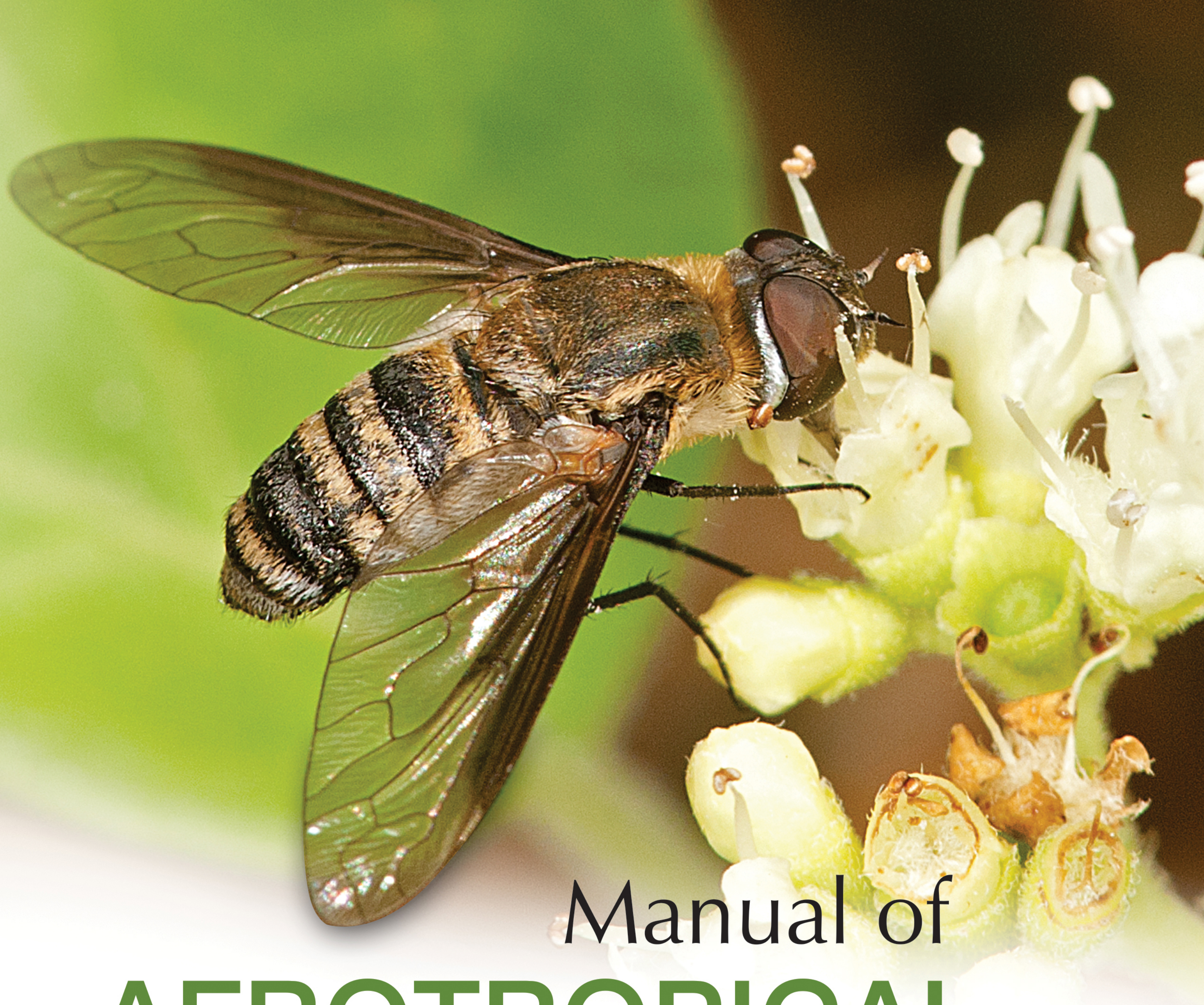

Manual of AFROTROPICAL DIPTERA

Volume 2

Edited by Ashley H. Kirk-Spriggs & Bradley J. Sinclair
With photographs by Stephen A. Marshall

SURICATA 5

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SURICATA 5

Manual of
Afrotropical Diptera

Volume 2

Nematocerous Diptera and lower Brachycera

Edited by
Ashley H. Kirk-Spriggs & Bradley J. Sinclair

Editorial Assistance
Burgert S. Muller

SANBI
Biodiversity for Life
South African National Biodiversity Institute

Pretoria, South Africa
2017

SURICATA

Suricata is the generic name of the suricate (*meerkat*), which is near-endemic to the arid western parts of southern Africa (occurring in Namibia, South Africa and Botswana; and just entering into a very small area in the extreme south of Angola). Behaviourally, suricates are socially inclusive and innately inquisitive, symbolising the commitment of South African National Biodiversity Institute (SANBI) to include all biodiversity and serve all of Africa and the scientific curiosity that precedes and drives research and publication of research results. Sister journal to SANBI's *Strelitzia*, *Suricata* is a peer-reviewed journal and publishes original and applied research, such as monographs, revisions, checklists, red lists, atlases and faunas of any taxa belonging to Regnum Animalia (the Animal Kingdom).

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LIMONIIDAE and TIPULIDAE 14

(Crane Flies)

Herman de Jong

Fig. 14.1. Copulating pair of *Dicranoptycha* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Minute- to very large-sized (body length: 1.5–50 mm; up to 60 mm in extralimital species), elongate nematoceran flies, with elongate wings and very long, slender legs (Figs 1–8).

Head (Figs 9–16, 135) with large compound eyes; ocelli absent; vertex usually low, sometimes raised as conical extension (e.g., *Hexatoma* Latreille, *Hovatipula* Alexander), anteriorly produced into lobe in *Toxorhina* (*Ceratocheilus* Wesché) (Fig. 13) and *Trichoneura* (*Ceratolimnobia* Alexander); head anteriorly produced into rostrum, usually about as long as remainder of head; rostrum longer than remainder of head in *Helius* Le Peletier & Serville and *Geranomyia* Haliday (Fig. 12), up to approximate body length in *Elephantomyia* Osten Sacken (Fig. 11) and *Toxorhina* Loew (Fig. 13); rostrum tipped with nasus in Tipulidae (Figs 9, 10); palpus usually 5-segmented, terminal segment long (most Tipulidae), or short (most Limoniidae); number of segments reduced in several taxa; antennae inserted between eyes, number of flagellomeres usually ranging from 11–14; flagellomeres fused in several taxa, resulting segments and entire antenna often long (*Hexatoma*); number of flagellomeres diagnostic for higher taxa; flagellomeres generally globular or cylindrical, produced in some taxa (e.g., *Rhipidia* Meigen); flagellum elongate, exceeding length of body in males of several species (*Hexatoma*, *Leptotarsus* Guérin-Méneville and *Maekistocera* Wiedemann).

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Thorax dorsally with V-shaped transverse suture (Fig. 9). Wing (Figs 22–129) elongate, with distinct anal vein; branching of radial and medial veins near apical ⅓ of wing in almost linear transverse line (the cord); venation variable and diagnostic for higher taxa; wings reduced in several taxa, especially montane species (*e.g.*, Figs 117, 130). Legs usually elongate and slender, breaking readily at suture between trochanter and femur; tibiae generally with ventral spurs at apex,


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Figs 14.2–8. Photographs of living Afrotropical Limoniidae and Tipulidae: (2) *Nephrotoma* sp. (Tipulidae) (Madagascar); (3) *Nephrotoma* sp. (Tipulidae) (Namibia); (4) Copulating pair of *Hovamyia apicistyla* Alexander (Limoniidae) (Madagascar); (5) Copulating pair of *Dolichopeza* (*Trichodolichopeza*) sp. (Tipulidae) (South Africa); (6) *Tipula* (*Acutipula*) sp. (Tipulidae) (Madagascar); (7) *Nephrotoma* sp. (Tipulidae) (South Africa); (8) *Conosia* sp. (Limoniidae) (Madagascar). Photographs © S.A. Marshall.

except in Chioneinae and few other taxa (number of spurs on fore to hind legs expressed as spur formula, *e.g.*, 1 : 2 : 2).

Abdomen elongate, slender, usually cylindrical; terminalia at apex of abdomen; complicated structures of male terminalia typical of species (*e.g.*, Figs 131, 132); female ovipositor (Fig. 133) usually elongate and sclerotised, in some taxa short and fleshy.

Egg symmetrical or asymmetrical elliptical, oval, spindle-shaped or kidney-shaped; diameter circular; both ends rounded, one or both ends truncate, or one or both ends slender, nipple-shaped or as acute point; colour varies between yellowish white, yellowish, grey, brown or black to glossy black; chorion clothed in regular, geometrical meshwork of microscopic sculptural elements, irregular, oblong relief of ribs, or irregularly placed warts varying in size and shape (Candan *et al*. 2005; Cramer 1968; Hemmingsen & Johns 1975; Lindner 1958*a*); eggs in some Tipulidae with terminal filament, usually coiled up like cap at posterior pole; extended filament up to several times length of egg (serves as anchor to attach egg to substrate in aquatic and semi-aquatic habitats (Cramer 1968; Hemmingsen 1952; Hemmingsen & Jensen 1972)).

Larvae (Fig. 136) elongate; head capsule distinct, posterior ⅔ retracted into prothorax; head capsule sclerotised anteriorly, ventrally and often dorsolaterally reduced, in some taxa reduced to sclerotised rods; mandibles opposed, moving in horizontal or oblique plane; abdominal segments smooth, or with transverse rows of fine setae; transverse creeping welts or fleshy projections present in some taxa; respiratory system functionally metapneustic, a few taxa apneustic; apical segment with pair of spiracles surrounded by lobe-like projections of varying length and sclerotisation, often fringed with setae, setae elongate in aquatic taxa; anal papillae, or membranous anal lobes, of variable length usually present (Alexander & Byers 1981: 156; Brindle 1967; Gelhaus 1986, 2009: 194).

Pupae (Fig. 137) elongate, obtect; respiratory system propneustic, peripneustic or amphipneustic; appendages of head and thorax visible in sheaths; palpal sheaths usually short and straight in Limoniidae, curved or recurved at apex in Tipulidae; thoracic respiratory organs of various forms, well-developed or very small, long and cylindrical, straight or curved, rod-like, branched, ear-shaped or terminating in spine; thoracic mesonotum with high transverse crest in more derived Chioneinae; legs sheaths parallel to each other, usually much longer than wing sheaths; in Chioneinae sheaths of mid legs much shorter than other legs; transverse rows of stiff setae or spines usually present posteriorly on abdominal segments; genital sheaths usually with spines; pupae of Limoniidae often in silken tube clothed in detritus (Alexander 1920; Brindle 1967; Gelhaus 2009: 194; Oosterbroek & Theowald 1991).

Adult Tipulidae *sensu lato* may be superficially confused with Tanyderidae (see Chapter 15) and Ptychopteridae (see Chapter 27). Both these families lack the anal vein that characterises the Tipulidae *sensu lato*. Tanyderidae are distinguished by the presence of five radial veins that reach the wing margin and Ptychopteridae may be recognised by the distinct basal appendage to the halter (the prehalter).

Biology and immature stages

Crane fly adults are usually encountered in damp situations, often in the vicinity of open water, but also in shaded spots in forests, heaths, grasslands, cultivated areas and urban environments. Adults mainly occur close to areas where the immature stages develop, although cases of long distance dispersal are known. The majority of species are dependent on the presence of freshwater, having aquatic or semi-aquatic immature stages. Depending on the species, larvae develop in flowing or standing water, often in moss cushions, or mats of algae growing on boulders or rocks, along the margins of streams and ponds in rich organic material, in phytothelmata containing water, in rotting plant material (including logs) and in decaying wood in various stages of decomposition. The larvae of a score of species, especially in the subfamily Limoniinae, develop in saline environments, either in inland saline marshes, in mangrove forests or in the inter-tidal zone of rocky coasts. Others are terrestrial, occurring in moist to rather dry soil (Alexander & Byers 1981: 156; de Jong *et al*. 2008; Gelhaus 2009: 194).

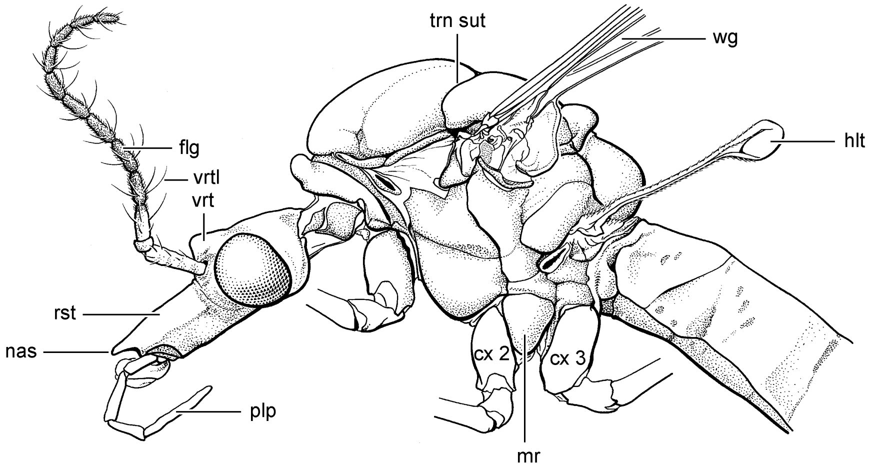
Crane flies occur from sea level to above the tree zone in montane habitats (*e.g.*, *Tipula* (*Tipula*) *hollanderi* Theowald, 1977, up to 3,800 m in the Bale Mountains, Ethiopia, *T.* (*T.*) *lobeliae* Alexander, 1956, up to 4,400 m on Mount Elgon, Kenya and *T.* (*T.*) *subaptera* Freeman, 1950, up to 4,750 m on Mount Kilimanjaro, Tanzania (Alexander 1956; Freeman 1950; Theowald 1977, 1984)). As compared to the immature stages, adults are short-lived; the adult stage lasting at most a few weeks. The majority of species appear to a have a one-year life cycle, although several species are known to have more than one generation per year. Others, especially in the cooler zones of the Earth, have a life cycle that may take several years (Pritchard 1983). Adults are generally non-feeding and only occasionally take up liquids, such as honeydew. Species with elongate mouthparts, e.g., *Elephantomyia*, *Geranomyia*, *Helius* and *Toxorhina*, regularly visit flowers in order to ingest nectar.

Feeding takes place during the larval stages. The majority of Tipuloidea are plant-feeders, either as saprophytophages, macrophytophages or microphytophages. Larvae of some groups, especially of the subfamily Limnophilinae of the Limoniidae and the non-Afrotropical Pediciidae, are predators.

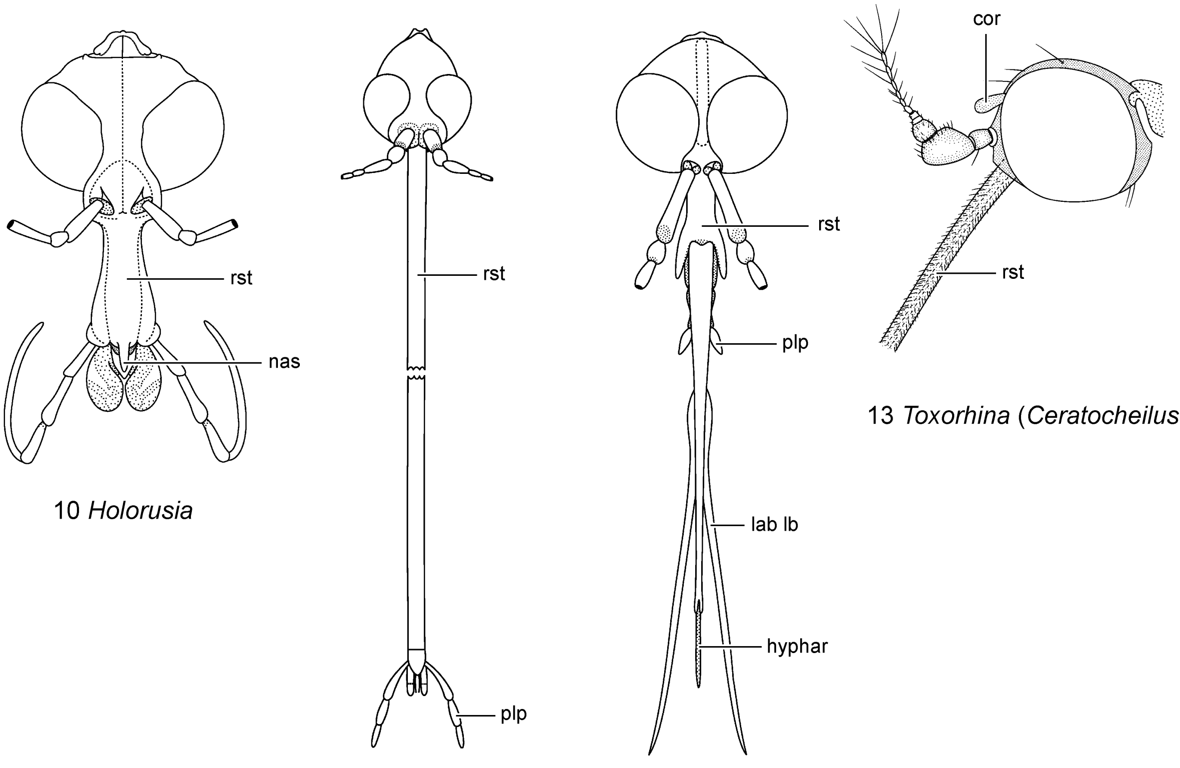
The number of eggs deposited varies between around 200 in Tipulidae to less than 100 in Limoniidae (Cramer 1968). Knowledge of the immature stages of Afrotropical crane flies relies heavily on the monograph by Wood (1952), on the crane flies of the south-west Cape, South Africa. Wood presented detailed accounts of the adults and immatures of South African crane flies with a range of information on the biology of the species.

Economic significance

A number of phytophagous crane fly species are classified as pests. Their larvae attack young plants and can damage seedling crops, such as wheat and rice, as well as pastures, grassland, gardens and lawns (Alexander 1954; Byers 2002; Kim & Lee 2002, 2003*b*, 2005*b*, 2007). Harmful species are known in *Nephrotoma* Meigen, *Tipula* L. *sensu stricto* and *Tipula* (*Yamatotipula* Matsumura), but there are apparently no records of species causing damage in the Afrotropical Region.



9 *Tipula*



10 *Holorusia*

11 *Elephantomyia*

12 *Geranomyia*

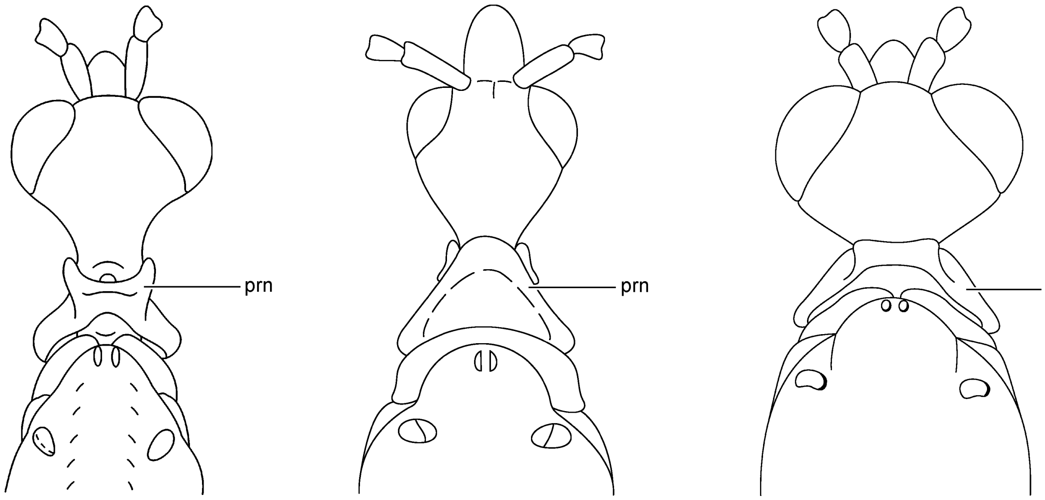
13 *Toxorhina* (*Ceratocheilus*)

Figs 14.9–13. Head and thorax and heads of Limoniidae and Tipulidae: (9) head and thorax of *Tipula* sp., lateral view (most of wing and legs omitted) (non-Afrotropical); (10) head of *Holorusia* sp., dorsal view; (11) same, *Elephantomyia* sp.; (12) same, *Geranomyia* sp.; (13) same, *Toxorhina* (*Ceratocheilus*) *alexanderi* Tjeder, lateral view (only base of mouthparts illustrated). Fig. 9 (after Alexander & Byers 1981, fig. 2), Figs 10–12 (after Crampton 1943, figs 1F, 3A, 4H, respectively), Fig. 13 (after Tjeder 1981, fig. 1).

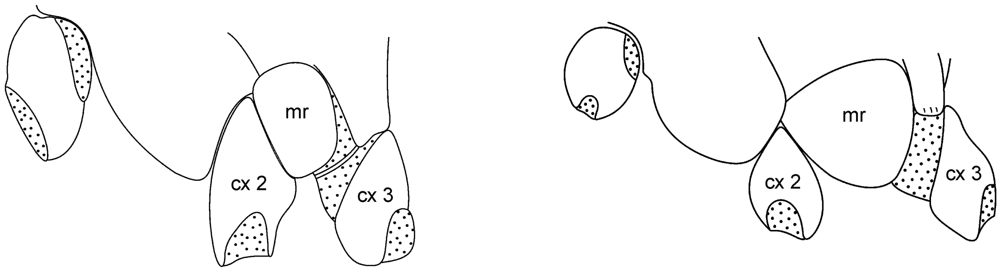
Abbreviations: cor – corniculus; cx – coxa; flg – flagellum; hlt – halter; hyphar – hypopharynx; lab lb – labial lobe; mr – meron; nas – nasus; plp – palpus; rst – rostrum; trn sut – transverse suture; vrt – vertex; vrtl – verticil; wg – wing.

Classification

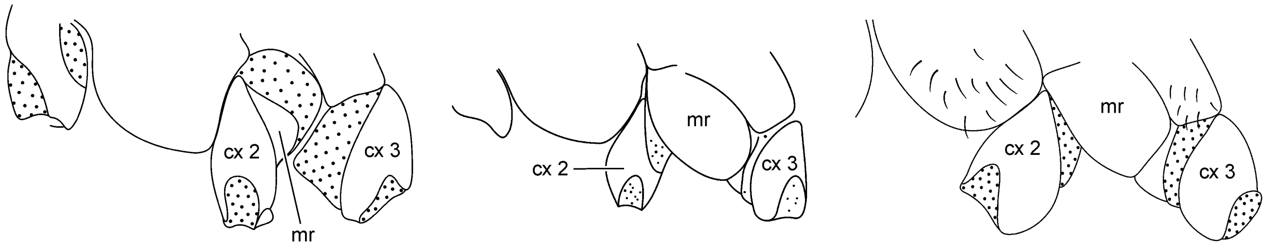
Together with non-Afrotropical Cylindrotomidae and Pediciidae, the Limoniidae and Tipulidae are grouped in the superfamily Tipuloidea. The crane fly families Limoniidae and Tipulidae are dealt with here in a single chapter for several reasons. Most importantly, the monophyly of the tipuloid family level taxa remains to be firmly established and the current higher level classification represents a conventional concept, rather than a robust scientific hypothesis. As a consequence the families cannot be separated conclusively. The Limoniidae are often referred to as "short-palped crane flies" in contrast to the Tipulidae or "long-palped crane flies". Both families, however, contain taxa that challenge this seemingly straightforward division. Other characters generally used to distinguish between the families (e.g., number of antennal segments,



14 *Pseudolimnophila* 15 *Limnophila* 16 *Pilaria*



17 *Neolimnophila* 18 *Crypteria*



19 *Gonomyia* 20 *Rhabdomastix* 21 *Erioptera*

Figs 14.14–21. Head and anterior part of thorax and ventral section of thorax of Limoniidae: (14) head and anterior part thorax of *Pseudolimnophila* sp., dorsal view; (15) same, *Limnophila* sp.; (16) same, *Pilaria* sp.; (17) ventral section thorax of *Neolimnophila* sp., lateral view (indicating position and shape of meron); (18) same, *Crypteria* sp.; (19) same, *Gonomyia* sp.; (20) same, *Rhabdomastix* sp.; (21) same, *Erioptera* sp. Figs 14–21 (after Edwards 1938, figs 13a–b, 17a–e).

Abbreviations: cx – coxa; mr – meron; prn – pronotum.

presence or absence of a rostrum, of a nasus and of the apex of the subcostal wing vein (*Sc*), position of crossvein *m–cu*, body size, *etc*.), do not hold either, especially when the world fauna is considered. C.P. Alexander combined the families of Tipuloidea in the vast majority of papers he published on Afrotropical crane flies. Treatment of Limoniidae and Tipulidae as a single chapter also concurs with North American authors, who treat this superfamily as a single family (Tipulidae *sensu lato*) in the *Manual of Nearctic Diptera* (Alexander & Byers 1981: 153) and the *Manual of Central American Diptera* (Gelhaus 2009: 193) (*Contributions to a Manual of Palaearctic Diptera* (Papp & Darvas 1997, 1998, 2000*a*, *b*) did not cover the Tipuloidea).

The position of the Tipuloidea in the higher classification of the Diptera remains a controversial issue. Traditionally, the Tipuloidea were considered the phylogenetically most "primitive" clade of the order Diptera, a position substantiated in several more recent publications (Blagoderov *et al*. 2007; Hennig 1973: 20; Michelsen 1996; Wood & Borkent 1989: 1340). Based on a phylogenetic analysis of morphological characters of the immature stages and adults, Oosterbroek & Courtney (1995) postulated an arrangement in which Tipuloidea, together with the non-Afrotropical Trichoceridae, are sister-group of the combined Anisopodidae and Brachycera. The position of the Tipuloidea as close relatives of the Brachycera was also recognised by Yeates & Wiegmann (1999, 2005: 20) and Yeates *et al*. (2007). The last named authors later abandoned this view in favour of an ordering in which the Tipuloidea represent one of the earlier clades of the Diptera that branched off after the Culicomorpha (Lambkin *et al*. 2013). This scheme agrees with the results of one of the analyses undertaken by Bertone *et al*. (2008).

The taxonomic rank assigned to the group dealt with in this chapter is also a matter of different interpretations. Old World and South American authors generally recognise four families within the superfamily Tipuloidea, *viz*. Cylindrotomidae (non-Afrotropical), Limoniidae, Pediciidae (non-Afrotropical) and Tipulidae, whereas North American authors assign subfamily rank to these taxa, grouping them in one family Tipulidae (*e.g.*, Alexander & Byers 1981: 153; Gelhaus 2009: 193). In this chapter the classification of the online *Catalogue of the Craneflies of the World* (Oosterbroek 2016) is followed at all taxonomic levels and four families are recognised, only two of which are represented in the Afrotropics. This is also the classification adopted by the online *Systema Dipterorum* (Pape & Thompson 2014).

Relatively few investigations are available on the phylogenetic relationships of the major groups within the Tipuloidea. Oosterbroek & Theowald (1991) examined relationships at the genus-group level, based on morphological information on the immature stages. Starý (1992) analysed a set of morphological characters pertaining to the adult stage at the familial and subfamilial levels. Ribeiro (2008) published a morphological phylogenetic analysis of 104 species of Tipuloidea, focusing on Limnophilinae. Petersen *et al*. (2010) presented a combined morphological and molecular study, based on 45 species sampled across the superfamily. Zhang *et al*. (2016) sequenced complete and vitually complete mitochondrial genomes of some Tipuloidea and used these in a phylogenetic analysis of families of the Diptera. In general, the results of these studies tend to indicate the same major groupings at the subfamilial or familial level, but except for a commonly found sister-group relationship between Cylindrotomidae and Tipulidae and a basal position of the Pediciidae, the postulated relationships between the major groups tend to differ among the various hypotheses. Indepth phylogenetic analyses that incorporate representatives of the majority of genus level taxa of Tipuloidea are not available and the monophyly of the currently recognised families has yet to be established.

At lower taxonomic levels, phylogenetic studies have been published on subfamilies, genera, subgenera and species-groups (*e.g.*, de Jong 1994; Gelhaus 2005; Oosterbroek 1980; Ribeiro 2008, 2009; Starkevic 2012; Tangelder 1985; Young 1987), but none of these studies has focused on the Afrotropical fauna.

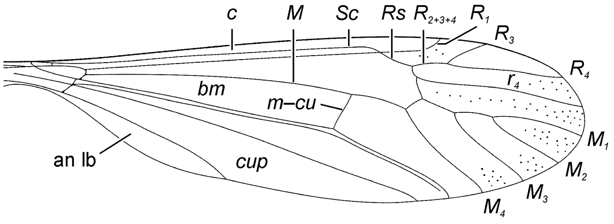
Identification

The number of described valid species of Tipuloidea is about 15,360, of which *ca* 1,390 are known from the Afrotropical Region (Oosterbroek 2016). Two of the four families of Tipuloidea are absent from the region, *viz*. the Cylindrotomidae and the Pediciidae. Both families are present in all other zoogeographical regions, except Antarctica and their absence from the Afrotropical Region is an interesting subject for future research. Another remarkable group that is absent from the Afrotropical Region are the Ctenophorinae, a probably monophyletic subfamily of the Tipulidae of which the larvae are wood-inhabiting. Ctenophorinae are a mainly Nearctic, Palaearctic and Oriental group, with only very few species known from Central and northern South America and two species known from the Australasian/Oceanian parts of Indonesia.

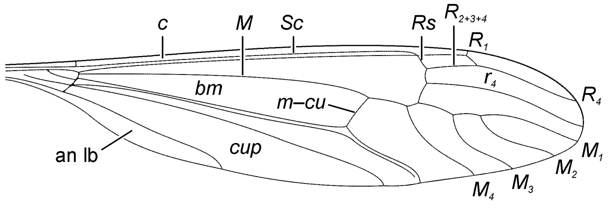
Limoniidae is the largest family of the superfamily Tipuloidea, with more than 10,525 described species globally and *ca* 1,045 species in the Afrotropics. The family Tipulidae comprises more than 4,275 species, of which approximately 340 are Afrotropical. Comparison of the total number of species known for the different zoogeographical regions indicates that the Afrotropical Region is less species-rich than any of the other regions. This at least partly reflects the modest attention given to the study of Afrotropical crane flies during the past decades. Some Afrotropical Tipuloidea species are restricted to mountainous areas and reduction of the wings is a common feature in many of these (*e.g.*, Fig. 117). Various stages of reduction are known and sometimes variation occurs within a species, depending on the elevations at which a population occurs. Atrophy of the wings is known in *Molophilus* Curtis *sensu stricto*, *Quathlambia*, *Symplecta* Meigen *sensu stricto* (Limoniidae: Chioneinae), *Austrolimnophila* Alexander *sensu stricto* (Limoniidae: Limnophilinae), *Platylimnobia* Alexander (Limoniidae: Limoniinae), *Leptotarsus* (*Longurio* Loew), *Nephrotoma* and *Tipula sensu stricto* (Tipulidae).

Original descriptions of Afrotropical crane flies appeared in a plethora of papers. More than 85% of the known fauna was described by C.P. Alexander, who published his first paper on Afrotropical Tipuloidea in 1912 and his last, dealing with the crane flies of Comoros, in 1979. Besides the long series of papers with a focus on descriptions of new Afrotropical species, Alexander published comprehensively on the fauna of the Ruwenzori Range, Uganda (1956), Madagascar (1963) and

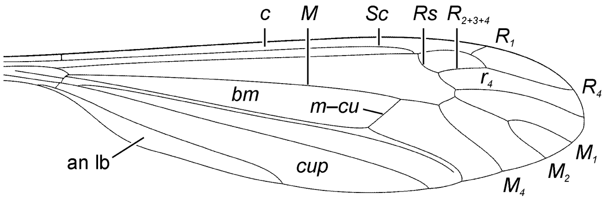
South Africa (1964). These papers include identification keys to genera and subgenera of the respective areas. Alexander's 1956 paper moreover includes identification keys to all the then known Afrotropical species of Tipuloidea, occurring between approximately 20°N and 20°S latitude, while his work on the crane fly fauna of South Africa (1964) includes keys to the then known species occurring south of approximately 16°S latitude. Wood (1952) meticulously examined the crane fly fauna of the south-west Cape, providing a wealth of information on the early stages as well as the adults. Wood provided identification keys to adults and, where applicable, to the immature stages of the species discussed. Besides the identification



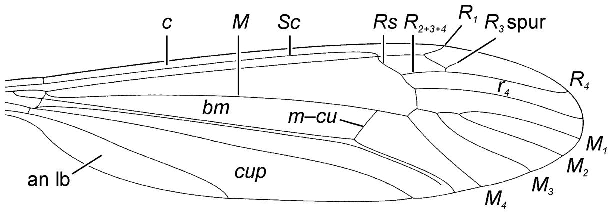
22 *Dolichopeza* (*Afrodolichopeza*)



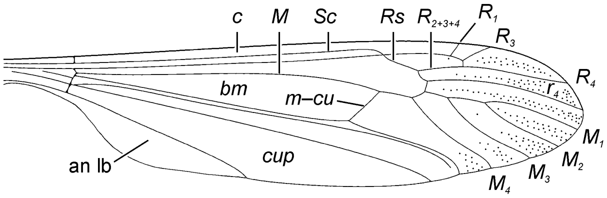
23 *Dolichopeza* (*Dolichopeza*)



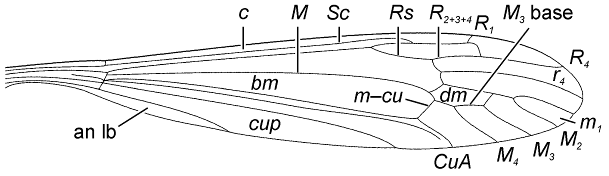
24 *Dolichopeza* (*Eudolichopeza*)



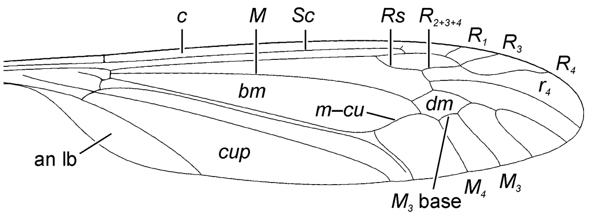
25 *Dolichopeza* (*Prodolichopeza*)



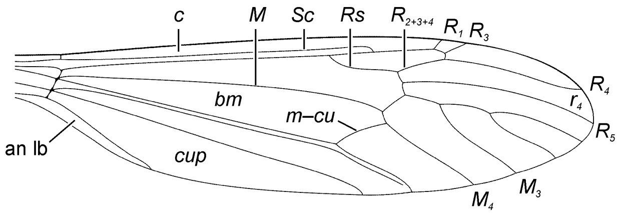
26 *Dolichopeza* (*Trichodolichopeza*)



27 *Goniotipula*



28 *Holorusia*



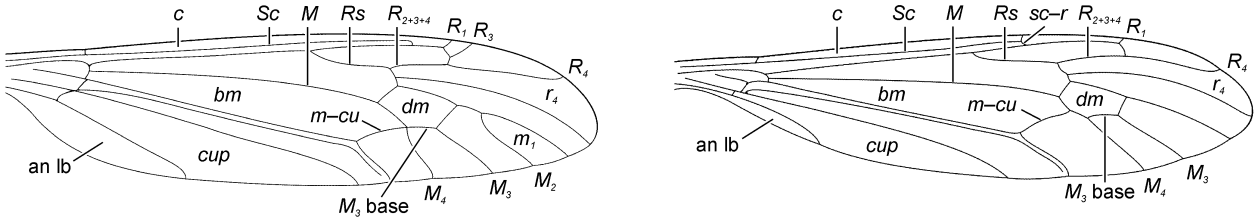
29 *Hovapeza*

Figs 14.22–29. Wings of Tipulidae (dorsal views): (22) *Dolichopeza* (*Afrodolichopeza*) *anitra* Alexander; (23) *D.* (*Dolichopeza*) *corybantes* Alexander; (24) *D.* (*Eudolichopeza*) *lipophleps* Alexander; (25) *D.* (*Prodolichopeza*) *malagasya* Karsch; (26) *D.* (*Trichodolichopeza*) *hirtipennis* Alexander; (27) *Goniotipula cuneipennis* Alexander; (28) *Holorusia inventa* (Walker); (29) *Hovapeza tisiphone* (Alexander). Figs 22–24 (after Alexander 1956, figs 55–57), Figs 25, 29 (after Alexander 1963, figs 45, 47), Figs 26–28 (after Alexander 1964, figs 32, 15, 10, respectively).

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *c* – costal cell; *CuA* – anterior branch of cubital vein; *cup* – posterior cubital cell; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.

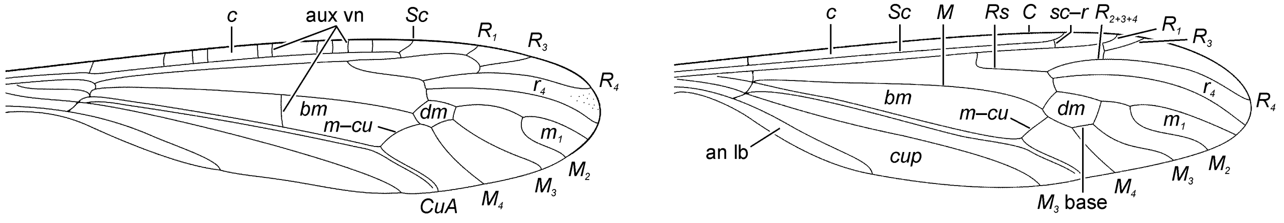
key to the six species of *Nephrotoma* known to occur in Réunion Is. (Alexander 1957), the species of *Tipula* (*Acutipula*) known from Madagascar (Alexander 1960*b*) and the four species of Limoniidae recorded from Saint Helena Is. (Alexander 1977), no other useful identification keys to the Afrotropical crane fly fauna are currently available.

The identification key to genera and subgenera provided below is based on the published keys of Alexander (1956, 1963, 1964) and Wood (1952). These have been adapted to include all Afrotropical genera and subgenera and all forms currently known from the Afrotropics. It follows the current classification of the Tipuloidea as much as possible



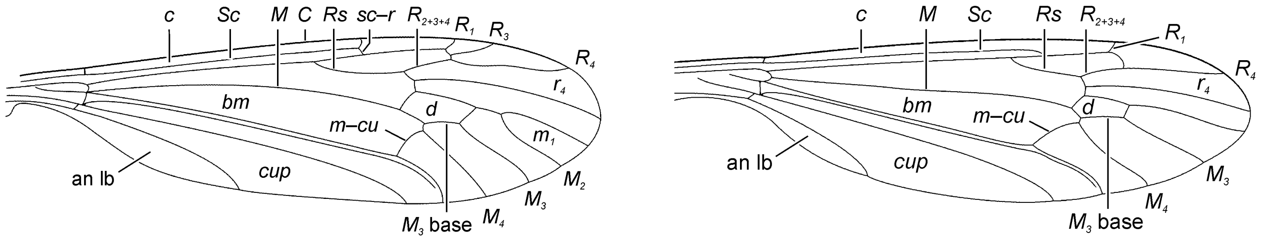
30 *Hovatipula*

31 *Idiotipula*



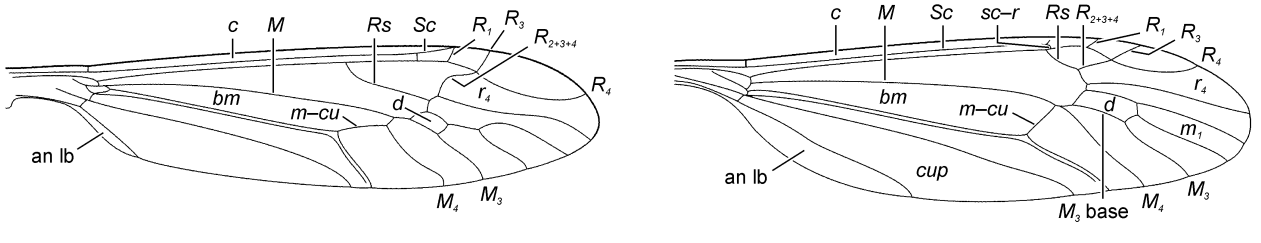
32 *Keiseromyia*

33 *Leptotarsus* (*Leptotipula*)



34 *Leptotarsus* (*Longurio*)

35 *Leptotarsus* (*Xenotipula*)



36 *Megistocera*

37 *Nephrotoma*

Figs 14.30–37. Wings of Tipulidae (dorsal views): (30) *Hovatipula megalothorax* (Alexander); (31) *Idiotipula confluens* Alexander; (32) *Keiseromyia polyphragma* Alexander; (33) *Leptotarsus* (*Leptotipula*) *limnophiloides* (Alexander); (34) *L.* (*Longurio*) *albicubitalis* (Alexander); (35) *L.* (*Xenotipula*) *munroi* (Alexander); (36) *Maekistocera filipes filipes* (F.); (37) *Nephrotoma tincta* (Walker). Figs 30, 32, 36 (after Alexander 1963, figs 42, 43, 39), Figs 31, 33, 34, 35, 37 (after Alexander 1964, figs 12, 14, 22, 13, 16, respectively).

Abbreviations: an lb – anal lobe; aux vn – auxiliary vein; *bm* – basal medial cell; *c* – costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *M* – medial vein, or media; m_1 – first medial cell; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

and successively deals with the Tipulidae, Limoniidae: Limnophilinae, Chioneineae and Limoniinae. Brachypterous and sub-apterous crane flies are dealt with in the final part of the key.

Identification of crane flies at the generic and subgeneric levels relies heavily on wing venation characters. For this reason, an extensive set of labeled illustrations of wings (Figs 22–129) supports the identification key to the genera and subgenera of Afrotropical crane flies. Most illustrations were originally derived from publications by Alexander.

Due to the ease with which adult Limoniidae and Tipulidae shed their legs, they should initially be preserved in individual paper packets to later be relaxed and either direct-pinned or card-pointed with the legs tucked-in (see Chapter 2).

Key to genera of Afrotropical Limoniidae and Tipulidae

1. Wings fully-developed (*e.g.*, Figs 22–116, 118–129). 2

– Wings reduced (*e.g.*, Figs 117, 130) 122

2. Terminal segment of palpus usually elongate, longer than two preceding segments combined (short in *Hovatipula*, *Keiseromyia* Alexander, *Leptotarsus*); antenna with 13 or fewer segments; head generally produced into rostrum, about as long as remainder of head (*e.g.*, Figs 9, 10); nasus usually distinct (*e.g.*, Figs 9, 10); wing with apex of subcostal vein (*Sc*) commonly atrophied (present or partly present in *Holorusia* Loew, *Idiotipula* Alexander, *Keiseromyia*, *Leptotarsus*, *Maekistocera* and *Nephrotoma*); apex of veins R_1 and R_3 (if present) closely approximated; fork of vein M_{3+4} in basal section of discal or discal medial cell (*d* or *dm*); crossvein *m–cu* usually at or close to fork of vein M_{3+4}; vein *CuA* constricted at crossvein *m–cu*; false vein just posterior of vein *CuA*, extending almost to wing margin (e.g., Figs 22–44); large-sized species, commonly with wing > 10 mm in length or more (TIPULIDAE [in part]) 3

– Terminal segment of palpus not elongate, usually subequal to preceding segment; antennae usually with 14–16 segments (6–10 in *Hexatoma*, 14 in some Limoniinae, 16 in virtually all other groups); head not or only slightly produced (*e.g.*, Figs 14–16) or if markedly produced (*Elephantomyia*, *Geranomyia* and *Toxorhina*; Figs 11–13), then greatly extended, exceeding ½ length of body, more modestly produced in *Helius*; without distinct nasus; wing with apex of subcostal vein (*Sc*) developed; apices of veins R_1 and R_3 usually separate; fork of vein M_{3+4} in apical section of discal or discal medial cell (*d* or *dm*); crossvein *m–cu* far removed from fork of vein M_{3+4}, usually at or close to fork of vein *M*, in some cases (*Antocha* Osten Sacken, *Idiocera* Dale, *Orimarga* Osten Sacken and *Thaumastoptera* Mik), positioned some distance before this fork; vein *CuA* straight, generally not constricted at crossvein *m–cu*; false vein posterior of vein *CuA* ending almost opposite or before crossvein *m–cu*; small- or medium-sized species, commonly with wing < 10 mm in length (LIMONIIDAE [in part]) 26

3. Wing with auxiliary crossveins in costal cell (*c*) and basal-medial cell (*bm*) (Fig. 32). . . . . *Keiseromyia* Alexander

– Wing without auxiliary crossveins in costal cell (*c*) and basal-medial cell (*bm*) (*e.g.*, Figs 22–31, 33–44) 4

4. Wing vein *Sc* very long, extending to beyond fork of vein *Rs*, almost joining apex of vein R_1; vein R_{2+3+4} strongly angulate at or near mid length; crossvein *m–cu* joining vein M_4 well before discal cell (*d*) (Fig. 36); antenna of male excessively lengthened, approximately 4 × length of wing . . . . *Maekistocera* Wiedemann

– Wing vein *Sc* usually shorter; vein R_{2+3+4} not angulate; crossvein *m–cu* rarely joining vein M_4 (*Hovapeza* Alexander, certain *Nephrotoma*, *Leptotarsus*, *Tipula* (*Afrotipula* Alexander), and *Tipula* (*Yamatotipula*)) (e.g., Figs 22–31, 33–35, 37–44); antenna of male shorter, at most approximately of wing length (some *Leptotarsus*) 5

5. Anal lobe of wing extensive, produced basad of arculus; cell *cup* produced basad of arculus; vein R_4 strongly arcuate at or near mid length, markedly narrowing at cell r_4 (Fig. 28); apex of femora with comb of small, blackened, spinoid setae (Fig. 134). . . . . *Holorusia* Loew

– Anal lobe of wing usually more restricted, not produced basad of arculus; cell *cup* narrowed at or near level of arculus (except in *Hovatipula*, Fig. 30, but then other characters differ); vein R_4 not conspicuously arcuate, cell r_4 not markedly constricted (*e.g.*, Figs 22–27, 29–31, 33–35, 37–44); apex of femur without spinoid setae. 6

6. Wing with discal or discal medial cell (*d* or *dm*) open by atrophy of base of vein M_3, outer medial field thus appearing pectinate; crossvein *m–cu* joining vein M_4 (*Hovapeza*; Fig. 29), or crossvein *m–cu* positioned far before fork of vein *M* (*Dolichopeza* Curtis *sensu lato*; Figs 22–26). 7

– Wing with discal or discal medial cell (*d* or *dm*) closed, base of vein M_3 present; crossvein *m–cu* commonly beyond fork of vein *M* (before fork of vein *M* in most *Nephrotoma* and some *Tipula sensu lato*) (*e.g.*, Figs 27, 30, 31, 33–35, 37–44) 12

7. Wing vein *Rs* rather long, originating well before end of vein *Sc*; vein R_3 reaching wing margin; crossvein *m–cu* beyond fork of vein *M* on vein M_4 (Fig. 29) . . . . *Hovapeza* Alexander

– Wing vein *Rs* very short, originating near end of vein *Sc*; vein R_3 usually more or less atrophied; crossvein *m–cu* on vein *M* before its fork (*e.g.*, Figs 22–26) . . . . *Dolichopeza* Curtis *sensu lato* 8

8. Wing with 3 branches of vein *M* reaching wing margin (Fig. 24) . . . . *Dolichopeza* (*Eudolichopeza* Alexander)

– Wing with 4 branches of vein *M* reaching wing margin (*e.g.*, Figs 22, 23, 25, 26) 9

9. Outer wing cells with macrotrichia (*e.g.*, Figs 22, 26) 10

– Outer wing cells without macrotrichia (*e.g.*, Figs 23, 25) 11

10. Wing vein R_3 present, distinct, reaching margin; outer cells with sparse macrotrichia (Fig. 22) . . . . *Dolichopeza* (*Afrodolichopeza* Alexander)

– Wing vein R_3 usually atrophied, at most represented by short basal spur, not reaching wing margin, or faintly preserved in some South African species; outer cells with abundant macrotrichia (Fig. 26) . . . . *Dolichopeza* (*Trichodolichopeza* Alexander)

11. Nasus present; legs relatively short . . . . *Dolichopeza* (*Prodolichopeza* Alexander)

– Nasus absent; legs long and slender . . . . *Dolichopeza* Curtis *sensu stricto*

12. Wing crossvein *sc–r* opposite or slightly beyond base of short vein *Rs*; apex of subcostal vein (*Sc*) usually weakly-developed; cell m_1 sessile or short-petiolate; usually vein M_4 arising at or before base of discal cell (*d*); crossvein *m–cu* commonly before fork of vein *M*, in rare cases at or beyond fork on M_{3+4} (Fig. 37) . . . . *Nephrotoma* Meigen

– Wing crossvein *sc–r* some distance beyond base of longer *Rs*, commonly at or near mid length of this vein; apex of subcostal vein (*Sc*) atrophied or developed; cell m_1 usually long-petiolate (absent in *Idiotipula*, some *Leptotarsus* (*Longurio*), *L.* (*Xenotipula* Alexander) and sessile in *Tipula* (*Afrotipula*)); crossvein *m–cu* at or close to fork of M_{3+4}, rarely at or close to fork of vein *M* (*Goniotipula* Alexander, *Leptotarsus* (*Longurio*) and some *Tipula* (*Schummelia* Edwards)) (*e.g.*, Figs 27, 30, 31, 33–35, 38–44) 13

13. Wing vein M_2 absent; cell m_1 absent (*e.g.*, Figs 31, 35) 14

– Wing vein M_2 present; cell m_1 present (*e.g.*, Figs 27, 30, 33, 34, 38–44) 16

14. Wing very long and narrow, *ca* 7 × as long as broad . . . . *Leptotarsus* (*Longurio* Loew) [in part]

– Wing shorter and broader, *ca* 4 × as long as broad (*e.g.*, Figs 31, 35) 15

15. Tibial spurs absent . . . . *Idiotipula* Alexander

– Tibial spurs present . . . . *Leptotarsus* (*Xenotipula* Alexander)

16. Wing with anal lobe very narrow, wing appearing petiolate; apex of subcostal vein (*Sc*) atrophied (Fig. 27); male terminalia with 1 gonostylus; female with short fleshy ovipositor. . . . *Goniotipula* Alexander

– Wing with anal lobe distinct, wing base short; apex of subcostal vein (*Sc*) commonly developed in *Leptotarsus* and *Hovatipula*, atrophied in *Tipula* (*e.g.*, compare Figs 30, 33, 34 with 38–44); male terminalia with 2 gonostyles (except in rare species of *Leptotarsus*); female with ovipositor usually elongate, sclerotised (except in a few *Leptotarsus* with short fleshy ovipositor) 17

17. Wing with apex of subcostal vein (*Sc*) commonly complete and vein *Sc* ending in costal vein (*C*) (*e.g.*, Figs 33, 34) or developed as a short spur; antenna of males of certain species elongate, almost as long as body, with inconspicuous verticils; male terminalia of simple structure; gonocoxite developed; inner gonostylus commonly with rows or groups of modified spinoid setae 18

– Wing with apex of subcostal vein (*Sc*) atrophied and vein *Sc* not ending in costal vein (*C*) (*e.g.*, Figs 38–44); antenna of male short or only moderately lengthened; flagellomeres usually with long conspicuous verticils; male terminalia more complex in structure; gonocoxite commonly fused with sternite 9, often fused with tergite 9 to form continuous ring; inner gonostylus without groups of spinoid setae . . . . *Tipula* L. *sensu lato* 20

18. Wing crossvein *m–cu* positioned close to fork of vein *M*, well removed from vein M_4 (Fig. 33) . . . . *Leptotarsus* (*Leptotipula* Alexander)

– Wing crossvein *m–cu* positioned near mid length of discal or discal medial cell (*d* or *dm*), close to or joining vein M_4 (*e.g.*, Figs 30, 34) 19

19. Palpus with terminal segment very small, present as small elongate cone, shorter than fourth palpal segment; head with vertical tubercle forming slender erect lobe (Fig. 135); wing venation as illustrated in Fig. 30 . . . . *Hovatipula* Alexander

– Palpus with terminal segment longer than fourth palpal segment, usually distinctly longer; head with vertical tubercle stout, not erect; wing venation as illustrated in Fig. 34 . . . . *Leptotarsus* (*Longurio* Loew) [in part]

20. Wing cell m_1 sessile (Fig. 39) (calypter bare; claws of male simple) . . . . . . *Tipula* (*Afrotipula* Alexander)

– Wing cell m_1 petiolate (*e.g.*, Figs 38, 40–44) (calypter bare or with macrotrichia; claws of male simple or toothed) 21

21. Wing cell m_4 *ca* 2 × as wide at base as at apex; crossvein *m–cu* positioned before or at fork of vein *M* (Fig. 41) . . . . *Tipula* (*Schummelia* Edwards)

– Wing cell m_4 not 2 × as wide at base as at apex; crossvein *m–cu* positioned at fork of vein M_{3+4} or beyond on vein M_4 (*e.g.*, Figs 38, 40, 42–44) 22

22. Wing vein *Rs* long, *ca* 2 × longer than crossvein *m–cu* (*e.g.*, Figs 43, 44) 23

– Wing vein *Rs* shorter, < 2 × longer than crossvein *m-cu*, usually subequal to or shorter than crossvein *m–cu* (*e.g.*, Figs 38, 40, 42) 24

23. Rostrum about as long as remainder of head; nasus distinct; antennal flagellomere 1 not much longer than flagellomere 2; *r* cells of wing without macrotrichia (Fig. 43). . . . . *Tipula* L. *sensu stricto*

– Rostrum distinctly shorter than remainder of head; nasus small to virtually absent; antennal flagellomere 1 distinctly longer than flagellomere 2, especially in male; *r* cells of wing with scattered macrotrichia (Fig. 44) . . . . *Tipula* (*Yamatotipula* Matsumura)

24. Wing vein R_4 markedly sinuous; cell m_3 with width at wing margin similar to that at base of cell (Fig. 40); basal antenna flagellomeres elongate; male terminalia with tergite and sternite separated by pale membrane . . . . *Tipula* (*Savtshenkia* Alexander)

– Wing vein R_4 less sinuous; cell m_3 with width at wing margin much broader than that at base of cell (*e.g.*, Figs 38, 42); basal antenna flagellomeres not elongate; male terminalia with sclerites fused into virtually continuous ring 25

25. Wing with discal medial cell (*dm*) large, about as long as or longer than vein *Rs*; anal lobe of wing distinct, broad (Fig. 38); tibial spur formula 1 : 2 : 2, spurs not accompanied by spinoid setae . . . . *Tipula* (*Acutipula* Alexander)

– Wing with discal cell (*d*) small, shorter than vein *Rs*; anal lobe of wing narrow (Fig. 42); tibial spur formula 1 : 1 : 2, spurs surrounded by group of spinoid setae . . . . *Tipula* (*Spinitipula* Alexander)

26. Wing vein *R* with 4 branches reaching wing margin (*e.g.*, Figs 45–52, 54–61, 63–67, 70–78, 81–84, 86–89, 91–94, 96) 27

– Wing vein *R* with at most 3 branches reaching wing margin (*e.g.*, Figs 53, 62, 68, 69, 79, 80, 85, 90, 95, 97–129) 28

27. Tibial spurs present; wing usually with 4 *M* veins in some cases 2 or 3; apical section of vein R_1 usually short (*e.g.*, Figs 45–52, 54–61, 63–67) (LIMNOPHILINAE [in part]) 33

– Tibial spurs absent; wing with 3 *M* veins; apical section of vein R_1 usually elongate (*e.g.*, Figs 70–78, 81–84, 86–89, 91–94, 96) (CHIONEINAE [in part]) 57

28. Head length, including extended mouthparts, up to ½ body length or more (*Elephantomyia*, *Geranomyia*, *Toxorhina*; Figs 11–13) (LIMONIINAE [in part]) 88

– Head not with extended mouthparts or if produced then notably shorter than ½ body length (*Helius*) 29

29. Wing vein R_1 with free apex absent, at most present as a spur (*e.g.*, Figs 127, 128) or vein *R* directly fusing with costal vein (*C*) (*e.g.*, Fig. 129) (LIMONIINAE [in part]) 88

– Wing vein R_1 with free apex present; vein *R* not directly fusing with costal vein (*C*) (*e.g.*, Figs 53, 62, 68, 69, 79, 80, 85, 90, 95, 97–126) 30

30. Wing crossvein *m–cu* basal from fork of vein *M*, at distance greater than length of crossvein *m–cu* (*e.g.*, Figs 100, 115–117, 120) (LIMONIINAE [in part]) 88

– Wing crossvein *m–cu* close to fork of vein *M* (*e.g.*, Figs 53, 62, 68, 69, 79, 80, 85, 90, 95, 97–99, 101–114, 118, 119, 121–126) 31

31. Antennae 14-segmented (LIMONIINAE [in part]) 88

– Antennae either 16-segmented or with 12 or fewer segments 32

32. Antennae 12-segmented at most (LIMNOPHILINAE [in part]). 33

– Antennae 16-segmented (CHIONEINAE [in part]) 57

33. Antennal segments reduced in number, commonly 6 or 7 in male, 9 or 10 in female; antenna of male in some cases excessively lengthened, exceeding body length . . . . . . *Hexatoma* Latreille *sensu lato* 34

– Antennal segments commonly 16 in number, if fewer then reduction resulting from fusion of basal flagellar segments, total apparent number less than 10. 35

34. Wing with discal medial cell (*dm*) open by atrophy of vein M_3, and crossvein *m–m*; only 2 medial veins (interpreted as veins M_1 and M_4), reaching wing margin (Fig. 55). . . . *Hexatoma* (*Parahexatoma* Alexander)

– Wing with discal medial cell (*dm*) closed; 4 medial veins or 3 medial veins (interpreted as veins M_1, M_3 and M_4), reaching wing margin (Fig. 54). . . . . *Hexatoma* (*Eriocera* Macquart)

35. Wing with 3 *M* veins reaching wing margin (*e.g.*, Figs 50, 53, 62, 64) 36

– Wing with 4 *M* veins reaching wing margin (*e.g.*, Figs 45–49, 51, 52, 56–61, 63, 65–67) 40

36. Outer cells of wing membrane with macrotrichia; vein R_2 absent; discal medial cell (*dm*) closed (Fig. 64). . . . . *Paradelphomyia* (*Oxyrhiza* de Meijere)

– Outer cells of wing membrane without macrotrichia; vein R_2 present; discal medial cell (*dm*) closed or open (*e.g.*, Figs 50, 53, 60, 62). 37

37. Wing with discal medial cell (*dm*) closed, base of vein M_3 present; and/or base of vein R_5 short, perpendicular to vein R_{2+3+4} (*e.g.*, Figs 50, 60). 38

– Wing with discal medial cell (*dm*) open by atrophy of base of vein M_3; base of vein R_5 elongate, forming sharp angle with vein R_{2+3+4} (*e.g.*, Figs 53, 62) 39

38. Wing vein R_{2+3+4} long, *ca* ⅔ length of vein *Rs* or *ca* 5 × length of basal section of vein R_5; discal medial cell (*dm*) elongate, almost as long as distal section of vein M_1; crossvein *m–cu* at or near mid length of discal medial cell (*dm*) (Fig. 50) . . . . *Ctenolimnophila* (*Campbellomyia* Alexander)

– Wing vein R_{2+3+4} short, *ca* ¼ length of vein *Rs* or 2 × length of basal section of vein R_5; discal medial cell (*dm*) shorter than distal section of vein M_{1+2}, with crossvein *m–cu* at or near ¼ its length (discal medial cell (*dm*) open in *L.* (*L.*) *difficilis* Alexander, 1920) (Fig. 60) . . . . . . *Limnophila* Macquart *sensu stricto* [in part]

39. Wing vein R_3 present as spur (Fig. 53). . . . . *Eupilaria* Alexander

– Wing vein R_3 absent (Fig. 62) . . . . *Medleromyia* Alexander

40. Wing with auxiliary crossvein in cell *bm* (*e.g.*, Figs 51, 52) 41

– Wing without auxiliary crossvein in cell *bm* (*e.g.*, Figs 45–49, 56–61, 63, 65–67) 42

41. Wing with auxiliary crossvein in cell r_3 (Fig. 51) . . . . *Dicranophragma* Osten Sacken *sensu stricto*

– Wing with auxiliary crossvein in cell *bm*, not in cell r_3 (Fig. 52) . . . . *Eloeophila* Rondani

42. Wing without arculus; base of vein *M* removed from wing base (Figs 46, 47); legs often with flattened elongate scales in addition to normal setae. . . . . *Austrolimnophila* Alexander *sensu lato* 43

– Wing with arculus; base of vein *M* close to wing base (*e.g.*, Figs 45, 48, 49, 56–61, 63, 65–67); legs without flattened elongate scales in addition to normal setae 44

43. Wing with auxiliary crossvein in basal ½ of cell *sc* (Fig. 47). . . . . *Austrolimnophila* (*Phragmocrypta* Alexander)

– Wing without auxiliary crossvein in basal ½ of cell *sc* (Fig. 46) . . . . *Austrolimnophila* Alexander *sensu stricto*

44. Wing with discal medial cell (*dm*) open by atrophy of crossvein *m–m* (*e.g.*, Figs 58, 59) 45

– Wing with discal medial cell (*dm*) closed, crossvein *m–m* present (*e.g.*, Figs 45, 48, 49, 56, 57, 60, 61, 63, 65–67). 46

45. Wing vein R_{2+3+4} about as long as vein R_2 (Fig. 58) . . . . *Limnophila* (*Elporiomyia* Alexander) [in part] (*L.* (*E.*) *woodiana* Alexander, 1964)

– Wing vein R_{2+3+4} much longer than vein R_2 (Fig. 59). . . . . *Limnophila* (*Hovalimnophila* Alexander)

46. Pronotum narrow, margins produced anteriorly into lateral lobes (Fig. 14) . . . . *Pseudolimnophila* Alexander *sensu lato* 47

– Pronotum broad, margins not produced anteriorly into lateral lobes (e.g., Figs 15, 16) 48

47. Wing with auxiliary crossvein in cell r_3 (Fig. 66) . . . . *Pseudolimnophila* (*Calolimnophila* Alexander)

– Wing without auxiliary crossvein in cell r_3 (Fig. 67) . . . . *Pseudolimnophila* Alexander *sensu stricto*

48. Antenna with basal 3–5 flagellomeres developed ventrally, without ventral verticils; male terminalia with outer gonostylus not bidentate at apex in most species 49

– Antenna with basal 3–5 flagellomeres not developed ventrally, all with ventral verticils; male terminalia with outer gonostylus bidentate at apex 50

49. Male terminalia with outer gonostylus in form of slender glabrous rod, terminating in single acute spine; gonapophyses in form of paddle-like blades; aedeagus elongate with apex narrowed and strongly recurved; female terminalia elongate and heavily sclerotised at apices . . . . . . *Afrolimnophila* Alexander

– Male terminalia with outer gonostylus setiferous; gonapophyses in form of flattened blades that extend into acute spines; aedeagus short and stout, apex blunt or membranous; female terminalia short and fleshy . . . . *Limnophila* (*Elporiomyia* Alexander) [in part]

50. Wing with apex of subcostal vein (*Sc*) positioned well before apex of vein R_1; base of vein R_5 short, almost perpendicular to vein R_{2+3+4} (e.g., Figs 57, 60, 61, 63, 65); tibial spurs well-developed 51

– Wing with apex of subcostal vein (*Sc*) ending close to apex of vein R_1; base of vein R_5 elongate, forming sharp angle with vein R_{2+3+4} and/or vein R_4 (*e.g.*, Figs 48, 49, 56); tibial spurs absent 55

51. Head not narrowed posteriorly, not produced into slender neck (Fig. 16) . . . . *Pilaria* Sintenis

– Head narrowed posteriorly, produced into slender neck (*e.g.*, Fig. 15) 52

52. Wing membrane with strong macrotrichia at apex (Fig. 57) . . . . *Limnophila* (*Dasylimnophila* Alexander)

– Wing membrane without strong macrotrichia at apex (e.g., Figs 60, 61, 63) 53

53. Male terminalia with outer gonostylus setiferous. . . . .*Neolimnomyia* Séguy

– Male terminalia with outer gonostylus bare 54

54. Wing membrane with distinct heavily maculate brown pattern. . . . .*Limnophila* (*Nesolimnophila* Alexander)

– Wing membrane without distinct heavily maculate brown pattern . . . . *Limnophila* Macquart *sensu stricto* [in part]

55. Wing vein *Rs* close to and parallel with vein R_1 (in direct longitudinal alignment with vein R_{2+3+4}); vein R_3 strongly curved (upturned), cephalad near apex (Fig. 56); palpus 5-segmented . . . . *Lecteria* Osten Sacken *sensu stricto*

– Wing vein *Rs* not close to and parallel with vein R_1; vein R_3 not strongly curved (upturned) at apex (*e.g.*, Figs 48, 49); palpus 2-segmented 56

56. Wing cell *c* with series of weak crossveins; crossvein *r–m* positioned far distad to or beyond outer end of discal medial cell (*dm*) (Fig. 49) . . . . *Conosia* Wulp

– Wing cell *c* without series of weak crossveins; crossvein *r–m* more basal in position at or before mid length of discal medial cell (*dm*) (*e.g.*, Fig. 48) . . . . *Clydonodozus* Enderlein

57. Wing vein R_1 ending at or near mid length of wing; anterior branch of vein *Rs* short, erect or suberect, ending before ¾ length of wing (Fig. 90) . . . . *Styringomyia* Loew

– Wing vein R_1 ending at or beyond ⅔ length of wing; anterior branch of vein *Rs* long, elongate, ending beyond ¾ length of wing (*e.g.*, Figs 68–89, 91–96). 58

58. Mid and hind coxae closely approximated; thorax with meron not larger than mid coxa (*e.g.*, Figs 17, 19). 59

– Mid and hind coxae more separated; thorax with meron larger than mid coxa (producing “pot-bellied” appearance) (*e.g.*, Figs 18, 20, 21) 71

59. Wing with 2 branches of vein *Rs* reaching wing margin (e.g., Figs 79, 80, 85, 95) 60

– Wing with 3 branches of vein *Rs* reaching wing margin (*e.g.*, Figs 73, 77, 78, 81, 83, 84, 86, 94) 63

60. Wing vein *Rs* in direct longitudinal alignment with vein R_5; subcostal vein (*Sc*) long, terminating at level of fork of vein *Rs* (Fig. 85) . . . . *Limnophilomyia* (*Eulimnophilomyia* Alexander)

– Wing vein *Rs* not in longitudinal alignment with vein R_5; subcostal vein (*Sc*) short, terminating well before level of fork of vein *Rs* (*e.g.*, Figs 79, 80, 95) 61

61. Wing vein R_2 and arculus absent (Fig. 79). . . . .*Gonomyia* (*Leiponeura* Skuse) [in part]

– Wing vein R_2 and arculus present (*e.g.*, Figs 80, 95) 62

62\. Wing with crossvein *r–m* positioned beyond fork of vein *Rs* (Fig. 95); legs with normal setation only, without flattened scales . . . . *Teucholabis* Osten Sacken *sensu stricto*

– Wing with crossvein *r–m* positioned before fork of vein *Rs* (Fig. 80); legs with abundant flattened scales. . . . . *Gymnastes* Brunetti *sensu stricto*

63\. Wing veins R_3 and R_4 at base of cell r_3 subparallel, gradually diverging near wing margin; cell r_3 deep, longer than its petiole; discal medial cell (*dm*) closed (*e.g.*, Figs 77, 84, 86) 64

– Wing veins R_3 and R_4 strongly diverging from base of cell r_3 onwards; cell r_3 often shorter than its petiole; discal medial cell (*dm*) often open (*e.g.*, Figs 73, 78, 81, 83, 94). 66

64\. Wing vein *Rs* not in direct longitudinal alignment with vein R_5; wing membrane with pattern (Fig. 77) . . . . *Eugnophomyia* Alexander

– Wing vein *Rs* in direct longitudinal alignment with vein R_5; wing membrane without pattern (except for pterostigma) (*e.g.*, Figs 84, 86) 65

65\. Wing with crossvein *sc–r* positioned well before apex of subcostal vein (*Sc*); crossvein *r–m* positioned close to fork of vein *Rs*; vein A_1 straight or gently sinuate (Fig. 84); legs with abundant scales additional to normal setation; claws simple . . . . *Idiognophomyia* Alexander

– Wing with crossvein *sc–r* positioned near apex of subcostal vein (*Sc*); crossvein *r–m* positioned far beyond fork of vein *Rs*; vein A_1 convexly arched (Fig. 86); legs with normal setation; claws with microscopic teeth . . . .*Limnophilomyia* Alexander *sensu stricto*

66\. Wing vein R_2 present (*e.g.*, Figs 73, 94). 67

– Wing vein R_2 absent (*e.g.*, Figs 78, 81, 83) 68

67\. Wing cell r_3 shorter than its petiole (Fig. 94) . . . . *Teucholabis* (*Euparatropesa* Alexander)

– Wing cell r_3 longer than its petiole (Fig. 73) . . . . *Ellipteroides* (*Progonomyia* Alexander)

68\. Wing crossvein *m–cu* at least its own length before fork of vein *M*; discal medial cell (*dm*) open; arculus present (Fig. 83). . . . .*Idiocera* Dale *sensu stricto*

– Wing crossvein *m–cu* at or close to fork vein *M*; discal medial cell (*dm*) open or closed; arculus present, or absent (*e.g.*, Figs 78, 81) 69

69\. Subcostal wing vein (*Sc*) ending opposite base of vein *Rs* or virtually so; cell r_5 narrowed towards wing margin; arculus absent (Fig. 78); legs without scales . . . . *Gonomyia* Meigen *sensu lato* 70

– Subcostal wing vein (*Sc*) ending opposite or beyond mid length of vein *Rs*; cell r_5 virtually parallel-sided; arculus present (Fig. 81); legs with abundant flattened scales . . . . *Hovamyia* Alexander

70\. Wing cell r_3 large; vein R_{2+3+4} subequal to or shorter than vein R_4 (Fig. 78) . . . .*Gonomyia* Meigen *sensu stricto*

– Wing cell r_3 small to minute; vein R_{2+3+4} longer than vein R_4. . . .*Gonomyia* (*Leiponeura* Skuse) [in part]

71\. Wing with 2 branches of vein *Rs* reaching wing margin (Figs 68, 69). . . . . *Atarba* Osten Sacken *sensu lato* 72

– Wing with 3 branches of vein *Rs* reaching wing margin (e.g., Figs 70–72, 74–76, 82, 87–89, 91–93, 96). 73

72\. Tibial spurs present . . . .*Atarba* Osten Sacken *sensu stricto*

– Tibial spurs absent . . . . *Atarba* (*Atarbodes* Alexander)

73\. Wing with veins R_{2+3} and R_{4+5} developed and vein *Rs* ending in cell r_3 or in direct longitudinal alignment with vein R_4, or vein R_{4+5} not developed and vein *Rs* in direct alignment with vein R_4 (*e.g.*, Figs 87, 93) 74

– Wing vein *Rs* either ending in cell r_4 or in direct alignment with vein R_{2+3+4} (e.g., Figs 70–72, 74–76, 82, 88, 89, 91, 92, 96). 75

74\. Wing with veins R_{2+3} and R_{4+5} developed and vein *Rs* ending in cell r_3 or in direct longitudinal alignment with vein R_4; veins R_{2+3} and R_5 not perpendicular (Fig. 87); male terminalia with gonostylus bipartite . . . .*Molophilus* Curtis *sensu stricto*

– Wing vein *Rs* in direct alignment with vein R_4; veins R_{2+3} and R_5 perpendicular at base (Fig. 93); male terminalia with gonostylus single . . . . *Tasiocera* (*Dasylimnophilus* Goetghebuer)

75\. Wing cells with macrotrichia or flattened scales 76

– Wing cells bare without macrotrichia or flattened scales. 78

76. Wing vein A_1 long and sinuous not divergent from vein *CuP* (e.g., Fig. 74) . . . . *Erioptera* Meigen *sensu stricto* [in part]

– Wing vein A_1 short and rather straight divergent from vein *CuP* (e.g., Figs 88, 96) 77

77. Wing cell r_3 shorter than its petiole; discal medial cell (*dm*) open (Fig. 88) . . . . *Ormosia* (*Neserioptera* Alexander)

– Wing cell r_3 longer than its petiole; discal medial cell (*dm*) closed (Fig. 96) . . . *Trichotrimicra* Alexander

78. Wing cell r_3 short, about as long as or shorter than its petiole (e.g., Figs 71, 72, 89). 79

– Wing cell r_3 longer than its petiole (e.g., Figs 70, 74–76, 82, 91, 92). 81

79. Wing vein R_2 absent (Fig. 89) . . . . *Rhabdomastix* Skuse *sensu stricto*

– Wing vein R_2 present (e.g., Figs 71, 72). . . . . *Cheilotrichia* Rossi *sensu lato* 80

80. Wing with discal medial cell (*dm*) closed (Fig. 71) . . . . *Cheilotrichia* Rossi *sensu stricto*

– Wing with discal medial cell (*dm*) open by atrophy of crossvein *m–m* (Fig. 72) . . . . *Cheilotrichia* (*Empeda* Osten Sacken)

81. Wing with crossvein *sc–r* positioned near apex of subcostal vein (*Sc*) (Fig. 82); antenna of male elongate . . . . *Hoverioptera* Alexander *sensu stricto*

– Wing with crossvein *sc–r* removed from apex of subcostal vein (*Sc*) (e.g., Figs 70, 74–76, 91, 92); antenna short in both sexes 82

82. Wing vein *Rs* long and straight, usually subequal in length to outer radial branches; crossvein *sc–r* positioned almost opposite outer end of vein *Rs*, well removed from base of vein *Rs*; crossvein *m–cu* positioned beyond fork of vein *M*, at or near mid length of vein M_{3+4} (Fig. 70); male terminalia with single gonostylus; female terminalia with blunt, fleshy ovipositor . . . . *Baeoura* Alexander

– Wing vein *Rs* usually short, commonly less than length of outer radial branches; crossvein *sc–r* usually positioned just beyond base of vein *Rs*, in some cases opposite mid length; crossvein *m–cu* positioned at or shortly before fork of vein *M* (e.g., Figs 74–76, 91, 92); male terminalia with gonostylus bipartite; female terminalia with elongate, sclerotised ovipositor 83

83. Wing with discal medial cell (*dm*) closed (Figs 91, 92) . . . . *Symplecta* Meigen *sensu lato* 84

– Wing with discal medial cell (*dm*) open (Figs 74–76) . . . . *Erioptera* Meigen *sensu lato* 86

84. Wing vein A_1 forked at apex (Fig. 91) . . . . *Symplecta* (*Podoneura* Bergroth)

– Wing vein A_1 unforked at apex (e.g., Fig. 92) 85

85. Wing membrane unpatterned; antenna with apical 3 flagellomeres abruptly smaller than preceding flagellomeres . . . . *Symplecta* (*Trimicra* Osten Sacken)

– Wing membrane patterned; antenna with apical 3 flagellomeres gradually reduced in size. *Symplecta* (*Psiloconopa* Zetterstedt)

86. Wing membrane unpatterned; antenna with basal flagellomeres more or less fused; male terminalia with inner gonostylus simple, near mid length bent at right angle into a spine. *Erioptera* (*Meterioptera* Alexander)

– Wing membrane pale, dark patterned; antenna with basal flagellomeres distinct; male terminalia with inner gonostylus more complex, not bent at right angle into a spine 87

87. Wing vein A_1 long and sinuous, apical part subparallel to wing margin (Fig. 74) . . . . *Erioptera* Meigen *sensu stricto* [in part]

– Wing vein A_1 short, not sinuous, apical part not subparallel to wing margin (Fig. 75). . . . . *Erioptera* (*Mesocyphona* Osten Sacken)

88. Wing vein R_2 absent (veins R_1 and R_4 well separated) (e.g., Figs 106, 108–110, 122, 123); rostrum more or less developed, at least as long as remainder of head in *Helius*, much longer in *Elephantomyia* (Fig. 11) and *Toxorhina* (Fig. 13). 89

– Wing vein R_2 present (obscured in certain *Trichoneura* Loew and in *Xenolimnobia* Alexander; e.g., Figs 97–105, 107, 111–116, 118–121, 124–129); rostrum undeveloped, except in *Geranomyia*, in which rostrum plus labial palpus and hypopharynx are greatly lengthened, to approximately ½ body length or more (Fig. 12) 95

89. Rostrum about as long as remainder of head or slightly longer; antenna with apical flagellomeres with short verticils, at most about length of flagellomeres, usually shorter . . . . *Helius* Le Peletier & Serville *sensu lato* 90

– Rostrum much longer than remainder of head, about as long as ½ body length, or more (*e.g.*, Figs 11, 13); antenna with apical flagellomeres with long verticils 93

90. Wing with discal medial cell (*dm*) open; crossvein *m–cu* positioned before fork of vein *M* . . . . *Helius* (*Rhamphidina* Alexander)

– Wing with discal medial cell (*dm*) closed or open, if open then crossvein *m–cu* positioned beyond fork of vein *M* (*e.g.*, Figs 108–110). 91

91. Wing veins *Sc* and R_1 apices close to each other, distance between them approximately as long as crossvein *m–cu*; crossvein *sc–r* positioned before apex of subcostal vein (*Sc*); crossvein *r–m* present; crossvein *m–cu* positioned before fork of vein *M* (Fig. 110) . . . . . . *Helius* (*Rhamphidioides* Alexander)

– Wing veins *Sc* and R_1 widely separated at apices, distance between them greater than length of crossvein *m–cu*; crossvein *sc–r* close to apex of subcostal vein (*Sc*); *r–m* present or absent; crossvein *m–cu* positioned at or beyond fork of vein *M* (e.g., Figs 108, 109) 92

92. Wing vein *Rs* short compared to vein R_4 (Fig. 108) or longer; male terminalia with gonostylus bifid . . . . *Helius* Le Peletier & Serville *sensu stricto*

– Wing vein *Rs* slightly or distinctly longer than vein R_4 (Fig. 109); male terminalia with gonostylus single . . . . *Helius* (*Prohelius* Alexander)

93. Wing veins R_1 and R_4 elongate, terminating near wing apex (Fig. 106); palpus 5-segmented; legs with setae simple. . . . . *Elephantomyia* Osten Sacken *sensu stricto*

– Wing veins R_1 and R_4 short, terminating in anterior margin of wing or R_1 short and R_4 absent (Figs 122, 123); palpus 2-segmented; legs with setae deeply forked. . . . . *Toxorhina* Loew *sensu lato* 94

94. Wing vein *Rs* unbranched: vein R_4 absent and only vein R_5 reaching wing margin (Fig. 123) . . . . *Toxorhina* Loew *sensu stricto*

– Wing vein *Rs* with 2 branches: veins R_4 and R_5 reaching wing margin (Fig. 122) . . . . *Toxorhina* (*Ceratocheilus* Wesché)

95. Wing with crossvein *m–cu* basal to fork of vein *M*, distance greater than length of crossvein *m–cu*; discal medial cell (*dm*) open (*e.g.*, Figs 100, 115, 116, 120). 96

– Wing with crossvein *m–cu* close to or apical to fork of vein *M*, or if basal then distance not or scarcely as long as crossvein *m–cu*; discal medial cell (*dm*) open or closed (*e.g.*, Figs 97–99, 101–105, 107, 111–114, 118, 119, 121, 124–129). 99

96. Wing with discal medial cell (*dm*) open by atrophy of base of vein M_3; crossvein *m–cu* basal to fork of vein *M*, by several times its length; anal lobe distinct (Fig. 120) . . . . *Thaumastoptera* Mik *sensu stricto*

– Wing with discal medial cell (*dm*) open by atrophy of crossvein *m–m*; crossvein *m–cu* basal to fork of vein *M*, by approximately its length or by several times its length; anal lobe distinct or narrow (*e.g.*, Figs 100, 115, 116). 97

97. Wing crossvein *m–cu* approximately its own length before fork of vein *M*, positioned near level of fork of vein *Rs*; vein *Rs* straight, to slightly concave; anal lobe distinct (Fig. 100) . . . . *Antocha* (*Orimargula* Mik)

– Wing crossvein *m–cu ca* 4 or 5 × its length before fork of vein *M*, positioned near base of vein *Rs*; vein *Rs* curved, convex near its base; anal lobe relatively narrow (*e.g.*, Figs 115, 116) . . . . *Orimarga* Osten Sacken *sensu lato* 98

98. Wing broad, approximately 3 × as long as wide, conspicuously patterned with dark brown; auxiliary crossveins in cells *c*, r_1 and *br* (Fig. 116); femora blackened at apices, enclosing a narrow pale subterminal ring . . . . *Orimarga* (*Protorimarga* Alexander)

– Wing narrow, approximately 4–4.5 × as long as wide; no auxiliary crossveins in any of the cells (Fig. 115); femora uniform in colour . . . .*Orimarga* Osten Sacken *sensu stricto*

99. Wing cell r_1 narrow, veins R_1 and R_{2+3+4} closely approximated; R_1 elongate, R_2 lying far distad, beyond level of outer end of discal medial cell (*dm*); crossvein *m–cu* beyond fork of vein *M*; a conspicuous pale fold in distal end of cell *cua*, vein *CuP* thus appearing forked (indicated as dashed line on Fig. 105); legs with abundant flattened scales additional to normal setae; claws simple. . . . .*Dicranoptycha* Osten Sacken

– Wing cell r_1 broader, veins R_1 and R_{2+3+4} wider apart; R_2 (if present) more basal in position, except where entire cord and veins beyond it lie far distad, usually at or before level of outer end of discal medial cell (*dm*); crossvein *m–cu* at or close to fork of vein *M*, rarely (*Libnotes* Westwood, *Limonia* Meigen) beyond; without fold in cell *cua* (*e.g.*, Figs 97–99, 101–104, 107, 111–114, 118, 119, 121, 124–129); legs without flattened scales; claws commonly toothed or spined. 100

100. Wing vein *Rs* in direct alignment with crossvein *r–m*; vein *Rs* forked basal, usually near mid length of wing; vein *CuA* apex close to vein *CuP* apex, or fused with vein *CuP*; vein A_1 short and convex (*e.g.*, Figs 124–126). . . . . *Trentepohlia* Bigot *sensu lato* 101

– Wing vein *Rs* not in direct alignment with crossvein *r–m*; vein *Rs* fork in apical ½ of wing; vein *CuA* apex not close to vein *CuP* apex (except for *Dicranomyia* (*Euglochina*); vein A_1 longer, rather straight or sinuous (*e.g.*, Figs 97–99, 101–104, 107, 111–114, 118, 119, 121, 127–129) 103

101. Wing with discal medial cell (*dm*) closed, emanating 4 *M* veins that reach wing margin (Fig. 124). . . . .*Trentepohlia* (*Mongoma* Westwood)

– Wing with discal medial cell (*dm*) closed (e.g., Fig. 125), or discal medial cell (*dm*) open by atrophy of vein M_3 (e.g., Fig. 126), 3 *M* veins reaching wing margin 102

102. Wing with discal medial cell (*dm*) closed, vein M_3 present; veins *CuA* and *CuP* not fused apically (Fig. 125). . . . . *Trentepohlia* (*Paramongoma* Brunetti)

– Wing with discal medial cell (*dm*) open by atrophy of vein M_3; veins *CuA* and *CuP* fused apically (Fig. 126). . . . . *Trentepohlia* Bigot *sensu stricto*

103. Antenna with 16 flagellomeres; free apex of wing vein R_1 absent or present as spur (e.g., Figs 127, 128), or R_1 directly merging with costal vein (*C*) (e.g., Fig. 129) 104

– Antenna with 14 flagellomeres; free apex of wing vein R_1 present, short (e.g., Figs 97–99, 101–104, 107, 111–114, 118, 119, 121). 106

104. Wing vein R_1 merging with costal vein (*C*); discal medial cell (*dm*) open (Fig. 129) . . . . *Xenolimnobia* Alexander

– Wing vein R_1 with free apex absent or present as short spur; discal medial cell (*dm*) closed (*e.g.*, Figs 127, 128). . . . .*Trichoneura* Loew *sensu lato* 105

105. Anterior vertex of head produced into a lobe or corniculus (*e.g.*, Fig. 13); wing membrane conspicuously patterned with brown. . . . . *Trichoneura* (*Ceratolimnobia* Alexander)

– Anterior vertex of head not produced into a lobe or corniculus; wing membrane unpatterned . . . . *Trichoneura* (*Xipholimnobia* Alexander)

106. Wing with discal medial cell (*dm*) open (e.g., Figs 99, 104, 118). 107

– Wing with discal medial cell (*dm*) closed (e.g., Figs 97, 98, 101–103, 107, 111–114, 119, 121) . . .110

107. Subcostal wing vein (*Sc*) very long, ending virtually opposite vein R_2; vein *Rs* elongate; anal lobe narrow (Fig. 99) . . . .*Amphilimnobia* Alexander

– Subcostal wing vein (*Sc*) short, ending virtually opposite base of vein *Rs*; anal lobe distinct or narrow (e.g., Figs 104, 118) 108

108. Wing with discal medial cell (*dm*) open by atrophy of base of vein M_3; anal lobe narrow . . . .*Dicranomyia* (*Pseudoglochina* Alexander)

– Wing with discal medial cell (*dm*) open by atrophy of crossvein *m–m*; anal lobe distinct (e.g., Figs 104, 118). 109

109. Antennal flagellomeres produced ventrally; male terminalia with rostral spines of inner gonostylus on common basal tubercle . . . . *Rhipidia* (*Eurhipidia* Alexander)

– Antennal flagellomeres not produced ventrally; male terminalia with rostral spines directly inserted on inner gonostylus. . . . . *Dicranomyia* (*Idioglochina* Alexander)

110. Mouthparts with rostrum, labial palpus and hypopharynx produced; combined structure longer than remainder of head, usually considerably so (Fig. 12). . . . . *Geranomyia* Haliday

– Mouthparts not conspicuously produced as above 111

111. Wing narrow, with narrow anal lobe; crossvein *sc–r* present some distance before base of vein *Rs*; cord of wing lying far distad (e.g., Figs 103, 121) 112

– Wing broad, with distinct anal lobe; crossvein *sc–r* usually at or beyond base of vein *Rs*; cord of wing in normal position from ¾ wing length (e.g., Figs 97, 98, 101, 102, 111–114, 119) 113

112. Wing vein *Rs* notably short; vein R_3 absent (Fig. 103) . . . . *Dicranomyia* (*Euglochina* Alexander)

– Wing vein *Rs* long; vein R_3 projecting as spur (Fig. 121) . . . . *Thrypticomyia* Skuse

113. Antennal flagellomeres more or less branched or produced ventrally, more strongly so in male (producing a bipectinate, unipectinate, or subpectinate condition); wing membrane often covered with small dark “freckles” (Fig. 119) . . . .*Rhipidia* Meigen *sensu stricto*

– Antennal flagellomeres simple, not branched or produced; wing membrane without "freckles" (*e.g.*, Figs 97, 98, 101, 102, 111–114) 114

114. Subcostal wing vein (*Sc*) ending close to base of vein *Rs* (in some cases slightly before or beyond) (Fig. 102) . . . . *Dicranomyia* Stephens *sensu stricto* [in part] and *Limonia* Meigen [in part]

– Subcostal wing vein (*Sc*) ending some distance beyond base of vein *Rs* (*e.g.*, Figs 97, 98, 101, 111–114). 115

115. Subcostal wing vein (*Sc*) extending to beyond fork of vein *Rs*; vein *Rs* short and oblique, crossvein *m–cu* near mid-length of vein M_{3+4} beneath discal medial cell (*dm*) . . . . *Libnotes* Westwood *sensu stricto*

– Subcostal wing vein (*Sc*) not extending to opposite fork of vein *Rs*; vein *Rs* longer and usually more arcuate; crossvein *m–cu* at, slightly before, or only slightly beyond fork of vein *M* (*e.g.*, Figs 97, 98, 101, 111–114). 116

116. Wing membrane with macrotrichia in stigmal area or covering greater part of membrane (*e.g.*, Figs 98, 113, 114). 117

– Wing membrane without macrotrichia (*e.g.*, Figs 97, 101, 111, 112) 119

117. Wing membrane with macrotrichia extensively covering wing membrane (Fig. 98). . . . . *Achyrolimonia* Alexander [in part]

– Wing membrane with macrotrichia confined to stigmal area (Fig. 114) or to stigmal area and wing apex (Fig. 113) . . . . *Metalimnobia* Matsumura *sensu lato* 118

118. Wing membrane with macrotrichia in stigmal area and wing apex, not remarkably glossy (Fig. 113); femora yellow with 4 narrow, dark brown bands; male terminalia with inner gonostylus with elongate rostrum bearing 2 long spines inserted on elevation; gonapophysis terminating in short acute spine . . . . *Metalimnobia* (*Lasiolimonia* Alexander)

– Wing membrane with macrotrichia in stigmal area only, remarkably glossy (Fig. 114); femora otherwise coloured; male terminalia with inner gonostylus with short robust rostrum bearing 2 short spines; gonapophysis terminating in elongate, slender extension . . . . *Metalimnobia* (*Tricholimonia* Alexander)

119. Eyes touching above and below antennae; male terminalia with gonocoxite with complicated ventromedial lobe; inner gonostylus intricately built. . . . . *Atypophthalmus* Brunetti *sensu stricto*

– Eyes not touching above and below antennae; male terminalia with gonocoxite with simple ventromedial lobe; inner gonostylus less intricately built 120

120. Male terminalia with inner and outer gonostylus present; inner gonostylus with elongate, slender rostrum, with dorsal spine and/or spine on elevation at base. . . . . *Achyrolimonia* Alexander [in part] and *Libnotes* (*Afrolimonia* Alexander) [in part]

– Male terminalia with inner gonostylus present only; inner gonostylus a slender, elongate structure, without dorsal spine and/or spine on elevation at base 121

121. Male terminalia with inner gonostylus bearing spines . . . . . . *Libnotes* (*Afrolimonia* Alexander) [in part]

– Male terminalia with inner gonostylus not bearing spines . . . . *Limonia* Meigen

122. Palpus with terminal segment elongate, longer than penultimate segment; antenna commonly with 13 segments; 9, 10, 11 or 12 segments in *Leptotarsus* (TIPULIDAE [in part]) 123

– Palpus with terminal segment short, not or scarcely longer than penultimate segment; antenna with 11, 12, 14 or 16 segments (LIMONIIDAE [in part]). 126

123. Wing not longer than halter; apical segment of palpus short . . . . . *Leptotarsus* (*Longurio* Loew) [in part]

– Wing longer than halter; apical segment of palpus short or long 124

124. Apical segment of palpus short. . . . . *Leptotarsus* (*Longurio* Loew) [in part]

– Apical segment of palpus long 125

125. Ground colour yellowish or orange-yellow, with dark markings; rostrum shorter than remainder of head . . . . *Nephrotoma* Meigen [in part]

– Ground colour greyish brown; rostrum about as long as remainder of head . . . . *Tipula* L. *sensu stricto* [in part]

126. Antenna 14-segmented; tibiae without spurs (LIMONIINAE [in part]) . . . . *Platylimnobia* Alexander

– Antenna 16-segmented; tibiae with or without spurs 127

127. Tibial spurs present (LIMNOPHILINAE [in part]) . . . . *Austrolimnophila* Alexander *sensu stricto* [in part] (*A. buxtoni* Alexander, 1956)

– Tibial spurs absent (CHIONEINAE [in part]) 128

128. Legs with abundant flattened scales among normal setae; female terminalia with short ovipositor . . . . *Quathlambia* Alexander (*Q. stuckenbergi* Alexander, 1956)

– Legs with normal setae; female terminalia with elongate ovipositor 129

129. Male terminalia not inverted . . . . *Symplecta* Meigen *sensu stricto* (*S. holdgatei* (Freeman, 1962))

– Male terminalia inverted . . . .*Molophilus* Curtis *sensu stricto* [in part] (*M. nannopterus* Alexander, 1956)

Synopsis of the fauna

***Achyrolimonia* Alexander** (Limoniidae: Limoniinae)**.** A genus of *ca* 35 described species, recorded from all zoogeographical regions, except the Neotropical Region and Antarctica. Eighteen species occur in the Afrotropical Region, from Guinea in the west to Comoros and Madagascar in the east. *Achyrolimonia* is probably a polyphyletic group, with species exhibiting affinities with *Dicranomyia* and allied genera. Some species of *Achyrolimonia* can be easily recognised by the wing membrane being extensively clothed in macrotrichia; subcostal vein (*Sc*) not reaching the fork of vein *Rs*; and the discal medial cell (*dm*) closed (Fig. 98). Other species are harder to separate from related taxa of Limoniinae. A few Palaearctic species have been reared from larvae occurring in the fruiting bodies of agaric fungi and from wood of deciduous and coniferous trees. In wood they probably occur in fungal hyphi (Brindle 1967; N.P. Krivosheina 2009, 2011*a*; Krivosheina & Krivosheina 2011: 190; Podeniene 2003). No identification keys are currently available to Afrotropical species.

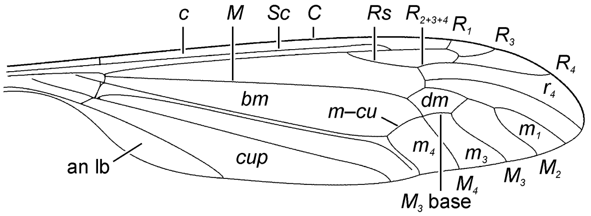
***Afrolimnophila* Alexander** (Limoniidae: Limnophilinae)**.** A genus of *ca* 40 described species, occurring in all zoogeographical regions, except the Australasian/Oceanian and Neotropical Regions and Antarctica, with most recorded from the Afrotropical and Oriental Regions. The Afrotropical fauna comprises 12 described species, restricted to the central parts of the continental Afrotropics, but absent from southern Africa and the Indian Ocean islands. *Afrolimnophila* can be recognised by the absence of auxiliary crossveins; a closed discal medial cell (*dm*); presence of four *M* veins that reach the wing margin (Fig. 45); ventrally produced basal antennal flagellomeres; and details of the male and female terminalia. Immature stages have been reported from aquatic and semi-aquatic situations, occurring along the margins of streams and in marshes and moist soil (Mendl 1978: 371). Alexander (1956, under *Limnophila*, subgenus *Afrolimnophila*) presented an identification key to the then known Afrotropical species.

***Amphilimnobia* Alexander** (Limoniidae: Limoniinae)**.** An endemic monotypic genus, with the single species, *A. leucopeza* Alexander, 1920, only known from Cameroon. The genus is characterised by the long subcostal wing vein (*Sc*), which terminates near the level of vein R_2 (Fig. 99). Biology and immatures stages remain unknown.

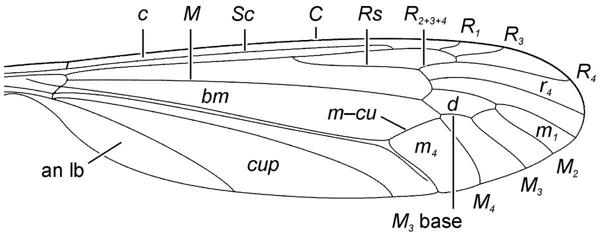
***Antocha* Osten Sacken** (Limoniidae: Limoniinae)**.** A genus of *ca* 160 described species occurring in all zoogeographical regions, except Antarctica, with most recorded from the Oriental and Palaearctic Regions. *Antocha* is divided into three subgenera, of which only *Antocha* (*Orimargula* Mik) is represented in the Afrotropics. *Antocha* (*Orimargula*) comprises 42 valid species, half of which occur in the Afrotropics, where the subgenus is widespread. The subgenus is characterised by the wide wing, with a virtually straight vein *Rs*; reduced radial and medial veins; the basal position of crossvein *m–cu*; and a distinct anal lobe (Fig. 100). Immature stages of a few *A.* (*Orimargula*) species are known. The apneustic larvae occur on vertical cliff and rock faces, in moss with running water and in fast-flowing streams. They obtain their oxygen directly from water (Alexander 1931; Bangerter 1929; Hinton 1965; Mendl 1978: 369); their life strategy concurring with that of other *Antocha* species (Alexander 1920; Brindle 1967; Fuller & Hynes 1987; Needham & Christensen 1927; Podeniene 2003; Yamagishi 1977; Young & Gelhaus 2000). Alexander (1956; 1964: 338) presented identification keys to Afrotropical species.

***Atarba* Osten Sacken** (Limoniidae: Chioneinae)**.** A genus of *ca* 160 described species occurring in all zoogeographical regions, except Antarctica, with only a few occurring in the Nearctic and Palaearctic Regions and *ca* 100 in the Neotropical Region. *Atarba* is divided into three subgenera, of which the subgenera *Atarba sensu stricto* and *A.* (*Atarbodes* Alexander) are represented in the Afrotropics. *Atarba* belongs to the group of Chioneinae with a large meron (*e.g.*, Figs 18, 20, 21). It differs from the other genera with a large meron by the presence of only three *R* veins that reach the wing margin (*e.g.*, Figs 68, 69). The two subgenera that occur in the Afrotropical Region can be separated by the presence (*Atarba sensu stricto*), or absence (*A.* (*Atarbodes*)) of tibial spurs. Two species of *Atarba sensu stricto* are described from South Africa. Immature stages of the Nearctic species *A. picticornis* Osten Sacken, 1869 and the Australasian/Oceanian (New Zealand) species *A. viridicolor* Alexander, 1922, are known, both occurring in wet, rotten hardwood logs (Alexander 1931; Rogers 1927). The Afrotropical fauna of *Atarba* (*Atarbodes*) comprises eight species, distributed in the south-eastern part of the continental Afrotropics, with three recorded from Madagascar. A further two species are known from the eastern Palaearctic. The biology and immature stages of the subgenus remain unknown. Alexander (1956; 1964: 371) presented identification keys to Afrotropical species.

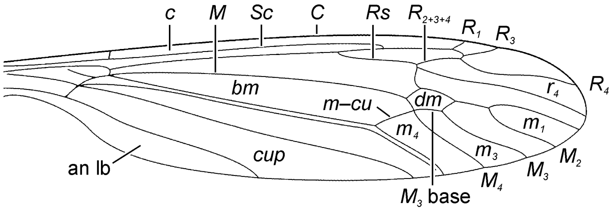
***Atypophthalmus* Brunetti** (Limoniidae: Limoniinae)**.** A genus of *ca* 50 described species occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. *Atypophthalmus* is divided into two subgenera of which *Atypophthalmus sensu stricto* is represented with 28 species in the Afrotropics. The genus is widespread in the region and is remarkably species-rich in the Indian Ocean islands of Comoros, Madagascar, Mauritius, Réunion Is. and Seychelles. The species can best be recognised by the complicated structure of the male terminalia, including the ventromedial lobe of the gonocoxite and the intricately built gonostylus. Larvae of the



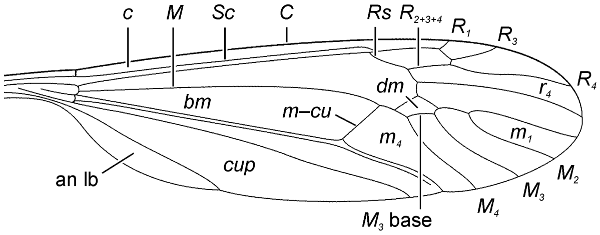
38 *Tipula* (*Acutipula*)



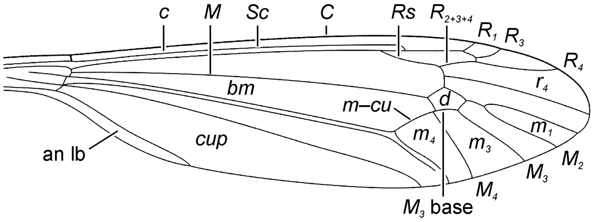
39 *Tipula* (*Afrotipula*)



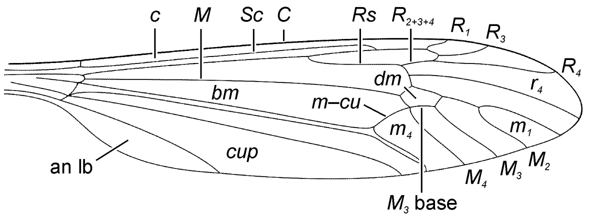
40 *Tipula* (*Savtshenkia*)



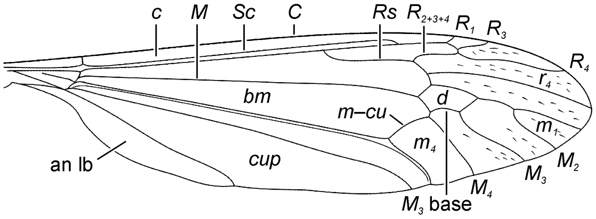
41 *Tipula* (*Schummelia*)



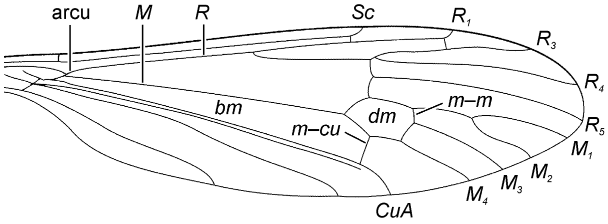
42 *Tipula* (*Spinitipula*)



43 *Tipula* (*Tipula*)



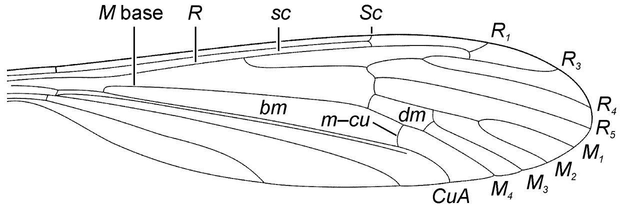
44 *Tipula* (*Yamatotipula*)



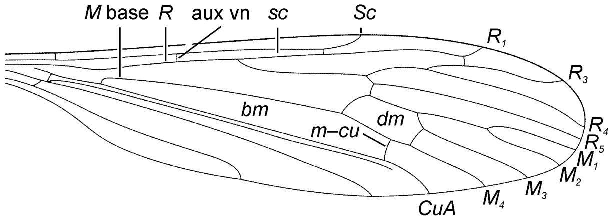
45 *Afrolimnophila*

Figs 14.38–45. Wings of Tipulidae and Limoniidae (dorsal views): (38) *Tipula* (*Acutipula*) *pomposa* Bergroth; (39) *T.* (*Afrotipula*) *infracta* Alexander; (40) *T.* (*Savtshenkia*) *draconis* Alexander; (41) *T.* (*Schummelia*) *scylla* Alexander; (42) *T.* (*Spinitipula*) *citricornis* Alexander; (43) *T.* (*Tipula*) *soror soror* Wiedemann; (44) *T.* (*Yamatotipula*) *setosipennis* Alexander; (45) *Afrolimnophila dichroica* (Alexander). Figs 38, 40, 41, 43 (after Alexander 1964, figs 18, 20, 19, 1, respectively), Fig. 39 (after Alexander 1955*a*, fig. 4), Fig. 42 (after Alexander 1963, fig. 49), Fig. 45 (after Alexander 1956, fig. 133).

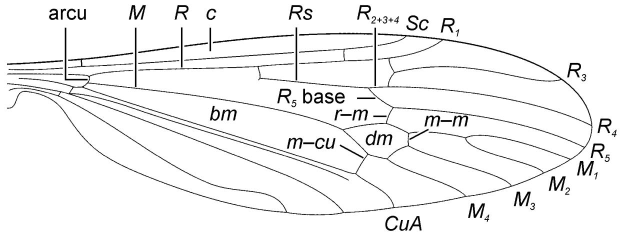
Abbreviations: an lb – anal lobe; arcu – arculus; *bm* – basal medial cell; *c* – costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.



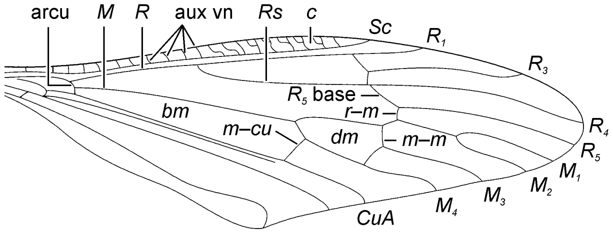
46 *Austrolimnophila* (*Austrolimnophila*)



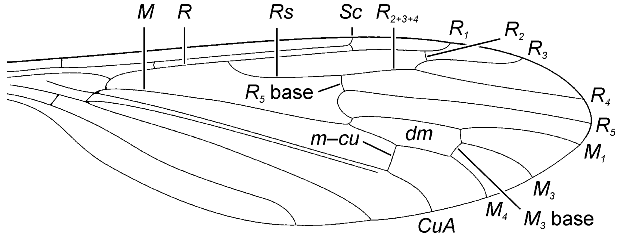
47 *Austrolimnophila* (*Phragmocrypta*)



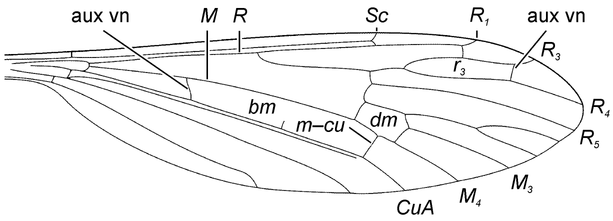
48 *Clydonodozus*



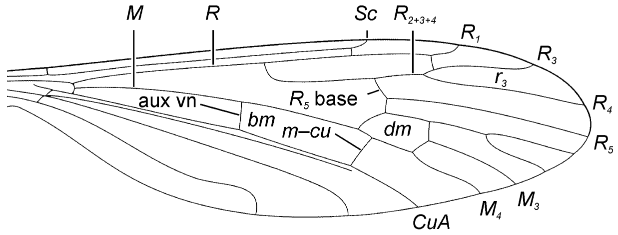
49 *Conosia*



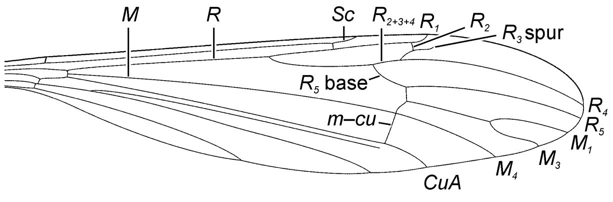
50 *Ctenolimnophila* (*Campbellomyia*)



51 *Dicranophragma* (*Dicranophragma*)



52 *Eloeophila*



53 *Eupilaria*

Figs 14.46–53. Wings of Limoniidae (dorsal views): (46) *Austrolimnophila* (*Austrolimnophila*) *echidnoides* Alexander; (47) *A.* (*Phragmocrypta*) *maumau* Alexander; (48) *Clydonodozus stuckenbergi* Alexander; (49) *Conosia irrorata irrorata* (Wiedemann); (50) *Ctenolimnophila* (*Campbellomyia*) *madagascariensis* Alexander; (51) *Dicranophragma* (*Dicranophragma*) *multiguttula* (Alexander); (52) *Eloeophila subannulata* (Alexander); (53) *Eupilaria nigeriana* Alexander. Figs 46, 47 (after Alexander 1956, figs 114, 117), Figs 48, 49, 52 (after Alexander 1964, figs 79, 78, 70, respectively), Fig. 50 (after Alexander 1963, fig. 68), Fig. 51 (after Alexander 1974, fig. 31), Fig. 53 (after Alexander 1972, fig. 21).

Abbreviations: arcu – arculus; aux vn – auxiliary vein; *bm* – basal medial cell; *c* – costal cell; *CuA* – anterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc* – subcostal cell.

Palaearctic species, *A. inustus* (Meigen, 1818), have been collected from fruiting bodies of solid fungi and wood of deciduous trees, where they probably occur in fungal hyphi (N.P. Krivosheina 2009, 2011*b*; Krivosheina & Krivosheina 2011: 193). De Meijere (1916) recorded the larvae of the Oriental species, *A. umbratus* (de Meijere, 1911), from green algae covering submerged objects in standing and flowing waters. No identification keys are available to Afrotropical species.

***Austrolimnophila* Alexander** (Limoniidae: Limnophilinae)**.** A genus of *ca* 200 described species, occurring in all zoogeographical regions, except Antarctica, with the majority of species recorded from the Afrotropical, Australasian/Oceanian and Neotropical Regions. The genus is divided into five subgenera, two of which are represented in the Afrotropics. The majority of the *ca* 50 Afrotropical representatives of *Austrolimnophila sensu stricto* occur to the east of the Great Rift Valley and in southern Africa, with a remarkable concentration of *ca* 20 species occurring in Madagascar. Only two species are recorded from West Africa (Nigeria). *Austrolimnophila sensu stricto* can be recognised by the rather "complete" wing venation, with three vein *Rs* branches and four vein *M* branches reaching the wing margin; the closed discal medial cell (*dm*); the position of crossvein *m–cu*, which touches the discal medial cell near mid length; in combination with the absence of the arculus and the associated rather distal base of vein *M* (Fig. 46). Known larvae of *Austrolimnophila* are all wood-inhabiting. Wood (1952) reported the breeding of the South African species *A. griseiceps* (Alexander, 1921), from a barkless decaying log of *Halleria capensis* L. (Scrophulariaceae) in a forest clearing removed from a stream, *A. medialis* (Alexander, 1921), from rotting logs in the immediate vicinity of small streams in forest areas and *A. thornei* (Wood, 1952), from a saturated decomposing log of *Cunonia capensis* L. (Cunoniaceae) over a shallow streamlet. Larvae of extralimital *Austrolimnophila* have been reared from beneath bark and from decaying wood of deciduous and coniferous trees (Alexander 1920; Brindle 1967; Brindle & Bryce 1960; N.P. Krivosheina 2009, 2010*a*; Krivosheina & Krivosheina 2011: 179; Podeniene 2003). The subgenus *A.* (*Phragmocrypta* Alexander) is endemic to the Afrotropical Region, with five species distributed in the central parts of the continental Afrotropics. It differs from the other subgenera of *Austrolimnophila* by the presence of an auxiliary crossvein in wing cell *sc* (Fig. 47). The biology and immature stages of *A.* (*Phragmocrypta*) remain unknown, but probably have a similar lifestyle to *Austrolimnophila sensu stricto*. Alexander (1955*b*, 1956, 1964: 350) and Wood (1952, as *Pseudolimnophila*) presented identification keys to Afrotropical species.

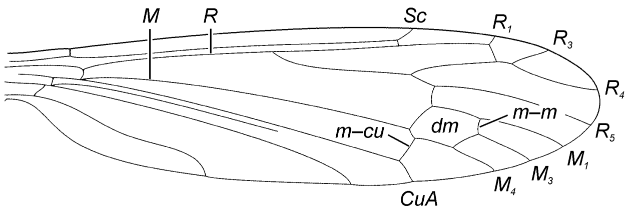
***Baeoura* Alexander** (Limoniidae: Chioneinae)**.** A genus of *ca* 70 described species, occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. Ten species occur in the Afrotropics, mostly restricted to South Africa, with individual species also known from Malawi, Mozambique and Nigeria. *Baeoura* belongs to the group of genera in the subfamily Chioneinae with the meron large (*e.g.*, Figs 18, 20, 21). It is characterised by the long and straight *Rs* wing vein; the subapical position of crossvein *sc–r* relative to the apex of vein *Sc*; the distal position of crossvein *m–cu* relative to the fork of vein *M* (Fig. 70); the presence of a single gonostylus of the male terminalia; and a short ovipositor in the female. Wood (1952) recorded the pupae of the South African species *B. claripennis* (Alexander, 1921) and *B. witzenbergi* (Wood, 1952); the pupae of *B. claripennis* were found flattened against small boulders at the edges of pools along the margins of streams; those of *B. witzenbergi* were recovered from similar muddy sand spits. Alexander (1964: 407) presented an identification key to South African species.

***Cheilotrichia* Rossi** (Limoniidae: Chioneinae)**.** A genus of *ca* 120 described species occurring in all zoogeographical regions, except Antarctica. The genus is divided into two subgenera, *Cheilotrichia sensu stricto* and *C.* (*Empeda* Osten Sacken), both of which are represented in the Afrotropical Region. *Cheilotrichia* belongs to the group of genera in the subfamily Chioneinae with the meron large (*e.g.*, Figs 18, 20, 21). Distinguishing features for the genus are the absence of macrotrichia on the wing membrane; four branches of vein *R* reaching the wing margin; and the short cell r_3 (*e.g.*, Figs 71, 72). The subgenera are separated by the presence (*Cheilotriochia sensu stricto*) (Fig. 71), or absence (*C.* (*Empeda*)), of wing crossvein *m–m* and hence absence of a closed discal medial cell (*dm*) (Fig. 72). The subgenus *Cheilotriochia sensu stricto* is small, with three species known from the Afrotropics, recorded from Madagascar, South Africa and Zimbabwe. Immature stages of the subgenus remain unknown. Only two species of the subgenus *C.* (*Empeda*) are Afrotropical: *C. bonaespei* (Alexander, 1917) and *C. telacantha* Alexander, 1960, both known from South Africa. Immature stages of the western Palaearctic species, *C. cinerascens* (Meigen, 1804) and the Nearctic species, *C. stigmatica* (Osten Sacken, 1869), have been reported from the margins of streams and marshy soils (Brindle 1967; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 187; Lévy 1919; Mendl 1978: 374; Podeniene 2003; Reusch 1988; Sandrock 1978; Young & Gelhaus 2000). Alexander (1964: 414) presented an identification key to South African species.

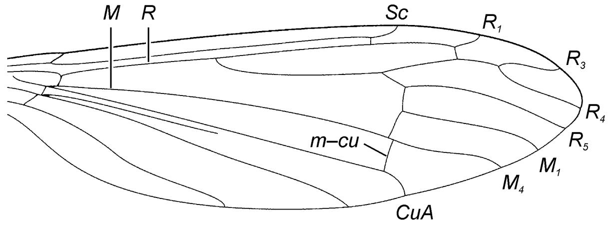
***Clydonodozus* Enderlein** (Limoniidae: Limnophilinae)**.** A genus of 23 described species occurring in the Afrotropical and Oriental Regions; 16 are Afrotropical. The genus is distributed in Central Africa and is absent from southern Africa and Madagascar. *Clydonodozus* is readily distinguished by the long subcostal vein (*Sc*), which terminates close to the apex of vein R_1; the robust and angular vein *Rs*; the full set of veins *Rs* and *M* branches; the presence of the arculus; the closed discal medial cell (*dm*) (Fig. 48); the short palpus and the absence of tibial spurs. The biology and immature stages remain unknown. Alexander (1956) presented an identification key to Afrotropical species.

***Conosia* Wulp** (Limoniidae: Limnophilinae)**.** A genus of nine described species occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions (Fig. 8). With the exception of the Oriental species *C. insularis* Alexander, 1942 and *C. minuscula* Alexander, 1958, both restricted to the Indian Peninsula, all species occur in the Afrotropical Region. Most Afrotropical species are endemic to small areas of the region, but *C. angustissima* Alexander, 1927 and *C. irrorata irrorata* (Wiedemann, 1828) are widespread. The latter occurs over much of the continental Afrotropics and is also represented in the Australasian/Oceanian, Oriental and Palaearctic Regions. *Conosia* can be easily recognised by the produced prescutum, which covers the head; and the peculiar wing venation, with the series of auxiliary crossveins in cell *c* and the distal position of crossvein *r–m*, relative to the large discal medial cell (*dm*) (Fig. 49). The tibiae lack spurs and the palpus is short. Wood (1952) provided a detailed account of the larva and pupa of the widespread Afrotropical species *C. angustissima* (erroneously cited as *C. irrorata*).

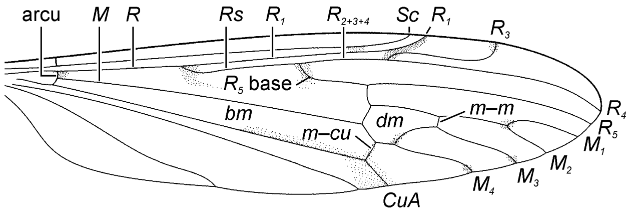
Numerous larvae were collected in wet sandy gravel and reddish silt on the edge of a small trickle of water *ca* 50–75 mm in depth. Judging from the structures of the head, the larvae are predatory as are most other known larvae of Limnophilinae.



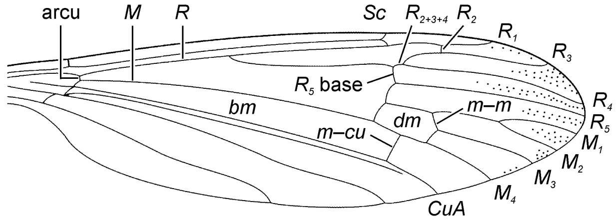
54 *Hexatoma* (*Eriocera*)



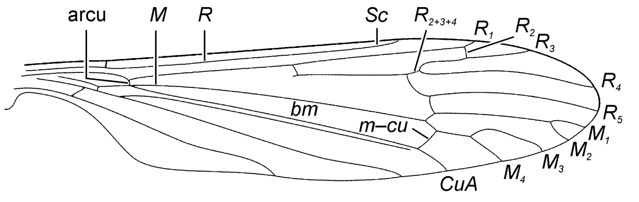
55 *Hexatoma* (*Parahexatoma*)



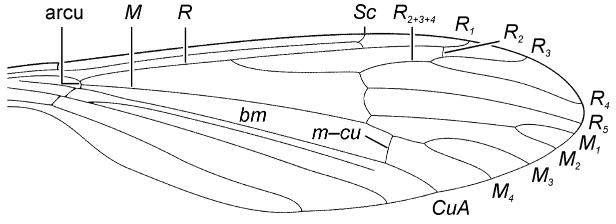
56 *Lecteria* (*Lecteria*)



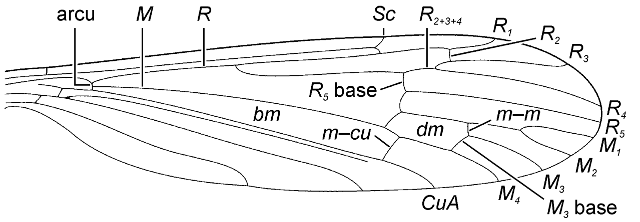
57 *Limnophila* (*Dasylimnophila*)



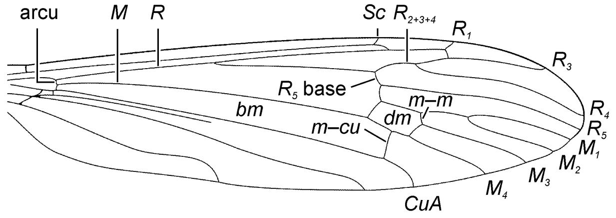
58 *Limnophila* (*Elporiomyia*)



59 *Limnophila* (*Hovalimnophila*)



60 *Limnophila* (*Limnophila*)



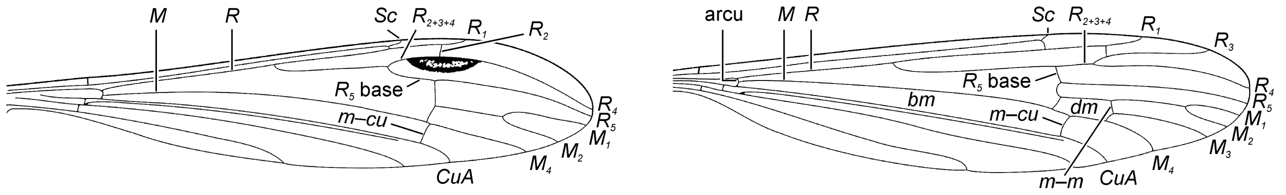
61 *Limnophila* (*Nesolimnophila*)

Figs 14.54–61. Wings of Limoniidae (dorsal views): (54) *Hexatoma* (*Eriocera*) *pusilloides* Alexander; (55) *H.* (*Parahexatoma*) *pauliani* Alexander; (56) *Lecteria* (*Lecteria*) *africana africana* Alexander; (57) *Limnophila* (*Dasylimnophila*) *stuckenbergiana* Alexander; (58) *L.* (*Elporiomyia*) *woodiana* Alexander; (59) *L.* (*Hovalimnophila*) *malitiosa* (Alexander); (60) *L.* (*Limnophila*) *sikorai* Alexander; (61) *L.* (*Nesolimnophila*) *luteifemorata* Alexander. Figs 54, 55, 59, 60, 61 (after Alexander 1963, figs 71, 72, 65, 66, 64, respectively), Fig. 56 (after Alexander 1920, fig. 2), Fig. 57 (after Alexander 1965, fig. 31), Fig. 58 (after Alexander 1964, fig. 74).

Abbreviations: arcu – arculus; *bm* – basal medial cell; *CuA* – anterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.

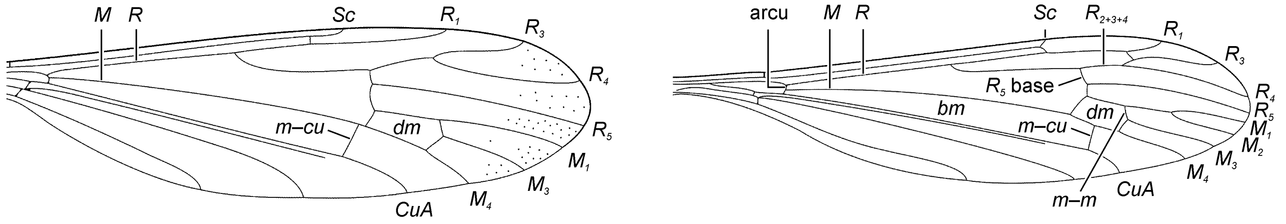
Alexander (1955*c*, 1956, 1964: 376) presented identification keys to Afrotropical species.

Ctenolimnophila **Alexander** (Limoniidae: Limnophilinae)**.** A genus of 15 described species occurring in the Afrotropical, Australasian/Oceanian and Neotropical Regions. *Ctenolimnophila* is divided into three subgenera of which only one, *C.* (*Campbellomyia* Alexander), is represented in the Afrotropics with a single species, *C.* (*C.*) *madagascariensis* Alexander, 1960, endemic to Madagascar. It can be recognised by the



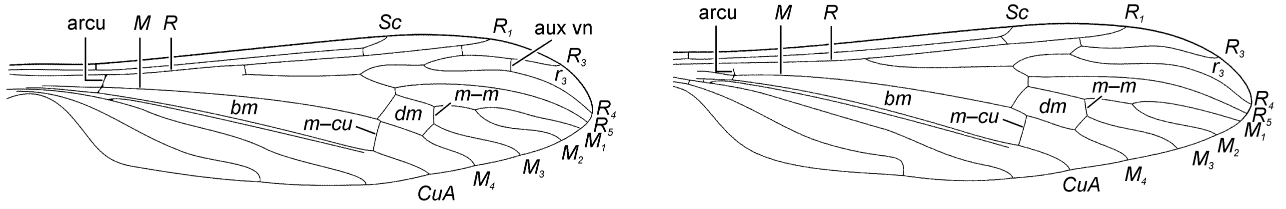
62 *Medleromyia*

63 *Neolimnomyia*



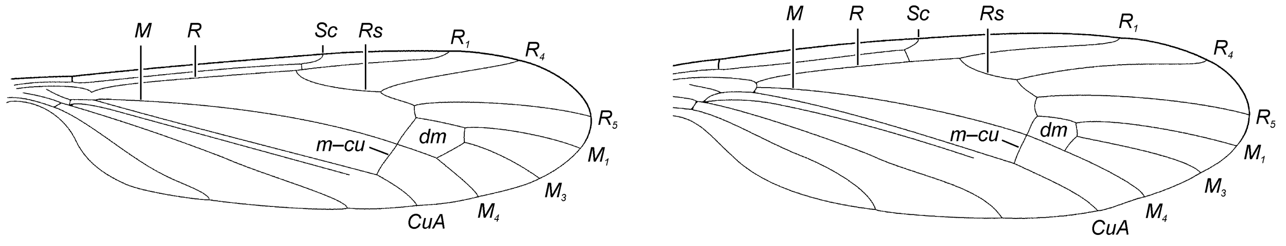
64 *Paradelphomyia* (*Oxyrhiza*)

65 *Pilaria*



66 *Pseudolimnophila* (*Calolimnophila*)

67 *Pseudolimnophila* (*Pseudolimnophila*)



68 *Atarba* (*Atarba*)

69 *Atarba* (*Atarbodes*)

Figs 14.62–69. Wings of Limoniidae (dorsal views): (62) *Medleromyia nigeriana* Alexander; (63) *Neolimnomyia fumivena* (Alexander); (64) *Paradelphomyia* (*Oxyrhiza*) *faurei* (Alexander); (65) *Pilaria chionomera* Alexander; (66) *Pseudolimnophila* (*Calolimnophila*) *rex* Alexander; (67) *P.* (*Pseudolimnophila*) *senex* Alexander; (68) *Atarba* (*Atarba*) *capensis* Alexander; (69) *A.* (*Atarbodes*) *tergata* Alexander. Fig. 62 (after Alexander 1974, fig. 40), Figs 63, 66, 67 (after Alexander 1956, figs 135, 97, 98, respectively), Figs 64, 68 (after Alexander 1964, figs 66, 72), Fig. 65 (after Alexander 1970, fig. 29), Fig. 69 (after Alexander 1963, fig. 73).

Abbreviations: arcu – arculus; aux vn – auxiliary vein; *bm* – basal medial cell; *CuA* – anterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.

long petiole of cell r_3; the closed and elongate discal medial cell (*dm*); the presence of three *M* veins reaching the wing margin; and the position of crossvein *m–cu*, which touches the discal medial cell near its mid length (Fig. 50). The biology and immature stages of the genus remain unknown.

***Dicranomyia* Stephens** (Limoniidae: Limoniinae)**.** The largest genus of the Limoniidae with *ca* 1,115 described species occurring in all zoogeographical regions, except Antarctica. In its present concept, the genus and most of the included subgenera are polyphyletic. According to the current classification the genus is divided into 24 subgenera. More than 730 species are included in the subgenus *Dicranomyia sensu stricto*, of which only 55 species are known from the Afrotropics. The subgenus is widespread and is recorded from most of the Indian and Atlantic Ocean island groups: Cabo Verde, Madagascar, Mauritius, Réunion Is., Saint Helena Is., Seychelles and Tristan da Cunha Is. (incl. Gough Is.). Wood (1952) discussed the immature stages of the South African species *D. capicola* Alexander, 1921 and *D. peringueyi* Alexander, 1917. Larvae of *D. capicola* were found on moss along the edges of a rapidly flowing streamlet. Larvae of *D. peringueyi* are wood-feeders that were found tunnelling in a decaying log. Prior to pupation they gather fragments of masticated wood and frass, with which they impregnate a jelly tube that is secreted by the salivary glands. Pupation takes place within this tube. The larvae of the majority of *Dicranomyia* species that are known in the immature stages are aquatic or semi-aquatic. Dependant on the species, they occur on algae, mosses and liverworts, in and along streams, sometimes on vertical rock walls (Alexander 1920, 1931; Brindle 1967; Bryce 1957; Coe 1941; Dittmar 1955; Hemmingsen *et al*. 1959; Krivosheina & Krivosheina 2011: 192; Mendl 1978: 368; Podeniene 2003; Reusch 1988; Sandrock 1978; Suren & Winterbourn 1991; Thienemann 1909; Werner *et al*. 2007; Williams 1943; Winterbourn 2000: 113; Winterbourn *et al*. 2006; Young & Gelhaus 2000), in wet boggy habitats, feeding on decaying organic matter, fungal hyphi and mosses (Jones *et al*. 2003; Mendl 1978: 368; Krivosheina & Krivosheina 2011: 192; Podeniene 2003; Wood 1952), in inland saline habitats (Alexander 1931; Brindle 1967), in marshes of brackish tidal flats (Brindle 1967; Krivosheina & Krivosheina 2011: 192; Mendl 1978: 368; Rogers 1932; Szadziewski 1979; Tokunaga 1940; Young & Gelhaus 2000), in the tidal zone of rocky coasts (Alexander 1931; Seligo 1931; Tokunaga 1933, 1938, 1939, 1940), in fruiting bodies of fungi (N.P. Krivosheina 2009, 2010*c*; Krivosheina & Krivosheina 2011: 192). Others occur as leaf-miners of various plant species (*Cyrtandra*: Gesneriaceae; Alexander 1920; Swezey 1913, 1915), or in decaying wood, where they probably occur in fungal threads (Anderson 1982; Dudley & Anderson 1982; N.P. Krivosheina 2009; Mendl 1978: 368; Winterbourn 1996; Winterbourn *et al*. 2006; Young & Gelhaus 2000). The subgenus *Dicranomyia* (*Euglochina* Alexander) is a relatively small group with 17 described species globally, of which two are known from the Afrotropical Region. The subgenus occurs in the central part of Africa and is not recorded from South Africa or Madagascar, although it is recorded from Comoros. *Dicranomyia* (*Euglochina*) can be easily identified by the long and slender wings, with the majority of veins shifted to the very apex of the wing (Fig. 103). The biology and immature stages of *D*. (*Euglochina*) remain unknown. *Dicranomyia* (*Idioglochina* Alexander) comprises 28 species, three of which are Afrotropical. The Afrotropical species occur in Comoros, Mauritius, Seychelles and South Africa. The species can be recognised by a short vein *Sc* that terminates at the level of the base of vein *Rs*; an open discal medial cell (*dm*) as a result of the atrophy of crossvein *m–m* (Fig. 104), in combination with cylindrical flagellomeres. Known larvae of *D*. (*Idioglochina*) are marine and are known from algal growths on rocky coasts that are submerged by the tide, from coral reefs between the tide marks and from mangrove seashore swamps (Alexander 1931; Saunders 1928; Tokunaga 1930, 1936, 1940). *Dicranomyia* (*Pseudoglochina* Alexander) comprises 25 species of which a single species, *D*. (*P*.) *pamela* (Alexander, 1960), is Afrotropical and known from Malawi. Typical features are the short vein *Sc* and the open discal medial cell as a result of the reduction of the base of vein M_3. The biology and immature stages of *D*. (*Pseudoglochina*) remain unknown. Alexander (1956 (as *Limonia*), 1964: 306 (as *Limonia* subg. *Dicranomyia*, *Euglochina*, *Idioglochina* and *Pseudoglochina*), 1977) presented identification keys to Afrotropical species.

***Dicranophragma* Osten Sacken** (Limoniidae: Limnophilinae)**.** A genus of *ca* 50 described species occurring in all zoogeographical regions, except the Australasian/Oceanian and Neotropical Regions and Antarctica. The genus is divided into three subgenera, of which *Dicranophragma sensu stricto* is represented by three species in the central part of the continental Afrotropics. *Dicranophragma* is most easily recognised by the presence of an auxiliary crossvein in wing cell r_3; cell *bm* of the Afrotropical species moreover exhibits two auxiliary crossveins, or a complete basal crossvein and a more apical posterior spur connected to vein *CuA* (Fig. 51). The immature stages of only a few *Dicranophragma* species are known that are aquatic, or semi-aquatic and occur in rich organic mud in cool, shaded woods and marshes (Alexander 1920; Brindle 1967; Brindle & Bryce 1960; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 181; Podeniene 2003; Rogers 1930; Young & Gelhaus 2000). No identification keys are available to Afrotropical species.

***Dicranoptycha* Osten Sacken** (Limoniidae: Limoniinae)**.** A genus of *ca* 85 described species occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica; 31 species occur in the Afrotropics. The largest concentration occurs in Madagascar, where 22 species have been reported (Fig. 1). *Dicranoptycha* can best be recognised by the pale fold in wing cell *cua* that connects to vein *CuP*. Other remarkable features are the distal position of vein R_2, which lies far beyond the discal medial cell (*dm*) and the position of crossvein *m–cu* that connects to the discal medial cell near its mid length (Fig. 105, dotted line). In Nearctic species, larvae and pupae have been found to be terrestrial and to occur in rich humus soil, where they reside in the uppermost zone. Running water is not necessary for the development of the immature stages (Alexander 1919, 1920; Young 1987; Young & Gelhaus 2000). Alexander (1956) presented an identification key to the then known continental Afrotropical species.

***Dolichopeza* Curtis** (Tipulidae)**.** A genus of more than 300 described species occurring in all zoogeographical regions, except Antarctica (Fig. 5). The genus is divided into 11 subgenera, five of which are represented in the Afrotropics. The genus can be distinguished by the wing venation, with the very short vein *Rs*; the absence of the discal medial cell (*dm*); and position of crossvein *m–cu* relative to the fork of vein *M* (*e.g.*, Figs 22–26); together with the presence of the remarkably slender and elongate legs in most species (Fig. 5). The subgenus *D.* (*Afrodolichopeza* Alexander) includes four species and is endemic to the Afrotropics. It is distributed in the Ruwenzori Range and Virunga Mountains stretching from Lake Albert to Lake Edward and Lake Kivu. *Dolichopeza* (*Afrodolichopeza*) differs from the other subgenera by the presence of wing vein R_3, four *M* veins and macrotrichia in the cells at the wing apex (Fig. 22). The biology and immature stages of *D.* (*Afrodolichopeza*) remain unknown. *Dolichopeza sensu stricto* includes more than 80 species, of which only four occur in the Afrotropics. The subgenus is restricted to the eastern part of the continental Afrotropics and is absent from southern Africa and Madagascar. *Dolichopeza sensu stricto* is characterised by the atrophy of wing vein R_3, the absence of macrotrichia on the wing membrane and the absence of a nasus (Fig. 23). Larvae of Nearctic and Palaearctic species of the subgenus *Dolichopeza sensu stricto* are semi-aquatic, occurring in damp to relatively dry moss, often on vertical surfaces (Alexander 1931; Brindle 1960*b*; Byers 1961, 2002; Chiswell 1956; Podeniene 2003; Theowald 1957, 1967, 1978: 364; Young & Gelhaus 2000). The biology and immature stages of Afrotropical species remain unknown. The single species of the subgenus *D.* (*Eudolichopeza* Alexander), *D.* (*E.*) *lipophleps* Alexander, 1956, is known from the Ruwenzori Mountains of Uganda. *Dolichopeza* (*Eudolichopeza*) is distinguished by the presence of three *M* veins (Fig. 24), whereas the other subgenera of *Dolichopeza* have four *M* veins. The biology and immature stages of the subgenus remain unknown. *Dolichopeza* (*Prodolichopeza* Alexander) includes four species, one of which, *D.* (*P.*) *malagasya* Karsch, 1886, occurs in Madagascar and is the type species of the subgenus. Typical features for *D.* (*Prodolichopeza*) are the presence of a nasus and the relatively short legs. The biology and immature stages of *D.* (*Prodolichopeza*) remain unknown. Almost all of the 25 species of the *Dolichopeza* (*Trichodolichopeza* Alexander) are Afrotropical, except for *D.* (*T.*) *sparsihirta* Alexander, 1943, which occurs in China. The Afrotropical species are mainly distributed in the south-eastern parts of the continental Afrotropics and in Madagascar. The South African fauna is especially rich, with 17 known species. A remarkable feature of the subgenus is the presence of abundant macrotrichia on the membrane of the wing apex (Fig. 26). A similar character is also known in *D.* (*Afrodolichopeza*). Both subgenera differ in the presence or absence of vein R_3: it is atrophied in *D.* (*Trichodolichopeza*) and fully-developed in *D.* (*Afrodolichopeza*). Wood (1952) referred to the immature stages of two *D.* (*Trichodolichopeza*) spp., *D.* (*T.*) *hirtipennis* Alexander, 1917 and *D.* (*T.*) *flavifrons* Alexander, 1925. Larvae were found in or beneath wet to saturated mats, or cushions of moss and liverworts on the sides of waterfalls, or on roots in the flowing rill and streams. The larvae of *D.* (*T.*) *flavifrons* were found exclusively in moss cushions on rocks projecting from a stream, but were absent in the moss on the actual banks of the same stream. Alexander (1956, 1964: 282) and Wood (1952) presented identification keys to Afrotropical species.

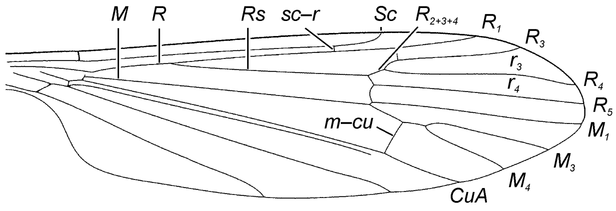
***Elephantomyia* Osten Sacken** (Limoniidae: Limoniinae)**.** A genus of *ca* 135 described species occurring in all zoogeographical regions, except Antarctica. The genus is divided into four subgenera of which *Elephantomyia sensu stricto* is represented with *ca* 40 species in the Afrotropics. The subgenus is widespread in the Afrotropics, recorded from Comoros, Madagascar and Seychelles. The genus is most easily recognised by the presence of the elongated mouthparts (Fig. 11), in combination with the absence of wing vein R_2 and the long veins R_1 and R_4 (Fig. 106). Wood (1952) described the larvae and pupae of the South African species, *E. montana* Alexander, 1934 and what he regarded as *E. aurantiaca* Alexander, 1917. The larvae of *E. montana* were collected from a log of *Halleria capensis* that had fallen over a forest stream. The larvae, identified as *E. aurantiaca*, were collected in a cushion of moss and liverworts on a waterfall and in moss in a small cascade. The larvae and pupae differ remarkably in their physical features and habitat choice from other known immature stages of *Elephantomyia* and probably represent a misidentification (Hynes 1997). Immature stages of *Elephantomyia sensu stricto* are known from a number of Nearctic, Palaearctic and Oceanian species and all occur in rotting wood of deciduous or coniferous trees (Alexander 1920; Bangerter 1934; Hynes 1990, 1997; N.P. Krivosheina 2009, 2010*b*; Krivosheina & Krivosheina 2011: 180; Rogers 1927, 1930; Starý & Salmela 2004; Young & Gelhaus 2000). Alexander (1955*c*, 1956, 1964: 366) and Wood (1952) presented identification keys to Afrotropical species.

***Ellipteroides* Becker** (Limoniidae: Chioneinae)**.** A genus of *ca* 125 species occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica. The genus is divided into six subgenera of which only the subgenus *E.* (*Progonomyia* Alexander) occurs in the Afrotropics. The six Afrotropical species are all endemic to South Africa. *Ellipteroides* has a small meron (as in Fig. 19) and is furthermore distinguished by the presence of vein R_2, the strongly divergent veins R_3 and R_4, and the elongate cell r_3 (Fig. 73). Wood (1952) reported the larvae of *E. nigrobimbo* (Alexander, 1934), from saturated organic sand on the margins of a forest rill. Pupation took place in dry sand spits sheltered by rocks. Adults of *E. nigrobimbo* scurried in stone-fly fashion over boulders and small stones protruding from the stream. Alexander (1964: 381, as *Gonomyia* subgenus *Progonomyia*) presented an identification key to South African species.

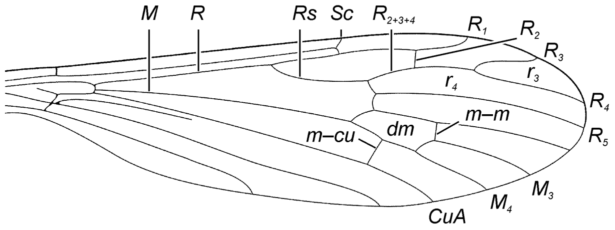
***Eloeophila* Rondani** (Limoniidae: Limnophilinae)**.** A relatively small genus of *ca* 85 described species occurring in all zoogeographical regions, except the Australasian/Oceanian and Neotropical Regions and Antarctica. The genus is widespread in the Afrotropics, where nine species are known. *Eloeophila* can be distinguished by the presence of an auxiliary crossvein near the mid length of wing cell *bm* (Fig. 52). Wood (1952) dealt with the immatures of the South African species noting that *E. dubiosa* (Alexander, 1917) occurs in gravely sandy spits and in organic saturated mud at margins of shallow streamlets and rills. As with known Nearctic and Palaearctic *Eloeophila* larvae (Bangerter 1928; Brindle 1967; Brindle & Bryce 1960; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 181; Mendl 1978: 371; Podeniene 2003; Podeniene & Gelhaus 2010; Reusch 1988; Sandrock 1978), the larva of *E. dubiosa* are adapted to a predatory lifestyle. Alexander (1956, 1964: 358 (as *Limnophila* subgenus *Elaeophila*) presented identification keys to Afrotropical species.

***Erioptera* Meigen** (Limoniidae: Chioneinae)**.** A genus of *ca* 280 described species occurring in all zoogeographical regions, except Antarctica. The genus is divided into 10 subgenera;

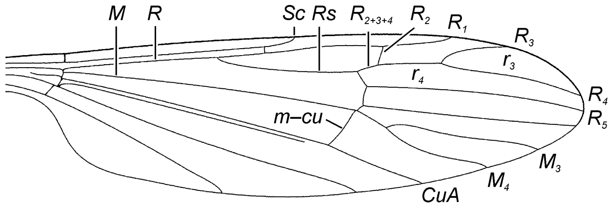
three of which occur in the Afrotropics: *Erioptera sensu stricto*, *E.* (*Mesocyphona* Osten Sacken) and *E.* (*Meterioptera* Alexander). *Erioptera* has a large meron (Fig. 21) and venational characters include the position of crossvein *sc–r* just distal to the base of vein *Rs*, three branches of vein *Rs* reaching the wing margin, elongate cell r_3 and the open discal medial cell (*dm*) (e.g., Figs 74–76). The subgenera can be separated by the absence (*E.* (*Meterioptera*)), or presence (*Erioptera sensu*



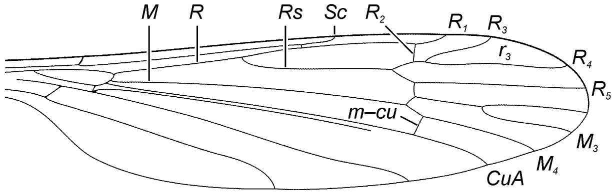
70 *Baeoura*



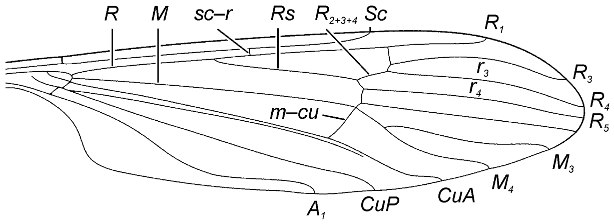
71 *Cheilotrichia* (*Cheilotrichia*)



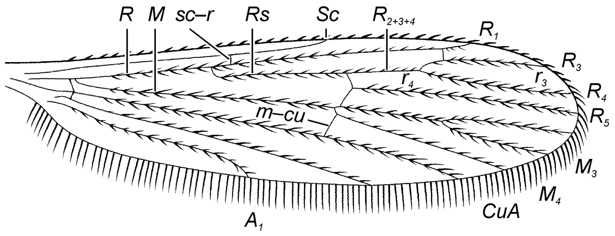
72 *Cheilotrichia* (*Empeda*)



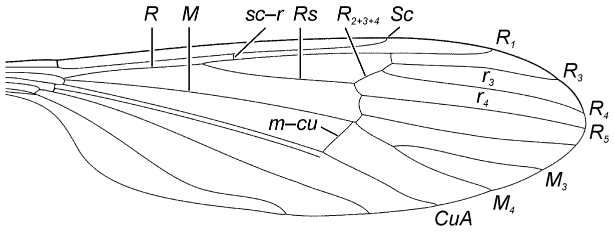
73 *Ellipteroides* (*Progonomyia*)



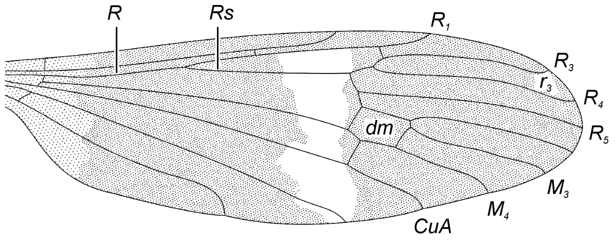
74 *Erioptera* (*Erioptera*)



75 *Erioptera* (*Mesocyphona*)



76 *Erioptera* (*Meterioptera*)

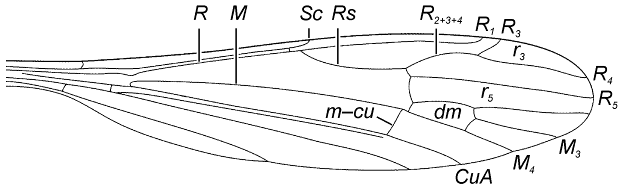


77 *Eugnophomyia*

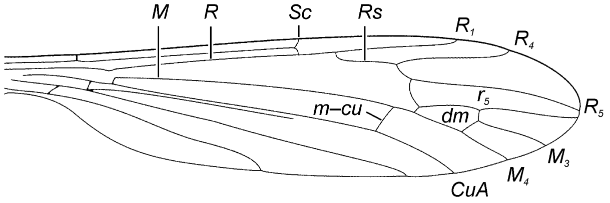
Figs 14.70–77. Wings of Limoniidae (dorsal views): (70) *Baeoura claripennis* (Alexander); (71) *Cheilotrichia* (*Cheilotrichia*) *guttipennis* Alexander; (72) *C.* (*Empeda*) *bonaespei* (Alexander); (73) *Ellipteroides* (*Progonomyia*) *natalensis* (Alexander); (74) *Erioptera* (*Erioptera*) *peringueyi* Bergroth; (75) *E.* (*Mesocyphona*) *albicapitella* (Edwards); (76) *E.* (*Meterioptera*) *persinuata* Alexander; (77) *Eugnophomyia elegans* (Wiedemann). Figs 70, 72, 73, 74, 76 (after Alexander 1964, figs 72, 105, 83, 106, 119, respectively), Fig. 71 (after Alexander 1963, fig. 87), Fig. 75 (after Edwards 1912, fig. 13), Fig. 77 (Alexander 1917, fig. 15).

Abbreviations: A_1 – first branch of anal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

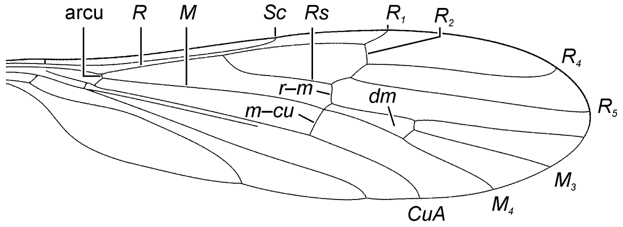
stricto, *E.* (*Mesocyphona*)), of a wing membrane pattern and the length and shape of vein A_1, which is long and sinuous, apically parallel to the wing margin in *Erioptera sensu stricto* and in *E.* (*Meterioptera*) and shorter, less sinuous and not parallel to the wing margin in *E.* (*Mesocyphona*). *Erioptera sensu stricto* includes more than 140 species and occurs in all zoogeographical regions, except Antarctica. The Afrotropical fauna includes 22 species distributed over the entire region. Known larvae of *Erioptera* are found in aquatic and semi-aquatic environments, especially along the margins of streams and



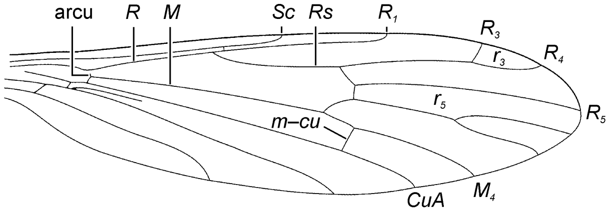
78 *Gonomyia* (*Gonomyia*)



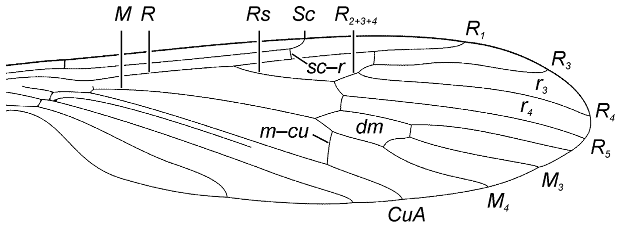
79 *Gonomyia* (*Leiponeura*)



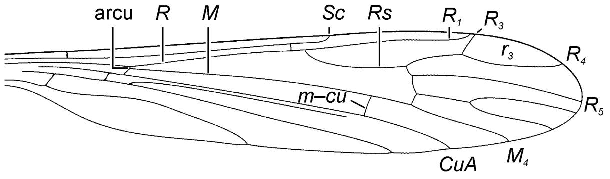
80 *Gymnastes* (*Gymnastes*)



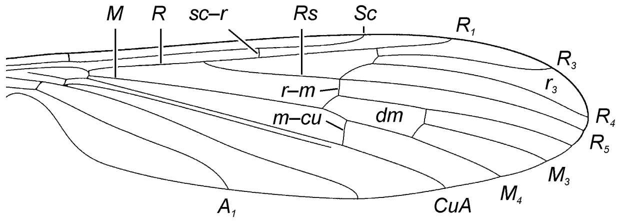
81 *Hovamyia*



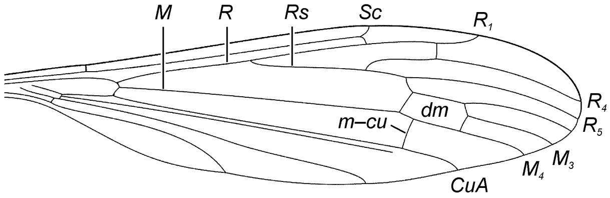
82 *Hoverioptera* (*Hoverioptera*)



83 *Idiocera* (*Idiocera*)



84 *Idiognophomyia*



85 *Limnophilomyia* (*Eulimnophilomyia*)

Figs 14.78–85. Wings of Limoniidae (dorsal views): (78) *Gonomyia* (*Gonomyia*) *sparsisetosa* Alexander; (79) *G.* (*Leiponeura*) *houtensis* Alexander; (80) *Gymnastes* (*Gymnastes*) *teucholaboides* (Alexander); (81) *Hovamyia polyperiscelis* Alexander; (82) *Hoverioptera* (*Hoverioptera*) *ambricola* (Alexander); (83) *Idiocera* (*Idiocera*) *malagasica* (Alexander); (84) *Idiognophomyia keiseri* Alexander; (85) *Limnophilomyia* (*Eulimnophilomyia*) *abnormalis* Alexander. Fig. 78 (after Alexander 1960*c*, fig. 25), Figs 79, 80, 85 (after Alexander 1964, figs 87, 99, 103), Figs 81–84 (after Alexander 1963, figs 82, 88, 84, 80, respectively).

Abbreviations: arcu – arculus; A_1 – first branch of anal vein; *CuA* – anterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

standing waters. *Erioptera* (*Mesocyphona*) includes 66 species globally of which only two species are recorded from the Afrotropics, *viz*. *E. albicapitella* (Edwards, 1912) and *E. maculosa* (Edwards, 1912), which are restricted to Seychelles. Immatures of several Nearctic and Palaearctic species of *E.* (*Mesocyphona*) have been found in aquatic and semi-aquatic situations along the margins of streams and standing waters (Alexander 1920, 1931; Krivosheina & Krivosheina 2011: 188; Podeniene 2009; Rogers 1930, 1931; Young & Gelhaus 2000). *Erioptera* (*Meterioptera*) is a small subgenus with 29 described species, 12 of which are Afrotropical. The other species occur in the Australasian/Oceanian (8 species), Oriental (10) and Palaearctic (2) Regions. Some species exhibit overlap between the Australasian/Oceanian, Oriental and Palaearctic Regions. *Erioptera* (*Meterioptera*) is distributed over the entire Afrotropical Region. In Hawaii, Williams (1943) bred the originally eastern Palaearctic species *E. bicornifer* Alexander, 1921, from mud and Hynes (1990) reported the larvae of the New Caledonian *E. raphidostyla* Alexander, 1978, from the base of rotting palm fronds. Alexander (1956, 1964: 416) presented identification keys to Afrotropical species.

***Eugnophomyia* Alexander** (Limoniidae: Chioneinae)**.** A genus of 30 species occurring in the Afrotropical, Nearctic and Neotropical Regions, of which nine species occur in the Afrotropics. The genus is restricted to the eastern part of the continental Afrotropics, mainly in the south-east, including Madagascar. *Eugnophomyia* has a small meron (as in Fig. 19); three vein *Rs* branches reach the wing margin; cell r_3 is deep; the discal medial cell (*dm*) is present; and the wing membrane is patterned with fascia (Fig. 77). Rogers (1928, 1930) reported the larvae of the Nearctic species *E. luctuosa* (Osten Sacken, 1860), from the decomposing hearth wood of cavities in living trees. Alexander (1956, 1964: 379 (as *Gnophomyia*)) presented identification keys to Afrotropical species.

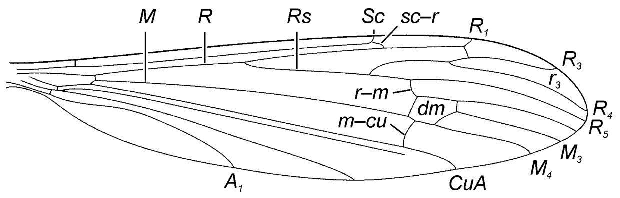
***Eupilaria* Alexander** (Limoniidae: Limnophilinae)**.** A genus with only 19 described species occurring in the Afrotropical and Oriental Regions. A single species, *E. nigeriana* Alexander, 1972, is known from Nigeria in the Afrotropics. It can be recognised by the slender wing with reduced venation, exhibiting a spurred vein R_3; absence of one of the *M* veins; and an open discal medial cell (*dm*) (Fig. 53). The biology and immature stages remain unknown.

***Geranomyia* Haliday** (Limoniidae: Limoniinae)**.** A genus of *ca* 345 species, representing one of the larger genera in the Limoniinae, occurring in all zoogeographical regions, except Antarctica. No subgenera are distinguished within the genus. *Geranomyia* can be recognised by the elongate mouthparts, with the rostrum, labial palpus and hypopharynx all lengthened (Fig. 12). Thirty-four species occur in the Afrotropics, where the genus is widespread. It is recorded from Madagascar, Réunion Is. and Seychelles. Wood (1952) described the immature stages of *G. rubrithorax* Alexander, 1921 and *G. sexocellata* Alexander, 1921. The larvae and pupae of *G. rubrithorax* were collected in a feeble trickle of water some 100–250 mm wide, where they were confined to the pendulous filaments of moss in the water. At another locality, larvae and pupae of *G. sexocellata* occurred in jelly tubes besprinkled with minute sand grains. These were also attached to the pendulous filaments of moss plants in a trickle of water. Immature stages of extralimital species were collected in algal growths on vertical cliff and rock faces (Alexander 1931; Rogers 1930; Young & Gelhaus 2000), in algal growths in the tidal zone of rocky shores (Alexander 1931; Brindle 1967; Krivosheina & Krivosheina 2011: 190; Saunders 1930; Seurat 1924; Stubbs 2003; Tokunaga 1940; Toye 1967), along stream margins (Bangerter 1929; Young & Gelhaus 2000), in jelly tubes and droplet-like jelly blobs on leaves of various plants (Beaver & Ryan 1998; Edwards 1934; Hingston 1932: 342). Alexander (1956, 1964: 306 (as *Limonia* subgenus *Geranomyia*) presented identification keys to Afrotropical species.

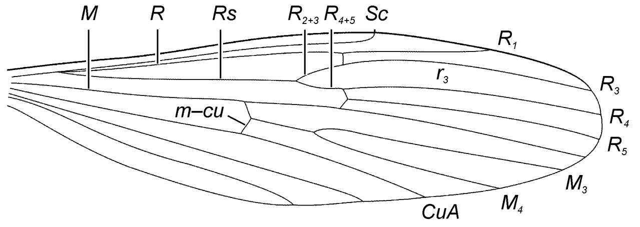
***Goniotipula* Alexander** (Tipulidae)**.** An endemic genus of two species, *G. cuneipennis* Alexander, 1921 and *G. lindneri* Mannheims, 1961, both restricted to the Cape Province of South Africa. Remarkable features for *Goniotipula* include the slender-based wing, which barely exhibits an anal lobe, the absence of vein R_3 (Fig. 27), presence of a single gonostylus in the male terminalia and the short ovipositor in the female. Wood (1952) described the larva and pupa of *G. cuneipennis*; numerous larvae were dug out from the rich soil beneath a carpet of rotting leaves in a shady wood. Mannheims (1961) listed the differences between the two species.

***Gonomyia* Meigen** (Limoniidae: Chioneinae)**.** A genus of *ca* 600 described species, representing one of the largest genera of the Tipuloidea, occurring in all zoogeographical regions, except Antarctica. The genus is divided into nine subgenera of which *Gonomyia sensu stricto* and *G.* (*Leiponeura* Skuse) are represented in the Afrotropics. *Gonomyia* has a small meron (Fig. 19); two or three vein *Rs* branches reach the wing margin; vein R_2 is absent; cell r_3 when present is short; cell r_5 narrows towards wing margin; the arculus is absent; and crossvein *m–cu* is close to the fork of vein *M* (e.g., Figs 78, 79). The size of cell r_3 is used to distinguish between *Gonomyia sensu stricto* and *G.* (*Leiponeura*), but this character is unsatisfactory and a re-analysis of subgeneric concepts is required. *Gonomyia sensu stricto* is almost entirely restricted to the eastern part of the continental Afrotropics, with a single species, *G. syrraxis* Alexander, 1955, recorded from Madagascar and two, *G. matileana* Alexander, 1979 and *G. moheliana* Oosterbroek, 2009, from Comoros. A single species, *G. pauliana* Nielsen, 1966, is recorded from Cabo Verde. Immature stages of a few Nearctic and Palaearctic species of *Gonomyia sensu stricto* have been found in semi-aquatic situations along the margins of flowing and standing waters (Alexander 1930; Brindle 1967; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 187; Podeniene 2003; Young & Gelhaus 2000). *Gonomyia* (*Leiponeura*) comprises *ca* 325 species, of which 44 species are widely distributed in the Afrotropics. Wood (1952) recorded the larvae and pupae of the South African *G. sulphurelloides* Alexander, 1920, just below the surface of a low mound of saturated gravely sand 150–300 mm removed from the edge of a stream. Larvae of the Nearctic species of *G.* (*Leiponeura*) were found in similar situations (Alexander 1920, 1931; Byers 2002; Rogers 1930, 1931; Young & Gelhaus 2000). Alexander (1956, 1964: 381) and Wood (1952) presented identification keys to Afrotropical species.

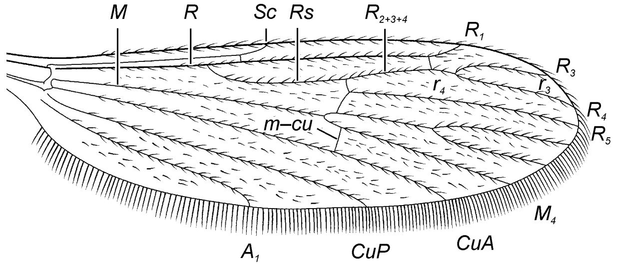
***Gymnastes* Brunetti** (Limoniidae: Chioneinae)**.** A genus with *ca* 40 described species occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. The genus is divided into three subgenera, of which only *Gymnastes sensu stricto* occurs in the Afrotropics. The subgenus includes



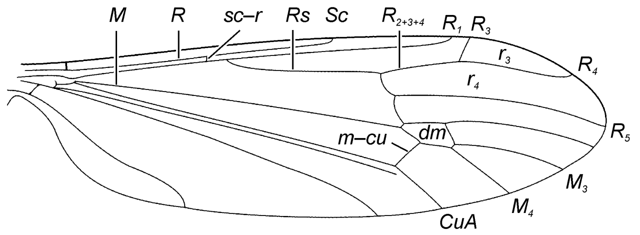
86 *Limnophilomyia* (*Limnophilomyia*)



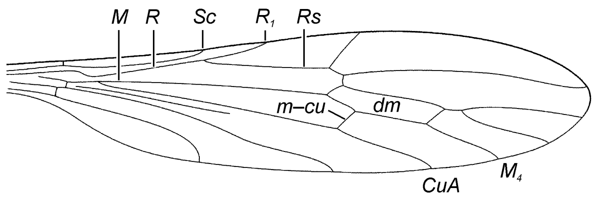
87 *Molophilus* (*Molophilus*)



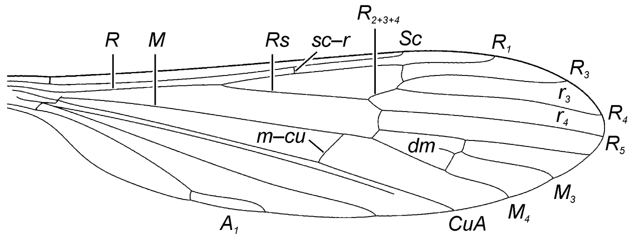
88 *Ormosia* (*Neserioptera*)



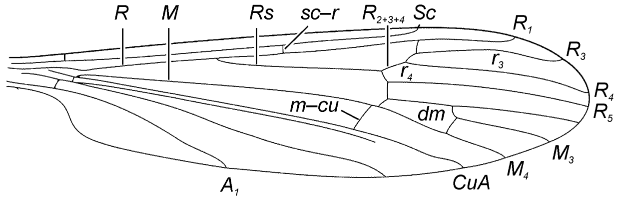
89 *Rhabdomastix* (*Rhabdomastix*)



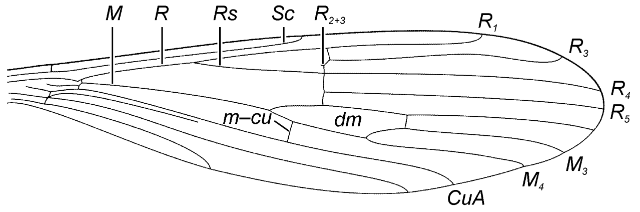
90 *Styringomyia*



91 *Symplecta* (*Podoneura*)



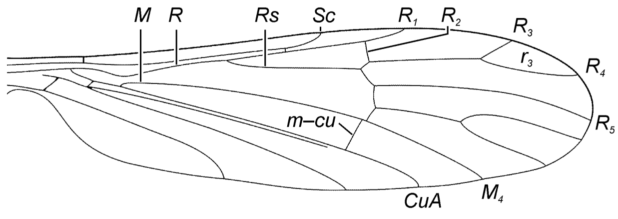
92 *Symplecta* (*Trimicra*)



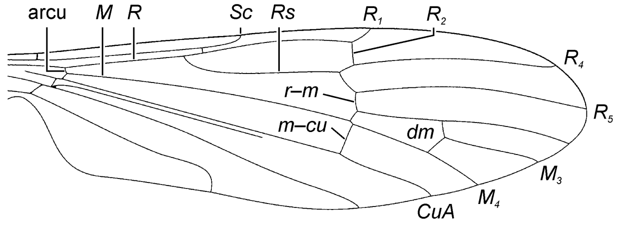
93 *Tasiocera* (*Dasymolophilus*)

Figs 14.86–93. Wings of Limoniidae (dorsal views): (86) *Limnophilomyia* (*Limnophilomyia*) *lacteitarsis* (Alexander); (87) *Molophilus* (*Molophilus*) *africanus* Riedel; (88) *Ormosia* (*Neserioptera*) *perpusilla* Edwards; (89) *Rhabdomastix* (*Rhabdomastix*) *indigena* Alexander; (90) *Styringomyia stuckenbergi* Alexander; (91) *Symplecta* (*Podoneura*) *anthracogramma anthracogramma* (Bergroth); (92) *S.* (*Trimicra*) *pilipes* (F.); (93) *Tasiocera* (*Dasymolophilus*) *hova* Alexander. Figs 86, 89–91 (after Alexander 1964, figs 102, 98, 115, 108, respectively), Fig. 87 (after Riedel 1914, fig. 10), Fig. 88 (after Edwards 1912, fig. 12), Fig. 92 (after Alexander 1977, fig. 38), Fig. 93 (after Alexander 1963, fig. 91).

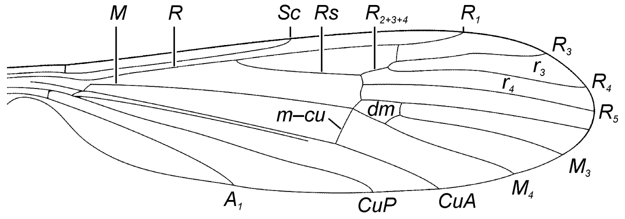
Abbreviations: A_1 – first branch of anal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.



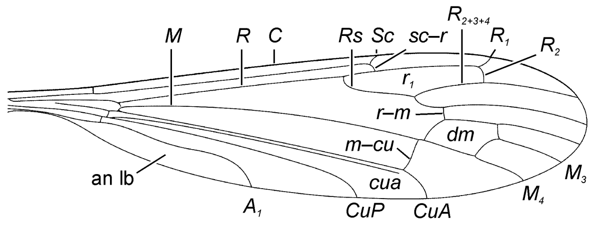
94 *Teucholabis* (*Euparatropesa*)



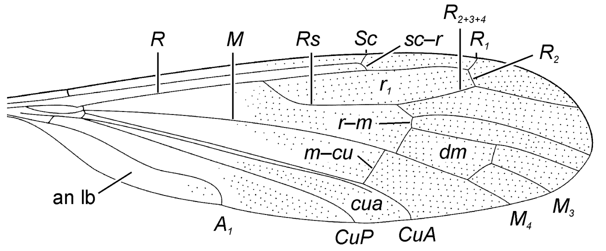
95 *Teucholabis* (*Teucholabis*)



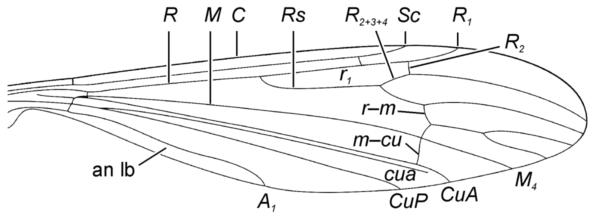
96 *Trichotrimicra*



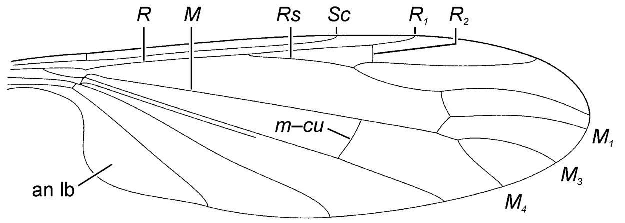
97 *Achyrolimonia*



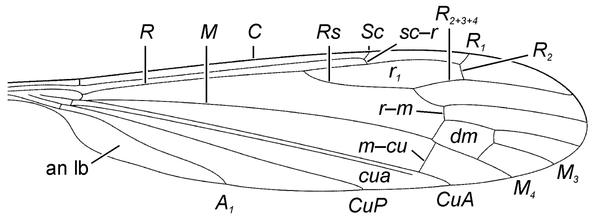
98 *Achyrolimonia*



99 *Amphilimnobia*



100 *Antocha* (*Orimargula*)



101 *Atypophthalmus* (*Atypophthalmus*)

Figs 14.94–101. Wings of Limoniidae (dorsal views): (94) *Teucholabis* (*Euparatropesa*) *witteana* Alexander; (95) *T.* (*Teucholabis*) *nodipes marleyi* Alexander; (96) *Trichotrimicra hirtipennis* (Alexander); (97) *Achyrolimonia bisalba* (Alexander); (98) *A. persuffusa* (Alexander); (99) *Amphilimnobia leucopeza* Alexander; (100) *Antocha* (*Orimargula*) *transvaalia* (Alexander); (101) *Atypophthalmus* (*Atypophthalmus*) *thaumastopyga* (Alexander). Figs 94, 98 (after Alexander 1970, figs 40, 16, respectively), Figs 95, 96, 100 (after Alexander 1964, figs 101, 110, 52, respectively), Figs 97, 101 (after Alexander 1961, figs 3, 10), Fig. 99 (after Alexander 1956, fig. 107).

Abbreviations: arcu – arculus; A_1 – first branch of anal vein; an lb – anal lobe; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; r_3 – third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

12 species, of which three occur in the afforested areas of Central Africa. *Gymnastes* has the meron small (e.g., Fig. 19); the wing venation is rather peculiar, with a short vein *Sc*; vein R_1 terminates in the anterior wing margin; two vein *Rs* branches reach the wing margin; and with an elongate and narrow discal medial cell (*dm*) from which three *M* veins reach the wing margin; and a large anal lobe (Fig. 80). The legs of *Gymnastes sensu stricto* are also clothed in abundant flattened scales. The biology and immature stage of the genus remain undescribed. Alexander (1956) presented an identification key to the three Afrotropical species.

***Helius* Le Peletier & Serville** (Limoniidae: Limoniinae)**.** A genus of *ca* 240 described species, being one of the larger genera of the Limoniinae, occurring in all zoogeographical regions, except Antarctica. The genus is divided into nine subgenera, four of which are recorded from the Afrotropics. *Helius* can be recognised by the modestly elongate rostrum, in combination with the absence of wing vein R_2 (e.g., Figs 108–110). *Helius sensu stricto* is widespread in the Afrotropics, with 23 described species, one of which occurs in Comoros and Madagascar. *Helius sensu stricto* is distinguished from other subgenera occurring in the Afrotropics by the widely separate apices of veins *Sc* and R_1; crossvein *sc–r* being close to the apex of vein *Sc*; the generally closed discal medial cell (*dm*); and the presence of crossvein *r–m* (Fig. 108). Known larvae of *Helius sensu stricto* are aquatic and occur in dead plant material in or near water, in submerged stems of water dock, or in moist soil (Alexander 1920; Bangerter 1929; Brindle 1967; Cramer 1968; Krivosheina & Krivosheina 2011: 185; Podeniene 2002, 2003; Przhiboro 2003; Reusch 1988; Tjeder 1958; Young & Gelhaus 2000). The subgenus *H.* (*Prohelius* Alexander) is endemic to the Afrotropics and, although it only includes three species, is widespread over the continental Afrotropics. *Helius* (*Prohelius*) can be distinguished by wing vein R_5 that originates from the dorsal margin of the discal medial cell (*dm*) (Fig. 109). This character is, however, also expressed in extralimital species that are currently classified in *Helius sensu stricto*. The biology and immature stages of *H.* (*Prohelius*) remain unknown. The subgenus *H.* (*Rhamphidina* Alexander) is also endemic to the Afrotropics, with the single species, *H.* (*R.*) *camerounensis* (Alexander, 1920), recorded from Cameroon and Nigeria. The discal medial cell is open and the *R* veins are strongly divergent. The larvae and pupae of this species remain unknown. *Helius* (*Rhamphidioides* Alexander) is the third subgenus endemic to the Afrotropics, with two described species, *H.* (*R.*) *alluaudi* (Riedel, 1914), recorded from Uganda and *H.* (*R.*) *venustissimus* (Alexander, 1920), known from Cameroon and Nigeria. The subgenus can be recognised by the proximity of the apices of veins *Sc* and R_1; the presence of crossvein *r–m*; and the basal position of crossvein *m–cu* relative to the discal medial cell (Fig. 110). The biology and immature stages of these species remain unknown. Alexander (1956, 1964: 336) presented identification keys to Afrotropical species.

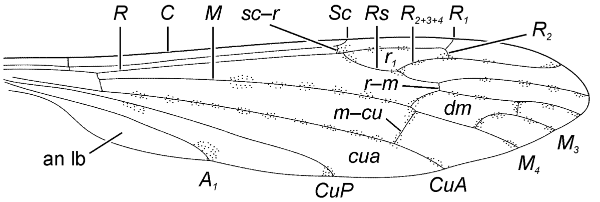
***Hexatoma* Latreille** (Limoniidae: Limnophilinae)**.** A genus of over 600 species, being one of the most speciose genera of Tipuloidea, occurring in all zoogeographical regions, except Antarctica. The genus is divided into six subgenera two of which occur in the Afrotropics. *Hexatoma* can be recognised by the reduced number of flagellomeres, probably the result of fusion of segments. The segments are often remarkably elongate. The subgenus *H.* (*Eriocera* Macquart) is widespread in the Afrotropical Region and occurs in the continental Afrotropics and in Madagascar and Seychelles. A total of 29 *H.* (*Eriocera*) spp. are reported from the Afrotropics. The subgenus is characterised by the presence of a closed discal medial cell (*dm*), from which either three or four *M* veins reach the wing margin (Fig. 54). The biology and immature stages of Afrotropical species remain unknown. Known larvae of Nearctic and Palaearctic species are aquatic or semi-aquatic and are predatory (Alexander 1915*b*, 1920, 1931; Alexander & Lloyd 1914; Cook 1949; Mendl 1978: 372; Przhiboro *et al*. 2009; Rogers 1930; Young & Gelhaus 2000). The subgenus *H.* (*Parahexatoma* Alexander) is endemic to the Afrotropical Region. Only a single species, *H.* (*P.*) *beieri* Alexander, 1970, is known from the continental Afrotropics (Tanzania), the remaining 11 species are endemic to Madagascar (9 species) and Seychelles (2). Species of *H.* (*Parahexatoma*) have the discal medial cell open and only two *M* veins that reach the wing margin. The biology and immature stages of the subgenus remain unknown. Alexander (1955*b*, 1956, 1964: 364) presented identification keys to Afrotropical species.

***Holorusia* Loew** (Tipulidae)**.** A genus of 117 described species occurring in all zoogeographical regions, except the Neotropical Region and Antarctica. The Afrotropical fauna comprises 11 species that are widespread in the region and are further recorded from Cabo Verde, Comoros, Madagascar, Mauritius, Réunion Is., São Tomé and Príncipe and Socotra Is. (Yemen). Species of *Holorusia* are most easily distinguished by their large size; the strong constriction of wing cell r_4; the large anal lobe; and the presence of a row of strong black spines at the apex of all femora (Fig. 134). Although the larvae of *Holorusia* species belong to the largest of the crane flies, only a few species have been described in the literature. They occur in rich organic matter at the edges of streams (Alexander 1920, 1931; Kellogg 1901; Young 2004: 797). Alexander (1964: 242 (as *Ctenacroscelis*)) presented an identification key to South African species.

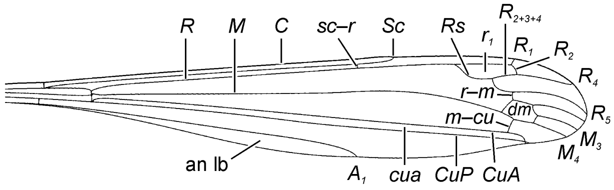
***Hovamyia* Alexander** (Limoniidae: Chioneinae)**.** An endemic Afrotropical genus with nine species, almost exclusively known from Comoros and Madagascar (Fig. 4). A single species, *H. venustipes* (Alexander, 1920), is widespread in West Africa. *Hovamyia* has the meron small (as in Fig. 19); the wing venation is reduced, with three *Rs* branches and three *M* branches that reach the wing margin; R_2 is absent and the discal medial cell (*dm*) is open (Fig. 81); legs are provided with abundant flattened scales. The biology and immature stages remain unknown. No identification keys are available to species.

***Hovapeza* Alexander** (Tipulidae)**.** An endemic genus of two species restricted to Madagascar. *Hovapeza costofuscata* Alexander, 1958, is known from the north and *H. tisiphone* (Alexander, 1951), from the central parts of the island. *Hovapeza* can be recognised by the absence of the discal medial cell (*dm*), which resulted from the atrophy of the base of vein M_3 (Fig. 29). This character is also found in the genus *Dolichopeza*, from which *Hovapeza* differs by its relatively long vein *Rs*, complete vein R_3 and position of crossvein *m–cu* which joins vein M_4 distal of the fork of vein *M*. The biology and immature stages remain unknown. No identification keys are available to species.

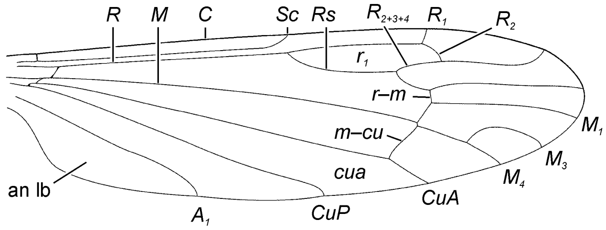
***Hovatipula* Alexander** (Tipulidae)**.** An endemic genus of four species restricted to Madagascar, occurring in the northern



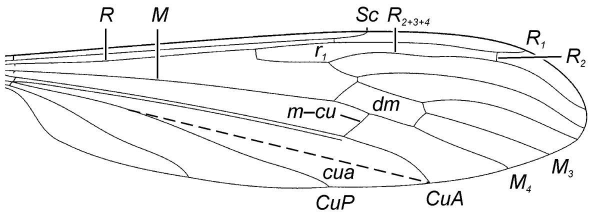
102 *Dicranomyia* (*Dicranomyia*)



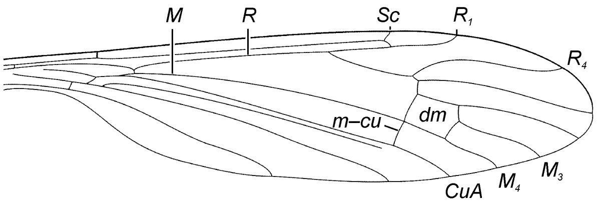
103 *Dicranomyia* (*Euglochina*)



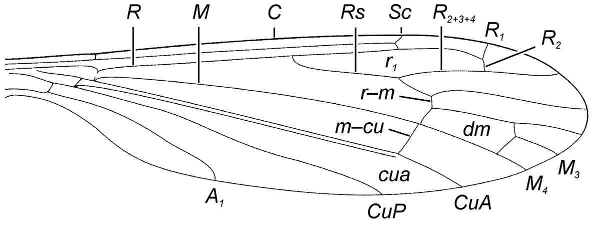
104 *Dicranomyia* (*Idioglochina*)



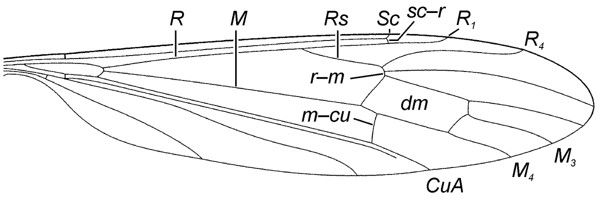
105 *Dicranoptycha*



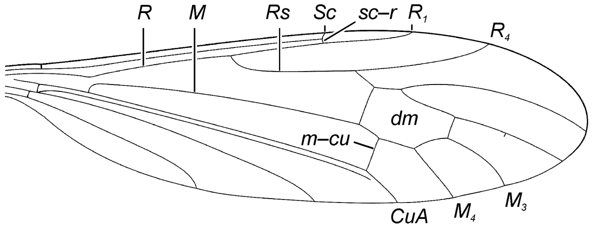
106 *Elephantomyia* (*Elephantomyia*)



107 *Geranomyia*



108 *Helius* (*Helius*)

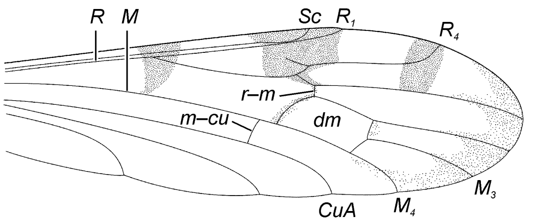


109 *Helius* (*Prohelius*)

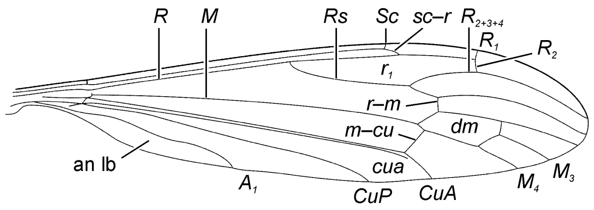
Figs 14.102–109. Wings of Limoniidae (dorsal views): (102) *Dicranomyia* (*Dicranomyia*) *guttula* Alexander; (103) *D.* (*Euglochina*) *connectans* Alexander; (104) *D.* (*Idioglochina*) *lightfooti* Alexander; (105) *Dicranoptycha atricolor* Alexander; (106) *Elephantomyia* (*Elephantomyia*) *maculistigma* (Enderlein); (107) *Geranomyia rudebecki* (Alexander); (108) *Helius* (*Helius*) *bifurcus* Alexander; (109) *H.* (*Prohelius*) *edwardsianus* Alexander. Fig. 102 (after Alexander 1915*a*, fig. 9), Figs 103, 107 (after Alexander 1964, figs 49, 63), Fig. 104 (after Alexander 1917, fig. 2), Figs 105, 108, 109 (after Alexander 1956, figs 95, 103, 106), Fig. 106 (after Alexander 1963, fig. 75).

Abbreviations: A_1 – first branch of anal vein; an lb – anal lobe; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

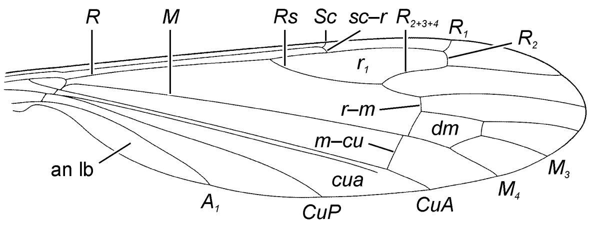
and eastern parts of the island. *Hovatipula* is characterised by the slender erect vertical lobe on the head; the very short palpus; the position of wing crossvein *m–cu* near the mid length of the wide discal medial cell (*dm*) and close to the base of vein M_4 (Fig. 30); and the presence of black spines on the inner gonostylus of the male terminalia. The biology and immatures remain unknown. No identification keys are available to species.



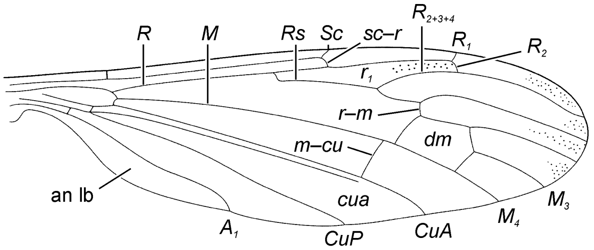
110 *Helius* (*Rhamphidioides*)



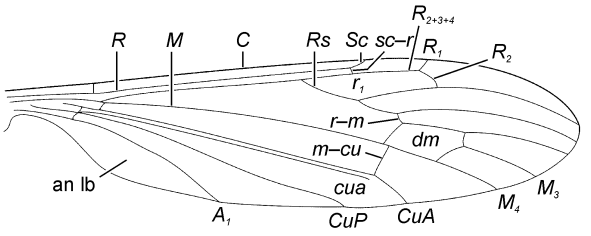
111 *Libnotes* (*Afrolimonia*)



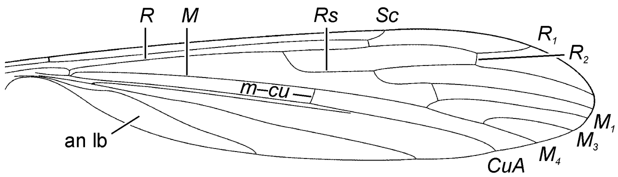
112 *Limonia*



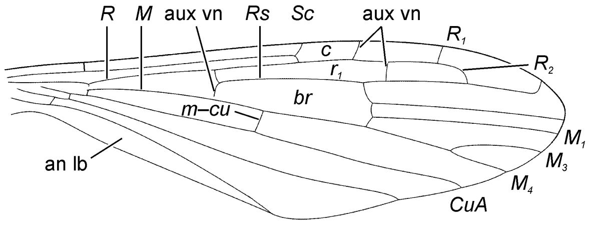
113 *Metalimnobia* (*Lasiolimonia*)



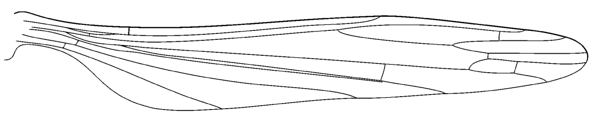
114 *Metalimnobia* (*Tricholimonia*)



115 *Orimarga* (*Orimarga*)



116 *Orimarga* (*Protorimarga*)



117 *Platylimnobia*

Figs 14.110–117. Wings of Limoniidae (dorsal views): (110) *Helius* (*Rhamphidioides*) *alluaudi* (Riedel); (111) *Libnotes* (*Afrolimonia*) *oligacantha* (Alexander); (112) *Limonia argopoda* Alexander; (113) *Metalimnobia* (*Lasiolimonia*) *oligotricha* (Alexander); (114) *M.* (*Tricholimonia*) *renaudi* (Alexander); (115) *Orimarga* (*Orimarga*) *mashonensis* Alexander; (116) *O.* (*Protorimarga*) *bequaertiana* (Alexander); (117) *Platylimnobia brinckiana* Alexander. Fig. 110 (after Riedel 1914, fig. 9), Fig. 111 (after Alexander 1956, fig. 82), Fig. 112 (after Alexander 1960*a*, fig. 9), Fig. 113 (after Alexander 1955*a*, fig. 11), Fig. 114 (after Alexander 1963, fig. 52), Figs 115, 117 (after Alexander 1964 figs 54, 53, respectively), Fig. 116 (after Alexander 1930, fig. 1).

Abbreviations: A_1 – first branch of anal vein; an lb – anal lobe; aux vn – auxiliary vein; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

Hoverioptera **Alexander** (Limoniidae: Chioneinae)**.** A genus of two monotypic subgenera, *Hoverioptera sensu stricto* and *H.* (*Tesserioptera* Mendl & Geiger). The single species of *H.* (*Tesserioptera*) is recorded from the Palaearctic Region (Switzerland); the single species of *Hoverioptera sensu stricto*, *H. ambricola* (Alexander, 1951), occurs in Comoros and Madagascar. *Hoverioptera* has the meron large (as in Figs 18, 20, 21); vein *Sc* is rather short and terminates at the mid length of vein *Rs*; crossvein *sc–r* occurs near the apex of vein *Sc*; vein R_2 is present; cell r_3 is elongate (Fig. 82); and the male antenna is elongate. The biology and immature stages remain unknown. No identification keys are available to species.

Idiocera **Dale** (Limoniidae: Chioneinae)**.** A genus of *ca* 140 described species, occurring in all zoogeographical regions, except Antarctica. The genus is divided into two subgenera: *I.* (*Euptilostena* Alexander) and *Idiocera sensu stricto*, of which the latter occurs in the Afrotropics. *Idiocera sensu stricto* is represented by 19 species, most in the eastern parts of the continent, with a few from Madagascar and one species recorded from Mauritius and Seychelles. Seven *Idiocera sensu stricto* species are known from the Afrotropical part of the Arabian Peninsula and *I. spuria* (Bergroth, 1888), is widespread throughout the Afrotropics. *Idiocera* is a genus of the subfamily Chioneinae with the meron small (as in Fig. 19); vein R_2 is absent; cell r_3 is short and wide; the arculus is absent; the discal medial cell (*dm*) is open; and crossvein *m–cu* lies basal to the fork of vein *M* (Fig. 83). A few Nearctic species of *Idiocera* have been reported from semi-aquatic situations along the margins of flowing waters (Young & Gelhaus 2000). No identification keys are available to Afrotropical species.

Idiognophomyia **Alexander** (Limoniidae: Chioneinae)**.** A genus of eight described species occurring in the Afrotropical, Nearctic and Palaearctic Regions, four of which occur in the Afrotropics. Three Afrotropical *Idiognophomyia* species. are endemic to South Africa (one to Madagascar). *Idiognophomyia* has the meron small (as in Fig. 19); vein *Sc* is rather long, terminating near the position of vein R_2; vein *Rs* is in direct longitudinal alignment with vein R_5; cell r_3 is deep (Fig. 84); and the legs are clothed in abundant flattened scales. Immature stages of the Nearctic species, *I. comstocki* (Alexander, 1947) and *I. enniki* Alexander, 1975, were reared from decaying Yucca (Alexander 1975; Byers 1974). Alexander (1964: 378) presented an identification key to the South African species.

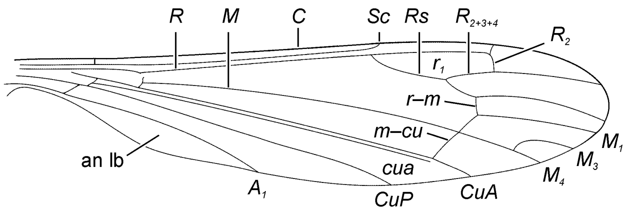
Idiotipula **Alexander** (Tipulidae)**.** An endemic monotypic genus, with the single described species, *I. confluens* Alexander, 1921, described from KwaZulu-Natal Province (as Zululand), South Africa. The wing of *Idiotipula* lack veins R_3 and M_2, thus only three *R* veins and three *M* veins reach the wing margin (Fig. 31). A similar venation is expressed in *Leptotarsus* (*Xenotipula*) (Fig. 35), from which *Idiotipula* differs in the absence of the tibial spurs. The biology and immature stages of the species remain unknown.

Keiseromyia **Alexander** (Tipulidae)**.** An endemic monotypic genus, with the single described species, *K. polyphragma* Alexander, 1963, restricted to Madagascar. It is easily distinguished by the series of auxiliary crossveins in wing cell *c* and the auxiliary crossvein that cuts cell *bm* into two halves (Fig. 32). The biology and immature stages of the species remain unknown.

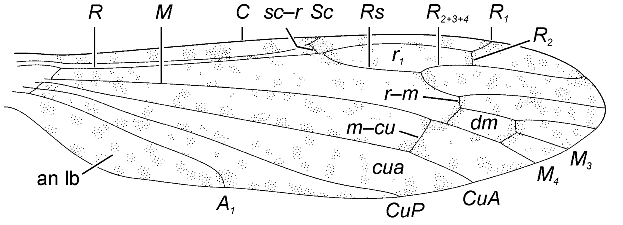
Lecteria **Osten Sacken** (Limoniidae: Limnophilinae)**.** A genus of *ca* 40 described species, occurring in the Afrotropical, Neotropical and Oriental Regions. *Lecteria* is divided into three subgenera of which only *Lecteria sensu stricto* occurs in the Afrotropical Region. *Lecteria* is characterised by the long wing vein *Sc*, which terminates close to the apex of vein R_1; the close approximation of vein *Rs* and its anterior branches to vein R_1; the elongate base of vein R_5 (Fig. 56); the short palpus; and the absence of tibial spurs. *Lecteria sensu stricto* includes 29 species, 18 of which are Afrotropical. The subgenus is widespread in the contintental Afrotropics, but is absent from the oceanic islands. The biology and immature stages of the genus remain unknown. Alexander (1956) presented an identification key to Afrotropical species.

Leptotarsus **Guérin-Méneville** (Tipulidae)**.** A genus of *ca* 325 species occurring in all zoogeographical regions, except Antarctica. The genus is divided into over 20 subgenera, only three of which occur in the Afrotropics. Characters expressed in most species include the preserved apex of wing vein *Sc* (*e.g.*, Figs 33, 34) and the short palpus. The wings of several Afrotropical species are reduced in size, often to about the length of the halters or even shorter in some cases. The antennae lack the whorls of verticilis to be found, for example, in *Nephrotoma* and *Tipula* spp. The subgenus *L.* (*Leptotipula* Alexander) is endemic to the Afrotropics, with *L. edwardsianus* (Alexander, 1920), occurring in Cameroon, Ghana and Nigeria and *L. limnophiloides* (Alexander, 1917), in South Africa. One of the characters used to distinguish *L.* (*Leptotipula*) is the position of wing crossvein *m–cu*, which joins the discal medial cell (*dm*) near its base, well removed from the origin of vein M_4 (Fig. 33). The biology and immature stages of *L.* (*Leptotipula*) remain unknown. The subgenus *L.* (*Longurio* Loew) includes 98 species, 44 of which are Afrotropical. In the Afrotropical Region *L.* (*Longurio*) is exceptionally well-represented in, and restricted to, the southern part of the region, with 30 species recorded from South Africa, eight from Madagascar and four more from Mozambique and Zimbabwe. Subapterism is a common feature in the South African species of *L.* (*Longurio*). Reduction of the wing may vary between short, but elongate and slender wings, with a complete venation, to short sac-like structures lacking distinct venation. Both sexes may have reduced wings, in other species only the females are short winged, while a few species are fully-winged in both sexes. Wood (1952) examined the early stages of 13 South African *L.* (*Longurio*) spp. The larvae are terrestrial and occur in two different habitat types: either in rather dry soil beneath clumps of Restiaceae on mountain slopes; or in damp soil beneath carpets of rotting leaves in dense woods. The subgenus *L.* (*Xenotipula* Alexander) includes two species: *L.* (*X.*) *cisatlaticus* (Alexander, 1937), from Brazil and *L.* (*X.*) *munroi* (Alexander, 1921), from South Africa. The venation of *L.* (*X.*) *munroi* is remarkable in the presence of only three *R* veins and three *M* veins that reach the wing margin (Fig. 35), a character also found in the genus *Idiotipula* (Fig. 31). *Leptotarsus* (*Xenotipula*) has tibial spurs, which are absent in *Idiotipula*. The biology and immature stages of *L.* (*Xenotipula*) remain unknown. Alexander (1956, 1964: 245 (as *Longurio*)) and Wood (1952) presented identification keys to Afrotropical species.

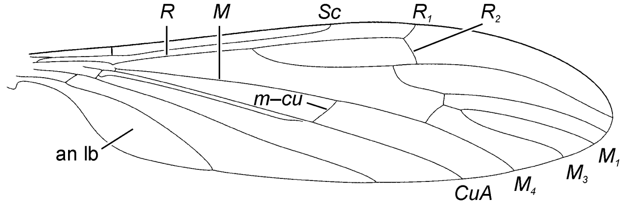
Libnotes **Westwood** (Limoniidae: Limoniinae)**.** A genus of *ca* 290 species occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. The genus is divided into eight subgenera, only two of which, *Libnotes* (*Afrolimonia* Alexander) and *Libnotes sensu stricto*, are recorded from the Afrotropics; *Libnotes* (*Afrolimonia* Alexander) is almost exclusively so, with 38 species. The subgenus is widespread on the continent and representatives are recorded from Comoros, Madagascar, Mauritius, Seychelles and the Arabian Peninsula. Alexander (1965) provided differences from the very similar subgenus *Libnotes sensu stricto*, *i.e.*, position of wing crossvein *m–cu* close to the fork of vein *M* and the less recurved apices of the outer radial veins. These characters do not, however, suffice to separate the two subgenera satisfactorily. Wood (1952) investigated the immature stages of *L. subapicalis subapicalis* (Alexander, 1930),



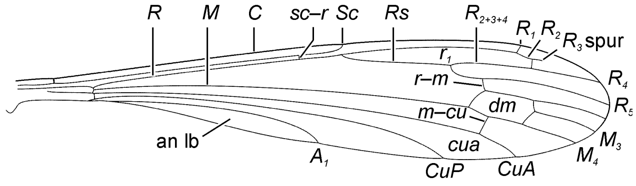
118 *Rhipidia* (*Eurhipidia*)



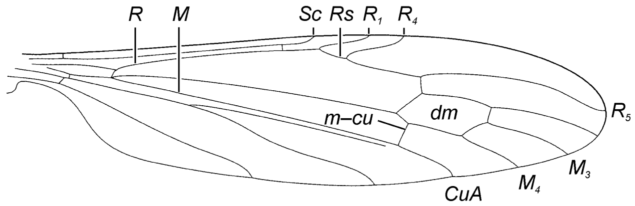
119 *Rhipidia* (*Rhipidia*)



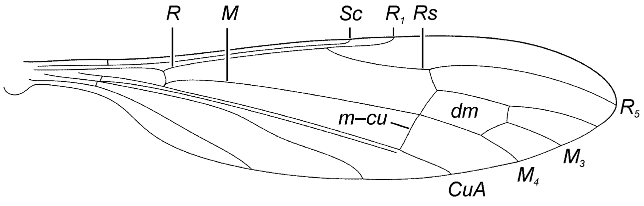
120 *Thaumastoptera* (*Thaumastoptera*)



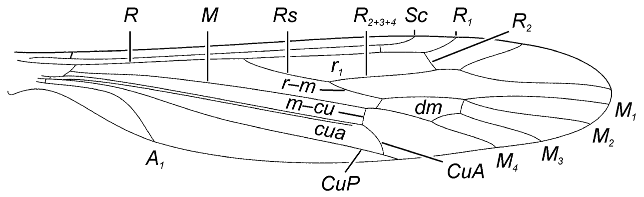
121 *Thrypticomyia*



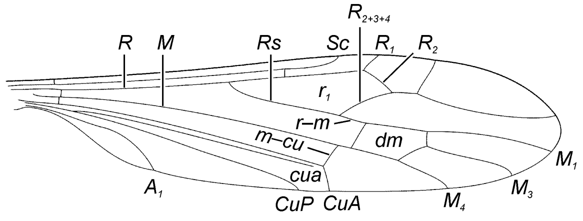
122 *Toxorhina* (*Ceratocheilus*)



123 *Toxorhina* (*Toxorhina*)



124 *Trentepohlia* (*Mongoma*)



125 *Trentepohlia* (*Paramongoma*)

Figs 14.118–125. Wings of Limoniidae (dorsal views): (118) *Rhipidia* (*Eurhipidia*) *submorionella* (Alexander); (119) *R.* (*Rhipidia*) *afra* Bergroth; (120) *Thaumastoptera* (*Thaumastoptera*) *natalensis* Alexander; (121) *Thrypticomyia bigeminata* (Alexander); (122) *Toxorhina* (*Ceratocheilus*) *drysdalei* Alexander; (123) *T.* (*Toxorhina*) *cuthbertsoni* Alexander; (124) *Trentepohlia* (*Mongoma*) *albilatissima* Alexander; (125) *Tr.* (*Paramongoma*) *nigeriensis* Alexander. Figs 118, 124, 125 (after Alexander 1956, figs 66, 101, 100, respectively), Fig. 119 (after Alexander 1917, fig. 5), Figs 120, 122, 123 (after Alexander 1964, figs 51, 116, 117), Fig. 121 (after Alexander 1963, fig. 55).

Abbreviations: A_1 – first branch of anal vein; an lb – anal lobe; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

the larvae of which were collected in damp rotting humus in a tree hole. According to Wood (1952: 181), "… [t]he slimy shiny larvae actively burrow through the humus, feeding as they go." Upon pupation, the larva secretes a tube of glutinous saliva around minute pieces of debris, forming a woody cocoon within which pupation occurs. Larvae of Palaearctic species of *L.* (*Afrolimonia*) are also wood-inhabiting, dependent on species, occurring beneath bark and in wood of either deciduous or coniferous trees (Krivosheina 2008; N.P. Krivosheina 2009; Krivosheina & Krivosheina 2011: 191, 195; Podeniene 2003). *Libnotes sensu stricto* includes *ca* 150 species, with only a single Afrotropical species, *L. libnotina* (Alexander, 1934), occurring in South Africa and Zimbabwe. Immature stages of a few Australasian/Oceanian, Oriental and Palaearctic species of *Libnotes sensu stricto* are known; these occur in fruiting bodies of fungi, beneath the bark of various species of coniferous and deciduous trees, in sap concentrations (Krivosheina 2008; N.P. Krivosheina 2009; Krivosheina & Krivosheina 2011: 191, 195), or in decaying debris behind old leaf sheaths, in tree holes, phytotelmata and similar moist to wet situations (Alexander 1920, 1931; Williams 1943). No identification keys are available to Afrotropical species.

Limnophila **Macquart** (Limoniidae: Limnophilinae)**.** In its current concept, the genus *Limnophila* includes *ca* 200 species, occurring in all zoogeographical regions, except Antarctica. There is no doubt that it represents a polyphyletic group and the classification reflects our poor understanding of the species. *Limnophila* is divided into 14, often very small subgenera, aside from *Limnophila sensu stricto*, which includes the majority of species. Five subgenera are represented in the Afrotropical Region. The subgenus *L.* (*Dasylimnophila* Alexander) is endemic to Madagascar, with two described species, for which the immature stages are unknown. The subgenus can be recognised by the presence of macrotrichia on the membrane of the wing apex (Fig. 57). The subgenus *L.* (*Elporiomyia* Alexander) is endemic to the Afrotropics and includes three South African species and a single species from Madagascar. *Limnophila* (*Elporiomyia*) can be recognised by the presence of ventrally-produced basal antennal flagellomeres and details of the male and female terminalia. Wood (1952) discussed the immature stages of the South African *L.* (*E.*) *crepuscula* Wood, 1952 and *L.* (*E.*) *nox* Alexander, 1921. Larvae of both species are aquatic; those of *L.* (*E.*) *crepuscula* were collected in the more moist areas of a stream bed over which percolated a thin film of water; those of *L.* (*E.*) *nox* in saturated mud beneath the water line. Their structure suggests a predatory lifestyle. The subgenus *L.* (*Hovalimnophila* Alexander) is endemic to Madagascar and includes the single species *L.* (*H.*) *malitiosa* (Alexander, 1951), for which the immature stages are unknown. This subgenus can be distinguished by the open discal medial cell (*dm*) (crossvein *m–m* absent) and the relatively long petiole of cell r_3 (Fig. 59). The subgenus *Limnophila sensu stricto* includes *ca* 145 described species, eight of which occur in the Afrotropics. The subgenus is recorded from Madagascar (5 species) and the adjacent continental Afrotropical Region. *Limnophila sensu stricto* is a "dumping ground" and includes species that do not easily fit into other defined subgenera. Known larvae of *Limnophila sensu stricto* are semi-aquatic and predatory (Alexander 1920, 1931; Brindle 1967; Brindle & Bryce 1960; Krivosheina & Krivosheina 2011: 181; Podeniene 2002, 2003; Podeniene & Gelhaus 2010). The subgenus *L.* (*Nesolimnophila* Alexander) is endemic to Madagascar and includes three described species. Species are characterised by a heavily dotted pattern on the wing. The immature stages remain unknown. Alexander (1956, 1964: 358) and Wood (1952) presented identification keys to Afrotropical species.

Limnophilomyia **Alexander** (Limoniidae: Chioneinae)**.** An endemic genus of 11 described species, divided into two subgenera; the monotypic *L.* (*Eulimnophilomyia* Alexander) and *Limnophilomyia sensu stricto*. The single species of *L.* (*Eulimnophilomyia*), *L.* (*E.*) *abnormalis* Alexander, 1964, occurs in South Africa, *Limnophilomyia sensu stricto* comprises 10 species widespread over the continental Afrotropics. *Limnophilomyia* has the meron small (as in Fig. 19); the subcostal vein (*Sc*) is rather long and terminates at the level of the fork of vein *Rs*; crossvein *sc–r* is positioned near the apex of vein *Sc*; vein *Rs* is in direct longitudinal alignment with vein R_5; vein R_3 is present (*L.* (*Limnophilomyia*)), or absent (*L.* (*Eulimnophilomyia*)), the discal medial cell (*dm*) is present and three *M* veins reach the wing margin from the discal medial cell (*e.g.*, Figs 85, 86). Wood (1952) found larvae of the South African *L.* (*L.*) *lacteitarsis* (Alexander, 1921), in a decaying log of *Cunonia capensis* L. (Cunoniaceae), on the edge of a waterfall pool, most of which were 25–75 mm below the water's surface. Wood suggested that larvae inhabit the roots and rotting stems of reeds in open treeless areas. In these situations the adults are found among the reeds that overgrow and partially conceal the true stream. In another situation pupae were found in a damp rotten log near a streamlet in a small group of trees. Alexander (1956, 1964: 403) presented identification keys to Afrotropical species of *Limnophilomyia*.

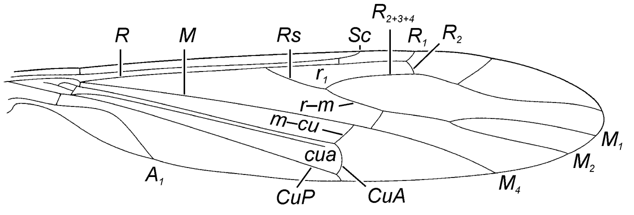
Limonia **Meigen** (Limoniidae: Limoniinae)**.** A genus of *ca* 215 species occurring in all zoogeographical regions, except Antarctica. The systematics of the genus is in need of revision, partly due to its long history as a "dumping ground" for a wide diversity of limoniid forms. Several genus-group level taxa have been separated in the past from *Limonia*, but it is still a polyphyletic group and a satisfactory characterisation of the genus cannot be provided. *Limonia* in its current concept is not divided into subgenera. The Afrotropical fauna of *Limonia* includes 13 species that are positively attributable to the genus, plus four species for which their generic affiliation remains to be ascertained. The genus is widespread in the region, with two species recorded from Comoros. Alexander (1956, 1964: 306) presented identification keys to Afrotropical species of "*Limonia*".

Medleromyia **Alexander** (Limoniidae: Limnophilinae)**.** An endemic genus with two species described from Nigeria, the larvae and pupae of which remain unknown. *Medleromyia* is distinguished by the slender wings with a reduced venation; two *Rs* veins and three *M* veins reaching the wing margin; the base of R_5 is long; and the discal medial cell (*dm*) is absent (Fig. 62). The species *M. nigeriana* Alexander, 1974, is characterised by the presence of a setuliferous pocket immediately posterior to vein R_4, a feature absent in *M. destituta* Alexander, 1976. No identification key is available to species of *Medleromyia*.

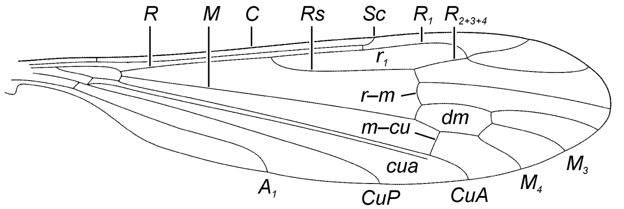
Maekistocera **Wiedemann** (Tipulidae)**.** A genus of three recognised species, recorded from the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical and Oriental Regions. Its only representative in the Afrotropics, *M. filipes filipes* (F., 1805), is widespread, being reported from the entire sub-

Saharan area and Madagascar. *Maekistocera* is easily recognised by the peculiar wing venation (Fig. 36), the extremely elongate and slender antennae in the male; and the likewise elongate and slender legs in both sexes. Larvae of *Maekistocera* are aquatic and are known to occur in calcareous waters (Rogers 1949; Young 2004: 780).

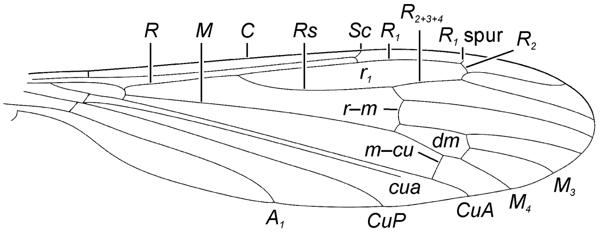
Metalimnobia **Matsumura** (Limoniidae: Limoniinae)**.** A genus of *ca* 50 species occurring in the Afrotropical, Neotropical, Oriental and Palaearctic Regions. The genus is divided into three subgenera, of which two, *M.* (*Lasiolimonia* Alexander) and *M.* (*Tricholimonia* Alexander), occur in and are endemic to, the Afrotropics. The genus can be recognised by the



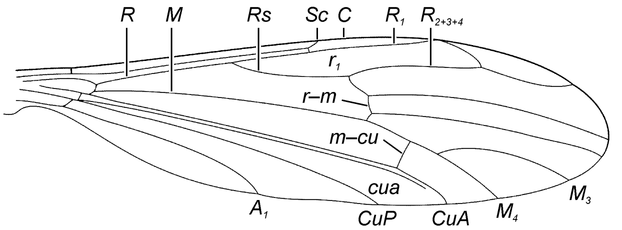
126 *Trentepohlia* (*Trentepohlia*)



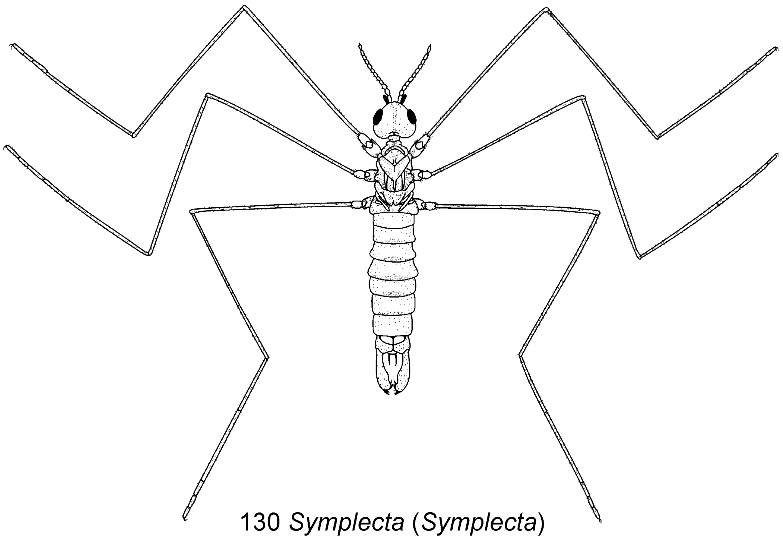
127 *Trichoneura* (*Ceratolimnobia*)



128 *Trichoneura* (*Xipholimnobia*)



129 *Xenolimnobia*



130 *Symplecta* (*Symplecta*)

Figs 14.126–130. Wings and habitus of Limoniidae (dorsal views): (126) wing of *Trentepohlia* (*Trentepohlia*) *alluaudi* Alexander; (127) same, *Trichoneura* (*Ceratolimnobia*) *munroi* (Alexander); (128) same, *T.* (*Xipholimnobia*) *madagascariensis* (Alexander); (129) same, *Xenolimnobia camerounensis* Alexander; (130) habitus of male *Symplecta* (*Symplecta*) *holdgatei* (Freeman). Figs 126, 128 (after Alexander 1963, figs 78, 51, respectively), Fig. 127 (after Alexander 1964, fig. 56), Fig. 129 (after Alexander 1974, fig. 18), Fig. 130 (after Jones *et al.* 2003, fig. 27).

Abbreviations: A_1 – first branch of anal vein; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_{2+3+4} – upper branch of radial sector; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein.

presence of macrotrichia in the stigmal area; in some species these are also present at the wing apex (*e.g.*, Figs 113, 114). *Metalimnobia* (*Lasiolimonia*) includes three described species with a central to western distribution. The macrotrichia in this subgenus are present in the stigmal area and at the wing apex (Fig. 113). The immature stages of *M.* (*Lasiolimonia*) spp. remain unknown. The subgenus *M.* (*Tricholimonia*) includes 10 species; it is widespread and a single species, *M.* (*T.*) *renaudi* (Alexander, 1955), is recorded from Madagascar. The wing macrotrichia in *M.* (*Tricholimonia*) are restricted to the stigmal area (Fig. 114). Larvae and pupae of the subgenus are currently unknown, but may (together with *M.* (*Lasiolimonia*)), be fungivorous, as most known larvae of the subgenus *Metalimnobia sensu stricto* appear to be (Alexander 1920; Brindle 1967; Bryce 1957; Buxton 1960; Chandler 2010: 431; Hackman & Meinander 1979; Johnson 1906; N.P. Krivosheina 2009; Krivosheina & Krivosheina 2010, 2011: 191; Lindner 1958*b*; Podeniene 2003; Podeniene *et al*. 2010; Salmela & Starý 2009; Young & Gelhaus 2000). Alexander (1956 (as *Limonia congoensis*-group)) presented an identification key to Afrotropical species.

***Molophilus* Curtis** (Limoniidae: Chioneinae)**.** A genus of *ca* 1,000 described species and one of the largest genera in the Tipuloidea, occurring in all zoogeographical regions, except Antarctica. The genus is currently divided into 11 subgenera, of which only *Molophilus sensu stricto* occurs in the Afrotropics. *Molophilus sensu stricto* includes *ca* 870 species globally, with only 22 species in the Afrotropics, but this probably reflects the relatively poor state of our knowledge of the local fauna rather than actual diversity. The subgenus is distributed over the entire continental Afrotropical Region and Madagascar. *Molophilus* belongs to a group of genera in the subfamily Chioneinae with the meron large (as in Figs 18, 20, 21). The small size, distinctive wing venation, with vein *Rs* ending in cell r_3, crossvein *r–m* lying apical to the fork of vein *Rs* (Fig. 87) and the usually abundant macrotrichia on the wing veins, make it rather easy to recognise *Molophilus*. It may only be confused with *Tasiocera*, in which crossvein *r–m* lies at the level of the fork of vein *Rs* (Fig. 93) and which only has a single gonostylus in the male terminalia, whereas *Molophilus* has two gonostyli. A number of Nearctic and Palaearctic species of *Molophilus* have been recorded from semi-aquatic areas (Alexander 1915*b*, 1920; Alexander & Lloyd 1914; Brindle 1967; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 186; Lehmann & Reusch 2009; Mendl 1978: 375; Okely 1979; Podeniene 2003, 2009; Reusch 1988; Reusch & Hohmann 2009; Reusch & Schrankel 2006; Young & Gelhaus 2000). Known Nearctic and Palaearctic larvae are aquatic or semi-aquatic and predatory (Alexander 1920; Brindle 1967; Brindle & Bryce 1960; Cameron 1917; Coe 1941; Crisp & Lloyd 1954; Gerbig 1913; Krivosheina & Krivosheina 2011: 186; Mendl 1978: 375; Podeniene 2003; Reusch 1988; Rogers 1930; Sandrock 1978; Young & Gelhaus 2000). Alexander (1956, 1964: 424) presented identification keys to Afrotropical species.

***Neolimnomyia* Séguy** (Limoniidae: Limnophilinae)**.** A genus of 10 species occurring in the Afrotropical and Palaearctic Regions, eight of which are endemic to the Afrotropical Region, where the genus is widespread. A single species, *N. ranavalona* (Alexander, 1965), is known from Madagascar. The wing venation of *Neolimnomyia* is of the general limnophiline type (Fig. 63), but species can be recognised on features of the male terminalia. The larvae of Palaearctic species are semi-aquatic and predatory (Brindle1967; Brindle & Bryce 1960; Podeniene 2003; Reusch 1988). Alexander (1956 (as *Limnophila*, *filata* group), 1964: 358 (as *Limnophila*, *cf. Neolimnomyia*)) presented identification keys to Afrotropical species.

***Nephrotoma* Meigen** (Tipulidae)**.** One of the larger genera of the Tipuloidea, with *ca* 475 recognised species occurring in all zoogeographical regions, except Antarctica (Figs 2, 3, 7). *Nephrotoma* includes 124 species in the Afrotropics, is widespread in the region, and has been recorded from Comoros, Madagascar, Réunion Is., São Tomé and Príncipe. *Nephrotoma* can be most easily recognised by the wing venation, with the relatively short vein *Rs*, at least partly present at the apex of vein *Sc*; crossvein *m–cu* that commonly joins vein *M* basal to the discal cell (*d*); and the sessile, or at most, very short petiolate cell m_1 (Fig. 37). *Nephrotoma* are usually yellow, or orange-yellow in ground colour, with a distinct brown to black pattern on head, thorax and abdomen. The dark colouration can be extensive in certain species so as to obscure the light ground colour. Parts of the integument are often shiny. Immature stages of *Nephrotoma* are terrestrial and larvae typically occur in damp soil where they feed on the roots of plants (Alexander 1931; Brindle 1960*b*; Byers 2002; Chiswell 1956; Kim & Lee 2005*a*; Kramer & Withers 2007; Podeniene 2003; Rogers 1931; Theowald 1957, 1967). Wood (1952) described the immatures of two species occurring in South Africa (*N. antennata* (Wiedemann, 1820) and *N. petiolata* (Macquart, 1838)). Alexander (1956, 1957, 1960*b*, 1964: 266) and Wood (1952) presented identification keys to Afrotropical species.

***Orimarga* Osten Sacken** (Limoniidae: Limoniinae)**.** A genus of almost 150 species occurring in all zoogeographical regions, except Antarctica. The genus is divided into three subgenera, of which *Orimarga sensu stricto* and *O.* (*Protorimarga* Alexander) are represented in the Afrotropics. *Orimarga sensu stricto* includes *ca* 130 species, of which 13 occur in the Afrotropics, about half of which are restricted to Comoros, Madagascar, Seychelles and United Arab Emirates. The remainder of Afrotropical *Orimarga sensu stricto* species are widespread over the continental Afrotropics. Compared to *O.* (*Protorimarga*), the wing is narrow, about four times as long as wide (Fig. 115). *Orimarga* larvae have not yet been properly described, but they appear to be aquatic to semi-aquatic (Mendl 1978: 369; Podeniene 2003; Stubbs 2003). *Orimarga* (*Protorimarga*) is endemic to the Afrotropics, with the single species, *O.* (*P.*) *bequaertiana* (Alexander, 1930), described from Liberia. It differs from species of the subgenus *Orimarga sensu stricto* by the relatively broad wings that exhibit a number of auxiliary crossveins in cells *c*, r_1 and *br* (Fig. 116). The immature stages of *O.* (*P.*) *bequaertiana* remain unknown. Alexander (1956, 1964: 345) presented identification keys to Afrotropical species of *Orimarga*.

***Ormosia* Rondani** (Limoniidae: Chioneinae)**.** A genus of *ca* 225 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. The genus is divided into four subgenera, of which only the monotypic subgenus *O.* (*Neserioptera* Alexander) is Afrotropical, with the single species, *O.* (*N.*) *perpusilla* Edwards, 1912, being endemic to Seychelles. The immature stages of the species remain unknown. *Ormosia* has the meron large (as in Figs 18, 20, 21); wing vein *Sc* is rather short and terminates near the base of vein *Rs*; crossvein *sc–r* is positioned near the apex of vein *Sc*; three long vein *Rs* branches and three *M* veins reach the wing margin; the discal medial cell (*dm*) is open; and the wing veins are clothed in abundant microtrichia (Fig. 88). Known immature stages of *Ormosia sensu stricto* are aquatic, or semi-aquatic and occur in or along streams and in moist soil (Alexander 1931; Bangerter 1930; Cameron 1917; Kramer & Withers 2007; Lantsov 2009; Young & Gelhaus 2000).

***Paradelphomyia* Alexander** (Limoniidae: Limnophilinae)**.** A genus with just over 80 described species occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica. The genus is divided into two subgenera, one of which, *P.* (*Oxyrhiza* de Meijere), is represented in the Afrotropics. Fourteen species are known from the Afrotropics, where the subgenus is widespread, although absent from Madagascar and adjoining Indian Ocean island groups. *Oxyrhiza* can be recognised by the presence of macrotrichia in the outer wing cells, in combination with the absence of vein R_2, a closed discal medial cell (*dm*) and three *M* veins that reach the wing margin (Fig. 64). Immature stages are known for a handful of species. Larvae are semi-aquatic and occur in moist, or marshy soils, humus near streams and in mud (Brindle 1967; Brindle & Bryce 1960; Crisp & Lloyd 1954; Krivosheina & Krivosheina 2011: 179; Podeniene 2002, 2003; Reusch 1988; Young & Gelhaus 2000). Alexander (1956, 1964: 348) presented identification keys to Afrotropical species.

***Pilaria* Sintenis** (Limoniidae: Limnophilinae)**.** A genus of *ca* 40 species occurring in all zoogeographical regions, except Antarctica. Eight species are distributed in central parts of the continental Afrotropics. *Pilaria* exhibits a complete limnophiline venation (Fig. 65); the head is not narrowed posteriorly and lengthened into a "neck" (Fig. 16); and the tarsi of most, but not all species are extensively white. Known Nearctic and Palaearctic larvae are aquatic or semi-aquatic and are predatory (Alexander 1920; Brindle 1958, 1967; Brindle & Bryce 1960; Cameron 1917; Coe 1941; Crisp & Lloyd 1954; Gerbig 1913; Krivosheina & Krivosheina 2011: 181; Mendl 1978: 372; Podeniene 2003; Reusch 1988; Rogers 1930; Sandrock 1978; Young & Gelhaus 2000). Alexander (1956) presented an identification key to Afrotropical species.

***Platylimnobia* Alexander** (Limoniidae: Limoniinae)**.** An endemic genus of five described species, all confined to South Africa. *Platylimnobia* is characterised by the reduced wings (Fig. 117). The biology and immature stages remain unknown. Alexander (1964: 342) presented an identification key to Afrotropical species.

***Pseudolimnophila* Alexander** (Limoniidae: Limnophilinae)**.** A genus of *ca* 75 species occurring in all zoogeographical regions, except the Australasian/Oceanian Region and Antarctica. The genus is divided into two subgenera, both of which occur in the Afrotropics. The genus can be distinguished by the narrow pronotum, of which the sides are anteriorly produced as lateral lobes (Fig. 14). The subgenus *P.* (*Calolimnophila* Alexander) is endemic to the region and includes 13 species, widespread in the continental Afrotropics, as well as Comoros, Madagascar and Mauritius. *Pseudolimnophila* (*Calolimnophila*) can be distinguished from the subgenus *Pseudolimnophila sensu stricto* by the presence of the auxiliary crossvein in wing cell r_3 (*e.g.*, Figs 66, 67). The biology and immature stages of *P.* (*Calolimnophila*) remain unknown. *Pseudolimnophila sensu stricto* includes 18 widespread species in the Afrotropics, including two in Madagascar. Known larvae of Nearctic and Palaearctic *Pseudolimnophila sensu stricto* are predatory, aquatic or semi-aquatic. They occur in open and shaded marshes, in rich organic soils and along stream margins (Alexander 1920; Brindle 1958*b*, 1967; Brindle & Bryce 1960; Crisp & Lloyd 1954; Hinton 1954; Hudson 1920; Krivosheina & Krivosheina 2011: 180; Podeniene 2002, 2003; Reusch 1988; Rogers 1926, 1930; Young & Gelhaus 2000). Alexander (1955*c*, 1956, 1964: 355) and Wood (1952) presented identification keys to Afrotropical species.

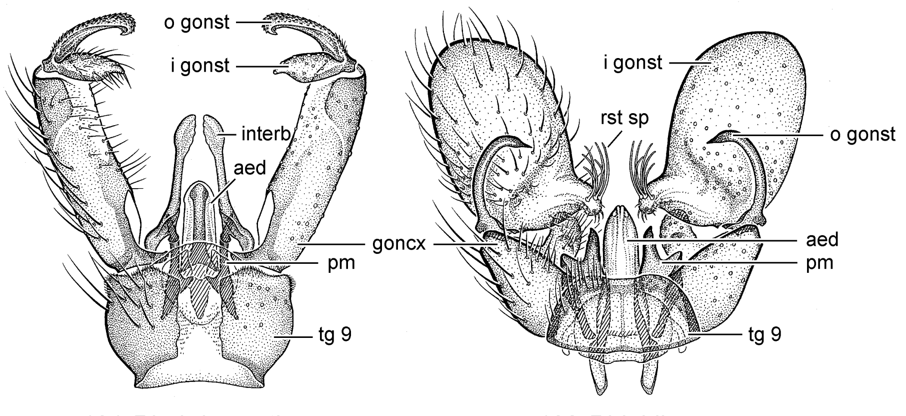
***Quathlambia* Alexander** (Limoniidae: Chioneinae)**.** An endemic monotypic genus, with the single species, *Q. stuckenbergi* Alexander, 1956, being confined to South Africa. *Quathlambia* has reduced wings and halteres and can be recognised by this combination of characters, plus the presence of abundant flattened scales on the legs. The eggs of *Quathlambia* are large, as are those in the purportedly related genera *Baeoura*, *Cryptolabis*, *Idiognophomyia* and *Phantolabis*. The biology and immature stages of *Quathlambia* remain unknown.

***Rhabdomastix* Skuse** (Limoniidae: Chioneinae)**.** A genus of *ca* 125 species occurring in all zoogeographical regions, except Antarctica. The genus is divided into two subgenera, of which *Rhabdomastix sensu stricto* is present in the Afrotropics with three species, *R.* (*R.*) *afra* Wood, 1952, *R.* (*R.*) *indigena* Alexander, 1958 and *R.* (*R.*) *tugela* Alexander, 1964, all endemic to South Africa. *Rhabdomastix* has the meron large (Fig. 20); the subcostal wing vein (*Sc*) is rather long; crossvein *sc–r* is well-removed from the apex of vein *Sc*, located near the base of vein *Rs*; vein *Rs* is long; vein R_2 is absent; cell r_3 is short and wide; and three *M* veins reach the wing margin from the discal medial cell (*dm*) (Fig. 89). Wood (1952) recorded the larvae of the South African species *R.* (*R.*) *afra*, from small gravely sand spits beneath small rocks in a stream. The pupae occurred in drier regions of the spits, where the sand was raised 50–75 mm above water level. Larvae of Nearctic and Palaearctic *Rhabdomastix* species are also recorded from aquatic and semi-aquatic habitats (Hynes 1969; Krivosheina & Krivosheina 2011: 185; Podeniene 2001, 2003; Reusch & Schrankel 2006). Starý (2003, 2004) discussed the phylogenetic position and classification of *Rhabdomastix*. Alexander (1964: 405) presented an identification key to Afrotropical species.

***Rhipidia* Meigen** (Limoniidae: Limoniinae)**.** A genus of *ca* 230 species occurring in all zoogeographical regions, except Antarctica. The genus is divided into two subgenera: *R.* (*Eurhipidia* Alexander) and *Rhipidia sensu stricto*, both of which occur in the Afrotropics. Most species of *Rhipidia* can be easily recognised by the comb-like antennae in males and ventrally-produced flagellomeres in females and by the freckled wing membrane (Fig. 119). Eight species of *R.* (*Eurhipidia*) occur in the Afrotropics, three of which are known from Madagascar and a single species in both Mauritius and Réunion Is. The discal medial cell (*dm*) of *R.* (*Eurhipidia*) is open by atrophy of crossvein *m–m* (Fig. 118). The larvae and pupae of *R.* (*Eurhipidia*) remain unknown. *Rhipidia sensu stricto* comprises 200 species globally, of which 17 widespread species occur in the Afrotropics, including Comoros, Madagascar and Seychelles. Immature stages of Nearctic and Palaearctic *Rhipidia* species are recorded from wood of deciduous trees, sap concentrations on trees, slimy masses of myxomycetes and the fruiting bodies of fungi (Alexander 1920, 1931; Brindle 1967; Johnson 1910; N.P. Krivosheina 2009; Krivosheina & Krivosheina 2011: 193, 197; MacGowan 2005; Podeniene 2003; Reusch 1988; Sandrock 1978; Tjeder 1958; Young & Gelhaus 2000). Alexander (1956, 1964: 306 (as *Limonia*, subgenus *Rhipidia*)) presented identification keys to Afrotropical species.

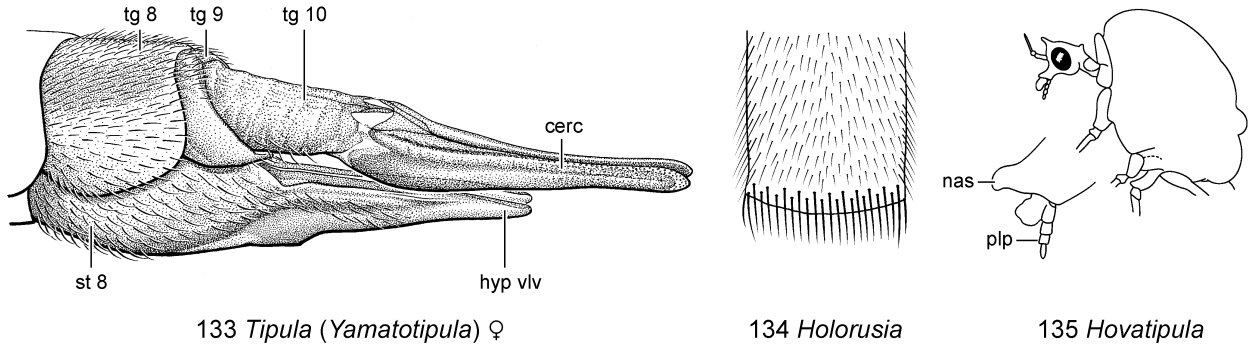
Styringomyia **Loew** (Limoniidae: Chioneinae)**.** A genus of *ca* 165 described species occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. Fifty-five species are recorded from the Afrotropics, where the genus is widespread. *Styringomyia* can be easily distinguished by the flattened appearance and the peculiar wing venation, with the extremely short vein R_1, which terminates near the mid length of the wing on the fore margin, two branches of vein *Rs* reach the wing margin, of which the anterior one is short and erect, or suberect, and the elongate discal medial cell (*dm*) from which three *M* veins reach the wing margin (Fig. 90). Australasian/Oceanian and Oriental species have been reared from rotting plant material, such as banana fibre, organic remains of dead tree trunks, rotting palm fronds and mats of organic material consisting of branches and leaves (Edwards 1924; Hynes 1990). Alexander (1956, 1964: 425) presented identification keys to Afrotropical species. Podenas (2012) provided an overview of the species occurring in Ghana, including an identification key.

Symplecta **Meigen** (Limoniidae: Chioneinae)**.** A genus of *ca* 100 described species occurring in all zoogeographical regions, including Antarctica. The genus is divided into five subgenera, only one of which, *S.* (*Hoploerioptera* Alexander) is absent from the Afrotropics. *Symplecta* has the meron large (as in Figs 18, 20, 21); wing vein *Sc* is long and reaches the level of vein R_2; crossvein *sc–r* is well-removed from the apex of the subcostal vein (*Sc*) and is located near the mid length of vein *Rs*; vein *Rs* is long and rather straight; cell r_3 is deep; the discal medial cell (*dm*) is closed; three *M* veins reach the wing margin from



131 *Rhabdomastix* ♂

132 *Rhipidia* ♂



133 *Tipula* (*Yamatotipula*) ♀

134 *Holorusia*

135 *Hovatipula*

Figs 14.131–135. Male and female terminalia, femur, head and thorax of Tipulidae: (131) male terminalia of *Rhabdomastix subfascigera* Alexander, dorsal view (non-Afrotropical); (132) same, *Rhipidia lecontei* (Alexander), dorsal view (non-Afrotropical); (133) ovipositor of *Tipula* (*Yamatotipula*) *noveboracensis* Alexander, lateral view (non-Afrotropical); (134) apex of femur of *Holorusia hespera* Arnaud & Byers, dorsal view; (135) head and thorax of *Hovatipula megalothorax* (Alexander), lateral view. Figs 131–133 (Alexander & Byers 1981, figs 6, 5, 7, respectively), Fig. 134 (after Vane-Wright 1967, fig. 15), Fig. 135 (after Alexander 1955*b*, fig. 5).

Abbreviations: aed – aedeagus; cerc – cercus; goncx – gonocoxite; hyp vlv – hypogynial valve; i gonst – inner gonostylus; interb – interbase; nas – nasus; o gonst – outer gonostylus; plp – palpus; pm – paramere; rst sp – rostral spine; st – sternite; tg – tergite.

the discal medial cell; and crossvein *m–cu* is located just basal of the discal medial cell (*e.g.*, Figs 91, 92). The small subgenus *S.* (*Podoneura* Bergroth) includes a single Palaearctic species and seven Afrotropical species that are widespread throughout the region. It can be recognised by the fork at the apex of wing vein A_1 (Fig. 91). The biology and immature stages of *S.* (*Podoneura*) remain unknown. The subgenus *S.* (*Psiloconopa* Zetterstedt) comprises 60 species, of which only one species, *S.* (*P.*) *rutshuruensis* (Alexander, 1956), is recorded from Central Africa in the Afrotropics. It is distinguished from other *Symplecta* species by the wing, which are patterned with large ocellate markings. Known immature stages of *S.* (*Psiloconopa*) are semi-aquatic, occurring in soil along the margins of streams (Alexander 1931; Brindle 1967; Dittmar 1955; Krivosheina & Krivosheina 2011: 187; Podeniene 2003, 2009; Reusch 1988; Young & Gelhaus 2000). *Symplecta sensu stricto* is a small subgenus of 18 described species globally, of which the Holarctic and Oriental species *S.* (*S.*) *hybrida* (Meigen, 1804) occurs in the United Arab Emirates and the flightless *S.* (*S.*) *holdgatei* (Freeman, 1962) in Gough Is. (Tristan du Cunha group). Larvae of *Symplecta* are either semi-aquatic or develop in decomposing plant material (Alexander 1920, 1931; Bruch 1939; Fritz 1982; Johannsen 1934; Jones *et al*. 2003; Krivosheina & Krivosheina 2011: 188; Podeniene 2003, 2009; Reusch 1988; Young & Gelhaus 2000). The small subgenus *S.* (*Trimicra* Osten Sacken) includes seven species in the Australasian/Oceanian Region (New Zealand), one of which, *S.* (*T.*) *pilipes* (F., 1787), is ubiquitous and also occurs in the Afrotropics, where it is widespread. *Symplecta* (*Trimicra*) can be distinguished by the unpatterned wing membrane; unforked vein A_1 (Fig. 92) and the abruptly smaller apical three flagellomeres. Larvae of *S.* (*T.*) *pilipes* have been reported from a wide range of habitats, varying from coastal algal growths that are submerged by the tide, to gravely sand spits in, or along, margins of streams and rivers (Alexander 1920, 1931; Tokunaga 1930, 1940; Williams 1943; Wood 1952; Young & Gelhaus 2000). Alexander (1956 (as *Erioptera*, subgenera *Podoneura*, *Psiloconopa*, *Trimicra*), 1964: 416 (as *Erioptera*, subgenera *Podoneura*, *Trimicra*) presented identification keys to Afrotropical species.

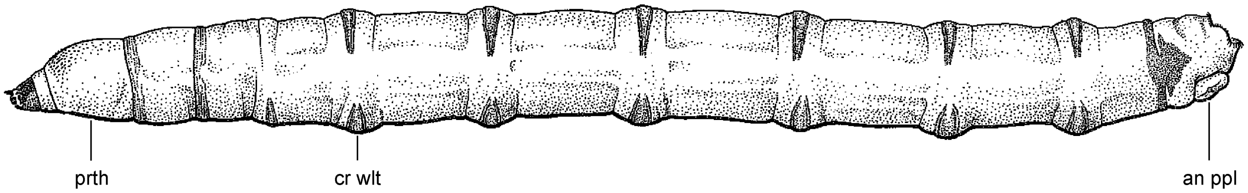
***Tasiocera* Skuse** (Limoniidae: Chioneinae)**.** A genus of *ca* 75 species occurring in all zoogeographical regions, except Antarctica. The genus is divided into two subgenera, *T.* (*Dasymolophilus* Goetghebuer) and *Tasiocera sensu stricto*, which does not occur in the Afrotropics. *Tasiocera* belongs to the group of genera in the subfamily Chioneinae with the meron large (as in Figs 18, 20, 21). The only taxon with which it may be confused is *Molophilus*, from which it differs by the close position of the bases of veins R_{2+3} and R_5 and crossvein *r–m* (Fig. 93), and the presence of a single gonostylus of the male terminalia (two gonostyles in *Molophilus*). The subgenus *T.* (*Dasymolophilus*) includes 34 species, of which 15 occur in the Afrotropics. Afrotropical species have a mainly south-eastern distribution, with a remarkable number of species occurring in the Comoros, Madagascar, Réunion Is., or Seychelles. *Tasiocera* (*Dasymolophilus*) larvae are phytosaprophagous, occurring in semi-aquatic situations in the soil, or in decomposing wood (Alexander 2002; Ashe *et al*. 2007; Reusch & Hohmann 2009). Alexander (1956, 1964: 410) presented identification keys to Afrotropical species.

***Teucholabis* Osten Sacken** (Limoniidae: Chioneinae)**.** A species-rich genus of *ca* 310 described species occurring in all zoogeographical regions, except Antarctica. The genus is divided into four subgenera, two of which, *T.* (*Euteucholabis* Alexander) and *T.* (*Paratropesa* Schiner) do not occur in the Afrotropics. The subgenus *T.* (*Euparatropesa* Alexander) includes 19 species, of which one species occurs in the Afrotropics, *T.* (*E.*) *witteana* Alexander, 1956, reported from Central Africa. It is characterised by the small meron (as in Fig. 19); the relatively short wing vein R_1; rather straight vein *Rs*; distinct vein R_2; short and wide cell r_3; and the open discal medial cell (*dm*) (Fig. 94). The immatures of this species remain unknown. *Teucholabis sensu stricto* is a large subgenus, with > 275 described species. Seven taxa, all recognised as subspecies of *T.* (*T.*) *nodipes* Speiser, 1913, are Afrotropical. Collectively they can be recognised by the short wing vein R_1; rather elongate and curved vein *Rs*; distinct vein R_2; absence of vein R_3; and the closed discal medial cell from which three *M* veins reach the wing margin (Fig. 95); the subspecies can be separated on colouration of the thorax, legs and wings. Larvae of the Nearctic *T.* (*T.*) *complexa* Osten Sacken, 1860, have been reported from wet rotten hardwood logs (Alexander 1920; Rogers 1927, 1930, 1931; Young & Gelhaus 2000); larvae of the Palaearctic species *T.* (*T.*) *yezoensis* Alexander, 1924, have been found in *Maackia* (Fabaceae), *Phellodendron* (Rutaceae), aspen, birch, maple and oak (M.G. Krivosheina 2009; N.P. Krivosheina 2009; Krivosheina & Krivosheina 2011: 184). Alexander (1956, 1964: 400) presented identification keys to Afrotropical species.

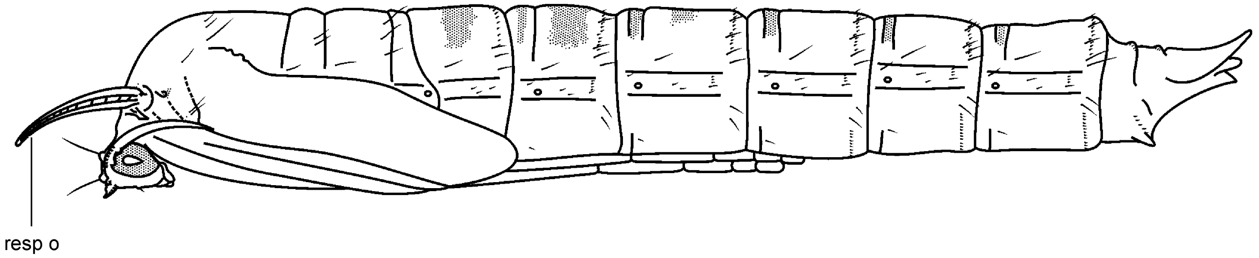
***Thaumastoptera* Mik** (Limoniidae: Limoniinae)**.** A small genus of nine described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. The genus is divided into two subgenera, only one of which, *Thaumastoptera sensu stricto*, is represented in the Afrotropics. *Thaumastoptera sensu stricto* includes eight species globally, one of which is endemic to South Africa and one endemic to Madagascar. *Thaumastoptera sensu stricto* can be recognised by the open discal medial cell (*dm*), resulting from the loss of crossvein m_3–m_4; the basal position of crossvein *m–cu* relative to the fork of vein *M*; and the distinct anal lobe (Fig. 120). Immature stages are known for the western Palaearctic species *T.* (*Thaumastoptera*) *calceata* Mik, 1866, the larvae of which occur in caddis-fly-like cases that they construct from leaf fragments. They occur in cold springs and amongst detritus in mud near small woodland streams (Alexander 1931; Brindle 1967; Lenz 1920; Mendl 1978: 369; Vaillant 1956). No identification key is available for Afrotropical species.

***Thrypticomyia* Skuse** (Limoniidae: Limoniinae)**.** A genus of 38 described species occurring in the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Five species occur in the Afrotropics, some with rather widespread distributions. *Thrypticomyia seychellensis* Edwards, 1912, for example, is recorded from Comoros, São Tomé and Príncipe, Seychelles and Sierra Leone. *Thrypticomyia* can be recognised by the remarkably slender and elongate wing (Fig. 121), which is reminiscent of the wing of *Dicranomyia* (*Euglochina*) (Fig. 103), but without exhibiting the concentration of veins terminally at the wing apex and vein *Rs* is rather long in *Thrypticomyia*. The biology and immature stages remain unknown. No identification key is available for Afrotropical species.

***Tipula* L.** (Tipulidae)**.** About half of the *ca* 5,000 described species of Tipulidae *sensu stricto* are included in the genus *Tipula*, occurring in all zoogeographical regions, except Antarctica (Fig. 6). The genus is divided into 40 subgenera, seven of which are represented in the Afrotropical Region. *Tipula* can be distinguished from other crane flies by the presence of a whorl of distinct verticilis at the enlarged bases of the antennal flagellomeres (Fig. 9); absence of the apex of the subcostal wing vein (*Sc*); presence of vein M_2; crossvein *m–cu* at or close to the fork of vein M_{3+4} (e.g., Figs 38–44); the male terminalia with two paired gonostyles; and the absence of groups of spines on the inner gonostylus. The subgenus *T.* (*Acutipula* Alexander) was based on the Afrotropical species *T.* (*A.*) *gaboonensis* Alexander, 1920, recorded from Angola, Cameroon, Gabon and Nigeria. *Tipula* (*Acutipula*) includes *ca* 200 species, 71 of which occur in the Afrotropics. The subgenus is widespread in the region and 14 species have been described from Madagascar (Fig. 6). *Tipula* (*Acutipula*) can be distinguished from other subgenera of *Tipula* by the relatively short vein *Rs*, which is about as long as crossvein *m–cu*; the petiolate cell m_1; the large discal medial cell (*dm*); the relatively narrow cell m_4; and the well-developed anal lobe (Fig. 38). Known larvae of *T.* (*Acutipula*) occur in aquatic and semi-aquatic situations, mainly in concentrations of rich organic material along the margins of streams and standing water (Alexander 1931; Brindle 1957, 1958*c* 1960*b*; Chiswell 1956; Crisp & Lloyd 1954; Lantsov 2012; Podeniene 2001, 2003; Theowald 1957, 1967, 1978: 364; Vogtenhuber 2007). Wood (1952) discussed the larvae of the South African species *T.* (*A.*) *jocosa* Alexander, 1917 and *T.* (*A.*) *pomposa* Bergroth, 1888. The subgenus *Tipula* (*Afrotipula* Alexander) includes three species and is endemic to the montane regions of East and southern Africa (Ethiopia, Kenya, Malawi, Rwanda and Uganda). The subgenus is characterised by the short rostrum; the sessile wing cell m_1; the tibial spur formula (1 : 1 : 2); the simple tarsal claws in the male; and the bifid outer gonostylus of the male terminalia. The immature stages of *T.* (*Afrotipula*) remain unknown. The mainly Palaearctic subgenus *T.* (*Savtshenkia* Alexander) includes 13 species in the Afrotropics, that are mainly distributed in the montane areas around Lake Victoria in the Great Rift Valley; the single species, *T.* (*S.*) *draconis* Alexander, 1964, is known from the Drakensberg in South Africa. The Afrotropical species of *T.* (*Satvshenkia*) can be distinguished from other Afrotropical species of *Tipula* by the shape of the male terminalia: tergite 9 is broad and has a widely emarginate posterior margin; and the inner gonostylus has a typical shape. External features that can help to separate *T.* (*Savtshenkia*) from other *Tipula* spp. include the elongate antennal flagellomeres; short vein *Rs*; sinuous vein R_4; petiolate cell m_1; and the rather narrow cell m_4 (Fig. 40). Known larvae occur in aquatic, or semi-aquatic moss, but immatures of Afrotropical species have not yet been reported (Alexander 1931; Brindle 1957, 1958*c*, 1960*a*, *b*; Bryce 1956; Chiswell 1956; Gelhaus 1986; Lantsov 1982; Podeniene 2003; Theowald 1957, 1967, 1978: 365; Young & Gelhaus 2000). De Jong (1994) provided a phylogenetic analysis of the subgenus. The subgenus *T.* (*Schummelia* Edwards) includes *ca* 70 species globally, including three Afrotropical species. One of these, *T.* (*S.*) *dolichopezoides* Alexander, 1920, is widespread and known from Democratic Republic of Congo, Kenya, Nigeria and Uganda; *T.* (*S.*) *jacksoniana* Alexander, 1956, is recorded from Uganda and *T.* (*S.*) *scylla* Alexander, 1964, from Zimbabwe. *Tipula* (*Schummelia*) can be distinguished from other subgenera of *Tipula* by the petiolate cell m_1, and the relatively wide cell m_4 (Fig. 41). Larvae occur in semi-aquatic



136 *Limonia*



137 *Austrolimnophila* (*Austrolimnophila*)

Figs 14.136–137. Larva and pupa of Limoniidae: (136) larva of *Limonia* sp., lateral view (non-Afrotropical); (137) pupa of *Austrolimnophila (Austrolimnophila) medialis* (Alexander), lateral view. Fig. 136 (Alexander & Byers 1981, fig. 82), Fig. 137 (after Wood 1952, fig. 63).

Abbreviations: an ppl – anal papilla; cr wlt – creeping welt; prth – prothorax; resp o – respiratory organ.

situations, such as the hygropetric zone of marshes and seepage areas along streams (Alexander 1931; Brindle 1957, 1958*c*, 1960*b*; Chiswell 1956; Gelhaus 1986; Podeniene 2003; Theowald 1957, 1967, 1978: 365; Young 2004: 783; Young & Gelhaus 2000). The immature stages of Afrotropical species of the subgenus remain unknown. The subgenus *T.* (*Spinitipula* Alexander) is endemic to Madagascar. It includes three species, one of which, *T.* (*S.*) *citricornis* Alexander, 1955, occurs in the west; the other two, *T.* (*S.*) *lactineipes* Alexander, 1961 and *T.* (*S.*) *spinimarginata* Alexander, 1951, occur in the east of the island. The subgenus can be distinguished from other *Tipula* species by the small discal cell; the narrow anal lobe (Fig. 42); the tibial spur formula (1 : 1 : 2); and the presence of a groups of straight spinoid setae around the tibial spurs. Immature stages of the subgenus remain unknown. The subgenus *Tipula sensu stricto* has a mainly Afrotropical and Palaearctic distribution and includes 28 species, of which 18 occur in the Afrotropical Region. The subgenus can be distinguished from other species of *Tipula* by the combination of a well-developed rostrum and nasus (Fig. 9); long vein *Rs*; the petiolate cell m_1; the relatively narrow cell m_4; the absence of macrotrichia on the membrane at the wing apex (Fig. 43); and the presence of the large outer gonostylus that covers most of the inner gonostylus of the male terminalia. In the Afrotropical Region the subgenus is restricted to montane areas, ranging from Ethiopia to South Africa. *Tipula sensu stricto* is absent from Madagascar. A remarkable feature in some species is the reduced wings, which usually occur in the female only. Males of species that are fully-winged at lower elevations may exhibit reduction of the wings in populations that occur at higher elevations (Theowald 1977, 1984). Theowald (1984) revised the subgenus and provided a phylogenetic and zoogeographical analysis. The larvae of some Palaearctic species of *Tipula sensu stricto* can cause economic damage to crops and grasslands (Brindle 1957, 1958*a*, *c*, 1960*a*, *b*; Chiswell 1956; Theowald 1957, 1967, 1978: 364). Two of these have been transported by humans and occur as pests in the Nearctic Region, while one has reached the Neotropical Region (Gelhaus 2009: 195; Peck 2007; Peck & Held 2007: 113; Young *et al.* 2000). These pest species have not yet been reported from the Afrotropical Region. The mainly Holarctic subgenus *T.* (*Yamatotipula* Matsumura) includes 124 species globally. The South African species *T. setosipennis* Alexander, 1920, is attributed to *T.* (*Yamatotipula*), but its phylogenetic affinity to other species of the subgenus requires re-examination. The biology and immature stages of *T.* (*Y.*) *setosipennis* remain unknown. Larvae of true *T.* (*Yamatotipula*) are known from aquatic and semi-aquatic situations (Alexander 1920, 1931; Brindle 1957, 1958*c*, 1959, 1960*b*; Chiswell 1956; Foote 1963; Gelhaus 1986; Kim & Lee 2004; Rogers 1930, 1933, 1942; Theowald 1957, 1967, 1978: 364; Young & Gelhaus 2000); larvae of several eastern Palaearctic species occur as pests in rice fields (Kim & Lee 2002, 2003*b*, 2005*b*, 2006, 2007). Alexander (1956, 1960*b*, 1964: 294) and Wood (1952) presented identification keys to Afrotropical species.

***Toxorhina* Loew** (Limoniidae: Limoniinae)**.** A genus of *ca* 150 species, almost exclusively restricted to the Southern Hemisphere, occurring in the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical and Oriental Regions. As with the genus *Elephantomyia*, *Toxorhina* is characterised by the extremely elongate rostrum (*e.g.*, Fig. 13). The two genera can be separated using the relative length of wing veins R_1 and R_4 and the number of antennal flagellomeres. *Toxorhina* is divided into three subgenera, of which *T.* (*Ceratocheilus* Wesché) and *Toxorhina sensu stricto* are represented in the Afrotropics. *Toxorhina* (*Ceratocheilus*) includes 77 species, 24 of which are recorded from the Afrotropics. The subgenus is widespread in the continental Afrotropics, as well as Comoros, Madagascar, Mauritius, Réunion Is. and Seychelles. *Toxorhina* (*Ceratocheilus*) is distinguished by vein *Rs* emitting two branches that reach the wing margin (Fig. 122). Hynes (1990, 1997) investigated the New Caledonian species *T.* (*C.*) *caledonica* Alexander, 1948, larvae of which develop at the base of decomposing palm fronds. *Toxorhina sensu stricto* currently includes 68 species, 12 of which occur in the Afrotropics. *Toxorhina sensu stricto* is distinguished by vein *Rs* being unbranched (Fig. 123). The biology and immature stages of *Toxorhina sensu stricto* remain unknown. Alexander (1956, 1964: 429) presented identification keys to Afrotropical species.

***Trentepohlia* Bigot** (Limoniidae: Limoniinae)**.** A genus of *ca* 300 described species occurring in all zoogeographical regions, except the Nearctic Region and Antarctica. The genus is divided into seven subgenera, three of which are recorded from the Afrotropics. *Trentepohlia* is distinguished by the basal position of the base of wing vein *Rs*; the longitudinal alignment of vein *Rs* and crossvein *r–m*; and, most significantly, the close approximation or fusion of the apical sections of veins *CuA* and *CuP*. Twenty-two species of *T.* (*Mongoma* Westwood) occur in the Afrotropics, with a remarkable concentration of 11 species in Madagascar. *Trentepohlia* (*Mongoma*) is distinguished by four veins originating from the discal medial cell (*dm*) that reach the wing margin (Fig. 124). The biology and immature stages of the subgenus *T.* (*Mongoma*) remain unknown. The subgenus *T.* (*Paramongoma* Brunetti) includes 51 species, of which seven species occur in the Afrotropics, where the subgenus is widespread. *Trentepohlia* (*Paramongoma*) are distinguished in having the discal medial cell closed; three *M* veins; and the apices of veins *CuA* and *CuP* approximate, but not fused (Fig. 125). As far as is known, larvae of *T.* (*Paramongoma*) species develop in water collected in the axils of plants (Alexander 1920, 1931). *Trentepohlia sensu stricto* includes 88 species, of which 50 occur in the Afrotropics. The subgenus is widespread, with a concentration of 11 species found in Madagascar; another concentration occurs in West Africa, where 18 species are reported from Nigeria and Cameroon. *Trentepohlia sensu stricto* is distinguished in having an open discal medial cell and the apices of veins *CuA* and *CuP* fused (Fig. 126). The biology and immature stages of *Trentepohlia sensu stricto* remain unknown. Alexander (1956, 1964: 396) presented identification keys to Afrotropical species.

***Trichoneura* Loew** (Limoniidae: Limoniinae)**.** A genus of 10 described species occurring in the Afrotropical, Australasian/Oceanian and Oriental Regions. The genus is divided into three subgenera of which *T.* (*Ceratolimnobia* Alexander) and *T.* (*Xipholimnobia* Alexander) are represented in the Afrotropics. The genus is characterised by the reduction of the apex of vein R_1, the closed discal medial cell (*dm*), the presence of 3 *M* veins originating from the discal medial cell (*e.g.*, Figs 127, 128). *Trichoneura* (*Ceratolimnobia*) includes the single species, *T.* (*C.*) *munroi* (Alexander, 1920), endemic and widespread in the Afrotropics (including Madagascar). *Trichoneura* (*Ceratolimnobia*) is characterised by the presence of a so-called corniculus on the vertex of the head (as in Fig. 13) and by brownish patterned wings with a venation as in Fig. 127. The biology and immature stages remain unknown. *Trichoneura* (*Xipholimnobia*) includes eight species, of which two species are Afrotropical, one occurring in Madagascar, the other in Cameroon and Nigeria. The vertex of the head has no corniculus and the wing membrane is unpatterned (Fig. 128). The biology and immature stages of the subgenus remain unknown. There are no identification keys available to Afrotropical species.

Trichotrimicra **Alexander** (Limoniidae: Chioneinae)**.** An endemic genus widespread in the Afrotropical Region, recorded from Nigeria to Kenya and South Africa. It includes nine species, none of which have been reared and the immature stages and biology remain unknown. *Trichotrimicra* are distinguished in having the meron large (as in Fig 18, 20, 21); the wing membrane entirely clothed in macrotrichia; three vein *Rs* branches and three *M* veins that reach the wing margin; cell r_3 deep; and the discal medial cell (*dm*) closed (Fig. 96). Alexander (1956 (as *Ormosia*, subgenus *Trichotrimicra*), 1964: 412 (as *Ormosia*)) presented identification keys to Afrotropical species.

Xenolimnobia **Alexander** (Limoniidae: Limoniinae)**.** An endemic monotypic genus, with the single species, *X. camerounensis* Alexander, 1926, restricted to Cameroon and Nigeria. It is distinguished in having the apex of wing vein R_1 fused for some distance with the costal vein (*C*) (Fig. 129). The biology and immature stages of *X. camerounensis* remain unknown.

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TANYDERIDAE

15

(Primitive Crane Flies)

R. Isaí Madriz

Fig. 15.1. Male of *Peringueyomyina barnardi* Alexander (South Africa).

Diagnosis

[Based on *Peringueyomyina*, the only genus in the region].

Small to large flies, length, excluding rostrum and terminalia 8.6–9.9 mm. Adults with elongated body and cylindrical abdomen (Fig. 1).

Head with mouthparts conspicuous, with elongated rostrum in some species; eyes with ommatrichia; ocelli absent; cervical sclerites prominent, often elongate, creating appearance of long neck; *Peringueyomyina* dichoptic above, contiguous ventrally, eyes with ommatrichia; antenna with 16 flagellomeres; rostrum (Fig. 1) heavily-sclerotised and elongate, exceeding combined length of head and thorax, bearing mouthparts at terminal end.

Thorax with legs as long or longer than body. Wing (Figs 2, 3) with 5 radial, 4 medial, and 2 cubital veins reaching wing margin; often patterned with irregular bands of brown infuscation

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 479–485.

in non-Afrotropical genera; with conspicuous anal lobe; usually sexually dimorphic in size, shape and brightness of bands; *Peringueyomyina* with wing membrane hyaline (Figs 2, 3), except for pterostigma and extra microtrichia on vein R_1, distal to vein R_{2+3} fork (Fig. 4), in between cells *sc* and r_1; veins with prominent microtrichia; no auxiliary crossveins.

Abdomen of *Peringueyomyina* with male terminalia (Figs 5–9) 0.3 × length of remaining abdomen; gonocoxite as long as thorax, tubular in shape, 11.2 × longer than wide, with row of stout, setiform sensilla inserted medially (Fig. 7); gonostylus as long as gonocoxite, 22.0 × longer than wide, with 34 stout setiform sensilla inserted medially (Fig. 6); aedeagus bifurcate, each ramus 24.0 × longer than wide (Figs 5, 8, 9); female terminalia (Figs 10–12) with 2 spermathecae (Fig. 12).

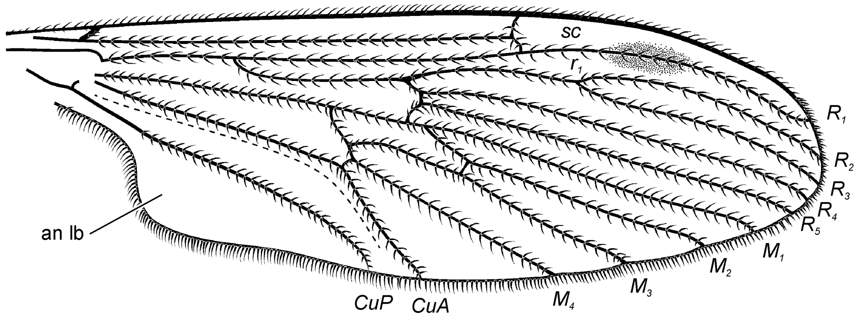
Larvae (Figs 13–18) aquatic, eucephalic with heavily sclerotised head capsule, somewhat dorsoventrally flattened; anal prolegs present on abdominal segment 9, each with 2 rows of retractile, crochet-shaped claws; *Peringueyomyina* fourth-instar larval length 18.0–26.1 mm; width 1.7–2.2 mm; dirty-white in colour; head capsule dark brown (Figs 13–15); amphipneustic; abdomen with 3 pairs of fleshy filaments (Figs 16–18), 1 on abdominal segment 8, 1 on abdominal segment 9 and 1 inserted at base of anal prolegs.

Pupa with "No cephalic crest; breathing horns small, widening to a funnel shape; leg sheaths unequal in length, the fore tarsi the shortest; venation on wing pads typically peringueyomyinan; abdominal segment eight with finger-like lobes, the other segments having a transverse row of spines near the posterior margin; cauda prominent, as in general description." (Wood 1952: 12).

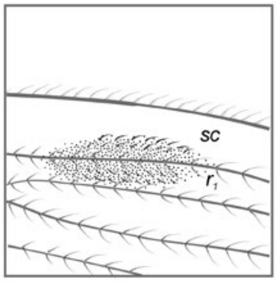
Although adult Tanyderidae are similar in appearance to Limoniidae and Tipulidae (see Chapter 14) and other long-legged flies, tanyderids can be easily differentiated through wing venation by the presence of 5 radial and 2 cubital veins.

Biology and immature stages

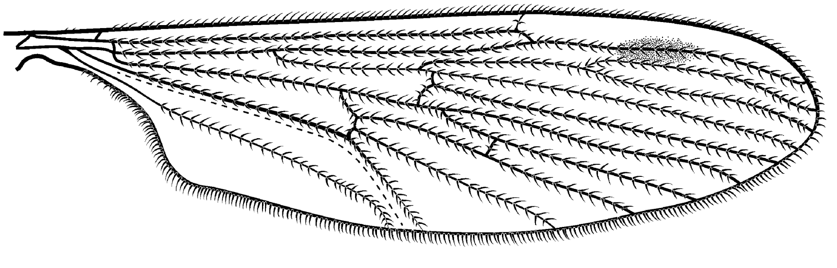
Tanyderidae are among the most ancient Diptera, with fossils dating to the Lower Jurassic (201.3 ± 0.6 MYA) (Ansorge 1994; Skibińska *et al*. 2014), but little is known regarding the biology of the family. Adults are most frequently found resting singly near



2 *Peringueyomyina* ♀



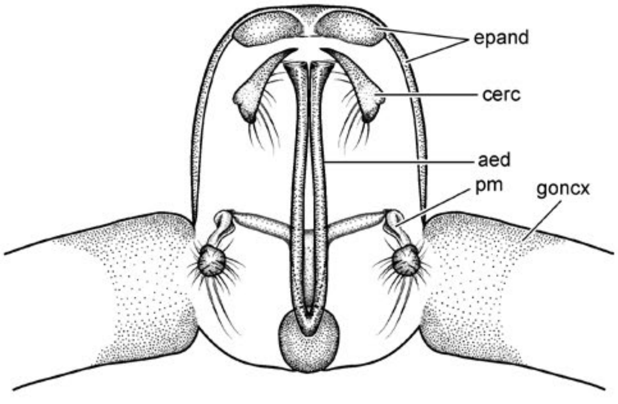
4 *Peringueyomyina*



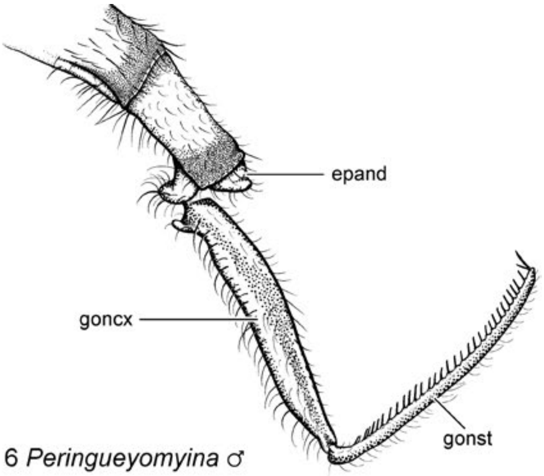
3 *Peringueyomyina* ♂

Figs 15.2–4. Wings of Tanyderidae: (2) *Peringueyomyina barnardi* Alexander, dorsal view ♀; (3) same ♂; (4) same, detail of pterostigma, both sexes.

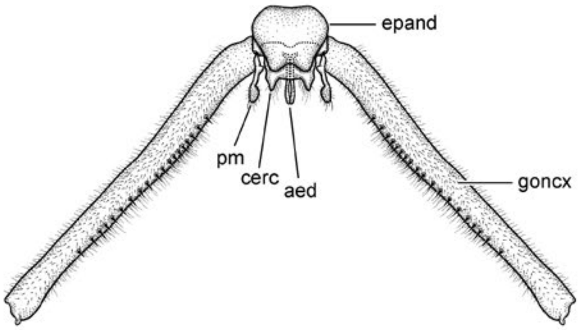
Abbreviations: an lb – anal lobe; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *sc* – subcostal cell.



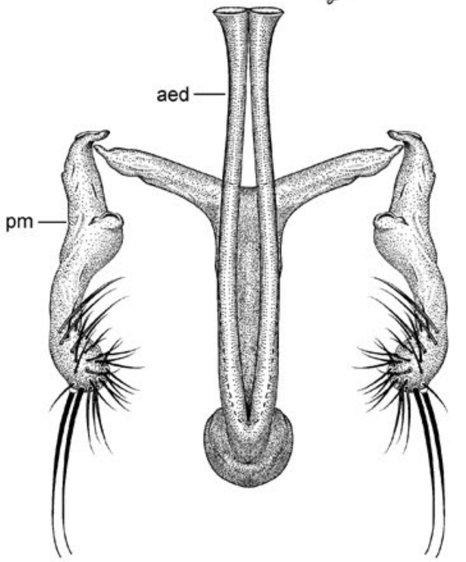
5 *Peringueyomyina* ♂



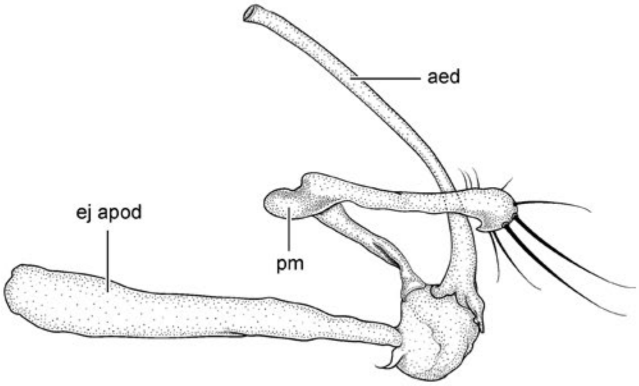
6 *Peringueyomyina* ♂



7 *Peringueyomyina* ♂



8 *Peringueyomyina* ♂



9 *Peringueyomyina* ♂

Figs 15.5–9. Male terminalia of Tanyderidae: (5) *Peringueyomyina barnardi* Alexander, terminalia in part, caudal view; (6) same, entire terminalia, lateral view of right side; (7) same, terminalia with gonostylus removed, dorsal view; (8) same, phallic structure, caudal view; (9) same, lateral view.

Abbreviations: aed – aedeagus; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm – paramere.

streams and rivers, on the underside of marginal vegetation, large rocks, or beneath bridges. Species of the non-Afrotropical genera, *Mischoderus* Handlirsch, *Protanyderus* Handlirsch and *Protoplasa* Osten Sacken, have been collected infrequently at porch lights and with the use of black lights. While most of the literature and museum collections suggest tanyderids are rare, mating swarms (Alexander 1930; Wood 1952) and a considerable number of larvae have been encountered (Wood 1952; Madriz, unpubl.), which may reflect collecting bias and our insufficient knowledge of the life history of this group.

All known species, for which the immature stages are known, have aquatic larvae. Species of the non-Afrotropical genera, *Araucoderus* Alexander, *Mischoderus*, *Protanyderus*, *Protoplasa* and *Radinoderus* Handlirsch and Afrotropical *Peringueyomyina* Alexander, are free-living, occurring in or near cobble and sand bottom streams (Alexander 1930; Anthon 1988; Exner & Craig 1976; Knight 1963; Krzremiński & Judd 1997: 282; Podeniene & Gelhaus 2013; Rose 1963; Wood 1952); species of the Australian genus *Eutanyderus* Alexander and non-Afrotropical *Radinoderus* have been found mining in soft, saturated wood along stream margins (Colless & McAlpine 1991: 742; Hinton 1966; Krzremiński & Judd 1997: 282). Observations suggest that larvae of some species migrate to drier, sandy areas prior to pupation (Alexander 1930; Knight 1964: 238; Madriz unpubl.; Wood 1952). Although the duration of the pupal stage is unknown for Afrotropical *Peringueyomyina*, this stage may last 7–15 days in other species (Alexander 1930; Madriz, unpubl.).

Peringueyomyina larvae have been found beneath large boulders in white gravel and sand pits along the edges of forest streamlets. For additional information on the biology of *Peringueyomyina barnardi* Alexander, 1921, refer to Wood (1952).

Economic significance

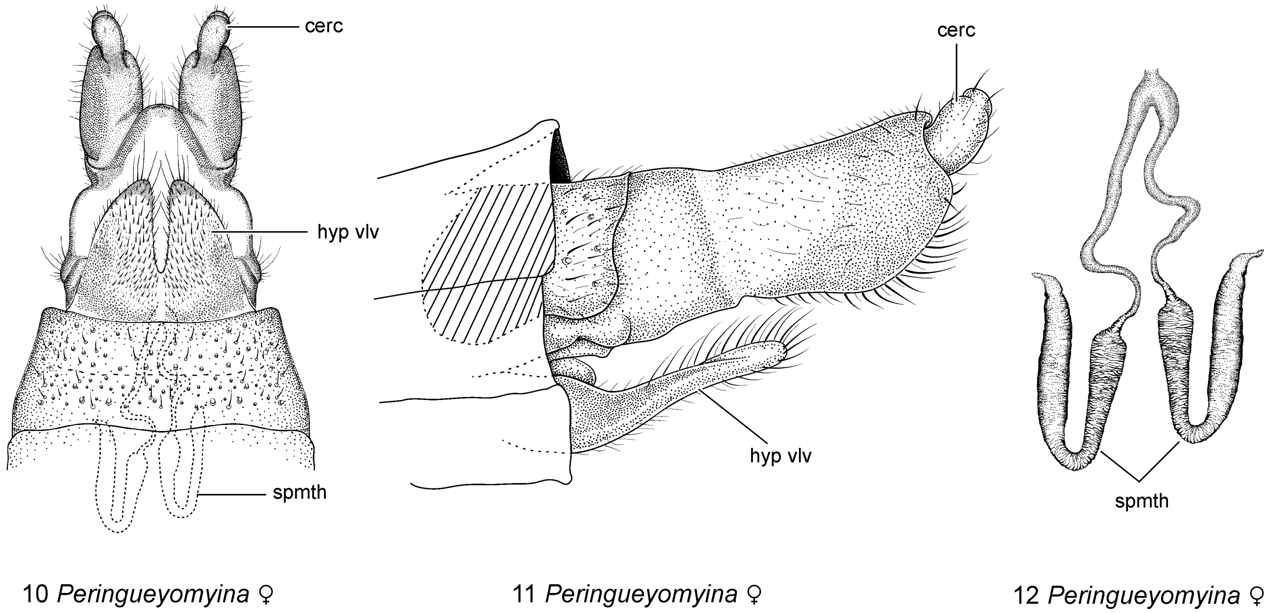
Tanyderids are not of economic or medical importance.

Classification

Tanyderids have long been described as "primitive", based primarily on their wing venation (Alexander 1930; Colless & McAlpine 1991: 742; Crampton 1930; Exner & Craig 1976; Rohdendorf 1974: 44; Williams 1933), yet few attempts have been made to place the family in a phylogenetic context. Results of morphological phylogenetic analyses have suggested a close relationship between Tanyderidae and Ptychopteridae (Hennig 1973: 55; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1342) and more recently Blephariceridae (Lambkin *et al*. 2013). In contrast, recent analyses based on molecular data strongly support a sister-group relationship between Blephariceridae and Tanyderidae + Psychodidae (Bertone *et al*. 2008; Wiegmann *et al*. 2011). There is currently no suprageneric classification within Tanyderidae. Thorough studies of adult and immature morphology are required to corroborate any previous phylogenetic hypotheses, as well as to clarify the phylogenetic placement of Tanyderidae within Diptera.

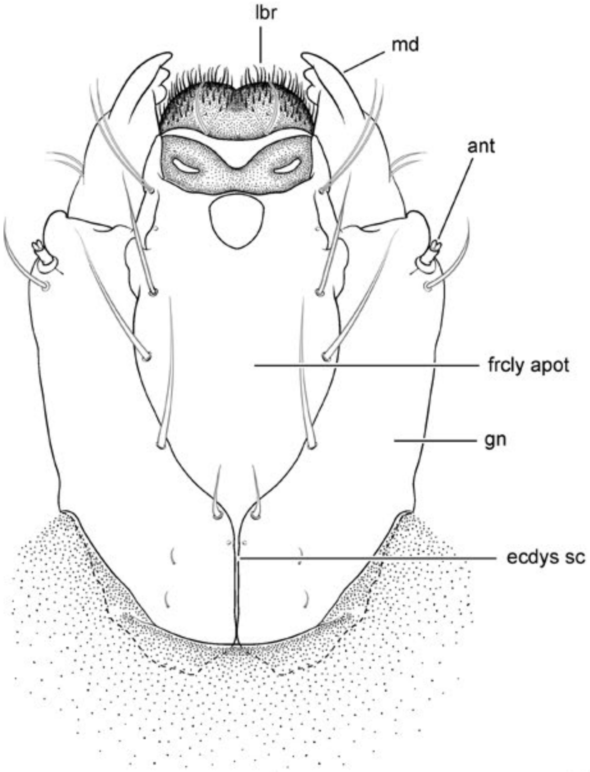
Identification

Identification of tanyderid species has traditionally relied on wing venation characters, but despite this, characters of the male (Borkent & Sinclair 2012) and female terminalia provide important information for the identification of species. Adult

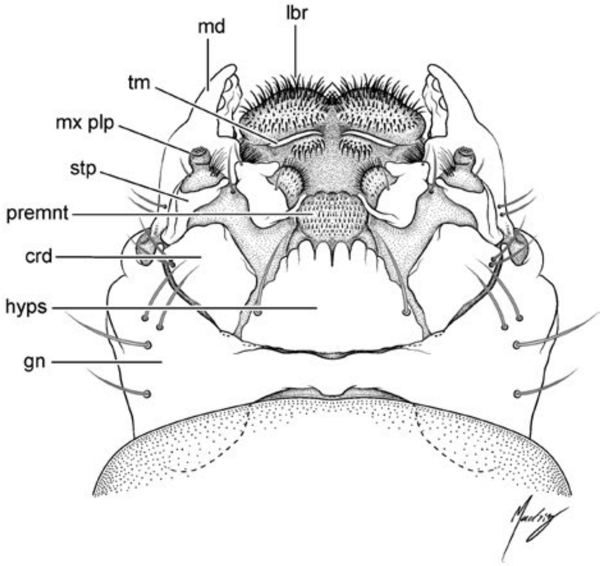


Figs 15.10–12. Female terminalia and spermathecae of Tanyderidae: (10) *Peringueyomyina barnardi* Alexander, terminalia ventral view; (11) same, lateral view; (12) same, spermathecae, ventral view.

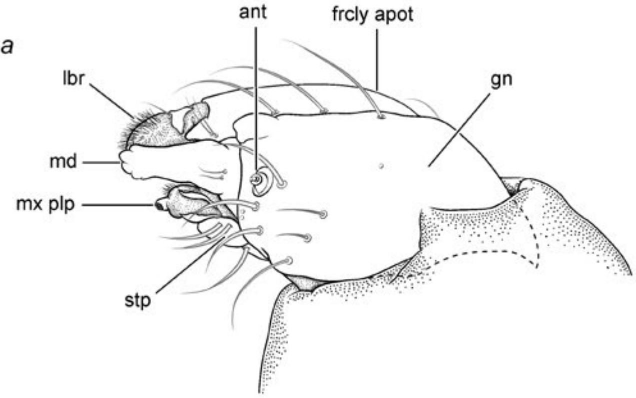
Abbreviations: cerc – cercus; hyp vlv – hypogynial valve; spmth – spermatheca.



13 *Peringueyomyina*



14 *Peringueyomyina*



15 *Peringueyomyina*

Figs 15.13–15. Larval head capsule of Tanyderidae: (13) *Peringueyomyina barnardi* Alexander, dorsal view; (14) same, ventral view; (15) same, lateral view.

Abbreviations: ant – antenna; crd – cardo; ecdys sc – ecdysial scar; frcly apot – frontoclypeal apotome; gn – gena; hyps – hypostoma; lbr – labrum; md – mandible; mx plp – maxillary palpus; premnt – prementum; stp – stipes; tm – torma.

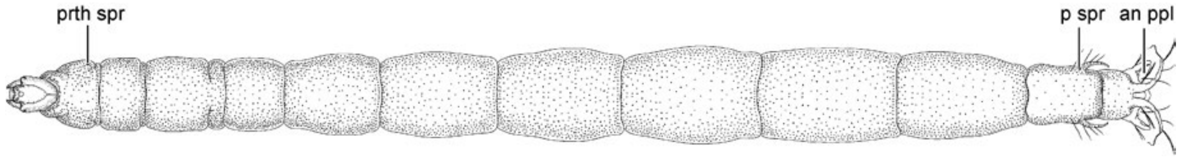
Tanyderidae are normally collected into paper packets for later mounting (see Chapter 2).

Synopsis of the fauna

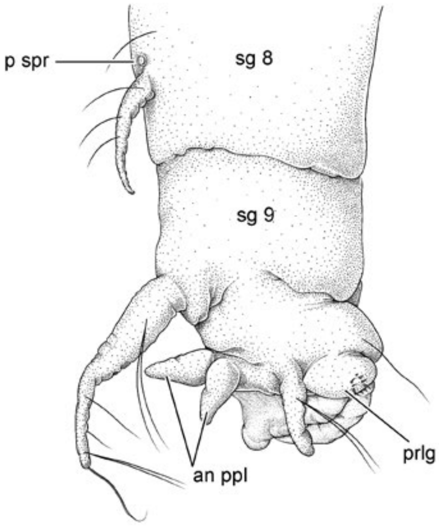
The family currently comprises 38 extant species, divided into 10 genera globally, with the greatest diversity found in the Southern Hemisphere. In the Afrotropical Region the family is represented by the monotypic genus *Peringueyomyina*. Its geographical range is restricted to Fynbos in the ancient Cape Fold Mountains of South Africa (Duxbury & Barraclough 1994; Kirk-Spriggs & Stuckenberg 2009: 178; Stuckenberg 1962).

Larvae identified as *Protoplasa fitchii* Osten Sacken, 1859 were sampled during several studies of the macro-invertebrate fauna of the Ikpoba River in southern Nigeria (Victor & Ogbeibu 1985, 1986, 1991; Ogbeibu & Victor 1989), but larval identifications have not been corroborated. This would represent a significant range extension for the genus *Protoplasa*, currently restricted to the eastern Nearctic Region and for this reason the genus is not listed below as occurring in the Afrotropical Region.

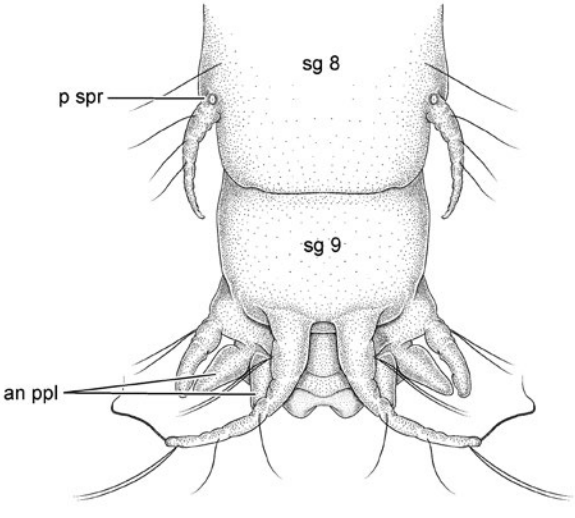
Peringueyomyina **Alexander.** An endemic monotypic genus. The single species, *P. barnardi*, is known only from South Africa and its conservation status was reviewed by Duxbury & Barraclough (1994) (see Chapter 10). Among tanyderids, *P. barnardi* is easily identifiable by its unique tubular rostrum bearing small mouthparts apically. It is also the only known extant tanyderid without a patterned wing. In *P. barnardi*, there is a small pterostigma near the wing apex (Fig. 4). Wing venation is strikingly similar to the fossil *Macrochile spectrum* Loew, 1851 from Baltic amber.



16 *Peringueyomyina*



17 *Peringueyomyina*



18 *Peringueyomyina*

Figs 15.16–18. Larva habitus and terminal segments of Tanyderidae: (16) larval habitus of *Peringueyomyina barnardi* Alexander, dorsal view; (17) same, terminal segments 8 and 9, lateral view; (18) same, dorsal view.

Abbreviations: an ppl – anal papillae; p spr – posterior spiracle; prlg – proleg; prth spr – prothoracic spiracle; sg – segment.

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BLEPHARICERIDAE 16

(Net-winged Midges or Torrent Midges)

Gregory W. Courtney

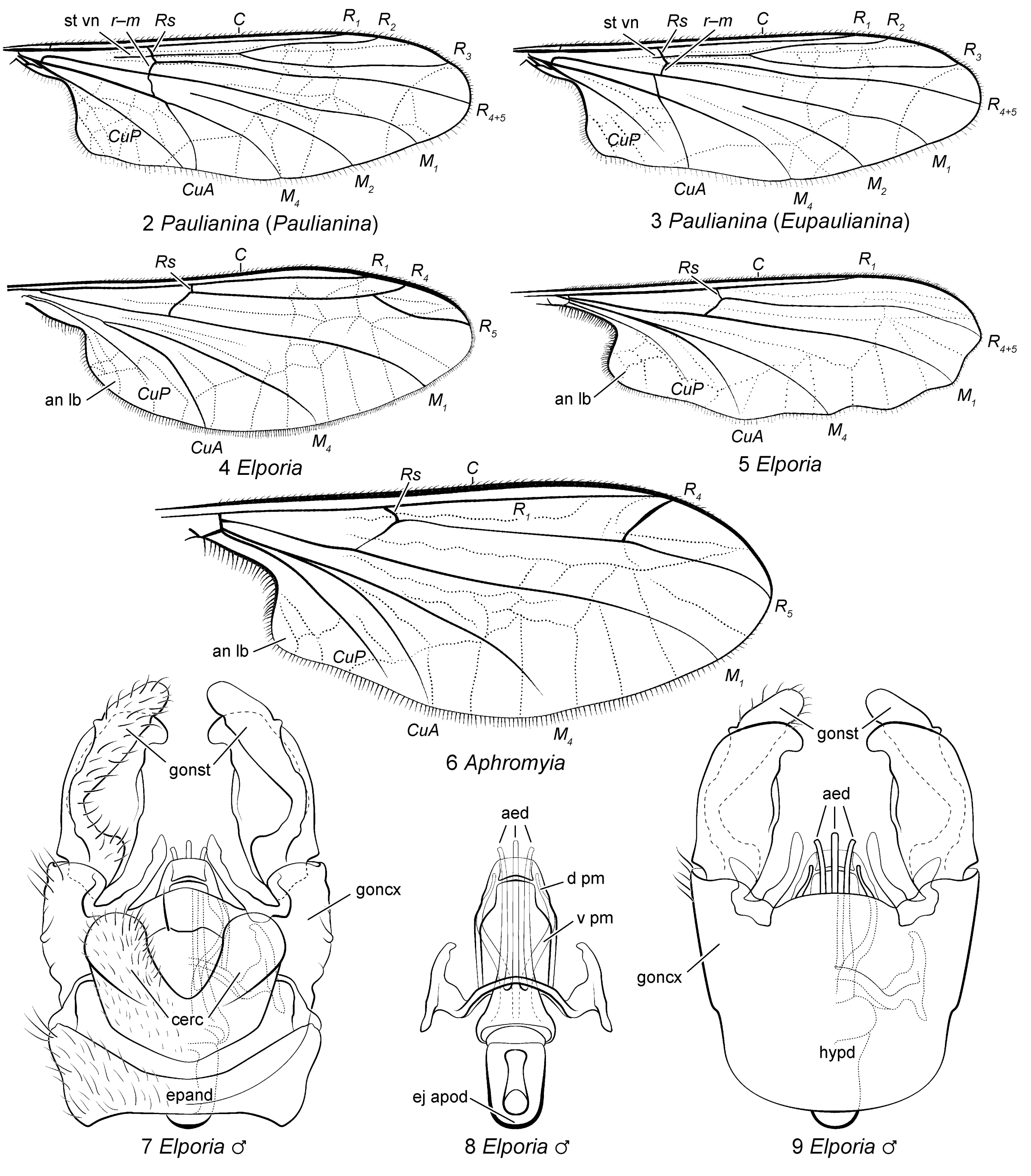
Fig.16.1. Male of *Edwardsina* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized nematoceran flies (wing length: 4–8 mm) (Fig. 1). Adults slender, with elongate legs (Fig. 1); most species dull brown or grey, without conspicuous patterns; some species with silvery, or opalescent pruinescence; mouthparts reduced, or well-developed, often sexually dimorphic; palpus with 3–5 palpal segments; head dichoptic to holoptic, often sexually dimorphic; dorsal ocelli present; antenna elongate, with 11–13 flagellomeres; wing with net-like pattern of folds; male terminalia dorsoflexed; female with 3 spermathecae, spherical to oblong.

Larva cylindrical to ovoid, ventrally flattened (Figs 10–15, 18–24); respiratory system apneustic; eucephalous, cranium well-developed dorsally, reduced ventrally to accommodate enlarged mouthparts; mouthparts include robust mandibles and enlarged maxillae, bearing prominent lacinial and galeal

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 487–496.



2 *Paulianina* (*Paulianina*)

3 *Paulianina* (*Eupaulianina*)

4 *Elporia*

5 *Elporia*

6 *Aphromyia*

7 *Elporia* ♂

8 *Elporia* ♂

9 *Elporia* ♂

Figs 16.2–9. Wings and male terminalia of Blephariceridae: (2) right wing of *Paulianina* (*Paulianina*) *umbra* Stuckenberg, dorsal view; (3) same, *P.* (*Eupaulianina*) *alexanderi* Stuckenberg; (4) same, *Elporia flavopicta* (Edwards); (5) same, *El. uniradius* Barnard; (6) same, *Aphromyia stuckenbergi* Courtney; (7) male terminalia of *El. uniradius*, dorsal view; (8) same (aedeagus and parameres) of *El. uniradius*; (9) same, *El. uniradius*, ventral view.

Abbreviations: aed – aedeagus; an lb – anal lobe; *C* – costal vein; cerc – cercus; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; d pm – dorsal paramere; ej apod – ejaculatory apodeme; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; st vn – stump vein; v pm – ventral paramere.

lobes and maxillary palpus (Figs 16, 17); body with six divisions, including cephalic division (fused head, thorax and abdominal segment 1) and anal division (abdominal segments 7–10); each division with single suctorial disc midventrally and paired gill tufts ventrolaterally (Figs 11, 22, 24); most species with 1 lateral proleg each side; anal division ventrally with 4 thick, digitiform anal papillae.

Pupa semiovoid, ventrally flattened, slightly to strongly convex dorsally (Figs 25–33), attached immovably to substrate; branchial sclerite (fused pronotum and mesonotum), bears pair of distinct respiratory organs anterodorsally; respiratory organ transverse, comprising either 4 thin lamellae, or complex series of elevated and secondarily differentiated integument or swellings (Figs 34, 36, 38); abdominal integument dorsally with microtubercles, variably shaped and arranged (Figs 35, 37, 39); abdominal segments 4–6 each with pair of adhesive pads ventrolaterally.

Although adults of some species superficially resemble certain Tipulidae *sensu lato* (see Chapter 14), Chironomidae (see Chapter 35) and other nematocerous flies, they are separated by wing venation. Pupae may be confused with those of mountain midges (Deuterophlebiidae – non-Afrotropical), but their respiratory organs differ (deuterophlebiid respiratory organs with common base and 3–4 tubular filaments). Although true suctorial discs are unique to larval blephariceridis, some Psychodidae larvae (*Neomaruina* Vaillant, *Neotelmatoscopus* Tonnoir) (see Chapter 24), have superficially similar pad-like structures ventrally.

Biology and immature stages

Net-winged midges are among the most highly specialised of aquatic flies. The immature stages are highly modified to life in flowing water. Larvae (Figs 10–15, 18–24) are remarkable in the presence of a complex cephalic division (fused head, thorax and abdominal segment 1) and the series of ventral suctorial discs. Pupae (Figs 25–33) are also distinctive, being streamlined, somewhat compressed, and attached immovably to the substrate. Despite their distinctive appearance, wide distribution, trophic significance and potential as bioindicators, data regarding net-winged midges remain scattered and incomplete.

Net-winged midges occur in and around a variety of streams, from small headwater seepages to large rivers. Larvae attach to rocks, through the action of their six ventral suctorial discs, which function on smooth substrata (*e.g.*, water-polished rocks), but generally not on wood, leaves, or sedimentary rocks. Larval locomotion is slow and complex, involving predictable sequences of suctorial disc attachment and detachment (Frutiger 1998). Larvae feed exclusively on periphyton, especially diatoms (Alverson & Courtney 2002; Alverson *et al*. 2001; Dudley *et al*. 1990; Georgian & Wallace 1983).

Pupation usually occurs on the upper, downstream faces of rocks, on emergent rocks in splash zones, or along stream margins. The pupal stage typically lasts 2–3 weeks, but can vary with species and stream temperature. Pupae remain attached until eclosion. The emerging adult splits the pupal ecdysial lines by applying downward pressure against the substrate. Field and laboratory observations indicate that adults of at least some species cannot simply crawl out of the pupal case, relying partly on the aid of current or an air bubble. Because the wings develop to full size within the pupal case and merely unfold during emergence, adults can fly immediately upon reaching the waters' surface.

Adult blephariceridis rarely venture beyond the riparian zone, where they frequent the undersides of branches extending over the stream, or beneath wet, overhanging and emergent rocks. Adult *Paulianina* Alexander are known to also use spiders' webs as resting sites for individuals, or chains of adults (Stuckenberg 1958). Females of some species are insect predators, sucking the hemolymph of other insects. The food of males and non-mandibulate females, including those of most Afrotropical species, is unknown, but nectarivory is likely. Adults of most species are short-lived (1–2 weeks). Mating presumably occurs shortly after eclosion and copulating individuals often rest on riparian vegetation, or emergent rocks. Ovipositing females usually cement small clusters of eggs to wet rocks, or just beneath the water surface. In some species, the female will crawl beneath the water to oviposit on submerged rocks. Genetic studies suggest that most populations, of at least some species, are endemic to individual stream catchments (Wishart & Hughes 2001, 2003).

Detailed studies of life-history are not available for most Afrotropical blephariceridis, with information on the majority of species based primarily on collection records. Temperate species of net-winged midge are mostly univoltine, whereas tropical species may be multivoltine, or exhibit highly asynchronous development. Collection records from South Africa (*e.g.*, Barnard 1947; Edwards 1915, 1933; Stuckenberg 1955, 1956: 391, 1961, 1962), suggest that most species of *Elporia* Edwards are univoltine, but with two major phenological patterns: one with egg hatch and most larval development in spring and early summer (*e.g.*, *El. natalensis* Stuckenberg, 1955); and the other with egg hatch in autumn, or early winter and most larval development during winter (*e.g.*, *El. marieps* Stuckenberg, 1961). Data on *Paulianina* (*e.g.*, Stuckenberg 1958), suggest that Malagasy species are quite different, with many species probably bivoltine or multivoltine and their life-histories influenced, at least partly, by precipitation. During the Malagasy dry season (April–November), most species probably survive in egg diapause. With the onset of the rainy, warm season (December–March), egg-hatch begins and probably continues for several weeks, leading to asynchronous life-histories (Courtney 2003: 705). Additional details regarding general blepharicerid biology are provided elsewhere (Alexander 1963; Courtney 2000*a*: 15, 2000*b*, 2003: 705; Hogue 1981: 191; Zwick 1977).

Economic significance

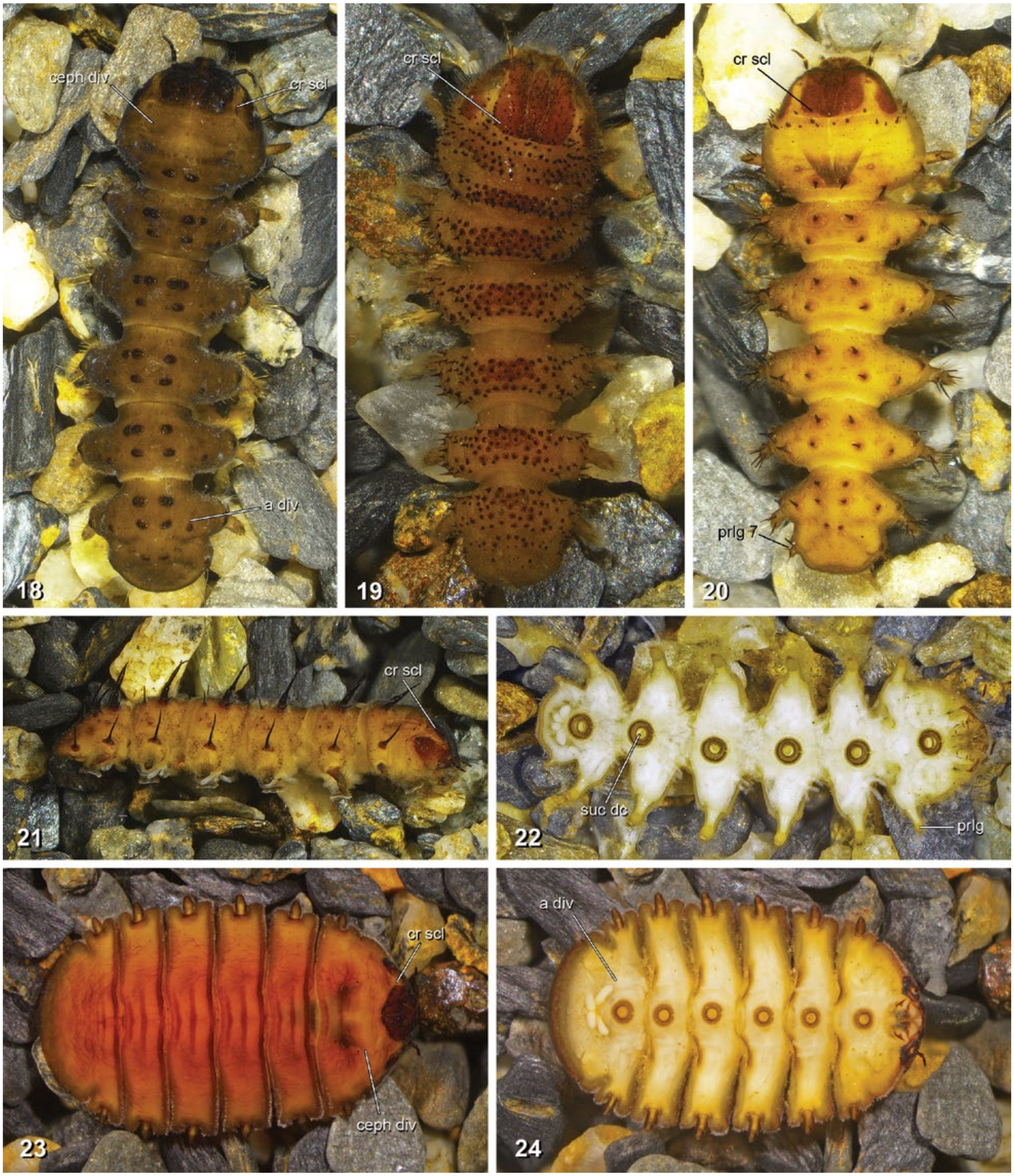
Although sometimes considered rare, blephariceridis can be locally abundant (Stuckenberg 1955, 1956; Wishart & Hughes 2001) and important in the trophic relationships of stream ecosystems (Anderson 1992). These flies may also play an important role as fish food, at least seasonally (Courtney & Duffield 2000). Furthermore, because blephariceridis inhabit clean, cool, well-oxygenated streams, these flies are potentially valuable bioindicators of water quality (Courtney *et al*. 2008: 747; Lenat 1993).

Classification

The placement of Blephariceridae within the wider context of Diptera has been problematic. Cladistic hypotheses based

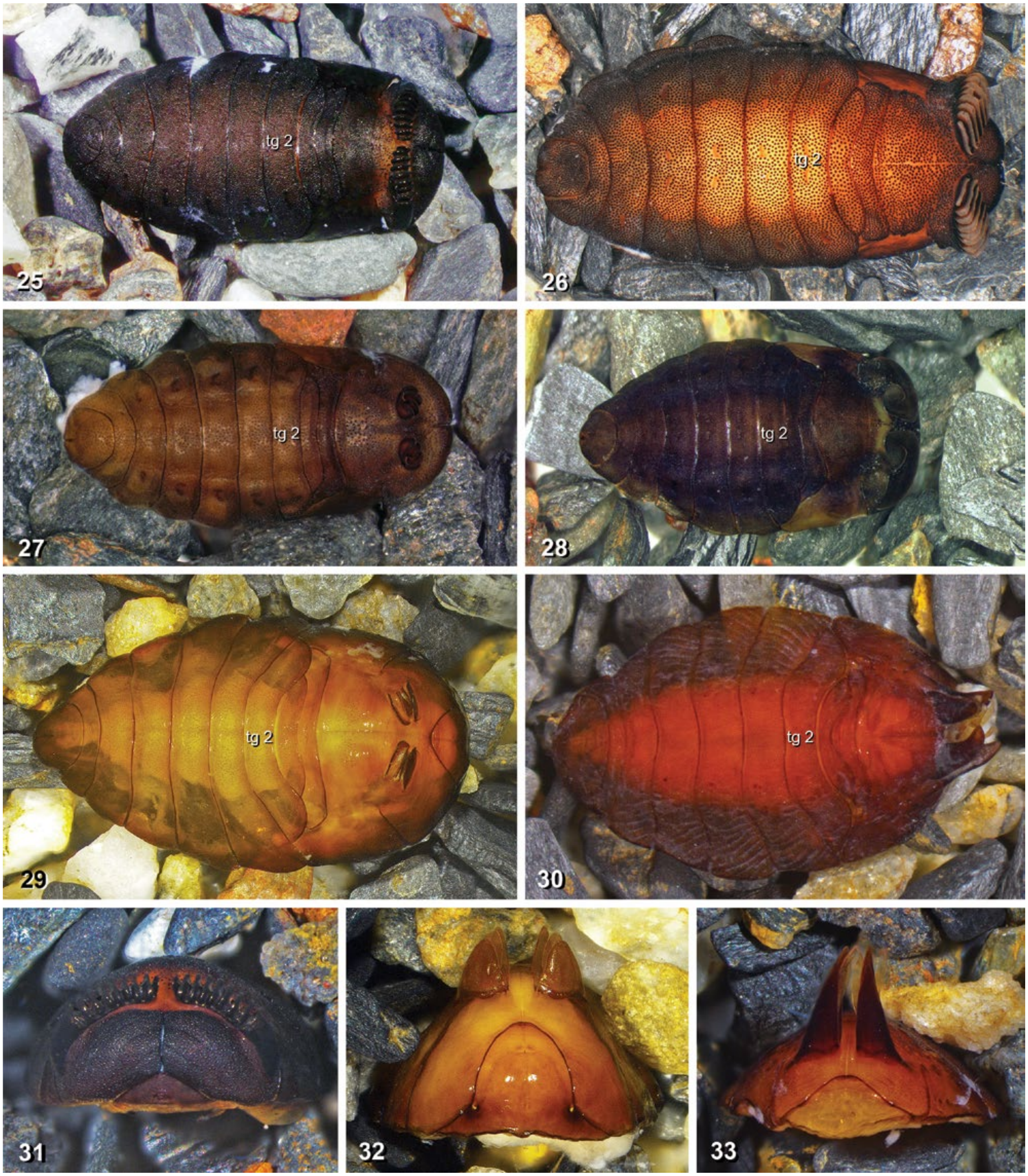
Figs 16.10–17. Larval habitus and features of Blephariceridae (Edwardsininae): (10) larval habitus of *Paulianina* (*Paulianina*) *umbra* Stuckenberg, dorsal view; (11) same, ventral view; (12) same, *P*. (*P.*) *ingens* Stuckenberg, dorsal view; (13) same, *P*. (*Eupaulianina*) *rivalis* Stuckenberg; (14) *P.* (*Eu*.) *alexanderi* Stuckenberg, dorsal view; (15) same, ventral view; (16) mouthparts of *P*. (*P*.) *umbra*, oblique ventral view; (17) same, *P*. (*Eu*.) *silva* Stuckenberg, ventral view.

Abbreviations: a div – anal division; an ppl – anal papilla; ceph div – cephalic division; cr scl – cranial sclerite; gll – gill; int seg – intercalary segment; lab – labium; lbr – labrum; lc – lacinia; md – mandible; mx plp – maxillary palpus; prlg – proleg; suc dc – suctorial disc.



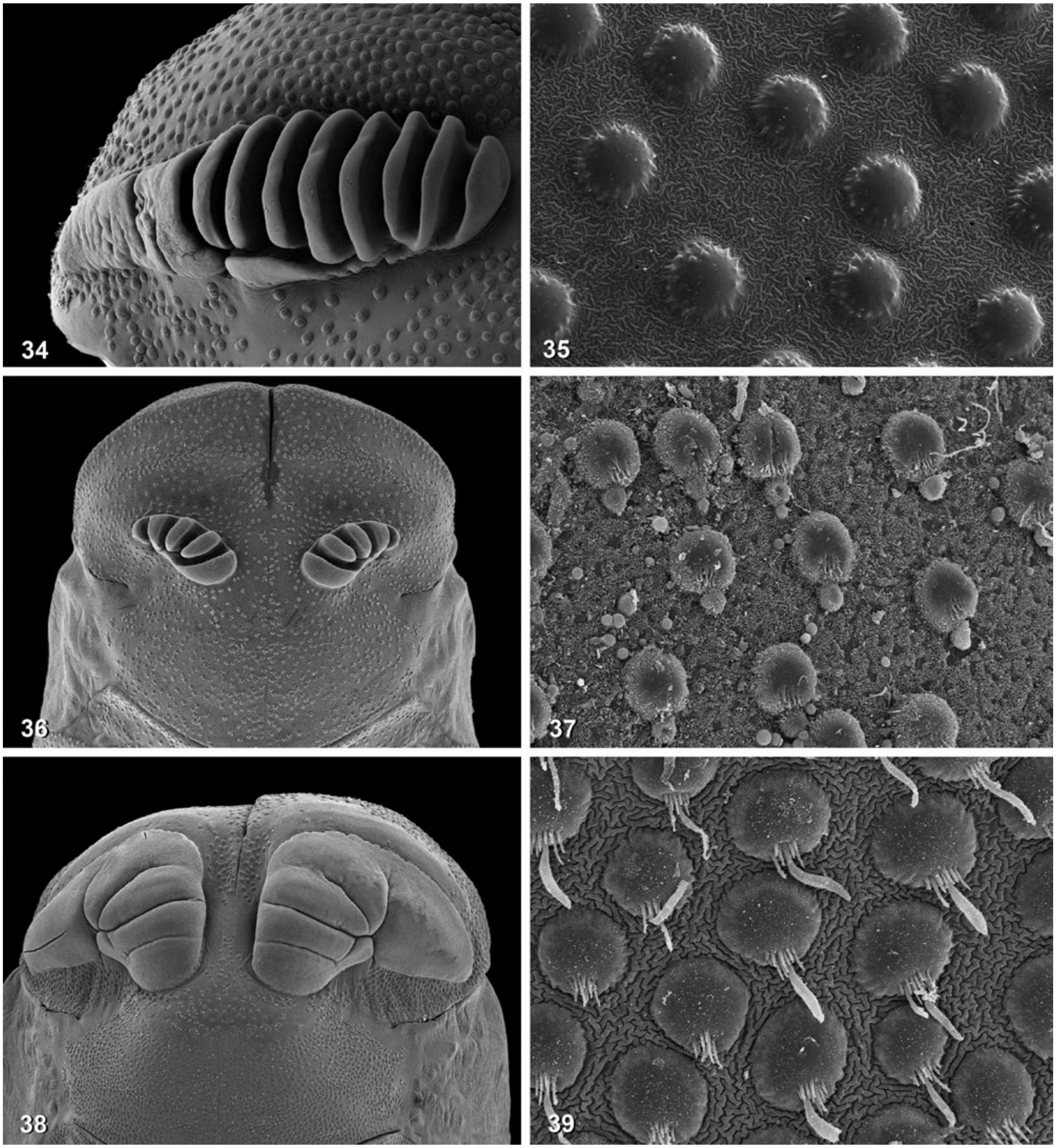
Figs 16.18–24. Larval habitus of Blephariceridae (Blepharicerinae): (18) *Elporia capensis* Edwards, dorsal view; (19) same, *El. spinulosa* Edwards; (20) same, *El. copra* Barnard; (21) *El. hystrix* (Edwards), lateral view; (22) *El. uniradius* Barnard, ventral view; (23) *Aphromyia stuckenbergi* Courtney, dorsal view; (24) same, ventral view.

Abbreviations: a div – anal division; ceph div – cephalic division; cr scl – cranial sclerite; prlg – proleg; suc dc – suctorial disc.



Figs 16.25–33. Pupal habitus of Blephariceridae: (25) *Paulianina* (*Paulianina*) *umbra* Stuckenberg, dorsal view; (26) same, *P.* (*P.*) sp.; (27) same, *P.* (*Eupaulianina*) *pamela* Stuckenberg; (28) same, *P.* (*Eu.*) *alexanderi* Stuckenberg; (29) same, *Elporia saltatrix* Stuckenberg; (30) same, *Aphromyia stuckenbergi* Courtney; (31) *P.* (*P.*) *umbra*, frontal view; (32) same, *El. saltatrix*; (33) same, *A. stuckenbergi*.

Abbreviation: tg – tergite.



Figs 16.34–39. Scanning electron micrographs of pupal Blephariceridae (all dorsal views): (34) left respiratory organ of *Paulianina* (*Paulianina*) *umbra* Stuckenberg; (35) same, abdominal microsculpture indicating papillae; (36) thorax and respiratory organs of *P.* (*Eupaulianina*) *pamela* Stuckenberg; (37) same, abdominal microsculpture indicating papillae; (38) thorax and respiratory organs of *P.* (*Eu.*) *silva* Stuckenberg; (39) same, abdominal microsculpture indicating papillae.

on morphological data (*e.g.*, Courtney 1991; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1333), have consistently placed Blephariceridae as sister-group to Deuterophlebiidae (non-Afrotropical), forming the infraorder Blephariceromorpha (sometimes including the non-Afrotropical Nymphomyiidae). More recent studies using exclusively (Bertone *et al*. 2008) or primarily molecular data (Wiegmann *et al*. 2011), however, provide compelling evidence that blephariceridsmay reside in the infraorder Psychodomorpha, as sister-group to the Tanyderidae + Psychodidae.

Blephariceridae are currently known from 30 genera and nearly 330 species, with representatives in all zoogeographical regions, except Antarctica (and including several oceanic islands such as Madagascar, New Zealand, Sri Lanka). The family comprises two subfamilies, Edwardsininae and Blepharicerinae. The subfamily Edwardsininae exhibits a largely Gondwanan distribution, being restricted to the Southern Hemisphere (Australasian Region, southern Neotropical Region and Afrotropical Region (Madagascar)), whereas Blepharicerinae occur in both hemispheres.

The Afrotropical blepharicerid fauna is comprised of three described genera, the Malagasy edwardsinine *Paulianina*, South African blepharicerine *Elporia* and recently described Malagasy blepharicerine *Aphromyia* (Courtney 2015). *Paulianina* is further subdivided into two subgenera: *Paulianina sensu stricto* and *P*. (*Eupaulianina* Stuckenberg). All genera have relatively restricted distributions, with *Aphromyia* and *Paulianina* endemic to Madagascar and *Elporia* occurring only in South Africa. Immature stages of an unnamed species are known from the Kumbo massif (Banso Mountains) in north-west Cameroon (Germain *et al*. 1967) and nearby parts of southern Nigeria (Stuckenberg *in litt*., 2003). Although perhaps related to *Elporia*, the affinities of this species remain uncertain until adults can be studied.

Identification

Much of our knowledge on Afrotropical blepharicerids is based on several short notes, species descriptions and regional surveys (*e.g.*, Alexander 1952, 1956; Barnard 1947; Courtney 2003: 702, 2015; Edwards 1912, 1915, 1916, 1932, 1933; Germain *et al*. 1967; Paulian 1953; Stuckenberg 1958, 1961, 1962). Of these, the most comprehensive studies focused on the fauna of South Africa's Western Cape Province (Barnard 1947), KwaZulu-Natal Province (Stuckenberg 1955) and the former Transvaal (Stuckenberg 1961) and of Madagascar (Stuckenberg 1958). All of these comprehensive treatments are well-illustrated and contain identification keys to adults, pupae and/or larvae of the known resident fauna. All life stages should be preserved initially in ethanol, with adults later dried and pinned (*e.g.*, Courtney 2000*b*; see Chapter 2).

Keys to genera of Afrotropical Blephariceridae

Adults

1\. Wing venation normal; costal vein (*C*) encircling entire wing; 3 branches of radial sector and 2 branches of medial sector reaching wing margin; vein M_2 present; vein *Rs* with backward stump vein (Figs 2, 3); fore, mid and hind legs of approximately same length; fore tibia with single spur; female terminalia with cercus simple (EDWARDSININAE) . . . . *Paulianina* Alexander 2

– Wing venation reduced; costal vein (*C*) ending near apex of wing; 1 or 2 branches of radial sector and 1 branch of medial sector reaching wing margin; vein M_2 absent; vein *Rs* without stump vein (*e.g.*, Figs 4–6); hind leg much longer than fore and mid legs; fore tibia lacking spurs; female terminalia with cercus ending in small, finger-shaped distal lobe (BLEPHARICERINAE) 3

2\. Palpus 4-segmented; radial sector of wing with long stump vein, length greater than length of *r–m* crossvein (Fig. 2); tibial spur formula: 1 : 1 : 1 . . . . *Paulianina* Alexander *sensu stricto*

– Palpus 5-segmented; radial sector of wing with short stump vein, length equal to or shorter than length of *r–m* crossvein (Fig. 3); tibial spur formula: 1 : 0 : 1. . . . . *Paulianina* (*Eupaulianina* Stuckenberg)

3\. Head dichoptic or holoptic; eye divided laterally into upper and lower divisions; anal lobe of wing rounded (Fig. 4) or angular (Fig. 5) and third branch of radius divided (Fig. 4) or simple (Fig. 5); tibial spur formula: 0 : 0 : 2 (South Africa) . . . .*Elporia* Edwards

– Head dichoptic; eyes simple and undivided; anal lobe of wing angular and third branch of radius divided (Fig. 6); tibial spur formula: 0 : 0 : 1 (Madagascar) . . . . *Aphromyia* Courtney

Larvae

1\. Posterior margin of cranial sclerite complete dorsolaterally; intercalary segments distinct (Figs 10, 12–14) (EDWARDSININAE). . . . . *Paulianina* Alexander 2

– Posterior margin of cranial sclerite usually split dorsolaterally; intercalary segments absent (*e.g.*, Figs 18–21, 23) (BLEPHARICERINAE) 3

2\. Lacinia enlarged, approximately ½ length of head (Figs 11, 16); all intercalary segments complete (Figs 10, 12); anal division trilobed, without prolegs. . . . . *Paulianina* Alexander *sensu stricto*

– Lacinia not enlarged, approximately ⅕ length of head (Figs 15, 17); first intercalary segment divided medially (Figs 13, 14); anal division with single median lobe and lateral prolegs . . . . *Paulianina* (*Eupaulianina* Stuckenberg)

3. Body cylindrical; dorsal surface usually with plates, spines and/or stout setae (Figs 18–21); antenna with 2–3 segments (if 2, then segments separated by membranous region); proleg 7 usually prominent (visible dorsally) (Fig. 20) (South Africa) . . . . *Elporia* Edwards

– Body flattened dorsoventrally or "chiton-shaped"; dorsal surface without plates, spines and/or stout setae (except for stout setae on dorsolateral margins of each body division) (Figs 23, 24); antenna 2-segmented, without membranous region; proleg 7 reduced (not visible dorsally) (Fig. 23) (Madagascar) . . . . *Aphromyia* Courtney

Pupae

1. Respiratory organ variable, comprised of 5 or more swellings or lamellae, most lamellae oriented obliquely or parallel to longitudinal axis of body (Figs 25–28, 31, 34, 36, 38); abdominal tergite 2 large, extended laterally to margin of pupa (Figs 25–28) (Madagascar) (EDWARDSININAE) . . . . *Paulianina* Alexander 2

– Respiratory organ comprised of 4 erect lamellae, each lamella oriented perpendicular to longitudinal axis of body (*e.g.*, Figs 29, 30, 32, 33); abdominal tergite 2 not extended laterally to margin of pupa (*e.g.*, Figs 29, 30) (BLEPHARICERINAE) 3

2. Respiratory organ with 8–9 distinct lamellae (Figs 25, 26, 31, 34); body shape elongate-ovoid, not compressed dorsoventrally; abdominal papillae without spinelets or projections (Fig. 35) . . . . *Paulianina* Alexander *sensu stricto*

– Respiratory organ with 5–7 swellings (or thick lamellae) (Figs 27, 28, 36, 38); body shape ovoid, strongly compressed dorsoventrally (in most species); abdominal papillae with well-developed spinelets and/or projections (Figs 37, 39) . . . . *Paulianina* (*Eupaulianina* Stuckenberg)

3. Respiratory lamellae short, length subequal to width; inner and outer lamellae of subequal width (Figs 29, 32) (South Africa) . . . . *Elporia* Edwards

– Respiratory lamellae elongate, at least 3 × longer than wide; inner lamellae much narrower than outer lamellae (Figs 30, 33) (Madagascar) . . . . *Aphromyia* Courtney

Synopsis of the fauna

***Aphromyia* Courtney** (Blephariceriinae)**.** An endemic monotypic genus. The single species, *A. stuckenbergi* Courtney, 2015, is known only from the Central highlands (Andringitra massif) of Madagascar. Due to habitat degradation, this species may now be extinct. Recent attempts to recollect the species at the type locality have proved unsuccessful.

***Elporia* Edwards** (Blepharicerinae)**.** An endemic genus, known from 19 described species, restricted to the Cape Fold Mountains and Great Escarpment of South Africa. There is a possibility that further species may be discovered. Identification keys to species from various subregions of South Africa were provided by Barnard (1947) and Stuckenberg (1955, 1961).

***Paulianina* Alexander** (Edwardsininae)**.** An endemic genus of eight described species restricted to Madagascar, including three species in the subgenus *Paulianina sensu stricto* and five species in the subgenus *P.* (*Eupaulianina*). Numerous undescribed species from both subgenera are known. Several species are known only from a single life stage. All species occur from the Central highlands and Evergreen rainforest biomes on the east side of the island. Due to habitat degradation, it is likely that some of these species are extinct. Identification keys to species were provided by Stuckenberg (1958).

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BIBIONIDAE 17

(March Flies or Lovebugs)

John Skartveit

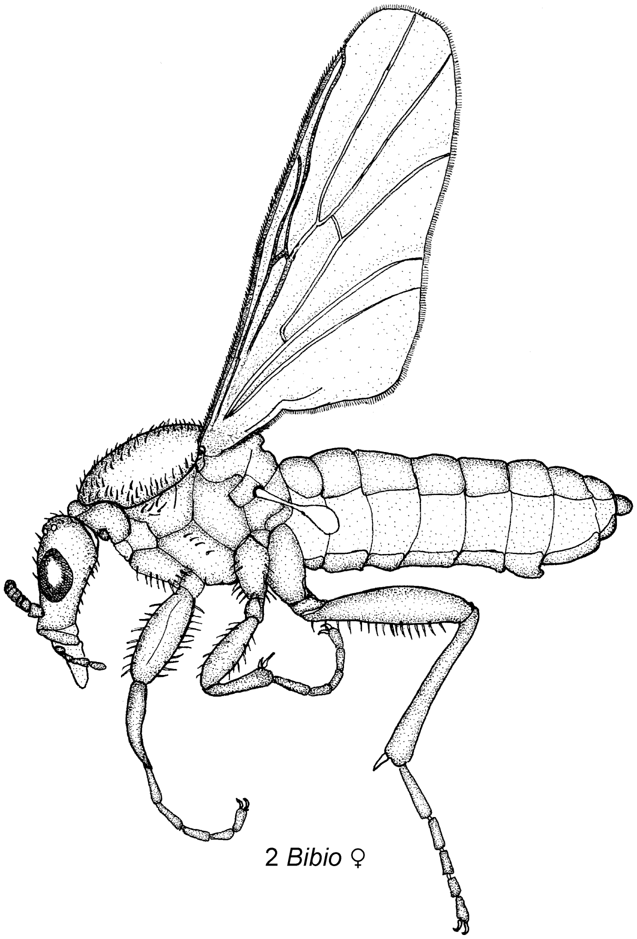
Fig. 17.1. Female of *Plecia* sp. (Tanzania) (photograph © S.A. Marshall).

Diagnosis

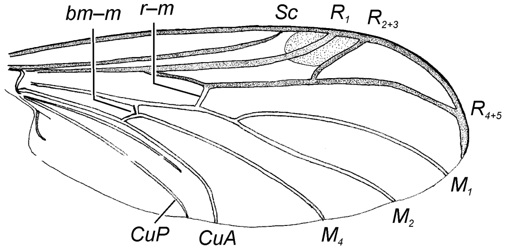
Moderately small- to medium-sized flies (body length: 2.5–15.0 mm), with relatively long legs, rather robust bodies and broad wings. Sexual dimorphism pronounced: males generally black, except thorax, which may be reddish; females often yellowish, brownish or reddish.

Head (Figs 2, 6, 7) strongly sexually dimorphic: male holoptic with compound eye subdivided into dorsal and ventral sections; female broadly dichoptic; compound eye rather small and rounded, usually with prominent intraocular setae, but may be absent, especially in females; ventral section of male eye homologous with female eye (Zeil 1983*a*), with smaller ommatidia, those of dorsal section enlarged; 3 ocelli situated on prominent tubercle posterodorsally on head; antennae shorter than head with 6–14 antennomeres, subcylindrical, situated anterior to margin of compound eye; scape short and transverse; pedicel often slightly enlarged, more or less inverted-conical; 4–12 subspherical to subcylindrical flagellomeres, usually somewhat wider than long, lacking long setae or conspicuous, large sensillae; distal flagellomere often smaller than others, 2 or 3 outer flagellomeres may be partially fused and poorly defined; palpus 4- or 5-segmented, approximately as long as antenna; some species of *Plecia* Wiedemann and *Dilophus* Meigen, with moderately elongate rostrum; proboscis

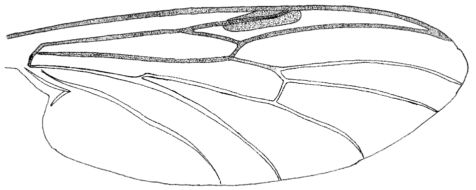
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 497–504.



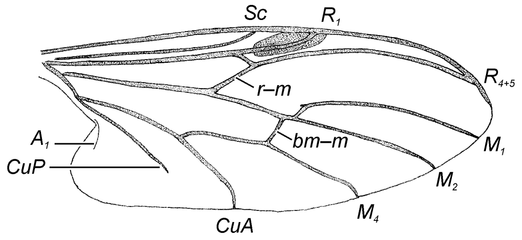
2 *Bibio* ♀



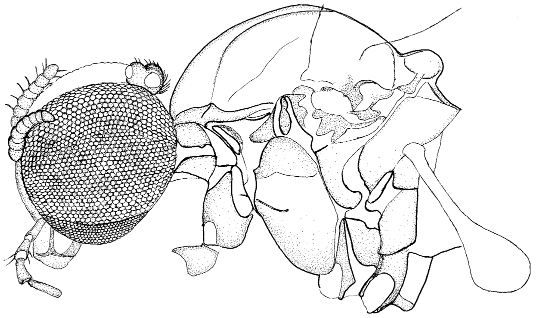
3 *Plecia*



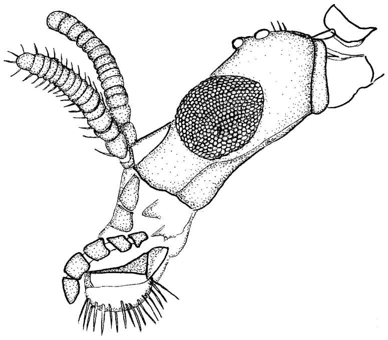
4 *Bibio*



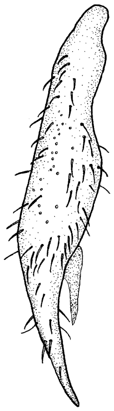
5 *Dilophus*



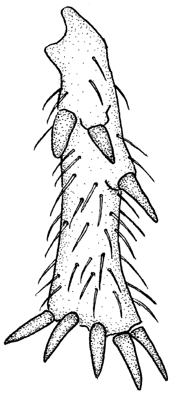
6 *Plecia* ♂



7 *Dilophus* ♀



8 *Bibio*



9 *Dilophus*

Figs 17.2–9. Habitus, wings, heads and tibiae of Bibionidae: (2) habitus of *Bibio breviceps* Loew ♀, lateral view (most setation omitted); (3) wing of *Plecia bilobata* Hardy, dorsal view; (4) same, *Bibio* sp. (non-Afrotropical); (5) same, *Dilophus nuptus* Speiser; (6) head and thorax of *Plecia bilobata* ♂, lateral view; (7) head of *D. nuptus* ♀, lateral view; (8) fore tibia of *Bibio* sp., dorsal view; (9) fore tibia of *D. nuptus*, lateral view.

Abbreviations: A_1 – first branch of anal vein; *bm–m* – basal medial crossvein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

usually short (may be prolonged and telescopically extended in *Dilophus*); labellum cushion-shaped, setulose.

Thorax (Figs 2, 6) usually predominantly clothed in abundant, relatively long pile, but may be virtually bare, particularly in some *Plecia*; pronotum moderately well-developed, with prominent lateral lobes; in *Dilophus* with transverse rows of spines on pronotum and frontal part of mesonotum; mesonotum large, more or less convex, usually with deep sulci delimiting dorsocentral and supra-alar areas; scutellum small, but prominent. Legs simple, moderately long and slender in *Plecia*, in Bibioninae legs shorter and more thickened; fore femur spindle-shaped, somewhat flattened; fore tibia relatively short; in *Dilophus* fore tibia cylindrical, with several protruding sharp spines in mesal part and ring of spines apically (Fig. 9) (similar spines may be partly developed on mid tibia); in *Bibio* Geoffroy, fore tibia with long, sharp apical projection anteriorly (Fig. 8); bibionines with group of rounded coeloconical sensillae on inner surface of all tibiae; tibial spurs always present, moderately large, usually sharp and curved, sometimes spoon-shaped (Fig. 2); tarsi 5-segmented, frequently with basal segment of hind tarsus thickened, but otherwise unmodified; tarsal claws simple; empodium and pulvilli feather-like. Wing (Figs 3–5) generally large and relatively broad, often fumose, but rarely patterned, venation distinctive, of general bibionomorph type; all known Afrotropical species macropterous; *Sc* and R_1 veins long, running more or less parallel to costa; radial sector simple (Bibioninae) or forked (Pleciinae); vein *M* forked; *r–m* crossvein situated medially on wing; in Pleciinae *bm–m* crossvein situated in medial part of wing, connecting basal part of vein M_4 with stem of vein *M*, in Bibioninae in apical ½, connecting distal part of vein M_4, either to vein *M* (just before fork) or vein M_2; veins M_4 and *CuA* usually reaching hind margin of wing; vein *CuP* and anal vein usually weak; vein A_1 just visible as short hook-shaped vein at base of anal lobe; no closed anal cell; pterostigma more or less prominent, sometimes indistinctive; no discal cell.

Abdomen (Fig. 2) with lateral sclerites well-developed, long and slender in male, stout in female, usually densely clothed in relatively short pile (most omitted from Fig. 2); tergites and sternites 1–8 well-developed in both sexes; male terminalia (Fig. 10) with epandrium (tergite 9) well-developed, often bilobed, occasionally divided into 2 separate parts, basally fused to hypandrium (sternite 9); gonocoxites well-developed, fused medially with hypandrium (sternite 9); gonostylus well-developed, in Bibioninae with plesiomorphic form, attached to inner distal end of gonocoxite directed mesally; gonostylus more or less sickle-shaped in *Bibio*, usually short and digitiform in *Dilophus*; morphology of terminalia varies greatly in *Plecia*, but gonostylus usually attached mesally and directed more or less ventrad, shape variable, often bilobed, 1 lobe often with slender tip or hook; female terminalia with tergite 9 well-developed, but sometimes reduced medially, tergite 10 small; cercus large and prominent, 2-segmented in *Plecia*, 1-segmented in Bibioninae; sternite 8 with variably developed hypogynial valves, often divided by mesal cleft; sternite 9 (genital fork) generally conspicuous; hypoproct usually prominent, membranous and pilose; 3 more or less globular spermathecae and 2 accessory glands present.

Bibionids are morphologically quite distinctive, but may superficially resemble some Empididae (Chapter 51) and Therevidae (Chapter 49).

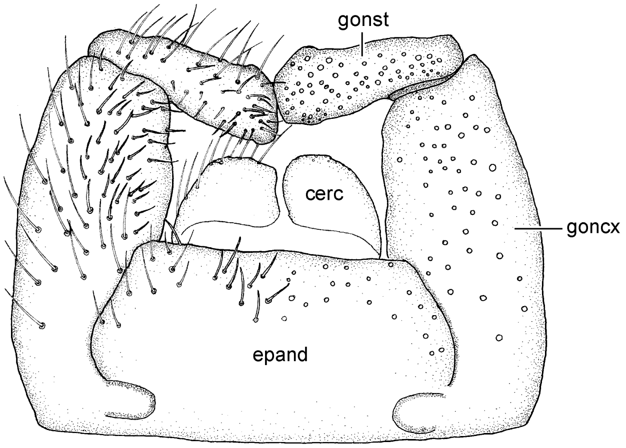
Biology and immature stages

Eggs have been described for relatively few species (Bollow 1954; Morris 1921; Pinto & Amorim 1996). Bibionine eggs are white to cream coloured, subcylindrical, with hemispherical ends and appear matt, due to the microsculpture of the chorion. Pleciine eggs may be spindle-shaped, jet-black and shiny (Buschman & Kuitert 1975), but it is not known if this applies in general, or is confined to a few species. Eggs are deposited in the soil in humid conditions, often in egg-masses of several hundred eggs (a female's entire output) in an earthen cell excavated by the female.

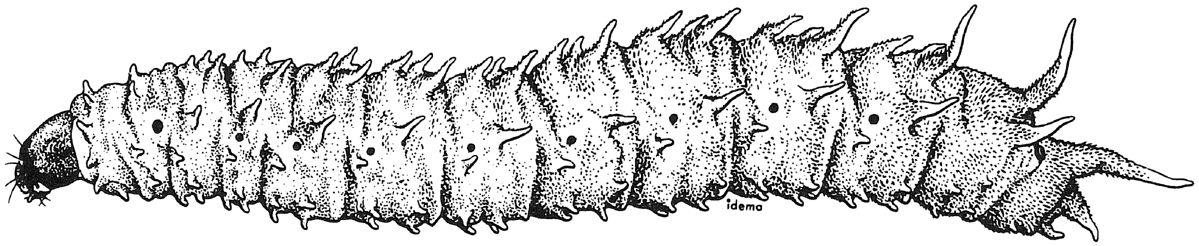
Bibionid larvae (Figs 11–13) are relatively archaic with a number of plesiomorphic traits (Hennig 1948: 81; Skartveit 2002). They are elongate and cylindrical without prolegs; the colour is typically white to pale brown in Bibioninae and greyish in Pleciinae. Segmental borders are discontinuous, with tergites and sternites lying in a staggered pattern. The head capsule is well-developed, strongly sclerotised, pigmented and non-retractable. Bibionid mouthparts were first treated in detail by Morris (1917), subsequent work has added little substantially to this. The mandibles are short and robust, with 3–5 molar teeth, although these are often worn down towards the end of each instar. The maxillae are stout, with conical sensillae on the palpus and on stipes. The labium is variously shaped and has a group of conical sensillae medially on the ventral surface. The cuticle is tough and leathery and is clothed in abundant, minute sclerotised scales that often bear spines. Cuticular setae sparse and short, except in first-instar *Bibio* larvae, which have numerous long setae, some of which may be virtually as long as the body (Morris 1917). The body in most species has numerous, wart-like to finger-like fleshy projections (*e.g.*, Morris 1917; Strenzke 1951). The respiratory system (described in detail by Schultz 1917) is holopneustic, except in first-instar larvae, which have only one pair of spiracles. Functional spiracles occur on the lateral margins of all segments, except the mesothoracic and sub-terminal, those on the last segment being inserted more dorsally and are at least twice as large as other spiracles. The spiracles of the last body segment carry ecdysal scars which are useful for identification (Hardy 1981: 218): pleciine larvae have 1 scar, *Bibio* species 2 and *Dilophus* species usually 3 scars, at least in European species (*e.g.*, Hennig 1948: 83; Morris 1921; Skartveit 2002). The alimentary canal has been described by Schultz (1917) and Frouz *et al*. (2002).

Bibionines pupate freely in a small earthen cell in the soil or in rotten wood (Brauns 1954: 41). Penthetriine and pleciine species may apparently pupate within the last larval skin (Brauns 1954: 39), but information on this is sparse. Pupae exhibit pronounced sexual dimorphism (Morris 1917), with the female pupae being considerably larger, with stouter abdomens and smaller heads than male pupae. Head-, wing- and leg-cases are obvious in the pupa, as is the segmentation of the abdomen. The pupal stage normally lasts several weeks, but may be as short as nine days under laboratory conditions (Skartveit 1997: 45).

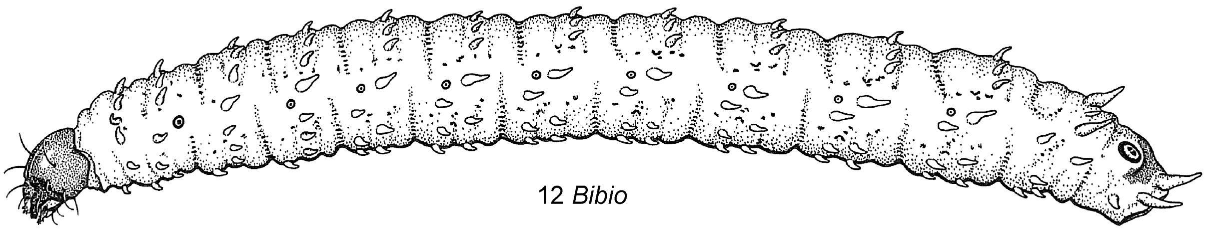
Very little information, other than collecting data, has been published on the biology and behaviour of Afrotropical bibionids. The information provided here is based largely on Palaearctic species which have received more attention.



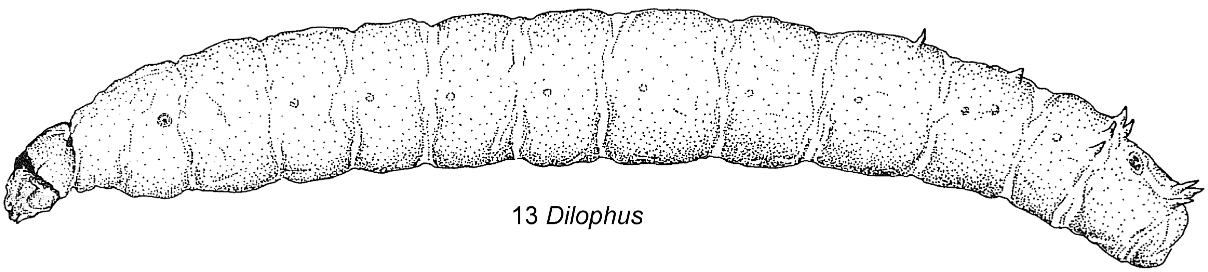
10 *Dilophus* ♂



11 *Plecia*



12 *Bibio*



13 *Dilophus*

Figs 17.10–13. External male terminalia and larvae of Bibionidae: (10) external male terminalia of *Dilophus antipedalis* Meigen, dorsal view; (11) larva of *Plecia* sp., lateral view (non-Afrotropical); (12) same, *Bibio* sp. (non-Afrotropical); (13) same, *Dilophus* sp. (non-Afrotropical). Figs 11, 12 (Hardy 1981, figs 12, 14), Fig. 13 (Skartveit 1997, fig. 14).

Abbreviations: cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus.

Bibionid larvae are principally phytosaprophagous and occur in humid, terrestrial environments, most commonly within leaf litter. Some species may feed to a large extent on living roots and tubers (D'Arcy Burt & Blackshaw 1991), on lichens (Skartveit 2002), or in soft dead wood (Allen 1974). Bibionine larvae generally occur in dense aggregations, each aggregation originating from one or more egg clutches. Mixed-species aggregations are known (Skartveit 2002). Pleciine larvae may be more solitary (Strenzke 1951), but may also be found in aggregations (Hetrick 1970). Larvae commonly occur in high densities in suitable habitats and most likely contribute significantly to the recycling of plant material through their chewing action, thus speeding microbial decomposition (Karpachevsky *et al.* 1968). Larval development undergoes seven instars and probably most commonly takes a year, although some species in Europe have two generations per year and some montane species take at least two years to develop (Skartveit & Solhøy 1997). Nothing appears to be published on bibionid larvae in the Afrotropical Region, except that they were found in the diet of Armored shrew, *Scutisorex somereni* (Thomas) (Mammalia: Insectivora), in Democratic Republic of Congo (Churchfield *et al*. 2007).

Adult bibionids are predominantly diurnal, but a few species have been commonly collected at light (Skartveit *et al*. 2005), demonstrating nocturnal activity. While some bibionids do not feed in the adult stage, others are frequent flower visitors, where they ingest nectar and probably also pollen. Males hover above vegetation, attempting to intercept females that may fly by (Zeil 1983*b*). Adult bibionids are commonly preyed upon by predaceous Diptera (*e.g.*, Skartveit 1996), spiders and ants, while birds appear to be rather minor predators of these flies. The red and black colour commonly exhibited in *Plecia* spp. may mimic certain noxious Hymenoptera, although it is not known if flies themselves are distasteful to predators.

Afrotropical bibionids are most abundant in montane woodlands and heathlands. The genus *Plecia* also occurs in lowland rainforests. Bibionids may be numerous in cultivated areas, particularly in grassy places, but since the larvae are highly susceptible to desiccation they are rare in dry habitats (Skartveit & Kaplan 1996). The family has been recorded at elevations up to 3500 m in Africa, but probably occurs even higher, where suitably humid conditions occur, as they have been found at elevations over 5000 m in the Himalayas (Skartveit 1997: 43).

Economic significance

In Europe, some bibionines may occasionally be notable pests of crops (e.g., barley, hops, maize, oats, potatoes, rye, sugar beet, tobacco and wheat), vegetables (*e.g.*, asparagus, cabbage, cauliflower, celery, cucumber, lettuce, peas, rhubarb, strawberries and tomatoes), as well as lawns and other amenity grass, the larvae destroying plant roots and tubers (D'Arcy Burt & Blackshaw 1991). Sometimes the main damage is caused by birds uprooting plants in order to feed on the larvae beneath (Dahlsson 1974), although there appears to be no record of such damage in Africa. Abundant larvae may be an important food source for various animals, such as moles and galliform birds. Being abundant shredders of dead plant material, the larvae probably contribute significantly to nutrient cycling in soil environments.

In North America mass accumulations of swarming bibionids along highways cause problems by clogging automobile ventilation systems, causing engine overheating, as well as ruining car paint (Callahan & Denmark 1973). Such damage is unlikely in Africa since automobile densities are far lower and large mass occurrences of bibionids have not been recorded.

Those species that are frequent flower-visitors may be of some importance as pollinators, although few attempts have been made to investigate this in detail. Johnson & Steiner (1994) found that bibionids were by far the most common visitors to flowers of the Cape orchid, *Disa obtusa* (Orchidaceae) and did effectively pollinate these flowers, while Goldblatt *et al*. (2005), noted that *Bibio longirostris* Rondani, 1863, is the only visitor to the flowers of *Melasphaerula ramosa* (Iridaceae) in South Africa and flies carry pollen from this plant, although the plant may also self-pollinate.

Classification

The sister-group of the Bibionidae is probably the non-Afrotropical Hesperinidae (Blaschke-Berthold 1994; Fitzgerald 2004: 34–36), which some previous authors have included as a subfamily of the Bibionidae. These two families make up the Bibionoidea *sensu* Blaschke-Berthold (1994) (= Bibionidae *sensu* Hardy 1981). Candidates as sister-group to the Bibionoidea are the non-Afrotropical Pachyneuridae (including Cramptonomyiidae) (Blaschke-Berthold 1994; Fitzgerald 2004: 34–36), the Mycetophiliformia (Pinto & Amorim 2000: 12), or a clade containing both these groups (Oosterbroek & Courtney 1995). Bibionoidea, Myctophiliformia and Pachyneuridae *sensu lato* make up the Bibionomorpha (Blaschke-Berthold 1994; Oosterbroek & Courtney 1995), in which the non-Afrotropical family Axymyiidae may also be included (Oosterbroek & Courtney 1995; Spangenberg *et al*. 2012). There is also some evidence supporting the inclusion of the Anisopodidae in this clade (Spangenberg *et al.* 2012; Yeates *et al.* 2007).

The family has traditionally been divided into two subfamilies (Bibioninae and Pleciinae) and seven extant genera, although more recently Pinto & Amorim (2000: 91) placed the genus *Penthetria* Meigen in a subfamily of its own (Penthetriinae). In the Afrotropical Region Bibioninae are represented by the genera *Bibio* and *Dilophus* and Pleciinae by the genus *Plecia*. Bibionids are distributed worldwide, except for the Polar regions and some Pacific Ocean islands. The subfamily Bibioninae appears to have most species in temperate areas, whereas the genus *Plecia* is predominantly tropical. *Dilophus* is most diverse in the Southern Hemisphere, while *Bibio* (in the extant fauna) is mainly a Northern Hemisphere genus. The presence of some seemingly archaic species of *Bibio* in southern Africa suggests a Southern Hemisphere origin for the genus.

Earliest fossil bibionids are known from the Upper Triassic (Olsen *et al*. 1978). This family is very abundant in some Tertiary lacustrine sediment from North America, Europe and Asia (Evenhuis 1994: 122–133; James 1937; Thèobald 1937: 133–143, 222–236, *etc*.) and a number of species have also been described from amber (Gee *et al*. 2001; Skartveit 2009). The only known fossil bibionids from Africa originate from the

Cretaceous of Botswana, approximately 93 million years B.P. (Rayner 1987). Interestingly, the species, which has not yet been named, belongs in the genus *Bibiodes* Coquillett, which currently only occurs in North America and Asia, although a number of Tertiary fossils have been found in Europe (Skartveit 2009).

Identification

The genera *Penthetria* (Penthetriinae), *Bibionellus* Edwards and *Enicoscolus* Hardy (Bibioninae) have not thus far been recorded from the Afrotropical Region, whereas the genus *Bibiodes* is only known from fossils.

Keys to genera of Afrotropical Bibionidae

Adults

1. Fore legs simple; radial sector of wing furcated (Fig. 3) (PLECIINAE) . . . . *Plecia* Wiedemann

– Fore femur strongly thickened (*e.g.*, Fig. 2), tibia modified with apical projection or spines (*e.g.*, Figs 8, 9); radial sector of wing undivided (*e.g.*, Figs 2, 4, 5) (BIBIONINAE) 2

2. Thorax with 2 transverse rows of spines on pronotum and mesonotum; fore tibia with mesal spines and a circlet of apical spines (Fig. 9) . . . . *Dilophus* Meigen

– Thorax without transverse rows of spines; fore tibia more or less thickened, with dorsal projection and ventral spur (Fig. 8) . . . . *Bibio* Geoffroy

Larvae

No Afrotropical bibionid larvae have been described to date. The following key is, therefore, based on Palaearctic species.

1. Posterior spiracle with 1 large ecdysal scar . . . . *Plecia* Wiedemann

– Posterior spiracle with at least 2 ecdysal scars 2

2. Posterior spiracle with 3 or more ecdysal scars . . . . *Dilophus* Meigen

– Posterior spiracle with 2 ecdysal scars. . . . . *Bibio* Geoffroy

Synopsis of the fauna

A catalogue of Afrotropical bibionids was published by Hardy (1980), who recorded 47 species of *Plecia*, 14 species of *Bibio* and 14 species of *Dilophus* from the Afrotropical Region. Subsequently, only three additional Afrotropical species of *Plecia* have been described (Skartveit 2004). It is likely that a number of undescribed species remain to be discovered, although bibionids appear to have been collected in most parts of Africa, including Madagascar, during colonial periods and considerable material from Africa is housed in some European museums. All the currently recognised African species (except the three described by Skartveit (2004)), were monographed by D. Elmo Hardy (1950*a*, 1951*a*, 1952*a*) and 51 of the 75 species were also described by him (Hardy 1948, 1949, 1950*a*, *b*, 1951*a*, *b*, 1952*a*, *b*, *c*, 1955, 1960*a*, *b*, 1961, 1962), for this reason there are probably few, if any, unrecognised synonymies in the group. Records of Bibionidae from the Arabian Peninsula were summarised by Deeming (2009).

***Bibio* Geoffroy** (Bibioninae)**.** The genus includes approximately 194 currently recognised species worldwide, of which 14 have been recorded from the Afrotropical Region. The Afrotropical species were keyed by Hardy (1950*a*). In addition, the widespread Palaearctic species *B. hortulanus* (L. 1758) occurs in the Arabian Peninsula (Deeming 2009).

***Dilophus* Meigen** (Bibioninae)**.** The genus includes approximately 195 currently recognised species worldwide, of which 14 occur in the Afrotropical Region. No Afrotropical species occur outside the ecozone apart from *D. antipedalis* Meigen, 1818, which appears to occur at high elevations in East Africa as well as in the Mediterranean province. Records of the Palaearctic *D. femoratus* Meigen, 1804, from Africa (*e.g.*, Hardy 1951*a*) are almost certainly erroneous, as this species occurs in relatively cold climates in Europe. The Afrotropical species were keyed by Hardy (1951*a*). In the Arabian Peninsula, the Afrotropical species *D. erythraeus* Bezzi, 1906 occurs in Yemen, while the southern Palaearctic species *D. tridentatus* Walker, 1848 occurs in Saudi Arabia and United Arab Emirates (Deeming 2009).

***Plecia* Wiedemann** (Pleciinae)**.** This genus is mainly pantropical and includes approximately 256 currently recognised species worldwide, of which 47 occur in the Afrotropical Region. The Afrotropical species were keyed by Skartveit (2004).

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KEROPLATIDAE 18

(Predaceous Fungus Gnats)

Vladimir Blagoderov and Jan Ševčík

Fig. 18.1. Copulating pair of *Macrocera* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized gnats (body length: 3–15 mm), yellowish to dark brown, or black in colour, with transparent wings, often with dark markings (Fig. 1).

Head usually with 3 ocelli; median ocellus small or absent in a few genera (*Rofelia* Matile and a few non-Afrotropical taxa: some *Keroplatus* Bosc spp., *Neoditomyia* Lane & Sturm, *Placoceratias* Enderlein, *Platyceridion* Tollet and *Tylparua* Edwards); ocelli absent in non-Afrotropical *Hesperodes* Coquillett, *Langkawiana* Ševčík, *Sciarokeroplatus* Papp & Ševčík, *Srilankana* Matile and *Vockerothia* Matile; antenna with scape and pedicel short, flagellum 14-segmented, in some species of subfamily Macrocerinae very long (several times longer than body), in subfamily Keroplatinae (tribe Keroplatini), usually with laterally compressed segments (Figs 3, 63), often pectinate or produced dorsally and ventrally (Fig. 55); in tribe Orfeliini cylindrical or slightly compressed laterally (Figs 64–69); palpus in Keroplatini reduced, porrect, with palpifer and 1 or 2 palpal segments (Fig. 61); in Orfeliini and Macrocerinae with 4 palpal segments (Figs 60, 64, 67–69); mouthparts in some genera elongate (e.g., Fig. 56).

Thorax with anepisternum setulose in most Macrocerinae, but setulose or bare in Keroplatinae (Figs 60–71); mediotergite bare or setulose. Scutellum in some genera with large membranous basal area (Figs 51–54). Wing membrane usually without macrotrichia (except some Macrocerinae); subcostal

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 505–525.

vein (*Sc*) ending at costal vein (*C*); veins *R* and *M* fused for short distance (except in *Asynaphleba* Matile, Fig. 33 and non-Afrotropical *Paleoplatyura* Meunier). Legs with fore tibia with 1 apical spur, mid and hind tibia with 1 or 2 spurs.

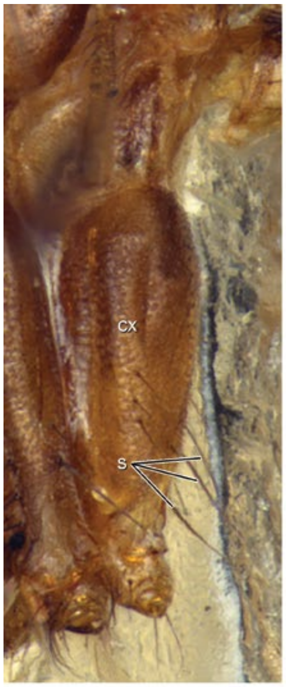
Abdomen usually long and slender, sometimes compressed laterally or dorsoventrally, or expanded laterally; sternite 1 well-developed in the non-Afrotropical subfamily Arachnocampinae, but reduced to varying degrees in other subfamilies; male segment 8 often shorter than 7 and telescopic; male terminalia follow the general pattern for Sciaroidea (*e.g.*, Mycetophilidae, Chapter 20); epandrium (tergite 9) extremely variable in size and shape, sometimes desclerotised to fully membranous medially, bearing incision at base or apex, or

2 *Macrocera* 3 *Paracerotelion*

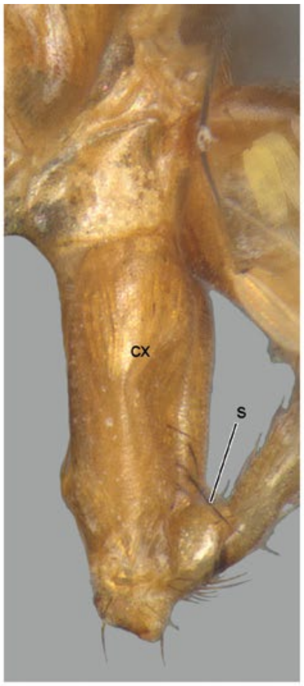
4 *Taulyrpa*

Figs 18.2–4. Habitus of Keroplatidae (lateral views): (2) *Macrocera africana* Freeman; (3) *Paracerotelion flavicauda* Matile; (4) *Taulyrpa caeruleovittata* Matile.

Abbreviation: ant – antenna.

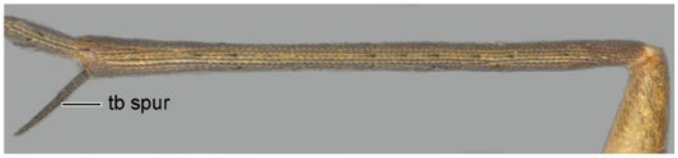


5 *Chiasmoneura* (*Prochiasmoneura*)



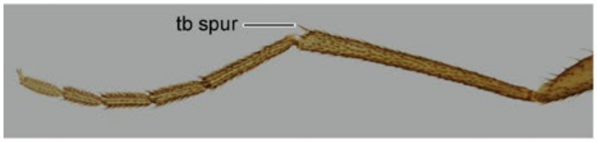
6 *Chiasmoneura* (*Synesostyla*)

10 *Monocentrota*



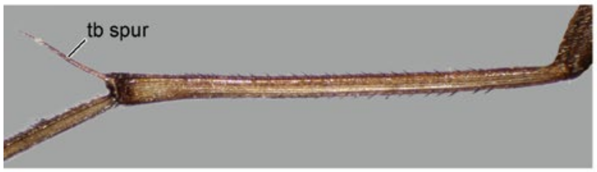
11 *Taulyrpa*

12 *Isoneuromyia*



7 *Micromacrocera*

13 *Lyprauta*



8 *Hikanoptilon*

14 *Truplaya* (*Truplaya*)

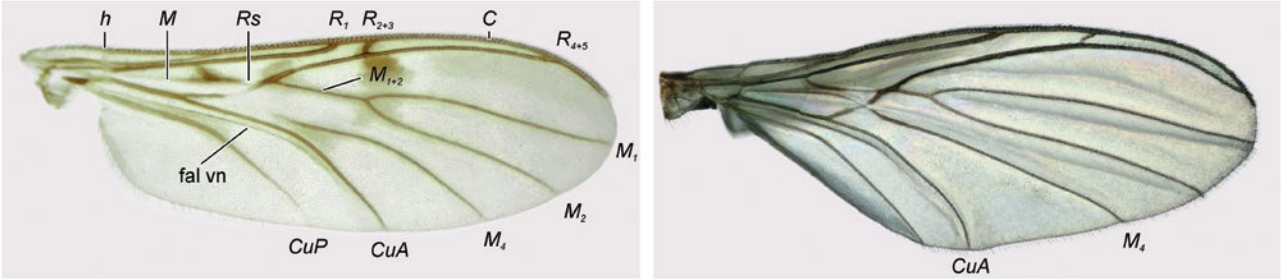
9 *Tolletia*

15 *Laurypta*

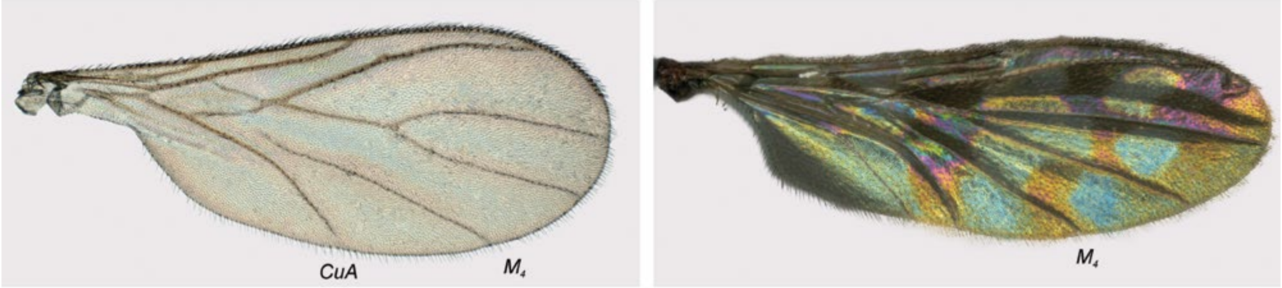
Figs 18.5–15. Leg features of Keroplatidae: (5) hind coxa of *Chiasmoneura* (*Prochiasmoneura*) *tripunctata* Matile, lateral view; (6) same, *C.* (*Synesostyla*) *stylata* Matile; (7) hind leg of *Micromacrocera stenobasis* Papp, ventral view; (8) hind tibia of *Hikanoptilon demoulini* Matile, anterior view; (9) same, *Tolletia vrydaghi* (Tollet), ventral view; (10) mid tibia of *Monocentrota aethiopica* Matile, ventral view; (11) same, *Taulyrpa* sp., dorsal view; (12) hind tibia of *Isoneuromyia* sp., ventral view; (13) fore tibia of *Lyprauta bezanozano* Matile, anterior view; (14) hind tibia of *Truplaya* (*Truplaya*) *calogastra* Speiser, anterior view; (15) mid tibia of *Laurypta laevis* (Enderlein), anterior view.

Abbreviations: cx – coxa; s – seta(e); tb cm – tibial comb; tb spur – tibial spur.

with additional lateral, basal or median processes that may be longer than gonocoxite (Figs 83, 85, 86); hypandrium (sternite 9) fused with gonocoxites ventromedially (forming gonocoxal synsclerite) (Figs 82–84), conspicuous only in Arachnocampinae; dorsal surface of gonocoxite significantly reduced; gonostylus varying dramatically in shape and size (Figs 82, 86), being represented by simple tubes with 2 apical teeth plesiomorphically (*Macrocera* Meigen and some other tribe Macrocerini); gonocoxal apodeme usually elongated, apically directed, sometimes reduced and pointing ventrally (non-Afrotropical *Robsonomyia* Matile & Vockeroth), or reduced entirely (*Truplaya* Edwards and related genera); aedeagus plesiomorphically with sclerotised distiphallus (= fused parameres) and membranous basiphallus; distiphallus membranous in Macrocerini and some Keroplatini, basiphallus sclerotised in Arachnocampinae and some Keroplatini; aedeagus may be disproportionally elongated anteriorly (= ejaculatory apodeme), penetrating deeply into abdomen (*Truplaya*-group (Figs 85, 86)); parameres usually well-developed, sometimes extending beyond gonocoxites (in non-Afrotropical *Arachnocampa* Edwards, *Cerotelion* Rondani and *Duretina* Matile) or reduced (*Placoceratias*); female terminalia with tergite 8 well-developed and larger then sternite 8, partially invaginated in Macrocerinae and significantly reduced in Keroplatinae (Figs 87, 89); sternite 8 separated into 2 sclerites in all Keroplatidae (*e.g.*, Fig. 87), except Arachnocampinae, in which this is deeply notched apically; tergite 9 varying from fully sclerotised in Arachnocampinae, to partly membranous or fused with tergite 10 in Macrocerinae, to entirely membranous



16 *Micrepimera* 17 *Macrocera*



18 *Micromacrocera* 19 *Angazidzia*

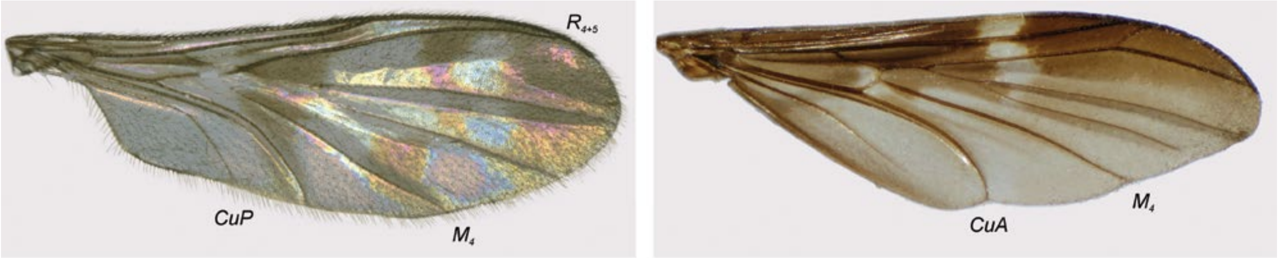
20 *Chiasmoneurella* 21 *Chiasmoneura* (*Prochiasmoneura*)

Figs 18.16–21. Wings of Keroplatidae (dorsal views): (16) *Micrepimera berentiana* Ševčík & Papp; (17) *Macrocera africana* Freeman; (18) *Micromacrocera stenobasis* Papp; (19) *Angazidzia insolita* Matile; (20) *Chiasmoneurella edwardsiana* Matile; (21) *Chiasmoneura* (*Prochiasmoneura*) *pulchella* Matile.

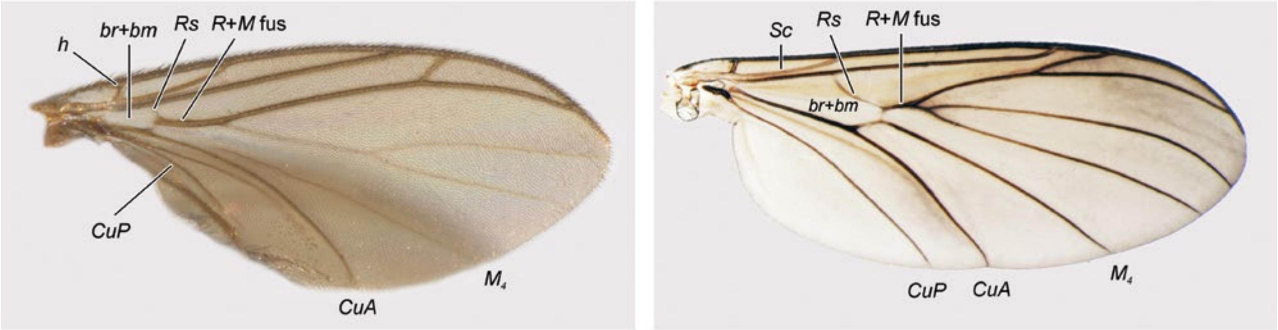
Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; fal vn – false vein; *h* – humeral crossvein; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Rs* – radial sector; M_{1+2} – fused first and second branch of media.

in Keroplatinae (*e.g.*, Figs 87, 88); sternite 9 visible only in non-Afrotropical *Arachnocampa*, and *Macrocera* and *Angazidzia* Matile, but reduced in all other genera to a narrow band; sternite 10 usually present and sclerotised; cercus 2-segmented in Arachnocampinae and Macrocerinae and 1-segmented in Keroplatinae (*e.g.*, Figs 87–89) (secondary membranisation gives appearance of 2-segmented cercus in some genera (Matile 1990)); usually 2 spermathecae present, although some *Chiasmoneura* spp. with 3 and *Cerotelion striatum* (Gmelin, 1790) with 1.

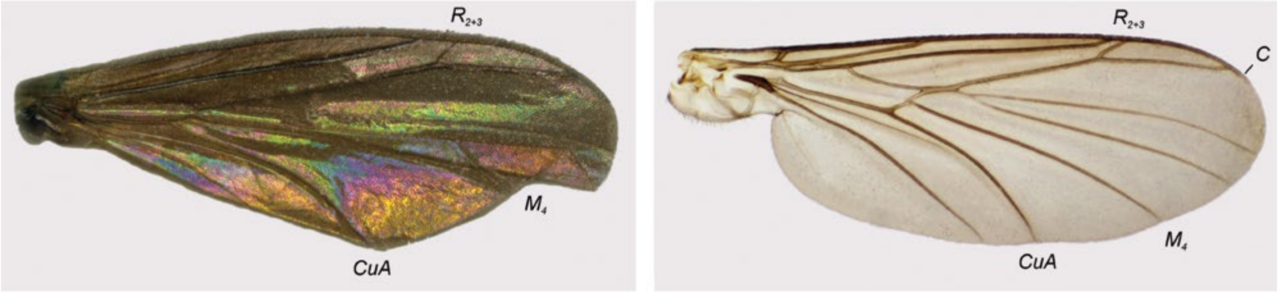
Larvae large, appearing worm-like, with abdomen secondarily segmented (Figs 90, 91), with well-developed head capsule (Figs 93, 94), often invaginated partly into thorax (Fig. 92), ovate in Arachnocampinae, pentangular in Macrocerinae and quadrangular in Keroplatinae; 2 pairs of stemmata; antenna (Figs 92, 93) very large in Macrocerinae and some Orfeliini and relatively small in *Keroplatus*; labrum (Fig. 92) with well-developed lateral lobes; frontoclypeal apotome (Fig. 92) relatively wide posteriorly; post-occipital area often membranous; gena (Figs 93, 94) with well-developed posterior incisions; tentorium well-developed in Arachnocampinae, but with reduced anterior arms in other subfamilies; anal segment with 2 (Arachnocampinae, Macrocerinae and Orfeliini) or 4 lobes (Keroplatini); larval respiratory system believed to be functionally apneustic, although prothoracic and reduced abdominal spiracles have been reported for larvae of several genera (Matile 1990).



22 *Chiasmoneura* (*Synesostyla*) 23 *Hikanoptilon*



24 *Tolletia* 25 *Afrokeroplatus*



26 *Ctenoceridion* 27 *Paracerotelion*

Figs 18.22–27. Wings of Keroplatidae (dorsal views): (22) *Chiasmoneura* (*Synesostyla*) *stylata* Matile; (23) *Hikanoptilon demoulini* Matile; (24) *Tolletia vrydaghi* Tollet; (25) *Afrokeroplatus ashleyi* Ševčík, Mantič & Blagoderov; (26) *Ctenoceridion freemani* Matile; (27) *Paracerotelion flavicauda* Matile.

Abbreviations: *br+bm* – basal medial cell + basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *h* – humeral crossvein; M_4 – fourth branch of media; *R+M* fus – radial medial vein fusion; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.

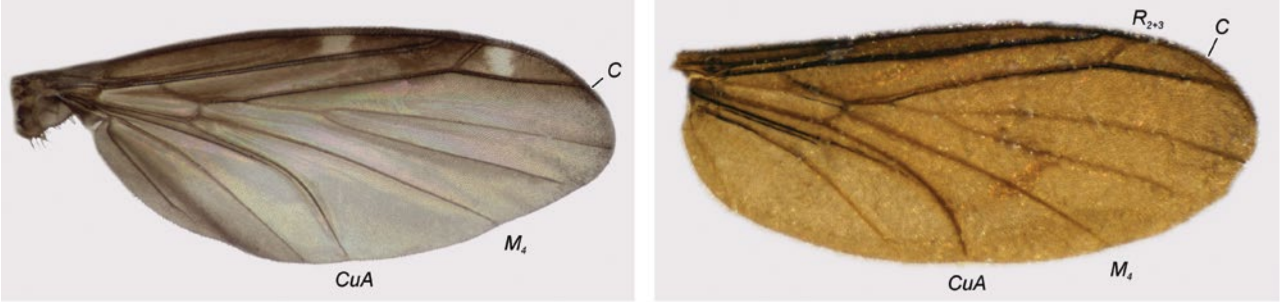
The hypothesis of monophyly of Keroplatidae is based solely on larval characters: respiratory system apneustic; Malpighian tubule system cryptonephridial; oesophagus approximately as long as midgut, mandibles long and narrow; sensillum S2 absent; abdomen ringed with fine hypodermal pigmented fascia; salivary secretion strongly acidic (Matile 1990).

Adult Keroplatidae may be confused with some Mycetophilidae (see Chapter 20), but are usually separable based on wing venation characters. In Keroplatidae the radio-medial fusion (Fig. 24, *R+M* fus) is usually present and the base of vein M_4 is invariably connected to vein *Rs* by a short transverse or oblique vein.

Biology and immature stages

Adults occur mostly in the undergrowth of forests, in shaded places alongside streams and on tree trunks, but also in meadow and steppe habitats. They can be swept from low vegetation, under overhanging rocks and fallen tree trunks, especially along banks of streams. As with other fungus gnats (Sciaroidea), very good collecting results can be achieved using Malaise traps.

Larvae and females of most keroplatids remain unknown particularly in the Afrotropical Region. The only Afrotropical species of Keroplatidae for which larvae have been described



28 *Heteropterna* (*Heteropterna*)

29 *Heteropterna* (*Scrobicula*)

30 *Tergostylus*

31 *Keroplatus*

32 *Cloeophoromyia*

33 *Asynaphleba*

Figs 18.28–33. Wings of Keroplatidae (dorsal views): (28) *Heteropterna* (*Heteropterna*) *ghesquierei* Tollet; (29) *H.* (*Scrobicula*) *balachowskyi* Matile; (30) *Tergostylus alberti* Matile; (31) *Keroplatus heimi* Matile; (32) *Cloeophoromyia mirei* Matile; (33) *Asynaphleba stuckenbergi* Matile.

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

are *Heteropterna balachowskyi* Matile, 1970, *Keroplatus heimi* Matile, 1970, *Tergostylus flavifemoratus* (Tollet, 1955) and *T. incolumis* Matile, 1974 (Matile 1970, 1974*b*). Outside the region larvae are most often associated with wood-decaying fungi (*e.g.*, Polyporaceae), where they spin hygroscopic webs, often covered with acidic salivary secretions, used for collecting spores, or ensnaring small living invertebrate prey (Fig. 90). Pupation occurs in a spun silk cocoon. Species of the Australasian subfamily Arachnocampinae (*Arachnocampa*) and a few genera of Keroplatinae (*Keroplatus*, *Mallochinus* Edwards, *Orfelia* Costa), have bioluminescent larvae (Matile 1990).

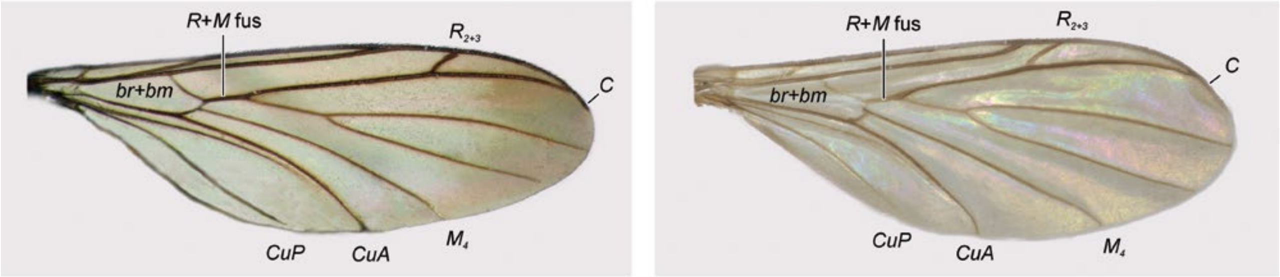
Economic significance

Most Keroplatidae are not known to have specific economic importance, however species of the genus *Arachnocampa* may form large aggregates in caves of New Zealand and Australia, representing a spectacular tourist attraction.

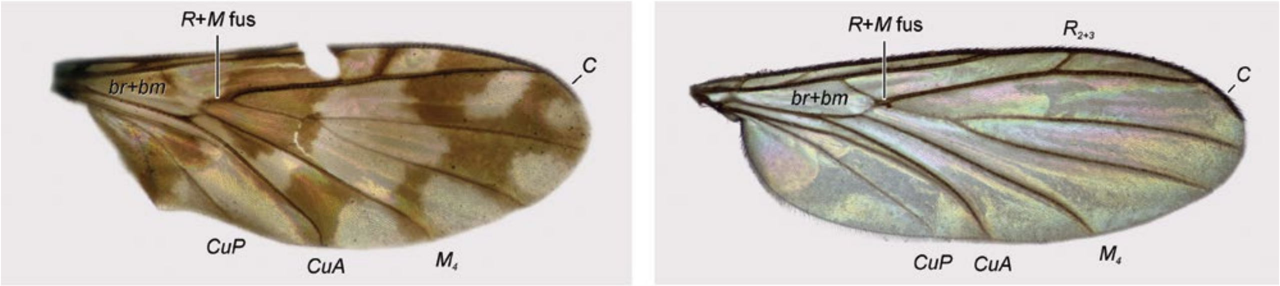
Classification

Keroplatidae, as a family group name, was proposed by Rondani (1856, as Ceroplatina). As is the case with other fungus

34 *Schizocyttara* 35 *Maborfelia*



36 *Rofelia* 37 *Monocentrota*



38 *Proceroplatus* 39 *Neoplatyura*

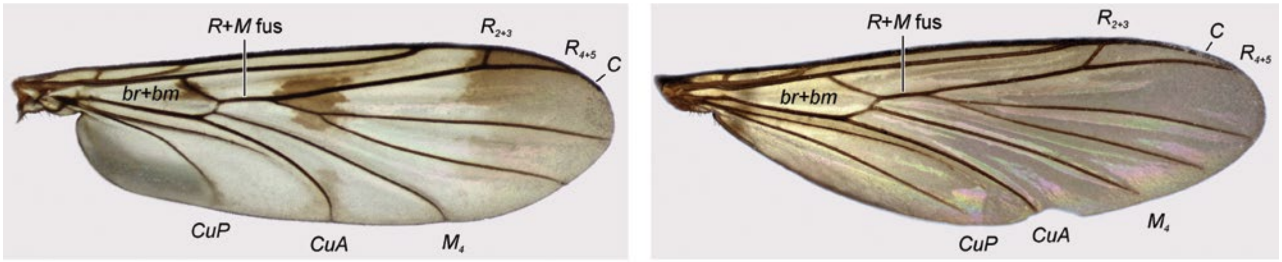
Figs 18.34–39. Wings of Keroplatidae (dorsal views): (34) *Schizocyttara turneri* Matile; (35) *Maborfelia picta* Matile; (36) *Rofelia rothiana* Matile; (37) *Monocentrota* sp.; (38) *Proceroplatus aedon* Vanschuytbroeck; (39) *Neoplatyura axillariger* Enderlein.

Abbreviations: *br* – basal radial cell; *br+bm* – basal medial cell + basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *M* – medial vein, or media; M_4 – fourth branch of media; *R+M* fus – radial medial vein fusion; R_1 – anterior branch of radius; R_{2+3} – second branch of radius.

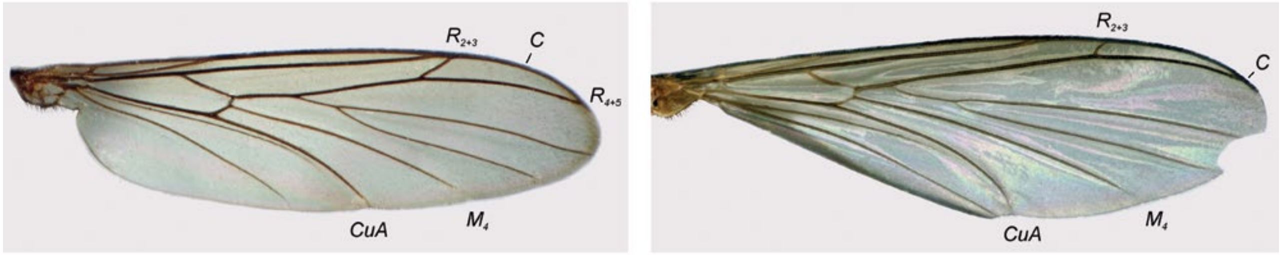
gnat families of the superfamily Sciaroidea, it was formerly included as a subfamily of the Mycetophilidae, but was first used at familial level by Tuomikoski (1966). The phylogenetic position of the family is still the subject of discussion, but sister-group relationships between Keroplatidae and non-Afrotropical Diadocidiidae and between this clade and the remainder of the Sciaroidea, excluding non-Afrotropical Ditomyiidae, were proposed by Amorim & Rindal (2007), Chandler (2002), Hippa & Vilkamaa (2005) and Matile (1997). Quantitative phylogenetic analyses have not yet revealed sufficient resolution to resolve phylogenetic relationships within the Bibionomorpha (*e.g.*, Lambkin *et al*. 2013; Wiegmann *et al*. 2011). The most recent attempt was that of Ševčík *et al*. (2016), who proposed a sister-group relationship of the Keroplatidae clade (including Lygistorrhinidae) to the clade containing Diadocidiidae (non-Afrotropical), Mycetophilidae, Sciaridae and the genera of Sciaroidea *incertae sedis*.

Following Matile (1990) and Evenhuis (2006) the family is divided into four subfamilies: Arachnocampinae, Macrocerinae, Keroplatinae and Sciarokeroplatinae. Nine known species of Arachnocampinae are distributed exclusively in the Australasian Region (Australia, Tasmania and New Zealand). The only known species of Sciarokeroplatinae occurs in Taiwan and the Shaanxi Province, China. Macrocerinae and Keroplatinae each consist of two tribes: Macrocerini and Robsonomyiini and Keroplatini and Orfeliini, respectively. Concept and circumscription of the two tribes of Keroplatinae may be a topic of debate, particularly in light of probable paraphyly of Orfeliini with respect to Keroplatini (Matile 1990).

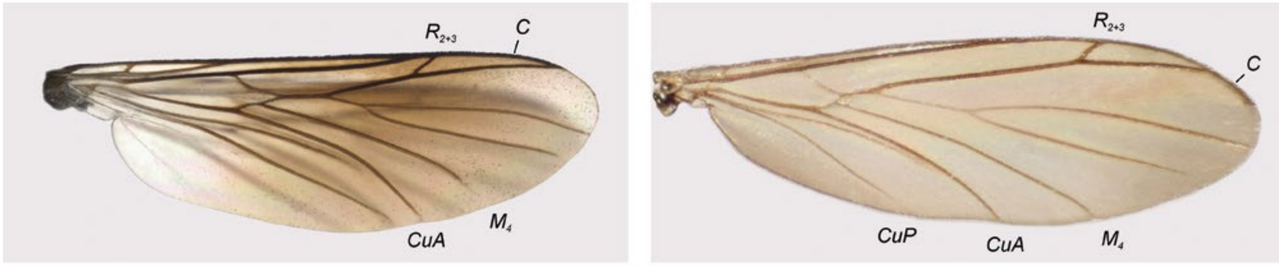
Keroplatidae are known (although still undescribed) from the fossil record since the Early Cretaceous (Blagoderov *et al*. 2002: 238). Forty-three species in fifteen genera are described from the Cretaceous of Burma, France, Spain, the Eocene of the United States, China and India, the Oligocene of Europe and the Holocene of Tanzania and, particularly, from Baltic amber (Upper Eocene) (Evenhuis 2006; Solórzano Kraemer & Evenhuis 2008). A rich undescribed fauna of Keroplatidae is also known from Burmese amber (Blagoderov & Grimaldi 2004).



40 *Rutylapa* 41 *Ralytupa*



42 *Taulyrpa* 43 *Xenoplatyura*



44 *Isoneuromyia* 45 *Lyprauta*

Figs 18.40–45. Wings of Keroplatidae (dorsal views): (40) *Rutylapa annulata* Matile; (41) *Ralytupa angusta* Matile; (42) *Taulyrpa caeruleovittata* (Matile); (43) *Xenoplatyura villiersi* Matile; (44) *Isoneuromyia* sp.; (45) *Lyprauta bezanozano* Matile.

Abbreviations: *br+bm* – basal medial cell + basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_4 – fourth branch of media; *R+M* fus – radial medial vein fusion; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

Identification

Currently the family Keroplatidae is divided into four subfamilies: Arachnocampinae (6 species), Macrocerinae (250), Keroplatinae (*ca* 760) and Sciarokeroplatinae (1) (Evenhuis 2006; Matile 1990; Papp & Ševčík 2005). Detailed diagnoses for known genera of Arachnocampinae, Macrocerinae and Keroplatinae: Keroplatini were provided by Matile (1990).

A catalogue of the world species of Keroplatidae was compiled by Evenhuis (2006). Regional keys to genera exist for the Nearctic (Vockeroth 1981), Palaearctic (Hutson *et al*. 1980; Søli *et al*. 2000; Zaitzev 1994) and Central America (Vockeroth 2009); keys to world genera and species for most of the genera of Macrocerinae and Keroplatini were published by Matile (1990), the key for Keroplatini was updated by Ševčík *et al*. (2015). Regional keys for species were provided for *Macrocera*, *Xenoplatyura* Malloch and *Cloeophoromyia* (Matile 1970), *Ralytupa* Edwards (Matile 1975) and *Truplaya* (Matile 1978).

Keroplatidae are best collected in alcohol and dissected and mounted on slides or critical-point-dried for later point-mounting; larger specimens can be direct- or micro-pinned in the field (see Chapter 2).

Key to genera of Afrotropical Keroplatidae

1. Head with cerebral sclerite distinct (*e.g.*, Figs 49, 50); mid and hind tibiae without apical combs (*e.g.*, Fig. 7); wing vein M_4 often curved at base of vein *CuA* (*e.g.*, Figs 17, 18) (MACROCERINAE) 2

– Head with cerebral sclerite absent (*e.g.*, Figs 56, 59, 73–81); mid and hind tibiae with at least 1 apical comb (*e.g.*, Figs 9, 13, except in *Kibaleana* Kurina, Mantič & Ševčík); wing vein M_4 never bent at base of vein *CuA* (*e.g.*, Figs 23–48) (KEROPLATINAE) 9

2. Thorax with anepimeron reduced to small rounded sclerite, not extending between katepisternum and laterotergite (see Matile 1990, fig. 415); mid and hind tibiae without spurs (see Ševčík & Papp 2011, fig. 1). . . . . *Micrepimera* Matile

– Thorax with anepimeron extending ventrally to reach between katepisternum and laterotergite (*e.g.*, Figs 60, 61); mid and hind tibiae with spurs (*e.g.*, Fig. 7) 3

3. Male (and often female) antenna at least as long (often 2 × and more as long) as body length (Fig. 2); palpal segments 3–4 × longer than wide (Fig. 60); wing vein M_4 weakened, but not interrupted at base (Fig. 17); pulvilli longer than tarsal claws (see Matile 1990, fig. 50). . . . . *Macrocera* Meigen

– Male antenna as long as or shorter than body length; palpal segments moniliform or at most 2 × as long as wide (*e.g.*, Fig. 61); wing vein M_4 often widely interrupted at base (*e.g.*, Figs 17–22); pulvilli not longer than tarsal claws 4

4. Tibial spur formula 1 : 2 : 1; both spurs shorter than diameter of tibia at apex (Fig. 7) . . . . *Micromacrocera* Papp

– Tibial spur formula 1 : 2 : 2; at least outer spur subequal to diameter of tibia at apex or longer (*e.g.*, Figs 9–15) 5

5. Wing with vein R_{2+3} (Fig. 20); scutellum bearing setae (Fig. 72; see Matile 1990: fig. 325); male terminalia with gonocoxites much broader than pregenital segments, forming 2 dorsal, widely divergent hollow processes . . . . *Chiasmoneurella* Matile

– Wing without vein R_{2+3} (e.g., Fig. 19); scutellum bare; male terminalia with gonocoxites slightly wider than pregenital segments, their dorsal surface reduced 6

6. Wing vein M_4 weakened at base (Fig. 19; see Matile 1990, fig. 259); male terminalia with epandrium (tergite 9) large, deeply indented at midline and extended by 2 long basal apodemes; gonocoxite without ventral membranous area; gonostylus trilobed (see Matile 1990, figs 260, 261); female tergite 9 entirely concealed beneath tergite 8 (see Matile 1990, fig. 262) . . . . *Angazidzia* Matile

– Wing vein M_4 more or less widely interrupted at base (Figs 21–22); male terminalia with epandrium (tergite 9) smaller, transverse, not emarginate, without apodemes; gonocoxite bearing ventral membranous area more or less well-developed; gonostylus simple or bilobed; female tergite 9 well-developed and not obscured beneath tergite 8 (see Matile 1990, figs 273, 288, 312) . . . . . . *Chiasmoneura* de Meijere 7

7. Wing membrane with dark brown markings, contrasting with well-defined white maculae; petiole and base of *M*-fork often absent; vein *CuP* widely interrupted and strongly angulate at apex. . . . . [*Chiasmoneura sensu stricto*]

– Wing membrane with lighter brown markings, blending with blurry-edged white maculae; only base of vein *M* absent; vein *CuP* complete or extending almost to wing margin, not angulate at apex (*e.g.*, Figs 21, 22). 8

8. Head with cerebral sclerite as long as broad, entirely bare (Fig. 49); hind coxa with numerous posterior setae (Fig. 5); male terminalia with gonostylus bidentate; hypandrium (sternite 9) not visible;

membranous area of gonocoxite simple (see Matile 1990, figs. 302–305); female tergite 9 partly membranous (see Matile 1990, fig. 288) . . . . *Chiasmoneura* (*Prochiasmoneura* Matile)

– Head with cerebral sclerite longer than wide, setulose (Fig. 50); hind coxa with single posterior apical seta (Fig. 6); male terminalia with gonostylus deeply lobed; hypandrium (sternite 9) visible; membranous area of gonocoxite limited by deep depression basally, with pair of apical processes (see Matile 1990, fig. 311); female tergite 9 entirely sclerotised (see Matile 1990, fig. 312) . . . . *Chiasmoneura* (*Synesostyla* Matile)

9. Mouthparts reduced, palpus reduced to 1 or 2 segments, terminal palpal segment thickened, often porrect (*e.g.*, Fig. 55); antenna usually modified, compressed or pectinate, only rarely elongate (*e.g.*, Figs 3, 55, 63) (KEROPLATINI) 10

– Mouthparts usually well-developed, sometimes elongated, rarely reduced; palpus normally with 4 segments in addition to palpifer, sometimes reduced, but then terminal segment never thickened and porrect (*e.g.*, Figs 56–58, 67–69); antenna usually filiform, rarely thickened, or pectinate (*e.g.*, Figs 57–59, 73, 76, 78) (ORFELIINI) 18

10. Antennal flagellum pectinate, sometimes with very short projections in females (*e.g.*, Fig. 55). 11

– Antennal flagellum laterally flattened and broadened (only broadened in some cases) (*e.g.*, Figs 3, 63) 14

11. Thorax with laterotergite setulose (Fig. 62); head with face entirely setulose (Fig. 55); hind tibiae without outer spurs (Fig. 8) . . . . *Hikanoptilon* Matile

– Thorax with laterotergite bare (*e.g.*, Figs 52, 54); head with face bare or bearing only short setae in ventral $^1/_2$; hind tibiae with outer spurs (*e.g.*, Fig. 9) 12

12. Tibial macrotrichia irregularly arranged; scutellum with large almost isosceles triangular membranous area below (Fig. 51) . . . . *Ctenoceridion* Matile

– Tibial macrotrichia regularly arranged in rows, at least on outer side (*e.g.*, Fig. 9); scutellum with membranous area below in shape of narrow fascia, Y-shaped or absent (*e.g.*, Fig. 52) 13

13. Wing with basal cell (*br+bm*) very small and short, its apex near level of humeral vein (*h*); vein *CuP* markedly shortened; radial sector (*Rs*) considerably shorter than radio-medial fusion (Fig. 24) . . . . *Tolletia* Matile

– Wing with basal cell (*br+bm*) normal in size, its apex near level of end of subcostal vein (*Sc*), vein *CuP* reaching wing margin; radial sector (*Rs*) longer than radio-medial fusion (Fig. 25). . . . . *Afrokeroplatus* Ševčík, Mantič & Blagoderov

14. Tibial macrotrichia irregularly arranged (except sometimes near apex); wing vein R_{2+3} terminating at costal vein (*C*) (*e.g.*, Figs 27–29) 15

– Tibial macrotrichia regularly arranged in rows, at least in apical ⅓; wing vein R_{2+3} terminating at costal vein (*C*) or at vein R_1 (*e.g.*, Fig. 31) 17

15. Membranous area below scutellum narrow, slightly wider medially (Fig. 52). . . . . *Paracerotelion* Matile

– Membranous area below scutellum depressed and triangular (Figs 53, 54) . . . . *Heteropterna* Skuse 16

16. Membranous area below scutellum in shape of large equilateral triangle (Fig. 53); antenna with ventral macrosetae on flagellomeres absent or much shorter than flagellomere 6, terminal flagellomere without apical process . . . . *Heteropterna sensu stricto*

– Membranous area below scutellum small in shape of isosceles triangle (Fig. 54); antennal flagellomeres with well-developed dorsal and ventral macrosetae (as long or longer than flagellomere 6), terminal flagellomere with apical process (see Matile 1990, fig. 627) . . . . *Heteropterna* (*Scrobicula* Matile)

17. Thorax with laterotergite bare (Fig. 73); wing vein R_{2+3} terminating in costal vein (*C*) (Fig. 30). . . . . *Tergostylus* Matile

– Thorax with laterotergite setose (Fig. 74); wing vein R_{2+3} terminating in vein R_1 (Fig. 31) . . . . *Keroplatus* Bosc

18. Proboscis as long as or longer than ½ greatest diameter of eye; only basal lobe of labellum elongated (Fig. 56); wing narrow (Fig. 32) . . . . *Cloeophoromyia* Matile

– Proboscis short or reduced (*e.g.*, Figs 57, 66, 68, 69); structure of labellum different; wing broad (*e.g.*, Figs 33–35) 19

19. Palpus very small, reduced to 2–3 moniliform segments; radial-medial fusion absent (with transverse radial–medial crossvein (*r–m*) only) (Fig. 33). . . . . *Asynaphleba* Matile

– Palpus normal, 4-segmented, often elongated (at least the terminal segment) (*e.g.*, Figs 57–59, 66, 68, 69, 71); radial-medial fusion present (e.g., Figs 34–41) 20

20. Wing base with vein *M* distinct, at least indicated by sharp sclerotised fold dividing the basal cell (*br+bm*) in two; vein R_{2+3} terminating in costal vein (*C*); vein *CuP* reduced, but ending beyond the apex of basal cell (Fig. 34) . . . . *Schizocyttara* Matile

– Wing base without vein *M* or vein reduced to faint trace; vein R_{2+3} terminating in costal vein (*C*); vein *CuP* reduced, not exceeding the apex of basal cell (*br+bm*) (*e.g.*, Figs 36–41) 21

21. Wing vein R_{2+3} terminating in vein R_1 (Fig. 35); thorax with laterotergite setulose; scutum uniformly clothed in setulae (Fig. 64) . . . . *Maborfelia* Matile

– Wing vein R_{2+3} absent or terminating in costal vein (*C*) (e.g., Figs 36–48); thorax with laterotergite setulose or bare; scutum with bare fasciae or uniformly clothed in setulae 22

22. Thorax with laterotergite setulose (*e.g.*, Fig. 76) 23

– Thorax with laterotergite bare (*e.g.*, Figs 67–71) 25

23. Head with 2 ocelli (Fig. 75); thorax with anepisternum bare. . . . . *Rofelia* Matile

– Head with 3 ocelli (e.*g.*, Figs 76, 78); thorax with anepisternum bare or setose 24

24. Thorax with scutum with broad, bare fasciae (Fig. 76); wing membrane without distinct markings (Fig. 37). . . . . *Monocentrota* Edwards

– Thorax with scutum uniformly setulose (Fig. 77); wing membrane with distinct markings (Fig. 38) . . . .*Proceroplatus* Edwards

25. Anterior thoracic spiracle with short setae on posterior and sometimes anterior margin (*e.g.*, Figs 66, 67). 26

– Anterior thoracic spiracle without short setae on posterior and anterior margin (*e.g.*, Figs 70, 71) . . . 29

26. Wing veins M_4 and *CuA* setulose dorsally (Fig. 39); thorax with metepisternum bare . . . .*Neoplatyura* Malloch

– Wing veins M_4 and *CuA* bare dorsally (e.*g.*, Figs 40–42); thorax with metepisternum with a few setulae or rarely bare (*e.g.*, Figs 67, 68) 27

27. Costal wing vein (*C*) extending beyond apex of vein R_{4+5} (Fig. 40); thorax with mediotergite with posterior setae or sometimes bare (Fig. 79). . . . . *Rutylapa* Edwards

– Costal wing vein (*C*) not extending beyond vein R_{4+5} (e.*g.*, Figs 41, 42); thorax with mediotergite with lateral seta or dorsal macrotrichia, or bare (e.*g.*, Fig. 68). 28

28. Mid tibia with 2 (outer and inner) tibial spurs (as in Figs 12, 14); thorax with mediotergite with 2 patches of lateral recumbent setae (Fig. 80); anterior thoracic spiracle never with setae on anterior margin (Fig. 67). . . . . *Ralytupa* Edwards

– Mid tibia with 1 (inner) tibial spur only (Fig. 11); thorax with mediotergite with dorsal pubescence or bare; anterior thoracic spiracle often with setae on anterior margin . . . . *Taulyrpa* Edwards

29. Head with frons bearing a few short erect setae above and between bases of antennae (Fig. 59); male terminalia often with tergite 9 remarkably long (Figs 85, 86). . . . . *Xenoplatyura* Malloch

– Head with frons entirely bare; male terminalia with tergite 9 of regular size 30

30. At least wing veins M_4 and *CuA* setulose dorsally; thorax with mediotergite bare (Fig. 69); scutum with bare longitudinal strips or uniformly setulose (Fig. 78); tibial macrotrichia arranged in regular rows (Fig. 12). . . . . *Isoneuromyia* Brunetti

– All wing veins bare (*e.g.*, Figs 45–48); thorax with mediotergite bare or setose (*e.g.*, Fig. 71); scutum usually uniformly setulose (*e.g.*, Fig. 81); tibial macrotrichia arranged irregularly or in regular rows (*e.g.*, Figs 13, 14) 31

31. Thorax with mediotergite bare 32

– Thorax with mediotergite setulose (*e.g.*, Fig. 71). 34

32. Wing vein *CuP* reaching wing margin (Fig. 46); tibial macrotrichia arranged irregularly on basal ½ (Fig. 14). . . . . *Truplaya* Edwards 33

– Wing vein *CuP* ending before wing margin (Fig. 45); tibial macrotrichia in regular rows for most of length (Fig. 13) . . . . *Lyprauta* Edwards

33. Thorax with prosternum bare (Fig. 58) . . . .*Truplaya sensu stricto*

– Thorax with prosternum setulose (Fig. 57) . . . .*Truplaya* (*Truplayella* Matile)

34. Wing vein R_{2+3} absent; mid and hind tibiae without apical combs . . . . *Kibaleana* Kurina, Mantič & Ševčík

– Wing vein R_{2+3} present; mid and hind tibiae with apical combs 35

35. Mid and hind tibiae with external spurs only (Fig. 15); thorax with metepisternum setulose; scutum uniformly setulose (Fig. 81) . . . . *Laurypta* Edwards

– Mid and hind tibiae with 2 spurs; thorax with metepisternum bare; scutum with bare paracrostichal fascia (Fig. 71) . . . . *Pyrtulina* Matile

Synopsis of the fauna

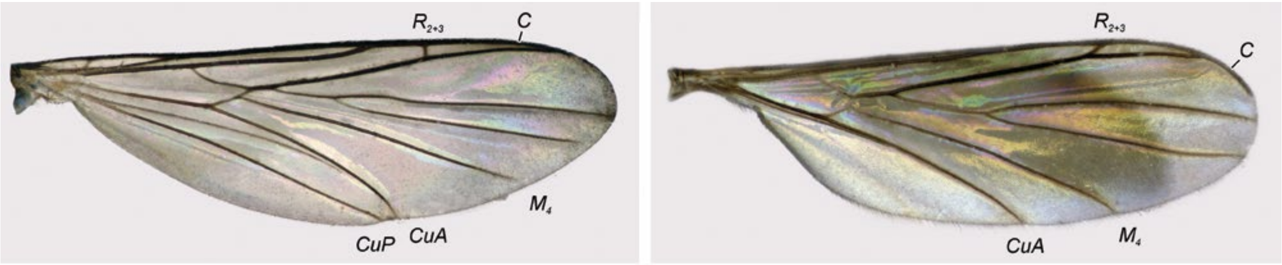
A total of 176 species of Keroplatidae are known to occur in the Afrotropical Region (Evenhuis 2006; Papp 2008; Ševčík & Papp 2011), but a number of species still await description in collections. Many additional species will undoubtedly be discovered, especially when surveys are conducted in poorly-studied areas.

Afrokeroplatus Ševčík, Mantič & Blagoderov (Keroplatinae: Keroplatini)**.** An endemic monotypic genus, with the single species, *A. ashleyi* Ševčík, Mantič & Blagoderov, 2015, recorded from South Africa (Ševčík *et al*. 2015). Biology and immature stages of the species remain unknown.

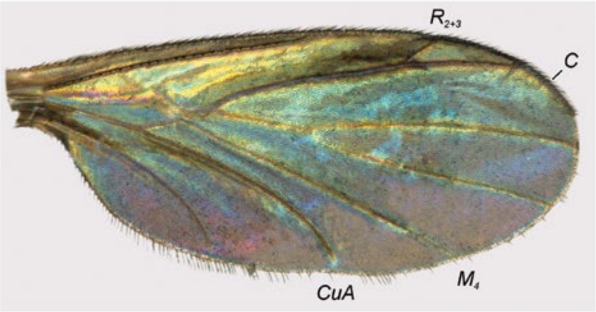
Angazidzia **Matile** (Macrocerinae: Macrocerini)**.** An endemic monotypic genus, with the single species, *A. insolita* (Matile, 1972), recorded from Comoros and Madagascar (Matile 1972*b*, 1979). Biology and immature stages of the species remain unknown.

Asynaphleba **Matile** (Keroplatinae: Orfeliini)**.** An endemic monotypic genus, with the single species, *A. stuckenbergi* Matile, 1974, known from the Cape Province of South Africa (Matile 1974*a*: 520). Biology and immature stages of the species remain unknown.

Chiasmoneura **Matile** (Macrocerinae: Macrocerini)**.** A genus of 17 described species in three subgenera, known from the Afrotropical, Australasian/Oceanian and Oriental Regions. Five species of the subgenus *C.* (*Prochiasmoneura* Matile) are described from the continental Afrotropics (Côte d'Ivoire, Kenya, Nigeria and Uganda) and three species of the endemic subgenus *C.* (*Synesostyla* Matile) are known from Comoros and Réunion Is. (Matile 1990). Biology and immature stages of the genus remain unknown.



46 *Truplaya* (*Truplaya*) 47 *Laurypta*



48 *Pyrtulina*

Figs 18.46–48. Wings of Keroplatidae (dorsal views): (46) *Truplaya* (*Truplaya*) *calogastra* Speiser; (47) *Laurypta laevis* (Enderlein); (48) *Pyrtulina dubia* Matile.

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_4 – fourth branch of media; R_{2+3} – second branch of radius.

***Chiasmoneurella* Matile** (Macrocerinae: Macrocerini)**.** An endemic monotypic genus, with the single species, *C. edwardsiana* Matile, 1972, described from Uganda (Matile 1972*c*). Biology and immature stages of the species remain unknown.

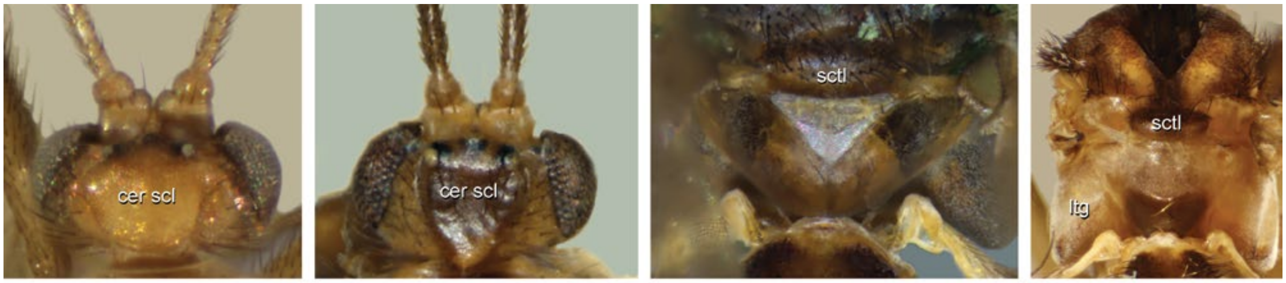
***Cloeophoromyia* Matile** (Keroplatinae: Orfeliini)**.** An endemic genus of six described species, recorded from Cameroon, Central African Republic, Côte d'Ivoire and Nigeria (Matile 1970). Biology and immature stages of the genus remain unknown. An identification key to Afrotropical species was provided by Matile (1970).

***Ctenoceridion* Matile** (Keroplatinae: Keroplatini)**.** A genus of four species recorded from the Afrotropical, Nearctic, Oriental and Palaearctic Regions. One species, *C. freemani* Matile, 1972, in the nominal subgenus is known from South Africa (Matile 1972*d*). Biology and immature stages of the species remain unknown.

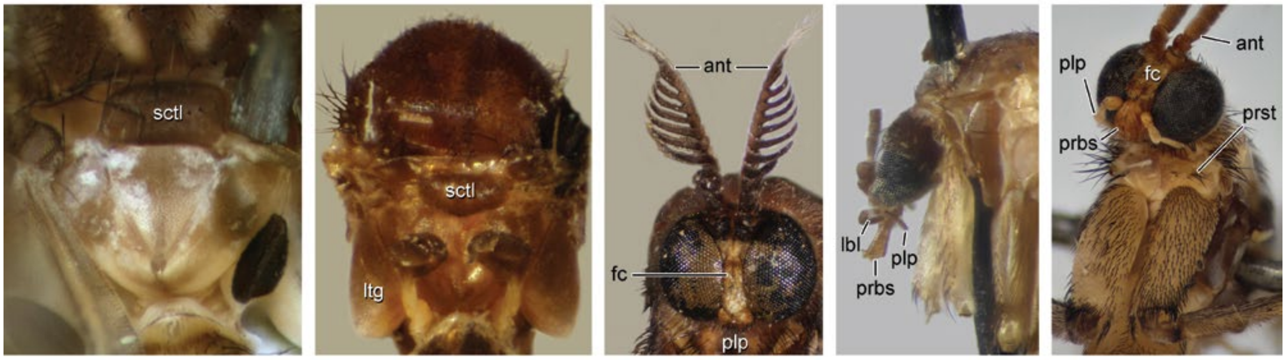
***Heteropterna* Skuse** (Keroplatinae: Keroplatini)**.** A genus of 26 described species recorded from the Afrotropical, Australasian/Oceanian, Nearctic, Neotropical and Oriental Regions. One species of the nominative subgenus, *H.* (*H.*) *ghesquierei* Tollet, 1950, is recorded from Côte d'Ivoire and Democratic Republic of Congo (Tollet 1950) and one species of subgenus *H.* (*Scrobicula*), *viz*. *H.* (*S.*) *balachowskyi* Matile, 1970, recorded from Central African Republic and Côte d'Ivoire (Matile 1970). Biology is summarised by Matile (1990). Larvae make webs underneath polypore fungi, sometimes forming colonies including all larval stages. Larvae of *H.* (*S.*) *balachowskyi* were collected in a pile of dead wood.

***Hikanoptilon* Matile** (Keroplatinae: Keroplatini)**.** An endemic monotypic genus, with the single species *H. demoulini* Matile, 1990, described from Democratic Republic of Congo (Matile 1990). Biology and immature stages of the species remain unknown.

***Isoneuromyia* Brunetti** (Keroplatinae: Orfeliini)**.** A genus of 56 described species, recorded from the Australasian/Oceanian, Nearctic, Neotropical, Oriental and Palaearctic Regions. The genus is not formally recorded from the Afrotropics, but several undescribed species are known from collections. Biology and immature stages of the genus remain unknown.



49 *Chiasmoneura* (*Prochiasmoneura*) 50 *Chiasmoneura* (*Synesostyla*) 51 *Ctenoceridion* 52 *Paracerotelion*



53 *Heteropterna* (*Heteropterna*) 54 *Heteropterna* (*Scrobicula*) 55 *Hikanoptilon* 56 *Cloeophoromyia* 57 *Truplaya* (*Truplayella*)

Figs 18.49–57. Head and thoracic features of Keroplatidae: (49) cerebral sclerite of *Chiasmoneura* (*Prochiasmoneura*) *pulchella* Matile, dorsal view; (50) same, *C.* (*Synesostyla*) *stylata* Matile; (51) postscutellum of *Ctenoceridion freemani* Matile, posterior view; (52) same, *Paracerotelion flavicauda* Matile; (53) same, *Heteropterna* (*Heteropterna*) *ghesquierei* Tollet; (54) same, *H.* (*Scrobicula*) *balachowskyi* Matile; (55) head of *Hikanoptilon demoulini* Matile, frontal view; (56) same, *Cloeophoromyia mirei* Matile; (57) head and thorax of *Truplaya* (*Truplayella*) *calogastra* Speiser, frontal view.

Abbreviations: ant – antenna; cer scl – cerebral sclerite; fc – face; lbl – labellum; ltg – laterotergite; plp – palpus; prbs – proboscis; prst – prosternum; sctl – scutellum.

***Keroplatus* Bosc** (Keroplatinae: Keroplatini)**.** A genus of 26 extant species occurring in all zoogeographical regions, except Antarctica. Two species, *K. fuscomaculatus* Tollet, 1955 and *K. heimi* Matile, 1970, are recorded from the Afrotropics, from Central African Republic and Democratic Republic of Congo (Matile 1970; Tollet 1955). Biology is summarised in Matile (1990). Larvae build nets beneath bracket fungi or dead wood covered with encrusting fungi. Larvae are sporophagous, rarely zoophagous, although constructed nets do not appear to be poisonous to small invertebrates, as is the case with some other Keroplatidae. Fourth-instar larvae of some Palaearctic species are bioluminescent.

***Kibaleana* Kurina, Mantič & Ševčík** (Keroplatinae: Orfeliini). An endemic monotypic genus, with the single species, *K. apicospinosa* Kurina, Mantič & Ševčík, 2017, described from Uganda (Kurina *et al.* 2017). Biology and immature stages of the species remain unknown.

***Laurypta* Edwards** (Keroplatinae: Orfeliini)**.** A genus of six described species recorded from the Afrotropical, Australasian/Oceanian, Oriental and Palaearctic Regions. Two species are recorded from the Afrotropics: *L. laevis* (Enderlein, 1910) from Seychelles and *L. scalaris* (Matile, 1970) from Cameroon, Central African Republic, Côte d'Ivoire and Democratic Republic of Congo (Matile 1970, 1974*b*, 1988). Biology and immature stages of the genus remain unknown.

***Lyprauta* Edwards** (Keroplatinae: Orfeliini)**.** A genus of 26 described species, recorded from the Afrotropical, Australasian, Neotropical, Nearctic and Palaearctic Regions. Four species are recorded from the Afrotropics: *L. bezanozano* Matile, 1977 and *L. bilucida* Matile, 1977 from Madagascar; *L. brunneicauda* (Matile, 1970) from Cameroon; and *L. chambordi* (Matile, 1974) from Central African Republic (Matile 1970, 1974*b*, 1977). Biology and immature stages of the genus remain unknown.

58 *Truplaya* (*Truplaya*)

59 *Xenoplatyura*

60 *Macrocera*

61 *Angazidzia*

62 *Hikanoptilon*

63 *Tergostylus*

Figs 18.58–63. Head and thoracic features of Keroplatidae: (58) head and thorax of *Truplaya* (*Truplaya*) *testaceofasciata* Matile, frontal view; (59) head of *Xenoplatyura villiersi* Matile, frontal view; (60) head and thorax of *Macrocera africana* Freeman, lateral view; (61) same, *Angazidzia insolita* Matile; (62) same, *Hikanoptilon demoulini* Matile; (63) same, *Tergostylus alberti* (Tollet).

Abbreviations: anepm – anepimeron; ant – antenna; fc – face; fr – frons; kepst – katepisternum; ltg – laterotergite; plp – palpus; prst – prosternum.

Maborfelia **Matile** (Keroplatinae: Orfeliini)**.** An endemic monotypic genus, with the single species *M. picta* Matile, 1988, recorded from Côte d'Ivoire and Nigeria (Matile 1988). Biology and immature stages of the species remain unknown.

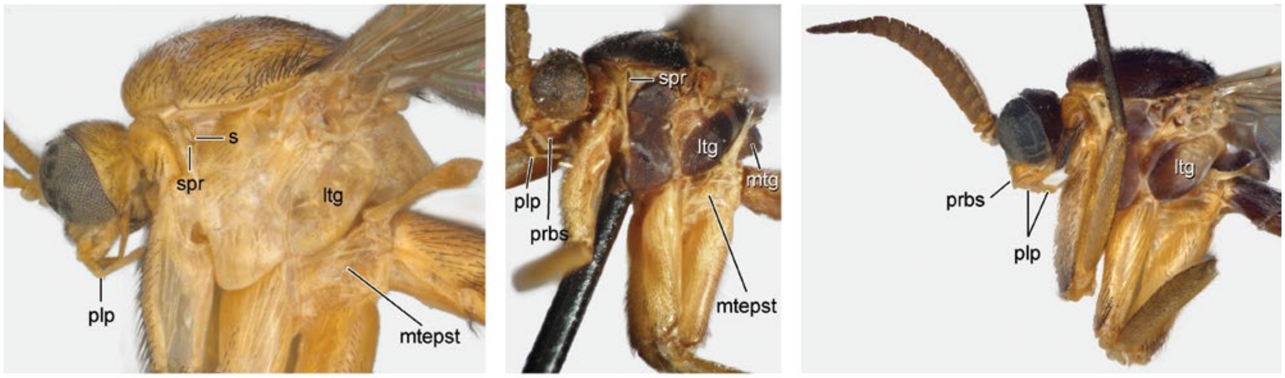
Macrocera **Meigen** (Macrocerinae: Macrocerini)**.** A genus of *ca* 200 described species, occurring in all zoogeographical regions, except Antarctica. Twenty-six species have been recorded from the Afrotropical Region, including nine from Madagascar (Fig. 1), six from Cameroon, five from Uganda, four from Democratic Republic of Congo, three from Comoros, two species each from Kenya, Oman and South Africa and one species from Central African Republic, Croset Is., Ethiopia, Ghana, Côte d'Ivoire, Malawi, Mozambique, Réunion Is., São Tomé and Príncipe, Tanzania and Zimbabwe (Freeman 1970; Matile 1972*b*, 1972*c*, 1977, 1979; Tollet 1955). The biology of the immature stages is summarised by Matile (1990). Larvae are predacious and catch their prey (insects or other small invertebrates), by building a web beneath rocks or inside cavities. An identification key to Afrotropical species was provided by Matile (1970).

Micrepimera **Matile** (Macrocerinae: Robsonomyiini)**.** A genus of three described species, two of which occur in the Oriental Region. One species, *M. berentiana* Ševčík & Papp, 2011, is known from the Afrotropics (Madagascar). Biology and immature stages of the genus remain unknown.

Micromacrocera **Papp** (Macrocerinae: Macrocerini)**.** An endemic monotypic genus, with the single species, *M. stenobasis* Papp, 2008, known from indigenous forest in the Eastern Cape Province, South Africa (Papp 2008). Biology and immature stages of the species remain unknown.

Monocentrota **Edwards** (Keroplatinae: Orfeliini)**.** A genus of 13 described species, recorded from the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Four species are recorded from the Afrotropics: *M. descarpentriesi* (Matile, 1972) and *M. griveaudi* (Matile, 1972) from Madagascar; *M. comoreana* Matile, 1979 from Comoros; and *M. aethiopica* Matile, 1974 from Cameroon and Mozambique (Matile 1972*b*, 1974*b*, 1979). Biology and immature stages of the genus remain unknown.

64 *Maborfelia* 65 *Neoplatyura* 66 *Neoplatyura*



67 *Ralytupa* 68 *Taulyrpa* 69 *Isoneuromyia*

Figs 18.64–69. Head and thoracic features of Keroplatidae (lateral views): (64) *Maborfelia picta* Matile; (65) *Neoplatyura axillariger* (Enderlein); (66) same, detail of thoracic spiracle; (67) *Ralytupa* sp.; (68) *Taulyrpa caeruleovittata* Matile; (69) *Isoneuromyia* sp.

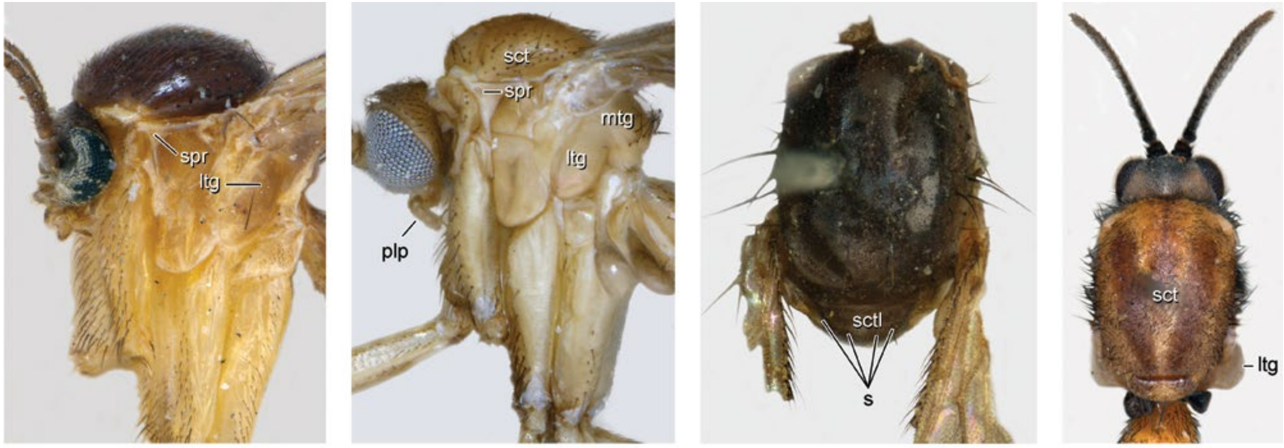
Abbreviations: ltg – laterotergite; mtepst – metepisternum; mtg – mediotergite; plp – palpus; prbs – proboscis; s – seta; spr – spiracle.

Neoplatyura **Malloch** (Keroplatinae: Orfeliini)**.** A genus of 51 described species, occurring in all zoogeographical regions, except Antarctica. Five species are described from the Afrotropical Region, one from Ethiopia, Kenya, Seychelles and South Africa, one species from Côte d'Ivoire and Nigeria and one species each from Cameroon, Comoros and Madagascar (Matile 1970, 1972*b*, 1974*a*: 522, 1979, 1988). Biology and immature stages of the genus remain unknown.

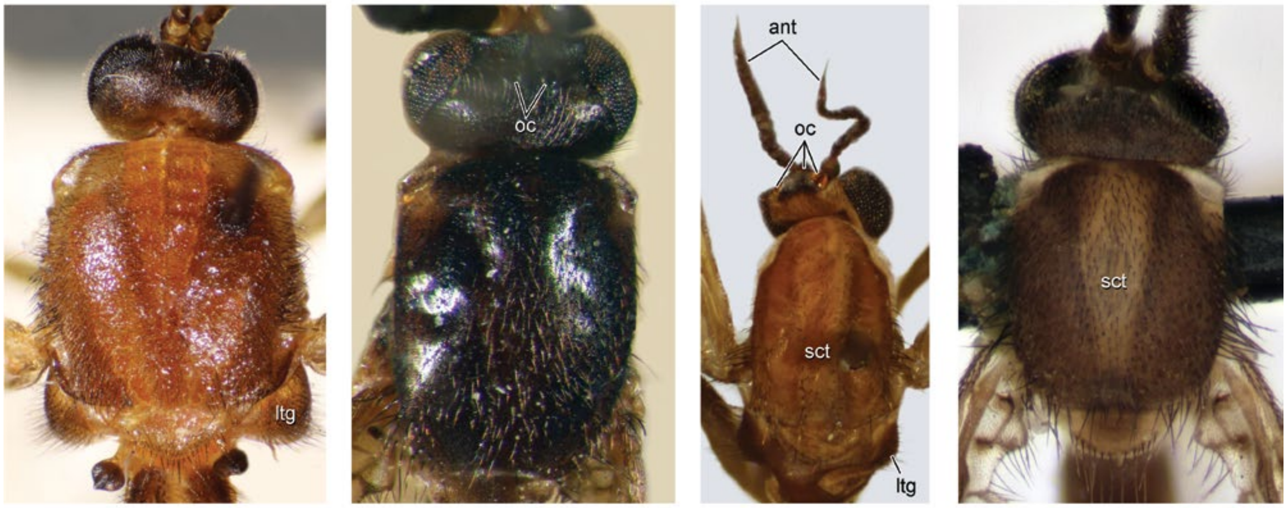
Paracerotelion **Matile** (Keroplatinae: Keroplatini)**.** An endemic monotypic genus, with the single species *P. flavicauda* Matile, 1974, recorded from South Africa (Matile 1974*a*: 514). Biology and immature stages of the species remain unknown.

Proceroplatus **Edwards** (Keroplatinae, Orfeliini)**.** A genus of 38 described species recorded from all zoogeographical regions, except Antarctica. Five species are known from the Afrotropics, recorded from Cameroon, Central African Republic, Democratic Republic of Congo, Tanzania (two species each) and Malawi and Réunion Is. (one species each) (Matile 1970, 1972*b*, 1974*b*). Biology and immature stages of the genus remain unknown.

Pyrtulina **Matile** (Keroplatinae: Orfeliini)**.** A genus of three described species, occurring in the Afrotropical and Australasian/Oceanian (New Caledonia) Regions. One species, *P. pumila* Matile, 1977, is recorded from Madagascar (Matile



70 *Laurypta* 71 *Pyrtulina* 72 *Chiasmoneurella* 73 *Tergostylus*



74 *Keroplatus* 75 *Rofelia* 76 *Monocentrota* 77 *Proceroplatus*

Figs 18.70–77. Heads and thoraces of Keroplatidae: (70) head and thorax of *Laurypta laevis* (Enderlein), lateral view; (71) same, *Pyrtulina dubia* Matile; (72) thorax of *Chiasmoneurella edwardsiana* Matile, dorsal view; (73) head and thorax of *Tergostylus alberti* Matile, dorsal view; (74) same, *Keroplatus heimi* Matile; (75) same, *Rofelia rothiana* (Matile); (76) same, *Monocentrota aethiopica* Matile; (77) same, *Proceroplatus aedon* (Vanschuytbroeck).

Abbreviations: ant – antenna; ltg – laterotergite; mtg – mediotergite; oc – ocellus; plp – palpus; s – setae; sct – scutum; sctl – scutellum; spr – spiracle.

1977) in the Afrotropics. Biology and immature stages of the genus remain unknown.

***Ralytupa* Edwards** (Keroplatinae: Orfeliini)**.** A genus of 37 described species, almost exclusively known from the Afrotropical Region (36 species), with the type species of the genus described from the Oriental Region (Thailand). Twelve species have been recorded from both Cameroon and Nigeria, eleven from Côte d'Ivoire, eight from Central African Republic, six from Uganda, three from Ghana, two from Sierra Leone and Tanzania and one from Liberia. One species each are recorded from Democratic Republic of Congo, South Africa and Sudan (Matile 1970, 1972*a*, 1974*b*, 1975, 1988). Biology and immature stages of the genus remain unknown. An identification key to Afrotropical species was provided by Matile (1975).

***Rofelia* Matile** (Keroplatinae: Orfeliini)**.** An endemic monotypic genus, with the single species *R. rothiana* (Matile, 1972), described from Madagascar (Matile 1972*b*). Biology and immature stages of the species remain unknown.

***Rutylapa* Edwards** (Keroplatinae: Orfeliini)**.** A genus of 18 described species, recorded from the Afrotropical, Australasian, Oriental and Palaearctic Regions. Six species are recorded from the Afrotropics, three species from Madagascar, two from Central African Republic and one from Réunion Is. (Matile 1970, 1972*b*, 1977). Biology and immature stages of the genus remain unknown.

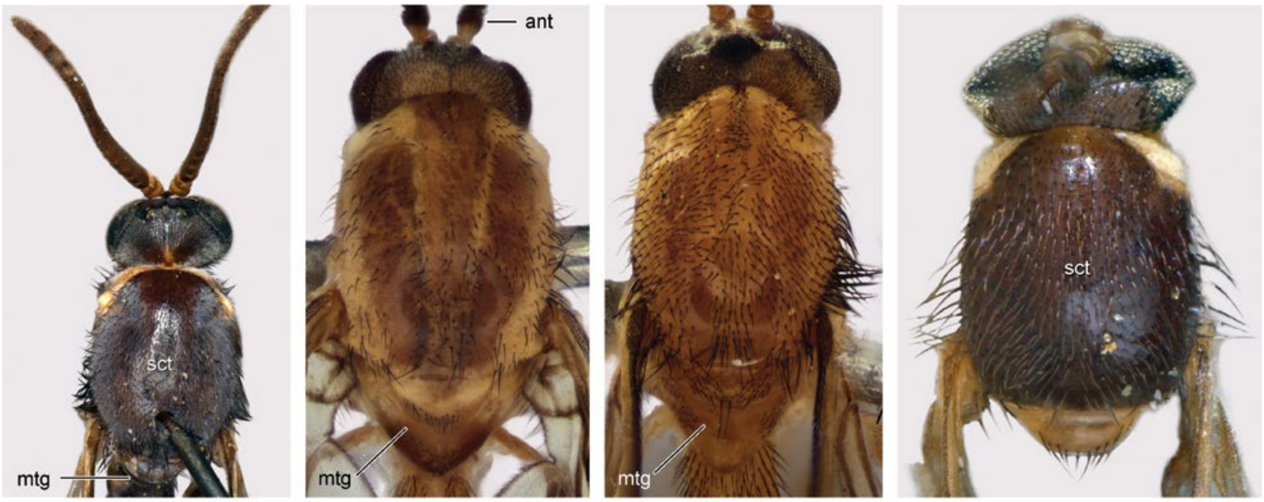
***Schizocyttara* Matile** (Keroplatinae: Orfeliini)**.** An endemic genus of two described species, *S. brincki* (Matile, 1974) and *S. turneri* (Matile, 1974), both described from South Africa (Matile 1974*a*: 517). Biology and immature stages of the genus remain unknown.

***Taulyrpa* Edwards** (Keroplatinae: Orfeliini)**.** A genus of five described species, recorded from the Afrotropical and Neotropical Regions. The two Afrotropical species, *T. caeruleovittata* (Matile, 1972) and *T. stuckenbergi* Matile, 1977, were both described from Madagascar (Matile 1972*b*). Biology and immature stages of the genus remain unknown.

***Tergostylus* Matile** (Keroplatinae: Keroplatini)**.** An endemic genus of six described species, two recorded from Bioko Is. (Equatorial Guinea) (as Fernando Póo), three from Central African Republic, two each from Cameroon and Democratic Republic of Congo and one from Côte d'Ivoire (Matile 1990). Although the biology remains unknown, larvae have been found on polypore fungi growing on dead wood, primarily in a corner formed by the upper surface of the bracket fungus and the trunk (Matile 1970, 1974*a*).

***Tolletia* Matile** (Keroplatinae: Keroplatini)**.** An endemic monotypic genus, with the single species, *T. vrydaghi* (Tollet, 1955), recorded from Bioko Is. (Equatorial Guinea) (as Fernando Póo), Cameroon, Central African Republic, Democratic Republic of Congo and Nigeria (Evenhuis 2006). Biology and immature stages of the species remain unknown.

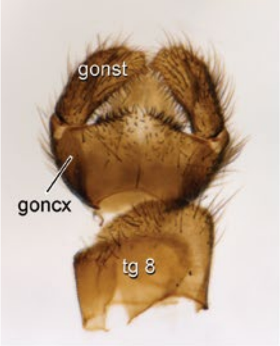
***Truplaya* Edwards** (Keroplatinae: Orfeliini)**.** A genus of 27 described species, four occurring in the Oriental Region and one in the Palaearctic (Israel). Twenty-two species are recorded from the Afrotropics, with the subgenus *Truplayella* being endemic. Eight species are recorded from Côte d'Ivoire, six from both Democratic Republic of Congo and Nigeria, three from both Angola and Uganda, two from Republic of Congo, Kenya, Liberia, Madagascar, South Africa and Tanzania and one from Benin, Burkina Faso, Cameroon, Guinea, Malawi, Rwanda, Sierra Leone and Zimbabwe (Matile 1978). Biology and immature stages of the genus remain unknown. An identification key to Afrotropical species was provided by Matile (1978).



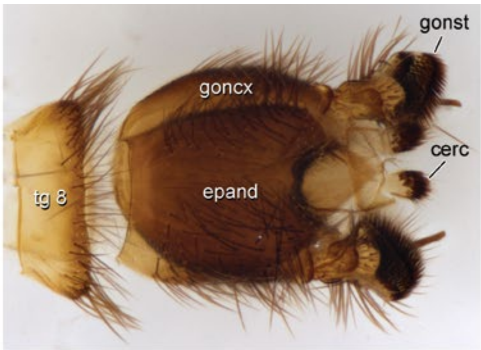
78 *Isoneuromyia* 79 *Rutylapa* 80 *Ralytupa* 81 *Laurypta*

Figs 18.78–81. Heads and thoraces of Keroplatidae (dorsal views): (78) *Isoneuromyia* sp.; (79) *Rutylapa annulata* Matile; (80) *Ralytupa angusta* Matile; (81) *Laurypta laevis* (Enderlein).

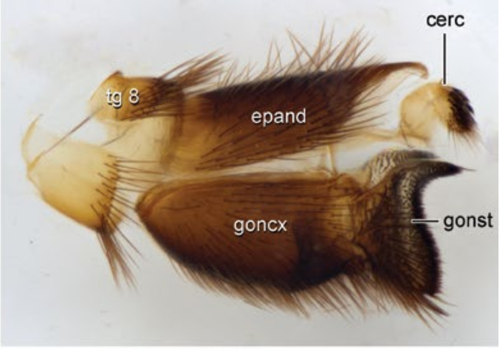
Abbreviations: ant – antenna; mtg – mediotergite; sct – scutum.



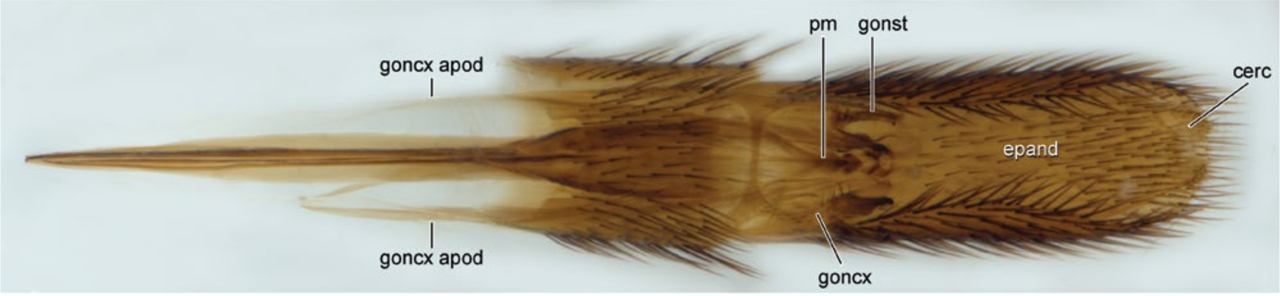
82 *Ctenoceridion* ♂



83 *Ralytupa* ♂

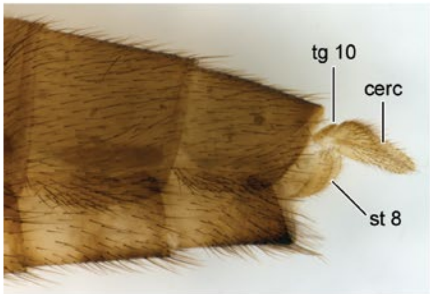


84 *Ralytupa* ♂

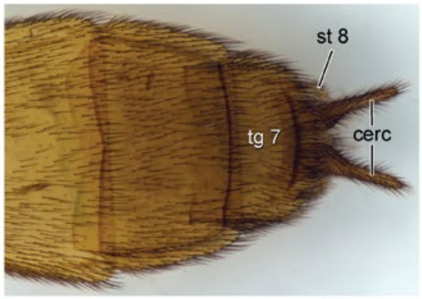


85 *Xenoplatyura* ♂

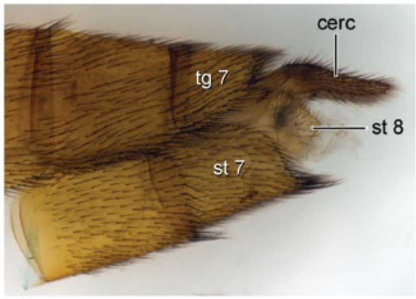
86 *Xenoplatyura* ♂



87 *Ctenoceridion* ♀



88 *Ralytupa* ♀



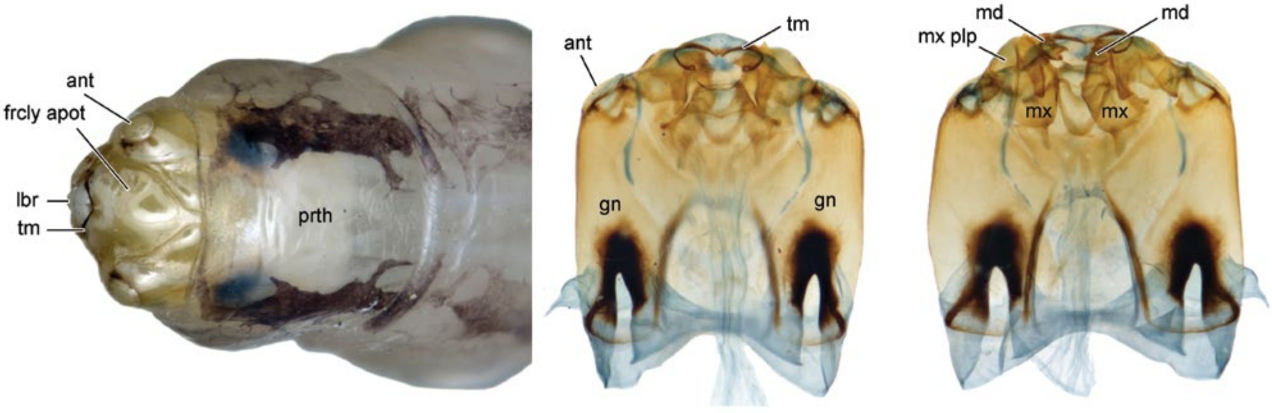
89 *Ralytupa* ♀

Figs 18.82–89. Male and female terminalia of Keroplatidae: (82) male terminalia of *Ctenoceridion* sp., ventral view; (83) same, *Ralytupa bacillata* Matile, dorsal view; (84) same, lateral view; (85) same, *Xenoplatyura* sp., ventral view; (86) same, lateral view; (87) female terminalia of *Ctenoceridion* sp., lateral view; (88) same, *Ralytupa* sp., dorsal view; (89) same, lateral view.

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; pm – paramere; st – sternite; tg – tergite.

90 *Keroplatus*

91 *Keroplatus*



92 *Keroplatus* 93 *Keroplatus* 94 *Keroplatus*

Fig. 18.90–94. Immature stages of Keroplatidae (all non-Afrotropical): (90) living larvae of *Keroplatus* sp. on bracket fungus; (91) habitus of fourth-instar larva of *Keroplatus* sp., dorsal view; (92) same, head, dorsal view; (93) same, head capsule, dorsal view; (94) same, ventral view.

Abbreviations: ant – antenna; frcly apot – frontoclypeal apotome; gn – gena; lbr – labrum; md – mandible; mx – maxilla; mx plp – maxillary palpus; prth – prothorax; rect ppl – rectal papilla; tm – torma.

Xenoplatyura **Malloch** (Keroplatinae: Orfeliini)**.** A genus of 50 species occurring in all zoogeographical regions, except Antarctica. Twenty-four species are recorded from the Afrotropical Region, including eight species from Cameroon, four from South Africa; two each from Central African Republic and Nigeria and one species each from: Burkina Faso, Côte d'Ivoire, Guinea, Madagascar, Malawi, Mali, Oman, Senegal, Seychelles and Togo (Chandler 2000; Matile 1970, 1972*b*, 1974*a*: 525, 1974*b*, 1984, 1988, 1998). Numerous undescribed species are available in various collections.

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LYGISTORRHINIDAE 19

(Long-beaked Fungus Gnats)

Vladimir Blagoderov

Fig. 19.1. *Lygistorrhina sanctaecatharinae* Thompson (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized gnats (body length: 2.5–7.0 mm), with characteristically reduced wing venation and elongate abdomen and legs (Figs 1, 2, 9); colour light brown to black with, or without, orange, yellow, or white markings. For detailed diagnosis see (Hippa *et al*. 2005).

Head round (*Seguyola* Matile) (Fig. 9), or conical posteriorly (*Lygistorrhina* Skuse) (Fig. 3), with or without distinct row of postocular setae of variable size; 2 (*Seguyola*), or 3 (*Lygistorrhina*) closely approximated ocelli, sometimes median ocellus smaller in size; head dichoptic or holoptic, with ommatrichia; compound eye with ommatidia often larger dorsally; antenna cylindrical, shorter, or up to 2 × as long as thorax; often with flagellomeres of contrasting colours; antenna of *Seguyola* with 11 flagellomeres (Fig. 9), *Lygistorrhina* with 14 flagellomeres (Fig. 3), each flagellomere with strong dorsal setae; mouthparts forming proboscis, composed of 1-segmented palpus, hypopharynx and labella (Fig. 3), very short in *Seguyola* (Fig. 9), long (up to abdomen length) in *Lygistorrhina* (Fig. 3); palpus without sensory pit.

Thorax (Fig. 3) short, seemingly globular; mesonotum evenly setulose; scutellum small, with subapical row of setae;

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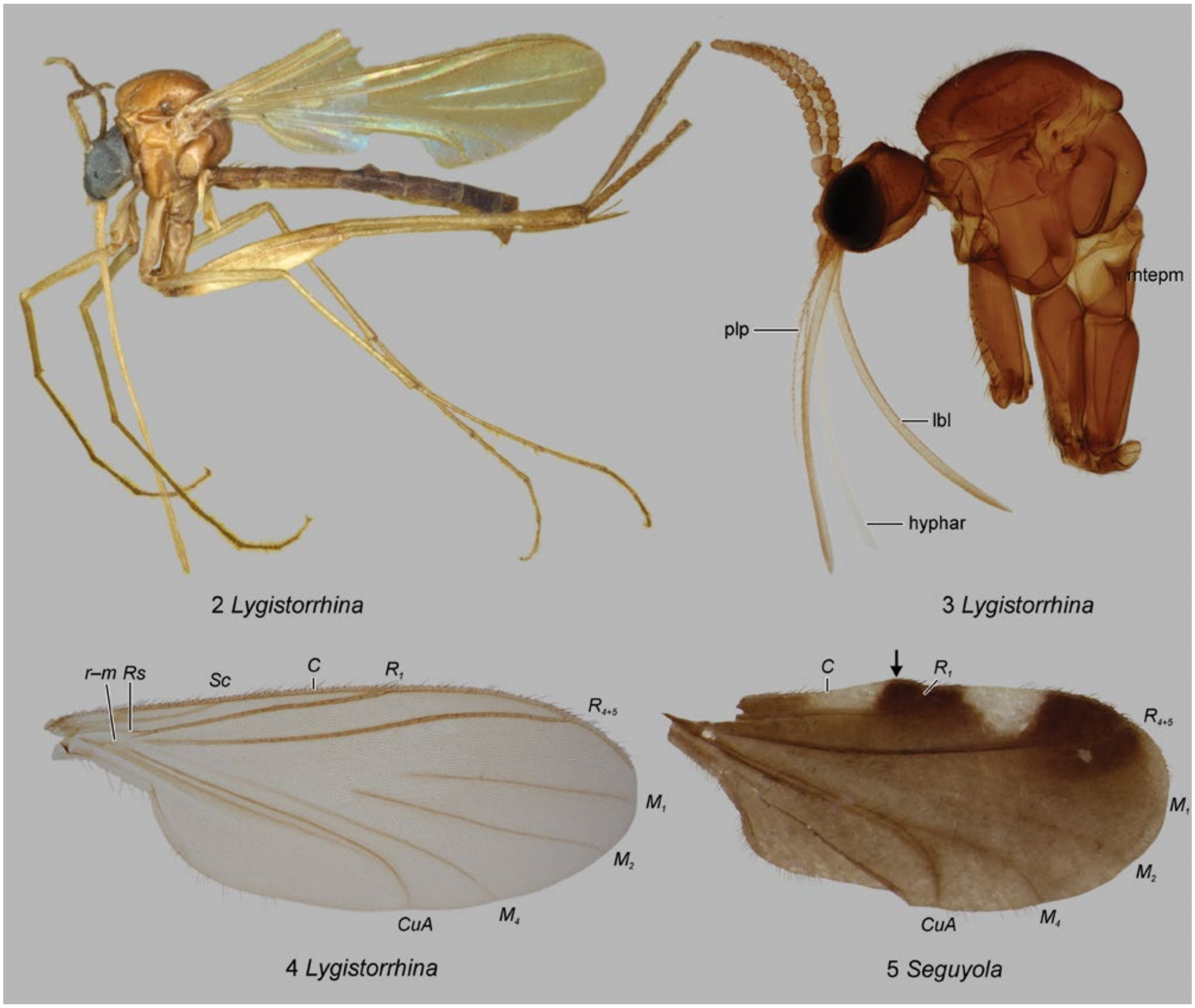
laterotergite strongly produced lateroventrally, with marginal row of setae (*Lygistorrhina*), or dispersed setae (*Seguyola*); antepronotum and proepisternum setulose; other thoracic pleura bare; suture between anepisternum and katepisternum distinct, or somewhat absent anteriorly; metepisternum, plus metepimeron, higher than wide, weakly sclerotised, with more strongly sclerotised anterior and posterior margins; phragma not produced into abdomen. Wing (Figs 4, 5), with costal vein (*C*) extending beyond apex of vein R_{4+5}, in *Segyuola* with swelling at mid length, proximal to apex of vein R_1; vein *Sc* very short, often weak, ending free, or joining wing margin; vein R_1 usually short, ending proximal to mid length of wing (well beyond in *L. magna* Matile, 1996); base of vein *Rs*, crossvein *r–m* and base of M_4 very short, often virtually indiscernible, if present, near base of wing; anal lobe distinct; anal veins very short; vein R_{4+5} unbranched; basal part of vein *M* reduced to a fold; base of veins M_1 and M_2 usually reduced, veins often not reaching wing margin; vein M_4 short, connected to *CuA* by *m–cu* crossvein, or free at base; wing membrane with macrotrichia not arranged in rows. Legs long, delicate; tibial spurs 1 : 2 : 2 (1 : 1 : 2 or 0 : 1 : 2 in some non-Afrotropical genera, Hippa *et al*. 2005); hind leg often enlarged, with femora, tibia and tarsomere 1 thickened, club-shaped (Figs 2, 9); claws simple, pointed, or blunt; pulvilli seta-like; empodium absent.



Figs 19.2–5. Habitus, head and thorax and wings of Lygistorrhinidae: (2) habitus of *Lygistorrhina edwardsina* (Matile), lateral view; (3) head and thorax of *L*. cf. *austroafricana* Blagoderov, Papp & Hippa, lateral view; (4) same, wing, dorsal view; (5) same, *Seguyola vicina* Matile (arrow indicates swelling on costal vein adjacent to vein R_1).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; hyphar – hypopharynx; lbl – labellum; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; mtepm – metepimeron; plp – palpus; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial-medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein.

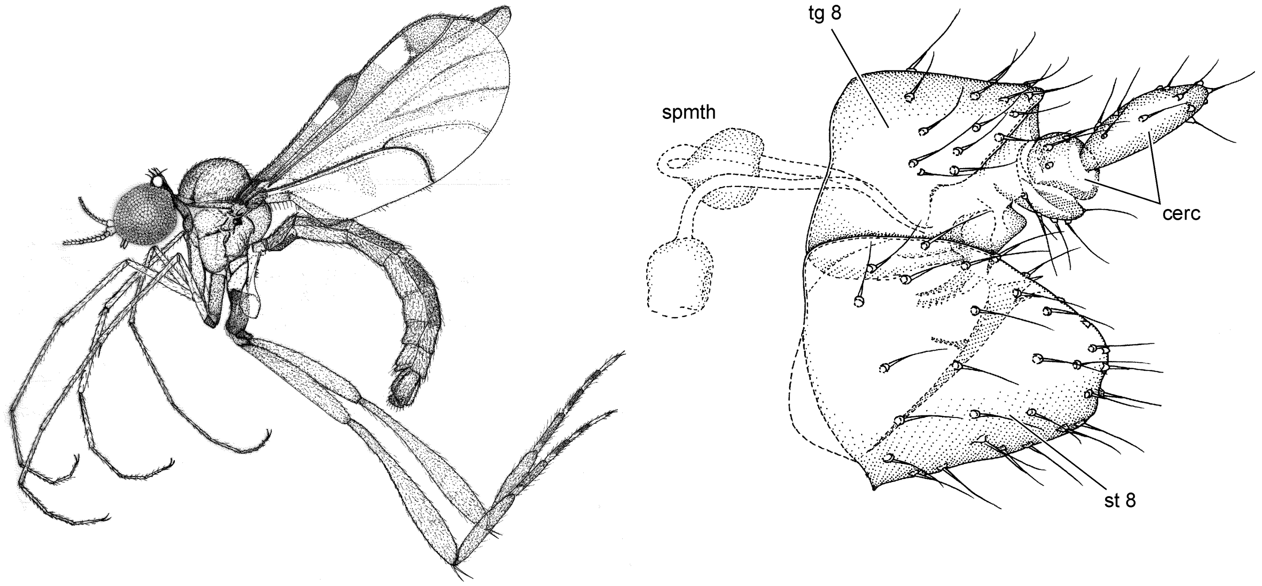
Abdomen with male sternite 9 (hypandrium) absent; tergite 9 (epandrium) with funnel-shaped apodeme extending anteriorly into abdomen; gonocoxites fused basoventrally, but with distinct cleft posteriorly; gonostylus bacilliform (in Cenozoic taxa), usually with long basomedial seta and apical teeth (absent in non-Afrotropical *Loyugesa* Grimaldi & Blagoderov), apical part often with numerous short spinose setae; aedeagus membranous, except dome-shaped paramere (Figs 6, 7); females in studied taxa with 2-segmented cercus; 2 sclerotised spermathecae present (Fig. 10).

Lygistorrhinidae are easily distinguished from other Sciaroidea by combination of modified mouthparts, reduced wing venation and enlarged hind leg with club-like tibia.

6 *Seguyola* ♂

7 *Seguyola* ♂

8 *Lygistorrhina* ♀



9 *Seguyola* ♂

10 Lygistorrhinidae sp. ♀

Figs 19.6–10. Male and female terminalia and habitus of Lygistorrhinidae: (6) male terminalia of *Seguyola variegata* Matile, dorsal view; (7) same, ventral view; (8) female terminalia of *Lygistorrhina cf. austroafricana* Blagoderov, Papp & Hippa, lateral view; (9) male habitus of *Seguyola variegata* Matile; (10) female terminalia of Lygistorrhinidae sp., lateral view. Figs 6, 7, 9 (courtesy J. Kjaerandsen, CC BY-NC 2.0 UK), Fig. 10 (Hippa *et al.* 2005, fig. 12A, © Magnolia Press 2005).

Abbreviations: cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm – paramere; spmth – spermatheca; st – sternite; tg – tergite; tg apod – tergite apodeme.

Biology and immature stages

Lygistorrhinidae are quite rare in collections and their biology is virtually unknown. Individual specimens and, less often, swarms have been sampled in Malaise traps from warm temperate and tropical forests. Adult *Lygistorrhina* are known as flower visitors (Ollerton *et al.* 2009; pers. obs.). The immature stages remain unknown.

Economic significance

No species of Lygistorrhinidae are known to have any economic importance.

Classification

Edwards (1925) first recognised Lygistorrhinidae as a subfamily of Mycetophilidae (Lygistorrhininae). Hendel (1936) first used it at family rank, although some North American authors even now prefer to include the family in Mycetophilidae *sensu lato* (Vockeroth 1981, *et auctt*.) Tuomikoski (1966) proposed the inclusion of *Lygistorrhina* in the family Keroplatidae, but this view was not accepted, either by Thompson (1975), or Matile (1990*a*). Matile (1997), Blagoderov & Grimaldi (2004) and Hippa & Vilkamaa (2005, 2006) suggested sister-group relationships between Lygistorrhinidae and Mycetophilidae. The more recent molecular phylogenetic studies of Bertone *et al*. (2008) and Wiegmann *et al.* (2011) do not provide strong support for the position of Lygistorrhinidae within the superfamily Sciaroidea.

Lygistorrhinidae comprises 50 species in 15 genera (Fungus Gnats Online Team 2014; Pape *et al*. 2011), including 13 species in one extant and seven extinct genera. Extant genera + *Parisognoriste* Blagoderov + *Palaeognoriste* Blagoderov, Hippa & Nel, from the Eocene ambers of Europe, form a monophyletic group, being a crown-group with respect to Cretaceous taxa (Blagoderov & Grimaldi 2004; Blagoderov *et al*. 2010). Recently the family is distributed worldwide in warm temperate and tropical forests.

Identification

An identification key to recent world genera was provided by Hippa *et al*. (2005). Keys to *Lygistorrhina* were provided by Matile (1990*b*) and Blagoderov *et al*. (2013). No recent keys to *Seguyola* are available. Lygistorrhinidae are best preserved direct into ethanol for later slide-mounting (see Chapter 2).

Key to genera of Afrotropical Lygistorrhinidae

1. Proboscis long, 4 X or more as long as height of head (Figs 2, 3); wing with costal vein (C) without swelling at apex of vein R_1 (Fig. 4) . . . . *Lygistorrhina* Skuse

– Proboscis short, at most ½ × height of head (Fig. 9); wing with costal vein (*C*) with swelling at apex of vein R_1 (Fig. 5, indicated with arrow) . . . .*Seguyola* Matile

Synopsis of the Fauna

Fifteen genera and 50 species have been described globally, although diversity of the family may be significantly higher. Only two genera, *Lygistorrhina sensu stricto* and *Seguyola*, have been recorded from the Afrotropical Region.

***Lygistorrhina* Skuse.** A genus of 22 described species, occurring in all zoogeographical regions, except Antarctica. Six described species are known from the Afrotropical Region, all belonging to the nominative subgenus. One additional unnamed species is known, based on the description of a female from Madagascar (Matile 1990*b*). Additional species are expected to occur in the region, especially in tropical forests. The writer has examined recent material (including males) from Réunion Is. and the genus has also been recently reported from Mauritius (A.H. Kirk-Spriggs, pers. comm. 2017). Identification keys for species are provided by Matile (1990*b*) and (Blagoderov *et al*. 2013).

***Seguyola* Matile.** An endemic Afrotropical genus, known from two described species, *S. variegata* Matile, 1990 and *S. vicina* Matile, 1990, both confined to equatorial Africa (Matile 1996). Additional species are expected to occur in the region, especially in forests. No identification key is available and species can only be identified by reference to the original descriptions.

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MYCETOPHILIDAE 20

(Fungus Gnats)

Geir Søli

Fig. 20.1. Female of *Clastobasis* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized, slender to moderately robust gnats (body length: 1.7–9.4 mm) (Figs 1–10). Colour varied; body commonly dull yellowish, brown, or black, rarely brightly marked. Wing sometimes infuscate or with markings. Legs with elongate coxae; tibia with strong apical spurs and, in most genera, well-developed setae (bristles). Eyes not meeting above antennae. Wing venation rather simple, commonly with distinct anterior (M_1+M_2) and posterior (M_4 and *CuA*) forks; basal median cell (*bm*) extends from level of humeral vein (*h*) to wing margin.

Head (Figs 11–16) with posterior surface commonly flat, to slightly concave, more deeply concave in, e.g., *Parempheriella* Matile (Fig. 4); head inserted below level of upper margin of strongly arched thorax; eyes usually situated on more ventral part of head, widely separated above; complete eye bridge present in the Oriental genus *Paramanota* Tuomikoski; occiput sometimes with row of strong setae just posterior to eye, connected across vertex, e.g., *Allactoneura* de Meijere (Fig. 8) and *Manota* Williston (Figs 6, 13); vertex with 3 ocelli arranged in deep to very shallow triangular arrangement, median ocellus usually in front of lateral ocelli, sometimes reduced or absent (Mycomyinae); lateral ocelli commonly inserted close to eye

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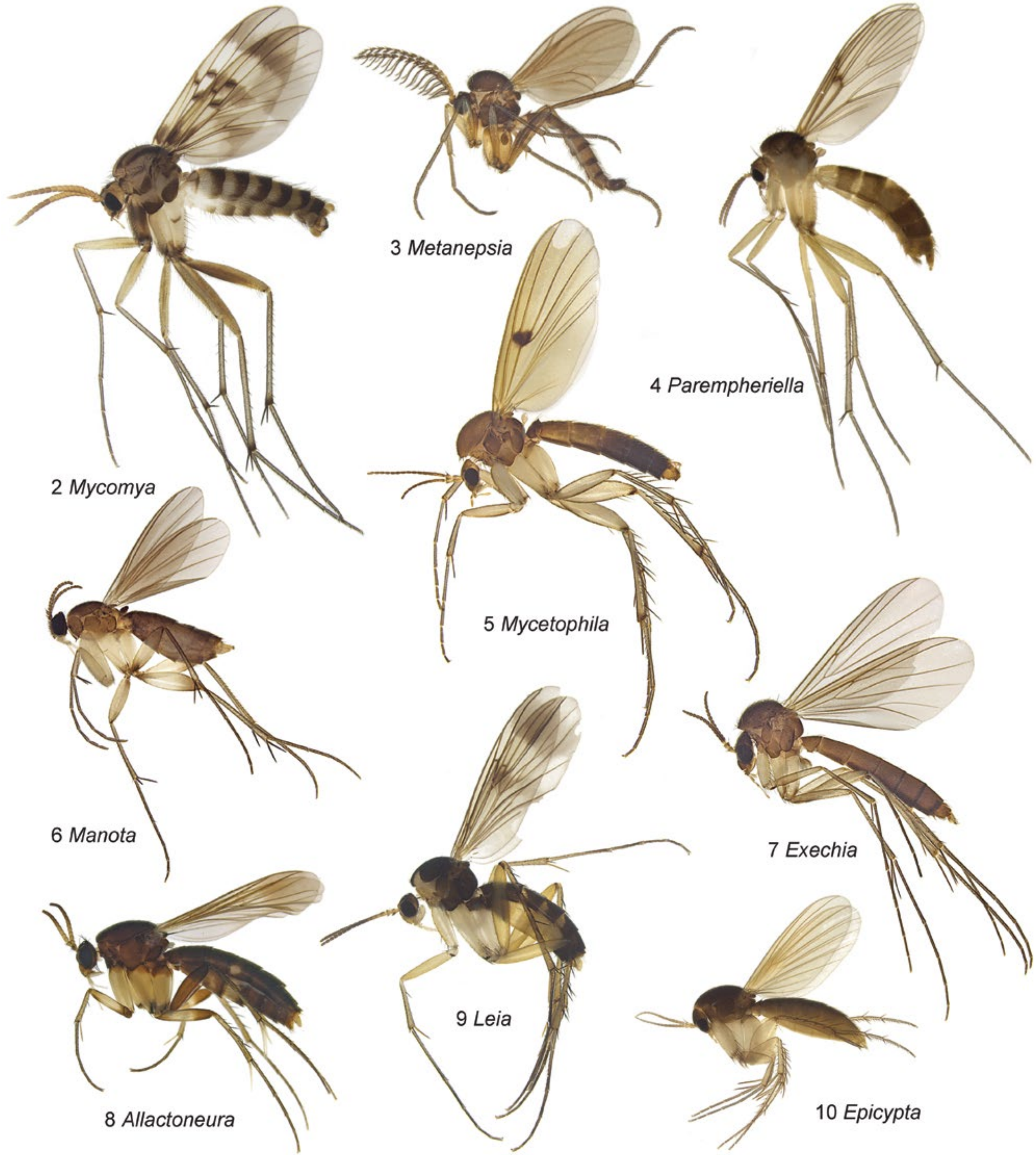
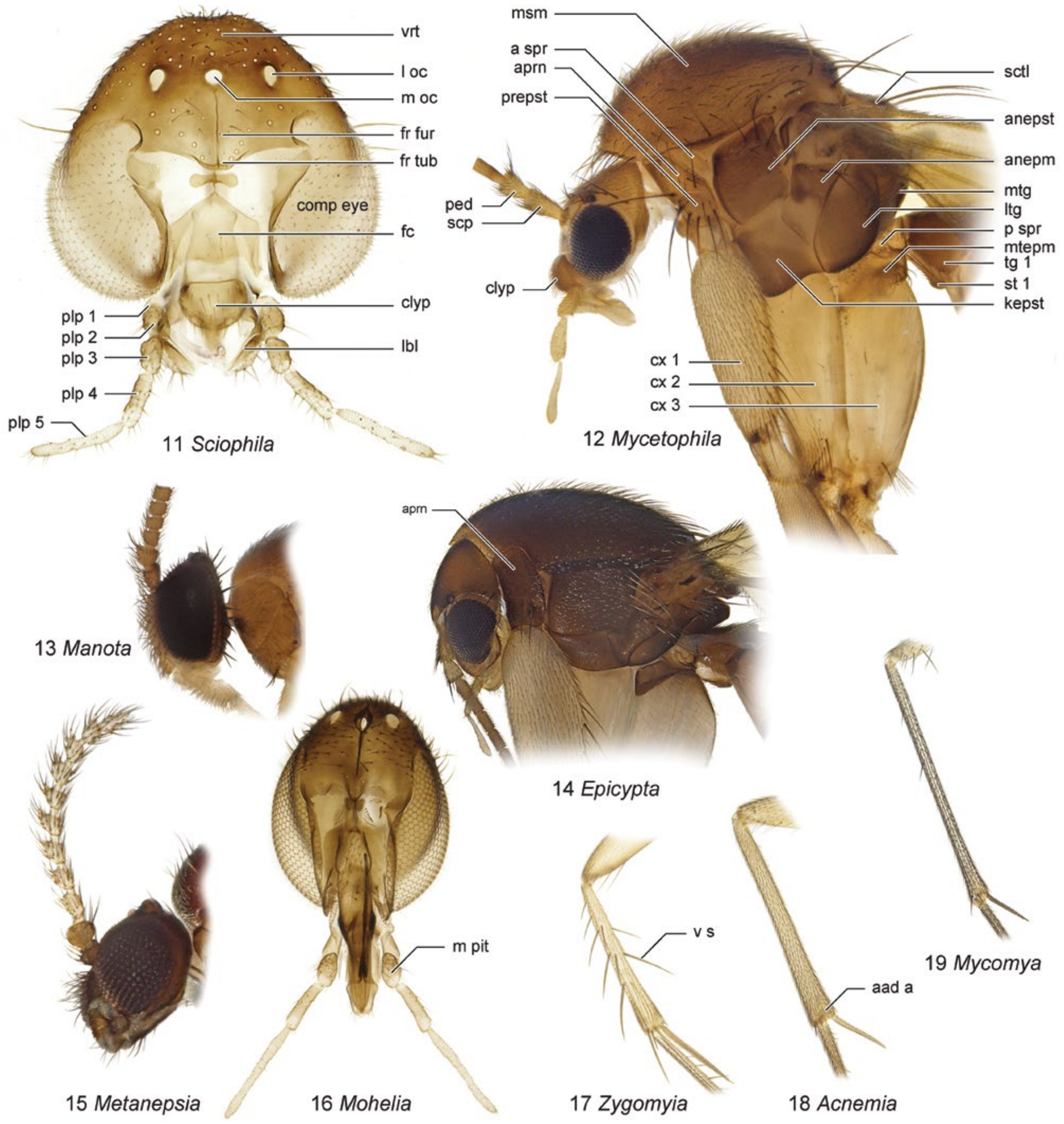


Figs 20.2–10. Habitus of Afrotropical Mycetophilidae (lateral views): (2) *Mycomya* sp.; (3) *Metanepsia* sp.; (4) *Parempheriella* sp.; (5) *Mycetophila* sp.; (6) *Manota* sp.; (7) *Exechia* sp.; (8) *Allactoneura* sp.; (9) *Leia* sp.; (10) *Epicypta* sp.

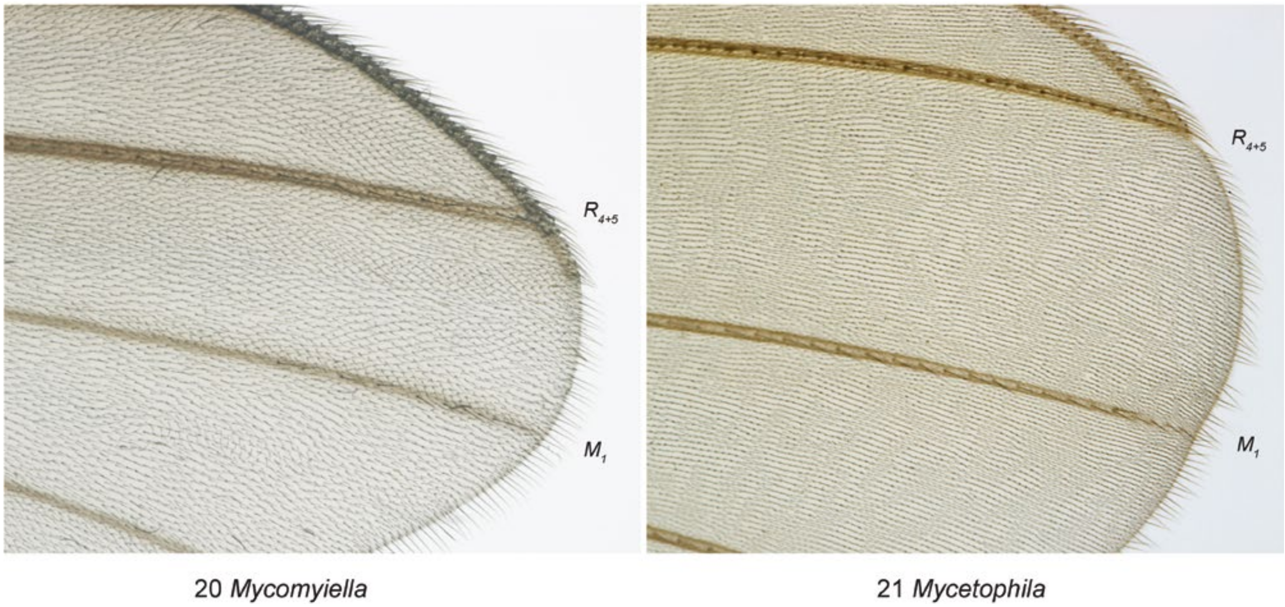


Figs 20.11–19. Heads, thoraces and legs of Mycetophilidae: (11) head of *Sciophila kakumensis* Søli, frontal view; (12) head and thorax of *Mycetophila* sp., lateral view; (13) head of *Manota* sp., lateral view; (14) head and thorax of *Epicypta* sp., lateral view; (15) head of *Metanepsia* sp., lateral view ♀; (16) head of *Mohelia* sp., frontal view; (17) mid tibia of *Zygomyia* sp., lateral view; (18) fore leg of *Acnemia* sp., lateral view; (19) same, *Mycomya* sp., lateral view.

Abbreviations: a spr – anterior spiracle; aad a – anteroapical depressed area; anepm – anepimeron; anepst – anepisternum; aprn – antepronotum; clyp – clypeus; comp eye – compound eye; cx – coxa; fc – face; fr fur – frontal furrow; fr tub – frontal tubercle; kepst – katepisternum; l oc – lateral ocellus; lbl – labellum; ltg – laterotergite; m oc – median ocellus; m pit – median pit; msm – mesonotum; mtepm – metepimeron; mtg – mediotergite; oc – ocellus; p spr – posterior spiracle; ped – pedicel; plp – palpal segment; prepst – proepisternum; scp – scape; sctl – scutellum; st – sternite; tg – tergite; v s – ventral seta (bristle); vrt – vertex.

margin; all ocelli absent only in *Syndocosia* Speiser; frons between ocelli and antennal bases bare, or setulose medially, often produced into distinct frontal tubercle (Fig. 11); frontal furrow sometimes present, running between median ocellus and frontal tubercle (Fig. 11); antenna usually inserted at, or slightly above middle of head; length varying from ½ to 2 × length of mesonotum; antenna with scape and pedicel sometimes with numerous strong setae (Fig. 12); flagellum usually thread-like, serrated to strongly pectinate in some species of *Dziedzickia* Johannsen and *Metanepsia* Edwards (Fig. 3); principally with 14 flagellomeres, but reduced to 8–9 in females of undescribed Afrotropical *Metanepsia* (Fig. 15) and 12–13 in both sexes of some undescribed Afrotropical *Exechia* Winnertz; each flagellomere usually cylindrical, longer than broad, sometimes compressed, or flattened (*Boletiniella* Matile, *Dziedzickia*, *Metanepsia*), clothed in short setulae, sometimes with interspersed short setae; face usually broad and setulose, very high in *Manota*; clypeus (Fig. 11) commonly rounded, setulose, forming sclerite below face, somewhat prolonged in *Dinempheria* Matile, sometimes virtually entirely fused with face; well-developed cibarial pump, attached to lateral parts of clypeus, nearly always present; labrum present, or absent, with or without setae; mouthparts normal, slightly prolonged in *Mohelia* Matile (Fig. 16); labella usually large and fleshy, pillow-like, with pseudotracheae, but greatly reduced in, *e.g.*, *Metanepsia* (Fig. 15); lacinia usually small, weakly-sclerotised; palpus principally 5-segmented, although first 2 segments usually very short, sometimes partly, or entirely, fused and barely visible in dry-mounted specimens; third segment, commonly referred to as antepenultimate segment, invariably well-developed, usually with modified, often club-shaped setae arranged in median pit (Fig. 16); terminal and penultimate segments both commonly longer than third, sometimes distinctly longer; rarely entirely reduced, as in *Metanepsia* (Fig. 15).

Thorax stout, about as high as long (Fig. 2), to more compressed and distinctly longer than high (Figs 8, 10); thoracic sclerites varying considerably in size, shape and distinctness; lateral cervical sclerite triangular, bare; antepronotum well-developed, usually setulose, dorsally fused with postpronotum, forming bare, collar-like structure above neck, ventrally partly, or entirely, fused with proepisternum, suture between latter usually distinct, but poorly-developed in, *e.g.*, *Epicypta* Winnertz (Fig. 14); proepimeron less conspicuous, usually triangular, but very prominent in, *e.g.*, *Allactoneura*; anterior thoracic spiracle located between antepronotum and anepisternum; shape of mesonotum varies from evenly to highly arched, with anterior parapsidal suture and median transverse suture; vestiture of mesonotum variable, usually comprising setulae and setae, either evenly dispersed, or arranged in clearly defined lines; mediotergite usually bare, more rarely with medially and/or laterally, arranged setae; laterotergite prominent, ovate, bare or setulose, varying from evenly arched to strongly protruding, sometimes with pronounced longitudinal keel; anepisternum invariably well-developed, triangular, quadrate to subquadrate, in some genera greatly developed, usually at expense of katepisternum (*e.g.*, *Epicypta*, Fig. 14), with or without setulae and setae; anterior and posterior basal area usually recognisable; katepisternum (preepisternum 2) separated from anepisternum by anapleural suture, commonly about as large as anepisternum, but sometimes much narrower, *e.g.*, *Epicypta*, usually bare; anepimeron strongly narrowed ventrally, commonly bare, but in several Mycetophilini genera upper border with row of strong setae; metanotum narrow, bare, situated posterior to mediotergite, laterally fused with metapleuron by membranous area; distinct pleural suture dividing metapleuron into anterior metepisternum and posterior metepimeron; posterior spiracle located below laterotergite and above metapleuron (Fig. 12). Wing usually *ca* 2.7 × as long as wide, but



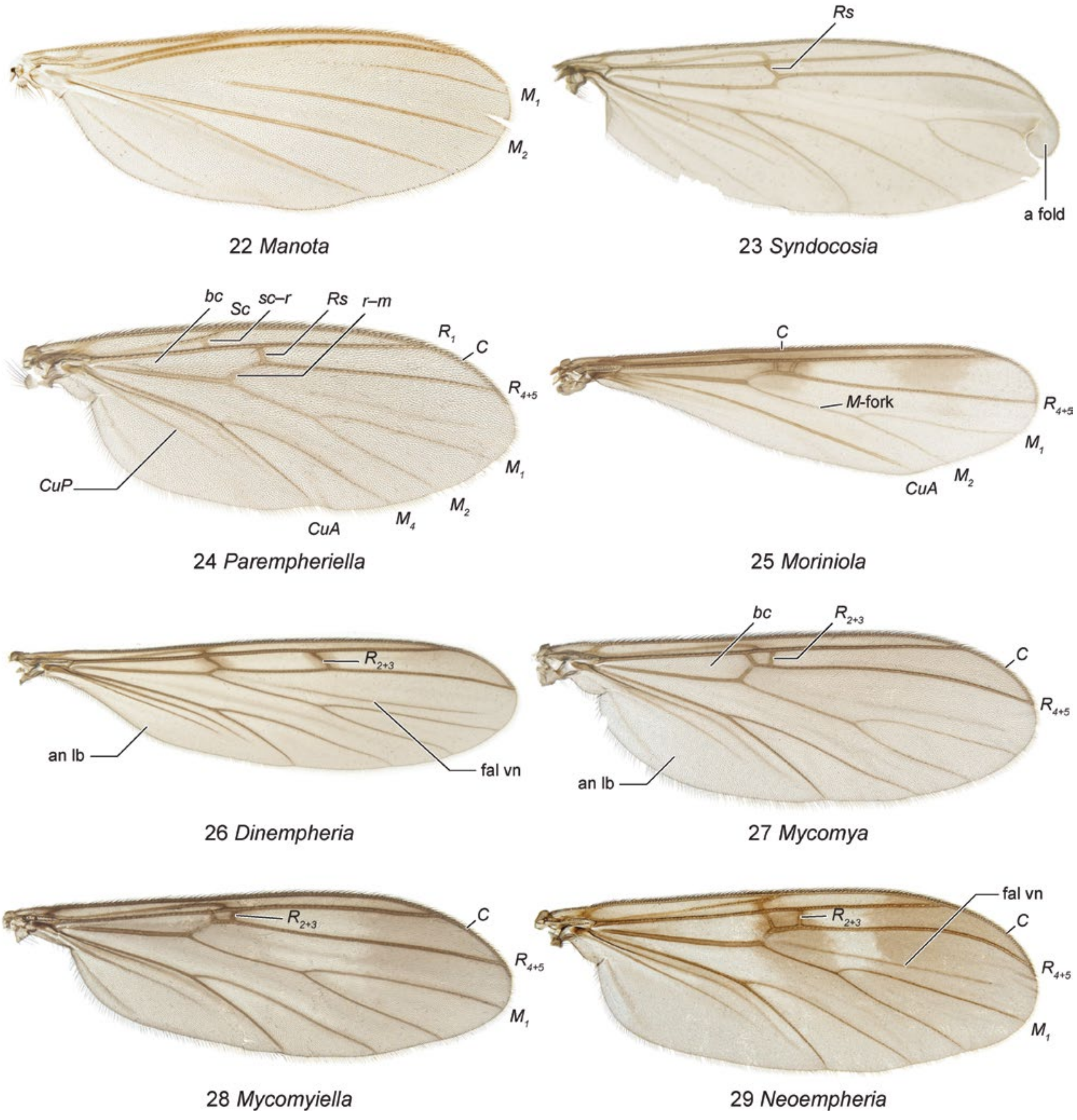
20 *Mycomyiella*
21 *Mycetophila*

Figs 20.20–21. Wing apex of Mycetophilidae (dorsal views): (20) *Mycomyiella* sp.; (21) *Mycetophila* sp.

Abbreviations: M_1 – first branch of media; R_{4+5} – third branch of radius.

aspect ratio varies from 2–3.5; *Allactoneura* peculiar in ability to fold wings longitudinally at rest in vespid-like manner (Fig. 8); wing membrane commonly transparent (Figs 6, 7), sometimes with dark wing apex and/or additional transverse fascia, maculae, or with anterior border infuscate (Figs 2, 5, 9); usually densely clothed in microtrichia on both sides, often with few to numerous macrotrichia, or true setae; if microtrichia absent, setae present on greater part of membrane; microtrichia arranged in fine, regular lines in Mycetophilinae (Fig. 21), more irregularly so in other subfamilies (Fig. 20); wing venation rather variable, much used in classification; venation slightly reduced in, *e.g.*, *Acnemia* Winnertz (Fig. 32) and *Moriniola* Matile (Fig. 25), more reduced still in *Azana* Walker (Fig. 30) and *Manota* (Fig. 22); radius (*R*) invariably with setae, not uncommonly both dorsally and ventrally; veins *M* and *CuA* with or without setae, usually on dorsal side only; costal vein (*C*) commonly ends at apex of vein R_{4+5}, but in numerous genera extending beyond this point, ending between apices of veins R_{4+5} and M_1 (Figs 41, 44); subcostal vein (*Sc*) always traceable, commonly well-developed, short and bent towards vein *R* in several genera of Mycetophilinae; humeral crossvein (*h*) invariably present; crossvein *sc–r* frequently present between base of humeral vein (*h*) and apex of vein *Sc*; vein *Sc* not uncommonly reduced beyond crossvein *sc–r*, thus apparently ending in vein *R*; vein R_1 usually extends close to apex of wing, considerably shorter in tribe Leiini (*e.g.*, *Mohelia*, Fig. 40); radial sector (*Rs*) commonly located in basal ½ of wing; veins R_{2+3} and R_{4+5} branching out together, the latter continues towards apex of wing; vein R_{2+3} sometimes present as short, almost vertical vein ending in vein R_1, enclosing small radial cell, as in many Mycomyinae (Figs 26–29); within Gnoristinae presence of vein R_{2+3} appears rather unstable, even at specific level; crossvein *r–m* (often termed anterior transversal), short, vertical to virtually horizontal; veins M_1 and M_2 commonly forming anterior fork with long, or short, common stem, with single branch in *Azana* (Fig. 30) and *Moriniola* (Fig. 25), proximal portion of 1 or both branches sometimes atrophied, or entirely reduced (*e.g.*, *Manota*, Fig. 22); distinct fold line between veins R_{4+5} and M_1 present in several Mycomyinae (*e.g.*, *Dinempheria*, Fig. 26), sometimes also shorter and weaker fold line between veins M_2 and M_4; behind veins M_2 are M_4 and *CuA*, which in most genera form posterior fork with common stem; vein M_4 sometimes reduced, or proximally atrophied, vein *CuA* strongly sinuous in *Acrodicrania* Skuse (Fig. 36); rare genus *Paradoxa* Marshall (Fig. 39) displays unique pattern in which vein *CuP* meets vein *CuA*, forming closed cell *cua*; a false vein, usually weak and fold-like, is frequently present between veins *CuA* and *CuP*, vein *CuP* may be well-developed sometimes virtually reaching wing margin as in *Epicypta* (Fig. 53); anal vein, A_1, often present as short, slightly curved vein as in, e.g. *Allodia* (Fig. 49); halter with knob rounded or more elongate. Legs (Figs 17–19) long and slender in a few Afrotropical genera, e.g., *Afrocnemia* Matile, *Leptomorphus* Curtis and *Syndocosia*; coxae invariably elongated and stout; male mid coxa of some *Mycomya* Rondani with anterior hook-like process distally; femora usually slender; mid and hind femora sometimes markedly swollen, or laterally compressed, e.g., *Epicypta* (Fig. 10); tibiae usually slender, with vestiture variable, with short setae arranged irregularly (Fig. 18), or in regular rows (Fig. 19), usually with strong setae (bristles) varying in strength and arrangement; fore tibia with anteroapical depressed area, bearing fine setae, arranged in 1, or more, rows, or more irregularly (Fig. 18) in depressed area, minute, or seemingly absent (in some non-Afrotropical genera upper ½ of mid tibia in male, sometimes also female, sometimes with specialised sensory area); 1 apical spur present on fore tibia; 2 each on mid and hind tibiae, 1 of which may be very short; tarsi usually slender, very long in *Afrocnemia*; tarsal claws rarely simple, usually with 1 or more teeth ventrally; pulvilli absent; empodium, if present, variable in size.

Abdomen long and slender to more short and stout; tergites and sternites 1–6 in male and 1–7 in female usually well-developed, except sternite 1 often reduced in size, V-shaped, sometimes lacking setulae; some or all of sternites 2–7 often with pair of submedian, or sublateral, weakly-sclerotised lines, sometimes also with similar median line (fold lines), which allow sternites to be partially folded longitudinally; male (Figs 57–60) often with reduced segments 7 and 8, sometimes telescoped into segment 6, as in most Mycetophilini (e.g., Figs 5, 7); male terminalia, *i.e.*, segment 9 and associated structures, extremely varied in form, but with apparently constant basic pattern: tergite and sternite 9; pair of lateral gonocoxites, each with an articulated gonostylus; pair of submedian parameres, each principally articulated laterally with gonocoxites and bearing aedeagus between them (structure of parameres and aedeagus often difficult to determine) and anus-bearing proctiger; partly reduced segment 10 sometimes present between tergite 9 and proctiger free, or more or less fused with former; gonocoxites separate, or broadly, or entirely fused ventromedially, in latter case probably by fusion with sternite 9; sometimes with distinct gonocoxal lobes distally; gonostylus particularly varied, sometimes slender and tapering, but more often with lobes, or processes, bearing variety of setulae, spines, or striate areas (lamellae) (Figs 57, 60); aedeagus commonly rather simple; outline of parameres varied, usually accompanied by long parameral apodemes; aedeagus and parameres suspended between gonocoxites by gonocoxal apodemes; development of tergite 9 varies, sometimes as distinct sclerite above gonocoxites, not uncommonly bearing spines or processes; proctiger varies from positioned immediately above aedeagus and parameres, to below posterior end of tergite 9; proctiger consists of pair of lateral unsegmented cerci and ventral hypoproct, which is commonly weak, sometimes medially divided, or fused with cercus; female (Figs 61–63) with tergite and sternite 8 usually well separated; tergite 8 sometimes seemingly fused with tergite 9; sternite 8 short, or long, with pair of rounded, or tapered lobes posteriorly, representing hypogynial valves (gonocoxites 8), often clothed in both strong and smaller setae; hypopygial valve commonly with pair of flattened outgrowths invaginated above (gonapophyses 8), being variable in shape and degree of sclerotisation; membranous, fringe-like structure between and above invaginated valves represents labia (*sensu* Søli 1997a); tergite 9 usually distinct and well-developed, setulose, or bare, sometimes with distinct median incision; sternite 9 usually fused laterally with tergite 9 and invaginated (gonapophyses 9) forming genital fork, commonly weakly sclerotised, with membranous areas; some outgrowths (genital fork) usually surrounding opening of spermathecal duct (gonopore); tergite 10 short, or absent, with or without setae; sternite 10 usually well-developed, rarely absent, or strongly reduced, commonly with median groove, probably serving as egg guide, with or without setae; lateral border frequently fused with



22 *Manota*

23 *Syndocosia*

24 *Parempheriella*

25 *Moriniola*

26 *Dinempheria*

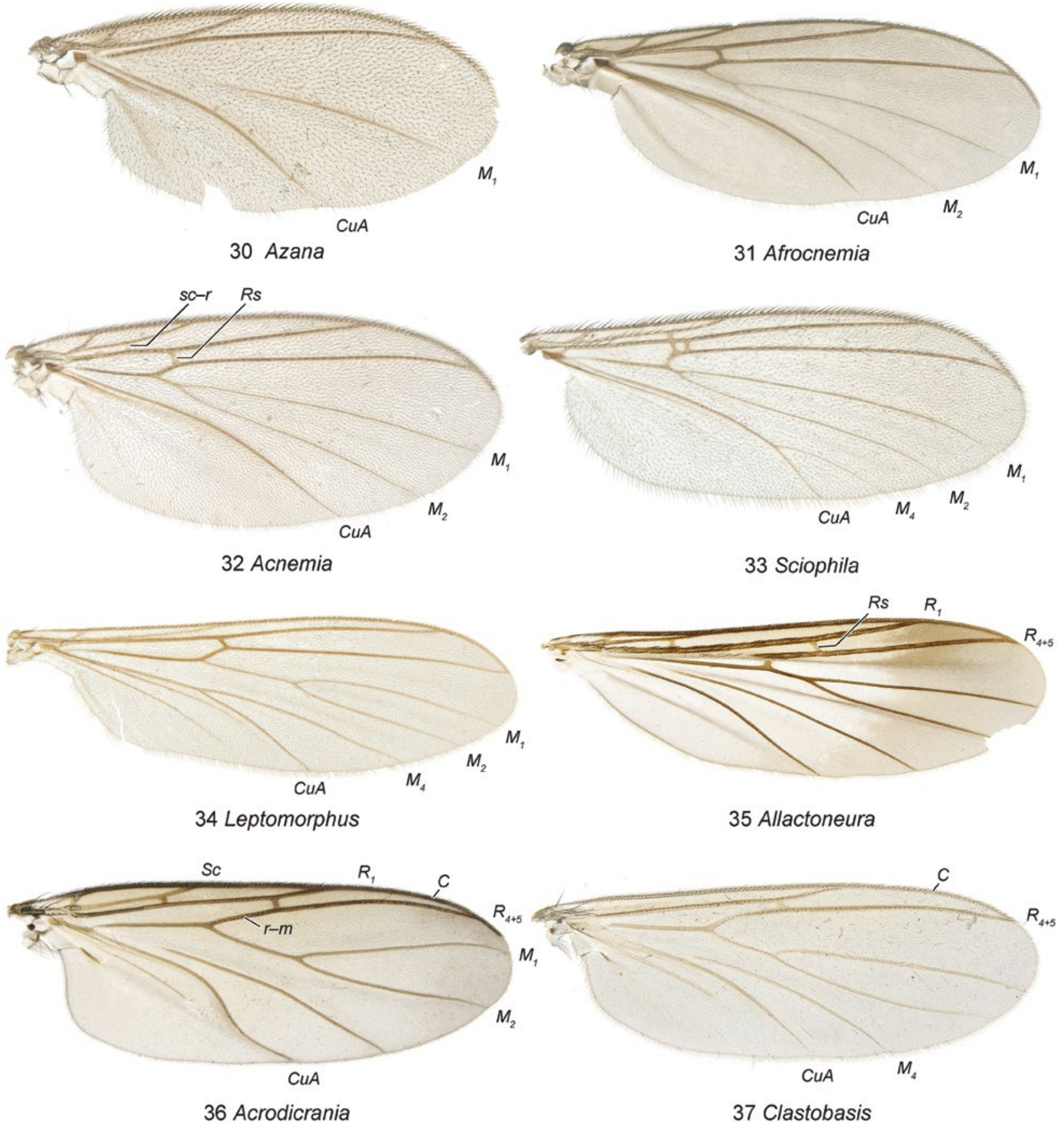
27 *Mycomya*

28 *Mycomyiella*

29 *Neoempheria*

Figs 20.22–29. Wings of Mycetophilidae (dorsal views): (22) *Manota* sp.; (23) *Syndocosia* sp.; (24) *Parempheriella* sp.; (25) *Moriniola* sp.; (26) *Dinempheria* sp.; (27) *Mycomya* sp.; (28) *Mycomyiella* sp.; (29) *Neoempheria* sp.

Abbreviations: a fold – apical fold; an lb – anal lobe; *bc* – basal costal cell; *bm* – basal medial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; fal vn – false vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.


30 *Azana*

31 *Afrocnemia*

32 *Acnemia*

33 *Sciophila*

34 *Leptomorphus*

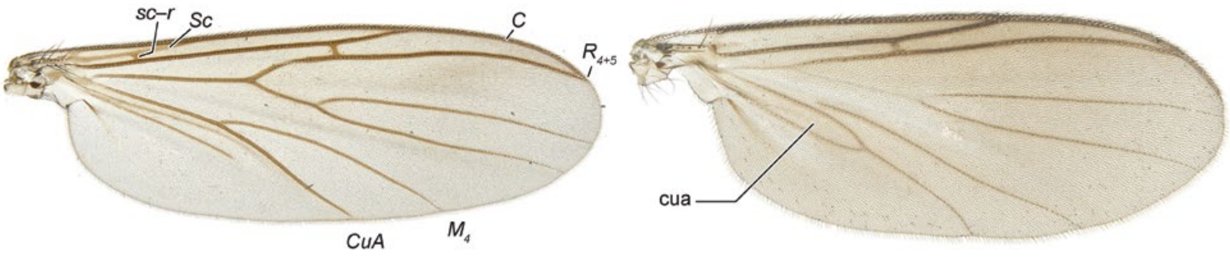
35 *Allactoneura*

36 *Acrodicrania*

37 *Clastobasis*

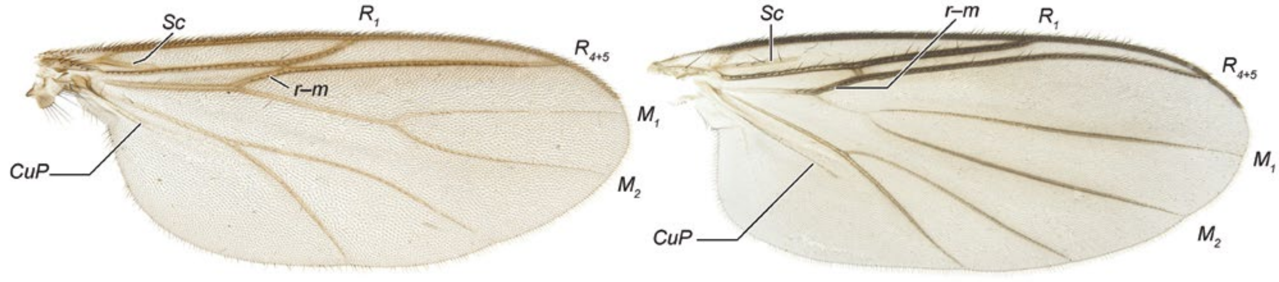
Figs 20.30–37. Wings of Mycetophilidae (dorsal views): (30) *Azana* sp.; (31) *Afrocnemia* sp.; (32) *Acnemia* sp.; (33) *Sciophila* sp.; (34) *Leptomorphus* sp.; (35) *Allactoneura* sp.; (36) *Acrodicrania* sp.; (37) *Clastobasis* sp.

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.



38 *Leia*

39 *Paradoxa*

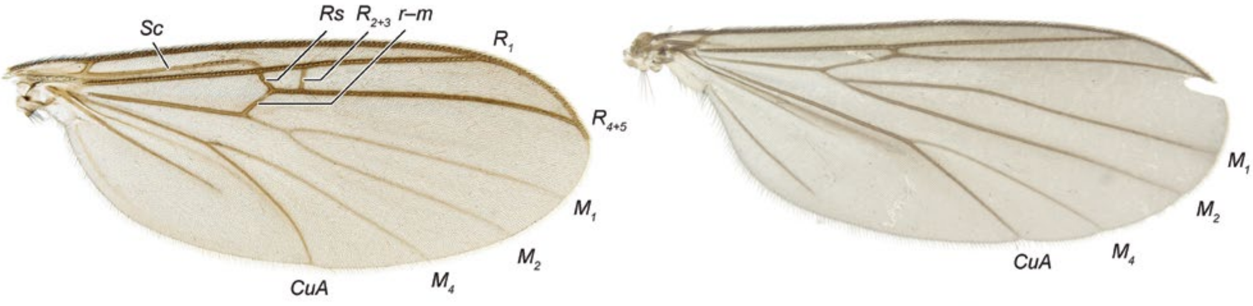


40 *Mohelia*

41 *Docosia*

42 *Synapha*

43 *Metanepsia*

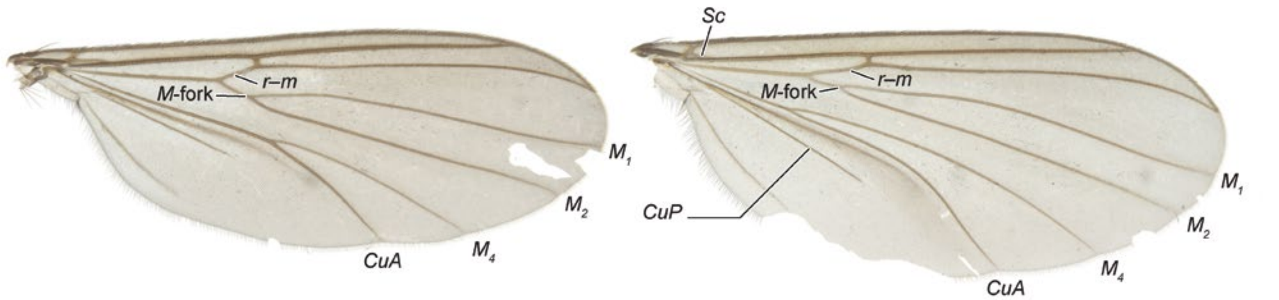


44 *Dziedzickia*

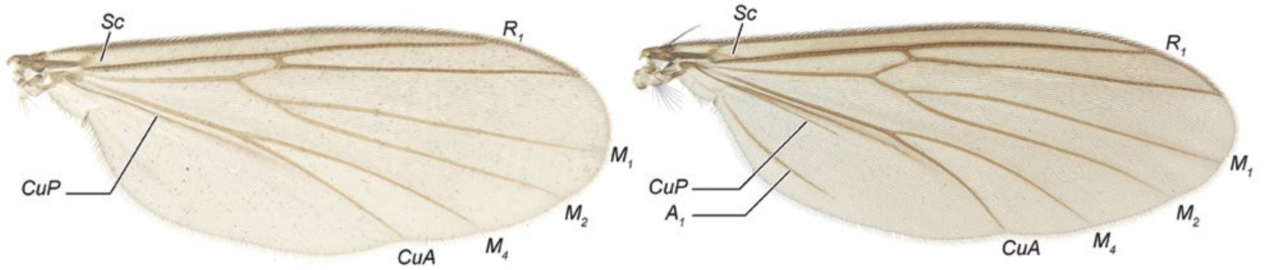
45 *Exechia*

Figs 20.38–45. Wings of Mycetophilidae (dorsal views): (38) *Leia* sp.; (39) *Paradoxa paradoxa* Jaschhof; (40) *Mohelia* sp.; (41) *Docosia* sp.; (42) *Synapha* sp.; (43) *Metanepsia* sp.; (44) *Dziedzickia* sp.; (45) *Exechia* sp.

Abbreviations: *C* – costal vein; *cua* – anterior cubital cell; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; *sc–r* – subcostal–radial crossvein.

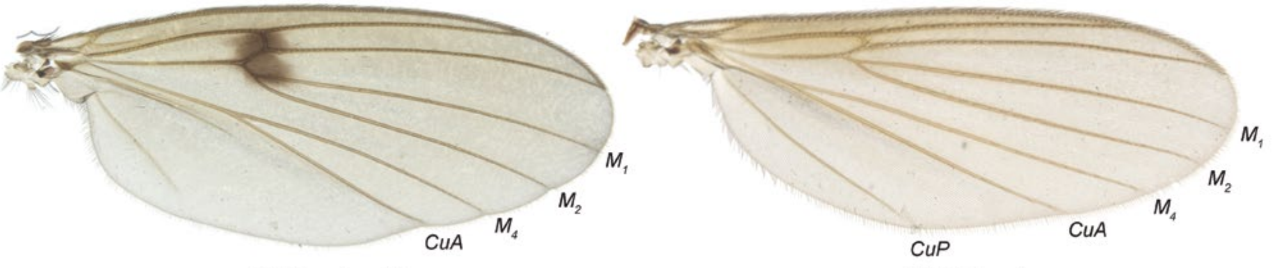


46 *Pseudexechia* 47 *Rymosia*



48 *Brevicornu* 49 *Allodia*

50 *Trichonta* 51 *Phronia*



52 *Mycetophila* 53 *Epicypta*

Figs 20.46–53. Wings of Mycetophilidae (dorsal views): (46) *Pseudexechia* sp.; (47) *Rymosia* sp.; (48) *Brevicornu* sp.; (49) *Allodia* sp.; (50) *Trichonta* sp.; (51) *Phronia* sp.; (52) *Mycetophila* sp.; (53) *Epicypta* sp.

Abbreviations: A_1 – first branch of anal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_1 – anterior branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

hypoproct; 1 or 2-segmented cercus articulates with last sclerotised tergite; cercus varying in form, being elongate, slender, curved and tapering; 2 membranous spermathecae present (not visible in macerated specimens).

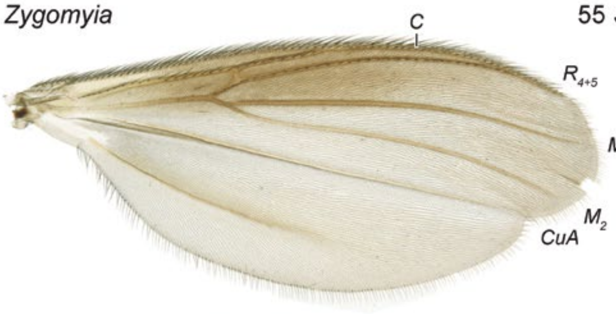
Mycetophilidae superficially resemble representatives of other families in the superfamily Sciaroidea, in particular Sciaridae (see Chapter 21) and some Keroplatidae (see Chapter 18). The missing eye bridge helps to distinguish them from the Sciaridae and unlike Keroplatidae, Mycetophilidae have the veins of the anterior and posterior forks separate from the wing base. A more comprehensive account of the adult morphology can be found in Søli (1997*a*).

Egg ovate, often pear-shaped, to slender, or boat-shaped; external surface often with longitudinal ridges, or complex network of forked interconnecting ridges; chorionic structures of egg shell of five species of Mycetophilidae were studied by Plachter (1981), who found egg shells both with, and without, plastron and chorion that was uniform, 1-layered, or complex and multi-layered. The egg structures in species of *Mycomya* and *Neoempheria* Osten Sacken were studied by Mazzini *et al*. (1990, 1992*a*, *b*).

Larvae usually whitish, cylindrical and slender (Fig. 64); ventral part of head capsule typical, with epicranial plates meeting only at single point, so that posterior tentorial bridge is absent (Fig. 66); reduced, 1-segmented antenna also typical (Fig. 65); labrum (Figs 65, 66) poorly sclerotised and fleshy, supported by sclerotised frame that articulates with 2 moveable arms, each of which carries fan-shaped premandible; mandible (Fig. 68) lamelliform, toothed along inner margin, with 5–8 prostheca near inner basal angle, prostheca long and pectinate to short and blunt; maxilla (Fig. 67) consisting of an inner blade-like lobe (galea) and an outer oval lobe (palpifer), blade-like lobe serrated along inner margin and ending in sclerotised bar that lies dorsal to basal plate-like cardo; oval lobe with distal circular membranous area (maxillary palpus) carrying several papillae, strongly prolonged and apically tapered in *Sciophila* Meigen; body with 3 thoracic and 9 abdominal segments; each thoracic segment bare, or virtually so; 9–11 ventral creeping welts between segments of thorax and abdomen; each welt with armature of spicules and hooks; larva with 1 pair of thoracic, and at most, 7 pairs of abdominal spiracles; respiratory system hemipneustic in most groups, very rarely propneustic as in the Holarctic genus *Speolepta* Edwards; most larvae in the subfamily Mycetophilinae free of creeping welts; rarely ovate and flattened, covered in a sticky layer of mucus (*Epicypta*), or with hard, dark conical case formed from frass and larval excrement (some *Phronia* Winnertz); larvae in several Sciophilinae and Mycomyinae often occurring in mucous tubes, or in silky webs formed from salivary excretion and without creeping welts. Comprehensive accounts of the larval stages are provided by Madwar (1937) and Plachter (1979*a*, *b*).

Pupae with leg sheaths side by side, rarely partly overlapping distinct visible tibial spurs; thorax characteristic, strongly arched with sessile undivided prothoracic spiracle; all species with 6 abdominal spiracles, except for Mycetophilinae, with 5; pupae found in soil, or in solid tubes, are typical in having spicules covering surface of abdomen, by contrast all pupae surrounded by webs or cocoons have very smooth cuticle.

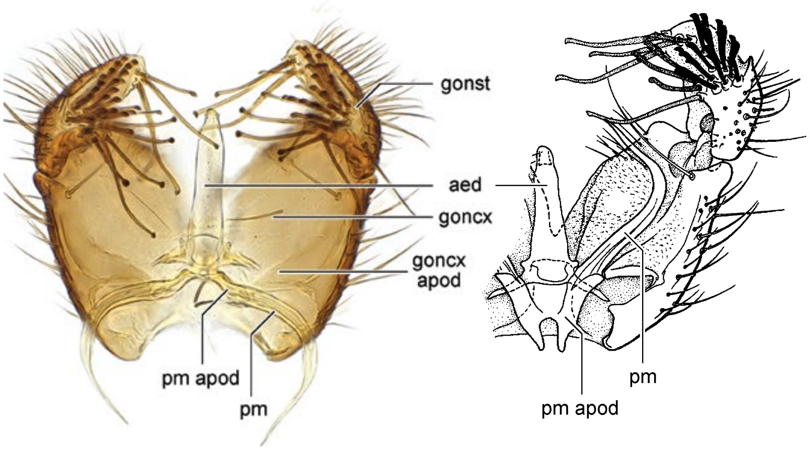
54 *Zygomyia* 55 *Sceptonia*



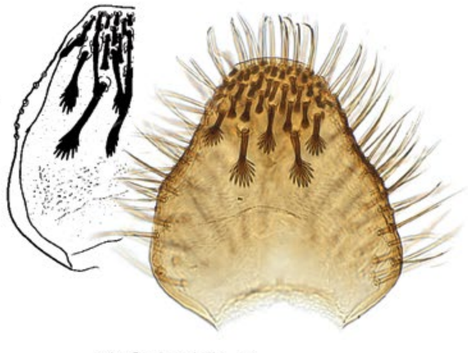
56 *Platyprosthiogyne*

Figs 20.54–56. Wings of Mycetophilidae (dorsal views): (54) *Zygomyia* sp.; (55) *Sceptonia* sp.; (56) *Platyprosthiogyne* sp.

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; R_{4+5} – third branch of radius.



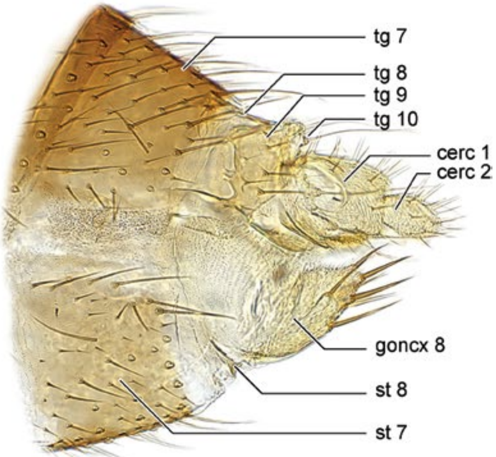
57 *Sciophila* ♂



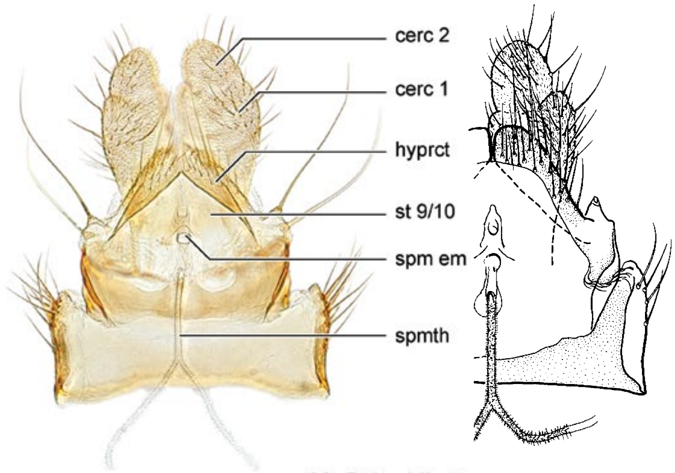
58 *Sciophila* ♂

59 *Mycomya* (*Mycomyopsis*) ♂

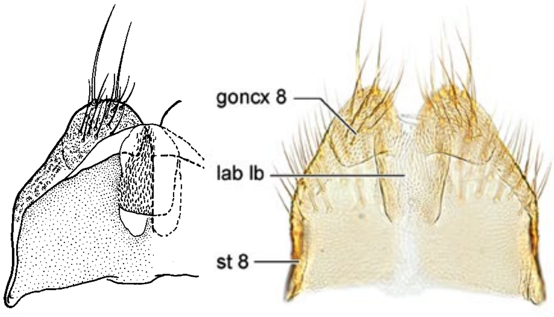
60 *Exechia* ♂



61 *Sciophila* ♀



62 *Sciophila* ♀



63 *Sciophila* ♀

Figs 20.57–63. Male and female terminalia of Mycetophilidae: (57) male terminalia of *Sciophila kakumensis* Søli, ventral view (tergite 9 removed); (58) same, tergite 9, ventral view; (59) *Mycomya* (*Mycomyopsis*) sp., tergites 9 and 10, dorsal view; (60) gonostylus of *Exechia* sp., lateral view (from inside); (61) female terminalia of *S. kakumensis*, lateral view; (62) same, tergal parts, ventral view; (63) female terminalia, sternite 8 and appendages of *S. kjaerandseni* Søli, dorsal view. Figs 57, 58, 62, 63 (Søli 1997, figs 57, 58, 22, 23, respectively).

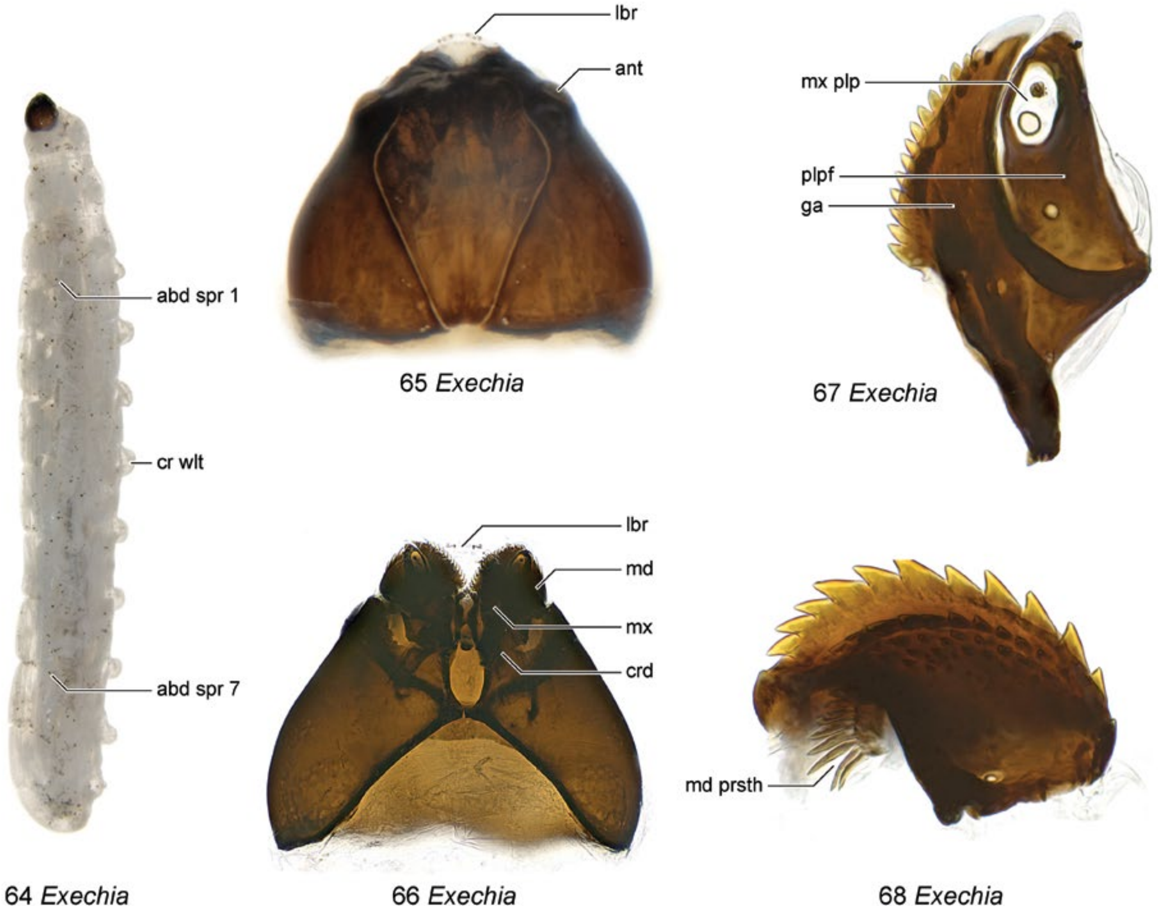
Abbreviations: aed – aedeagus; cerc – cercus; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hyprct – hypoproct; hyp vlv – hypogynial valve; pm – paramere; pm apod – parameral apodeme; spm em – spermathecal eminence; spmth – spermatheca; st – sternite; tg –tergite.

A study describing the pupae of 21 species, representing most families of Sciaroidea, including most subfamilies of Mycetophilidae, is provided by Plachter (1979*c*).

Biology and immature stages

Despite being common in both temperate and tropical regions, our knowledge of the biology of fungus gnats remains poor, especially for the tropics. Adults are most abundant in humid areas, especially moist woodlands. During the day adults, especially the subfamily Mycetophilinae, congregate in damp, dark places, such as overhanging stream banks and cavities under tree roots. Several species are common in caves, mines and in smaller subterranean cavities (*e.g.*, Kjærandsen 1993; Kurina 1996). Species of the Holarctic genus *Speolepta* are regular inhabitant of caves in all life stages, even if adults are regularly encountered outside. Many species of fungus gnats can be swept from undergrowth in woods. Little is known regarding their nocturnal activity, but some species appear to rest in secluded spots during the day, as they are almost exclusively sampled in traps deployed during the night. Although the majority of temperate species occur in woodlands, some species appear to prefer grassland, or open habitats (Ševčík & Roháček 2008), but little is known regarding the biology of fungus gnats in such environments, or in dry forests, both in temperate and tropical regions.

Fungus gnats in more than 10 genera are documented as being important and effective pollinators of the botanical families Araceae, Liliaceae, Orchidaceae (possibly including pseudocopulation) and Saxifragaceae (Barriault *et al*. 2010; Gaskett 2011; Goldblatt *et al*. 2004; Mesler *et al*. 1980; Okuyama *et al*. 2004; Tremblay & Ackerman 2007). These results are based on studies in temperate regions and very little is known regarding their role as pollinators in the Afrotropical Region. Larvae are usually found in fungi, under brackets and bark, in old tree trunks, in decaying plants, soil, *etc*. Only scattered reports on the larval diet and behaviour exist from the tropics and our



64 *Exechia* 65 *Exechia* 66 *Exechia* 67 *Exechia* 68 *Exechia*

Figs 20.64–68. Larval features of Mycetophilidae: (64), larval habitus of *Exechia frigida* (De Geer), lateral view (non-Afrotropical); (65) same, head capsule, dorsal view; (66) same, ventral view; (67) same, left maxilla, ventral view; (68) same, left mandible, ventral view.

Abbreviations: abd spr – abdominal spiracle; ant – antenna; cr wlt – creeping welt; crd – cardo; ga – galea; lbr – labrum; md – mandible; md prsth – mandibular prostheca; mx – maxilla; mx plp – maxillary palpus; plpf – palpifer.

knowledge is almost exclusively based on studies undertaken in Europe. Recent contributions and reviews include those of Jakovlev (2011, 2012). Larvae of species in the subfamily Mycetophilinae are mostly found in soft ground fungi, but some species prefer a wide range of lignicolous fungi, fleshy or woody. Most groups of fungi and even Myxomycetes, have been reported as larval breeding media for fungus gnats and both polyphagy and oligophagy have been documented. Species in the remaining subfamilies have a more varied biology, several with larvae that develop in fungi or under bark. The larvae often occur in a small mucilaginous tube supported by threads and in some species these may be covered in a dry irregular sometimes communal web. Species of the genera *Docosia* Winnertz and *Leia* Meigen have been found in the nests of birds and mammals, in which they probably feed on mycelium. *Mycomya* spp. have been reared from fungi associated with dead wood. In the rainforests of Central African Republic, Matile (1972*b*) observed larvae of *Viridivora* feeding on mosses and liverworts and suggested that this behaviour may also apply to other species. Pupation usually takes place in the soil, but some species pupate in the host fungus. Within the subfamily Sciophilinae a large number of genera have pupae that hang in a sparse web of salivary threads. Several species of Hymenoptera in the families Braconidae, Ichneumonidae and Proctotrupidae have been reported as parasites of fungus gnats (Kolarov & Bechev 1995; Šedivý & Ševčík 2003). A protozoan (Trypanosomatidae) has been found in the gut of larvae of *Leia* (Gibbs 1959), and in North America a nematode (Steinernematidae) has been reported from adult *Mycetophila* Meigen (Poinar 1992).

Economic significance

As the ecological role of fungus gnats is poorly known, their economic significance is difficult to assess. In areas where wild mushrooms are extensively used as human food, the larvae of fungus gnats have long been considered as pests. Larvae of fungus gnats have also been reported to infest cultivated mushrooms causing extensive damage through their feeding action (*e.g.*, Sasakawa 1992; Sueyoshi & Murakami 2012; Tobar *et al*. 2010), or by serving as vectors of harmful nematodes (Tsuda *et al*. 1996). Larvae of the Afrotropical species, *Leia arsona* Hutson, 1978, have been recorded as feeding on stored root ginger in London (Hutson 1978). The importance of fungus gnat larvae in decomposition of organic matter is virtually unknown (Binns 1981, for review). As numerous species feed on fungal mycelium penetrating dead organic material, such as rotting tree trunks and branches, their role in decomposition may be more important than commonly recognised, *e.g.*, by carrying putrefactive micro-organisms into the decaying material (Irmler *et al*. 1996). In temperate regions the fungus gnat fauna has proved to be a good bioindicator of undisturbed forests (Økland 1994, 1996). As mentioned above, fungus gnats may also be of vital importance in the pollination of certain flowers, especially orchids.

Classification

The family Mycetophilidae is regarded by most contemporary authors to comprise a monophyletic group (Amorim & Rindal 2007; Rindal *et al*. 2009; Ševčík *et al*. 2013). The family belongs to the infraorder Bibionomorpha (*e.g*., Wiegmann *et al*. 2011) and has commonly been included in the superfamily Sciaroidea, together with the families Bolitophilidae (non-Afrotropical), Cecidomyiidae, Diadocidiidae (non-Afrotropical), Ditomyiidae (non-Afrotropical), Lygistorrhinidae, Keroplatidae, Sciaridae and Rangomaramidae (non-Afrotropical) (Amorim & Rindal 2007; Wood & Borkent 1989: 1339). Phylogenetic relationship among the families included in the infraorder remains unresolved.

Following Edwards (1925*a*), the family has traditionally been divided into three subfamilies, Manotinae, Sciophilinae and Mycetophilinae. The last two mentioned subfamilies have been divided into a varying number of tribes: Sciophilinae into Gnoristini, Leiini, Metanepsiini, Mycomyini and Sciophilini and Mycetophilinae into Exechiini and Mycetophilini. Despite an ongoing debate regarding their delimitation, these tribes (except Exechiini and Mycetophilini), are today commonly treated at the subfamilial level. Notwithstanding, a recent molecular study by Ševčík *et al*. (2013), has demonstrated that the three genera in "Metanepsiinae" do not form a monophyletic group, but are nested within the Gnoristinae. Among the commonly recognised subfamilies, the monophyly of the Gnoristinae is probably the least well-supported, both by morphological and molecular data. For convenience the common practice of dividing the family in subfamilies is, however, followed here.

Identification

There is no comprehensive identification key covering the entire Afrotropical fauna of fungus gnats, but useful contributions can be found in Matile (1992 (Gnoristinae), 1998*b* (Sciophilinae, in part)) and Väisänen (1994) (Mycomyinae). Moreover, Vockeroth (1981: 228), Søli *et al*. (2000: 63) and Vockeroth (2009: 268) provide useful keys covering the Nearctic, Palaearctic, and Central American regions, respectively. At the generic level, available identification keys are noted in the "Synopsis of the fauna" section (below). In the field Mycetophilidae are best stored in alcohol, or micro-pinned for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Mycetophilidae

1. Legs with trichia arranged in regular rows along entire length of tibia (*e.g.,* Fig. 19). 2
– Legs with trichia irregularly arranged along entire length of tibia (*e.g.,* Fig. 18), although sometimes tending to form rows towards apex 13
2. Head with row of very strong, erect, posteriorly directed setae on occiput (behind eye) (Fig. 13); wing without apparent *M*-fork, branches present as detached veins (Fig. 22) (MANOTINAE). . . . . *Manota* Williston

– Head without such strong posteriorly directed setae on occiput (behind eye); wing with apparent *M*-fork (*e.g.*, Fig. 25) 3

3. Head invariably with 2 or 3 ocelli, the lateral touching eye margin (*e.g.*, Figs 12, 14); wing vein R_{2+3} absent; microtrichia on wing membrane, especially towards apex, arranged in more or less regular longitudinal lines (*e.g.*, Fig. 21) (MYCETOPHILINAE) 28

– Head with 2 ocelli, inserted far from eye margin; rarely, ocelli absent; wing vein R_{2+3} present, or absent; microtrichia on wing membrane not clearly arranged in lines (as in *e.g.*, Fig. 20) (MYCOMYINAE) . . . 4

4. Head without ocelli; wing usually with striking apical fold in males; vein R_{2+3} absent (Fig. 23) . . . . *Syndocosia* Speiser

– Head with ocelli; wing without striking apical fold (*e.g.*, Fig. 27) 5

5. Tibiae without strong setae (bristles); wing with costal vein (*C*) produced beyond apex of vein R_{4+5} (as in Fig. 24) . . . . *Viridivora* Matile

– Tibiae with strong setae (bristles), about as long as apical width of tibia, often longer; wing with costal vein (*C*) ending at apex of vein R_{4+5}, or produced beyond 6

6. Wing with single vein, *CuA*, posteriorly to vein M_2 (Fig. 25); scutellum without long apical setae . . . . *Moriniola* Matile

– Wing with fork (M_4 and *CuA*) posteriorly to vein M_2 (*e.g.*, Fig. 24); scutellum with long apical setae 7

7. Wing without vein R_{2+3}; costal vein (*C*) produced well beyond apex of vein R_{4+5} (Fig. 24) . . . . *Parempheriella* Matile 8

– Wing with vein R_{2+3}; costal vein (*C*) ending at apex of vein R_{4+5} (*e.g.*, Fig. 27) or produced beyond (*e.g.*, Fig. 28) 9

8. Antenna with median flagellomeres as long as broad; palpus with terminal segment thread-like, much longer than penultimate segment; wing with subcostal vein (*Sc*) ending near level of apex of basal cell (*bc*), commonly before; point of furcation of posterior fork (M_4 and *CuA*) at level of base of crossvein *r–m* (rarely slightly before) (Fig. 24) . . . . *Parempheriella sensu stricto*

– Antenna with median flagellomeres shorter than wide; palpus with terminal segment about as long as penultimate segment; wing with subcostal vein (*Sc*) ending at, or after, level of apex of basal cell (*bc*); point of furcation of posterior fork (M_4 and *CuA*) before base of crossvein *r–m* . . . . *Parempheriella* (*Parempherina* Matile)

9. Thorax with laterotergite setulose (careful observation required as setae may be pale and difficult to discern); wing with anal lobe reduced (Fig. 26) . . . . *Dinempheria* Matile

– Thorax with laterotergite bare; wing with anal lobe normal (*e.g.*, Fig. 27) 10

10. Wing with costal vein (*C*) ending at apex of vein R_{4+5} (Fig. 27) . . . . *Mycomya* Rondani 11

– Wing with costal vein (*C*) produced beyond apex of R_{4+5} (*e.g.*, Figs 28, 29) 12

11. Male terminalia with tergite 9 with 2 well-separated median combs (Fig. 59) . . . . *Mycomya* (*Mycomyopsis* Väisänen)

– Male terminalia with tergite 9 without well-separated median combs . . . . *Mycomya sensu stricto*

12. Wing membrane without false vein between veins R_{4+5} and M_1; wing without distinct markings (Fig. 28) . . . . *Mycomyiella* Matile

– Wing membrane with false vein between veins R_{4+5} and M_1; wing with, or without, conspicuous dark markings (Fig. 29) . . . . *Neoempheria* Osten Sacken

13. Thorax with mediotergite setulose; wing membrane with numerous distinct macrotrichia and usually also microtrichia (*e.g.*, Figs 30, 33) (SCIOPHILINAE) 14

– Thorax with mediotergite bare; wing membrane without macrotrichia, or at most, with a few short macrotrichia near posterior margin, always with dense microtrichia (*e.g.*, Fig. 38) 18

14. Wing with only 2 major veins (M_1, *CuA*) posterior to radial veins; without forks (Fig. 30) . . . . *Azana* Walker

– Wing with anterior fork (M_1+M_2) and 1 or 2 posterior veins (*e.g.*, Fig. 31) 15

15. Wing with complete anterior fork (M_1+M_2) and 1 vein (*CuA*) posteriorly to it (*e.g.*, Figs 31, 32) 16

– Wing with both anterior (M_1+M_2) and posterior (M_4 and *CuA*) forks complete (*e.g.*, Fig. 33) 17

16. Wing without crossvein *sc–r* (Fig. 31); fore leg with tarsomere 1 at least 1.5 × as long as tibia, sometimes considerably so; head with lateral ocelli separated by less than individual width from eye margin . . . . *Afrocnemia* Matile

– Wing with crossvein *sc–r* (Fig. 32); fore leg with tarsomere 1 slightly shorter than tibia; head with lateral ocelli inserted far from eye margin, separated by at least 3 × individual width . . . . . . *Acnemia* Winnertz

17. Wing with point of furcation of posterior fork (M_4 and *CuA*) beyond point of furcation of anterior fork (M_1+M_2); vein M_4 sometimes obsolete basally (Fig. 33) . . . .*Sciophila* Meigen

– Wing with point of furcation of posterior fork (M_4 and *CuA*) before point of furcation of anterior fork (M_1+M_2); M_4 complete (Fig. 34). . . . . *Leptomorphus* Curtis

18. Wing vein R_1 short, usually about as long as crossvein *r–m* and ending in basal ⅔ of wing (*e.g.*, Fig. 36); if vein R_1 longer (*ca* 3–4 × as long as *r–m* in *Docosia*), then stem of anterior fork (M_1+M_2) about as long as crossvein *r–m* (*e.g.,* Fig. 41); head with lateral ocellus close to eye margin (except in *Mohelia*), with, or without, median ocellus (LEIINAE) 19

– Wing vein R_1 long, several times as long as crossvein *r–m*, nearly always ending in distal ⅓ of wing (*e.g.*, Fig. 44); if vein R_1 ending in basal ⅔ of wing (*Metanepsia*), then stem of anterior fork (M_1+M_2) *ca* 10 × as long as crossvein *r–m* (*e.g.*, Fig. 43); head with lateral ocellus inserted far from eye margin; median ocellus present (GNORISTINAE). 25

19. Wings longitudinally folded; radial veins densely clothed in slightly flattened setae (Figs 8, 35); head with several strong, recurved, posteriorly directed setae on occiput (Fig. 8); abdomen densely clothed in flattened, blade-shaped setae. . . . . *Allactoneura* de Meijere

– Wings not longitudinally folded; radial veins with a single row of setae; occiput with at most a few posteriorly directed setae; abdomen with evenly dispersed normal setae 20

20. Hind tibia with numerous strong setae (bristles) at least 2 × as long as apical width of tibia (*e.g.*, Fig. 9) 21

– Hind tibia without strong setae (bristles) longer than width of tibia (as in Fig. 2) 23

21. Wing with costal vein (*C*) produced beyond apex of vein R_{4+5}; subcostal vein (*Sc*) ending in costal vein; vein *CuA* distinctly sigmoid (Fig. 36). . . . . *Acrodicrania* Skuse

– Wing with costal vein (*C*) ending at vein R_{4+5}; subcostal vein (*Sc*) free, or ending in costal vein; vein *CuA* straight or virtually so (*e.g.*, Figs 37, 38) 22

22. Wing vein M_4 distinctly detached proximally, running more or less parallel with vein *CuA* towards base of wing; subcostal vein (*Sc*) weak, ending free; crossvein *sc–r* absent (Fig. 37); head with lateral ocelli touching eye margin; antenna with proximal part of each flagellomere dark, giving antenna conspicuous banded appearance (Fig. 1); thorax more or less unicoloured, usually light yellowish (Fig. 1). . . . *Clastobasis* Skuse

– Wing vein M_4 attached or slightly detached from vein *CuA*, in latter case curving distinctly towards vein *CuA* proximally; subcostal vein (*Sc*) distinct, ending in costal vein (*C*); crossvein *sc–r* present (Fig. 38); head with lateral ocelli close, but not touching eye margin; antenna not appearing banded (Fig. 9); thorax usually with contrasting pattern between brown and yellow (Fig. 9). . . . .*Leia* Meigen

23. Wing with posterior fork incomplete; vein *CuP* joining vein *CuA*, forming conspicuous, closed cell *cua* (Fig. 39) . . . . *Paradoxa* Marshall

– Wing with posterior fork (M_4 and *CuA*) complete; vein *CuP* not joining vein *CuA*, to form conspicuous cell *cua* (*e.g.*, Figs 40, 41) 24

24. Wing with stem of anterior fork (M_1+M_2) 3 × as long as crossvein *r–m*; subcostal vein (*Sc*) short, ending at vein *R* (Fig. 40); mouthparts somewhat prolonged (Fig. 16). *Mohelia* Matile

– Wing with stem of anterior fork (M_1+M_2) barely longer than crossvein *r–m*; subcostal vein (*Sc*) long, ending free (Fig. 41); mouthparts not prolonged . . . . *Docosia* Winnertz

25. Wing with point of furcation of posterior fork (M_4 and *CuA*) opposite point of furcation of anterior fork (M_1+M_2) and subcostal vein (*Sc*) ending in costal vein (*C*) (Fig. 42) . . . . *Synapha* Meigen

– Wing with point of furcation of posterior fork (M_4 and *CuA*) usually before point of furcation of anterior fork (M_1+M_2), if opposite point of furcation of anterior fork, then subcostal vein (*Sc*) ending in radial vein (R_1) (*e.g.*, Fig. 44) 26

26. Wing crossvein *r–m* extremely short, barely longer than vein *Rs*; wing roundish, about 2 × as long as broad (Fig. 43); mouthparts reduced and palpus with only 1 visible segment (Fig. 15) . . . . *Metanepsia* Edwards

– Wing crossvein *r–m* long, at least 1.5 × as long as vein *Rs*; wings normal, distinctly longer than 2 × width (*e.g.*, Fig. 44); mouthparts normal; palpus with at least 3 well-separated segments 27

27. Wing with subcostal vein (*Sc*) ending free, or at vein *R*; crossvein *sc–r*, if present, close to apex of vein *Sc*; vein R_{2+3} present or absent; veins posteriorly to vein *R* normal, ending at wing margin (Fig. 44) . . . .*Dziedzickia* Johannsen

– Wing with subcostal vein (*Sc*) ending in costal vein (*C*); crossvein *sc–r* located about midway along vein *Sc*; vein R_{2+3} absent; veins posteriorly to vein *R* distally atrophied, not reaching wing margin . . . . *Boletiniella* Matile

28. Thorax with anepisternum bare (*e.g.*, Fig. 7) (EXECHIINI) 29

– Thorax with anepisternum with strong setae at least near upper margin (*e.g.*, Fig. 12) (MYCETOPHILINI) 34

29. Wing with point of furcation of posterior fork (M_4 and *CuA*) beyond level of point of furcation of anterior fork (M_1+M_2) (*e.g.*, Figs 45, 46) 30

– Wing with point of furcation of posterior fork (M_4 and *CuA*) before, or opposite, level of point of furcation of anterior fork (M_1+M_2) (*e.g.*, Figs 47–49) 31

30. Thorax with mesonotum with discal setae (Fig. 7); wing with crossvein *r–m* > 2 × as long as stem of *M*-fork (Fig. 45); abdomen with pale markings (when present), usually situated towards fore margin of tergites. . . . . *Exechia* Winnertz

– Thorax with mesonotum without discal setae; wing with crossvein *r–m* about as long as stem of *M*-fork (Fig. 46); pale abdominal markings (if present), usually situated towards hind margins of tergites . . . . *Pseudexechia* Tuomikoski

31. Wing with subcostal vein (*Sc*) ending free; vein *CuP* strong, extending well beyond point of furcation of posterior fork (M_4 and *CuA*) (Fig. 47); thorax with mediotergite sometimes with some dark, short setae on lower part . . . . *Rymosia* Winnertz

– Wing with subcostal vein (*Sc*) ending at vein R_1; vein *CuP* faint and short, not extending beyond point of furcation of posterior fork (M_4 and *CuA*) (care should be taken not to interpret the false vein between veins *CuA* and *CuP* as vein *CuP*) (*e.g.*, Figs 48, 49); thorax with mediotergite bare 32

32. Thorax with mesonotum with most of disc evenly clothed in prostrate setae . . . . . *Brevicornu* Marshall

– Thorax with mesonotum with most of disc devoid of setae, or with erect setae arranged in rows . . . . *Allodia* Winnertz 33

33. Thorax with mesonotum without setae over most of disc . . . . *Allodia sensu stricto*

– Thorax with mesonotum with several erect setae . . . . *Allodia* (*Brachycampta* Winnertz)

34. Thorax with anepimeron without setulae and setae 35

– Thorax with anepimeron with setulae and setae (*e.g.*, Fig. 12) 36

35. Hind coxa with basal seta; wing with subcostal vein (*Sc*) ending free or at vein *R*; point of furcation of posterior fork (M_4 and *CuA*) before, opposite or very slightly beyond point of furcation of anterior fork (M_1+M_2) (Fig. 50). . . . . *Trichonta* Winnertz

– Hind coxa without basal seta; wing with subcostal vein (*Sc*) ending free; point of furcation of posterior fork (M_4 and *CuA*) well beyond point of furcation of anterior fork (M_1+M_2) (Fig. 51). . . . . *Phronia* Winnertz

36. Wing with posterior fork (M_4 and *CuA*) (*e.g.*, Figs 52, 53) 37

– Wing without posterior fork, only single vein (*CuA*) present (*e.g.*, Figs 54–56) 38

37. Wing vein M_4 slightly divergent from vein M_2, but parallel with, or convergent towards, vein *CuA* (Fig. 52); thorax with ventral border of mesonotum above antepronotum nearly straight, only slightly curved (Fig. 12) . . . . *Mycetophila* Meigen

– Wing vein M_4 parallel with vein M_2, but slightly divergent from vein *CuA* (Fig. 53); thorax with upper portion of antepronotum inserted into sharp incision in lower border of mesonotum (Fig. 14) . . . . *Epicypta* Winnertz and *Platurocypta* Enderlein

38. Mid tibia with 1 or more short to long ventral setae (bristles) (Fig. 17); wing vein *CuA* slightly diverging from vein M_2 (Fig. 54) . . . . *Zygomyia* Winnertz

– Mid tibia without ventral setae; wing vein *CuA* parallel, or converging towards vein M_2 (*e.g.*, Figs 55, 56) 39

39. Wing with costal vein (*C*) ending at apex of vein R_{4+5} (Fig. 55) . . . . *Sceptonia* Winnertz

– Wing with costal vein (*C*) produced well beyond apex of vein R_{4+5} (*e.g.*, Fig. 56) 40

40. Thorax with mesonotum with shiny median keel anteriorly; wing without incision near apex of vein *CuA* . . . . *Aspidionia* Colless

– Thorax with mesonotum normal; wing with distinct incision near apex of vein *CuA* (Fig. 56) . . . . *Platyprosthiogyne* Enderlein

Synopsis of the fauna

The family Mycetophilidae currently includes more than 4,000 described, extant species in about 150 genera. Thirty-eight genera are recorded from the Afrotropics, nine of which are endemic to the region. Another four genera have a very restricted distribution, known only from the Australasian and/or the Oriental Regions outside the Afrotropics. Five genera are listed here, that were not included in Matile (1980*a*), the most recent species account for the Afrotropical Region. The undescribed species mentioned below were identified from collections of the Natural History Museum (London, UK), The Natural History Museum, University of Oslo (Oslo, Norway) and the National Museum (Bloemfontein, South Africa).

***Acnemia* Winnertz** (Sciophilinae)**.** A genus of 39 described species recorded from all zoogeographical regions, except the Australasian Region and Antarctica. The vast majority of species occur in the Holarctic Realm. Only one species, *A. falkei* Matile & Vockeroth, 1977, described from Uganda, is known from the Afrotropical Region. In the subfamily Sciophilinae, *Acnemia* is recognised by the combination of a single vein posteriorly to the vein *M*-fork; and the presence of crossvein *sc–r* (Fig. 32). The biology and immature stages of Afrotropical species remain unknown.

***Acrodicrania* Skuse** (Leiinae)**.** A small genus of eight described species, recorded from the Afrotropical, Australasian and Oriental Regions. The single Afrotropical species, *A. africana* Edwards, 1925, is only known from South Africa (Edwards 1925*b*), where it appears to be locally common. In the subfamily Leiinae, *Acrodicrania* is recognised by the combination of the lateral ocelli close to the eye margin; the wing without a complete posterior fork; and the strikingly sinuous vein *CuA*. The biology and immature stages remain unknown.

***Afrocnemia* Matile** (Sciophilinae)**.** Until recently, *Afrocnemia* was only known from the Afrotropical Region, with three described species from Central African Republic, but a fourth species from Israel, originally described as *Acnemia* (Chandler 1994), was added by Borkent & Wheeler (2013). In the tribe Sciophilini, this rare genus is recognised by the combination of a single posterior vein, the absence of crossvein *sc–r* (Fig. 31) and the elongate tarsi of the fore leg. The biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Matile (1998*b*).

***Allactoneura* de Meijere** (Leiinae)**.** A small genus of eight extant species recorded from the Afrotropical, Oceanian/Australasian, Oriental and Palaearctic Regions. One species, *A. argentosquamosa* Enderlein, 1910, occurs in the Afrotropical Region, described from Seychelles (Enderlein 1910) and later recorded from Madagascar and Mauritius. Additional specimens have been examined from Burundi, Democratic Republic of the Congo and Tanzania. The systematics remains unclear, but more than one species certainly exists. *Allactoneura* spp. are readily distinguishable by their ability to fold their wings longitudinally in a wasp-like fashion (Fig. 8). Furthermore, the radial wing veins are densely clothed in flattened, almost scale-like setae (Fig. 35). The biology and immature stages remain unknown.

***Allodia* Winnertz** (Mycetophilinae: Exechiini)**.** A genus of *ca* 95 extant species, recorded from all zoogeographical regions, except Antarctica, with the majority described from the Palaearctic Region. Two species have been reported from the Afrotropical Region: one undescribed species of *Allodia sensu stricto* from Cameroon and one species from the Comoros, in the subgenus *A.* (*Brachycampta* Winnertz) (Matile 1979a). In Afrotropical genera of the subfamily Mycetophilinae, *Allodia* and *Brevicornu* can be distinguished in having the anepisternum bare; the wing with long and well-developed median and cubital forks; vein *Sc* ending at vein *R*; and a normally-developed anal vein (Fig. 49). As opposed to *Brevicornu*, *Allodia* has the mesonotum bare, or with erect setae. The biology and immature stages of Afrotropical species remain unknown.

***Aspidionia* Colless** (Mycetophilinae: Mycetophilini)**.** A genus with only two described species, one Afrotropical, the other Australasian. The single Afrotropical species, *A. balachowskyi* Matile, 1974, was described from Comoros (Matile 1974*b*). Among genera in the subfamily Mycetophilinae with a single cubital vein, *Aspidionia* is unique in having the mid anterior portion of the mesonotum developed into a shiny median keel; and in having an evenly curved wing border, without a distinct incision near the apex of vein *CuA* (*cf*. Colless 1966, fig. 8), as in *Platyprosthiogyne* (Fig. 56). The biology and immature stages remain unknown.

***Azana* Walker** (Sciophilinae)**.** A small genus with 14 extant species, known from all zoogeographical regions, except the Australasian Region and Antarctica. Two species occur in the Afrotropical Region, described from Côte d'Ivoire and Gabon, respectably (Matile 1998*a*), but additional undescribed species have been recognised from Nigeria (Matile 1980a: 225), Burundi, Madagascar and Tanzania. *Azana* is distinguished by the unique wing venation, with only two major veins posterior to radius (Fig. 30). Species vary in size and colouration, from dusty brown to bright yellow. The biology and immature stages of Afrotropical species remain unknown.

***Boletiniella* Matile** (Gnoristinae)**.** This endemic monotypic genus, with the single described species *B. nigrifemur* Matile, 1973, was erected by Matile (1973*a*), based on specimens from Bioko Is. (Equatorial Guinea) (as Fernando Póo) and Cameroon, but was later recorded from Gabon (Matile 1992). The species can be identified on the combination of the flattened antennae and the atrophied wing veins of the anterior and the posterior forks, which do not reach the wing margin. The biology and immature stages remain unknown.

***Brevicornu* Marshall** (Mycetophilinae: Exechiini)**.** The genus comprises more than 80 extant species, known from all zoogeographical regions, except Antarctica, with most described from the Palaearctic Region. One undescribed species is reported from Cameroon in the Afrotropical Region (Matile 1980*a*: 228), but the genus appears to be not uncommon in forested areas. Together with *Allodia*, *Brevicornu* is the only Afrotropical genus in the subfamily Mycetophilinae, with the anepisternum bare; the wing with long and well-developed median and cubital forks; vein *Sc* ending at vein *R*; and a normally developed anal vein (Fig. 48). Of the two, aforementioned genera *Brevicornu* is the only genus with the mesonotum clothed in numerous prostrate setae (*i.e.*, setae lying flat against the body). It may also be useful to examine male and female terminalia, as *Brevicornu* usually have elongated terminalia, as opposed to those in *Allodia*. The biology and immature stages of Afrotropical species remain unknown.

***Clastobasis* Skuse** (Leiinae)**.** A small genus comprising 16 extant species, recorded from all zoogeographical regions, except the Nearctic and Neotropical Regions and Antarctica. Six species are recorded from the Afrotropical Region, described from Comoros, Oman, Senegal, Seychelles and Tanzania, but the genus appears to be widespread and locally common and numerous species await description. The genera *Leia* and *Clastobasis* are frequently confused in collections, due to their very similar wing venation (compare Figs 37 and 38), but the latter genus can be recognised based on their smaller size, colouration (usually unicolourous yellowish) and conspicuous banded antennae (Fig. 1). For identification see Matile (1973*b*, 1979*a*) and Chandler (2000). The biology and immature stages of Afrotropical species remain unknown.

***Dinempheria* Matile** (Mycomyinae)**.** An endemic Afrotropical genus with seven described species. It appears to be most common in lowland rainforests in Central Africa and additional species await description. Within the subfamily Mycomyinae, species of *Dinempheria* are easily identified based on their slender body; long legs; narrow wings with the anal lobe reduced (Fig. 26); and a setulose laterotergite. Species described to date are figured in Matile (1979*b*) and Väisänen (1994). The larvae are gregarious and spin webs and have been found on the underside of sporophores of Agaricaceae. Larvae of two species were described by Matile (1979*b*).

***Docosia* Winnertz** (Leiinae)**.** A genus of *ca* 80 extant species two-thirds of which occur in the Palaearctic Region. The genus is known from all zoogeographical regions, however, except the Australasian Region and Antarctica. Kurina & Ševčík (2012) reported *Docosia gilvipes* (Haliday *in* Walker, 1856) from South Africa (both sexes). A further eight specimens from four additional localities in South Africa have been examined, but as this material only comprises females, they could not be identified to species. Thus, Kurina & Ševčík's (2012) suggestion that *D. gilvipes* may represent an introduced species must remain an open question. Systematically, the genus takes an intermediate position between the subfamilies Gnoristinae and Leiinae, but due to the relatively short wing vein R_1 (Fig. 41), is commonly included in the Leiinae. *Docosia* can be separated from other genera in the subfamily in having the wing with complete anterior and posterior forks and a strong, long and abruptly ending vein *Sc* (Fig. 41). The biology and immature stages of Afrotropical species remain unknown.

***Dziedzickia* Johannsen** (Gnoristinae)**.** A genus of more than 60 species, recorded from all zoogeographical regions, except the Australasian Region and Antarctica, two-thirds of which occur in the Neotropics. Five species are recorded from the Afrotropical Region. As commonly treated, *Dziedzickia* covers a large, diverse assemblage of species globally, which are certainly paraphyletic (*e.g.*, Matile 1992; Ševčík *et al*. 2011, 2013). In genera in the subfamily Gnoristinae, *Dziedzickia* can be identified on the following combination of characters: presence of well-developed mouthparts; wing with long vein *Sc* ending free, or in vein *R*; point of furcation of posterior fork distinctly before point of furcation of anterior fork; and vein R_{2+3} present or absent (Fig. 44). Some species have distinctly serrated antennae that may even be branched, as in some *Metanepsia* (Fig. 3). The biology and immature stages of Afrotropical species remain unknown. An identification key, that includes the five described Afrotropical species, was provided by Matile (1992), but several additional species await description.

***Epicypta* Winnertz** (Mycetophilinae: Mycetophilini)**.** A large genus of *ca* 150 extant species, known from all zoogeographical regions, except Antarctica, with most by far described from the Neotropical Region. Twenty-one species have been recorded from the Afrotropical Region. The closely related genus *Platurocypta* Enderlein was erected, based on material from Seychelles and today comprises 19 species from all regions, 11 occurring in the Afrotropics. As previously noted by Chandler (1981), distinctions between *Epicypta* and *Platurocypta* remain vague and problematic and the validity of the two genera remains unresolved. Afrotropical material, studied for preparation of this chapter, exhibit continuous variations in all characters commonly used to separate the two genera (*i.e.*, branches of anterior and posterior forks with, or without setae; posterior fork branching before, or after, anterior fork; costal vein ending at apex of vein R_{4+5}, or produced beyond vein R_{4+5} (Fig. 53); antepronotum and proepisternum completely, or partially fused (Fig. 14); and the chaetotaxy of mesonotum, antepronotum and propleuron (Fig. 14)). As Matile (1979*a*) pointed out, *Epicypta* and *Platurocypta* require a comprehensive revision, preferably also including parts of *Mycetophila*. Consequently, *Epicypta* and *Platurocypta* are not separated in the above generic key. Most Afrotropical species in the two genera were described from Bioko Is. (Equatorial Guinea) (as Fernando Póo) and Comoros and the male terminalia are illustrated by Matile (1973*a*, 1979*a*). The biology and immature stages of Afrotropical species remain unknown.

***Exechia* Winnertz** (Mycetophilinae: Exechiini). A large genus of *ca* 170 described species, known from all zoogeographical regions, except the Neotropical Region and Antarctica, with most from the Holarctic Realm. Ten species have been described from the Afrotropical Region (Chandler 2000; Matile 1980*a*), but the genus appears to be locally very common and numerous species await description. In the Afrotropical Region *Exechia* and *Pseudexechia* are the only genera within the subfamily Mycetophilinae with a short posterior wing fork and thorax with a bare anepisternum. Of the two genera, *Exechia* is the only one with numerous strong setae on the mesonotum. The biology and immature stages of Afrotropical species remain unknown.

***Leia* Meigen** (Leiinae)**.** A genus of more than 150 described species, recorded from all zoogeographical regions, except Antarctica, about two-fifths from the Neotropical Region. The genus is common and widespread in the Afrotropical Region and 23 species have been recorded. Within Leiinae, *Leia* is easily confused with *Clastobasis* (see above), but can be separated on the combination of wing with costal vein produced beyond apex of vein R_{4+5}; distinct vein *Sc* ending at costal vein (C); and presence of crossvein *sc–r* (Fig. 38). Larvae of the Afrotropical species, *L. arsona* Hutson, 1978, have been observed feeding on stored root ginger in London (Hutson 1978). There has been no attempt to compile an identification key for the Afrotropical species and a thorough revision of the genus is required.

***Leptomorphus* Curtis** (Sciophilinae)**.** A genus of 45 extant species, recorded from all zoogeographical regions, except

Antarctica (Borkent & Wheeler 2012). Ten species are recorded from the Afrotropical Region, originating in West and Central Africa (7 species) and one species each from Madagascar, South Africa and Tanzania. *Leptomorphus* spp. are large mycetophilids with long legs and rather slender wings (Fig. 34). Matile (1977) recognised four subgenera, of which three are represented in the Afrotropics. The phylogenetic analysis of Borkent & Wheeler (2012), however, did not recover support for Matile's subgeneric classification and this is not followed here. The biology and immature stages of Afrotropical species remain unknown. Borkent & Wheeler (2012) provided an identification key for all extant species.

***Manota* Williston** (Manotinae)**.** A very large genus of more than 250 described species, known from all zoogeographical regions, except Antarctica. The genus appears to be common and widespread in the Afrotropical Region, with 56 described species, most by Hippa & Kurina (2012), Hippa (2008), Jaschhof & Mostovski (2006), Kurina & Hippa (2014), Matile (1972*a*, 1979*a*) and Søli (1993). *Manota* is the single representative of the subfamily Manotinae occurring in the region. *Manota* are pale coloured, rather small species (2.5–3.5 mm) and can be recognised in having the fine tibial setae in regular rows; a conspicuous row of strong, erect occipital setae just behind the compound eye (Fig. 13); and reduced wing venation, with very short vein R_1, and M_1 and M_2 proximally reduced (Fig. 22). The biology and immature stages of Afrotropical species remain unknown.

***Metanepsia* Edwards** (Gnoristinae)**.** A genus of nine described species, confined to the Afrotropical and Oriental Regions, seven of which occur in the Afrotropics. The genus is chiefly identified on the basis of the roundish, often infuscate wing, with a short vein R_1 (Fig. 43) and the reduced mouthparts (Fig. 15); males also have asymmetrical antennal flagellomeres and sometimes even deeply-branched antennae (Fig. 3). The systematic position of this, in many respects, rather divergent genus, has been much discussed and is here included in the subfamily Gnoristinae, following Ševčík *et al*. (2013). The biology and immature stages remain unknown. Identification keys to described Afrotropical species were provided by Matile (1971, 1974*c*, 1980*b*), but numerous species await description.

***Mohelia* Matile** (Leiinae)**.** This endemic monotypic genus, was described based on material from Comoros (Matile 1979*a*). Recently two more species were described from South Africa, and one from Mauritius (Oliveira 2015). At least four additional species are known from Malawi (Oliveira 2015), Burundi, Madagascar, South Africa and Tanzania. *Mohelia* can be recognised by the combination of hind tibia without strong setae, short wing vein R_1 and the anterior fork with long stem (Fig. 40). The genus is closely related to the Neotropical genus *Aphrastomyia* Coher & Lane and their phylogenetic relationship requires further investigation. The biology and immature stages remain unknown.

***Moriniola* Matile** (Mycomyinae)**.** An endemic monotypic genus, with the single described species, *M. grilloti* Matile, 1976, described from Democratic Republic of Congo (Matile 1976*a*). *Moriniola* is the only genus in the subfamily Mycomyinae with narrow wings and a single vein behind the anterior fork (Fig. 25). The biology and immature stages remain unknown.

***Mycetophila* Meigen** (Mycetophilinae: Mycetophilini)**.** The largest genus in the family, with *ca* 700 extant species, recorded from all zoogeographical regions, except Antarctica, with most species described from the Neotropical and Palaearctic Regions. Four species are described from the Afrotropical Region (Matile 1980*a*: 229), but additional species await description. Within the tribe Mycetophilini, *Mycetophila* have both the anterior and posterior wing forks complete, with vein M_4 slightly divergent from vein M_2, but parallel with, or convergent toward, vein *CuA* (Fig. 52). The biology and immature stages of Afrotropical species remain unknown.

***Mycomya* Rondani** (Mycomyinae)**.** A large genus comprising more than 350 species, recorded from all zoogeographical regions, except Antarctica. Eleven subgenera are recognised, two of which (*Mycomya sensu stricto* and *M.* (*Mycomyopsis* Väisänen)), have been recorded from the Afrotropical Region, with seven and two species, respectively. Within Mycomyinae, *Mycomya* are best recognised based on the presence of wing vein R_{2+3}; absence of the fold line between veins R_{4+5} and M_1; and costal vein ending at apex of vein R_{4+5} (Fig. 27). The biology and immature stages of Afrotropical species remain unknown.

***Mycomyiella* Matile** (Mycomyinae)**.** An endemic Afrotropical genus with nine described species. The genus appears to be rather common in the Afrotropics, particularly in Afromontane forests and species have been described from Bioko Is. (Equatorial Guinea) (as Fernando Póo), Cameroon, Ghana, South Africa and Tanzania. Within Mycomyinae, *Mycomyiella* can be recognised by the combination of wing vein R_{2+3} present; costal vein produced beyond apex of vein R_{4+5}; and absence of a fold line between veins R_{4+5} and M_1 (Fig. 28). The biology and immature stages remain unknown. An identification key for all known species was provided by Gammelmo (2004).

***Neoempheria* Osten Sacken** (Mycomyinae)**.** A genus of *ca* 120 extant species, recorded from all zoogeographical regions, except Antarctica, with more than half described from the Neotropical Region. Eleven species are recorded from the Afrotropical Region, six from Bioko Is. (Equatorial Guinea) (as Fernando Póo) and Comoros (Matile 1973*a*, 1979*a*). Within Mycomyinae, *Neoempheria* can be recognised on the combination of presence of wing vein R_{2+3}, costal vein produced beyond apex of vein R_{4+5}; presence of fold line between veins R_{4+5} and M_1; and the wing commonly with dark markings (Fig. 29). One species, tentatively included in the monotypic and poorly known subgenus *Syndocosiella* Väisänen in the genus *Syndocosia* (see below), may key out together with *Neoempheria*. In contrast to species in *Neoempheria*, this species has wing vein *Sc* ending in vein *C*. Larvae of *N. ombrophila* Matile, 1975, were observed in a web on the underside of the sporophore of Agaricaceae (Delobel & Matile 1976).

***Paradoxa* Marshall** (Leiinae)**.** An interesting small genus, known from two species, one from the Australasian Region (New Zealand) and one from the Afrotropical Region (South Africa). The Afrotropical species, *P. paradoxa* Jaschhof, 2006, is illustrated by Jaschhof (2006). The genus is easily recognised by its unique wing venation, with a closed cell *cua* (Fig. 39). The biology and immature stages remain unknown.

***Parempheriella* Matile** (Mycomyinae)**.** With the exception of a single species recorded from South Korea, this genus is confined to the Afrotropical Region. Two subgenera are recognised, *P.* (*Parempherina* Matile), with four described species and *Parempheriella sensu stricto*, with 34 described species, but numerous additional Afrotropical species of this common and widespread genus await description. Most species were described and keyed by Matile (1974*a*). Within Mycomyinae, *Parempheriella* can be chiefly recognised by the absence of wing vein R_{2+3} and the costal vein produced well beyond apex of vein R_{4+5} (Fig. 24). The biology and immature stages remain unknown.

***Phronia* Winnertz** (Mycetophilinae: Mycetophilini)**.** A large genus of *ca* 150 extant species, known from all zoogeographical regions, except Antarctica, with most from the Holarctic Realm. Four species have been described from the Afrotropical Region, one from Seychelles and three from Comoros (Matile 1979*a*). Undescribed species are known from Madagascar, South Africa, Tanzania and Uganda. Within the subfamily Mycetophilinae, the two genera *Phronia* and *Trichonta* are distinguished by the combination of the setulose anepisternum and bare anepimeron. Some key characters used to separate the two genera in the Holarctic, fail when applied to Afrotropical material. Although *Phronia* seemingly always has the hind coxa without a basal seta and the posterior wing fork distinctly shorter than in *Trichonta*, with veins M_4 and *CuA* often reaching the wing margin (Fig. 51). The more rounded dorsal appendage of the gonostylus in *Phronia* also helps to separate males in the two genera. The biology and immature stages of Afrotropical species remain unknown.

***Platurocypta* Enderlein**. See *Epicypta*.

***Platyprosthiogyne* Enderlein** (Mycetophilinae: Mycetophilini)**.** An endemic Afrotropical genus with three described species, recorded from Cameroon, Comoros and Seychelles (Matile 1974*b*, 1980*a*: 229). Among genera in the subfamily Mycetophilinae with a single cubital wing vein, *Platyprosthiogyne* can be recognised in having the mid tibia without ventral setae; the mesonotum without an anterior median keel; the costal vein produced well beyond the apex of vein R_{4+5}; and the wing border with a distinct incision near the apex of vein *CuA* (Fig. 56). The biology and immature stages remain unknown.

***Pseudexechia* Tuomikoski** (Mycetophilinae: Exechiini)**.** A genus of 23 extant species, known from all zoogeographical regions, except the Australasian and Neotropical Regions and Antarctica, with most described from the Palaearctic Region. Seven species have been described from the Afrotropical Region (Kjærandsen 1994). *Exechia* and *Pseudexechia* are the only Afrotropical genera in the subfamily Mycetophilinae with a short posterior wing fork (Fig. 46) and bare anepisternum. As opposed to *Exechia*, the mesonotum is devoid of larger setae in *Pseudexechia*. The biology and immature stages of Afrotropical species remain unknown.

***Rymosia* Winnertz** (Mycetophilinae: Exechiini)**.** A genus of 80 extant species, known from all zoogeographical regions, except the Australasian Region and Antarctica, with most species described from the Palaearctic Region. The genus appears to be rare in the Afrotropics and Matile (1980*a*: 228) listed two species from Kenya and Tanzania; the former being questionable, as the record appears to be based on an erroneous identification of a European species. Additional undescribed species are known from Burundi, Kenya, Madagascar and Tanzania. *Rymosia* is unique among Afrotropical genera in the subfamily Mycetophilinae, by the combination of a bare anepisternum; wings with long and well-developed anterior and posterior forks; vein *Sc* ending free; and presence of a long and strong vein *CuP* (Fig. 47). The biology and immature stages of Afrotropical species remain unknown.

***Sceptonia* Winnertz** (Mycetophilinae: Mycetophilini)**.** A genus of 33 described species, occurring in all zoogeographical regions, except Antarctica. One species was described from Tanzania (Bechev 1994) and an undescribed species was previously reported from South Africa (Matile 1980*a*: 230). Among genera in the subfamily Mycetophilinae with a single cubital vein, *Sceptonia* can be recognised in having the mid tibia without ventral setae and the costal vein of the wing not extending beyond the apex of vein R_{4+5} (Fig. 55). The biology and immature stages of Afrotropical species remain unknown.

***Sciophila* Meigen** (Sciophilinae)**.** A large genus of *ca* 170 extant species occurring in all zoogeographical regions, except the Australasian Region and Antarctica. The genus appears common and widespread in the Afrotropical Region, with 21 described and numerous undescribed species. *Sciophila* is best recognised by the relatively broad wing, with numerous macrotrichia; presence of vein R_{2+3}; and the short posterior fork (Fig. 33). The biology and immature stages of Afrotropical species remain unknown. The identification key provided by Søli (1997*b*) deals with the majority of Afrotropical species.

***Synapha* Meigen** (Gnoristinae)**.** A genus of 30 extant species recorded from all zoogeographical regions, except Antarctica, but appears most common in the Southern Hemisphere. The genus appears rather widespread in the Afrotropical Region, with five described and several undescribed species. Among genera in the subfamily Gnoristinae, Afrotropical *Synapha* can be identified based on the short posterior wing fork (Fig. 42). The biology and immature stages of Afrotropical species remain unknown. The five described Afrotropical species were keyed by Matile (1992).

***Syndocosia* Speiser** (Mycomyinae)**.** An endemic Afrotropical genus of eight or nine described species. *Syndocosia* is mainly recognised in having the ocelli entirely reduced. A new monotypic subgenus *S.* (*Syndocosiella*) was erected to contain *S. ekoicola* Väisänen, 1982, known from a single, poorly-preserved specimen from Nigeria. The tentative inclusion of the species in *Syndocosia* was based almost exclusively on characters of the male terminalia, as the species diverges markedly in other respects: its size is almost half that of the other species, the ocelli are present and the wing has vein R_{2+3} and no apical fold (as in Fig. 23) (Väisänen 1982). Pending a more detailed analysis, the new subgenus has been omitted from the above identification key. Following the description provided by Väisänen (1982), *S. ekoicola* would key out together with the genus *Neoempheria*, but wing vein *Sc* ends in vein R_1 and not in *C* as in *Neoempheria*. The remaining eight species are described based on material from Central African Republic and Tanzania and most are keyed by Matile (1976*b*). Undescribed species have been reported from Bioko Is. (Equatorial Guinea) (as Fernando Póo), Côte d'Ivoire and Democratic Republic of Congo (Matile 1976*b*) and additional undescribed species are known from Burundi and Tanzania. The biology and immature stages remain unknown.

***Trichonta* Winnertz** (Mycetophilinae: Mycetophilini)**.** A rather large genus of *ca* 110 extant species, recorded from all zoogeographical regions, except Antarctica, most of which occur in the Holarctic Realm. Only one species, *T. sincera* Gagné, 1981, described from Central African Republic, has been recorded from the Afrotropical Region (Gagné 1981), but undescribed species are known from Madagascar. Within the subfamily Mycetophilinae, the two genera *Trichonta* and *Phronia* are distinguished by the combination of the setulose anepisternum and bare anepimeron; for further details on the separation of the two genera, see *Phronia* (above). The biology and immature stages of Afrotropical species remain unknown.

***Viridivora* Matile** (Mycomyinae)**.** An endemic Afrotropical genus with two described species, recorded from Bioko Is. (Equatorial Guinea) (as Fernando Póo) (Matile 1973*a*) and Central African Republic (Matile 1972*b*). In the subfamily Mycomyinae, *Viridivora* is unique in the absence of strong tibial setae. The two known species have yellowish wings, without maculae, and a costal vein extending well beyond the apex of vein R_{4+5}. In rainforest, Matile (1972*b*) observed larvae of *Viridivora* feeding on mosses and liverworts growing on tree trunks. The larvae occurred under a thin, silky web.

***Zygomyia* Winnertz** (Mycetophilinae: Mycetophilini)**.** A large genus of *ca* 90 species, recorded from all zoogeographical regions, except Antarctica. Four described species occur in the Afrotropical Region, described from Cameroon and Ethiopia (Kurina 2012), but the genus is also recorded from Central African Republic, Comoros (Matile 1980*a*: 230) and Uganda. Among genera in the subfamily Mycetophilinae with a single cubital vein, *Zygomyia* can be recognised in having the mid tibia with one or more, ventral setae (Fig. 17) and wing vein M_4 clearly divergent from vein M_2 (Fig. 54). The biology and immature stages of Afrotropical species remain unknown.

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SCIARIDAE 21

(Black Fungus Gnats)

Frank Menzel and Jane E. Smith

Fig. 21.1. Male of *Sciara differens* (Lengersdorf) (South Africa) (photograph © S.A. Marshall).

Diagnosis

Very small- to medium-sized gnats (body length: 0.7–8.0 mm), rarely up to 15 mm in tropical species; often uniformly dark brown to black (Figs 2, 63), but some species with more contrasting reddish or yellow colouration on antennal bases, thoracic sclerites, abdominal sclerites, abdominal pleural membranes and male terminalia structures (Fig. 1).

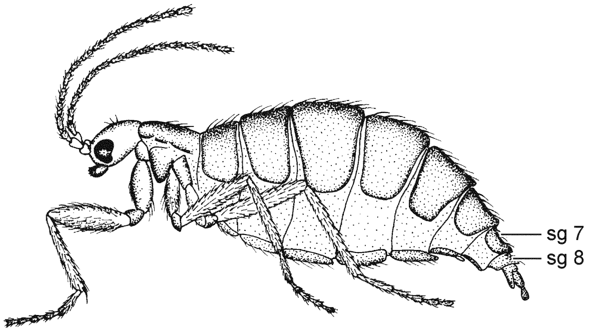
Head usually rounded (Figs 5, 6), rarely flattened, elongate-oval (Fig. 3) or with conspicuously prolonged face, clypeus and mouthparts (Fig. 7); face and clypeus with roundish tufts or elongate bands of setae; clypeus ending ventrally in tapered mouthparts (labrum, hypopharynx, maxilla, labium and labella); head capsule laterally with large compound eyes, dorsally with 3 ocelli in triangular arrangement; eye bridge usually complete medially, with or without ommatidia (Fig. 5), usually with 1–4 rows of ommatidia, 5–9 rows in larger species, rarely vestigial (Fig. 6); antenna consisting of scape, pedicel and 14 flagellomeres (together forming the flagellum); scape and pedicel sub-globular (Fig. 5), scape rarely bowl-shaped (Fig. 7), pedicel rarely elongate-cylindrical; flagellomeres mostly longer in male than in female, often with longer setae; flagellomeres with broad, cylindrical basal portions and narrower necks (Figs 14–22), usually with sharp edge between both parts; surface of basal portion smooth (Figs 14, 17) or variously structured

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 557–580.

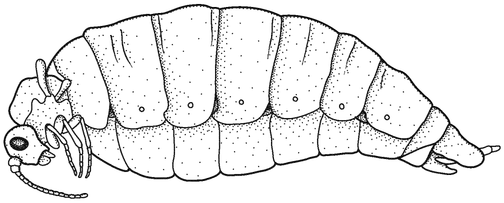
(Figs 15, 16, 20, 21), with coarse setae, often with fine sensilla (Fig. 22); neck smooth, without node-like swelling and sensilla, occasionally bicoloured with dark ring on apex (Fig. 15); setae usually about as long as width of basal portion (Fig. 19) or shorter (Figs 14–16), rarely markedly dense and short (*e.g.*, *Rhynchomegalosphys* Lengersdorf), or conspicuously long (then in connection with long necks, *e.g.*, *Epidapus* Haliday and *Euricrium* Enderlein) (Figs 17, 18) or long and arranged in circular whorls (males of some *Cratyna* Winnertz *sensu stricto*); palpus long, usually 3-segmented (Figs 23–27), in some genera foreshortened, 1- or 2-segmented (Figs 28–33), only in *Sciarotricha biloba* Hippa & Vilkamaa, 1994 extremely long, 4-segmented; all palpal segments with setae, palpal segment 1 (segment 2 in *S. biloba*) with translucent sensilla forming sensory area (Figs 23, 25, 27–31) or sensory pit (Figs 26, 32, 33).

Thorax usually flatly arched, often dark brown to black in colour (Fig. 2), paler in small species (*e.g.*, *Corynoptera* Winnertz, *Epidapus* and *Pnyxia* Johannsen), occasionally honey-coloured laterally (*Dolichosciara* Tuomikoski, *Euricrium* and some species-groups of *Bradysia* Winnertz) or entirely reddish orange (some species of *Sciara* Meigen) (Fig. 1); rarely thorax highly arched, similar to Mycetophilidae (*Dolichosciara*), or flattened, with reduced thoracic sclerites (*e.g.*, females with reduced wings in the genera *Epidapus* and *Pnyxia*) (Figs 3, 8); mesonotum with setae of varying sizes laterally and/or dorsally; katepisternum subtriangular, usually high (Fig. 11), attenuated, wedge-shaped (Fig. 12) or shortened and small (Fig. 13); posterior pronotum usually bare, occasionally with short seta(e) (*e.g.*, *Sciara*, *Cratyna* and *Pnyxia*); laterotergite and posterior episternum usually bare, rarely with setal group (*Sciarotricha* Hippa & Vilkamaa and *Scythropochroa* Enderlein); scutellum sparsely covered in short setae, mostly with longer and stronger setae (2 or 4 setae in pairs, or more setae diffusely arranged). Wing as in Figs 34–47; membrane hyaline or fumose, brownish to blackish in larger species, with dense microtrichia; macrotrichia only present in one named Afrotropical species (*Trichosia ghesquierei* Lengersdorf, 1938); wing venation (*e.g.*, Fig. 34) rather uniform, typically with strong anterior veins bearing macrotrichia (veins *C*, *R*, R_1, R_{4+5}) and 2 weaker or thinner vein forks usually without macrotrichia (M_1+M_2 and M_4+CuA); costal vein (C) extending beyond R_{4+5} (extension of *C* between R_{4+5} and M_1 indicated as "c"; distance between apex of R_{4+5} and apex of M_1, indicated as "w") (Figs 34, 46); only one functional crossvein (radial sector (*Rs*)), typically short, perpendicular to veins R/R_1 and $r\text{–}m/R_{4+5}$; vein $M+CuA$ shorter than crossvein *bm–m* (Figs 34, 38) or longer than *bm–m* crossvein (Figs 35, 40); exceptionally *m–cu* crossvein present and vein $M+CuA$ absent (*Pnyxia*, Fig. 39) or vein M_1 absent (*Amesicrium* Enderlein, Fig. 47); anal lobe well-developed (*e.g.*, Figs 34–37, 40–43) or reduced (Figs 38, 39, 46); halter (Figs 9, 10) with knob and stem variable in colour and length, H–K index = 1.8–2.5 (= ratio of halter length (H) to knob length (K), relevant in identification of small species); knob with short setae, often in

2 *Lobosciara* ♂



3 *Pnyxia* ♀

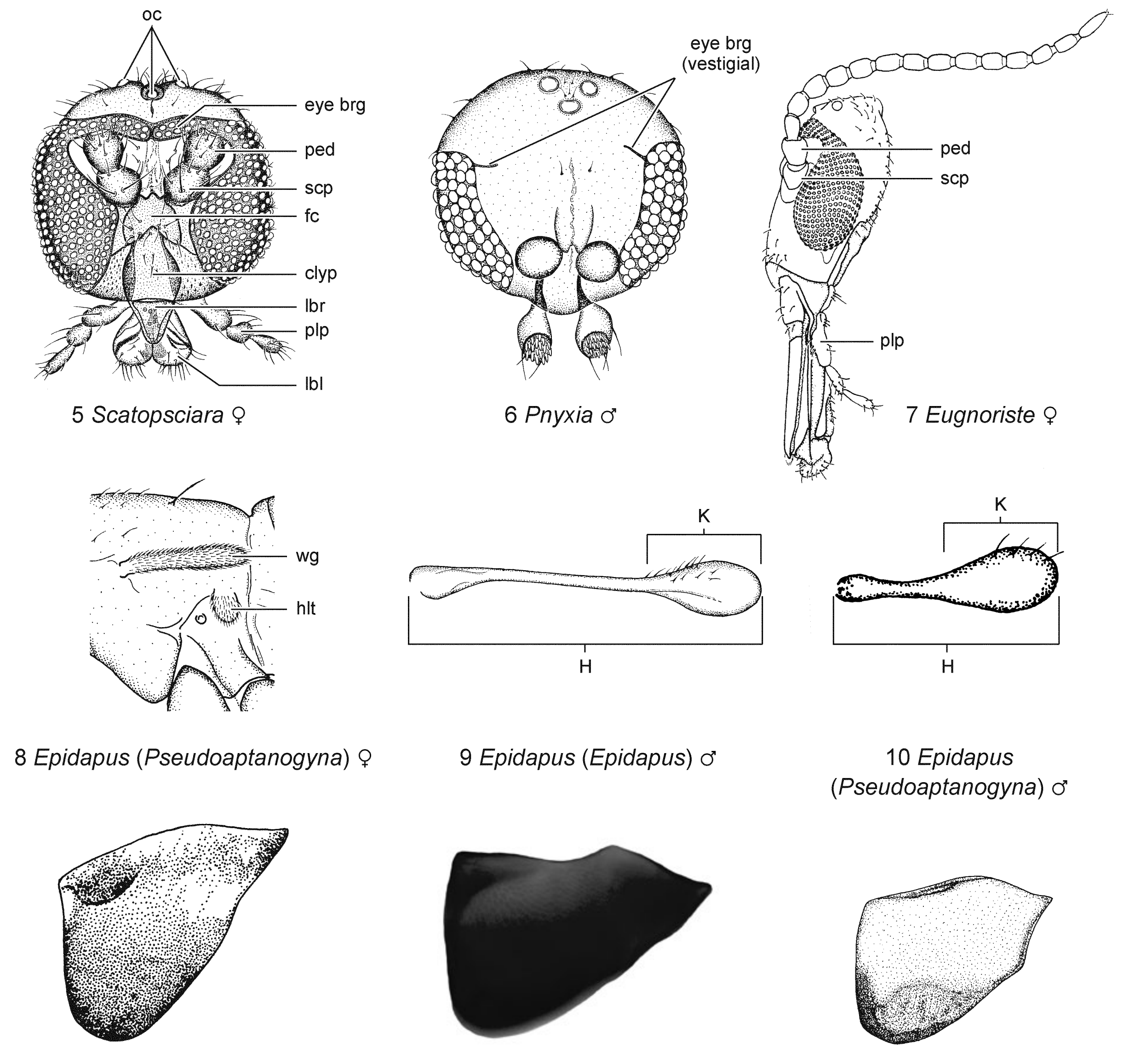


4 *Epidapus* (*Pseudoaptanogyna*) ♀

Figs 21.2–4. Habitus of Sciaridae (lateral views): (2) male of *Lobosciara bilobata* Vilkamaa & Hippa (mounted in Canada balsam, terminalia removed, see Fig. 62); (3) apterous female of *Pnyxia scabiei* (Hopkins); (4) micropterous female of *Epidapus pallidus* (Séguy). Fig. 2 (Menzel & Smith 2009, fig. 1), Fig. 3 (Menzel & Mohrig 2000, fig. 428), Fig. 4 (after Séguy 1961, fig. 1).

Abbreviation: sg – segment.

1 or 2 rows. Legs long and strong (Fig. 1), occasionally slender (Fig. 2) or shorter and thickened (Figs 3, 4); legs dark brown to black, pale grey or yellow; tibiae and tarsi (Figs 48, 49) densely clothed in short, coarse setae; tibiae often with short, dark and spinose setae (conspicuously strong, stiff setae); hind tibia occasionally with complete posterodorsal row of spinose setae (*e.g.*, *Bradysia* and *Corynoptera*), fore tibia with apical spur and modified anteroapical depressed area (Figs 50–58), apices of mid and hind tibiae usually with 2 spurs subequal or distinctly unequal in size (Fig. 59), rarely with single spur (*Scatopsciara*



5 *Scatopsciara* ♀

6 *Pnyxia* ♂

7 *Eugnoriste* ♀

8 *Epidapus* (*Pseudoaptanogyna*) ♀

9 *Epidapus* (*Epidapus*) ♂

10 *Epidapus* (*Pseudoaptanogyna*) ♂

11 *Bradysia* ♂

12 *Euricrium* ♂

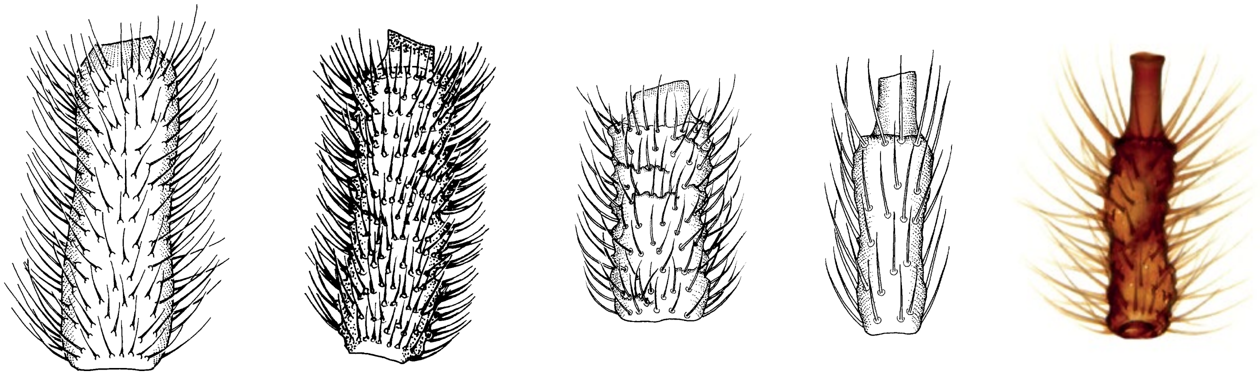
13 *Hyperlasion* ♂

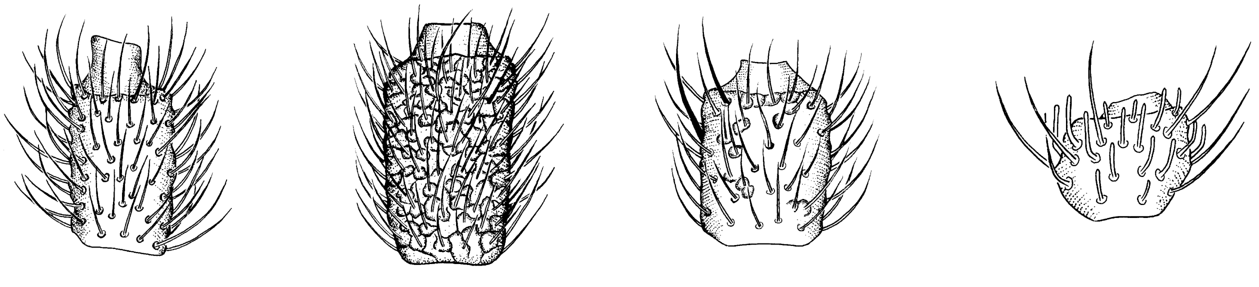
Figs 21.5–13. Heads, halteres and katepisterna of Sciaridae: (5) head of *Scatopsciara* sp., frontal view ♀ (non-Afrotropical); (6) same, *Pnyxia scabiei* (Hopkins), dorsofrontal view ♂; (7) same, *Eugnoriste capensis* Steffan, lateral view ♀; (8) rudiments of wing and halter of *Epidapus* (*Pseudoaptanogyna*) sp., lateral view ♀ (non-Afrotropical); (9) halter of *Epidapus* (*Epidapus*) sp., lateral view ♂ (non-Afrotropical); (10) same, *Epidapus* (*Pseudoaptanogyna*) sp. ♂; (11) katepisternum of *Bradysia* sp., lateral view ♂ (non-Afrotropical); (12) same, *Euricrium* sp. ♂; (13) same, *Hyperlasion* sp. ♂. Figs 5, 6, 8–11 (Menzel & Mohrig 2000, figs 48, 50, 255, 260, 292, 70a, respectively), Fig. 13 (Menzel *et al.* 2013, fig. 14), Fig. 7 (Steffan 1967, fig. 1c).

Abbreviations: clyp – clypeus; eye brg – eye bridge; fc – face; H – halter length; hlt – halter; K – halter knob length; lbl – labellum; lbr – labrum; oc – ocellus; ped – pedicel; plp – palpus; scp – scape; wg – wing.

Edwards); tarsal claws usually untoothed (Fig. 60), sometimes with fine teeth (Fig. 61) or strong teeth (Fig. 62).

Male preabdomen (segments 1–8) subcylindrical, sclerites usually more or less uniformly setose, rarely with setae accumulated in groups or bare (Fig. 64); pleural membrane bare; postabdomen (= hypopygium, including all parts posterior to segment 8) clearly distinct from preabdomen (Fig. 66); hypopygium mainly consisting of plate-like tergite 9 dorsally, ventrobasally fused gonocoxites, gonostyli connected to gonocoxites by basolateral articulations, aedeagal complex ventrally and cerci dorsally; gonocoxites with more or less V-shaped (*e.g.*, Figs 69–71), U-shaped (*e.g.*, Fig. 74) or semicircular ventral emargination (*e.g.*, Figs 75, 76), usually with 1 strong seta ventroapically (Fig. 68), in *Dolichosciara* and *Lobosciara* Steffan with 2–4 such setae (Fig. 67); ventral surface and margin of emargination with setae of various lengths, usually randomly dispersed, sometimes accumulated in groups or on lobes basolaterally or basomedially (Fig 63), especially basomedial group of setae on inner membrane (Fig. 73) and basomedial lobe (Fig. 66) with broad relevance in taxonomy; gonostylus (Figs 81–92) of varying size, form and colouration: outline straight or bent, slender or swollen, sometimes excavated (concave) on inner surface (Fig. 83), apex with spines (Figs 83, 84, 92) or with tooth (Figs 88, 89, 91), often in species-specific combinations (Figs 85–87, 90); inner surface with setae of various lengths, usually with spines varying in size and translucence (Figs 81, 86), in *Pseudolycoriella* Menzel & Mohrig and *Lycoriella* Frey with 1–3 long whiplash setae in different positions (Figs 82, 86); aedeagal complex (Figs 65, 66) consisting of fused parameres (tegmen), with aedeagal membrane ventrally and ejaculatory apodeme; paramere (tegmen) shield-like, with basolateral apodemes of varying size, form and sclerotisation; aedeagal membrane with area of small teeth (apparently with unusually strong microtrichia); paramere (tegmen) often with species-specific substructures apically, marginally and/or centrally (*e.g.*, Figs 71, 72); ejaculatory apodeme generally rod-like, varying in size and degree of sclerotisation, sometimes with basal modifications (Figs 65, 77, 80); cerci present as pair of large setose lobes dorsal to paramere (tegmen), usually clearly protruding beyond apex of paramere (Figs 63, 66); female preabdomen (segments 1–6 or 7) largely as in male, but with clear tendency to taper towards end; postabdomen (= ovipositor, including all parts posterior to segments 6 or 7) largely in correspondence to groundplan in Sciaroidea (*e.g.*, Hippa & Vilkamaa 2005, fig. 7; Søli 1997, fig. 37B), with well-developed

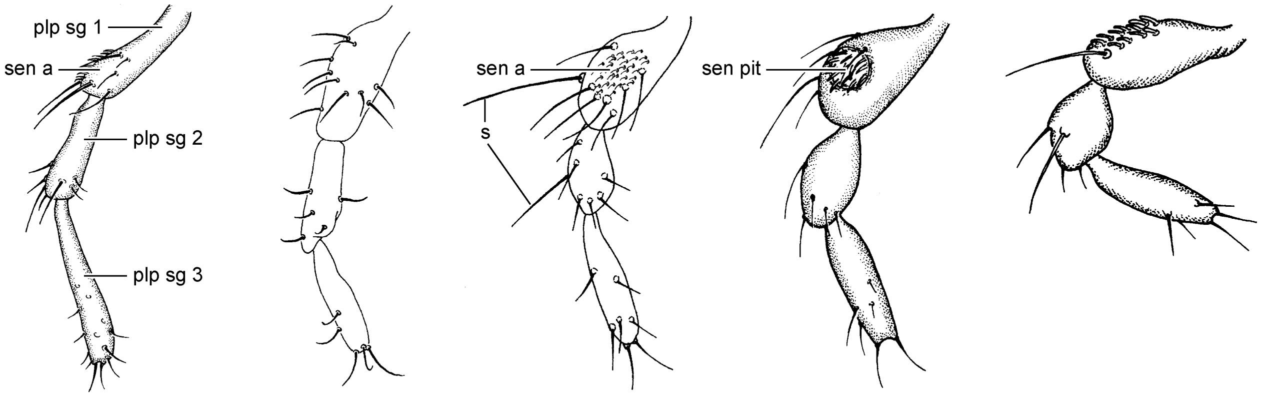

14 *Sciara* ♂
15 *Dolichosciara* ♂
16 *Bradysia* ♂
17 *Epidapus* (*Epidapus*) ♂
18 *Euricrium* ♂


19 *Pseudolycoriella* ♂
20 *Lobosciara* ♂
21 *Scythropochroa* ♀
22 *Ceratiosciara* ♀

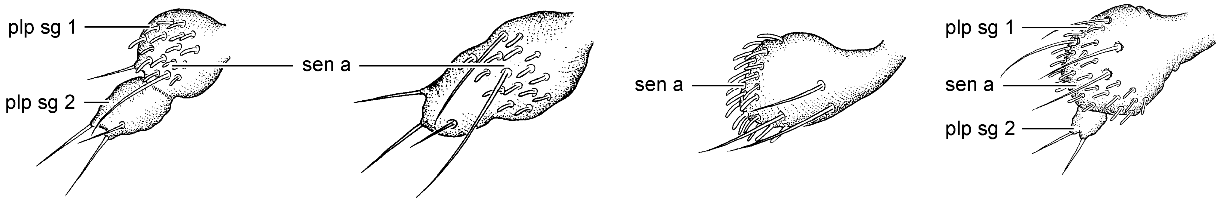
Figs 21.14–22. Antennal flagellomere 4 of Sciaridae (lateral views): (14) *Sciara hemerobioides* (Scopoli) ♂; (15) *Dolichosciara flavipes* (Meigen) ♂ (non-Afrotropical); (16) *Bradysia ocellaris* (Comstock) ♂; (17) *Epidapus* (*Epidapus*) *gracilipes* Menzel ♂; (18) *Euricrium longitibiale* (Lengersdorf) ♂; (19) *Pseudolycoriella microcteniuni* (Yang & Zhang) ♂; (20) *Lobosciara bilobata* Vilkamaa & Hippa ♂; (21) *Scythropochroa latefurcata* Enderlein ♀; (22) *Ceratiosciara corniculata* Enderlein ♀. Figs 14, 15 (Menzel & Mohrig 2000, figs 483, 416, respectively), Figs 16, 17, 19–22 (Menzel & Smith 2009, figs 9, 28, 44, 3, 50, 15, respectively).

hypogynial valves, large tergite 9, internalised and modified sternite 9 (often referred to as genital fork or vaginal furca), small segment 10 and 2-segmented cerci; female terminalia highly uniform, poorly investigated, without taxonomic relevance.

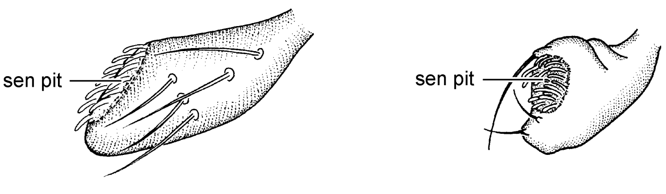
Sciaridae are readily separated from other Sciaroidea by the typical wing venation. The families Keroplatidae (see Chapter 18), non-Afrotropical Bolitophilidae, Diadocidiidae and Ditomyiidae, and all the unplaced genera of the *Heterotricha*-group (see Chapter 23), differ in having a distinct, vertical or diagonal *m–cu* crossvein (in sciarids only present in *Pnyxia*, Fig. 39). Apart from the absence of the eye bridge, Mycetophilidae (see Chapter 20) differ from Sciaridae in having a narrower, more lanceolate *M*-fork, which is much longer than vein M_{1+2}, while in Sciaridae the *M*-fork and vein M_{1+2} are subequal in length, with the *M*-fork rather bell-shaped. Furthermore, the insertion of the abdomen in the thorax is narrower in



23 *Dolichosciara* ♂ 24 *Eugnoriste* ♀ 25 *Angustosciara* ♂ 26 *Lycoriella* (*Lycoriella*) ♂ 27 *Corynoptera* ♂



28 *Epidapus* (*Zuhalia*) ♂ 29 *Epidapus* (*Zuhalia*) ♂ 30 *Epidapus* (*Epidapus*) ♂ 31 *Cosmosciara* ♂



32 *Scythropochroa* ♀ 33 *Hyperlasion* ♂

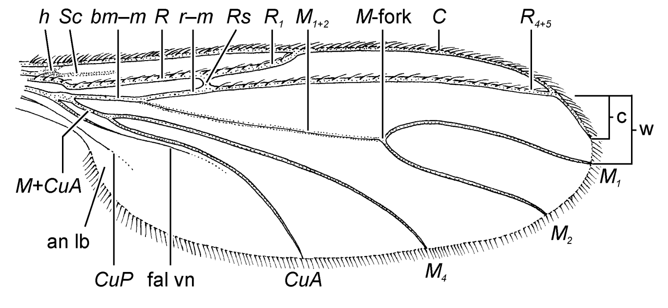
Figs 21.23–33. Palpi of Sciaridae (lateral views): (23) *Dolichosciara flavipes* (Meigen) ♂ (non-Afrotropical); (24) *Eugnoriste capensis* Steffan ♀; (25) *Angustosciara robusta* Rudzinski ♂; (26) *Lycoriella* (*Lycoriella*) *sativae* (Johannsen) ♂; (27) *Corynoptera fatigans* (Johannsen) ♂ (non-Afrotropical); (28) *Epidapus* (*Zuhalia*) *nanus* Menzel ♂; (29) same; (30) *Epidapus* (*Epidapus*) *gracilipes* Menzel ♂; (31) *Cosmosciara perniciosa* (Edwards) ♂; (32) *Scythropochroa latefurcata* Enderlein ♀; (33) *Hyperlasion viridiventris* (Frey) ♂. Figs 23, 26, 27, 33 (Menzel & Mohrig 2000, figs 55, 56, 184, 216), Fig. 24 (Steffan 1967, fig. 1b), Fig. 25 (Rudzinski 1997*c*, fig. 1a), Figs 28–32 (Menzel & Smith 2009, figs 34, 33, 29, 24, 48, respectively).

Abbreviations: plp sg – palpal segment; s – seta; sen a – sensory area; sen pit – sensory pit.

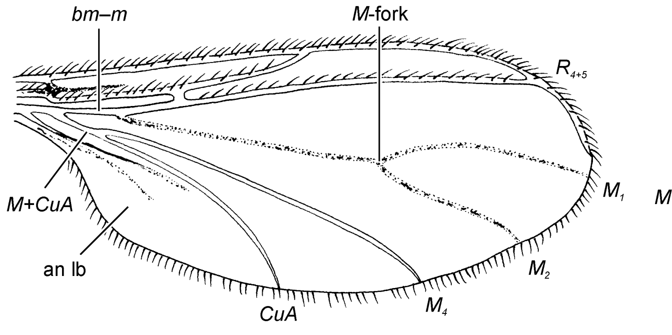
Mycetophilidae, exposing more of the mediotergite and the mesothoracic phragma is never as greatly extended into the abdomen as in Sciaridae (Fig. 2). The possession of tibial spurs distinguishes the Sciaridae (as well as the other families of Sciaroidea, except Rangomaramidae) from the family Cecidomyiidae (see Chapter 22), which is important to note, as Sciaridae and Cecidomyiidae have a complete eye bridge.

Biology and immature stages

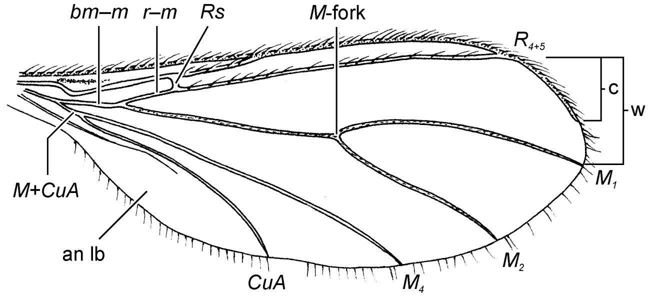
Sciarids occur in virtually all terrestrial habitats, including lowland rainforest, cloud forest, dry forest, mangrove, river and lake margins, meadow, pasture, wasteland, savanna and desert; although they are less species-rich in open and dry habitats. Almost nothing is known about the particulars of



34 *Bradysia* ♀ 35 *Scythropochroa* ♀



36 *Ceratiosciara* ♀ 37 *Scatopsciara* ♂



38 *Hyperlasion* ♂ 39 *Pnyxia* ♂

Figs 21.34–39. Wings of Sciaridae (dorsal views): (34) *Bradysia impatiens* (Johannsen) ♀; (35) *Scythropochroa latefurcata* Enderlein ♀; (36) *Ceratiosciara corniculata* Enderlein ♀; (37) *Scatopsciara atomaria* (Zetterstedt) ♂; (38) *Hyperlasion viridiventris* (Frey) ♂; (39) *Pnyxia scabiei* (Hopkins) ♂. Fig. 34 (Menzel *et al.* 2003, fig. 9), Figs 35, 36 (Menzel & Smith 2009, figs 51, 17, respectively), Figs 37–39 (Menzel & Mohrig 2000, figs 458, 215, 78, respectively).

Abbreviations: an lb – anal lobe; *bm–m* – basal medial crossvein; *C* – costal vein; c – distance between apex of R_{4+5} and end of costal vein (*C*); *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; fal vn – false vein; *h* – humeral crossvein; *M+CuA* – median vein + anterior branch of cubital vein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; *M*-fork – medial vein fork; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; w – distance between apex of R_{4+5} and apex of M_1.

biology and immature stages of Afrotropical sciarids. More detailed information is available from the Holarctic Realm for seven species with cosmopolitan distributions, including the Afrotropics, in the genera *Bradysia* (3 species), *Cosmosciara* Frey (1), *Lycoriella* (2) and *Pnyxia* (1) (see "Synopsis of the fauna" section below); all were found reproducing in greenhouses, mushroom farms or laboratories and are pests of economic importance. Further details and literature were summarised by Menzel & Mohrig (2000: 25), Menzel *et al.* (2006), Mohrig *et al.* (2013) and Steffan (1966).

Sciaridae are phytophagous (*e.g.*, *Dolichosciara* and *Sciara*), xylophagous (*e.g.*, *Scythropochroa*), phytosaprophagous (*e.g.*, *Bradysia*, *Corynoptera* and *Scatopsciara*), or mycophagous (*Lycoriella sensu stricto*) (Menzel & Mohrig 2000: 22; Shin *et al.* 2013). Generally speaking, sciarid larvae develop in a variety of decaying plant material. The number of species known to feed on living plant tissue, such as roots, or as miners in plant stems, is relatively small; the same applies to fungus-feeders. Larvae are, therefore, most numerous in soils rich in decaying plant litter or in rotten wood attacked by fungi. The tree canopy with higher humus layers, although poorly studied for Sciaridae, also provides habitat for larval development (Floren 2004; Schulz & Menzel 2000). Some exceptional sciarid species occur exclusively in ants' nests (myrmecophilous species) (*e.g.*, Evenhuis *et al.* 2007: 3) or termitaria (termitophilous species) (*e.g.*, Sutou *et al.* 2012).

In temperate zones the life cycle of species takes between 15 and 135 days, dependant on temperature and moisture (Menzel & Mohrig 2000: 14). Mating takes place on the surface of the ground or on tree logs and leaves, often immediately following eclosion of the female from the pupa and eggs are laid in batches within the first 9 days of a female's life. The female produces an average of 30 eggs, varying between 10 and 130 per female. In species in the Holarctic Realm, the egg stage lasts 2–30 days, the four larval instars 9–70 days and the pupal stage 4–36 days. Adults are short-lived (2–10 days) and survive by imbibing drops of water, or rarely, by feeding on nectar of flowers or other carbohydrate-rich sources. From a behavioural point of view, adult Sciaridae are nimble runners, but relatively weak fliers. Mass movements of larvae ("army worms") in columns of up to 10 metres are well-documented from the Palaearctic (*e.g.*, Menzel & Mohrig 2000: 17; Sutou *et al.* 2011) and are also known from the Nearctic (United States), Neotropical (Venezuela) and Oriental (Indonesia and Philippines) Regions.

The cylindrical larva (*e.g.*, Fig. 93), is characterised by the eucephalous black head capsule and the 12-segmented, white, semi-translucent body. The first-instar larva has a metapneustic respiratory system, the second- and third-instars a propneustic system and the fourth-instar larva a hemipneustic system. The last instar has one anterior (prothoracic) and seven abdominal spiracles (*e.g.*, Fig. 93), while abdominal segment 8 lacks spiracles (hemipneustic condition). The terminal abdominal segment is lobate and is used in locomotion, assisted by small ventral creeping welts on each of the other abdominal segments. These welts have irregular rows of fine spicules and the other parts of the integument are usually bare. The head capsule (*e.g.*, Fig. 95) consists dorsally of a long triangular frontal plate situated between the lateral parts of the genae. The clypeal plate is trapezoidal, is well-demarcated from the frontal plate and the labrum ends dorsally in two lobe-like sensory humps with needle-like sensory setae. The antennae are reduced to heart-shaped plates at the base of the mandibles and the eyes are indicated as single ommatidia, by lightly pigmented areas posterior to the excavated bases of the antennal plates. The labrum comprises a fleshy lobe dorsally, with two lateral sensory protuberances and two central sensory areas in circular pits. The ventral part of the labrum is formed of two areas, with comb-like rows of fine teeth. The large mandibles are inserted laterally and have three or four strong teeth. Both maxillae on the ventral side consist of a triangular cardo and an outer lying stipe, with the maxillary palpus, formed of a flat sensory area. The inner parts are represented by the large laciniae with 6–7 coarse teeth. The small setae II are located on the inner base of laciniae arranged in pairs. The mentum with the reduced labial palpi, lies between the cardo and the salivary gland opens anterior to the base of the hypopharynx. The main parts of the head capsule are formed laterally and ventrally by the genae. The shape of the ventral margins of the genae, with two different wide bridges enclosing a distinct piriform membranous area, is typical for sciarid larvae.

Black fungus gnats develop within so-called "mummy" pupae (*e.g.*, Fig. 94). All body parts and appendages are clearly visible and the surface of the pupal integument corresponds to the sheaths of antennae, wings and legs. Both cerci and gonostyli are also enclosed in separate sheaths. Unlike many fungus gnats, sciarid pupae lack the humpbacked, strongly arched thorax. The leg sheaths are adjacent and straight. The wing complex and antennal sheaths, as with the leg sheaths, lie against the body and are directed towards the abdomen. The positions of the compound eyes, palpi, prefons, proboscis and labrum are distinctly visible on the ventral side. On the dorsal side, below the wing sheaths, which extend to abdominal segment 2, are the sheaths of the halters. The prothoracic stigmata are wide and lie on a short, blunt elevation. The abdomen is 9-segmented and clothed in short, wart-like spines; these more densely arranged on the tergites and the terminal segment. The abdominal stigmata are located in pairs on segments 2–7.

Additional information (including figures) on the morphology and terminology of characters of the immature stages and their importance in identification is provided by Blaschke-Berthold (1988), Krivosheina *et al.* (1987), Menzel & Mohrig (1997: 54; 2000: 49), Steffan (1966), Sutou & Ito (2004) and Sutou *et al.* (2007).

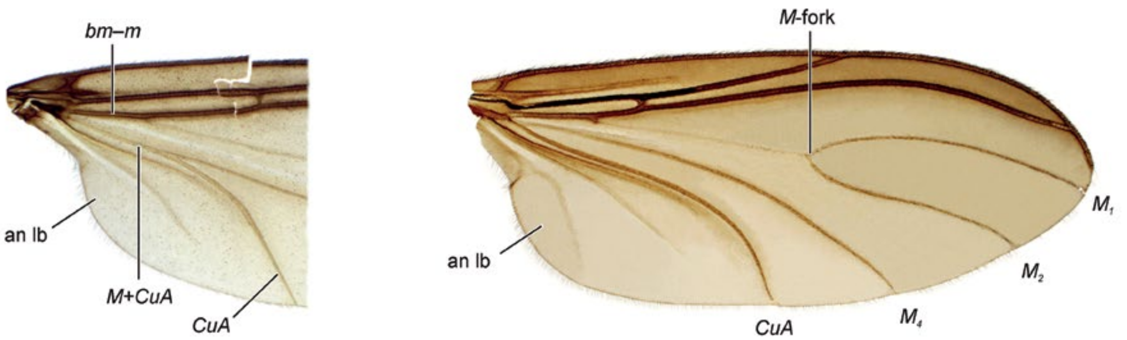
Economic significance

In Sciaridae there is a general tendency to settle in urban habitats (including all kinds of green spaces and human dwellings) and in rural areas (including animal stables, dung and compost heaps and greenhouses). Immature stages are easily transported by human activities from one place to another, often over great distances, together with soil or different plant products (*e.g.*, vegetables, fruits, flowers, timber and tree logs). So it does not come as a surprise that certain species not only find optimal conditions, but are pests in agricultural monocultures, mushroom cultures and forestry nurseries (Hurley *et al.* 2007, 2010; Menzel & Mohrig 2000: 25; Menzel *et al.* 2003, 2006). In human homes and greenhouses they are imported with plant pots, compost or other breeding substrates (*e.g.*, *Bradysia impatiens* (Johannsen, 1912), *B. ocellaris* (Comstock, 1882), *B. tilicola* (Loew, 1850) and *Cosmosciara perniciosa* (Edwards, 1922)). Studies on young pot plants revealed that the root system can be severely damaged through both larval feeding action and accumulations of larval frass. Root hairs, tubers and young shoots are especially at risk, leading to total destruction of plants; *e.g.*, *B. impatiens* on carnation plants (Santini & Lucchi 1994) and *Pnyxia scabiei* (Hopkins, 1895) on potato tubers (Gui 1933; Hopkins 1895).

Observations of sciarids causing damage in agriculture concern numerous crops, including beans, beets, cucumbers, melons, peas, peppers, potatoes, tomatoes and wheat. Damage was also observed on ornamental plants (*e.g.*, begonias, cacti, campanulas, cyclamen, geraniums, lucerne, lupins, orchids, poinsettias and primulas), in which cases larvae invade the root system and hollow out the water-storing parts (summarised by Menzel & Mohrig 2000: 24; Menzel *et al.* 2003, 2006). As a result of their physical activities, larvae were found to create entry wounds that allowed secondary bacterial and fungal infections (Menzel & Mohrig 2000: 24). High abundances of sciarid adults have been observed in plantations of banana, cocoa, coffee and oil palm, especially near accumulations of plant litter, including heaps of crop residues (pers. obs.). These observations also suggest damage in other plant cultures that have not yet been studied.

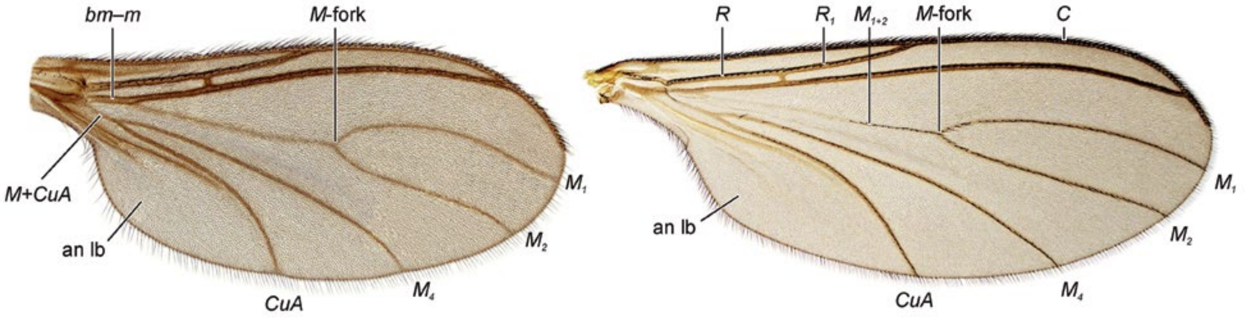
Mushroom cultures, with their warm-humid climate and beds of compost (straw with animal manure), are ideal places for the mass development of other sciarid species (*e.g.*, *Lycoriella sativae* (Johannsen, 1912) and *L. ingenua* (Dufour, 1839)) (Menzel & Mohrig 2000: 25; Menzel *et al.* 2006). The larvae of these mycophagous species infest the compost produced for mushroom cultures, browse on the fungal mycelium and burrow in the mushrooms' fruiting bodies (*e.g.*, Santini & Lucchi 1994; Symes 1921).

Although hard to quantify in economic terms, Sciaridae play an important role in the maintenance of ecosystem functions, *e.g.*, as decomposers of plant material (compost, fallen leaves, pine needles, tree bark and deadwood) or animal wastes (cow and horse manure), in food chains and webs (as prey of nematodes, spiders, predatory insects and amphibians) and even as pollinators (Rulik *et al.* 2008; Vogel & Martens 2000).



40 *Rhynchomegalosphys* ♂

41 *Sciara* ♂



42 *Pseudolycoriella* ♂

43 *Dolichosciara* ♂

Figs 21.40–43. Wings of Sciaridae (mounted in Canada balsam, dorsal views): (40) *Rhynchomegalosphys aethiops* Lengersdorf ♂ (basal section only); (41) *Sciara differens* (Lengersdorf) ♂; (42) *Pseudolycoriella patronata* Rudzinski ♂; (43) *Dolichosciara fabulosa* Rudzinski ♂.

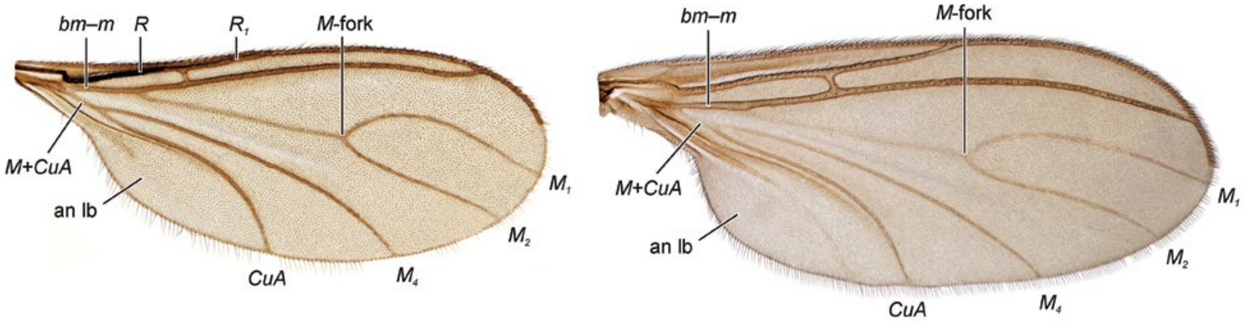
Abbreviations: an lb – anal lobe; *bm–m* – basal medial crossvein; *C* – costal vein; *CuA* – anterior branch of cubital vein; *M+CuA* – median vein + anterior branch of cubital vein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; *R* – radius, or radial vein; R_1 – anterior branch of radius.

Classification

The species-rich family Sciaridae occur in all zoogeographic regions of the Earth, including Antarctica and the subantarctic islands (Evenhuis 1989: 799; Frenot *et al.* 2005; Hughes *et al.* 2005). There are currently *ca* 2,720 extant species, classified in 83 genera and 45 subgenera (summarised here, based on an unpublished world catalogue). The Palaearctic fauna is the best researched in terms of Sciaridae taxonomy and diversity; none of the other faunas are adequately studied, not even at the generic level. The number of world species, including those remaining to be collected and named, appears inestimable and there have been few studies into the species richness of particular habitats or regions, especially outside the Palaearctic. As a matter of fact, the sciarid inventory continues to uncover new species, even in the best-studied areas of Europe, while faunistic studies of extra-Holarctic sciarids develop easily into challenging enterprises, due to the high proportion of undescribed diversity at all taxonomic levels.

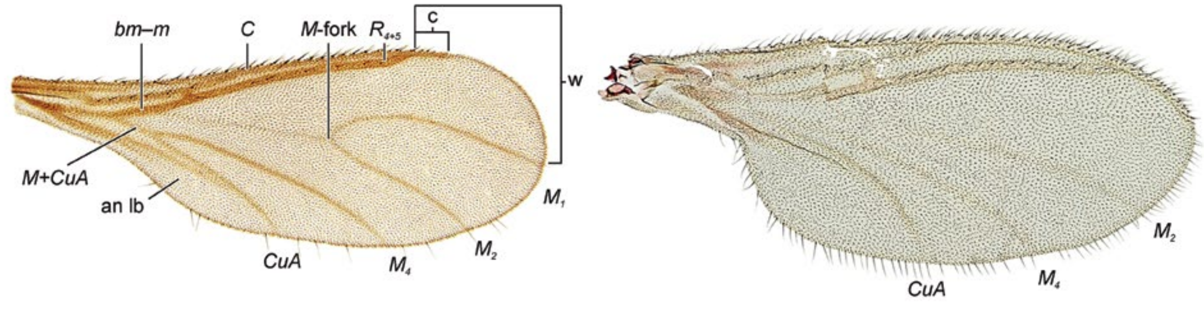
Sciaridae are accepted as a distinct family within the infraorder Bibionomorpha and the superfamily Sciaroidea (*e.g.*, Ševčík *et al.* 2016). The monophyly of the family was only exceptionally questioned in recent years, notably by Hippa & Vilkamaa (2005, 2006*a*), who included *Sciarosoma* Chandler in the Sciaridae (a genus usually considered unassigned to family; see Chapter 23), as well as the genus *Rangomarama* Jaschhof & Didham (usually classified in a family of its own, Rangomaramidae; see Chapter 23), to refer only to extant taxa. As regards the sister-group of the Sciaridae, phylogenetic analyses based on morphological characters resulted in heavily conflicting hypotheses (*e.g.*, Amorim & Rindal 2007; Hippa & Vilkamaa 2005, 2006*a*; Wood & Borkent 1989). The same is true of molecular phylogenetic analyses (*e.g.*, Ševčík *et al*. 2016; Wiegmann *et al*. 2011). Moreover, morphological and molecular evidence are not in accordance with each other, rendering the sister-group of the Sciaridae an unresolved issue.

Early attempts to classify the Sciaridae into subfamilies and tribes (Enderlein 1911; Lengersdorf 1928–30: 5) are no longer accepted and applied, as these subdivisions were not supported by autapomorphic characters (see Menzel & Mohrig 2000: 650). Already Frey (1942: 15) rejected these early classifications and instead preferred to apply what he called three "levels of specialisation". Subsequent authors of revisions, handbooks and catalogues (*e.g.*, Menzel & Mohrig 1997, 2000; Mohrig *et al*. 2013; Steffan 1966, 1980, 1981) did not sub-classify the family beyond the level of genus in the past 75 years.



44 *Euricrium* ♂

45 *Lobosciara* ♀



46 *Epidapus* (*Afromoehnia*) ♂

47 *Amesicrium* ♀

Figs 21.44–47. Wings of Sciaridae (mounted in Canada balsam, dorsal views): (44) *Euricrium afrum* Lengersdorf ♂; (45) *Lobosciara bilobata* Vilkamaa & Hippa ♀; (46) *Epidapus* (*Afromoehnia*) *breviatus* (Rudzinski) ♂; (47) *Amesicrium nanum* Enderlein ♀.

Abbreviations: an lb – anal lobe; *bm–m* – basal medial crossvein; c – distance between apex of R_{4+5} and end of costal vein (C); *C* – costal vein; *CuA* – anterior branch of cubital vein; *M+CuA* – median vein + anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; *R* – radius, or radial vein; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; w – distance between apex of R_{4+5} and apex of M_1.

The higher classification of Sciaridae remains a contentious issue and many genera from the Southern Hemisphere are poorly defined. The first suggestions and modern attempts to subdivide the Sciaridae in subfamilies were published by Menzel & Mohrig (2000: 650) and Hippa & Vilkamaa (2005) on the basis of adult external morphology and by Shin *et al*. (2013) based on molecular characters. Even so, a robust phylogenetic system of the Sciaridae has not yet been achieved. This discussion can only be continued, however, once the non-Holarctic type species are revised and more information is available regarding the sciarid fauna of the Southern Hemisphere.

Identification

Adult sciarid specimens collected in the field or reared in the laboratory for all scientific purposes are best-preserved in 70% ethanol (see Chapter 2). Specimens need to be permanently mounted on microscope slides for study using a transmitted light microscope; the routine method for identifying species using morphological characters. As this preparation is time-consuming and expensive, usually only males are slide-mounted, the body in lateral view (*e.g*., Fig. 2) and the male terminalia in ventral view under a separate cover-slip on the same slide (*e.g*., Fig. 63). Procedures for preparing slide-mounted specimens from ethanol-preserved sciarid material were described in detail by Menzel & Mohrig (2000: 44) and Steffan (1966).

Detailed examination of the male terminalia is crucial for identifying species. Male genitalic structures providing taxonomic characters are: the gonocoxites (*e.g*., outline, presence of setal groups or lobes), the paramere (tegmen) (*e.g*., shape, conspicuous modifications) and the gonostyli (*e.g*., number and arrangement of teeth, spines and conspicuous setae, especially at the apex and inner surface). A separately prepared wing may be helpful for the identification of very small species or black coloured specimens. Too excessive dissecting of specimens (*i.e*., separation of head, legs and abdomen, see Chapter 2, Figs 2.66–68) is not recommended for sciarids, as thoracic sclerites may be destroyed and sensitive isolated body parts may be distorted and damaged. Canada balsam or Euparal should be used as mounting media. As a rule, females can be identified mostly only to genus or subgenus level, as the female terminalia are highly uniform and as they lack species-specific characters. Larval and pupal characters are also of limited value in identification, due to the fact that globally the immature stages of only 45 sciarid species are described to some extent. Most recent efforts to apply molecular characters (DNA barcodes) for identifying Sciaridae species are promising and apparently useful in uncovering hidden biodiversity (Shin *et al*. 2013). One of the major challenges is to build a reference library of DNA barcodes from specimens that were authoritatively identified using morphological characters (note that slide-mounted specimens cannot be used in this respect).

In the Afrotropics, identification of species is problematic, due to a lack of modern taxonomic revisions and identification tools (identification keys and collections of authoritatively identified specimens). As a rule, most of the species descriptions published before 1967 are of limited or no use for the purpose of identification. It is estimated that at least one-half of these species names are in need of verification by type study. Taxonomic authors of Afrotropical Sciaridae names in the years 1838–1961 are: J.M.F. Bigot, M. Bezzi, F.W. Edwards, G. Enderlein, J.-J. Kieffer, F. Lengersdorf, J.P.M. Macquart, R. Paulian, E. Séguy, P.G.E. Speiser and C.G. Thomson. Recent taxonomic studies of Afrotropical Sciaridae resulted in several significant publications (Hippa & Vilkamaa 1994, 2005; Hippa *et al*. 1998; Menzel 2017; Menzel & Smith 2007, 2009; Menzel *et al*. 2013; Mohrig & Röschmann 2005; Rudzinski 1997*a*–*e*, 1999, 2000, 2003; Rudzinski & Baumjohann 2012; Steffan 1967; Vilkamaa & Hippa 1994). Afrotropical sciarid material examined and referred to in publications in the years 1838–2013 originates from Cameroon, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea, Ethiopia, Ghana, Guinea, Kenya, Madagascar, Seychelles, Sierra Leone, South Africa, Tanzania, Togo, Tristan da Cunha Is., Uganda, United Arab Emirates and Zimbabwe.

The identification key presented below is based on the Afrotropical genera and species included in the checklist of Menzel (2017). Several genus-group names are not included here (for reasons explained in the "Synopsis of the fauna" section below), namely: *Apelmocreagris* Enderlein, *Trichosia* Winnertz, *Zygoneura* Meigen (all family Sciaridae), *Faratsiho* Paulian (lower Diptera *incertae sedis*), *Psectrosciara* Kieffer (Scatopsidae; see Chapter 26), *Heterotricha* Loew and *Rhynchoheterotricha* Freeman (both Sciaroidea *incertae sedis*; see Chapter 23).

Key to genera of Afrotropical Sciaridae

1. Wing with *M*-fork reduced in female sex; vein M_1 absent, vein M_2 weakly developed (Fig. 47) (only female holotype known) . . . . *Amesicrium* Enderlein

– Wing with *M*-fork well-developed in both sexes; vein M_1 present, forming *M*-fork with vein M_2 (*e.g*., Figs 34–39, 41–46) or female wing greatly reduced (*e.g*., Figs 3, 4, 8) 2

2. Compound eyes very large, berry-shaped, with dense ommatidia between antennal scape and ocelli; eye bridge 8–9 facets wide; palpus 4-segmented, with unmodified sensory area on palpal segment 2; thorax with laterotergite setose; male terminalia with gonocoxite extended apicoventrally, with pointed process, without long setae; gonostylus bilobed, divided into ventral and dorsal lobes (see Hippa & Vilkamaa 2005, figs 3A, 4D, 5A, 6B–C) . . . . *Sciarotricha* Hippa & Vilkamaa

– Compound eyes smaller, roundish-oval to kidney-shaped (*e.g*., Figs 5–7), larger areas between antennal scape and ocelli without ommatidia; eye bridge up to 6 facets wide (*e.g*., Fig. 5) or vestigial (*e.g*., Fig. 6); palpus at most 3-segmented (*e.g*., Fig. 23), with unmodified sensory area or distinct sensory pit on palpal segment 1 (*e.g*., Figs 25–33); thorax with laterotergite bare; male terminalia with gonocoxite not extended apicoventrally (*e.g.*, Figs 69–80), without pointed process, with long seta(e) (*e.g.*, Figs 67, 68); gonostylus undivided (*e.g.*, Figs 81–92) 3

3. Posterior wing veins (M_1, M_2, M_4, *CuA*, sometimes also M_{1+2} distally) in both sexes entirely or partly with macrotrichia (*e.g.*, Figs 41, 43) 4

– Posterior wing veins (M_1, M_2, M_{1+2}, M_4, *CuA*) in both sexes without macrotrichia (*e.g.*, Figs 34–40, 42, 44–46) or wings of female greatly reduced (*e.g.*, Figs 3, 4, 8) 6

4. Necks of antennal flagellomeres uniformly brown, bottle-shaped, without sharp edge between basal portion and neck (Fig. 14); neck of flagellomere 4 distinctly wider than long; thorax with postpronotum setose; anteroapical depressed area of fore tibia with dense patch of fine setae (Fig. 50) . . . . *Sciara* Meigen

– Necks of antennal flagellomeres bicoloured (base pale, apex with dark ring), with sharp edge between basal portion and neck (*e.g.*, Fig. 15); neck of flagellomere 4 *ca* as long as wide; thorax with postpronotum bare; anteroapical depressed area of fore tibia with irregular row of spinose setae, without basal carina (*e.g.*, Fig. 54), or with single comb-like row of stronger setae, with basal carina (*e.g.*, Fig. 55) 5

5. Thorax with mesonotum slightly arched; wing small and narrow, with reduced, slightly convex anal lobe (as in Fig. 38); veins M_1, M_2 and M_4 with macrotrichia distally, veins *CuA* and M_{1+2} bare; vein R_1 very short, merged with costal vein (*C*) well before point of furcation of *M*-fork; anteroapical depressed area of fore tibia with single comb-like row of strong setae, with basal carina (2 × as wide as in Fig. 55); tarsal claws without teeth (as in Fig. 60); basal portion of antennal flagellomeres smooth, without scarred surface; palpal segments moderately long, palpal segment 1 swollen and humped, palpal segment 2 short, with 1 long seta (Fig. 25); male terminalia with gonocoxites ventrally without setose basal lobe (Fig. 71), with single long seta apicoventrally (as in Fig. 68); gonostylus broad, strongly convex medially, a wing-like bulge present dorsomedially, with spines in 2 distinct groups; paramere (tegmen) sclerotised, with strong, relatively long basolateral apodemes (Fig. 71) . . . .*Angustosciara* Rudzinski

– Thorax with mesonotum highly arched (similar to Mycetophilidae); wing large and broad, with well-developed, strongly convex anal lobe (Fig. 43); veins M_1, M_2, M_4 and *CuA* clothed in macrotrichia throughout, sometimes also M_{1+2} distally; vein R_1 long, merging with costal vein (*C*) at or near point of furcation of *M*-fork; anteroapical depressed area of fore tibia with irregular row of spinose setae, without basal carina (Fig. 54); tarsal claws with strong teeth (Fig. 62); basal portion of antennal flagellomeres with very rough, mostly scarred surface (Fig. 15); all palpal segments long and narrow, palpal segment 1 slender (Fig. 23), palpal segment 2 long, without conspicuously long seta; male terminalia with gonocoxites ventrally with setose basal lobe (as in Fig. 66), usually with 2–4 long setae apicoventrally (Fig. 67); gonostylus narrow, compact, flat to slightly concave medially, with single group of spines; paramere (tegmen) membranous, with narrow, short basolateral apodemes (as in Fig. 66) . . . . *Dolichosciara* Tuomikoski

6. Anteroapical depressed area of fore tibia with distinct comb-like row of stronger or spinose setae, with carina at apex (*e.g.*, Figs 55, 56) 7

– Anteroapical depressed area of fore tibia with dense patch of setae, with or without arcuate margin (*e.g.*, Figs 51, 52), or distinctly reduced (*e.g.*, Figs 57, 58); if setae arranged in irregular row, then this row not straight and without comb-like carina (*e.g.*, Fig. 53). 9

7. Anteroapical depressed area of fore tibia with comb-like row of setae on low bulge (Fig. 56); mid and hind tibiae with one spur either absent or ½–⅔ shorter than the other (Fig. 59); wing vein R_1 very short, shorter than ½ length of vein R (Fig. 37) . . . .*Scatopsciara* Edwards *sensu stricto*

– Anteroapical depressed area of fore tibia with comb-like row of setae, but without bulge (*e.g.*, Fig. 55); mid and hind tibiae either with 2 subequal spurs or one spur at most ¼–⅕ shorter than the other; wing vein R_1 longer than ⅔ length of vein R (*e.g.*, Figs 34, 44) 8

8. Thorax with katepisternum high, triangular (Fig. 11); mesonotum with strong, long setae laterally and dorsally in addition to short setae; wing with *M*-fork long-attenuated to bow-shaped; veins M_1 and M_2 at base weakly arched, towards apex evenly curved and almost parallel (Fig. 34); antennal flagellomeres with short necks, at most as long as wide (Fig. 16); basal portion of male flagellomere 4 moderately long, with uniformly dense setae; femora and tibiae robust; fore femur usually swollen; mid and hind tibiae with 2 subequal spurs . . . . *Bradysia* Winnertz *sensu lato*

– Thorax with katepisternum attenuated, wedge-shaped (Fig. 12); mesonotum with only sparse, short setae; wing with *M*-fork bell-shaped, wider basally than distally; vein M_1 at base highly arched, towards apex s-shaped; vein M_2 almost linear (Fig. 44); antennal flagellomeres with slender necks (Fig. 18), distinctly longer than wide; basal portion of male flagellomere 4 with long, erect setae, often with tendency to form spiral crowns at base and tip of basal portion (not figured); femora and tibiae narrow; fore femur slender; mid and/or hind tibiae with one spur ¼–⅕ shorter than the other . . . . *Euricrium* Enderlein

9. Wing vein *M+CuA* (in both sexes) very long, distinctly longer than crossvein *bm–m* (*e.g.*, Figs 35, 40) 10

– Wing vein *M+CuA* (in both sexes) at most as long as crossvein *bm–m* (*e.g.*, Figs 34, 36–38, 42, 44–46) or *M+CuA* absent in wing-reduced males (*e.g.*, Fig. 39) and females (*e.g.*, Figs 3, 4, 8) 11

10. Wing vein *CuA* distinctly angled (Fig. 40); head elongate-oval; compound eyes narrow, kidney-shaped; face and clypeus (especially in female) greatly elongated (similar to Fig. 7); palpus long, 3-segmented; palpal segment 1 narrow, with unmodified sensory area (as in Fig. 23); basal portions of antennal flagellomeres with very dense, short setae, entire surface with honeycomb-like structure (as in Fig. 20); thorax with antepronotum, mesonotum and scutellum with only sparse, small setae (without thick, long setae); posterior episternum without setal group; anteroapical depressed area of fore tibia undifferentiated, very dense with short and fine setae (without diagnostic differences with other tibial setae); male terminalia with paramere (tegmen) narrow, with excessively long basolateral apodemes (Fig. 65) . . . . *Rhynchomegalosphys* Lengersdorf

– Wing vein *CuA* evenly curved (Fig. 35); head roundish; compound eyes large; face and clypeus short (as in Fig. 5); palpus short, 1-segmented; palpal segment 1 swollen, with shallow sensory pit (Fig. 32); basal portions of antennal flagellomeres with coarse, long setae, surface only partially with honeycomb-like structure (Fig. 21); thorax with antepronotum, mesonotum and scutellum with dense, large setae; posterior episternum with setal group; anteroapical depressed area of fore tibia differentiated, dense with spinose setae in distal ½ (Fig. 51); male terminalia with paramere (tegmen) broader, with short basolateral apodemes . . . . *Scythropochroa* Enderlein

11. Antenna very short in female, with strongly shortened and convex expanded flagellomeres (Fig. 22); flagellomeres 1–6 with asymmetrical, ventrally swollen basal portions; female flagellomere 4 at most 0.9 × as long as wide, flagellomeres 7–12 shorter and wider than flagellomeres 2–6, basal portions only 0.6–0.7 × as long as wide; necks extremely short (Fig. 22); basal portions with sparse setae and conspicuously long sensilla; compound eyes reduced laterally; wing large (Fig. 36), with well-developed anal lobe (only female holotype known). . . . . *Ceratiosciara* Enderlein

– Antenna distinctly longer in both sexes, with longer, cylindrical flagellomeres (*e.g.*, Figs 16, 17, 19, 20); all flagellomeres with symmetrical basal portions (not swollen ventrally); flagellomere 4 in both sexes at least 1.3 × as long as wide, flagellomeres 7–12 narrower than flagellomeres 2–6, usually with higher length to width index (longer than 1.5 ×); necks longer (*e.g.*, Figs 17, 19); basal portions denser setose, without sensilla or with distinctly weaker sensilla; compound eyes usually large, roundish (if eyes narrower, then female head with long mouthparts (*e.g.*, Fig. 7) or female with small eyes (*e.g.*, Fig. 6) and greatly reduced wings (*e.g.*, Figs 3, 4, 8)) 12

12. Head elongate-oval; compound eyes narrow, kidney-shaped; female face, clypeus and mouthparts greatly elongated (Fig. 7); palpus 3-segmented, palpal segment 1 with short setae (Fig. 24) (only female of *E. capensis* Steffan, 1967 known) . . . . *Eugnoriste* Coquillett

– Head roundish, compound eyes large (*e.g.*, Fig. 5) or head flattened, compound eyes reduced, egg-shaped, with distinctly reduced eye bridge (*e.g.*, Fig. 6); face, clypeus and mouthparts short (as in Fig. 5) or vestigial; if palpus 3-segmented, then with conspicuously long seta on palpal segment 1 (*e.g.*, Figs 25–27). 13

13. Basal portions of flagellomeres with honeycomb-like structure (Fig. 20); male terminalia with gonocoxites with 3–4 long setae apicoventrally (as in Fig. 67), ventrally with 2–4 setose basal lobes (Fig. 63), basal ½ of inner ventral margin of gonocoxites with setal groups in pairs; gonostylus conspicuously slender, rod-shaped (Fig. 63). . . . . *Lobosciara* Steffan

– Basal portions of flagellomeres without honeycomb-like structure (*e.g.*, Figs 16, 17, 19); male terminalia with gonocoxites with single long seta apicoventrally (*e.g.*, Fig. 68), without modification ventrobasally (*e.g.*, Figs 72, 75–80) or with basomedial group of setae on inner membrane (*e.g.*, Fig. 73) or only with single setose lobe ventrobasally (*e.g.*, Fig. 66); basal ½ of inner ventral margin of gonocoxites without lobe-like group of setae; gonostylus not rod-shaped (elongate-oval, spherically widened, conically narrowed to triangular or with distinctly angled apex) (*e.g.*, Figs 81–92). 14

14. Palpal segment 1 with single long seta, without short setae (*e.g*, Fig. 27) 15

– Palpal segment 1 (sometimes only segment) with 1 conspicuously long seta and 1 or more shorter setae (*e.g.*, Figs 25, 26, 28, 29, 33) or only with short setae (*e.g.*, Figs 30, 31) 16

15. Scutellum with 2 large marginal setae; tarsal claws without teeth (as in Fig. 60); anteroapical depressed area of fore tibia denser setose, with curved margin (as in Fig. 52); flagellomeral necks approximately as long as wide (as in Fig. 19); abdominal tergites 5 and 6 without bulges and conspicuous setal

groups, tergites 7 and 8 not foreshortened, setose; male terminalia with gonostylus swollen, deeply concave medially, with spines at apex and on inner surface (Fig. 83); paramere (tegmen) rounded . . . . *Corynoptera* Winnertz *sensu lato* (*C. parvula*-group)

– Scutellum with 4 large marginal setae; tarsal claws with strong teeth (as in Fig. 62); anteroapical depressed area of fore tibia with irregular row of setae, without margin (as in Fig. 54); flagellomeral necks shorter than wide (as in Fig. 21); abdominal tergites 5 and 6 with lobe-like, bulged extensions and conspicuous setal groups (Fig. 64); abdominal tergites 7 and 8 distinctly shortened, bare or with single pair of setae (Fig. 64); male terminalia with gonostylus narrow, slightly concave medially, without spines at apex and on inner surface (as in Fig. 63); paramere (tegmen) trapezoid . . . . . .*Tergosciara* Rudzinski

16. Male terminalia with gonostylus with single long whiplash seta (*e.g.*, Figs 82, 86) or with several whiplash setae; anteroapical depressed area of fore tibia usually with curved margin (*e.g.*, Fig. 52) 17

– Male terminalia with gonostylus without long whiplash seta(e) (*e.g.*, Figs 81, 87–92); anteroapical depressed area of fore tibia without curved margin (*e.g.*, Figs 51, 57, 58) 18

17. Palpal segment 1 with deep sensory pit (Fig. 26); scutellum with 2 large marginal setae; tarsal claws toothless (as in Fig. 60); anteroapical depressed area of fore tibia denser setose, with strongly curved margin (Fig. 52); male terminalia with gonocoxites ventrally with basal lobe (Fig. 66) or basomedial group of setae on inner membrane (Fig. 73); gonostylus strongly tapered towards apex (Figs 73, 86), with sparse setae and tooth apically, 1 or more upcurved whiplash setae sub-basomedially (Fig. 86); inner surface of gonostylus with > 5 hyaline spines between tooth and whiplash seta(e) . . . . *Lycoriella* Frey *sensu stricto*

– Palpal segment 1 with unmodified sensory area (as in Fig. 25); scutellum with 4 or more large marginal setae; tarsal claws with fine teeth (as in Fig. 61); anteroapical depressed area of fore tibia with tendency to straight row of setae, with or without weakly curved margin (Fig. 53); male terminalia with gonocoxites ventrally without basal lobe or basomedial group of setae on inner membrane (Fig. 72), sometimes ventrobasally with dense setae on inner margin; gonostylus elongate-oval to kidney-shaped (Figs 72, 82), with fur-like, dense setae and without tooth apically, 1 or more downcurved whiplash setae sub-apicomedially; inner surface of gonostylus with 1–2 stronger spines subapically (Fig. 82) . . . .*Pseudolycoriella* Menzel & Mohrig

18. Thorax with katepisternum high, triangular, broadly rounded ventrally (*e.g.*, Fig. 11); anteroapical depressed area of fore tibia denser setose, with strong setae (similar to Figs 51, 52), but without curved margin; spurs strong, dagger-like (*e.g.*, Fig. 52), mid- and hind tibiae with 2 subequal spurs; large and robust species (male body length: 2.8–4.5 mm) 19

– Thorax with katepisternum attenuated, wedge-shaped, narrowly rounded ventrally (*e.g.*, Fig. 12) or small, short, triangular (*e.g.*, Fig. 13); anteroapical depressed area of fore tibia undifferentiated (*e.g.*, Fig. 58) or weakly differentiated (setae only slightly stronger and denser; *i.e.*, Fig. 57), spurs narrow, pen-like (Figs 57, 58); mid and/or hind tibiae with 1 long and 1 shorter spur; small, gracile species (male body length: 0.7–1.8 mm) 20

19. Wing vein R_{4+5} with macrotrichia only dorsally (as in Fig. 36); palpus long, 3-segmented (similar to Fig. 24); palpal segment 1 slender, segments 2–3 long; male terminalia with gonocoxites long, ventral emargination V-shaped (as in Fig. 69); gonostylus long, narrow, apex pointed and distinctly angled (Fig. 87), apex of gonostylus with group of spines and narrow, multi-pointed tooth (as in Fig. 88); paramere (tegmen) shorter than wide, without conspicuous modifications . . . . *Archicratyna* Mohrig

– Wing vein R_{4+5} with dorsal and ventral macrotrichia in distal ½ (as in Fig. 35); palpus shorter, 1–3-segmented (similar to Figs 27–29), if palpus 3-segmented, then segment 1 swollen and segments 2–3 distinctly shorter; male terminalia with gonocoxites short, ventral emargination semicircular (as in Fig. 76); gonostylus stout, apex not angled (short-oval, spherical or triangular); inner surface of gonostylus with group(s) of spines; apex of gonostylus toothless (similar to Fig. 81) (subgenus *Cratyna sensu stricto*), or with long, single pointed tooth (similar to Fig. 89) (subgenus *Peyerimhoffia* Kieffer); paramere (tegmen) *ca* as long as wide, bulging marginally (subgenus *Peyerimhoffia*), or with conspicuous modifications ventrally, such as central ridge, semicircular transverse carina or finger-like process (subgenus *Cratyna sensu stricto*) . . . . *Cratyna* Winnertz

20. Eye bridge vestigial (Fig. 6); antennal pedicel of male cylindrically prolonged; wing of male narrow, narrowly rounded in anterior ½ (Fig. 39), veins M_1 and M_2 forming V-shaped *M*-fork, radial sector (*Rs*) inclined to *r–m* crossvein and vein R_{4+5}, *m–cu* crossvein present, vein *M+CuA* absent, therefore veins M_4 and *CuA* merging in *m–cu* far apart (Fig. 39); thorax with postpronotum setose; gonostylus with tiny hook-like tooth subapically (Fig. 80); female apterous (Fig. 3), with flattened, elongate-oval head (Fig. 3). . . . . *Pnyxia* Johannsen

– Eye bridge complete, with or without ommatidia (as in Fig. 5); antennal pedicel of male spherical; wing of male not conspicuously narrow, widely rounded in anterior ½ (*e.g.*, Figs 38, 46), veins M_1 and M_2 curved basally and apically, *M*-fork rather bell-shaped, radial sector (*Rs*) perpendicular to *r–m* crossvein and vein R_{4+5}, *m–cu* crossvein absent, vein *M+CuA* present (*e.g.*, Fig. 38); thorax with postpronotum bare; male terminalia with gonostylus without apical tooth (*e.g.*, Figs 81, 92), or with distinct longer tooth (*e.g.*, Figs 88–91); female with well-developed or vestigial wing and halter (*e.g.*, Fig. 8), with roundish head (*e.g.*, Fig. 5) (only unknown female of *Epidapus gracilipes* Menzel, 2007 may be apterous) 21

21. Palpus 1-segmented, with sensory pit (Fig. 33); male terminalia with paramere (tegmen) longer than wide (Fig. 76); gonostylus elongate-oval, with apex broadly rounded, toothless, with groups of spines medially (Figs 76, 81); antennal pedicel of female cylindrically prolonged . . . . . . *Hyperlasion* Schmitz

– Palpus 1- or 2-segmented, with unmodified sensory area (*e.g.*, Figs 28–31); male terminalia with paramere (tegmen) shorter than wide (*e.g.*, Figs 77–79); gonostylus with apex pointed (*e.g.*, Figs 89–92) or narrowly rounded (*e.g.*, Fig. 88), with tooth (*e.g.*, Figs 88–91), if apical tooth absent, then with apical group of spines (*e.g.*, Fig. 92); antennal pedicel of female spherical 22

22. Male terminalia with gonostylus narrowly rounded apically, with straight, multi-pointed tooth subapically (Fig. 88); female usually with well-developed wing, rarely micropterous (polymorphic) . . . . *Cosmosciara* Frey

– Male terminalia with gonostylus pointed apically, with curved, single pointed tooth (Figs 89–91) or group of spines apically (Fig. 92); female at most with short, rudimentary wing and halter (Fig. 8) (only *Epidapus* (*Pseudoaptanogyna*) with known female in the Afrotropics, Fig. 4) . . . . . *Epidapus* Haliday 23

23. Male terminalia with apex of gonostylus toothless, but with group of spines (Fig. 92); anteroapical depressed area of fore tibia with slightly coarser and denser setae (as in Fig. 57); male thorax with katepisternum foreshortened, small (as in Fig. 13) (only female of *Epidapus* (*P.*) *pallidus* (Séguy, 1961) known in the Afrotropics, Fig. 4) . . . . *Epidapus* (*Pseudoaptanogyna* Vimmer)

– Male terminalia with apex of gonostylus toothed (*e.g.*, Figs 89–91); anteroapical depressed area of fore tibia sparse, light (without diagnostic differences in setae at apex of fore tibia) (similar to Fig. 58); male thorax with katepisternum attenuated, wedge-shaped (as in Fig. 12) 24

24. Palpal sensory area situated apically (Fig. 30); male terminalia with paramere (tegmen) rounded (Fig. 78); gonostylar apical tooth long, *ca* ½ as long as gonostylar body (Fig. 89) (female only known from Holarctic species, apterous) . . . . *Epidapus sensu stricto*

– Palpal sensory area situated dorsally (*e.g.*, Figs 28, 29); male terminalia with paramere (tegmen) trapezoid (*e.g.*, Fig. 79); gonostylar apical tooth short, at most ¼ as long as gonostylar body (*e.g.*, Figs 90, 91) 25

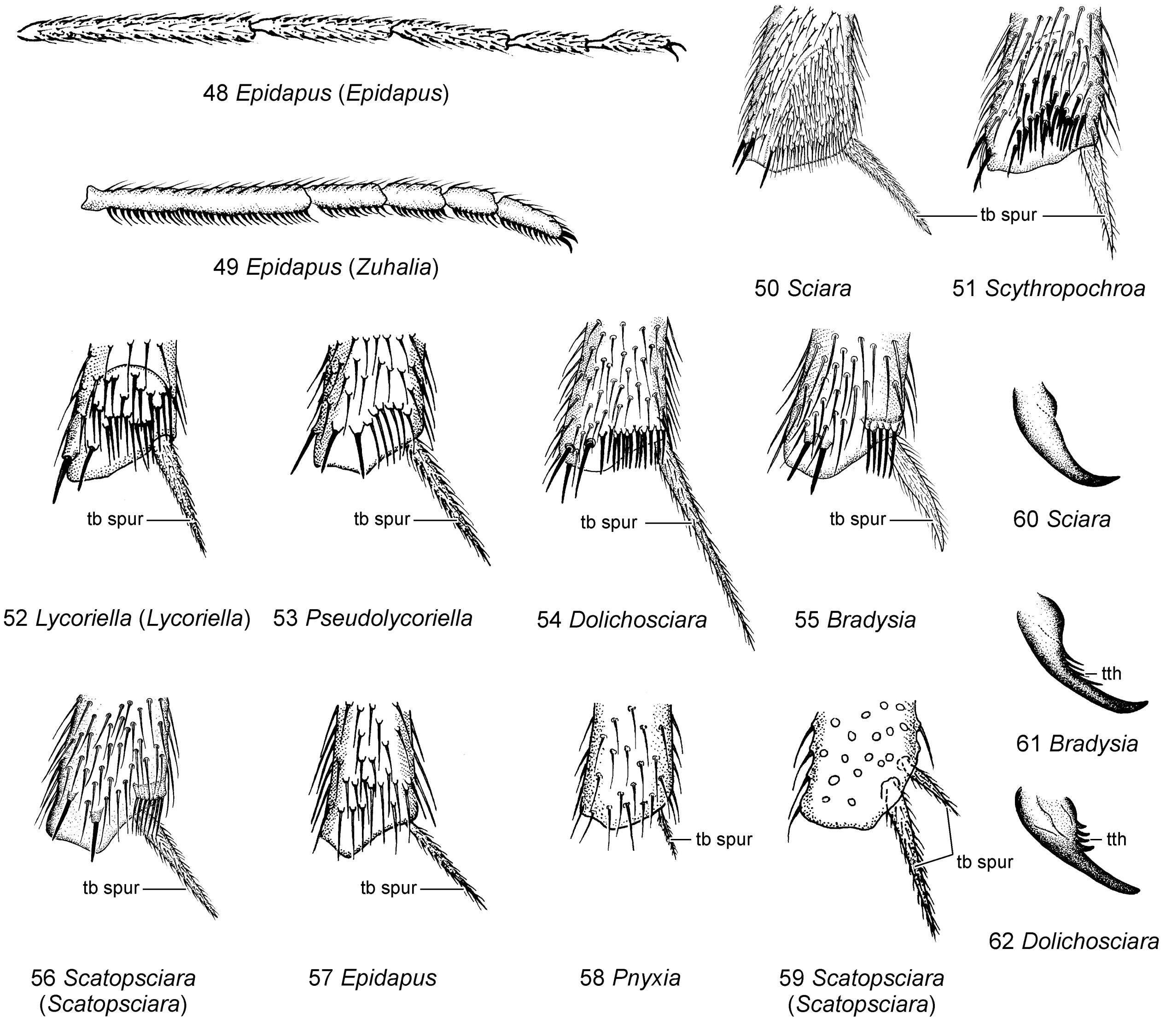
25. Male wing with distinctly reduced anal lobe, costal vein (*C*) very short, barely reaching beyond apex of vein R_{4+5}, c = ⅕ w (Fig. 46); legs short and strong; tarsi roundish, evenly setose, without dense, coarse row of setae (as in Fig. 48); halter with short stem (H–K index < 2.0) (as in Fig. 10); palpus 1-segmented; neck of male antennal flagellomere 4 short, *ca* as long as wide; male terminalia with gonostylus pointed, strongly curved and angled apically, slender, not swollen basally (Fig. 91); apex of gonostylus without hyaline spines (female unknown) . . . . *Epidapus* (*Afromoehnia* Rudzinski)

– Male wing with well-developed anal lobe; costal vein (*C*) long, extending beyond wing apex, c > ⅔ w (as in Fig. 38); legs long and slender; tarsi flattened and keel-shaped, with dense, coarse row of setae (as in Fig. 48); halter with long stem (H–K index > 2.0) (as in Fig. 9); palpus 2-segmented (Fig. 28), if both segments fused into one, then fusion marked by constriction (Fig. 29); neck of male antennal flagellomere 4 distinctly longer than wide (as in Fig. 17); male terminalia with gonostylus pointed, slightly curved, not angled apically, swollen basally (Fig. 90); apex of gonostylus with hyaline spines near tooth (female unknown) . . . . *Epidapus* (*Zuhalia* Koçak & Hüseyinoğlu)

Synopsis of the fauna

Steffan (1980) catalogued 18 genera and 58 species of Sciaridae as occurring in the Afrotropical Region. Two of these genera and species were subsequently determined not to belong to the Sciaridae (Chandler 2002; Hippa & Vilkamaa 2006*a*, *b*), but to the *Heterotricha*-group (see Chapter 23): *Heterotricha relicta* Edwards, 1925 (type species of the genus *Afrotricha* Chandler) and *Rhynchoheterotricha stuckenbergae* Freeman, 1960 (type species of the genus *Rhynchoheterotricha* Freeman). Furthermore, Menzel & Smith (2009: 19) transferred *Psectrosciara mahensis* Kieffer, 1912 to the Scatopsidae (see Chapter 26) and Menzel (2017) classified *Faratsiho microptera* Paulian, 1956 in the lower Diptera as *incerta sedis*. The genera *Trichosia* Winnertz and *Zygoneura* Meigen were previously reported from the Afrotropics, based on misidentified specimens, but actually do not (see below). Considering these taxonomic decisions and other results (published descriptions, synonymies and records) into account, there are currently 101 species of Sciaridae known to occur in the Afrotropics. Of these, 78 species in 23 genera remain to be properly classified and the remaining 23 species have not yet been studied and are therefore, regarded as Sciaridae *incertae sedis* for the time being. Kirk-Spriggs & Stuckenberg (2009: 186) estimated the Afrotropical fauna to contain 2,000 + species of Sciaridae.

Amesicrium **Enderlein.** An endemic monotypic genus, with the single species, *A. nanum* Enderlein, 1911, confined to Seychelles (Enderlein 1911, 1912). It was initially excluded from the family Sciaridae on the basis of the cecidomyiid-like


48 *Epidapus* (*Epidapus*)
49 *Epidapus* (*Zuhalia*)
50 *Sciara*
51 *Scythropochroa*
52 *Lycoriella* (*Lycoriella*)
53 *Pseudolycoriella*
54 *Dolichosciara*
55 *Bradysia*
60 *Sciara*
61 *Bradysia*
56 *Scatopsciara* (*Scatopsciara*)
57 *Epidapus*
58 *Pnyxia*
59 *Scatopsciara* (*Scatopsciara*)
62 *Dolichosciara*

Figs 21.48–62. Leg structures of Sciaridae (lateral views): (48) pretarsus and tarsal segments of *Epidapus* (*Epidapus*) *atomarius* (De Geer) ♂ (non-Afrotropical); (49) same, *Epidapus* (*Zuhalia*) *nanus* Menzel ♂; (50) anterior apex of fore tibia of *Sciara hemerobioides* (Scopoli) ♂; (51) same, *Scythropochroa latefurcata* Enderlein ♀; (52) same, *Lycoriella* (*Lycoriella*) *riparia* (Holmgren) ♂ (non-Afrotropical); (53) same, *Pseudolycoriella morenae* (Strobl) ♂ (non-Afrotropical); (54) same, *Dolichosciara flavipes* (Meigen) ♂ (non-Afrotropical); (55) same, *Bradysia bishopi* Steffan ♂; (56) same, *Scatopsciara* (*Scatopsciara*) *vitripennis* (Meigen) ♀; (57) same, *Epidapus* sp. ♂ (non-Afrotropical); (58) same, *Pnyxia scabiei* (Hopkins) ♂; (59) spurs on mid tibia of *Scatopsciara* (*Scatopsciara*) *vitripennis* (Meigen) ♂; (60) pretarsal claw of *Sciara* sp.; (61) same, *Bradysia* sp.; (62) same, *Dolichosciara* sp. Figs 49, 51, 55 (Menzel & Smith 2009, figs 35, 49, 6, respectively), Figs 50, 52–54, 57–62 (Menzel & Mohrig 2000, figs 485, 376, 438, 81, 261, 426, 449, 87a–c, respectively).

Abbreviations: tb spur – tibial spur; tth – tooth.

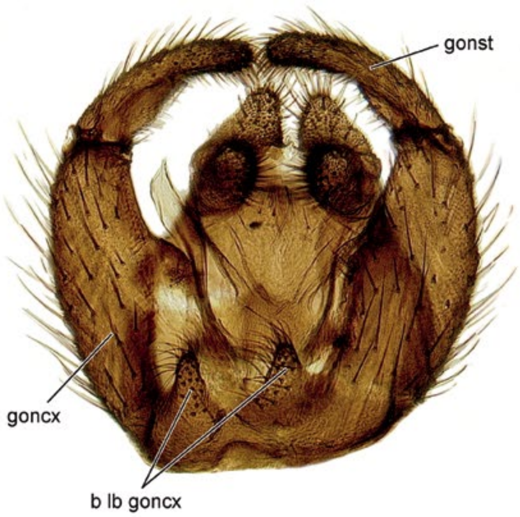
female characters described by Enderlein (Menzel & Smith 2009: 19), but was later re-instated in the Sciaridae by Menzel (2017). The type habitat was described as woodland of Capucin trees, *Northia seychellana* Hook.f. (Sapotaceae) at *ca* 609 m elevation. The male, immature stages and biology of the species remain unknown.

Angustosciara **Rudzinski.** An endemic monotypic genus, with the single species, *A. robusta* Rudzinski, 1997, described from grasslands of South Africa (Rudzinski 1997*c*). The biology and immature stages remain unknown.

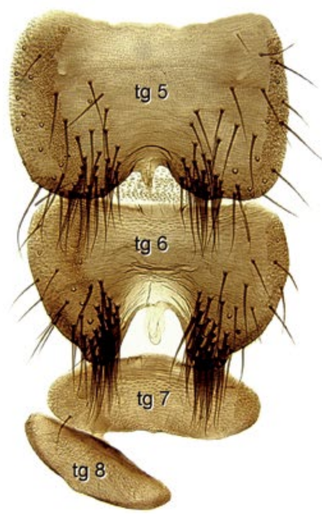
[***Apelmocreagris*** **Enderlein.** Synonymised with *Sciara* Meigen by Menzel (2017). See comments below under *Sciara*.]

Archicratyna **Mohrig.** A genus of four species, three of which were described from Dominican amber (Miocene) (Mohrig & Röschmann 2005). The extant type species, *A. zimbabweensis* Mohrig, 2005, was described from Matopus National Park, Zimbabwe. The biology and immature stages remain unknown.

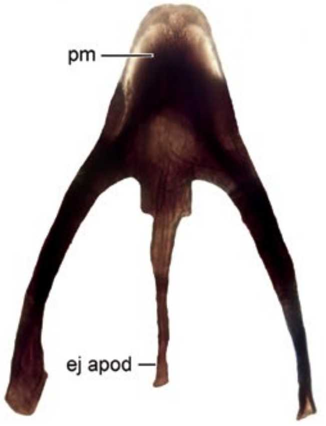
Bradysia **Winnertz *sensu lato*** (= *Neosciara* Pettey)**.** A polyphyletic genus of more than 450 described species, occurring in



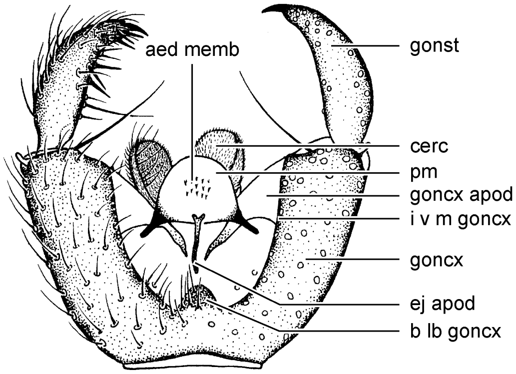
63 *Lobosciara* ♂



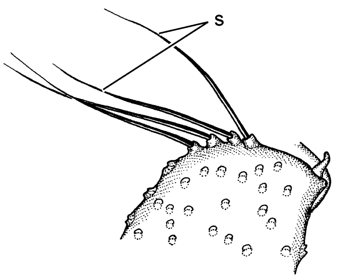
64 *Tergosciara* ♂



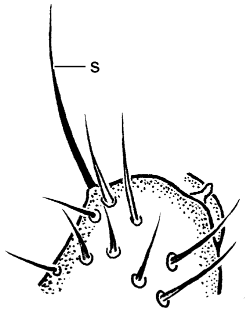
65 *Rhynchomegalosphys* ♂



66 *Lycoriella* (*Lycoriella*) ♂



67 *Dolichosciara* ♂



68 *Pseudolycoriella* ♂

Figs 21.63–68. Abdomen and male terminalia of Sciaridae (Figs 63–65 mounted in Canada balsam): (63) terminalia of *Lobosciara bilobata* Vilkamaa & Hippa, ventral view; (64) tergites 5–8 of *Tergosciara laciniata* Rudzinski, dorsal view; (65) aedeagal complex of *Rhynchomegalosphys aethiops* Lengersdorf (paramere (tegmen) and ejaculatory apodeme in ventral view); (66) terminalia of *Lycoriella* (*Lycoriella*) *ingenua* (Dufour), ventral view; (67) apex of right gonocoxite of *Dolichosciara flavipes* (Meigen), ventral view (non-Afrotropical); (68) same, *Pseudolycoriella setigera* (Hardy), ventral view. Fig. 63 (Menzel & Smith 2009, fig. 2), Figs 66, 67 (Menzel & Mohrig 2000, figs 89, 415).

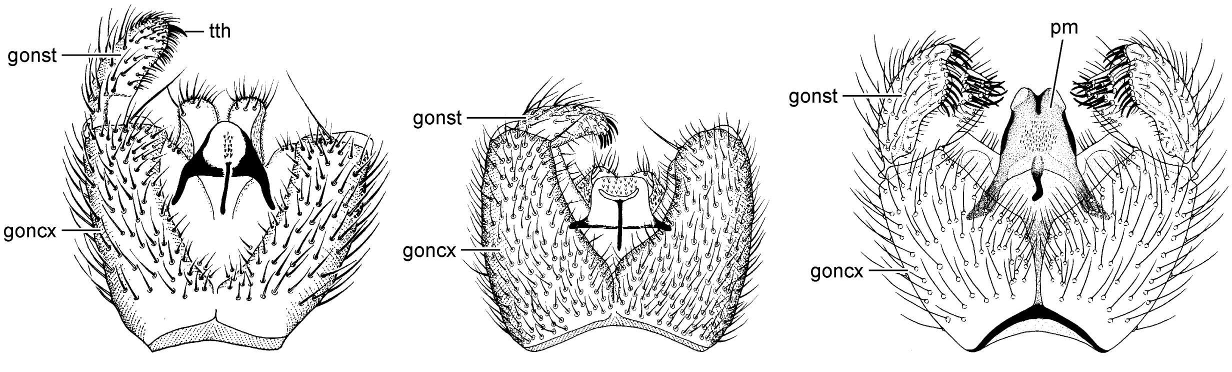
Abbreviations: aed memb – aedeagal membrane; b lb goncx – basal lobe of gonocoxite; cerc – cercus; ej apod – ejaculatory apodeme; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; i v m goncx – inner ventral margin of gonocoxite; pm – paramere (tegmen); s – seta; tg – tergite.

all zoogeographical regions (including Antarctica) and subdivided into 21 species-groups. Nineteen Afrotropical species belong here, representing six of these species-groups: the *B. fallaciosa*-group, *B. hilaris*-group, *B. pallipes*-group, *B. rufescens*-group, *B. spatitergum*-group and *B. tilicola*-group. *Bradysia novalobata*, described by Rudzinski (1997*a*, e), represents a different genus and was excluded as *incerta sedis* by Menzel (2017). Some virtually cosmopolitan *Bradysia* species (that also occur in the Afrotropics) are important pests in greenhouses and forestry nurseries (Hurley *et al*. 2007, 2010; Menzel *et al*. 2003, 2013): *B. impatiens* (Johannsen, 1912) (= *B. difformis* Frey, 1948), *B. ocellaris* (Comstock, 1882) (= *B. tritici* (Coquillett, 1895)) and *B. tilicola* (Loew, 1850) (= *B. amoena* (Winnertz, 1867)). Immature stages of these pest species are known from the Holarctic Realm, where larvae are phytophagous or phytosaprophagous.

***Ceratiosciara* Enderlein.** An endemic monotypic genus, with the single species, *C. corniculata* Enderlein, 1911, described from Mahé Is. in Seychelles and later recorded from Mahé Is., North Is. and Silhouette Is. (Menzel & Smith 2009: 29). The species is only known from females, which were collected in a habitat characterised by guava plants, lantana flowers and Coco-de-mer palms. The male, immature stages and details of the biology of the species remain unknown.

***Corynoptera* Winnertz *sensu lato*.** A polyphyletic genus, with more than 300 named species, occurring in all zoogeographical regions, except Antarctica. *Corynoptera* is subdivided into 18 species-groups, of which only the *C. parvula*-group occurs in the Afrotropics, represented by *C. minuta* (Hippa & Vilkamaa, 1994) from South Africa and *C. latistylata* (Hardy, 1956) from Seychelles and United Arab Emirates (Menzel & Heller 2007; Menzel & Smith 2009). The immature stages and biology of the two Afrotropical species remain unknown; larvae of Holarctic species of the *C. parvula*-group are known to be phytosaprophagous.

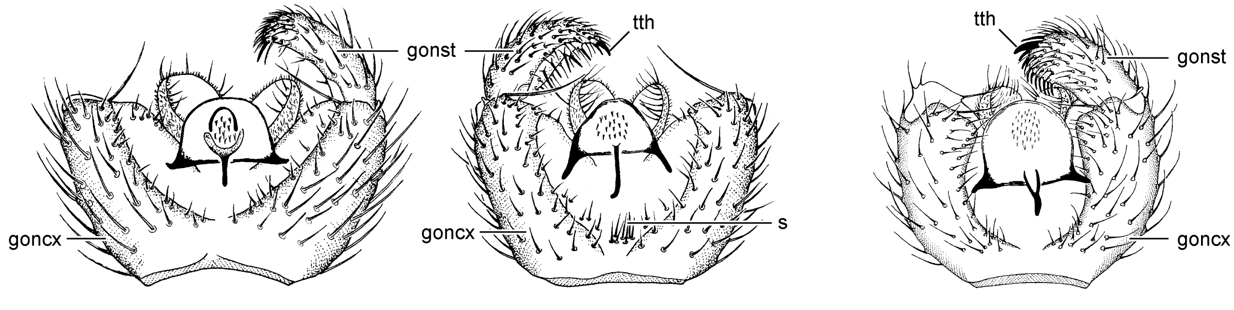
***Cosmosciara* Frey.** A widespread genus of five described species occurring in all zoogeographical regions, except Antarctica (Menzel & Heller 2007). Only the virtually cosmopolitan species *C. perniciosa* (Edwards, 1922) is known from the Afrotropical Region, collected from beaches on Tristan da Cunha Is. and Seychelles (Frey 1954; Menzel & Smith 2009: 32). Extralimital specimens of *C. perniciosa* were mostly recorded



69 *Bradysia* ♂

70 *Bradysia* ♂

71 *Angustosciara* ♂



72 *Pseudolycoriella* ♂

73 *Lycoriella* (*Lycoriella*) ♂

74 *Scatopsciara* (*Scatopsciara*) ♂

Figs 21.69–74. Male terminalia of Sciaridae (ventral views): (69) *Bradysia forficulata* (Bezzi); (70) *B. spatitergum* (Hardy); (71) *Angustosciara robusta* Rudzinski; (72) *Pseudolycoriella microcteniuni* (Yang & Zhang); (73) *Lycoriella* (*Lycoriella*) *sativae* (Johannsen); (74) *Scatopsciara* (*Scatopsciara*) *vitripennis* (Meigen). Figs 69, 73 (Menzel *et al*. 2013, figs 1, 20), Figs 70, 72 (Menzel & Smith 2009, figs 11, 42), Fig. 71 (Rudzinski 1997*c*, fig. 1f), Fig. 74 (Menzel & Mohrig 2000, fig. 446).

Abbreviations: goncx – gonocoxite; gonst – gonostylus; pm – paramere (tegmen); s – setae; tth – tooth.

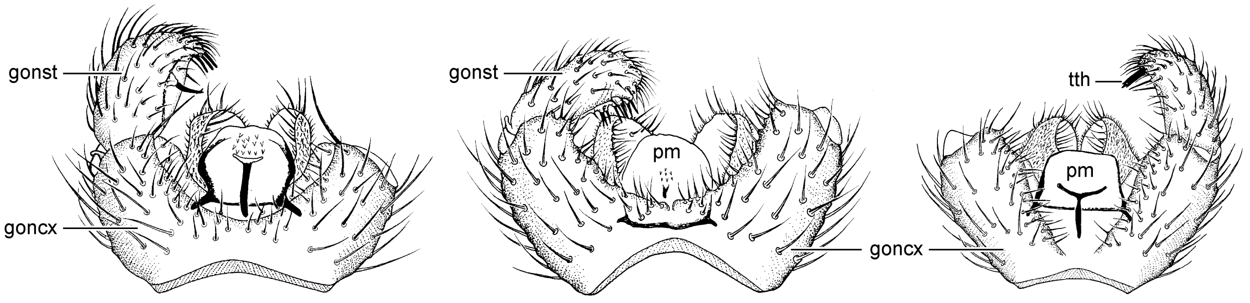
near human settlements, in gardens, farms, greenhouses and laboratories (Menzel *et al.* 2013). This phytophagous species is an important pest, especially of young plants, *e.g.*, cucumbers (Edwards 1922) and is easily spread with agricultural produce (Steffan 1973*a*). The polymorphism of adults, immature stages and biology of *C. perniciosa* were described from the Palaearctic Region and Hawaii (*e.g.*, Madwar 1937; Steffan 1973*b*).

Cratyna **Winnertz.** A large genus of 138 described species, occurring in all zoogeographical regions, except Antarctica, and classified in five subgenera (Menzel & Mohrig 2000; Mohrig & Menzel 2014). Ten species in two subgenera were described from the continental Afrotropics: nine species of *Cratyna* Winnertz *sensu stricto* (two species from Cameroon, one from Democratic Republic of Congo, three from Ghana, one from South Africa and two from Zimbabwe) and one species of the subgenus *C.* (*Peyerimhoffia* Kieffer) from South Africa (Hippa *et al.* 1998; Menzel 2017; Mohrig & Menzel 2014; Rudzinski & Baumjohann 2012).

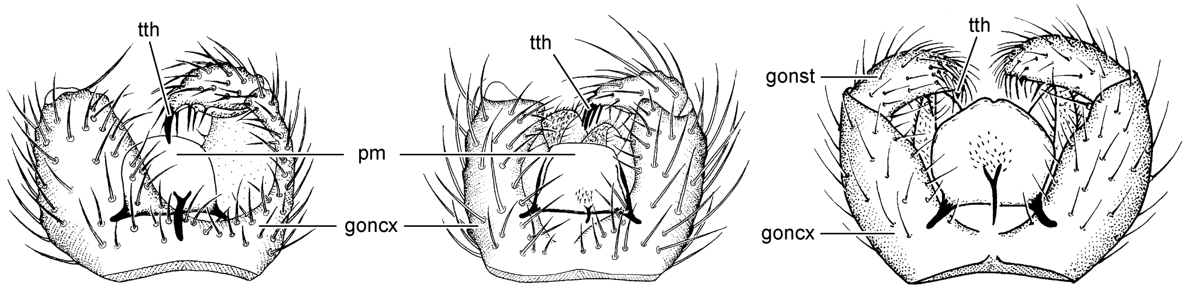
Dolichosciara **Tuomikoski.** A genus of 49 species globally, most of which occur in the Oriental and Palaearctic Regions (Menzel 2017). The single Afrotropical species, *D. fabulosa* Rudzinski, 2000, was described from Madagascar at an elevation of 2,060 m (Rudzinski 2000). The biology and immature stages of *D. fabulosa* remain unknown, but larvae of Palaearctic *Dolichosciara* species are phytophagous.

Epidapus **Haliday.** A widespread, virtually cosmopolitan genus of 78 described species, classified in six subgenera and six species-groups. Four Afrotropical species of *Epidapus* are known from Guinea, Seychelles and South Africa (Menzel 2017; Menzel & Heller 2007; Menzel & Smith 2007, 2009): *E. gracilipes* Menzel, 2007 (*Epidapus sensu stricto*; *E. atomarius*-group); *E. pallidus* (Séguy, 1961) (*Pseudoaptanogyna* Vimmer (= *Afrosciara* Séguy); *E. subcarpaticus*-group), *E. nanus* Menzel, 2007 (*Zuhalia* Koçak & Hüseyinoğlu (= *Macrotarsus* Mohrig, *preocc.*)) and *E. breviatus* (Rudzinski, 1999) (*Afromoehnia* Rudzinski). *Epidapus gracilipes* and *E. nanus* (both from Seychelles) were found on the invasive plant *Lantana camara* L. (Verbenaceae) (Menzel & Smith 2007) and *E. pallidus* (from Guinea and Seychelles) in soil on rotting plants (Séguy 1961). All known females of *Epidapus* are apterous or brachypterous. The immature stages and biology of Afrotropical *Epidapus* species remain unknown, but larvae of Holarctic species are phytosaprophagous.

Eugnoriste **Coquillett.** A genus of five named species occurring in the Afrotropical, Nearctic and Neotropical Regions. The single Afrotropical species, *E. capensis*, was described from



75 *Corynoptera* ♂ 76 *Hyperlasion* ♂ 77 *Cosmosciara* ♂



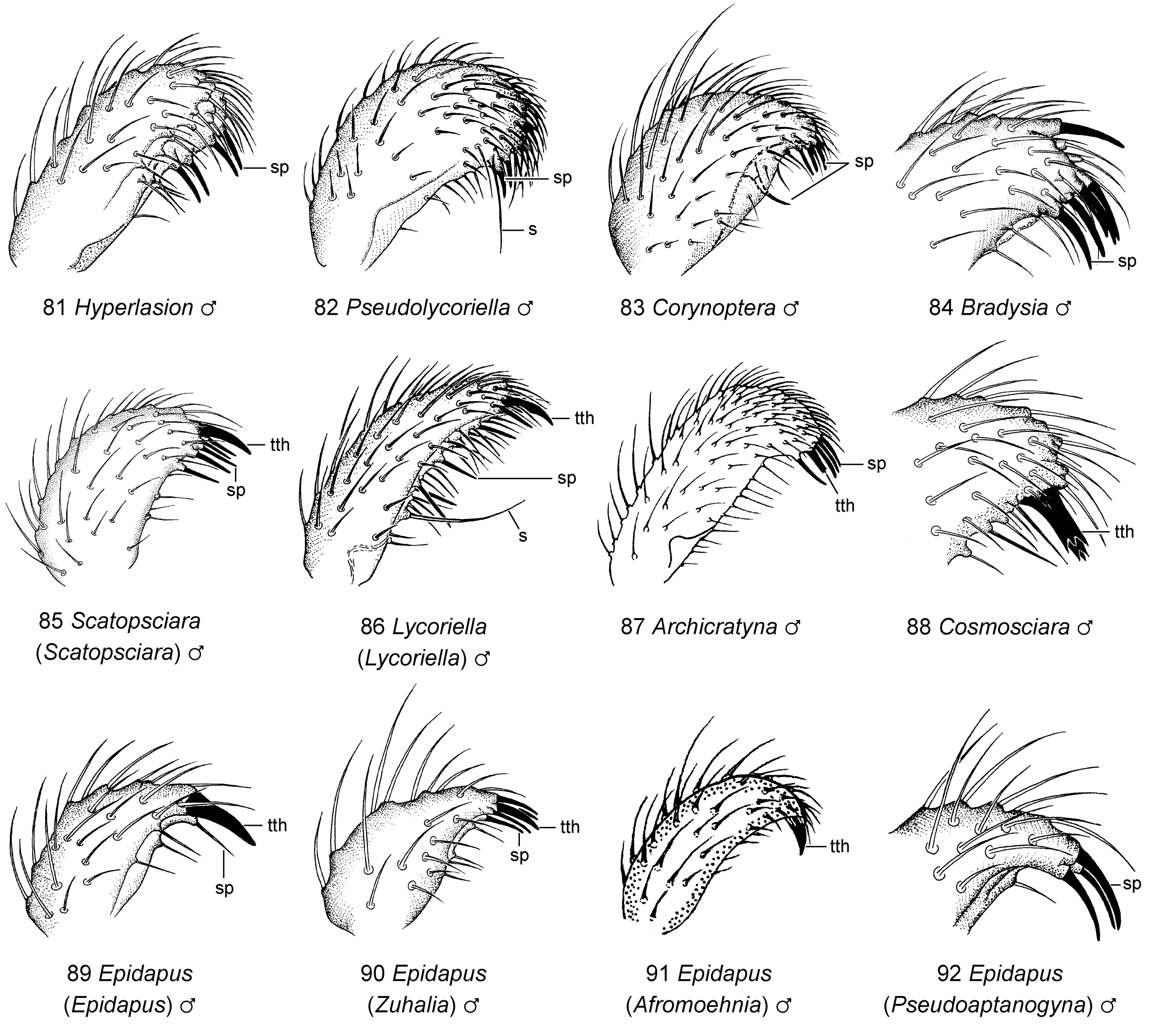
78 *Epidapus* (*Epidapus*) ♂ 79 *Epidapus* (*Zuhalia*) ♂ 80 *Pnyxia* ♂

Figs 21.75–80. Male terminalia of Sciaridae (ventral views): (75) *Corynoptera latistylata* (Hardy); (76) *Hyperlasion viridiventris* (Frey); (77) *Cosmosciara perniciosa* (Edwards); (78) *Epidapus* (*Epidapus*) *gracilipes* Menzel; (79) *E.* (*Zuhalia*) *nanus* Menzel; (80) *Pnyxia scabiei* (Hopkins). Figs 75, 77–79 (Menzel & Smith 2009, figs 18, 21, 26, 30), Fig. 76 (Menzel *et al.* 2013, fig. 8); Fig. 80 (Menzel & Mohrig 2000, fig. 427).

Abbreviations: goncx – gonocoxite; gonst – gonostylus; pm – paramere (tegmen); tth – tooth.

South Africa on the basis of two females (Steffan 1967). The male, immature stages and biology of the species remain unknown, but presence of a long proboscis suggests it may be a visitor in tubular flowers.

Euricrium **Enderlein** (= *Mapiria* Edwards, = *Muhabbetiola* Koçak, = *Zygomma* Enderlein, *preocc*.)**.** A genus of 20 described species occurring in the Afrotropical, Nearctic and Neotropical Regions. There are five species in the Afrotropics, described from Democratic Republic of Congo and Kenya, some of which were treated as *Bradysia* and *Zygoneura* (Steffan 1980: 232, 234). Menzel (2017) and Mohrig & Menzel (2014) recorded *E. afrum* Lengersdorf, 1939, *E. africanum* (Lengersdorf, 1938), *E. diabolicum* (Lengersdorf, 1938), *E. longitibiale* (Lengersdorf, 1939) and *E. pernitidum* (Edwards, 1914) from the Afrotropical Region. The biology and immature stages remain unknown.



81 *Hyperlasion* ♂
82 *Pseudolycoriella* ♂
83 *Corynoptera* ♂
84 *Bradysia* ♂
85 *Scatopsciara* (*Scatopsciara*) ♂
86 *Lycoriella* (*Lycoriella*) ♂
87 *Archicratyna* ♂
88 *Cosmosciara* ♂
89 *Epidapus* (*Epidapus*) ♂
90 *Epidapus* (*Zuhalia*) ♂
91 *Epidapus* (*Afromoehnia*) ♂
92 *Epidapus* (*Pseudoaptanogyna*) ♂

Figs 21.81–92. Details of male terminalia of Sciaridae (gonostylus, ventral views): (81) *Hyperlasion aliens* Mohrig; (82) *Pseudolycoriella setigera* (Hardy); (83) *Corynoptera latistylata* (Hardy); (84) *Bradysia bishopi* Steffan (apex); (85) *Scatopsciara* (*Scatopsciara*) *atomaria* (Zetterstedt); (86) *Lycoriella* (*Lycoriella*) *ingenua* (Dufour); (87) *Archicratyna zimbabweensis* Mohrig; (88) *Cosmosciara perniciosa* (Edwards) (apex); (89) *Epidapus* (*Epidapus*) *gracilipes* Menzel; (90) *E.* (*Zuhalia*) *nanus* Menzel; (91) *E.* (*Afromoehnia*) *breviatus* (Rudzinski); (92) *E.* (*Pseudoaptanogyna*) *pallidus* (Séguy) (apex). Figs 81–84, 88–90, 92 (Menzel & Smith 2009, figs 40, 46, 19, 5, 22, 27, 31, 37, respectively), Fig. 85 (Menzel & Mohrig 2000, fig. 459), Fig. 86 (Menzel *et al.* 2013, fig. 19), Fig. 87 (Mohrig & Röschmann 2005, fig. 6a).

Abbreviations: s – seta; sp – spine; tth – tooth.

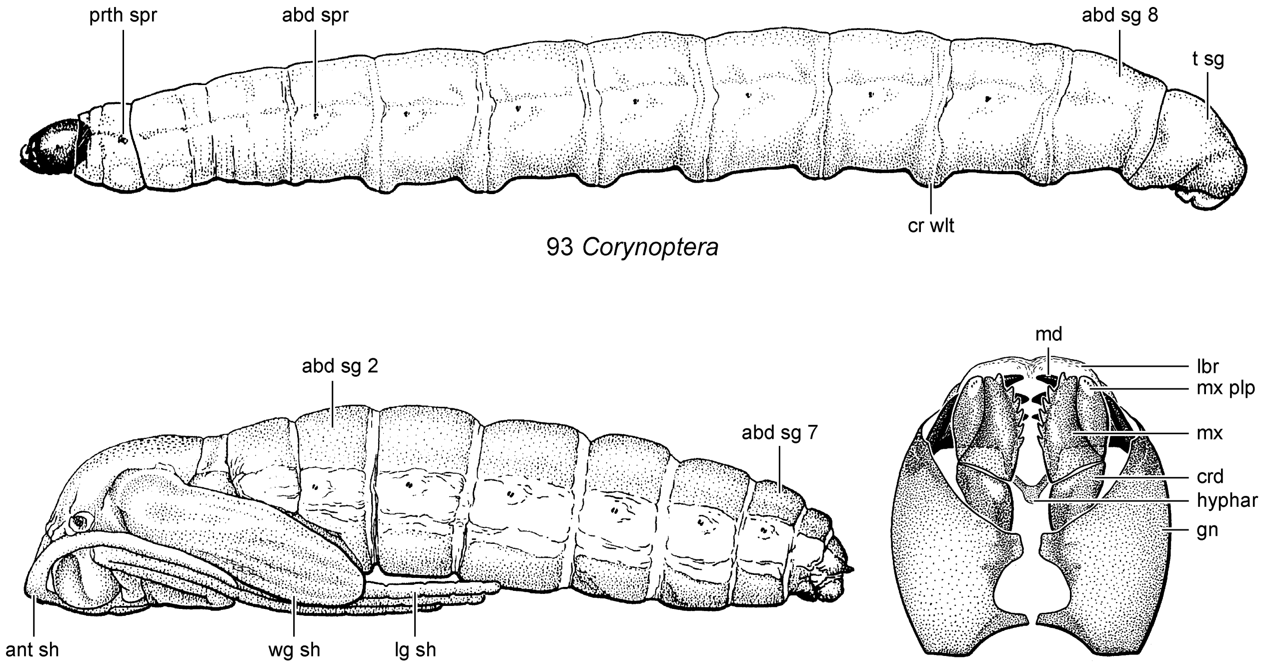
[***Faratsiho*** **Paulian.** An endemic monotypic genus from Madagascar, excluded from the Sciaridae and transferred to lower Diptera as *incerta sedis* by Menzel (2017). The micropterous female of the type species, *F. microptera* Paulian, 1956, were found in a wet sinkhole (Paulian 1956). The male, immature stages and biology remain unknown.]

[***Heterotricha*** **Loew.** A genus excluded from the Sciaridae by Chandler (2002), with the Afrotropical species *Heterotricha relicta* Edwards, 1925 (now in *Afrotricha* Chandler) treated in Chapter 23 (*Heterotricha*-group).]

Hyperlasion **Schmitz.** A genus of eight named species occurring in the Afrotropical, Australasian, Neotropical and Palaearctic Regions. Three species are present in the Afrotropics: *H. aliens* Mohrig, 2004, only known from Seychelles (Menzel & Smith 2009: 38), *H. wasmanni* Schmitz, 1918, only recorded from Zimbabwe (Mohrig 2004) and *H. viridiventris* (Frey, 1945) only known from the Tristan da Cunha Is. group (Menzel *et al.* 2013). These species occur in greenhouses and in nature (open woodlands, grasslands and wetlands). Immature stages and biology remain unknown; only the undescribed, phytophagous larva of *H. wasmanni* was reported from the Palaearctic Region (Menzel & Mohrig 2000: 346).

Lobosciara **Steffan.** A small genus of five species, occurring in the Afrotropical, Australasian and Oriental Regions, with most in the Oriental Region (Vilkamaa & Hippa 1994). The single Afrotropical species, *L. bilobata* Vilkamaa & Hippa, 1994, was collected in Seychelles in primary forest canopies on an unidentified fungus (Menzel & Smith 2009). Immature stages and biology of *Lobosciara* species remain unknown.

Lycoriella **Frey.** A virtually cosmopolitan genus of 85 named species, classified in three subgenera and four species-groups, with most of the species occurring in the Holarctic Realm. Two truly cosmopolitan species of *Lycoriella sensu stricto* are known from the Afrotropical Region: *L. ingenua* (Dufour, 1839) (= *L. mali* (Fitch, 1856)) and *L. sativae* (Johannsen, 1912) (= *L. castanescens* (Lengersdorf, 1940)). Both are important pests in greenhouses and mushroom farms, but were also found in a broad variety of natural habitats (including abandoned nests of wasps, birds and small mammals) (Chidziya *et al.* 2013; Menzel *et al.* 2006, 2013). As a rule, species of *Lycoriella sensu stricto* are associated with fungi, often in combination with plant litter (Menzel & Mohrig 2000: 380). Immature stages and biology of both mycophagous species were described from the Holarctic under different names, e.g. Binns (1979, 1981), Blaschke-Berthold (1988), Krivosheina *et al.* (1987), Madwar (1937), Martín-Cruiz *et al.* (2015), Santini & Lucchi (1994) and Symes (1921).



93 *Corynoptera*

94 *Corynoptera*

95 *Corynoptera*

Figs 21.93–95. Immature stages of Sciaridae: (93) larva of *Corynoptera* sp., lateral view (non-Afrotropical); (94) same, pupa, lateral view; (95) same, larval head capsule, ventral view. Figs 93, 94 (after Steffan 1981, figs 35, 34, respectively and Menzel & Mohrig 2000, figs 37, 38), Fig. 95 (Steffan 1981, fig. 33).

Abbreviations: abd sg – abdominal segment; abd spr – abdominal spiracle; ant sh – antenna sheath; cr wlt – creeping welt; crd – cardo; gn – gena; hyphar – hypopharynx; lbr – labrum; lg sh – leg sheath; md – mandible; mx – maxilla; mx plp – maxillary palpus; prth spr – prothoracic spiracle; t sg – terminal segment; wg sh – wing sheath.

Pnyxia **Johannsen.** A genus of four described species, occurring in all zoogeographical regions, except Antarctica. The apterous female of *Peyerimhoffia tanyae* was described from Madagascar by Paulian (1961) and is a synonym of the virtually cosmopolitan type species *P. scabiei* (Hopkins, 1895) (Menzel 2017). *Pnyxia scabiei* is a phytophagous species, frequently spread by humans in agricultural produce. It is certainly present in the continental Afrotropics and may have been introduced to Madagascar. Chiefly synanthropic, this species causes damage in greenhouses, especially in Europe and the United States. It has been reared from seedlings or tubers of potato, cucumber, tomato and narcissus bulbs; also occurring in pot plants, stable manure and mushroom beds and seldom observed in natural habitats, including caves (summarised by Menzel & Mohrig 2000: 25; Menzel *et al.* 2006; Mohrig *et al.* 2013). Details of the biology, life history and immature stages were provided by Gui (1933), Hopkins (1895), Madwar (1934) and Osmola (1970), to name a few.

[***Psectrosciara*** **Kieffer.** A genus excluded from the Sciaridae and transferred to the Scatopsidae (Menzel & Smith 2009: 19), with the type species *P. mahensis* Kieffer, 1912 from Seychelles, a junior synonym of *P. brunnescens* (Brunetti, 1911) (see Chapter 26)].

Pseudolycoriella **Menzel & Mohrig.** A large, virtually cosmopolitan genus of 120 described species, subdivided into eight species-groups, most of which occur in the Southern Hemisphere. In the Afrotropical Region ten species of the *P. bruckii*-group occur (Menzel & Smith 2009: 40; Rudzinski 1997*d*, 2003) that is identical with the *P. bruckii*-group of *Lycoriella* (*Hemineurina*) *sensu* Rudzinski (1997*d*). The biology and immature stages of Afrotropical species remain unknown. Larvae of Holarctic *Pseudolycoriella* are phytosaprophagous.

[***Rhynchoheterotricha*** **Freeman.** The genus *Rhynchoheterotricha* and type species *R. stuckenbergae* Freeman, 1960, were originally described in the family Sciaridae, but were later transferred to the *Heterotricha*-group (Chandler 2002) (see Chapter 23).]

Rhynchomegalosphys **Lengersdorf.** An endemic monotypic genus, with the single species, *R. aethiops* Lengersdorf, 1931, confined to Madagascar (Lengersdorf, 1931). The biology and immature stages of the species remain unknown.

Scatopsciara **Edwards.** A large, virtually cosmopolitan genus of 116 mostly Holarctic species, classified in two subgenera and five species-groups. Two widespread species of *Scatopsciara sensu stricto* occur in the Afrotropical Region (Kenya and United Arab Emirates): *S. atomaria* (Zetterstedt, 1851) and *S. vitripennis* (Meigen, 1818) (= *quinquelineata* (Macquart, 1834)) (Edwards 1914; Menzel 2017). Immature stages and biology of *Scatopsciara* species remain undescribed. The habitats of both phytosaprophagous species are only known from the Holarctic Realm (*e.g.*, Menzel *et al.* 2006; Mohrig *et al.* 2013).

Sciara **Meigen** (= *Lycoria* Meigen, = *Apelmocreagris* Enderlein)**.** A genus of 56 accepted species, occurring in all zoogeographical regions, except Antarctica. Eight Afrotropical species are recognised. One species, *S. thoracica* Macquart, 1838, described from Madagascar, is listed in Mohrig & Menzel (2014) with three synonyms under the generic name *Apelmocreagris* Enderlein, as *A. thoracica* (Macquart, 1838) (= *bibionea* (Speiser, 1909); = *bibionea* var. *miniaticeps* (Enderlein, 1911); = *ruficollis* (Walker, 1848)). The female syntypes (male unknown) of the type species of *Apelmocreagris*, namely *Lycoria bibionea* Speiser from Tanzania, are not yet located and revised, but a number of pinned females of this species in the collection of the Museum für Naturkunde, Berlin, clearly belong to the genus *Sciara* (Menzel 2017). *Sciara thoracica* is reported in the literature from Cameroon, Democratic Republic of Congo, Equatorial Guinea, Kenya, Madagascar, South Africa, Tanzania, Togo and Uganda (*e.g.*, Edwards 1914; Menzel 2017). The other accepted *Sciara* species in accordance with the characteristics of *Sciara* Meigen *sensu* Menzel & Mohrig (2000: 515) are: *S. aurosa* Rudzinski, 1997; *S. bullastylata* Rudzinski, 1997; *S. denticornis* (Lengersdorf, 1939); *S. differens* (Lengersdorf, 1938); *S. hemerobioides* (Scopoli, 1763); *S. maculithorax* (Lengersdorf, 1938); and *S. rimiscutellata* Enderlein, 1912. Twenty-one others, *e.g.* listed by Steffan (1980: 233), are only known from the original poor descriptions. These may represent synonyms or may be transferred, following revision of types in different genera. Immature stages and biology of Afrotropical species remain unknown, but the larvae of Palaearctic *Sciara* are phytophagous.

Sciarotricha **Hippa & Vilkamaa.** An endemic monotypic genus, with the single species, *S. biloba* Hippa & Vilkamaa, 2005, only known from a large series of both sexes from the Brandberg massif (Namibia's highest mountain). The describers regarded the adult morphology of *S. biloba* as so extraordinary they classified the species in a subfamily of its own (Sciarotrichinae). The type habitat was noted as bushy Karoo-Namib shrubland in a river valley. Immature stages and biology remain unknown.

Scythropochroa **Enderlein.** A genus of 24 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions; of these, 21 species are only known from the Southern Hemisphere. The single Afrotropical species, *S. latefurcata* Enderlein, 1911, is endemic to Seychelles (Mahé Is. and Saint Anne Is.). The male, immature stages and biology of the species remain unknown (Enderlein 1911; Menzel & Smith 2009: 43).

Tergosciara **Rudzinski.** An endemic monotypic genus, with the single species, *T. laciniata* Rudzinski, 1997, only known from the former Transvaal of South Africa (Rudzinski 1997*b*). Immature stages and biology of the species remain unknown.

[***Trichosia*** **Winnertz.** A mostly Holarctic genus; currently not known from the Afrotropical Region. Lengersdorf's (1938) generic classification of *Trichosia ghesquierei* Lengersdorf, 1938, is based upon a misidentification. This species represents a different genus and was excluded from the genus *Trichosia* (as *incerta sedis*) by Menzel (2017).]

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CECIDOMYIIDAE 22

(Gall Midges)

Netta Dorchin, Keith M. Harris and Mathias Jaschhof

Fig. 22.1. Undetermined species of Cecidomyiidae (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small midges (Figs 1–9), with wing length usually 1–5 mm, exceptionally up to 10 mm; body colouration of live (or recently killed) specimens usually light to dark brown, often conspicuously red, orange or yellow.

Head with eyes usually holoptic; ocelli absent (except in most Lestremiinae and Micromyinae); antennae usually long, usually with 10–14 bead-like flagellomeres, sometimes up to 20 or more, or reduced to fewer than 10; male and female flagellomeres each with thread-like circumfila, or other specialised sensoria and often with appreciable sexual dimorphism.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 581–599.

Thorax with wing venation generally reduced to three main veins, *R_1*, *R_{4+5}* and *M_4+CuA* (*M_4* sometimes lost) (except in Catotrichinae, Lestremiinae, most Micromyinae and some Porricondylinae, where vein *M_{1+2}* may also be present). Legs long, without tibial spurs; tarsomere 1 much shorter than tarsomere 2 (except in all Catotrichinae, Lestremiinae and Micromyinae, in which tarsomere 1 is longer than tarsomere 2); many Heteropezini (in Winnertziinae) with fewer than 5 tarsomeres.

Abdomen elongate-cylindrical or elongate-ovate, with distinct tergites and sternites on 7–8 segments; male terminalia diverse (Figs 24–27), usually less elaborate than in many other Sciaroidea, with gonocoxite and gonostylus invariably present, but aedeagus and parameres of many Porricondylinae and Cecidomyiinae form complex structures (parts of which may be difficult to homologise); Cecidomyiinae are peculiar in having the gonocoxites not fused ventrally; tergite 9 reduced to simple dorsal plate; sternite 9 greatly reduced and fused with gonocoxites; ejaculatory apodeme absent; tergite 10 absent, or indistinguishably fused with hypoproct; sternite 10 membranous, or fused with hypoproct; aedeagus relatively small, transparent, often rod-like and sometimes flanked by mediobasal lobes of gonocoxites (identification of species in many groups relies heavily on detailed structure of the male terminalia, which may be complicated by considerable variation of this basic pattern); female terminalia with ovipositor in Catotrichinae, most Lestremiinae and Micromyinae rather short, with 2-segmented cercus, that of many other Cecidomyiidae may be protrusible, sometimes very long, telescopic and tapered (Fig. 34), occasionally aciculate (Fig. 33), but generally not greatly extended, with specialised sensorial, or otherwise modified, 1-segmented cercus (Figs 35, 36), often fused into single lamella (Figs 28–32); 1 or 2 spermathecae present in many primitive species, but absent in Porricondylinae and Cecidomyiinae.

Third-instar larvae (Fig. 38) with head capsule greatly reduced; prothoracic segment with ventral, median, sclerotised spatula (Figs 38–42), a synapomorphy for the family that is secondarily lost in many species; body colour white, yellow, orange to bright red.

Pupae (Fig. 37) often with horn-like structures of various shapes at antennal bases and on face, often with dorsal rows of spinules across abdominal segments, which aid in breaking out of the gall or soil shortly before adult eclosion; cephalic setae minute to very long; prothoracic spiracle often elongate and tapering, pupal characters sometimes critical for species identification in groups where adult morphology is generally uniform.

Cecidomyiidae adults superficially resemble some other Sciaroidea, but differ from them, with the exception of Rangomaramidae (a small family endemic to New Zealand), by the absence of tibial spurs and the costal vein of the wing entirely surrounding wing margin, usually with slight break at the juncture with vein *R_{4+5}*. The combination of small size, fragility and reduced wing venation readily distinguishes most Cecidomyiidae from related sciaroids.

Biology and immature stages

As far as is known, larvae of Catotrichinae, Lestremiinae, Micromyinae, Porricondylinae and Winnertziinae all feed on fungal hyphae in decaying plant tissues in soil, leaf litter, dead wood and similar substrates, or within fungal sporophores. Larvae of some species of Cecidomyiinae are also essentially mycophagous, but most are phytophagous, feeding directly on living plants, and in many instances, inducing galls of diverse shapes and structures in leaves, stems, buds or flowers (*e.g.*, Figs 43–51). Most of these species are restricted to development on one, or a few, closely related host-plants. Larvae of other species are zoophagous, feeding as predators on insects and mites, and a few are specialised endoparasites in aphids and psyllids, or are inquilines in galls made by other cecidomyiids or other insects.

Larval digestion is extra-intestinal and the larva is the main and usually the only feeding stage. Larval development may be completed within a few days, but in many species is extended many months or even years by larval diapause within galls, or other affected plant parts, or in soil and other substrates.

Pupae generally develop rapidly, over a few days or weeks, and adult life is brief, often restricted to a single day at least in phytophagous species. Sex ratios tend to be strongly skewed in favour of females, and adult males tend to emerge before females and have a shorter life expectancy. Information on biological and ecological strategies and varied life history patterns has been summarised in Gagné (1989), Harris (1994) and Yukawa & Rohfritsch (2005).

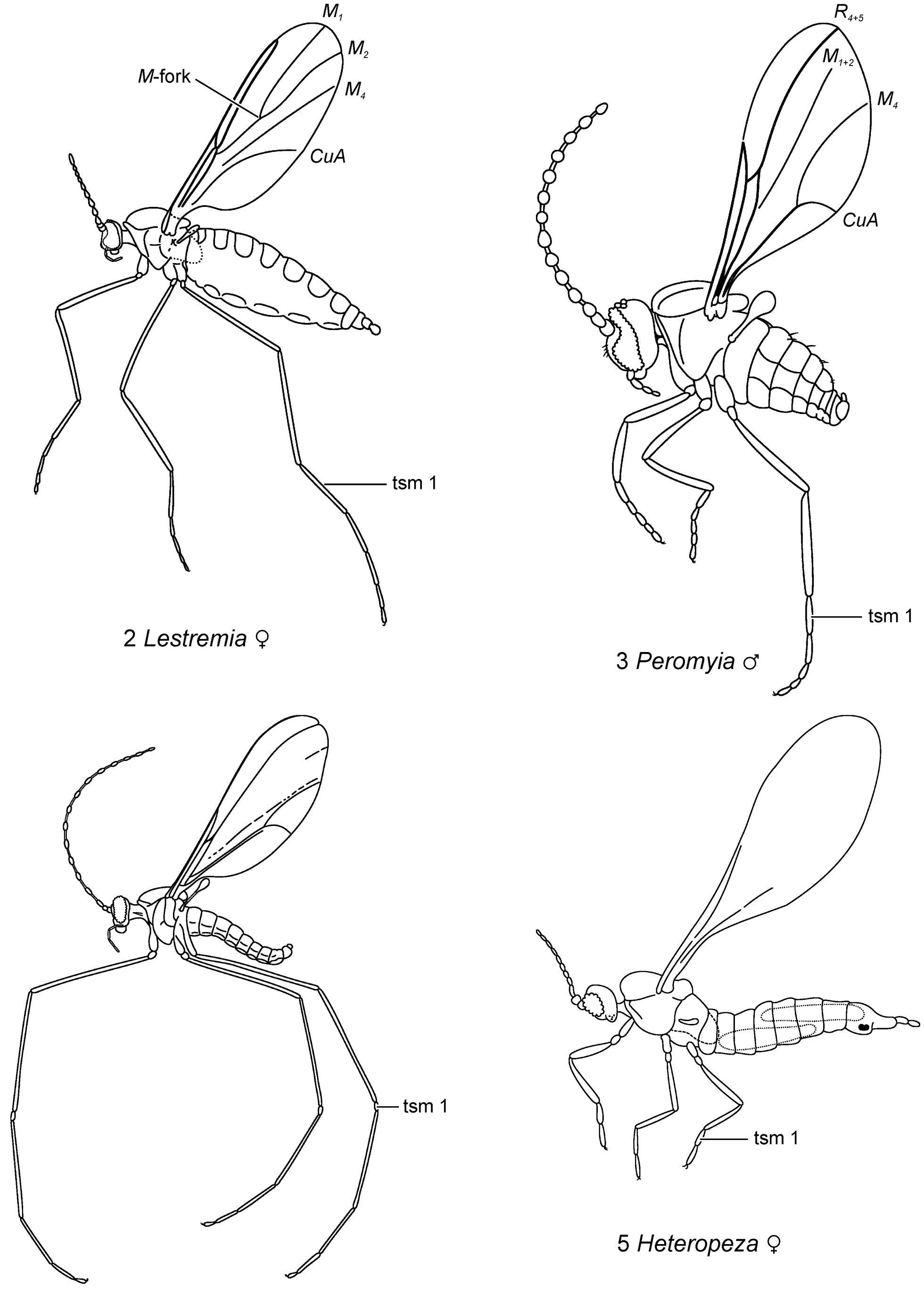
Economic significance

Two species, the African Rice gall midge, *Orseolia oryzivora* Harris & Gagné, 1982 and the Sorghum midge, *Stenodiplosis sorghicola* (Coquillett, 1889), reduce grain yields of rice and sorghum, respectively and are important pests of those crops in the Afrotropical Region. Other species that may be of local importance include the Millet grain midge, *Geromyia penniseti* (Felt, 1920), and the Sesame pod midge, *Asphondylia sesami* Felt, 1916. Some species are potentially beneficial as pollinators of cacao, as predators on coccoids (mealybugs and scale insects), mites and other pests, or as phytophagous biocontrol agents for use against weeds (see Chapter 5).

Classification

Several studies (Chandler 2010: 3; Matile 1997; Wood & Borkent 1989: 1351) placed the Cecidomyiidae in the superfamily Sciaroidea, and recent analyses of morphological and molecular characters agree with Matile (1990, 1997), who suggested a sister-group relationship between Cecidomyiidae and the remainder of Sciaroidea (*e.g.*, Bertone *et al*. 2008; Lambkin *et al*. 2013). However, Sciaroidea phylogeny is still in dispute (Amorim & Rindal 2007; Bertone *et al.* 2008), including the unresolved classification of the so-called unplaceable Sciaroidea to the family level (see Chapter 23).

The Cecidomyiidae are no doubt a monophyletic group (Jaschhof & Jaschhof 2009) and are divided into six subfamilies: Catotrichinae, Lestremiinae, Micromyinae, Winnertziinae, Porricondylinae and Cecidomyiinae (Gagné & Jaschhof 2014; Jaschhof & Jaschhof 2013). Within these major divisions, a number of supertribes and tribes have been recognised



2 *Lestremia* ♀

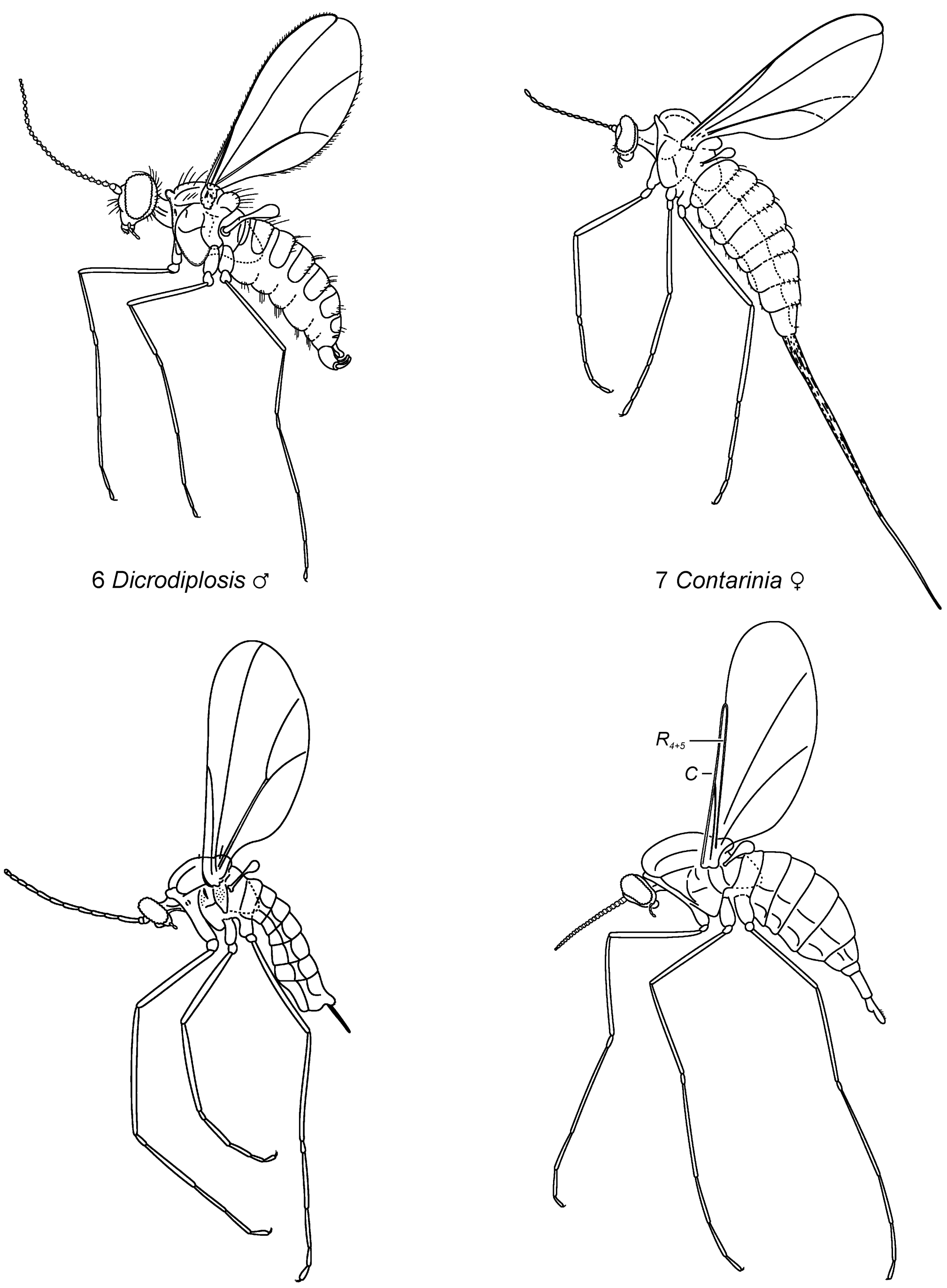
3 *Peromyia* ♂

5 *Heteropeza* ♀

4 *Porricondyla* ♂

Figs 22.2–5. Habitus of adult Cecidomyiidae (lateral views): (2) *Lestremia* sp. ♀; (3) *Peromyia* sp. ♂; (4) *Porricondyla* sp. ♂; (5) *Heteropeza* sp. ♀. Fig. 3 (after Jaschhof & Jaschhof 2009: 6), Fig. 4 (after Panelius 1965, fig. 2).

Abbreviations: *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_{1+2}– first and second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_{4+5} – third branch of radius; tsm – tarsomere.



6 *Dicrodiplosis* ♂

7 *Contarinia* ♀

8 *Asphondylia* ♀

9 *Lasioptera* ♀

Figs 22.6–9. Habitus of adult Cecidomyiidae (lateral views): (6) *Dicrodiplosis* sp. ♂; (7) *Contarinia* sp. ♀; (8) *Asphondylia* sp. ♀; (9) *Lasioptera* sp. ♀.

Abbreviations: *C* – costal vein; R_{4+5} – third branch of radius.

but, with many cecidomyiid species still unknown and undescribed, this classification will require substantial modification in future. In the world catalogue of Cecidomyiidae (Gagné & Jaschhof 2014), many genera remain unassigned to tribal or other suprageneric categories, especially in Cecidomyiinae, which is the largest and biologically most diverse subfamily. An overview of the latest Cecidomyiinae classification was provided by Gagné & Jaschhof (2014).

Identification

Identification of cecidomyiids is generally difficult, partly due to their small size and fragility, but chiefly due to the inadequacy of taxonomic studies, both in quality and quantity. This is especially the case in the Afrotropical Region where, apart from species that are of importance or of interest to agriculturalists and other applied biologists, little is known about cecidomyiids in the major ecosystems. Afrotropical species were catalogued by Harris (1980), but there have been few attempts to make extensive collections, and even when collections have been available, the biological data has been inadequate (especially for specimens caught in flight or collected using passive collection techniques without host records), and there have been insufficient taxonomic resources available to deal with them adequately.

Fewer than 200 Afrotropical species have been formally described and it has been estimated that there may be up to 10,000 undescribed species (Kirk-Spriggs & Stuckenberg 2009: 184). The following key to genera must, therefore, be used in this context. It includes some virtually cosmopolitan and well-defined genera, but a number of mostly monotypic genera erected by Kieffer are excluded and regarded as *nomina dubia* (Harris & Dorchin 2012). There have been no revisionary studies directed mainly at Afrotropical Cecidomyiidae, but Harris (1968) reviewed the known predators on Coccoidea in a worldwide context, and many publications by Gagné contain much relevant information, especially his contributions to the *Manual of Nearctic Diptera* (Gagné 1981), the *Manual of Central American Diptera* (Gagné & Jaschhof 2009), and his accounts of *The plant-feeding gall midges of North America* (Gagné 1989) and *The gall midges of the Neotropical Region* (Gagné 1994). A key to the Palaearctic genera of Cecidomyiidae was provided by Skuhravá (1997), to the Holarctic genera of Lestremiinae and Micromyinae by Jaschhof & Jaschhof (2009), and to the Holarctic genera of Winnertziinae and Porricondylinae by Jaschhof & Jaschhof (2013), but all these are likely to be of limited use in the Afrotropical Region. Larvae have been dealt with by Mamaev & Krivosheina (1965), but mostly for some European genera, so that is not a comprehensive treatment.

The named taxa of Afrotropical Lestremiinae (3 genera, 3 species), Micromyinae (3 genera, 3 species), Winnertziinae (1 genus, 1 species), and Porricondylinae (6 genera, 13 species), are not taken into account here and are not keyed below the level of subfamily, as they are only partly revised to modern standards (see "Synopsis of the fauna" below). Also, their number is considered to be negligible compared with the diversity of unknown genera and species that can realistically be expected to occur in the Afrotropics. Most genera of Cecidomyiinae that are based on specimens caught in flight, or are solely based on females or larvae, are inadequately characterised and are, therefore, also excluded from this key. In addition, it must be appreciated that there are probably thousands of undescribed species of Cecidomyiidae and possibly hundreds of unrecognised genera in the Afrotropics and that these unknowns cannot be covered by this key. All recorded genera are noted in the "Synopsis of the fauna" section (below), which contains additional information that may facilitate identification.

Identification of cecidomyiids is generally difficult, partly due to their small size and fragility, necessitating preservation of reared specimens in ethanol for later slide-mounting (see Chapter 2), but chiefly due to the inadequacy of taxonomic studies, both in quality and quantity.

Provisional key to genera of Afrotropical Cecidomyiidae

1. Ocelli usually present; first tarsomere clearly longer than second (*e.g.*, Figs 2, 3). 2

– Ocelli absent; first tarsomere much shorter than second (*e.g.*, Figs 4–9), except in Winnertziinae. 3

2. Wing vein M_{1+2} furcate, stem shorter than *M*-fork (*e.g.*, Fig. 2) (LESTREMIINAE) . . . (not keyed further)

– Wing vein M_{1+2} simple (*e.g.*, Fig. 3), or if furcate then stem longer than *M*-fork, or vein M_{1+2} absent (MICROMYINAE). . . . . (not keyed further)

3. Male terminalia with gonocoxites joined ventrally (e.g., Fig. 24); female terminalia with cercus usually 2-segmented; wing vein *Rs* if present as strong as other veins (e.g., Fig. 10) 4

– Male terminalia with gonocoxites not joined ventrally (*e.g.*, Figs 25–27); female terminalia with cercus 1-segmented; wing vein *Rs* absent or incomplete and weaker than other veins (*e.g.*, Figs 12–15), except in Stomatosematidi (*e.g.*, Fig. 11) (CECIDOMYIINAE) 5

4. Antennal flagellomeres without circumfila; thorax with both anepisternum and anepimeron usually bare; wing vein *CuA* absent (WINNERTZIINAE) . . . . (not keyed further)

– Antennal flagellomeres with circumfila; thorax with anepisternum often setulose, anepimeron virtually always setulose; wing vein *CuA* absent or present (PORRICONDYLINAE). . . . . (not keyed further)

5. Antenna almost invariably with 12 flagellomeres in both sexes; male flagellomeres cylindrical in Asphondyliini (*e.g.*, Fig. 18) and a few other species, but generally binodal, with narrow waist and/

or bare internode and distal neck; each node with thread-like circumfila (*e.g.*, Figs 19–21); sockets of basally recurved setae inconspicuous; post-vertical peak, bearing 2 large forwardly directed setae, often present in both sexes; male terminalia generally without mediobasal gonocoxite lobes ("parameres" of many publications) sheathing aedeagus (*e.g.*, Figs 25–27) (CECIDOMYIIDI) 14

– Antennae with more or fewer flagellomeres, often varying between sexes and with size of individuals; male flagellomeres similar to female's, generally evenly cylindrical, not binodal, and each with only a single set of interconnected circumfila (*e.g.*, Figs 22, 23); sockets of basally recurved setae usually bulbous and conspicuous; post-vertical peak absent; male terminalia generally with mediobasal gonocoxite lobes ("parameres") sheathing aedeagus 6

6. Antenna with 13 flagellomeres in male and female, the last with a narrow terminal elongation; male terminalia with gonocoxites splayed, free, mediobasal gonocoxite lobes not clasping aedeagus; wing vein *Rs* complete, as strong as vein R_1 (Fig. 11) (STOMATOSEMATIDI) . . . . *Stomatosema* Kieffer

– Antenna with different numbers of flagellomeres in male and female, usually more, or fewer than 13; male terminalia with gonocoxites not splayed (except in some *Lauthia* spp.), mediobasal gonocoxite lobes at least partially clasping aedeagus; wing vein *Rs* absent (LASIOPTERIDI). 7

7. Wing vein R_{4+5} running very close and virtually parallel to costal vein (*C*), joining it well before wing apex, usually before or at *ca* ½ length (*e.g.*, Fig. 9), often obscured by dense covering of scales; female ovipositor with various groups of modified setae, including group of lateral setae just beyond tergite 8 and with modified setae on cercal segment, often large and hooked, inserted on sclerotised plates just before apical lamella (*e.g.*, Fig. 28) (LASIOPTERINI) 8

– Wing vein R_{4+5} not running close to costal vein (*C*), usually joining it closer to wing apex (*e.g.*, Fig. 15); female ovipositor without groups of modified setae and lacking sclerotised plates on cercal segment 12

8. Female ovipositor with preapical sclerotised plates, bearing large hooked setae, as well as shorter, pointed setae (*e.g.*, Fig. 28) 9

– Female ovipositor with preapical sclerotised plates reduced, bearing some short setae, but no large hooked setae (Fig. 29) . . . . *Izeniola* Fedotova

9. Female ovipositor with aculeus (*e.g.*, Figs 30, 31) 10

– Female ovipositor without aculeus (*e.g.*, Fig. 28) 11

10. Aculeus of female ovipositor curved ventrally (convex) (Fig. 30) . . . . *Baldratia* Kieffer

– Aculeus of female ovipositor curved dorsally (concave) (Fig. 31). . . . . *Stefaniola* Kieffer

11. Female abdominal segment 8 inflated; preapical plate of cercus bare, except for long hook-like setae dorsally (Fig. 32) . . . . *Afrolasioptera* Dorchin

– Female abdominal segment 8 not inflated; preapical plate of cercus with short, pointed setae in addition to long hook-like setae dorsally (Fig. 28) . . . . *Lasioptera* Meigen

12. Larvae induce artichoke bud galls on *Ochna arborea* Burch.ex DC (Ochnaceae). . . . *Ochnephila* Kieffer

– Larvae develop on other host-plants. 13

13. Antennal scape elongate, *ca* 3 × as long as broad; hind femora enlarged, 3 × as long and 2 × as wide as mid femora . . . . *Trotteria* Kieffer

– Antennal scape not elongate, about as long as broad; hind femora not enlarged, about same size as mid femora. . . . . *Dasineura* Rondani

14. Male antennal flagellomeres cylindrical, each with single set of interconnected circumfila (*e.g.*, Fig. 18) 15

– Male antennal flagellomeres binodal, each with 2 or 3 separate sets of circumfila (*e.g.*, Figs 19–21) . . . 17

15. Female antennae with terminal flagellomeres progressively shorter distally, ending with small spherical, or subspherical, terminal flagellomere (ASPHONDYLIINI) 38

– Female antennae with distal flagellomeres not progressively shorter and not ending in small spherical, or subspherical, terminal flagellomere 16

16. Larvae induce spherical galls on leaves of *Combretum galpinii* Engl. & Diels (Combretacaeae) . . . . *Lopesiella* Tavares

– Larvae predaceous, feeding on mealybugs (*Pseudococcus* and *Pulvinaria* spp.) . . . .*Megommata* Barnes

17. Male antennal flagellomeres bifilar, with 1 set of looped circumfila on basal node and 1 set on distal node (*e.g.*, Fig. 21). 18

– Male antennal flagellomeres trifilar, with 1 set of looped circumfila on basal node and 2 sets on distal node (*e.g.*, Fig. 19), one of which may be reduced to simple girdling thread (*e.g.*, Fig. 20) 22

18. Female ovipositor telescopic, often long and finely tapering; retracting into abdomen; cerci reduced (*e.g.*, Fig. 34) 19

– Female ovipositor not retracting into abdomen; cerci not reduced; larvae induce leaf galls on *Mangifera indica* L. (Anacardiaceae) . . . . *Procontarinia* Keiffer & Cecconi

19. Larvae induce multilocular woody terminal and lateral bud galls on *Lannea fulva* (Engl.) Engl. (Anacardiaceae). . . . . *Stephodiplosis* Tavares

– Larvae develop on other plant genera, with or without gall induction. 20

20. Larval sternal spatula reduced to broad, quadrate, short shaft, with 1 or 2 narrow terminal teeth; larvae of known species induce galls on *Acacia* spp. (Fabaceae) . . . .*Acacidiplosis* Gagné

– Larval sternal spatula with long shaft and bilobed anterior blade, or sternal spatula absent 21

21. Larval sternal spatula absent in third-instar larva; adult abdominal tergites lacking lateral setae; larvae of known species feed on developing ovaries in seed heads of Poaceae (grasses and cereal crops) without gall induction. . . . . *Stenodiplosis* Reuter

– Larval sternal spatula present in third-instar larva, usually with long shaft and bilobed anterior blade (Fig. 39); adult abdominal tergites with lateral setae; larvae of most known species induce galls on various plant genera and are usually host-specific . . . . *Contarinia* Rondani

22. Male antennal flagellomeres each with appressed, girdling proximal circumfilum on distal node (*e.g.*, Fig. 20) 23

– Male antennal flagellomeres each with looped, proximal circumfilum on distal node (*e.g.*, Fig. 19). . . 24

23. Both sexes with unusually long necks and enlarged mouthparts (Fig. 16) . . . . *Farquharsonia* Collin

– Both sexes with short, normal sized, necks and mouthparts . . . . *Bremia* Rondani

24. Male antennal flagellomeres with some circumfilar loops much longer than others. . . . . *Farquharsonia* Collin

– Male antennal flagellomeres with circumfilar loops of approximately equal length (*e.g.*, Fig. 19). . . . 25

25. Larvae phytophagous, with or without gall induction 26

– Larvae either zoophagous, feeding on other insects and mites, or mycophagous, feeding on fungi . . . 33

26. Larvae feed on Poaceae (cereal crops and/or wild grasses) 27

– Larvae feed on other host-plants 28

27. Larvae feed on ovaries in seed heads without gall induction; third-instar larva lacks sternal spatula. . . . . *Geromyia* Coutin & Harris

– Larvae induce hollow, elongate terminal bud galls on developing shoots of cultivated and wild rice (*Oryza* spp.) and on various grasses*;* third-instar larva with sternal spatula (Fig. 41) . . . . *Orseolia* Kieffer & Massalongo

28. Larvae induce galls on stems, leaves or fruits, generally host-specific 29

– Larvae feed in flowers of *Protea repens* L. (Proteaceae) without gall induction . . . . . *Resseliella* Seitner

29. Larvae induce galls on *Acacia* spp. (Fabaceae) 30

– Larvae induce galls on other host-plants. 31

30. Wing with strong *Rs* vein arising from R_1 around mid-length; third-instar larvae with eight terminal papillae, with very short, corniform setae, each on short projection . . . . *Lopesia* Rübsaamen [in part]

– Wing with incomplete vein *Rs* situated before mid-length of vein R_1; third-instar larvae with four (possibly eight) terminal papillae reduced and indistinct . . . .*Athidiplosis* Gagné

31. Larvae induce leaf galls on *Parinari* spp. (Chrysobalanaceae) (*e.g.*, Fig. 50) . . . . *Calodiplosis* Tavares and *Lopesia* Rübsaamen [in part]

– Larvae induce bud or stem galls on other host-plants 32

32. Larvae induce stem galls on *Colophospermum mopane* (Benth.) Leonard (Fabacaeae) . . . . *Delodiplosis* Tavares

– Larvae induce terminal bud galls on *Tarchonanthus camphoratus* L. (Asteracaeae) . . . .*Afrodiplosis* Felt

33. Larvae zoophagous, feeding on mites and/or insects. 34

– Larvae mycophagous, feeding in exposed positions on mycelium and/or spores of pathogenic basidiomycete fungi (rusts or mildews), on leaves and other plant parts . . . . *Mycodiplosis* Rübsaamen

34. Cercus of female terminalia with ventral brush-like array of short, thin-walled, blunt-ended, modified sensory setae (*e.g.*, Fig. 36). 35

– Cercus of female terminalia with setula-like setae not grouped into ventral brush-like array 36

35. Tarsal claws with strong basal tooth on all legs; female antennal flagellomeres with short necks; larvae of known Afrotropical species specialised predators on mealybugs, especially *Planococcus, Phenacoccus*, *Pseudococcus* and *Nipaecoccus* spp. . . . . *Dicrodiplosis* Kieffer

– Tarsal claws without strong basal tooth; female antennal flagellomeres with long, narrow necks (Fig. 19); larvae of known species specialised or generalised predators on various groups of arthropods, including mites, mealybugs, scale insects, other cecidomyiid larvae, and lepidopterous caterpillars . . . .*Lestodiplosis* Kieffer

36. Holoptic compound eyes divided into 3 separate sections by scarcity, or complete absence of ommatidia laterally (*e.g.*, Fig. 17) 37

– Holoptic compound eyes not clearly divided into 3 separate sections; ommatidia contiguous . . . . *Silvestriola* Skuhravá

37. Tarsal claws with basal tooth at least on fore legs . . . .*Diadiplosis* Felt and *Triommata* Barnes

– Tarsal claws without basal tooth . . . . *Trisopsis* Kieffer

38. Female ovipositor in form of needle-like, sclerotised rod, without terminal cerci, retracting straight into abdomen (*e.g.*, Fig. 33); first tarsomere with ventroapical spur 39

– Female ovipositor long, fine and thread-like, retracting into partial coil within abdomen, with minute terminal cerci; first tarsomere without ventroapical spur. . . . .*Schizomyia* Kieffer

39. Palpus 3-segmented. . . . .*Asphondylia* Loew

– Palpus 4-segmented. 40

40. Male terminalia without mediobasal gonocoxite lobes . . . .*Aposchizomyia* Gagné

– Male terminalia with mediobasal gonocoxite lobes. . . . . *Tetrasphondylia* Kieffer

Synopsis of the fauna

About 200 valid species have been described from the Afrotropical Region and many additional unnamed species are known. The following synopsis lists all genera reported from the Afrotropical Region in published work, with some additional unpublished records in brackets. It also indicates some notable synonymies. Genera that were considered *nomina dubia* by Harris & Dorchin (2012) are also listed in brackets. No keys to Afrotropical species and no biological information are available for any of the following genera unless otherwise indicated.

***Acacidiplosis* Gagné** (Cecidomyiinae: Cecidomyiidi: Cecidomyiini)**.** An endemic Afrotropical genus. Larvae of the 13 named species induce bud galls on *Acacia* spp. (Fabaceae) in Kenya. An identification key was provided by Gagné & Marohasy (1993).

***Actilasioptera* Gagné** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** Occurring in the Australasian and Oriental Regions. Six species have been named and three unnamed species have been recorded from United Arab Emirates in the Arabian Peninsula (Harris & van Harten 2010: 599). All known species induce leaf galls on mangrove, *Avicennia* spp. (Acanthaceae), and undiscovered species may be present in suitable habitats along the coast of East Africa.

***Afrodiplosis* Felt** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single named species, *A. tarchonanthi* Felt, 1926, is known from the Western and Eastern Cape Provinces of South Africa and induces conspicuous bud galls on *Tarchonanthus camphoratus* L. (Asteraceae).

***Afrolasioptera* Dorchin** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** An endemic monotypic genus. Larvae of the single named species, *A. tumida* Dorchin, 2007, induce bud galls on *Elytropappus rhinocerotis* Less. (Asteraceae) in South Africa (Dorchin & Gullan 2007). A second, undescribed species is also known.

***Allarete* Pritchard** (Lestremiinae: Lestremiini)**.** Mainly occurring in the Holarctic Realm and Oriental Region. Twelve named species are known, with one species, *A. africana* (Enderlein, 1911), described from Tanzania and subsequently recorded from Ghana and Somalia.

***Anodontoceras* Yukawa** (Micromyinae: Micromyini)**.** Occurring in the Palaearctic, Oriental and Afrotropical Regions, represented by three named species, one of which, *A. harrisi* Jaschhof & Jaschhof, 2009, was described from South Africa.

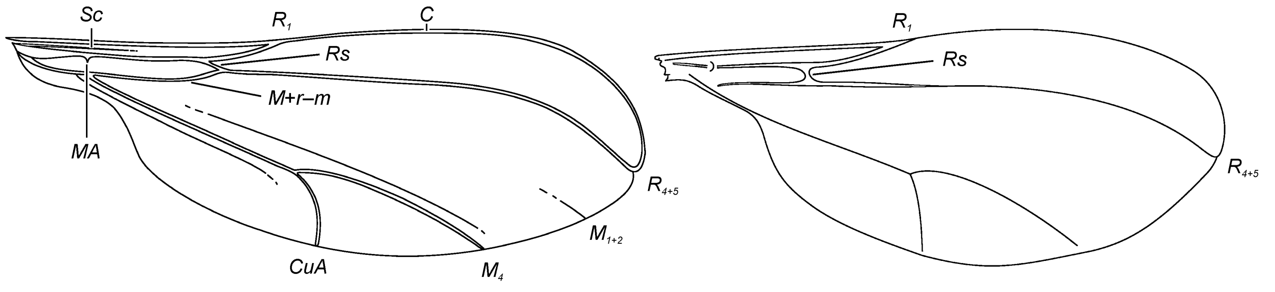
[***Aplecus* Kieffer.** *Nomen dubium*].

***Aposchizomyia* Gagné** (Cecidomyiinae: Cecidomyiidi: Asphondyliini)**.** An endemic Afrotropical genus, with six species described from Kenya that induce galls on *Acacia* spp. (Fabaceae) (Gagné & Marohasy 1993).

***Arthrocnodax* Rübsaamen** (Cecidomyiinae: Cecidomyiidi: Lestodiplosini)**.** A virtually cosmopolitan genus with 49 named species. The only recorded Afrotropical species, *A. moricola* Kieffer, 1910, described from South Africa, was transferred to the genus *Lestodiplosis* by Gagné (2004: 189). The monotypic *Microdiplosis* Tavares is probably a junior synonym of *Arthrocnodax* (see below). Larvae are mostly specialised predators on eriophyoid mites (Acari).

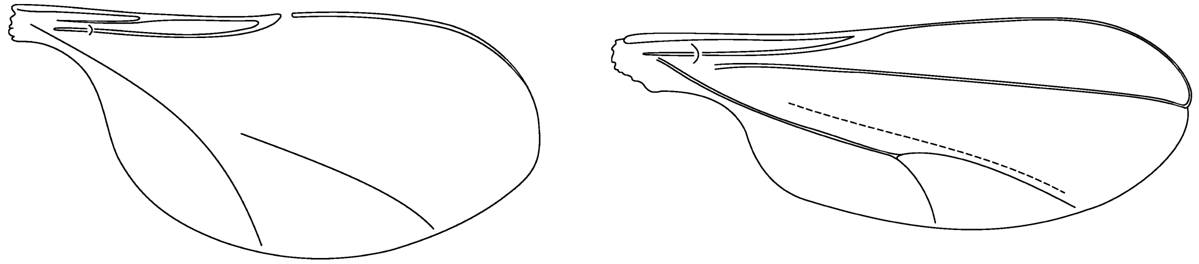
Asphondylia **Loew** (Cecidomyiinae: Cecidomyiidi: Asphondyliini)**.** A virtually cosmopolitan genus with 320 named species. Fifteen Afrotropical species have been named, but some of these are represented only by specimens caught in flight and are considered to be *nomina dubia*. Numerous species from Asteraceae await description and many additional species have been reared from Asteraceae and Aizoaceae in South Africa and Namibia (Dorchin, unpubl.). The genus probably numbers hundreds of undescribed species in southern Africa alone. Larvae are phytophagous, inducing galls on flowers, buds, stems or other aerial parts of plants. Most species are restricted to development on a few related host-plants, but some have wider host ranges. Galls are always accompanied by a symbiotic fungus.

Asynapta **Loew** (Porricondylinae: Asynaptini)**.** Mainly occurring in the Holarctic Realm and Oriental Region, with 44



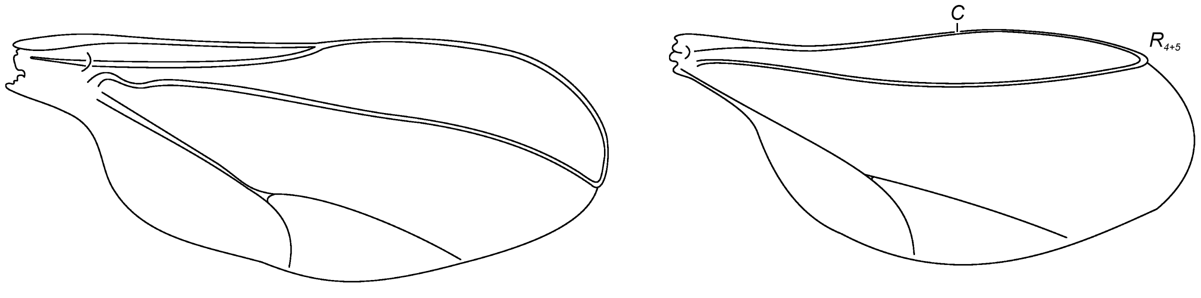
10 *Porricondyla*

11 *Stomatosema*



12 *Lasioptera*

13 *Asphondylia*



14 *Orseolia*

15 *Dasineura*

Figs 22.10–15. Wings of Cecidomyiidae (dorsal views): (10) *Porricondyla* sp.; (11) *Stomatosema* sp.; (12) *Lasioptera* sp.; (13) *Asphondylia* sp.; (14) *Orseolia* sp.; (15) *Dasineura* sp. Fig. 10 (after Gagné 1994, fig. 11).

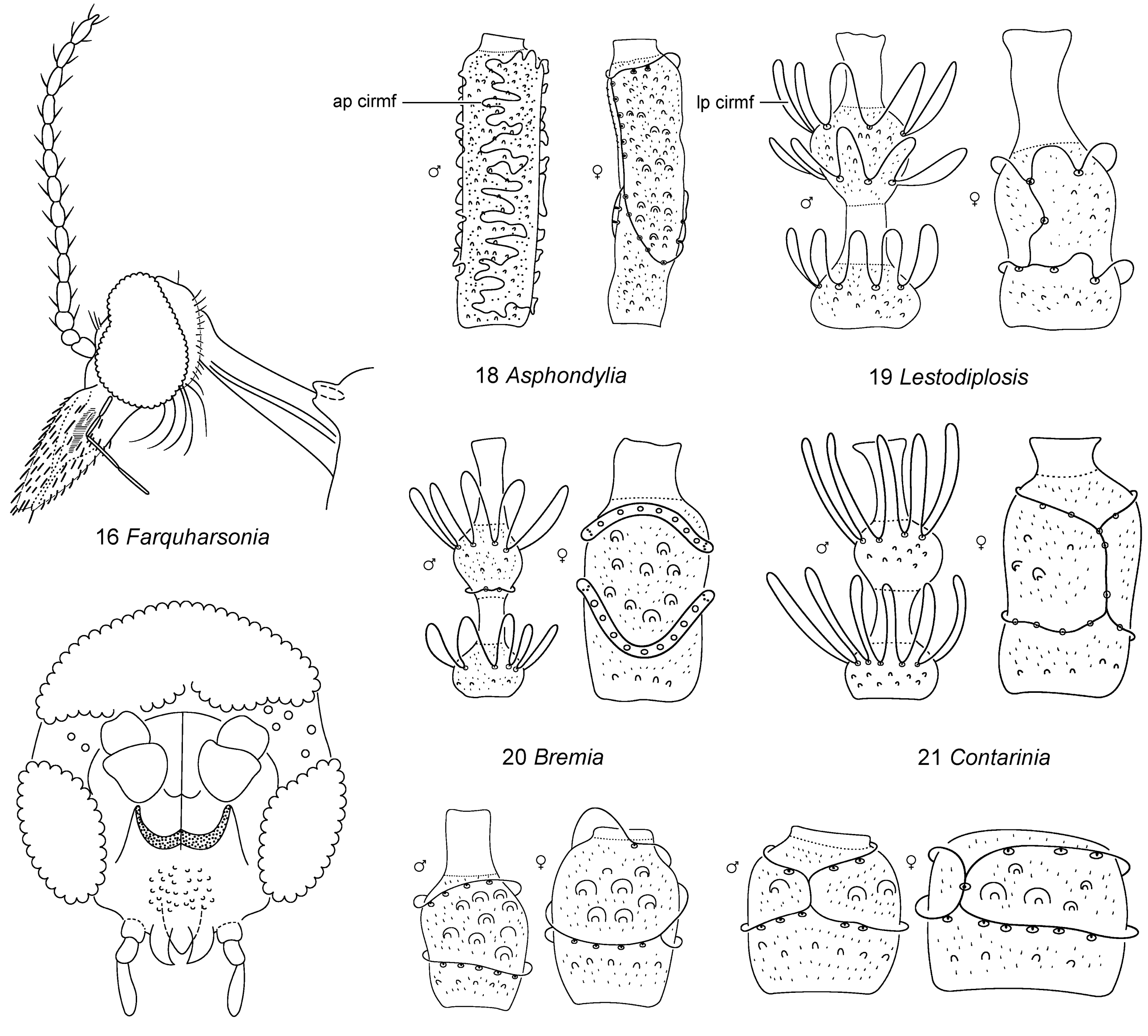
Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; *M+r–m* – media + radial-medial crossvein; M_{1+2} – first and second branch of media; M_4 – fourth branch of media; *MA* (arculus) – anterior branch of media; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *Rs* – radial sector; *Sc* – subcostal vein.

named species. Six species occur in the Afrotropics, five from Somalia and one from Seychelles.

Athidiplosis **Gagné** (Cecidomyiinae: Cecidomyiidi)**.** An endemic Afrotropical genus. Larvae of the two species, *A. bullata* Gagné, 1993 and *A. walteri* Gagné, 1993, known only from Kenya, induce stem galls in *Acacia* spp. (Fabaceae).

[***Baeodiplosis*** **Kieffer.** *Nomen dubium*].

Baldratia **Kieffer** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** Occurring in the Palaearctic (central Asia and the Mediterranean basin) and Afrotropical Regions, with 38 described and numerous undescribed species, all from Chenopodiaceae hosts. Larvae are gall inducers, mostly in stems and leaves, or occur in plant tissues without forming galls. Two named species have been recorded from the Afrotropics – the type species, *B. salicorniae* Kieffer, 1897 (later recorded by Houard (1922: 227) from Eritrea) and *B. orientalis* Möhn, 1969, from Arabia.



16 *Farquharsonia*

18 *Asphondylia*

19 *Lestodiplosis*

20 *Bremia*

21 *Contarinia*

17 *Diadiplosis*

22 *Dasineura*

23 *Lasioptera*

Figs 22.16–23. Heads and antennal flagellomeres of Cecidomyiidae: (16) head of *Farquharsonia* sp., lateral view; (17) same, *Diadiplosis* sp., frontal view; (18) antennal flagellomeres of *Asphondylia* sp., dorsal view (♂ left, ♀ right); (19) same, *Lestodiplosis* sp.; (20) same, *Bremia* sp.; (21) same, *Contarinia* sp.; (22) same, *Dasineura* sp.; (23) same, *Lasioptera* sp.

Abbreviations: ap cirmf – appressed circumfila; lp cirmf – looped circumfila.

Several undescribed species are known from Chenopodiaceae in South Africa and Namibia (Dorchin, unpubl.).

Bremia **Rondani** (Cecidomyiinae: Cecidomyiidi: Aphidoletini)**.** A virtually cosmopolitan genus with 19 named species. Two Afrotropical species have been described, *B. agilis* (Felt, 1920) and *B. legrandi* Harris, 1981. The biology is generally unknown, but larvae are probably predaceous, and *B. legrandi* was recorded as a predator on dragonfly (Odonata) eggs in Gabon (Harris 1981).

[***Cacoplecus*** **Kieffer.** *Nomen dubium*].

Calodiplosis **Tavares** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single named species, *C. parinarii* Tavares, 1908, described from Mozambique, induces leaf galls on *Parinari* spp. (Chrysobalanaceae). The illustrated original description indicates, however, that this species could be assigned to *Lopesia* Rübsaamen.

[***Chaetodiplosis*** **Kieffer.** *Nomen dubium*].

Chrysodiplosis **Kieffer** (Cecidomyiinae: Cecidomyiidi)**.** The genus, currently with two species, was based on the single known specimen of *C. pulchricornis* Kieffer, 1911, from Seychelles. This genus is probably a junior synonym of *Diadiplosis* Felt.

Clinodiplosis **Kieffer** (Cecidomyiinae: Cecidomyiidi: Clinodiplosini)**.** A virtually cosmopolitan genus with 104 named species. The single named Afrotropical species, *C. insularum* Kieffer, 1911, based on two specimens from Seychelles, is considered to be a *nomen dubium* (Harris & Dorchin 2012). Larvae are variously mycophagous, secondary invaders of damaged plant tissues, or primarily phytophagous, as inquilines in other cecidomyiid galls, or as gall inducers.

Clinophaena **Kieffer** (Porricondylinae: unplaced to tribe)**.** An endemic monotypic genus known only from Seychelles. The male holotype of *Holoneurus mahensis* Kieffer, 1911, the only species included in the genus, is available in the Natural History Museum, London and awaits restudy.

[***Coccodiplosis*** **de Meijere.** Synonymised with *Diadiplosis*].

Conarete **Pritchard** (Lestremiinae: Lestremiini)**.** Mainly occurring in the Holarctic Realm and Oriental Region, with 12 named species. *Conarete calcuttaensis* (Nayar, 1949), originally described from India, is recorded from South Africa and Togo.

[***Conodiplosis*** **Kieffer.** *Nomen dubium*].

Contarinia **Rondani** (Cecidomyiinae: Cecidomyiidi: Cecidomyiini)**.** A large virtually cosmopolitan genus with more than 300 named species. At least five Afrotropical species are known, including *C. citri* Barnes, 1944, which affects citrus flowers in Mauritius (Harris & Yukawa 1980) and *C. coffeae* Harris, 1970, which induces blisters on young *Coffea arabica* L. (Rubiaceae) berries growing at high elevations in Uganda (Harris 1970). Larvae are phytophagous, feeding on various aerial plant parts with, or without, gall induction. Some Afrotropical species that develop in seed heads of grasses and cereal crops (Poaceae), are included in *Stenodiplosis* by Gagné & Jaschhof (2014) (see below).

[***Ctenodiplosis*** **Kieffer.** *Nomen dubium*].

Dasineura **Rondani** (Cecidomyiinae: Lasiopteridi: Dasineurini)**.** A virtually cosmopolitan genus comprising about 470 named species. Only six Afrotropical species have been named, mostly from Ethiopia, but several undescribed species are known from various Asteraceae hosts (Dorchin, unpubl.). One species is known from *Coffea arabica* L. (Rubiaceae) in Democratic Republic of Congo and three species have been introduced into South Africa from Australia for the biological control of *Acacia* spp. (Fabaceae) and *Leptospermum laevigatum* (Gaertn.) F.Muell. (Myrtaceae) (Dorchin & Adair 2011; Kolesik *et al*. 2005). Larvae are phytophagous, living on various aerial parts of plants, with or without gall induction, and some are inquilines in galls induced by other organisms.

Delodiplosis **Tavares** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. Larvae of *D. copaibae* Tavares, 1908, induce stem galls on *Copaiba mopane* (J. Kirk ex Benth.) Kuntze (Fabaceae) in Mozambique.

Diadiplosis **Felt** (Cecidomyiinae: Cecidomyiidi)**.** A virtually cosmopolitan, mainly tropical genus of 30 named species. Afrotropical species reviewed by Harris (1968) were later revised and partly reassigned by Gagné (1994: 182). Larvae are specialised predators of whiteflies and coccoids (especially mealybugs). Eight Afrotropical species are known, all as predators on mealybugs (*Planococcus*, *Pseudococcus* spp., *etc*.).

Dicrodiplosis **Kieffer** (Cecidomyiinae: Cecidomyiidi)**.** A virtually cosmopolitan genus of 13 named species, the larvae of which are predators on coccoids (especially mealybugs). Four species have been recorded from the Afrotropics, one of which, *D. manihoti* Harris, 1981, is a widespread predator on mealybugs, including the Cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Pseudococcidae) (Harris 1981; Harris & van Harten 2006).

Endaphis **Kieffer** (Cecidomyiinae: Cecidomyiidi: Lestodiplosini)**.** Occurring in the Holarctic Realm and Oriental Region with eight named species. An unnamed species is known from Ghana. Larvae are internal parasitoids of aphids.

Eohormomyia **Felt** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single named species, *E. howardi* Felt, 1915, is known from Mozambique, based on a single female caught in flight.

[***Erosomyia*** **Felt.** Synonymised under *Procontarinia*].

Farquharsonia **Collins** (Cecidomyiinae: Cecidomyiidi)**.** An endemic Afrotropical genus, known from adults of two species, *F. manicata* (Edwards, 1929) and *F. rostrata* Collin, 1922, distinguished by exceptionally long necks. Adults of *F. rostrata* were observed hovering over ants and coccoids in West Africa.

Geromyia **Coutin & Harris** (Cecidomyiinae: Cecidomyiidi)**.** Three named species are known from Africa, India and Japan. One of these, the Millet grain midge, *G. penniseti*, is a pest of cultivated pearl millet, *Pennisetum glaucum* (L.) R.Br. (Poaceae) in Africa and India. Larvae feed on and destroy developing ovaries and reduce grain yields.

Haplusia **Karsch** (Winnertziinae: Diallactiini)**.** A virtually cosmopolitan genus with 19 named species, also known from Baltic amber. One Afrotropical species, *H. alexanderi* (Felt, 1921), is known from Cameroon. The genus as currently delimited is very likely not monophyletic and is in need of revision.

Heterobremia **Felt** (Cecidomyiinae: Cecidomyiidi: Aphidoletini)**.** An endemic monotypic genus, known from a single male of *H. furcata* Felt, collected from spiders' webs in a hollow tree near the Ulou River, Cameroon. In his original description, Felt (1920) noted that midges representing several different species were present in large numbers. He described a female from the same collection as *Homobremia agilis* (now included in *Bremia*), but suggested that it may be the opposite sex of *H. furcata*.

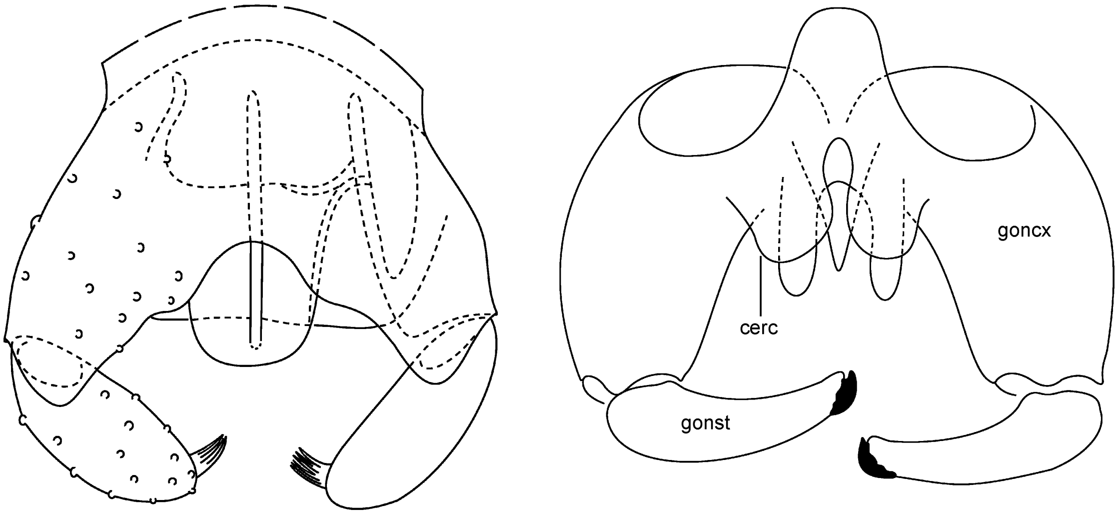
[***Holodiplosis*** **Kieffer.** *Nomen dubium*].

[***Izeniola*** **Fedotova** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** A Palaearctic genus of three species described from galls on Chenopodiaceae, one of which may occur in Eritrea (Dorchin 2001)].

[***Johnsonomyia*** **Felt.** Synonymised with *Haplusia*].

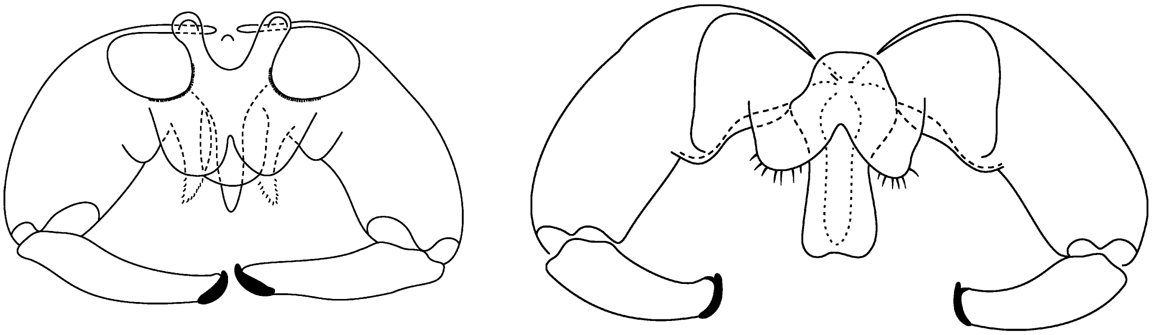
[***Kalodiplosis*** **Felt.** Synonymised with *Diadiplosis*].

Karshomyia **Felt** (Cecidomyiinae: Cecidomyiidi: Karshomyiini)**.** A virtually cosmopolitan genus of 49 named species. The only Afrotropical species, *K. atricauda* (Kieffer, 1913), was caught in Kenya and assigned to this genus by Harris (1980: 246). The biology of most species is unknown, but some have



24 *Leptosyna* ♂

25 *Contarinia* ♂



26 *Dicrodiplosis* ♂

27 *Orseolia* ♂

Figs 22.24–27. Male terminalia of Cecidomyiidae: (24) *Leptosyna* sp., ventral view; (25) *Contarinia* sp., dorsal view; (26) same, *Dicrodiplosis* sp.; (27) same, *Orseolia* sp.

Abbreviations: cerc – cercus; goncx – gonocoxite; gonst – gonostylus.

been reared from fungi and others are associated with decaying plant material.

***Kimadiplosis* Gagné** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single described species, *K. diversa* Gagné, 1993, is only known from its larva and was described from leaf-roll galls on *Acacia tortilis* Hayne (Fabaceae) in Kenya (Gagné & Marohasy 1993).

[***Lasiodiplosis* Kieffer.** *Nomen dubium*].

***Lasioptera* Meigen** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** A virtually cosmopolitan genus of 130 named species. Six species have been described from various parts of the Afrotropics. Larvae are phytophagous and most species induce galls, especially in plant stems. Others occur as inquilines in vacated galls and at least one species is a facultative predator.

***Lauthia* Kieffer** (Cecidomyiinae: Lasiopteridi: Ledomyiini)**.** A virtually cosmopolitan genus of 28 named species. Three species described from Seychelles are considered to be *nomina dubia* (Harris & Dorchin 2012).

***Ledomyia* Kieffer** (Cecidomyiinae: Lasiopteridi: Ledomyiini)**.** A virtually cosmopolitan genus of 25 named species mostly reared from freshly-cut logs. Not recorded from continental Africa, but three of four species described from Seychelles by Kieffer are considered to be *nomina dubia* (Harris & Dorchin 2012).

[***Lepidobremia* Kieffer.** *Nomen dubium*].

[***Lepidodiplosis* Kieffer.** *Nomen dubium*].

***Lestodiplosis* Kieffer** (Cecidomyiinae: Cecidomyiidi: Lestodiplosini)**.** A virtually cosmopolitan genus of 181 named species. Seven species have been recorded from the Afrotropics, including a species from Madagascan copal, but most are considered *nomina dubia*. Larvae are specialised or generalist predators on other invertebrates, including other cecidomyiids, mites, lepidopterous caterpillars and even, in one case, on a millipede. The biology of only two of the Afrotropical species is known.

***Lestremia* Macquart** (Lestremiinae: Lestremiini)**.** A virtually cosmopolitan genus of 18 named species. Only one Afrotropical species is known, *L. ugandae* Barnes, 1936, from Uganda.

***Lopesia* Rübsaamen** (Cecidomyiinae: Cecidomyiidi: Lopesiini)**.** A mainly Neotropical genus of 23 named species, three of which occur in the Afrotropical Region. *Lopesia parinarii* Tavares, 1908, is known from Mozambique, where it induces leaf galls on *Parinari capensis* Harv. (as *P. mobola*) (Chrysobalanaceae); *L. armata* Gagné, 1993 and *L. niloticae* Gagné, 1993, induce leaf-roll galls on *Acacia* spp. (Fabaceae) in Kenya.

***Lopesiella* Tavares** (Cecidomyiinae: Cecidomyiidi: Lopesiini)**.** An endemic monotypic genus. The single named species, *L. combreti* Tavares, was described from Mozambique, where it induced globular galls on leaves of *Combretum galpinii* Engl. & Diels (Combretaceae). In his original description, Tavares (1908) described and illustrated the galls, both sexes and the pupae, and rediscovery should, therefore, be relatively easy.

***Megommata* Barnes** (Cecidomyiinae: Cecidomyiidi)**.** An Afrotropical and Oriental genus known from six named species. Larvae of species for which the biology is known are specialised predators on coccoids, especially *Pulvinaria* spp. The three named Afrotropical species were reviewed by Harris (1968).

***Microdiplosis* Tavares** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single described species, *M. zambezensis* Tavares, 1908, was described from Mozambique, living as a commensal in galls induced on *Royena* sp. (Ebenaceae) by an unidentified eriophyoid mite. The original description and the accompanying illustrations indicate that this genus is probably a junior synonym of *Arthrocnodax* Rübsaamen, larvae of which are well known as specialised predators on eriophyoid mites in plant galls in the Holarctic Realm.

***Micromya* Rondani** (Micromyinae: Micromyini)**.** A mostly Holarctic and Oriental genus of 11 named species. An unnamed species of this genus is known to occur in South Africa (Harris 1980: 239).

***Microplecus* Kieffer** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single named species, *M. brevipalpis* Kieffer, 1913, was described from Tanzania, based on one male caught in flight; its biology remains unknown.

***Mitodiplosis* Kieffer** (Cecidomyiinae: Cecidomyiidi)**.** An endemic monotypic genus. The single described species, *M. graminis* Kieffer, 1914, known from South Africa, was taken from the grass *Ehrharta villosa* Schult.f. (Poacaeae); its biology is otherwise unknown.

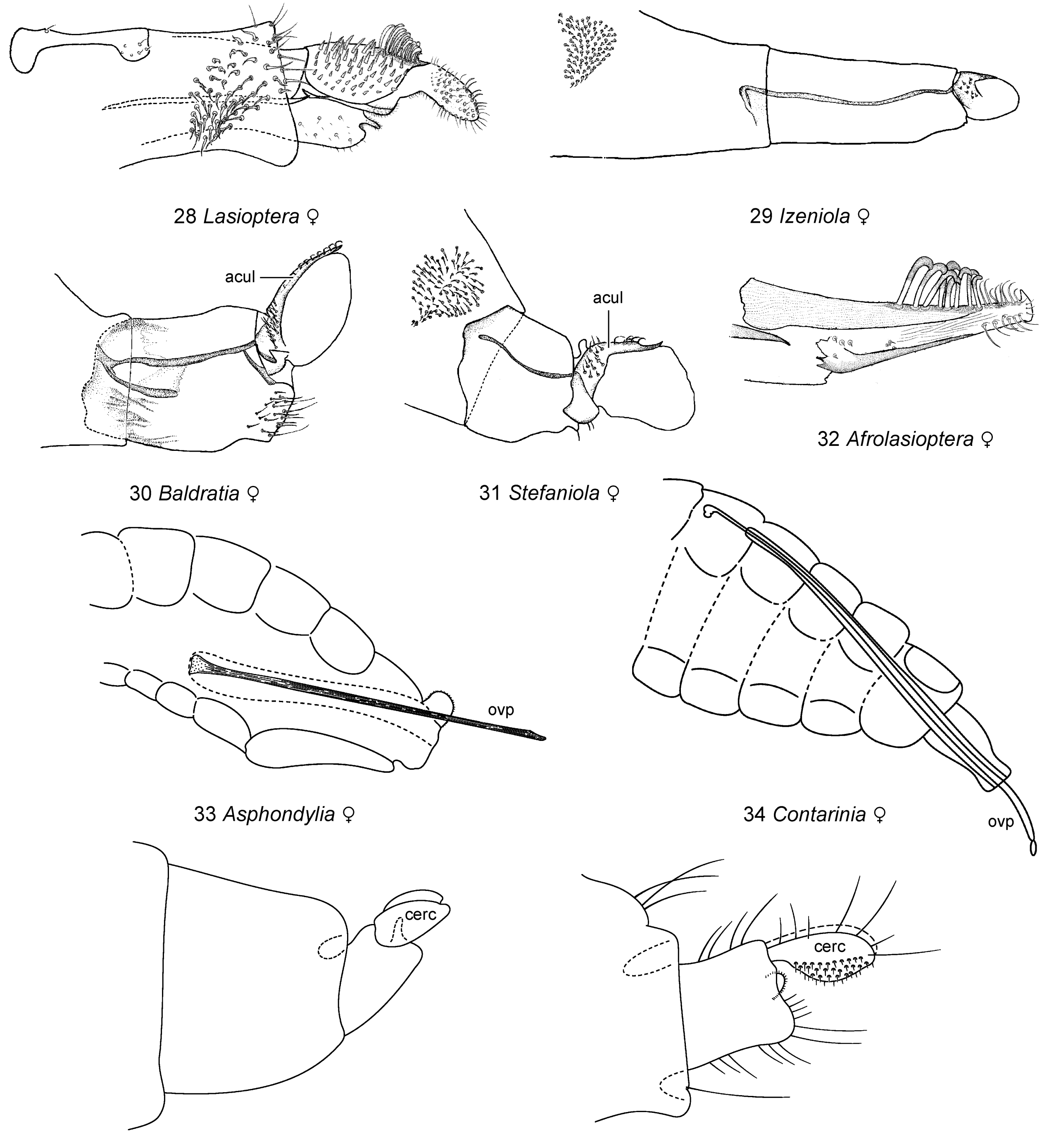
***Monardia* Kieffer** (Micromyinae: Micromyini)**.** A mostly Holarctic genus with four subgenera: *M.* (*Antennardia* Mamaev), *Monardia sensu stricto*, *M.* (*Trichopteromyia* Williston) and *M.* (*Xylopriona* Kieffer), with a total of 52 named species. The only Afrotropical species, *M.* (*T.*) *latipennis* (Kieffer, 1911), is known from a female collected in Seychelles. Its synonymy with *M.* (*T.*) *modesta* Williston, 1894, a species described from the Caribbean, needs to be reconsidered.

[***Monilipennella* Del Guercio.** Synonymised under *Lasioptera*].

***Mycodiplosis* Rübsaamen** (Cecidomyiinae: Cecidomyiidi: Mycodiplosini)**.** A virtually cosmopolitan genus of 46 named species. Larvae are mycophagous, feeding on pathogenic fungi (mostly rusts and mildews) developing on living plants. Only two Afrotropical species have been described: *M. hemileiae* Barnes, 1939, that develops on Coffee rust, *Hemileia vastatrix* Berk. & Broome (Uredinales) and *M. hemileiae* (Barnes, 1939), on Wheat leaf rust, *Puccinia triticina* Erikss. (Uredinales).

***Nanodiplosis* Kieffer** (Cecidomyiinae: Cecidomyiini)**.** An endemic monotypic genus. The single named species, *N. squamosus* (Kieffer, 1911), was described from Seychelles, based on one male caught in flight.

***Neostenoptera* Meunier** (Winnertziinae: Heteropezini)**.** Known from African copal (*N. kiefferi* Meunier, 1901) and from one extant species, *N. congoensis* Gagné, 1979, from Democratic Republic of Congo.



28 *Lasioptera* ♀

29 *Izeniola* ♀

30 *Baldratia* ♀

31 *Stefaniola* ♀

32 *Afrolasioptera* ♀

33 *Asphondylia* ♀

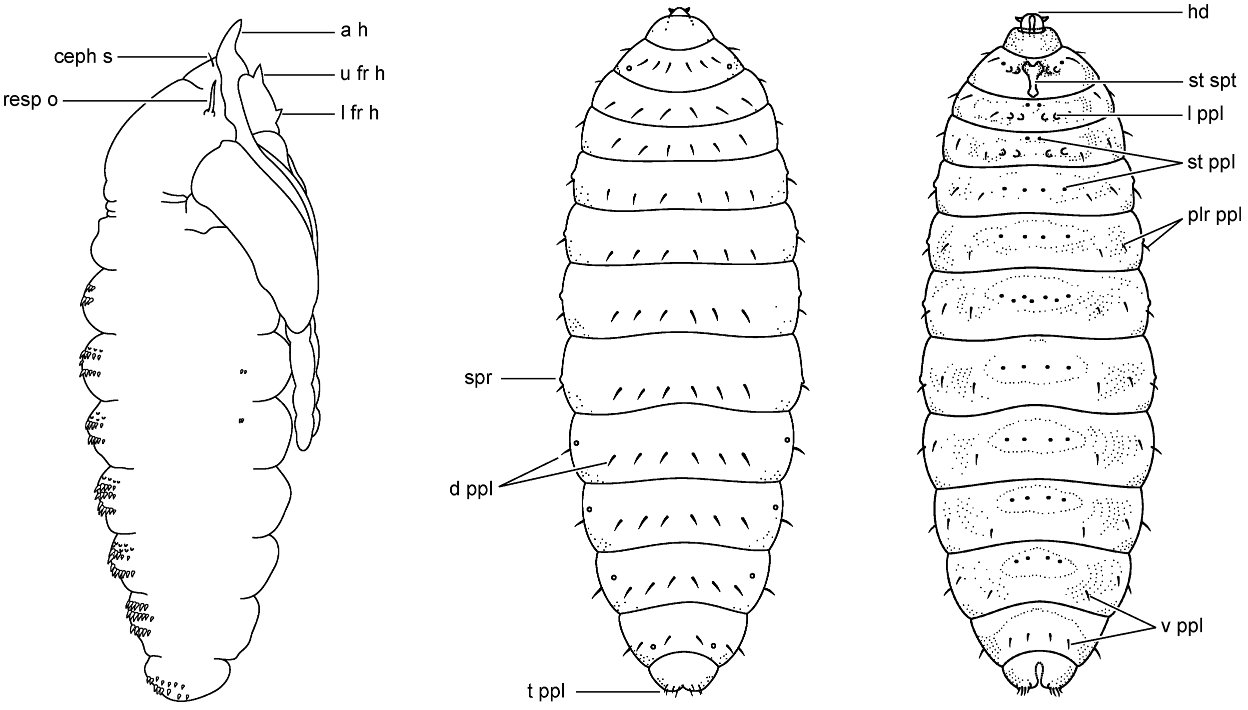
34 *Contarinia* ♀

35 *Orseolia* ♀

36 *Dicrodiplosis* ♀

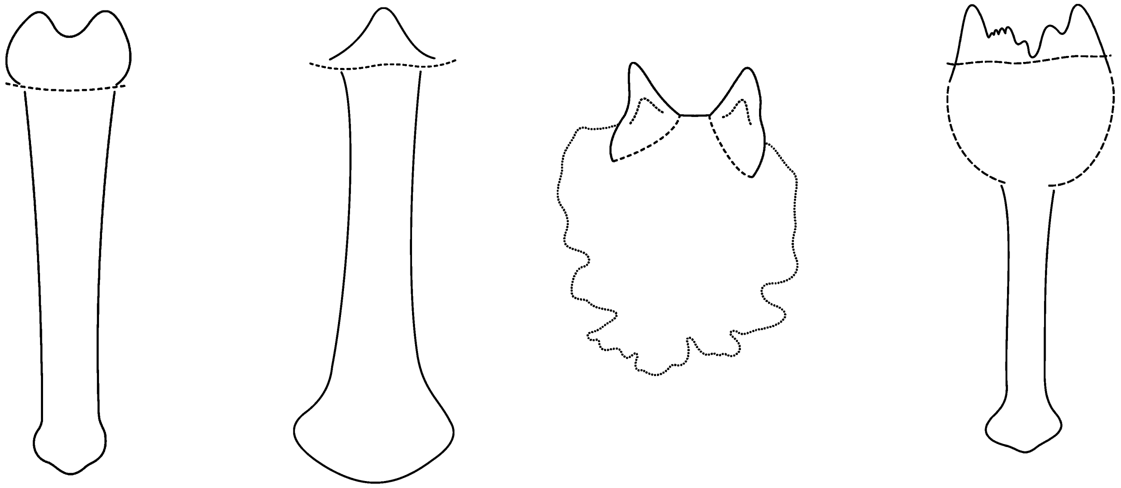
Figs 22.28–36. Female ovipositors of Cecidomyiidae (lateral views): (28) *Lasioptera* sp.; (29) *Izeniola* sp.; (30) *Baldratia* sp.; (31) *Stefaniola* sp.; (32) *Afrolasioptera* sp.; (33) *Asphondylia* sp.; (34) *Contarinia* sp.; (35) *Orseolia* sp.; (36) *Dicrodiplosis* sp.

Abbreviations: acul – aculeus; cerc – cercus; ovp – ovipositor.



37 *Asphondylia*

38 *Dasineura*



39 *Contarinia*

40 *Dicrodiplosis*

41 *Orseolia*

42 *Asphondylia*

Figs 22.37–42. Features of pupae and larvae of Cecidomyiidae: (37) pupa of *Asphondylia* sp., lateral view; (38) larva of *Dasineura* sp., dorsal view (left), ventral view (right); (39) sternal spatula of *Contarinia* sp.; (40) same, *Dicrodiplosis* sp.; (41) same, *Orseolia* sp.; (42) same, *Asphondylia* sp. Fig. 37 (after Gagné 1994, fig. 108), Fig. 38 (after Gagné 1989, fig. 19).

Abbreviations: a h – anterior horn; ceph s – cephalic seta; d ppl – dorsal papillae; hd – head; l fr h – lower frontal horn; l ppl – lateral papillae; plr ppl – pleural papillae; resp o – respiratory organ; spr – spiracle; st ppl – sternal papillae; st spt – sternal spatula; t ppl – terminal papillae; u fr h – upper frontal horn; v ppl – ventral papillae.

Ochnephila **Kieffer** (Cecidomyiinae: Lasiopteridi)**.** An endemic monotypic genus. The single described species, *O. socialis* Kieffer, 1914, is known only from the female collected in South Africa. Larvae induce artichoke bud galls on *Ochna arborea* Burch.ex DC. (Ochnaceae).

Orseolia **Kieffer & Massalongo** (Cecidomyiinae: Cecidomyiidi)**.** A Palaearctic, Afrotropical and Oriental genus of 28 named species. Three Afrotropical species have been described and additional undescribed species are known. Larvae induce galls in grasses and cultivated cereals (Poaceae) and two species are major pests of rice in Asia and Africa (see Chapter 5).

[***Orthodiplosis*** **Kieffer.** *Nomen dubium*].

[***Pachydiplosis*** **Kieffer.** *Nomen dubium*].

[***Perodiplosis*** **Kieffer.** *Nomen dubium*].

Peromyia **Kieffer** (Micromyinae: Peromyiini)**.** A virtually cosmopolitan genus of 160 named species, also known from Baltic amber. The single named Afrotropical species, *P. seychellensis* (Kieffer, 1911), was described from Seychelles.

[***Planodiplosis*** **Kieffer.** *Nomen dubium*].

[***Plecophorus*** **Kieffer.** *Nomen dubium*].

Porricondyla **Rondani** (Porricondylinae: Porricondylini)**.** A virtually cosmopolitan genus of 75 named species, also known from Baltic amber, but several of these are not *Porricondyla sensu stricto*. Three Afrotropical species described from Kenya are considered to be *nomina dubia* (Harris & Dorchin 2012).

Procontarinia **Kieffer & Cecconi** (Cecidomyiinae: Cecidomyiidi: Cecidomyiini)**.** A mainly Oriental genus of 15 named species, but with some species established as invasive aliens elsewhere. Only one species, *P. matteiana* Kieffer & Cecconi, 1906, is known to be established in the Afrotropics. Larvae induce galls on Mango, *Mangifera indica* L. (Anacardiaceae); the only known host-plant.

[***Pseudendaphis*** **Barnes.** Synonymised under *Endaphis*].

Pseudocamptomyia **Parnell** (Porricondylinae: Asynaptini)**.** One Nearctic and two Afrotropical species were described: *P. africana* Mamaev & Zaitzev, 1997 and *P. palpata* Mamaev & Zaitzev, 1997, both from Somalia. It is questionable, however, whether these two species truly belong to this genus.

[***Rabdophaga*** **Westwood** (Cecidomyiinae: Lasiopteridi: Dasineurini)**.** A Holarctic genus of 77 named species. Larvae are phytophagous, with many inducing galls on willows (*Salix* spp.) and, to a lesser extent, on other Salicaceae. The only Afrotropical species that was formerly assigned to this genus, *R. oleiperda* Del Guercio, 1918, has been transferred to *Dasineura* (Gagné 2004: 136)].

Radulella **Del Guercio** (Cecidomyiinae: Lasiopteridi)**.** An endemic monotypic genus. The only named species, *R. aureocephala* Del Guercio, 1918, is known from Eritrea on *Olea chrysophylla* Lam. (Oleaceae).

Resseliella **Seitner** (Cecidomyiinae: Cecidomyiidi)**.** A virtually cosmopolitan genus of 55 named species, with a varied biology. The only known Afrotropical species, *R. proteae* Gagné, 1983, develops in flowers of *Protea repens* (L.) L. (Proteacae) in South Africa. Larvae of many known species occur beneath bark or in flower heads.

Schizomyia **Kieffer** (Cecidomyiinae: Cecidomyiidi: Asphondyliini)**.** A virtually cosmopolitan genus of 55 named species. Six species have been described from the Afrotropical Region, including three from South Africa and one from Madagascar. Larvae are phytophagous and many induce galls.

Seychellepidosis **Spungis** (Porricondylinae: Porricondylini)**.** An endemic monotypic genus erected by Spungis (2007) for *S. spinosa* from Seychelles.

[***Silvestrina*** **Kieffer.** Preoccupied. See *Silvestriola*].

Silvestriola **Skuhravá** (Cecidomyiinae: Cecidomyiidi)**.** A virtually cosmopolitan genus of 14 named species. One virtually cosmopolitan species, *S. cincta* (Felt, 1907), has been recorded from South Africa in the Afrotropics. As far as is known, larvae are predators on mites and other arthropods.

Stefaniola **Kieffer** (Cecidomyiinae: Lasiopteridi: Lasiopterini)**.** A Palaearctic genus of *ca* 110 named species, although many additional undescribed species are known. Three species have been tentatively recorded from Eritrea (Dorchin 2001) and numerous undescribed species are known from Chenopodiaceae and possibly Aizoaceae in South Africa and Namibia (Dorchin, unpubl.). The genus as currently delimited is not monophyletic and is in need of thorough revision. All species are associated with Chenopodiaceae. Larvae induce simple or complex galls in leaves, stems, and buds, or occur in plant tissues without inducing galls.

Stenodiplosis **Reuter** (Cecidomyiinae: Cecidomyiidi: Cecidomyiini)**.** A virtually cosmopolitan genus of 11 named species, plus some currently assigned to *Contarinia*. Four Afrotropical species are known, one of which, the Sorghum midge, *S. sorghicola*, is a major pantropical pest of grain sorghums (see Chapter 5). Larvae feed on developing ovaries in inflorescences of grasses and cereal crops (Poaceae).

Stephodiplosis **Tavares** (Cecidomyiinae: Cecidomyiidi)**.** Only two species are known, one from Mozambique, the other from New Zealand. The Afrotropical species, *S. lanneae* Tavares, 1908 (type species of the genus), induces multilocular woody galls on *Lannea fulva* (Engl.) Engl. (Anacardaceae).

Stomatosema **Kieffer** (Cecidomyiinae: Stomatosematidi)**.** A virtually cosmopolitan genus of 18 named species. Four Afrotropical species, recorded from Kenya and Tanzania, are considered to be *nomina dubia* (Harris & Dorchin 2012).

Tetrasphondylia **Kieffer** (Cecidomyiinae: Cecidomyiidi: Asphondyliini)**.** An endemic monotypic genus. The single species, *T. terminaliae* (Tavares, 1908), known from Mozambique, induces galls on *Terminalia sericea* (Roxb.) Wight & Arn. (Combretaceae). Kieffer erected this genus and separated it from *Asphondylia* solely on the basis of the 4-segmented maxillary palpus. The genus should probably be synonymised under *Asphondylia*.

[***Tricampylomyza*** **Kieffer** (Micromyinae)**.** An endemic monotypic genus, known only from Cameroon. *Nomen dubium*].

[***Trichopteromyia*** **Williston.** Treated as a subgenus of *Monardia*].

Triommata **Barnes** (Cecidomyiinae: Cecidomyiidi)**.** Only two species known; one from India and Sri Lanka, the other, *T. coccotroctes* Barnes, 1931 (type species of the genus), from Sierra Leone and Democratic Republic of Congo. Larvae are predators on mealybugs (Pseudococcidae). The genus is close to *Diadiplosis* (see above).

Trisopsis **Kieffer** (Cecidomyiinae: Cecidomyiidi: Lestodiplosini)**.** A virtually cosmopolitan genus of 25 named species, all presumably predators on mites and other small arthropods. Three species are known from the Afrotropical Region, *T. alluaudi* Kieffer, 1913 (Kenya), *T. oleae* Kieffer, 1912 (South Africa) and *T. nana* (Kieffer, 1911) (Seychelles), but two of these (*T. alluaudi* and *T. nana*), are considered to be *nomina dubia* (Harris & Dorchin 2012).

[***Trissodiplosis*** **Kieffer.** *Nomen dubium*].

Tropaprionus **Jaschhof & Jaschhof** (Micromyinae: Aprionini)**.** A genus of six Palaearctic and one Oriental/Afrotropical species (Jaschhof & Jaschhof 2011). *Tropaprionus indicus* (Jaiswal, 1988), originally described from India, was subsequently recorded from Togo and Madagascar.

Trotteria **Kieffer** (Cecidomyiinae: Lasiopteridi: Trotterini)**.** A Holarctic, Neotropical and Afrotropical genus of 23 named species. The only known Afrotropical species, *T. sesami* Barnes, 1931, is an inquiline recorded from galls of *Asphondylia sesami*

Figs 22.43–50. Galls induced by Afrotropical Cecidomyiidae: (43) *Asphondylia* sp. stem gall on *Carpobrotus acinaciformis* (L.) L.Bolus (Aizoaceae); (44) leaf gall on *Antimima tuberculosa* (L.Bolus) H.E.K.Hartmann (Aizoaceae); (45) bud galls on *Eriocephalus* sp. (Asteraceae); (46) stem and bud galls on *Elytropappus rhinocerotis* Less. (Asteraceae); (47) bud galls on *Cliffortia ruscifolia* L. (Rosaceae); (48) bud gall on *Acacia tortilis* (Forssk.) Hayne (Fabaceae); (49) leaf gall on *Plectranthus grallatus* Briq. (Lamiaceae); (50) stem gall on *Parinari capensis* Harv. (Chrysobalanaceae); (51) bud galls on *Thamnochortis* sp. (Restionaceae). Figs 47–51 (courtesy S. Neser).

Felt on *Sesamum angustifolium* (Oliv.) Engl. (Pedialaceae) in Tanzania. Larvae of most species occur in galls of Asphondyliini, as inquilines or successors.

[***Winnertzia* Rondani** (Winnertziinae: Winnertziini). A mostly Holarctic genus of 105 named species. The only known Afrotropical species, *W. mahensis* (Kieffer, 1911), recorded from Seychelles, is considered to be a *nomen dubium* (Harris & Dorchin 2012)].

***Xenhormomyia* Felt** (Cecidomyiinae: Cecidomyiidi)**.** An endemic Afrotropical genus. The two described species, *X. africana* Felt, 1920 and *X. natalensis* Felt, 1920 (both from South Africa), are based on a single male and a single female, respectively.

***Zatsepinomyia* Mamaev & Zaitzev** (Porricondylinae: Porricondylini)**.** An endemic Afrotropical genus. The two described species, *Z. inopina* Mamaev & Zaitzev, 1997 and *Z. intercalaris* Mamaev & Zaitzev, 1997, were described from Somalia.

***Zeuxidiplosis* Kieffer** (Cecidomyiinae: Cecidomyiidi)**.** The Palaearctic monotypic species *Z. giardi* (Kieffer, 1896) was introduced into South Africa in 1972, for biological control of St. John's wort, *Hypericum perforatum* L. (Clusiaceae) and has become established (Gordon & Neser 1986).

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HETEROTRICHA-GROUP 23

(Sciaroidea, unassigned to family)

Mathias Jaschhof

Fig. 23.1. Male of *Rhynchoheterotricha stuckenbergae* Freeman (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized (body length: 2.0–6.0 mm), yellowish to blackish brown gnats, usually lacking conspicuous markings (Fig. 1).

The gnats in question, often referred to as the unplaceable Sciaroidea, have the size and habitus typical of many other sciaroids, especially among the families Sciaridae and Mycetophilidae. They are recognisable by their slender bodies with long, filamentous antennae and long legs (Fig. 1). As a polyphyletic group, species exhibit much variation in vein patterns, terminalia and other morphological structures. They differ from the Sciaroidea families as currently defined (see "Classification" below), by the following combination of characters:

Head with 14 subcylindrical flagellomeres, with short, randomly distributed sensilla ("setae"), flagellomeres longer in male (Fig. 2) than in female (Fig. 3); palpus 5-segmented (see Jaschhof *et al*. (2006) for a possible exception), in *Madagotricha* Jaschhof & Jaschhof 2-segmented.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 601–605.

Thorax with postnotal phragma well-developed, projecting into abdomen (Jaschhof 2004, figs 10–18). Wing membrane hyaline, usually with macrotrichia (absent in one species of *Rhynchoheterotricha* Freeman); venation as in Figs 4–7, with *r–m* crossvein usually present, more or less oblique, but may be extremely short (*Nepaletricha* Chandler), or absent, with radius and media either touching at a point (*Kenyatricha* Chandler, Fig. 5), or fused for short distance (*Madagotricha*, Fig. 4); vein M_{1+2} complete, with stem and fork; fork as long as stem or longer; *bm–m* crossvein shorter, or longer than *m–cu* (Chandler 2002), together forming a vein virtually parallel to vein *R*; base of vein M_4 always distinct, very short in *Sciarosoma* Chandler; veins M_4 and *CuA* joining near wing base; *CuP* and anal veins not reaching wing margin. [Venation of *Ohakunea*-group (not present in the Afrotropics) differs from above pattern in vein M_{1+2} being weak, or incomplete and the bases of vein *Rs* and adjacent veins being strongly relocated to wing base]. Legs with tibial spurs present.

Abdomen with terminalia more complex than in many other Sciaroidea, especially in females; ovipositor, as far as is known, with conspicuously long, strong setae.

Biology and immature stages

Immature stages are entirely unknown and details of the adult biology are extremely scarce (see *Rhynchoheterotricha* under "Synopsis of the fauna" below). Phenological observations suggest that many, or perhaps most, species are adapted to temperate environments, including montane zones of the tropics. Adult flies appear to have a relatively short flight period, usually in early summer at higher latitudes in both hemispheres. Most species, for which details of the collecting habitat are known, exhibit preferences for old-growth forest, *i.e.*, with abundance of dead wood and associated wood-decomposing fungi (Jaschhof & Didham 2002; Jaschhof *et al*. 2006). There is, therefore, every indication that these sciaroids, like many others, belong to the saproxylic guild. Such empirical knowledge, general as it is, may assist in obtaining specimens for research purposes, given that most species are very rarely encountered.

Economic significance

No species of economic importance have been documented in the literature.

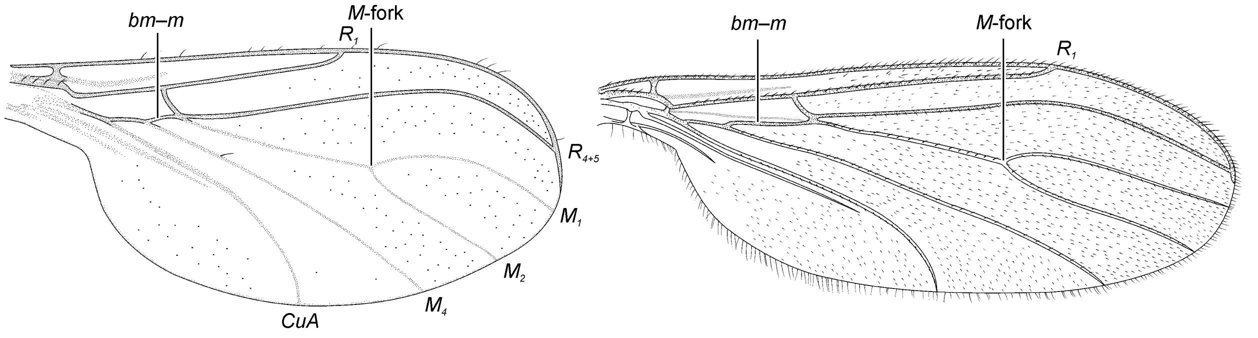
2 *Sciarosoma* ♂

3 *Sciarosoma* ♀

Figs 23.2–3. Habitus of *Heterotricha*-group (Sciaroidea, unassigned to family) (lateral views): (2) male of *Sciarosoma nigriclava* (Strobl) (non-Afrotropical); (3) same, female. Figs 2, 3 (Jaschhof *et al*. 2006, figs 1, 2).

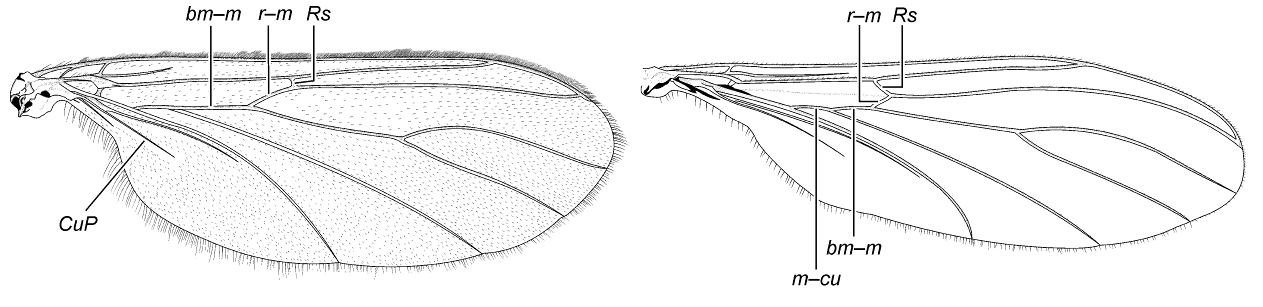
Classification

The Sciaroidea in question were until recently referred to by dipterists as the *Heterotricha*-group, a loosely defined assemblage of five genera and 17 species, all – except for two Baltic (Eocene) amber fossils – from the Southern Hemisphere. Chandler (2002) showed this group to be polyphyletic and its members as not belonging to one of the traditionally recognised families, where some species had been occasionally placed in the past. He defined the *Heterotricha*-group more strictly than had been done previously and introduced seven new genera and 11 new species. In the same year, Jaschhof & Didham (2002) introduced the sciaroid family Rangomaramidae for five new species from New Zealand, all classified in the new genus *Rangomarama*. These two papers catalysed efforts to search for enigmatic Sciaroidea and to resolve their systematic position above the generic level. While the first goal was accomplished successfully, the second has so far proved to be too ambitious. On the one hand, between 2004 and 2014 different authors described a further 23 new species and six new genera of unplaceable Sciaroidea. On the other hand, three studies (Amorim & Rindal 2007; Hippa & Vilkamaa 2005, 2006a), addressing the phylogeny and family classification of the Sciaroidea (including the unplaceables) generated hypotheses that were in conflict with each other and, in the writer's opinion (Jaschhof 2011), lacking convincing support. Moreover, Amorim & Rindal's (2007) new concept for the Rangomaramidae was based on methodologically disputable analyses and was, therefore, rejected by Jaschhof (2011). Pending a phylogenetic hypothesis that is better-founded than previous ones, Jaschhof (2011) proposed to retain the family Rangomaramidae in its original sense and to consider the following genera (listed alphabetically) as Sciaroidea *incertae sedis* for the time being: *Afrotricha* Chandler (South Africa, 1 sp.); *Anisotricha* Chandler (New Zealand, 2 spp.); *Cabamofa* Jaschhof (Costa Rica, 1 sp.); *Chiletricha* Chandler (southern Neotropics, 8 spp.); *Colonomyia* Colless (Neotropical and Australasian/Oceanian Regions, 9 spp.); *Eratomyia* Amorim & Rindal (northern South America, 2 spp.); *Freemanomyia* Jaschhof (a replacement name for *Pterogymnus* Freeman; southern Neotropics, 1 sp.); *Heterotricha* Loew (1 extant southern European sp., 3 fossil Baltic amber spp.); *Insulatricha* Jaschhof



4 *Madagotricha*

5 *Kenyatricha*



6 *Afrotricha*

7 *Rhynchoheterotricha*

Figs 23.4–7. Wings of *Heterotricha*-group (Sciaroidea, unassigned to family) (dorsal views): (4) *Madagotricha ranomafanae* Jaschhof & Jaschhof; (5) *Kenyatricha elgon* (Chandler); (6) *Afrotricha relicta* (Edwards); (7) *Rhynchoheterotricha stuckenbergae* Freeman. Fig. 4 (after Jaschhof & Jaschhof 2007, fig. 1C), Figs 5–7 (after Chandler 2002, figs 15, 16, 53).

Abbreviations: *bm–m* – basal medial crossvein; *CuA* –anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector.

(New Zealand, 3 spp.); *Kenyatricha* (eastern Africa, 2 spp.); *Madagotricha* (Madagascar, 1 sp.); *Nepaletricha* (Oriental Region, 6 spp.); *Ohakunea* Tonnoir & Edwards (Neotropical and Australasian/Oceanian Regions, 5 spp.); *Rhynchoheterotricha* (South Africa, 2 spp.); *Rogambara* Jaschhof (Central America, 1 sp.); *Sciaropota* Chandler (Japan, 1 sp.); *Sciarosoma* (Europe, 1 sp.); and *Starkomyia* Jaschhof (New Zealand, 1 sp.). *Cabamofa*, *Colonomyia*, *Ohakunea* and *Rogambara* appear to form a monophyletic group, the *Ohakunea*-group of Jaschhof (2005), or the subfamily Ohakuneinae of the Rangomaramidae *sensu* Amorim & Rindal (2007). Furthermore, a monophyletic *Heterotricha*-group is likely to comprise all the genera ending with *–tricha*, plus the genus *Eratomyia* (Hippa & Vilkamaa 2005: fig. 2; Jaschhof & Jaschhof 2007). The relationships of *Freemanomyia*, *Sciaropota*, *Sciarosoma* and *Starkomyia* to each other and to other Sciaroidea are controversially discussed (Amorim & Rindal 2007; Chandler 2002; Hippa & Vilkamaa 2005, 2006*a*; Jaschhof 2004).

All unplaceable Sciaroidea found in the Afrotropics belong to the *Heterotricha*-group *sensu stricto*. The phylogenetic hypotheses of Chandler (2002), Hippa & Vilkamaa (2005, fig. 2) and Jaschhof & Jaschhof (2007) suggest biogeographic affinities between Afrotropical genera and Neotropical (*Rhynchoheterotricha* + *Chiletricha*), Palaearctic (*Afrotricha* + *Heterotricha*) and Oriental (*Kenyatricha* + *Nepaletricha*) elements, as well as straightforward intra-Afrotropical relationships (*Kenyatricha* + *Madagotricha*).

Identification

Unplaceable Sciaroidea occur in all zoogeographic regions of the world, except the Nearctic Region and Antarctica. Most of the 19 genera and 56 species (53 extant) occur in either the Neotropical or Australasian/Oceanian Regions. Dipterists not familiar with Sciaroidea often believe the unplaceables to belong to the Sciaridae (in the case of members of the *Ohakunea*-group), the (non-Afrotropical) Diadocidiidae (due to superficial resemblance in wing venation), or Mycetophilidae (due to overall resemblance). Such misidentification is not surprising, given the fact that both the Sciaridae and Mycetophilidae are large, morphologically diverse families and each includes several unusual species. Without going into too great detail, unplaceable Sciaroidea differ from Sciaridae in possessing both the base of wing vein M_4 and macrotrichia on the wing membrane (note that wing macrotrichia are present in a very few Sciaridae and are absent in one *Rhynchoheterotricha*), as well as more complex male terminalia structures; from Mycetophilidae in having the postnotal phragma well-developed (not rudimentary); and from Diadocidiidae in the much shorter base of wing vein *Rs* and the horizontal rather than vertical crossvein *bm–m* plus base of vein M_4. As regards the identification of Afrotropical species, important papers are Chandler (2002), Hippa & Vilkamaa (2006*b*) and Jaschhof & Jaschhof (2007). There are indications of unnamed species (Jaschhof & Jaschhof 2007), a fact that should be borne in mind, especially when working on sciaroids from Madagascar, the East African mountains, or South Africa.

Key to genera of unassigned Afrotropical Sciaroidea

1. Wing crossvein *r–m* absent (*e.g.*, Figs 4, 5); thorax with metepisternum bare 2
– Wing crossvein *r–m* present (*e.g.*, Figs 6, 7); thorax with metepisternum setulose 3
2. Palpus 2-segmented; wing vein R_1 ending before level of vein *M*-fork (Fig. 4) . . . . *Madagotricha* Jaschhof & Jaschhof
– Palpus 5-segmented; wing vein R_1 ending beyond level of vein *M*-fork (Fig. 5) . . . *Kenyatricha* Chandler
3. Thorax with laterotergite setulose; wing with base of vein *Rs* shorter than crossvein *r–m* (Fig. 6); proboscis normal . . . . *Afrotricha* Chandler
– Thorax with laterotergite bare; wing with base of vein *Rs* and crossvein *r–m* of equal length (Fig. 7); proboscis ½ as long as head height, or longer. . . . . *Rhynchoheterotricha* Freeman

Synopsis of the fauna

The Afrotropical Region has four known genera and six described species of the *Heterotricha*-group, none of which occurs outside of the region.

Afrotricha **Chandler.** An endemic monotypic genus. *Afrotricha relicta* (Edwards, 1925) (described as *Heterotricha*), is known from both sexes, collected in the Cape Province of South Africa in 1917 and has not been collected subsequently. Biology and immature stages remain unknown.

Kenyatricha **Chandler.** An endemic genus of two described species. *Kenyatricha elgon* (Chandler, 2002) and *K. mulanje* Chandler, 2002, are known from Afromontane habitats in Kenya and Malawi. The descriptions of both species were based on males alone and each has been collected only once, in 1982 and 1984, respectively. Biology and immature stages remain unknown.

Madagotricha **Jaschhof & Jaschhof**. An endemic monotypic genus. *Madagotricha ranomafanae* Jaschhof & Jaschhof, 2007, is only known from a series of males collected in Ranomafana National Park, Madagascar in 2002. Biology and immature stages remain unknown.

Rhynchoheterotricha **Freeman.** An endemic genus of two described species. *Rhynchoheterotricha* are remarkable in possessing an elongate proboscis (actually the clypeus, or clypeus plus labium), which is excessively long in *R. stuckenbergae* Freeman, 1960 (Fig. 1) and much shorter in *R. chandleri*

Hippa & Vilkamaa, 2006. The former species was observed visiting flowers of an unspecified heather, *Erica* sp. (Ericaceae), which according to Chandler (2002), is the only biological information available for any member of the *Heterotricha*-group. *Rhynchoheterotricha* are known from only a very few specimens and immature stages remain unknown.

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PSYCHODIDAE 24

(Sand Flies, Moth Flies or Owl Flies)

Gunnar M. Kvifte and Rüdiger Wagner

Fig. 24.1. Male of *Clogmia albipunctata* (Williston) (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Adults small- to medium-sized lower Diptera (wing length: 1–6 mm) (Figs 1–4), with body shape humpbacked; wings held erect, roof-like or horizontally over abdomen at rest; adults with flight short and erratic; antennae with hyaline sensory rods (termed ascoids); palpus 3- to 5-segmented; ocelli absent; wing shape variable, with vein *Sc*, 4–5 *R* veins, 4 *M* veins, 1–2 *Cu* veins of which *CuP* is restricted to wing base (Figs 18–25); crossveins reduced, or confined to *Sc* and/or basal cells. Morphology highly variable between subfamilies, thus each subfamily is diagnosed separately below.

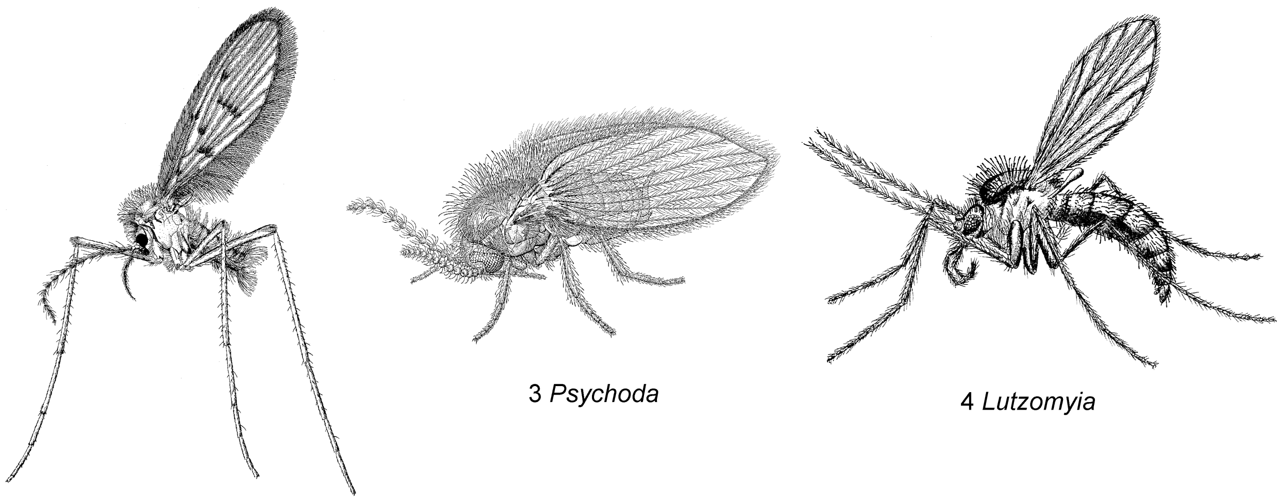
Bruchomyiinae: habitus of adults (Fig. 2) slender, legs longer than body, vestiture developed. Head with compound eye oval; antenna with 14–111 elongate cylindrical flagellomeres, ascoids bulbous, petiolate, shorter than flagellomeres, usually paired; palpus 5-segmented; female mouthparts without functional mandibles. Thorax with wing long, lanceolate, distally rounded (Fig. 18); vein *R* 5-branched; jugum undeveloped.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 607–632.

Abdomen with male terminalia inverted by torsion of segments 7 and 8; gonocoxite cylindrical; gonostylus usually without spines; male with paired testes and ejaculatory ducts, but only single phallotrema in Afrotropical species; epandrium without appendage; cercus simple; female with 1 spermatheca and spermathecal duct, distal part often wider and well-sclerotised. Larvae (Fig. 61) similar to Phlebotominae; antenna 1-segmented; abdominal segments without creeping welts; segment 8 with 2 lateral posterior spiracles; respiratory system amphipneustic; terminal complex with 2 short setae; pseudo-segmentation adumbrate.

Phlebotominae: habitus of adult (Fig. 4) slender, legs longer than body. Head with compound eye oval; antenna with 14 elongate cylindrical, or pyriform flagellomeres; ascoids digitiform, shorter than flagellomeres; palpus 5-segmented; female mouthparts with functional mandibles. Thorax with wing long, lanceolate, distally pointed (Fig. 20); vein *R* 5-branched; *CuP* reduced; jugum weakly or undeveloped. Abdomen with male terminalia inverted by torsion of segments 7 and 8, each by approximately 90°; gonocoxite cylindrical, with parameres with 1 to several lobes (*e.g.*, Figs 31, 32); gonostylus with at least 1, usually several, spiniform setae (Figs 28–32); male with paired testes, ejaculatory ducts and aedeagal filaments; epandrium usually reduced and membranous; epandrium with fixed appendages present, with or without tenacula; cercus present, simple; female with paired spermathecae and spermathecal ducts. Larvae (Fig. 62) elongate, slightly sclerotised, consisting of head with 3-segmented antennae, thorax, eight abdominal segments with ventral creeping welts and terminal segment with 4 long setae of about ½ body length; posterior spiracles present laterally on segment 8; pseudo-segmentation adumbrate.

Psychodinae: habitus of adult (Figs 1, 3) stout, short-legged, vestiture developed. Head with compound eye reniform, usually with dorsal extension (eye bridge, Figs 5, 6); antenna with 8–14 flagellomeres; ascoids (Figs 12–16) paired, or multiple, highly variable in shape; palpus 4-segmented; female mouthparts without functional mandibles; males of some genera with club- or sac-shaped structures posteriorly on head (cornicula, Fig. 9). Thorax with wing lanceolate to oval, distally rounded or pointed (Figs 22–25); vein *R* 5-branched; jugum usually well-developed; prothorax and/or mesothorax in males of some genera with eversible, or permanently everted structures for display and pheromone release. Abdomen with male terminalia inverted by full rotation of segment 9; gonocoxite usually curved cylindrical, with parameral complex only partially sclerotised; gonostylus usually tapering, but variable; male with paired testes and 3 pairs of accessorial glands; ejaculatory duct unpaired, unsclerotised (muscular), with 1 phallotrema; epandrium present, with jointed muscular appendages present, invariably with tenacula (Figs 34–41, 43, 47, 49); cercus absent; female with single genital opening; spermathecae and ducts reduced; structures superficially similar to spermatheca often present. Larvae (Figs 65, 67–95, 97, 98) heavily sclerotised, cylindrical, sometimes flattened, with ventral suction discs in some genera (Figs 89, 91, 93); pseudo-segmentation in 26–27 body rings (annuli) (Fig. 97); antenna with several to numerous setulose, digitiform or differently shaped sensillae from an oval base; thoracic segments divided into 2, abdominal segment 1 into 2 or 3, segments 2–7 each into 3 annuli; usually each annulus with tergal plates divided on first 3 annuli (Figs 67, 68); each segment with identical numbers and positions of true setae (with basal ring): prothorax with 22 pairs, mesothorax to abdominal segment 7 each with 18 pairs; number and shape of accessory setae variable; terminal complex (segments 8–11, Figs 68, 82, 84–86, 88, 89), differently shaped, probably related to larval ecological requirements, comprising a dorsal and ventral pair of flabellar processes on each side of the posterior spiracle openings; processes and setulae keep the spiracles dry; respiratory system amphipneustic.

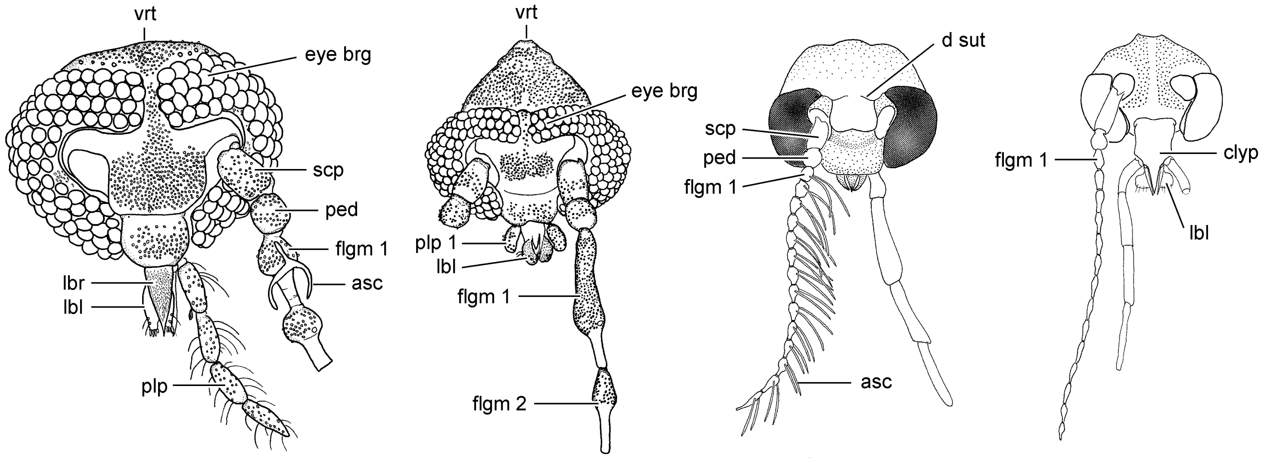


2 *Nemopalpus*

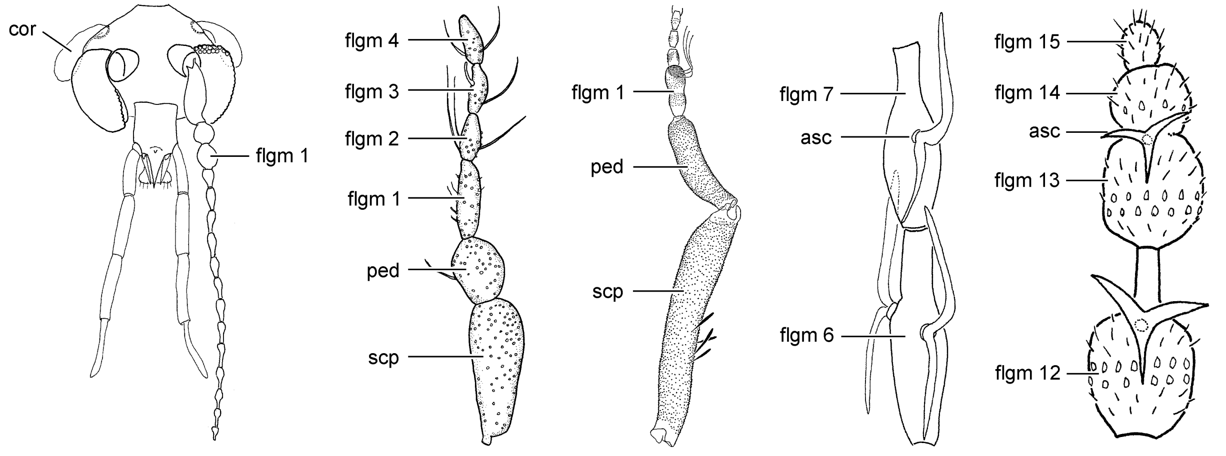
3 *Psychoda*

4 *Lutzomyia*

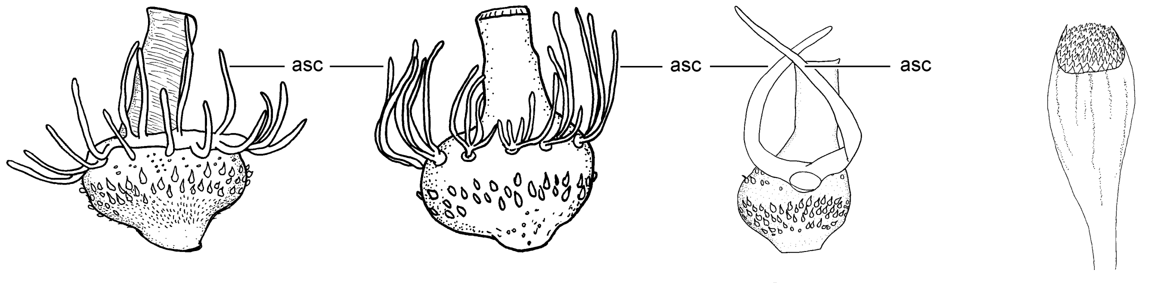
Figs 24.2–4. Habitus of adult Psychodidae: (2) *Nemopalpus transvaalensis* Stuckenberg, lateral view ♀; (3) same, *Psychoda* sp.; (4) same, *Lutzomyia cruciata* (Coquillett) (non-Afrotropical). Fig. 2 (Wagner & Stuckenberg 2016, fig. 1), Fig. 3 (Quate & Vockeroth 1981, fig. 1), Fig. 4 (Wagner & Ibáñez-Bernal 2009, fig. 2).



5 *Psychoda* 6 *Potophila* 7 *Setomima* 8 *Mystropsychoda* ♀



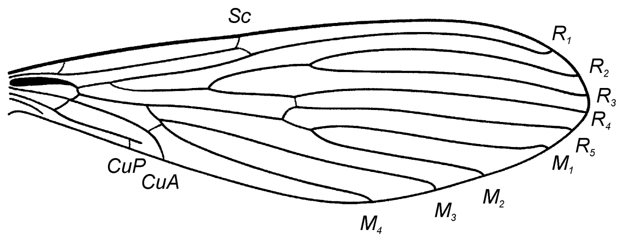
9 *Mystropsychoda* ♂ 10 *Abcharis* 11 *Clytocerus* 12 *Threticus* 13 *Psychoda*



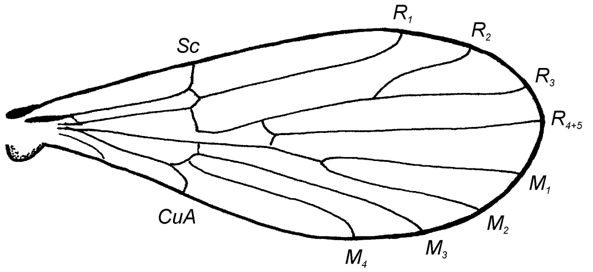
14 *Paramormia* 15 *Neotelmatoscopus* 16 *Clogmia* 17 *Parvidens* ♀

Figs 24.5–17. Heads, antennae, hypopharynx and cibarium of Psychodidae: (5) head of *Psychoda divaricata* Duckhouse, frontal view (non-Afrotropical); (6) same, *Potophila verrucosa* Kvifte; (7) same, *Setomima senegambica* Wagner; (8) same, *Mystropsychoda tansanica* Wagner & Andersen ♀; (9) same, *Mystropsychoda tansanica* Wagner & Andersen ♂; (10) antennal segments 1–6 of *Abcharis* sp., dorsal view (with ascoids); (11) same *Clytocerus excelsior* Duckhouse; (12) antennal segments 6–7 of *Threticus tanganicus* Wagner & Andersen, dorsal view; (13) antennal segments 12–15 of *Psychoda alternata* Say, dorsal view; (14) flagellomere of *Paramormia ustulata* (Walker), dorsal view (non-Afrotropical); (15) same, *Neotelmatoscopus* sp.; (16) same, *Clogmia albipunctata* (Williston); (17) hypopharynx and cibarium of *Parvidens arida* (Davidson), dorsal view. Fig. 6 (Kvifte 2014*a*, fig. 1A), Fig. 7 (Wagner 1983, fig. 1), Figs 8, 9, 12 (Wagner & Andersen 2007, figs 7, 14, 33), Fig. 11 (Duckhouse 1987, fig. 125), Fig. 17 (after Niang *et al*. 2004, figures unnumbered).

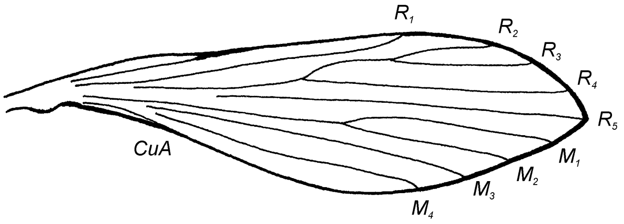
Abbreviations: asc – ascoid; clyp – clypeus; cor – corniculum; d sut – dorsal suture; eye brg – eye bridge; flgm – flagellomere; lbl – labellum; lbr – labrum; ped – pedicel; plp – palpus; scp – scape; vrt – vertex.



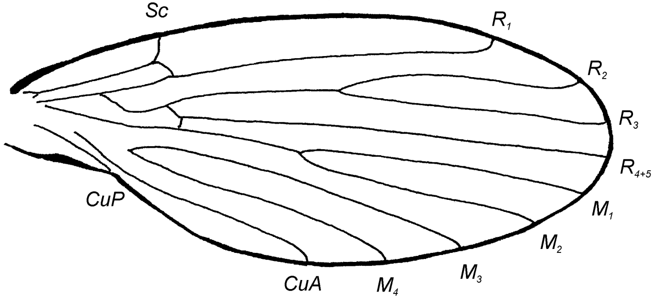
18 *Nemopalpus*



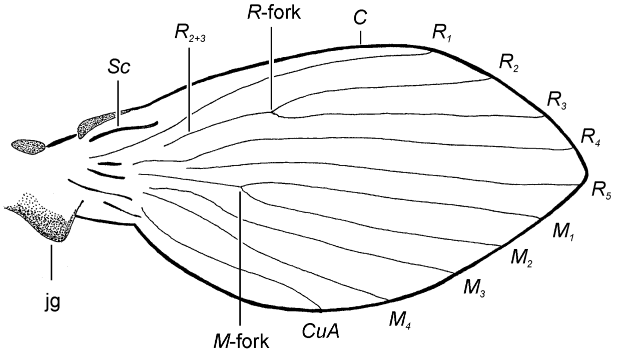
19 *Sycorax*



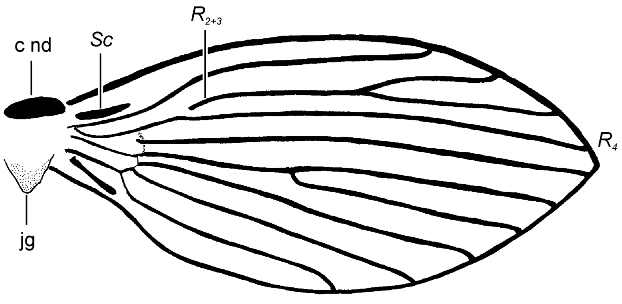
20 *Phlebotomus*



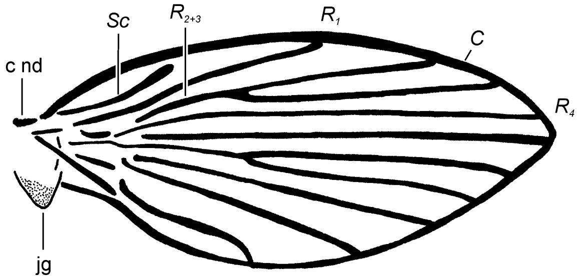
21 *Trichomyia*



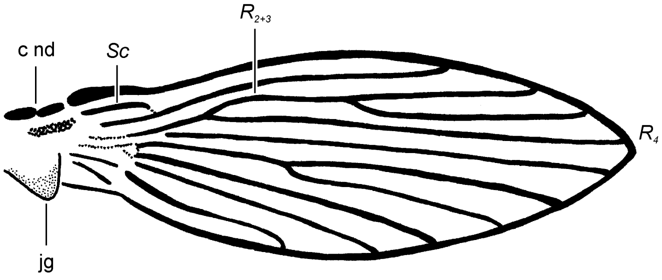
22 *Clogmia*



23 *Potophila*



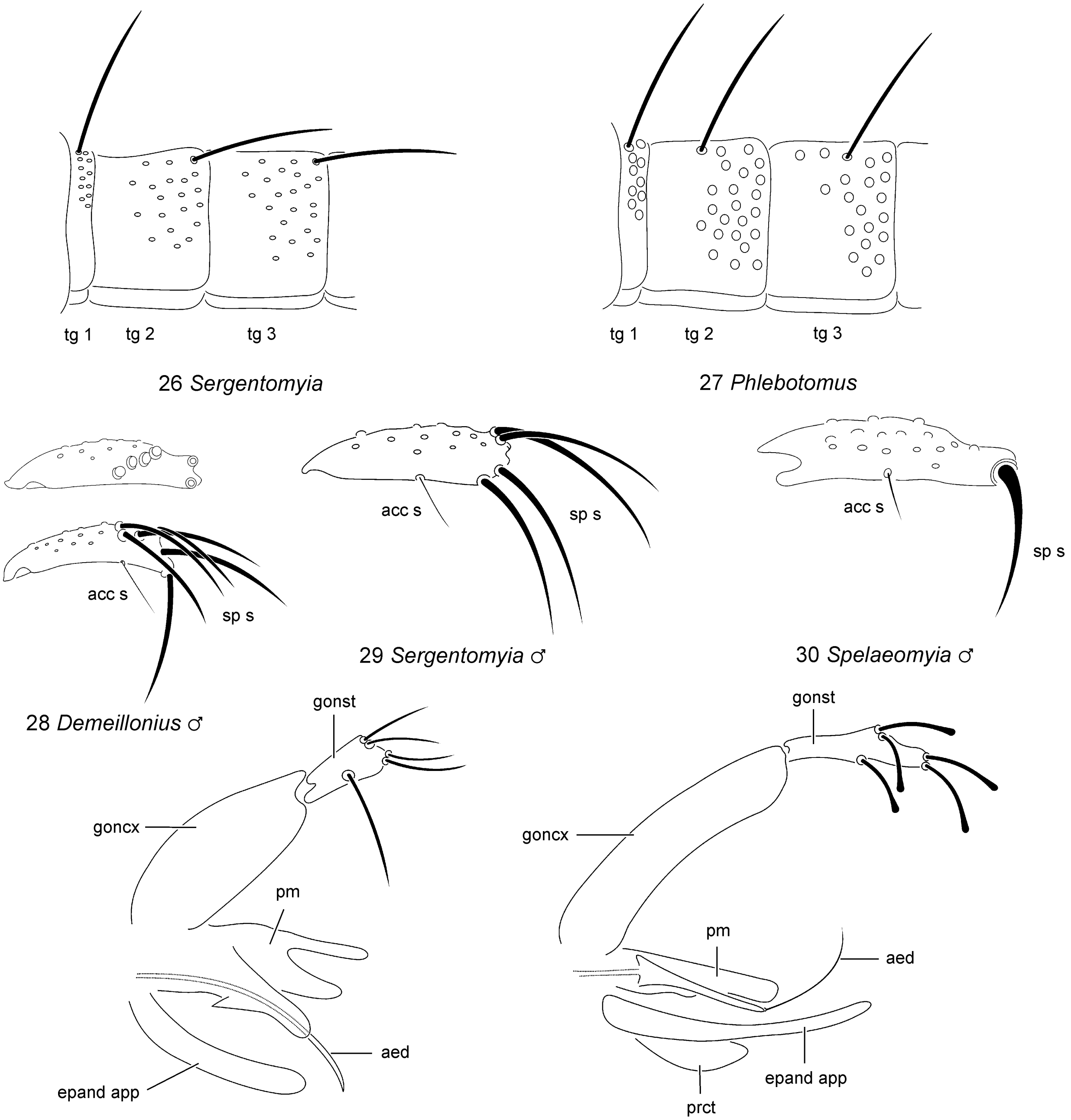
24 *Elsahowia*



25 *Mormia*

Figs 24.18–25. Wings of Psychodidae (dorsal views): (18) *Nemopalpus* sp.; (19) *Sycorax* sp. (non-Afrotropical); (20) *Phlebotomus* sp. (non-Afrotropical); (21) *Trichomyia* sp. (non-Afrotropical); (22) *Clogmia albipunctata*; (23) *Potophila verrucosa* Kvifte; (24) *Elsahowia* sp.; (25) *Mormia* sp. Fig. 23 (Kvifte 2014*a*, fig. 1B), Figs 24, 25 (after Duckhouse 1978, figs 145, 113, respectively),

Abbreviations: *C* – costal vein; c nd – costal node; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; jg – jugum; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3} – second branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; R_5 – lower branch of third branch of radius; *R*-fork – radial vein fork; *Sc* – subcostal vein.



26 *Sergentomyia*

27 *Phlebotomus*

28 *Demeillonius* ♂

29 *Sergentomyia* ♂

30 *Spelaeomyia* ♂

31 *Parvidens* ♂

32 *Phlebotomus* ♂

Figs 24.26–32. Abdomens and male terminalia of Psychodidae: (26) abdominal tergites 1–3 of *Sergentomyia* sp., lateral view; (27) same, *Phlebotomus* sp.; (28) gonostylus of *Demeillonius* sp., dorsolateral view (with spines below; without spines above); (29) same, *Sergentomyia* sp.; (30) same, *Spelaeomyia* sp.; (31) male terminalia and parameres of *Parvidens* sp., lateral view; (32) same, *Phlebotomus* sp. Figs 26–32 (after Niang *et al*. 2004, figures unnumbered).

Abbreviations: acc s – accessory seta; aed – aedeagus; epand app – epandrial appendage; goncx – gonocoxite; gonst – gonostylus; pm – paramere; prct – proctiger; sp s – spiniform seta; tg – tergite.

Sycoracinae: habitus of adult stout, small, short-legged, vestiture reduced. Head with compound eye oval; antenna with 13–14 cylindrical, fusiform, or pyriform flagellomeres; ascoids in Afrotropical species shorter than flagellomeres; palpus 4-segmented; female mouthparts with functional mandibles. Thorax with wing oval (Fig. 19); vein *R* 4-branched; jugum weakly developed. Abdomen with male terminalia not inverted in Afrotropical species; gonocoxites cylindrical, with complex parameres; gonostylus in Afrotropical species with single strong terminal spine (Fig. 33); male with paired, unsclerotised testes and ejaculatory ducts and 1 phallotrema; epandrium present without lobes or appendages; cerci simple; female with paired spermathecae. Larvae (Figs 63, 96) of known species small, flattened, heavily sclerotised, large posterior spiracles on lateral sclerites of segment 8; respiratory system metapneustic; all tergites of larval instars 1–3 split; in larval instar 4 only tergites of prothorax and mesothorax divided.

Trichomyiinae: habitus of adult stout, short-legged, vestiture developed or reduced. Head with compound eye oval; antenna with 13–14 elongate cylindrical, pyriform, or nodiform flagellomeres; ascoids paired to multiple, digitiform; palpus 3- or 4-segmented; female mouthparts without functional mandibles. Thorax with wing (Fig. 21) oval; vein *R* 4-branched; jugum weakly developed; male terminalia inverted by torsion of segments 7 and 8; gonocoxite cylindrical, often with complex parameres; gonostylus variable; male with paired unsclerotised testes and ejaculatory ducts and 1 or 2 phallotremata; epandrium present without lobes or appendages; cerci simple, or modified into clasping structures; female with paired spermathecae and ducts and single genital opening. Larva (Figs 64, 66) thin, elongate, head heavily sclerotised, with 1-segmented antenna, thoracic and abdominal segments weakly sclerotised; small posterior spiracles present laterally on segment 8; pseudosegmentation adumbrate; respiratory system amphipneustic.

Adult psychodids are superficially similar to some Corethrellidae (see Chapter 29), Simuliidae (see Chapter 32), Thaumaleidae (see Chapter 33) and Cecidomyiidae (see Chapter 22), but can be separated on the much higher number of developed wing veins.

Biology and immature stages

The life cycle of Psychodidae encompasses the egg, four larval instars, the pupa and adult. Development time is dependent on temperature and availability of nutrients; under optimal environmental conditions the life cycle may be as short as 1–2 weeks (*Psychoda* Latreille spp.), or as much as 2 years (in alpine populations of *Bazarella atra* Vaillant, 1955, see Vaillant (1983*a*: 339)). Reproduction is usually sexual, but parthenogenesis or facultative parthenogenesis is known in several species. A few species are larviparous, depositing first-instar larvae rather than eggs directly on the substrate.

Bruchomyiinae and Phlebotominae are terrestrial in their larval development, feeding on damp organic matter. Both subfamilies are difficult to locate as larvae in the field. Hanson (1961, 1968) provides a summary of larval habitats of Phlebotominae: they were found on the surface of fallen dead leaves on forest floors, in debris, burrowing in loose soils rich in organic material and in the burrows of mammals and land tortoises. Colonies of several species are permanently kept in laboratories, where larvae can be fed on a standardised diet consisting of, *e.g*., rabbit droppings and liver (*e.g*., Anez & Oviedo 1985). Instructions to establish and maintain sandfly colonies in the laboratory are provided by Killick-Kendrick *et al*. (1977) and Volf & Volfova (2011).

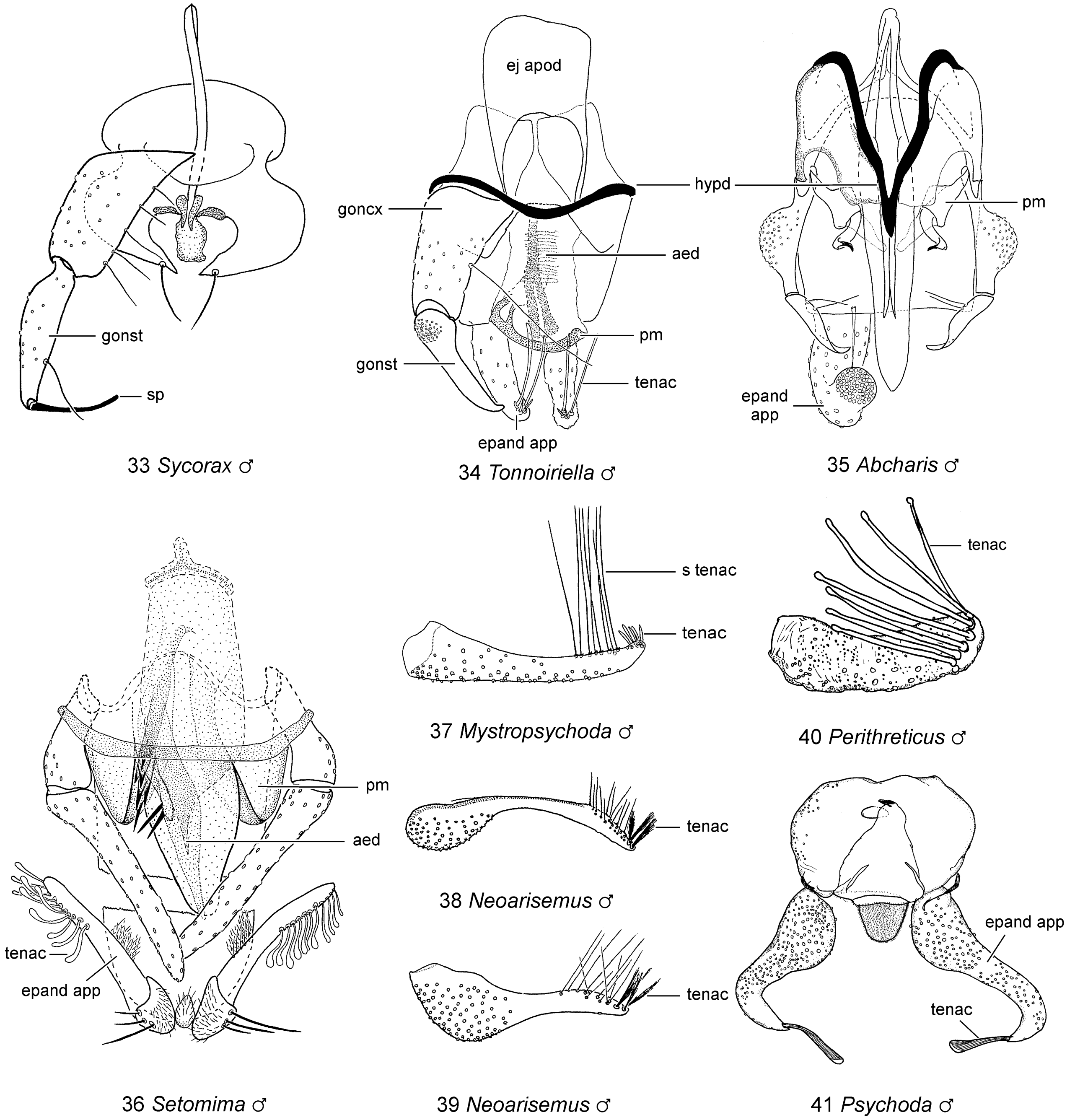
The habits of bruchomyiine larvae are more poorly understood. They have been discovered together with Phlebotominae larvae, feeding on decaying organic matter. One species from New Zealand was found to develop in rotting wood (Duckhouse 1980) and larvae and pupae of an unidentified Neotropical species were mentioned by Williams (2003), as being myrmecophilous. *Bruchomyia argentina* Alexander, 1920 and *Nemopalpus nearcticus* Young, 1974 have been reared from egg to adult on the same breeding media used for phlebotomine larvae (Mahmood & Alexander 1992; Satchell 1953).

Most information on Psychodinae larvae is based on Palaearctic and Nearctic taxa (*e.g*., Vaillant 1971, 1972*a*, *b*, 1973, 1974, 1975, 1983*a*, *b*). Larvae of Afrotropical Psychodinae remain virtually unknown, with the exception of very few descriptions by Vaillant (1963) and Duckhouse (1985, 1987). The best known Afrotropical Psychodinae larva is that of *Neomaruina* Vaillant, which is adapted to fast-flowing torrent streams, where it alternates between being submerged and living hygropetrically (Duckhouse 1985; Vaillant 1963). Otherwise, basic information concerning larval biology is mainly derived from Palaearctic and Nearctic species. Palaearctic Psychodinae are among the taxonomically best known Diptera larvae, as the body surface is well-sclerotised and bears tergal sclerites with accessorial and true setae; the size, shape and position of which enable species determinations in many cases. Basic conditions for larval development include a suitable substrate in which to live and feed and an appropriate amount of moisture and permanent access to atmospheric oxygen. Most taxa of Psychodinae in the Palaearctic Region are detritivores, associated with marginal freshwater habitats, such as the margins of streams and springs, phytotelmata, or water-logged soils. There are, however, also species found in fungal fruiting bodies, leaf litter and compost, decaying wood, carrion and vertebrate dung. A few species are opportunistic myiasis agents, although confirmed cases of this are rare (Taylan-Ozkan *et al*. 2004; Tu *et al*. 2007).

Sycoracinae larvae have only been described from the Palaearctic Region. They occur in aquatic mosses, or leaf litter, mostly in spring and stream habitats with high lime contents (Duckhouse 1972; Wagner 1997: 134).

All known larvae of Trichomyiinae have been found in decaying wood (Duckhouse 1978; Keilin 1914). Adult collections in various parts of the world suggest an association with natural forests and dieback trees.

Adult Phlebotominae and Sycoracinae have functional mandibles and females feed on vertebrate blood. In the Afrotropical Region, it generally appears that *Phlebotomus* Rondani & Berte *in* Rondani feeds on avian and mammalian blood, *Sergentomyia* França & Parrot on reptilian blood and Sycoracinae on amphibian blood (frogs and toads). Phlebotominae can serve as vectors for trypanosomes, notably *Leishmania* and the European *Sycorax silacea* Haliday *in* Curtis, 1893 has been



33 *Sycorax* ♂

34 *Tonnoiriella* ♂

35 *Abcharis* ♂

36 *Setomima* ♂

37 *Mystropsychoda* ♂

38 *Neoarisemus* ♂

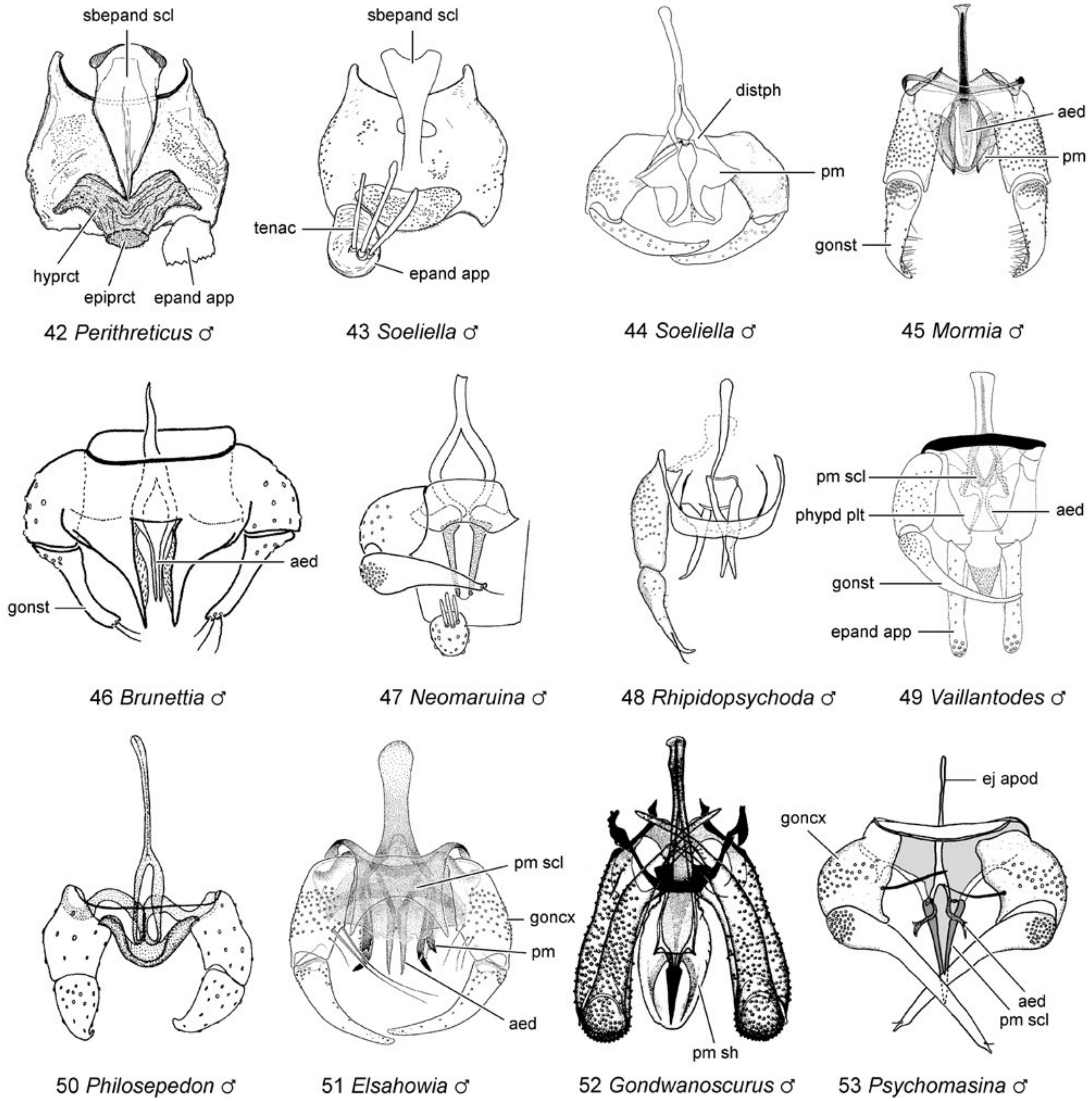
39 *Neoarisemus* ♂

40 *Perithreticus* ♂

41 *Psychoda* ♂

Figs 24.33–41. Male terminalia of Psychodidae: (33) male terminalia of *Sycorax usambarica* Wagner & Andersen, ventral view; (34) same, *Tonnoiriella fasciola* Wagner & Andersen, dorsal view; (35) same, *Abcharis insignis* (Eaton); (36) same, *Setomima senegambica* Wagner; (37) epandrial appendages of *Mystropsychoda pallida* (Tonnoir), lateral view; (38) same, *Neoarisemus angularis* Duckhouse; (39) same, *N. youngi* Duckhouse; (40) same, *Perithreticus anderseni* Kvifte; (41) tergite 9, hypoproct and epandrial appendages of *Psychoda divaricata* Duckhouse, dorsal view (non-Afrotropical). Figs 33, 34 (Wagner & Andersen 2007, figs 5, 40), Fig. 36 (Wagner 1983, fig. 3), Figs 37–39 (Duckhouse 1987, figs 122, 7, 32, respectively), Fig. 40 (Kvifte 2015*b*, fig. 1H).

Abbreviations: aed – aedeagus; ej apod – ejaculatory apodeme; epand app – epandrial appendage; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; pm – paramere; s tenac – setiform tenaculum; sp – spine; tenac – tenaculum.



42 *Perithreticus* ♂ 43 *Soeliella* ♂ 44 *Soeliella* ♂ 45 *Mormia* ♂

46 *Brunettia* ♂ 47 *Neomaruina* ♂ 48 *Rhipidopsychoda* ♂ 49 *Vaillantodes* ♂

50 *Philosepedon* ♂ 51 *Elsahowia* ♂ 52 *Gondwanoscurus* ♂ 53 *Psychomasina* ♂

Figs 24.42–53. Male terminalia of Psychodidae: (42) epandrium of *Perithreticus anderseni* Kvifte, dorsal view; (43) same, *Soeliella platypenis* Kvifte; (44) gonopods and aedeagus of *Soeliella platypenis* Kvifte, dorsal view; (45) same, *Mormia dycei* Duckhouse; (46) same, *Brunettia howelli* Wagner & Andersen; (47) terminalia of *Neomaruina usambaria* Wagner & Andersen, dorsal view; (48) gonopods and aedeagus of *Rhipidopsychoda boettgeri* (Wagner), dorsal view; (49) terminalia of *Vaillantodes margaretae* (Wagner), dorsal view (non-Afrotropical); (50) gonopods and aedeagus of *Philosepedon africanus* Wagner, dorsal view; (51) same, *Elsahowia zombae* Duckhouse; (52) same, *Gondwanoscurus socotrensis* Ježek & Tkoč; (53) same, *Psychomasina violina* Kvifte. Figs 42–44, 48 (Kvifte 2015*b*, figs 1G, 2E, 2D, 3C), Fig. 45 (Duckhouse 1978, fig. 114), Figs 46, 47 (Wagner & Andersen 2007, figs 64, 20, respectively), Fig. 49 (Wagner 1988, fig. 21), Fig. 50 (after Wagner 1979, fig. 21), Fig. 51 (Duckhouse 1987, fig. 101), Fig. 52 (Ježek & Tkoč 2012, fig. 28), Fig. 53 (Kvifte 2015*a*, fig. 8).

Abbreviations: aed – aedeagus; distph – distiphallus; ej apod – ejaculatory apodeme; epand app – epandrial appendage; epiprct – epiproct; goncx – gonocoxite; gonst – gonostylus; hyprct – hypoproct; phypd plt – posthypandrial plate; pm – paramere; pm scl – parameral sclerites; pm sh – parameral sheath; sbepand scl – subepandrial sclerite; tenac – tenaculum.

shown to transmit microfilarial worms between frogs (Desportes 1941). It is not known whether Trichomyiinae, Bruchomyiinae or Psychodinae feed as adults.

The sexual behaviour of psychodids in general appears to be complicated. Males appear to locate females based on species-specific pheromones and also produce their own pheromones, which are used in courtship (Feuerborn 1922; Spiegel *et al*. 2011). The sensilla of psychodid antennae appear to function in perception of pheromones and many taxa in Psychodinae and Bruchomyiinae also possess specialised secondary sexual characters, linked with release and perception of chemical cues (Faucheux & Gibernau 2010; Feuerborn 1922). Visual and tactile displays are also used (Elger 1979, 1981). Some Sycoracinae and Phlebotominae are known to mate in leks and specific aggregation pheromones have been demonstrated in the latter subfamily (Spiegel *et al*. 2011).

Economic significance

Approximately 70 species of Phlebotominae are of high medical importance as vectors of pathogenic protozoans, notably *Leishmania*. Infections with these parasites cause the deadly disease leishmaniasis, which exists in multiple forms. Cutaneous leishmaniasis is a skin disease which often leaves permanent scars, whereas visceral leishmaniasis can kill up to 95% of patients, if appropriate treatment is not available. In the Afrotropical Region, the disease is endemic, with most cases reported from Ethiopia, South Sudan and Sudan. There are probably many unreported cases elsewhere on the continent. The principal vectors in East Africa are *Phlebotomus orientalis* Parrot, 1936 and *Phlebotomus martini* Parrot, 1936 (Elnaiem 2011).

Other subfamilies are of minor or no economic importance. The drain flies *Clogmia albipunctata* (Williston, 1893) (Fig. 1) and *Psychoda alternata* Say, 1824 may occur in large numbers in sewage treatment plants, hospitals, kitchens and bathrooms and are, therefore, often considered nuisance pests (Boumans *et al*. 2009; Coombs *et al*. 1996; Faulde & Spiesberger 2012). Both species have also been associated with cases of myiasis – the infection of human tissues with fly larvae (*e.g*., Tu *et al*. 2007). In some cases, however, these synanthropic moth flies can also be beneficial organisms and at least *Psychoda alternata* may improve efficiency of sewage treatment percolating filters by slowing down the accumulation of biofilm (Williams & Taylor 1968).

Classification

Psychodid monophyly is comparatively robust, being supported by a suite of morphological characters, including: body with dense vestiture; antennae with membranous sensory filaments (ascoids); wing with reduced anal area; second basal cell and wing vein shortened; distal part of wing without crossveins; females with 0, 1 or 2 spermathecae; and male terminalia inverted 180° (Hennig 1972; Quate & Vockeroth 1981: 293). Monophyly is also supported by most published molecular studies (*e.g*., Bertone *et al*. 2008; Wiegmann *et al*. 2011).

Several competing hypotheses have been proposed as to which taxon constitutes the sister-group of the Psychodidae. Published morphological studies have yielded mixed results, due to high levels of homoplasy within the family (Curler & Moulton 2012*b*). Wood & Borkent (1989: 1340) resolved the family as sister to a clade consisting of Trichoceridae (non-Afrotropical), Anisopodidae, Scatopsidae, Synneuridae (non-Afrotropical) and Perissommatidae (non-Afrotropical), mainly based on characters of the larval mouthparts. Using an expanded morphological dataset, Oosterbroek & Courtney (1995) resolved the family's nearest relatives to be a clade consisting of Tipulomorpha (including Trichoceridae), Anisopodidae and Brachycera. More recently, Lambkin *et al*. (2013) suggested a relationship with a Bibionomorpha concept, including the taxa Trichoceridae, Anisopodidae, Scatopsidae, Cecidomyiidae, Sciaroidea and Bibionidae. No broad scale morphological studies are available, however, that consider character distributions within all subfamilies of Psychodidae. Molecular evidence suggests the sister taxon of the Psychodidae to be the Tanyderidae (Bertone *et al*. 2008; Curler & Moulton 2012*b*; Wiegmann *et al*. 2011).

Extant Psychodidae are usually classified in a single family, comprising six extant subfamilies: Bruchomyiinae, Horaiellinae, Phlebotominae, Psychodinae, Sycoracinae and Trichomyiinae. With the exception of the highly specialised Oriental subfamily Horaiellinae, all psychodid subfamilies occur in the Afrotropical Region. Some authors consider the group to consist of two families, *i.e*., Psychodidae and Phlebotomidae (Azar *et al*. 1999; Williams 1993), although this arrangement is impractical, given that phylogenetic relationships between psychodid subfamilies remain unresolved. Given the probable sister-group relationship between the subfamilies Phlebotominae and Psychodinae (Curler & Moulton 2012*b*), recognising phlebotomines as a separate family would necessitate separate familial status for all currently recognised subfamilies and this system is not adopted here.

Extant Bruchomyiinae occur on the southern continents, reaching north to the southern borders of the Nearctic and Palaearctic Regions. The Neotropical genus *Bruchomyia* Alexander was originally placed in the family Tanyderidae. Two genera, *Eutonnoiria* Alexander and *Nemopalpus* Macquart, occur in the Afrotropical Region. The generic classification of world Bruchomyiinae is currently under revision (Wagner & Stuckenberg 2016).

Several competing systems exist for the classification of Old World Phlebotominae. Rispail & Léger (1998) and Depaquit *et al*. (2008) are followed here, in recognising *Demeillonius* Davidson, *Grassomyia* Theodor, *Parvidens* Theodor & Meshghali, *Spelaeomyia* Theodor and *Spelaeophlebotomus* Theodor as separate genera, although many authors still consider these taxa as subgenera of *Sergentomyia*, or *Phlebotomus* (*e.g*. Walter Reed Biosystematics Unit 2013).

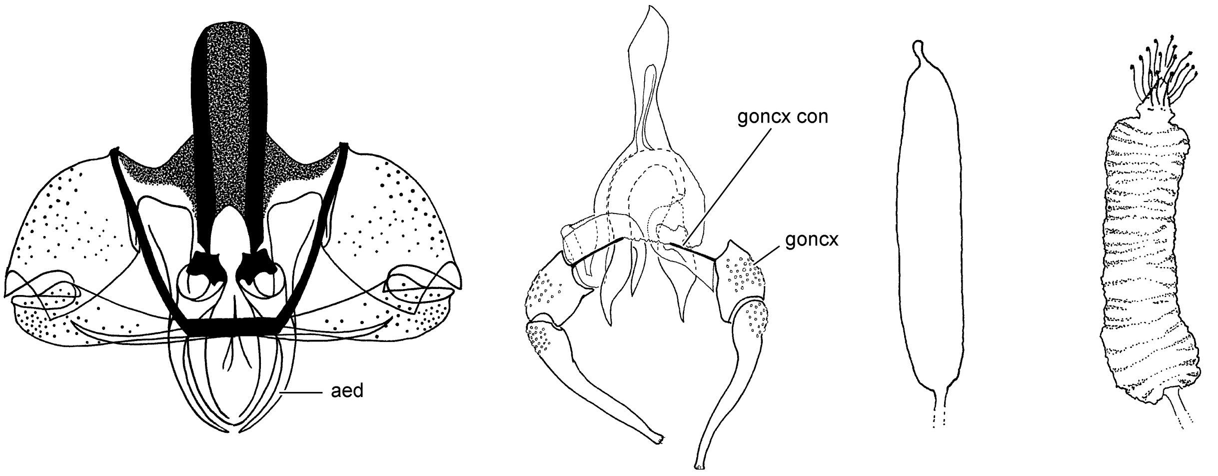
Extant Trichomyiinae are currently classified in the single genus *Trichomyia* Haliday *in* Curtis, but this arrangement is unsatisfactory, as the group is very ancient and morphologically diverse. Trichomyiinae still requires to be subdivided phylogenetically, although some tentative classifications exist, which divide the subfamily into two informal groups (Group A and Group B *sensu* Duckhouse 1965) and/or into eight subgenera (Araújo & Bravo 2012, 2013; Bravo & Araújo 2013).

Three genera of the subfamily Sycoracinae are recognised by the majority of authors (Curler & Jacobson 2012; Duckhouse 1972; Santos *et al*. 2009), although it has also been suggested that these should rather be treated as subgenera (Ježek 1999). This question is beyond the scope of this chapter, given that all Afrotropical species are included in *Sycorax sensu stricto*.

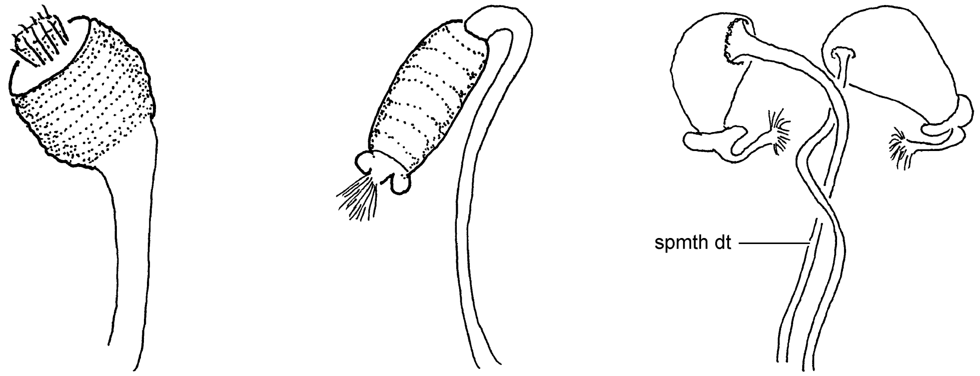
The classification of Psychodinae has a long and convoluted history and remains controversial. Fourteen tribal or subtribal level taxa have been proposed by various authors, although few of these have been supported by phylogenetic analyses (*e.g*., Duckhouse 1985, 1987; Ježek 1983; Kvifte 2015*b*; Quate 1959; Quate & Brown 2004). For this reason tribes are not applied here, as a robust classification is still lacking. Applying the classification of Kvifte (2012), however, all taxa that key out at couplet 23, in the identification key below, belong to the tribe Psychodini and all taxa that key out at couplet 30 belong to the tribe Paramormiini.

Identification

Identification of Afrotropical Psychodidae remains problematic. Most Phlebotominae can be identified using Abonnenc (1972), Lewis (1982, *Phlebotomus* only) and Niang *et al*. (2000, 2004, West Africa). Few sources are available for the remaining subfamilies. The fauna was recently catalogued by Kvifte (2012), a classification later modified by Kvifte (2015*b*).



54 *Iranotelmatoscopus* ♂ 55 *Threticus* ♂ 56 *Parvidens* ♀ 57 *Demeillonius* ♀



58 *Grassomyia* ♀ 59 *Phlebotomus* ♀ 60 *Spelaeomyia* ♀

Figs 24.54–60. Male and female terminalia of Psychodidae: (54) aedeagus and gonopods of *Iranotelmatoscopus hajiabadi* Ježek, dorsal view; (55) same, *Threticus tanganicus* Wagner & Andersen; (56) female spermatheca of *Parvidens iranicus* Lewis & Mesghali, dorsal view; (57) same, *Demeillonius transvaalensis* (Sinton); (58) same, *Grassomyia squamipleuris* Qutubuddin; (59) same, *Phlebotomus alexandri* Sinton; (60) same, *Spelaeomyia darlingi* Lewis & Kirk. Fig. 54 (Ježek 1987, fig. 10), Fig. 55 (Wagner & Andersen 2007, fig. 35), Figs 56–60 (after Niang *et al*. 2004, figures unnumbered).

Abbreviations: aed – aedeagus; goncx – gonocoxite; goncx con – gonocoxal condyle; spmth dt – spermathecal duct.

The key presented below is largely based on these sources, incorporating additional information from Ježek & Tkoč (2012), Kvifte (2011, 2014*a*, 2015*a*, *b*) and Tkoč & Ježek (2013).

An identification key to South African Bruchomyiinae was published by Stuckenberg (1962) and remains useful, despite covering only half the known Afrotropical fauna of the subfamily. Species-level identification keys are still unavailable for Afrotropical Sycoracinae and Trichomyiinae. The last comprehensive identification key to Afrotropical Psychodinae was published by Satchell (1955); but is now outdated and of little use at the generic level. Species-level identification is possible for some genera, applying the identification keys in Satchell (1955) and Duckhouse (1975, 1978, 1985, 1987). In the Arabian Peninsula, the described species can be identified using Ježek & van Harten (2009: 708). References to species identification keys are provided in the "Synopsis of the fauna" section below, if available.

The larva of *Neoarisemus prodiguosus* Duckhouse, 1978 was briefly described by Duckhouse (1978, 1987), but insufficient details were included to incorporate the genus into the below larval identification key. In addition, the majority of Afrotropical genera remain unknown in the larval stages (see "Synopsis of the fauna" section below).

The below key to adult Psychodidae is in most cases only applicable to males. Psychodidae can be collected using most standard collection techniques and are usually preserved in ethanol for later slide-mounting (see Chapter 2). For accurate examination of terminalia, specimens must usually be macerated and slide-mounted prior to identification.

Keys to genera of Afrotropical Psychodidae

Adults

1. Palpus 3- or 4-segmented; wing vein *R* 4-branched (*e.g.*, Figs 19, 21) 2

– Palpus 4- or 5-segmented; wing vein *R* 5-branched (*e.g.*, Figs 18, 20, 22) 3

2. Female with functional mandibles; wing vein *CuA* ending in costal vein (*C*) before end of basal cells (Fig. 19); male terminalia with gonostylus with terminal spine (Fig. 33) . . . . *Sycorax* Haliday *in* Curtis

– Female without functional mandibles; wing vein *CuA* reaching beyond end of basal cells (Fig. 21); male terminalia with gonostylus without terminal spine . . . . *Trichomyia* Haliday *in* Curtis

3. Palpus 5-segmented; wing lanceolate to cuneiform (*e.g.*, Figs 2, 4, 18, 20); eyes never with dorsal extension towards midline, without suture between eyes; male terminalia with ventral pair of appendages not articulated at base, with or without tenacula 4

– Palpus 4-segmented; wing lanceolate to ovoid (*e.g.*, Figs 22–25); eyes usually with dorsal extension towards midline (eye bridge, *e.g.*, Figs 5, 6), if eye bridge absent, then often with dorsal suture between eyes (*e.g.*, Fig. 7); male terminalia with ventral pair of appendages jointed, carrying spatulate to feather-like tenacula (e.g., Figs 34–41, 43) (PSYCHODINAE) 12

4. Female with functional mandibles; male terminalia with gonostylus with 1–6 spiniform setae (*e.g.*, Figs 28–32) (PHLEBOTOMINAE) 5

– Female without functional mandibles; male terminalia with gonostylus terminally with or without very short spiniform setae (BRUCHOMYIINAE) 11

5. Abdominal tergites 2–6 with erect setulae, their alveoli of similar sizes to those on tergite 1 (*e.g.*, Fig. 27); male terminalia with gonostylus with 3–5 spiniform setae; accessory setae usually absent; female cibarium with or without teeth 6

– Abdominal tergites 2–6 with setulae mostly recumbent, their alveoli much smaller than on tergite 1 (*e.g.*, Fig. 26); male terminalia with gonostylus with 1–6 spiniform setae; female cibarium with teeth (*e.g.*, Fig. 17) 8

6. Palpus with segment 3 longer than segment 5; wing vein *M*-fork at level of *r–m* crossvein . . . . *Spelaeophlebotomus* Theodor

– Palpus with segment 5 longer than segment 3; wing vein *M*-fork distal to *r–m* crossvein 7

7. Thorax with anepisternum with 1 patch of setae; male terminalia with paramere bilobate or not (Fig. 32), if bilobate, then lower lobe not dorsoventrally compressed, without row of stout spines; female spermathecal wall ornamented (Fig. 59) . . . . *Phlebotomus* Rondani & Berte *in* Rondani

– Thorax with anepisternum with 2 patches of setae; male terminalia with paramere bilobate, lower lobe partially flattened (Fig. 31), with row of stout spines; female spermathecal wall unornamented (Fig. 56) . . . . *Parvidens* Theodor & Mesghali

8. Male terminalia with gonostylus with 1 or 2 spines (Fig. 30); female spermatheca large and sac-like; spermathecal duct with large bulge near junction with spermatheca (Fig. 60); legs elongate . . . . *Spelaeomyia* Theodor

– Male terminalia with gonostylus with 4–6 spines (*e.g.*, Figs 28, 29); female spermatheca tubular or capsular; spermathecal duct without large bulge near junction with spermatheca; legs not particularly elongate. 9

9. Male antenna with first flagellomere without ascoids; female antennae without paired ascoids; thorax with anepisternum with 2 patches of setae; female spermatheca with rows of spicules (Fig. 58) . . . . *Grassomyia* Theodor

– Male antenna usually with first flagellomere with ascoids, if ascoids absent, then male terminalia with gonostylus with 6 spines; female antennae with paired ascoids on flagellomeres 1–13; thorax with anepisternum without patches of setae; female spermatheca without rows of spicules 10

10. Male terminalia with gonostylus with 6 spines (Fig. 28); female spermathecae striated, apically with cluster of spines (Fig. 57) . . . . *Demeillonius* Davidson

– Male terminalia with gonostylus with 4 spines (Fig. 29); female spermathecae not as above . . . . *Sergentomyia* França & Parrot

11. Antenna with more than 100 flagellomeres . . . . *Eutonnoiria* Alexander

– Antenna with 14 flagellomeres. *Nemopalpus* Macquart

12. Antenna with flagellomeres fusiform (barrel- or bead-shaped) (*e.g.*, Figs 7, 10, 11) 13

– Antenna with flagellomeres nodiform (with basal setulose trunk and bare distal neck) (*e.g.*, Figs 5, 6, 8, 9, 12–17). 17

13. Antennal scape more than 3 × length of pedicel (Fig. 11); first flagellomere distally with wavy brush of setae (Fig. 11); male head usually with cornicula (as in Fig. 9) . . . . *Clytocerus* Eaton

– Antennal scape less than 3 × length of pedicel (*e.g.*, Figs 7, 10); first flagellomere without distal brush of setae; male head invariably without cornicula 14

14. Antenna with first flagellomere about as long as second; terminalia asymmetrical; epandrial appendages of male terminalia without subapical setulae 15

– Antenna with first flagellomere at least 2 × as long as second, often longer (*e.g.*, Fig. 10); terminalia symmetrical or asymmetrical; epandrial appendages of male terminalia with subapical patch of setiform tenacula, in addition to apical patch of tenacula (*e.g.*, Figs 37–39) 16

15. Antennal ascoids very short, shorter than flagellomere bearing them; tenacula with apices fringed; aedeagus symmetrical or asymmetrical, paramere asymmetrical (Fig. 34) . . . . *Tonnoiriella* Vaillant

– Antennal ascoids elongate, more than 2 × length of flagellomere bearing them (Fig. 7); tenacula with apices complete; aedeagus and paramere asymmetrical (Fig. 36) . . . . *Setomima* Enderlein

16. Eye bridge absent; male terminalia with hypandrium pointed medially and parameres bifurcate basally (Fig. 35) . . . . *Abcharis* Tkoč & Ježek

– Eye bridge present; male terminalia with hypandrium straight medially and parameres not bifurcate . . . . *Mormopericomiella* Ježek & van Harten

17. Origin of wing vein R_{2+3} distal to origin of vein R_5 (*e.g.*, Figs 23, 25), often fused with R_4, giving the appearance of an R_{2+3+4}. 18

– Origin of wing vein R_{2+3} basal to or at same level as origin of vein R_5 (*e.g.*, Figs 22, 24) 23

18. Eye bridge absent, clypeus elongate, more than ⅔ projecting in front of eyes (Figs 8, 9). . . . . *Mystropsychoda* Duckhouse

– Eye bridge present 19

19. Eye bridge separated medially by at least 0.5 × an eye facet diameter (*e.g.*, Figs 5, 9) 20

– Eye bridge contiguous 22

20. Eye bridge comprising 4 rows of eye facets (as in Fig. 5); wing vein R_5 ending at wing apex, radial fork basal of medial fork; male terminalia with aedeagus asymmetrical; epandrial appendages bulbous at base, distally narrow, with short, feather-like tenacula (Figs 38, 39). . . . . *Neoarisemus* Botoşaneanu & Vaillant

– Eye bridge comprising 3 rows of eye facets (*e.g.*, Fig. 6); wing vein R_5 ending below wing apex, radial fork distal of medial fork; male terminalia with aedeagus symmetrical or asymmetrical; epandrial appendages evenly tapering or of equal width throughout length. 21

21. Antennal flagellum with segment 1 much longer than segment 2 (Fig. 6); wing with costal vein (C) with node at base more than 2 × width of rest of costa (Fig. 23), aedeagus asymmetrical. . . . . *Potophila* Kvifte

– Antennal flagellum with segment 1 at most ¾ length of segment 2; wing with costal vein (*C*) with node at base less than 2 × width of rest of costa, aedeagus symmetrical . . . . *Promormia* Ježek

22. Male terminalia with aedeagus racket-shaped, not flanked by triangular processes, but may have triangular extensions on each paramere (Fig. 45); gonostylus mostly without apical setae; epandrial appendages with 1 distal patch of tenacula that are fringed apically . . . . *Mormia* Enderlein

– Male terminalia with aedeagus usually narrow, with diamond-shaped widening at midlength, flanked by 2 triangular extensions (Fig. 46); gonostylus with apical setae (Fig. 46); epandrial appendages with 2 types of tenacula, apical ones simple, rod-like, subapical ones with complex apical expansions . . . . *Brunettia* Annandale

23. Antennal ascoids with 2–4 branches, 1 branch posteriorly directed, 1–3 branches anteriorly directed, usually Y-shaped (*e.g.*, Figs 5, 12, 13); apical flagellomeres (11–14) round, much smaller than other flagellomeres; occasionally flagellomere 13 and/or 14 reduced or fused (*e.g.*, Fig. 13); male terminalia with aedeagus symmetrical or asymmetrical (PSYCHODINI). 24

– Antennal ascoids, if multi-branched, with all branches pointing in same direction (*e.g.*, Figs 15, 16); male terminalia with aedeagus symmetrical in all known Afrotropical species (PARAMORMIINI) 31

24. Labellum flat, with row of apical teeth (*e.g.*, Fig. 5). 25

– Labellum bulbous, without row of apical teeth (*e.g.*, Figs 6, 8) 27

25. Eyebridge without dorsal suture (Fig. 5); male terminalia with epandrial appendages with single distal tenaculum (Fig. 41) . . . .*Psychoda* Latreille

– Eyebridge with dorsal suture developed at least laterally (*e.g.*, Fig. 7); male terminalia with epandrial appendages with distal row of several tenacula 26

26. Antennal ascoids 3-branched (as in Fig. 5); male terminalia symmetrical (Fig. 47) . . . .*Neomaruina* Vaillant

– Antennal ascoids 2-branched (as in Fig. 12); male terminalia asymmetrical (Fig. 48) . . . . *Rhipidopsychoda* Vaillant

27. Male terminalia with tenacula of epandrial appendages in 1 apical group of rod-like tenacula and 1 subapical group of filiform tenacula with complex apical expansions . . . .*Trichopsychoda* Tonnoir

– Male terminalia with tenacula all apical and rod-like, evenly tapering or of same width apically as basally 28

28. Antennal ascoids 2-branched (Fig. 12); male terminalia asymmetrical (Fig. 55); gonocoxites with long, narrow condyles . . . .*Threticus* Eaton

– Antennal ascoids 3-branched; male terminalia symmetrical; gonocoxal condyles usually different . . . 29

29. Male terminalia with epandrial appendages with 2 tenacula. . . . .*Philosepedon* Eaton

– Male terminalia with epandrial appendages with 3 or more tenacula 30

30. Male terminalia with distiphallus extending further than parameres, hypoproct concave anteriorly at mid-point (Fig. 42); epandrial appendages with at least 7 tenacula (Fig. 40) . . . . . *Perithreticus* Vaillant

– Male terminalia with distiphallus expanded into 2 large and partially fused plates (Fig. 44); hypoproct straight anteriorly at mid-point (Fig. 43); epandrial appendages with 3 tenacula (Fig. 43). . . . . *Soeliella* Kvifte

31. Wing with apex of subcostal vein (*Sc*) terminating closer to vein R_1 than to costal vein (*C*) (*e.g.*, Fig. 22). 32

– Wing with apex of subcostal vein (*Sc*) terminating closer to costal vein (*C*) than to vein R_1 (in dubious cases antennal flagellomeres with ascoids with more than 2 filiform apices) (*e.g.*, Fig. 14) 34

32. Antennal flagellum with 1 pair of ascoids on each segment (Fig. 16); ascoids with 2–6 branches in Afrotropical species . . . .*Clogmia* Enderlein

– Antennal flagellum with more than 1 pair of ascoids on each antennal segment (*e.g.*, Fig. 15); ascoids with 1–5 branches 33

33. Antennal ascoids with 1–3 branches; head with vertex developed (as in Fig. 6); male terminalia with parameral sheath with areas of different sclerotisation (Fig. 52), epandrium longer than wide. . . . . *Gondwanoscurus* Ježek

– Antennal ascoids with 5 branches; head with vertex reduced (as in Fig. 5); male terminalia with parameral sheath membranous, without area of different sclerotisation, epandrium shorter than wide . . . . *Neotelmatoscopus* Tonnoir

34. Base of antennal ascoids elongate, circling at least ⅓ of antennal segment diameter, more than 12 filiform ascoid apices visible (Fig. 14) . . . . *Paramormia* Enderlein

– Base of antennal ascoids rounded (as in Fig. 16), ascoids either single or V-shaped, digitiform to filiform 35

35. Male terminalia with stem of ejaculatory apodeme narrowly rod-shaped (Fig. 53); parameral sclerites broadly fused to form elongate, V-shaped median protuberance reaching beyond apices of gonocoxites (Fig. 53) . . . . *Psychomasina* Ježek

– Male terminalia with stem of ejaculatory apodeme broadly spatulate to U-shaped; parameral sclerites absent, or narrowly fused to form V- to X-shaped "furca", not extending beyond apices of gonocoxites (*e.g.*, Figs 49, 51) 36

36. Head with elongate cornicula (as in Fig. 9, but stalked); male terminalia with aedeagus distally with sickle-shaped lateral appendages, with convex end laterally . . . . *Panimerus* Eaton

– Head without cornicula; male terminalia with aedeagus not as above 37

37. Male terminalia with posthypandrial dorsal plate (Fig. 49); a dorsal plate (ventral prior to genital torsion), arising from hypandrium covering both V-shaped parameral sclerites and distal end of aedeagus . . . . *Vaillantodes* Wagner

– Male terminalia without posthypandrial dorsal plate. 38

38. Wing with expanded area anterior to subcostal vein (*Sc*) (Fig. 24); wing membrane with sparse setula scars; male terminalia with 2 pairs of processes flanking aedeagus; aedeagal complex not enclosed within sheath (Fig. 51) . . . . *Elsahowia* Duckhouse

– Wing without expanded area anterior to subcostal vein (*Sc*); wing membrane bare; male terminalia with at most 1 pair of processes flanking aedeagus; aedeagal complex enclosed within sheath or not. . . . 39

39. Antennal ascoids as short as node of same flagellomere; wing with vein R_5 situated at apex; male terminalia with aedeagus distally U-shaped, flanked by jointed appendages (Fig. 54) . . . . *Iranotelmatoscopus* Ježek

– Antennal ascoids typically longer than node of same flagellomere, sometimes reduced; wing with vein R_5 situated posterior to apex; male terminalia with aedeagus U-shaped or not, with or without jointed appendages . . . . *Telmatoscopus auctt.*, *nec* Eaton

Larvae

1. Body shorter (< 2 mm); asselliform, with no evident pseudo-segmentation; head and prothorax retractable into body (*e.g.*, Figs 63, 96) (SYCORACINAE) . . . . *Sycorax* Haliday *in* Curtis

– Body longer (> 2 mm); elongate, with slight or evident pseudo-segmentation; head and prothorax not retractable into body 2

2. Body well-sclerotised, with up to 27 pseudo-segments (annuli), mostly covered with well-sclerotised tergal plates; abdomen with 7 segments; posterior spiracles close to one another, dorsally on sclerotised tube on terminal complex of segments 8 and following segments (*e.g.*, Figs 65, 90, 92, 94, 95, 97, 98) (PSYCHODINAE) 5

– Body sclerotisation and pseudo-segmentation less pronounced; abdomen with 8 segments and terminal complex; posterior spiracles laterally on segment 8. 3

3. Larvae micropilose, thin; more than 10 × longer than wide, without terminal setae (Figs 64, 66) (TRICHOMYIINAE). . . . . *Trichomyia* Haliday *in* Curtis

– Larvae setose; less than 10 × longer than wide, with elongate true and accessory setae on terminal complex (*e.g.*, Figs 61, 62) 4

4. Terminal complex with remarkably long setae, more than ½ body length (*e.g.*, Fig. 62) (PHLEBOTOMINAE). . . . . (not keyed further)

– Terminal complex with setae shorter, as long as an abdominal segment (*e.g.*, Fig. 61) (BRUCHOMYIINAE). . . . . (not keyed further)

5. Larvae generally weakly-sclerotised, appearing pale (Fig. 98); tergal plates on annuli often reduced in size or even absent; antenna consisting of 1 or 2 elongate sensilla (Fig. 72); hypostoma without teeth (Fig. 79); preanal plate absent . . . . *Psychoda* Latreille

– Larvae usually well-sclerotised, appearing dark, with 36 tergal plates on annuli usually large, not reduced in size; antenna consists of 2 or more sensilla of different size and shape (*e.g.*, Figs 70, 71, 73); hypostoma with 1 or more teeth (*e.g.*, Figs 68, 74–78, 80, 81); preanal plate present. 6

6. Abdomen with ventral suction discs (*e.g.*, Figs 89, 91, 93) 7
– Abdomen without ventral suction discs 8
7. Body not clearly "waisted" (Fig. 90); suction discs subrectangular, connected to one another (Figs 89, 91); suction disc diameter almost as wide as body width . . . . *Neomaruina* Vaillant
– Body with several clear "waists" (Figs 92, 93); suction discs circular, at some distance from one another (Fig. 93); suction disc diameter less than 50% of body width . . . . *Neotelmatoscopus* Tonnoir
8. Antenna inserted on remarkably pronounced processes on head (*e.g.*, Fig. 70) 9
– Antenna inserted immediately on head capsule, not on pronounced processes (*e.g.*, Figs 71–73) . . . 10
9. Body with 26 pseudo-segments (annuli); abdominal segment 1 with only 2 annuli; hypostoma with a single row of teeth; lateroanal plates absent; siphon short, or absent; tergal plates with numerous elongate accessory setae . . . . *Clytocerus* Eaton
– Body with 27 pseudo-segments (annuli); abdominal segment 1 with 3 annuli; hypostoma (*e.g.*, Fig. 75) with 2 medial teeth; prothorax with 4 large tergites; mesothorax, metathorax and abdominal segments without large plates, but with only very small dorsal and dorsolateral ones, without adanal plates or setae (BRUNETTIINI) . . . .(see note under *Brunettia* below)
10. Body dorsoventrally flattened, with furcate lateral projections (Fig. 87); head capsule sub-triangular; hypostoma (Fig. 74) with single median tooth; ventral flabellar processes *ca* 3 × longer than dorsal processes, with long setae (Figs 65, 97). . . . . *Tonnoiriella* Vaillant
– Body not dorsoventrally flattened, without furcate lateral projections; head capsule sub-oval; hypostoma with 3 to many teeth, sometimes arranged in several rows; ventral flabellar processes at most 2 × longer than dorsal 11
11. Prothoracic spiracles absent; preanal plate formed of thin cross sclerite (Fig. 83); body with 19 tergites; mesotergites and metatergites of abdominal segments fused; hypostoma (Fig. 77) with 2 lateral projections with toothed margins. . . . . *Philosepedon* Eaton
– Prothoracic spiracles present, often prominent; preanal plate well-developed (*e.g.*, Figs 82, 84), oval or rectangular; body invariably with more than 19 tergites; mesotergites and metatergites of abdominal segments separate; hypostoma of different shape, without lateral projections. 12
12. Respiratory siphon very short or undeveloped (*e.g.*, Fig. 85); terminal tip of larvae appearing rounded; true setae present on preanal plate at some distance from distal margin 13
– Respiratory siphon well-developed, more or less elongate (*e.g.*, Fig. 82); true setae present on preanal plate close to, or at distal margin (*e.g.*, Fig. 82). 14
13. Hypostoma with single tooth medially; tergal plates and siphonal segment without accessory setae; prothoracic spiracles at apex of shaft (petiolate) . . . . *Trichopsychoda* Tonnoir
– Hypostoma (Fig. 80) with several differently shaped teeth; tergal plates and siphonal segment with accessory setae (Fig. 85), prothoracic spiracles without shaft . . . . *Mormia* Enderlein
14. Antenna with 2 short sensillae; tergites and terminal complex without accessory setae; preanal plate oval, wider than long (Fig. 82) . . . . *Threticus* Eaton
– Antenna with more than 2 elongate sensillae; at least some tergites and terminal complex usually with accessory setae; preanal plate longer than wide 15
15. Hypostoma with only 3 teeth along entire width (*e.g.*, Figs 76, 78) 16
– Hypostoma with numerous teeth along entire width 17
16. Hypostoma with 3 sharp teeth (Fig. 78) . . . . *Clogmia* Enderlein
– Hypostoma with 1 large, sharp median tooth and 2 short, blunt lateral teeth, with a deep notch basally to median tooth, so hypostoma appears very narrow in centre (Fig. 76) . . . . *Setomima* Enderlein
17. Head capsule with number of lateral spines (Fig. 73); prothoracic spiracles elongate; hypostoma with teeth blunt. . . . . *Paramormia* Enderlein
– Head capsule without lateral spines; prothoracic spiracles short; hypostoma with well-developed teeth 18
18. Terminal complex with numerous tiny lateral setae, usually with 4 pairs of dorsal and 4 pairs of lateral accessory setae and usually 4 longitudinal rows of knobs (Fig. 86); head wider than long . . . . *Vaillantodes* Wagner
– Terminal complex without tiny lateral setae, other than 4 pairs of dorsal and lateral accessory setae; head longer than wide (Fig. 71) . . . . *Panimerus* Eaton

Synopsis of the fauna

***Abcharis* Tkoč & Ježek** (Psychodinae)**.** A genus of 18 described species occurring in the Afrotropical, Australasian and Oriental Regions. Although the centre of diversity is the Oriental Region, the type species, *A. insignis* (Eaton, 1913), was described from Seychelles and an undescribed species is known from Uganda (G.M. Kvifte, pers. obs.). In most published literature this genus is referred to as *Notiocharis* Eaton, but Tkoč & Ježek (2013) point out that this name is unavailable. Adults occur mainly in moist forests and mangrove swamps, but the biology and immature stages remain unknown. No keys relevant to the Afrotropical Region are available.

***Brunettia* Annandale** (Psychodinae)**.** A genus of more than 110 described species occurring in the Afrotropical, Australasian, Neotropical, Oriental and Palaearctic Regions. Three species are recorded from the Afrotropics, but their taxonomy is unresolved. According to Duckhouse (1991) and Bravo (2006), all three species appear to belong to the subgenus *Brunettia sensu stricto* (contrary to the statement in Wagner & Andersen (2007)). Larvae of this subgenus remain unknown and the larval characters provided in the above key are based on two different subgenera of the closely related genus or subgenus *Atrichobrunettia* Satchell, based on Vaillant & Withers (1990) and Duckhouse (1994). These known larvae are semi-aquatic, having been found in waterlogged calcareous tufas and in leaf litter in the outer marginal zone of a rainforest stream. Duckhouse (1978) provided a key to two of the three described Afrotropical species.

***Clogmia* Enderlein** (Psychodinae)**.** A genus of *ca* 30 described species occurring in all zoogeographical regions, except Antarctica. The genus is in need of revision, but six species occur in the Afrotropics, described from Cabo Verde, Madagascar, Malawi, Sierra Leone and South Africa (Kvifte 2012). The type species and probably most commonly encountered species, *C. albipunctata*, is a widespread synanthropic moth-fly, occurring commonly in bathrooms and kitchens in tropical, subtropical and warm-temperate climates throughout the world, including most Afrotropical countries. It was considered as an invasive alien species in South Africa by Kirk-Spriggs (2011: 132), but as its geographical origin is not known, it may well be native to the Afrotropical Region. The larva is described in detail by Vaillant (1971: 2). The majority of species develop in water-filled tree-holes and other phytotelmata (Duckhouse 1978). Keys to species are not available.

***Clytocerus* Eaton** (Psychodinae)**.** A genus of 38 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions (Curler & Moulton 2012*a*), with 15 species recorded from the Afrotropics. The genus is divided into two subgenera: *Clytocerus sensu stricto* and C. (*Boreoclytocerus* Duckhouse). The former appears to be endemic to the Afrotropics and the latter restricted to the Holarctic Realm. Larvae are known for some Palaearctic species of *C.* (*Boreoclytocerus*), which Vaillant (1983*a*: 345) notes as saprophytic in running waters, or as dendrolimnobionts. Most Afrotropical species can be determined using the identification key provided by Duckhouse (1975).

***Demeillonius* Davidson** (Phlebotominae)**.** An endemic monotypic genus, with the single described species, *D. transvaalensis* (Sinton, 1933), recorded from South Africa (Davidson 1980). *Demeillonius* was originally described as a subgenus of *Sergentomyia*. Biology and immature stages remain unknown.

***Elsahowia* Duckhouse** (Psychodinae)**.** An endemic Afrotropical genus of five described species, recorded from Madagascar, Malawi, South Africa and Tanzania. The biology and immature stages remain unknown (Duckhouse 1978). A key to species was provided by Duckhouse (1978).

***Eutonnoiria* Alexander** (Bruchomyiinae)**.** An endemic monotypic genus, with the single species, *E. edwardsi* (Tonnoir, 1939) described from three specimens collected on a dead tree in the Ruwenzori Mountains of Uganda (Tonnoir 1939: 38). Biology and immature stages remain unknown.

***Gondwanoscurus* Ježek** (Psychodinae)**.** A genus of eight described species occurring mainly in the Oriental Region. A single species, *G. socotrensis* Ježek & Tkoč, 2012, is recorded from Socotra Is. (Yemen), close to the Horn of Africa (Ježek & Tkoč 2012); and an additional undescribed species is known from Tanzania (G.M. Kvifte, pers.obs.). Biology and immature stages remain unknown.

***Grassomyia* Theodor** (Phlebotominae)**.** A genus of six described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Five species are recorded from the Afrotropics, and can be identified using Abonnenc (1972). One Afrotropical species also occurs in the Mediterranean province and Middle East and an additional species is recorded from the Oriental Region. Adults feed on reptilian and amphibian blood (Abonnenc 1972). Immature stages remain unknown.

***Iranotelmatoscopus* Ježek** (Psychodinae)**.** A genus of three described species occurring in the Afrotropical and Palaearctic Regions. The single Afrotropical species, *I. hajiabadi* Ježek, 1987, described from Iran, has subsequently been recorded from *wadis* (ephemeral desert streams) in United Arab Emirates in the Arabian Peninsula (Ježek & van Harten 2009: 697). The other two known species of the genus occur in North Africa and southern Europe. Biology and immature stages remain unknown.

***Mormia* Enderlein** (Psychodinae)**.** A large genus of about 75 described species occurring in the Afrotropical, Nearctic, Palaearctic and possibly the Oriental Region. Six species are recorded from the Afrotropics, in the subgenera *M.* (*Hemimormia* Krek) and *M.* (*Limomormia* Vaillant) (treated as full genera by Kvifte 2012). Larvae are semi-terrestrial and occur in moist soils and mud (Vaillant 1974: 133). The Afrotropical species were reviewed and keyed by Duckhouse (1978), but this work must be regarded as incomplete, as half of the known species have been described after its publication.

***Mormopericomiella* Ježek & van Harten** (Psychodinae)**.** An endemic monotypic genus, with *M. yemenensis* Ježek & van Harten, 2002 recorded from United Arab Emirates and Yemen in the Arabian Peninsula, where it occurs in *wadis* (ephemeral desert streams). In addition, Kvifte (2012) placed *Telmatoscopus pilosternatus* Satchell, 1955, in *Mormopericomiella*, but as pointed out by Tkoč & Ježek (2013), this species possibly belongs in a different, undescribed genus.

***Mystropsychoda* Duckhouse** (Psychodinae)**.** An endemic genus of four described species, most of which appear to be widespread in the Afrotropics (Wagner & Andersen 2007:

290). Some species have been shown to occur in streams (Duckhouse 1987). Larvae remain unknown, but the pupa was described by Tonnoir (1922) from a stony stream bed. Most species can be identified using Duckhouse (1975).

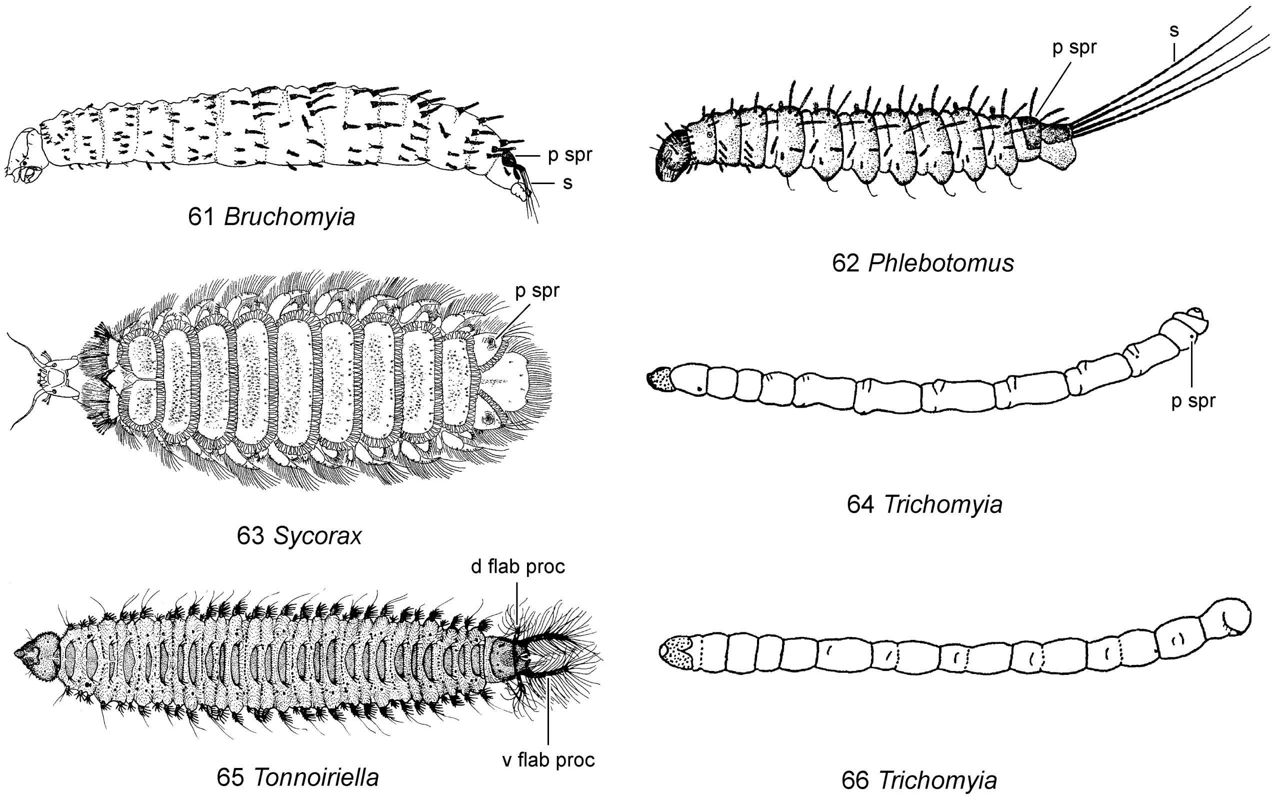
Nemopalpus **Macquart** (Bruchomyiinae)**.** A genus of nine described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Species described from the Australasian, Nearctic and Neotropical Regions belong to different genera. Five species are recorded from the Afrotropics, all from Namibia and South Africa. Disjunctions between the Canary Islands and southern Africa were discussed by Kirk-Spriggs & McGregor (2009). The South African species are associated with forests and the Namibian species with the abodes of rock hyraxes, *Procavia capensis* (Pallas) (Procaviidae) (Stuckenberg 1978). Stuckenberg (1962) provides a key to the South African species.

Neoarisemus **Botoşaneanu & Vaillant** (Psychodinae)**.** A genus of 26 described species occurring in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions. Eighteen species have been described from the Afrotropics, most of which can be identified using the key in Duckhouse (1978). Larvae mainly occur in stream habitats and Duckhouse (1978, 1987) described the larva of *N. prodiguosus* Duckhouse, 1978.

Neomaruina **Vaillant** (Psychodinae)**.** An endemic genus of five species described from mountain ranges in Malawi, Tanzania and Uganda. Larvae were described by Vaillant (1963: 333) and Duckhouse (1985) and appear to occur both semi-aquatically in water films, or fully aquatic, submerged in rapidly-flowing streams. The pupa was described by Duckhouse (1985), who also provided a key to most of the known species.

Neotelmatoscopus **Tonnoir** (Psychodinae)**.** A genus of 13 described species occurring in the Oriental Region. The genus is not formally recorded from the Afrotropics, but an undescribed species was mentioned by Kvifte (2011). The larvae are adapted to water films and the splash zones of fast-flowing streams and all life stages are treated by Curler & Courtney (2009).

Panimerus **Eaton** (Psychodinae)**.** A genus of *ca* 15 described species occurring in the Afrotropical and Palaearctic Regions. The only Afrotropical species that can be reliably attributed to the genus is *P. sarai* (Salamanna, 1975), recorded from Yemen in the Arabian Peninsula and the south-western Palaearctic (Ježek & van Harten 2002). In addition, a similar undescribed species is known from Uganda (G.M. Kvifte, pers. obs.). The larvae of several western Palaearctic species have been



61 *Bruchomyia*

62 *Phlebotomus*

63 *Sycorax*

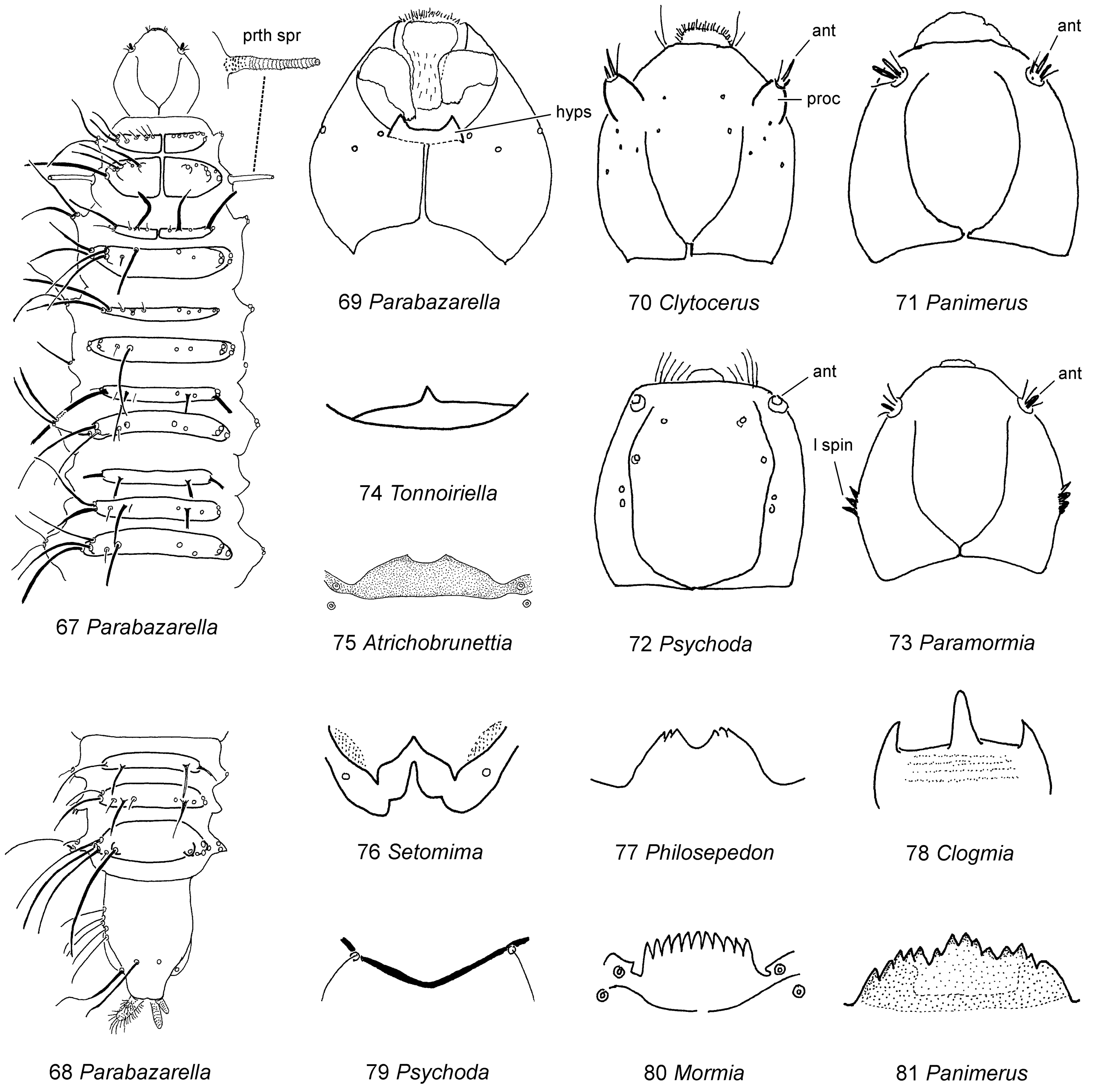
64 *Trichomyia*

65 *Tonnoiriella*

66 *Trichomyia*

Figs 24.61–66. Larval habitus of Psychodidae: (61) *Bruchomyia* sp., lateral view (non-Afrotropical); (62) *Phlebotomus* sp., dorsolateral view (non-Afrotropical); (63) *Sycorax* sp., dorsal view (non-Afrotropical); (64) *Trichomyia* sp., lateral view (non-Afrotropical); (65) *Tonnoiriella* sp., dorsal view (non-Afrotropical); (66) *Trichomyia* sp., ventral view. Fig. 61 (Jung 1958*a*, fig. 15), Fig. 62 (Theodor 1958, fig. 14), Figs 63, 64, 66 (Jung 1958*b*, figs 34, 73, 74).

Abbreiations: d flab proc – dorsal flabellar process; p spr – posterior spiracle; s – seta; v flab proc – ventral flabellar process.



67 *Parabazarella*

69 *Parabazarella*

70 *Clytocerus*

71 *Panimerus*

74 *Tonnoiriella*

75 *Atrichobrunettia*

72 *Psychoda*

73 *Paramormia*

68 *Parabazarella*

76 *Setomima*

77 *Philosepedon*

78 *Clogmia*

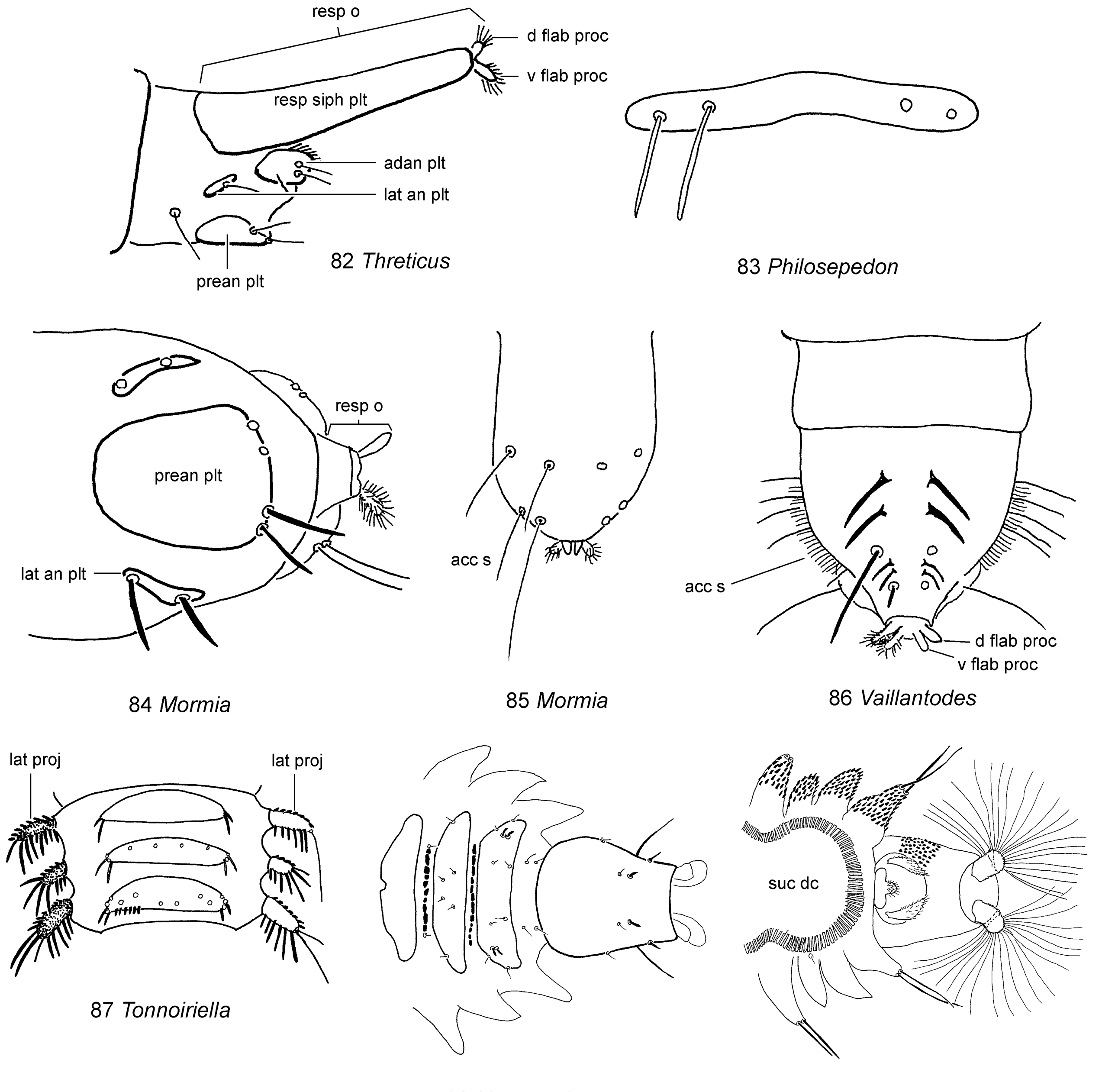
79 *Psychoda*

80 *Mormia*

81 *Panimerus*

Figs 24.67–81. Larval features of Psychodidae: (67) head, thorax and abdominal segments 1 and 2 of *Parabazarella* sp., dorsal view (non-Afrotropical); (68) same, abdominal segment 7 and terminal complex, dorsal view; (69) same, head, ventral view; (70) head capsule of *Clytocerus* sp., dorsal view (non-Afrotropical); (71) same, *Panimerus* sp. (non-Afrotropical); (72) same, *Psychoda* sp. (non-Afrotropical); (73) same, *Paramormia* sp. (non-Afrotropical); (74) hypostoma of *Tonnoiriella pulchra* (Eaton), ventral view (non-Afrotropical); (75) same, *Atrichobrunettia angustipennis* (Tonnoir) (non-Afrotropical); (76) same, *Setomima nitida* (Banks) (non-Afrotropical); (77) same, *Philosepedon* sp. (non-Afrotropical); (78) same, *Clogmia albipunctata* (Williston); (79) same, *Psychoda* sp. (non-Afrotropical); (80) same, *Mormia bryophila* Vaillant (non-Afrotropical); (81) same, *Panimerus* sp. (non-Afrotropical). Figs 70–73, 78, 81 (Vaillant 1971, figs 167, 168, 5, 3, 86, 6, respectively), Fig. 75 (Vaillant & Withers 1990, fig. 14), Figs 76, 80 (Vaillant 1975, figs 379, 16, respectively), Fig. 77 (Vaillant 1974, fig. 255).

Abbreviations: ant – antenna; hyps – hypostoma; l spin – lateral spinule; proc – process; prth spr – prothoracic spiracle.



82 *Threticus*

83 *Philosepedon*

84 *Mormia*

85 *Mormia*

86 *Vaillantodes*

87 *Tonnoiriella*

88 *Neomaruina*

89 *Neomaruina*

Figs 24.82–89. Larval features of Psychodidae: (82) terminal complex of *Threticus* sp., lateral view (non-Afrotropical); (83) preanal plate of *Philosepedon* sp., ventral view (non-Afrotropical); (84) terminal complex of *Mormia* sp., ventral view (siphon not developed) (non-Afrotropical); (85) same, *Mormia* sp., dorsal view (non-Afrotropical); (86) same, *Vaillantodes occidentalis* (Wagner) (non-Afrotropical); (87) abdominal segment 4 of *Tonnoiriella pulchra*, dorsal view (non-Afrotropical); (88) abdominal segment 7 and terminal complex of *Neomaruina* sp., dorsal view; (89) same, ventral view. Figs 82, 83 (Vaillant 1971, figs 6, 2, respectively), Fig. 86 (Vaillant 1974, fig. 6).

Abbreviations: acc s – accessory seta; ada plt – adanal plate; d flab proc – dorsal flabellar process; lat an plt – lateroanal plate; lat proj – lateral projection; prea plt – preanal plate; resp o – respiratory organ; resp siph plt – respiratory siphon plate; suc disc – suction disc; v flab proc – ventral flabellar process.

described and known larvae occur at the margins of springs and slow-flowing waters or in mud in swamps (Vaillant 1972*a*: 64).

***Paramormia* Enderlein** (Psychodinae)**.** A genus of uncertain circumscription, with *ca* 15 species described from the Palaearctic, Nearctic, Neotropical and Oriental Regions. A single species, *P. fluviatilis* Ježek, 2004, is known from the Afrotropical Region, described from Madagascar (Ježek 2004). Larvae from elsewhere occur at the margins of stagnant and slow-flowing waters, with some species having very broad habitat tolerances (Vaillant 1972*a*: 55).

***Parvidens* Theodor & Mesghali** (Phlebotominae)**.** A genus of four described species occurring in the Afrotropical and Palaearctic Regions. Three rare species are recorded from the Afrotropics, from Ethiopia, Kenya, Mauritania, Namibia and Sudan. They feed on mammalian and reptilian blood and are occasionally sampled locally in large numbers (Quate 1964). It is unknown, however, whether they are instrumental in the transmission of *Leishmania* (Léger *et al*. 2008). Afrotropical species can be identified by reference to Abonnenc (1972) and Davidson (1982).

***Perithreticus* Vaillant** (Psychodinae)**.** A genus of two described species occurring in the Afrotropical and Nearctic Regions. One Afrotropical species, *P. anderseni* Kvifte, 2015 was described from Tanzania by Kvifte (2015*b*). Biology and immature stages remain unknown.

***Philosepedon* Eaton** (Psychodinae)**.** A genus of uncertain circumscription with *ca* 90 described species occurring in all zoogeographical regions, except Antarctica. Six Afrotropical species were attributed to *Philosepedon* by Kvifte (2012), but affinities of these species are not fully established and they may not necessarily be closely related to the Palaearctic species complex that the type species belongs to. Omelková & Ježek (2012) listed three Afrotropical species in their treatment of the world fauna, which is followed here and in the above identification key, although it is likely that the true phylogenetic relationships of at least some of these species lie elsewhere (Kvifte 2015*b*). *Philosepedon sensu stricto* are viviparous and larvae are deposited directly onto the dead snails on which they feed. It remains unclear whether Afrotropical species share the same biology. No identification keys are available covering the Afrotropical fauna.

***Phlebotomus* Rondani & Berte *in* Rondani** (Phlebotominae)**.** A genus of *ca* 140 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions, with *ca* 30 species recorded from the Afrotropics, including several of the most common synanthropes. Afrotropical species are classified in the subgenera *P.* (*Adlerius* Nitzulescu), *P.* (*Anaphlebotomus* Theodor), *P.* (*Larroussius* Nitzulescu), *P.* (*Legeromyia* Rahola, Depaquit, Makanga & Paupy), *P.* (*Paraphlebotomus* Theodor), *Phlebotomus sensu stricto* and *P.* (*Synphlebotomus* Theodor) (Rahola *et al.* 2013). Most can be identified using Lewis (1982). *Phlebotomus* females feed primarily on mammalian blood and include the most important *Leishmania* vectors in the Old World.

***Potophila* Kvifte** (Psychodinae)**.** An endemic monotypic genus, with the single species, *P. verrucosa* Kvifte, 2014, described from the Usambara Mountains (Eastern Arc Mountains) of Tanzania. Biology and immature stages remain unknown (Kvifte 2014*a*).

***Promormia* Ježek** (Psychodinae). A genus comprising two described species occurring in the Palaearctic Region (Ježek 1994; Kvifte 2012). Kvifte (2012) suggested that no described Afrotropical species fit within the diagnosis of *Promormia* as provided by Ježek (1984), but an undescribed species from Uganda has later been found to correspond closely in morphology to the Palaearctic species of the genus (G.M. Kvifte, pers. obs.). Biology and immature stages remain unknown.

***Psychoda* Latreille** (Psychodinae)**.** A highly diverse and heterogeneous genus of more than 400 described species, occurring in all zoogeographical regions, including some Antarctic islands. Fifty species have been recorded from the Afrotropics. Usually the most commonly encountered genus in collections, both in terms of number of species and of individuals (Kvifte 2011; Satchell 1955). The majority of *Psychoda* spp. are terrestrial to semi-terrestrial as larvae, varying from extreme generalists to specialists on, *e.g.*, dung or fungal fruiting bodies (Satchell 1947; Svensson 2009; Withers 1988). The last identification key to Afrotropical species was published by Satchell (1955), but this must be used with care as undescribed species are commonly encountered.

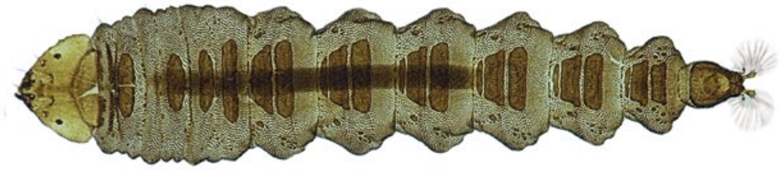
***Psychomasina* Ježek** (Psychodinae)**.** An endemic genus with three described species confined to Kenya and Madagascar (Ježek 2004; Kvifte 2015*a*). A key to species was provided by Kvifte (2015*a*). Biology and immature stages remain unknown.

***Rhipidopsychoda* Vaillant** (Psychodinae)**.** A genus of three described species occurring in the Afrotropical and Oriental Regions. Two Afrotropical species, *R. nana* (Tonnoir, 1922) and *R. boettgeri* (Wagner, 1979), have been described, recorded from Democratic Republic of Congo. Their larvae are unknown, but *R. boettgeri* has been reared from a mountain stream (Wagner 1979). An identification key to species was provided by Kvifte (2015*b*).

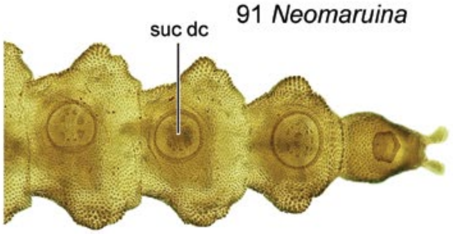
***Sergentomyia* França & Parrot** (Phlebotominae)**.** The most widespread and diverse genus of Phlebotominae in the Afrotropics, with over 90 described species from all over the continent. It otherwise occurs in the Oriental and Palaearctic Regions. *Sergentomyia* is divided into the following subgenera: *S.* (*Capensomyia* Davidson), *S.* (*Parrotomyia* Theodor), *S.* (*Rondanomyia* Theodor), *Sergentomyia sensu stricto*, *S.* (*Sintonius* Nitzulescu), *S.* (*Trouilletomyia* Randrianambinintsoa, Léger, Robert & Depaquit) and *S.* (*Vattieromyia* Depaquit, Léger, & Robert) (Depaquit *et al*. 2008; Randrianambinintsoa *et al.* 2014). In much of the literature, *Demeillonius* Davidson, *Grassomyia* Theodor, *Parvidens* Theodor & Mesghali and *Spelaeomyia* Theodor are also considered subgenera of *Sergentomyia*. Their separation, as applied here, follows Rispail & Léger (1998) and Depaquit *et al*. (2008). Adults of *Sergentomyia* have traditionally been considered to largely feed on reptilian blood, but recent DNA screenings of blood meals has revealed that they are also able to feed on mammalian blood, including that of humans (*e.g.*, Anjili *et al*. 2011; Mutinga *et al*. 1994). Some species may possibly be minor vectors of *Leishmania* (Mutinga *et al*. 1994). Most of the species can be identified using Abonnenc (1972).

90 *Neomaruina*

91 *Neomaruina*



92 *Neotelmatoscopus*

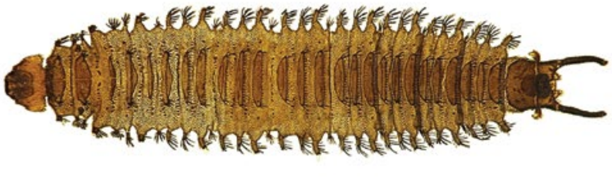


93 *Neotelmatoscopus*

94 *Clytocerus*

95 *Peripsychoda*

96 *Sycorax*



97 *Tonnoiriella*

98 *Psychoda*

Figs 24.90–98. Larval habitus and features of Psychodidae: (90) larval habitus of *Neomaruina* sp. dorsal view; (91) same, abdominal segments 5–7 and terminal complex, ventral view; (92) larval habitus of *Neotelmatoscopus* sp., dorsal view (non-Afrotropical); (93) same, abdominal segments 5–7 and terminal complex, ventral view (indicating suction discs) (non-Afrotropical); (94) larval habitus of *Clytocerus* sp., lateral view (non-Afrotropical); (95) same, *Peripsychoda* sp., dorsal view (non-Afrotropical); (96) same, *Sycorax* sp. (exuvia) (non-Afrotropical); (97) same, *Tonnoiriella* sp. (non-Afrotropical); (98) same, *Psychoda sigma* Kincaid, dorsolateral view. Fig. 98 (photograph C. Matthieu – UMR CNRS 502).

Abbeviation: suc disc – suction disc.

***Setomima* Enderlein** (Psychodinae)**.** A genus of 14 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Ten species are described from the Afrotropics, identifiable using Duckhouse (1987). The only known larva is that of the Nearctic species, *S. nitida* (Banks, 1894), which has been reared from oak tree-holes and from liquid chicken guano (Quate 1955; Vaillant 1975: 164).

***Soeliella* Kvifte** (Psychodinae)**.** An endemic monotypic genus, with *S. platypenis* Kvifte, 2015 described from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania. Biology and immature stages remain unknown (Kvifte 2015*b*).

***Spelaeomyia* Theodor** (Phlebotominae)**.** A genus of 11 described species occurring in the Afrotropical and Oriental Regions. Five species have been described from the Afrotropics, all of which are cavernicolous (Abonnenc 1972). *Spelaeomyia darlingi* Lewis & Kirk, 1954 has also been recorded as a locally abundant species in some villages in Mali (Berdjane-Brouk *et al*. 2012). The feeding habits of *S. mirabilis* Parrot & Wanson, 1939, were studied by Vattier-Bernard (1971), who found adults to feed exclusively on the blood of bats, but human DNA has been detected in the blood meals of *S. darlingi* (Berdjane-Brouk *et al*. 2012). Since the latter species is also known as a host of *Leishmania*, it may be instrumental in disease transmission (Berdjane-Brouk *et al*. 2012). For identification see Abonnenc (1972).

***Spelaeophlebotomus* Theodor** (Phlebotominae). An endemic genus, with two described species, *S. gigas* (Parrot & Schwetz, 1937), and *S. minteri* (Lewis, 1982). Both appear to be strictly cavernicolous, with *S. gigas* being widespread in West Africa (Abonnenc 1972; Lewis 1982; Vattier-Bernard & Trouillet 1984) and *S. minteri* recorded from a single cave in Tanzania (Lewis 1982). In feeding experiments, *S. gigas* was shown to feed on a wide range of mammalian hosts, including bats, porcupines, mice and man (Vattier-Bernard 1971). The two species can be separated using Lewis (1982).

***Sycorax* Haliday *in* Curtis** (Sycoracinae)**.** A genus with 41 described species occurring in all zoogeographical regions, except the Nearctic Region and Antarctica (Curler & Jacobson 2012). Four species are described from the Afrotropics, but no recent revision is available. The genus is mainly aquatic in the larval stages and some adults are known to feed on amphibian (frog and toad) blood (Wagner 1997: 134).

***Telmatoscopus auctt., nec* Eaton** (Psychodinae)**.** The Afrotropical species listed by Kvifte (2012) as included in this genus are unlikely to be closely related to the type species of the genus, *T. advena* (Eaton, 1893) and probably form a paraphyletic assemblage of superficially similar species. For a detailed discussion of the nomenclatural history of the genus, see Kvifte (2014*b*). A revision of the Afrotropical fauna is urgently required.

***Threticus* Eaton** (Psychodinae)**.** A genus of 21 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Some species in the Australasian and Oriental Regions have also been attributed to this genus, but are in need of revision and may belong in different genera. Four species have been described from the Afrotropics, recorded from Ghana, Kenya, South Africa and Tanzania. In the Holarctic species, larvae are associated with leaf litter in springs and streams (Curler & Moulton 2010; Vaillant 1972*b*: 100). Afrotropical species have not been revised and no keys are available.

***Tonnoiriella* Vaillant** (Psychodinae)**.** A genus of 22 described species occurring in the Afrotropical and Palaearctic Regions. Four species have been described from the Afrotropics, recorded from the Democratic Republic of Congo, South Africa and Tanzania. The larva of one Palaearctic species, *T. pulchra* (Eaton, 1893), has been described, occurring in water films on the underside of stones and leaves at the margins of streams and springs (Satchell 1949). Afrotropical species often occur in large numbers near small aquatic habitats and Wagner (1979) recorded almost 50 specimens of *T. drepanopenis* (Duckhouse, 1975) from a mountain stream in Democratic Republic of Congo. Keys to species are not currently available.

***Trichomyia* Haliday *in* Curtis** (Trichomyiinae)**.** A genus of more than 150 described species occurring in all zoogeographical regions, except Antarctica. Only five species have been described from the Afrotropics, but the genus is commonly collected and many species await description. All known larvae bore in rotting wood (Duckhouse 1978). The fauna is in need of revision both globally and locally and no indentification key covers the Afrotropical Region.

***Trichopsychoda* Tonnoir** (Psychodinae). A genus of 22 described species occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. A single species, *T. africana* Satchell, 1955, is recorded from Democratic Republic of Congo and South Africa in the Afrotropics. The only species for which the larva is known is the Palearctic *T. hirtella* (Tonnoir, 1919), which is terrestrial and occurs in decaying vegetable matter and fruit (Vaillant 1974: 129).

***Vaillantodes* Wagner** (Psychodinae)**.** A genus of eight described species occurring in the Afrotropical and Palaearctic Regions. A single species, *V. ypsilon* Wagner & Andersen, 2007 was described from Tanzania in the Afrotropics. The larva of *V. occidentalis* (Wagner, 1987) was described by Vaillant (1972*b*: 79), under the name *Panimerus fraudulentus* (Eaton, 1896). The larva was found in the sandy margin of a slow-flowing stream. Identification keys to species are currently unavailable.

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ANISOPODIDAE 25

(Wood Gnats or Window Gnats)

E. Geoffrey Hancock

Fig. 25.1. Female of *Silvicola* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Adults small- to medium-sized nematoceran flies (body length: 3.0–15.0 mm), with slender body and legs (Figs 1–5).

Head with 3 ocelli; antenna 16-segmented, tapering; flagellomeres cylindrical, elongating slightly towards apex, variegated in colour in Afrotropical *Sylvicola* Harris (Fig. 10); uniformly dark in other genera, apart from white apical flagellomere in *Mesochria* Enderlein; compound eyes in *Sylvicola* dichoptic in females, holoptic in males, *Mesochria* contiguous in females for *ca* 12 facets, males for > 20, *Olbiogaster* Osten-Sacken separate in both sexes; face convex; palpus either 4-segmented (*Mesochria*, *Mycetobia* Meigen), or 5-segmented (*Olbiogaster*, *Sylvicola*); segment 3 with 1 sensory pit (2 in female *Sylvicola*), but due to fusion of the joints these pits appear to be in basal segment in *Mycetobia* and *Mesochria*.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 633–640.

Thorax convex, without distinct transverse suture; scutum and scutellum setulose, with setae weakly-developed; pleural sutures distinct. Wings lie flat over abdomen in resting position (Fig. 1); anal lobe well-developed, alula present in *Olbiogaster* and *Sylvicola* (Figs 8, 9); wing patterns present in *Sylvicola* (Figs 1, 2, 3, 9), pterostigma present in *Olbiogaster* (Figs 4, 8); crossvein *sc–r* absent; membrane densely microtrichose and additionally with macrotrichia in *Sylvicola* (Fig. 9); vein *M* 4-branched, discal cell (*d*) present in *Olbiogaster* and *Sylvicola* (Figs 8, 9), or vein *M* 3-branched, discal cell (*d*)

2 *Sylvicola* ♀

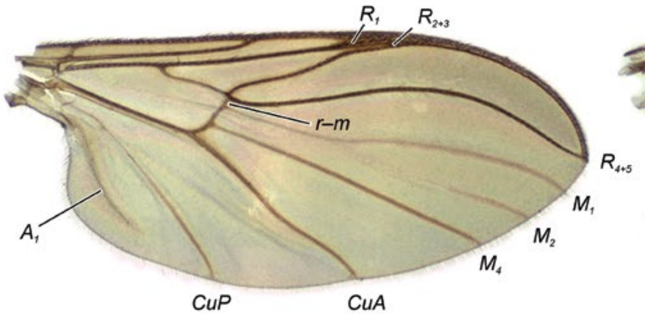
3 *Sylvicola* ♂


4 *Olbiogaster* ♀

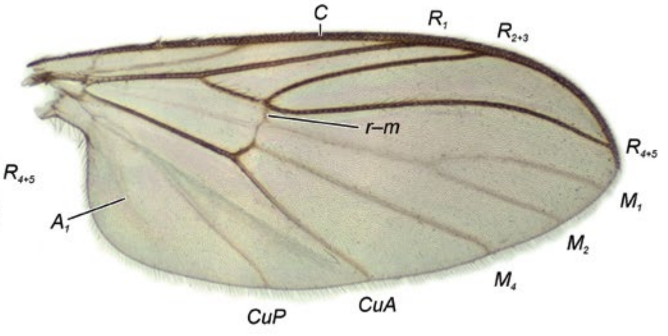
5 *Mesochria* ♂

Figs 25.2–5. Habitus of Anisopodidae (lateral views): (2) *Sylvicola annulicornis* Edwards (Kenya) ♀; (3) same ♂; (4) *Olbiogaster* sp. (Angola) ♀; (5) *Mesochria medicorum* Edwards (Ghana) ♂. Photographs R. Lyszkowski.

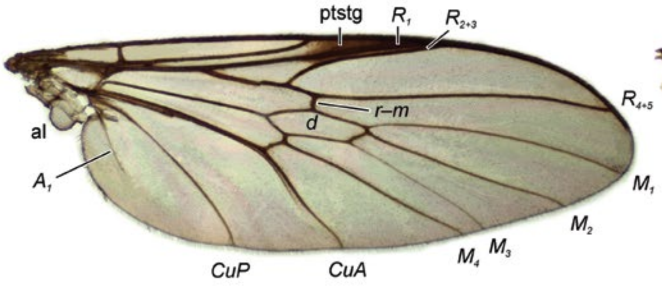
Abbreviation: tsm 1 – tarsomere 1.



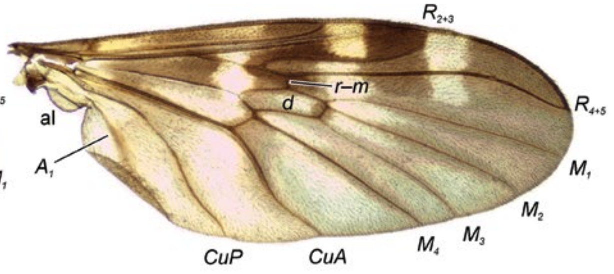
6 *Mesochria*



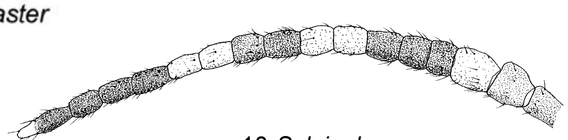
7 *Mycetobia*



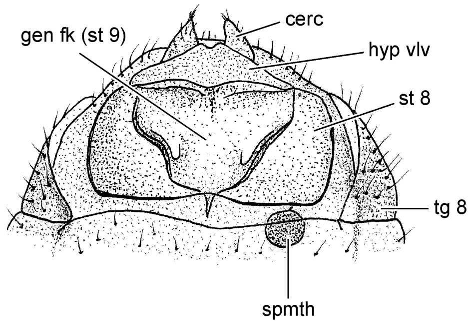
8 *Olbiogaster*



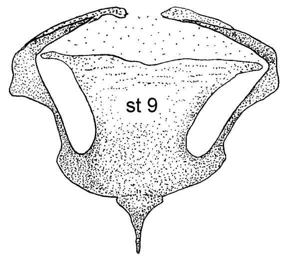
9 *Sylvicola*



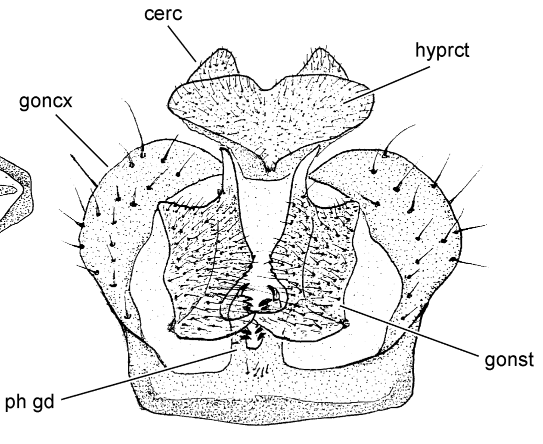
10 *Sylvicola*



11 *Sylvicola* ♀



12 *Sylvicola* ♀



13 *Sylvicola* ♂

Figs 25.6–13. Wings, antenna and male and female terminalia of Anisopodidae: (6) wing of *Mesochria medicorum* Edwards, dorsal view; (7) same, *Mycetobia pallipes* (Meigen) (non-Afrotropical); (8) same, *Olbiogaster* sp. (non-Afrotropical); (9) *Sylvicola annulicornis* (Edwards); (10) antenna of *Sylvicola* sp., lateral view; (11) female terminalia of *Sylvicola* sp., ventral view; (12) same, detail of genital fork (sternite 9), ventral view; (13) male terminalia of *S. annulicornis*, ventral view. Figs 6–9 (photographs A.H. Kirk-Spriggs).

Abbreviations: *A_1* – first branch of anal vein; al – alula; *C* – costal vein; cerc – cercus; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *d* – discal cell; gen fk – genital fork; goncx – gonocoxite; gonst – gonostylus; hyprct – hypoproct; hyp vlv – hypogynial valve; *M_1* – first branch of media; *M_2* – second branch of media; *M_3* – third branch of media; *M_4* – fourth branch of media; ph gd – phallic guide; ptstg – pterostigma; *R_1* – anterior branch of radius; *R_{2+3}* – second branch of radius; *R_{4+5}* – third branch of radius; *r–m* – radial–medial crossvein; spmth – spermatheca; st – sternite; tg – tergite.

absent in *Mesochria* and *Mycetobia* (Figs 6, 7); vein *CuA* slightly sinuous in *Mesochria*, very slightly so in *Mycetobia* (Figs 6, 7), more strongly sinuous in *Olbiogaster* and *Sylvicola* (Fig. 9). Legs without strong spines; fore coxae long; fore tibia usually with 1 apical spur, mid and hind tibiae usually with 2 finely pubescent apical spurs; inner apex of hind tibia with comb of setae, less extensive in *Olbiogaster*; empodium setulose; hind tarsomere 1 swollen in males of Afrotropical *Sylvicola* (Fig. 3).

Abdomen elongate, parallel-sided; male terminalia (Fig. 13) rotated up to 180°, usually visible externally (may be retracted in dried specimens); cercus prominent in *Olbiogaster*, as are lobes of hypoproct; gonostylus usually well-developed, except in *Mesochria* and *Mycetobia*; aedeagus may be complex in conjunction with parameres, ending internally in long coiled structure in *Sylvicola*; female terminalia (Fig. 11) with cercus well-developed, often very large in *Olbiogaster*; 3 spermathecae in *Olbiogaster*, 2 in *Mesochria* and *Mycetobia*, 1 in *Sylvicola* (Fig. 11). One of the principal key characters for distinguishing female species is in the morphology of the genital fork (sternite 9) (Fig. 12).

Due to the lack of a discal cell (*d*) on the wing, *Mesochria* and *Mycetobia* may be confused with some Mycetophilidae (see Chapter 20). The fork of wing veins R_{2+3} and R_{4+5} is situated at, or before, crossvein *r–m* in Anisopodidae, but distal to crossvein *r–m* in Mycetophilidae. Mycetophilidae usually also have very prominent tibial spurs and the head often smaller and tucked, at least slightly, beneath the thorax.

Biology and immature stages

In nature anisopodids have a strong relationship with forests, hence one of their vernacular names "wood gnats". This association is a product of saprophagous larval development in wet, decaying, or fermenting organic matter, of mainly plant origin, although animal carcases, or dung, are sometimes exploited. One temperate species is also known to invade living plants (Hancock 1989). Typical larval substrates include rotting fruits and plant stems, fermenting sap, rot holes, water pockets and other phytotelmata in trees, epiphytic plants and in the ground flora. In the Afrotropics there are rearing records from fruits of species of *Conopharyngea* (Apocynaceae) (Cuthbertson 1939; Freeman 1959), *Solanum* (Solanaceae) (Copeland *et al*. 2009) and, from preserved specimen data labels, the plants *Cossonia* (Brassicaceae), *Culcasia* (Araceae), *Phoenix* (Arecaceae) and *Tabernaemontana* (Apocynaceae) are indicated. The discovery of *Sylvicola* developing in decaying or fallen forest fruits in studies by Copeland *et al*. (2009) was also reported in Australian rainforest habitats by Atkinson (1985), confirming that they share this breeding medium with tephritoids, Drosophilidae and other insects.

In the Afrotropics, *Olbiogaster* larvae are known from rot holes in trees and in other regions have been reared from rotten wood (Edwards 1928; Fuller 1935). *Mycetobia* larvae have been found in tree holes in Europe and are part of the characteristic insect fauna of exudations of tree sap, where *Sylvicola* can also be found. The species *Mesochria medicorum* Edwards, 1928, was described from adults reared from rotting banana fibre in Ghana (Edwards 1928). The known substrates are not exclusive and it is likely that some species from each of the genera may share substrates with those of others.

The alternative vernacular name "window gnats" is derived from their occasional association with buildings, where some species breed in association with organic waste. Adults have been observed feeding on nectar in flowers, but can often be located near the substrate in which oviposition takes place. Males of some species form "dancing", or mating, swarms. Females oviposit close to the substrate in batches of up to 50 eggs suspended within jelly, which protects them from desiccation and possibly predation prior to hatching. Anisopodid larvae writhe like miniature snakes and this serpentine movement can be vigorous if disturbed. Pupae are active and move to a drier zone prior to adult eclosion.

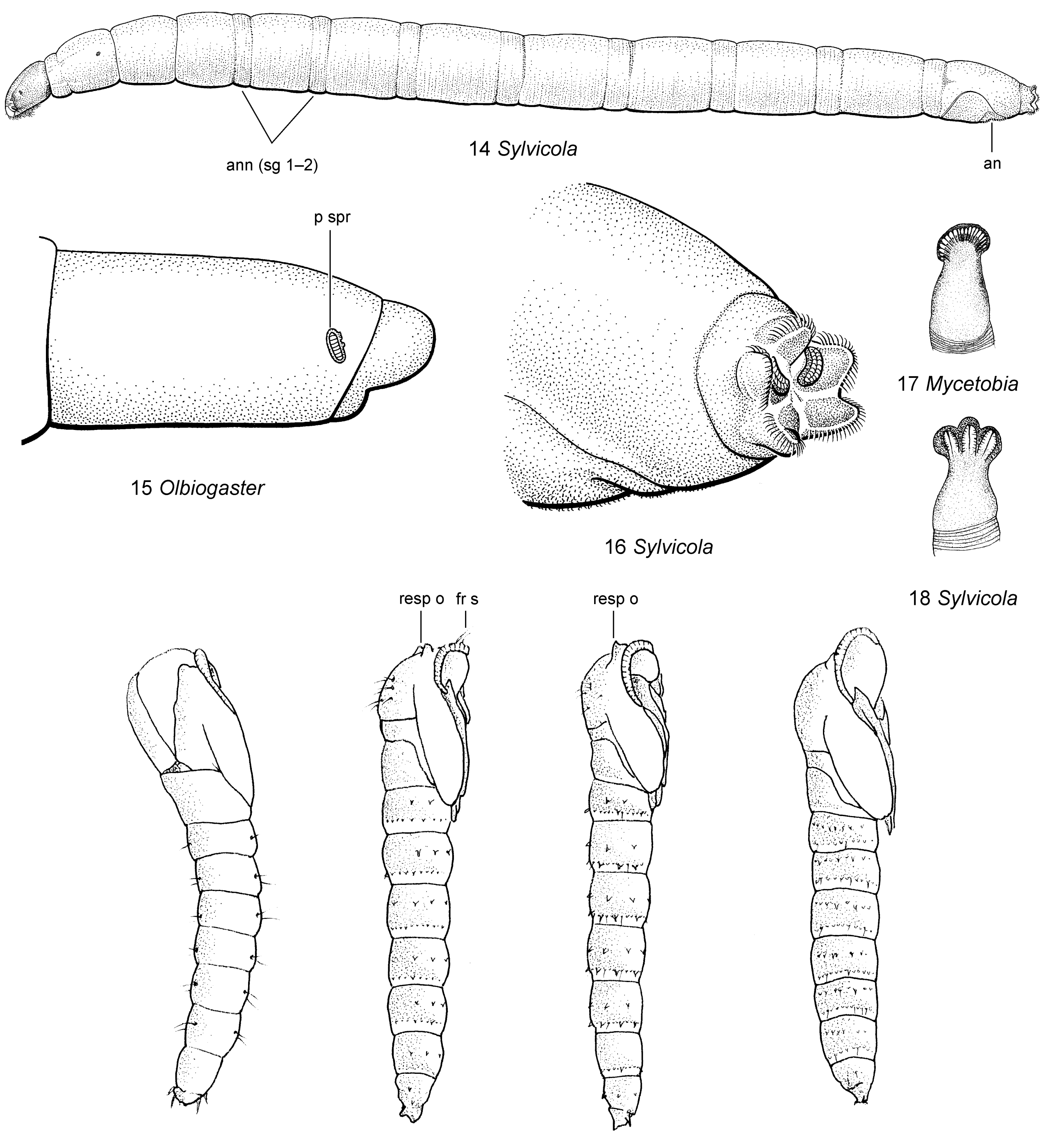
Larvae are amphineustic and in *Mesochria*, *Mycetobia* and *Sylvicola* (Fig. 14), have a unique perianal shield on segment 8, a smooth area of large hypodermal cells surrounding the ventral anus. Species of *Olbiogaster* lack this perianal shield, but share the family characteristic of abdominal segments 1–7 divided into two unequal parts by annular constrictions (Fig. 14). In *Mycetobia* and *Sylvicola* there is a well-defined terminal spiracular field (Fig. 16). *Olbiogaster* larvae lack this; the spiracles lying dorsolaterally and anterior to the anus (Fig. 15). Larvae may be patterned with reddish brown markings on the integument, at least on the thoracic segments in *Sylvicola* and in some *Olbiogaster*; those of *Mycetobia*, that have been reared, are unpigmented. The prothoracic spiracles of *Sylvicola* have 3 large papillae (Fig. 18); mycetobiines usually have more than 15 papillae (Fig. 17).

Olbiogaster pupae (Fig. 19) are also quite different from those of other genera (Figs 20–22). The abdominal segments lack spicules (Fuller 1935; Keilin & Tate 1940), but bear instead lateral spines, one pair on segment 2, two pairs on segments 3–7 (Fig. 19). The other genera have varying combinations of rings of small and larger spicules anteriorly, or posteriorly (Figs 20–22). Detailed descriptions of larval and pupal morphology and anatomy were provided by Keilin & Tate (1940).

The numbers of species yet to be found is potentially higher than currently known. Collecting and rearing larvae from sap runs, rotting fruits and other decaying vegetable matter in forest habitat may reveal additional species and, as in other saprophagous groups, there are often opportunities created in disturbed areas, or secondary forest, for such species to breed. Adults of *Sylvicola* are also frequently sampled in forested areas, using hanging traps baited with fermenting liquids and fruit baits (A.H. Kirk-Spriggs, pers. comm. 2014; see also Pratt & Pratt 1980).

Economic significance

Sylvicola are known from a very wide range of situations, which include animal carcases (Hancock 1990) and myiasis in living vertebrates (Smith & Taylor 1966). The family, therefore, has implications for both forensic science and medical entomology. They can be a component of the fauna of sewage treatment works (Tomlinson 1946) and so contribute to the breakdown of organic waste. Their presence in decaying fruits, vegetables, or fermentation products, is secondary rather than causative.



Figs 25.14–22. Larvae and pupae of Anisopodidae: (14) larval habitus of *Sylvicola punctatus* (F.), lateral view (non-Afrotropical); (15) larval posterior segment of *Olbiogaster africanus* Edwards, lateral view; (16) same, *S. punctatus*, posterolateral view; (17) larval prothoracic spiracle of *Mycetobia* sp., lateral view; (18) same, *Sylvicola* sp.; (19) pupal habitus of *O. africanus*, lateral view; (20) same, *Sylvicola* sp.; (21) same, *Mycetobia* sp.; (22) same, *Mesochria medicorum* Edwards. Figs 14–16 (Peterson 1981, figs 19, 21, 22), Figs 17–22 (after Keilin & Tate 1940, figs 49, 14, 81, 41, 61, 84, respectively).

Abbreviation: an – anus; ann (sg 1–2) – annulus (segments 1–2); fr s – frontal seta; p spr – posterior spiracle; resp o – respiratory organ.

Classification

The family formerly consisted of five genera and nearly 100 species globally, as reviewed by Edwards (1928), but has increased subsequently to six genera and over 120 species. Anisopodidae are monophyletic in the superfamily Anisopodoidea. Edwards (1928) and more recent authors (e.g., Peterson 1981: 310; Thompson & Rogers 1992), refer to the "chequered", or "unsettled" taxonomic and nomenclatural history of the family and constituent genera. Recent phylogenetic analyses of the Diptera including molecular evidence support the placement of Anisopodidae as basal within the Bibionomorpha, summarised in Spangenberg *et al*. (2012). Although there has been unanimity in the monophyly of the Anisopodidae, there have been and are various opinions on ranking within it. The elevation of anisopodid genera to higher taxononomic levels (Amorim & Tozoni, 1994) has not been adopted generally. Recent European literature place *Mesochria* and *Mycetobia* in the separate family Mycetobiidae and the *Mycetobia* split into three genera (Krivosheina 1997; Mamaev 1987). Thompson (2006) pointed out that elevation of genera to higher ranks should be based on the age of their origin, for which there is little supporting evidence in this case. Extensive fossil wing remains of an "anisopodiform" type, used alone to place such finds within the group, are inconclusive in the absence of other preserved remains and several have been removed from the family (Michelsen 1999).

Since the suggested splitting into several families and genera proposed in the analysis by Amorim & Tozoni (1994), which also summarises much of the earlier descriptive literature, little has been published. Michelsen (1999) rejected the morphological characters used to separate *Sylvicola* into two zoogeographical elements, Laurasian and Gondwanan (Amorim & Tozoni 1994) and suggested retention of the single family Anisopodidae. To simplify treatment here, this approach has been adopted in common with Thompson (2006) and Hancock & Amorim (2009: 342). It seems clear, however, that the situation will generate further discussion.

The Anisopodidae are usually divided into two subfamilies: the Anisopodinae (comprising the world genera *Olbiogaster* and *Sylvicola* and the solely Neotropical genera *Carreraia* Corrêa and *Lobogaster* Philippi) and the Mycetobiinae (comprising the world genera *Mesochria* and *Mycetobia*). Adults of the two subfamilies are distinguished on the basis of absence of a discal cell in Mycetobiinae. Mycetobiines also have a three-segmented palpus; this being four-segmented in anisopodines.

Identification

For the family as a whole, Edwards (1928) provided a key to the world genera and species known at that time. An updated generic key by Thompson & Rogers (1992) included currently known genera. Examination of both male and female terminalia is important for distinguishing many species. With shrinkage of dry-preserved males it may be necessary to clear, or soften specimens, in order to manipulate these to see key characters; females require clearing to examine sternite 9 (genital fork, also sometimes referred to as vaginal apodeme). Terminalia have rarely been figured for species occurring beyond the Palaearctic Region. Adult Anisopodidae are best either direct-pinned (for larger specimens), or micro-pinned in the field for later double-mounting (see Chapter 2).

Keys to genera of Afrotropical Anisopodidae

Adults

1. Wing with discal cell (*d*); vein *M* 4-branched (*e.g.*, Figs 8, 9) (ANISOPODINAE) 2

– Wing without discal cell (*d*); vein *M* 3-branched (*e.g.*, Figs 6, 7) (MYCETOBIINAE) 3

2. Wing membrane with macrotrichia (Fig. 9); wing variably patterned, with well-defined markings (Figs 1–3, 9); antennae shorter than head and thorax combined (Figs 1–3) . . . . *Sylvicola* Harris

– Wing membrane without macrotrichia (Fig. 8); wing hyaline, with darkened pterostigma (Figs 4, 8); antennae longer than head and thorax combined (Fig. 4) . . . . *Olbiogaster* Osten-Sacken

3. Wing vein R_{2+3} ending in costa; costal vein (*C*) extending beyond vein R_{4+5}; vein A_1 very faint (Fig. 7) . . . . *Mycetobia* Meigen

– Wing vein R_{2+3} meeting vein R_1 before costa; costal vein (*C*) ending at vein R_{4+5}; vein A_1 well-developed (Fig. 6) . . . . *Mesochria* Enderlein

Larvae

[The larvae of *Mesochria* are unknown.]

1. Anal shield absent; posterior spiracles not terminal (Fig. 15); head capsule heavily sclerotised; antennae prominent . . . . *Olbiogaster* Osten-Sacken

– Anal shield present; posterior spiracles with prominent terminal spiracular field (*e.g.*, Figs 14, 16); head capsule weakly-sclerotised; antennae hidden 2

2. Anal shield asymmetrically divided, with posterior section smaller (Fig. 14); prothoracic spiracle with 3 large papillae (Fig. 18); larval integument with reddish brown pigmented thoracic pattern . . . . *Sylvicola* Harris

– Anal shield divided into approximately equal parts; prothoracic spiracles with numerous small papillae, invariably more than 3, usually *ca* 20 (Fig. 15); larval integument pale, unpigmented . . . . *Mycetobia* Meigen

Pupae

1. Abdominal segments 2–7 bearing distinct setae, but no spicules (Fig. 19) . . . *Olbiogaster* Osten-Sacken

– Abdominal segments 2–7 bearing spicules, but no setae (*e.g.*, Figs 20–22) 2

2. Frontal setulae long (Fig. 20) . . . . *Sylvicola* Harris

– Frontal setulae very short or absent (*e.g.*, Figs 21, 22) 3

3. Abdominal segments with anterior ring consisting of row of larger spicules, with a few smaller ones; respiratory organ conspicuous, extending to at least level of antennal sheath; short frontal setulae sometimes present (Fig. 21) . . . . *Mycetobia* Meigen

– Abdominal segments with both anterior and posterior rings comprising a few larger spicules and many smaller ones; respiratory organ inconspicuous; frontal setulae absent (Fig. 22) . . . . . . *Mesochria* Enderlein

Synopsis of the fauna

The world fauna of Anisopodidae comprises 120 species in six genera. Seventeen species in four genera are described from the Afrotropical Region: *viz*. *Mesochria*, *Mycetobia*, *Olbiogaster* and *Sylvicola*. None of these genera are endemic to the Afrotropical Region.

***Mesochria* Enderlein** (Mycetobiinae)**.** A genus of 11 described species occurring in the Afrotropical, Neotropical and Oriental Regions. Five species are described from the Afrotropical Region. A key to adults of all *Mesochria* species was provided by Thompson (2006), but this does not recognise that the antenna of *M. medicorum* Edwards, 1928, has a white terminal flagellomere and so breaks down at that couplet. This may have been following Stuckenberg (1961), who contrasted Madagascan with continental Afrotropical species, by their white antennal terminal flagellomere. Examination of the types and other preserved specimens of Afrotropical and Malagasy species, indicate that they are not separable on this character, as they all have white apices to their antennae. In practice it appears to be the apical half of the apical segment that is white, not the entire segment, which itself is longer than the previous segments. This can be seen also in some *Sylvicola* species (*e.g.*, Fig. 10) and is a character that may vary within and between different zoogeographical regions. The immature stages of *Mesochria* are known only from a pupal exuvium from rotting banana fibre in Ghana from which the type specimen of *M. medicorum* was reared (Edwards 1928; Keilin & Tate 1940).

***Mycetobia* Meigen** (Mycetobiinae)**.** A genus of 28 described species occurring mainly in the Holarctic Realm. In the Afrotropical Region the genus is only known from an unidentified female from the Ethiopian Highlands. This indicates an overlap between the Palaearctic and the Afrotropical fauna in this area. Immature stages are associated with sap runs and rot holes in the Palaearctic Region (Hancock *et al*. 1996) and from unpublished data from the Neotropics. The only identification key to adult *Mycetobia* available is for the Palaearctic fauna by Mamaev (1987).

***Olbiogaster* Osten-Sacken** (Anisopodinae)**.** A genus of 45 described species, occurring in the Afrotropical, Australasian (4 species), Neotropical (33) and Palaearctic (1) Regions. Seven species are recorded from the Afrotropical Region. The wings of *Olbiogaster* spp. are hyaline, only darkened in the stigmal area (Figs 4, 8), but can be slightly infuscated towards the apex. The inner comb at the apex of the hind tibia of *Olbiogaster* was stated to be absent by Edwards (1928). Although such a comb is clearly visible in Neotropical species, it is also present in Afrotropical species, although smaller and more indistinct. Immature stages are little known, but have been reared in West Africa from a tree rot hole (Edwards 1928) and in Australia from rotten wood (Fuller 1935). There are no published identification keys to Afrotropical species, other than Edwards (1928).

***Sylvicola* Harris** (Anisopodinae)**.** A genus of 70 described species, occurring in all zoogeographical regions, except Antarctica. Only four named species occur in the Afrotropics, described by Edwards (1928), Tollet (1956) and Vanschuytbroek (1965). Reliance mainly on wing pattern and body colouration indicates that cryptic species will be discovered, once male and female terminalia characters are examined from longer series, as has occurred in other zoogeographical regional faunas. *Sylvicola* are unique within the family, in possessing macrotrichia and the known tropical species also have a patterned wing membrane (Figs 1–3, 9). There are a considerable number of Afrotropical specimens of *Sylvicola* in museum collections and many of these have been reared from decaying fruits, often in the context of agricultural or horticultural situations. This is in keeping with their known saprophagous habits and provides one technique to develop in searching for these in various habitats. Seeking immature stages and rearing to adult would probably reveal additional species. Immature stages are generally saprophagous and have been reared from a wide range of both decaying plant and animal matter. In the Afrotropics this has been mainly from decaying fruits. The genus is in need of revision and no modern key to *Sylvicola* adults for the Afrotropics has been published. Edwards (1928) remains the only work, which includes them, based on the total world fauna known at that time.

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SCATOPSIDAE 26

(Minute Black Scavenger Flies or Dung Midges)

Jean-Paul Haenni and Dalton de Souza Amorim

Fig. 26.1. Undetermined sex of *Anapausis* sp. nr. *soluta* (Loew) (non-Afrotropical) (photograph © A. Poledniček).

Diagnosis

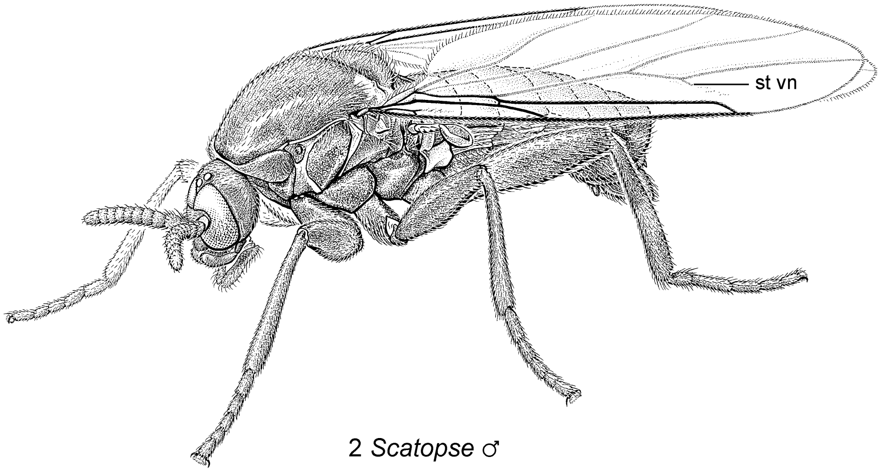
Minute- to small-sized midges (overall length: 0.5–4.0 mm) (Fig. 1), usually black or dark brown in colour, sometimes fulvous or yellow-marked, usually with a somewhat elongated, parallel-sided body. Inconspicuous short pubescence more or less developed on body and legs, microtrichosity widespread in some genera, absent or greatly reduced in others.

Head with antennae (Figs 1, 2, 14) longer than height of head, anteriorly directed, flagellum with 8–10 short flagellomeres (in Afrotropical genera); eyes virtually always holoptic, forming bridge over antennae; 3 ocelli present; palpus 1-segmented (Figs 12, 13).

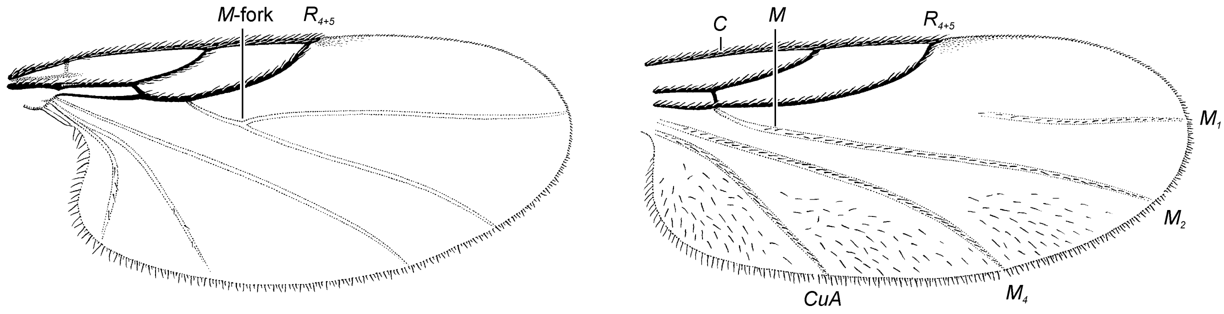
Thorax laterally compressed in most genera (rather quadrate in some Colobostematini); mesonotum usually convex; scutellum simple; anterior spiracle in most genera on separate

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 641–651.

sclerite originally part of the proepimeron (Figs 15, 16); postnotal phragma strongly developed, extending into 1–3 abdominal segments. Legs short and simple in Afrotropical genera; fore coxa often elongate. Wing with characteristic venation (Figs 3–11), only radial veins sclerotised, posterior veins usually hyaline, rarely infuscate; subcostal vein (*Sc*) incomplete; apices of veins R_1 and R_{4+5} joining costal vein (*C*), well separated or close to each other; crossvein *r–m* in most cases very short or absent, due to fusion of vein M_{1+2} to base of vein R_{4+5}, oblique or most often horizontal, continuous with basal part of vein *M*;

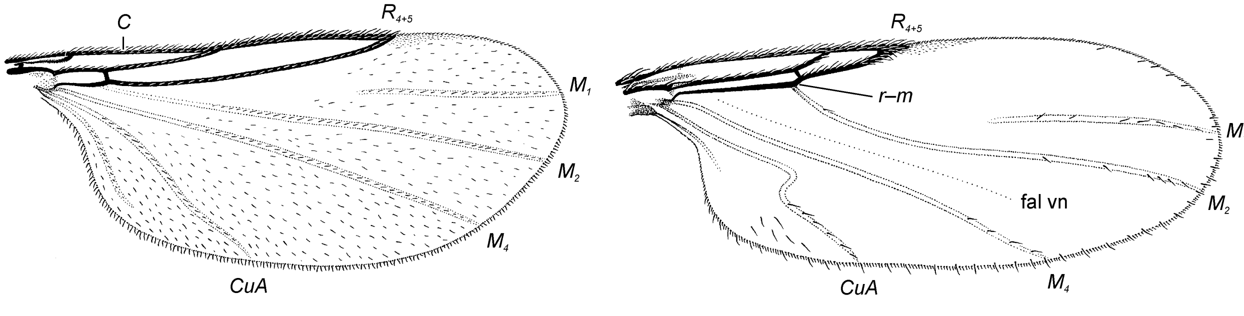


2 *Scatopse* ♂



3 *Ectaetia* ♂

4 *Anapausis* ♀



5 *Psectrosciara* ♀

6 *Thripomorpha* ♀

Figs 26.2–6. Habitus and wings of Scatopsidae: (2) habitus of *Scatopse notata* (L.), dorsolateral view ♂; (3) wing of *Ectaetia* sp., dorsal view (non-Afrotropical); (4) same, *Anapausis soluta* (Loew) (non-Afrotropical); (5) same, *Psectrosciara californica* (Cole) (non-Afrotropical); (6) same, *Thripomorpha truncatum* (Cook) (non-Afrotropical). Figs 2–5 (Cook 1981, figs 1, 4, 5, 10), Fig. 6 (after Cook 1981, fig. 6).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; fal vn – false vein; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; st vn – stump vein.

M-fork usually complete, sometimes base of vein M_1 absent; veins M_4 and *CuA* invariably present, but fork not visible; in most genera base of vein *M* connecting with vein M_4 very close to wing base; macrosetae often present on posterior veins and on wing membrane in some genera; halter with large knob, stem with or without macrosetae.

Abdomen with 7 fully-developed pregenital segments; sternite 1 unsclerotised, in Swammerdamellini genera sternites 2–5 with different degrees of sclerotisation; abdominal pleurites longitudinally ribbed, with modified microtrichia; pregenital segment 7 variously modified; male terminalia often complex, in most genera capsule-like (Fig. 20), with variously and highly modified parts, their transformations obscuring homologies; aedeagus short or long, diversely modified; sperm pump (Fig. 19) well-sclerotised, connected to genital capsule (Aspistinae, Psectrosciarinae, Ectaetiinae), or free from terminalia in abdomen (Scatopsinae); female terminalia (Fig. 21) with tergite and sternite 8 variously modified, bearing pair of usually dorsal spiracles; tergite 10 mesally divided in Scatopsinae ("cercus" of former authors); only 1 well-sclerotised spermatheca present.

Scatopsidae may be confused with some Bibionidae (see Chapter 17) and Simuliidae (see Chapter 32), which possess similarly-shaped antennae, but are easily distinguished from the former by their minute size and from both families by the 1-segmented palpus. Most Sciaridae (see Chapter 21) and Cecidomyiidae: Lestremiinae (see Chapter 22) also possess an eye-bridge above the antennae and in some cases quite similar wing venation, but the shorter antenna, with short flagellomeres and the longitudinally-ribbed abdominal pleural membranes are distinctive to Scatopsidae. One may also confuse Scatopsidae with some Ceratopogonidae (see Chapter 34), but the shape of the antenna and the presence of ocelli allow easy recognition.

Biology and immature stages

Very little is known regarding the life-cycle and biology of the Scatopsidae and virtually nothing has been recorded for the Afrotropical fauna. Larvae (Fig. 22) have a peripneustic respiratory system, with the posterior spiracles dorsal, positioned at the apex of elongate sclerotised processes in Scatopsinae (Fig. 23). The larval mouthparts are adapted to microphagy. The life-cycle is completed within 3–4 weeks in the two widespread synanthropic species *Coboldia fuscipes* (Meigen, 1830) and *Scatopse notata* (L., 1758). All known larvae are saprophagous, developing in a wide variety of substrates, both vegetable and animal and in various types of soil. Decaying vegetable material, especially rotten plants and fruits, are usually preferred. Other locations in which larvae have been found include mushrooms, dung (including hyrax dropping in Namibia, A.H. Kirk-Spriggs, *in litt*.), carrion, tree holes (filled with rotten wood, or with water), decaying bark of dead trees, leaf litter, gravel banks of rivers, salt marshes and wet and marshy soils. Myrmecophily has been observed in Palaearctic representatives of the genera *Colobostema* Enderlein and *Holoplagia* Enderlein (Donisthorpe 1927: 137; Köhler 2011). Pupation takes place within the last instar larval skin. Pupa (Fig. 24) with a pair of dorsal prothoracic horn-like respiratory organs protruding through the ecdysial slit of the larva. A review of our knowledge of the immature stages of the family and their media of development was published by Haenni & Vaillant (1994). For a complete description of the larva and pupa see Haenni (1997).

Imagos are rather inconspicuous midges that can be found in practically all kinds of habitats. Adults of some genera may be quite frequently found feeding on flowers and may act as pollinators. All three known Afrotropical species of *Anapausis* Enderlein have been collected on *Lobelia* (Campanulaceae) and *Senecio* (Asteraceae) flowers, in East African mountain ranges. Mass occurrences are sometimes observed. Alluaud & Jeannel (*in* Edwards 1914, footnote, pp. 58–59, here translated), for example, commented for *Anapausis absoluta* Edwards, 1914 that they "... can be found in incalculable numbers in the *Senecio* and *Lobelia* inflorescences at about 3,000 m elevation. Beating but one inflorescence of *Lobelia* nr 150 […] around camp III would fill our parasols with hundreds of these Diptera". Such populations can sometimes be observed in several scatopsid species, with thousands of midges aggregated on the surface of soil, tree trunks, low vegetation or bushes (Fritz 1984).

Economic significance

Coboldia fuscipes is a virtually cosmopolitan species that has become widespread through human activities all over the world, including the Afrotropical Region. Larvae of this species develop in a wide variety of decaying organic matter, both under anthropogenic or natural conditions. In recent years *C. fuscipes* has been reported as a serious pest in mushroom cultivation in Asia (South Korea and Iran) (Choi *et al*. 2000; Talebi *et al*. 2003). No damage due to this species has, however, been reported from the Afrotropical Region.

Classification

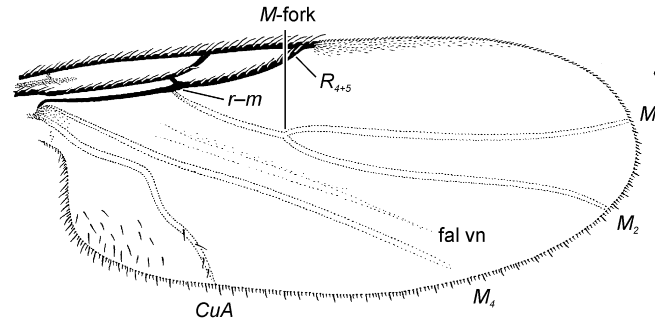
The family Scatopsidae clearly belongs to a monophyletic group, the superfamily Scatopsoidea, together with the non-Afrotropical family Canthyloscelidae (Amorim 2000). More recently, the non-Afrotropical family Valeseguyidae, with a single extant species and some extinct species from Oligocene Dominican (Grimaldi 1991) and Cretaceous Myanmar amber (Amorim & Grimaldi 2006), was transferred in the latter paper from the Anisopodidae (in which it was formerly regarded as a subfamily), to the Scatopsoidea.

About 380 species of Scatopsidae have been described globally in 36 genera and four subfamilies: Aspistinae (two exclusively Holarctic genera), Ectaetiinae (one genus, no Afrotropical representatives), Psectrosciarinae (two genera, present in the Afrotropics) and Scatopsinae (31 genera, at least 15 of which have Afrotropical representatives). The Scatopsinae are divided into four tribes: Colobostematini, Rhegmoclematini, Scatopsini and Swammerdamellini, all of which occur in the Afrotropical Region.

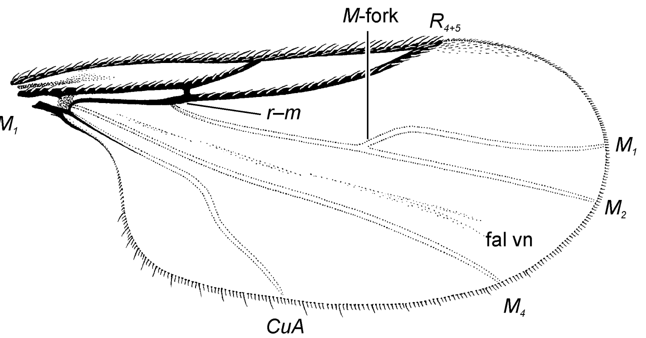
Identification

The Scatopsidae of the Afrotropical Region are still very poorly known, both taxonomically and faunistically. The few published papers consist mainly of haphazard descriptions of species, usually with no identification keys, with the exception of a revision of *Colobostema* spp. (Haenni 1993) and two faunistic papers dealing with the fauna of South Africa (Cook 1965) and Seychelles (Haenni 2009).

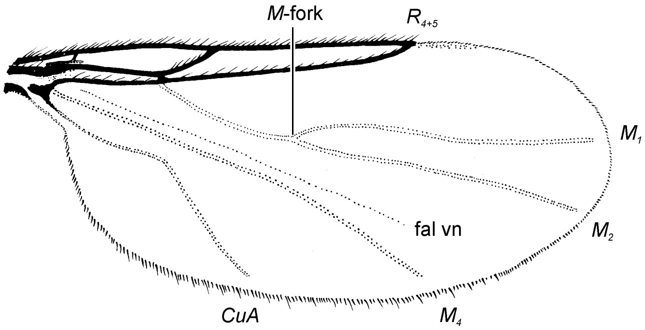
External features of adults, especially wing venation, will allow identification of scatopsids in most cases to the generic level, but the study of terminalia is required for specific identification. Although quite uniform in external habitus, scatopsid species in most genera display an outstanding diversity in terminalia and in the shape and ornamentation of pregenital tergites and sternites in both sexes. Dissection and maceration of the tip of abdomen is required, especially for



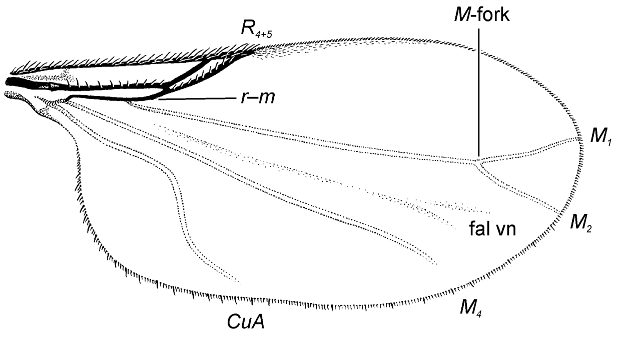
7 *Rhegmoclemina* ♀



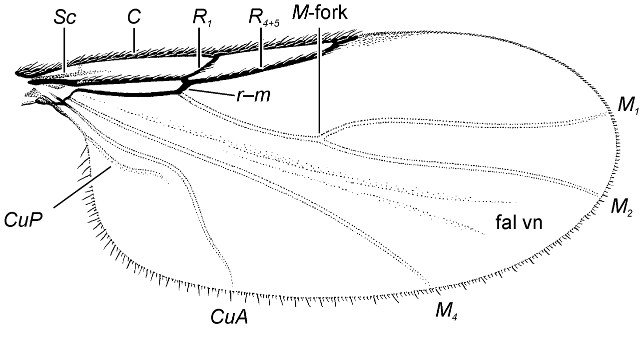
8 *Colobostema* ♀



9 *Octaseps* ♀



10 *Swammerdamella* ♀



11 *Coboldia* ♀

Figs 26.7–11. Wings of Scatopsidae (dorsal views): (7) *Rhegmoclemina bimaculata* (Melander) (non-Afrotropical); (8) *Colobostema variatum* Cook (non-Afrotropical); (9) *Octaseps alata* Haenni & Amorim; (10) *Swammerdamella obtusa* Cook (non-Afrotropical); (11) *Coboldia fuscipes* (Meigen). Figs 7, 8, 10, 11 (Cook 1981, figs 8, 9, 7, 3, respectively), Fig. 9 (Haenni & Amorim 2016, fig. 1).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* –posterior branch of cubital vein; fal vn – false vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *M*-fork – medial vein fork; R_1 – anterior branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

dry preserved material. In Swammerdamellini the preparation and slide-mounting of the entire insect may be necessary. Scatopsids are best preserved directly into alcohol in the field for later observation and preparation of terminalia where necessary. They can alternatively be dry-pinned, either double-mounted using micro-pins, or are point-mounted (see Chapter 2).

The following identification key is based upon the keys to Palaearctic genera provided by Haenni (1997) and for world genera by Amorim (2009). Only genera recorded from the Afrotropical Region are included in the key below, although some genera likely to occur in the Afrotropics are placed in square brackets. These non-Afrotropical genera are not listed in the "Synopsis of the fauna" section below.

Key to genera of Afrotropical Scatopsidae

1. Wing crossvein *r–m* absent; stem of *M*-fork arising from vein R_{4+5} (Fig. 3); hind tibia club-shaped, flattened, strongly swollen in apical ⅓ (ECTAETIINAE). . . . . [*Ectaetia* Enderlein]

– Wing crossvein *r–m* present, even if very short, often oblique or horizontal (*e.g.*, Figs 4–11); stem of *M*-fork arising from just before or below transverse vein (base of R_{4+5}); hind tibia normally developed, at most slightly enlarged apically 2

2. Wing fold (or "false vein") absent between veins M_2 and M_4 (*e.g.*, Figs 4, 5); posterior veins and membrane with macrosetae; *M*-fork incomplete, base of vein M_1 absent; vein *CuA* virtually straight, or only slightly undulated; male terminalia with sperm-pump directly attached to genital capsule (PSECTROSCIARINAE). 3

– Wing fold ("false vein") present between veins M_2 and M_4, sometimes furcate apically (*e.g.*, Figs 6–11); posterior veins and membrane with or without macrosetae; *M*-fork complete, base of vein M_1 usually present (except in *Thripomorpha*, with clearly visible fold between veins M_2 and M_4 and sigmoid vein *CuA*); male terminalia with sperm-pump lying free in abdomen, attached to terminalia only by elongate sperm duct (or endophallus) (SCATOPSINAE). 4

3. Wing vein R_{4+5} long, joining costal vein (*C*) gradually, with smooth, gentle curve (Fig. 5); body elongate, strongly compressed laterally . . . .*Psectrosciara* Kieffer

– Wing vein R_{4+5} shorter, joining costal vein (*C*) rather abruptly, apically with an angle close to 90° (Fig. 4); body neither particularly elongate, nor strongly compressed laterally . . . . *Anapausis* Enderlein

4. Stem of halter devoid of setae; macrosetae present on posterior wing veins and membrane posteriorly in some genera (*e.g.*, Figs 6, 7) (no macrosetae in Afrotropical *Parascatopse* Cook and non-Afrotropical *Diamphidicus* Cook) (RHEGMOCLEMATINI) 5

– Stem of halter with at least a few setae; macrosetae absent on posterior wing veins and membrane (*e.g.*, Figs 8–11) 10

5. Wing vein R_{4+5} long, reaching costal vein (*C*) well beyond mid length of wing; base of vein M_1 complete 6

– Wing vein R_{4+5} shorter, joining costal vein (*C*) in vicinity of mid length of wing, or slightly beyond (*e.g.*, Figs 6, 7); base of vein M_1 complete (*e.g.*, Fig. 7), or incomplete (*e.g.*, Fig. 6) 7

6. Macrosetae present posterior to vein *CuA*; *M*-fork longer than stem . . . . . [*Holoclema* Amorim & Haenni]

– Macrosetae absent on posterior wing veins or membrane; *M*-fork shorter than stem. . . . .[*Diamphidicus* Cook]

7. Wing with *M*-fork incomplete, with base of vein M_1 either lacking for a distance (Fig. 6), or clearly interrupted at extreme base; macrosetae present on veins M_1, M_2, or both . . . .*Thripomorpha* Enderlein (incl. *Rhegmoclema* Enderlein *sensu* Amorim 2009)

– Wing with *M*-fork complete, with base of vein M_1 present, not interrupted; macrosetae absent on veins M_1 and M_2, present only on veins M_4 and *CuA* (*e.g.*, Fig. 7) (entirely absent in known Afrotropical *Parascatopse*). 8

8. Antennal flagellum with 10 flagellomeres; macrosetae absent on wing membrane posterior to vein *CuA* . . . . *Neorhegmoclemina* Cook

– Antennal flagellum with 8 flagellomeres; macrosetae on wing membrane posterior to vein *CuA* either present or absent 9

9. Male abdominal sternite 7 shield-shaped (Fig. 18); at least 1–2 macrosetae present on wing membrane posterior to vein *CuA*; thorax with distinct row of supra-alar setae . . . . *Rhegmoclemina* Enderlein

– Male abdominal sternite 7 not shield-shaped; macrosetae absent on membrane posterior to vein *CuA*; thorax without distinct row of supra-alar setae . . . . *Parascatopse* Cook

10. Wing vein R_{4+5} long, extended well beyond mid-length of wing (*e.g.*, Fig. 9); palpus small, usually rounded apically 11

– Wing vein R_{4+5} short, reaching costal vein (C) at most in the vicinity of mid-length of wing (*e.g.*, Figs 10, 11); palpus elongate, pointed or rounded apically, sometimes enormously developed, as long as eye in profile (*Psacotes* Haenni & Amorim, Fig. 12) (SWAMMERDAMELLINI) 16

11. Thorax stout; mesonotum as wide as long, or virtually so (COLOBOSTEMATINI [in part]). 12

– Thorax narrow; mesonotum considerably longer than wide 13

12. Eye-bridge developed above antennae; tarsi yellow, strongly contrasting with dark legs; wing vein M_1 angled in basal ¼, with complete (♀), or incomplete (♂) auxiliary crossvein joining veins M_1 to R_{4+5} (Fig. 13). . . . . *Holoplagia* Enderlein

– Eyes closely approximated above antennae, but no true eye-bridge present; tarsi not yellow, not strongly contrasting with dark legs; wing with vein M_1 angled in basal ¼, bearing at most a short anteriorly-directed stump vein (Fig. 8) . . . . *Colobostema* Enderlein

13. Thoracic anterior spiracular sclerite rounded, or square anterodorsally (similar to Fig. 16); abdominal sternite 6 with transversal cluster of spiniform setae medially, close to posterior margin (COLOBOSTEMATINI [in part]). . . . . *Ferneiella* Cook

– Thoracic anterior spiracular sclerite with acute anterodorsal projection (*e.g.*, Fig. 15); abdominal sternite 6 devoid of spiniform setae (SCATOPSINI) 14

14. Wing vein M_1 angled in basal ¼, bearing an anteriorly directed stump vein (Fig. 2); male hind tarsomere 1 widened, spinose, shorter than tarsomere 2 (Fig. 2) . . . . *Scatopse* Geoffroy

– Wing vein M_1 simple, neither angled in basal ¼, nor bearing an anteriorly directed stump vein (*e.g.*, Fig. 9); male hind tarsomere 1 simple, longer than tarsomere 2 15

15. Labella strongly developed in Afrotropical species; base of wing vein *CuA* neither markedly thickened, nor densely microtrichose; suture between thorax and abdomen simple; no sclerotised area present around spiracle on pleural membrane of abdominal segment 7 . . . . *Apiloscatopse* Cook

– Labella normally developed; base of wing vein *CuA* markedly thickened (Fig. 9), densely beset with enlarged spinose microtrichia on dorsal surface; suture between thorax and abdomen laterodorsally in shape of thickened, elevated rim; sclerotised area present around spiracle on pleural membrane of abdominal segment 7 . . . . *Octaseps* Haenni & Amorim

16. Wing with *M*-fork shorter than stem; vein *CuA* with a double bend, sigmoid, not reaching wing margin (Fig. 10); abdomen with only 6 pregenital segments visible externally; male terminalia with segment 7 concealed within segment 6. . . . . *Swammerdamella* Enderlein

– Wing with *M*-fork longer than stem; vein *CuA* with single bend, virtually reaching posterior margin of wing nearly at a right angle (*e.g.*, Fig. 11); abdomen with 7 pregenital segments visible externally; male terminalia with segment 7 not concealed within segment 6 17

17. Palpus pointed apically; thoracic anterior spiracular sclerite large, rather quadrate, 2 × as long as high, spiracular opening comparatively small; male terminalia with tergite 7 asymmetrically produced posteriorly into narrow spatulate process (Fig. 17); aedeagus elongated, coiled; female sternite 7 with median rounded posterior emargination. . . . . *Coboldia* Melander

– Palpus rounded apically; thoracic anterior spiracular sclerite differently shaped, spiracle opening comparatively large (*e.g.*, Fig. 16); male terminalia with tergite 7 variously modified, but never asymmetrically produced posteriorly; aedeagus never coiled, variously shaped, usually short; female sternite 7 with posterior margin not emarginate. 18

18. Male terminalia with genital capsule compressed laterally, with ventrally directed beak-like projection of modified tergite 9 and aedeagal plate neither conical nor projecting ventrally . . . . *Quateiella* Cook

– Male terminalia with genital capsule not compressed laterally, without ventrally directed beak-like projection of modified tergite 9, with aedeagal plate strongly developed, conical, projecting ventrally . . . . *Psacotes* Haenni & Amorim

Synopsis of the fauna

There has been little progress in our knowledge of Afrotropical Scatopsidae since Cook (1980), who listed 34 species from the region. To date, 53 species in 17 genera are known to occur in the Afrotropical Region, five of which were described from other regions. There are numerous undescribed species known in collections and the true species richness of the family, although difficult to predict, probably amounts to several hundred species. Kirk-Spriggs & Stuckenberg (2009:

186) predicted that 400+ (90% of species) probably await description. Three species described by early authors, namely *Rhegmoclema peringueyi* (Enderlein, 1923), *Scatopse brevitruncata* (Duda, 1928) and *S. divergens* (Duda, 1928), cannot be currently attributed to any genus on the bases of their poor original descriptions.

***Anapausis* Enderlein** (Psectrosciarinae)**.** A genus of 43 described species, occurring in all zoogeographical regions, except Antarctica. Three species are known from the Afrotropical Region, apparently isolated at higher elevations on East Africa mountains (Mt Kenya, Mt Kinangop and Mt Elgon) (Edwards 1914; Freeman 1989), and one undescribed species is known from the southern Arabian Peninsula. The biology and immature stages remain unknown.

***Apiloscatopse* Cook** (Scatopsinae: Scatopsini)**.** An essentially Holarctic genus of 19 described species, occurring in the Afrotropical, Nearctic and Palaearctic Regions. There is one described South African species (Cook 1965: 477), known only from the female, the generic placement of which remains questionable. The immature stages of one European species have been described from leaf litter and mushrooms (Haenni 1981; Seddon 1985).

***Coboldia* Melander** (Scatopsinae: Swammerdamellini)**.** The virtually cosmopolitan species *C. fuscipes* is the only representative of the genus. It has been spread by humans to most parts of the world and is recorded from Ghana, Kenya, South Africa and St. Helena Is. in the Afrotropical Region (Cook 1980: 236). Larvae have been found in a wide variety of decaying organic matter.

***Colobostema* Enderlein** (Scatopsinae: Colobostematini)**.** A genus of 65 described species, occurring in all zoogeographical regions, except Antarctica. Eight described species occur in the Afrotropical Region, including one in Madagascar (Cook 1965: 478; Duda 1928; Haenni 1993) and four additional undescribed species are known. Immature stages are unknown, but some European species appear to be myrmecophilous. The Afrotropical species were keyed by Haenni (1993).

***Ferneiella* Cook** (Scatopsinae: Colobostematini)**.** A genus of three described species, occurring in the Australasian and Palaearctic Regions. One undescribed species known from the Afrotropical Region is considered likely to belong to the genus.

***Holoplagia* Enderlein** (Scatopsinae: Colobostematini)**.** A genus of ten described species, occurring in the Afrotropical, Australasian, Neotropical, Oriental and Palaearctic Regions. One pantropical species, *H. guamensis* (Johannsen, 1946), has been recorded from Ghana (Cook 1957) and Madagascar (Haenni 2006). Larvae of *H. guamensis* have been obtained from *Calathea violacea* (Roscoe) Lindl. (Marantaceae) (Amorim 2009: 354).

***Neorhegmoclemina* Cook** (Scatopsinae: Rhegmoclematini)**.** A genus of 11 described species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. The genus is poorly known, with two described Afrotropical species recorded from South Africa (Cook 1965: 473) and one undescribed species. The immature stages and biology remain unknown.

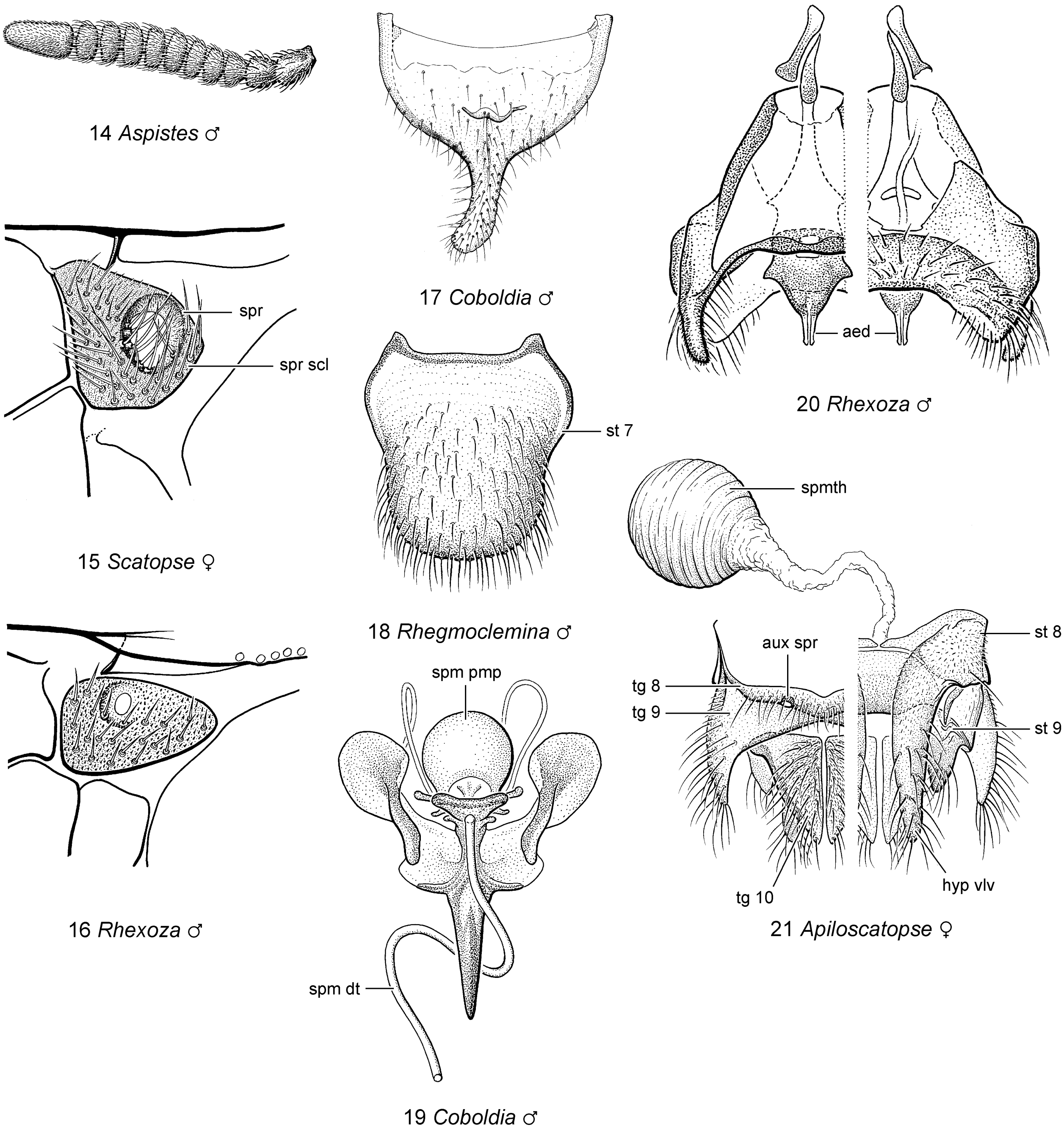
***Octaseps* Haenni & Amorim** (Scatopsinae: Scatopsini)**.** An endemic monotypic genus, with the single described species, *O. alata* Haenni & Amorim, 2016, recorded from South Africa. The biology and immature stages remain unknown.

***Parascatopse* Cook** (Scatopsinae: Rhegmoclematini)**.** A genus of eight described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica. Two species are recorded from the Afrotropical Region, from Democratic Republic of Congo and Madagascar, respectively (Cook 1962; Haenni 2006), but two additional undescribed species

12 *Psacotes* 13 *Holoplagia*

Figs 26.12–13. Habitus of adult Scatopsidae (lateral views): (12) *Psacotes gigantipalpus* Haenni & Amorim ♂; (13) *Holoplagia guamensis* (Johannsen) ♂. Fig. 12 (photograph M. Borer), Fig. 13 (photograph G. Haldimann).

Abbreviations: *C* – costal vein; plp – palpus; r_{4+5}–m_1 – auxiliary crossvein.


14 *Aspistes* ♂

15 *Scatopse* ♀

16 *Rhexoza* ♂

17 *Coboldia* ♂

18 *Rhegmoclemina* ♂

19 *Coboldia* ♂

20 *Rhexoza* ♂

21 *Apiloscatopse* ♀

Figs 26.14–21. Antenna, spiracular sclerite, segment 8 and terminalia of Scatopsidae: (14) antenna of *Aspistes* sp., lateral view (non-Afrotropical); (15) left spiracular sclerite of *Scatopse notata* (L.), lateral view; (16) same, *Rhexoza incisa* Cook (non-Afrotropical); (17) male tergite 7 of *Coboldia fuscipes* (Meigen), dorsal view; (18) male sternite 7 of *Rhegmoclemina bimaculata* (Melander) (non-Afrotropical); (19) sperm pump of male *C. fuscipes*, dorsal view; (20) male terminalia of *R. incisa*, ventral view (left), dorsal view (right); (21) female terminalia of *Apiloscatopse uncinata* (Melander), ventral view (left), dorsal view (right) (non-Afrotropical). Figs 14–16, 18–21 (Cook 1981, figs 11, 20, 21, 17, 22, 23, respectively), Fig. 17 (illustration M. Rapp).

Abbreviations: aed – aedeagus; aux spr – auxiliary spiracle; hyp vlv – hypogynial valve; spm dt – sperm duct; spm pmp – sperm-pump; spmth – spermatheca; spr – spiracle; spr scl – spiracular sclerite; st – sternite; tg – tergite.

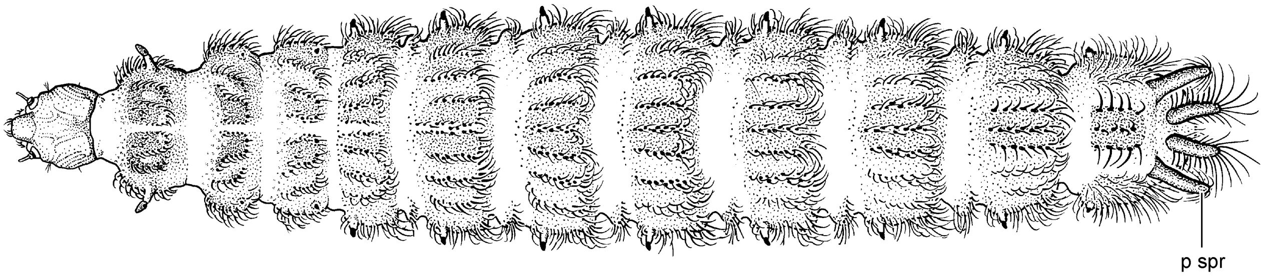
are known. Several species of *Parascatopse* are halophilous and are restricted to sea shores and saline soils. Immature stages of one European species have been described by Szadziewski (1979).

***Psacotes* Haenni & Amorim** (Scatopsinae: Colobostematini)**.** An endemic Afrotropical genus, with three described species recorded from Botswana, Democratic Republic of Congo and Tanzania respectively (Haenni & Amorim 2016). The biology and immature stages remain unknown.

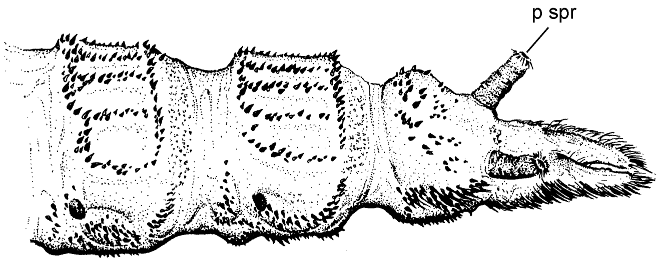
***Psectrosciara* Kieffer** (Psectrosciarinae)**.** A genus of 25 described species, occurring in all zoogeographical regions, except Antarctica. Only two species are recorded from the Afrotropical Region (South Africa and Seychelles, respectively) (Cook 1965: 480; Kieffer 1912), although five additional species await description. Immature stages of the genus remain unknown.

***Quateiella* Cook** (Scatopsinae: Swammerdamellini)**.** A genus of four described species previously known only from the Nearctic and Palaearctic Regions; one undescribed species is known from the Afrotropical Region. Nearctic species of the genus have been reared from various rotting plants, but the immature stages remain undescribed.

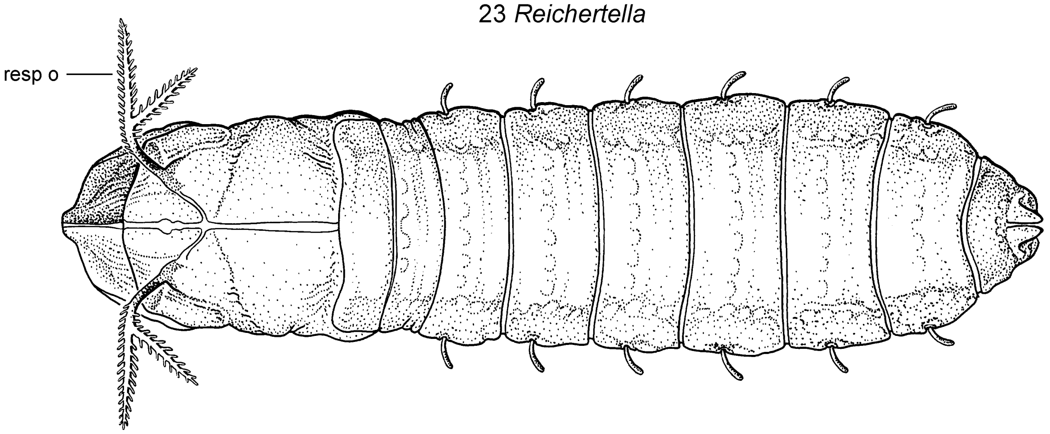
***Rhegmoclemina* Enderlein** (Scatopsinae: Rhegmoclematini)**.** A widespread genus of 24 described species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic



22 *Rhexoza*



23 *Reichertella*



24 *Rhexoza*

Figs 26.22–24. Immature stages of Scatopsidae: (22) larval habitus of *Rhexoza* sp., dorsal view (non-Afrotropical); (23) tip of abdomen of larva of *Reichertella geniculata* (Zetterstedt), laterodorsal view (non-Afrotropical); (24) pupal habitus of *Rhexoza* sp., dorsal view (non-Afrotropical). Figs 22, 24 (Cook 1981, figs 24, 25), Fig. 23 (Haenni 1997, fig. 28).

Abbreviations: p spr – posterior spiracle; resp o – respiratory organ.

Regions. Three described species (Duda 1928; Cook 1960; Haenni 2007) and three undescribed species are recorded or known from the Afrotropics. Immature stages remain unknown, although one European species has been reared from gravel beds of rivers (Haenni & Godfrey 2009).

***Scatopse* Geoffroy** (Scatopsinae: Scatopsini)**.** A Holarctic genus of seven described species. One species, *S. notata*, is virtually cosmopolitan and synanthropic, spread by humans to almost all parts of the world. In the Afrotropical Region, *S. notata* has been recorded so far only from the South Atlantic Nightingale Is. (in the Tristan da Cunha group) by Hänel & Haenni (2007). Larvae of this species have been found in a wide variety of decaying organic matter (e.g., rotten plant or vegetables remains, fungi and the droppings and dung of birds and mammals).

***Swammerdamella* Enderlein** (Scatopsinae: Swammerdamellini)**.** A genus of 36 described species, occurring in all zoogeographical regions except Antarctica. Four species have been described to date from the Afrotropical Region (Cook 1962, 1965: 476; Duda 1928). Immature stages have not been described, but adults have emerged from peat bogs, marshy soils and rotten grass leaf piles.

***Thripomorpha* Enderlein** (incl. *Rhegmoclema* Enderlein, *sensu* Amorim 2009) (Scatopsinae: Rhegmoclematini)**.** A genus of 51 described species, occurring in all zoogeographical regions, except Antarctica. The genus is the most speciose in the Afrotropical Region, with 15 described species (Cook 1955, 1960, 1962, 1964, 1965: 470; Edwards 1914; Freeman 1996; Haenni 1989, 2006; Speiser 1920) and two undescribed species. Several species are apparently restricted to high elevations in East African mountain ranges and two species are endemic to the Indian Ocean islands. Many species appear to be restricted to damp soil, but immature stages remain unknown.

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PTYCHOPTERIDAE 27

(Phantom Crane Flies or Fold-winged Crane Flies)

Andrew Fasbender

Fig. 27.1. Female of *Ptychoptera* cf. *madagascariensis* Alexander (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Medium to large (body length: 7–35 mm) crane fly-like nematoceran flies (Fig. 1).

Head roughly triangular; ocelli absent; compound eyes hemispherical, forming lateral margins of head capsule; antennae with 13–14 flagellomeres (in Ptychopterinae), or 18–21 flagellomeres (in Bittacomorphinae); labrum triangular; mouthparts simple, with prominent labella; maxillary palpus 5-segmented, terminal segment often elongate.

Thorax box-like, higher than broad, with prominent prescutal suture ending in a triangular posterior point in Ptychopterinae, indistinct in Bittacomorphinae; pleural sclerites with indistinct, or absent, anepisternal suture; meron fused with epimeron, metapleural suture absent in Ptychopterinae. Wing (Fig. 4) with 4 radial branches reaching wing margin, 3 branches

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 653–657.

of medial vein reaching wing margin in Ptychopterinae (2 in Bittacomorphinae), and 2 branches of cubital reaching margin; wings often with infuscate banding in Ptychopterinae; halter with distinctive polyp-like lobe anteriorly at base (termed prehalter). Legs elongate, longer than overall length of rest of body.

Abdomen elongate; abdominal segment 2 extended; sternite 3 with accessory copulatory organ in some male *Ptychoptera* Meigen, posterior abdominal segments slightly telescoping in Ptychopterinae; female terminalia (Fig. 9) with tergites 8–9 concealed by tergite 7 in Ptychopterinae, exposed in Bittacomorphinae; cerci heavily sclerotised and modified into ovipositor in Ptychopterinae, shorter and more membranous in Bittacomorphinae; male terminalia unrotated, with bilobate epandrium forming distinct epandrial claspers (Fig. 6), not fused with hypandrium (Fig. 5); parameres separate and stylate, or fused to form bridge, in Ptychopterinae base of paramere shifted posterior on dorsal surface of gonocoxite; gonopods (Fig. 5) simple, or complex, free of hypandrium; hypandrium (Fig. 5) separated into distinctive basal and terminal divisions, often with articulated spathate lobes on basal division; aedeagus (Figs 7, 8) rotated dorsally in Ptychopterinae, with large sperm sac, well-defined ejaculatory apodeme, prominent lateral ejaculatory processes and variable subapical sclerite ventral to phallotrema.

Larva vermiform in shape (Fig. 2), metapneustic, with distinctive retractile respiratory siphon; eucephalous, cranium with well-defined subgenal sclerite; labrum with prominent brushes; mandible broad, divided into molar and incisor lobes, with mandibular comb; maxilla with lateral and medial setal brushes; maxillary palpus peg-like; prementum with circular apex, with ring of dentitions; postmentum serrated and bridge-like in Ptychopterinae, simple and fused to subgenal sclerite in Bittacomorphinae; thoracic segments short, slightly nodiform; abdominal segments 1–6 cylindrical, each with posterior annular creeping welt in Ptychopterinae; integument smooth and glabrous with sparse chaetotaxy in Ptychopterinae, with prominent tubercles present in Bittacomorphinae; ventral pair of prolegs weakly-developed on abdominal segments 1–3, with single sickle-shaped claw on each; abdominal segments posterior to segment 6 developed into conical anal division, housing respiratory siphon and 2 retractile anal papillae.

Pupa fusiform (Fig. 3), propneustic, thoracic respiratory organs unevenly developed: right organ hypertrophied in Ptychopterinae and *Bittacomorpha* Westwood, left organ hypertrophied in *Bittacomorphella* Alexander; Ptychopterinae with tarsi parallel, Bittacomorphinae with fore tarsus lying over mid tarsus; abdominal segments with numerous rows of tubercles, ringed with apical dentitions and elongate trichoid sensilla; posterior margins of segments with creeping welts in Ptychopterinae; male terminalia primordium readily apparent, morphology variable between species-groups.

Adult Ptychopteridae superficially resemble several other families of lower Diptera (*i.e.*, Tipuloidea, Tanyderidae (see Chapter 15), Sciaroidea, and non-Afrotropical Trichoceridae), based on the compact thorax and elongate legs and abdomen. Adults can be readily distinguished from all other Diptera by the prehalter. Wing venation is also distinctive, lacking the anal vein of Tipuloidea and Trichoceridae, with less than four branches of the medial vein reaching the wing margin (unlike Tanyderidae). Sciaroidea have three, or fewer, branches of the radial vein reaching the wing margin, compared to the four of Ptychopteridae.

Biology and immature stages

Larval Ptychopteridae reside in saturated organic sediments, such as groundwater seepages and the depositional areas of small to medium streams. The larvae use brushes of macrotrichia on the labrum and maxillae to sift fine organic particles from the sediment (Mattingly 1987; Wolf *et al*. 1997). The characteristic respiratory siphon is extended into oxygenated water above the substrate (Alexander 1920; Hodkinson 1973; Peus 1958; Wolf & Zwick 2001). Larvae experience significant mortality (Wolf & Zwick 2001), with predation by larval Tabanidae and Limnephilidae (Trichoptera) observed in the Nearctic Region (G.W. Courtney, pers. comm. 2013). Pupation occurs in the larval habitat, with mature pupae travelling to the surface of the substrate for eclosion. Adults remain near the natal habitat, typically resting on the upper surface of emergent vegetation and fly in a straight, direct manner between different perches. Males copulate with recently emerged females, which oviposit in the same habitat. Adults retain functional mouthparts (including a well-developed cibarium) and have been recorded feeding on honeydew (Scherbakov & Lukashevich 2005). Wolf & Zwick (2001) found the Palaearctic species *Ptychoptera* (*Paraptychoptera*) *paludosa* Meigen, 1804, to be univoltine, with an emergence of eight weeks. The Nearctic taxa *P*. (*Ptychoptera*) *quadrifasciata* Say, 1824 and *Bittacomorpha clavipes* F., 1781, however, have an extended emergence of over four months and probably have multiple generations during the summer months (Bowles 1998; Rogers 1942). In more thoroughly studied regions, multiple *Ptychoptera* spp. have been found in sympatric association, often facilitated by partitioning microhabitats, such as standing *versus* flowing water (Fasbender, pers. obs.; Harris & Carlson 1978; Stubbs 1993: 24–30).

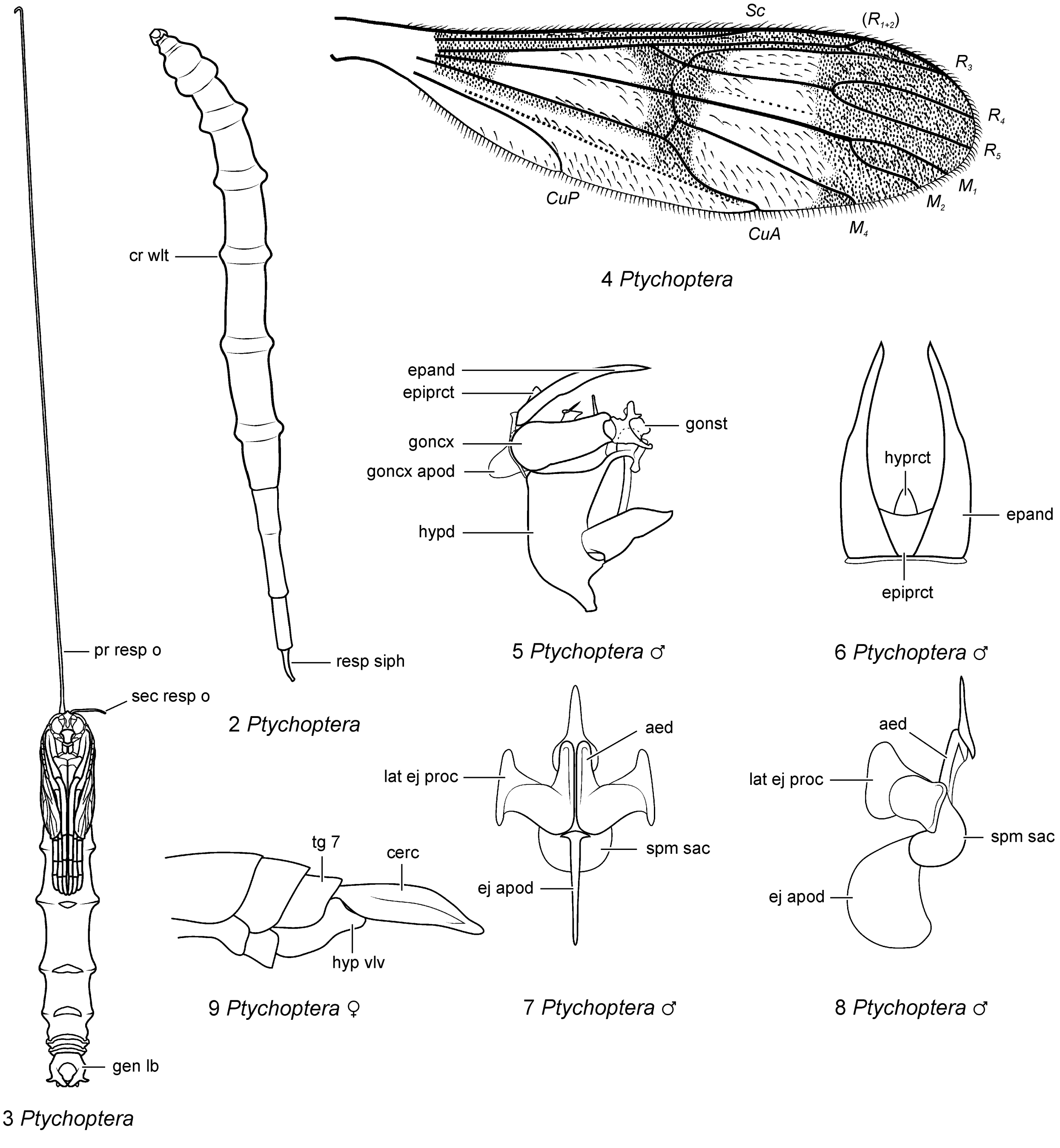
Ecological information for Afrotropical taxa is severely lacking. Stuckenberg (1983) provides a brief synopsis of habitats of the Afrotropical fauna. He notes that most *Ptychoptera* spp. are associated with montane forests, including gallery forest, and tend to reside in shaded pools. An exception is *P*. (*Pt*.) *kosiensis* Stuckenberg, 1983, which is found in coastal “swamp-forest” in eastern South Africa. Previous workers have hypothesised that Ptychopteridae is a group associated with temperate montane environments (Alexander 1927; Hancock *et al*. 2006; Stuckenberg 1983). The extensive species diversity of the Oriental Region and the discovery of both *Ptychoptera* and *Bittacomorpha* in Central America as far south as Costa Rica (Fasbender, pers. obs.), seem to contradict this view. Rather, the absence of Ptychopteridae in South America and its comparatively poor diversity in the Afrotropics is more likely due to historical biogeographic processes than current climatic conditions.

Economic significance

No species of economic significance are currently known.

Classification

The placement of Ptychopteridae within the wider context of Diptera has been problematic. The family is very ancient, with fossils that can be definitively assigned to the group dating to at least the Early Jurassic (Lukashevich 2008) and potentially the Late Triassic (Barth *et al*. 2011). Fossil evidence of the



Figs 27.2–9. Larva, pupa, wing and terminalia of Ptychopteridae: (2) larva of *Ptychoptera sculleni* (Alexander), dorsal view (non-Afrotropical); (3) same, male pupa, ventral view; (4) wing of *P. africana* (Alexander), dorsal view; (5) same, male terminalia, lateral view; (6) same, epandrium, dorsal view; (7) same, aedeagus, anterior view; (8) same, lateral view; (9) female terminalia of *P. africana*, lateral view. Fig. 3 (courtesy R.I. Madriz).

Abbreviations: aed – aedeagus; cerc – cercus; cr wlt – creeping welt; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; gen lb – genital lobe; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hyp vlv – hypogynial valve; hypd – hypandrium; hyprct – hypoproct; lat ej proc – lateral ejaculatory process; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; pr resp o – primary respiratory organ; R_{1+2} – anterior branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; resp siph – respiratory siphon; *Sc* – subcostal vein; sec resp o – secondary respiratory organ; spm sac – sperm sac; tg – tergite.

extant subfamilies is known only from Eurasia until past the separation of Laurasia and Gondwana (Lukashevich 2008). No Afrotropical fossils of the family have been described.

Most cladistic morphological hypotheses have placed Ptychopteridae as sister-group to the Tanyderidae, forming the infraorder Ptychopteromorpha (Hennig 1973: 24; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1358). The characters associating ptychopterids with tanyderids are either plesiomorphic or of problematic assessment; the sole "synapomorphy" of a foldable fifth tarsomere is not consistently distributed in Ptychopteridae. Furthermore, molecular analyses have not supported this morphological hypothesis, placing Tanyderidae closer to Psychodidae (Curler & Moulton 2012; Wiegmann *et al*. 2011). Culicomorpha has been suggested as sister-group to Ptychopteromorpha (Oosterbroek & Courtney 1995), but the evidence is equivocal.

Ptychopteridae comprises two extant subfamilies: Bittacomorphinae and Ptychopterinae. Bittacomorphinae is found in the Nearctic and Oriental Regions. Ptychopterinae has a Holarctic distribution, extending into the Afrotropical Region (including Madagascar). Currently, Ptychopterinae comprises the single genus *Ptychoptera*, with *ca* 70 species globally. *Ptychoptera* (*Paraptychoptera* Tonnoir) is represented by *P*. (*Pa*.) *surcoufi* Séguy, 1925, in Algeria, but does not enter the Afrotropics. *Ptychoptera* (*Ptychoptera*) is a heterogenous collection of species (Zwick & Starý 2003) and will be subdivided as part of an ongoing revision (Fasbender & Courtney, in prep). One author suggested that *P*. (*Pt*.) *capensis* Alexander, 1920, was related to the European *P*. (*Pt*.) *albimana* F., 1787 (Freeman 1959). The characters cited to support this hypothesis are, however, rather superficial and probably represent symplesiomorphies. Afrotropical *Ptychoptera* do not exhibit a strong association with the *Ptychoptera* spp. of North Africa and the western Palaearctic, but more closely resemble taxa from the Oriental Region, especially the Malay Archipelago. Further examination is required to determine the phylogenetic affinities and establish a biogeographic context for the Afrotropical species.

Identification

Unfortunately, there is currently no functional key for all Afrotropical species of *Ptychoptera*. The two best works are Freeman (1959) and Alexander (1928), of which only Freeman's contains illustrations. The three Malagasy species are keyed by Alexander (1957), including illustrations. Hutson (1980) catalogues the Afrotropical taxa, although no identification keys or diagnoses are provided. There has been very little taxonomic work on larvae of the family, with the only works useful for distinguishing species limited to the western Palaearctic fauna (Hansen 1981; Stubbs 1993: 18). There are no recorded larval collections of the group from the Afrotropical Region. The state of pupal taxonomy is even more rudimentary than that of the larvae and it is only possible to distinguish between genera (Alexander 1920, 1927, 1981: 327–328).

Synopsis of the fauna

***Ptychoptera* Meigen** (Ptychopterinae)**.** A genus of *ca* 70 described species, occurring in the Afrotropical, Nearctic, northern Neotropical, Oriental and Palaearctic Regions. Eight recognised species occur in the Afrotropical Region; five widely distributed continental species and three confined to Madagascar. Five additional species were described in the first half of the 20th century, but were synonymised by Freeman (1959). This work is in need of review however, as at least one name, *P*. (*Pt*.) *schoutedeni* Alexander, 1956, was synonymised under the wrong species. Species of the genus are similar in habitus to large fungus gnats, with most Afrotropical species displaying bright banding on the body and patterned wings. Thorough sampling for this genus has occurred in only a few areas, primarily the Albertine Rift and coastal South Africa. West Africa is particularly poorly sampled, with known species recorded from only a single specimen (*P*. (*Pt*.) *camerounensis* Alexander, 1921), or a limited number of localities (*P*. (*Pt*.) *africana* Alexander, 1920). The three species known from Madagascar are also recorded only from the type localities and are of questionable phylogenetic association with the mainland fauna. Recent investigations of the more thoroughly studied faunas of the Nearctic and western Palaearctic have revealed multiple new species (Fasbender, pers. obs.; Krzeminski & Zwick 1993; Ujvárosi *et al*. 2011; Zwick & Starý 2003) and it appears likely that there are additional species awaiting discovery in the Afrotropical Region. Indeed, there is evidence that some of the disjunct populations of *P*. (*Pt*.) *africana* and *P*. (*Pt*.) *uelensis* Alexander, 1928, represent distinct species, contrary to the findings of Freeman (1959). Further collecting is required, however, before drawing definitive conclusions, as many of the species synonymised with *P*. (*Pt*.) *uelensis* were described from female holotypes.

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DIXIDAE 28

(Meniscus Midges or Dixid Midges)

Jan Ševčík and Vladimir Blagoderov

Fig. 28.1. Male of *Dixella nova* Walker (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

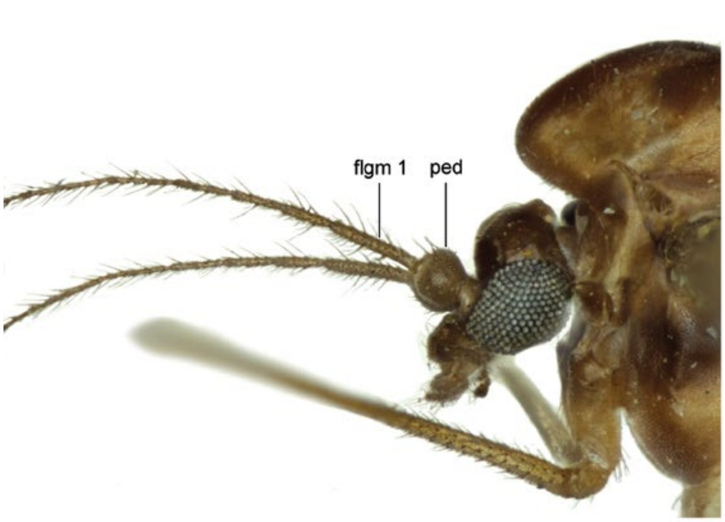
Medium-sized (body length: 4.0–8.0 mm), yellowish to dark brown midges with elongated legs (Fig. 1), antennae without long setulae (non-plumose), wing membrane without scales or macrotrichia, vein R_{2+3} distinctly arched (Figs 4, 5). See Peters (1981: 329) for detailed diagnosis of Dixidae.

Head with relatively large, dichoptic eyes (Figs 2, 3), more widely separated dorsally than ventrally; ocelli absent (Fig. 3); antenna long, with scape and pedicel enlarged (Figs 2, 3), but scape much shorter, flagellum with 14 elongated articles (3–10 × as long as broad); female mouthparts non-functional, reduced to short proboscis; labrum triangular; mandibles short and thin; palpus long, 5-segmented; labellum short and wide.

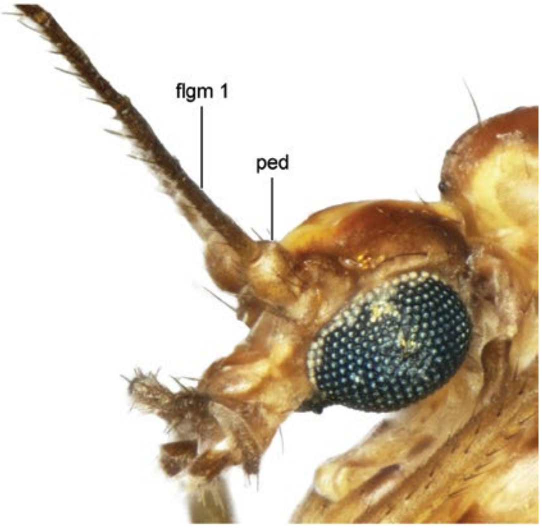
Thorax humpbacked in profile (Figs 1, 2); mesonotum usually with dark longitudinal fascia; katepisternum well-developed, with or without central group of setae. Wing membrane without macrotrichia or scales (either hyaline in most species of *Dixella* Dyar & Shannon or with dark markings in *Dixa* Meigen); subcostal vein (*Sc*) ending in costal vein (*C*) at *ca* ½ wing length; 4 radial and 3 medial veins present; vein R_{2+3} strongly arched (Figs 4, 5); crossvein *m–m* interrupted or complete; vein *CuP* long, reaching wing margin; halter long. Legs long and thin (Fig. 1), with coxae relatively short; hind tibia slightly to significantly expanded distally.

Abdomen elongate and narrow, with 4 pairs of spiracles on anterior segments; male terminalia (Figs 6, 7) rotated 180°, this rotation occurring between segments 5 and 8; gonocoxite with

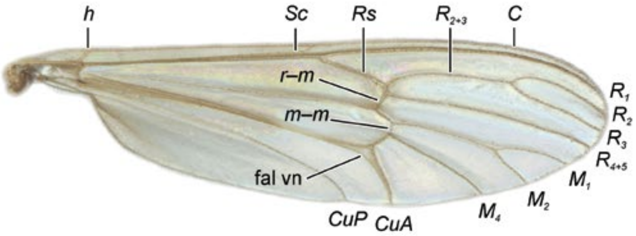
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 659–663.



2 *Dixa*



3 *Dixella*



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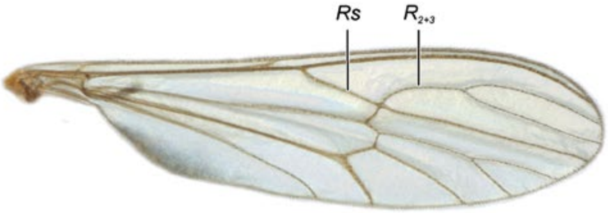
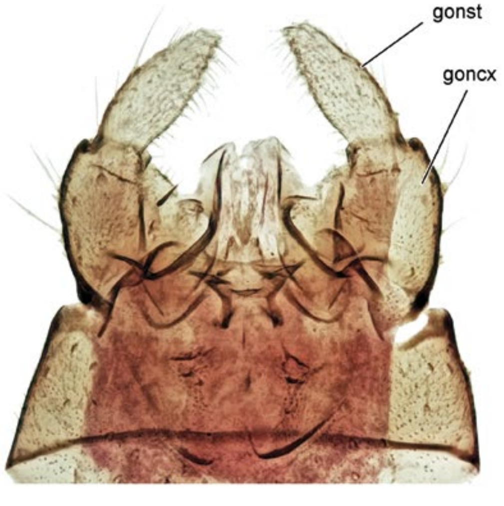


5 *Dixella*



6 *Dixa* ♂

7 *Dixella* ♂

Figs 28.2–7. Head and antennae, wings and male terminalia of Dixidae: (2) head and antenna of *Dixa bicolor* Wood, dorsolateral view; (3) same, *Dixella harrisoni* Freeman; (4) wing of *D. bicolor*, dorsal view; (5) same, *D. harrisoni*; (6) male terminalia of *D. bicolor*, dorsal view; (7) male terminalia of *D. harrisoni*, dorsal view. Figs 2–7 (© Trustees of Natural History Museum, London).

Abbreviations: ap lb goncx – apical lobe of gonocoxite; *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; fal vn – false vein; flgm – flagellomere; goncx – gonocoxite; gonst – gonostylus; *h* – humeral crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *m–m* – medial crossvein; ped – pedicel; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3} – second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein.

or without apical and sometimes with basal lobe; apical lobe of gonocoxite almost as long as gonostylus in *Dixella* species (Fig. 7); gonostylus short to long, species-specifically shaped; female terminalia with large, slightly sclerotised cerci; tergite and sternite 9 of species-specific shape; 1 round to elliptical sclerotised spermatheca present; bursa frequently with sclerotised structures resembling cones or spines (see Peters 1981, figs 5, 6).

Larva (Fig. 8) overall shape elongate, cylindrical; head capsule conspicuously black, highly mobile, with characteristic elongated antennae and palpi; 1 or 2 pairs of abdominal prolegs present; caudal respiratory apparatus complex. Head capsule complete; antenna 1-segmented; frontoclypeal apotome trapezoidal, narrowed frontally; maxillary palpus 1-segmented, similar in shape to antenna; thoracic sclerites distinct, without spiracles; abdomen 10-segmented, with pair of retractable prolegs on segment 1 or segments 1 and 2; distal abdominal segments with ventral ambulatory combs; dorsum of anterior segments sometimes with complex plumose setulae arranged in a circular crown (corona); segment 8 with pair of spiracles on dorsum, each with postspiracular process extended laterally; segment 9 with unpaired median sclerite (postanal process), a pair of paddle-shaped posterolateral processes and pair of anterolateral plates; several distinctive features of larvae (crowns, combs, terminal complex) are widely used for identification of species (see Disney 1974, 1999).

Pupa generally similar to Culicidae (see Chapter 31), but not as mobile, with widely separated respiratory organs (their shape used for species identification, e.g., Disney 1999); abdomen elongated and curved beneath cephalothorax.

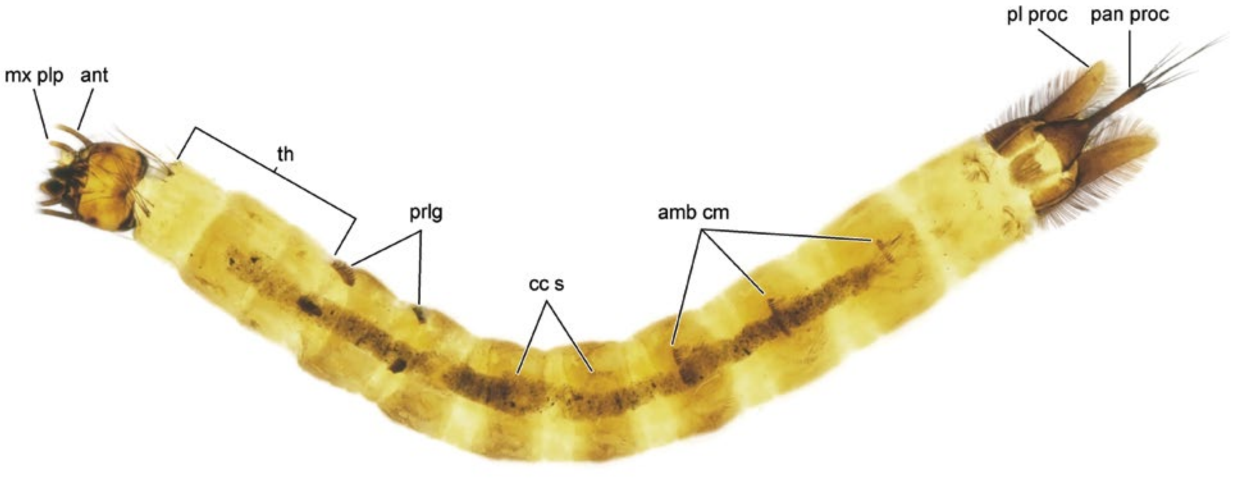
Adult Dixidae may be superficially confused with some small Limoniidae (see Chapter 14) or non-Afrotropical Trichoceridae, but can be separated by their strongly curved wing vein R_{2+3} and the absence of crossvein-like R_2. Dixidae resemble Chaoboridae (see Chapter 30) and Culicidae (see Chapter 31) in body size, but are easily distinguished from these by the bare wing membrane, non-plumose male antennae, elongate legs and non-functional mouthparts in females.

Biology and immature stages

The biology of Dixidae in general is discussed by Nowell (1951). The biology of Afrotropical species of the family is poorly understood and larvae of most species remain unknown or have not been associated with adult forms. The larvae of three Afrotropical species have been described (Disney 1974; Wood 1934).

Eggs are laid in gelatinous masses at the water edge. Larval Dixidae are aquatic; *Dixa* prefer running waters, while those of *Dixella* occur in calmer or stagnant waters. Larvae are filter-feeders and lie in the meniscus before emerging from the water onto rocks, moss or emergent vegetation for pupation. While crawling, larvae maintain an inverted U-shaped position, with the head in the water, the terminal segments with stigmata on the meniscus (hence their vernacular name) and the mid-section outside the water, covered with a thin film of water. Pupae are able to swim, but are usually encountered above the waters' surface, glued to sections of grass or to rocks with gelatinous secretion.

Adults are poor fliers, do not feed and occur near the larval habitat. They usually rest on emergent or overhanging vegetation or in moist crevices near the larval habitat. Males sometimes form small leks or swarms in the same locations, typically at dusk.



8 *Dixa*

Fig. 28.8. Larval habitus of Dixidae: *Dixa lunata* Edwards, dorsal view. Fig. 8 (slide-mount: © Trustees of Natural History Museum, London).

Abbreviations: amb cm – ambulatory combs; ant – antenna; cc s – circular crown setae; mx plp – maxillary palpus; pan proc – postanal process; pl proc – posterolateral process; prlg – proleg; th – thorax.

Economic significance

Dixidae are not known to have specific economic importance.

Classification

Dixidae are poorly understood phylogenetically. There are *ca* 180 described species globally (Pape *et al*. 2011; Wagner *et al*. 2008) in nine genera, most of which occur in the Holarctic Realm. The family as a whole has generally been neglected or overlooked and generic classification is especially in need of revision. It is classified as a part of the infraorder Culicomorpha and superfamily Culicoidea, where it represents the sister group to the Corethrellidae + Chaoboridae + Culicidae (*e.g*., Borkent 2012; Wagner 1997: 299; Wiegmann *et al*. 2011). Traditionally, the family is divided into three subfamilies: Dixinae, Meringodixinae and Paradixinae, but validity of these, as well as generic classification, is questionable (Wagner 1997: 302).

Fossil Dixidae are known from Baltic amber (Upper Eocene–Lower Oligocene) and Upper Palaeocene–Lower Eocene of Denmark. More recently Mesozoic representatives of the family have been identified from several deposits of Lower to Upper Jurassic of Middle Asia and Middle Jurassic of Siberia (Lukashevich 1997), although these may represent a stem-group of recent Dixidae.

Identification

Only two genera and eight species are known from the Afrotropical Region. Seven species belong to *Dixa* and a single species to *Dixella*. However, both the species described from Madagascar (based on female holotypes only) require further study and some of these may well be shown to belong to a different genus (*e.g*., *Nothodixa* Edwards (K. Moulton, pers. comm. 2016)) as soon as males are associated and a worldwide generic revision of Dixidae is completed.

The types of most species are housed in the Natural History Museum, London. All hitherto described continental Afrotropical species can be identified using the revision of Freeman (1956) and the additional two Malagasy species by reference to the original descriptions in Alexander (1957).

All stages are best preserved in 70% ethanol in the field for later slide-mounting in the laboratory (Disney 1999), although adults can be micro-pinned for later double-mounting (see Chapter 2).

Keys to genera of Afrotropical Dixidae

Adults

1. First antennal flagellomere relatively short, at most 3 × as long as pedicel, slightly tapering (Fig. 2); wing membrane with dark markings, at least over *r–m* crossvein; vein R_{2+3} branching from vein *Rs* before junction with *r–m* crossvein (Fig. 4); male terminalia with gonocoxite with at most a short process apically, not reaching ½ length of gonostylus (Fig. 6) . . . . *Dixa* Meigen

– First antennal flagellomere relatively long and cylindrical, at least 3 × as long as pedicel (Fig. 3); wing membrane hyaline (Fig. 5); vein R_{2+3} branching from vein *Rs* at junction with *r–m* crossvein; male terminalia with gonocoxite with long curved process apically, almost as long as gonostylus (Fig. 7) . . . . *Dixella* Dyar & Shannon

Larvae

1. Abdominal segments 2–7 with dorsal circular crowns of setae (Fig. 8). . . . . *Dixa* Meigen

– Abdominal segments 2–7 without dorsal crowns of setae . . . . *Dixella* Dyar & Shannon

Synopsis of the fauna

***Dixa* Meigen** (Dixinae)**.** A genus of *ca* 100 described species, occurring in the Afrotropical and Oriental Regions and Holarctic Realm. Seven species are recorded from the Afrotropics. Two are widespread in Central and southern Africa (*D. camerounensis* Alexander, 1926 and *D. claripennis* Séguy, 1938) and two are endemic to Madagascar (*D. hova* Alexander, 1957 and *D. stuckenbergi* Alexander, 1957; both known only from the female holotypes). *Dixa bicolor* Wood, 1933 appears to be the most abundant species in South Africa. The biology and immature stages of the majority of species remain unknown. Species can only be reliably identified by reference to the original descriptions and male terminalia.

***Dixella* Dyar & Shannon** (Dixinae)**.** A genus of *ca* 60 described species, occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions and the Holarctic Realm. The single described species, *D. harrisoni* (Freeman, 1956), occurs in South Africa (Olifantsvlei nr. Johannesburg, Gauteng Province) and is only known from the type material (single male and female). The biology and immature stages remain unknown. The species can only be identified by reference to the original description.

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CORETHRELLIDAE 29

(Frog-biting Midges)

Art Borkent

Fig. 29.1. Female of *Corethrella wirthi* Stone, feeding on the frog, *Hyla femoralis* Bosc (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

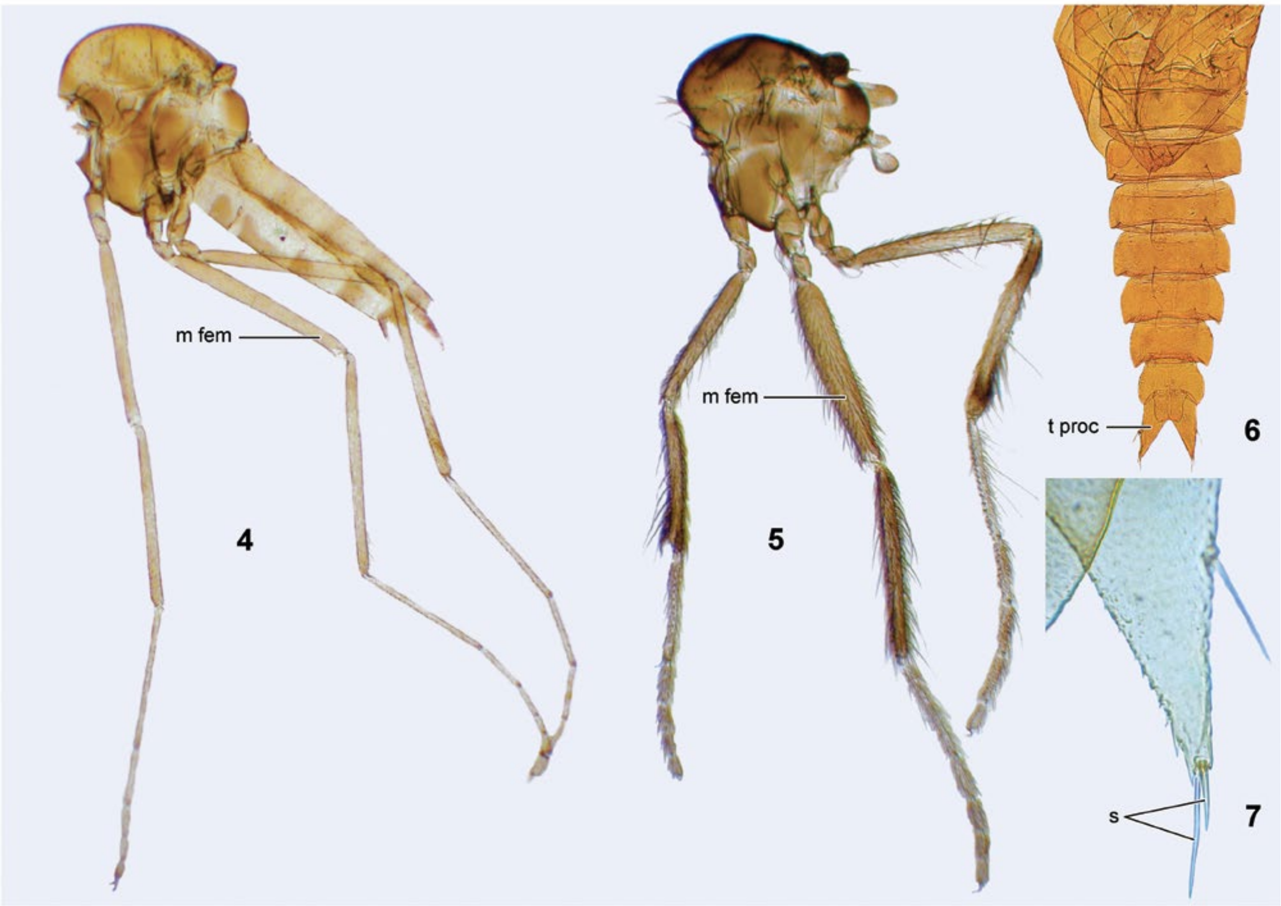
Small biting midges (wing length: 1.1–1.9 mm) (Fig. 1), with wing venation similar to Culicidae (see Chapter 31), with vein *R* 4-branched, vein *M* 3-branched and vein *Cu* 2-branched; branches of veins *Rs* and *M* virtually parallel to each other, but vein R_1 closer to vein *Sc*, or lying nearly midway between veins *Sc* and R_2 (Fig. 8); legs with mid femur thicker than both fore and hind femora (Figs 4, 5); male terminalia (Fig. 9) simple, with gonocoxite moderately elongate, parameres fused medially, with single prong extending posteriorly; aedeagus membranous.

Larva (unknown from Afrotropical Region) (Figs 10, 11), mosquito-like in overall habitus, but with antennae originating medially and folded laterally against head capsule when at rest; head capsule with lateral row of strong spines; well-developed abdominal respiratory siphon present.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 665–670.

2 *Corethrella*

3 *Corethrella*



4–7 *Corethrella*

Figs 29.2–7. Adult females feeding on calling male frogs in Borneo Is.; adult thorax and pupa of Corethrellidae: (2) *Corethrella nanoantennalis* Borkent & Grafe on thorax and legs of the frog, *Ansonia longidigita* (Inger); (3) *C. mitra* Borkent & Grafe on area surrounding nares of the frog, *Limnonectes leporinus* (Andersson) (note reddish abdomens of engorged females) (both non-Afrotropical); (4) thorax of *C. harrisoni* Freeman, lateral view; (5) same, *C. picticollis* Edwards, lateral view; (6) pupal exuviae of *C. appendiculata* Grabham, dorsal view (non-Afrotropical); (7) apical portion of terminal process of pupal exuviae of *C. appendiculata*, dorsal view. Figs 2–3 (after Borkent & Grafe 2012, figs 3A, 3B), Figs 4–7 (after Borkent 2008, figs 38D, 45D, 108B, 100C, respectively).

Abbreviations: m fem – mid femur; s – seta; t proc – terminal process.

Pupa (unknown from Afrotropical Region) (Figs 6–7), with respiratory organ well-developed, open-ended; third leg curled beneath wing sheath; length of cephalothorax (measured from anterior margin to apex of wing sheath), about equal to length of remaining abdomen (posterior to apex of wing sheath); apex of abdomen not curled under thorax; 2 pointed terminal processes, each with 2 subapical elongate setae.

Adult Corethrellidae may be initially confused with some Chironomidae (see Chapter 35), but may be distinguished by their wing venation, with deeply forked veins R_{2+3} and M_{1+2}; the short R_1 vein separates them from the Chaoboridae (see Chapter 30); and the presence of well-developed crossveins *r–m* and *bm–m* near the mid length of the wing separates them from some similar Psychodidae (see Chapter 24). Larvae may be initially confused with some small Culicidae or Psychodidae larvae, but the large antennae (Fig. 11) and head capsule (Fig. 10), with a lateral row of strong spines are unique to the Corethrellidae. Pupae are unique among the Diptera, in having the third leg S-shaped and positioned beneath the wing sheath, the palpus being posteromedially directed and with 2 pointed terminal processes (Fig. 6), each with 2 subapical elongate setae (Fig. 7).

Biology and immature stages

Corethrellidae, with the single genus *Corethrella* Coquillett, is one of the more fascinating families of nematocerous Diptera. Unlike other blood-sucking flies, adult females are attracted by the calls of male frogs. They only feed at night and are able to hear and locate their hosts from substantial distances, flying to the frogs and feeding on their blood (Figs 1–3). Only a few mosquitoes, in the genera *Uranotaenia* Lynch Arribálzaga (Borkent & Belton 2006) and *Mimomyia* Theobald (Toma *et al*. 2005) are able to do the same. Little is known otherwise regarding the behaviour of *Corethrella* adults. Adult females have never been observed feeding on frogs in Africa but, considering they have biting mouthparts and have other modifications related to biting frogs, this is likely due to the lack of directed research. Laboratory observations indicate the occurrence of swarming and mating pairs assume a venter-to-venter position (Silva & Bernal 2013). Frog call traps using the playback of frog calls of less than 4 kHz at night can be used to capture adult females. In the New World tropics and Borneo Is., for example, the call of *Hyla gratiosa* Le Conte, despite being a frog from the eastern United States, attracted many Corethrellidae. This type of trap, essentially a speaker broadcasting a frog call and placed over a fan blowing into a collecting bag (*e.g.*, a bulbless CDC trap) (Borkent 2008: figs 1A, B; McKeever & Hartberg 1980), has never been used in the Afrotropical Region. Alternately, a speaker placed over a pan of dilute, soapy water can also be used to capture adults (Amaral & Pinho 2015). Using frog calls successfully utilised in other regions and those of local frogs (*e.g.*, Carruthers & du Preez 2011), will likely result in fresh samples.

Adult females of at least some *Corethrella* spp. are vectors of *Trypanosoma* Gruby, between their male frog hosts (Johnson *et al*. 1993). Based on phylogenetic patterns, the fossil record and distribution patterns, it is likely the association between *Corethrella*, frogs and *Trypanosoma* is an ancient one, originating in the Jurassic Period. Because Afrotropical species represent earlier lineages within the genus and considering that nothing is known regarding their biology, it would be fascinating to study these interactions in the region.

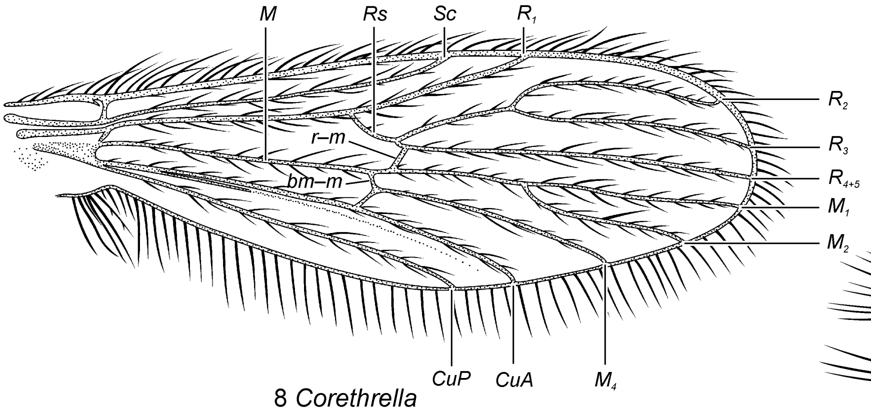
Immature stages of Afrotropical *Corethrella* spp. are unknown, but elsewhere are restricted to small aquatic habitats, either in pools at the edges of streams or marshes (and some from the hyporheic zone), or from a variety of phytotelmata (plant-held waters). Corethrellidae were formerly considered to be members of Culicidae and considering the large number of studies of mosquito larvae in the Afrotropical Region, none of which have reported a *Corethrella* larva or pupa, it seems most likely that immature stages of Afrotropical species occur in obscure groundwater habitats.

Larvae spend most of their time submerged, sometimes for extended periods and each anchors itself to the substrate, either with the two pairs of strong spines at the apex of the siphon, or the posterior pair only. As such, they are often upside-down on the bottom substrate or hang on the side of a container. Larvae are ambush predators, preying on moving organisms that are generally smaller than themselves. Larger prey may be taken by ingesting part of the prey and then "snipping" off the remainder, including the head capsule of some larger mosquito larvae, with synchronous use of the mandibles when it is not possible to ingest more. When an insect, crustacean, nematode or large rotifer is moving nearby, larvae either twist their bodies to bring their heads close to the prey (sometimes assuming a U-shaped position), or may slowly and stealthily extend their body length by about ⅓ its normal length for more distant prey. When the head is close enough, larvae lash at the prey, grab it with at least the mandibles, and ingest it. In the absence of sufficient food in the laboratory *Corethrella* larvae may become cannibalistic. The escape response of *Corethrella* larvae is to wriggle backward, as do Dixidae, Culicidae and some Chaoboridae (*Eucorethra* Underwood), and either hide in the bottom or work their way into the meniscus and part way up the side of a container.

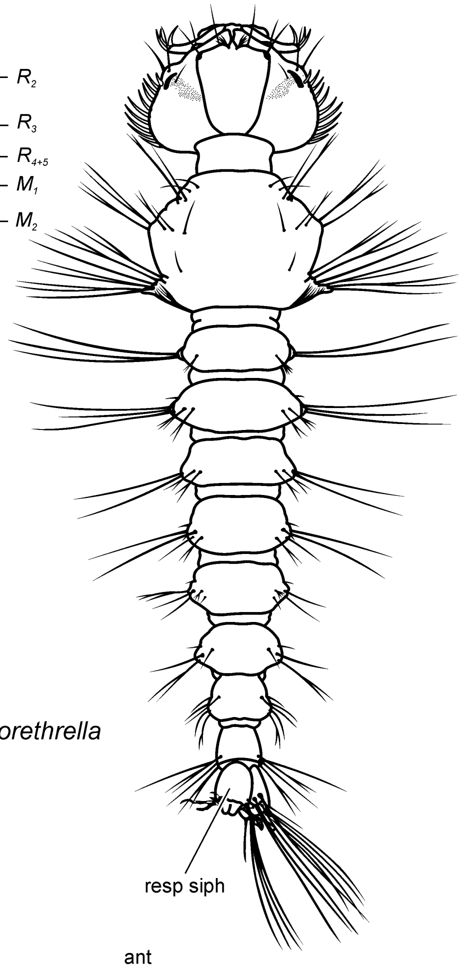
Larvae of some species of *Corethrella* are an important component of phytotelm communities, influencing host size, distribution, growth pattern and behaviour of other species and play a critical role in community structure (Alto *et al*. 2005; Beaver 1983; Bradshaw & Holzapfel 1984, 1985; Griswold & Lounibos 2005*a*, *b*, 2006; Kitching 2000; Lounibos 1983). Although studied primarily in tree holes in Florida and in *Nepenthes* (Nepenthaceae) in South-east Asia, the widespread distribution of *Corethrella* in phytotelmata makes it likely that they are important components of the communities found in these habitats, especially in tropical climates. It is unknown what impact *Corethrella* larvae living in groundwater habitats have on their communities.

Pupae are lethargic and generally remain at the surface, with some lying horizontal, some at about a 45° angle and some hanging vertically. A few days are sufficient for the adults to emerge.

All biological observations were compiled and summarised by Borkent (2008) in a comprehensive monograph of the family worldwide. Supplementary information on the species from Borneo Is. was published by Borkent & Grafe (2012).



8 *Corethrella*



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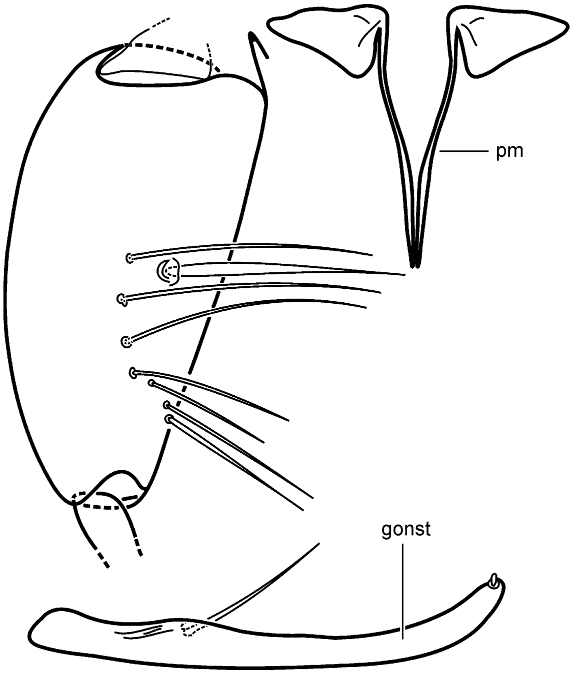
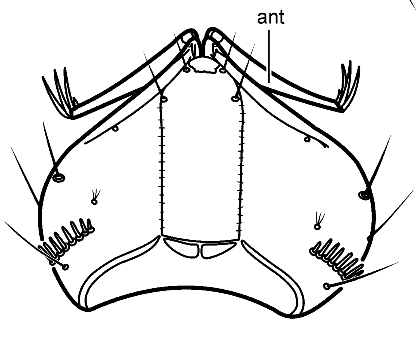


9 *Corethrella*



11 *Corethrella*

Figs 29.8–11. Wing, male terminalia and larva of Corethrellidae: (8) wing of *Corethrella* sp.; (9) male terminalia of *C. harrisoni* Freeman, dorsal view, with parameres, gonostylus displaced; (10) larva of *C. calathicola* Edwards, dorsal view (non-Afrotropical); (11) larval head of *C. towadensis* Okada & Hara, dorsal view (non-Afrotropical). Fig. 8 (after Cook 1981, fig. 3), Fig. 9 (after Borkent 2008, fig. 83D), Fig. 10 (after Edwards 1930, fig. 1a), Fig. 11 (after Okada & Hara 1962, fig. 7).

Abbreviations: ant – antenna; *bm–m* – basal medial crossvein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; gonst – gonostylus; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; pm – paramere; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; resp siph – respiratory siphon; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein.

Economic significance

Adult females of some *Corethrella* spp. are vectors of *Trypanosoma* Gruby (Tryanosomatidae) parasites between male frogs, but the immediate impact of this transmission is unknown. Biting and transmitting a parasite has likely played a role in the evolution of call diversification and behaviour in anurans.

Classification

The family Corethrellidae is a member of the superfamily Culicoidea and is the sister-group of the Chaoboridae + Culicidae. Together these three are the sister-group of the Dixidae. These relationships appear to be well-supported by larval, pupal and adult synapomorphies (Borkent 2012). Worldwide, the 107 extant species of *Corethrella* are found between 50°N and 50°S, but most are found between 30°N and 30°S and below 1500 m in elevation (Borkent 2008).

Seven fossil species of *Corethrella* are known, with the oldest of these from 121 million year old Lebanese amber (Borkent 2008). All extant and fossil species were catalogued by Borkent (2014), other than a recently described species from China (Yu *et al*. 2013) and Brazil (Amaral & Pinho 2015).

A phylogenetic analysis of the genus, including its relationships to other Culicomorpha and those between the extant and fossil species of *Corethrella* on a worldwide basis, was provided by Borkent (2008). Further species from Borneo Is. were described and interpreted by Borkent & Grafe (2012).

Identification

Five of the six named Afrotropical species were described and keyed by Borkent (2008). Giłka & Szadziewski (2009) redescribed a Saudi Arabian species from United Arab Emirates. All are known only from adults.

Synopsis of the fauna

Only the single genus *Corethrella* is known from the Afrotropical Region.

***Corethrella* Coquillett**. A genus occurring in all zoogeographical regions, except Antarctica, with 107 named species globally, six of which occur in the Afrotropical Region, recorded from South Africa, Uganda, West Africa and United Arab Emirates. A recent survey using CDC light traps in Madagascar revealed the presence of seven species, at least six of which are undescribed (Robert & Borkent 2014), indicating the likelihood of further undiscovered species in the Afrotropical Region and the use of frog-call traps will certainly provide new records.

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CHAOBORIDAE 30

(Phantom Midges)

Art Borkent

Fig. 30.1. Female of *Chaoborus ceratopogones* (Theobald) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

[Based on *Chaoborus*; the only genus in the region].

Small to moderately-sized non-biting midges (wing length: 1.5–3.5 mm) (Figs 1, 7), with wing venation similar to that of Culicidae (vein R_1 ending at vein C close to apex of veins R_2, R_3 and R_{4+5}; vein M with 3 branches) (Fig. 8); head with mouthparts short (Figs 7, 9); antenna with 9–13 flagellomeres, plumose in males (Figs 1, 7); terminalia of male (Fig. 10) with elongate, slender gonocoxite and gonostylus; the only sclerotised intromittent structures are 2 separate, articulated parameres; aedeagus membranous.

Pupa (Figs 6, 11) with apical terminal processes (as paddles), each with 2 lateral and 1 medial rib supporting clear membrane, and short mouthparts; respiratory organ narrow apically, lacking obvious plastron. In living specimens, abdomen

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 671–675.

hanging straight down or slightly curved (unlike the tightly curled abdomen of Culicidae).

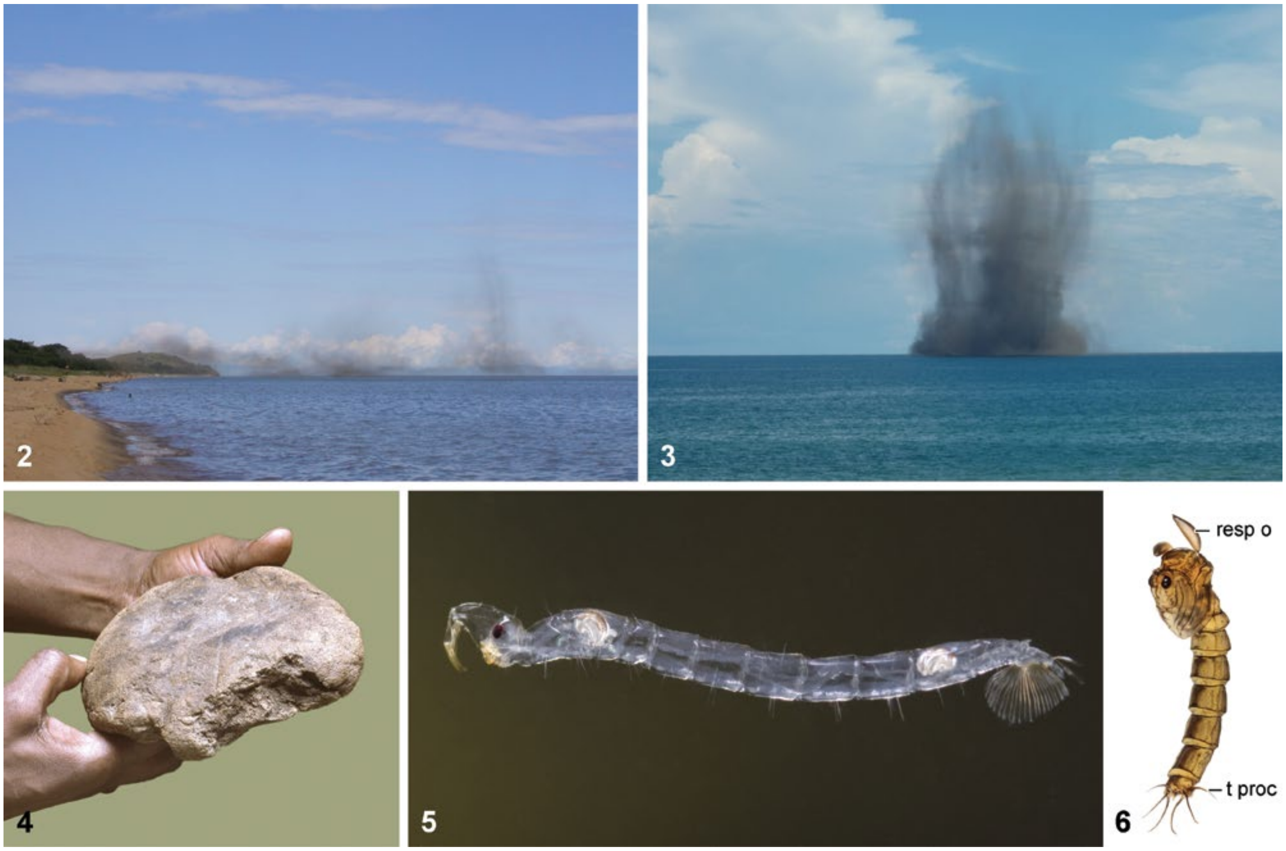
Larva (Figs 5, 12) highly distinctive, mostly transparent in life; head capsule laterally compressed, with prehensile antennae, the bases of these abutting medially; without spiracles, but with pair of prominent air sacs in both thorax and abdominal segment 7.

Adult Chaoboridae may be superficially confused with some Chironomidae (see Chapter 35), but are distinguished by their wing venation, with deeply forked veins R_{2+3} and M_{1+2}. Their elongate vein R_1 separates them from species of the Corethrellidae (see Chapter 29) and their relatively short mouthparts from Culicidae (see Chapter 31).

Biology and immature stages

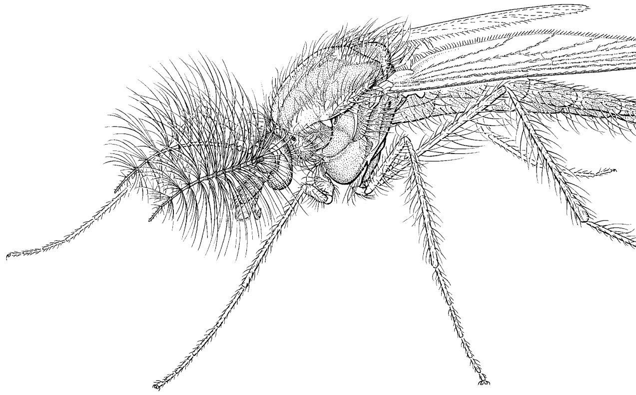
Chaoboridae, with the single genus *Chaoborus* Lichtenstein in the Afrotropical Region, may be strikingly abundant, particularly in some East African lakes (such as Lakes Victoria, Edward and Malawi), where adults of some species occurred in such vast numbers that swarms appeared as dark clouds (Figs 2, 3). Some swarms may be as high as 100 m (Verbeke 1957) and form the largest swarms of any insect on Earth. Mating occurs on land, or over water, either early in the morning or at dusk (McGowan 1975). Hare & Carter (1986) discussed the presence of parthenogenic populations of *C. anomalus* Edwards, 1930, a unique condition in the family. In lakes with high populations, pupal exuviae may be so dense as to form floating islands on lakes. Eggs are laid at night, either singly, or embedded together in a single gelatinous matrix, depending on the species (MacDonald 1956; McGowan 1975).

Chaoboridae, like most other nematocerous Diptera, have four larval instars. The life cycle of *C. anomalus* and *C. pallidipes* (Theobald, 1911) lasts about two months, the larvae growing for most of that time (about seven weeks) and with the pupal stage lasting 2–3 days and the adults surviving only a few days more. At Lake Victoria, there are two overlapping generations, so that there is an adult emergence every month, with peak emergence two days after the new moon (MacDonald 1953, 1956). Adult peak emergence occurs at, or somewhat

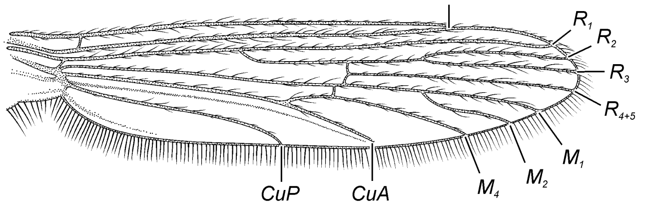


Figs 30.2–6. Swarming adults and larva and pupa of Chaoboridae: (2, 3) swarm of *Chaoborus edulis* Edwards on Lake Malawi; (4) *Kungu* cake (compressed adult *C. edulis*, consumed as human food); (5) larva of *Chaoborus* sp., lateral view; (6) pupa of *C. trivittatus* (Loew), anterolateral view (non-Afrotropical). Fig. 2 (photograph: S. Anamchara), Fig. 3 (photograph: A. Orr), Fig. 4 (source Natural History Museum, London), Fig. 5 (photograph J. Hamrsky); Fig. 6 (photograph T. Murray).

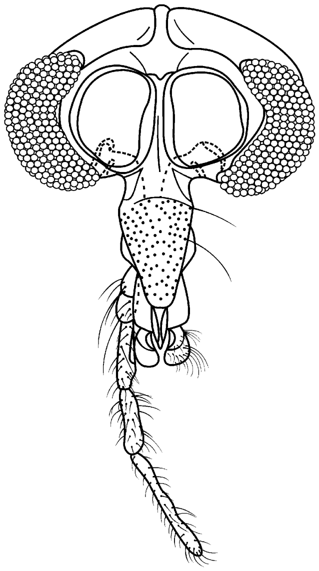
Abbreviations: resp o – respiratory organ; t proc – terminal process.



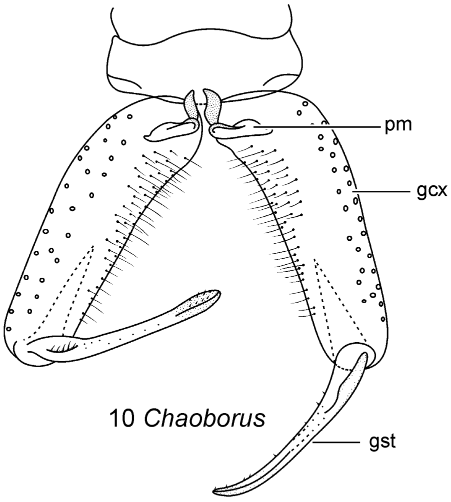
7 *Chaoborus*



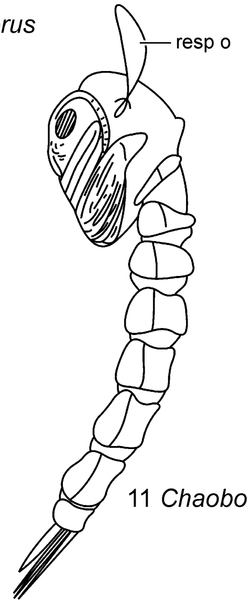
8 *Chaoborus*



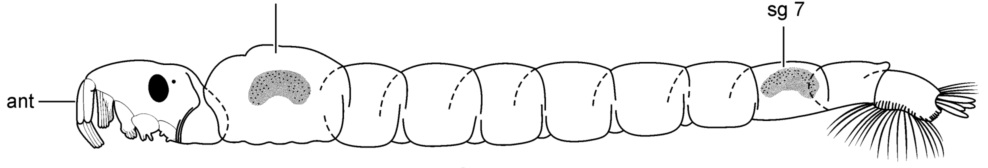
9 *Chaoborus*



10 *Chaoborus*



11 *Chaoborus*



12 *Chaoborus*

Figs 30.7–12. Habitus, wing, head, male terminalia, pupa and larva of Chaoboridae: (7) habitus of *Chaoborus americanus* (Johannsen) (non-Afrotropical); (8) same, wing, dorsal view (non-Afrotropical); (9) head of *C. crystallinus* (De Geer), anterior view (antennae removed) (non-Afrotropical); (10) male terminalia of *C. freemani* Verbeke, dorsal view; (11) pupa of *C. trivittatus* (Loew), lateral view (non-Afrotropical); (12) same, larva, lateral view (non-Afrotropical). Fig. 7 (after Cook 1981, fig. 1), Fig. 8 (after Cook 1981, fig. 2), Fig. 9 (after Sæther 1972, fig. 2A), Fig. 10 (after Verbeke 1958, fig. 41), Fig. 11 (after Borkent 1979, fig. 5B), Fig. 12 (after Borkent 2009, fig. 3).

Abbreviations: ant – antenna; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; gcx – gonocoxite; gst – gonostylus; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; pm – paramere; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; resp o – respiratory organ; *Sc* – subcostal vein; sg – segment; th – thorax.

before, the time of the new moon in all lake species (Hare & Carter 1986). Low light levels at this time likely increase the survival rate of mature fourth-instar larvae and pupae as they occur at the surface (Irvine 1997). McGowan (1974) noted *C. anomalus* and *C. ceratopogones* (Theobald, 1903), were more abundant during the rainy seasons at Lake George, but Hare & Carter (1986) found *C. ceratopogones* more abundant during the dry season in Nigeria.

Larvae are an important component of the lentic community and are often abundant in standing water, from small pools to large lakes. McGowan (1974) recorded up to 7,990 larvae per m^2 in the benthos of Lake George, Uganda and noted that the two *Chaoborus* spp. that occur there (*C. anomalus* and *C. ceratopogones*), made up 65–85% of all macroscopic organisms in the benthos. Because they are planktonic, *Chaoborus* larvae are restricted to standing waters, although they may sometimes be found in rivers, or streams, when flood waters have inundated nearby ponds or lakes, or when large reservoirs have released water rapidly. Although very abundant in Lakes Victoria, Albert, Edward, Malawi and George (and lakes elsewhere in Africa), *Chaoborus* are absent from Lakes Tanganyika, Kivu and Turkana, likely because of a combination of fish predation, high temperatures and low oxygen levels (Halat & Lehman 1996).

The transparent larvae are predaceous and hang horizontally in the water (Fig. 5). They await passing prey, which they detect with sensory setae and lash sideways to capture as food. Feeding of chaoborid larvae in lakes is known to influence the size, morphology, distribution and species composition of crustacean zooplankton (Hanazato & Ooi 1992; Irvine 1997; Pagano *et al*. 2003; Tollrian 1993). In smaller water bodies, larvae also feed on small insects, such as chironomid larvae.

Larvae have the remarkable capability of controlling gas in their air sacs. Species that occur in larger water bodies have a diurnal vertical rhythm, in which they slowly rise up in the water during early night (and hence may be found near the surface at that time) and sink into the benthos or, if the lake is deep, sometimes to great depths (*e.g.*, 230 m), during daylight hours (Green *et al*. 1973; Irvine 1997; MacDonald 1956; McGowan 1974; Verbeke 1957). The first-instars of lake-dwelling species remain in the upper layers and it is the larger, subsequent instars which have the diurnal vertical migration (the second less so than the third and fourth). The diurnal vertical migration is a response to escape predation by fish, which are generally restricted to the oxygenated upper layers of a lake and otherwise have poorer eyesight at night. One cichlid fish species, *Konia dikume* Trewavas, in Cameroon, however, appears to have evolved specifically to prey more efficiently on *C. ceratopogones* larvae (Green *et al*. 1973). This fish species has nearly double the haemoglobin concentration and a higher blood volume than other cichlid fishes, and these adaptations allow it to dive down into the deoxygenated hypolimnion and prey on *Chaoborus* larvae as they rise at dusk or descend at dawn, effectively extending its feeding time. An unnamed cichlid species was recently described as a specialist feeding on *Chaoborus* larvae and pupae in Lake Chilingali, Malawi (Tyers *et al*. 2014).

Subfossil *Chaoborus* larval structures have been used to interpret the past trophic states of African lakes (Rumes *et al*. 2005).

Economic significance

The vast swarms of *Chaoborus* at some East African lakes are a source of food for local people. The missionary and explorer David Livingstone (1813–1873) was apparently the first European to report this phenomenon at Lake Malawi (as Lake Nyasa) (Livingston 1875: 261). Locals gather adults to press into *Kungu* cakes (Edwards 1930) (Fig. 4), by swinging hemispherical baskets attached to long poles into the dense clouds of midges (which also include Chironomidae). The midges are then compressed into solid masses, molded into cakes, dried in the sun and later consumed in various ways. Cranston (1994: 372) indicated the possibility that large numbers of *Chaoborus* adults may be the cause of allergic reactions in Entebbe, Uganda (although Chironomidae may be the partial, or entire, culprit).

The larvae of those *Chaoborus* spp. that occur in lakes are known to strongly influence zooplankton community structure and, consequentially, the entire ecosystem of such lakes. Larvae are the predominant food of some fishes, including some important fishery species (Allison *et al*. 1996; Duponchelle *et al*. 2005; Green *et al*. 1973; Verbeke 1957).

Classification

Chaoboridae are the sister-group of the Culicidae (Borkent 2012), with which they share numerous features. The 51 extant species of Chaoboridae known worldwide are divided into six genera and *Chaoborus*, with 43 described species, includes the majority of these. The family is ancient, with numerous fossils known since the Jurassic period (176 MYA) (Borkent 2014) and it is clear that they have been important members of the lentic aquatic community for a considerable time. Ogawa (2007) provided a phylogenetic analysis of the family and many included species, and reviewed previous hypotheses of relationships.

Identification

Borkent (2014) cataloged the species of Chaoboridae worldwide and provided references to keys, descriptions of all known life stages, ecological studies and bionomic information.

Synopsis of the fauna

Only the single genus *Chaoborus* is known from the Afrotropical Region, with eight described species. The four species that commonly occur in Africa's lakes, *C. anomalus*, *C. ceratopogones*, *C. edulis* Edwards, 1930 and *C. pallidipes* are moderately well understood, but the remaining four are described only as adults and their biologies remain unknown.

***Chaoborus* Lichtenstein**. This genus occurs in all zoogeographical regions, except Antarctica, with 43 recognised species. A key to adults, detailed descriptions and distributions of seven of the eight Afrotropical species were provided by Verbeke (1958), with some details of adult structures also provided by Verbeke (1957). Verbeke (1958) considered

C. fuscinervis a synonym of *C. edulis*, but Hare & Carter (1986) discussed the significant differences between the two. The pupae of three species, *C. anomalus*, *C. ceratopogones* and *C. edulis*, have been described and Verbeke (1957) provided a key to separate *C. anomalus* and *C. ceratopogones*. The larvae of four species have been described and three of these: *C. anomalus*, *C. ceratopogones* and *C. pallidipes*, were keyed by Green & Young (1976). The fourth species, *C. edulis*, does not appear to be distinguishable from *C. pallidipes* (or perhaps was misidentified) (McGowan 1976).

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CULICIDAE 31

(Mosquitoes)

Maureen Coetzee

Fig. 31.1. Female of *Toxorhynchites* (*Toxorhynchites*) *brevipalpis* Theobald (Tanzania) (photograph © S.A. Marshall).

Diagnosis

Small- to medium-sized (body length: 4–13 mm), slender-bodied nematoceran flies (Fig. 1); head with proboscis of male and female conspicuous, scaly, forwardly-projecting; usually with numerous scales on body, legs and wing veins, of varying colours, including white, silvery, yellowish, brown, black and bluish, some with metallic sheen; posterior margin of wing with fringe of scales (Jupp 1996: 1; Service 1980: 22, 1990: 3) (Figs 3, 9–24); males usually distinguished from

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 677–692.

females by the highly plumose antennae (Figs 2, 27), while living adults of the two subfamilies Anophelinae and Culicinae can be recognised by their resting positions (Figs 4, 5).

Head globular, with prominent compound eye (Fig. 2); occiput with erect scales posteriorly, vertex with broad, and/or narrow, decumbent scales; antenna multi-segmented, plumose in males in most genera, giving feathery appearance (Figs 2, 27), in females delicate, with 5–7 short setae arising from base of each flagellomere (Figs 3, 26); palpus scaly, arising from below clypeus, either short, or as long as proboscis (Figs 2, 26, 27); proboscis scaly, forwardly-projecting.

Thorax clothed in scales dorsally, sometimes bearing rows of setae; lateral pleural sclerites with or without scales and setae. Scutellum usually trilobed in subfamily Culicinae (Figs 31, 35), evenly rounded in Anophelinae (Fig. 28), with scales or setae. Wing (Figs 3, 9–25) long, narrow, veins with scales dorsally and ventrally, posterior margin of wing with fringe of outstanding narrow scales. Legs long and slender (Figs 1, 3).

Abdomen long and slender (Fig. 3); tergites and sternites 1–8 well-developed; female terminalia with paired cerci that may be withdrawn into terminal segments; male terminalia with jointed claspers; paramere heavily-sclerotised, positioned ventral to claspers; female terminalia of limited use in differentiating species, but male terminalia often of taxonomic value.

Adult Culicidae superficially resemble midges of the families Chaoboridae (see Chapter 30), Chironomidae (see Chapter 35) and Dixidae (see Chapter 28), but are easily distinguishable by the prominent forwardly-projecting, elongated mouthparts.

Biology and immature stages

The aquatic larval stages (Figs 6, 43, 44) have a well-developed head, a pair of antennae, stemmata, a bulbous thorax, absence of prolegs and only one pair of dorsal spiracles on the last segment of the abdomen (Anophelinae) (Fig. 44), or situated at the end of a respiratory siphon (Culicinae) (Figs 6, 43). Anopheline larvae lie parallel with the meniscus of the water, feeding on surface debris (Fig. 44), while all other mosquitoes hang head down and are mostly bottom-feeders (*e.g.*, Figs 6, 43), but some are predaceous.

Only female mosquitoes take blood, as they require a protein meal for egg development. Not all species require blood, however, and indeed all females of the tribe Toxorhynchitini require only the nectar of flowers in order to develop egg batches. Male mosquitoes lack mouthparts adapted for piercing skin and, therefore, do not suck blood. Some species of culicines can survive for extended periods without laying eggs, *e.g.*, when over-wintering. An occasional blood meal will be taken, but the female will only venture out of her refuge once environmental conditions are conducive for oviposition. Some species of mosquitoes can lay their first batch of eggs without taking a blood-meal, but thereafter require a blood-meal for every subsequent gonotrophic cycle (Service 1980: 26).

Male mosquitoes usually eclose from their pupal cases before females and are only ready for mating once the apical segments of the abdomen have rotated 180°, which takes about 24 hours (Dahan & Koekemoer 2013). In many species, males attract females by the formation of swarms around dusk, using various markers on the ground or above, *e.g.*, around tree branches, and swarm for approximately 20 minutes. The majority of swarms are single-species males (Assogba *et al*. 2013; Dabire *et al*. 2013*a*), but in the *Anopheles* (*Cellia*) *gambiae* Giles, 1902 complex, mixed swarms of *An*. *coluzzii* Coetzee & Wilkerson, 2013 and *An*. *gambiae* may be found (Dabire *et al*. 2013*b*), but mating remains assortative within species. In general, larger males are more successful in mating than their smaller counterparts (Sawadogo *et al*. 2013).

Female mosquitoes can oviposit from 30–300 eggs at a time, depending on the species. Some species (*e.g.*, *Culex* L. and *Anopheles* Meigen), deposit their eggs directly onto the surface of the water, while others, such as *Aedes* Meigen spp., lay their eggs above the water level on damp substrates. Such eggs can usually withstand desiccation. Eggs are normally blackish in colour and ovoid (Fig. 7), but there is considerable variation, for example, *Toxorhynchites* Theobald eggs do not turn black following oviposition (Muspratt 1951), while some species of *Mansonia* Blanchard have skittle-shaped eggs, that are glued onto the under-surface of floating vegetation (Jupp 1996: 23; Service 1980: 61). The eggs of the subfamily Anophelinae are characterised by air sacks that allow these to float on the surface of the water (Figs 41, 42).

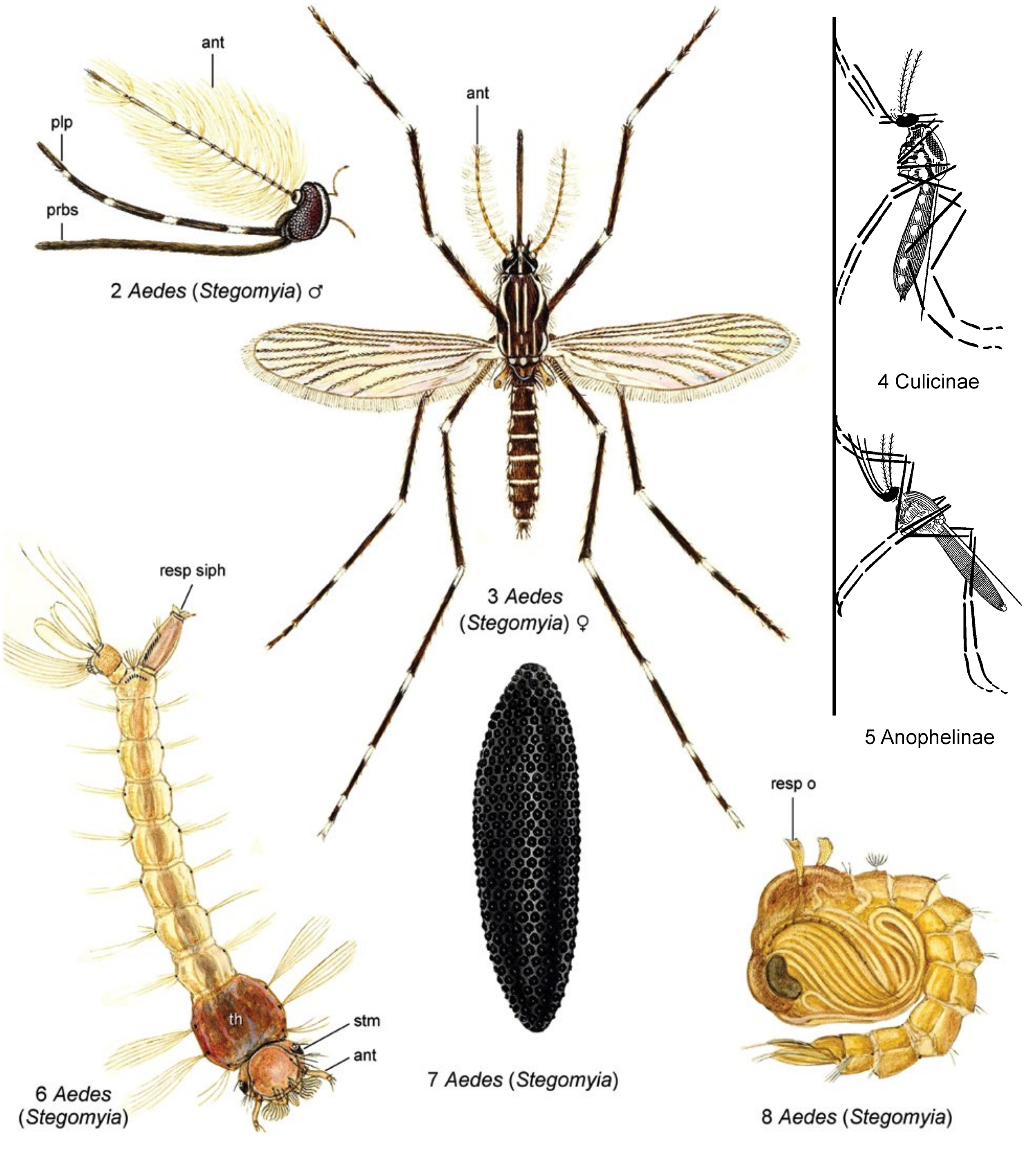
Mosquito larvae occur in a wide range of aquatic habitats, including temporary rainwater pools, artificial water containers, tree holes, crab holes, leaf axils, impoundments, swamps and slow-moving streams. They are mostly filter-feeders, feeding on algae, yeasts, bacteria, protozoans and other microorganisms, but some are predaceous. Larvae go through four moulting stages and development from first-instar larva to pupa may last from 7–30 days, depending on the species and on temperature. Larvae of *Anopheles* can be recognised by their feeding and breathing positions, lying parallel with the meniscus of the water (Fig. 44). Culicine larvae usually browse over the substratum in search of food and only come to the surface of the water to breathe through a respiratory siphon (Figs 6, 43). Species of the genera *Mansonia* and *Coquillettidia* Dyer have highly specialised siphons that pierce roots, or stems of aquatic vegetation, to obtain oxygen from air cells in the aerenchyma tissue of plants.

Pupae of all mosquitoes are comma-shaped (*e.g.*, Fig. 8) and are capable of brisk movement, using the paddles at the tip of the abdomen. They do not feed during this stage. They breathe through respiratory organs on the cephalothorax (Fig. 8), with pupae of *Mansonia* and *Coquillettidia* having modified trumpets for breathing through plant stems. The pupal stage usually lasts 2–3 days before adult eclosion.

Economic significance

Mosquitoes play an important role in the transmission of human and animal diseases, such as malaria, filariasis and various arboviruses (Jupp 1996: 4; Service 1980: 46). Hence, they are one of the best-studied families within the Diptera (see Chapter 6).

The most significant mosquito-borne disease is malaria. Parasites of the genus *Plasmodium* Marchiafava & Celli



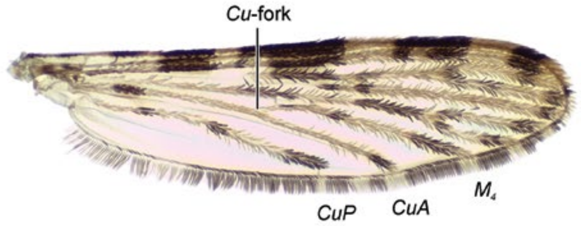
Figs 31.2–8. Life stages of *Aedes* (*Stegomyia*) *aegypti* L. and resting positions of adult Culicinae and Anophelinae (Culicidae): (2) head of adult *Ae. aegypti*, lateral view ♂; (3) same, habitus, dorsal view ♀; (4) Culicinae adult resting position, lateral view; (5) same, Anophelinae; (6) larva of *Ae. aegypti*, dorsal view; (7) same, egg, dorsal view; (8) same, pupa, lateral view. Figs 2–8 (after Coetzee *et al*. 2009, original paintings by N. Lighton).

Abbreviations: ant – antenna; plp – palpus; prbs – proboscis; resp o – respiratory organ; resp siph – respiratory siphon; stm – stemmata; th – thorax.

9 *Aedeomyia* (*Lepiothauma*)

10 *Aedes* (*Stegomyia*)

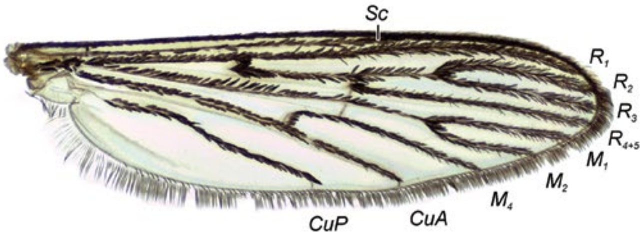
11 *Aedes* (*Mucidus*)



12 *Anopheles* (*Cellia*)

13 *Coquillettidia* (*Coquillettidia*)

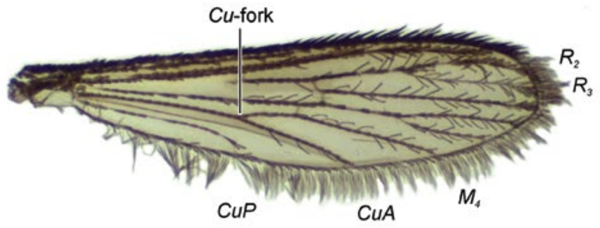
14 *Culex* (*Culex*)



15 *Culiseta* (*Allotheobaldia*)

16 *Eretmapodites*

17 *Ficalbia*



18 *Hodgesia*

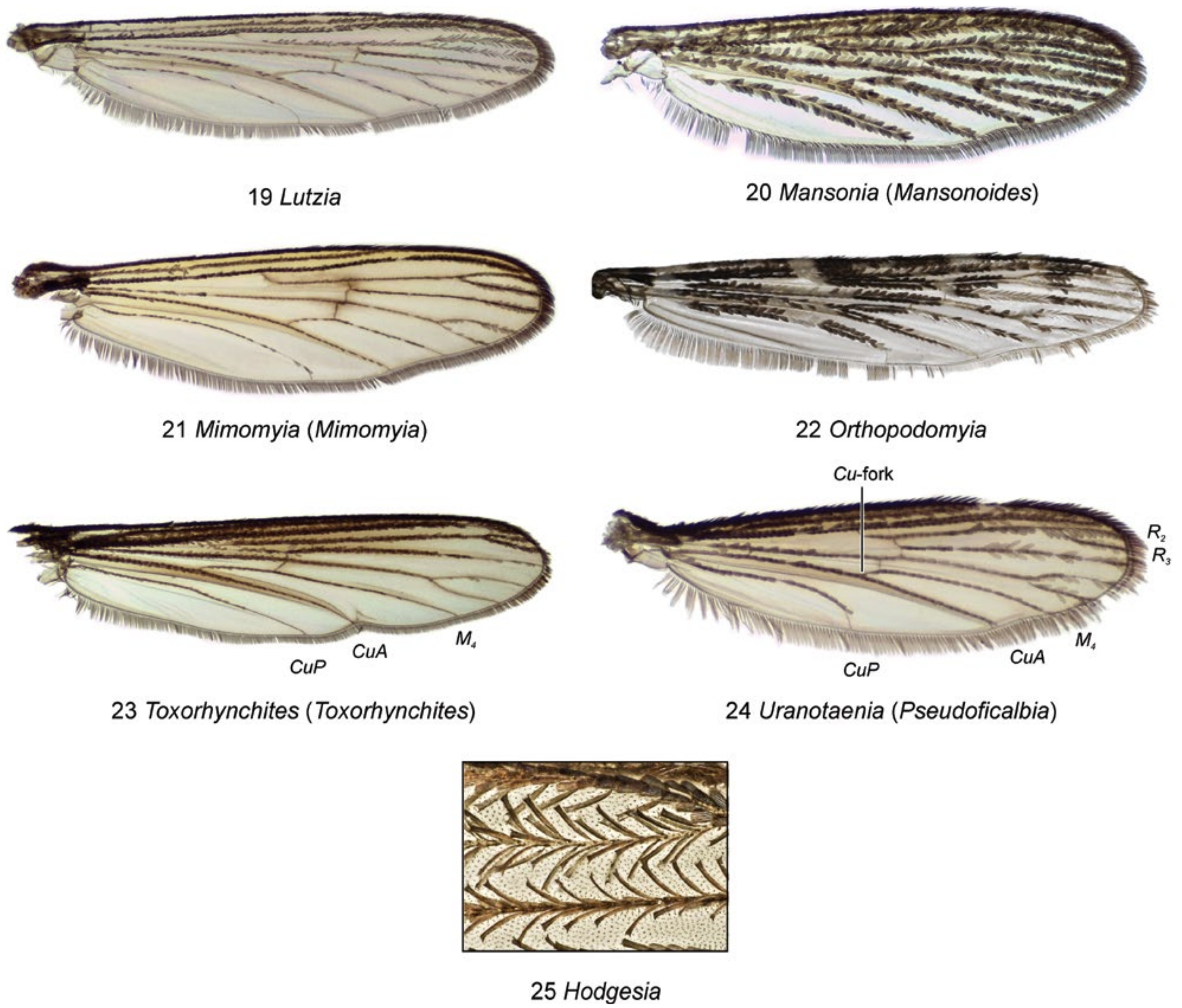
Figs 31.9–18. Wings of Culicidae (dorsal view): (9) *Aedeomyia* (*Lepiothauma*) *africana* Neveu-Lemaire; (10) *Aedes* (*Stegomyia*) *aegypti* (L.); (11) *Ae.* (*Mucidus*) *sudanensis* Edwards; (12) *Anopheles* (*Cellia*) *gambiae* Giles; (13) *Coquillettidia* (*Coquillettidia*) *aurites* (Theobald); (14) *Culex* (*Culex*) *annulioris* Theobald; (15) *Culiseta* (*Allotheobaldia*) *longiareolata* (Macquart); (16) *Eretmapodites chrysogaster* Graham; (17) *Ficalbia nigra* (Theobald); (18) *Hodgesia sanguinae* Theobald. Photographs A.H. Kirk-Spriggs.

Abbreviations: *CuA* – anterior branch of cubital vein; *Cu*-fork – cubital vein fork; *CuP* – posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

(Plasmodiidae) are transmitted to humans only by *Anopheles* mosquitoes, but other species of plasmodia that affect non-humans, *e.g.*, primates, birds and reptiles (Garnham 1966: 11), may be transmitted by culicine mosquitoes. In the Afrotropical Region, malaria remains the number one killer of pregnant women and children under five years of age (WHO 2015: x) and plays a major role in contributing to poverty in many African countries. In the Afrotropical Region malaria parasites are transmitted chiefly by species in the *An*. *gambiae* complex and the *An*. (*Cellia*) *funestus*-group, with other species playing minor roles in restricted parts of Central Africa (*e.g.*, *An*. (*Cellia*) *moucheti* Evans, 1925 and *An*. (*Cellia*) *nili* (Theobald, 1904)), coastal West Africa (*An*. (*Cellia*) *melas* (Theobald, 1903)) and East/southern Africa (*An*. (*Cellia*) *merus* Dönitz, 1902) (Sinka *et al*. 2010).

The causative agent of Bancroftian filariasis, commonly known as "elephantiasis", is a nematode transmitted by both anopheline (*An*. *gambiae* and *An*. *funestus* Giles, 1900) and culicine mosquitoes (*Culex* (*Culex*) *quinquefasciatus* Say, 1823), in the Afrotropical Region (Service 1980: 49).

At least 13 arboviruses have been isolated from Culicidae in the Afrotropical Region (Jupp 1996: 4), the common ones


19 *Lutzia*

20 *Mansonia* (*Mansonoides*)

21 *Mimomyia* (*Mimomyia*)

22 *Orthopodomyia*

23 *Toxorhynchites* (*Toxorhynchites*)

24 *Uranotaenia* (*Pseudoficalbia*)

25 *Hodgesia*

Figs 31.19–25. Wings of Culicidae (dorsal view): (19) *Lutzia tigripes* de Grandpré & de Charmoy; (20) *Mansonia* (*Mansonoides*) *africana* (Theobald); (21) *Mimomyia* (*Mimomyia*) *plumosa* (Theobald); (22) *Orthopodomyia fontenillei* Brunhes & Hervy; (23) *Toxorhynchites* (*Toxorhynchites*) *brevipalpis* Theobald; (24) *Uranotaenia* (*Pseudoficalbia*) *nivipous* Theobald; (25) detail of wing scales of *Hodgesia sanguinae* Theobald. Figs 19–21, 23, 24 (photographs A.H. Kirk-Spriggs).

Abbreviations: *CuA* – anterior branch of cubital vein; *Cu*-fork – cubital vein fork; *CuP* – posterior branch of cubital vein; M_4 – fourth branch of media; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius.

being yellow fever virus (*Aedes* (*Stegomyia*) *aegypti* L., 1762), West Nile and Sindbis (*Culex* (*Culex*) *univittatus* Theobald, 1901), chikungunya (*Aedes* (*Diceromyia*) *furcifer* (Edwards, 1913)) and Rift Valley fever (*Culex* (*Culex*) *theileri* Theobald, 1903).

Larvae of *Toxorhynchites* spp. and *Lutzia tigripes* (de Grandpré & de Charmoy, 1901) are predacious on other Culicidae larvae and have been investigated as possible agents for biological control of larvae of disease transmitting mosquitoes (Service 1990: 38). *Toxorhynchites* spp., in particular, were viewed as promising biological control agents, due to their preference for "container" habitats (used tyres, discarded tin cans, tree holes, *etc*.) and, therefore, a possible control measure for the yellow fever vector (*Ae. aegypti*). Unfortunately, they did not prove to be useful, due to their cannibalistic habits that included their siblings, and it was not possible to increase the *Toxorhynchites* population size sufficiently to ensure control of vector mosquitoes. *Bacillus thuringiensis* var. *israelensis* has proven to be the most effective bacterial agent for larval control.

Classification

Culicidae is classified in the Culicomorpha, assigned to the superfamily Culicoidea. Culicoidea comprises Dixidae, Corethrellidae, Chaoboridae and Culicidae (Wood & Borkent 1989: 1359) and this morphological classification is supported by the molecular analysis of Wiegmann *et al*. (2011), based on nuclear and mitochrondrial DNA analysis.

Harbach (2007) recently reviewed the classification and phylogeny of the family Culicidae based on analysis of morphological and molecular data. Up-to-date information can be obtained from two websites: the Walter Reed Biosystematics Unit (http://www.wrbu.org) and the Mosquito Taxonomic Inventory (http://mosquito-taxonomic-inventory.info/). The family Culicidae is currently classified into two subfamilies: Anophelinae and Culicinae (Harbach 2007; White 1980: 114). The Anophelinae are characterised by both sexes having the palpus almost as long as the proboscis (*e.g*., Fig. 26), in males clubbed apically (*e.g*., Fig. 27) and the scutellum evenly rounded or strap-like (*e.g*., Fig. 28). Culicinae females have the palpus less than half as long as the proboscis (*e.g*., Fig. 29) and the scutellum in both sexes usually trilobed (*e.g*., Figs 31, 35) (Jupp 1996: 7; Service 1990: 4).

Identification

Culicidae occur virtually worldwide, with over 3,600 valid species and sub-species currently recognised in 41 genera and 174 subgenera (Wilkerson *et al*. 2015). Only 22% of these occur in the Afrotropics, where there are more than 780 species of mosquitoes belonging to 16 genera (Harbach 2007, 2013; Walter Reed Biosystematics Unit: http://www.wrbu.org). Only one genus, *Eretmapodites* Theobald, is endemic to the Afrotropical Region (White 1980: 114).

There are currently three keys available for the identification of genera of adult Afrotropical Culicidae. Service (1990: 18) provided keys for all genera, Jupp (1996: 33) provided keys for the southern African Culicinae (excluding *Hodgesia* Theobald) and Huang (2001), provided pictorial keys for all genera, as well as subgenera of *Aedes*. The larval key provided below follows Coetzee (2003: 64), which was based on the early works of Hopkins (1952: 33) and Mattingly (1971: 21). The keys presented below include all major characteristics from all these publications.

Adult mosquitoes are usually transported live to the laboratory where they are induced to lay eggs. Egg batches are reared to fourth-instar, at which time larvae are isolated individually. The larval and pupal exuviae are mounted in a medium, such as ® Entellan (Merck) and accession codes given to link them to the emergent adult. All progeny from a single female would have one common identifier, with each sibling having its own unique accession code. In addition, where species complexes require molecular identification, a subsample of the progeny is stored on silica gel for polymerase chain reaction (PCR) assays. Mosquitoes can also be micro-pinned in the field for later double-mounting (see Chapter 2) but this is not appropriate for those belonging to species complexes.

Keys to genera of Afrotropical Culicidae

Adults

1. Palpus about as long as proboscis in both sexes (Fig. 26), in males swollen apically (Fig. 27); abdomen largely devoid of scales . . . . *Anopheles* Meigen

– Palpus of female short, at most ½ length of proboscis, in male often exceeding length of proboscis, not swollen apically; abdomen completely or largely clothed in dense, uniform covering of scales 2

2. Proboscis long and recurved (Fig. 29); scutellum with posterior margin evenly rounded with evenly distributed setae; posterior wing margin with small indentation near vein *CuA* (Fig. 23); very large mosquitoes (body length: 8–13 mm), with metallic green, blue, or violet abdomens (Fig. 1) . . . . *Toxorhynchites* Theobald

– Proboscis straight (*e.g*., Fig. 26) (except for *Malaya* (Fig. 30) which is upturned); scutellum with posterior margin usually trilobed (Fig. 35, setation omitted), with setae in 3 tufts on all lobes (*e.g*., Fig. 31); posterior wing margin without indentation near vein *CuA* (*e.g*., Figs 9–22, 24); smaller mosquitoes (body length: 2.5–10 mm), with at most silvery metallic scales on abdomen (*e.g*., Fig. 3) 3

3. Wing vein *CuP* ending about level with base of *Cu*-fork (*e.g.*, Figs 18, 24); upper calypter without fringe of scales (*e.g.*, Fig. 37); small-sized species (body length: 2.5–4.0 mm). 4

– Wing vein *CuP* ending well beyond base of *Cu*-fork (*e.g.*, Fig. 12); upper calypter wholly or partially with fringe of scales (*e.g.*, Fig. 38); medium-sized species (body length: 4.5–7.0 mm) 6

4. Wing veins R_2 and R_3 shorter than their stem vein (Fig. 24); abdomen without silvery markings. . . . . *Uranotaenia* Lynch Arribálzaga

– Wing veins R_2 and R_3 equal to or longer than their stem vein (*e.g.*, Fig. 18); abdomen black, with silvery markings 5

5. Proboscis setulose, upturned and distinctly swollen apically (Fig. 30); wing veins with outstanding scales lacking notches at apices . . . . *Malaya* Leicester

– Proboscis bare, straight, not swollen apically, except sometimes slightly so in male; wing veins with outstanding scales on distal ½ notched at apices (Figs 18, 25). . . . . *Hodgesia* Theobald

6. Antenna shorter than proboscis, segments short and thick; palpus short in both sexes; very scaly flies, with large tufts of sub-erect scales on apices of mid and hind femora (Fig. 34) . . . . *Aedeomyia* Theobald

– Antenna as long or longer than proboscis, slender, unmodified in both sexes; female palpus short, male palpus about as long as proboscis; not very scaly flies, without tufts of sub-erect scales on apices of mid and hind femora 7

7. Thoracic postspiracular setae present (*e.g.*, Fig. 33); female abdomen blunt, or pointed apically. 8

– Thoracic postspiracular setae absent (*e.g.*, Fig. 36); female abdomen blunt apically 10

8. Wing with dorsal membrane with mixed pale and dark, very broad scales (Fig. 20); tarsal claws of female simple, not toothed on fore and mid tarsomeres . . . . *Mansonia* Blanchard

– Wing with dorsal membrane without mixed pale and dark scales (*e.g.*, Figs 3, 10, 14, 16); tarsal claws of female usually toothed on fore and mid tarsomeres 9

9. Thorax partly or largely yellowish; occiput of head, thoracic pleura and posterior and lateral margins of abdominal terga, with broad, metallic silvery scales . . . . *Eretmapodites* Theobald

– Thorax dark; occiput of head, thoracic pleura and posterior and lateral margins of abdominal terga without broad metallic silvery scales. . . . . *Aedes* Meigen

10. Thoracic spiracular setae present (*e.g.*, Fig. 32). 11

– Thoracic spiracular setae absent. 12

11. Thoracic postspiracular and sub-spiracular scales present (Fig. 32) . . . . *Culiseta* Felt

– Thoracic postspiracular and sub-spiracular scales absent . . . .*Lutzia* Theobald

12. Both sexes with fore and mid tarsomeres 1 distinctly longer than remaining 4 tarsomeres combined; tarsomere 4 much shorter than tarsomere 5 . . . .*Orthopodomyia* Theobald

– Both sexes with fore and mid tarsomeres 1 equal to or shorter than remaining 4 tarsomeres combined; tarsomere 4 equal to or longer than tarsomere 5 in female, but often shorter in male. 13

13. Larger species (body length: 5.7–8.0 mm); integument and scales predominantly yellow or black, if black then scales on thoracic terga and legs with purple or black sheen . . . . *Coquillettidia* Dyer

– Smaller species (body length: 3–6 mm); integument and scales not yellow or black 14

14. Pulvilli present, pad-like (Figs 39, 40); hind tarsal claws very small and inconspicuous . . . .*Culex* L.

– Pulvilli absent; hind tarsal claws variable 15

15. Wing with alula fringed with narrow scales (Figs 17, 38) . . . . *Ficalbia* Theobald

- Wing with alula bare or with flat decumbent scales (Figs 21, 37) . . . . *Mimomyia* Theobald

Larvae (fourth-instar)

1. Respiratory siphon absent (*e.g.*, Fig. 44); seta 1 on most abdominal segments palmate (Fig. 45) . . . .*Anopheles* Meigen

– Respiratory siphon present (*e.g.*, Figs 6, 43); seta 1 on abdominal segments never palmate. 2

2. Abdominal segment 8 with large, lateral sclerotised plates (comb plates) (*e.g.*, Fig. 46) 3

– Abdominal segment 8 without large, lateral sclerotised plates (*e.g.*, Fig. 49) 6

3. Head with labral brushes comprised of *ca* 10 strong curved spines (Fig. 47); abdominal comb scales and siphon pecten spines absent (Fig. 46) . . . . *Toxorhynchites* Theobald

– Head with labral brushes unmodified, comprised of numerous very fine setae; abdominal comb scales present, set at margin of lateral sclerotised plate (*e.g.*, Fig. 48); siphon with pecten spines present, or absent 4

4. Abdominal segments 6–8 with large sclerotised dorsal plates; comb with 2, rarely more, rows of long slender scales distal on margin of sclerotised comb plate (Fig. 48). . . . . *Orthopodomyia* Theobald

– Abdominal segments 6–8 without large sclerotised dorsal plates; comb with single row of scales (*e.g.*, Fig. 49) 5

5. Antenna very large, greatly flattened, *ca* ¼ as wide as long (Fig. 50); respiratory siphon with pair of long, curved spines apically (Fig. 51). . . . . *Aedeomyia* Theobald

– Antenna neither large, nor flattened; respiratory siphon without pair of long, curved spines apically. . . . . *Uranotaenia* Lynch Arribálzaga

6. Head with labral brushes comprised of strong setae, edged on one side by sharp teeth for predation . . . . *Lutzia* Theobald

– Head with labral brushes unmodified, comprised of numerous fine setae 7

7. Head with all setation poorly-developed (*e.g.*, Figs 52, 53); respiratory siphon conical, with serrated saw-like processes towards apex (*e.g.*, Fig. 54) 8

– Head with setation well-developed (*e.g.*, Fig. 50) or poorly-developed, but with respiratory siphon tube-like, without serrated, saw-like processes towards apex 9

8. Antenna with portion beyond subapical setae flexible, about as long as basal portion (Fig. 53); abdominal comb formed of 4–10 sharp, pointed scales . . . . *Coquillettidia* Dyer

– Antenna with portion beyond subapical setae rigid, much shorter than basal portion (Fig. 52); abdominal comb formed of 2–3 blunt-ended scales (Fig. 55) . . . . *Mansonia* Blanchard

9. Respiratory siphon with dorsal or subdorsal row of 4 or 5 multiple-branched tufts of setae (Fig. 56) . . . . *Malaya* Leicester

– Respiratory siphon with at most 2 such multiple-branched tufts of setae of which one, if present, is subdorsal, the other lateral (*e.g.*, Fig. 57) 10

10. Respiratory siphon with more than 1 subventral tuft of setae (Fig. 57), usually numerous tufts present, but may be very small and inconspicuous, or consist of a single seta. *Culex* L.

– Respiratory siphon with only single subventral tuft of setae (*e.g.*, Fig. 58) 11

11. Respiratory siphon with seta 1 inserted well before ⅓ of length from base (*e.g.*, Fig. 58). 12

– Respiratory siphon with seta 1 inserted at least ⅓ of distance from base (*e.g.*, Fig. 49) 14

12. Abdominal comb forming patch of numerous small scales (Fig. 58) . . . . *Culiseta* Felt

– Abdominal comb forming single row of not more than *ca* 10 scales (*e.g.*, Fig. 49) 13

13. Head with frontoclypeal setae 5, 6 and 7 large, very conspicuous (Fig. 50) . . . . *Ficalbia* Theobald

– Head with frontoclypeal setae 5, 6 and 7 small and inconspicuous (as in Figs 52, 53). . . . . *Hodgesia* Theobald

14. Abdominal segment 10 with seta 3 at least 3-branched (Fig. 59). . . . . *Mimomyia* Theobald

– Abdominal segment 10 with seta 3 either 1-branched (*e.g.*, Fig. 49), or rarely, 2-branched (*e.g.*, Fig. 60) 15

15. Abdominal segment 10 with seta 4 with 4 1-branched, or 2-branched setae, the bases of which do not form barred areas (setae arising from individual alveoli) (Fig. 60); pecten reduced, with at most 4 spines (Fig. 60) . . . . *Eretmapodites* Theobald

– Abdominal segment 10 with seta 4 frequently with more than 4 2-branched setae, the bases of which invariably form conspicuous barred areas (setae arising from cuticular structures resembling bars); pecten with at least 8 spines (Fig. 49) . . . . *Aedes* Meigen

Synopsis of the fauna

***Aedeomyia* Theobald** (Culicinae: Aedeomyiini)**.** A genus of seven species occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions. Four species in two subgenera occur in the Afrotropical Region, that are readily distinguished from all other Culicinae, in having conspicuous tufts of suberect scales at the apices of the mid and hind femora (Fig. 34). Adult females feed mostly on avian blood in tree canopies, but have been recorded feeding on humans. Larvae are found in swamps, or abandoned borrow-pits, in association with living vegetation. See Fig. 9 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 64), Hopkins (1952: 73) and Service (1990: 78).

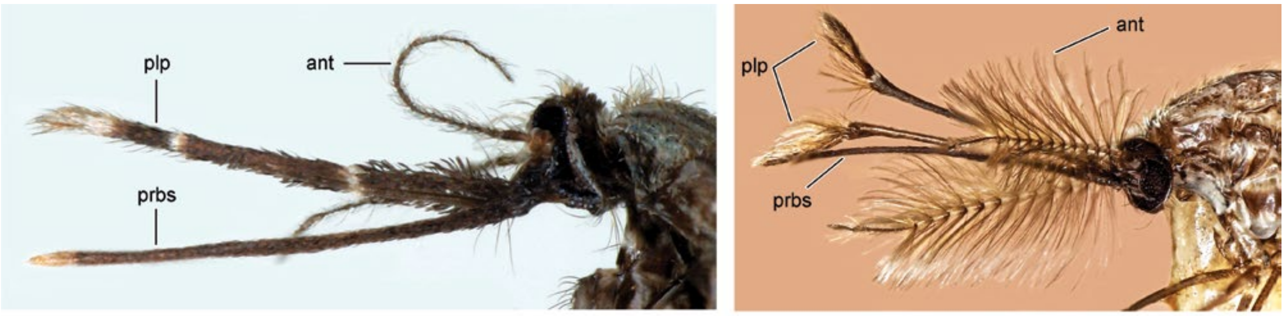
***Aedes* Meigen** (Culicinae: Aedini)**.** A genus of at least 965 species in 71 subgenera occurring in all zoogeographical regions, except Antarctica, but best represented in the Old World and Nearctic Region (Wilkerson *et al.* 2015). In the Afrotropical Region, 19 subgenera with *ca* 230 species are currently recognised. The genus belongs to the tribe Aedini with extensive revisions proposed in recent times (Reinert 2000; Reinert *et al.* 2004, 2006, 2008, 2009; Wilkerson *et al*. 2015). The genus *Aedes* was split into 74 genera by Reinert and co-workers, mostly based on quantitative cladistic analyses (see Reinert *et al.* 2009). While Wilkerson *et al*. (2015) do not challenge the phylogenetic hypotheses generated by these analyses, they point out that the identification of the new genera can only be achieved by combinations of characters states and not by simple, consistent diagnostic characters. This, together with a desire to retain stability and utility in the classification of the Aedini, led them to assign all aedine genera proposed between 2000 and 2009 to subgenera of *Aedes*, and all new subgenera to informal species-groups. The keys presented above treat *Aedes* as a single genus, inclusive of all subgeneric ranks, in line with the recommendations of Wilkerson *et al.* (2015). Incomplete keys to the subgenera of adult mosquitoes can be found in Huang (2001) and Jupp (1996: 36). The tribe Aedini contains several species of medical importance, including the efficient urban yellow fever virus vector *Ae. aegypti*. Many species are vectors of filarial parasites and various arboviruses. Larval habitats are usually temporary water bodies, as eggs rely on direct rainfall or river flooding to hatch, many being tree hole or container breeders. Larvae are primarily bottom-feeders and browse over mud or debris. Some species have predatory larvae and others can tolerate high salinities. Eggs are also able to withstand desiccation, sometimes for years between rains. See Figs 10, 11 for examples of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 106) and Hopkins (1952: 116).

***Anopheles* Meigen** (Anophelinae: Anophelini)**.** A genus of over 485 species occurring in all zoogeographical regions, except Antarctica, with over 130 recorded in three subgenera from the Afrotropical Region (Harbach 2015). *Anopheles* is the only genus of the subfamily Anophelinae present in the Afrotropics. It spans the entire continent (Sinka *et al*. 2010) and includes vectors of malarial and filarial parasites and the arbovirus known as *o'nyong nyong* (Gillies & Coetzee 1987: 2; Gillies & de Meillon 1968: 5; Service 2012: 67). Three subgenera, *Anopheles sensu stricto*, *An*. (*Cellia* Theobald) and *An.* (*Christya* Theobald) (Harbach & Kitching 2016), occur across the Afrotropics, with medically important species being largely confined to the subgenus *An*. (*Cellia*). Afrotropical species have been extensively studied for over 100 years and descriptions of species can be found in the monographic publications of de Meillon (1947), Evans (1938), Gillies & Coetzee (1987) and Gillies & de Meillon (1968). The occurrence of species-complexes is, however, a well-known phenomenon within *Anopheles* that complicates the taxonomy and systematics of the genus (Coetzee & Koekemoer 2013; Hunt & Coetzee 1995: 90). These are species that are morphologically indistinguishable, but can be identified on chromosomal or molecular characteristics, and may exhibit clear behavioural differences, although this is not always the case (Coetzee *et al*. 2013). While the current list of valid named species of *Anopheles* in the Afrotropics stands at 134 (Harbach 2015), many genetically recognised species await formal description and naming (Coetzee *et al*. 2013; Cohuet *et al*. 2003; Spillings *et al*. 2009) and many more await discovery. Adult *Anopheles* mosquitoes are easily recognised by their resting position on vertical surfaces, with the abdomen held at an angle of 45° (Fig. 5). Larval habitats range from high-salinity waters on coastal planes, to freshwater streams, mineral springs, temporary rain pools and puddles created by animal spoor around water bodies. Larvae of all but two species possess well-developed abdominal palmate setae that enable them to maintain the characteristic horizontal position in the water. See Fig. 12 for an example of the wing of the genus. A pictorial identification key to Afrotropical species was provided by Gillies & Coetzee (1987: 12).

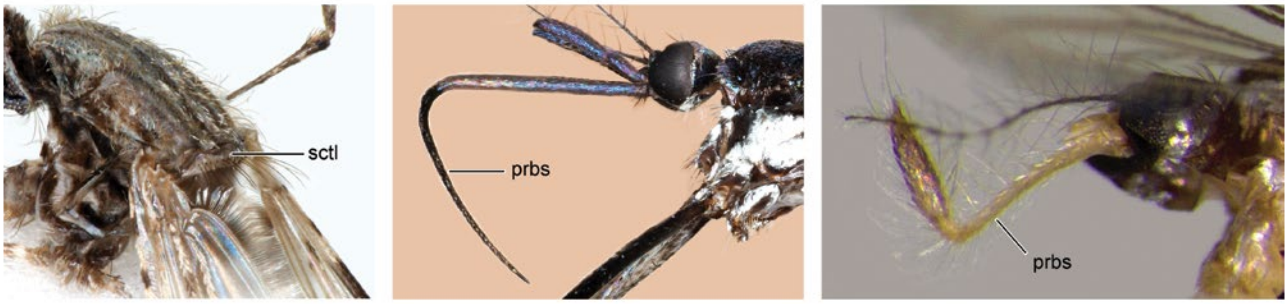
***Coquillettidia* Dyer** (Culicinae: Mansoniini)**.** A genus of 57 species, occurring in all zoogeographical regions, except Antarctica, with 22 species recorded from the Afrotropics, most of which feed on avian blood. Larvae and pupae require aquatic vegetation for development, such as *Pistia* (Araceae), or *Salvinia* (Salviniaceae), either rooted or floating in swamps and marshes. They remain attached to plant stems and are very rarely collected in nets or scoops. They only leave these plants during moulting and upon eclosion. See Fig. 13 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 88), Hopkins (1952: 103) and Service (1990: 135).

***Culex* L.** (Culicinae: Culicini)**.** A large genus of 763 species, occurring in all zoogeographical regions, except Antarctica, with 136 species in eight subgenera recorded from the Afrotropics. The genus contains efficient vectors of filarial parasites and numerous arboviruses affecting humans and livestock. The genus also contains vectors of avian malaria parasites. Adults feed on a wide range of avian, mammalian and reptilian blood, but relatively few feed on humans. *Culex* larvae breed in a wide variety of aquatic habitats, from natural pools, to pit latrines and blocked drains. See Fig. 14 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 242) and Hopkins (1952: 246).

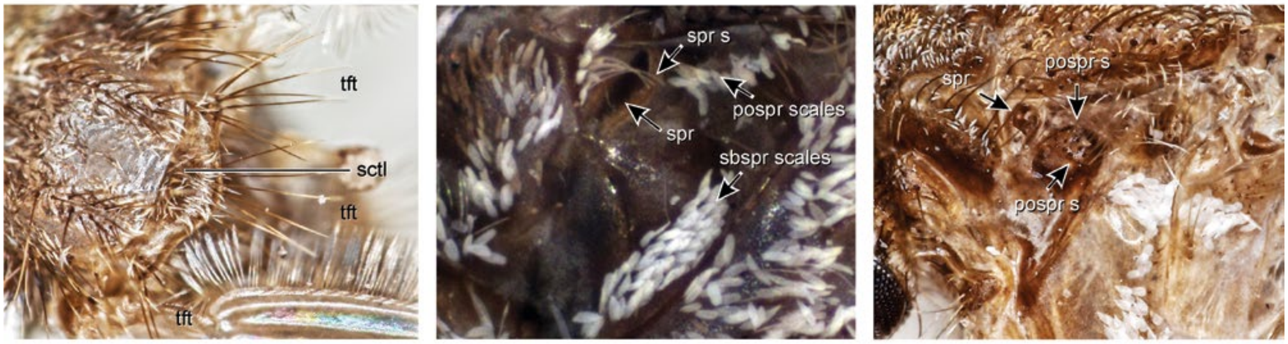
***Culiseta* Felt** (Culicinae: Culisetini)**.** A genus of 37 species occurring in all zoogeographical regions, except the Neotropics and Antarctica. Only two widely distributed species are known to occur in the Afrotropics, each in its own subgenus (one of which is endemic to the Region). Adults are known to feed on avian blood and on humans, but are of no known



26 *Anopheles* (*Cellia*) ♀ 27 *Anopheles* (*Cellia*) ♂



28 *Anopheles* (*Cellia*) 29 *Toxorhynchites* (*Toxorhynchites*) 30 *Malaya*

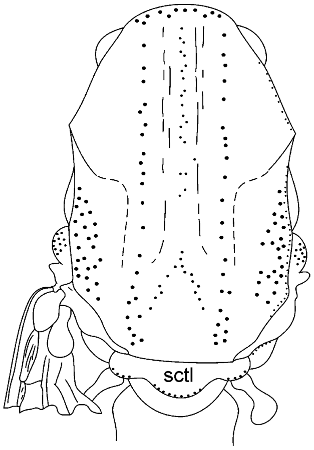


31 *Culex* (*Culex*) 32 *Culiseta* (*Allotheobaldia*) 33 *Mansonia* (*Mansonoides*)

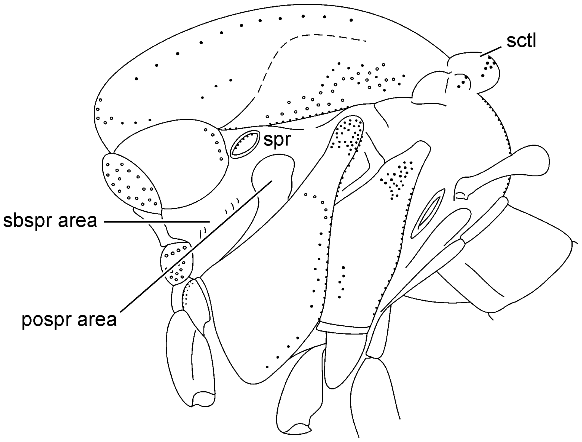
34 *Aedomyia* (*Lepiothauma*)

Figs 31.26–34. Head, thoraces and leg characters of Culicidae: (26) head, proboscis and palpus of *Anopheles* (*Cellia*) *gambiae* Giles (Anophelinae), lateral view ♀; (27) same, head and palpus ♂; (28) same, scutellum, dorsolateral view; (29) head and proboscis of *Toxorhynchites* (*Toxorhynchites*) *brevipalpis* Theobald, lateral view ♀; (30) same, *Malaya taeniarostris* Theobald; (31) scutellum of *Culex* (*Culex*) *quinquefasciatus* Say (Culicinae), dorsal view; (32) thorax of *Culiseta* (*Allotheobaldia*) *longiareolata* (Macquart), lateral view; (33) same, *Mansonia* (*Mansonoides*) *africana* (Theobald); (34) legs of *Aedeomyia* (*Lepiothauma*) *furfurea* (Enderlein), lateral view.

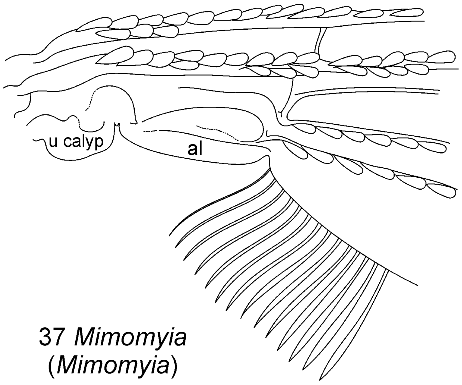
Abbreviations: ant – antenna; plp – palpus; pospr s – postspiracular setae; pospr scales – postspiracular scales; prbs – proboscis; sbspr scales – subspiracular scales; sctl – scutellum; spir s – spiracular seta; spr – spiracle; tft – tuft.



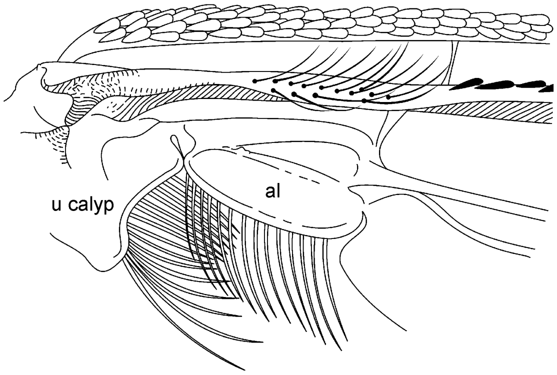
35 Culicinae



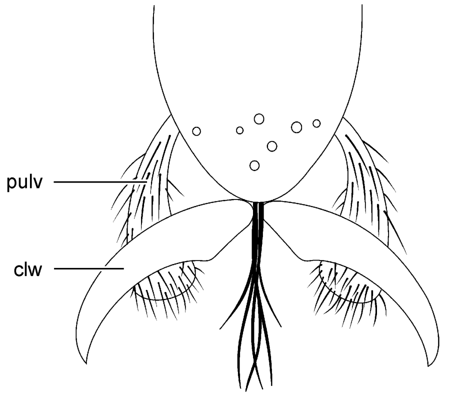
36 Culicinae

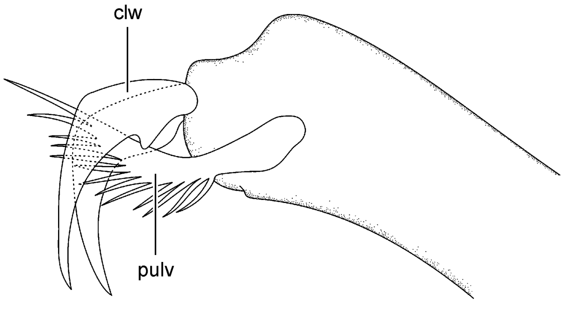


37 *Mimomyia* (*Mimomyia*)



38 *Ficalbia*





40 *Culex* (*Culex*)

39 *Culex* (*Culex*)

Figs 31.35–40. Thorax, wing and leg characters of Culicidae: (35) thorax of Culicinae, dorsal view (major setation omitted); (36) same, lateral view; (37) base of wing of *Mimomyia* (*Mimomyia*) *hispida* Theobald, dorsal view; (38) same, *Ficalbia circumtestacea* Theobald; (39) pulvilli of *Culex* (*Culex*) *pipiens* L., dorsal view; (40) same, lateral view. Figs 35–39 (after Edwards 1941, figs 1a, 1b, 4b, 4d, 3c, respectively).

Abbreviations: al – alula; clw – claw; pospr area – postspiracular area; pulv – pulvillus; sbspr area – sub-spiracular area; sctl – scutellum; spr – spiracle; u calyp – upper calypter.

medical importance. Larvae have been found in pools, barrels and cattle dips and indigenous species are restricted to tree holes. See Fig. 15 for an example of the wing of the genus. An identification key to Afrotropical species was provided by Service (1990: 82).

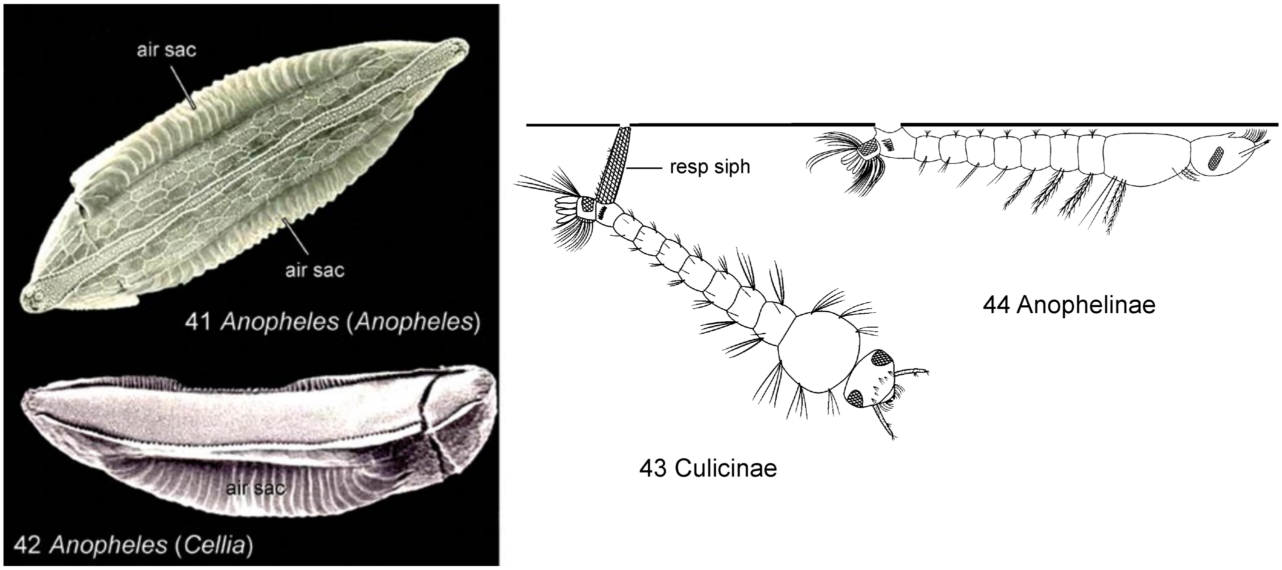
Eretmapodites **Theobald** (Culicinae: Aedini)**.** An endemic genus of 48 known species; larvae of only 20 species are known. Adults have unique ornamentation of black abdominal terga, with metallic silvery scales and sterna mainly covered with golden yellowish scales. Adult females can be collected feeding on humans, particularly in shaded forests, banana and other plantations. A few arboviruses have been isolated from *Eretmapodites* spp. and some species have been infected with Rift Valley and yellow fever viruses in the laboratory, but have not been shown to be vectors in nature. Larvae occur in small collections of water in fallen leaves, discarded tins, snails' shells, plant-axils and rarely tree holes. Some species have larvae that are predatory on other culicid larvae. See Fig. 16 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 224), Hopkins (1952: 226) and Service (1990: 157).

Ficalbia **Theobald** (Culicinae: Ficalbiini)**.** A genus of eight species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions, with four widely distributed species recorded in the Afrotropics. Females do not feed on humans, but are sometimes collected in biting catches and light traps. Larvae are found in clear, stagnant water with vegetation, swamp margins and ditches. See Fig. 17 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 73) and Service (1990: 97).

Hodgesia **Theobald** (Culicinae: Hodgesiini)**.** A genus of 11 species, occurring in the Afrotropics and tropical parts of the Australasian and Oriental Regions, with four species recorded from the Afrotropics, mostly from Central and West Africa. Two species have been recorded from Uganda, but not from other East African countries. Adults are distinguished from all other culicids, in having wing scales notched at the tips. Females take blood meals, but little else is known regarding their biology, except that one species can be a persistent and irritating biter of humans. Larvae occur in swampy areas. See Figs 18, 25 for examples of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 37), Hopkins (1952: 85) and Service (1990: 36).

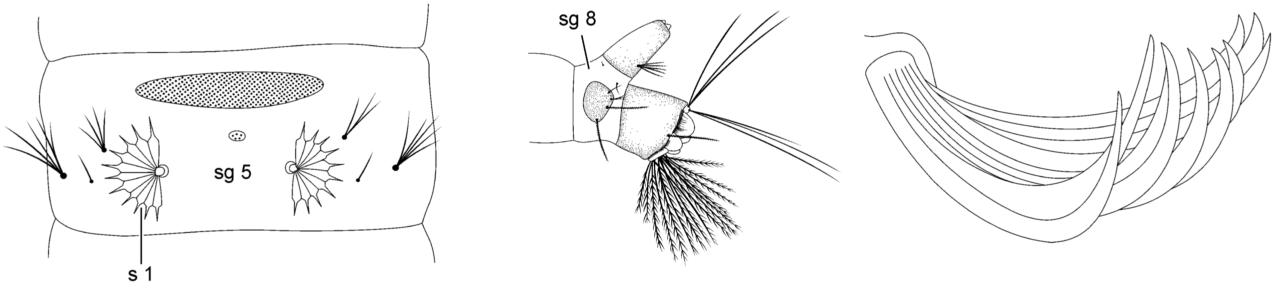
Lutzia **Theobald** (Culicinae: Culicini)**.** A genus of seven species, occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions, previously regarded as a subgenus of *Culex*. Only one species, *Lt. tigripes*, occurs in the Afrotropics, which has predatory larvae, occurring in tree holes and artificial containers. Adult females are blood-feeders and are quite common in many parts of the region. See Fig. 19 for an example of the wing of the genus. A description of *Lt. tigripes* was provided by Edwards (1941: 246) and Jupp (1996: 106).

Malaya **Leicester** (Culicinae: Sabethini)**.** A genus of 12 species, occurring in the Afrotropical, Australasian and Oriental Regions, with only six species recorded from the Afrotropics. *Malaya* is distinguished from all other culicids by the jointed and distally swollen proboscis (Fig. 30). As with *Toxorhynchites* (see below), females do not take blood meals and are peculiarly adapted to feeding on food produced by "cocktail" ants, *Crematogaster* spp. (Hymenoptera: Formicidae), that occur mainly on trees. The specialised proboscis is inserted into the



Figs 31.41–44. Stereoscan micrographs of eggs and line drawings of larval Culicidae resting positions: (41) egg of *Anopheles* (*Anopheles*) *coustani* Laveran, dorsal view; (42) same, *An.* (*Cellia*) *gambiae* Giles; (43) resting position at waters' surface of Culicinae; (44) same, Anophelinae. Figs 43, 44 (after Coetzee 2003, fig. 4.3).

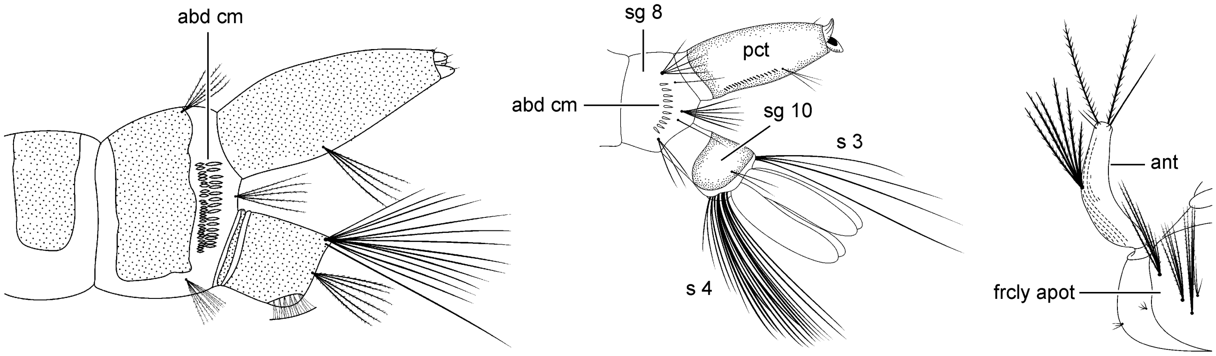
Abbreviation: resp siph – respiratory siphon.



45 *Anopheles* (*Cellia*)

46 *Toxorhynchites* (*Toxorhynchites*)

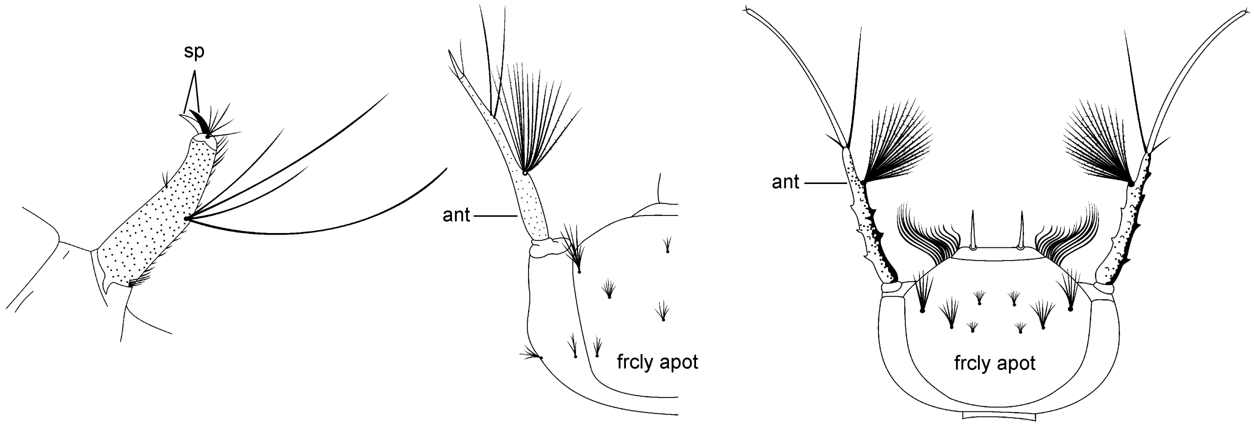
47 *Toxorhynchites* (*Toxorhynchites*)



48 *Orthopodomyia*

49 *Aedes* (*Stegomyia*)

50 *Aedeomyia* (*Lepiothauma*)



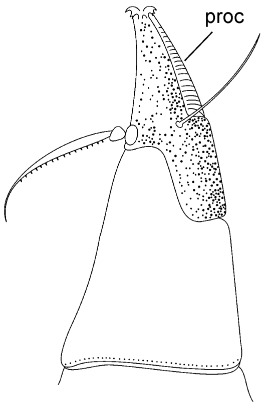
51 *Aedeomyia* (*Lepiothauma*)

52 *Mansonia* (*Mansonoides*)

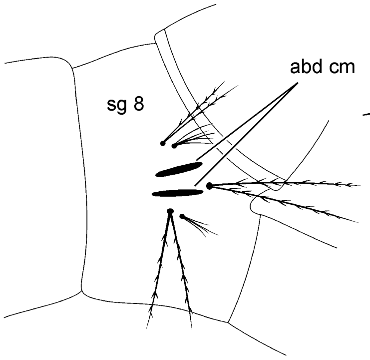
53 *Coquillettidia* (*Coquillettidia*)

Figs 31.45–53. Larval characters of Culicidae: (45) abdominal segment 5 of *Anopheles* (*Cellia*) sp. (Anophelinae), dorsal view; (46) terminal abdominal segments of *Toxorhynchites* (*Toxorhynchites*) sp. (Culicinae), lateral view; (47) same, labral brushes, lateral view; (48) terminal abdominal segments of *Orthopodomyia arboricollis* Theobald, lateral view; (49) same, *Aedes* (*Stegomyia*) sp., lateral view; (50) head of *Aedeomyia* (*Lepiothauma*) sp., dorsal view; (51) same, respiratory siphon, lateral view; (52) head of *Mansonia* (*Mansonoides*) sp., dorsal view; (53) same, *Coquillettidia* (*Coquillettidia*) sp. Figs 45–47, 50–53 (after Coetzee 2003, figs 4.6A–F, H), Fig. 48 (after Service 1990, fig. 149), Fig. 49 (after Coetzee 2003, fig. 4.7G).

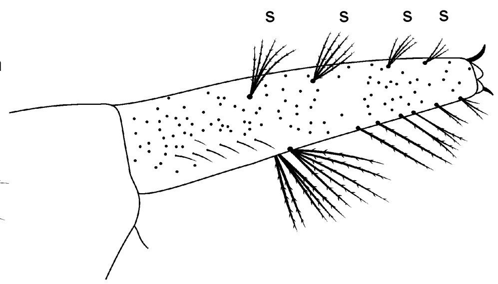
Abbreviations: abd cm – abdominal comb; ant – antenna; frcly apot – frontoclypeal apotome; pct – pectin; s – seta; sg – segment; sp – spine.



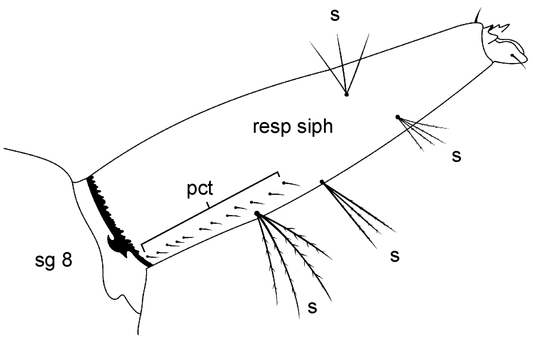
54 *Coquillettidia* (*Coquillettidia*)



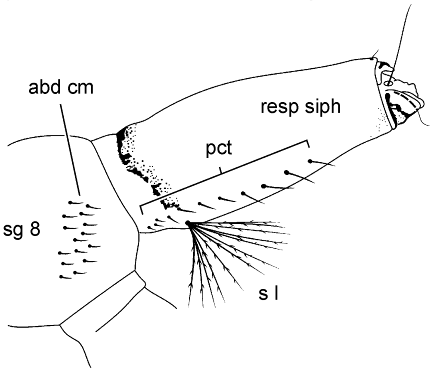
55 *Mansonia* (*Mansonoides*)



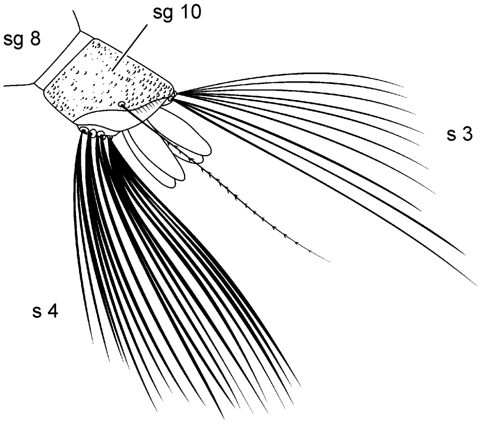
56 *Malaya*



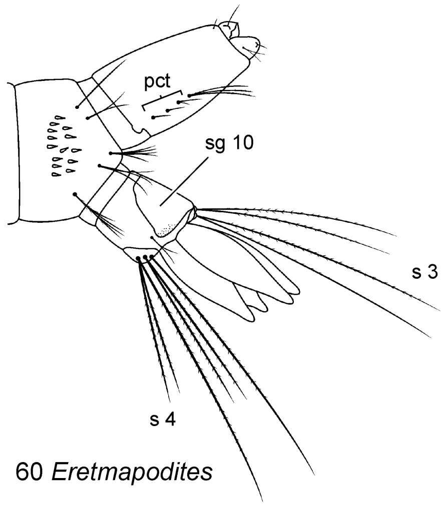
57 *Culex* (*Culex*)



58 *Culiseta* (*Allotheobaldia*)



59 *Mimomyia* (*Mimomyia*)



60 *Eretmapodites*

Figs 31.54–60. Larval characters of Culicidae (lateral views): (54) respiratory siphon of *Coquillettidia* (*Coquillettidia*) sp.; (55) abdominal segment 8 of *Mansonia* (*Mansonoides*) sp.; (56) respiratory siphon of *Malaya* sp.; (57) same, *Culex* (*Culex*) sp.; (58) same, *Culiseta* (*Allotheobaldia*) sp.; (59) abdominal segment 10 of *Mimomyia* (*Mimomyia*) sp.; (60) terminal abdominal segments of *Eretmapodites* sp. Fig. 54 (after Coetzee 2003, fig. 4.6G), Figs 55–60 (after Coetzee 2003, figs 4.7A–F).

Abbreviations: abd cm – abdominal comb; pct – pectin; proc – process; resp siph – respiratory siphon; s – seta; sg – segment.

ants' mouthparts and sucks up honeydew, which ants obtain from plant bugs. When not in use, the jointed proboscis is folded backwards beneath the body, a highly unusual condition in culicids. The larvae are known for only three of the six Afrotropical species, which have been found breeding in plant axils. An identification key to Afrotropical species was provided by Service (1990: 31).

***Mansonia* Blanchard** (Culicinae: Mansoniini)**.** A genus of 23 species, occurring in all zoogeographical regions, except Antarctica, with two species recorded from the Afrotropics. Both are important vectors of several arboviruses. Although they are not vectors of human filarial parasites they do, however, transmit filaria affecting cats, dogs and cattle. Larval habits are the same as those of *Coquillettidia* (see above). See Fig. 20 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 88), Hopkins (1952: 103) and Service (1990: 135).

***Mimomyia* Theobald** (Culicinae: Ficalbiini)**.** A genus of 44 species, occurring in the Afrotropical, Australasian and Oriental Regions, with 30 species, in three subgenera, recorded from the Afrotropics. One subgenus, *Mi*. (*Ingramia* Edwards), is known only from the Indian Ocean island states of Comoros and Madagascar. Little is known regarding adult biology, but species are rarely collected biting humans. Larval habitats are the same as for *Ficalbia* (see above), but *Mi*. (*Ingramia*) spp. prefer tree holes, leaf axils and pitchers of pitcher plants. See Fig. 21 for an example of the wing of the genus. An identification key to Afrotropical species was provided by Service (1990: 101).

***Orthopodomyia* Theobald** (Culicinae: Orthopodomyiini)**.** A genus of 38 species, occurring in the Afrotropical, Neotropical and Oriental Regions, with 14 widely distributed species recorded from the Afrotropics. Very little is known regarding their biology, but none of the Afrotropical species have been recorded as feeding on humans. Larvae occur mainly in tree holes. See Fig. 22 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 71) and Service (1990: 86).

***Toxorhynchites* Theobald** (Culicinae: Toxorhynchitini)**.** A relatively large genus of 88 species, occurring in the tropical parts of the Afrotropical, Australasian, Neotropical and Oriental Regions, with 28 species in two subgenera recorded from the Afrotropics. They are the largest known mosquitoes in the world and adults are highly ornamental (Fig. 1), possessing iridescent blue, green, or purple scaling, with large yellow or white tufts of scales at the apex of the abdomen. Adult females feed on nectar, or fruit juices, and as they do not possess piercing mouthparts (Fig. 29), cannot suck blood and are, therefore, of no medical importance. Larvae prey on the larvae of other culicids and have been investigated as a means of biological control in some parts of the world, but without great success, due to their cannibalistic habits. Larvae occur mainly in "container habitats", such as tree holes, bamboo stumps, discarded tins and tyres, which are not the preferred habitats of most of the medically important culicid species. See Fig. 23 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 23), Hopkins (1952: 36) and Service (1990: 23).

***Uranotaenia* Lynch Arribálzaga** (Culicinae: Uranotaeniini)**.** A relatively large genus of 265 species, occurring in all zoogeographical regions, except Antarctica, with 114 species in two subgenera recorded from the Afrotropics. Adult females feed on avian, mammalian and reptilian blood, but are not implicated in disease transmission. Larvae possess a relatively short respiratory siphon and so adopt an almost horizontal position at the waters' surface somewhat resembling *Anopheles* larvae and this may cause confusion between these two genera. Larval habitats range from tree holes and leaf axils, to shaded pools and swamps with vegetation. See Fig. 24 for an example of the wing of the genus. Identification keys to Afrotropical species were provided by Edwards (1941: 41), Hopkins (1952: 51) and Service (1990: 41).

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SIMULIIDAE 32

(Blackflies)

Ferdinand C. de Moor

Fig. 32.1. Female of *Simulium* (*Nevermannia*) *nigritarse* Coquillett (South Africa) (photograph © S.A. Marshall).

Diagnosis

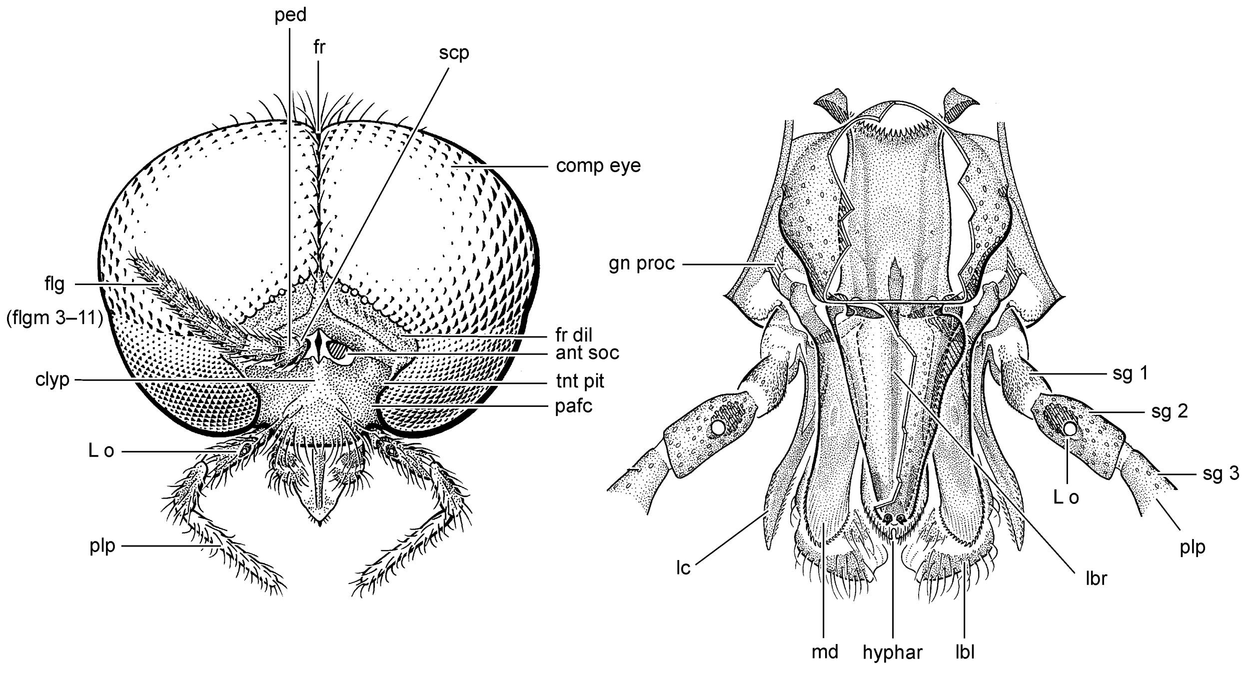
Small (wing length: 1.5–6.0 mm), compact, humpbacked nematocerous flies, with short antennae and characteristic wing venation (Fig. 1).

Head of female dichoptic, compound eyes (Fig. 1) with uniformly sized ommatidial facets (Fig. 1); male head holoptic (Figs 2, 9, 10), eyes with large dorsal facets and smaller ventral facets (Fig. 2); eyes apilose in both sexes (*e.g.*, Fig. 2); antenna short and thick (Figs 1, 2, 4, 5–8), forwardly directed, dorsal across front of eyes; scape and pedicel more bulbous than flagellum with 9 flagellomeres (Fig. 2), more compacted subcylindrical in females, more elongated subcylindrical in males; hypognathous head with downwardly-projecting short, cylindrical proboscis, formed by stylets or syntrophium (paired mandibles and lacinia of maxillae, labrum and hypopharynx) and labium which forms back of proboscis and is composed of divided premental plate and pair of fleshy lobe-like labella (Fig. 3); palpus considerably longer than proboscis (Fig. 4), with terminal segment usually much longer than preceding two segments (Fig. 2); females in blood-feeding species (Fig. 3) with toothed lacinia and mandibles (not toothed in males and non-biting females).

Thorax short and high, comprised mostly of mesothorax to accommodate flight muscles (Fig. 4); pronotum formed by pair of dorsolateral pronotal lobes, connected by narrow transverse

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 693–728.

strip, hidden beneath anterior mesonotal margin; lateral propleura extending ventrally to coxal attachments of fore legs; mesonotum dorsally comprised of scutum (Fig. 4), with pair of anterior, dorsolateral processes and bluntly-triangular scutellum, separated from scutum by transverse suture; katepisternum (Fig. 4) swollen (in lateral view) to accommodate vertical flight muscles, bounded by katepisternal sulcus; pleural membrane (Fig. 4) soft and membranous situated below scutum and in front of wing base (diagnostically broader and more distinct in Simuliidae than in almost any other dipteran family), usually bare, but in some species setulose; postnotum (Fig. 4) smooth convex or roof-like, sloping downward from scutellum to base of abdomen. Wing (Fig. 4) short and broad, with well-developed anal lobe; veins *C*, *Sc*, R_1, *Rs* and *M* fully-formed, open, tubular veins, veins M_1, M_2, M_4, *CuA*, *CuP* and A_1 only raised arches on wing membrane; false vein (submedian fold) situated between veins M_2 and M_4, arising near base of M_4 and forked at *ca* ⅔ distance from origin; humeral crossvein (*h*), situated proximally between costal (*C*) and subcostal veins (*Sc*) (Fig. 4); *r–m* crossvein formed of minute connection between veins *Rs* and *M*, where the latter deflects posteriorly before branching (Fig. 4); basal medial cell (*bm*) present in *Paracnephia* Rubtsov at origin of median and cubital veins (absent in *Simulium* Latreille) (as in Figs 11, 12); socketed setulae and spinules, or only socketed setulae, present on all tubular veins, except vein *M*, sometimes lacking on veins *Sc* and *R*, these situated either on dorsal or ventral surface of tubular veins, dependant on whether veins form ridges (*i.e.*, have a positive-upper veins *C*, *R* and R_1) or valleys (*i.e.*, negative-lower veins *Sc* and *Rs*) projecting above and below plane of wing; halter at same horizontal level, immediately behind wing, on metathorax (Fig. 4). Legs short and stout, subequal to body length (Figs 1, 4); coxae, trochanters and femora similar on all legs; tibiae slightly dilated towards distal end before narrowing apically (Figs 4, 23–29); basitarsus (tarsomere 1) the longest, equalling or exceeding length of other four tarsomeres forming eutarsus (Figs 4, 23–29); tarsomere 4 heart-shaped, bearing pad of water repellent setulae on underside; tarsomere 5 bearing pair of terminal tarsal claws; tarsi of fore legs and tarsomere 1 of hind leg varying in size and shape in different species (offering useful specific diagnostic features); flange-like lobe (calcipala) (*e.g.*, Figs 4, 20), extending terminally from inner side of hind tarsomere 1 and depression (pedisulcus) (*e.g.*, Figs 4, 20, 21), forming proximal narrowing of tarsomere 2 (shape, size and presence or absence of calcipala and pedisulcus important diagnostic features); claws distally with minute setiform empodium between; claws similar in structure on all legs (Fig. 4), but females exhibit diagnostic specialisation, sometimes bifid, or else with variously-shaped teeth and more curved talon-like appearance, than observed in males (Figs 23–29); male claws overarched by large umbrella-like grapple, varying in shape and structure in different species.



2 *Simulium* ♂

3 *Simulium*

Figs 32.2–3. Head and mouthparts of Simuliidae: (2) head of *Simulium* (*S.*) *decorum* Walker, frontal view (non-Afrotropical) ♂; (3) mouthparts of *Simulium* (*Psilozia*) *vittatum* Zetterstedt, frontal view (non-Afrotropical). Figs 2, 3 (Peterson 1981, figs 3, 8).

Abbreviations: ant soc – antennal socket; clyp – clypeus; comp eye – compound eye; flg – flagellum; flgm – flagellomeres; fr – frons; fr dil – frontal dilation; gn proc – genal process; hyphar – hypopharynx; L o – Lutz's organ; lbl – labellum; lbr – labrum; lc – lacinia; md – mandible; pafc – parafacial; ped – pedicel; plp – palpus; scp – scape; sg – segment; tnt pit – tentorial pit.

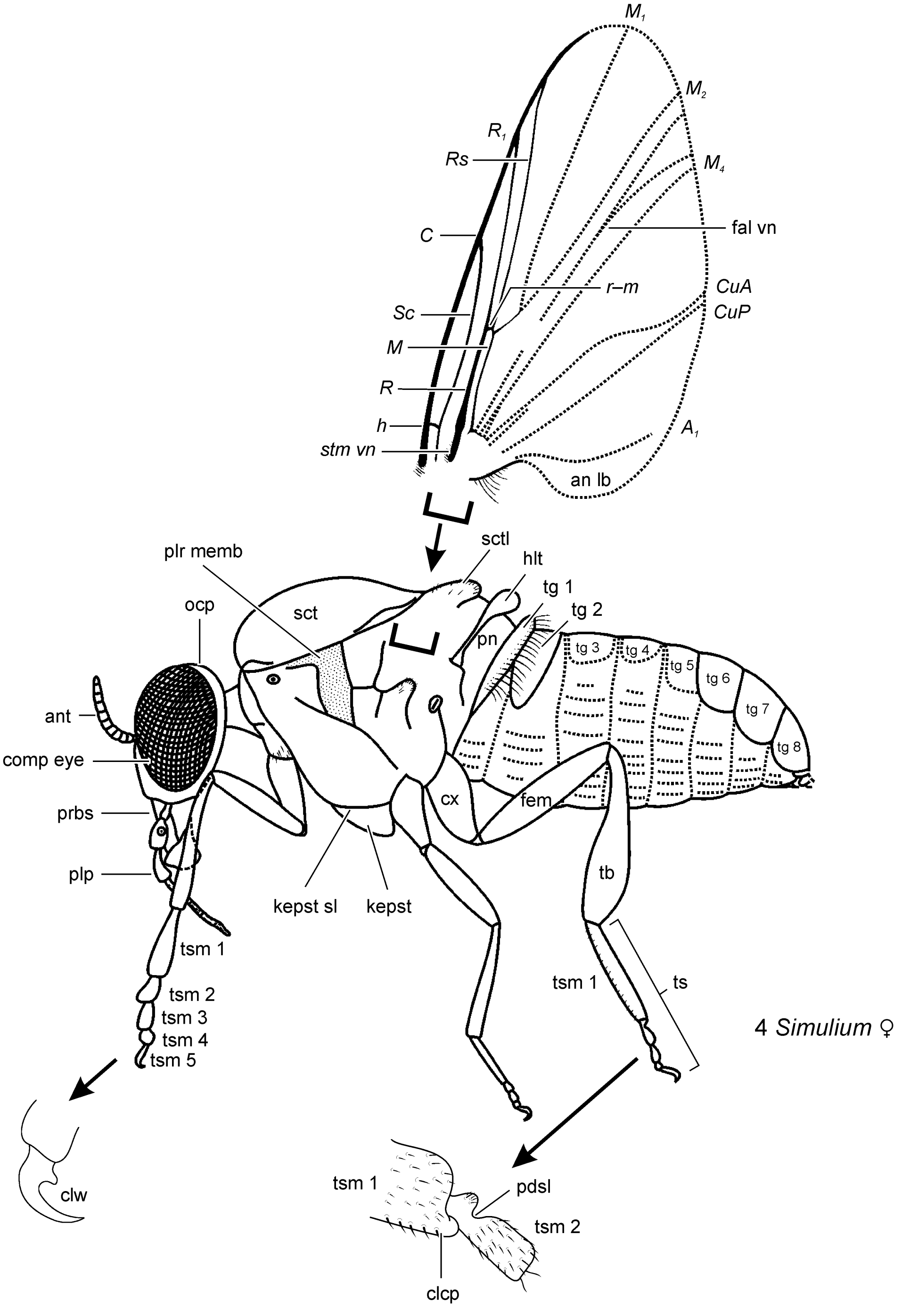
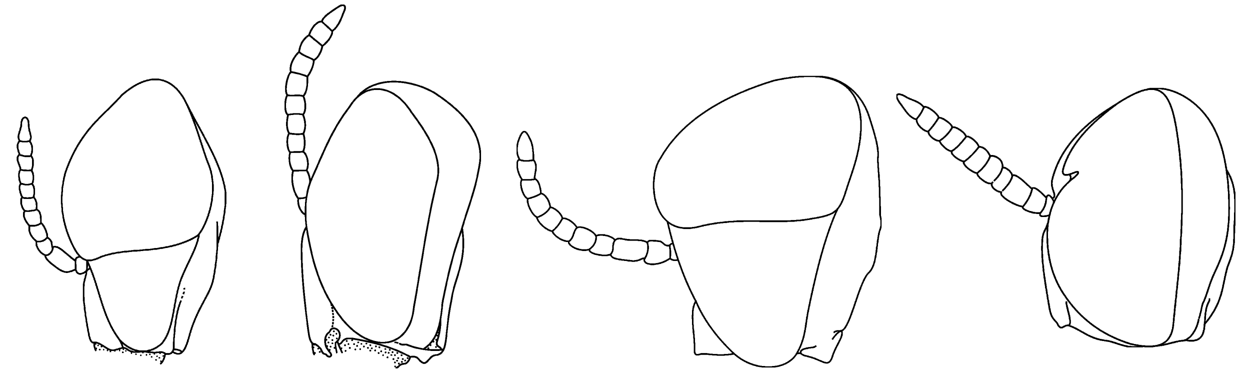


Fig. 32.4. External features of *Simulium* sp., lateral view ♀ (wing detached; left bottom insert tarsal claw; right bottom insert hind leg). Fig. 4 (after Crosskey 1990, fig. 12.1).

Abbreviations: A_1 – first branch of anal vein; an lb – anal lobe; ant – antenna; *C* – costal vein; clcp – calcipala; clw – claw; comp eye – compound eye; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; cx – coxa; fal vn – false vein; fem – femur; *h* – humeral crossvein; hlt – halter; kepst – katepisternum; kepst sl – katepisternal sulcus; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; ocp – occiput; pdsl – pedisulcus; plp – palpus; plr memb – pleural membrane; pn – postnotum; prbs – proboscis; *R* – radius, or radial vein; R_1 – anterior branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcostal vein; sct – scutum; sctl – scutellum; *stm vn* – stem vein; tb – tibia; tg – tergite; ts – tarsus; tsm – tarsomere.

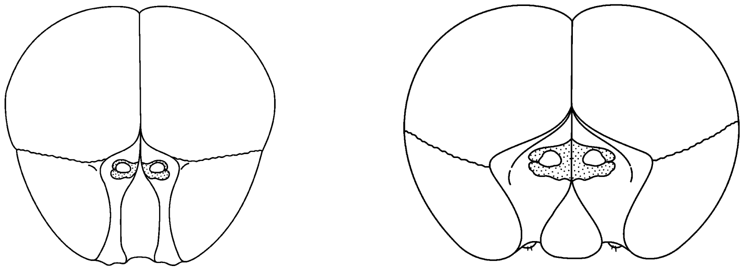


5 *Simulium* (*Afrosimulium*) ♂

6 *Simulium* (*Afrosimulium*) ♀

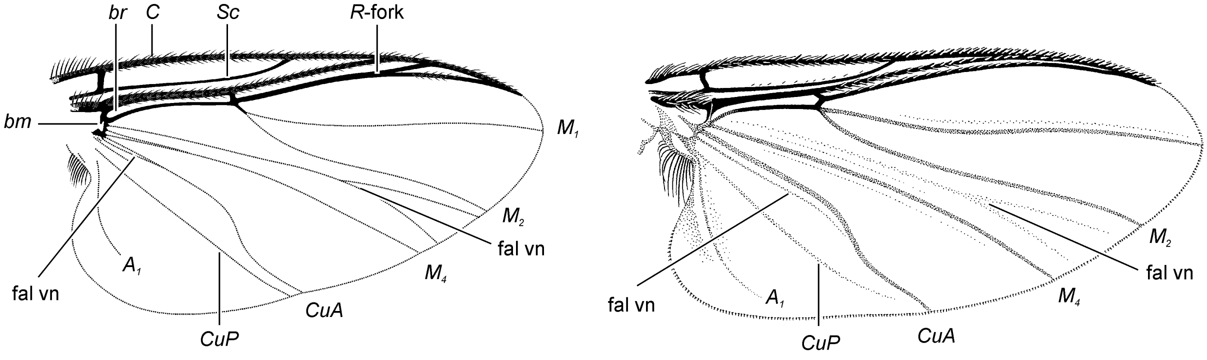
7 *Simulium* ♂

8 *Simulium* ♀



9 *Simulium* (*Afrosimulium*) ♂

10 *Simulium* ♂



11 *Prosimulium*

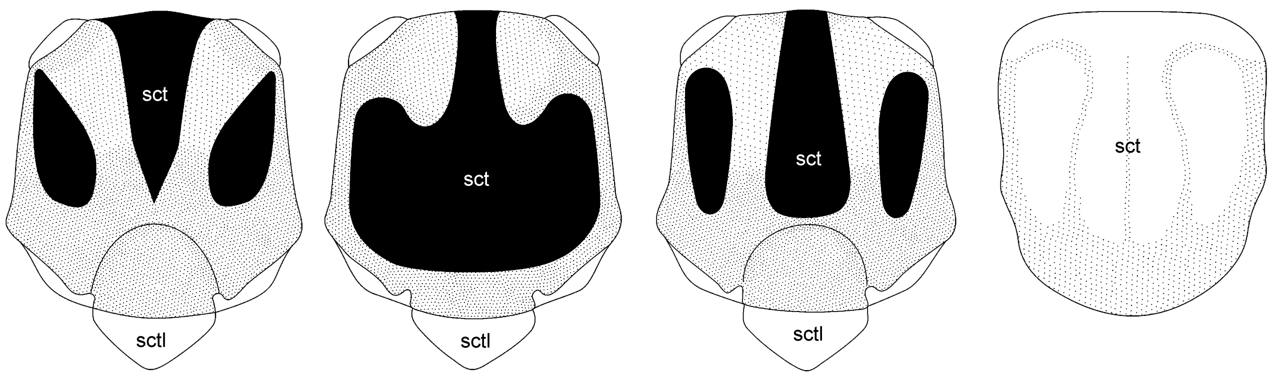
12 *Simulium* (*Simulium*)

Figs 32.5–12. Heads and wings of Simuliidae: (5) head of *Simulium* (*Afrosimulium*) *gariepense* de Meillon, lateral view ♂; (6) same ♀; (7) same, *S.* (*Simulium*) sp. ♂; (8) same ♀; (9) same, *S.* (*Af.*) *gariepense*, frontal view ♂; (10) same, *S.* (*Simulium*) sp.; (11) wing of *Prosimulium* sp., dorsal view (non-Afrotropical); (12) same, *S.* (*S.*) *venustum* Say (non-Afrotropical). Figs 5–11 (after Crosskey 1969, figs 67, 68, 65, 66, 62, 61, respectively), Fig. 12 (Peterson 1981, fig. 28).

Abbreviations: A_1 – first branch of anal vein; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; fal vn – false vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *R*-fork – radial vein fork; *Sc* – subcostal vein.

Abdomen composed of segments 1–10, nine of which are clearly visible (Fig. 4); segment 10 in both sexes formed by plates and structures associated with terminalia (Figs 31, 73–75); size of abdomen varying enormously, becoming greatly distended and rotund in females after imbibing blood meal or when abdomen filled with fully matured eggs prior to oviposition; sclerotised tergites present dorsally on segments 1–9 (Fig. 4), tergite 10 reduced in female (Figs 73–75); male with separate tergites on segments 1–8, a sclerotised ring formed by fusion of epandrium and hypandrium (tergite and sternite 9) (Fig. 31); tergite 1 in form of prominent collar-like flange with dense fringe of long setulae, present in both sexes (Fig. 4), but more prominent in male; small ventral sclerotised sternites may be present on some or all segments; male terminalia (Figs 30, 31) with hypopygium that cannot be rotated (males must adopt inverted position during copulation); hypopygium (Figs 30, 31) formed of aedeagus and pair of gonopods, comprising gonocoxite and hinged apical gonostylus (Figs 30, 31); aedeagus forming fleshy median bulbous projection with terminal genital opening surrounded by sclerotised structures, comprising unpaired ventral plate, unpaired median sclerite and paired parameres (plates attached to fleshy aedeagus and connected to dorsal inner edges of gonocoxites and lateral edges of ventral plate) (Figs 30, 31); either side of genital opening with aedeagal membrane bearing parameral spines that are (in some species), also directly attached to ends of parameres (*e.g.*, Figs 30, 31, 33, 35, 36); variations observed in sclerotised components of hypopygium offer best characters to distinguish different simuliid species; female terminalia (Figs 72–75) with sternite 8 modified, with hardened, slightly concave median genital plate, with pair of fleshy median terminal hypogynial valves separated by oval-shaped ovipositor notch; sternite 9 with sclerotised backwardly directed Y-shaped genital fork, with anterior facing stem supporting dorsal wall of vagina and upwardly bent wing-like arms, forming sclerotised dorsal front surface of genital recess (Figs 72, 73); segment 10 in female bearing small, sclerotised, mid-dorsal tergal plate, a pair of downwardly directed anal lobes and pair of backwardly-directed cerci.

Larvae (Fig. 82) recognised by club-shaped body with swollen posterior abdomen, with median ventral disc-like terminal abdominal proleg, presence of distinct pair of labral fans on rounded, fully-sclerotised head capsule (Figs 93, 94) and single median ventral thoracic proleg immediately beneath head (Figs 82, 83, 85, 87, 89). Head (Figs 93, 94) comprising elongated, barrel-shaped, fully-sclerotised capsule, with large frontal oral cavity around which mouthparts are attached and large posterior opening (the occipital foramen), behind which thorax attached; ground colour of head capsule ranging from creamy-white, straw-yellow, to red or blackish brown, usually with pattern of head maculae and patches, formed by pigment accumulations, often indicating positioning of head muscle attachments; patterns stand out as dark maculae or patches against paler background (positive head maculae) or as pale patches within an area of more darkly pigmented cuticle (negative head maculae) (Figs 99–109); head capsule pigmentation generally pale in newly-moulted larvae of all instars, more pigmented as larva ages, capsule divided into lower hull-shaped plate, forming floor and sides of head and upper, slightly-convex plate, the dorsal frontoclypeal apotome (Fig. 93); lower plate, although a single sclerotised unit, divided into 2 lateral postgenae and anteromedian hypostoma (Fig. 94); paired postgenae usually entirely fused ventrally, leaving posterior membranous postgenal cleft, shape and size of cleft diagnostic in different species (*e.g.*, Figs 120–140); hind margin of postgenae narrowly rimmed along dorsal margin as far as ventral postgenal cleft by darkly-pigmented post-occiput; as larvae grow, develop and moult through seven instars, a pair of tiny, oval cervical sclerites become visible within dorsal margin of post-occiput (Figs 110, 111); sclerites separate from margin in final instar larvae of all *Simulium* species (Fig. 111), but remain connected in the final instars of *Paracnephia* spp. (Fig. 110); dorsolaterally postgenae with pair of darkly-pigmented, light-sensitive stemmata on each side, comprising small oval-shaped anterior and larger comma-shaped posterior one; ventrally hypostoma forming raised projection in front of postgenae and bearing row of usually 9 heavily-sclerotised non-socketed teeth along anterior margin (*e.g.*, Figs 112–119); teeth diagnostic in shape, size and number for different species; hypostoma broadens posteriorly, forming triangular shape and rigidly fuses with postgenae; on inner side of each of tapering margins with row of hypostomal setae numbering from 3–18 (dependant on species); alignment of these setae ranges from parallel with outer margin, to diverging inwards from margin posteriorly; postgenal region behind hypostoma to start of postgenal cleft forming postgenal bridge (Fig. 94); anterior margins of postgenal plate strengthened to form 2 vertically-oriented X-shaped buttresses, lower pair supporting base of mandibles and upper pair bases of "cephalic fans" recognised and embryologically proven to be labral fans (Craig 1969, 1974; Planchon 1844) and antennae; antenna inserted just above base of labral fans (Figs 93, 94), tapering, tubular with 3-articles, with terminal article bearing long sensory cone and 2 sensory papillae, often mistakenly considered as fourth article, in subgenus *S.* (*Xenosimulium* Crosskey) secondarily annulations give appearance of six or more articles (Fig. 95); prominent, retractile labral fans present (Figs 93, 94), each comprising a complex of four separate fans, a primary fan, secondary fan, median fan and a scale fan, all arising from fan stem connected laterally to upper part of labrum by membranous cuticle; each fan ray of primary fan with numerous inwardly-facing secondary rays of similar or varying length, forming fringes of stout microtrichia, often interlocking with those of adjacent rays, thus creating efficient bipectinate filtering mesh; structure, size and shape of primary fan rays species-specific; labrum (Fig. 94) formed of hollow subtriangular lobe overhanging entrance to cibarium, situated medially between two labral fan stem bases; mandible (Fig. 94) situated below labral fan stem base, with inner edges facing down and inwards towards cibarium; mandible elongated in shape, laterally flattened and contracted distally to form subconical apical prominence, with strong sclerotised teeth; unsclerotised mandibular cleft extending from base of mandible to *ca* ⅓ of its length on inner side; outer margin of mandible sclerotised, gradually arched from base to apical prominence; mandibular serrations on ventral pre-apical surface, followed by number of spinose comb teeth and finally strong, well-defined apical teeth, these forming good diagnostic features (*e.g.*, Figs 96–98); up to seven sets of mandibular brushes present, of which terminal covering brush (which extends over mandibular tip) is most prominent; maxilla (Fig. 94), situated below mandibles and above hypostoma, comprises rounded lower lobe, bearing 3 dense setulose brushes and cylindrical unsegmented maxillary palpus; labium and hypopharynx (Fig. 94)

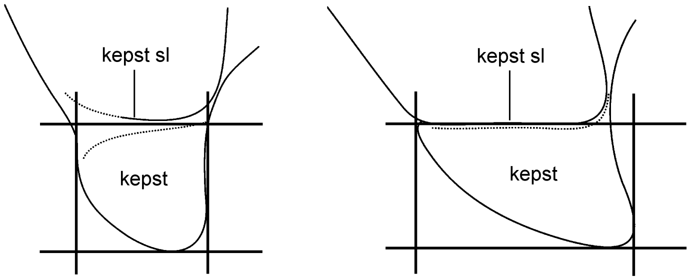


13 *Simulium* (*Edwardsellum*) ♂

14 *Simulium* (*Simulium*) ♂

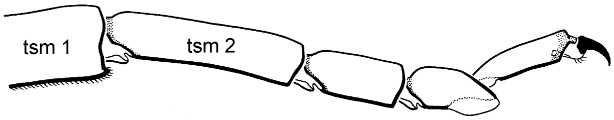
15 *Simulium* (*Metomphalus*) ♂

16 *Simulium* (*Metomphalus*) ♀

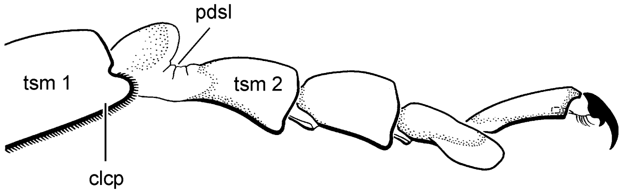


17 *Paracnephia*

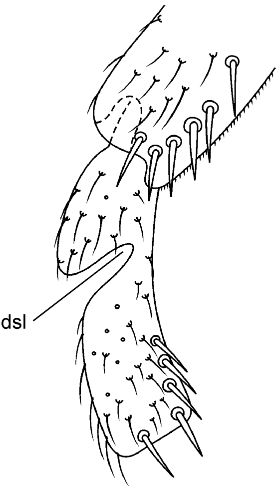
18 *Simulium*



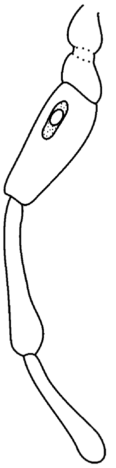
19 *Prosimulium*



20 *Simulium* (*Simulium*)



21 *Simulium* (*Afrosimulium*)



22 *Simulium* (*Afrosimulium*)

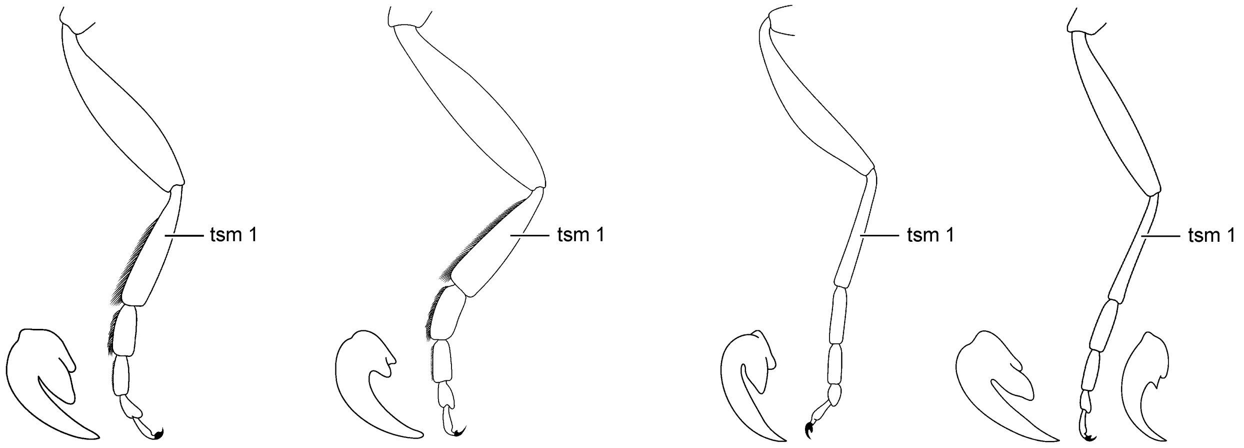
Figs 32.13–22. Thoracic, leg features and palpus of Simuliidae: (13) scutal pattern of *Simulium* (*Edwardsellum*) sp., dorsal view ♂; (14) same, *S.* (*Simulium*) *nitidifrons* Edwards ♂ (non-Afrotropical); (15) same, *S.* (*Metomphalus*) sp. ♂; (16) same, *S.* (*Met.*) *medusaeforme* Pomeroy ♀; (17) katepisternum and katepisternal sulcus of *Paracnephia* sp., lateral view; (18) same, *Simulium* sp.; (19) hind tarsomeres of *Prosimulium ursinum* (Edwards), lateral view ♀ (non-Afrotropical); (20) same, *Simulium* (*Simulium*) *arcticum* Malloch ♀ (non-Afrotropical); (21) hind tarsomere 2 and apex of tarsomere 1 of *Simulium* (*Afrosimulium*) *gariepense* de Meillon, lateral view; (22) palpus of *S.* (*Af.*) *gariepense*, lateral view ♀. Figs 13–15, 17, 18, 21, 22 (after Crosskey 1969, figs 77, 75, 76, 18, 19, 306, 305, respectively), Fig. 16 (after Freeman & Meillon 1953, fig. 55a), Figs 19, 20 (Peterson 1981, figs 19, 20).

Abbreviations: clcp – calcipala; kepst – katepisternum; kepst sl – katepisternal sulcus; pdsl – pedisulcus; sct – scutum; sctl – scutellum; tsm – tarsomere.

in Simuliidae combined to form labiohypopharyngeal complex (Chance 1970; Craig 1977), located below and between bases of maxillae and above hypostomium, with only bristly tip visible.

Thorax not distinct from abdomen, but recognisable by presence of certain external and internal structures (Fig. 82); single finger-like, distally tapered ventral thoracic proleg, protruding forwards from just below postgenal cleft, distally forming small, cylindrically-shaped apical proleg-head, with circlet of 20–50 outwardly directed oblique rows, each with 6–15 hooks arranged along outer rim of proleg-head; central area of head formed of oval-shaped cuticular disc devoid of hooks; developing buds of legs, wings and halteres visible as pale imaginal buds, or histoblasts in thoracic region, becoming increasingly more prominent in later instar larvae; development of pupal gill histoblast (Fig. 82) begins as small prothoracic bud above fore leg bud, which enlarges during development to become equal in size to imaginal wing-bud in final seventh-instar larva; gill histoblast turns dark brown just prior to pupation; shape and structure of gill histoblast can be diagnostic in final-instars.

Abdomen (Fig. 82) 9-segmented (segmentation not clearly discernible, but recognised from embryological evidence

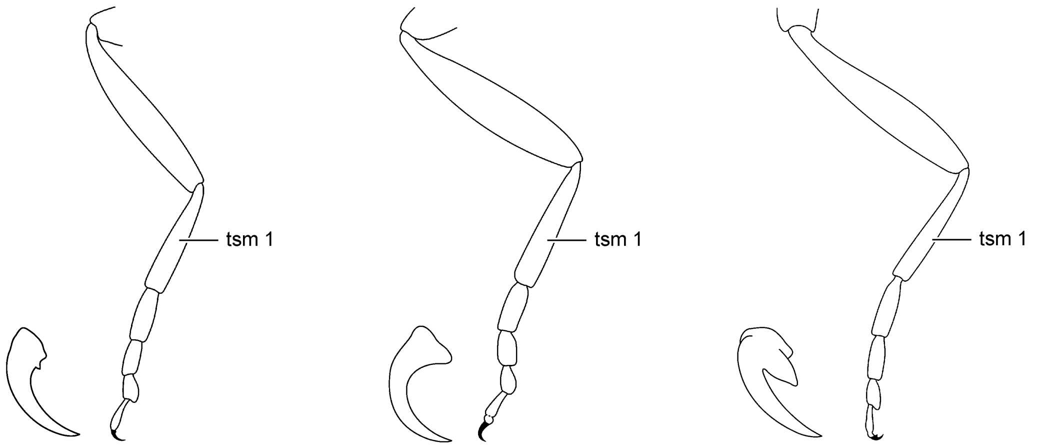


23 *Simulium* (*Phoretomyia*)

24 *Simulium* (*Edwardsellum*)

25 *Simulium* (*Pomeroyellum*)

26 *Simulium* (*Nevermannia*)



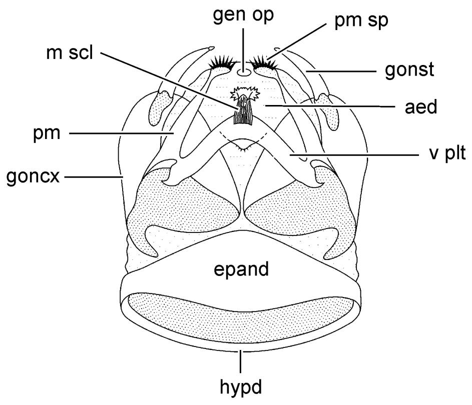
27 *Simulium* (*Lewisellum*)

28 *Simulium* (*Metomphalus*)

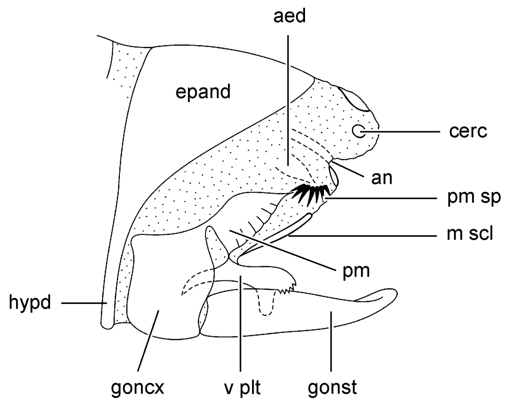
29 *Simulium* (*Byssodon*)

Figs 32.23–29. Fore tibia and tarsus of Simuliidae, with tarsal claws of females's enlarged (lateral views); (23) *Simulium* (*Phoretomyia*); (24) *S.* (*Edwardsellum*); (25) *S.* (*Pomeroyellum*); (26) *S.* (*Nevermannia*); (27) *S.* (*Lewisellum*); (28) *S.* (*Metomphalus*); (29) *S.* (*Byssodon*). Figs 23–29 (after Crosskey 1969, figs 81, 82, 78–80, 83, 87, respectively).

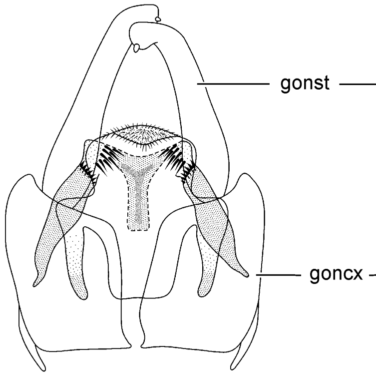
Abbreviation: tsm – tarsomere.



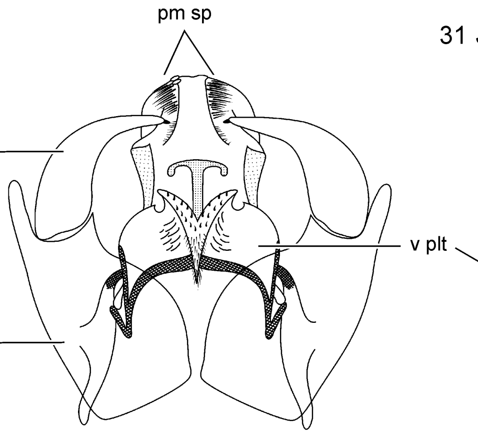
30 *Simulium* ♂



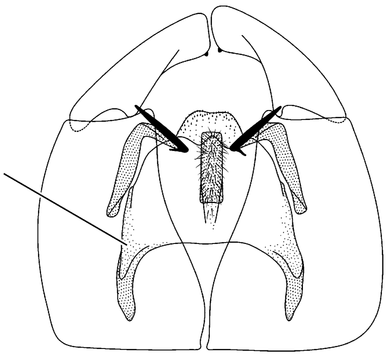
31 *Simulium* ♂



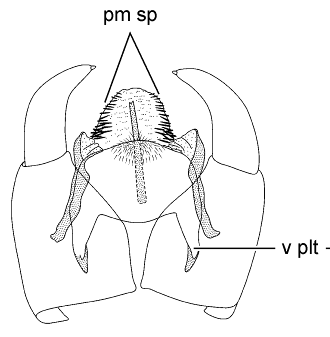
32 *Simulium* (*Freemanellum*) ♂



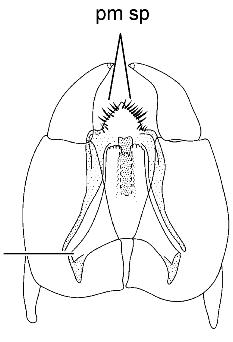
33 *Simulium* (*Edwardsellum*) ♂



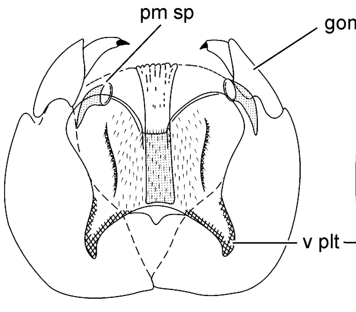
34 *Simulium* (*Nevermannia*) ♂



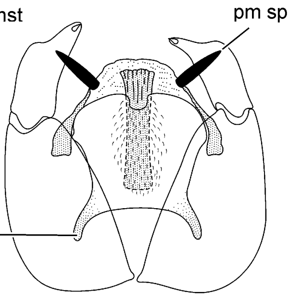
35 *Simulium* (*Anasolen*) ♂



36 *Simulium* (*Metomphalus*) ♂



37 *Simulium* (*Meilloniellum*) ♂



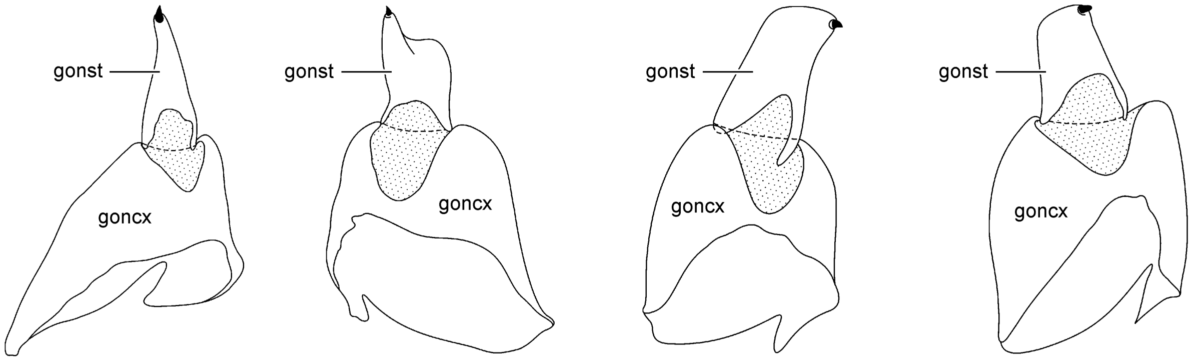
38 *Simulium* (*Lewisellum*) ♂

Figs 32.30–38. Male terminalia of Simuliidae: (30) morphology of male terminalia of *Simulium* sp., ventral view; (31) same, lateral view; (32) hypopygium of *S.* (*Freemanellum*), ventral view; (33) same, *S.* (*Edwardsellum*); (34) same, *S.* (*Nevermannia*); (35) same, *S.* (*Anasolen*); (36) same, *S.* (*Metomphalus*); (37) same, *S.* (*Meilloniellum*); (38) same, *S.* (*Lewisellum*). Figs 30, 31 (after Crosskey 1990, figs 12.9a, 12.8a, respectively), Figs 32, 34–36, 38 (after Crosskey 1969, figs 91, 88, 90, 92, 89, respectively), Figs 33, 37 (after Freeman & de Meillon 1953, figs 68d, 32e, respectively).

Abbreviations: aed – aedeagus; an – anus; cerc – cercus; epand – epandrium; gen op – genital opening; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; m scl – median sclerite; pm – paramere; pm sp – parameral spines; v plt – ventral plate.

(Craig 1969), adorned with variously-shaped fine, to course scales or setulae (cuticular macrotrichia) (*e.g.*, Figs 84, 86, 88, 90); larvae of *Simulium* (*Edwardsellum*) *damnosum* Theobald, 1903 *sensu lato* with prominent, dorsal abdominal humps, clothed in dense, dark scales, also present on most regions of abdomen (Fig. 89); abdominal proleg at terminal end of abdomen, posterior and ventral to anus, considerably larger than thoracic proleg; abdominal proleg with posterior circlet of 150–225 rows of 25–45 hooks in mature larvae (Fig. 82); X-shaped anal sclerite situated between anus and proleg; retractile rectal papillae (Figs 82, 91) with 3 large lobes arising from common base, lobes can be further subdivided into numerous secondary lobules depending on species (Fig. 92); pair of posterior ventral processes (ventral tubercles) discernible immediately in front of abdominal proleg in larvae of some, but not all species (Fig. 82).

Pupae of Simuliidae recognisable due to general shape, distinctive pupal respiratory organs and adherence within silken cocoon attached to underwater substrates (Figs 141, 142); obtect sedentary pupae of *Simulium* embedded in shoe- or slipper-shaped cocoons (Figs 141–144) and those of *Paracnephia* wedged in mats of communal silk, often linked to aquatic mosses; distinctive in having well-developed prothoracic respiratory organs (pupal gills), that are diagnostic in shape and branching pattern; abdomen adorned dorsally and ventrally with forwardly-turned hooks and combs that anchor them within their silken pupal cocoons (Figs 145, 146); male and female pupae recognised by developing compound eyes, with large dorsal eye facets of males being diagnostic; external features of simuliid pupae offer numerous diagnostic features; size range of body length, excluding pupal respiratory organs, from 3–5 mm; head and thorax forming large hump-backed unit (cephalothorax) separate

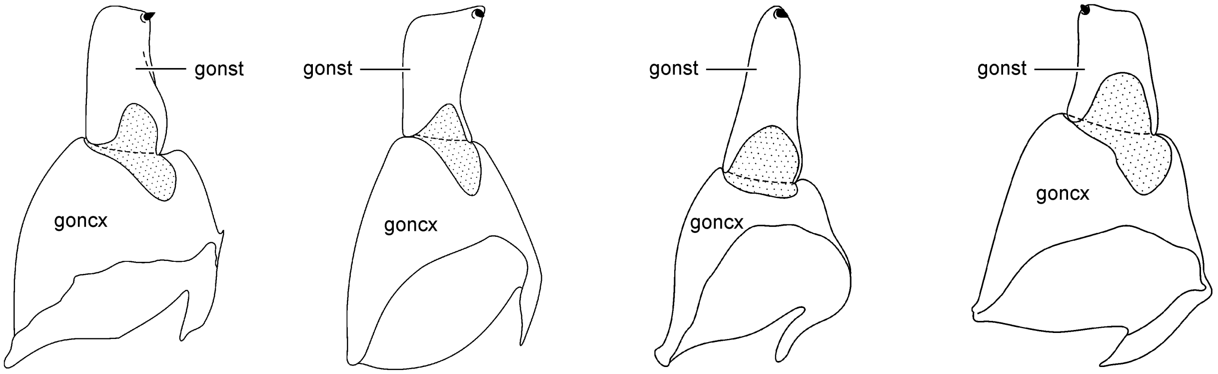


39 *Simulium* (*Phoretomyia*) ♂

40 *Simulium* (*Lewisellum*) ♂

41 *Simulium* (*Pomeroyellum*) ♂

42 *Simulium* (*Pomeroyellum*) ♂



43 *Simulium* (*Nevermannia*) ♂

44 *Simulium* (*Nevermannia*) ♂

45 *Simulium* (*Xenosimulium*) ♂

46 *Simulium* (*Anasolen*) ♂

Figs 32.39–46. Male terminalia of Simuliidae: (39) gonocoxite and gonostylus of *Simulium* (*Phoretomyia*), lateral view; (40) same, *S.* (*Lewisellum*); (41) same, *S.* (*Pomeroyellum*); (42) same; (43) same, *S.* (*Nevermannia*) *ruficorne* species-group; (44) same; (45) same, *S.* (*Xenosimulium*); (46) same, *S.* (*Anasolen*). Figs 39–46 (after Crosskey 1969, figs 146, 145, 140, 141, 143, 144, 148, 149, respectively).

Abbreviations: goncx – gonocoxite; gonst – gonostylus.

from 9-segmented abdomen (Figs 145, 146); upper surface of head formed of flattened plate that lifts during eclosion, allowing adult to emerge; head, antenna, eyes, mouthparts, fore and mid legs and wing clearly visible in ventral view; thorax bearing paired pupal gills inserted laterally above head and outwardly directed to opening of enclosing silken cocoon (Figs 141, 142); shape, size, variation of structure, branching and number of pupal gill filaments, vary enormously between different species and offers clearest diagnostic features for identifying blackfly species (Crosskey 1990: 314) (*e.g.*, Figs 148–196); pupal abdominal segments with simple or divided, forwardly-directed hooks on sternites of segments 5–7 and tergites of segments 3–4, that assist to anchor pupae firmly into silk lining of cocoon (Figs 145, 146); sometimes also backwardly-directed spine combs on tergites of last 3 or 4 abdominal segments; *Paracnephia* with abdominal segment 9 bearing pair of terminal hooks (Fig. 147) that are absent in *Simulium*.

Adult Simuliidae may be confused with other small, stout-bodied fly families, such as Bibionidae (see Chapter 17), Scatopsidae (see Chapter 26), Empididae (see Chapter 51) and Phoridae (see Chapter 59), but are distinguished by the distinctive wing venation, cigar-shaped 11-articled antenna and low-slung head in front of an arched thorax, giving them a humpbacked appearance (Fig. 1).

Biology and immature stages

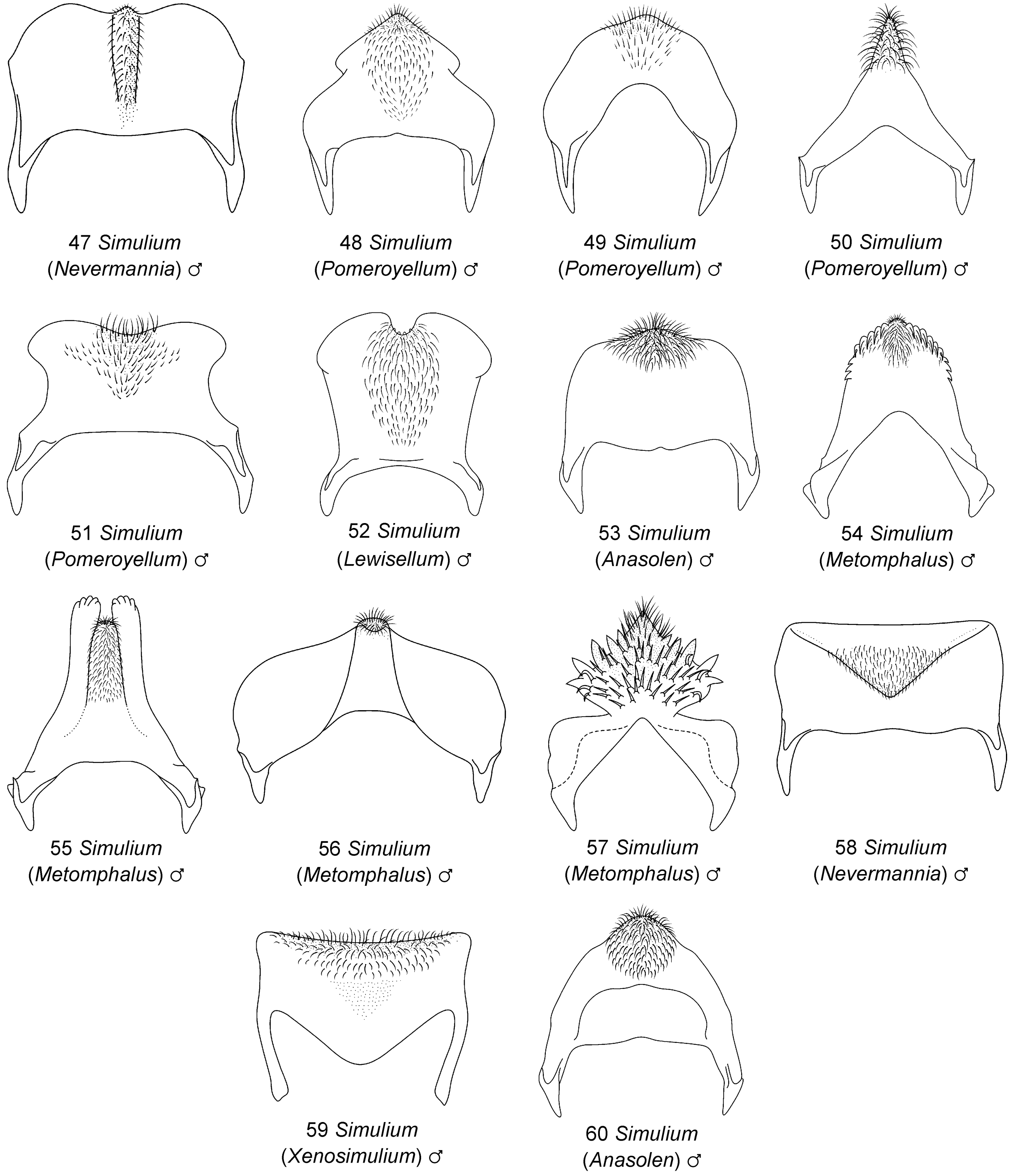
Larval and pupal stages of blackflies are among the insects best adapted to life in swift-flowing water and the absence of running water is, in most cases, a limiting factor preventing the presence of larvae and pupae. The pupae are obligate sedentary, fixed to substrates, and larvae have limited locomotive powers, relying on flowing water to provide food, remove waste (egestion and excretion) and supply dissolved oxygen at the required high levels. All simuliid species are found in flowing freshwater, although *S.* (*Meilloniellum*) *adersi* Pomeroy, 1922, a widespread species throughout the Afrotropical Region, has been recorded from highly saline and even brackish estuarine waters and along the windswept shores of Lake Victoria, where wave action simulates flowing water conditions (Crosskey 1990: 204; Gibbins 1934). Another widespread species, *S.* (*Nevermannia*) *ruficorne* Macquart, 1838, has been recorded from small trickles of water in northern Namibia, where water temperatures reach 36.2°C (de Moor *et al*. 2000). Larvae of different species colonise stones, submerged vegetation or any other firm substratum in moderate to swift-flowing waters.

A larva will spin a patch of silk onto the substratum, to which it attaches by means of the circlets of hooks on the terminal abdominal proleg. It will remain in a semi-upright position facing downstream of the flowing water and twist its body in such a way as to position the head and curved concave surface of the labral fans to face the flowing water, when feeding. In this feeding position the labral fan rays are extended sideways in fan-like fashion, the bipectinate setae filter fine particulate matter from the water. The fans are periodically retracted, to face the cibarium, and the mandibles, with their terminal covering brush of setulae, scrape off attached particles. Larvae are extremely efficient biological filterers and are able to extract small particles (0.1–350 μm) from the water (Wallace & Merritt 1980). Food extracted from the suspended detritus in the water column comprises diatoms, other algae, tiny invertebrates and even bacteria.

Movement of larvae within the region of favoured substrate is a slow tedious process. A new patch of silk is spun by the larva next to the patch in which the abdominal proleg is anchored. The larva anchors the circlets of hooks on the thoracic proleg onto this new patch and then releases its hold of the abdominal proleg attached to the old patch of silk. The larva then loops the abdominal proleg round to attach to the same patch where the thoracic proleg is attached after which the thoracic proleg is detached. The larva is thus able to move around on the substrate by repeating this slow, looping form of locomotion. When disturbed, or during certain developmental stages in the lifecycle, the larvae can detach themselves from their silken holdfast and become part of the organic drift in rivers. Evasive escape can be achieved by releasing hold on the silk patch, but leaving a silken anchor thread attached while drifting downstream. The larva is then carried away from the immediate threat, but remains in contact with the region of favoured swift-flowing water and are able to climb back upstream again along the silk thread. Larvae of different species show preferences for settling on selected substrata in a flow of water that optimises their feeding efficiency and gives them maximal protection from natural enemies. The preferred substrata may be stones, boulders or bedrock in swift-flowing water, trailing aquatic vegetation or roots from marginal vegetation in slower flowing currents. Larvae can even form phoretic associations on the bodies of Crustacea (crabs, prawns and shrimps), or on Ephemeroptera (Crosskey 1990: 214).

Larvae of all Afrotropical species (studied to date), go through seven instars prior to pupation (Crosskey 1990: 132). The structure of the pupal cocoon varies greatly and indicates flowing water conditions in which different Simuliidae species occur (Crosskey 1990: 306). Two basic forms of cocoon can be identified, slipper-shaped cocoons (Figs 141, 143) are elongate posteriorly-tapering bags of silk attached to the substrate along the ventral surface, with an anterior semi-circular opening from which the head and thorax of the pupa extrude; shoe-shaped cocoons (Figs 142, 144) are similar in structure, but with a circular to oval-shaped anterior opening, with a collar extending along the ventral surface, thus raising the opening above the substrate, creating the so-named “heel” of the “shoe” (Fig. 144). Variations include an elongated “heel” forming a boot-shaped cocoon or a slipper-shaped cocoon, with “hood” or “windows” on the side, giving a fenestrate appearance. The pupal gills have an external plastron surface, composed of fine interlaced filaments that trap air and thus form functional physical organs for respiration, they are hollow, filled with water, and connect *via* a thickened base to the pharate adult fly’s thoracic spiracles, where the exchange of oxygen takes place. The water-filled pupal gills serve to equilibrate pressure under water, preventing the collapse of these respiratory organs, even under pressure of 10 m of water (Hinton 1964).

The late seventh-instar larva is deceptive, being a pharate pupa within the skin of a larva (Hinton 1958). Although apolysis has already taken place, the larval cuticle is retained until actual shedding at ecdysis. This then serves to identify the physiologically functional pupa from the definitive morphological pupa. Towards the end of the pupal stage, apolysis occurs again and the pharate adult is then retained in the pupal skin.



47 *Simulium* (*Nevermannia*) ♂

48 *Simulium* (*Pomeroyellum*) ♂

49 *Simulium* (*Pomeroyellum*) ♂

50 *Simulium* (*Pomeroyellum*) ♂

51 *Simulium* (*Pomeroyellum*) ♂

52 *Simulium* (*Lewisellum*) ♂

53 *Simulium* (*Anasolen*) ♂

54 *Simulium* (*Metomphalus*) ♂

55 *Simulium* (*Metomphalus*) ♂

56 *Simulium* (*Metomphalus*) ♂

57 *Simulium* (*Metomphalus*) ♂

58 *Simulium* (*Nevermannia*) ♂

59 *Simulium* (*Xenosimulium*) ♂

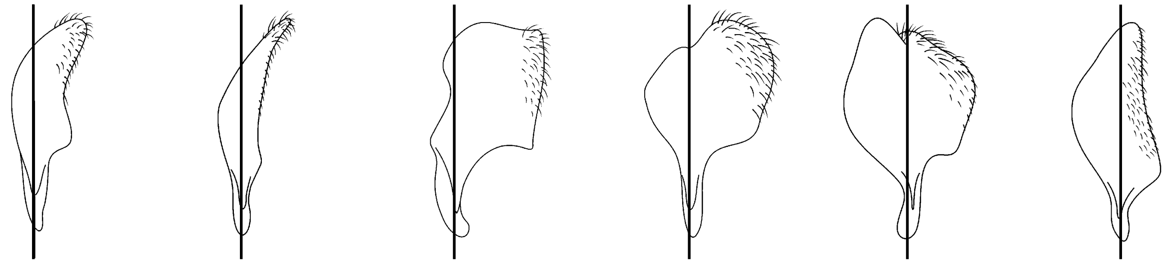
60 *Simulium* (*Anasolen*) ♂

Figs 32.47–60. Male terminalia of Simuliidae: (47) male ventral plate of *Simulium* (*Nevermannia*) *ruficorne* species-group, ventral view; (48) same, *Simulium* (*Pomeroyellum*) *alcocki* species-group; (49) same; (50) same; (51) same, *S.* (*Po.*) *cervicornutum* species-group; (52) same, *S.* (*Lewisellum*) sp.; (53) same, *S.* (*Anasolen*) sp; (54) same, *S.* (*Metomphalus*) *medusaeforme* species-group; (55) same; (56) same, *S.* (*Met.*) *bovis* species-group; (57) same; (58) same, *S.* (*N.*) *loutetense* species-group; (59) same, *S.* (*Xenosimulium*) sp.; (60) same, *S.* (*An.*) sp. Figs 47–60 (after Crosskey 1969, figs 101, 96–99, 105, 108, 114, 116, 115, 117, 103, 104, 109, respectively).

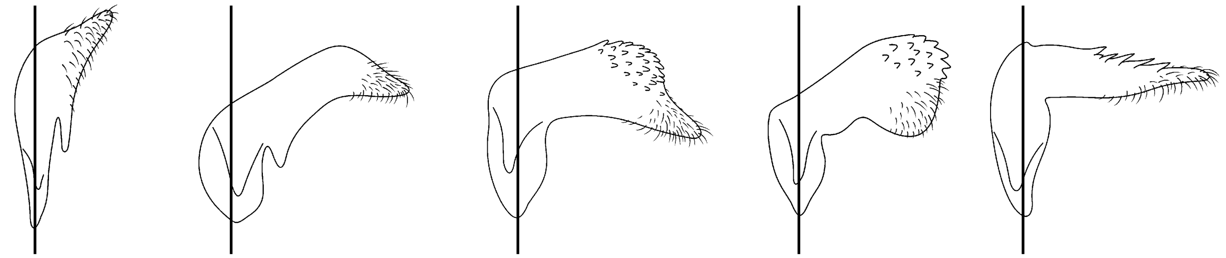
Once metamorphosis is completed the fully formed adult accumulates air between the body and the enclosing pupal skin. The pupal skin then splits lengthwise, dorsally between the head and thorax and the adult floats to waters' surface in a bubble of air and takes to flight immediately

Adults are, virtually without exception, visibly sexually dimorphic with holoptic males and dichoptic females. Premating sexual behaviour often involves the formation of swarms, comprised almost entirely of males, around some prominent feature (swarm marker) in the landscape, near to the larval breeding site at the base of rapids, or around animals from which the females are known to take blood (Crosskey 1990: 362). The females are attracted to the swarms or concentrate at the sites where the males group and this male behaviour, although not obligatory, enhance the chances of successful mating. It is in the more temperate regions, where dense populations of blackfly larvae develop in rivers, that male swarms are most frequently encountered. In the more tropical regions such swarms are rarely found and observed mating has been only sporadically recorded (Crosskey 1990: 362). Because of difficulties associated with successful mating (with the requirements of the male having to grasp the female and invert the genital apparatus before successful copulation can occur), copulation invariably takes place on the ground or on vegetation around which males congregate. Copulation and spermatophore transfer usually takes 20 seconds or less, but there are records of this lasting up to 30 minutes (Crosskey 1990: 376). The hardened spermatophore, inserted by the male, is held in place in the females' genital recess (between the hypogynial valve, anal lobes and wings of the genital forks). From here the spermatophore is opened by the female and all the sperm (from 600–7000 in number) are released, to be stored and nourished in the single spermatheca. If the eggs of the female are mature, the spermatophore can directly release the sperm to fertilise the eggs.

As a source of additional energy for flight activity, adults of both sexes feed on nectar from flowers. Females, although in some species capable of developing eggs autogenously, usually require a blood-meal for extra protein to mature their eggs. Adult flies are frequently found resting on vegetation near rivers. Blackflies are active almost exclusively during daylight hours and exhibit greatest intensity of flight activity when barometric pressure is declining (Wellington 1974). There are generally two peaks of flight activity, the first early in the morning and the second late in the afternoon and these peaks have been recorded in temperate and tropical regions (Roberts & Irving-Bell 1985). Female simuliids generally fly upstream before ovipositing and this behaviour is seen as a compensation for the downstream flow, carrying larvae in the drift away from

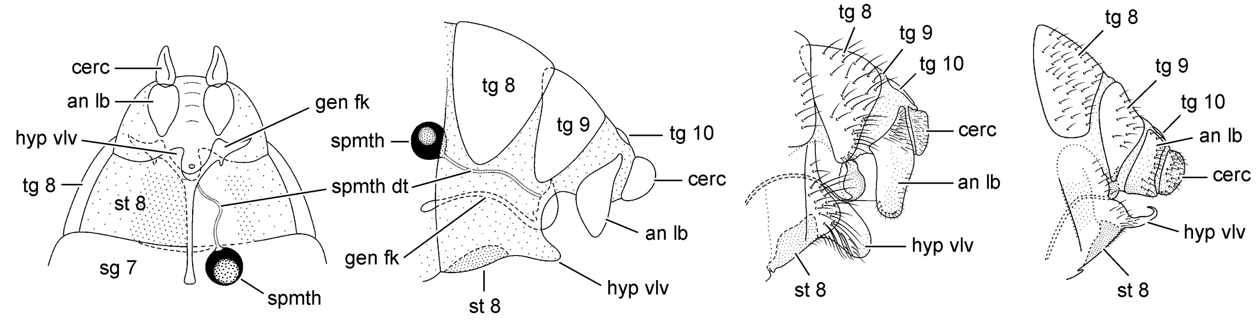


61 *Simulium* (*Pomeroyellum*) ♂ 62 *Simulium* (*Pomeroyellum*) ♂ 63 *Simulium* (*Pomeroyellum*) ♂ 64 *Simulium* (*Nevermannia*) ♂ 65 *Simulium* (*Meilloniellum*) ♂ 66 *Simulium* (*Lewisellum*) ♂

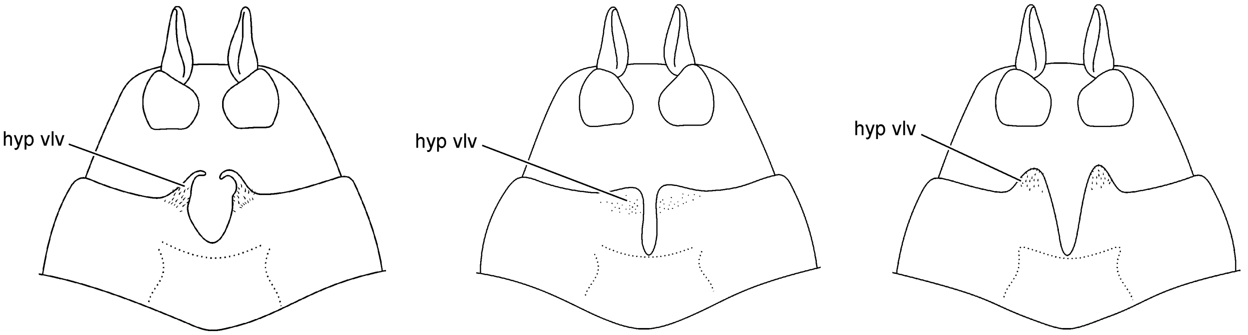


67 *Simulium* (*Xenosimulium*) ♂ 68 *Simulium* (*Anasolen*) ♂ 69 *Simulium* (*Metomphalus*) ♂ 70 *Simulium* (*Metomphalus*) ♂ 71 *Simulium* (*Metomphalus*) ♂

Figs 32.61–71. Male terminalia of Simuliidae (vertical line indicates profile at 90° axis from base of ventral plate): (61) ventral plate of *Simulium* (*Pomeroyellum*) *alcocki* species-group, left lateral profile; (62) same; (63) same; *S.* (*Po.*) *kenyae* species-group; (64) same; *S.* (*Nevermannia*) *ruficorne* species-group; (65) same; *S.* (*Meilloniellum*) sp.; (66) same; *S.* (*Lewisellum*) sp.; (67) same; *S.* (*Xenosimulium*) sp.; (68) same; *S.* (*Anasolen*) sp.; (69) same; *S.* (*Metomphalus*) *medusaeforme* species-group; (70) same; *S.* (*Met.*) *bovis* species-group; (71) same; *S.* (*Met.*) *albivirgulatum* Wanson & Henrard. Figs 61–71 (after Crosskey 1969, figs 120–122, 125–127, 129, 132–135).



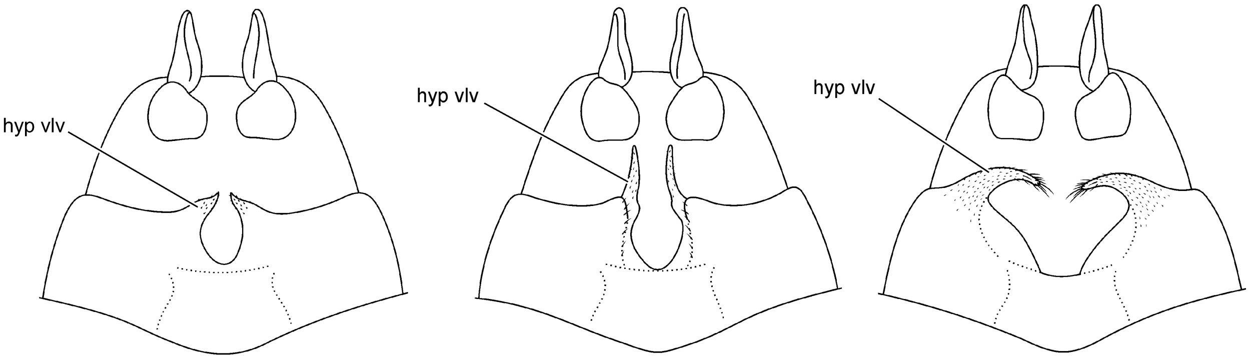
72 *Simulium* ♀ 73 *Simulium* ♀ 74 *Simulium* (*Freemanellum*) ♀ 75 *Simulium* ♀



76 *Simulium* (*Metomphalus/Edwardsellum*) ♀

77 *Simulium* (*Pomeroyellum/Meilloniellum/Lewisellum*) ♀

78 *Simulium* (*Meilloniellum*) ♀



79 *Simulium* (*Anasolen*) ♀ 80 *Simulium* (*Metomphalus*) ♀ 81 *Simulium* (*Xenosimulium*) ♀

Figs 32.72–81. Female terminalia of Simuliidae: (72) morphology of female terminalia of *Simulium* sp., ventral view; (73) same, lateral view; (74) female terminalia of *Simulium* (*Freemanellum*) sp., lateral view; (75) same, *Simulium* sp.; (76) same, *S.* (*Metomphalus / Edwardsellum*), ventral view; (77) same, *S.* (*Pomeroyellum / Meilloniellum / Lewisellum*); (78) same, *S.* (*Meilloniellum*) sp.; (79) same, *S.* (*Anasolen*) sp.; (80) same, *S.* (*Metomphalus*) *wellmanni* Roubaud; (81) same, *S.* (*Xenosimulium*) sp. Figs 72, 73 (after Crosskey 1990, figs 12.8b, 12.9b), Figs 74–81 (after Crosskey 1969, figs 163, 162, 159, 156–158, 160, 161, respectively).

Abbreviations: an lb – anal lobe; cerc – cercus; gen fk – genital fork; hyp vlv – hypogynial valve; sg – segment; spmth – spermatheca; spmth dt – spermathecal duct; st – sternite; tg – tergite.

where the eggs are laid (Müller 1954). Ovipositing behaviour in different simuliid species follows a distinct pattern of techniques: freely scattering eggs on the waters' surface, dabbing the abdomen on a thin film of water over bedrock while releasing eggs onto the substrate (a few at a time), laying eggs on the floating surface of plant matter, or laying eggs in patches, layers or strings under partially-submerged stones and plants after having crawled under water to select a suitable area to lay their eggs. The size and number of eggs laid and the number of gonotrophic cycles (recorded as up to five) that a species undertakes also varies between species.

Although some species of blackfly in the *S.* (*E.*) *damnosum sensu lato* complex are able to fly distances of up to 5.27 km in less than five hours, in most species flight is usually confined to shorter bursts of activity, with an average duration of 75 minutes recorded in *S.* (*Edwardsellum*) *sirbanum* Vajime & Dunbar, 1975 (Crosskey 1990: 396). Nonetheless, simuliids in the *S. damnosum sensu lato* complex have been recorded to disperse over distances greater than 500 km across the wet season Intertropical Conversion Zone in West Africa (Garms & Walsh 1987: 208). Migratory flight behaviour, which is particularly important in the spread of Simuliidae to other rivers systems, has serious medical and veterinary implications.

Blackflies have many natural enemies, comprising parasites and predators that obtain nourishment from their aquatic and adult stages. Parasites include fungi, protozoa and nematodes and predators include larvae and nymphs of numerous aquatic insects, adult Odonata, species of several Diptera families, Crabronidae wasps, spiders, fishes and birds (Crosskey 1990: 246, 484; de Moor 1992; Gess & Gess 2014: 76, 80).

Economic significance

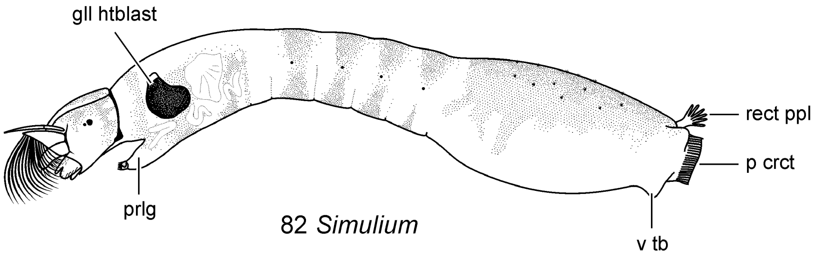
Due to the biting behaviour of female blackflies (the mouthparts are used to cut the skin creating a wound and pool of blood that is imbibed), the physical damage to the host's skin can lead to secondary infections. Due to the high number of blackflies that appear periodically at certain times of the year, these blood-sucking pests can have dire negative economic impacts, by significantly decreasing the productivity of livestock farmers. The biting flies cause loss of condition in animals through loss of blood; infections, sickness (through viral and parasite transmissions) and can even cause the death of poultry and mammalian livestock. Due to such effects, the species concerned may be accorded pest status. Only a handful of species can be considered pests in the Afrotropical Region and these are generally confined within the subgenera *S.* (*Metomphalus* Enderlein), *S.* (*Meilloniellum* Rubtsov) and *S.* (*Nevermannia* Enderlein). The species, or more appropriately complexes of species, recognised as occasionally attaining pest status are *S.* (*Met.*) *chutteri* Lewis, 1965, *S.* (*Met.*) *bovis* de Meillon, 1930, *S.* (*Met.*) *hargreavesi* Gibbins, 1934, *S. damnosum sensu lato*, *S.* (*N.*) *nigritarse* Coquillett, 1901 and *S.* (*Me.*) *adersi* (Palmer & de Moor 1998).

From a medical standpoint, problematic blackflies include all species that are known to be vectors of the filarial nematode worm *Onchocerca volvulus* (Onchocercidae), which is responsible for causing "river blindness" in humans in tropical regions of Africa and America (Crosskey 1990: 568). The main vectors of *O. volvulus* in the Afrotropics include a number of species within the *S.* (*E.*) *damnosum sensu lato* complex, as well as *S.* (*Lewisellum*) *neavei* Roubaud, 1915, *S.* (*L.*) *ethiopiense* Fain & Oomen, 1968 and *S.* (*L.*) *woodi* de Meillon, 1930, all with phoretic larvae on crabs and *S.* (*Met.*) *albivirgulatum* Wanson & Henrard, 1944, a large river species (Crosskey 1990: 569).

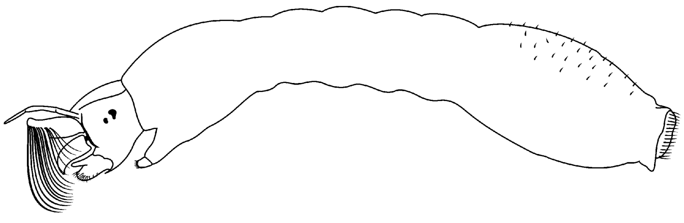
There are a number of mammalophilic and ornithophilic species that cause sufficient problems to warrant veterinary intervention. The species that feed preferentially on avian blood can usually be recognised by the presence in the female of a bulbous or elongated ventral tooth on each tarsal claw, giving it a bifid appearance. This tooth aids in obtaining a holdfast on the feathers of avian hosts while taking a bloodmeal. Besides the physical traumatic impact that large numbers of biting flies have on livestock, they also spread viral diseases and are vectors of nematode parasites to birds and mammals. Pests on poultry are vectors of a number of species of protozoan blood parasites in the genus *Leucocytozoon* (Leucocytozoidae) that cause a malaria-like disease. Two important species are *L. schoutedeni*, a parasite of domestic poultry and *L. neavei*, a parasite of guinea fowl (Fallis *et al*. 1973*a*). There is also a record of *Trypanosoma numidae* parasites transmitted to birds by *S.* (*Me.*) *adersi* in Tanzania (Fallis *et al*. 1973*b*). A large number of species of filarial parasites in the genus *Onchocerca* (Onchocercidae) are also transmitted to mammalian livestock and wild game by blackfly vectors. There is an extensive literature on the topic of disease vectors, which is beyond the scope of the chapter and the review of Crosskey (1990) expands considerably on this topic.

Classification

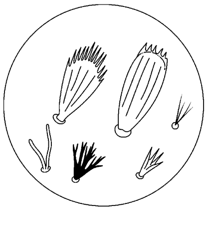
The phylogenetic relationship of the family Simuliidae is well-established within the nematoceran Diptera (Sæther 2000). The family was placed in the superfamily Chironomoidea, together with Ceratopogonidae, Chironomidae and Thaumaleidae (Currie & Adler 2008). Based on molecular evidence, however, Bertone *et al*. (2008) recommended the establishment of the new superfamily Simulioidea to accommodate Simuliidae + Thaumaleidae. Within the family Simuliidae, relationships are, however, not as clearly defined (Moulton 2000, 2003) and this is evidenced in the history of classification of the group. Linnaeus (1758: 603) originally placed *Simulium* in the genus *Culex* and the genus *Simulium* was only established by Latreille in 1802. The taxon group "*Simuliites*" was created by Newman (1834) and this provided the basis for establishment of the family name. In 25 publications between 1914 and 1943 G. Enderlein created some 50 genera within the family (Adler *et al*. 2004: 126). In contrast, Edwards (1931: 121) recognised only two genera, *Parasimulium* Malloch and *Simulium*, with seven subgenera in the latter genus (*S.* (*Austrosimulium* Tonnoir), *S.* (*Cnephia* Enderlein), *S.* (*Eusimulium* Roubaud), *S.* (*Gigantodax* Enderlein), *S.* (*Morops* Enderlein), *S.* (*Prosimulium* Roubaud) and *Simulium sensu stricto*). Smart (1945) produced the first comprehensive monographic review of the family and suggested a reduction of higher taxa, containing two subfamilies Parasimuliinae (with one genus *Parasimulium*) and Simuliinae containing five genera, excluding *Eusimulium* and *Morops*, derived from the subgenera proposed by Edwards (1931: 121). Grenier & Rageau (1960)



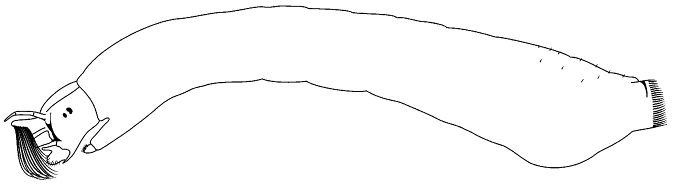
82 *Simulium*



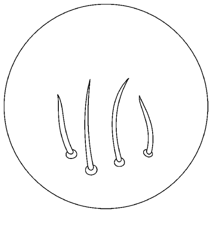
83 *Simulium* (*Pomeroyellum*)



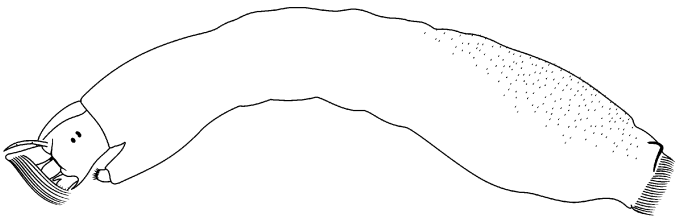
84 *Simulium* (*Pomeroyellum*)



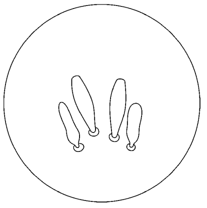
85 *Simulium* (*Metomphalus*)



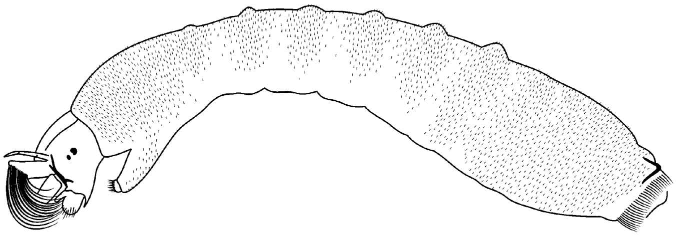
86 *Simulium* (*Metomphalus*)



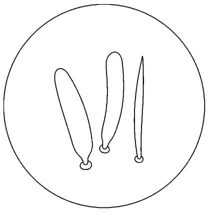
87 *Simulium* (*Metomphalus*)



88 *Simulium* (*Metomphalus*)



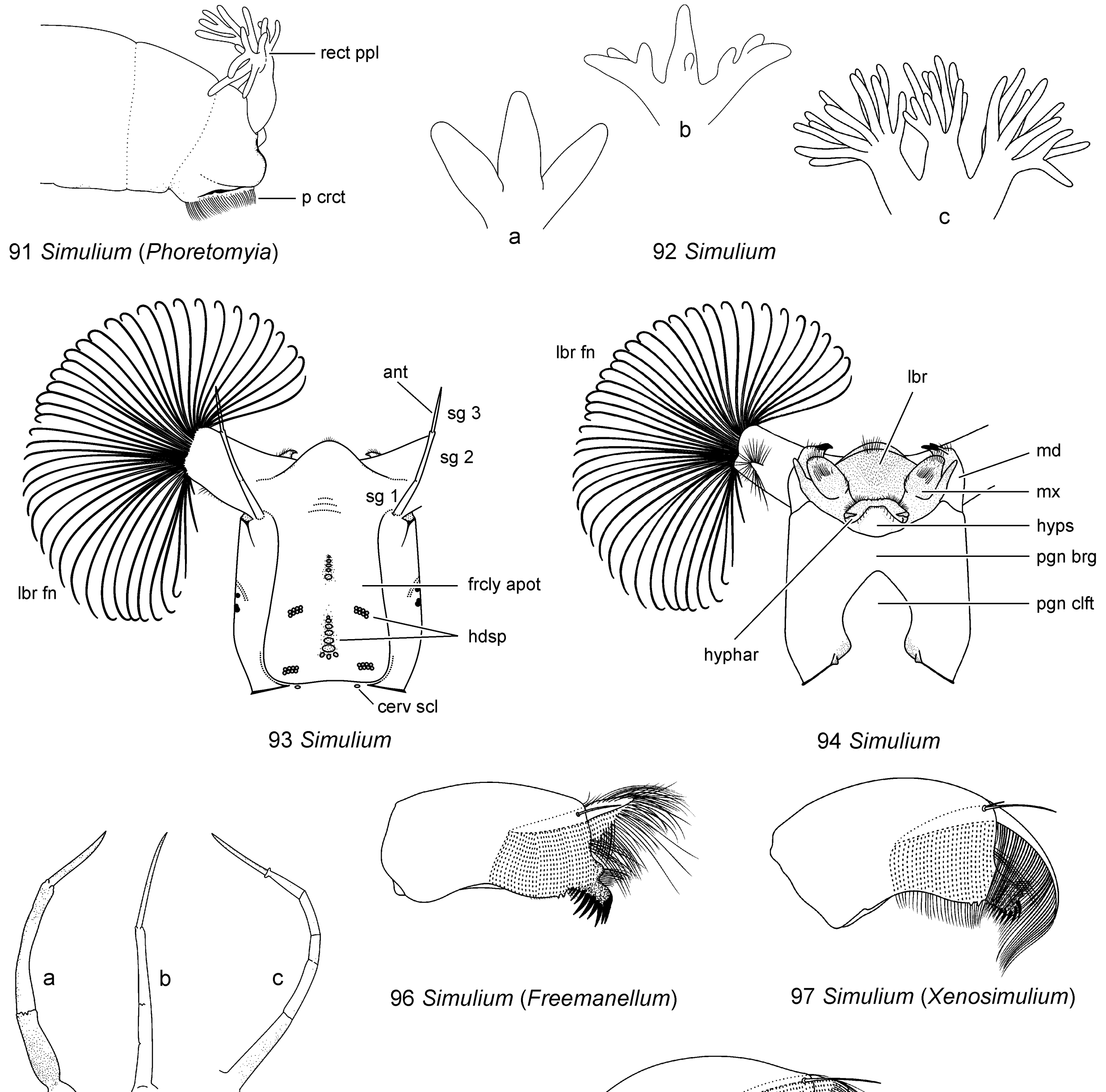
89 *Simulium* (*Edwardsellum*)



90 *Simulium* (*Edwardsellum*)

Figs 32.82–90. Larval habitus and features of Simuliidae: (82) larval features of *Simulium* sp, lateral view (non-Afrotropical); (83) larval habitus of *S.* (*Pomeroyellum*) sp., lateral view; (84) same, detail of abdominal setal structure; (85) larval habitus of *S.* (*Metomphalus*) *medusaeforme* species-group, lateral view; (86) same, detail of abdominal setal structure; (87) larval habitus of *S.* (*Met.*) *bovis* species-group, lateral view; (88) same, detail of abdominal setal structure; (89) larval habitus of *S.* (*Edwardsellum*) sp, lateral view; (90) same, detail of abdominal setal structure. Figs 82–90 (after Crosskey 1969, figs 7, 224–231).

Abbreviations: gll htblast – gill histoblast; p crct – posterior circlet; prlg – proleg; rect ppl – rectal papillae; v tb – ventral tubercle.



Figs 32.91–98. Larval features of Simuliidae: (91) terminal abdominal segments of *Simulium* (*Phoretomyia*) sp., lateral view; (92) examples of rectal papillae in Simuliidae; (93) structure of head of *Simulium* sp., dorsal view; (94) same, ventral view; (95) examples of antennal structure in Simuliidae; (96) left mandible of *Simulium* (*Freemanellum*) sp., inner view; (97) same, *Simulium* (*Xenosimulium*) sp.; (98) same, *Simulium* (*Metomphalus*) sp. Figs 91–98 (after Crosskey 1969, figs 285, 10, 14, 15, 288–290, 295, 296, 294, respectively).

Abbreviations: ant – antenna; cerv scl – cervical sclerite; frcly apot – frontoclypeal apotome; hdsp – head spots; hyphar – hypopharynx; hyps – hypostoma; lbr – labrum; lbr fn – labral fan; md – mandible; mx – maxilla; p crct – posterior circlet; pgn brg – postgenal bridge; pgn clft – postgenal cleft; rect ppl – rectal papillae; sg – segment.

accepted three subfamilies in Simuliidae (Parasimuliinae, Prosimuliinae and Simuliinae), with Simuliinae comprised of three tribes: Cnephiini (*Cnephia sensu lato*), Austrosimuliini (*Austrosimulium*, *Gigantodax*) and Simuliini (*Simulium sensu lato*).

The most recent classification of Simuliidae has been derived from the work of two prominent researchers I.A. Rubtsov and R.W. Crosskey. Rubtsov (1974) produced a detailed classification, taking into account the evolution, phylogeny and classification of the family and recognised 59 genera in four subfamilies: Gymnopaidinae, Parasimuliinae, Prosimuliinae (containing the genera *Gigantodax*, *Paracnephia*, *Procnephia* Crosskey and *Prosimulium*) and Simuliinae (containing five tribes and all other genera). Crosskey (1981: 3, 1988: 425) published a classification dividing the family into two subfamilies Prosimuliinae and Simuliinae, together containing nine tribes. In a more recent update Crosskey & Howard (1997: 10) recognised only two subfamilies Parasimuliinae (*Parasimulium*) and Simuliinae (containing all other blackfly genera placed in the tribes Prosimuliini and Simuliini). This classification is adopted in this chapter.

Afrotropical blackflies are all classified in the subfamily Simuliinae and tribe Simuliini. The species placed in the genus *Paracnephia* pose some interesting dilemmas, in that their phylogenetic placement is somewhat tentative, as the wing venation in the genus *Paracnephia* is considered derived, due to the lack of a fork in vein *Rs*, but many of the other characters, such as the absence of spinules on the costal vein (C), and other wing veins, the lack of a pedisulcus and poorly developed calcipala, structurally poorly formed pupal cocoons and the development of sharp terminal spines on the abdomen of the pupa, as well as the unseparated cervical sclerites in the final instar larva, are all indicative of an underived (plesiomorphic) condition. Crosskey & Howard (1997: 18) raised the subgenus *Paracnephia* to generic level, retaining its status as subgenus for a number of the known species and added *Procnephia* as a second subgenus in this grouping. The Australasian genus *Cnephia* was also added to this genus, but not designated further subgeneric status.

By using the banding pattern observed on the giant polytene chromosomes extracted from the salivary glands of mature larvae, or from the malpighian tubules of adult blackflies, the pattern of chromosomal inversions can be analysed and be used to develop cytological transformation series (Adler *et al*. 2004: 60). Such studies have been used to designate over 70 cytoforms within the *S. damnosum sensu lato* species complex and some of these have been recognised as representing good species, based on detailed morphotaxonomic, behavioural or molecular information (Adler & Crosskey 2015*a*).

With the advent of cytotaxonomy and molecular characterisation of species Currie & Adler (2008) conservatively predicted that the total number of species of blackfly that can be recognised will increase by 32.2% for the Afrotropical Region.

Identification

As Simuliidae include a number of species of medical and veterinary importance they have been relatively well-studied systematically, biologically and ecologically in all stages of their life cycle (Crosskey 1990: 3). There are currently 2,175 extant species in the family with 1,820 recognised globally as belonging to the genus *Simulium* (Adler & Crosskey 2015*a*). This genus has, therefore, become a taxonomically unmanageable unit and the use of subgeneric taxon and species-group names have been supported by most researchers studying blackflies (Crosskey 1990: 44). There are also many cryptic species that are morphologically very difficult to identify and a further division, that of sibling or aphanic species (*sensu* Steyskal 1972), has been accepted.

In most cases, the description of blackfly species has been based on the adult stage, usually the male, but as the pupal stage in blackflies is very distinctive a number of species have been described using only this stage, particularly from Madagascar (Elouard *et al*. 1996; Pilaka & Elouard 1997, 1999*a*, *b*). Following the classification proposed by Crosskey (1981: 3, 1988: 425), 211 species in two genera (*Simulium* and *Paracnephia*) are currently recognised from the Afrotropical Region (Adler & Crosskey 2015*a*). With the exception of *S*. (*Byssodon* Enderlein) and *S*. (*Nevermannia*), at the subgeneric level the Afrotropical species of Simuliidae are all endemic.

Identification keys and descriptions of species, mostly for adults and pupae, but also a number of keys to larvae, can be found in Carvalho (1962), Crosskey (1960, 1969), Dang & Peterson (1981), de Moor (2003), Elouard (2003), Elouard & Pilaka (2001), Freeman & de Meillon (1953), Lewis (1965*a*, *b*), Lewis & Raybould (1974) and Palmer (1991).

Insufficient characters could be found in the literature to key adult females of the subgenera *S*. (*Nevermannia*) and *S*. (*Meilloniellum*), so females of these two subgenera are treated together in the below identification key.

The below identification key to larvae is primarily intended for the identification of final, or penultimate instars, although earlier instars can be identified in many cases. The effectiveness of the key is greatly enhanced if used in conjunction with the key to pupae. In many instances the dissection and examination of pupal gill histoblasts in final-instar larvae will significantly aid identification. No satisfactory characters separating the larvae of the subgenera *Paracnephia* (*Procnephia*) and *Paracnephia sensu stricto* have been found in the literature or from the limited material available, so larvae are only keyed to the generic level below.

Pupae with 8-filamented respiratory organs are recorded for three subgenera: *S*. (*Lewisellum* Crosskey), *S*. (*Meilloniellum* Rubtsov) and *S*. (*Pomeroyellum* Rubtsov) and some careful discretion is required to separate these groups. Rearing pupae through to the adult stage, as well as examination of larval material from the same collection site will assist. As identification to specific level is in many instances relatively easy, the below identification key facilitates identification to the level of species-group where feasible.

Adult Simuliidae are usually micro-pinned in the field for later double-mounting (see Chapter 2). Immature stages are usually preserved direct into ethanol.

Keys to genera of Afrotropical Simuliidae

Adults

1. Hind tarsomere 2 without pedisulcus (as in Fig. 19); wing with basal medial cell (*bm*) (as in Fig. 11); thorax with katepisternum (viewed in profile) approximately equal in length and depth (Fig. 17) . . . . . *Paracnephia* Rubtsov 2

– Hind tarsomere 2 with pedisulcus (Fig. 20); wing without basal medial cell (*bm*) (Fig. 12); thorax with katepisternum (viewed in profile) distinctly longer than deep (Fig. 18) . . . . . *Simulium* Latreille 3

2. Wing with costal vein (*C*) with socketed setae only; hind tarsomere 1 without calcipala, or calcipala small and indistinct (as in Fig. 19) . . . . . *Paracnephia* (*Procnephia* Crosskey)

– Wing with costal vein (*C*) with socketed setae and spinules; hind tarsomere 1 with calcipala, moderately to well-developed (as in Fig. 20) . . . . . *Paracnephia sensu stricto*

3. Hind tarsomere 1 with calcipala barely discernible (Fig. 21); terminal segment of palpus not longer than penultimate segment (Fig. 22); head (in frontal view) equal in width and height, tapering ventrally (Fig. 9); posterior margin of eye (in lateral view) extending backwards medially (Figs 5, 6) . . . . . *Simulium* (*Afrosimulium* Crosskey)

– Hind tarsomere 1 with calcipala distinct, well-developed (*e.g.*, Fig. 20); terminal segment of palpus distinctly longer than penultimate segment (*e.g.*, Fig. 2); head (in frontal view) distinctly wider than high, not distinctly tapered ventrally (*e.g.*, Fig. 10); posterior margin of eye (in lateral view) not extended backwards medially (*e.g.*, Figs 7, 8) 4

4. Wing with basal section of radial vein (*R*) bare . . . . . *Simulium* (*Byssodon* Enderlein)

– Wing with basal section of radial vein (*R*) setose (as in Fig. 12) 5

5. Head holoptic, eyes with large dorsal facets and smaller ventral facets (*e.g.*, Fig. 2) (separate key to males) 6

– Head dichoptic, eyes with uniformly sized facets dorsally and ventrally (*e.g.*, Figs 1, 4) (separate key to females) 16

6. Thorax with katepisternum setose; ground colour of thorax orange to dark reddish brown; terminalia with gonostylus long and slender, exceeding length of gonocoxite (Fig. 32) . . . . . *Simulium* (*Freemanellum* Crosskey) [in part]

– Thorax with katepisternum bare; ground colour of thorax almost invariably black; terminalia with gonostylus shorter than gonocoxite, rarely subequal in length (*e.g.*, Figs 33–38) 7

7. Fore tarsus conspicuously dilated, bearing dorsal setose crest; tarsomere 1 3.5–5.0 × as long as its greatest width (*e.g.*, Figs 23, 24) 8

– Fore tarsus not conspicuously dilated, without dorsal setose crest; tarsomere 1 5.5–8.0 × as long as its greatest width (*e.g.*, Figs 25–29) 9

8. Thorax with scutum with sharply defined black and silver-grey pattern, with dark posteriorly tapering median macula and two dorsolateral, forwardly tapering maculae (Fig. 13); terminalia (Fig. 33) with hypopygium with numerous parameral spines; ventral plate strongly arched in profile, with numerous teeth and diverging basal arms; gonostylus truncate and gonocoxite extending beyond base of gonostylus . . . . . *Simulium* (*Edwardsellum* Enderlein) [in part]

– Thorax with scutum without pattern, or with broad dark median longitudinal fascia, flanked by paler lateral areas; terminalia (as in Fig. 34) with hypopygium with 1 large parameral spine, sometimes also second shorter spine, or with only rudimentary spines; ventral plate not arched in profile, lamellate with small basal arms not toothed; gonostylus apically tapered to conical (Fig. 39) . . . . . *Simulium* (*Phoretomyia* Crosskey) [in part]

9. Terminalia (*e.g.*, Figs 34, 37, 38) with hypopygium with 1 outwardly directed dagger- or scythe-shaped parameral spine on each side; ventral plate rectangular, lamellate or triangular in shape (*e.g.*, Figs 47–52), without toothed surface and more or less straight in profile (*e.g.*, Figs 61–66); thorax with scutum without pattern of pale grey and dark markings 10

– Terminalia (*e.g.*, Figs 35, 36) with hypopygium with multiple, variously placed parameral spines on each side; ventral plate of varied form, often complex, with toothed surface (*e.g.*, Figs 53–57), usually strongly angulate in profile (*e.g.*, Figs 67–71); thorax with scutum frequently with bold pattern of pale grey and dark markings, if not then at least exhibiting traces of silvery grey shoulder patches 13

10. Terminalia (*e.g.*, Figs 37, 40) with gonostylus abruptly narrowed at *ca* ⅔ its length, forming conical apical extension; ventral plate longer than wide or sub-quadrate, with small basal arms and an indented median apical notch (*e.g.*, Figs 37, 52) 11

– Terminalia (*e.g.*, Figs 41–44) with gonostylus not abruptly narrowed apically; ventral plate wider than long or sub-triangular, with moderately long basal arms (*e.g.*, Figs 47–51) 12

11. Small species (wing length: 1.9–2.5 mm); terminalia (Fig. 37) with basal region of ventral plate (between basal arms), extended medially, sometimes bilobed in appearance . . . . *Simulium* (*Meilloniellum* Rubtsov) [in part]

– Large species (wing length: 2.6–3.6 mm); terminalia (Fig. 38) with basal region of ventral plate (between basal arms), evenly rounded. . . . . *Simulium* (*Lewisellum* Crosskey) [in part]

12. Terminalia with ventral plate wider than long, rectangular in shape, with well-developed shoulders and setulose median keel (Figs 34, 47) . . . . *Simulium* (*Nevermannia* Enderlein) *ruficorne*-group

– Terminalia with ventral plate sub-rectangular, with downwardly-sloping shoulders or plate triangular (Figs 48–50), if plates rectangular, then without strong median setulose keel (Fig. 51) . . . . *Simulium* (*Pomeroyellum* Rubtsov) [in part]

13. Thorax with scutum with pruinescence, silver-grey shoulder marks, or with bold black and pale grey pattern (as in Figs 14, 15); terminalia with ventral plate of diverse shape and form, usually sub-triangular and apically toothed (Figs 36, 54–57, 69–71) . . . . *Simulium* (*Metomphalus* Enderlein) [in part]

– Thorax with scutum without pruinescence, silver-grey shoulder marks, or black and pale-grey pattern; terminalia with ventral plate never toothed and not as above 14

14. Terminalia with ventral plate broadly rectangular, usually with median downturned setulose apical lip (Fig. 58); thorax with pleural membrane bare . . . . *Simulium* (*Nevermannia* Enderlein) *loutetense*-group

– Terminalia with ventral plate less broadly rectangular, with downwardly sloping shoulders (*e.g.*, Fig. 60) or with basal region of plate with convex rounded median extension between arms (*e.g.*, Fig. 59); thorax with pleural membrane setulose 15

15. Terminalia with ventral plate with well-developed square shoulders and elongate, parallel basal arms, apical margin setulose across most of width (Fig. 59), in profile plate only gently curved (Fig. 67); gonostylus gradually tapering to apex (Fig. 45) (confined to Madagascar) . . . . *Simulium* (*Xenosimulium* Crosskey) [in part]

– Terminalia with ventral plate with sloping shoulders or sub-triangular and short basal arms, apical margin setulose, only setose along median region (Figs 53, 60), in profile plate strongly bent or angulate in relation to basal arms (Fig. 68); gonostylus abruptly truncated apically (Fig. 46) (confined to continental Afrotropics) . . . . *Simulium* (*Anasolen* Enderlein) [in part]

16. Thorax with katepisternum setulose; ground colour of thorax reddish to dark red-brown; terminalia with hypogynial valves fleshy, protruding ventrally; anal lobes moderately to extensively produced ventrally (Fig. 74). . . . . *Simulium* (*Freemanellum* Crosskey) [in part]

– Thorax with katepisternum bare; ground colour of thorax almost invariably black; terminalia with hypogynial valves and anal lobes not produced ventrally (*e.g.*, Fig. 75). 17

17. Fore tarsus conspicuously dilated, bearing dorsal setulose crest; tarsomere 1 3.5–5.0 × as long as its greatest width (*e.g.*, Figs 23, 24) 18

– Fore tarsus not conspicuously dilated, without dorsal setulose crest; tarsomere 1 5.5–8.0 × as long as its greatest width (*e.g.*, Figs 25–27) 19

18. Hind leg with tarsomere 1 creamy white throughout most of its length, sharply contrasting with other black tarsomeres; terminalia with hypogynial valves extended, slender and inwardly curled (Fig. 76); thorax with scutum with blue-grey dusty appearance (viewed from in front). . . . . *Simulium* (*Edwardsellum* Enderlein) [in part]

– Hind leg with all tarsi (including tarsomere 1) black; terminalia with hypogynial valves bluntly rounded, not extended (as in Fig. 77); thorax with scutum densely clothed in pale yellow to golden, or copper-coloured scales . . . . *Simulium* (*Phoretomyia* Crosskey) [in part]

19. Terminalia with pointed sub-triangular, or slender attenuated straight, or spiralled hypogynial valves (*e.g.*, Figs 76, 79–81); tarsal claws simple or with minute basal tooth only (*e.g.*, Fig. 28); thorax with pleural membrane often setulose 20

– Terminalia with short bluntly rounded, or truncate lobe-like hypogynial valves (*e.g.*, Figs 77, 78); tarsal claws usually with large basal tooth (*e.g.*, Figs 25, 26); thorax with pleural membrane bare (except in *S.* (*Meilloniellum*) *adersi* Pomeroy, 1922) 22

20. Terminalia with large medially directed, clasper-like hypogynial valves, densely setulose apically (Fig. 81); anal lobe ventrally extended (as in Fig. 74); abdominal segment 7 with distinctly-shaped brown sclerotised sternite (confined to Madagascar) . . . . *Simulium* (*Xenosimulium* Crosskey) [in part]

– Terminalia with slender attenuate, or short triangular, hypogynial valves, not densely setulose apically (*e.g.*, Figs 76, 79, 80); anal lobe not ventrally extended (*e.g.*, Fig. 75); abdominal segment 7 with pale membranous sternite (not confined to Madagascar) 21

21. Terminalia with long slender attenuate hypogynial valves, often curled apically (Figs 75, 76, 80); thorax with scutum with 3 longitudinal thin dark curved lines (visible when viewed from front) (Fig. 16); tarsal claws simple, without basal tooth . . . . *Simulium* (*Metomphalus* Enderlein) [in part]

– Terminalia with short sub-triangular hypogynial valves, apical tips medially directed (Fig. 79); thorax with scutum without distinctive pattern; tarsal claws without, or with only small basal tooth . . . . *Simulium* (*Anasolen* Enderlein) [in part]

22. Tarsal claws with large basal tooth (small in *S.* (*Nevermannia*) *speculiventre* Enderlein, 1914) (*e.g.*, Figs 25, 26); hind tibiae usually with dark sub-basal fascia; legs in most cases extensively pale; abdomen with silvery-yellow or silver scales; generally small species (wing length: 1.8–2.8 mm); pupae not attached to other arthropods 23

– Tarsal claws with small or minute basal tooth (*e.g.*, Fig. 27); hind tibiae without dark sub-basal fascia; legs usually entirely black; abdomen with yellow to golden, sometimes black scales; large species (wing length: 2.7–3.6 mm); pupae attached to prawns, crabs or mayfly nymphs 24

23. Abdominal tergites 6–8 with only sparse, fine inconspicuous setae, appearing bare and shiny black (except in *S.* (*Po.*) *merops* de Meillon, 1950 and *S.* (*Po.*) *evillense* Fain, Hallot & Bafort, 1966, with pale scales on all tergites) . . . . *Simulium* (*Pomeroyellum* Rubtsov) [in part]

– Abdominal tergites evenly and densely clothed in pale scales, not shiny black on tergites 6–8 . . . . *Simulium* (*Nevermannia* Enderlein) and *S.* (*Meilloniellum* Rubtsov) [in part]

24. Abdominal segments 1 and 2 clothed in pale yellow to deep golden scales, strongly contrasting with remaining abdominal segments, black with coppery brown scales; pupae attached to mayfly nymphs or freshwater prawns . . . . *Simulium* (*Phoretomyia* Crosskey) [in part]

– Abdominal segments evenly clothed in pale yellow or golden scales, often interspersed with red-brown coppery scales, sometimes with fascia of dark scales basally on segments 3 and 4, anterior and posterior segments not strongly contrasted; pupae attached to crabs, occasionally to freshwater prawns . . . . *Simulium* (*Lewisellum* Crosskey) [in part]

Larvae

1. Cervical sclerites merged with upper ends of post-occiput in final instars (Fig. 110); hypostoma with large fusiform teeth aggregated in 3 separate groups, sometimes only median tooth prominent (Figs 112, 113); frontoclypeal apotome widest at *ca* ⅓ distance from posterior margin (Fig. 99) (subgenera not keyed further) . . . . *Paracnephia* Rubtsov

– Cervical sclerites separated from upper ends of post-occiput in final instars (Fig. 111); hypostoma with simple teeth, not aggregated into 3 separate groups (Figs 114–117); frontoclypeal apotome widest near posterior margin (Figs 101–109) . . . . *Simulium* Latreille 2

2. Larvae attached to river crabs or prawns; hypostoma with even row of 13 apical teeth (Fig. 117); head elongated, with frontoclypeal apotome rounded posteriorly (Fig. 100); postgenal cleft small, quadrate (Fig. 139) . . . . *Simulium* (*Lewisellum* Crosskey) [in part]

– Larvae attached to mayfly nymphs or freshwater prawns; hypostoma not with even row of apical teeth; head more rounded with frontoclypeal apotome basally flattened (*e.g.*, Figs 101–109); postgenal cleft of various shapes (*e.g.*, Figs 120–138) 3

3. Larvae attached to mayfly nymphs or freshwater prawns; posterior abdominal proleg and circlet of hooks in ventral position (Fig. 91); postgenal cleft not discernible (Fig. 140) . . . . *Simulium* (*Phoretomyia* Crosskey)

– Larvae not attached to mayfly nymphs; posterior abdominal proleg and circlet of hooks in sub-terminal position (*e.g.*, Figs 83, 85, 87, 89); postgenal cleft discernible of various shapes and sizes (*e.g.*, Figs 120–138) 4

4. Abdominal segments 1–5 with paired dorsolateral subconical tubercles (Fig. 89); cuticle of entire body, including anterior proleg, clothed in prominent, elongated scale-like setae (Fig. 89) . . . . *Simulium* (*Edwardsellum* Enderlein)

– Abdominal segments 1–5 without paired dorsolateral subconical tubercles (at most abdominal segments with slightly produced protrusions, not clothed in dense setae) (*e.g.*, Figs 82, 83, 85, 87); if cuticle with conspicuous simple scales, then these not extending onto anterior proleg 5

5. Dorsal cuticle of body adorned with prominent, large, flat scales; postgenal cleft elongated and sub-elliptical (Fig. 126) (*S.* (*Met.*) *albivirgulatum*) . . . . *Simulium* (*Metomphalus* Enderlein) [in part]

– Dorsal cuticle of body bare or with sparse covering of scales, or with abundant minute, setula-like or fan-shaped setae; large fan-like setae if present confined to posterodorsal part of abdomen (*e.g.*, Figs 83–88); postgenal cleft of various shapes, but not as in Fig. 126 6

6. Ventral tubercles absent (*e.g.*, Figs 85, 87); rows of hypostomal setae diverging posteriorly from lateral margins of hypostoma, median and corner teeth of hypostoma not strongly prominent (*e.g.*, Figs 115, 116); head pigmentation pattern always positive or indistinctive (*e.g.*, Figs 106–109) 7

– Ventral tubercles present, subconical, sometimes small and rounded (*e.g.*, Figs 82, 83); rows of hypostomal setae lying virtually parallel to lateral margins of hypostoma, median and corner teeth of hypostoma strongly prominent (*e.g.*, Fig. 114); head pigmentation pattern negative (*e.g.*, Figs 101–103) or positive (*e.g.*, Figs 104, 105) 12

7. Abdominal cuticle without scales; primary brush of mandibles very prominent, extending far beyond end of mandible, main apical tooth of mandible reduced, not larger than other teeth (*e.g.*, Figs 96, 97); hypostomal teeth greatly reduced (*e.g.*, Figs 118, 119) 8

– Abdominal cuticle dorsally with at least small scales, or fine scattered simple setae on last few segments (*e.g.*, Figs 85–88); primary brush of mandibles not projecting far beyond end of mandible and main apical tooth larger than other teeth (*e.g.*, Fig. 98); hypostomal teeth visible and prominent (*e.g.*, Figs 115, 116). 9

8. Postgenal cleft large, elongated and mitre-shaped (Fig. 121); rectal papillae with numerous finger-like secondary lobules (as in Fig. 92c); antenna with 3 articles, with terminal cone, without secondary annulations (as in Figs 95a, 95b) (continental Afrotropics). . . . . *Simulium* (*Freemanellum* Crosskey)

– Postgenal cleft small and pentagonal-shaped (Fig. 122); rectal papillae simple without secondary lobules (as in Fig. 92a); antenna with secondary annulations, appearing to consist of 6–8 articles (as in Fig. 95c) (confined to Madagascar) . . . . *Simulium* (*Xenosimulium* Crosskey)

9. Postgenal cleft small, much shorter than postgenal bridge and forming square or rounded notch (Fig. 120); rectal papillae with numerous secondary lobules (as in Fig. 92c); hypostomal setae numerous, 8–24 in each row, but usually 12–18 (Fig. 115) . . . . *Simulium* (*Anasolen* Enderlein)

– Postgenal cleft large, rounded (*e.g.*, Figs 127, 129, 130), sagittate (*e.g.*, Figs 123–125), sub-cordate (*e.g.*, Fig. 128) or elongate (*e.g.*, Fig. 121), but always much longer than postgenal bridge; rectal papillae simple or with secondary lobules (*e.g.*, as in Figs 92a, 92b); hypostomal setae various, but never more than 10 per row. 10

10. Postgenal cleft sub-cordate, postgenal bridge minute (Fig. 128); rectal papillae simple; head capsule faintly pigmented posteriorly; hypostomal setae 4 per row . . . . *Simulium* (*Afrosimulium* Crosskey)

– Postgenal cleft rounded or sagittate (*e.g.*, Figs 123–127, 130); rectal papillae simple or with secondary lobules; head capsule pigmentation positive or indiscernible; hypostomal setae from 3–10 per row 11

11. Hypostomal setae 3 (occasionally 4) per row; postgenal cleft large and sub-circular (Fig. 130); rectal papillae with finger-like secondary lobules . . . . *Simulium* (*Byssodon* Enderlein)

– Hypostomal setae 4–8 (rarely up to 10) per row (Fig. 116); postgenal cleft large and sagittate to sub-circular (Figs 124, 125, 127); rectal papillae simple, or with secondary lobules. . . . . *Simulium* (*Metomphalus* Enderlein) [in part]

12. Head pigmentation pattern positive (Figs 104, 105) (positive head pigmentation also occurs in some species of *S.* (*Pomeroyellum*), so is advisable to examine pupal respiratory organs to confirm identification); postgenal cleft much smaller than postgenal bridge (Figs 131, 132) (except in *S.* (*N.*) *loutetense* species-group in which postgenal cleft is elongated and larger than the postgenal bridge (Fig. 133)) . . . . *Simulium* (*Nevermannia* Enderlein)

– Head pigmentation pattern usually negative (positive in some species of *S.* (*Pomeroyellum*)), forming H-shape on frontoclypeal apotome (*e.g.*, Figs 101–103); postgenal cleft longer than or equal to length of postgenal bridge 13

13. Postgenal cleft sub-equal to postgenal bridge, rounded (Fig. 138); ventral tubule rounded and small, rather inconspicuous; cuticle of abdomen adorned with small simple, or slightly fusiform setae . . . . *Simulium* (*Meilloniellum* Rubtsov)

– Postgenal cleft of various shapes (Figs 134–137); ventral tubule subconical and well-developed; cuticle of abdomen posterodorsally adorned with large scales, or small divided setae (except in *S.* (*Po.*) *kenyae* species-group, with setae absent) . . . . *Simulium* (*Pomeroyellum* Rubtsov)

Pupae

1. Last abdominal segment with pair of elongated strong terminal spines (Fig. 147); cuticle of abdomen with strongly sclerotised tergal and sternal plates . . . . *Paracnephia* Rubtsov 2

– Last abdominal segment with pair of small, blunt or slightly thorn-like tubercles; cuticle of abdomen not strongly sclerotised. . . . .*Simulium* Latreille 3

2. Pupal respiratory organ with 6–7 filaments, with apically converging inter-twined apices (Figs 148, 149). . . . . *Paracnephia* (*Procnephia* Crosskey)

– Pupal respiratory organ with 10–22 filaments, or with 6 apically divergent filaments (Figs 150, 151) . . . .*Paracnephia sensu stricto*

3. Pupae attached to mayfly nymphs, river crabs or river prawns 4

– Pupae not attached to mayfly nymphs, river crabs or river prawns 5

4. Pupae attached to mayfly nymphs or river prawns; pupal respiratory organ (Figs 152–154) with 10–95 slender filaments arising from common base and arranged in semicircular fashion; cocoon much reduced, only covering abdomen . . . . *Simulium* (*Phoretomyia* Crosskey)

– Pupae attached to river crabs or prawns; pupal respiratory organ (Fig. 155) with 8 long slender filaments (3 sub-branches branched further 3 : 3 : 2); cocoon usually longer than length of body . . . .*Simulium* (*Lewisellum* Crosskey)

5. Pupal respiratory organ (*e.g.*, Figs 156, 157) with 3 robust, tapering, flattened, leaf-like or rounded branches 6

– Pupal respiratory organ a single stem, with or without terminal branches, with 4 or more slender unbranched or numerous branched filaments, or with more than one type of filament which may or may not be branched (*e.g.*, Figs 158–196) 7

6. Pupal respiratory organ (Fig. 156) with 3 leaf-like, flattened branches with smooth unsculptured walls . . . . *Simulium* (*Byssodon* Enderlein)

– Pupal respiratory organ (Fig. 157) with 3 strongly tapering tube-like branches with nodular sculpturing (*S.* (*Af.*) *gariepense* de Meillon, 1953) . . . . *Simulium* (*Afrosimulium* Crosskey)

7. Pupal cocoon shoe-shaped, with "heel", usually with well-developed neck (*e.g.*, Figs 142, 144) (in one species *S.* (*Met.*) *albivirgulatum* with inconspicuous neck); dorsally abdominal segments 6–8 without spine combs 8

– Pupal cocoon slipper-shaped (*e.g.*, Figs 141, 143), sometimes with indistinct neck; dorsally abdominal segments 6–8 with well-developed, backwardly directed spine combs (*e.g.*, Fig. 145) 14

8. Pupal respiratory organ with 4 filaments (Figs 158, 159) . . . . *Simulium* (*Freemanellum* Crosskey)

– Pupal respiratory organ with more than 4 filaments or branches 9

9. Pupal respiratory organ (Figs 160, 161) with 8–19 sharp-pointed filaments with blackened tips, of one type of filament only . . . .*Simulium* (*Anasolen* Enderlein)

– Pupal respiratory organ (*e.g.*, Figs 162–166) with rounded terminal ends without sharp darkened tips, usually robust and often branched, frequently with basal arms and secondary filaments 10

10. Pupal respiratory organ (Figs 162, 163) consisting of 6 or 9 large, thin-walled tubular branches arising between pair of large thin-walled curved basal arms, all branches pale and essentially of same form . . . . *Simulium* (*Edwardsellum* Enderlein)

– Pupal respiratory organ consisting of slender filaments without basal arms or of stout tubular primary filaments, with basal arms and thinner secondary filaments sometimes also on basal arms 11

11. Pupal respiratory organ (Figs 164–166) without basal arm, comprised of 6–19 slender filaments (confined to Comoros and Madagascar). . . . . *Simulium* (*Xenosimulium* Crosskey)

– Pupal respiratory organ (Figs 167–172) consisting of stout or tubular primary branches, often with basal arms and thinner secondary filaments (widespread Afrotropics) . . . . *Simulium* (*Metomphalus* Enderlein) 12

12. Pupal respiratory organ (Fig. 170) ending in large number of equally sized filaments, arising from 5 basal branches; pupal cocoon with indistinct neck . . . . . *Simulium* (*Met.*) *albivirgulatum* Wanson & Henrard

– Pupal respiratory organ (e.g., Figs 167–169, 171, 172) with stout primary branched filaments and variously sized thinner secondary filaments, or rounded tubular branches; pupal cocoon with distinct neck (e.g., Fig. 144) 13

13. Pupal respiratory organ (Figs 167–169) with distinct basal arms, with or without secondary filaments and large central branches without terminal filaments; abdominal segment 5 with pair of ventral hooks on each side . . . . *Simulium* (*Met*.) *medusaeforme*-group

– Pupal respiratory organ (Figs 171, 172) without basal arms; large central branches usually with terminal filaments; abdominal segment 5 without ventral hooks on each side, sometimes with single minute hook on each side . . . . *Simulium* (*Met*.) *bovis*-group

14. Pupal respiratory organ (Figs 173–180) variously branched with 4 or 6 filaments, sometimes with 4 thin terminal filaments arising from single or once-divided robust tubular filament; cocoon usually without, but occasionally with indistinct neck . . . . *Simulium* (*Nevermannia* Enderlein)

– Pupal respiratory organ various, but never with 4–6 filaments; cocoon without distinct neck (indistinct neck in *S*. (*Po*.) *kenyae* de Meillon, 1940) 15

15. Pupal respiratory organ (Figs 181, 182) with 8 or 11 filaments (note: *S*. (*Lewisellum*) and some *S*. (*Pomeroyellum*) also have 8 filaments) . . . . *Simulium* (*Meilloniellum* Rubtsov)

– Pupal respiratory organ (Figs 183–196) with 20 or fewer filaments, but never with 4–6 filaments and of varied form, but never arranged in semi-circular fashion . . . . . . *Simulium* (*Pomeroyellum* Rubtsov) 16

16. Pupal respiratory organ (Figs 183–185) formed of single, long, forwardly directed tube or tube branching into 8 apical thread-like filaments arising from ⅓ to ⅔ of the way up tube . . . . *Simulium* (*Po*.) *schoutedeni*-group

– Pupal respiratory organ with common basal stem, with numerous branching slender filaments, or dividing into 2 simple broad arms, or with broad arms branching off a number of short-stout secondary arms 17

17. Pupal respiratory organ (Figs 186–188) with 7–20 filaments, sometimes arising from common basal stem, if with 8 filaments that arise in pairs near base, then it belongs to *S*. (*Po*.) *kenyae*-group with only recognised species *S*. (*Po*.) *kenyae* (Fig. 189) otherwise . . . . *Simulium* (*Po*.) *alcocki*-group

– Pupal respiratory organ (Figs 190–196) arising from base and dividing into 2 simple arms, or else with branching secondary series of short, stout arms . . . . *Simulium* (*Po*.) *cervicornutum*-group

Synopsis of the fauna

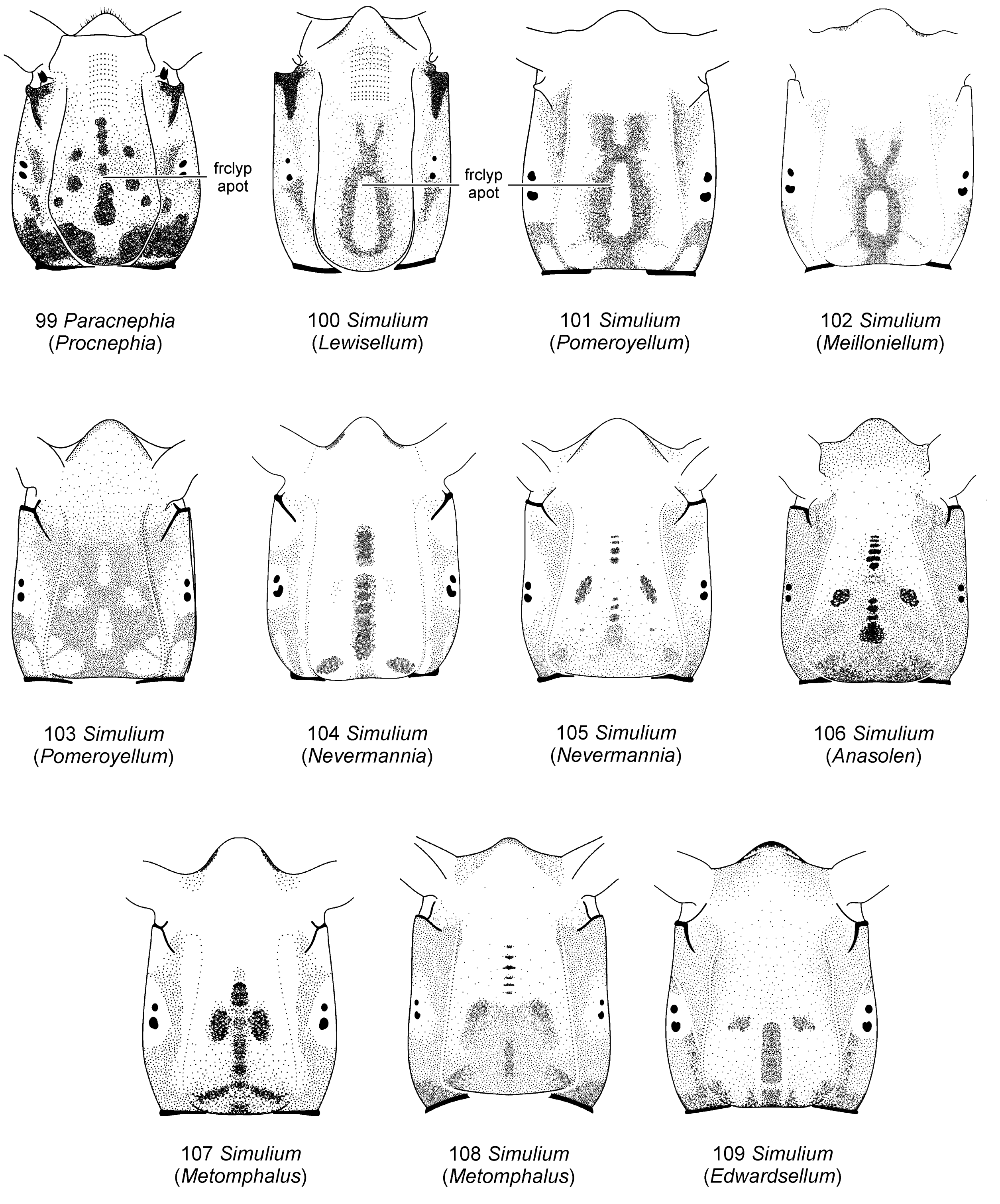
The Afrotropical species of blackfly can be divided into several ecological categories that closely reflect the subgeneric divisions of the family. The distribution and ecology of many southern African species is discussed by Palmer & de Moor (1998).

***Paracnephia* Rubtsov** (Simuliinae: Simuliini)**.** A genus of 19 described species occurring in the Afrotropical and Australasian Regions. In the Afrotropics the genus is divided into two subgenera, *Paracnephia sensu stricto*, with six described species and *P*. (*Procnephia* Crosskey) with three species (Adler & Crosskey 2015*a*). The 10 described Australian species are considered to be phylogenetically closely related to the Afrotropical species, but are currently unassigned to subgenera (Adler & Crosskey 2015*a*). It can be surmised that species in the genus reflect a relic Gondwana austral distribution. The genus shares morphological and ecological similarities with European *Prosimulium*. Larvae and pupae of both subgenera are found in mosses attached to rocks in swift-flowing waters and pupae form a communal silken mat. The two Afrotropical subgenera are dealt with separately below.

***Paracnephia* (*Procnephia* Crosskey)** (Simuliinae: Simuliini)**.** An endemic subgenus, with three described species, *P*. (*Pr*.) *damarensis* (de Meillon & Hardy, 1951), described from Namibia, *P*. (*Pr*.) *morotoensis* McCrae & Prentice, 1965, from Uganda and *P*. (*Pr*.) *rhodesiana* (Crosskey, 1968), from Zimbabwe (Adler & Crosskey 2015*a*). Species are usually found in ephemeral streams on outcrops of ancient geological formations, such as granite outcrops near Harare, Zimbabwe and on granitic inselbergs, such as the Brandberg massif in the Namib Desert of Namibia. Immature stages have been described for all species in the original descriptions of the species by authors. An identification key was provided by Crosskey (1968).

Paracnephia sensu stricto (Simuliinae: Simuliini)**.** An endemic subgenus divided into two species-groups: the *P*. (*P*.) *brincki* species-group, with the single species, *P*. (*P*.) *brincki* (de Meillon, 1955), from the Western Cape, South Africa and the *P*. (*P*.) *muspratti* species-group, with five described species, all except *P*. (*P*.) *herero* (Enderlein, 1935) (from Namibia), recorded from the Western Cape, South Africa (Adler & Crosskey 2015*a*). In the south-western Cape sedimentary deposits of Table Mountain Sandstone and some granitic outcrops where streams only flow intermittently support several species. Mature larvae, pupae and adults have been collected in late spring to early summer (September–December), but very little is known about the biology and ecology of the species found in southern Africa. An identification key to some species was provided by Freeman & de Meillon 1953.

***Simulium* Latreille** (Simuliinae: Simuliini)**.** The largest genus in the Simuliidae, with 1,745 described species occurring in



99 *Paracnephia* (*Procnephia*)

100 *Simulium* (*Lewisellum*)

101 *Simulium* (*Pomeroyellum*)

102 *Simulium* (*Meilloniellum*)

103 *Simulium* (*Pomeroyellum*)

104 *Simulium* (*Nevermannia*)

105 *Simulium* (*Nevermannia*)

106 *Simulium* (*Anasolen*)

107 *Simulium* (*Metomphalus*)

108 *Simulium* (*Metomphalus*)

109 *Simulium* (*Edwardsellum*)

Figs 32.99–109. Larval head capsules of Simuliidae (dorsal views): (99) *Paracnephia* (*Procnephia*) sp.; (100) *Simulium* (*Lewisellum*) sp.; (101) *S.* (*Pomeroyellum*) sp.; (102) *S.* (*Meilloniellum*) sp.; (103) *S.* (*Po.*) sp.; (104) *S.* (*Nevermannia*) sp.; (105) *S.* (*N.*) sp.; (106) *S.* (*Anasolen*) sp.; (107) *S.* (*Metomphalus*) sp.; (108) *S.* (*Met.*) sp.; (109) *S.* (*Edwardsellum*) sp. Figs 99–109 (after Crosskey 1969, figs 48, 283, 232–240, respectively).

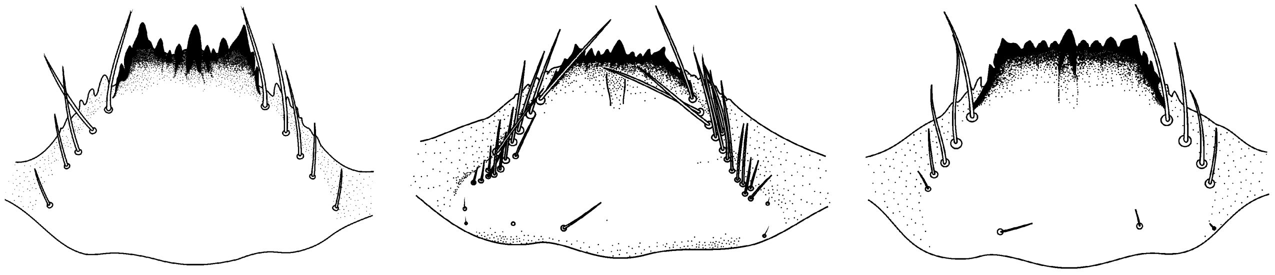
Abbreviation: frcly apot – frontoclypeal apotome.

all zoogeographical regions. The Afrotropical fauna comprises 198 described species that are currently divided into 11 subgenera that are dealt with separately below.

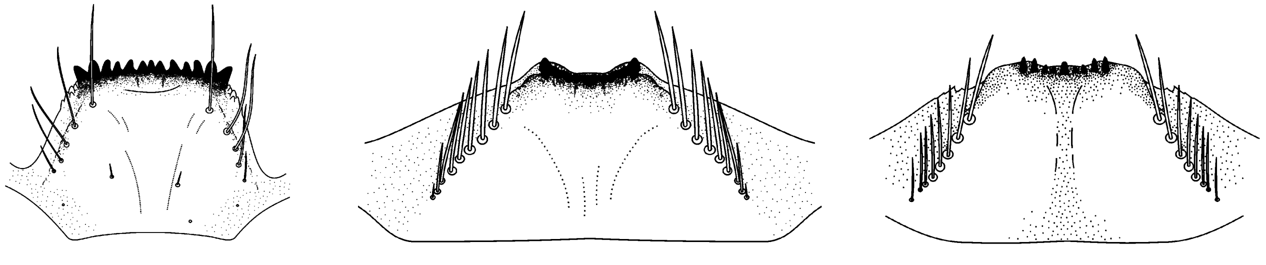
***Simulium* (*Afrosimulium* Crosskey)** (Simuliinae: Simuliini)**.** An endemic monotypic subgenus, with the single described species, *S.* (*Af.*) *gariepense* de Meillon, 1953, recorded from Lesotho, Namibia and South Africa (Adler & Crosskey 2015a). The species is adapted to the slower-flowing stretches of large, turbid rivers, such as the Orange River in South Africa. It may in fact be one of the few species that is able to survive on muddy substrata. Following the construction of impoundments and

110 *Paracnephia* 111 *Simulium*

112 *Paracnephia* (*Procnephia*) 113 *Paracnephia* (*Paracnephia*)



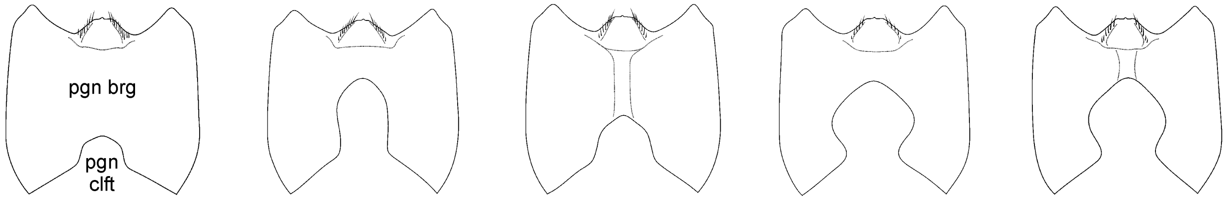
114 *Simulium* (*Nevermannia*) 115 *Simulium* (*Anasolen*) 116 *Simulium* (*Metomphalus*)



117 *Simulium* (*Lewisellum*) 118 *Simulium* (*Freemanellum*) 119 *Simulium* (*Xenosimulium*)

Figs 32.110–119. Larval head features of Simuliidae: (110) posterior margin of head of final-instar larvae of *Paracnephia* sp., dorsal view; (111) same, *Simulium* sp.; (112) apical hypostomal teeth of *Paracnephia* (*Procnephia*) sp., dorsal view; (113) same, *Paracnephia* (*Paracnephia*) sp.; (114) apical hypostomal teeth and setal arrangement of *S.* (*Nevermannia*) sp., dorsal view; (115) same, *S.* (*Anasolen*) sp.; (116) same, *S.* (*Metomphalus*) sp.; (117) same, *S.* (*Lewisellum*) sp.; (118) same, *S.* (*Freemanellum*) sp.; (119) same, *S.* (*Xenosimulium*) sp. Figs 110–119 (after Crosskey 1969, figs 20, 21, 49, 53, 272, 275, 278, 268, 276, 277, respectively).

Abbreviation: cerv scl – cervical sclerite.



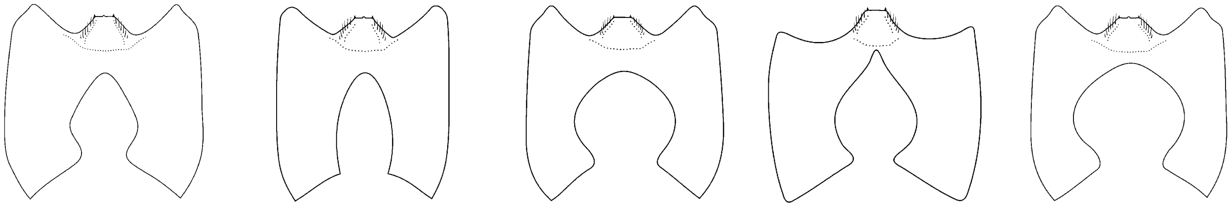
120 *Simulium* (*Anasolen*)

121 *Simulium* (*Freemanellum*)

122 *Simulium* (*Xenosimulium*)

123 *Simulium* (*Metomphalus*)

124 *Simulium* (*Metomphalus*)



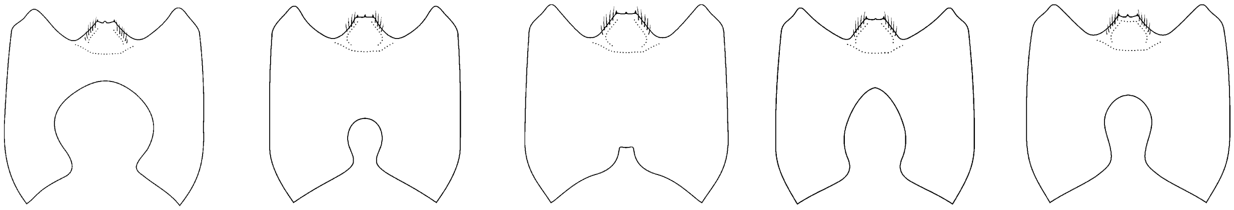
125 *Simulium* (*Metomphalus*)

126 *Simulium* (*Metomphalus*)

127 *Simulium* (*Metomphalus*)

128 *Simulium* (*Afrosimulium*)

129 *Simulium* (*Edwardsellum*)



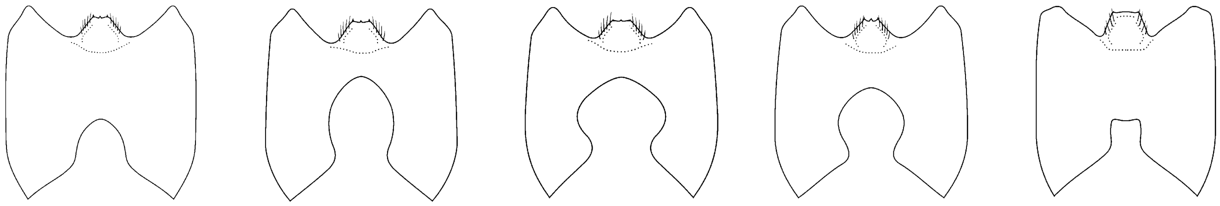
130 *Simulium* (*Byssodon*)

131 *Simulium* (*Nevermannia*)

132 *Simulium* (*Nevermannia*)

133 *Simulium* (*Nevermannia*)

134 *Simulium* (*Pomeroyellum*)



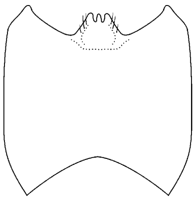
135 *Simulium* (*Pomeroyellum*)

136 *Simulium* (*Pomeroyellum*)

137 *Simulium* (*Pomeroyellum*)

138 *Simulium* (*Meilloniellum*)

139 *Simulium* (*Lewisellum*)



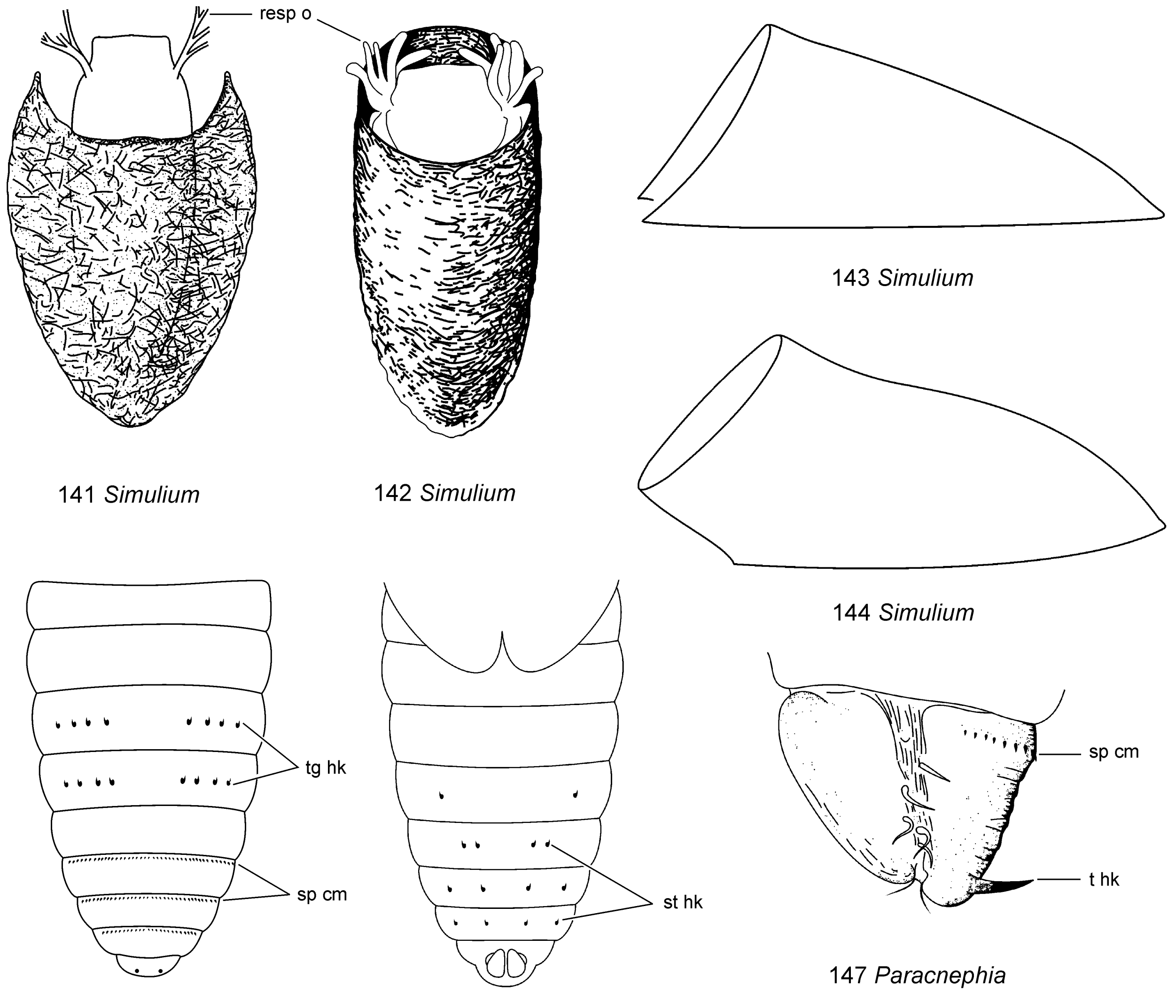
140 *Simulium* (*Phoretomyia*)

Figs 32.120–140. Larval head capsule and postgenal cleft of Simuliidae (ventral views): (120) *Simulium* (*Anasolen*) sp.; (121) *S.* (*Freemanellum*) sp.; (122) *S.* (*Xenosimulium*) sp.; (123) *S.* (*Metomphalus*) *medusaeforme* species-group; (124) same; (125) same; (126) *S.* (*Met.*) *bovis* species-group; (127) same; (128) *S.* (*Afrosimulium*); (129) *S.* (*Edwardsellum*); (130) *S.* (*Byssodon*); (131) *S.* (*Nevermannia*) *ruficorne* species-group; (132) same; (133) *S.* (*N.*) *loutetense* species-group; (134) *S.* (*Pomeroyellum*) *alcocki* species-group; (135) *S.* (*Po.*) *schoutedeni* species-group; (136) *S.* (*Po.*) *cervicornutum* species-group; (137) *S.* (*Po.*) *kenyae* de Meillon; (138) *S.* (*Meilloniellum*) sp.; (139) *S.* (*Lewisellum*) sp.; (140) *S.* (*Phoretomyia*) sp. Figs 120–140 (after Crosskey 1969, figs 253–260, 261, 262, 243–252), Fig, 128 (after de Moor 2003, fig. 5.6L).

Abbreviations: pgn brg – postgenal bridge; pgn clft – postgenal cleft.

development of larval blackfly population control programmes along the Orange River this species has become rare and should be considered threatened (Palmer 1997) and Palmer & Palmer (1995) have recommended measures to protect the species. Immature stages of the species were described by de Meillon (1953) and Car (1983).

***Simulium* (*Anasolen* Enderlein)** (Simuliinae: Simuliini)**.** A near-endemic subgenus of 11 described species, all recorded from the Afrotropical Region, but with one species, *S.* (*An.*) *nili* Gibbins, 1934 also recorded from Saudi Arabia and Yemen in the Arabian Peninsula (Adler & Crosskey 2015a). The majority of species are torrenticolous, or cascade-inhabiting, favouring cool clear mountain streams. They are found in the swiftest of flows, even clinging to rock surfaces and trailing roots in waterfalls. Species are recorded from glacier-melt streams in Kenya at elevations of up to 5,000 m (Crosskey 1969). They include species with some of the largest individuals, larvae growing up to 13 mm in length and adults occasionally attaining a wingspan of 20 mm. *Simulium* (*An.*) *dentulosum* Roubaud, 1915 is the most widespread species, recorded from 22 continental Afrotropical countries, plus Bioko Is. (Equatorial Guinea) and



141 *Simulium*

142 *Simulium*

143 *Simulium*

144 *Simulium*

145 *Simulium*

146 *Simulium*

147 *Paracnephia*

Figs 32.141–147. Pupal features of Simuliidae: (141) slipper-shaped pupal cocoon of *Simulium* sp. (with embedded pupa), dorsal view; (142) same, shoe-shaped cocoon; (143) same, slipper-shaped cocoon, lateral view; (144) same, shoe-shaped cocoon; (145) pupal abdomen of *Simulium* sp., dorsal view; (146) same, ventral view; (147) pupal terminal abdominal segment of *Paracnephia*, lateral view. Figs 141–147 (after Crosskey 1969, figs 164–168, 171, 44, respectively).

Abbreviations: resp o – respiratory organ; sp cm – spine comb; st hk – sternal hooks; t hk – terminal hook; tg hk – tergal hooks.

São Tomé and Príncipe. Eight of the eleven recognised species are recorded from the cascading high mountain streams of eastern Africa in Democratic Republic of Congo, Rwanda and Uganda and these are frequently the only simuliids found at elevations above 3,000 m. *Simulium* (*An.*) *rhodesiense* de Meillon, 1942 is the only southern African species restricted to Zimbabwe. Immature stages have been described by most authors describing species. Identification keys were provided by Freeman & de Meillon (1953).

***Simulium* (*Byssodon* Enderlein)** (Simuliinae: Simuliini)**.** A subgenus of 12 described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Four species are recorded from the Afrotropics: *S.* (*B.*) *bifila* Freeman & de Meillon, 1953, from Central African Republic and South Sudan, *S.* (*B.*) *trisphaerae* Wanson & Henrard, 1944, confined to Democratic Republic of Congo and two widely distributed species: *S.* (*B.*) *tridens* Freeman & de Meillon, 1953, recorded from 13 Afrotropical countries and *S.* (*B.*) *griseicolle* Becker, 1903, recorded from 15 and from Egypt in the Palaearctic (Adler & Crosskey 2015*a*). Species of the subgenus occur in very large rivers and Crosskey (1969) considers that Simuliidae adapted to large rivers, such as the Nile, have been able to maintain a dispersal route between Europe and Africa, even during extreme drought conditions. Drought would create severe ecological and geographical barriers to other simuliid species, not specialised and adapted to conditions in larger rivers, and thus prevented their dispersal. In West Africa *S.* (*B.*) *griseicolle* has been recorded as a pest on poultry (Crosskey 1960). Immature stages have been described by authors describing species. Identification keys were provided by Freeman & de Meillon (1953).

***Simulium* (*Edwardsellum* Enderlein)** (Simuliinae: Simuliini)**.** An endemic subgenus of 27 described species. The *S.* (*E.*) *damnosum* Theobald, 1903 *sensu lato* complex of species is represented by at least 26 named cytoform or morphoform varieties that are not designated formal specific taxonomic status (Adler & Crosskey 2015*a*). Some of these varieties, excluding the true *S.* (*E.*) *damnosum sensu stricto*, represent some of the most common and widespread blackflies in southern Africa (Palmer & de Moor 1998, 1999). Regulation of rivers by humans has favoured varieties in this complex, causing considerable increase in their distribution in recent times (Palmer & de Moor 1999). The larvae and pupae of this complex of species are found on stones and trailing vegetation in the swift-flowing waters of medium-sized rivers. Population densities in medium-sized rivers and below impoundments are often high. Besides the *S.* (*E.*) *damnosum* complex, there are 27 additional species of *S.* (*Edwardsellum*) recognised in the Afrotropical Region (Adler & Crosskey 2015*a*). The adults of a number of these species have been recorded biting humans, poultry and livestock and some of the named species and varieties of the *S.* (*E.*) *damnosum sensu lato* complex are recorded as transmitters of the filarial nematode *Onchocerca volvulus*, being the causal agent of onchocerciasis, or river blindness, in humans (Crosskey 1990: 559). The pupal stages have been described for most species by authors. Four distinct larvae not designated to species were described by Gouteux (1975). Multivariate approaches to allow morphotaxonomic identification of sibling species have been proposed by Wilson *et al*. (1993) and pictorial keys to identify some species and species-groups within the *S.* (*E.*) *damnosum* complex were published by Dang & Peterson (1980). Guides and keys to cytospecies and cytotypes of the *S.* (*E.*) *damnosum* complex based on the larval polytene chromosomes have been published by Boakye (1993), Krueger (2006), Krueger *et al*. (2005) and Post *et al*. (2007, 2011). The most comprehensive and up-to-date treatment to cytospecies is provided by Adler & Crosskey (2015*b*).

***Simulium* (*Freemanellum* Crosskey)** (Simuliinae: Simuliini)**.** An endemic subgenus of seven described species. Four species occur in southern Africa (one also in Tanzania), two species in the highlands of eastern Africa and one widespread species, *S.* (*F.*) *manense* Elsen & Escaffre, 1976, occurs in West Africa, extending to Malawi, Tanzania and Uganda. The majority of species in this subgenus are torrenticolous, or cascade-inhabiting, favouring cool clear mountain streams. They are found in the swiftest of flows, even clinging to rock surfaces and trailing roots in waterfalls. *Simulium* (*F.*) *debegene* de Meillon, 1934 is the most common species in southern Africa. It is restricted to cascades and waterfalls where water quality is excellent. Two other species, *S.* (*F.*) *hirsutilateris* de Meillon, 1937 and *S.* (*F.*) *empopomae* de Meillon, 1937, have similar ecological requirements, but are more restricted in distribution. These three species occur along the eastern parts of South Africa, but are absent from the southern and western Cape. *Simulium* (*F.*) *hessei* Gibbins, 1941 is endemic to the southern and south-western Cape. Palmer (1991) described the larva of *S.* (*F.*) *hessei*. Pupal stages have been described for most species by authors. Identification keys were provided by Freeman & de Meillon (1953).

***Simulium* (*Lewisellum* Crosskey)** (Simuliinae: Simuliini)**.** An endemic subgenus of nine described species, mainly distributed in East and Central Africa. Larval and pupal stages attach themselves to river crabs or Atyidae prawns occurring in small streams, probably a means of avoiding predation, but also considered as an adaptation to being "piggy-backed" in and out of small bodies of water that periodically dry up. Immature stages have been described for *S.* (*L.*) *neavei* Roubaud, 1915, *S.* (*L.) nyaslandicum* de Meillon, 1930 and *S.* (*L.*) *woodi* de Meillon, 1930, by Freeman & de Meillon (1953) and immature stages of most other species were described by the authors. An identification key to most species was provided by Lewis & Raybould (1974).

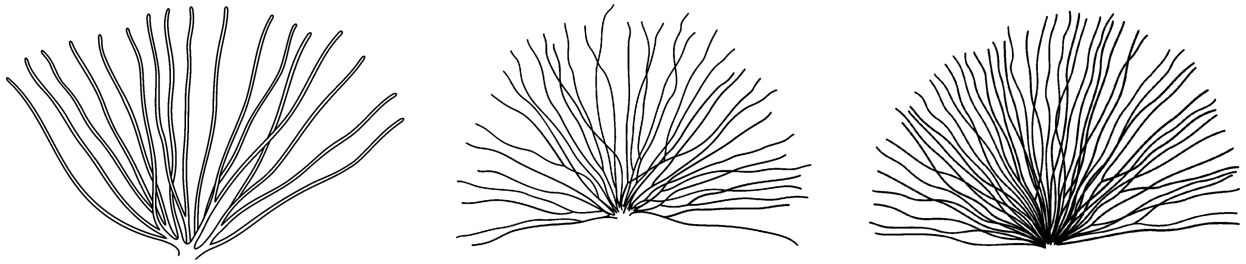
***Simulium* (*Meilloniellum* Rubtsov)** (Simuliinae: Simuliini)**.** A near endemic subgenus with five described species recorded from the Afrotropical Region, one species of which, *S.* (*Me.*) *yemenense* Crosskey & Garms, 1982, is described from Yemen, extending northwards into Saudi Arabia in the Palaearctic (Adler & Crosskey 2015a). *Simulium* (*Me.*) *adersi* Pomeroy, 1922 is widespread in the continental Afrotropics, Comoros, Madagascar and Mauritius and is an adaptable species common in small- to medium-sized rivers, favouring slow-flowing waters. Because ecological conditions in large rivers vary widely, *S.* (*Me.*) *adersi* is frequently found coexisting with many other *Simulium* spp. in medium to large rivers. It has also been recorded from regions where wave action occurs in lakes and on a few occasions from saline brackish waters, showing its high tolerance of, or adaptability to, a range of ecological conditions. *Simulium adersi* is a pest on poultry and is recorded as biting farmworkers (Palmer & de Moor 1998). *Simulium* (*Me.*) *hirsutum* Pomeroy, 1922 is also widespread, frequently found in mountain streams where water quality is excellent. It is

148 *Paracnephia* (*Procnephia*)

149 *Paracnephia* (*Procnephia*)

150 *Paracnephia* (*Paracnephia*)

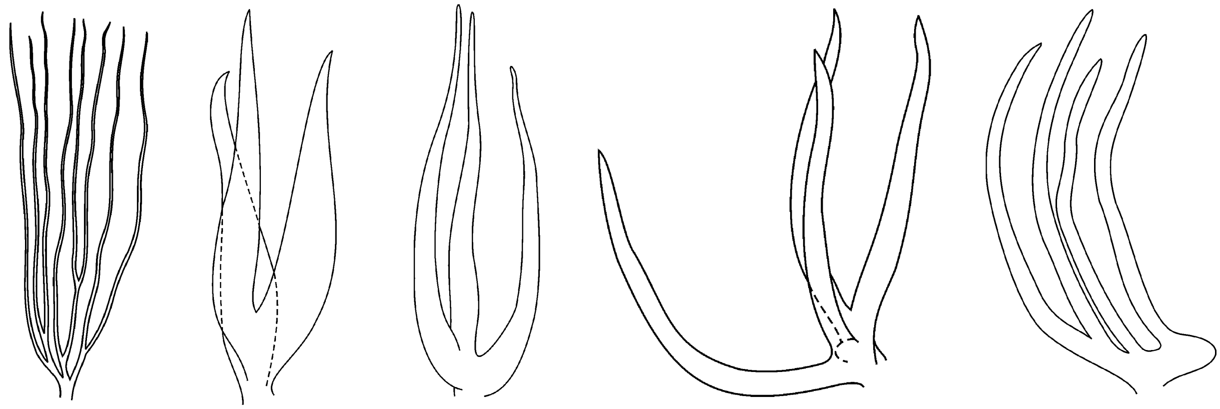
151 *Paracnephia* (*Paracnephia*)



152 *Simulium* (*Phoretomyia*)

153 *Simulium* (*Phoretomyia*)

154 *Simulium* (*Phoretomyia*)



155 *Simulium* (*Lewisellum*)

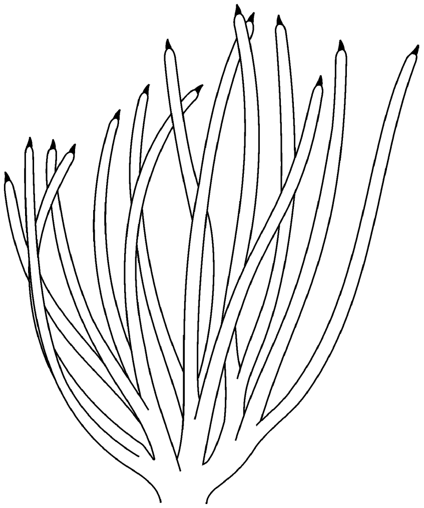
156 *Simulium* (*Byssodon*)

157 *Simulium* (*Afrosimulium*)

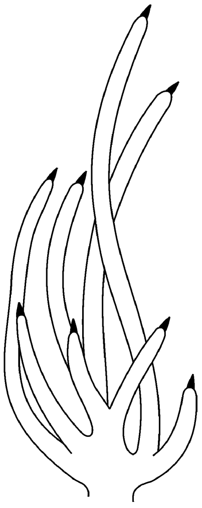
158 *Simulium* (*Freemanellum*)

159 *Simulium* (*Freemanellum*)

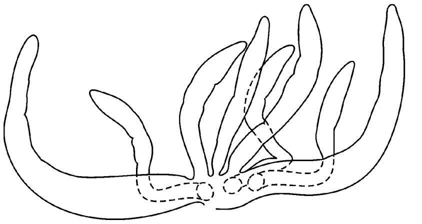
Figs 32.148–159. Pupal respiratory organs of Simuliidae (lateral views): (148) *Paracnephia* (*Procnephia*) sp.; (149) same; (150) *P.* (*Paracnephia*) sp.; (151) same; (152) *Simulium* (*Phoretomyia*) sp.; (153) same; (154) same; (155) *S.* (*Lewisellum*) sp.; (156) *S.* (*Byssodon*) sp.; (157) *S.* (*Afrosimulium*) *gariepense* de Meillon; (158) *S.* (*Freemanellum*) sp.; (159) same. Figs 148–159 (after Crosskey 1969, figs 38–41, 197, 198, 199, 195, 222, 223, 205, 206, respectively).



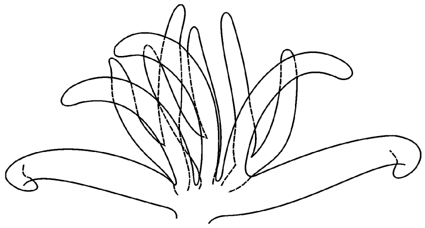
160 *Simulium* (*Anasolen*)



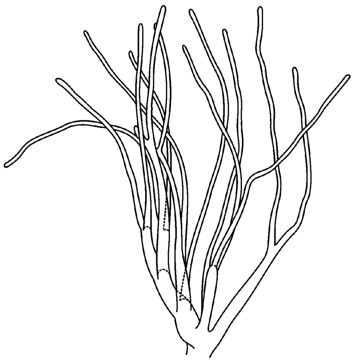
161 *Simulium* (*Anasolen*)



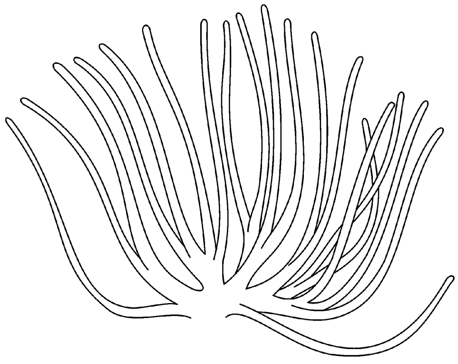
162 *Simulium* (*Edwardsellum*)



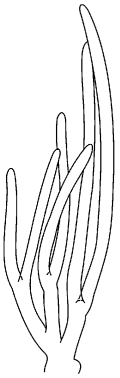
163 *Simulium* (*Edwardsellum*)



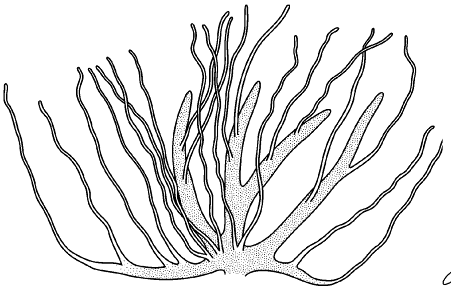
164 *Simulium* (*Xenosimulium*)



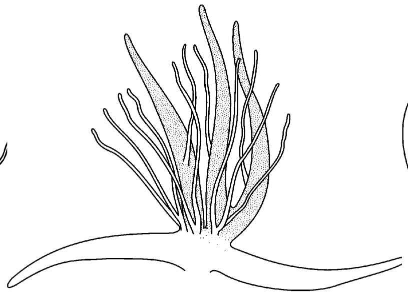
165 *Simulium* (*Xenosimulium*)



166 *Simulium* (*Xenosimulium*)



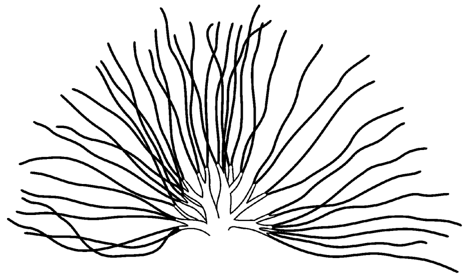
167 *Simulium* (*Metomphalus*)



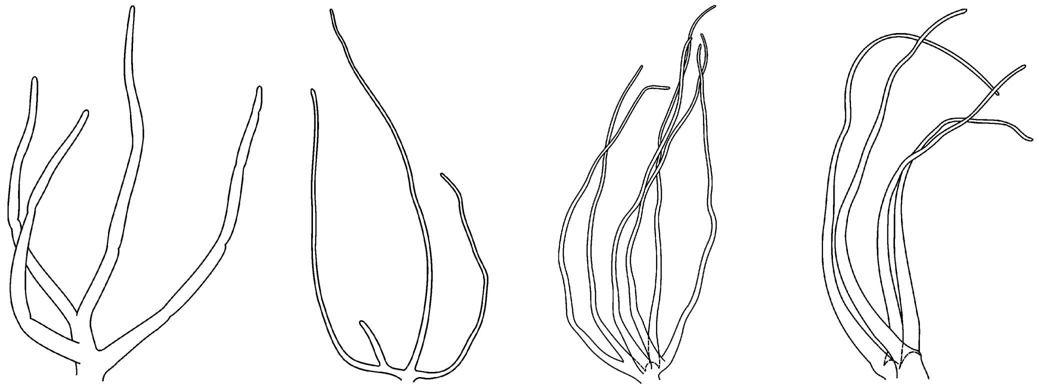
168 *Simulium* (*Metomphalus*)

169 *Simulium* (*Metomphalus*)

Figs 32.160–169. Pupal respiratory organs of Simuliidae (lateral views): (160) *Simulium* (*Anasolen*) sp.; (161) same; (162) *S.* (*Edwardsellum*) sp.; (163) same; (164) *S.* (*Xenosimulium*) sp.; (165) same; (166) same; (167) *S.* (*Metomphalus*) *medusaeforme* species-group; (168) same; (169) same. Figs 160–169 (after Crosskey 1969, figs 203, 204, 209, 210, 200–202, 211–213, respectively).



170 *Simulium* (*Metomphalus*) 171 *Simulium* (*Metomphalus*) 172 *Simulium* (*Metomphalus*)



173 *Simulium* (*Nevermannia*) 174 *Simulium* (*Nevermannia*) 175 *Simulium* (*Nevermannia*) 176 *Simulium* (*Nevermannia*) 177 *Simulium* (*Nevermannia*)

178 *Simulium* (*Nevermannia*) 179 *Simulium* (*Nevermannia*) 180 *Simulium* (*Nevermannia*) 181 *Simulium* (*Meilloniellum*) 182 *Simulium* (*Meilloniellum*)

Figs 32.170–182. Pupal respiratory organs of Simuliidae (lateral views): (170) *Simulium* (*Metomphalus*) *bovis* species-group; (171) same; (172) same; (173) *S.* (*Nevermannia*) *ruficorne* species-group; (174) same; (175) *S.* (*N.*) *loutetense* species-group; (176) same; (177) same; (178) *S.* (*N.*) *ruficorne* species-group; (179) same; (180) same; (181) *S.* (*Meilloniellum*) sp.; (182) same. Figs 170–179, 181, 182 (after Crosskey 1969, figs 214–216, 174–180, 193, 194, respectively), Fig. 180 (after Elouard & Pilaka 1996, fig. 11.1c).

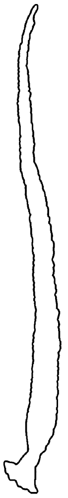
almost indistinguishable from *S.* (*Me.*) *adersi* and its occurrence in southern Africa may be more common than estimated at present (Palmer & de Moor 1998). Two of the other three species have a Central to North African distribution and one species is found in the Arabian Peninsula. Immature stages have been described for *S.* (*Me.*) *urundiense* Fain, 1950 and *S.* (*Me.*) *sexiens* de Meillon 1944 by Freeman & de Meillon (1953) and immatures stages of most other species have been described by authors. An identification key was provided by de Meillon (1953).

***Simulium* (*Metomphalus* Enderlein)** (Simuliinae: Simuliini)**.** An endemic subgenus of 33 described species (Adler & Crosskey 2015*a*). Species belonging to this subgenus are most frequently found on stones and trailing vegetation in the swift turbulent waters of medium- to large-sized rivers. In the *S.* (*Met.*) *bovis* species-group there are 12 species of which eight can be considered as large river species. *Simulium* (*Met.*) *chutteri* Lewis, 1965, a species found in the swiftest of currents in rapids on the Vaal and Orange Rivers of South Africa, can at certain times of the year be found at densities of up to 400,000 individuals or 700 g dry weight mass of blackfly per square metre of river bottom (de Moor 1982). This species is the most serious simuliid pest in southern Africa and much research has gone into devising methods for controlling and eradicating the species (Palmer 1997 and references therein). *Simulium* (*Met.*) *bovis* de Meillon, 1930 occurs in the middle to lower reaches of large warm, alkaline rivers and is widespread in the Afrotropics, being a voracious cattle biter. Other large river species, *S.* (*Met.*) *fragai* Abreu, 1960 and *S.* (*Met.*) *arnoldi* Gibbins, 1937, are recorded from the Kunene and Zambezi Rivers, respectively. The *S.* (*Met.*) *medusaeforme* species-group is represented by 21 species in the Afrotropical Region and two of these are also recorded from Madagascar. The larvae of these species are often not easy to distinguish and pupae often reveal better diagnostic characters. Three species are widely distributed in the continental Afrotropics, *S.* (*Met.*) *medusaeforme* Pomeroy, 1920 is found in a wide range of stream and river types with water quality varying from excellent to poor (Palmer & de Moor 1998). This species has adapted to river regulation and is frequently common below impoundment outlets and artificial waterways. It is usually found in the upper to middle reaches of medium-sized rivers. *Simulium* (*Met.*) *hargreavesi* Gibbins, 1934 is also widespread and prefers similar flow and water conditions. Of interest is that this species replaced *S.* (*Met.*) *chutteri* as the dominant species in the Vaal River near Warrenton following a prolonged drought, causing lower water flow and increased growth of aquatic macrophytes, transforming the river from a normal silty turbid to a very clear-water river (Car & de Moor 1984). *Simulium* (*Met.*) *vorax* Pomeroy, 1922 is restricted to fast-flowing rivers and waters of moderate to excellent quality. It is also widespread and often found together with *S.* (*Met.*) *medusaeforme* in large rivers (Palmer & de Moor 1998). Most of the other species of the subgenus are restricted in their distribution and are mostly confined to cool, clear, swift-flowing mountain streams. Immature stages for most species have been described by authors describing species. Palmer (1991) described the larvae of *S.* (*Met.*) *letabum* de Meillon, 1935 and a number of species are described or re-described by Crosskey (1960, 1969) and Freeman & de Meillon (1953). Identification keys were provided by Crosskey (1960), Freeman & de Meillon (1953) and Lewis (1965*a*, *b*).

***Simulium* (*Nevermannia* Enderlein)** (Simuliinae: Simuliini)**.** A subgenus of 227 described species, occurring in the Australasian, Afrotropical, Oriental and Palaearctic Regions (Adler & Crosskey 2015*a*). Species of the subgenus are the most widespread of all simuliids in the Afrotropical Region, with the greatest diversity of species. Two species-groups occur in the region, the *S.* (*N.*) *loutetense* species-group comprising four species, with *S.* (*N.*) *loutetense* Grenier & Ovazza, 1951 widespread in the tropics, *S.* (*N.*) *milloti* Grenier & Doucet, 1949 occurring only in Madagascar, *S.* (*N.*) *narcaeum* de Meillon, 1950 recorded only from South Africa and *S.* (*N.*) *rutherfoordi* de Meillon, 1937 occurring in southern Africa and Democratic Republic of Congo. Species of the *S.* (*N.*) *loutetense* species-group are found in cool, clear, swift-flowing streams. The *S.* (*N.*) *ruficorne* species-group comprises 69 species of which 34 occur in the Afrotropics, while the other species extend into the Australasian, Oriental and Palaearctic Regions. *Simulium* (*N.*) *nigritarse sensu lato* is considered to comprise a complex of 19 or more sibling species (Fain & Dujardin 1983), of which at least three are known from southern Africa (Palmer & de Moor 1998). *Simulium* (*N.*) *ruficorne* is one of the most widely distributed species, extending into North Africa (Morocco) and the Middle East (Israel, Jordan, Oman, Saudi Arabia, Syria and Yemen). It is also one of the first colonisers of recently inundated streams (Harrison 1966). As a coloniser of newly formed streams it is able to colonise even desert streams and can also tolerate a wide variety of polluted waters. It is found in a wide spectrum of flowing-water conditions from the smallest of trickles to large rivers, but favours slow to moderate flow. It is recorded as a pest on poultry (Palmer & de Moor 1998). Immature stages have been described for many species by the authors describing the species. Palmer (1991) described the larvae of *S.* (*N.*) *rutherfoordi* and *S.* (*N.*) *katangae* Fain 1951 and Fain & Dujardin (1983) described the larvae of a number of species. A number of species from Madagascar are only known from descriptions of the pupae (Elouard 2003). Identification keys were provided by Crosskey (1960, 1969), Elouard (2003) and Freeman & de Meillon (1953).

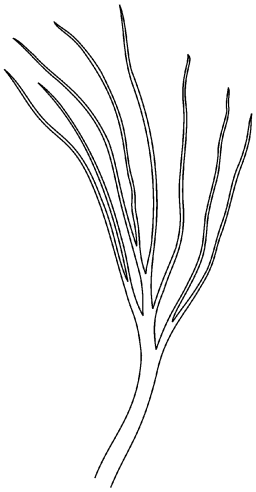
***Simulium* (*Phoretomyia* Crosskey)** (Simuliinae: Simuliini)**.** An endemic subgenus of 15 described species (Adler & Crosskey 2015*a*), having larval and pupal stages that attach to Oligoneuriidae, Heptageniidae and Baetidae mayflies and rarely Atyidae prawns occurring in small streams and rivers. The larvae exhibit specialisation for attachment to host insects, with the posterior abdominal proleg being situated ventrally. Pupae have modified spine combs on the abdomen to increase purchase inside the much reduced pupal cocoon. Two species in the subgenus *S.* (*Phoretomyia*) in Madagascar have adopted phoretic associations with Atyidae prawns (*S.* (*Ph.*) *desirei* Pilaka & Elouard, 1999), or with Oligoneuriidae mayflies (*S.* (*Ph.*) *kiangaraense* Pilaka & Elouard, 1999) (Elouard 2003: 721; Pilaka & Elouard 1999*b*). Immature stages have been described for most species by authors describing species. Identification keys to some of the species were provided by Freeman & de Meillon (1953) and Gouteux (1978).

***Simulium* (*Pomeroyellum* Rubtsov)** (Simuliinae: Simuliini)**.** An endemic subgenus of 47 described species, being the most species-rich of all subgenera in the Afrotropical Region (Adler & Crosskey 2015*a*). Larvae and pupae of the majority of species



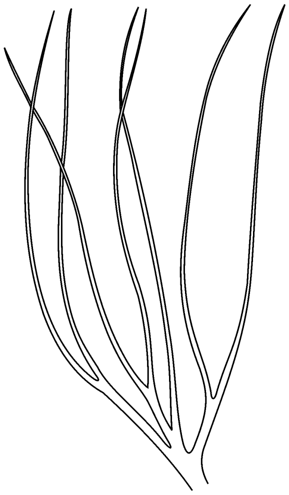
183 *Simulium*
(*Pomeroyellum*)

184 *Simulium*
(*Pomeroyellum*)

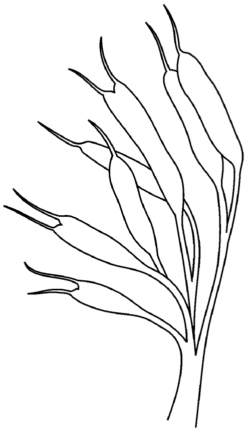


185 *Simulium*
(*Pomeroyellum*)

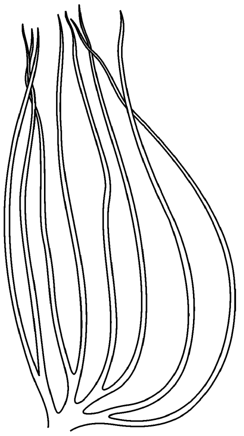
186 *Simulium*
(*Pomeroyellum*)



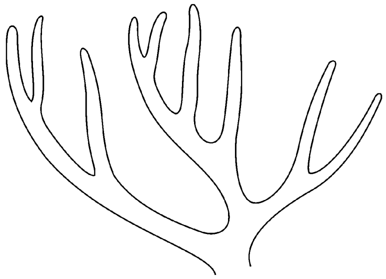
187 *Simulium*
(*Pomeroyellum*)



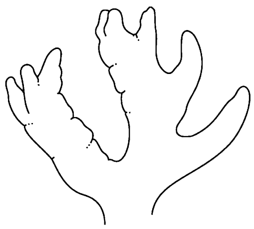
188 *Simulium*
(*Pomeroyellum*)



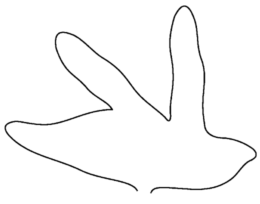
189 *Simulium*
(*Pomeroyellum*)



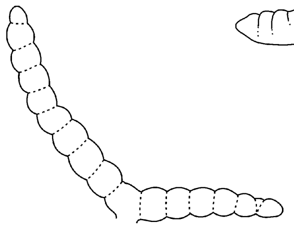
190 *Simulium*
(*Pomeroyellum*)



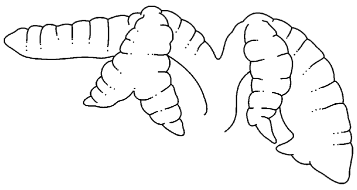
191 *Simulium*
(*Pomeroyellum*)



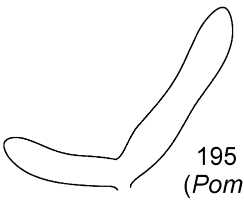
192 *Simulium*
(*Pomeroyellum*)



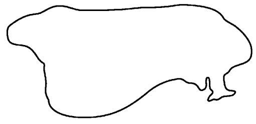
193 *Simulium*
(*Pomeroyellum*)



194 *Simulium*
(*Pomeroyellum*)



195 *Simulium*
(*Pomeroyellum*)



196 *Simulium*
(*Pomeroyellum*)

Figs 32.183–196. Pupal respiratory organs of Simuliidae (lateral views): (183) *Simulium* (*Pomeroyellum*) *schoutedeni* species-group; (184) same; (185) same; (186) *S.* (*Po.*) *alcocki* species-group; (187) same; (188) same; (189) same; (190) *S.* (*Po.*) *cervicornutum* species-group; (191) same; (192) same; (193) same; (194) same; (195) same; (196) same. Figs 183, 196 (after de Moor 2003, figs 5.10G, 5.10M), Figs 184–195 (after Crosskey 1969, figs 181, 185, 182, 183, 186, 184, 187–192, respectively).

attach themselves to dead leaves, trailing roots and grasses in slow-flowing waters of small streams. Some species, however, occur in rapids and in swift-flowing waters of large rivers. The subgenus is divided into four species-groups: the *S.* (*Po.*) *alcocki* Pomeroy, 1922 species-group, with 25 species; the *S.* (*Po.*) *cervicornutum* Pomeroy, 1920 species-group, with 14 species; the *S.* (*Po.*) *kenyae* de Meillon, 1940 species-group, represented by the single species *S.* (*Po.*) *kenyae*; and the *S.* (*Po.*) *schoutedeni* Wanson, 1947 species-group, with six species. In all four species-groups the majority of species have a distribution largely confined to the tropics, but a few have extended their range into the more temperate parts of South Africa, with *S.* (*Po.*) *harrisoni* Freeman & de Meillon, 1953 and *S.* (*Po.*) *merops* de Meillon, 1950 restricted to small afforested streams in the Western Cape, South Africa (Palmer & de Moor 1998). Four species in the *S.* (*Po.*) *cervicornutum* species-group are endemic to Madagascar and *S.* (*Po.*) *unicornutum* Pomeroy, 1920 is widespread in headwater streams in the continental Afrotropics and in Madagascar. *Simulium* (*Po.*) *cervicornutum* is common in small- to medium-sized, clear alkaline streams and can tolerate moderate pollution. *Simulium* (*Po.*) *rotundum* Gibbins, 1936 and *S.* (*Po.*) *mcmahoni* de Meillon, 1940 are widespread species common in warm alkaline streams and medium-sized rivers, where they are often associated with other species found near impoundment outlets, such as *S.* (*Nevermannia*) *nigritarse* and *S.* (*Edwardsellum*) *damnosum sensu lato*. In the *S.* (*Po.*) *alcocki* species-group, *S.* (*Po.*) *alcocki* and *S.* (*Po.*) *impukane* de Meillon, 1936 are widespread in mountain foothill and temporary streams and both species are tolerant of moderate pollution. Immature stages have been described for *S.* (*Po.*) *cervicornutum* by Gibbins (1936); *S.* (*Po.*) *unicornutum* Pomeroy 1920 by Gibbins (1936) and Grenier & Rageau (1949); *S.* (*Po.*) *alcocki* by Roubaud & Grenier (1943); *S.* (*Po.*) *garmsi* Crosskey, 1969 by Freeman & de Meillon (1953) and Garms & Hausermann (1968); *S.* (*Po.*) *bequaerti* Gibbins 1936, *S.* (*Po.*) *harrisoni* Freeman & de Meillon, 1953 and *S.* (*Po.*) *merops* de Meillon 1950 by Palmer (1991); the immatures of most other species have been described by authors. Identification keys were provided by Crosskey (1960, 1969), Pilaka & Elouard (1999*a*), Elouard (2003: 717) and Freeman & de Meillon (1953).

***Simulium* (*Xenosimulium* Crosskey)** (Simuliinae: Simuliini)**.** An endemic subgenus of five species, four of which are restricted to Madagascar and one, *S.* (*X.*) *imerinae* Roubaud, 1905, to Comoros and Madagascar (Adler & Crosskey 2015*a*). They are considered closely related to the subgenera *S.* (*Anasolen*) and *S.* (*Freemanellum*) and also ecologically similar in their requirements for large boulders or bedrock as substrates in swift-flowing to cascading waters. The species have all been recorded biting humans and livestock, but none are vectors of diseases (Elouard 2003: 719). Immature stages have been described for all the species by authors. An identification key was provided by Elouard (2003: 717).

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THAUMALEIDAE 33

(Seepage Midges or Trickle Midges)

Bradley J. Sinclair

Fig. 33.1. Female of *Afrothaumalea stuckenbergi* Sinclair (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small midges (wing length: 1.5–5.0 mm) (Fig. 1), with body stocky, yellow to dark brown in colour.

Head (Fig. 1) small, round; eyes large, males and females holoptic, ommatrichia lacking; ocelli absent; antenna dark, pedicel globular, slightly larger than scape, male flagellum non-plumose, 10 flagellomeres; palpus 5-segmented.

Thorax (Fig. 1) strongly arched dorsally, lacking transverse suture; scutellum acute apically; postnotum strongly convex. Wing (Fig. 4) broad, with costal vein (*C*) reduced beyond wing tip; crossvein (R_{2+3}) joining vein R_1; vein R_{4+5} with dorsal bend; microtrichia generally confined to veins (also on membrane in the non-Afrotropical genus *Trichothaumalea* Edwards); crossveins restricted to basal ¼ of wing; upon death wings often characteristically folded across sides of body along

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 729–732.

transverse weakening proximal to main veins. Legs short, slender; tibiae lacking spurs.

Abdomen with male terminalia (Figs 5, 6) unrotated, symmetrical; epandrium and hypandrium fused laterally into ring sclerite; aedeagus comprising membranous tube; paramere paired, or fused medially into single process; ventral plate (= gonocoxal plate) broadly fused laterally with gonocoxites, or appearing as pair of medial processes; gonostylus normally simple, with, or without, apical spine-like setae; cercus well-developed, positioned subapically; female cercus 1-segmented; sternite 8 shield-shaped; hypogynial valve short to elongate; 2 unpigmented, elongate spermathecae present.

Living larvae are readily identified in the field by their unique lateral jerking motion when escaping predators or capture (Thienemann 1909). Larva (Fig. 2) elongate, cylindrical; head hypognathous (Fig. 3); colour of larvae due to chromatocytes of fat body beneath transparent cuticle (Fig. 2); mandible with multi-toothed comb on apical part; unpaired prolegs on prothorax and terminal segment, each armed with series of crochets, those of prothoracic proleg in single transverse row; amphipneustic with dorsolateral spiracle on prothorax and elongate, transverse spiracular plate on abdominal segment 8, flanked by pair of short, conical fleshy lobes (absent in *Afrothaumalea* Stuckenberg); paired sclerotised, finger-like procerci bearing dark setae posterior to spiracular plate.

Pupa subcylindrical, quadrate in cross-section (dorsoventrally flattened in *Afrothaumalea* and *Trichothaumalea*); apical portion of abdomen posteriorly directed; palpus posteromedially-directed, apices of palpi separated medially; thorax with dorsal crenulations; fore and mid leg sheaths projecting straight and slightly beyond wing sheaths; hind leg S-shaped beneath wing, projecting along posterior margin of wing sheath (Borkent 2012, fig. 19B); respiratory organ short, cylindrical, truncate apically, with spiracular openings encircling apex; abdomen with lateral open spiracles on segments 2–7, 3–7, 4–7, or 5–7; terminal processes hook-like or absent.

Adult Thaumaleidae may be superficially confused with Simuliidae (see Chapter 32), but can be distinguished by the distinctive wing venation, with R_{2+3} appearing as a crossvein and R_{4+5} usually with a dorsal bend (Fig. 4).

Biology and immature stages

All life stages of Thaumaleidae are restricted to madicolous or hygropetric habitats: thin films of water flowing over rock surfaces (Sinclair & Marshall 1987; Thienemann 1909; Vaillant 1956). Habitats include streams cascading over large rocks, spray zones of boulders in streams and seepages near waterfalls and roadcuts. Adults are apparently non-feeding and have not been observed visiting flowers. Larvae are herbivores, scraping diatoms from the rock face of seepage habitats (Leathers 1922). Thaumaleid larvae apparently have a large and unfixed number of instars with some 9, or 15–20 reported (Borkent 2012; Mandaron 1963). Larvae are the most exposed life stage and are preyed upon by empidoid flies searching wet rock faces (Sinclair & Marshall 1987). Fungal symbiontic Harpellales (Trichomycetes), or gut fungi, have been studied in several species of Northern Hemisphere thaumaleid larvae (Lichtwardt *et al*. 2001; White & Lichtwardt 2004).

The family is confined to temperate zones, normally in hilly or mountainous regions. In the Afrotropical Region Thaumaleidae are restricted to South Africa. Larvae have been collected in the Drakensberg (Giant's Castle Reserve), KwaZulu-Natal Province (Sinclair & Stuckenberg 1995), the Cederberg, Western Cape Province (Sinclair 2015) and captured in macroinvertebrate surveys of the upper reaches of the Buffalo River, Eastern Cape Province (Palmer *et al*. 1994).

Adults are weak fliers, hovering around the seepage face, or stream, usually observed resting on wet rocks, or on overhanging vegetation. No aerial mating swarms are formed and pairs *in copula* have been observed on riparian vegetation in tail-to-tail position (Borkent *et al*. 2008; Mandaron 1963). General biology and life history of Thaumaleidae are reviewed by Disney (1999) and Wagner (2002).

Economic significance

No species of economic importance are currently known. The family is considered a suitable taxon for biomonitoring and assessment of seepage areas and spring-fed reaches of brooks in Finland (Salmela *et al*. 2007).

Classification

The family Thaumaleidae is currently assigned to the superfamily Simulioidea (Culicomorpha), which also includes Simuliidae (Bertone *et al*. 2008; Wiegmann *et al*. 2011), or Simuliidae and Ceratopogonidae (Borkent 2012). The monophyly of the traditional superfamily Chironomoidea (comprising: Chironomidae, Ceratopogonidae, Simuliidae and Thaumaleidae), is now in doubt (Sinclair *et al*. 2007; Woodley *et al*. 2009: 81). A single negative impression fossil, *Mesothaumalea fossilis* Kovalev, 1989, is known from the Late Jurassic / Early Cretaceous (Kovalev 1989).

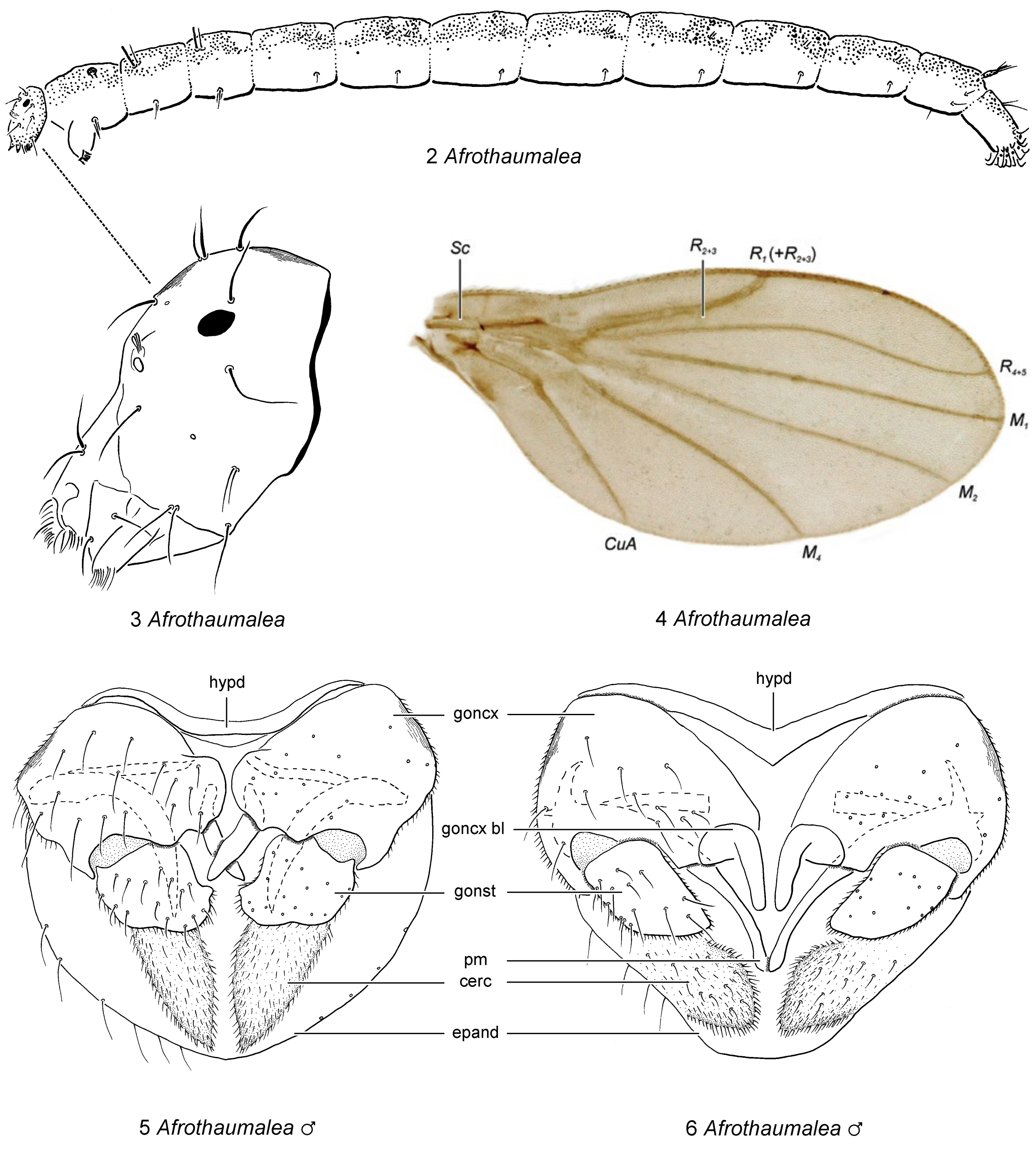
The family is small, with 184 described species worldwide. There are 7–8 recognised genera, where *Protothaumalea* Vaillant is either considered a distinct European genus (Wagner 2002), or a synonym of *Androprosopa* Mik (Sinclair 1996). *Afrothaumalea* appears closely related to the Australian and southern Chilean genus *Niphta* Theischinger, on the basis of reduced setae on the first vein ($R_1(+R_{2+3})$) (Sinclair & Stuckenberg 1995).

Identification

Thaumaleidae are readily recognised on the basis of the male terminalia (Figs 5, 6). A key to males of Afrotropical Thaumaleidae (*i.e.*, *Afrothaumalea*) is presented in Sinclair (2015). Thaumaleidae are best collected direct into ethanol for later critical-point-drying (see Chapter 2).

Synopsis of the fauna

Only a single genus is known from the Afrotropical Region. The family is little known, based on only a few, mostly adult specimens, collected from South Africa. Concerted collecting efforts are required in South Africa and other African countries


2 *Afrothaumalea*

3 *Afrothaumalea*

4 *Afrothaumalea*

5 *Afrothaumalea* ♂

6 *Afrothaumalea* ♂

Figs 33.2–6. Larva, wing and male terminalia of Thaumaleidae: (2) larval habitus of *Afrothaumalea pamelae* Stuckenberg, lateral view; (3) same, larval head capsule, lateral view; (4) wing of *A. capensis* Sinclair & Stuckenberg, dorsal view; (5) male terminalia of *A. pamelae*, ventral view; (6) same, *A. capensis*. Fig. 4 (photograph J. Kjærandsen), Fig. 5 (after Stuckenberg 1960, fig. 2), Fig. 6 (after Sinclair & Stuckenberg 1995, fig. 6).

Abbreviations: cerc – cercus; *CuA* – anterior branch of cubital vein; epand – epandrium; goncx – gonocoxite; goncx bl – gonocoxal blade; gonst – gonostylus; hypd – hypandrium; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; pm – paramere; R_1 $(+R_{2+3})$ – anterior branch of radius; R_{2+3} (crossvein) – second branch of radius; R_{4+5} – third branch of radius; *Sc* – subcostal vein.

to assess the true diversity of Afrotropical Thaumaleidae. Given the record of larvae from an aquatic invertebrate survey (Palmer *et al*. 1994), it is likely that the family is much more common than records indicate.

***Afrothaumalea* Stuckenberg.** A genus endemic to the Afrotropical Region, characterised by having the first basal cell of the wing divided into two secondary cells (Fig. 4) (Stuckenberg 1961: 409). *Afrothaumalea* is apparently widespread in South Africa, but highly disjunct and localised. The conservation status of the genus in southern Africa was reviewed by Duxbury & Barraclough (1994) (see Chapter 10). Three widely separated species are described from South Africa: *A. pamelae* Stuckenberg, 1960 (Drakensberg), *A. capensis* Sinclair & Stuckenberg, 1995 (Maanschynkop) and *A. stuckenbergi* Sinclair, 2015 (Cederberg). The larva of *A. pamelae* has been described (Sinclair & Stuckenberg 1995) and the pupa of *A. stuckenbergi* was described by Sinclair (2015). A single female specimen is known from Knysna in the Eastern Cape Province and possibly represents an undescribed species.

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CERATOPOGONIDAE 34

(Biting Midges)

Art Borkent

Fig. 34.1. Male of *Serromyia morio* (F.) (non-Afrotropical) (photograph © R. Andrade).

Diagnosis

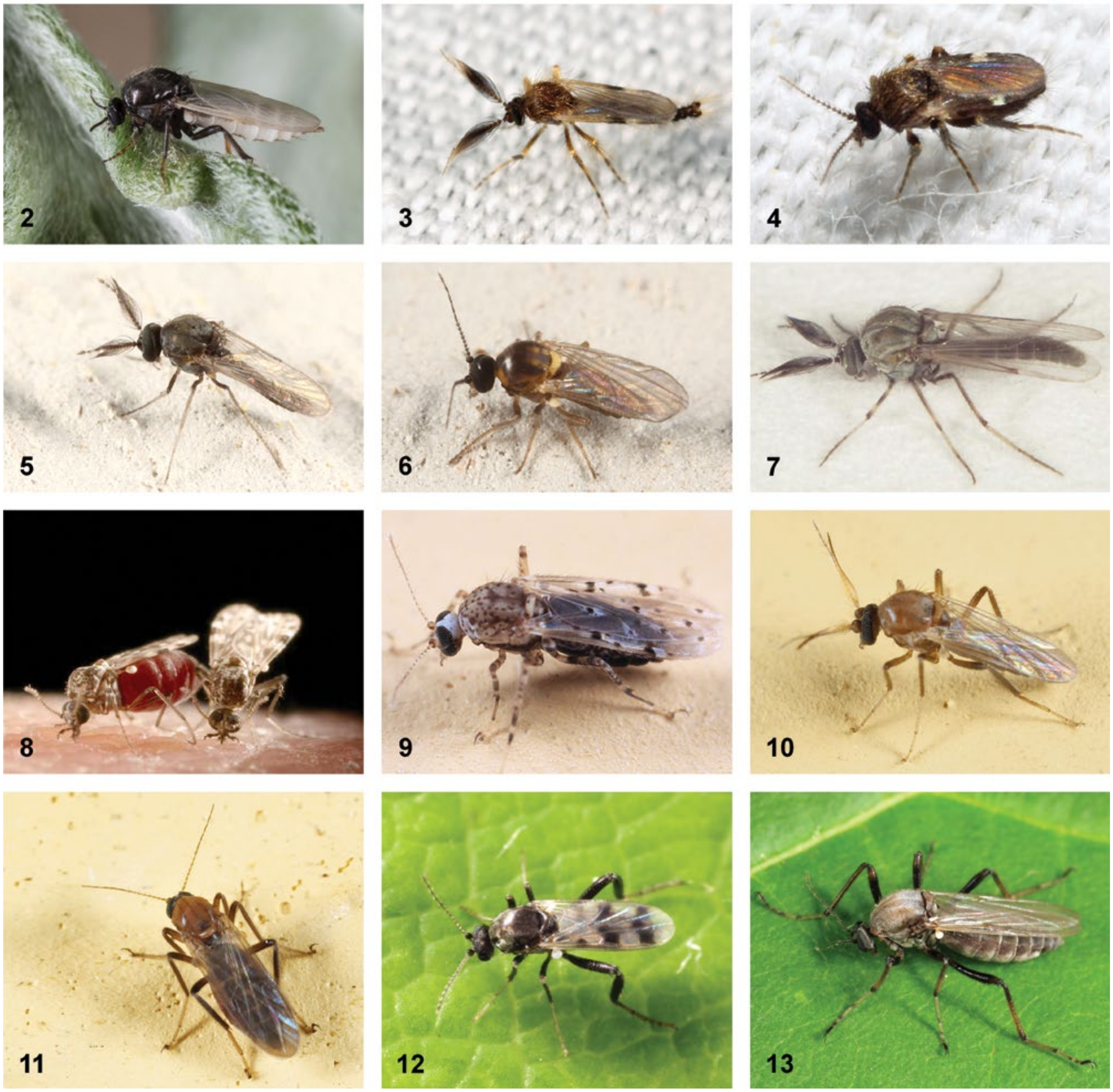
Adults small- to medium-sized biting midges (wing length: 0.4–7.0 mm) (Figs 1–39) with body colour from almost entirely black to pale brown, green (in life, yellow in alcohol), in some with parts white, some variously patterned on body, legs and wings.

Head with ommatidia from broadly separated dorsally (Figs 40, 41, 51), moderately separated (Figs 44, 45), narrowly separated, or contiguous at midline (Figs 42, 43, 46–50), bare, or with short interspersed spicules and eyes appearing pubescent; ocelli absent; antenna generally with 13 flagellomeres (Figs 52–57) (some with as few as 9; these and others with varying degrees of fusion (Fig. 58)); most males with plumose antennae (Figs 34, 54, 56), but feminised in some (Figs 44, 55); most females with mouthparts with well-developed labrum with basal torma, paired apically serrate mandibles, paired long, slender laciniae (with or without retrorse teeth), 4- or 5-segmented palpus, with third segment bearing capitate sensilla on undifferentiated surface, or in variably sized pit, well-developed labium terminating in two lobes termed labellum (Fig. 43); vertebrate feeders with finely-toothed mandibles (to cut into host), laciniae with retrorse teeth (to hold mouthparts in place); others feeding on invertebrates with coarsely toothed mandibles, simple laciniae; some non-biting, with mouthparts reduced, mandibles and laciniae without teeth, shorter, more slender; males with similar mouthparts, but with mandibles and laciniae reduced (either without teeth or with few small teeth) and palpal sensory pit smaller than female or absent, with fewer capitate sensilla (some with these on surface of segment).

Thorax and included sclerites variably shaped, with setae of scutum arranged in rows or scattered; paratergite with (Fig. 67) or without setae; anepisternum and katepisternum with or

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 733–812.

without setae; anepisternum divided into anterior and posterior portions by broad (Figs 68, 69) or narrow (Fig. 37) anepisternal cleft; postnotum without medial longitudinal groove. Wing with 1–3 radial veins reaching anterior margin, usually with 3 median vein branches (vein M_2 may be weak basally or absent, some only visible with phase contrast microscopy), reaching wing margin (Figs 35, 36, 75, 76, 79, 84); *r–m* crossvein absent (*Leptoconops* Skuse, Fig. 110), or present; wings overlapping each other, held flat over abdomen in living individuals at rest (except in some *Stilobezzia* Kieffer) (Figs 1–19). Legs, especially of females, variously modified, with or without variably distributed spines; fore leg shorter than hind leg (Figs 32–39); tarsomere 1 of each leg equal to, or longer than, tarsomere 2 (except in some *Forcipomyia* Meigen) (Figs 170, 173, 190,



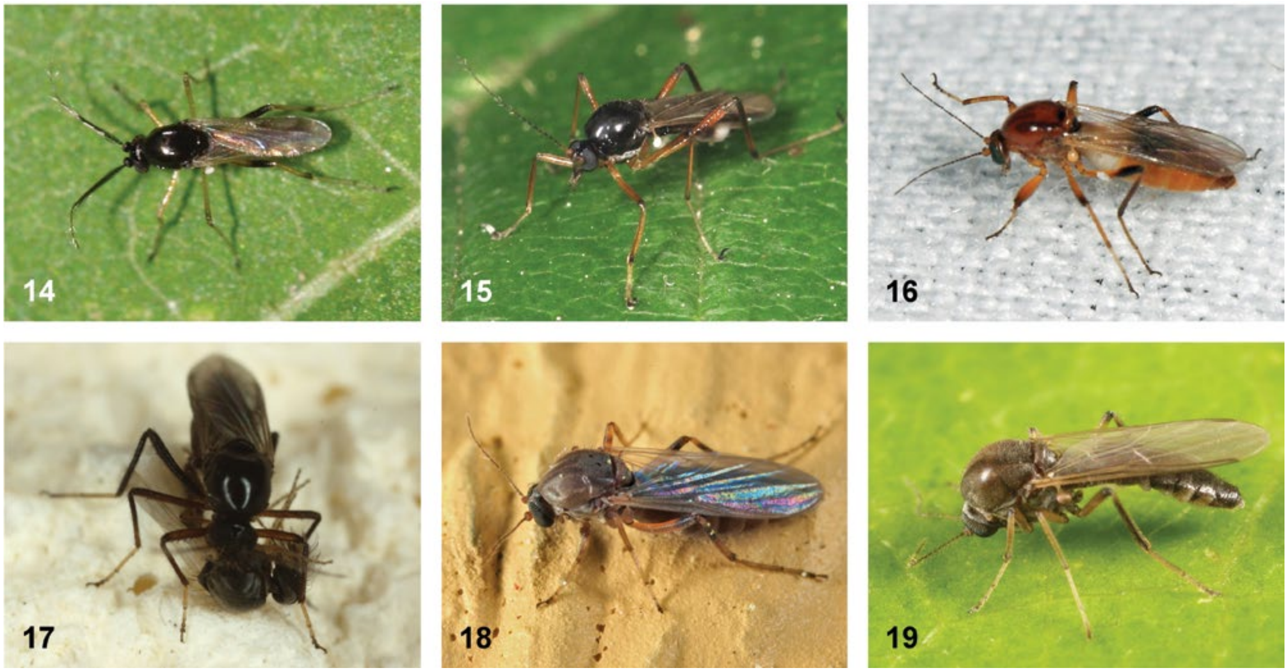
Figs 34.2–13. Habitus of adult Ceratopogonidae (all non-Afrotropical): (2) *Leptoconops* sp. ♀; (3) *Forcipomyia* (*Lepidohelea*) sp. ♂; (4) *Forcipomyia* (*Forcipomyia*) sp. ♀; (5) *Atrichopogon* sp. ♂; (6) same, ♀; (7) *Dasyhelea* sp. ♂; (8) *Culicoides nubeculosus* (Meigen) ♀ feeding on human; (9) *Alluaudomyia paraspina* Wirth ♀; (10) *Stilobezzia* sp. ♂; (11) same, ♀; (12) *Allohelea* sp. ♀; (13) *Sphaeromias longipennis* (Loew) ♀. Fig. 2 (photograph © A. Abela), Figs 3–6 (photographs T.C. Murray), Fig. 7 (photograph A. Liberta), Fig. 8 (Wilson *et al*. 2008, fig. 1), Figs 9–13 (photographs T.C. Murray).

199–201); tarsal claws of females variably modified in size and shape; empodium absent to well-developed.

Abdomen with male terminalia with well-developed epandrium and hypandrium (Figs 261, 266); epandrium with or without apicolateral process, bearing 1 or more setae (Figs 262, 267–272); most with gonocoxite and gonostylus well-developed (Figs 261–265), fused in *Nilobezzia* Kieffer (Fig. 289); gonostylus markedly reduced in size in a few genera (Figs 283, 291); aedeagus (ventral plate of other Culicomorpha) generally with overall triangular shape (*e.g.*, Figs 261, 263, 264), but otherwise variable in shape (*e.g.*, Figs 271, 274); parameres articulated or fused with gonocoxal apodemes, separate or variably fused, in some forming single medial structure (*e.g.*, Figs 261, 262, 265, 278, 282, 284); cercus small and ventral to apex of epandrium to large and more apically placed; female with relative sizes of segments 6–9 variable (*e.g.*, Figs 293, 294, 297); sternite 8 variably modified, with (*e.g.*, Figs 300, 301) or without setal tufts; sternite 9 fused or separate medially; cercus small to large; tergite 7 and variably tergites 2–6, with anteriorly directed apodemes bearing eversible sacs in Palpomyiini and Stenoxenini (Fig. 303); 1–3 spermathecae present (in many with 2 well-developed and 1 tiny), variably shaped.

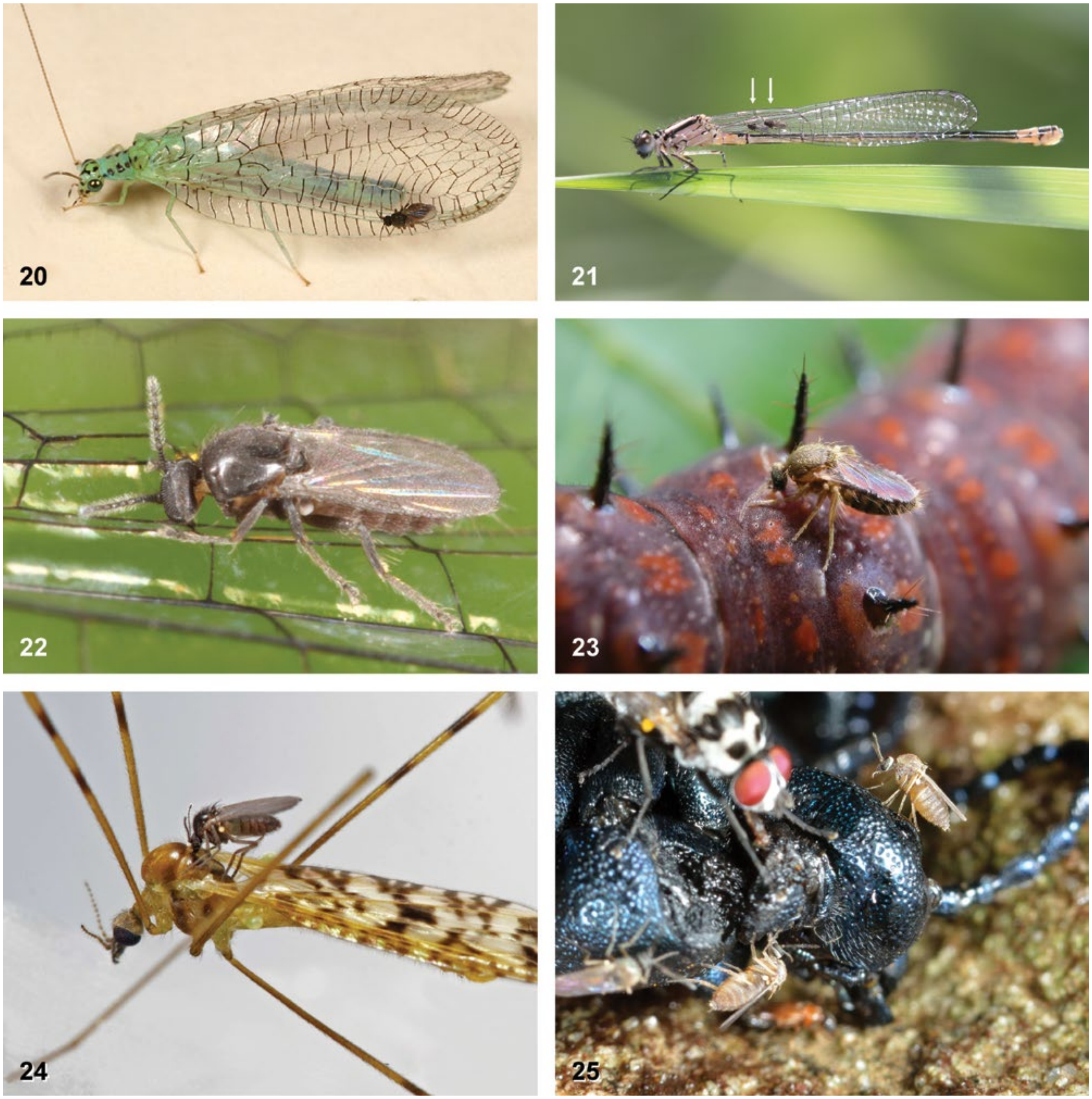
Larva differing markedly in different subfamilies, but all with well-developed head capsule (Figs 304–317), well-developed pharyngeal complex (Figs 314, 315) and no open spiracles. Leptoconopinae (here with only *Leptoconops*) with prognathous head capsule, highly modified mouthparts, bearing elongate internal apodemes posteriorly directed into prothorax (Figs 304, 310, 311); abdominal segments with secondary divisions (Fig. 304), in life often reddish in colour. Forcipomyiinae with hypognathous head capsule; body with well-developed setae/spines often borne on tubercles, with anterior and posterior prolegs (Figs 305, 306). Dasyheleinae with head capsule anteroventrally directed, with posterior proleg (with or without division of crochets medially) (Fig. 307). Ceratopogoninae long, slender, without prolegs (other than first-instar *Culicoides*), head capsule prognathous, with setae fine, slender, except in some at posterior of terminal abdominal segment (Figs 308, 309).

Pupa (described in detail by Borkent 2012, 2014), with cephalothorax somewhat larger dorsoventrally than abdomen, apical portion of abdomen nearly always posteriorly directed in life (except in one Oriental species) (Figs 318–325); slender, in some retaining larval exuviae posteriorly (some Forcipomyiinae) (Fig. 319); mouthparts and thoracic appendages fused to each other and/or remainder of cephalothorax (Figs 322, 324). Head with or without tubercles; dorsal apotome variably shaped (Figs 318, 325); anterolateral cephalic sclerite well-developed, broadly meeting or divided medially by dorsal apotome (Fig. 318); antenna elongate, apex extending posteriorly to various points along anterior margin of wing (Figs 322, 324); mouthparts short, restricted to area anterior to fore coxae / trochanters; apex of labrum narrowly to broadly rounded; mandible present or absent; maxilla present (most of those with biting adult females) or absent (most of those with non-biting adult females); palpus posteriorly directed or posteromedially, apices of palpi separated medially; exuviae with head entirely



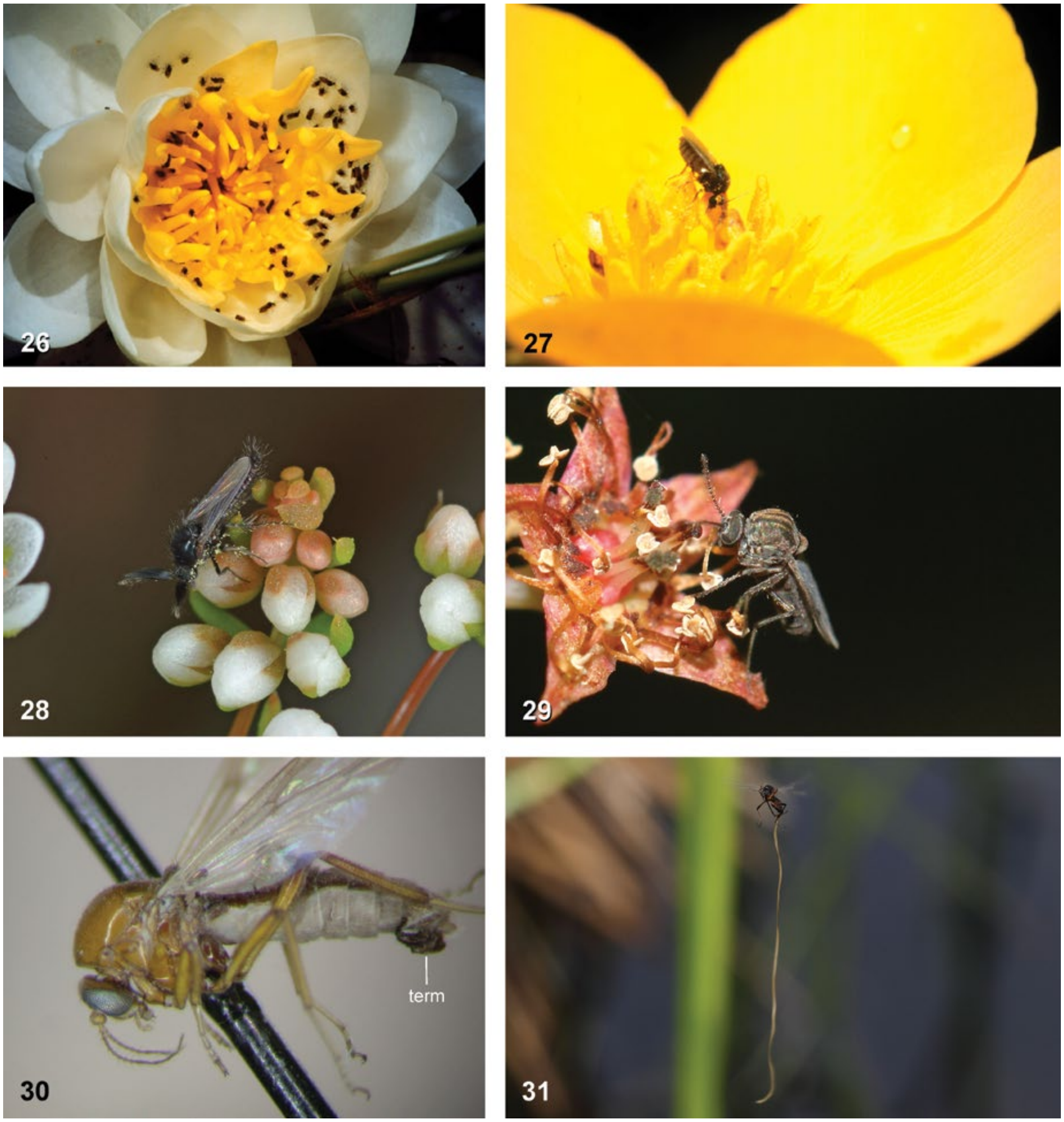
Figs 34.14–19. Habitus of adult Ceratopogonidae (all non-Afrotropical): (14) *Clinohelea* (*Clinohelea*) *bimaculata* (Loew) ♂; (15) *C. curriei* (Coquillett) ♀; (16) *Palpomyia rufa* (Loew) ♀; (17) *P. serripes* (Meigen) ♀ feeding on ♂ *Atrichopogon* sp.; (18) *Bezzia* sp. ♀; (19) *Phaenobezzia opaca* (Loew) ♀. Figs 14–16, 18, 19 (photographs T.C. Murray), Fig. 17 (photograph © M. Deml, http://www.biolib.cz/en/).

detached dorsally, fused posteriorly to fore coxae/trochanters, not distorted from original shape; cephalic sensilla present in variable numbers and sizes, some on tubercles on dorsal apotome, anterolateral cephalic sclerite, labrum, ocular area, antenna. Thorax with or without tubercles; prothorax with or without ventrolateral extension abutting against lateral margin of palpus (not visible in four genera); respiratory organ well-developed, undivided, with series of small apical pores (some with additional more basal pores); tubular, of varying shape, surface with or without annulations, with or without spicules;



Figs 34.20–25. Adult Ceratopogonidae behaviour: (20) *Forcipomyia* (*Trichohelea*) *eques* (Johannsen) ♀, on wing of *Chrysopa chi* Fitch (Neuroptera) (non-Afrotropical); (21) *F.* (*Pterobosca*) *paludis* (Macfie) ♀, on wing of *Ischnura elegans* (Vander Linden) (Odonata) (non-Afrotropical); (22) same, on wing of undetermined damselfly (Odonata) (non-Afrotropical); (23) *F.* (*Microhelea*) *fuliginosa* (Meigen) ♀, on caterpillar of *Dione juno* (Cramer) (Lepidoptera) (non-Afrotropical); (24) *Atrichopogon* sp. ♀, on Tipulidae (Diptera) (non-Afrotropical); (25) *Atrichopogon* sp. ♀, on Meloidae (Coleoptera) (South Africa). Fig. 20 (photograph T.C. Murray), Figs 21, 22 (photographs G. Kunz), Fig. 23 (photograph K. Nishida), Figs 24, 25 (photographs © S.A. Marshall).

hind leg curled under wing; fore leg extending partway to or near apex of wing; apical portion of hind leg visible in lateral view along posterior margin of wing or not visible and under wing, apex abutting apex of mid leg (Figs 322, 324); metathorax either narrow to broad band undivided medially or divided medially by mesothorax, extending posterolaterally from halfway length of abdominal tergite 1 to posterior to anterolateral margin of abdominal tergite 2, apex separate to broadly abutting hind leg; thoracic sensilla with setae, non-bifurcated or bifurcated, arising from flat cuticle or from tubercles, some campaniform sensilla; setae and campaniform sensilla in varying numbers and distribution along anterior margin of thorax,



Figs 34.26–31. Adult Ceratopogonidae behaviour (all non-Afrotropical, except Fig. 28): (26) *Atrichopogon* sp. ♀, on inflorescence of *Nymphea* (Nymphaeaceae); (27) same, on inflorescence of *Potentilla* (Rosaceae); (28) same, on inflorescence (South Africa); (29) *Dasyhelea* ♀, on inflorescence; (30) *Palpomyia* sp. ♀, with dried ♂ terminalia attached to terminalia; (31) *Mallochohelea nitida* (Macquart) ♀, flying with ribbon of eggs. Figs 26–28 (photographs © S.A. Marshall), Fig. 29 (photograph J.A. Gaspar), Fig. 31 (photograph T. Barton).

Abbreviation: term – terminalia.

dorsally, in some above wing base, metathorax. Abdomen: circular in cross-section; with or without tubercles; without open spiracles; segments without pleural membrane, some with ventral membranous disc on one or more of sternites 5–7 (Fig. 322); terminal process posteriorly rounded (in *Leptoconops* only) or pointed, short to elongate, dorsally curved and hook-like, lobe-like, or conical (Figs 318, 320–325); abdominal sensilla variable in distribution, size on each segment; setae, bifurcated or non-bifurcated, arising from flat cuticle or tubercles. Terminal process posteriorly rounded (only in *Leptoconops*) or pointed.

Adult Ceratopogonidae are superficially similar to some Chironomidae (see Chapter 35), but may be distinguished by the combination of a lack of a medial groove on the postnotum (otherwise only in podonomine Chironomidae) and lack of *m–cu* wing crossvein (present in Podonominae). Larvae have a distinctive, well-developed pharyngeal complex (Figs 314, 315), that is superficially similar to those of some, much larger and metapneustic (with terminal spiracles) Ptychopteridae (non-Afrotropical). Pupae may be superficially confused with those of Psychodidae (see Chapter 24), but the presence of apical pores on the respiratory organ distinguishes Ceratopogonidae, as well as the presence of the S-shaped hind leg tucked beneath the wing.

Biology and immature stages

The Ceratopogonidae, commonly known as "biting midges", "no-see-'ums" or "sand flies" (the last name also applied to some Psychodidae), are a remarkably diverse and interesting family of biting flies. Representatives of this family, with 6,267 named species arranged in 111 genera, occur in virtually all terrestrial areas on Earth, from coastal areas to high mountain peaks (to an elevation of least 4,200 m on Mt Everest, Nepal), and from the tropics to the high arctic (within 150 km of permanent polar ice) and subantarctic islands. Adults are one of the most abundant dipteran families represented in most insect traps and are particularly common in Malaise and light trap collections (*e.g.*, Bickel & Tasker 2004: 892; Brown 2005; Kitching *et al*. 2004; Meiswinkel *et al*. 2004*a*: 95). Immatures may be found in an amazing diversity of habitats with even a moderate amount of moisture, from rotting vegetation or dung, to wet mosses, seeps, epiphytes and tiny rock pools, to the benthic regions of large rivers and lakes (Glukhova 1979). Most taxa are found in the substrates of ponds, marshes, bogs, fens and wet, often muddy, margins of streams and rivers. Some *Atrichopogon* Kieffer and *Forcipomyia* species have terrestrial larvae that occur beneath rotting bark and on algae, mosses and other moist habitats. The earlier lineages of the family are generally restricted to smaller habitats and the more recently evolved lineages of the non-pest tribes Heteromyiini, Hebetulini, Johannsenomyiini, Sphaeromiini, Palpomyiini and Stenoxenini are generally in larger aquatic habitats, such as rivers and lakes (although some representatives of these tribes may also occur in smaller habitats). When in such substrates as wet soil, mud or sand, larvae rarely occur deeper than 5 cm from the surface. Larvae of some species of biting midges are quite rare and difficult to locate, but some species of *Culicoides* Latreille may occur in vast numbers in wet soils, manure, or particularly in dairy wastewater ponds, with abundances of over 7,000 per 30 ml of mud recorded from such a pond (Mullens & Lii 1987). Meiswinkel (1989) reported 512 adult *Culicoides bolitinos* Meiswinkel, 1989, emerging from half of a large Cape buffalo pat.

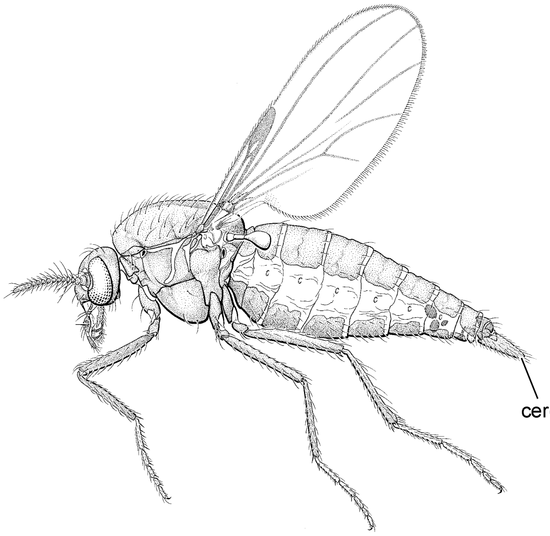
Although primarily known as significant biting pests and vectors of various diseases, biting midges as a group are a vital and important part of ecosystems. The vast majority of species are not pests at all and play important roles in a wide array of habitats. The adults of some species are important pollinators (*e.g.*, Figs 26–29) of such plants as cacao (without them we would not enjoy chocolate!) and rubber trees and the larvae of many are important predators of other organisms in aquatic systems. Adults of most biting midges actually ingest hemolymph or liquified body fluids from other insects (as ectoparasites or predators) (*e.g.*, Figs 20–25) and some may possibly be important vectors of viruses and spiroplasmas that may kill caterpillars. It is worth pointing out, that even the pest species that attack humans and livestock provide an important role by restricting human development in certain regions, thereby helping to preserve some habitats and biodiversity during a time when ecological destruction is rampant and many species are under great threat or have already become extinct.

The immatures of Ceratopogonidae are the most poorly known of any of the biting flies, with only 2% known as eggs, 9% known as larvae and 13% known as pupae for the global fauna of 6,267 species (Borkent 2014; 2016*a*). In the Afrotropical Region, with 928 species, only 1%, 5% and 9% are known as eggs, larvae and pupae, respectively, and of these, 76% of larvae and 60% of pupae are of species of *Culicoides*, *Dasyhelea* Kieffer and *Forcipomyia*. Of the 53 described genera of Afrotropical Ceratopogonidae, 33 are not known, either as larvae or pupae, indicating how little investigation of immatures has taken place in the region. Of these 33 genera, nine are known as at least pupae from outside the Afrotropical Region. As such, some information presented here is based on extralimital species.

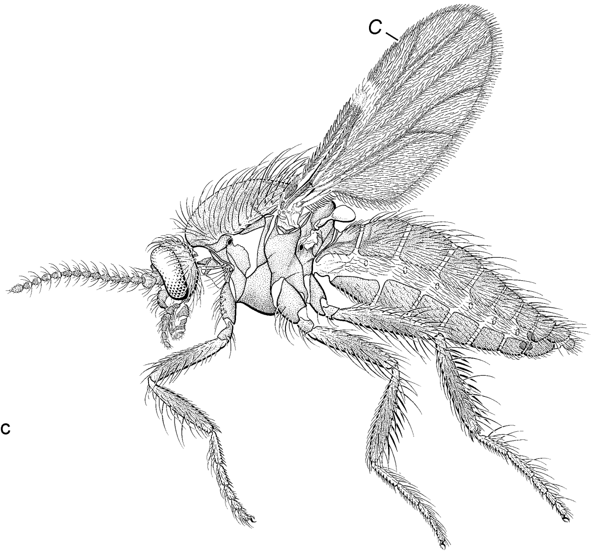
Borkent (2014) provided the first identification keys to pupae at the generic level and included all genera known globally. Larvae can be easily recognised to subfamily, but the differences between genera of the subfamily Ceratopogoninae are generally subtle (Glukhova 1979) and poorly understood, especially in areas outside of Europe.

Species of Ceratopogonidae all share a basic life cycle, with an egg stage, which generally lasts a few days, four larval instars which make up the bulk of their lifespan, a short-lived pupal stage and male and female adults (of variable longevity, but generally not longer than one week; some adult *Culicoides* live for months). Only two non-Afrotropical species of *Culicoides* are known to be parthenogenetic. The total life cycle in many species takes one year, but under favourable, warm conditions, may take as little as 8–10 days from egg to adult (for multivoltine species) (Meiswinkel 1992). A variety of environmental factors have been studied for a few pest species and these indicate that temperature, moisture levels, chemical composition of the substrate and population density affect the rate of development of immatures.

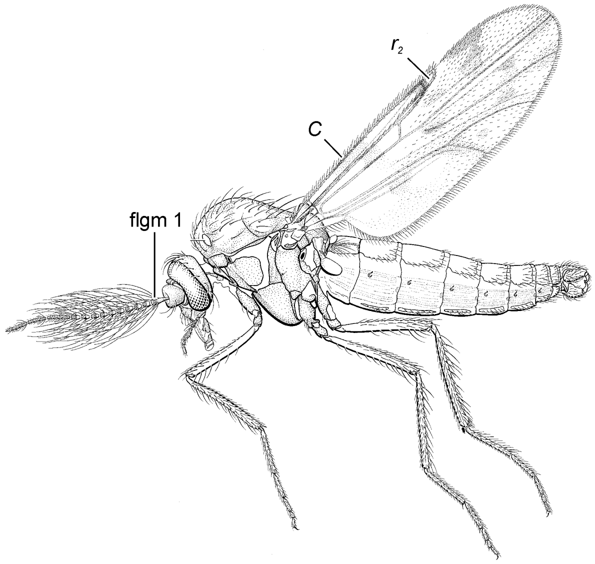
In northern and southern temperate regions, it is almost always the third- or fourth-instar larvae that diapause and overwinter, although a few species have been recorded as overwintering



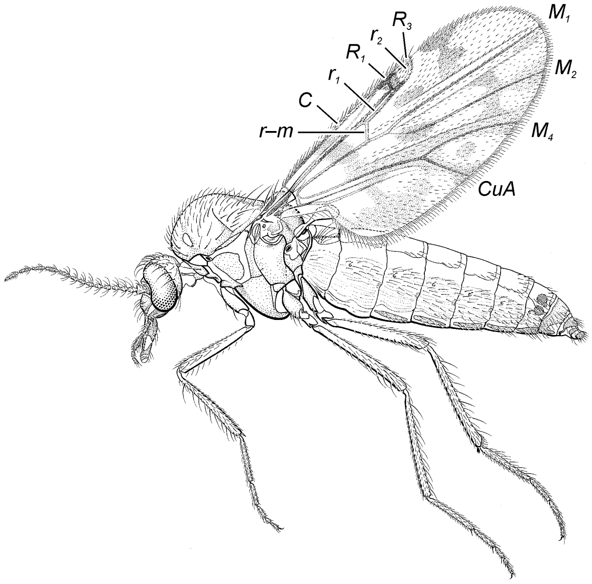
32 *Leptoconops* (*Holoconops*) ♀



33 *Forcipomyia* (*Forcipomyia*) ♀



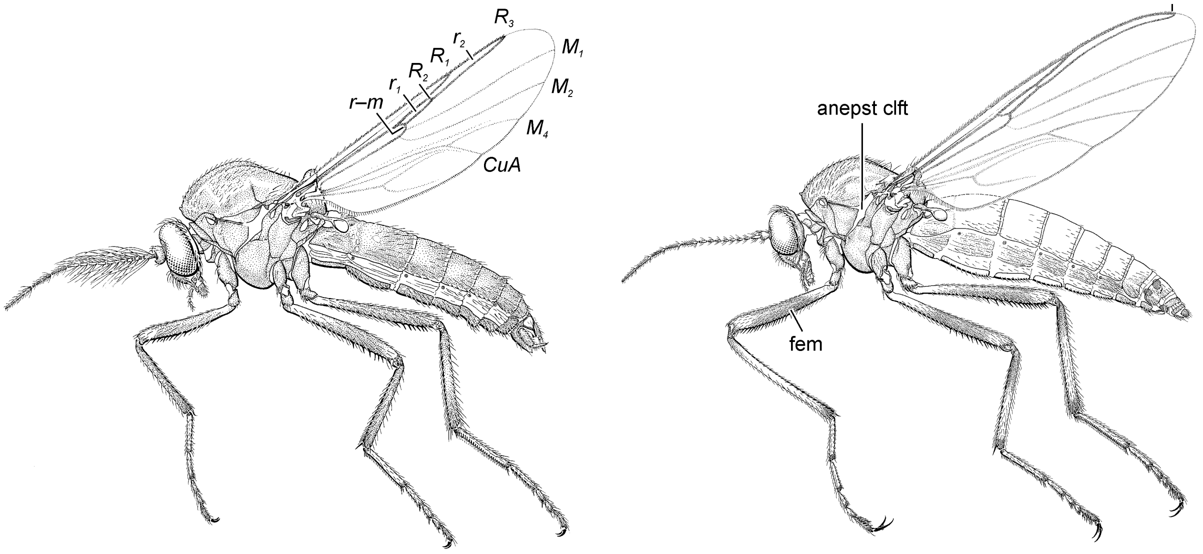
34 *Culicoides* ♂



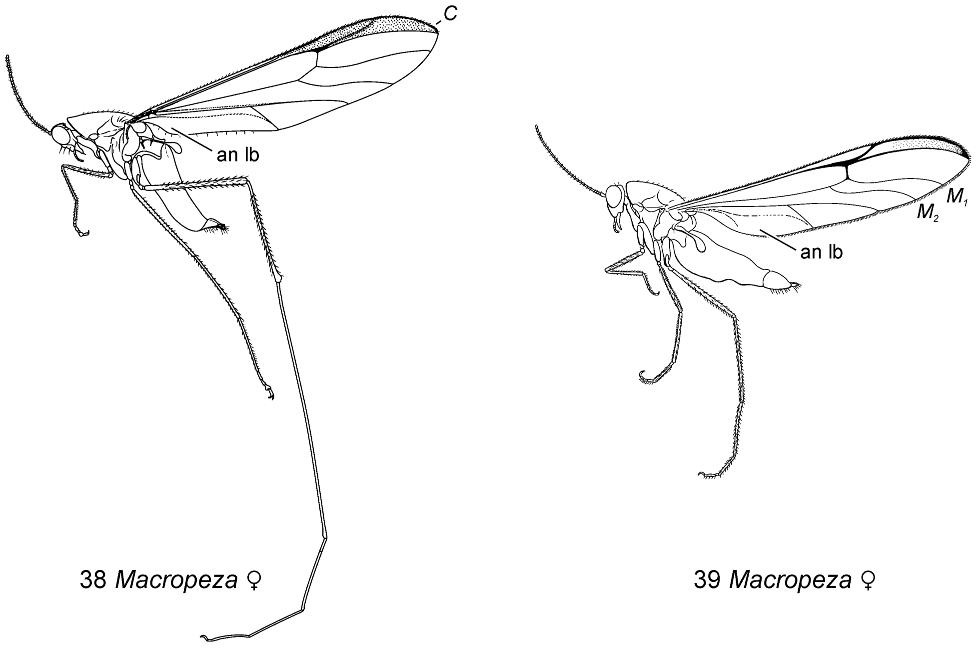
35 *Culicoides* ♀

Figs 34.32–35. Habitus of adult Ceratopogonidae (all non-Afrotropical): (32) *Leptoconops* (*Holoconops*) sp. ♀; (33) *Forcipomyia* (*Forcipomyia*) *bipunctata* (L.) ♀; (34) *Culicoides yukonensis* Hoffman ♂; (35) same, ♀. Figs 32–35 (Downes & Wirth 1981, figs 2, 11–13).

Abbreviations: *C* – costal vein; cerc – cercus; *CuA* – anterior branch of cubital vein; flgm – flagellomeres; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; *r–m* – radial–medial crossvein.



36 *Sphaeromias* ♂ 37 *Sphaeromias* ♀



38 *Macropeza* ♀ 39 *Macropeza* ♀

Figs 34.36–39. Habitus of adult Ceratopogonidae: (36) *Sphaeromias longipennis* (Loew) ♂ (non-Afrotropical); (37) same, ♀ (non-Afrotropical); (38) *Macropeza longipes* (Séguy) ♀; (39) *M. nigra* (Séguy) ♀. Figs 36, 37 (Downes & Wirth 1981, figs 14, 15), Figs 38, 39 (after Séguy 1931, figs 1, 2).

Abbreviations: anepst clft – anepisternal cleft; an lb – anal lobe; *C* – costal vein; *CuA* – anterior branch of cubital vein; fem – femur; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – second branch of radius; r_2 – second radial cell; R_3 – lower branch of second branch of radius; *r–m* – radial–medial crossvein.

as eggs. Emerging adults are, therefore, generally more diverse in spring and early summer than later in the season. In subtropical or warm temperate areas, some species complete two or more generations before going into diapause as larvae. No adults are known to overwinter in cold regions, but at least some species do so in warm temperate and subtropical regions (Nevill 1971). Our understanding of the life cycle of tropical species is poor and those studies that have been undertaken have focused on species of *Culicoides*. Some species are clearly more abundant and diverse during the wet season in areas with a distinct dry-wet season. Dipeolu (1976*b*), for example, found 33 *Culicoides* species to be more abundant during an early rain peak in April and a higher late rain peak in October in Nigeria and Diarra *et al*. (2014) reported peak abundance correlated with the rainy seasons in Senegal. In tropical regions with a less distinctive seasonality, it appears that some species may occur as adults throughout the year. South Africa, with its relatively southern geographical position and generally higher elevations, has stronger seasonal patterns of abundance, with some *Culicoides* species in higher numbers and more diverse (or present only) during the warmer months (Meiswinkel *et al*. 2004*b*; Venter *et al*. 1996*a*, 1997, 2014*a*). For most of South Africa adult *Culicoides* are totally absent from light traps for less than one month.

Eggs are laid directly on or very close to the microhabitat in which the larvae later develop, either separately, in loose groups, in gelatinous masses (*Dasyhelea*, uniquely C-shaped), or arranged in closely-packed strings (*e.g.*, Fig. 31) (some genera of Johannsenomyiini). Eggs are generally not desiccation resistant and need to remain at least moist to survive. Larvae hatch by using a small tooth on the dorsum of the head capsule to break open the eggshell. They begin feeding almost immediately on micro-organisms, or in the case of some Ceratopogoninae, on small invertebrates. The behaviour of the immatures of each of the four subfamilies differs substantially and is discussed separately, as follows:

Larvae of Leptoconopinae are reddish and have unique, secondarily divided abdominal segments (Fig. 304). Those of the markedly modified *Leptoconops* are elongate and rather sluggish as they move through wet sand (freshwater, saline and marine beaches), or wet alkaline, clay soils (which may be cracked at the surface), sweeping their heads as they browse on micro-organisms. They use their powerful mandibles (with very elongate apodemes) to assist moving themselves through the substrate. The larvae of the generally plesiomorphic Australian genus *Austroconops* Wirth & Lee (Borkent & Craig 2004) are also elongate, but with assistance of their anterior and posterior prolegs, move in a similar snake-like manner to larvae of Ceratopogoninae. They feed on micro-organisms and some on small invertebrates.

Larvae of Forcipomyiinae are aquatic, semi-aquatic or terrestrial (Figs 305, 306). When in aquatic habitats, they are generally restricted to lentic (standing) waters, although a few are known from streams and small rivers, associated with mosses and algae. They retain the plesiomorphic anterior and posterior prolegs and, therefore, can walk on surfaces above or beneath water using these. Representatives of this subfamily have a unique mode of feeding, in which the larvae graze moist or submerged surfaces for micro-organisms or algae, sweeping their heads back and forth with a rapid motion, as they move along using their anterior and posterior prolegs. Some species feed on decaying vegetation (or the associated micro-organisms) and a few may be found associated with manure. The larvae of most species have specialised setae along the length of their bodies that secrete a sticky fluid that repels ants (Hinton 1955), while in others the secretion appears to keep the cuticle moist for respiration and have an anti-microbial function (Urbanek *et al*. 2011, 2012).

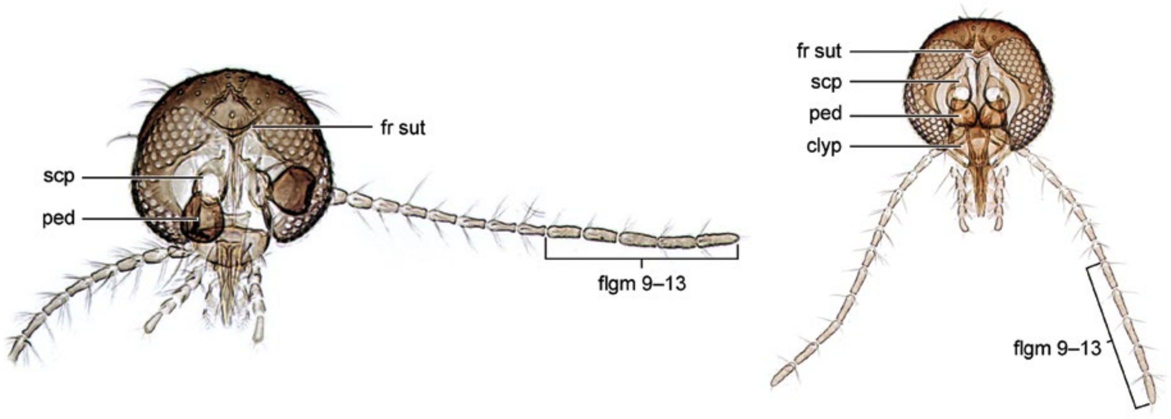
Larvae of Dasyheleinae (Fig. 307), with the single, but species-rich genus *Dasyhelea*, are aquatic and semi-aquatic. They feed on micro-organisms or are sometimes scavengers and propel themselves rather sluggishly along the substrate using their mouthparts and posterior crochets. Most species occur in small water bodies, such as those in epiphytes, tree holes, broken or damaged bamboo, rotten banana stems, fruit husks and small rock pools, including those on the margins of streams and rivers. A few species are common in mangrove swamps and salt marshes. Larvae may also be found in very wet vegetation.

Larvae of Ceratopogoninae, the most species-rich subfamily, are prognathous, lack prolegs and hooks (at least in instars 2–4) and the abdominal segments are not secondarily divided (Figs 308, 309). They have a characteristic snake-like motion, working their way slowly or rapidly through wet substrates, ingesting micro-organisms, nematodes or larger prey; at times some species are cannibalistic. In some habitats, biting midge larvae are an important biological control on other insects. Larvae of most species that leave the substrate swim with a characteristic, rapid, sinuous movement (Linley 1986), similar to that of many aquatic nematodes. Larvae of the species-rich genus *Culicoides*, with 1,368 species recorded from all zoogeographical regions other than Antarctica, may be found in decaying vegetation and fruits, herbivore manure (for some, rather dry dung), epiphytes, tree holes, wet mud, mangrove swamps and an array of other aquatic habitats, but then always in muddy/detritus substrates. In streams and rivers, Ceratopogoninae larvae may be an important source of food for other invertebrates and fishes. In general, the most early lineages of the subfamily are in smaller habitats and either feed on micro-organisms or small prey (*e.g.*, nematodes), whereas those in more recent lineages, such as the Hebetulini, Heteromyiini, Johannsenomyiini, Palpomyiini and Sphaeromiini, are generally found in larger bodies of water: ponds, marshes, lakes and rivers and can feed on larger prey, in some instances, being able to work a hole through the cuticle of their host with their mouthparts and feeding on the interior tissues. Glukhova (1979) provided a detailed synopsis of the larvae of the Ceratopogoninae, with many details of behaviour, habitat, morphology, development and more. Although in Russian (not available to some readers), an unpublished English translation is available from most current ceratopogonid systematists.

Larvae of Ceratopogonidae generally pupate on wet substrates, near to, or on the primary larval substrate (some pupate submerged). Pupae of Ceratopogonidae (Borkent 2014) are sluggish (likely to avoid predation) and move the abdomen slowly, in more or less circular movements until they find an appropriate resting position amongst the substrate or abut floating matter at the waters' surface, where the paired respiratory organs are able to obtain air. Pupae of most genera become agitated if floating freely or when they are not lodged against or on some form of substrate.

40 *Leptoconops* (*Holoconops*) ♂ 41 *Leptoconops* (*Megaconops*) ♀

42 *Culicoides* ♂ 43 *Culicoides* ♀



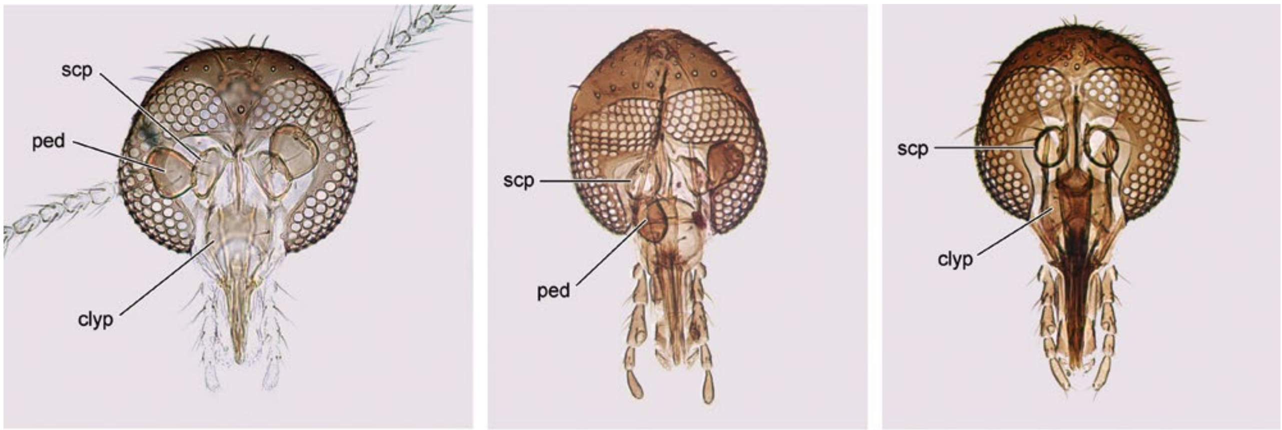
44 *Fanthamia* ♂ 45 *Fanthamia* ♀

Figs 34.40–45. Heads of Ceratopogonidae (anterior views): (40) *Leptoconops* (*Holoconops*) *catawbae* (Boesel) ♂ (non-Afrotropical); (41) *L.* (*Megaconops*) *floridensis* Wirth ♀ (non-Afrotropical); (42) *Culicoides yukonensis* Hoffman ♂ (non-Afrotropical); (43) same, ♀; (44) *Fanthamia draconis* de Meillon & Downes ♂; (45) *F. ornatipennis* (de Meillon) ♀. Figs 41–43 (Downes & Wirth 1981, figs 4, 46, 47).

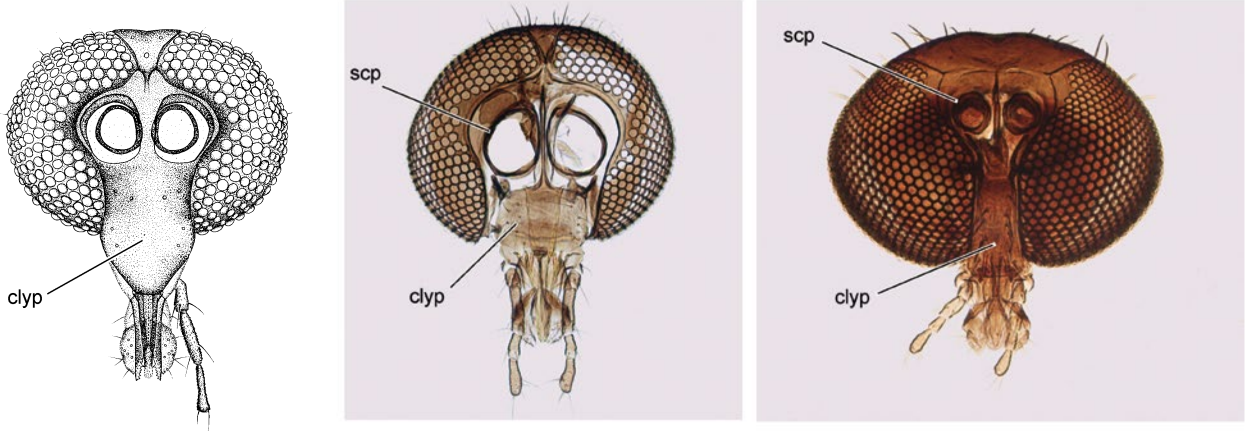
Abbreviations: clyp – clypeus; flgm – flagellomeres; fr sut – frontal suture; lbl – labellum; lbr – labrum; lc – lacinia; md – mandible; ped – pedicel; plp sg – palpal segment; scp – scape; tm – torma.

Pupae of *Leptoconops* have a distinctive behaviour, in which they remain at or below the substrate surface (generally sand) until shortly before emergence, when they wriggle upward and stand erect on the tip of the abdomen shortly prior to adult eclosion. Pupae of Australian *Austroconops* behave as those of most Ceratopogoninae. When larvae of Forcipomyiinae pupate, many retain the larval exoskeleton on the posterior end of the body (Fig. 319), likely to retain the protective measures provided by the repellent exudate remaining on the setae of the larval exuviae (Hinton 1955; Urbanek *et al*. 2011). Pupae of most Ceratopogoninae embed themselves in wet substrates with only the top of the head and/or only the tip of the respiratory organs exposed to the air. Borkent & Craig (2001) described an unusual pupa of a *Stilobezzia* species from the Neotropics that uses the respiratory organs to obtain oxygen by piercing submerged leaves of floating plants. The same species-group of *Stilobezzia* is also present in the Afrotropics and has the same pupal modifications. Pupae of some genera of Johannsenomyiini have a peculiar and distinctive means of resting in which larvae emerge from water, approach or are washed against the meniscus of emergent plants or other substrate and wiggle their way out of the water. Once at a certain distance above the water line (variable even intraspecifically), the larva pupates. The pupa then wriggles further upward and with the aid of membranous discs on sternites 6–7 (and sometimes sternite 5) (Fig. 322) adpressed firmly against the substrate, is held securely in place. Further pupal modifications and behaviour are discussed by Borkent (2014).

Upon eclosion, adults share a behaviour common to many other nematoceran Diptera: following eclosion, the soft, emergent adults rest briefly (including voiding their meconium) and then fly to a nearby spot to complete the hardening of the cuticle. On average, males emerge slightly earlier than females, so that they are ready to mate as soon as females emerge, but there is a broadly overlapping emergence period for the two



46 *Notoceratopogon* ♀ 47 Undescribed genus ♂ 48 Undescribed genus ♀



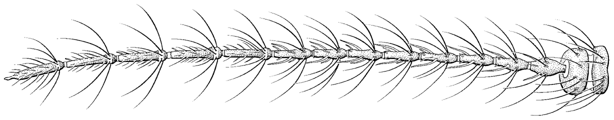
49 *Parabezzia* ♀ 50 *Johannsenomyia* ♂ 51 *Macropeza* ♂

Figs 34.46–51. Heads of Ceratopogonidae (anterior views): (46) *Notoceratopogon* sp. ♀; (47) Undescribed genus ♂; (48) same, ♀; (49) *Parabezzia* sp. ♀ (non-Afrotropical); (50) *Johannsenomyia* sp. ♂ (non-Afrotropical); (51) *Macropeza albitarsis* Meigen ♂ (non-Afrotropical). Figs 49 (Borkent *et al*. 2009, fig. 7).

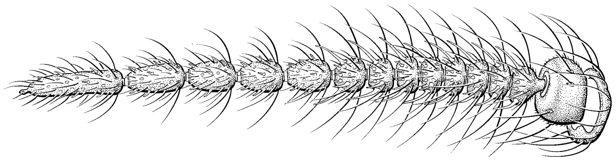
Abbreviations: clyp – clypeus; ped – pedicel; scp – scape.

sexes. Adults are generally crepuscular and more active at lower light levels, with at least some species of *Culicoides* being active nocturnally (Fall *et al*. 2015*b*, *c*). Males of most species form swarms of varying sizes near the habitat from which they emerged, while others appear to fly singly, apparently in search of females. Some species do not form swarms and males of these generally have a reduced antennal plume and markedly enlarged terminalia, mating on substrates (Downes 1978). Such taxa in the Afrotropics have not been studied in this regard. The sites where swarming males congregate are often species-specific and are associated with a particular marker, such as above a dark rock, or next to a tree branch at a certain height above the ground. Females fly through these swarms and the male, attracted by the wing beat frequency of the female and secreted female pheromones, grabs the passing female and either copulates during flight or mating couples land on the substrate. Some females (see below) enter swarms of males of their own species and feed on them while copulating. Males are able to twist their terminalia 180°, so that the flying or resting couple face away from each other. Copulation generally takes only a few minutes or less. Males produce and insert a two-chambered spermatophore into the female terminalia and the sperm are then released and find their way to the female spermathecae. Following mating, females of species that require a blood meal disperse in search of a suitable host, generally in close proximity, but in some species up to four kilometres distance. Adult sex ratios in Ceratopogonidae tend to be close to 1 : 1 near the site of emergence, therefore, with the number of males rapidly decreasing with distance from the site of emergence.

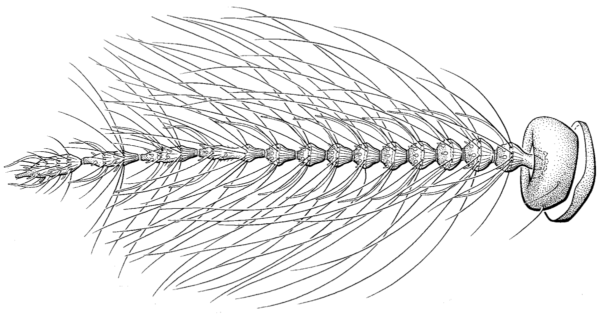
Taxa that occur in small and temporary habitats tend to be better dispersers than those in permanent habitats, where females generally remain closer to the habitat in which they developed. This is reflected in a global zoogeographical pattern of generic diversity of Ceratopogonidae, including the Afrotropics, where species of the widespread genera *Atrichopogon*,



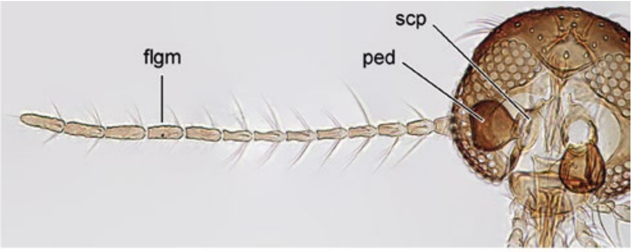
52 *Forcipomyia* (*Caloforcipomyia*) ♀



53 *Forcipomyia* (*Trichohelea*) ♀

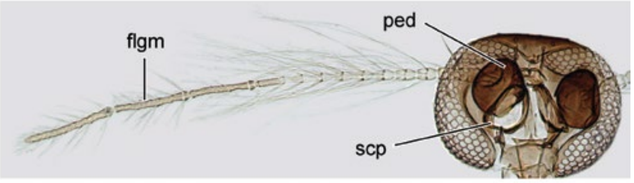


54 *Dasyhelea* ♂

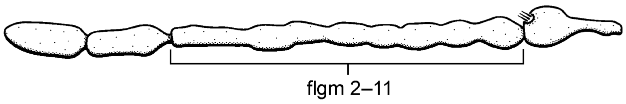


55 *Fanthamia* ♂

56 *Stilobezzia* (*Acanthohelea*) ♂



57 *Schizonyxhelea* ♂



58 *Brachypogon* (*Brachypogon*) ♂

Figs 34.52–58. Antennae and heads of Ceratopogonidae: (52) antenna of *Forcipomyia* (*Caloforcipomyia*) *glauca* Macfie, lateral view ♀ (non-Afrotropical); (53) same, *F.* (*Trichohelea*) *eques* (Johannsen) ♀ (non-Afrotropical); (54) same, *Dasyhelea pseudoincisurata* Waugh & Wirth ♂ (non-Afrotropical); (55) head of *Fanthamia draconis* de Meillon & Downes, frontal view ♂; (56) same, *Stilobezzia* (*Acanthohelea*) *fuscula* Wirth ♂ (non-Afrotropical); (57) same, *Schizonyxhelea thomsenae* Wirth ♂ (non-Afrotropical); (58) antenna of *Brachypogon* (*Brachypogon*) *corneti* Grogan & de Meillon, lateral view ♂. Figs 52–54 (Downes & Wirth 1981, figs 58, 60, 64), Fig. 58 (after Grogan & de Meillon 1993, fig. 2).

Abbreviations: flgm – flagellomere; ped – pedicel; scp – scape.

Culicoides, *Dasyhelea* and *Forcipomyia*, which commonly occur in temporary habitats, are the only genera found, even on distant volcanic islands, such as Réunion Is. and Galápagos Is. (Borkent 1991). The immatures of these taxa are generally in such small, temporary habitats as manure, fungi, wet mosses, decaying vegetation, seeps, small pools and mud at the margins of larger aquatic habitats. The generic diversity of continental areas, including islands of continental origin, such as Seychelles with 17 genera, is much higher, with additional taxa that are generally associated with more stable habitats.

The diversity of feeding behaviours on vertebrates and invertebrates exhibited by female adult Ceratopogonidae globally is truly remarkable, with hosts including: fishes (emergent mud skippers in South-east Asia), amphibians (frogs, toads), and reptiles (lizards and marine, freshwater and terrestrial turtles), birds and mammals (within the vertebrates) and a wide array of invertebrate hosts (see below). It appears likely that most bird and mammal species are fed upon by at least one species of Ceratopogonidae. Some vertebrate-feeders are highly host-specific, while others incorporate a range of hosts. The mouthparts of female Ceratopogonidae reflect the type of host (Borkent 1995: 129); those with coarsely-toothed mandibles feed on insects and those with finely-toothed mandibles feed on vertebrates (there are a few exceptions in species of *Forcipomyia*, which pierce the soft skin of caterpillars). Within the vertebrate feeding groups, there is a further correlation between the numbers of capitate sensilla on the third palpal segment, which detect carbon dioxide emanating from their hosts, and the size of the host. Those with fewer sensilla tend to have larger hosts.

Overall, the host type makes phylogenetic sense. Feeding on vertebrate blood is restricted to the earliest lineages of Ceratopogonidae and is a homologous behaviour shared with other vertebrate blood-feeding groups in the Culicomorpha (*i.e.*, some Chironomidae, Corethrellidae, Culicidae and Simuliidae) (Borkent & Craig 2004). Of the 111 extant genera known in Ceratopogonidae, blood-feeding on vertebrates is restricted to four genera, namely *Austroconops*, *Culicoides*, *Forcipomyia* (only in the subgenus *F.* (*Lasiohelea* Kieffer)) and *Leptoconops*, with females requiring a blood meal to develop one or more clutches of eggs. Within this group of vertebrate-feeders, females of *Austroconops*, *F.* (*Lasiohelea*) and *Leptoconops* have the plesiotypic feature of feeding diurnally, a feature shared with the closely related Simuliidae (Borkent 2012; Borkent & Craig 2004). The crepuscular and nocturnal feeding of most species of *Culicoides* is a derived feature within the family.

Females of some species of Ceratopogonidae are able to develop eggs without any additional food (autogenous), but most require a blood meal to do so (anautogenous). Vertebrate feeders are able to locate their host initially by tracking the downwind plumes of carbon dioxide and other odours produced by their intended hosts. As the biting midges get closer, further cues, such as size, shape and colour of the host, movement, heat and skin secretions direct them to specific locations on the host. Most species appear to prefer specific sites on the host, often at a certain height from the ground. Virtually nothing is known how invertebrate feeders locate their hosts, other than the attractiveness of the chemical cantharidin for some *Atrichopogon* species, that feed on blister beetles (Coleoptera: Meloidae) (Fig. 25) and the likely use of vision by some female Ceratopogoninae to find swarms of midges upon which they subsequently feed (see below).

Specific environmental conditions are required before females can begin to fly and feed. Obviously, daytime temperatures have an important effect (flight does not take place if too cold, and in many, if too hot) and high winds, generally more than 8 km/hour, severely restrict or prevent flight. Other factors have been discovered which affect rates of attack in vertebrate-feeders: movement of host, time of day, temperature, light intensity (or the change in light in light intensity), humidity, type of surrounding habitat (open or heavily wooded), precipitation and the number of closely congregated hosts.

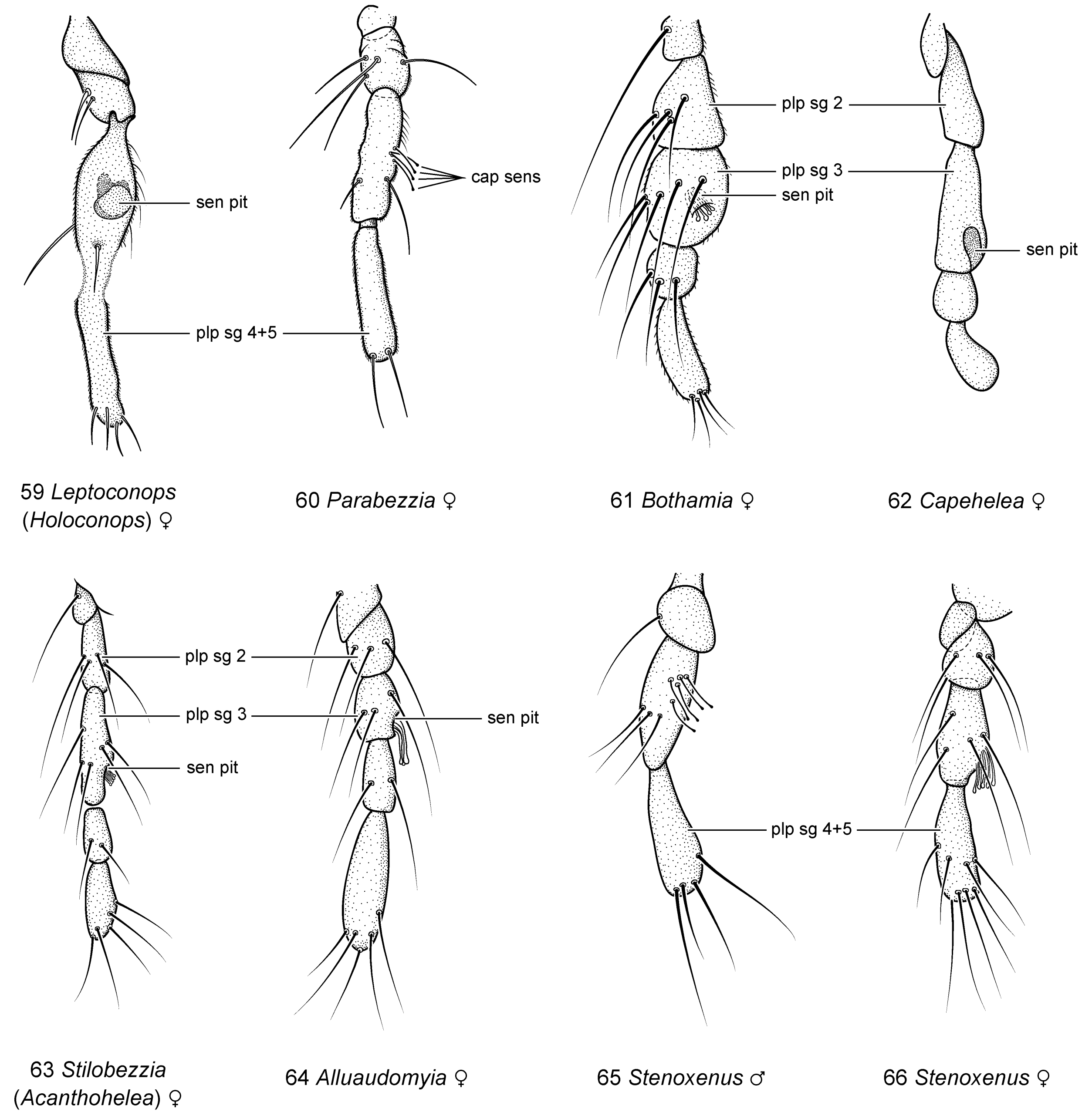
Austroconops species are restricted to two species in south-western Australia and at least one of which feeds on humans and kangaroos (Borkent & Craig 2004). Females of several *Leptoconops* species are diurnal feeders on humans and other mammals in the Afrotropics (Clastrier 1981, 1983*d*; de Meillon & Hardy 1953; Laurence & Mathias 1972). *Leptoconops* (*Styloconops*) *spinosifrons* (Carter, 1921) is a pest on some marine beaches in East Africa, Madagascar and Seychelles and *L. nevilli* Clastrier, 1981 has been reported causing painful bites in South Africa (Nevill 1975: 3, 1983). Two species of *F.* (*Lasiohelea*) feed on humans in the Afrotropics: *F. anthropophila* (Harant, Huttel & Huttel, 1951) and *F. lefanui* Carter, 1916, with the hosts of the remaining ten unknown, but likely to be vertebrates. Fall *et al*. (2015*c*) reported high incidences of diurnal attacks on horses and sheep in Senegal by an unidentified species of *F.* (*Lasiohelea*).

Culicoides is the most notorious genus of biting midges. Adult females of this genus may occur in large numbers in localities where there is appropriate and abundant habitat. Meiswinkel *et al*. 2004*a*: 125, for example, include a photograph of two jars containing an impressive 1,054,620 adult *Culicoides*, 99.4% of which were *C. imicola* Kieffer, 1913, sampled with a black light with a down draught fan on a single night in South Africa! The bite of female *Culicoides* species (sometimes unnoticed at the time), can produce painful and itching welts entirely out of proportion to their small size. Although 159 *Culicoides* species are known in the Afrotropics, only a few have been recorded as feeding on humans, although sometimes in vast numbers. Further details regarding their significant medical, veterinary and economic importance are discussed in the "Economic significance" and "Synopsis of the fauna" sections below.

The excellent fossil record for biting midges provides evidence of the antiquity of the female adult vertebrate blood-sucking habit. Species of both *Austroconops* and *Leptoconops* were present 125–129 MYA (Lebanese amber) and the earliest fossils of *Culicoides* are known from 90–94 MYA (New Jersey amber). Fossil *F.* (*Lasiohelea*) are recorded from 41–48 MYA (Sakhalin amber). Some of these fossils have swollen abdomens and mouthpart structures, that indicate they were feeding on vertebrate blood, and some females of at least two Cretaceous *Culicoides* species likely fed on dinosaurs (Borkent 1995: 129). Clearly, the relationship between biting midges and their vertebrate hosts is an ancient one.

Otherwise, female Ceratopogonidae draw hemolymph or liquefied tissues from other insects. This habit has evolved at least three times within the family: once in the Forcipomyiinae, once in the subgenus *Culicoides* (*Trithecoides* Wirth & Hubert) and once in a monophyletic group in the subfamily Ceratopogoninae (those in the sister-group of Culicoidini).

Biting habits of adult female Forcipomyiinae, including the only two genera *Atrichopogon* and *Forcipomyia*, are remarkably diverse and independently derived from the insect feeding by the predaceous genera in most Ceratopogoninae. Globally



59 *Leptoconops* (*Holoconops*) ♀

60 *Parabezzia* ♀

61 *Bothamia* ♀

62 *Capehelea* ♀

63 *Stilobezzia* (*Acanthohelea*) ♀

64 *Alluaudomyia* ♀

65 *Stenoxenus* ♂

66 *Stenoxenus* ♀

Figs 34.59–66. Right palpi of Ceratopogonidae (anterior views): (59) *Leptoconops* (*Holoconops*) *bequaerti* (Kieffer) ♀ (non-Afrotropical); (60) *Parabezzia* sp. ♀ (non-Afrotropical); (61) *Bothamia demeilloni* Meiswinkel ♀; (62) *Capehelea steli* de Meillon & Wirth ♀; (63) *Stilobezzia* (*Acanthohelea*) *kindiae* Clastrier ♀; (64) *Alluaudomyia fimbriatinervis* Clastrier ♀; (65) *Stenoxenus* sp. ♂; (66) *S. pastorianus* Clastrier ♀. Figs 59, 60 (after Borkent *et al*. 2009, figs 48, 52), Fig. 61 (after Meiswinkel 1987, fig. 5), Fig. 62 (after Wirth & Grogan 1988, fig. 15c), Fig. 63 (after Clastrier 1988*b*, fig. 6), Fig. 64 (after Clastrier 1958, fig. 31), Fig. 66 (after Clastrier 1982*b*, fig. 1E).

Abbreviation: cap sens – capitate sensilla; plp sg – palpal segment; sen pit – sensory pit.

(except Antarctica), adult female Forcipomyiinae act as ectoparasites of large insects, with some sucking hemolymph from their hosts for extended periods of time (in some for hours or days) (*e.g.*, Figs 20–25). Various species ingest hemolymph from Phasmatodea, Tettigoniidae (Orthoptera), Lepidoptera caterpillars, Symphyta larvae (Hymenoptera), blister and oil beetles (Meloidae), spiders (Araneae), crane flies (Tipulidae), mosquitoes (Culicidae), the various prey items caught in spiders' webs and the wing veins of dragonflies and damselflies (Odonata), lacewings (Neuroptera) and Lepidoptera (Borkent & Rocha Filho 2006; McCrae 1967; Wirth 1956*a*, 1972, 1980; Wirth & Messersmith 1971). There are only a few records of *Atrichopogon* and *Forcipomyia* feeding on insects in the Afrotropics and these are noted in the "Synopsis of the fauna" section below.

As noted above, species of the subgenus *Forcipomyia* (*Lasiohelea*) are the only Forcipomyiinae that are vertebrate feeders. Adult females of *Dasyhelea*, the only genus in the Dasyheleinae, have reduced mouthparts and do not suck blood or hemolymph from either vertebrates or invertebrates.

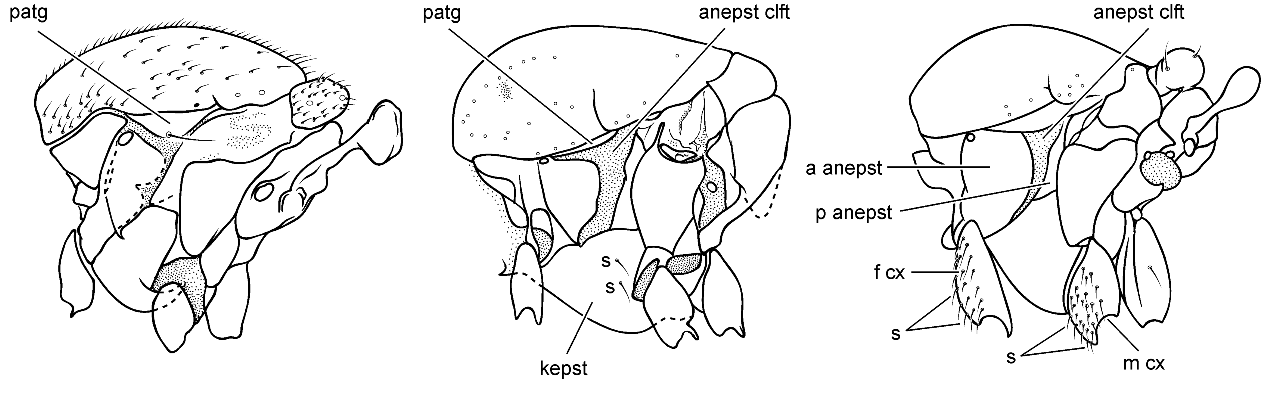
Adult females of many *Culicoides* (*Trithecoides*) species have a remarkable habit, in which they draw "second-hand" blood from blood-fed mosquitoes or phlebotomine psychodids (Ma *et al*. 2013; Wirth & Hubert 1989). Some research (Das Gupta 1964; Paimpali 1996) suggests that these species may also draw hemolymph from the mosquito itself.

Adult females in the subfamily Ceratopogoninae, other than those of most *Culicoides*, are predators and feed on other flying insects that are approximately the same sizes as themselves (Downes 1978). In general, a female flies into a swarm of male non-biting midges (Chironomidae), grabs an individual and soon settles on the ground or surrounding vegetation (*e.g.*, Fig. 17). Injected proteolytic enzymes dissolve the internal organs and tissues of the prey and the female then sucks up the liquefied contents as a rich protein-lipid meal. In some representatives of the tribes Heteromyiini, Johannsenomyiini, Sphaeromiini and Palpomyiini females may enter a male swarm of the same species and while copulation takes place, pierce the body of the male and suck out the contents. Such females may later be found with the dried male terminalia still attached to their own abdomen, after the bulk of the dried male has broken away (*e.g.*, Fig. 30). The males of these taxa, therefore, provides their own bodies as nutrition for females and leaves an effective mating plug to ensure no further mating takes place.

After obtaining a blood meal, females require several days for their eggs to develop, during which time some females seek out suitable habitats to lay their eggs (depending how far they are from the site of emergence) (Kettle 1995). Females of some *Leptoconops* species have a peculiar behaviour, in which they rest by burying themselves just beneath the sand surface. Other adult Ceratopogonidae rest on surrounding vegetation. Females oviposit 30–450 eggs, dependant on the species.

There are two components to natural dispersal of adults: the first is wing-propelled flight, used by females to locate relatively nearby hosts and suitable habitats (Kluiters *et al*. 2015); and the second is wind-borne dispersal, in which adults are caught in wind streams, generally at heights of 0.5–2 kilometres, 10–40 km/hour and at temperatures of 12–35°C. Adult *Culicoides* (and some other genera) have been collected as "aerial plankton" with aircraft and are quite able to disperse to distant islands (Borkent 1991; Kirk-Spriggs & McGregor 2009). There is reasonable indirect evidence that wind-dispersed *Culicoides* spread diseases into new regions 130–200 (and perhaps 700) km from sites of emergence.

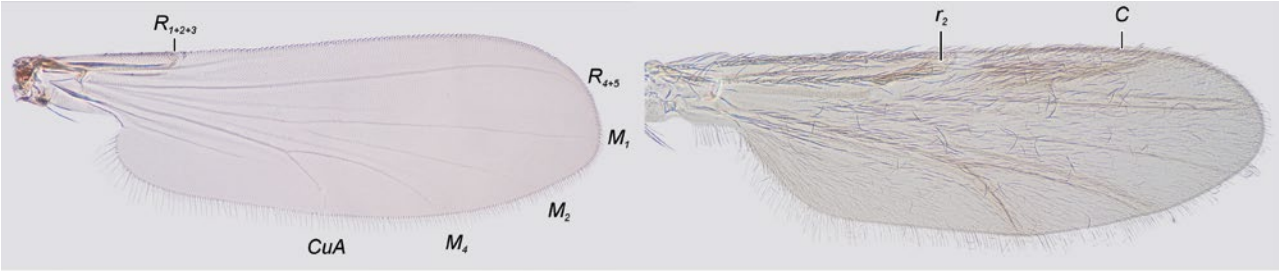
Both sexes of many Ceratopogonidae also require sugar sources to fuel flight as well as influencing egg production in females (Kaufmann *et al*. 2015). The taxa generally involved in nectar-feeding are also those in early lineages of the family, such as the subfamilies Dasyheleinae, Forcipomyiinae, Leptoconopinae, and within the Ceratopogoninae, representatives



67 *Atrichopogon* 68 *Brachypogon* 69 *Parabezzia*

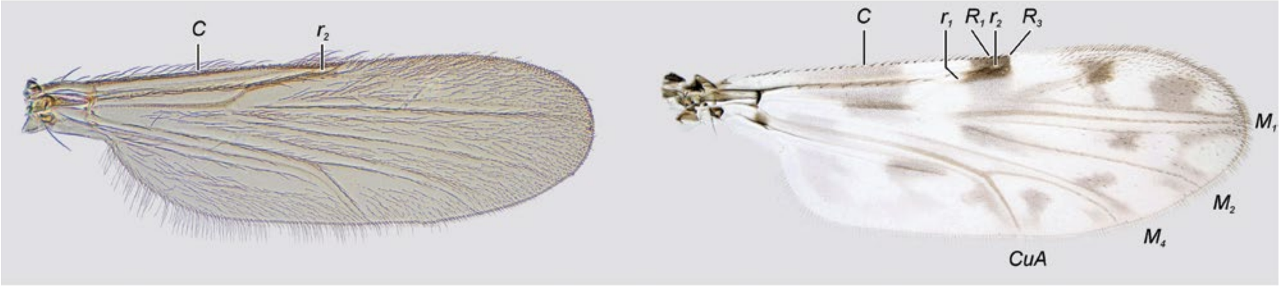
Figs 34.67–69. Thoraces of Ceratopogonidae (lateral views; all non-Afrotropical): (67) *Atrichopogon* sp. ♀; (68) *Brachypogon* sp. ♀; (69) *Parabezzia bystraki* Grogan & Wirth ♂. Fig. 67 (after Szadziewski *et al*. 1997, fig. 48), Fig. 68 (after Borkent 1992), Fig. 69 (after Borkent *et al*. 2009, fig. 29.55).

Abbreviations: a anepst – anterior anepisternum; anepst clft – anepisternal cleft; f cx – fore coxa; kepst – katepisternum; m cx – mid coxa; p anepst – posterior anepisternum; patg – paratergite; s – seta(e).

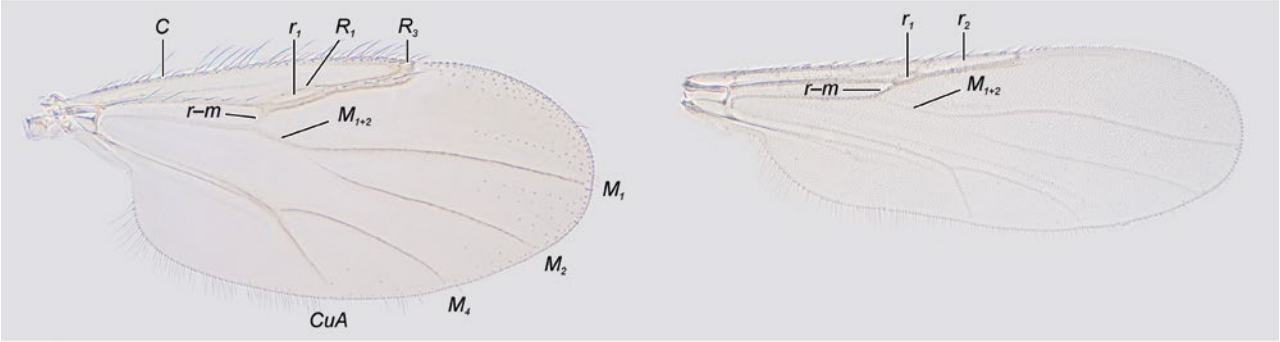


70 *Leptoconops* (*Holoconops*) ♂ 71 *Forcipomyia* (*Forcipomyia*) ♂

72 *Forcipomyia* (*Lasiohelea*) ♂ 73 *Atrichopogon* ♂



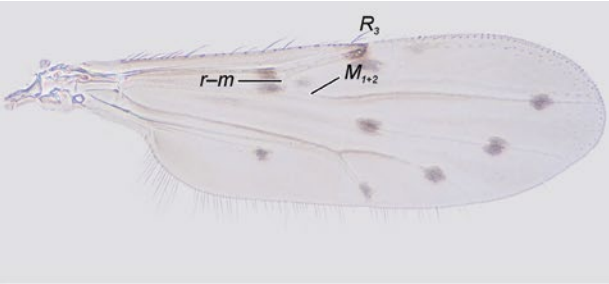
74 *Dasyhelea* ♂ 75 *Culicoides* ♂



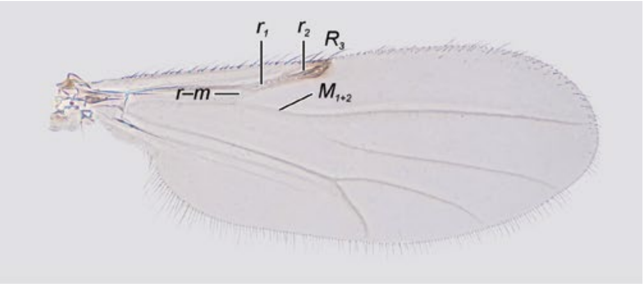
76 *Fanthamia* ♂ 77 *Schizonyxhelea* ♂

Figs 34.70–77. Wings of male Ceratopogonidae (dorsal views) (all non-Afrotropical, except Fig. 76): (70) *Leptoconops* (*Holoconops*) *catawbae* (Boesel); (71) *Forcipomyia* (*Forcipomyia*) *bipunctata* (L.); (72) *F.* (*Lasiohelea*) *fairfaxensis* Wirth; (73) *Atrichopogon downesi* Wirth; (74) *Dasyhelea flavifrons* (Guérin-Méneville); (75) *Culicoides occidentalis* Wirth & Jones; (76) *Fanthamia draconis* de Meillon & Downes; (77) *Schizonyxhelea bulla* (Thomsen).

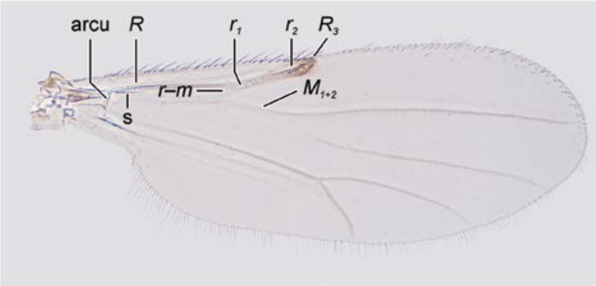
Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_{1+2+3} – fused first and second branch of radius; r_2 – second radial cell; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.



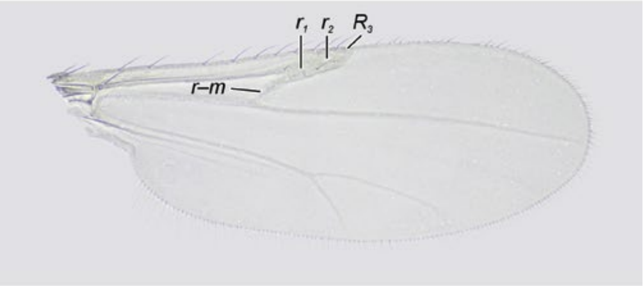
78 *Alluaudomyia* ♂



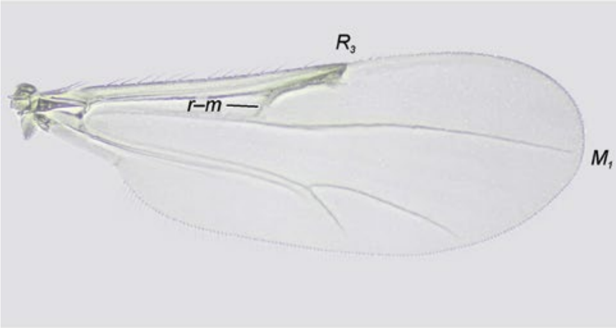
79 *Alluaudomyia* ♂



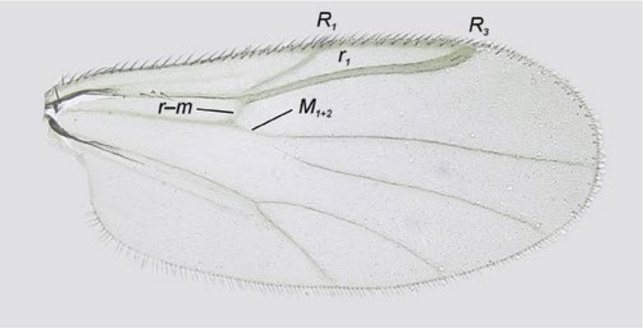
80 *Alluaudomyia* ♂



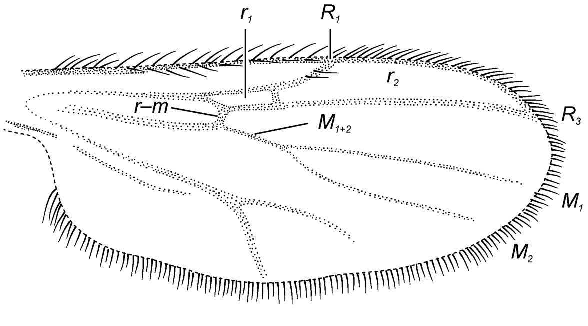
81 *Brachypogon* (*Isohelea*) ♂



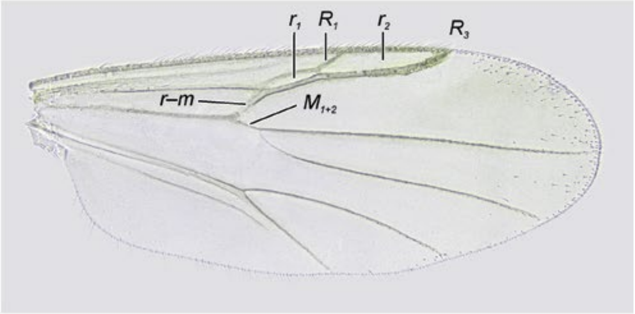
82 *Brachypogon* (*Brachypogon*) ♂



83 *Afrohelea* ♂



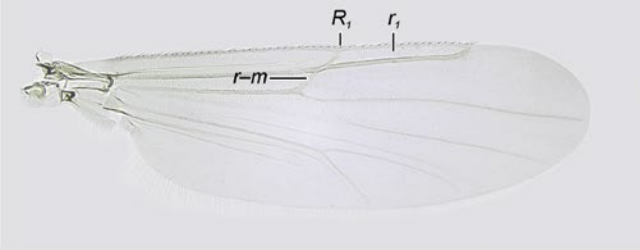
84 *Luciamyia* ♂



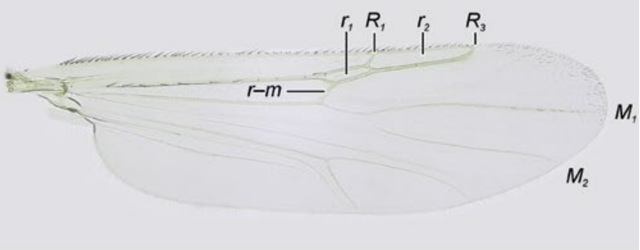
85 Undescribed genus ♂

Figs 34.78–85. Wings of male Ceratopogonidae (dorsal views): (78) *Alluaudomyia bella* (Coquillett) (non-Afrotropical); (79) *A. parva* Wirth (non-Afrotropical); (80) *Alluaudomyia* sp.; (81) *Brachypogon* (*Isohelea*) sp. (non-Afrotropical); (82) *B.* (*Brachypogon*) *canadensis* Downes (non-Afrotropical); (83) *Afrohelea capensis* (de Meillon & Hardy); (84) *Luciamyia biloba* de Meillon; (85) Undescribed genus. Fig. 84 (after Wirth & Grogan 1988, fig. 30e).

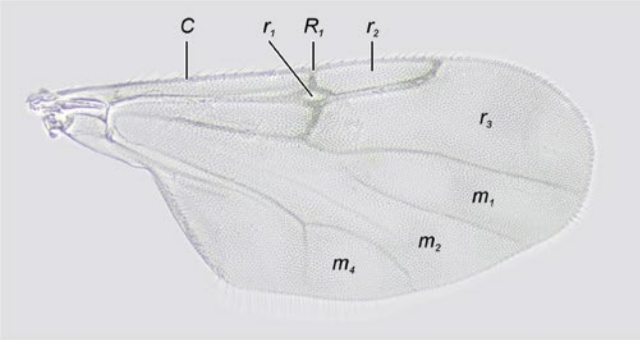
Abbreviations: arcu – arculus; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; *r–m* – radial–medial crossvein; s – seta.



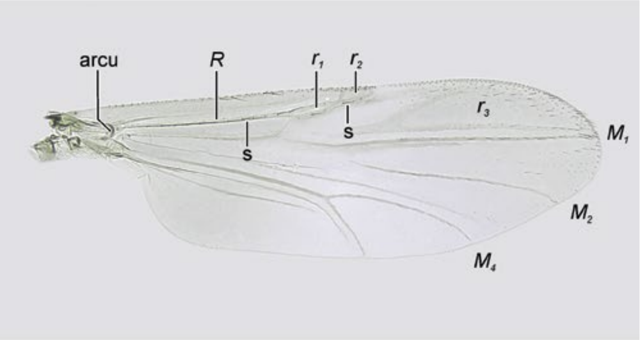
86 *Stilobezzia* (*Eukraiohelea*) ♂



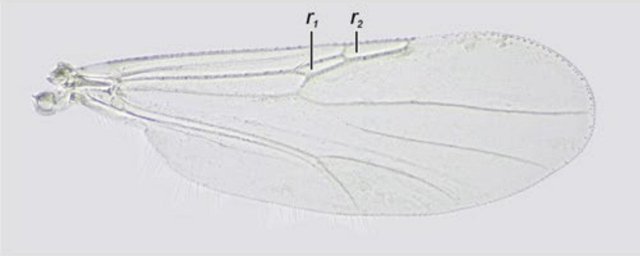
87 *Stilobezzia* (*Acanthohelea*) ♂



88 *Stiloculicoides* ♂

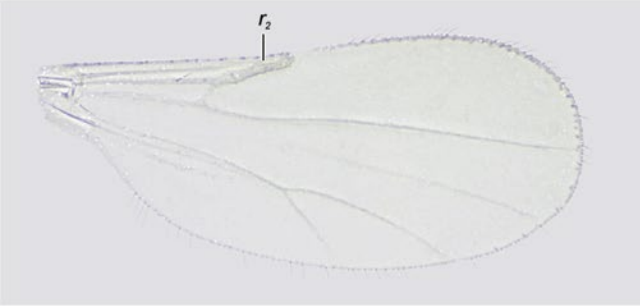


89 *Capehelea* ♂

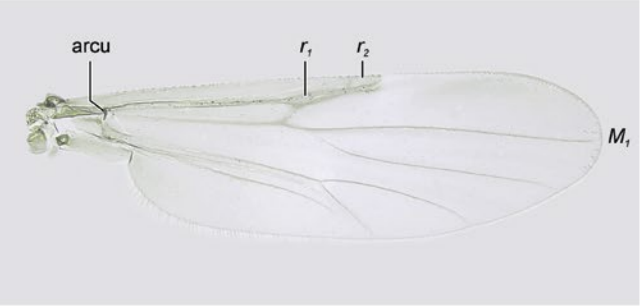


90 *Kolenohelea* ♂

91 *Bothahelea* ♂



92 *Notoceratopogon* ♂



93 *Ceratohelea* ♂

Figs 34.86–93. Wings of male Ceratopogonidae (dorsal views): (86) *Stilobezzia* (*Eukraiohelea*) *elegantula* (Johannsen) (non-Afrotropical); (87) *S.* (*Acanthohelea*) *lutea* (Malloch) (non-Afrotropical); (88) *Stiloculicoides africanus* Clastrier; (89) *Capehelea steli* de Meillon & Wirth; (90) *Kolenohelea monticola* de Meillon & Downes; (91) *Bothahelea phelpsi* Grogan & Wirth; (92) *Notoceratopogon minutus* de Meillon & Downes; (93) *Ceratohelea advena* (de Meillon).

Abbreviations: arcu – arculus; *C* – costal vein; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; m_4 – fourth medial cell; M_4 – fourth branch of media; *R* – radius, or radial vein; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein; s – seta.

of the genera *Brachypogon* Kieffer, *Ceratopogon* Meigen (endemic to the Holarctic), *Culicoides* and *Stilobezzia*. These taxa also have early roots in the Cretaceous, when angiosperms were evolving diverse flower structures (Borkent 1996, 2000*a*: 404). Representatives of these genera are often common on flowers, particularly those that are small, white or green. Some species, primarily those in *Dasyhelea* and *Forcipomyia*, with relatively hairy bodies, are important pollinators of some commercial trees, such as cacao (Dessart 1961, 1962; Kaufmann 1974, 1975*a*, *b*, *c, d*: 77; Wirth & Derron 1976), avocado (de Meillon & Wirth 1979a) and rubber (Warmke 1951, 1952; Wirth 1956*b*) (the last named not studied in the Afrotropics). Ollerton *et al*. (2009) demonstrated that *Forcipomyia* species are important pollinators of *Ceropegia* (Apocynaceae) in the Afrotropics and other species of Ceratopogonidae are likely to be pollinators of numerous other plants in the region, although further research is required to confirm this.

Comprehensive phylogenetic studies are still required, which would help provide a predictive framework to better interpret the biology of biting midges and their role as vectors. Although some applied scientists believe that it is sufficient to restrict studies to pest species, it is clear that an understanding of non-pest relatives provides important comparative information allowing for a better interpretation of virtually every feature of pest species. Phylogenetic studies, which interpret the genealogical relationships of all representatives of a given group, provide an important reference system to interpret the behaviour, population dynamics, phenology, vector capacity, host types and other characteristics of pest species. For example, understanding that vertebrate biters in the genera *Austroconops*, *Culicoides*, *Leptoconops* and *Forcipomyia* (*Lasiohelea*) are all early lineages within the family and that their biting habit is homologous to each other and to those of Simuliidae (blackflies) and Culicidae (mosquitoes), strongly suggests that many of their feeding strategies and behaviours are also homologous. In such instances, we can reasonably apply many of the conclusions of studies of one species to the others.

Economic significance

Biting midges are notorious as nasty biters, pestering humans and domestic animals and as vectors of harmful pathogens. Their economic impact in the Afrotropics has been and continues to be great. Meiswinkel *et al*. (2004*a*: 97) provided an excellent overview of *Culicoides*-borne diseases and their vectors, concentrated on South Africa and Borkent (2004: 114) and Purse *et al*. (2015) gave a global perspective, including the Afrotropical Region, of the main viral diseases noted here, while Wirth *et al*. (1980: 150) provided a summary of earlier pertinent studies. Females of species of *Leptoconops* and *F*. (*Lasiohelea*) are not known to vector any organisms in the Afrotropical Region.

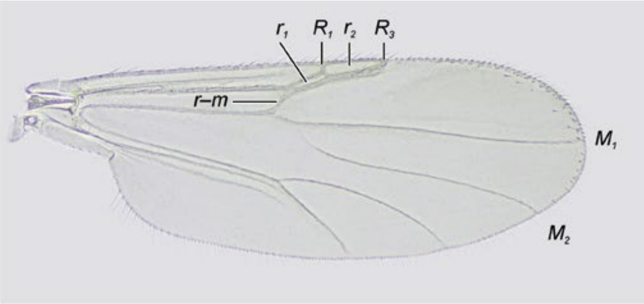
Due to their small size, many Ceratopogonidae species are able to pass through window screens and mesh that normally prevent the entry of biting flies and these can make life insufferable in many areas. Some species occur in such high concentrations that outdoor activities become intolerable and livestock are traumatised (Khamala 1975; White 1977). Their bite, both in terms of pain and the resulting welt, often seems entirely out of proportion to their small size.

Globally, various species of *Culicoides*, *Forcipomyia* (*Lasiohelea*) and *Leptoconops* are vectors of 76 viruses, 35 protozoa and 27 species of nematodes (Borkent 2004: 114, with some modifications), of which 26 viruses, two protozoa and nine nematodes occur in the Afrotropical Region. Nearly all of these organisms are vectored by species of *Culicoides*, with limited evidence of *Leptoconops* vectoring nematodes and *Forcipomyia* (*Lasiohelea*) vectoring three viruses, *Leishmania* and two species of nematodes. It is worth noting that there are varying levels of evidence for these as vectors; finding a virus, for example, in a blood-sucking ceratopogonid species is not evidence that it is a vector. There is little doubt that there are many additional vertebrate diseases transmitted by biting midges, but critical information is lacking concerning most of these. There have been difficulties in establishing captive breeding colonies of some species (only one species in the Afrotropics; Walker & Davies (1971)) and their small size and nocturnal behaviour have limited some aspects of field studies.

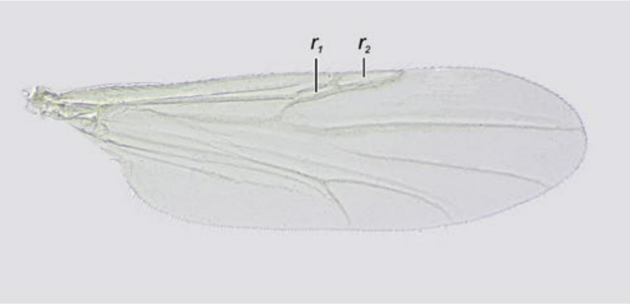
As pests of humans, large numbers of adult female *Culicoides* have been recorded in West Africa, as well as Angola, Ethiopia, Kenya, South Sudan and Sudan (Austen 1909, 1912; Carter *et al*. 1920*a*; Khamala 1975; Nicholas 1953; White 1977), although even at low concentrations midges may be irritating. At least one species of *Leptoconops* is a serious pest as a diurnal feeder on marine beaches (Laurence & Mathias 1972). Species of *Forcipomyia* (*Lasiohelea*) do not appear to be as seriously troublesome to humans anywhere in the Afrotropics. Elsewhere in the world, adult female *Culicoides* afflicting humans in large numbers can have a severe impact on forestry, dam building, tourism and other outdoor activities (Hendry 2011: 1; Linley & Davies 1971), but these effects have not been studied in the Afrotropics. Vast numbers of female *Culicoides* may afflict domesticated animals with, for example, over a million females (mostly of *C. imicola*, a vector of Bluetongue virus), sampled with a light trap in one night, deployed near a group of horses in South Africa (Meiswinkel *et al*. 2004*a*: fig. 5:21).

In some areas outside of the Afrotropical Region, large numbers of biting female *Culicoides* can cause a seasonally recurrent dermatitis in horses, cattle and sheep (resulting from an allergic reaction to midge bites), termed “sweet itch” or hypersensitivity (Schaffartzik *et al*. 2012). Although not yet reported from the Afrotropics, such conditions probably also occur in the region (Meiswinkel *et al*. 2004*a*: 98).

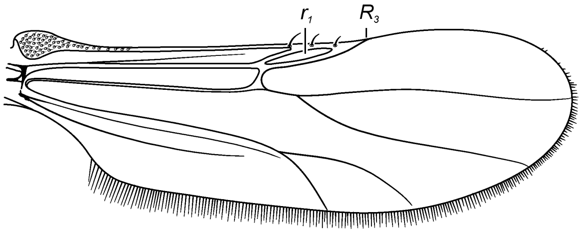
Of the many viruses, protozoa and nematodes vectored by species of Ceratopogonidae globally, humans in the Afrotropics are impacted directly by only three filarial nematode parasites, which are transmitted by species of *Culicoides*. Of these *Mansonella perstans* (Manson) is the most prevalent, having been reported from 33 countries in the Afrotropical Region, often with very high infection rates (frequently over 90%), especially in children (Noireau *et al*. 1990; Simonsen *et al*. 2011, 2014: 738; Uttah *et al*. 2011). It is one of the most poorly understood of tropical diseases, largely because it primarily affects poor rural populations, with no apparent symptoms (only in adults following initial exposure). Primary vectors have been identified as *C. austeni* Carter, Ingram & Macfie, 1920, *C. fulvithorax* (Austen, 1912), *C. grahamii* Austen, 1909 and *C. inornatipennis* Carter, Ingram & Macfie, 1920. In a molecular examination of potential vectors in Senegal, however, Bassene *et al*. (2015) cast doubt on *Culicoides* being vectors of nematodes.



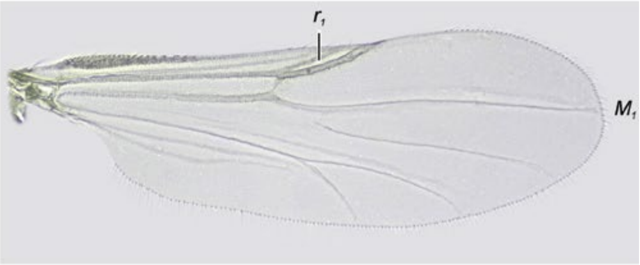
94 *Ankylohelea* ♂



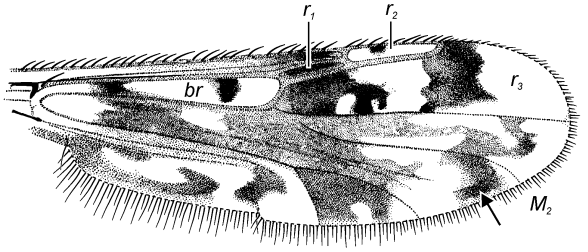
95 *Neohelea* ♂



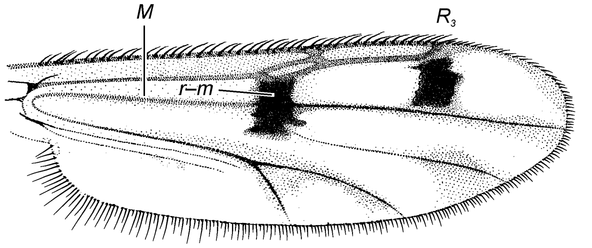
96 *Parabezzia* ♂



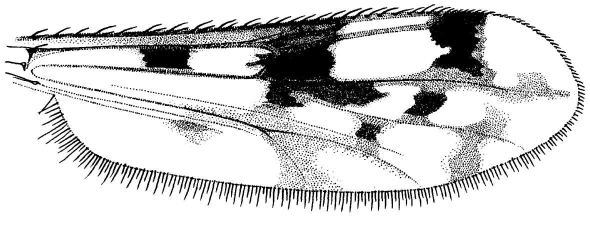
97 *Parabezzia* ♂



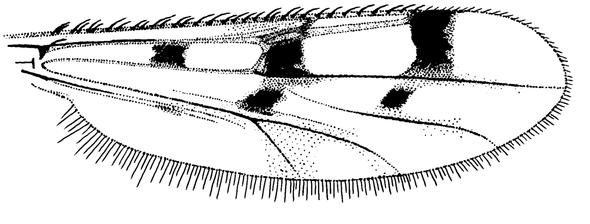
98 *Monohelea* ♂



99 *Downeshelea* ♂



100 *Allohelea* ♂

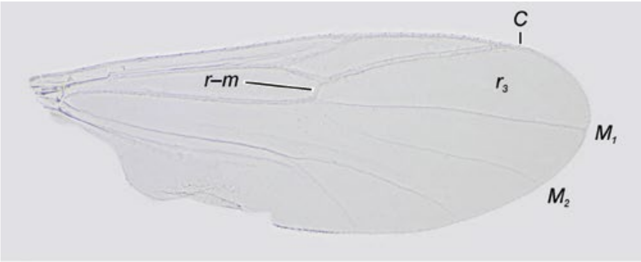


101 *Allohelea* ♂

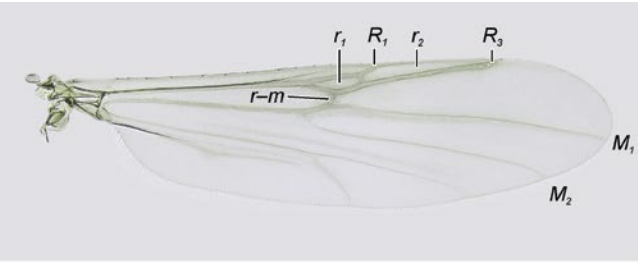
Figs 34.94–101. Wings of male Ceratopogonidae (dorsal views): (94) *Ankylohelea montana* de Meillon & Wirth; (95) *Neohelea pastoriana* Clastrier; (96) *Parabezzia falcipennis* Clastrier; (97) *Parabezzia* sp. (non-Afrotropical); (98) *Monohelea pallida* Clastrier & Delécolle (S-shaped pigmentation patch arrowed); (99) *Downeshelea bimaculata* Clastrier & Delécolle; (100) *Allohelea afra* Clastrier & Delécolle; (101) *A. paucimaculata* Clastrier & Delécolle. Fig. 96 (after Clastrier 1960*b*, fig. 25), Figs 98–101 (after Clastrier & Delécolle 1990, figs 15A, 13A, 1B, 6A, respectively).

Abbreviations: *br* – basal radial cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein.

The other two species of nematodes, *Mansonella rodhaini* (Peel & Chardome) and *M. streptocerca* (Macfie & Corson) are of lesser importance and are more restricted geographically (Fisher *et al*. 1997; Richard-Lenoble *et al*. 1988). There is evidence that *M. rodhaini* primarily infects chimpanzees. Other filaria nematodes vectored by species of Ceratopogonidae are recorded from bovines, equines, various primates and amphibians (frogs) (Borkent 2004: 114).

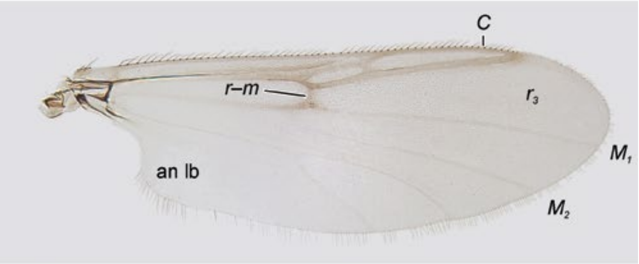


102 *Neurobezzia* ♂

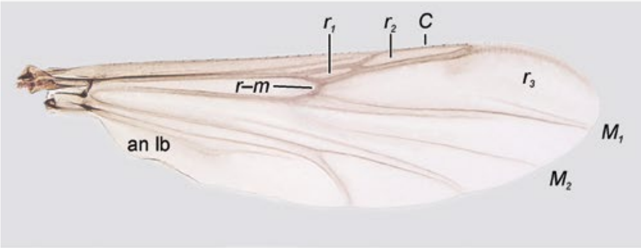


103 *Clinohelea* (*Clinohelea*) ♂

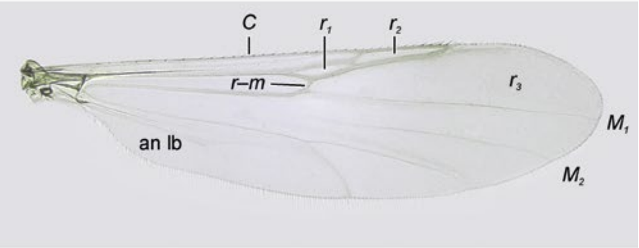
104 *Tetrahelea* ♂



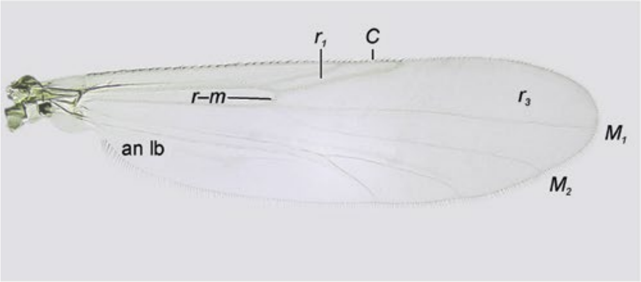
105 *Jenkinshelea* ♂



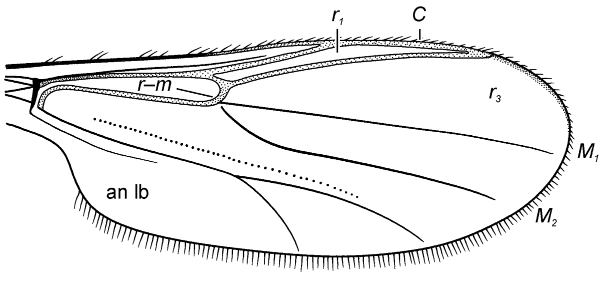
106 *Dibezzia* ♂



107 *Palpomyia* ♂



108 *Bezzia* ♂



109 *Bezzia* ♂

Figs 34.102–109. Wings of male Ceratopogonidae (dorsal views) (all non-Afrotropical, except Fig. 109): (102) *Neurobezzia granulosa* (Wirth); (103) *Clinohelea* (*Clinohelea*) *curriei* (Coquillett); (104) *Tetrahelea pictipennis* (Kieffer); (105) *Jenkinshelea albaria* (Coquillett); (106) *Dibezzia debenhamae* Wirth & Ratanaworabhan; (107) *Palpomyia altispina* Grogan & Wirth; (108) *Bezzia bivittata* (Coquillett); (109) *B. griseipes* Clastrier, Rioux & Descous. Fig. 109 (after Clastrier *et al*. 1961, fig. 26).

Abbreviations: an lb – anal lobe; *C* – costal vein; *M_1* – first branch of media; *M_2* – second branch of media; *R_1* – anterior branch of radius; *r_1* – first radial cell; *r_2* – second radial cell; *R_3* – lower branch of second branch of radius; *r_3* – third radial cell; *r–m* – radial–medial crossvein.

The impact on domestic animals of various pathogens vectored by species of *Culicoides* is immense (see Chapter 5). There are five primary and several minor viruses of primary importance (as discussed below).

Bluetongue virus (BT) is a viral disease of cattle, sheep, goats, camelids and wild ruminants. It is particularly damaging in sheep, where up to half of infected animals may die. In cattle and goats the disease primarily affects the animal's reproductive ability. Bluetongue virus is virtually cosmopolitan, with different unrelated vectors in various regions of the world. In the Afrotropical Region the primary vectors are the widely distributed *C. imicola* (also present in southern Europe and the Oriental Region) and *C. bolitinos* (restricted to the Afrotropical Region) (Meiswinkel *et al*. 2004*a*: 99; Venter 2015), although a number of other species may also play a role (Wirth & Dyce 1985: 151). A valuable review of this disease in South Africa was provided by Coetzee *et al*. (2012). Considering the rapid northward expansion of BT into Europe with the acquisition of new vectors in that region (Carpenter *et al*. 2009), it is increasingly imperative that the disease, its vectors and its distribution be better understood in the Afrotropics. In some sub-Saharan countries, BT appears to be benign and at least some indigenous ruminant breeds appear to have achieved a balance with the virus (unlike ruminant breeds from elsewhere, which develop severe symptoms).

African Horse Sickness (AHS) is a miserable disease of horses with often devastating impacts and mortality rates up to 90% for infected animals (Zientara *et al*. 2015). In 1959–1960, a near and mid-east epidemic killed 300,000 horses and in 1854–1855 this disease claimed 40% of the horses of the Cape of Good Hope colony in just eight months, with 70,000 deaths. The disease continues to be a threat to African and southern European equids, although various treatments, including vaccinations, are available. Nevertheless, the disease continues to have an immense impact in the Afrotropics (Aklilu *et al*. 2014; Diouf *et al*. 2013). For example, more than 1,500 horses have died from AHS in South Africa since 2005 (Venter *et al*. 2014*b*) and 1,169 horses died in Senegal in 2007 alone (Fall *et al*. 2015*a*). The primary vectors of the disease are the widespread and abundant *C. imicola* and the more geographically restricted *C. bolitinos* (Meiswinkel & Paweska 2003). *Culicoides oxystoma* Kieffer, 1910 has been implicated as a vector in Senegal (Fall *et al*. 2015*b*). The disease also occurs in zebras and local donkeys without any apparent significant impact (elsewhere donkeys may be affected) (Hess 1988).

Akabane virus occurs in domestic ruminants and a wide variety of vertebrates and is widespread in the Afrotropics. It causes abortions and deformities in at least domestic animals (Al-Busaidy *et al*. 1987; Elhassan *et al*. 2014; Meiswinkel *et al*. 2004*a*: 98). The primary vector of Akabane virus is *C. imicola*.

Epizootic haemorrhagic disease (EHD) is another widely distributed infectious virus, transmitted by *Culicoides* species, that affects wild and domestic ruminants (Paweska *et al*. 2005; Savini *et al*. 2011). The disease can kill and other symptoms vary according to the host and area (in some Afrotropical countries its clinical symptoms are minimal). Within the Afrotropics several *Culicoides* species have been implicated as vectors (Paweska *et al*. 2005). Recent outbreaks have been reported for Réunion Is. (Cêtre-Sossah *et al*. 2014; Desvars *et al*. 2015).

Bovine ephemeral fever is a widely distributed disease that infects cattle and water buffalo and antibodies to the virus have been detected in various wild ruminants, hedgehogs, giant rats and possibly birds and humans in the Afrotropics (Blasdell *et al*. 2012). It can result in death, abortion and loss of milk production in cattle (Venter *et al*. 2003) and is primarily vectored in the Afrotropics by *C. imicola* and *C. coarctatus* Clastrier & Wirth, 1961.

There are 21 other viruses, two other protozoa and six nematodes recorded from various animals (mostly domestic), or which have been isolated from *Culicoides* females in the Afrotropics (Borkent 2004: 114), but their economic impact is uncertain. Without doubt there are many more vectored organisms yet to be discovered, especially among wild mammal and bird species.

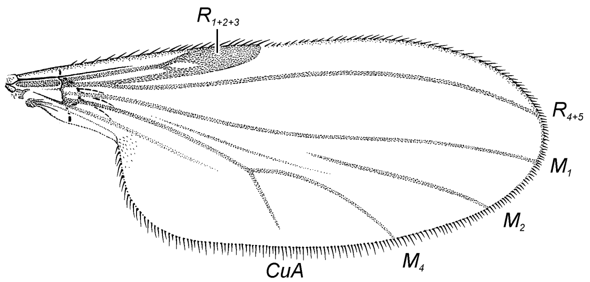
Seasonality of adult midges affects the incidence of disease outbreaks. Except in areas where some adults are active all year round, organisms transmitted by Ceratopogonidae must find a reservoir in resident hosts. In some areas, the disease must be re-introduced, either by dispersing, infected biting midges or by the introduction of infected hosts.

It is worth noting, that most species of vertebrate feeding biting midges are of no or little medical or veterinary significance. In reality, the natural hosts of the majority of species remain unknown (although structure of mouthparts indicates they feed on vertebrates). The true culprits, as biting pests and/or as vectors of diseases, are restricted to a few species. For example, of the 159 *Culicoides* species in the Afrotropical Region, only a few have been recorded as biting humans and of these, just six occur in large enough numbers to be considered serious pests of humans.

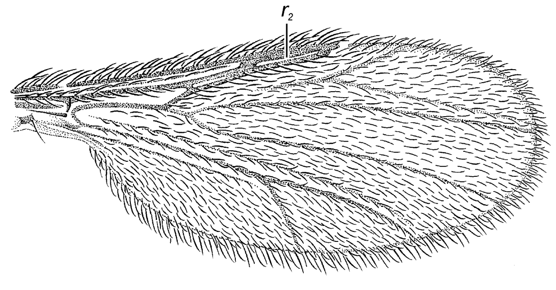
Classification

Ceratopogonidae are sister-group to Simuliidae + Thaumaleidae and all three form the superfamily Simulioidea (Borkent 2012). Globally there are 6,267 extant species of biting midges ascribed to 111 genera (Borkent 2016*a*). Extant Ceratopogonidae are divided into four subfamilies and these differ significantly from one another in all life stages (other than the egg). Overall, the phylogenetic relationships between the subfamilies, and some genera within these, are reasonably well established, but there remain significant sections, especially in the tribes Ceratopogonini, Heteromyiini, Johannsenomyiini, Sphaeromiini and Palpomyiini for which relationships between many genera remain uncertain (Borkent 1995: 86; 2000*a*: 388, 2014).

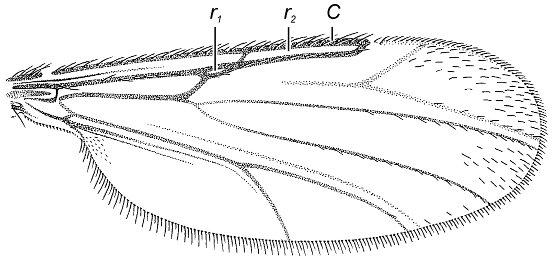
Leptoconopinae is sister-group to all remaining Ceratopogonidae and includes two genera: the highly modified *Leptoconops* with a global distribution (except Antarctica) and comprising 150 species; and the overall plesiomorphic relict genus *Austroconops*, with two species restricted to south-western Australia (Borkent & Craig 2004). Forcipomyiinae and Dasyheleinae are sister-groups and together form the sister-group of the fourth subfamily, Ceratopogoninae. Forcipomyiinae includes only two genera, *Atrichopogon* and *Forcipomyia*, but each of these is markedly diverse, with 527 and 1,154 species, respectively, both recorded from all zoogeographical regions other than Antarctica (Borkent 2016*a*). At least some representatives of



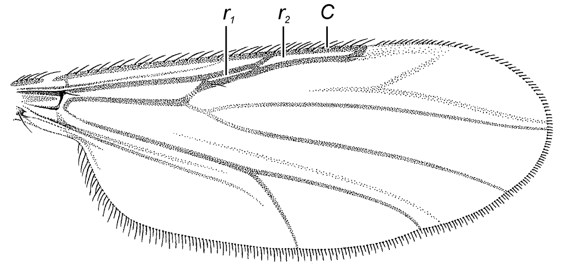
110 *Leptoconops* (*Holoconops*) ♀



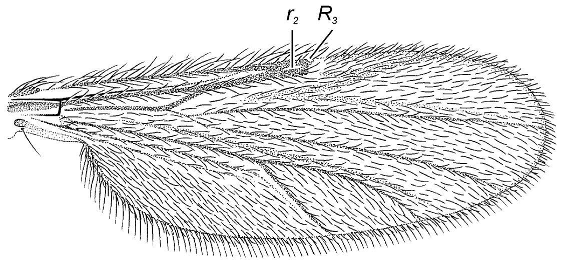
111 *Forcipomyia* (*Lasiohelea*) ♀



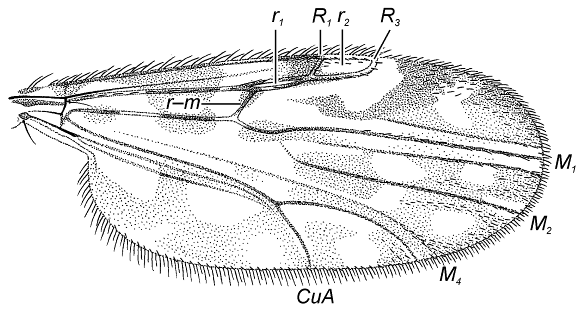
112 *Atrichopogon* ♀



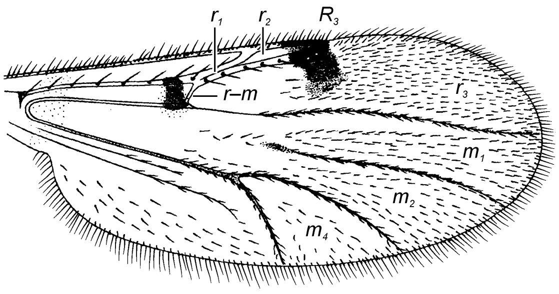
113 *Atrichopogon* ♀



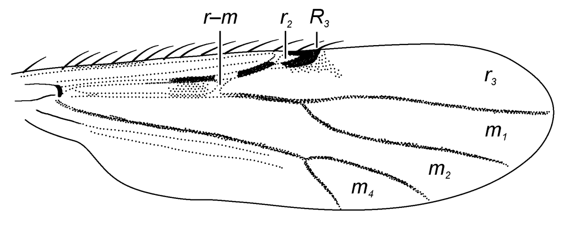
114 *Dasyhelea* ♀



115 *Culicoides* ♀



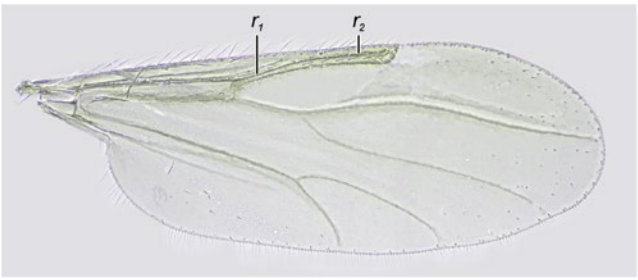
116 *Alluaudomyia* ♀



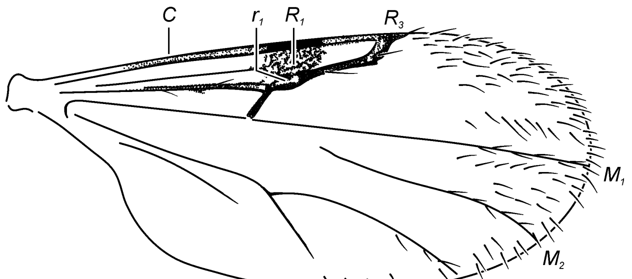
117 *Alluaudomyia* ♀

Figs 34.110–117. Wings of female Ceratopogonidae (dorsal views) (all non-Afrotropical, except Fig. 117): (110) *Leptoconops* (*Holoconops*) sp.; (111) *Forcipomyia* (*Lasiohelea*) *fairfaxensis* Wirth; (112) *Atrichopogon levis* (Coquillett); (113) *Atrichopogon* sp.; (114) *Dasyhelea pseudoincisurata* Waugh & Wirth; (115) *Culicoides insignis* Lutz; (116) *Alluaudomyia meridian* Clastrier; (117) *A. lunata* de Meillon & Wirth. Figs 110–115 (after Downes & Wirth 1981, figs 2, 17, 16, 18, 19, 21, respectively), Fig. 116 (after Clastrier 1978, fig. 1A), Fig. 117 (after de Meillon & Wirth 1983*a*, fig. 26).

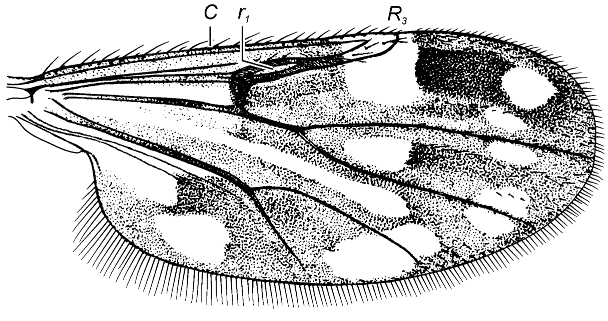
Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; R_1 – anterior branch of radius; r_1 – first radial cell; R_{1+2+3} – fused first and second branch of radius; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.



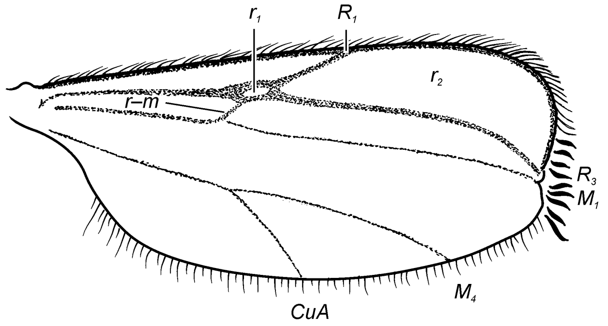
118 *Alluaudomyia* ♀



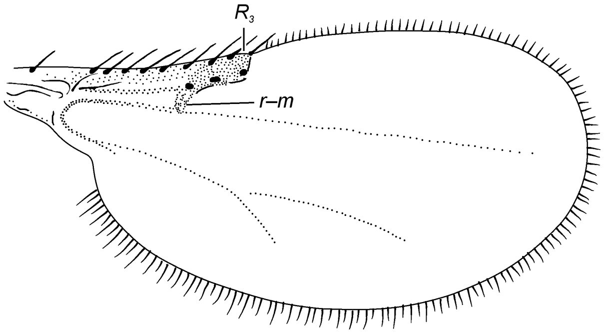
119 *Fanthamia* ♀



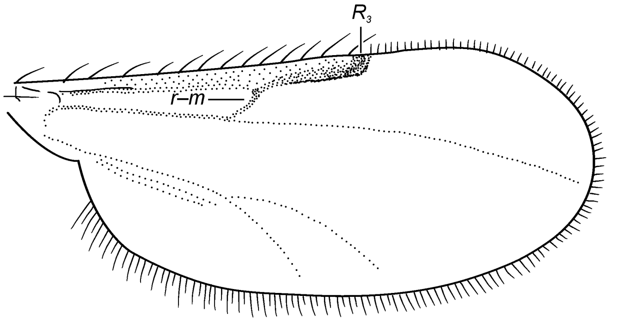
120 *Fanthamia* ♀



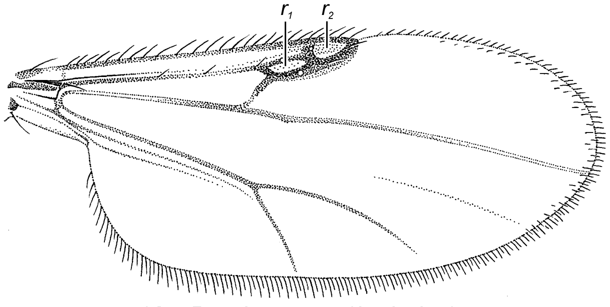
121 *Luciamyia* ♀



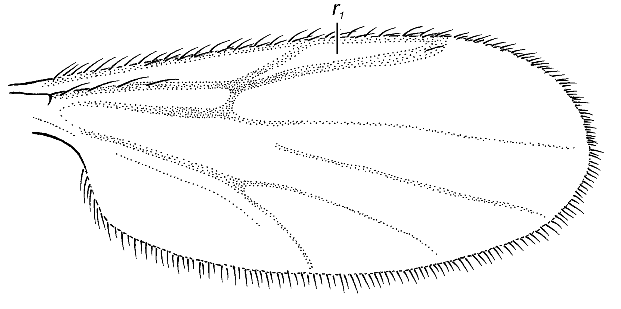
122 *Brachypogon* (*Brachypogon*) ♀



123 *Brachypogon* (*Brachypogon*) ♀



124 *Brachypogon* (*Isohelea*) ♀



125 *Afrohelea* ♀

Figs 34.118–125. Wings of female Ceratopogonidae (dorsal views): (118) *Alluaudomyia* sp.; (119) *Fanthamia adulator* (de Meillon); (120) *F. ornatipennis* (de Meillon); (121) *Luciamyia biloba* de Meillon; (122) *Brachypogon* (*Brachypogon*) *corneti* Grogan & de Meillon; (123) *B.* (*B.*) *corius* (de Meillon & Hardy); (124) *B.* (*Isohelea*) *stigmalis* (Coquillett) (non-Afrotropical); (125) *Afrohelea capensis* (de Meillon & Hardy). Figs 119, 120 (after de Meillon 1939c, figs 11d, 12a), Figs 121, 125 (after Wirth & Grogan 1988, figs 30d, 2e, respectively), Figs 122, 123 (after Grogan & de Meillon 1993, figs 4, 13), Fig. 124 (after Downes & Wirth 1981, fig. 24).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; *r–m* – radial–medial crossvein.

both genera are abundant and common in Malaise and light traps. *Forcipomyia*, on the one hand, includes 35 subgenera globally and, although many species remain undescribed, it has a solid taxonomic basis for further interpretation of the morphologically diverse adults, larvae and pupae. The classification of *Atrichopogon*, on the other hand, is largely unresolved for most of the world fauna, including the Afrotropics and most species cannot be identified with certainty. Dasyheleinae includes the single genus *Dasyhelea*, with 622 species globally (Borkent 2016*a*). Although some subgenera are recognised, these are difficult to apply on a world basis. The Ceratopogoninae includes the vast majority of genera in the family, with 106 genera and 3,812 species globally. The subfamily, with its characteristic and distinctive eel-like larva, is divided into eight tribes. The potentially paraphyletic Culicoidini is sister-group to all remaining Ceratopogoninae and includes three genera, namely *Culicoides*, *Paradasyhelea* Macfie and *Washingtonhelea* Wirth & Grogan. The last two genera are of minute midges of limited distribution and diversity. It is *Culicoides*, with 1,368 species globally, that is the best known and notorious genus in the family. This is further divided into 31 subgenera and 38 species-groups (these unplaced to subgenus). The remaining species, which make up 13% of the genus, are unplaced. There has been virtually no cladistic study of any of these and there remains a great need for comparative morphology and phylogenetic interpretation (Borkent 2016*b*). The Ceratopogonini includes many of the early lineages within the subfamily (other than Culicoidini) and is clearly paraphyletic in relation to the remaining tribes. For example, the Ceratopogonini genus *Echinohelea* Macfie is sister-group to Heteromyiini + Hebetulini + Johannsenomyiini + Sphaeromiini + Palpomyiini + Stenoxenini and a group of Ceratopogonini genera, including *Parabezzia* Malloch is sister-group to all these aforementioned taxa. The Heteromyiini includes seven genera, of which three occur in the Afrotropical Region, but there is a question of the monophyly of this tribe (Borkent 1998). Genera of Sphaeromiini *sensu lato* were recently divided into three tribes by Borkent (2014, 2015): Hebetulini, Johannsenomyiini and Sphaeromiini *sensu stricto*, with 1, 17 and 11 genera, respectively and with 1, 8 and 4 of these, respectively occurring in the Afrotropical Region. Hebetulini forms the sister-group of Johannsenomyiini + Sphaeromiini + Palpomyiini + Stenoxenini and Sphaeromiini is sister-group to Palpomyiini + Stenoxenini. The Palpomyiini with six genera has three of these in the Afrotropical Region, but is questionably monophyletic. Its sister-group, Stenoxenini, with two genera (one in the Afrotropics) is monophyletic.

Ceratopogonidae are notable in having a remarkable fossil record, with 283 species described in 45 genera (20 extinct) (Borkent 2016*a*), with many thousands of specimens present in over 17 major amber deposits, ranging from relatively young Dominican amber (15–20 MYA) to the oldest Lebanese amber (125–129 MYA) (Borkent 2000*a*: 355). In general, there is excellent congruence between the relative age of fossils and the current understanding of phylogenetic relationships: increasingly older fossils include only successively earlier lineages within the family. For example, the oldest extant lineage of Ceratopogonidae, including both genera of Leptoconopinae, *Austroconops* and *Leptoconops*, are the only extant genera of Diptera in 125–129 MYA Lebanese amber. The oldest fossil is represented by a compression fossil wing from England dated at 142 MYA (Borkent *et al*. 2013). There is an extinct subfamily, Lebanoculicoidinae, found only in Cretaceous deposits, which forms the sister-group to all other Ceratopogonidae, extant and extinct. Meunier (1912) described four species from Madagascan copal, but the specimens are lost and are of uncertain identity. Madagascan copal is mostly post-World War II (Penney & Preziosi 2010: 299), but may be as old as several hundreds of thousands of years.

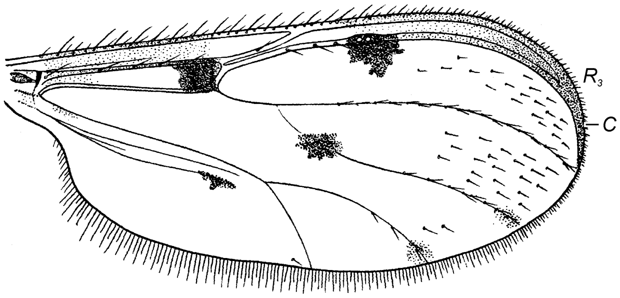
Although 6,267 species of extant Ceratopogonidae are now described, it would be reasonable to estimate that there are at least another 9,000 morphologically distinct species on Earth. Within the Afrotropical Region, with 928 described species, there are clearly many species remaining to be described and understood. Kirk-Spriggs & Stuckenberg (2009: 184) predicted that upwards of 69% of species occurring in the Afrotropics may be undescribed. Taxonomic studies are required for virtually all genera comprising more than a few species, including those of the vertebrate-feeding groups. Ceratopogonidae is the only family of biting flies for which distribution maps and an identification key to the Afrotropical species of the main biting groups does not exist; the best we have are identification keys to species of *Culicoides* occurring in a few areas (see "Synopsis of the fauna" section below).

Large tracts of the continental Afrotropics have only been superficially sampled, if at all. For example, most species were originally described from (in descending numbers) South Africa (246 species), Democratic Republic of Congo (119), Senegal (60), Guinea (59), Republic of Congo (49), Nigeria (44) and Zimbabwe (34). Most other sub-Saharan countries have had few if any species described from them (*e.g*., Niger (0), Botswana (0), Central African Republic (1), Zambia (2), Côte d'Ivoire (4), Malawi (8) and Gambia (10)). For most of these countries, the species described have been from one or a few collections and a concerted collecting effort is required throughout most of the Afrotropics.

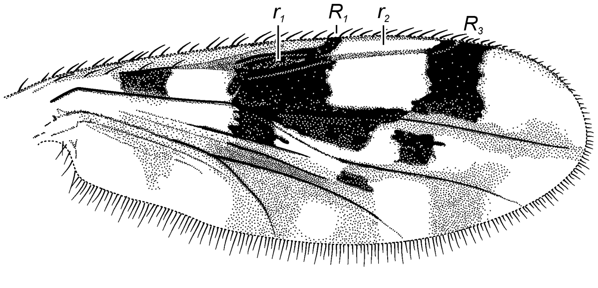
The above estimates of the number of undescribed species reflect our understanding of morphological species (species that can be distinguished using morphological characters alone). In the closely related families Chironomidae and Simuliidae it has been demonstrated that many species are distinguishable only through study of chromosomes and/or molecular investigation and it is almost a certainty that the same applies to Ceratopogonidae. Chromosome study will likely be highly limited within the Ceratopogonidae, as their polytene chromosomes (very broad chromosomes with distinct banding patterns) are poorly defined (Urbanek *et al*. 2013). Barcoding of species and other molecular techniques will clearly be an important tool for better understanding some species and has already been applied to some species of *Culicoides* from the Afrotropical Region including, for example, some very similar species of the *C. imicola* species complex (Meiswinkel & Linton 2003; Sebastiani *et al*. 2001) and those in the *C. schultzei* species-group (Augot *et al*. 2013; Bakhoum *et al*. 2013).

Identification

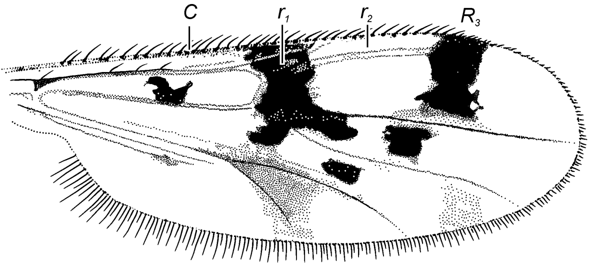
In an important publication on Afrotropical Ceratopogonidae, de Meillon & Wirth (1991) provided a generic identification key to the genera and subgenera of Ceratopogonidae of the region, based primarily on adult females. This provided



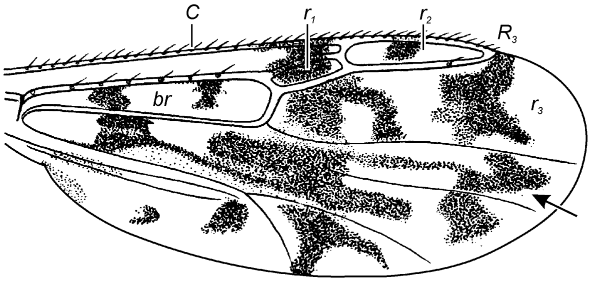
126 *Paralluaudomyia* ♀



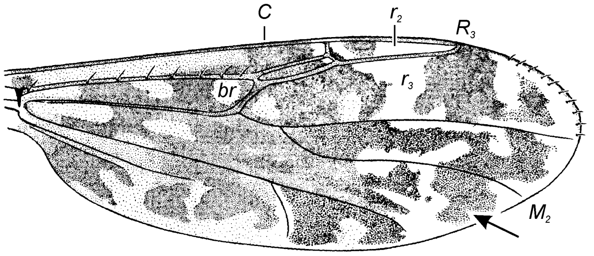
127 *Allohelea* ♀



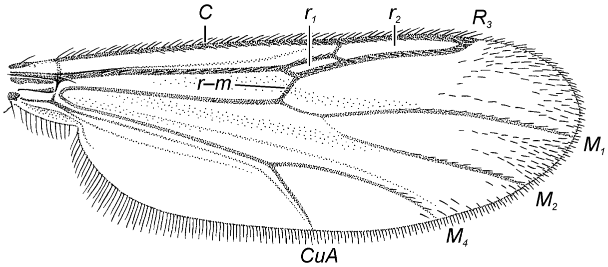
128 *Allohelea* ♀



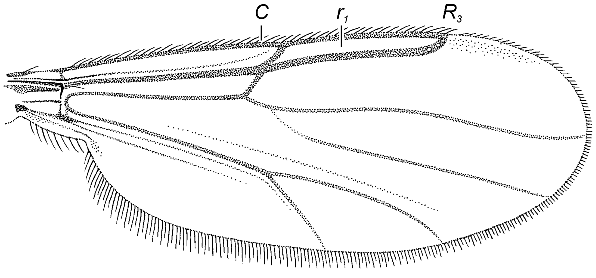
129 *Monohelea* ♀



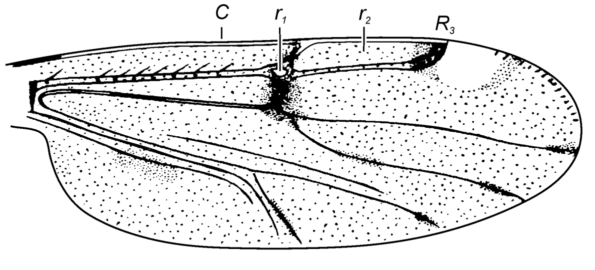
130 *Monohelea* ♀



131 *Stilobezzia* (*Acanthohelea*) ♀



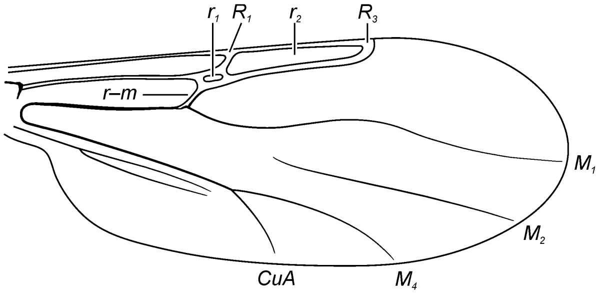
132 *Stilobezzia* (*Eukraiohelea*) ♀



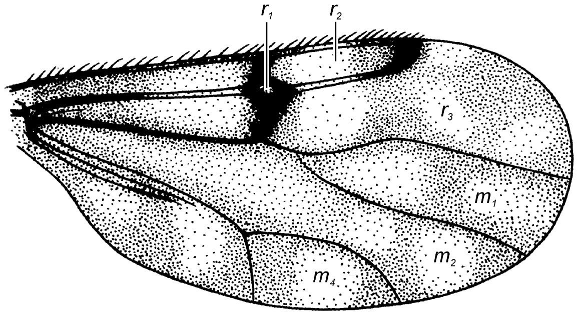
133 *Stilobezzia* (*Stilobezzia*) ♀

Figs 34.126–133. Wings of female Ceratopogonidae (dorsal views): (126) *Paralluaudomyia maculata* Clastrier; (127) *Allohelea afra* Clastrier & Delécolle; (128) *A. guineensis* Clastrier & Delécolle; (129) *Monohelea chalybeata* Clastrier (S-shaped pigmentation patch arrowed); (130) *M. legrandi* Clastrier (S-shaped pigmentation patch arrowed); (131) *Stilobezzia* (*Acanthohelea*) *lutea* (Malloch) (non-Afrotropical); (132) *S.* (*Eukraiohelea*) *elegantula* (Johannsen) (non-Afrotropical); (133) *S.* (*Stilobezzia*) *paucimaculata* Clastrier. Figs 126, 129 (after Clastrier 1960*b*, figs 10, 20), Figs 127, 128 (after Clastrier & Delécolle 1990, figs 3A, 5A), Fig. 130 (Clastrier 1984*a*, fig. 1), Figs 131, 132 (Downes & Wirth 1981, figs 30, 29, respectively), Fig. 133 (after Clastrier 1984*d*, fig. 2A).

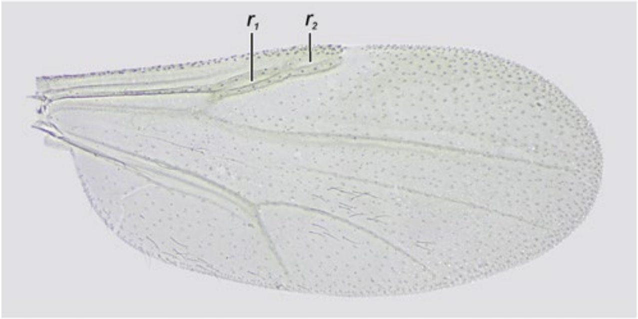
Abbreviations: *br* – basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein.



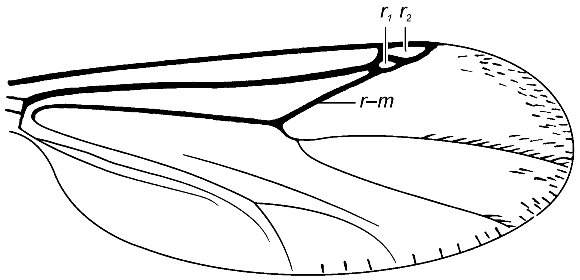
134 *Schizonyxhelea* ♀



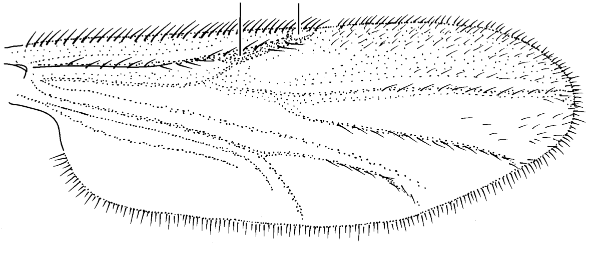
135 *Stiloculicoides* ♀



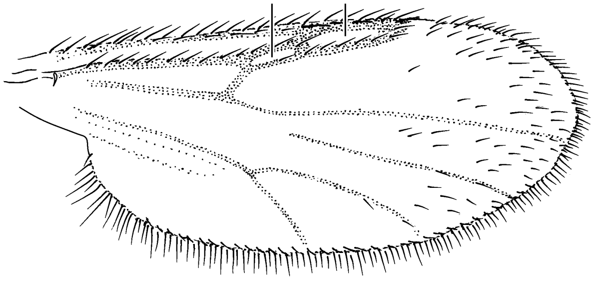
136 *Bothamia* ♀



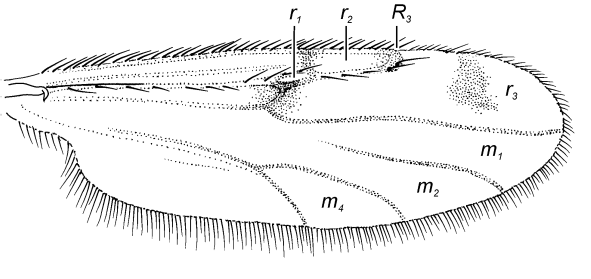
137 *Stilobezzia* (*Acanthohelea*) ♀



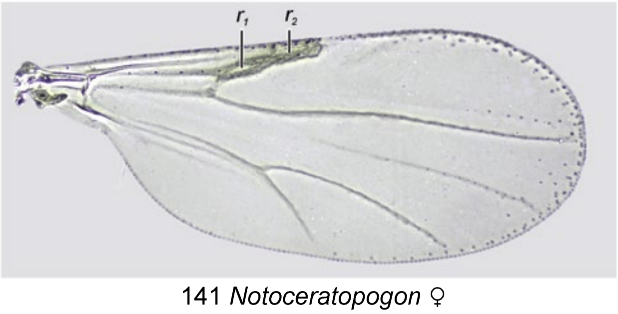
138 *Capehelea* ♀



139 *Kolenohelea* ♀



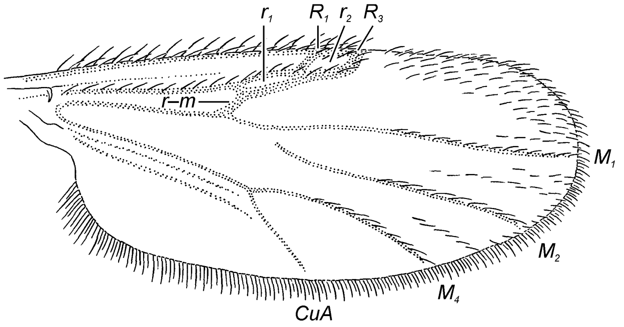
140 *Kolenohelea* ♀



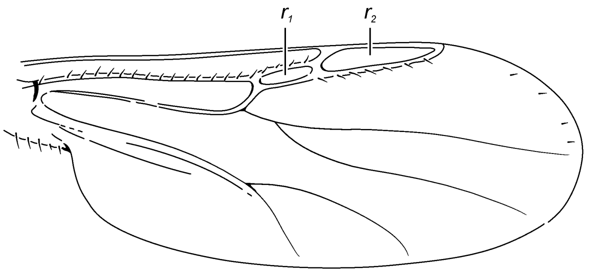
141 *Notoceratopogon* ♀

Figs 34.134–141. Wings of female Ceratopogonidae (dorsal views): (134) *Schizonyxhelea afra* (Clastrier); (135) *Stiloculicoides congoensis* Clastrier; (136) *Bothamia demeilloni* Meiswinkel; (137) *Stilobezzia* (*Acanthohelea*) *singularis* (Clastrier); (138) *Capehelea steli* de Meillon & Wirth; (139) *Kolenohelea dycei* de Meillon & Wirth; (140) *K. luciae* de Meillon & Wirth; (141) *Notoceratopogon vockerothi* de Meillon & Downes. Fig. 134 (after Clastrier 1991, fig. 1), Fig. 135 (Clastrier 1993, fig. 12), Fig. 136 (Meiswinkel 1987, fig. 2), Fig. 137 (after Clastrier 1985 fig. 35), Fig. 138 (Wirth & Grogan 1988, fig. 15g), Fig. 139 (de Meillon & Wirth 1981*a*, fig. 11), Fig. 140 (de Meillon & Wirth 1983*a*, fig. 41).

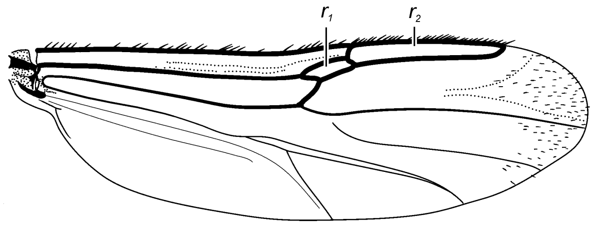
Abbreviations: *CuA* – anterior branch of cubital vein; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein.



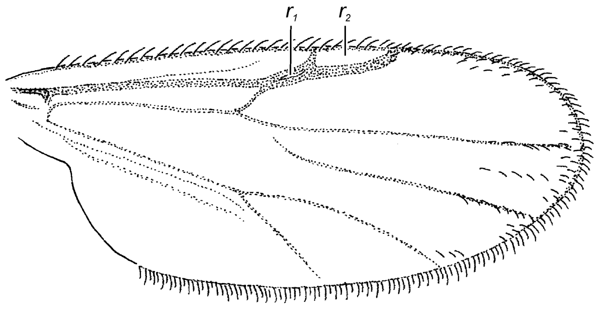
142 *Ceratohelea* ♀



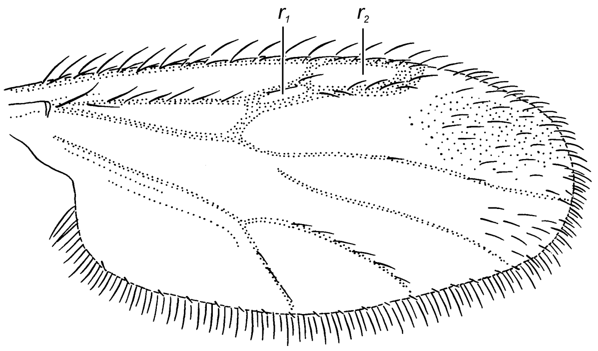
143 *Neohelea* ♀



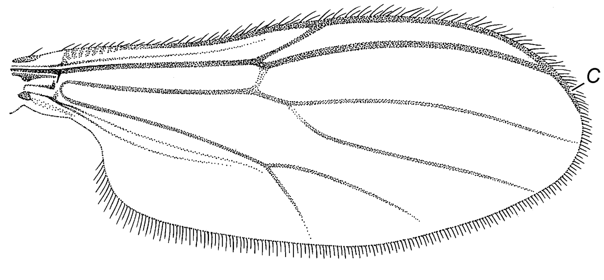
144 *Afrostilobezzia* ♀



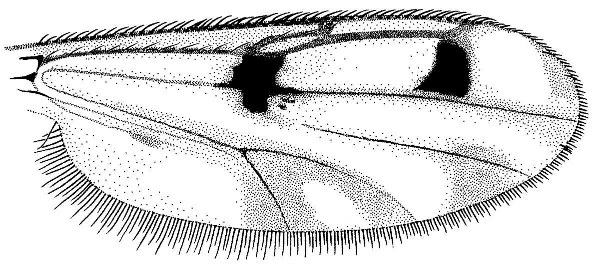
145 *Ankylohelea* ♀



146 *Calcarhelea* ♀



147 *Parabezzia* ♀

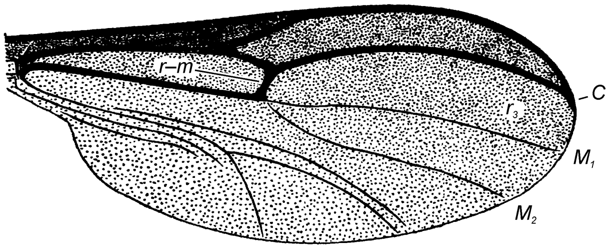


148 *Downeshelea* ♀

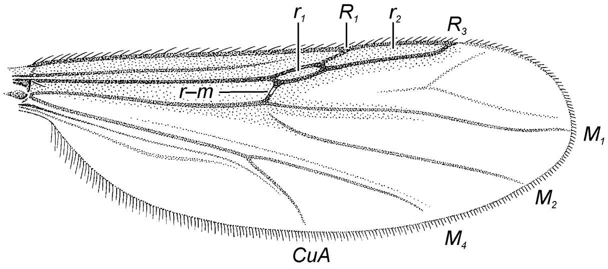
149 *Bothahelea* ♀

Figs 34.142–149. Wings of female Ceratopogonidae (dorsal views): (142) *Ceratohelea advena* (de Meillon); (143) *Neohelea pastoriana* Clastrier; (144) *Afrostilobezzia clastrieri* Szadziewski & Dominiak; (145) *Ankylohelea montana* de Meillon & Wirth; (146) *Calcarhelea bimater* (de Meillon & Hardy); (147) *Parabezzia eupetiolata* Grogan & Wirth (non-Afrotropical); (148) *Downeshelea bimaculata* Clastrier & Delécolle; (149) *Bothahelea phelpsi* Grogan & Wirth. Figs 142, 145, 146, 149 (after Wirth & Grogan 1988, figs 17e, 5d, 13b, 9b, respectively), Fig. 143 (after Clastrier 1988a, fig. 1A), Fig. 144 (after Szadziewski & Dominiak 2015, fig. 1a), Fig. 147 (Downes & Wirth 1981, fig. 31), Fig. 148 (after Clastrier & Delécolle 1990, fig. 14A).

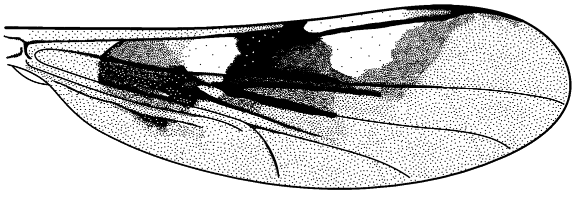
Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; *r–m* – radial–medial crossvein.



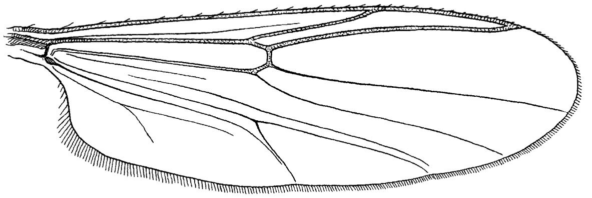
150 *Neurobezzia* ♀



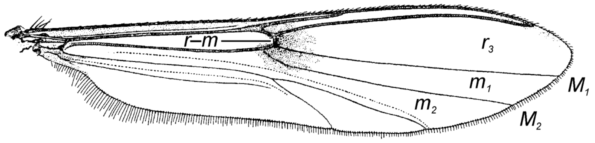
151 *Echinohelea* (*Echinohelea*) ♀



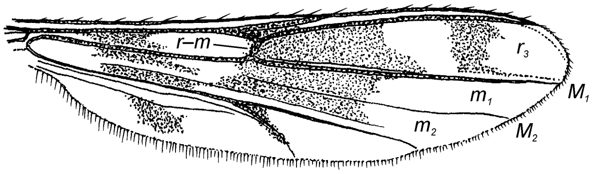
152 *Clinohelea* (*Clinohelea*) ♀



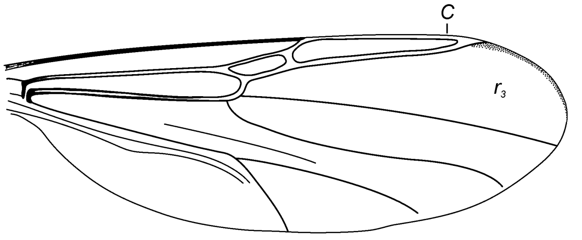
153 *Pellucidomyia* ♀



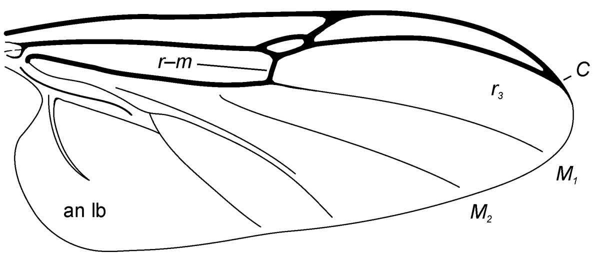
154 *Tetrabezzia* ♀



155 *Tetrabezzia* ♀



156 *Hebetula* ♀



157 *Jenkinshelea* ♀

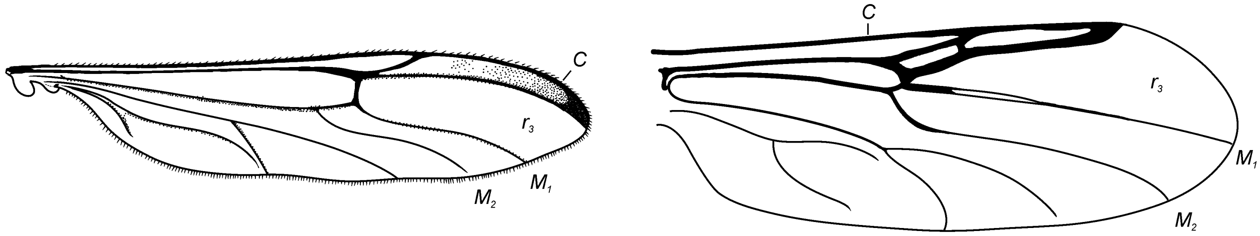
Figs 34.150–157. Wings of female Ceratopogonidae (dorsal views): (150) *Neurobezzia tsacasi* Clastrier; (151) *Echinohelea* (*Echinohelea*) *lanei* Wirth (non-Afrotropical); (152) *Clinohelea* (*Clinohelea*) *trimaculata* Clastrier; (153) *Pellucidomyia ugandae* Macfie; (154) *Tetrabezzia argentea* Ingram & Macfie; (155) *T. pictipennis* (Kieffer) (non-Afrotropical); (156) *Hebetula hexacantha* (Kieffer); (157) *Jenkinshelea djalonensis* Clastrier. Figs 150, 156 (after Clastrier 1983*c*, figs 29F, 27F, respectively), Fig. 151 (Downes & Wirth 1981, fig. 28), Fig. 152 (after Clastrier 1983*b*, fig. 13), Fig. 153 (Macfie 1939*b*, fig. 10), Fig. 154 (Ingram & Macfie 1923, fig. 25), Fig. 155 (de Meillon & Wirth 1991, fig. 320), Fig. 157 (after Clastrier 1983*a*, fig. 1A).

Abbreviations: an lb – anal lobe; *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein.

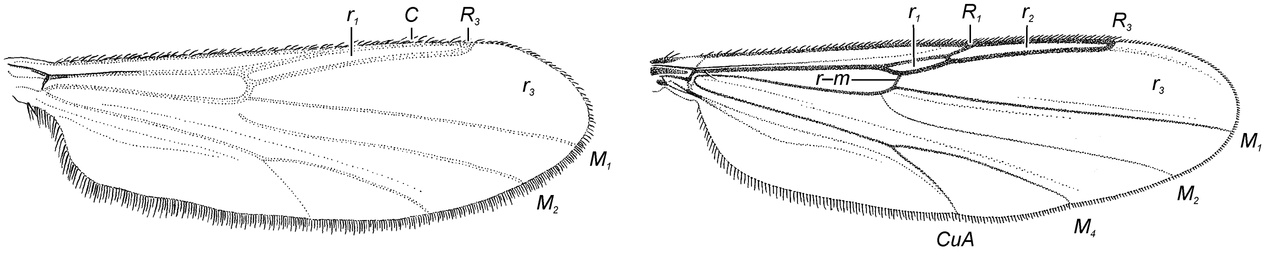
a working backbone for this contribution, although the identification key below includes males and was otherwise highly modified. De Meillon & Wirth (1991) otherwise included a diagnosis of each genus and subgenus (other than *Culicoides*), a synopsis of the immature stages and biology and a list of the included species (sometimes only as modifications to the *Catalogue of the Diptera of the Afrotropical Region* (Wirth *et al*. 1980: 150)). Another important resource is the identification key to and synopsis of the Ceratopogonini of the world by Wirth & Grogan (1988), which included numerous genera that occur in the Afrotropics. The diverse fauna of Seychelles, with species in 14 genera, was described by Clastrier (1983*c*) and Wirth *et al*. (1980: 150) provided a brief, but valuable synopsis of earlier taxonomic work.

The following identification key to adults of genera known from the Afrotropical Region includes males of genera for the first time. The males of *Afrostilobezzia* Szadziewski & Dominiak, *Congohelea* Wirth & Grogan, *Paralluaudomyia* Clastrier and *Xenohelea* Kieffer remain unknown. In preparation of the new identification key provided here, all included genera were examined first-hand (both males and females, if known), other than the male of *Bothamia* Meiswinkel, the male and female of *Luciamyia* de Meillon and females of *Afrostilobezzia* and *Metacanthohelea* Wirth & Grogan.

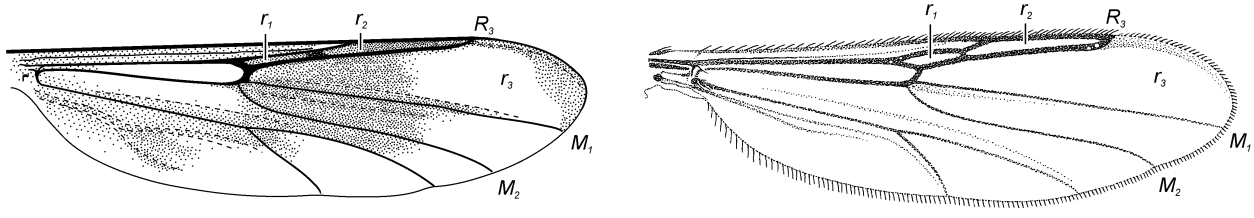
The male of the monotypic genus *Calcarhelea* Wirth & Grogan is known, but the single specimen is lost (M. Coetzee, pers. comm. 2016) and as a number of its features are uncertain, it could not be included in the below key. Based on what is known, it will key only to couplet 19, because although it has a feminised antenna, it is uncertain whether this includes the feminisation of the scape and pedicel (as in Figs 44, 55). If the scape and pedicel are not feminised (which is most likely), then the male would key to couplet 31. The male terminalia of the genus is illustrated here (Fig. 264) and readers can compare



158 *Macropeza* ♀ 159 *Mackerrasomyia* ♀



160 *Nilobezzia* ♀ 161 *Mallochohelea* ♀



162 *Sphaeromias* ♀ 163 *Palpomyia* ♀

Figs 34.158–163. Wings of female Ceratopogonidae (dorsal views): (158) *Macropeza nigra* (Séguy); (159) *Mackerrasomyia zumpti* de Meillon & Wirth; (160) *Nilobezzia yasumatsui* Wirth & Ratanaworabhan (non-Afrotropical); (161) *Mallochohelea smithi* (Lewis) (non-Afrotropical); (162) *Sphaeromias pistiae* (Ingram & Macfie); (163) *Palpomyia plebeja* (Loew) (non-Afrotropical). Fig. 158 (after Séguy 1931, fig. 647), Fig. 159 (after de Meillon & Wirth 1979*c*, fig. 1), Fig. 160 (Wirth & Ratanaworabhan 1981*b*, fig. 2), Figs 161, 163 (Downes & Wirth 1981, figs 43, 40), Fig. 162 (after Ingram & Macfie 1922, fig. 20).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; r_2 – second radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; *r–m* – radial–medial crossvein.

this to any South African specimens which have a wing length of *ca* 1.5 mm, a wing venation similar to that of the female (Fig. 146), but with the costal ratio (length of wing measured from arculus/length of costa (C) measured from arculus) = 0.77 and fewer macrotrichiae and densely spiculose eyes. Furthermore, it is somewhat uncertain whether the male is correctly associated with the holotype female (Wirth & Grogan 1988: 35).

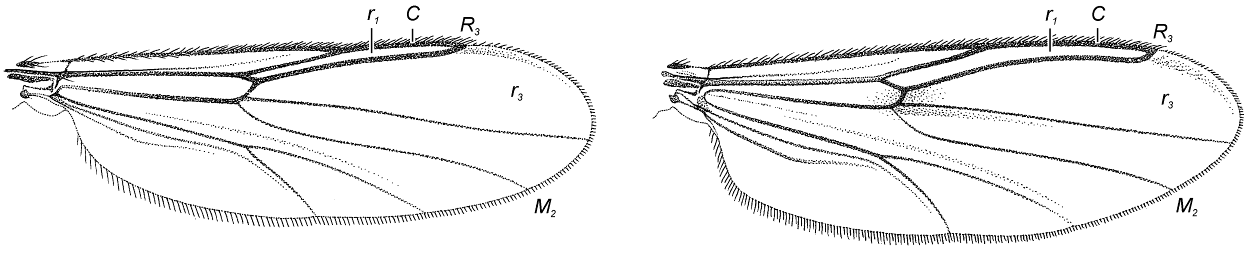
There is a need to confirm the generic placement of a substantial number of species of Johannsenomyiini, Sphaeromiini and *Palpomyia* Meigen, which are known only from males. Generic concepts in many instances have been defined based primarily or solely on female features and further study and cladistic interpretation are sorely needed (Borkent 2014). As such, readers will notice that the males of some *Sphaeromias* Curtis and *Palpomyia* are keyed more than once and this likely indicates, in part, the misplacement of at least some of these.

Schizonyxhelea Clastrier, a genus with tiny individuals, was recently redefined by Borkent (2015) and now includes Afrotropical species.

The adult and larval identification keys will work for some specimens that are preserved in alcohol. The identification of many genera requires slide-mounted material for the uninitiated, although with skill and patience many minute characters may also be observed in alcohol-preserved specimens. Some wing veins may be difficult to see in some taxa. For alcohol-preserved specimens, tilting the wing may help to see faint wing veins and with slide material, phase contrast microscopy provides the best resolution.

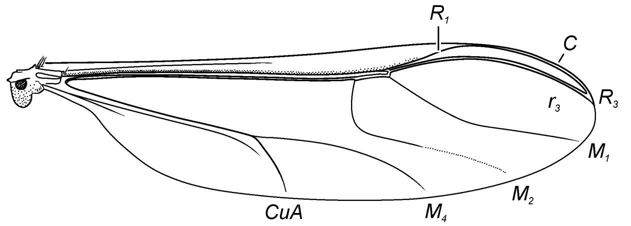
The homology of the first and second radial cells in some genera of Ceratopogonidae remains uncertain if reduced (either cell may be absent or vein R_2 may be absent with r_1 and r_2 fused). First and second radial cells are indicated with the abbreviations r_1 and r_2 on the figures included in this chapter for convenience, but do not necessarily imply homology. When the two tarsal claws at the end of a leg are the same size, they are referred to as being equal; conversely when they differ in size they are referred to as unequal. Differences between claws of different legs are described as such. Palisade setae are defined as setae that form a single row of basally thick, relatively short setae on the ventral surface of tarsomere 1 of the hind leg in most genera of Ceratopogoninae (those other than in the Culicoidini) (Urbanek *et al*. 2015). At least those setae which are situated basally on the tarsomere have their bases abutting, or virtually abutting. Those that are more distal may have adjacent bases, or be separated from one another by a short distance. Palisade setae are stouter than other setae on the tarsomere and taper close to their apices. The costal ratio represents the length of the costal vein (C) from the wing base (measured from the arculus; Figs 80, 89, 91), divided by the total wing length. Radial cells are measured according to their inner membranous length.

Considering the relatively limited sampling conducted in the Afrotropical Region, it seems likely that both new genera and species not yet recognised from the region are still to be discovered. It is noteworthy that 17 genera in the region are each known from only one species. Furthermore, some Southern Hemisphere genera, such as *Paradasyhelea* (also one species in the Pacific north-west of USA), *Austrohelea* Wirth & Grogan and *Macrurohelea* Ingram & Macfie are currently known from



164 *Bezzia* ♀

165 *Phaenobezzia* ♀



166 *Stenoxenus* ♀

Figs 34.164–166. Wings of female Ceratopogonidae (dorsal views): (164) *Bezzia nobilis* (Winnertz) (non-Afrotropical); (165) *Phaenobezzia pistiae* (Ingram & Macfie); (166) *Stenoxenus pastorianus* Clastrier, 1982. Figs 164, 165 (Downes & Wirth 1981, figs 41, as *B. setulosa*, 42), Fig. 166 (after Clastrier 1982*b*, fig. 1A).

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell.

the Australasian Region and southern South America and may well be present in southern Africa (as Gondwanan elements). The diversification of the family over time (Borkent 2000*a*) is consistent with at least some linages of Ceratopogonidae being old enough to be influenced by such ancient geological events. Other genera have very small individuals and/or have scattered distributions elsewhere, but are not known from the Afrotropics. The genus *Nannohelea* Grogan & Wirth, for example, is known from Algeria, Colombia, Costa Rica, Papua New Guinea and Sri Lanka and these very minute midges (wing length: 0.35–0.75 mm) may have been overlooked (or are not yet collected) from sub-Saharan Africa.

There are no previously published identification keys to larvae occurring in the Afrotropical Region and the identification key provided below is rather limited and is based mostly on extralimital species. As noted above, only 5% of Afrotropical species are known as larvae and 76% of these are of species of the genera *Culicoides*, *Dasyhelea* and *Forcipomyia*. Of the 53 described Afrotropical genera, 42 are unknown as larvae in the Afrotropics and there is a great need to rear and study the morphology of these. Many Afrotropical genera of the subfamily Ceratopogoninae occur in the Palaearctic Region and therefore the larval identification key by Glukhova (1979) for the fauna of the former Soviet Union may prove helpful. Larvae of this subfamily are, however, often strikingly similar and are challenging to identify even in the Palaearctic fauna.

Of the 53 described Afrotropical genera, 30 can be identified as pupae using the worldwide identification key of Borkent (2014), although for some these are based on extralimital species. The remaining 23 genera are currently unknown in this stage, but most of these, if not all, are probably rare; 11 belong to endemic monotypic genera.

The below identification key to larvae will allow for identification of specimens preserved in alcohol, other than those of Ceratopogoninae (from couplet 5 onwards). Further identification requires slide-mounting (Borkent & Spinelli 2007: 35). Descriptions of the larvae of some further genera were provided by de Meillon & Wirth (1991), but these were not diagnosed or keyed. Of the 49 genera of the subfamily Ceratopogoninae known from sub-Saharan Africa, only six are known as larvae from this region. Another 14 genera are known as species from elsewhere.

Adult and immature Ceratopogonidae are best collected directly into ethanol, using several different methods. For adults, fine-meshed Malaise traps (see Chapter 2) placed near wetter habitats are very productive and light traps using UV fluorescent tubes in similar localities are effective. For those studying species of *Culicoides*, adding a source of CO_2 will often markedly increase the numbers of female *Culicoides* collected. Sweeping with a fine-meshed aerial net is an excellent method of collecting and often samples species which are not collected by various other trapping methods; adults are often slow to emerge from the detritus in the bottom of an aerial net and 2 × or 4 × reading glasses are useful to detect the smallest individuals. Emergence traps are also a valuable collecting method to obtain adults (Havelka 1976; Knausenberger 1987).

Pupae occur in a wide array of aquatic habitats or moist substrates (*e.g.*, wet leaves, dung, decaying vegetation, fungi, *etc*.). In lotic or lentic habitats, pupae are never in open water, but are found abutting or on surrounding, somewhat emergent substrates; some representatives of the Johannsenomyiini are able to crawl *ca* 15 cm up emergent vegetation. Virtually all pupae can be sampled by submerging appropriate substrates in buckets of water and retrieving these as they slowly work their way to the surface and float at or move upwards from the edge of the water (sometimes taking 20 minutes to do so). Larvae are found in similar habitats, but may occur almost anywhere near the surface of submerged substrates (including the benthos of lakes), as well as in the same moist habitats noted for pupae. Larvae therefore require a variety of collecting techniques, with Berlese funnels being effective to collect those of Forcipomyiinae (Saunders 1959). Larvae of most Ceratopogonidae can be sampled by placing substrates in water in white pans, watching for their rapidly undulating and distinctive swimming behaviour and then removing them with a pipette for rearing. Larvae of Ceratopogoninae and *Leptoconops* can often be retrieved in large numbers (and sometimes reared) by using various floatation methods using salts or sugar (Davies & Linley 1966; Mullens & Rodriguez 1984).

As most species of Ceratopogonidae are small, virtually all need to be slide-mounted. There are a variety of techniques available (see Chapter 2), but many produce poor results. A slower method, which produces excellent specimens, is described in detail by Borkent & Spinelli (2007: 35). Additional specimens should be pinned (or glued to the side of a pin), fresh in the field and placed in a freezer to be freeze-dried for two months, or dried from ethanol with a critical-point-drier or using HMDS. Alcohol specimens eventually become impossible to slide mount because of changes to muscle tissue.

Keys to genera of Afrotropical Ceratopogonidae

Adults

1. Eyes widely separated medially, without frontal suture (Figs 40, 41); palpus 4-segmented (only 1 segment, composed of fused segments 4+5, beyond elongate and/or swollen segment 3) and with membranous gap between segment 3 and fused 4+5 (Figs 40, 59); wing without crossvein *r–m*, radial cells 1–3 fused into swollen unit (Figs 70, 110); without palisade setae on hind tarsomere 1 (Fig. 167); male terminalia with gonostylus with apical socketed peg (Fig. 260); female terminalia with cercus short (as in Figs 33, 293) or elongate (Figs 32, 292) (LEPTOCONOPINAE) . . . . *Leptoconops* Skuse

– Eyes abutting, narrowly separated or widely separated medially, with frontal suture (*e.g.*, Figs 42, 44, 45); palpus 4- or 5-segmented, but if 4-segmented, then never with membranous gap between terminal two segments (*e.g.*, Figs 60–66); wing with crossvein *r–m* (*e.g.*, Figs 76, 84, 115, 121); 1–2 radial cells distinct or if fused or absent (*e.g.*, Figs 82, 122, 123), then crossvein *r–m* clearly present; with (*e.g.*, Figs 170–172, 178) or without (*e.g.*, Figs 168, 169) palisade setae on hind tarsomere 1; male terminalia with gonostylus without apical, socketed peg (*e.g.*, Figs 261–272) although apex may be pointed (*e.g.*, Figs 267, 269, 274, 278); female terminalia with cercus short (*e.g.*, Figs 293, 294, 297–303) 2

2. Hind tarsomere 1 with scattered setae or at most row of coarse setae (but these not forming tight row, especially basally on tarsomere), stout sub-basal spine absent (*e.g.*, Figs 168, 169); female with 2 small, equal claws on each leg (*e.g.*, Figs 187, 188); with (*e.g.*, Figs 185, 186) or without (*e.g.*, Figs 187, 188) well-developed empodium 3

– Hind tarsomere 1 with row of palisade setae, with at least more basal setae with abutting bases, some groups with additional pronounced stout sub-basal spine (*e.g.*, Figs 170–172, 178, 240); females with 2 small, equal claws on each leg (*e.g.*, Figs 217–219) or with 1–2 claws on one or more legs which in some are large and if 2, these equal or unequal (*e.g.*, Figs 190–193, 195–198, 213, 216, 228, 240); without well-developed empodium 6

3. Costal wing vein (*C*) reaching well beyond middle of wing (Figs 73, 112, 113); both radial cells well-developed, with second radial cell elongate and usually moderately wide (Figs 73, 112, 113); paratergite well-developed, with 1 stout, large and 0–5 more slender, shorter setae (Fig. 67) . . . . *Atrichopogon* Kieffer

– Costal wing vein (*C*) short or long (*e.g.*, Figs 33–35, 71, 72, 74, 75), if long then second radial cell either wide (*e.g.*, Figs 34, 35, 75, 115) or narrow (*e.g.*, Figs 71, 74, 111, 114); paratergite narrow (as in Fig. 68), without setae 4

4. Apical antennal flagellomere with (Figs 52, 53) or without terminal "nipple", that is constricted basally; tarsal claws strongly curved (Figs 185, 186); empodium vestigial or well-developed (Figs 185, 186) . . . . *Forcipomyia* Meigen

– Apical antennal flagellomere without terminal "nipple" (although may be strongly tapered) (*e.g.*, Fig. 54); tarsal claws only slightly curved (*e.g.*, Figs 187, 188); empodium poorly developed. 5

5. Wing with or without well-defined radial cells (Figs 34, 35, 75, 115), wing with or without distinct patterns of dark and/or light pigmentation (Figs 34, 35); female mandible well-developed, serrate (Fig. 43); male with setae on antennal flagellomere 1, about as long as those on following flagellomeres (Fig. 34); male flagellomeres not sculptured; fore leg with tibial spur; male terminalia with symmetrical parameres (Fig. 263) (CULICOIDINI) . . . . *Culicoides* Latreille

– Wing with slit-like, difficult to define radial cells (Figs 74, 114); wing without distinct pattern of dark pigmentation (some weakly patterned); female mandible poorly developed, non-serrate; male with setae on antennal flagellomere 1 short, less than ½ length of those on following flagellomeres (Fig. 54); male flagellomeres sculptured (Fig. 54); fore leg without tibial spur; male terminalia with symmetrical or asymmetrical parameres (Fig. 262) (DASYHELEINAE) . . . .*Dasyhelea* Kieffer

6. Wing vein M_{1+2} forked beyond *r–m* crossvein (medial fork petiolate) (*e.g.*, Figs 76–80, 83–85), in some, base of vein M_2 absent (*e.g.*, Figs 81, 82, 119, 122–125) 7

– Wing vein M_{1+2} forked at or before *r–m* crossvein (medial fork sessile, not petiolate) (*e.g.*, Figs 102–109, 150–166); base of vein M_2 present, or if absent, then with M_2 extending basally to at least level of *r–m* 63

7. Palpus 4-segmented, only 1 segment distal to that bearing sensory pit and/or capitate sensilla (Fig. 60); male wing with single radial cell and slight dip along anterior margin where vein R_3 meets costal vein (*C*) (Figs 96, 97); female costal vein long, extending almost to wing tip (Fig. 147); female head with clypeus fused laterally to eyes (Fig. 49); fore and mid coxae of male with dense, long spine-like setae (Fig. 69) . . . . *Parabezzia* Malloch

– Palpus 5-segmented, 2 segments distal to that bearing sensory pit and/or capitate sensilla (*e.g.*, Figs 61–64); male wing with radial cells variable, but anterior margin straight; female costal vein short to long (extending to wing tip); female head with clypeus separated laterally from eyes by membrane (*e.g.*, Figs 45, 46, 48); male coxae without long spine-like setae (coarse setae present in some). 8

8. Hind femur moderately to greatly swollen distally, with stout ventral spines in close-set distal series (*e.g.*, Figs 1, 220, 222) 9

– Hind femur slightly to somewhat swollen, without stout ventral spines in series 10

9. Male with > 0.58 of apex of hind femur bearing stout ventral spines (Fig. 1, as the female Fig. 220); female with fore and mid tarsal claws with rounded or straight base, distal portion curved; female hind claws either single and elongate (Figs 220, 221), or if short and equal, then lacking inner tooth . . . . *Serromyia* Meigen

– Male with < 0.43 of apex of hind femur bearing stout ventral spines (Fig. 222); female tarsal claws distinctly bent at base, distal portion straight; female hind claws short and equal, with well-developed inner tooth. . . . . *Metacanthohelea* Wirth & Grogan

10\. Males (*Afrostilobezzia*, *Congohelea* & *Paralluaudomyia* unknown; *Calcarhelea* not sufficiently described, see "Identification" section above) 11

– Females 34

11\. Hind leg with single long tarsal claw and small basal tooth (Fig. 173) . . . . *Allohelea* Kieffer [in part]

– Hind leg with two equal or subequal tarsal claws (*e.g.*, Figs 174–177). 12

12\. Wing with characteristic pattern of pigmentation, 2 dark pigmentation patches in cell *br* (these merging posteriorly in *M. legrandi* Clastrier, 1984) and 2 in cell r_3 (forming more or less single line of four patches), also with at least patch in second radial cell and somewhat S-shaped patch (arrowed) near apex of vein M_2 (Fig. 98); thorax and at least hind femur and tibia with patterned pigmentation; terminalia with aedeagus with distinctive anteromedial loop (Fig. 276). . . . . *Monohelea* Kieffer [in part]

– Wing without pattern of pigmentation, or if present not as above (*e.g.*, Figs 78, 99); pigmentation of thorax and legs variable, with or without pattern; terminalia with aedeagus variable, but not with anteromedial loop (*e.g.*, Figs 266, 267, 272, 273) 13

13\. Wing vein R_3 extending to near wing tip (costal ratio (length of wing measured from arculus / length of costa (C) measured from arculus) > 0.90) (Fig. 84); hind tarsomeres 2 and 3 with stout, strongly bent, pale spines (Fig. 174) . . . . *Luciamyia* de Meillon [in part]

– Wing vein R_3 not extending to near wing tip (costal ratio < 0.85) (*e.g.*, Figs 78–83, 85); hind tarsomeres 2 and 3 with slender or stout, straight, pale to dark setae or spines (as in Fig. 173) 14

14\. Wing with characteristic pattern of pigmentation, strikingly similar to that of some *Culicoides*, with round or oblong white areas on otherwise darkly pigmented membrane, with virtually round white patches at apex of each of cells r_3, m_1, m_2 and m_4 and others more basally (*e.g.*, Fig. 88) 15

– Wing with or without pigmentation, but not with rounded pale patches on otherwise darkly pigmented membrane (e.g., Figs 78, 79, 93, 99) 16

15\. Wing with 2 radial cells; vein R_1 extending to costal vein (C) (Fig. 88). . . . . *Stiloculicoides* Wirth & Grogan [in part]

– Wing with 1 radial cell developed; apical portion of vein R_1 not extending to costal vein (C) (Fig. 76). . . . . *Fanthamia* de Meillon [in part]

16\. Wing with 2 main dark pigmentation patches, one over *r–m* crossvein and base of vein *M* and the other posterior to apical portion of vein R_3, some further lighter patches present apically and posteriorly (Fig. 99); tarsomeres 4 elongate and cylindrical (Fig. 175) . . . . *Downeshelea* Wirth & Grogan [in part]

– Wing without pigmentation, or if present, then not as above (e.g., Figs 89–95); if pattern similar to above (some *Stilobezzia*), then tarsomeres 4 short and cordiform (e.g., Fig. 176) 17

17\. Wing with 1, broad, elongate radial cell (*e.g.*, Figs 83, 86) 18

– Wing with either 2 radial cells (in some slit-like and narrow) (*e.g.*, Figs 77, 79, 81, 85, 87), or if 1 present, then this short and narrow (*e.g.*, Fig. 92), or without apparent radial cell (*e.g.*, Fig. 82) 19

18\. Radial wing cell broad at base, with vein R_1 about as long as *r–m* crossvein (Fig. 86); terminalia with aedeagus divided medially (Fig. 273) . . . . *Stilobezzia* Kieffer [in part]

– Radial wing cell narrow, with vein R_1 at least 2 × as long as *r–m* crossvein (Fig. 83); terminalia with aedeagus continuous medially (Fig. 265) . . . . *Afrohelea* Wirth [in part]

19\. Antenna entirely feminised, lacking plume, with flagellomeres 9–13 longer than preceding flagellomeres; scape small and narrow (relative to rest of head), oblong, with dorsal flange; pedicel narrow (*e.g.*, Figs 44, 55) 20

– Antenna characteristically male, with or without plume, with flagellomeres 11–13 longer than preceding flagellomeres (or only flagellomeres 12, 13 longer, but then flagellomere 11 fused to more basal flagellomeres (*e.g.*, Fig. 58)), in some with flagellomeres nearly equal in length; scape wide, without flange; pedicel wide, well-developed (*e.g.*, Figs 56, 57) 21

20\. Wing vein R_1 without apical portion or not extending to costal vein (C) (only first radial cell developed or without radial cell apparent) (Fig. 76); head capsule (not including mouthparts) about as long as wide (Fig. 44) . . . . *Fanthamia* de Meillon [in part]

– Wing vein R_1 extending to costal vein (C) (2 radial cells developed) (Fig. 85); head capsule narrow and elongate (Fig. 47) . . . . .Undescribed genus [in part]

21. Wing with both radial cells well-developed, second radial cell longer than first radial cell (*e.g.*, Figs 77, 87, 90, 94, 95); terminalia with aedeagus divided (Fig. 273) or continuous medially (in some only transverse band present) (*e.g.*, Figs 270–272, 274). 22

– Wing with 0–2 radial cells, in some first radial cell slit-like (*e.g.*, Fig. 91), in others both radial cells slit-like (*e.g.*, Figs 78, 80), but if with both well-developed (*e.g.*, Figs 79, 81, 89, 93), then second radial cell equal to or shorter than first; terminalia with aedeagus continuous medially, transverse band absent (*e.g.*, Figs 266, 267, 269, 271, 272) 26

22. Terminalia with epandrium without apicolateral process or process small (setose cercus present) (*e.g.*, Figs 270, 273, 275); aedeagus continuous medially (*e.g.*, Fig. 270), divided medially (*e.g.*, Fig. 273) or with transverse band (*e.g.*, Fig. 275) 23

– Terminalia with epandrium with apicolateral process thick, well-developed (*e.g.*, Figs 271, 272, 274); aedeagus continuous medially, without transverse band (*e.g.*, Figs 271, 272, 274) 25

23. All tarsal claws with well-developed inner tooth (Figs 196–198); terminalia with aedeagus continuous medially (Fig. 270) . . . .*Ankylohelea* de Meillon & Wirth [in part]

– All tarsal claws without inner tooth (in some with just extreme apices of claws bifid); terminalia with aedeagus divided medially (*e.g.*, Fig. 273) or with transverse band present (e.g., Fig. 275) 24

24. Terminalia with aedeagus divided medially (Fig. 273); terminalia without heavily sclerotised transverse band ventral to parameres . . . .*Stilobezzia* Kieffer [in part]

– Terminalia with aedeagus greatly reduced or absent; terminalia with heavily sclerotised transverse band ventral to parameres (Fig. 275). . . . . *Schizonyxhelea* Clastrier [in part]

25. Length of antennal flagellomeres 11–13/1–10 *ca* 0.5; all legs with tarsomere 4 without abruptly bent whip-like setae . . . . *Neohelea* Clastrier [in part]

– Length of antennal flagellomeres 11–13/1–10 > 0.8; all legs with tarsomere 4 with abruptly bent whip-like setae (Fig. 177) . . . .*Kolenohelea* de Meillon & Wirth [in part]

26. Wing with radial cells entirely fused (Fig. 82) or with 2 short, virtually equal radial cells (Figs 81); antennal flagellomeres 2–11 fused (Fig. 58); thorax with katepisternum with 1 or more lateral setae (can be viewed in specimens in alcohol by holding specimen upright and viewing along plane of thoracic pleura in outline) (Fig. 68). . . . . *Brachypogon* Kieffer [in part]

– Wing with 1–2 radial cells, of variable relative sizes, in some slit-like, narrow (*e.g.*, Figs 78–80, 89, 91–93); antennal flagellomeres either separate or variably fused, but none with 10–11 fused; thorax with katepisternum without setae. 27

27. Wing with pigmentation patches at least over apex of vein R_3 (Fig. 79), in some with additional patches and/or narrow partial pigmentation of wing veins (Fig. 78) . . . . *Alluaudomyia* Kieffer [in part]

– Wing without pattern of pigmentation 28

28. Wing with macrotrichia present over most of wing (Fig. 136); terminalia with epandrium without apicolateral processes (with only an elongate seta at posterolateral corner) (Fig. 266) . . . . *Bothamia* Meiswinkel

– Wing with macrotrichia restricted to near apex of wing (*e.g.*, Fig. 89), in some to very margin (*e.g.*, Fig. 93) or entirely absent (*e.g.*, Fig. 91); terminalia with epandrium with (*e.g.*, Figs 267–269) or without apicolateral processes 29

29. Costal ratio < 0.6, radial cells poorly defined, narrow or fused (Fig. 92). . . . . *Notoceratopogon* de Meillon & Downes

– Costal ratio > 0.5; both radial cells clearly present (*e.g.*, Figs 79, 89, 93) or with only first radial cell slit-like, elongate and narrow (*e.g.*, Figs 80, 91) 30

30. Wing with only 1 seta on radial vein (*R*) (basal to radial cells), situated near arculus (*e.g.*, Figs 80, 91); membrane without macrotrichia; hind tarsomere 1 without sub-basal stout thick spine 31

– Wing with several setae along length of radial vein (*R*) (basal to radial cells) in addition to single seta situated near arculus (*e.g.*, Figs 89, 93); membrane with at least some macrotrichia subapically (in some just short of apex) (*e.g.*, Fig. 89); hind tarsomere 1 with (*e.g.*, Fig. 178) or without stout thick sub-basal spine 32

31. Hind tarsal comb with setae similar in length (as in Figs 170, 172); terminalia with anterior margin of gonocoxite near level of anterior margin of laterally shortened segment 9 (Fig. 269). . . . . *Bothahelea* Grogan & Wirth

– Hind tibial comb with ventral-most seta markedly elongate as a spine (Fig. 179); terminalia with anterior margin of gonocoxite situated more distally on laterally elongate segment 9 (as in Figs 270, 274) . . . . *Alluaudomyia* Kieffer [in part]

32. Abdominal tergite 1 without lateral patch of elongate setae; terminalia with epandrium with apicolateral process of epandrium broad and elongate (Figs 271, 272) . . . .*Kolenohelea* de Meillon & Wirth [in part]

– Abdominal tergite 1 with lateral patch of elongate setae; terminalia with epandrium with apicolateral process of epandrium either slender (*e.g.*, Fig. 267) or broad and short (*e.g.*, Fig. 268) 33

33. Wing with macrotrichia more broadly distributed in cell r_3 and on veins M_1, M_2 and M_4 (Fig. 89); hind tarsomere 1 with 2 stout thick sub-basal spines (Fig. 178); terminalia with epandrium with apicolateral process slender, elongate (Fig. 267) . . . . *Capehelea* de Meillon & Wirth [in part]

– Wing with macrotrichia restricted to near apical margin and a few at very apex of vein M_1 (Fig. 93); hind tarsomere 1 without stout, thick sub-basal spine; terminalia with epandrium with apicolateral process broad, short (Fig. 268) . . . . *Ceratohelea* Wirth & Grogan [in part]

34. Apex of wing bilobed, with enlarged scale-like setae and modified macrotrichia (Fig. 121). . . . . *Luciamyia* de Meillon [in part]

– Apex of wing rounded, without modified setae and macrotrichia (*e.g.*, Figs 119, 120, 122–125). . . . 35

35. Wing vein R_3 extending to wing apex; costal vein (C) extending beyond apex of vein R_3 (Fig. 126) . . . .*Paralluaudomyia* Clastrier

– Wing vein R_3 extending at most to 0.9 of wing length; costal vein (C) not extending beyond apex of vein R_3 (e.g., Figs 127–133) 36

36. Wing with characteristic pattern of pigmentation, with 2 dark pigmentation patches in cell *br* (these merging posteriorly in *M. legrandi*) and 2 in cell r_3 (forming more or less single line of 4 patches), at least 1 patch also present in second radial cell and somewhat S-shaped patch (arrowed) near apex of vein M_2 (Figs 129, 130); thorax and at least hind femur and tibia with patterned pigmentation; terminalia with 2 unequal spermathecae, the smaller one usually with long thread-like sclerotisation of duct (Fig. 293) . . . . *Monohelea* Kieffer [in part]

– Wing without pattern of pigmentation, or if present, not as above (*e.g.*, Figs 127, 128, 133, 148); pigmentation of thorax and legs variable, with or without pattern; terminalia with spermatheca either not visible (hyaline in some), 1 spermatheca (plus in some with minute second), or if 2 spermathecae present, then these subequal (smaller of two without long thread-like sclerotisation of duct); in some with minute third. 37

37. Wing without radial cells or only one present (in *Fanthamia* with apical portion of vein R_1 not extending to costal vein (C) (*e.g.*, Figs 116–120, 122, 123, 125, 132) 38

– Wing with 2 radial cells, in some first radial cell slit-like (*e.g.*, Figs 124, 127, 128, 131, 133, 134–141) 43

38. Wing with 1 elongate, well-developed, broad radial cell (*e.g.*, Figs 116, 117, 125, 132) 39

– Wing without radial cell (R_1, R_2, R_3 fused apically, as R_{1+2+3}) (e.g., Figs 122, 123), or if 1 cell present, then this either short, virtually oval (in *Fanthamia* with apical portion of vein R_1 not extending to costal vein (C) (only first radial cell developed)) (*e.g.*, Figs 119, 120), or elongate and extremely narrow (*e.g.*, Fig. 118). 41

39. Tarsal claws of all legs equal (Figs 217–219). . . . .*Afrohelea* Wirth [in part]

– Tarsal claws of all legs unequal or with single claw with basal tooth (*e.g.*, Figs 191–193, 202–204) . . . 40

40. Wing with prominent colour pattern, with at least black pigmentation patches over, or just basal to *r–m* crossvein and over apex of vein R_3, in some with additional patches and/or narrow partial pigmentation of wing veins (Figs 116, 117); fore femur without ventral spines; hind tarsomere 1 with only single row of palisade setae (Fig. 170); fifth tarsomeres without ventral spines (Figs 202–204) . . . . *Alluaudomyia* Kieffer [in part]

– Wing without pigmentation patches; fore femur with 1–2 short, stout thick ventral spines (Fig. 189); hind tarsomere 1 with at least 1½ rows of palisade setae (Fig. 171); tarsomeres 5 each with 1 or 2 pairs of thick ventral spines (Fig. 190). . . . .*Stilobezzia* Kieffer [in part]

41. Wing with markedly elongate, single, slit-like radial cell (Fig. 118); hind tibial comb with 2 ventral-most setae, spine-like, particularly elongate and thick (Fig. 194) . . . . *Alluaudomyia* Kieffer [in part]

– Wing without radial cells (R_1, R_2, R_3 fused apically) (e.g., Figs 122, 123), or if 1 cell present, then this either short, virtually oval (in *Fanthamia* with apical portion of vein R_1 not extending to costal vein (C) (only one radial cell developed)) (e.g., Figs 119, 120); hind tibial comb with setae similar in length 42

42. Wing with first radial cell present, second absent (apical portion of vein R_1 if present, not extending to costal vein (*C*)) and vein R_3 extending well past apex of first radial cell (Figs 119, 120); thorax with katepisternum without setae . . . . *Fanthamia* de Meillon [in part]

– Wing without radial cells (these fused), or with 1 very short apical cell (Figs 122, 123); thorax with katepisternum with 1 or more lateral setae (discernible in specimens in alcohol by holding specimen upright and viewing along plane of thoracic pleura in outline) (Fig. 68) . . . *Brachypogon* Kieffer [in part]

43. Fore (Fig. 212) and mid (Fig. 213) tarsal claws equal, hind leg with single claw (Figs 214–216, with or without basal tooth 44

– Tarsal claws not as above 45

44. Hind tarsal claw with basal tooth (Figs 214, 215) . . . . *Allohelea* Kieffer [in part]

– Hind tarsal claw without basal tooth (Fig. 216) . . . . *Downeshelea* Wirth & Grogan [in part]

45. Wing with short radial cells, equal or nearly equal in size (Fig. 124); thorax with katepisternum with 1 or more lateral setae (discernible in specimens in alcohol by holding specimen upright and looking along plane of thoracic pleura in outline) (Fig. 68) . . . . *Brachypogon* Kieffer [in part]

– Wing with radial cells either well-developed (elongate) (*e.g.*, Figs 131, 133, 134, 139, 140, 142–146), or with first radial cell slit-like, radial cells unequal in size (Figs 116, 138, 141); thorax with katepisternum without setae 46

46. All legs each with single tarsal claw, with basal tooth (in some with tooth somewhat elongate, but clearly fused to claw) (*e.g.*, Figs 191–193, 202–210) 47

– All legs each with both tarsal claws present, from equal or virtually equal in size (*e.g.*, Figs 196–201), to some or all unequal, claws each with or without basal tooth 56

47. Wing with characteristic pigmentation pattern, strikingly similar to that of some *Culicoides*, with pattern of dark and pale pigmentation, including virtually round white patches near apex of each of cells r_3, m_1, m_2 and m_4 (Fig. 135) . . . . *Stiloculicoides* Wirth & Grogan [in part]

– Wing with (*e.g.*, Figs 116, 117, 140) or without pigmentation, but not with rounded pale patches surrounded by dark pigmentation in cells r_3, m_1, m_2 and m_4 48

48. Wing with abundant macrotrichia to base (Fig. 136); palpal segments 3 and 4 short, stout (Fig. 61) . . . . *Bothamia* Meiswinkel

– Wing without macrotrichia, or at most with macrotrichia mostly restricted to distal ½ (*e.g.*, Figs 116, 131, 139); palpal segments 3 and 4 variable, from short, stout to markedly elongate, slender (*e.g.*, Figs 62–64) 49

49. Wing with second radial cell short, sub-ovate (*e.g.*, Fig. 138) or with crossvein *r–m* longer than combined lengths of two radial cells (Fig. 137) 50

– Wing with second radial cell, elongate, *ca* 2 × or more length of first radial cell (in some first radial cell slit-like or appearing fused); crossvein *r–m* shorter than combined lengths of two radial cells (*e.g.*, Figs 116, 117, 131, 133, 134, 139, 140, 143) 51

50. Hind tarsomere 1 with single row of palisade setae (as in Fig. 170); wing crossvein *r–m* shorter than combined lengths of two radial cells (Fig. 138) . . . . *Capehelea* de Meillon & Wirth [in part]

– Hind tarsomere 1 with at least partial second row of palisade setae (Fig. 171); wing crossvein *r–m* longer than combined lengths of two radial cells (Fig. 137) . . . . *Stilobezzia* Kieffer [in part; *S. singularis* Clastrier, 1985]

51. Wing with first radial cell rhomboidal (*e.g.*, Figs 131, 133, 134) 52

– Wing with first radial cell oval to slit-like, not rhomboidal (*e.g.*, Figs 116, 117, 139, 140, 143) 53

52. Terminalia with 2 moderately to well-developed spermathecae (also minute third), oval or almost circular in shape (as in Fig. 294) . . . . *Stilobezzia* Kieffer [in part]

– Terminalia with 1 well-developed spermatheca, with thick, bent neck (Fig. 295) . . . . *Schizonyxhelea* Clastrier [in part]

53. Wing with prominent pigment pattern, with at least black pigmentation patches over, or just basal to *r–m* crossvein and over apex of vein R_3, in some with additional patches and/or narrow partial pigmentation of wing veins (Figs 116, 117) . . . . *Alluaudomyia* Kieffer [in part]

– Wing without pigmentation patches, or if present then with patch in cell r_3, distal to apex of vein R_3 (Fig. 140) 54

54. Terminalia with 1 well-developed spermatheca, with thick, sharply bent neck (Fig. 295) . . . . *Schizonyxhelea* Clastrier [in part]

– Terminalia with 1–2 well-developed spermathecae, oval or nearly circular in shape, neck very short or long and slender (*e.g.*, Fig. 296) 55

55. All legs with tarsomere 4 without recurved whip-like setae . . . . *Neohelea* Clastrier [in part]

– All legs with tarsomere 4 with recurved whip-like setae (Fig. 195) . . . *Kolenohelea* de Meillon & Wirth

56. Fore femur with 3 stout, widely spaced ventral spines (Fig. 223) . . . . *Congohelea* Wirth & Grogan

– Fore femur without ventral spines 57

57. Head (excluding mouthparts) narrow and elongate (Fig. 48) . . . . Undescribed genus [in part]

– Head about as long as wide (*e.g.*, Fig. 46) 58

58. Wing without macrotrichia (Fig. 149); terminalia greatly modified, with sternites 6 and 7 short (*ca* ½ length of sternite 5); segment 8 large, sub-cylindrical, with anteroventral margin somewhat bilobed; segment 9 long (lateral margin as long as lateral margin of segment 8), narrow (sub-quadrate in outline) and with dorsomedial line of weakness (Fig. 297); terminalia with 1 large and 1 tiny spermathecae (Fig. 297) . . . . *Bothahelea* Grogan & Wirth

– Wing with macrotrichiae, in some sparse apically (*e.g.*, Figs 141, 142, 145, 146); terminalia unmodified, with sternites 6, 7 and 8 almost equally long; segment 8 tapering, with anteroventral margin straight or slightly and evenly curved; segment 9 short (lateral margin < ⅔ length of lateral margin of segment 8), wide (*ca* 3 × wider than long) and complete medially (*e.g.*, Fig. 294); terminalia with 2 moderately-sized spermathecae, in some a tiny third (*e.g.*, Fig. 294) 59

59. Wing with radial wing cells sub-equal in length (*e.g.*, Figs 141, 142); hind tarsomere 1 without thick sub-basal spine 60

– Wing with second radial cell *ca* 2–3 × length of first (*e.g.*, Figs 144–146); hind tarsomere 1 with (as in Figs 172, 219) or without thick sub-basal spine 61

60. Antennal flagellomeres without sensilla coeloconica (very short sensilla surrounded by thin spicules); costal ratio: 0.45–0.56 (Fig. 141); spermathecae with irregular, wrinkled walls (Fig. 298) . . . . *Notoceratopogon* de Meillon & Downes

– Antennal flagellomere 12 with sensilla coeloconica; costal ratio: 0.72 (Fig. 142); female spermathecae with smooth walls (as in Fig. 296) . . . . *Ceratohelea* Wirth & Grogan [in part]

61. Wing with first radial cell rhomboidal (Fig. 144) . . . . *Afrostilobezzia* Szadziewski & Dominiak

– Wing with first radial cell oval to narrow, not rhomboidal (*e.g.*, Figs 145, 146) 62

62. Tarsal claws each with inner tooth (Figs 196–198) . . . . *Ankylohelea* de Meillon & Wirth [in part]

– Tarsal claws on at least fore and hind legs each without inner tooth (Figs 199–201) . . . . *Calcarhelea* Wirth & Grogan

63. Fore tarsomere 5 swollen (*e.g.*, Figs 181, 224) or if not swollen (*e.g.*, Figs 183, 227), then with band of wing pigmentation, including at least *r–m* crossvein and base of vein M_2, to basal portion of cells r_3, m_1 and m_2 (*e.g.*, Figs 154, 155); female tarsomeres 5 each without ventral stout, black spines (batonnet spines) (*e.g.*, Figs 224, 225, 227, 228) (HETEROMYIINI) 64

– Fore tarsomere 5 not swollen, or if swollen then with at least 1 pair of thick ventral spines (batonnet spines) (some *Macropeza*); wing without pattern of pigmentation or, if present then not with defined wide band extending from *r–m* crossvein and base of vein M_2 to basal portion of cells r_3, m_1 and m_2 (some with entire wing infuscated), or if with defined wide fascia (1 species of *Sphaeromias*, Fig. 162), then female tarsomeres 5 with batonnet spines (*e.g.*, Fig. 254); female tarsomeres 5 with or without ventral stout, black batonnet spines (*e.g.*, Figs 229–237, 241–243, 245, 247–254) 69

64. Males 65

– Females 67

65. Wing pale, without pigmentation pattern; terminalia with parameres broadly fused (Fig. 278) . . . . *Pellucidomyia* Macfie [in part]

– Wing at least somewhat darkened (anterior infuscation) (Fig. 103), some with pigmentation pattern (*e.g.*, Fig. 104); terminalia with parameres separate (*e.g.*, Fig. 280) or only partially fused (*e.g.*, Fig. 279) 66

66. Apex of hind tarsomere 4 bifid and spinose (Fig. 182); fore tarsomere 5 swollen medially, wider than those of mid- and hind legs (Fig. 181) . . . . *Clinohelea* Kieffer [in part]

– Apex of hind tarsomere 4 undivided, without spines (Fig. 184); fore tarsomere 5 slender, similar to those of mid- and hind legs (Fig. 183) . . . . *Tetrabezzia* Kieffer [in part]

67. Hind tarsomere 5 with 1 or 2 tarsal claws, *ca* length of tarsomere 5 (Fig. 225); hind leg slightly longer than other legs, with tarsomere 2 less than ½ length of tarsomere 1 . . . . . . *Clinohelea* Kieffer [in part]

– Hind tarsomere 5 with single, extremely elongate claw, much longer than tarsomere 5 (in some with much shorter basal tooth) (*e.g.*, Figs 228, 240); hind leg strikingly elongate, tarsomere 2 at least ¾ length of tarsomere 1 (*e.g.*, Fig. 240) 68

68. Hind leg with single tarsal claw, without short basal tooth (Fig. 240); tarsomeres 4 of fore- and mid leg cordiform, without spines (Figs 238, 239); wing pale, without markings . . . . *Pellucidomyia* Macfie [in part]

– Hind leg with single tarsal claw, with short basal tooth (Fig. 228); tarsomeres 4 of fore- and mid leg bifid, spinose (Fig. 227); wing with pigmentation pattern (Figs 154, 155) . . . . . . *Tetrabezzia* Kieffer [in part]

69. All femora with elongate, ventrally- and anteroventrally directed spines (Fig. 211); male terminalia large, with gonocoxites fused dorsally and ventrally (Fig. 277); female terminalia with sternite 8 large and plate-like (Fig. 299) . . . . *Echinohelea* Macfie

– Femora with (*e.g.*, Figs 246, 250–252, 255, 258) or without (Figs 256, 257) elongate or stout spines, but if present these ventrally directed; male terminalia small or large, gonocoxites not fused (*e.g.*, Figs 282–284); female terminalia with sternite 8 moderately developed (*e.g.*, Figs 301–303). 70

70. Costal wing vein (*C*) extending well beyond apex of vein R_3 (Figs 102, 150); bases of veins M_1 and M_2 closely approximated at *r–m* crossvein (Figs 102, 150) . . . . *Neurobezzia* Wirth & Ratanaworabhan

– Costal wing vein (*C*) not extending beyond apex of vein R_3 or slightly so (*e.g.*, Figs 105–109, 156, 158–166), or if with long extension, then base of vein M_2 well basal to *r–m* crossvein, distant from base of vein M_1 (*e.g.*, Fig. 157) 71

71. Males (males of *Xenohelea* unknown). 72

– Females 86

72. Terminalia with gonostylus reduced in size to small articulated stub or not articulated and fused to gonocoxite (*e.g.*, Figs 289, 291) 73

– Terminalia with gonostylus at least moderately developed, articulated (*e.g.*, Figs 281–284, 285–288, 290). 74

73. Thorax with anepisternum with numerous elongate setae; terminalia with gonocoxite reduced in size to small stub (much narrower than width of gonocoxite) (Fig. 291) . . . *Phaenobezzia* Haeselbarth [in part]

– Thorax with anepisternum without setae; terminalia with gonocoxite and gonostylus fused and elongate (Fig. 289) . . . . *Nilobezzia* Kieffer [in part]

74. Palpus 4-segmented (segments 4 and 5 fused) (Fig. 65) . . . . *Stenoxenus* Coquillett [in part]

– Palpus 5-segmented (as in Figs 61–64) 75

75. Head (in anterior view) with ommatidia (eye facets) broadly separated medially, ventral ommatidia larger than dorsal ommatidia; clypeus narrow; antennal scape small (Fig. 51). . . . . *Macropeza* Meigen [in part]

– Head (in anterior view) with ommatidia (eye facets) narrowly or moderately separated medially, ventral and dorsal ommatidia of equal diameter; clypeus wide; antennal scape well-developed (*e.g.*, Fig. 50) 76

76. Anal lobe of wing well-developed, almost forming 90° angle basally (Fig. 105) . . . . *Jenkinshelea* Macfie [in part]

– Anal lobe of wing not well-developed, forming much less than a 90° angle basally (Figs 106–109) 77

77. Tarsomere 5 of at least hind leg with batonnet spines (Fig. 180); each tarsal claw with short, but well-developed, blunt outer tooth (Fig. 180) . . . . *Johannsenomyia* Malloch [in part]

– Tarsomeres 5 without thick spines, or if present then these more slender and sharply pointed; each tarsal claw without inner or outer tooth 78

78. Wing with 1 radial cell (Figs 108, 109) . . . . *Bezzia* Kieffer [in part]

– Wing with 2 radial cells (Figs 106, 107) 79

79. Terminalia with gonocoxite elongate, slender, apex well posterior to apex of epandrium and cercus (Fig. 281). . . . . *Dibezzia* Kieffer [in part]

– Terminalia with gonocoxite relatively short and thick, to elongate and slender, but apex extending to or just beyond apex of epandrium and cercus (*e.g.*, Figs 282–284, 285–288) .80

80. Fore femur with or without ventral spines; terminalia with parameres fused basally, with apical, parallel-sided fork (*e.g.*, Figs 282, 288) 81

– Fore femur with ventral spines; terminalia with parameres separate, or if fused not as above (*e.g.*, Figs 284, 286, 290). 82

81. Fore femur without ventral spines . . . . *Mallochohelea* Wirth [in part]

– Fore femur with ventral spines . . . .*Hebetula* Wirth & Debenham [in part]

82. Terminalia with gonostylus short (*e.g.*, Fig. 283) 83

– Male terminalia with gonostylus elongate (*e.g.*, Figs 284–287) 84

83. Terminalia with gonostylus rounded apically, parameres separate (Fig. 283) . . . . *Neosphaeromias* Das Gupta & Wirth [in part]

– Terminalia with gonostylus pointed apically (as in Fig. 290), parameres fused, with apex forming single rounded bulb (as in Fig. 286, but without spicules) . . . . . *Palpomyia* Meigen [in part; only *P. singularis*]

84. Terminalia with parameres fused, apically bulbous and pubescent (Figs 284, 286, 287) . . . . *Sphaeromias* Curtis [in part; *S. corsoni*], *Homohelea* Kieffer [in part], *Palpomyia* Meigen [in part; *P. fusca, P. kurwana*]

– Terminalia with parameres separate, or if fused then apical portion not bulbous and pubescent (*e.g.*, Fig. 285, as in Fig. 290) 85

85. Terminalia with parameres separate (Fig. 285) . . . . *Palpomyia* Meigen [in part], *Sphaeromias* Curtis [in part; *S. eugenei*, *S. pistiae*], *Mackerrasomyia* Debenham [in part], *Anebomyia* Borkent [in part]

– Terminalia with parameres fused at least in part (as in Figs 282, 290) . . . . *Palpomyia* Meigen [in part], *Sphaeromias* Curtis [in part; *S. litoraurea*]

86. Wing vein M_2 strongly curved near base (Fig. 166); palpus 4-segmented (Fig. 66). . . . .*Stenoxenus* Coquillett [in part]

– Wing vein M_2 not, or only slightly curved near base (*e.g.*, Figs 158–165); palpus 5-segmented (as in Figs 61–64). 87

87. Tarsomere 5 with stout black, blunt ventral spines (batonnet spines) (*e.g.*, Figs 229–237, 241–243); abdominal tergites without anteriorly directed apodemes; sternite 8 with (*e.g.*, Figs 300, 301), or without (*e.g.*, Fig. 302), posterior setal tufts of long, medially overlapping, curved setae (HEBETULINI, JOHANNSENOMYIINI, SPHAEROMIINI) 88

– Tarsomere 5 without ventral spines, or if with some ventral spines then these slender with sharp tips or only moderately developed (*e.g.*, Fig. 259); abdomen with at least tergite 7 with (*e.g.*, Fig. 303), or without tergal apodemes (not visible in some teneral or young specimens); sternite 8 without setal tufts (*e.g.*, Fig. 303) (PALPOMYIINI) 100

88. Tarsal claws unequal, at least on hind leg (*e.g.*, Figs 247–249), or with single long claw with basal tooth (*e.g.*, Figs 232–237, 241–243) 89

– Tarsal claws equal on all legs (*e.g.*, Figs 245, 250–253) 92

89. Tarsal claws unequal on mid- and hind legs, equal on fore leg (Figs 247–249) . . . . *Johannsenomyia* Malloch [in part]

– Tarsal claws unequal on all legs (*e.g.*, Figs 232–237, 241–243) 90

90. All legs with tarsal claws each with 1 short to very short pointed tooth, with blunt external basal tooth (Figs 232–234); tarsomeres 5 with 3 or more pairs of batonnet spines throughout length (Figs 232–234). . . . . *Dibezzia* Kieffer [in part]

– All legs with tarsal claws each single, with slender basal tooth (*e.g.*, Figs 235–237, 241–243); tarsomeres 5 with batonnet spines variable (*e.g.*, Figs 235–237, 241–243) 91

91. Thorax with mesonotum shiny black; tarsomeres 5 with 2–3 pairs of ventral batonnet spines on basal portion only (Figs 235–237); tarsomeres 4 cordiform (Figs 235–237) . . . .*Hebetula* Wirth & Debenham [in part]

– Thorax with mesonotum densely whitish to greyish pruinescent; tarsomeres 5 with 4 or more pairs of ventral batonnet spines along entire length (Figs 241–243); tarsomeres 4 cylindrical (Figs 241–243) . . . . *Xenohelea* Kieffer

92. Tarsal claws each with basal internal and external teeth, internal teeth flat and laminate (closely adpressed) (Fig. 244); tarsomeres 5 with 12–16 short stout batonnet spines (Fig. 245); fore femur markedly swollen with 15–20 stout ventral spines (Fig. 246) . . . . . *Neosphaeromias* Das Gupta & Wirth [in part]

– Tarsal claws each with basal internal (*e.g.*, Fig. 254) or external tooth (*e.g.*, Figs 229–231), but not both in combination, internal teeth slender, not adpressed; tarsal batonnet spines and fore femur variable 93

93. Tarsal claws gently curved distally, with or without slender basal tooth on internal side (*e.g.*, Fig. 254) 94

– Tarsal claws straight or flattened distally (gently curved in *Anebomyia hansfordi* (de Meillon & Wirth, 1983)), with blunt basal external tooth, at least on one pair of legs (*e.g.*, Figs 229–231) 96

94. Costal wing vein (C) extending to *ca* 0.75 of wing length (Fig. 159); fore femur markedly swollen, with numerous short, stout ventral spines (Fig. 250) . . . . *Mackerrasomyia* Debenham [in part]

– Costal wing vein (C) extending from *ca* 0.75 (*e.g.*, Fig. 162) nearly to wing tip (*e.g.*, Fig. 37); fore femur slender, with or without spines (*e.g.*, Fig. 37) 95

95. Tarsomere 5 with 1–2 basal pairs of batonnet spines (Fig. 253) . . . . *Homohelea* Kieffer [in part]

– Tarsomere 5 with 3 or more pairs of batonnet spines (Fig. 254) . . . . *Sphaeromias* Curtis [in part]

96. Costal wing vein (C) relatively short, costal ratio: 0.74–0.85 (e.g., Figs 160, 161) 97

– Costal wing vein (C) long, extending almost to wing tip, costal ratio: > 0.90 (*e.g.*, Figs 38, 157, 158) 99

97. Wing with 1–2 radial cells, membrane usually whitish (Fig. 160), anterior veins usually pale, not prominent; thorax with mesonotum dull, usually with dense whitish to greyish pruinescence; terminalia with sclerite just ventral or anterior to ventromedial extension of sternite 9 (Fig. 300). . . . . *Nilobezzia* Kieffer [in part]

– Wing with 2 radial cells (*e.g.*, Fig. 161); membrane greyish hyaline, veins usually infuscated, more anterior veins prominent; thorax with mesonotum usually shiny yellow to black, with little or no pruinescence; terminalia without sclerite ventral or anterior to ventromedial extension of sternite 9 (although there may be ridge or slight ventral extension of sternite 9) 98

98. Femora without ventral spines; terminalia with tufts of long setae on sternite 8 (Fig. 301) . . . . *Mallochohelea* Wirth [in part]

– At least fore femur with 1 or more ventral spines; terminalia without setal tufts on sternite 8 (Fig. 302) . . . . *Anebomyia* Borkent [in part]

99. Wing with very large angular anal lobe (Fig. 157) . . . . *Jenkinshelea* Macfie [in part]

– Wing with very shallow to moderately large anal lobe (Figs 38, 39). . . . . . .*Macropeza* Meigen [in part]

100. Wing with 2 radial cells (Fig. 163) . . . . *Palpomyia* Meigen [in part]

– Wing with 1 radial cell (Figs 164, 165) 101

101. Costal wing vein (C) moderately short, with costal ratio: 0.67–0.75 (Fig. 164); fore femur with (Fig. 258) or without stout ventral spines; tarsomere 5 with or without stout ventral setae . . . . *Bezzia* Kieffer [in part]

– Costal wing vein (C) more elongate, with costal ratio: > 0.80 (Fig. 165); fore femur without stout ventral spines; tarsomere 5 with slender ventral setae with sharp, bent tips (Fig. 259) . . . . *Phaenobezzia* Haeselbarth [in part]

Larvae

1. Proleg present on prothorax (Figs 305, 306); head capsule hypognathous to prognathous (Figs 305, 306); with stout setae on head capsule and body (Figs 305, 306) (FORCIPOMYIINAE) 2

– Proleg absent on prothorax (*e.g.*, Figs 304, 307–309); head capsule anteroventrally directed (*e.g.*, Fig. 307) or prognathous (*e.g.*, Figs 304, 308, 309); without stout setae on head capsule and body anterior to anal segment (*e.g.*, Figs 304, 308, 309) 3

2. Body somewhat flattened dorsoventrally, with lateral tubercles (Fig. 306) . . . . *Atrichopogon* Kieffer

– Body cylindrical in cross-section, without lateral tubercles (Fig. 305) . . . . *Forcipomyia* Meigen

3. Head capsule anteroventrally directed (Fig. 307); terminal segment of abdomen with series of crochets, sometimes arranged as 2 groups (often retracted and difficult to discern in alcohol material), never with elongate setae (Fig. 307) (DASYHELEINAE) . . . . *Dasyhelea* Kieffer

– Head capsule prognathous; terminal segment of abdomen simple, without crochets, with or without elongate setae (*e.g.*, Figs 304, 308, 309). 4

4. Head capsule somewhat weakly pigmented, with well-developed, posteriorly directed apodemes extending into prothorax (Figs 304, 310, 311); abdomen with segments secondarily divided (Fig. 304) (LEPTOCONOPINAE) . . . . *Leptoconops* Skuse

– Head capsule well-developed, lacking apodemes posterior to margin of head capsule (*e.g.*, Figs 312–317); abdomen with segments normal, not secondarily divided (*e.g.*, Figs 308, 309) (CERATOPOGONINAE). 5

5. Head capsule with all setae simple (*e.g.*, Figs 312–315) 6

– Head capsule with 1 or more of setae s, u and posterior o plumose (*e.g.*, Figs 316, 317) 7

6. Head capsule very small compared to rest of body. . . . . *Serromyia* Meigen

– Head capsule normally sized (Fig. 308) . . . . *Culicoides* Latreille

7. Head capsule with posteroventral margin with posteriorly projecting triangular process (Fig. 317) . . . . *Sphaeromias* Curtis

– Head capsule with posteroventral margin straight, somewhat curved or rounded . . . . (CERATOPOGONINI [in part], JOHANNSENOMYIINI, PALPOMYIINI)

Synopsis of the fauna

Although no up-to-date published catalogue is available, there are currently 928 named species, placed in 53 named genera of Ceratopogonidae recorded from the Afrotropical Region. A world catalogue of species is kept current by Borkent (2016*a*) and which, when compared to the catalogues of Wirth *et al*. (1980) and Segerman (1996), the modifications noted by de Meillon & Wirth (1991), as well as additional literature, allowed for a list of African species to be determined. There are certainly many additional species awaiting description, especially in the genera *Atrichopogon*, *Culicoides*, *Dasyhelea*, *Forcipomyia* and *Stilobezzia*. In addition, the report of an Undescribed genus here, based on a quite limited survey of material, also likely indicates the presence of significant additional diversity.

Species of the family may be found at all elevations and in virtually every habitat where there is even a little moisture. De Meillon & Wirth (1991) provided an excellent source of information on each genus, other than *Culicoides*, for the Afrotropical fauna. Borkent (2014) described all known pupae of the world (45 genera), provided bionomic information and listed all references describing eggs, larvae and pupae of all Ceratopogonidae. Four fossil species, all in *Ceratopogon*, are recorded from Madagascan copal by Meunier (1912), but the specimens are lost and the true identity of the species is uncertain.

Afrohelea **Wirth** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus with the single described species, *A. capensis* (de Meillon & Hardy, 1954), recorded from a few localities in the Western Cape Province of South Africa (de Meillon & Hardy 1954). Wirth (1965) and Wirth & Grogan (1988: 13) suggested the genus may be closely related to *Echinohelea*. Males lack a well-developed plume, suggesting that they do not swarm. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

Afrostilobezzia **Szadziewski & Dominiak** (Ceratopogoninae: Ceratopogonini)**.** This recently recognised endemic genus includes two Afrotropical species restricted to West Africa (Szadziewski & Dominiak 2015). *Afrostilobezzia ornatithorax* Clastrier, 1988, previously placed in *Stilobezzia*, is recorded from Guinea and the other, *A. clastrieri* Szadziewski & Dominiak, 2015 is restricted to Nigeria. Only female adults are known. Szadziewski & Dominiak (2015) considered the genus to be sister-group of the diverse and virtually cosmopolitan genus *Stilobezzia*. Immatures remain unknown. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

Allohelea **Kieffer** (Ceratopogoninae: Ceratopogonini)**.** A genus of 59 described species occurring in all zoogeographical regions, except Antarctica. Sixteen species occur in the Afrotropical Region, recorded mostly from Democratic Republic of Congo, Ghana, Guinea, Republic of Congo, South Africa and one species from Seychelles. Males are unique in the family in having an enlarged hind leg and a single hind claw (Fig. 173), as in the predaceous female (Fig. 12). The monotypic genus *Boreohelea* Clastrier & Delécolle, was recently placed as a junior synonym of *Allohelea* by Alwin-Kownacka *et al*. (2016). Its type species *A. afrotropica* (Clastrier & Delécolle, 1990), known only from the female holotype, is the only representative of this genus with plain wings. Other species have wing pigmentation over at least crossvein *r–m* and distal to vein R_3 (Figs 100, 101, 127, 128). The pupa of one Afrotropical species, *A. mimas* (de Meillon, 1939) has been described and was collected among grass in a stream (de Meillon 1939*a*, as *Monohelea*). The larva and pupa of a Palaearctic species have been described (Borkent 2014), the only other immatures known. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. An identification key, mostly to male adults, was provided by Clastrier & Delécolle (1990).

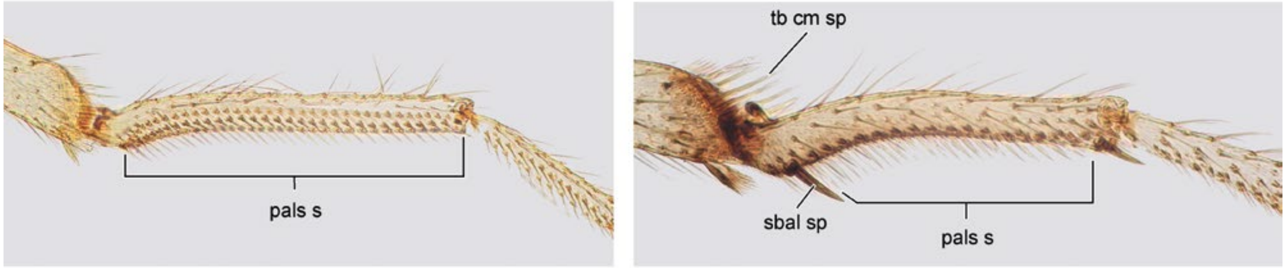
***Alluaudomyia* Kieffer** (Ceratopogoninae: Ceratopogonini)**.** A diverse genus of 206 described species occurring in all zoogeographical regions, except Antarctica. Forty-six species are recorded from the Afrotropical Region. *Alluaudomyia* keys out twice (for males) and three times (for females) in the above identification key, in part due to what is likely an undescribed species from Madagascar which lacks a pigmentation pattern. The wing of this species is more or less uniformly pigmented brown, as are the legs and remainder of the body. The species is known only from a male and female that are slide-mounted and housed in the Swedish Museum of Natural History. Adults of *Alluaudomyia* are otherwise small, generally brightly patterned predaceous midges (Fig. 9), with larvae that inhabit a variety of aquatic habitats where they typically swim rapidly on the surface film (a unique and distinctive behaviour). One African species, *A. maculithorax* (Carter, Ingram & Macfie, 1921), has been described as a larva and three (*A. claudia* de Meillon, 1942, *A. maculithorax* and *A. natalensis* de Meillon, 1939), have been described as pupae (Borkent 2014; de Meillon 1939*b*; Mayer 1955). Immatures have been collected from debris at stream margins with abundant vegetation in Democratic Republic of Congo, where larvae were predaceous on larvae of *Forcipomyia*. Other immatures have been found in such habitats as ponds, streams, stagnant water with abundant organic material, swampy mud and a tree hole in a mango tree. The larvae of nine species and the pupae of 20 extralimital species have been described and have been additionally collected from bogs, fens, swamps, tree holes and the margins of streams, creeks, rivers and lakes

167 *Leptoconops* (*Holoconops*) ♀

168 *Forcipomyia* (*Forcipomyia*) ♀

169 *Culicoides* ♀

170 *Alluaudomyia* ♀

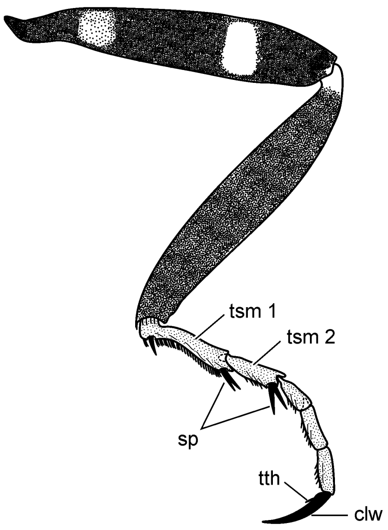


171 *Stilobezzia* (*Acanthohelea*) ♀

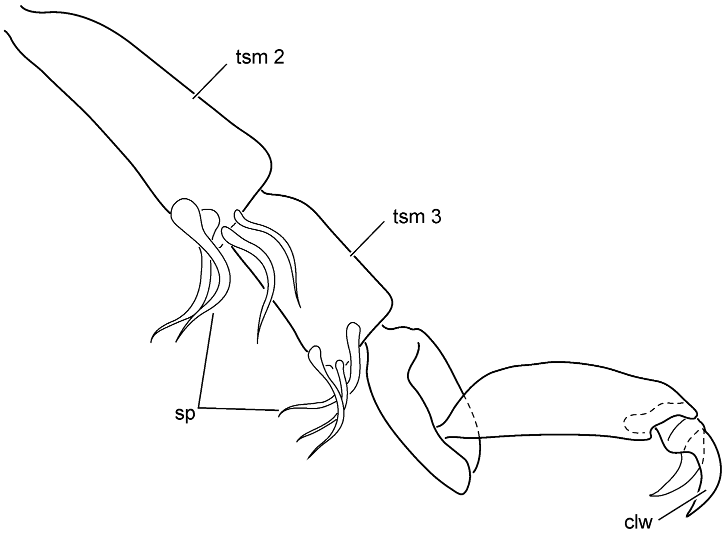
172 *Kolenohelea* ♀

Figs 34.167–172. Tarsomere 1 of right hind legs of female Ceratopogonidae (posterior views) (all non-Afrotropical, except Fig. 172): (167) *Leptoconops* (*Holoconops*) *catawbae* (Boesel); (168) *Forcipomyia* (*Forcipomyia*) *bipunctata* (L.); (169) *Culicoides variipennis* (Coquillett); (170) *Alluaudomyia parva* Wirth; (171) *Stilobezzia* (*Acanthohelea*) *lutea* (Malloch); (172) *Kolenohelea mira* de Meillon & Wirth.

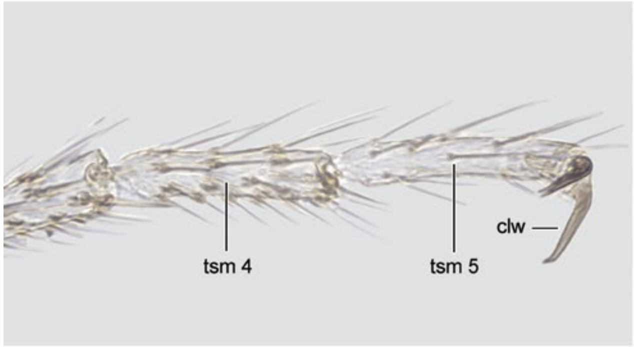
Abbreviations: pals s – palisade setae; sbal sp – sub-basal spine; tb – tibia; tb cm sp – tibial comb spine; tsm – tarsomere.



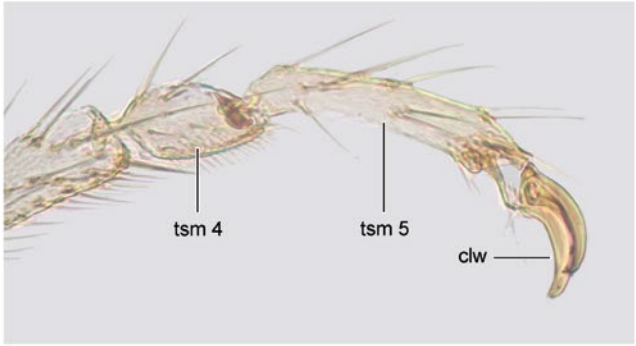
173 *Allohelea* ♂



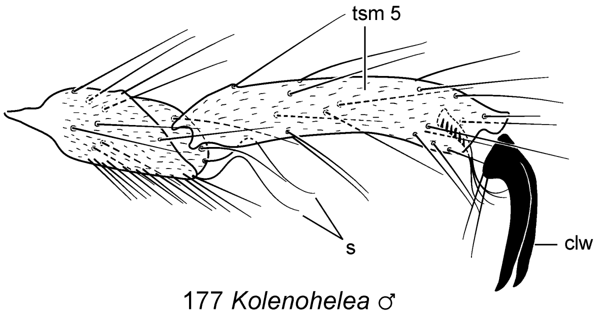
174 *Luciamyia* ♂



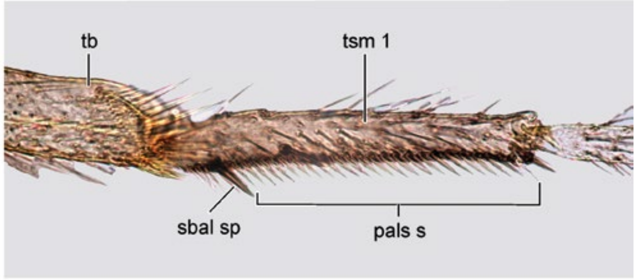
175 *Downeshelea* ♂



176 *Stilobezzia* (*Acanthohelea*) ♂



177 *Kolenohelea* ♂



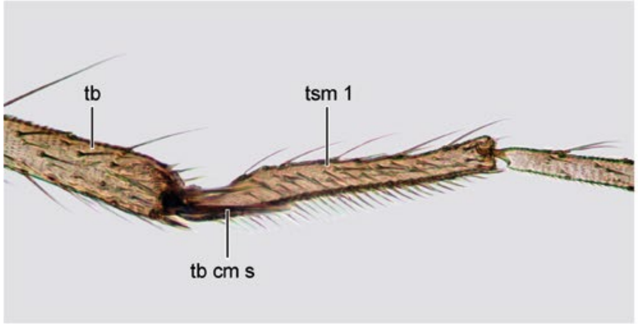
178 *Capehelea* ♂

Figs 34.173–178. Leg features of male Ceratopogonidae: (173) right hind leg of *Allohelea afra* Clastrier & Delécolle, posterior view; (174) hind tarsomeres 2–5 of *Luciamyia biloba* de Meillon, lateral view; (175) hind tarsomeres 4–5 of *Downeshelea stonei* (Wirth), lateral view (non-Afrotropical); (176) same, *Stilobezzia* (*Acanthohelea*) *lutea* (Malloch) (non-Afrotropical); (177) same, *Kolenohelea uysorum* de Meillon, Meiswinkel & Wirth; (178) right hind tarsomere 1 of *Capehelea steli* de Meillon & Wirth, posterior view. Fig. 173 (after Clastrier & Delécolle 1990, fig. 2A), Fig. 174 (after Wirth & Grogan 1988, fig. 30k), Fig. 177 (after de Meillon *et al*. 1982, fig. 23).

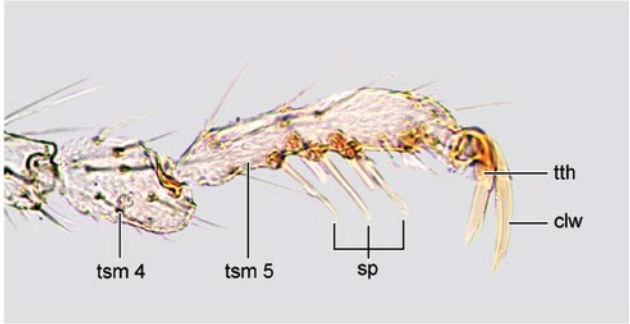
Abbreviations: clw – claw; pals s – palisade setae; s – seta; sbal sp – sub-basal spine; sp – spine; tb – tibia; tsm – tarsomere; tth – tooth.

(Borkent 2014). Some species have been reared from wet leaves and mud associated with the aforementioned habitats. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (as in Fig. 17) (Downes 1978). A worldwide identification key to species by de Meillon (1939*b*) included 12 species from the Afrotropical Region. Those Afrotropical species with only two pigmentation patches on the wing (basal to *r–m* crossvein and at the apex of vein R_3) were keyed by de Meillon & Wirth (1983*a*) (who did not include *A. anserina* de Meillon & Wirth, 1983). The remainder require an examination of the primary taxonomic literature to identify these.

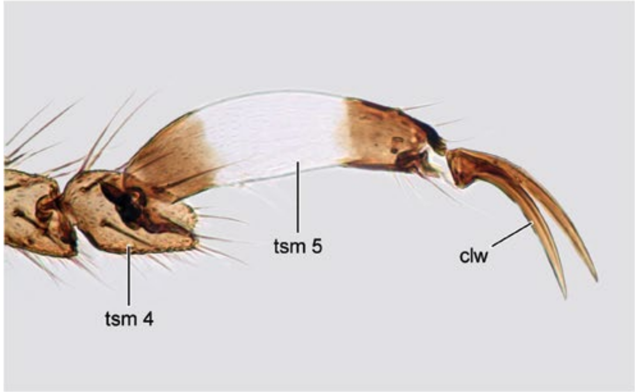
***Anebomyia* Borkent** (Ceratopogoninae: Johannsenomyiini)**.** A recently recognised genus of nine species occurring in the Afrotropical, Palaearctic (China) and Nearctic Regions. Further



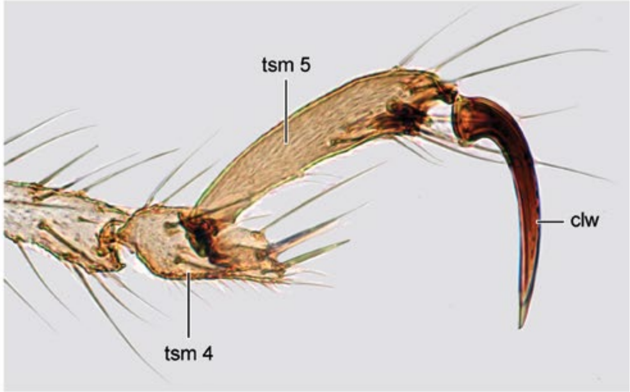
179 *Alluaudomyia* ♂



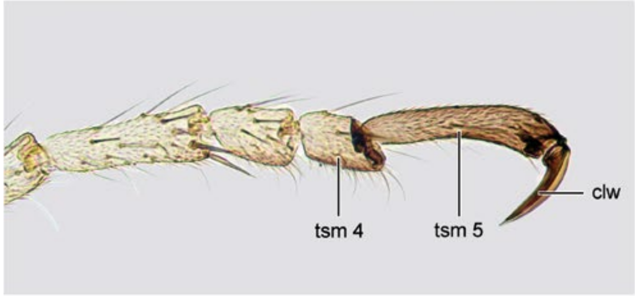
180 *Johannsenomyia* ♂



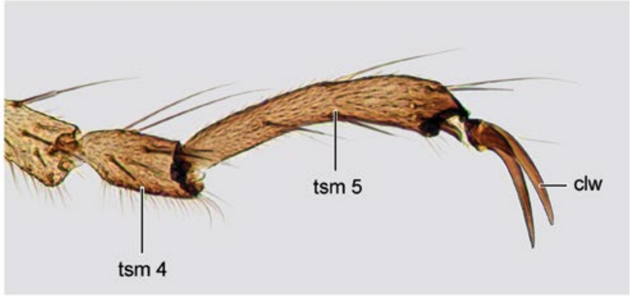
181 *Clinohelea* (*Clinohelea*) ♂



182 *Clinohelea* (*Clinohelea*) ♂



183 *Tetrabezzia* ♂



184 *Tetrabezzia* ♂

Figs 34.179–184. Leg features of male Ceratopogonidae (lateral views): (179) right hind tarsomere 1 of *Alluaudomyia* sp., posterior view; (180) hind tarsomeres 4–5 of *Johannsenomyia argentata* (Loew) (non-Afrotropical); (181) fore tarsomeres 4–5 of *Clinohelea* (*Clinohelea*) *curriei* (Coquillett) (non-Afrotropical); (182) same, hind tarsomeres 4–5; (183) fore tarsomeres 4–5 of *Tetrabezzia pictipennis* (Kieffer) (non-Afrotropical); (184) same, hind tarsomeres 4–5.

Abbreviations: clw – claw; sp – spine; tb cm s – tibial comb seta; tb – tibia; tsm – tarsomere; tth – tooth.

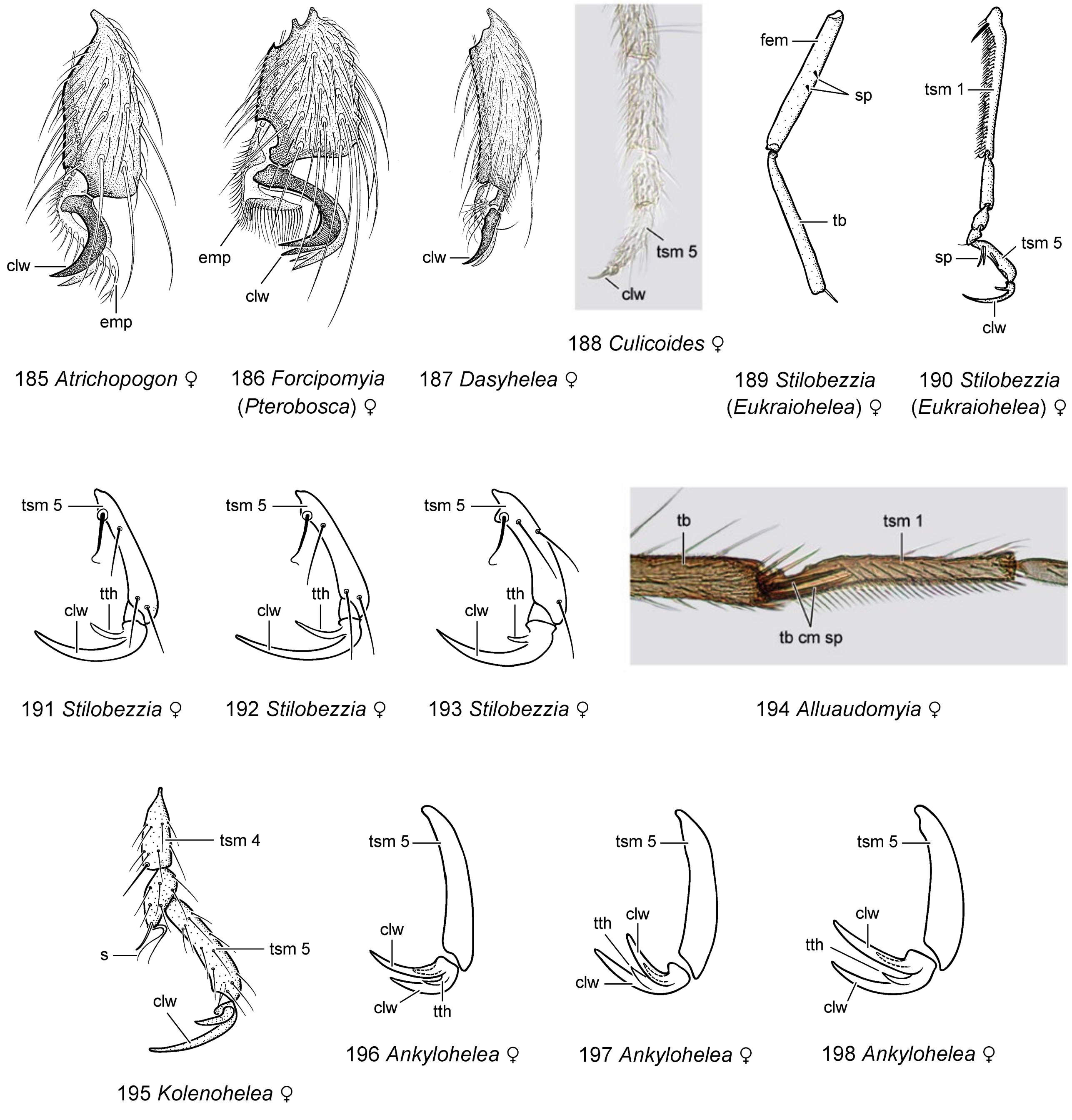
study of species of the virtually cosmopolitan genus *Mallochohelea* Wirth, from which *Anebomyia* was separated, will likely reveal additional species requiring transfer. Six species occur in the Afrotropics, restricted to Kenya, Madagascar and South Africa (Borkent 2014, 2015). All are known as both sexes, other than *A. aukurabis* (de Meillon & Wirth, 1983), which is known only as a female. Adults are of moderate size, with a wing length of 2–3 mm and are slender to moderately stout. The only Afrotropical immatures known are those of the pupa of *A. fluminea* (Borkent, 2014), collected from the margin of a water storage tank (de Meillon & Wirth 1981*b*). Otherwise, the larva and pupa of one Nearctic species are known, from algae-covered pond weeds and the margin of a small lake (Borkent 2014). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Females are cannibalistic on males during copulation, as evidenced by the collection of females with their abdomens bearing a male's dried terminalia (a known relationship in a number of other genera (Downes 1978)). *Mallochohelea kirki* (Macfie, 1939), known only as a female, will key to *Anebomyia* in the above identification key, but its generic placement is uncertain and it therefore remain in *Mallochohelea* (Borkent 2016*a*). *Anebomyia siricis* (de Meillon, 1961) and *A. fluminea* (de Meillon & Wirth, 1981) can be keyed with the identification key to species of *Mallochohelea* provided by de Meillon & Wirth (1981*b*), but identification of the remaining four species requires study of the original descriptions.

***Ankylohelea* de Meillon & Wirth** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *A. montana* de Meillon & Wirth, 1987, is known as both sexes from a single locality in South Africa (de Meillon & Wirth 1987*b*). Adults are small and brown and the male has a somewhat reduced plume (with sparse long verticils), suggesting that this species does not swarm. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Atrichopogon* Kieffer** (Forcipomyiinae)**.** A genus of 527 described species occurring in all zoogeographical regions, except Antarctica. Sixty-four species are recorded from the Afrotropical Region. The overall systematics of the genus is chaotic and most Afrotropical species cannot be identified with confidence (as is the case in the rest of the world). Adults have a uniquely swollen paratergite bearing at least one stout seta. Globally, 7% of species are known as larvae and pupae, but in the Afrotropical Region the larvae and pupae have been described for only two species (*A. ochrosoma* (Ingram & Macfie, 1921) (Ingram & Macfie 1921) and *A. victoriae* de Meillon, 1942 (Mayer 1955)). Larvae are aquatic to terrestrial and have distinctive elongate dorsal setae and tubercles (Fig. 306) (a feature shared with many *Forcipomyia*, see Fig. 305). They creep on substrates using their anterior and posterior prolegs, grazing on micro-organisms and algae (Nielsen 1951). Pupae also have tubercles and retain the larval exuviae on their abdomens (Fig. 319). Immature stages are particularly rich in morphological features (unlike adults) and will be an important component of the future systematics of the group in the Afrotropics (and elsewhere). Adults are a common component of most samples from Malaise and light traps and both sexes are often on flowers (especially those that are small and white), where they obtain nectar (but see below) (Figs 5, 6, 26–28). In spite of their virtually ubiquitous presence, observations of female adult blood-sucking are few, with records of feeding on other animals for only 10 described species of *Atrichopogon* (worldwide) on either true or false blister beetles (Coleoptera: Meloidae and Oedemeridae) or the wings of Lepidoptera (Borkent & Rocha Filho 2006). Other unnamed species have been observed feeding on Tipulidae (Fig. 24), mealybugs or dead earthworms. Downes & Smith (1969) observed unidentified *Atrichopogon* feeding on dead insects in a spider web and Marshall *et al*. (2016) observed a species feeding on termites recently captured by a spider in Ecuador. In the Afrotropical Region, this chapter provides the first report of *Atrichopogon* (females) feeding on Meloidae in South Africa (Fig. 25) although Hemp *et al*. (1999) recorded two unnamed species of *Atrichopogon* (males and females) at cantharidin (also produced by Meloidae and Oedemeridae) traps in Kenya, Tanzania and Uganda. A few species of *Atrichopogon*, unique within the biting nematocerous flies, derive their female specific food by piercing pollen grains and sucking pollen sap (Borkent & Rocha Filho 2006; de Meillon & Wirth 1989; Downes 1955). Goetghebuer (1935, 1948) provided identification keys to species from Democratic Republic of Congo and de Meillon & Wirth (1989) discuss the Afrotropical species placed in the subgenus *A.* (*Psilokempia* Enderlein). Boorman & van Harten (2002) described species from the Arabian Peninsula.

***Bezzia* Kieffer** (Ceratopogoninae: Palpomyiini)**.** A genus of 324 described species occurring in all zoogeographical regions, except Antarctica. Of the 39 species recorded from the Afrotropical Region, 18 are known only from males, seven from females only and 14 from both sexes. Adult females have abdominal tergal apodemes that are present in females of other representatives of the tribes Palpomyiini and Stenoxenini (Fig. 303). Globally, 9% of species are known as larvae (Fig. 309) and 16% as pupae (Fig. 324). In the Afrotropics, the larva and pupa of *B. albicornis* (Meigen, 1818) (as *B. strobli* Kieffer, 1919), the pupae of *B. africana* Ingram & Macfie, 1923 and *B. amana* de Meillon & Wirth, 1981 have been described (Borkent 2014; de Meillon & Wirth 1981*b*; Glukhova 1979). Afrotropical larvae of 11 species, although not described, have been recorded from rice fields, seepage pools, margin of a brackish stream, hoof prints in a sandy creek bed, stream margins, rivers, margins of a water storage impoundment and from moss on a wall (de Meillon & Wirth 1991). Among adult collections, this is the most common genus in the tribe Palpomyiini in the Afrotropics (Fig. 18). Females have coarsely-serrated mandibles and have been observed feeding on nematocerous Diptera of nearly equal size in other regions (as in Fig. 17) (Downes 1978). Females are also cannibalistic on males during copulation and upon completion, the dry husk of the male body breaks off, leaving the male's terminalia still clasped onto that of the female, thereby functioning as a mating plug (as in Fig. 30) (Downes 1978). Female adults have eversible abdominal sacs that are attached to internal tergal apodemes and that are everted at times during flight (Borkent & Craig 1994). Haeselbarth (1975) provided a partial identification key to 16 Afrotropical species in the *B. africana* species-group. Boorman & van Harten (2002) described species from the Arabian Peninsula.

***Bothahelea* Grogan & Wirth** (Ceratopogoninae: Ceratopogonini)**.** An endemic genus of three described species, *B. nama* de Meillon & Wirth, 1987 from South Africa and *B. gigantostyla* Grogan & Wirth, 1983 and *B. phelpsi* Grogan & Wirth,



185 *Atrichopogon* ♀

186 *Forcipomyia* (*Pterobosca*) ♀

187 *Dasyhelea* ♀

188 *Culicoides* ♀

189 *Stilobezzia* (*Eukraiohelea*) ♀

190 *Stilobezzia* (*Eukraiohelea*) ♀

191 *Stilobezzia* ♀

192 *Stilobezzia* ♀

193 *Stilobezzia* ♀

194 *Alluaudomyia* ♀

195 *Kolenohelea* ♀

196 *Ankylohelea* ♀

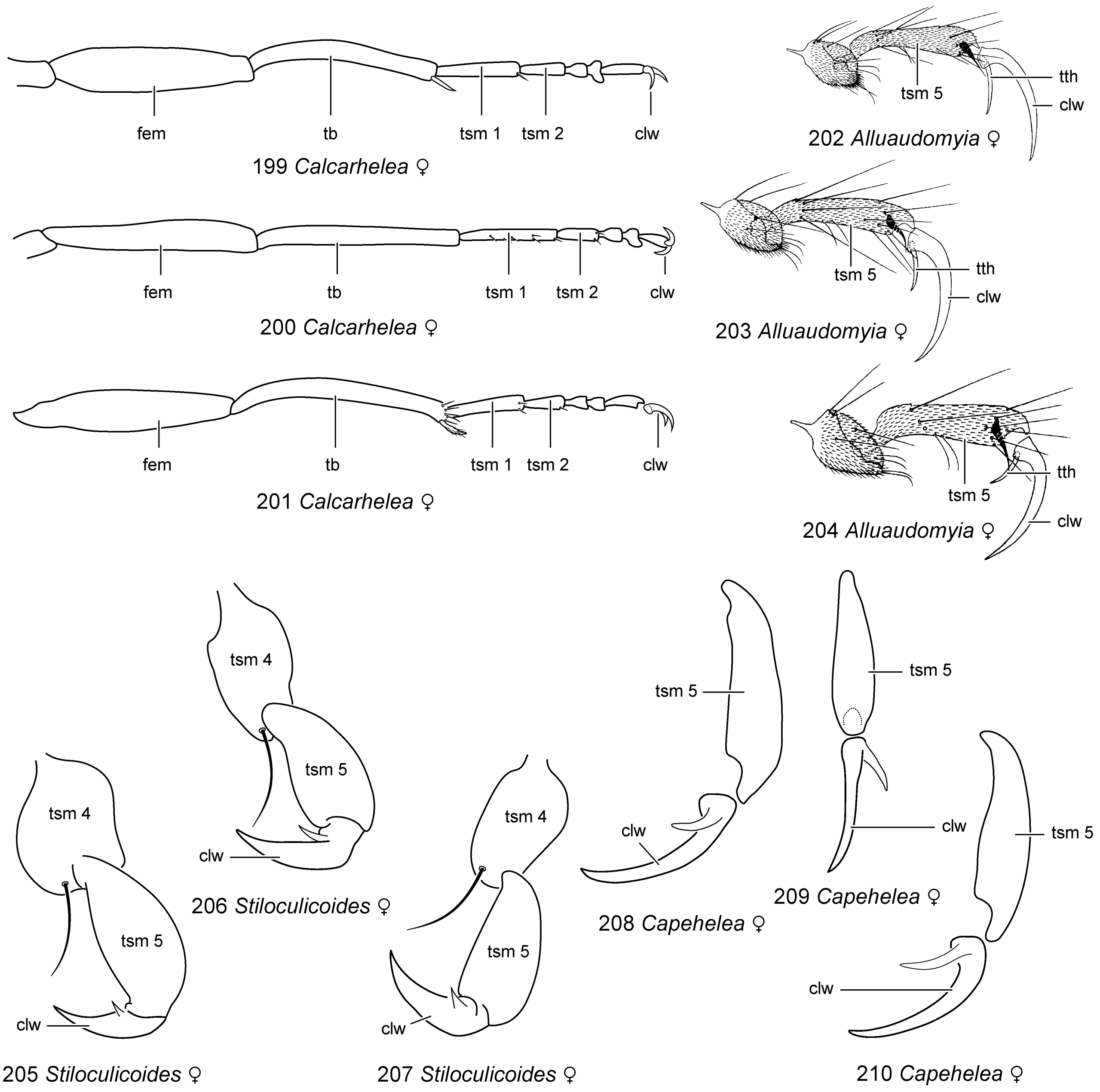
197 *Ankylohelea* ♀

198 *Ankylohelea* ♀

Figs 34.185–198. Leg features of female Ceratopogonidae (lateral views): (185) hind tarsomere 5 of *Atrichopogon levis* (Coquillett) (non-Afrotropical); (186) same, *Forcipomyia* (*Pterobosca*) *fusicornis* (Coquillett) (non-Afrotropical); (187) same, *Dasyhelea pseudoincisurata* Waugh & Wirth (non-Afrotropical); (188) same, *Culicoides arboricola* Root & Hoffman (non-Afrotropical); (189) fore femur and tibia of *Stilobezzia* (*Eukraiohelea*) *elegantula* (Johannsen) (non-Afrotropical); (190) same, hind tarsomere 1–5; (191) fore tarsomere 5 of *Stilobezzia* sp.; (192) same, mid tarsomere 5; (193) same, hind tarsomere 5; (194) hind tarsal comb and tarsomere 1 of *Alluaudomyia* sp.; (195) hind tarsomeres 3–5 of *Kolenohelea ornata* Clastrier; (196) fore tarsomere 5 of *Ankylohelea montana* de Meillon & Wirth; (197) same, mid tarsomere 5; (198) same, hind tarsomere 5. Figs 185–187 (Downes & Wirth 1981, figs 65–67), Figs 189, 190, 196–198 (after Wirth & Grogan 1988, figs 47h, 47i, 5f, respectively), Figs 191–193 (after Clastrier 1983*d*, fig. 34G), Fig. 195 (after Clastrier 1984*c*, fig. 2G).

Abbreviations: clw – claw; emp – empodium; fem – femur; s – seta; sp – spine; tb – tibia; tb cm sp – tibial comb spine; tsm – tarsomere; tth – tooth.

1983 from Zimbabwe. Adults of both sexes have been collected with either truck traps or with light traps (de Meillon & Wirth 1987*a*; Grogan & Wirth 1983). Male terminalia are large and bulbous, with the epandrium with enlarged apicolateral processes. Immatures remain unknown and the specific larval habitats of species in this genus are unknown. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.



199 *Calcarhelea* ♀

200 *Calcarhelea* ♀

201 *Calcarhelea* ♀

202 *Alluaudomyia* ♀

203 *Alluaudomyia* ♀

204 *Alluaudomyia* ♀

205 *Stiloculicoides* ♀

206 *Stiloculicoides* ♀

207 *Stiloculicoides* ♀

208 *Capehelea* ♀

209 *Capehelea* ♀

210 *Capehelea* ♀

Figs 34.199–210. Leg features of female Ceratopogonidae (lateral views): (199) fore leg of *Calcarhelea bimater* (de Meillon & Hardy); (200) same, mid leg; (201) same, hind leg; (202) fore tarsomeres 4–5 of *Alluaudomyia magoebai* de Meillon, Meiswinkel & Wirth; (203) same, mid tarsomeres 4–5; (204) same, hind tarsomeres 4–5; (205) fore tarsomeres 4–5 of *Stiloculicoides ugandae* (Ingram & Macfie); (206) same, mid tarsomeres 4–5; (207) same, hind tarsomeres 4–5; (208) fore tarsomere 5 of *Capehelea steli* de Meillon & Wirth; (209) same, mid tarsomere 5; (210) same, hind tarsomere 5. Figs 199–201, 205–207, 208–210 (after Wirth & Grogan 1988, figs 13f–h, 48e, 15e), Figs 202–204 (de Meillon *et al.* 1982, figs 13–15).

Abbreviations: clw – claw; fem – femur; tb – tibia; tsm – tarsomere; tth – tooth.

***Bothamia* Meiswinkel** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus with the single described species, *B. demeilloni* Meiswinkel, 1987, described as small, yellowish brown adults, sampled with light traps in various locations in the former northern Transvaal, South Africa. These light traps were situated near small shallow lakes (termed *vleis* in the original description), in a town garden and on the grounds of a hospital (Meiswinkel 1987). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Brachypogon* Kieffer** (Ceratopogoninae: Ceratopogonini)**.** A genus of 201 described species of small, black midges occurring in all zoogeographical regions, except Antarctica. The genus is divided into three subgenera as recognised by Debenham (1991), Grogan (1982) and Wirth & Grogan (1988: 26). *Brachypogon sensu stricto* adults are generally smaller in size, with 0–1 or more rarely two setae on palpal segment 4, 0–1 radial cells, vein M_2 usually absent, the wing without macrotrichia and usually with one well-developed spermatheca. The subgenus *B.* (*Isohelea* Kieffer) are generally larger in size, with two, or rarely one or three setae on palpal segment 4, usually with two small radial cells, vein M_2 usually present, the wing usually with macrotrichia and usually two, rarely one, well-developed spermatheca (Wirth & Grogan 1988: 27). Readers will note the repeated use of "usually" and "rarely" in this characterisation, indicating the poor separation of some species. The subgenus *B.* (*Sarrissohelea* Debenham) includes five Oriental or Australasian species. The Afrotropical Region includes 34 species, with 28 of these in *Brachypogon sensu stricto* and six in *B.* (*Isohelea*) (a sixth species *B.* (*I.*) *albipennis* (Kieffer, 1921) is *nomen dubium*). There are numerous undescribed species in the Holarctic Realm and it appears likely that there are also numerous undescribed species in the Afrotropics. Female adults of species of *Brachypogon* have coarse mandibular teeth and feed on other nematocerous Diptera of similar size, generally entering swarms of Chironomidae to catch their prey. No immatures have been described from the Afrotropics, although *B. africanus* de Meillon, 1929 was reared from a pupa collected in an exposed pool in South Africa. Larvae and pupae are known for four and seven species, respectively, from extralimital localities (Borkent 2014). Immatures generally occur in such small to moderately-sized lentic habitats as pools, marshes, bogs and fens, as well as the mud, sand or detritus at the margins of streams and creeks. At least within the Nearctic, species are diverse and often common in bogs and fens. Grogan & de Meillon (1993) reported nine new species from Senegal and provided an identification key to Afrotropical males (25 species) and females (11 species). They did not include a species described concurrently by Boorman & van Harten (2002) and Grogan & Wirth (1993: 30). Since then six species has been described (Grogan & de Meillon 1997; Szadziewski *et al*. 2011).

***Calcarhelea* Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *C. bimater* (de Meillon & Hardy, 1953) based on one male and four females from the Cape Province, South Africa. The single known male is not keyed here, but may be recognised based on the features discussed above (see "Identification" section). The male terminalia illustrated by Wirth & Grogan (1988: 113) differs in some subtle details from that provided by de Meillon & Hardy (1954) and the former is used here. Furthermore, there is a question as to whether the sexes are correctly associated (Wirth & Grogan 1988: 35). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

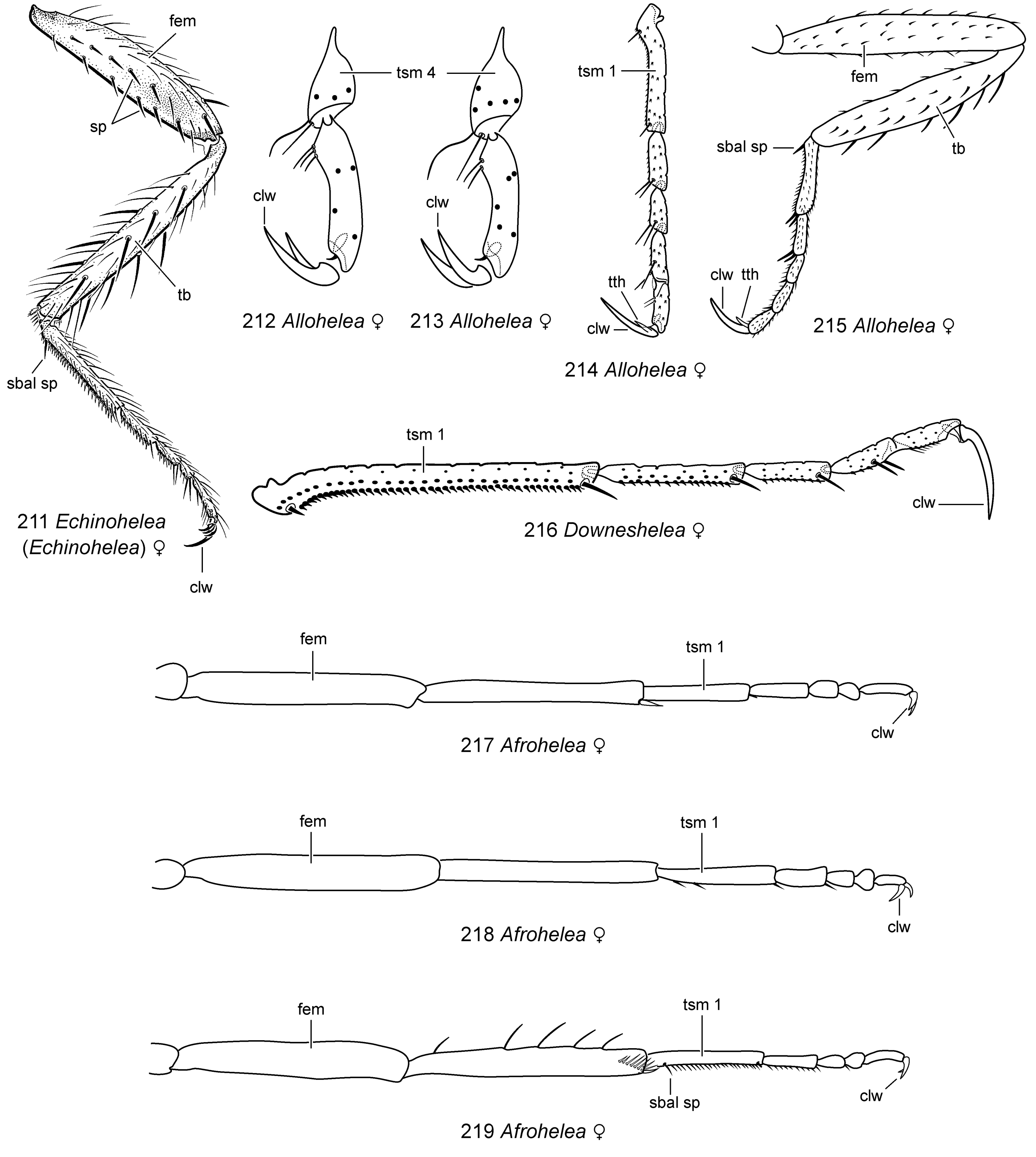
***Capehelea* de Meillon & Wirth** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *C. steli* de Meillon & Wirth, 1987, known only from 2 males and 1 female from the Cape Province, South Africa (de Meillon & Wirth 1987*b*). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Ceratohelea* Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *C. advena* (de Meillon, 1959), known from a male and 2 females from Zimbabwe. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Clinohelea* Kieffer** (Ceratopogoninae: Heteromyiini)**.** A genus of 40 elegant, predaceous species occurring in all zoogeographical regions, except Antarctica. Seven species occur in the Afrotropical Region, although their scattered distributions suggests that further species are likely present. Adults (Figs 14, 15) have long, slender legs and dark pigmentation patches on the wings. Immatures are undescribed from the Afrotropics, but *C. hygropetrica* Clastrier, 1983 has been reared from roots, moss and organic material in shallow rock pools and *C. trimaculata* Clastrier, 1983 was reared from the muddy margins of a rice paddy (de Meillon & Wirth 1991). Larvae of four and pupae of seven species have been described from elsewhere, where they have been sampled from the margins of streams, fens, seepage areas into a lake and rock pools (Borkent 2014; Knausenberger 1987). Females have coarsely-serrated mandibles and have been observed feeding on chaoborids and chironomids of nearly equal size in other regions (as in Fig. 17) (Downes 1978). Females are also cannibalistic on males during copulation and upon completion, the dry husk of the male body breaks off, leaving the male's terminalia still clasped onto that of the female, thereby functioning as a mating plug (as in Fig. 30) (Downes 1978). There is no identification key to Afrotropical species, but recent authors discuss the differences between the taxa (Clastrier 1983*b*; de Meillon & Wirth 1981*c*).

***Congohelea* Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *C. fuligipennis* (Clastrier, 1960), known from a single dark brown female, collected with a light trap from Republic of Congo (Wirth & Grogan 1988: 46). The fore femur has three widely spaced ventral spines. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Culicoides* Latreille** (Ceratopogoninae: Culicoidini)**.** A genus of 1,368 described species, the largest in the family (Figs 8, 34, 35), occurring in all zoogeographical regions, except Antarctica. The 175 validly named and described Afrotropical



211 *Echinohelea* (*Echinohelea*) ♀

212 *Allohelea* ♀

213 *Allohelea* ♀

214 *Allohelea* ♀

215 *Allohelea* ♀

216 *Downeshelea* ♀

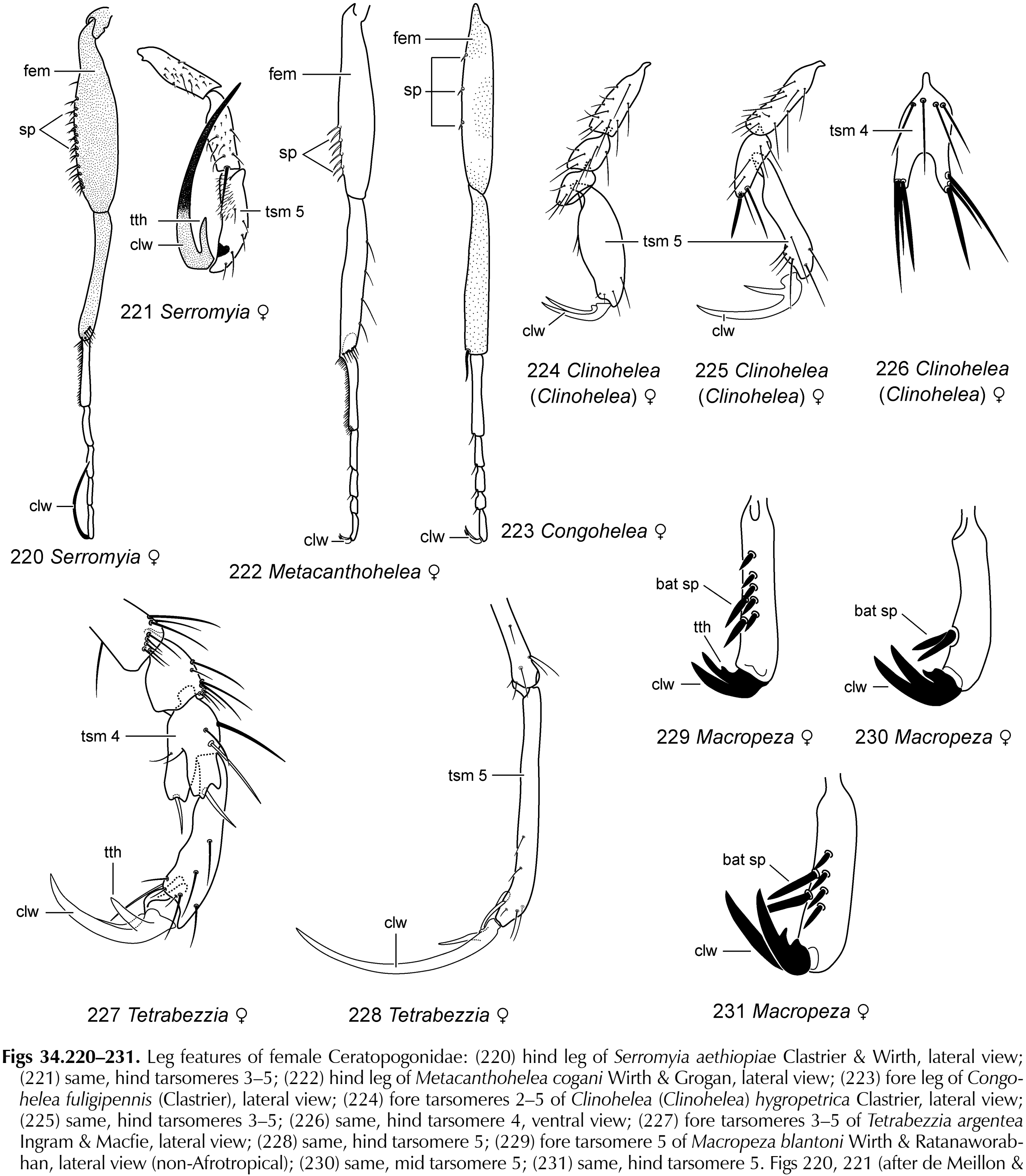
217 *Afrohelea* ♀

218 *Afrohelea* ♀

219 *Afrohelea* ♀

Figs 34.211–219. Leg features of female Ceratopogonidae (lateral views): (211) hind leg of *Echinohelea* (*Echinohelea*) *lanei* Wirth (non-Afrotropical); (212) fore tarsomeres 4–5 of *Allohelea afrotropica* (Clastrier & Delécolle); (213) same, mid tarsomeres 4–5; (214) same, hind tarsomeres 1–5; (215) hind leg of *A. johannseni* (Wirth) (non-Afrotropical); (216) hind tarsomeres 1–5 of *Downeshelea bimaculata* Clastrier & Delécolle; (217) fore leg of *Afrohelea capensis* (de Meillon & Hardy); (218) same, mid leg (219) same, hind leg. Fig. 211 (Downes & Wirth 1981, fig. 71), Figs 212, 213, 214, 216 (after Clastrier & Delécolle 1990, figs 12H, 14F), Figs 215, 217–219 (after Wirth & Grogan 1988, figs 3c, 2k–m, respectively).

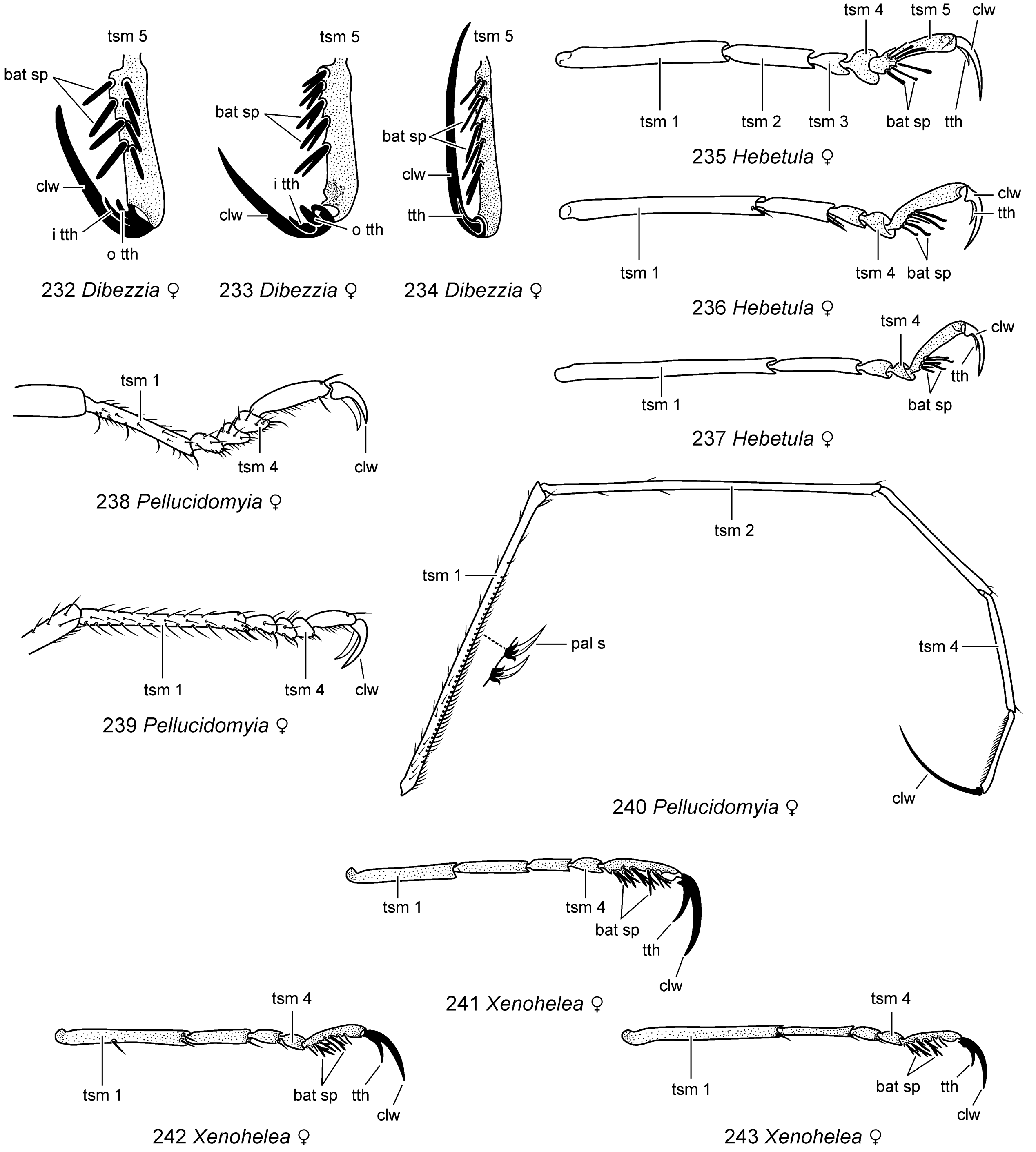
Abbreviations: clw – claw; fem – femur; sbal sp – sub-basal spine; sp – spine; tb – tibia; tsm – tarsomere; tth – tooth.



220 *Serromyia* ♀
221 *Serromyia* ♀
222 *Metacanthohelea* ♀
223 *Congohelea* ♀
224 *Clinohelea* (*Clinohelea*) ♀
225 *Clinohelea* (*Clinohelea*) ♀
226 *Clinohelea* (*Clinohelea*) ♀
227 *Tetrabezzia* ♀
228 *Tetrabezzia* ♀
229 *Macropeza* ♀
230 *Macropeza* ♀
231 *Macropeza* ♀

Figs 34.220–231. Leg features of female Ceratopogonidae: (220) hind leg of *Serromyia aethiopiae* Clastrier & Wirth, lateral view; (221) same, hind tarsomeres 3–5; (222) hind leg of *Metacanthohelea cogani* Wirth & Grogan, lateral view; (223) fore leg of *Congohelea fuligipennis* (Clastrier), lateral view; (224) fore tarsomeres 2–5 of *Clinohelea* (*Clinohelea*) *hygropetrica* Clastrier, lateral view; (225) same, hind tarsomeres 3–5; (226) same, hind tarsomere 4, ventral view; (227) fore tarsomeres 3–5 of *Tetrabezzia argentea* Ingram & Macfie, lateral view; (228) same, hind tarsomere 5; (229) fore tarsomere 5 of *Macropeza blantoni* Wirth & Ratanaworabhan, lateral view (non-Afrotropical); (230) same, mid tarsomere 5; (231) same, hind tarsomere 5. Figs 220, 221 (after de Meillon & Wirth 1983*b*, figs 6, 14), Figs 222, 223 (after Wirth & Grogan 1988, figs 32l, 19h, respectively), Figs 224–226 (after Clastrier 1983*a*, figs 6–8), Figs 227, 228 (after Ingram & Macfie 1923 figs 24b, 24d), Figs 229–231 (after Wirth & Ratanaworabhan 1972, fig. 1i).

Abbreviations: bat sp – batonnet spine; clw – claw; fem – femur; sp – spine; tsm – tarsomere; tth – tooth.



232 *Dibezzia* ♀ 233 *Dibezzia* ♀ 234 *Dibezzia* ♀

235 *Hebetula* ♀

236 *Hebetula* ♀

237 *Hebetula* ♀

238 *Pellucidomyia* ♀

239 *Pellucidomyia* ♀

240 *Pellucidomyia* ♀

241 *Xenohelea* ♀

242 *Xenohelea* ♀ 243 *Xenohelea* ♀

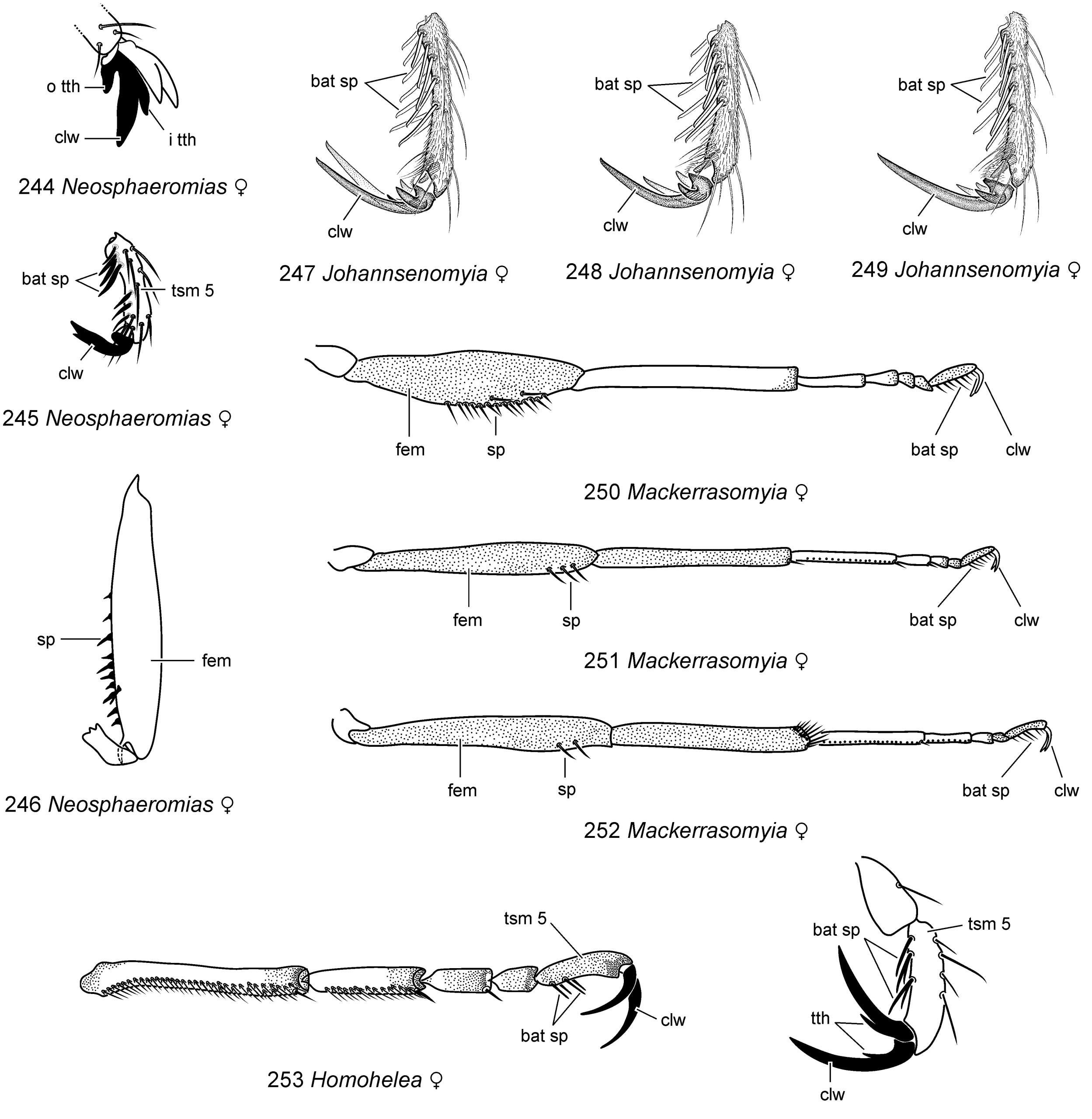
Figs 34.232–243. Leg features of female Ceratopogonidae (lateral views): (232) fore tarsomere 5 of *Dibezzia debenhamae* Wirth & Ratanaworabhan (non-Afrotropical); (233) same, mid tarsomere 5; (234) same, hind tarsomere 5; (235) fore tarsomeres 1–5 of *Hebetula tonnoiri* (Lee) (non-Afrotropical); (236) same, mid tarsomeres; (237) same, hind tarsomeres 1–5; (238) fore tarsomeres 1–5 of *Pellucidomyia ugandae* Macfie; (239) same, mid tarsomeres 1–5; (240) same, hind tarsomeres 1–5; (241) fore tarsomeres 1–5 of *Xenohelea nuansriae* Wirth & Ratanaworabhan (non-Afrotropical); (242) same, mid tarsomeres 1–5; (243) same, hind tarsomeres 1–5. Figs 232–234 (after Wirth & Ratanaworabhan 1981*a*, fig. 1f), Figs 235–237 (after de Meillon & Wirth 1991, fig. 323), Figs 238–240 (after Macfie 1939*a*, figs 10I–III), Figs 241–243 (after Wirth & Ratanaworabhan 1981*b*, fig. 3I).

Abbreviations: bat sp – batonnet spine; clw – claw; i tth – inner tooth; o tth – outer tooth; pal s – palisade setae; tsm – tarsomere.

species are widely distributed throughout the region. *Culicoides* is the largest and undoubtedly the most important genus of Ceratopogonidae, in terms of human and animal health. Numerous additional species remain undescribed and there are significant geographical gaps where the genus has never been sampled. Meiswinkel *et al*. (2004*a*: 103) reported that ⅓ of the 112 species known from South Africa alone were undescribed, a fraction still valid today, as no subsequent species have been described from there since (Meiswinkel *et al*. 2004*b*: recognised "> 120" species from South Africa). Labuschagne (2015) indicated the presence of 101 species in South Africa. Only two Afrotropical species have been described from the region in the 21st century, *C. tuttifrutti* Meiswinkel, Cornet & Dyce, 2003, from South Africa and *C. candolfii* Delécolle, Paupy, Rahola & Mathieu, 2013, from Gabon. Labuschagne (2015) described four new species from South Africa in her unpublished thesis. Further to this, distributions of the described species are mostly poorly understood. Fall *et al*. (2015a), for example, discovered an additional 19 species of *Culicoides* for Senegal by sampling five localities near the coast using a horse bait trap and two light traps. Rawlings *et al*. (1998) sampled with light traps for 12 nights at four villages in Gambia and reported 14 species, of which five were new to the country. Similarly, Gordon *et al*. (2015) collected 51 species for Zimbabwe, with 10 of these new to the country (and some undescribed). It is certain that wider surveys with additional and a variety of trap types would sample numerous additional species from these and other localities. Aside from a significant number of morphologically distinct species that require description from the Afrotropics, there are, as elegantly shown by Meiswinkel (1989, 1991, 1992), Meiswinkel & Linton (2003) and Sebastiani *et al*. (2001), species complexes, which require resolution to determine the true identity of species. Recent barcoding has also helped to define and understand some species of *Culicoides* (Augot *et al*. 2013; Bakhoum *et al*. 2013). Afrotropical species are classified into eight subgenera, seven species-groups (not ascribed to subgenera) and with an additional 40 unplaced species. The classification of Afrotropical species is particularly messy and one need only compare the arrangement in the following to see major discrepancies in the placement of many species: Boorman & Dipeolu (1979); Glick (1990); Itoua *et al*. (1987); and Khamala & Kettle (1971). There are significant opportunities to interpret morphological synapomorphies present, but almost entirely unreported, in adults, pupae and larvae of species of *Culicoides*, that would replace the present unstable classification with one based on phylogenetic relationships (Borkent 2016*b*). A global classification of all included species is provided by Borkent (2016*b*), but, as noted in that work, this is almost entirely based on phenetics. Although the classification does not present the latest arrangements (to avoid the inclusion of some recent changes that are clearly unjustified and would result in further taxonomic problems), it is likely the best arrangement of species available. In spite of their medical and veterinary significance, there is no identification key to species of the entire region. Of all biting fly groups, this genus is by far the most poorly understood from virtually every aspect of systematics. The following provide regional identification keys; names for some species have changed (these can be checked in the world catalogue (Borkent 2016*a*, *b*)): Boorman (1989): female adults of species from Oman, United Arab Emirates and Yemen, with additional records from these states by Boorman & van Harten (2002) and Szadziewski *et al*. (2011); Boorman & Dipeolu (1979): female adults of 47 species from Nigeria; Caeiro (1961): female adults of 24 species from Angola; Carter *et al*. (1920*b*): male and female adults of 17 species from Ghana (as Gold Coast); Colaço (1946): female adults from the Afrotropical Region (badly out of date); Cornet & Nevill (1980): males and females of clear-winged species from the Afrotropics; Fiedler (1951): female adults of 22 species from South Africa (badly out of date); Glick (1990): male and female adults of 55 species from Kenya; Goetghebuer (1935): female adults of 13 species from Democratic Republic of Congo; Khamal & Kettle (1971): male and female adults of 61 species from "East Africa", the results of sampling with light traps along a transect from Queen Elisabeth National Park, Uganda to Mombasa, Kenya (see Glick 1990 for major changes to this work); and Labuschagne (2015): key to 91 species and a wing atlas to 101 species in South Africa. The following provide identification keys to Afrotropical species in specific species-groups, although for some it is unclear how a given group may be recognised as such: Cornet & Brunhes (1994): male and female adults of the *C. schultzei* species-group (but see Bakhoum *et al*. 2013); Itoua & Cornet (1986): female adults of the *C. milnei* species-group; Meiswinkel & Dyce (1989): male and female adults of 10 species of *C.* (*Synhelea* Kieffer); Meiswinkel (1995): male and female adults of the *C. imicola* group; and Meiswinkel (2004): discussion of species of *C.* (*Avaritia* Fox). Probably the best known area is South Africa, where most work has been undertaken (*e.g.*, Labuschagne *et al*. 2007; Meiswinkel & Linton 2003; Meiswinkel *et al*. 2004*a*: 103, 2004*b*; Rawlings *et al*. 2003; Sebastiani *et al*. 2001; Venter & Meiswinkel 1994; Venter *et al*. 1996*a*, *b*, 1997). The genetic structure of populations of *C. imicola* in East and South Africa has been studied by Onyango *et al*. (2015). As wing patterns are so important in the identification of most *Culicoides*, some other regions have "wing atlases" including photographs of all species, as well as antennal sensilla patterns and some morphometric data (*e.g.*, Dyce *et al*. 2007: 1; Wirth *et al*. 1985, 1988). A similar publication would be very useful to help identify female adults of Afrotropical *Culicoides*, at least as a stopgap measure, until fully functional identification keys and a comprehensive taxonomic monograph become available. Labuschagne (2015) provided a wing atlas to the species of South Africa. The distributions of species of *Culicoides* (like those of virtually all other Ceratopogonidae), are poorly known, other than the distributions within South Africa for 91 species by Labuschagne (2015). Otherwise, distribution maps are available for only a few species (*e.g.*, Meiswinkel & Linton 2003). Furthermore, it is clear that many species prefer specific habitats (*e.g.*, Dipeolu 1976*a*). Becker *et al*. (2013) showed how human habitats impact the distribution of some *Culicoides* in Namibia. Immatures are poorly known with 9% of Afrotropical species known as larvae (Figs 308, 312–315) and 17% as pupae (Fig. 321) (Borkent 2014). Identification keys to some immatures are available, even though it is not possible to recognise the groups as such: Nevill (1969): eight larvae and seven pupae of South African species; Nevill & Dyce (1994): pupae of the *C. similis* species-group; Nevill *et al*. (2007): pupae of the *C. imicola* species-group; Nevill *et al*. (2009): pupae of two dung breeding *C.* (*Avaritia*). Nevill (1969) described methods of collecting, rearing and studying all stages. Female adults of some species are important vectors of various pathogens (see "Economic significance" section above). An excellent summary of the species of Afrotropical *Culicoides* as vectors, in the light of systematics, is provided by Meiswinkel *et al*. (2004*a*: 93). Afrotropical species of *Culicoides* are also important by virtue of their large numbers and are notorious as blood-feeding flies, irritatingly biting humans and domestic animals. Large numbers of adult female *Culicoides* of six species have been recorded severely biting humans: *C. fulvithorax* in Ethiopia (White 1977) and in Cameroon and Nigeria (Nicholas *et al*. 1953); *C. austeni* and *C. inornatipennis* in Cameroon and Nigeria (Nicholas *et al*. 1953); *C. trifasciellus* Goetghebuer, 1935 in Kenya (April–June) (Khamala 1975); *C. grahamii* widely distributed in the Afrotropics (Austen 1909; Caeiro 1961; Carter *et al*. 1920*a*; White 1977); and *C. leucostictus* Kieffer, 1911 in South Africa (Nevill & Nevill 1995). In addition, White (1977) reported *C. kingi* Austen, 1912 and *C. milnei* Austen, 1909 biting humans in Ethiopia, but these identifications require verification. Other animals can attract vast numbers, with females of species biting various species of reptiles, birds and mammals. In South-east Asia, one species, *C. garciai* Wirth & Hubert, 1989 even bites fish (emergent mud skippers). Females of some species of the subgenus *C*. (*Trithecoides*), many of which have coarsely-toothed mandibles, are unique in feeding on recently blood-fed mosquitoes (Culicidae) and phlebotomine sand flies (Psychodidae), although this behaviour is unknown for the two Afrotropical species; at least those of *C*. (*T*.) *fulvithorax* feed on humans and a variety of ruminants (de Meillon 1961; Glick 1990). Little is known regarding native hosts of most species of *Culicoides*, but Meiswinkel & Braack (1994) showed how five species are specialised to feed on the ears of elephants and use their dung as larval breeding sites. They also summarise and discuss further records of wild host preferences. It is highly likely that most and perhaps all ungulates, at least, are attacked by the females of one or more species of *Culicoides*, as indicated by the presence by various viral antibodies in many game animals as a reaction to viruses known to be vectored by species of *Culicoides*. The use of small mammals and birds as hosts is very poorly investigated, but these are also likely sources of blood for females of various species of *Culicoides* (Braverman & Hulley 1979; Braverman & Phelps 1981). The presence of finely-toothed mandibles for most species of Afrotropical *Culicoides* indicates that these are likely to feed on vertebrates (Borkent 1995: 129). The genus has a long history of biting vertebrates, with fossils of 47 species known mostly from various ambers (a few Tertiary species are compression fossils), the oldest being from New Jersey 90–94 MYA (Borkent 1996, 2000*a*: 355, *b*: 453). Evidence from mouthpart structures of female adults indicates that at least two Cretaceous species fed on the blood of dinosaurs (Borkent 1995: 129). Extant species that have been reared are known from numerous types of environments and these are generally small, or are restricted to aquatic or subaquatic habitats and include the following: damp or wet decomposing vegetation, manure, fungi, different types of phytotelmata, including tree holes, seed husks, springs, seeps, bogs, fens, swamps, pond and lake margins, mangrove swamps, salt marshes, stream and river margins; one species is recorded from the shells of giant land snails (Braverman 1978; Glick 1990; Khamala 1971; Meiswinkel *et al*. 2004*a*: 95; Nevill 1969). Although there are many types of habitat represented for *Culicoides*, it is clear that individual species are often quite restricted where they may be found (Dipeolu 1976*a*) and their habitat can often be described with precision. Most *Culicoides* are crepuscular, some are nocturnal feeders and a few are also diurnal (Auriault 1977; El Sinnary *et al*. 1985; Fall *et al*. 2015*b*, *c*; Itoua *et al*. 1987; Service 1969, 1971). Some nocturnal species of *Culicoides* are more active when the Moon is shining and some coastal species respond to ocean tides. The circadian activity of most species of Afrotropical *Culicoides* is, however, poorly understood in the region. Numbers also vary during the seasons or under various climatic conditions (see "Biology and immature stages" section above). Female *Culicoides* develop a distinctive brown to burgundy-red pigment of the abdomen following a blood meal and at least some species also develop further pigmentation of the abdominal sternites and tergites 2–3 (Braverman & Mumcuoglu 2009; Dyce 1969). Because biting midges only become infected after a blood meal, these useful features allows for the identification of individuals that may be vectoring organisms. There is no evidence that viruses are transmitted transovarially in Ceratopogonidae and early emerging individuals are therefore free of viral infection.

***Dasyhelea* Kieffer** (Dasyheleinae)**.** A common and mainly diurnal genus of 622 described species, occurring in all zoogeographical regions, except Antarctica, although there are certainly many more undescribed species (Fig. 7). The 114 Afrotropical species are difficult to identify and there is a need for a revision of the entire genus. Classification of the genus remains difficult, with subgeneric concepts applied locally in various regions. The situation in the Afrotropical fauna is particularly poor. The larvae of eight Afrotropical species and the pupae of 15 have been described and globally a total of 54 and 90, respectively, have been described (Borkent 2014). Pupae are morphologically diverse (Fig. 320), providing good prospects for future cladistic analysis, but larvae are generally rather homogeneous (Fig. 307). Adult females have reduced, non-biting mouthparts and both sexes are common on many flowers (particularly those that are small and white), where they feed on nectar (Fig. 29). Larvae are generally aquatic grazers on algae and detritus (some are at least opportunistic carrion-feeders (McLachlan 1981)) and occur in small aquatic habitats, such as tree holes and other phytotelmata, rock pools, on algal growth on wet mud, sand or soil or at the surface of ponds or puddles, fungi, hot springs, seeps, in moist decaying plant material and in extremely saline (but terrestrial) habitats. A few species are associated with coastal tidal areas. The larvae of *D. thompsoni* de Meillon, 1936 are desiccation resistant and are able to survive dry rock pools by encysting in capsules of hardened mucus and reviving once water reappears (McLachlan 1981; McLachlan & Ladle 2001). There are no adequate identification keys to species occurring in the region, although the following are useful for some species: Boorman & van Harten (2002): males from Yemen; Carter *et al.* (1921): males and females from Ghana; de Meillon & Downes (1986): Afrotropical species similar to *D. salta* de Meillon & Downes, 1986 (no diagnosis of this group of species is provided); de Meillon (1942*a*: 11): Afrotropical species of the *D. fusca* species-group (no diagnosis provided); and Goetghebuer (1933): males from Democratic Republic of Congo.

***Dibezzia* Kieffer** (Ceratopogoninae: Johannsenomyiini)**.** A genus of five described species, restricted to the Afrotropical and Oriental Regions. The single Afrotropical species, *D. gideoni* de Meillon & Wirth, 1981, is known from four females, sampled with a light trap from one locality in the former Transvaal of South Africa. As such, the male, as characterised in the identification key provided above, is based on species from the Oriental Region (known only for *D. debenhamae* Wirth & Ratanaworabhan, 1981 and *D. prominens* (Johannsen, 1932)).



244 *Neosphaeromias* ♀

247 *Johannsenomyia* ♀

248 *Johannsenomyia* ♀

249 *Johannsenomyia* ♀

245 *Neosphaeromias* ♀

250 *Mackerrasomyia* ♀

251 *Mackerrasomyia* ♀

246 *Neosphaeromias* ♀

252 *Mackerrasomyia* ♀

253 *Homohelea* ♀

254 *Sphaeromias* ♀

Figs 34.244–254. Leg features of female Ceratopogonidae (lateral views): (244) fore tarsal claw (one of two) of *Neosphaeromias afrotropicalis* Clastrier; (245) same, hind tarsomere 5; (246) same, fore femur; (247) fore tarsomere 5 of *Johannsenomyia argentata* (Loew) (non-Afrotropical); (248) same, mid tarsomere 5; (249) same, hind tarsomere 5; (250) fore leg of *Mackerrasomyia wongsirii* Wirth & Ratanaworabhan (non-Afrotropical); (251) same, mid leg; (252) same, hind leg; (253) hind tarsomeres 1–5 of *Homohelea iberica* Delécolle, Blasco-Zumeta & Rieb (non-Afrotropical); (254) mid leg tarsomeres 4–5 of *Sphaeromias meeseri* de Meillon. Figs 244–246 (after Clastrier 1983*b*, figs 5K, L, C, respectively), Figs 247–249 (Downes & Wirth 1981, figs 85–87), Figs 250–252 (after Wirth & Ratanaworabhan 1981*b*, fig. 1G), Fig. 253 (after Delécolle *et al*. 1997, fig. 11), Fig. 254 (after de Meillon 1942*b*, fig. 6c).

Abbreviations: bat sp – batonnet spine; clw – claw; fem – femur; i tth – inner tooth; o tth – outer tooth; sp – spine(s); tsm – tarsomere; tth – tooth.

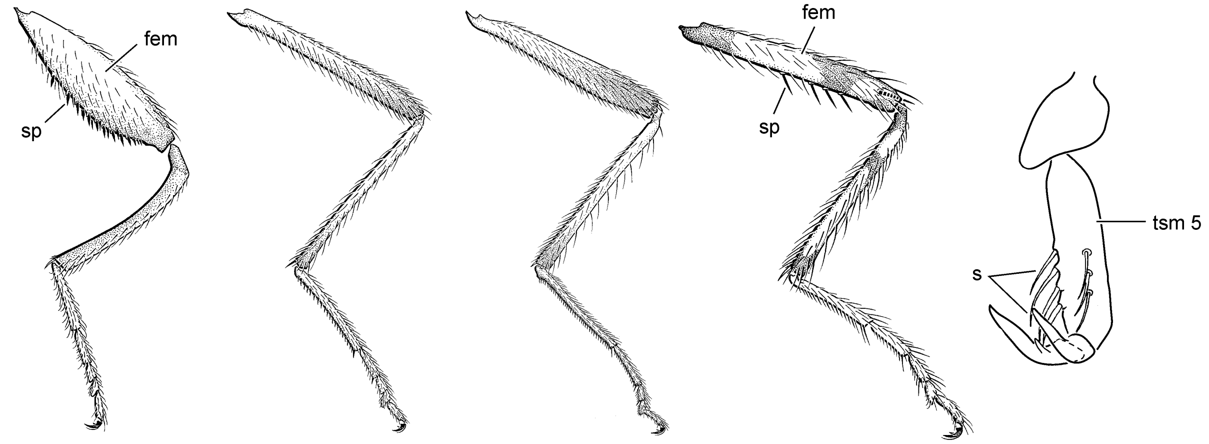
Dibezzia brevistila Kieffer, 1911, from Bangladesh, is doubtfully placed in this genus (Wirth & Ratanaworabhan 1981*a*). Adults have been reared in the Oriental Region from bamboo peat and a tree hole. Larvae remain unknown, but the pupae of two Oriental species have been described (Borkent 2014). Females have mandibles with coarse teeth, indicating that they are predaceous, likely on other nematocerous Diptera of similar size.

***Downeshelea* Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** A genus of 35 described species occurring in all zoogeographical regions, except the Palaearctic Region and Antarctica. The Afrotropical Region includes only two species: *D. bimaculata* Clastrier & Delécolle, 1990, known only from a male from Côte d'Ivoire; and *D. nigeriae* (Ingram & Macfie, 1922), known only from a female from Nigeria. Adults have a characteristic pair of pigment patches on the wing, over the *r–m* crossvein and just posterior to the apex of vein R_3, that is otherwise known only in a few *Stilobezzia* spp. (Clastrier 1986*a*: 365). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immatures remain unknown.

***Echinohelea* Macfie** (Ceratopogoninae: Ceratopogonini)**.** A genus of 27 described species occurring in all zoogeographical regions, except the Palaearctic Region and Antarctica. Five species are recorded from the Afrotropical Region as follows: from Burkina Faso, Guinea and Liberia from a few specimens (specimens from elsewhere are occasionally common in Malaise and sweep net samples). Clastrier (1984*b*) provided identification keys to both sexes. The distinctive adults are patterned and bright yellow to golden brown in colour, have numerous spines on the legs and both sexes have the proboscis long and the antennel flagellum elongate. Species are strikingly similar to one another and are somewhat difficult to identify. The pupa of one species (Nearctic) has been described (Borkent 2014). Two Afrotropical species have been reared from rich, organic soil near a backwater or wet rocks and from sludge in the bottom of a drain (Clastrier 1984*b*). Nearctic species have been reared from a wet forest floor, from under bark of a rotting log and from damp, dark brown mud in a roadside ditch (Borkent 2014). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

***Fanthamia* de Meillon** (Ceratopogoninae, Ceratopogonini)**.** An endemic genus of 14 species, 11 of which are restricted to South Africa, one to South Africa and Uganda, one to Zimbabwe and one to Democratic Republic of Congo. All specimens have been collected with light traps (most frequently), Malaise traps or sweeping. Several species from South Africa were collected at over 1,400 meters elevation. The specimen of *F. ornatipennis* (de Meillon, 1939) from Uganda was collected at 1,981 m, the species from Zimbabwe at 1,483 m and the species from Democratic Republic of Congo at 2,300 m. This suggests that this genus is largely restricted to South Africa and in more northern locations, to high elevations in East Africa. The immatures of this genus remain unknown. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. An identification key to the 12 species known at that time, mainly to males, was provided by de Meillon & Downes (1986), with two further species described subsequently by de Meillon & Wirth (1987*a*).

***Forcipomyia* Meigen** (Forcipomyiinae)**.** The second most species-rich genus in the family, with 1,154 described species, occurring in all zoogeographical regions, except Antarctica. One hundred and twenty-seven described species occur in the

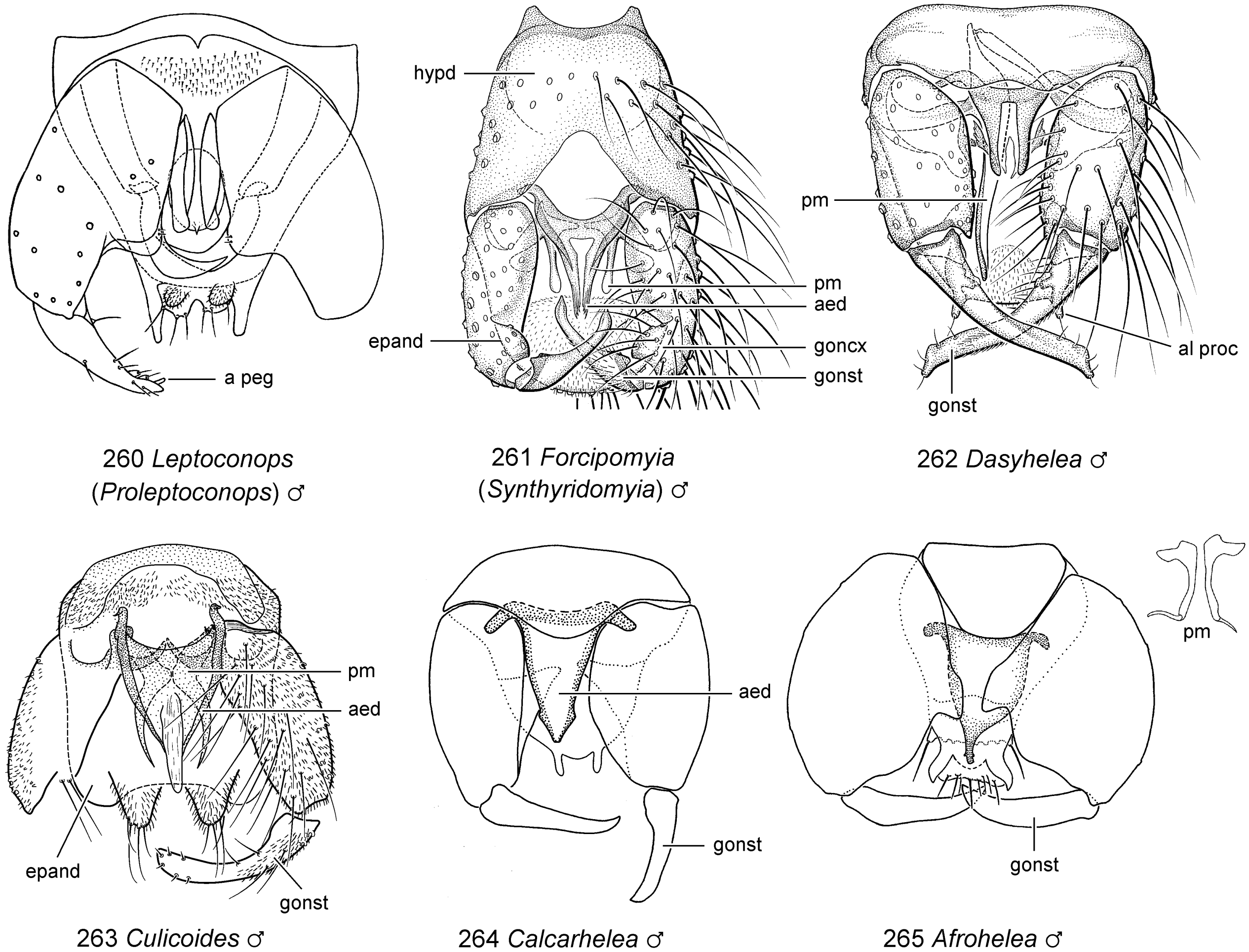


255 *Palpomyia* ♀ 256 *Palpomyia* ♀ 257 *Palpomyia* ♀ 258 *Bezzia* ♀ 259 *Phaenobezzia* ♀

Figs 34.255–259. Leg features of female Ceratopogonidae (lateral views) (all non-Afrotropical): (255) fore leg of *Palpomyia plebeja* (Loew); (256) same, mid leg; (257) same, hind leg; (258) fore leg of *Bezzia nobilis* (Winnertz); (259) hind tarsomeres 4–5 of *Phaenobezzia mellipes* Wirth & Ratanaworabhan. Figs 255–258 (Downes & Wirth 1981, figs 90–92, 94, as *B. setulosa*), Figs 259 (after Wirth & Ratanaworabhan 1981*b*, fig. 9E).

Abbreviations: fem – femur; s – seta; sp – spine; tsm – tarsomere.

Afrotropical Region, but numerous undescribed species should be expected. Adult *Forcipomyia* are the most common genus in nearly every type of trap and appear to be virtually ubiquitous and cosmopolitan, where even a little moisture is present (Figs 3, 4, 33). Globally, the genus is divided into 36 subgenera, 17 of which occur in the Afrotropics. Fourteen of these global subgenera (nine Afrotropical) are well defined as both adults and immatures, so that the overall classification of the genus is relatively stable. Larvae (*e.g.*, Fig. 305) and pupae (*e.g.*, Fig. 318) are remarkably diverse morphologically (Borkent 2014; Saunders 1957), with most bearing a variety of stout, elongate setae, some of which are secretory in the larval stage and likely used to keep the cuticle moist in terrestrial taxa (Urbanek *et al*. 2011), or functioning to repel predators (Hinton 1955). Globally, the larvae of 142 and the pupae of 143 species of *Forcipomyia* have been described (Borkent 2014). In the Afrotropical Region, only nine species have been described as larvae and eight as pupae, with the additional, but questionable, association of the immatures of *F.* (*Pterobosca* Macfie) *hutsoni* Wirth & Ratanaworabhan, 1976 (Wirth & Ratanaworabhan 1976). With the exception of female adults of the subgenus *F.* (*Lasiohelea*), which feed on vertebrates (see "Economic significance" section above), female *Forcipomyia* feed (globally) on other insects substantially larger than themselves (e.g., caterpillars, katydids, Odonata, Lepidoptera; see "Biology and immatures stages" section above) (*e.g.*, Figs 20–23), or do not feed at all (mandibles reduced). Afrotropical records include caterpillars (Macfie 1937), wings of Odonata (Clastrier &



260 *Leptoconops* (*Proleptoconops*) ♂

261 *Forcipomyia* (*Synthyridomyia*) ♂

262 *Dasyhelea* ♂

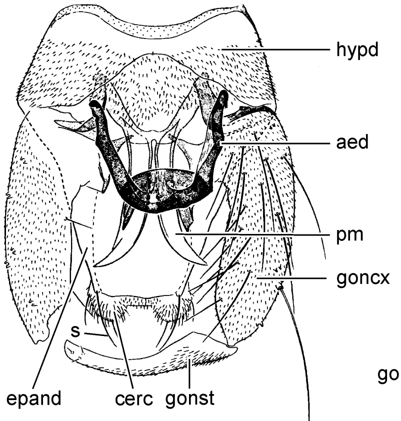
263 *Culicoides* ♂

264 *Calcarhelea* ♂

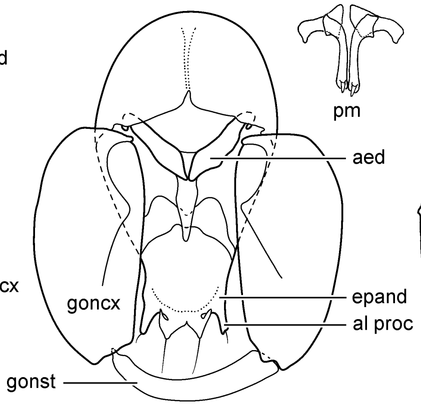
265 *Afrohelea* ♂

Figs 34.260–265. Male terminalia of Ceratopogonidae (ventral views): (260) *Leptoconops* (*Proleptoconops*) *dixi* de Meillon; (261) *Forcipomyia* (*Synthyridomyia*) *acidicola* (Tokunaga) (non-Afrotropical); (262) *Dasyhelea pseudoincisurata* Waugh & Wirth (non-Afrotropical); (263) *Culicoides imicola* Kieffer; (264) *Calcarhelea bimater* (de Meillon & Hardy); (265) *Afrohelea capensis* (de Meillon & Hardy) (parameres indicated separately). Fig. 260 (Clastrier 1983*c*, fig. 3G), Figs 261, 262 (Downes & Wirth 1981, figs 98, as *F. colemani*, 100), Fig. 263 (Meiswinkel 1989, fig. 19), Figs 264, 265 (Wirth & Grogan 1988, figs 13d, e, 2g, h, respectively).

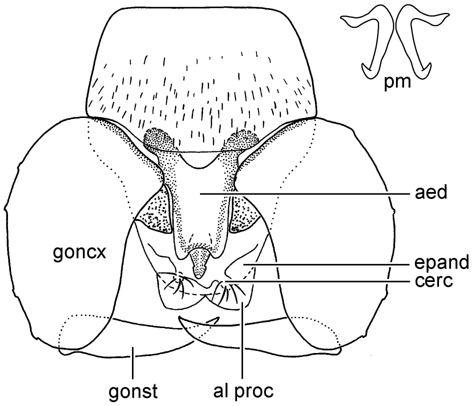
Abbreviations: a peg – apical peg; aed – aedeagus; al proc – apicolateral process; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; pm – paramere.



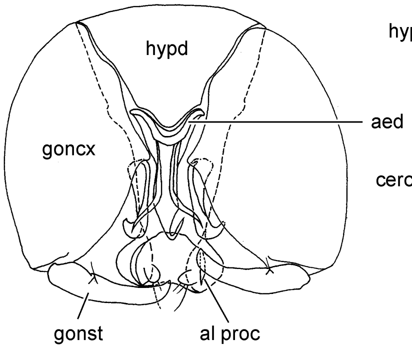
266 *Bothamia* ♂



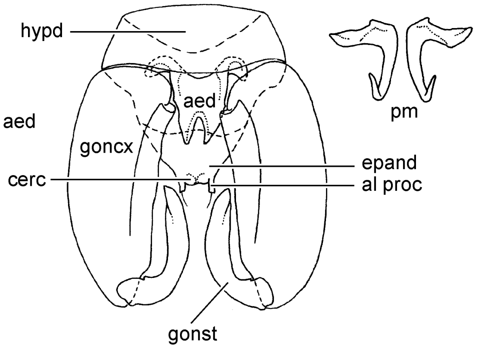
267 *Capehelea* ♂



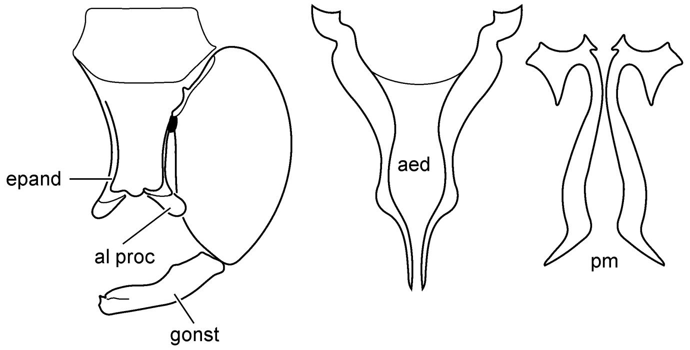
268 *Ceratohelea* ♂



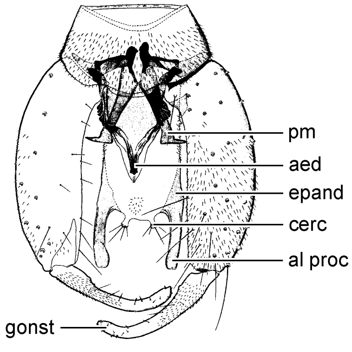
269 *Bothahelea* ♂



270 *Ankylohelea* ♂



271 *Kolenohelea* ♂

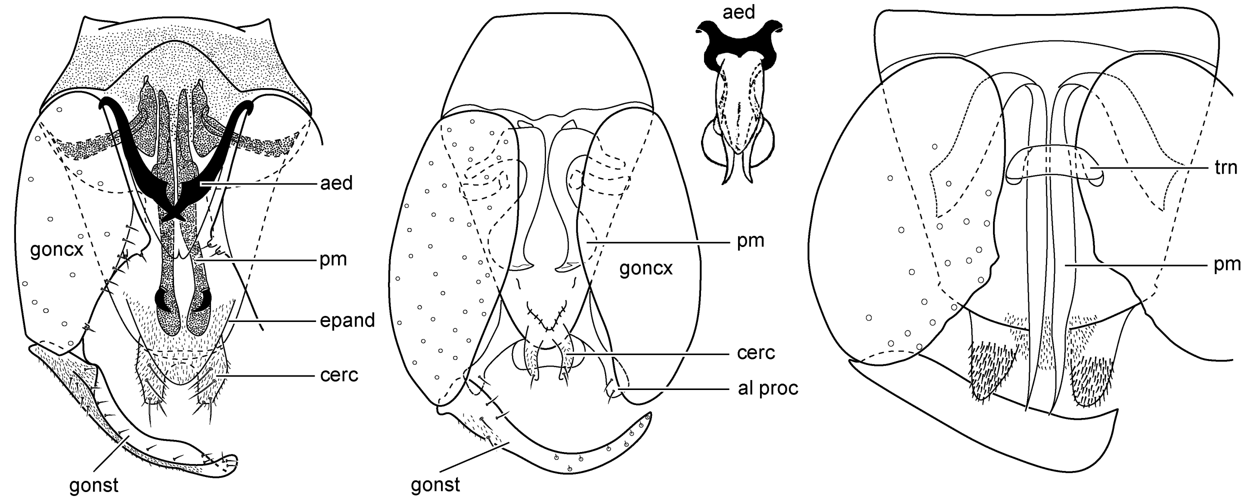


272 *Kolenohelea* ♂

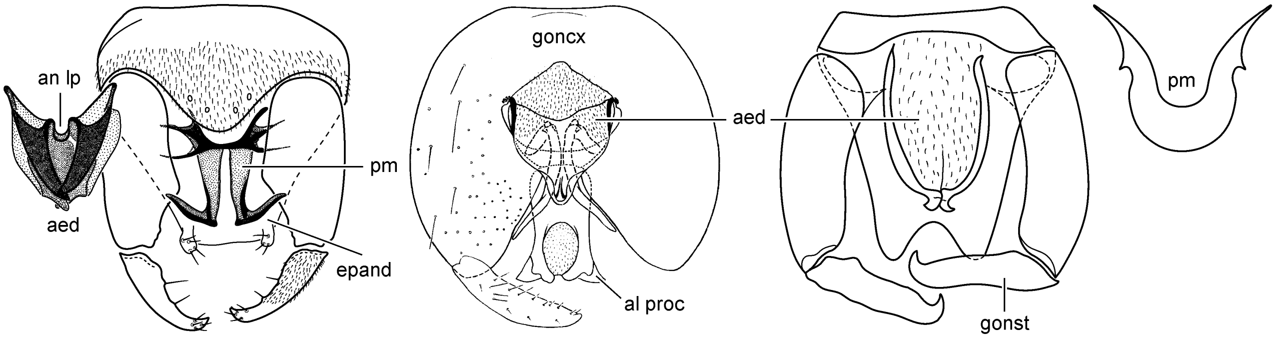
Figs 34.266–272. Male terminalia of Ceratopogonidae (ventral views): (266) *Bothamia demeilloni* Meiswinkel; (267) *Capehelea steli* de Meillon & Wirth (parameres indicated separately); (268) *Ceratohelea advena* (de Meillon) (parameres indicated separately); (269) *Bothahelea phelpsi* Grogan & Wirth; (270) *Ankylohelea montana* de Meillon & Wirth (parameres indicated separately); (271) *Kolenohelea dycei* de Meillon & Wirth (aedeagus and parameres indicated separately); (272) *K. uysorum* de Meillon, Meiswinkel & Wirth. Fig. 266 (Meiswinkel 1987, fig. 8), Figs 267–270 (after Wirth & Grogan 1988, figs 17k, l, 15h, 9i, 5h, i, respectively), Fig. 271 (after de Meillon & Wirth 1981*a*, figs 6–8), Fig. 272 (de Meillon *et al*. 1982, fig. 19).

Abbreviations: aed – aedeagus; al proc – apicolateral process; cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; pm – paramere; s – seta.

Legrand 1984; Wirth 1956*a*; Wirth & Ratanaworabhan 1976) and adult Lepidoptera (Lane 1977), on the thoraces of Tipulidae (McCrae 1967) and Culicidae (Macfie 1949; McCrae 1967) and on a spider (Clastrier & Legrand 1991). These records are few and far between, however, and it remain a mystery why, considering how diverse and abundant females may be, that there are so few observations of females feeding in the Afrotropics and elsewhere. Females of some *Forcipomyia* spp. lack serrate mandibles and, therefore, probably do not feed on other insects or have any other prey (*e.g.*, *F.* (*Caloforcipomyia* Saunders) and some species of *Forcipomyia sensu stricto*). Adult *Forcipomyia* are hairy and to fuel flight both males and females feed on nectar and are important pollinators of a variety of plants. The best studied pollinators are those belonging to the subgenus *F.* (*Euprojoannisia* Brèthes) and *Forcipomyia sensu stricto*, which are common on flowers of cacao. Other species of the genus also pollinate other plants such as rubber and avocado (see "Biology and immature stages" section above). Adult *F.* (*Synthyridomyia* Saunders) are often common on Umbelliferae. Adults of *F.* (*Rhinohelea* de Meillon & Wirth) have markedly elongate mouthparts that likely indicate that these are also important as pollinators in the *Erica* heath of the Cape Province, South Africa, where they have been collected (Kirk-Spriggs & Stuckenberg 2009: 159). Larvae of *Forcipomyia* range from aquatic to terrestrial and are present in such habitats as the margin of springs (including hot springs), submerged or close to and above



273 *Stilobezzia* (*Stilobezzia*) ♂ 274 *Neohelea* ♂ 275 *Schizonyxhelea* ♂

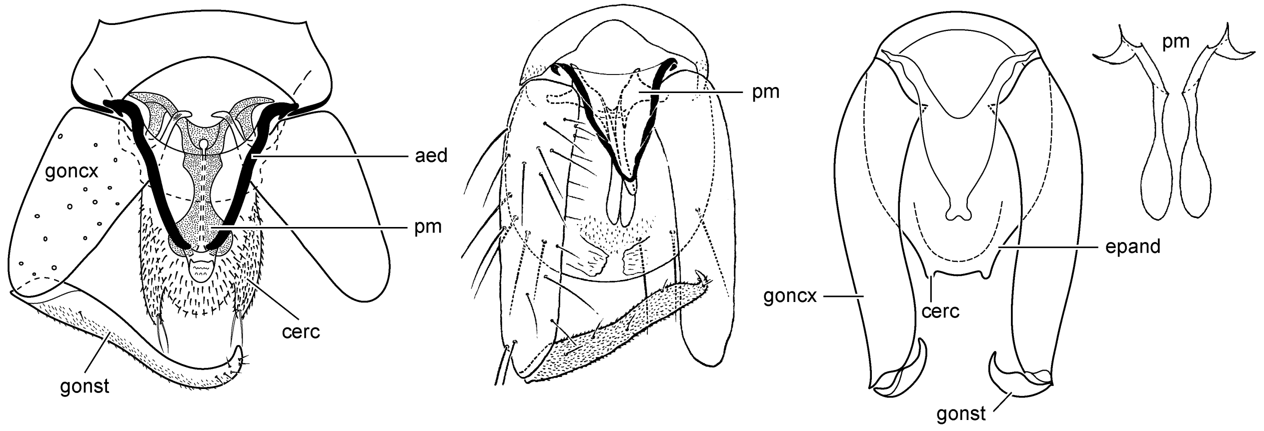


276 *Monohelea* ♂ 277 *Echinohelea* (*Echinohelea*) ♂ 278 *Pellucidomyia* ♂

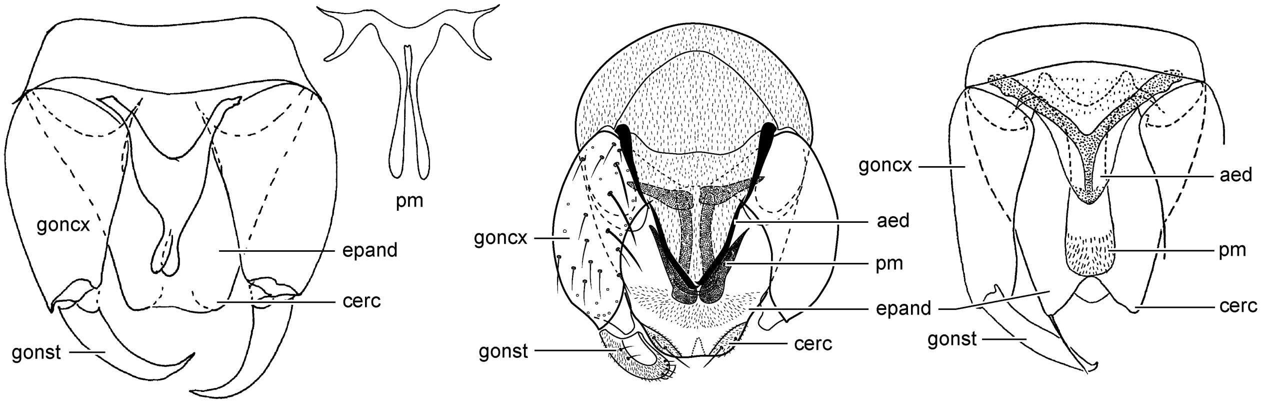
Figs 34.273–278. Male terminalia of Ceratopogonidae (ventral views): (273) *Stilobezzia* (*Stilobezzia*) *pastoriana* Clastrier; (274) *Neohelea pastoriana* Clastrier (aedeagus indicated separately); (275) *Schizonyxhelea afra* (Clastrier); (276) *Monohelea pallida* Clastrier & Delécolle (aedeagus indicated separately); (277) *Echinohelea* (*Echinohelea*) *pastoriana* Clastrier; (278) *Pellucidomyia wirthi* (Lane) (parameres indicated separately) (non-Afrotropical). Fig. 273 (after Clastrier 1986b, fig. 13), Fig. 274 (after Clastrier 1988*a*, figs 1I, K), Fig. 275 (after Clastrier 1991, fig. 9), Fig. 276 (after Clastrier & Delécolle 1990, fig. 15F), Fig. 277 (Clastrier 1984*d*, fig. 3F), Fig. 278 (after Wirth & Ratanaworabhan 1971, figs 1O, P).

Abbreviations: aed – aedeagus; al proc – apicolateral process; an lp – anteromedial loop; cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm – paramere; trn bd – transverse band.

the water line in various phytotelmata, undersides of leaves on the ground, on wet rock faces, sap flows, manure, rotting vegetative matter, beneath tree bark of dead trees or logs, inside the stems of *Lobelia bequaertiana* De Wild (Campanulaceae), mossy rotting wood in deep shade and moist and rotten cacao-pod husks. They feed on a variety of micro-organisms, fungi and algae and may even be predaceous on Culicidae larvae (at least in the laboratory; Carter 1919) (de Meillon & Wirth 1991). Pupae of many species form a somewhat circular group, with their heads directed inward and keeping the cast larval skin on the posterior portion of their abdomens, with the elongate larval skin retaining some repellent fluid on the stout secretory setae. This likely functions as an effective barrier against predators at the pupal stage. This genus will almost certainly reward a future systematist with a wealth of cladistic information and the opportunity to phylogenetically interpret the remarkable diversity of adult and larval behaviour (both in Africa and elsewhere). Currently, our understanding of the phylogenetic relationships within the genus is virtually non-existent, although most of the subgenera are likely monophyletic. De Meillon & Wirth (1991) provided an identification key to subgenera, chiefly based on female adults, presenting a summary of morphology in each life stage and a summary of biology. An identification key to males of the subgenera occurring in the Australasian Region (Debenham 1987), included all subgenera occurring in the Afrotropics, other than the distinctive *F.* (*Rhinohelea*), with elongate mouthparts and unique male terminalia (de Meillon & Wirth (1979*b*) and the subgenus *F.* (*Saliohelea* Wirth & Ratanaworabhan), with two species described (or re-described) by Wirth & Ratanaworabhan (1978). Descriptions and an identification key to all Afrotropical species was published by Dessart (1963). Subsequently, identification keys have appeared for the following subgenera: both



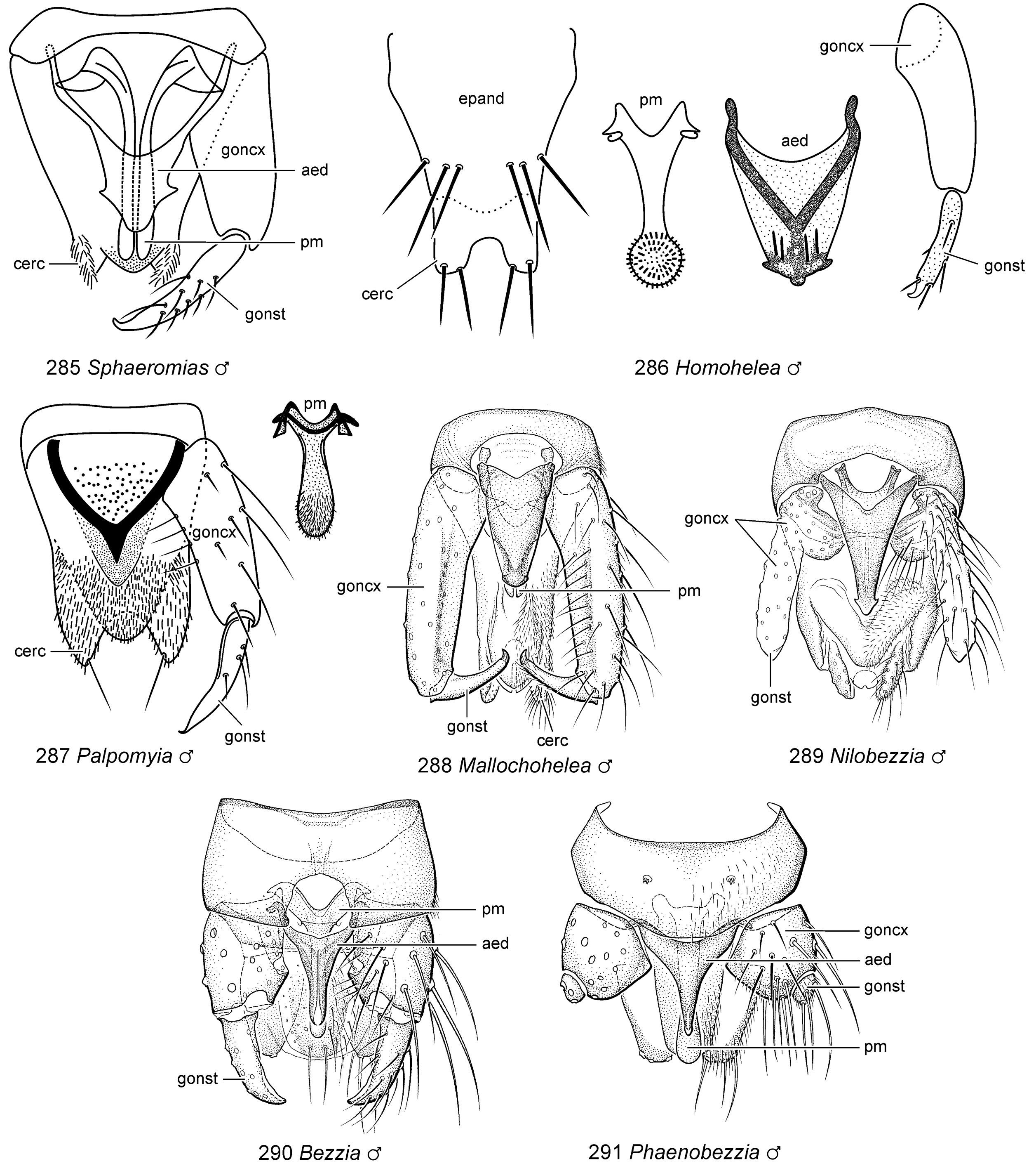
279 *Clinohelea* (*Clinohelea*) ♂ 280 *Tetrabezzia* ♂ 281 *Dibezzia* ♂



282 *Hebetula* ♂ 283 *Neosphaeromias* ♂ 284 *Sphaeromias* ♂

Figs 34.279–284. Male terminalia of Ceratopogonidae (ventral views): (279) *Clinohelea* (*Clinohelea*) *trimaculata* Clastrier; (280) *Tetrabezzia africana* Clastrier; (281) *Dibezzia debenhamae* Wirth & Ratanaworabhan (parameres indicated separately) (non-Afrotropical); (282) *Hebetula tonnoiri* (Lee) (parameres indicated separately) (non-Afrotropical); (283) *Neosphaeromias afrotropicalis* Clastrier; (284) *Sphaeromias corsoni* (Ingram & Macfie). Fig. 279 (after Clastrier 1983*a*, fig. 20), Fig. 280 (Clastrier 1982*a*, fig. 1O), Fig. 281 (after Wirth & Ratanaworabhan 1981*a*, fig. 1f), Fig. 283 (after Clastrier 1983*b*, fig. 6B), Fig. 284 (after Ingram & Macfie 1924, fig. 3B).

Abbreviations: aed – aedeagus; cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm – paramere.



285 *Sphaeromias* ♂

286 *Homohelea* ♂

287 *Palpomyia* ♂

288 *Mallochohelea* ♂

289 *Nilobezzia* ♂

290 *Bezzia* ♂

291 *Phaenobezzia* ♂

Figs 34.285–291. Male terminalia of Ceratopogonidae (ventral views): (285) *Sphaeromias eugenei* de Meillon & Wirth; (286) *Homohelea telmatoscopa* (Ingram & Macfie) (epandrium + cercus, parameres, aedeagus, gonocoxite + gonostylus indicated separately); (287) *Palpomyia fusca* de Meillon (parameres indicated separately); (288) *Mallochohelea albibasis* (Malloch) (non-Afrotropical); (289) *Nilobezzia minor* (Wirth) (non-Afrotropical); (290) *Bezzia nobilis* (Winnertz) (non-Afrotropical); (291) *Phaenobezzia pistiae* (Ingram & Macfie). Fig. 285 (after de Meillon & Wirth 1987*a*, fig. 95), Fig. 286 (after Ingram & Macfie 1921, figs 15a–d), Fig. 287 (after de Meillon 1938, figs 1b, c), Figs 288–291 (Downes & Wirth 1981, figs 116, 119, 112, as *B. setulosa*, 114, respectively).

Abbreviations: aed – aedeagus; cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm – paramere.

sexes of *F*. (*Thyridomyia* Saunders) (de Meillon & Wirth 1981*c*); males of *F*. (*Schizoforcipomyia* Chan & Leroux) (de Meillon *et al*. 1982); both sexes of *F*. (*Phytohelea* Remm) (de Meillon & Wirth 1979*d*); males of *F*. (*Pedilohelea* de Meillon & Wirth) (de Meillon & Wirth 1980); and females of *F*. (*Trichohelea* Goetghebuer) (Lane 1977).

Hebetula **Wirth & Debenham** (Ceratopogoninae: Hebetulini)**.** A genus of 22 described species restricted to the Afrotropical, Australasian and Oriental Regions. Two species, known only from females, occur in the Afrotropics: *H. bequaerti* (Goetghebuer, 1933), from Democratic Republic of Congo; and *H. hexacantha* (Kieffer) from Seychelles. Males are characterised in the above identification key based on extralimital species. Immatures are only known as the pupa of the Australasian/Oceanian *H. tonnoiri* (Lee, 1948) and have been reared from moss in a creek and the margin of a river (Borkent 2014). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

Homohelea **Kieffer** (Ceratopogoninae: Sphaeromiini)**.** A genus of 19 described species, confined to the Afrotropical, Australasian (Guam Is.), Oriental and Palaearctic Regions, with seven species recorded from the Afrotropics. Males and females are known for only two Afrotropical species: *H. delanoe* (de Meillon, 1942) and *H. telmatoscopus* (Ingram & Macfie, 1921). The remaining five species are known only as females (in the adult stage). Larvae of this genus remain unknown, but pupae have been described for three Afrotropical species (Borkent 2014), collected from a river margin, a brackish marsh, ponds and ground pools. Ingram & Macfie (1921: 358) noted pupae to be common in "… puddles of dirty water near a stand-pipe". Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Females were keyed by de Meillon & Wirth (1981*b*).

Jenkinshelea **Macfie** (Ceratopogoninae: Johannsenomyiini)**.** A genus of 20 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Borkent 2014), eight of which occur in the Afrotropics, recorded from Ghana, Guinea, South Africa and Zimbabwe. Larvae of the genus are known only for a Nearctic species. Pupae are associated for five species, two of which occur in the Afrotropics (Borkent 2014). Immatures of Afrotropical species have been reared from stream and river margins, rice fields, marshes, ponds and dead leaves in a swamp. A Nearctic species has been reared from a lake margin (Borkent 2014). Some pupae of this genus, and several other Johannsenomyiini, have distinctive membranous discs on the ventrum of the abdomen (as in Fig. 322), which are used to adhere to emergent vegetation or other substrates. Some adult representatives of the genus may be difficult to distinguish from those of *Macropeza* (see below). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Females are also cannibalistic on males during copulation as evidenced by the collection of females with abdomens bearing a male's dried terminalia (a known relationship in a number of other genera (Downes 1978)). There is no published identification key to adults, but Clastrier (1983*a*) and de Meillon & Wirth (1983*a*) discuss differences between species.

Johannsenomyia **Malloch** (Ceratopogoninae: Johannsenomyiini)**.** A genus of 27 described species, occurring in all zoogeographical regions, except Antarctica, but restricted to North Africa in the Palaearctic (Borkent 2016*a*). Six species are known from the Afrotropical Region, recorded from Democratic Republic of Congo, Nigeria and South Africa. The larva and pupa of only one Nearctic species are known (Borkent 2014). Mayer (1957) described the pupa of the Afrotropical *J. albidorsata* (de Meillon, 1937) (as *Dicrohelea* Kieffer), but this was based on a misidentification of a specimen of *Bezzia* (Borkent 2014). Immatures from elsewhere have been reared from river margins, a pond and lakes. Williams (1955) described how mature larvae of the Nearctic *J. argentata* (Loew, 1861) burrowed into the sand on a lake beach to pupate. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Females are cannibalistic on males during copulation as evidenced by the collection of females with their abdomens bearing a male's dried terminalia (a known relationship in a number of other genera) (de Meillon & Wirth 1981*a*; Downes 1978). There is no published identification key to adults available.

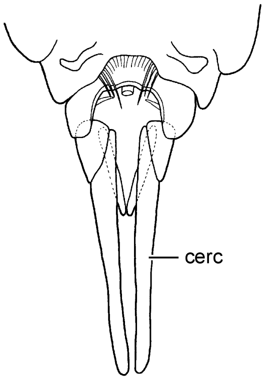
Kolenohelea **de Meillon & Wirth** (Ceratopogoninae: Ceratopogonini)**.** A genus of 19 described species occurring in the Afrotropical (17 species) and Palaearctic Regions (2). Thirteen Afrotropical species are recorded from South Africa, one from Cameroon, South Africa and Zimbabwe and three from Guinea. Immatures remain unknown. Adults have been collected with light traps (most), Malaise traps or by sweeping. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. De Meillon & Wirth (1981*a*) provided an identification key to the four species known at that time. Male terminalia are distinctive for most of the subsequently described species and a new identification key is required that incorporates these and the two species known only as females (Clastrier 1984*c*).

Leptoconops **Skuse** (Leptoconopinae)**.** A genus of 150 described species occurring in all zoogeographical regions, except Antarctica and 18 of these occur in the Afrotropical Region. The genus is divided into six subgenera, four of which occur in the Afrotropics: *Leptoconops* (*Holoconops* Kieffer) has six Afrotropical species, *L*. (*Leptoconops*) five, *L*. (*Proleptoconops* Clastrier) five and *L*. (*Styloconops* Kieffer) two. An overview of the species of *L*. (*Holoconops*) was provided by Clastrier (1981). De Meillon & Wirth (1983*a*) provided an identification key to the seven species, but this was misprinted and unusable. The larvae of 14 species and pupae of 14 (some of these not the same as those described as larvae), have been described globally, but the only Afrotropical species described in these stages is the widely distributed *L. spinosifrons*; a diurnal biting pest on the coastal beaches of Kenya, Madagascar, Seychelles and Tanzania (and those of the Oriental and Australasian Regions) (Laurence & Mathias 1972). Immatures of this genus are restricted to wet or damp sand or sandy soil (generally freshwater or marine beaches protected from wave action), seepage areas in desert oases, and wet margins of salt flats, cracked clay soils, halomorphic, calcareous soil and the margin of vernal ponds in xeric areas. Species in this group often occur in dry habitats otherwise inhospitable to most other Ceratopogonidae. Adults of both sexes have the unusual habit of burrowing into sand to rest and for females to lay their eggs. Females (*e.g*., Figs 2, 32) have fine mandibular teeth, reflecting their biting habit on vertebrate hosts, which are diurnal. Hosts in the Afrotropical Region include humans, cattle and horses, but extralimital species are known to bite a wide range of vertebrates, including lizards, tortoises, birds, bats and other mammals (Clastrier & Wirth 1978; Mullens *et al*. 1997; Široký *et al*. 2007; Wirth & Atchley 1973), suggesting that further investigation of the Afrotropical species may also result in host records beyond those now known for the region. Adults of at least some extralimital *Leptoconops* are important pollinators (Wiesenborn 2003) (e.g., Fig. 2). A key to African subgenera was provided by de Meillon & Wirth (1991). Clastrier (1983*d*) described and keyed species of the subgenus *L*. (*Leptoconops*) (including *L*. (*L.*) *dixi* de Meillon, 1936, which is now in the subgenus *L*. (*Proleptoconops*)).

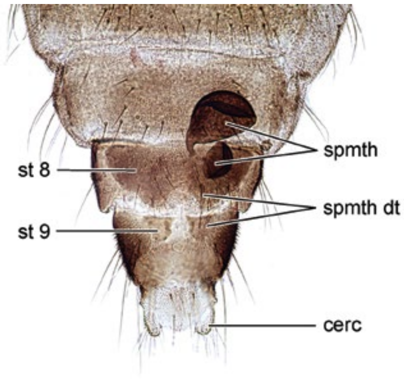
***Luciamyia* de Meillon** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *L. biloba* de Meillon, 1937, known from one male and one female sampled with a net over marshy ground in South Africa. The female is the only Ceratopogonidae with an apically bilobed wing (Fig. 121). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

***Mackerrasomyia* Debenham** (Ceratopogoninae: Sphaeromiini)**.** A genus of eight described species, occurring in the Afrotropical, Australasian and Oriental Regions, with the single Afrotropical species, *M. zumpti* de Meillon & Wirth, 1979, sampled with a light trap in Zimbabwe. The immatures of this genus remain unknown. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

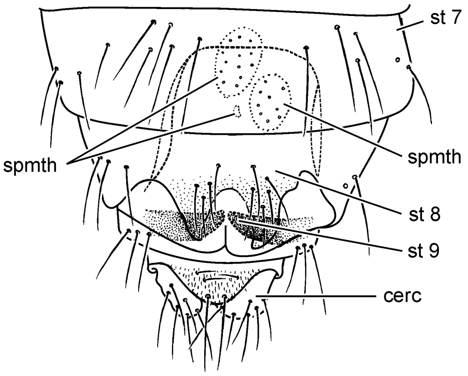
***Macropeza* Meigen** (Ceratopogoninae: Johannsenomyiini)**.** A genus of 22 described species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Sixteen species



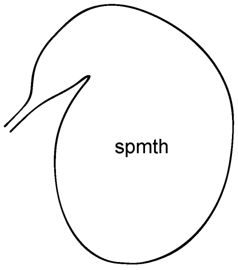
292 *Leptoconops* (*Megaconops*) ♀



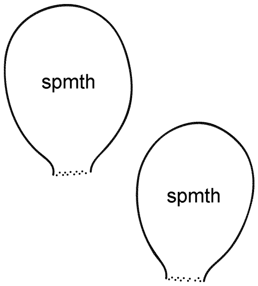
293 *Monohelea* ♀



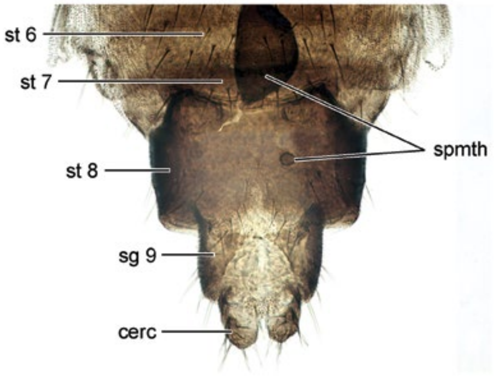
294 *Afrostilobezzia* ♀



295 *Schizonyxhelea* ♀



296 *Neohelea* ♀

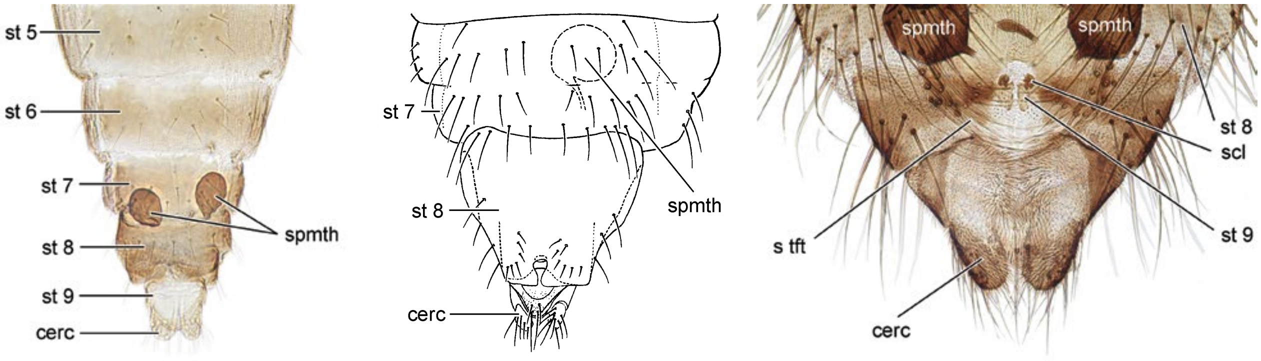


297 *Bothahelea* ♀

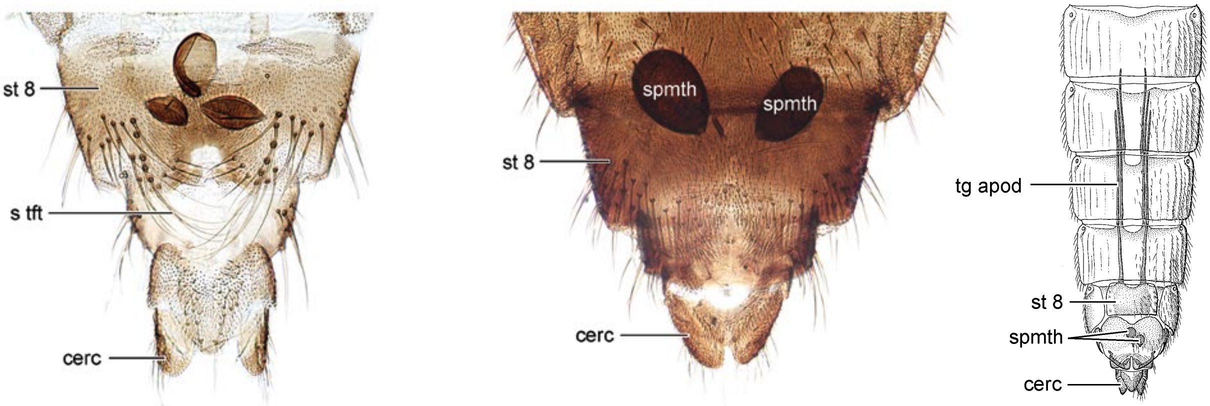
Figs 34.292–297. Female terminalia of Ceratopogonidae (ventral views): (292) *Leptoconops* (*Megaconops*) *floridensis* Wirth (non-Afrotropical); (293) *Monohelea ornata* Wirth (non-Afrotropical); (294) *Afrostilobezzia ornatithorax* (Clastrier); (295) spermatheca of *Schizonyxhelea afra* (Clastrier); (296) same, *Neohelea pastoriana* Clastrier; (297) *Bothahelea phelpsi* Grogan & Wirth. Fig. 292 (after Wirth & Atchley 1973, fig. 2d), Fig. 294 (after Clastrier 1988*a*, fig. 26), Fig. 295 (after Clastrier 1991, fig. 4), Fig. 296 (after Clastrier 1988*a*, fig. 1E).

Abbreviations: cerc – cercus; sg – segment; spmth – spermatheca(e); spmth dt – spermathecal duct; st – sternite.

are confined to the Afrotropical Region: one from Madagascar, two from Mozambique, one from Nigeria, two from Senegal and Sierra Leone, respectively and eight from South Africa. Seven Afrotropical species are known only as males and nine only as females, suggesting the strong possibility that at least some are conspecific with representatives of the opposite sex. Globally, the larvae of two species and the pupae of four are known (Borkent 2014). Of these, Afrotropical species are known as larva and pupa for *M. natalensis* (de Meillon, 1937) (as *Macroptilum* Becker) and pupae for two others. Immatures have been collected from mud and among plants at stream and river margins, impoundments and from aquatic plants (*Pistia stratiotes* L. (Araceae)). Some pupae of the genus, and several other Johannsenomyiini, have distinctive membranous discs on the ventrum of the abdomen (as in Fig. 322), which are used to adhere to emergent vegetation or other substrates. There are problems diagnosing adults of this genus. Males of all species, including the type, have at least partially fused parameres of the male terminalia and many, including some Afrotropical species, lack parameres with a ventrally recurved hook-like process, as characterised by de Meillon & Wirth (1991). The distinctive male head, as indicated in the above identification key, is likely a good synapomorphy for the genus (or at least a group of species). The type species of the genus, *M. albitarsis* Meigen, 1818, has a well-developed anal lobe of the wing (although not as large as in some *Jenkinshelea*). Further study of the distinction between these two genera is required. Description of the pupa, by Borkent (2014) indicated that the genus is monophyletic for those few taxa studied. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Females are cannibalistic on males during copulation as evidenced by the collection of females with their abdomens bearing a male's dried terminalia (a known relationship in a number of other genera (de Meillon 1961, as a *Macroptilum*)). The most recent identification key by Macfie (1939*a*), includes 10 Afrotropical species as part of a larger identification key to all species of Ceratopogonidae in which the thorax is narrowed anteriorly and more or less conical. One species, previously ascribed to the genus, as *M. geari* de



298 *Notoceratopogon* ♀ 299 *Echinohelea* (*Echinohelea*) ♀ 300 *Nilobezzia* ♀



301 *Mallochohelea* ♀ 302 *Anebomyia* ♀ 303 *Palpomyia* ♀

Figs 34.298–303. Female terminalia of Ceratopogonidae (ventral views): (298) *Notoceratopogon vockerothi* de Meillon & Downes; (299) *Echinohelea* (*Echinohelea*) *pastoriana* Clastrier; (300) *Nilobezzia mallochi* Wirth (non-Afrotropical); (301) *Mallochohelea pullata* (Wirth) (non-Afrotropical); (302) *Anebomyia fluminea* (de Meillon & Wirth); (303) *Palpomyia lineata* (Meigen) (non-Afrotropical). Fig. 299 (after Clastrier 1984*d*, fig. 1l), Fig. 303 (Downes & Wirth 1981, fig. 123).

Abbreviations: cerc – cercus; s tft – setal tuft; scl – sclerite; spmth – spermatheca(e); st – sternite; tg apod – tergal apodeme.

Meillon & Wirth, 1981, was recently transferred to *Pellucidomyia* Macfie (Borkent 2014).

***Mallochohelea* Wirth** (Ceratopogoninae: Johannsenomyiini)**.** A genus of 45 described species occurring in all zoogeographical regions, except Antarctica (Borkent 2014, 2015, 2016*a*). This genus is represented by six species in the Afrotropical Region, one each from Kenya and Mozambique and four species from South Africa. *Mallochohelea kirki* will key to *Anebomyia* in the above identification key; although the generic placement of the species remain uncertain, it is here treated as *Mallochohelea* (Borkent 2016*a*). Of the six Afrotropical species, two are known only as males (*M. errinae* (de Meillon, 1940) and *M. sanctaeluciae* (de Meillon)) and four only as females (*M. kirki*, *M. luaboensis* (de Meillon, 1959), *M. sidis* (de Meillon, 1959) and *M. turneri* (Ingram & Macfie, 1923)), suggesting the possibility that some of opposite sexes in South Africa may be conspecific. The only immature known from the Afrotropical Region is the pupa of *M. errinae* collected from a river (Borkent 2014). Otherwise, larvae are known for four and pupae for 11 extralimital species, collected from stream and river margins, a thermal stream, impoundments, ponds and lakes (Borkent 2014). Pupae of the genus and several other Johannsenomyiini have distinctive membranous discs on the ventrum of the abdomen (Fig. 322), which are used to adhere to emergent vegetation or other substrates. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (as in Fig. 17) (Downes 1978). Females are also cannibalistic on males during copulation and upon completion, the dry husk of the male body breaks off, leaving the male's terminalia still clasped onto that of the female, thereby functioning as a mating plug (as in Fig. 30) (de Meillon & Wirth 1987*a*; Downes 1978). The setal tufts on sternite 8 of females (Fig. 301) of the genus and some other Johannsenomyiini are probably important in producing long ribbons of eggs during flight (Fig. 31) and which are subsequently deposited in aquatic habitats. De Meillon & Wirth (1981*b*) provided an identification key to five Afrotropical species (the omitted *M. sanctaeluciae* (de Meillon, 1937) is discussed) and include two others, *A. siricis* and *A. fluminea*, which are now ascribed to the genus *Anebomyia*.

***Metacanthohelea* Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *M. cogani* Wirth & Grogan, 1988, known from males and females from Aldabra Is. (Seychelles) and a single female from Kenya, at an elevation of 1,280 m, certainly an unusual distribution. The small, dark brown adults are similar to many species of *Serromyia* and have a swollen hind femur, with 14 large ventral spines in the distal half. Females have equal hind claws, each with an inner tooth and have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

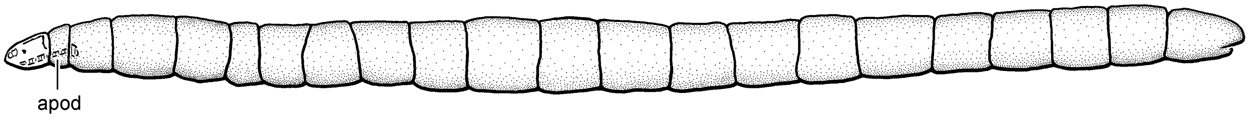
***Monohelea* Kieffer** (Ceratopogoninae: Ceratopogonini)**.** A genus of 88 described species known from all zoogeographical regions, except Antarctica. Ten species occur in the Afrotropical Region, four from Democratic Republic of Congo, one from Gabon, two from Guinea, one from Republic of Congo, one from Senegal and one from South Africa. Four species are known from both sexes, three from males only and three from females only. Adults have wings with characteristic black and grey pigmentation patches, brightly banded legs and females have single, large hind tarsal claws. Overall, species tend to be similar to one another, with primary differences in the male terminalia. Immatures have not been described for Afrotropical species, but the larva of one Palaearctic species and the pupae of two Nearctic species are known and have been reared from *Sphagnum* moss from lake margins and a swamp, or *Sphagnum* bogs (Borkent 2014). Afrotropical adults have been reared from roots and soil at the margins of puddles, seeps, a backwater and a swamp (Clastrier & Delécolle 1990). Adults of Afrotropical species have also been sampled in light and Malaise traps (Clastrier 1984*a*; Clastrier & Delécolle 1990). Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (as in Fig. 17) (Downes 1978). No identification key to adults is available, but Clastrier (1984*a*) and Clastrier & Delécolle (1990) discussed some differences between species.

***Neohelea* Clastrier** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *N. pastoriana* Clastrier, 1988, known from two males and one female, collected with a sweep net near a stream in Guinea (Clastrier 1988*a*). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Clastrier (1988*a*) indicated the presence of sensilla coeloconica on the subapical flagellomeres of the male and female antenna of this species. Re-examination of specimens indicates that these are, at best, difficult to discern. These are similar, however, to those reported for *Capehelea steli*, perhaps indicating a phylogenetic relationship. Immature stages and biology of the species remain unknown.

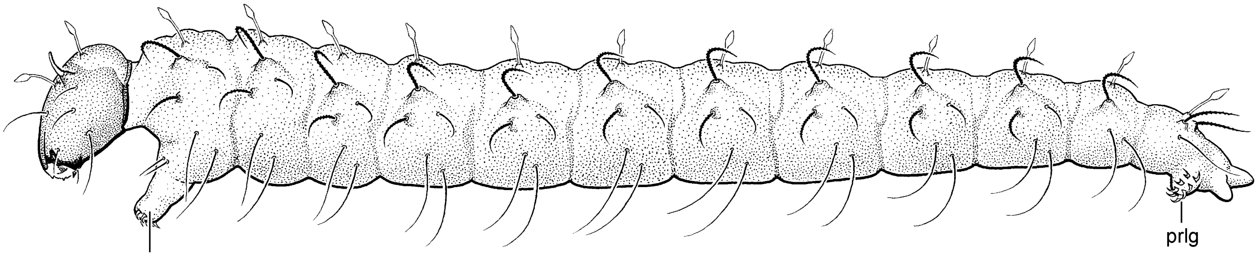
***Neosphaeromias* Das Gupta & Wirth** (Ceratopogoninae: Johannsenomyiini). A genus of four described species restricted to the Australasian/Oceanian (only Solomon Is.), Afrotropical and Oriental Regions. One species is known from the Afrotropics: *N. afrotropicalis* Clastrier, 1983 from Guinea. The male will key out in the above identification key, but other *Neosphaeromias* from elsewhere have more elongate gonostyli of the male terminalia, indicating a need for caution, should further species be discovered in the Afrotropics. Immatures are unknown, but adult *N. afrotropicalis* were reared from mud in a rice field, a pond margin and from vegetation in a small stream. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

***Neurobezzia* Wirth & Ratanaworabhan** (Ceratopogoninae: Ceratopogonini)**.** A genus of three described species, one from the Nearctic, one from China (Hubei Province, a single female) and one, *N. tsacasi* Clastrier, 1983, from Seychelles (a single female) in the Afrotropical Region. Although appearing to form a monophyletic group, further research (and material) is required. The male is characterised in the above identification key on the basis of the male of the Nearctic *N. granulosa* (Wirth, 1952) (Borkent 1998). Immatures are unknown. The Nearctic species is present in bogs and near lakes. The specific locality and habitat of *N. tsacasi* on Mahé Is. in Seychelles is unknown (Clastrier 1983*c*). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size.

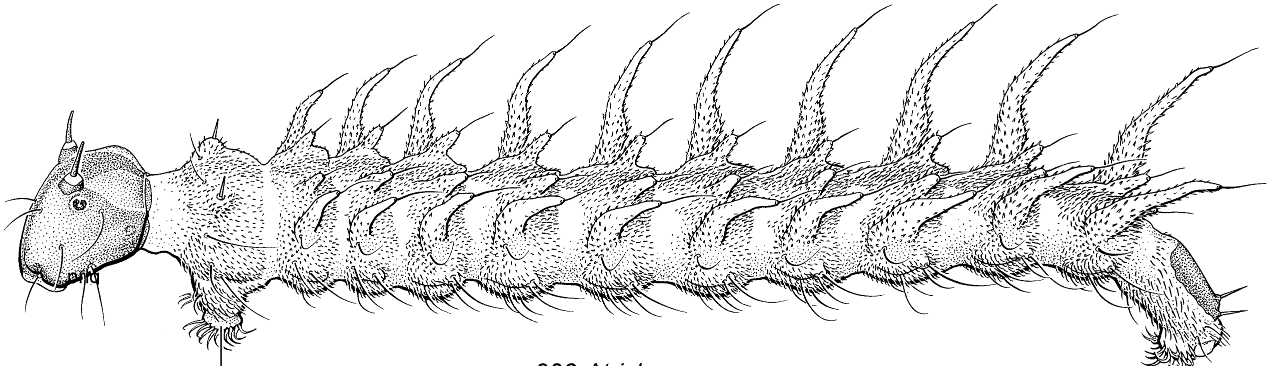
***Nilobezzia* Kieffer** (Ceratopogoninae: Johannsenomyiini)**.** A genus of 74 described species occurring in all zoogeographical



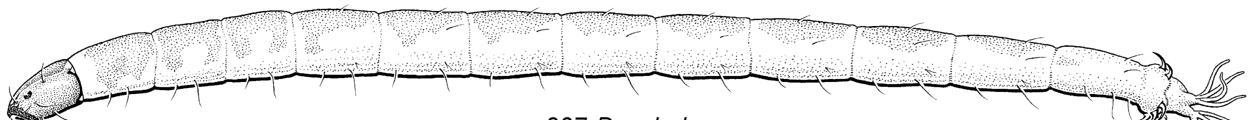
304 *Leptoconops* (*Styloconops*)



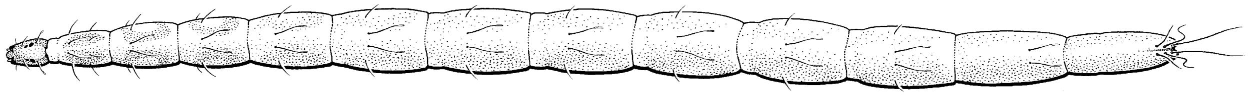
305 *Forcipomyia*



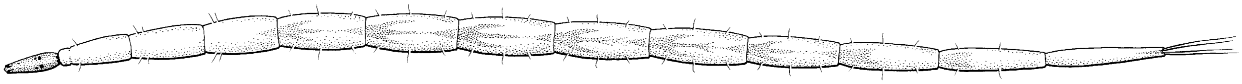
306 *Atrichopogon*



307 *Dasyhelea*



308 *Culicoides*



309 *Bezzia*

Figs 34.304–309. Habitus of fourth-instar larvae of Ceratopogonidae: (304) *Leptoconops* (*Styloconops*) *spinosifrons* (Carter), lateral view; (305) *Forcipomyia* sp., lateral view (non-Afrotropical); (306) *Atrichopogon fusculus* (Coquillett), lateral view (non-Afrotropical); (307) *Dasyhelea* sp., lateral view (non-Afrotropical); (308) *Culicoides* sp., dorsal view (non-Afrotropical); (309) *Bezzia* sp., dorsal view (non-Afrotropical). Fig. 304 (after Laurence & Mathias 1972, fig. 1), Figs 305–309 (Downes & Wirth 1981, figs 130, 131 (as *A. polydactylus* Nielsen), 132–134).

Abbreviations: apod – apodeme; crt – crochets; prlg – proleg.

regions, except Antarctica (Borkent 2016*a*). Nine species are known from the Afrotropical Region, from Ghana, Gambia, Cameroon and South Africa (1 species), Senegal (1), Seychelles (1), South Africa (3), South Sudan (2) and Zimbabwe (1). Seven of the species are known in the adult stage only as females and the remaining two as both sexes. Males of these species have a markedly modified and unique form of terminalia, which is rotated and bent ventrally (so the ventral surface is oriented anteriorly) and the gonostylus is fused to the gonocoxite (Fig. 289). Worldwide, the larvae of five and the pupae of 17 species have been described (Borkent 2014). Of these, in the Afrotropical Region, the larva and pupa of one species and only the pupae of two species are described (Borkent 2014) and these have been reared from sparse vegetation at the margin of a small, deep lake, the margins of a river and reservoir, grassy wetlands and from sand in shallow waters of a river (de Meillon & Wirth 1991). Otherwise extralimital species have been collected from lakes, ponds, salt marshes, reservoirs, creeks and rivers (Borkent 2014). Some pupae of this genus and several other Johannsenomyiini have distinctive membranous discs on the ventrum of their abdomens (as in Fig. 322), which are used to adhere to emergent vegetation or other substrate. Adults of two species have been collected with light traps. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (Giłka 2003). Females are also cannibalistic on males during copulation and upon completion, the dry husk of the male body breaks off, leaving the male's terminalia still clasped onto that of the female, thereby functioning as a mating plug (as in Fig. 30) (Downes 1978). An identification key to Afrotropical species is unavailable.

***Notoceratopogon* de Meillon & Downes** (Ceratopogoninae: Ceratopogonini)**.** An endemic genus of small- to moderately-sized midges known from four South African species. Adult males are known for all four species and females for two of these. Three of the species, *N. alcides* (de Meillon & Hardy, 1954), *N. minutus* de Meillon & Downes, 1986 and *N. vockerothi* de Meillon & Downes, 1986 are recorded from the Drakensberg at 1,400–2,265 m. The fourth species, *N. natalensis* (de Meillon, 1937), was collected as six adults male swarming over marshy ground at St. Lucia near the east coast and about 300 km NE of the Drakensberg. As such, the genus has a very restricted distribution. The immatures remain unknown. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. De Meillon & Downes (1986) mistakenly recorded the genus as present in Zimbabwe. There is no identification key, but de Meillon & Downes (1986) discuss the differences between the included species.

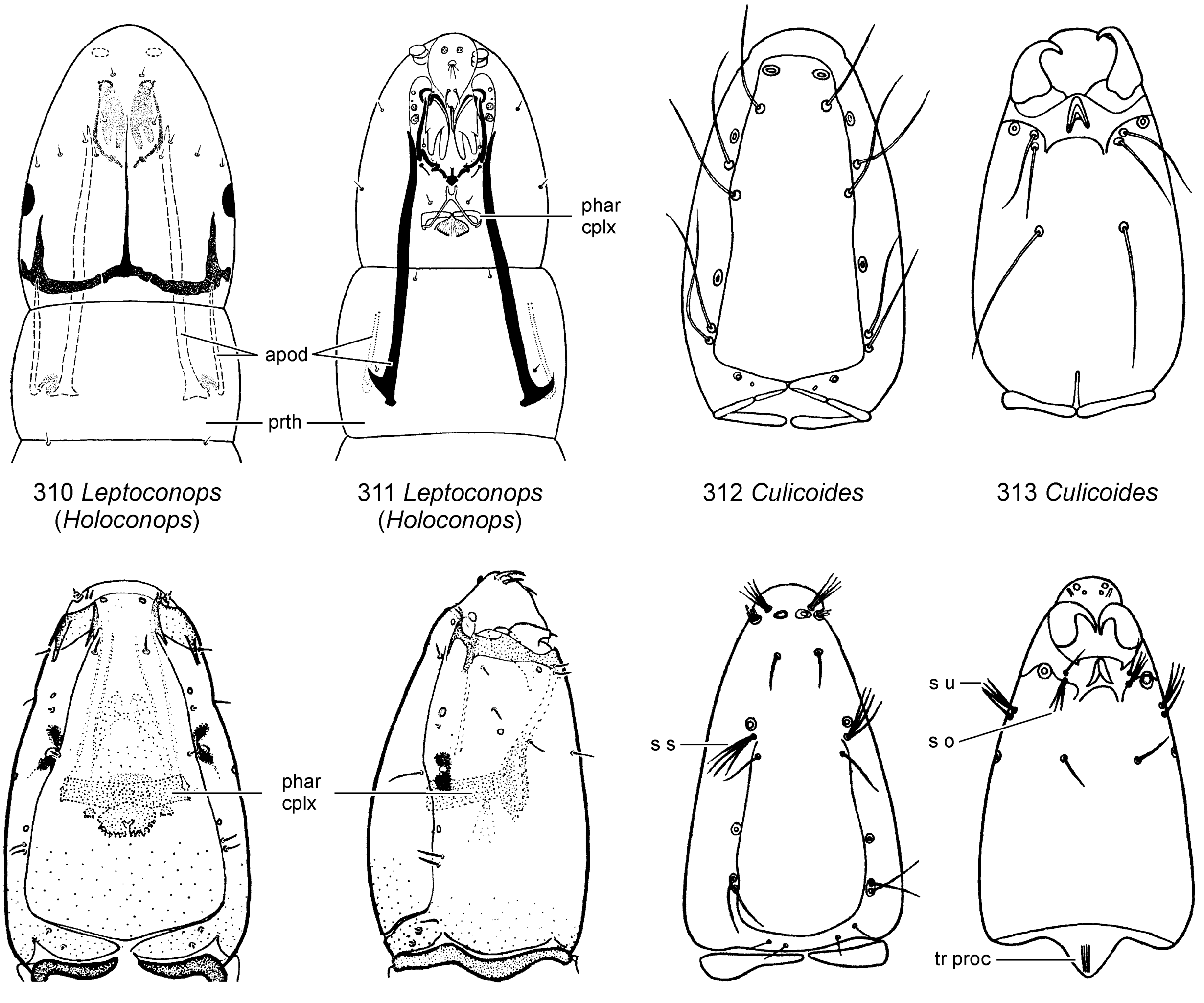
***Palpomyia* Meigen** (Ceratopogoninae: Palpomyiini)**.** A large genus of 271 described species, occurring in all zoogeographical regions, except Antarctica. Thirty-one species are recorded from the Afrotropical Region and of these, 19 are known only as females, nine only as males and the remaining three from both sexes. Adults vary from small to large, slender to moderately robust midges (Figs 16, 17), with the anterior femur variably thick and bearing ventral spines. Like other representatives of the tribes Palpomyiini and Stenoxenini, females have eversible abdominal sacs and internal tergal apodemes (Borkent & Craig 1994) (Fig. 303). Globally, the larvae of 23 and pupae of 41 species have been described, but within the Afrotropical Region the pupa of only one species is known (Borkent 2014) (Fig. 325). Three Afrotropical species have been reared from a swamp, river margins and from an exposed pool (de Meillon & Wirth 1991). Globally immatures have been collected from streams, hot springs, river margins, marshes, bogs, fens, ponds, lakes and reservoirs (Borkent 2014). Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies, including other ceratopogonids (Fig. 17) of nearly equal size and small mayflies in other regions (Downes 1978; Giłka 2003). Females are also cannibalistic on males during copulation and upon completion, the dry husk of the male body breaks off, leaving the male's terminalia still clasped onto that of the female, thereby functioning as a mating plug (Fig. 30) (Downes 1978). Female adults have eversible abdominal sacs that are attached to internal tergal apodemes and that are everted at times during flight (Borkent & Craig 1994). There is no identification key to all species, but de Meillon & Wirth (1987*a*) provided an identification key to those species in which only the fore femur has spines. Macfie (1939*b*) provided an identification key to ten species known at that time (including additional species now placed elsewhere) and Goetghebuer (1948: 16) keyed six species from Democratic Republic of Congo. Together these authors key out all species other than *P. armigera* de Meillon & Downes, 1986, *P. bicolor* Macfie, 1941, *P. ebejeri* Boorman & Harten, 2002, *P. fusca* de Meillon, 1938, *P. kurwana* de Meillon & Wirth, 1987, *P. magali* de Meillon & Wirth, 1981, *P. mahyoubi* Boorman & Harten, 2002, *P. nakali* Boorman & Harten, 2002, *P. oliffi* de Meillon & Hardy, 1954, *P. singularis* de Meillon, 1937, *P. tauffliebi* Vattier & Adam, 1966 and *P. vittata* Clastrier, Rioux & Descous, 1961.

***Parabezzia* Malloch** (Ceratopogoninae: Ceratopogonini)**.** A genus of 44 described species, 39 of which are restricted to the New World and five species occur in the Old World. One species occurs in Algeria in the Palaearctic and one species in Sri Lanka in the Oriental Region. Three species occur in the Afrotropical Region: *P. falcipennis* Clastrier from Republic of Congo and *P. stagni* de Meillon & Wirth, 1981 and *P. obscura* de Meillon & Wirth, 1981, from South Africa. The female wing has a costal extension well beyond the apex of vein R_3 and extending to, or near to the apex of the wing (Fig. 147). Males have unique (in the Afrotropical Region) spinose fore and mid coxae (Fig. 69). Larvae are unknown for this genus (see Borkent 2014), but the pupae of eight species have been described, including for the Afrotropical Region, the pupa of *P. stagni*, collected from a ground water pool (Borkent 2014). Elsewhere, pupae have been collected from the margins of streams, rivers and ponds. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (as in Fig. 17) (Downes 1978). No identification key to Afrotropical species is available.

***Paralluaudomyia* Clastrier** (Ceratopogoninae: Ceratopogonini)**.** An endemic monotypic genus, with the single described species, *P. maculata* Clastrier, 1960, known only from a single female collected with a light trap at Buku N'Situ (= M'Bouku), M'Vouti District, Republic of Congo (Clastrier 1960*a*, 1960*b*). The female has a distinctive elongate single radial cell extending almost to the wing apex (Fig. 126). The mandible of the female has not been described, but likely has coarse teeth, indicating that it probably feeds on other nematocerous Diptera of a similar size. Immature stages and biology of the species remain unknown.

Pellucidomyia **Macfie** (Ceratopogoninae: Heteromyiini)**.** A genus with nine species of elegant, moderately-sized midges, occurring in the New World and the Australasian and Afrotropical Regions. Three species occur in the Afrotropics: *P. ugandae* Macfie, 1939 from Uganda; *P. sambulena* (de Meillon, 1942) from Mozambique; and *P. geari* (de Meillon & Wirth, 1981) from South Africa. The last two named may be conspecific (Borkent 2014). Adults are rare and females are unusual (but not unique), in having a greatly elongated hind leg with a single elongate claw. In the Afrotropics, only the pupa of *P. geari* is known, collected from the margin of a water storage impoundment. The larva and pupa of the Australian *P. leei* Wirth, 1960 are the only other immatures known and have been sampled from small streams and creeks and the backwaters of a creek. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. No identification key to Afrotropical species is available.

Phaenobezzia **Haeselbarth** (Ceratopogoninae: Palpomyiini)**.** A genus of 34 described species occurring in the New World and the Afrotropical, Oriental and Palaearctic Regions. Of these, 14 occur throughout most of the Afrotropics, including one species from Seychelles (Clastrier 1983*c*). The male terminalia has a strikingly reduced gonostylus (Fig. 291) that may be absent.



310 *Leptoconops* (*Holoconops*)

311 *Leptoconops* (*Holoconops*)

312 *Culicoides*

313 *Culicoides*

314 *Culicoides*

315 *Culicoides*

316 *Sphaeromias*

317 *Sphaeromias*

Figs 34.310–317. Head capsules of fourth-instar larvae of Ceratopogonidae: (310) *Leptoconops* (*Holoconops*) *gallicus* Clastrier, dorsal view (non-Afrotropical); (311) same, ventral view; (312) *Culicoides punctatus* (Meigen), dorsal view (non-Afrotropical); (313) same, ventral view; (314) *Culicoides nubeculosus* (Meigen); (315) same, ventral view; (316) *Sphaeromias pictus* (Meigen), dorsal view (non-Afrotropical); (317) same, ventral view. Figs 310, 311 (Clastrier 1972, figs 1A, 1B, as *L. kerteszi*), Figs 312, 313, 316, 317 (after Glukhova 1979, figs 68.1, 68.2, 18.A1, 18A2, respectively), Figs 314, 315 (after Lawson 1951, figs 5, 4).

Abbreviations: apod – apodeme; phar cplx – pharyngeal complex; prth – prothorax; s o – seta o; s s – seta s; s u – seta u; tr proc – triangular process.

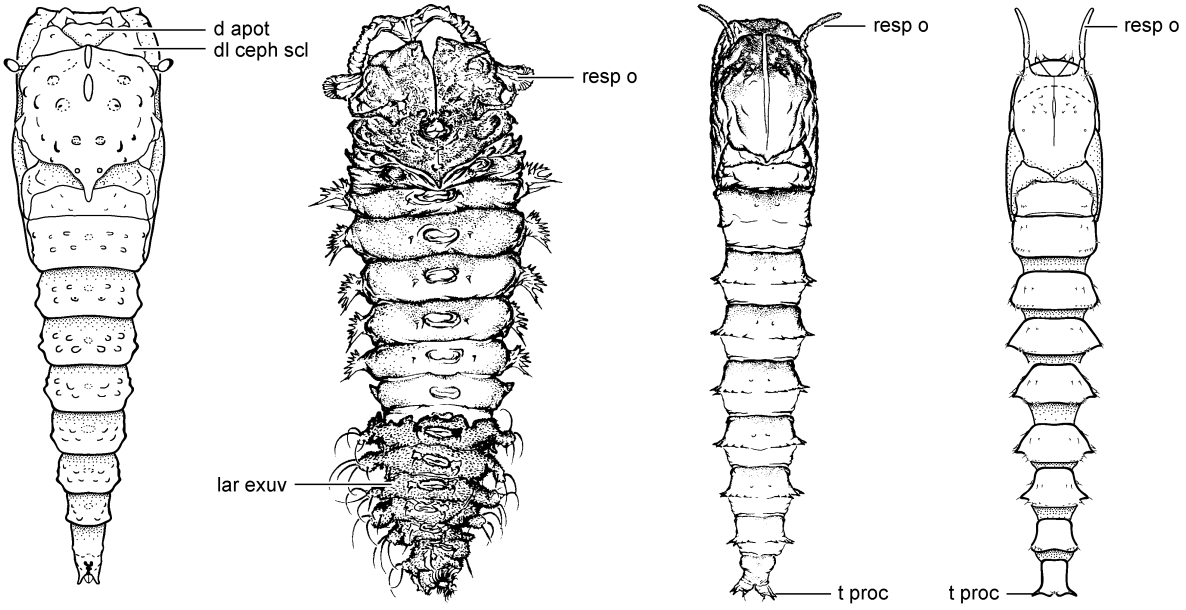
Females (Fig. 19) have eversible abdominal sacs and internal tergal apodemes (Borkent & Craig 1994), like other representatives of the tribes Palpomyiini and Stenoxenini. Of Afrotropical species, the larva and pupa of *P. pistiae* (Ingram & Macfie, 1921) and only the pupae of four others are described (Borkent 2014; Haeselbarth 1965). These and two other Afrotropical species have been collected from margins of streams and a water storage impoundment, the backwaters of streams, rice fields and from the floating vegetation of *Pistia stratiotes*. De Meillon (1942*a*: 13) reported *P. pistiae* to be common in marshes, backwaters of rivers and in lakes, amongst vegetation. Outside the region, the larvae of two and the pupae of four other species have been described, from stream and river margins, seepage pools, marshes (usually among vegetation) and the margins of lakes and reservoirs. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Female adults have eversible abdominal sacs that are attached to internal tergal apodemes and that are everted at times during flight (Borkent & Craig 1994) (as in Fig. 303). Identification keys to males and females of the seven Afrotropical species known at that time were provided by Haeselbarth (1965).

***Schizonyxhelea* Clastrier** (Ceratopogoninae: Ceratopogonini)**.** A genus of 15 described species occurring in the New World and the Afrotropical and Oriental Regions. There is also an undescribed species from the Australasian Region (Borkent 2014). This genus was newly recorded from the Afrotropical Region by Borkent (2015) and there are probably more names that need to be transferred from *Stilobezzia* in the future, after types have been examined. Adults are tiny and, at least in the New World, may be relatively common. Males have a distinctive and unique heavily sclerotised transverse band ventral to the parameres of the male terminalia and a reduced aedeagus. The adults are tiny and have a reduced wing venation (Figs 77, 134). The larvae and pupae of two New World species have been described and were collected from mud from the margins of a bog, from the grassy margin of a marsh, from mud, pond weeds and *Sphagnum* and from wet mud in a small seep, which flowed into the outflow of a larger spring (Borkent 2014). Immatures are unknown from the Afrotropical Region, but adults have been reared from a root mat covered with moss situated on the margin of a seep and from mud from rice paddies (Clastrier 1991). Adults have also been collected with light traps. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. The three Afrotropical species, *S. afra* (Clastrier, 1991) from Guinea, *S. afrotropica* (Clastrier, 1991) from Guinea and *S. corneti* (Clastrier, 1991) from Burkina Faso, can be identified with the identification key provided by Clastrier (1991), which includes some other extralimital species, as species of *Stilobezzia*.

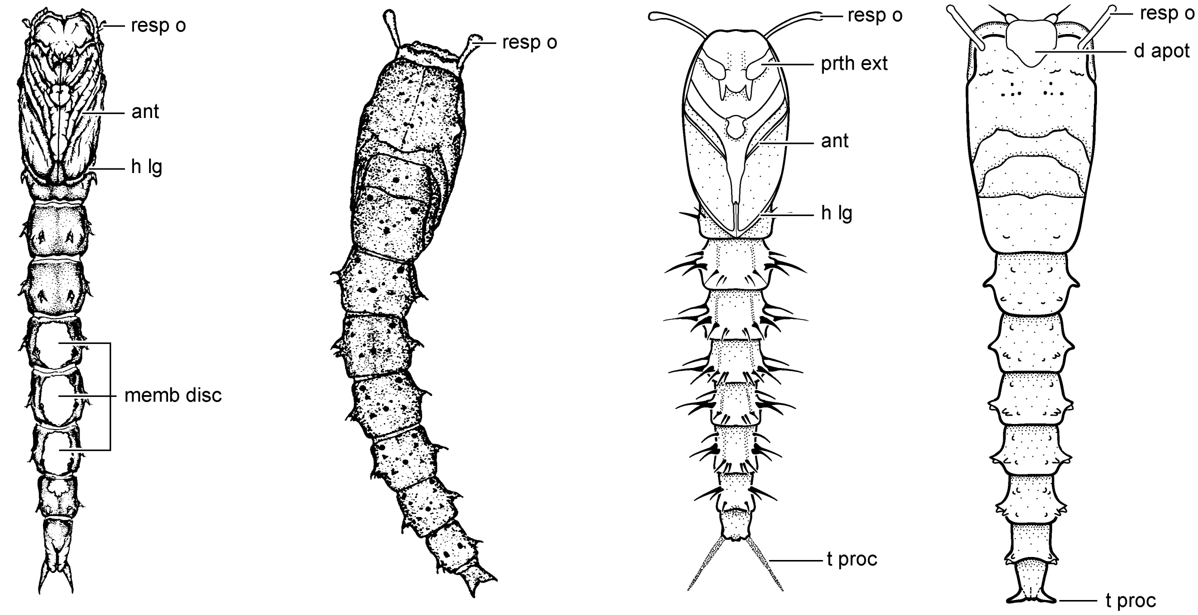
***Serromyia* Meigen** (Ceratopogoninae: Ceratopogonini)**.** A genus of 37 described species occurring in all zoogeographical regions, except the Neotropics and Antarctica (Borkent 2016*a*). Twelve species are recorded from the Afrotropical Region: one species from United Arab Emirates; one species from Oman and Yemen; one species from Gambia; seven from South Africa; one from Madagascar; and one from Seychelles. Adults have a distinctive swollen hind femur, with at least two rows of ventral spines on at least the distal 0.58 of femur (Figs 1, 220) (see also *Metacanthohelea*, Fig. 222). Immatures are unknown from the Afrotropical Region, but the larva and pupa of one species, the larva of one species and the pupa of another species are known from the Holarctic Realm. These were collected from bogs, fens, in mosses at lake margins, in mud associated with marshlands, wet meadows, streams or small rivers (Borkent 2014). At least within the Holarctic Realm, species are restricted to wooded areas; *S. silvatica* de Meillon & Downes, 1986 from the Drakensberg was collected in an area of Fynbos and open grassland. Adults in the Afrotropical Region have been collected by sweeping, Malaise traps, light traps and truck traps. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (Borkent & Bissett 1990; Downes 1978). Females are also cannibalistic on males during copulation (Edwards 1920). Nearly all known males and females were keyed by de Meillon & Wirth (1983*b*). The subsequently described *S. silvatica*, known only from a female, is unique in the Afrotropical fauna in having small, equal hind claws. The lone species from Seychelles, *S. festiva* Kieffer, 1911, was redescribed by Clastrier (1983*c*). One species from United Arab Emirates was described by Szadziewski *et al.* 2011 and a record of one otherwise Palaearctic species from Oman and Yemen was recorded by Boorman & van Harten (2002).

***Sphaeromias* Curtis** (Ceratopogoninae: Sphaeromiini)**.** A genus of 30 described species occurring in all zoogeographical regions, except the Neotropics and Antarctica (Borkent 2016*a*). These large ceratopogonids (Figs 13, 36, 37) are known from six species in the Afrotropical Region. Male *S. eugenei* de Meillon & Wirth, 1987 and *S. pistiae* (Ingram & Macfie, 1922) have separate, non-spiculose parameres and *S. litoraureus* Ingram & Macfie, 1921 have partially fused parameres, unlike those of other *Sphaeromias*. Some adults are the largest of all Ceratopogonidae, with a wing length of some females of > 5 mm. The wing pigmentation of *S. pistiae* is similar to that of many Heteromyiini and distinctive. Immatures have not been described for Afrotropical species, but adults have been reared from *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae), *Pistia stratiotes*, from peat soil in *Rhizophora* mangroves and shady swamps (de Meillon & Wirth 1991). Elsewhere species have been found in rivers and lakes (sometimes in blanket algae) (Figs 316, 317, 323). Larvae of species in the Holarctic Realm are reported from the benthos of lakes. Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (Giłka 2003). An identification key to the four species known from males and the five known from females was provided by de Meillon & Wirth (1987*a*), but this include *N. theileri* de Meillon & Wirth, 1981, now placed in *Nilobezzia*.

***Stenoxenus* Coquillett** (Ceratopogoninae: Stenoxenini)**.** A genus of 21 described species known from the New World and the Afrotropical and Oriental Regions. Three species occur in the Afrotropical Region: *S. pauliani* Vattier & Adam, 1966 from Republic of Congo; *S. pastorianus* Clastrier, 1982 from Guinea; and *S. usutae* de Meillon, 1959 from South Africa. Larvae and pupae of this genus remain unknown. Males and females of *S. pastorianus* have been reared from soil taken from shallow pools of water on a sandstone plateau in Guinea. The remaining two species, known only from females, were sampled with light traps. This genus is closely related to *Paryphoconus* Enderlein, the only two genera in the tribe Stenoxenini and the eggs of both genera have a distinctive



318 *Forcipomyia* (*Thyridomyia*) 319 *Atrichopogon* 320 *Dasyhelea* 321 *Culicoides*



322 *Mallochohelea* 323 *Sphaeromias* 324 *Bezzia* 325 *Palpomyia*

Figs 34.318–325. Habitus of pupae of Ceratopogonidae (all non-Afrotropical): (318) *Forcipomyia* (*Thyridomyia*) *rugosa* Chan & Le Roux, dorsal view; (319) *Atrichopogon muelleri* (Müller), dorsal view (with larval exuviae on posterior of abdomen); (320) *Dasyhelea flavifrons* (Guérin-Méneville), dorsal view; (321) *Culicoides sonorensis* Wirth & Jones, dorsal view; (322) *Mallochohelea munda* (Loew), ventral view; (323) *Sphaeromias fasciatus* (Meigen), dorsal view; (324) *Bezzia glabra* (Coquillett), ventral view; (325) *Palpomyia* sp., dorsal view. Fig. 318 (after Chan & LeRoux 1970, fig. 5G), Figs 319, 320, 322 (after Szadziewski *et al*. 1997, figs 27, 29 as *D. versicolor* (Winnertz), 30)), Fig. 321 (after Borkent 2014, fig. 3A), Fig. 323 (Mayer 1934, fig. 68), Fig. 324 (after Thomsen 1937, fig. 97), Fig. 325 (after Grogan & Wirth 1979, fig. 3B).

Abbreviations: ant – antenna; d apot – dorsal apotome; dl ceph scl – dorsolateral cephalic sclerite; h lg – hind leg; lar exuv – larval exuviae; memb disc – membranous disc(s); prth ext – prothoracic extension; resp o – respiratory organ; t proc – terminal process.

terminal nipple-like constriction, with a fringed subapical collar (a synapomorphy of the tribe). Female *Stenoxenus* have a strikingly different M_2 wing vein (Fig. 166), compared to males and other representatives of the family. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. Adult females have eversible abdominal sacs that are attached to internal tergal apodemes that are everted at times during flight (Borkent & Craig 1994). No identification key to Afrotropical species is available.

Stilobezzia **Kieffer** (Ceratopogoninae: Ceratopogonini)**.** A genus of 344 species of common, often brightly coloured and patterned predaceous midges, occurring in all zoogeographical regions, except Antarctica. Of these, 70 species occur in the Afrotropical Region (Figs 10, 11). The genus is divided into four subgenera, three of which are represented in the region: *Stilobezzia sensu stricto* (35 species), *S.* (*Acanthohelea* Kieffer) (32) and *S.* (*Eukraiohelea* Ingram & Macfie) (3). The phylogenetic relationships between species of *Stilobezzia* remain uncertain and the genus warrants a detailed cladistic analysis to test the reality of the current division into four subgenera (Borkent 2014). Clastrier (1976) recognised that the current subgenera (at that time with three subgenera), were artificial and correctly suggested further characters (primarily of the antennae, wings and thoracic chaetotaxy), to interpret the group, although these were not interpreted cladistically. He divided the genus into a number of sections and groups and, although these are useful to distinguish some taxa occurring in the Afrotropical Region, he did not provide an identification key. The resultant complex portrayal of the genus makes it difficult to identify species of this group. The larvae of two and the pupae of four Afrotropical species have been described and these and others have been reared from the margins of streams, ponds and lakes, swamps, rice fields, rock pools and wet tree cavities (de Meillon & Wirth 1991). Elsewhere, the larvae of 11 and pupae of 25 species have been described. These and others reared, but not described occur in a wide variety of aquatic and semi-aquatic habitats, including such additional habitats as springs, swamps, bogs, fens, rock pools, and soil in tidal marshes. The remarkably modified respiratory organs of *S. poikiloptera* (Ingram & Macfie, 1922), are used to pierce the submerged roots of aquatic plants to obtain oxygen for the pupa (Borkent & Craig 2001). Females have coarsely-serrated mandibles and have been observed feeding on nematocerous flies of nearly equal size in other regions (Downes 1978; Giłka 2003). Clastrier (1986a) keyed the five species in the *S. subviridis* species-group and redescribed those previously described by Goetghebuer from the Afrotropics and Clastrier (1988*b*) keyed the four species Clastrier (1976) recognised as his "section 4". There is a need to develop an identification key to all the species occurring in the region.

Stiloculicoides **Wirth & Grogan** (Ceratopogoninae: Ceratopogonini)**.** A small genus of six species restricted to the Afrotropical (5 species) and Palaearctic Regions (1). Afrotropical taxa are known from three species from Guinea, one from Republic of Congo and one from Cameroon and Uganda. Immatures are undescribed, but two female adults of *S. ugandae* (Ingram & Macfie, 1923) were reared from leaf mould at the base of a palm tree in Cameroon (de Meillon & Hardy 1954, as *Stilobezzia*). Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. The name of the genus refers to the similarity of the wings (Figs 88, 135) to those of some species of *Culicoides*. Clastrier (1993) provided an identification key to the adults of all species (two of which are known only from females).

Tetrabezzia **Kieffer** (Ceratopogoninae: Heteromyiini)**.** A small genus of six described species restricted to the Afrotropical (4 species) and Oriental Regions (2). Afrotropical species are known from Guinea, Madagascar, Mozambique and Nigeria (Borkent 2016*a*). Adults are large and slender, with patterned wings and the hind tarsus of the female is greatly elongated. Although the immatures are undescribed, *T. africana* Clastrier, 1982 was reared from roots and moss in shallow rock pools. Adults have also been collected with light traps and two female *T. argentea* Ingram & Macfie, 1923 were collected hovering during the day. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. There is no published identification key to adults, but Clastrier (1982*a*) discusses differences between all four Afrotropical species.

Undescribed Genus (Ceratopogoninae: Ceratopogonini)**.** A genus represented by two unnamed species that have well-developed wing venation (Fig. 85) similar to that of a number of other genera (*e.g.*, Figs 139, 142, 143, 146) and the legs similar to those of *Fanthamia* (swollen hind femora, female with equal claws). The male terminalia are large (somewhat similar to that of *Ceratopogon gigaforceps* Remm, 1973; Borkent & Grogan 1995). The elongate, narrow head readily distinguishes the new genus from others. The head of *Calcarhelea bimater* (de Meillon & Hardy, 1953) is also somewhat slender (at least in the female; male not examined), but in that species the head is not as narrow and the eyes are widely separated (abutting medially in the undescribed genus). Nothing is known about the immatures. The presence of coarse mandibular teeth for females of both species indicates they probably feed on other nematocerous Diptera of a similar size. Of the two species, one is based on 1 male and 3 females from the Sederberg Mountains, South Africa (in California Academy of Sciences, USA) and the other, represented by a single female, from Cathedral Peak, KwaZulu-Natal, South Africa (in Canadian National Collection, Ottawa).

Xenohelea **Kieffer** (Ceratopogoninae: Sphaeromiini)**.** A genus of 14 described species restricted to the Afrotropical (2 species) and Oriental Regions (12). *Xenohelea spinosipes* (Goetghebuer, 1948), is known from Democratic Republic of Congo and *X. galatea* de Meillon, 1942 from Mozambique and South Africa. Males are unknown for the genus. The wing illustrated as that of the Afrotropical species *X. spinosipes* by Goetghebuer (1948) is mislabelled and is actually that of *Culicoides schultzei* (Enderlein, 1908) (as *C. irroratus* Goetghebuer, 1948). Larvae of the genus remain unknown and the pupa of only one species (*X. galatea*) has been described (Borkent 2014). It was collected from among debris in a small clear stream in Mozambique (de Meillon 1942*a*: 23). An adult has been collected with a light trap. Females have coarse mandibular teeth, indicating that they probably feed on other nematocerous Diptera of a similar size. No identification key to Afrotropical species is available.

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CHIRONOMIDAE 35

(Non-biting Midges)

Torbjørn Ekrem, Patrick Ashe, Trond Andersen and Elisabeth Stur

Fig. 35.1. Male of *Kiefferulus brevibucca* (Kieffer) (South Africa) (photograph © S.A. Marshall).

Diagnosis

Minute- to moderately large-sized midges (overall length: 1–13 mm; wing length: 0.6–8.0 mm) (Fig. 1), colour from white to pale yellowish green, to entirely black, sometimes with pigmented pattern on body, legs and/or wings.

Head (Figs 43, 44) with well-developed compound eyes, often with non-contiguous dorsomedian extensions; male antenna most often long and plumose, with low flat scape, globose pedicel and 6–15 flagellomeres; female antenna with fewer setae, smaller pedicel and 4–7 or 10–15 flagellomeres; mouthparts largely reduced, functional mandibles absent (except in females of *Archaeochlus* Brundin and non-Afrotropical *Austrochlus* Cranston), labellum and palpus present, usually well-developed.

Thorax (Figs 37–42) variable with regard to setation and development of antepronotal lobes; mesonotum dorsally convex in winged species, giving a more or less "hunchbacked" appearance; postnotum usually with median longitudinal

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groove. Wing usually narrower in male, broader in female; reductions and other shapes occur in taxa with specific life history adaptations; wings in resting position flat or tent-like over abdomen; costal vein (*C*) reaching at most to apex of wing; membrane hyaline, sometimes with dark markings, or rarely nearly all dark; microtrichia present, short true setae (macrotrichia) also present on wing cells and/or veins in a number of taxa; calypter bare or fringed with setae; 2 or 3 branches of vein *R*, 2 of vein *M*, 1 of vein *Cu* usually reaching wing margin (*e.g.*, Fig. 6). Legs usually long and thin (shorter and stouter in some groups of ground mating species); fore leg longest, mid leg shortest; male fore tarsus with or without conspicuously long setae ("beard"); fore tarsus shorter than tibia, except in subfamily Chironominae (fore tarsus usually longer than tibia); first tarsomere longer than second; claws pointed or toothed; pulvilli present or absent (Figs 45–48).

Abdomen with 7 (female) or 8 (male) pregenital segments; in some taxa the male terminalia can be rotated up to 180° at junction between segments 7 and 8; male tergite 9 (epandrium) frequently with posteromedian extension (anal point); well-developed gonocoxite and gonostylus; appendages on gonocoxite variably developed in number and shape, often forming complex structures (Figs 49–108); female terminalia with tergite 8 usually unmodified (strongly reduced in Telmatogetoninae); segment 8 with large sternal plate and postero-medial lobes and processes; tergite 9 well-developed, sometimes divided, with ventrolateral expansion or prolongation (= gonocoxite 9 *sensu* Sæther 1980) variably developed, often with protruding bulge; sternite 9 mostly membranous; genital fork ("furca") well-developed; segment 10 undifferentiated, including genital plate and bearing the free, lobe-formed cerci.

Chironomidae are superficially similar to Chaoboridae (see Chapter 30), Culicidae (see Chapter 31) and Ceratopogonidae (see Chapter 34), but can be separated from these as adults by the combination of the maximum of 7 wing veins reaching the wing margin; the costal vein (*C*) ending before or at the wing apex (Figs 2–36); the postnotum usually with a median longitudinal groove (Fig. 37); and the usually reduced mouthparts (Figs 43, 44).

Biology and immature stages

A comprehensive overview of Chironomidae morphology, systematics, biology, ecology and behaviour was provided by Armitage *et al*. (1995). Although new knowledge has emerged over the past two decades, this work still provides the best overview of chironomid biology.

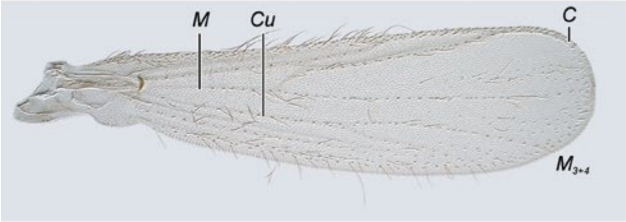
The immature stages of most Chironomidae species inhabit freshwater, but the larvae of numerous species are associated with semi-terrestrial, terrestrial, or even marine coastal habitats. Chironomids have been recorded from all zoogeographical regions of the world and even continental Antarctica is home to three species (Cranston 1995*a*: 1). At the time of writing there are 6,359 species described worldwide (Ashe & O'Connor 2009, 2012, unpubl.), but estimates of 10–15,000 species have been suggested (Cranston 1995*a*: 2).

Thus, Chironomidae is one of the most successful and widely distributed families of Diptera. The remarkable diversity and the many adaptations to particular environments make it difficult to generalise, or treat comprehensively the various aspects of the biology of non-biting midges within the framework of this *Manual*. This section, therefore, provides the most commonly observed biologies of the various life stages of Chironomidae, with special focus on the Afrotropical fauna. Given their wide distribution, high diversity and old age, the biogeography of Chironomidae is interesting in an evolutionary perspective. Some of the knowledge related to the Afrotropical Region was summarised by Sæther & Ekrem (2003), and Cranston *et al*. (2010) tested Brundin's (1966) hypotheses on transantarctic relationships using a dated molecular phylogeny.

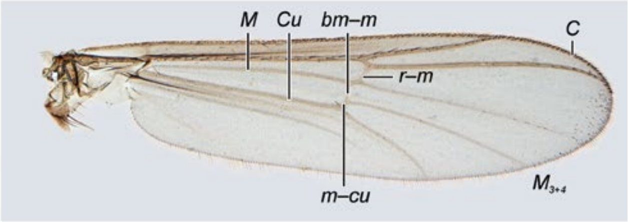
The females of most Chironomidae species lay numerous eggs in a gelatinous matrix; single-egg oviposition is known only in the subfamily Telmatogetoninae (Cranston 1995*c*: 12). The shape of the egg mass and arrangement of eggs differs among taxa and appears to be phylogenetically significant at subfamily level (Nolte 1993), but more detailed investigation is required. Oviposition behaviour varies by taxon and habitat, but in aquatic species eggs are typically laid on the waters' surface, attached to solid surfaces, such as stones, leaf litter, or macrophytes (Nolte 1993). The females of some species oviposit directly into the water, however, and communal oviposition generating large aggregates of egg masses has been observed to occur in several subfamilies (Pinder 1995*a*: 89).

Chironomid larvae have characteristics typical for nematocerous Diptera: a well-developed, complete, non-retractile head capsule; well-developed mandibles, operating in an oblique to horizontal plane; and a narrow, elongate, segmented body that lacks true legs (Figs 109–111). They can usually be separated from other Diptera larvae by having paired prolegs on the first thoracic and last abdominal segments, a pair of dorsal procerci with apical tufts of setae on the last abdominal segment, and by the absence of spiracles (Figs 109, 110). Posterior spiracles are present only in some Podonominae and prolegs may be variably fused or lacking, particularly in certain terrestrial species (Fig. 111). In these cases, chironomid larvae are difficult to separate from those of Thaumaleidae (see Chapter 33) or Ceratopogonidae (see Chapter 34), but the anteriorly directed mouthparts (Figs 112–116), as well as the poorly sclerotised and unmodified pharynx is typical of Chironomidae.

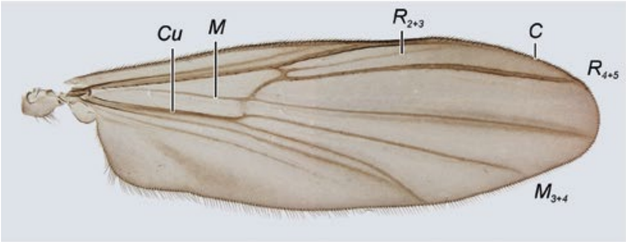
Chironomid larvae have four instars. The first instar in aquatic species is typically more or less free-swimming and exposed to drift, until settling on a suitable substrate. The remaining instars of aquatic species are benthic, free-living, or sedentary, frequently building variably shaped tubes or shelters in the surrounding substrate using salivary secretions as glue. These structures can be transportable or fixed to the substrate and are sometimes central to the feeding strategy (*e.g.*, in *Rheotanytarsus* Thienemann & Bause). Instars 2–4 may occur on different types of substrate (depending on specialisation), including algal mats, macrophytes, submersed dead wood, or muddy to rocky sediments. Some species mine in plants or even induce and inhabit true galls (Jäger-Zürn *et al*. 2013), others occur phoretically, or as endo- or ectoparasites on various animals. The more general habitats are numerous, making Chironomidae one of the most ecologically diverse insect groups. They inhabit all kinds of lotic and lentic waters, including glacial streams, cold and hot springs, thin water films, brooks, rivers, lakes, ponds, phytotelmata, rock pools and salt lakes. There are also



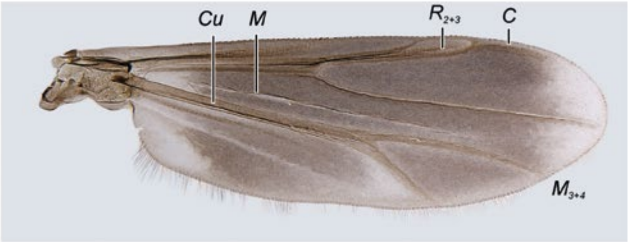
2 *Aphrotenia*



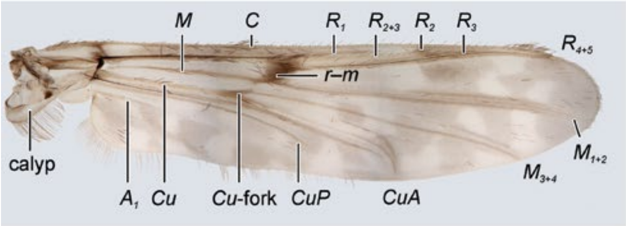
3 *Archaeochlus*



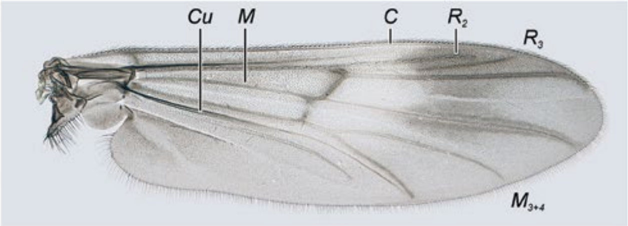
4 *Diamesa*



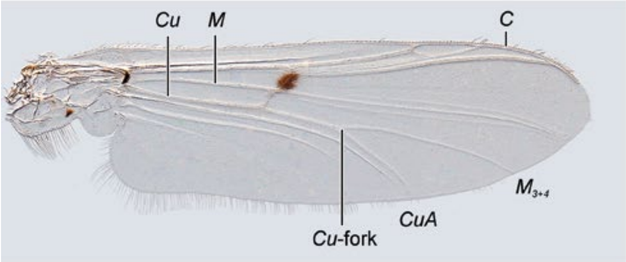
5 *Usambaromyia*



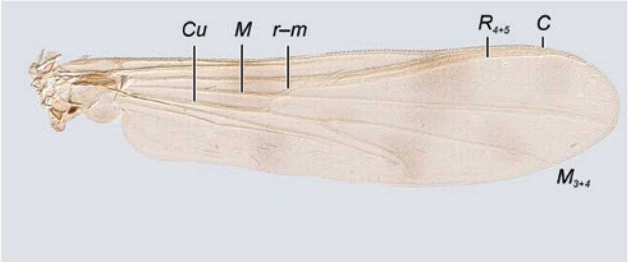
6 *Ablabesmyia* (*Karelia*)



7 *Coelotanypus*



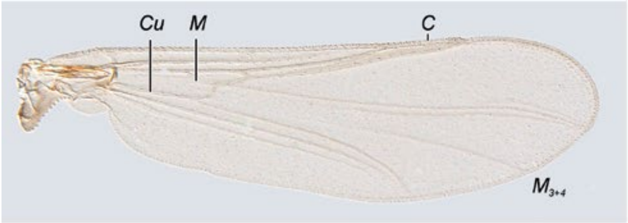
8 *Djalmabatista*



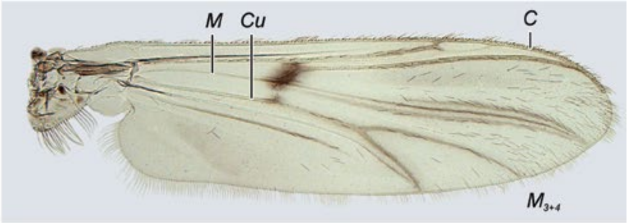
9 *Lepidopelopia*

Figs 35.2–9. Wings of Chironomidae males: (2) *Aphrotenia tsitsikamae* Brundin; (3) *Archaeochlus biko* Cranston, Edward & Colless; (4) *Diamesa freemani* Willassen & Cranston; (5) *Usambaromyia nigrala* Andersen & Sæther; (6) *Ablabesmyia* (*Karelia*) *nilotica* (Kieffer); (7) *Coelotanypus* sp.; (8) *Djalmabatista reidi* (Freeman); (9) *Lepidopelopia annulator* (Goetghebuer). Photographs T. Ekrem and E. Stur.

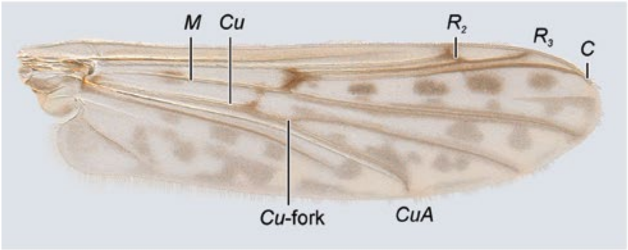
Abbreviations: A_1 – first branch of anal vein; *bm–m* – basal–medial crossvein; *C* – costal vein; calyp – calypter; *Cu* – cubitus; *CuA* – anterior branch of cubital vein; *Cu*-fork – cubital vein fork; *CuP* – posterior branch of cubital vein; *M* – media; M_{1+2} – fused first and second branch of media; M_{3+4} – fused third and fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3} – second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.



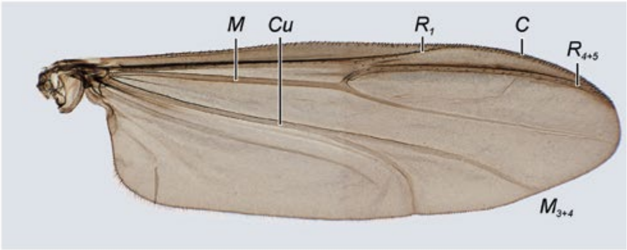
10 *Nilotanypus*



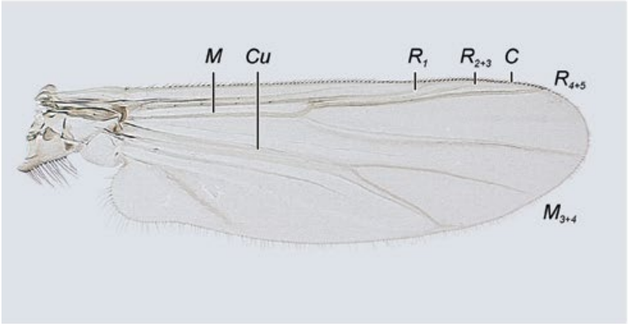
11 *Procladius* (*Holotanypus*)



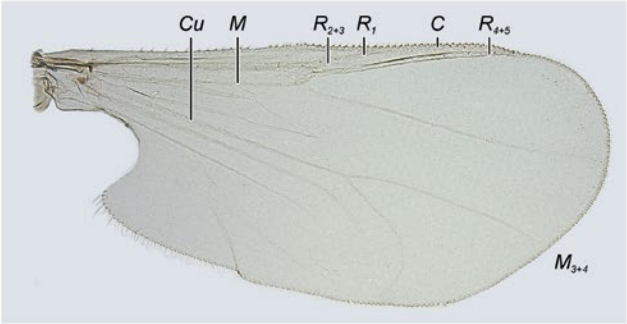
12 *Tanypus* (*Tanypus*)



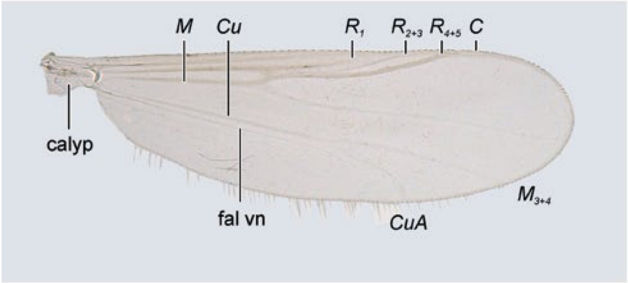
13 *Telmatogeton*



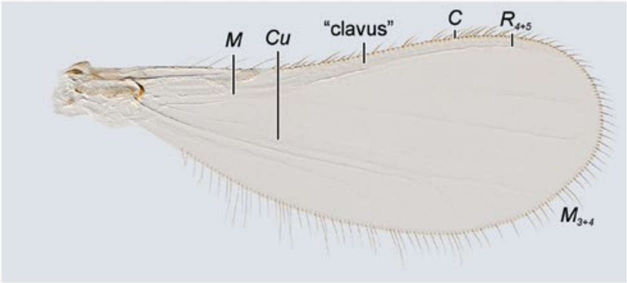
14 *Cardiocladius*



15 *Clunio*



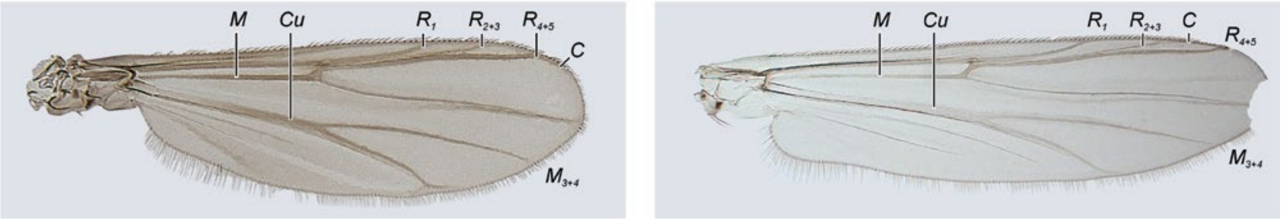
16 *Colosmittia*



17 *Corynoneura*

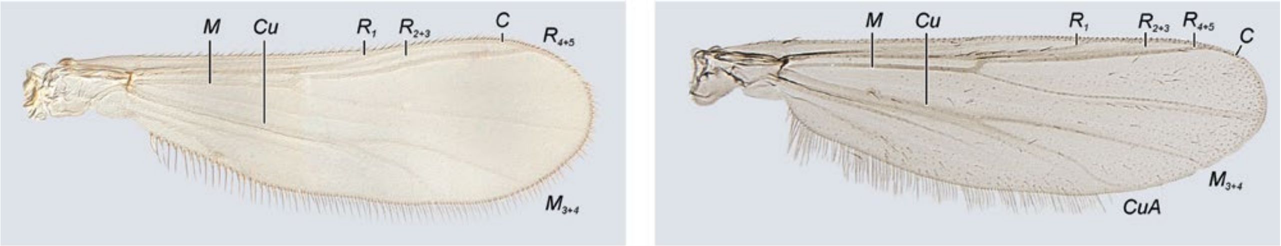
Figs 35.10–17. Wings of Chironomidae males: (10) *Nilotanypus comatus* (Freeman); (11) *Procladius* (*Holotanypus*) sp.; (12) *Tanypus* (*Tanypus*) *brevipalpis* (Kieffer); (13) *Telmatogeton goughi* Sæther & Andersen; (14) *Cardiocladius* sp.; (15) *Clunio jonesi* Sæther & Andersen; (16) *Colosmittia clavata* Andersen & Sæther; (17) *Corynoneura* sp. Photographs T. Ekrem and E. Stur.

Abbreviations: *C* – costal vein; calyp – calypter; *Cu* – cubitus; *CuA* – anterior branch of cubital vein; *Cu*-fork – cubital vein fork; fal vn – false vein; *M* – media; M_{3+4} – fused third and fourth branch of media; R_1 – anterior branch of radius; R_2 – upper branch of second branch of radius; R_{2+3} – second branch of radius; R_3 – lower branch of second branch of radius; R_{4+5} – third branch of radius.



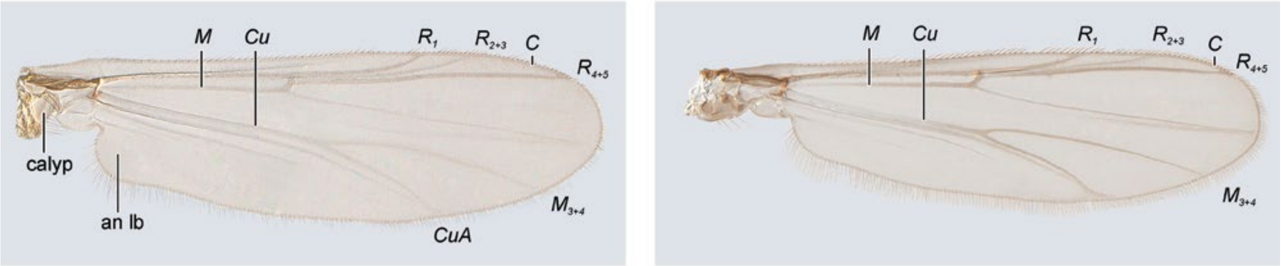
18 *Cricotopus* (*Cricotopus*)

19 *Cricotopus* (*Paratrichocladius*)



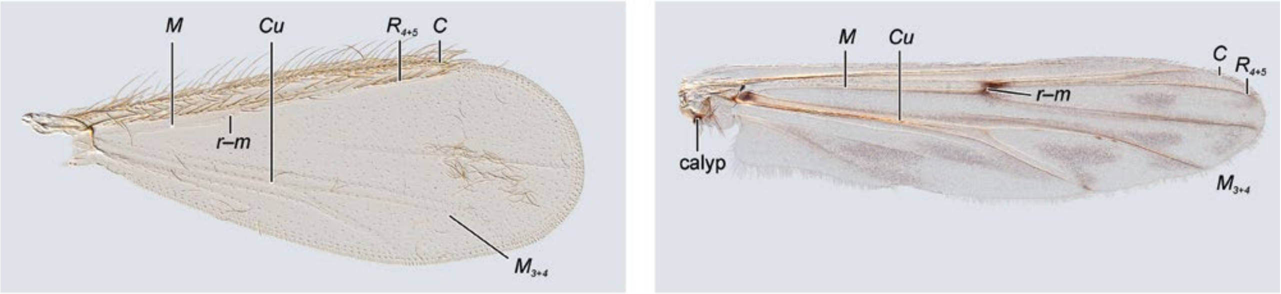
20 *Georthocladius* (*Georthocladius*)

21 *Parametriocnemus*



22 *Psectrocladius* (*Psectrocladius*)

23 *Rheocricotopus* (*Psilocricotopus*)



24 *Afrozavrelia*

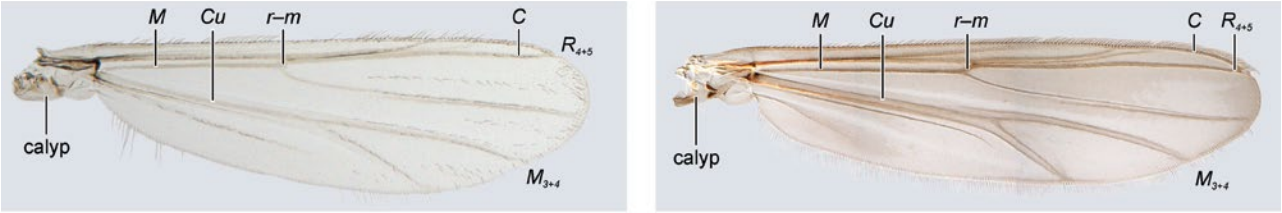
25 *Chironomus* (*Chironomus*)

Figs 35.18–25. Wings of Chironomidae: (18) *Cricotopus* (*Cricotopus*) sp. ♂; (19) *Cricotopus* (*Paratrichocladius*) sp. ♂; (20) *Georthocladius* (*Georthocladius*) *longicalcaneum* Sæther & Andersen ♂; (21) *Parametriocnemus* sp. ♂; (22) *Psectrocladius* (*Psectrocladius*) sp. ♂; (23) *Rheocricotopus* (*Psilocricotopus*) sp. ♂; (24) *Afrozavrelia kribiensis* (Kieffer) ♀; (25) *Chironomus* (*Chironomus*) sp. ♂. Photographs T. Ekrem and E. Stur.

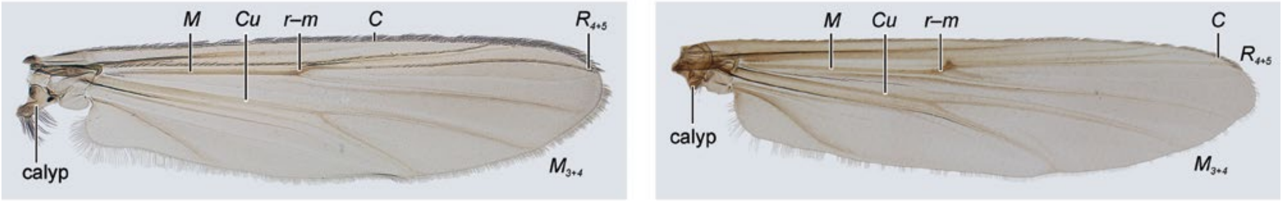
Abbreviations: an lb – anal lobe; *C* – costal vein; calyp – calypter; *Cu* – cubitus; *CuA* – anterior branch of cubital vein; *M* – media; M_{3+4} – fused third and fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

species with semi-aquatic, semi-terrestrial or terrestrial larvae, typically associated with wet or moist organic matter. A few taxa are even known to be truly marine. Terrestrial species almost exclusively occur in the subfamily Orthocladiinae, while marine species occur in the subfamilies Chironominae, Orthocladiinae and Telmatogetoninae. A special adaptation of an Afrotropical species is particularly noteworthy. The larvae of *Polypedilum* (*Polypedilum*) *vanderplanki* Hinton, 1951, inhabit temporary granite pools and can resist dehydration and drought for 17 years (Adams 1983; Hinton 1951, 1960) or more. Desiccated larvae tolerate high levels of gamma radiation and have an impressive capability to repair DNA (Gusev *et al*. 2010). Other species, including the recently described *P*. (*P*.) *ovahimba* Cranston, 2014 from Namibia, are also reported to tolerate desiccation and dehydration in temporary pools (Cranston 2014; Pinder 1995*b*: 128), but none yet as extreme as *P*. *vanderplanki*.

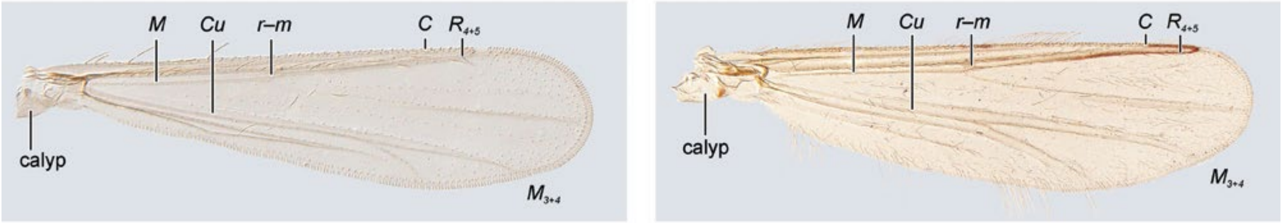
Most Chironomidae larvae are microphagous, ingesting detritus, small algae, or decaying plant or animal tissues. Some feed on tissues of living plants, others are carnivorous on oligochaetes, chironomid larvae, zooplankton, or more rarely, other freshwater invertebrates (Berg 1995: 136). Symbioses are also common, forming associations with other freshwater invertebrates, such as sponges, bryozoans, molluscs or insects, particularly Ephemeroptera (Jacobsen 1995: 317); larvae of the



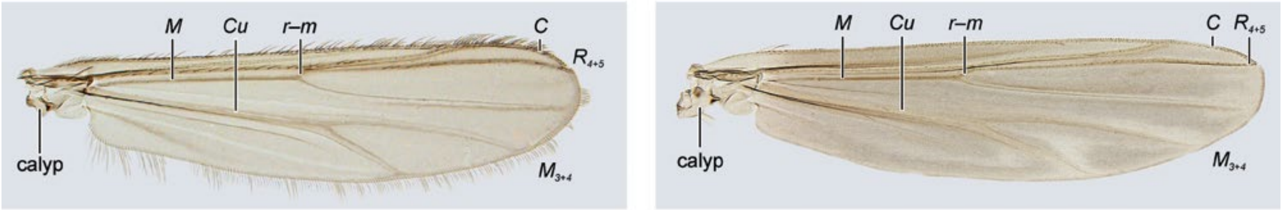
26 *Cladotanytarsus* (*Cladotanytarsus*) 27 *Dicrotendipes*



28 *Henrardia* 29 *Madachironomus*



30 *Neostempellina* 31 *Neozavrelia*



32 *Parachironomus* 33 *Polypedilum* (*Cerobregma*)

Figs 35.26–33. Wings of Chironomidae males: (26) *Cladotanytarsus* (*Cladotanytarsus*) sp.; (27) *Dicrotendipes* sp.; (28) *Henrardia quadrispinosa* Goetghebuer; (29) *Madachironomus lakazana* Andersen; (30) *Neostempellina* sp.; (31) *Neozavrelia* sp.; (32) *Parachironomus acutus* (Goetghebuer); (33) *Polypedilum* (*Cerobregma*) sp. Photographs T. Ekrem and E. Stur.

Abbreviations: *C* – costal vein; calyp – calypter; *Cu* – cubitus; *M* – media; M_{3+4} – fused third and fourth branch of media; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

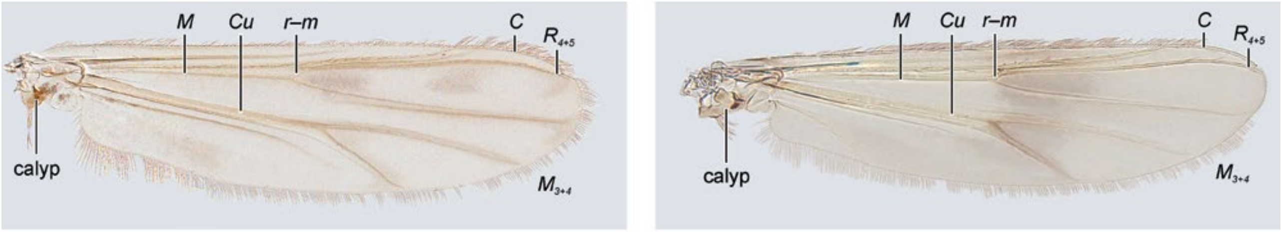
Neotropical genus *Ichthyocladius* Fittkau occur phoretically on catfish (Fittkau 1974; Mendes *et al*. 2004).

Chironomid pupae are typically comma-shaped or relatively straight, with a swollen cephalothorax and dorsoventrally flattened abdomen (Figs 117–119). They are similar to pupae in several other aquatic nematoceran families, and their wide morphological variation, including reduction and disappearance of some structures, makes it difficult to distinguish all Chironomidae pupae by any single trait or combination of characters. Most of them can be recognised, however, by the presence of an undivided swimming lobe without reinforced structural support. The pupa and cast pupal skins (exuviae) often possess characteristic features for recognition of species, genera and higher taxonomic ranks within Chironomidae. Such characters may occur almost anywhere on the pupal body, but where present, the paired thoracic respiratory organs, various armaments of abdominal tergites and the terminal swimming lobes are of particular importance. Pupae exhibiting reductions in morphological features are more difficult to separate. In free-living species, the pupae can hang beneath the water surface like those of mosquitoes (subfamilies Tanypodinae and Podonominae), or be mobile in the benthos (Aphroteniinae). The thoracic respiratory organs in these species (except Aphroteniinae) are typically tubular, with an apical respiratory surface (plastron plate). In the remaining subfamilies pupae generally occur in some kind of tube or shelter, provided by the fourth-instar larva. The thoracic organs in these species are of variable shape, but lack a plastron plate and function as gills.

The Chironomidae pupal stage is short, ranging from a few hours to a couple of days. In mature pupae the features of the enclosed (pharate) adult are usually clearly visible through the pupal skin. In aquatic species the pupa rises actively, or passively, to the water surface for adult emergence. The imago ecloses from the pupal skin in less than a minute and usually leaves more or less immediately after the wings have hardened, flying to solid ground to rest (Langton 1995: 169).

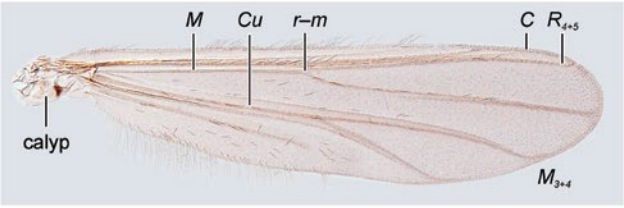
Adults of extant Chironomidae species (with very few exceptions) are non-biting (hence the family's vernacular name); if feeding at all during their comparatively short life spans, they consume nectar or honey dew. Adults of most species are flying midges, but brachypterous and apterous forms exist, particularly in more extreme habitats, such as at high elevations or latitudes. Water surface skimmers with poor flight are also known from most zoogeographical regions and some genera (such as the marine *Pontomyia* Edwards) include flightless forms only. Although flying midges typically form mating swarms after more-or-less synchronised emergence, non-flying species are adapted to ground mating and a suite of morphological traits often reflect this (*e.g*., loss of male antennal plume, ability to rotate the male terminalia, reduced wings, stouter legs, *etc*.). A chironomid swarm comprises predominantly males from a few to millions of individuals. Although single swarms can include more than one species, these aggregations usually comprise a single species only (Armitage 1995*a*: 194). Chironomid swarms typically build over or around some natural or artificial marker (a tree, bush, rock, boat, car, *etc*.). They can form at all times during the day, but are weather-dependent and considerably more common around sunrise and/or sunset.

Although the majority of chironomid species are bisexual, parthenogenesis is not uncommon. Both facultative and obligatory parthenogenesis is documented in various genera in the subfamilies Chironominae (tribe Tanytarsini) and Orthocladiinae. For example, the only known species of *Paratanytarsus* Thienemann & Bause from the Afrotropical Region is the parthenogenetic and virtually cosmopolitan *P. grimmii* (Schneider,



34 *Polypedilum* (*Polypedilum*)

35 *Stenochironomus*



36 *Tanytarsus*

Figs 35.34–36. Wings of Chironomidae males: (34) *Polypedilum* (*Polypedilum*) sp.; (35) *Stenochironomus* sp.; (36) *Tanytarsus pallidulus* Freeman. Photographs T. Ekrem and E. Stur.

Abbreviations: *C* – costal vein; calyp – calypter; *Cu* – cubitus; *M* – media; M_{3+4} – fused third and fourth branch of media; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

1885), a frequent inhabitant of water supply systems (Langton *et al*. 1988).

Economic significance

Chironomids do not transmit diseases to other living organisms, but can be a nuisance to humans if appearing in large numbers. This occurs in and around a variety of habitats and nearly 100 species of the subfamilies Chironominae, Orthocladiinae and Tanypodinae are reported to have nuisance potential (*e.g.*, Ali 1995: 339). The concentration of midges can be so large that they become a hazard to traffic and inhibit human outdoor activities, as adults can be inhaled or fly into the mouth, eyes or ears. Since many species are attracted to light, these mass occurrences are often particularly disturbing for people and economically damaging to tourism and other industries near water bodies where they occur. The nuisance and potential danger of chironomids are sometimes further intensified by allergic reactions to haemoglobins or haemoglobin-derived substances from all life stages (Cranston 1995*b*: 365). Many instances of allergic reactions to Chironomidae are known from most parts of the world; perhaps the best-investigated early case occurred in Sudan, where people living along the River Nile developed asthma, caused primarily by the species *Cladotanytarsus lewisi* (Freeman, 1950) (Cranston 1995*b*: 365; Lewis 1956).

Although chironomids themselves are not known to transmit diseases, their presence can be of relevance to disease outbreaks. Chironomid egg masses in freshwater have been shown to serve as reservoirs for strains of the bacterium *Vibrio cholerae* in India, Israel and Africa (Broza & Halpern 2001; Broza *et al*. 2010: 357; Halpern *et al*. 2004).

Chironomids are an important food source for a variety of wildlife. Fishes, amphibians, birds, bats and a range of invertebrates are known to take advantage of various life stages of Chironomidae as food (Armitage 1995*b*: 423). As such, chironomids are important (and sometimes crucial) elements of food chains and are important for both terrestrial and freshwater ecosystems. Laboratory and large-scale rearing of Chironomidae has been successfully implemented and used for production of fish food. The ability of many species to live in nutrient-rich and oxygen-poor aquatic environments gives chironomids a potential role as biological filters of wastewaters (Armitage 1995*b*: 423).

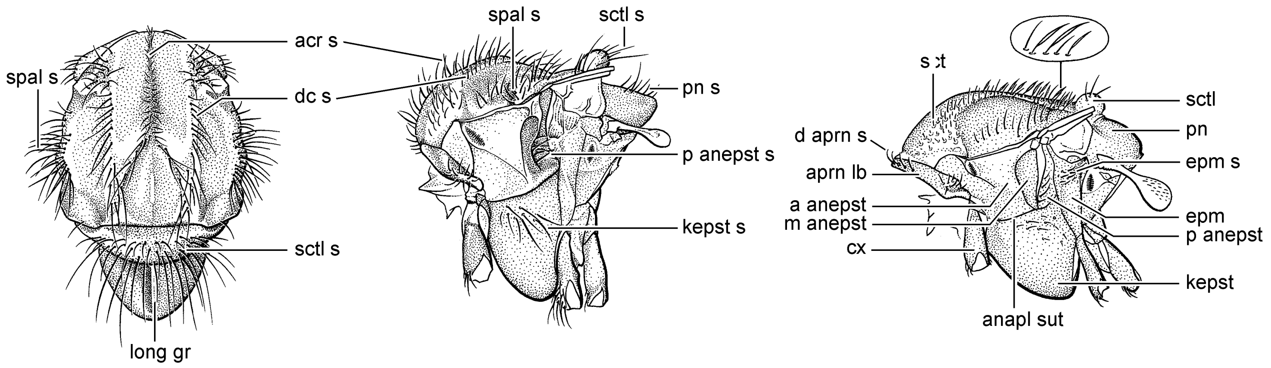
Adult midges can also play a role as pollinators, particularly in northern or high-elevation areas, where chironomids are abundant and frequently visit flowers to collect heat from the sun (Kevan 2007). Some pollination, or at least increased chances for fertilisation, is also expected in situations where adults are attracted to flowers to seek nectar and/or pollen (Armitage 1995*a*: 222). Cases in which pollination by chironomids is economically significant are unknown, however, and few documented records of flower-visiting Chironomidae exist for the Afrotropics.

Invasive freshwater weeds are a considerable challenge in many African freshwater ecosystems and of great economic significance. This is particularly true for Water-hyacinth, *Eichhornia crassipes* (Mart.) Solms. (Pontederiaceae), Water lettuce, *Pistia stratiotes* L. (Araceae) and Water fern, *Salvinia molesta* D.Mitch. (Salviniaceae) (Labrada & Fornasari 2002). Given that the larvae of some chironomid species mine in leaves, stems or roots of living aquatic plants, non-biting midges have been suggested as potential biological agents for the control of pest aquatic macrophytes, such as *Hydrilla verticillata* (L.f.) Royle (Bennett & Buckingham 2000: 307) or *Lagarosiphon major* Ridl. Moss ex Wager (both Hydrocharitaceae) (Earle *et al*. 2013). Copeland *et al*. (2012) were, however, unable to find any species of African Chironomidae suitable for biological control of *Hydrilla*.

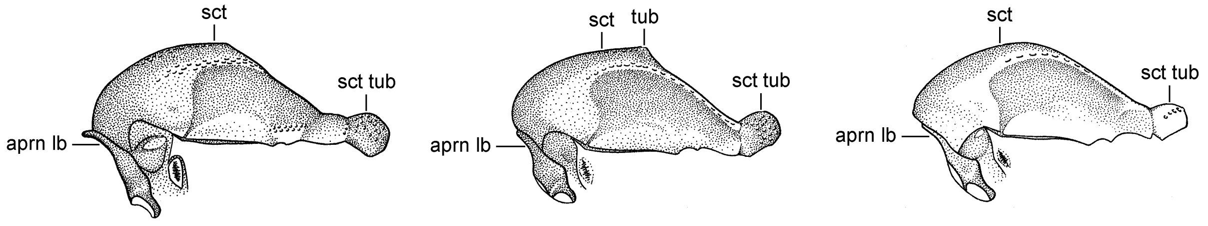
Classification

The placement of Chironomidae in Culicomorpha is undisputed in the literature, but relatively recent studies provide some conflicting evidence on phylogenetic placement within this infraorder. Based on morphological data, the Chironomidae has been placed as sister to Ceratopogonidae (Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1333), to Simuliidae (Sæther 2000*a*) or to the remaining Culicomorpha (Borkent 2012). Using partial 18S ribosomal RNA sequences, Pawlowski *et al*. (1996) also placed Chironomidae as sister to the remaining Culicomorpha, but Ptychopteridae and the non-Afrotropical Nymphomyiidae were not included in their dataset. A later study using both ribosomal and three protein coding nuclear markers indicated sister-group relationships between Ceratopogonidae and Chironomidae (Bertone *et al*. 2008). This relationship was confirmed through analyses of an extensive dataset containing 30 kb of data from 14 nuclear loci and full mitochondrial genomes (Wiegmann *et al*. 2011). Both studies present good support for Culicomorpha, but some differences concerning relationships within the infraorder. In Bertone *et al*. (2008) Simuliidae and Thaumaleidae constitute a monophyletic group sister to the remaining Culicomorpha, while in Wiegmann *et al*. (2011) these families, albeit with poor branch support, group with Ceratopogonidae and Chironomidae in the traditional superfamily Chironomoidea.

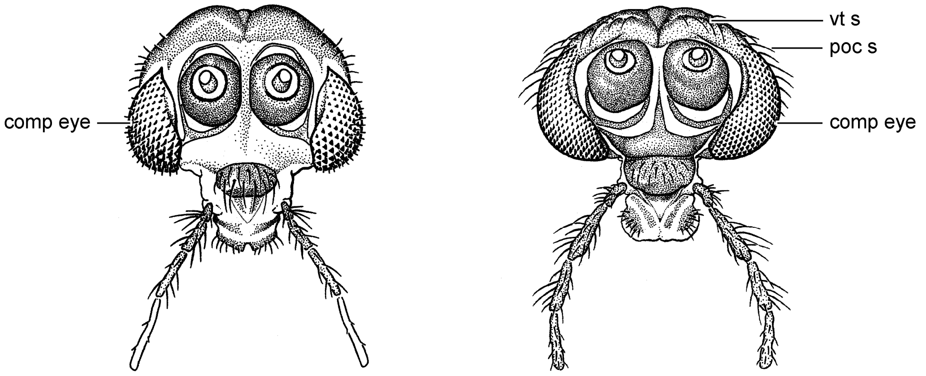
The monophyly of the family Chironomidae is supported by both morphology and molecular data (Cranston *et al*. 2012; Sæther 2000*b*). The oldest known chironomid fossil is *Aenne triassica* Krzemiński & Krzemińska, 1999, from late Triassic deposits in the United Kingdom (Krzemiński & Jarzembowski 1999). Analyses of molecular divergence rates indicate that the most recent ancestor of Chironomidae evolved in the Early to Mid Triassic, *ca* 250–210 MYA (Bertone *et al*. 2008; Cranston *et al*. 2012; Wiegmann *et al*. 2011). All eleven extant subfamilies were likely present in the Late Jurassic, 150 MYA; the respective monophyly, or near monophyly, of all these subfamilies has been confirmed by molecular data (Cranston *et al*. 2012). Several hypotheses on the subfamilial relationships within Chironomidae have been proposed over the past 50 years (Cranston *et al*. 2012; Sæther 2000*b*; and references therein). All hypotheses post-Brundin (1966) agree on the close relationship between Chironominae, Orthocladiinae, Diamesinae and Prodiamesinae (*i.e.*, semifamily Chironomoinae), but the placement of Buchonomyiinae and Telmatogetoninae has been especially unstable. A comprehensive molecular phylogeny of Chironomidae places Telmatogetoninae as sister to Chironomoinae and Buchonomyiinae as sister to the remaining Chironomidae (Cranston *et al*. 2012). The subfamilies



37 *Ablabesmyia* 38 *Psectrotanypus* 39 *Limnophyes*



40 *Chironomus* 41 *Stictochironomus* 42 *Polypedilum* (*Tripodura*)



43 *Nanocladius* 44 *Orthocladius* (*Pogonocladius*)

Figs 35.37–44. Thoraces and heads of Chironomidae males (all non-Afrotropical): (37) thorax of *Ablabesmyia* sp., dorsal view; (38) thorax of *Psectrotanypus dyari* (Coquillett), lateral view; (39) same, *Limnophyes brachytomus* (Kieffer); (40) dorsal part of thorax of *Chironomus* sp., lateral view; (41) same, *Stictochironomus* sp.; (42) same, *Polypedilum* (*Tripodura*) *simulans* Townes; (43) head of *Nanocladius* sp., frontal view; (44) same, *Orthocladius* (*Pogonocladius*) *consobrinus* (Holmgren). Figs 37–44 (Oliver 1981, figs 26, 28, 40, 46, 47, 48, 20, 21, respectively).

Abbreviations: a anepst – anterior anepisternum; acr s – acrostichal seta; anapl sut – anapleural suture; aprn lb – antepronotal lobe; comp eye – compound eye; cx – coxa; d aprn s – dorsal antepronotal seta; dc s – dorsocentral setae; epm – epimeron; epm s – epimeral setae; kepst – katepisternum; kepst s – katepisternal setae; long gr – longitudinal groove; m anepst – median anepisternum; p anepst – posterior anepisternum; p anepst s – posterior anepisternal setae; pn – postnotum; pn s – postnotal setae; pn s – postnotal setae; poc s – postocellar seta; sct – scutum; sct tub– scutal tubercle; sctl – scutellum; sctl s – scutellar setae; spal s – supra-alar seta; tub – tubercle; vt s – vertical setae.

Usambaromyiinae and Chilenomyiinae were not represented in the dataset however.

The subfamily Aphroteniinae was established by Brundin (1966: 326) based on three species-poor genera from the Southern Hemisphere. In a review of the Australian Aphroteniinae, Cranston & Edward (1992) added a second species to *Aphrotenia* Brundin, synonymised *Anaphrotenia* with *Aphroteniella* Brundin and expanded the information on geographical distribution and morphology, based on previously unknown life stages of several taxa. Two species, the South African *Aphrotenia tsitsikamae* Brundin, 1966 and *A. barnardi* Brundin, 1966, are known from the Afrotropical Region.

The subfamily Buchonomyiinae is monogeneric, with *Buchonomyia thienemanni* Fittkau, 1955, *B. burmanica* Brundin & Sæther, 1978 and *B. brundini* Andersen & Sæther, 1995 as the only extant species. The subfamily has not been recorded from the Afrotropical Region, but given its current distribution (Europe, North Africa, Iran, Myanmar, Central America) and age it may be present there.

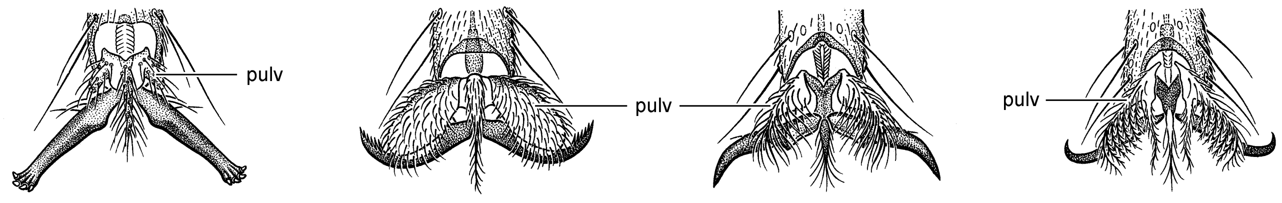
Chilenomyia paradoxa Brundin, 1983 is the only species in the subfamily Chilenomyiinae. It is known only from dense *Nothofagus* forests in South Chile (Brundin 1983). The immatures remain unknown, but may occur in small brooks in the area (Brundin 1983). The subfamily is not likely to be present in the Afrotropical Region.

Chironominae is the largest subfamily worldwide, with 2,802 species (Ashe & O'Connor, unpubl.). Fifty-seven genera are recorded from the Afrotropical Region. Larvae inhabit all kinds of aquatic habitats (including the open ocean and saline lakes) and each life stage exhibits distinctive features characteristic for the subfamily. Its monophyly is supported by molecular data (Cranston *et al*. 2012). The monotypic genera *Kribiomyia* Kieffer (type species: *K. longipalpis* Kieffer, 1921), *Kribiopelma* Kieffer (type species: *K. albida* Kieffer, 1921) and *Kribioxenus* Kieffer (type species: *K. pallidus* Kieffer, 1921) and their respective type species have been recorded from the Afrotropical Region and treated as valid taxa by some authors in the past. The genus *Kribiobius* Kieffer (type species: *K. ploenensis* Kieffer, 1922) is almost certainly a junior synonym of *Chironomus* Meigen in the current sense, but the later described African *K. modestus* Kieffer, 1923 appears to belong to an as yet unnamed, different genus. Thus *Kribiobius*, as defined by its type species, does not have any known representatives in the Afrotropical Region. Due to the fact that all corresponding original descriptions are inadequate for recognition and the respective name-bearing type specimens are presumed lost, these genus and species names are here regarded as *nomina dubia*.

Representatives of Diamesinae typically inhabit cool, montane areas. The subfamily is most species-rich in the Holarctic Realm, but there are taxa characteristic of the Southern Hemisphere, several of which were described by Brundin (1966). Two genera have been recorded from the Afrotropical Region: *Diamesa* Meigen from East African mountains and *Harrisonina* Freeman from South Africa and Zimbabwe (Willassen & Cranston 1986). Four other genera, *Boreoheptagyia* Brundin, *Potthastia* Kieffer, *Pseudodiamesa* Goetghebuer and *Sympotthastia* Pagast, have not been recorded from the Afrotropics but may occur (see identification key below).

The subfamily Orthocladiinae is highly species- and genera-rich, with immatures in all aquatic (including marine) and many semi-terrestrial and terrestrial habitats. At the time of writing, 2,432 species are known globally. Many genera are cosmopolitan, or virtually so, in their distribution; 47 genera are recorded from the Afrotropics. The Afrotropical fauna mainly consists of widely distributed genera, but there are some endemics (see "Synopsis of the fauna" below). Orthocladiinae is probably the least understood group of Afrotropical chironomids and new records, species and even genera can be expected.

Afrotropical Podonominae consist of two genera, *Afrochlus* Freeman and *Archaeochlus* Brundin, considered sister taxa to a group of 12 other genera globally (Cranston & Edward 1998; Cranston *et al*. 2002, 2010, 2012). Many genera have a Southern Hemisphere distribution and their phylogenetic relationships were applied by Brundin (1966) as evidence for trans-Antarctic relationships in Gondwanan midges. Subsequent dated molecular phylogenies confirm many of Brundin's details concerning the timing and locations of historical events in the Southern Hemisphere (Cranston *et al*. 2010). Immature stages and adults of the monotypic *Afrochlus* are found in



45 *Chaetocladius* (*Chaetocladius*)

46 *Psectrocladius* (*Psectrocladius*)

47 *Sergentia*

48 *Polypedilum* (*Polypedilum*)

Figs 35.45–48. Tarsomeres 5 and tarsal claws of Chironomidae males (all non-Afrotropical): (45) *Chaetocladius* (*Chaetocladius*) *piger* (Goetghebuer), ventral view; (46) *Psectrocladius* (*Psectrocladius*) *simulans* (Johannsen); (47) *Sergentia coracina* (Zetterstedt); (48) *Polypedilum* (*Polypedilum*) *nubeculosum* (Meigen). Figs 45–48 (Oliver 1981, figs 75 (as *Chaetocladius stamfordi*), 76, 73 (as *Phaenopsectra*), 74, respectively).

Abbreviation: pulv – pulvillus.

and around granitic outcrop seepages in Zimbabwe, whereas *Archaeochlus* species are associated with similar seepages, temporary streams and ephemeral riverbed pools in Lesotho, Eastern Cape, South Africa and Namibia (Cranston & Edward 1998; Cranston *et al*. 2002; P.S. Cranston, pers. comm. 2015).

The subfamily Prodiamesinae was erected by Sæther (1976), based on three genera previously placed in Diamesinae or Orthocladiinae (*Monodiamesa* Kieffer, *Odontomesa* Pagast and *Prodiamesa* Kieffer). It was later expanded to include *Compteromesa* Sæther (Sæther 1981) and almost certainly also includes *Propsilocerus* Kieffer (Cranston *et al*. 2012), although the last named genus has not yet been transferred formally, pending further investigation of unsampled "basal" Orthocladiinae. The known distribution of Prodiamesinae is largely Holarctic, but *Monodiamesa* is recorded from southern Chile (Andersen 1996) and the Oriental Region and *Odontomesa* occurs in the last named region (Ashe & O'Connor 2009: 73). None of the constituent genera have been recorded from the Afrotropical Region.

The subfamily Tanypodinae, as currently defined, goes back to Thienemann & Zavřel (1916), who based it mainly on characteristic features of the immature stages. The larval mouthparts differ markedly from those of other Chironomidae, in comprising a well-developed ligula and paired paraligulae, associated with a predatory life style (Figs 112, 113). Moreover, the larval antennae are retractile into the head capsule. There are 54 genera globally, 19 of which are recorded from the Afrotropical Region. The larvae of most species are free-swimming or crawling, but some burrow in bottom mud (Epler 2001). Tanypodinae are found in virtually all kinds of freshwater habitats, including rivers, streams and ditches, lakes, ponds, springs, phytotelmata and marshes. Larvae of one species, the North American *Ablabesmyia janta* (Roback, 1959), have been observed to live symbiotically on unionid mussels (Cranston & Epler 2013: 62; Roback 1976).

Telmatogetoninae is a small subfamily with predominantly marine species (Cranston 1995*d*: 44). The only known representatives in freshwater are two torrenticolous species of *Telmatogeton* Schiner species from the Hawaiian Islands (Newman 1988) and one *Thalassomya* Schiner (*T. reissi* Oliveira, 2000) from a river in Kenya (Oliveira 2000). Aside from these, larvae of Telmatogetoninae are associated with algae growing on rocks in coastal marine environments. Both described genera (*Telmatogeton* and *Thalassomya*) and a total of five species are recorded from the Afrotropical Region.

The subfamily Usambaromyiinae is monotypic, with the single species, *Usambaromyia nigrala* Andersen & Sæther, 1994, recorded from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen & Sæther 1994). The immature stages remain unknown. Based on adult morphology the subfamily is suggested as sister to the Tanypodinae (Sæther 2000*b*).

Identification

Unless one is very familiar with the local or regional chironomid fauna sampled in a particular study, morphological identification of any life stage of non-biting midges usually requires dissection of specimens and slide-mounting for determinations to specific or even generic level (see Chapter 2). In addition, maceration in dilute potassium hydroxide (KOH), lactic acid or enzymes may be necessary to examine diagnostic internal characters. Species-level identification can be challenging, however, even when high-quality optics with good magnification are employed. This applies especially for adult females and larvae, as these life stages possess fewer species-specific characters and are often not associable with the available descriptions of and scientific names given to adult males.

In light of these difficulties with identifications to species, Chironomidae are frequently omitted from biodiversity assessments. The use of short, standardised DNA sequence markers for specific identifications (so-called DNA barcoding; Hebert *et al*. 2003) has greatly increased the potential for including chironomids in studies of community ecology, bioinventories and conservation biology. The usefulness of DNA barcodes to associate life stages and discover new species has been documented in several studies (Anderson *et al*. 2013; Ekrem & Stur 2007; Ekrem *et al*. 2007, 2010; Silva *et al*. 2013). The steadily increasing library of DNA barcodes of Afrotropical species available in the *Barcode of Life Data System* (BOLD; Ratnasingham & Hebert 2007) now comprises more than 200 barcodes of *ca* 90 species (data from December 2015).

For decades the most widely used literature for the identification of Chironomidae at generic level have been the keys and diagnoses to Holarctic Chironomidae written by experts in the field and edited by Torgny Wiederholm (Wiederholm 1983, 1986, 1989), but also the keys in the *Manual of Nearctic Diptera* (Oliver 1981: 423), in *A Contribution to the Manual of Palaearctic Diptera* (Sæther *et al*. 2000: 113) and more recently, the *Manual of Central American Diptera* (Spies *et al*. 2009: 437) are classic contributions. A revised and updated version of the volume on Holarctic Chironomidae larvae was published recently (Andersen *et al*. 2013*a*). Identification literature to species is most often present in taxonomic revisions at the generic level (see "Synopsis of the fauna" below), but a number of noteworthy keys to immature stages from larger zoogeographical regions exists for pupal exuviae (Langton 1991; Langton & Visser 2003) and larvae (Epler 1995, 2001). Moreover, P.S. Cranston has produced an electronic Lucid key to genera of Chironomidae larvae (Cranston 2011) and a quite useful webpage with Australian emphasis that includes illustrated diagnostic descriptions of numerous genera (Cranston 2010). For the Afrotropical Region, no general identification key has been published since Freeman's monumental works on the Chironomidae of Africa south of the Sahara (Freeman 1955, 1956, 1957, 1958).

At the time of writing, the total number of scientifically named Chironomidae species recorded from the Afrotropical Region stands at 604. Many additional species and possibly dozens of new genera have been identified in museums and in private collections, but are still awaiting formal description and classification. For this reason the below identification key must be viewed as provisional and reader should be aware that not all specimens will key successfully, as these may belong to undescribed genera.

The identification key provided below is based on adult males only, but females can also be keyed to subfamilies, tribes and some to genera if terminalia and antennae are not required for their identification. Although only known from females, the genus *Lepidopodus* Freeman is included, since males are expected to have the same key characters.

In the key that follows, identification to genus requires dissection and slide-mounting. Genera that are currently not recognised as present in the Afrotropical Region, but might be found there, are indicated in square brackets. With the exception of *Endochironomus* Kieffer, these genera are not included in the "Synopsis of the fauna" section below. For identification keys to pupal exuviae and larvae of Afrotropical genera the respective Holarctic keys in Andersen *et al*. (2013) and Wiederholm (1986) are recommended, as these provide information on the majority of Afrotropical genera for which the immature stages are known.

Chironomid adults and immature stages are best preserved directly into ethanol in the field, for later slide-mounting as required (see Chapter 2). High-concentration ethanol (96%) should be used for immatures, while a slightly diluted solution (80–85%) is better for adults to avoid breakage of legs and antennae. This conservation strategy is "DNA-friendly" and will preserve the DNA of sampled specimens over many years if kept dark and cool.

Key to genera of Afrotropical Chironomidae

1. Wing with crossvein between medial vein (*M*) and cubital vein (*Cu*) or between veins *M* and M_{3+4} (*e.g.*, Figs 3, 4, 6–12) 2

– Wing without crossvein between veins *M* and *Cu* and between veins *M* and M_{3+4} (*e.g.*, Figs 2, 5, 13–36) 6

2. Wing without vein R_{2+3} (*e.g.*, Fig. 3); costal vein (*C*) reaching wing apex, if shorter then male terminalia with gonocoxal appendage 2 digitiform (*e.g.*, Fig. 51). 3

– Wing usually with vein R_{2+3} (*e.g.*, Figs 4–6), if absent, then male terminalia with gonocoxal appendage 2 not digitiform or absent (*e.g.*, Fig. 60); costal vein (*C*) not reaching wing apex. 5

3. Wing with *bm–m* and *m–cu* crossveins positioned close to middle of wing, or in distal ½ (*e.g.*, Fig. 3); wing base with first axillary sclerite without setae (PODONOMINAE). 4

– Wing with crossveins positioned in basal part of wing, clearly proximal to *r–m* crossvein; wing base with first axillary sclerite with setae (BUCHONOMYIINAE) . . . . [*Buchonomyia* Fittkau]

4. Palpus normally developed, 5-segmented; setation of body and legs long and slender . . . . *Archaeochlus* Brundin

– Palpus reduced, 4-segmented; setation of body and legs short and stout. . . . . *Afrochlus* Freeman

5. Terminal antennal flagellomere in male shorter than penultimate flagellomere; wing vein R_{2+3} usually forked, if simple or absent, then membrane clothed in setae (TANYPODINAE). 16

– Terminal antennal flagellomere in male longer than penultimate flagellomere; wing vein R_{2+3} simple, unforked; membrane at most with a few setae in distal ½ (*e.g.*, Fig. 4) (DIAMESINAE [in part]). 12

6. Legs with tibial spurs and combs absent on all legs; small midges (wing length: *ca* 1 mm) with male terminalia (Fig. 49) small compared to rest of abdomen (APHROTENIINAE). . . . . . *Aphrotenia* Brundin

– Legs with at least 1 tibial spur and/or tibial comb present on mid and hind legs; size variable, but male terminalia not small compared to rest of abdomen (*e.g.*, Figs 63–108) 7

7. Thorax with anterior anepisternum with cluster of sensilla chaetica; wing membrane (Fig. 5) black, with more pale apex and base (USAMBAROMYIINAE) . . . . *Usambaromyia* Andersen & Sæther

– Thorax with anterior anepisternum without cluster of sensilla chaetica; wing membrane not as above (*e.g.*, Figs 13, 14, 25) 8

8. Wing vein R_{2+3} absent; veins R_1 and R_{4+5} widely separated (*e.g.*, Fig. 13); fore coxa enlarged; all tarsomeres 4 cordiform (TELMATOGETONINAE) 9

– Wing vein R_{2+3} usually present, if absent then veins R_1 and R_{4+5} narrowly separated by no more than width of a vein (*e.g.*, Figs 14–23); fore coxa only occasionally enlarged in species with reduced antenna; tarsomere 4 cordiform only in *Cardiocladius* Kieffer and *Harrisonina* Freeman 10

9. Tarsomere 5 simple; thorax with numerous acrostichal setae; palpus 5-segmented. . . *Thalassomya* Schiner

– Tarsomere 5 trilobed; thorax without acrostichal setae; palpus reduced, with no more than 3 segments . . . . *Telmatogeton* Schiner

10. Fore tarsomere 1 shorter than tibia; hind tibial combs, when present, consisting of free spiniform setae; male terminalia (Figs 63–90) with gonostylus flexibly attached to gonocoxite and usually folded inwards 11

– Fore tarsomere 1 usually longer than tibia, if slightly shorter, hind tibial combs consisting of basally fused spines; male terminalia (*e.g.*, Figs 91–108) with gonostylus usually rigidly attached to gonocoxite and posteriorly directed (except *Stictochironomus* Kieffer with movable gonostylus) (CHIRONOMINAE) 92

11. Mid leg longest, hind leg shortest; tarsomere 1 of hind leg thickened, bearing paired thick spines on oblique apex, not longer than tarsomere 2 (DIAMESINAE [in part]: HARRISONINI) . . . . *Harrisonina* Freeman

– Mid leg shortest; tarsomere 1 of hind leg normally developed, without thick, paired spines (ORTHOCLADIINAE). 41

12. Thorax with dorsocentral setae divided in 2 groups, anteriorly and posteriorly on mesonotum; "frontal tubercles" large conical (see Oliver 1989, fig. 7.2) (BOREOHEPTAGYINI) . . . . [*Boreoheptagyia* Brundin]

– Thorax with dorsocentral setae in row on mesonotum (e.g., Figs 37–39); head with "frontal tubercles", if present small and indistinct (DIAMESINI) 13

13. Tarsomere 4 cordiform. 14

– Tarsomere 4 cylindrical 15

14. Wing vein R_{4+5} without setae; head without inner vertical setae; male terminalia with 2 aedeagal lobes (see Oliver 1989, fig. 7.8) . . . . [*Potthastia* Kieffer]

– Wing vein R_{4+5} with setae (Fig. 4); head with inner vertical setae; male terminalia (Fig. 52) with 1 aedeagal lobe . . . . *Diamesa* Meigen

15. Wing vein R_{2+3} ending midway between veins R_1 and R_{4+5}; head with inner vertical setae; eye with obvious dorsomedian elongation (see Oliver 1989, fig. 7.10) . . . .[*Pseudodiamesa* Goetghebuer]

– Wing vein R_{2+3} ending ¼ way between veins R_1 and R_{4+5}; head without inner vertical setae; eye with slight dorsomedian elongation (see Oliver 1989, fig. 7.12) . . . . [*Sympotthastia* Pagast]

16. Tarsomeres 4 cordiform (bilobed) and shorter than tarsomere 5; comb on hind tibia double (see Murray & Fittkau 1989, fig. 5.9F); wing with vein R_2 not connected to vein R_3 (e.g., Fig. 7). 17

– Tarsomeres 4 cylindrical, not or only slightly shorter than tarsomere 5; comb on hind tibia formed of single row of setae or entirely absent; wing with either vein R_2 connected to vein R_3 (e.g., Fig. 12), or both these veins entirely absent (e.g., Fig. 9) 18

17. Thorax without scutal tubercle; postnotal setae present (as in Fig. 38) . . . . *Clinotanypus* Kieffer

– Thorax with scutal tubercle (as in Fig. 41); postnotal setae absent. . . . . *Coelotanypus* Kieffer

18. Wing crossvein between veins *M* and *Cu* positioned some distance before *Cu*-fork (e.g., Fig. 12) . . . 19

– Wing crossvein between veins *M* and *Cu* terminating in vein M_{3+4} (positioned beyond *Cu*-fork) (e.g., Fig. 6) 21

19. Wing with distance between *Cu*-fork and crossvein less than ⅓ as long as vein *CuA* (Fig. 12); scutal tubercle oval or dome-shaped . . . . *Tanypus* Meigen

– Wing with distance between *Cu*-fork and crossvein at least ½ as long as vein *CuA* (e.g., Fig. 8); scutal tubercle absent 20

20. Eye strongly iridescent; thorax, legs and abdomen vividly pigmented; male terminalia (Fig. 56) with gonostylus sharply hooked with apical and subapical lobes . . . . *Djalmabatista* Fittkau

– Eye not iridescent; body pigmentation not as above; male terminalia (Fig. 61) with gonostylus less sharply hooked, with or without posterior "heel" and inner lobe . . . . *Procladius* Skuse

21. Wing with costal vein (*C*) produced beyond vein R_{4+5} by a distance at least as long as *r–m* crossvein; thorax with postnotal setae (as in Fig. 38). 22

– Wing with costal vein (*C*) not, or at most produced beyond vein R_{4+5} by distance less than the length of *r–m* crossvein (e.g., Figs 6, 9); thorax without postnotal setae 26

22. Thorax with scutal tubercle 23

– Thorax without scutal tubercle 24

23. Fore leg with distinct tibial comb (see Murray & Fittkau 1989, fig. 5.23F); claw of mid leg simple, apically pointed . . . . *Macropelopia* Thienemann

– Fore leg without tibial comb; claw on mid leg apically cusp-shaped or spatulate . . . .*Fittkauimyia* Karunakaran

24. Pulvilli absent; fore leg with distinct tibial comb (Murray & Fittkau 1989, fig. 5.23F). . . . . [*Natarsia* Fittkau]

– Pulvilli present; fore leg without tibial comb. 25

25. Male terminalia with epandrium without posterior row of setae; gonostylus long, reaching *ca* ⅔ gonocoxite length . . . . . *Psectrotanypus* Kieffer

– Male terminalia with epandrium with posterior row of setae; gonostylus shorter, not reaching ⅔ gonocoxite length . . . . . *Apsectrotanypus* Fittkau

26. Legs with numerous flattened scale-like setae (visible over 200 × magnification); tarsomere 1 white, with central dark brown ring; tarsomere 2 dark brown in basal ½, white in apical ½; tarsomeres 3 and 4 dark brown; tarsomere 5 pale brown . . . . . *Lepidopelopia* Harrison

– Legs without scale-like setae; tarsi without above pattern or unpatterned 27

27. Thorax with acrostichal setae divergent around the prescutellar field (Fig. 37); male terminalia (Fig. 54) with gonostylus elongate and narrow, with characteristic cochleariform apex (indicated with arrow) . . . . . *Ablabesmyia* Johannsen

– Thorax with acrostichal setae not divergent around the prescutellar field; male terminalia with gonostylus not as above 28

28. Male terminalia with dorsomedial lobe 29

– Male terminalia without dorsomedial lobe (*e.g.*, Figs 58, 59) 33

29. Male terminalia with epandrium without posterior row of setae, with dorsomedial lobe simple, reduced to a short rounded lobe . . . . . *Chrysopelopia* Harrison

– Male terminalia with epandrium with posterior row of setae, without dorsomedial lobe, if present, then more elongate and strongly developed or complex often bilobed (see Murray & Fittkau 1989, fig. 5.17F) or with lateral appendage or filaments 30

30. Thorax with scutal tubercle 31

– Thorax without scutal tubercle 32

31. Male terminalia with dorsomedial lobe broad, bilobed and pubescent; mid leg with tarsomere 3 without apical brush . . . . . [*Thienemannimyia* (*Hayesomyia* Murray & Fittkau)]

– Male terminalia with dorsomedial lobe elongate, *ca* ½ as long as gonocoxite, with complete or partial row of filaments; mid leg with tarsomere 3 with apical brush of 5–7 strong setae . . . . . *Conchapelopia* Fittkau

32. Mid tarsomere 3 with apical brush of several strong setae; male terminalia with paramere simple . . . . . [*Rheopelopia* Fittkau]

– Mid tarsomere 3 without apical brush of setae; male terminalia with paramere broad, anteriorly forked . . . . . *Thienemannimyia* Fittkau *sensu stricto*

33. Male terminalia (Fig. 58) with gonostylus equally broad for most of its length, not gradually tapering to apex . . . . . *Monopelopia* (*Cantopelopia* Roback)

– Male terminalia with gonostylus broad basally, gradually tapering to apex (*e.g.*, Fig. 59) 34

34. Eye pubescent (microtrichia between ommatidial lenses shorter than height of lenses); apical antennal flagellomere with wavy setae . . . . . *Nilotanypus* Kieffer

– Eye bare (without microtrichia); apical antennal flagellomere with straight setae 35

35. Wing with costal vein (*C*) ending beyond, at or slightly before apex of vein *M* 36

– Wing with costal vein (*C*) ending distinctly before apex of vein *M* 38

36. Hind leg without tibial comb; male terminalia with epandrium without posterior row of setae . . . . . *Trissopelopia* Kieffer

– Hind leg with tibial comb; male terminalia with epandrium with posterior row of setae 37

37. Legs with main tooth of spur on fore leg and on outer (smaller) spur on mid and hind legs short, only slightly longer than remaining side teeth, these spurs thus having a semi-lyrate shape (see Murray & Fittkau 1989, fig.5.43D); inner spurs on mid and hind legs with long main tooth; wing membrane with distinct fascia; adults not pale, with darker pigmentation . . . . . [*Zavrelimyia* (*Zavrelimyia* Fittkau)]

– Legs with all tibial spurs elongate, never semi-lyrate in shape, with main tooth considerably longer than side teeth (see Murray & Fittkau 1989, fig. 5.20E); wing membrane unmarked; adults very pale, virtually white . . . . . [*Krenopelopia* Fittkau]

38. Thorax with scutal tubercle; fore, mid and hind legs all with similar lyrate tibial spurs, with outermost teeth usually not significantly longer or stronger than the others . . . . . *Larsia* Fittkau

– Thorax without scutal tubercle; tibial spurs not all similar or lyrate, sometimes semi-lyrate, invariably at least 1 spur with a significantly longer and stronger tooth 39

39. Wing with costal vein (*C*) ending midway between apices of veins *M* and M_{3+4}; mid tibia with 2 spurs; male terminalia with epandrium posteriorly without row of setae. . . . .*Zavrelimyia* (*Paramerina* Fittkau)

– Wing with costal vein (*C*) ending above or slightly beyond apex of vein M_{3+4}; mid tibia with 1 spur; male terminalia with epandrium posteriorly with either continuous row of setae, or an interrupted row with a few lateral setae on each side 40

40. Hind tibia with 1 spur; male terminalia (Fig. 59) with epandrium posteriorly with a few lateral setae on each side or bare; terminal antennal flagellomere clearly demarcated from penultimate flagellomere . . . . *Monopelopia* Fittkau *sensu stricto*

– Hind tibia without spurs; male terminalia with epandrium posteriorly with continuous transverse row of setae; terminal antennal flagellomere almost fused to penultimate flagellomere. . . . .[*Labrundinia* Fittkau]

41. Wing veins R_1 and R_{4+5} short and thick, fused with costal vein (*C*) in thick "clavus" ending before midlength of wing (*e.g.*, Fig. 17) 42

– Wing veins R_1, R_{2+3} (if present) and vein R_{4+5} narrow, elongate separated from costal vein (*C*) until their respective meeting with vein *C* beyond midlength of wing (*e.g.*, Figs 16, 18, 21) 45

42. Male terminalia (Fig. 69) with genital segment internally with gonocoxal apodeme dilated, inverted V- or U-shaped, with no trace of oral projections . . . . *Corynoneura* Winnertz

– Male terminalia with genital segment internally with gonocoxal apodeme narrow, straight, or convex, anterolateral corners slightly to strongly projecting orally 43

43. Male terminalia without gonocoxal appendages or distal lobe . . . .*Notocladius* Harrison

– Male terminalia with gonocoxal appendages 1 and 2, or large distal lobe 44

44. Male terminalia with gonocoxite with large distal lobe; without appendages 1 and 2 . . . . *Corynoneurella* Brundin

– Male terminalia (Fig. 89) with gonocoxite without large distal lobe; with well-developed, rounded to triangular appendage 1; appendage 2 often elongated, adpressed to inner margin of gonocoxite . . . .*Thienemanniella* Kieffer

45. Eye (*e.g.*, Fig. 43) microtrichiose, *i.e.*, microtrichia extending beyond ommatidia 46

– Eye (*e.g.*, Fig. 44) bare or pubescent, *i.e.*, microtrichia if present not extending beyond ommatidia. . . 54

46. Thorax with dorsocentral setae erect, frequently arising from pale areas on scutum 47

– Thorax with dorsocentral setae decumbent, not arising from pale areas on scutum. . . . . *Cricotopus* Wulp [in part]

47. Antennal flagellomere 1 much longer than flagellomere 2; palpus 2-segmented; male terminalia (Fig. 67) with epandrium extending posteriorly to cover gonocoxites; tarsomere 3 *ca* 2 × length of tarsomere 2 . . . . *Clunio* Haliday

– Antennal flagellomere 1 subequal to flagellomere 2; palpus 4- or 5-segmented; male terminalia (*e.g.*, Figs 71, 78, 88) with epandrium shorter, not covering gonocoxites; tarsomere 3 subequal or shorter than tarsomere 2 48

48. Male terminalia without anal point 49

– Male terminalia with anal point 50

49. Wing vein R_{4+5} ending opposite or proximal to end of vein M_{3+4}; thorax without acrostichal setae; eye without dorsomedial extension . . . .*Eukiefferiella* Thienemann [in part]

– Wing vein R_{4+5} ending distal to end of vein M_{3+4} (Fig. 19); thorax with acrostichal setae; eye with slight dorsomedial extension . . . .*Cricotopus* (*Paratrichocladius* Santos Abreu)

50. Antenna with 1 strong subapical seta . . . . *Smittia* Holmgren [in part]

– Antenna without strong subapical seta 51

51. Male terminalia (*e.g.*, Fig. 78) with anal point broad, sparsely to densely clothed in short to moderately long setae 52

– Male terminalia (*e.g.*, Fig. 87) with anal point narrow, not clothed in setae 53

52. Male terminalia with anal point densely clothed in setae; calypter bare; antennal flagellomere number and plume reduced . . . . *Thalassosmittia* Strenzke & Remmert

– Male terminalia (Fig. 78) with anal point sparsely clothed in longer setae; calypter with a few setae; antenna with 13 flagellomeres, fully plumed . . . . *Mesocricotopus* Brundin

53. Thorax medially with 2 acrostichal setae at most; head with remains of reduced ocelli (“frontal tubercles”); area behind eye deeply excavated; male terminalia as illustrated in Fig. 80. . . . . *Nanocladius* Kieffer

– Thorax with acrostichal setae more numerous, usually beginning near anterior margin of scutum; head without frontal tubercles; area behind eye not excavated; male terminalia as illustrated in Fig. 87 . . . . *Rheocricotopus* Brundin

54. Wing membrane with setae at least subapically (e.g., Fig. 21) 55

– Wing membrane bare (e.g., Fig. 14) 64

55. Male terminalia with gonostylus bifurcate, lobes of subequal length, gonostylar tooth (“megaseta”) absent . . . . *Elpiscladius* Harrison & Cranston

– Male terminalia (e.g., Figs 82, 90) with gonostylus simple, “megaseta” present 56

56. Male terminalia with gonostylar tooth (“megaseta”) broad, comb-like. . . . . . . *Compterosmittia* Sæther

– Male terminalia with “megaseta” simple. 57

57. Thorax with dorsal antepronotal setae; eye with long, rectangular dorsomedial extension . . . . *Tokyobrillia* Kobayashi & Sasa

– Thorax without dorsal antepronotal setae; eye with at most short, wedge-shaped dorsomedial extension (long and parallel-sided only in *Parametriocnemus*) 58

58. Wing vein R_{4+5} invariably and costal vein (*C*) usually ending proximal to apex of vein M_{3+4}. 59

– Wing vein R_{4+5} usually and costal vein (*C*) invariably ending opposite or distal to apex of vein M_{3+4} (e.g., Fig. 21) 60

59. Eye with comparatively long, wedge-shaped dorsomedial extension; thorax with acrostichal setae (e.g., Figs 37, 38) long, beginning near antepronotum; dorsocentral setae uniserial or irregularly biserial; male terminalia as illustrated in Fig. 83 . . . . *Paraphaenocladius* Thienemann

– Eye rounded, without dorsomedial extension; thorax without acrostichal setae; dorsocentral setae irregularly multiserial anteriorly; male terminalia as illustrated in Fig. 79 . . . . . . *Molleriella* Sæther & Ekrem

60. Thorax with acrostichal setae weak, hooked or scalpellate, inserted at some distance from antepronotum 61

– Thorax with acrostichal setae (e.g., Figs 37, 38) strong, suberect, beginning near antepronotum 62

61. Male terminalia (Fig. 63) with anal point long, with lateral setae; thorax with acrostichal setae scalpellate . . . . *Antillocladius* Sæther

– Male terminalia with anal point absent or small, developed only as setulose, microtrichiose protuberance on epandrium; thorax with acrostichal setae hooked . . . . *Gymnometriocnemus* Edwards

62. Wing vein *CuA* more or less straight . . . . *Metriocnemus* Wulp

– Wing vein *CuA* curved or sinuous (e.g., Fig. 21) 63

63. Eye with dorsomedial extension long, parallel-sided; male terminalia (Fig. 82) with anal point long, without apical setae or occasionally with small setae . . . . *Parametriocnemus* Goetghebuer

– Eye with dorsomedial extension wedge-shaped; male terminalia with anal point short, triangular, with strong apical setae . . . . *Pseudorthocladius* Goetghebuer [in part]

64. Scutum (Fig. 39) with epimeron, posterior anepisternum and usually katepisternum and dorsal antepronotum with setae; often some humeral setae and/or prescutellar setae lanceolate . . . *Limnophyes* Eaton

– Scutum with epimeron, posterior anepisternum and dorsal antepronotum invariably and katepisternum usually bare; without lanceolate humeral and prescutellar setae 65

65. Male terminalia with anal point strongly sclerotised, very long and narrow with apical indentations, without setae or microtrichia . . . . *Freemaniella* Sæther

– Male terminalia with anal point not as above, if long, then never with apical indentations 66

66. Wing membrane strongly punctuated, microtrichia distinct at 60 × magnification 67

– Wing membrane moderately to finely punctuated, microtrichia not distinct at 60 × magnification (e.g., Fig. 14) 69

67. Legs with prominent lateral spines on spurs of mid and hind tibiae, projecting outwards . . . .*Chaetocladius* Kieffer

– Legs with lateral spines on spurs of mid and hind tibiae more or less adpressed to shaft of spur 68

68. Male terminalia (Fig. 64) with anal point hyaline, semicircular to subtriangular; thorax with acrostichal setae strong, decumbent, inserted close to antepronotum . . . . *Bryophaenocladius* Thienemann

– Male terminalia (Fig. 84) with anal point not hyaline, with setae and microtrichia; thorax with acrostichal setae moderately strong, inserted close to antepronotum . . . . *Paratrissocladius* Zavřel

69. Tarsomere 4 more or less cordiform, shorter than tarsomere 5 . . . . *Cardiocladius* Kieffer

– Tarsomere 4 cylindrical, generally longer than tarsomere 5 70

70. Male terminalia (Fig. 72) with anal point long and strong, with unique strong lamellate setae laterally and apicodorsally. . . . . *Doithrix* Sæther & Sublette

– Male terminalia with anal point variably developed, but never with strong, lamellate setae 71

71. Calypter with at least 1 seta (*e.g.*, Fig. 22). 72

– Calypter bare (*e.g.*, Fig. 16) 82

72. Pulvilli pad-like or pectinate, at least ½ length of claw (*e.g.*, Fig. 46). 73

– Pulvilli absent, vestigial or small, never as long as ½ length of claw 76

73. Wing vein *CuA* more or less strongly curved (*e.g.*, Fig. 20); antenna with subapical, strong seta 74

– Wing vein *CuA* straight (*e.g.*, Fig. 22); antenna without subapical strong seta 75

74. Male terminalia (Figs 73, 74) with gonostylus with outer corner; legs usually with pseudospurs on tarsomere 1 and often 2 of mid and hind legs . . . . *Georthocladius* Strenzke

– Male terminalia with gonostylus without outer corner; legs without pseudospurs . . . . *Pseudorthocladius* Goetghebuer [in part]

75. Wing with vein R_{2+3}; anal lobe normal (Fig. 22) . . . .*Psectrocladius* Kieffer

– Wing without vein R_{2+3} (indiscernible); anal lobe slightly reduced. . . . .*Paradoxocladius* Harrison

76. Male terminalia with epandrium with strongly elevated longitudinal ridge with lateral setae, without true anal point . . . . *Mesosmittia* Brundin

– Male terminalia with epandrium without strongly elevated ridge 77

77. Male terminalia without anal point. . . . .*Eukiefferiella* Thienemann [in part]

– Male terminalia with anal point 78

78. Thorax without acrostichal setae or if rarely present, then extremely fine, short and indistinct 79

– Thorax with acrostichal setae always distinct even if short 81

79. Male terminalia with gonocoxal appendage 1 distinct, collar-like or hook-shaped . . . . *Orthocladius* Wulp [in part]

– Male terminalia with gonocoxal appendage 1 poorly defined, gently rounded or absent 80

80. Male terminalia with anal point evenly tapering to pointed apex . . . . *Tvetenia* Kieffer

– Male terminalia with anal point parallel-sided, narrow with rounded apex. . . . . *Parorthocladius* Thienemann

81. Thorax with acrostichal setae beginning some distance from anterior margin of scutum, short, often hooked or scalpellate. . . . .*Synorthocladius* Thienemann

– Thorax with acrostichal setae beginning close to anterior margin of scutum, weak to strong, never hooked or scalpellate. . . . .*Orthocladius* Wulp [in part]

82. Antenna with 1 strong, straight subapical seta 83

– Antenna without strong subapical seta 84

83. Male terminalia with epandrium divided into 2 setigerous lobes by longitudinal fissure, without anal point . . . .*Semiocladius* Sublette & Wirth

– Male terminalia (Fig. 88) with epandrium not divided into 2 setigerous lobes by longitudinal fissure, with anal point . . . . *Smittia* Holmgren [in part]

84. Thorax without acrostichal setae 85

– Thorax with acrostichal setae 87

85. Thorax with tuft of microtrichia on mid scutum . . . . *Parakiefferiella* Thienemann

– Thorax without such tuft on mid scutum 86

86. Male terminalia with anal point narrowly triangular, pointed without microtrichia and setae; gonostylus with large basal or apically angled crista dorsalis, lateral basal lobe or deep subapical invagination . . . . *Lobosmittia* Sæther & Andersen

– Male terminalia with anal point absent or weakly-developed, wide-based clothed in microtrichia, with a few lateral setae; gonostylus without crista dorsalis, lateral lobe or deep subapical invagination . . . . *Krenosmittia* Thienemann & Krüger

87. Thorax with acrostichal setae setula-like, beginning at antepronotum and reaching mid scutum . . . . *Ionthosmittia* Sæther & Andersen

– Thorax with 2–16 short, non-scalpellate acrostichal setae on mid scutum, not beginning at antepronotum 88

88. Palpus strongly reduced, 4- or 5-segmented; antennae with 12–13 flagellomeres; wing cuneiform with short to very long costal extension; thorax with median lobes of antepronotum strongly reduced . . . 89

– Palpus not reduced, 5-segmented; antennae with 13 flagellomeres; wing cueniform to anal lobe well-developed with short to very long costal extension; thorax with median lobes of antepronotum reduced to well-developed 90

89. Palpus 4-segmented; eye not protruding; wing (Fig. 16) with costal vein (*C*) slightly extended beyond vein R_{4+5}, with long false vein; male terminalia (Fig. 68) without anal point . . . . *Colosmittia* Andersen & Sæther

– Palpus 5-segmented; eye protruding; wing with costal vein (*C*) strongly extended beyond vein R_{4+5}; male terminalia with anal point (Fig. 76) . . . . *Lerheimia* Andersen & Sæther

90. Thorax with 4–16 acrostichal setae; male terminalia with at least apex of anal point free of microtrichia . . . . *Allocladius* Kieffer

– Thorax with 2 acrostichal setae; male terminalia with anal point usually entirely clothed in microtrichia 91

91. Male terminalia with virga (spiniform process at end of phallus) consisting of median spine or plate, with additional lateral groups of spinules on each side; thorax with antepronotal lobes well-developed medially. . . . . *Hydrosmittia* Ferrington & Sæther

– Male terminalia (Fig. 86) with virga without lateral groups of spinules or if present, then needle-like; thorax with median antepronotal lobes reduced . . . . *Pseudosmittia* Edwards

92. Wing (*e.g.*, Figs 24, 30, 31, 36) crossvein *r–m* in a more or less straight line and continuous with vein R_{4+5}, or oblique if wing reduced; calypter without setae; wing cells usually with setae at least near apex of wing (TANYTARSINI) 93

– Wing (*e.g.*, Figs 25, 27–29, 32–35) crossvein *r–m* oblique to vein R_{4+5}; if wing cells with setae, then calypter with fringe of setae (CHIRONOMINI and PSEUDOCHIRONOMINI) 110

93. Marine water skaters; fore and hind legs very long; male antennae long, filiform without plume; wing reduced . . . . [*Pontomyia* Edwards]

– Not marine water skaters; fore and hind legs normally developed; male antenna normally developed not filiform with plume; wing normally developed 94

94. Male terminalia with gonostylus reduced to short, narrow peg, with long apical seta; eye with long microtrichia between ommatidia and dorsomedian extension . . . . *Afrozavrelia* Harrison

– Male terminalia (*e.g.*, Figs 99, 100) with gonostylus normally developed; if eye with long microtrichia present between ommatidia then without dorsomedian extension 95

95. Eye with long microtrichia between ommatidia 96

– Eye without long microtrichia between ommatidia 97

96. Mid and hind tibiae with 2 apical combs each, each comb including a small spur; male terminalia with anal tergite band of epandrium partly or entirely encircling median setae; gonocoxite without appendage 1a . . . . [*Zavrelia* Kieffer, Thienemann & Bause]

– Mid and hind tibiae with 2 apical combs each, combs without spurs; male terminalia (Fig. 99) with anal tergite band of epandrium T-shaped; gonocoxite with appendage 1a . . . . *Neostempellina* Reiss

97. Mid and hind tibiae with respective combs fused or narrowly separated. 98

– Mid and hind tibiae with respective combs clearly separated 100

98. Each mid and hind tibiae with 2 spurs projecting from the apical combs; male terminalia with anal point with crests as wide as long . . . . *Paratanytarsus* Thienemann & Bause

– Mid and hind tibiae with apical combs usually without spurs, occasionally with single spur on each tibia; male terminalia with anal point with crests longer than wide 99

99. Male terminalia with anal tergite bands of epandrium long, curved posteriorly towards anal point; transverse gonocoxal apodeme with oral protrusions . . . . [*Micropsectra* Kieffer]

– Male terminalia with anal tergite bands of epandrium short, not curved posteriorly towards anal point; transverse gonocoxal apodeme without oral protrusions. . . . . *Nidnurbia* Säwedal

100. Minute species, wing length < 0.7 mm; male terminalia (Fig. 106) without anal tergite bands; anal point triforked. . . . . *Seppia* Ekrem & Sæther

– Larger species, wing length > 0.7 mm; male terminalia with anal tergal bands; epandrium with anal point never triforked 101

101. Male terminalia with anal point with tuft of strong lamellae, lacking longitudinal crests; gonostylus short and stout; gonocoxite with appendage 2a reduced to minute tubercle . . . *Friederia* Sæther & Andersen

– Male terminalia with anal point without tuft of strong lamellae, if with lamellar structures, then longitudinal crests invariably present; gonostylus normally developed; gonocoxite with appendage 2a well-developed or entirely absent 102

102. Scutum usually with central tubercle (not clearly discernible in type material of Afrotropical *S. reissi* Lehmann, 1981); male terminalia with anal tergite bands transverse, encircling median setae . . . . *Stempellina* Thienemann & Bause

– Scutum without central tubercle; male terminalia with anal tergite bands of various shapes, but never encircling median setae 103

103. Male terminalia with anal tergite bands transverse, meeting medially, but limited to anterior margin of epandrium . . . . *Stempellinella* Brundin

– Male terminalia (*e.g.*, Figs 100, 108) with anal tergite bands separate and curving towards anal point, or clearly T-, V- or Y-shaped 104

104. Male terminalia with anal point well-developed with characteristic groove that is wide at anal point base and extends as a thinner slit towards anal point apex; gonocoxal appendage 2a usually with some lamellae fused to a plate; gonostylus sometimes abruptly constricted in distal third . . . . *Rheotanytarsus* Thienemann & Bause

– Male terminalia with anal point weakly-developed without characteristic groove, if anal point with groove or crests, then never as described above; gonocoxal appendage 2a invariably with separated lamellae; gonostylus not abruptly constricted in distal third.... 105

105. Male terminalia (Fig. 92) with gonocoxal appendage 2a with branched lamellae; eye without dorsomedian extension . . . . *Cladotanytarsus* Kieffer

– Male terminalia with gonocoxal appendage 2a with simple lamellae of various shapes, never branched; eye usually with dorsomedian extension 106

106. Male terminalia with anal point with posteriorly arising pair of anteriorly directed rods or bars (lamellae), the latter fused in some species . . . . *Virgatanytarsus* Pinder

– Male terminalia with anal point without structures as above, although dorsally or posteriorly directed spines or lamellae may be present 107

107. Male terminalia (*e.g.*, Fig. 100) with epandrium without anal crests on or near anal point 108

– Male terminalia (*e.g.*, Fig. 108) with epandrium with anal crests on or near anal point 109

108. Male terminalia (Fig. 100) with gonocoxal appendage 1 of virtually same size as gonostylus, appendage 1a absent; wing as illustrated in Fig. 31 . . . . *Neozavrelia* Goetghebuer & Thienemann

– Male terminalia (Fig. 108) with gonocoxal appendage 1 clearly smaller than gonostylus, appendage 1a absent or present; wing as illustrated in Fig. 36 . . . . *Tanytarsus* Wulp [in part]

109. Male terminalia with anal point with crests, without spines or spinules . . . .[*Sublettea* Roback]

– Male terminalia (Fig. 108) with anal point usually without crests, if crests present then spines or spinules present in between . . . . *Tanytarsus* Wulp [in part]

110. Fore tibial apex with obvious, basally combed or feathered spur similar to those present on mid and hind tibiae (PSEUDOCHIRONOMINI) 111

– Fore tibial apex without a spur similar to those present on mid and hind tibiae, although a short or long spine on a tibial scale may be present (CHIRONOMINI) 112

111. Male terminalia (Fig. 95) with anal point on epandrium . . . . *Madachironomus* Andersen

– Male terminalia (Fig. 96) without anal point on epandrium . . . . *Manoa* Fittkau

112. Legs clothed in scales as well as setae (male unknown). . . . . *Lepidopodus* Freeman

– Legs clothed in setae only 113

113. Antennal flagellum 11-segmented; fore tibial apex with 2 rounded scales, inner scale barely projecting beyond outer one 114

– Antennal flagellum 13-segmented; fore tibial apex with a noticeably projecting, well-developed scale and/or spine 140

114. Mid and hind tibial combs fused, lacking spurs; male terminalia with gonocoxal appendage 1 bent, swollen subapically, with apical inner lobe bearing pair of setae (see Freeman 1957, fig. 11k) . . . . *Nilomyia* Kieffer

– If mid and hind tibial combs fused, then combs including projecting spurs; male terminalia with gonocoxal appendage 1 not as described above 115

115. Palpus reduced with segments round or oval, each at most 2.5 × longer than broad, segments 4–5 often fused; male terminalia with anal tergite without setae; gonocoxal appendage 1 broad and straight, with dense microtrichia, but without setae, gonocoxal appendage 2 elongate and bowed . . . . *Zuluchironomus* Harrison

– Without the above combination of characters 116

116. Thorax with antepronotal lobes separated medially (see Cranston *et al*. 1989*a*, fig. 10.24A–C). . . . 117

– Thorax with antepronotal lobes fused (although often notched) medially (*e.g*., Figs 40, 41). 120

117. Thorax with median gap between antepronotal lobes more or less broadly V-shaped; abdominal tergites 2 or 3–6 anteromedially with a bare oval or racquet-shaped impression (may be indistinct); male terminalia with gonocoxal appendage 1 composed of setulose base and bare, relatively slender distal part; anal point narrow basally, slightly widened distally . . . . *Glyptotendipes* Kieffer

– Thorax with median gap between antepronotal lobes narrower; abdominal tergites without racquet-shaped impressions; male terminalia with gonocoxal appendage 1 broad, with numerous short setae; anal point broad 118

118. Male terminalia with gonocoxal appendage 1 more or less elongate, with dense apical tufts of long, fine setae (see Epler *et al*. 1998, figs 1, 2); appendage 2 with narrowed, upturned apex bearing several setae . . . . *Acinoretracus* Epler, Harrison & Hare

– Male terminalia with gonocoxal appendage 1 rounded, clothed in long, dense setae, or short and wide with few setae; appendage 2 without narrowed upturned apex 119

119. Male terminalia with gonocoxal appendage 1 rounded, clothed in long, dense setae; epandrium with median setae absent; gonostylus usually with numerous short subapical inner setae . . . [*Axarus* Roback]

– Male terminalia with gonocoxal appendage 1 short, wide with a few setae, clothed in normal short microtrichia; epandrium with median setae long; gonostylus with only a few subapical inner setae . . . . *Xenochironomus* Kieffer

120. Male terminalia (*e.g*., Fig. 97) with gonocoxal appendage 2 never with dense setae, although often with microtrichia, usually small, sometimes absent. 121

– Male terminalia (*e.g*., Figs 91, 94) with gonocoxal appendage 2 at least partially setulose, invariably well-developed, elongate, cylindrical to racquet-shaped 136

121. Male terminalia with gonocoxal appendage 2 elongate, long and subcylindrical, reaching at least as far as posterior as anal point, covered with microtrichia, but without true setae. . . . . . . *Kloosia* Kruseman

– Male terminalia (*e.g*., Fig. 97) with gonocoxal appendage 2 not as above, never reaching as far to posterior as anal point of epandrium 122

122. Male terminalia with all gonocoxal appendages strongly reduced or vestigial 123

– Male terminalia (*e.g*., Fig. 97) with gonocoxite showing at least one distinct gonocoxal appendage 124

123. Male terminalia with gonostylus elongate, curved and usually with distinctly narrower proximal section that begins near junction with gonocoxite . . . . *Cladopelma* Kieffer

– Male terminalia with gonostylus relatively short, straight or slightly curved, without distinctly narrower section. . . . . *Harnischia* Kieffer

124. Male terminalia (Fig. 93) with gonocoxal appendage 2 entirely concealed beneath appendage 1 in dorsal view, without microtrichia, but with a few setae (2–8); head usually with "frontal tubercles" . . . . *Cryptochironomus* Kieffer

– Male terminalia (*e.g.*, Fig. 97) with gonocoxal appendage 2, if present, never entirely concealed beneath appendage 1 and rarely with setae; head usually without "frontal tubercles" 125

125. Male terminalia without gonocoxal appendage 2 126

– Male terminalia with gonocoxal appendage 2 128

126. Male terminalia with gonostylus virtually straight, without basal-median expansion, its dorsal aspect usually with distinct longitudinal contour ("keel"); head with "frontal tubercles". . . . .*Demicryptochironomus* Lenz

– Male terminalia (*e.g.*, Fig. 97) with gonostylus distinctly curved or kinked, usually with basal-median expansion, its dorsal aspect without distinct longitudinal contour; head often without "frontal tubercles" 127

127. Male terminalia (Fig. 97) with gonostylus with apical tooth; setulose protrusions present on each side of anal point . . . . *Microchironomus* Kieffer

– Male terminalia with gonostylus without apical tooth; no setulose protrusions on each side of anal point . . . . *Cryptotendipes* Beck & Beck

128. Scutum with strong central tubercle (*e.g.*, Fig. 41) 129

– Scutum without central tubercle (or weakly developed in some *Parachironomus* Lenz) 131

129. Male terminalia with epandrium with pair of digitiform, setulose posterolateral projections (see Cranston *et al*. 1989*a*, fig. 10.23) . . . . *Gillotia* Kieffer

– Male terminalia with epandrium without posterolateral digitiform projections 130

130. Ratio of length of last antennal flagellomere to remaining flagellomeres (*i.e.*, antennal ratio): 1.2–1.3; wing length: 1.2–1.7 mm; male terminalia with gonocoxal appendage 2 with long microtrichia, but lacking setae . . . . [*Rheomus* Laville & Reiss]

– Antennal ratio: 1.5–4.0; wing length: 1.8–2.4 mm; male terminalia with gonocoxal appendage 2 usually with several setae, rarely 0–1 . . . . *Cyphomella* Sæther

131. Male terminalia (*e.g.*, Fig. 101) with gonocoxal appendage 1 digitiform, without microtrichia, bearing 2–3 setae 132

– Male terminalia with gonocoxal appendage 1 pediform to rectangular, microtrichiose, with > 3 setae (except in *Saetheria* Jackson) 133

132. Male terminalia with gonostylus clavate, widest in middle; gonocoxal appendage 1 with setae not arising from distinct pits. . . . . *Robackia* Sæther

– Male terminalia (Fig. 101) with gonostylus not clavate, widest elsewhere than in middle; gonocoxal appendage 1 with setae arising from distinct pits . . . . *Parachironomus* Lenz

133. Male terminalia with gonocoxal appendage 2 indicated only as weak inner expansion of medial gonocoxite contour . . . . [*Chernovskiia* Sæther]

– Male terminalia with gonocoxal appendage 2 forming distinct lobe 134

134. Thorax without acrostichal setae; male terminalia with gonocoxal appendage 1 broadly rectangular . . . .*Beckidia* Sæther

– Thorax with acrostichal setae; male terminalia with gonocoxal appendage 1 more or less pediform 135

135. Male terminalia with anal tergite bands of epandrium distinctly Y-shape. . . . .[*Saetheria* Jackson]

– Male terminalia with anal tergite bands of epandrium entirely fused or at most, shallowly Y- or T-shaped . . . . *Paracladopelma* Harnisch

136. Male terminalia usually with gonocoxal appendage 2 very broad, somewhat racquet-shaped; if appendage 2 narrow, then not strongly bowed dorsoventrally and appendage 1 thin with apical median extension . . . . *Kiefferulus* Goetghebuer

– Male terminalia (*e.g.*, Fig. 94) with gonocoxal appendage 2 narrow, usually subcylindrical; if appendage 1 thin with apical median extension, then appendage 2 strongly bowed dorsoventrally 137

137. Male terminalia (Fig. 94) with gonocoxal appendage 2 strongly bowed dorsoventrally, often narrow basomedially and clubbed, or variably divided subapically; sternite 6 often with ventral accessory setae . . . .*Dicrotendipes* Kieffer

– Male terminalia with gonocoxal appendage 2 subcylindrical; sternite 6 without ventral accessory setae 138

138. Palpus with 2–5 segments and mid and hind tarsomeres strongly reduced; male terminalia with anal point apically truncated . . . . *Chironomus* (*Baeotendipes* Kieffer)

– Palpal segments normally developed; tarsomeres rarely reduced; male terminalia with anal point variably shaped, but never truncate 139

139. Male terminalia with digitiform part of gonocoxal appendage 1 arising dorsomedially from large basal microtrichiose lobe, continuing more or less medially, so that basal portion extends posterior to digitiform part . . . . [*Einfeldia* Kieffer]

– Male terminalia with digitiform part of gonocoxal appendage 1 arising apically, or medially, from variably sized basal microtrichiose lobe, continuing posteriorly so that digitiform part extends posterior to base (Fig. 91) . . . . *Chironomus sensu stricto,* *Chironomus* (*Benthalia* Lipina) and [*C.* (*Lobochironomus* Ryser, Wülker & Scholl)]

140. Male terminalia with anal tergite with 1 or more dorsomedial lobes or projections bearing setae . . . . *Nilothauma* Kieffer

– Male terminalia with anal tergite without dorsomedial setulose lobes or projections 141

141. Apical mid tibial combs with 4–6 spurs (4–5 on outer comb; 0–1 on inner comb) (see Amakye & Sæther 1993, fig. 1E) . . . .*Henrardia* Goetghebuer

– Apical mid tibial combs with 2 spurs at most (0–1 on outer comb; 0–1 on inner comb) 142

142. Antennae not plumose, each flagellomere with whorl of *ca* 4 short setae (see Freeman 1958, fig. 9c) . . . . *Kribiothauma* Kieffer

– Antennae plumose, each flagellomere with whorl of numerous long setae (as in Fig. 1) 143

143. Scutum strongly projecting, with apical notch; palpus strongly reduced (see Amakye & Sæther 1992, fig. 3A, B) . . . .*Collartomyia* Goetghebuer

– Scutum usually not projecting, but if strongly projecting, then apical notch lacking; palpus normally developed 144

144. Apex of fore tibia with low scale at most, lacking spine-like extension 145

– Apex of fore tibia with well-developed scale and/or spine-like extension .146

145. Calypter fringed with setae; fore femur apicomedially with patch of posteriorly directed setae; male terminalia (Fig. 98) with gonostylus normally developed. . . . . *Microtendipes* Kieffer

– Calypter bare; fore femur without patch of posteriorly directed setae; male terminalia with gonostylus extremely short . . . . *Paralauterborniella* Lenz

146. Male terminalia with gonocoxal appendage 2 fused to inner side of gonocoxite, except at apex. . . . . [*Fissimentum* Cranston & Nolte]

– Male terminalia (*e.g.*, Fig. 103) with gonocoxal appendage 2 basally fused to gonocoxite only 147

147. Male terminalia with anal point short, apically bulbous; gonocoxal appendage 1 with long, narrow, thorn-like apex (see Freeman 1958, fig. 7b) . . . . *Kribiocosmus* Kieffer

– Male terminalia with anal point not short and apically bulbous; gonocoxal appendage 1 without thorn-like apex 148

148. Male terminalia with gonocoxal appendage 2a. 149

– Male terminalia without gonocoxal appendage 2a 151

149. Scutum with obvious median tubercle . . . .*Conochironomus* Freeman

– Scutum without obvious median tubercle 150

150. Legs with 2 combs on mid and hind tibia with spur . . . .*Paratendipes* Kieffer

– Legs with only 1 of 2 combs on mid and hind tibia with spur . . . .*Skusella* Freeman

151. Calypter bare or at most with 5 setae 152

– Calypter (*e.g.*, Fig. 35) with at least 5, usually many more setae 157

152. Thorax with pronotum reduced, not visible from above; wing membrane unmarked; fore femora and tibia slightly swollen and club-like apically; pulvilli weak, scarcely distinguishable; male terminalia with tergite 8 anteriorly tapered. . . . . *Kribiodosis* Kieffer

– Without the above combination of characters 153

153. Wing membrane with dark pattern; legs dark ringed; fore femur apically swollen. 154

– Wing membrane unmarked; legs unicolourous; fore femur apically cylindrical. 155

154. Abdominal tergites 2–7 with long longitudinal ridge, bearing brush of dark setae; wing membrane with numerous dark maculae; thorax with small scutal tubercle . . . . *Zavreliella* Kieffer

– Abdominal tergites without longitudinal ridge, bearing brush of dark setae; wing membrane with 2 dark fascia (see Freeman 1958, plate 2o); thorax without scutal tubercle . . . . *Kribiodorum* Kieffer

155. Male terminalia with anal tergite bands long, reaching anal point; gonocoxal appendage 1 basomedially with group of setae . . . . *Pagastiella* Brundin [in part]

– Male terminalia with anal tergite bands short, not extending beyond mid tergite, never reaching anal point; gonocoxal appendage 1 without basomedial group of setae. 156

156. Mid and hind tibia with spur on inner apical comb only; with pulvilli, simple *ca* ½ claw length . . . . [*Lauterborniella* Thienemann & Bause]

– Mid and hind tibia with spur on both inner and outer combs; without pulvilli. . .*Lunditendipes* Harrison

157. Wing membrane with macrotrichia, anal point of terminalia never trifid. 158

– Wing membrane without macrotrichia, or if macrotrichia present, then anal point of terminalia trifid 160

158. Male terminalia with long and evenly distributed setae on inner subapical margin of gonostylus; tergite 8 anteriorly tapered . . . . *Polypedilum* (*Pentapedilum* Kieffer)

– Male terminalia with short and clumped setae on inner subapical margin of gonostylus; tergite 8 not tapered anteriorly 159

159. Fore tarsus usually without conspicuously long setae (“beard”); wing length < 4.0 mm . . . . *Phaenopsectra* Kieffer

– Fore tarsus with conspicuously long setae (“beard”); wing length > 4.0 mm. . . . . . . [*Sergentia* Kieffer]

160. Abdominal tergite 8 strongly tapered anteriorly . . . . *Polypedilum* Kieffer [in part]

– Abdominal tergite 8 not or at most weakly tapered 161

161. Scutum extending well beyond anterior apex of reduced antepronotal lobes 162

– Scutum (*e.g.*, Fig. 41) extending to apex of divided antepronotal lobes. 163

162. Male terminalia with anal tergite bands strongly developed; gonocoxal appendage 1 with pad-like microtrichiose and setulose base with digitiform extension. . . . . *Xestotendipes* Harrison

– Male terminalia (Fig. 107) with anal tergite bands weakly developed; gonocoxal appendage 1 not as above, without digitiform extension . . . . *Stenochironomus* Kieffer

163. Calypter fringe reduced to maximum of 6 setae; eye with dorsomedial extension extending no further medially than mid pedicel; fore tibia with apical spur abruptly delimited, narrow, pointed and off-set . . . . *Pagastiella* Brundin [in part]

– Calypter fringe well-developed, with at least 10 setae; eye with strong dorsomedial extension, extending to inner margin of pedicel; fore tibia with or without apical spur, when present not off-set 164

164. Mid and hind tibia almost invariably with 2 spurs apically (1 on each comb); fore tarsus (except in *Nilodosis grisea* Freeman, 1957) with conspicuously long setae (“beard”) 165

– Mid tibia never with more than 1 spur apically, hind tibia apically with 0–2 spurs; fore tarsus with or without conspicuously long setae (“beard”) 166

165. Legs with large pulvilli, nearly extending to claw apex; fore tibial scale with short, slender spine. . . . . [*Endochironomus* Kieffer]

– Legs without pulvilli; fore tibial scale with long, strong curved spine . . . . *Nilodosis* Kieffer

166. Thorax with scutal tubercle (Fig. 41); male terminalia with distinct articulation between gonocoxite and gonostylus; tibiae often banded . . . . *Stictochironomus* Kieffer

– Thorax without scutal tubercle; male terminalia without articulation between gonocoxite and gonostylus; tibiae never banded 167

167. Male terminalia with gonocoxal appendage 1 with basal, setiferous part, subcylindrical, not set-off from more apical part; fore tarsomere 1 white, mid and hind tarsomere 1 white with brown bands . . . . *Synendotendipes* Grodhaus

– Male terminalia with gonocoxal appendage 1 with basal, broad, setiferous part, more or less clearly delimited from apical part; all tarsi dark . . . . [*Tribelos* Townes]

Synopsis of the fauna

***Ablabesmyia* Johannsen** (Tanypodinae)**.** A genus of 93 described species that occurs in all zoogeographical regions, except Antarctica – it is currently the most speciose genus in the Tanypodinae. The genus is divided into four subgenera, two of which occur in the Afrotropical Region, *Ablabesmyia sensu stricto* with nine and *A.* (*Karelia* Roback) with four species. Adult males of the two subgenera can be separated by the shape of the subterminal seta of the gonostylus, which is pointed in *A.* (*Karelia*) and apically expanded in *Ablabesmyia sensu stricto*. McLachlan (1969) described and figured the larvae and pupae of two species, *A.* (*A.*) *appendiculata* (Kieffer, 1923) and *A.* (*K.*) *nilotica* (Kieffer, 1923), from Lake Kariba in Zimbabwe. Harrison (1991) described the larva and pupal exuviae of *A.* (*A.*) *dusoleili* Goetghebuer, 1935 and the presumptive larva (with some pupal features visible) of *A.* (*A.*) *rimae* Harrison, 1991, from lakes in Ethiopia. *Ablabesmyia* larvae (*e.g.*, Figs 109, 112), occur in a wide variety of habitats, including small and large standing and flowing waters from cold temperate to warm tropical climatic zones (Cranston & Epler 2013: 62). See Fig. 6 for an example of the wing of the genus, Fig. 37 for the thorax and Fig. 54 for the male terminalia. An identification key to all Afrotropical species is unavailable.

***Acinoretracus* Epler, Harrison & Hare** (Chironominae: Chironomini)**.** An endemic genus erected on four known species previously placed in *Dicrotendipes* Kieffer (Epler *et al*. 1998). Larval, pupal and adult stages were described (Epler *et al*. 1998). The genus has been recorded from numerous countries throughout tropical Africa. Subfossil specimens of *Acinoretracus* sp. near *multispinosus* (Freeman, 1957) have been reported from lakes in equatorial East Africa (Eggermont & Verschuren 2004). An identification key to species was provided by Epler *et al*. (1998).

***Afrochlus* Freeman** (Podonominae)**.** An endemic monotypic genus, with the single species, *A. harrisoni* Freeman, 1964, recorded from wet granitic outcrops in Zimbabwe. A systematic revision including phylogenetic placement and description of immature stages was published by Cranston & Edward (1998).

***Afrozavrelia* Harrison** (Chironominae: Tanytarsini)**.** An endemic, monotypic genus, with the single species, *A. kribiensis* (Kieffer, 1923), recorded from Cameroon, South Africa and Zimbabwe. Kieffer (1923) originally placed *A. kribiensis* in *Zavrelia* Kieffer, but as well-documented by Harrison (2004*a*), *Afrozavrelia* is easily distinguished from *Zavrelia* in all life stages. Immature stages of *Afrozavrelia* are inhabitants of clear streams and montane rivers, at least in South Africa (Ekrem & Stur, pers. obs.; Harrison 2004*a*). See Fig. 24 for an illustration of the wing of *A. kribiensis*.

***Allocladius* Kieffer** (Orthocladiinae)**.** A genus of 25 described species that occurs in all zoogeographical regions, except Antarctica and Oceania (Ashe & O'Connor 2012: 115). Nine species are known from the Afrotropical Region, most of these from mountainous areas in East Africa (Ferrington & Sæther 2011). One species, *A. lusciniolus* Sæther & Andersen, 2011, from Tristan da Cunha, Nightingale and Gough islands, is parthenogenetic (Sæther & Andersen 2011). *Allocladius* larvae appear to be truly aquatic, as they have been found in ponds, rivers and streams, but some of them are probably also able to survive in moist sandy substrata (Andersen *et al.* 2013*b*: 202). Immature stages of the Afrotropical species remain undescribed, but larvae and pupae of extralimital species were characterised by Ferrington & Sæther (2011). An identification key to species was provided by Ferrington & Sæther (2011).

***Antillocladius* Sæther** (Orthocladiinae). A genus of 28 described species that occurs in the Neotropical, Nearctic, Palaearctic and Oriental Regions (Ashe & O'Connor 2012: 121). The genus is here recorded from the Afrotropical Region for the first time based on an undescribed species from the West Usambara Mountains (Eastern Arc Mountains), in Tanzania (Fig. 63). This record must be regarded as tentative, however, as adults have eyes with long microtrichia between the ommatidia. Most *Antillocladius* larvae appear to be terrestrial or semi-terrestrial; they have been collected in moss and lichens on stones and tree trunks and also in seeps near streams and impoundments (Andersen *et al.* 2013*b*: 203). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 203) and Coffman *et al.* (1986: 160), respectively. An identification key to the males of *Antillocladius* was provided by Mendes *et al.* (2011).

***Aphrotenia* Brundin** (Aphroteniinae)**.** A genus of three described species that occurs in the Afrotropical and Australasian Regions. The genus was erected by Brundin (1966: 338), based on two species, *A. tsitsikamae* Brundin, 1966 and *A. barbardi* Brundin, 1966, collected in the south-western Cape of South Africa. Larval and pupal stages were described for both species (Brundin 1966), although the larva of *A. tsitsikamae* was not associated with certainty. The species appear to prefer mountainous brooks and streams in afforested areas. Later records of the genus include *A. australiensis* Cranston & Edward, 1992 and unassociated larvae from south and south-east Australia (Cranston & Edward 1992). See Fig. 2 for an example of the wing of the genus. An identification key to Afrotropical species was provided by Brundin (1966: 338).

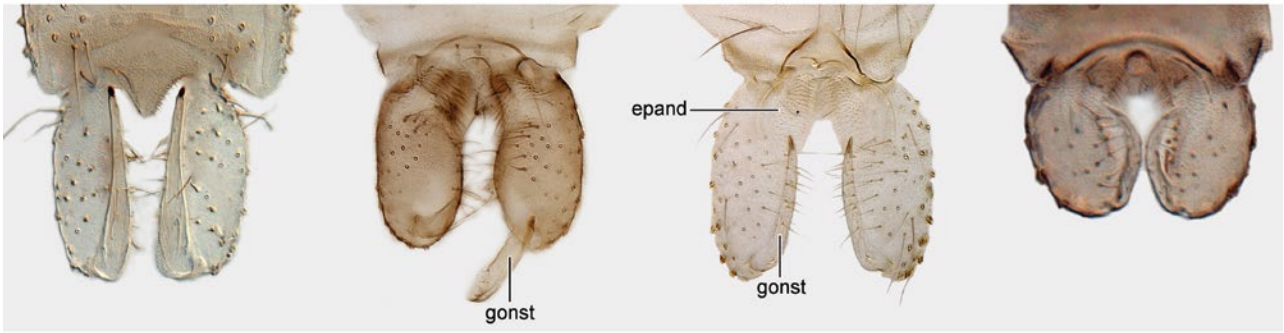
***Apsectrotanypus* Fittkau** (Tanypodinae)**.** A genus of seven named species that occurs in all zoogeographical regions, except Antarctica and Oceania. One species, *A. unicolor* (Freeman, 1954), is recorded from the Afrotropical Region, where it was collected at a waterfall on the Berg River, South Africa

(Ashe & O'Connor 2009: 128). Larvae of *Apsectrotanypus* occur in small, cool, flowing waters (Cranston & Epler 2013: 46). Immature stages of the Afrotropical species are undescribed.

***Archaeochlus* Brundin** (Podonominae)**.** An endemic genus of three described species, all occurring in southern Africa (Lesotho and Namibia). The genus was revised, including descriptions of all known life stages, by Cranston *et al*. (1987). Larvae of *A. drakensbergensis* Brundin, 1966 and *A. bicirratus* Brundin, 1966, are known to inhabit temporary streams that flow over rock faces, whereas larvae of *A. biko* Cranston, Edward & Colless, 1987, have been reared from ephemeral pools in the Kuiseb River, Namibia (Cranston 2010). See Fig. 3 for an example of the wing of the genus and Fig. 51 for the male terminalia. An identification key to species was provided by Cranston *et al*. (1987).

49 *Aphrotenia* ♂ 50 *Telmatogeton* ♂ 51 *Archeochlus* ♂ 52 *Diamesa* ♂

53 *Usambaromyia* ♂ 54 *Ablabesmyia* (*Karelia*) ♂ 55 *Coelotanypus* ♂ 56 *Djalmabatista* ♂



57 *Lepidopelopia* ♂ 58 *Monopelopia* (*Cantopelopia*) ♂ 59 *Monopelopia* (*Monopelopia*) ♂ 60 *Nilotanypus* ♂

Figs 35.49–60. Male terminalia of Chironomidae (dorsal views): (49) *Aphrotenia tsitsikamae* Brundin; (50) *Telmatogeton goughi* Sæther & Andersen; (51) *Archaeochlus biko* Cranston, Edward & Colless; (52) *Diamesa freemani* Willassen & Cranston; (53) *Usambaromyia nigrala* Andersen & Sæther; (54) *Ablabesmyia* (*Karelia*) *nilotica* (Kieffer) (cochleariform apex of gonostylus arrowed); (55) *Coelotanypus* sp.; (56) *Djalmabatista reidi* (Freeman); (57) *Lepidopelopia annulator* (Goetghebuer); (58) *Monopelopia* (*Cantopelopia*) sp.; (59) *M*. (*Monopelopia*) sp.; (60) *Nilotanypus comatus* (Freeman). Photographs T. Ekrem and E. Stur.

Abbreviations: aed lb – aedeagal lobe; epand – epandrium; goncx app 2 – gonocoxal appendage 2; gonst – gonostylus.

***Beckidia* Sæther** (Chironominae: Chironomini)**.** Sæther (1977) erected the genus *Beckiella* based on three species, two occurring in the Holarctic Realm and *B. hirsti* (Freeman, 1957) recorded from Chad, Democratic Republic of Congo, Namibia, Nigeria and Sudan (de Moor *et al.* 2000; Freeman 1957: 400; Hare & Carter 1987; Harrison 2004*b*). Sæther (1979) replaced the original genus name *Beckiella* with *Beckidia*, due to junior homonymy of the former with the oribatid genus *Beckiella* Grandjean. Three additional species have been described since, two from the Russian Far East (Zorina 2006) and one from India in the Oriental Region (Bhattacharya *et al*. 1985). However, the original description of the Indian species, *Beckidia nigrotibia* Bhattacharya, Dutta & Chaudhuri, 1985 (*op. cit.*), does not match Sæther's (1977) diagnosis and should probably be placed in a different genus. Immature stages of Afrotropical species remain unknown. Identification keys to species were provided by Sæther (1977) and Zorina (2006), the latter including Holarctic species only.

***Bryophaenocladius* Thienemann** (Orthocladiinae). A species-rich genus of 117 described species that occurs in all zoogeographical regions, except Antarctica and Oceania (Ashe & O'Connor 2012: 138). Fifteen species are known from the Afrotropical Region including the Arabian Peninsula (Andersen & Mendes 2010: 570; Andersen & Schnell 2000; Wang *et al*. 2002). Most species are terrestrial or semi-terrestrial as larvae, but a few are aquatic (Andersen *et al.* 2013*b*: 206). Immature stages of Afrotropical species remain undescribed, but generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 205) and Coffman *et al.* (1986: 162), respectively. Identification keys to males are available for Afrotropical species (Wang *et al*. 2002) and for the Arabian Peninsula (Andersen & Mendes 2010: 569).

***Cardiocladius* Kieffer** (Orthocladiinae)**.** A genus of 19 described species that occurs in all zoogeographical regions, except Antarctica and Oceania (Ashe & O'Connor 2012: 160). Four species are known from the Afrotropical Region, *C. africanus* Freeman, 1955 from Democratic Republic of Congo, Ethiopia, South Africa and Zimbabwe, *C. hessei* Freeman 1956 from South Africa, *C. latistilus* Freeman, 1956 from Réunion Is., South Africa, Swaziland and Zimbabwe and *C. oliffi* Freeman, 1956 from Ethiopia, Madagascar, South Africa and Togo. Larvae occur in fast-flowing waters and are often associated with the immature stages of blackflies (Simuliidae), on which they are reported to be predaceous (Andersen *et al.* 2013*b*: 208). Generic diagnoses for Holarctic larva and pupa were provided by Andersen *et al.* (2013*b*: 207) and Coffman *et al.* (1986: 163), respectively. According to G.A. Halvorsen (pers. comm. 2015), however, the immatures of the Afrotropical species show similarities to the immatures of *Eukiefferiella* Thienemann. The pupa of *C. hessei* was described by Lehmann (1979). See Fig. 14 for an example of the wing of the genus and Fig. 66 for the male terminalia. An identification key to the males of Afrotropical species was provided by Freeman (1956: 321).

***Chaetocladius* Kieffer** (Orthocladiinae)**.** A species-rich genus of 64 described species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 165). Two species are known from the Afrotropics (Harrison 1992), *C. awasae* Harrison, 1992, from Ethiopia and *C. melaleucus* (Meigen, 1818), originally described from Europe and recorded from Uganda; both belong to the subgenus *Chaetocladius sensu stricto*. The immature stages occur in wet leaves, mud and among plants in springs, streams, ditches, ponds and in permanent and ephemeral pools. Larvae of most species can be characterised as semi-aquatic, but a few are truly aquatic (Andersen *et al.* 2013*b*: 209). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 208) and Coffman *et al.* (1986: 164), respectively. See Fig. 45 for an example of tarsomere 5 and the claws of the genus.

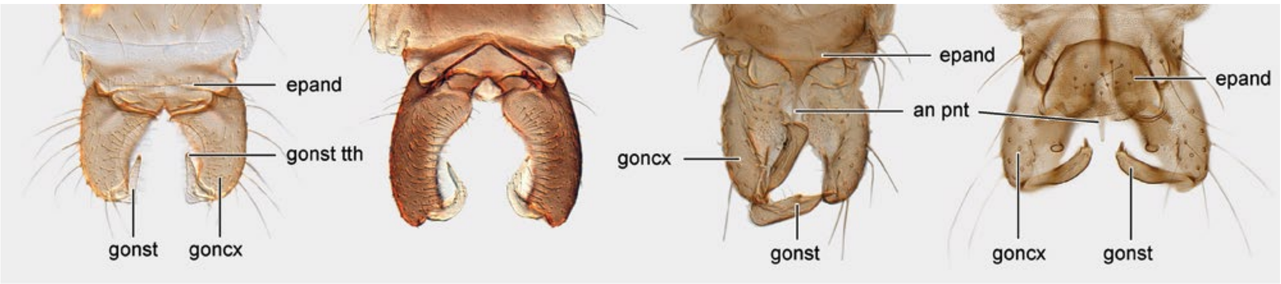
***Chironomus* Meigen** (Chironominae: Chironomini)**.** A genus with *ca* 300 described species that occurs in all zoogeographical regions, except Antarctica. Nineteen species in three subgenera are recorded from the Afrotropical Region. The intra-generic classification of *Chironomus* is uncertain and in need of a molecular systematic revision. Here, the writers follow the broad definition of the genus, as proposed by Epler *et al*. (2013) and treat the taxa *Baeotendipes* Kieffer, *Benthalia* Lipina and *Chironomus sensu stricto* as subgenera of *Chironomus*. *Chironomus* (*Baeotendipes*) includes two known species, *C.* (*B.*) *noctivagus* (Kieffer, 1911) from Europe and North Africa and *C.* (*B.*) *ovazzai* (Freeman, 1957), described from Ethiopia (Freeman 1957) and also recorded from Mozambique and South Africa. Larvae of *C.* (*Baeotendipes*) inhabit saline pools (Cranston *et al.* 1989*a*: 363). The only Afrotropical species so far included in *C.* (*Benthalia*) is *C.* (*B.*) *hamatus* Freeman, 1957 from Democratic Republic of Congo, previously placed in *Endochironomus* (Ekrem & Stur 2016). *Chironomus sensu stricto* includes 18 species in the Afrotropical Region, the majority of which were reviewed by Dejoux (1968), Freeman (1957) or Harrison (1996). Larvae (Figs 110, 115) and pupae (Fig. 119) of many species in *Chironomus sensu stricto* are fairly eurytopic and are associated mostly with lakes, ponds or rivers (Harrison 1996). See Fig. 25 for an example of the wing of the genus, Fig. 40 for the thorax and Fig. 91 for the male terminalia. Identification keys that include all Afrotropical species are unavailable.

***Chrysopelopia* Harrison** (Tanypodinae)**.** An endemic monotypic genus, with the single described species, *C. corusca* Harrison, 1978, only known from the type locality in Zimbabwe (Harrison 1978). Adult males were collected close to a stream; thus, the unknown immatures are probably rheophilic. A more detailed adult male generic diagnosis is required.

***Cladopelma* Kieffer** (Chironominae: Chironomini)**.** A genus of 20 described species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. The generic placement of the single known Afrotropical species, *Cladopelma inflexum* (Freeman, 1957) was recently confirmed by Ekrem & Stur (2016). The species has been recorded as adults from Chad, Malawi, Niger and Sudan. Yan *et al*. (2008a) provided a key to *Cladopelma* that includes *C. inflexum*.

***Cladotanytarsus* Kieffer** (Chironominae: Tanytarsini)**.** A genus of 77 described species that occurs in all zoogeographical regions, except Antarctica and Oceania (Giłka 2011). Twelve species of the subgenus *Cladotanytarsus sensu stricto* are known from the Afrotropics, many of them as adults only. Larvae of *Cladotanytarsus* may be found in both, standing and flowing waters (Ekrem 1999*a*; Freeman 1958; Harrison 2004*b*). See Fig. 26 for an example of the wing of the genus. No comprehensive identification key to species of the subgenus *Cladotanytarsus* is available.

Clinotanypus **Kieffer** (Tanypodinae)**.** A genus of 44 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2009: 50). Two subgenera are recognised, but only *Clinotanypus sensu stricto* occurs in the Afrotropics, with five named species. The larva and pupa of *C.* (*C.*) *maculatus* Freeman, 1955 were described by McLachlan (1969) from Lake Kariba (Zimbabwe), where it is usually found in bottom mud. Harrison (1991) described the larva of *C.* (*C.*) *claripennis* Kieffer, 1918 from lakes in Ethiopia, where it feeds on oligochaetes. Larvae of *Clinotanypus* prefer soft sediments in shallow, warm water bodies ranging widely in size and water quality, including ponds, lakes and slow-flowing streams and rivers (Cranston & Epler 2013: 49). The Afrotropical species can be identified using the identification key

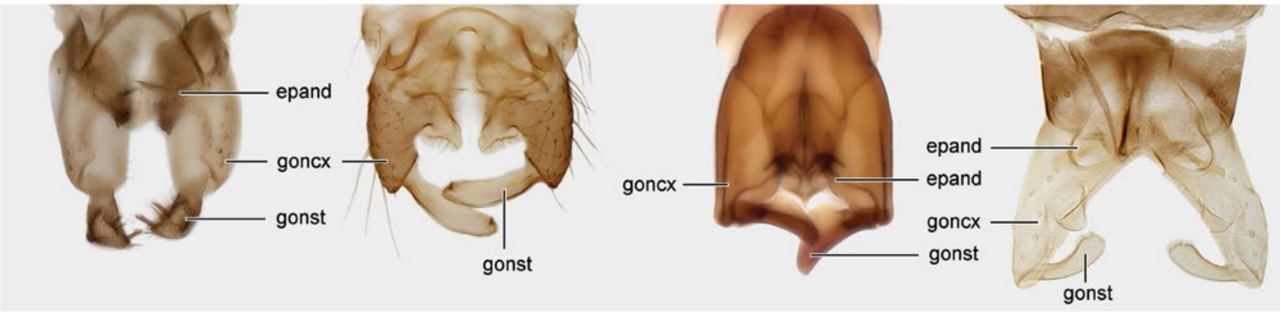


61 *Procladius* (*Holotanypus*) ♂

62 *Tanypus* (*Tanypus*) ♂

63 *Antillocladius* ♂

64 *Bryophaenocladius* ♂

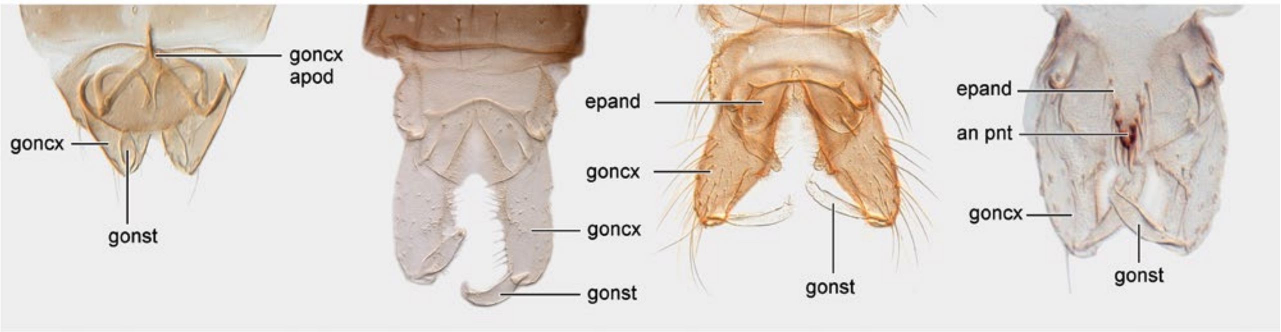


65 *Bryophaenocladius* ♂

66 *Cardiocladius* ♂

67 *Clunio* ♂

68 *Colosmittia* ♂



69 *Corynoneura* ♂

70 *Cricotopus* (*Cricotopus*) ♂

71 *Cricotopus* (*Paratrichocladius*) ♂

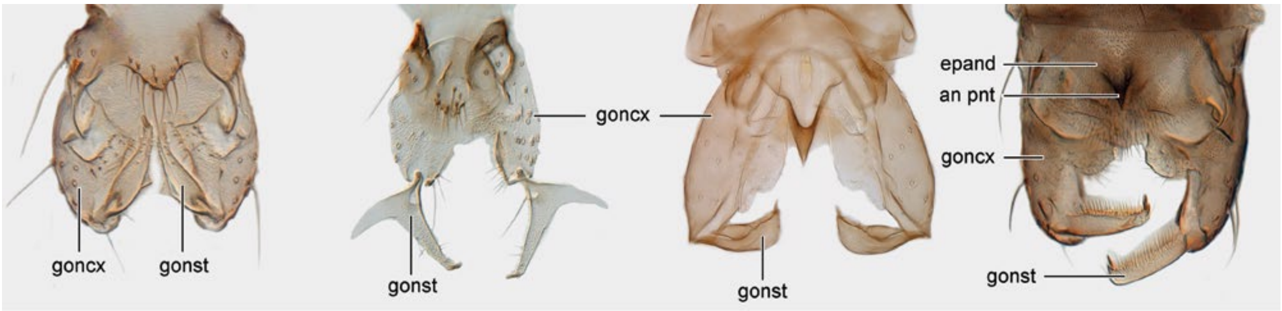
72 *Doithrix* ♂

Figs 35.61–72. Male terminalia of Chironomidae (dorsal views): (61) *Procladius* (*Holotanypus*) sp.; (62) *Tanypus* (*Tanypus*) *brevipalpis* (Kieffer); (63) *Antillocladius* sp.; (64) *Bryophaenocladius* sp.; (65) *B. usambarensis* Andersen & Schnell; (66) *Cardiocladius* sp.; (67) *Clunio jonesi* Sæther & Andersen; (68) *Colosmittia clavata* Andersen & Sæther; (69) *Corynoneura* sp.; (70) *Cricotopus* (*Cricotopus*) sp.; (71) *Cricotopus* (*Paratrichocladius*) sp.; (72) *Doithrix longipes* Sæther & Andersen. Photographs T. Ekrem and E. Stur.

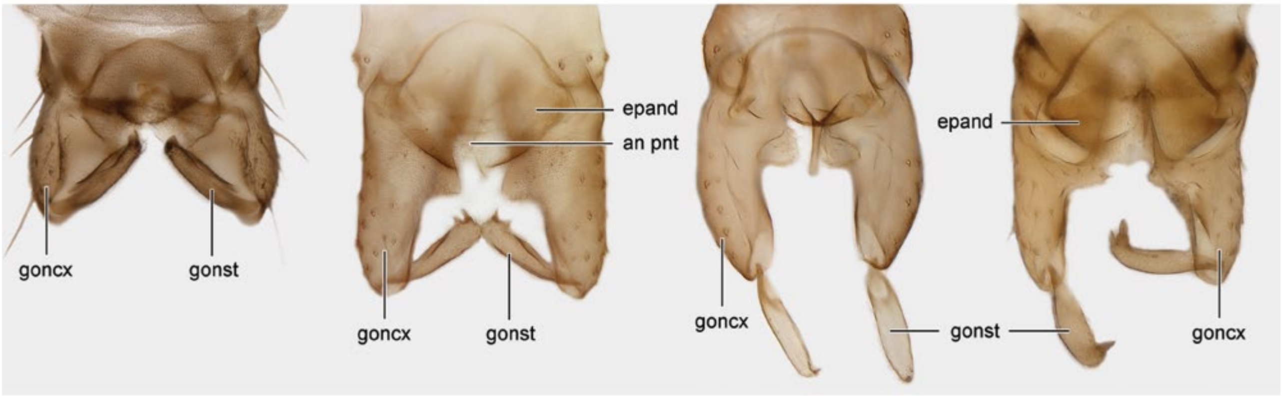
Abbreviations: an pnt – anal point; epand – epandrium; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; gonst tth – gonostylar tooth.

provided by Freeman (1955), modified by Freeman (1956) to include *C.* (*C.*) *verbekei* Freeman, 1956.

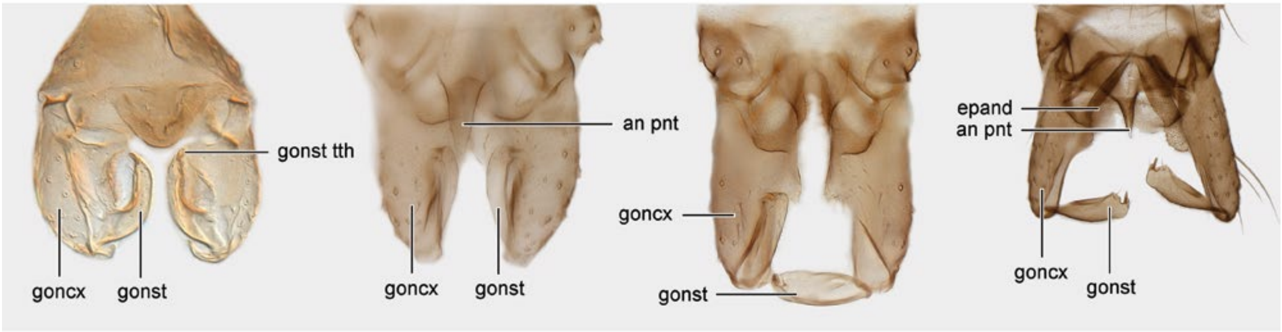
Clunio **Haliday** (Orthocladiinae). A genus of 25 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 180). Three species are known from the Afrotropical Region, *C. africanus* Hesse, 1937 from South Africa, *C. gerlachi* Sæther, 2004 from Seychelles and *C. jonesi* Sæther & Andersen, 2011 from Gough Is. Larvae are marine and occur in the intertidal zone, particularly



73 *Georthocladius* (*Georthocladius*) ♂ 74 *Georthocladius* (*Georthocladius*) ♂ 75 *Ionthosmittia* ♂ 76 *Lerheimia* ♂



77 *Limnophyes* ♂ 78 *Mesocricotopus* ♂ 79 *Molleriella* ♂ 80 *Nanocladius* (*Nanocladius*) ♂



81 *cf. Parakiefferiella* ♂ 82 *Parametriocnemus* ♂ 83 *Paraphaenocladius* ♂ 84 *Paratrissocladius* ♂

Figs 35.73–84. Male terminalia of Chironomidae (dorsal views): (73) *Georthocladius* (*Georthocladius*) *amakyei* Sæther & Andersen; (74) *G.* (*G.*) *longicalcaneum* Sæther & Andersen; (75) *Ionthosmittia caudiga* Sæther & Andersen; (76) *Lerheimia scopulata* Andersen & Sæther; (77) *Limnophyes* sp.; (78) *Mesocricotopus* sp.; (79) *Molleriella kaputu* Andersen; (80) *Nanocladius* (*Nanocladius*) sp.; (81) *cf. Parakiefferiella* sp.; (82) *Parametriocnemus* sp.; (83) *Paraphaenocladius crassicaudatus* Sæther & Wang; (84) *Paratrissocladius* sp. Photographs T. Ekrem and E. Stur.

Abbreviations: an pnt – anal point; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; gonst tth – gonostylar tooth.

on rocky shores (Andersen *et al.* 2013*b*: 210). Females are wingless, almost vermiform. Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 210) and Coffman *et al.* (1986: 166), respectively. See Fig. 15 for an example of the male wing of the genus. An identification key to all Afrotropical species is unavailable.

***Coelotanypus* Kieffer** (Tanypodinae)**.** A genus of 21 described species that occurs in the Afrotropical, Australasian, Nearctic and Neotropical Regions. Only one named species, *C. africanus* Freeman, 1955, is known from the Afrotropics, with a distribution that comprises Cameroon, Nigeria and Sierra Leone (Ashe & O'Connor 2009: 140). Larvae of *Coelotanypus* occur in benthic sediments of lakes, artificial impoundments, slow-flowing reaches of rivers and old riverbeds (Cranston & Epler 2013: 50). The immature stages of the only known Afrotropical species remain unknown. See Fig. 7 for an example of the wing of the genus and Fig. 55 for the male terminalia.

***Collartomyia* Goetghebuer** (Chironominae: Chironomini)**.** An endemic genus with two described species: *C. hirsuta* (Goetghebuer, 1936), from Democratic Republic of Congo, South Africa and Uganda; and *C. discaudata* Amakye, 1995 from Ghana (Amakye 1995). The latter species is, however, certainly not congeneric with *C. hirsuta*. *Collartomyia discaudata* is here regarded as a valid species, but is unplaced in Chironomini and here follows the stricter definition of *Collartomyia* presented by Amakye & Sæther (1992). *Collartomyia* is close to *Polypedilum* Kieffer and the larvae of *C. hirsuta* feed on pupae of the caddis fly family Hydropsychidae (Amakye & Sæther 1992).

***Colosmittia* Andersen & Sæther** (Orthocladiinae)**.** A genus of three described species that occurs in the Afrotropical and Neotropical Regions (Ashe & O'Connor 2012: 185). The genus was erected based on *C. clavata* Andersen & Sæther, 1994, from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen & Sæther 1993). Recently two species have been described from Central and South America. The immature stages remain unknown.

***Compterosmittia* Sæther** (Orthocladiinae)**.** A genus of 16 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 185). One undescribed species is known from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania. Larvae have been found in phytotelmata (plant-held waters), including internodes of bamboo, rot holes in trees and axillary fluid (Andersen *et al.* 2013*b*: 211). Larvae and pupae are very similar to those in *Limnophyes* Eaton. A generic diagnosis for the larva was provided by Andersen *et al.* (2013*b*: 210); the pupa of an unidentified species from Tasmania was described by Cranston & Kitching (1995: 229).

***Conchapelopia* Fittkau** (Tanypodinae)**.** A genus of 43 described species that occurs in the Holarctic Realm, the Afrotropical and Oriental Regions, with records from the Neotropical and Australasian Regions requiring confirmation. Cranston & Epler (2013: 39) have reduced the previously separate genus *Helopelopia* Roback to subgeneric status in *Conchapelopia*. Only the subgenus *Conchapelopia sensu stricto*, with five described species, is known from the Afrotropics (Ashe & O'Connor 2009: 52). Larva and pupa of one of these, *C.* (*C.*) *trifascia* (Freeman, 1954), was described by Harrison (1991) and the pupa of *C.* (*C.*) *zairensis* Lehmann, 1979 by Lehmann (1979); both species occur in mountain rivers and streams. Larvae of *Conchapelopia* range from stenothermic inhabitants of flowing waters and lakes, to warm eurythermic species (Cranston & Epler 2013: 82). An identification key to all Afrotropical species is unavailable.

***Conochironomus* Freeman** (Chironominae: Chironomini)**.** A genus of six described species that occurs in the Afrotropical, Australasian and Oriental Regions. Three described species are recorded from the Afrotropics (Cranston & Hare 1995): *C. acutistilus* (Freeman, 1955) from Burkina Faso, Democratic Republic of Congo, Nigeria, Rwanda, Sierra Leone, Uganda and Zimbabwe; *C. avicula* (Freeman, 1955) from Cameroon, Democratic Republic of Congo, Madagascar, Nigeria, Republic of Congo and Senegal; and *C. deemingi* Cranston & Hare, 1995 from Nigeria. *Conochironomus* larvae inhabit sediments of lakes and rivers (Cranston & Hare 1995). An identification key to species was provided by Cranston & Hare (1995).

***Corynoneura* Winnertz** (Orthocladiinae)**.** A genus of 97 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 188). Three species are known from the Afrotropical Region: *C. cristata* Freeman, 1953 from South Africa and Zimbabwe; *C. dewulfi* Goetghebuer, 1935 from Democratic Republic of Congo, Ethiopia, South Africa, Tanzania, Uganda and Zimbabwe; and *C. elongata* Freeman, 1953 from South Africa and Zimbabwe. Larvae occur in virtually all types of aquatic habitats, from standing waters to fast-flowing streams (Andersen *et al.* 2013*b*: 212). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 211) and Coffman *et al.* (1986: 167), respectively. The larva and pupa of *C. dewulfi* have been described and figured (Harrison 1992; Lehmann 1979). An identification key to the males of Afrotropical species was provided by Freeman (1956: 361).

***Corynoneurella* Brundin** (Orthocladiinae)**.** A genus based on *C. paludosa* Brundin, 1949 from the Palaearctic Region (Ashe & O'Connor 2012: 204). A second species, *C. afra* (Lehmann, 1981) is known from Democratic Republic of Congo (Lehmann 1981). The pupa was described by Lehmann (1981) and redescribed by Fu *et al.* (2010).

***Cricotopus* Wulp** (Orthocladiinae)**.** Following recent synonymy with *Paratrichocladius* (Cranston & Krosch 2015), *Cricotopus* contains 262 described species and occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 205, 487). Seven subgenera are recognised, including the monotypic *C.* (*Maurius* Lehmann), based on *C.* (*M.*) *kisantuensis* Goetghebuer, 1934 from Democratic Republic of Congo (Lehmann 1981). A further 20 species of the genus are known from the Afrotropics, seven of which are assigned to the subgenus *Cricotopus sensu stricto*, three to *C.* (*Paratrichocladius* Santos Abreu) and the remaining ten are subgenerically unplaced. Larvae (Fig. 114) inhabit all types of freshwater, and to a lesser extent, saline coastal and inland waters. They are frequently associated with aquatic plants, including algae and some mine living parts of aquatic macrophytes (Andersen *et al.* 2013*b*: 214). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 212, 245) and Coffman *et al.* (1986: 167, 196), respectively. The pupae of several Afrotropical species were described and figured by Lehmann (1979, 1981) and Harrison (1992), including the pupae of *C.* (*M.*) *kisantuensis* and *C.* (*P.*) *micans* (Kieffer, 1918). See Figs 18, 19 for examples of wings of the two subgenera with Afrotropical representatives and Figs 70, 71 for the male terminalia. An identification key to most adult males of Afrotropical species was provided by Freeman (1956: 303, 314).

***Cryptochironomus* Kieffer** (Chironominae: Chironomini)**.** A genus of 57 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor unpubl.). The genus belongs to the *Harnischia* genus complex, which includes many genera and a world total of more than 140 described species (Silva *et al.* 2010). All Afrotropical representatives of this complex that were known at the time were reviewed and keyed as adult males by Freeman (1957), but in his classification all of these were placed in a single subgenus, "*Chironomus* (*Cryptochironomus*)", rather than being ascribed to separate genera as in the current system. Some of these species, e.g., "*C.* (*Cr.*)" *melutensis* Freeman, 1957 and "*C.* (*Cr.*)" *reidi* Freeman, 1957, have valid names, but require revision for placement in established or new genera. More recent authors assigned nine species known from tropical Africa to *Cryptochironomus* in the modern, much restricted sense, all to the nominotypical subgenus *Cr.* (*Cryptochironomus*). Larvae occur in both running and standing waters. No comprehensive recent identification key exists for Afrotropical species, but some revised descriptions have been provided (Andersen & Mendes 2010: 581; Lehmann 1979).

***Cryptotendipes* Beck & Beck** (Chironominae: Chironomini)**.** A genus of 23 species, most of which occur in the Holarctic Realm, while there are two published records from the Oriental Region and one from the Neotropical Region. The single named species from the Afrotropical Region is *C. graminicolor* (Kieffer, 1925), known from Burkina Faso, Chad, Ethiopia, Kenya, Mali, South Africa and Sudan, as well as from Mediterranean North Africa. This species has been placed in *Cryptotendipes* at least since the description of the pupa (Azzouzi 1992). An identification key to some *Cryptotendipes* species was provided by Yan *et al*. (2005), but this does not include *C. graminicolor*. The male of this species was, however, treated by Freeman (1957, as "*Chironomus* (*Cryptochironomus*)").

***Cyphomella* Sæther** (Chironominae: Chironomini)**.** A genus comprising four described species that occur in the Holarctic Realm and a morphologically different species of questionable inclusion in the Afrotropical Region. *Cyphomella camelus* (Kieffer, 1925), was originally described from the River Nile in Egypt and has been recorded from Chad, Democratic Republic of Congo, South Sudan and Sudan (Freeman 1957). Immature stages of some *Cyphomella* species were described by Sæther (1977), but little is known about their biology. An identification key to adult males in the genus was provided by Yan *et al.* (2011), and Freeman (1957) keyed *C. camelus* among the many other species in his "*Chironomus* (*Cryptochironomus*)".

***Demicryptochironomus* Lenz** (Chironominae: Chironomini)**.** A genus of 31 described species that occurs in all zoogeographical regions, except the Neotropics, Oceania and Antarctica (Yan *et al.* 2008*b*). Two species are known from the Afrotropics, *D. cinereithorax* (Goetghebuer, 1934) from Chad, Democratic Republic of Congo, South Africa and Zimbabwe (tentatively placed in the subgenus *D.* (*Irmakia* Reiss)) and *D. zairensis* Lehmann, 1979, from Democratic Republic of Congo (placed in the subgenus *Demicryptochironomus sensu stricto*) (Reiss 1988*b*). Pupal stages are required to confirm the subgeneric placements. Immature stages and biology remain unknown for Afrotropical species; larvae of Holarctic species occur in soft sediments of lakes and rivers (Cranston *et al.* 1989*a*). An identification key to adult males was provided by Yan *et al.* (2008*b*).

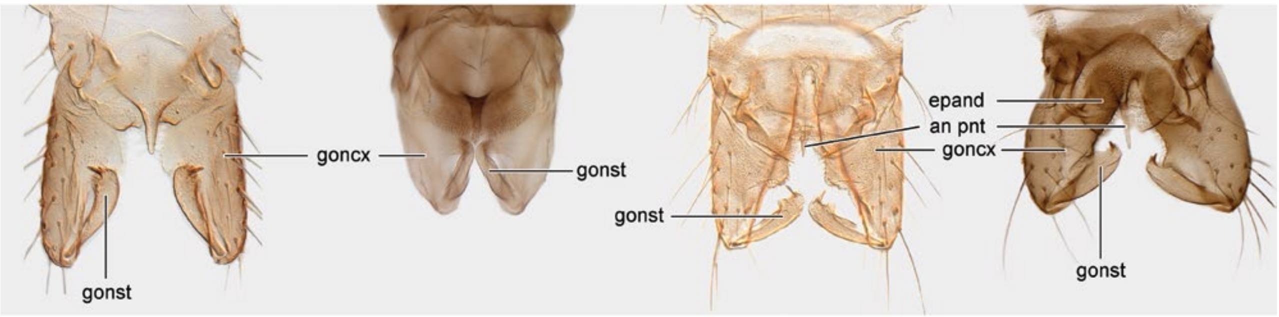
***Diamesa* Meigen** (Diamesinae: Diamesini)**.** A genus of 107 described species that occurs in all zoogeographical regions, except Oceania and Antarctica. The genus is a typical element of the Holarctic alpine regions and is only represented by three species in the Afrotropics. Distribution is restricted to East African mountain ranges, where larvae of two species have been found in high elevation streams and proglacial tarns on Mount Kenya, while adults of the third species are known from locations near various kinds of waters in the Ruwenzori Mountains of Uganda (Willassen & Cranston 1986). An identification key to all Afrotropical species is unavailable.

***Dicrotendipes* Kieffer** (Chironominae: Chironomini)**.** A genus of 85 described species that occurs in all zoogeographical regions, except Antarctica. Fourteen species are recorded from the Afrotropics for many of which the immatures are known (Epler 1988; Harrison 1996). Larvae occur in a variety of standing waters, including marginal sediments of pools in slow-flowing rivers. See Fig. 27 for an example of the wing of the genus. An identification key to adult males of Afrotropical species was provided by Epler (1988).

***Djalmabatista* Fittkau** (Tanypodinae)**.** A genus of 12 described species that occurs in all zoogeographical regions, except Antarctica and Oceania (Ashe & O'Connor 2009: 54). The single described Afrotropical species, *D. reidi* (Freeman, 1955), is recorded from Cameroon, Chad, Ghana, Guinea, Sudan and Togo, as well as Saudi Arabia in the Arabian Peninsula and India in the Oriental Region. Larvae appear to prefer low alkalinity to weakly acidic waters and may be found in lakes, ponds, springs, large and small rivers, as well as temperate to tropical lentic and lotic depositional habitats (Cranston & Epler 2013: 52). The immature stages of *D. reidi* remain undescribed.

***Doithrix* Sæther & Sublette** (Orthocladiinae)**.** A genus of 12 described species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 262). Two Afrotropical species, *D. amegabei* Sæther & Andersen, 1996 and *D. longipes* Sæther & Andersen, 1996, are described from Ghana (Sæther & Andersen 1996). Larvae are probably semi-terrestrial, occurring at the margins of small streams and seepage areas (Andersen *et al.* 2013*b*: 216). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 215) and Coffman *et al.* (1986: 170), respectively.

***Elpiscladius* Harrison & Cranston** (Orthocladiinae)**.** An endemic monotypic genus, with the single species, *E. capicola* Harrison & Cranston, 2007, described from the Western Cape Province, South Africa, where the immature stages are xylophylous in mountain streams (Cranston 2008; Harrison & Cranston 2007).

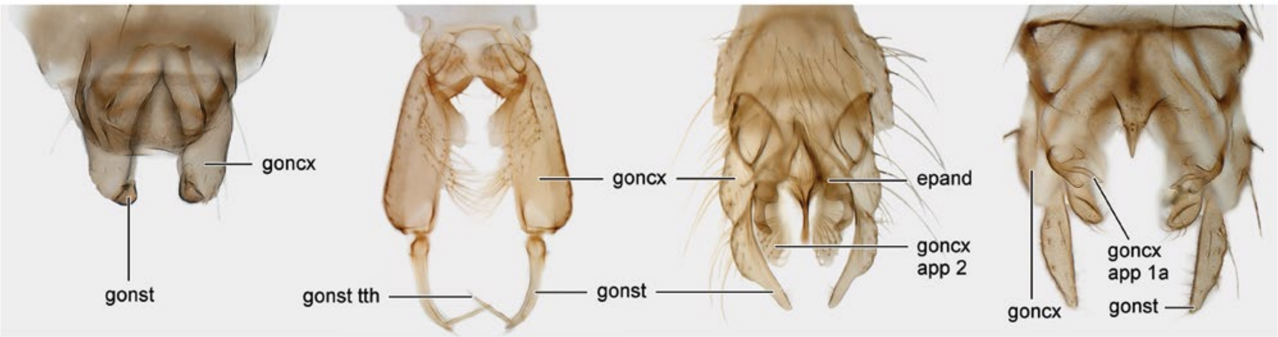


85 *Psectrocladius* (*Psectrocladius*) ♂

86 *Pseudosmittia* ♂

87 *Rheocricotopus* (*Psilocricotopus*) ♂

88 *Smittia* ♂

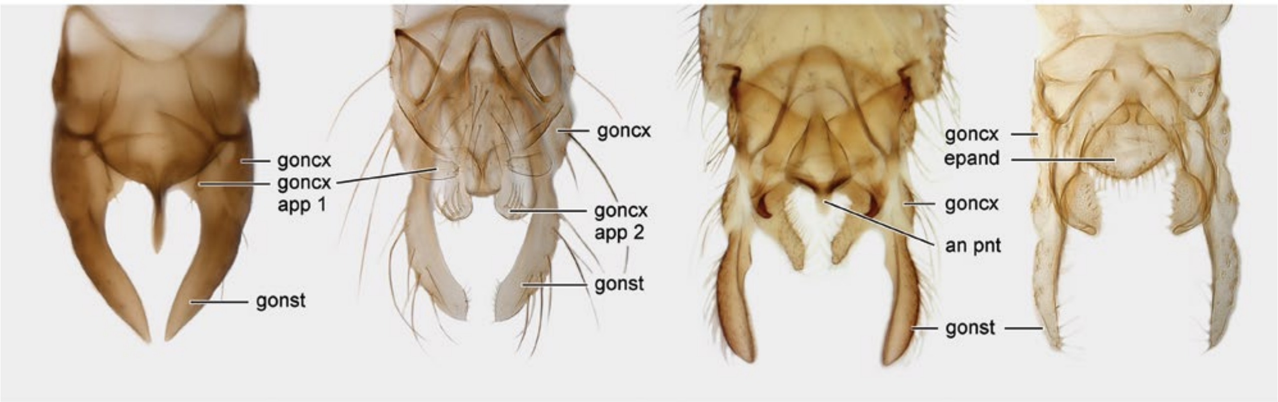


89 *Thienemanniella* ♂

90 *Tokyobrillia* ♂

91 *Chironomus* (*Chironomus*) ♂

92 *Cladotanytarsus* (*Cladotanytarsus*) ♂



93 *Cryptochironomus* (*Cryptochironomus*) ♂

94 *Dicrotendipes* ♂

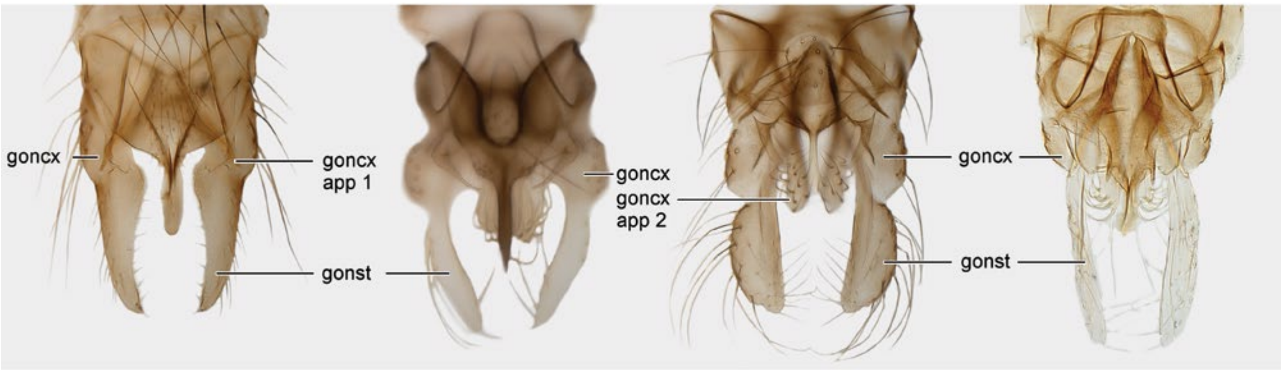
95 *Madachironomus* ♂

96 *Manoa* ♂

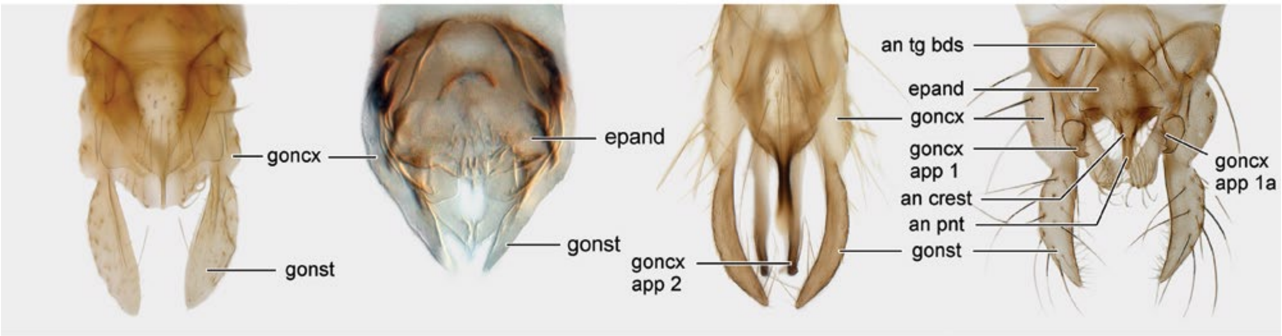
Figs 35.85–96. Male terminalia of Chironomidae (dorsal views): (85) *Psectrocladius* (*Psectrocladius*) sp.; (86) *Pseudosmittia* sp.; (87) *Rheocricotopus* (*Psilocricotopus*) sp.; (88) *Smittia* sp.; (89) *Thienemanniella* sp.; (90) *Tokyobrillia anderseni* Sæther & Wang; (91) *Chironomus* (*Chironomus*) sp.; (92) *Cladotanytarsus* (*Cladotanytarsus*) sp.; (93) *Cryptochironomus* (*Cryptochironomus*) *niligenus* (Kieffer); (94) *Dicrotendipes* sp.; (95) *Madachironomus lakazana* Andersen; (96) *Manoa tangae* Andersen & Sæther. Photographs T. Ekrem and E. Stur.

Abbreviations: an pnt – anal point; epand – epandrium; goncx – gonocoxite; goncx app 1 – gonocoxal appendage 1; goncx app 1a – gonocoxal appendage 1a; goncx app 2 – gonocoxal appendage 2; gonst – gonostylus; gonst tth – gonostylar tooth.

97 *Microchironomus* ♂ 98 *Microtendipes* ♂ 99 *Neostempellina* ♂ 100 *Neozavrelia* ♂



101 *Parachironomus* ♂ 102 *Polypedilum* (*Cerobregma*) ♂ 103 *Polypedilum* (*Polypedilum*) ♂ 104 *Polypedilum* (*Tripodura*) ♂



105 *Polypedilum* (*Uresipedilum*) ♂ 106 *Seppia* ♂ 107 *Stenochironomus* ♂ 108 *Tanytarsus* ♂

Figs 35.97–108. Male terminalia of Chironomidae (dorsal views): (97) *Microchironomus deribae* (Freeman); (98) *Microtendipes* sp.; (99) *Neostempellina* sp.; (100) *Neozavrelia* sp.; (101) *Parachironomus acutus* (Goetghebuer); (102) *Polypedilum* (*Cerobregma*) sp.; (103) *P.* (*Polypedilum*) sp.; (104) *P.* (*Tripodura*) sp.; (105) *P.* (*Uresipedilum*) sp.; (106) *Seppia trifurca* Ekrem & Sæther; (107) *Stenochironomus* sp.; (108) *Tanytarsus pallidulus* Freeman. Photographs T. Ekrem and E. Stur.

Abbreviations: an crest – anal crest; an pnt – anal point; an tg bds – anal tergite bands; epand – epandrium; goncx – gonocoxite; goncx app 1 – gonocoxal appendage 1; goncx app 1a – gonocoxal appendage 1a; goncx app 2 – gonocoxal appendage 2; goncx app 2a – gonocoxal appendage 2a; gonst – gonostylus.

Endochironomus **Kieffer** (Chironominae: Chironomini)**.** A genus previously represented by six Afrotropical species (Freeman 1957, 1961), but all have been transferred to other genera, following the re-definition of *Endochironomus* by Grodhaus (1987). *Endochironomus acutistilus* Freeman, 1955 and *E. avicula* Freeman, 1955 now belong to *Conochironomus* (Cranston & Hare 1995); *E. disparilis* (Goetghebuer, 1936) and *E. pruinosus* (Freeman, 1961) to *Kiefferulus* (Cranston & Judd 1989; Ekrem & Stur 2016); *E. hamatus* (Freeman, 1957) to *Chironomus* (*Benthalia*) (Ekrem & Stur 2016) and *E. woodi* (Freeman, 1957) to *Synendotendipes* (Ekrem & Stur 2016). "True" *Endochironomus* larvae from other regions are facultative leaf-miners (Cranston *et al*. 1989*a*: 377).

Eukiefferiella **Thienemann** (Orthocladiinae)**.** A genus of 87 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 268). Three species are known from the Afrotropical Region: *E. angustistilus* Freeman, 1953 from South Africa and possibly Senegal; *E. clavigera* (Freeman, 1956) from Madagascar and South Africa; and *E. kivuensis* Lehmann, 1979 from Democratic Republic of Congo. The immature stages inhabit flowing waters of all types (Andersen *et al.* 2013*b*: 219). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 218) and Coffman *et al.* (1986: 173), respectively. The pupa of *E. kivuensis* was described by Lehmann (1979). An identification key to all Afrotropical species is unavailable.

Fittkauimyia **Karunakaran** (Tanypodinae)**.** A genus of six named species that occurs in all zoogeographical regions, except Antarctica and Oceania. A single Afrotropical species, *F. petersi* (Freeman, 1955), is recorded from Burkina Faso, Democratic Republic of Congo, Nigeria and Tanzania (Ashe & O'Connor 2009: 157). *Fittkauimyia* larvae occur in rivers and the littoral region of lakes, generally in tropical and subtropical regions (Cranston & Epler 2013: 53). The immature stages of *F. petersi* remain undescribed.

Freemaniella **Sæther** (Orthocladiinae)**.** An endemic monotypic genus described by Sæther (1976), based on *Chaetocladius eastopi* Freeman, 1956 from Kenya (Freeman 1956). The biology and immature stages remain unknown.

Friederia **Sæther & Andersen** (Chironominae: Tanytarsini)**.** An endemic monotypic genus, with the single species, *F. villosa* Sæther & Andersen, 1998, described from Ankasa Game Production Reserve in western Ghana (Sæther & Andersen 1998). Immature stages and biology remain unknown.

Georthocladius **Strenzke** (Orthocladiinae)**.** A genus of 10 described species that occurs in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions (Ashe & O'Connor 2012: 291). Two species, *G. amakyei* Sæther & Andersen, 1996 and *G. longicalcaneum* Sæther & Andersen, 1996, were described from Ghana, both in the subgenus *Georthocladius sensu stricto* (Sæther & Andersen 1996). Larva occurs in bogs, seeps and small streams (Andersen *et al.* 2013*b*: 222). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013b: 221) and Coffman *et al.* (1986: 176), respectively. See Fig. 20 for an example of the wing of the genus.

Gillotia **Kieffer** (Chironominae: Chironomini)**.** A genus of three named species, one in the Holarctic Realm, one in the Oriental Region, and one (with unknown immature stages), from the Afrotropical Region. A few additional undescribed species are known from other regions (Cranston 2010; Cranston *et al.* 1989*a*). *Gillotia* was included in *Chironomus* (*Cryptochironomus*) by Freeman (1957), but was revalidated by Sæther (1977). The Afrotropical type species of the genus, *G. trifida* Freeman, 1957, is widespread and has at least been recorded from Benin, Burkina Faso, Chad, Namibia, Nigeria, Senegal, South Sudan, Sudan and Zimbabwe (Bidwell & Clarke 1977; Dejoux 1976, 1984*a*; Freeman 1957; Freeman & Cranston 1980: 191; Harrison 2004*b*).

Glyptotendipes **Kieffer** (Chironominae: Chironomini)**.** A genus of 45 named species that occurs in the Holarctic Realm and Oriental Region (Epler *et al.* 2013: 413), with one species from the Oceanian Region. Three subgenera are recognised and one undescribed species, not currently assigned to a subgenus, is reported from the Afrotropical Region (Epler *et al.* 2013: 413). Larvae of Holarctic species are recorded from detritus-rich littoral sediments and from "Aufwuchs" in lakes and small water bodies; less often in running water. Larvae of several species mine submerged plants, bryozoans or sponges or occur beneath immersed tree bark.

Gymnometriocnemus **Edwards** (Orthocladiinae)**.** A genus of 17 described species that occurs in the Afrotropical, Australasian, Nearctic, Neotropical and Palaearctic Regions (Ashe & O'Connor 2012: 294; Stur & Ekrem 2015). Two species, *G. benoiti* (Freeman, 1956) recorded from Democratic Republic of Congo and *G. mahensis* (Kieffer, 1911) recorded from Seychelles (Sæther 2004) and possibly Burkina Faso, are known from the Afrotropics, both in the subgenus *Gymnometriocnemus sensu stricto*. Larvae appear to be solely terrestrial, occurring in humus-rich soils, cultivated fields and meadows (Andersen *et al.* 2013*b*: 223). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 222) and Coffman *et al.* (1986: 177), respectively.

Harnischia **Kieffer** (Chironominae: Chironomini)**.** A genus of 20 described species that occurs in all zoogeographical regions, except Antarctica, the Neotropics and Oceania. Two species are recorded from the Afrotropics, *H. curtilamellata* (Malloch, 1915) from Ethiopia, Nigeria, South Africa, Sudan and Togo and *H. lacteiforceps* (Kieffer, 1923) from Chad, Democratic Republic of Congo, Senegal, South Africa and Sudan (Bidwell & Clarke 1977; Dejoux 1984*a*; Freeman & Cranston 1980: 191; Harrison 1996). Larvae of *Harnischia* occur on soft sediments predominantly in clean lakes and larger rivers (Epler *et al*. 2013: 415).

Harrisonina **Freeman** (Diamesinae: Harrisonini)**.** An endemic monotypic genus, with the single species, *H. petricola* Freeman, 1956, recorded from Komga in the Eastern Cape Province, South Africa and Zimbabwe (Cranston *et al*. 2012; Harrison 1965). The genus constitutes the tribe Harrisonini and is aberrant compared to other diamesines, in lacking the crossvein between wing veins *M* and *Cu* in adults. It was placed originally within the Orthocladiinae (Freeman 1956), but based on a combination of adult characters, Brundin argued its placement as sister-group to the tribes Diamesini and Protanypini (Brundin 1966: 368). Placement of the genus in the Diamesinae is supported by molecular data, but phylogenetic analyses, including seven genera in this subfamily, places *Harrisonina* as sister to *Heptagyia* Philippi (Cranston *et al*. 2012). Immature stages and adults have been found in a thin water film running over stones in a temporary mountain stream in the former Transvaal, South Africa (Brundin 1966: 423) and in Komga and other locations in Eastern Cape Province where it is very characteristic of newly flowing temporary streams (P.S. Cranston, pers. comm. 2015).

***Henrardia* Goetghebuer** (Chironominae: Chironomini)**.** An endemic monotypic genus, with the single described species, *H. quadrispinosa* Goetghebuer, 1936, recorded from Benin, Burkina Faso, Democratic Republic of Congo, Nigeria, Republic of Congo and Senegal. Males and females were redescribed by Amakye & Sæther (1993). The biology and immature stages remain unknown. See Fig. 28 for an example of the wing of the genus.

***Hydrosmittia* Ferrington & Sæther** (Orthocladiinae)**.** A genus of 13 described species that occurs in the Afrotropical, Nearctic and Palaearctic Regions (Ashe & O'Connor 2012: 323). Four species are known from the Afrotropical Region, *H. falsicostata* Ferrington & Sæther, 2011 from Mt Kenya and *H. annulata* Ferrington & Sæther, 2011, *H. soelii* Ferrington & Sæther, 2011 and *H. tenuistylata* Ferrington & Sæther, 2011, from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania. Larvae are truly aquatic, occurring in submerged moss and algal growth on stones in streams, rivers, canals, waterfalls and lakes (Andersen *et al.* 2013*b*: 228). Immature stages of Afrotropical species remain undescribed, but larvae and pupae of extralimital species were described by Ferrington & Sæther (2011). An identification key to species was provided by Ferrington & Sæther (2011).

***Ionthosmittia* Sæther & Andersen** (Orthocladiinae)**.** A genus with two species, one each from the Afrotropical and Palaearctic Regions (Ashe & O'Connor 2012: 328). The genus was originally erected based on *I. caudiga* Sæther & Andersen, 1995 from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Sæther & Andersen 1995). The biology and immature stages remain unknown. See Fig. 75 for an example of the male terminalia of the genus.

***Kiefferulus* Goetghebuer** (Chironominae: Chironomini)**.** A genus of 27 named species that occurs in all zoogeographical regions, except Antarctica (Cranston *et al.* 1990; Epler *et al.* 2013; Spies *et al.* 2009). Following the synonymisation of *Carteronica* Kieffer and *Nilodorum* Kieffer with *Kiefferulus* (Cranston *et al*. 1990) and the placement of *Endochironomus pruinosus* in *Kiefferulus* (Ekrem & Stur 2016), there are now eight described species from the Afrotropical Region. Immature stages are found predominantly in small water bodies throughout the Afrotropics, but also in lakes and saline environments (Cranston *et al*. 1990; Harrison 1996). See Fig. 1 for an example of the adult male habitus of the genus. An identification key to all Afrotropical species is unavailable.

***Kloosia* Kruseman** (Chironominae: Chironomini)**.** A genus of four named species that occurs in the Holarctic Realm and the Afrotropical and Oriental Regions. The genus was revised by Reiss (1988*a*), who also described an Afrotropical species, *K. africana* Reiss, 1988, from the upper potamon of a stream in the Meru National Park of central Kenya. The subsequent records of this species from Ethiopia and South Africa (Harrison 1996) were due to misidentification, either of the widespread Palaearctic (*e.g.*, circum-Mediterranean) *K. pusilla* (L., 1767), or of a closely related species (M. Spies, pers. comm. 2015; based on Harrison material at the Zoologische Staatssammlung München). There is also a male from Kenya determined as *K. pusilla* by F. Reiss. The pupa of *K. africana* has been described (Reiss 1988*a*) and the pupa and larva of *K. pusilla* have been treated under various now synonymous names (Langton & Visser 2003; Reiss 1988). Larvae are also known for some hitherto non-Afrotropical species (Epler *et al.* 2013: 417).

***Krenosmittia* Thienemann & Krüger** (Orthocladiinae)**.** A genus of 20 named species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 330). Two species are known from the Afrotropical Region, *K. brevitarsis* (Freeman, 1953) from South Africa and Zimbabwe and *K. ignota* Lehmann, 1981 from Democratic Republic of Congo. Larvae occur in springs and rivers (Andersen *et al.* 2013*b*: 229). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 228) and Coffman *et al.* (1986: 182), respectively.

***Kribiocosmus* Kieffer** (Chironominae: Chironomini)**.** A genus of three named species that occurs in the Afrotropical and Oriental Regions. The genus was originally based on *K. ornatipes* Kieffer, 1921 from Cameroon (Kieffer 1921). A second species has been described from Oriental Japan (Yamamoto 1993) and a third from India (Dutta & Chaudhuri 1995). The Afrotropical species occurs in the modern states of Democratic Republic of Congo, Ghana, Guinea, Mali and Niger (Dejoux 1984*b*; Freeman 1958: 318). Immature stages remain unknown.

***Kribiodorum* Kieffer** (Chironominae: Chironomini)**.** A genus of two named species that occurs in the Nearctic and Afrotropical Regions. A third species is known from pupa and adults from South-east Asia in the Oriental Region (Cranston 2010). The only known Afrotropical species, *K. pulchrum* Kieffer, 1921, described from Cameroon, is distributed in Benin, Democratic Republic of Congo, Ghana, Nigeria, South Africa, South Sudan, Sudan, Togo and Zimbabwe (Dejoux 1984*a*; Freeman 1958; Hare & Carter 1987). Immature stages of *K. pulchrum* remain unknown. Larvae of the only other named species (the North American *K. perpulchrum* (Mitchell, 1908)), are associated with dead wood in flowing waters (Epler *et al.* 2013: 418).

***Kribiodosis* Kieffer** (Chironominae: Chironomini)**.** An endemic monotypic genus, described for five different species from the Kribi area of Cameroon, but four of the names were subsequently synonymised under the fifth and only remaining valid name (Freeman 1958: 324). *Kribiodosis clavigera* Kieffer, 1921 has been recorded from a number of countries in West and Central Africa (Dejoux 1984*b*; Freeman 1958; Lehmann 1981). Immature stages remain undescribed, but Lehmann (1981) recorded larvae among wood and plant debris in a stream near Kisangani, Democratic Republic of Congo.

***Kribiothauma* Kieffer** (Chironominae: Chironomini)**.** An endemic monotypic genus, with the single species, *K. pulchellum* Kieffer, 1921, described from Cameroon and recorded later from the KwaZulu-Natal Province, South Africa (Freeman 1958: 327; Harrison 2001). A larva tentatively placed in *Kribiothauma* was described by Harrison (2001).

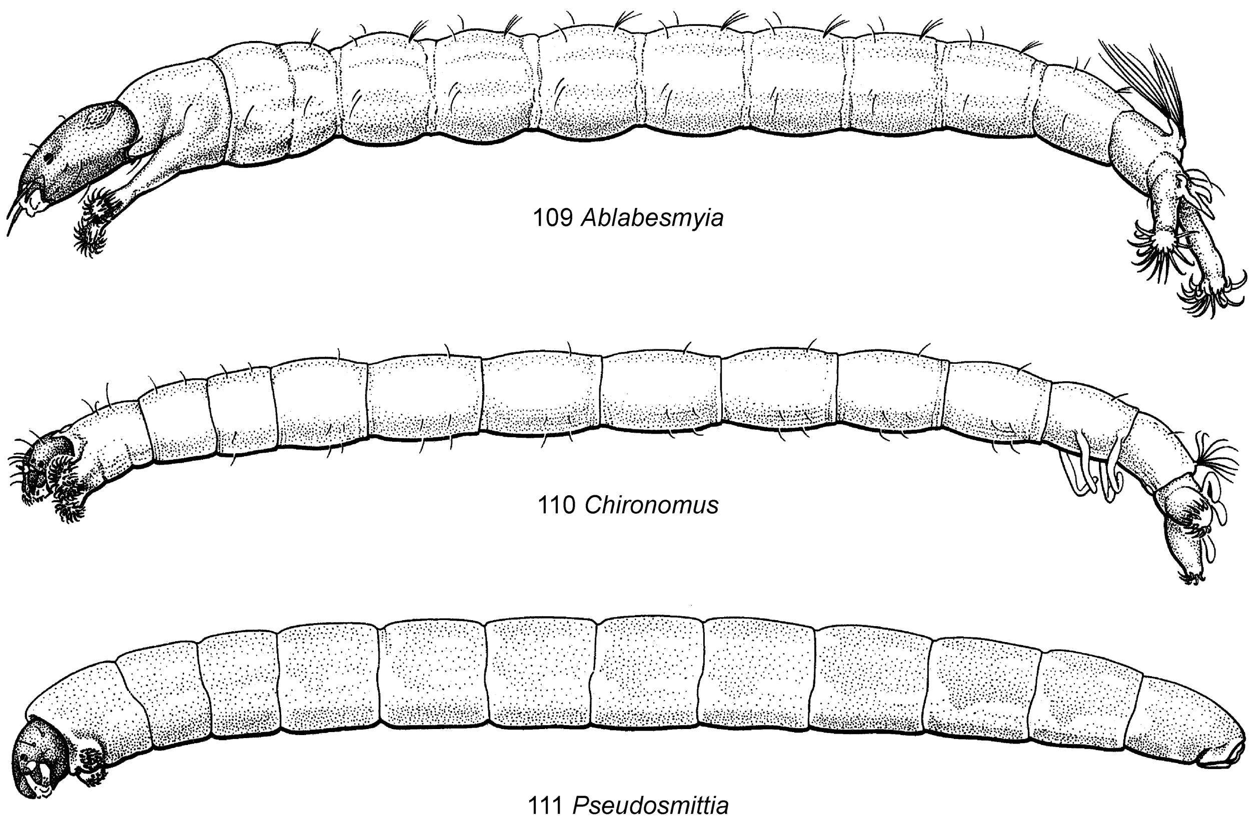
Larsia **Fittkau** (Tanypodinae)**.** A genus of 28 named species that occurs in all zoogeographical regions, except Antarctica, with nine species in the Afrotropics. The pupal exuviae of *L. africana* Lehmann, 1979, was described from a montane river in the eastern part of Democratic Republic of Congo (Lehmann 1979). *Larsia* includes some species for which larvae are moderately cold stenothermic and occur in many habitats, including springs, ditches, streams, small standing waters and the littoral zone of lakes, whereas others in the Southern Hemisphere are associated with both lotic and standing warm waters (Cranston & Epler 2013: 68). Some regional publications include identification keys to species, but no comprehensive key including all Afrotropical species exists.

Lepidopelopia **Harrison** (Tanypodinae)**.** A monotypic genus, with the single species, *L. annulator* (Goetghebuer, 1935), known from Democratic Republic of Congo, Ghana and Tanzania (Ashe & O'Connor 2009: 171). It is the only described genus of Tanypodinae with scale-like setae (Harrison 1970), which otherwise are known from few other chironomid genera. The biology and immature stages remain unknown. See Fig. 9 for an example of the wing of the genus and Fig. 57 for the male terminalia.

Lepidopodus **Freeman** (Chironominae: Chironomini)**.** An endemic monotypic genus, erected for *L. nigratipes* (Kieffer, 1911), known only from the female holotype collected on Mahé Is. in Seychelles (Freeman 1958: 326; Sæther 2004). The genus is nevertheless included in the key above, as the legs of the unknown male are expected to carry both, scales and setae as in the female. The biology and immature stages remain unknown.

Lerheimia **Andersen & Sæther** (Orthocladiinae)**.** An endemic genus, erected based on *L. scopulata* Andersen & Sæther, 1993, from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen & Sæther 1993*b*). Three additional species are known, *L. aviculata* Andersen & Sæther, 1993 and *L. villangulata* Andersen & Sæther, 1993, both from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania and *L. wulfi* (Freeman, 1956) from Democratic Republic of Congo. The biology and immature stages remain unknown. An identification key to adult males was provided by Andersen & Sæther (1993*b*).

Limnophyes **Eaton** (Orthocladiinae)**.** A genus of 93 named species that occurs in all zoogeographical regions, except the Oceanian Region (Ashe & O'Connor 2012: 336). Four species are known from the Afrotropical Region: *L. bubo* Sæther, 1990 recorded from Uganda; *L. lobiscus* Sæther, 1990 from Kenya and Uganda; *L. minimus* (Meigen, 1818) a virtually cosmopolitan species, recorded from Ethiopia, Kenya, South Africa



109 *Ablabesmyia*

110 *Chironomus*

111 *Pseudosmittia*

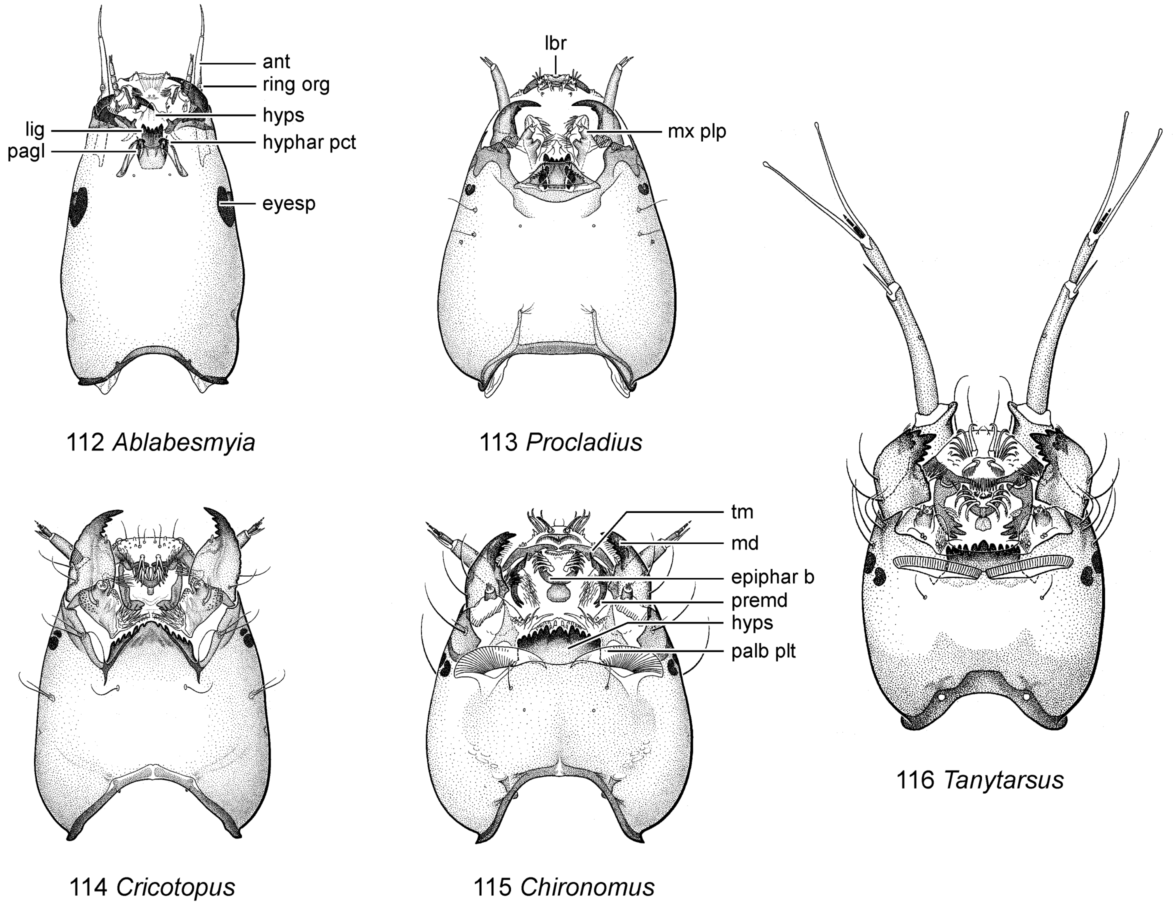
Figs 35.109–111. Larval habitus of Chironomidae (lateral views) (all non-Afrotropical): (109) *Ablabesmyia* sp.; (110) *Chironomus* sp.; (111) *Pseudosmittia* sp. Figs 109–111 (Oliver 1981, figs 114–116).

and Gough, Inaccessible and Nightingale Is. in the South Atlantic; and *L. natalensis* (Kieffer, 1914) from the Nearctic and Palaearctic Regions and from Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Rwanda, South Africa, Sudan, Uganda and Zimbabwe in the Afrotropics. Larvae are found in many aquatic, semi-terrestrial and terrestrial habitats (Andersen *et al.* 2013*b*: 231). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 230) and Coffman *et al.* (1986: 183), respectively. The immatures of *L. minimus* and *L. natalensis* were described by Sæther (1990). See Fig. 39 for an example of the wing of the genus and Fig. 77 for the male terminalia. An identification key to adult males was provided by Sæther (1990).

Lobosmittia **Sæther & Andersen** (Orthocladiinae)**.** A genus of three named species that occurs in the Afrotropical, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 363). The genus was erected based on *L. basilobata* Sæther & Andersen, 1993, from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Sæther & Andersen 1993). The biology and immature stages remain unknown.

Lunditendipes **Harrison** (Chironominae: Chironomini)**.** An endemic monotypic genus, with the single species, *L. tropicus* Harrison, 2000, recorded from tropical and subtropical regions of north-eastern South Africa and Zimbabwe (Harrison 2000). The biology and immature stages remain unknown.

Macropelopia **Thienemann** (Tanypodinae)**.** A genus of 18 named species that occurs in all zoogeographical regions, except Antarctica and Australasia. Cranston & Epler (2013: 39) incorporated *Bethbilbeckia* Fittkau & Murray as a subgenus of *Macropelopia*. Thus, the genus is now divided into two subgenera, but only *Macropelopia sensu stricto* occurs in the Afrotropical Region, with the single described species, *M.* (*M.*) *marmorata* (Freeman, 1955), from the Western Cape Province,



112 *Ablabesmyia*

113 *Procladius*

114 *Cricotopus*

115 *Chironomus*

116 *Tanytarsus*

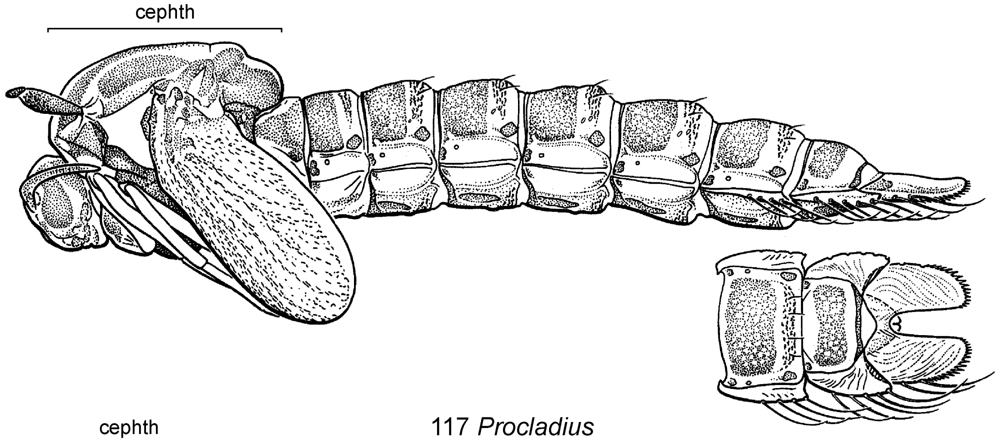
Figs 35.112–116. Larval head capsules of Chironomidae (all non-Afrotropical): (112) head capsule of *Ablabesmyia* sp., ventral view; (113) same, *Procladius* sp.; (114) same, *Cricotopus* sp.; (115) same, *Chironomus* sp.; (116) same, *Tanytarsus* sp. Figs 112–116 (Oliver 1981, figs 117, 118, 122, 119, 120 (as *Micropsectra*), respectively).

Abbreviations: ant – antenna; epiphar b – epipharyngeal bar; eyesp – eye spot; hyphar pct – hypopharyngeal pecten; hyps – hypostoma; lbr – labrum; lig – ligula; md – mandible; mx plp – maxillary palpus; pagl – paraglossa; palb plt – paralabial plate; premd – premandible; ring org – ring organ; tm – torma.

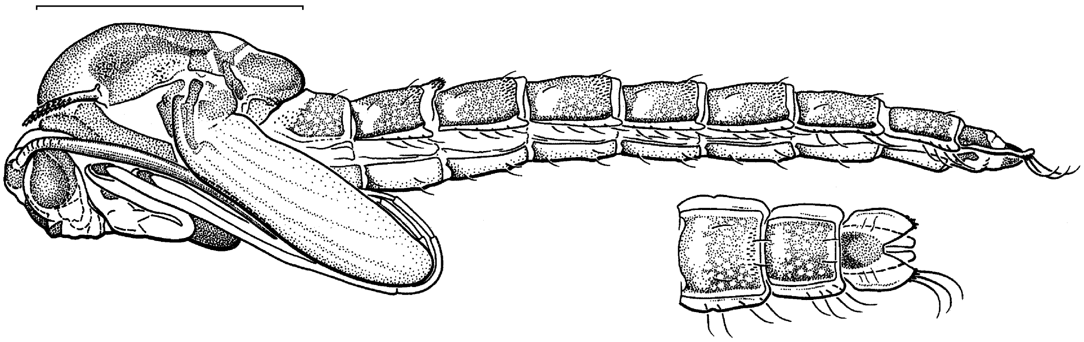
South Africa (Ashe & O'Connor 2009: 174). Larvae of *Macropelopia* occur in fine sediments in cool water bodies (springs, brooks, lakes and bogs) (Cranston & Epler 2013: 54). The immature stages of *M.* (*M.*) *marmorata* remain unknown.

***Madachironomus* Andersen** (Chironominae: Pseudochironomini)**.** An endemic genus from Madagascar with two known species (Andersen 2016). The biology and immature stages remain unknown. See Fig. 29 for an example of the wing of the genus and Fig. 95 for the male terminalia.

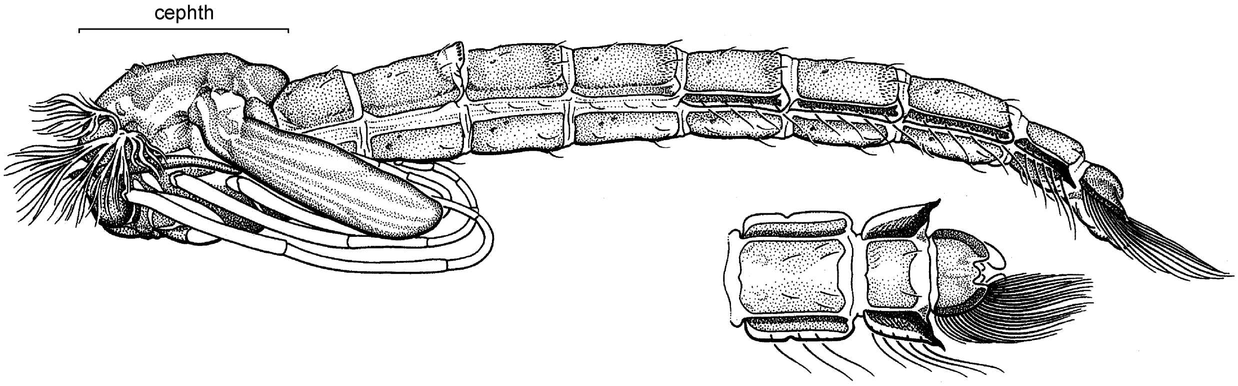
***Manoa* Fittkau** (Chironominae: Pseudochironomini)**.** The genus is one of two Afrotropical genera in the tribe Pseudochironomini, which may be redefined according to recent



117 *Procladius*



118 *Orthocladius*



119 *Chironomus*

Figs 35.117–119. Pupal habitus of Chironomidae (lateral views) (all non-Afrotropical), with enlargements of terminalia (dorsal views): (117) *Procladius* sp.; (118) *Orthocladius* sp.; (119) *Chironomus* sp. Figs 117–119 (Oliver 1981, figs 138, 140, 139, respectively).

Abbreviation: cephth – cephalothorax.

works (*e.g.*, Epler *et al.* 2013). *Manoa* was erected based on the single species, *M. obscura* Fittkau, 1963, from the Amazon region of South America (Fittkau 1963). Two additional species have been described: *M. tangae* Andersen & Sæther, 1997 from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen & Sæther 1997) and *M. pahayokeensis* Jacobsen, 2002 from the Nearctic Region (Jacobsen & Perry 2002). Adults of *M. tangae* Andersen & Sæther, 1997 are morphologically very similar to those of *M. obscura*, but can be differentiated by characters of the head and thorax (Andersen & Sæther 1997). The biology and immature stages of *M. tangae* remain unknown. See Fig. 96 for an example of the male terminalia of the genus.

***Mesocricotopus* Brundin** (Orthocladiinae)**.** A genus of two named species that occurs in the Afrotropical, Nearctic and Palaearctic Regions (Ashe & O'Connor 2012: 367). The genus is recorded from the Afrotropical Region based on unidentified larvae from lakes and streams in the Eastern Cape Province, South Africa (Harrison 2004*b*). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 232) and Coffman *et al.* (1986: 185), respectively.

***Mesosmittia* Brundin** (Orthocladiinae)**.** A genus of 18 named species that occurs in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 368). Three species are known from the Afrotropics: *M. cristaga* Sæther, 1996 recorded from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania; *M. nigerrima* (Kieffer, 1918) from Democratic Republic of Congo, Ethiopia and South Africa; and *M. patrihortae* Sæther, 1986, a virtually cosmopolitan species, recorded from South Africa in the Afrotropical Region. The immatures are considered to be terrestrial (Andersen *et al.* 2013*b*: 233); a generic diagnosis for larva was provided by Andersen *et al.* (2013*b*: 233). An identification key to Afrotropical species is unavailable.

***Metriocnemus* Wulp** (Orthocladiinae)**.** A genus of 75 named species that occurs in all zoogeographical regions, except Oceania and Antarctica (Ashe & O'Connor 2012: 371). Six species are known from the Afrotropical Region, all in the subgenus *Metriocnemus sensu stricto*. Larvae occur in mosses, phytotelmata, springs, ditches, streams and lakes and a few species are hygropetric (Andersen *et al.* 2013*b*: 234). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 233) and Coffman *et al.* (1986: 186), respectively. An identification key to adult males of most Afrotropical species was provided by Freeman (1956: 294).

***Microchironomus* Kieffer** (Chironominae: Chironomini)**.** A genus of 13 named species that occurs in the Afrotropical, Australasian and Oriental Regions and the Holarctic Realm. Three species are recorded from the Afrotropics: *M. deribae* (Freeman, 1957) from Chad, Ethiopia, Kenya, Sudan and the Palaearctic Region; and *M. lendli* (Kieffer, 1918) and *M. tener* (Kieffer, 1918), both widespread in the Afrotropical, Oriental, Palaearctic and Australasian/Oceanian Regions. The immature stages of all three species are known (*e.g.*, Epler *et al.* 2013; Kugler 1971; Langton & Visser 2003 (*M. lendli* as *Leptochironomus stilifer*); Pagast 1931 (*M. tener* as *Chironomus* (*Leptochironomus*) *balticus*)). Larvae of *M. deribae* are known to inhabit saline lakes, but several other larval types have been recorded in Lake Awasha, Ethiopia (Harrison 1996). An identification key to known adult males of Afrotropical species was provided by Yan & Wang (2006).

***Microtendipes* Kieffer** (Chironominae: Chironomini)**.** A genus of 55 named species that occurs in the Afrotropical, Australasian and Oriental Regions (with an unnamed species reported from the Neotropics) and in the Holarctic Realm (Xin *et al.* 2012). Thirteen Afrotropical species are recorded. For some of these, generic placement remains uncertain (Epler *et al.* 2013: 423). The immature stages of *M. lentiginosus* Freeman, 1955 were described by Amakye & Sæther (1992). An identification key to adult males of the majority of Afrotropical species was provided by Freeman (1958: 311), the remaining species were described by Freeman (1961) or Lehmann (1979, 1981).

***Molleriella* Sæther & Ekrem** (Orthocladiinae)**.** A genus of two named species that occurs in the Afrotropical and Palaearctic Regions. The genus was erected based on *M. calcarella* Sæther & Ekrem, 1999 from the Netherlands in the Palaearctic (Sæther & Ekrem 1999). The record from the Afrotropical Region is based on the recently described, *M. kaputu* Andersen, 2014, from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen 2014). The immature stages remain unknown, but the larva of the European species is considered to be terrestrial (Sæther & Ekrem 1999).

***Monopelopia* Fittkau** (Tanypodinae)**.** Cranston & Epler (2013: 39) reduced *Cantopelopia* Roback (only known from the Afrotropical and Nearctic Regions), to a subgenus of *Monopelopia*, which was later supported by Silva & Ekrem (2016). Both subgenera occur in the Afrotropics, *Monopelopia sensu stricto*, with one described species, *M.* (*M.*) *pavida* Harrison, 1978 from Nigeria and Sudan; and the subgenus *M.* (*Cantopelopia* Roback), with two species, *M.* (*C.*) *meilloni* (Freeman, 1955) from Benin, Democratic Republic of Congo, Niger, Senegal, South Africa and Zimbabwe and *M.* (*C.*) *robacki* Lehmann, 1979 from Democratic Republic of Congo. Additionally, one undescribed species of each subgenus is documented from South Africa and Tanzania, respectively (Figs 58, 59). Larval habitats of *Monopelopia* include small to very small pools of boggy acid water, ponds, creeks, sub-coastal pools and phytotelmata (in the water of bromeliad plants and tree holes) (Cranston & Epler 2013: 69). The immature stages of Afrotropical species remain unknown. An identification key to all Afrotropical species is unavailable, but some species were keyed in regional publications.

***Nanocladius* Kieffer** (Orthocladiinae)**.** A genus of 37 named species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 390). Seven species are known from the Afrotropical Region, all in the subgenus *Nanocladius sensu stricto.* Larvae of this subgenus occur in streams, rivers, lakes and ponds and some are symphoretic on immature Corydalidae (Megaloptera) (Andersen *et al.* 2013*b*: 235). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 234) and Coffman *et al.* (1986: 187), respectively. The larva and pupa of *N.* (*N.*) *saetheri* Harrison, 1994 are described, recorded from Ethiopia and South Africa. Pupae of *N.* (*N.*) *jannae* Lehmann, 1979 and *N.* (*N.*) *ortosi* Lehmann, 1979, are described, both recorded from Democratic Republic of Congo and Ethiopia and *N.* (*N.*) *acutus* Lehmann, 1981, recorded from Democratic Republic of Congo (Harrison 1994; Lehmann 1979, 1981). See Fig. 43 for an example of the head of the genus. Identification keys to adults of Afrotropical species were provided by Harrison (1994).

***Neostempellina* Reiss** (Chironominae: Tanytarsini)**.** A genus of six described species that occurs in the Afrotropical and Oriental Regions and the Holarctic Realm. The two species recorded from the Afrotropics, *N. abnormis* (Lehmann, 1981) and *N. saetosa* (Lehmann, 1981), are unusual in having long microtrichia between the ommatidia of the adult eye ("hairy" appearance). Both species were originally described, in the genus *Tanytarsus*, from a stream near Kisangani in Democratic Republic of Congo (Lehmann 1981). All known larvae (Holarctic Realm only) occur in streams and springs and construct transportable cases, which are strongly curved. See Fig. 30 for an example of the wing of the genus. An identification key to adult males was provided by Guo & Wang (2004), but does not include *N. saetosa*.

***Neozavrelia* Goetghebuer & Thienemann** (Chironominae: Tanytarsini)**.** A genus of 26 described species that occurs in all zoogeographical regions, except the Neotropics, Oceania and Antarctica (Ekrem 2006; Giłka 2012). It was previously unknown from the Afrotropical Region, but material has been examined of three adult males of an undescribed species from Malawi (Figs 31, 100). The immature stages of the Afrotropical representative are unknown; other species are known to inhabit streams, rivers, lakes, peat pits, hygropetric situations or hot springs (Epler *et al*. 2013: 449).

***Nidnurbia* Säwedal** (Chironominae: Tanytarsini)**.** An endemic monotypic genus, with the single named species, *N. capicola* (Freeman, 1955), described from the Cape Province, South Africa (Säwedal 1982). The immature stages remain unknown, but an unassociated pupal exuviae collected at the type locality has been examined that resembles those in the genus *Micropsectra*. Given that *Micropsectra* has not been recorded from the Afrotropical Region, this specimen may represent *N. capicola*.

***Nilodosis* Kieffer** (Chironominae: Chironomini)**.** A genus of two formally described species that occur in West and Central Africa, but with several unnamed forms from the Australasian, Neotropical and Oriental Regions (Tang & Yamamoto 2012). The two Afrotropical species, *N. fusca* Kieffer, 1922, recorded from Benin, Burkina Faso, Democratic Republic of Congo, Guinea, Nigeria, Sudan, Togo, Uganda and Zimbabwe, and *N. grisea* Freeman, 1957 from Democratic Republic of Congo, were revised by Cranston & Spies (1999). The immature stages inhabit lakes and lentic areas in rivers, but do not occur in mesotrophic or eutrophic situations (Cranston & Spies 1999).

***Nilomyia* Kieffer** (Chironominae: Chironomini). A monotypic genus, with the single named species, *N. aculeata* Kieffer, 1921, originally described from Sudan and later recorded from Senegal, as well as from North Africa, the Near East and Romania in the Palaearctic Region (Dejoux 1976; Sæther & Spies 2013). The pupa and larva are known, but undescribed (M. Spies, pers. comm. 2015); the biology remains unknown.

***Nilotanypus* Kieffer** (Tanypodinae)**.** A genus of nine named species that occurs in all zoogeographical regions, except Oceania and Antarctica. Two species occur in the Afrotropics, *N. comatus* (Freeman, 1953) from Burkina Faso, Chad, Democratic Republic of Congo, Ethiopia, Guinea, Madagascar, Mali, Nigeria, Senegal, South Africa, Togo, Uganda and Zimbabwe and *N. remotissimus* Kieffer, 1923 from Sudan (Ashe & O'Connor 2009: 185). The larva and pupa of one of these, *N. comatus*, was described by Harrison (1991) from stony torrents of rivers in Ethiopia. Larvae of *Nilotanypus* inhabit flowing waters, especially with sandy beds (Cranston & Epler 2013: 70). See Fig. 10 for an example of the wing of the genus and Fig. 60 for the male terminalia.

***Nilothauma* Kieffer** (Chironominae: Chironomini)**.** A genus of 44 named species that occurs in all zoogeographical Regions, except Antarctica (Mendes & Andersen 2009). The genus was revised relatively recently (Adam & Sæther 1999; Mendes & Andersen 2009); 11 species are recorded from the Afrotropical Region. Afrotropical species are known from running waters, while non-Afrotropical species occur in standing waters and springs (Adam & Sæther 1999). The immature stages of several species have been described. Identification keys to the known life stages of Afrotropical species were provided by Adam & Sæther (1999).

***Notocladius* Harrison** (Orthocladiinae)**.** An endemic monotypic genus, erected based on *N. capicola* Harrison, 1997, from the Western Cape Province, South Africa (Harrison 1997). The larvae and pupae may occur in vast numbers on the surface of stones and rocks in the fast current in second and third order mountain streams and rivers and were described by Harrison (1997).

***Orthocladius* Wulp** (Orthocladiinae)**.** A genus of 150 named species that occurs in the Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 410). Six subgenera are recognised, but all ten named species known from the Afrotropical Region are unplaced. Willassen & Cranston (1986), however, recorded the larva of an unnamed species belonging to the subgenus *O.* (*Eudactylocladius* Thienemann) from Mount Kenya. The larvae and pupae (Fig. 117) inhabit all types of flowing waters, lakes, ponds, swamps and moist earth and some species also mine submerged wood (Andersen *et al*. 2013*b*: 239). Generic diagnoses for the larva and pupa were provided by Andersen *et al*. (2013*b*: 238) and Coffman *et al*. (1986: 189), respectively. See Fig. 44 for an example of the head of the genus. An identification key to males of Afrotropical species was provided by Freeman (1953: 331), but most of the species regarded by Freeman as belonging to *Orthocladius* are now ascribed to other genera.

***Pagastiella* Brundin** (Chironominae: Chironomini)**.** A genus of two named species that occurs in the Palaearctic and Nearctic Regions. There are no formally named species recorded from the Afrotropical Region, but the genus has been recorded and a *P.* "sp. A" was described from a damaged male from KwaZulu-Natal Province, South Africa (Harrison 2001). Immature stages from other zoogeographical regions are known to inhabit the littoral and sublittoral of lakes and slow-flowing rivers; those of the Afrotropical species have not been described.

***Parachironomus* Lenz** (Chironominae: Chironomini)**.** A genus of 72 named species that occurs in all zoogeographical regions, except Antarctica. Six species are recorded from the Afrotropical Region, but some of these may well belong to other (established or undescribed) genera, as they do not fit the current diagnosis for *Parachironomus* that is based largely on Holarctic forms. One of these species, the widespread Afrotropical *P. unicalcar* (Freeman, 1957), was fixed as the type species of *Kribiocryptus* Kieffer, 1921 under its earlier but invalid name *K. flaviventris* Kieffer, 1921. The inclusion of *K. unicalcar* in *Parachironomus* possess an unresolved nomenclatural problem, as it renders this genus name invalid as a junior synonym of *Kribiocryptus*. The immature stages of *K. unicalcar* are known, but undescribed (for a sketch of the pupa, see Dejoux *et al.* 1983). Diagnosing *Kribiocryptus*, as opposed to *Parachironomus*, would be relatively easy for the adult male and pupa, but problematic for the larva (M. Spies, pers. comm. 2015). *Parachironomus* larvae are associated with standing and flowing waters of different types. Some occur in association with Bryozoa, as ectoparasites on other invertebrates, or mine submerged stems and leaves (Epler *et al*. 2013: 426). Harrison (1996) described an unnamed larva from Lake Awasa, Ethiopia. See Fig. 32 for an example of the wing of the genus and Fig. 101 for the male terminalia (note that the figured species (*P. acutum*) is far from "typical" for *Parachironomus*, especially concerning the male hypopygium and may have to be placed in another genus). Identification keys to adult males of all Afrotropical species, except *P. nigrofasciatus* (Freeman, 1961), were provided by Freeman (1958: 384), within his very broadly defined subgenus *Chironomus* (*Cryptochironomus*).

***Paracladopelma* Harnisch** (Chironominae: Chironomini)**.** A poorly defined, probably not monophyletic genus of 48 named species recorded from all zoogeographical regions, except the Neotropics, Oceania and Antarctica. Five species occur in the Afrotropical Region, but as in *Parachironomus* (see above), some are likely to not be retained in *Paracladopelma* following a thorough revision. Larvae are most often associated with sandy substrata in lakes, streams and small rivers (Epler *et al*. 2013). Immature stages of Afrotropical species remain undescribed. An identification key to adult males was provided by Yan *et al.* (2008*c*), but should be used with caution as it includes a number of species belonging to different genera and misinterprets a number of critical morphological data.

***Paradoxocladius* Harrison** (Orthocladiinae)**.** An endemic monotypic genus, erected based on *P. mangoldi* Harrison, 2000 from the KwaZulu-Natal Province, South Africa. The immature stages occur in the upper, stony reaches of rivers and were described by Harrison (2000).

***Parakiefferiella* Thienemann** (Orthocladiinae)**.** A genus of 43 named species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 457). Four species are known from the Afrotropical Region (Ferrington & Sæther 1995: 369): *P. biloba* (Freeman, 1953) recorded from South Africa and Zimbabwe; *P. ephippium* (Freeman, 1956) recorded from Benin and South Africa; *P. harrisoni* (Freeman, 1956) recorded from South Africa and Sudan; and *P. minax* Ferrington & Sæther, 1995 recorded from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania. Larvae are found most frequently in standing waters although some species also inhabit running waters (Andersen *et al.* 2013*b*: 242). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 242) and Coffman *et al.* (1986: 192), respectively. The pupa of *P. ephippium* was described by Lehman (1979). See Fig. 81 for an example of the male terminalia of the genus. An identification key to all Afrotropical species is unavailable.

***Paralauterborniella* Lenz** (Chironominae: Chironomini)**.** A genus of two named species: *P. nigrohalteralis* (Malloch, 1915), which is widely distributed in the Holarctic Realm and reported from the Afrotropical and Neotropical Regions, and *P. manii* (Maheshwari & Maheshwari, 2002) from India in the Oriental Region. In the Afrotropics, *P. nigrohalteralis* has been recorded from Namibia and South Africa (Harrison 2001). Its larvae are known from soft sediments in the littoral of lakes (Epler *et al.* 2013), but probably also occur in flowing waters (Harrison 2001; Spies *et al.* 2009).

***Parametriocnemus* Goetghebuer** (Orthocladiinae)**.** A genus of 35 named species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 469). Three species are known from the Afrotropical Region: *P. capensis* (Freeman, 1954) recorded from South Africa and Togo; *P. fordi* (Freeman, 1956) from Uganda; and *P. scotti* (Freeman, 1953) from Ethiopia, Kenya, Madagascar, South Africa, Uganda, Zambia and Zimbabwe. Larvae occur in springs, streams and rivers (Andersen *et al.* 2013*b*: 244). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 243) and Coffman *et al.* (1986: 194), respectively. The pupa of *P. scotti* was described and figured by Lehmann (1979). See Fig. 21 for an example of the wing of the genus. The three Afrotropical species were keyed by Freeman (1956: 294), as *Metriocnemus*.

***Paraphaenocladius* Thienemann** (Orthocladiinae)**.** A genus of 25 named species that occurs in all zoogeographical regions, except Australasia and Antarctica (Ashe & O'Connor 2012: 476). Three species are known from the Afrotropical Region: *P. crassicaudatus* Sæther & Wang, 1995 recorded from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania; *P. cuneipennis* (Freeman, 1961) from Madagascar; and *P. dewulfi* (Goetghebuer, 1936) from Saudi Arabia and from Democratic Republic of Congo, South Africa, Tanzania and Zimbabwe. Most larvae are reported to be terrestrial, inhabiting meadows and damp soil near springs. Semi-aquatic or perhaps truly aquatic species occur in springs and streams (Andersen *et al.* 2013*b*: 244). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 244) and Coffman *et al.* (1986: 194), respectively. An identification key to adult males was provided by Sæther & Wang (1995).

***Paratanytarsus* Thienemann & Bause** (Chironominae: Tanytarsini)**.** A genus of *ca* 52 named species that occurs in all zoogeographical regions, except Antarctica, but is most diverse in the Holarctic Realm. The only species known from the Afrotropical Region is the parthenogenetic and virtually cosmopolitan *P. grimmii* (Schneider, 1885); its larvae inhabit standing waters and frequently infest water supply systems (Langton *et al*. 1988), and *Paratanytarsus praecellens* Giłka, 2009 from the United Arab Emirates (Giłka 2009).

***Paratendipes* Kieffer** (Chironominae: Chironomini)**.** A genus of 38 named species that occurs in the Afrotropical and Oriental Regions and the Holarctic Realm (Qi *et al.* 2009). Six species are known from the Afrotropical Region. Larvae occur on soft sediments and sandy bottoms in running and standing waters (Epler *et al.* 2013). The immature stages of Afrotropical species have not been described, but an identification key to adult males was provided by Freeman (1957: 420).

Paratrissocladius **Zavřel** (Orthocladiinae)**.** A genus of three named species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 494). Two species are reported from the Afrotropical Region, *P. excerptus* (Walker, 1856) recorded from the Palaearctic and Oriental Regions, with an uncertain record from Senegal in the Afrotropical Region and *P. natalensis* (Freeman, 1956) recorded from South Africa. Larvae occur in sand and mud in streams and rivers, where they build long tubes of sand and detritus (Andersen *et al.* 2013*b*: 246). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 246) and Coffman *et al.* (1986: 196), respectively.

Parorthocladius **Thienemann** (Orthocladiinae)**.** A genus of seven named species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 495). The genus is recorded from the Afrotropical Region by Cranston *et al*. (1983: 190), but without any named species. Larvae inhabit small bodies of flowing waters, including springs and shallow bodies of still water (Andersen *et al.* 2013*b*: 247). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 247) and Coffman *et al.* (1986: 197), respectively.

Phaenopsectra **Kieffer** (Chironominae: Chironomini)**.** A genus of 11 named species that occurs in all zoogeographical regions, except the Oriental and Australasian Regions and Antarctica. The widely distributed *P. flavipes* (Meigen, 1818) has been reported from the Afrotropical Region (Democratic Republic of Congo), although with slight morphological differences from European specimens (Lehmann 1981). The larvae of *P. flavipes* are eurythermic and eurytopic and are found in running as well as standing waters (Lehmann 1981).

Polypedilum **Kieffer** (Chironominae: Chironomini)**.** The largest genus of Chironomidae, with 501 described species that occurs in all zoogeographical regions, except Antarctica. Sæther *et al*. (2010) proposed the division the genus into nine subgenera, but did not provide complete, workable diagnoses and left several critical taxa formally invalid by failing to meet the requirements of the International Code of Zoological Nomenclature (ICZN 1999). Eight of these putative subgenera have representatives in the Afrotropics, but only those not labelled with asterisks in the following list are recognised as valid, using diagnoses established prior to Sæther *et al*. (2010): *Polypedilum sensu stricto*, *P.* (*Cerobregma* Sæther & Sundal), *P.* (*Kribionympha* Kieffer*), *P.* (*Pentapedilum* Kieffer), *P.* (*Probolum* Andersen & Sæther*), *P.* (*Tripedilum* Kieffer*), *P.* (*Tripodura* Townes) and *P.* (*Uresipedilum* Oyewo & Sæther). A total of 85 Afrotropical species are named, including two that are unassigned to subgenera (*P. alticola* Kieffer, 1911 and *P. fuscum* Freeman, 1954). *Polypedilum* larvae are known from virtually all kinds of standing and flowing waters. The larvae of at least one species, *P.* (*P.*) *vanderplanki* Hinton, 1951, inhabit temporary pools and are capable of surviving desiccation, even for years (see "Biology and immature stages" section above) (Epler *et al*. 2013: 432). A second Afrotropical species assumed to be desiccation tolerant is *P.* (*P.*) *ovahimba* Cranston, 2014, recently described in all life stages from rock pools on the Waterberg Plateau, Namibia (Cranston 2014). See Figs 33, 34 for examples of wings of the genus, Fig. 42 for the thorax, Fig. 48 for tarsomere 5 and claws and Figs 102–105 for the male terminalia. Useful identification keys to a number of Afrotropical species in various subgenera were provided by Oyewo & Sæther (1998), Sæther & Oyewo (2008), Sæther & Sundal (1998) and Vårdal *et al.* (2002).

Procladius **Skuse** (Tanypodinae)**.** The second most speciose genus of Tanypodinae, with 69 described species that occur in all zoogeographical regions, except Antarctica. The eight named Afrotropical species belong to the three recognised subgenera, *P.* (*Holotanypus* Roback) with three, *Procladius sensu stricto* with four and *P.* (*Psilotanypus* Kieffer) with one species (Ashe & O'Connor 2009: 59). Adult males of the three subgenera can be separated on characters of the male terminalia, namely the absence or presence of a posterior "heel" on the gonostylus and/or inner lobe of the gonocoxite. Harrison (1991) described larval and some pupal features (from a prepupal larva) of one species, *P.* (*H.*) *brevipetiolatus* (Goetghebuer, 1935) from lakes in Ethiopia. Larvae (Fig. 113) and pupae (Fig. 118) of the majority of *Procladius* species prefer muddy substrata of standing or slow-flowing water bodies, especially ponds and small lakes, but a few species also inhabit the profundal zone of large, deep lakes (Cranston & Epler 2013: 56). A revision of the genus is urgently required, but evidence of seasonal and environmental polymorphism makes this problematic, with a combined molecular and morphological study being essential to resolve specific boundaries.

Psectrocladius **Kieffer** (Orthocladiinae)**.** A genus of 63 named species that occurs in all zoogeographical regions, except Australasia, Oceania and Antarctica (Ashe & O'Connor 2012: 507). One species in the subgenus *Psectrocladius sensu stricto*, (*P.* (*P.*) *viridescens* Freeman, 1953), is recorded from South Africa and Zimbabwe in the Afrotropical Region (Freeman 1953) and a second species (*P.* (*P.*) *limbatellus* (Holmgren, 1869)), occurs in the Nearctic and Palaearctic Regions, extending southwards into United Arab Emirates in the Arabian Peninsula (Andersen & Mendes 2010: 575). Larvae are eurytopic (Andersen *et al.* 2013*b*: 251). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 250) and Coffman *et al.* (1986: 199), respectively. See Fig. 46 for an examples of tarsomere 5 and claws of the genus and Fig. 85 for the male terminalia.

Psectrotanypus **Kieffer** (Tanypodinae)**.** A genus of seven described species that occurs in the Afrotropical and Oriental Regions and the Holarctic Realm, while confirmation of a record from the Neotropical Region is required. The one Afrotropical species, *P. schwetzi* (Freeman, 1955) is reported from Burundi, Rwanda and Uganda (Ashe & O'Connor 2009: 220). Larval *Psectrotanypus* occur in ponds, bogs, small bodies of water and slow-flowing streams; some species appear pollution tolerant and one species is associated with elevated salinity in coastal rock pools (Cranston & Epler 2013: 58). Immature stages of the Afrotropical *P. schwetzi* remain unknown. See Fig. 38 for an example of the thorax of the genus. Some species were keyed in regional publications and *P. schwetzi* can be identified from the description in Freeman (1955).

Pseudorthocladius **Goetghebuer** (Orthocladiinae)**.** A genus of 57 described species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 529). Two species, both belonging to subgenus *Pseudorthocladius sensu stricto*, *P.* (*P.*) *bernadetti* Lehmann, 1979 recorded from Democratic Republic of Congo and *P.* (*P.*) *similis* Freeman, 1953, from Democratic Republic of Congo, Senegal and

South Africa are known from the Afrotropical Region. Larvae occur in mosses, the margins of spring-fed streams and in hygropetric situations (Andersen *et al.* 2013*b*: 252). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 251) and Coffman *et al.* (1986: 201), respectively.

***Pseudosmittia* Edwards** (Orthocladiinae)**.** A genus of 102 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 539). Seventeen species are known from the Afrotropical Region (Ferrington & Sæther 2011): *P. danconai* (Marcuzzi, 1947) distributed in the Afrotropical, Nearctic and Palaearctic Regions and recorded from United Arab Emirates in the Arabian Peninsula (Andersen & Mendes 2010: 576). Most larvae appear to be semi-terrestrial to semi-aquatic (Andersen *et al.* 2013*b*: 253). In the Afrotropical Region, only the larva and pupa of *P. danconai* are known: those of extralimital species were described by Ferrington & Sæther (2011). An identification key to species was provided by Ferrington & Sæther (2011).

***Rheocricotopus* Brundin** (Orthocladiinae)**.** A genus of 74 described species that occurs in all zoogeographical regions, except Oceania and Antarctica (Ashe & O'Connor 2012: 558). Three species are known from the Afrotropical Region, all belonging to the subgenus *R.* (*Psilocricotopus* Sæther): *R.* (*P.*) *capensis* (Freeman, 1953) recorded from Democratic Republic of Congo, Ethiopia, Lesotho, South Africa, Tanzania, Togo and Zimbabwe; *R.* (*P.*) *cereofasciatus* (Goetghebuer, 1934) recorded from Democratic Republic of Congo, Madagascar and Zimbabwe; and *R.* (*P.*) *metallescens* (Goetghebuer, 1934) recorded from Cameroon, Chad, Democratic Republic of Congo, Nigeria, Sierra Leone and Sudan. Larvae occur on plants and stones in streams and rivers and are found rarely in the littoral zone of lakes (Andersen *et al.* 2013*b*: 254). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 254) and Coffman *et al.* (1986: 203), respectively. The pupa of *R.* (*P.*) *capensis* was described and figured by Lehmann (1979).

***Rheotanytarsus* Thienemann & Bause** (Chironominae: Tanytarsini)**.** A genus of 107 described species that occurs in all zoogeographical regions, except Antarctica. Twenty-one known species occur in the Afrotropical Region, many of which were described or re-described relatively recently (Harrison 2004*a*; Kyerematen & Sæther 2000). Larvae are rheobionts and typically filter-feed on particles in the drift, using self-spun nets suspended on projections from their characteristic cases. Immature stages of several Afrotropical species have been described (Harrison 2004*a*; Kyerematen & Sæther 2000; Lehmann 1979). Identification keys to known life stages of all Afrotropical species, except *R. shebelensis* Harrison, 2004, were provided by Kyerematen & Sæther (2000).

***Robackia* Sæther** (Chironominae: Chironomini)**.** A genus of five named and several undescribed species that occurs in all zoogeographical regions, except Oceania, Australasia and Antarctica. The collections of the Zoologische Staatssammlung München (Germany) hold numerous specimens of various life stages from a number of Afrotropical countries; this material was identified as *Robackia* and sorted to several species by F. Reiss, but no descriptions have yet been published (M. Spies, pers. comm. 2015). In the Holarctic Realm, larvae occur on sandy substrates in rivers and streams and the littoral of lakes (Epler *et al*. 2013: 433).

***Semiocladius* Sublette & Wirth** (Orthocladiinae)**.** A genus of six described species that occurs in the Afrotropical, Australasian, Oceanian and Palaearctic Regions (Ashe & O'Connor 2012: 581). A single species is known from the Afrotropics, *S. brevicornis* (Tokunaga, 1964), recorded from Australasia and Oceania and from Seychelles in the Afrotropical Region (Sæther 2004). Larvae occur in the marine intertidal zone and splash zone pools above the high tide level, as well as the mid-tidal section of an estuary (Andersen *et al.* 2013*b*: 256). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 256) and Coffman *et al.* (1986: 206), respectively.

***Seppia* Ekrem & Sæther** (Chironominae: Tanytarsini)**.** An endemic monotypic genus, with the single species, *S. trifurca* Ekrem & Sæther, 2000, recorded from Ankasa Game Production Reserve in western Ghana (Ekrem & Sæther 2000: 79). Adults are minute, with a wing length of less than 0.7 mm. See Fig. 106 for a figure of the male terminalia of the genus. The biology and immature stages remain unknown.

***Skusella* Freeman** (Chironominae: Chironomini)**.** A genus of three formally described species that occurs in the Afrotropical, Australasian and Oriental Regions. Two species are known from the Afrotropics, *S. pallidipes* (Kieffer, 1921), widespread in West and Central Africa, and *S. freemani* Harrison, 2002, from the Northern Province, South Africa. Immature stages of Afrotropical species remain undescribed, but the larva and pupa of *S. subvittata* Freeman, 1961 from Australia and a *Skusella* larva from Thailand were described by Cranston (2010). Adults of *S. freemani* have been captured at light near permanent alkaline springs and spring riffles (Harrison 2001). Harrison (2001) provided a differential diagnosis for adults of the two Afrotropical species.

***Smittia* Holmgren** (Orthocladiinae)**.** A species-rich genus of 83 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 582). Eight named species are known from the Afrotropical Region. Most larvae are terrestrial, occurring in damp soil, but at least one species is aquatic (Andersen *et al.* 2013*b*: 257). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 256) and Coffman *et al.* (1986: 206), respectively. See Fig. 88 for an example of the male terminalia in the genus. No modern identification key that incorporates all valid species is available.

***Stempellina* Thienemann & Bause** (Chironominae: Tanytarsini)**.** A genus of 18 described species that occurs in all zoogeographical regions, except Antarctica (Epler *et al*. 2013: 452). Only *S. reissi* Lehmann, 1981, described from the adult male and pupa, is known from the Afrotropics. The species was collected in a stream near Kisangani, Democratic Republic of Congo (Lehmann 1981), but the larva and biology remain unknown.

***Stempellinella* Brundin** (Chironominae: Tanytarsini)**.** A genus of 19 described species that occurs in all zoogeographical regions, except Antarctica. The genus was revised and two species described from the Afrotropical Region by Ekrem (2007). *Stempellinella chambiensis* (Goetghebuer, 1935) apparently has a very wide distribution, mainly in the Southern Hemisphere (including the Afrotropical, Australasian and Neotropical Regions), while *S. truncata* (Freeman, 1958) has been recorded only from fast-flowing montane streams and small rivers in South Africa (Ekrem 2007). One possible additional species from Lake Tana, Ethiopia (Ashe *et al*. 1987) (on slide in Zoologische Staatssammlung München, Germany), has been identified (by T. Ekrem) as "*Stempellinella cf. edwardsi*". Immature stages of *S. chambiensis* and *S. truncata* are described (Ekrem 2007); identification keys to known life stages were provided by Ekrem (2007).

***Stenochironomus* Kieffer** (Chironominae: Chironomini)**.** A genus of 86 described species that occurs in all zoogeographical regions, except Antarctica. Twelve formally described species are known from the Afrotropical Region, none of which are placed in any of the subgenera established for Holarctic and Neotropical species (Borkent 1984). The larvae are obligate miners in living and dead immersed plant (including woody) material (Epler *et al*. 2013: 436). The larva and pupa of one Afrotropical species, *S. africus* Lehmann, 1981, are known (Lehmann 1981). See Fig. 35 for an example of the wing of the genus. An identification key to adult males of Afrotropical species, except *S. africus* and *S. unicalcar* Freeman, 1961, was provided by Freeman (1957: 410).

***Stictochironomus* Kieffer** (Chironominae: Chironomini)**.** A genus of 39 described species that occurs in all zoogeographical regions, except the Neotropics and Antarctica. Six species are recorded from the Afrotropics. Larvae occur on soft sediments in the profundal or on sandy bottoms in the littoral zone of mesotrophic to oligotrophic lakes, streams and slow-flowing rivers (Epler *et al*. 2013: 436; Harrison 1996). An identification key to adult males of Afrotropical species was provided by Freeman (1958: 305).

***Synendotendipes* Grodhaus** (Chironominae: Chironomini)**.** A genus of eight described species, seven of which occur in the Holarctic Realm. The single species that occurs in the Afrotropical Region, *S. woodi* (Freeman, 1957), was transferred from the genus *Endochironomus* (Ekrem & Stur 2016). The species appears to be widespread in the Afrotropics, with records from Burkina Faso, Ghana, Madagascar, Malawi, Nigeria, Senegal and Uganda. The immature stages and biology of *S. woodi* remain unknown. Holarctic species in the genus occur in standing and slow-flowing waters, where the larvae of at least some species are leaf-miners (Epler *et al*. 2013: 437).

***Synorthocladius* Thienemann** (Orthocladiinae)**.** A genus of eight described species that occurs in all zoogeographical regions, except Oceania and Antarctica (Ashe & O'Connor 2012: 610). *Synorthocladius lobiger* (Freeman, 1953), recorded from South Africa, is the only known species from the Afrotropical Region (Freeman 1953). The larvae inhabit both standing and flowing waters (Andersen *et al.* 2013*b*: 261). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 261) and Coffman *et al.* (1986: 210), respectively.

***Tanypus* Meigen** (Tanypodinae)**.** A genus of 31 described species that occurs in all zoogeographical regions, except Oceania and Antarctica. This genus is divided into two recognised subgenera. The five named species in the Afrotropics all belong to the subgenus *Tanypus sensu stricto*. The larvae occur in sediments in standing and slow-flowing waters, especially in temperate to warm regions, where they can tolerate high nutrient and salinity levels (Cranston & Epler 2013: 60). Immature stages of the Afrotropical species remain unknown. See Fig. 62 for an example of the male terminalia of the genus. No modern identification key that incorporates all valid species is available, but Freeman (1955: 48) keyed all Afrotropical species, except *T.* (*T.*) *complanatus* Sæther, 2004.

***Tanytarsus* Wulp** (Chironominae: Tanytarsini)**.** The second most species-rich genus in the subfamily Chironominae, with 358 described species represented in all zoogeographical regions, except Antarctica. Thirty-six named species are known from the Afrotropics, but five are regarded as doubtful, leaving 31 recognisable species. Several of these were described during the past 15 years (Ekrem 1999*b*, 2001; Ekrem & Harrison 1999; Ekrem & Stur 2007: 87; Harrison 2004*a*; Stur & Ekrem 2000). An identification key to species was provided by Ekrem (2001). *Tanytarsus* larvae (Fig. 116) have been found in a range of habitats from pristine freshwater springs to saline lakes.

***Telmatogeton* Schiner** (Telmatogetoninae)**.** A genus of 29 described species that occurs in all zoogeographical regions. Except for a few freshwater species from Hawaii, the genus mainly comprises species associated with the marine intertidal zone. Adults are able to fly, but do not swarm and pairs encounter and copulate on rocks in the splash zone (Cranston 1989: 19). Three species are known from the Afrotropical Region, two from South Africa (Wirth 1947) (*T. minor* (Kieffer, 1914) also from Namibia (Kirk-Spriggs *et al*. 2001)) and one species from Gough Is., Tristan da Cunha Is. and Inaccessible Is. (Sæther & Andersen 2011). The immature stages of *T. minor* and *T. sanctipauli* Schiner, 1866 have been described (Hesse 1934; Wirth 1947), while *T. goughi* Sæther & Andersen, 2011 remain unknown. See Fig. 13 for an example of the wing of the genus and Fig. 50 for the male terminalia. An identification key to Afrotropical Telmatogetoninae was provided by Kirk-Spriggs *et al*. (2001), but does not include *T. goughi*.

***Thalassomya* Schiner** (Telmatogetoninae)**.** A genus of 12 described species that occurs in all zoogeographical regions, except Antarctica. As with *Telmatogeton* species noted above, most *Thalassomya* species are associated with the marine intertidal zone (Cranston 1989: 19). Two species are recorded from the Afrotropics, with *T. reissi* Oliveira, 2000, described from inland Kenya (Amboseli National Park) (Oliveira 2000). Immature stages remain unknown, so it is unclear whether species of the genus inhabit fresh or local inland saline waters in the area. The other Afrotropical species, *T. africana* Edwards, 1926, was described from Dar es Salaam, Tanzania. An identification key to Afrotropical Telmatogetoninae was provided by Kirk-Spriggs *et al*. (2001), but does not include *T. reissi*.

***Thalassosmittia* Strenzke & Remmert** (Orthocladiinae)**.** A genus of 11 described species that occurs in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions (Ashe & O'Connor 2012: 614). A single species, *T. christinae* Sæther & Andersen, 2011 from Gough Is. is known in the Afrotropical Region (Sæther & Andersen 2011). With two exceptions the larvae are all marine littoral dwellers (Andersen *et al.* 2013*b*: 264). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 263) and Coffman *et al.* (1986: 211), respectively.

***Thienemanniella* Kieffer** (Orthocladiinae)**.** A genus of 54 described species that occurs in all zoogeographical regions, except Antarctica (Ashe & O'Connor 2012: 618). Six species are known from the Afrotropical Region (Fu *et al*. 2010). Larvae occur in most lotic habitats, from fast-flowing streams to slow-flowing ditches and rivers (Andersen *et al.* 2013*b*: 265). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 264) and Coffman *et al.* (1986: 213), respectively. The pupa of *T. fuga* Lehmann, 1979, recorded from Democratic Republic of Congo, South Africa and Tanzania, is described and figured by Lehmann (1979). Identification keys to adults of Afrotropical species were provided by Fu *et al*. (2010).

***Thienemannimyia* Fittkau** (Tanypodinae)**.** A genus of 28 valid species that occurs in all zoogeographical regions, except Oceania and Antarctica. With the reduction of *Hayesomyia* Murray & Fittkau to a subgenus of *Thienemannimyia* (Cranston & Epler 2013: 39), the genus now comprises two subgenera. A single species of *Thienemannimyia sensu stricto*, *T*. (*T.*) *tinctoria* (Freeman, 1955), occurs in the Afrotropical Region, which is known only from the type locality, the Mooi River, South Africa (Ashe & O'Connor 2009: 238). Larvae occur in both lotic and lentic waters, in streams, rivers and lakes (Cranston & Epler 2013: 87). Immature stages of the Afrotropical *T*. (*T.*) *tinctoria* remain unknown. No modern identification key incorporates all valid species, but some species were keyed in regional publications.

***Tokyobrillia* Kobayashi & Sasa** (Orthocladiinae)**.** A genus of two described species that occurs in the Afrotropical, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 638). A single species, *T. anderseni* Sæther & Wang, 1995 from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania is known from the Afrotropical Region (Sæther & Wang 1992). The immature stages remain unknown. See Fig. 90 for an example of the male terminalia of the genus.

***Trissopelopia* Kieffer** (Tanypodinae)**.** A genus of seven described species that occurs in the Holarctic Realm and the Afrotropical and Oriental Regions. A single species, *T. montivaga* Harrison, 1978, is recorded from the Afrotropics, apparently restricted to South Africa (Ashe & O'Connor 2009: 240). Larvae occur especially in groundwater-fed springs, mountain brooks and in the littoral of lakes (in northern latitudes) and in low order streams (Cranston & Epler 2013: 76). Immature stages of the Afrotropical species *T. montivaga* remain unknown.

***Tvetenia* Kieffer** (Orthocladiinae)**.** A genus of 27 described species that occurs in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Ashe & O'Connor 2012: 643). The genus is recorded from the Afrotropics based on two species, one named and one unnamed. *Tvetenia calvescens* (Edwards, 1929) is widespread in the Holarctic Realm and is recorded from Democratic Republic of Congo, Ethiopia and South Africa in the Afrotropics. An unnamed Afrotropical species is mentioned by Cranston *et al*. (1989*b*: 250), but the country is not specified. Larvae inhabit flowing waters (Andersen *et al.* 2013*b*: 269). Generic diagnoses for the larva and pupa were provided by Andersen *et al.* (2013*b*: 268) and Coffman *et al.* (1986: 215), respectively. The pupa of *T. calvescens* was described and figured by Lehmann (1979).

***Usambaromyia* Andersen & Sæther** (Usambaromyiinae)**.** An endemic monotypic genus, with the single species, *U. nigrala* Andersen & Sæther, 1994, described from the West Usambara Mountains (Eastern Arc Mountains) of Tanzania (Andersen & Sæther 1994). *Usambaromyia* is the sole genus in this subfamily and immature stages remain unknown.

***Virgatanytarsus* Pinder** (Chironominae: Tanytarsini)**.** A genus of seven described species that occurs in the Afrotropical and Palaearctic Regions. Three species are recorded from the Afrotropics, *V. aboensis* Harrison, 2004, *V. arduennensis* (Goetghebuer, 1922) and *V. nigricornis* (Goetghebuer, 1935), the last two mentioned being quite widely distributed in the continental Afrotropics (Cranston & Judd 1989; Freeman & Cranston 1980: 201; Kugler & Reiss 1973). The Afrotropical *V. subreflexens* (Freeman, 1955) is regarded as a junior synonym of *V. arduennensis*, although small morphological differences exist (Cranston & Judd 1989; Kugler & Reiss 1973). Species boundaries in *Virgatanytarsus* are challenging, however, and future molecular and morphological studies, particularly of immature *V. subreflexens*, may dissolve accepted synonymies. The immatures of some species were described by Kugler & Reiss (1973) (as the *Tanytarsus triangularis*-group). Larvae occur in small rivers and the littoral of lakes. No modern identification key that incorporates all valid species is available.

***Xenochironomus* Kieffer** (Chironominae: Chironomini)**.** A genus of 19 described species that occurs in all zoogeographical regions, except Oceania and Antarctica. The genus was revised recently; three species are known from the Afrotropical Region (Fusari *et al*. 2013). Immature stages of Afrotropical species remain unknown. The larvae of most *Xenochironomus* species are obligate miners in freshwater sponges in standing and flowing waters; one species from New Zealand is associated with freshwater Mollusca (Fusari *et al*. 2013). An identification key to known life stages was provided by Fusari *et al.* (2013).

***Xestotendipes* Harrison** (Chironominae: Chironomini)**.** An endemic monotypic genus erected on males and a female of *X. sufflavus* Harrison, 2000 from the Eastern Cape Province, South Africa and Zimbabwe (Harrison 2000). The genus shares morphological similarities with *Xestochironomus* Sublette & Wirth and likely represents a second Afrotropical genus in the *Stenochironomus* complex (Harrison 2000). The "African larval form" described by Borkent (1984) was collected a few kilometres from the type locality of *X. sufflavus* and may represent the larva of this species (Harrison 2000).

***Zavreliella* Kieffer** (Chironominae: Chironomini)**.** A genus of 14 described species that occurs in all zoogeographical regions, except Antarctica (Epler *et al.* 2013), with the single species, *Z. marmorata* (Wulp, 1858), recorded from the Afrotropical Region. This species is widely distributed and only absent from the Neotropical and Oceanian Regions and Antarctica. Larvae construct transportable cases amongst vegetation in small bodies of standing water. *Zavreliella marmorata* (in older literature often referred to under its junior synonym, *Lauterborniella fuscoguttata* (Kieffer, 1922)), appears to be widespread in the Afrotropical Region (Dejoux 1984*a*, 1984*b*; Freeman & Cranston 1980: 192). Immature stages of *Zavreliella* (including *Z. marmorata*) were diagnosed and figured in Cranston (2010), Epler *et al.* (2013), Pinder & Reiss (1986) and Reiss (1990).

Zavrelimyia **Fittkau** (Tanypodinae)**.** A genus of *ca* 50 valid species that occurs in all zoogeographical regions, except Antarctica. Only the subgenus *Z.* (*Paramerina*), previously recognised at genus level (Silva & Ekrem 2015), occurs in the Afrotropics (Ashe & O'Connor 2009: 58) with thirteen recorded species in the region. The pupa of *Z.* (*P.*) *fittkaui* Lehmann, 1981 and the mature larva (with some pupal features) of *Z.* (*P.*) *ababae* Harrison, 1991 are the only known immatures from the Afrotropics (Lehmann 1981; Harrison 1991). Both these species occur in montane rivers and streams. Larvae of *Z.* (*Paramerina*) are eurythermic, occurring in a variety of standing waters of all sizes, but are also present in small lotic habitats, including pools in rivers (Cranston & Epler 2013: 71). A comprehensive identification key to all described species is unavailable, but some species were keyed in regional publications.

Zuluchironomus **Harrison** (Chironominae: Chironomini)**.** An endemic monotypic genus, with the single described species, *Z. demoori* Harrison, 2000, known only from South Africa (Harrison 2000). Associated larvae and pupae are not known with certainty, but a larval form that could not be placed in an existing genus has been described from the same river system in KwaZulu-Natal Province (Harrison 2000). Larvae probably occur in running waters (Harrison 2000).

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VERMILEONIDAE 36

(Wormlions)

Norman E. Woodley and Vaughn R. Swart

Fig. 36.1. Male of *Vermipardus* nr. *univittatus* (Stuckenberg) (South Africa) (photograph © S.A. Marshall).

Diagnosis

Medium-sized flies (length: 7–15 mm), elongate and slender in general form (Fig. 1), brownish to yellowish or sometimes dark greyish in colour, scutum usually more or less vittate, male abdomen sometimes silvery pruinescent dorsally.

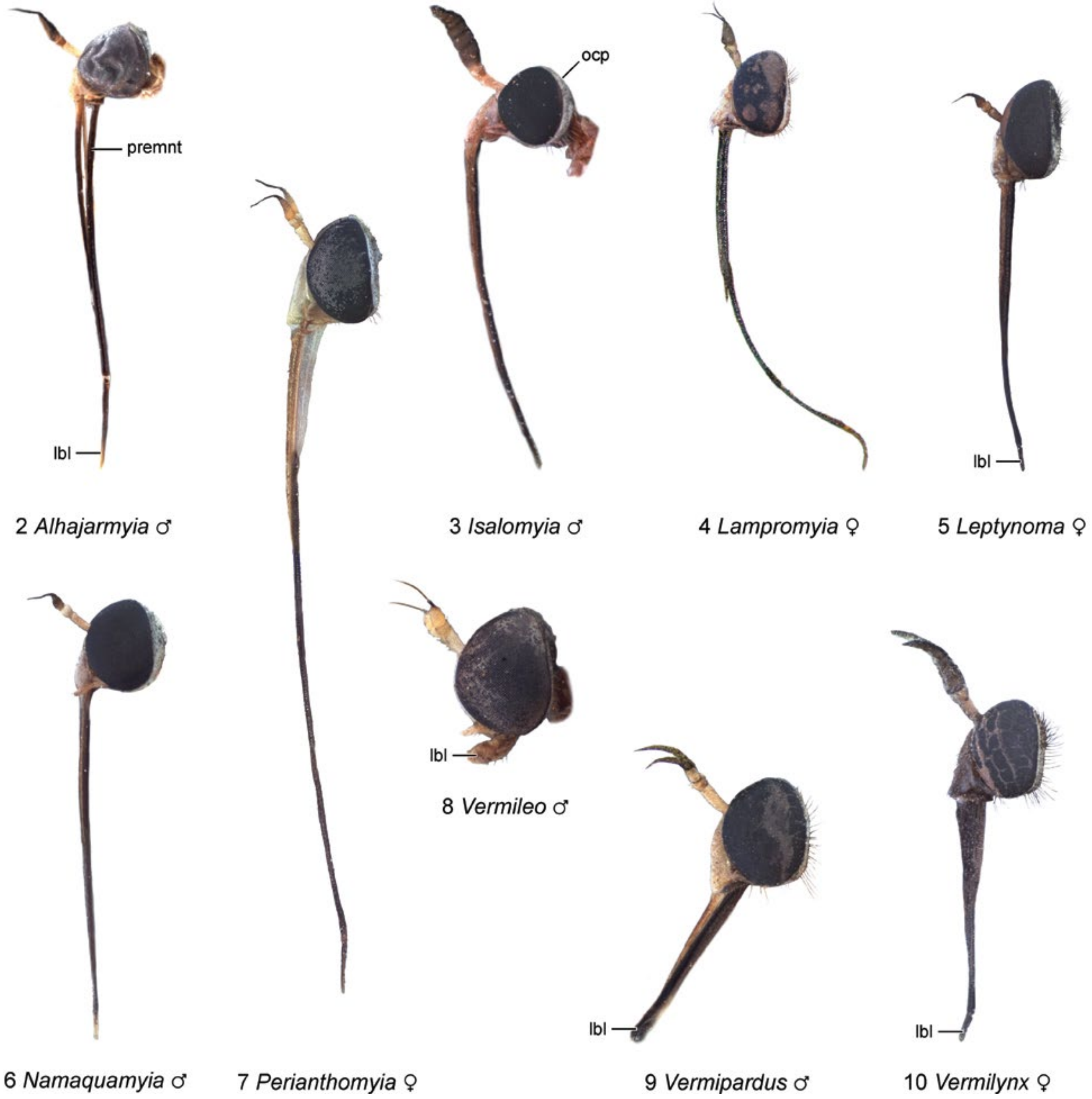
Eyes bare, separate in both sexes, although frons can be narrowed in some males; antenna (Figs 11–23) with scape twice length of pedicel; flagellum varying from having eight more or less unmodified flagellomeres to having postpedicel conical or elongate, with long, apical stylus composed of 2 or more flagellomeres that is often arista-like; clypeus weakly convex to strongly convex, projecting ventrally; mouthparts short, labellum fleshy in *Vermileo* Macquart (Fig. 8), but in most Afrotropical species elongate, slightly to several times longer than head height (Figs 2–7, 10), prementum well sclerotised and rigid, labellum reduced; palpus 2-segmented, basal segment slender, cylindrical, apical segment thicker, sometimes acutely conical apically, some taxa with palpus 1-segmented, clavate.

Thorax unmodified. Scutellum evenly rounded apically, flattened dorsally. Legs simple, elongate and slender (Fig. 1); hind femur more elongate, slightly to moderately clavate; hind

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 865–875.

tibia cylindrical, but thickened apically in a few species; tibial spurs 1 : 2 : 2, but fore tibial spurs reduced or absent in some species of *Leptynoma* Westwood; tarsi with empodium and pulvilli small, sometimes reduced to virtually absent. Wing (Figs 24–32) elongate, membrane usually uniformly coloured, but a few species with some contrastingly dark markings, alula virtually absent, anal lobe sometimes reduced; vein R_4 ending anterior to wing apex, in a few taxa near apex; vein R_5 ending well posterior to apex; cell m_3 usually closed at wing margin, but narrowly to moderately open in a minority of taxa, cell *cua* open at wing margin, closed at wing margin in rare cases.

Abdomen elongate, slender, slightly enlarged and blunt posteriorly; male terminalia (Figs 33–35) with aedeagus comprising



2 *Alhajarmyia* ♂ 3 *Isalomyia* ♂ 4 *Lampromyia* ♀ 5 *Leptynoma* ♀

6 *Namaquamyia* ♂ 7 *Perianthomyia* ♀ 8 *Vermileo* ♂ 9 *Vermipardus* ♂ 10 *Vermilynx* ♀

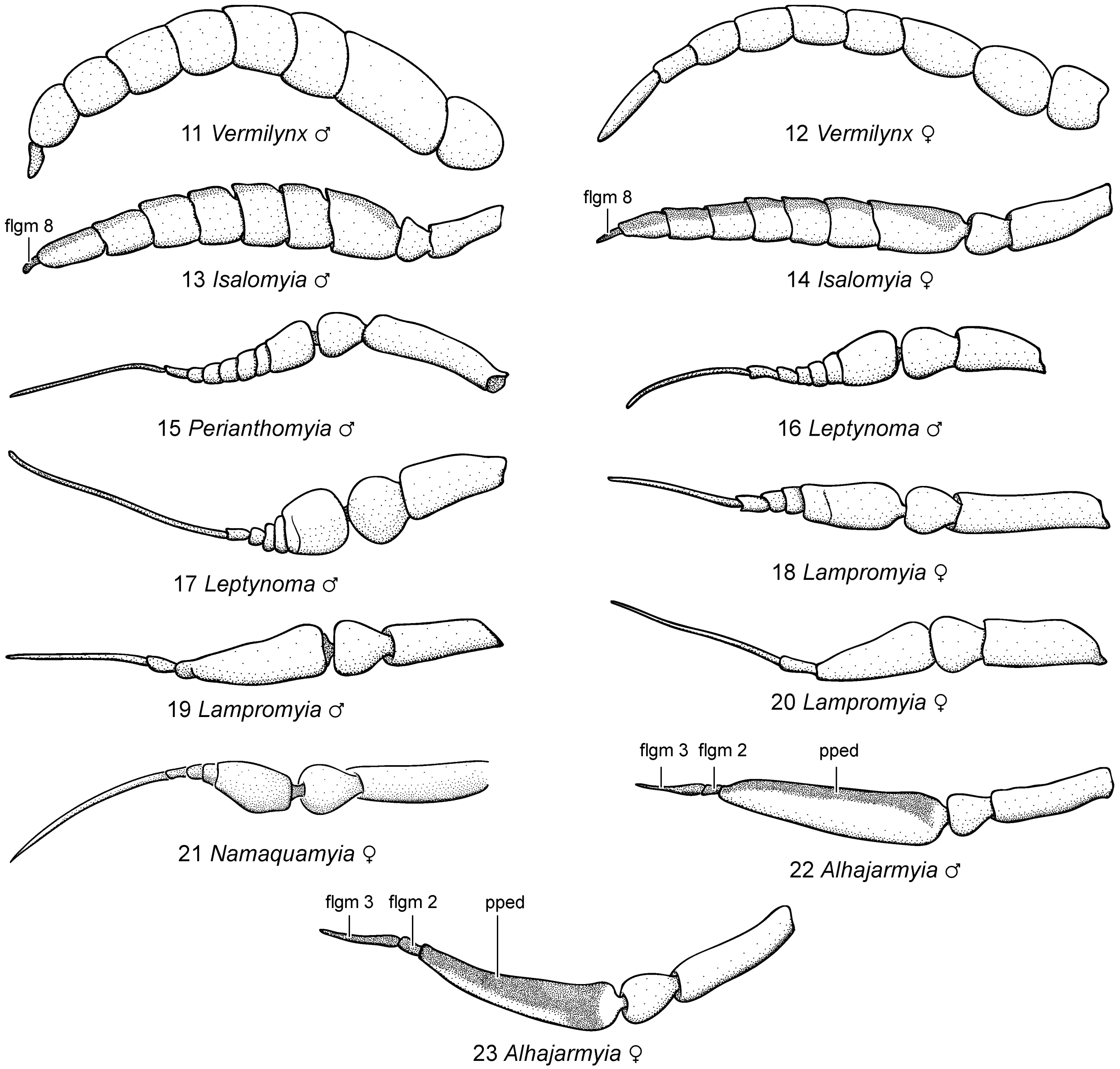
Figs 36.2–10. Heads of Vermileonidae (lateral views): (2) *Alhajarmyia stuckenbergi* Swart, Kirk-Spriggs & Copeland ♂; (3) *Isalomyia irwini* Stuckenberg ♂; (4) *Lampromyia rebecca* Stuckenberg ♀; (5) *Leptynoma namaquaensis* (Stuckenberg) ♀; (6) *Namaquamyia manselli* (Stuckenberg) ♂; (7) *Perianthomyia monticola* (Stuckenberg) ♀; (8) *Vermileo vermileo* (L.) ♂ (non-Afrotropical); (9) *Vermipardus intermedius* (Stuckenberg) ♂; (10) *Vermilynx vansoni* (Stuckenberg) ♀. Figs 2–10 (photographs B.S. Muller).

Abbreviations: lbl – labellum; ocp – occiput; premnt – prementum.

sclerotised tube with ejaculatory apodeme in form of slender, irregularly curved rod, situated within aedeagal tube; epandrium (tergite 9) rounded; female terminalia with cercus 2-segmented (Fig. 36); 3 spermathecae present.

Larval body (Figs 37, 38) gradually widening posteriorly, with distinctive morphology, featuring conspicuous body setae, single proleg on abdominal segment 1 and distinctive comb of stout spine-like abdominal tubercles on dorsal side of abdominal segment 7.

Adult vermileonids are easily recognised by their distinctive habitus, combined with the presence of a spur on the fore tibia (absent in only a few species), the wing with the alula virtually



Figs 36.11–23. Antennae of Vermileonidae (lateral views): (11) *Vermilynx jasoni* Stuckenberg ♂; (12) same ♀; (13) *Isalomyia irwini* Stuckenberg ♂; (14) same ♀; (15) *Perianthomyia maculata* (Stuckenberg) ♂; (16) *Leptynoma namaquaensis* (Stuckenberg) ♂; (17) *L. appendiculata* (Bezzi) ♂; (18) *Lampromyia pilosula* Engel ♀; (19) *La. rebecca* Stuckenberg ♂; (20) *La. flavida* Engel & Cuthbertson ♀; (21) *Namaquamyia manselli* (Stuckenberg) ♀; (22) *Alhajarmyia umbraticola* (Stuckenberg & Fisher) ♂; (23) same ♀. Figs 11, 12 (after Stuckenberg 1996*a*, figs 1, 2), Figs 13, 14, 22, 23 (after Stuckenberg 2003, figs 4–7), Figs 15–20 (after Stuckenberg 1996*b*, figs 2–7), Fig. 21 (after Stuckenberg 2000*b*, fig. 11).

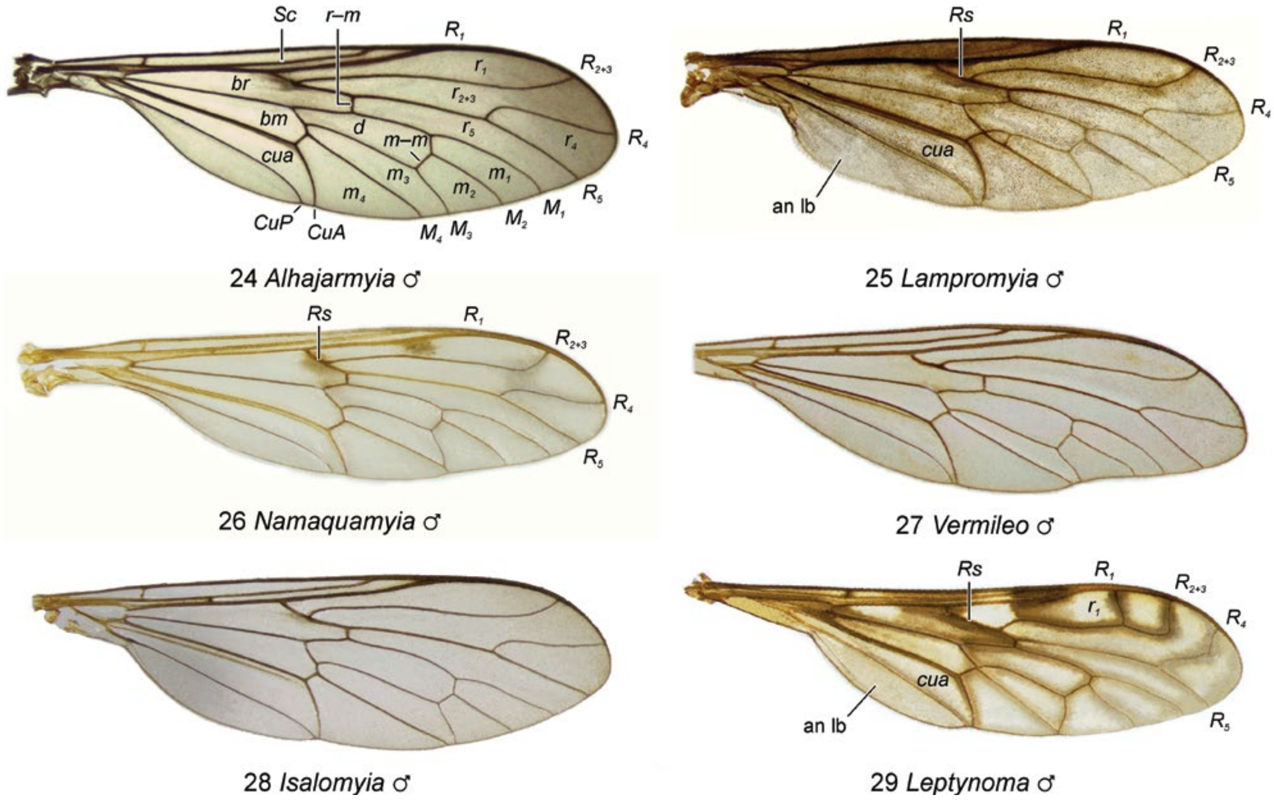
Abbreviations: flgm – flagellomere; pped – postpedicel.

absent and the antennal stylus composed of several flagellomeres. Vermileonids resemble leptogastrine Asilidae (see Chapter 48) in general appearance, but the latter lack tibial spurs, have a setiform empodium, piercing mouthparts and a postpedicel with only a single segment and an arista-like stylus.

Biology and immature stages

Larvae of Vermileonidae (Figs 37, 38), commonly known as wormlions, are remarkable in that they construct a conical pit to trap other insects, similar to that of antlions (Neuroptera: Myrmeleontidae). Ludwig *et al*. (2001) investigated different aspects of larval morphology (mouthparts, prolegs, abdominal combs). Ludwig *et al*. (1996) provided diagnoses of the larval mouthparts and Hafez & El-Moursy (1956) described the external and internal morphology of *Vermileo* from Egypt in detail.

Pits are constructed in fine sand and dust at the entrances of caves or overhangs or at the base of trees, cliffs or large boulders and in man-made situations, such as old stone walls, along houses, beneath bridges (Devetak 2008), *etc*., where they prey on other insects. Devetak (2008) and Devetak & Arnett (2015) investigated preferred substrate particle size in the genera *Vermileo* and *Lampromyia*, Hemmingsen (1963) and Lackinger (1973) compared pit building between antlions and wormlions and Marshall (2012: 196) mentioned that pits are usually protected by overhanging rocks or some sort of shelter. Larvae are usually crowded under these suitably sheltered spots. When prey fall into a pit they are maneuvered to the centre of the pit by the larva. If the larva does not capture the prey immediately by wrapping around its victim, the larva flings dirt by flicking its body, inevitably collapsing the walls of the pit and bringing the prey within striking distance. With a rapid strike the larva wraps the anterior end of its body around the prey thus restraining it. Prey is paralysed within minutes and often drawn into the sand. Once the larva has completed feeding on the prey it flings the corpse out of the pit and rebuilds the trap. Ludwig *et al*. (1996) provided detailed observations on feeding



24 *Alhajarmyia* ♂

25 *Lampromyia* ♂

26 *Namaquamyia* ♂

27 *Vermileo* ♂

28 *Isalomyia* ♂

29 *Leptynoma* ♂

Figs 36.24–29. Wings of Vermileonidae (dorsal views): (24) *Alhajarmyia stuckenbergi* Swart, Kirk-Spriggs & Copeland ♂; (25) *Lampromyia flavida* Engel & Cuthbertson ♂; (26) *Namaquamyia manselli* (Stuckenberg) ♂; (27) *Vermileo vermileo* (L.) ♂ (non-Afrotropical); (28) *Isalomyia irwini* Stuckenberg ♂; (29) *Leptynoma namaquaensis* (Stuckenberg) ♂.

Abbreviations: an lb – anal lobe; *bm* – basal medial cell; *br* – basal radial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *d* – discal cell; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–m* – medial crossvein; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; *Rs* – radial sector.

behaviour, Dor *et al*. (2014) investigated how hunger and ecological factors shape investment in foraging and Scharf & Dor (2015) focused on starvation tolerance in vermileonid larvae.

Adults are rarely observed or collected in nature and most known specimens are reared from larvae. Vermileonid adults are apparently short lived (Nagatomi *et al*. 1999: 118, 126) and feed on floral nectar. Wheeler (1930) observed captive vermileonid females ovipositing eggs into the sand by thrusting the abdominal tip downward into the sand, consequently each site becomes a pit. Hemmingsen & Nielsen (1971) provided detailed accounts of oviposition behaviour in the genera *Lampromyia* and *Vermileo*

Virtually all literature on the biology of vermileonids is summarised in detail by Nagatomi *et al.* (1999).

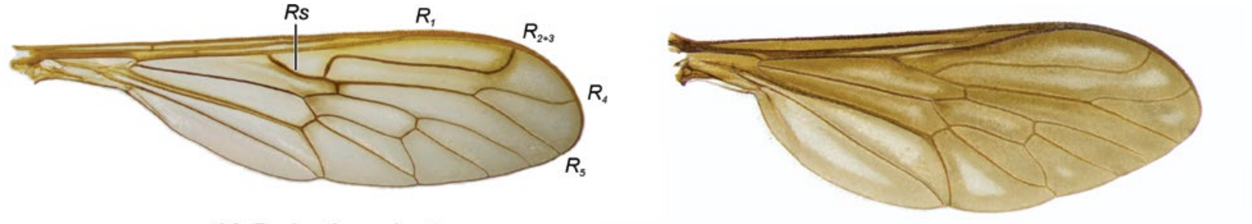
Economic significance

No species are known to have economic importance.

Classification

Vermileonidae are representatives of the infraorder Tabanomorpha of the "orthorrhaphous" Brachycera and are the apparent sister-group to the remaining families of the order (Kerr 2010). The history of placement of the family has been fairly convoluted. Traditionally they have been considered part of the Rhagionidae, usually as a separate subfamily (*e.g.*, Hennig 1973: 39; Stuckenberg 1960: 218). Nagatomi (1977) elevated the group to family status as Vermileonidae, but was uncertain as to its relationships to other lower Brachycera. Teskey (1981: 532) followed Nagatomi's lead, and suggested that vermileonids had a relationship among the Asiloidea. Woodley (1989: 1382) considered the family as part of the Tabanomorpha, but as *incertae sedis*. Griffiths (1994) placed the Vermileonidae as a separate infraorder of the Brachycera and Ovtshinnikova (2000) proposed that the Vermileonidae are the sister-group to the Xylophagomorpha near the base of the Brachycera, based on studies of musculature of the male terminalia. Subsequent work based on morphology pointed toward placement of Vermileonidae as the most primitive family of the infraorder Tabanomorpha (Sinclair *et al*. 1994; Yeates 2002; Zloty *et al*. 2005), while molecular analyses recovered the vermileonids as sister-group to the Rhagionidae (Wiegmann *et al*. 2000, 2003) within Tabanomorpha. More recent work, based on both morphological and molecular data, retain the vermileonids within Tabanomorpha with varying relationships to the other families depending on the data analysed (Kerr 2010; Wiegmann *et al.* 2011). The combined data set used by Kerr (2010) resulted in the relationships: (Vermileonidae (Pelecorhynchidae (Athericidae) (Tabanidae))) (Rhagionidae). One can conclude that the Vermileonidae are certainly a representative of the Tabanomorpha and probably one of the basal lineages.

Currently there are 11 genera of Vermileonidae comprising 61 species currently recognised globally. Nagatomi *et al*. (1999) provided a world catalogue and key to genera known at that time, however, four additional genera and 31 species have subsequently been recognised in the Afrotropical Region. The greatest species diversity is found in the Afrotropical Region (31 species) followed by the western Palaearctic Region (14), China and the Oriental Region (11), Mexico and the Caribbean (4) and the Nearctic Region (2). Nine of the 11 vermileonid genera occur in the Afrotropics and all but four of the Afrotropical species occur only in southern Africa. There is no subfamilial classification within the family. At the time of Stuckenberg (1960), 13 Afrotropical species were known that were placed in two genera and one subgenus. Stuckenberg's continued



30 *Perianthomyia* ♂

31 *Vermilynx* ♂

32 *Vermipardus* ♂

Figs 36.30–32. Wings of Vermileonidae (dorsal views): (30) *Perianthomyia phantasma* (Stuckenberg) ♂; (31) *Vermilynx vansoni* (Stuckenberg) ♂; (32) *Vermipardus univittatus* (Stuckenberg) ♂.

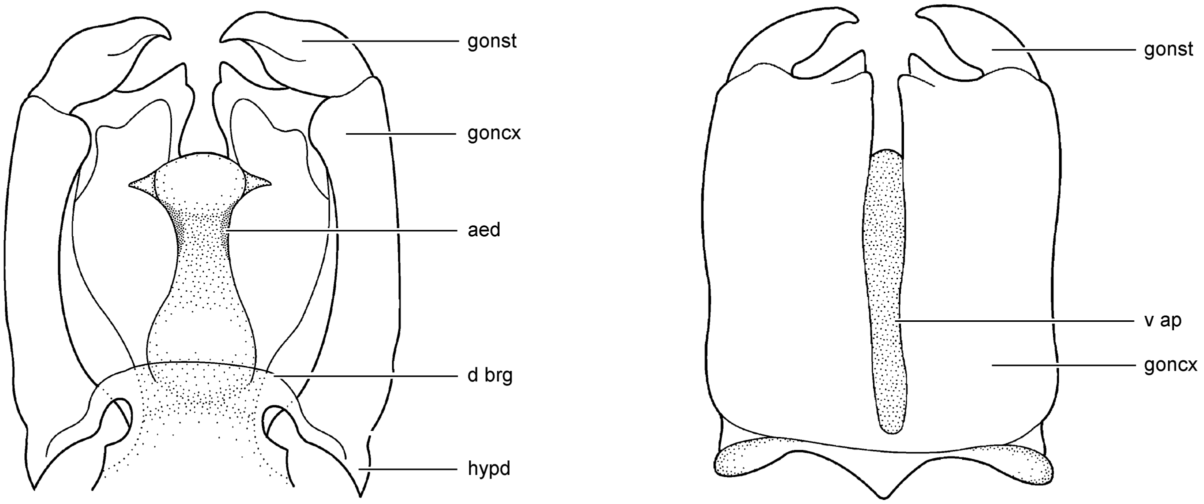
Abbreviations: R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Rs* – radial sector.

interest in the family resulted in the description of 17 additional species and his various cladistic studies and discoveries resulted in the splitting of *Lampromyia* and description of several new genera (Stuckenberg 1995*a*, 1996*b*, 2000*b*, 2003). A synthesis of morphological characters scored for all species and analysed using modern phylogenetic methods is required, however, to validate generic concepts.

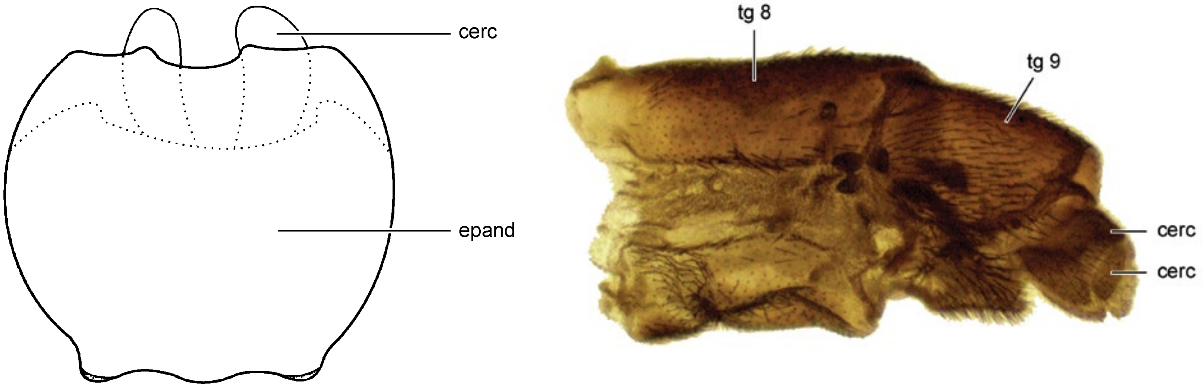
Identification

Stuckenberg (1996*b*, 2000*b*) published identification keys to the genera that occur in the southern continental Afrotropics, the latter paper treating six genera. References for species-level identification keys where available are provided in the "Synopsis of the fauna" section below. Vermileonids are rarely collected as adults. Numerous taxa are known only from reared specimens, but Malaise traps can be effective for collecting some specimens (*e.g.*, Stuckenberg 2003). While there are certainly undescribed species in the Afrotropical Region, it is likely that the fauna is currently fairly well known. Kirk-Spriggs & Stuckenberg (2009: 187), for example, predicted that *ca* 12 species probably await discovery and description, representing 29% of the described fauna.

Field sampled and reared vermileonid adults are best direct-pinned in the field (see Chapter 2). Larvae can be collected from pits by hand or by using a spoon, tea strainer or small



33 *Alhajarmyia* ♂ 34 *Alhajarmyia* ♂



35 *Alhajarmyia* ♂ 36 *Alhajarmyia* ♀

Figs 36.33–36. Male and female terminalia of Vermileonidae: (33) male terminalia of *Alhajarmyia stuckenbergi* Swart, Kirk-Spriggs & Copeland, dorsal view (epandrium removed); (34) same, ventral view; (35) same, epandrium, dorsal view; (36) same, female terminalia, lateral view. Figs 33–36 (after Swart *et al.* 2015, figs 12, 16, 20, 22).

Abbreviations: aed – aedeagus; cerc – cercus; d brg – dorsal bridge; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd - hypandrium; tg – tergite; v ap – ventral aperture.

sieve and be transported to the laboratory in glass or plastic tubes filled with very fine sand and/or dust, from the original substrate. They may then either be placed together in a single large container, ensuring that there is enough space between the pits, or be placed individually into separate containers. Smaller individual containers should be slightly wider than the pit. Keeping a record of when larvae feed is important for optimum development and this is easier if stored in individual containers. Removing dried-up corpses of insects once larvae have fed ensures that feeding takes place without obstacles. Larvae pupate underground and once adults emerges they can survive for *ca* 2–5 days.

Key to genera of Afrotropical Vermileonidae

1. Proboscis shorter than head height (Fig. 8), prementum obscured by large, fleshy labellum; face only slightly convex, evenly rounded in profile ("Sudan") . . . . *Vermileo* Macquart

– Proboscis slightly to considerably longer than head height (*e.g.*, Figs 2–7, 9, 10), prementum slender, sclerotised, with reduced labellum; face convex, projecting ventrally in profile (Kenya, Oman, southern Africa & Madagascar) 2

2. Antennal flagellum composed of 3 segments (postpedicel and flagellomeres 2 & 3) (Figs 22, 23), the first much more robust > 2 × as long as flagellomeres 2 and 3 combined (Kenya & Oman) . . . . *Alhajarmyia* Stuckenberg

– Antennal flagellum almost invariably with more than 3 flagellomeres (*e.g.*, Figs 11–18, 21), but if only 3 present, then flagellomere 1 short, conical, much shorter than flagellomeres 2 and 3 combined (southern Africa & Madagascar) 3

3. Occipital region of head enlarged (Fig. 3), in lateral view slightly thicker than base of antenna; antenna with 8 flagellomeres, terminal flagellomere much more slender and shorter than penultimate flagellomere (Figs 13, 14) (endemic to Madagascar) . . . . *Isalomyia* Stuckenberg

– Occipital region of head not enlarged (*e.g.*, Figs 2, 4–10), in lateral view considerably less than ½ width of eye; antenna variable, often with fewer than 8 flagellomeres (Figs 17–21), if 8 present, then apical flagellomere not significantly more slender and shorter than penultimate flagellomere (*e.g.*, Figs 12, 15, 16), except in male of *Vermilynx* (Fig. 11) (confined to southern continental Afrotropics) 4

4. Antenna with 8 flagellomeres, terminal flagellomere short, at most length of preceding 3 flagellomeres combined (*e.g.*, Figs 11, 12); proboscis relatively short, rigid, projecting downwards (*e.g.*, Figs 9, 10) 5

– Antenna with 8 or fewer flagellomeres, terminal flagellomere elongate and slender, at least length of remaining flagellomeres combined (*e.g.*, Figs 15–21); proboscis more elongate, capable of posterior flexure between legs (*e.g.*, Figs 4–7) 6

5. Labellum laterally compressed, short, subtriangular, paired labella fused over *ca* ½ their length (Fig. 9), bearing stiff setae; pulvilli well-developed, elongate with narrow basal stem, empodium similar, but moderately smaller . . . . *Vermipardus* Stuckenberg

– Labellum elongate tubular, dorsoventrally flattened (in dried specimens), paired labella separated over their entire length, although usually held pressed together (Fig. 10), without setae; pulvilli minute and inconspicuous, empodium vestigial . . . . *Vermilynx* Stuckenberg

6. Wing veins R_4 and R_5 only moderately divergent, R_4 ending near wing apex (Fig. 26); antenna with 5 flagellomeres, terminal flagellomere much longer than remaining flagellomeres combined (Fig. 21) . . . . *Namaquamyia* Stuckenberg

– Wing veins R_4 and R_5 strongly divergent, R_4 ending distinctly anterior to wing apex (*e.g.*, Figs 29, 30); antenna with number of flagellomeres variable, but often > 5 7

7. Wing with base of vein R_{2+3} originating perpendicular to vein *Rs*, then bending almost at right angle near vein R_1 in basal section (Fig. 30); antenna with 8 flagellomeres, terminal flagellomere about as long as remaining flagellomeres combined (Fig. 15) . . . . *Perianthomyia* Stuckenberg

– Wing with base of vein R_{2+3} originating at acute angle to vein *Rs* then virtually straight, not approaching R_1 in basal section (*e.g.*, Figs 25, 29); antenna with fewer than 8 flagellomeres (*e.g.*, Figs 16–20). 8

8. Hind tibia gradually thickened toward apex, where about same diameter as hind femur; wing membrane patterned, with conspicuous dark macula in cell r_1 near end of vein R_1; anal lobe reduced, at most as wide as cell *cua*, reduction especially noticeable proximally (Fig. 29) . . . . *Leptynoma* Westwood

– Hind tibia more or less cylindrical, apically more slender than diameter of the hind femur; wing membrane without pattern, although evenly darkened costally; anal lobe not reduced, wider than cell *cua* (Fig. 25) . . . . *Lampromyia* Macquart

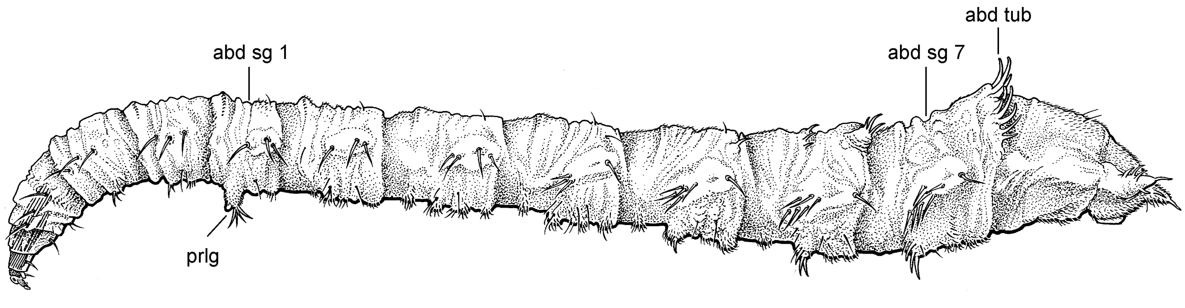
Synopsis of the fauna

***Alhajarmyia* Stuckenberg.** An endemic genus of two described species, *A. stuckenbergi* Swart, Kirk-Spriggs & Copeland, 2015 from the Eastern Arc Mountains of Kenya (Swart *et al*. 2015) and *A. umbraticola* (Stuckenberg & Fisher, 1999) recorded from the Western Hajar Mountains of northern Oman (Stuckenberg & Fisher 1999). The latter species was originally described in *Lampromyia* and the genus *Alhajarmyia* was subsequently erected by Stuckenberg (2003) to accommodate the species. The larvae of *L. umbraticola* were collected in fine dusty sediment on the floor of deeply shaded rock overhangs, caves and deserted houses at elevations of 1800–2500 m at sites that were not exposed to sunlight and were sheltered from rainfall. *Alhajarmyia stuckenbergi* was collected at Kasigau Mountain and the Taita Hills of Kenya, which represented the first vermileonid known to occur in East Africa (Swart *et al*. 2015). An identification key to the two species was provided by Swart *et al*. (2015).

***Isalomyia* Stuckenberg.** A monotypic genus with the single described species, *I. irwini* Stuckenberg, 2002, known only from Madagascar, being the sole vermileonid recorded from the island. The species is currently known from a single locality in Isalo National Park. The first specimen was reared from a larva collected on a shelf under a cliff overhang (Stuckenberg 2002a) and subsequent specimens were collected at the same locality using a Malaise trap (Stuckenberg 2003). Recent larval material was collected in Madagascar in 2014 from Anja Nature Reserve, 12 km south of Ambalavao, which may represent the same or an undescribed species (A.H. Kirk-Spriggs, pers. comm. 2016).

***Lampromyia* Macquart.** A genus of 13 described species, 10 of which occur in the Canary Islands and the Mediterranean region across northern Africa to Sicily and in Spain and southern France (Kehlmaier 2014), with a disjunct group of three species from Zimbabwe, Lesotho and South Africa. Disjunctions in the genus were mapped and discussed at length

37 *Vermipardus*



38 *Vermileo*

Figs 36.37–38. Larval habitus of Vermileonidae: (37) *Vermipardus intermedius* (Stuckenberg) (South Africa); (38) *Vermileo comstocki* Wheeler, lateral view (non-Afrotropical). Fig. 38 (Teskey 1981, fig. 5).

Abbreviations: abd sg – abdominal segment; abd tub – abdominal tubercle; prlg – proleg.

by Kirk-Spriggs & McGregor (2009). Stuckenberg (1996*b*) published a key to the three Afrotropical species and later (Stuckenberg 1998*a*) presented a cladistic analysis of the 12 species known at that time from all regions.

***Leptynoma* Westwood.** An endemic genus of five species known only from south-western South Africa and southern Namibia. Considered a synonym of *Lampromyia* for many years, this genus was reinstated at the generic level by Stuckenberg (1996*b*) and at that time also included the species now placed in *Perianthomyia*. Stuckenberg (2000*b*) elevated *Perianthomyia* to generic level, leaving the five species now considered *Leptynoma* in the genus. Stuckenberg (1996*b*) published a key to the four species known at that time. *Leptynoma kirkspriggsi* Stuckenberg, 1998 was subsequently described from the Succulent karoo biome of southern Namibia (Stuckenberg 1998*b*) and compared with the previously known species. In this same paper a cladogram was presented with hypothesised relationships of the species.

***Namaquamyia* Stuckenberg.** An endemic monotypic genus with the single described species, *N. manselli* (Stuckenberg, 2000), only known from Namaqualand, South Africa. It was discovered in the *sandveld*, a strip of loose sands between the Orange and Olifants Rivers (Stuckenberg 2000*b*). The original generic name was *Namamyia* Stuckenberg, but since this was preoccupied a replacement name, *Namaquamyia*, was proposed by Stuckenberg (2002*b*).

***Perianthomyia* Stuckenberg.** An endemic genus of three species, known only from Namibia and the Northern and Western Cape Provinces of South Africa. Stuckenberg (1996*b*) published a key to the two species known at the time, *P. maculata* (Stuckenberg, 1960) and *P. phantasma* (Stuckenberg, 1996), when this taxon was considered a subgenus of *Leptynoma*. A third species was described, *P. monticola* (Stuckenberg, 2000), from the Brandberg massif, Namibia, *ca* 400 km north of the nearest record of other species of Vermileonidae (Stuckenberg 2000*a*) in Namibia. *Perianthomyia monticola* was reared from larvae collected in ephemeral riverbeds and adults have been attracted to light in large numbers (A.H. Kirk-Spriggs, pers. comm. 2016). *Perianthomyia* was not ranked as a distinct genus until 2000 (Stuckenberg 2000*b*).

***Vermileo* Macquart.** A genus of 10 described species found in the south-western United States south to Costa Rica (Woodley 2009: 482), Cuba, Jamaica, southern Europe and Sudan (Nagatomi *et al*. 1999: 72). Edwards (1935) described *V. niloticus* from "Sudan", without further locality data from specimens reared from larvae. Stuckenberg (1965) reviewed the status of *V. niloticus* compared to *V. vermileo* (L., 1758) and two other Palaearctic species and concluded it to be a valid species. Stuckenberg (1965: 495) stated that an unnamed Egyptian record based on larvae probably referred to *V. niloticus*. The type material of *V. niloticus* was described from specimens collected by Efflatoun and others in Egypt and these specimens have subsequently been confirmed as conspecific (C. Kehlmaier, pers. comm. 2016). Otherwise, nothing is known regarding the biology of the species.

***Vermilynx* Stuckenberg.** An endemic genus of two described species that are only known from the Richtersveld region in northern Namaqualand in north-western South Africa and southern Namibia (Stuckenberg 2000*b*: fig. 6), *V. vansoni* (Stuckenberg, 1965) and *V. jasoni* Stuckenberg, 1996 (Stuckenberg 1995*a*, 1996*a*). Apparently two undescribed species are known from the Northern and Western Cape Provinces of South Africa (Stuckenberg 2000*a*), extending the known distribution farther south in western South Africa. Stuckenberg (1996*a*: 198) provided character information on how to separate the two described species.

***Vermipardus* Stuckenberg.** An endemic genus of 13 described species recorded from Lesotho and South Africa. Originally described as a subgenus of *Lampromyia*, it was later elevated to generic status (Stuckenberg 1995*b*). The genus ranges along the Great Escarpment in eastern South Africa, westward near the coast to the Cape Peninsula (Stuckenberg 1997, fig. 1). Stuckenberg (1995*b*) published a key to the 10 species known at the time and later (Stuckenberg 1997) described three additional species. In the latter paper he provided a key to species of the south-west Cape, omitting only *V. barracloughi* Stuckenberg, 1997 from the identification keys. It is easily recognised, however, in that the wing lacks an *m–m* crossvein, so that it lacks a closed discal cell (*d*), which is unique in the genus (although apparent in an aberrant paratype of *V. sylphe* Stuckenberg, 1995).

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RHAGIONIDAE 37

(Snipe Flies)

Peter H. Kerr and Bradley J. Sinclair

Fig. 37.1. Male of *Chrysopilus* sp. (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Slender flies, lacking bristle-like setae (body length: *ca* 5–11 mm) (Fig. 1). Body colour generally drab; yellow, grey, brown, or black.

Head with male compound eyes holoptic, or narrowly separated; female eyes widely separated; antenna with scape small; pedicel and first flagellomere round or conical, bearing elongate terminal arista-like stylus (Fig. 7), or tapered, comprising 3–8 flagellomeres (Figs 5, 6); adult with convex, bulbous clypeus; labella fleshy (Figs 6, 7), with short or sclerotised and elongate proboscis (Fig. 2); palpus 1- or 2-segmented.

Thorax with legs elongate and delicate; tibial spurs 0 : 2 : 1 or 0 : 2 : 2. Wing hyaline, or with some dusky brown colouration (Kerr 2010; figs 44–64); vein R_{4+5} branched (*i.e.*, vein R_4 present); discal (*d*) cell [absent in *Litoleptis* Chillcott (non-Afrotropical)]

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 877–883.

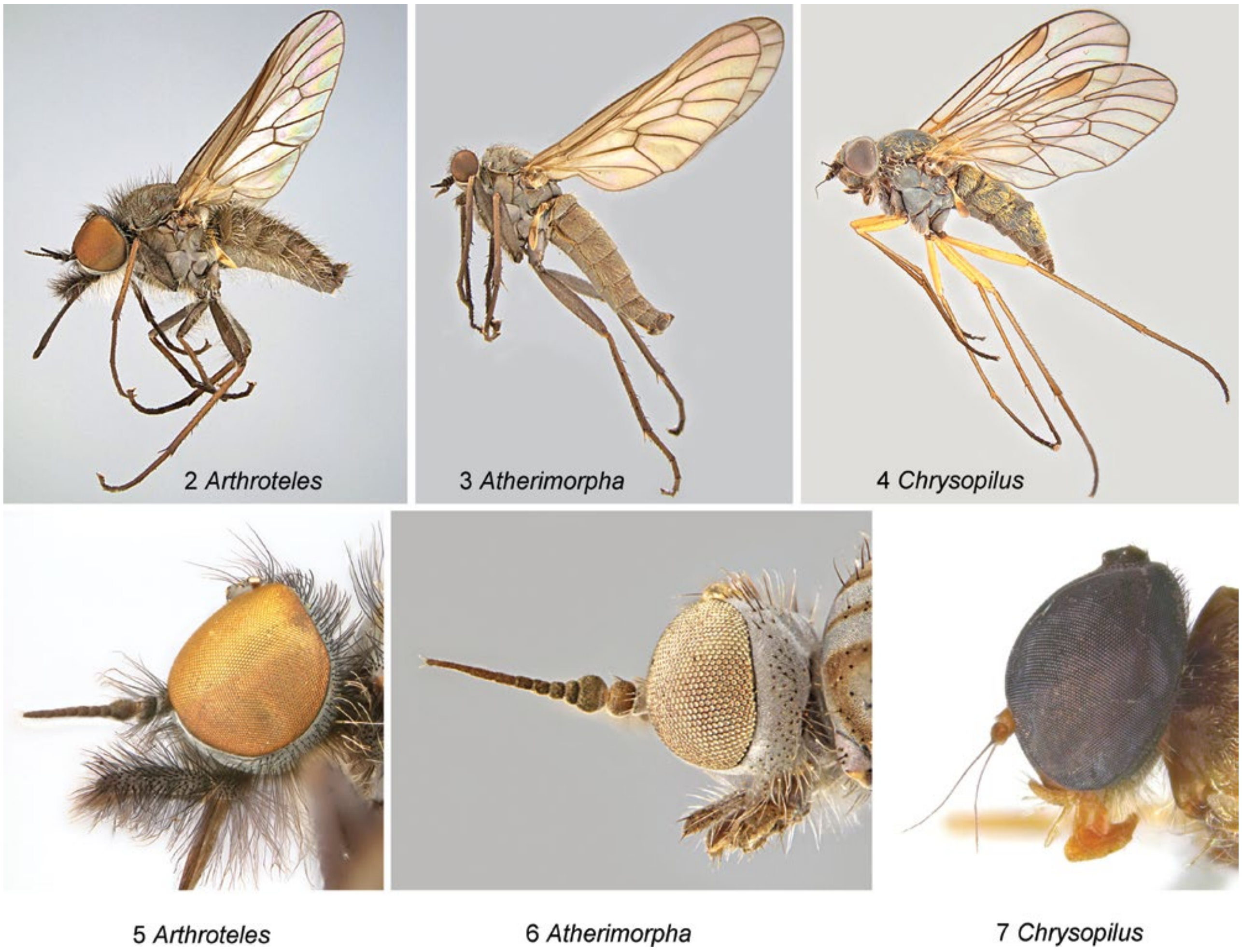
and veins M_3 and M_4 usually present [M_3 rarely absent or reduced in some non-Afrotropical genera]; cell *cua* open or closed near wing margin (Figs 8–10).

Abdomen tapered posteriorly; female ovipositor telescopic; cercus 2-segmented (Figs 11, 12); 3 spermathecae spherical or elongate, with or without sclerotisation; male terminalia with simple epandrium; epandrial sclerite wider than long; hypandrium entirely fused to gonocoxites (*Chrysopilus* Macquart), or hypandrium separated from gonocoxites by complete suture (*Arthroteles* Bezzi and *Atherimorpha* White); gonostylus simple; aedeagal tines absent (Fig. 13).

Eggs somewhat sausage-shaped, unsculptured, pale to light brown; only eggs of *Symphoromyia* Frauenfeld (non-Afrotropical) have been described (Sommerman 1962).

Larvae elongate, cylindrical and cream-coloured; body cuticle generally smooth; tapered at anterior end, with retractile head; mandible divided into two components: heavily sclerotised distal hook, with, or without, external groove on adoral surface and an inverted U-shaped basal mandibular sclerite; mandibular brush of sclerotised spines at posterior margin of basal sclerite, lacking articulated mandibular rod; larval stemmata visible beneath sclerotised lateral margin of head capsule (Fig. 17) (Courtney *et al*. 2000: 104; Sinclair 1992); respiratory system amphipneustic (not apneustic); prothoracic spiracles small, reduced; posterior spiracles on posterior face of terminal segment; creeping welts present on abdominal segments 1–6 or 1–7 (Fig. 14); terminal segment possesses lobes or tubercles, surrounding posterior spiracular face (Fig. 16) (Courtney *et al*. 2000: 103, 107; James & Turner 1981: 484; Kerr 2010).

Pupa cylindrical, generally with truncate posterior end; antenna on face, not apical; thorax lacking distinct setae; prothoracic spiracle on short dorsolateral protuberance; legs extending slightly beyond wings; abdominal spiracles on short prominence on segments 2–7; abdominal segments with marginal row of spine-like projections (Fig. 15) (Greene 1926; Hobby & Smith 1962).


2 *Arthroteles*
3 *Atherimorpha*
4 *Chrysopilus*
5 *Arthroteles*
6 *Atherimorpha*
7 *Chrysopilus*

Figs 37.2–7. Habitus and heads of Rhagionidae: (2) habitus of *Arthroteles bombyliiformis* Bezzi, lateral view; (3) same, *Atherimorpha bevisi* Stuckenberg; (4) same, *Chrysopilus* sp. (non-Afrotropical); (5) head of *Ar. bombyliiformis*, lateral view; (6) same, *At. latipennis* Stuckenberg; (7) same, *Chrysopilus fimbriatus* Bezzi.

Rhagionids are recognised by their bulbous clypeus and may be separated from other families that share this character (Athericidae; see Chapter 38 and Tabanidae; see Chapter 39), by the lack of a scale-like elevation immediately posterior to the posterior thoracic spiracle.

Biology and immature stages

Few details regarding the biology of Afrotropical rhagionids are known and the immature stages of the Afrotropical genera *Atherimorpha* and *Arthroteles* remain unknown. As larvae, the virtually cosmopolitan genus *Chrysopilus* may be aquatic, associated with streamside vegetation, or as for most rhagionid larvae, may be found in moist soils that are rich in organic matter. Larvae are reportedly predators of oligochaetes and soft-bodied insect larvae (Roberts 1969; Thomas 1997: 312 and references therein).

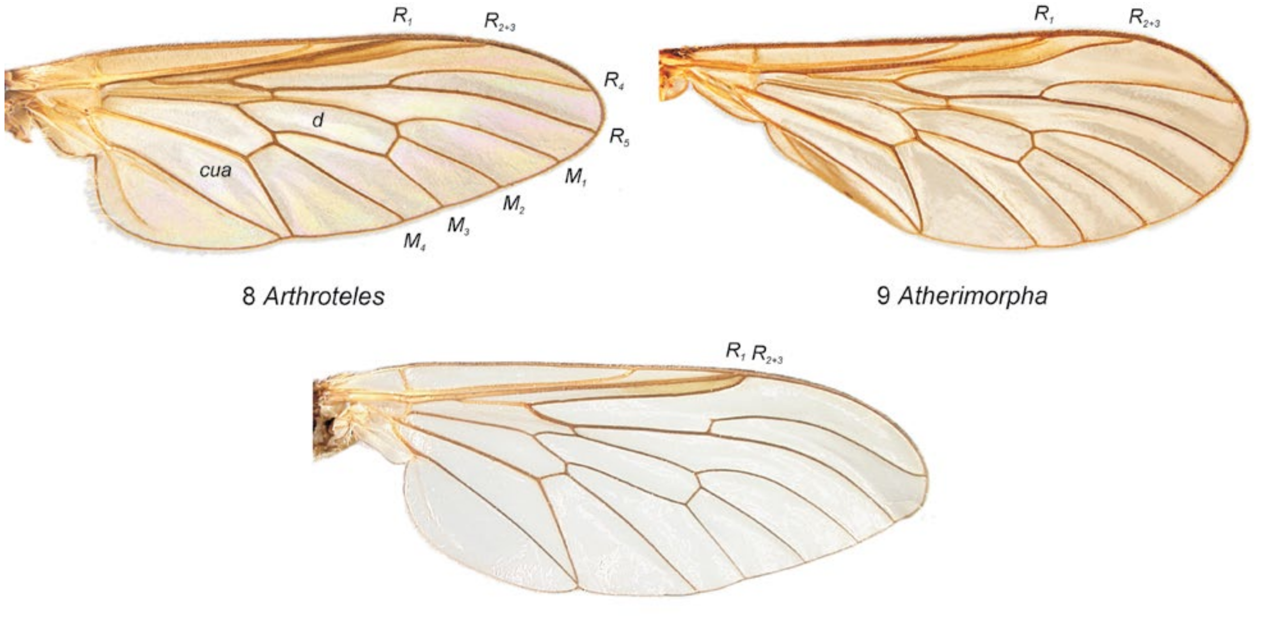
Adult *Arthroteles* are noteworthy for their specialised flower-feeding behaviour and are restricted to the Cape Fold Mountains of the Western Cape Province and the scarp mountains of eastern South Africa. Stuckenberg (1956a) reported that *A. cinerea* Stuckenberg, 1956, resembles bombyliids in flight and is most frequently collected on flower heads of *Helichrysum* spp. (Asteraceae). Interestingly, *Arthroteles* spp. apparently exhibit species-specific, or virtually species-specific, periods of flight activity. Historically, *A. cinerea* adults are collected in March, *A. bombyliiformis* Bezzi, 1926, in August or September and *A. orophila* Stuckenberg, 1956, in November. Flight activity of *A. longipalpis* Nagatomi & Nagatomi, 1990, occurs in July and may overlap to some degree with that of *A. bombyliiformis*. Records of Afrotropical *Atherimorpha* indicate that they are also mostly collected in mountainous regions. In all habitats, it appears that *Atherimorpha* spp. gravitate towards small, slow-moving streams, which presumably provide moist soil substrates for larval development. *Chrysopilus* are known to perch on leaves within gallery forests, in woodlands, and well-vegetated meadows and males of some species are known to swarm.

Economic significance

No species of economic importance are currently documented in the literature.

Classification

The concept of Rhagionidae has become generally more exclusive as relationships among primitive brachyceran genera have become better understood. Kerr (2010) provides the most recent classification scheme for the family, recognising four subfamilies based on a combined data set (morphological and 28S rDNA): Arthrocerinae, Chrysopilinae, Rhagioninae and Spaniinae. The non-Afrotropical genera *Bolbomyia* Loew



8 *Arthroteles*

9 *Atherimorpha*

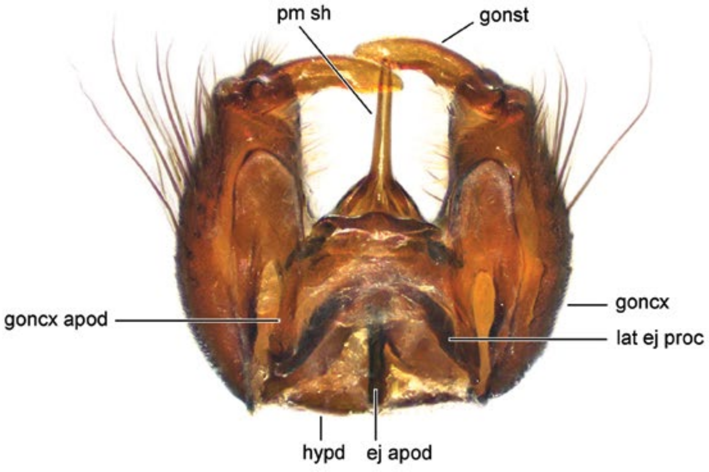
10 *Chrysopilus*

Figs 37.8–10. Wings of Rhagionidae: (8) *Arthroteles bombyliiformis* Bezzi, dorsal view; (9) *Atherimorpha monsaemontis* Stuckenberg; (10) *Chrysopilus* sp. (non-Afrotropical).

Abbreviations: *cua* – anterior cubital cell; *d* – discal cell; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

11 *Arthroteles* ♀

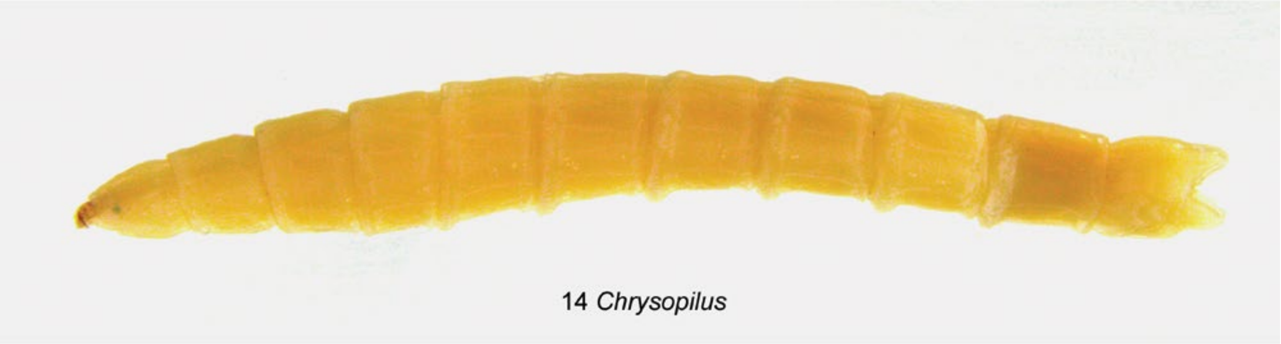
12 *Arthroteles* ♀

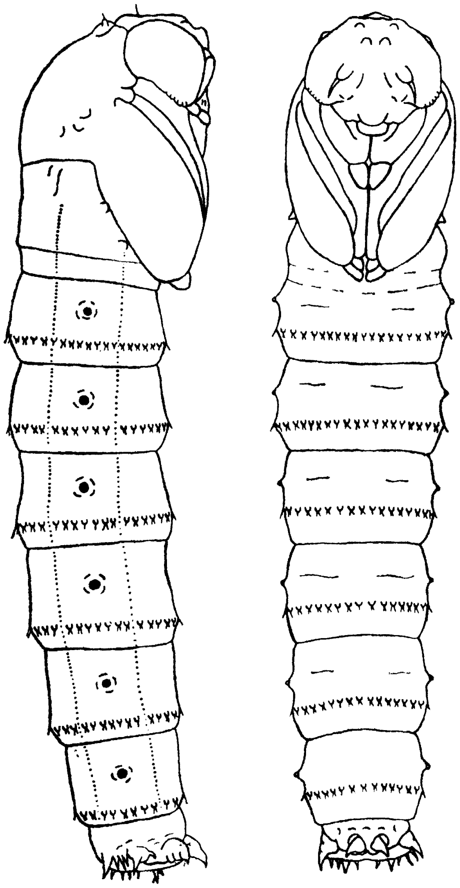


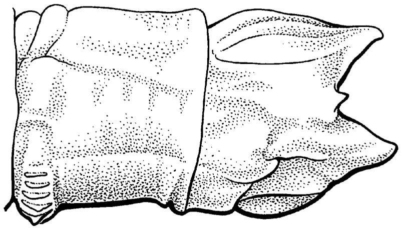
13 *Arthroteles* ♂

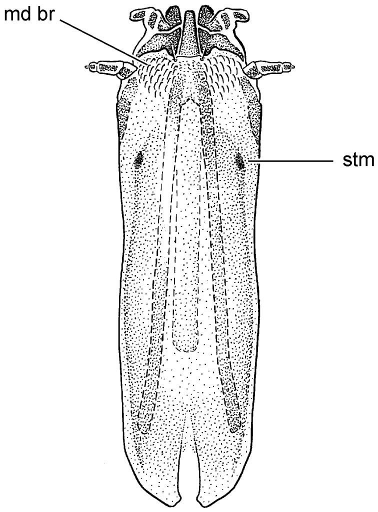
Figs 37.11–13. Terminalia of Rhagionidae: (11) female terminalia of *Arthroteles bombyliiformis* Bezzi, lateral view; (12) same, ventral view; (13) same, male terminalia, dorsal view (epandrium and proctiger removed).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; lat ej proc – lateral ejaculatory process; pm sh – parameral sheath; st – sternite; tg – tergite.


14 *Chrysopilus*


15 *Chrysopilus*


16 *Chrysopilus*



17 *Chrysopilus*

Figs 37.14–17. Larvae and pupae of Rhagionidae (non-Afrotropical): (14) larval habitus of *Chrysopilus* sp., lateral view; (15) pupal habitus of *Chrysopilus* sp., lateral (left) and ventral (right) views; (16) larval terminal segments of *Chrysopilus* sp., lateral view; (17) larval head capsule of *Chrysopilus* sp., dorsal view. Fig. 15 (after Hobby & Smith 1962, figs 7, 8), Fig. 16 (James & Turner 1981, fig. 21), Fig. 17 (after James & Turner 1981, fig. 15).

Abbreviations: md br – mandibular brush; stm – stemmata.

and *Austroleptis* Hardy, previously included in the Rhagionidae, are now assigned to two monogeneric families.

Rhagionidae now contain approximately 700 species in 16 genera, most of which occur in north and south temperate regions (Kerr 2010). Within the Afrotropical Region, two subfamilies are represented, Rhagioninae (*Arthroteles, Atherimorpha* and questionably *Rhagio* F.) and Chrysopilinae (*Chrysopilus*).

Rhagioninae is supported by the unique form of the endoaedeagal process, which is strongly laterally compressed. *Rhagio* and its nearest relatives are also united in having the lateral ejaculatory processes integrated into the sperm sac membrane (Kerr 2010). The chrysopilines are supported by three synapomorphies: the presence of metallic or scale-like thoracic setae; a reduced proepimeron sclerite; and flattened, appressed setae on the legs, especially the femur (Kerr 2010). *Chrysopilus* is the largest genus of the family with a global distribution. It is also the most commonly encountered rhagionid genus in the Afrotropics.

Identification

Illustrations of the mouthparts, antenna, wing, male and female terminalia and an identification key to *Arthroteles* were provided by Stuckenberg (1956*a*) and a new species was illustrated by Nagatomi & Nagatomi (1990*a*). A key to Malagasy *Chrysopilus*, with illustrations of diagnostic features, was provided by Stuckenberg (1965) and the *Chrysopilus* of South Africa were treated by Stuckenberg (1997). The *Atherimorpha* species of southern Africa were revised by Nagatomi & Nagatomi (1990*b*), building on the contribution of Stuckenberg (1956*b*). Oldroyd (1939: 15) reported three specimens of *Rhagio* from South Africa (as Pondoland and Zululand). These were re-examined here and represent a yellow species of *Atherimorpha* (possibly *A. flavicorpus* Nagatomi & Nagatomi, 1990). Stuckenberg (1960: 270) reported additional specimens tentatively identified as *Rhagio* from the south-western Cape, South Africa, but apparently the specimens concerned were in very poor condition.

Key to genera of Afrotropical Rhagionidae

1. First antennal flagellomere bearing long arista-like stylus apically (*e.g.*, Fig. 7); wing vein R_{2+3} strongly arched, terminating close to apex of vein R_1 (*e.g.*, Figs 1, 10) 2

– First antennal flagellomere followed by 5–8 tapered flagellomeres (*e.g.*, Figs 5, 6); wing vein R_{2+3} not arched, distant from apex of vein R_1 (*e.g.*, Figs 8, 9) 3

2. Hind tibia with 1 spur . . . . *Chrysopilus* Macquart

– Hind tibia with 2 spurs. . . . . [*Rhagio* F.]

3. Proboscis short and fleshy (not specialised for flower-feeding) (Figs 3, 6); eyes in male narrowly dichoptic . . . . *Atherimorpha* White

– Proboscis elongate and sclerotised (specialised for flower-feeding) (Fig. 2); eyes in male usually holoptic (Fig. 5) (except in *A. longipalpis*). . . . . *Arthroteles* Bezzi

Synopsis of the fauna

There are just over 40 species of Rhagionidae known to occur in the Afrotropical Region, although the true number is likely to be considerably greater, as many species of the genus *Chrysopilus* remain undescribed.

***Arthroteles* Bezzi** (Rhagioninae)**.** An endemic genus of four species, all apparently restricted to South Africa. The genus is distinguished by the forward projecting and elongate proboscis (Fig. 2); a specialised adaptation for flower-feeding (Stuckenberg 1956*a*) and 2-segmented palpus. The genus is strictly montane, with species in the Natal Drakensberg and Cape Fold Mountains, with distinct species-specific flight periods (Kerr 2010; Stuckenberg 1956*a*, 1962). The biology and immature stages remain unknown.

***Atherimorpha* White** (Rhagioninae)**.** A genus of 51 described species (1 extinct), occurring in the Afrotropical, Neotropical and Oceanian/Australasian Regions. *Atherimorpha* is a Gondwanan element, distributed in south-east Australia, Tasmania and temperate South America (Nagatomi & Nagatomi 1990*b*; Stuckenberg 1962). Twelve species occur in the Afrotropics, apparently confined to Lesotho and South Africa. Some species have only been collected during the winter months (*e.g.*, *A. crassitibia* Nagatomi & Nagatomi, 1990). The genus is distinguished by the form of the antenna, fleshy proboscis and 2-segmented palpus (Fig. 6) (Kerr 2010). An identification key to the South African species was provided by Nagatomi & Nagatomi (1990*b*). The biology and immature stages remain unknown.

***Chrysopilus* Macquart** (Chrysopilinae)**.** A genus of 361 described species (3 extinct), occurring in all zoogeographical regions, except Antarctica. Thirty-seven species are recorded from the Afrotropics, the majority of which occur in Madagascar (the single rhagionid genus known to occur there) and Stuckenberg (1997) detailed the distribution of the genus across the region. The *Chrysopilus* fauna of the Afrotropics is poorly known, however, with most species only known from the type localities and appear confined to narrow distributional ranges (Stuckenberg 1997). *Chrysopilus* is characterised by the arista-like stylus (Fig. 7), 1-segmented palpus, and single hind tibial spur.

[***Rhagio* F.** (Rhagioninae). A genus of 167 described species occurring throughout the Holarctic Realm. Immature stages of the genus occur in damp, humus rich soils. A single specimen of *R. conspicuus* (Meigen, 1804) was recorded from United Arab Emirates by Deeming (2010), but is considered a doubtful record, due to the absence of suitable habitat. For this reason the genus is included in the above key in square brackets representing a questionable record.]

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ATHERICIDAE 38

(Water Snipe Flies)

Norman E. Woodley

Fig. 38.1. Male of *Suragina milloti* (Séguy) (Madagascar) (photograph © S.A. Marshall).

Diagnosis

Medium-sized flies (body length: 5.5–12 mm) (Fig. 1), sometimes with patterned wings.

Head of female with eyes widely separated, in males ranging from virtually holoptic to widely separated and not sexually dimorphic; antenna with scape and pedicel short, flagellum composed of 2 flagellomeres, flagellomere 1 small, ovoid to usually kidney-shaped, with flagellomere 2 in form of an elongate arista-like stylus, inserted dorsally in all Afrotropical species (Figs 7, 9–11); clypeus typically convex, bulbous, but this may be poorly developed in *Pachybates* Bezzi; proboscis slightly elongate, usually about as long as head height; with labella well-developed, sometimes mouthparts adapted for blood-feeding; palpus 2-segmented, basal segment small, ovoid, apical segment elongate and usually curved ventrally (Figs 9–11).

Thorax unmodified; posterior spiracle with scale-like elevation immediately posterior to it. Scutellum evenly rounded apically. Legs simple, sometimes elongate and delicate, or

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 885–891.

having femora and tibiae strongly thickened, male of *Trichacantha* Stuckenberg with hind legs enlarged and elongate (Fig. 7); tibial spurs usually 0 – 2 – 2, 0 – 1 – 2, or absent in *Trichacantha* except for highly enlarged and modified spur on hind tibia in males (Fig. 7). Wing (Figs 12, 13) ranging from hyaline to distinctly patterned; vein R_{2+3} ending in costal vein (*C*) proximal to, or at apex of vein R_1; vein M_3 usually present, absent in one species (Fig. 13); cell *cua* elongate, closed just before wing margin, but widely open in *Trichacantha*.

Abdomen about as wide as thorax, only slightly tapered posteriorly, apex sometimes somewhat blunt; male terminalia (Fig. 14) with hypandrium fused with gonocoxites, gonocoxal apodemes very elongate and aedeagal tines present; female cercus 1-segmented, about as long as wide, rounded posteriorly; 3 spermathecae present.

Larvae (Fig. 15) with head small, retractable into thorax; abdomen with distinctive morphology, including paired abdominal prolegs on segments 1–7 and segment 8 with single, unpaired proleg (absent in *Atrichops* Verrall); prolegs apically with curved, simple claws (crochets), other fleshy processes usually present on abdominal segments 2–7 and longer ones sometimes present on segment 8.

2 *Pachybates*

3 *Suragina* 4 "*Atherix*" 5 *Atrichops* 6 *Suragina*

Figs 38.2–6. Hind legs, hind coxa and proepimeron of Athericidae (lateral views): (2) hind legs of *Pachybates braunsi* (Bequaert); (3) hind coxa of *Suragina* sp.; (4) same, "*Atherix*" sp.; (5) proepimeron of *Atrichops* sp. (non-Afrotropical); (6) same, *Suragina* sp. Fig. 2 (photograph B. Muller), Fig. 4 (photograph A.H. Kirk-Spriggs).

Abbreviations: cx – coxa; prepm – proepimeron; proc – process; tb – tibia; tsm – tarsomere.

Adult Athericidae are easily recognised by the presence of the postspiracular scale on the metathorax, shared only with Tabanidae (see Chapter 39), from which they can be immediately separated by their modified antenna with slender stylus and their more delicate habitus. Athericids closely resemble Rhagionidae (see Chapter 37) in general form, but rhagionids have no postspiracular scale and usually have a more tapered abdomen.

Biology and immature stages

As far as is known, the immature stages of Athericidae are strictly aquatic. Larvae usually occur in rocky or gravelly riffle areas of flowing streams (Nagatomi 1962; Webb 1995). Larvae are predaceous and can be fed in the laboratory on oligochaetes and chironomid larvae (Neff 1965). Larval stages are well known in the Palaearctic Region and each genus usually has a distinctive morphology (Rozkošný & Nagatomi 1997: 443, 444). Presumed larvae of *Suragina* Walker have been collected in South Africa (Stuckenberg 1965: 92), but no larvae of athericids have been reared or described from the Afrotropical Region. Adults are usually collected on vegetation near streams and adults of *Pachybates* and *Trichacantha* are known to form large aggregations (Bequaert 1921; Stuckenberg 1955) that resemble swarms of bees, similar to the behaviour of *Atherix* Meigen in north temperate regions. Adults of some genera, including *Atrichops* and *Suragina*, are known, depending on the species, to feed on amphibian, avian and mammalian blood (Stuckenberg 2000). Nagatomi (1962) provided a comprehensive review of the biology of both adults and larvae of Japanese species, which probably has general applicability to species in other regions.

Economic significance

No species, including those that feed on blood, are known to have economic significance.

Classification

Athericidae are included in the infraorder Tabanomorpha and are sister-group to the Tabanidae (Woodley 1989: 1381). Stuckenberg (1973) was the first to recognise athericids as a family separate from the Rhagionidae *sensu stricto* and elegantly outlined the character evidence supporting their relationship to the Tabanidae. Prior to that athericids had been considered part of the Rhagionidae. All subsequent phylogenetic studies have supported this sister-group relationship (*e.g.*, Kerr 2010; Zloty *et al*. 2005).

Ten genera of Athericidae are currently recognised globally (Stuckenberg 2000), divided into two subfamilies. Stuckenberg (1973) presented evidence that *Dasyomma* Macquart (confined to southern South America and Australia) is sister-group to the remaining genera, erecting the subfamily Dasyommatinae for the genus and placed all remaining genera in the subfamily Athericinae. No rigorous cladistic analysis has been undertaken, however, that includes all athericid genera. Most of the described genera are well characterised, but the generic concept of *Suragina* on a world level is not fully satisfactory (Stuckenberg 2000). That being said, the athericid genera recognised in South Africa are the most poorly understood. Species that were once assigned to *Atherix* that occur there are now not considered congeneric with the Holarctic species (Nagatomi 1984*b*; Stuckenberg 1980, 2000), and Stuckenberg (1960: 275) stated, concerning *Pachybates*, "… clear-cut distinctions from *Atherix* [*i.e.*, the South African species] are not easy to draw as many of the characters are sexual or based on comparative proportions, and are unequally developed between the sexes." Thus, the South African genera are badly in need of revision to properly place the species that occur there.

About 100 species of Athericidae are described, with greatest species diversity in the south temperate regions. Twenty-two described species occur in the Afrotropical Region and although additional undescribed species certainly exist, the number of species in the family is not likely to become significantly greater with additional study and collecting.

Identification

Stuckenberg's (1960) chapter treats the known Afrotropical genera of athericids (as part of Rhagionidae), except *Atrichops* (not known to occur in the Afrotropics in 1960), as well as the South African species, with identification keys. Bezzi (1926) treated some South African species and his original descriptions are useful. Stuckenberg's (1965) paper on the rhagionids of Madagascar provides identification information for the two species of *Suragina* that occur there. Stuckenberg (1980) catalogued the Afrotropical athericids and only one species, *Atrichops stuckenbergi* Nagatomi, 1984, has subsequently been described.

Key to genera of Afrotropical Athericidae

1. Wing cell *cua* widely open at wing margin (Figs 7, 8, 12); mid tibia of male without apical spurs, hind tibia with 1 very large, rigid, curved spur (Fig. 7), female without tibial spurs (Eastern Cape Province, South Africa) . . . . *Trichacantha* Stuckenberg

– Wing cell *cua* usually closed at or before wing margin (*e.g.*, Fig. 13), occasionally very narrowly open; mid tibia of both sexes with 1, or usually 2, apical spurs, hind tibia with 2 spurs (widespread) 2

2. Femora stout, especially on hind legs, and hind tibia also strongly thickened (Fig. 2); tarsomere 1 of hind leg slightly produced ventrally, so its apex is oblique; both sexes strongly dichoptic (Western Cape Province, South Africa). . . . . *Pachybates* Bezzi

– Femora not unusually stout, hind tibia not strongly thickened; tarsomere 1 of hind leg not produced ventrally, truncate at apex; eyes usually much more narrowly separated in male than in female (widespread) 3

3. Anterior apex of hind coxa with distinct sharp spur-like process (*e.g.*, Fig. 3); female head with frons partly with velvety-black vestiture (small patches in some *Atrichops*); slender, often brightly coloured species, with long legs (widespread) 4
– Anterior apex of hind coxa without distinct sharp spur-like process (Fig. 4); female head with frons without velvety-black vestiture; more compact, dully coloured species with proportionately shorter legs (South Africa) . . . . *"Atherix"* Meigen
4. Thorax with proepimeron with ventrally directed flap-like process (Fig. 5); tibial spurs 0 – 1 – 2; female head with margins of frons distinctly diverging dorsally, with lateral velvety-black patches on dorsal part; antennal bases narrowly separated . . . . *Atrichops* Verrall
– Thorax with proepimeron without ventrally directed process (Fig. 6); tibial spurs 0 – 2 – 2; female head with margins of frons virtually parallel-sided, or slightly convergent dorsally, with dorsal part anterior to ocellar tubercle entirely velvety-black; antennal bases more widely separated . . . . . . *Suragina* Walker

Synopsis of the Fauna

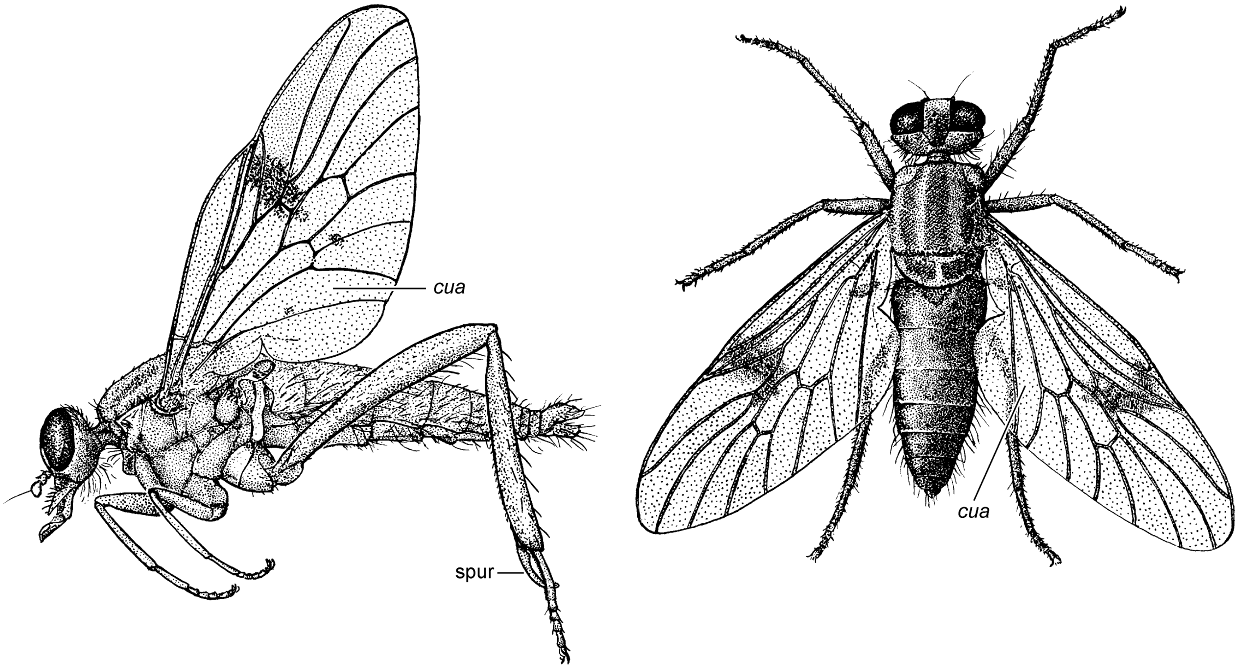
***"Atherix"* Meigen** (Athericinae)**.** A small genus of *ca* seven species occurring in the Nearctic and Palaearctic Regions. Five additional South African species have been placed in the genus (Stuckenberg 1960), but were subsequently considered unplaced species (Stuckenberg 1980) and are now considered not to be congeneric with the north temperate species (Nagatomi 1984*b*; Stuckenberg 2000) and thus are not combined with a generic name. Presumably these were what Stuckenberg (2000: 157) referred to as "… several undescribed South African genera." Nagatomi (1984*b*: 96) separated the South African species from true *Atherix* by the former having narrower parafacials and a narrower female frons. These species require further study to be placed in context within the family with respect to the Northern Hemisphere species (which include the type species for the genus). Stuckenberg (1960: 270) provided an identification key to the South African species placed here. One species, *A. kar* Stuckenberg, 1960, was found "… in considerable numbers on herbage lining the banks of two densely-shaded little streams running through montane forest …" (Stuckenberg 1960: 273). No other biological information is known about the South African species.

***Atrichops* Verrall** (Athericinae)**.** A small genus with 11 described species occurring primarily in the Oriental and Palaearctic Regions, with only one Afrotropical species, *A. stuckenbergi* Nagatomi, 1984, known from Kenya (Nagatomi 1984*a*). Nagatomi (1979: 281) noted that B.R. Stuckenberg (*in litt*.) mentioned a single specimen from Central Africa that was undescribed and it is not known whether this is conspecific with the Kenyan material. Adult females of European and Japanese species of *Atrichops* have been observed feeding on amphibian blood (Nagatomi 1962).

***Pachybates* Bezzi** (Athericinae)**.** A small genus of two species and one subspecies known only from the Western Cape Province, South Africa. Stuckenberg (1960) described *P. incompleta adeps* Stuckenberg as a subspecies from the Cape Peninsula, while *P. i. incompleta* (Bezzi, 1926) is known from other parts of the Western Cape Province. The characters used to separate the two taxa, however, appear to indicate that *P. i. adeps* should be considered a separate species. Stuckenberg (1960: 275) provided a key to all three taxa. The first species described that is now placed in *Pachybates*, *P. braunsi* (Bequaert, 1921) (Fig. 2), was observed to form large aggregations similar to north temperate *Atherix*. Bequaert (1921: 3), citing a letter from Dr. H. Brauns (*in litt*.), stated: "… [this species] is at home along the margin of swiftly running brooks near Cape Town. One finds females and males of it on stones that emerge above the water (the female is smaller and black), bunched together in masses as large as a man's head; every moment pieces the size of a fist break away from the mass …".

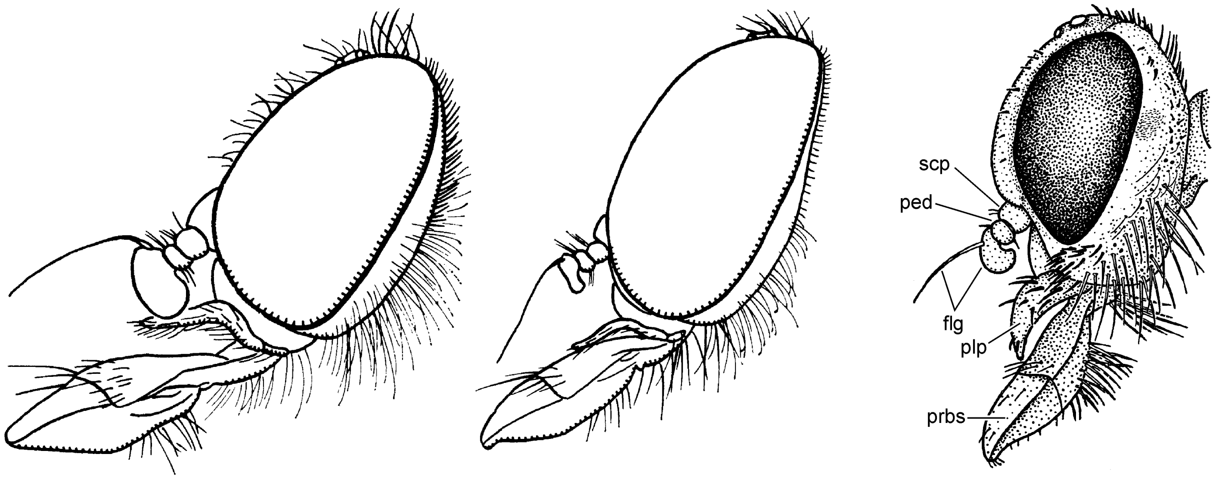
***Suragina* Walker** (Athericinae)**.** A genus of *ca* 45 species occurring in all zoogeographic regions, except Antarctica. Thirteen species occur in the Afrotropical Region, ranging from Nigeria, Chad and Uganda, south to South Africa and Madagascar. The two species known from Madagascar are the only athericids recorded from the island. The majority of Afrotropical *Suragina* spp. were described under the name *Atrichops*, which was more or less considered synonymous with *Suragina* at the time. More recently, *Atrichops* has been recognised as a valid genus (see Stuckenberg 1965: 91, for brief summary). Despite earlier confusion, all Afrotropical species currently assigned in *Suragina* are probably correctly placed. Stuckenberg (1960: 293) treated the South African species, but did not include an identification key. He later dealt with the two species occurring in Madagascar (Stuckenberg 1965). Adults of at least some *Suragina* spp. congregate on vegetation near water, but do not form masses (Stuckenberg 1960: 284). Adult females of a few species have been recorded feeding on mammalian blood, including humans (Nagatomi 1962), and Stuckenberg & Young (1973) reported *Suragina bivittata* (Bezzi, 1926) feeding on the Giant eagle owl (*Bubo lacteus* Temminck) in the Mpumalanga Province (former eastern Transvaal), South Africa. Stuckenberg (2000) speculated that females of all species of *Suragina* feed on blood of vertebrate hosts. There are specimens known of an undescribed athericid from Madagascar that will key to *Suragina* in the above identification key, but these have a highly modified first flagellomere that is very strongly bilobed, with the lobes slender so that the flagellomere appears C-shaped. The writer's inclination is to regard these as a species of *Suragina* with a highly autapomorphic antennal flagellum, but only further study will resolve status and placement of the flies that have this character.

***Trichacantha* Stuckenberg** (Athericinae)**.** A monotypic genus with the single species, *T. atranupta* Stuckenberg, 1955, recorded only from the Eastern Cape Province, South Africa (Stuckenberg 1955, 1960: 280). The species is sexually dimorphic (Figs 7, 8). The male is a robust, yellowish orange fly, with greatly enlarged hind legs with a large, curved apical tibial spur. The female is more brownish, with hind legs that are not enlarged or modified. Stuckenberg (1960: 282) provided an account of the behaviour of adult flies, and stated: "The flies were found clustering under a section of a fairly low-lying bridge overhanging a swift flow of water. The cluster consisted almost entirely of dead females and batches of eggs, and some living females engaged in oviposition. Numerous males attending females were present elsewhere on the underside of the bridge and on the supporting piles." The immature stages remain unknown.



7 *Trichacantha* ♂

8 *Trichacantha* ♀



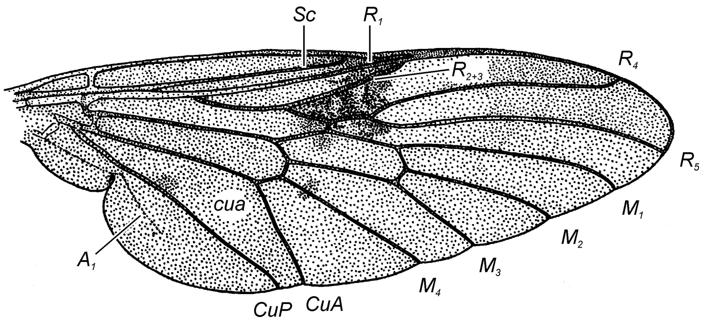
9 *Suragina* ♀

10 *Suragina* ♂

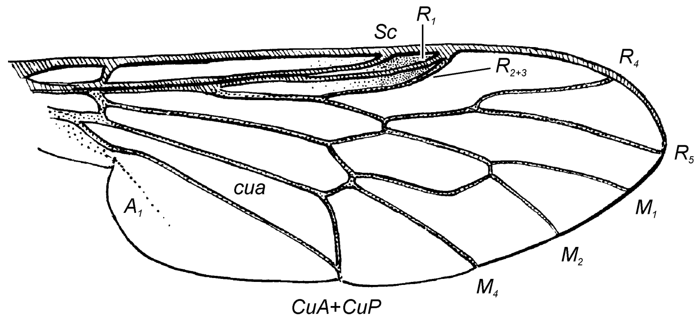
11 *Trichacantha* ♂

Figs 38.7–11. Habitus and heads of Athericidae: (7) habitus of *Trichacantha atranupta* Stuckenberg, lateral view ♂; (8) same, dorsal view ♀; (9) head of *Suragina milloti* (Séguy), lateral view ♀; (10) same ♂; (11) same, *T. atranupta* ♂. Figs 7, 8 (Stuckenberg 1960, figs 77, 78), Figs 9, 10 (Stuckenberg 1965, figs 3, 4), Fig. 11 (Stuckenberg 1955, fig. 3).

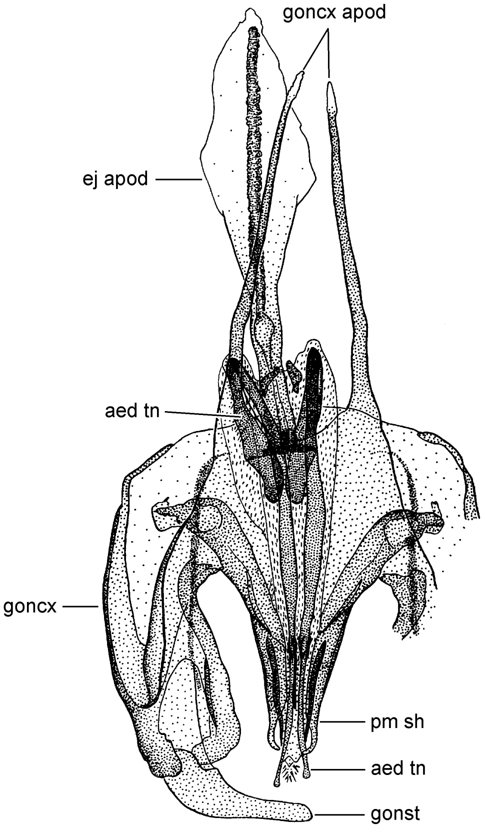
Abbreviations: *cua* – anterior cubital cell; flg – flagellum; ped – pedicel; plp – palpus; prbs – proboscis; scp – scape.



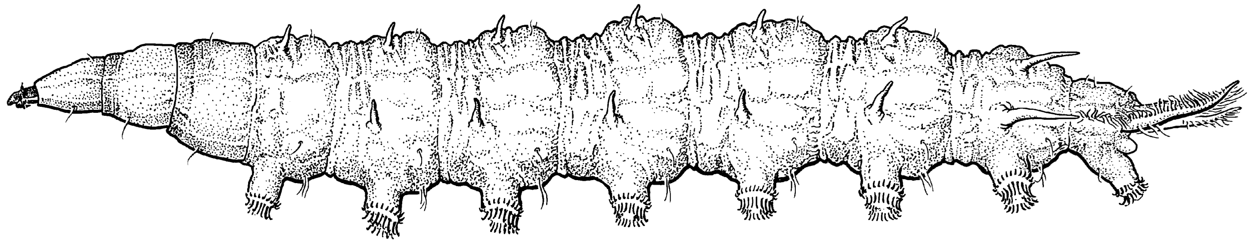
12 *Trichacantha* ♀



13 *Pachybates* ♀



14 *Suragina* ♂



15 *Atherix*

Figs 38.12–15. Wings, male terminalia and larva of Athericidae: (12) wing of *Trichacantha atranupta* Stuckenberg, dorsal view ♀; (13) same, *Pachybates incompleta adeps* Stuckenberg ♀; (14) male genital capsule of *Suragina monogramma* (Bezzi), dorsal view, epandrium and proctiger removed. (15) larval habitus of *Atherix* sp., lateral view (non-Afrotropical). Fig. 12 (Stuckenberg 1955, fig. 4), Fig. 13 (Stuckenberg 1960, fig. 73), Fig. 14 (after Stuckenberg 1973, fig. 1), Fig. 15 (Webb 1981, fig. 7).

Abbreviations: A_1 – first branch of anal vein; aed tn – aedeagal tine; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *CuP* – posterior branch of cubital vein; ej apod – ejaculatory apodeme; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; pm sh – parameral sheath; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Sc* – subcostal vein.

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TABANIDAE 39

(Horse Flies, Deer Flies and Clegs)

John Chainey

Fig. 39.1. Female of *Tabanus taeniola* Palisot de Beauvois (Namibia) (photograph © S.A. Marshall).

Diagnosis

Medium- to large-sized, generally robust-looking flies (body length: 6–25 mm) (Figs 1–11), with body often densely clothed in pruinescence, giving flies a dusted appearance; body and legs clothed in setulae, but virtually devoid of setae; numerous species of subfamilies Chrysopsinae and Tabaninae with beautifully coloured compound eyes during life, often with brilliant green, purple or red maculae or fasciae (Figs 3–5), these colours and patterns sometimes useful in identification, but advisable to note colours when specimens fresh, as colours lost or obscured after death (sometimes possible to temporarily restore patterns, by placing specimens in relaxing chamber).

Head (Figs 12, 13) generally large, at least as wide as mesonotum; compound eyes invariably dichoptic in females, separated by frons, usually holoptic in males (Figs 4, 6, 11), but in some species narrowly separated and in very few cases similar to females (Fig. 2); males of numerous species with upper eye facets greatly enlarged (often area of enlarged facets dark centrally, surrounded by pale area) (Fig. 4); in most species the colouration of the eye is formed by the reflections of the lenses of individual facets, hence acting like reflective sunglasses (Lunau & Knüttel 1995); frons (Fig. 12) usually with 1 or more bare, slightly raised areas (calli), often reduced to narrow line in Pangoniinae (Fig. 14); sometimes with raised ocellar triangle at vertex, which may include 3 ocelli; frons becomes median

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 893–913.

occipital sclerite on occiput; subcallus situated below frons and above antennae (Fig. 12); clypeus sometimes large and protuberant (Fig. 23), area between clypeus and eyes being parafacial; antenna (Figs 15–17) comprising scape, pedicel and flagellum; flagellum usually the longest segment, divided into 3–8 flagellomeres; basal flagellomere invariably the largest, often with dorsal projection (generally referred to as "tooth"), this projection may be forwardly-produced, exceptionally with

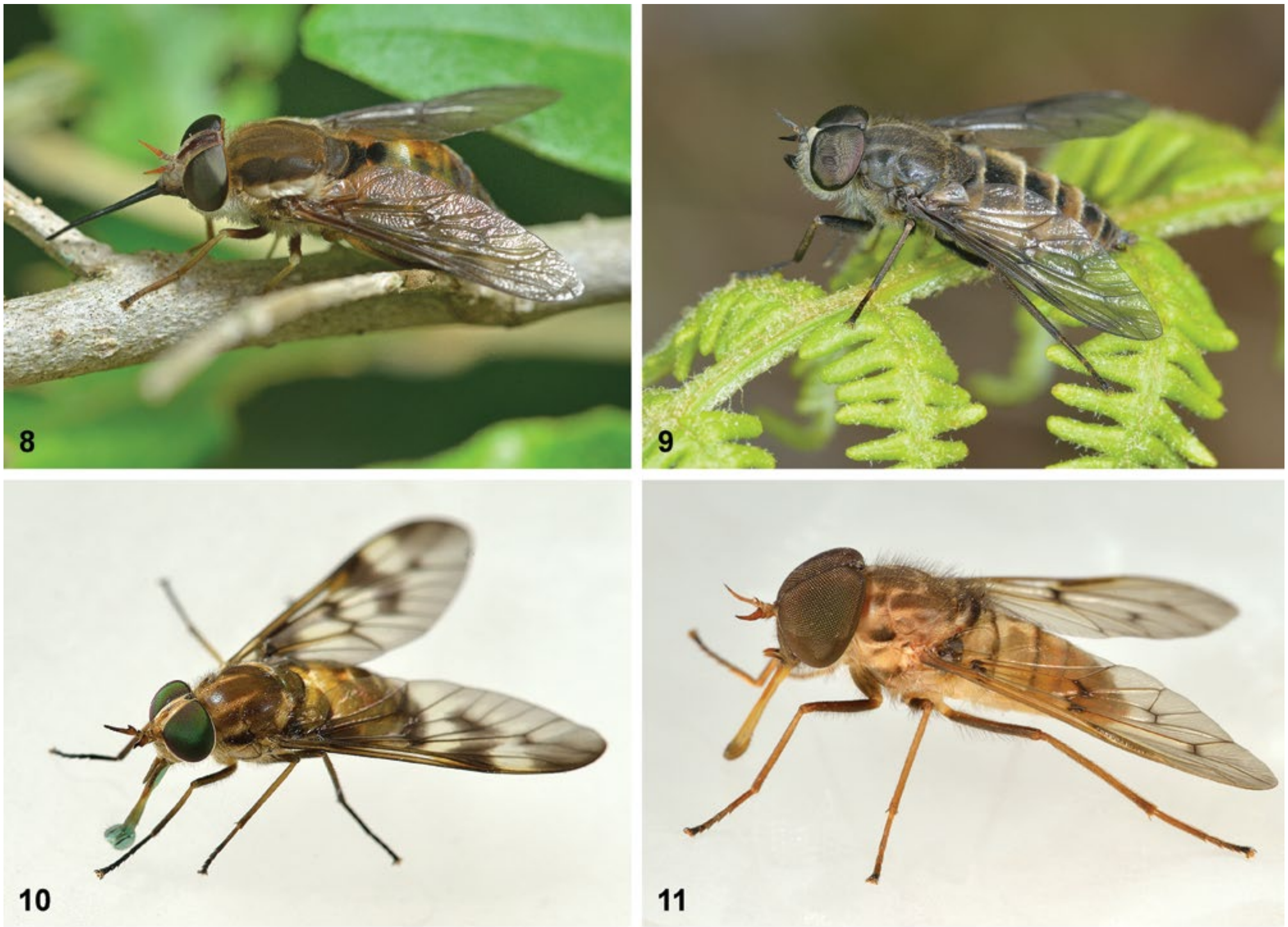
Figs 39.2–7. Habitus of Afrotropical Tabanidae: (2) copulating pair of *Rhigioglossa* (*Rhigioglossa*) *nitens* Chainey (South Africa); (3) *Chrysops obliquefasciatus* Macquart (Namibia); (4) *Tabanus gratus* Loew (Namibia); (5) *Haematopota* sp. (South Africa); (6) *Ancala* sp. (Namibia); (7) *T. biguttatus* Wiedemann (South Africa). Photographs © S.A. Marshall.

2 dorsal projections (Fig. 17), remainder of flagellum sometimes referred to as stylus; arista invariably absent; palpus 2-segmented, with basal segment generally small and apical segment (Figs 12, 13) generally long and tapered in females, more rounded in males, held close to base of proboscis; females of many species with proboscis adapted for blood-feeding, with well-developed blade-like mandibles and maxillae; together with the hypopharynx and labrum, these structures held within trough-like labium, at apex of which is the labellum, which may be large (Fig. 13) – this combined structure termed the syntrophium; sclerotised part of labium attached to head by ventral rostral membrane, which allows stretching to gain additional functional length (Morita 2011).

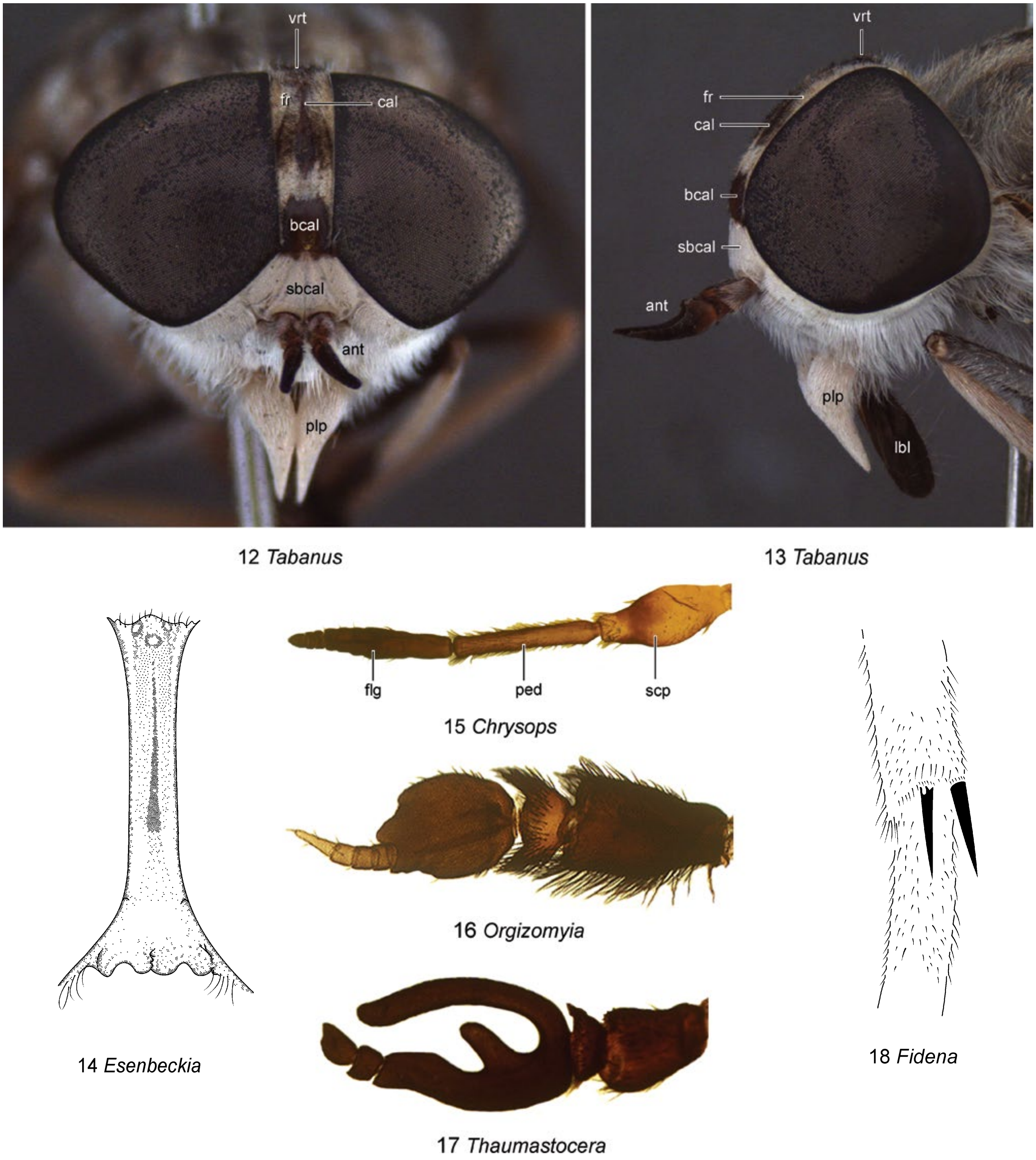
Thorax with legs with paired apical spurs on mid tibia and sometimes hind tibia (Fig. 18); tarsi with pulvilliform empodium (Chapter 3, fig. 49), hence apparently each with 3 pulvilli. Wing (Figs 24–41) hyaline or distinctly patterned; large cells *br*, *bm* and *d* invariably present (Fig. 29); cell *cua* usually closed near wing margin (Fig. 29); cells r_5 and m_3 sometimes closed at, or before, wing margin (Fig. 24); vein R_4 invariably reaching wing margin before apex, vein R_5 reaching posterior margin (Fig. 29); basicosta bare or setulose (Fig. 29); alula and upper and lower calypteres well-developed (Figs 28, 30; Chapter 3, fig. 44b).

Abdomen with male terminalia generally unremarkable, being simple and uniform below tribal level (Mackerras 1954; Morita 2008*a*); male (Fig. 42) with gonocoxite fused with hypandrium and gonostylus single, or occasionally bifid (Pangoniini); epandrium either entire or divided; tergite 10 absent; female (Fig. 43) with tergite 10 divided and sternite 8 large.

The family Tabanidae can be readily separated from other similar sized Diptera by the structure of the antennae, pulvilliform empodium, the wing venation and the almost complete absence of setae on the body and legs. Some Tabanidae are superficially similar to Nemestrinidae (see Chapter 43) and Apioceridae (see Chapter 46) in the field. Both Nemestrinidae and Apioceridae differ in wing venation, with vein M_1 (and R_5 where present) curving up to reach the costal vein (C) before (anterior to) the apex of the wing; these veins always reach the posterior margin of the wing in Tabanidae.



Figs 39.8–11. Habitus of Afrotropical Tabanidae: (8) *Philoliche* (*Philoliche*) *rondani* (Bertoloni) (South Africa); (9) *Rhigioglossa* (*Perisilvius*) sp. nr. *designata* (Oldroyd) (South Africa); (10) *Tabanocella* (*Tabanocella*) sp. nr. *maculata* Surcouf (Madagascar); (11) *Aegophagamyia* (*Triclida*) *longirostris* (Séguy) (Madagascar). Photographs © S.A. Marshall.



Figs 39.12–18. Heads, frons, antennae and hind tibia of Tabanidae: (12) head of *Tabanus taeniola* Palisot de Beauvois, frontal view; (13) same, lateral view; (14) frons of *Esenbeckia peruviana* Burger, frontal view (non-Afrotropical); (15) antenna of *Chrysops* sp., lateral view; (16) same, *Orgizomyia zigzag* Palisot de Beauvoist; (17) same, *Thaumastocera akwa* Grünberg; (18) hind tibia of *Fidena flavipennis* (Kröber), ventral view (non-Afrotropical). Figs 12, 13 (photographs A.H. Kirk-Spriggs), Figs 14, 18 (after Burger 2009, figs 15b, 3, respectively).

Abbreviations: ant – antenna; bcal – basal callus; cal – callus; flg – flagellum; fr – frons; lbl – labellum; ped – pedicel; plp – palpus; sbcal – subcallus; scp – scape; vrt – vertex.

Biology and immature stages

Afrotropical Tabanidae are associated with a wide range of habitat types, occurring in forest, savanna and desert, montane and coastal biomes. Most species appear to be sedentary in habits and none are known to be migratory. Very few species are shared with neighbouring zoogeographical regions, but the presence of *Tabanus taeniola* Palisot de Beavois, 1806 (Fig. 1), in Aldabra Is. (Seychelles) and Madagascar may indicate occasional long-distance dispersal and this species has been taken on ships off the east coast of Africa (pers. obs.).

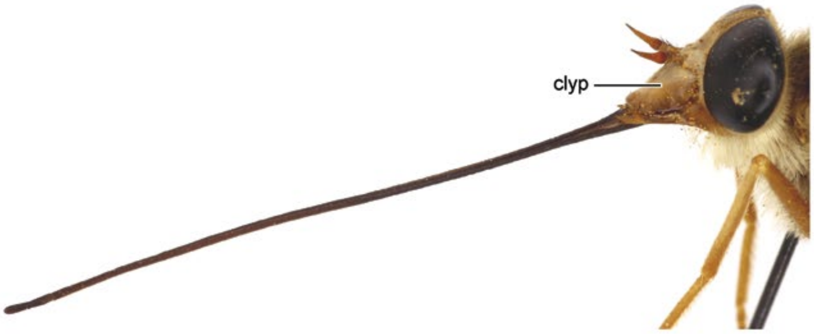
Eggs are often laid in large masses, close to the substrate in which the larvae develop, *e.g.*, on surrounding vegetation. Larvae (Fig. 44) are generally cylindrical in form, reaching a length of at least 46 mm in larger species, such as *Tabanus biguttatus* Wiedemann, 1830. They may occur in mud, sand, soil and a variety of other semi-aquatic or aquatic situations, e.g., the larvae of *Ancala fasciata* (F., 1775) are adapted to living in aquatic vegetation and are notable for their green colouration, while those of others, particularly some species of the tribe Rhinomyzini, occur in the rot holes of trees. Tabanid larvae are generally predaceous; the mandibles (Fig. 45) are equipped with a duct, through which passes the venom with which they subdue their prey. They feed on other invertebrates and are cannibalistic, at least in captivity. They may also attack vertebrates, such as frogs and in some situations will also attack man and presumably other large mammals. Larvae may be long-lived and the larval stage may last more than one season, dependant on conditions. Pupation occurs below ground, close to the substrate occupied by the larva. The pupa (Fig. 46) is mobile, but is usually positioned vertically, enabling it to work its way to the surface for adult eclosion. Under conditions of drying mud, larvae of some Afrotropical species construct hollow mud cylinders in the ground prior to pupation (*e.g.*, Fig. 47); these include *Tabanus taeniola* and *T. biguttatus*. These cylinders prevent the pupae from becoming exposed by cracks forming as the mud dries, and also enables the pupa to retreat away from the surface of the mud if conditions become excessively hot (Lamborn 1938). For some genera and many species, however, the immature stages remain unknown. These include all endemic genera and species occurring in Madagascar and other Indian Ocean islands. Important


19 *Chrysops*


20 *Chrysops*


21 *Sphecodemyia*


22 *Jashinea*



23 *Philoliche*

Figs 39.19–23. Habitus and head of Tabanidae: (19) habitus of *Chrysops silaceus* Austen, dorsal view; (20) same, *Ch. dimidiatus* Wulp; (21) same, *Sphecodemyia infuscata* Oldroyd; (22) same, *Jashinea jacoti* (Bouvier); (23) head of *Philoliche* (*Philoliche*) sp., lateral view.

Abbreviation: clyp – clypeus.

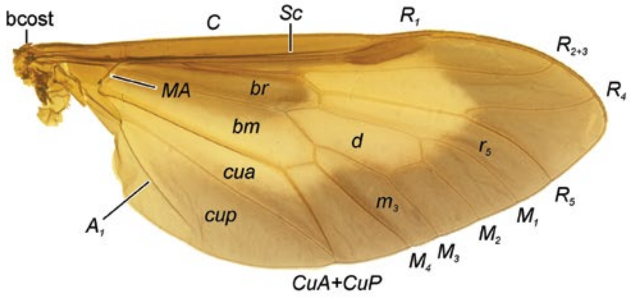
24 *Aegophagamyia* (*Aegophagamyia*)

25 *Chrysops*

26 *Chrysops*

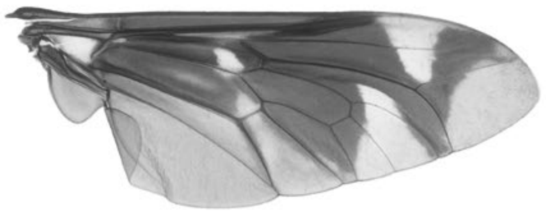
27 *Chrysops*

28 *Chrysops*



29 *Chrysops*

30 *Gressittia*



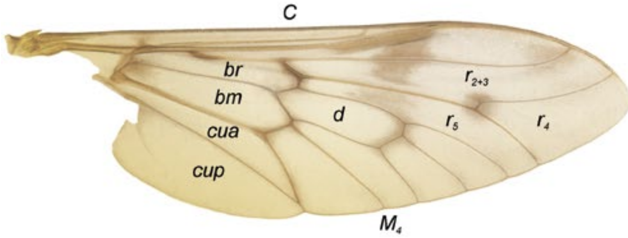
31 *Orgizomyia*

Figs 24.24–31. Wings of Tabanidae (dorsal views): (24) *Aegophagamyia* (*Aegophagamyia*) sp.; (25) *Chrysops silaceus* Austen; (26) *Ch. streptobalius* Speiser; (27) *Ch. petersi* Oldroyd; (28) *Ch. longicornis* Macquart; (29) *Ch. woodi* Neave; (30) *Gressittia pulchripennis* (Austen); (31) *Orgizomyia zigzag* (Macquart).

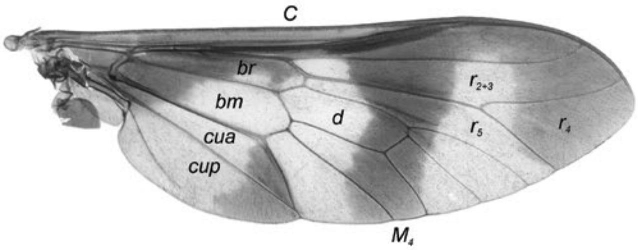
Abbreviations: A_1 – first branch of anal vein; al – alula; bcost – basicosta; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; *MA* – anterior branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *Sc* – subcostal vein.

32 *Sphecodemyia*

33 *Thriambeutes*



34 *Tabanocella* (*Tabanocella*)



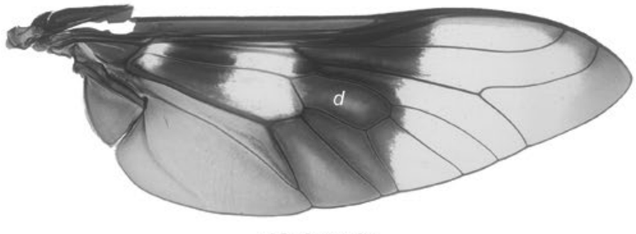
35 *Tabanocella* (*Tabanocella*)

36 *Hippocentrum*

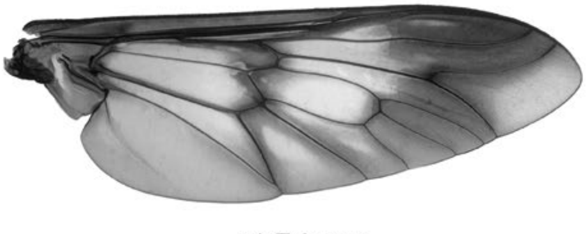
37 *Haematopota*

38 *Thaumastocera*

39 *Euancala*



40 *Ancala*



41 *Tabanus*

Figs 39.32–41. Wings of Tabanidae (dorsal views): (32) *Sphecodemyia lamborni* Austen; (33) *Thriambeutes mesembrinoides* (Surcouf); (34) *Tabanocella* (*Tabanocella*) *alveolata* (Surcouf); (35) *T*. (*Tabanocella*) *stimulans* (Austen); (36) *Hippocentrum versicolor* Austen; (37) *Haematopota pulchella* Edwards; (38) *Thaumastocera akwa* Grünberg; (39) *Euancala maculatissima* (Macquart); (40) *Ancala africana* (Gray); (41) *Tabanus marmoratus* Surcouf.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *cup* – posterior cubital cell; *d* – discal cell; M_4 – fourth branch of media; r_{2+3} – second + third radial cell; R_3 – lower branch of second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell.

works on the immature stages of Afrotropical Tabanidae include those of Goodwin (1982) and Neave (1915).

Adults of both sexes may be found at rest, or feeding at flowers, with some *Philoliche* Wiedemann spp. possessing a long proboscis, specifically adapted to feeding at particular flowers (Johnson 2010) (Figs 8, 23). Specimens of *Rhigioglossa* Wiedemann *sensu stricto* are frequently found covered in pollen (Fig. 2), suggesting that flower-feeding is important in this group. Females of most species also feed on mammalian (including humans) (Fig. 5) and/or reptilian blood, although records of flies feeding on avian blood are less common. The method of blood-sucking is unsubtle, with the blade-like mandibles being used to slash their way into a blood vessel, with the resultant flow of blood being taken up through the labella. The blood meal has the function of providing protein for egg production. In other regions, females of some species have the ability to lay one batch of eggs without a blood meal (autogeny), but this capability is little known in the Afrotropical fauna. Large, hot objects such as cars frequently attract tabanids (pers. obs.), indicating that the stimuli the flies use to find their hosts include size and temperature. Moreover, tabanids have been shown to be excellent detectors of carbon dioxide, or other odours, such as 1-Octen-3-ol (octenol) and ammonia (French & Kline 1989; Hayes *et al*. 1993; Hribar *et al*. 1992), a way to recognise living animals. Methods of attack are poorly documented for the Afrotropical Region, but *Chrysops* Meigen spp. elsewhere usually target the head. Many species are diurnal, but some are crepuscular, and a number of Afrotropical species are now known to be nocturnal and frequently come to lights (Lancaster & Haddow 1970). Mating behaviour has been little studied in the Afrotropics, but Corbet & Haddow (1962) reported on noise and swarming behaviour of males above forest canopies in Uganda. Wilkerson *et al*. (1985) suggest that the presence of enlarged eye facets in the males of some species may relate to mating behaviour at low light densities; alternatively, the enlarged facets may provide a larger focal length (Th. Zeegers, pers. comm. 2015).

Few details of parasites and predators of Tabanidae have been published in the literature and Jenkins (1964: 35) provided a summary. Tabanid egg masses are parasitised by parasitic Hymenoptera, including *Telenomus kingi* Crawford (Platygastridae) in the Afrotropics, which may result in significant control of numbers (Jenkins 1964: 35).

Predators of tabanid larvae are poorly documented in the Afrotropics, but include birds (Kopij *et al*. 2004; Taylor & Perlo 1998: 175). Afrotropical predators of adult tabanids also include birds (Fry *et al*. 1988: 250; Keith *et al*. 1992: 181; Urban *et al*. 1997: 483). Such predation is probably opportunistic, rather than targeted. In Madagascar, however, Tabanidae formed 9.7% of food given to nestlings of the endemic Chabert vanga, *Leptopterus chabert* (Müller) (Vangidae) (Schulenberg 2013: 820). Tabanids are also predated upon by certain invertebrates, including *Bembix capensis* Lepeletier de Saint Fargeau and *B. moebii* Handlirsch (Hymenoptera: Crabronidae) (Gess & Gess 1991; Neave 1915) and various species of Asilidae (Diptera). The collections of the Natural History Museum, London include a number of Tabanidae taken as prey by several Asilidae genera (especially *Promachus* Loew). While it is difficult to draw too many conclusions from these limited data, it does suggest that *Haematopota* spp. are much more subject to predation by Asilidae than similarly sized *Chrysops* spp.

Economic significance

Tabanids can be significant pests of livestock, through the transmission of disease and in loss of productivity, as large numbers of biting flies distract animals from feeding (see Chapter 5). The painful bites are unlikely to be ignored by hosts, whose counteractions encourage the mechanical transmission of disease. Some Afrotropical species, e.g., *Atylotus agrestis* (Wiedemann, 1828) and *Tabanus taeniola* (Fig. 1), are involved in the mechanical transmission of pathogens that cause diseases in livestock, such as anaplasmosis, bovine besnoitiosis and *surra* (Foil 1989; Krinsky 1976; Chapter 5). Tabanids have also been implicated in transmission of *Trypanosoma vivax* (Trypanosomatidae), although the relative impact of this in the Afrotropics remains unclear, owing to the widespread presence of *tsetse* (Glossinidae) vectors (Desquesnes & Dia 2003). Little is known of the effects of tabanids on most indigenous animals, but hosts are likely to include many primates and game animals and also larger reptiles, such as turtles in coastal habitats, or crocodiles along river margins. Three species, *Ancala africana* (Gray, 1832), *Tabanus biguttatus* (Fig. 7) and *T. taeniola* (Fig. 1) are known, however, to have an important influence on the diurnal behaviour of hippopotamus in Zululand (Tinley 1964). Genera with species known to bite humans (based on label data on specimens in the Natural History Museum, London and pers. obs.), include *Aegophagamyia* Austen, *Chrysops*, *Cydistomyia* Taylor, *Haematopota* Meigen, *Orgizomyia* Grünberg, *Philoliche*, *Rhigioglossa*, *Tabanocella* Bigot and *Tabanus* L.

Some *Chrysops* spp. are of particular importance as cyclical vectors of *Loa loa* filariasis, the non-fatal, but debilitating disease of humans and monkeys (see Chapter 6). The main foci for the disease is in West Africa, where the main vectors to humans are *C. silaceus* Austen, 1907 (Fig. 19; wing Fig. 25) and the similar *C. dimidiatus* Wulp, 1885 (Fig. 20). White (1977) stated that *C. streptobalius* Speiser, 1912 (wing Fig. 26) was the vector of *Loa loa* in Ethiopia, but this statement was based on a mixed series of specimens, that included both *C. streptobalius* and *C. distinctipennis* Austen, 1906. Vectors of the simian form of the disease include *C. centurionis* Austen, 1911 and *C. langi* Bequaert, 1930.

In other regions, tabanid larvae have been recorded as biting humans in certain situations, e.g., workers in paddy fields (Otsuru & Ogawa 1959), with their venom causing unpleasant wounds. Species of the genus *Philoliche* are known to be important pollinators of endemic plants in the South African Fynbos flora (Morita 2008*b*).

Classification

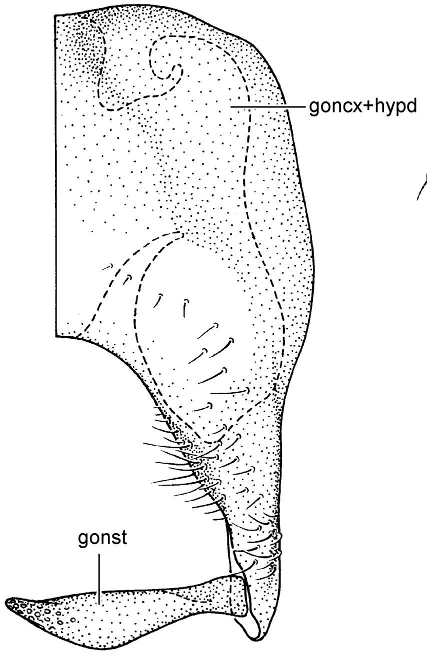
The Tabanidae have long been recognised as a distinct family within the lower Brachycera. They have traditionally been divided into four subfamilies (Mackerras 1954), although the genera of the Scepsidinae have sometimes been placed in their own subfamilies. Morita (2008*a*) suggests that this arrangement may not be correct, with just two subfamilies (Pangoniinae and Tabaninae) being one possible scenario. More recently an analysis by Lessard *et al*. (2013) has supported the monophyly of the subfamilies Chrysopsinae, Pangoniinae and Tabaninae (Scepsidinae was not included in the study).

The Pangoniinae are generally considered the oldest group within the Tabanidae, dating back to the Late Jurassic (165–145 MYA) (Martins-Neto 2003). Most species have the mouthparts with a long proboscis, the antennal flagellum divided into 8 segments and the subcostal wing vein (*Sc*) invariably bare ventrally. Four tribes are now generally recognised and likely to be monophyletic (Pangoniini, Philolichini, Scionini and the Neotropical Mycteromyiini), with the first two named occurring in the Afrotropical Region; a fifth tribe (Goniopsini) has been proposed by Lessard *et al*. (2013) for the monotypic genus *Goniops* Aldrich, but is Nearctic.

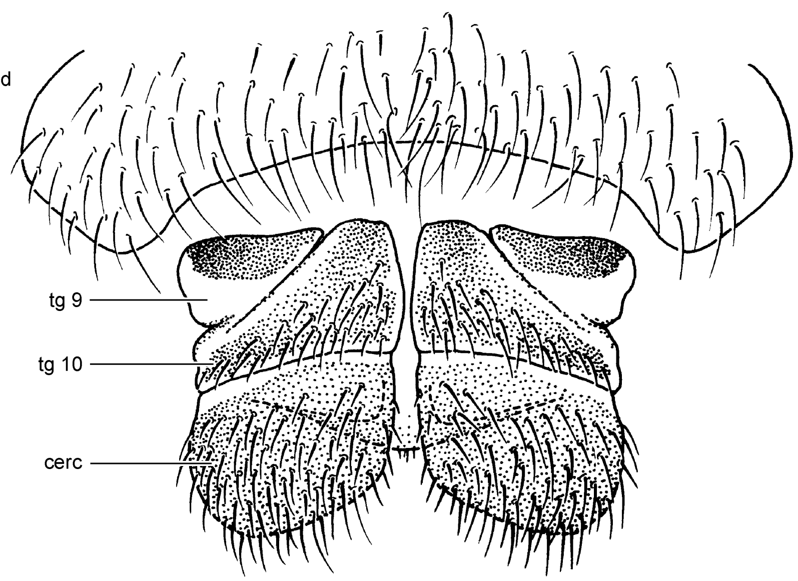
The Scepsidinae is a small group of coastal flies that have greatly reduced mouthparts. Three genera have been included in the subfamily, including two in the Afrotropical Region. It is not certain that these genera form a natural group and it may be that the apparent similarity of the genera is the result of convergence. The recent molecular study of Turcatel (2014) suggests that *Adersia* Austen may belong within the tribe Chrysopsini.

The Chrysopsinae is perhaps the most diverse group within the Tabanidae. Three tribes are recognised (Bouvieromyiini, Chrysopsini and Rhinomyzini), all of which occur in the Afrotropical Region. Recent studies suggest the monophyly of the first two tribes is not established and is especially uncertain for the Bouvieromyiini (Bayless 2012; Turcatel 2014). Chrysopsinae include small- to large-sized flies, often with distinctively patterned wings. The antennal flagellum consists of a basal plate and stylus of 3–4 terminal flagellomeres (the basal plate being frequently produced dorsally) and the subcostal wing vein (*Sc*) is bare ventrally in most Bouvieromyiini (*Paulianomyia* Oldroyd being the exception, with a few setulae) and Chrysopsini, but setulose in Rhinomyzini. Mackerras (1954) considered this subfamily to be intermediate between Pangoniinae and Tabaninae and a more recent study supports that view (Morita 2008*a*).

The Tabaninae are the most derived subfamily and include some of the most familiar of all tabanid species. Three tribes are usually recognised (Diachlorini, Haematopotini and Tabanini). A recent study of the Diachlorini using DNA-analysis indicates, however, that this group is paraphyletic (Bayless 2012). As far as the Afrotropical fauna is concerned, all Diachlorini are suggested as belonging to a separated Chasmiini. A number of Afrotropical genera were, however, not included in this analysis and Diachlorini is retained here. It is also suggested that Haematopotini is integrated into the tribe Tabanini, but likewise, few Afrotropical taxa were included in the study and so this major change is not adopted here. The subfamily is diverse in appearance and is most easily characterised by the absence of a pair of spurs on the hind tibiae (an exception is the chrysopsine genus *Thaumastocera* Grünberg, which also



42 *Chrysops* ♂



43 *Chrysops* ♀

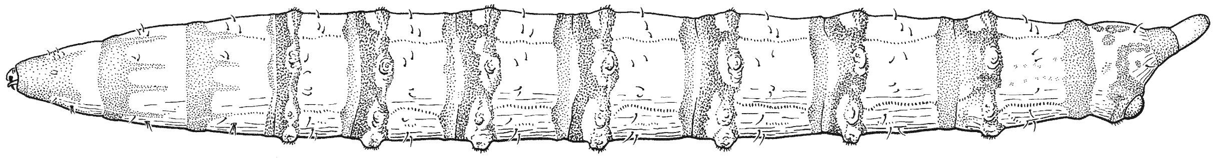
Figs 39.42–43. Male and female terminalia of Tabanidae: (42) male gonopod of *Chrysops cincticornis* Walker, dorsal view of right side; (43) same, female terminalia, dorsal view (both non-Afrotropical). Figs 42, 43 (Pechuman & Teskey 1981, figs 47, 41, respectively).

Abbreviations: cerc – cercus; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; tg – tergite.

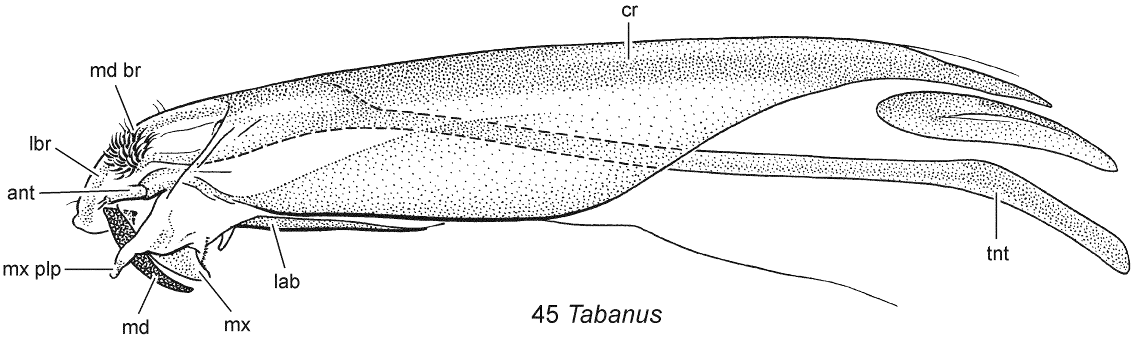
lacks these spurs) and the subcostal wing vein (*Sc*), which is invariably setulose ventrally.

Identification

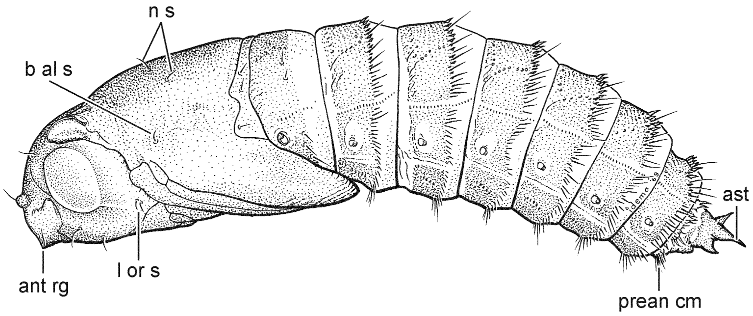
The monograph of Oldroyd (1952, 1954, 1957) remains the standard work on Afrotropical Tabanidae. The identification keys to genera below are largely an adaptation from the keys published in that work, but with additions as appropriate. A number of small genera and subgenera were proposed since then, including *Alocella* (Quentin 1990), *Atelozomyia* (Dias 1987*a*), *Bartolomeudiasiella* (Dias 1987*b*), *Gressittia* (Philip & Mackerras 1960), *Mackerrasia* (Dias 1956*a*), *Oldroydiella* (Dias 1955), *Picromyza* (Quentin 1979), *Orgizocella* (Quentin 1990), *Seguytabanus* (Paulian 1962), *Stuckenbergina* (Oldroyd 1962) and *Tabanocella* (*Tabanocellinus*) (Dias 1966). Many of these proposals lack support for the monophyly of the groups involved and, therefore, need to be reconsidered. Generic reviews have included *Philoliche* (*Ommatiosteres* Enderlein) (Chainey 1983), *Philoliche sensu stricto* (Morita 2008*b*) and *Rhigioglossa* (Chainey 1987).



44 *Tabanus*



45 *Tabanus*



46 *Hybomitra*

47 *Tabanus*

Figs 39.44–47. Immature stages of Tabanidae and mud cylinder: (44) larval habitus of *Tabanus reinwardtii* Wiedemann, lateral view; (45) same, head capsule, lateral view; (46) pupa of *Hybomitra epistates* (Osten Sacken), lateral view (all non-Afrotropical); (47) mud cylinder formed by larval *Tabanus* sp. Figs 44, 45, 46 (Pechuman & Teskey 1981, figs 51, 56, 61), Fig. 47 (photograph © M.J.R. Hall).

Abbreviations: ant – antenna; ant rg – antennal ridge; ast – aster; b al s – basal alar seta; cr – cranium; l or s – lateral orbital seta; lab – labium; lbr – labrum; md – mandible; md br – mandibular brush; mx – maxilla; mx plp – maxillary palpus; n s – notal setae; prean cm – preanal comb; tnt – tentorium.

The below identification key is intended purely for identification purposes and the placement of genera within the key should not be taken to infer relationships. Many characters of tabanid genera are only apparent in females, and consequently, males may be difficult to identify unless associated with females. It is essential that specimens are in good condition; in particular, care should be taken to ensure that the fragile antennae are preserved. With experience, many tabanid genera can be recognised by their overall appearance, although this is difficult to translate into key characters. Two genera, *Alocella* Quentin, and *Orgizocella* Quentin and one undescribed genus could not be included in the below identification key, but details of these are provided in the "Synopsis of the fauna" section below (indicated by square brackets).

Specimens of Tabanidae should be collected dry and ideally direct-pinned when fresh (see Chapter 2). They may be stored in dry layers of tissue for pinning at a later stage, but this increases the risk of losing important appendages, such as the antennae. Storage of Tabanidae in spirit is not recommended as the liquid obscures colours and patterns and unless critical-point-dried, it can be difficult to prevent shrivelling if dried out for pinning at a later stage.

Key to genera of Afrotropical Tabanidae

1. Mouthparts greatly reduced; sandy-grey species, inhabiting beaches, or sand-dunes (SCEPSIDINAE) 2

– Mouthparts not greatly reduced, proboscis at least ½ as long as head height, if proboscis greatly reduced, then not sandy-grey, beach or dune-inhabiting species 3

2. Head of female with frons about as wide as high; males with eyes holoptic, or narrowly separated; wing veins M_2 and M_3 present and reaching wing margin . . . . *Adersia* Austen

– Head with frons in both sexes extremely broad, much wider than high; males with eyes not holoptic; wing veins M_2 and M_3 absent . . . . *Braunsiomyia* Bequaert

3. Wing with subcostal vein (*Sc*) bare ventrally, or at most with 1 or 2 setae; antennal flagellum with 6–8 clearly differentiated segments (*e.g.*, Fig. 15) 4

– Wing with short setae present ventrally along the length of subcostal vein (*Sc*); antennal flagellum with no more than 5 segments. 27

4. Antennal flagellum with 7–8 clearly differentiated flagellomeres; eye bare; female head with frons diverging towards subcallus (as in Fig. 14); wing membrane rarely with bold pattern of bands or maculae, although may be bicoloured or darkened along veins (Fig. 8) (PANGONIINAE: PHILOLICHINI) . . . . *Philoliche* Wiedemann 5

– Antennal flagellum with basal flagellomeres fused to form basal plate, leaving 3 or 4 distinct terminal flagellomeres, or eye setulose; female head with frons either converging or diverging towards subcallus; wing membrane frequently with bold pattern of bands or maculae 13

5. Antennal bases widely separated, by more than length of antennal scape. 6

– Antennal bases closely approximated, separated by less than length of antennal scape 8

6. Head with clypeus protuberant (*e.g.*, Fig. 23); parafacial narrow; rarely with ocelli at vertex. 7

– Head with clypeus not protuberant (as in Fig. 13); parafacial broad (at narrowest point, *ca* ½ width of clypeus); with ocelli at vertex . . . . *Philoliche* (*Returneria* Oldroyd)

7. Head with clypeus with shiny, bare patch laterally; fore tibia in males never with forwardly-projecting dorsal "lappets" . . . .*Philoliche* (*Stenophara* Enderlein)

– Head with clypeus entirely pruinescent; fore tibia in males sometimes with forwardly-projecting "lappets" . . . .*Philoliche sensu stricto*

8. Head with clypeus entirely bare and shiny; palpus with second segment swollen . . . . *Philoliche* (*Phara* Walker)

– Head with clypeus not entirely bare and shiny; palpus with second segment flattened, often with central groove 9

9. Wing cell m_3 closed at or before wing margin. . . . . *Philoliche* (*Dorcaloemus* Austen)

– Wing cell m_3 open at wing margin.. 10

10. Female head with 3 ocelli at vertex . . . . *Philoliche* (*Buplex* Austen)

– Female head without ocelli at vertex 11

11. Labella with filamentous outgrowths . . . . *Philoliche* (*Subpangonia* Surcouf)

– Labella without filamentous outgrowths 12

12. Head with parafacial narrow; wing membrane sometimes bicoloured . . . .*Philoliche* (*Ommatiosteres* Enderlein)

– Head with parafacial broad; wing membrane not bicoloured, although sometimes with dark subapical macula . . . . *Philoliche* (*Maverica* Oldroyd)

13. Wing cell m_3 closed at or before wing margin (Fig. 24) (CHRYSOPSINAE: BOUVIEROMYIINI [in part]) . . . .*Aegophagamyia* Austen 14

– Wing cell m_3 open at wing margin (e.g., Fig. 25). 15

14. Head with frons broad (3–4 × as high as wide at base), parallel-sided, without callus; wing vein M_1 bent upwards to meet vein R_5 well before wing margin (Fig. 24). . . . . *Aegophagamyia sensu stricto*

– Head with frons narrow, often with sides converging basally, with distinct callus; wing vein M_1 straight meeting vein R_5 close to wing margin . . . . *Aegophagamyia* (*Triclida* Enderlein)

15. Antennal flagellum with 8 flagellomeres, although separation of basal 3 may be incomplete; wing membrane without pattern, but cell r_5 may be closed at or before wing margin (PANGONIINAE: PANGONIINI). 16

– Antennal flagellum with basal plate and 3 or 4 distinct terminal flagellomeres; wing membrane may be patterned, but cell r_5 never closed at or before wing margin (CHRYSOPSINAE [in part]) 17

16. Eye setulose; wing cell r_5 closed at or before wing margin. . . . . *Stuckenbergina* Oldroyd

Eye bare; wing cell m_3 open at wing margin (as in Fig. 25) . . . . Undescribed genus A

17. Head with clypeus or parafacial with shiny bare areas; antennal scape at least 2 × as long as high (*e.g.*, Fig. 15); wing membrane usually with conspicuous pattern; eye in living flies with complex pattern of maculae or with distinct bands (CHRYSOPSINI) 18

– Head with clypeus and parafacial usually pruinescent, or occasionally entirely shiny, but without discrete shiny areas; antennal scape short, barely longer than high; wing membrane hyaline, or if tinted, rarely with crossband, or with maculae at forks, or extreme base may be contrastingly dark; eye in living flies without pattern (BOUVIEROMYIINI [in part]) 19

18. Eye in living flies with pattern of irregular blotches (Fig. 3); wing membrane with conspicuous pattern, that often includes distinct crossband (Figs 25–29) (widespread continental Afrotropical Region) . . . .*Chrysops* Meigen

– Eye in living flies with 3 straight fasciae; wing membrane without distinct crossband, although sometimes uniformly darkened (Madagascar) . . . . *Picromyza* Quentin

19. Wing membrane with distinct crossband, crossing discal cell (*d*) and an additional dark area filling apex (Fig. 30) . . . .*Gressittia* Philip & Mackerras

– Wing membrane without distinct pattern, or if so then without transverse brown band 20

20. Head with frons very narrow, *ca* 10 × longer (measured from base to vertex) than wide at base; wing with subcostal vein (*Sc*) with 1 or 2 setae ventrally; large dark brown flies (18–20 mm), without distinct body or wing membrane pattern (endemic to Madagascar) . . . . *Paulianomyia* Oldroyd

– Head with frons broader, 6 × (or less) longer (measured from base to vertex) than wide at base; wing with subcostal vein (*Sc*) entirely bare ventrally; small- to medium-sized flies < 18 mm (*e.g.*, Figs 2, 9), often with distinct pattern on body or wing membrane (continental Afrotropical Region and Madagascar) 21

21. Antennal stylus with segments elongate, each distinctly longer than broad; pedicel with or without indistinct dorsal tooth; eye bare; female head with frons narrow and parallel-sided; index length ratio at least 1–6 (frontal index = width at base where frons joins subcallus, against length from base to vertex, when both points are viewed in same plane); callus linear, narrow and inconspicuous; larger species (females > 14 mm; males > 12 mm), with remarkably long wings, when folded over abdomen apex of discal cell (*d*) about at level of apex of abdomen (Madagascar). . . . .*Rhinomyzopsis* Enderlein

– Antennal stylus with segments usually not elongate, if elongate, then also with pedicel with strong dorsal tooth; eye setulose; female head with frons virtually square, broader; index length ratio at most 1–5, often much greater; wing of normal length, discal cell (*d*) not reaching apex of abdomen (continental Afrotropical Region). . . . . *Rhigioglossa* Wiedemann 22

22. Female head with frons pruinescent, broader than high; eyes clearly separated in male; subcallus sometimes greatly enlarged (as in Fig. 12). . . . . *Rhigioglossa* (*Pronopes* Loew)

– Female head with frons usually much higher than broad, if very broad, then mostly bare and shiny; eyes not clearly separated in male; subcallus not greatly enlarged 23

23. Head with frons broad, about as wide as high; body almost entirely shiny black; head with subshiny subcallus, clypeus and parafacial; female head with frons broad, shiny, with indistinct callus; antennal flagellum with prominent dorsal tooth . . . . *Rhigioglossa* (*Pseudoscaptia* Enderlein)

– Head with frons narrower, clearly longer than wide at base; body often with distinct pattern; head mainly pruinescent; female head with frons pruinescent, often with distinct callus. 24

24. Female head with frons entirely pruinescent, without callus; wing membrane hyaline or lightly tinted, with base contrastingly dark brown, as far as vein *MA* (as in Fig. 29) . . . . *Rhigioglossa* (*Dasycompsa* Enderlein)

– Female head with frons not entirely pruinescent, but with distinct callus or mainly shiny; wings membrane variable, but not contrastingly dark brown as far as vein *MA* 25

25. Female head with frons mostly shiny black, with only narrow tomentose fasciae at margins (most extensive in *R. pusilla* (Schiner, 1868)); median occipital sclerite distinctly shiny; eye bare or if with short setulae (*R. pusilla*), then these inconspicuous; eyes occasionally widely separated in male; subcallus usually setulose at margins; proboscis often unusually long and slender . . . . . *Rhigioglossa sensu stricto*

– Female head with frons not extensively shiny (tomentose at least on dorsal ⅓); median occipital sclerite dull tomentose; eyes setulose, or bare, never widely separated in males; subcallus not setulose at margins; proboscis not unusually long and slender 26

26. Eye distinctly setulose (viewed at low magnification), or if setulae short and inconspicuous (female *R. fallax* (Austen, 1912)), then head with frontal callus virtually filling basal ½ of frons. . . . . *Rhigioglossa* (*Mesomyia* Macquart)

– Eye bare (viewed at low magnification), or microscopically setulose; female head with frontal callus essentially linear in form, although generally expanding towards base . . . . . . *Rhigioglossa* (*Perisilvius* Enderlein)

27. Hind tibia with pair of ventral spurs apically (as in Fig. 18) (CHRYSOPSINAE: RHINOMYZINI [in part]) 28

– Hind tibia without pair of ventral spurs apically 36

28. Antennal scape large and shiny, similar in size to discoid flagellum, which lacks a dorsal process (Fig. 16); female palpus with segment 2 slender and pointed at tip . . . . *Orgizomyia* Grünberg

– Antennae slender or antennal flagellum with strong dorsal forwardly-projecting spine; scape not large and shiny, not similar in size to discoid flagellum; female palpus sometimes with segment 2 swollen and blunt-tipped 29

29. Head with clypeus prominent, developed into bare, shiny "snout"; antenna slender, flagellum without dorsal spine; wing membrane may be mainly dark or strongly patterned (Fig. 32) . . . . *Sphecodemyia* Austen

– Head with clypeus not prominent or if swollen, then antennal flagellum with strong dorsal spine; wing membrane rarely without distinct pattern. 30

30. Antennal flagellum without forwardly-projecting dorsal spine; female palpus with segment 2 swollen or not blunt-tipped; fore tibia swollen . . . . *Thriambeutes* Grünberg

– Antennal flagellum usually with distinct forwardly-projecting dorsal spine; female palpus with segment 2 either swollen or not; fore tibia usually not swollen 31

31. Head with subcallus distinctly prominent; female palpus with segment 2 swollen and blunt-tipped . . . 32

– Head with subcallus not prominent; female palpus with segment 2 not swollen and blunt-tipped. . . . 34

32. Antennal scape > 2 × as long as broad; large species (> 20 mm), obvious wasp-mimics with bicolourous wing membrane (yellow anteriorly, darkened posteriorly), suggesting two wings. . . . . *Seguytabanus* Paulian

– Antennal scape < 2 × as long as broad; smaller species (usually < 20 mm), not obvious wasp mimics 33

33. Smaller, pale brown species (*ca* 10 mm); antennal flagellum with dorsal tooth only slightly produced; head with clypeus not swollen; wing membrane dark, with pale band running through apices of basal cells *br* and *bm* . . . . *Oldroydiella* Dias

– Larger, dark red-brown to blackish species (at least 14 mm); antennal flagellum with strongly-produced dorsal spine; head with clypeus sometimes strongly swollen; wing membrane variable, sometimes brightly coloured (Fig. 22) . . . . *Jashinea* Oldroyd

34. Antennal flagellum usually with strong forwardly-projecting dorsal spine; wing membrane patterned, often brown along costal vein (*C*), this area expanding across base of basal cells *br*, *bm* and most of cell r_4, also expanding into band across cells r_{2+3} and r_5 the apex of the discal cell (*d*) and reaching margin at vein M_4; also a dark macula at apices of cells *cua* and *cup* (Figs 34, 35) . . . . . . *Tabanocella* Bigot 35

– Antennal flagellum without strong dorsal spine; small *Tabanus*-like species without wing membrane pattern, although pterostigma prominent . . . . *Mackerrasia* Dias

35. Abdomen metallic blue . . . . *Tabanocella* (*Tabanocellinus* Dias)

– Abdomen not metallic blue . . . . *Tabanocella sensu stricto*

36. Antennal flagellum with 4 flagellomeres; in living flies wings held roof-like over abdomen, not spread out into V-shape (TABANINAE: HAEMATOPOTINI) 37

– Antennal flagellum with 5 flagellomeres; in living flies wings held out in V-shape 38

37. Head mostly shiny, including frons, clypeus and parafacial, therefore, frons without pair of dark maculae above low transverse callus, without dark central fascia above these; antennal scape long and slender, nearly 6 × as long as pedicel; wing membrane entirely brown, or with 3–4 pale bands (Fig. 36) . . . . *Hippocentrum* Austen

– Head mostly dull; frons, with pair of dark maculae above low transverse callus (Fig. 5), often with dark central fascia above these; antennal scape rarely as long or slender, often only 2 or 3 × as long as pedicel; wing membrane with pattern of numerous pale maculae, or streaks that cluster around forks of veins to form a “rosette” (Fig. 37) (Note: 1 species has the wing entirely black, except for a short clear band close to wing apex) . . . . *Haematopota* Meigen

38. Head with fully functional ocelli at vertex; antennal flagellum with long forwardly-projecting dorsal spine (Fig. 17); fore tibia distinctly swollen; black species, with strongly patterned wing membrane, blackish at base, a central band leaving apices of basal cells *br* and *bm* clear and dark maculae at end of veins R_3 and R_4 and base of vein R_4 (Fig. 38) (CHRYSOPSINAE: RHINOMYZINI [in part]) . . . . *Thaumastocera* Grünberg

– Head without ocelli at vertex or ocelli vestigial; antennal flagellum without long forwardly-projecting dorsal spine; if fore tibia swollen, then not black species with strongly patterned wing membrane 39

39. Wing with basicosta bare or rarely with 1 or 2 setae; membrane without distinct pattern (TABANINAE: DIACHLORINI) 40

– Wing with basicosta densely setulose, as dense as on basal section of costal vein (*C*); membrane sometimes with distinct pattern (TABANINAE: TABANINI) 47

40. Female head with frontal callus divided medially . . . . *Bartolomeudiasiella* Dias

– Female head with frontal callus undivided medially 41

41. Female head with frons about as wide as high; callus almost entirely absent, reduced to 2 minute shiny dark maculae at base of frons. . . . .*Atelozomyia* Dias

– Female head with frons distinctly higher than wide; callus clearly present. .42

42. Female head with frontal callus separated from eye margins, bordered by short setulae on either side; eye conspicuously setulose . . . . *Atelozella* Bequaert

– Female head with frontal callus not separated from eye margins, or if separated, then eye not conspicuously setulose 43

43. Female head with frons diverging towards subcallus, with index length ratio of 2–2.5; basal callus often filling base of frons; subcallus often shiny; eye setulose, although setulae may be short. 44

– Female head with frons parallel-sided, only slightly divergent, at most with index length ratio of 3–7; basal callus usually not filling base of frons; subcallus subshiny at most; eye setulose or not 45

44. Female head with basal callus filling base of frons; median callus much narrower, but joined to basal callus; eye without pattern in living flies (southern Africa) . . . . *Limata* Oldroyd

– Female head with basal callus not filling base of frons, separated from eye; median callus large and rounded, at most narrowly joined to basal callus; eye banded in living flies (Madagascar). . . . . *Seguyiella* Dias

45. Antennal flagellum unusually slender, without dorsal tooth; terminal flagellomeres as long as rest of antenna; head with frontal callus filling base of frons (coastal species) . . . . *Neavella* Oldroyd

– Antennal flagellum of normal proportions, with dorsal tooth; terminal flagellomeres shorter than rest of antenna; head with frontal callus not filling base of frons (species not confined to coasts) . . . . *Cydistomyia* Taylor 46

46. Female head with frons broader, with index length ratio of 3–5.5; eye often with short setulae visible at low magnification (10 ×) (continental Afrotropical species) . . . . *Cydistomyia* (*Amanella* Oldroyd)

– Female head with frons narrower, with index length ration of 6.5–7; eye bare at low magnification (10 ×) (confined to Mauritius) . . . . *Cydistomyia* (*Tabanotelum* Oldroyd)

47. Wing membrane with pattern of dense brown maculae on clear background (Fig. 39) . . . . *Euancala* Enderlein

– Wing membrane without such pattern 48

48. Fore tibia strongly inflated; wing membrane with broad transverse brown band crossing discal cell (*d*) (Figs 6, 40); body sometimes bright green . . . . *Ancala* Enderlein

– Fore tibia not strongly inflated; wing membrane without distinct pattern, or if so, then without transverse brown band crossing discal cell (*d*); body never bright green 49

49. Eye light to reddish brown in dry specimens (light green or greenish yellow in living flies); female head with frontal calli on frons reduced to small maculae, or absent; basal callus without dorsal extension; wing membrane invariably without distinct pattern, although costal cell (*c*) may be tinted yellow . . . . *Atylotus* Osten Sacken

– Eye black in dried specimens (bright green to blackish in living flies); female head with at least basal callus of frons larger, basal callus often with dorsal extension; wing membrane sometimes distinctly patterned. 50

50. Eye densely and conspicuously setulose; head with basal callus of frons with tuft of setulae along either side; setulose bee-like species; abdomen partly shiny, without longitudinal fascia or rows of pale triangular markings . . . . "*Therioplectes*" Zeller

– Eye not conspicuously setulose; head with basal callus of frons without tuft of setulae along either side; not setulose bee-like species; abdomen often with longitudinal fascia or rows of pale triangular markings 51

51. Head with frons with basal callus square, filling base of frons and shiny patch also present at vertex; subcallus not swollen or shiny; eye with short setulae; antennal scape arched forward over base of pedicel; wing membrane hyaline, or slightly darkened, but without distinct pattern. . . . "*Hybomitra*" Enderlein

– Head with frons variable, if basal callus fills base of frons and vertex shiny, then subcallus swollen and shiny, or with large separate median callus; eye usually bare; antennal scape not arched forward over base of pedicel; wing membrane sometimes with distinct pattern (*e.g.*, Fig. 41) . . . . *Tabanus* L.

Synopsis of the fauna

With a large mammalian fauna potentially serving as hosts, the continental Afrotropical Region should be expected to be rich in tabanid species and indeed *ca* 800 species in some 35 genera are currently recognised, although the status of some genera remains uncertain (Chainey 2003). This is perhaps rather less than might have been anticipated, as compared to the *ca* 4,500 species in *ca* 150 genera currently recognised globally.

All currently recognised tabanid subfamilies and most tribes are represented in the Afrotropics, with the exception of the tribe Scionini, which is confined to the Australasian and Neotropical Regions and the Neotropical tribe Mycteromyiini. Within the Afrotropical Region, the Malagasy fauna is very distinctive (Chainey 2003; Zeegers 2014), with a number of endemic genera and subgenera, but is entirely lacking in the otherwise species-rich genera *Haematopota* and *Philoliche*; the absence of the latter genus in Madagascar is all the more remarkable given that there are two species recorded from Mauritius.

The blood-sucking habit of female tabanids has ensured that this group has received considerable taxonomic attention and there are expected to be relatively few undescribed species in the Afrotropics. The Madagascan fauna is less well known, however, with a number of genera known only from type specimens and many additional species to be described (Zeegers 2014). The distribution of many species is likely to be affected by the preference for and availability of particular hosts, but little research has been undertaken to investigate these factors.

***Adersia* Austen** (Scepsidinae)**.** An endemic genus of six small- to medium-sized grey, or sandy-looking species, with greatly reduced mouthparts, that occurs on the coasts of southern and eastern Africa, extending northwards to the Arabian Peninsula. Larvae of *A. oestroides* (Karsch, 1888), occur in sand between neap and spring tide lines and can survive five hours submersed (Usher 1972). An identification key to species was provided by Oldroyd (1957: 308).

***Aegophagamyia* Austen** (Chrysopsinae: Bouvieromyiini)**.** An endemic genus of 36 described species and several undescribed (Th. Zeegers, pers. comm. 2015). *Aegophagamyia* are mostly small flies (Fig. 11), with distinctive wing venation (Fig. 24). Two species of the nominate subgenus occur along the coasts of East Africa north to Kenya and two additional species are recorded from Madagascar and other Indian Ocean islands. In addition, 32 species of the subgenus *A.* (*Triclida* Enderlein) occur in Madagascar and the Indian Ocean islands; this subgenus may be best treated as a separate genus (Th. Zeegers, pers. comm. 2015). Distribution in Madagascar includes coasts, open areas and both deciduous western forest and eastern rainforest. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Oldroyd (1957: 265), supplemented by Burger (1992).

[***Alocella* Quentin** (Chrysopsinae: Rhinomyzini)**.** An endemic monotypic genus, only known from the type series of the single Malagasy species *A. seguyi* Quentin, 1990. Material was not examined in preparation of this chapter, but it is considered likely to belong to the genus *Tabanocella*. The main difference appears to be wing pattern, which is mostly black, with a number of small clear maculae. Biology and immature stages of the species remain unknown. It was not possible to include the genus in the above identification key.]

***Ancala* Enderlein** (Tabaninae: Tabanini)**.** An endemic genus of robust species, with orange bodies and distinctively banded wings (Figs 6, 40), or in the case of the remarkable *A. fasciata* (F., 1775), with body bright green (at least when fresh). Eyes may be pale green in life (Fig. 6), being similar to *Atylotus* in this respect. Seven species occur throughout most of the Afrotropics, including the Arabian Peninsula, although the genus is absent from Madagascar. As in the adult, the immature stages of *A. fasciata* are also green, are aquatic, and are found in floating vegetation (Goodwin 1982; Oldroyd 1954: 93). An identification key to species was provided by Oldroyd (1954: 89).

***Atelozella* Bequaert** (Tabaninae: Diachlorini)**.** An endemic genus of two species: *A. fuelleborni* (Enderlein, 1923) and *A. subulta* Oldroyd, 1957. Both are very rare in collections and are only known from Tanzania. Biology and immature stages of the genus remain unknown. Identification requires reference to the original descriptions provided by Oldroyd (1954: 62, 1957: 468).

***Atelozomyia* Dias** (Tabaninae: Diachlorini)**.** An endemic monotypic genus known only from the poorly-preserved female holotype of the type species, *A. thalassae* Dias, 1987, from Namibia. Biology and immature stages of the species remain unknown.

***Atylotus* Osten Sacken** (Tabaninae: Tabanini)**.** A widespread genus of *ca* 70 species occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. Twenty-two species are recorded from the Afrotropics, their range including Madagascar and Oman in the Arabian Peninsula. Many species are poorly known, but *A. agrestis* (Wiedemann, 1828) is very common and widespread; its range including Madagascar and is the only tabanid species recorded from Cabo Verde (Duarte 2013). *Atylotus* are generally small- to medium-sized species, with the wing membrane lacking distinct patterning and often with distinct sublateral maculae on the abdominal tergites. As opposed to most other Tabanini, the colouration of the eye does not originate from the lenses of the facets and is pale greenish in life (*Ancala* may be similar in this respect). Goodwin (1982) described the immature stages of the two widespread species, *A. agrestis* and *A. albipalpus* (Walker, 1850). An identification key to species was provided by Oldroyd (1954: 112).

***Bartolomeudiasiella* Dias** (Tabaninae: Diachlorini)**.** An endemic monotypic genus, with the single distinctive species, *B. atlanticus* Dias, 1987, occurring in the Namib Desert of Namibia. The frons is divergent towards the antennae and is almost as wide as high; the medially divided frontal callus is unlike any other species of the tribe Diachlorini. Biology and immature stages of the species remain unknown.

***Braunsiomyia* Bequaert** (Scepsidinae)**.** An endemic monotypic genus, with the single described species, *B. cinerea* (Surcouf, 1921), confined to the coasts of Mozambique and South Africa. *Braunsiomyia cinerea* is a medium-sized greyish species, with greatly reduced mouthparts and distinctive wing venation, with the frons much wider than high in both sexes. Biology and immature stages of the species remain unknown, but there is some evidence to suggest the species prefers drier sandy habitats than do coastal species of *Adersia* (Usher 1972).

***Chrysops* Meigen** (Chrysopsinae: Chrysopsini)**.** A genus of *ca* 250 described species occurring in all zoogeographical regions, except Antarctica, being poorly represented in the Australasian Region. Forty-three species are recorded from the continental Afrotropics and Madagascar, both in open and forested habitats, although no species are yet recorded from the Afrotropical part of the Arabian Peninsula. *Chrysops* are generally small species, with long antennae and boldly patterned wings (Figs 3, 15, 19, 20, 25–29). In living flies the eyes are brilliantly coloured, with a complex pattern of maculae and bands (Fig. 3). *Chrysops* includes the principal vectors of *Loa loa* filariasis in humans and monkeys (see Chapter 6). The immature stages of a number of species are known (Goodwin 1982). An identification key to species was provided by Oldroyd (1957: 57).

***Cydistomyia* Taylor** (Tabaninae: Diachlorini)**.** A genus of *ca* 120 described species occurring in the Afrotropical, Australasian and Oriental Regions. Nineteen species are recorded from the Afrotropics, ascribed to two subgenera of questionable validity. The endemic subgenus *C.* (*Amanella* Oldroyd) includes 17 small- to medium-sized species, usually with short setulae on the eye, but generally rather nondescript, without wing pattern, found mostly in South Africa, but with a few species recorded from East Africa as far north as Kenya. The poorly known subgenus *C.* (*Tabanotelum* Oldroyd) includes two medium- to large-sized species (*ca* 18 mm), known only from Mauritius. Oldroyd (1957: 27) provided information on the larva of one species of the subgenus *C.* (*Amanella*). An identification key to species was provided by Oldroyd (1954: 75, as *Amanella*), supplemented by Usher (1965).

***Euancala* Enderlein** (Tabaninae: Tabanini)**.** An endemic genus, based on one (or possibly two) very distinctively patterned species (wing Fig. 39). The type species, *E. maculatissima* (Macquart, 1838), occurs throughout much of the Afrotropical Region, but is absent from the Arabian Peninsula and Madagascar. The form *E. irrorata* (Surcouf, 1909), that occurs in afforested areas from Sierra Leone to Angola, is sometimes treated as a distinct species. Bayless (2012) suggested that *Euancala* may be sister to a group containing *Haematopota* and *Hippocentrum*. Neave (1915) provided descriptive information on the immature stages, which were found in a dried up stream bed.

***Gressittia* Philip & Mackerras** (Chrysopsinae: Bouvieromyiini)**.** A genus of *ca* 12 described species occurring in the Afrotropical and Oriental Regions. The majority of these pattern-winged species (Fig. 30) occur in the Oriental Region (Philip & Mackerras 1960). The single Afrotropical species, *G. pulchripennis* (Austen, 1937) is only known from two male specimens from Kenya. Biology and immature stages of the genus remain unknown.

***Haematopota* Meigen** (Tabaninae: Haematopotini)**.** A genus of *ca* 475 described species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. The largest genus of Tabanidae in the Afrotropics, with over 250 currently recognised continental species (including the Arabian Peninsula); by contrast, the absence of the genus from Madagascar and other Indian Ocean islands is remarkable. *Haematopota* are small- to medium-sized species (Fig. 5) with characteristic wing patterns (Fig. 37) and frons. In living flies the eyes have a pattern of zigzag bands (Fig. 5) and flies rest with their wings held tight alongside the body, giving a roof-like appearance. They occur in a variety of habitats, with a few species being found at high elevations. The general distribution of the genus is, however, likely linked to the occurrence of wild hoofed mammals, perhaps explaining its absence from Madagascar. The immature stages of this large genus remain poorly known (Goodwin 1982; Neave 1915). An identification key to species-groups and keys to species were provided by Oldroyd (1952: 23), supplemented by Dias & Sousa (1958) for the *H. tumidicornis*-group.

***Hippocentrum* Austen** (Tabaninae: Haematopotini)**.** An endemic genus of five described species, occurring throughout the tropical forest belt of the continental Afrotropics, but absent from the Arabian Peninsula and Madagascar. *Hippocentrum* are small- to medium-sized species, with largely shiny heads and distinctive wing patterns (Fig. 36). They form the sister-group for *Haematopota*. The biology and immature stages of the genus remain unknown. For identification of species see the descriptions of Oldroyd (1952: 7).

[***"Hybomitra"* Enderlein** (Tabaninae: Tabanini)**.** About 14 species have sometimes been ascribed to this mostly Holarctic genus. It is doubtful, however, that they belong here and they may be better placed within the genus *Tabanus*. Zeegers (2005) suggested that Afrotropical species ascribed to *Therioplectes* may belong with *Hybomitra*, but they differ in having the eyes unbanded in living flies. The immature stages are known for a few species (Goodwin 1982). An identification key to species was provided by Oldroyd (1954: 137).]

***Jashinea* Oldroyd** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of five mainly forest-inhabiting species, distributed from Ghana to Zimbabwe, with two further species from eastern Madagascar. The monophyly of the genus is not well established (Zeegers 2014) and should probably include the species placed in *Oldroydiella*. *Jashinea* are medium- to large-sized species, often with patterned wings (Fig. 22). The larvae of *J. jacoti* (Bouvier, 1936) were recorded from tree rot holes of a *Brachystegia* sp. (Fabaceae) by Lamborn (1938) (as *J. bicolor* (Austen, 1937)), although no description was provided. They were found singly and were cannibalistic in captivity. An identification key to species was provided by Oldroyd (1957: 150).

***Limata* Oldroyd** (Tabaninae: Diachlorini)**.** An endemic genus of six described species known only from Namibia and South Africa. *Limata* are small- to medium-sized species with a broad frons and usually a shiny, or partly shiny, subcallus in females and setulose eyes that are not banded in living flies. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Oldroyd (1954: 68).

***Mackerrasia* Dias** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of one, or possibly two, small species described from Madagascar. These species may be ascribable to the genus *Tabanocella*, differing only in the lack of a strong dorsal spine on the antennal flagellum and lack of wing pattern in the type species *M. simplicicornis* (Austen, 1912). The genus occurs in both eastern rainforests and deciduous dry forests. Immature stages of the genus remain unknown. The identification key to *Tabanocella* spp. by Oldroyd (1957: 167) includes these species.

***Neavella* Oldroyd** (Tabaninae: Diachlorini)**.** A near endemic genus of five coastal species. There are four or five Afrotropical species: *N. albipectus* (Bigot, 1859), recorded from Kenya, Madagascar, Seychelles and Tanzania (Zanzibar Is.), plus the Indian Ocean islands of Aldabra, Amirante and Astove (all Seychelles); *N. verstraeteni* Leclercq, 1981 (possibly includes *N. madagascariensis* Chainey & Timmer, 1986, from Madagascar, but treated as a distinct species by Mohammad *et al*. (2010)); *N. notopleuralis* Oldroyd, 1954 from Socotra Is. (Yemen); and *N. producticornis* (Austen, 1912) from Kenya, Mozambique and Tanzania. *Neavella sylvioides* Mohammad, Badrawy & Abu El-Hassan, 2010, was recorded from Egypt, just within the Palaearctic Region. The very slender antennal flagellum without a dorsal projection is a notable feature of the genus. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Chainey & Timmer (1986), but excludes *N. verstraeteni*.

***Oldroydiella* Dias** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of two small species, *O. fallax* (Macquart, 1846) from South Africa and *O. tenebrosa* Dias, 1959, from Mozambique; both are doubtfully distinct from the genus *Jashinea*. Biology and immature stages of the genus remain unknown. The identification key to *Jashinea* (as *Hinea* Adams) spp. by Oldroyd (1957: 150) includes these species.

[***Orgizocella* Quentin** (Chrysopsinae: Rhinomyzini)**.** An endemic genus known from three species, *O. pauliani* Quentin, 1990, *O. seyrigi* (Séguy, 1951) and *O. viettei* Quentin, 1990, confined to Madagascar, all from the eastern rainforests. Only one male specimen of the type species of this genus, *O. seyrigi*, was available for study, but it is considered likely to belong to the genus *Tabanocella* and it was not possible to include the genus in the above key. The main difference appears to be the blackish wing pattern, which exhibits some similarity to *Orgizomyia*. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Quentin (1990).]

***Orgizomyia* Grünberg** (Chrysopsinae: Rhinomyzini)**.** An endemic monotypic genus, currently with the single Malagasy species, *O. zigzag* (Macquart, 1855), with a distinctive wing pattern (Fig. 31). Additionally, there is an undescribed species (Zeegers 2014) and possibly this genus should include *Thriambeutes*. Label data indicate that local people particularly fear this species for its painful bite. It occurs in a variety of forest types. Biology and immature stages of the species remain unknown.

***Paulianomyia* Oldroyd** (Chrysopsinae: Bouvieromyiini)**.** A poorly known endemic monotypic genus confined to

Madagascar. The type species, *P. rufa* Oldroyd, 1957, is large and is notable for having one or two setae on the otherwise bare underside of the subcostal vein (*Sc*). A further two Malagasy species included in *Rhigioglossa* (*Perisilvius*) may belong here or to *Rhinomyzopsis*. Biology and immature stages of the species remain unknown.

***Philoliche* Wiedemann** (Pangoniinae: Philolichini)**.** A large genus of *ca* 100 species, mostly occurring in the Afrotropical Region, but with a few species in the Australasian and Oriental Regions. *Philoliche* occurs throughout the continental Afrotropics south of the Sahara through to Oman in the Arabian Peninsula. Two species are recorded from Mauritius, but curiously, none from Madagascar. Outside the Afrotropical Region, there are several Indo-Malayan species and two species from New Caledonia also placed in *Philoliche*. The monotypic Palaearctic genus *Ectinocerella* Séguy is almost certainly ascribable to *Philoliche* and is close to *P.* (*Buplex*), although this synonymy has not been formally published. Several subgenera are currently recognised, but there may be a case for readjusting this arrangement, for example, molecular studies have indicated that *P.* (*Subpangonia*) nests within nominate *Philoliche* (Morita 2008*a*). The proboscis is generally long, longer than the head height (Figs 8, 23) and in a few species it is much longer than the body. The eye colour in living flies (Fig. 8) is rarely recorded, but it appears that they are generally dark, lacking the brilliant colours and patterns apparent in Chrysopsinae and Tabaninae. The subgenera may be summarised as follows: *P.* (*Returneria*) with five species from Namibia and South Africa; *P.* (*Stenophara*) with 20 widespread species from Senegal and Somalia to Mozambique and Namibia; *Philoliche sensu stricto* with 11 widespread species from Guinea-Bissau and Ethiopia to Mozambique and Namibia; *P.* (*Phara*) with 19 species from eastern Democratic Republic of Congo and Tanzania to South Africa; *P.* (*Dorcaloemus*) with nine species from Democratic Republic of Congo and Ethiopia to South Africa and Zambia; *P.* (*Buplex*) with 10 species, mostly South Africa, but with one species from the Kenyan coast; *P.* (*Subpangonia*) with one species from the forest zone from Ghana to Democratic Republic of Congo; *P.* (*Ommatiosteres*) with 23 species from Cameroon and Ethiopia to Namibia and South Africa (also Oman and Yemen in the Arabian Peninsula); and *P.* (*Maverica*) with two species from Democratic Republic of Congo to Namibia and South Africa. The two species recorded from Mauritius are not ascribed to a subgenus. Other than an unconfirmed report by Neave (1915), the biology and immature stages of this large genus remain unknown. An identification key to species was provided by Oldroyd (1957: 322), to the subgenus *P.* (*Ommatiosteres*) by Chainey (1983) and to the *Philoliche* (*Philoliche*) *aethiopica* complex by Morita (2008*b*).

***Picromyza* Quentin** (Chrysopsinae: Chrysopsini)**.** An endemic genus of four described and five undescribed species (Zeegers 2015) confined to Madagascar (Burger 1992), occurring in both eastern rainforests and deciduous dry forests. *Picromyza* are similar to *Chrysops* in many ways, but differs in lacking wing patterns and have a pattern of three straight bands, rather than maculae on the eyes in living flies. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Zeegers (2015) and Oldroyd (1957: 58) included three species in his key to the *Chrysops woodi* species-group.

***Rhigioglossa* Wiedemann** (Chrysopsinae: Bouvieromyiini)**.** A genus of 47 described species occurring in the Afrotropical (44 species) and Australasian (3) Regions. As currently recognised, this is a diverse genus with six subgenera (Chainey 1987). Further study may well reveal that some of these taxa deserve recognition at the generic level. Most of the species are from South Africa, but the genus is represented in most of the Afrotropical Region. Three Australian species are also placed here. Many species are rare in collections and several are known only from type specimens. The subgenera may be summarised as follows: *R.* (*Pronopes*) with three species from South Africa; *R.* (*Pseudoscaptia*) with three species from South Africa; *R.* (*Dasycompsa*) with two widespread species in afforested habitats from Liberia to South Africa (former Transvaal); *Rhigioglossa sensu stricto* with six species from Namibia and South Africa; *R.* (*Mesomyia*) with seven species from southern and eastern Africa (a further three species in Australia); and *R.* (*Perisilvius*) with 22 species from southern and eastern Africa (also two species in Madagascar; but see above). Specimens of *Rhigioglossa sensu stricto* are frequently covered in pollen (Fig. 2) and some regularly rest in inflorescences. Immature stages remain unknown. An identification key to species was provided by Chainey (1987).

***Rhinomyzopsis* Séguy** (Chrysopsinae: Bouvieromyiini)**.** An endemic Malagasy genus consisting of up to four rarely collected species with remarkably long wings. It was previously placed in *Mesomyia* (= *Rhigioglossa*) and is somewhat intermediate between this genus and *Paulianomyia*. As well as the type species *R. longipennis* Séguy, 1950, two Malagasy species included in *Rhigioglossa* (*Perisilvius*) may belong here (or to *Paulianomyia*). An additional undescribed species is also known (Th. Zeegers, pers. comm. 2015). Biology and immature stages remain unknown.

***Seguyiella* Dias** (Tabaninae: Diachlorini)**.** An endemic monotypic genus, with the single species, *S. seyrigi* (Séguy, 1955), described from south-western Madagascar. It is a small species with banded, setulose eyes and shiny subcallus (Chainey & Timmer 1986). The species should possibly be included within *Limata*. Biology and immature stages of the species remain unknown.

***Seguytabanus* Paulian** (Chrysopsinae: Rhinomyzini)**.** An endemic monotypic genus, with the single species, *S. oldroydi* Paulian, 1962, described from Madagascar related to *Jashinea* (and possibly synonymous). A very obvious wasp mimic with the wing yellow anteriorly and darkened posteriorly, hence suggesting two wings (Zeegers 2015). Biology and immature stages of the species remain unknown.

***Sphecodemyia* Austen** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of five medium- to large-sized species that are often distinctively patterned (Fig. 32). The five species are recorded from Côte d'Ivoire to Mozambique and are largely confined to afforested habitats; the genus is absent from the Arabian Peninsula and Madagascar. The immature stages of *S. lamborni* Austen, 1937 have been found in tree rot holes, where they are gregarious, but exhibit no signs of the cannibalistic habits of many other tabanids (Lamborn 1938). An identification key to species was provided by Oldroyd (1957: 133).

***Stuckenbergina* Oldroyd** (Pangoniinae: Pangoniini)**.** An endemic genus of two little known and rather nondescript setulose-eyed species, *S. africana* Oldroyd, 1962 and *S. callani*

Oldroyd, 1962, both described from South Africa (Oldroyd 1962). Biology and immature stages of the genus remain unknown. An identification key is currently unavailable and referral to the original descriptions provided by Oldroyd (1962: 52) is required for specific identification.

***Tabanocella* Bigot** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of 28 described species, 16 of which occur throughout most of the continental Afrotropical Region, but are absent from the Arabian Peninsula. A further 12 species occur in a variety of forest types in Madagascar and the Comoros; two of which have been ascribed to the subgenus *T.* (*Tabanocellinus*), although such placement may only be justified for the type species of the subgenus (*T. metallica* Oldroyd, 1957). *Tabanocella* is possibly paraphyletic (Zeegers 2014), *e.g.*, *T. aurea* Oldroyd, 1957, *T. metallica* and *Mackerrasia simplicicornis* may form a monophyletic group. *Tabanocella* are small- to medium-sized species (Fig. 10), usually with a long dorsal spine on the antennal flagellum and distinctively patterned wings (Figs 34, 35). Most continental Afrotropical species have the appearance of large *Chrysops* spp., but with different head structure. The wing patterns of Malagasy species are rather more diverse (Fig. 10). The immature stages are undescribed, although Davey & O'Rourke (1951) provided some biological information. An identification key to species was provided by Oldroyd (1957: 167), supplemented by Usher (1965).

***Tabanus* L.** (Tabaninae: Tabanini)**.** A genus of *ca* 1,200 described species occurring in all zoogeographical regions, except Antarctica. The genus occurs throughout the Afrotropics with *ca* 130 described species. *Tabanus* are diverse in appearance and range in size from small- to very large-sized species (Figs 1, 4, 7), with the wing either clear (Figs 1, 4), or distinctly patterned (*e.g.*, *T. marmorosus* Surcouf, 1909) (Fig. 41). They occur in almost all habitat types and are often numerous where they occur. One species, *T. taeniola* (Fig. 1) is the most widespread of all Afrotropical Tabanidae, extending up the Nile valley into the Palaearctic Region and also occurring in Madagascar and even Aldabra Is. (Seychelles). Molecular studies by Morita (2008*a*) and Bayless (2012), suggest that *Tabanus* as currently understood may be paraphyletic, as the very different genus *Haematopota* clustered with Nearctic *Hybomitra rhombica* (Osten Sacken, 1876) and *T. aegrotus* Osten Sacken, 1877, but not the Afrotropical *T. biguttatus*. The immature stages of a number of species have been described and include species that construct mud cylinders for pupation (Fig. 47). An identification key to species was provided by Oldroyd (1954: 125).

***Thaumastocera* Grünberg** (Chrysopsinae: Rhinomyzini)**.** An endemic genus with two described species, *T. akwa* Grünberg, 1906, described from Cameroon and *T. cervaria* Séguy, 1935 (including *T. boueti* Séguy, 1946 (Chainey 1981)), described from Democratic Republic of Congo, both forest species. The genus is found from Guinea and Sierra Leone east to Uganda and south to Angola. *Thaumastocera* are black species with heavily marked wings (Fig. 38). Larvae have been found in trees rot holes (Oldroyd 1954: 54), while Goodwin (1976) provided information on the pupae of *T. akwa*. An identification key to species was provided by Oldroyd (1954: 51).

[***"Therioplectes"* Zeller** (Tabaninae: Tabanini)**.** Two montane species have been assigned to this Palaearctic genus, *T. canofasciatus* (Austen, 1912) from Kenya and Tanzania and *T. ruwenzorii* (Ricardo, 1908) described from the Ruwenzori Mountains of Uganda. Zeegers (2005) excluded these Afrotropical species from the genus *Therioplectes* in his review and suggested they may be better placed in *Hybomitra*, although they differ in lacking eye bands in living flies. Although these species are likely to share affinities with the Palaearctic fauna, it is highly doubtful that they belong to this genus and it may be more appropriate to erect a new genus to accommodate them. A third species, *T. zumpti* (Dias, 1956), from South Africa is here considered not closely related to the two aforementioned species, based on comparison with the original description and figure of the frons provided by Dias (1956*b*, fig. 1); its placement remains unclear. Biology and immature stages of the genus remain unknown. An identification key to species was provided by Oldroyd (1954: 134).]

***Thriambeutes* Grünberg** (Chrysopsinae: Rhinomyzini)**.** An endemic genus of four medium-sized species, often with distinctively patterned wings (*e.g.*, *T. mesembrinoides* (Surcouf, 1908) (Fig. 33). The four species occur from Togo to Botswana and Mozambique. The genus may not be separable from *Orgizomyia* (Zeegers 2014). Larvae of *T. v-album* (Surcouf, 1908) were recorded from rot holes of *Sterculia* (Malvaceae) trees by Lamborn (1938), although no description was provided. An identification key to species was provided by Oldroyd (1957: 143).

[**Undescribed genus A** (Pangoniinae: Pangoniini)**.** A recently discovered genus from Madagascar, with characters suggesting a relationship with the Neotropical genus *Protosilvius* Enderlein (Zeegers 2015).]

[**Undescribed genus B** (Pangoniinae: Pangoniini)**.** A genus known from a single male specimen from Ethiopia (Oldroyd 1957: 454). Oldroyd provided a description, but did not name the genus in the absence of female specimens. It has conspicuously setulose eyes and unusually slender antennae. The genus is not included in the above identification key.]

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XYLOMYIDAE 40

(Xylomyid Flies or Wood Soldier Flies)

Norman E. Woodley

Fig. 40.1. Female of *Solva* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

[Based on *Solva*; the only genus in the region].

Small to medium-sized flies (body length: 5–10 mm), dark brown to black, abdomen reddish brown to black, in most species with narrow pale fasciae on posterior margins of abdominal tergites. Legs mostly pale yellow, sometimes marked with darker colouration (Figs 1, 2).

Head (Figs 1–3) with eyes separate in both sexes; antenna with scape and pedicel short; flagellum short to moderate in length, not longer than head width, with 8 more or less uniform flagellomeres, elongate-conical to gradually tapered toward apex, flagellomere 8 conical, sharply tapered at apex into a slender, bare mucro; clypeus flat to weakly convex; mouthparts short, labella fleshy (Figs 2, 3); palpus 2-segmented (sometimes appearing 1-segmented), porrect to reflexed dorsally; basal segment small, cylindrical; apical segment elongate, cylindrical to moderately inflated distally.

Thorax (Figs 1, 2) unmodified. Scutellum short, evenly rounded apically. Legs simple, hind pair more elongate; hind femur (Fig. 5) weakly to strongly inflated, with tubercles on ventral surface; tibial spurs small, 0 : 2 : 2, occasionally 0 : 2 : 1; tarsi with empodium pulvilliform. Wing (Figs 1, 2, 4) moderately long, usually hyaline, sometimes weakly infuscate, never with distinct colour pattern; vein R_{4+5} invariably forked; vein R_5 ending very near wing apex; cell m_3 closed before wing margin; anal (*cua*) cell elongate, closed slightly before wing margin.

Abdomen (Figs 1, 2) about as wide as thorax; anterior five tergites virtually parallel-sided, or only slightly tapered; posterior segments conically tapered; first abdominal tergite often

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 915–918.

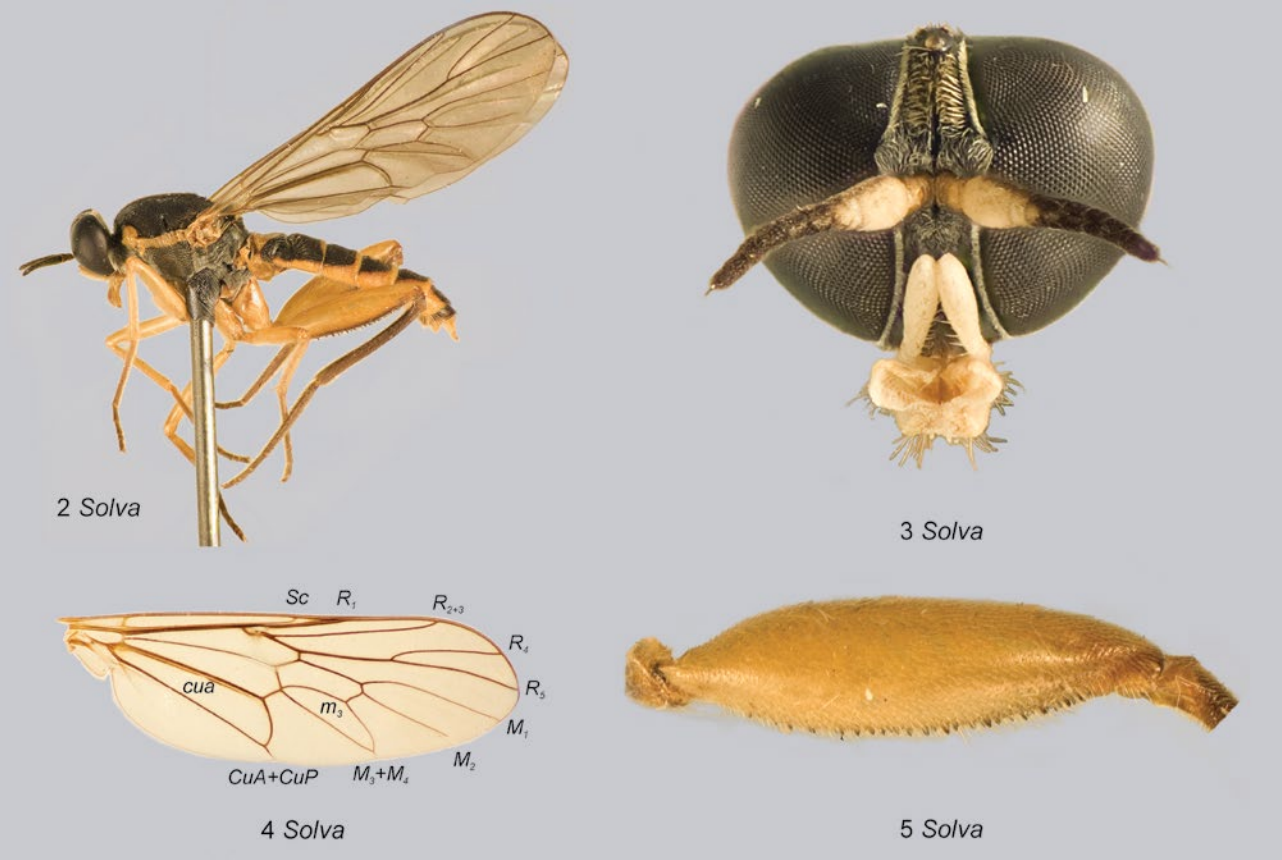
extensively membranous medially; male terminalia (Figs 6, 7) differ considerably between species, very species-specific, ranging from short and wide, to elongate; gonocoxites sometimes with paired dorsal processes, gonocoxal apodemes extremely reduced or absent; gonostyli generally simple without processes; aedeagus usually strongly tapered posteriorly, sometimes quite reduced in size; female cercus 2-segmented, first segments laterally compressed and appressed against each other; female with 2 spermathecae present, ducts very elongate.

Xylomyidae may possibly be confused with some species of Therevidae (see Chapter 49), but therevids have a setiform empodium and lack tibial spurs. Otherwise, they are unlikely to be confused with other Afrotropical families.

Larvae (Fig. 8) with a distinctive morphology featuring a shagreened appearance with cuticular plates of calcium carbonate. Most of head capsule exserted; dorsum of prothorax and mesothorax usually with smooth dorsal field; posterior spiracles in cleft at apex of terminal abdominal segment; transverse row of tooth-like denticles present anterior to anal opening on ventral surface of terminal abdominal segment (Woodley 2009, figs 2, 3). Larval pupation within last larval skin.

Biology and immature stages

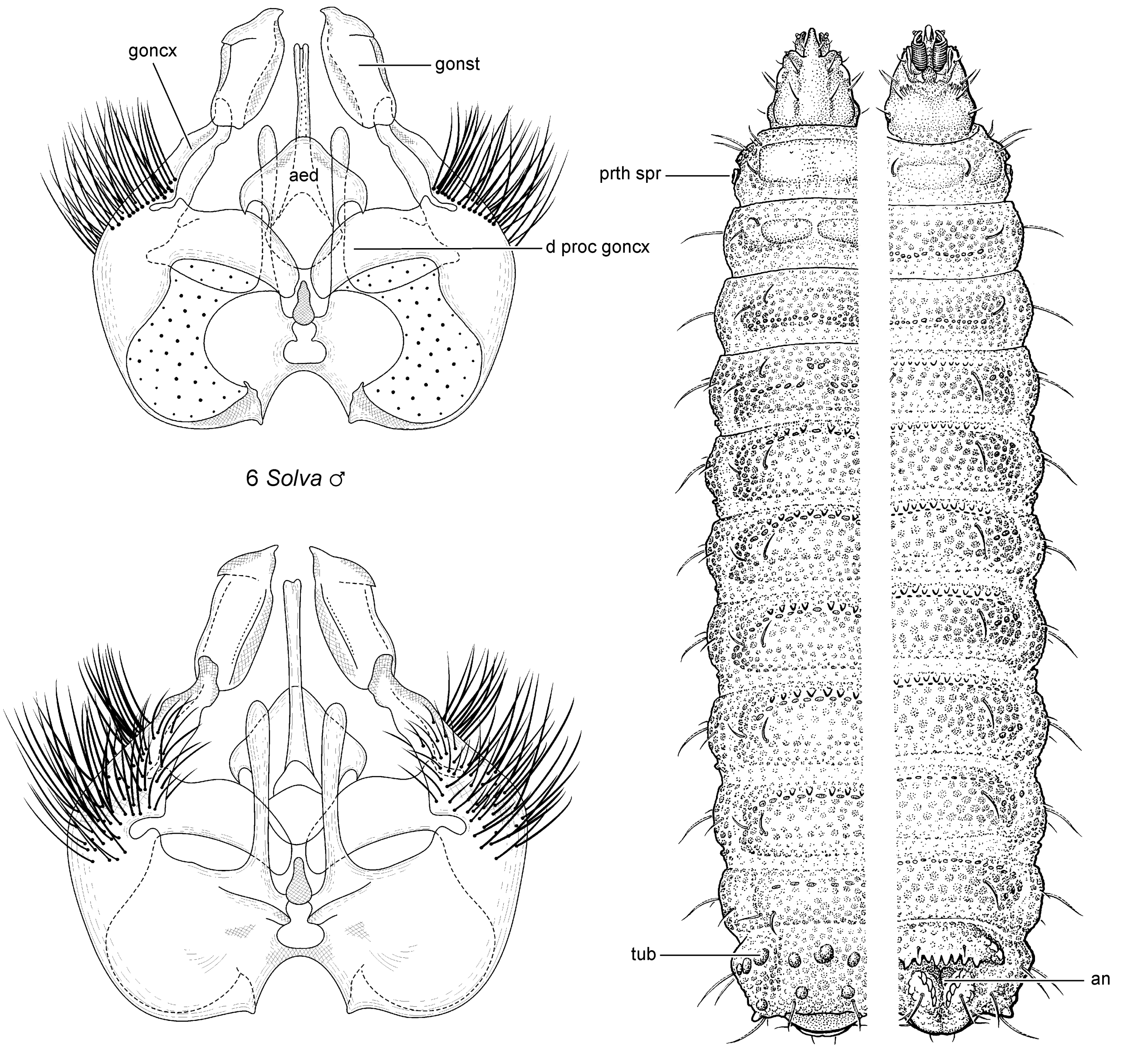
Immature stages of *Solva* Walker, the only xylomyid genus known from the Afrotropical Region, are best known in the Palaearctic Region (Krivosheina 1976; Rozkošný 1973), where they are usually found under bark of various fallen hardwood trees, similar to those in the Nearctic Region. It is most likely that larvae are scavengers, as they are found in decaying plant material, rather than healthy plants and their mouthparts are unsuited for predation (Sinclair 1992). Krivosheina (1976), however, reported *S. schnitnikowi* Pleske, 1928, from roots of *Ferula* (Apiaceae). Kühbandner (1995) described the larva and pupa of *S. caprerae* (Becker, 1908), reared from an old stem of *Euphorbia canariensis* L. (Euphorbiaceae) from the Canary Islands. The biology of tropical species is poorly understood.



Figs 40.2–5. Habitus, head, wing and hind femur of Xylomyidae: (2) habitus of *Solva* sp., lateral view ♀; (3) same, head, anterior view; (4) same, wing, dorsal view; (5) same, hind femur, posterior view.

Abbreviations: *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; m_3 – third medial cell; M_3+M_4 – third branch of media + fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Sc* – subcostal vein.

Specimens of an unidentified *Solva* sp. from Philippines (in the United States National Museum (USNM)), were reared from Breadfruit, *Atrocarpus communis* Forst. (Moraceae). Specimens from another unidentified *Solva* sp. from Kenya (USNM) were reared from Ivy gourd, *Coccinea grandis* (L.) J. Voigt (Curcurbitaceae), although the plant part in which they were found was unspecified. Engel & Cuthbertson (1937) briefly described the larva and pupa of *S. caffra* (Bigot, 1879), from specimens reared from decaying tubers of Sweet potato, *Ipomoea* sp. (presumably *I. batatas* (L.) Lam.) (Convolvulaceae) in Zimbabwe (as Southern Rhodesia). Adults are not commonly encountered, but are frequently collected in Malaise traps. Females of *Solva* spp. apparently range far more widely than males, as they make up the majority of specimens captured in Malaise traps, or alternatively, adult female flies may live longer than male flies.



6 *Solva* ♂

7 *Solva* ♂

8 *Solva*

Figs 40.6–8. Male terminalia and larva of Xylomyidae: (6) male terminalia of *Solva flavoscutellaris* (Matsumura), dorsal view (non-Afrotropical); (7) same, ventral view; (8) larva of *Solva pallipes* (Loew), dorsal view (left) ventral view (right) (non-Afrotropical). Figs 6, 7 (after Nagatomi & Tanaka 1971, figs 12D, 12E), Fig. 8 (James 1981, figs 7, 8).

Abbreviations: aed – aedeagus; an – anus; d proc goncx – dorsal process of gonocoxite; goncx – gonocoxite; gonst – gonostylus; prth spr – prothoracic spiracle; tub – tubercle.

Economic significance

No species are known to have economic significance.

Classification

Xylomyidae are members of the infraorder Stratiomyomorpha of the "orthorrhaphous" Brachycera and are the sister-group to the Stratiomyidae (Woodley 1989: 1376–1377), a placement corroborated by further morphological data (Sinclair 1992) and molecular data (Wiegmann *et al*. 2003). Larvae of the two families are very similar and pupation takes place in the last larval skin, a feature unique in the lower Brachycera. Woodley (2011) presented some data on the phylogeny of the genera within the family.

Woodley (2011) published a catalogue of world Xylomyidae; there are four genera, namely: *Arthropeina* Lindner, *Coenomyiodes* Brunetti, *Solva*, and *Xylomya* Rondani, containing 138 species currently recognised. The greatest species diversity is found in the Palaearctic (46 species) and Oriental (62 species) Regions. Only six species are recognised as valid from the Afrotropical Region, all in the genus *Solva*. Stuckenberg (1980: 252) placed one Afrotropical species, *S. aurolimbata* (Lindner, 1935), in *Hanauia* Enderlein, a genus considered a synonym of *Solva*, at least since Nagatomi & Tanaka (1971). This was presumably because Lindner (1935) originally described *S. aurolimbata* in *Hanauia*. It is probable that some undescribed *Solva* exist in the Afrotropics, but based on material examined by the writer, the species diversity is not great in the region.

Identification

Woodley (2011) provided a key to the four world genera of Xylomyidae. The Afrotropical species are poorly known, the existing literature consisting primarily of isolated species descriptions. A modern revision of the Afrotropical fauna is badly needed. The male terminalia are complex and very diagnostic at the specific level. The female spermathecae also exhibit some promise for species diagnoses. Xylomyidae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Synopsis of the Fauna

***Solva* Walker**. A genus of 100 described species occurring in all zoogeographic regions, except Antarctica. Six valid species of *Solva* have been described from the Afrotropical Region, with only one name in synonymy (Woodley 2011). These Afrotropical species have been recorded, or examined, by the writer from Burundi, Ghana, Kenya, Malawi, Sierra Leone, South Africa, Sudan, Tanzania, Uganda and Zimbabwe. They have been poorly-collected in the Afrotropics; it seems likely that they occur in most wooded and forested areas in the region. Based on our knowledge of the fauna and unidentified material examined here, it appears likely that 10 or fewer undescribed Afrotropical species exist. This outlook could change if wide-scale Malaise trapping reveals additional species diversity in under-sampled Afrotropical regions. Despite extensive Malaise trapping of Diptera in Madagascar, *Solva* has not been found there (M. Hauser, pers. comm. 2013).

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STRATIOMYIDAE 41

(Soldier Flies)

Martin Hauser, Norman E. Woodley and Diego A. Fachin

Fig. 41.1. Male of *Gongrosargus* sp. (Madagascar) (photograph © P. Bertner).

Diagnosis

Small- to large-sized flies (body length: 2–28 mm), highly varied in shape and colouration (Figs 1–102), wings hyaline to variously infuscate or patterned (Figs 156–232); some species mimicking wasps and bees, particularly in flight and in colour (Figs 2, 3, 6, 14, 15, 27, 41, 42, 86).

Head with eyes various, male eyes often holoptic (Figs 106, 112), sometimes dichoptic (Figs 108, 119, 122), female eyes invariably dichoptic (Figs 111, 113, 117, 120); antenna with scape and pedicel usually short, flagellum with 5–8 flagellomeres (in non-Afrotropical species sometimes reduced to one flagellomere), highly varied in shape (Figs 123–149), terminal flagellomere sometimes oblong (Figs 129, 144, 145), cone-shaped (Figs 123, 138, 148), lanceolate (Figs 132, 137) or arista-like stylus (Figs 126, 130, 143); frons in females well-developed, occasionally widening towards vertex (Fig. 104) and frequently with evident postocular region (Figs 113, 117, 118, 120); face usually flat or evenly rounded, but occasionally tuberculate or conically produced (Figs 31, 62); mouthparts

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 919–979.

typically short, with fleshy labellum, but lateral area of labellum sometimes sclerotised, occasionally narrowed; palpus usually 2-segmented, occasionally 1-segmented, sometimes more or less concealed in subcranial cavity or vestigial.

Thorax (including scutum) unmodified, but with long supra-alar spines in two genera (Figs 35, 65). Scutellum short, unarmed (Figs 24–26), or with pair of apical spines of various sizes (Figs 15, 66), or less commonly with 4 or more marginal spines (Figs 44, 46). Wing (Fig. 156) with membrane hyaline, infuscate, or occasionally with distinct pattern (Figs 157–232); costal vein (*C*) ending before wing tip; radial veins characteristically crowded towards anterior margin; veins R_{4+5} or R_5 ending well before wing apex; cell m_3 open; vein M_3 usually present and long, but sometimes reduced or absent (Figs 195, 203); discal cell (*d*) characteristically reduced in size, as compared to Xylomyidae and situated in anterior ½ of wing; cell *cua* elongate, closed (Fig. 156). Legs usually simple, occasionally hind leg elongate (Fig. 39), femora sometimes clavate and with spines (Figs 51, 52, 53, 154); fore and hind tibiae without apical spurs, mid tibia usually without spurs, but with single tiny spur only in *Allognosta* Osten Sacken in the Afrotropical fauna (Fig. 153, arrowed).

Abdomen highly varied in shape, ranging from short and rounded to elongate (Figs 12, 39), sometimes clavate (Fig. 53) to triangular (Fig. 79); male terminalia (Figs 233–236) with phallic complex trifid in vast majority of Afrotropical taxa (Figs 235, 236), occasionally bifid, modifications include lobes partly to entirely fused, sometimes with additional elongate lateral processes; female terminalia with cercus usually 2-segmented (Fig. 237), occasionally 1-segmented, not strongly modified, cerci distinctly separated by tergite 10; female almost invariably with 3 spermathecae, rarely with only 2, ducts moderately elongate, usually with distinct hinge-like bend (*e.g.*, Ururahy-Rodrigues & Pujol-Luz 2000, figs 2, 5), genitalic fork simple (Fig. 238), but often species-specific.

Larvae with distinctive morphology, including shagreened appearance, cuticular "warts" (Figs 239–242), exerted head capsule (Fig. 241) and well-developed setae on all segments; aquatic larvae with characteristic fringe of hydrofuge setae at posterior end (Fig. 242), surrounding cleft that houses posterior spiracles; larval pupation within last larval skin.

Although Stratiomyidae are one of the most morphologically diverse groups of Diptera, they are easy to recognise. Their


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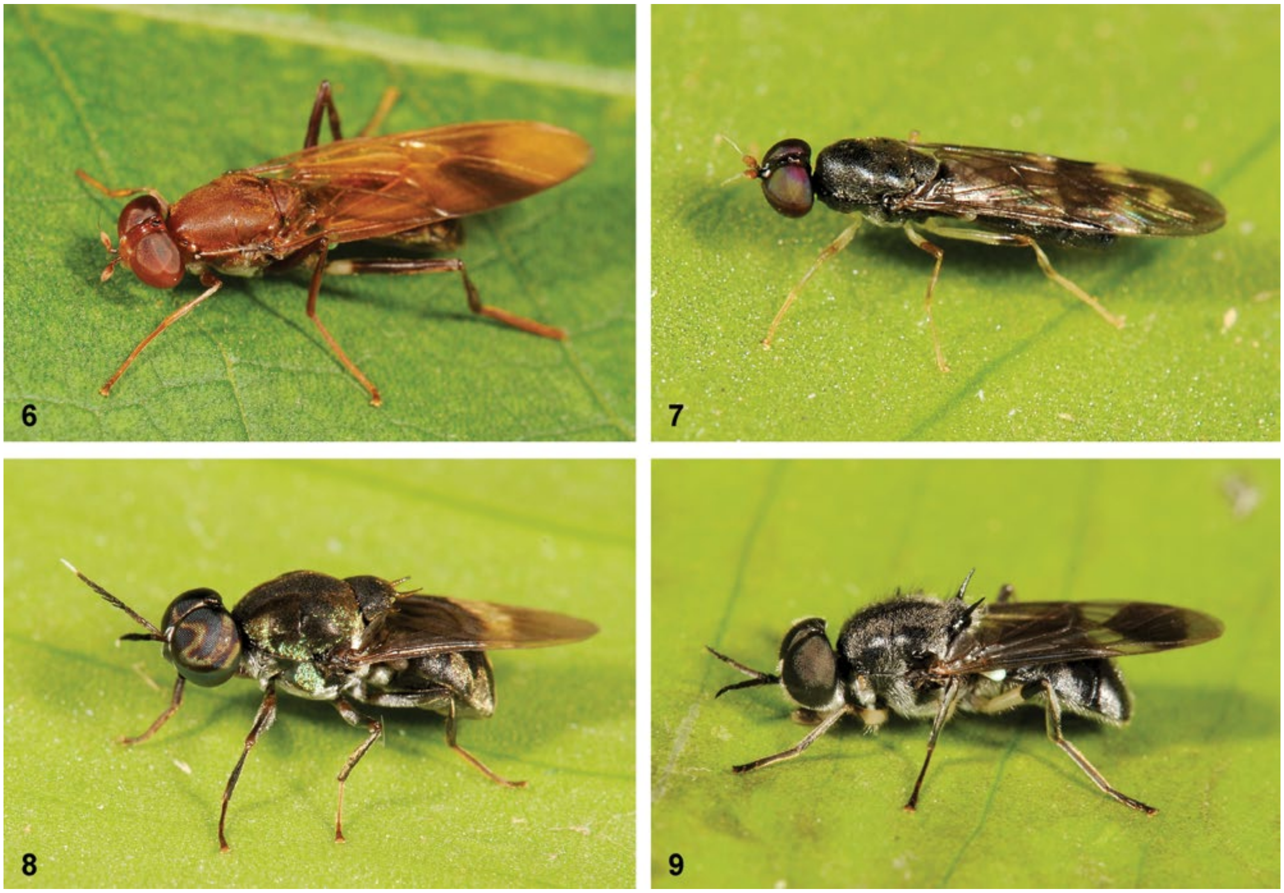
Figs 41.2–5. Photographs of living Afrotropical Stratiomyidae: (2) *Ptecticus posticus* (Wiedemann) ♂ (Tanzania); (3) *Ampsalis terminalis* James ♂ (Madagascar); (4) *Zulumyia* sp. ♂ (South Africa); (5) *Psapharomys* sp. ♀ (Namibia). Figs 2–4 (photographs © S.A. Marshall), Fig. 5 (photograph © P. Bertner).

distinctive wing venation, with the radial veins crowded anteriorly and the small discal cell (*d*), is characteristic (Fig. 156). They may possibly be confused with Xylomyidae (see Chapter 40), but this family has 2 tibial spurs on the mid leg and 1 or 2 on the hind leg. The nematocerous family Anisopodidae (see Chapter 25) has a wing venation that is somewhat similar to stratiomyids, but these flies have more than two palpal segments, more than eight flagellomeres and wing cell *cua* is broadly open at the wing margin. Syrphidae (see Chapter 60) superficially resemble some stratiomyids, but syrphid wing venation differs in having the venation less crowded toward the costal margin (C) and having a much larger discal cell and a false vein through cells *br* and r_{4+5}.

Biology and immature stages

Immature stages of Stratiomyidae occur in a variety of habitats. They are usually associated with decaying plant matter, ranging from leaf litter to rotting fruits. Some, particularly representatives of the subfamily Pachygastrinae, are found beneath the bark of fallen trees (Figs 239, 240). Larvae of the subfamilies Raphiocerinae (non-Afrotropical), Nemotelinae and Stratiomyinae (Fig. 242) are aquatic, occurring in a variety of wet habitats, ranging from ponds and rivers, to tree holes and other more transient water sources, such as seepage areas. The larvae of several Neotropical species have been recently described, providing new information on the subfamilies: Chiromyzinae (Pujol-Luz & Vieira 2000; Viana *et al*. 2003); Clitellariinae (Viana *et al*. 2003; Xerez *et al*. 2004); Pachygastrinae (Marques & Xerez 2009; Pujol-Luz & Xerez 1999; Pujol-Luz *et al*. 2016*b*; Xerez & Gracia 2008; Xerez & Lopes 2009; Xerez & Pujol-Luz 2001; Xerez *et al*. 2002, 2003); Sarginae (Pujol-Luz & Leite 2001; Viana & Xerez 2002); Chrysochlorininae (Iide 1965); Raphiocerinae (Pujol-Luz *et al*. 2004); and Hermetiinae (Pujol-Luz *et al.* 2016*a*). Bučánková *et al*. 2009 described the larva and pupa of the Oriental species *Pegadomyia pruinosa* Kertész, 1916 and summarised all the described Pachygastrinae larvae globally. The larva and puparium of the Oriental *Oplodontha rubrithorax* (Macquart, 1838) was illustrated in detail by Nerudová *et al*. (2015). James (1981: 498), McFadden (1967) and Rozkošný (1982: 22, 1983: 219) summarised what is known regarding the biology of stratiomyid larvae in North America and Europe, but little has been published on Afrotropical taxa. James (1940) illustrated the terminal four segments of the pupal case of *Oplodontha albipennis* (Macquart, 1838)



Figs 41.6–9. Photographs of living Afrotropical Stratiomyidae: (6) *Gongrosargus maculipennis* (Lindner) ♀ (Madagascar); (7) *Enypnium obscura* (Bigot) ♂ (Ghana); (8) *Isomerocera quadrilineata* (F.) ♂ (Ghana); (9) *Nigritomyia loewii* (Brauer) ♂ (Ghana). Figs 6–9 (photographs © S.G. Gaimari).

(as *Hoplodonta stricticella*). Lachaise & Lindner (1973) published ecological information on a few species from Côte d'Ivoire that included information on larval habitats. Kühbandner (1985) described the larva of *Odontomyia smaragdifera* (Lindner, 1938) from Kenya, without being aware that Lachaise & Lindner (1973) had earlier described the larva of the same species. Engel & Cuthbertson (1939) described the larva of *Ptecticus posticus* (Wiedemann, 1830). Lindner (1938) described and illustrated the pupa of *Sargus opulentum* (Grünberg, 1915). Lachaise & Lindner (1973) attempted to classify the species found in the vicinity of a field station in Côte d'Ivoire into three ecological groups: forest-dwellers, savanna-dwellers and ubiquitous species.

Adult soldier flies often occur on leaves in sunny patches in forest habitats and some adults, particularly Stratiomyinae and some Clitellariinae, frequent flowers. Adults of Sarginae and Hermetiinae usually occur near larval food sources, where males congregate and form small territories awaiting females (N.E. Woodley, pers. obs.). Males of some taxa hover singly in small aerial territories, similar to the behaviour of male syrphids, while others form conspecific swarms, ranging from a few to many individuals. Corbet & Haddow (1962) published some brief notes regarding *Tinda nigra* (Macquart, 1935) swarming above a forest canopy in Uganda at sunset. Oldroyd (1964: 114) mentioned that *Platyna hastata* (F., 1805) swarmed in patches of sunlight in West Africa and the same species was observed swarming in sun spots in forest clearings in Democratic Republic of Congo (A.H. Kirk-Spriggs, pers. comm. 2016). Stratiomyids can be abundant in Malaise traps, but rarely come to light, indicating that they are primarily diurnal.

Economic significance

Very few Stratiomyidae are of economic importance. A few species of the non-Afrotropical subfamily Chiromyzinae have been implicated as pests of grass crops. The larvae of these species occur in soil and two species, *Inopus flavus* (James, 1968) and *I. rubriceps* (Macquart, 1847), are considered pests of sugarcane in Australia (Bull 1976), with the latter also apparently inflicting extensive damage to lawns and pastures through its feeding action on grass roots. *Inopus rubriceps* was introduced into New Zealand, where it is considered a major pest of pastures and maize crops on North Island (Macfarlane & Andrew 2000). It was also accidentally introduced into California in the United States around 1948 (Kessel 1948), and that population still exists and is slowly spreading (E. Fisher, pers. comm. 2005), but has not assumed pest status. *Tana paulseni* (Philippi, 1865) has been listed as a pest of wheat, rye grass and pastures in Chile (González *et al*. 1973: 34). Recently another Chiromyzinae, *Chiromyza vittata* Wiedemann, 1820, has been identified as a pest of coffee plantations in Brazil (Pujol-Luz 1999). The larva was described in detail, together with biological observation by Pujol-Luz & Vieira (2000).

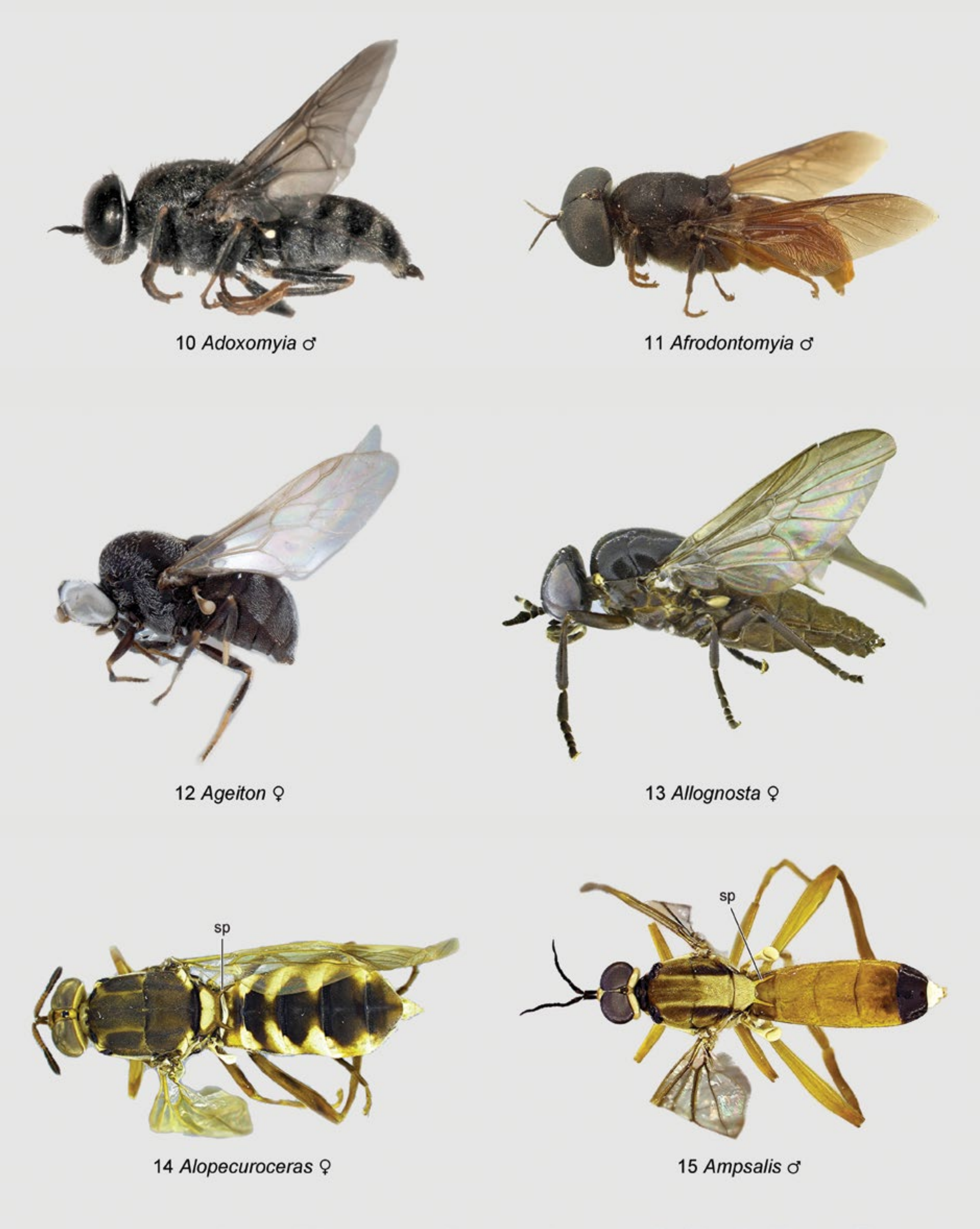
One species, *Hermetia illucens* (L., 1758), known as the Black soldier fly, is a very general scavenger in the larval stage that occurs in a wide variety of decaying organic material. As a result of human commerce, *H. illucens* has been spread virtually throughout all warmer regions of the world (Leclercq 1969, 1997; Roháček & Hora 2013). Very rare cases of human intestinal and cutaneous myiasis caused by this species have been recorded (Adler & Brancato 1995; Calderón-Arguedas *et al*. 2005; Meleney & Harwood 1935). In the past few decades, there has been a burgeoning interest in the use of larval *H. illucens* for organic waste control, composting and as animal food supplements. It has been studied as an agent for manure control (Sheppard *et al*. 1994), for controlling house fly infestations in chicken production (Furman *et al*. 1959; Sheppard 1983) and as a food supplement for fish (Bondari & Sheppard 1981) and pigs (Newton *et al*. 1977). More recently, there has been considerable interest in using *H. illucens* as an agent for composting (Lalander *et al*. 2015). An Internet search on "Black soldier fly" demonstrates that this use is reaching a household level. Because of their broad spectrum of immature food sources, the larvae can be found on corpses and are used for the estimation of the post-mortem interval in forensic entomology (Lord *et al*. 1994; Pujol-Luz *et al*. 2008). The discovery of potential antimicrobial substances in the larva is stimulating new research in medicine (Chu *et al*. 2014; Park *et al*. 2014).

Classification

Stratiomyidae are representatives of the infraorder Stratiomyomorpha and are sister-group to the Xylomyidae (Woodley 1989: 1376), a placement corroborated by morphological (Sinclair 1992; Sinclair *et al*. 1994) and molecular studies (Wiegmann *et al*. 2003). Larvae of the two families are similar and pupation takes place in the last larval skin, a feature unique in the lower Brachycera. Woodley (2001) presented some data on the phylogeny of the subfamilies and summarised general information on the recognised subfamilies and their biology. Subsequently, Brammer & von Dolen (2007) published a phylogenetic study based on DNA sequences which recovered most recognised subfamilies as monophyletic, except for Clitellariinae and Stratiomyinae (see below for further details). Brammer & von Dolen (2010) presented another phylogeny, based on morphological data, which recovered similar results, except Sarginae and Antissinae were not recovered as monophyletic. Additional phylogenetic study is required, particularly in poorly characterised subfamilies such as the Clitellariinae, to further resolve the phylogenetic relationships of the family. The following paragraphs give a brief overview of the twelve subfamilies recognised by Woodley (2001), of which eight occur in the Afrotropical Region, as well as the three tribes of Stratiomyinae. Further general information on the classification of the family, including discussion of subfamilies that do not occur in the Afrotropical Region, can be found in Woodley (2001). Woodley (2001) provided a solid taxonomic and nomenclatural foundation for all the described Afrotropical genera and species, which was updated by Woodley (2011) and Hauser *et al*. (2017).

Parhadrestiinae is a small subfamily only comprising the Chilean genus *Parhadrestia* James, with two species and the Cretaceous Canadian amber fossil genus *Cretaceogaster* Teskey.

Chiromyzinae is a distinct subfamily with reduced mouthparts, which is found in South America and the Australasian Region. Many representatives of this group are light to dark brown and resemble rhagionids. Several species appear to be pests and have been transported accidently into other regions of the world. No species are known from the Afrotropical Region.



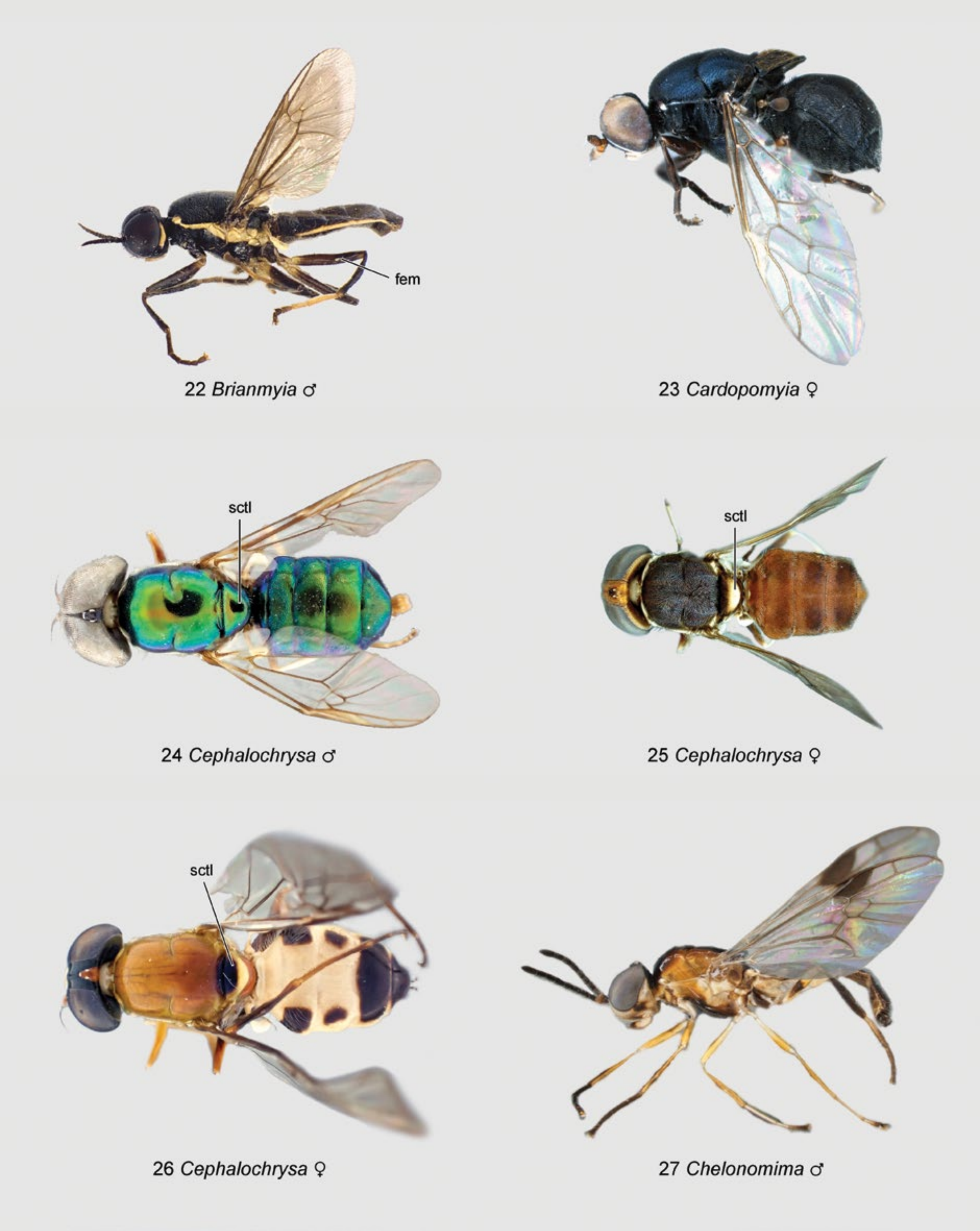
Figs 41.10–15. Habitus of Stratiomyidae: (10) *Adoxomyia argenteofasciata* (Bezzi), lateral view ♂; (11) same, *Afrodontomyia gracilis* (Curran) ♂; (12) same, *Ageiton ater* Kertész ♀; (13) same, *Allognosta* sp. ♀; (14) *Alopecuroceras atripluma* James, dorsal view ♀; (15) same, *Ampsalis terminalis* James ♂.

Abbreviation: sp – spine.

16 *Apotomaspis* ♀
17 *Argyrobrithes* ♂
18 *Ashantina* ♀
19 *Aspidacantha* ♂
20 *Aspidacanthina* ♀
21 *Brachycara* ♀

Figs 41.16–21. Habitus of Stratiomyidae (lateral views): (16) *Apotomaspis nigeriana* Lindner ♀; (17) *Argyrobrithes* sp. ♂; (18) *Ashantina antennata* Kertész ♀; (19) *Aspidacantha atra* Kertész ♂; (20) *Aspidacanthina exigua* Lindner ♀; (21) *Brachycara ventralis* Thomson ♀.

Abbreviations: msm – mesonotum; proc – process; sctl – scutellum.



22 *Brianmyia* ♂

23 *Cardopomyia* ♀

24 *Cephalochrysa* ♂

25 *Cephalochrysa* ♀

26 *Cephalochrysa* ♀

27 *Chelonomima* ♂

Figs 41.22–27. Habitus of Stratiomyidae: (22) *Brianmyia stuckenbergi* Woodley, lateral view ♂; (23) same, *Cardopomyia* sp. ♀; (24) *Cephalochrysa lucens* (Lindner), dorsal view ♂; (25) same, *Cephalochrysa* sp. ♀; (26) same; (27) *Chelonomima* sp., lateral view ♂. Fig. 22 (after Woodley 2012, fig. 1).

Abbreviations: fem – femur; sctl – scutellum.

Beridinae are small- to moderately sized flies (body length: 5–9 mm) that are characterised in having an abdomen with six or seven larger segments and major abdominal tergites with subapical grooves (Fig. 155). This subfamily mainly occurs in temperate regions or at higher elevations, but several genera are primarily tropical. Woodley (1995) provided a comprehensive revision of the genera of this subfamily. Only the Afrotropical fauna is depauperate, where the subfamily is represented by only a few species of *Allognosta* (*e.g.*, Fig. 13).

Antissinae are characterised by the presence of a mid-tibial spur and representatives of this small subfamily are restricted to Australia and South America. No species are known from the Afrotropical Region

Pachygastrinae is a species-rich subfamily that occurs globally. The 90 described species in the Afrotropical Region are divided into 40 genera, many of them with only one or two species. Most of the genera are not well defined and many species are undescribed. They are small- to moderate-sized flies (body length: 2–12 mm) and are varied in appearance and morphology, often with modified scutellar and antennal structures. The main character used to define the subfamily is the absence of wing vein M_3 (Fig. 159), but this state occurs sporadically in other subfamilies (*e.g.*, Figs 181, 188, 189, 203). Nonetheless, most of the taxa placed in the subfamily probably form a monophyletic group. Lindner (1966*a*) published a key to continental Afrotropical genera, but it separates some genera on superficial characters and is incomplete due to subsequently described taxa. A modern generic revision is badly needed. Larvae of most species occur beneath the bark of fallen trees (Figs 239, 240). The larvae of *Sternobrithes tumidus* Loew, 1856 were found in humus at the bases of young *Raphia hookeri* G. Mann & H. Wendl. (as *Raphia gigantea*) (Palmaceae) by Lachaise & Lindner (1973) in Côte d'Ivoire.

Clitellariinae is a heterogeneous group that includes genera that are not readily assignable to other subfamilies. With twelve species in four genera, the subfamily is not very diverse in the Afrotropical Region. The subfamily lacks a rigorous diagnosis based on synapomorphic characters and recent phylogenetic studies centred on the subfamily, using both morphological and molecular data, have indicated that the group is polyphyletic (Brammer & von Dolen 2007, 2010). Clitellariinae possess a relatively plesiomorphic antennal flagellum with eight flagellomeres (Figs 123–125, 137, 149) and have wing vein M_3 present (Fig. 157). Larvae of this subfamily inhabit various types of decaying organic matter, often in the remains of fleshy plants or beneath bark (McFadden 1967).

Chrysochlorininae is a small subfamily, with only eight recognised genera, two of which occur in the Afrotropics. These are large flies that resemble Hermetiinae, except that the terminal antennal flagellomere is an arista-like stylus. They differ from Sarginae in having eight antennal flagellomeres and having wing crossvein *m–cu* connected to vein M_4 (Fig. 173) (only *Gongrosargus* Lindner and *Formosargus* James in the Sarginae have the *m–cu* crossvein connected to vein M_{3+4} – see Fig. 182). There are only four described Afrotropical species and nothing is known regarding their biology.

Hermetiinae are large, wasp-like flies, related to Sarginae and Chrysochlorininae, but are distinguished from these in having the terminal antennal flagellomere modified, at least in part, into a long, flattened, vane-like style (Fig. 131). The distinction between Hermetiinae and Chrysochlorininae is muddied by genera such as *Chaetohermetia* Lindner (non-Afrotropical) which has the terminal flagellomere arista-like apically, but is not entirely aristate. It is possible that these two taxa should be combined into a single subfamily. The Afrotropical fauna is small, consisting of three described species of *Hermetia* Latereille, one of which (*H. illucens*) is introduced as an invasive species in much of the Afrotropics (Kirk-Spriggs 2011: 125).

Sarginae is a species-rich subfamily with a global distribution. Currently, 114 species are described in 13 genera in the Afrotropical Region, but many undescribed species are known. They are related to the Chrysochlorininae and Hermetiinae, as all three subfamilies share a strongly concave posterior region to the head. It is separated from these in having a reduced number of antennal flagellomeres (5 or 6) (Figs 126, 130, 143) and by having wing crossvein *m–cu* connected to vein M_4 (Fig. 170) (except in *Gongrosargus* (Fig. 182) and in the Oriental genus *Formosargus*). World genera are in need of a rigorous revision and the Afrotropical fauna is particularly problematic. This is partly due to the fact that the Malagasy fauna is diverse and poorly studied. Compounding the problem, Erwin Lindner described numerous species, mostly from Madagascar, using the generic name *Chrysochroma* Williston, which is unambiguously a synonym of *Sargus* F. Few, if any, of these species are congeneric with *Sargus* as now recognised. Thus, 35 Afrotropical species were unplaced generically in Woodley (2001). Of these, most could be assigned to a genus (Hauser *et al*. 2017), but eight species remain unplaced. Adults of Sarginae usually occur in the vicinity of decaying plant matter, such as fallen forest fruits or animal dung, where the immatures could be found feeding on different organs and tissues in a plant, as shown for the Neotropical *Merosargus* Loew in Fontenelle *et al*. (2012). Males in many species patrol small territories in these habitats awaiting females that are attracted to the larval food source (N.E. Woodley, pers. obs.).

Raphiocerinae are elongate, often brightly coloured and have patterned wings. This small subfamily occurs mainly in the Neotropics, but one species is described from the Oriental Region. No species are known from the Afrotropical Region.

Stratiomyinae are characterised in having aquatic larvae with a coronet of setae surrounding the posterior spiracular cavity (Fig. 242). Adults have six antennal flagellomeres (Figs 134, 138) (in some genera there are only five); sometimes the terminal flagellomere is modified into an arista-like stylus (Figs 135, 136, 141). Flies in this subfamily often occur on flowers, at least in temperate regions. Some Afrotropical species mimic wasps and bees, such as *Nyassamyia andreniformis* (Lindner, 1935) (Fig. 66) and are particularly convincing when in flight. The generic limits, particularly of the genera similar to *Odontomyia* Meigen, require revision. Three tribes were recognised by Woodley (2001), the Oxycerini, Prosopochrysini and Stratiomyini.

Oxycerini are predominantly found in the Nearctic, Oriental and Palearctic Regions. They are generally smaller in size than representatives of the tribe Stratiomyini, but are otherwise similar in general appearance. They differ from Stratiomyini and most Prosopochrysini in having wing crossvein *m–cu* connected to vein M_{3+4} (Fig. 207). The Afrotropical Region has 13 described

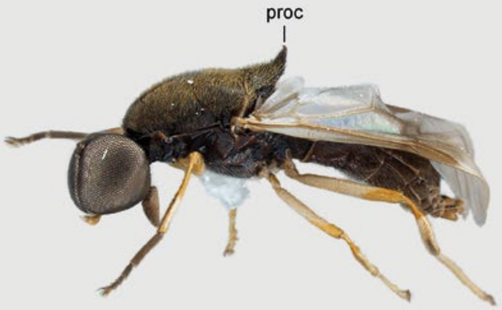
28 *Chloromyia* ♀

29 *Chrysochlora* ♂

30 *Chrysochromioides* ♀

31 *Crocutasis* ♂

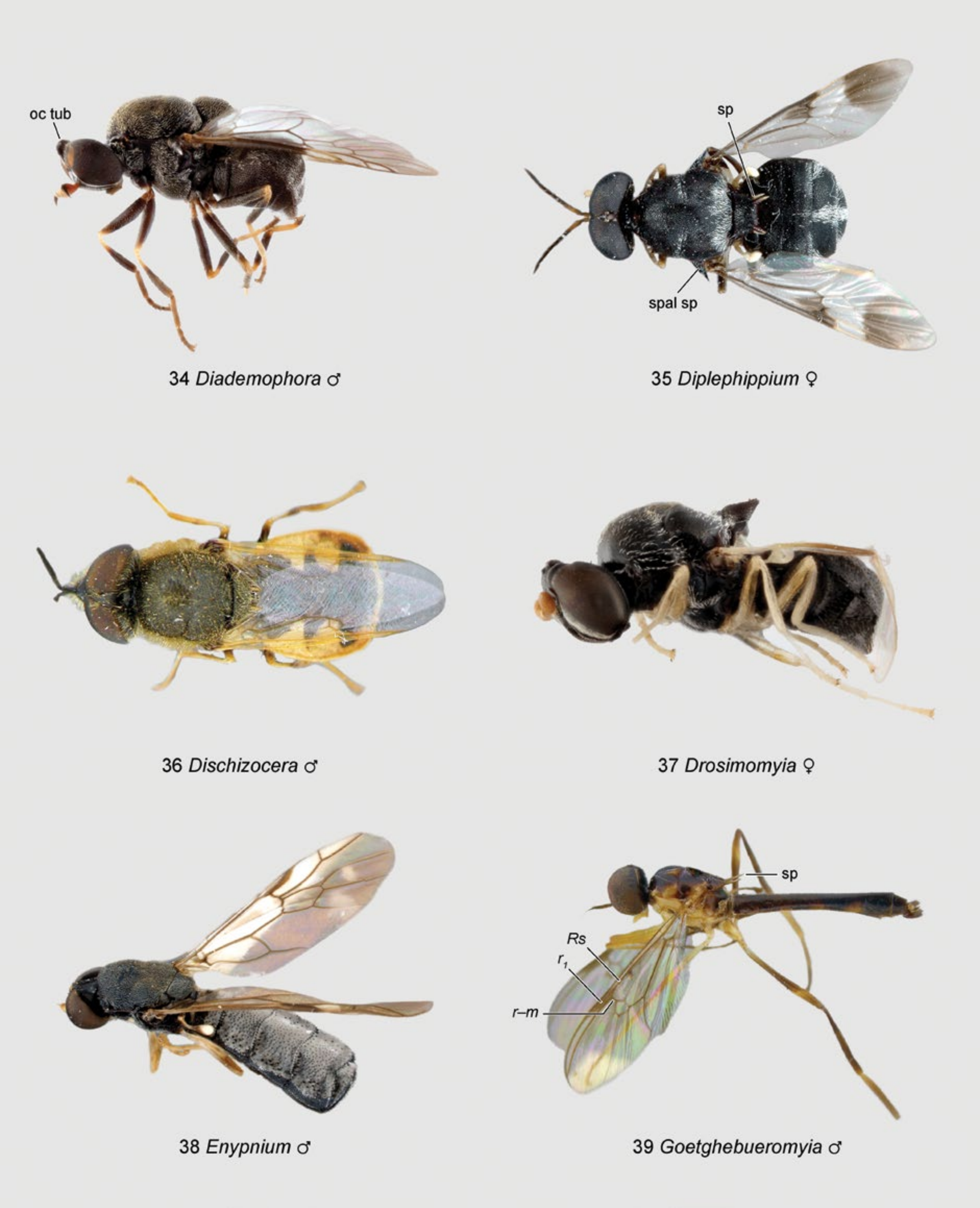
32 *Cyphoprosopa* ♂



33 *Dactylotinda* ♂

Figs 41.28–33. Habitus of Stratiomyidae: (28) *Chloromyia tuberculata* James, dorsal view ♀; (29) *Chrysochlora amethystina* (F.), lateral view ♂; (30) same, *Chrysochromioides micropunctata* Brunetti ♀; (31) same, *Crocutasis abyssinica* Lindner ♂; (32) same, *Cyphoprosopa lindneri* James, ♂; (33) same, *Dactylotinda saegeri* Lindner ♂.

Abbreviations: *d* – discal cell; fc – face; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; proc – process.



34 *Diademophora* ♂

35 *Diplephippium* ♀

36 *Dischizocera* ♂

37 *Drosimomyia* ♀

38 *Enypnium* ♂

39 *Goetghebueromyia* ♂

Figs 41.34–39. Habitus of Stratiomyidae: (34) *Diademophora ruandaensis* Lindner, lateral view ♀; (35) *Diplephippium snyderi* James, dorsal view ♂; (36) same, *Dischizocera zumpti* Lindner ♂; (37) *Drosimomyia* sp., lateral view ♀; (38) *Enypnium* sp., dorsolateral view ♂; (39) *Goetghebueromyia paradoxa* Lindner, lateral view ♂.

Abbreviations: oc tub – ocellar tubercle; r_1 – first radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector; sp – spine; spal sp – supra-alar spine.

species, 12 in the genus *Oxycera* Meigen and one in *Stuckenbergiola* Lindner. The biologies of flies in this tribe are relatively well-known only in Europe. Larvae occur primarily in moss in marshes, streams and seepage areas, where they are scavengers, sometimes feeding on algae (Rozkošný 1983: 94). Adults are usually collected by sweeping near larval habitats, but males of at least some species form conspecific swarms (Woodley 2001).

Prosopochrysini (frequently termed Myxosargini in older literature) are more elongate and slender than other Stratiomyinae and some species have patterned wings (Fig. 189). Eleven of the 13 Afrotropical species are endemic to Madagascar, as are six of the eight Afrotropical genera. The group is poorly studied phylogenetically, but has been characterised in having the antennae inserted dorsal to the lower eye margin and in having wing vein *CuP* sinuate (Figs, 168, 174, 181, 188, 189, 209) (James & McFadden 1979). Further study is required to properly define the tribe and solidify generic concepts. In a number of species wing vein M_3 is absent (Figs 174, 181, 188, 189, 191, 209), which has resulted in some Afrotropical genera being placed in the subfamily Pachygastrinae. As species in these genera have six antennal flagellomeres (Figs 128, 135, 136, 141) and a different conformation of the discal wing cell (*d*) as compared to Pachygastrinae, Woodley (2011) transferred them to the tribe Prosopochrysini. Very little is known regarding the biology of the tribe, but the presence of hydrofuge setae at the posterior end of the larva indicates that they are aquatic.

Stratiomyini are small- to relatively large-sized, robust flies. They frequently resemble bees or wasps and many frequent flowers as adults. There are 81 species in eight, often poorly defined genera. They differ from the tribe Oxycerini in being generally larger in size and in having wing crossvein *m–cu* connected to vein M_4 (Figs 203, 228) and from Prosopochrysini in being more robust in general form. Representatives of this tribe lack a modified terminal flagellomere which is often simply cone-shaped and never arista-like or elongate (Figs 138, 148). Larvae are aquatic and occur in lakes, ponds and streams (McFadden 1967; Rozkošný 1982: 158) and more transient aquatic situations, such as temporary pools (Lachaise & Lindner 1973), or tree holes (Woodley 2001; Yanoviak 2001).

Nemotelinae is poorly defined in phylogenetic terms (Woodley 2001). Forty-two species in four genera occur in the Afrotropical Region, with *Nemotelus* Geoffroy being by far the most species-rich genus and the only one represented in Madagascar. The subfamily is characterised in having six antennal flagellomeres and crossvein *m–cu* connected to vein M_{3+4} (Figs 167, 190, 215). Larvae of *Nemotelus* are aquatic and exhibit some similarities with the larvae of Stratiomyinae, but those of other genera included here remain largely unknown. Adults sometimes frequent flowers and species of *Brachycara* Thomson are only found near ocean shores in warm climates, with larvae presumably occurring nearby.

Identification

There has never been a published general treatment of the Stratiomyidae of the Afrotropical Region. Most published taxonomic work comprises species descriptions, most of which are poorly illustrated, if at all. There has been virtually no true revisionary work. Mason (1997*b*) published a comprehensive revision of Afrotropical Nemotelinae which is the only work that treats a subfamily with more than one genus. Modern revisionary work has been undertaken for a few individual genera and these works are cited in the individual generic treatments below.

Larger specimens should be direct-pinned and smaller species micro-pinned in the field for later double-mounting in the laboratory (see Chapter 2).

Key to genera of Afrotropical Stratiomyidae

1. Abdominal segments 6 and 7 relatively undifferentiated, not retracted into abdomen; tergites 2–6 with distinctly impressed transverse subapical grooves (Fig. 155); mid tibia with tiny apical spur (Fig. 153, arrowed) (BERIDINAE) . . . . *Allognosta* Osten Sacken

– Abdominal segments 6 and 7 reduced in size, usually retracted into abdomen, thus abdomen appearing 5-segmented (*e.g.*, Fig. 41); abdominal tergites lacking subapical grooves; mid tibia without apical spur 2

2. Wing with 3 median (*M*) veins (some *Odontomyia* with vein M_3 present as short stump vein, less than ½ length of other *M* veins) (*e.g.*, Figs 186, 191, 197, 203, 228) 3

– Wing with 4 median (*M*) veins (*e.g.*, Figs 190, 206, 221) 64

3. Wing with *m–cu* crossvein connected to vein M_4 (*e.g.*, Figs 156, 174) 4

– Wing with *m–cu* crossvein connected to vein M_{3+4} (*e.g.*, Figs 159, 163, 228) (PACHYGASTRINAE & STRATIOMYINAE [in part]) 10

4. Scutellum without spines (Fig. 60); wing vein *CuP* absent (Fig. 197) (SARGINAE [in part]) . . . . *Microsargus* Lindner

– Scutellum with pair of spines (*e.g.*, Figs 68, 70); wing vein *CuP* present (*e.g.*, Fig. 174) (STRATIOMYINAE [in part]) 5

5. Delicate flies with abdomen elongate (Fig. 32); lower calypter virtually linear, without lobe developed laterally (as in Fig. 152); wing membrane almost entirely clothed in microtrichia; vein R_4 absent (Fig. 174) . . . . *Cyphoprosopa* James

– Robust flies with abdomen rounded (e.g., Figs 36, 69); lower calypter with well-developed, conspicuous lobe arising laterally, mostly clothed in long setulae (e.g., Fig. 150); wing membrane largely devoid of microtrichia; wing vein R_4 present (e.g., Fig. 203) or rarely absent (Fig. 204) 6

6. Terminal antennal flagellomere blunt at apex, concave on posterior surface, sometimes notched at apex, appearing bifurcate . . . . *Dischizocera* Lindner

– Terminal antennal flagellomere conically tapered, never notched or bifurcate (e.g., Fig. 138) 7

7. Eye densely pilose, with setulae as long as antennal scape; eyes in male slightly separated on upper frons; body almost entirely black in colour (Fig. 31) . . . . *Crocutasis* Lindner

– Eye usually bare, if pilose, then setulae much shorter than antennal scape; eyes in male almost invariably contiguous on upper frons; colour variable, but usually not entirely black (e.g., Figs 68–70) 8

8. Wing with discal cell (*d*) greatly reduced, small to absent, *r–m* crossvein absent as discal cell (*d*) broadly fused with radial sector (*Rs*) anteriorly; veins M_1 and M_2 absent or at most vein M_2 faintly discernible; vein *CuP* likewise very weak to absent beyond base, with cell *cua* undefined (Fig. 204) . . . . *Oplodontha* Rondani

– Wing with discal cell (*d*) not reduced, not usually fused with radial sector (*Rs*) anteriorly, *r–m* crossvein distinct, sometimes punctiform; vein M_2 weak, but distinct, extending at least halfway to wing margin, usually longer; vein M_1 variable, occasionally absent, but usually ranging from a short stump vein near discal cell (*d*) to complete, sometimes basal portion reduced; vein *CuP* weak, but distinct, with cell *cua* defined (e.g., Fig. 203) 9

9. Antennal scape and pedicel elongate, together only slightly shorter than flagellum, both segments subequal in length; male scutum clothed in dense silvery pilosity obscuring surface; vein M_3 invariably present . . . . *Catatasis* Kertész

– Antennal scape and pedicel not elongate, together distinctly shorter than flagellum, both segments sometimes subequal, but scape frequently longer than pedicel (Fig. 138); male scutum not clothed in dense silvery pilosity; some species with wing vein M_3 only present as stump vein . . . . *Odontomyia* Meigen

10. Scutellum with 2 (e.g., Fig. 48), 4 (e.g., Fig. 46), 6 (e.g., Fig. 44), 8 or 10 spines 11

– Scutellum without spines (e.g., Fig. 42), or with single central spine (e.g., Fig. 80) 25

11. Scutellum with 4 or more spines 12

– Scutellum with 2 spines 17

12. Scutellum with 4 spines 13

– Scutellum with 6 or more spines 16

13. Antennal flagellomeres 3–5 with dorsoventral processes, thus slightly bipectinate (Fig. 113); vestiture of thorax and abdomen partly composed of small metallic scales (Figs 8, 46) . . . . . *Isomerocera* Enderlein

– Antennal flagellomeres 3–5 without processes (e.g., Figs 129, 147); vestiture of thorax and abdomen not composed of small, metallic scales (e.g., Figs 35, 97) 14

14. Thorax with supra-alar spine near wing base (Fig. 35); each pair of scutellar spines orientated at different planes, apical pair longer than scutellum (Fig. 35); antennal flagellum cylindrical, terminal flagellomere shorter than basal 7 flagellomeres (Fig. 129) . . . . *Diplephippium* Speiser

– Thorax without supra-alar spine near wing base (e.g., Fig. 97); all 4 scutellar spines orientated in same plane (e.g., Fig. 97), length variable; terminal flagellomere longer than basal 7 flagellomeres (Fig. 147) 15

15. Scutellar spines longer than scutellum; scutellum at 45° angle to mesonotum; thorax and abdomen brownish to brownish yellow, with some black markings; abdomen roundish, wider than thorax . . . . *Tindacera* Lindner

– Scutellar spines much shorter than scutellum (Fig. 97); scutellum virtually in same plane as mesonotum; thorax and abdomen black, without distinct markings (Fig. 97); abdomen distinctly longer than wide, only marginally wider than thorax . . . . *Tinda* Walker

16. Head with oral margin not produced ventrally (Figs 111, 112); scutellum with 6 spines (Fig. 44) . . . . *Hexacraspis* Enderlein

– Head with oral margin produced ventrally (Fig. 116); scutellum with 8–10 spines (Fig. 75) . . . . *Oxymyia* Kertész

17. Antenna with 8 flagellomeres, terminal flagellomere unmodified, cone-shaped (Fig. 115); wing vein R_4 present (Fig. 193). . . . . *Meristomeringina* James

– Antenna with 6 flagellomeres, terminal flagellomere unmodified cone-shaped (*e.g.*, Fig. 148), elongate (*e.g.*, Fig. 134) or modified as arista-like stylus (*e.g.*, Figs 136, 141); wing vein R_4 present or absent (*e.g.*, Figs 188, 228) (STRATIOMYINAE [in part]) 18

18. Robust flies with abdomen rounded (Fig. 99); lower calypter with well-developed, conspicuous lobe arising laterally, mostly clothed in long setulae (as in Fig. 150); wing membrane largely devoid of microtrichia; vein R_4 present (Fig. 228); antennal scape > 5 × as long as broad at apex, pedicel > 3 × as long as broad at apex (Fig. 148) . . . . *Zulumyia* Lindner

– Delicate flies with abdomen elongate (*e.g.*, Figs 39, 48, 53); lower calypter virtually linear, without lobe developed laterally (as in Fig. 152), at most with inconspicuous widening along margin; wing membrane with microtrichia evident at least apically beyond discal cell (*d*), usually present over most of wing; vein R_4 absent (*e.g.*, Figs 168, 188, 189, 191); antennal scape < 3 × as long as broad at apex, pedicel < 2 × as long as broad at apex (*e.g.*, Figs 134–136, 141) (PROSOPOCHRYSINI [in part]) 19

19. Hind femur strongly thickened, with large ventral tooth-like process near apex (*e.g.*, Figs 51, 52, 154), mid femur sometimes also conspicuously thickened (Fig. 53) (confined to Madagascar) 20

– Mid and hind femora unmodified (*e.g.*, Fig. 22), without armature, or with small spines (*Keiseria* Lindner) (Madagascar & continental Afrotropics) 22

20. Antennal flagellomeres 1–5 forming very short, conical complex; terminal flagellomere arista-like, > 3 × as long as complex (Fig. 135); head and body black in colour (Fig. 49). . . . . . . *Lampetiopus* Lindner

– Antennal flagellomeres 1–5 forming elongate cylindrical to elongate conical complex; terminal flagellomere in form of pubescent arista-like stylus 1–2 × as long as complex (*e.g.*, Fig. 136); head yellowish, body colour variable (*e.g.*, Figs 51–53) 21

21. Mid femur more strongly thickened than hind femur (Fig. 53), both with only single, subapical tooth . . . . *Madagascarina* Lindner

– Mid femur not nearly as strongly thickened as hind femur (Fig. 52), without subapical tooth; hind femur with numerous denticles anterior to large, subapical tooth (Figs 51, 52, 154). . . . . *Madagascara* Lindner

22. Scutellar spines only *ca* ½ length of scutellum; antenna almost cylindrical, flagellomeres 1–5 only slightly tapered, with flagellomere 6 almost as wide as flagellomere 5 at base, evenly, conically tapering to sharp apex (South Africa) . . . . *Brianmyia* Woodley

– Scutellar spines as long as or longer than scutellum (*e.g.*, Figs 39, 48); antennal flagellum either strongly tapered toward apex, with terminal flagellomere arista-like (*e.g.*, Fig. 141), or elongate with rounded apex (*e.g.*, Fig. 134) (widespread Afrotropics) 23

23. Antennal flagellum elongate, oblong-shaped, rounded apically (Fig. 134); antenna much longer than head (Fig. 48) (confined to Madagascar) . . . . *Keiseria* Lindner

– Antennal flagellum not oblong-shaped, strongly tapered toward apex, terminal flagellomere arista-like (*e.g.*, Fig. 141); antenna at most as long as head (Figs 39, 76) (continental Afrotropics and Madagascar) 24

24. Abdomen slender, subparallel-sided (Fig. 39); median wing vein (*M*) evident throughout entire length between cells *bm* and *br*; wing without maculae or dark markings (Fig. 181) (Central Africa) . . . . *Goetghebueromyia* Lindner

– Abdomen spatulate, broadest at abdominal segment 4 (Fig. 76); median wing vein (*M*) fading in basal part between cells *bm* and *br*; with apical wing macula and infuscation around discal cell (*d*) (Fig. 209) (confined to Madagascar) . . . . *Pachyberis* James

25. Scutellum with median, spine-like digitate process (*e.g.*, Figs 33, 80); overall length > 5 mm 26

– Scutellum without median spine-like digitate process (*e.g.*, Fig. 96); scutellum sometimes with process/extension, but then overall length < 4 mm (*e.g.*, Fig. 19) 28

26. Abdomen narrow, almost 2 × as long as wide (Fig. 33); terminal arista-like flagellomere inserted dorsally and subapically in female and apically in male . . . . *Dactylotinda* Lindner

– Abdomen greatly widened, much wider than thorax (*e.g.*, Fig. 79); terminal flagellomere with arista-like stylus apically (*e.g.*, Fig. 142) 27

27. Antenna elongate, especially scape and pedicel; terminal flagellomere forming short, slender arista-like stylus shorter than remainder of flagellum (Fig. 142); male abdomen with large patch of brilliant, silvery pubescence (Fig. 79) . . . . *Platyna* Wiedemann

– Antenna short and compact; terminal flagellomere forming an arista-like stylus that is longer than remainder of flagellum (Fig. 80); male abdomen without large patch of brilliant, silvery pubescence (Fig. 80). . . . . *Platynomorpha* Grünberg

28. Terminal antennal flagellomere similar to preceding ones, broad, lanceolate, oblong-shaped or cone-shaped, sometimes with different vestiture to preceding ones; antenna with elongate, cylindrical flagellum (*e.g.*, Figs 127, 140, 146); body form elongate (*e.g.*, Figs 27, 77, 96) 29

– Terminal antennal flagellomere highly variable, but distinctly tapered in some way and much narrower than basal flagellomeres, most commonly arista-like (e.g., Fig. 107), but may be in form of pubescent lanceolate style, which is much more narrow than preceding flagellomeres (*e.g.*, Figs 109, 121), or lanceolate and strongly tapered into filament (*e.g.*, Fig. 132); body form highly variable (*e.g.*, Figs 12, 67, 81). 31

29. Antenna distinctly shorter than head (Fig. 77); flagellomeres 7 and 8 short, cone-shaped, without obvious stiff, dense setae; flagellomere 8 minute, shorter than flagellomere 7 in male, subequal in female (Fig. 140) . . . . *Parameristomerinx* Woodley

– Antenna longer than head (*e.g.*, Figs 27, 96); flagellomeres 7 and 8 equal in length (*e.g.*, Fig. 127) or longer than preceding flagellomeres in both sexes, clothed in stiff, dense setae (*e.g.*, Fig. 146) 30

30. Antennal scape and pedicel short, virtually as long as broad and of subequal length (Fig. 127); antennal flagellomeres 1–8 of almost equal size and shape (Fig. 127), each short cylindrical and evenly pubescent with short, stiff black setulae; moderately slender, Sarginae-like flies, most species predominantly yellowish in colour (Fig. 27) . . . . *Chelonomima* Enderlein

– Antennal scape and pedicel elongate, at least 2 × as long as broad, sometimes pedicel longer than scape (Fig. 146); antennal flagellomeres 1–6 similar in size and shape, with some short, stiff pubescence, but terminal 2 flagellomeres conspicuously larger and much more densely pubescent, the terminal flagellomere virtually as long as three basal flagellomeres combined (Fig. 146); larger, more robust flies, predominantly black dorsally (Fig. 96) . . . . *Thorasena* Macquart

31. Terminal two antennal flagellomeres with bristly black setulae, noticeably longer and more conspicuous than vestiture of more basal flagellomeres (*e.g.*, Figs 107, 132); antenna distinctly elongate, flagellum much longer than wide; abdomen elongate, distinctly longer than thorax, flat dorsally (*e.g.*, Figs 18, 43); large flies > 5.5 mm in length 32

– Terminal two antennal flagellomeres without conspicuous black setulae (*e.g.*, Fig. 103), although flagellomere 8 may differ in colour due to vestiture (*e.g.*, Fig. 121); antenna and abdomen highly variable (*e.g.*, Figs 12, 98); size highly variable, but most taxa < 5.5 mm in length 33

32. Terminal antennal flagellomere arista-like, with pilosity restricted to base, virtually equal in length to flagellomeres 1–7 combined (Fig. 107); male eyes dichoptic; face in both sexes somewhat protuberant below antennae, not evenly rounded (Fig. 107) . . . . *Ashantina* Kertész

– Terminal antennal flagellomere with pilosity over more than basal ½, shorter than length of flagellomeres 1–7 combined (Fig. 132); male eyes holoptic; face in both sexes evenly rounded below antennae. . . . .*Hermetiomima* Grünberg

33. Eye pilose (*e.g.*, Fig. 122) 34

– Eye bare (sometimes with a few microscopic setulae) (*e.g.*, Figs 103, 120, 121) 36

34. Wing with pterostigma short and triangular (Fig. 214), this part of wing weakened and easily folded (often appearing folded in preserved specimens) . . . . *Psapharomys* Grünberg [in part]

– Wing with pterostigma longer than broad (Fig. 229), this part of wing not weakened and capable of folding (not appearing folded in preserved specimens) 35

35. Head with lower oral margin produced ventrally, bilobed (Fig. 122); male eyes widely separated on frons; lower frons immediately above antennae deeply depressed; larger species (body length: 5.5 mm). . . . . Undescribed genus A

– Head with lower oral margin not produced ventrally, not bilobed; male eyes holoptic; lower frons immediately above antennae not depressed; smaller species (body length: 2.4–3.6 mm) . . . . *“Eupachygaster” lasiops* (Speiser, 1922)

36. Wing vein R_{2+3} arising distinctly beyond crossvein *r–m* (e.g., Fig. 163), or if *r–m* absent, then beyond point where discal cell (*d*) is fused to radial sector (*Rs*) (*e.g.*, Figs 159, 224). 37

– Wing vein R_{2+3} arising before crossvein *r–m* (*e.g.*, Fig. 186), or close to fusion of discal cell (*d*) with radial sector (*Rs*) (*e.g.*, Fig. 214) 42

37. Abdomen distinctly longer than wide, flat dorsally (Fig. 56); head longer than high (Fig. 56), distinctly wider than thorax; habitus rather Clitellariinae-like . . . . *Meristomerinx* Enderlein

– Abdomen almost circular in dorsal view, dorsally convex (*e.g.*, Fig. 12); head higher than long (*e.g.*, Fig. 17), about as wide as thorax; habitus typically Pachygastrinae-like 38

38. Terminal antennal flagellomere thickened, stylate (*e.g.*, Figs 103, 109, 121, 145), either cylindrical or bilaterally flattened and vane-like. 39

– Terminal antennal flagellomere slender, aristate (*e.g.*, Figs 104, 106). 41

39. Terminal antennal flagellomere whitish in colour, at least at apex (Figs 121, 145) . . . . *Sternobrithes* Loew

– Terminal antennal flagellomere of antenna entirely black in colour (*e.g.*, Fig. 109) 40

40. Ocellar tubercle not abnormally elevated (Fig. 103); terminal antennal flagellomere rounded at apex (Fig. 103); male eyes contiguous or separated on frons. . . . . *Argyrobrithes* Grünberg

– Ocellar tubercle strongly elevated (Fig. 109); terminal antennal flagellomere tapering abruptly to pointed apex (Fig. 109); male eyes contiguous at middle of frons . . . . *Diademophora* Lindner

41. Head in profile almost 1.5 × as high as broad (Fig. 12); antennal arista-like terminal flagellomere black to brown, never white at apex (Fig. 106); wing with discal cell (*d*) broadly connected to radial sector (*Rs*), crossvein *r–m* absent (Fig. 159); female frons with white setae along eye margin, but without setal patch above antenna (continental Afrotropics) . . . . *Ageiton* Kertész

– Head in profile as high as broad or slightly higher than broad (Fig. 23); antennal arista-like terminal flagellomere entirely white or at least apex white (Fig. 104); wing with discal cell (*d*) narrowly connected to radial sector (*Rs*), crossvein *r–m* present, but short, often punctiform (Fig. 169); female frons with white setae along eye margin and setal patch above antenna (Fig. 104) (confined to Madagascar) . . . . *Cardopomyia* Kertész

42. Terminal antennal flagellomere bilaterally flattened, invariably black in colour (*e.g.*, Figs 105, 144). . . . 43

– Terminal antennal flagellomere arista-like (*e.g.*, Figs 108, 114), sometimes appearing thickened (*e.g.*, Fig. 139), but not bilaterally flattened; black or white in colour 44

43. Male eyes dichoptic; ocellar triangle distinctly elevated (Fig. 67); antennal pedicel without finger-like projection (continental Afrotropics) . . . . *Nyplatys* Séguy

– Male eyes holoptic; ocellar triangle normal (Fig. 89); antennal pedicel in most species with finger-like projection (Fig. 105) (confined to Madagascar). . . . . *Ptilinoxus* Lindner

44. Wing vein R_4 absent (*e.g.*, Figs 165, 227) 45

– Wing vein R_4 present (*e.g.*, Fig. 205). 50

45. Scutellum with 1 short, button-shaped process (Fig. 19); head hemispherical in profile (Fig. 19). . . . . *Aspidacantha* Kertész

– Scutellum simple, without process (as in Fig. 98); head shape variable (as in Figs 20, 98) 46

46. Head almost spherical in lateral view (Fig. 98); antennal flagellum compact, higher than long, with arista-like terminal flagellomere inserted near middle in profile and somewhat lateral to apex . . . . *Zabrachia* Coquillett

– Head higher than long (*e.g.*, Fig. 20); antenna shape variable. 47

47. Femora extensively black in colour (Fig. 54) . . . . *Marangua* Lindner

– Femora mainly or entirely yellow in colour (*e.g.*, Figs 20, 37) 48

48. Frons of head without maculae of setae above antenna . . . . *Drosimomyia* Kertész

– Frons of head with pair of silver maculae above antennae (as in Fig. 108). 49

49. Antennae inserted above middle of head in profile (Fig. 19). . . . . *Aspidacanthina* Lindner

– Antennae inserted below middle of head in profile . . . . *Diargemus* Kertész

50. Larger species, > 4 mm in length; abdomen round, triangular or elongate (*e.g.*, Figs 38, 81); male eyes often holoptic, rarely dichoptic 51

– Smaller species, < 4 mm in length; abdomen invariably round (*e.g.*, Fig. 64); male eyes invariably dichoptic (except in Malagasy *Otionigera* Lindner and *Lophoteles* Loew from Seychelles) 57

51. Head higher than long; male eyes dichoptic. 52

– Head longer than high (females) (*e.g.*, Figs 117, 118, 120) or round (males); male eyes holoptic 54

52\. Abdomen round, as wide as long; male abdomen without silver pubescence . . . . *"Neopachygaster" valida* Lindner, 1938

– Abdomen parallel-sided, rectangular (*e.g.*, Fig. 38) or triangular "flask"-shaped (*e.g.*, Fig. 81); male abdomen with or without silver pubescence 53

53\. Wing membrane brownish, with 3 pale maculae visible to the naked eye beyond discal cell (*d*) (Figs 7, 180); male abdomen elongate, sides straight, gradually widening posteriorly (Fig. 38); female abdomen elongate oval; face with dark pilosity only . . . . *Enypnium* Kertész

– Wing membrane with pale brownish infuscation, but without maculae (Fig. 213); abdomen of male strongly widened to third segment, flask-shaped (Fig. 81), that of female more ovate, only slightly longer than wide; face with pale pilosity and silvery tomentose margins . . . . *Platynomyia* Kertész

54\. Wing with pterostigma triangular (Fig. 214); wing often bent (Fig. 5) . . . *Psapharomys* Grünberg [in part]

– Wing with pterostigma linear, rectangular (*e.g.*, Figs 216, 223); wing not bent (*e.g.*, Fig. 7) 55

55\. Wing cell *cua* very distinctive, vein *CuA* straight, making closure of cell *cua* rectilinear, both distal angles of cell close to 90° (Fig. 223) . . . . *Steleoceromys* Grünberg

– Wing cell *cua* without vein *CuA* closing at 90° (*e.g.*, Figs 186, 216) 56

56\. Terminal antennal flagellomere arista-like, inserted distinctly dorsal (female) to slightly dorsal (male) (continental Afrotropics) . . . . *Hypoceromys* Lindner

– Terminal antennal flagellomere arista-like, inserted apically (both sexes) (confined to Madagascar) . . . . *Pseudoxymyia* Lindner

57\. Terminal antennal segment with long, black setae dorsally and ventrally, considerably longer than thickness of segment; male eyes holoptic (confined to Seychelles) . . . . *Lophoteles* Loew

– Terminal antennal segment without long setae, sometimes with short, white setae that are shorter than thickness of segment (e.g., Fig. 139); male eyes dichoptic (except in Malagasy *Otionigera* Lindner) (continental Afrotropics & Madagascar) 58

58\. Abdomen considerably longer than wide, longer than thorax; legs entirely yellow; antennae inserted below middle of head in profile; frons shiny black . . . . *Anargemus* Lindner

– Abdomen almost circular in dorsal view, or wider than long; legs and antennae variable; frons often with silvery tomentose maculae 59

59\. Terminal antennal flagellomere arista-like, with short, dense, white pubescence (Fig. 139); male eyes holoptic (confined to Madagascar) . . . . *Otionigera* Lindner

– Terminal antennal flagellomere arista-like, thin, setula-like; male eyes dichoptic (continental Afrotropics & Madagascar) 60

60\. Scutellum strongly upwardly directed, at least at 90° angle to plane of mesonotum (*e.g.*, Fig. 16) . . . 61

– Scutellum not as strongly upwardly directed, forming *ca* 45° angle to plane of mesonotum (as in Fig. 37) 63

61\. Antennal flagellum higher than long, kidney-shaped, inserted well above middle of head in profile; scutellum with slightly button-shaped process apically, appearing sub-triangular in dorsal view, apparently with silvery setulae near base, with bright silvery pilosity; wing entirely pale in colour . . . . *Diplopeltina* Lindner

– Antennal flagellum round in profile, inserted above or below middle of head in profile; scutellum without apical process, without bright silvery pilosity; wing with some darkening of veins 62

62\. Scutellum rounded in dorsal view; mesonotum with yellowish gold pilosity on dorsum (Fig. 16) . . . . *Apotomaspis* Lindner

– Scutellum sharply triangular in dorsal view; mesonotum with some silvery pilosity on dorsum . . . . *Pachyacantha* Lindner

63\. Wing membrane not darkened near base (Figs 63, 199); antennae inserted at middle of head in profile, or above; terminal antennal flagellomere arista-like, not distinctly pubescent; scutellum more triangular in dorsal view . . . . *Neopachygaster* Austen

– Wing membrane darkened near base; antennae inserted below middle of head in profile; terminal antennal flagellomere arista-like, apparently with dense brownish pilosity; scutellum semi-circular in dorsal view . . . . *Pithomyia* Kertész

64\. Antennal flagellum with 8 discernible flagellomeres (flagellomere 7 may be minute and difficult to detect) (*e.g.*, Figs 123–125, 131) 65

– Antennal flagellum with 5 (*e.g.*, Figs 126, 143), 6, or rarely 7 discernible flagellomeres (*e.g.*, Figs 110, 130). 74

65. Scutellum with 2 marginal spines (*e.g.*, Figs 3, 9, 14, 15) (CLITELLARIINAE) 66

– Scutellum without marginal spines (*e.g.*, Fig. 42) 72

66. Scutum with large supra-alar spine just dorsal to wing base (Figs 9, 65) (continental Afrotropics). . . . .*Nigritomyia* Bigot

– Scutum without supra-alar spine dorsal to wing base, at most with small tubercle (*e.g.*, Figs 10, 15, 100) (Madagascar & continental Afrotropics) 67

67. Wing vein R_4 absent (Fig. 230); terminal flagellomere as long as 7 preceding flagellomeres combined, blunt at apex, not tapering, but same width as preceding flagellomeres (continental Afrotropics) . . . . Undescribed genus B

– Wing vein R_4 present (*e.g.*, Figs 162, 232); terminal flagellomere shorter than preceding flagellomeres combined (*e.g.*, Figs 125, 149), terminal flagellomere often much thinner than preceding flagellomeres and strongly tapered towards apex (*e.g.*, Figs 123, 124) (continental Afrotropics & Madagascar) 68

68. Wing vein R_{2+3} arising in close proximity to crossvein *r–m* (Fig. 231); terminal antennal flagellomere significantly shorter than flagellomere 1; scutellum with spines very small, difficult to discern (continental Afrotropics) . . . . Undescribed genus C

– Wing vein R_{2+3} arising distal to crossvein *r–m* (*e.g.*, Figs 157, 161); terminal antennal flagellomere of equal length or significantly longer than flagellomere 1 (e.g., Fig. 124); scutellum with spines small, to large (e.g., Figs 3, 14, 15), invariably clearly visible (continental Afrotropics & Madagascar). 69

69. Antennal flagellomeres 1–5 forming conical complex with flagellomeres closely appressed and not distinctly separated, flagellomeres 6 and 7 often reduced, much smaller than preceding ones (Fig. 123); black coloured species with silver setulae (Fig. 10) (continental Afrotropics) . . . . . . *Adoxomyia* Kertész

– Antennal flagellomeres 1–5 more elongate and cylindrical and more distinctly demarcated, flagellomeres 6 and 7 not reduced, similar to preceding ones (*e.g.*, Figs 124, 125, 149); yellow and orange coloured species, if black then without silver setulae (confined to Madagascar) 70

70. Antennal flagellomeres 7 and 8 densely setulose (Fig. 124), with setulae greater in length than diameter of flagellomeres; wing membrane yellowish with brownish markings (Fig. 161); large flies, generally > 15 mm in length (Fig. 14). . . . .*Alopecuroceras* Lindner

– Antennal flagellomeres 7 and 8 not densely setulose (*e.g.*, Figs 125, 149); wing membrane unicolourous (*e.g.*, Figs 162, 232); smaller flies, generally < 15 mm in length 71

71. Scutellum with spines as long as scutellum (Fig. 15); eyes essentially bare, with only sparse, minute setulae, difficult to discern; abdomen widening posteriorly, widest at *ca* segment 4 (Fig. 15). . . . . *Ampsalis* Walker

– Scutellum with spines about ⅓ as long as scutellum or less; eyes with distinct setulae although these may be sparse; abdomen elongate ovoid, widest at *ca* segments 2–3 (Fig. 102) . . . . . Undescribed genus D

72. Terminal antennal flagellomere elongate, laterally flattened, blade-like (Fig. 131), with bristly setulae, especially ventrally; face with medial, ventrally directed conical process (HERMETIINAE). . . . . *Hermetia* Latreille

– Terminal antennal flagellomere arista-like without bristly setulae; face without medial, conical process (CHRYSOCHLORININAE) 73

73. Antennal flagellomeres 1–5 forming small complex that is almost the same diameter as pedicel (Fig. 29); terminal flagellomere much longer than length of flagellomeres 1–7 combined. . . .*Chrysochlora* Latreille

– Antennal flagellomeres 1–5 forming large complex that is much greater in diameter than pedicel (Fig. 82); terminal flagellomere shorter than length of flagellomeres 1–7 combined . . . *Porpocera* Enderlein

74. Scutellum with 2 marginal spines (*e.g.*, Figs 66, 74) (STRATIOMYINAE [in part]) 75

– Scutellum without marginal spines (*e.g.*, Fig. 24) 78

75. Lower calypter sub-linear, without lobe developed laterally (as in Fig. 152), at most with inconspicuous widening along margin; wing membrane with microtrichia evident at least apically beyond discal cell (*d*), usually present on most of membrane surface (*e.g.*, Fig. 207) (OXYCERINI) 76

– Lower calypter with well-developed, conspicuous lobe arising laterally, mostly clothed in long setulae (as in Fig. 150); wing membrane largely devoid of microtrichia (*e.g.*, Figs 158, 201) (STRATIOMYINI [in part]) 77

76. Terminal antennal flagellomere arista-like, considerably more slender than basal flagellomeres 1–4 . . . . *Oxycera* Meigen

– Terminal antennal flagellomere lanceolate-shaped, only slightly more slender than basal flagellomeres 1–4 . . . . *Stuckenbergiola* Lindner

77. Eye with silvery white, curved setulae (Fig. 66); with longer, denser setae on body, resembling bees. . . . . *Nyassamyia* Lindner

– Eye bare (Fig. 11), setae on body shorter, not resembling bees . . . . *Afrodontomyia* James

78. Antenna with terminal flagellomere ranging from being similar to penultimate flagellomere to slender and cone-shaped, < 2 × length of basal flagellomeres combined (*e.g.*, Fig. 21); wing crossvein *m–cu* connected to vein M_{3+4} (*e.g.*, Figs 190, 215) (NEMOTELINAE) 79

– Antenna with terminal flagellomere arista-like, several times length of basal flagellomeres combined (*e.g.*, Figs 110, 126, 130); wing crossvein *m–cu* connected to vein M_4 (*e.g.*, Figs 170, 195) (*m–cu* connected to vein M_{3+4} only in the Malagasy genus *Gongrosargus* (Fig. 182)) (SARGINAE) 82

79. Palpus discernible near posterior part of oral cavity, especially second segment which is blackish and ovoid; head with face rounded, not conically produced; larger flies > 6 mm in length (*e.g.*, Figs 50, 84). 80

– Palpus reduced, not easily discernible, often vestigial or absent; head with face usually distinctly conically produced (*e.g.*, Fig. 62); smaller flies, usually < 6 mm in length, although larger individuals of a few species exceed 6 mm (*e.g.*, Figs 21, 62) 81

80. Abdominal tergite 5 not declivous, gently curving downward posteriorly, without transverse depression; wing membrane hyaline to weakly infuscate, not obviously brown (Fig. 190); scutellum black on at least basal ½ (Fig. 50); antenna much shorter than head (Fig. 50), except in one species . . . . *Lasiopa* Brullé

– Abdominal tergite 5 strongly declivous posteriorly, with distinct transverse depression sub-medially; wing membrane distinctly brown infuscate (Fig. 215); scutellum mostly yellowish to dark orangish (Fig. 84); antenna as long as or longer than head (Fig. 84) . . . . *Pselaphomyia* Kertész

81. Wing membrane, except extreme base, densely set with conspicuous microtrichia (Fig. 167); head with face evenly receding below antennae (Fig. 21); associated with ocean shorelines . . . . *Brachycara* Thomson

– Wing membrane with extensive areas devoid of microtrichia (Fig. 198), inconspicuous where present; head with face conically produced below antennae (Fig. 62), but sometimes weakly; usually near water, but not necessarily ocean shorelines. . . . . *Nemotelus* Geoffroy

82. Antenna with basal complex of flagellum sub-cylindrical, if wider than pedicel then only slightly so; arista-like terminal flagellomere white in colour, inserted virtually at centre of basal complex; female with postocular region widening dorsally (Fig. 72); mostly yellowish flies with parts of head black, sometimes with brownish bands on abdomen (Figs 72, 73) . . . . *Otochrysa* Lindner

– Antenna with basal complex of flagellum more ovoid or bilaterally flattened (*e.g.*, Figs 126, 130, 143); arista-like terminal flagellomere brown to black in colour, usually inserted dorsoapically on basal complex (*e.g.*, Fig. 119); colour of body variable. 83

83. Median wing vein (*M*) present throughout entire length between cells *bm* and *br* (*e.g.*, Figs 217, 221) 84

– Median wing vein (*M*) weakly developed at base, only discernible distally (*e.g.*, Figs 196, 222). 89

84. Lower calypter with distinct lobe (as in Figs 150, 151) 85

– Lower calypter mostly linear without distinct lobe (*e.g.*, Fig. 152) 88

85. Wing crossvein *m–cu* connected to vein M_{3+4} (Fig. 182); female antenna with acute process on both inner and outer sides of pedicel, projecting into flagellum (Figs 110, 130) (confined to Madagascar) . . . . *Gongrosargus* Lindner

– Wing crossvein *m–cu* connected to vein M_4 (*e.g.*, Fig. 172); female antenna without acute process (as in Fig. 126), or if present, then only on inner side (as in Fig. 143) (continental Afrotropics & Madagascar) 86

86. Eye densely setulose . . . . *Chloromyia* Duncan

– Eye bare or with some microscopic setulae 87

87. Wing vein R_{2+3} in close proximity to crossvein *r–m* (Fig. 220) . . . . *Sagaricera* Grünberg

– Wing vein R_{2+3} distal to crossvein *r–m* (Fig. 221). . . . . *Sargus* F. [in part]

88. Antenna with inner side of pedicel without finger-like projection (as in Fig. 126); face projected as much as frontal callus; wing vein R_{2+3} distal to crossvein *r–m* (Fig. 210); scutellum triangular with tiny process at apex; male eyes holoptic, meeting for short distance (Fig. 78) . . . . . *Paraptecticus* Grünberg

– Antenna with inner side of pedicel with finger-like projection (Fig. 119); face not projected as much as frontal callus; wing vein R_{2+3} usually proximal to crossvein *r–m* (Fig. 217); scutellum round; male eyes dichoptic (Fig. 119) . . . . *Ptecticus* Loew

89. Wing veins M_1 and M_3 often weakly developed, as compared to veins M_2 and M_4 (*e.g.*, Fig. 195); antenna with flagellar complex small, short-cylindrical to ovoid, about as long as or shorter than scape + pedicel; female head with very broad frons, strongly widening towards vertex; vein R_4 present or absent (*e.g.*, Figs 30, 195) 90

– Wing veins M_1 and M_3 slightly (if at all) fainter than veins M_2 and M_4 (*e.g.*, Figs 170, 196, 218); antenna with flagellar complex variable, but often larger than described above (*e.g.*, Figs 126, 143); female head with frons shorter (broader in some *Cephalochrysa* Kertész and *Microptecticus* Lindner), frequently weakly widened towards vertex (*e.g.*, Figs 25, 26); vein R_4 invariably present (*e.g.*, Figs 170, 196, 218) 91

90. Wing veins M_1 and M_3 very weakly developed, sometimes absent, much fainter than M_2 and M_4 (Fig. 195); discal cell (*d*) very small, sometimes with one or more of its sectors weakened; vein R_4 present or absent; female frons rarely with 2 circular white maculae; female abdomen often as broad as long . . . . *Microchrysa* Loew

– Wing veins M_1 and M_3 slightly weakened, but not as described above (Fig. 30); discal cell (*d*) larger, its sectors not weakened (Fig. 30); vein R_4 absent (Fig. 30); female frons with 2 circular white maculae; female abdomen more elongate . . . .*Chrysochromioides* Brunetti

91. Lower calypter without projection (as in Fig. 152) or at most with very small rudimentary projection (Fig. 151); male eyes dichoptic (Fig. 59); elongate species (Figs 58, 59) . . . . *Microptecticus* Lindner

– Lower calypter with distinct large projection (*e.g.*, Fig. 150); male eyes dichoptic or holoptic (*e.g.*, Figs 24, 87); often broad species (*e.g.*, Figs 24–26) 92

92. Head with occiput with fringe of erect, posteriorly-oriented pale setulae; male eyes dichoptic. . . . . *Sargus* F. [in part]

– Head with occiput without fringe of erect, posteriorly-oriented pale setulae; male eyes holoptic or virtually so (*e.g.*, Figs 24, 87) 93

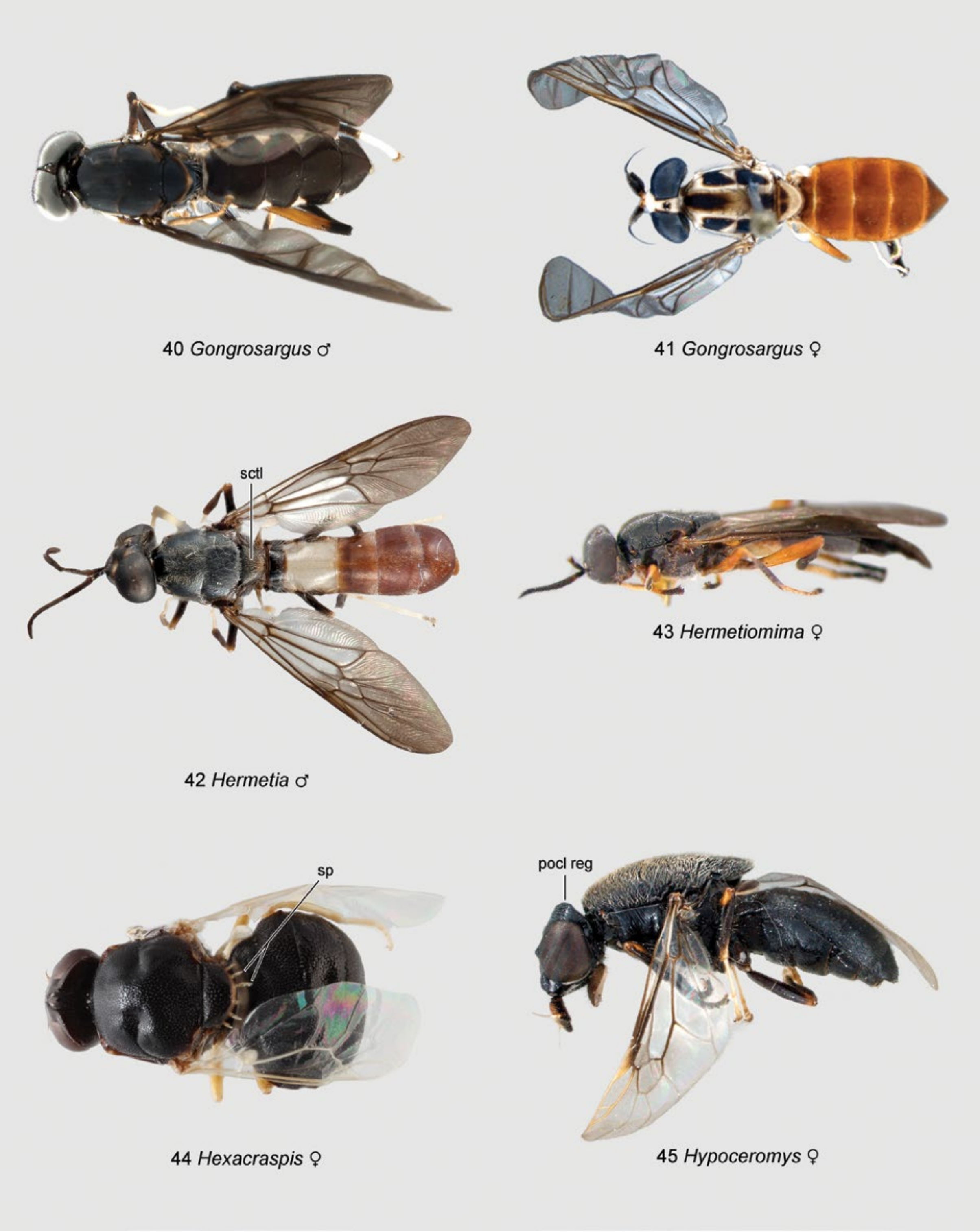
93. Abdomen broad (Figs 24–26); male eyes entirely holoptic (Fig. 24), eyes with two different ommatidia sizes, smaller on ventral ½ and larger dorsally; lobe of calypter large, round (Fig. 150); female antenna with inner side of pedicel without acute process (Fig. 126). . . . .*Cephalochrysa* Kertész

– Abdomen often more elongate (Figs 87, 88); male eyes often slightly separated (Figs 87, 88), eyes with only one size of ommatidia; lobe of calypter more oval-shaped; female antenna with inner side of pedicel often with acute process (Fig. 143). . . . . *Ptectisargus* Lindner

Synopsis of the fauna

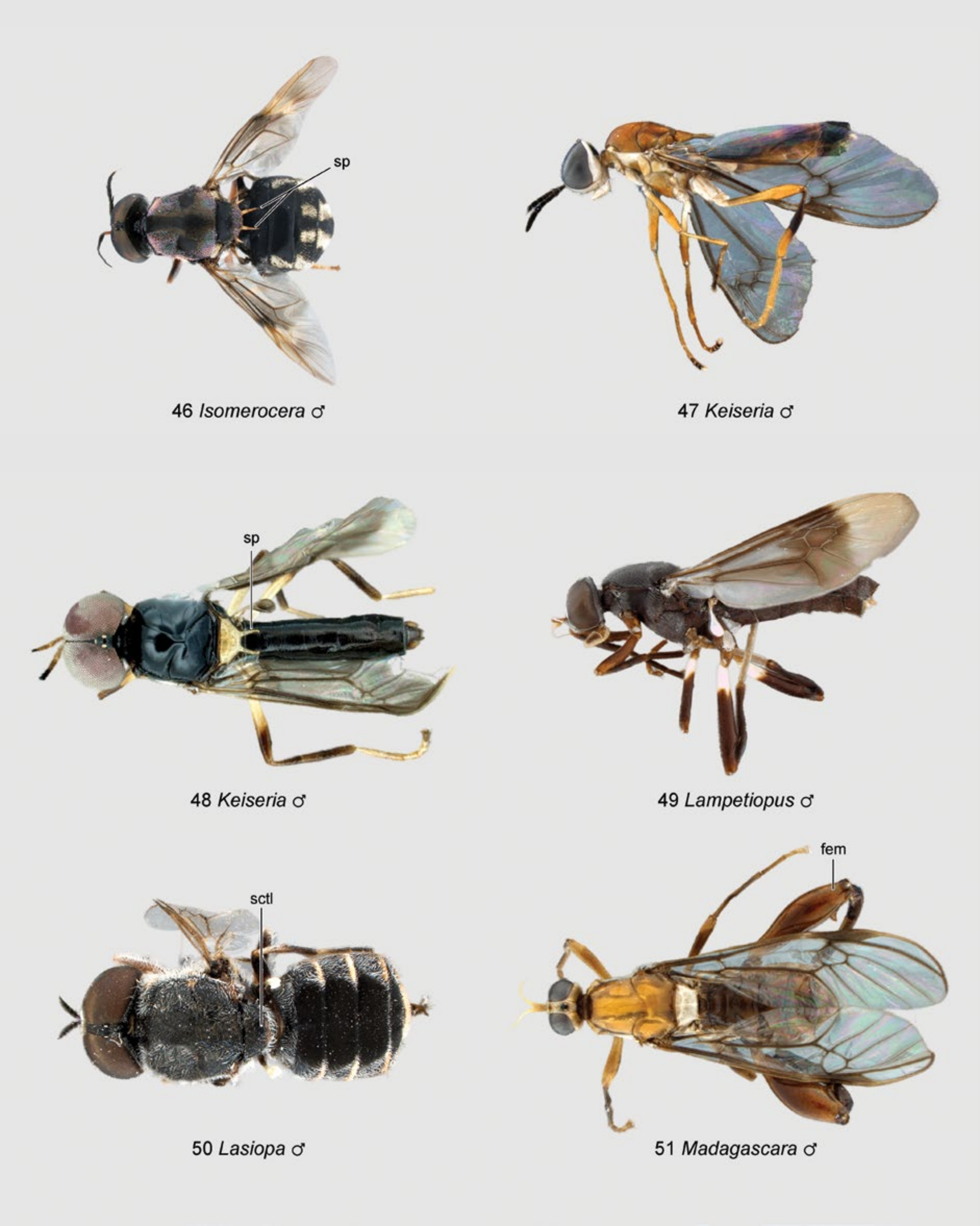
There are *ca* 367 genera of Stratiomyidae currently recognised globally (Hauser *et al.* 2017; Woodley 2001, 2011), 86 of which occur in the Afrotropical Region. The first catalogue of Afrotropical Stratiomyidae was provided by James (1980), but is now completely outdated and superseded by the world catalogue of Woodley (2001). Approximately 2,850 species are described in the world fauna (Woodley 2001, 2011 and recent papers), of which 376 occur in the Afrotropical Region. The fauna of Madagascar is clearly distinct, missing several continental elements and being very diverse in Sarginae and relatively poor in Pachygastrinae. There are certainly undescribed species in the Afrotropics, with the fauna of Madagascar being the most poorly studied. Kirk-Spriggs & Stuckenberg (2009: 186), for example, predicted that 35+ species may await description. Nonetheless, studies of unidentified Afrotropical museum material does not indicate a large number of undescribed taxa from the region, as is the case for the Neotropical fauna.

Adoxomyia **Kertész** (Clitellariinae)**.** A genus of nearly 40 species, occurring in all zoogeographical regions, except the Australasian Region and Antarctica, with most species occurring in the Nearctic and Palaearctic Regions. Woodley (2011) synonymised the Afrotropical genera *Haplephippium* Speiser and *Mixoclitellaria* Lindner with *Adoxomyia*, so seven species now occur in the Afrotropical Region. Five species are fairly widespread in Central and Southern Africa, one species is found in the Arabian Peninsula (Hauser 2008: 592) and one is endemic to Socotra Is. (Yemen) (Hauser 2002; Tkoc & Rozkošný 2014). *Adoxomyia* species are usually dark brown to black with silver or golden setae and have a compact body shape. Some species have a significant variation in size and males are usually smaller than females. The immature stages of



Figs 41.40–45. Habitus of Stratiomyidae: (40) *Gongrosargus* sp., dorsal view ♂; (41) same, *Gongrosargus* sp. ♀; (42) same, *Hermetia myieriades* Speiser ♂; (43) *Hermetiomima rufipes* Lindner, lateral view ♀; (44) *Hexacraspis sexspinosa* (Macquart), dorsal view ♀; (45) *Hypoceromys* sp., lateral view ♀.

Abbreviations: pocl reg – postocular region; sctl – scutellum; sp – spine.



46 *Isomerocera* ♂

47 *Keiseria* ♂

48 *Keiseria* ♂

49 *Lampetiopus* ♂

50 *Lasiopa* ♂

51 *Madagascara* ♂

Figs 41.46–51. Habitus of Stratiomyidae: (46) *Isomerocera quadrilineata* (F.), dorsal view ♂; (47) *Keiseria* sp., lateral view ♂; (48) *Keiseria* sp., dorsal view ♂; (49) *Lampetiopus umbrosus* Lindner, lateral view ♂; (50) *Lasiopa* sp., dorsal view ♂; (51) same, *Madagascara* sp. ♂.

Abbreviations: fem – femur; sctl – scutellum; sp – spine.

the genus are only known for three Nearctic and one Oriental species (*A. heminopla* (Wiedemann, 1819) that also occurs in the Arabian Peninsula) (McFadden 1967). The Nearctic species were found in rotting cacti, while *A. heminopla* was collected from the tuberous root of *Kaempferia* (Zingiberaceae) (McFadden 1967) and was "… found in rotten stems of the papaya, plantain, wood-apple and in the bark of *Erythrissa* [*sic*] sp." (possibly *Erythrina* sp.) (Brunetti 1923: 90). No identification key to Afrotropical species is currently available.

***Afrodontomyia* James** (Stratiomyinae: Stratiomyini)**.** A genus of eight Afrotropical species and one Oriental (Indian) species, that was not examined and may or may not be congeneric with the Afrotropical species. These are large, robust flies (Fig. 11) with some species exceeding 20 mm in length, which are probably the largest Stratiomyini. The abdomen is often coloured dull red or green. Most species occur in Central Africa, but with one each from East and West Africa. The biology and immature stages remain unknown. James (1952*b*) provided an identification key to most species.

***Ageiton* Kertész** (Pachygastrinae)**.** An endemic monotypic genus with the single species *A. ater* Kertész, 1914, widespread in the Afrotropical Region. The species is robust and black with silver setae covering the body. The genus (Figs 12, 159) is very similar to *Cardopomyia* (Figs 23, 169) from Madagascar and these may be synonymised in future. The biology and immature stages of the species remains unknown.

***Allognosta* Osten Sacken** (Beridinae)**.** A genus of *ca* 60 described species, occurring in all zoogeographical regions, except Antarctica, with diversity concentrated in the Oriental Region. *Allognosta* is the only genus of the subfamily Beridinae occurring in the Afrotropical Region. There are four described Afrotropical species which were treated by Woodley (1987*b*, 2000), all of which occur in the continental Afrotropics: *A. bwamba* Woodley, 1987 (Democratic Republic of Congo, Ghana, Rwanda and Uganda); *A. njombe* Woodley, 2000 (Malawi and Tanzania); *A. stuckenbergae* Lindner, 1961 (South Africa); *A. tessmanni* Enderlein, 1921 (Democratic Republic of Congo, Equatorial Guinea, Kenya, Sierra Leone and Uganda). There is one undescribed species from Madagascar (Figs 13, 153, 155, 160), but otherwise there are unlikely to be many undescribed Afrotropical species. Most species are dark brown to black in colour, but some extralimital species have yellow patterns on the abdomen or pleura. Species of *Allognosta* generally occur in montane or temperate regions. The biology and immature stages of Afrotropical species remain unknown. The larva of the Nearctic species *A. fuscitarsis* (Say, 1823) has been described (Johannsen 1922; McFadden 1967). Woodley (2000) presented an identification key to described Afrotropical species.

***Alopecuroceras* Lindner** (Clitellariinae)**.** An endemic genus of two species confined to Madagascar, *A. atripluma* James, 1960 and *A. coloratum* Lindner, 1936. These are large, elongate, yellowish brown flies with darker markings on the body (Fig. 14) and wings (Fig. 161). The biology and immature stages remain unknown. James (1960) provided characters to distinguish the two species.

***Ampsalis* Walker** (Clitellariinae)**.** Three Oriental and two Afrotropical species have been placed in this genus. James (1960) described *A. terminalis* from Madagascar with some doubt regarding its generic placement. Later, James (1975) expressed further doubts of the generic placement of the Afrotropical species when he described *A. dichromata*, which is here included in Undescribed genus D (Figs 102, 149, 232). Woodley (2001) commented that the Malagasy species differed from the type species of *Ampsalis* from Indonesia. *Ampsalis terminalis* (Figs 3, 15, 125, 162) is here retained in this genus pending a revision of these generic concepts and is the only Afrotropical species placed here, but two undescribed species close to *A. terminalis* from Madagascar are known. These flies are colourful, yellowish and red, with brown and black markings, often a white head and the apical tergite invariably white. The biology and immature stages of the species remain unknown.

***Anargemus* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *A. basalis* Lindner, 1965, only known from the unique female holotype from South Africa, which was not studied in preparation of this chapter. The genus is not very well characterised and belongs to a group of small, rather non-descript genera that are poorly understood. The biology and immature stages of the species remain unknown.

***Apotomaspis* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *A. nigeriana* Lindner, 1972 (Fig. 16), only known from the unique female holotype from Nigeria. Examination of the type specimen revealed that it is very likely allied to Afrotropical species of *Neopachygaster*. The biology and immature stages of the species remain unknown.

***Argyrobrithes* Grünberg** (Pachygastrinae)**.** A genus of eight described species distributed throughout the Old World tropics from Papua New Guinea through Asia, Madagascar and the Afrotropical Region. Four species are known from the Afrotropical Region. The genus is likely related to *Ageiton*, *Cardopomyia*, *Diademophora*, *Sternobrithes* and the Australasian *Gabaza* Walker. Several undescribed species are known from Madagascar. The genus is characterised by the elongated last flagellomere and the compact body shape. The biology and immature stages remain unknown. No key to Afrotropical species is currently available.

***Ashantina* Kertész** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *A. antennata* Kertész, 1914 (Figs 18, 107, 164), widespread in the Afrotropical Region. The long antennae are highly characteristic (Fig. 107). The species is likely a wasp mimic, with its long antenna and elongate body. The biology and immature stages of the species remain unknown.

***Aspidacantha* Kertész** (Pachygastrinae)**.** An endemic genus of three described Afrotropical species (*A. aethiops* Lindner, 1939 from Uganda and *A. minuta* (Lindner, 1966) from South Africa) and the type species, which occurs from the Palaearctic (Israel, Egypt), into the Afrotropics (*A. atra* Kertész, 1916 (Fig. 19) from Democratic Republic of Congo, Ethiopia, Tanzania, Uganda, United Arab Emirates and Zimbabwe). All of these small black species are characterised by the loss of wing vein R_4 (Fig. 165), a more or less pointed scutellum (Fig. 19) and with pubescent maculae above the antenna (Fig. 108). It is uncertain whether *A. aethiops* and *A. minuta* are congeneric with the type. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

52 *Madagascara* ♂

53 *Madagascarina* ♂

54 *Marangua* ♀

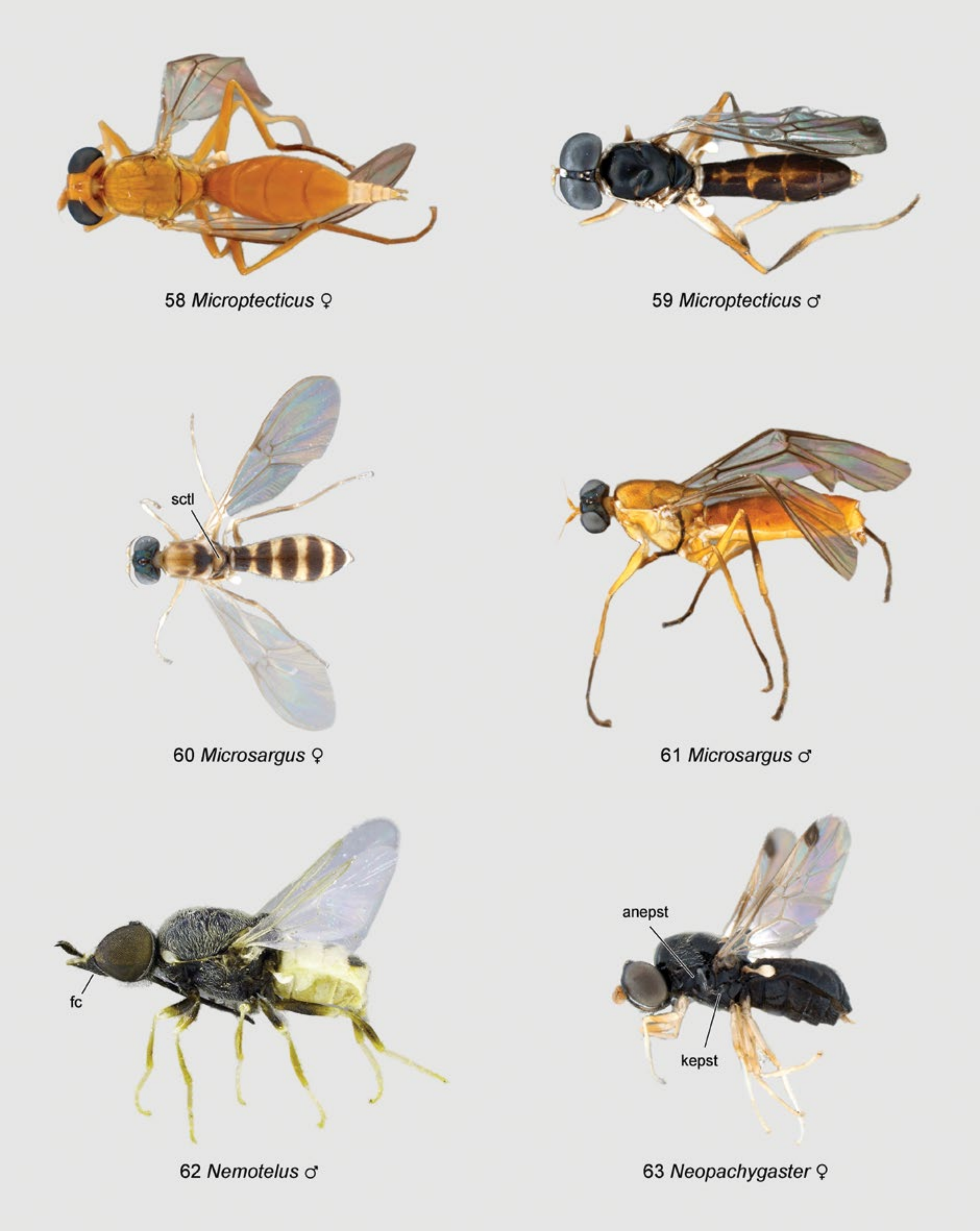
55 *Meristomeringina* ♀

56 *Meristomerinx* ♂

57 *Microchrysa* ♂

Figs 41.52–57. Habitus of Stratiomyidae: (52) *Madagascara woodleyi* Schacht & Heuck, lateral view ♂; (53) *Madagascarina beyeri* Lindner, dorsal view ♂; (54) *Marangua* sp., lateral view ♀; (55) *Meristomeringina mimetes* James, dorsal view ♀; (56) *Meristomerinx camerunensis* Enderlein, lateral view ♂; (57) *Microchrysa flaviventris* (Wiedemann), dorsal view ♂.

Abbreviation: fem – femur.



58 *Microptecticus* ♀

59 *Microptecticus* ♂

60 *Microsargus* ♀

61 *Microsargus* ♂

62 *Nemotelus* ♂

63 *Neopachygaster* ♀

Figs 41.58–63. Habitus of Stratiomyidae: (58) *Microptecticus* sp., dorsal view ♀; (59) same, *Microptecticus* sp. ♂; (60) same, *Microsargus* sp. ♀; (61) *Microsargus* sp., lateral view ♂; (62) same, *Nemotelus niloticus* Olivier ♂; (63) same, *Neopachygaster stigma* Lindner ♀.

Abbreviations: anepst – anepisternum; fc – face; kepst – katepisternum; sctl – scutellum.

Figs 41.64–69. Habitus of Stratiomyidae: (64) *Neopachygaster kiboensis* Lindner, dorsal view ♂; (65) *Nigritomyia loewii* (Brauer), lateral view ♀; (66) *Nyassamyia deceptor* (Curran), anterolateral view ♂; (67) *Nyplatys cultellata* (Lindner), lateral view ♂; (68) *Odontomyia* sp., anterolateral view ♀; (69) *O. limbifacies* Bigot, dorsal view ♀.

Abbreviations: oc tr – ocellar triangle; sp – spine; spal sp – supra-alar spine.

70 *Oplodontha* ♂

71 *Otionigera* ♀

72 *Otochrysa* ♀

73 *Otochrysa* ♂

74 *Oxycera* ♂

75 *Oxymyia* ♂

Figs 41.70–75. Habitus of Stratiomyidae: (70) *Oplodontha* sp., dorsal view ♂; (71) *Otionigera* sp., lateral view ♀; (72) *Otochrysa* sp., dorsal view ♀; (73) same ♂; (74) same, *Oxycera* sp. ♂; (75) *Oxymyia epacta* Kertész, lateral view ♂.

Abbreviations: pocl reg – postocular region; sp – spine.

***Aspidacanthina* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *A. exigua* Lindner, 1966 (Figs 20, 166), described from Democratic Republic of Congo. Following examination of the type series, it is very likely that this species is allied to Afrotropical species ascribed to *Neopachygaster*. The biology and immature stages of the species remain unknown.

***Brachycara* Thomson** (Nemotelinae)**.** A genus of eight described species occurring in all zoogeographical regions, except Antarctica. Only *B. ventralis* Thomson, 1869 (Figs 21, 167), is known from the Afrotropical Region, recorded from Seychelles (including Aldabra Is.), but it may occur elsewhere in the region in suitable habitats. Although this species has been reported to range widely in the Indian and Pacific Ocean regions, it likely occurs only in the Indian Ocean (Woodley 2001). One undescribed species is known from Madagascar. Most species have a black head and thorax with some white markings and a white to yellowish abdomen. Species of the genus are associated with ocean shorelines and occur on remote oceanic islands. The larvae of the Galapagos species, *B. digitata* James, 1966 occur in leaf litter beneath *Sesuvium* (Aizoaceae) (B.J. Sinclair, pers. comm. 2017). Mason (1997*b*: 170) provided a well-illustrated discussion of *B. ventralis* as well as some extralimital species. Mason (1997*b*: 28) provided an identification key to genera of Afrotropical Nemotelinae. No identification key to Afrotropical species is currently available.

***Brianmyia* Woodley** (Stratiomyinae: Prosopochrysini)**.** A recently described, endemic monotypic genus (Woodley 2012), with the single species, *B. stuckenbergi* Woodley, 2012 (Figs 22, 168), recorded only from the Drakensberg Mountains of South Africa. It is a very characteristic species with black body colouration and a yellowish line along the lateral margin of the thorax and abdomen. It is the only genus of Prosopochrysini known from South Africa and nothing is known regarding the biology and immature stages of the species.

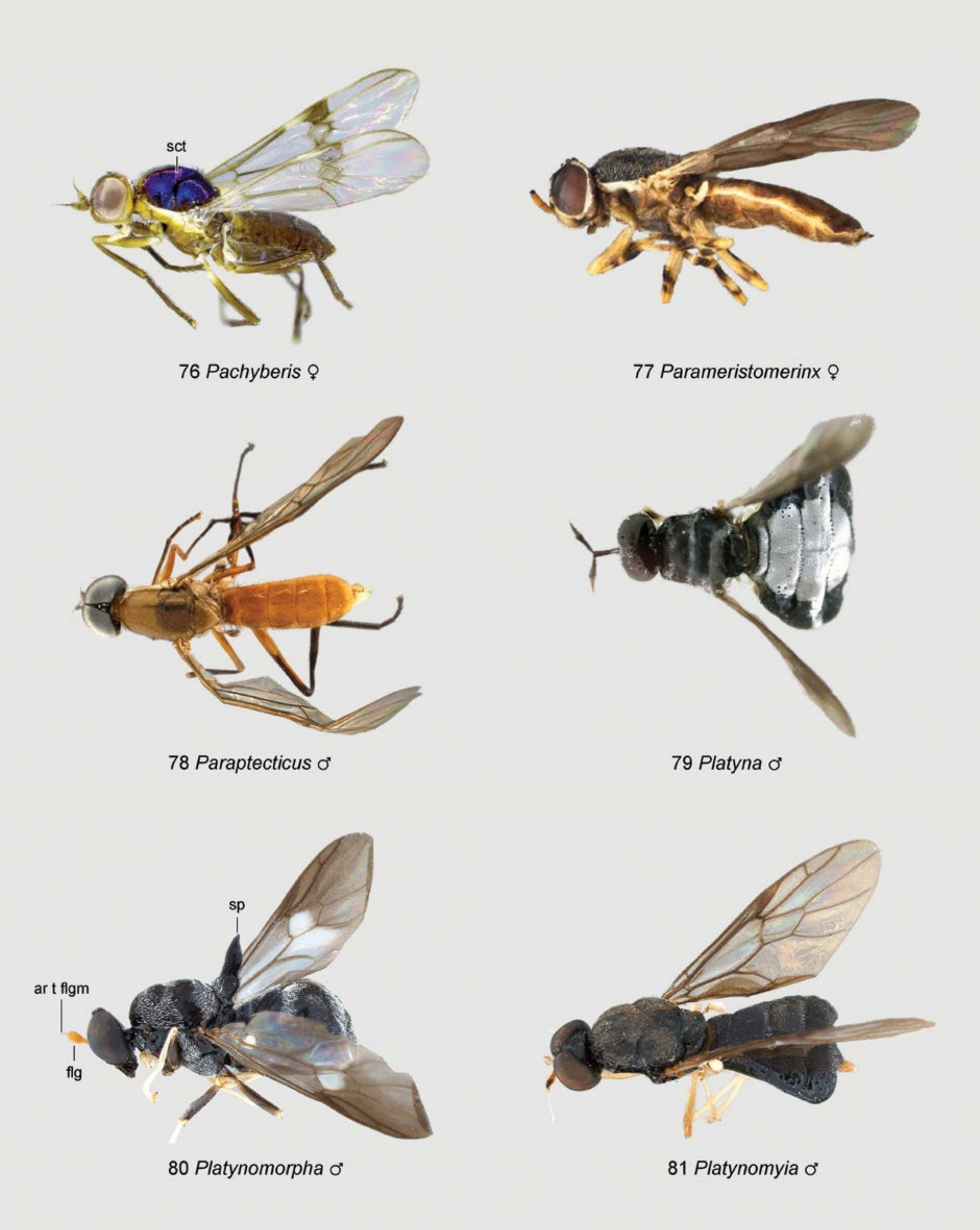
***Cardopomyia* Kertész** (Pachygastrinae)**.** An endemic genus of three described Malagasy species, *C. parvicornis* (Lindner, 1959), *C. robusta* Kertész, 1916 and *C. vesicularis* (Lindner, 1966). *Cardopomyia robusta* is by far the most common stratiomyid in Malaise trap samples from Madagascar, accounting for more than half of all Stratiomyidae specimens collected. There are five additional undescribed species (Figs 23, 104, 169) known from Madagascar. Most species are black, with distinct white setal patterns on the thorax, others have dense golden setae on the thorax or have a blue metallic luster covering the thorax. The genus is closely related to *Ageiton*. The biology and immature stages of the species remain unknown. No identification key to species is currently available.

***Catatasis* Kertész** (Stratiomyinae: Stratiomyini)**.** A poorly-defined Afrotropical genus of two described species that differs little from *Odontomyia*. The type species of the genus, *C. clypeata* Kertész, 1912, from Seychelles is almost entirely black with yellow legs. A second species, *C. congoensis*, was described in the genus by Lindner (1955*b*) from Democratic Republic of Congo, but differs in a number of respects from the type species. It has a shorter antennal scape and pedicel, the flagellum has a blunt apex, the male scutum is only partly clothed in dense golden pilosity and the abdomen is mostly pale with black markings. It appears to be more similar to *Dischizocera* than to the type species of *Catatasis*, although it also has quite faint wing veins distal to cell *m*, similar to species of *Oplodontha*. The biology and immature stages remain unknown. No identification key to species is currently available.

***Cephalochrysa* Kertész** (Sarginae)**.** A genus of 31 described species occurring in all zoogeographical regions, except Antarctica. Of these, 18 species occur in the Afrotropical Region, recorded from all parts of the continental Afrotropics and Madagascar. A global revision of the subfamily Sarginae is required to determine whether all species belong to the genus. The type species of the genus was described from Madagascar and there are at least 20 undescribed species known from the island. Adults can be recognised in having a large, broad body (Figs 24–26), the male eyes are entirely holoptic (Fig. 24), with different sizes of ommatidia, the antennae are short, but with conspicuous segmentation (Fig. 126) and females frequently have a broad frons (Figs 25, 26) and larger antenna. Important characteristics distinguishing *Cephalochrysa* from many other Sarginae genera, include the very large and flat lobe of the calypter (Fig. 150) and wing vein *M* only discernible distally (Fig. 170). They exhibit a wide variety of species-specific colouration, ranging from black, brown, orange, red and ivory to green and blue metallic. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

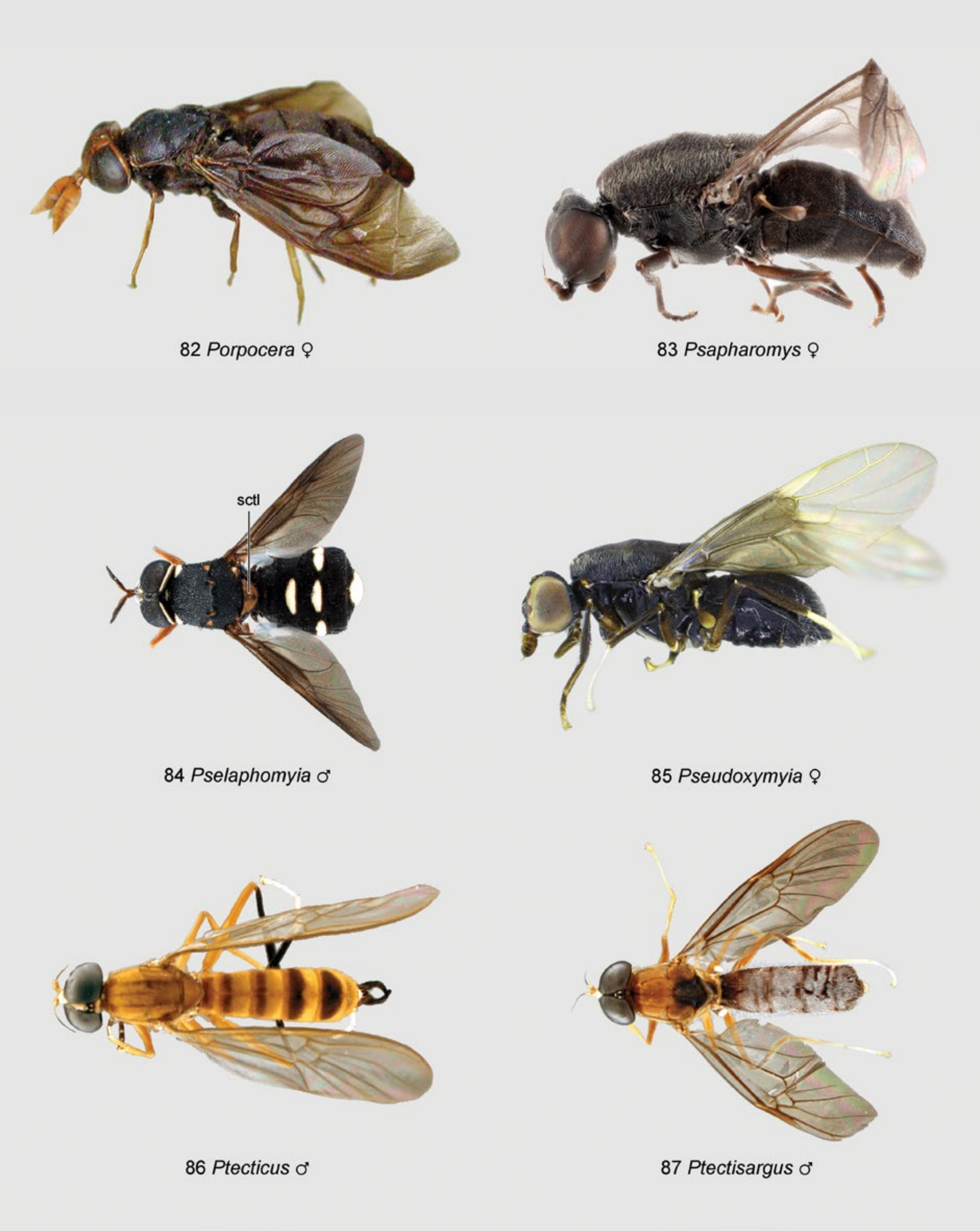
***Chelonomima* Enderlein** (Pachygastrinae)**.** A small genus of four described species occurring in the Afrotropical and Oriental Regions. Three species occur in the Afrotropics: *C. gracilis* James, 1949, from Burundi, Democratic Republic of Congo and Uganda (the type species); *C. partiticeps* Enderlein, 1914, from Benin, Burundi, Cameroon, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea, Liberia, Malawi, Nigeria, Republic of Congo, Sierra Leone and Uganda; and *C. proloxocera* Speiser, 1922, from Cameroon. Species are very characteristic among Afrotropical Stratiomyidae with long antenna (Fig. 127) and often light brown body colouration (Fig. 27). It remains questionable whether the single Oriental species, *C. signata* de Meijere, 1924 is congeneric with the Afrotropical species, but the type is lost and the description very rudimentary, but this species may belong in the Oriental genus *Pseudomeristomerinx* Hollis. The biology and immature stages remain unknown. An identification key to Afrotropical species was provided by James (1949*b*).

***Chloromyia* Duncan** (Sarginae)**.** A small genus of seven described species, occurring in the Afrotropical, Oriental and Palaearctic Regions, with one European species introduced into the Nearctic Region. The genus is essentially defined in the subfamily Sarginae based on pilose eyes. Four species occur in the Afrotropics recorded from East Africa and southern Africa: *C. bella* (Loew, 1856), from South Africa and Zimbabwe; *C. caeligera* Lindner, 1939, from Kenya; *C. cingulata* Lindner, 1972, from South Africa; and *C. tuberculata* James, 1952 (Figs 28, 172) from Kenya, Rwanda, Tanzania and Uganda. At least some Afrotropical species, e.g., *C. tuberculata* (Figs 28, 172), have a general appearance and black to dark brown bodies, in contrast to the metallic coloured European species (which includes the type species of the genus), so they may eventually be transferred elsewhere. Lindner (1955*a*) described the genus *Afrosargus*, based on a species that is a



Figs 41.76–81. Habitus of Stratiomyidae: (76) *Pachyberis stigmaticalis* James, lateral view ♀; (77) same, *Parameristomerinx copelandi* Woodley ♀; (78) *Paraptecticus viduatus* Grünberg, dorsal view ♂; (79) same, *Platyna hastata* (F.) ♂; (80) *Platynomorpha* sp., lateral view ♂; (81) *Platynomyia edwardsi* Lindner, dorsolateral view ♂. Fig 77 (after Woodley 2010, fig. 4).

Abbreviations: ar t flgm – arista-like terminal flagellomere; flg – flagellum; sct – scutum; sp – spine.



82 *Porpocera* ♀

83 *Psapharomys* ♀

84 *Pselaphomyia* ♂

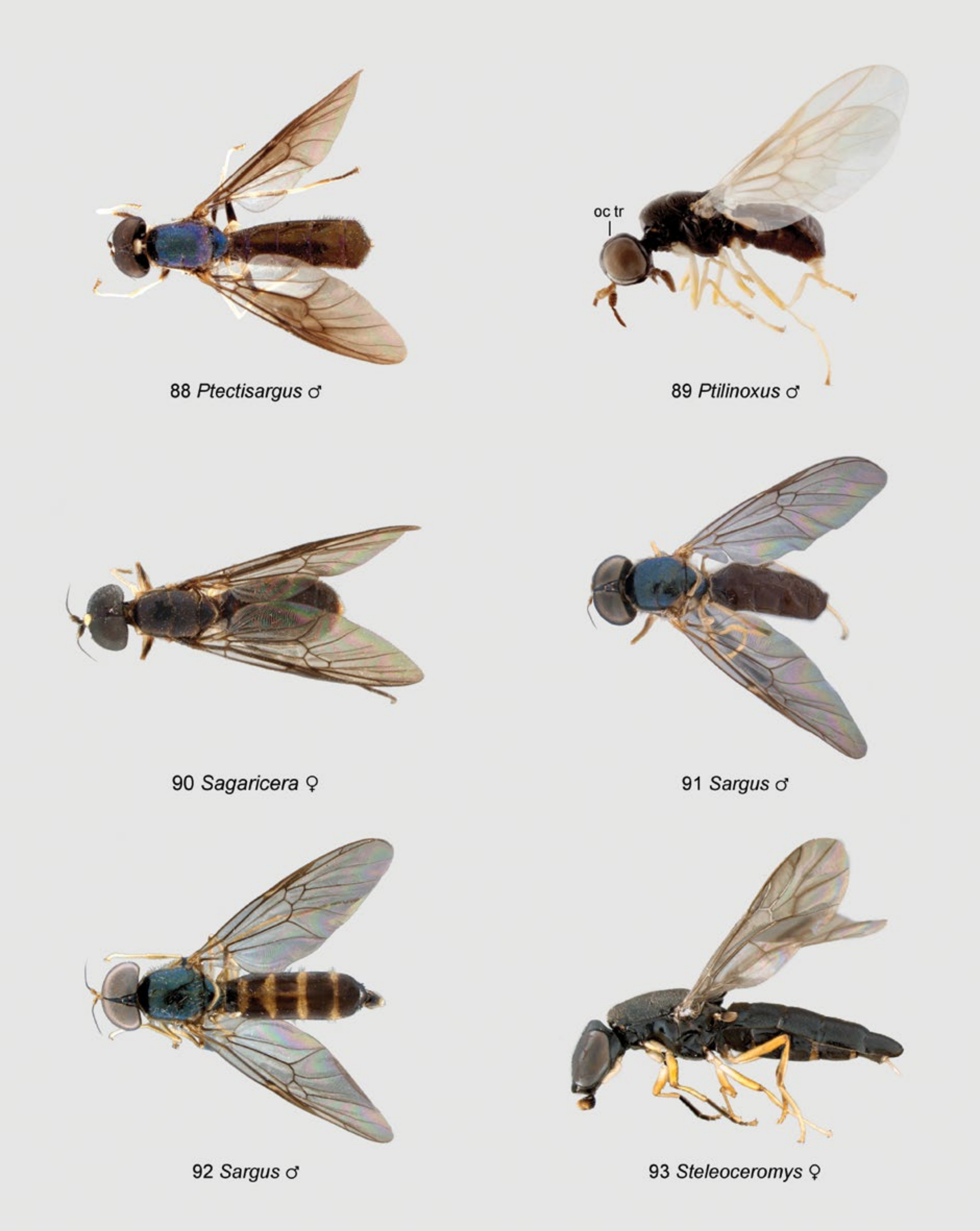
85 *Pseudoxymyia* ♀

86 *Ptecticus* ♂

87 *Ptectisargus* ♂

Figs 41.82–87. Habitus of Stratiomyidae: (82) *Porpocera horrida* Lindner, dorsolateral view ♀; (83) *Psapharomys* sp., lateral view ♀; (84) *Pselaphomyia nigripennis* (Bigot), dorsal view ♂; (85) *Pseudoxymyia* sp., lateral view ♀; (86) *Ptecticus* sp., dorsal view ♂; (87) same, *Ptectisargus argentipellitus* (Lindner) ♂.

Abbreviation: sctl – scutellum.



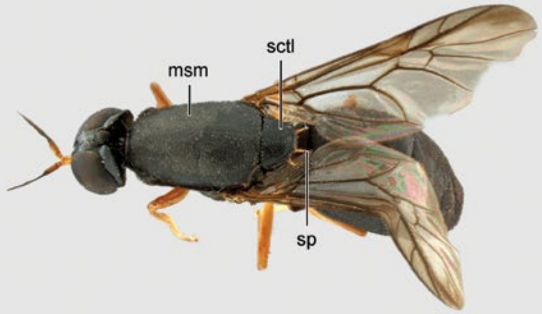
Figs 41.88–93. Habitus of Stratiomyidae: (88) *Ptectisargus abditus* (Lindner), dorsal view ♂; (89) *Ptilinoxus fallax* Lindner, lateral view ♀; (90) *Sagaricera analis* (Macquart), dorsal view ♀; (91) same, *Sargus* sp. ♂; (92) same, dorsal view ♂; (93) *Steleoceromys anthracina* Grünberg, lateral view ♀.

Abbreviation: oc tr – ocellar triangle.

94 *Sternobrithes* ♂

95 *Stuckenbergiola* ♂

96 *Thorasena* ♂



97 *Tinda* ♀

98 *Zabrachia* ♀

99 *Zulumyia* ♀

Figs 41.94–99. Habitus of Stratiomyidae: (94) *Sternobrithes* sp., lateral view ♂; (95) same, *Stuckenbergiola jugorum* Lindner ♂; (96) same, *Thorasena* sp. ♂; (97) *Tinda* sp., dorsal view ♀; (98) *Zabrachia madagascariensis* Lindner, lateral view ♀; (99) *Zulumyia expansa* James, dorsal view ♀.

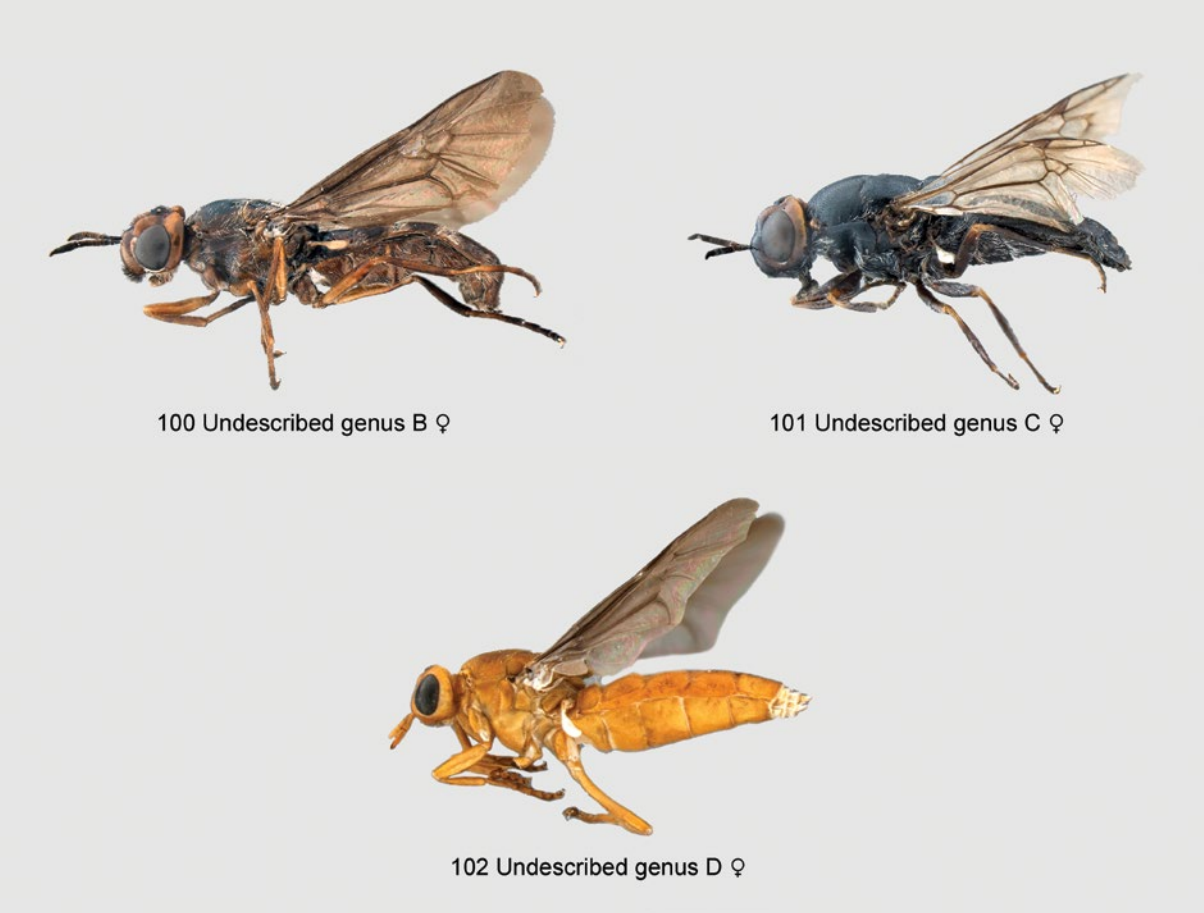
Abbreviations: msm – mesonotum; pocl reg – postocular region; sctl – scutellum; sp – spine.

synonym of *C. tuberculata*, so although that genus is currently synonymised under *Chloromyia*, it may be resurrected for some Afrotropical species in the future. Nothing is known regarding their biology. Immatures of both European species have been described that occur in garden soil, dung and beneath bark (Rozkošný 1982: 116). No identification key to Afrotropical species is currently available.

***Chrysochlora* Latreille** (Chrysochlorininae)**.** Of the five species currently placed in the genus, two occur in the Afrotropical Region. The type species, *C. amethystina* (F., 1805) (Figs 29, 173) was described from Mauritius and has also been further recorded from Madagascar. The *m–cu* crossvein is connected to vein M_{3+4}. *Chrysochlora amethystine* is a very distinct large fly, with dark brown wings and green metallic reflexions on the thorax and metallic purple on the abdomen. Iide (1968) provided a detailed redescription of this species. The other Afrotropical species, *C. cooksoni* Lindner, 1966, is recorded from South Africa and Zimbabwe, but has not been studied in preparation of this chapter. The Indonesian *C. lineata* de Meijere, 1913 belongs in the Sarginae and the two species described by Ricardo (1929) from Samoa are actually male and female of the same species and should not be included in the genus according to Iide (1968). The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

***Chrysochromioides* Brunetti** (Sarginae)**.** An endemic monotypic genus with the species, *C. micropunctata* Brunetti, 1926 (Fig. 30), described from a single female from Democratic Republic of Congo. The male specimen of an undescribed species mentioned by Lindner (1966*a*) could not be located in the Royal Museum for Central Africa, Belgium. The genus resembles *Microchrysa*, and wing vein R_4 is absent (Fig. 30) (as in some species of *Microchrysa*), and wing veins M_1 and M_3 are more distinct (Fig. 30) than in *Microchrysa* (Fig. 195). Without a male and additional comparative material the position and circumscription of this genus remains unclear. The biology and immature stages of the species remain unknown.

***Crocutasis* Lindner** (Stratiomyinae: Stratiomyini)**.** A poorly known monotypic genus with the species, *C. abyssinica* Lindner, 1935 (Fig. 31), apparently known only from the unique holotype from Ethiopia. The type was examined in preparation of this chapter and is clearly a male (Fig. 31), not a female as Lindner (1935) supposed. Other than having densely pilose



Figs 41.100–102. Habitus of Stratiomyidae (lateral views): (100) Undescribed genus B ♀; (101) Undescribed genus C ♀; (102) Undescribed genus D ♀.

eyes, this genus is similar to *Odontomyia*. The biology and immature stages of the species remain unknown.

***Cyphoprosopa* James** (Stratiomyinae: Prosopochrysini)**.** An endemic monotypic genus known from a single species, *C. lindneri* James, 1975 (Figs 32, 128, 174), from Madagascar. The colourful species has a yellow thorax and abdomen with black markings. Beyond the original characterisation by James (1975), little is known about the species. The biology and immature stages of the species remain unknown.

***Dactylotinda* Lindner** (Pachygastrinae)**.** An endemic monotypic genus known from the single species, *D. saegeri* Lindner, 1965 (Figs 33, 175), recorded from Côte d'Ivoire, Democratic Republic of Congo and Ghana. The species is characterised by its long slender body and the upcurved and pointed scutellum (Fig. 33). This genus is likely related to *Hypoceromys*, *Psapharomys*, *Pseudoxymyia* and *Steleoceromys*, with which it shares the distinct elongate female head shape. The biology and immature stages of the species remain unknown.

***Diademophora* Lindner** (Pachygastrinae)**.** An endemic monotypic genus with the single species, *D. ruandaensis* Lindner, 1955 (Figs 34, 109, 176), recorded from Cameroon and Rwanda. The genus is characterised by the brown, laterally flattened terminal antennal flagellomere and the strongly raised ocellar tubercle (Fig. 109). This genus may be congeneric with *Argyrobrithes* (Fig. 17). The biology and immature stages of the species remain unknown.

***Diargemus* Kertész** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *D. flavipes* Kertész, 1916, known only from the unique female holotype from South Africa, which is now destroyed. *Diargemus flavipes* is a small, black, rather non-descript species, which should likely be grouped together with other Afrotropical species described as *Neopachygaster* and not be placed in a separate genus. The biology and immature stages of the species remain unknown.

***Diplephippium* Speiser** (Pachygastrinae)**.** An endemic genus of three species: *D. amphicentrium* Speiser, 1908, from Tanzania; *D. snyderi* James, 1949 (Figs 35, 177), from Liberia; and *D. tessmanni* Grünberg, 1915, from Equatorial Guinea, Malawi and Mozambique. The genus is unusual in the subfamily Pachygastrinae in having a long spine above the wing base (Fig. 35). The general habitus is similar to that of Clitellariinae. The biology and immature stages remain unknown. An identification key to species was provided by James (1949*a*).

***Diplopeltina* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *D. skaifei* Lindner, 1972, described from South Africa. The type material of this species was not examined in preparation of this chapter, but it is likely to belong to a genus of Afrotropical species described under *Neopachygaster* and may need to be sunk as part of a future revision. The biology and immature stages of the species remain unknown.

***Dischizocera* Lindner** (Stratiomyinae: Stratiomyini)**.** A small endemic genus of five described species, ranging from Uganda in East Africa, south to South Africa. This genus is very similar to *Odontomyia* (Figs 36, 178), differing in the structure of the antennal flagellum, in which the apex is blunt with the terminal flagellomere concave on the posterior side and in some species distinctly bilobed. The flagellum has only five readily discernable flagellomeres. The biology and immature stages remain unknown. James (1957) included an identification key to four of the five species and Lindner (1965) described and illustrated the fifth known species.

***Drosimomyia* Kertész** (Pachygastrinae)**.** A genus of four described species, one from the Oceanian Region (Vanuatu) and three from the Afrotropical Region: *D. mercurialis* Lindner, 1939, from Uganda; *D. natalensis* Kertész, 1916, from South Africa; and *D. oldroydi* James, 1949, from Eritrea. Whether all three species belong to the same genus requires verification. The genus is characterised by the high insertion of the antenna on the face, the indentated frons (Fig. 37), and the lack of vein R_4 (Fig. 179). Larvae of *D. oldroydi* have been reared from branches of *Euphorbia abyssinica* J.F. Gmel. (Euphorbiaceae), in Eritrea (James 1949*b*). An identification key to Afrotropical species was provided by James (1950).

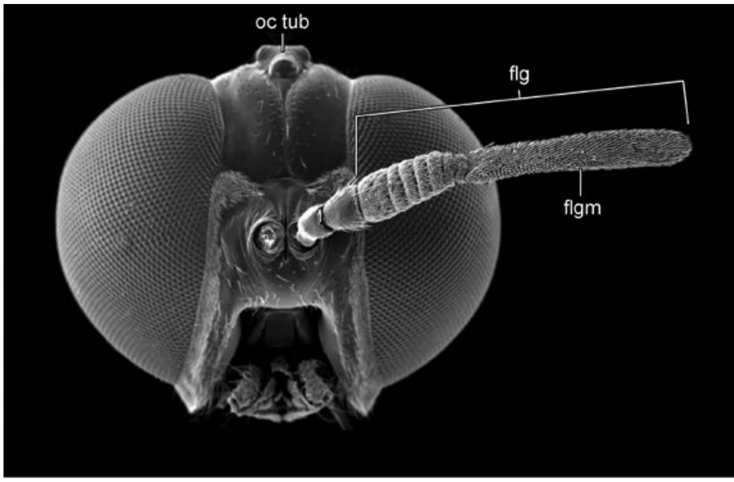
***Enypnium* Kertész** (Pachygastrinae)**.** An endemic genus of two described species: *E. obscura* (Bigot, 1891) from Côte d'Ivoire and *E. quadripunctatum* Kertész, 1914, from Cameroon, Central African Republic, Democratic Republic of Congo, Ghana and Liberia. The genus is characterised by the distinct maculae on the wings (Figs 7, 180) and by silver pubescence on the male abdomen (Fig. 38). Adults have been observed to fly slowly up and down the margins of forests (M. Hauser, pers. obs.); the biology and immature stages otherwise remain unknown. No identification key to species is currently available, although the two described species may be conspecific.

***Eupachygaster* Kertész** (Pachygastrinae)**.** A genus of five described species, originally erected for the European species *E. tarsalis* (Zetterstedt, 1842). The genus also includes a second Palaearctic species, one Neotropical, one Australasian and one Afrotropical species. The Afrotropical species, *E. lasiops* Speiser, 1922 described from Cameroon, clearly does not belong in this genus and should be placed in a new genus (therefore the name is indicated with quotation marks in the above identification key). This species is likely related to *Enypnium* and *Platynomyia*. The other non-European species of *Eupachygaster* should probably also be excluded and placed in other genera.

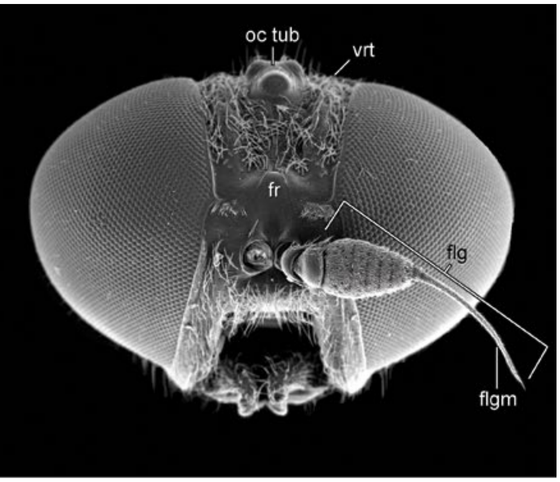
***Goetghebueromyia* Lindner** (Stratiomyinae: Prosopochrysini)**.** An endemic monotypic genus, with the single species, *G. paradoxa* Lindner, 1938 (Figs 39, 181), recorded from Central and East Africa, ranging from Democratic Republic of Congo to Kenya. *Goetghebueromyia* is an elongate, rather delicate, long-legged fly (Fig. 39). The biology and immature stages of the species remain unknown.

***Gongrosargus* Lindner** (Sarginae)**.** A genus of eleven described and several undescribed species, endemic to Madagascar. *Gongrosargus* species are variably coloured, ranging from dark and metallic to mostly yellow (Figs 1, 6, 40, 41). Species range from 10–20 mm in length, so some can be quite large. Lindner (1959) applied a single character to diagnose the genus: crossvein *m–cu* connected to vein M_{3+4} (in older literature stated as absence of wing crossvein *m–cu*) (Fig. 182). It is unclear if this character state alone defines a monophyletic group, as it also expressed in the Oriental genus *Formosargus* James. The genus is unusual among sargines, although not unique, in having strongly sexually dimorphic antennae. In the male the antennal flagellum is small, only slightly larger than the pedicel, which is not produced into the inner side of the flagellum. The female flagellum is significantly larger than the male flagellum (Figs 110, 130) and the pedicel is strongly, narrowly produced into the inner and outer side of the flagellum; a unique characteristic within Sarginae. Additionally, the presence of more than five antennal flagellomeres (certainly six, but sometimes there appears to be seven) (Fig. 130), may indicate that this genus does not belong to Sarginae, but may instead be related to Chrysochlorininae. The biology and immature stages remain unknown. No identification key to species is currently available.

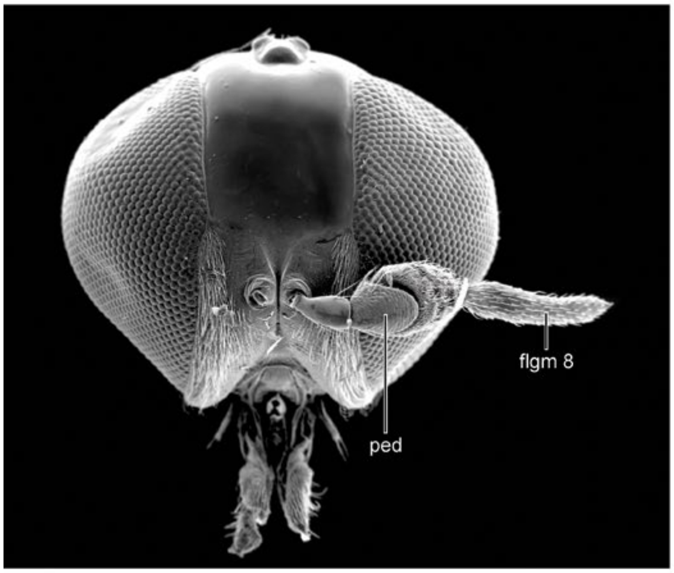
Hermetia **Latreille** (Hermetiinae)**.** A genus of *ca* 75 described species, occurring in all zoogeographical regions, except Antarctica, that is particularly diverse in the Neotropics. Three species are recorded from the Afrotropical Region:



103 *Argyrobrithes* ♀



104 *Cardopomyia* ♀



105 *Ptilinoxus* ♀

106 *Ageiton* ♂

Figs 41.103–106. Heads of Stratiomyidae (frontal views): (103) stereoscan micrograph of head of *Argyrobrithes* sp. ♀; (104) same, *Cardopomyia* sp. ♀; (105) same, *Ptilinoxus* sp. ♀; (106) light micrograph of *Ageiton ater* Kertész ♂.

Abbreviations: flg – flagellum; flgm – flagellomere; fr – frons; oc tub – ocellar tubercle; ped – pedicel; styl – stylus; vrt – vertex.

H. illucens (L., 1758) has been introduced from the New World to warmer parts of the globe through human commerce and is widespread in the Afrotropics (including Madagascar). *Hermetia myieriades* Speiser, 1913 (Figs 42, 131, 183) is recorded from Cameroon, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea and Togo and *H. pennicornis* Bezzi, 1908, known from Central African Republic, Côte d'Ivoire, Democratic Republic of Congo, Equatorial Guinea, Gabon, Liberia and Nigeria. *Hermetia* are moderately to large-sized flies, that superficially resemble wasps in flight and many species have translucent colouration on the second abdominal segment (Fig. 42), giving the impression of a petiolate abdomen. Known larvae of *Hermetia* are scavengers in decaying vegetation (Schremmer 1986). There are specimens of *H. pennicornis* in the National Museum of Natural History (USA) from Liberia that were reared from oil palm petioles. No identification key to Afrotropical species is currently available.

***Hermetiomima* Grünberg** (Pachygastrinae). An endemic genus of two described and one undescribed species from Central Africa. *Hermetiomima melaleuca* Grünberg, 1915, is recorded from Cameroon, Democratic Republic of Congo,

107 *Ashantina* ♀ 108 *Aspidacantha* ♂

109 *Diademophora* ♀ 110 *Gongrosargus* ♀

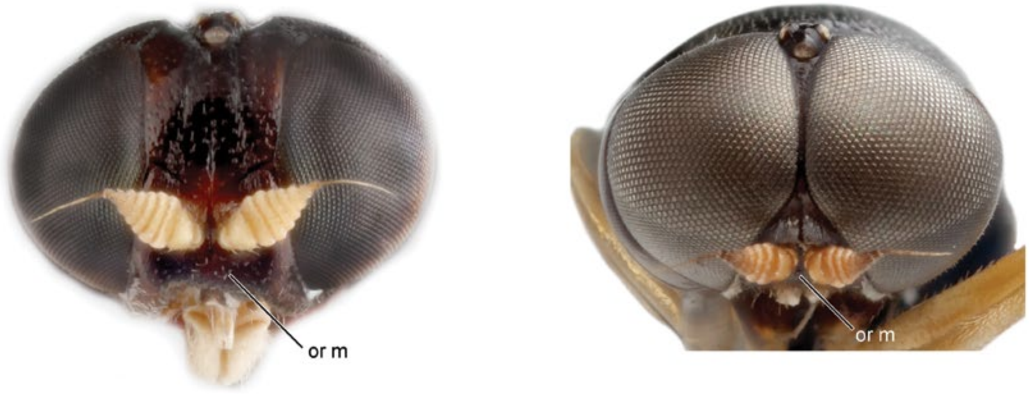
Figs 41.107–110. Heads of Stratiomyidae: (107) *Ashantina antennata* Kertész, frontolateral view ♀; (108) *Aspidacantha atra* Kertész, frontal view ♂; (109) same, *Diademophora ruandaensis* Lindner ♀; (110) same, *Gongrosargus* sp. ♀.

Abbreviations: ar t flgm – arista-like terminal flagellomere; fc – face; flgm – flagellomere; lan styl – lanceolate stylus; oc tub – ocellar tubercle; proc – process.

Equatorial Guinea, Tanzania and Uganda and *H. rufipes* Lindner, 1938 (Figs 43, 132, 184) was described from Democratic Republic of Congo. They are moderately sized, blackish flies (Fig. 43) with long antennae that probably resemble wasps when in flight. The biology and immature stages remain unknown. No identification key to species is currently available.

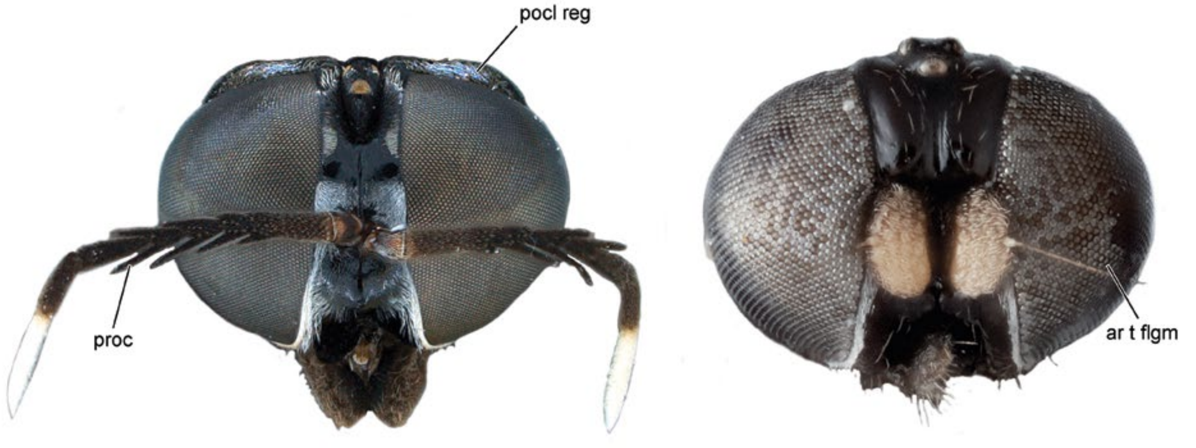
***Hexacraspis* Enderlein** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *H. sexspinosa* (Macquart, 1846) (Figs 44, 111, 112, 133, 185), described from South Africa. The genus is characterised by a compact black body, with six yellow spines on the scutellum. It is relatively similar to *Oxymyia epacta* Kertész, 1916 (Figs 75, 116, 208) and the two species may be congeneric, both occurring in South Africa. The biology and immature stages of the species remain unknown.

***Hypoceromys* Lindner** (Pachygastrinae)**.** An endemic genus of five described species: *H. albisetosa* Lindner, 1935, recorded from Cameroon, Democratic Republic of Congo, Nigeria and Sierra Leone; *H. australis* Lindner, 1958, from South Africa and Zimbabwe; *H. jamesi* (Lindner, 1965), from Sudan; *H. nigripes* (Lindner, 1938) from Democratic Republic of Congo; and *H. similis* Lindner, 1952, from South Africa. The genus is characterised by the elongate female face (Fig. 45) and the slightly dorsally inserted arista-like terminal flagellomere. Although females are highly characteristic, males have a virtually round head with very small antennae. This is likely the reason why Lindner described only females and described the males in different genera. The biology and immature stages remain unknown. No identification key to species is currently available.



111 *Hexacraspis* ♀

112 *Hexacraspis* ♂



113 *Isomerocera* ♀

114 *Marangua* ♀

Figs 41.111–114. Heads of Stratiomyidae (frontal views): (111) *Hexacraspis sexspinosa* (Macquart) ♀; (112) same, ♂; (113) *Isomerocera quadrilineata* (F.) ♀; (114) *Marangua* sp. ♀.

Abbreviations: ar t flgm – arista-like terminal flagellomere; or m – oral margin; pocl reg – postocular region; proc – process.

Isomerocera **Enderlein** (Pachygastrinae)**.** An endemic genus of two relatively large and colourful species, *I. heteraspis* James, 1949, described from Uganda and *I. quadrilineata* (F., 1787) (Figs 8, 46, 113, 187), which is widespread in the region. The pectinate antenna and the metallic reflecting scales on the rather large-sized body resemble the Asian genus *Ptilocera* Wiedemann. The biology and immature stages remain unknown. A highly detailed revision of the genus was published by Mason & Rozkošny (2015), which included an identification key to the two species.

Keiseria **Lindner** (Stratiomyinae: Prosopochrysini)**.** An endemic genus of five described and several undescribed species confined to Madagascar (Figs 47, 48, 134, 188). The genus is unique among Afrotropical Prosopochrysini in having a subcylindrical antennal flagellum (*e.g.*, Fig. 134), that is not tapered and has flagellomere 6 rounded apically. Lindner (1966*b*: 23) stated that at least some species have spines on the ventral surface of the hind femur. The biology and immature stages remain unknown. No identification key to species is currently available.

Lampetiopus **Lindner** (Stratiomyinae: Prosopochrysini)**.** Currently an endemic monotypic genus, with the single species, *L. umbrosus* Lindner, 1936 (Figs 49, 135, 189), described from Madagascar. At least one additional undescribed species is known from Madagascar. Woodley (2011) transferred the genus to the tribe Prosopochrysini from the subfamily Pachygastrinae, where it had been previously placed, based on the absence of wing vein M_3. The hind femur has an apical tooth which is very similar to those of *Madagascara* and *Madagascarina* and might be a character that indicates a close relationship

115 *Meristomeringina* ♀

116 *Oxymyia* ♂

117 *Psapharomys* ♀

118 *Psapharomys* ♀

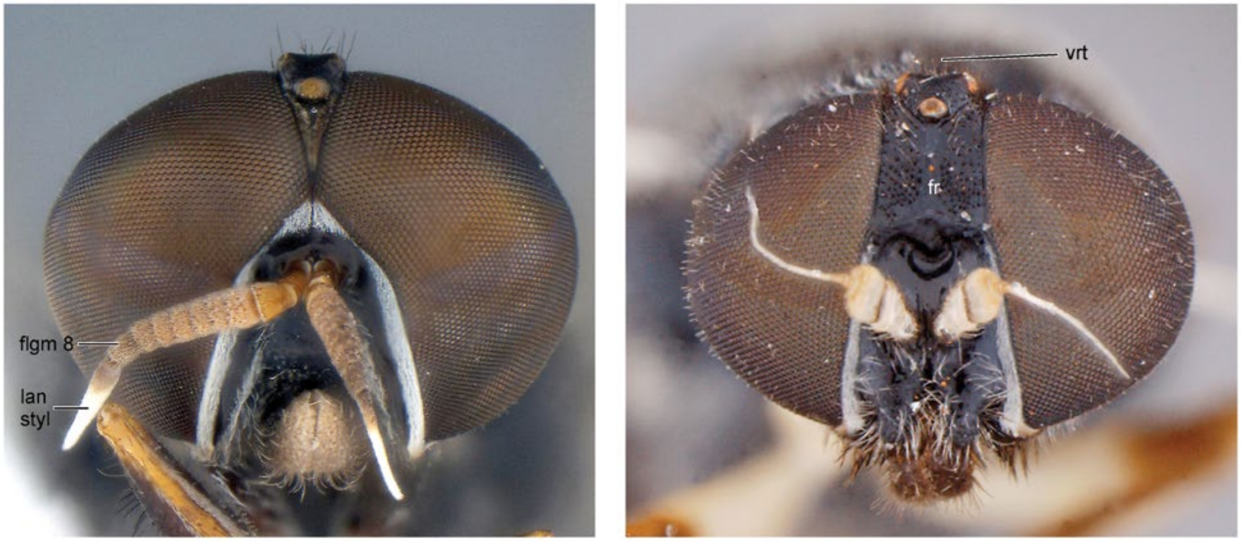
Figs 41.115–118. Heads of Stratiomyidae: (115) *Meristomeringina* sp., frontal view ♀; (116) same, *Oxymyia epacta* Kertész ♂; (117) *Psapharomys* sp., dorsal view ♀; (118) same, lateral view ♀.

Abbreviations: or m – oral margin; pocl reg – postocular region.

between these three genera. The biology and immature stages remain unknown. In the original paper describing the genus, Lindner (1936) provided illustrations of the features that distinguish the species.

***Lasiopa* Brullé** (Nemotelinae)**.** A genus of 17 described and two undescribed species, most of which occur in the Palaearctic, with one species in the Oriental Region and three in the Afrotropics. Two Afrotropical species, *L. edentula* (Wiedemann, 1824) and *L. martinezi* Mason, 1997, occur only in South Africa and *L. rhodensiensis* Lindner, 1952, is also known from Botswana, Mozambique, Namibia, South Africa and Zimbabwe. Two additional undescribed species are known from South Africa and Kenya respectively. Species are rather compact and dark with some pale maculation on the abdomen (Fig. 50). Nothing is known regarding the biology of the genus in the

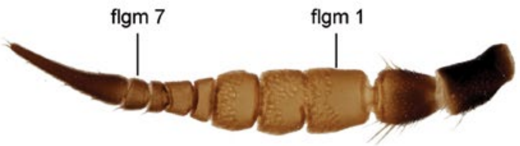
119 *Ptecticus* ♂ 120 *Steleoceromys* ♀



121 *Sternobrithes* ♂ 122 Undescribed genus A ♂

Figs 41.119–122. Heads of Stratiomyidae: (119) *Ptecticus* sp., frontolateral view ♂; (120) *Steleoceromys* sp. dorsolateral view ♀; (121) *Sternobrithes* sp., frontal view ♂; (122) same, Undescribed genus A ♂.

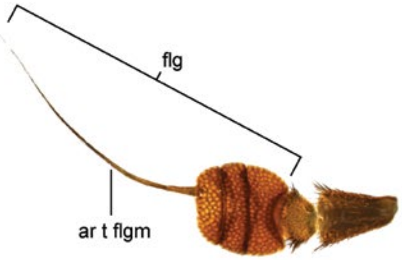
Abbreviations: ar t flgm – arista-like terminal flagellomere; flgm – flagellomere; fr – frons; pocl reg – postocular region; proc – process; lan styl – lanceolate stylus; vrt – vertex.



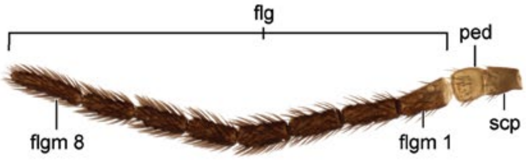
123 *Adoxomyia* ♂

124 *Alopecuroceras* ♀

125 *Ampsalis* ♀



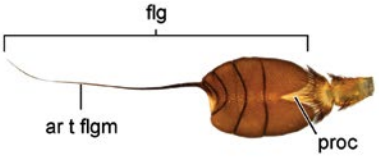
126 *Cephalochrysa* ♂



127 *Chelonomima* ♂

128 *Cyphoprosopa* ♂

129 *Diplephippium* ♂



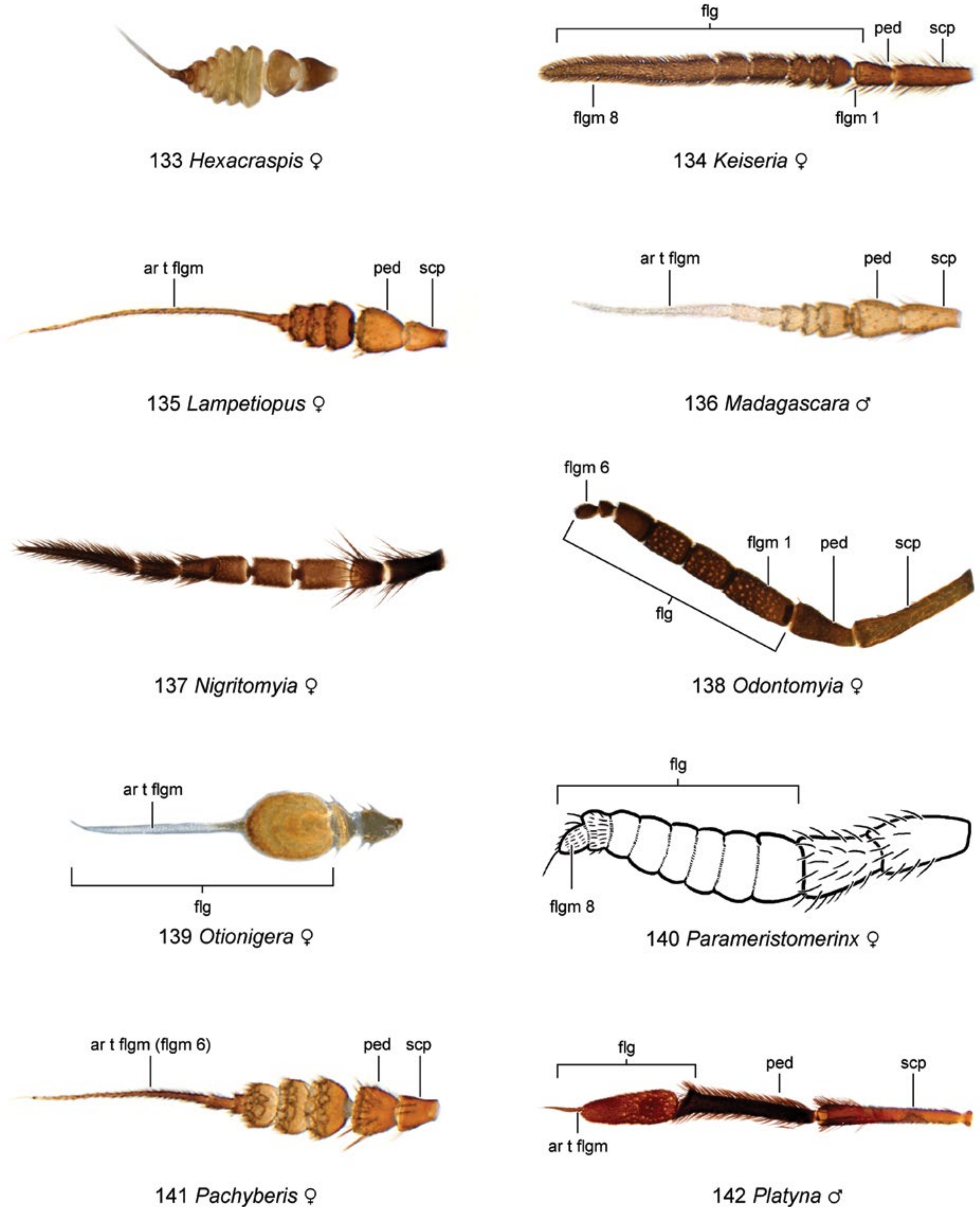
130 *Gongrosargus* ♂

131 *Hermetia* ♂

132 *Hermetiomima* ♀

Figs 41.123–132. Antennae of Stratiomyidae (lateral views): (123) *Adoxomyia* sp. ♂; (124) *Alopecuroceras atripluma* James ♀; (125) *Ampsalis terminalis* James ♀; (126) *Cephalochrysa* sp. ♂; (127) *Chelonomima* sp. ♂; (128) *Cyphoprosopa lindneri* James ♂; (129) *Diplephippium snyderi* James ♂; (130) *Gongrosargus* sp. ♀; (131) *Hermetia myieriades* Speiser ♂; (132) *Hermetiomima rufipes* Lindner ♀.

Abbreviations: ar t flgm – arista-like terminal flagellomere; flg – flagellum; flgm – flagellomere; ped – pedicel; proc – process; scp – scape; styl – stylus.



133 *Hexacraspis* ♀ 134 *Keiseria* ♀ 135 *Lampetiopus* ♀ 136 *Madagascara* ♂ 137 *Nigritomyia* ♀ 138 *Odontomyia* ♀ 139 *Otionigera* ♀ 140 *Parameristomerinx* ♀ 141 *Pachyberis* ♀ 142 *Platyna* ♂

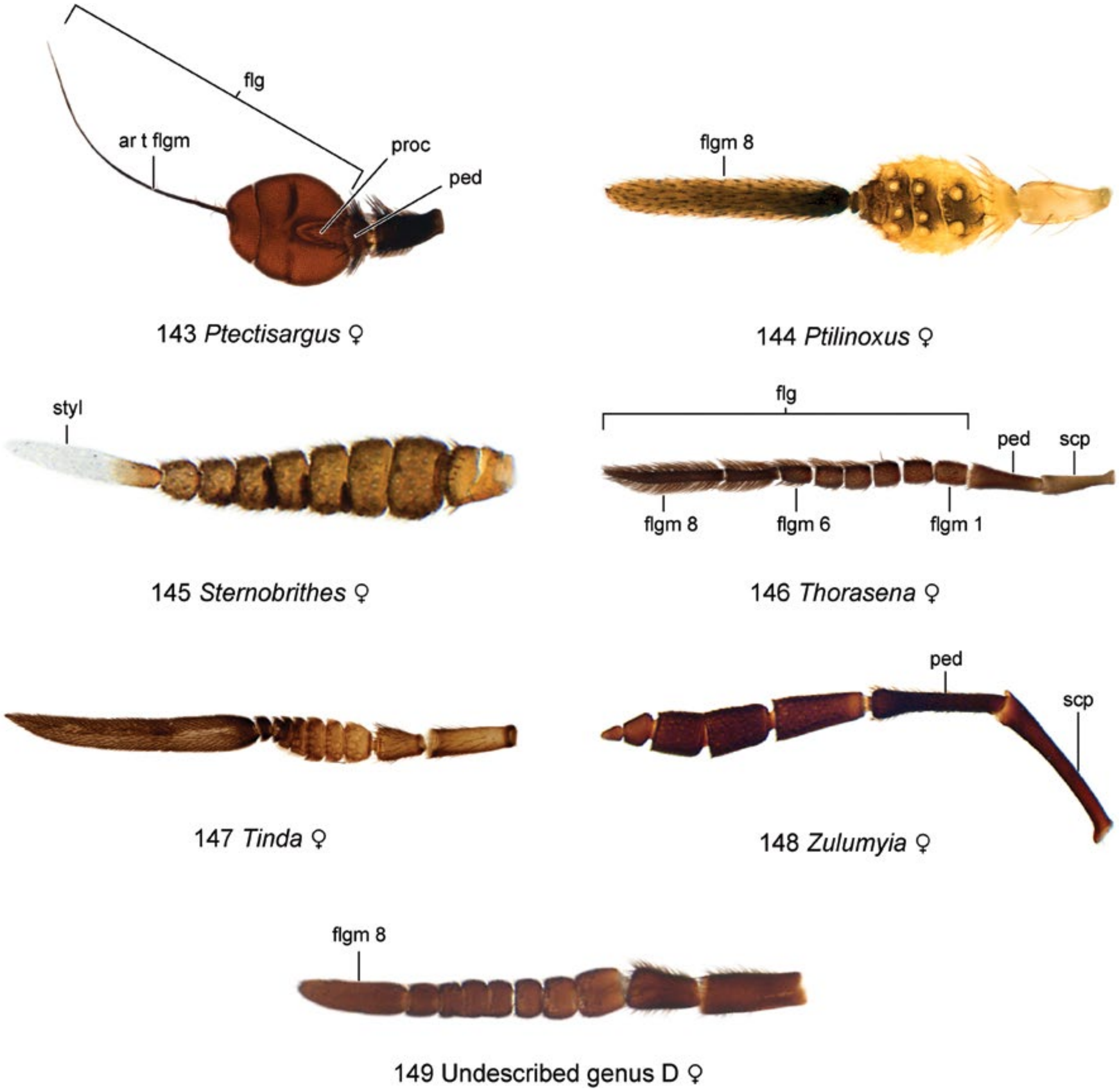
Figs 41.133–142. Antennae of Stratiomyidae (lateral views): (133) *Hexacraspis sexspinosa* (Macquart) ♀; (134) *Keiseria* sp. ♀; (135) *Lampetiopus* sp. ♀; (136) *Madagascara* sp. ♂; (137) *Nigritomyia loewii* (Brauer) ♀; (138) *Odontomyia* sp. ♀; (139) *Otionigera* sp. ♀; (140) *Parameristomerinx copelandi* Woodley ♀; (141) *Pachyberis stigmaticalis* James ♀; (142) *Platyna hastata* (F.) ♂. Fig. 140 (after Woodley 2010, fig. 6).

Abbreviations: ar t flgm – arista-like terminal flagellomere; flg – flagellum; flgm – flagellomere; ped – pedicel; scp – scape.

Afrotropics, but adults of extralimital species have been collected on flowers (Rozkošný 1983: 19). The larva of one European species has been described (Schremmer 1953). Mason (1997*b*: 31) provided a thorough taxonomic treatment of the Afrotropical species known at that time.

Lophoteles **Loew** (Pachygastrinae)**.** A genus of 12 species occurring in the Australasian Region (mainly Papua New Guinea), with one recently described species from the Philippines (Rozkošný 2013). The type species, *L. plumula* Loew 1858, was described from the Marshall Is. in the Pacific and was recorded from Seychelles by Kertész (1914). From Kertész's description it is clear that the specimens from Seychelles belong to this genus, but it is doubtful that these specimens are conspecific with *L. plumula*. The specimens mentioned by Lindner (1974) from Comoros belong to the genus *Ptilinoxus*. The small black species are characterised by the antennal arista clothed in dense dorsal and ventral setae, giving it a feather-like appearance. The biology and immature stages remain unknown. No identification key to species is currently available.

Madagascara **Lindner** (Stratiomyinae: Prosopochrysini)**.** An endemic genus of two described species confined to Madagascar, *M. seyrigi* Lindner, 1936 and *M. woodleyi* Schacht & Heuck, 2006 (Fig. 52). The latter species differs from the former in having a slightly more compact antennal flagellum and



143 *Ptectisargus* ♀

144 *Ptilinoxus* ♀

145 *Sternobrithes* ♀

146 *Thorasena* ♀

147 *Tinda* ♀

148 *Zulumyia* ♀

149 Undescribed genus D ♀

Figs 41.143–149. Antennae of Stratiomyidae (lateral views): (143) *Ptectisargus abditus* (Lindner) ♀; (144) *Ptilinoxus* sp. ♀; (145) *Sternobrithes* sp. ♀; (146) *Thorasena* sp. ♀; (147) *Tinda* sp. ♀; (148) *Zulumyia expansa* James ♀; (149) Undescribed genus D ♀.

Abbreviations: ar t flgm – arista-like terminal flagellomere; flg – flagellum; flgm – flagellomere; ped – pedicel; proc – process; scp – scape; styl – stylus.

even more robustly enlarged hind femora (Schacht & Heuck 2006). Two additional undescribed species are known from Madagascar (Figs 51, 136, 191), both with enlarged hind tibia with large femoral teeth (Fig. 154). The biology and immature stages remain unknown. No identification key to species is currently available.

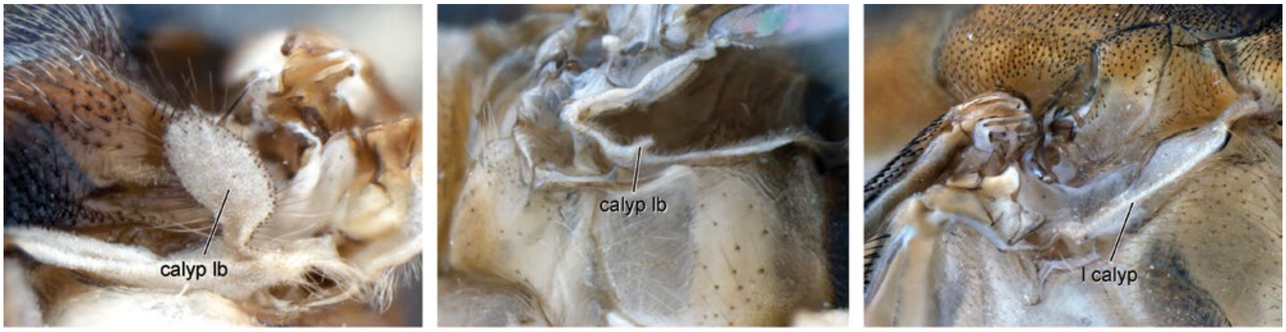
***Madagascarina* Lindner** (Stratiomyinae: Prosopochrysini)**.** An endemic monotypic genus, with the single species, *M. beyeri* Lindner, 1967 (Fig. 53), confined to Madagascar. In Madagascar, there are three genera of Prosopochrysini which have a large subapical tooth on the hind femur, but this genus is unique in also having a tooth on the mid femur, which is considerably more enlarged than the hind femur (Fig. 53). The biology and immature stages remain unknown. Lindner (1967, fig. 1) provided a habitus illustration of the species.

***Marangua* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *M. pygmaea* Lindner, 1960, described from Tanzania. This is probably the smallest Afrotropical Stratiomyidae, being less than 2 mm in length (Figs 54, 114, 192). The species may belong to a group of small black Afrotropical Pachygastrinae that are described in the genus *Neopachygaster*. The biology and immature stages remain unknown.

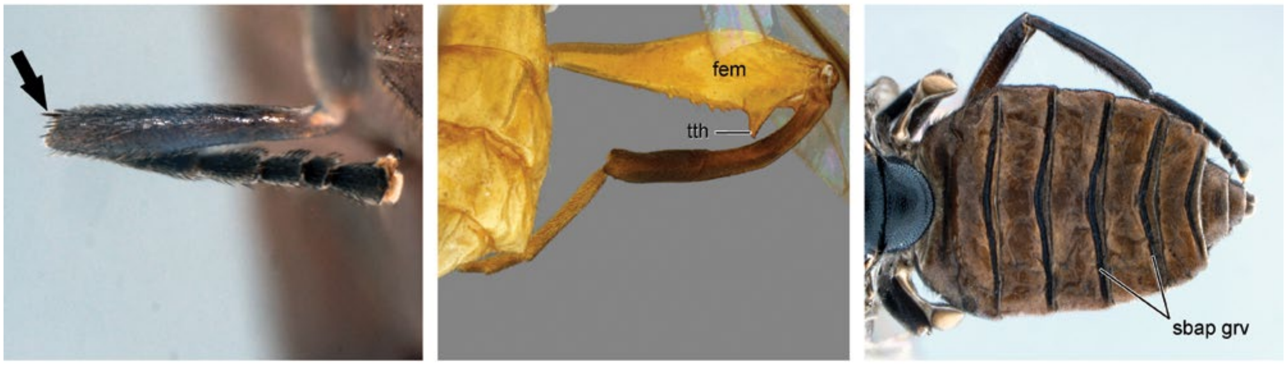
***Meristomeringina* James** (Pachygastrinae)**.** An endemic genus of six described species that occur from West Africa (Togo) through Central Africa, south to Zimbabwe. All species are quite similar in appearance, mostly blackish (Figs 55, 115) and are most reliably identified by reference to the male terminalia. *Meristomeringina* is the only Afrotropical genus of the subfamily Pachygastrinae with two scutellar spines (Fig. 55). The biology and immature stages remain unknown. Woodley (1987*a*) revised the genus and provided an identification key to species.

***Meristomerinx* Enderlein** (Pachygastrinae)**.** An endemic genus of two described species, *M. camerunensis* Enderlein, 1914 (Figs 56, 194), from Cameroon, Côte d'Ivoire and Zimbabwe and *M. proxima* Lindner, 1972, from South Africa. The dull black to brown body has a yellowish margin along the thorax and abdomen, together with mainly yellowish legs. The biology and immature stages remain unknown. A revision of the genus was provided by Woodley (1997).

***Microchrysa* Loew** (Sarginae)**.** A genus of 42 described species, occurring in all zoogeographical regions, except Antarctica. With 21 species, the Afrotropical Region is the most species-rich. The genus is widespread in the Afrotropics, including



150 *Cephalochrysa* ♀ 151 *Microptecticus* ♀ 152 *Ptecticus* ♀



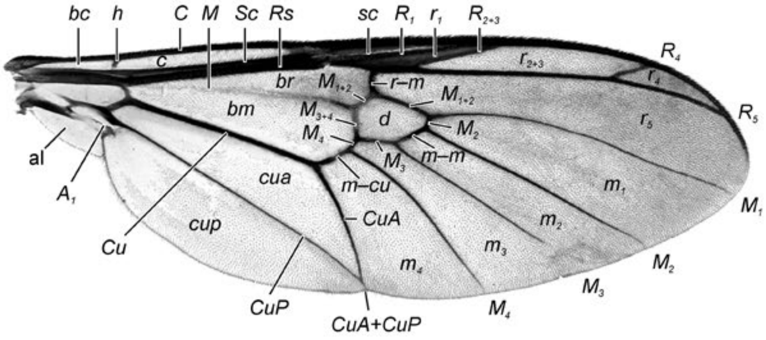
153 *Allognosta* ♀ 154 *Madagascara* ♀ 155 *Allognosta* ♀

Figs 41.150–155. Calypters, legs and abdomen of Stratiomyidae: (150) calypter of *Cephalochrysa* sp., lateral view ♀; (151) same, *Microptecticus* sp. ♀; (152) same, *Ptecticus* sp. ♀; (153) mid tibia of *Allognosta* sp., dorsal view ♀ (arrow indicates spur); (154) hind leg of *Madagascara* sp., dorsal view ♀; (155) abdomen and hind leg of *Allognosta* sp., dorsal view ♀.

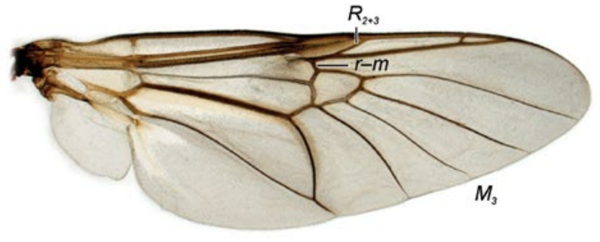
Abbreviations: calyp lb – calypter lobe; fem – femur; l calyp – lower calypter; sbap grv – subapical groove; tth – tooth.

Madagascar and Seychelles. *Microchrysa* species are generally small, metallic green flies (Fig. 57), sometimes with partially yellow colouration. The usually short, ovoid abdomen may be more elongate and slender in a few Afrotropical species. The discal wing cell (*d*) is usually small (Fig. 195). Larvae from Europe which occur in animal dung and various types of decaying plant matter (Rozkošný 1982: 129). A detailed revision of the genus was provided by Mason (1997*a*), which included an identification key.

Microptecticus **Lindner** (Sarginae)**.** An endemic genus of four described species, *M. ambiguus* Lindner, 1966, *M. dimidiatus*

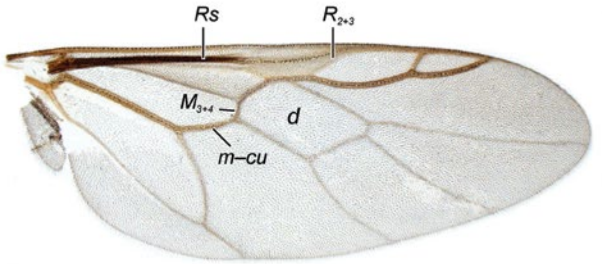


156 *Cephalochrysa* ♀



157 *Adoxomyia* ♂

158 *Afrodontomyia* ♀



159 *Ageiton* ♀

160 *Allognosta* ♀

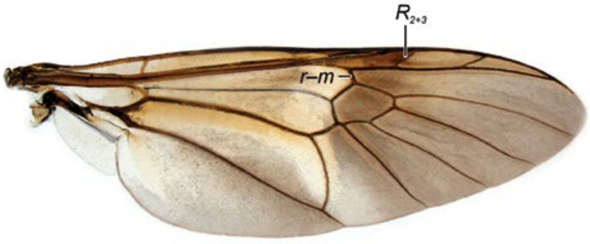
Figs 41.156–160. Wings of Stratiomyidae (dorsal views): (156) *Cephalochrysa* sp. ♀; (157) *Adoxomyia heminopla* (Wiedemann) ♂; (158) *Afrodontomyia* sp. ♀; (159) *Ageiton ater* Kertész ♀; (160) *Allognosta* sp. ♀.

Abbreviations: A_1 – first branch of anal vein; al – alula; *bc* – basal costal cell; *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *Cu* – cubital vein or cubitus; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *h* – humeral crossvein; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein.

Lindner, 1936, *M. magnicornis* (Lindner, 1936) and *M. stuckenbergi* (Lindner, 1936) confined to Madagascar. At least eight undescribed species are known from Madagascar (Figs 58, 59). Despite its name, the genus does not closely resemble *Ptecticus*. The medial wing vein (*M*) between cells *bm* and *br* is only discernible distally (Fig. 196), while in *Ptecticus* it is strong for its entire length (Fig. 217) and the female antenna is much larger than in *Ptecticus*. Species with a metallic scutum are quite common in *Microptecticus*, but rare in *Ptecticus* and not evident in Afrotropical *Ptecticus*. Species are also much smaller than those of *Ptecticus* being distinctly less than 10 mm in length. Nothing is known regarding the biology of the genus. No identification key to species is currently available.

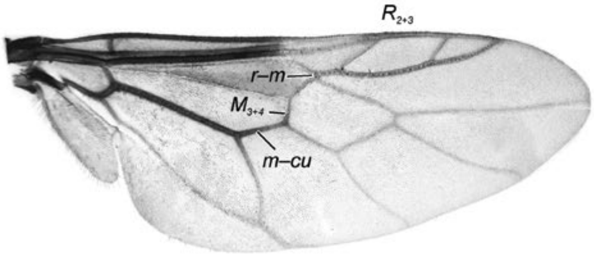
***Microsargus* Lindner** (Sarginae)**.** Currently an endemic monotypic genus, with the single species, *M. stuckenbergi* Lindner, 1958, confined to South Africa. Three undescribed species are known from Côte d'Ivoire, Kenya, Togo and Uganda. *Microsargus* are small slender sargines (Figs 60, 61) that are rare in collections, easily recognised by the absence of wing veins *CuP*, M_3 and R_4 which is a very rare combination in this subfamily (Fig. 197). Both sexes have a metallic head, with a broad frons that strongly widens towards the vertex and a mostly yellowish body (Figs 60, 61). The biology and immature stages remain unknown.

***Nemotelus* Geoffroy** (Nemotelinae)**.** A large genus of *ca* 190 described species that is widespread in the New World, as well as the Afrotropical and Palaearctic Regions. Thirty-five species are recorded from the Afrotropics, almost all of which are confined to South Africa, although two are endemic to Madagascar and two are known from United Arabic Emirates (Hauser 2008, 2014) (Figs 62, 198). Mason (1997*b*: 28) recognised three genera that are here treated as the genus *Nemotelus*,



161 *Alopecuroceras* ♀

162 *Ampsalis* ♀



163 *Argyrobrithes* ♀

164 *Ashantina* ♀

165 *Aspidacantha* ♀

166 *Aspidacanthina* ♀

Figs 41.161–166. Wings of Stratiomyidae (dorsal views): (161) *Alopecuroceras atripluma* James ♀; (162) *Ampsalis terminalis* James ♀; (163) *Argyrobrithes* sp. ♀; (164) *Ashantina antennata* Kertész ♀; (165) *Aspidacantha atra* Kertész ♀; (166) *Aspidacanthina* sp. ♀.

Abbreviations: M_{3+4} – fused third and fourth branch of media; *m–cu* – medial–cubital crossvein; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein.

following Woodley (2001), due to the lack of phylogenetic study supporting their recognition as separate genera. Of the generic units that Mason recognised, *Epideicticus* Kertész is the most distinctive, being restricted to the Afrotropics with the exception of one species described by James (1974) from Colombia that may be similar, but not actually related. Species are small- or medium-sized, often with a conical projected face. The colouration is mainly black, but males of numerous species have a white abdomen, often with some black markings, while the female abdomen is often black with some white maculae or entirely black. Adults of at least some *Nemotelus* species occur on flowers, usually near aquatic habitats where the larvae occur. Only the larvae of a few Palaearctic and Nearctic species have been described, which occur in standing (sometimes quite saline) water (Rozkošný 1982: 28). Mason (1997*b*: 35) revised the Afrotropical fauna and provided an identification key to species. Hauser (2008: 598) discussed two species from the United Arab Emirates and later Hauser (2014: 697) described an additional species from United Arab Emirates.

Neopachygaster **Austen** (Pachygastrinae)**.** A genus of 17 described species occurring in the Afrotropical, Nearctic and Palaearctic Regions. Nine species occur in the central part of the Afrotropical Region. It is doubtful that all species currently ascribed to the genus are congeneric with the European type species. Most described Afrotropical species appear to belong to the same lineage, in which several other described genera could be included. Most of these genera are described on species-specific characters that may not be supported following a thorough revision. Genera that may fall into this group are: *Anargemus* Lindner, *Apotomaspis*, *Aspidacanthina*, *Diargemus*, *Diplopeltina*, *Drosimomyia*, *Marangua*, *Nyplatys*, *Pachyacantha*

167 *Brachycara* ♀

168 *Brianmyia* ♂

169 *Cardopomyia* ♀

170 *Cephalochrysa* ♀

171 *Chelonomima* ♂

172 *Chloromyia* ♀

Figs 41.167–172. Wings of Stratiomyidae (dorsal views): (167) *Brachycara* sp. ♀; (168) *Brianmyia stuckenbergi* Woodley ♂; (169) *Cardopomyia* sp. ♀; (170) *Cephalochrysa* sp. ♀; (171) *Chelonomima* sp. ♂; (172) *Chloromyia tuberculata* James ♀. Fig. 168 (after Woodley 2012, fig. 4).

Abbreviations: *CuP* – posterior branch of cubital vein; *d* – discal cell; *M* – medial vein or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector.

and *Pithomyia*. Different species display rather unique characters, such as an apical wing macula (Figs 63, 199), an entirely silver pubescent body (in males) (Fig. 64), an enlarged scutellum, *etc*., but all these species have the antennae inserted on a pair of small tubercles (see Lindner 1939, fig. 2) and an L-shaped patch of silver setulae along the posterior margin of the anepisternum and the dorsal part of the katepisternum (Fig. 63). Rozkošný (1983: 177) summarised what is known regarding the larva of European species, which occur beneath the bark of rotten trees, as do most known Pachygastrinae larvae. No identification key to Afrotropical species is currently available.

***Nigritomyia* Bigot** (Clitellariinae)**.** A genus of 14 described species that occur in the Afrotropical, Australasian and Oriental Regions, with the majority occurring in the last-named region. The Afrotropical fauna is represented by the single species, *N. loewii* (Brauer, 1882) (Figs 65, 137, 200), which occurs in West and Central Africa. The wings have dark brown patches, the body is dark with silver metallic setae throughout and there is a long spine on each side above the wing base. An additional one or two undescribed species are known from South Africa. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

***Nyassamyia* Lindner** (Stratiomyinae: Stratiomyini)**.** An endemic genus of two species, *N. deceptor* (Curran, 1928) (Fig. 66), described from Democratic Republic of Congo and *N. andreniformis*, recorded from Malawi and South Africa. There is at least one additional undescribed species known from South Africa and Zambia. Both described species are densely pubescent and probably mimic bees (Fig. 66). A museum specimen of *N. andreniformis* was examined with its pupal skin mounted with the adult and a label "… pupae from rothole in tree". No identification key to species is currently available.

***Nyplatys* Séguy** (Pachygastrinae)**.** An endemic genus with two species, *N. niger* Séguy, 1938 and *N. cultellata* (Lindner, 1939) (Figs 67, 202), described from Kenya and Uganda respectively. Additional records of the genus are known from

173 *Chrysochlora* ♂ 174 *Cyphoprosopa* ♂

175 *Dactylotinda* ♂ 176 *Diademophora* ♀

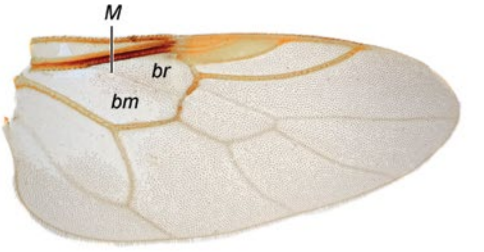
177 *Diplephippium* ♂ 178 *Dischizocera* ♂

Figs 41.173–178. Wings of Stratiomyidae (dorsal views): (173) *Chrysochlora amethystina* (F.) ♂; (174) *Cyphoprosopa lindneri* James ♂; (175) *Dactylotinda saegeri* Lindner ♂; (176) *Diademophora ruandaensis* Lindner ♀; (177) *Diplephippium snyderi* James ♂; (178) *Dischizocera zumpti* Lindner ♂.

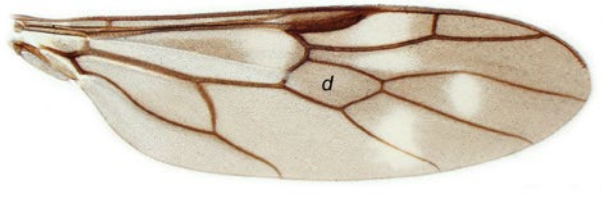
Abbreviations: *CuP* – posterior branch of cubital vein; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein.

Burundi, Democratic Republic of Congo and Ethiopia. There may be additional undescribed species in the region, but a thorough revision of the genus is required. The genus is characterised by the laterally flattened terminal antennal flagellomere, but otherwise fits very well with Afrotropical species described in *Neopachygaster*. A revision of the small Pachygastrinae is required to clarify the generic status of the species. The biology and immature stages of the species remain unknown. No identification key to Afrotropical species is currently available.

***Odontomyia* Meigen** (Stratiomyinae: Stratiomyini)**.** A large genus of *ca* 215 species occurring in all zoogeographical regions, except Antarctica. The genus is widespread, over virtually the entire continental Afrotropics, together with Madagascar and Seychelles with forty-five species. The genus *Cyrtopus* Bigot is here regarded as a synonym of *Odontomyia*, following Rozkošný & Woodley (2010). Generic limits in the tribe Stratiomyini are not well defined, if the world fauna is considered. Conversely, some Afrotropical genera, such as *Catatasis*, *Crocutasis* and *Dischizocera*, include species that could arguably be autapomorphic species-groups within *Odontomyia*. The genus displays a large variety of colour patterns and size, but has a very characteristic compact, slightly dorsoventrally flattened habitus (Figs 68, 69). Larvae are aquatic, and while the biologies of European species are relatively well known (Rozkošný 1982: 163), very little is understood about Afrotropical species. Label data cited in Lindner (1972: 31) noted that *O. lamborni* Lindner, 1938, was "… bred in rothole in *Sterculia* sp. and *Brachystegia* sp. …" Lachaise & Lindner (1973) published life history information on two species, *O. smaragdifera* and *O. magnifica* Lachaise & Lindner, 1973, occurring in savanna habitats in Côte d'Ivoire. The larvae of both species occur in small puddles on granite outcrops and take a year or more for development. During dry seasons the larvae aestivate in organic detritus in the puddle depressions. Kühbandner (1985) described the larva of *O. smaragdifera* from Kenya, being

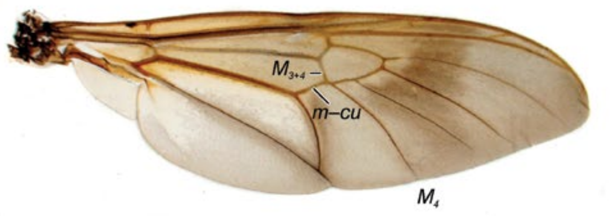


179 *Drosimomyia* ♀



180 *Enypnium* ♂

181 *Goetghebueromyia* ♂



182 *Gongrosargus* ♂

183 *Hermetia* ♂

184 *Hermetiomima* ♀

Figs 41.179–184. Wings of Stratiomyidae (dorsal views): (179) *Drosimomyia* sp. ♀; (180) *Enypnium obscura* (Bigot) ♂; (181) *Goetghebueromyia paradoxa* Lindner ♂; (182) *Gongrosargus* sp. ♂; (183) *Hermetia myieriades* Speiser ♂; (184) *Hermetiomima* sp. ♀.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *d* – discal cell; *M* – medial vein, or media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein.

unaware of the previous work of Lachaise & Lindner (1973). No identification key to Afrotropical species is currently available.

Oplodontha **Rondani** (Stratiomyinae: Stratiomyini)**.** This genus of *ca* 20 known species occurs in the Afrotropical, Oriental and Palaearctic Regions, with 16 species that are widely distributed in the continental Afrotropics (Fig. 70). Two of the more widespread species, *O. dispar* (Macquart, 1838) and *O. pulchriceps* Loew, 1858, are recorded from Madagascar. The genus is characterised by the small discal cell (*d*) (Fig. 204) and superficially resemble small *Odontomyia*. Larvae are undoubtedly aquatic, as this habitat has been documented for the common European species, *O. viridula* (F., 1775) (Rozkošný 1982: 204). The pupal case of *Oplodontha albipennis* (as *Hoplodonta stricticella*) was described by James (1940). Lindner (1961) provided an identification key to some Afrotropical species.

Otionigera **Lindner** (Pachygastrinae)**.** Currently an endemic monotypic genus, with the single species, *O. acuticornis* Lindner, 1966, confined to Madagascar (Figs 71, 139, 205). At least one additional undescribed species is known from Madagascar. The males have holoptic eyes, with larger ommatidia dorsally and the terminal flagellomere is snow white pubescent (Fig. 139). The biology and immature stages remain unknown.

Otochrysa **Lindner** (Sarginae)**.** An endemic monotypic genus, with the single species, *O. bicolor* Lindner, 1938, recorded from Central African Republic and Democratic Republic of Congo. Specimens of this genus are rare in collections, but several additional specimens have been examined from Kenya and Uganda, that may represent a different species (Figs 72, 73, 206). The body is pale brown with dark brown abdominal markings and a pitch black head. The biology and immature stages remain unknown.

185 *Hexacraspis* ♂ 186 *Hypoceromys* ♀

187 *Isomerocera* ♂ 188 *Keiseria* ♂

189 *Lampetiopus* ♂ 190 *Lasiopa* ♂

Figs 41.185–190. Wings of Stratiomyidae (dorsal views): (185) *Hexacraspis sexspinosa* (Macquart) ♂; (186) *Hypoceromys* sp. ♀; (187) *Isomerocera quadrilineata* (F.) ♂; (188) *Keiseria* sp. ♂; (189) *Lampetiopus umbrosus* Lindner ♂; (190) *Lasiopa* sp. ♂.

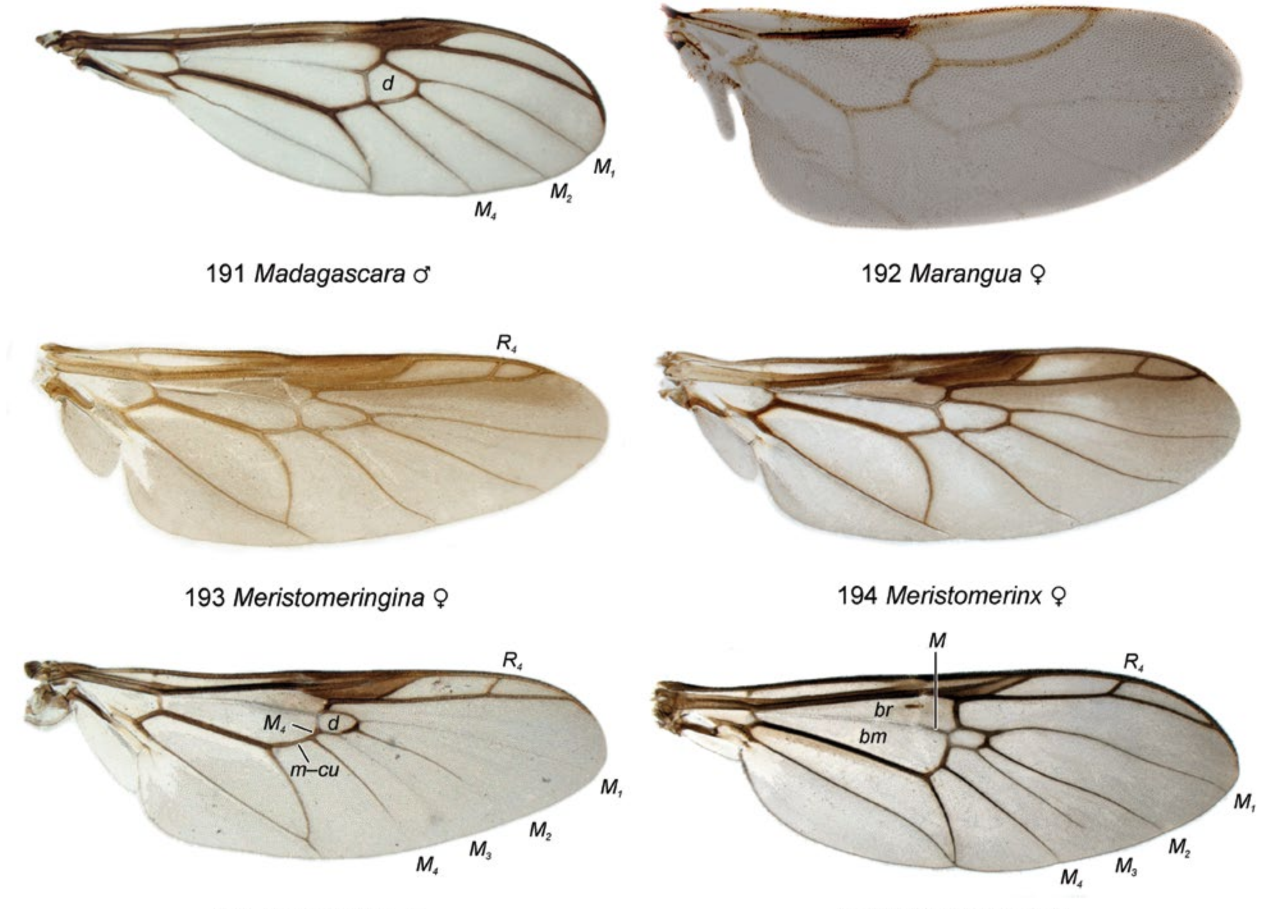
Abbreviations: *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *d* – discal cell; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_{2+3} – second branch of radius; *r–m* – radial–medial crossvein.

Oxycera **Meigen** (Stratiomyinae: Oxycerini)**.** A genus of *ca* 95 species, occurring in all zoogeographical regions, except the Australasian and Neotropical Regions and Antarctica, being most diverse in the Palaearctic. Twelve described species occur in the Afrotropical Region, most of which are poorly known and difficult to identify (Fig. 74). Numerous species are black with yellow to white markings and invariably with long spines on the scutellum. Species that lack wing vein R_4 (Fig. 207) were formerly placed in the genus *Heraclina* Lindner now considered a synonym of *Oxycera*. The majority of larvae are aquatic and often prefer hygropetric habitats (Hauser 2014: 697). Rozkošný (1982: 94) summarised the biology of European species. No identification key to Afrotropical species is currently available.

Oxymyia **Kertész** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *O. epacta* Kertész, 1916, described from Cape Province, South Africa. The genus is very similar to *Hexacraspis* (Figs 44, 111, 112), but easily separated by the prolonged lower face (Figs 75, 116). The biology and immature stages of the species remain unknown.

Pachyacantha **Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single described South African species, *P. crassiventris* Lindner, 1952, possibly belonging to a group of Afrotropical species described in *Neopachygaster*. No material of this genus was examined in preparation of this chapter. The biology and immature stages of the species remain unknown.

Pachyberis **James** (Stratiomyinae: Prosopochrysini)**.** An endemic monotypic genus, with the single species, *P. stigmaticalis* James, 1975 (Figs 76, 141, 209), confined to Madagascar. It is the only Afrotropical prosopochrysine with a metallic coloured scutum (Fig. 76). The wing has a distinctly darkened cell r_1 with the infuscation extending to the discal cell (*d*) (Fig. 209). James (1975: 480) noted that antennal flagellomere 6 is "… distinctly longer than the five basal flagellomeres



191 *Madagascara* ♂ 192 *Marangua* ♀

193 *Meristomeringina* ♀ 194 *Meristomerinx* ♀

195 *Microchrysa* ♂ 196 *Microptecticus* ♀

Figs 41.191–196. Wings of Stratiomyidae (dorsal views): (191) *Madagascara* sp. ♂; (192) *Marangua* sp. ♀; (193) *Meristomeringina* sp. ♀; (194) *Meristomerinx camerunensis* Enderlein ♀; (195) *Microchrysa* sp. ♂; (196) *Microptecticus dimidiatus* Lindner ♀.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *d* – discal cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_4 – upper branch of third branch of radius.

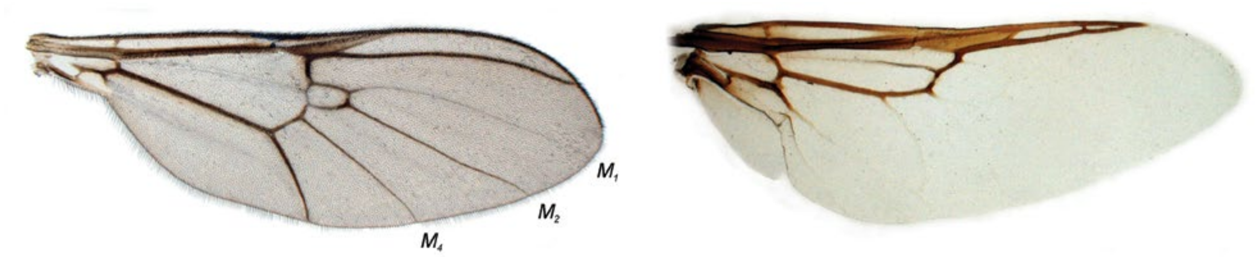
combined …", although his figure of the head and antennae (James 1975, fig. 10) portrays the length of the style as being almost equal in length to flagellomeres 1–5 combined, which is also true for the material studied (Fig. 141). The biology and immature stages of the species remain unknown.

***Parameristomerinx* Woodley** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *P. copelandi* Woodley, 2010 (Figs 77, 140), described from Arabuko-Sokoke Forest, Kenya, the most pristine patch of coastal forest left in East Africa. The biology and immature stages of the species remain unknown.

***Paraptecticus* Grünberg** (Sarginae)**.** An endemic monotypic genus, with the single species, *P. viduatus* Grünberg, 1915 (Figs 78, 210), recorded from Central Africa. It is a mostly yellowish species (Fig. 78), that appears superficially similar to *Ptecticus*, but unlike that genus, has a distinctly pointed scutellum. The biology and immature stages of the species remain unknown.

***Pithomyia* Kertész** (Pachygastrinae)**.** An endemic genus of two species, *P. laevifrons* Kertész, 1916, the type species described from South Africa and *P. stuckenbergi* James, 1975, from Madagascar. It remains unclear whether these two species are congeneric. The type species was not examined in preparation of this chapter and it is possible that this genus is congeneric with the group of Afrotropical species described in *Neopachygaster*. There are several undescribed species known from Madagascar that are related to *P. stuckenbergi*. The biology and immature stages remain unknown. No identification key to species is currently available.

***Platyna* Wiedemann** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *P. hastata* F., 1805 (Figs 79, 142, 211), which is widespread in West and East Africa. It is a very distinctive species with a long antenna (Fig. 142)



197 *Microsargus* ♀

198 *Nemotelus* ♂

199 *Neopachygaster* ♀

200 *Nigritomyia* ♀

201 *Nyassamyia* ♀

202 *Nyplatys* ♂

Figs 41.197–202. Wings of Stratiomyidae (dorsal views): (197) *Microsargus* sp. ♀; (198) *Nemotelus* sp. ♂; (199) *Neopachygaster stigma* Lindner ♀; (200) *Nigritomyia loewii* (Brauer) ♀; (201) *Nyassamyia* sp. ♀; (202) *Nyplatys cultellata* (Lindner) ♂.

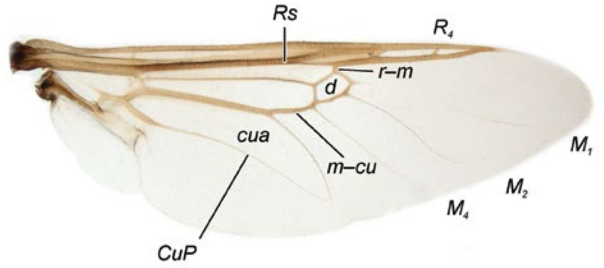
Abbreviations: M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media.

and a broad abdomen that is silver pubescent in males (Fig. 79). The biology and immature stages of the species remain unknown.

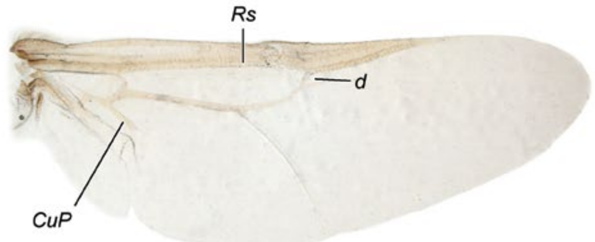
***Platynomorpha* Grünberg** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *P. doryphora* Grünberg, 1915, described from Equatorial Guinea and Cameroon. There is at least one new species from Kenya and the genus is recorded from West and Central Africa (Cameroon, Democratic Republic of Congo, Equatorial Guinea, Ghana, Liberia, Rwanda and Uganda). The genus is superficially similar to *Platyna*, with its long pointed scutellum, but has an entirely different antenna (Fig. 80). The biology and immature stages of the species remain unknown.

***Platynomyia* Kertész** (Pachygastrinae)**.** An endemic Central and East African genus of two described species, *P. dimorpha* Kertész, 1916, from Democratic Republic of Congo, Kenya and Uganda and *P. edwardsi* Lindner, 1939 (Figs 81, 213), from Burundi, Democratic Republic of Congo, Kenya, Tanzania and Uganda. This distinct genus with dichoptic males, appears to be related to *Enypnium* and "*Neopachygaster*" *valida*. The biology and immature stages remain unknown. No identification key to species is currently available.

***Porpocera* Enderlein** (Chrysochlorininae)**.** An endemic genus of two described uncommon species, *P. fibulata* Enderlein, 1914, from South Africa and Zimbabwe and *P. horrida* Lindner, 1958 (Fig. 82) from Zimbabwe. These large brownish to yellowish species have an unusual antennal flagellum, in which



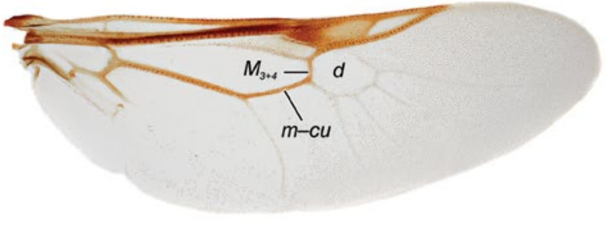
203 *Odontomyia* ♀



204 *Oplodontha* ♂

205 *Otionigera* ♀

206 *Otochrysa* ♂



207 *Oxycera* ♂

208 *Oxymyia* ♂

Figs 41.203–208. Wings of Stratiomyidae (dorsal views): (203) *Odontomyia* sp. ♀; (204) *Oplodontha* sp. ♂; (205) *Otionigera* sp. ♀; (206) *Otochrysa* sp. ♂; (207) *Oxycera* sp. ♂; (208) *Oxymyia epacta* Kertész ♂.

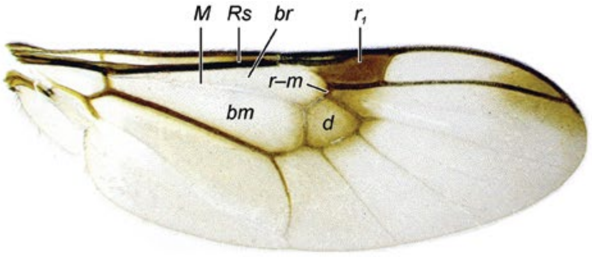
Abbreviations: *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *d* – discal cell; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector.

flagellomeres 1–5 are enlarged and closely approximated, forming a large, semi-inflated complex with the terminal flagellomere ending in an apical, short arista-like stylus. The biology and immature stages remain unknown. No identification key to species is currently available.

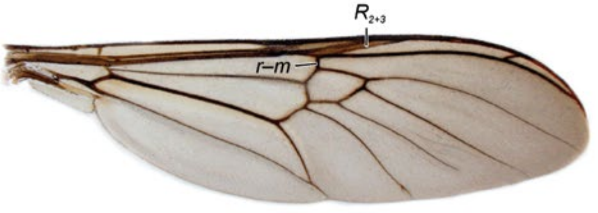
Psapharomys **Grünberg** (Pachygastrinae)**.** Currently an endemic monotypic genus, with the single species, *P. salebrosa* Grünberg, 1915, described from Democratic Republic of Congo and Equatorial Guinea, but with at least two additional undescribed species known from Kenya (Figs 83, 117, 118, 214). The genus is characterised by the triangular pterostigma (Fig. 214), which facilitates the folding of the wing (Fig. 5) (similar to *Stegana* Meigen in the Drosophilidae). At least one species from Kenya has densely setulose eyes. The genus may be closely related to the genera *Hypoceromys* and *Steleoceromys*. The biology and immature stages remain unknown.

Pselaphomyia **Kertész** (Nemotelinae)**.** An endemic genus of two species, *P. manselli* Mason, 1997 and *P. nigripennis* (Bigot, 1887) (Figs 84, 215), both from South Africa. Species are black, with conspicuous yellow markings on the abdomen and brown wings. The biology and immature stages remain unknown. The genus was revised by Mason (1997*b*: 39), who included an identification key to species.

Pseudoxymyia **Lindner** (Pachygastrinae)**.** Currently an endemic monotypic genus, with the single described species, *P. flavitarsis* Lindner, 1959, confined to Madagascar, but at least three additional undescribed species are known, also from



209 *Pachyberis* ♀

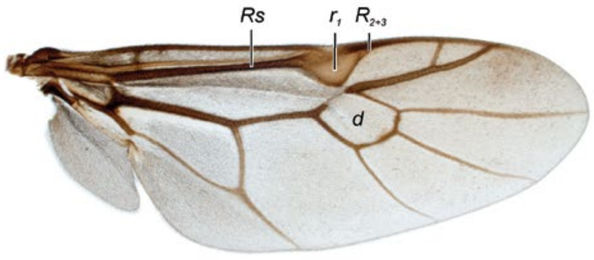


210 *Paraptecticus* ♂

211 *Platyna* ♂

212 *Platynomorpha* ♂

213 *Platynomyia* ♂



214 *Psapharomys* ♀

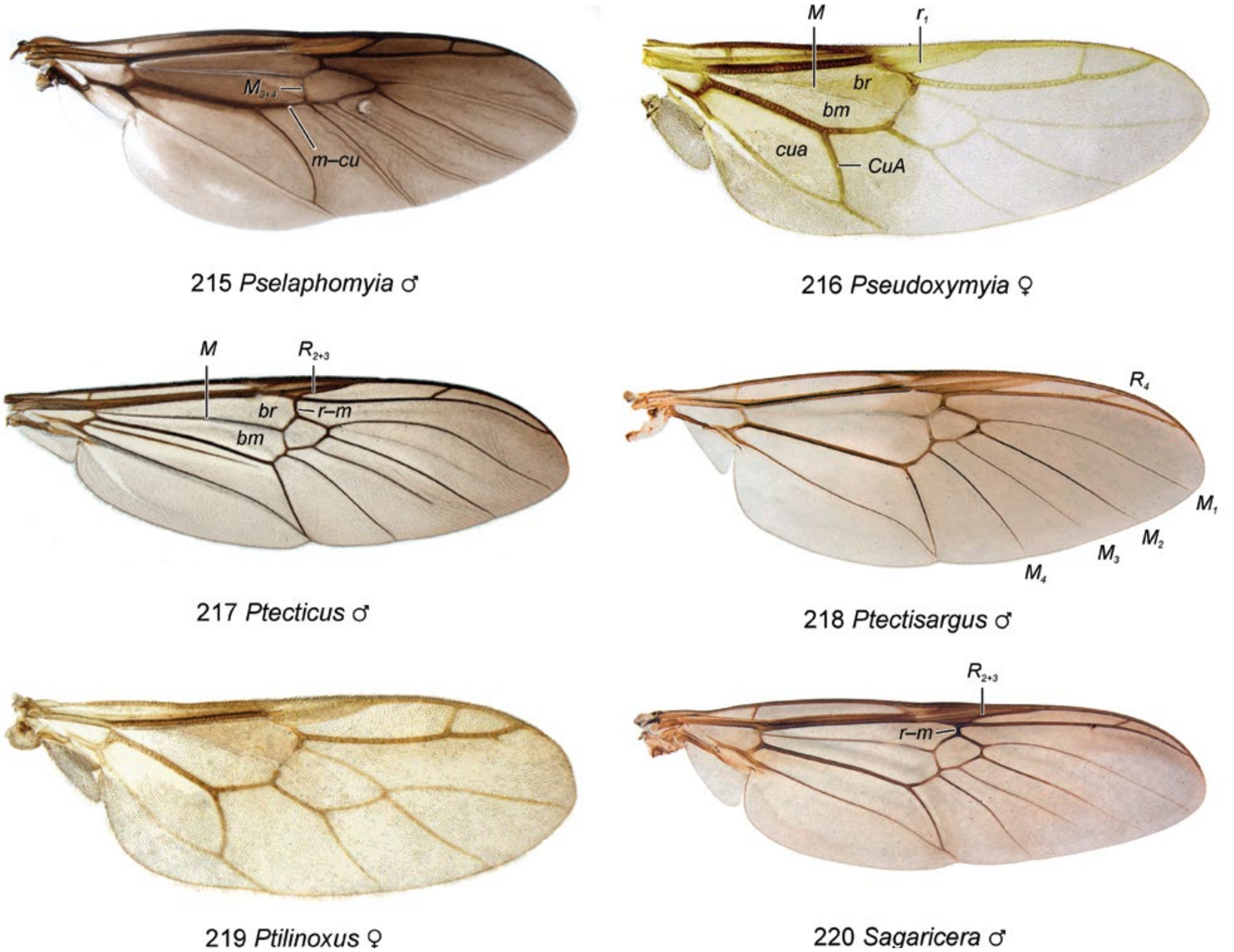
Figs 41.209–214. Wings of Stratiomyidae (dorsal views): (209) *Pachyberis stigmaticalis* James ♀; (210) *Paraptecticus viduatus* Grünberg ♂; (211) *Platyna hastata* (F.) ♂; (212) *Platynomorpha* sp. ♂; (213) *Platynomyia edwardsi* Lindner ♂; (214) *Psapharomys* sp. ♀.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *d* – discal cell; *M* – medial vein, or media; r_1 – first radial cell; R_{2+3} – second branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector.

Madagascar (Figs 85, 216). Females (Fig. 85) have a similar head shape to *Hypoceromys*. The biology and immature stages remain unknown.

Ptecticus **Loew** (Sarginae)**.** A genus of *ca* 140 described species occurring in all zoogeographical regions, except Antarctica. Eleven species are currently recorded from the Afrotropical Region (Figs 2, 86, 119, 217), with two described and at least two undescribed species known from Madagascar. The genus is widespread in the continental Afrotropics, with *P. posticus* (Wiedemann, 1830) being particularly common and widely distributed. All Afrotropical species are yellowish to black in colour and non-metallic, while Asian species often display metallic colouration on the thorax and abdomen. Lachaise & Lindner (1973) reported the immatures of *P. posticus* (as *P. elongatus* (F., 1787)), developing in the decomposing fruits of *Pandanus candelabrum* P. Beauv. (Pandanaceae) in Côte d'Ivoire. Extralimital species are known to develop in a variety of decomposing plant material and are probably not host-specific. Adults are fast fliers that resemble wasps in flight. Only the larva of *Ptecticus posticus* is described by Engel & Cuthbertson (1939). James (1952*a*) published an identification key to the species from the continental Afrotropics.

Ptectisargus **Lindner** (Sarginae)**.** An endemic genus of 13 described species from Comoros and Madagascar (Figs 87, 88, 218). At least ten undescribed species are known from Madagascar. *Ptectisargus* have an elongate body shape, with colouration varying from yellowish to strongly metallic blue, purple or green (Figs 87, 88). Some species resemble



215 *Pselaphomyia* ♂

216 *Pseudoxymyia* ♀

217 *Ptecticus* ♂

218 *Ptectisargus* ♂

219 *Ptilinoxus* ♀

220 *Sagaricera* ♂

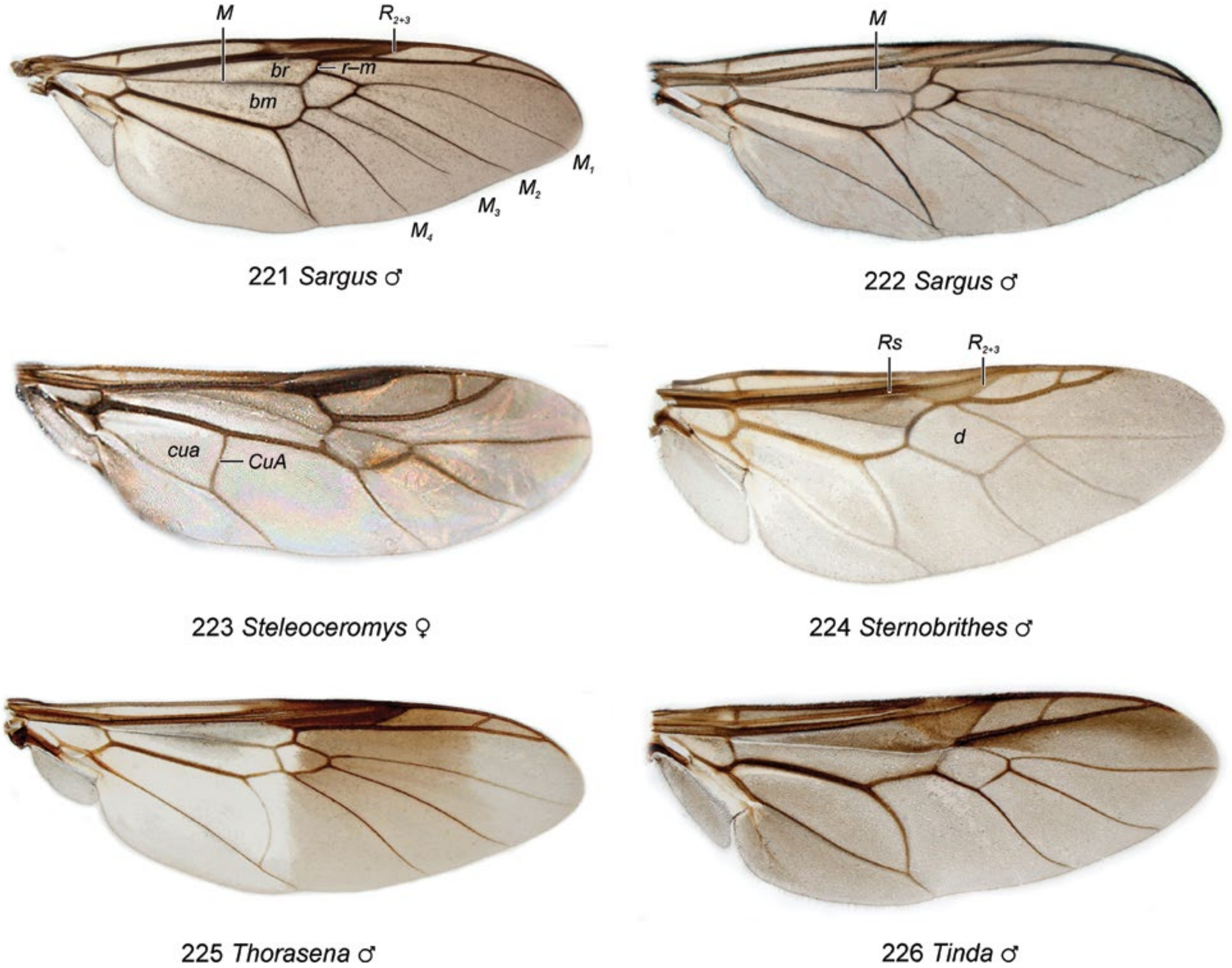
Figs 41.215–220. Wings of Stratiomyidae (dorsal views): (215) *Pselaphomyia nigripennis* (Bigot) ♂; (216) *Pseudoxymyia* sp. ♀; (217) *Ptecticus* sp. ♂; (218) *Ptectisargus abditus* (Lindner) ♂; (219) *Ptilinoxus fallax* Lindner ♀; (220) *Sagaricera analis* (Macquart) ♂.

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; r_1 – first radial cell; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein.

Cephalochrysa, but unlike this genus the male eyes do not touch each other entirely and the ommatidia are all of the same size. The female frons is also often narrower than in *Cephalochrysa* and commonly the antennal pedicel has a finger-like, acute or rounded projection into the flagellum (Fig. 143). The biology and immature stages remain unknown. No identification key is currently available.

***Ptilinoxus* Lindner** (Pachygastrinae)**.** An endemic genus, of two described species, *P. fallax* Lindner, 1966 (Figs 89, 105, 144, 219) and *P. interruptum* (Lindner, 1966), confined to Madagascar, but at least one undescribed species is also known from Madagascar. The genus is characterised by the laterally flattened terminal flagellomere (Figs 105, 144) and holoptic eyes. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

***Sagaricera* Grünberg** (Sarginae)**.** An endemic genus of two described species, *S. aenescens* Grünberg, 1915 (described from the male only) and *S. analis* (Macquart, 1838) (Figs 90, 220), both of which are widespread from West to East Africa. One specimen of an apparently undescribed species has been examined that probably belongs to this genus, although the pedicel is not as strongly produced into the flagellar complex. In *S. aenescens* the male has a greatly modified antennal flagellum, in which the basal complex has the flagellomeres apparently entirely fused into a more or less crescent-shaped structure and the arista-like terminal flagellomere inserted dorsally, almost at the apex of the dorsal part. The apparent female of this species has a much less modified flagellum with distinct flagellomeres. *Sagaricera analis* has a much more typical sargine flagellum, but is otherwise similar. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.



221 *Sargus* ♂

222 *Sargus* ♂

223 *Steleoceromys* ♀

224 *Sternobrithes* ♂

225 *Thorasena* ♂

226 *Tinda* ♂

Figs 41.221–226. Wings of Stratiomyidae (dorsal views): (221) *Sargus* sp. ♂; (222) same; (223) *Steleoceromys anthracina* Grünberg ♀; (224) *Sternobrithes* sp. ♂; (225) *Thorasena* sp. ♂; (226) *Tinda* sp. ♂.

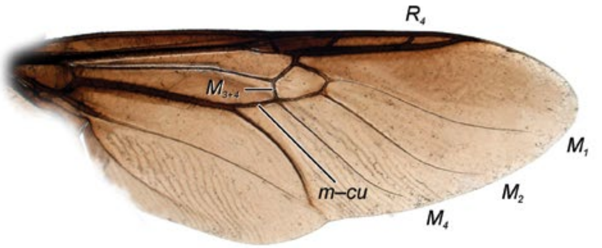
Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *d* – discal cell; *M* – medial vein, or media; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector.

***Sargus* F.** (Sarginae)**.** A genus of *ca* 110 described species occurring in all zoogeographical regions, except Antarctica. Nineteen species are recorded from the Afrotropical Region. The genus has been used as a "dumping ground" in the past and is clearly paraphyletic, with some Afrotropical species likely belonging to other genera (Figs 91, 92). One group has the palpus reduced and consists of several described and undescribed species, some species have vein *M* distinct and others have this vein fading in the basal half (Figs 221, 222). True *Sargus* species occur in the continental Afrotropics and Madagascar. The genus is in need of revision, but would be better undertaken on a global basis, rather than region by region. The biology of European *Sargus* species was well summarised by Rozkošný (1982: 25). No identification key to Afrotropical species is currently available.

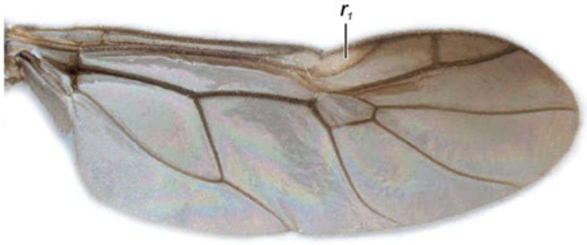
***Steleoceromys* Grünberg** (Pachygastrinae)**.** An endemic genus, with two species, *S. anthracina* Grünberg, 1915, recorded from Cameroon, Côte d'Ivoire, Democratic Republic of Congo and Nigeria and *S. procera* (Lindner, 1966) from Democratic Republic of Congo. These highly elongate and narrow species (Figs 93, 120) are characterised by the right angle closure of wing cell *cua* (Fig. 223). The biology and immature stages of the species remain unknown. No identification key to Afrotropical species is currently available.

***Sternobrithes* Loew** (Pachygastrinae)**.** An endemic genus of three described species: *S. picticornis* (Bigot, 1879) and *S. tumidus* Loew, 1857, which are widespread in the Afrotropical Region, including Cabo Verde (it is not clear which of the two species occurs in the Cape Verde Is.), while *S. mercurialis*

227 *Zabrachia* ♀

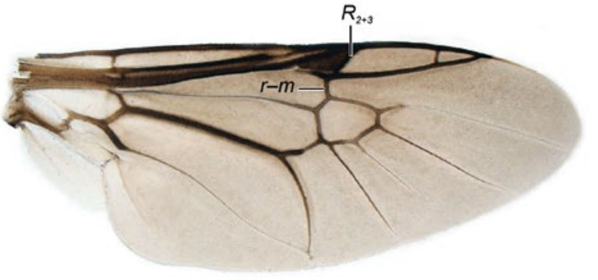


228 *Zulumyia* ♀



229 Undescribed genus A ♂

230 Undescribed genus B ♀



231 Undescribed genus C ♀

232 Undescribed genus D ♀

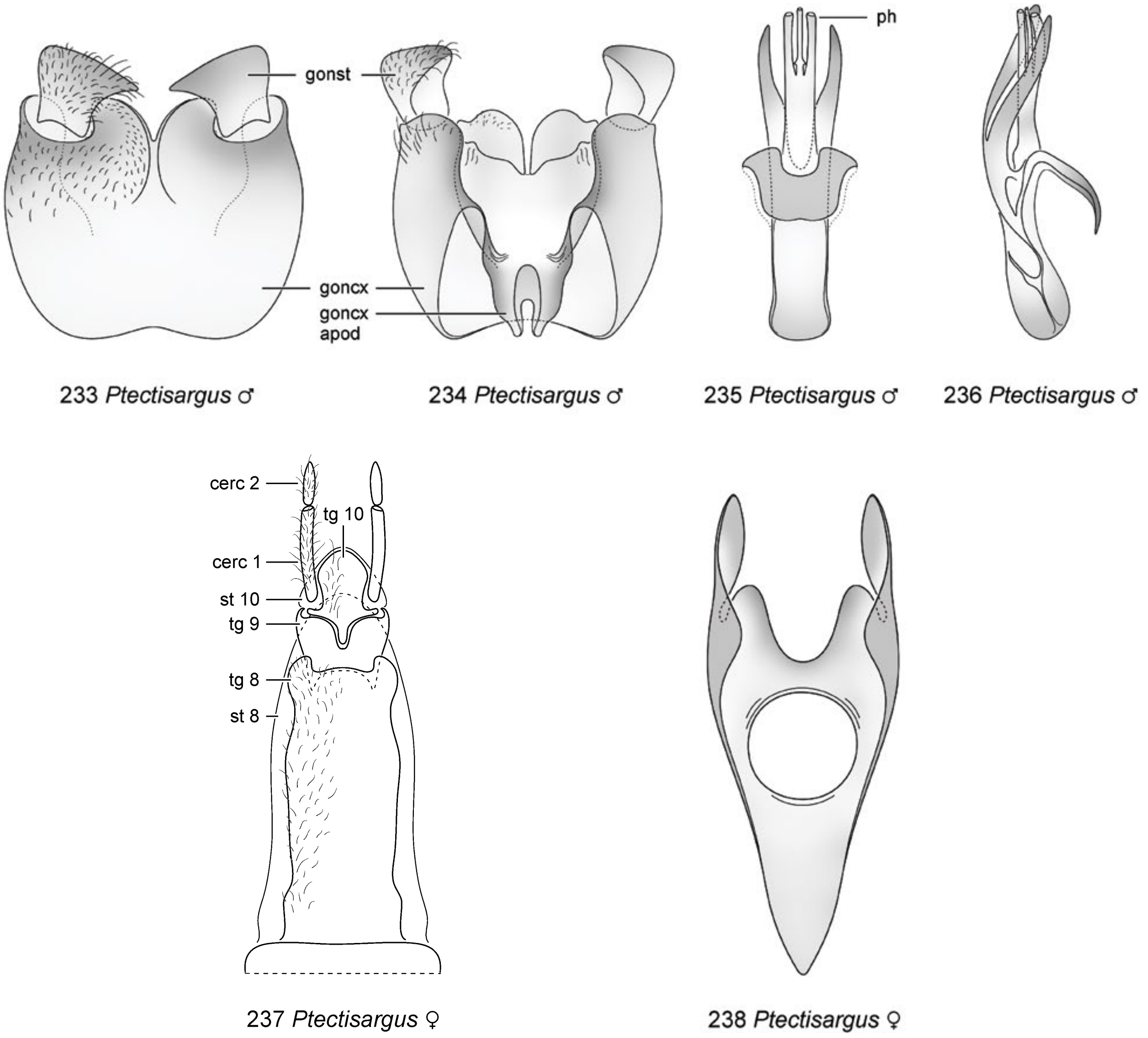
Figs 41.227–232. Wings of Stratiomyidae (dorsal views): (227) *Zabrachia madagascariensis* Lindner ♀; (228) *Zulumyia expansa* James ♀; (229) Undescribed genus A ♂; (230) Undescribed genus B ♀; (231) Undescribed genus C ♀; (232) Undescribed genus D ♀.

Abbreviations: M_1 – first branch of media; M_2 – second branch of media; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; r_1 – first radial cell; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein.

(Lindner, 1938) is only know from the male holotype from Democratic Republic of Congo. This genus is very similar to *Ageiton*, *Argyrobrithes*, *Cardopomyia* and *Diademophora* sharing a similar body shape and a very similar wing venation. The terminal flagellomere is invariably white, in contrast to most other related genera (Figs 94, 121, 145). The larvae of *Sternobrithes tumidus* Loew, 1856 occur in humus at the bases of young *Raphia hookeri* G. Mann & H. Wendl. (as *Raphia gigantea* A. Chev.) (Palmaceae) in Côte d'Ivoire (Lachaise & Lindner, 1973). No identification key to Afrotropical species is currently available.

***Stuckenbergiola* Lindner** (Stratiomyinae: Oxycerini)**.** An endemic monotypic genus, with the single species, *S. jugorum* Lindner, 1965 (Fig. 95), recorded from Lesotho and South Africa. Known collection localities are above 2,000 m elevation. This genus is larger than *Oxycera* and has longer, denser setae covering the body. Biology and immature stages of the species remain unknown.

***Thorasena* Macquart** (Pachygastrinae)**.** An endemic genus of two described species, *T. pectoralis* (Wiedemann, 1824) from Bioko Is. (Equatorial Guinea), Cameroon, Côte d'Ivoire,



233 *Ptectisargus* ♂ 234 *Ptectisargus* ♂ 235 *Ptectisargus* ♂ 236 *Ptectisargus* ♂

237 *Ptectisargus* ♀ 238 *Ptectisargus* ♀

Figs 41.233–238. Male and female terminalia of Stratiomyidae: (233) male terminalia of *Ptectisargus abditus* (Lindner), ventral view ♂; (234) same, dorsal view; (235) same, phallic complex, dorsal view ♂; (236) same, lateral view ♂; (237) same, female terminalia (last tergite), dorsal view; (238) same, genital fork, dorsal view.

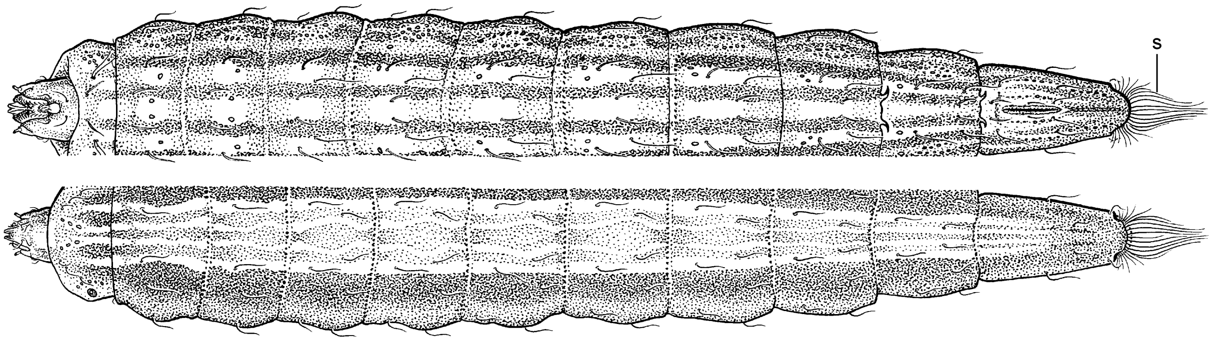
Abbreviations: cerc – cercus; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; ph – phallus; st – sternite; tg – tergite.

Democratic Republic of Congo, Guinea and Nigeria and *T. fenestrata* (James, 1949), from Democratic Republic of Congo, Kenya, Liberia, Namibia, South Africa and Zimbabwe. One undescribed species from Kenya has been examined. *Thorasena* are blackish flies (Fig. 96) that sometimes have a translucent second abdominal tergite (Fig. 96) and long antenna (Fig. 146), so they likely resemble wasps in flight. The biology and immature stages remain unknown. No identification key to species is currently available. Woodley (2010) discussed the taxonomy of *T. fenestrata*, the most common and widespread species.

239 Pachygastrinae

240 Pachygastrinae

241 *Hermetia*



242 *Odontomyia*

Figs 41.239–242. Larval habitus of Stratiomyidae: (239) Pachygastrinae sp. (non-Afrotropical); (240) same; (241) *Hermetia* sp. (242) *Odontomyia* sp., ventral view (above), dorsal view (below) (non-Afrotropical). Figs 239–241 (photograph © M. Bertone), Fig. 242 (James 1981, figs 74, 75).

Abbreviation: s – setae

***Tinda* Walker** (Pachygastrinae)**.** A genus of seven described species, occurring in the Afrotropical, Australasian and Oriental Regions, with five species in the Afrotropics (Figs 97, 147, 226), most of which occur in West Africa, but some are very widely distributed, covering more than one zoogeographical region. Some species are recorded from the Indian oceanic islands of Réunion Is. (France) and Seychelles. A modern revision is required in order to test species concepts. The species in the genus have long antennae with a laterally flattened antennal arista. They are invariably dark black with the wings bent, likely to mimic beetles. The biology and immature stages remain unknown. No identification key to Afrotropical species is currently available.

***Tindacera* Lindner** (Pachygastrinae)**.** An endemic monotypic genus, with the single species, *T. quadrispinosa* Lindner, 1961, described from South Africa. No material of this genus was studied in preparation of this chapter. The biology and immature stages remain unknown.

Undescribed genus A (Pachygastrinae)**.** A genus represented by one species and specimen from Kenya. It is characterised by setulose eyes and a downward-pointed face (Figs 122, 229). The biology and immature stages of the species remain unknown.

Undescribed genus B (Clitellariinae)**.** A genus represented by two undescribed species from South Africa. These are medium-sized, brownish to black species, with the antennae longer than the head, the terminal flagellomere elongate (Fig. 100) and wing vein R_4 absent (Fig. 230). The biology and immature stages remain unknown.

Undescribed genus C (Clitellariinae)**.** A genus represented by two undescribed species from South Africa, which are very similar in habitus to Undescribed genus B (noted above). The species differ, however, in the structure of the antenna (Fig. 101), wing venation (Fig. 231) and size of the scutellar spines. The biology and immature stages remain unknown.

Undescribed genus D (Clitellariinae)**.** A new genus needs to be erected for *Ampsalis dichromatica* James, 1975, which is clearly not congeneric with other Malagasy species ascribed to the genus. James (1975) noted clear differences between the two species of the genus, but retained both in *Ampsalis*. There are at least three additional undescribed species that belong here from Madagascar. Species range in colour from entirely yellow (Fig. 102) to black with brown or entirely black species and often have a distinct white margin at the wing apex (Fig. 232). The biology and immature stages remain unknown.

***Zabrachia* Coquillett** (Pachygastrinae)**.** A genus of 22 described species occurring in all zoogeographical regions, except Australasia and Antarctica. *Zabrachia* are mostly small, non-descript species (Fig. 98) that lack wing vein R_4 (Fig. 227), but it remains unclear whether all species of the genus are congeneric with the Nearctic type species *Z. polita* Coquillett, 1901. The Afrotropical fauna is represented by the single species, *Z. madagascariensis* Lindner, 1959 (Figs 98, 227), which is endemic to Madagascar. Rozkošný (1983) summarised what is known regarding the larvae of European species. No identification key to Afrotropical species is currently available.

***Zulumyia* Lindner** (Stratiomyinae: Stratiomyini)**.** A distinctive endemic genus of three described species: *Z. dissimilis* (Brunetti, 1926), from Kenya, Malawi South Africa and Zimbabwe; *Z. expansa* James, 1957 (Figs 99, 148, 228), from Mozambique and Zimbabwe; and *Z. signifera* James, 1957, from Uganda. *Zulumyia* are mostly dark in colouration with infuscate wings (Figs 99, 148, 228). At least one additional undescribed species is known from South Africa (Fig. 4). The biology and immature stages remain unknown. James (1957) provided an identification key to the three described species.

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ACROCERIDAE 42

(Small-headed Flies or Spider Flies)

Shaun L. Winterton and David A. Barraclough

Fig. 42.1. Copulating pair of *Psilodera hessei* Schlinger (South Africa) (photograph © S.A. Marshall).

Diagnosis

The family Acroceridae can be diagnosed as follows (based on Schlinger 2009: 552, with amendments):

Small- to large-sized flies (body length: 3–20 mm), compound eyes large and holoptic in both sexes. Body shape typically robust, relatively varied in shape and size among subfamilies: distinctively hump-backed in Philopotinae (Fig. 2), while Acrocerinae (Fig. 1) and Panopinae (Fig. 14) usually possess a large pilose thorax and globose abdomen. Body colouration usually dark brown or black; sometimes bright metallic green, blue or purple; some species with contrasting yellow, white and black markings.

Head rounded; holoptic in both sexes, disproportionately smaller than rest of body in some genera; mouthparts with shape variable, ranging from absent to greatly elongate (sometimes longer than body), when elongate then labellum often bifid; palpus present or absent; antenna 3-segmented, styliform, or elongate and cylindrical, in which case sometimes laterally flattened.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 981–993.

Thorax robust; pile variable, ranging from absent, to dense and erect; macrosetae absent; postpronotal lobes sometimes greatly enlarged, meeting medially in Philopotinae. Wing hyaline, or sometimes infuscate, typically with regular corrugation of membrane; venation complete to wing margin (Fig. 22), or reduced to varying degrees; when complete, then wing cell r_{4+5} typically subdivided by crossvein *r–m2* and cell m_3 closed; in all acrocerid wings, when venation is reduced posteriorly and distally, then invariably with concomitant strengthening of anterior and basal veins; calypter very large. Legs with tibia sometimes with 1 (rarely multiple) apical spine-like process; apical tarsomere with fleshy, pulvilliform empodium and large claws.

Abdomen with pile frequently dense and erect, sometimes very short and sparse; male terminalia relatively simple in form, rotated 180° to 360° on axis (*e.g.*, Figs 23–27); epandrium with well-developed cercus; gonocoxites robust, completely or partially fused with gonostylus; phallus elongate; parameral sheath entirely enclosing endophallus; gonopore typically subterminal; ejaculatory apodeme poorly-developed; female terminalia relatively simple in structure, typically apical on abdomen, rarely migrated anteriorly (along ventral surface) towards base of abdomen in non-Afrotropical species (*e.g.*, *Rhysogaster* Aldrich).

Larva (Fig. 28) hypermetamorphic between instars; first-instar minute (< 1.0 mm), free-living planidium, comprising cephalic region, 3-segmented thorax and 9-segmented abdomen (segments poorly defined in *Acrocera* Meigen); first-instar larva metapneustic, later instars amphipneustic with prothoracic spiracles apparently non-functional (Nartshuk 1997: 469). Thorax and abdomen typically with elongate setae in rows on each segment (lacking in *Acrocera*). Later instars endoparasitoids, with white rounded body and creeping welts ventrally. Last instar larva (Fig. 28) emerges from host to pupate. Prepupa and pupa white, turning brown prior to adult eclosion. Pupa


2 *Africaterphis* 3 *Dimacrocolus* 4 *Thyllis*


5 *Thyllis* 6 *Sabroskya* 7 *Ogcodes*

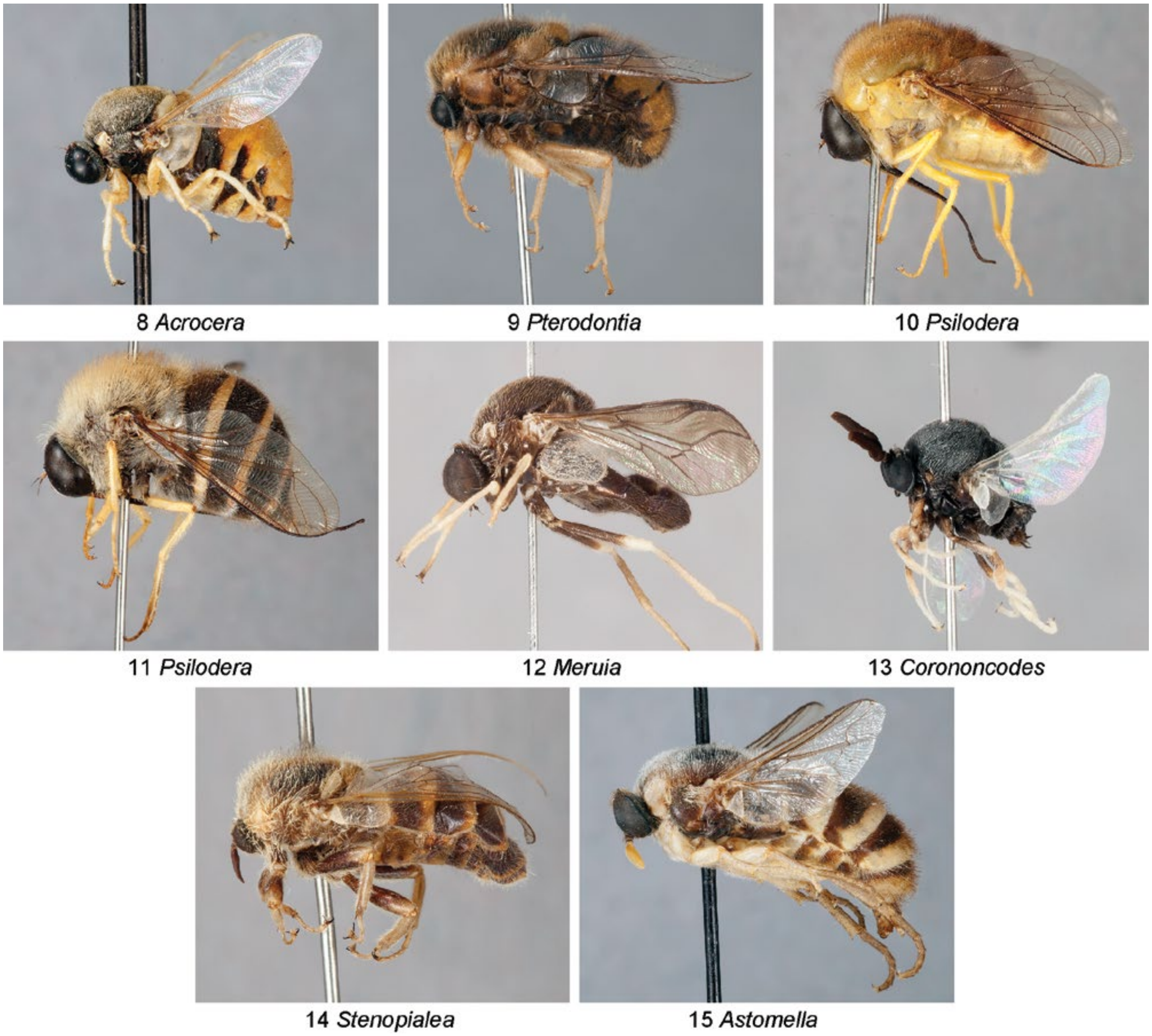
Figs 42.2–7. Habitus of Acroceridae (lateral views): (2) *Africaterphis acroceroides* Sabrosky ♂; (3) *Dimacrocolus pauliani* Schlinger ♂; (4) *Thyllis* sp. ♀; (5) *Thyllis splendens* Brunetti ♂; (6) *Sabroskya schlingeri* Winterton & Gillung ♂; (7) *Ogcodes* sp. ♂. Photographs S.L. Winterton.

(Fig. 29) often with rows of processes on head to adhere to silken moulting bed spun by host.

A morphologically diverse group, particularly within the three subfamilies, but characteristics, such as the distinctively enlarged calypter, pulvilliform mediolobus of the empodium and lack of macrosetae on the body, readily distinguish Acroceridae from all other Diptera. Morphological convergence is frequent among flies exhibiting wasp mimicry, especially in parasitoid groups. Some genera of Bombyliidae (see Chapter 45) superficially resemble acrocerids, but the empodium is setiform (with mediolobus absent) and wing cell r_{4+5} is never bisected by crossvein *r–m2*. Some Nemestrinidae (see Chapter 43) are also similar to acrocerids, but have highly distinctive wing venation. Many calyptrate flies have enlarged calypteres, but are easily differentiated based on wing venation and absence of a mediolobus, along with the presence of macrosetae on the thorax and abdomen, which are absent in Acroceridae.

Biology and immature stages

Acrocerid larvae are specialised parasitoids of spiders, in almost all cases as endoparasitoids. Records of acrocerids parasitising Acari are rare and are known for both extant (Sferra 1986) and extinct taxa (Kerr & Winterton 2008), although none


8 *Acrocera*
9 *Pterodontia*
10 *Psilodera*
11 *Psilodera*
12 *Meruia*
13 *Corononcodes*
14 *Stenopialea*
15 *Astomella*

Figs 42.8–15. Habitus of Acroceridae (lateral views): (8) *Acrocera* sp. ♂; (9) *Pterodontia mellii* Erichson ♀; (10) *Psilodera affinis* Westwood ♂; (11) *Psilodera confusa* Schlinger ♂; (12) *Meruia somereni* Sabrosky ♀; (13) *Corononcodes* sp. ♂; (14) *Stenopialea primitiva* Schlinger ♀; (15) *Astomella* sp. ♀. Photographs S.L. Winterton.

have been reared from living examples to confirm or identify the acrocerid species in question. Adult females oviposit large numbers of microtype eggs, either on branches and foliage, or the eggs are scattered during flight (Schlinger 1987: 322).

The first-instar is a free-living planidium, which actively seeks out a spider host by crawling, looping or jumping, with the aid of well-developed setae, spines and a caudal suction disk (Nartshuk 1997: 470). First-instars of *Acrocera* are distinct from other Acroceridae in lacking setal pile and having the abdomen with numerous annulations obscuring the regular segmentation (Overgaard Nielsen *et al*. 1999; Schlinger 1981: 580).

Most host records for Acroceridae involve rearing of mature larvae from infested spiders (reviewed in Schlinger 1987, table 24), but observations of infestation of the host by the planidium stage are rare. Previous summaries of acrocerid life histories by Schlinger (1981: 580, 1987: 324) and Nartshuk (1997: 470) state that the planidium enters the spider directly through the cuticle of the cephalothorax, opisthosoma, or leg joint, but these appear to have not been verified by direct observations. More recently, Overgaard Nielsen *et al*. (1999) described the novel mechanism of self-injection of *Acrocera orbicula* (F., 1787) into a wolf spider, in which first-instars attach externally to the cuticle by cutting a hole in the integument, but do not enter the host. During the following seven days it is presumed that the attached first-instar larva feeds directly on the host hemolymph. During subsequent moulting the endoparasitic second-instar is injected directly into the spider *via* the junction of the oral cavity and leg wound, leaving the exuviae of the ectoparasitic first-instar intact and covering the site of infection. It is possible that this is the mechanism for infection by many or all spider flies, but is yet to be observed in other species. All larvae eventually locate in the opisthosoma and attach to the book lung *via* the posterior spiracle for respiration (Nartshuk 1997: 471; Schlinger 1981: 580, 1987: 324). Schlinger (1987: 580) proposed that once attached the larva may enter a state of diapause for several months (Acrocerinae) up to 10 years (Panopinae) and upon cessation of diapause the actively feeding larva completes its life cycle relatively quickly (days to weeks), undergoing up to four instars. There is limited direct observational evidence to support these hypotheses of diapause and instar number (the typical number being three) and there is a need for further study. It has also been suggested that acrocerid larvae only infect juvenile spiders (Schlinger 1987: 580; Winterton *et al*. 2007), but it is likely that all life stages are susceptible to infection, as several authors have recorded rearings from adult spiders (*e.g*., Eickstedt 1971; Montgomery 1903).

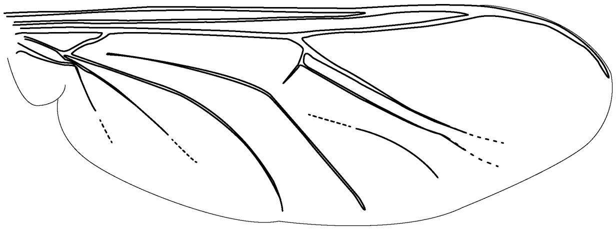
Most spider hosts exhibit no obvious external indication of parasitism, although Barraclough & Croucamp (1997) reported an example where the host abdomen was noticeably enlarged when parasitised by a larva of *Ogcodes* Latreille. It has been repeatedly reported that the host will display some confused and/or agitated behaviour during the final stages of parasitism and that emergence of the parasitoid corresponds with the premoulting behaviour of the spider (spinning of a substrate premoulting web) (*e.g*., Barneche *et al*. 2012; Barraclough & Croucamp 1997; Cady *et al*. 1993). A causative relationship between the production of the premoulting web and parasite emergence can only be speculative at this time, but the presence of the hook-like processes on the head and/or abdomen of the spider fly, which are used to attach to the web, suggest that this is not coincidental. The last instar acrocerid larva typically only kills the host shortly prior to emergence, when it consumes the entire contents of the host body, leaving an empty, unbroken exoskeleton (Nartshuk 1997: 476).

While super-parasitism is common in early instars, usually only a single acrocerid adult ultimately emerges from its host (Cady *et al*. 1993; Overgaard Nielsen *et al*. 1999). Multiple emergences of larvae from a single host are more likely found in Panopinae, which attack large Mygalomorphae spiders capable of sustaining multiple individuals (Schlinger 1987: 326). The only exception to the exclusive endoparasitic mode in Acroceridae is found in the Chilean genus *Carvalhoa* Koçak & Kemal (= *Sphaerops* Philippi), which is reported to remain ectoparasitic on its host spider for at least three weeks (Schlinger 1987: 326). It is unknown if the entire life cycle is spent as an ectoparasite, but Schlinger (1987: 326) reports this ectoparasitic behaviour in multiple rearings of later instars.

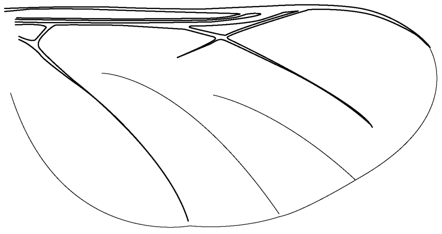
Host records for acrocerids parasitising spiders are known for at least 60 species, recorded from *ca* 25 spider families (Schlinger 2003: 736). Schlinger (1987, table 24) presented an extensive list of spider taxa parasitised by acrocerids, while Winterton *et al*. (2007) mapped host use onto a phylogeny of the family based on molecular data. These studies clearly demonstrate that Panopinae are host-specific to Mygalomorphae spiders, while Acrocerinae and Philopotinae are host-specific to Aranaeomorphae spiders. Only the genera *Acrocera* and *Carvalhoa* have been reared from Haplogynae spiders, while Philopotinae and all remaining Acrocerinae, have only been reared from Entelegynae. The virtually cosmopolitan genera (*Acrocera*, *Ogcodes* and *Pterodontia* Gray) have been reared from numerous hosts in multiple spider families, while most geographically restricted and species-poor genera tend to be more host-specific, generally within a single spider family (Schlinger 1987: 326). The pattern of host use in Acroceridae is not highly specific, even at the familial level, but certain trends are apparent and host preference generally follows spider guilds (Cady *et al*. 1993). The spider guild most susceptible to parasitism by Acroceridae includes those families in which the spiders are cursorial, or occupy sac, tangle, or funnel-like web retreats (Cady *et al*. 1993; Overgaard Nielsen *et al*. 1999). Very few records exist of acrocerids parasitising true web-dwelling spiders and exceptions typically involve tangle-web spiders (*e.g*., Theridiidae), where the spider may still be proximal to the substrate.

Economic significance

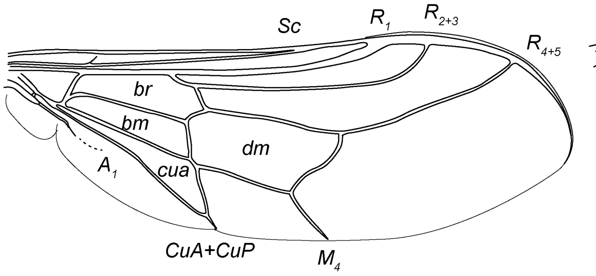
Acroceridae have limited economic significance, although adults of some species are known to be important pollinators in ecological systems. In the Nearctic Region the genus *Eulonchus* Gerstaecker is a frequent pollinator and has been found carrying large pollen loads (Borkent & Schlinger 2008; Cole 1919). In the Neotropical Region, *Holops* Philippi, *Lasia* Wiedemann, *Megalybus* Philippi and *Philopota* Wiedemann are known as pollinators of various plant species, including Orchidaceae, with pollinia recorded on some flies (Carvalho & Machado 2006; Stuardo Oritz 1980). In the Afrotropical Region, studies by Goldblatt *et al*. (1997) and Potgieter *et al*. (1999, 2007) on the southern African fauna have examined in detail the pollination efficacy of *Psilodera* Gray on Lamiaceae



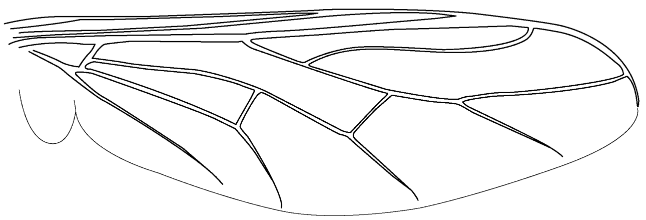
16 *Ogcodes*



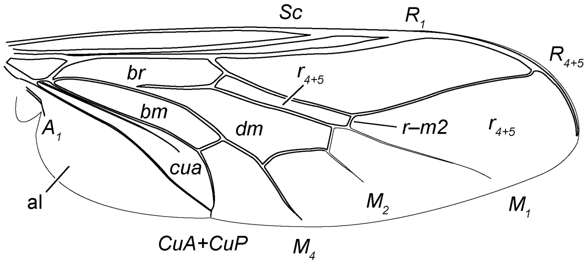
17 *Corononcodes*



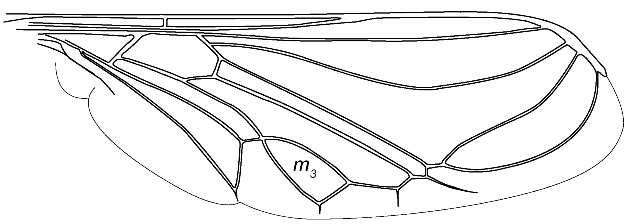
18 *Pterodontia*



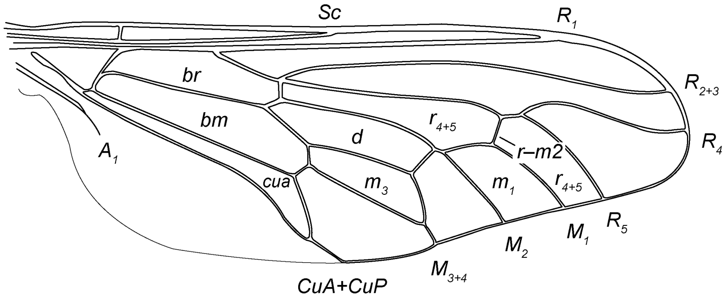
19 *Acrocera*



20 *Sabroskya*



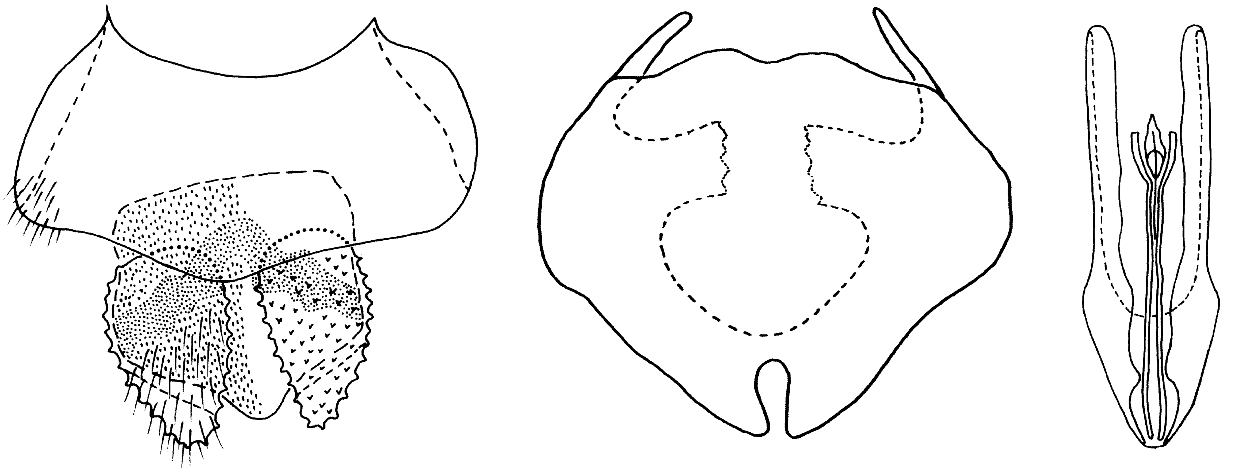
21 *Psilodera*



22 *Stenopialea*

Figs 42.16–22. Wings of Acroceridae (dorsal views): (16) *Ogcodes* sp. ♂; (17) *Corononcodes* sp. ♂; (18) *Pterodontia davisi* Paramonov ♀ (non-Afrotropical); (19) *Acrocera* sp. ♂; (20) *Sabroskya schlingeri* Winterton & Gillung ♂; (21) *Psilodera* sp. ♂; (22) *Stenopialea primitiva* Schlinger ♀.

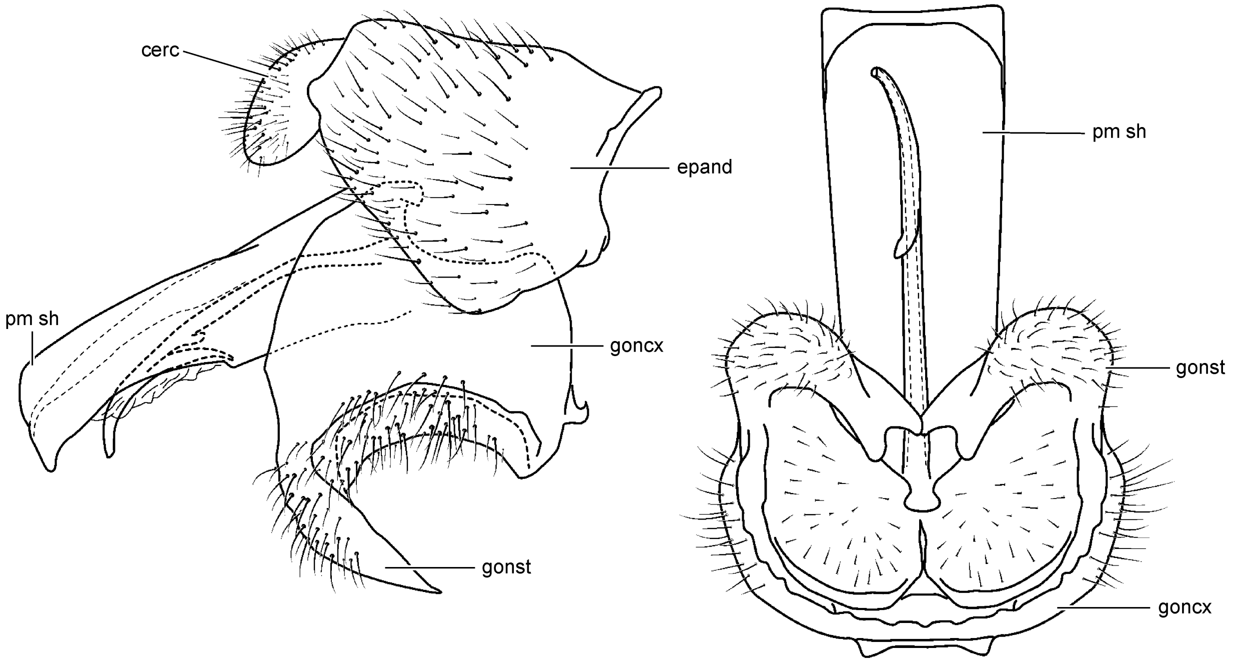
Abbreviations: A_1 – first branch of anal vein; al – alula; *bm* – basal medial cell; *br* – basal radial cell; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *d* – discal cell; *dm* – discal medial cell; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_3 – third medial cell; M_{3+4} – fused third and fourth branches of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; r_{4+5} – fourth + fifth radial cell; R_5 – lower branch of third branch of radius; *r–m2* – second radial–medial crossvein; *Sc* – subcostal vein.



23 *Africaterphis* ♂

24 *Africaterphis* ♂

25 *Africaterphis* ♂



26 *Panops* ♂

27 *Panops* ♂

Figs 42.23–27. Male terminalia of Acroceridae: (23) epandrium and postgenital segments of *Africaterphis acroceroides* (Sabrosky), dorsal view; (24) same, gonocoxites, ventral view; (25) same, phallus, dorsal view (26) terminalia, *Panops baudini* Lamarck, (non-Afrotropical), lateral view; (27) same, ventral view. Figs 23–25 (courtesy J. Gillung), Figs 26, 27 (after Winterton 2012, fig. 17).

Abbreviations: cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; pm sh – parameral sheath.

and Iridaceae. Potgieter (2009) found that six species of *Plectranthus* (Lamiaceae) were solely or partly reliant on pollination by *Psilodera*. That said, while adult acrocerids are frequent components of pollinator guilds in various ecosystems, their relative primacy as requisite pollinators remain uncertain and requires additional research.

Classification

Acroceridae are an enigmatic group of parasitoid flies in the lower Brachycera, the phylogenetic position of which is yet to be determined with any certainty. Traditionally, spider flies have been placed with Nemestrinidae in Nemestrinoidea, based on a shared larval parasitoid life history (Woodley 1989: 1383), but subsequent quantitative phylogenetic analyses of both morphology and DNA sequences have not recovered the superfamily as monophyletic (Wiegmann *et al*. 2003, 2011; Yeates 2002). Moreover, acrocerids have been placed in these analyses as sister to non-Afrotropical Hilarimorphidae, or more commonly as sister to the remaining Muscomorpha, exclusive of Nemestrinidae.

The monophyly of Acroceridae is well-established and is based on synapomorphic characters, such as the antennal flagellum being composed of a single flagellomere; enlarged lower calypter; and obligate endoparasitoid life history on spiders (Woodley 1989: 1383; Yeates 2002). The bisection of wing cell r_{4+5} by crossvein *r–m2* is an apparent synapomorphy for the family, but is lost in taxa where the wing venation is reduced (Winterton 2012). Three subfamilies are recognised: Acrocerinae, Philopotinae and Panopinae (Schlinger 1987: 320). Panopinae were considered by Schlinger (1987: 326) as the sister to the remaining Acroceridae, but phylogenetic analysis of molecular data by Winterton *et al*. (2007) found that Acrocerinae were rendered paraphyletic relative to Philopotinae and Panopinae, and that Panopinae were recovered in a more derived position.

Acrocerinae are typically small- to medium-sized flies with a large thorax, globose abdomen and a relatively small, rounded head. The subfamily is the most species-rich globally and comprises 236 extant and extinct (fossil) species in 23 genera. Yet only a small proportion of the acrocerine fauna is represented in the Afrotropics, with only 38 species in six genera (Barraclough 1984; Schlinger 1960*a*, *b*; Winterton & Gillung 2012). *Meruia* Sabrosky, *Psilodera* and *Sabroskya* Schlinger are endemic to the region, while *Acrocera*, *Ogcodes* and *Pterodontia* are more widely distributed. Synapomorphies for Acrocerinae are lacking, but certain characteristics in combination readily separate the subfamily from Philopotinae and Panopinae, including: antennae styliform; tibial spines absent (both shared with Philopotinae); postpronotal lobes widely separated (shared with Panopinae); and wing humeral crossvein frequently reduced (Winterton & Gillung 2012). *Pterodontia* has tibial spines similar to those found in Panopinae, but this was shown to have been acquired through convergence by Winterton *et al*. (2007). In their phylogenetic analysis based on molecular data, Winterton *et al*. (2007) showed that *Acrocera* formed a sister-group relationship with the South American genus *Carvalhoa* in a clade sister to the remainder of the family. The remaining Acrocerinae formed a paraphyletic grade sister to Panopinae. Genera such as *Pterodontia* and *Ogcodes* are some of the most derived Acrocerinae. It is estimated that the clade comprising *Acrocera* and *Carvalhoa* diverged from the remaining Acroceridae during the Early Jurassic (*ca* 200 MYA), with the remaining stem Acrocerinae diverging from Philopotinae and subsequently from Panopinae during the Late Jurassic (*ca* 150 MYA) and Early Cretaceous (*ca* 135 MYA) (Winterton *et al*. 2007).

The oldest fossil Acroceridae are known from Late Jurassic deposits (*e.g*., *Archocyrtus gibbosus* Ussatchev, 1968 and *Juracyrtus kovlevi* Nartshuk, 1996; both Acrocerinae), and Grimaldi *et al*. (2011) suggested that the divergence age estimates for the family and much of the internal hierarchy based on molecular data may be overestimated. Fossil Acrocerinae


28 *Exetasis*

29 *Exetasis*

Figs 42.28–29. Immature stages of Acroceridae: (28) last instar (post emergence from host) of *Exetasis jujuyensis* Gillung (non-Afrotropical); (29) same, pupa. Figs 28, 29 (after Barneche *et al*. 2012, figs 7, 8).

are also known from much younger Baltic (*ca* 45 MYA) (*e.g.*, *Glaesoncodes completinervis* Hennig, 1968, *Villalites electrica* Hennig, 1966) and Dominican (*ca* 20 MYA) amber deposits (*Ogcodes exotica* Grimaldi, 1995). Grimaldi *et al*. (2011) recently described *Schlingeromyia minuta* Grimaldi & Hauser, 2011, from Cretaceous-aged amber deposits, but left it *incertae sedis* within Acroceridae. Placement in Acrocerinae seems appropriate based on a series of characters, including the relatively complete wing venation, with veins reaching the wing margin, presence of cell m_3, the apparent widely separated postpronotal lobes and a body shape that is not particularly arched. None of these characters are present in philopotines and the absence of tibial spines preclude placement in Panopinae. Relationships among most of the genera of this subfamily are still poorly understood and are in need of further quantitative study.

Philoptinae are very small- to medium-sized flies with characteristically arched bodies, in some cases extremely so, such that the head is close to the tip of the abdomen in certain species of *Thyllis* Erichson. Currently, there are 65 extant and fossil species in 15 genera globally, with 16 species in four genera recorded from the Afrotropics (Gillung & Winterton 2011; Schlinger 1960*b*). Monophyly of Philopotinae is strongly supported, with all species being highly distinctive, with a characteristic arched body shape and postpronotal lobes enlarged and meeting medially to form a collar behind the head. Other characters that define this subfamily include antennal flagellum styliform, tibial spines always absent, wing costal vein margin ending apically in the radial field, and cell m_3 absent. Gillung & Winterton (2011) distinguished two morphological groups of Philopotinae differentiated based on the relative complement of wing veins and closed cells. In the Afrotropical Region both types are found, with *Dimacrocolus* Schlinger, *Parahelle* Schlinger and *Thyllis* being representatives of the group with relatively complete wing venation, while *Africaterphis* Schlinger is the only representative of the group with greatly reduced wing venation. Winterton *et al*. (2007) estimated the age of this group at 153 MYA during the Late Jurassic. *Dimacrocolus*, *Parahelle* and *Thyllis* form a close group of relatively derived genera in southern Africa and Madagascar, originating during the Early–Mid Cretaceous. The reduced wing venation of *Africaterphis* indicates clear affinities with Palaearctic genera, both extant (*Oligoneura* Bigot) and extinct (*e.g.*, *Prophilopota* Hennig). Numerous fossil philopotines are known from Baltic Amber (including some undescribed species), but from no other deposits. Philopotinae already described from these amber deposits include *Eulonchiella eocenia* Meunier, 1912, *Archaeterphis* Hauser & Winterton and *Prophilopota* (Gillung & Winterton 2011; Hauser & Winterton 2007; Hennig 1966).

Panopinae display a large range of body size, ranging from very small species of *Corononcodes* Speiser, to very large species of *Exetasis* Walker and *Lasia*. Adults are typically large, robust flies, with a very large and pilose thorax and abdomen. The length of the mouthparts may vary considerably, ranging from highly reduced or absent, to much longer than the body. Synapomorphies defining Panopinae include: elongate antennal flagellum (longer than head length) that is tapered, cylindrical to paddle-shaped, never stylate; wing venation typically complete with cells m_3, *d*, *bm* and basal r_{4+5} present (reduced in *Corononcodes* only); and tibial spines present (reduced in *Corononcodes* and absent in *Apsona* Westwood) (Winterton 2012). Panopinae are relatively species-rich in many parts of the world, with 121 species in 22 genera, yet with only 16 species in three genera recorded from the Afrotropics. Only one genus (*Stenopialea* Speiser) is endemic to the Afrotropical Region and although *Astomella* Latreille and *Corononcodes* are well-represented, they also have species in the western Palaearctic. There is a strong tendency for reduction in wing venation in more derived genera in all subfamilies but this phenomenon is least developed in Panopinae, although *Corononcodes* exhibits extreme reduction in wing venation, presumably associated with the small body size of many species of this genus. All other genera display remarkably conserved and relatively plesiomorphic wing venation, with all wing cells and veins largely present and exhibiting few dramatic modifications in size and shape across the group. Schlinger (1987: 326, 2003: 736) hypothesised that Panopinae were the "primitive" basal subfamily of Acroceridae, largely based on the retention of several plesiomorphic morphological character states and the specificity of this group as parasitoids on the relatively "primitive" Mygalomorphae spiders. A phylogenetic analysis of DNA sequence data by Winterton *et al*. (2007) found the opposite to be the case, with Panopinae recovered as a derived clade, diverging from acrocerine lineages during the Early Cretaceous. Surprisingly, no fossils are known for this subfamily.

Identification

There is currently no complete key to world genera of Acroceridae. Recent regional keys are available for the genera of acrocerids of Australasia (Winterton 2012), Brazil (Gillung & Carvalho 2009), the Neotropical (Schlinger 2009: 553; Schlinger *et al*. 2013) and Palaearctic Regions (Nartshuk 1997: 478). Taxon-based keys to extinct and extant world genera are available for Philopotinae (Gillung & Winterton 2011) and Acrocerinae (Winterton & Gillung 2012). Barraclough (2000) provided a key to Namibian Acroceridae. Older keys are available in Schlinger (1960*a*, 1961). Acroceridae are best micro-pinned in the field for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Acroceridae

1. Thorax with postpronotal lobes greatly enlarged, meeting, or virtually meeting, along midline to form collar for head; body shape greatly arched (*e.g.*, Figs 2–5) (PHILOPOTINAE) 3

– Thorax with postpronotal lobes not greatly enlarged, separate along midline; body rarely arched (*e.g.*, Figs 6–15) 2

2. Antenna styliform, usually with terminal setae; tibiae without apical spines (except *Pterodontia*) (*e.g.*, Figs 6–12) (ACROCERINAE) 6

– Antenna with elongate flagellum, cylindrical or flattened, without terminal seta; tibiae with apical spines (reduced in *Corononcodes*) (e.g., Figs 13–15) (PANOPINAE). 11

3. Wing venation reduced, presenting only 1 or 2 branches of vein *M* and only 1 basal cell (*br*) (East, Central and southern Africa). . . . . *Africaterphis* Schlinger

– Wing venation relatively complete with all branches of vein *M* and also discal (*d*) and r_{4+5} cells (widely distributed) 4

4. Palpus present; legs very long; male wing with tufted projection at base of costal vein (*C*) (Madagascar) . . . . *Dimacrocolus* Schlinger

– Palpus absent; legs of regular length; male wing without tufted projection at base of costal vein (*C*) (Madagascar and southern Africa) 5

5. Eyes clearly pilose (southern Africa and Madagascar) . . . . *Thyllis* Erichson

– Eyes very sparsely pilose (setae barely visible) or bare (Madagascar) . . . . *Parahelle* Schlinger

6. Mouthparts greatly elongate, often as long as or longer than, body (Figs 1, 10, 11); wing cell m_3 present (Fig. 21) (southern Africa). . . . . *Psilodera* Gray

– Mouthparts reduced in length, shorter than head length (e.g., Figs 6–9, 12); wing cell m_3 absent (widely distributed) 7

7. Antenna inserted on upper ½ of head, usually proximal to antennal tubercle (Fig. 8) (widely distributed, except Australia) . . . . *Acrocera* Meigen

– Antenna inserted on lower ½ of head, adjacent to mouthparts (widely distributed) (e.g., Figs 6, 7, 9, 12). 8

8. Thorax with antepronotum produced anteriorly as collar-like process behind head (e.g., Figs 6, 12); wing cell *dm* and proximal cell r_{4+5} separate (e.g., Fig. 20) 9

– Thorax with antepronotum not forming collar-like process behind head (e.g., Figs 7, 9); wing cell *dm* and proximal cell r_{4+5} fused to form large single cell (e.g., Fig. 18), or cells absent (e.g., Fig. 16) 10

9. Thorax greatly enlarged dorsally (less developed in female) (Fig. 12); wing veins R_{2+3} and R_{4+5} curved anteriorly, then reflexed towards wing apex; vein M_2 reaching wing margin; alula absent (Fig. 12) (Kenya) . . . . *Meruia* Sabrosky

– Thorax rounded, but not greatly enlarged; wing veins R_{2+3} (when present) and R_{4+5} straight to curved slightly; vein M_2 not reaching wing margin; alula present (Fig. 20) (southern Africa) . . . . . . *Sabroskya* Schlinger

10. Mouthparts present; wing with 5 closed cells (*i.e.*, non-marginal); most wing veins reaching wing margin (Fig. 18); tibial spines present (virtually cosmopolitan) . . . . *Pterodontia* Gray

– Mouthparts absent; wing with 1 or 2 cells present, most cells lost due to reduction in number of wing veins; veins rarely reaching wing margin (Fig. 16); tibial spines absent (virtually cosmopolitan) . . . . *Ogcodes* Latreille

11. Wing venation greatly reduced (Fig. 17) (throughout Africa and Mediterranean province) . . . . *Corononcodes* Speiser

– Wing venation not reduced, most veins and cells present (e.g., Fig. 22) (Afrotropical and Palaearctic Regions). 12

12. Antenna inserted on lower ½ of head (Fig. 15); wing with costal vein (*C*) ending in radial field; vein R_{4+5} not forked; only 2 medial veins present, neither reaching wing margin (Afrotropical and Palaearctic Regions). . . . . *Astomella* Latreille

– Antenna inserted on upper ½ of head (Fig. 14); wing with costal vein (*C*) ending at vein *CuA+CuP*; vein R_{4+5} forked; 3 medial veins reaching wing margin (Fig. 22) (southern Africa). . . . . . *Stenopialea* Speiser

Synopsis of the fauna

Currently, 422 species of both extinct and extant Acroceridae are placed in 58 genera, divided into three subfamilies. All three subfamilies are represented in the Afrotropical Region, with 65 species described in 13 genera, eight of which are endemic. Modern revisions are required for genera such as *Acrocera*, *Ogcodes*, *Psilodera* and *Thyllis*.

***Acrocera* Meigen** (Acrocerinae) (Figs 8, 19)**.** A virtually cosmopolitan genus of 53 described species, recorded from all major zoogeographical regions, except notably absent from Australasia. *Acrocera* is the second-most species-rich genus of Acroceridae globally. Eight species are described from the Afrotropics, all from southern Africa (Barraclough 1984; Sabrosky 1950; Schlinger 1960*a*). *Acrocera* is easily diagnosed based on the stylate antenna positioned close to the antennal tubercle;

eyes apilose; reduced mouthparts; reduced wing venation, with fusion of cells *br*, m_3, r_{4+5} and *d* into a single composite cell *dm*; a single medial vein proximating wing margin; frequent reduction and loss of veins R_{2+3} and R_4; and typically bulbous male terminalia. The body shape is characteristic, with a large round thorax, bulbous abdomen and small, rounded head. The typical acrocerine, *Acrocera* represents (along with *Carvalhoa*) the sister-group to all other acrocerids. The larvae of *Acrocera* have characters that distinguish them from other acrocerid larvae, including weakly-sclerotised body segments in early instars and lack of long body setation (Overgaard Nielsen *et al*. 1999; Schlinger 1960*b*). As opposed to all other Acrocerinae, which are exclusively parasitoids of Entelegynae spiders, *Acrocera* and *Carvalhoa* are known to be exclusive parasitoids of Haplogynae spiders (Winterton *et al.* 2007). Identification keys to Afrotropical species were provided by Schlinger (1960*a*) and Barraclough (1984).

Africaterphis **Schlinger** (Philopotinae) (Figs 2, 23–25)**.** An endemic genus of two described species, *A. acroceroides* (Sabrosky, 1950), recorded from Democratic Republic of Congo, Mozambique and Zimbabwe and *A. gertschi* (Schlinger, 1960), from South Africa. The body is distinctively arched and can be differentiated from other Afrotropical philopotine genera by the highly reduced wing venation and apilose eyes. *Africaterphis* is the only philopotine genus with reduced wing venation in the Afrotropical Region and has clear phylogenetic affinities with the Palaearctic genera *Oligoneura* and *Prophilopota*. The spider host of this rarely collected genus is unknown. Identification keys to Afrotropical species were provided by Schlinger (1960*a*) and Barraclough (1984).

Astomella **Latreille** (Panopinae) (Fig. 15)**.** A distinctive genus of 13 described species occurring in the Afrotropical, Oriental and Palaearctic Regions, seven of which are recorded from the Afrotropics, described from Namibia, South Africa and Tanzania (Barraclough 1984, 1991*a*). The genus is easily diagnosed from other Afrotropical panopine acrocerids by the antennae located on the lower half of head, eyes pilose, costal vein ending at wing apex, vein R_{4+5} not forked, and only two medial veins present. Females have the terminalia located midway along the venter of the abdomen, a feature shared with the Oriental genus *Rhysogaster* Aldrich. *Astomella* has been reared from spiders in the families Ctenizidae, Migidae and Theraphosidae (Barraclough 1984; Schlinger 1987, table 24). Identification keys to Afrotropical species were provided by Schlinger (1960*a*) and Barraclough (1984, 1991*a*).

Corononcodes **Speiser** (Panopinae) (Figs 13, 17)**.** A genus of five described species occurring in the Afrotropical and Palaearctic Regions. Four of the five described species are known from South Africa, while the fifth species is known from the Mediterranean province (Barraclough 2001). This genus is unique among spider flies, especially Panopinae, due to the small size of males of some species and highly reduced wing venation. *Corononcodes* is distinguished from other Afrotropical Panopinae by the entirely black colouration and highly reduced wing venation. Reduction in wing venation is rare in Panopinae, but is found to varying degrees in *Corononcodes* and *Astomella*; for example, the costal vein ending at the wing apex is found only in these two genera, while it is circumambient in all other Panopinae. Identification keys to Afrotropical species were provided by Barraclough (1984, 2001) and Kehlmaier *et al.* (2014).

Dimacrocolus **Schlinger** (Philopotinae) (Fig. 3)**.** An endemic monotypic genus with the single species, *D. pauliani* Schlinger, 1961, restricted to Madagascar and known from relatively few specimens. *Dimacrocolus pauliani* is a spectacular philopotine acrocerid with greatly elongate legs and specialised tufts at the base of the wings in the male (Schlinger 1961). Other characters that distinguish this species include the presence of palpi, apilose eyes, and relatively complete wing venation. *Dimacrocolus* is closely elated to the genera *Parahelle* and *Thyllis*. The spider hosts of this rarely collected genus remain unknown.

Meruia **Sabrosky** (Acrocerinae) (Fig. 12)**.** An endemic monotypic genus, with the single species, *M. somereni* Sabrosky, 1950, known only from Kenya. *Meruia somereni* is distinguished from other Acrocerinae by the modified wing venation (radial veins thickened and bent anteriorly), stylate antennae adjacent to mouthparts, wing costal vein ending at wing apex, beyond R_{4+5}, and antenotum forming a collar behind head. Sabrosky (1950) described the genus based on a single male specimen, but a female specimen from the Coast Province of Kenya has recently been discovered (unpubl.). The female has a similarly enlarged thorax and modified wing veins, but not as pronounced as in the male. *Meruia* is a highly derived acrocerine genus closely related to *Glaesoncodes* Hennig, *Ogcodes*, *Pterodontia* and *Sabroskya*, based on wing venation and the presence of stylate antennae adjacent to the highly reduced mouthparts (Winterton 2012). *Meruia* is the likely sister genus to *Sabroskya*, as both have the antenotum forming a collar behind the head and wing venation with cell m_3 fused with the discal cell (*d*) to form cell *dm*, but not fused with proximal cell r_{4+5} (Schlinger 1960*b*; Winterton & Gillung 2012). The hosts of this rarely collected genus remain unknown.

Ogcodes **Latreille** (Acrocerinae) (Figs 7, 16)**.** A species-rich, virtually cosmopolitan genus, with 115 species occurring in all zoogeographical regions, except Antarctica. Only 10 species are described from the Afrotropics and are widely distributed throughout Central and southern Africa, including Madagascar (Barraclough 1984; Sabrosky 1950; Schlinger 1960*a*, *b*, *c*). Individuals of *Ogcodes* are typically small- to medium-sized black and white-yellow flies, with sparse pilosity, small spherical heads and a globose abdomen. Schlinger (1960*c*) divided the genus into three subgenera, although this has not been widely adopted. *Ogcodes* can be differentiated from all other Acrocerinae by the antennae located on the ventral side of the head adjacent to the mouthparts; eyes apilose; wing venation greatly reduced, with most wing cells and vein R_{2+3} absent and most medial and cubital veins incomplete, or present, but barely sclerotised. *Ogcodes* is a highly derived acrocerid genus sister to *Pterodontia*. The genus has been reared from spiders in a number of families: Agelenidae, Amaurobiidae, Anyphaenidae, Araneidae, Clubionidae, Gnaphosidae, Lycosidae, Oxyopidae, Philodromidae, Psechridae, Salticidae, Theridiidae, and Thomisidae. Identification keys to Afrotropical species were provided by Schlinger (1960*a*) and Barraclough (1984).

Parahelle **Schlinger** (Philopotinae)**.** An endemic monotypic genus confined to Madagascar. It can be differentiated from other Afrotropical genera in the subfamily by the minutely pilose eyes, regular length legs, absence of palpi, and relatively complete wing venation. Schlinger (1961) stated that the eyes were bare in this genus, but actually they are minutely pilose, with very short and sparsely distributed setae. Moreover, Schlinger (1961) suggested that this species was closely related to *Helle* Osten Sacken from New Zealand and *Megalybus* from Chile. Winterton *et al*. (2007), however, indicated that it is actually more closely related to *Thyllis*, but did not include *Dimacrocolus* in their analyses. Considering that the only character separating *Parahelle* from *Thyllis* is the presence or absence of eye pilosity, the status of the two genera should be re-examined. The spider hosts of this genus remain unknown.

***Psilodera* Gray** (Acrocerinae) (Figs 1, 11, 21)**.** A charismatic genus endemic to southern Africa, with 10 described species from South Africa and Zimbabwe (Schlinger 1960*a*, *b*, 1972). One species, originally recorded from India, *P. aurata* (Brunetti, 1920), was subsequently found to be a synonym of a South African species *P. bipunctata* Wiedemann, 1819 and the anomalous distribution record confirmed as erroneous (Barraclough 1991*b*; Schlinger 1960*b*). These flies have a similar habitus to panopines, with medium to large body size, densely pilose body, elongate mouthparts, and complete wing venation. The aristate flagellum and lack of tibial spines clearly place them in Acrocerinae, with DNA sequence data placing them as an intermediate group closely related to *Holops* and more derived Acrocerinae genera (Winterton *et al*. 2007). The plesiomorphic characteristics exhibited by *Psilodera* led Schlinger (1972) to suggest that the genus represented an ancestral stock for genera, such as *Cyrtus* Latreille, *Hadrogaster* Schlinger, *Nipponcyrtus* Schlinger and *Turbopsebius* Schlinger. *Psilodera* can be distinguished from other Acrocerinae by the large pilose body with bulbous abdomen; elongate mouthparts, typically longer than the body; antennae located at middle of head; eye bare; wing with cells m_3, *d* and r_{4+5} present; costal margin circumambient; and posterior radial veins curved anteriorly to join margin before wing apex. The wing venation of *Psilodera*, specifically the curvature of radial veins anteriorly, is very similar to various panopine genera, such as *Eulonchus* and *Lasia*. This genus is in need of monographic revision. The spider hosts of this genus remain unknown. An identification key to Afrotropical species was provided by Schlinger (1960*a*).

***Pterodontia* Gray** (Acrocerinae) (Figs 9, 18)**.** A virtually cosmopolitan genus of 20 species occurring in all zoogeographical regions, except Antarctica. Two widely distributed species occur throughout the eastern Afrotropical Region. *Pterodontia aerivaga* Séguy, 1962, is known from Ethiopia, while *P. smithi* Johnson, 1898, is more widely distributed throughout eastern Africa (Sabrosky 1950; Schlinger 1960*a*, *b*). Species of *Pterodontia* typically have a large, pilose thorax and globose abdomen; very small head with dense pile on the eyes; and often an extremely enlarged calypter, sometimes half the length of the wing. *Pterodontia* is unique among Acrocerinae, in that tibial spines are present, which led some authors to place the genus in Panopinae (*e.g*., Schlinger 1960*a*, *b*). Evidence in support of placement in Acrocerinae, include the presence of stylate antennae, reduced wing venation, and the host range of *Pterodontia* exclusively as parasitoids of Aranaeomorphae spiders (Schlinger 1987, table 24). Analysis of DNA sequence data placed *Pterodontia* in a well-supported, highly derived position in Acrocerinae and sister to *Ogcodes* (Winterton *et al*. 2007). Stylate antennae located adjacent to the mouthparts supports placement of *Pterodontia* in a clade with *Glaesoncodes*, *Meruia*, *Ogcodes* and *Sabroskya*. Moreover, reduction in medial wing veins and fusion of major wing cells (*i.e*., r_{4+5}, *dm* and m_3) into a single composite cell supports the sister-group relationship of this genus with *Ogcodes*. *Pterodontia* has been reared from a wide range of araneomorph spider families including Araneidae, Lycosidae, Salticidae and Theridiidae (Schlinger 1987, table 24).

***Sabroskya* Schlinger** (Acrocerinae) (Figs 6, 20)**.** An endemic genus of three species described from Malawi and South Africa (Barraclough 1984; Schlinger 1960*b*; Winterton & Gillung 2012). *Sabroskya* is in a clade of derived Acrocerinae, which along with its putative sister genus *Meruia*, is grouped with *Glaesoncodes* and the widely distributed genera *Ogcodes* and *Pterodontia* (Grimaldi 1995; Winterton & Gillung 2012). *Sabroskya* can be differentiated from other Acrocerinae genera by the antennae located on the ventral side of the head adjacent to the mouthparts, eyes pilose and the presence of separate wing cells *dm* and r_{4+5} and three medial veins. Vein R_{2+3} is variably present in this genus and its weaker sclerotisation or absence in other genera (*e.g*., *Acrocera*, *Ogcodes*), suggests that it is phylogenetically labile and structurally non-essential in wing flight mechanics in some acrocerids. The spider hosts of this genus remain unknown. The most recent identification key to Afrotropical species was provided by Winterton & Gillung (2012).

***Stenopialea* Speiser** (Panopinae) (Figs 14, 22)**.** An endemic genus of four species described from Malawi and South Africa (Barraclough 1985). The generic affinities of this genus are obscure and it may be closely related to South American genera, such as *Ocnaea* Erichson and *Pialea* Erichson, based on wing venation and antennal and mouthpart characteristics (Schlinger 1956). *Stenopialea* can be differentiated from other Afrotropical genera of Panopinae by the antennae located on the upper half of the head, eyes densely pilose, female terminalia located terminally on the abdomen, wing with a full complement of wing veins and cells, and costal margin ending at vein *CuA+CuP*. The spider hosts of this genus remain unknown. Identification keys to Afrotropical species were provided by Barraclough (1985) and Schlinger (1960*a*).

***Thyllis* Erichson** (Philopotinae) (Figs 4, 5)**.** An endemic genus of 12 described species restricted to the southern continental Afrotropics and Madagascar. *Thyllis* can be distinguished by the relatively complete wing venation, regular length of the legs, pilose eyes and lack of palpi. Some Malagasy species have the most extremely arched bodies of any acrocerids, with the head close to the tip of the abdomen. *Thyllis splendens* Brunetti, 1926, is a relatively large, spectacular species from Madagascar that is entirely metallic green-violet, with lateral spine-like processes on the abdomen (Fig. 5) (Schlinger 1961). This genus has been previously treated in part by Schlinger (1960*a*, *b*; 1961), but is in need of a comprehensive revision. *Thyllis crassa* (F., 1805) has been reared from a species of Miturgidae (Schlinger 1987, table 24). Identification keys to Afrotropical species were provided by Séguy (1962) and Schlinger (1961).

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NEMESTRINIDAE 43

(Tangle-veined Flies)

David A. Barraclough

Fig. 43.1. Female of *Moegistorhynchus* sp. (South Africa) (photograph © A. Pauw).

Diagnosis

Moderate to large, typically robust and compact flies (body length: 5–25 mm) (Fig. 1), but diverse in form and appearance; body variously coloured; dorsum of thorax and abdomen often with conspicuous and complex pruinescent markings (often vittae and maculae or rounded areas) (Fig. 2); setae lacking, without pilosity, or pilosity present to varying degrees, often long and dense, with some species remarkably bee-like; wing elongate, ranging from slender and largely hyaline, to broader, with complex and striking dark patterning and occasionally almost entirely dark brown and opaque (Figs 2, 5–9).

Head with eyes holoptic to dichoptic in males, typically dichoptic in females; eye always bare, or virtually so; ocelli present (except in *Atriadops* Wandolleck); antenna small to minute, with scape and pedicel compact and variously developed; flagellum unsegmented in Trichopsideinae, or in the Nemestrininae segmented, with first flagellomere short and rounded, to elongate-conical, followed by relatively elongate and slender stylus, comprising 1–3 flagellomeres, stylus sometimes shortened, invariably bare (Figs 3, 4); facial region moderately and evenly concave in profile to deeply convex/excavate and concealed, with deep vertical groove on either side beneath antenna in *Nycterimyia* Lichtwardt, or with deep horizontal

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 995–1003.

groove beneath antennal insertions in *Atriadops*; mouthparts highly variable in form and size; proboscis reduced, vestigial or difficult to discern in *Atriadops*, *Nycterimyia* and *Trichopsidea* Westwood, to remarkably elongate (albeit slender) reaching 2–3 × body length in some *Moegistorhynchus* Macquart and *Prosoeca* Schiner; palpus slender and well-developed, although vestigial in forms with reduced proboscis.

Thorax unmodified; about equal in length, width and depth. Scutellum short and relatively broad, often with submarginal groove (Fig. 2). Legs slender (but shorter and stouter in *Atriadops* and *Nycterimyia*); tibiae without apical spurs; tarsal claws well-developed (exceptionally so in *Moegistorhynchus*). Wing typically longer than body, often slender, but notably broad basally in *Atriadops*; unusual in shape in several genera: may be sinuous along hind margin in *Nycterimyia* (Fig. 8), sharply tapered apically, or virtually so, in *Atriadops* (Fig. 7) and occasionally with prominent anterior costal flexure (notably males of *Stenobasipteron* Lichtwardt, Fig. 6); wing venation variable and highly complex, typified by “diagonal vein” (Fig. 7), commencing from vein R_1 at about basal ⅖ of wing and traversing diagonally (virtually in straight line) across apical ½–⅗ of wing to terminate at hind margin *ca* ¼–⅖ length of wing from apex (Figs 2, 5–9); “diagonal vein” comprises sections of veins *Rs*, R_{4+5}, crossvein *r–m*, veins M_1, M_2, and M_4; all apical veins terminate on costa anterior to wing apex (except in *Atriadops*, in which vein M_2 terminates posterior to wing apex) (Fig. 7); in *Moegistorhynchus*, *Nemestrinus* Latreille, *Prosoeca* and *Stenobasipteron* all veins run parallel to hind margin of wing; extensive apical reticulation present in radial and medial sectors (cells divided by numerous reticulate apical veins) in apical ⅓ of wing distal to “diagonal vein” in *Moegistorhynchus* (Fig. 2) and two species of *Nemestrinus*.

Abdomen usually at least as wide as thorax, widest at about mid length; male terminalia with epandrium invariably free and typically prominent and well-developed (Figs 14, 15); hypandrium present and free in genera of Nemestrininae (Figs 14, 15), otherwise absent; cercus well-developed; phallus consisting of simple, or variously modified tubular structure (Figs 14, 15); female terminalia with ovipositor of two types: either elongate, retractile, with short apical cerci (Nemestrininae) (Fig. 12), or cerci greatly lengthened, appressed to each other, with curved, sabre-like form (Fig. 13); 2–3 spermathecae present.

Immature stages (only formally described for *Trichopsidea*), with four larval instars: first-instar minute and planidiform; second-instar cylindrical and tapering at each extremity, cuticle very thin and transparent; third-instar similar, but becoming opaque; fourth-instar (Fig. 16) stout, dorsoventrally flattened, with series of folds and tubercles, posterior spiracles only slightly raised above body surface.

Pupa (Fig. 17) obtect, with abdominal section broadest; segment 8 with pair of broad flattened spines terminally, set transversely and dorsally directed.

The family is most readily recognised (in the vast majority of species) by venational characters: the presence of characteristic apical veins running parallel to the hind margin of the wing and terminating anterior to its apex; and by the “diagonal vein” (an oblique linear combination of veins and crossveins crossing the apical ⅓–½ of wing) (Figs 2, 5–9). Nemestrinidae are distinctive flies and can often be immediately recognised in the laboratory and in the field. They may, however, be confused with Acroceridae (especially the genus *Psilodera* Gray) (see Chapter 42) and many Bombyliidae (see Chapter 45). These last two named families can be distinguished from the Nemestrinidae by the combination of a lack of a “diagonal vein” and the apical veins of the wing not being inserted on the costa anterior to the wing tip; *Psilodera* spp. also have a more rotund abdomen and a smaller, downwardly directed head.

Biology and immature stages

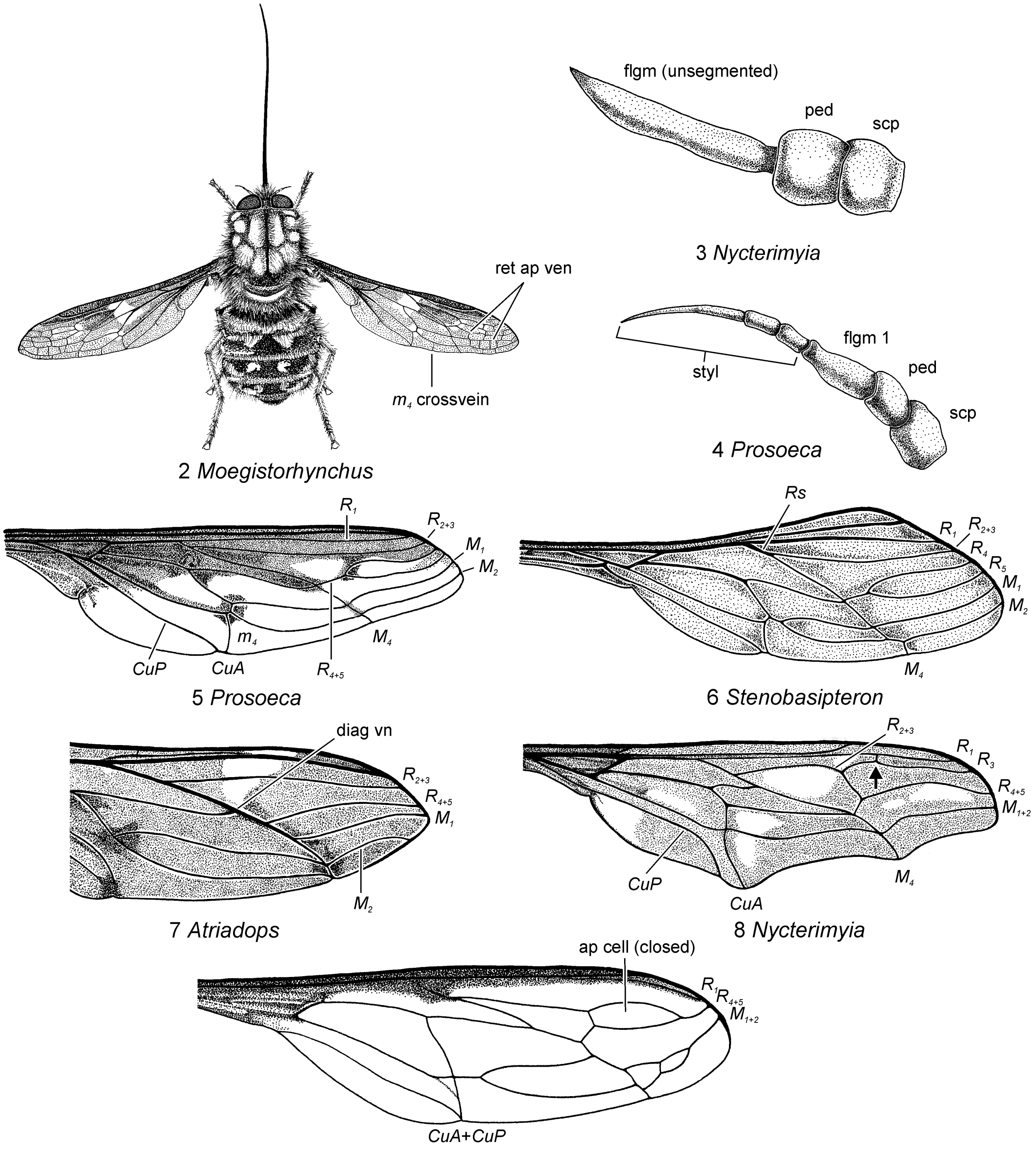
Known larvae of Nemestrinidae are largely internal parasitoids of the nymphs and adults of Orthoptera (Acrididae) and the immature stages of scarabaeid beetles, although *Atriadops* has been reared from katydids (Orthoptera: Tettigoniidae) in Japan (Kanmiya 1987) and Mantodea (Tarachodidae) in Gambia, West Africa (Haenni & Borer 2007).

Adult nemestrinids (especially the subfamily Nemestrininae), are fast fliers; the genus *Atriadops* is a notable exception, as are probably other species in the subfamily Trichopsideinae. They often hover at or in the vicinity of flowers, where they feed on nectar, making a characteristic high-pitched buzzing or humming sound. In some parts of the Afrotropics adults are most abundant at certain times of the year. For example, in the eastern provinces of South Africa, many species are particularly active during the autumn months.

Haenni & Borer (2007) reported *Atriadops vespertilio* (Loew, 1858) as a parasitoid of *Galepsus* (*Lydamia*) *nimulensis* (Giglio-Tos) (Mantodea: Tarachodidae) in Gambia, West Africa, in a grassland area with sandy soil. This represents the only known record of a Mantodea host for the Nemestrinidae. Interestingly, Bequaert (1937) also refers to the fact that the genus is collected from grassland and savanna areas and preliminary observations suggest this to be correct. Bequaert also noted that *A. vespertilio* is a poor flier and is thus easily collected, which appears to confirm much earlier reports in the literature. The wide distribution of the genus suggests that it targets a diverse range of hosts.

A pollination guild of long-tubed flowers centred on *Moegistorhynchus longirostris* (Wiedemann, 1819) was established in the literature by Manning & Goldblatt (1997), who reported it pollinating (partly or exclusively), 20 late spring and early summer flowering species of Geraniaceae, Iridaceae and Orchidaceae. Goldblatt & Manning (2000) also attribute *M. longirostris* and an undescribed species to the *Moegistorhynchus-Philoliche* guild, together with two species of *Philoliche* Wiedemann (Tabanidae) and two of *Prosoeca*. The guild operates along the western and south-western coasts and adjacent mountains in the winter rainfall zone (Goldblatt & Manning 2006). Pauw *et al*. (2009) published a significant paper on *M. longirostris*, discussing the coevolutionary processes between it and the long-tubed flowers it pollinates.

Despite an intensive focus by pollination biologists and entomologists in South Africa, very little is known about the life history and immature stages of Nemestrininae. An undetermined species of *Prosoeca* in the KwaZulu-Natal midlands of South



2 *Moegistorhynchus*

3 *Nycterimyia*

4 *Prosoeca*

5 *Prosoeca*

6 *Stenobasipteron*

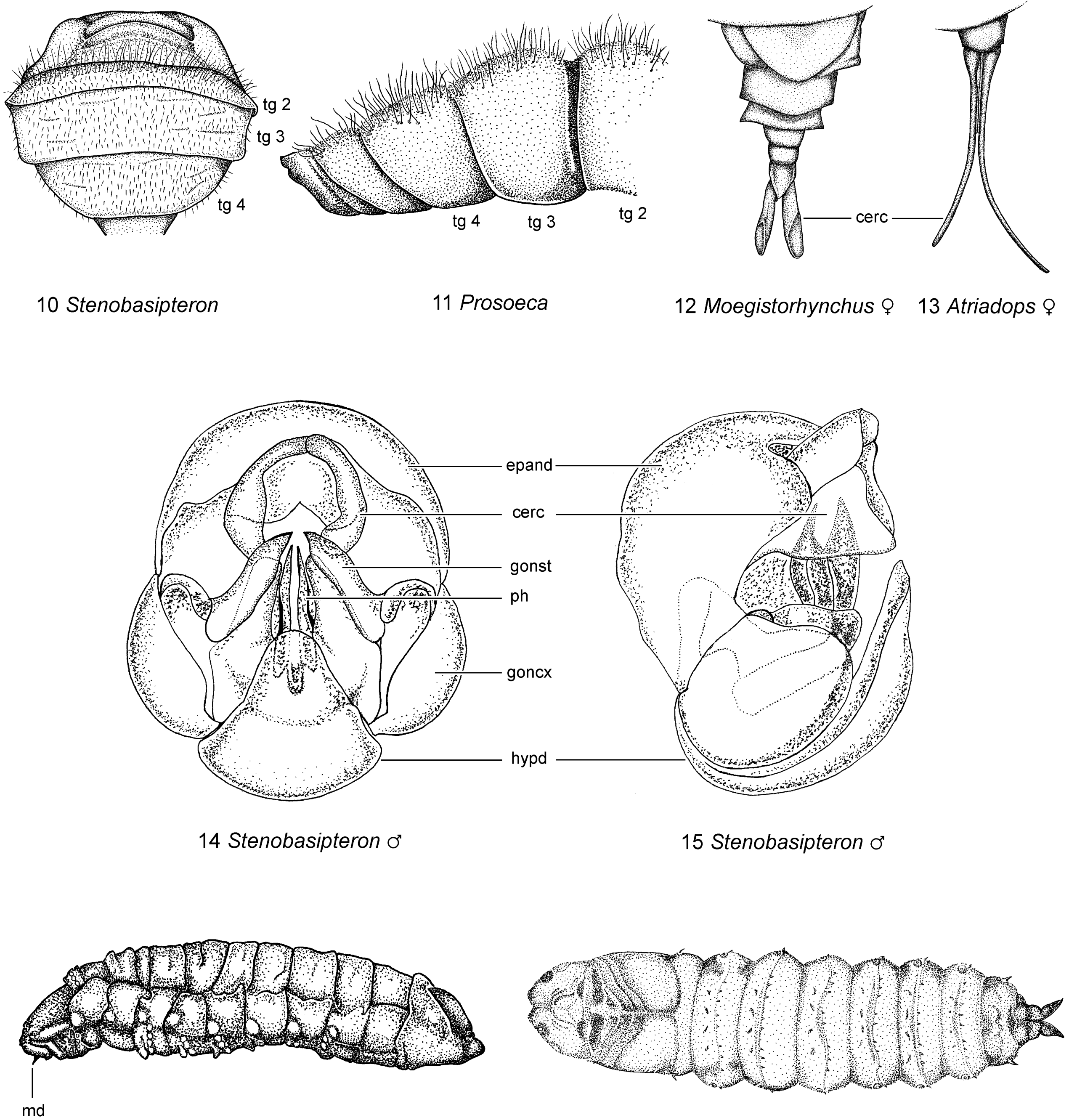
7 *Atriadops*

8 *Nycterimyia*

9 *Trichopsidea*

Figs 43.2–9. Habitus, antennae and wings of Nemestrinidae: (2) habitus of *Moegistorhynchus* sp., dorsal view; (3) antenna of *Nycterimyia capensis* Bezzi, lateral view; (4) same, *Prosoeca robusta* Bezzi; (5) wing of *P. peringueyi* Lichtwardt, dorsal view; (6) same, *Stenobasipteron wiedemanni* Lichtwardt; (7) same, *Atriadops* sp.; (8) same, *N. capensis* Lichtwardt; (9) same, *Trichopsidea costata* (Loew).

Abbreviations: ap cell – apical cell; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; diag vn – diagonal vein; flgm 1 – first flagellomere; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; m_4 – fourth medial cell; ped – pedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; R_5 – lower branch of third branch of radius; ret ap ven – reticulate apical venation; *Rs* – radial sector; *Sc* – subcostal vein; scp – scape; styl – stylus.



10 *Stenobasipteron* 11 *Prosoeca* 12 *Moegistorhynchus* ♀ 13 *Atriadops* ♀

14 *Stenobasipteron* ♂ 15 *Stenobasipteron* ♂

16 *Trichopsidea* 17 *Atriadops*

Figs 43.10–17. Abdomens, terminalia and immature stages of Nemestrinidae: (10) abdomen of *Stenobasipteron wiedemanni* Lichtwardt, dorsal view; (11) same, *Prosoeca* sp., lateral view; (12) female terminalia of *Moegistorhynchus longirostris* (Wiedemann), dorsal view; (13) same, *Atriadops* sp.; (14) male terminalia of *Stenobasipteron* sp., ventral view; (15) same, oblique lateral view; (16) fourth-instar larva of *Trichopsidea costata* (Loew), lateral view; (17) pupa of *Atriadops vespertilio* (Loew), ventral view. Fig. 16 (after Greathead 1958, fig. 9), Fig. 17 (after Haenni & Borer 2007, fig. 3).

Abbreviations: cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; md – mandible; ph – phallus; tg – tergite.

Africa has, however, been observed flying (in late summer and autumn), adjacent to the branches of dead trees. In one instance the fly was apparently ovipositing in crevices in wood (J. Roff, pers. comm. 2014). If these observations are confirmed, these species may well be parasitoids of cerambycid beetles (given their large size).

Four plant pollination guilds, centred on species of *Prosoeca*, are established in the literature (Johnson 2010): the *P. peringueyi* Lichtwardt, 1920 guild (18 species pollinated); the *P. ganglbaueri* guild (20 species pollinated); the *P. longipennis* (Loew, 1858) guild (5 species pollinated); and a guild of six plant species pollinated by an undetermined *Prosoeca* sp. Our understanding of these guilds has, however, changed with continuing research by pollination biologists. For example, in an important recent paper by Newman *et al*. (2014), 17 floral guild members are now recorded as pollinated in all or part of their range by *P. longipennis*. Recent research by Karolyi *et al*. (2012, 2013) has also provided new insights into the adaptations for nectar-feeding in the mouthparts of long-proboscid species of *Prosoeca*.

The habitat preference of *Stenobasipteron* is of interest, in that the commonest species, *S. wiedemanni* Lichtwardt, 1910, is thought to be restricted to forests or closed-canopy habitat in South Africa (Potgieter & Edwards 2005). This is unusual in the Nemestrinidae, although *Prosoeca* spp. have been encountered in sunlit patches at forest margins (pers. obs.). Potgieter & Edwards (2005) described a separate pollination guild centred on *S. wiedemanni*. *Stenobasipteron wiedemanni* was previously considered part of the *P. ganglbaueri* guild by Goldblatt & Manning (2000), but Potgieter & Edwards (2005) recorded the species as a pollinator of 19 plant species in six families (Acanthaceae, Balsaminaceae, Gesneriacae, Iridaceae, Lamiaceae and Orchidaceae).

Trichopsidea is recorded as a parasitoid of grasshoppers (Orthoptera: Acrididae) throughout its range and Greathead's (1958, 1960, 1967) treatment of the genus should be referred to for detail on taxonomy and biology. Acridid hosts in the Afrotropical Region include *Dociostaurus maroccanus* (Thunberg), *Locustana paradalina* (Walker) and *Schistocerca gregaria* (Forskål) (*e.g*., Greathead 1958; Léonide 1962; Potgieter 1929). More information exists on the biology of *Trichopsidea costata* (Loew, 1858) than any other Afrotropical species of Nemestrinidae. According to Greathead (1958), and based also on his synopsis of other literature, adults likely emerge after rains and lay a large number of eggs into cracks in bark and in the soil. After the minute first-instar planidial larvae hatch, and following wind dispersion, they enter a grasshopper host through the thoracic or abdominal inter-segmental membrane (usually only one larva per host), with moulting commencing after the formation of a respiratory tube to the exterior. The larva lies in the abdomen of the host with its anterior end facing the same direction as the head of the host. Three instars follow over about two weeks, with the larvae feeding mainly on hemolymph and the fat body (and the fourth-instar on the gonads). The final instar larva emerges by rupturing the membranes near the base of the abdomen, behind the base of the hind legs. Following emergence, the host grasshopper dies, or if surviving a short period, is unable to reproduce. On exiting the host, the final instar larvae burrow into the nearby sand, where pupation is likely to be induced (sometimes after years of diapause) by moisture in the soil (the breeding of resident grasshopper populations is also induced by rainfall), with eclosion of adults after about two weeks. Greathead could not determine the impact of the parasitoid habit on grasshopper populations in the Afrotropics, but outside the region (Léonide 1969; Prescott 1960) the control of grasshopper populations has been noted and Prescott (1960) documented a parasitism rate of up to 90%.

Economic significance

Nemestrinidae currently have no direct economic significance, but have the potential to be used as biological control agents of pest grasshoppers and locusts (Orthoptera: Acrididae). They are also important pollinators of numerous attractive flowering plants, especially flowers with long-tubed corollas and species guilds that have been identified. This has direct relevance to ecotourism, especially in the Western Cape Province, South Africa, which is part of the Cape Floristic Region (the smallest of the world's six floral kingdoms, although of exceptional interest because of its many endemic species).

Classification

Bernardi (1973) published a revision of and classified the world fauna of Nemestrinidae into five extant subfamilies: Atriadopsinae, Cyclopsideinae, Hirmoneurinae, Nemestrininae and Trichopsideinae. Later, Papavero & Bernardi (2009) also recognised five subfamilies of Nemestrinidae, with the Atriadopinae (corrected spelling) and Falleniinae replacing the Atriadopsinae and Trichopsideinae, respectively. Barraclough (2006) recognised only the Nemestrininae (*Moegistorhynchus*, *Prosoeca* and *Stenobasipteron*) and Trichopsideinae (*Atriadops*, *Nycterimyia* and *Trichopsidea*) in the Afrotropical fauna.

Woodley (2009: 558) briefly discussed the unsatisfactory nature of our understanding of relationships in the Nemestrinoidea and the phylogenetic placement of the Nemestrinidae and it is clear that further research is required. Woodley (1989: 1383) placed the Nemestrinidae with the Acroceridae, in the superfamily Nemestrinoidea, based on the shared endoparasitic lifestyle of the two families. This tenuous relationship has been discussed by various authors. Yeates (1994) found the superfamily to be paraphyletic, while Nagatomi (1992) and Griffiths (1994) found the superfamily better placed in the Tabanomorpha. Yeates (2002) again showed that the Nemestrinoidea were paraphyletic and formed the two basal clades of the Muscomorpha. Yeates *et al*. (2007), however, found the Nemestrinoidea to be monophyletic. More recently, in a molecular estimate of Diptera relationships, Wiegmann *et al*. (2011) placed the Nemestrinidae as the sister-group to the non-Afrotropical Xylophagidae, being basal to the Tabanomorpha and with the Acroceridae in the Asiloidea.

Identification

Globally there are *ca* 275 described species of Nemestrinidae and the family is most speciose in the Afrotropical, Australasian, Neotropical and Palaearctic Regions and notably depauperate in the Nearctic with only six described species (Teskey

1981: 587). There are currently 52 described Afrotropical species, although many additional new species await description and the fauna could potentially comprise more than 80 species and represent the richest Nemestrinidae fauna in the Southern Hemisphere. Bernardi (1989) and Papavero & Bernardi (2009) catalogued 55 and 64 species from the Australasian and Neotropical Regions, respectively. Bernardi (1973, 1976, 1977), revised the world fauna, provided a catalogue of genera and species and suggested a higher-level classification for the family. A key to the genera of the Afrotropical Region is included in Bernardi (1973), although this work does not include identification keys to species. Bezzi (1924) had previously provided an identification key to genera, but this is now entirely outdated. Barraclough (2006) published a detailed and annotated identification key to South African genera.

With respect to published keys to described species in the family, the following publications are most pertinent: Barraclough (2005*a*) [*Nycterimyia*]; Barraclough (2005*b*) [*Stenobasipteron*]; Bequaert (1935) [*Moegistorhynchus*]; Bezzi (1924) [*Prosoeca*]; Greathead (1967) [*Trichopsidea*] and Sack (1933) [*Nemestrinus*]. It should be noted, however, that the identification key of Bezzi (1924) to the then known species of *Prosoeca* is of little value and recourse should be made to the original descriptions in order to confirm or make determinations; a new and revised key is much needed. For identification and information on the morphology of immature stages of Afrotropical nemestrinids, reference should be made to Greathead (1958).

Numerous morphological characters can assist with the identification of nemestrinid species. Despite the complexity of wing venation, venational characters may be of limited value in the group, especially given that there can be significant intraspecific variation and sometimes the presence of auxiliary veins, crossveins and cells. The length of the proboscis relative to body length is especially useful for distinguishing species of *Moegistorhynchus*, *Prosoeca* and *Stenobasipteron*. Characters relating to the colouring and patterning of the wings, abdomen and thoracic dorsum are most valuable, as are the development and disposition of pilosity on these areas. The structure and form of the antenna (especially the flagellum) is also of some value. Characters of the postabdomen and terminalia offer great potential for future taxonomic studies, including the shape and development of the female spermathecae and also of the male gonocoxite, gonostylus, epandrium, hypandrium and phallus. Nemestrinidae are collected by hand-netting and are best direct-pinned in the field (see Chapter 2).

Key to genera of Afrotropical Nemestrinidae

1. Ocelli lacking in both sexes; wing strongly tapered apically (Fig. 7); vein M_2 curved posteriorly to terminate posterior to wing apex (Fig. 7) . . . . *Atriadops* Wandolleck

– Ocelli present in both sexes; wing not strongly tapered apically (*e.g.*, Figs 5, 6); all apical veins terminating anterior to wing apex (*e.g.*, Figs 2, 5, 6, 8, 9) 2

2. Wing veins R_1 and R_3 connected by apparent crossvein (Fig. 8, arrowed); hind wing margin with characteristic sinuous appearance (less evident in female); antenna with undivided flagellum (Fig. 3) . . . . *Nycterimyia* Lichtwardt

– Wing with radial veins not connected by apparent crossvein (except sometimes in *Moegistorhynchus*, but then apical ½ of wing extensively reticulate (*e.g.*, Fig. 2)); hind wing margin without sinuous appearance; antenna with flagellum having several basal segments, plus a stylus (*e.g.*, Fig. 4), or flagellum unsegmented in *Trichopsidea* 3

3. Proboscis vestigial or absent; antennal flagellum unsegmented; wing with at least 1 apical cell closed, venation here irregular, with auxiliary cell/s sometimes developed (Fig. 9) . . . . *Trichopsidea* Westwood

– Proboscis well-developed, typically longer than head length; antennal flagellum segmented; wing without crossvein in apical ½ (*e.g.*, Figs 5, 6), except in *Moegistorhynchus*, but then this section extensively reticulate (*e.g.*, Fig. 2) 4

4. Head with face projecting forwards, snout-like in profile (infrequently encountered flies from north-eastern fringe of Afrotropical Region, *i.e.*, Ethiopia, Sudan and United Arab Emirates). . . . . . *Nemestrinus* Latreille

– Head with face not prominent in profile, not projecting forwards, or snout-like in profile (sub-Saharan flies, restricted to southern Africa) 5

5. Wing with extensive apical reticulation in radial and medial sectors (cells divided by numerous auxiliary crossveins) in apical ⅓ distal to "diagonal vein" (Fig. 2); cell m_4 divided by 1 or 2 crossveins (Fig. 2) . . . . *Moegistorhynchus* Macquart

– Wing lacking reticulation in apical ⅓ (Figs 5–9); cell m_4 not divided by a crossvein, or crossveins 6

6. Wing base conspicuously narrowed, resulting from notable narrowing of alula (Fig. 6); wing membrane often appearing mostly brown-infuscate, never with prominent markings (Fig. 6); abdominal dorsum with posterior ½ of tergite 2 and entire surfaces of tergites 3 and 4, with short, recumbent vestiture (Fig. 10), obvious, long, erect pilosity usually absent (Fig. 10); striking body markings absent . . . . *Stenobasipteron* Lichtwardt

– Wing base typically relatively broad, usually not obviously narrowed and with alula not reduced (Fig. 5); wing membrane ranging from mostly hyaline, to strongly patterned, or largely dark infuscate (Fig. 5); abdominal dorsum with posterior ½ of tergite 2 and/or much of tergites 3 and 4 typically with obvious, erect vestiture (Fig. 11), variable in length and density; striking body markings often present, particularly on dorsum of thorax and abdomen . . . . *Prosoeca* Schiner

Synopsis of the fauna

Nemestrinidae are especially speciose and abundant in South Africa, with the exception of the more arid parts of the north-west of the country. Of the 52 described Afrotropical species, more than 80% (43 species) are recorded from South Africa. This is likely to rise to *ca* 95% once the Afrotropical fauna is fully revised taxonomically. Dominant Nemestrininae probably occur in all nine South African provinces, fringing into southern Namibia and southern Botswana, through Lesotho, Swaziland and Zimbabwe and the western highlands of Mozambique and into Malawi. Bowden (1980: 374) refers to a report of Nemestrinidae observed flying in north-eastern Uganda, and if this is accurate, this observation probably represents a species of *Nemestrinus* (Nemestrininae), a genus recorded from adjoining Sudan and nearby Ethiopia (and recently also from the United Arab Emirates (UAE) by Deeming (2009)). In South Africa, the Nemestrininae occur in all habitats, except closed-canopy forest, although *Stenobasipteron wiedemanni* (see under genus *Stenobasipteron* below), is a notable exception. This habitat preference is likely to be replicated in other parts of southern Africa. The genus *Atriadops* is likely to be distributed throughout much of sub-Saharan Africa (but see under genus *Atriadops* below), while *Nycterimyia* and *Trichopsidea* are distributed in southern Africa, East Africa, Madagascar (one species of *Nycterimyia*), and north-east Africa and into the southern Palaearctic Region (*Trichopsidea*). The Malagasy fauna of Nemestrinidae is notably depauperate, with only two species, one of which is undescribed.

***Atriadops* Wandolleck** (Trichopsideinae)**.** A genus of seven described species largely restricted to the Old World, occurring in the Afrotropical, Australasian, Neotropical and Oriental Regions (Nagatomi 1978). A single, little-known species is recorded from the New World (Brazil and Costa Rica) (Bequaert 1937; Bernardi 1973; Lopes 1936; Woodley 2009: 559). The genus is widely distributed in sub-Saharan Africa and an undescribed species is known from northern Madagascar. Two species have been described from the Afrotropics, with one, *A. cinnamonea* Brunetti, 1929, apparently restricted to East Africa (Bowden 1980: 376). The fauna is in need of revision with, for example, at least two species known from South Africa alone (Barraclough 2006). The flies are not infrequent in collections and are occasionally pinned with the associated pupal exuviae.

***Moegistorhynchus* Macquart** (Nemestrininae)**.** An endemic genus of four described species restricted to south-western South Africa (Northern and Western Cape Provinces). At least three new species have been identified from montane areas in the southern part of the Western Cape (D.A. Barraclough, in prep.) and there may be additional undescribed species in Namaqualand (Northern Cape Province). The genus comprises large (15–20 mm), striking flies with conspicuously patterned wings and often with a remarkably elongate proboscis. *Moegistorhynchus longirostris* is by far the most commonly encountered species, with a range from the Western Cape into the Northern Cape. It has the longest proboscis of all known Diptera species worldwide (Barraclough & Slotow 2010), reaching 90–100 mm in some specimens.

***Nemestrinus* Latreille** (Nemestrininae)**.** A large genus of at least 66 species occurring mainly in the Palaearctic Region (Richter 1997: 466). Bowden (1980: 375), however, recorded two species (one with reticulate venation) from the Afrotropics: *N. abdominalis* Olivier, 1811, from Ethiopia and Sudan, and *N. fasciatus* Olivier, 1811, from Sudan. The material concerned was not examined in preparation of this chapter, so these records remain unconfirmed. Recently, however, Deeming (2009) recorded *N. rufipes* (Olivier, 1810) from United Arab Emirates in the Arabian Peninsula. This species is otherwise distributed across North Africa into Syria and Palestine (Deeming 2009). Note that although there are at least two references in the literature to *Nemestrinus* species occurring in "Arabic states" (Richter 1988: 173–178), no definite additional records could be found for the Afrotropical part of the Arabian Peninsula, although further records are probable. The genus includes large species, some with reticulate venation, as in the genus *Moegistorhynchus*, although a close phylogenetic relationship between these two genera has not been established.

***Nycterimyia* Lichtwardt** (Trichopsideinae)**.** A genus of 12 described species occurring in the Afrotropical, Australasian (Australia, New Guinea) and Oriental (Indonesia, Philippines, Taiwan) Regions (Bernardi 1973). Barraclough (2005*a*) revised the Afrotropical fauna and recorded only two species from the region, *N. bezzii* Lichtwardt, 1925, from Malawi and *N. capensis* Bezzi, 1924, from Kenya, Madagascar and South Africa. *Nycterimyia* is difficult to recognise as a nemestrinid, as the head is highly modified (facial region recessed, proboscis vestigial) and the wing venation is reduced and largely concealed by dark infuscation. It is a rarely collected taxon (the most infrequently encountered genus in southern Africa), probably because adults do not feed and the flight period must, therefore, be very short.

***Prosoeca* Schiner** (Nemestrininae)**.** A large endemic genus of 37 described species, being by far the largest and most morphologically diverse genus of Nemestrinidae in the Afrotropical Region. Unlike the genus *Stenobasipteron*, most species tend to be relatively robust flies (Barraclough 2006). About 90% of species (once revised) are likely to be recorded from South Africa, with the remainder recorded from Lesotho, Malawi, Mozambique, Namibia, Swaziland and Zimbabwe. *Prosoeca* spp. exhibit an extensive range of body and wing patterning, although the patterning is not evident in some species. Body size ranges from slightly more than 5 mm up to 24 mm. It is difficult to generalise regarding ecology and habitat preferences, but the genus is likely to occur in most biomes, although none of the species appear to be strictly forest dwellers.

A substantial number of new *Prosoeca* spp. await description and the fauna may eventually comprise over 50 species, despite the likelihood of additional new synonymies. Some of the widely distributed species of *Prosoeca*, such as *P. ganglbaueri* Lichtwardt, 1910, are likely (based on preliminary research) to be species complexes and a taxonomic review of such taxa is warranted. Unfortunately, the accurate identification of most *Prosoeca* spp. must await a thorough taxonomic revision, involving examination of all type material.

***Stenobasipteron* Lichtwardt** (Nemestrininae)**.** An endemic genus of three described species, confined to the south-eastern parts of the Afrotropics. In South Africa, where the genus is most speciose, it is restricted to the eastern summer rainfall provinces, especially the Eastern Cape and KwaZulu-Natal, although several undescribed species are represented in the north-eastern provinces of Limpopo and Mpumalanga, where the genus appears to have speciated extensively. The genus is further represented in western Mozambique, Swaziland and Zimbabwe, and historical records from Malawi require confirmation. Barraclough (2005*b*) reduced the number of *Stenobasipteron* spp. from five to three, following transfer of two species, *P. difficile* (Bequaert, 1925) (Zimbabwe) and *P. minimum* (Bezzi, 1924) (Western Cape, South Africa), to *Prosoeca*. *Stenobasipteron* spp. are moderately-sized to large flies, typically unicolourous, or virtually so, ranging in length from 10–18 mm. They typically differ from the genera *Moegistorhynchus* and *Prosoeca* in having a more slender facies, with the proboscis length ranging from *ca* 10–20 mm.

***Trichopsidea* Westwood** (Trichopsideinae)**.** A widespread genus of three species occurring in the Afrotropical, Australasian, Palaearctic and Nearctic Regions, each with a single species, although the Palaearctic and Afrotropical Regions share one: *T. costata* (the only African nemestrinid species that occurs outside the region). The hyaline wings of *T. costata* and its vestigial proboscis make it immediately recognisable in the Afrotropical fauna. The genus appears to be abundant in the arid northern parts of South Africa and is also recorded by Bowden (1980: 376) from Ethiopia, Kenya, Mozambique, Namibia and Somalia, and northwards into the southern Palaearctic. Greathead (1958) further recorded the genus from Sudan.

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MYTHICOMYIIDAE 44

(Micro Bee Flies)

Neal L. Evenhuis

Fig. 44.1. Female of *Cephalodromia montana* (Hesse) (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small flies (body length: 0.8–3.0 mm), usually bare, with projecting proboscis, thorax and abdomen of contrasting dark and pale-coloured patterns and hyaline wings (Fig. 1).

Head with indentation of inner eye margin near level of antennae; antenna with 2 flagellomeres and small, seta-like stylus inserted either apically, or subapically, on flagellomere 2; palpus extremely reduced, or absent.

Thorax with mesonotum rounded, sometimes with hump-backed appearance. Wings (Figs 27–36) held together over abdomen at rest (Fig. 1) (held outstretched, or at an angle in Bombyliidae); vein R_{4+5} unbranched; costal vein (C) ending just after end of vein R_{4+5} (or M_1 in Leylaiyinae); lacking vein *MA* (arculus) and vein M_3 (thus having 4, or fewer posterior cells); bases of some veins effaced (*Doliopteryx* Hesse) (Fig. 31).

Abdomen usually broader than thorax (Figs 21–23), rounded, with spiracles placed in tergites; body vestiture consists

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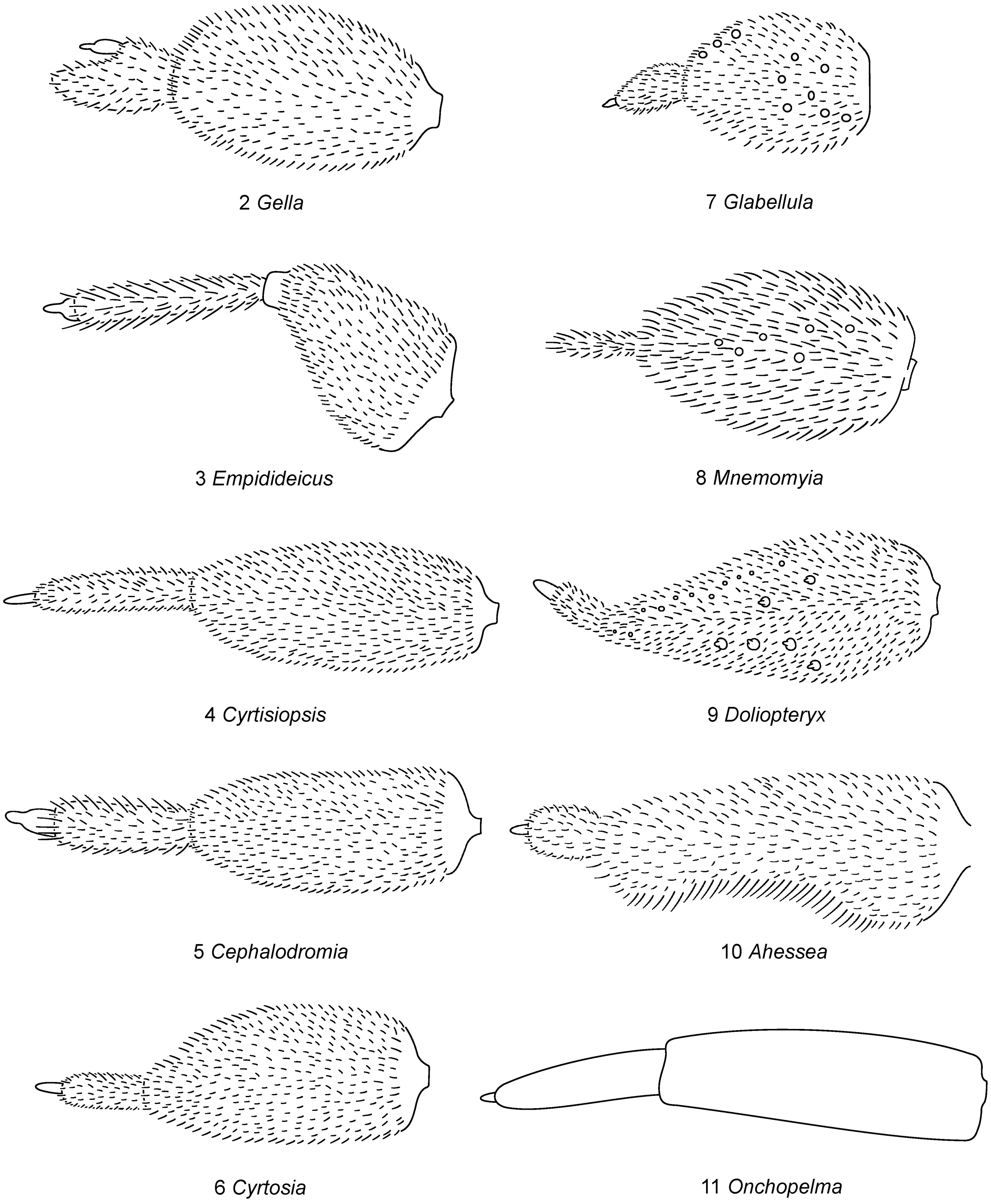


2 *Gella*

7 *Glabellula*

3 *Empidideicus*

8 *Mnemomyia*

4 *Cyrtisiopsis*

9 *Doliopteryx*

5 *Cephalodromia*

10 *Ahessea*

6 *Cyrtosia*

11 *Onchopelma*

Figs 44.2–11. Antennal flagellomeres of Mythicomyiidae (lateral views): (2) *Glella ashleyi* Greathead & Evenhuis; (3) *Empidideicus basutoensis* Hesse; (4) *Cyrtisiopsis singularis* Séguy; (5) *Cephalodromia fusca* (Séguy); (6) *Cyrtosia marginata* Perris; (7) *Glabellula natalensis* Hesse; (8) *Mnemomyia rostrata* Bowden; (9) *Doliopteryx tigrina* Evenhuis; (10) *Ahessea crassirostris* (Hesse); (11) *Onchopelma pulchellum* Hesse (diagrammatic).

of sparse pubescence, or minute setae on head, thorax and abdomen, tomentum always absent; male terminalia with epandrium consisting of single sclerite; true surstyli absent, but conspicuous pointed processes often present (termed "pseudosurstyli"); gonocoxites united basally, forming single plate, or absent altogether; gonostyli often absent, or reduced, present only in few genera; phallic complex comprising phallus (with single, bifid, or trifid tip), epiphallus, long thin gonocoxal, or epiphallic apodemes and relatively large ejaculatory apodeme, with associated lateral ejaculatory processes (rami and vanes); female postabdomen without sand chamber, rostrum, or spines on acanthophorites; female terminalia with 3 (rarely 2) spermathecae of various shapes and sizes (Figs 37–40), usually associated with long, thin apical spermathecal ducts and small, thin sperm pumps.

Mythicomyiidae are separated from Bombyliidae (see Chapter 45), by the abdominal spiracles inserted in tergites (situated in pleural membrane in Bombyliidae); unbranched wing vein R_{4+5} (branched into veins R_4 and R_5 in Bombyliidae); lack of vein *MA* (arculus) (present in Bombyliidae); presence of extremely long, thin gonocoxal, or epiphallic apodemes in male terminalia (apodemes reduced or absent in Bombyliidae); and caudal spines of pupae hooked 90° (spines hooked only 45°, or less in Bombyliidae). Augmenting the morphological characters, Mythicomyiidae is also a much older lineage than any known Bombyliidae, dating from the Middle Jurassic (*Palaeoplatypygus* Kovalev; Callovian: 163–168 MYA), with other genera known from the Cretaceous (*Procyrtosia* Hennig and *Proplatypygus* Zaitzev). By contrast, Bombyliidae are not known from fossil material older than Eocene amber deposits (Lutetian to Rupelian: 30–52 MYA) (Nel 2006).

Biology and immature stages

Little is known regarding the immature habits of Afrotropical mythicomyiids, but it can be assumed that the habits recorded for genera outside of the region also pertain to species found there. One endemic Afrotropical genus, *Psiloderoides* Hesse, has been recorded as egg pod predators of the Brown locust, *Locustana pardalina* (Walker) (Orthoptera: Acrididae) (Hesse 1967) and the egg pod predation habit is also known in other psiloderoidine genera in Australia (described taxa) and Argentina (undescribed taxa) (pers. obs.). Andersson (1974) recorded species of *Glabellula* Bezzi in Scandinavia as inquilines in nests of the ant genus *Formica* L. (Formicidae). Adults are weak fliers and those with mouthparts feed on nectar and pollen; flowers being the most common place they are encountered. Species of *Cephalodromia* Becker have been observed by the writer in KwaZulu-Natal Province, South Africa, hovering approximately 0.5 cm over prospective flowers for visitation, prior to terminating their wing beat and dropping onto these to feed.

Larvae of Afrotropical Mythicomyiidae are unknown, but those of the genus *Glabellula*, which occurs in the Afrotropics have been described and illustrated by Andersson (1974; for *G. arctica* (Zetterstedt)) (non-Afrotropical). They are white, approximately 5–6 mm long, 1 mm broad and slightly arcuate or straight. Andersson (1974) described the abdomen as having fat bodies, which were also described by Fuller (1938) for the Australian mythicomyiid *Acridophagus flavoscutellaris* (Roberts) (as "*Cyrtomorpha flavoscutellaris*") (non-Afrotropical). The larva is metapneustic, with inconspicuous spiracles on the first thoracic and eighth abdominal segments. The head capsule is weakly sclerotised, possessing rod-like antennae with a terminal cone-like apex and the metacephalic rods and tentorial arms are long, extending well into the first thoracic segment (Fig. 45). The body consists of 12 segments (Fig. 44), with small paired abdominal prolegs on the venter of segments 5–9 (abdominal segments 2–6) (Fig. 46). The terminal segment (12) possesses four apical abdominal prolegs (Fig. 47). Andersson (1974) observed these prolegs being used to manoeuvre the larvae in combination with the mandibles, which grab the substrate and pull the larva forward.

The pupal stage of Afrotropical mythicomyiids is represented by that illustrated for the pupal exuvium of *Psiloderoides mansfieldi* Hesse (by Hesse 1967) (Figs 41–43) and for *Glabellula* by those illustrated from a living specimen of *G. arctica* by Andersson (1974) (Fig. 48). Both possess the synapomorphic condition for Mythicomyiidae of a caudal armature (best illustrated in Fig. 42), consisting of slender hook-like processes curved 90° (these structures curved only 45° in Bombyliidae). Each pupa exhibits differences that are most likely related to habitat and behaviour. For example, *Glabellula* pupae do not have cephalic armature, while such thorn-like armature is found in *Psiloderoides mansfieldi*. This is related to the pupa of *Psiloderoides* needing to grasp the substrate to emerge away from the host (Hesse (1967) stated that pupae were collected in the soil away from grasshopper egg packets), while Andersson (1974) wrote that the pupae of *Glabellula* emerge in the ants' nests, since he observed pupae in the nests and collected adults when sifting contents of ants' nests. The colour of the *Glabellula* pupa begins white and slowly darkens until almost the entire pupa is black in colour. The living colour of *Psiloderoides* was not given by Hesse (1967), although it is probably also dark brown to blackish, as are most fully-developed bombylioid pupae. Andersson (1974) did not provide a detailed description of the *Glabellula* pupa, but it is of the typical bombylioid shape (curved upon itself), with small wing sheaths, rows of abdominal bristles and caudal armature, consisting of hook-like thorns curved 90°. There are no bristles or spines on the head or thorax, but sparse rows of thin bristles exist on the abdominal segments. The pupal exuvium of *Psiloderoides mansfieldi* also lacks bristles on the head and thorax, but cephalic armature is present, consisting of a pair of thorn-like processes on each side of the anterior portion of the head capsule (Fig. 43). The abdomen possesses rows of bristles on each segment that appear stronger than those found in *Glabellula* (Fig. 48).

Economic significance

No species of economic significance are known.

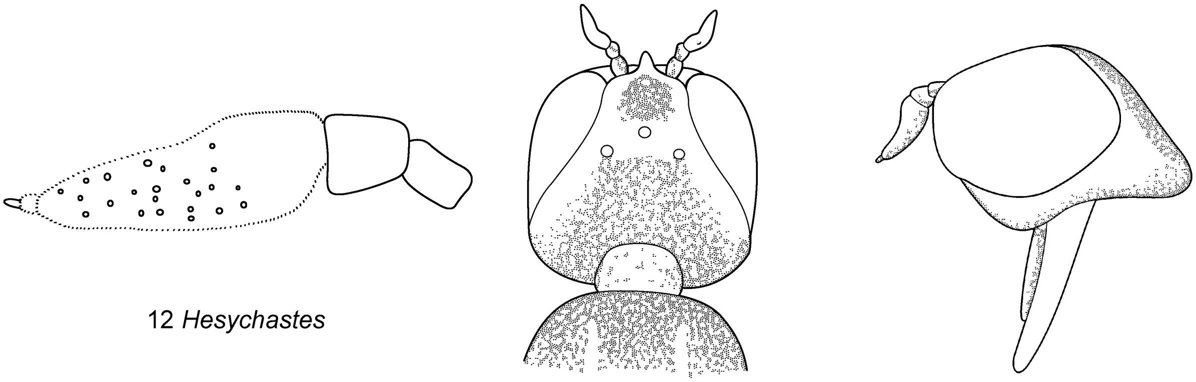
Classification

Mythicomyiidae are included in the Asiloidea, but their exact relationships with other families in that superfamily have been a point of contention. Due to their extremely small size and curious body shapes, some genera have at times been placed in Acroceridae (see Chapter 42) or Empididae *sensu lato* (see Chapters 51–55). Melander (1902) originally placed his new subfamily Mythicomyiinae in the Empididae *sensu lato*. Becker (1913), probably without knowledge of Melander's (1902) work, proposed the subfamily Cyrtosiinae (also comprising genera in now considered Mythicomyiidae) and placed it in the Bombyliidae, where mythicomyiids have long been treated.

Rohdendorf (1961) was the first to list the group (as Cyrtosiidae) as a family in the Bombylioidea in his proposed classification of the Diptera; and more formally (Rohdendorf 1964) proposed raising the group to familial level pending further analysis. Zaitzev (1992) was the first to provide characters warranting raising the group to familial level, but his lead was not followed by Yeates (1994) who, although placing the clade as the basal sister-group to the remainder of the Bombyliidae, treated the group as a subfamily of Bombyliidae. A number of works including Evenhuis (1994, 2002*b*, *c*, 2009, 2013), Evenhuis & Greathead (1999), Evenhuis *et al*. (2009), Greathead & Evenhuis (2001*a*), Grimaldi *et al*. (2011) and Irwin *et al*. (2003) have followed Zaitzev's lead and treated the group as a separate family. More recent molecular analyses by Trautwein (2009) and Trautwein *et al*. (2011) have shown the Mythicomyiidae to be placed in a separate clade with *Heterotropus* Loew and having a sister-group relationship to the Bombyliidae *sensu stricto* clade. Within the family, Greathead & Evenhuis (2001) proposed the subfamily classification followed here. Five of the six subfamilies known worldwide occur in the Afrotropical Region.

Identification

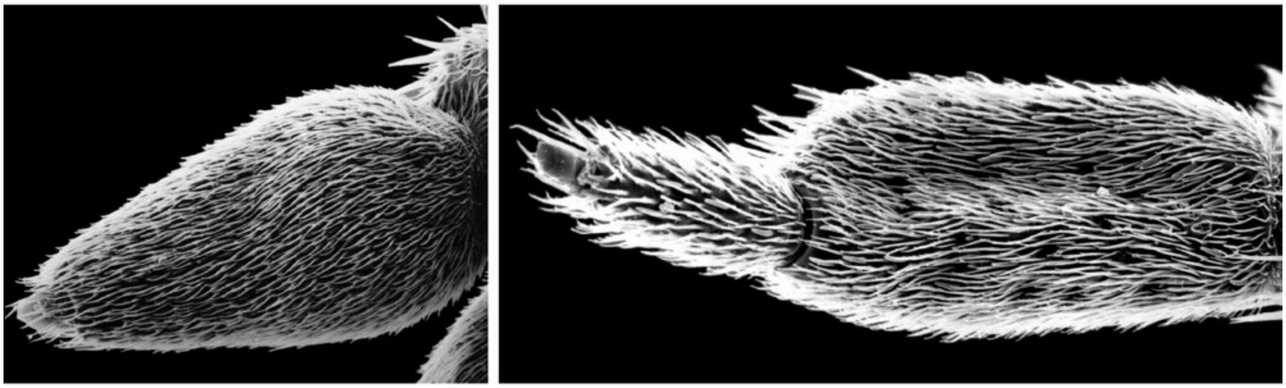
Mythicomyiids are found throughout most parts of the world, except the highest elevations and latitudes. They are not as common in the tropics, but genera such as *Cephalodromia* are known from these regions. Many of these "micro bee flies" have humpbacked thoraces and lack the dense vestiture common in Bombyliidae. Mythicomyiids have until recently not received much attention in the literature. Their small size has caused them to escape Malaise traps and aerial nets with large-mesh netting. Yellow pan trapping and fine-mesh netting has resulted



12 *Hesychastes*

13 *Hesychastes*

14 *Hesychastes*



15 *Leylaiya*

16 *Platypygus*

Figs 44.12–16. Antennal flagellomeres and heads of Mythicomyiidae: (12) flagellum of *Hesychastes solitus* Evenhuis, lateral view; (13) same, head, dorsal view; (14) same, head, lateral view; (15) SEM of flagellum of *Leylaiya mimnermia* Efflatoun, lateral view; (16) same, *Platypygus natalensis* Hesse. Fig. 12 (after Evenhuis 2001, fig. 2), Figs 13, 14 (after Evenhuis 2001, figs 1a, 1b).

in a tremendous amount of undescribed material of mythicomyiids from many parts of the world that are currently under revision. Due to their extremely small size and relatively soft bodies, it is strongly recommended they be preserved in fluid immediately after collection and be critical-point-dried when studied (see Chapter 2). Air dried specimens often have critical characters of the head and abdomen distorted, or impossible to discern, thus rendering them virtually useless to taxonomy.

The family has been little studied in the Afrotropical Region; the main papers being Hesse (1938, 1967) and Greathead & Evenhuis (2001*a*), the last mentioned presenting keys to genera and discussing the taxonomy and African faunal composition of each genus. The below key is based on the keys presented in Greathead & Evenhuis (2001a), with modifications to reflect additional genera and new characters found to distinguish genera.

Key to genera of Afrotropical Mythicomyiidae

1. Head prognathous, with extended lower occipital region; antennae inserted anterior to tip of oral margin (Figs 13, 14) . . . . *Hesychastes* Evenhuis

– Head more globular in shape, if occipital region extended posteriorly, then antennae inserted posterior to tip of oral margin (*e.g.*, Figs 17, 18) 2

2. Wing vein R_{4+5} ending in costal vein (*C*), at a level at or before end of vein M_2 (*e.g.*, Figs 28–31). 3

– Wing vein R_{4+5} ending in costal vein (*C*) at a level well beyond end of vein M_2 (*e.g.*, Figs 33, 35, 36). . . . 8

3. Wing with costal vein (*C*) ending at or near vein M_1; veins R_{4+5} and M_1 converging or parallel at wing margin (*e.g.*, Figs 27, 32) (LEYLAIYINAE) 4

– Wing with costal vein (*C*) ending at or near vein R_{4+5}; veins R_{4+5} and M_1 diverging at wing margin (*e.g.*, Figs 28, 30) (GLABELLULINAE). 5

4. Wing vein R_{2+3} present, ending in R_1 before costal vein (*C*), forming small triangular marginal cell (Fig. 32); antenna without evident second flagellomere . . . . *Pseudoglabellula* Hesse

– Wing vein R_{2+3} absent, no triangular marginal cell (Fig. 27); antenna with small second flagellomere (Fig. 15). . . . . *Leylaiya* Efflatoun

5. Wing vein R_{2+3} ending in vein R_1, forming small triangular cell r_1 (*e.g.*, Figs 29–31); clypeus normal, not well-developed and bulbous (*e.g.*, Fig. 25) 6

– Wing vein R_{2+3} absent (Fig. 28); clypeus large, bulbous (Figs 19, 20). . . . . *Mnemomyia* Bowden

6. Wing vein M_1 with basal portion evanescent or absent (Fig. 31) . . . . *Doliopteryx* Hesse

– Wing vein M_1 complete (*e.g.*, Figs 29, 30). 7

7. Abdominal tergum 2 with sclerotisation complete, not interrupted medially; antenna with stylus inserted subapically on second antennal flagellomere (Fig. 2); first antennal flagellomere width ½ to ⅓ its length, ovate . . . . *Glella* Greathead & Evenhuis

– Abdominal tergum 2 with sclerotisation interrupted medially (Fig. 23); antennal stylus inserted apically on second antennal flagellomere, or not evident; first antennal flagellomere width subequal to its length, often rounded (Fig. 7). . . . . *Glabellula* Bezzi

8. Wing vein R_{2+3} absent (Fig. 34); female spermathecae spherical with apical invagination (Fig. 37) (EMPIDIDEICINAE) . . . . *Empidideicus* Becker

– Wing vein R_{2+3} present (*e.g.*, Figs 26, 33, 35, 36); female spermathecae shaped otherwise (*e.g.*, Figs 38–40). 9

9. Wing vein R_{2+3} shorter than R_{4+5}, turned upward and meeting costal vein (*C*) much closer to end of vein R_1 than to end of vein R_{4+5} (*e.g.*, Fig. 26) (PSILODEROIDINAE). 10

– Wing vein R_{2+3} subequal in length to vein R_{4+5}, ending in costal vein (*C*) much closer to vein R_{4+5} than to vein R_1 (*e.g.*, Figs 33, 35, 36) (PLATYPYGINAE). 11

10. Proboscis much reduced, non-functional; habitus acrocerid-like (Fig. 26); head small, rounded; second antennal flagellomere much shorter than first; females large, males considerably smaller . . . . *Psiloderoides* Hesse

– Proboscis tubular, not reduced; habitus not acrocerid-like (Figs 21, 22); head not disproportionally small compared to thorax and abdomen; second antennal flagellomere ¾ size to equal in length to first (Fig. 11); females and males of equal size (Figs 21, 22) . . . . *Onchopelma* Hesse

11. Wing cell *dm* open distally, not closed by crossvein (*e.g.*, Fig. 33). 12

– Wing cell *dm* closed distally by crossvein (*e.g.*, Figs 35, 36) 13

12. Oral cavity with prominent ventral sulcus and produced posteriorly resulting in well-developed postgena (Figs 17, 18) . . . . *Cephalodromia* Becker

– Oral cavity without prominent ventral sulcus; postgena normal, or if produced posteriorly, a bulbous or blunt process, not pointed . . . . *Cyrtosia* Perris

13. Wing vein R_1 short, ending in costal vein (C) before level of *r–m* crossvein; vein *Sc* complete, ending in costal vein (C); crossvein *r–m* at middle of cell *dm* (Fig. 35); first antennal flagellomere with basoventral and apicoventral bulges (Fig. 10); female spermathecae with long sclerotised apical duct leading to bulbous, club-like and rounded reservoir (Fig. 39) . . . . *Ahessea* Greathead & Evenhuis

– Wing vein R_1 long, ending in costal vein (C) beyond level of crossvein *r–m*; vein *Sc* incomplete, not ending in costal vein (C) (*e.g.*, Fig. 36); first antennal flagellomere shaped as in Fig. 4, without such bulges basally or apically (*e.g.*, Fig. 16); crossvein *r–m* and female spermathecae not as above 14

14. Oral cavity with prominent ventral sulcus and produced posteriorly, resulting in well-developed postgena (as in Figs 17, 18) . . . . [*Cyrtisiopsis* Séguy]

– Oral cavity without prominent ventral sulcus; postgena normal, or if produced posteriorly, a bulbous or blunt process, not pointed . . . . *Platypygus* Loew

Synopsis of the Fauna

Of the 30 known extant genera worldwide, 14 are known from the Afrotropical Region. More than 380 species of Mythicomyiidae are known worldwide, more than 50 of which occur in the Afrotropical Region. Outside of the Nearctic, which has the highest number of species (183), due to the mega-diverse genus *Mythicomyia* Coquillett, the Afrotropical Region is one of the most diverse regions for Mythicomyiidae and, after study is completed on a number of speciose genera (*Empidideicus* and *Glabellula*), it could easily rival the Palaearctic for second most number of species worldwide.

***Ahessea* Greathead & Evenhuis** (Platypyginae)**.** An endemic monotypic genus. This genus is most similar to *Cyrtisiopsis*, but can be distinguished by the complete wing vein *Sc*; the position of crossvein *r–m* at the middle of cell *dm* (Fig. 35) and the first antennal flagellomere with distinctive apical and basal bulges (Fig. 10). *Ahessea crassirostris* (Hesse, 1967) characteristically has a very well-developed occiput and very long mouthparts. The detailed description of the genus by Hesse (1938) (as *Cyrtisiopsis*) serves to provide additional information on characterisation of the genus.

***Cephalodromia* Becker** (Platypyginae)**.** This genus (Fig. 1) is known from 18 species in the southern and eastern Palaearctic, Afrotropical and Oriental Regions. Many species were originally described in *Cyrtosia*. Eleven species are currently known from the regions covered in this *Manual*, most found primarily in South Africa. Little is known of their biology, but some adults in South Africa have been observed to aggregate, possibly for food or mating leks (S.A. Marshall, *in litt*.). Mühlenberg (1971) studied the courtship and mating behaviour of an undetermined species in Greece, which also showed evidence of aggregating. See Fig. 5 for an example of the antenna of this genus and Figs 17, 18 for the head.

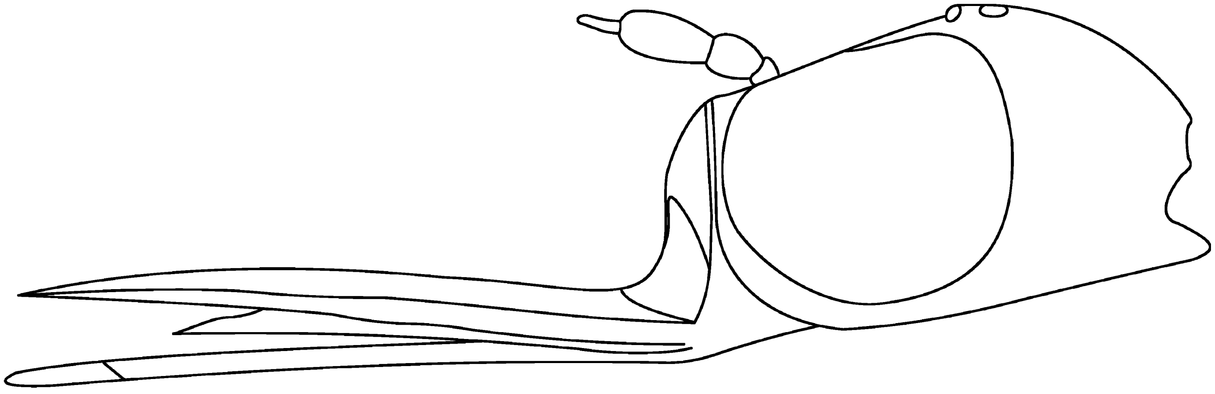
[***Cyrtisiopsis* Séguy** (Platypyginae)**.** Transfer of *C. crassirostris* Hesse to *Ahessea* in Greathead & Evenhuis (2001) has resulted in the restriction of this genus to three species in northern Africa and the eastern Mediterranean. It is included here in the event that future research may discover specimens from areas of the northern or eastern portions of the Afrotropical Region. See Fig. 36 for an example of the wing venation of this genus and Fig. 38 for an example of the spermathecal reservoir.]

***Cyrtosia* Perris** (Platypyginae)**.** This genus is known from the Palaearctic and Afrotropical Regions. Currently, 37 species are known, 9 of which are found in the regions covered by this *Manual*. Species that were described as *Cyrtosia* from Australia have been transferred to *Acridophagus* (Evenhuis 1989), which is a member of the subfamily Psiloderoidinae. See Fig. 6 for an example of the antenna of this genus and Fig. 33 for the wing.

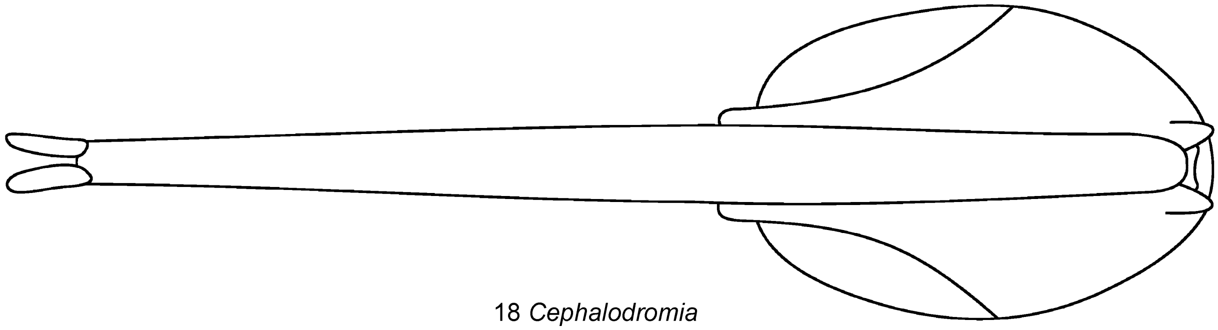
***Doliopteryx* Hesse** (Glabellulinae)**.** Originally, *Doliopteryx* was only known from four specimens representing two species. However, concentrated collecting by yellow pan and Malaise trapping [specimens examined in the revision by Evenhuis (2000)], has resulted in thousands of specimens representing 12 species from the Middle East, Egypt, Namibia, South Africa and Zimbabwe. Nine species are known from the Afrotropical Region; additional new species are known from the United Arab Emirates, Oman and western India (Evenhuis, unpubl.). See Fig. 9 for an example of the antenna of this genus and Fig. 31 for the wing.

***Empidideicus* Becker** (Empidideicinae)**.** This genus is predominantly Old World with high diversity in southern Africa and Arabia. Many undescribed forms are known from these areas, as well as Madagascar, India, Pakistan, Sri Lanka, Thailand, Flores Island (Indonesia) and the Kimberley Range of northern Australia (Evenhuis, unpubl.). Once revisionary work on this genus is completed, it is estimated that the number of species could easily triple or possibly quadruple. Currently, 40 species of this genus are known worldwide, with 20 described from the regions covered in this *Manual*, including one from Madagascar (Evenhuis 2007) and two from Socotra Is. (Yemen) (Greathead & Evenhuis 2001*b*). See Fig. 3 for an example of the antenna of this genus and Fig. 34 for the wing.

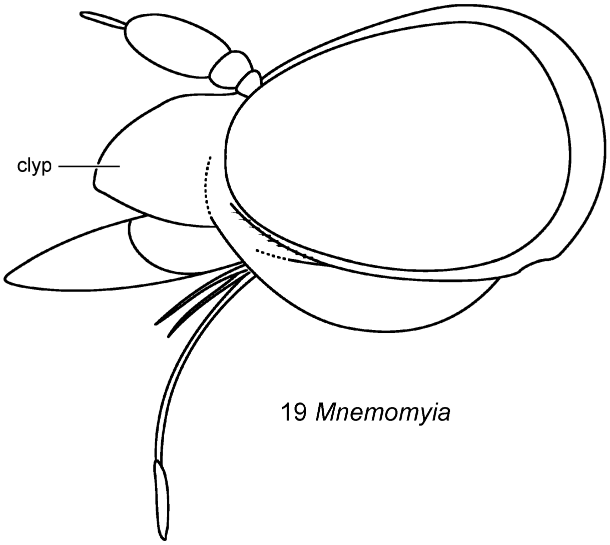
***Glella* Greathead & Evenhuis** (Glabellulinae)**.** A genus of two described species: one from Chile – *G. quebradae* (Hall); the other from Namibia – *G. ashleyi* Greathead & Evenhuis, 2001, which exhibits a clear disjunct distribution of the genus. It is a very rare genus, known only from a handful of specimens of each species. See Fig. 2 for an example of the antenna of



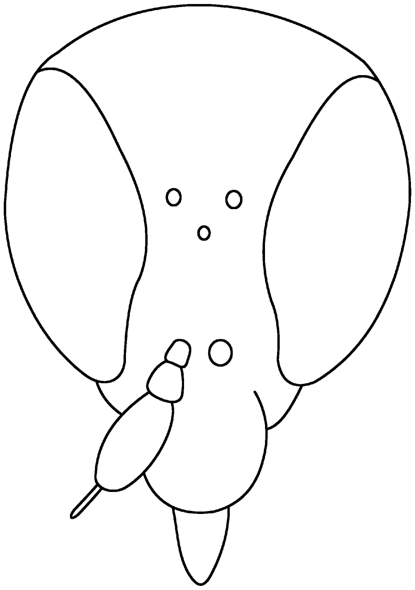
17 *Cephalodromia*



18 *Cephalodromia*



19 *Mnemomyia*



20 *Mnemomyia*

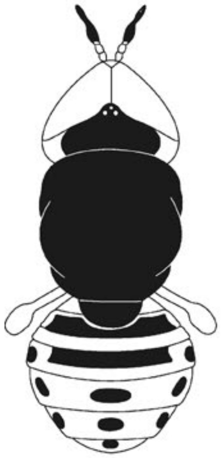
Figs 44.17–20. Head capsules of Mythicomyiidae (diagrammatic): (17) *Cephalodromia fusca* (Séguy), lateral view; (18) same, ventral view; (19) *Mnemomyia rostrata* Bowden, lateral view; (20) same, dorsal view.

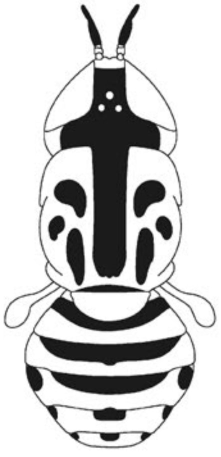
Abbreviation: clyp – clypeus.

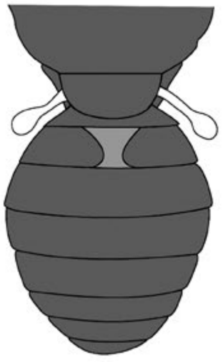
this genus, Fig. 29 for the wing venation and Fig. 40 for the spermathecal reservoir.

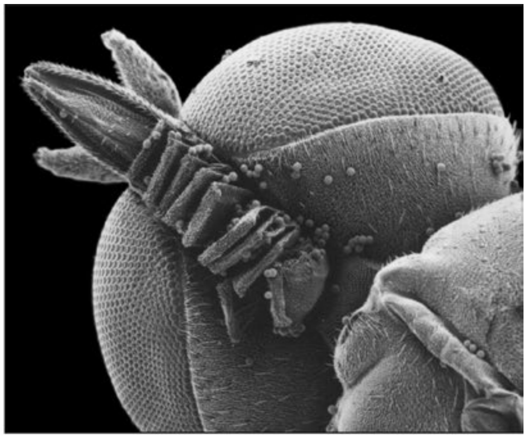
Glabellula **Bezzi** (Glabellulinae)**.** *Glabellula* (Fig. 25) is currently the subject of a world revision by the writer. More than 25 new species are being described, which will result in a total of some 40–50 species worldwide. The genus is virtually cosmopolitan, but localised in its range. It is found in North and South America, Europe, Asia, Africa, and Australia. It has not yet been recorded from the Oriental Region. Immatures have been recorded in Europe as ant inquilines in the nests of *Formica* and *Coptoformica* Müller spp. (Anderssen 1974). The genus is currently represented in the regions covered by this *Manual* by only two species, *G. natalensis* Hesse, 1967 (South Africa) and *G. thespia* Evenhuis, 2009 (United Arab Emirates), but a number of new species are awaiting description from southern Africa and Madagascar (Evenhuis, unpubl.). See Fig. 7 for an example of the antenna of this genus, Fig. 23 for the abdomen and Fig. 30 for wing venation.

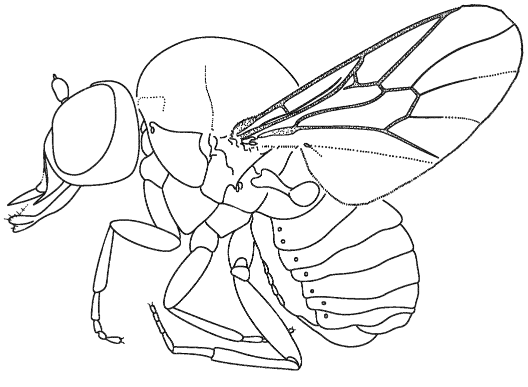
Hesychastes **Evenhuis** (unplaced to subfamily)**.** This unusual relict monotypic genus is only known from the Brandberg massif, Namibia, where it was sampled in Malaise and pan traps (Evenhuis 2001). Nothing is known of its life history and it is

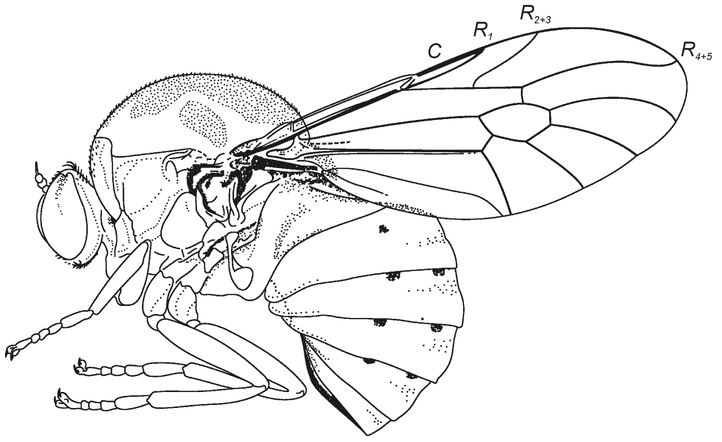

21 *Onchopelma* ♂


22 *Onchopelma* ♀


23 *Glabellula*


24 *Leylaiya*


25 *Glabellula*



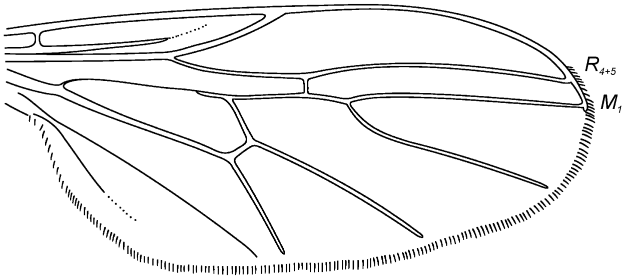
26 *Psiloderoides*

Figs 44.21–26. Dorsal features, head and habitus of Mythicomyiidae: (21) *Onchopelma brevifasciatum* Evenhuis, dorsal view ♂; (22) same female (showing sexual dimorphism); (23) abdomen of *Glabellula natalensis* Hesse, dorsal view ♂ (showing interruption of sclerotisation on abdominal tergum 2); (24) SEM of venter of head of *Leylaiya whiteheadi* Greathead & Evenhuis (showing accordion-like retracted proboscis); (25) habitus of female *G. natalensis* Hesse, lateral view; (26) same, *Psiloderoides mansfieldi* Hesse, lateral view. Figs 21, 22 (after Evenhuis 2002*a*, figs 1, 2).

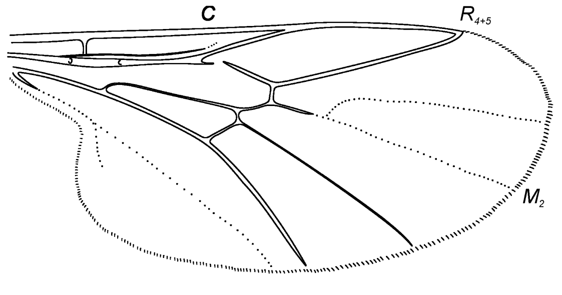
Abbreviations: *C* – costal vein; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

currently unplaced to subfamily. See Fig. 12 for an example of the antenna of the genus and Figs 13, 14 for the head.

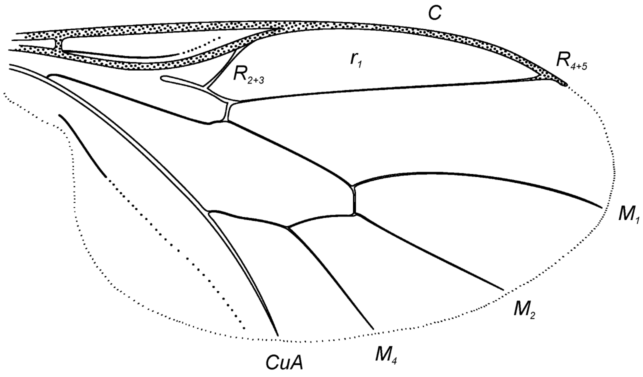
Leylaiya **Efflatoun** (Leylaiyinae)**.** Originally described and based on a single Egyptian species. Examination of the southern African genera *Euanthobates* Hesse and *Acoecus* Hesse, however, has revealed these to be congeneric with *Leylaiya*. Six species are currently known from the southern Palaearctic and Afrotropical Regions (Gharali & Evenhuis 2011); additional new species from western India, the United Arab Emirates, Oman, Namibia, and South Africa await description (Evenhuis, unpubl.). Five described species occur in the regions covered



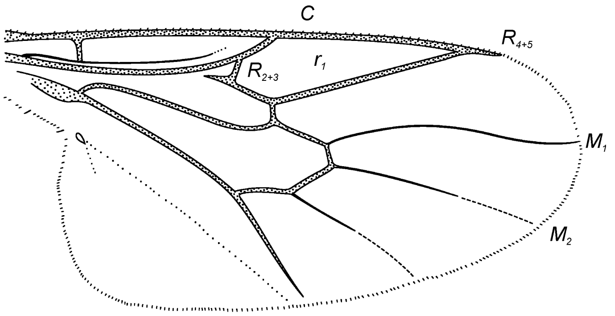
27 *Leylaiya*



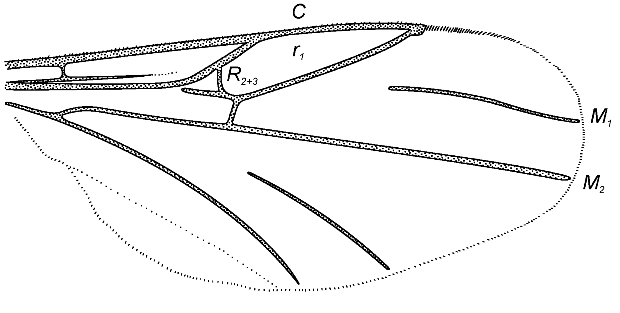
28 *Mnemomyia*



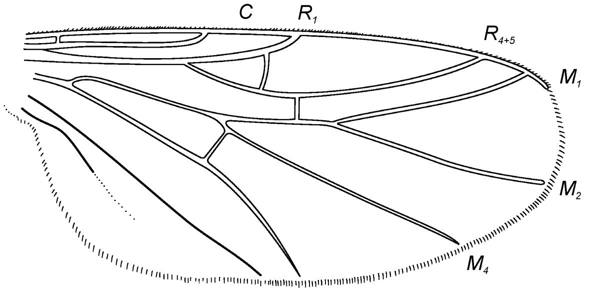
29 *Glella*



30 *Glabellula*



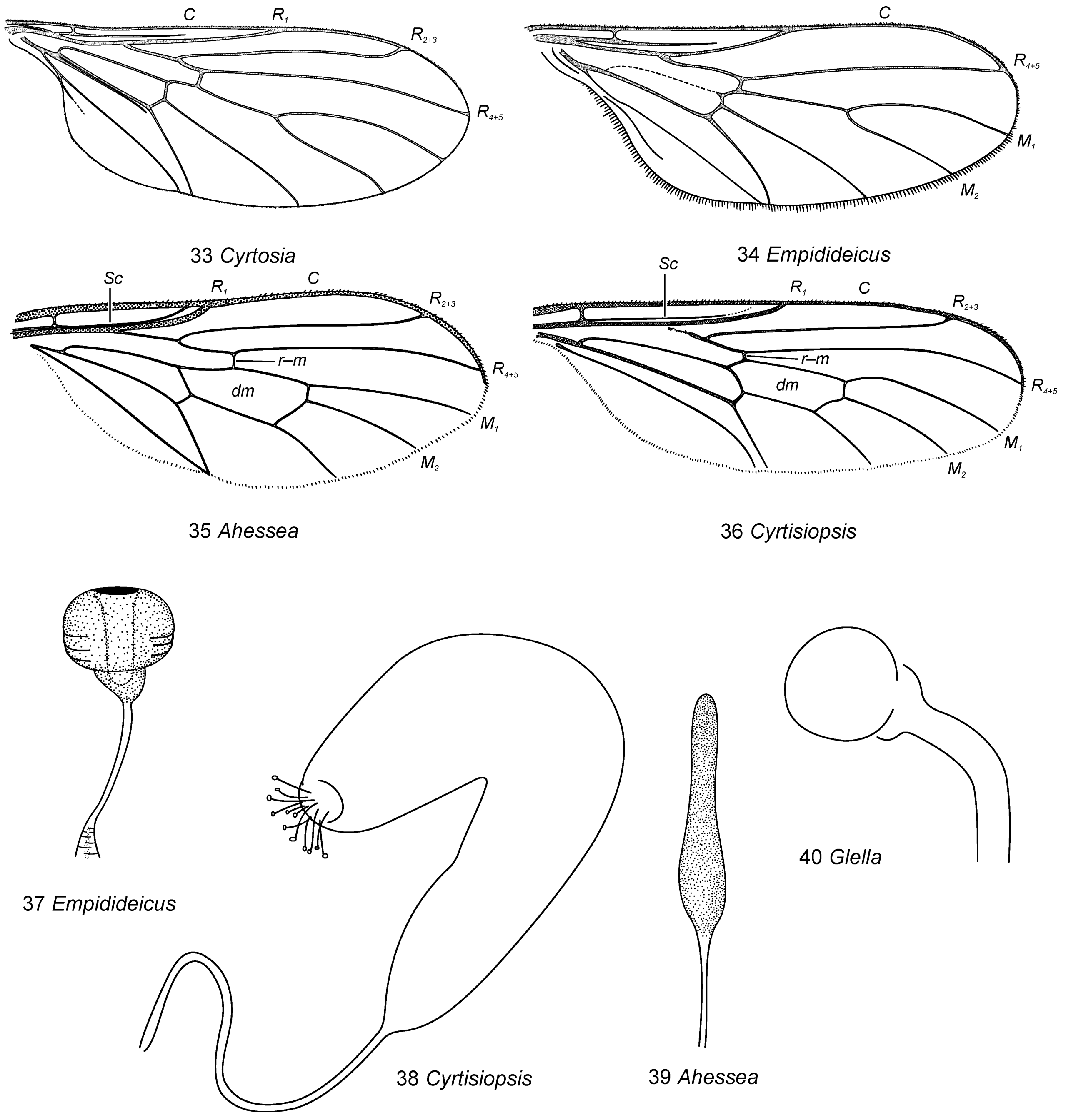
31 *Doliopteryx*



32 *Pseudoglabellula*

Figs 44.27–32. Wings of Mythicomyiidae (dorsal views): (27) *Leylaiya mellivora* (Hesse); (28) *Mnemomyia rostrata* Bowden; (29) *Glella ashleyi* Greathead & Evenhuis; (30) *Glabellula natalensis* Hesse; (31) *Doliopteryx welwitschia* Evenhuis; (32) *Pseudoglabellula meridionalis* Hesse.

Abbreviations: *C* – costal vein; *CuA* – anterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.



33 *Cyrtosia*

34 *Empidideicus*

35 *Ahessea*

36 *Cyrtisiopsis*

37 *Empidideicus*

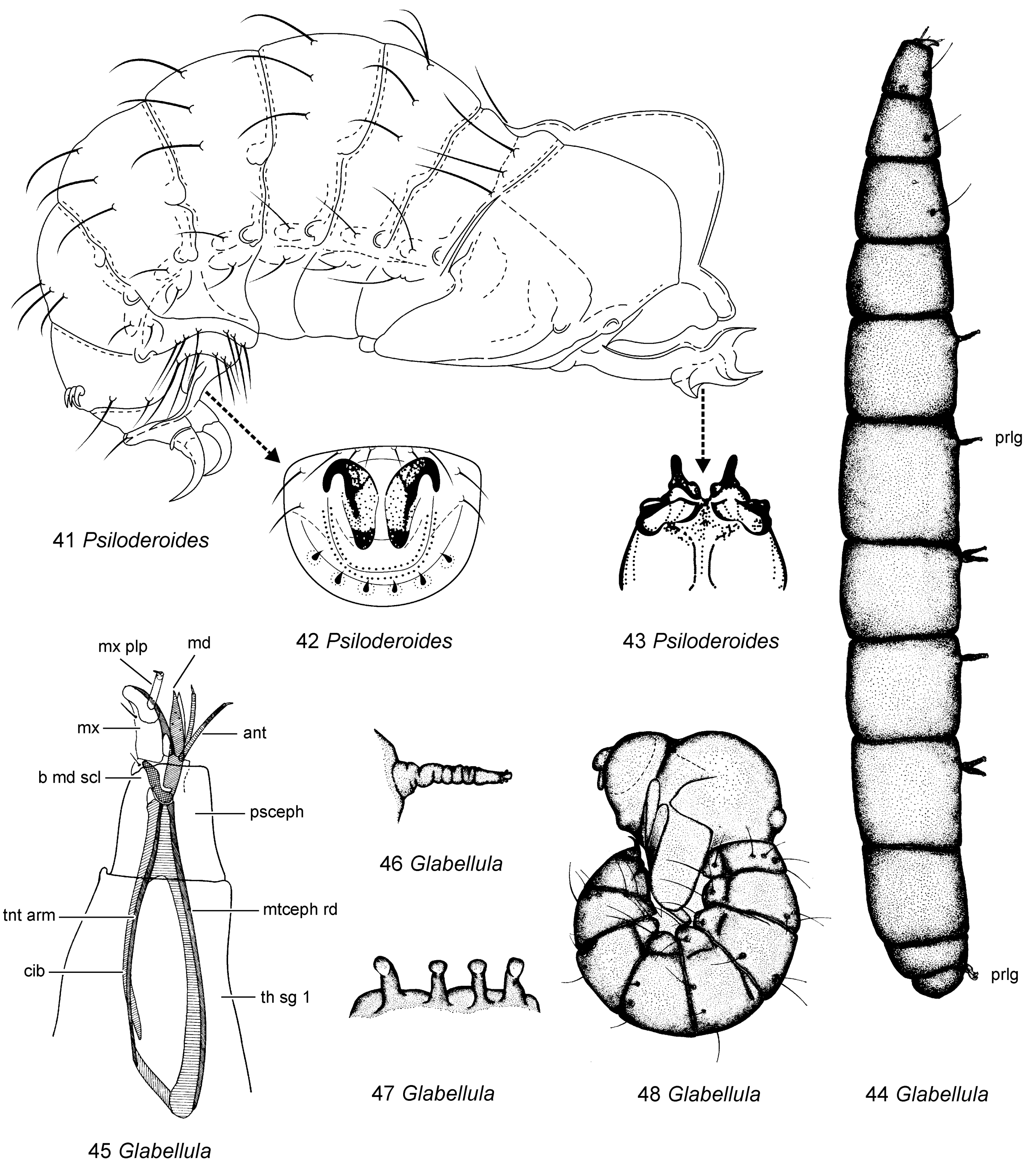
38 *Cyrtisiopsis*

39 *Ahessea*

40 *Glella*

Figs 44.33–40. Wings (dorsal views) and female spermathecal reservoirs (lateral views) of Mythicomyiidae: (33) wing of *Cyrtosia* sp.; (34) same, *Empidideicus turneri* Hesse; (35) same, *Ahessea crassirostris* (Hesse); (36) same, *Cyrtisiopsis singularis* (Séguy) (non-Afrotropical); (37) spermathecal reservoir of *Empidideicus socotrae* Greathead & Evenhuis; (38) same, *Cyrtisiopsis melleus* (Loew) (non-Afrotropical); (39) same, *Ahessea crassirostris* (Hesse); (40) same, *Glella ashleyi* Greathead & Evenhuis. Fig. 37 (after Greathead & Evenhuis 2001*a*, fig. 11).

Abbreviations: *C* – costal vein; *dm* – discal medial cell; M_1 – first branch of media; M_2 – second branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.



41 *Psiloderoides*

42 *Psiloderoides*

43 *Psiloderoides*

44 *Glabellula*

45 *Glabellula*

46 *Glabellula*

47 *Glabellula*

48 *Glabellula*

Figs 44.41–48. Immature stages of Mythicomyiidae: (41) pupal exuvium of *Psiloderoides mansfieldi* Hesse, lateral view; (42) same, detail of caudal armature, posterior view; (43) same, detail of cephalic armature, anterior view; (44) last instar larval habitus of *Glabellula arctica* (Zetterstedt), lateral view (non-Afrotropical); (45) same, detail of last instar larval mouthparts and anterior portion of larval body, lateral view; (46) same, detail of abdominal proleg found on segments 5–9, lateral view; (47) same, detail of apical abdominal prolegs of terminal segment 12, posterior view; (48) same, pupal habitus, lateral view. Figs 41–43 (after Hesse 1967, fig. 8), Figs 44–48 (after Andersson 1974, figs 1, 8, 3, 4, 5, respectively).

Abbreviations: ant – antenna; b md scl – basal mandibular sclerite; cib – cibarium; md – mandible; mtceph rd – metacephalic rod; mx – maxilla; mx plp – maxillary palpus; prlg – proleg; psceph – pseudocephalon; th sg – thoracic segment; tnt arm – tentorial arm.

by this *Manual*. Hull (1973) regarded his subgenus *Acoecus* to have "caeca-like" protuberances on the venter of the head. Close examination has revealed that Hull misinterpreted these "protuberances". They in fact form part of the proboscis, which retracts accordion-fashion into the open oral cavity of the venter of the head (Fig. 24). In South Africa, some species are pollinators of Aizoaceae: *L. whiteheadi* Greathead & Evenhuis, 2001 on *Conophytum pellucidum* Schwantes (Liede *et al*. 1991). Others have been sampled in yellow pan traps deployed in the vicinity of *Welwitschia mirabilis* Hook.f. (Welwitchiaceae) plants (Evenhuis, unpubl.) and may be involved in pollination of those ancient gymnosperms.

***Mnemomyia* Bowden** (Glabellulinae)**.** An endemic genus, apparently indigenous to Namibia and South Africa. Bowden (1975) created this southern African genus to comprise his new species *M. rostrata* and one additional species, *M. mellea* (Bezzi, 1908), the latter originally described in *Glabellula*. The genus is an unusual one and is characterised by the prominent bulging clypeus and flattened mesonotum. Bowden (1975) expressed concern that it was even a bombyliid, due to its anomalous characters. It does not fit well in the Glabellulinae and further research may reveal it to belong elsewhere, possibly the Leylaiyinae. Previously known from only two specimens representing two species, but recent collecting efforts has resulted in numerous individuals of many new species, especially so from Namibia. See Fig. 8 for an example of the antenna of the genus, Figs 19, 20 for the head and Fig. 28 for wing venation.

***Onchopelma* Hesse** (Psiloderoidinae)**.** An endemic genus, apparently indigenous to Namibia and South Africa, with seven known species. Evenhuis (2002*a*) revised the genus and provided an identification key to the species. Sexual dimorphism is exhibited in species of this genus (see Figs 21, 22), which is rarely shown in other Mythicomyiidae (exceptions include *Psiloderoides* in the Afrotropical Region, *Acridophagus* Evenhuis in the Australasian Region and *Mythicomyia* in the New World).

***Platypygus* Loew** (Platypyginae)**.** Primarily a Euro-Asian genus with most of its 13 described species occurring in western and central Asia with extreme geographical outliers in western North America and South Africa (Gharali *et al*. 2013). Only one species, *P. natalensis* Hesse, 1967, is known from South Africa. See Fig. 16 for an example of the antenna of the genus.

***Pseudoglabellula* Hesse** (Leylaiyinae)**.** This endemic genus was originally described based on a single specimen from South Africa. Additional males and females from Malaise and pan traps have been examined from Namibia. It remains an uncommon genus, but is not as rare as originally thought.

***Psiloderoides* Hesse** (Psiloderoidinae)**.** Only two species are known of this endemic South African genus with vestigial mouthparts, *P. mansfieldi* Hesse, 1967 (Fig. 26) and *P. dauresensis* Kirk-Spriggs & Evenhuis, 2008. The type species, *P. mansfieldi*, was reared as an egg-pod predator from the egg packets of the Brown locust, *Locustana pardalina* (Walker) (Hesse 1967). Nothing is known of the life history of *P. dauresensis*, but it is probably also an orthopteran egg-pod predator (Kirk-Spriggs & Evenhuis 2008).

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BOMBYLIIDAE 45

(Bee Flies)

Neal L. Evenhuis and Carlos Einicker Lamas

Fig. 45.1. Female of *Marleyimyia xylocopae* Marshall & Evenhuis (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized (body length: 2–20 mm), usually robust flies, often with long projecting proboscis, usually with a pattern of coloured scales and setulae and wing often with distinctive infuscation (*e.g.*, Figs 1, 6, 12, 14, 16). Many taxa, particularly Bombyliinae, are setulose and have a general resemblance to bees (*e.g.*, Figs 6–9) or wasps (Fig. 3), hence the vernacular name "bee flies".

Head in males frequently holoptic (*e.g.*, Fig. 25); antenna (Figs 39–53) with 1 or 2 flagellomeres, frequently with terminal seta-like stylus.

Thorax with pronotum reduced, not apparent in most genera. Legs long and slender; pulvilli pad-like, reduced or absent. Wing vein R_{4+5} branched; vein M_3 absent (4 or 3 posterior cells) (Figs 56–73).

Abdomen broad, rounded, or elongate and cylindrical; male terminalia (Figs 74–103) with epandrium comprising 1 sclerite; surstylus absent; gonocoxites almost invariably fused basally, bearing articulated gonostyli apically; aedeagus usually sheathed, often with elaborate parameral sheath; ejaculatory apodeme laterally compressed, usually well-developed; sperm pump usually well-developed; female terminalia with segment 8 modified to form sand-chamber in more apomorphic subfamilies (*e.g.*,

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1019–1055.

Anthracinae, Bombyliinae, Cythereinae, Ecliminae, Lomatiinae), but sometimes secondarily reduced or absent; acanthophorites present, usually bearing strong spines; normally 3 spermathecae present with sclerotised bulbs (Figs 104–106).

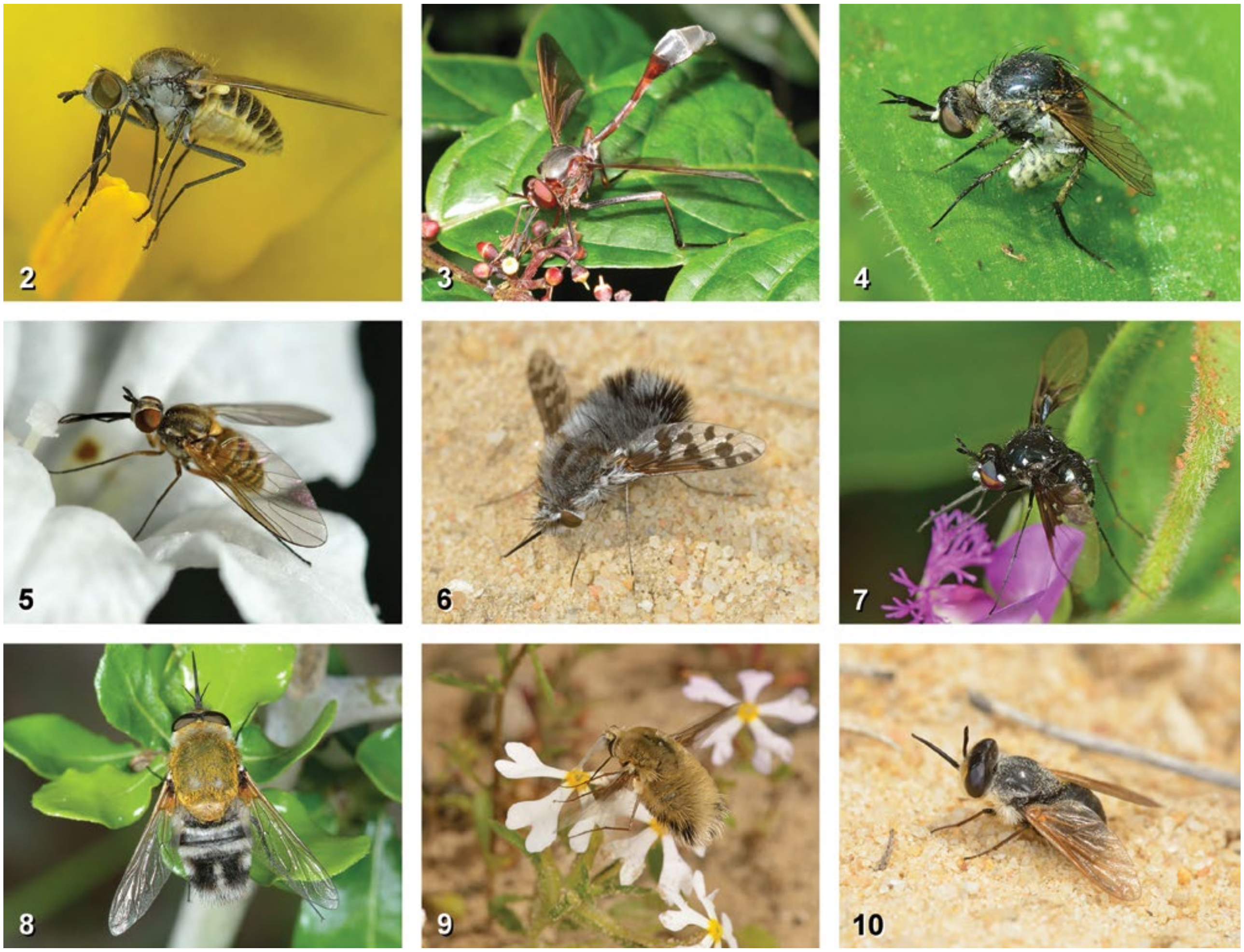
Adult Bombyliidae can be separated from Mythicomyiidae (see Chapter 44), formerly treated as a subfamily of Bombyliidae, by the branched wing vein R_{4+5}, presence of an arculus (vein *MA*) (except in *Heterotropus* Loew) and presence of abdominal spiracles in the pleural membrane and not the tergites. Immatures are separated in the pupal stage by the caudal armature not or slightly curved (these processes curved 90° in Mythicomyiidae).

Biology and immature stages

Adult Bombyliidae can often be found basking on the ground and females, of those subfamilies with an abdominal sand-chamber, can be commonly observed filling these with sand grains, by dipping the tip of the abdomen into fine sand. Most are capable of rapid flight and many Bombyliinae, particularly males, hover over a marker and/or patrol small "territories" in lekking area protection. Adults, except those with vestigial mouthparts, feed on nectar and pollen and many females are obligate pollen-feeders (a nourishing requirement for developing ova). Many Bombyliidae are thus major pollinators of many arid-area flowering plants, especially annuals.

Few studies have been undertaken on immatures in the Afrotropical Region, but all reared immatures are predators or parasitoids of arthropods. It seems likely that the ancestral state was a generalist predator in soil and that evolution proceeded towards specialisation on particular hosts in the soil, leading to ectoparasitism and ultimately endoparasitism.

Hull (1973) provided a detailed overview of the immature stages of Bombyliidae, which go through egg, three larval instars



Figs 45.2–10. Photographs of living Afrotropical Bombyliidae: (2) *Apolysis* sp. (South Africa); (3) *Systropus* (*Diaerops*) *marshalli* (Bezzi) (Guinea); (4) *Toxophora* sp. (South Africa); (5) *Phthiria flavicosta* Hesse (South Africa); (6) *Australoechus megaspilus* (Bezzi) (South Africa); (7) *Bombylella delicata* (Wiedemann) (South Africa); (8) *Eurycarenus* sp. (South Africa); (9) *Anastoechus* sp. (South Africa); (10) *Corsomyza* sp. (South Africa). Figs 2, 4–10 (photographs © S.A. Marshall), Fig. 3 (photograph © C. Woolley).

and a pupal stage, before metamorphosing into the adult fly. Berg (1940) gave a description of the immature stages of *Systoechus vulgaris* Loew, 1863 (non-Afrotropical). As most Bombyliidae are similar in morphology, Berg's descriptions of the life stages serve as a general description of most other genera of Bombyliidae and is used, for the most part, as the basis for the descriptions provided below.

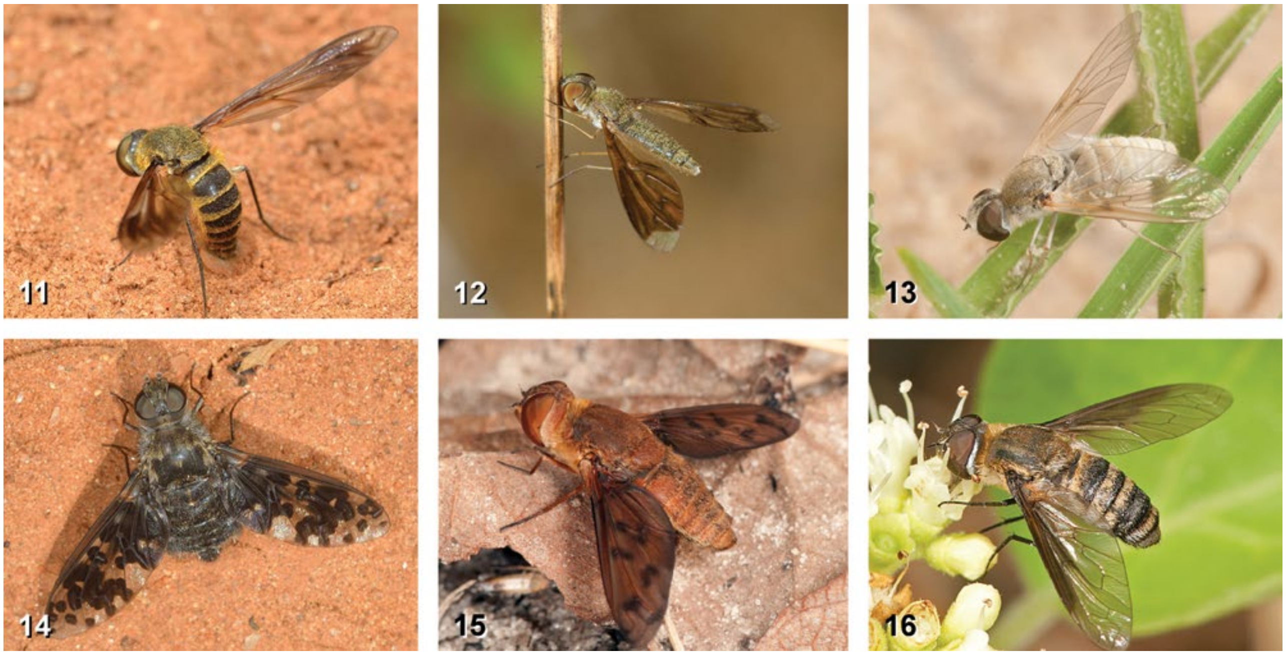
Eggs are ellipsoid and white, most without an evident operculum. Those of Toxophorinae (*e.g.*, *Systropus* Wiedemann and *Toxophora* Meigen), possess a collar-like ridge surrounding an operculum and are not covered with sand grains. It is presumed that this egg type corresponds to placement on or near a host, as opposed to eggs without an evident operculum and covered with fine sand grains, that are oviposited while the adult female hovers over the oviposition area.

The first-instar larva (*e.g.*, Fig. 107) is planidial, actively seeking a host after hatching. It is long, thin, cylindrical, and transparent, with three thoracic and nine abdominal segments. Each thoracic segment bears a pair of long curved setulae on the ventrolateral surface; the terminal abdominal segment bears two long curved setulae apically. Two prolegs are present on abdominal segments 2–6 and two pairs of prolegs are present on the posterior margin of segment 8. This stage has a metapneustic respiratory system with raised spiracles present only on the dorsolateral surface of abdominal segment 8.

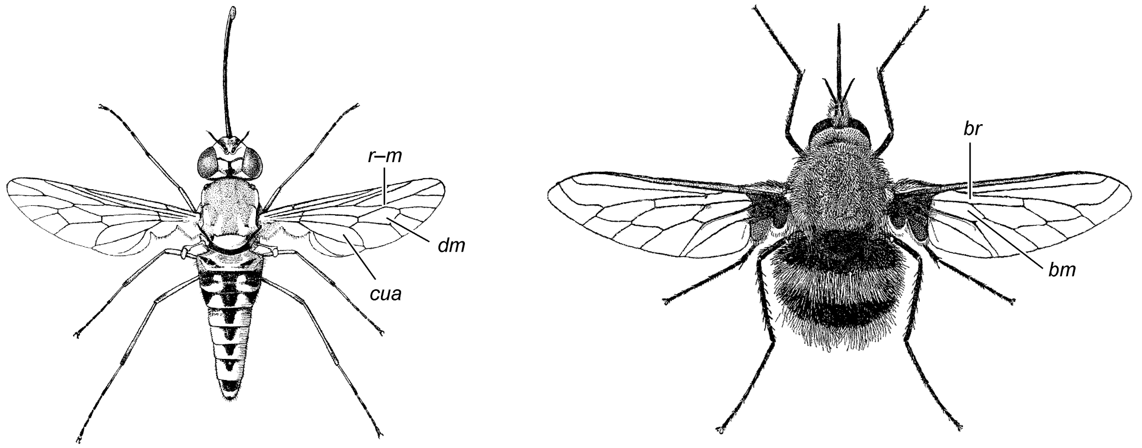
The much larger second-instar larva has three thoracic segments and nine abdominal segments. It is opaque, lacks prolegs, but has paired setulae lateroventrally on the three thoracic segments. This stage has an amphipneustic respiratory system, with prothoracic and penultimate abdominal spiracles.

The third-instar (Fig. 108) grows to about twice the length of the second-instar. The body is typically curved, crescent-like in curvature and whitish to yellowish in colour. Prolegs are absent, but weak setulae are present ventrolaterally on the thoracic segments. The respiratory system is amphipneustic, as in the second-instar.

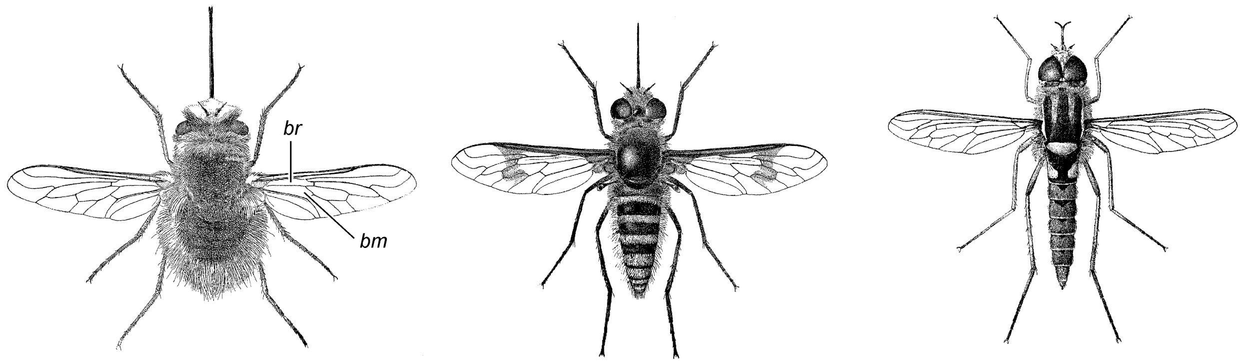
The pupal stage (Figs 109, 110) is the most commonly encountered – usually the exuvium after the adult has eclosed. The pupa is subequal in size to the third-instar. The colour of the living young pupa is yellowish, but becomes brown with age. The head capsule characteristically bears thorn- or barb-like processes (termed "cephalic armature"), that are divided into upper and lower sets of varying thickness, shape, and degree of sclerotisation; the upper pair are essentially the antennal sheaths; the lower ones are facial outgrowths and can be two to six pairs in number. These processes are used in manoeuvring through the soil and their morphology can be characteristic for identification to subfamily-, genus-, and/or (rarely) species-level. Some genera (*e.g.*, *Geron* Meigen), have these processes reduced or absent (Fig. 109) (Purrington & Evenhuis 2001) and this reduction may be a correlation to a non-soil-dwelling habitat. A long proboscis sheath is evident for long proboscis-bearing taxa, reduced or not evident for short or vestigial proboscis-bearing taxa. The thorax is generally bare, but some genera (*e.g.*, *Anthrax* Meigen) may possess long, dense wavy setulae along the posterodorsal margin. The wing and leg sheaths are bare, without modifications. Each abdominal



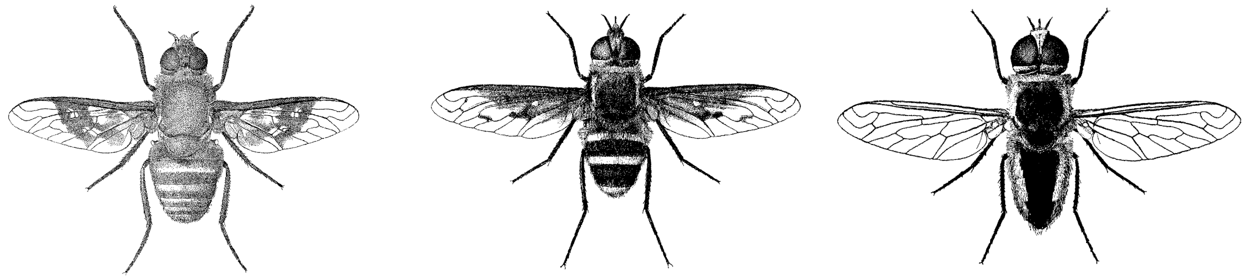
Figs 45.11–16. Photographs of living Afrotropical Bombyliidae: (11) *Notolomatia* sp. (South Africa) (♀ gathering sand into sand-chamber); (12) *Petrorossia plerophaia* Hesse (South Africa); (13) *Desmatoneura* sp. (South Africa); (14) *Anthrax* sp. (South Africa); (15) *Euligyra* sp. (South Africa); (16) *Defilippia luteicosta* (Bezzi) (South Africa). Photographs © S.A. Marshall.



17 *Heterotropus* 18 *Bombomyia*



19 *Anastoechus* 20 *Callostoma* 21 *Antonia*



22 *Thyridanthrax* 23 *Exoprosopa* 24 *Defilippia*

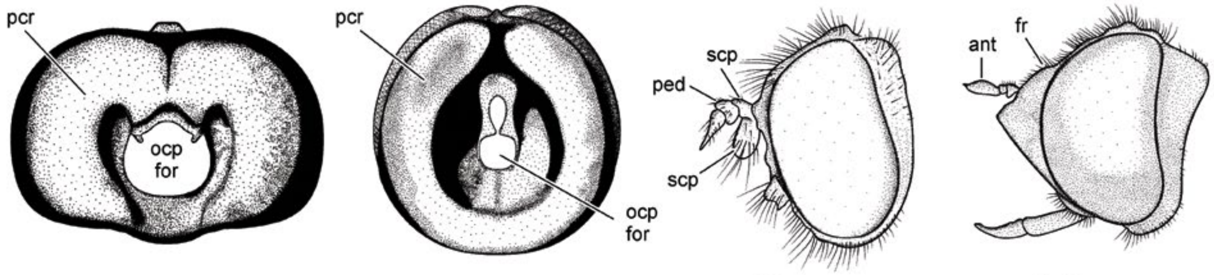
Figs 45.17–24. Habitus of Bombyliidae (dorsal views): (17) *Heterotropus aegyptiacus* Paramonov (non-Afrotropical); (18) *Bombomyia bombiformis* (Bezzi); (19) *Anastoechus exalbidus* (Wiedemann) (non-Afrotropical); (20) *Callostoma fascipenne* Macquart (non-Afrotropical); (21) *Antonia suavissima* Loew; (22) *Thyridanthrax polyphemus* (Wiedemann); (23) *Exoprosopa protuberans* Bezzi; (24) *Defilippia chionea* (Bezzi). Fig. 17 (Hull 1973, fig. 31), Fig. 18 (Bezzi 1924, fig. 1), Figs 19, 20 (Austen 1937, figs 11, 14), Figs 21, 23, 24 (Bezzi 1924, figs 10, 30, 38), Fig. 22 (Austen 1937, fig. 58).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *cua* – anterior cubital cell; *dm* – discal medial cell; *r–m* – radial–medial crossvein.

segment usually has a transverse dorsomedial ridge bearing thin L-shaped sclerotised barbs (frequently incorrectly termed “spines”), which are used for manoeuvring through soil; the number, size and thickness of these barbs vary among bee fly taxa, but are generally present in all soil-dwelling taxa and are absent in non-soil-dwelling taxa (*e.g.*, *Geron*; see Purrington & Evenhuis 2001). Setulae are present dorsally and laterally on all abdominal segments; the terminal abdominal segment possesses a pair of thorn-like processes termed “caudal armature”; these processes are either uncurved or slightly curved (always less than 90°) and thickly sclerotised apically.

Most adult female bee flies possess an area at the apex of the abdomen (surrounded by a dense and thick fringe of setulae), that is termed the “sand-chamber”. Females search for places with fine grains of sand and fill the sand-chamber with these grains of sand by movements of the acanthophorite spines at the tip of the abdomen, as the abdomen is dipped into the sand (*e.g.*, Fig. 11). While hovering in mid-air, females of the genera possessing a sand-chamber oviposit into holes or irregularities in the ground, by ejecting thin-walled, sticky eggs through this chamber, which contains previously-gathered fine sand particles adhering to the dense setulae. The eggs obtain a covering of fine sand grains when they are oviposited and are thus thought to be protected from desiccation. The more primitive clades within the family lack the characteristic sand-chamber found in the Anthracinae and Bombyliinae and instead have a tubular ovipositor. In Toxophorinae (one of the more primitive subfamilies containing genera without a sand-chamber), the eggs of *Geron* are thick-walled and have been observed by the senior writer being oviposited directly on leaf axils near the host (undetermined psychid caterpillars). Some genera among the sand-chamber subfamilies, that are more advanced phylogenetically, have reverted to a more tubular ovipositor, either having a reduced sand-chamber (*Beckerellus* Greathead), or having completely lost it (*Antonia* Loew, *Lepidochlaenus* Hesse and non-Afrotropical *Lordotus* Loew). Most hosts of Bombyliidae inhabit the soil, or are in close contact with it, where their bombyliid predator/parasitoids seek them out, *e.g.*, larvae of *Heterotropus* are predatory on soil insects, while some *Anthrax* are parasitic on mud-dauber wasps in arboreal situations. A few genera have species that are specialised predators of egg pods of Acridoidea (Orthoptera) (*e.g.*, *Anastoechus* Osten Sacken, *Callostoma*

25 *Geron* (*Geron*) ♂ 26 *Geron* (*Pseudoammictus*) ♂



27 *Bombylius* 28 *Pachyanthrax* 29 *Xenoprosopa* 30 *Tomomyza*

Figs 45.25–30. Heads of Bombyliidae: (25) *Geron* (*G.*) sp., frontal view ♂; (26) same, *G.* (*Pseudoammictus*) *heteropterus* (Wiedemann); (27) *Bombylius* sp., posterior view; (28) same, *Pachyanthrax telamon* (Bezzi); (29) *Xenoprosopa paradoxa* Hesse, lateral view; (30) same, *Tomomyza pictipennis* Hesse. Figs 27, 28 (after Theodor 1983, figs 13, 14), Figs 29, 30 (after Hesse 1956, figs 286, 14, respectively).

Abbreviations: ant – antenna; fr – frons; ocp for – occipital foramen; pcr – postcranium; ped – pedicel; scp – scape.

Macquart and *Systoechus* Loew), but most bombyliids are ectoparasitoids on larvae and pupae – chiefly Scarabaeoidea and Tenebrionidae (Coleoptera), Myrmeleontidae (Neuroptera), Noctuidae (Lepidoptera), and above all, ground-nesting bees and wasps (Hymenoptera). The mode of parasitism has developed to endoparasitism in the tribes Systropodini (on Lepidoptera: Limacodidae), Gerontini (on lepidopterous larvae in concealed situations) and Villini (on larvae and pupae in soil). Above-ground hosts are attacked by Toxophorini and Antoniinae (both on wasps) and many Anthracinae and Bombyliinae parasitise bees and wasps that nest in holes in the ground or in wood or that construct mud nests.

An excellent detailed host list was published by Merle (1975) for all Bombylioidea and was supplemented by a summary of hosts and parasites by Yeates & Greathead (1997).

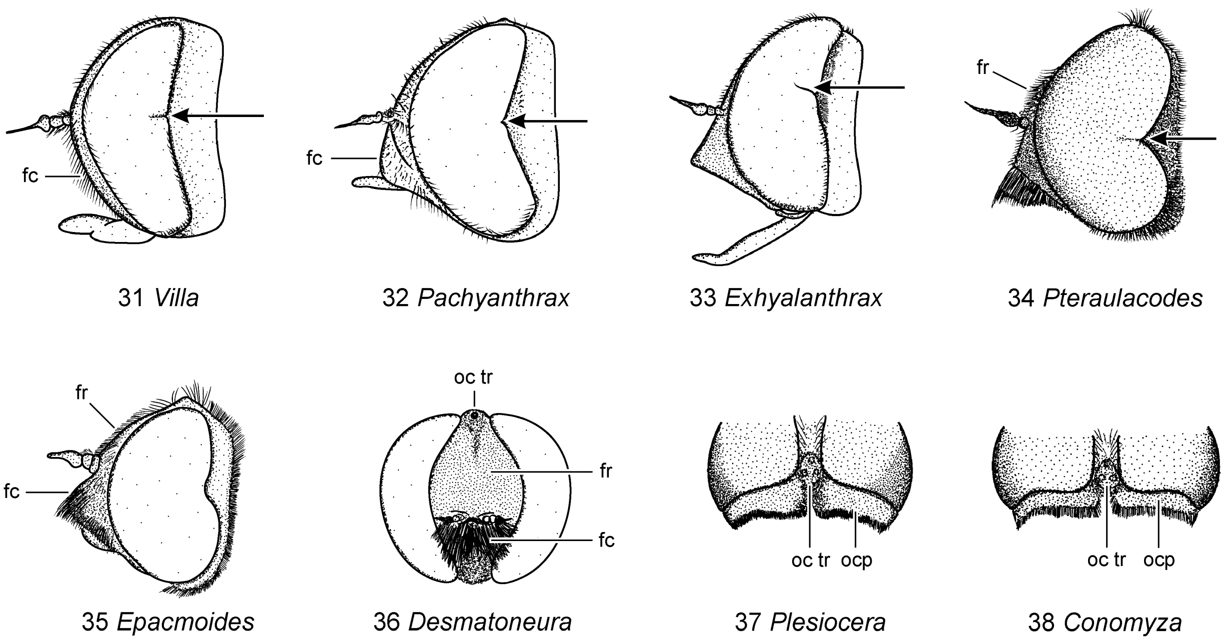
Economic significance

No species of economic significance are known. In the Afrotropics, however, some species of *Systoechus* have been assessed as potential biological control agents of acridoids (Axelsen *et al*. 2009; Greathead 1963) and those of *Exhyalanthrax* Becker were reviewed as having potential as biological control agents of *Glossina* Wiedemann spp. (Glossinidae) (Greathead 1980*c*).

Classification

Meigen (1820: viii) erected the family Bombyliidae by uniting the Anthracidae and Bombyliidae of earlier authors, the last two named groups each broadly equivalent to the divisions Homeophthalmae and Tomophthalmae of Bezzi (1924: 7). Schiner (1868: 116) grouped the genera known to him into four subfamilies. Becker (1913) reviewed the classification of the family, proposed additional subfamilies to accommodate the increasing number of recognised genera, and produced the first phylogenetic tree, based on his analysis of the generic characters used at that time, an arrangement that was followed until the 1960s. Becker's work was built upon by M. Bezzi, who also introduced formal subgeneric names for a number of genera, especially among the Exoprosopinae. His classification was published in the *Bombyliidae of the Ethiopian Region* (Bezzi 1924), along with a checklist of world genera and an identification key to African genera and species. All these workers relied heavily on characters of wing venation in defining their taxa.

Hesse (1938, 1956) demonstrated the importance of the male terminalia of Bombyliidae in distinguishing species, but largely missed their significance as characters for the separation of genera. Mühlenberg (1971) drew attention to the importance of the female terminalia and Theodor (1983) published a comprehensive illustrated study of male and female terminalia,

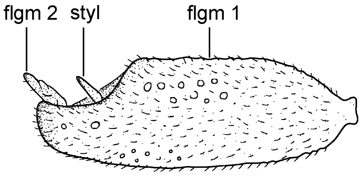


31 *Villa* 32 *Pachyanthrax* 33 *Exhyalanthrax* 34 *Pteraulacodes*

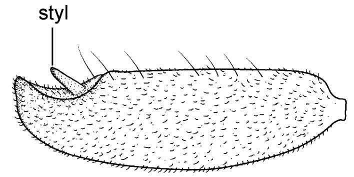
35 *Epacmoides* 36 *Desmatoneura* 37 *Plesiocera* 38 *Conomyza*

Figs 45.31–38. Heads of Bombyliidae: (31) *Villa hottentotta* (L.) (non-Afrotropical), lateral view (arrow indicates bisecting line); (32) same, *Pachyanthrax laconae* Greathead (arrow indicates bisecting line) (non-Afrotropical); (33) same, *Exhyalanthrax muscarius* (Pallas) (arrow indicates bisecting line); (34) same, *Pteraulacodes karooensis* Hesse (arrow indicates bisecting line); (35) same, *Epacmoides biumbonatus* (Bezzi); (36) *Desmatoneura nivea* (Rossi), frontal view (non-Afrotropical); (37) *Plesiocera psammophila* Hesse, dorsal view of occipital region; (38) same, *Conomyza semirufella* Hesse, lateral view. Figs 31–33 (after Greathead 1981, figs 1, 2, 3, as *E. vagans*), Figs 34, 37, 38 (after Hesse 1956, figs 129, 25*a*, 25*b*, respectively), Fig. 35 (after Hull 1973, fig. 650, as *E. albifrons*), Fig. 36 (after Engel 1936, fig. 168).

Abbreviations: fc – face; fr – frons; oc tr – ocellar triangle; ocp – occiput.

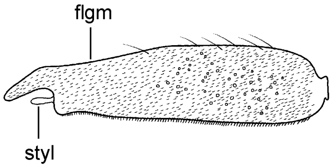


39 *Apolysis*

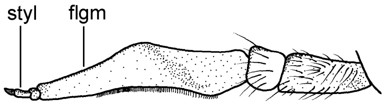


40 *Parageron*

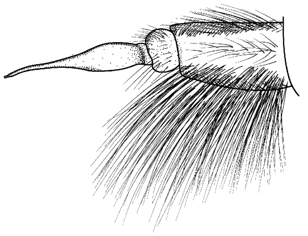
41 *Systropus* (*Systropus*)



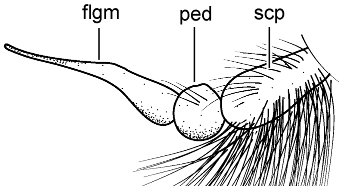
42 *Phthiria*



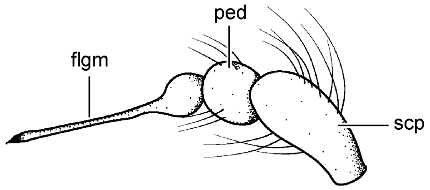
43 *Crocidium*



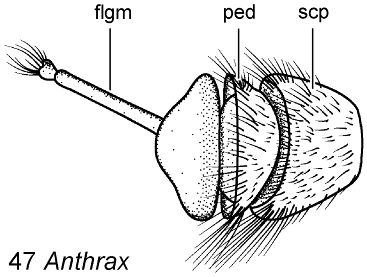
44 *Peringueyimyia*



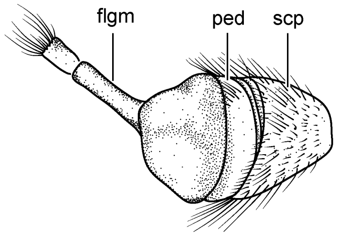
45 *Notolomatia*



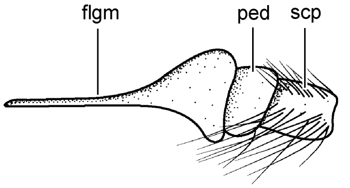
46 *Canariellum*



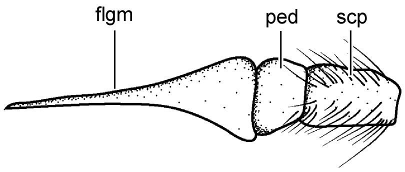
47 *Anthrax*



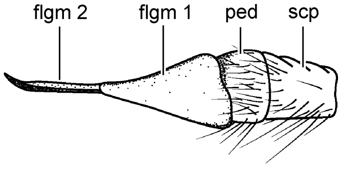
48 *Spogostylum*



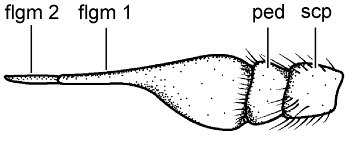
49 *Villa*



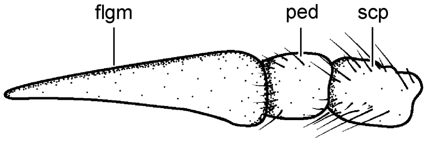
50 *Thyridanthrax*



51 *Pachyanthrax*



52 *Exhyalanthrax*



53 *Veribubo*

Figs 45.39–53. Antennae of Bombyliidae (lateral views): (39) *Apolysis flavifemoris* Hesse; (40) *Parageron lutescens* Bezzi (non-Afrotropical); (41) *Systropus* (*Systropus*) *angulatus* Karsch (non-Afrotropical); (42) *Phthiria gaedii* Wiedemann (non-Afrotropical); (43) *Crocidium phaeopteralis* Hesse; (44) *Peringueyimyia capensis* (Wiedemann); (45) *Notolomatia* sp.; (46) *Canariellum brunnipenne* Macquart; (47) *Anthrax pithecius* F.; (48) *Spogostylum punctipenne* (Wiedemann); (49) *Villa hottentotta* (L.) (non-Afrotropical); (50) *Thyridanthrax perspicillaris* (Loew); (51) *Pachyanthrax laconae* Greathead (non-Afrotropical); (52) *Exhyalanthrax muscarius* (Pallas) (non-Afrotropical); (53) *Veribubo gazella* Greathead. Figs 39, 40, 42 (after Evenhuis 1990, figs 12e, 19a, 43), Figs 41, 43, 44, 45, 46 (after Hull 1973, figs 87, 59, 120, 146, as *Lomatia*, 130A, as *Lomatia* (*Canariellum*), respectively), Figs 47, 48 (after Hesse 1956, figs 133, as *Anthrax conspurcata*, 134, as *Argyramoeba*), Figs 49–53 (after Greathead 1981, figs 4, 5, 7, 6, as *E. vagans*, 8, respectively).

Abbreviations: flgm – flagellomere; ped – pedicel; scp – scape; styl – stylus.

which was supplemented by Liu *et al*. (1995). Hull (1973) published the results of a world review of the family and attempted to reduce the increasing number of subfamily groups by the introduction of a tribal classification. His work was otherwise conservative in its reliance on the morphological characters favoured by Becker and Bezzi. He worked on his book over a long period without apparently re-reading earlier pages, with the result that, at times, he published conflicting conclusions on different pages and even proposed different names for the same taxa.

Critical morphological studies leading to phylogenetic analysis were initiated by Mühlenberg (1971), who showed that the Tomophthalmae formed a monophyletic group, but that the Homeophthalmae were paraphyletic. Earlier, however, Rohdendorf (1964) proposed a superfamily Bombylioidea to contain Bombyliidae, Cyrtosiidae (= Mythicomyiidae), Systropodidae and Usiidae, but did not provide an explanation of his proposal, or an allocation of genera to these families. Zaitzev (1992*a*) conducted detailed morphological studies, principally on the mouthparts of adults and, as a result, Zaitzev (1992*b*) accepted the superfamily concept of Rohdendorf, recognising Bombyliidae, Mythicomyiidae, Phthiriidae, Systropodidae and Usiidae, each of which he further divided into subfamilies.

Attempts were also made by other workers to develop a more satisfactory classification by incorporating features of the male and female terminalia into descriptions of supraspecific taxa. Notable among them were J. Bowden and D.J. Greathead, whose conclusions, developed during discussions over several years, were used in ordering the family for the *Catalogue of the Diptera of the Afrotropical Region* (Bowden 1980) and papers on the Arabian fauna (Greathead 1980*a*, *b*, 1988). Unfortunately, no full or formal explanations were published in those works.

Evenhuis (1990) published a phylogenetic analysis of the Phthiriinae and Usiinae, in which he made proposals for reallocation of some genera to other subfamilies. In a subsequent publication (Evenhuis 1991), he discussed the uncertainties over the limits of the family, but adopted a conservative classification incorporating his ideas. Yeates & Irwin (1992) studied African *Heterotropus* and postulated the possibility that the genus should be removed to its own subfamily. Yeates (1994) undertook a detailed morphological study and cladistic analysis of the Bombyliidae and close relatives in the Asilomorpha. He concluded that the Bombyliidae *sensu lato* (including Mythicomyiidae), were the sister-group of the non-Afrotropical Hilarimorphidae and together these formed a clade between the Acroceridae and Scenopinidae + Mydidae within the Asiloidea. He also retained the Heterotropinae within the family, based basally near the Mythicomyiidae on the resulting phylogenetic tree. Unpublished phylogenetic research led Evenhuis (1994: 338) to raise the Mythicomyiinae to family status, as the sister-group to the Bombyliidae, which has more recently been corroborated through molecular analysis (Trautwein 2009; Trautwein *et al*. 2011), in which the Mythicomyiidae were placed in a clade with Heterotropinae and Hilarimorphidae separate from the Bombyliidae *sensu stricto* clade. Following Zaitzev (1992*b*) and Evenhuis (1994) the Mythicomyiidae are here recognised at the familial level (see Chapter 44). Although Krivosheina (2012) reiterated the hypothesis that the Heterotropinae should be treated as a separate family, it is here treated within the Bombyliidae, pending further study.

Of the 16 subfamilies recognised in Bombyliidae, six are found only in the Old World. Almost 100 genera in 14 subfamilies are known from the Afrotropical Region and are treated here. Evenhuis & Greathead (1999) recognised more than 4,500 species globally, of which more than 1,400 occur in the

54 *Crocidium* 55 *Apolysis*

Figs 45.54–55. Hind coxae of Bombyliidae (ventrolateral views): (54) *Crocidium* sp. (arrow indicates mesal coxal peg); (55) *Apolysis namaensis* Hesse.

Abbreviations: cx – coxa; trc – trochanter.

Afrotropical Region. There are undoubtedly more species to be discovered, particularly in the less well surveyed tropical countries, although the family, particularly the sand-chamber subfamilies, are more diverse and species-rich in arid regions.

Identification

Greathead & Evenhuis (2001) provided comprehensive details on the morphology, biology and keys for identification, updating the previous keys of Hesse (1938, 1956).

The following identification key to genera of the Afrotropical Region follows primarily the keys in Greathead & Evenhuis (2001), excluding African genera not found in the Afrotropical Region, and is based chiefly on external characters that can be observed without dissection. In some instances, however, diagnostic characters of the male and female terminalia are required. These are essential for the identification of species in some genera, but in others the terminalia are extremely uniform. The key below is based primarily on males but, in some cases, female genitalic characters are critical for determination.

Bee flies are fragile insects and important characters of the antennae, legs and vestiture are easily lost, unless specimens are rapidly killed, preferably using a potassium cyanide killing vial, with ample crushed tissue to prevent damage (ethyl acetate can also be used, but takes much longer to kill and there is more resultant damage of specimen vestiture while individuals thrash around before death). For larger taxa, the number of specimens in such vials should be restricted to a minimum to prevent rubbing together of individuals. Killing vials or bottles also used for collecting Lepidoptera should be avoided (so as not to obscure critical features with scales) and bee flies should not be killed in bottles with Coleoptera, Orthoptera, or other robust insects that will trample them. Larger specimens are best collected individually in nets. Many smaller species are rare when applying such collecting methods and are instead more frequently collected using Malaise or yellow pan traps. Except for Apolysini, Phthiriinae and a few other small species lacking extensive setulae and scales, specimens collected in alcohol are best dried before they can be identified to species. The drying process must, however, be carefully controlled to prevent matting of the vestiture and collapsing of soft cuticular features, which can obscure critical characters. Specimens are best pinned soon after killing to avoid loss of vestiture while otherwise being stored in killing containers. Larger specimens should be direct-pinned in the field and smaller specimens micro-pinned for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Bombyliidae

1\. Head with postcranium flat or tumid, without concavity surrounding occipital foramen (*e.g.*, Fig. 27) 2

– Head with postcranium deep or shallow, with concavity surrounding occipital foramen (*e.g.*, Fig. 28) 44

2\. Wing without M_2 vein (3 posterior cells) (*e.g.*, Fig. 56) 3

– Wing with M_2 vein (4 posterior cells) (*e.g.*, Fig. 57) 11

3\. Antennal flagellum with subapical sulcus containing stylus (*e.g.*, Figs 39, 40) (USIINAE) 4

– Antennal flagellum without subapical sulcus (*e.g.*, Fig. 41) (TOXOPHORINAE) 5

4\. Antenna with articulated spine-like flagellomere 2 in addition to stylus (Fig. 39); wing cell *dm* open or closed by crossvein *dm–m*; narrow-bodied flies, usually < 3 mm (APOLYSINI). . . . . *Apolysis* Loew

– Antenna without flagellomere 2 (Fig. 40); wing cell *dm* invariably closed by crossvein *dm–m*; compact bee-like flies, usually > 3mm (USIINI) . . . . *Parageron* Paramonov

5\. Thorax with pronotum well-developed, with strong setae; mesothorax humped; proboscis as long as or shorter than head; body with dense scales (Fig. 4) (TOXOPHORINI) . . . . *Toxophora* Meigen

– Thorax with pronotum normal, without setae; mesothorax humped or not; proboscis elongate, longer than head; body without dense scales 6

6\. Thorax with metasternum normal, not elongate; mid and hind coxae not separated; abdomen tapered, but not conspicuously elongate, apex not swollen in males; body with fine setulae and scattered scales, usually whitish or brownish; not mimics of Hymenoptera (GERONTINI) . . . . *Geron* Meigen 7

– Thorax with metasternum elongate; mid and hind coxae widely separated; abdomen long, slender, tending to be swollen apically in males; body virtually bare, with short fine setulae only; mimics of Hymenoptera: Ichneumonidae, Sphecidae and Vespidae (SYSTROPODINI) . . . . . *Systropus* Wiedemann 8

7\. Male eyes holoptic (Fig. 25); gena narrow, distance between eyes across oral cavity slightly wider than across face below antennae (Fig. 25); tibiae with spicules from near their bases; thorax markedly humped and deep; origin of wing vein R_4 usually distal to crossvein *dm–m* . . . . . . *Geron sensu stricto*

– Male eyes dichoptic, separated by at least width of median ocellus (Fig. 26); gena broad, distance between eyes across oral cavity considerably wider than across face below antennae (Fig. 26); tibiae with spicules confined to apical ½; thorax not markedly humped and deep; origin of wing vein R_4 at level of crossvein *dm–m* . . . . *Geron* (*Pseudoammictus* Bigot)

8. Abdominal petiole composed of segments 2 and 3; head with face with dense tuft of setulae below antennae; body with black and yellow cuticle resembling *Sceliphron* spp. (Hymenoptera: Vespidae) . . . . *Systropus* (*Dimelopelma* Enderlein)

– Abdominal petiole composed of 3 or 4 segments; head with face with at most sparse setulae; body not with black and yellow cuticle resembling Hymenoptera: Vespidae 9

9. Wing with well-developed alula; subcostal vein (*Sc*) bare below; thoracic pleura with dense tufts of setulae; abdomen attenuate, petiole 4-segmented . . . . *Systropus* (*Teinopelmus* Bowden)

– Wing with alula greatly reduced; subcostal vein (*Sc*) with setulae below; thorax with propleuron at most with sparse pubescence; abdomen not markedly attenuate, petiole 3- or 4-segmented 10

10. Wing membrane if infuscate then unicolourous; body entirely black or with red or yellow areas; ligament between wing base and scutellum bare; thorax with metanotum poorly-developed; smaller species, not resembling Hymenoptera: Vespidae . . . . *Systropus sensu stricto*

– Wing membrane yellow at base and in costal area, apex darker, veins often with dark borders; body reddish; ligament between wing base and scutellum with setulae; thorax with metanotum well-developed; large species resembling *Belonogaster* Saussure spp. (Hymenoptera: Vespidae) (Fig. 3). . . . . *Systropus* (*Dierops* Enderlein)

11. Antennal postpedicel with apical sulcus containing stylus (Fig. 42) (PHTHIRIINAE) . . . . *Phthiria* Meigen

– Antennal postpedicel without apical sulcus, stylus arising from flagellomere 2 (*e.g.*, Fig. 43) 12

12. Hind leg with mesal coxal peg (as in Fig. 54, arrowed); mid leg with tibial spurs; antennal scape not swollen; abdomen elongate, narrow; body up to 6 mm in length, but usually less (CROCIDIINAE) 13

– Hind leg without mesal coxal peg (e.g., Fig. 55) (except in *Heterotropus*); mid leg without tibial spurs (except in *Othniomyia* Hesse); antennal scape sometimes swollen; abdomen ovate or chordate; body usually > 5 mm in length 14

13. Head with gena broad; wing membrane with or without maculae, hyaline or tinted; alula broad; axillary lobe broad, triangularly produced and rounded posteriorly; halter knob < 2 × as long as wide; asilid-like flies . . . . *Crocidium* Loew

– Head with gena narrow, virtually absent; wing membrane tinted or infuscated; alula narrow; axillary lobe not enlarged; halter knob *ca* 2 × as long as wide; empid-like flies . . . . . *Apatomyza* Wiedemann

14. Wing cell *cua* almost invariably closed; cell *dm* very wide at *r–m* crossvein (Fig. 17); body rather bare, without setae or scales; compact flies with pattern of dark and pale cuticle (HETEROTROPINAE). . . . . *Heterotropus* Loew

– Wing cell *cua* usually open; cell *dm* not markedly widened medially (*e.g.*, Figs 57–59); body usually with abundant setulae and/or scales, setae well-developed; broad or narrow-bodied, elongate flies 15

15. Antenna often thickened, scape usually shorter than flagellum; thorax with pronotum indistinct; body usually broad and densely setulose; wing normally broad, usually with well-developed alula; female with well-developed sand-chamber guarded by dense, long setulae (except in *Beckerellus*, but other characters do not differ); spermatheca with distinct terminal bulb (BOMBYLIINAE) 18

– Antenna elongate, rod-like, scape as long as, or longer than flagellum; thorax with pronotum distinct; body very narrow and elongate, bare, or with scales and sparse setulae only; wing very narrow, petiolate, with alula reduced; female with sand-chamber small, guarded only by row of stiff setulae on free margin of tergite 8; spermatheca without distinct terminal bulb (ECLIMINAE). 16

16. Thorax with spine-like setae on prothorax; wing with alula developed and with scales on membrane . . . . *Palintonus* François

– Thorax without spine-like setae on prothorax; wing with alula reduced, without scales on membrane 17

17. Alula wing cell broad; hind femora with strong setae ventrally . . . . *Thevenetimyia* Bigot

– Alula wing cell narrow; hind femora without strong setae ventrally. . . . . *Paratoxophora* Engel

18. Wing cell *dm* broad towards apex; radial sector (*Rs*) broad, with costal vein (*C*) tending to bulge forwards near wing apex (e.g., Fig. 60); mid leg with tibial spurs in some genera (CONOPHORINI) 41

– Wing cell *dm* broadest near middle; radial sector (*Rs*) not enlarged, with costal vein (*C*) more or less straight along anterior margin (*e.g.*, Figs 57, 58); mid leg invariably without tibial spurs (BOMBYLIINI) 19

19. Thorax with laterotergite invariably with setulae and wing cell r_5 usually closed at distance from margin; wing usually large, broad at base, with well-developed anal lobe and alula (*e.g.*, Fig. 57); hind femora invariably with well-developed setae ventrally; body invariably broad, setae usually well-developed; male terminalia with narrow or leaf-like gonostylus; ejaculatory apodeme usually large (*e.g.*, Fig. 77) 20

– Thorax with laterotergite bare and/or wing cell r_5 broadly open at wing margin; wing often small, narrowed at base, with at least alula reduced; hind femora often without setae ventrally; body usually more elongate, evenly narrow conical or cylindrical, setae usually weak, often setula-like, especially those posterior to wing; male terminalia often with long robust gonostylus ending in a curved point; ejaculatory apodeme usually small (*e.g.*, Fig. 76) 27

20. Head as wide as thorax; eye with hind margin indented; wing cell r_5 pointed and closed near wing margin; head and body with strong setae, including hind margins of abdominal tergites; head and body vestiture with gold scaling, with pattern of short black and white setulae and scales (Fig. 8); male terminalia with gonocoxite, bearing tuft of long stiff setae on dorsomedial surface (Figs 80, 81) . . . . *Eurycarenus* Bezzi

– Head usually narrower than thorax; eye with hind margin not indented; wing cell r_{4+5} closed and stalked; head and body vestiture with setulae long and dense; male terminalia (*e.g.*, Figs 82, 83) with gonocoxite without tuft of long stiff setae on dorsomedial surface, fine setae may be present 21

21. Wing cell *br* longer than cell *bm* (*e.g.*, Fig. 58), crossvein *r–m* sometimes equal in length to crossvein *m–cu*; membrane pattern various, sometimes with well-defined dark infuscation and/or isolated dark maculae; body vestiture various, often with black setulae and/or scaled patches; male terminalia with parameral sheath usually without clasper-like outgrowths (*e.g.*, Figs 82, 83) 22

– Wing cell *br* equal in length to cell *bm* (Fig. 57); crossvein *r–m* usually much shorter than crossvein *m–cu*, occasionally virtually as long; membrane infuscation, if present, diffuse and darker along anterior margin (Fig. 57); body vestiture fine and silky, with clipped appearance, at least on occiput and thorax, setulae white to straw-yellow, or brown shading to paler on underside; male terminalia with parameral sheath often with clasper-like outgrowths (Fig. 77) . . . . *Systoechus* Loew

22. Abdomen truncate, strongly tapered beyond tergite 4; male and female terminalia appearing similar, with cercus in female and process on gonocoxite in males projecting; female head with frons narrow, eyes separated by less than width of ocellar triangle; male terminalia with gonocoxite with robust elongate terminal lobes; gonostylus thick, parallel-sided, blunt (Figs 82, 83), or with small point and short setulae only; female with tubular ovipositor and vestigial sand-chamber; unlaid eggs large spherical, pigmented . . . . *Beckerellus* Greathead

– Abdomen ovate, gradually tapered beyond tergite 4; male and female terminalia normal; female head with frons at least as broad as ocellar triangle; male terminalia with gonocoxite with terminal lobes not longer than wide; gonostylus slender, pointed, crowned with long setulae at base, or broad with short, erect setulae; female with sand-chamber guarded by long silky setulae; unlaid eggs ellipsoidal, thin-walled, unpigmented 23

23. Male eyes adjoining for distance at least equal to length of ocellar triangle; head invariably distinctly narrower than thorax; palpus 1-segmented; legs usually very dark or black, with at least setae black; body cuticle mainly or entirely black; male terminalia with gonocoxite slender; gonostylus elongate slender, with tuft of long black setulae at base; parameral sheath usually without accessory structures 24

– Male eyes adjoining for less than length of ocellar triangle; head broad, sometimes as wide as thorax; palpus 2-segmented; legs pale, but bases of femora and tarsi sometimes darkened, setae almost invariable pale, at least in males; body cuticle generally with paler reddish or yellowish areas on callus, scutellum and margins of anterior abdominal tergites; male terminalia with gonocoxite broad; gonostylus usually broader and shorter, without long black setulae; parameral sheath often with large accessory structures (Figs 84, 85) . . . . *Parisus* Walker

24. Wing with *r–m* crossvein as long or longer than vein M_2 base; venation in radial sector (*Rs*) unstable, often with stump veins, sometimes with auxiliary vein complete (3 sub-marginal cells); body vestiture shaggy, with long setulae at margins of abdomen only, setae fine, sparse; setulae brown to blackish, with contrasting short white scale-like setulae, forming notopleural fasciae on thorax and maculae or bands on abdomen . . . . *Triplasius* Loew

– Wing with *r–m* crossvein much shorter than vein M_2 base, occasionally almost as long; venation normal; body vestiture more evenly distributed and differently coloured 25

25. Antennal scape at least 3 × length of pedicel; small relatively slender flies, with relatively long, slender legs; wing with alula long and narrow; body vestiture usually predominantly black, setulae long and tufted, usually with metallic or opalescent scales in maculae on frons and often on thorax and abdomen . . . . *Bombylella* Greathead

– Antennal scape at most 3 × length of pedicel; more robust and compact flies with shorter less slender legs; wing with alula broad; body vestiture often pale yellow to brown, if black, then without maculae of metallic or opalescent scales 26

26. Antennal scape *ca* 2 × length of pedicel; male eye with upper facets not enlarged; head with face short, with short, sparse setulae only; wing membrane with base black, remainder hyaline or tinged yellowish; body setulae short, with clipped appearance, usually with abundant black elements contrasting with areas of white, orange or grey (Fig. 18) . . . . *Bombomyia* Greathead

– Antennal scape more than 2 × length of pedicel; male eye with upper facets enlarged; head with face long, prominent, with long setulae; wing membrane pattern, if present, with basicosta often diffuse, sometimes with isolated maculae, rarely completely infuscate; body setulae usually long, sometimes tufted, rarely with clipped appearance, usually predominantly white to yellow or brown, with few black elements, if predominantly black, then without contrasting pattern of pale setulae . . . . . . *Bombylius* L.

27. Thorax with laterotergite setulose; wing cell r_5 open or closed at wing margin 28

– Thorax with laterotergite bare, but may be obscured by long setulae elsewhere on pleura and calypter, if so, then wing cell r_5 closed, with long stalk 32

28. Wing cell r_5 narrowed or closed at wing margin; palpus 2-segmented; body vestiture with setulae very short and sparse; male terminalia with gonocoxite very large, enclosing parameral sheath . . . . *Xerachistus* Greathead

– Wing cell r_5 broadly open, only slightly (if at all), narrowed towards wing margin; palpus 1- or 2-segmented; body vestiture with setulae not very short and sparse and/or with dense scales 29

29. Palpus 1-segmented; male eyes holoptic; wing with vein M_2 base considerably shorter than *r–m* crossvein; body with maculae of metallic scales at margins of frons and often on thorax and abdomen 30

– Palpus 2-segmented; male eyes dichoptic; wing with vein M_2 base about equal in length to *r–m* crossvein; body without metallic scales on frons, thorax and abdomen 31

30. Pulvilli well-developed; head (in male only) with frons usually without patches of silver scales either side of antennae; male terminalia with gonocoxite without prominent crest; parameral sheath, bearing paired horn-like outgrowths (Figs 78, 79) . . . . *Bombylisoma* Rondani

– Pulvilli undeveloped; head (in both sexes) with frons with patches of silver scales either side of antennae; male terminalia with gonocoxite with broad lobe-like apical crest; parameral sheath without paired horn-like outgrowths . . . . *Eremyia* Greathead

31. Body vestiture with setulae normal, long and evenly distributed; male terminalia with gonostylus broad, leaf-shaped; female with sand-chamber . . . . *Doliogethes* Hesse

– Body vestiture with setulae thick and frayed at ends, with dense scales; male terminalia with gonostylus long, narrow; female without sand-chamber . . . . *Lepidochlaenus* Hesse

32. Antennal scape markedly swollen, barrel-shaped; male terminalia with gonostylus long and sinuous. 33

– Antennal scape about equal in diameter to pedicel, if somewhat swollen, then hind femora with row of strong, but short setae ventrally; male terminalia with gonostylus usually broad, leaf-like, or with ventral spine (not long and leaf-like) 35

33. Head with face bare and shiny; hind femora with row of strong setae ventrally . . . . *Sisyrophanus* Karsch

– Head with face setulose, or if bare, then tomentose; hind femora without row of setae ventrally . . . 34

34. Small-sized species (< 5 mm in length); male eyes holoptic; palpus 2-segmented . . . . *Conophorina* Becker

– Medium- to large-sized species (> 5 mm in length); male eyes dichoptic; palpus 1-segmented . . . . *Dischistus* Loew

35. Wing narrow at base; basal comb undeveloped; cell r_5 broadly open 36

– Wing broad at base; basal comb well-developed; cell r_5 closed or only narrowly open 38

36. Male eyes holoptic; elongate, narrow-bodied flies; male terminalia with gonostylus with hook-like apex (Fig. 76) . . . . *Gonarthrus* Bezzi

– Male eyes dichoptic; broad-bodied flies, with short rounded abdomen; male terminalia with gonostylus leaf-shaped, pointed 37

37. Antenna modified, with flagellum markedly broad, with long setulae; wing with auxiliary vein (3 sub-marginal cells); membrane pilose at base . . . . *Sosiomyia* Bezzi

– Antenna unmodified, with flagellum narrow, without long setulae; wing without auxiliary vein (2 sub-marginal cells); membrane not pilose at base . . . . *Adelidea* Macquart

38. Abdomen round, with bee-like banded pattern of short setulae-like scales; tarsal claws toothed; pulvilli absent . . . . *Zinnomyia* Hesse

– Abdomen ovate, without bee-like pattern; tarsal claws untoothed; pulvilli present 39

39. Hind femora with row of setae ventrally; body not *Nemestrinus*-like, but with long shaggy setulae (*e.g.*, Fig. 6); male terminalia with gonostylus flat, leaf-like; parameral sheath slender and pointed 40

– Hind femora without row of setae ventrally; body *Nemestrinus*-like, with short sparse setulae and cuticle with pattern of dark and pale areas; male terminalia with gonostylus thick, round in cross-section; parameral sheath robust, not pointed . . . . *Isocnemus* Bezzi

40. Wing cell *br* longer than cell *bm* (Fig. 58); palpus 2-segmented . . . . *Australoechus* Greathead

– Wing cell *br* equal in length to cell *bm* (Fig. 19); palpus 1-segmented . . . . *Anastoechus* Osten Sacken

41. Antenna with 2 flagellomeres subequal in length (flagellomere 1 broad, flagellomere 2 narrow, rod-like); mid leg with tibial spurs; wing with auxiliary vein (3 sub-marginal cells) (Fig. 59); membrane glassy hyaline; scutellum bilobate, shiny at apex; body compact, humped, acrocerid-like; male eyes dichoptic, separated by more than width of median ocellus . . . . *Othniomyia* Hesse

– Antenna with large postpedicel, flagellomere 2 small or minute; mid leg with or without tibial spurs; wing usually without auxiliary vein; membrane not glassy hyaline, at least with faint basal infuscation, but often with extensive infuscation; scutellum rarely bilobate and shiny at apex; body not humped, not acrocerid-like; male eyes holoptic, or separated at vertex by no more than width of median ocellus 42

42. Antennal scape moderately swollen; postpedicel bare, frequently broad and dorsoventrally flattened; wing membrane with extensive dark mottled pattern, including dark maculae in middle of cells (Fig. 60); abdomen elongate; body uniformly dark blackish . . . . *Prorachthes* Loew

– Antennal scape not swollen; wing membrane hyaline, or with basicostal infuscation, more pronounced along margins of veins, more extensive in females; abdomen broad; body sometimes with pale markings 43

43. Mouthparts normally developed, proboscis extending for distance beyond oral cavity; antennal postpedicel lanceolate, with a few setulae on dorsal surface . . . . *Legnotomyia* Bezzi

– Mouthparts vestigial, proboscis concealed in oral cavity; antennal postpedicel without setulae, leaf-shaped. . . . . *Notolegnotus* Greathead & Evenhuis

44. Head with clypeus reaching antennal sockets 45

– Head with clypeus not reaching antennal sockets 49

45. Wing large, elongate, usually longer than body; antennal scape cylindrical or conical, without ventral apical bulge (*e.g.*, Figs 45, 46) (LOMATIINAE) 46

– Wing small, shorter than body; antennal scape with ventral apical bulge (*e.g.*, Fig. 29) 48

46. Eye with hind margin complete; thorax with mesonotum with numerous strong setae at sides; male terminalia with parameral sheath expanded at apex; spermathecal bulb elongate (PERINGUEYIMYIINI) . . . . *Peringueyimyia* Bigot

– Eye with hind margin indented; thorax with mesonotum with a few setae at sides, often inconspicuous anterior to wing; male terminalia with parameral sheath pointed apically; spermathecal bulb short (LOMATIINI) 47

47. Wing considerably longer than body, entirely infuscate; vein R_4 often with stump vein or angular bend, vein M_2 base at an angle toward margin, so cell *dm* appears truncated . . . . *Canariellum* Strand

– Wing slightly longer than body, not entirely infuscate, with at least apex hyaline; vein R_4 without stump vein, with rounded bend, vein M_2 base frequently virtually parallel to wing margin so cell *dm* appears pointed . . . . *Notolomatia* Greathead

48. Mouthparts elongate; labrum clothed in scales; palpus normal (ONIROMYIINAE) . . . *Oniromyia* Bezzi

– Mouthparts vestigial; labrum not clothed in scales; palpus lobed (XENOPROSOPINAE) . . . .*Xenoprosopa* Hesse

49. Eye without indentation on posterior margin, or any indication of bisecting line (*e.g.*, Fig. 30); wing vein R_{2+3} invariably arising at acute angle close to origin of vein *Rs*. 50

– Eye with indentation on posterior margin and at least indication of bisecting line (*e.g.*, Figs 31–34); if exceptionally both characters lacking (some Prorostomatini), then wing vein R_{2+3} arising at right angle at distance from origin of vein *Rs* 63

50. Head much broader than high (viewed from in front); antennae separated by no more than length of scape and pedicel combined; scape with short dorsal spine; body short and broad (MARIOBEZZIINAE). 51

– Head not markedly broader than high (viewed from in front), if so, then antennae separated by considerably more than length of flagellum; scape without short dorsal spine; body elongate, usually narrow 58

51. Head with frons inflated, or face very long and tumid; wing usually with auxiliary vein (3 sub-marginal cells) 52

– Head with frons not inflated or face long and tumid; wing usually without auxiliary vein (2 sub-marginal cells) (except in *Corsomyza tricellulata* Hesse, 1938) 54

52. Head with frons not inflated; face very long and tumid; antennae inserted nearer ocellar triangle than oral rim; flagellum narrow and linear; thorax without tuft of setulae posterior to metathoracic spiracle 53

– Head with frons inflated; face shorter and not tumid; antennae inserted just above oral rim; flagellum clubbed; thorax with tuft of setulae posterior to metathoracic spiracle . . . . . . *Callynthrophora* Schiner

53. Body vestiture with setulae dense in male, obvious in female. *Gnumyia* Bezzi

– Body vestiture with setulae sparse in both sexes, female virtually bare . . . .*Mariobezzia* Becker

54. Head with oral rim raised into prominent ridge; thorax without plumule; without tuft of setulae posterior to metathoracic spiracle 55

– Head with oral rim not raised into prominent ridge; thorax with plumule; with tuft of setulae posterior to metathoracic spiracle. 56

55. Antennae inserted midway between ocellar triangle and oral rim; thorax with 1 or more prealar setae . . . .*Megapalpus* Macquart

– Antennae inserted at oral rim; thorax without prealar setae . . . .*Zyxmyia* Bowden

56. Antennae inserted at oral rim; head without facial brush of stiff setulae 57

– Antennae inserted well above oral rim; head with facial brush of stiff, dense and conspicuous setulae . . . . *Corsomyza* Wiedemann

57. Body without adpressed scale-like setulae; wing cell *cua* broadly open; anal lobe narrow, alula markedly reduced; proboscis as long as head and thorax combined . . . . *Pusilla* Paramonov

– Body with dense adpressed scale-like setulae; wing cell *cua* closed or only narrowly open; anal lobe broad, alula well-developed; proboscis considerably shorter than head and thorax combined . . . .*Hyperusia* Bezzi

58. Head with frons produced to meet face, thus forming cone with antennae near apex (*e.g.*, Fig. 30); body vestiture virtually bare, with only minute setulae (TOMOMYZINAE) 59

– Head with frons flat or only slightly tumid; body vestiture with setulae and/or small scales, setae strong and conspicuous (CYTHEREINAE) 60

59. Body and legs predominantly reddish brown; abdomen cylindrical, humped in appearance; tergites 2–5 usually with depression at each side . . . .*Pantostomus* Bezzi

– Body and legs predominantly black; abdomen laterally compressed or flattened, not humped; tergites with at most very small shallow depressions at each side . . . .*Tomomyza* Wiedemann

60. Head with face very broad; antennae separated by more than length of scape; body vestiture with abundant setulae and/or scales as well as setae (*e.g.*, Fig. 20) (CYTHEREINI). 61

– Head with face not exceptionally broad; antennae separated by less than length of scape; body vestiture with sparse setulae and/or small scales, setae strong and conspicuous (ENICINI) 62

61. Wing cell r_5 closed and (usually) stalked . . . . *Callostoma* Macquart

– Wing cell r_5 open . . . . *Cytherea* F.

62. Wing cell r_1 divided by crossveins; head with frons with numerous strong setae; face with abundant setulae . . . . *Enica* Macquart

– Wing cell r_1 not divided by crossveins; head with frons with some stiff setulae only; face with few (if any) setulae . . . . *Nomalonia* Rondani

63. Head with frons and face protruding, with antennae inserted in groove between; body slender; abdomen elongate conical; rather bare flies with short setulae, but without distinct setae, cuticle with yellow and black pattern (Fig. 21); female without sand-chamber; 1 spermatheca present (ANTONIINAE) . . . . *Antonia* Loew

– Head with frons (at most) only slightly tumid, face protruding or not; body slender or broad, usually densely clothed in setulae and/or scales, with well-developed setae (*e.g.*, Figs 22, 23); female with sand-chamber well-differentiated; 3 spermathecae present (ANTHRACINAE) 64

64. Wing vein R_{2+3} originating at acute angle close to origin of radial sector (*Rs*) (*e.g.*, Fig. 61); head with face not produced or with oral rim slightly projecting; abdomen conical or elongate-ovate; palpus 2-segmented; male eyes holoptic (APHOEBANTINI) 65

– Wing vein R_{2+3} originating at right angle between origin of radial sector (*Rs*) and crossvein *r–m* (*e.g.*, Figs 63–65), exceptionally (some Prorostomatini), arising at acute angle close to origin of *Rs*, but then face produced; face projecting or smoothly rounded; abdomen conical, elongate-ovate or broad and flattened; palpus 1-segmented; male eyes dichoptic 67

65. Wing with auxiliary vein complete (3 sub-marginal cells) 66

– Wing with auxiliary vein incomplete (2 sub-marginal cells) . . . . *Cononedys* Hermann

66. Wing cell r_5 closed and stalked (Fig. 61); head with face with evenly-distributed setulae; frons with erect bristly setulae . . . . *Pteraulax* Bezzi

– Wing cell r_5 open not stalked; head with face with brush of bristly setulae at apex; frons with dense scales and fine setulae (Fig. 34) . . . . *Pteraulacodes* Hesse

67. Wing vein R_{2+3} usually originating closer to origin of radial sector (*Rs*) than to *r–m* crossvein; head with facial cone strongly developed, distinctly separated from frons (*e.g.*, Fig. 35); eye with hind margin usually without bisecting line; body narrow, elongate, abdomen not flattened (PROROSTOMATINI) 68

– Wing vein R_{2+3} originating closer to *r–m* crossvein than to radial sector (*Rs*) or opposite to it; head with face projecting to variable extent, but not distinctly separated from frons or smoothly rounded; eye with hind margin usually with bisecting line; body narrow, elongate, or broad, abdomen flattened 72

68. Wing with alula reduced or vestigial; eye with indentation very shallow 69

– Wing with alula broad; eye with indentation shallow or deep and angular 71

69. Wing membrane usually hyaline; vein R_{2+3} without stump vein near its base; fore and mid femora without strong setae; fore leg with tarsal claws usually markedly reduced 70

– Wings membrane with distinct basicostal infuscation; vein R_{2+3} sharply bent near its base, emitting a stump vein; all femora with strong setae; fore leg with tarsal claws at most only slightly smaller than mid tarsal claws . . . . *Coryprosopa* Hesse

70. Head with occiput long posterior to ocellar triangle, central groove deep, narrower than ocellar triangle (Fig. 37); fore tarsi at least as long as fore tibiae, without distinct spinules ventrally; tarsal claws markedly reduced or vestigial; male terminalia with large epiphallus . . . . *Plesiocera* Macquart

– Head with occiput short posterior to ocellar triangle, central groove as broad as ocellar triangle (Fig. 38); fore tarsi shorter than fore tibiae, with distinct spinules ventrally; fore tarsal claws scarcely smaller than mid tarsal claws; male terminalia with long and slender epiphallus . . . . *Conomyza* Hesse

71. Eye with hind margin only slightly emarginate; scutellum with hind margin rounded and dull. . . . . *Prorostoma* Hesse

– Eye with hind margin distinctly emarginate (Fig. 35); scutellum with hind margin emarginate or bilobed and shiny . . . . *Epacmoides* Hesse

72. Wing vein R_{2+3} usually originating before *r–m* crossvein; head with face rounded, not produced; femora without strong setae ventrally; body narrow, elongate to moderately broad, abdomen not broad or flattened (XERAMOEBINI) 73

– Wing vein R_{2+3} originating opposite *r–m* crossvein or very close to it (if, exceptionally, vein R_{2+3} originates before *r–m* crossvein, then face prominent); body broad; at least hind femora usually with row of strong setae ventrally; abdomen usually broad, flattened 76

73. Wing relatively broad, alula large, lobe-like; wing cell *dm* short, *r–m* crossvein situated well before middle of cell *dm*. 74

– Wing relatively narrow, alula reduced, narrow; wing cell *dm* long, *r–m* crossvein usually situated near middle of cell *dm* (*e.g.*, Fig. 62) 75

74. Head with frons broad at level of antennae, tumid, with silvery tomentum and fine setulae (Fig. 36); body narrow, abdomen conical; male terminalia with gonostylus elongate, rod-like; parameral sheath truncate apically (Fig. 86). . . . . *Desmatoneura* Williston

– Head with frons not unusually broad; body with small scales and coarse setulae; male terminalia with gonostylus broad at base, with curved pointed apical part; parameral sheath rounded apically with hook-like process (Fig. 87) . . . . *Xeramoeba* Hesse

75. Wing crossvein *r–m* situated before middle of cell *dm* (Fig. 62); body elongate, abdomen flattened, with setulae and sparse small scales; male terminalia with parameral sheath without spines on dorsal surface. . . . . *Petrorossia* Bezzi

– Wing crossvein *r–m* situated near middle of cell *dm*; body short, cylindrical; abdomen with scales, but without setulae; male terminalia with parameral sheath with spines on dorsal surface . . . . *Pipunculopsis* Bezzi

76. Antennal scape and pedicel quadrate, of similar width, flagellum elongate (*e.g.*, Figs 49–53); wing veins in radial sector (*Rs*) usually without recurrent appendices; thorax with mediotergite and laterotergite with setulae; abdomen usually clothed in adpressed scales of various colours, setulae fine, sparse 79

– Antenna remarkably compacted, flagellum terminating in a circlet of setulae (e.g., Figs 47, 48), often onion-shaped, narrow part usually with distinct suture; wing veins in radial sector (*Rs*) often with recurrent appendices (*e.g.*, Fig. 65); thorax with mediotergite and laterotergite bare; abdomen usually broad, ovate, usually with coarse setulae and scales not adpressed, usually mostly black, white or silvery and dull ochreous to brown (ANTHRACINI) 77

77. Wing cell r_4 divided by crossvein, cell r_5 closed and stalked (Fig. 63); vestiture on thorax and abdomen composed only of setulae . . . . *Dicranoclista* Bezzi

– Wing cell r_4 not divided by crossvein, cell r_5 open or occasionally closed at wing margin (*e.g.*, Figs 64, 65); vestiture on thorax and abdomen composed of scales and setulae 78

78. Antennal pedicel globular or disc-shaped, not moulded to flagellum (Fig. 47); wing membrane usually with more or less extensive infuscation, especially basally, seldom almost completely hyaline (Fig. 64); body vestiture with dense scales, lying flat, predominantly black with patches of white or silver scales on abdomen . . . . *Anthrax* Schrank

– Antennal pedicel flattened, closely applied to scape and flagellum, in some cases hollowed to receive flagellum (Fig. 48); wing membrane without extensive black basicostal infuscation, clear or maculate, sometimes with diffuse brownish infuscation at base and along anterior margin (Fig. 65); body vestiture without predominantly black, dense scales lying flat on abdomen . . . . *Spogostylum* Macquart

79. Wing usually without auxiliary vein between veins R_{2+3} and R_4 (2 sub-marginal cells) (*e.g.*, Figs 66–68); tarsal claws without tooth at base; pulvilli sometimes present (VILLINI) 80

– Wing with auxiliary vein between veins R_{2+3} and R_4 (3 sub-marginal cells) (*e.g.*, Figs 69–71), sometimes also cell r_4 divided by crossvein (4 sub-marginal cells) (*e.g.*, Fig. 72); tarsal claws with tooth (= conical pulvillus) at base (EXOPROSOPINI) 91

80. Mouthparts reduced, non-functional 81

– Mouthparts normally developed, functional 83

81. Head considerably narrower than thorax; wing cell *cua* narrowly open at wing margin; membrane with basicostal infuscation . . . . *Oestranthrax* Bezzi

– Head virtually as broad as thorax; wing cell *cua* closed before wing margin, with or without basicostal infuscation. 82

82. Mouthparts reduced, but palpus present . . . .*Marleyimyia* Hesse

– Mouthparts greatly reduced, concealed in slit, palpus absent . . . . *Villoestrus* Paramonov

83. Antennal flagellum usually onion-shaped (*e.g.*, Fig. 49), composed of 1 flagellomere; head with face rounded, at most only slightly bulging (*e.g.*, Fig. 31) 84

– Antennal flagellum conical (*e.g.*, Figs 50–53), frequently composed of 2 flagellomeres; head with face often strongly produced, conical, never entirely undeveloped (*e.g.*, Figs 32, 33) 85

84. Fore tibia with short setae, spiculate; pulvilli absent; wing membrane with at most narrow basicostal infuscation, male often with patch of silvery scales at base; body vestiture usually with extensive yellowish setulae, especially on thorax; abdomen with more or less distinctly banded pattern and 1 or more pairs of tufts of black scales at sides . . . . *Villa* Lioy

– Fore tibia smooth or with a few weak setae; pulvilli sometimes present; wing membrane with extensive dark pattern reaching hind margin at base, covering at least ½ its surface (Fig. 67), without silvery scales at base; body vestiture with extensive black setulae; abdomen with at most 2 white scale bands, remainder black, without contrasting tufts of black scales at sides. . . . . *Hemipenthes* Loew

85. Pulvilli present; body vestiture uniform whitish or yellowish 86

– Pulvilli absent; body vestiture usually including bands of scales of various colours, rarely entirely white or yellow 87

86 Eye with hind margin without bisecting line; legs with all tibiae spiculate; antennal flagellum with short flagellomere 2; wing membrane with diffuse basicostal infuscation; cell *cua* open; body vestiture composed chiefly of yellowish setulae. . . . . *Synthesia* Bezzi

– Eye with hind margin with bisecting line; fore leg with tibia smooth, other legs with only a few weak setae; antennal flagellum elongate, conical, without distinct flagellomere 2; wing membrane hyaline; cell *cua* closed at wing margin; body vestiture with setulae weakly-developed, except at sides of abdomen, composed predominantly of white (male) or yellowish (female) scales . . . . . . *Laminanthrax* Greathead

87. Antennal flagellum elongate, conical with minute, terminal bristle-like stylus (*e.g.*, Fig. 50); head with face weakly-developed; wing cell r_5 narrowed at margin; contact of cell m_4 with cell *dm* much shorter than basal vein of former (*e.g.*, Fig. 66); membrane often with extensive pattern; male terminalia with parameral sheath curled dorsally at apex (e.g., Fig. 94). 88

– Antennal flagellum elongate, conical with distinct second segment, or flagellum blade-shaped (*e.g.*, Figs 51–53); head with face often markedly produced (e.g., Fig. 32); wing cell r_5 narrowed or not; contact of cell m_4 with cell *dm* often long (*e.g.*, Fig. 68); membrane with pattern usually reduced, if extensive, then fully-developed in 1 sex only; male terminalia with parameral sheath truncate apically (*e.g.*, Figs 92, 93). 89

88. Wing with anal area very broad; *r–m* crossvein situated beyond middle of cell *dm*, its terminal vein oblique to wing margin; membrane with pattern dimidiate, uniform and dark; body vestiture with metallic scales, mainly black; abdomen with fringe of setulae at sides . . . . *Caecanthrax* Greathead

– Wing normally developed; *r–m* crossvein situated at middle of cell *dm*, its terminal vein more or less parallel with wing margin; membrane with infuscation paler at base, with hyaline maculae on crossveins ("window panes") (Fig. 66); body vestiture composed of black, brown, yellow and white elements; head with face with pale scaling; thorax with distinct pale notopleural fascia; abdomen banded, with dense setulae at sides of basal segments only (Fig. 22) . . . . *Thyridanthrax* Osten Sacken

89. Head with face rounded with abundant setulae (Fig. 32); antenna with 2 flagellomeres (Fig. 51); fore leg with claws greatly reduced, inner claw sometimes smaller than outer; wing membrane with pale infuscation at base and in costal cell (*c*), with, or without, dark infuscation medially, pattern equally developed in both sexes; cell r_{4+5} narrowed at margin; contact of cell m_4 with cell *dm* shorter than basal vein of former; abdomen chordate or elongate-ovate with setulae at sides and on dorsal surface sparse, not forming distinct rows across tergites; male terminalia with gonocoxite bearing crest of stiff, spine-like setulae (Figs 92, 93) . . . . *Pachyanthrax* François

– Head with face angularly produced (e.g., Fig. 33) with few (if any) setulae, but with dense scales; antenna with 1 or 2 flagellomeres (*e.g.*, Figs 52, 53); fore leg with claws large, inner and outer claws equally well-developed; wing membrane with various degrees of infuscation, often sexually dimorphic; cell r_5 barely narrowed at margin; contact of cell m_4 with cell *dm* longer than basal vein of former; abdomen elongate-ovate, or parallel-sided, with dense setulae at sides of tergite 1 only, with bristly setulae in rows at hind margins of tergites; male terminalia with gonocoxite with, or without crest, but if crested, then scarcely so, with normal setulae (*e.g.*, Figs 90, 91) 90

90. Head with face strongly-developed, conical, often forming an acute angle when viewed in profile (Fig. 33); antennal postpedicel elongate conical, with well-developed flagellomere 2 (Fig. 52); head usually with at least some metallic scales, often with dense patches above antennae; wing membrane usually with more or less well-developed dark basicostal infuscation, generally more extensively developed in female, rarely almost entirely hyaline; male terminalia with gonocoxite sometimes with crest; parameral sheath usually with pair of dorsal denticles or spines (Figs 90, 91). . . . . *Exhyalanthrax* Becker

– Head with face less strongly developed, blunt when viewed in profile; antennal postpedicel blade-shaped, lacking obvious flagellomere 2 (Fig. 53); head with a few setulae, without metallic scales, but yellow or white scales present on face; wing membrane with pattern, if present, variable, but more extensive in males, ending almost perpendicular to fore margin; male terminalia with gonocoxite invariably without crest, parameral sheath often spinulate . . . . *Veribubo* Evenhuis

91\. Wing with cell r_4 not divided into two by crossvein (3 sub-marginal cells) (*e.g.*, Figs 70, 71, 73) 92

– Wing with cell r_4 divided into two by auxiliary crossvein (4 sub-marginal cells) (Fig. 72) . . . . *Euligyra* Lambkin & Yeates

92\. Head with face rounded; proboscis projecting by as much as length of head; wing membrane with characteristic brown basicostal infuscation, continued as median band across wing at apex of cell *dm*, usually reaching posterior margin (Fig. 69); body often extensively brown or orange with brown to orange vestiture . . . . *Litorhina* Bowden

– Head with face projecting (although only slightly in *Atrichochira* Hesse); proboscis rarely projecting by as much as length of head; wing membrane with pattern and colouring usually otherwise, but if with *Litorhina*-like wing pattern, then proboscis not projecting and/or antennal postpedicel much longer than second segment 93

93\. Body and legs with setae weak, reduced in number; male terminalia with parameral sheath considerably widened at apex, pointed at either side (*e.g.*, Fig. 101); gonostylus simple, U-shaped; spermatheca narrow, thin-walled, elongate and unpigmented 94

– Body and legs with setae normally developed; male terminalia with parameral sheath not markedly widened at apex, without points at either side (Figs 99, 103); gonostylus differently shaped (*e.g.*, Figs 96–99, 102, 103); spermatheca thick-walled, usually pigmented, usually with rounded terminal bulb 95

94\. Body cuticle, especially frons, shiny, with iridescent or metallic scales . . . . *Micomitra* Bowden

– Body cuticle tomentose, not shiny, without iridescent or metallic scales on head or thorax . . . . *Atrichochira* Hesse

95\. Wing venation usually normal, rarely with appendices or subdivision of cells; cell r_5 open at margin (except in *Exoprosopa enigma* Greathead & Evenhuis, 2001, but then other characters do not differ); membrane pattern various, but rarely with veins bordered with infuscation and of different colour to infuscation in centres of cells, usually without isolated maculae on crossveins (*e.g.*, Fig. 71); body vestiture with setulae and scales of various colours, frequently with stripes or uniform colouring; male terminalia large; parameral sheath not chisel- or axe-shaped, apodemes large (*e.g.*, Figs 98, 99); spermathecae of various shapes, but not narrow, tubular and thick-walled 102

– Wing venation generally unstable, frequently with appendices and divided cells; cell r_5 sometimes closed at margin; membrane pattern often with veins bordered with different colour to centres of cells, frequently with isolated maculae (Fig. 70); body vestiture with setulae and scales black, brown and yellow to white, often mixed or arranged in ill-defined fasciae; male terminalia small; parameral sheath chisel- or axe-shaped, apodemes weak, usually not projecting outside enclosing gonocoxite (Figs 96, 97, 102, 103); spermathecae narrow, tubular and thick-walled . . . . *Heteralonia* Rondani 96

96\. Wing cell r_{2+3} divided by auxiliary crossvein; membrane with pattern comprising eye-like maculae on crossveins . . . . *Heteralonia sensu stricto*

– Wing cell r_{2+3} undivided by crossvein; membrane with maculae if present, not eye-like 97

97\. Wing cell r_5 divided by auxiliary crossvein, or closed with long stalk; membrane with pattern diffuse, usually pale, with paler borders to veins or small, darker maculae on crossveins, often paler at base, with darker diagonal middle band before hyaline apical band; if wing vein characters not present, then vestiture and wing pattern as described; body vestiture usually composed predominantly of pale sandy-coloured setulae and scales . . . . *Heteralonia* (*Zygodipla* Bezzi)

– Wing cell r_5 undivided by crossvein, open, if closed, then with at most with very short stalk; membrane with pattern various, but not as above; body vestiture usually brown to blackish 98

98\. Wing cell *dm* broad and angular at apex, emitting a stump vein into cell m_2 (*e.g.*, Fig. 70) 99

– Wing cell *dm*, if broad at apex, then not angular, without stump vein into cell m_2 100

99\. Wing cell m_2 divided by stump vein (5 posterior cells) . . . . *Heteralonia* (*Metapenta* Bezzi)

– Wing cell m_2 undivided (4 or 5 posterior cells) (Fig. 70) . . . . *Heteralonia* (*Acrodisca* Bezzi) [in part]

100\. Wing vein M_2 base long, sinuous, parallel to hind margin, so cell *dm* long and tapered at apex; membrane with pattern uniform in density, extensive, but often with clear macula or indentation over middle of cell *dm*; abdomen with scaling uniform in colour, or with bold division into areas of different colours . . . . *Heteralonia* (*Homalonia* Bowden)

– Wing vein M_2 base short and straight, or slightly sinuous and at an angle with hind margin, so cell *dm* tends to appear truncated at apex; membrane with pattern tending to be darker and denser along fore margin, to be composed of maculae or infuscated borders to veins, which may reach hind margin; abdomen with scaling of different colours, not differentiated into distinct areas, or with tendency to form paler band across base of tergite 2 101

101. Proboscis not or barely projecting; wing with anal area and alula normal, wing normally broad at base (Fig. 70); membrane with anterior infuscation merging into maculae or dark borders on veins in hind part; abdomen without appearance of fringe of dense scales at sides . . . . *Heteralonia* (*Acrodisca* Bezzi) [in part]

– Proboscis usually projecting, sometimes by more than length of head; wing with anal area narrow and alula reduced, so that wing appears petiolate; membrane with anterior infuscation sharply demarcated from hind part, that is tinged brownish; abdomen with fringe of dense scales at sides. . . . . *Heteralonia* (*Isotamia* Bezzi)

102. Eye with distinct setulae; body narrow; wing pedunculate, longer than body, membrane with extensive infuscation forming characteristic pattern and margined with short fine setulae. . . .*Diatropomma* Bowden

– Eye without distinct setulae; body usually broad; wing usually not pedunculate, membrane variously infuscate, or virtually hyaline, not margined with short setulae 103

103. Hind tibia with fringe of large erect scales, giving feathered appearance; body predominantly black, with chiefly black vestiture; wing membrane infuscate black, except at extreme apex. . . . . .*Pterobates* Bezzi

– Hind tibia with small, adpressed scales; body and vestiture of various colours; wing membrane with variety of patterns or almost entirely hyaline (*e.g.*, Figs 71, 73) 104

104. Spermathecal reservoir with apical portion rounded or fairly broadly cylindrical (*e.g.*, Figs 104, 106) 105

– Spermathecal reservoir long, narrow, if cylindrical, not broadly so (Fig. 105) . . . . *Balaana* Lambkin & Yeates

105. Spermathecal reservoir with tapered or nipple-like apex, with clear basal ring and sclerotised base of basal bulb (Fig. 104); thorax with dense white scales on katepisternum; abdomen dark with contrasting white scales (Fig. 24) . . . .*Defilippia* Lioy

– Spermathecal reservoir rounded or broadly cylindrical, not tapered or nipple-like apically (Fig. 106), without sclerotised basal portion to basal bulb; thorax with scales on katepisternum variable; abdomen variously patterned . . . . *Exoprosopa* Macquart

Synopsis of the Fauna

***Adelidea* Macquart** (Bombyliinae: Bombyliini)**.** An endemic genus of eight species known from the Eastern and Western Cape Provinces, South Africa. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938).

***Anastoechus* Osten Sacken** (Bombyliinae: Bombyliini) (Fig. 9)**.** A widespread genus of 92 described species, occurring in the Afrotropical (30 species) and Oriental (4) Regions and Holarctic Realm (63). Formerly considered to be closely-allied to *Bombylius* and *Systoechus*, *Anastoechus* has subsequently been shown to have the laterotergite bare (Greathead 1995) and is thus more closely related to the southern African genus *Australoechus* (Greathead & Evenhuis 2001). Although Afrotropical species have not been reared, some Holarctic species are recorded as predators in egg pods of Acrididae (Greathead 1963; Merle 1975). Identification keys for Afrotropical species were provided by Bezzi (1924: 73) and Hesse (1938).

***Anthrax* Scopoli** (Anthracinae: Anthracini) (Fig. 14)**.** A virtually cosmopolitan genus of almost 250 species, 54 of which occur in the Afrotropical Region. Theodor (1983: 194) recognised two groups of species, based on differences in the male and female terminalia. The first group has males without spines on the cercus, the gonocoxite truncate and the parameral sheath simple, with a hooked apex (Fig. 88); females with elongate club-shaped spermathecal bulbs, with a broad looped duct and short sperm pump. The second group has males with spines on the cercus, the gonocoxite with an elongate terminal process and the parameral sheath with a complex apical structure (Fig. 89); females with heavily-sclerotised spermathecal bulbs of various shapes, with usually narrow, straight ducts and a longer sperm pump. Immatures are ectoparasitoids on the larvae of bees and wasps (Merle 1975; Yeates & Greathead 1997). Identification keys to species were provided by Bowden (1964, for Ghana), François (1972, Senegal) and Hesse (1956, southern Africa).

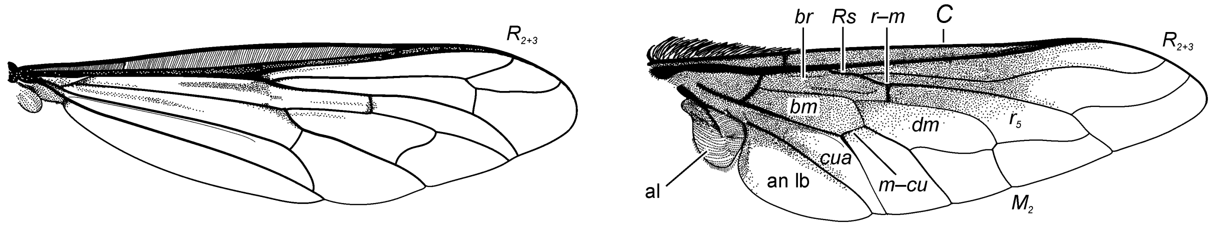
***Antonia* Loew** (Antoniinae) (Fig. 21)**.** A genus of 15 species, occurring in the Afrotropical and Palaearctic Regions, eight of which occur in the Afrotropics. *Antonia* spp. are elongate flies, with a striking pattern of yellow and black cuticle. Immatures are known to parasitise bees of the genus *Bembix* F. (Crabronidae) and a mud-dauber wasp. Identification keys to species were provided by Bezzi (1924: 137) and Hesse (1956).

***Apatomyza* Wiedemann** (Crocidiinae)**.** An endemic genus of 12 described species recorded from southern Africa

(Namibia and South Africa), with an undescribed species known from Madagascar (Lamas & Evenhuis, in prep.). Lamas *et al*. (2001) have shown that *Adelogenys* Hesse is a junior synonym. Immature stages and biology remain unknown. Lamas & Evenhuis (2005) and Lamas *et al*. (2001, 2003) reviewed the genus and Lamas *et al*. (2003) provided an identification key to species.

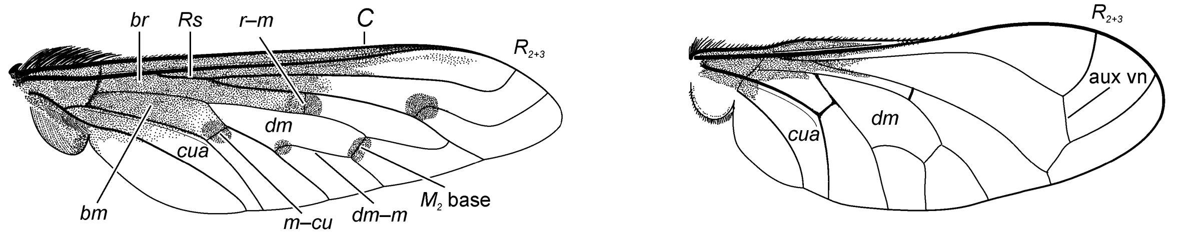
***Apolysis* Loew** (Usiinae: Apolysini) (Fig. 2). A genus of more than 120 species occurring in all zoogeographical regions, except the Australasian Region and Antarctica. Some 29 species occur in the Afrotropical Region. Evenhuis (1990) revised the generic concepts of *Apolysis* and showed that many species previously misidentified and described as *Oligodranes* Loew (Oligodraninae); belong to *Apolysis*, including all those present in Africa. Wing cell *dm* may be closed by a terminal crossvein or open. All species are greyish to pale coloured, small to minute, usually < 5 mm in length and often < 2 mm. Because of the small size of some species, they are sometimes mistaken for Mythicomyiidae. Gibbs (2011) provided a revised identification key to separate the tribes Apolysini and Usiini and the key can also be used to separate *Apolysis* from the similar-looking *Parageron* (see also below under *Parageron*). The pupa of an *Apolysis* sp. was recorded by Greathead (1999c), as parasitic on a wasp of the genus *Quartinia* André (Vespidae), which was nesting in the shell of the gastropod *Trigonephus* Pilsbry (Dorcasiidae). The species was subsequently reared from numerous individuals and identified as *A. hesseana* Evenhuis, 1990 (Greathead 2006). An identification key to Afrotropical species was provided by Hesse (1975), as *Apolysis* and *Oligodranes*.

***Atrichochira* Hesse** (Anthracinae: Exoprosopini)**.** A genus of four described species occurring in the Afrotropical and Australasian (two species) Regions. Two described species, *A. inermis* (Bezzi, 1912) from Malawi and *A. pediformis* (Bezzi, 1921) from Burundi, Malawi and South Africa, are recorded from the Afrotropics and a further undescribed species is known from Madagascar. The male and female terminalia are



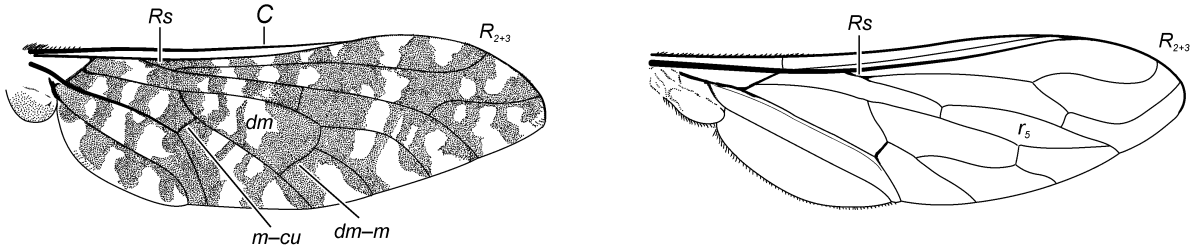
56 *Systropus* (*Systropus*)

57 *Systoechus*



58 *Australoechus*

59 *Othniomyia*



60 *Prorachthes*

61 *Pteraulax*

Figs 45.56–61. Wings of Bombyliidae (dorsal views): (56) *Systropus* (*Systropus*) *leptogaster* Loew; (57) *Systoechus robustus* Bezzi; (58) *Australoechus punctifer* (Bezzi); (59) *Othniomyia tylopelta* Hesse; (60) *Prorachthes conspersipennis* (Hesse); (61) *Pteraulax flexicornis* Bezzi. Figs 56, 57, 58 (after Bezzi 1924, figs 8, 5, 4, respectively), Figs 59, 60 (after Hesse 1938, figs 211, 198, respectively), Fig. 61 (after Hesse 1956, fig. 122).

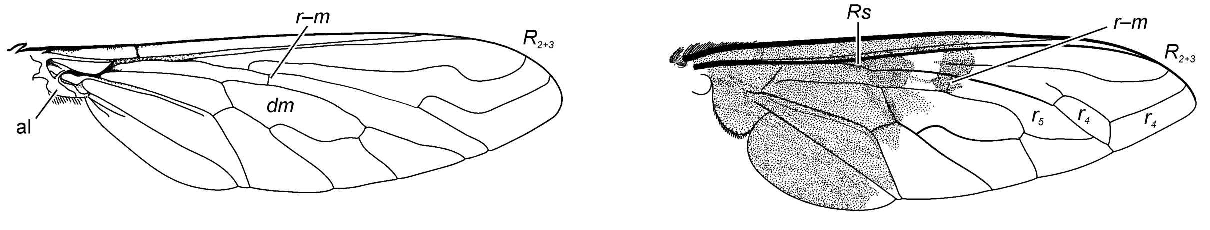
Abbreviations: al – alula; an lb – anal lobe; aux vn – auxiliary vein; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *cua* – anterior cubital cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; M_2 – second branch of media; *m–cu* – medial–cubital crossvein; R_{2+3} – second branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector.

very similar to those of *Micomitra*, but are quite distinct from other Afrotropical Exoprosopini. *Micomitra* and *Atrichochira* form a well-supported clade, along with the Australian genus *Pseudopenthes* Roberts (Lambkin *et al*. 2003). Immature stages and biology remain unknown.

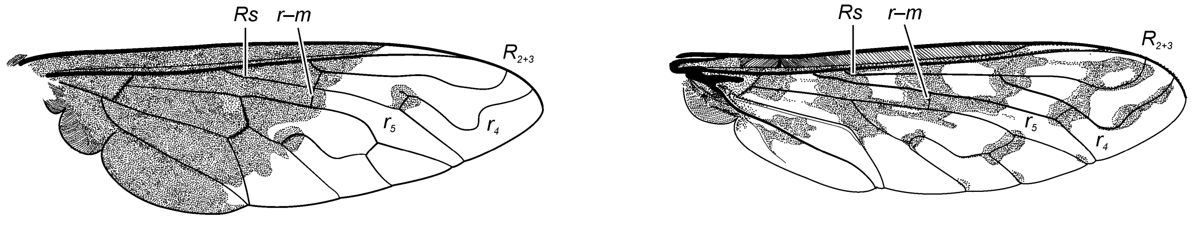
***Australoechus* Greathead** (Bombyliinae: Bombyliini) (Fig. 6)**.** An endemic genus of 29 species restricted to southern Africa (Namibia and South Africa). Greathead (1995) showed that the *Bombylius micans*-group of Bezzi (1924: 56), "Group 3" of Hesse (1938), have a bare laterotergite and so belong to this genus, which was described for that group. They resemble *Anastoechus* in the broad head and shaggy, bristly vestiture, but differ from that genus in the placement of the *r–m* crossvein. Immature stages and biology remain unknown. The identification key of Hesse (1938) (as "*Bombylius* "Group 3") can be used to key species.

***Balaana* Lambkin & Yeates** (Anthracinae: Exoprosopini)**.** A genus of ten species occurring in the Afrotropical (3 species), Australasian (7) and Palaearctic (3) Regions. The genus was erected by Lambkin et *al*. (2003) in their phylogenetic analysis of Exoprosopinae of the Australasian Region. The three species that occur in the Afrotropics (*B. efflatounbeyi* (Paramonov, 1928), *B. grandis* (Wiedemann, 1820) and *B. onusta* (Walker, 1852)), are confined to United Arab Emirates and Yemen in the Arabian Peninsula. Immature stages and biology remain unknown. An identification key to Afrotropical species is currently unavailable.

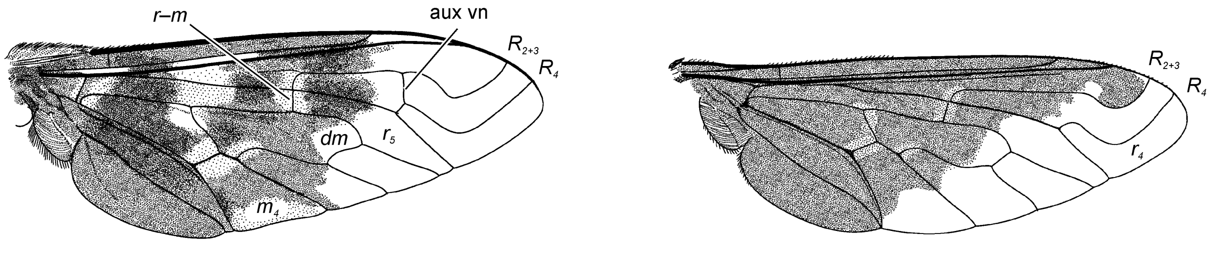
***Beckerellus* Greathead** (Bombyliinae: Bombyliini)**.** A genus of four species, three of which occur in the Afrotropical Region (*B. melanopus* (Bezzi), *B. obtusus* (Bezzi) and *B. terminatus* (Becker)). The genus *Beckerellus* is confined to southern Europe, the Middle East to Iran, and Africa and was proposed by Greathead (1995) for a group of anomalous species of *Bombylius*-like bee flies, in which there is convergence in some of the external characters of the sexes. The narrow frons and elongate cercus of the females has caused confusion between sexes. The enlargement of the anterior facets of the



62 *Petrorossia* 63 *Dicranoclista*



64 *Anthrax* 65 *Spogostylum*



66 *Thyridanthrax* 67 *Hemipenthes*

Figs 45.62–67. Wings of Bombyliidae (dorsal views): (62) *Petrorossia letho* (Wiedemann); (63) *Dicranoclista simpsoni* Bezzi; (64) *Anthrax aygulus* F.; (65) *Spogostylum princeps* Bezzi; (66) *Thyridanthrax perspicillaris* (Loew); (67) *Hemipenthes velutinus* (Meigen) (non-Afrotropical). Fig. 62 (after Hull 1973, fig. 383), Figs 63–66 (after Bezzi 1924, figs 16, 14, 15, 18, respectively), Fig. 67 (after Austen 1937, fig. 47),

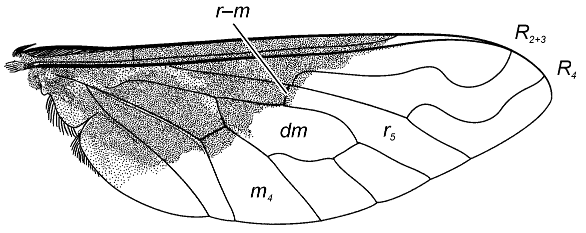
Abbreviations: al – alula; aux vn – auxiliary vein; *dm* – discal medial cell; m_4 – fourth medial cell; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector.

eye and tubular ovipositor of the female, with the large pigmented eggs suggest that these are accurately placed on the substrate, rather than ejected onto the soil surface as in other Bombyliinae. Oviposition has not been observed, however, and there are no rearing records for any species of the genus. An identification key to Afrotropical species is currently unavailable.

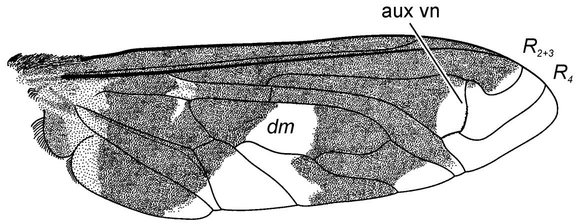
***Bombomyia* Greathead** (Bombyliinae: Bombyliini) (Fig. 18)**.** A genus of 21 species known from the Old World, 17 of which occur in the Afrotropical Region. *Bombomyia* was proposed by Greathead (1995), for the *Bombylius analis* (= *discoideus*) -group of Bezzi (1924: 32), Hesse's (1938) "Group 1 Section 2". They are all large, broad-bodied flies, with brightly coloured setulae and bear a resemblance to some bees of the genera *Bombus* Latrielle and *Anthophora* Latrielle (Apidae). The genus is found in Africa, the Palaearctic and India, with one very widespread species, *B. discoideus* (F., 1794), occurring from South Africa to central Europe and the Caucasus. See Figs 74, 75 for examples of the male terminalia of the genus. Immature stages and biology remain unknown. An identification key to species (as the *Bombylius discoideus*-group), was provided by Paramonov (1955).

***Bombylella* Greathead** (Bombyliinae: Bombyliini) (Fig. 7)**.** A genus of 24 species restricted to the Old World, 15 of which occur in the Afrotropical Region. This genus corresponds to the *Bombylius ornatus*-group of Bezzi (1924: 37), "Group 1 Section 3" of Hesse (1938). It is a predominantly African genus of rather slender delicately-built flies, mostly associated with dense savanna or forest vegetation. There are two records from South Africa of rearings from the dung balls of Scarabaeidae (Cambefort 1982). An identification key to species was provided by Greathead (1999a).

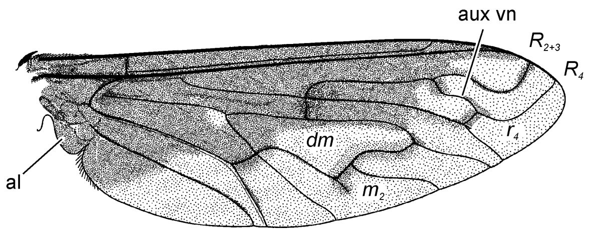
***Bombylisoma* Rondani** (Bombyliinae: Bombyliini)**.** A southern European and African genus of 38 species, with 23 species known from the Afrotropical Region. Some Palaearctic species



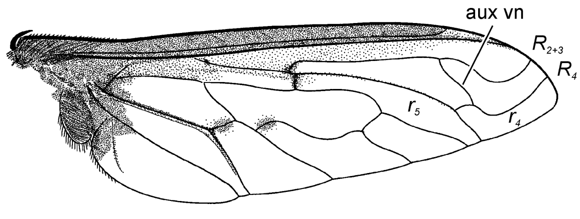
68 *Exhyalanthrax*



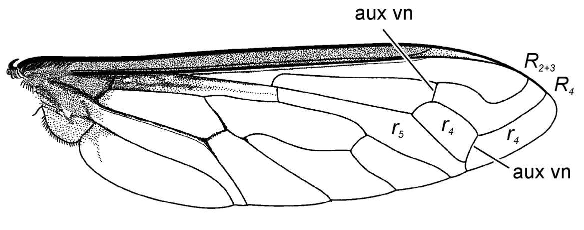
69 *Litorhina*



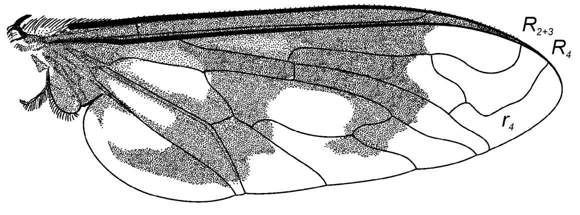
70 *Heteralonia* (*Acrodisca*)



71 *Exoprosopa*



72 *Euligyra*



73 *Balaana*

Figs 45.68–73. Wings of Bombyliidae (dorsal views): (68) *Exhyalanthrax transiens* (Bezzi); (69) *Litorhina dentifera* (Bezzi); (70) *Heteralonia* (*Acrodisca*) *spoliata* (Bezzi); (71) *Exoprosopa batrachoides* Bezzi; (72) *Euligyra atricosta* (Bezzi); (73) *Balaana grandis* (Meigen). Fig. 68 (after Austen 1929, fig. 8, as *Thyridanthrax transiens*), Figs 69–73 (Bezzi 1924, figs 19, as *Litorhynchus dentiferus*, 22, as *Exoprosopa spoliata*, 33, as *Exoprosopa batrachoides*, 430, as *Hyperalonia atricosta*, respectively).

Abbreviations: al – alula; aux vn – auxiliary vein; *dm* – discal medial cell; m_2 – second medial cell; m_4 – fourth medial cell; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein.

were at one time included in the genus *Dischistus* owing to the mistaken acceptance by many authors of the designation of *Bombylius minimus* Schrank, 1781 as genotype by Brunetti (1920: 273), which was later than the designation of *B. mystax* Wiedemann, 1818 as the type species by Becker (1913). The confusion led Hesse (1938) to propose a new genus *Chasmoneura* for South African species, unaware of the availability of the name *Bombylisoma* (Bowden 1973). *Bombylisoma* are similar in habitus to species of *Bombylella* (both have conspicuous shiny, silvery patches of scales on the head, thorax and abdomen) and both are encountered in similar habitats. Immature stages and biology remain unknown. An identification key to species was provided by Greathead (1996*b*).

***Bombylius* L.** (Bombyliinae: Bombyliini)**.** A genus occurring throughout the Holarctic Realm with species occurring as far south as Central America in the New World. More than 280 species are known globally, with 23 of these occurring in the Afrotropical Region. Greathead (1995) showed that most species of *Bombylius sensu lato* in Africa belong to other genera. As now defined, *Bombylius* is represented in the Afrotropical Region principally by the *Bombylius neithokris* Jaennicke, 1867 series (an identification key to species was provided by Greathead 1991*b*) and the *B. modestus* Loew, 1873 series of Bezzi (1924: 46–47) (an identification key to species provided by Greathead 1967). Afrotropical species have not been reared, but several Holarctic species are known as parasites in the nests of solitary bees (Merle 1975).

***Caecanthrax* Greathead** (Anthracinae: Villini)**.** A genus of three species with a primarily Eremian distribution, ranging from central Asia to the Middle East, but also onto the African continent. The Afrotropical distribution of each is as follows: *C. inauratus* (Klug, 1832) from Mali to Yemen (incl. Socotra Is.); *C. arabicus* (Macquart, 1840) from the United Arab Emirates; and *C. auratus* Greathead, 1980 from Yemen. The genus contains striking *Exoprosopa*-like species with a dimidiate wing pattern and contrasting black and gold or white scale patches on the abdomen. The first two species to be recognised were originally described as *Anthrax* and later placed in *Hemipenthes* or *Thyridanthrax*. Immature stages and biology remain unknown. An identification key to species was provided by Greathead (1980*b*).

***Callostoma* Macquart** (Cythereinae: Cythereini) (Fig. 20)**.** A genus of seven species occurring from the Middle East to Central Asia, India and Ethiopia. The Palaearctic species all have a distinctive pattern of black and white vestiture and a brown transverse infuscated band across the middle of the wing. The single Afrotropical species, *C. distinctum* Greathead, 1972, has a similar structure, except for minor differences in wing venation, but strikingly different pigmentation – yellowish vestiture and heavily infuscated wings, having a general resemblance to species of the genus *Rhagio* F. (Rhagionidae) (Greathead 1972). Nothing is known of the habits of the Ethiopian species, but Palaearctic species have been reared from egg pods of Acridoidea (Greathead 1963; Merle 1975).

***Callynthrophora* Schiner** (Mariobezziinae)**.** A poorly known endemic genus, known only from the type specimens of the three described: *C. capensis* Schiner, 1868; *C. hastaticornis* Hesse, 1938; and *C. marginifrons* Bezzi, 1921, from South Africa. Immature stages and biology remain unknown. An identification key to the three species was provided by Hesse (1938).

***Canariellum* Strand** (Lomatiinae: Lomatiini)**.** A genus of four species, three of which occur in the Afrotropical Region, distributed as follows: *C. acutangula* (Loew) and *C. transvaalense* Hesse from South Africa and *C. neavei* (Bezzi) from Malawi. The genus was erected for *Anthrax brunnipennis* Macquart, 1840, an endemic species from the Palaearctic Canary Is. and the genus was subsequently long-regarded as a synonym of *Lomatia* Meigen by authors who had not seen specimens. François (1970), however, collected a long series of *C. brunnipennis*, redescribed it and recognised *Canariellum* as a valid genus. Immature stages and biology remain unknown. An identification key to Afrotropical species is currently unavailable.

***Conomyza* Hesse** (Anthracinae: Prorostomatini)**.** An endemic genus known only from two species: *C. karooana* Hesse, 1956 and *C. semirufella* Hesse, 1956, from the Northern and Western Cape Provinces, South Africa. It was originally proposed by Hesse (1956) for one new species (and one new variety of it) that is very similar in appearance to *Plesiocera*. The variety has since been raised to species. Immature stages and biology remain unknown.

***Cononedys* Hermann** (Anthracinae: Aphoebantini)**.** A western Palaearctic and eastern Afrotropical genus of 13 species, only two of which occur in the Afrotropics: *C. bilobata* (Bezzi, 1924) and *C. inornata* (Greathead, 1967), from Ethiopia and Eritrea, respectively; both representing African extensions of Arabian Peninsula species. The genus may be the Old World counterpart to the New World genus *Aphoebantus* Loew. All the western Palaearctic and Afrotropical species examined by Greathead (1996*a*) were found to belong to the genus *Cononedys*, and other species determined as *Aphoebantus* from the Palaearctic may well belong here, once material is re-examined. Immature stages and biology remain unknown.

***Conophorina* Becker** (Bombyliinae: Bombyliini)**.** A poorly known endemic monotypic genus, with the single species, *C. bicellaris* Becker, 1920, from South Africa, resembling a small *Dischistus*. Immature stages and biology of the species remain unknown.

***Corsomyza* Wiedemann** (Mariobezziinae) (Fig. 10)**.** An endemic genus of 27 species, occurring predominantly in temperate southern Africa, including Namibia, South Africa and Zimbabwe. *Corsomyza* is the most speciose genus of the subfamily Mariobezziinae. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938).

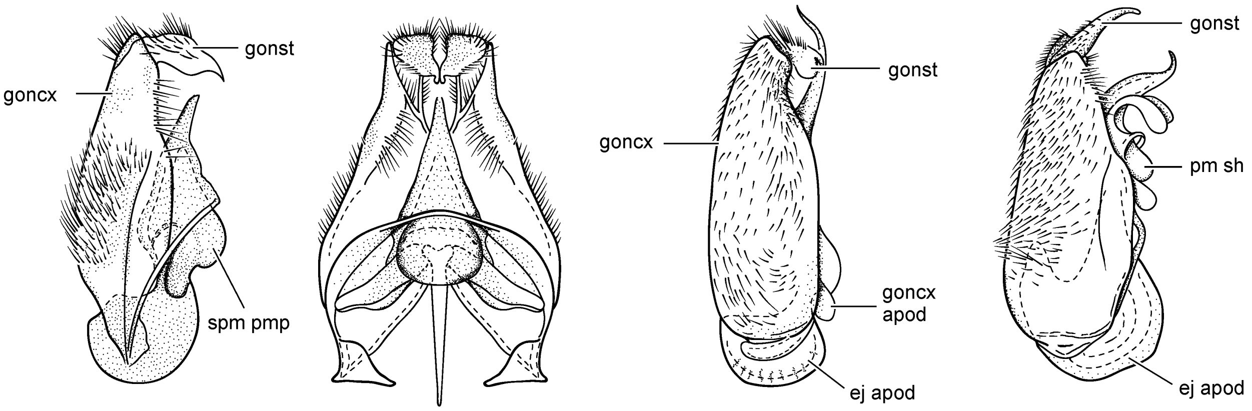
***Coryprosopa* Hesse** (Anthracinae: Prorostomatini)**.** A poorly known endemic monotypic genus, with the single species, *C. lineata* Hesse, 1956, recorded from the Northern and Western Cape Provinces, South Africa and Namibia. Immature stages and biology of the species remain unknown.

***Crocidium* Loew** (Crocidiinae)**.** A genus with an interesting distribution, being known only from Palaearctic Egypt (two species) and the Afrotropical Region (22 species); a further two species from South Africa are under description by Lamas & Evenhuis (in prep.). The distribution in Africa could be explained by dispersal through an arid corridor and subsequent isolation (Lamas & Nihei 2007), as there are no records from Central Africa. Immature stages and biology remain unknown. An identification key to all species was provided by Lamas *et al*. (2003).

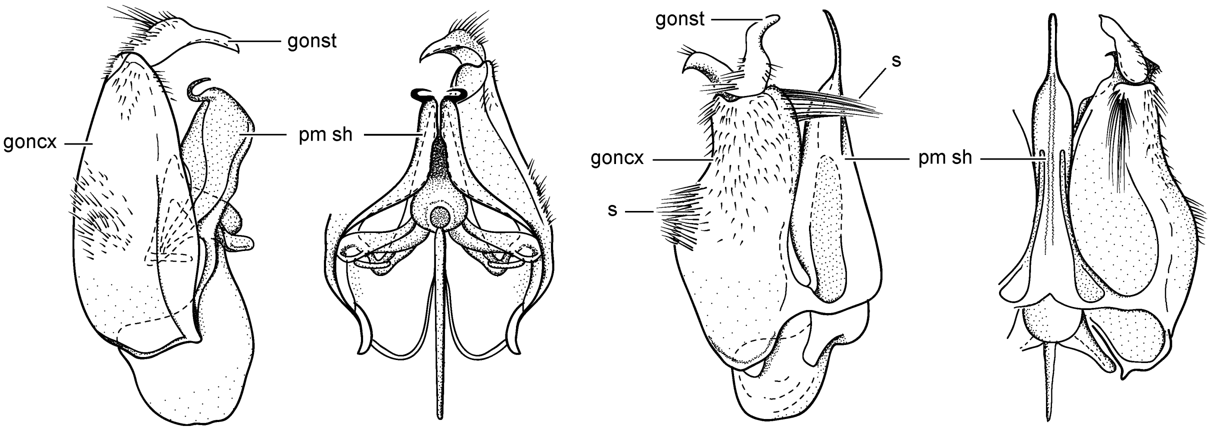
Cytherea **F.** (Cythereinae: Cythereini). A genus of 49 species occurring in the western Palaearctic and North Africa. Four Palaearctic species have distributions that extend into the Arabian parts of the Afrotropical Region. Immature stages have been reared from egg-pods of Acridoidea (Greathead 1963; Merle 1975). Identification keys to species were provided by Paramonov (1930) and Efflatoun (1945).

Defilippia **Lioy** (Anthracinae: Exoprosopini) (Figs 16, 24)**.** A genus of eight species, seven of which occur in the Afrotropical Region. *Defilippia* was raised to generic status by Lambkin *et al*. (2003), based on their phylogenetic analysis; however, they provided no key to distinguish it from other related genera. The genus includes species from the Afrotropical and Palaearctic Regions previously treated as *Exoprosopa* or *E*. (*Defilippia*). Immature stages and biology remain unknown. An identification key to species is currently unavailable.

Desmatoneura **Williston** (Anthracinae: Xeramoebini) (Fig. 13). A genus of 15 species, six of which occur in the Afrotropical Region. *Desmatoneura* occurs in all zoogeographical regions, except Antarctica, but with extremely disjunct populations in the Afrotropical, Nearctic, Oriental and Palaearctic Regions. François (1967) demonstrated that the genus *Chionamoeba* Sack is a synonym of *Desmatoneura* and Greathead (1988) found that *Chiasmella* Bezzi is also a synonym. The generic



74 *Bombomyia* ♂ 75 *Bombomyia* ♂ 76 *Gonarthrus* ♂ 77 *Systoechus* ♂



78 *Bombylisoma* ♂ 79 *Bombylisoma* ♂ 80 *Eurycarenus* ♂ 81 *Eurycarenus* ♂

Figs 45.74–81. Male terminalia of Bombyliidae (lateral views, unless otherwise stated): (74) *Bombomyia bombiformis* (Bezzi); (75) same, ventral view; (76) *Gonarthrus kalaharicus* Hesse; (77) *Systoechus mixtus* (Wiedemann); (78) *Bombylisoma senegalense* (Macquart); (79) same, ventral view; (80) *Eurycarenus dichopticus* Bezzi; (81) same, ventral view. Figs 74–81 (after Hesse 1938, figs 6, as *Bombylius bombiformis*, 166, as *Chasmoneura pectoralis* (Loew), 182, 141, 148, respectively).

Abbreviations: ej apod – ejaculatory apodeme; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; pm sh – parameral sheath; s – setae; spm pmp – sperm-pump.

identity of species is readily confirmed by the large conical parameral sheath and by the tumid frons, the latter which is lacking in other genera with a similar habitus, *e.g.*, species of *Xeramoeba*. Immature stages and biology remain unknown. An identification key to Afrotropical species was provided by Hesse (1956).

***Diatropomma* Bowden** (Anthracinae: Exoprosopini)**.** A small endemic genus comprising three East African species: *D. carcassoni* Bowden, 1962 from Kenya; *D. claudia* (François, 1960) from Burundi; and *D. annettae* Greathead & Evenhuis, 2001 from Tanzania. The genus is readily distinguished from other Exoprosopini, being slender, dark in colour, with petiolate, infuscated wings. As noted by François (1960), they resemble species of the genus *Baccha* F. (Syrphidae) and are weak fliers. All three species occur in arid savanna and thicket habitats. Immature stages and biology remain unknown. An identification key was provided by Greathead & Evenhuis (2001).

***Dicranoclista* Bezzi** (Anthracinae: Anthracini)**.** This genus has a strange disjunct distribution, with two species, *D. simpsoni* Bezzi, 1924 and *D. auliae* Greathead, 1993, known from the northern arid Afrotropical Region (Gambia, Senegal and Sudan) and the other two species occurring in the more arid parts of central and western North America. The male terminalia are similar to those of *Spogostylum*, but females have globular or broad tubular spermathecal bulbs and short ducts, with well-developed sperm pumps. Immature stages and biology remain unknown. The genus was reviewed by Greathead (1993), who provided an identification key.

***Dischistus* Loew** (Bombyliinae: Bombyliini)**.** A genus of 25 species occurring in the Afrotropical and Palaearctic Regions, seven of which occur in the Afrotropics. Hesse (1938) correctly recognised the South African species *D. mystax* as the type of the genus and that *Dischistus* is very close to its Mediterranean counterpart, *Acanthogeron* Bezzi, which Bowden (1973) formally reduced to a subgenus of *Dischistus*. *Acanthogeron* has since been regarded as a synonym of *Dischistus*, but as *Acanthogeron* spp. differ in wing venation and vestiture and are, therefore, readily separated; it is convenient to recognise *Acanthogeron* as a subgenus, as applied here, following Greathead & Evenhuis (2001). *Dischistus sensu stricto* all have brown vestiture composed of long upright setulae, while *D.* (*Acanthogeron*) spp. have much shorter and denser pale setulae. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938).

***Doliogethes* Hesse** (Bombyliinae: Bombyliini)**.** An endemic southern African genus, comprising 17 species from Namibia and South Africa. *Doliogethes* was proposed by Hesse (1938) for those species of *Dischistus* "Group 3" of Bezzi (1924: 91) that have dichoptic males, a tendency for reddening of the cuticle and entirely pale setae on the legs. Immature stages and biology remain unknown. Most species can be identified using the key provided by Hesse (1938).

***Enica* Macquart** (Cythereinae: Enicini)**.** An endemic monotypic genus, with the single species, *E. longirostris* (Wiedemann, 1819), recorded from the Western Cape Province, South Africa. *Enica longirostris* is extremely variable in size and resembles the non-Afrotropical *Cyllenia* Latreille in habitus. Immature stages and biology of the species remain unknown.

***Epacmoides* Hesse** (Anthracinae: Prorostomatini)**.** An endemic genus of three species (*E. biumbonatus* (Bezzi), *E. cryptochaunum* Hesse, and *E. xerophilus* Hesse) confined to southern Africa. Although given the name *Epacmoides*, the genus was proposed by Hesse (1956) for species more similar in appearance to *Plesiocera* and *Prorostoma* than to the New World genus *Epacmus* Osten Sacken. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1956).

***Eremyia* Greathead** (Bombyliinae: Bombyliini)**.** *Eremyia* was proposed by Greathead (1996*b*) for three species formerly in *Bombylisoma*, from the eastern half of the Eremian Realm. One species, *E. argentata* (Greathead, 1967), occurs in the Afrotropical Region, recorded from Eritrea and Yemen. Immature stages and biology of the species remain unknown. Species of the genus can be identified using the identification key to *Bombylisoma* spp. provided by Greathead (1996*b*).

***Euligyra* Lambkin & Yeates** (Anthracinae: Exoprosopini) (Fig. 15)**.** An endemic genus currently comprising six species. In their phylogenetic analysis, Lambkin *et al*. (2003) determined that the African species that they examined (previously assigned to *Ligyra* Newman), belong in the new genus *Euligyra*. *Ligyra* is, in their work, restricted to the Australasian Region, but may also include Australian species that range into adjacent Oriental areas. *Ligyra sensu lato* occurs virtually worldwide, contains almost 120 species and workers (*e.g.*, Bowden 1971), have postulated that the genus is highly varied and may actually comprise a complex of genera. Despite the characters provided by Lambkin *et al*. (2003), preliminary examination of numerous species of "*Ligyra*" from Africa (and dozens of species from other regions), in preparation of this chapter, has not corroborated any robust characters to separate *Euligyra* from *Ligyra*. Solving this taxonomic problem is beyond the scope of this *Manual*, so *Euligyra* is tentatively retained here pending further studies. If all Afrotropical species are eventually transferred to *Euligyra*, it will be known from 23 species. There are no records of immature hosts for Afrotropical species, but they may be similar to those for *Ligyra* from other areas, where they are recorded as parasitoids of the pupae of Scoliidae and Tiphiidae (Hymenoptera) (Merle 1975). Hesse (1956, as *Ligyra*) can be used to key species of putative *Euligyra* from the Afrotropics.

***Eurycarenus* Bezzi** (Bombyliinae: Bombyliini) (Fig. 8). A genus of 15 species occurring in the Afrotropical and Oriental (India) Regions, 14 of which occur in the Afrotropics. *Eurycarenus* is a very distinctive genus, at once recognised by the pattern of black, white and yellow vestiture, numerous black setae and broad head, with indented hind margins of the eyes. Immature stages and biology remain unknown. Identification keys to species were provided by Bowden (1964, for Ghana) and Hesse (1938, for southern Africa).

***Exhyalanthrax* Becker** (Anthracinae: Villini). A fairly widespread genus in the Old World (Afrotropical, Oriental and Palaearctic Regions), comprising 78 species, 46 of which occur in the Afrotropics. *Exhyalanthrax* have a characteristic appearance and formed Hesse's (1956) *Thyridanthrax* "Group 1". Hesse had shown that some species have sexually dimorphic wing infuscation and, most notably, that *E. lineus* (Loew, 1860) with hyaline wings was the male of *E. abruptus* (Loew, 1860) females with a dark basicostal infuscation. Species are commonly reared as parasitoids in the pupae of *Glossina* spp. and other dipterous puparia and have also been reared from the parasitoids and hosts of parasitic Diptera and Hymenoptera (Austen 1929; Greathead 1980*c*; Merle 1975; Yeates & Greathead 1997). Bezzi (1924: 193) provided an identification key to Afrotropical species and more recent keys include Hesse (1956) and Bowden (1964), all of which identify species in their former placement in *Thyridanthrax*.

***Exoprosopa* Macquart** (Anthracinae: Exoprosopini) (Fig. 23). A virtually cosmopolitan genus comprising almost 335 species, 172 of which occur in the Afrotropical Region. There is a bewildering diversity of wing patterns and vestiture, as a result of convergent evolution of cryptic and disruptive colour patterns (Lambkin 2001). This is not congruent with differences in male and female terminalia, considered to be of phylogenetic significance. Despite several of Bezzi's (1924) subgenera of *Exoprosopa* having been raised to generic status and some species-groups to separate genera, *Exoprosopa* remains a very large genus, being particularly diverse and speciose in the Afrotropics. Greathead & Evenhuis (2001) treated *Defilippia* as a junior synonym of *Exoprosopa*; however, Lambkin *et al*. (2003) showed it to be a good genus. Little is known of the life history, but there are a few records of rearings from cocoons of Hymenoptera and some more dubious records (Merle 1975). Identification keys to Afrotropical species were provided by Bowden (1964, for Ghana), François (1972, Senegal) and Greathead (2001, the *E. busiris*-group).

***Geron* Meigen** (Toxophorinae: Gerontini)**.** A virtually cosmopolitan genus, with even a few species found on Pacific Oceanic islands (Evenhuis 1989: 361). Of the 196 species globally, 64 are known from the Afrotropical Region. Hesse (1938) proposed the genus *Amictogeron* for African species with dark vestiture and a tendency for the wings to be tinged smoky-brown, various subtle differences in the external morphology, and in the male terminalia. Bowden (1974), however, showed that there is no clear distinction between species of *Amictogeron* and *Geron sensu stricto* and treated the former as a junior synonym of the latter. Bowden also synonymised *Pseudoammictus* Bigot with *Geron*, but Evenhuis (1979) resurrected it as a subgenus and Greathead & Evenhuis (2001) followed that treatment. There are few conspicuous external characters for distinguishing species in the genus, but males have complex terminalia and females possess a subgenital plate, providing both sexes with good characters for the separation of species. Examination of the terminalia is essential for accurate identification and many older distribution records, based solely on external characters are unreliable (Greathead 1999*b*). Records of parasitisation are few, but indicate that immatures are endoparasitoids in the pupae of Lepidoptera, including Psychidae, Pyralidae and Sesiidae (Merle 1975; Purrington & Evenhuis 2001; Yeates & Greathead 1997). Identification keys to Afrotropical species were provided by Hesse (1938, treating *Geron* and *Pseudoammictus* as separate genera) and Bowden (1974).

***Gnumyia* Bezzi** (Mariobezziinae)**.** A poorly known endemic genus of two species confined to southern Africa: *G. brevirostris* (Bezzi, 1921) from Namibia, South Africa and Zimbabwe; and *G. fuscipennis* Hesse, 1938, from South Africa. The genus is close in appearance to *Callynthrophora* and *Corsomyza*, but differs in antennal and facial characters. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938).

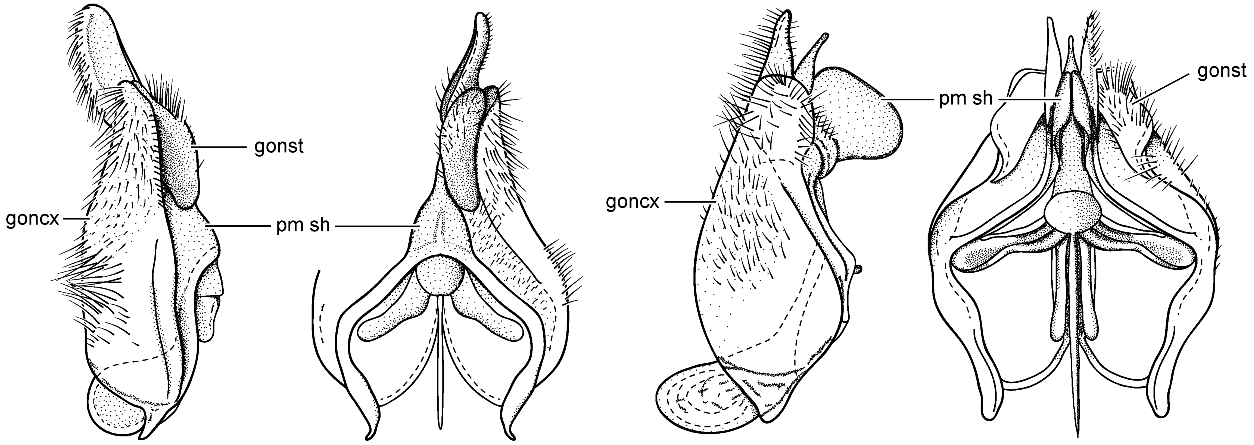
***Gonarthrus* Bezzi** (Bombyliinae: Bombyliini)**.** An endemic genus of 31 species widespread in the Afrotropical Region. They are generally narrow-bodied flies, with long white to yellowish setulae and are very uniform in appearance recalling *Geron* spp., with which they have been confused on occasion. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938).

***Hemipenthes* Loew** (Anthracinae: Villini)**.** A genus of 81 species occurring primarily in the Neotropical (27 spp.) and Oriental (8) Regions and the Holarctic Realm (56). Only one species, *H. ethiops* Greathead, 1967 (from Ethiopia), occurs in the Afrotropical Region. *Hemipenthes* spp. are *Anthrax*-like in external morphology (face not produced; single onion-shaped flagellum), but are *Villa*-like in appearance and colour, characteristically having the wing infuscated in the basal half or more. Immatures are hyperparasites of dipterous and hymenopterous parasitoids of Lepidoptera and Diprionidae (Hymenoptera) and their hosts (Merle 1975; Yeates & Greathead 1997).

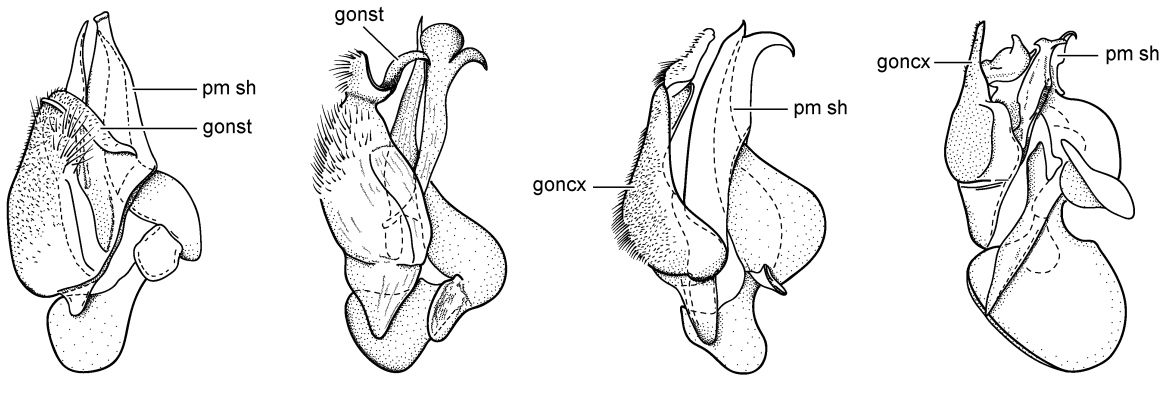
***Heteralonia* Rondani** (Anthracinae: Exoprosopini)**.** A genus of 142 species occurring in the Afrotropical, Oriental and Palaearctic Regions, with 72 species known from the Afrotropics. *Heteralonia* was erected to contain species of *Exoprosopa* with wing cell r_{2+3} divided by a crossvein. Bowden (1975) found that species in other subgenera of *Exoprosopa sensu* Bezzi (1924): (*H.* (*Acrodisca*); some *Defilippia*, *H.* (*Isotamia*), *H.* (*Mesoclis* Bezzi) non-Afrotropical, *H.* (*Metapenta*) and *H.* (*Zygodipla*)), all possess small male terminalia, with a simple axe-head-shaped epiphallus concealed between the fused gonocoxae and a weak ejaculatory apodeme, as well as a tendency to unstable wing venation, a characteristic dark wing pattern and dark vestiture. Bezzi (1924) grouped all these species in *Heteralonia* and divided it into subgenera, based on wing venation and the degree of reduction of the fore legs. Additionally, it has been found that species of *Heteralonia sensu* Bowden all have a similar spermathecal shape – small with narrow, tubular, thick-walled, unpigmented bulbs – which provides an unambiguous apomorphy to define the genus. Lambkin *et al*. (2003) synonymised the monotypic genus *Colossoptera* Bowden with *Heteralonia*, but did not indicate a subgeneric placement for its species. Their phylogenetic tree placed the lone species (*C. latipennis* (Brunetti, 1909)) in the same clade with *Heteralonia singularis* (Macquart, 1840), which is currently treated in *H.* (*Zygodipla*). The subgeneric characters of *Heteralonia*, if interpreted strictly, produce some anomalies: some southern African *Acrodisca*-like species lack the stump veins in the wing and so are strictly *Homolonia* spp., although they have the typical wing pattern, body size and colouration of *Acrodisca* spp.; similarly some Arabian *H.* (*Zygodipla*)-like species lack either a divided or a closed wing cell r_5, but have the membrane pattern and colouration of this subgenus; some Indian species can be placed in either *Acrodisca* or *Isotamia*, having the characters of both subgenera, and so on. Thus, the subgenera of *Heteralonia* are ill-defined and are retained here only as an aid to identification; the number of species in each is consequently open to interpretation. The six Afrotropical subgenera can be summarised as follows: *H.* (*Acrodisca*) is a widespread subgenus with striking wing patterns of infuscation and maculae, with species known from the Afrotropical, Oriental and Palaearctic

Regions (*ca* 22 species recorded from the Afrotropics); *Heteralonia sensu stricto* is an endemic subgenus known from only two species: *H. oculata* (Macquart, 1840), from Senegal to Eritrea and East Africa and *H. kaokoensis* (Hesse, 1956) from Namibia; *H.* (*Homalonia* Bowden), a subgenus occurring in the Afrotropical, Oriental and Palaearctic Regions (21 species restricted to the Afrotropics); *H.* (*Isotamia*), a subgenus occurring in the Afrotropical and Oriental Regions (6 species recorded from the Afrotropics); *H.* (*Metapenta*), an endemic subgenus, with ten species; and *H.* (*Zygodipla*), a subgenus occurring in the Afrotropical, Oriental and Palaearctic Regions (3 species recorded from the western Afrotropical Region). With regard to known biologies, there is only one reliable record of parasitisation, a record from the cocoon of a pompilid (Hymenoptera) (Yeates & Greathead 1997). The record from a locust in Merle (1975) is dubious. Identification keys to Afrotropical species were provided by Bowden (1964, for Ghana), François (1972, Senegal), Greathead (1967, Ethiopia and Eritrea) and Hesse (1956, southern Africa), with all species treated as *Exoprosopa*.

***Heterotropus* Loew** (Heterotropinae) (Fig. 17)**.** A genus of 48 species occurring in the Afrotropical, Oriental and Palaearctic Regions. Thirteen species are currently known from the Afrotropics, but additional new species are known from United Arab Emirates (Evenhuis, unpubl.). *Heterotropus* include small, odd-looking, bare flies with a pattern of black and yellow or ivory areas on the cuticle. The recent molecular studies of Trautwein (2009) and Trautwein *et al.* (2011) recovered *Heterotropus* in a clade with Hilarimorphidae (non-Afrotropical) and Mythicomyiidae and separated from Bombyliidae *sensu stricto*. Recent examination has found that all three groups share the character state of the lack of an arculus (vein *MA*) at the base



82 *Beckerellus* ♂ 83 *Beckerellus* ♂ 84 *Parisus* ♂ 85 *Parisus* ♂



86 *Desmatoneura* ♂ 87 *Xeramoeba* ♂ 88 *Anthrax* ♂ 89 *Anthrax* ♂

Figs 45.82–89. Male terminalia of Bombyliidae (lateral views, unless otherwise stated): (82) *Beckerellus terminatus* (Becker); (83) same, ventral view; (84) *Parisus aurantiacus* (Macquart); (85) same, ventral view; (86) *Desmatoneura meridionalis* (Hesse); (87) *Xeramoeba apricaria* Hesse; (88) *Anthrax pithecius* F.; (89) *A. aygulus* F. Figs 82–89 (after Hesse 1938, figs 21, as *Bombylius mollis*, 31, as *B. tinctipennis* var. *thornei*, 131, as *Chionamoeba meridionalis*, 132, as *C. meridionalis*, 135, as *Anthrax conspurcata*, 151, as *A. biflexus,* respectively).

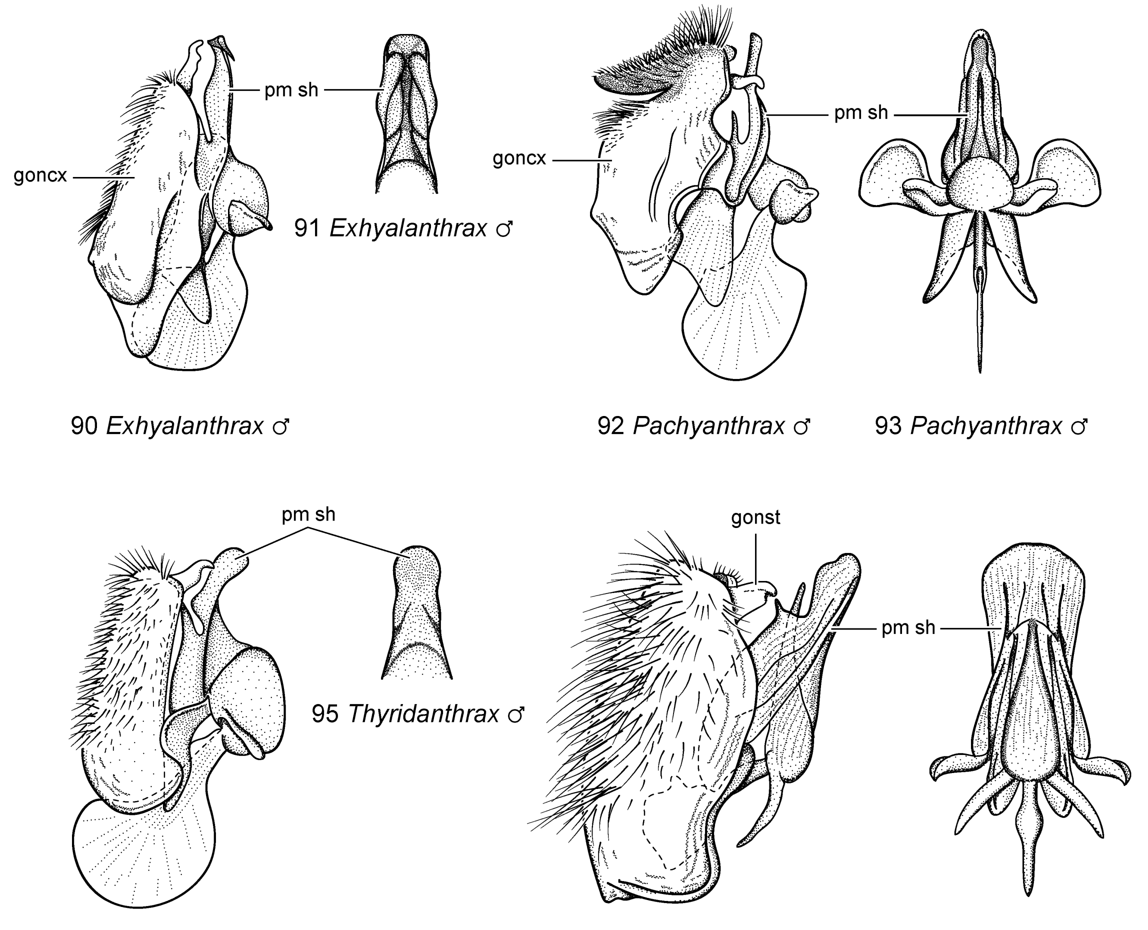
Abbreviations: goncx – gonocoxite; gonst – gonostylus; pm sh – parameral sheath.

of the wing (present in Bombyliidae *sensu stricto*). If this clade is confirmed through further studies, Heterotropinae may warrant being raised to familial level (*e.g.*, Krivosheina 2012), as has been done for the Mythicomyiidae. Larvae are elongate, therevid-like and are predacious in soil (Yeates & Irwin 1992). The most recent identification key to southern African species was provided by Greathead (2006).

Hyperusia **Bezzi** (Mariobezziinae)**.** An endemic genus of nine species, *Hyperusia* is similar in appearance to *Corsomyza*, but with a different distribution pattern. Species occur in tropical southern Africa and into central Tanzania, areas principally outside the Cape temperate region, where *Corsomyza* spp. predominate (Greathead 2000). Immature stages and biology remain unknown. An identification key to most species was provided by Greathead (2006).

Isocnemus **Bezzi** (Bombyliinae: Bombyliini)**.** An endemic monotypic genus, with the single species, *I. nemestrinus* Bezzi, 1924 (from Ethiopia), bearing a strong resemblance to species of the genus *Nemestrinus* Latreille (Nemestrinidae) in shape, vestiture and colouration. Immature stages and biology of the species remain unknown.

Laminanthrax **Greathead** (Anthracinae: Villini)**.** A genus of only two species occurring primarily in the south-western Palaearctic and in north-east Africa. One species, *L. chionophorus* (Bezzi, 1925), extends into the Afrotropical Region and is recorded from Eritrea and Ethiopia. *Laminanthrax* is the most plesiomorphic genus in the tribe Villini and has well-developed pulvilli (like those in Anthracini), unlike other genera included in the tribe, except *Synthesia*. Immature stages and biology of the species remain unknown.



91 *Exhyalanthrax* ♂

90 *Exhyalanthrax* ♂

92 *Pachyanthrax* ♂

93 *Pachyanthrax* ♂

95 *Thyridanthrax* ♂

94 *Thyridanthrax* ♂

96 *Heteralonia* (*Acrodisca*) ♂

97 *Heteralonia* (*Acrodisca*) ♂

Figs 45.90–97. Male terminalia of Bombyliidae (lateral views, unless otherwise stated): (90) *Exhyalanthrax abruptus* (Wiedemann); (91) same, apex of parameral sheath, ventral view; (92) *Pachyanthrax lutulentus* (Bezzi); (93) same, phallic complex, ventral view; (94) *Thyridanthrax perspicillaris* (Loew); (95) same, apex of parameral sheath, ventral view; (96) *Heteralonia* (*Acrodisca*) *umbrosa* (Hesse); (97) same, phallic complex, ventral view. Figs 90–97 (after Hesse 1956, figs 192, as *Thyridanthrax abruptus*, 198, as *Thyridanthrax lutulentus*, 199, as *Thyridanthrax subperspicillaris*, 231, as *Exoprosopa umbrosa*, respectively).

Abbreviations: goncx – gonocoxite; gonst – gonostylus; pm sh – parameral sheath.

***Legnotomyia* Bezzi** (Bombyliinae: Conophorini)**.** A genus of ten known species, occurring primarily in the Palaearctic Region, with one species, *L. striata* (Bischof, 1903), recorded from Kenya and Tanzania in the Afrotropics. Species of *Legnotomyia* are virtually bare and have a characteristic broad, rounded abdomen with, in most instances, a banded pattern of colouration. The wing infuscation is sexually dimorphic, being more intense and restricted in area in males. Immature stages and biology of the species remain unknown.

***Lepidochlaenus* Hesse** (Bombyliinae: Bombyliini)**.** An endemic monotypic genus, with the single species, *L. fimbriatus* Hesse, 1938, recorded from Namibia and western South Africa. Immature stages and biology of the species remain unknown.

***Litorhina* Bowden** (Anthracinae: Exoprosopini)**.** A fairly widespread genus occurring from the Palaearctic Region (two species) and the Afrotropical Region (35 species) to India (two species) in the Oriental Region. In Africa the genus is not known to occur north of the Sahara. Bowden (1975) explained the complex history of *Litorhynchus* Macquart, the name of which had become familiar from the work of Bezzi (*e.g.*, Bezzi 1924), Hesse (1956), and others for this distinctive African genus. After discovering the true identity of the type species, however, the name became a junior synonym of *Exoprosopa*, so that a new genus (*Litorhina*) was required for the remaining species in the genus. Immatures have been recorded from Tiphiidae and from nests of Sphecidae (Hymenoptera) (Merle 1975; Yeates & Greathead 1997). Identification keys to Afrotropical species were provided by François (1972, for Senegal) and Hesse (1956, southern Africa), all as *Litorhynchus*.

***Mariobezzia* Becker** (Mariobezziinae)**.** A genus of four species ranging from North Africa in the Palaearctic to India and Pakistan in the Oriental Region. Only one of the four species, *M. ebneri* Becker, 1922, is known from the north-eastern Afrotropical Region (Sudan). Immature stages and biology of the species remain unknown.

***Marleyimyia* Hesse** (Anthracinae: Villini)**.** An unusual genus with reduced mouthparts consisting of two species occurring in the Afrotropical Region (*M. natalensis* Hesse, 1956 and *M. xylocopae* Marshall & Evenhuis, 2015) and one from the Oriental Region (*M. goliath* (Oldroyd, 1951)). The genus was proposed by Hesse (1956) for his new South African species, *M. natalensis*, reared from immatures found in a log with cossid (Lepidoptera) pupae, and which did not correspond with *Oestranthrax* or *Villoestrus* (the only other two known genera at the time with reduced mouthparts). Subsequently, a second species was described from Peninsular Malaysia in the Oriental Region, based on two specimens that were reared from a single cossid host (Oldroyd 1951). Recently, Marshall & Evenhuis (2015) described a third species, *M. xylocopae* (Fig. 1), the second known from the Afrotropical Region. An additional undescribed species from Nigeria was reported by Bowden (1978). Marshall & Evenhuis (2015) presented a distribution map and photographs of the types of both Afrotropical species.

***Megapalpus* Macquart** (Mariobezziinae)**.** An endemic monotypic southern African genus, with the single species, *M. capensis* Hesse, 1938, recorded from South Africa. Hesse (1938) provided characters for the separation of two partially sympatric species, *M. capensis* (Eastern and Western Cape Provinces) and *M. nitidus* Macquart, 1840 (Western Cape Province). Specimens vary in the expression of these characters, however, and many show a combination of characters of the two putative species. Consequently, *M. nitidus* has been placed in synonymy with *M. capensis* and the genus is currently considered monotypic. *Megapalpus capensis* has been studied as a pollinator of *Pelargonium tricolor* Curtis (Geraniaceae) (McDonald & Walt 1992) and *Gorteria diffusa* Thunb. (Asteraceae) (Johnson & Midgley 1996). Immature stages and biology of the species remain unknown.

***Micomitra* Bowden** (Anthracinae: Exoprosopini)**.** A genus of 19 species occurring in the Afrotropical, Oriental and Palaearctic Regions. Eight species are restricted to the Afrotropics, including one species from Aldabra Is. and an undescribed species is known from Madagascar (Greathead & Evenhuis 2001). The male and female terminalia resemble those of *Atrichochira* and the two genera form a distinct clade, along with the Australasian genus *Pseudopenthes* Roberts (Lambkin *et al*. 2003). Immatures have been recorded as parasitic on Myrmeleontidae (Merle 1975). No recent identification keys to species are available, but Hesse (1956, as *Exoprosopa*) can be used to identify southern African species.

***Nomalonia* Rondani** (Cythereinae: Enicini)**.** An endemic genus of six species confined to South Africa. Hesse (1956) noted that this genus is barely separable from *Enica* (only on the basis of lack of wing crossveins and patches of setae on the face) and that, as such, may simply be a subgenus or synonym of *Enica*. The genus is retained here, pending further studies. Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1956).

***Notolegnotus* Greathead & Evenhuis** (Bombyliinae: Conophorini)**.** An endemic monotypic genus, with the single species, *N. brevis* Greathead & Evenhuis, 2001, described from Namibia. *Notolegnotus brevis* is superficially similar to a *Legnotomyia* sp., but is remarkable in having vestigial mouthparts. On close examination it also differs from *Legnotomyia* in having a leaf-shaped antennal flagellum without long setulae, the face not projecting and fine setulae on the laterotergite and the first abdominal tergite not interrupted medially (Greathead & Evenhuis 2001). Immature stages and biology of the species remain unknown.

***Notolomatia* Greathead** (Lomatiinae: Lomatiini) (Fig. 11)**.** An endemic genus of 97 described species. The genus was proposed for Afrotropical species formerly included in *Lomatia*, which is now restricted to the Palaearctic Region. Immature stages and biology remain unknown. Identification keys were provided by Bezzi (1924: 142) and Hesse (1956), all as *Lomatia*.

***Oestranthrax* Bezzi** (Anthracinae: Villini)**.** A genus of 15 species with reduced mouthparts, known from the Afrotropical, Oriental and Palaearctic Regions, five of which are restricted to the Afrotropics. *Oestranthrax* adults are seldom collected, presumably because they are unable to feed and adults have a brief life span. As with other genera of the tribe Villini with vestigial mouthparts, adults contain an unusual amount of fat and collected specimens tend to become "greasy" following drying. Little is known of the life history, with only one record as a parasitoid of Myrmeleontidae (Yeates & Greathead 1997). An identification key was provided by Hesse (1956).

***Oniromyia* Bezzi** (Oniromyiinae)**.** An endemic genus, with two described species: *O. caffrariae* Hesse, 1960, from the Eastern Cape Province, South Africa; and *O. pachycerata* (Bigot, 1892), from the Western Cape, South Africa. The subfamily Oniromyiinae was proposed by Greathead (1972) to contain the anomalous South African genus *Oniromyia*, which had previously been placed in the subfamily Cythereinae. Yeates (1994) substantiated this conclusion and noted that the scape, with ventral bulge and scales on the labrum, constituted synapomorphies for the subfamily. *Oniromyia* also has characters in common with *Xenoprosopa* however (see below). Immature stages and biology remain unknown.

***Othniomyia* Hesse** (Bombyliinae: Conophorini)**.** An endemic monotypic genus, with the single species, *O. tylopelta* Hesse, 1938, from the Western Cape, South Africa. The compact body with the thorax humped is reminiscent of Acroceridae. Immature stages and biology of the species remain unknown.

***Pachyanthrax* François** (Anthracinae: Villini)**.** A genus of 13 currently known species occurring in the Afrotropical, Oriental and southern Palaearctic Regions. Five species are restricted to the Afrotropics, but do not extend south into South Africa. After *Pachyanthrax* was described for a new species from Senegal, certain anomalous species that had been placed in *Thyridanthrax*, *Villa* or *Exoprosopa*, have been transferred to this genus. Immature stages and biology remain unknown. An identification key to Afrotropical species was provided by Bezzi (1924), as *Thyridanthrax*.

***Palintonus* François** (Ecliminae)**.** Known from a single Afrotropical species, *P. austeni* (Paramonov, 1949), originally placed in the New World genus *Lepidophora* Westwood (which is similar in appearance and also has scales on the wings). François (1964) showed that the African species differed in so many characters that it should be transferred to his new genus, *Palintonus*. Currently, the genus is only known from the forests of Democratic Republic of Congo and Uganda. A second species from Côte d'Ivoire is known only from a photograph (Lachaise & Bowden 1976). Recent investigations indicate that the genus is monophyletic (Rodrigues & Lamas, unpubl.). Immature stages and biology remain unknown.

***Pantostomus* Bezzi** (Tomomyzinae)**.** An endemic southern African genus of nine species that superficially resemble some South African Syrphidae of the genera *Melanostoma* Schiner, *Paragus* Latreille, or *Xanthogramma* Schiner. Adults of *Pantostomus* are frequently found visiting flowers of mesems (Mesembryanthemaceae) or Asteraceae. Immature stages remain unknown. An identification key to species was provided by Hesse (1956).

***Parageron* Paramonov** (Usiinae: Usiini)**.** A fairly widespread, primarily Palaearctic genus of 19 species, with only one species, *P. erythraeus* (Greathead, 1967), from Eritrea recorded from the Afrotropical Region. Species of *Parageron* are similar in appearance to *Apolysis*, frequently with greyish yellow to bright yellow bands on the abdomen, but are generally larger in body size. Gibbs (2011) clarified the generic concepts between *Apolysis*, *Parageron* and the non-Afrotropical *Usia* Latreille. *Parageron* can be separated from *Apolysis* by the male terminalia which are rotated 180° (35–145° in *Apolysis*). Immature stages and biology remain unknown.

***Paratoxophora* Engel** (Ecliminae)**.** An endemic monotypic genus, with the single species, *P. cuthbertsoni* Engel, 1936, recorded from southern and eastern Africa. *Paratoxophora* superficially resembles *Gonarthrus* and consequently had been included in the Bombyliinae, notably by Hesse (1938), however, it differs most conspicuously from *Gonarthrus* in the large size and structure of the male terminalia and in the dark bluish black cuticle and sparse vestiture and was placed in the Ecliminae by Evenhuis & Greathead (1999). Recent investigations indicate that the genus is monophyletic and corroborates its placement in the Ecliminae (Rodrigues & Lamas, unpubl.). Immature stages and biology of the species remain unknown.

***Parisus* Walker** (Bombyliinae: Bombyliini)**.** A predominantly southern African and south-western Asian (Oriental) genus, comprising 47 species, 44 of which occur in the Afrotropical Region. The genus was revived by Greathead (1995) for the majority of species in the *Bombylius mundus*-group of Bezzi (1924: 46) (= *Bombylius* "Group 2" of Hesse (1938, 1961)). Immature stages and biology remain unknown. An identification key to species was provided by Hesse (1938), as his *Bombylius* "Group 2".

***Peringueyimyia* Bigot** (Lomatiinae: Peringueyimyiini)**.** An endemic monotypic genus, with the single species, *P. capensis* Bigot, 1887, recorded from the Northern and Western Cape Provinces, South Africa. Formerly placed as a monotypic tribe in the subfamily Cylleniinae, Yeates (1994) transferred it to a monotypic tribe within the subfamily Lomatiinae. Immature stages and biology of the species remain unknown.

***Petrorossia* Bezzi** (Anthracinae: Xeramoebini) (Fig. 12)**.** A widespread Old World genus of 69 species, occurring in the Afrotropical, Australasian, Oriental and southern and eastern Palaearctic Regions. Twenty-eight species are recorded from the Afrotropical Region. Despite published identification keys (see below), species are difficult to accurately characterise based on external morphology, and the possible taxonomic significance of considerable variation in male terminalia characters has not been resolved. Host preference is apparently greatly varied, with species having been reared from the puparia of *Glossina* spp., cocoons of Tiphiidae, solitary bees and wasps and one from the egg mass of a spider (Merle 1975; Yeates & Greathead 1997). Identification keys to Afrotropical species were provided by Hesse (1956) and Bowden (1964).

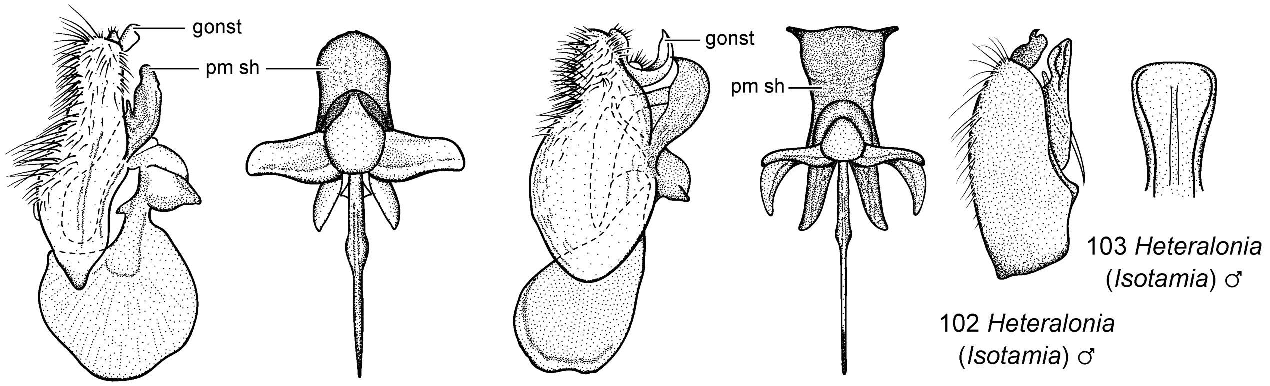
***Phthiria* Meigen** (Phthiriinae) (Fig. 5)**.** A genus of 73 currently known species, 22 of which are restricted to the Afrotropical Region. Evenhuis (1990) reviewed the genera of Phthiriinae, which restricted the distribution of *Phthiria* to the Old World and Chile in the Neotropical Region. Recent investigations have shown, however, that specimens from the latter country may not represent true *Phthiria* (Yamaguchi *et al.*, unpubl.). The majority of known African species have been recorded from North or southern Africa, although *P. fumata* (Greathead, 1966) was described from Kenya (as *Oligodranes*) and females of *P. crocogramma* Hesse, 1938 have been collected in Kenya, as have single specimens of two additional species. Thus, it is likely that further collecting in tropical Africa, especially

Malaise and yellow pan trapping, will indicate a more even distribution of species on the African continent. Immatures have been reared from Gelechiidae and Tortricidae (Lepidoptera) (Merle 1975). An identification key to species was provided by Hesse (1975).

***Pipunculopsis* Bezzi** (Anthracinae: Xeramoebini)**.** A genus of four species occurring in Palaearctic North Africa that is very similar in appearance to *Petrorossia*. One of these species, *P. bivittata* Bezzi, 1925, extends southwards into Sudan. Immature stages and biology of the species remain unknown. An identification key to species was provided by Zaitzev (2000).

***Plesiocera* Macquart** (Anthracinae: Prorostomatini)**.** A near endemic Afrotropical genus known from ten species, nine of which occur in the Afrotropical Region, with the type species *P. algira* Macquart, 1840, occurring in Palaearctic North Africa. Yeates (1994) noted that the type species differs from the southern African species, in possessing an indented eye margin and bisecting line. This character was noted by Hull (1973), who proposed the new genus *Calledax*, for the southern African species. *Calledax* was treated as a junior synonym of *Plesiocera* by Bowden (1980: 429). Yeates (1994), however, considered that when the composition of the Prorostomatini is revised, *Calledax* may well be revived and *Plesiocera* removed to another tribe. *Plesiocera ochraea* Greathead, 1967, a species that ranges from eastern Afrotropical Africa into northern and central Palaearctic Saudi Arabia, lacks the bisecting line and would thus be included in *Calledax sensu* Hull (1973). Immature stages and biology remain unknown. An identification key to eight southern African species was provided by Hesse (1956).

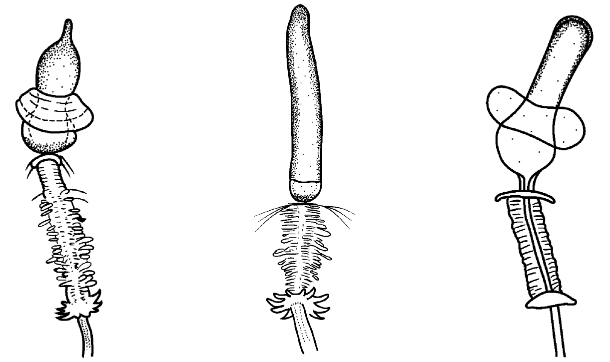
***Prorachthes* Loew** (Bombyliinae: Conophorini)**.** A western Palaearctic and southern African genus of ten species, two of



103 *Heteralonia* (*Isotamia*) ♂

102 *Heteralonia* (*Isotamia*) ♂

98 *Exoprosopa* ♂ 99 *Exoprosopa* ♂ 100 *Micomitra* ♂ 101 *Micomitra* ♂



104 *Defilippia* ♀ 105 *Balaana* ♀ 106 *Exoprosopa* ♀

Figs 45.98–106. Male terminalia and female spermathecae of Bombyliidae (lateral views, unless otherwise stated): (98) male terminalia of *Exoprosopa argentifrons* Macquart; (99) same, phallic complex, ventral view; (100) same, *Micomitra lucidipennis* Greathead & Evenhuis; (101) same, phallic complex, ventral view; (102) same, *Heteralonia* (*Isotamia*) *azanae* Greathead & Evenhuis; (103) same, apex of parameral sheath, ventral view; (104) female spermathecae of *Defilippia rubescens* (Bezzi); (105) same, *Balaana grandis* (Meigen); (106) same, *Exoprosopa enigma* Greathead & Evenhuis. Figs 98–101 (after Hesse 1956, figs 262, as *Exoprosopa argentifrons*, 273, as *E. iridipennis*), Figs 102, 103, 106 (after Greathead & Evenhuis 2001, fig. 123, 122, respectively), Figs 104, 105 (after Lambkin *et al.* 2003, figs 3D, 16J, respectively).

Abbreviations: gonst – gonostylus; pm sh – parameral sheath.

which occur in Namibia and South Africa: *P. conspersipennis* (Hesse) and *P. xerophilus* (Hesse). *Prorachthes conspersipennis*, originally described in *Cheilohadrus* Hesse, differs from that Palaearctic genus, in having a narrow spindle-shaped flagellum, rather than a broad flattened one. Otherwise, the genus is readily recognised by the mottled wings and dark vestiture. Immature stages and biology remain unknown. An identification key to species was provided by Paramonov (1940).

Prorostoma **Hesse** (Anthracinae: Prorostomatini)**.** An endemic monotypic genus, with the single species, *P. integra* Bezzi, 1956, recorded from South Africa. Hesse (1956) described this genus based on *P. integra*, previously placed in *Plesiocera*. Immature stages and biology of the species remain unknown.

Pteraulacodes **Hesse** (Anthracinae: Aphoebantini)**.** An endemic genus of two species: *P. hessei* Lindner, 1956, from Namibia; and *P. karooensis* Hesse, 1956, from South Africa. This genus is, as its names implies, very similar to *Pteraulax*, but differs by the characters provided in the above key. Immature stages and biology remain unknown. Contrary to the statement in Greathead & Evenhuis (2001), there are currently no identification keys to species.

Pteraulax **Bezzi** (Anthracinae: Aphoebantini)**.** A mainly Afrotropical genus, with eight species in southern Africa and one other species occurring in Iran in the Palaearctic Region. Immature stages and biology remain unknown. An identification key to Afrotropical species was provided by Hesse (1956).

Pterobates **Bezzi** (Anthracinae: Exoprosopini)**.** A genus of five species occurring in the Afrotropical, Oriental and Palaearctic Regions. Only one species, *P. apicalis* (Wiedemann, 1821), is known from South Africa in the Afrotropics. *Pterobates* spp. have a striking appearance and are readily recognised by their iridescent black scales on the body, almost entirely dark infuscated wing membrane and conspicuous long dark scales on the hind legs, that give the legs a feathered appearance. Immatures have been reared from a pompilid, a lepidopteran and a myrmeleontid (Yeates & Greathead 1997).

Pusilla **Paramonov** (Mariobezziinae)**.** An endemic monotypic genus, with the single species, *P. longirostris* Paramonov, 1954, known only from the unique holotype from Democratic Republic of Congo. Immature stages and biology of the species remain unknown.

Sisyrophanus **Karsch** (Bombyliinae: Bombyliini)**.** An endemic genus comprising eight species. The wings are similar to those of *Eurycarenus* spp. and like these, the head is broad and the body elongate, but these species differ in the colour of the vestiture, having few setae and in having entire hind margins to the eyes. Immature stages and biology remain unknown. An identification key to species was provided by Greathead (1997).

Sosiomyia **Bezzi** (Bombyliinae: Bombyliini)**.** An endemic monotypic genus, with the single species, *S. carnata* Bezzi, 1921, known only from the Northern Cape Province, South Africa. It is very similar to *Adelidea*, but with the flagellum broadened and with strong setulae. Immature stages and biology of the species remain unknown.

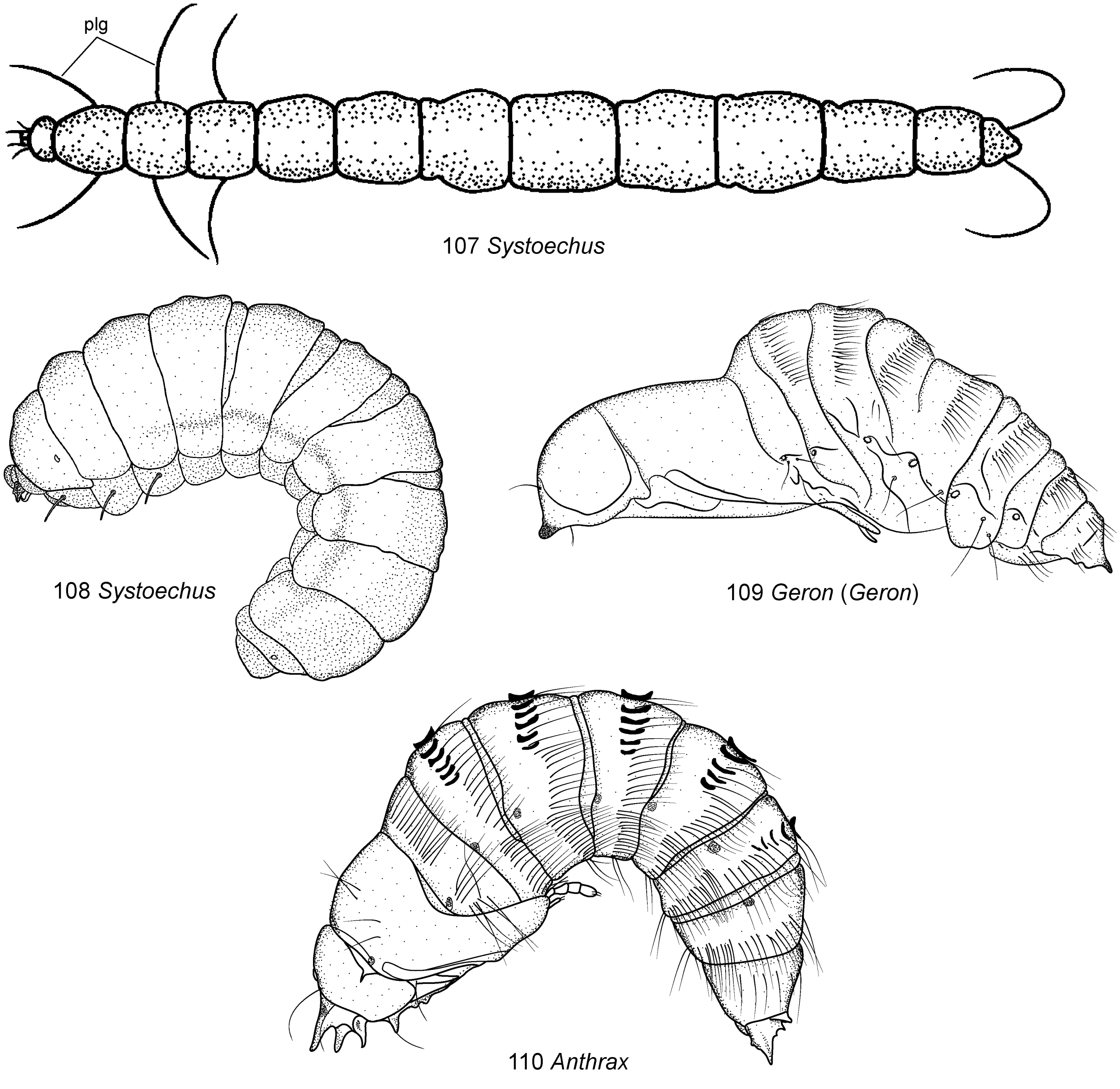
Spogostylum **Macquart** (Anthracinae: Anthracini)**.** A widespread Old World genus of 79 species, occurring in the Afrotropical, Oriental and Palaearctic Regions, 23 of which occur in the Afrotropics. Owing to confusion over the identity of the type species of *Spogostylum*, the name *Argyramoeba* Loew, an objective junior synonym, was in widespread use by many authors, e.g., Bowden (1964) and Hesse (1956), for species of this genus. Evenhuis (1985) provided a full account of the history of the underlying misconceptions. Immatures have been recorded as ectoparasitoids of solitary bees and wasps, predators in egg pods of Acrididae and also reared from the moth, *Loxostege frustalis* (Zeller) (Pyralidae) and its parasitoids (Merle 1975; Yeates & Greathead 1997). Identification keys to species were provided by Greathead (1967, for Ethiopia and Eritrea), Bowden (1964, West Africa) and Hesse (1956, southern Africa), all as *Argyramoeba*.

Synthesia **Bezzi** (Anthracinae: Villini)**.** An endemic monotypic genus, with the single species, *S. fucoides* Bezzi, 1921, recorded from the Northern Cape Province, South Africa. *Synthesia fucoides* has normally developed pulvilli, the eyes lack a bisecting line and the species exhibits other plesiomorphic characters. The immature stages of the species remain unknown.

Systoechus **Loew** (Bombyliinae: Bombyliini)**.** A primarily Old World genus of 117 described species, occurring in the Afrotropical, Oriental and Palaearctic Regions, with its centre of diversity in the Afrotropics, with 91 known species. *Systoechus* is extremely similar in appearance to *Bombylius*, but is recognised by its distinctive body colouration, different placement of the *r–m* crossvein and different parameral sheath of the male terminalia. All reared species are egg predators of Acridoidea (Greathead 1963; Merle 1975; Yeates & Greathead 1997). Identification keys to species were provided by Bowden (1964, western Africa), Greathead (1996*c*, eastern Africa) and Hesse (1938, southern Africa).

Systropus **Wiedemann** (Toxophorinae: Systropodini). A virtually cosmopolitan genus of 175 described species, occurring in all zoogeographical regions, except Antarctica, with 44 species recorded from the Afrotropical Region. Unlike most genera of Bombyliidae with affinities to xeric areas, *Systropus* are instead most abundant in dense vegetation, including forests. Although the tribe Systropodini is present in Baltic amber (Nel & De Ploëg 2004) and *Systropus* is known from Eocene/Oligocene compression fossils in the United Kingdom (Evenhuis 1994: 336), extant taxa of the tribe are absent from forests of the western Palaearctic; but the genus *Systropus* is particularly diverse further south in the Afrotropical Region and in Asia, especially eastern China and South-east Asia. All *Systropus* spp. have an elongate body and petiolate abdomen and some appear to mimic ammophiline Hymenoptera. They are relatively slow in flight and tend to hang from the fore legs when at rest, as do species of Bittacidae (Mecoptera) and Tipulidae. Bowden (1967) separated the Afrotropical species into four subgenera (although species from other regions have not been recognised within subgenera). These subgenera can be summarised as follows: *S.* (*Dierops*), represented by the single Afrotropical species, *S.* (*D.*) *marshalli* Bezzi, 1924 (Fig. 3), recorded from Democratic Republic of Congo, Equatorial Guinea, Kenya, Togo, Uganda and Zimbabwe; *S.* (*Dimelopelma*), known from six species, recorded from Democratic Republic of Congo, Equatorial Guinea, Kenya, Nigeria, Tanzania and Uganda; *Systropus sensu stricto*, represented by 31 species in the Afrotropics, including two species from Madagascar; and *S.* (*Teinopelmus*), represented by six fairly widespread species, from West Africa though the tropical countries of Democratic Republic of Congo, Sierra Leone and Equatorial Guinea, to Kenya and Mozambique. Immature stages are endoparasitoids of Limacodidae (Merle 1975; Yeates & Greathead 1997). An identification key was provided by Bowden (1967).

***Thevenetimyia* Bigot** (Ecliminae). A possibly relict genus of 37 species with disjunct populations in the western Nearctic (28 species), southern Palaearctic (5), Australia (6), New Caledonia (undescribed sp.), Japan (undescribed sp.) and Africa (1). One species, *T. quedenfeldti* (Engel, 1885), is known from one record in the Afrotropical Region (Mauritania) and one in the Palaearctic (Algeria). Recent investigations indicate paraphyly of the genus, with *T. quedenfeldti* being grouped with *Eclimus* Loew in a clade separate from the other *Thevenetimyia*



Figs 45.107–110. Immature stages of Bombyliidae: (107) first-instar planidial larva of *Systoechus vulgaris* Loew, dorsal view; (108) same, third-instar larva, lateral view; (109) pupa of *Geron* (*Geron*) *argutus* Painter, lateral view; (110) same, *Anthrax limatulus* Say (all non-Afrotropical). Figs 107, 108 (after Berg 1940, figs 1A, 3A), Fig. 109 (after Purrington & Evenhuis 2001, fig. 1A), Fig. 110 (after Hull 1973, fig. 4).

Abbreviation: plg – proleg.

(Rodrigues & Lamas, unpubl.). If these results are confirmed, the genus may no longer occur in the Afrotropical Region. Immature stages have been recorded from wood-boring beetles (Merle 1975). Hall (1969) published a world revision, including an identification key to species.

***Thyridanthrax* Osten Sacken** (Anthracinae: Villini) (Fig. 22)**.** A fairly widespread genus of 52 described species, occurring in all zoogeographical regions, except the Oriental Region and Antarctica, with ten species recorded from the Afrotropical Region. Once thought to be more variable in wing pattern and previously confused with species now in *Exhyalanthrax*, *Thyridanthrax* is now restricted to those species with hyaline areas within the infuscated part of the wing (fenestrate pattern), which equals Hesse's (1956) *Thyridanthrax* "Group 2". Immatures have been reared from cocoons of Sphecidae, pupae of Noctuidae and Tenebrionidae and the egg pods of Acrididae in the region (Merle 1975; Yeates & Greathead 1997). An identification key to Afrotropical species was provided by Greathead (1991*a*).

***Tomomyza* Wiedemann** (Tomomyzinae)**.** An endemic southern Africa genus, with 11 species, that are either similar in appearance to bees of the genus *Ceratina* Latreille (Apidae), or are wasp-like. Biology and immature stages remain unknown. An identification key to species was provided by Hesse (1956).

***Toxophora* Meigen** (Toxophorinae: Toxophorini) (Fig. 4)**.** A virtually cosmopolitan genus of 50 known species, 18 of which occur in the Afrotropical Region. *Toxophora* is extremely uniform in appearance, comprising species with elongate antennae and strong setae that are densely clothed in (usually black, sometimes iridescent) scales, with contrasting pale yellow or white colouration. They are quite common, but seldom abundant, so that most collections contain only one or very few specimens, often collected on the same occasion. Immature stages are parasitic in nests of solitary wasps (principally Eumeninae) and bees that are usually situated above ground (Merle 1975; Yeates & Greathead 1997). Identification keys to species were provided by Bowden (1964, for Ghana) and Hesse (1963, for southern Africa).

***Triplasius* Loew** (Bombyliinae: Bombyliini)**.** A genus of eight described species, occurring in the Afrotropical and Palaearctic Region, with four species recorded from the Afrotropics. The genus was treated by Bowden (1980: 391) as a synonym of *Bombylius*, but it was revived by Greathead (1995) to comprise a group of species that share an unstable wing venation and a striking colour pattern (treated by Hesse (1938), as his *Bombylius* "Group 1, Section 1"). Biology and immature stages remain unknown. An identification key to southern African species (as *Bombylius*, "Group 1, Section 1") was provided by Hesse (1938).

***Veribubo* Evenhuis** (Anthracinae: Villini). A genus of 30 described species, occurring in the Afrotropical and south-eastern Palaearctic Regions, with five species recorded from the Afrotropics. The genus was proposed by Hull (1973) (as *Thyridanthrax* subgenus *Tumulus* Hull, but unfortunately this name is preoccupied), for species with a 1-segmented robust flagellum. In contrast to *Exhyalanthrax* spp., males tend to have more developed wing patterns than females. The species now allocated to this genus indicate an Eremian distribution. Biology and immature stages remain unknown. There is currently no identification key to species.

***Villa* Lioy** (Anthracinae: Villini). A large, virtually cosmopolitan genus of 280 species, most of which are very similar looking. Currently, 46 species are known from the Afrotropical Region, many of which can only be reliably separated based on differences in the male terminalia. Immatures have been recorded as internal parasitoids of the pupae of Lepidoptera, Tabanidae and Myrmeleontidae (Merle 1975; Yeates & Greathead 1997). Although the genus is in dire need of revision, the identification key of Hesse (1956) can be used to identify species from southern Africa.

***Villoestrus* Paramonov** (Anthracinae: Villini). A genus of three described species, occurring in the Afrotropical and Palaearctic Regions, with the single species, *V. dimorphus* Hesse, 1956, described from South Africa, occurring in the Afrotropics. The genus has the most reduced mouthparts among the three genera of the tribe Villini with non-functional mouthparts (*Marleyimyia*, *Oestranthrax*, *Villoestrus*). Biology and immature stages remain unknown.

***Xenoprosopa* Hesse** (Xenoprosopinae). An endemic monotypic genus, with the single South Africa species, *X. paradoxa* Hesse, 1956, known only from the unique female holotype. Hesse (1956) noted that in life *X. paradoxa* rests on sand and that, with its whitish setation, elongate shape and conspicuously yellow-ringed abdomen and legs, it resembles a therevid or asilid. A cladistic analysis was published by Evenhuis (1992). Biology and immature stages remain unknown.

***Xerachistus* Greathead** (Bombyliinae: Bombyliini)**.** An endemic genus of five described species. Greathead (1995) showed that certain species of Hesse's (1938) *Bombylius* "Group 2" have an open, or virtually open, wing cell r_5, broad head and relatively narrow body, short vestiture and different male terminalia, warranting their transfer to his new genus. Biology and immature stages remain unknown. An identification key to southern African species (as *Bombylius* "Group 2") was provided by Hesse (1938).

***Xeramoeba* Hesse** (Anthracinae: Xeramoebini)**.** A genus of *ca* 13 species, occurring in the Afrotropical and southern Palaearctic Regions, with eight species known from the Afrotropics. The genus was described by Hesse (1956) for a new South African species near *Prothaplocnemis* Bezzi, namely *X. apricaria* Hesse, 1956. Subsequently, other Afrotropical species have been described and several Palaearctic species transferred to it from the tribe Anthracini and from the genus *Desmatoneura*. The genus *Gazlia* Zaitzev was found to be synonymous and was treated as such in Evenhuis & Greathead (2003). *Xeramoeba oophaga* (Zakhvatkin, 1931) is well known as an egg predator of Acrididae and another species, *X. infuscata* Greathead, 1967, has been reared from the pupa of a noctuid moth in the region (Greathead 1963; Merle 1975). There is currently no identification key to species

***Zinnomyia* Hesse** (Bombyliinae: Bombyliini)**.** An endemic genus of three described species: *Z. bifida* (Bezzi, 1924), from

South Africa; *Z. brincki* Hesse, 1955, from Namibia; and *Z. mira* Greathead, 1970, from Mali. The genus was proposed by Hesse (1955) for two species with a striking tabanid-like appearance. He remarked on the fact that one of these was collected at a much visited site on a single occasion only and speculated that it must either be very rare, or have a very limited flight period. The paucity of specimens of these striking flies in collections suggests that the species are indeed rare, but as specimens of the same species have been collected at widely-separated localities, it appears that they are, nonetheless, widespread. Biology and immature stages remain unknown. There is currently no identification key to species.

***Zyxmyia* Bowden** (Mariobezziinae)**.** An endemic monotypic genus, proposed by Bowden (1960) for an unusual-looking short-haired bombyliid, allied to the genera *Corsomyza*, *Hyperusia* and *Megapalpus*, but with shiny golden scales on the abdomen. The single species, *Z. megachile* Bowden, 1960, was described from Kenya and Tanzania. Biology and immature stages remain unknown.

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APIOCERIDAE 46

(Apiocerid Flies)

Torsten Dikow

Fig. 46.1. Male of *Apiocera* (*Pyrocera*) *painteri* Cazier (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

Afrotropical species are medium-sized (body length: 16–21 mm), brown to black flies, with grey pubescent patterned head, thorax and abdomen (Figs 1–3).

Head dichoptic in both sexes; frons virtually parallel-sided; vertex slightly depressed; ocelli circular; ocellar triangle formed by 2 posterior ocelli, anterior ocellus positioned at considerable distance anterior to posterior ocelli; antenna positioned in ventral ½ of head; antennal scapes separated proximally; postpedicel broadest medially, short; stylus composed of 1 element, with seta-like sensory element positioned apically on stylus; proboscis projecting beyond frontoclypeal suture; labellum well-developed; large pseudotracheae separated from prementum; palpus 2-segmented; distal segment laterally compressed, extending beyond frontoclypeal suture.

Thorax with postpronotal lobe entirely fused to mesonotum; cervical sclerite smoothly rounded and elevated above lateral postpronotum; prosternum separated from proepisternum, triangular in shape; proepisternum not fused to lateral

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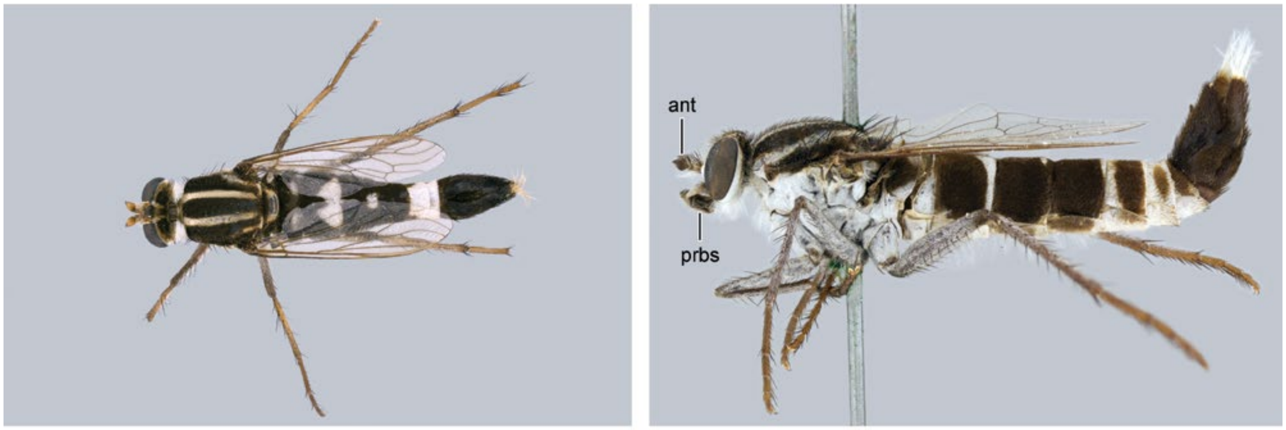
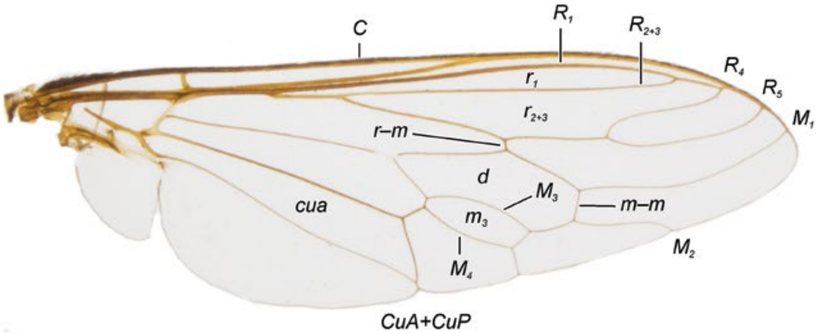


2 *Apiocera* (*Ripidosyrma*) ♂

3 *Apiocera* (*Ripidosyrma*) ♂



4 *Apiocera* (*Ripidosyrma*)

5 *Apiocera* (*Ripidosyrma*) ♂

6 *Apiocera* (*Ripidosyrma*) ♀

Figs 46.2–6. Habitus, wing and terminalia of Apioceridae: (2) habitus of *Apiocera* (*Ripidosyrma*) *alastor* (Walker), dorsal view ♂; (3) same, *A.* (*R.*) *braunsi* Melander, lateral view ♂; (4) same, wing, dorsal view; (5) same, male terminalia, lateral view; (6) same, female terminalia.

Abbreviations: a apod – anterior apodeme; acanth plt – acanthophorite plate; acanth sp – acanthophorite spine; ant – antenna; *C* – costal vein; cerc – cercus; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *d* – discal cell; epand – epandrium; goncx – gonocoxite; goncx apod – gonocoxal apodeme; hypd – hypandrium; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; *m–m* – medial crossvein; prbs – proboscis; R_1 – anterior branch of radius; r_1 – first radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; st – sternite; tg – tergite.

postpronotum, macrosetulose and setulose; anterior proepimeron, anterior and superoposterior anepisternum, anterior basalare and katepimeron asetose; 3 or more notopleural setae and 1 supra-alar and postalar seta present; scutellum large, mesopostnotum not visible in dorsal view; apical scutellar macrosetae present; metakatepisternum small and not visible between mesothoracic and metathoracic coxae; metathoracic coxa macrosetulose laterally, with blunt protuberance anteriorly. Legs with femur cylindrical throughout length, with 1 anteroventral row of macrosetae; proximal tarsomere as long as or longer than tarsomeres 2–3 combined; pulvillus with single dorsal ridge; setiform empodium absent. Wing membrane hyaline; cells r_1, r_{2+3}, m_3, and *cua* closed (Fig. 4); costal vein (*C*) circumambient, or terminating at vein *CuA+CuP*; auxiliary crossvein (R_3) absent; veins M_1 and M_2 separated; vein M_1 terminating in costal vein anterior to wing apex.

Abdomen elongate, tapered towards apex; male (Fig. 5) with tergites and sternites 1–8 fully-developed; abdominal tergites without anterodorsal apodemes; male terminalia with epandrium separated medially and joining proximally; hypandrium large, elongate; hypandrium and gonocoxite entirely free; short gonocoxal apodeme present; gonostylus present, positioned medially on gonocoxite; lateral ejaculatory apodeme small, triangular in shape; phallus with 1 functional phallic prong; gonocoxite with distal, feathery plume extending beyond tip of hypopygium (Figs 2, 3, 5); female terminalia (Fig. 6) with tergite 8 with apodeme on anterior margin, without auxiliary spiracle; sternite 8 plate-like, divided into 2 halves; tergites 9 and 10 entirely fused, acanthophorite spines present on acanthophorite plate (tergite 10); 3 equally large, poorly-sclerotised spermathecae present; furca shaped as an inverted U.

Apioceridae may possibly be confused in the field with certain medium-sized species of Asilidae (see Chapter 48). The non-predacious proboscis (Fig. 3), short antenna (Fig. 3) and peculiar wing venation (Fig. 4), however, will easily differentiate *Apiocera* Westwood from Asilidae.

Biology and immature stages

The immature stages of Afrotropical *Apiocera* are unknown and information on other species is scarce. Larvae and pupae of the Australian species *A.* (*Apiocera*) *maritima* Hardy, 1933 (English 1946), as well as the Nearctic *A.* (*Pyrocera*) *hispida* Cazier, 1941 (Toft & Kimsey 1982) (Figs 7–11), *A.* (*P.*) *haruspex* Osten Sacken, 1877 (Wharton 1982) and *A.* (*P.*) *painteri* Cazier, 1963 (Cazier 1963) have been described. All of these were found in sandy habitats (although not necessarily sand dunes) and the same habitat type is most probably also utilised by Afrotropical species. *Apiocera* larvae are believed to be predatory, feeding on other larvae, as is the case with the families Asilidae (see Chapter 48) and Mydidae (see Chapter 47). The head morphology of the fifth-instar larva (more or less flattened maxilla and laterally inserted maxillary palpus; Fig. 8) is more similar to those of Asilidae than to Mydidae – its closest relative. Imagines are nectar or pollen-feeders and their annual adult activity period may, therefore, coincide with the flowering of certain plant species. There is no evidence, however, that *Apiocera* rely on specific plant species for food. All specimens examined in collections were collected between December and February.

Economic significance

No species of Apioceridae are known to have economic importance.

Classification

Apioceridae is placed in the superfamily Asiloidea and is closely related to Asilidae and Mydidae. Hennig (1973), Irwin & Wiegmann (2001), Yeates (2002) and Yeates & Irwin (1996) have established the close phylogenetic relationship between Apioceridae and Mydidae, while Dikow (2009*a*, *b*) proposed that a clade (Apioceridae + Mydidae) is the sister-group to Asilidae, based on both morphological and molecular data. This set of relationships has also been supported by molecular analyses focusing on Asiloidea (Trautwein *et al*. 2010) and Diptera in general (Wiegmann *et al*. 2011).

Apioceridae has a unique distribution, in that the current 143 valid species are distributed in Australia (73 species), Chile (4), South Africa (3) and western North America (Canada, Mexico, United States, 64 species). The North American species are primarily Nearctic with a few species found in the Neotropical states of Mexico. Yeates & Irwin (1996) published the only phylogenetic hypothesis of relationships within the family and proposed to apply available genus-group names, plus a newly-described one to be ranked as subgenera of the single, worldwide genus *Apiocera*. These subgenera correspond to the zoogeographical distribution, in that the Australasian species are grouped in *A.* (*Apiocera*), the Neotropical (Chilean) species in *A.* (*Anypenus* Philippi), the Afrotropical species in *A.* (*Ripidosyrma* Hermann) and the Nearctic and Neotropical (Mexican) species in *A.* (*Pyrocera* Yeates & Irwin). Stuckenberg (1966) described the morphologically unique genus, *Tongamya*, from the South Africa/Mozambique border in Apioceridae, but this taxon was subsequently transferred to Mydidae by Yeates & Irwin (1996).

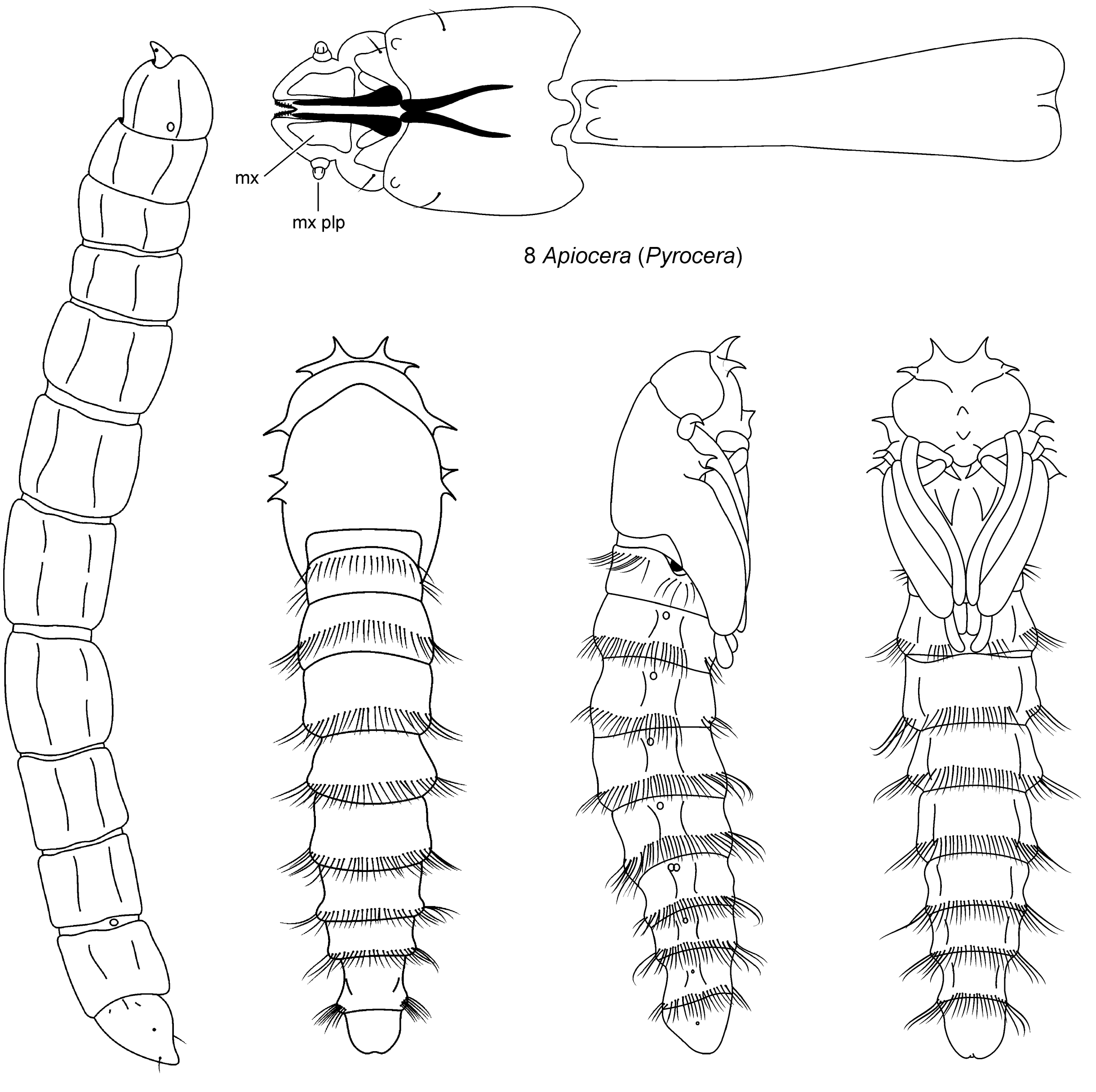
The study by Yeates & Irwin (1996) proposed that *A.* (*Pyrocera*) represents the sister-group to the Southern Hemisphere species and that the Afrotropical *A.* (*Ripidosyrma*) spp. are in turn the sister-group to the clade of Chilean and Australian species, which presents evidence for a true Gondwanan origin.

Identification

Yeates (1994) published a revision of the Afrotropical *Apiocera* and provided an identification key to the three valid species. The key relies in part on the pubescence of the thorax and it is pertinent to have well-preserved specimens at hand to make correct identifications. Apioceridae should be direct-pinned in the field (see Chapter 2).

Synopsis of the fauna

***Apiocera* Westwood.** A genus of 143 species, occurring in the Afrotropical, Australasian, Nearctic and Neotropical Regions. Three valid species (all in the subgenus *A.* (*Ripidosyrma*)) have been described from the Afrotropics, with one name in synonymy (Dikow & Agosti 2015; Yeates 1994). These Afrotropical species are restricted to South Africa, and in particular, to the Eastern Cape and Western Cape Provinces, from Graaff-Reinet and Willowmore in the east to the Tankwa Karoo National Park and the Ceres District in the west. In general, apiocerid flies are rarely collected and are scarce in collections, with Afrotropical species being no exception. Apioceridae (as is the case with Mydidae) may, however, be locally abundant and specialist collectors may be able to collect long series when visiting suitable habitat at the correct time of year. While the fauna has been recently reviewed (Yeates 1994), it is possible that additional fieldwork will reveal undescribed species, given that male specimens from Matjiesfontein and "Janfontein, Ceres Division" (Western Cape) have been examined (Dikow, unpubl.), which appear to be undescribed. *Apiocera* (*R.*) *badipeniculata* Yeates,



8 *Apiocera* (*Pyrocera*)

7 *Apiocera* (*Pyrocera*) 9 *Apiocera* (*Pyrocera*) 10 *Apiocera* (*Pyrocera*) 11 *Apiocera* (*Pyrocera*)

Figs 46.7–11. Fifth-instar larva and pupa of Apioceridae: (7) fifth-instar larva of *Apiocera* (*Pyrocera*) *hispida* Cazier (non-Afrotropical), lateral view (anterior top); (8) same, head, dorsal view (anterior left); (9) same, male pupa, dorsal view (anterior top); (10) same, lateral view; (11) same, ventral view. Figs 7–11 (after Toft & Kimsey 1982, figs 6, 2, 9–11, respectively).

Abbreviations: mx – maxilla; mx plp – maxillary palpus.

1994 is only known from a single collecting event, although Yeates (1994) identified other specimens from the same series as *A. alastor*. The remaining two species are more widespread, with *A.* (*R.*) *braunsi* (Fig. 3) found in the eastern and *A.* (*R.*) *alastor* (Fig. 2), transferred by Stuckenberg (1968) from Asilidae to *Apiocera*, in the western parts of their distribution range.

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MYDIDAE 47

(Mydas Flies)

Torsten Dikow

Fig. 47.1. Male of *Cephalocera* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

Afrotropical species small- to medium-sized (body length: 7–28 mm), yellow, light brown, grey, or black flies (Figs 1–11), with several species exhibiting mimicry of wasps (Figs 64, 65, 98, 99); palpus 1-segmented; antenna with apical seta-like sensory element positioned apically in cavity on postpedicel; thorax with postpronotal lobes only partly fused to scutum and lobes elevated above scutum posteriorly; metakatepisternum large and visible between mesothoracic and metathoracic coxa; majority of wing cells closed, wing microtrichia absent; pulvillus with single dorsal ridge, setiform empodium absent; male terminalia with gonostylus absent, male hypandrium reduced and fused to gonocoxites (forming a gonocoxite-hypandrial complex), male lateral ejaculatory processes absent.

The Afrotropical Mydidae exhibit the following features with *Tongamya* Stuckenberg, (Figs 10, 11, 96, 97) often the exemption to the rule, indicated by "(except T)" below:

Head dichoptic in both sexes (except T); face protruding distinctly, bearing mystacal setae (Figs 12–15, except T); frons parallel-sided to slightly converging dorsally (Figs 12–15); vertex slightly to considerably depressed (sometimes lateral margins

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1063–1095.

Figs 47.2–7. Photographs of living Mydidae: (2) *Eremomidas arabicus* Bequaert ♀ (United Arab Emirates); (3) same, ovipositing in sand dune; (4) same ♂; (5) *Leptomydas sardous* (Costa) ♀ (non-Afrotropical); (6) *Neolaparopsis puncturatus* Hesse ♂ (South Africa); (7) *Perissocerus arabicus* Bequaert ♂ (United Arab Emirates). Figs 2, 4, 7 (photographs © D. Gardner), Fig. 3 (photograph © B. Howarth), Fig. 5 (photograph © L. Lenzini), Fig. 6 (photograph © S.A. Marshall).

elevated above dorsal compound eye margin (Figs 12, 15, except T); anterior ocellus circular as in *Tongamya* (Fig. 11) to transversely oval in other genera (Fig. 12); ocellar triangle formed by 2 posterior, distinctly elongated ocelli positioned on ridge, anterior ocellus positioned at considerable distance anterior to posterior ocelli (Fig. 12, except T); antenna positioned in ventral ½ of head; antennal scapes proximally close together, almost touching (except T); postpedicel elongate and distinctly clubbed distally, composed of cylindrical proximal part and bulbous distal part separated by unsclerotised area (Figs 6, 8, except T); stylus reduced, only seta-like sensory element present; proboscis minute to long, extending beyond frontoclypeal suture; labellum either well-developed with large pseudotracheae separated from prementum or small and only forming distal tip of proboscis; palpus 1-segmented, usually short, in some species more than ½ as long as oral cavity.

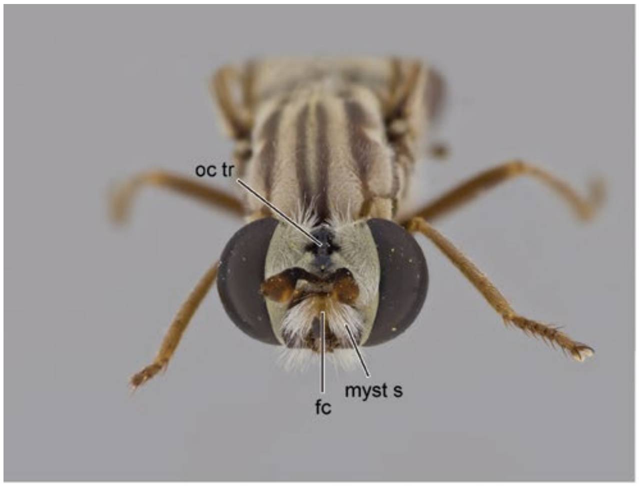
Thorax with postpronotal lobe only partially fused to mesonotum, lobes elevated above scutum posteriorly; cervical sclerite flat (except T with cone-shaped sclerite); prosternum dorsal margin with flange-like projection; prosternum fused to proepisternum; proepisternum fused to lateral postpronotum, setulose; anterior proepimeron, anterior anepisternum, anterior and posterior basalare bare; posterior anepisternum, katepimeron, anatergite, mediotergite (mesopostnotum) setose or bare; katatergite usually setose and flat, sometimes elevated and convex; metakatepisternum large and visible between mesothoracic and metathoracic coxa; scutum entirely smooth or microrugose; laterally usually with at least a few setae (Fig. 35), often densely setose (Fig. 29); short dorsocentral setae pre- and postsuturally developed; acrostichal setae only sometimes presuturally; notopleural, supra-alar and postalar setae absent (Fig. 29). Scutellum small, mediotergite (mesopostnotum) visible in dorsal view (Fig. 42, except T); apical and discal scutellar macrosetae usually absent. Legs with metathoracic coxa setulose laterally; median metathoracic trochanter setulose, sometimes macrosetulose; femur usually cylindrical throughout length (Fig. 10) or slightly expanded posteriorly (Fig. 33), several genera with distinctly clubbed hind femur (Fig. 51, either evenly clubbed or distinctly and abruptly clubbed in

Figs 47.8–11. Photographs of living Mydidae; (8) *Rhopalia* sp. ♂ (non-Afrotropical); (9) *Syllegomydas* (*Syllegomydas*) *palestinensis* Bequaert (non-Afrotropical) ♀; (10) *Tongamya miranda* Stuckenberg ♂ (South Africa); (11) same ♀. Figs 8, 9 (photographs © A. Weinstein), Figs 10, 11 (photographs © S.A. Marshall).

Abbreviation: oc tr – ocellar triangle.

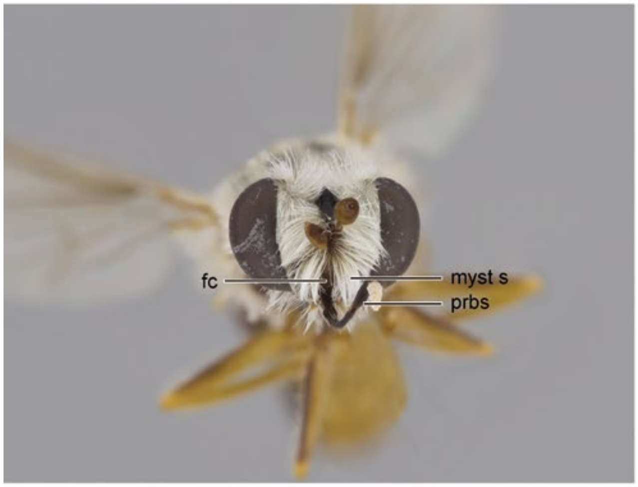
distal ½–⅓); hind femur usually with one anteroventral and one posteroventral row of macrosetae (sometimes with single row present or only a few distoventral macrosetae); femur additionally often with ventral spine-like macrosetae on elevated alveoli (Figs 27, 28); hind tibia usually straight, sometimes arched medially, usually without (Fig. 73), sometimes with ventral keel terminating in spine (Fig. 51); fore and mid proximal tarsomere as long as tarsomeres 2–3 combined (except T), hind proximal tarsomere usually longer than tarsomeres 2–3 combined; pulvillus usually well-developed with single dorsal ridge, sometimes reduced particularly in females, but never absent; setiform empodium absent. Wing membrane usually hyaline (Figs 2, 70), sometimes brown infuscate (Figs 31, 34), especially along veins; microtrichia absent; cells r_1, r_4 (usually), r_5 (usually), m_3 (except T), and *cua* closed (Figs 16–19, 30, 87); costal vein (*C*) rarely circumambient, usually terminating at veins R_1, R_5, or M_{1+2} (Figs 16–19, 23, 30, 42); stump vein (auxiliary crossvein R_3) usually present (Figs 17, 30), rarely absent (Fig. 62), in one genus connecting veins R_2 and R_4 (Figs 18, 85); veins M_1 and M_2 fused (Figs 16, 17, except T), veins M_{3+4} usually not terminating together into costal vein (*C*) (Fig. 16), sometimes terminating into costal vein (*C*) (Fig. 18).

Abdomen elongate, parallel-sided or slightly tapered towards apex, tergites 2–3 sometimes constricted forming “wasp-waist” (Fig. 98); tergite 2 on posterolateral margin with bullae (Fig. 1, except T and females of *Haplomydas* Bezzi); male tergites 1–7 well-developed; tergite 8 posteromedially weakly sclerotised, with anterior transverse sclerotised bridge connecting lateral sclerites (Fig. 100); abdominal tergites usually with 2 anterodorsal apodemes; sternite 6 usually simple ventrally, sometimes with clump of setae; sternite 8 usually simple (Fig. 106), sometimes



12 *Afroleptomydas* (*Afroleptomydas*) ♀

13 *Namibimydas* ♂



14 *Nothomydas* ♂

15 *Vespiodes* ♂

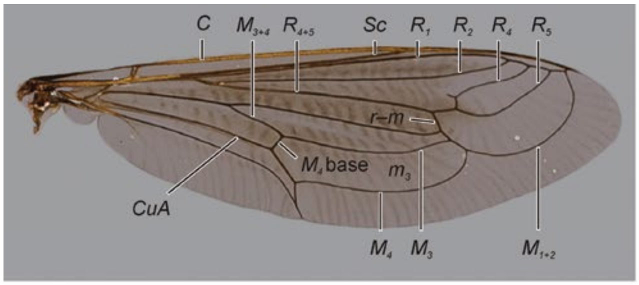
Figs 47.12–15. Heads of Afrotropical Mydidae (anterior views): (12) *Afroleptomydas* (*Afroleptomydas*) sp. ♀; (13) *Namibimydas psamminos* Dikow ♂; (14) *Nothomydas picketti* Dikow ♂; (15) *Vespiodes cerioidiformis* Hesse ♂.

Abbreviations: fc – face; myst s – mystacal setae; oc tr – ocellar triangle; prbs – proboscis.

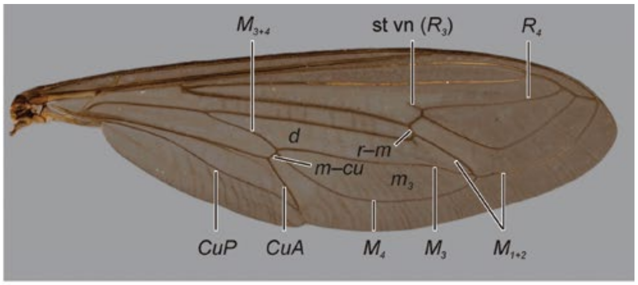
with median tooth posteromedially, divided into 2 halves, or directed ventrally (Fig. 100); male terminalia usually with epandrium fused medially (Fig. 110), sometimes separated medially and joined proximally (Fig. 101); hypandrium usually reduced, not differentiated and fused to gonocoxite, forming gonocoxite-hypandrial complex (Fig. 100), sometimes internal suprahypandrial sclerite present (Fig. 100, see definition in Dikow 2012: 107); gonocoxal apodeme usually absent, sometimes short apodeme present; gonostylus absent; gonocoxite usually without appendages (2 genera with palpus-like appendage present) (Figs 105, 108); subepandrial sclerite usually without protuberances (2 genera with median protuberance present); lateral ejaculatory apodeme absent; 1 or 2 phallic prongs, when 2 phallic prongs present, then often dorsal phallic epimere (see definition in Hesse 1969: 36) present (Figs 100, 109, 112); female tergite 8 usually with anterior apodeme (Fig. 115) and auxiliary spiracle (Fig. 115); sternite 8 plate-like, divided into 2 halves; tergites 9–10 usually entirely fused (Fig. 115), acanthophorite spines present on fused tergite 9–10 (Fig. 115), few genera with enlarged tergite 9, only partially fused tergite 9–10 and without acanthophorite spines on tergite 10 (Fig. 116); either 2 or 3 equally large, poorly to well-sclerotised spermathecae present (Figs 117–121, sometimes median spermatheca larger than lateral ones); genital fork usually ring-like (joined anteriorly and posteriorly, Figs 117–120), sometimes inverted U-shaped (joined anteriorly, separated posteriorly, Fig. 121), anterior genital fork apodeme present (Fig. 117), lateral genital fork apodeme (Fig. 119) and median genital fork bridge usually absent.

Larva robust with 12 apparent segments, with small, partly retractable head capsule and large conical tip (Fig. 129); head conical, heavily sclerotised; maxilla enlarged (Figs 127, 128), laterally compressed and extending laterally to form head capsule (Fig. 128); maxillary palpus inserted apically (Figs 125, 127), mandible hidden beneath maxilla (Fig. 128); labrum pointed; submentum forming ventral plate (Fig. 128); abdominal segments 1–7 with transverse proleg-like ridges anteroventrally; posterior spiracle on abdominal segment 8; segment 9 conical and tapered (Fig. 129).

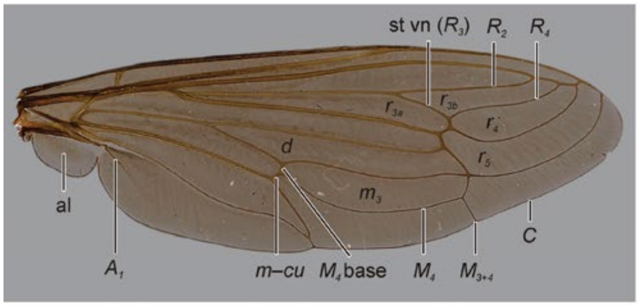
Pupa (*e.g.*, Figs 130–133) robust with appendages movable (exarate); head with 1 pair of cephalic and 2 pairs of antennal processes; abdominal segments 1–7 with row of posteroventrally oriented processes distally, particularly well-developed ventrally on segments 2–7; segment 9 with pair of caudally oriented apical processes.



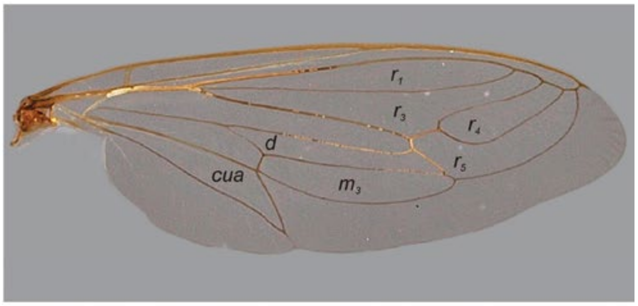
16 *Cephalocera*



17 *Mydaselpis*



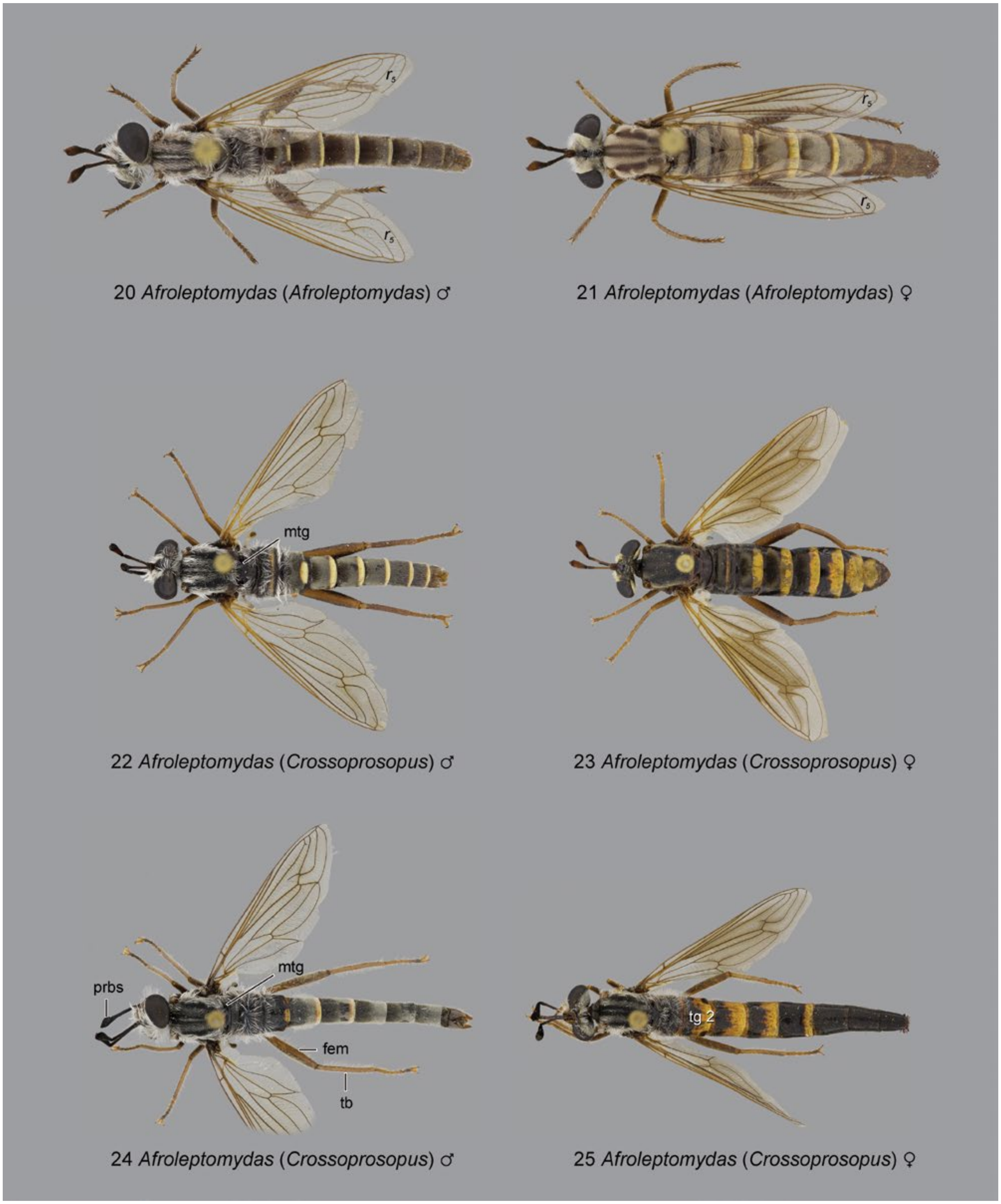
18 *Parectyphus*



19 *Syllegomydas* (*Syllegomydas*)

Figs 47.16–19. Wings of Afrotropical Mydidae (dorsal views): (16) *Cephalocera* sp.; (17) *Mydaselpis ngurumani* Dikow; (18) *Parectyphus namibiensis* Hesse; (19) *Syllegomydas* (*Syllegomydas*) *elachys* Dikow. Figs 17, 19 (Dikow 2010*a*, figs 43, 44), Fig. 18 (Lyons & Dikow 2010, fig. 38).

Abbreviations: A_1 – first branch of anal vein; al – alula; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *d* – discal cell; M_{1+2} – fused first and second branch of media; M_3 – third branch of media; m_3 – third medial cell; M_{3+4} – fused third and fourth branch of media; M_4 – fourth branch of media; *m–cu* – medial–cubital crossvein; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; r_3 – third radial cell; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein; st vn – stump vein.



20 *Afroleptomydas* (*Afroleptomydas*) ♂

21 *Afroleptomydas* (*Afroleptomydas*) ♀

22 *Afroleptomydas* (*Crossoprosopus*) ♂

23 *Afroleptomydas* (*Crossoprosopus*) ♀

24 *Afroleptomydas* (*Crossoprosopus*) ♂

25 *Afroleptomydas* (*Crossoprosopus*) ♀

Figs 47.20–25. Habitus photographs of Mydidae (dorsal views): (20) *Afroleptomydas* (*Afroleptomydas*) sp. ♂; (21) same ♀; (22) *A.* (*Crossoprosopus*) sp. ♂; (23) same ♀; (24) *A.* (*Crossoprosopus*) sp. ♂; (25) same ♀.

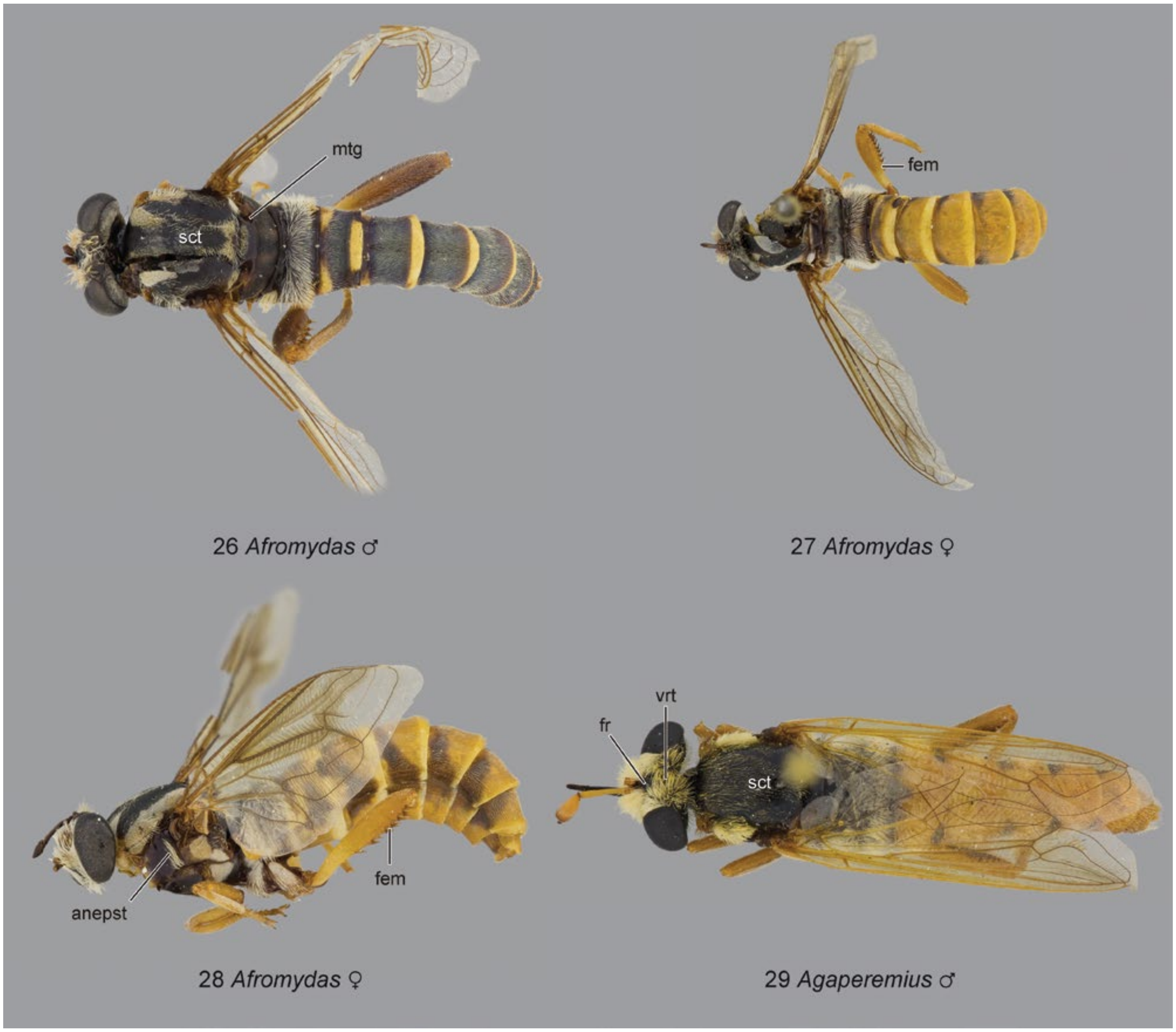
Abbreviations: fem – femur; mtg – mediotergite; prbs – proboscis; r_5 – fifth radial cell; tb – tibia; tg – tergite.

Mydidae are superficially similar to some Apioceridae (see Chapter 46) and Asilidae (see Chapter 48). The non-predacious proboscis, usually long antennae, peculiar wing venation (absence of wing microtrichia, closed cells r_1 *and cua*, and fused veins M_1 and M_2) and Hymenoptera-like flight easily differentiate Mydidae.

Biology and immature stages

The immature stages of Afrotropical Mydidae have so far only been described for the aberrant *Tongamya miranda* Stuckenberg, 1966 by Irwin & Stuckenberg (1972), who described and illustrated the first-instar larva (Figs 125–127). Information on extralimital larval and pupal morphology and behaviour is published for the Nearctic species *Mydas clavatus* (Drury, 1776) (Figs 128, 129) (Greene 1917; Wilcox 1981: 535), *M. maculiventris* (Westwood, 1835) (Genung 1959), *Rhaphiomidas acton* Coquillett, 1891 (Steinberg *et al*. 1998) and *R. terminatus* Cazier, 1941 (Hogue 1967), as well as the Neotropical species *Gauromydas heros* (Perty, 1833) (Wilcox & Papavero 1971; Zikan 1942, 1944), the largest known Diptera species (Calhau *et al*. 2015).

Mydidae larvae (Figs 122–124) are believed to be predatory, feeding on other insect larvae, as is the case with the families



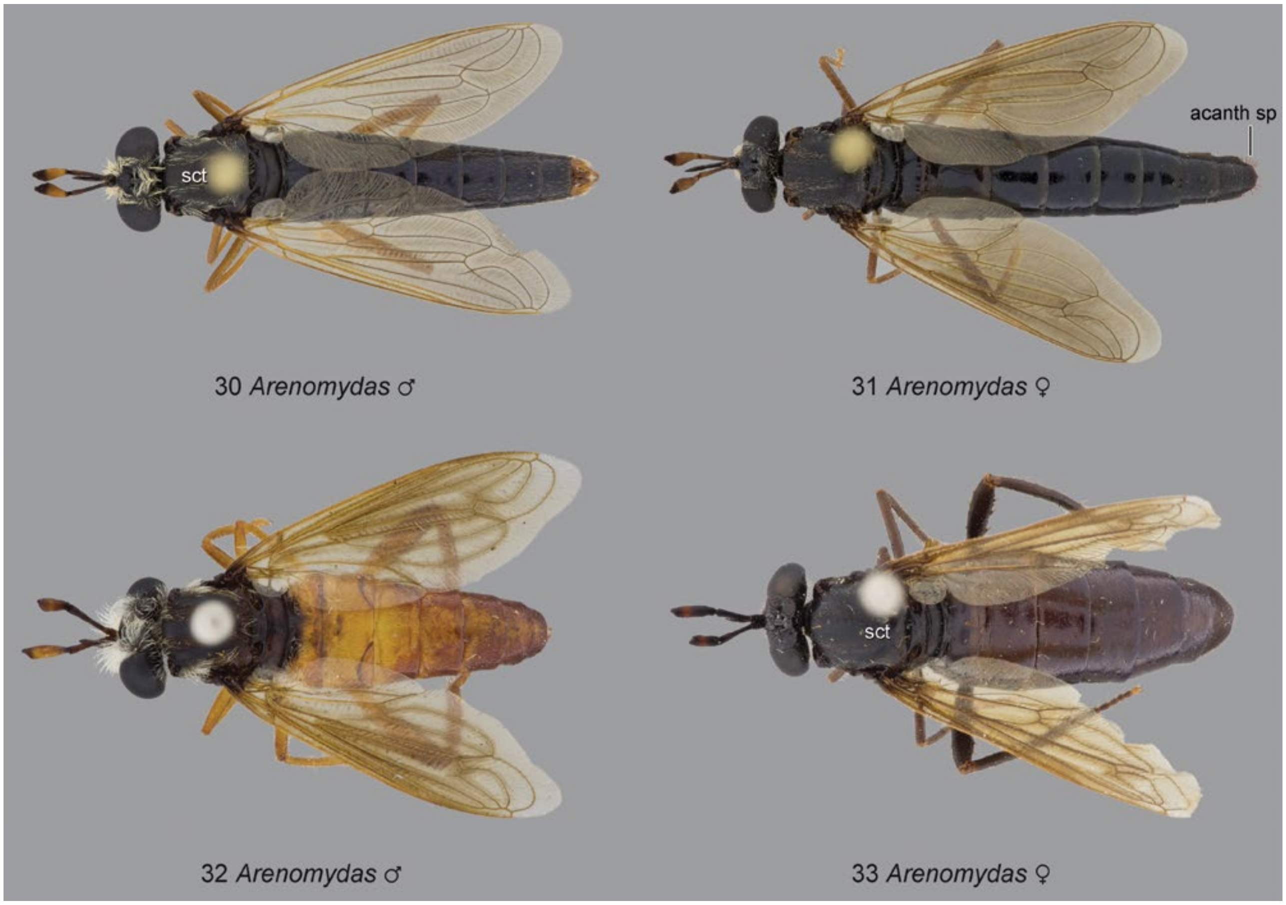
Figs 47.26–29. Habitus photographs of Mydidae: (26) *Afromydas guichardi* Bequaert, dorsal view ♂; (27) same ♀; (28) same, lateral view (Figs 27 and 28 with head rotated); (29) *Agaperemius hirtus* Hesse, dorsal view ♂.

Abbreviations: anepst – anepisternum; fem – femur; fr – frons; mtg – mediotergite; sct – scutum; vrt – vertex.

Apioceridae and Asilidae. The first known Afrotropical and Syllegomydinae pupae (Figs 130–133) are morphologically similar to Asilidae pupae and were collected by sifting loose sand (M.E. Irwin & B.S. Miller, pers. comms. 2015). Adults are pollen-feeders and their annual adult activity period may, therefore, coincide with the flowering of certain plant species. There is no evidence, however, that Mydidae rely on specific plant species for food. Some species with minute mouthparts, of which there are several in the Afrotropical Region, may not feed at all (Wharton 1982). Mydidae are very rarely observed and collected, but visiting the right habitat (usually sand dunes or sandy habitats) at the right time of the year can result in collection of several specimens. Several *Afroleptomydas* Bequaert species have been observed resting on termite mounts (S.K. & F.W. Gess, pers. comm. 2008), but the majority of species are encountered at rest on open sand or ground, much like Apioceridae and many Asilidae, low dry vegetation (Fig. 2), or on inflorescences (Fig. 1). The majority of Afrotropical species will oviposit in loose sand by using the acanthophorite spines to insert the abdomen deep into the substrate and sometimes almost the entire body (Fig. 3). Those genera most likely relying on decaying wood as larval and pupal habitat, *i.e.*, taxa without acanthophorite spines, such as *Afromydas* Bequaert, *Mydaselpis* Bezzi and *Vespiodes* Hesse, may rest further away from the ground, although no observations are currently available.

Several species exhibit mimicry of aculeate wasps, in particular the Mydaselpidini genera *Afromydas*, *Mydaselpis* and *Vespiodes*. Other genera, such as *Arenomydas* Hesse and *Namadytes* Hesse, include species that are at least partly yellow and may, therefore, resemble bees.

Sexual dimorphism may be quite pronounced within Mydidae species. Such dimorphism is predominant in the density of setation on the head, scutum and thoracic pleura, body size, the shape of the antennal postpedicel and also in general habitus. To illustrate this dimorphism, images of both males and females of the same species are provided. Compare, for example, males and females of *Cephalocerodes* Hesse (Figs 40, 41), *Eremomidas* Semenov (Figs 2, 4, 46, 47), *Halterorchis* Bezzi (Figs 48, 49), *Namadytes* (Figs 68, 69), *Neolaparopsis* Hesse (Figs 72, 73), *Perissocerus* Gerstaecker (Figs 86, 87) and *Syllegomydas* Becker (Figs 90–95). Males of *Halterorchis* and *Neolaparopsis* and females of *Cephalocerodes* are reported here for the first time and are



Figs 47.30–33. Habitus photographs of Mydidae (dorsal views): (30) *Arenomydas caerulescens* Hesse ♂; (31) same ♀; (32) *A. callosus* (Wiedemann) ♂; (33) same ♀.

Abbreviations: acanth sp – acanthophorite spine; sct – scutum.

associated with the known sex, while females of *Agaperemius* Hesse, *Mahafalymydas* Kondratieff, Carr & Irwin and *Mimadelphus* Hesse (but see *Halterorchis*) remain unknown.

Due to their extensive distribution in the Afrotropics, Mydidae adults can be observed throughout the year, although locally a particular taxon may only be active for a very short period (Wharton 1982). Several semi-desert-inhabiting species are active as adults in the Southern Hemisphere winter in July–August (data insufficient for species occurring in the Sahel and Sahara).

Economic significance

No species of Mydidae are known to have economic significance.

Classification

Mydidae is placed in the superfamily Asiloidea and is closely related to Apioceridae and Asilidae. Hennig (1973: 43), Irwin & Wiegmann (2001), Yeates (2002) and Yeates & Irwin (1996) established the close phylogenetic relationship between Apioceridae and Mydidae, while Dikow (2009*a*, *b*) proposed that a clade (Apioceridae + Mydidae) is sister-group to Asilidae, based on both morphological and molecular data. This set of relationships has also been supported by molecular analyses focusing on Asiloidea (Trautwein *et al*. 2010) and Diptera in general (Wiegmann *et al*. 2011).

Bequaert (1963), Wilcox & Papavero (1971) and Papavero & Wilcox (1974) published the first classifications of Mydidae with three, four and nine subfamilies, respectively. Bequaert's (1963) study focused on the Afrotropical fauna and he placed *Ectyphus* Gerstaecker in Mydinae and all remaining eight genera known at the time in the newly proposed subfamily Syllegomydinae. Wilcox & Papavero (1971) divided the Mydinae of Bequaert into the New World Mydinae and Afrotropical and Nearctic Ectyphinae, including *Ectyphus*. Yeates & Irwin (1996) published a phylogenetic hypothesis of relationships within Apioceridae, in which they re-delimited the family Mydidae. The Nearctic genus *Rhaphiomidas* Osten Sacken, Neotropical *Megascelus* Philippi, Australasian *Neorhaphiomidas* Norris and Afrotropical *Tongamya* Stuckenberg were transferred from the Apioceridae to the Mydidae in order to render the former monophyletic. *Rhaphiomidas* (as Rhaphiomidinae) and *Megascelus*, *Neorhaphiomidas* and *Tongamya* (as Megascelinae), were hypothesised to be the earliest divergences within Mydidae, respectively. With the addition of these two taxa there are now 11 currently recognised subfamilies. The hypothesis of the "basal" placement of Rhaphiomidinae and Megascelinae has since been supported by molecular (Irwin & Wiegmann 2001) and morphological data (Dikow 2009*a*). The relationships within Mydidae beyond the earliest divergences have not been adequately studied (see Yeates & Irwin 1996, fig. 68) and no modern morphological or molecular hypothesis has yet been published.

To date, representatives of five of the 11 subfamilies of Mydidae are known from the Afrotropical Region, *i.e.*, Ectyphinae (2 genera), Leptomydinae (3), Megascelinae (1), Rhopaliinae (2) and Syllegomydinae (24). Of these taxa, Syllegomydinae is found throughout the Afrotropics, except the Afrotropical part of the Arabian Peninsula, while Ectyphinae is restricted to Southern and Eastern Africa, Leptomydinae to the Arabian Peninsula, the north-eastern Afrotropics and Madagascar, Megascelinae to Southern Africa and Rhopaliinae to the north-eastern Afrotropics and the Arabian Peninsula.

Identification

The Afrotropical fauna has never been treated in a comprehensive way and no identification key to all genera exists. Bequaert (1938, 1940, 1951, 1959, 1961, 1963), Bezzi (1924) and Gerstaecker (1868) described most of the early species and the treatises of Hesse (1969, 1972) cover the diversity in Southern Africa. The keys in Hesse's 1969 and 1972 studies are difficult to use though as the couplets are often very long and confusing if one doesn't have specimens at hand that fit the detailed descriptions perfectly. Dikow (2010*a*, 2012), Dikow & Leon (2014) and Lyons & Dikow (2010) provided modern taxonomic revisions of several genera including identification keys to the species, which are also available online.

The identification key to genera provided below relies to a large degree on the chaetotaxy of thoracic sclerites and well-preserved field-pinned specimens are, therefore, most easily identified. Females are in general less setose than males and, for example, the presence of even a few short katatergal or posterior anepisternal setae is interpreted as being setose. In a few instances, the key relies on male terminalia features. Furthermore, in two couplets two genera are keyed out together, as these genera might have to be synonymised and more in-depth study is required.

The below identification key does not include eight "morphogenera" of Syllegomydinae from Southern Africa that have been identified and cannot be placed in any of the existing 32 Afrotropical genera included below. These will need to be described elsewhere and an updated key provided at that time. The identification key provided below can also be accessed electronically at https://asiloidflies.si.edu/content/online-identification-keys add http://bit.ly/Afrotropical_Mydidae_genera and will be updated when the new genera have been formally described. Mydidae should be preserved by direct-pinning in the field (see Chapter 2).

Key to genera of Afrotropical Mydidae

1. Antennal postpedicel composed of a single clubbed segment (Figs 10, 11); mystacal (facial) setae absent . . . . *Tongamya* Stuckenberg

– Antennal postpedicel composed of cylindrical proximal part and bulbous distal part, separated by membranous cuticle (*e.g.*, Fig. 6); mystacal (facial) setae present (*e.g.*, Figs 12–15) 2

2. Thorax with katatergite bare 3

– Thorax with katatergite setose (at least a few short setae present, often densely setose) 6

3. Wing cell r_4 closed; vein M_{3+4} present (terminating together at costal vein (*C*)) (*e.g.*, Figs 18, 85) 4

– Wing cell r_4 open; vein M_{3+4} absent (not terminating together at costal vein (*C*) or wing margin) 5

4. Wing stump vein (R_3) extending from vein R_4, but not reaching vein R_2 (Fig. 42); thorax with anatergite bare; posterior margin of anepisternum bare . . . . *Ectyphus* Gerstaecker

– Wing stump vein (R_3) connecting veins R_2 and R_4 (Figs 18, 85); thorax with anatergite setose; posterior margin of anepisternum setose . . . . *Parectyphus* Hesse

5. Proboscis minute; antennal postpedicel with cylindrical proximal part short, much shorter than bulbous distal part (Figs 7, 86, 87), this proximally expanded and narrower distally; head with vertex elevated above median compound eye margin . . . . *Perissocerus* Gerstaecker

– Proboscis long (extending beyond frontoclypeal suture); antennal postpedicel with cylindrical proximal part long, longer than bulbous distal part (Figs 8, 89), this more or less cylindrical; head with vertex slightly below median compound eye margin . . . . *Rhopalia* Macquart

6. Thorax with posterior margin of anepisternum setose (at least a few setae present, *e.g.*, in *Oreomydas* Hesse, often densely setose) (*e.g.*, Figs 51, 53) 7

– Thorax with posterior margin of anepisternum bare 16

7. Hind tibia with well-developed ventral keel, terminating in distinct spine (Figs 51, 53); hind femur greatly expanded; female without bullae on posterolateral margin of tergite 2 (Fig. 53) . . . . *Haplomydas* Bezzi

– Hind tibia without ventral keel; hind femur more or less cylindrical (only slightly expanded distally, *e.g.*, Fig. 24, a few taxa with somewhat expanded femur, *e.g.*, Figs 28, 83); females with bullae on posterolateral margin of tergite 2 (*e.g.*, Fig. 25) 8

8. Thorax with mediotergite (mesopostnotum) setose, at least laterally, usually also medially (*e.g.*, Figs 22, 24) 9

– Thorax with mediotergite (mesopostnotum) bare (*e.g.*, Fig. 26) 10

9. Proboscis long to very long, invariably projecting beyond frontoclypeal suture (Fig. 24); wing cell r_5 open (even if only narrowly so, Figs 20, 21) (restricted to Southern Africa, including southern Angola and southern Zambia) . . . . *Afroleptomydas* Bequaert

– Proboscis minute to short, but never projecting beyond frontoclypeal suture; wing cell r_5 (usually) closed (Figs 19, 95, but see Fig. 91) (widespread sub-Saharan Africa, with few species in Southern Africa) . . . . *Syllegomydas* Becker

10. Thorax with infra-halter sclerite present and setose (see definition in Dikow & Leon 2014: 37, figs 12b, c); male terminalia with 2 phallic prongs fused medially . . . . *Namadytes* Hesse

– Thorax with infra-halter sclerite absent; male terminalia with 2 phallic prongs invariably separated medially 11

11. Thorax with anatergite setose 12

– Thorax with anatergite bare 13

12. Hind femur cylindrical, not expanded distally (Fig. 71); thorax with posterior margin of anepisternum densely setose; larger flies (wing length: 11.2–17.7 mm) . . . . *Namibimydas* Hesse

– Hind femur distinctly expanded distally (Fig. 83); thorax with posterior margin of anepisternum only sparsely setose (1–4 setae, Fig. 83); smaller flies (wing length: 7.8–8.9 mm) . . . . *Oreomydas* Hesse

13. Proboscis very long, projecting beyond tip of antennal postpedicel (Figs 14, 78, 79) . . . . *Nothomydas* Hesse

– Proboscis long, projecting beyond frontoclypeal suture, but never beyond tip of antennal postpedicel (*e.g.*, Fig. 73) 14

14. Abdominal tergal setae with small alveoli (sockets) only, surface not punctate (Fig. 76); scutum smooth (Fig. 76) . . . . *Heteroleptomydas* Bequaert & *Nomoneuroides* Hesse

– Abdominal tergal setae with large, distinct alveoli, giving surface punctate appearance (*e.g.*, Figs 72, 73); scutum rugose (*e.g.*, Figs 72, 73) 15

15. Head with frons bare medially (directly anterior to anterior ocellus); thorax with posterior margin of anepisternum densely setose from dorsal to ventral margin (Fig. 28) (restricted to northern Somalia) . . . . *Afromydas* Bequaert

– Head with frons setose medially (at least a few setae present, directly anterior to anterior ocellus); thorax with posterior margin of anepisternum only sparsely setose dorsally (restricted to easternmost South Africa and southernmost Mozambique) . . . . *Neolaparopsis* Hesse

16. Base of wing vein M_4 and middle section of *CuA* fused for considerable distance (*m–cu* crossvein absent, base of vein M_4 connecting veins M_{3+4} and *CuA*, *e.g.*, Figs 16, 34); cell m_3 broad proximally (*e.g.*, Figs 16, 34). 17

– Base of wing vein M_4 and middle section of *CuA* separated by *m–cu* crossvein (*m–cu* connecting veins M_{3+4} and *CuA*, e.g., Fig. 17); cell m_3 narrow proximally (e.g., Figs 17–19) 18

17. Proboscis long, invariably extending well beyond frontoclypeal suture, often projecting beyond tip of antennal postpedicel (Figs 35, 37); thorax with anatergite bare; hind tibia with ventral keel at least proximally (restricted to southern Namibia, Eastern, Northern & Western Cape Provinces of South Africa) . . . . *Cephalocera* Latreille

– Proboscis short, usually minute, except extending just beyond frontoclypeal suture in *Cephalocerodes bequaerti* Hesse, 1969; thorax with anatergite setose; hind tibia entirely cylindrical (widely distributed throughout Southern Africa) . . . . *Cephalocerodes* Hesse

18. Proboscis minute (barely distinguishable) to short, never projecting beyond frontoclypeal suture. . . . 19

– Proboscis long, invariably projecting beyond frontoclypeal suture 25

19. Wing cell r_5 widely open (as in Fig. 18); hind tibia with well-developed ventral keel terminating in either spine or spine with distal macroseta; hind femur distinctly clubbed 20

– Wing cell r_5 closed (e.g., Fig. 19); hind tibia cylindrical, without ventral keel; hind femur not expanded (clubbed) 21

20. Anterior fore coxa and proepisternum with long macrosetae; head and scutum only sparsely short setose (Figs 44, 45); scutum slightly rugose (Figs 44, 45). . . . . *Eremohaplomydas* Bequaert

– Anterior fore coxa and proepisternum with long setae only (no macrosetae); head and scutum densely long setose (Figs 57, 58); scutum distinctly rugose (Fig. 59). . . . . *Lachnocorynus* Hesse

21. Scutellum with 2 lateral tufts of discal scutellar setae (Figs 48, 49, 63). . . . . *Halterorchis* Bezzi & *Mimadelphus* Hesse

– Scutellum without discal scutellar setae 22

22. Head with parafacial area (between tentorial pit and median eye margin) more than ½ width of central facial swelling (at same level) (more pronounced in females); light brown, grey pubescent, mostly bare flies (Figs 2, 4, 46, 47) (restricted to southern Arabian Peninsula) . . . . *Eremomidas* Semenov

– Head with parafacial area less than ½ width of central facial swelling (restricted to sub-Saharan Africa or Madagascar) 23

23. Discal wing cell (*d*) closed with long stalk (veins M_1 and M_3 merging before reaching *r–m* crossvein, Fig. 62); stump vein (R_3) on vein R_4 absent (Fig. 62) (restricted to Madagascar) . . . . *Mahafalymydas* Kondratieff, Carr & Irwin

– Discal wing cell (*d*) closed bluntly, with short stalk (veins M_1 and M_3 merging beyond *r–m* crossvein, *e.g.*, Figs 17); stump vein (R_3) on vein R_4 present (*e.g.*, Figs 17) (restricted to continental sub-Saharan Africa) 24

24. Median surface of hind tibia without long, erect setae; hind femur with ventral macrosetae on elevated alveoli; proboscis short, but extending to frontoclypeal suture (restricted to Kenya and Tanzania) . . . . *Mydaselpis* Bezzi [in part; *M. ngurumani* Dikow, 2010]

– Median surface of hind tibia with long, erect setae; hind femur without ventral macrosetae; proboscis very short, only extending halfway to frontoclypeal suture (restricted to north-westernmost Namibia) . . . . *Notosyllegomydas* Hesse

25. Thorax with anepimeron and katepimeron setose 26

– Thorax with anepimeron and katepimeron bare. 27

26. Restricted to Madagascar . . . . *Hessemydas* Kondratieff, Carr & Irwin

– Restricted to Sudan . . . . *Leptomydas* Gerstaecker

27. Surface of abdominal tergites punctate (setae on tergites with distinct alveoli, Fig. 65); abdominal tergite 10 in females without acanthophorite spines (*e.g.*, Fig. 99). 28

– Surface of abdominal tergites smooth (setae on tergites without distinct alveoli, Figs 31, 75); abdominal tergite 10 in females with acanthophorite spines (*e.g.*, Fig. 31) 29

28\. Male terminalia with phallic epimere (*sensu* Hesse 1969: 36) absent (restricted to Southern Africa) . . . . *Mydaselpis* Bezzi [in part]

– Male terminalia with phallic epimere distally simple and evenly rounded (throughout sub-Saharan Africa) . . . . *Vespiodes* Hesse

29\. Scutum rugose (except postalar callus, Figs 30, 33); abdomen broad proximally and tapering slightly distally (Figs 30, 32) . . . . *Arenomydas* Hesse

– Scutum smooth throughout, sometimes slightly punctate medially and sub-medially (*e.g.*, Figs 29, 74); abdomen parallel-sided throughout (*e.g.*, Figs 29, 74) 30

30\. Thorax with katatergite, anterolateral scutum and abdominal tergite 1 densely long setose (Fig. 29, females unknown); wing with alula large, medially overlapping with scutellum (when wings folded over abdomen, Fig. 29); head with frons and vertex densely long setose (Fig. 29) (restricted to southern Namibia and north-western South Africa) . . . . *Agaperemius* Hesse

– Thorax with katatergite, anterolateral scutum and abdominal tergite 1 sparsely short setose in both sexes (Fig. 74); wing with alula well-developed, but medially not touching scutellum (when wings folded over abdomen, Fig. 74); head with frons and vertex sparsely short setose (virtually bare, Figs 74, 75) (restricted to eastern and southern South Africa) . . . . *Nomoneura* Bezzi

Synopsis of the fauna

The earliest mydid species described from the Afrotropical Region is *Afroleptomydas* (*Afroleptomydas*) *westermanni* (Wiedemann, 1819) from the "Promontorium Bonae Spei" (= Cape of Good Hope) referring to south-western South Africa.

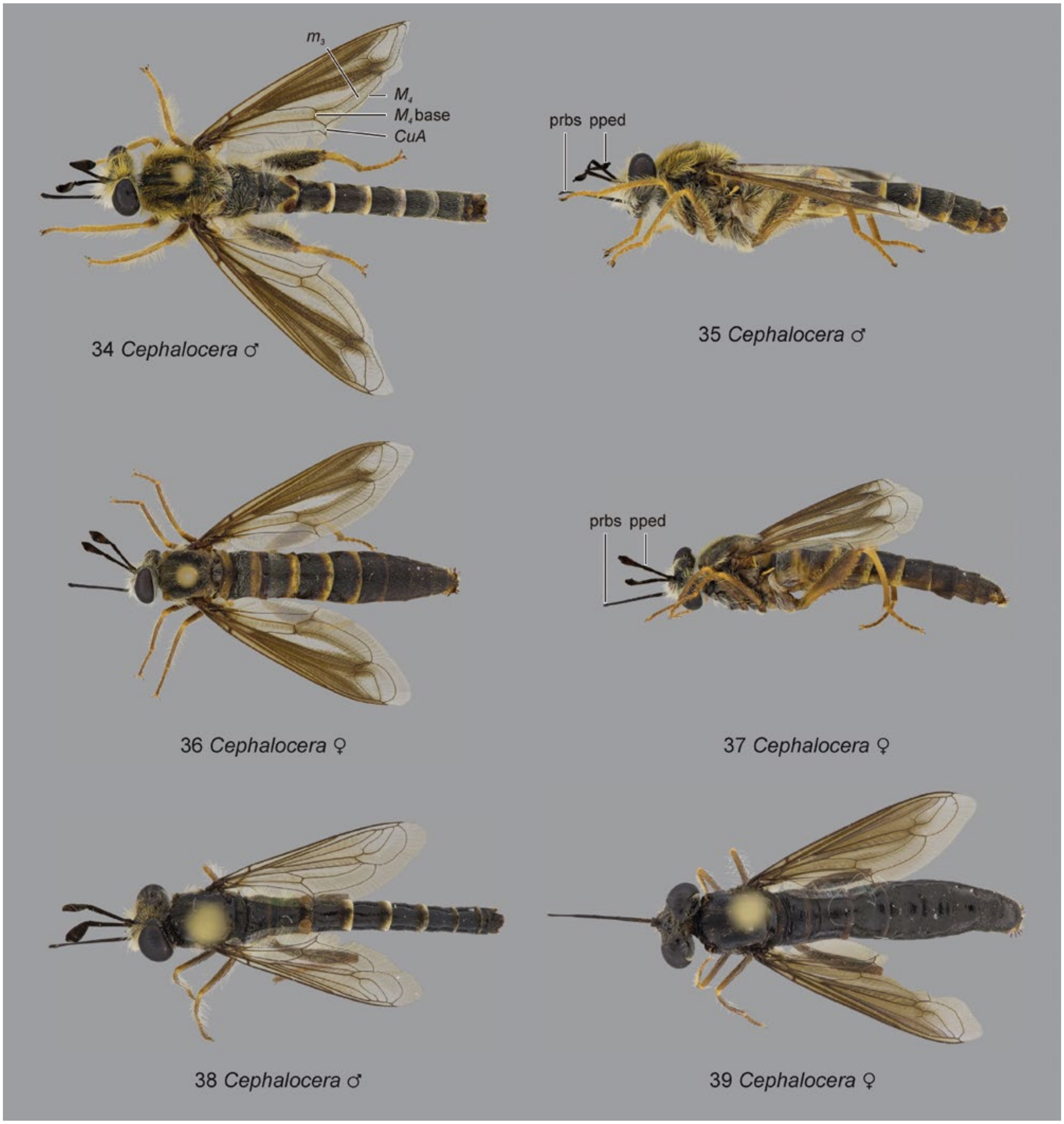
The Afrotropical fauna is the most diverse Mydidae fauna in the world. Of the 66 valid genera and 476 valid species known, 32 genera (48%) and 208 species (44%) occur in the region. Of the 32 genera, 28 are endemic to the Afrotropics and 20 (63%, 30% of world fauna) are endemic to Southern Africa. Similarly, 179 species (86%, 38% of world fauna) are endemic to Southern Africa alone and 161 species (77%, 34% of world fauna) are restricted to Namibia and South Africa. Kirk-Spriggs & Stuckenberg (2009: 185) predicted that *ca* 200 species (50%) of the Afrotropical fauna may await discovery and description.

The Ectyphinae and Syllegomydinae are especially speciose in the Afrotropics with seven species (70% of world fauna) and 189 species (92%), respectively, represented in the region. Less well represented are the Leptomydinae (4 species, 7% of world fauna), Megascelinae (2, 13%), and Rhopaliinae (6, 26%).

This synopsis is based on the study of more than 2,202 Afrotropical specimens, many of which were previously undetermined, from the major natural history collections and particularly those with substantial Afrotropical holdings. Of these, 35 specimens representing eight "morphogenera" of Syllegomydinae cannot be placed in any of the existing 32 Afrotropical genera and will need to be described elsewhere. The specimen occurrence data on which the below outlines are based can be accessed at http://gbif.org (Dikow 2016) and http://asiloidlfies.si.edu. In addition, the photographs of pinned specimens in Figs 20–99, plus additional views of the lateral habitus and head in anterior view, can be accessed electronically at Morphbank under Collection ID 859751 (http://www.morphbank.net/myCollection/?id=859751).

***Afroleptomydas* Bequaert** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 12, 20–25) of 88 species occurring in Southern Africa (including southern Angola and Zambia) and in particular in Namibia and western South Africa. *Afroleptomydas* is by far the most diverse genus in the Afrotropics and globally (19% of the world fauna). It is also the most often encountered Mydidae taxon in Southern Africa. Interestingly, the genus is absent, however, from the Indian Ocean coastline of eastern South Africa (part of the Eastern Cape and virtually entire KwaZulu-Natal Provinces). Specimens have been collected from September–May (with extremely few records for June and August and none for July). Sexual dimorphism varies from minimal to pronounced. The genus is distinguishable by the long proboscis (invariably extending beyond the frontoclypeal suture), the open wing cell r_5 (even if only narrowly so) and the setose katatergite, posterior anepisternum and mediotergite (mesopostnotum). Hesse (1969, fig. 7) distinguished two subgenera, *Afroleptomydas sensu stricto*, with 64 species (Figs 20, 21) and *A.* (*Crossoprosopus* Hesse) with 24 species (Figs 22–25). Many species appear to have extremely restricted distributions and are based on only a small series of specimens collected at a particular locality. Willowmore, in the Eastern Cape Province of South Africa, for example, is the type locality of no less than five *Afroleptomydas* species (along with two *Cephalocera* and one *Mydaselpis* species), based on collections made by J. Brauns (Londt 1998). While Brauns certainly also collected specimens in surrounding habitats, five species occurring in this southern Karoo environment exemplifies how diverse this taxon is in semi-desert environments. It is likely that new species await discovery, although some species may have been described more than once. The identification key to species provided by Hesse (1969) is cumbersome to use and identifying specimens originating far from the known type localities often proves problematic. In addition, the key does not include the ten species later described by Hesse (1972).

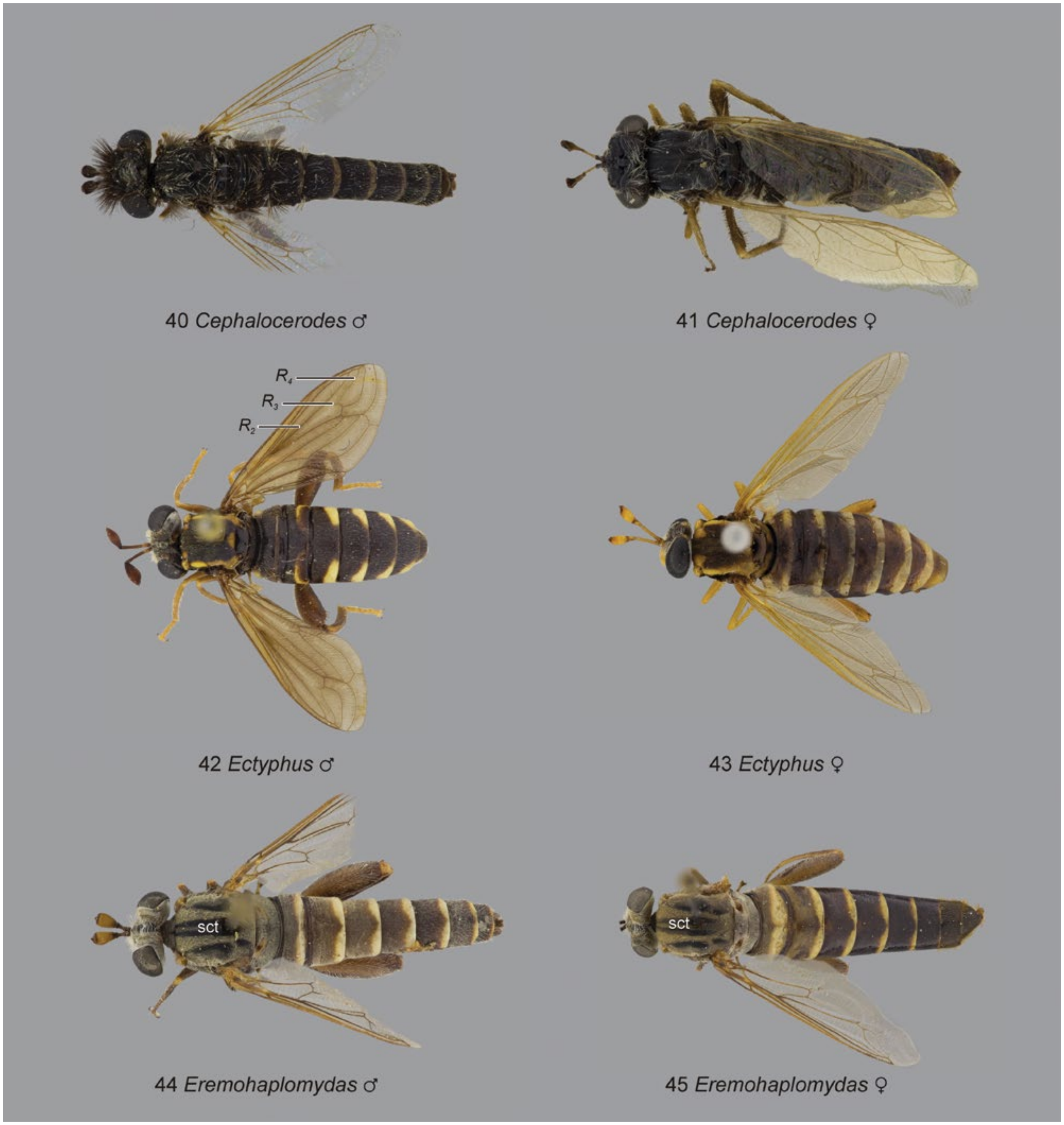
***Afromydas* Bequaert** (Syllegomydinae: Mydaselpidini)**.** An endemic monotypic genus (Figs 26–28) with the single described species, *A. guichardi* Bequaert, 1961, occurring in northern Somalia. The species is only known from the male holotype and single female paratype collected in April. Sexual dimorphism is minimal in the species. The genus is distinguishable by the setose posterior anepisternum, bare anatergite, punctate abdominal tergites and the female without acanthophorite spines. *Afromydas* is grouped together with the genera *Mydaselpis* and *Vespiodes* in the tribe Mydaselpidini. Females of these genera are unique within the subfamily Syllegomydinae, in having lost the acanthophorite spines. Within Mydidae, only the New World subfamilies Mydinae and Oriental Cacatuopyginae lack acanthophorite spines, which is an



Figs 47.34–39. Habitus photographs of Mydidae: (34) *Cephalocera imitata* Hesse, dorsal view ♂; (35) same, lateral view; (36) same, dorsal view ♀; (37) same, lateral view; (38) *Cephalocera* sp., dorsal view ♂; (39) same ♀.

Abbreviations: *CuA* – anterior branch of cubital vein; m_3 – third medial cell; M_4 – fourth branch of media; pped – postpedicel; prbs – proboscis.

indication that Mydaselpidini, like Mydinae, oviposit in decaying wood rather than soil. Dikow (2010a) mentioned that the three genera can only be distinguished based on the presence and shape of the phallic epimere (absent in *Mydaselpis*, present and distally simple and evenly rounded in *Vespiodes* and present and distally bifurcate in *Afromydas*). *Afromydas* keys out separately in the above identification key, as it is the only Mydaselpidini genus with a setose posterior anepisternum.



40 *Cephalocerodes* ♂

41 *Cephalocerodes* ♀

42 *Ectyphus* ♂

43 *Ectyphus* ♀

44 *Eremohaplomydas* ♂

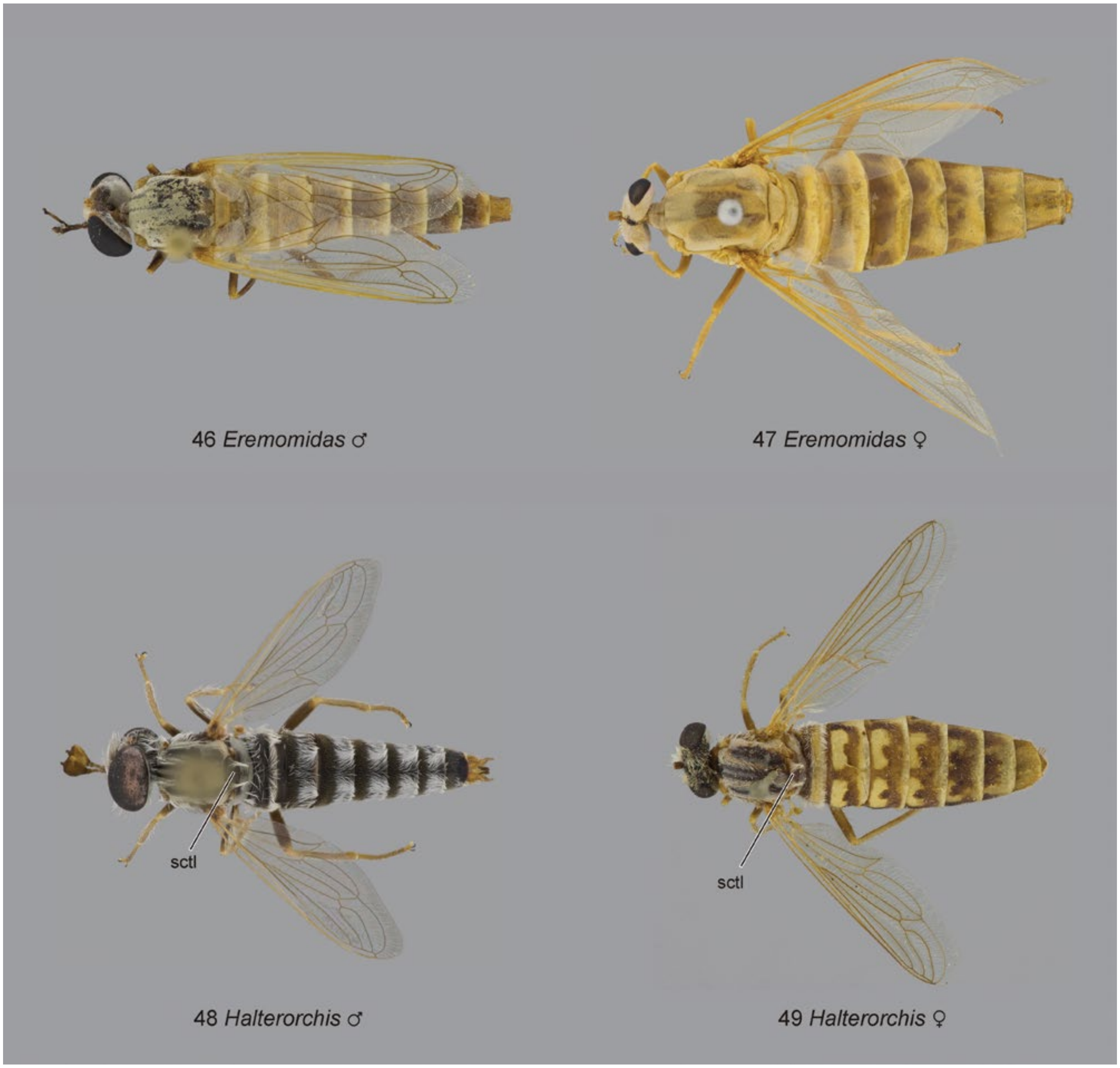
45 *Eremohaplomydas* ♀

Figs 47.40–45. Habitus photographs of Mydidae (dorsal views): (40) *Cephalocerodes eremobius* Hesse ♂; (41) same ♀; (42) *Ectyphus pinguis* Gerstaecker ♂; (43) same ♀; (44) *Eremohaplomydas desertorum* Bequaert ♂; (45) same ♀.

Abbreviations: R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; sct – scutum.

***Agaperemius* Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic monotypic genus (Fig. 29) with the single described species, *A. hirtus* Hesse, 1969, occurring in southern Namibia and north-western South Africa, known from three males only, all collected in October (females remain unknown). Wharton (1982) also recorded the genus from Gobabeb in the Namib Desert of Namibia, but the study of voucher specimens revealed that these specimens do not represent *Agaperemius*, but an undescribed genus and species. *Agaperemius* is distinguishable by the long proboscis (extending beyond the frontoclypeal suture) and the long setose frons, vertex, katatergite, anterolateral scutum and abdominal tergite 1.

***Arenomydas* Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 30–33) of nine species occurring in western South Africa with one record from southern Namibia. Specimens have been collected from September–November (very few records for August and December). Sexual dimorphism can be pronounced. The genus is distinguishable by the long proboscis (extending beyond frontoclypeal suture), the

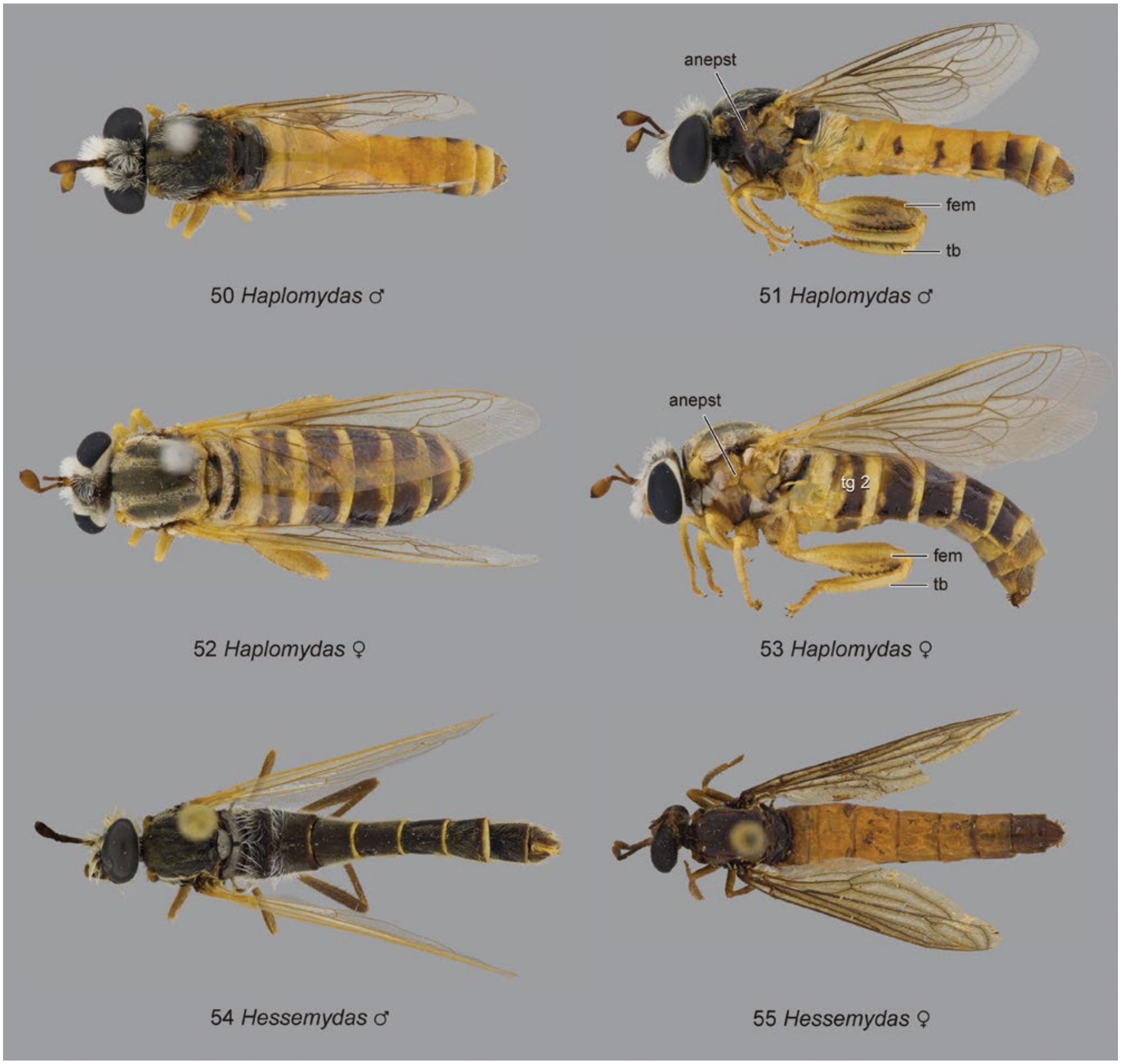


Figs 47.46–49. Habitus photographs of Mydidae (dorsal views): (46) *Eremomidas arabicus* (Bequaert) ♂; (47) same ♀; (48) *Halterorchis* sp. ♂; (49) *H. karooensis* Hesse ♀.

Abbreviation: sctl – scutellum.

rugose scutum (except the postalar callus) and broad abdomen that tapers slightly distally. An identification key to species was provided by Hesse (1969).

***Cephalocera* Latreille** (Syllegomydinae: Cephalocerini)**.** An endemic genus (Figs 1, 16, 34–39) of 28 species occurring in Namibia and South Africa. *Cephalocera* is the second-most diverse genus of Afrotropical Mydidae and is restricted in its distribution to western South Africa, particularly in the Succulent Karoo biome and the Cape Floristic Region, as well as southernmost Namibia. Specimens have been collected from August–November (few records for December). Sexual dimorphism is minimal. The genus is distinguishable by the long proboscis, which invariably extends well beyond the frontoclypeal suture and often beyond the tip of the antennal postpedicel, the ventral keel of the hind tibia and unique wing venation (veins M_4 and *CuA* merged for considerable distance, *m–cu* crossvein absent and base of vein M_4 connecting veins *M* and *CuA* and cell m_3 broad proximally, Figs 16, 34). *Cephalocera* is placed together with *Cephalocerodes* in the tribe Cephalocerini,

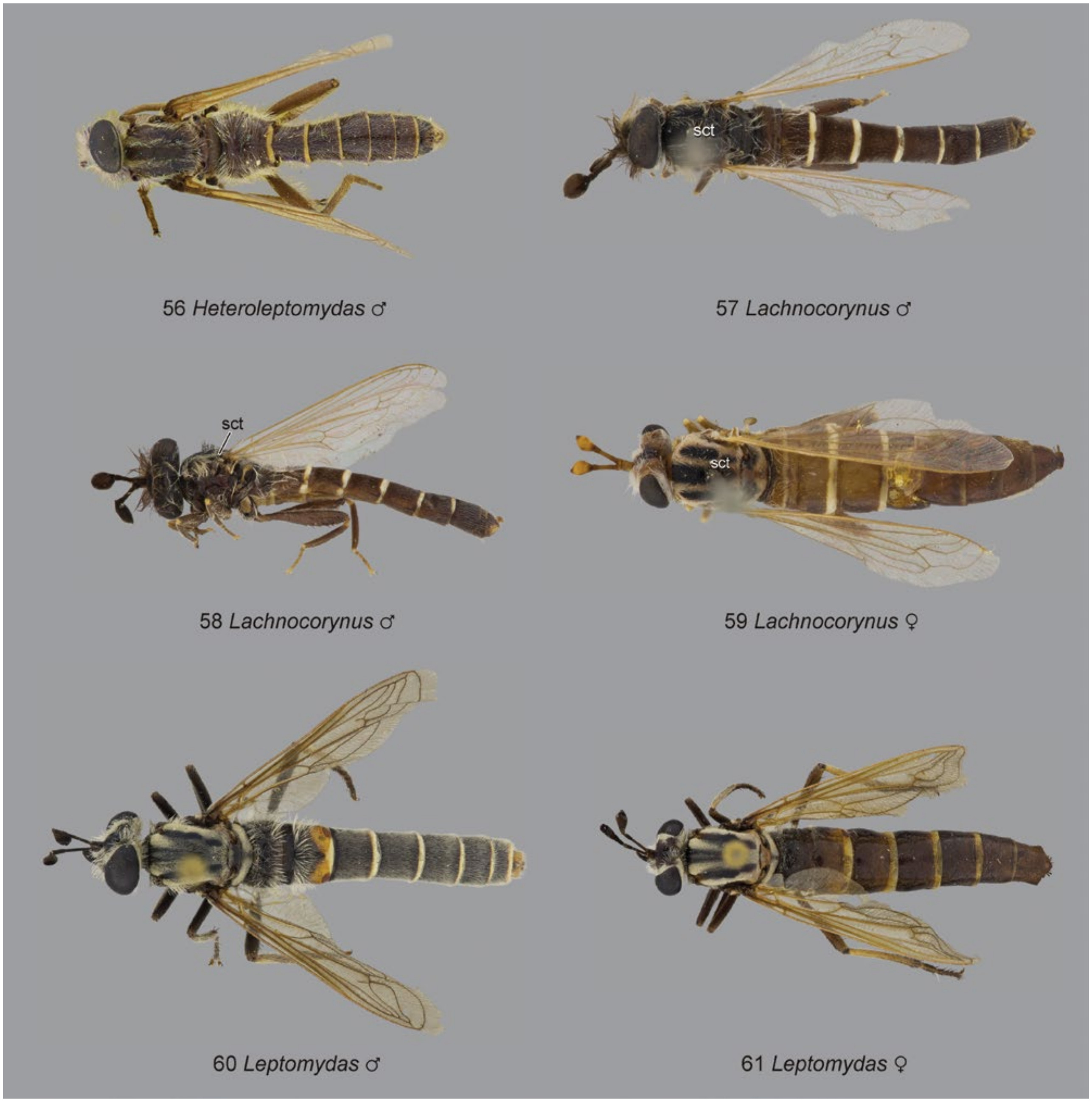


Figs 47.50–55. Habitus photographs of Mydidae: (50) *Haplomydas crassipes* Bezzi, dorsal view ♂; (51) same, lateral view; (52) same, dorsal view ♀; (53) same, lateral view; (54) *Hessemydas seyrigi* (Séguy), dorsal view ♂; (55) same ♀.

Abbreviations: anepst – anepisternum; fem – femur; tb – tibia; tg – tergite.

which is uniquely identified by the wing venation. An identification key to species was provided by Hesse (1969).

***Cephalocerodes* Hesse** (Syllegomydinae: Cephalocerini)**.** An endemic genus (Figs 40, 41) of three described species: *C. bequaerti* Hesse, 1969, from South Africa; *C. eremobius* Hesse, 1969 from Namibia; and *C. oldroydi* (Bequaert, 1963), from Zimbabwe. These species were described based on males alone and females remained unknown until a single specimen of an undescribed species was discovered. Specimens have been collected in May–July (one record in September). Sexual dimorphism is substantial. The genus is distinguishable by



Figs 47.56–61 Habitus photographs of Mydidae: (56) *Heteroleptomydas conopsoides* Bequaert, dorsal view ♂; (57) *Lachnocorynus chobeensis* Hesse, dorsal view ♂; (58) same, lateral view; (59) same, dorsal view ♀; (60) *Leptomydas turcicus* Bowden, dorsal view ♂ (non-Afrotropical); (61) same ♀.

Abbreviation: sct – scutum.

the short proboscis, the setose anatergite and the unique wing venation (veins M_4 and *CuA* merged for considerable distance, *m–cu* crossvein absent and base of vein M_4 connecting with veins *M* and *CuA* and cell m_3 broad proximally, as in Fig. 16). *Cephalocerodes* is placed together with *Cephalocera* in the tribe Cephalocerini. An identification key to species was provided by Hesse (1969).

***Ectyphus* Gerstaecker** (Ectyphinae)**.** An endemic genus (Figs 42, 43) of six described species occurring primarily in South Africa with a single species recorded from south-eastern Kenya. Sexual dimorphism is minimal. Specimens have been collected from September–February (none in October and single records for April and July). The genus is distinguishable by the closed r_4 wing cell, the presence of vein M_{3+4}, which terminates in the costal vein (C) and the bare anatergite. *Ectyphus* was recently revised by Lyons & Dikow (2010), who provided an identification key to species.

***Eremohaplomydas* Bequaert** (Syllegomydinae: Syllegomydini)**.** An endemic monotypic genus (Figs 44, 45), with the single described species, *E. desertorum* Bequaert, 1959, occurring in north-westernmost Namibia. Wharton (1982) also recorded the genus from Gobabeb in the central Namib Desert of Namibia and study of voucher specimens supports this. Specimens have been collected from April–May. Sexual dimorphism is minimal although females are larger than males. The genus is distinguishable by the very short proboscis, the widely open wing cell r_5, the well-developed ventral keel on the hind tibia and sparse setation on the head and scutum.

***Eremomidas* Semenov** (Leptomydinae)**.** A genus of five species, occurring primarily in the Palaearctic Region (Central Asia), with a single species, *E. arabicus* Bequaert, 1961 (Figs 2–4, 46, 47), from the Afrotropical Region. The species is recorded from Oman, United Arab Emirates and Yemen in the Arabian Peninsula (Dikow 2010*b*: 608). An undescribed species, known from three male specimens only, has been discovered from south-western Sudan that exhibits the same male terminalia configuration as *E. arabicus*. Afrotropical specimens of *Eremomidas* have been collected from September–October and in June. Sexual dimorphism is pronounced and females are considerably larger than males (when known). Morphological evidence suggests that *E. arabicus* and the undescribed species do not belong to *Eremomidas* and that the subfamilial classification within Leptomydinae is also questionable. *Eremomidas arabicus* is distinguishable by the large size (female wing length: 17.5–18.2 mm), closed wing cell r_5, the broad parafacial area (more than ½ width of central facial swelling at same level) and a distribution in the southern Arabian Peninsula. The male terminalia of *E. arabicus* and the undescribed species are unique in having an almost entirely fused epandrium medially, the phallus with bifid tip extending beyond the gonopore and a dorsal phallic epimere.

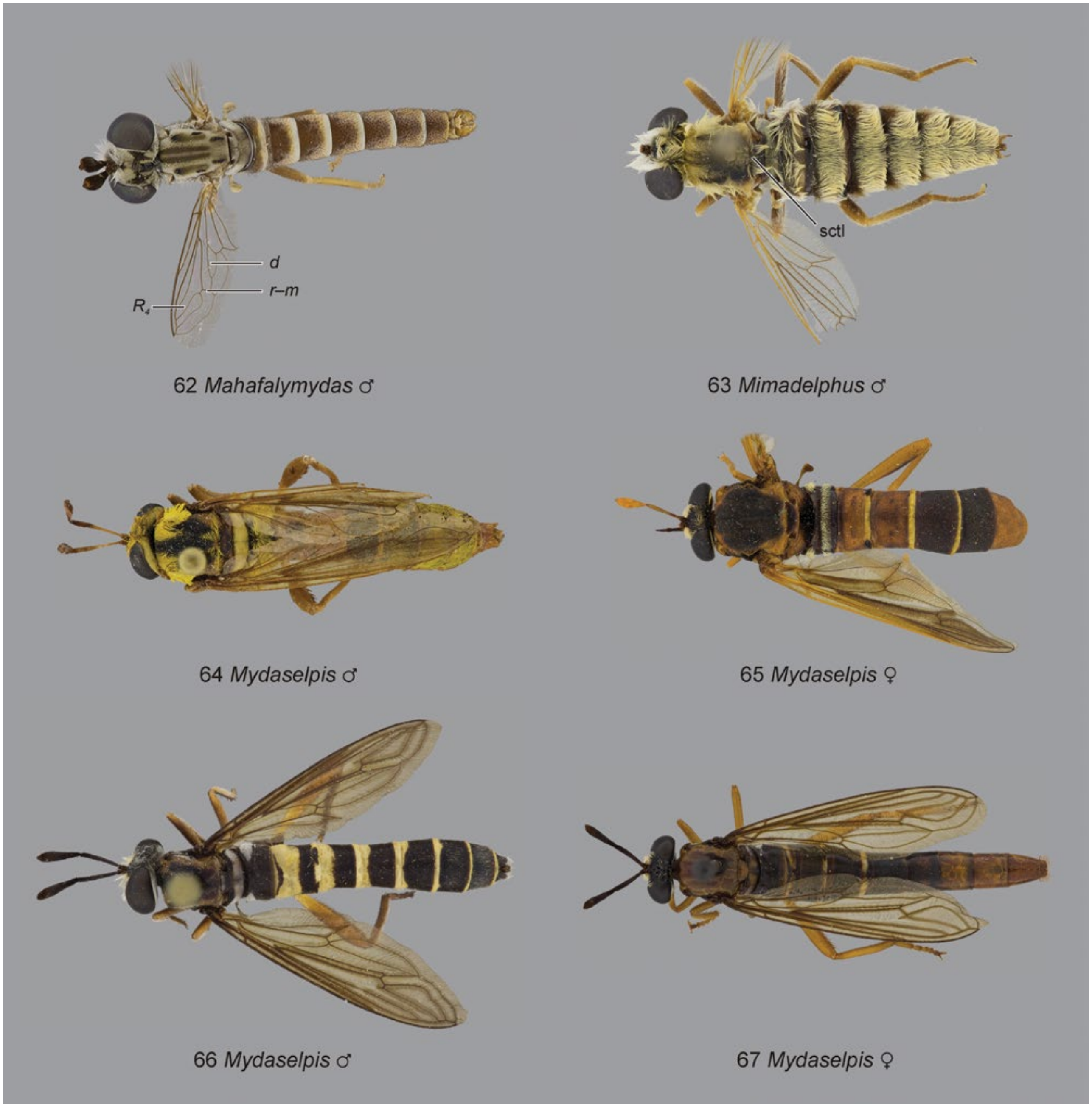
***Halterorchis* Bezzi** (Syllegomydinae: Halterorchini)**.** An endemic genus (Figs 48, 49) with two species, *H. inermis* Bezzi, 1924 and *H. karooensis* Hesse, 1969, occurring in western South Africa. Both species were initially based on female holotype specimens only, which are poorly-preserved. The discovery of a male specimen of an undescribed species, as well as the possible synonymy with *Mimadelphus* (based on a single male only), extend the knowledge of the genus somewhat. Specimens have been collected in March. Sexual dimorphism is pronounced. The genus is distinguishable by the minute proboscis, the bare posterior anepisternum and the two lateral tufts of discal scutellar setae. Dikow (2012) noted, that in the tribe Halterorchini there is a need to determine whether the supra-hypandrial sclerite, so far unique to *Namibimydas* and *Nothomydas*, is also present in *Halterorchis* (due to the paucity of male specimens none have been dissected). Wharton (1982) also recorded the genus from Gobabeb in the central Namib Desert of Namibia, but study of voucher specimens revealed that these do not represent *Halterorchis*. *Halterorchis* is placed, together with *Mimadelphus*, *Namibimydas* and *Nothomydas*, in the tribe Halterorchini. An identification key to the two Afrotropical species was provided by Hesse (1969).

***Haplomydas* Bezzi** (Syllegomydinae: Syllegomydini)**.** An endemic monotypic genus (Figs 50–53) with the single, distinctive species, *H. crassipes* Bezzi, 1924, recorded from Botswana, Mozambique, Namibia and Zimbabwe, but interestingly absent from South Africa. Specimens have been collected from March–May (with a single record in February). Sexual dimorphism is moderate. The genus is distinguishable by the well-developed ventral keel on the hind tibia terminating in a distinct spine and the greatly expanded hind femur. Females of *H. crassipes* appear to lack bullae on the posterolateral corner of abdominal tergite 2. *Heleomydas* Séguy, 1929 was synonymised with *Haplomydas* by Bequaert (1963).

***Hessemydas* Kondratieff, Carr & Irwin** (Leptomydinae)**.** An endemic genus (Figs 54, 55) with three species: *H. parkeri* Kondratieff, Carr & Irwin, 2005, *H. seyrigi* (Séguy 1960) and *H. tulear* Kondratieff, Carr & Irwin, 2005, from the state of Toliara, in south-western Madagascar (Kondratieff 2009; Kondratieff *et al*. 2005). Specimens have been collected from March–April and from September–November. Sexual dimorphism is minimal. The first species was described decades ago in the genus *Leptomydas* (*H. seyrigi*) and all currently recognised species were available in collections by 1984, but only a recent Malaise trap sampling project in Madagascar, which began in the early 2000s, ignited the description of the genus and new species. The genus is distinguishable by the setose katatergite, anepimeron and katepimeron and the long proboscis that extends beyond the frontoclypeal suture. These characteristics are shared with the genus *Leptomydas* and it is possible that *Hessemydas* represents a synonym of this widespread Northern Hemisphere genus. *Hessemydas* is the only Leptomydinae genus occurring in the Southern Hemisphere, as *Plyomydas* Wilcox & Papavero from the Neotropical Region has recently been transferred to the Mydinae (Castillo & Dikow 2017). An identification key to the three described species was provided by Kondratieff *et al*. (2005).

***Heteroleptomydas* Bequaert** (Syllegomydinae: Syllegomydini)**.** An endemic monotypic genus (Fig. 56) with the single described species, *H. conopsoides* Bequaert, 1963, occurring in south-eastern South Africa. The genus is known from the male holotype and a female non-type specimen, collected at Port St. Johns on the Indian Ocean coast from December–January. Sexual dimorphism is pronounced. The genus is distinguishable by the setose katatergite, bare anatergite, the setose posterior margin of the anepisternum, the long proboscis that extends beyond the frontoclypeal suture and the smooth scutal and abdominal cuticle. Hesse (1969) noted the constriction of abdominal segments 2–3 as a generic character, but this constriction in the holotype (Fig. 56, illustrated by Bequaert 1963, fig. 114), is more probably a preservation anomaly. *Heteroleptomydas* and *Nomoneuroides* key out together in the above identification key and are likely synonymous (see *Nomoneuroides* below).

***Lachnocorynus* Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 57–59) with two described species, *L. chobeensis* Hesse, 1969 from northern Botswana and *L. kochi* Hesse, 1969, from northern Namibia. An undescribed species is also known from north-eastern Zimbabwe. Specimens have been collected from July–August. Sexual dimorphism is pronounced. The genus is distinguishable by the very short proboscis, the widely open wing cell r_5, the well-developed ventral keel on the hind tibia and the long setation

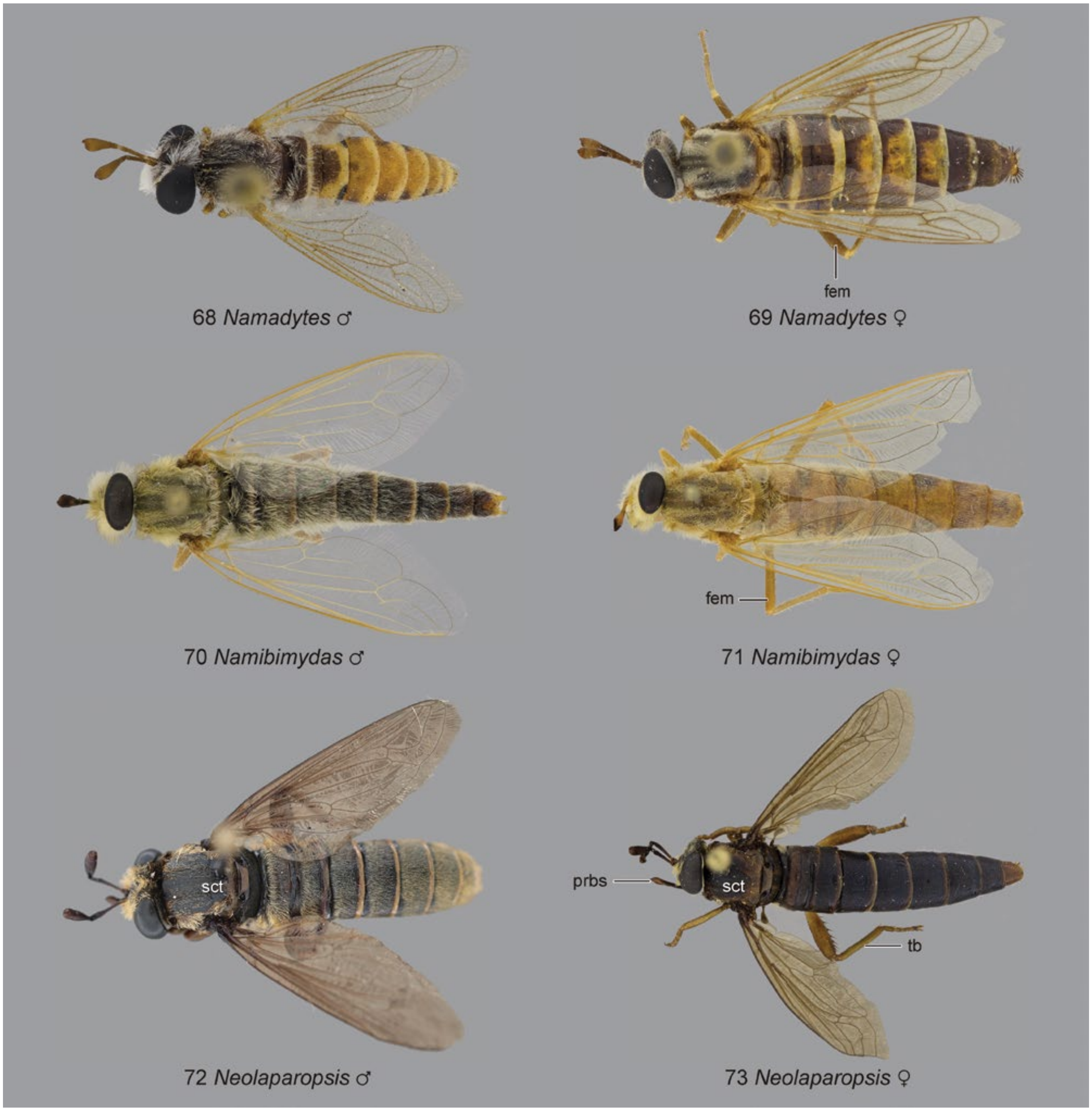


Figs 47.62–67. Habitus photographs of Mydidae (dorsal views): (62) *Mahafalymydas tuckeri* Kondratieff, Carr & Irwin ♂; (63) *Mimadelphus vellosus* Hesse ♂; (64) *Mydaselpis* sp. ♂; (65) *M. peringueyi* Bezzi ♀; (66) *M. ngurumani* Dikow ♂; (67) same ♀.

Abbreviations: *d* – discal cell; R_4 – upper branch of third branch of radius; *r–m* – radial–medial crossvein; sctl – scutellum.

on the head and scutum. An identification key to the two described species was provided by Hesse (1969).

Leptomydas **Gerstaecker** (Leptomydinae)**.** A genus of 18 described species (Figs 5, 60, 61), occurring primarily in the Palaearctic and Oriental Regions (Dikow 2010a). Only one species, *L. fulviventris* Bigot, 1885, is recorded from the Afrotropical Region, based on two specimens collected in north-eastern Sudan in April. This specific epithet is a homonym of *L. fulviventris* (Dufour, 1850) (which in turn is a junior synonym of the Palaearctic species *L. lusitanicus* (Wiedemann, 1830)). Sexual dimorphism is minimal. Bowden (1980: 326) combined *Rhopalia tutankhameni* Brunetti, 1929 with this genus, but that species belongs in *Rhopalia* (see below). The



Figs 47.68–73. Habitus photographs of Mydidae (dorsal views): (68) *Namadytes vansoni* Hesse ♂; (69) same ♀; (70) *Namibimydas psamminos* Dikow ♂; (71) same ♀; (72) *Neolaparopsis puncturatus* Hesse ♂; (73) same ♀.

Abbreviations: fem – femur; prbs – proboscis; sct – scutum; tb – tibia.

genus is distinguishable by the setose katatergite, anepimeron and katepimeron and the long proboscis that extends beyond the frontoclypeal suture (see also *Hessemydas* above).

Mahafalymydas **Kondratieff, Carr & Irwin** (Syllegomydinae)**.** An endemic genus (Fig. 62) with two described species, *M. wiegmanni* Kondratieff, Carr & Irwin, 2005 and *M. tuckeri* Kondratieff, Carr & Irwin, 2005, endemic to the state of Toliara in south-western Madagascar (Kondratieff *et al*. 2005), both only known from males. Specimens have been collected from September–October. *Mahafalymydas* species are very small (wing length: 4.3–5.0 mm) and have the two-pronged phallus characteristic of the subfamily Syllegomydinae. It is the only genus of this diverse Afrotropical radiation that occurs in Madagascar.

74 *Nomoneura* ♂

75 *Nomoneura* ♀

76 *Nomoneuroides* ♂

77 *Nomoneuroides* ♀

78 *Nothomydas* ♂

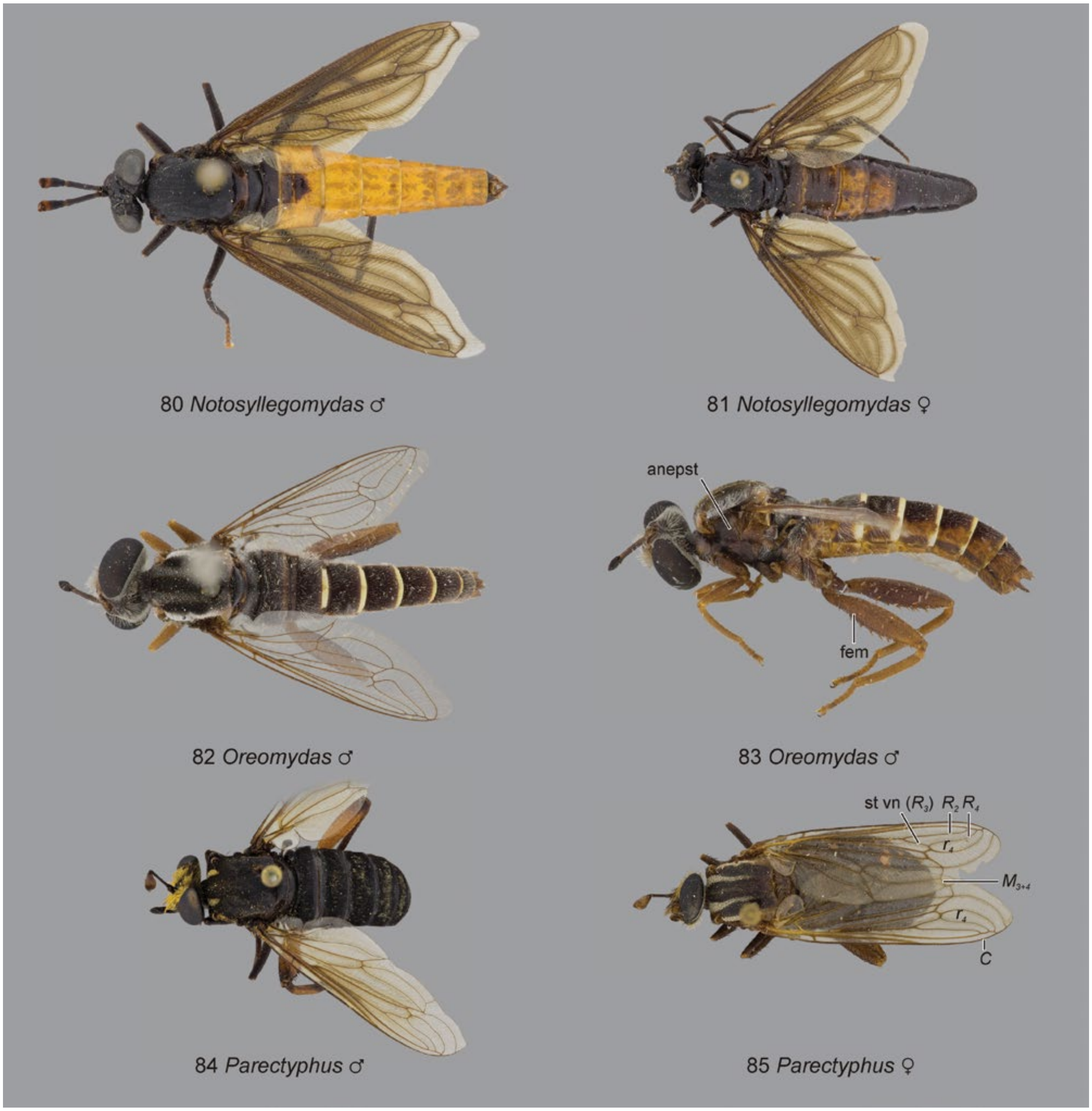
79 *Nothomydas* ♀

Figs 47.74–79. Habitus photographs of Mydidae (dorsal views): (74) *Nomoneura caffra* Hesse ♂; (75) same ♀; (76) *Nomoneuroides natalensis* Hesse ♂; (77) same ♀; (78) *Nothomydas picketti* Dikow ♂; (79) same ♀.

Abbreviations: al – alula; fr – frons; m_3 – third medial cell; prbs – proboscis; sct – scutum; vrt – vertex.

The genus is distinguishable by the unique wing venation (discal wing cell (*d*) closed with long stalk) and a distribution confined to Madagascar. The two species can be identified by reference to original descriptions of Kondratieff *et al*. (2005).

Mimadelphus **Hesse** (Syllegomydinae: Halterorchini)**.** An endemic monotypic genus (Fig. 63) with the single described species, *M. vellosus* Hesse, 1972, recorded from Namibia. Seasonality and females remain unknown. The genus is


80 *Notosyllegomydas* ♂

81 *Notosyllegomydas* ♀

82 *Oreomydas* ♂

83 *Oreomydas* ♂

84 *Parectyphus* ♂

85 *Parectyphus* ♀

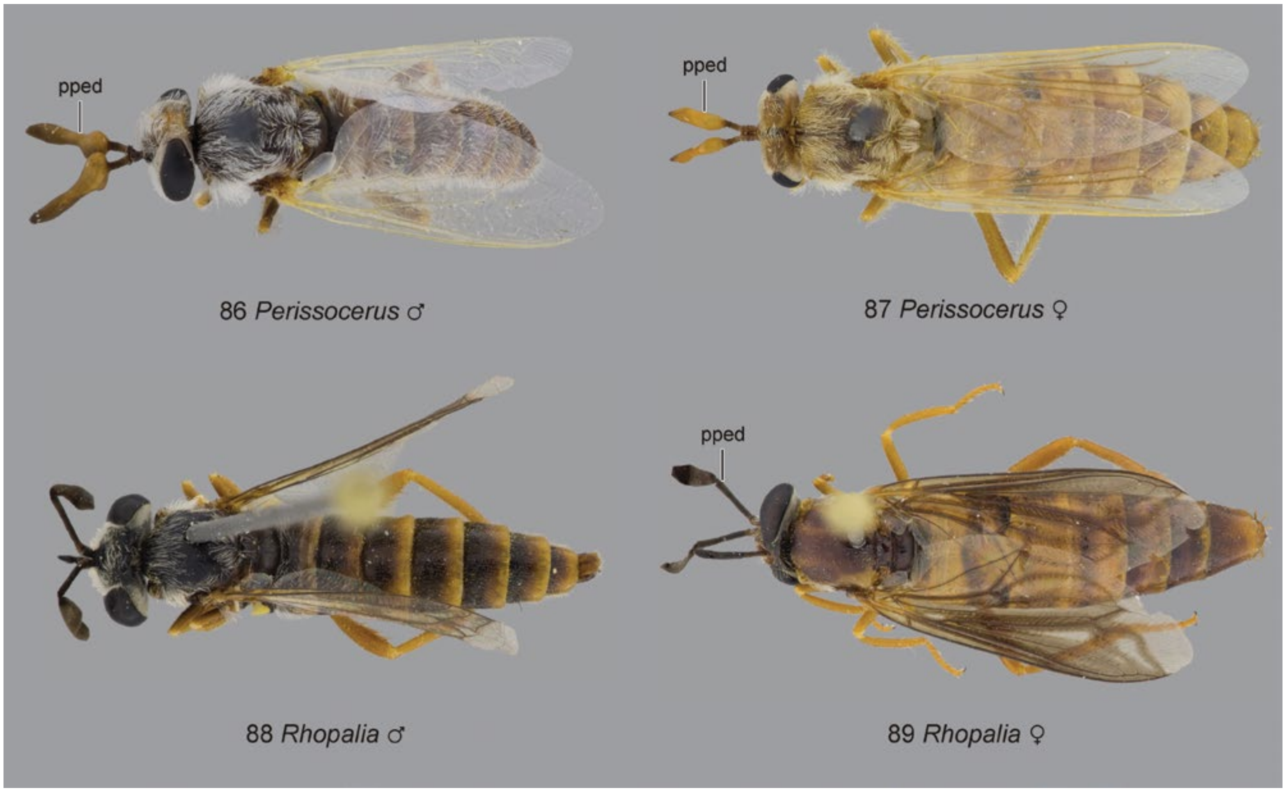
Figs 47.80–85. Habitus photographs of Mydidae: (80) *Notosyllegomydas brincki* (Bequaert), dorsal view ♂; (81) same, dorsal view ♀; (82) *Oreomydas luctuosus* (Bezzi), dorsal view ♂; (83) same, lateral view; (84) *Parectyphus namibiensis* Hesse, dorsal view ♂; (85) same, dorsal view ♀.

Abbreviations: anepst – anepisternum; *C* – costal vein; fem – femur; M_{3+4} – fused third and fourth branch of media; R_2 – upper branch of second branch of radius; R_3 – lower branch of second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; st vn – stump vein.

distinguishable by the minute proboscis, the bare posterior anepisternum and the two lateral tufts of discal scutellar setae. The type locality of *M. vellosus*, which is based on a single male specimen, is apparently unknown, but was likely collected in southern Namibia. Hesse (1972) suggested that this species may represent the unknown male of *Halterorchis* and this finding is supported here. Both genera are keyed out together in the above identification key, based on the presence of lateral tufts of discal scutellar setae. Further examination of specimens of both genera is required to establish the possible synonymy. *Mimadelphus* is placed, together with the genera *Halterorchis*, *Namibimydas* and *Nothomydas* in the tribe Halterorchini (see *Halterorchis* above).

Mydaselpis **Bezzi** (Syllegomydinae: Mydaselpidini)**.** An endemic genus (Figs 17, 64–67) of six species, occurring in Eastern (Kenya and Tanzania) and Southern Africa (Namibia, South Africa and Zimbabwe). Specimens have been collected from October–January (in Southern Africa, with a single record for April) and from June–July (in Eastern Africa). Sexual dimorphism is minimal. The genus is distinguishable by the bare posterior anepisternum, anepimeron and katepimeron, the punctate abdominal tergites, the somewhat constricted abdominal tergites 2–3 (exhibiting a "wasp waist"), females without acanthophorite spines (one species with acanthophorite spines) and males without a phallic epimere. The majority of species are only known from a single sex and several species exhibit mimetic colouration resembling various wasp taxa. *Mydaselpis ngurumani* is the only species in Eastern Africa and by contrast to all other species, the female possesses acanthophorite spines. The species was described in *Mydaselpis*, based on the male terminalia with the bifid phallus and the absence of a phallic epimere, but could also represent a new generic taxon. This species is keyed out separately from *Mydaselpis sensu stricto* in the above identification key. *Mydaselpis* is included in the tribe Mydaselpidini, along with genera *Afromydas* and *Vespiodes* (see *Afromydas* above). The possibility of synonymy between *Mydaselpis* and *Vespiodes* exists, as these two genera can only be distinguished based on the presence of a phallic epimere in males. While *Mydaselpis* primarily occurs in Southern Africa and *Vespiodes* occurs further north, the distributional ranges overlap in Zimbabwe and northern South Africa. An identification key to species was provided by Hesse (1969).

Namadytes **Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 68, 69) of three described species: *N. cimbebasiensis* Hesse, 1972, *N. maculiventris* (Hesse, 1969) and *N. vansoni* Hesse, 1969, occurring primarily in Namibia, with a few collecting localities in north-western South Africa. Specimens have been collected from February–June (with a few records in October). Sexual dimorphism is pronounced. The genus is distinguishable by the presence of the setose infra-halter

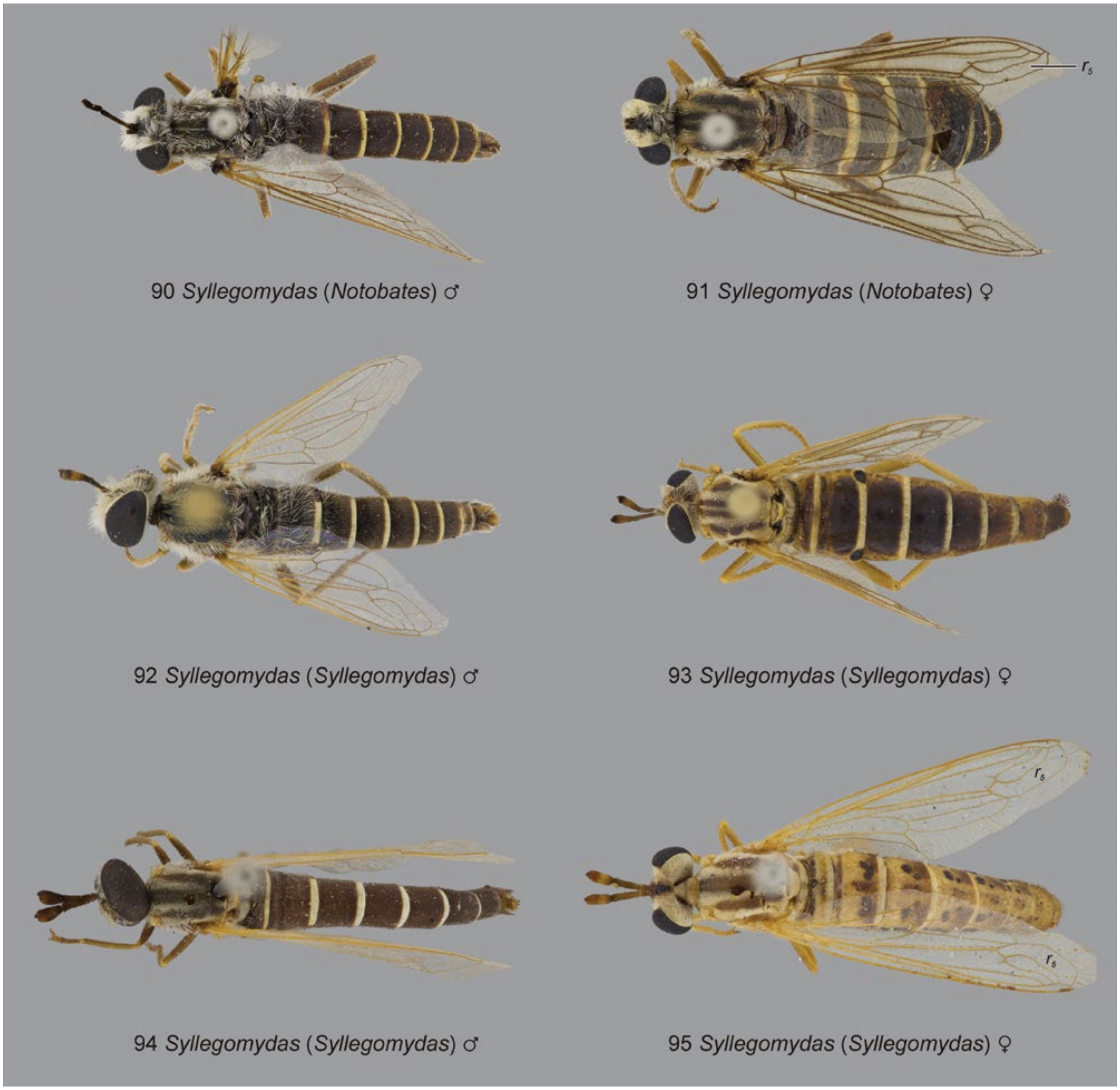


Figs 47.86–89. Habitus photographs of Mydidae (dorsal views): (86) *Perissocerus transcaspicus* Portschinsky ♂ (non-Afrotropical); (87) same ♀; (88) *Rhopalia* sp. ♂; (89) same ♀.

Abbreviation: pped – postpedicel.

sclerite (Dikow & Leon 2014), the setose katatergite and posterior anepisternum and the bare mediotergite (mesopostnotum). *Namamydas* Hesse, 1969 was synonymised with *Namadytes* by Hesse (1972). The genus was last revised by Dikow & Leon (2014), who provided an identification key for the three species.

***Namibimydas* Hesse** (Syllegomydinae: Halterorchini)**.** An endemic genus (Figs 13, 70, 71) of four species, occurring primarily in Namibia, with a single species in western South Africa. Specimens have been collected from January–February with single records for November and April. Sexual dimorphism is minimal. The genus is distinguishable by the setose katatergite and anatergite, the densely setose posterior margin of the anepisternum, the cylindrical hind femur and the large size (wing length: 11.2–17.7 mm). Three species possess a long proboscis that extends beyond the frontoclypeal suture, while one species from the interior of the Namib Desert in



90 *Syllegomydas* (*Notobates*) ♂

91 *Syllegomydas* (*Notobates*) ♀

92 *Syllegomydas* (*Syllegomydas*) ♂

93 *Syllegomydas* (*Syllegomydas*) ♀

94 *Syllegomydas* (*Syllegomydas*) ♂

95 *Syllegomydas* (*Syllegomydas*) ♀

Figs 47.90–95. Habitus photographs of Mydidae (dorsal views): (90) *Syllegomydas* (*Notobates*) *rhodesiensis* Bequaert ♂; (91) same ♀; (92) *Syllegomydas* (*Syllegomydas*) *astrictus* Dikow ♂; (93) same ♀; (94) *S.* (*S.*) *proximus* Séguy ♂; (95) same ♀.

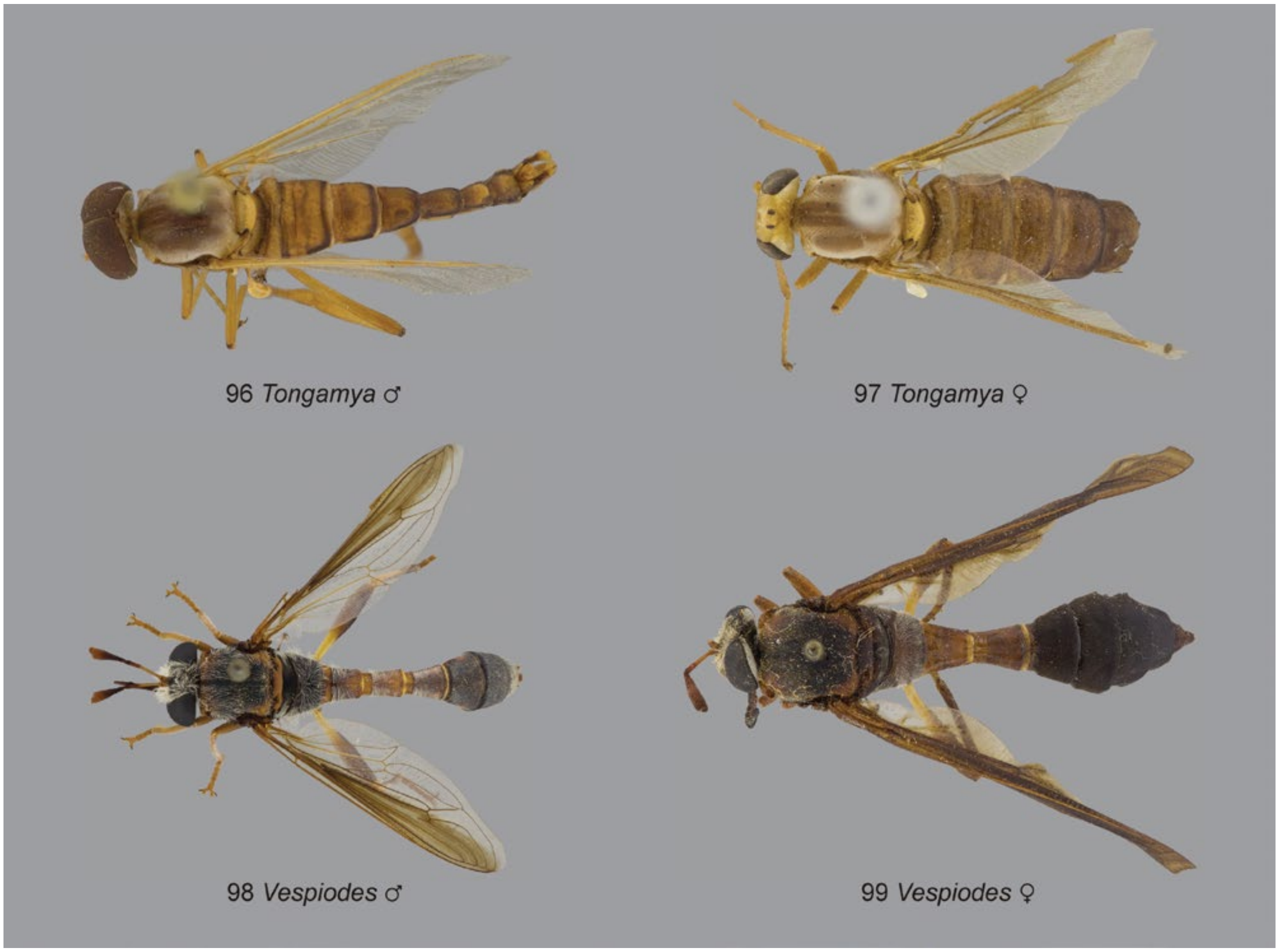
Abbreviation: r_5 – fifth radial cell.

Namibia exhibits a very short proboscis. *Namibimydas* is placed together with *Halterorchis*, *Mimadelphus* and *Nothomydas* in the tribe Halterorchini. The genus was last revised by Dikow (2012), who provided an identification key to species.

Neolaparopsis **Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 6, 72, 73) with the single described species, *N. puncturatus* Hesse, 1969, occurring in easternmost South Africa and adjacent southernmost Mozambique. Specimens have been collected from November–December and in February. Sexual dimorphism is pronounced. The genus is distinguishable by the setose katatergite and posterior anepisternum, the bare anatergite, the long proboscis that extends beyond the frontoclypeal suture and setae on the median frons (directly anterior to anterior ocellus). At the time of description, Hesse (1969) had only two female specimens at hand. Only through the discovery of female and male specimens collected during the same collecting event was it possible to associate the sexes.

Nomoneura **Bezzi** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 74, 75) of six described species, occurring primarily in South Africa, but also recorded from Mozambique and Zimbabwe. Specimens have been collected from August–February (with a single record for March). Sexual dimorphism is minimal. The genus is distinguishable by the setose katatergite, the bare anepimeron and katepimeron and the long proboscis that extends beyond the frontoclypeal suture. Hesse (1969) placed *N. bellardi* (Bertoloni, 1861), originally described from Inhambane, Mozambique and recorded from Zimbabwe, in this genus, but the type specimen has not been located, so the placement of the species requires verification. The only other Mydidae species known from Inhambane is *Syllegomydas* (*Notobates*) *dispar* (Loew, 1852), which is a valid species, known from the type and other specimens. Should *N. bellardi* be correctly placed in *Nomoneura*, it would be the only species of this genus to occur outside of South Africa. An identification key to species was provided by Hesse (1969).

Nomoneuroides **Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 76, 77) of three species, *N. brunneus* Hesse, 1969, *N. melas* Hesse, 1969 and *N. natalensis* Hesse, 1969, occurring in southern Mozambique and south-eastern South Africa. Specimens have been collected from December–February (single records for March and April). Sexual

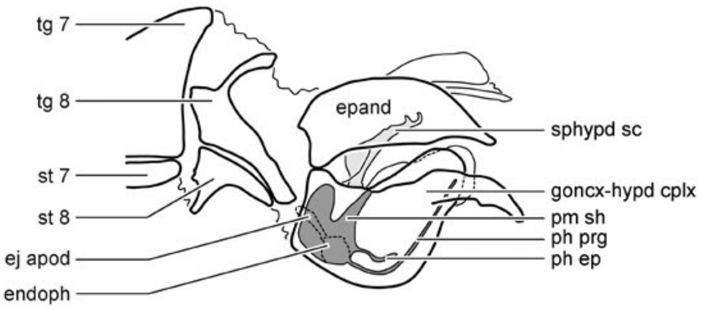


Figs 47.96–99. Habitus photographs of Mydidae (dorsal views): (96) *Tongamya miranda* Stuckenberg ♂; (97) same ♀ (tip of abdomen missing); (98) *Vespiodes cerioidiformis* Hesse ♂; (99) *V. katangensis* (Bequaert) ♀.

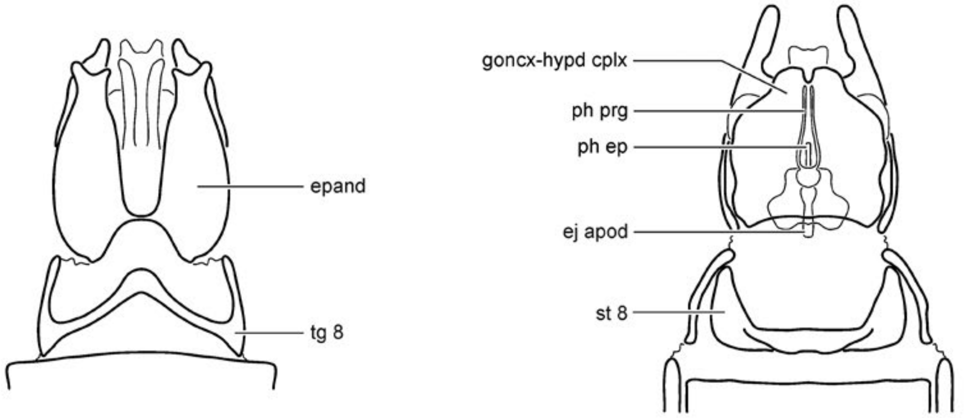
dimorphism is pronounced. The genus is distinguishable by the setose katatergite, bare anatergite, the setose posterior margin of the anepisternum, the long proboscis that extends beyond the frontoclypeal suture and smooth scutal and abdominal cuticle. *Heteroleptomydas* and *Nomoneuroides* key out together in the above identification key and these genera are likely synonymous. Both are confined to coastal sand dunes on the Indian Ocean coast of southern Mozambique and South Africa (Eastern Cape and KwaZulu-Natal Provinces). *Nomoneuroides* was originally based on specimens collected between Inhaca Island in the north and Durban in the south, while *Heteroleptomydas conopsoides* was based on specimens from Port St. Johns, much farther south (a distance of some 250 km). The discovery of specimens from habitats in between these two localities substantiates the possible synonymy. Furthermore, *N. melas* Hesse, 1969 (based on male and female type specimens) and *N. brunneus* Hesse, 1969 (based on females only) are likely synonyms as both type series originate from the same collecting event at Inhaca Is. An identification key to species was provided by Hesse (1969).

Nothomydas **Hesse** (Syllegomydinae: Halterorchini)**.** An endemic genus (Figs 14, 78, 79) of four species, occurring in south-western Namibia and north-westernmost South Africa. Specimens have been collected from September–November. Sexual dimorphism is pronounced. The genus is distinguishable by the very long proboscis that extends beyond the tip of the antennal postpedicel and the bare anatergite and mediotergite (mesopostnotum). *Nothomydas* is placed together with *Halterorchis*, *Mimadelphus*, and *Namibimydas* in the tribe Halterorchini. The genus was last revised by Dikow (2012), who provided an identification key to species.

Notosyllegomydas **Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 80, 81) with the single species, *N. brincki* (Bequaert, 1959), occurring in north-westernmost Namibia in April. Sexual dimorphism is minimal. The genus is distinguishable by the short proboscis (distinct, but not extending beyond frontoclypeal suture), the long erect setae on the median surface of the hind tibia, the closed wing cell r_5 and the bare posterior anepisternum. This species was originally described in *Syllegomydas*



100 *Nothomydas* ♂

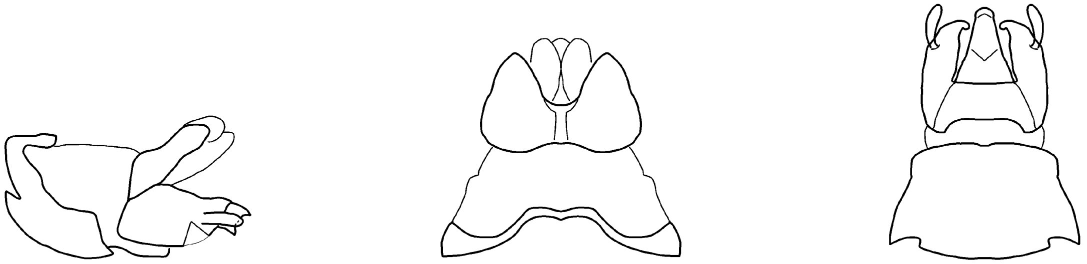


101 *Nothomydas* ♂

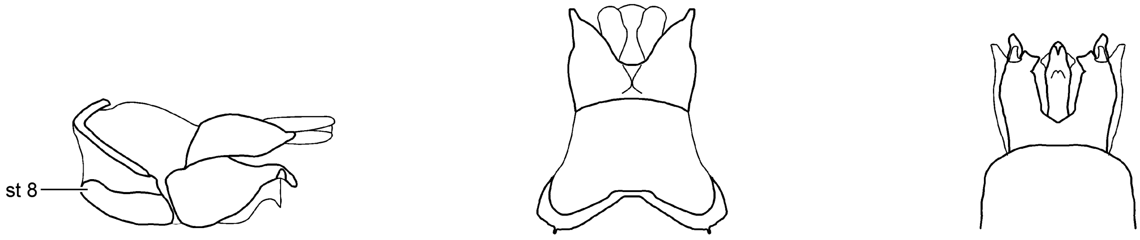
102 *Nothomydas* ♂

Figs 47.100–102. Male terminalia of Mydidae: (100) *Nothomydas picketti* Dikow, lateral view; (101) same, dorsal view; (102) same, ventral view. Figs 100–102 (Dikow 2012, figs 32–34).

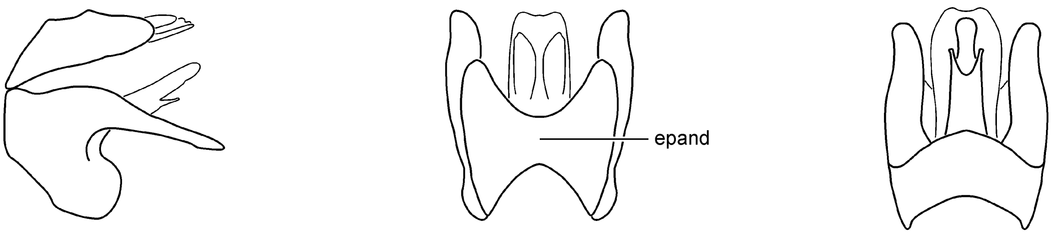
Abbreviations: ej apod – ejaculatory apodeme; endoph – endophallus; epand – epandrium; goncx-hypd cplx – gonocoxal-hypandrial complex; ph ep – phallic epimere; ph prg – phallic prongs; pm sh – parameral sheath; sphypd sc – supra-hypandrial sclerite; st – sternite; tg – tergite.



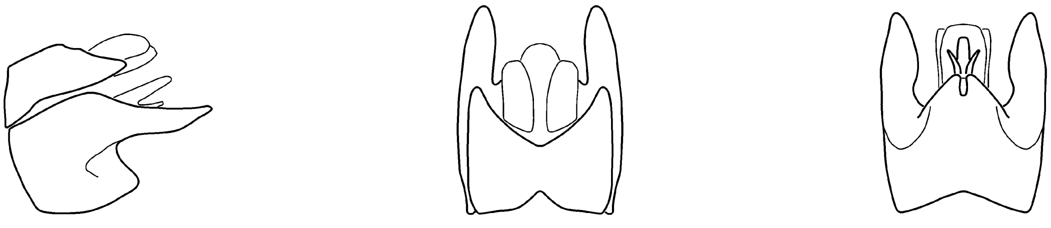
103 *Ectyphus* ♂ 104 *Ectyphus* ♂ 105 *Ectyphus* ♂



106 *Parectyphus* ♂ 107 *Parectyphus* ♂ 108 *Parectyphus* ♂



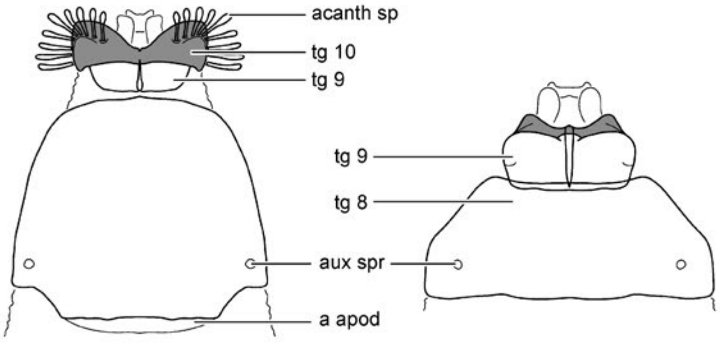
109 *Syllegomydas* (*Syllegomydas*) ♂ 110 *Syllegomydas* (*Syllegomydas*) ♂ 111 *Syllegomydas* (*Syllegomydas*) ♂



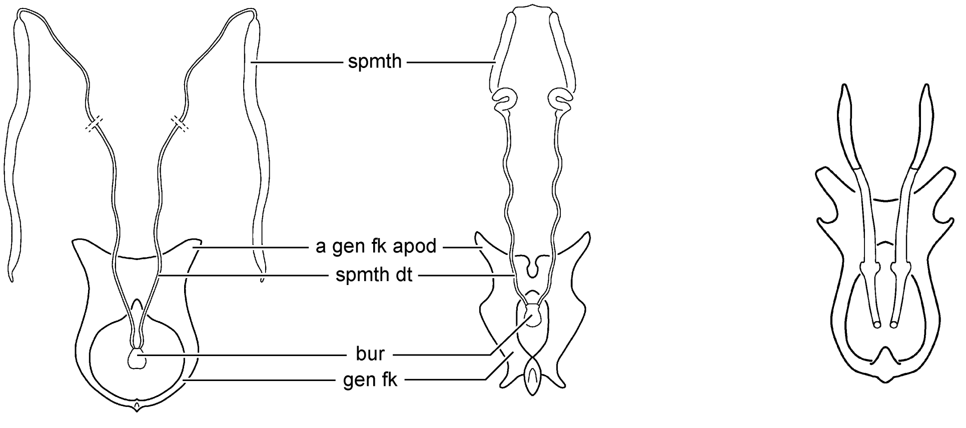
112 *Syllegomydas* (*Syllegomydas*) ♂ 113 *Syllegomydas* (*Syllegomydas*) ♂ 114 *Syllegomydas* (*Syllegomydas*) ♂

Figs 47.103–114. Male terminalia of Mydidae: (103) *Ectyphus pinguis* Gerstaecker, lateral view; (104) same, dorsal view; (105) same, ventral view; (106) *Parectyphus namibiensis* Hesse, lateral view; (107) same, dorsal view; (108) same, ventral view; (109) *Syllegomydas* (*Syllegomydas*) *astrictus* Dikow, lateral view; (110) same, dorsal view; (111) same, ventral view; (112) *S.* (*S.*) *dispar* (Loew), lateral view; (113) same, dorsal view; (114) same, ventral view. Figs 103–108 (Lyons & Dikow 2010, figs 29–22, 26–28), Figs 109–114 (Dikow 2010*a*, figs 21–23, 27–29).

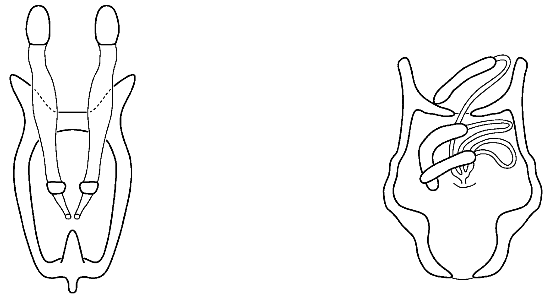
Abbreviations: epand – epandrium; st – sternite.



115 *Leptomydas* ♀ 116 *Vespiodes* ♀



117 *Namibimydas* ♀ 118 *Nothomydas* ♀ 119 *Mydaselpis* ♀



120 *Syllegomydas* ♀ 121 *Parectyphus* ♀

Figs 47.115–121. Female external and internal terminalia of Mydidae (dorsal views): (115) *Leptomydas lusitanicus* (Wiedemann) (non-Afrotropical); (116) *Vespiodes phaios* Dikow (tergite 10 indicated in grey); (117) *Namibimydas gaerdesi* Hesse; (118) *Nothomydas namaquensis* Hesse; (119) *Mydaselpis ngurumani* Dikow; (120) *Syllegomydas* (*Notobates*) *heothinos* Dikow; (121) *Parectyphus namibiensis* Hesse. Figs 117, 118 (Dikow 2012, figs 21, 22), Figs 119, 120 (Dikow 2010*a*, figs 19, 20); Fig. 121 (Lyons & Dikow 2010, fig. 30).

Abbreviations: a apod – anterior apodeme; bur – bursa; a gen fk apod – anterior genital fork apodeme; acanth sp – acanthophorite spine; aux spr – auxiliary spiracle; gen fk – genital fork; spmth – spermatheca; spmth dt – spermathecal duct; tg – tergite.

and later transferred to a new genus by Hesse (1969), which he based solely on literature study, without having studied the type specimens. *Notosyllegomydas brincki* can, however, be easily distinguished from *Syllegomydas*, based on the bare posterior anepisternum and the long setose median hind tibia.

Oreomydas **Hesse** (Syllegomydinae: Syllegomydini)**.** An endemic genus (Figs 82, 83) with the single described species, *O. luctuosus* (Bezzi, 1924), known from the two type specimens only, collected on the Matroosberg at an elevation of 1,200 m in south-western South Africa. Specimens have been collected in January. Sexual dimorphism is minimal. The genus is distinguishable by the setose katatergite and anatergite, the bare mediotergite (mesopostnotum), and an expanded metathoracic femur. Both, Bezzi (1924) and Hesse (1969) mention several differences to *Afroleptomydas* species, such as the less setose anepisternum, anepimeron and katatergite and shorter antennae. In addition, the mediotergite (mesopostnotum) is bare in *Oreomydas*, which distinguishes it from *Afroleptomydas* and *Syllegomydas*.

Parectyphus **Hesse** (Ectyphinae)**.** An endemic genus (Figs 18, 84, 85) with the single described species, *P. namibiensis* Hesse, 1972, occurring in Namibia and north-westernmost South Africa. Specimens have been collected from June–September. Sexual dimorphism is minimal. The genus is distinguishable by the bare katatergite, the setose anatergite, the closed wing cell r_4, presence of vein M_{3+4}, which terminates in the costal vein (*C*) and presence of a stump vein (R_3) connecting veins R_2 and R_4. The genus was last revised by Lyons & Dikow (2010).

Perissocerus **Gerstaecker** (Rhopaliinae)**.** A genus of seven species, occurring primarily in the Palaearctic Region, with three species found in the Afrotropics (Figs 7, 86, 87). The most widespread Afrotropical species, *P. arabicus* (Bequaert, 1961),

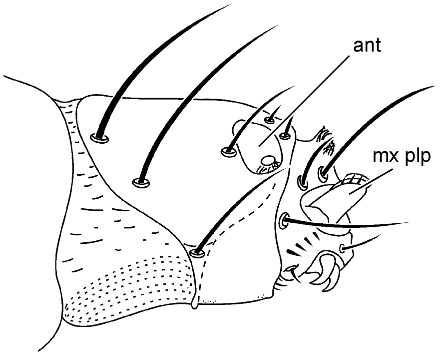
122 (?) *Syllegomydas*

123 (?) *Syllegomydas*

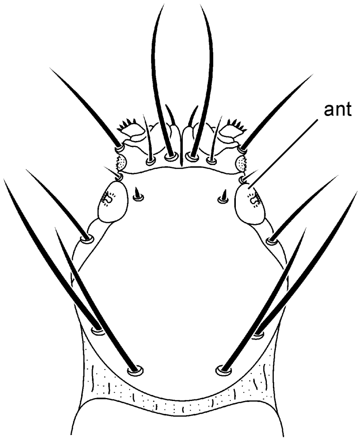
124 (?) *Syllegomydas*

Figs 47.122–124. Third-instar larva of Mydidae (Syllegomydinae) (note sand particles attached to larval cuticle): (122) larval habitus of (?) *Syllegomydas* sp., dorsal view; (123) same, lateral view; (124) same, ventral view.

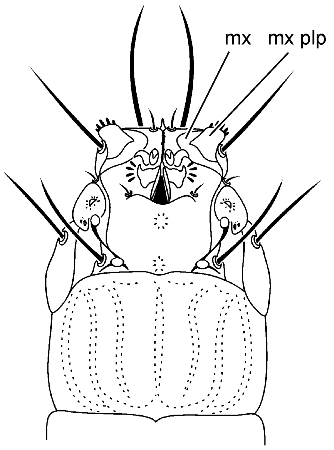
occurs in the United Arab Emirates and Yemen (Dikow 2010*b*: 612). The type species *P. abyssinicus* Gerstaecker, 1868 remains known only from the type specimen from "Abyssinia" [= Ethiopia] and *P. dumonti* Séguy, 1928, an otherwise Palaearctic species, has been recorded from the Tibesti Mountains in north-western Chad. Afrotropical species have been collected in October–November. Sexual dimorphism is pronounced. The genus is distinguishable by the minute proboscis, the bare katatergite, the open wing cell r_4 and the peculiar shape of the antennal postpedicel. These small flies are very rarely collected and a taxonomic revision is required. No identification key to Afrotropical species is available.



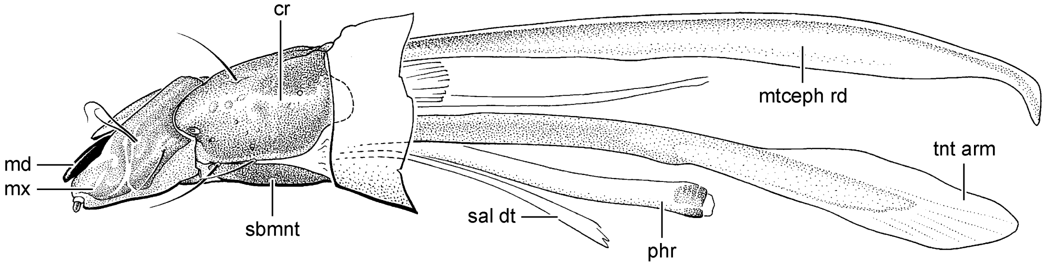
125 *Tongamya*



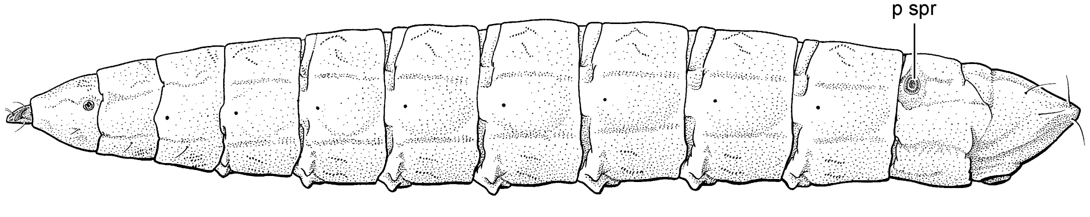
126 *Tongamya*



127 *Tongamya*



128 *Mydas*



129 *Mydas*

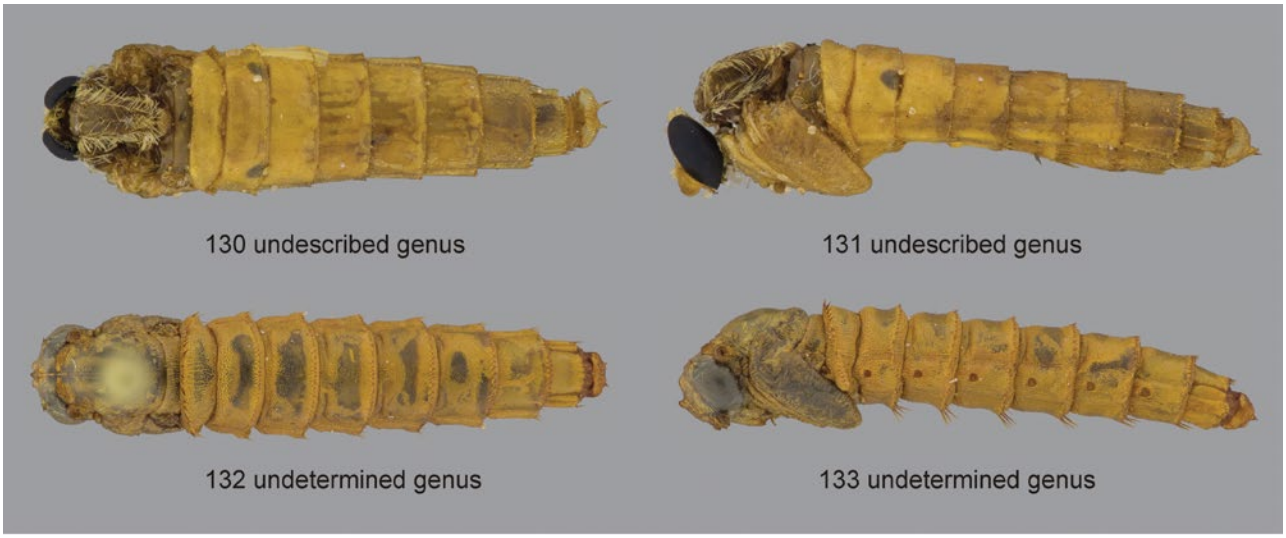
Figs 47.125–129. Larval features of first- and third-instar larvae of Mydidae: (125) head of first-instar larva of *Tongamya miranda* Stuckenberg, lateral view; (126) same, dorsal view; (127) same, ventral view; (128) head capsule and internal structures of third-instar larva of *Mydas clavatus* (Drury) (non-Afrotropical); (129) same, larval habitus of third-instar larva. Figs 125–127 (after Irwin & Stuckenberg 1972, figs 19–21), Figs 128, 129 (Wilcox 1981, figs 28, 29).

Abbreviations: ant – antenna; cr – cranium; md – mandible; mtceph rd – metacephalic rod; mx – maxilla; mx plp – maxillary palpus; phr – pharynx; p spr – posterior spiracle; sal dt – salivary duct; sbmnt – submentum; tnt arm – tentorial arm.

***Rhopalia* Macquart** (Rhopaliinae)**.** A genus of 15 species, occurring primarily in the Palaearctic Region, with three species found in the Afrotropics (Figs 8, 88, 89). Two species, *R. gyps* Bowden, 1987 and *R. olivieri* Macquart, 1838, are recorded from United Arab Emirates in the Arabian Peninsula (Deeming 2008: 602; Dikow 2010*b*: 612) and *R. tutankhameni* is known from eastern Sudan. Afrotropical specimens have been collected from March–May. Sexual dimorphism is minimal. The genus is distinguishable by the long proboscis that extends beyond the frontoclypeal suture, the bare katatergite, the open wing cell r_4 and the long cylindrical antennal postpedicel. Bowden (1980: 326) ascribed *R. tutankhameni* to *Leptomydas*, but the species belongs to *Rhopalia*, based on the unique wing venation of Rhopaliinae (vein R_5 ending in costal vein (*C*) and cell r_4 open). The two Afrotropical species occurring in the Arabian Peninsula can be identified by reference to Dikow (2010*b*).

***Syllegomydas* Becker** (Syllegomydinae: Syllegomydini)**.** A genus of 26 species, occurring primarily in the south-western Palaearctic Region (Mediterranean), with ten species recorded from the Afrotropics (Figs 9, 19, 90–95). Two Palaearctic species, *S. dallonii* Séguy, 1936 and *S. vittatus* (Wiedemann, 1828), penetrate the far northern Afrotropical Region in Chad and Sudan, respectively. The remaining eight species are endemic to the region and are distributed throughout sub-Saharan Africa and in particular in Eastern Africa. Specimens have been collected from May–August and from September–December (with a single record for March in Sudan). Sexual dimorphism is pronounced. The genus is distinguishable by the minute to short proboscis (never extending beyond the frontoclypeal suture), the closed wing cell r_5 (a few specimens with a narrowly open cell and a single undescribed species from western South Africa with widely open cell r_5) and the setose katatergite, posterior anepisternum and mediotergite (mesopostnotum). *Afroleptomydas* and *Syllegomydas* can be distinguished by the length of the proboscis and cell r_5, but the undescribed species from the Atlantic coast of South Africa exhibits a minute proboscis, as *Syllegomydas* and an open cell r_5, as in *Afroleptomydas*. Hesse (1969) distinguished two subgenera, *Syllegomydas sensu stricto* (five Afrotropical species) and *S.* (*Notobates* Hesse), the latter being endemic to the Afrotropics. Currently, there are four species placed in *S.* (*Notobates*) (Dikow 2010*a*; Hesse 1969) and *S. lamborni* Bequaert, 1951 should also be placed here. The placement of *S.* (*N.*) *dispar* (Loew, 1852) from Mozambique, which was listed as unplaced by Bowden (1980: 333), has been addressed by Dikow (2010*a*), who also provided the latest treatment of the genus. An undescribed species from the Namib Desert, Namibia and north-western South Africa, known only from three female specimens is the largest Afrotropical Mydidae with a wing length of 22 mm. A key to all species is unavailable, but species can be identified by reference to Hesse (1969) and Dikow (2010*a*).

***Tongamya* Stuckenberg** (Megascelinae)**.** An endemic genus (Figs 10, 11, 96, 97) of two species, *T. miranda* Stuckenberg, 1966 and *T. stuckenbergi* Irwin & Wiegmann, 2001, occurring in Angola, Botswana, Mozambique, Namibia and South Africa (Irwin & Wiegmann 2001), but only known from a few scattered collecting localities. Specimens have been collected from October–January (a record in April exists from Angola). Sexual dimorphism is pronounced and females are considerably larger than males. The genus is distinguishable by the antennal postpedicel composed of a single clubbed segment, the absence of mystacal (facial) setae and bullae on abdominal tergite 2, the peculiar wing venation and holoptic males. The genus was initially described in Apioceridae (Stuckenberg 1966) and later transferred to Mydidae by Yeates & Irwin (1996). This morphologically unique taxon is phylogenetically related to *Megascelus* Philippi from Chile and *Neorhaphiomidas* Norris from Australia, which represents a true Gondwanan radiation of the Megascelinae. Species of *Tongamya* are extremely rarely collected, but can be abundant at the right locality and time



Figs 47.130–133. Pupal habitus of Mydidae: (130) undescribed genus (Namib Desert, Namibia) with adult head and thorax partially extruded, dorsal view; (131) same, lateral view; (132) undetermined genus (possibly *Afroleptomydas* Bequaert, *Cephalocerodes* Hesse or *Namadytes* Hesse), dorsal view; (133) same, lateral view.

of year and were originally described from north-easternmost KwaZulu-Natal Province of South Africa (Stuckenberg 1966) and northern Namibia (Irwin & Wiegmann 2001). The genus might be more widespread and new populations or species might be encountered when suitable habitat is visited during the right time of the year. The two species can be identified by reference to Irwin & Wiegmann (2001).

***Vespiodes* Hesse** (Syllegomydinae: Mydaselpidini)**.** An endemic genus (Figs 15, 98, 99) of ten species, occurring throughout sub-Saharan Africa (Ghana to Kenya to northern South Africa), but with few collecting events. It is the only Mydidae genus known to date to occur in the tropical rainforests of central Africa. Specimens have been collected from February–May and from September–November. Sexual dimorphism is minimal. The genus is distinguishable by the bare posterior anepisternum, anepimeron and katepimeron, the punctate abdominal tergites, the constricted abdominal tergites 2–3 (exhibiting a "wasp waist"), females without acanthophorite spines and males with a distally simple phallic epimere. The majority of species are only known from one sex and several species exhibit mimetic colouration resembling various wasp taxa. *Vespiodes* is placed together with *Afromydas* and *Mydaselpis* in the Mydaselpidini (see *Afromydas* above). The genus may represent a junior synonym of *Mydaselpis* (see under that genus). A key to species was provided by Hesse (1969).

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ASILIDAE 48

(Assassin Flies or Robber Flies)

Jason G.H. Londt and Torsten Dikow

Fig. 48.1. Female of *Promachus* sp. with hymenopteran prey (Zambia) (photograph © R. Felix).

Diagnosis

Small- to very large-sized flies (body length: 4–65 mm; wing length: 4–40 mm) (Figs 101, 185), that are predatory, capturing insects on the wing, and to a lesser extent, resting insects or spiders.

Asilidae can be diagnosed as follows: labellum of proboscis fused to prementum at least ventrally; hypopharynx heavily sclerotised, with dorsal seta-like spicules; labrum short, at most ½ as long as labium; cibarium trapezoidal; vertex usually depressed (Figs 72, 73); postpronotal lobes fused to scutum (Figs 164, 184), extending medially; face with mystax (Fig. 1), usually macrosetose (Fig. 46), but sometimes only composed of setae near lower facial margin (Fig. 200); antenna positioned in dorsal ½ of head (Fig. 46); fore- and mid coxa positioned close together; legs virtually originating at same level to capture and hold prey (Fig. 46); metakatepisternum usually small (Fig. 46), except in Laphriinae (Fig. 162), not visible between mid and hind coxa.

Head dichoptic in both sexes; face usually protruding to some extent, forming facial swelling (Fig. 1), but in several taxa entirely plane (Fig. 200); face with mystacal macrosetae

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1097–1182.

forming mystax (Fig. 1), which varies in extent from only covering lower facial margin (Fig. 200) to entire face (Fig. 46); frons predominantly parallel-sided (Fig. 80), but strongly divergent in a few taxa (Fig. 81); vertex slightly (Fig. 70) to considerably depressed (Figs 72, 80); all 3 ocelli circular, placed on single ocellar triangle (Fig. 74); antenna positioned in dorsal ½ of head (Fig. 46); antennal scapes separated proximally; postpedicel of varying length and shape (Figs 34, 46, 58, 66); stylus of

Figs 48.2–7. Photographs of living Asilidae (Asilinae): (2) *Alcimus* sp. ♂ (Zambia); (3) same ♀; (4) *Apoclea inarticulata* Theodor ♂ (United Arab Emirates); (5) *Apoclea* sp. ♀ (United Arab Emirates); (6) *Congomochtherus penicillatus* (Speiser) ♂ (Tanzania); (7) *Dasophrys androclea* (Walker) ♀ (South Africa). Figs 2, 3 (photographs © R. Felix), Figs 4, 5 (photographs © H. Roberts), Fig. 6 (photograph © S.A. Marshall), Fig. 7 (photograph © J.G.H. Londt).

varying development, shape and position, often composed of 1 or 2 cylindrical or rod-like articles, plus seta-like sensory article distally (*e.g.*, Asilinae, Fig. 1; Brachyrhopalinae, Fig. 18; Leptogastrinae, Fig. 42; Ommatiinae, Fig. 46; Stenopogoninae, Fig. 54; Stichopogoninae, Fig. 58; Tillobromatinae, Fig. 61; and Willistonininae, Fig. 66), or stylus reduced, only seta-like sensory article present and positioned in cavity on postpedicel (*e.g.*, Laphriinae, Fig. 33); proboscis well-developed and strong, usually straight, extending beyond frontoclypeal suture (Fig. 46), single genus (*Ancylorhynchus* Berthold), with posteriorly curved proboscis resembling parrot's beak (Fig. 110); labellum small, fused to prementum at least ventrally, usually entirely fused; palpus 1- or 2-segmented, usually small, cylindrical, sometimes laterally compressed and prominent, often setose.

Thorax with postpronotal lobe entirely fused to scutum (Figs 164, 184), extending medially; cervical sclerite flat; prosternum dorsal margin with or without flange-like projection; prosternum either fused to or separated laterally from proepisternum; proepisternum fused to lateral postpronotum, setulose, sometimes macrosetose; antepronotum usually bare, sometimes setose and rarely macrosetose; postpronotum usually setose, sometimes macrosetose; anterior proepimeron, anterior anepisternum, anterior and posterior basalare usually setose, sometimes macrosetose (Fig. 1); posterior anepisternum, anepimeron and anatergite setose or bare (Fig. 1); several taxa with at least 1 macroseta on superoposterior angle of anepisternum; katatergite setose or macrosetose, usually elevated and convex; metakatepisternum usually small (Fig. 46), in Laphriinae, large and visible between mid- and hind coxa (Fig. 162); scutum usually smooth, sometimes punctate; dorsocentral setae of varying length and development pre- and postsuturally (Figs 1, 61); acrostichal setae usually present presuturally; several genera with scutal mane (Figs 10, 11, 194), composed of dense setae between rows of acrostichal and dorsocentral setae; notopleural, supra-alar and postalar setae usually present (Figs 1, 46, 58). Scutellum large; mediotergite (mesopostnotum) not visible in dorsal view (Fig. 201); apical and discal scutellar macrosetae absent (Fig. 200) or present (Figs 1, 142, 144). Legs with hind coxa setose or macrosetose laterally (Fig. 1); hind coxa in a few taxa with anterior peg-like process; median hind trochanter setose, sometimes expanded medially and macrosetose; femur usually cylindrical (Figs 1, 46) to at least slightly expanded distally (Figs 22, 40), one genus with greatly expanded fore femur (Fig. 52) and several genera with distinctly clubbed hind femur (Figs 34, 146, 228), sometimes with ventrodistal macrosetae mounted on tubercles; hind tibia usually straight, sometimes arched medially; proximal tarsomere as long as (Fig. 18) or sometimes longer than tarsomeres 2–3 combined (Fig. 200); pulvillus usually well-developed (Fig. 1), with two dorsal ridges, entirely reduced in several genera (Figs 25, 45, 66), or less commonly to small lobe visible at base of claw; setiform empodium usually present, sometimes reduced in length and rarely laterally compressed. Wing membrane usually hyaline (Fig. 195), sometimes darkened through brown staining (Figs 145, 159, 211), or patterned through white and brown staining (Figs 123, 157); membrane with microtrichia in many taxa, often covering entire or almost entire wing (Fig. 137) or with specific pattern; cell r_1 open (Figs 189, 199) or closed (Figs 83, 84, 145), when closed either by stalk (Fig. 145) or R_1 and R_{2+3} joining at point where they meet costal vein (*C*) (Figs 83, 233); cell r_4 open (Figs 83, 84, 145, 199); cell r_5 usually open (Figs 84, 145, 199), but often closed with stalk (Figs 83, 107, 233); cell m_3 open (Fig. 199) or closed (Figs 83, 84, 145); cell *cua* open (Fig. 199) or closed (Fig 83, 84); costal vein (*C*) usually circumambient (Figs 83, 84, 145, 199), sometimes terminating at veins *CuP* or *CuA+CuP* (Fig. 223) and even further anteriorly at vein R_4 (Fig. 221); auxiliary vein usually absent (Fig. 199), sometimes appearing as short stump vein on vein R_4 (Figs 85, 113, 223), in 4 genera long, connecting veins R_{2+3} and R_4 (Figs 84, 99, 201, 203); veins M_1 and M_2 never fused (Figs 83, 84, 199); alula usually well-developed (Figs 83, 84, 123), reduced in size in several genera (Fig. 197) and entirely reduced in a few genera (Fig. 171).

Abdomen elongate, parallel-sided (Fig. 201), sometimes slightly tapering distally (Fig. 203), or constricted between tergites 2–3 or 2–4 (Figs 145, 199), or dorsoventrally flattened (Figs 86, 88, 222); tergite 2 usually wider than long (Figs 145, 157, 199, 203), several genera with tergite 2 more than 5 × as long as wide (Fig. 172); abdominal tergites without anterodorsal apodemes; male and female tergites 1–8 well-developed; male and female sternites 1–8 usually well-developed and simple; tergites with (Figs 201, 227) or without lateral macrosetae (Fig. 199); male terminalia usually straight (Fig. 194), but often rotated up to 180° (Fig. 164); epandrium either separated and joined proximally (Figs 247, 278, 295), separated, not joined proximally (Fig. 285), or fused entirely medially (Figs 265, 273); hypandrium usually well-developed and distinct (Figs 240, 259, 278, 284, 292, 310), often reduced to varying degree (Fig. 271) or fused to gonocoxite forming gonocoxite + hypandrial complex (Figs 268, 275, 281, 197); gonocoxite of varying shape, often with species-specific characters (Figs 259, 262, 269, 287, 310); gonocoxal apodeme usually absent, sometimes present, either short or long; gonostylus of varying shape, often with species-specific characters (Figs 248, 261, 263, 269, 310); subepandrial sclerite usually without setae or protuberances; lateral ejaculatory apodeme present; 1–3 phallic prongs, usually short, sometimes long; female terminalia with tergite 8 usually simple, sometimes with anterior transverse apodeme (Fig. 306); ovipositor usually consisting of segment 8 and following segments (Figs 23, 53), but sometimes involving segment 5 or 6 and following segments; ovipositor for direct sand or soil oviposition, with tergite 10 divided into 2 acanthophorite plates with acanthophorite spines (Figs 22, 23, 53, 56–58, 136, 306), a few genera with strong macrosetae on cercus for sand or soil oviposition, ovipositor for other types of oviposition, such as egg-dropping, simple (Figs 42, 45), for placing eggs in vegetation often knife-like in taxon-specific arrangements of sclerites (Figs 7, 17, 252, 254), for placing eggs in decaying wood, simple (Fig. 37); either 2 or 3 equally large, poorly- to well-sclerotised spermathecae present, sometimes median spermatheca larger or smaller than lateral ones; genital fork usually either ring-like (joined anteriorly and posteriorly) or inverted U-shaped (joined anteriorly, separated posteriorly), anterior and lateral genital fork apodemes usually present.

Larva (*e.g.*, Figs 312–319) robust with 11 apparent segments, with small, partly retractable head capsule (Figs 312, 313); head dorso-ventrally flattened; maxilla dorso-ventrally flattened, divided into proximal part and movable distal part (Fig. 314); maxillary palpus inserted sub-apically (Fig. 314); mandibles pointed, stylet-like, not extending to apex of maxilla (Fig. 314); labrum pointed; submentum forming ventral plate; abdominal

Figs 48.8–13. Photographs of living Asilidae (Asilinae): (8) *Eremisca heleni* (Efflatoun) ♂ (left) and ♀ (right) *in copula* (United Arab Emirates); (9) *Melouromyia natalensis* (Ricardo) ♂ (South Africa); (10) *Neolophonotus* sp. ♂ (South Africa); (11) same; (12) *N. abuntius* (Walker) ♂ with heteropteran prey (South Africa); (13) *Philodicus* sp. ♂ with cicindelid prey (Namibia). Fig. 8 (photograph © H. Roberts), Fig. 9 (photograph © J.G.H. Londt), Figs 10, 11, 13 (photographs © S.A. Marshall), Fig. 12 (photograph © B. Londt).

segments 1–6 sometimes (Laphriinae) with contractile protuberances dorsally and laterally and proleg-like protuberances ventrally (Fig. 313) otherwise smooth (Fig. 312); posterior spiracle on apparent penultimate abdominal segment (Figs 312, 313); the caudal abdominal segment often appears partly divided and difficult to distinguish subdivision; apex of abdomen with taxon-specific sclerotised (hook-like) appendages.

Pupa (*e.g.*, Figs 320–323) robust with appendages movable (exarate); head with 2 pairs of antennal processes; abdominal segments 1–7 with row of posteroventrally-oriented processes dorsally; segment 9 with caudally-oriented terminal processes.

Asilidae are very distinct and should not be confused in the field with most Asiloidea. The three rarely collected species of the closely related Apioceridae (see Chapter 46) superficially resemble ground-perching robber flies, but their non-predacious proboscis, short antennae and peculiar wing venation easily differentiate them from Asilidae. In addition, Afrotropical *Apiocera* Westwood species run over the surface on slender legs and do not sit or perch. Some Mydidae (see Chapter 47) could also be confused with certain Asilidae species, but, likewise, the non-predacious proboscis, as well as long antennae, peculiar wing venation and resting position on the ground with the body almost touching the surface are unlike most assassin flies.

Biology and immature stages

An ecological classification has been attempted, based on observations of Afrotropical species and the structure of their ovipositor (Londt 1994*c*). Most of the information available is that recorded on specimen labels and in taxonomic literature. However, an analysis of 26 years of data from the semi-arid Karoo near Willowmore (Eastern Cape Province, South Africa) (Londt 1998*a*) and a year-long survey undertaken in a single mixed seasonal grassland habitat (KwaZulu-Natal Province, South Africa) (Londt 2002*c*) have been conducted. Dikow *et al*. (2009: 327) compared the species richness and endemicity of Asilidae in biodiversity hotspots, wilderness areas and comparable areas in the Afrotropical Region and concluded that the hotspots and wilderness areas *sensu* Conservation International (Mittermeier *et al*. 2003; Myers 2003), harbour more Asilidae species than comparable areas outside.

Figs 48.14–17. Photographs of living Asilidae (Asilinae): (14) *Promachus* sp. ♀ with asilid prey (*Microstylum* sp. ♂) (Namibia); (15) same ♂ (left) and ♀ (right) *in copula* (Namibia); (16) same ♀ (South Africa); (17) *Synolcus dubius* (Macquart) ♀ (South Africa). Figs 14, 15 (photographs © S.A. Marshall), Figs 16, 17 (photographs © J.G.H. Londt).

Dennis *et al*. (2013) summarised known information on the biology and morphology of immature stages. Oviposition commonly involves random egg-dropping, introduction of eggs directly into the ground (the ovipositors of those species involved usually being equipped with strong setae or spines with which to dig), or eggs are deposited into suitable crevices in plant material or pasted between leaves (females frequently being equipped with elongate, knife-like ovipositors). While studies


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Figs 48.18–23. Photographs of living Asilidae (Brachyrhopalinae and Dasypogoninae): (18) *Afroholopogon capensis* (Lindner) ♀ (South Africa); (19) *Afroholopogon* sp. (South Africa); (20) *Habropogon bussinowi* Bosák & Hradský ♂ (United Arab Emirates); (21) *Pegesimallus aulicus* (Wiedemann) ♀ (South Africa); (22) *Pegesimallus* sp., ovipositing in soil (South Africa); (23) same with isopteran prey (Zambia). Figs 18, 21 (photographs © J.G.H. Londt), Figs 19, 22 (photographs © S.A. Marshall), Fig. 20 (photograph © H. Roberts), Fig. 23 (photograph © R. Felix).

undertaken in other zoogeographical regions (e.g., Melin 1923; Musso 1978) reveal that larvae are predatory, feeding on subterranean invertebrates, very little detailed biological information exists. Assassin fly larvae most probably live in soil or in burrows in wood, but knowledge of Afrotropical species is largely confined to isolated descriptions of eggs, larvae and pupae. Some of the better known contributions are those of Engel (1929: larva and pupa of *Hyperechia* Schiner), Engel (1932: immatures of *Proagonistes* Loew), Engel & Cuthbertson (1934: immatures of *Alcimus* Loew and *Hyperechia*), Engel & Cuthbertson (1939: immatures of *Neolophonotus* Engel and *Promachus* Loew), Londt & Harris (1987: larvae of *Millenarius*

Figs 48.24–29. Photographs of living Asilidae (*incertae sedis* and Laphriinae): (24) *Oligopogon penicillatus* Loew ♂ (South Africa); (25) *Anypodetus* sp. ♂ (Namibia); (26) *A. fasciatus* Hermann ♀ (Namibia); (27) *Choerades* sp. ♂ (South Africa); (28) *Goneccalypsis* sp. ♂ (Tanzania); (29) *Hoplistomerus nobilis* Loew ♀ (South Africa). Figs 24, 26, 29 (photographs © T. Dikow), Figs 25, 27, 28 (photographs © S.A. Marshall).


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Figs 48.30–35. Photographs of living Asilidae (Laphriinae): (30) *Lamyra vorax* Loew ♀ with buprestid prey (Oman); (31) *Laphyctis* sp. ♂ (Namibia); (32) *Laxenecera albicincta* (Loew) ♂ (left) and ♀ (right) *in copula* (South Africa); (33) *Notiolaphria coerulescens* (Macquart) ♀ (Madagascar); (34) same ♂ (Mauritius); (35) *Nusa infumata* (Loew) ♂ with lepidopteran prey (Tanzania). Fig. 30 (photograph © M. Borer), Fig. 31 (photograph © T. Dikow), Fig. 32 (photograph © J.G.H. Londt), Figs 33, 35 (photographs © S.A. Marshall), Fig. 34 (photograph © D. Martiré).

dichaetus (Hull, 1967) (Figs 318–319) and Londt (1991: eggs and larvae of *Damalis femoralis* Ricardo, 1925).

Adult flies are predators, feeding exclusively on living prey, most frequently caught in flight, but sometimes actively hunting resting prey (*e.g.*, Leptogastrinae). The proboscis and internal sucking pump (cibarium) are well-developed for this purpose and harbour all of the morphological autapomorphies (see diagnosis, Dikow 2009*a*). Although there is scattered information concerning prey taken by assassin flies, Londt (1987*a*: 44, 2006*b*) summarises what is known regarding adult feeding in general. Predation of honeybees in particular (Londt 1993*a*) and Lepidoptera in general (Londt 1999*c*), have received attention, as well as the predation of robber flies by other robber flies (Fig. 14) (Londt 1995). In most instances, a broad range of prey is taken (Figs 1, 13, 23, 30, 35, 42, 43, 54, 55, 58, 60), but a few species appear to specialise (*e.g.*, *Hoplistomerus nobilis* Loew, 1858 (Fig. 29), primarily perches on large mammal dung and feeds almost exclusively on small dung beetles).

Male and female flies of the same species are morphologically identical (except the structures pertaining to the terminalia) (Figs 187–190), with females sometimes slightly larger (Figs 85–88). Only in very few Afrotropical species, *e.g.*, *Dasypletis vespertilio* (Engel, 1932) (Fig. 49) (Londt 2010*a*) and *Laxenecera albicincta* (Loew, 1852) (Fig. 32), is distinct sexual dimorphism evident. For the latter species, this dimorphism led to the description of the male and female as different species, *i.e.*, *L. albicincta* and *L. zonata* Loew, 1860, respectively. Males of several *Pegesimallus* Loew species exhibit long, laterally compressed setae on the mid and hind tibiae and tarsi, giving them a "feathered" appearance, which led to the description of the genus *Lagodias* Loew and only later was it found to be an exclusively male, sexually dimorphous character (Oldroyd 1974). Females and males of other species, *e.g.*, *Acnephalomyia* Londt species (Figs 85–88), exhibit some sexual dimorphism, but the sexes can be assigned to the correct species despite such differences.

Mating takes place in taxon-specific positions and involves, e.g., standing tail-to-tail (Figs 15, 32, 55), perching tail-to-tail (Fig. 63), or standing on top of each other (Fig. 59).

Economic significance

No species of Asilidae are known to have economic significance. Assassin flies, however, can have an effect on populations of their prey insects and spiders, including honeybees (Londt 1993*a*). As predatory flies, Asilidae may be seen as indicative of environmental health, *i.e.*, greater numbers and diversity of robber flies may indicate good environmental health.

Classification

Asilidae is placed in the superfamily Asiloidea and is closely related to Apioceridae and Mydidae. Dikow (2009*a*) summarised the history of placements of Asilidae within Asiloidea and proposed that a clade (Apioceridae + Mydidae) is sister-group to Asilidae, based on both morphological (Dikow 2009*a*) and molecular data (Dikow 2009*b*). This set of relationships has also been supported by molecular analyses focusing on Asiloidea (Trautwein *et al*. 2010) and Diptera in general (Wiegmann *et al*. 2011).

Artigas & Papavero (1988), Geller-Grimm (2004), Hull (1962) and Papavero (1973) followed a traditional classification based on overall morphological similarity. Dikow (2009*a*) published the only phylogenetic classification of Asilidae to date, but did not provide an updated identification key to world subfamilies. While that study was unable to include all genera known at the time (528), only 127 genera (24%) could not be placed in the phylogenetic classification, including 25 Afrotropical genera. Since 2009, 13 Afrotropical genera have been described and along with the 25 previously unplaced genera are here placed within this most recent classification. No new phylogenetic analyses have been conducted, but genera are placed in one of the 11 subfamilies based on presence of synapomorphic character states.

Of the 14 subfamilies recognised globally (Dikow 2009*a*), 11 are represented in the Afrotropical Region. Only the Australasian and Neotropical Bathypogoninae and Phellinae, as well as the Australasian and Holarctic Dioctriinae are not found within the confines of the region. The most diverse subfamilies in terms of number of genera and species are the Asilinae (41 genera, 574 species), Laphriinae (33, 201), Stenopogoninae (22, 269) and Brachyrhopalinae (16, 101), while several subfamilies are only represented by a few genera, such as Dasypogoninae (3 genera, 57 species), Stichopogoninae (6, 26), Tillobromatinae (2, 27) and Trigonomiminae (2, 61).

The subfamily Asilinae is a megadiverse taxon in the Afrotropics, comprising 41 genera (183 genera globally), 26 of which are endemic and 574 species. This subfamily is global in distribution, except Antarctica. While most Afrotropical genera (29) include less than 10 species, *Promachus* (97 species) and *Neolophonotus* (254) are extremely diverse and can be encountered throughout the region, with *Neolophonotus* being particularly common in Southern Africa. Eleven endemic genera are monotypic and an additional nine have 2–4 species each. Asilinae was newly delineated by Dikow (2009*a*), who combined the Apocleinae and Asilinae *sensu* Artigas & Papavero (1988) and Geller-Grimm (2004) as Apocleinae was shown to be paraphyletic. The genus *Tolmerus* Loew still requires clarification in an Afrotropical context (see below).

The subfamily Brachyrhopalinae is a medium diverse taxon in the Afrotropics, comprising 16 genera (currently 32 genera globally), 13 of which are endemic and 101 species. The subfamily is distributed globally with the exception of the Oceanian Region and Antarctica. Thirteen Afrotropical genera have less than ten species, three endemic genera are monotypic and the endemic genera *Afroholopogon* Londt (19 species) and *Rhabdogaster* Loew (39) are relatively diverse. Brachyrhopalinae was elevated to subfamily status by Dikow (2009*a*) and includes genera previously assigned to Dasypogoninae and Stenopogoninae *sensu* Artigas & Papavero (1988) and Geller-Grimm (2004).

The subfamily Dasypogoninae is a very small taxon in the Afrotropics, comprising three genera (17 genera globally), one of which is endemic and monotypic and 57 species. This subfamily is global in distribution, except Antarctica. Dasypogoninae was newly delineated by Dikow (2009*a*) as the monophyly

Figs 48.36–41. Photographs of living Asilidae (Laphriinae): (36) *Proagonistes praeceps* (Walker) ♀ (South Africa); (37) *Proagonistes* sp. ♀ (Namibia); (38) *Prytanomyia kochi* (Lindner) ♀ (Namibia); (39) *Stiphrolamyra* sp. ♂ (United Arab Emirates); (40) *Trichardis picta* Hermann ♂ (Namibia); (41) *T. leucocomus* Wulp ♂ (United Arab Emirates). Fig. 36 (photograph © J.G.H. Londt), Fig. 37 (photograph © S.A. Marshall), Figs 38, 40 (photographs © T. Dikow), Figs 39, 41 (photograph © H. Roberts).

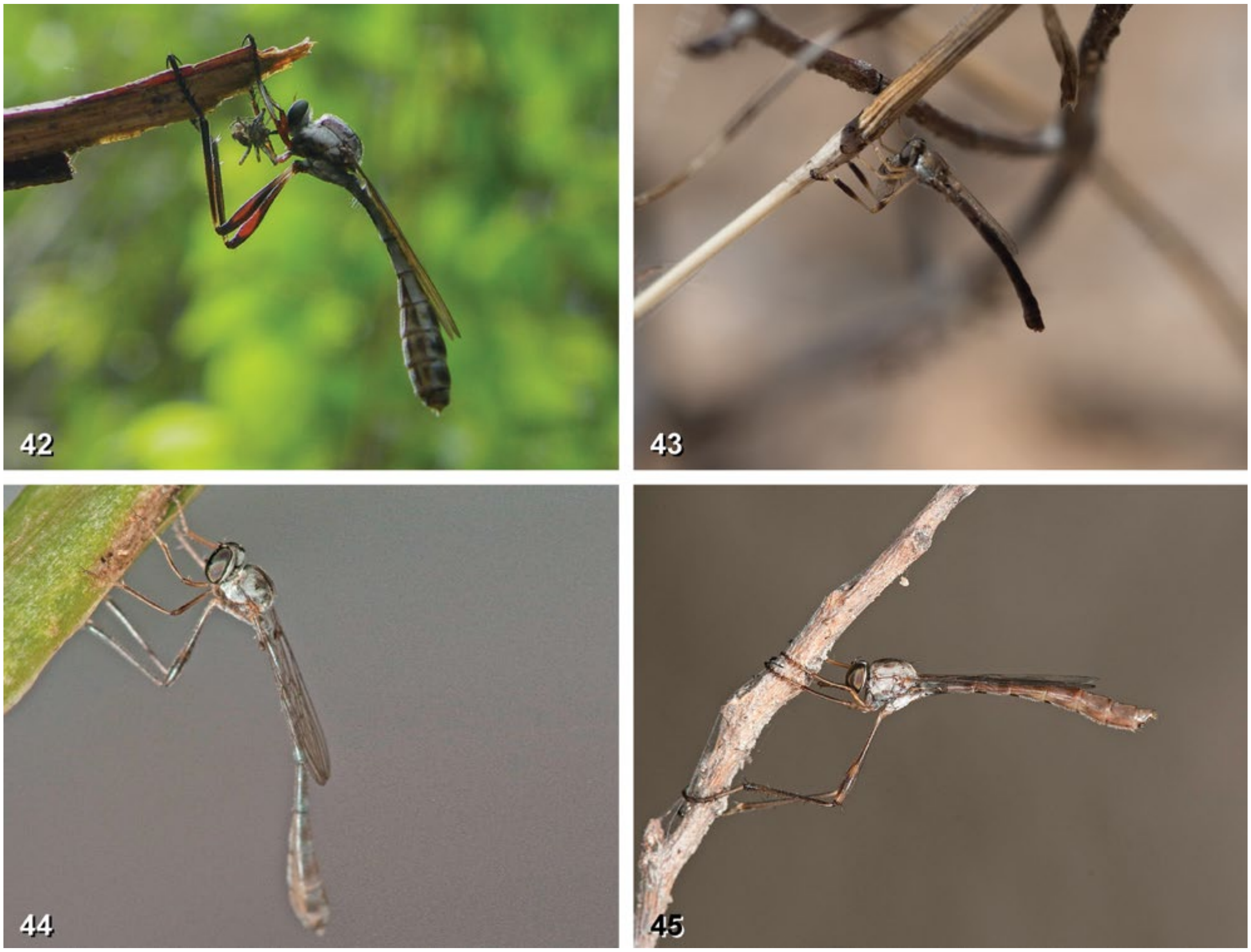
of the previous delineation *sensu* Geller-Grimm (2004) and Papavero (1973) could not be established and several genera were assigned to Brachyrhopalinae, none of which are Afrotropical.

The subfamily Laphriinae is a diverse taxon in the Afrotropics, comprising 33 genera (112 genera globally), 19 of which are endemic and 201 species. This subfamily is global in distribution, except Antarctica. Most genera (26) include less than 10 species and the majority of species are placed in four genera, each with 22–29 species. Laphriinae was newly delineated by Dikow (2009*a*), who combined the Laphriinae and Laphystiinae *sensu* Geller-Grimm (2004) and Papavero (1973) as Laphystiinae was shown to be paraphyletic.

The subfamily Leptogastrinae is a diverse taxon in the Afrotropics, comprising seven genera (18 genera globally), one of which is endemic and 150 species. This subfamily is almost global in distribution, being absent only from Chile, New Zealand and Antarctica. With the exception of *Lasiocnemus* Loew, all genera also occur outside the Afrotropical Region, primarily in the Old World, with *Schildia* Aldrich centred in the New World.

The subfamily Ommatiinae is a diverse taxon in the Afrotropics, comprising nine genera (13 genera globally), four of which are endemic and 132 species. This subfamily is global in distribution, except Antarctica. Three of the four endemic genera have between 1–3 species each, while *Afroestricus* Scarbrough has 21. Scarbrough (2010) published an identification key to Afrotropical genera and subgenera that has been adjusted and incorporated into the below key.

The subfamily Stenopogoninae is a highly diverse taxon in the Afrotropics, comprising 22 genera (currently 28 genera globally), 17 of which are endemic and 269 species. This subfamily is global in distribution, except Antarctica. Sixteen genera, 15 of which are endemic, have less than ten species and *Gonioscelis* Schiner with 40 species is the most diverse Afrotropical endemic. The global genus *Microstylum* Macquart



Figs 48.42–45. Photographs of living Asilidae (Leptogastrinae): (42) *Euscelidia* sp. ♀ with araneaen prey (South Africa); (43) *Leptogaster aganniphe* Janssens ♂ with dipteran prey (South Africa); (44) *Lobus* sp. ♀ (Tanzania); (45) *Mesoleptogaster* sp. ♀ (Namibia). Fig. 42 (photograph © J.G.H. Londt), Fig. 43 (photograph © T. Dikow), Figs 44, 45 (photographs © S.A. Marshall).

with 79 Afrotropical species is one of the most diverse taxa and occurs throughout the region. Stenopogoninae was newly delineated by Dikow (2009*a*), as the monophyly of the previous delineation *sensu* Artigas & Papavero (1988) and Geller-Grimm (2004) could not be established and genera are assigned to Bathypogoninae, Brachyrhopalinae (2 Afrotropical genera), Phellinae, Tillobromatinae (2) and Willistonininae (3).

The subfamily Stichopogoninae is a small taxon in the Afrotropics, comprising six genera (14 genera globally), one of which is endemic and 26 species. This subfamily is global in distribution, except Antarctica. Oldroyd (1963) included *Psilinus* Wulp and *Sporadothrix* Hermann in an identification key to the taxon. *Psilinus* is a synonym of *Rhabdogaster*, placed in Brachyrhopalinae and *Sporadothrix* is placed in Willistonininae. Bosák & Hradský (2011: 739) recorded two genera for the first time for the region.

The subfamily Tillobromatinae is a small taxon in the Afrotropics, comprising two endemic genera (three genera globally) and 27 species. Tillobromatinae only occurs in the Afrotropics, where it has its largest species diversity and in the Neotropics. Tillobromatinae was elevated to subfamily status by Dikow (2009*a*) and includes genera previously assigned to Stenopogoninae *sensu* Geller-Grimm (2004) and Papavero (1973).

The subfamily Trigonomiminae is a medium-sized taxon, comprising two Afrotropical genera (12 genera globally), one of which is endemic and 61 species. This subfamily has a global distribution, with the exception of the Oceanian Region and Antarctica. Oldroyd (1974) included *Oligopogon* Loew in an identification key to the taxon and in 1980 catalogued *Oligopogon* and *Oxynoton* Janssens in the tribe Xenomyzini (within Stenopogoninae at that time). *Oligopogon* is placed as *incertae sedis* here, following Dikow (2009*a*) and *Oxynoton* is placed in the subfamily Brachyrhopalinae.

The subfamily Willistonininae is a small taxon, comprising six Afrotropical genera (eight genera globally), five of which are endemic and 34 species. The subfamily is confined to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Figs 48.46–48. Photographs of living Asilidae (Ommatiinae): (46) *Cophinopoda pulchripes* (Bigot) ♀ (Réunion Is.); (47) *Ommatius* sp. ♂ (Tanzania); (48) same ♀ (United Arab Emirates). Fig. 46 (photograph © D. Martiré), Fig. 47 (photograph © S.A. Marshall), Fig. 48 (photograph © H. Roberts).


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Figs 48.49–54. Photographs of living Asilidae (Stenopogoninae): (49) *Daspletis vespertilio* (Engel) ♂ (South Africa); (50) *D. setithoracicus* (Ricardo) ♀ (South Africa); (51) *D. vulpes* Loew ♂ (South Africa); (52) *Gonioscelis* sp. ♂ (Namibia); (53) *Microstylum* sp. ♀ (South Africa); (54) same ♂ with coreid prey (South Africa). Figs 49, 54 (photographs © J.G.H. Londt), Figs 50, 52 (photographs © T. Dikow), Figs 51, 53 (photographs © S.A. Marshall).

Figs 48.55–60. Photographs of living Asilidae (Stenopogoninae and Stichopogoninae): (55) *Microstylum* sp. ♀ (left) and ♂ (right) *in copula*, ♀ with hymenopteran prey (Namibia); (56) *Scylaticus* sp. ♀ (South Africa); (57) *Rhadinus* sp. ♀ (United Arab Emirates); (58) *Stichopogon* sp. ♀ with coleopteran prey (South Africa); (59) *Stichopogon* sp. ♂ (above) and ♀ (below) *in copula* (South Africa); (60) *Stichopogon* sp. ♀ with araneaen prey (Zambia). Figs 55, 56, 58, 59 (photographs © S.A. Marshall), Fig. 57 (photograph © H. Roberts), Fig. 60 (photograph © R. Felix).

Figs 48.61–65. Photographs of living Asilidae (Tillobromatinae and Trigonomiminae): (61) *Hypenetes stigmatias* Loew ♂ (South Africa); (62) *Damalis* sp. ♀ (South Africa); (63) *D. speciosa* Loew ♀ (above, perching) and ♂ (below, upside-down) *in copula* (South Africa; see Londt 1991 for copulation sequence); (64) *Rhipidocephala* sp. ♂ (South Africa); (65) *Rhipidocephala* sp. ♀ (South Africa). Fig. 61 (photograph © J.G.H. Londt), Figs 62, 64 (photographs © S.A. Marshall), Figs 63, 65 (photographs © T. Dikow).

the Afrotropics (where it has its largest species diversity), the south-western Palaearctic and western Nearctic Regions. Willistonininae was elevated to subfamily status by Dikow (2009*a*) and includes genera previously assigned to Stenopogoninae *sensu* Artigas & Papavero (1988) and Geller-Grimm (2004).

Taxa such as Asilinae, Dasypogoninae, Laphriinae, Leptogastrinae, Ommatiinae, Stichopogoninae and Trigonomiminae are no doubt monophyletic in the delineation used in the synopsis below. Potential changes to taxon assignment are most probable for Brachyrhopalinae, Stenopogoninae and Tillobromatinae, as the monophyly needs to be tested by including additional genera from the world fauna.

The morphological phylogenetic analysis of Dikow (2009*a*) was unable to place the Afrotropical genus *Oligopogon* and Nearctic genus *Coleomyia* Wilcox & Martin in any of the 14 subfamily taxa and these are, therefore, placed as *incertae sedis* within Asilidae. *Akatiomyia* Londt is added here, as it is morphologically similar to *Oligopogon* and new phylogenetic research is required to place both genera.

Identification

Asilidae is the largest family of Afrotropical Diptera, currently with 1,684 described species, representing about 8% of the entire Diptera fauna (Kirk-Spriggs & Stuckenberg 2009: 175). The oldest assassin-fly descriptions from the Afrotropical Region were published by J.C. Fabricius and A.A.H. Lichtenstein from West Africa and South Africa between 1775 and 1796, *i.e.*, *Promachus fasciatus* (F., 1775) (Sierra Leone, Asilinae), *Teratopomyia cyanea* F., 1781 (South Africa, Brachyrhopalinae), *Asilus morio* F., 1794 ("Guinea", unplaced species), *A. bombylius* Lichtenstein, 1796 (South Africa, unplaced species), *A. melanotarsus* Lichtenstein, 1796 (South Africa, unplaced species) and *A. nigellus* Lichtenstein, 1796 (South Africa, unplaced species). The earliest comprehensive treatment of parts of the Afrotropical fauna was published by Loew (1860) focusing on the Southern African fauna.

Considering the global fauna, assassin flies are known to occur on all continents, except Antarctica and are diverse on many major islands/island groups, but are absent from


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Figs 48.66–68. Photographs of living Asilidae (Willistonininae): (66) *Acnephalomyia andrenoides* (Wiedemann) ♀ (South Africa); (67) *Sisyrnodytes* sp. ♂ (United Arab Emirates); (68) *Trichoura tankwa* Londt ♀ (South Africa). Fig. 66 (photograph © S.A. Marshall), Fig. 67 (photograph © H. Roberts), Fig. 68 (photograph © T. Dikow).

the Hawaiian Is. The greatest species diversity is found in semi-arid to arid environments and tropical rainforests. Londt (1998*a*) recorded 61 species from the semi-arid Karoo near Willowmore (Eastern Cape Province, South Africa) and Fisher (1985, 2009: 616) recorded 97 species from the Tambopata Reserve in Amazonian Peru and 108 species from La Selva Biological Station in a Central American lowland rainforest in Costa Rica.

In an Afrotropical context, robber flies occur in almost every biome, but appear to have their greatest diversity in arid habitats. Assassin flies have not been recorded from the South Atlantic Ocean islands of Ascension, St. Helena, Tristan da Cunha and Gough, as well as the Cape Verde Is. Taxonomically, Afrotropical species are best known from arid to semi-arid Southern Africa, as well as the savanna belt from western Africa through eastern Africa. The fauna of the tropical rainforest in western and Central Africa and the arid environments of the southern Arabian Peninsula is much less known, due largely to the paucity of material. Through the comprehensive revisionary work of the senior author over the past 40 years the fauna has been reviewed extensively and this is particularly true for Southern Africa.

The Afrotropical Asilidae fauna is one of the most diverse in the world. Of the 557 genera globally, 148 genera (26.6%) occur within the region and 1,684 species (*ca* 22% of the world fauna) are known to date, with many additional species awaiting description.

Although the Afrotropical fauna has been catalogued (Oldroyd 1980), no single comprehensive manuscript reviewing the assassin-fly fauna has been published. Oldroyd's (1970, 1974) reviews of regional faunas (Congo basin and Southern Africa), complete with identification keys to genera, are among the more useful general references for the region, in light of this contribution these are now outdated. Londt published a series of papers in the *Annals of the Natal Museum* entitled "Afrotropical Asilidae 1–33" between 1977 and 2000. In more than 55 additional manuscripts, the senior author reviewed many other genera and through contributions of other authors many taxa were studied, however, a few of the larger global genera still require attention (*e.g.*, *Leptogaster* Meigen, *Microstylum* and *Promachus*). The following eleven specialists have been the main contributors having each generated at least 50 specific names (currently valid or otherwise) – J.G.H. Londt (29% of fauna), H. Oldroyd (9%), H. Loew (6%), S.W. Bromley (6%), G. Ricardo (5%), J.P.M. Macquart (4%), F. Walker (3%), E. Janssens (3%), C.H. Martin (3%), E.O. Engel (3%) and A.G. Scarbrough (3%). The majority of genera occurring in the Afrotropical Region have likewise been described by few dipterists – J.G.H. Londt (44 genera, 30% of fauna, 42 endemic), H. Loew (26, 18%, 11), F. Hermann (13, 9%, 6), H. Oldroyd (10, 7%, 10) and F.M. Hull (7, 5%, 5).

Of the 148 genera in the Afrotropics, 91 (61.5%) are endemic to the region and 13 (8.8%) additional genera have their greatest species diversity and centre of distribution in the Afrotropics (four or less species known from outside the Afrotropical Region). There are 31 (20.9%) endemic, monotypic genera within the Afrotropical Region and 33 (22.4%) endemic genera with 2–4 species each. The most diverse endemic genus is *Gonioscelis* with 40 species followed by *Rhabdogaster* (39), *Dasophrys* Loew (32), *Rhipidocephala* Hermann (26), *Proagonistes* (22) and *Hypenetes* Loew and *Afroestricus*, each with 21 species. By far the most speciose genus in the Afrotropics is *Neolophonotus* with 254 Afrotropical species, which is also represented by two species in the Palaearctic Region and Oldroyd (1975: 147) disputes the presence of *Neolophonotus* in the Oriental Region. This genus is the most commonly encountered assassin-fly taxon particularly in Southern Africa where its centre of diversity lies.

There are 22 described species that have not, for a variety of reasons, been assigned to any Afrotropical genus (Oldroyd 1980: 373 lists 14 unplaced species). In all instances, the type specimens require re-examination and at least some of these appear to have been lost. A list of these species is provided here for reference, along with the country/region from where they were originally described: *Asilus bombylius* Lichtenstein, 1796 (South Africa), *A. forficula* Macquart, 1846 (South Africa), *A. gabonicus* Macquart, 1855 (Gabon), *A. incisuralis* Macquart, 1838 (South Africa), *A. melanotarsus* Lichtenstein, 1796 (South Africa), *A. morio* F., 1794 ("Guinea"), *A. natalicus* Macquart, 1855 (South Africa), *A. nigellus* Lichtenstein, 1796 (South Africa), *A. schedius* Walker, 1849 (South Africa), *Dasypogon aequalis* Walker, 1857 (South Africa), *D. atripennis* Macquart, 1834 (Senegal), *D. caffer* Wiedemann, 1828 (South Africa), *D. carvilius* Walker, 1849 (unknown), *D. fossius* Walker, 1849 (South Africa), *D. lenticepsa* Thomson, 1869 (South Africa), *D. reinhardi* Wiedemann, 1824 (South Africa), *D. tragicus* Wiedemann, 1828 (South Africa), *Dioctria stigmatizans* F., 1805 (Mauritius), *Lophonotus albiciliatus* Loew, 1854 (Egypt; Sudan), *L. dubius* Bezzi, 1892 (Somalia), *L. leucotaenia* Bezzi, 1906 (Eritrea) and *L. macropterus* Loew, 1854 (Nubien = Sudan).

Londt (2002*b*) published the most recent key to the then recognised subfamilies of Afrotropical Asilidae (*i.e.*, Apocleinae, Asilinae, Dasypogoninae, Laphriinae, Laphystiinae, Leptogastrinae, Ommatiinae, Stenopogoninae, Stichopogoninae and Trigonomiminae), which is superseded by the below identification key. Although efforts have been made to avoid the use of terminalia characters, this was not always possible and so, ideally, representatives of both sexes should be available when the below key is used. The Asilinae genus *Tolmerus* still requires clarification in an Afrotropical context (see below) and is not included in the below key.

The identification key provided below can also be accessed electronically at https://asiloidflies.si.edu/content/online-identification-keys and http://keys.lucidcentral.org/keys/phoenix/Afrotropical_Asilidae_genera/.

The photographs of pinned specimens in Figs 85–236 representing 69 genera, plus additional views of the head in anterior view, can be accessed electronically at Morphbank under Collection ID 860613 (http://www.morphbank.net/myCollection/?id=860613).

Larger specimens of Asilidae should be direct-pinned and smaller species micro-pinned in the field for later staging (see Chapter 2).

Key to genera of Afrotropical Asilidae

1. Abdominal tergite 2 not more than 4 × as long as wide (*e.g.*, Fig. 17); abdominal sternite 1 confined beneath tergite 1; wing with alula (*e.g.*, Fig. 84) and tarsi with pulvilli (*e.g.*, Fig. 46) usually present, but occasionally one or other may be absent 2

– Abdominal tergite 2 at least 5 × or more as long as wide (*e.g.*, Figs 42–45); abdominal sternite 1 extending *ca* halfway back beneath tergite 2; wing without alula (*e.g.*, Fig. 171) and tarsi without pulvilli (*e.g.*, Fig. 42) (LEPTOGASTRINAE) 15

2. Fore tibia without spine-like tibial processes (macrosetae may be present); thorax with prosternum either fused to or separated from proepisternum by membranous area 3

– Fore tibia with apical, unarticulated spur (*i.e.*, a spine-like process of distal tibial margin, somewhat sigmoid in shape, e.g., Fig. 23); thorax with prosternum separated from proepisternum by membranous area (DASYPOGONINAE) 21

3. Wing vein R_{2+3} ending in costal vein (*C*), cell r_1 thus open at wing margin (as in Fig. 185) 4

– Wing vein R_{2+3} joining vein R_1 proximal to end of R_1, cell r_1 thus closed, either stalked or closed at wing margin (as in Figs 83, 84) 10

4. Head with frons virtually same width at level of antennal insertion and vertex, or only slightly diverging (*e.g.*, Figs 74, 80); eye more or less oval or posterior margin slightly sinuate in ventral ¼ (*e.g.*, Figs 158, 224); thorax with prosternum either fused to or separated from proepisternum by membranous area 5

– Head with frons narrowed at level of antennal insertion, then abruptly diverging dorsally (frons much wider at vertex than at antennal insertion) (*e.g.*, Figs 58, 81); posterior margin of eyes distinctly sinuate in ventral ½ (*e.g.*, Fig. 60); thorax with prosternum fused to proepisternum, forming a precoxal bridge (STICHOPOGONINAE) 69

5. Antennal stylus with long setulae on all surfaces (either loosely arranged or tightly-packed) (*e.g.*, Fig. 197); wing with alula reduced (*e.g.*, Fig. 197) 6

– Antennal stylus without long setulae (*e.g.*, Fig. 220, *Rhipidocephala* sometimes with ventral setulae); wing with alula usually well-developed (*e.g.*, Figs 185, 186) 7

6. Antennal stylus robust, broader than distal end of postpedicel; stylus setulae short and tightly-packed; thorax with prosternum separated from proepisternum by membranous area (confined to Western Cape Province, South Africa) . . . . *Akatiomyia* Londt

– Antennal stylus narrower than distal end of postpedicel (Fig. 198); stylus setulae long and loosely arranged (Fig. 198); thorax with prosternum fused to proepisternum, forming precoxal bridge (Fig. 198) (widespread throughout Afrotropical Region) . . . . *Oligopogon* Loew

7. Head with tentorial pits well-developed, conspicuous anteroventrally (*e.g.*, Fig. 71); wing cell m_3 open (*e.g.*, Figs 137, 215) (TRIGONOMIMINAE) 8

– Head with tentorial pits small, slit-like, inconspicuous ventrally (*e.g.*, Fig. 78); wing cell m_3 open or closed (*e.g.*, Figs 163, 205) 9

8. Antennal postpedicel consisting of proximal bulb, with elongate, but undifferentiated distal part (resembling stylus) (Fig. 138); abdominal tergite 1 entirely sclerotised (Fig. 137); hind trochanter with posteriorly-directed, setose protuberance; fairly robust flies, often shiny yellow-brown with glistening wings (Figs 62, 63, 137, 138) . . . . *Damalis* F.

– Antennal postpedicel elongate, with distinct apical stylus (Fig. 216); abdominal tergite 1 often unsclerotised medially (Fig. 216); hind trochanter without protuberance; small, fragile, blackish flies (Figs 64, 65, 215, 216) . . . . *Rhipidocephala* Hermann

9. Female terminalia with divided tergite 10, bearing acanthophorite spines (may be difficult to discern in specimens with withdrawn terminalia) (e.g., Figs 189, 190, 306); thorax with anepisternum invariably without strong macroseta at superoposterior angle (e.g., Fig. 142); prosternum separated from proepisternum by membranous area 23

– Female terminalia simple, tergite 10 never divided, without acanthophorite spines (*e.g.*, Fig. 216); thorax with anepisternum usually with at least one macroseta at superoposterior angle, in front of wing insertion (*e.g.*, Fig. 228) (if absent, then pulvilli also absent); prosternum fused to proepisternum, forming precoxal bridge (LAPHRIINAE [in part]) 74

10. Wing vein R_{2+3} bent anteriorly at tip, joining vein R_1 just before or at costal vein (*C*) (*e.g.*, Figs 83, 233) 11

– Wing vein R_{2+3} closing cell r_1 by obvious, fairly straight stalk (e.g., Fig. 95) 13

11. Costal wing vein (*C*) circumambient (as in Fig. 84); hind femur slender, without ventrodistal macrosetae inserted on tubercles (confined to eastern and southern Africa) . . . . *Perasis* Hermann

– Costal wing vein (*C*) terminating at or before vein *CuA+CuP* (cell *cup* not bordered by costal vein (*C*)) (*e.g.*, Figs 83, 155, 233); hind femur stout, frequently with ventrodistal macrosetae inserted on tubercles (*e.g.*, Figs 156, 234) (throughout sub-Saharan Africa and/or southern Arabia) 12

12. Antennal postpedicel almost 2 × as long as scape and pedicel combined (Fig. 155); larger species (> 13 mm); hind femur with ventrodistal macrosetae inserted on tubercles; wing with patches of yellow-brown infuscation (Fig. 155) (throughout sub-Saharan Africa); . . . . . . *Hoplistomerus* Macquart

– Antennal postpedicel only slightly longer than scape and pedicel combined (Fig. 233); smaller species (< 13 mm); hind femur with or without ventrodistal macrosetae inserted on tubercles (Fig. 234); wing usually without infuscation (Fig. 233) (throughout sub-Saharan Africa and southern Arabia) . . . . *Trichardis* Hermann

13. Thorax with anepisternum invariably without strong macroseta at superoposterior angle (*e.g.*, Fig. 142); prosternum either fused to or separated from proepisternum by membranous area; palpus 1-segmented 14

– Thorax with anepisternum usually with at least one macroseta at superoposterior angle, in front of wing insertion (*e.g.*, Fig. 228) (if absent, then pulvilli also absent); prosternum fused to proepisternum, forming precoxal bridge; palpus 1- or 2-segmented (LAPHRIINAE [in part]). 78

14. Antennal stylus with long setulae (*e.g.*, Fig. 146); thorax with postmetacoxal area sclerotised (*i.e.*, postmetacoxal bridge complete) (OMMATIINAE) 102

– Antennal stylus without setulae (*e.g.*, Fig. 204); thorax with postmetacoxal area unsclerotised and membranous at least medially (ASILINAE) 110

15. Tarsal claws of unequal length, median claw shorter than lateral; wing veins *M* and *R* with trichoid spicules (reminiscent of setulae); thorax with long, posteriorly directed postsutural dorsocentral setae; male terminalia without surstylus (Fig. 281) (confined to south-western Madagascar). . . . . *Schildia* Aldrich

– Tarsal claws of equal length, median and lateral claws equally long; wing veins *M* and *R* without trichoid spicules; thorax usually without posteriorly directed postsutural dorsocentral setae; male terminalia invariably with distinct surstylus (*e.g.*, Figs 275, 278) (throughout Afrotropical Region) 16

16. Wing cell *cua* closed (as in Fig. 83). 17

– Wing cell *cua* open (as in Fig. 199). 18

17. Hind tibia enlarged, swollen, widest medially, with at least 2 long ventrally-angled setae on ventral surface (Figs 167, 168); hind femur in distal ¾ long setose on all surfaces (Figs 167, 168); wing membrane usually brown patterned (Fig. 167). . . . . *Lasiocnemus* Loew

– Hind tibia cylindrical, usually widest at distal tip, without long ventrally-angled setae on ventral surface (Fig. 104); hind femur in distal ¾ not long setose (Fig. 104); wing membrane never brown patterned (although sometimes appearing darker due to dense microtrichia) (Fig. 103) . . . . *Ammophilomima* Enderlein

18. Thorax with postpronotum medially with distinct, cylindrical, peg-like protuberance (Fig. 148) . . . . *Euscelidia* Westwood

– Thorax with postpronotum medially without protuberance (median postpronotum may be slightly elevated) (*e.g.*, Figs 172, 174, 176, 182) 19

19. Hind tibia with dorsal and ventral rows of short macrosetae (Figs 45, 181, 182); hind legs long, almost cylindrical throughout (Figs 45, 181, 182) . . . . *Mesoleptogaster* Frey

– Hind tibia without distinct rows of short macrosetae (single macrosetae may be present particularly towards distal tip) (*e.g.*, Fig. 44); hind legs not markedly elongated, at least femur distinctly clubbed distally (*e.g.*, Fig. 44) 20

20. Antennal postpedicel short (as long as, or marginally longer than scape and pedicel combined); male terminalia with hypandrium and gonocoxite fused to form "lobus"; surstylus without movable secondary ventral lobe, invariably bipartite distally; female terminalia often with long macrosetae distally on abdominal sternite 8 . . . . *Lobus* Martin

– Antennal postpedicel short or long (Figs 172, 174); male terminalia with hypandrium and gonocoxite invariably separated; surstylus invariably with movable secondary ventral lobe, with only single tip (sometimes more or less blunt with distinct dorso- and ventrodistal points); female terminalia without long macrosetae distally on abdominal sternite 8 . . . . *Leptogaster* Meigen

21. Fore tibial spur slender, sigmoid, not associated with proximal tarsal process, at most with group of stout, peg-like, black, tarsal macrosetae (Fig. 218); scutellum with 2 well-developed apical macrosetae (Fig. 217); male terminalia with epandrium and hypandrium unfused (suture distinctly visible). . . . . *Saropogon* Loew

– Fore tibial spur stout, associated with well-developed proximal tarsal process (*e.g*, Fig. 200); apical scutellar macrosetae highly reduced to absent (*e.g.*, Fig. 200); male terminalia with epandrium and hypandrium fused, forming continuous ring (no suture apparent) (*e.g.*, Fig. 262) 22

22. Head with ocellar tubercle prominent (Fig. 200); median occipital sclerite with 2 vertical macrosetae; postpronotal lobe without macrosetae (Fig. 200); weak dorsocentral macrosetae may be present postsuturally. . . . . *Pegesimallus* Loew

– Head with ocellar tubercle not prominent; median occipital sclerite with 4–6 vertical macrosetae; postpronotal lobe with 1–2 stout macrosetae; pre- and postsutural dorsocentral macrosetae present . . . . *Caroncoma* Londt

23. Thorax with anatergite setose (*e.g.*, Figs 108, 144, 186) 24

– Thorax with anatergite bare (*e.g.*, Figs 118, 222) 32

24. Antennal stylus composed of 2–3 distinctly discernible articles (1–2 segment-like articles plus apical seta-like sensory article) 25

– Antennal stylus reduced, composed of greatly reduced segment-like articles (not always evident) and apical seta-like sensory article in cavity on distal postpedicel 31

25. Head with occiput without macrosetae (*i.e.*, with weak postocular and occipital setae only). 26

– Head with occiput with obvious macrosetae (including postocular and occipital setae) (*e.g.*, Fig. 108) 27

26. Antennal scape distinctly longer than pedicel; eye : face width ratio < 1.1 : 1; male terminalia with hypandrium less than ½ as long as epandrial lobes. . . . . *Dioctobroma* Hull

– Antennal scape and pedicel of virtually same length; eye : face width ration > 1.3 : 1; male terminalia with hypandrium *ca* as long as epandrial lobes. . . . . *Dogonia* Oldroyd

27. Thorax with proepisternum with a few strong macrosetae in addition to setae (Fig. 108); antepronotum and scutum with very strong macrosetae, giving a bristly appearance (Fig. 108) . . . . *Anasillomos* Londt

– Thorax with proepisternum with setae only (some may be stronger than others, but never as strong as scutal macrosetae); antepronotum and scutum with setae or regular macrosetae 28

28. Abdominal tergite 1–4 with group of strong macrosetae dorsolaterally; antennal stylus composed of two articles (1 segment-like article, plus apical seta-like sensory article); male terminalia bulbous (Figs 295–297); female abdominal tergites 7 and 8 of virtually same length . . . . . *Ontomyia* Dikow & Londt

– Abdominal tergite 1 (only) with group of strong macrosetae dorsolaterally; antennal stylus composed of three articles (2 segment-like articles, plus apical seta-like sensory article); male terminalia slender, never bulbous; female abdominal tergite 8 distinctly shorter than tergite 7 (*Fishermyia* female unknown) 29

29. Head with facial swelling well-developed on entire face. . . . . *Oratostylum* Ricardo

– Head with facial swelling weak, only ventral margin moderately developed 30

30. Scutellum with 2 apical scutellar macrosetae; head with mystax occupying ventral ⅓ of face only; antennal postpedicel elongate, spindle-shaped, > 1.5 × as long as scape and pedicel combined (confined to Madagascar) . . . . *Fishermyia* Londt

– Scutellum with 4 or more apical scutellar macrosetae present; head with mystax occupying almost entire face, although sometimes weak in dorsal part; antennal postpedicel usually somewhat clavate, < 1.5 × as long as scape and pedicel combined (confined to southern Africa) . . . . . . *Remotomyia* Londt

31. Head with facial swelling occupying *ca* ¾ of face (Fig. 144); mystax entirely covering face (Fig. 144); thoracic pre- and postsutural dorsocentral setae well-developed; postmetacoxal membrane clothed in long setae (Fig. 144); wing vein M_1 not strongly arched anteriorly (Fig. 143) . . . . *Daspletis* Loew

– Head with facial swelling occupying at most ventral ½ of face (Figs 186, 188, 190); mystax primarily confined to ventral ½ of face (Figs 186, 188, 190); only postsutural dorsocentral setae well-developed; postmetacoxal membrane usually bare (Figs 186, 188, 190); wing vein M_1 usually strongly arched anteriorly (Figs 185, 187, 189) . . . . *Microstylum* Macquart

32. Costal wing vein (*C*) not circumambient, cell *cup* and alula without bordering vein *C* (*i.e.*, *C* terminates at or before point where vein *CuP* joins wing margin) (*e.g.*, Figs 91, 93, 105, 117, 211, 221, 223) 33

– Costal wing vein (*C*) circumambient (around entire wing margin, even when weakly-developed as in *Trichoura*) (*e.g.*, Fig. 157) 43

33. Tarsal claws with pulvilli minute or absent (*e.g.*, Fig. 224) (WILLISTONININAE [in part]) 34

– Tarsal claws with pulvilli well-developed (*e.g.*, Fig. 212) 38

34. Abdomen broad, obviously dorsoventrally flattened (width : length ratio of abdominal tergite 2 > 2) (*e.g.*, Figs 85, 222) 35

– Abdomen cylindrical, not obviously dorsoventrally flattened (width : length ratio of abdominal tergite 2 < 1.5) (*e.g.*, Figs 102, 224) 37

35. Costal wing vein (*C*) terminating before reaching vein *CuA+CuP* (*e.g.*, Fig. 221); cell r_5 closed and stalked (stalk frequently not reaching wing margin) (*e.g.*, Fig. 221) . . . . *Sisyrnodytes* Loew

– Costal wing vein (*C*) terminating at point where vein *CuA+CuP* reaches wing margin (*e.g.*, Fig. 85); cell r_5 open (*e.g.*, Fig. 85) 36

36. Wing cell m_3 open (Fig. 85); vein R_4 with short stump vein (Fig. 85); tarsal claws with pulvilli poorly developed, but clearly discernible; male terminalia with hypandrium somewhat flat or only gently concave. . . . . *Acnephalomyia* Londt

– Wing cell m_3 closed and stalked; vein R_4 without stump vein (Fig. 117); tarsal claws with pulvilli minute, difficult to discern; male terminalia with hypandrium distinctly cup-shaped . . . . *Astiptomyia* Londt

37. Small species (wing length: < 3.5 mm) (Fig. 101); tarsal claws without empodium (Fig. 102); wing without stump vein on vein R_4; thorax with scutal macrosetae well-developed, many times longer than accompanying setae. . . . . *Ammodaimon* Londt

– Larger species (wing length:> 6.0 mm) (Fig. 223); tarsal claws with well-developed empodium (Fig. 224); wing with short stump vein on vein R_4 (Fig. 223); thorax with scutal macrosetae moderately developed, not considerably longer than accompanying setae (Fig. 224) . . . . *Sporadothrix* Hermann

38. Thoracic postmetacoxal area sclerotised (*i.e.*, postmetacoxal bridge complete) (Fig. 212) . . . . *Rhabdogaster* Loew

– Thoracic postmetacoxal area entirely membranous 39

39. Thorax with scutum greatly elevated anterodorsally, hump-like . . . . *Oxynoton* Janssens

– Thorax with scutum of more usual shape, not hump-like 40

40. Hind coxa anteriorly with elongate, distally rounded, peg-like process . . . . *Ischiolobos* Londt

– Hind coxa anteriorly without peg-like process 41

41. Head with strong mystacal macrosetae extending over entire face (Fig. 106); thorax with 1–4 long postalar macrosetae (Fig. 106) . . . . *Amphisbetetus* Hermann

– Head with strong mystacal macrosetae either confined to lower ½ of face or absent (weak mystacal setae present) (*e.g.*, Figs 92, 94); thoracic postalar macrosetae usually absent (1 or 2 macrosetae in some species) (*e.g.*, Figs 92, 94). 42

42. Head with mystacal macrosetae more extensive, if restricted to single row on lower facial margin, then weaker mystacal setae also present on face (*e.g.*, Figs 92, 94); abdominal tergites usually bare (Figs 91–94) (primarily in Southern Africa) . . . . *Afroholopogon* Londt

– Head with mystacal macrosetae restricted to single row on lower facial margin; abdominal tergites primarily pubescent (small median bare maculae present) (Palaearctic & southern Arabian Peninsula) . . . . *Wadipogon* Bosák & Hradský

43. Palpus 1-segmented (usually fairly robust and curved, such that their distal ends converge) 44

– Palpus 2-segmented (weak distal segment may be tucked away in oral cavity) 46

44. Proboscis with spine-like processes distally; antennal stylus not clearly differentiated, apical seta-like sensory article situated sub-apically in cavity on postpedicel. . . . . *Hynirhynchus* Lindner

– Proboscis of more usual form, without spine-like processes distally (*e.g.*, Figs 152, 208); antennal stylus clearly differentiated, apical seta-like sensory article situated apically in cavity on stylus 45

45. Proboscis shorter than antenna (Fig. 152); mystax occupying ventral ⅓ of face (Fig. 152); male mid tarsomeres 4–5 with highly modified, rather spade-shaped setae (usually reddish in colour) (Fig. 152) . . . . *Habropogon* Loew

– Proboscis longer than antenna (Fig. 208); mystax occupying ventral ½ of face (Fig. 208); male mid tarsomeres 4–5 with regular setae only (Fig. 208) . . . . *Pycnomerinx* Hull

46. Head almost circular in anterior view (*i.e.*, face narrow) (*e.g.*, Fig. 69) 47

– Head distinctly wider than high in anterior view (*e.g.*, Fig. 70) 51

47. Thorax with katatergite bare 48

– Thorax with katatergite setose (*e.g.*, Fig. 98) 49

48. Fore femur with large, proximoventral spinose process (*i.e.*, strongly raptorial) (Figs 52, 150) . . . . *Gonioscelis* Schiner

– Fore femur of more usual form, without large spinose process . . . . *Stenopogon* Loew

49. Thoracic dorsocentral macrosetae developed pre- and postsuturally (Fig. 154) . . . . *Haroldia* Londt

– Thoracic dorsocentral macrosetae developed only postsuturally (*e.g.*, Fig. 98) 50

50. Antennal stylus composed of two articles (1 segment-like article, plus apical seta-like sensory article) (Fig. 98); male terminalia with hypandrium usually bifurcate distally . . . . *Afroscleropogon* Londt

– Antennal stylus composed of three articles (2 segment-like articles plus apical seta-like sensory article); male terminalia with hypandrium usually simple . . . . *Rhacholaemus* Hermann

51. Proboscis strongly downwardly-curved, resembling a parrot's beak (Fig. 110) . . . . *Ancylorhynchus* Berthold

– Proboscis of more usual form, not strongly downwardly-curved (*e.g.*, Fig. 134) 52

52. Head with facial swelling strongly projecting ventrally only (not dorsally), giving pointed, nose-like appearance; mystacal macrosetae largely confined to small area at apex of facial swelling . . . . *Lycostommyia* Oldroyd

– Head with facial swelling not projecting ventrally, of more usual form; mystacal macrosetae placed more widely on facial swelling (Figs 134, 136) 53

53. Head with mystax occupying entire face, even if weakly-developed dorsally (*e.g.*, Fig. 134) 54

– Head with mystax not occupying entire face, with distinct gap between dorsal mystacal setae and antennal sockets (*e.g.*, Fig. 220) 59

54. Antennal postpedicel widening toward middle (in lateral view), apical ½ appearing strongly incised ventrally (*P. astroptica* Londt, 1994) . . . . *Pedomyia* Londt [in part]

– Antennal postpedicel either distinctly laterally compressed or cylindrical 55

55. Antennal postpedicel distinctly laterally compressed, strap-like; stylus laterally compressed . . . . *Hermannomyia* Oldroyd

– Antennal postpedicel more or less cylindrical (may appear slightly laterally compressed) (Figs 133, 134); stylus more or less cylindrical 56

56. Large, bee-mimicking flies (wing length: > 15 mm) (Figs 119, 120); palpus large, well-developed (Fig. 120); thoracic anepimeral macroseta absent (Fig. 120) . . . . *Bana* Londt

– Small flies (wing length: < 10 mm) (*e.g.*, Figs 129, 130, 133–136); palpus moderately developed (*e.g.*, Figs 130, 134, 136); thoracic anepimeral macroseta usually present (*e.g.*, Figs 130, 136) 57

57. Male terminalia club-like (Fig. 134); epandrium greatly developed, hemispherical; hypandrium greatly reduced . . . . *Corymyia* Londt

– Male terminalia of more usual form (*e.g.*, Fig. 130); epandrium not greatly developed; hypandrium not greatly reduced 58

58. Head with mystax well-developed, occupying entire face (Fig. 130); scutellum with numerous apical scutellar setae, usually some discal scutellar setae (central area usually bare) (Fig. 129); male terminalia with gonocoxite with two sub-equal, pointed, distal processes, lateral one with at most a small tumid dorsodistal projection . . . . *Connomyia* Londt

– Head with mystax moderately developed, occupying entire face, but usually weak dorsally; scutellum usually with few apical scutellar setae, rarely few discal scutellar setae present; male terminalia with gonocoxite with lateral process having distal or dorsodistal flange-like process . . . . *Danomyia* Londt

59. Thorax with anepimeral macroseta; hind tarsus with empodium laterally compressed and blade-like . . . . *Empodiodes* Oldroyd

– Thorax without anepimeral macroseta; hind tarsus with empodium seta-like, not laterally compressed and blade-like 60

60. Head with facial swelling strongly developed in ventral ¾, dorsal part distinctly defined (*e.g.*, Fig. 158) 61

– Head with facial swelling at most moderately developed, dorsal part not distinctly defined (*e.g.*, Fig. 220). 62

61. Body not entirely metallic blue-black (Fig. 158); antennal postpedicel strongly club-shaped, subequal to length of scape and pedicel combined (Fig. 158); wing largely transparent with dark maculae (especially "pterostigma-like" marking at base of cell r_1) (Fig. 157). . . . . *Hypenetes* Loew

– Body entirely metallic blue-black; antennal postpedicel elongate, cylindrical, *ca* 2 × as long as scape and pedicel combined; wing fairly uniformly black . . . . *Teratopomyia* Oldroyd

62. Head with mystax occupying at most ventral ⅓ of face (*e.g.*, Figs 180, 236) 63

– Head with mystax occupying at least ventral ½ of face (*e.g.*, Fig. 220) 67

63. Wing cells *cua* and m_3 closed and stalked (Fig. 235); male terminalia with hypandrium reduced, largely fused with gonocoxites (WILLISTONININAE [in part]). . . . . *Trichoura* Londt

– Wing cells *cua* and m_3 open at wing margin (even if only narrowly); male terminalia with hypandrium moderately well-developed, not fused with gonocoxites 64

64. Male terminalia with epandrial lobes separated, only joined proximally 65

– Male terminalia with epandrial lobes fused medially for at least proximal ½ of length. 66

65. Larger flies (wing length: > 5 mm) . . . . *Antiscylaticus* Londt

– Smaller flies (wing length: < 5 mm) . . . . *Microphontes* Londt

66. Scutellum with discal setae (*ca* 4); male terminalia with epandrial lobes fused medially for virtually entire length (only slight distal indentation) . . . . *Irwinomyia* Londt

– Scutellum without discal setae (Fig. 180); male terminalia with epandrial lobes fused medially for *ca* ½ length . . . . *Macroetra* Londt

67. Antennal postpedicel widening toward middle (in lateral view), apical ½ appearing strongly incised ventrally. . . . . *Pedomyia* Londt [in part]

– Antennal postpedicel spindle-shaped (*e.g.*, Fig. 219) 68

68. Male terminalia with epandrial lobes short, fused medially for *ca* ⅓ length; male hypandrium elongate, ventrally directed with upturned distal region. . . . . *Agrostomyia* Londt

– Male terminalia with epandrial lobes long, entirely separated medially or very narrowly joined proximally; male hypandrium more or less straight and distally directed. . . . . *Scylaticus* Loew

69. Tarsi without pulvilli 70

– Tarsi with pulvilli (even if only weakly developed) 71

70. Wing cell m_3 open (Fig. 213); head with mystacal setae dorsoventrally flattened (Fig. 214). . . . . *Rhadinus* Loew

– Wing cell m_3 closed; head with mystacal setae circular in cross-section . . . . *Turkmenomyia* Paramonov

71. Tarsi with pulvilli weakly developed, about ½ length of tarsal claw (confined to Kenya) . . . . *Nanoculcita* Londt & Copeland

– Tarsi with pulvilli well-developed, almost reaching distal end of tarsal claw. 72

72. Head with 2 well-developed ocellar macrosetae (Fig. 81); wing cell m_3 with long stalk at base (Fig. 225); usually small, or even tiny flies (body length: < 10 mm) (Figs 58–60, 225, 226); habitat sandy banks of streams, rivers and lakes. . . . . *Stichopogon* Loew

– Head with ocellar macrosetae weak or absent (*e.g.*, Fig. 126); wing cell m_3 with short basal stalk or stalk absent (*e.g.*, Fig. 125); habitat not as above 73

73. Thorax with scutum entirely grey pubescent (Fig. 125); larger flies (body length: > 10 mm) (littoral zones on East African coast and Indian Ocean islands) . . . . *Clinopogon* Bezzi

– Thorax with scutum bare; smaller flies (body length: < 10 mm) (confined to southern Arabian Peninsula) . . . . *Dichropogon* Bezzi

74. Tarsi with pulvilli poorly developed (*ca* ½ length of tarsal claw) (Fig. 206) . . . . . *Prytanomyia* Özdikmen

– Tarsi with pulvilli well-developed (as long as or slightly shorter than tarsal claw) (*e.g.*, Fig. 164) 75

75. Thorax with anepisternum with strong macroseta on superoposterior angle; small flies (body length: < 8 mm); head with face narrower than width of one eye in anterior view; antennal scape 2 × as long as pedicel . . . . . *Gerrolasius* Hermann

– Thorax with anepisternum without obvious strong macroseta on superoposterior angle; larger flies (body length: > 8 mm); head with face as wide or wider than width of one eye; antennal scape < 2 × as long as pedicel 76

76. Head with mystax composed almost entirely of fine setae, uniformly covering face; fine setae of thorax and abdomen longish and soft; no conspicuous macrosetae on body; wing cell r_5 usually closed; bee-like in appearance . . . . . *Pilophoneus* Londt

– Head with mystax composed of strong macrosetae, largely restricted to ventral facial margin (*e.g.*, Fig. 164); fine setae of thorax and abdomen minute; thoracic and abdominal macrosetae conspicuous and moderately well-developed (*e.g.*, Fig. 164); wing cell r_5 open (*e.g.*, Fig. 163); not bee-like in appearance 77

77. Scutellum with apical macrosetae moderately developed; antennal postpedicel virtually as long as scape and pedicel combined; thorax and abdomen extensively bare . . . . . *Ericomyia* Londt

– Scutellum without apical macrosetae (Fig. 163); antennal postpedicel considerably longer than scape and pedicel combined (Fig. 164); thorax and abdomen entirely setose (Figs 163, 164) . . . . . *Laphyctis* Loew

78. Thorax with postmetacoxal area sclerotised (*i.e.*, postmetacoxal bridge complete, no suture evident) 79

– Thorax with postmetacoxal area membranous (some *Proagonistes* with almost complete bridge, but dorsoventral suture evident) 84

79. Larger flies (body length: > 10 mm) (confined to Madagascar) 80

– Small to tiny flies (body length: < 10 mm) (confined to sub-Saharan Africa) 81

80. Male terminalia with cercus short, barely extending beyond tip of epandrium . . . . . *Katharma* Oldroyd

– Male terminalia with cercus very long, extending well beyond tip of epandrium . . . . . *Katharmacercus* Tomasovic

81. Antennal postpedicel without stylus, with seta-like sensory article inserted just beyond ½ length; thorax with scutum without distinct macrosetae anteriorly; anatergite bare; scutellum with tubercular projection apically . . . . . *Afromosia* Londt

– Antennal postpedicel with distinct stylus, seta-like sensory article inserted sub-apically and laterally on postpedicel; thorax with scutum anteriorly with pair of small macrosetae; anatergite setose; scutellum simple, smoothly rounded 82

82. Antennal stylus as long as or longer than scape; head with postocular macrosetae weakly developed . . . . . *Dichaetothyrea* de Meijere

– Antennal stylus shorter than scape; head with postocular macrosetae well-developed 83

83. Head with face wide (eye : face width ratio < 1.5); mystax of males with dorsoventrally flattened, shiny scale-like macrosetae (Fig. 28); thorax with scutum shiny, at most slightly puncticulate (Fig. 28) . . . . . *Goneccalypsis* Hermann

– Head with face narrow (eye : face width ratio > 1.5); mystax of both sexes without laterally situated dorsoventrally flattened scale-like setae; thorax with scutum punctate . . . . . *Loewinella* Hermann

84. Wing vein M_3 with apical portion perfectly aligned with proximal portion of vein M_2 (forming cross) (confined to Madagascar) . . . . . *Orthogonis* Hermann

– Wing veins not so aligned (*e.g.*, Figs 111, 123, 159, 227) (except in *Anypodetus nigrifacies* Ricardo, 1925, in which alignment is almost perfect) (widespread Afrotropical Region) 85

85. Proboscis long, narrow and laterally compressed (knife-like) (as in Fig. 124) 86

– Proboscis short to moderate in length, often stout, somewhat triangular in cross-section (*e.g.*, Fig. 228) 88

86. Hind femur considerably expanded mediodistally and with ventrodistal macrosetae inserted on tubercles . . . . . *Storthyngomerus* Hermann

– Hind femur not obviously expanded mediodistally, with only regular ventrodistal macrosetae (not inserted on tubercles) (*e.g.*, Fig. 124) 87

87\. Antennal postpedicel at most 2 × as long as scape and pedicel combined (Fig. 124); female ovipositor short and not markedly tubular; smaller (body length: < 20 mm), not obviously robust, setaceous, or bee-like flies (Figs 27, 123, 124). . . . . . *Choerades* Walker

– Antennal postpedicel > 2 × as long as scape and pedicel combined; female ovipositor somewhat elongate, tubular; large (body length: > 20 mm), robust, setaceous, bee-like flies. . . . . . *Dasyllina* Bromley

88\. Palpus laterally compressed and leaf-like (*e.g.*, Fig. 160); female ovipositor projecting distally as slender tube (*e.g.*, Fig. 159) 89

– Palpus cylindrical in cross-section (*e.g.*, Fig. 228); female ovipositor short, not markedly tubular 92

89\. Wing cell r_5 closed (Fig. 159); broad flies, bee-like in appearance (mimicking carpenter bees) (Figs 159, 160). . . . . . *Hyperechia* Schiner

– Wing cell r_5 open; not broad and bee-like in appearance. 90

90\. Head with facial swelling only weakly developed; antennal postpedicel virtually as long as scape and pedicel combined . . . . . . *Andrenosoma* Rondani

– Head with facial swelling well to strongly developed; antennal postpedicel *ca* 1.5 × as long as scape and pedicel combined. 91

91\. Larger flies (body length: > 20 mm) mimicking pompilid wasps (Figs 36, 37); thorax with scutum blackish (sometimes with red-brown lateral parts) (Fig. 37) . . . . . . *Proagonistes* Loew

– Smaller flies (body length: < 20 mm); thorax with scutum brown-yellow to reddish, clothed in golden setae . . . . . . *Systropalpus* Hull

92\. Wing vein M_2 not reaching wing margin. . . . . . *Ctenota* Loew

– Wing vein M_2 reaching wing margin (*e.g.*, Figs 161, 169, 227) 93

93\. Head with postgena well-developed, with ventral flange-like projection (in lateral view) (*e.g.*, Fig. 162) 94

– Head with postgena simple, not ventrally extended and flange-like (*e.g.*, Figs 112, 166, 170, 192). . . . 95

94\. Hind leg greatly elongate (hind femur *ca* 2 × as long as mid femur) (Fig. 162); abdomen somewhat constricted in anterior ½ (Fig. 161); larger flies (body length: *ca* 20–36 mm) (Figs 30, 161, 162). . . . . . *Lamyra* Loew

– Hind leg normally proportioned (hind femur not more than 1.5 × as long as mid femur) (Fig. 228); abdomen more or less parallel-sided, not noticeably constricted (Fig. 227); smaller flies (body length: *ca* 10–27 mm) (Figs 39, 227, 228) . . . . . . *Stiphrolamyra* Engel

95\. Wing cell r_5 closed (*e.g.*, Fig. 169) 96

– Wing cell r_5 open (*e.g.*, Figs 111, 165, 192) 98

96\. Palpus bulbous (virtually spherical); mystax composed of fine setae only . . . . . . *Afromelittodes* Oldroyd & Van Bruggen

– Palpus not markedly bulbous (cylindrical) (*e.g.*, Fig. 170); mystax composed of strong macrosetae (*e.g.*, Fig. 170) 97

97\. Antennal postpedicel with numerous well-developed dorsal setulae (Fig. 169); scape usually *ca* 2 × as long as pedicel (Fig. 169); often rather bee-like in appearance (Figs 32, 169, 170) . . . . . . *Laxenecera* Macquart

– Antennal postpedicel without setulae; scape only slightly longer than pedicel; never bee-like in appearance . . . . . . *Nusa* Walker

98\. Tarsi without pulvilli (Fig. 112); thorax with anepisternum without macrosetae on superoposterior angle (Fig. 112) . . . . . . *Anypodetus* Hermann

– Tarsi with pulvilli (*e.g.*, Figs 166, 192); thorax with anepisternum with strong macrosetae on superoposterior angle (Figs 166, 192). 99

99\. Antennal postpedicel bearing well-defined segment-like stylus, tipped with terminal pit-enclosed seta-like sensory article (Fig. 165). . . . . . *Laphystotes* Oldroyd

– Antennal postpedicel simple, tipped with terminal, obliquely positioned pit-enclosed seta-like sensory article (*e.g.*, Fig. 191) 100

100\. Generally pale yellow-brown to red-brown flies; legs entirely yellow-brown to red-brown . . . . . . *Smeryngolaphria* Hermann

– Generally dark red-brown to black flies; legs extensively or entirely blackish (*e.g.*, Figs 191, 192) 101

101. Head of male with mystax at least laterally overlaid by shiny scale-like setae (Fig. 34); wing with proximal ½ transparent, distal ½ uniformly clothed in dense microtrichia. . . . . *Notiolaphria* Londt

– Head in both sexes with mystax not overlaid by shiny scale-like setae (Fig. 192); wing membrane more extensively clothed in black microtrichia (Fig. 192). . . . . *Nannolaphria* Londt

102. Head with mystax with some dorsal macrosetae arranged in two distinct vertical rows (*e.g.*, Figs 47, 48, 90). 103

– Head with mystax simple, dorsal setae not arranged in distinct vertical rows (*e.g.*, Fig. 46, 130, 184) 108

103. Scutellum without apical macrosetae; antennal stylus with ventral setulae arranged in single row . . . .*Metommatius* Hull

– Scutellum with apical macrosetae (*e.g.*, Figs 89, 146); antennal stylus with ventral setulae arranged in two distinct divergent rows (*e.g.*, Figs 90, 146) 104

104. Head with facial swelling moderately well-developed (at least in ventral ½) (*e.g.*, Fig. 90). 105

– Head with facial swelling only weakly developed ventrally (*e.g.*, Fig. 146) 106

105. Head with facial swelling moderately well-developed, abruptly produced in ventral ⅔ (Fig. 90); proboscis more or less cylindrical medially (only slightly higher than wide), shorter than compound eye (in lateral view) (Fig. 90); antennal postpedicel small, virtually as wide as scape (Fig. 89); thorax with 2–3 stout, long presutural dorsocentral macrosetae (Fig. 89) . . . .*Afroestricus* Scarbrough

– Head with facial swelling less developed, with only ventral ½ developed; proboscis oval in diameter medially (higher than wide), as long as or slightly longer than compound eye (in lateral view); antennal postpedicel wider than scape; thorax with short presutural dorsocentral macrosetae . . . . *Longibeccus* Scarbrough

106. Abdominal tergites 2–4 strongly constricted laterally (Fig. 145) . . . .*Emphysomera* Schiner

– Abdomen tergites 2–4 more or less parallel-sided (not noticeably constricted) (*e.g.*, Figs 47, 48). 107

107. Thorax with stout macroseta on anepimeron; male mystax usually narrow, individual macrosetae tapering evenly from proximal to distal; male abdominal sternites 3–4 without pattern of erect macrosetae and/or dense setae (Figs 47, 48) . . . .*Ommatius* Wiedemann

– Thorax usually without macroseta on anepimeron, if present, then only setose, rarely macrosetose; male mystax usually with several thick macrosetae of uniform diameter medially, tapering only at or just before apex; male abdominal sternites 3–4 with pattern of erect macrosetae and/or dense setae . . . . *Pygommatius* Scarbrough & Marascia

108. Head with face narrow at antennal insertion, < ⅕ as wide as head at greatest width; antennal postpedicel 2–6 × as long as scape and pedicel combined (Fig. 184); stylus short, much shorter than postpedicel (Fig. 184) . . . .*Michotamia* Macquart

– Head with face wide, > ⅕ as width of head; antennal postpedicel short, virtually as long as scape or scape and pedicel combined (Fig. 46); stylus long, usually > 3 × as long as postpedicel (*e.g.*, Fig. 46) 109

109. Head with mystax composed of dense macrosetae medially (Figs 46, 132); numerous ocellar setae positioned fan-like posteriorly; antennal stylus with setulae short, arranged in single row (Fig. 132); larger robust flies (body length: > 10 mm) (Figs 46, 131, 132) . . . .*Cophinopoda* Hull

– Head with mystax composed of sparse setae medially; only 2 ocellar setae posteriorly; antennal stylus with setulae long, arranged in two rows; smaller flies (body length: < 9 mm) . . . . . *Thallosia* Oldroyd

110. Thorax with anatergite bare (although setae may be present on mediotergite (mesopostnotum)) (*e.g.*, Figs 100, 114, 142, 178, 194, 196, 202, 204, 230, 232) 111

– Thorax with anatergite setose (*e.g.*, Figs 96, 128) 136

111. Antennal stylus composed of two articles (one segment-like article plus apical seta-like sensory article); head with facial swelling weakly developed ventrally (*e.g.*, Figs 100, 114, 202, 204); dorsocentral macrosetae only postsuturally (*e.g.*, Figs 100, 114, 178, 202, 204) 112

– Antennal stylus composed of three articles (two unequal segment-like articles plus apical seta-like sensory article); head with facial swelling not distinctly defined or gently convex (Figs 17, 142, 194, 196, 230, 232); thorax with dorsocentral macrosetae usually inserted pre- or postsuturally (*e.g.*, Figs 142, 194, 196, 230, 232) 118

112. Wing with complete auxiliary vein on vein R_4 (connecting veins R_{2+3} and R_4) (as in Fig. 84; Figs 99, 201, 203). 113

– Wing either without auxiliary vein on vein R_4 or with only short stump vein on vein R_4 (*e.g.*, Figs 113, 178). 116

113. Wing either with auxiliary vein long, or running parallel to vein R_{4+5} for considerable distance before reaching fork of veins R_4 and R_5 (*e.g.*, Figs 84, 203); cell r_4 short, diverging rapidly near wing margin (*e.g.*, Fig. 203); posterior wing margin with microtrichia arranged in single row (aligned in same plane as wing membrane); scutellum with 8 or more apical macrosetae (*e.g.*, Fig. 203); discal scutellar setae and macrosetae present (Fig. 204) 114

– Wing either with auxiliary vein shorter, or at most running parallel to vein R_{4+5} for short distance (*e.g.*, Figs 99, 201); cell r_4 long, diverging gradually towards wing margin (*e.g.*, Figs 99, 201); posterior wing margin with microtrichia arranged in two rows (diverging from plane of wing membrane); scutellum with fewer than 8 apical macrosetae (*e.g.*, Figs 99, 201); discal scutellar setae composed of setae only (no macrosetae) (*e.g.*, Figs 99, 201) 115

114. Head with vertex of regular width, with ocellar tubercle of regular shape and size (Figs 77, 203); ocellar tubercle usually not visible in lateral view (Fig. 204) . . . . *Promachus* Loew

– Head with vertex wide, entirely occupied by ocellar tubercle; ocellar tubercle distinctly visible in lateral view . . . . *Tuberconspicus* Tomasovic

115. Wing with auxiliary vein very short (virtually as long as section of vein R_4 between fork of vein R_{4+5} and point at which crossvein joins R_4) (Fig. 99) . . . . *Alcimus* Loew

– Wing with auxiliary vein longer (Fig. 201). . . . . *Philodicus* Loew

116. Wing without stump vein on vein R_4 (Fig. 178); female ovipositor telescopic, comprised of abdominal segments 5 and following (confined to Madagascar & Mauritius) . . . . *Lycoprosopa* Hull

– Wing with short stump vein (st vn) on vein R_4 (*e.g.*, Fig. 113); female ovipositor not obviously telescopic, comprising abdominal segments 8 and following (confined to West Africa, Arabian Peninsula & North Africa) 117

117. Scutellum with 2 apical macrosetae (Figs 113, 115); hind coxa with 2–3 lateral macrosetae; wing cell r_5 open or closed (Figs 113, 115); female ovipositor tubular; cercus spinose with well-developed macrosetae . . . . *Apoclea* Macquart

– Scutellum with 4–6 apical macrosetae; hind coxa with single lateral macroseta; wing cell r_5 open; female ovipositor laterally compressed; cercus without macrosetae. *Erax* Scopoli

118. Head with dorsal postocular setae short to moderately long, at most weakly proclinate (*e.g.*, Fig. 232) 119

– Head with dorsal postocular setae long, markedly proclinate (*e.g.*, Figs 12, 142, 194, 196, 230). 123

119. Antennal stylus distinctly longer than postpedicel (*e.g.*, Fig. 232) 120

– Antennal stylus shorter or virtually same length as postpedicel 121

120. Thorax with postpronotal lobes with macrosetae in addition to fine setae; hind coxa with single lateral macroseta; posterior wing margin with microtrichia arranged in two rows (diverging from plane of wing membrane) . . . . *Dysclytus* Loew

– Thorax with postpronotal lobes with fine setae only (Fig. 232); hind coxa with 4–5 lateral macrosetae; posterior wing margin with microtrichia arranged in single row (lying in same plane as wing membrane) . . . . *Torasilus* Londt

121. Thorax with dorsocentral macrosetae well-developed pre- and postsuturally; hind coxa with more than 2 lateral macrosetae. . . . . *Zelamyia* Londt

– Thorax with dorsocentral macrosetae well-developed only postsuturally; hind coxa with 2 lateral macrosetae. 122

122. Female cercus with fine setae only (without dorsodistal projection) . . . . *Acasilus* Londt

– Female cercus with fine setae and dorsodistal spine-like projection . . . . *Juxtasilus* Londt

123. Posterior wing margin with microtrichia arranged in 2 rows (diverging from plane of wing membrane) . . . . *Robertomyia* Londt

– Posterior wing margin with microtrichia arranged in single row (lying in same plane as wing membrane) 124

124. Wing cell r_5 closed well before wing margin . . . . *Megadrillus* Bigot

– Wing cell r_5 open (*e.g.*, Figs 141, 193, 195, 229) 125

125. Female ovipositor at least 2 × as long as high (in lateral view) (as in Figs 252, 253) 126

– Female ovipositor < 2 × as long as high (in lateral view) (Figs 254, 255) 130

126. Hind coxa with at least one lateral macroseta together with fine setae (*e.g.*, Figs 17, 230) 127

– Hind coxa with fine setae only (without macrosetae) 129

127. Discal wing cell (*d*) markedly constricted at mid length (Fig. 229) . . . . *Synolcus* Loew

– Discal wing cell (*d*) not markedly constricted at mid length (*e.g.*, Fig. 141) 128

128. Head with facial swelling smoothly (if only slightly) convex (Fig. 142); antennal stylus as long as or slightly longer than postpedicel (Fig. 142); thorax with scutum not markedly humped (Fig. 142); scutal mane (*i.e.*, long, tightly-packed, fine setae arranged in narrow strip mid-dorsally) undeveloped (Fig. 142) . . . . *Dasophrys* Loew

– Head with facial swelling undeveloped; antennal stylus shorter than postpedicel; thorax with scutum markedly humped; scutal mane well-developed . . . . *Gibbasilus* Londt

129. Scutellum with > 6 apical macrosetae; scutal mane (*i.e.*, long, tightly-packed, fine setae arranged in narrow strip mid-dorsally) well-developed, but without clearly discernible acrostichal macrosetae . . . . *Hippomachus* Engel

– Scutellum with 6 or fewer apical macrosetae; scutal mane well-developed with clearly discernible acrostichal macrosetae . . . . *Labarus* Londt

130. Female terminalia with ovipositor laterally compressed, distinctly longer than high (in lateral view) (Figs 254, 255); cercus smoothly rounded distally (Fig. 255); male terminalia (Figs 240–242), with abdominal sternite 8 with bifurcate medial process distally; phallus long, Z-shaped, each straight section being of similar length and general development . . . . *Millenarius* Londt

– Female terminalia with ovipositor usually tubular in form, but if somewhat laterally compressed, then never distinctly longer than high (in lateral view); male terminalia (Figs 243–235), with abdominal sternite 8 usually without medial process distally (if process present, then never bifurcate, but knob-like or in form of smoothly-rounded dorsoventrally flattened projection); male phallus short to moderately long, usually fairly straight, but if somewhat Z-shaped, then basal section invariably much more robust than other sections . . . . *Neolophonotus* Engel 131

131. Hind coxa with fine setae only; thorax with postpronotal lobe invariably with setae 132

– Hind coxa with at least 1 (often more) lateral macroseta in addition to fine setae; thorax with postpronotal lobe with or without setae 133

132. Thorax with scutal mane (*i.e.*, long, tightly-packed, fine setae arranged in narrow strip mid-dorsally), usually weakly developed, with only weak, loosely arranged, usually pale coloured setae (rarely absent) in posterior part or absent anteriorly; if scutal mane present, then not bicoloured (black anteriorly, pale yellow or white posteriorly) . . . . *Neolophonotus angustibarbus*-group

– Thorax with scutal mane well-developed, with longish setae arranged loosely or as tightly-packed row; scutal mane unicolourous black along entire length (may be bordered by smaller pale coloured setae) . . . . *Neolophonotus suillus*-group

133. Thorax with postpronotal lobes setose with several setae 134

– Thorax with postpronotal lobes bare (rarely with 1–3 isolated, erect setae) 135

134. Thorax with scutal mane (*i.e.*, long, tightly-packed, fine setae arranged in a narrow strip mid-dorsally), weakly to moderately developed, bicolourous (black setae anteriorly, white setae posteriorly) . . . . *Neolophonotus chionthrix*-group

– Thorax with scutal mane usually well-developed, unicolourous black (may be bordered by pale coloured setae; exceptions with white setae anteriorly and black setae posteriorly) . . . . *Neolophonotus comatus*-group

135. Thorax with scutal mane bicolourous (black setae anteriorly, black or yellow-white setae posteriorly) or unicolourous (white setae along entire length) . . . . *Neolophonotus pellitus*-group

– Thorax with scutal mane unicolourous black (often bordered by pale coloured setae; exceptions with white setae anteriorly and black setae posteriorly) . . . . *Neolophonotus squamosus*-group

136. Scutellum with 4 or more apical macrosetae 137

– Scutellum with 3 or fewer apical macrosetae (*e.g.*, Figs 95, 127) 138

137. Head with facial swelling confined to lower ½ of face; male terminalia with phallus straight. . . . . *Eremisca* Hull

– Head with facial swelling well-developed; male terminalia with phallus strongly curved . . . . *Machimus* Loew

138. Female abdominal sternites 1–5 pubescent, sternites 6–10 shiny and bare; female ovipositor telescopic, comprised of segment 6 and following abdominal segments. . . . .*Astochia* Becker

– Female abdominal sternites 1–6 (at least) pubescent; female ovipositor more or less conical, comprised of segment 8 and following abdominal segments 139

139. Antennal stylus composed of 2 articles (1 segment-like article, plus apical seta-like sensory article) (some Malagasy species with 3 articles) 140

– Antennal stylus composed of 3 articles (2 clearly evident segment-like articles, plus apical seta-like sensory article) 141

140. Mid femur swollen and with conspicuous cluster of well-developed macrosetae ventrally; proboscis curved upwards distally; thorax with dorsocentral macrosetae developed only postsuturally; female sternites 1–6 pubescent, sternites 7–9 shiny and bare; female cercus spinose, with well-developed macrosetae . . . . *Hoplopheromerus* Becker & *Curvirostris* Tomasovic

– Mid femur not conspicuously swollen, without cluster of well-developed macrosetae ventrally; proboscis straight; thorax with dorsocentral macrosetae developed pre- and postsuturally; female sternites 1–7 pubescent, sternites 8–9 shiny and bare; female cercus finely setose . . . . *Heligmonevra* Bigot

141. Thorax with postpronotal lobe (and much of scutum) clothed in uniformly short setae (some species have setae of intermediate length, Fig. 96); hind coxa usually with 2 lateral macrosetae (Fig. 96); male terminalia with epandrium with characteristic sub-apical dorsomedial lobe; male phallus straight, laterally compressed with at most tiny distal prongs; female ovipositor relatively short, only slightly laterally compressed distally . . . .*Afromochtherus* Lehr

– Thorax with postpronotal lobe with fine, long setae (e.g., Fig. 128); hind coxa usually with 1 lateral macroseta (*Notomochtherus* with *ca* 3 long, weak setae, barely differentiated from accompanying setae, e.g., Fig. 128); male terminalia with epandrium and phallus differently developed; female ovipositor of various forms 142

142. Male terminalia with phallus strongly curved, exceptionally long, often coiled; terminal abdominal segments with characteristic deep (laterally compressed) appearance; hypandrium not markedly constricted medially . . . .*Valiraptor* Londt

– Male terminalia with phallus more or less straight to bowed; terminal abdominal segments tubular, not laterally compressed; hypandrium slightly (*Notomochtherus*) to markedly constricted medially. . . .143

143. Hind femur uniformly dark red-brown to black (proximal or distal end may be paler) (e.g., Fig. 6) . . . 144

– Hind femur chiefly yellow, with or without distinct dark red-brown or blackish marks or fascia (e.g., Figs 9, 121). 146

144. Hind coxa with *ca* 3 weakly developed lateral macrosetae; male terminalia with phallus abruptly bent upwards at virtually mid length; female ovipositor broader than deep . . . . *Notomochtherus* Londt

– Hind coxa with single lateral macroseta; male terminalia with phallus more of less straight or with slight curve 145

145. Thorax with dorsocentral setae well-developed pre- and postsuturally; female terminalia with cercus finely setose; ovipositor laterally compressed; male terminalia with phallus of characteristic shape (shaft gently bowed, prongs short and weakly developed, sperm pump proximally situated (see Theodor 1976)) . . . . *Cerdistus* Loew

– Thorax with dorsocentral setae only well-developed postsuturally (Figs 6, 128); female terminalia with cercus usually spinose, short macrosetae dorsally or finely setose with strongly sclerotised, upturned tip; ovipositor conical; male terminalia with phallus of characteristic development (more or less straight or slightly sinuous, prongs short and moderately well-developed, lateral pair upwardly directed, median prong downwardly directed, sperm pump distally situated (see Londt & Tsacas 1987)) . . . . *Congomochtherus* Oldroyd

146. Hind femur almost entirely yellow (may have poorly defined pale brown patches or dark distal ends) (e.g., Fig. 122) 147

– Hind femur with well-defined dark red-brown patches or fascia (other than dark distal ends) (e.g., Fig. 9). 150

147. Antennal scape and trochanters blackish (e.g., Fig. 122) 148

– Antennal scape and trochanters yellowish 149

148. Confined to Southern Africa. . . . . *Caenoura* Londt

– Confined to Central Africa (*T. kivuensis* (Tsacas, 1969)). . . . . *Tsacasiella* Lehr [in part]

149. Head with facial swelling occupying ventral ½ of face and moderately developed; male terminalia not greatly elongate; epandrium with dorsomedial process; male gonocoxite not markedly elongate; gonostylus elongate, considerably longer than gonocoxite; phallus downwardly-curved distally, prongs minute. . . . . *Sphagomyia* Londt

– Head with facial swelling occupying < ½ of face and only weakly developed; male terminalia greatly elongate; epandrium usually with small ventrodistal process; male gonocoxite, gonostylus and phallus long, narrow and relatively straight. . . . . *Tsacasiella* Lehr [in part]

150. Male abdominal sternite 8 with prominent distomedial process . . . . *Gongromyia* Londt

– Male abdominal sternite 8 without prominent distomedial process. 151

151. Antennal postpedicel at least 2 × as long as scape; male terminalia with epandrium characteristically shaped, shortish, converging strongly distally; phallus bent abruptly upwards at virtually mid length and with 3 short, well-developed terminal prongs. . . . . *Dikowmyia* Londt

– Antennal postpedicel < 2 × as long as scape; male terminalia with epandrium and phallus of different shape. 152

152. Male terminalia with epandrium with complicated arrangement of lobes and processes distally; female ovipositor shortish, broad proximally, laterally compressed distally . . . . *Aneomochtherus* Lehr

– Male terminalia with epandrium simple, without lobes and processes; female ovipositor longish, laterally compressed for most of length . . . . *Melouromyia* Londt

Synopsis of the fauna

Ecological comments below follow Londt (1994*c*) and are based on personal observations as well as more recently available field photographs. The oviposition strategy is likewise based on personal observations together with ovipositor morphology.

***Acasilus* Londt** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *A. tigrimontis* Londt, 2005, confined to South Africa (Londt 2005*a*). The species inhabits semi-desert habitat and adults probably perch within and/or at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation.

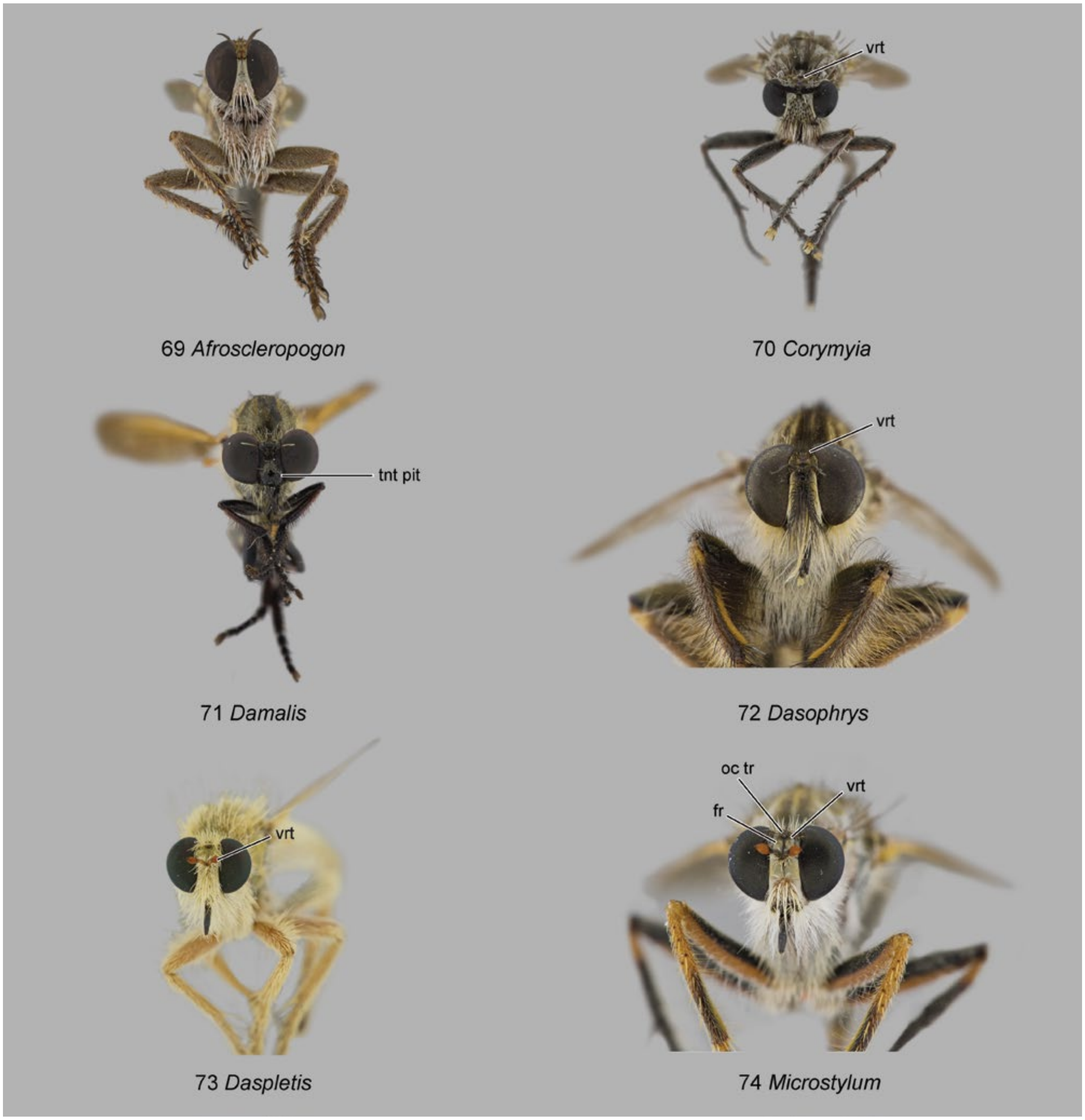
Acnephalomyia Londt (Willistonininae)**.** An endemic genus of seven small- to medium-sized, bee-like species (Figs 66, 85–88), confined to Southern Africa (Namibia and South Africa) (Londt 2010*c*). The genus inhabits desert, Fynbos, grassland, savanna, semi-desert and woodland habitats and adults perch on stones or on the ground (Fig. 66). Oviposition takes place in sand or soil. Londt (2010*c*) provided an identification key to the seven species.

***Afroestricus* Scarbrough** (Ommatiinae)**.** An endemic genus of 20 species of small- to large-sized flies (Figs 89, 90) described by Scarbrough (2005). The genus is widely distributed, in Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Cameroon, Chad, Democratic Republic of Congo, Gabon, Malawi, Republic of Congo and Zambia), East Africa (Burundi, Eritrea, Ethiopia, Kenya, Rwanda, Tanzania and Uganda), the southern Arabian Peninsula (Yemen), West Africa (Gambia, Ghana, Mali, Mauritania, Niger and Nigeria) and the Indian Ocean islands (Madagascar) (Scarbrough 2005). The genus inhabits savanna and woodland habitats and adults perch either on the ground or within or at the tips of shrubs and bushes. The oviposition strategy remains unknown, but probably involves random egg-dropping. Other useful references on the genus include Londt (2010*b*, 2012*a*) and Tomasovic & De Bakker (2010). Scarbrough (2005) provided an identification key to species.

***Afroholopogon* Londt** (Brachyrhopalinae)**.** An endemic genus of 19 described species of small- to medium-sized, bee-like species (Figs 18, 19, 91–94) (Londt 2005*b*). The distribution of the genus is centred in Southern Africa (Botswana, Namibia, South Africa, Swaziland and Zimbabwe), but is also recorded from East Africa (Eritrea and Kenya) and the southern Arabian Peninsula (Yemen and Oman). The genus inhabits grass in Fynbos, grassland, savanna, semi-desert and woodland habitats and adults perch either on rocks or within, or at the tips of grasses, shrubs and bushes (Figs 18, 19). Oviposition takes place in sand or soil. Other useful references to the genus include Londt (1994*a*). Londt (2005*b*) provided an identification key to all species.

***Afromelittodes* Oldroyd & Van Bruggen** (Laphriinae)**.** An endemic genus of two large-sized, bee-mimicking species confined to Southern Africa: *A. mimos* Londt, 2003 and *A. solis* Oldroyd & Van Bruggen, 1963 (both from Namibia and South Africa) (Londt 2003). The genus inhabits savanna and woodland habitats and adults perch within trees. Oviposition takes place on or in vegetation. Other useful references to the genus include Oldroyd & Van Bruggen (1963). Londt (2003) provided an identification key to the two species.

***Afromochtherus* Lehr** (Asilinae)**.** An endemic genus of 15 medium- to large-sized species (Figs 95, 96) reviewed by Londt (2002*b*) and Londt & Vieira (2013). The genus is fairly widespread throughout the Afrotropics and occurs in Southern Africa (Botswana, Namibia, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo, Malawi and Zambia), East Africa (Kenya and Tanzania) and the Indian Ocean islands (Madagascar). The genus inhabits Fynbos, grassland, savanna, semi-desert and woodland habitats and adults perch on the ground, on stones and rocks, within shrubs and bushes, or at the tips of branches. Oviposition takes place in sand or soil. Other useful references to the genus include Tomasovic (2006) and Tsacas (1969). An identification key to continental



69 *Afroscleropogon*

70 *Corymyia*

71 *Damalis*

72 *Dasophrys*

73 *Daspletis*

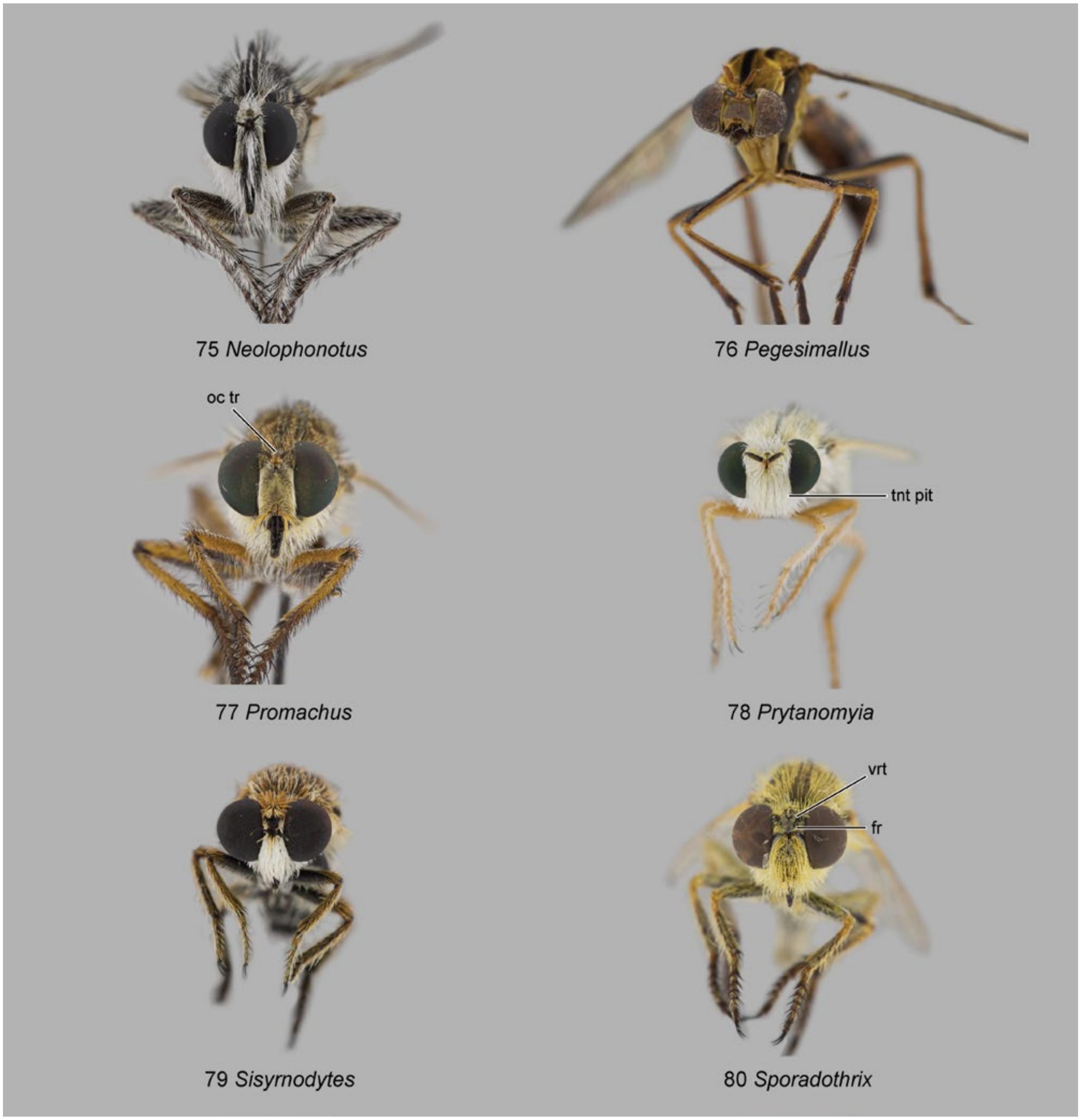
74 *Microstylum*

Figs 48.69–74. Heads of Afrotropical Asilidae (anterior views): (69) *Afroscleropogon* sp. ♀; (70) *Corymyia antimelas* Londt ♂; (71) *Damalis femoralis* Ricardo ♂; (72) *Dasophrys androclea* (Walker) ♂; (73) *Daspletis setithoracicus* (Ricardo) ♂; (74) *Microstylum* sp. ♂.

Abbreviations: fr – frons; oc tr – ocellar triangle; tnt pit – tentorial pit; vrt – vertex.

Afrotropical species was provided by Londt (2002*c*) and the Malagasy species by Londt & Vieira (2013).

Afromosia **Londt** (Laphriinae)**.** An endemic monotypic genus, with the single small-sized species, *A. barkemeyeri* Londt, 2015, confined to Central Africa (Cameroon) (Londt 2015*a*). The habitat and ecology of the species remain unknown, but it probably occurs at forest margins or in woodland savanna. Oviposition probably takes place through random egg-dropping or into vegetation.



75 *Neolophonotus* 76 *Pegesimallus*

77 *Promachus* 78 *Prytanomyia*

79 *Sisyrnodytes* 80 *Sporadothrix*

Figs 48.75–80. Heads of Afrotropical Asilidae (anterior views): (75) *Neolophonotus* sp. ♂; (76) *Pegesimallus calvifrons* Londt ♀; (77) *Promachus amastrus* (Walker) ♂; (78) *Prytanomyia kochi* (Lindner) ♀; (79) *Sisyrnodytes subater* Oldroyd ♀; (80) *Sporadothrix gracilis* Hermann ♂.

Abbreviations: fr – frons; oc tr – ocellar triangle; tnt pit – tentorial pit; vrt – vertex.

***Afroscleropogon* Londt** (Stenopogoninae)**.** An endemic genus of seven medium-sized species (Figs 69, 97, 98) confined to Southern Africa (Botswana, Namibia and South Africa) (Londt 1999*d*). The genus inhabits Fynbos, grassland, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. A useful additional reference is Oldroyd (1974), who treated species under the name *Stenopogon* Loew. Londt (1999*d*) provided an identification key to species.

***Agrostomyia* Londt** (Brachyrhopalinae)**.** An endemic monotypic genus, with the single medium-sized species, *A. dimorpha* Londt, 1994, confined to Southern Africa (Namibia and South Africa) (Londt 1994*b*). Other useful references include Londt (1999*d*). The species inhabits savanna and grassland habitats and adults perch on the ground or within grass. Oviposition takes place in sand or soil.

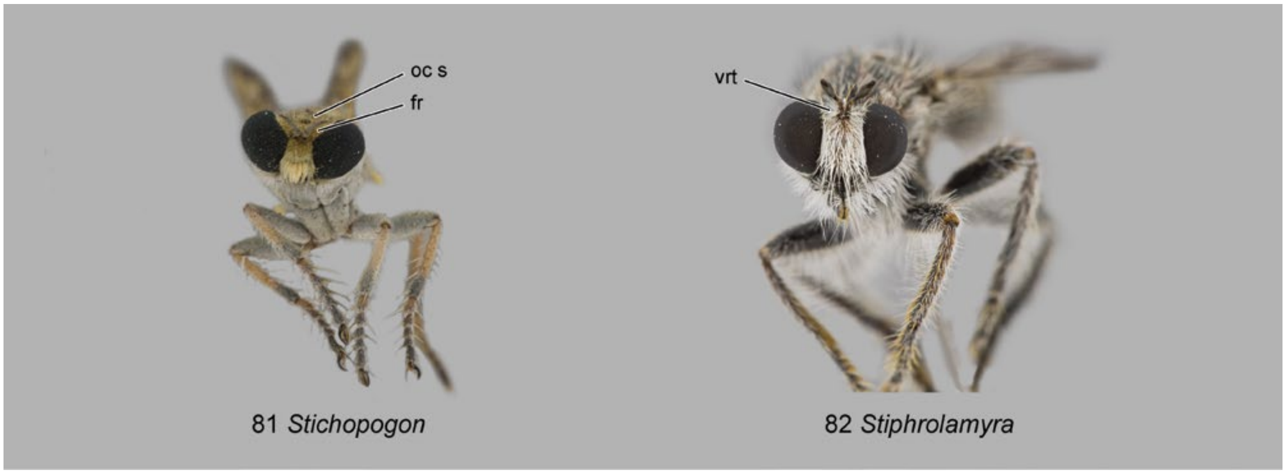
***Akatiomyia* Londt** (*incerta sedis*)**.** An endemic monotypic genus, with the single small-sized, black species, *A. eremnos* Londt, 2013, confined to Southern Africa (South Africa) (Londt 2013*a*). The species inhabits Fynbos habitats and adults perch at the tips of shrubs and bushes. Oviposition takes place in sand or soil.

***Alcimus* Loew** (Asilinae)**.** A medium-sized genus of 18 described very large-sized species (Figs 2, 3, 99, 100), requiring modern revision. Currently, considered an Afrotropical endemic, although it may occur in the south-western Palaearctic Region. The genus is widespread throughout sub-Saharan Africa, being recorded from Southern Africa (South Africa and Zimbabwe), Central Africa (Malawi), East Africa (Ethiopia, Kenya, Sudan, Tanzania and Uganda) and West Africa (Gambia and Senegal). The genus inhabits grassland, savanna and woodland habitats and adults perch on the ground, including river banks, on rocks, or at the tips of shrubs and bushes (Figs 2, 3). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1933, 1934, 1935, 1936, 1937, 1938, 1939) and Engel & Cuthbertson (1934). Other useful references include Engel & Cuthbertson (1934), Londt (2005*a*, 2010*b*) and Oldroyd (1974). No identification key to Afrotropical species is currently available.

***Ammodaimon* Londt** (Willistonininae)**.** A small endemic genus of two small-sized, bee-like species (Figs 101, 102), *A. acares* Londt, 1985 and *A. platythrix* Londt, 2010, confined to Southern Africa (Namibia) (Londt 1985*c*). Unpublished records indicate that the genus also occurs in South Africa. The genus inhabits grassland and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (2010*c*) provided an identification key to the two species.

***Ammophilomima* Enderlein** (Leptogastrinae)**.** A medium-sized genus of 41 large-sized species (Figs 103, 104), recorded from the Afrotropical and Oriental Regions and reviewed by Janssens (1953) and Martin (1973). The ten Afrotropical species are recorded from Central Africa (Cameroon and Democratic Republic of Congo), East Africa (Burundi and Kenya) and West Africa (Nigeria), although most species are recorded from Democratic Republic of Congo. There are unpublished records of the genus from Angola, Central African Republic, Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Liberia, Malawi, Mozambique, Togo and Uganda. The biology remains unknown, but the genus probably inhabits forest habitats and adults perch within or at the tips of shrubs and bushes. Oviposition probably takes place through random egg-dropping. Other useful references include Janssens (1955) and Oldroyd (1970). Martin (1973) provided an identification key to Afrotropical species.

***Amphisbetetus* Hermann** (Brachyrhopalinae)**.** A genus of 12 small-sized, often bee-like species (Figs 105, 106), primarily known from the south-western Palaearctic Region, but also recorded from the Australasian Region. The single Afrotropical species, *A. hermanni* Bosák & Hradský, 2011, is confined to the southern Arabian Peninsula (United Arab Emirates) (Bosák



Figs 48.81–82. Heads of Afrotropical Asilidae (anterior views): (81) *Stichopogon hermanni* Bezzi ♂; (82) *Stiphrolamyra diaxantha* (Hermann) ♂.

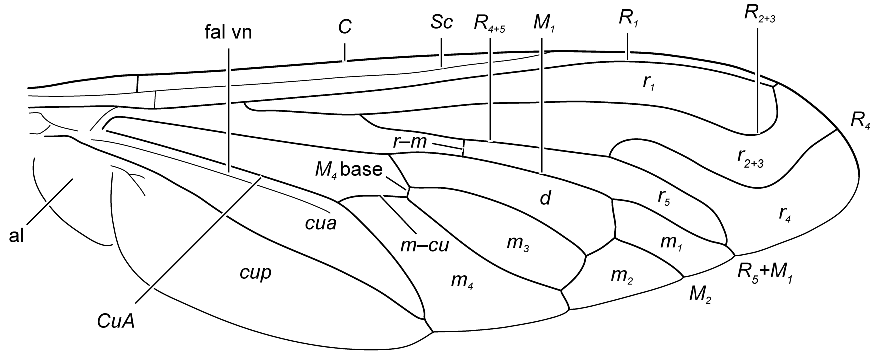
Abbreviations: fr – frons; oc tr – ocellar triangle; vrt – vertex.

& Hradský 2011: 729). Other useful references include Efflatoun (1937) and Theodor (1980). The biology remains unknown, but the genus probably inhabits semi-desert habitats and adults probably perch on the ground or on low vegetation. Oviposition takes place in sand or soil.

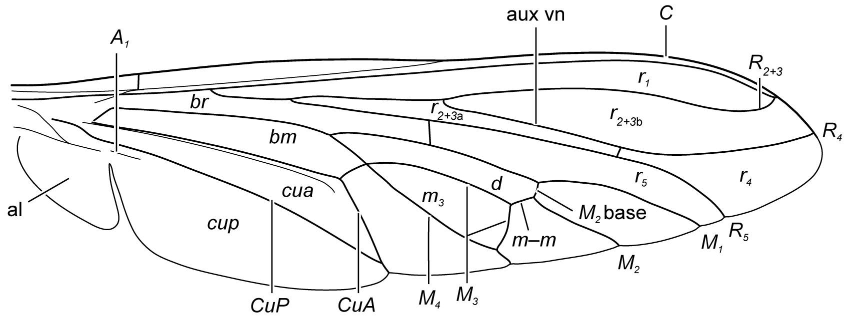
***Anasillomos* Londt** (Stenopogoninae)**.** An endemic genus of two medium-sized species (Figs 107, 108), *A. chrysopos* Londt, 1983 and *A. juergeni* Dikow, 2015, confined to Southern Africa (Botswana, Namibia and South Africa) (Dikow 2015). The genus inhabits grassland, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Dikow & Londt (2000*b*) and Londt (1983*c*). Dikow (2015) provided an identification key to the two species.

***Ancylorhynchus* Berthold** (Stenopogoninae)**.** A large genus of 50 medium- to large-sized, wasp-like species (Figs 109, 110, 292–294, 298–300), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. The 27 Afrotropical species were reviewed by Londt (2011) and are widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo, Malawi and Zambia), East Africa (Burundi, Eritrea, Kenya, Somalia, Sudan and Tanzania) and West Africa (Côte d'Ivoire, Gambia, Ghana and Nigeria). The genus inhabits forest (possibly), Fynbos, grassland, savanna, semi-desert and woodland habitats and adult perch on the ground, on rocks and at the tips of grass. Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1935, 1936). Other useful references include Bromley (1936), Oldroyd (1970, 1974) and Londt (2010*b*). Londt (2011) provided an identification key to Afrotropical species.

***Andrenosoma* Rondani** (Laphriinae)**.** A genus of 64 medium- to large-sized species, occurring in all zoogeographical



83 *Hoplistomerus*

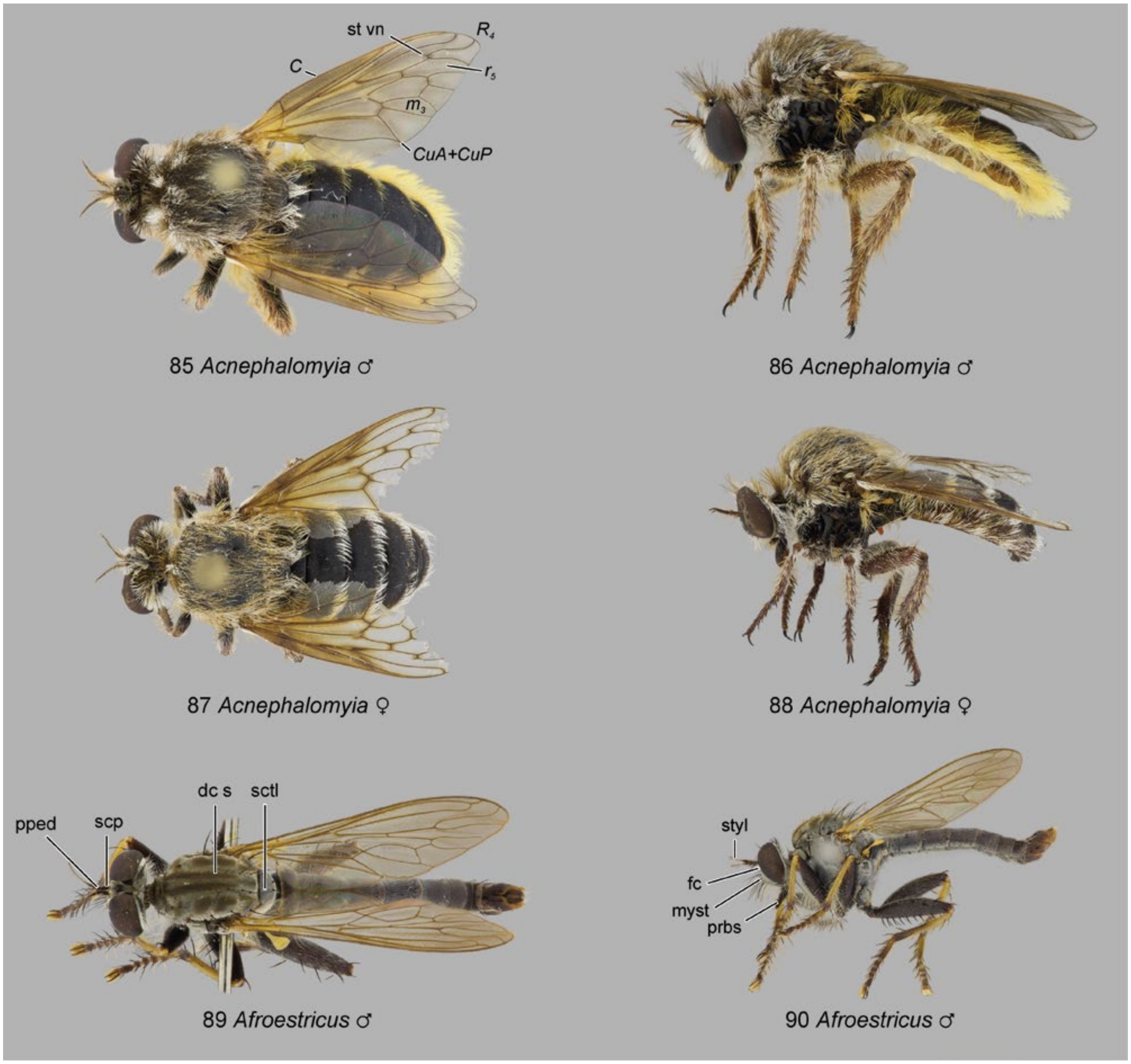


84 *Promachus*

Figs 48.83–84. Wings of Afrotropical Asilidae (dorsal views): (83) *Hoplistomerus nobilis* Loew; (84) *Promachus amastrus* (Walker).

Abbreviations: *A_1* – first branch of anal vein; al – alula; aux vn – auxiliary vein; *bm* – basal medial cell; *br* – basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; fal vn – false vein; *M_1* – first branch of media; *m_1* – first medial cell; *M_2* – second branch of media; *m_2* – second medial cell; *M_3* – third branch of media; *m_3* – third medial cell; *M_4* – fourth branch of media; *m_4* – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; *R_1* – anterior branch of radius; *r_1* – first radial cell; *R_{2+3}* – second branch of radius; *r_{2+3}* – second + third radial cell; *r_4* – fourth radial cell; *R_4* – upper branch of third branch of radius; *R_{4+5}* – third branch of radius; *r_5* – fifth radial cell; *R_5* – lower branch of third branch of radius; *R_5+M_1* – lower branch of third branch of radius + first branch of media; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.

regions, except Antarctica. Two species occur in the Afrotropical Region, *A. boranicum* Corti, 1895 and *A. serpentina* (Bezzi, 1908), that are widespread throughout sub-Saharan Africa, recorded from Southern Africa (South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo and Malawi), East Africa (Ethiopia and Kenya) and West Africa (Côte d'Ivoire). The biology is poorly known, but species probably inhabit forest, savanna and woodland habitats and adults probably perch within shrubs, bushes and trees. Oviposition takes place in vegetation. The immature stages of the extralimital species, *Andrenosoma cruentum* (McAtee, 1919) (Figs 320–323) were described by Dennis & Barnes (2014). Other useful references include Engel & Cuthbertson (1937), Oldroyd (1970), the unpublished thesis of Fisher (1986) and Tomasovic (2010). No identification key to Afrotropical species is currently available.

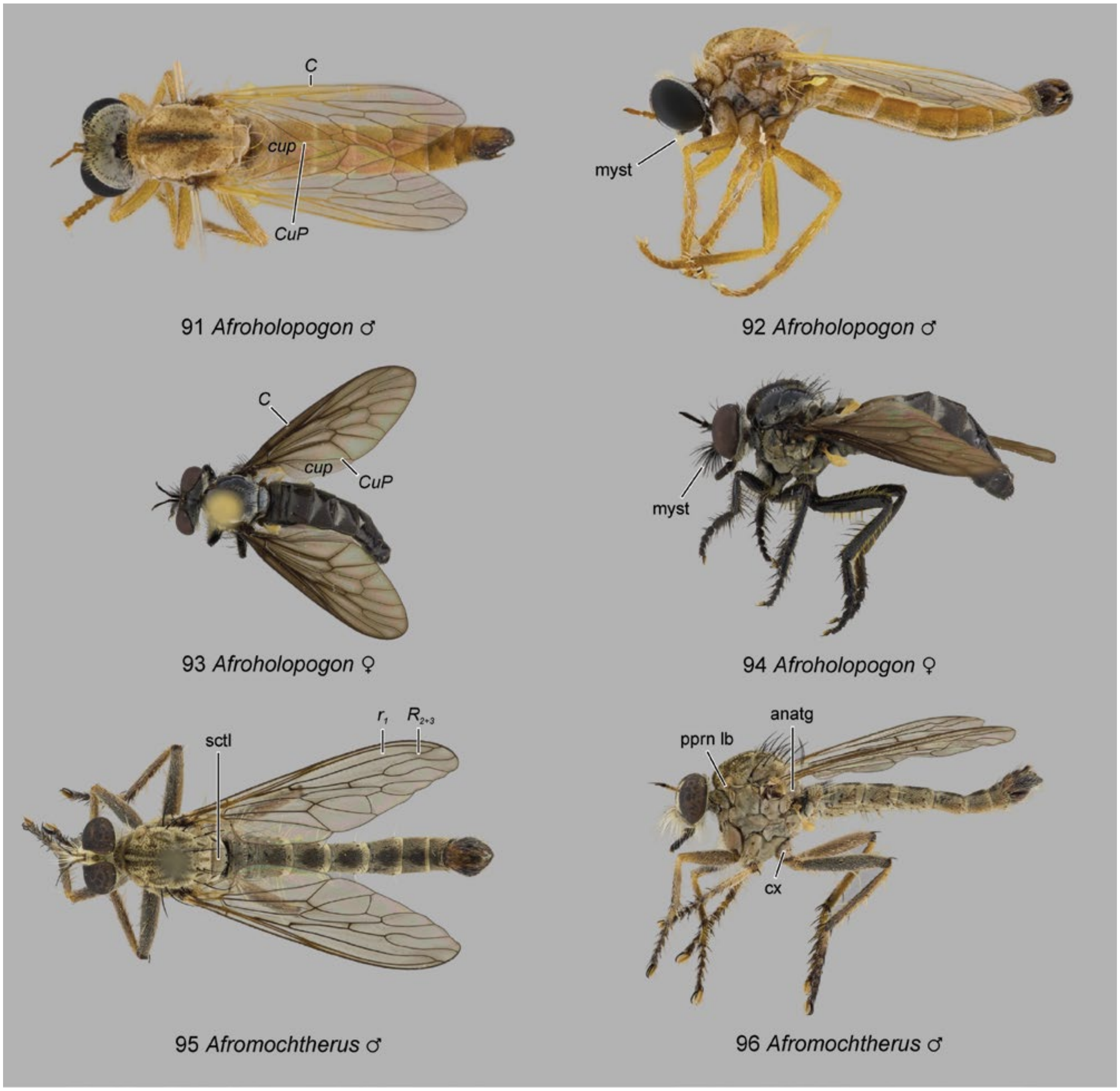


Figs 48.85–90. Habitus photographs of Asilidae: (85) *Acnephalomyia* sp. ♂, dorsal view; (86) same, lateral view; (87) *Acnephalomyia* sp. ♀, dorsal view; (88) same, lateral view; (89) *Afroestricus chiastoneurus* (Speiser) ♂, dorsal view; (90) same, lateral view.

Abbreviations: *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; dc s – dorsocentral seta; fc – face; m_3 – third medial cell; myst – mystax; pped – postpedicel; prbs – proboscis; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; scp – scape; sctl – scutellum; st vn – stump vein; styl – stylus.

***Aneomochtherus* Lehr** (Asilinae)**.** A genus of 63 medium-sized species, occurring in the Afrotropical, Oriental and Palaearctic Regions. The three Afrotropical species, *A. africanus* (Ricardo, 1919), *A. deserticolus* (Karsch, 1888) and *A. monobia* (Speiser, 1910), are confined to East Africa (Kenya and Tanzania) and were reviewed by Londt (2002*b*). Habitat requirements of the genus remain unknown, but probably comprise savanna and woodland habitats and adults probably perch within and/or at the tips of trees and shrubs. Oviposition takes place on or in vegetation. Londt (2002*b*) provided an identification key to Afrotropical species.

***Antiscylaticus* Londt** (Brachyrhopalinae)**.** An endemic monotypic genus, with the single medium-sized species, *A. snowi* Londt, 2010, confined to West Africa (Gambia) (Londt 2010*b*, 2012*a*). The species inhabits grassland habitats and



91 *Afroholopogon* ♂ 92 *Afroholopogon* ♂

93 *Afroholopogon* ♀ 94 *Afroholopogon* ♀

95 *Afromochtherus* ♂ 96 *Afromochtherus* ♂

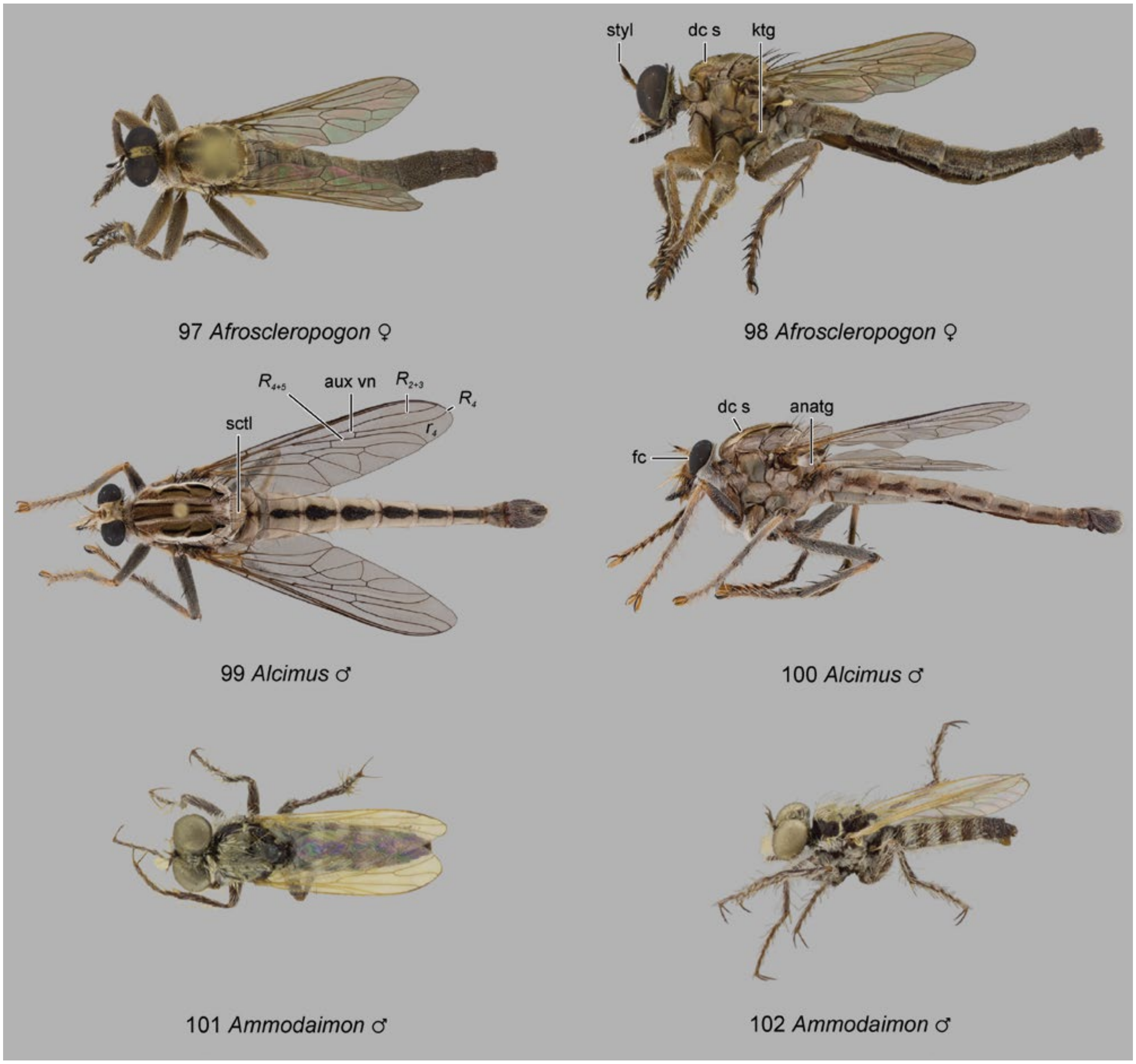
Figs 48.91–96. Habitus photographs of Asilidae: (91) *Afroholopogon* sp., dorsal view ♂; (92) same, lateral view; (93) *Afroholopogon* sp., dorsal view ♀; (94) same, lateral view; (95) *Afromochtherus mendax* (Tsacas), dorsal view ♂; (96) same, lateral view.

Abbreviations: anatg – anatergite; *C* – costal vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; cx – coxa; myst – mystax; pprn lb – postpronotal lobe; r_1 – first radial cell; R_{2+3} – second branch of radius; sctl – scutellum.

adults probably perch on the ground or within and at the tips of grass. Oviposition takes place in sand or soil.

***Anypodetus* Hermann** (Laphriinae)**.** An endemic genus of eight medium-sized, bee-like species (Figs 25, 26, 111, 112, 264–266) reviewed by Londt (2000*a*). The genus is more or less confined to Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe) and Central Africa (Zambia). The genus inhabits open sandy places in forest, grassland, savanna, semi-desert and woodland habitats and adults perch on the ground, but have also been observed to perch on low vegetation (Figs 25, 26). The oviposition strategy is unknown, but probably takes place directly into sand. Other useful references include Oldroyd (1974). Londt (2000*a*) provided an identification key to species.

***Apoclea* Macquart** (Asilinae)**.** A genus of 21 medium-sized species (Figs 4, 5, 113–116), occurring in the Afrotropical,



97 *Afroscleropogon* ♀

98 *Afroscleropogon* ♀

99 *Alcimus* ♂

100 *Alcimus* ♂

101 *Ammodaimon* ♂

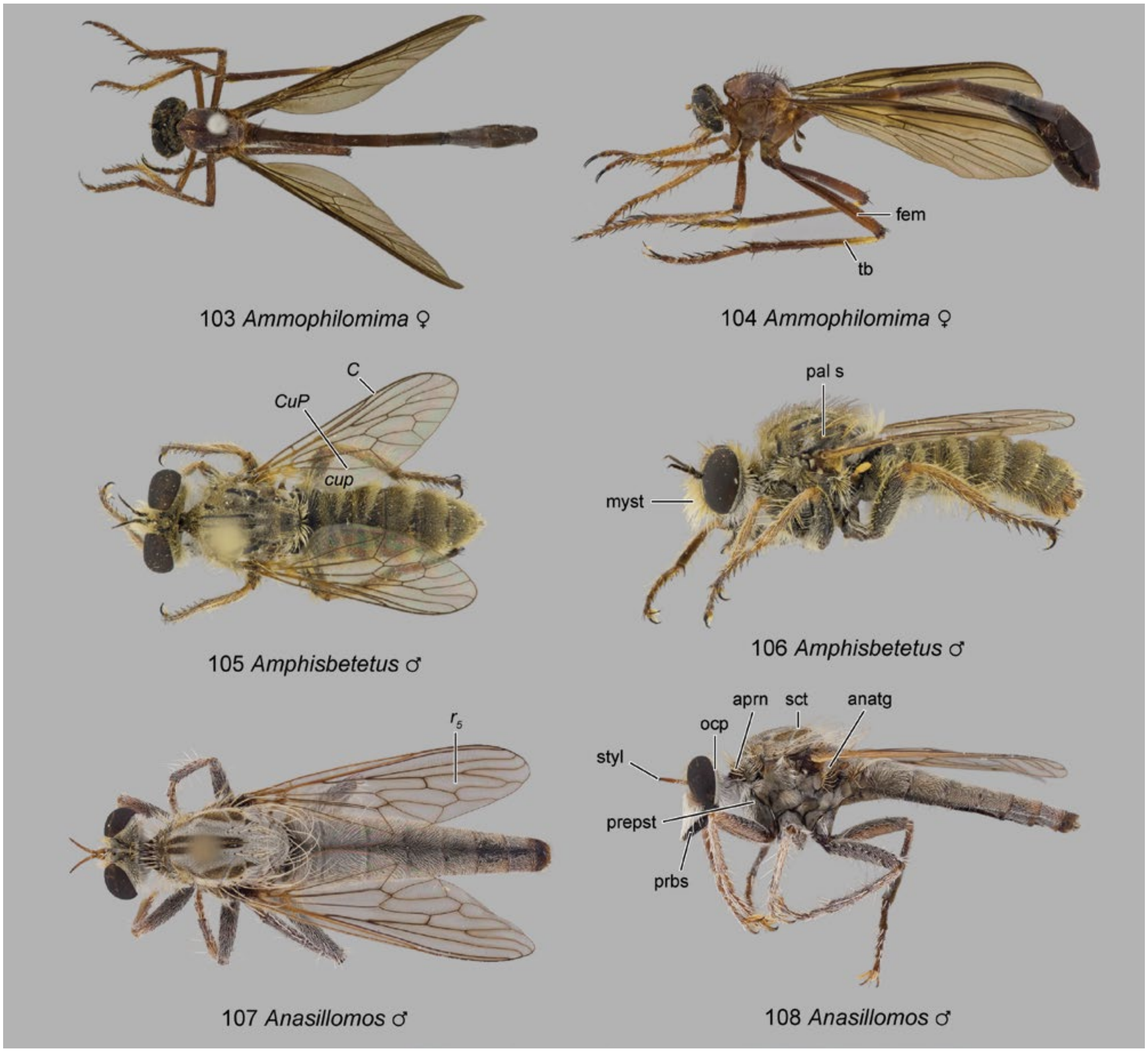
102 *Ammodaimon* ♂

Figs 48.97–102. Habitus photographs of Asilidae: (97) *Afroscleropogon* sp., dorsal view ♀; (98) same, lateral view; (99) *Alcimus* sp., dorsal view ♂; (100) same, lateral view; (101) *Ammodaimon* sp., dorsal view ♂; (102) same, lateral view.

Abbreviations: anatg – anatergite; aux vn – auxiliary vein; dc s – dorsocentral seta; fc – face; ktg – katatergite; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; sctl – scutellum; styl – stylus.

Oriental and Palaearctic Regions. Four species are recorded from the Afrotropics, from East Africa (Sudan), the southern Arabian Peninsula (Oman, United Arab Emirates and Yemen) and West Africa (Niger). Unpublished records are also known for Djibouti and Senegal. The genus inhabits desert and semi-desert habitats and adults perch on the ground or on low vegetation (Figs 4, 5). Oviposition probably takes place in sand or soil. Other useful references include Bosák & Hradský (2011), Efflatoun (1934, 1937), Londt (2005*a*) and Walker & Pittaway (1987). No identification key to Afrotropical species is currently available.

***Astiptomyia* Londt** (Willistonininae)**.** An endemic monotypic genus, with the single small, bee-like species, *A. bikos* Londt, 2010 (Figs 117, 118), confined to Southern Africa (Namibia) (Londt 2010*c*). The species inhabits desert and semi-desert



Figs 48.103–108. Habitus photographs of Asilidae: (103) *Ammophilomima auripennis* Janssens, dorsal view ♀; (104) same, lateral view; (105) *Amphisbetetus favillaceus* (Loew), dorsal view ♂ (non-Afrotropical); (106) same, lateral view; (107) *Anasillomos juergeni* Dikow, dorsal view ♀; (108) same, lateral view.

Abbreviations: anatg – anatergite; aprn – antepronotum; *C* – costal vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; fem – femur; myst – mystax; ocp – occiput; pal s – postalar seta; prbs – proboscis; prepst – proepisternum; r_5 – fifth radial cell; sct – scutum; styl – stylus; tb– tibia.

habitats and adults probably perch on the ground. Oviposition takes place in sand or soil.

Astochia **Becker** (Asilinae)**.** A genus of 44 large-sized species, occurring in the Afrotropical, Australasian (possibly), Oriental and Palaearctic Regions (Geller-Grimm 2004). Five species reviewed by Londt (1982*b*) occur in the Afrotropics that are widespread throughout sub-Saharan Africa, recorded from Southern Africa (South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo and Malawi), East Africa (Kenya, Tanzania and Uganda), the southern Arabian Peninsula (Yemen) and West Africa (Nigeria and Sierra Leone). The genus inhabits savanna and woodland habitats and adults perch at the tips of grass, shrubs and bushes. Oviposition takes place on or in vegetation. Other useful references include Londt (2002*b*). Londt (1982*b*) provided an identification key to the five Afrotropical species.

Bana **Londt** (Stenopogoninae)**.** An endemic genus described by Londt (1992*b*), comprising two large-sized, bee-like species (Figs 119, 120), *B. apicida* Londt, 1992 and *B. madiba* Londt, 2013, confined to Southern Africa (Namibia and South Africa) (Londt 2013*b*). The genus inhabits grassland, savanna and semi-desert habitats and adults perch on the ground or at the tips of grass, shrubs and bushes. Oviposition takes place in sand or soil. Londt (2013*b*) provided an identification key to the two species.

Caenoura **Londt** (Asilinae)**.** An endemic genus of two small- to medium-sized species (Figs 121, 122), described by Londt (2002*b*), *C. annulitarsis* (Loew, 1858) and *C. sinuatus* (Loew, 1858), confined to Southern Africa (Lesotho, South Africa and Zimbabwe). The genus inhabits grassland, savanna and woodland habitats and adults perch within grass. Oviposition takes place on or in vegetation. Londt (2002*b*) provided an identification key to the two species.

Caroncoma **Londt** (Dasypogoninae)**.** An endemic monotypic genus described by Londt (1980*b*), with the single medium-sized species, *C. atrimaculatus* (Oldroyd, 1960), confined to the Indian Ocean islands (Madagascar). The species probably inhabits forest habitats and adults probably perch on the ground or within or at the tips of shrubs and bushes. Oviposition takes place in sand or soil. Other useful references include Oldroyd (1960*a*).

Cerdistus **Loew** (Asilinae)**.** A genus of 64 medium-sized species, occurring in the Afrotropical, Australasian (doubtfully), Oriental and Palaearctic Regions (Geller-Grimm 2004). The single Afrotropical species, *C. griseola* (Oldroyd, 1960), was recorded from Madagascar by Oldroyd (1960*b*), but remains doubtful and requires revision, along with Palaearctic species. Geller-Grimm (2002) further records an undescribed species from Socotra Is. (Yemen). The genus inhabits either forest (Madagascar) or semi-desert (Socotra Is.) habitats and adults perch within and/or at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation. Other useful references include Londt (2002*b*).

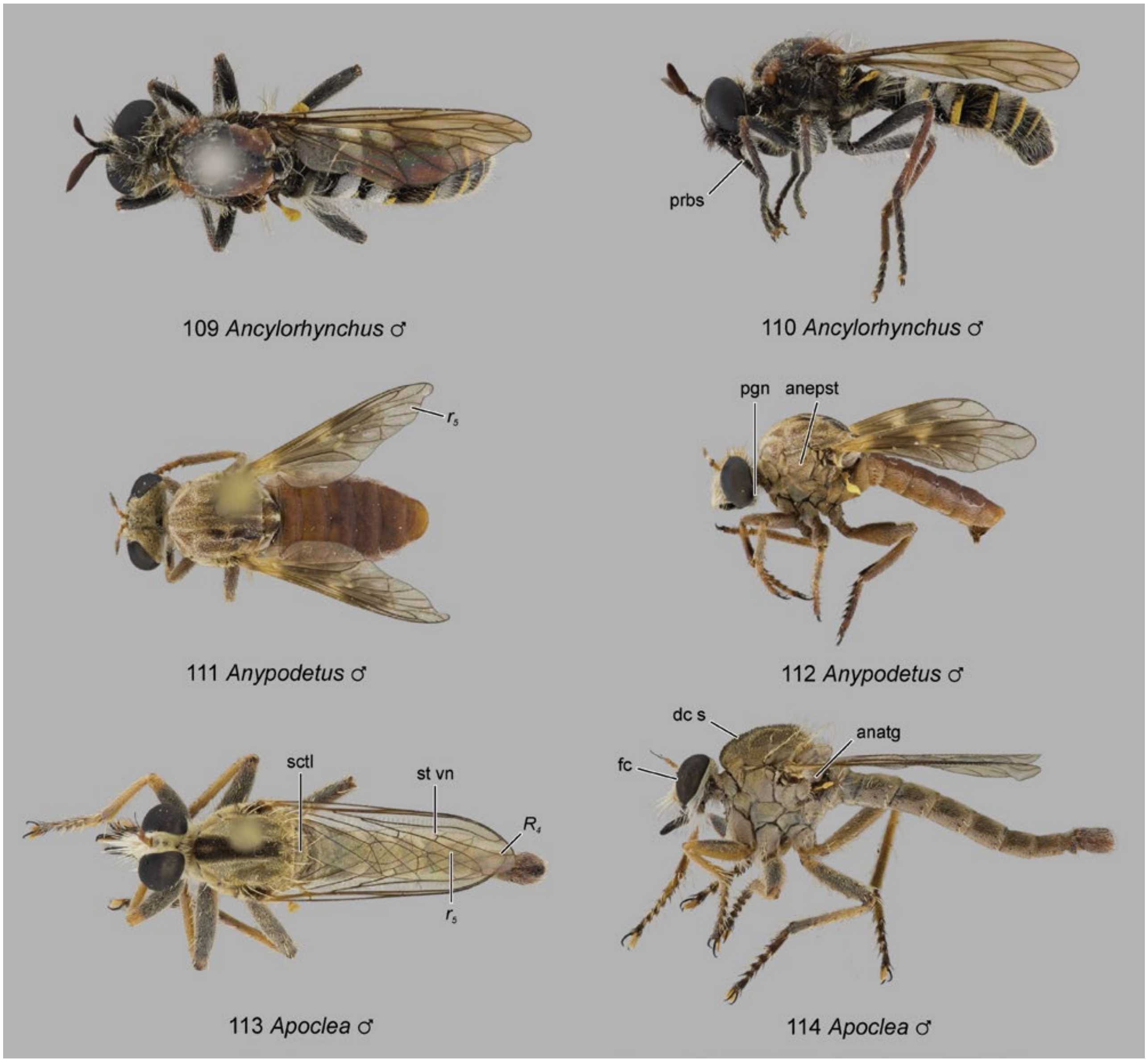
Choerades **Walker** (Laphriinae)**.** A genus of 75 medium-sized, bee-like species (Figs 27, 123, 124), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Twenty-five species occur in the Afrotropics, but the genus requires modern revision. Londt (1977) reviewed the Southern African species, while Londt (2015*a*) discussed the genus and transferred species then catalogued as *Laphria* to this and other genera. Species of the genus are widespread throughout sub-Saharan Africa, recorded from Southern Africa (Mozambique, South Africa and Zimbabwe), Central Africa (Cameroon, Democratic Republic of Congo, Gabon, Malawi and Republic of Congo), East Africa (Uganda) and West Africa (Côte d'Ivoire, Gambia, Ghana, Liberia, Nigeria and Sierra Leone). A single record for an Indian Ocean island (Seychelles) requires confirmation. The genus inhabits forest habitats (including thick coastal bush) and adults perch at the tips of shrubs, bushes and trees and within trees. Oviposition takes place on or in vegetation (wood). Some biological information (as *Laphria*) was provided by Cuthbertson (1936). Other useful references include Oldroyd (1970), who produced a key to Afrotropical *Laphria*, that includes species now assigned to *Choerades*, Oldroyd (1974), who keyed the Southern African species (also under the name *Laphria*), Bromley (1935), Tomasovic (2007, 2008*a*) and Londt (2015*a*). No useful identification key to Afrotropical species is currently available.

Clinopogon **Bezzi** (Stichopogoninae)**.** A genus of nine medium-sized species (Figs 125, 126), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Two species occur in the Afrotropics, *C. nicobarensis* (Schiner, 1868) and *C. reginaldi* (Séguy, 1955). This littoral genus is distributed along almost the entire eastern coastline of Africa (*C. nicobarensis*) and Tromelin Is. (*C. reginaldi*). The genus inhabits maritime beach habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Londt & Copeland (2017), Oldroyd (1974) and Séguy (1955). Although Londt (1979*b*) briefly reviewed the Afrotropical species, the genus requires modern revision and no identification key to Afrotropical species is currently available.

Congomochtherus **Oldroyd** (Asilinae)**.** An endemic genus of seven medium-sized species (Figs 6, 127, 128), reviewed by Londt & Tsacas (1987) and Londt (2014*c*). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Namibia, South Africa and Zimbabwe), Central Africa (Angola, Cameroon, Democratic Republic of Congo, Republic of Congo and Zambia), East Africa (Kenya, Tanzania and Uganda) and West Africa (Nigeria). The genus inhabits Fynbos, grassland, savanna and woodland habitats and adults perch on the ground, on stones, riverbanks and other riparian habitats, including rocks surrounded by water (Fig. 6). Oviposition probably takes place in riverine sand or soil. Other useful references include Londt (2002*b*) and Oldroyd (1970). Londt (2014*c*) provided an identification key to the seven species.

Connomyia **Londt** (Stenopogoninae)**.** A near endemic genus of 22 medium-sized, bee-like species (Figs 129, 130), occurring in the Afrotropical and Oriental Regions. The 20 Afrotropical species were reviewed by Londt (1993*c*) and are widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo and Malawi), East Africa (Eritrea, Kenya and Tanzania) and West Africa (Burkina Faso, Gambia, Mali, Nigeria and Senegal). The genus inhabits Fynbos, grassland, savanna and woodland habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Londt (2010*b*). Londt (1993*c*) provided an identification key to Afrotropical species.

Cophinopoda **Hull** (Ommatiinae)**.** A genus of 11 large- to very large-sized species (Figs 46, 131, 132), occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions. Five species occur in the Afrotropics, that were reviewed by Tsacas & Artigas (1994) and are confined to the Indian Ocean islands of Comoros, Europa Is., Madagascar (incl. Sainte-Marie Is.), Mauritius (Maurice Is.), Réunion Is., Seychelles (incl. Aldabra and Cosmoledo Is.) and Socotra Is. (Yemen). The biology remains unknown, but species apparently inhabit "dry forest, scrub" and other island vegetation and adults probably perch at the tips of shrubs and bushes (Fig. 46). The oviposition strategy probably involves random egg-dropping. Other useful references include Martin (1964). Tsacas & Artigas (1994) provided an identification key to the five Afrotropical species.

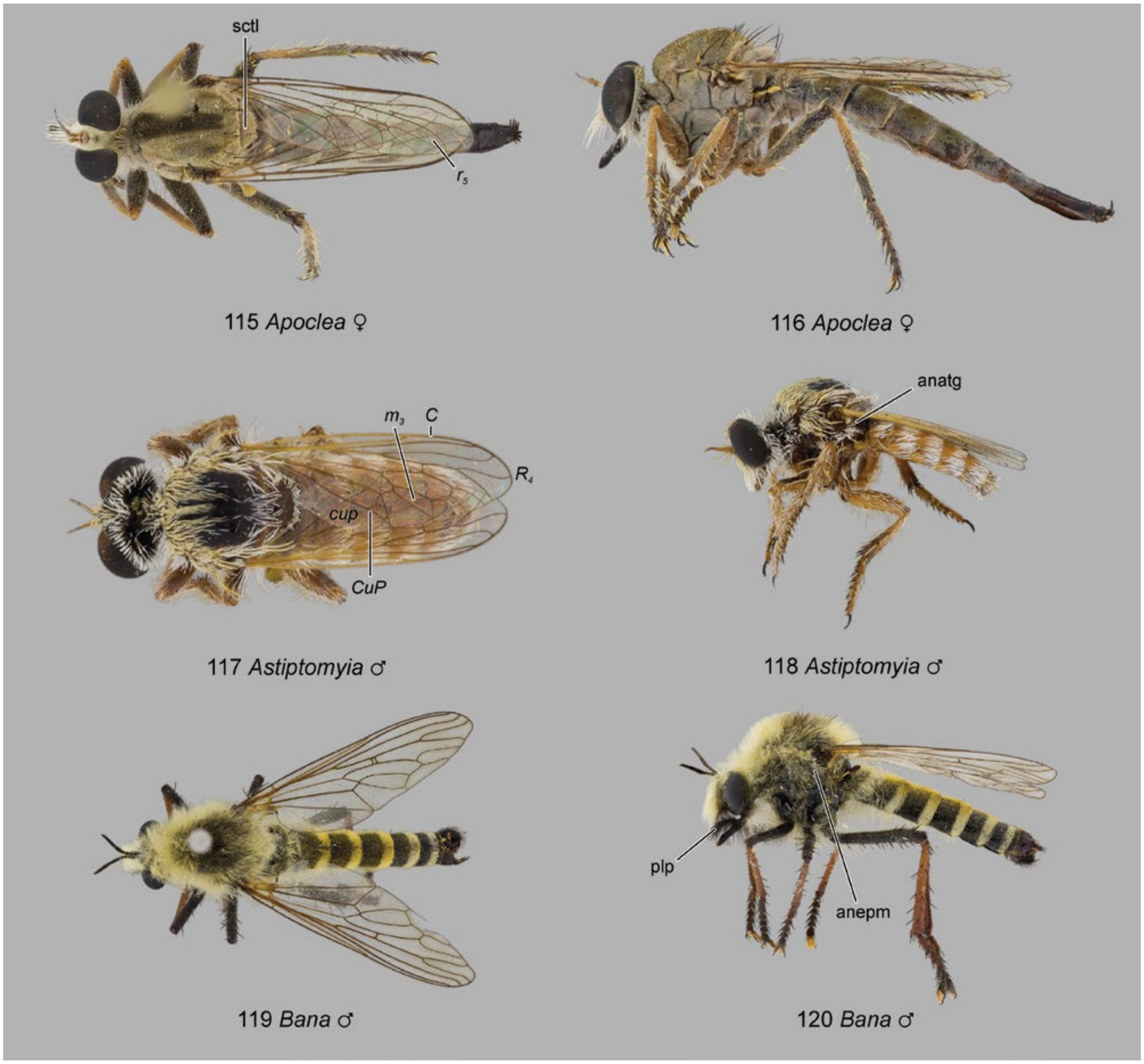


Figs 48.109–114. Habitus photographs of Asilidae: (109) *Ancylorhynchus unifasciatus* (Loew), dorsal view ♂; (110) same, lateral view; (111) *Anypodetus fascipennis* Engel, dorsal view ♂; (112) same, lateral view; (113) *Apoclea* sp., dorsal view ♂; (114) same, lateral view.

Abbreviations: anatg – anatergite; anepst – anepisternum; dc s – dorsocentral seta; fc – face; pgn – postgena; prbs – proboscis; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; sctl – scutellum; st vn – stump vein.

***Corymyia* Londt** (Stenopogoninae)**.** An endemic genus of four small-sized species (Figs 70, 133–136), confined to Southern Africa (South Africa) (Londt 1994*b*). The genus inhabits grassland, Fynbos and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (1994*b*) provided an identification key to the four species.

***Ctenota* Loew** (Laphriinae)**.** A genus of seven medium- to large-sized species, occurring in the Afrotropical and Palaearctic Regions. Two species occur in the Afrotropics, *C. molitrix* Loew, 1873 and *C. ruficornis* (Wulp, 1899), confined to the southern Arabian Peninsula (United Arab Emirates and Yemen) and East Africa (Sudan). The genus most probably inhabits semi-desert habitats and adults probably perch on the ground, on stones or in riparian habitats. Oviposition takes place in sand or soil. Other useful references include Efflatoun (1934), who provided an excellent description of the type species (*C. molitrix*), which occurs in Egypt, Hull (1962), Theodor (1980) and Bosák



115 *Apoclea* ♀

116 *Apoclea* ♀

117 *Astiptomyia* ♂

118 *Astiptomyia* ♂

119 *Bana* ♂

120 *Bana* ♂

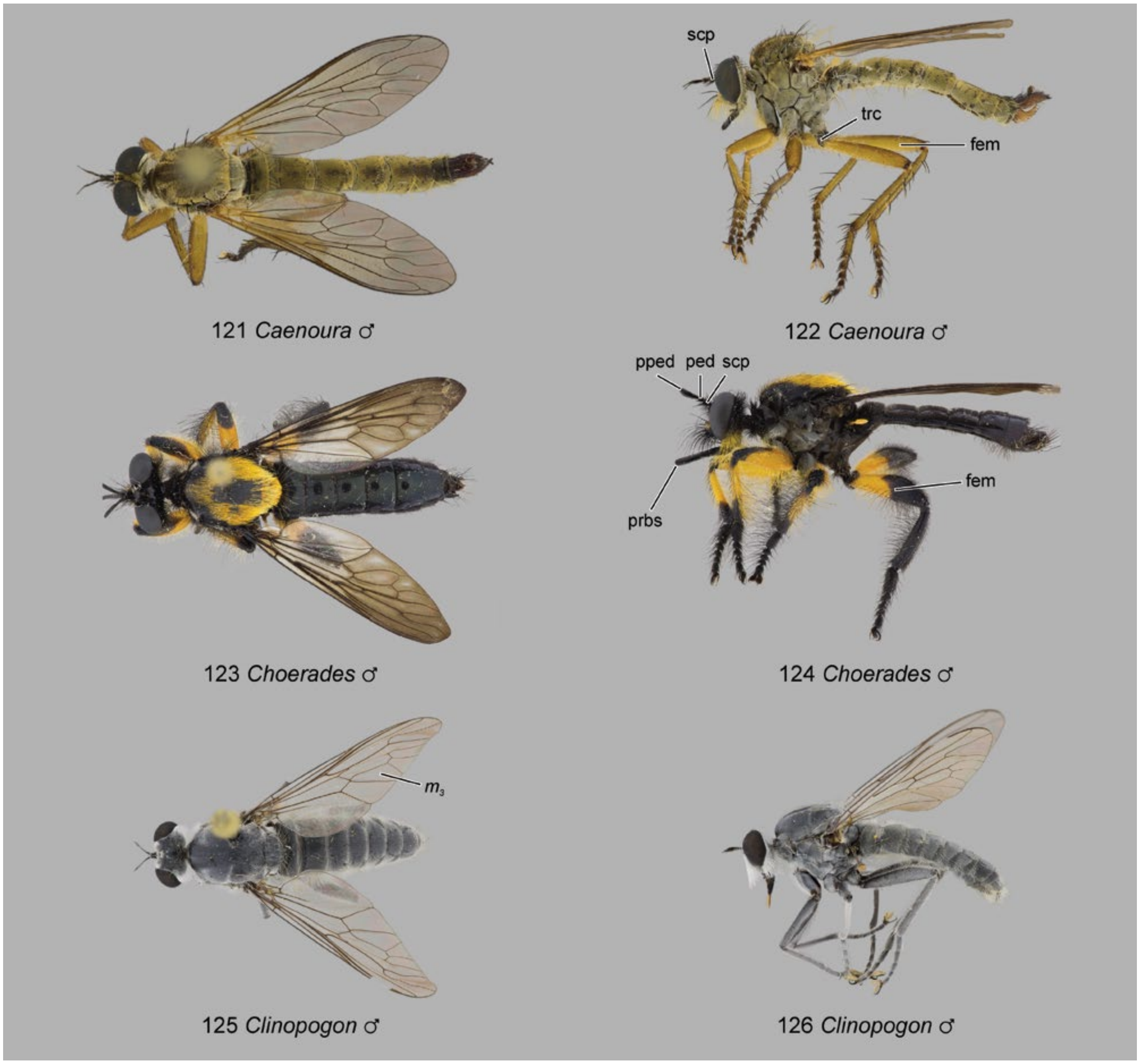
Figs 48.115–120. Habitus photographs of Asilidae: (115) *Apoclea* sp., dorsal view ♀; (116) same, lateral view; (117) *Astiptomyia bikos* Londt, dorsal view ♂; (118) same, lateral view; (119) *Bana apicida* Londt, dorsal view ♂; (120) same, lateral view.

Abbreviations: anatg – anatergite; anepm – anepimeron; *C* – costal vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; m_3 – third medial cell; plp – palpus; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; sctl – scutellum.

& Hradský (2011). No identification key to Afrotropical species is currently available.

Curvirostris **Tomasovic** (Asilinae)**.** An endemic monotypic genus, with the single large-sized species, *C. dupontae* Tomasovic, 2015, confined to West Africa (Côte d'Ivoire) (Tomasovic 2015). The species inhabits forest margin habitats and adults probably perch at the tips of shrubs, bushes and trees. The oviposition strategy remains unknown. *Curvirostris* and *Hoplopheromerus* key out together in the above identification key and these genera are potentially synonymous.

Damalis **F.** (Trigonomiminae)**.** A large genus of 107 medium-sized species (Figs 62, 63, 71, 137–140, 307–309), occurring in the Afrotropical, Oriental and Palaearctic Regions. Thirty-five species are recorded from the Afrotropics, which were reviewed by Londt (1989*a*) and Oldroyd (1960*a*). The genus is widespread throughout the Afrotropics, recorded from



121 *Caenoura* ♂

122 *Caenoura* ♂

123 *Choerades* ♂

124 *Choerades* ♂

125 *Clinopogon* ♂

126 *Clinopogon* ♂

Figs 48.121–126. Habitus photographs of Asilidae: (121) *Caenoura annulitarsis* (Loew), dorsal view ♂; (122) same, lateral view; (123) *Choerades bella* (Loew), dorsal view ♂; (124) same, lateral view; (125) *Clinopogon nicobarensis* (Schiner), dorsal view ♂; (126) same, lateral view.

Abbreviations: fem – femur; m_3 – third medial cell; ped – pedicel; pped – postpedicel; prbs – proboscis; scp – scape; trc – trochanter.

Southern Africa (Mozambique, South Africa and Zimbabwe), Central Africa (Angola, Cameroon, Central African Republic, Democratic Republic of Congo, Malawi and Zambia), East Africa (Kenya, Tanzania and Uganda), West Africa (Benin, Côte d'Ivoire, Ghana, Guinea, Liberia, Nigeria and Sierra Leone) and the Indian Ocean islands (Madagascar). Aspects of the biology of *D. femoralis* Ricardo, 1925 were published by Londt (1991). The genus inhabits forest (margins), Fynbos, grassland, savanna and woodland habitats and adults perch within grass and at the tips of grass, shrubs, bushes and trees (Figs 62, 63). Oviposition takes place through random egg-dropping. Some biological information was provided by Cuthbertson (1938, as *Lophurodamalis* Hermann) and eggs and larvae were described by Londt (1991). Londt (1989*a*) and Oldroyd (1960*a*) provided identification keys to the continental Afrotropical and Malagasy species, respectively.

***Danomyia* Londt** (Stenopogoninae)**.** An endemic genus of nine medium-sized, bee-like species, centred in Southern Africa (Botswana, South Africa and Zimbabwe), but also recorded from Central Africa (Chad) and East Africa (Sudan) (Londt 1993*c*). The genus inhabits grassland, savanna and woodland habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (1993*c*) provided an identification key to the nine species.

***Dasophrys* Loew** (Asilinae)**.** A large endemic genus of 32 medium- to large-sized species (Figs 7, 72, 141, 142), reviewed by Londt (1981*b*) who later added an additional species (Londt 1985*a*). The genus is confined to Southern Africa (Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe) and inhabits forest and woodland habitats and adults perch within and at the tips of shrubs and bushes (Fig. 7). Oviposition takes place on or in woody vegetation. Some biological information was provided by Cuthbertson (1936). Other useful references include Londt (2005*a*). Londt (1981*b*) provided the most recent identification key to species, but see Londt (1985*a*) for an additional species.

***Daspletis* Loew** (Stenopogoninae)**.** An endemic genus of nine medium- to very large-sized species (Figs 49–51, 73, 143, 144), confined to Southern Africa (Botswana, Namibia, South Africa, Zimbabwe) (Londt 2010*a*), with unpublished records from Mozambique. Tomasovic (2016) described a new species from Gabon, but the generic assignment is questionable. The genus inhabits grassland, savanna and semi-desert habitats and adults perch on the ground or on low vegetation (Figs 49–51). Oviposition takes place in sand or soil. Other useful references include Londt (1983*c*, 1985*a*) and Tomasovic & Constant (2013). Londt (2010*a*) provided the most recent identification key to species, but see Tomasovic (2016) for an additional species.

***Dasyllina* Bromley** (Laphriinae)**.** An endemic monotypic genus, with the single large-sized, bee-like species, *D. fulvithorax* Bromley, 1935, confined to Central Africa (Democratic Republic of Congo). The biology remains unknown, but the species probably inhabits forest or woodland habitats and adults probably perch within or at the tips of shrubs, bushes and trees. Oviposition probably takes place on or in vegetation. Other useful references include Bromley (1935), Londt (1988*b*) and Oldroyd (1970).

***Dichaetothyrea* De Meijere** (Laphriinae)**.** A genus of two small-sized species, occurring in the Afrotropical and Oriental Regions. The single Afrotropical species, *D. calvifrons* Londt, 1982, is confined to the Indian Ocean islands (Madagascar) (Londt 1982*a*). The biology remains unknown, but the species probably inhabits forest habitats and adults probably perch within and/or at the tips of shrubs and bushes. Oviposition probably takes place through random egg-dropping.

***Dichropogon* Bezzi** (Stichopogoninae)**.** A genus of five small-sized species, occurring in the Afrotropical and Palaearctic Regions. *Dichropogon* was formerly treated as a subgenus of *Stichopogon* (Geller-Grimm 2004; Hull 1962), but was recently elevated to full generic status for south-western Palaearctic species. A single species, *D. tenebrosus* Bosák & Hradský, 2011, is recorded from the Afrotropics, confined to the southern Arabian Peninsula (United Arab Emirates) (Bosák & Hradský 2011: 741). The biology of the species remains unknown, but is probably similar to that of semi-desert inhabiting *Stichopogon* species, with adults probably perching on the ground. Oviposition takes place in sand or soil.

***Dikowmyia* Londt** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *D. mediorus* Londt, 2002, confined to Southern Africa (South Africa) (Londt 2002*b*). The species inhabits grassland habitats and adults probably perch within and at the tips of grass. Oviposition probably takes place in or on vegetation.

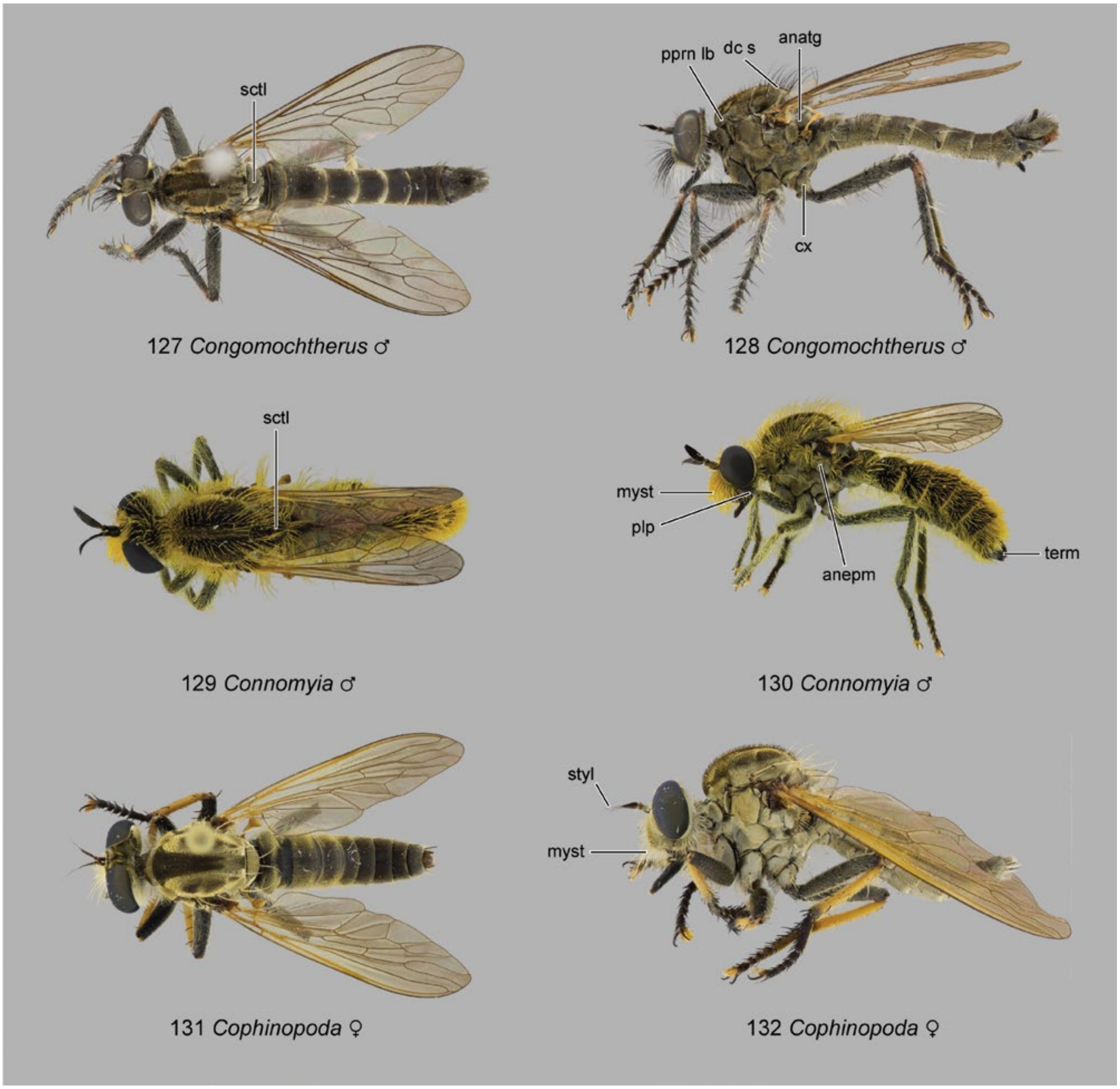
***Dioctobroma* Hull** (Stenopogoninae). An endemic monotypic genus, with the single medium-sized species, *D. flavoterminatus* Hull, 1962, confined to Southern Africa (Botswana and Namibia) (Hull 1962). The biology of the species remains unknown, but it probably inhabits grassland, savanna and semi-desert habitats and adults probably perch on the ground. Oviposition takes place in sand or soil. Other useful references include Londt (1983*c*) and Dikow & Londt (2000*b*).

***Dogonia* Oldroyd** (Stenopogoninae)**.** An endemic monotypic genus, with the single medium- to large-sized species, *D. saegeri* Oldroyd, 1970, confined to Central Africa (Democratic Republic of Congo). The genus was described by Oldroyd (1970) and was reviewed by Londt (2008*a*). The biology of the species remains unknown, but it probably inhabits forest habitats and adults probably perch on the ground or at the tips of shrubs and bushes. Oviposition takes place in sand or soil.

***Dysclytus* Loew** (Asilinae)**.** An endemic monotypic genus, with the single large-sized species, *D. firmatus* Walker, 1857, confined to Southern Africa (South Africa) (Londt 1979*a*). The species inhabits savanna and woodland habitats and adults perch at the tips of shrubs and bushes. Oviposition takes place on or in vegetation. Other useful references include Londt (2005*a*) and Oldroyd (1974).

***Emphysomera* Schiner** (Ommatiinae)**.** A genus of 21 medium-sized species (Figs 145, 146), occurring in the Afrotropical, Australasian and Oriental Regions. Four species are recorded from the Afrotropics, that are widespread and recorded from Southern Africa (Botswana, Mozambique, South Africa, Swaziland and Zimbabwe), Central Africa (Chad, Democratic Republic of Congo, Gabon, Malawi and Zambia), East Africa (Kenya, Tanzania and Uganda), West Africa (Côte d'Ivoire, Gambia, Ghana, Guinea, Liberia, Senegal and Sierra Leone) and the Indian Ocean islands (Madagascar) (Scarbrough & Marascia 1996). The genus inhabits forest and woodland habitats and adults perch at the tips of shrubs and bushes. Oviposition takes place through random egg-dropping. Other useful references include Londt (2010*b*). Scarbrough & Marascia (1996) provided an identification key to the four species.

***Empodiodes* Oldroyd** (Stenopogoninae)**.** An endemic genus of four small- to medium-sized species, confined to Southern Africa (Namibia and South Africa). The genus was described by Oldroyd (1972) and was reviewed by Londt (1992*a*, 2012*c*). The genus inhabits grassland, Fynbos and savanna habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (2012*c*) provided an identification key to the four species.



127 *Congomochtherus* ♂

128 *Congomochtherus* ♂

129 *Connomyia* ♂

130 *Connomyia* ♂

131 *Cophinopoda* ♀

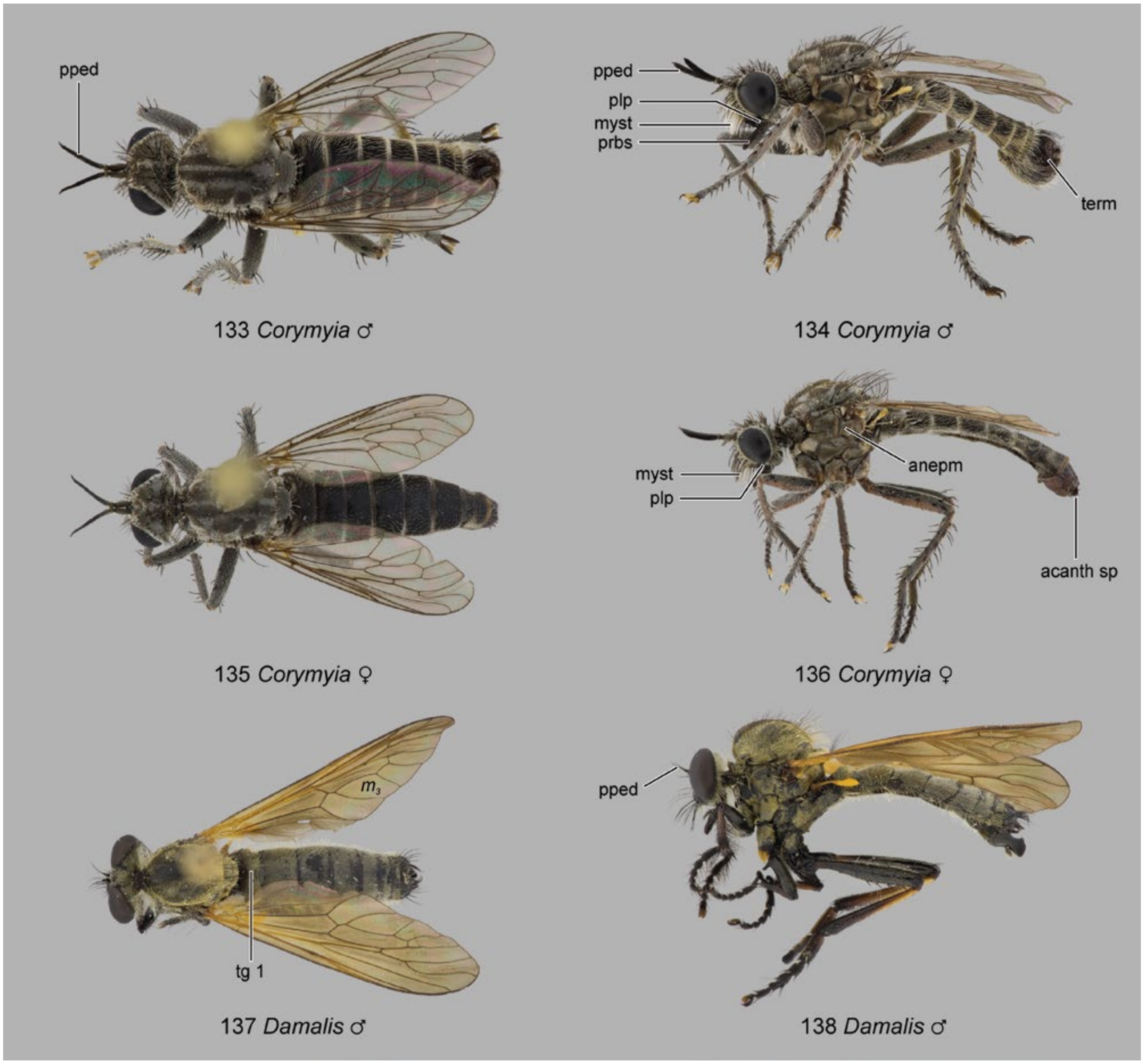
132 *Cophinopoda* ♀

Figs 48.127–132. Habitus photographs of Asilidae: (127) *Congomochtherus elferinki* Londt & Tsacas, dorsal view ♂; (128) same, lateral view; (129) *Connomyia leonina* (Engel), dorsal view ♂; (130) same, lateral view; (131) *Cophinopoda pulchripes* (Bigot), dorsal view ♀; (132) same, lateral view.

Abbreviations: anatg – anatergite; anepm – anepimeron; cx – coxa; dc s – dorsocentral seta; myst – mystax; plp – palpus; pprn lb – postpronotal lobe; sctl – scutellum; styl – stylus; term – terminalia.

***Erax* Scopoli** (Asilinae)**.** A genus of 27 medium-sized species occurring in the Afrotropical and Palaearctic Regions. Three species, *E. albiceps* Macquart, 1850, *E. costalis* (Wulp, 1899) and *E. nigrotinctus* (Becker, 1909), occur in the Afrotropics, confined to East Africa (Kenya) and the southern Arabian Peninsula (Yemen). The genus probably inhabits desert and semi-desert habitats and adults probably perch on the ground. The oviposition strategy remains unknown, but may take place in sand or soil. Other useful references include Londt (2005*a*). No identification key to Afrotropical species is currently available.

***Eremisca* Hull** (Asilinae)**.** A genus of 17 medium-sized species (Fig. 8), occurring in the Afrotropical and Palaearctic Regions. The single Afrotropical species, *E. heleni* (Efflatoun, 1934), is confined to the southern Arabian Peninsula (Oman and United Arab Emirates) (Lehr 1988*b*). The genus probably inhabits desert and semi-desert habitats and adults perch on



133 *Corymyia* ♂ 134 *Corymyia* ♂
135 *Corymyia* ♀ 136 *Corymyia* ♀
137 *Damalis* ♂ 138 *Damalis* ♂

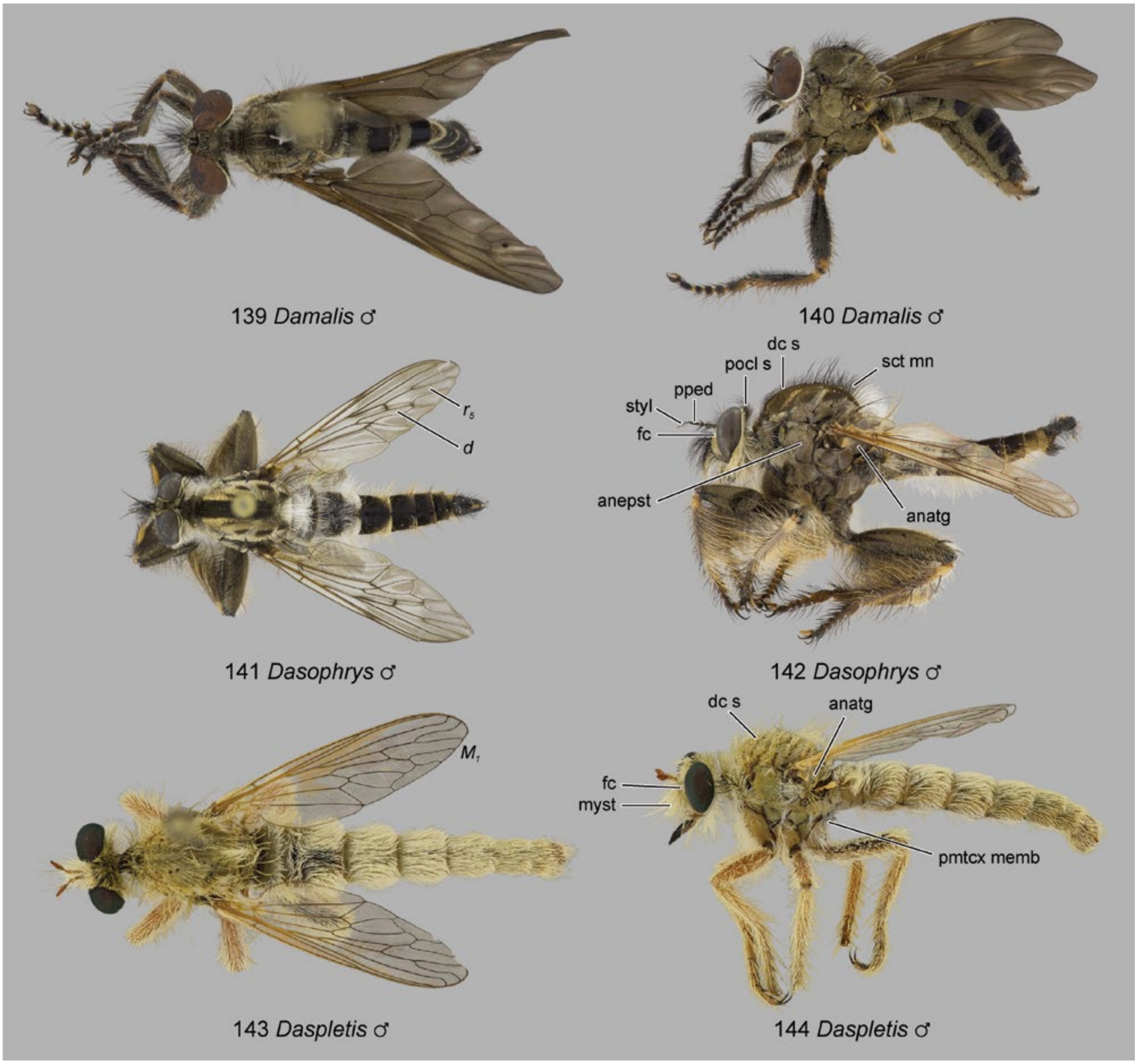
Figs 48.133–138. Habitus photographs of Asilidae: (133) *Corymyia melas* Londt, dorsal view ♂; (134) same, lateral view; (135) *C. antimelas* Londt, dorsal view ♀; (136) same, lateral view; (137) *Damalis femoralis* Ricardo, dorsal view ♂; (138) same, lateral view.

Abbreviations: acanth sp – acanthophorite spine; anepm – anepimeron; m_3 – third medial cell; myst – mystax; plp – palpus; pped – postpedicel; prbs – proboscis; term – terminalia; tg – tergite.

the ground (Fig. 8). Oviposition probably takes place in sand or soil. Other useful references include Bosák & Hradský (2011) and Theodor (1980).

***Ericomyia* Londt** (Laphriinae)**.** An endemic monotypic genus, with the single medium-sized, bee-like species, *E. atomentosa* (Oldroyd, 1960), confined to the Indian Ocean islands (Madagascar) (Londt 2015*a*). The biology of the species remains unknown, but it probably inhabits forest habitats and adults probably perch at the tips of shrubs, bushes and trees. Oviposition may involve random egg-dropping or placement of eggs on or in dead wood. Other useful references include Oldroyd (1960*a*).

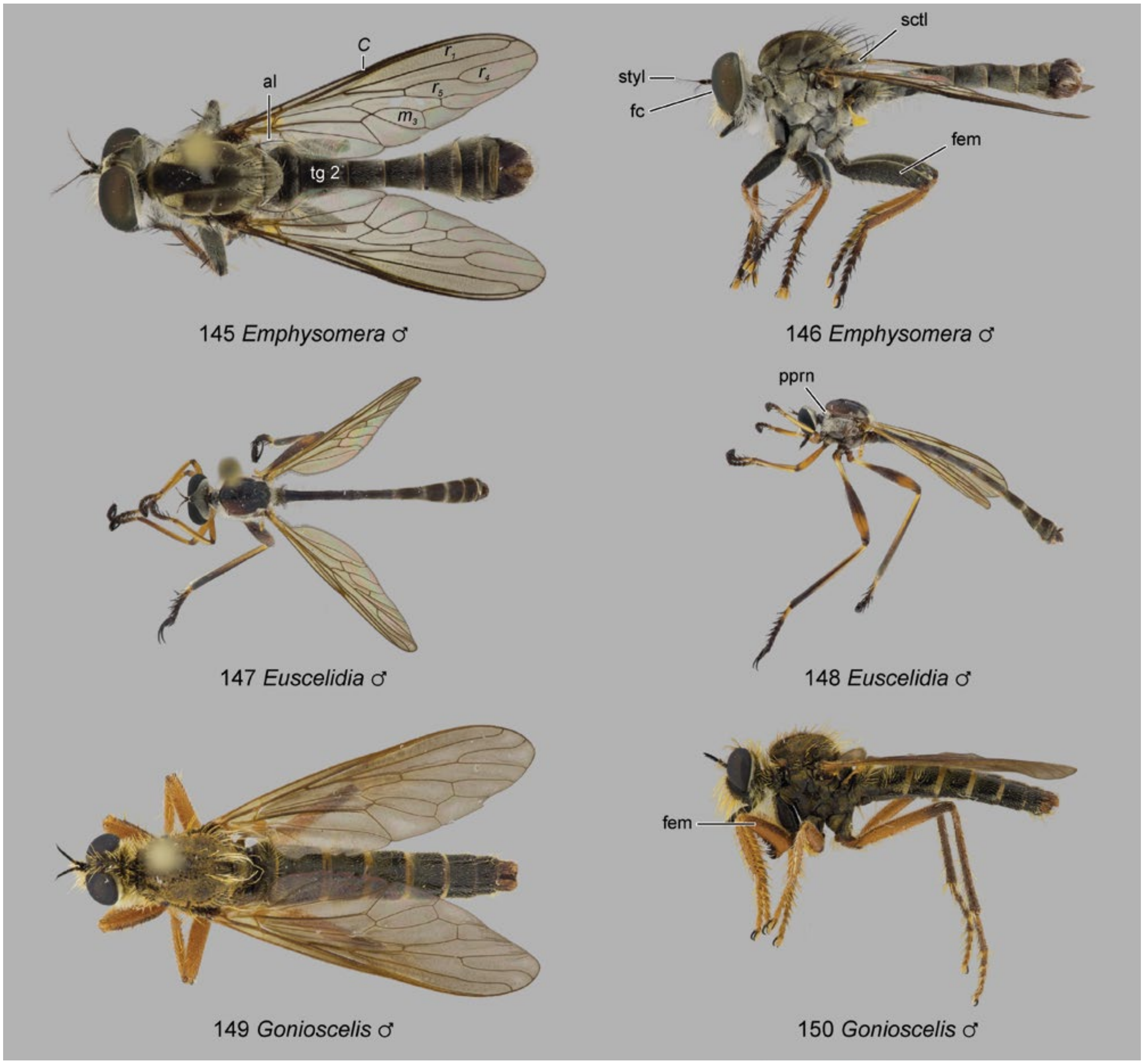
***Euscelidia* Westwood** (Leptogastrinae)**.** A large genus of 68 medium-sized species (Figs 42, 147, 148, 275–277), occurring



Figs 48.139–144. Habitus photographs of Asilidae: (139) *Damalis annulata* Loew, dorsal view ♂; (140) same, lateral view; (141) *Dasophrys androclea* (Walker), dorsal view ♂; (142) same, lateral view; (143) *Daspletis setithoracicus* (Ricardo), dorsal view ♂; (144) same, lateral view.

Abbreviations: anatg – anatergite; anepst – anepisternum; *d* – discal cell; dc s – dorsocentral seta; fc – face; M_1 – first branch of media; myst – mystax; pmtcx memb – postmetacoxal membrane; pocl s – postocular seta; pped – postpedicel; r_5 – fifth radial cell; sct mn – scutal mane; styl – stylus.

in the Afrotropical, Oriental and Palaearctic Regions. The 55 Afrotropical species are widespread throughout the region, reported from Southern Africa (Botswana, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Cameroon, Central African Republic, Chad, Democratic Republic of Congo, Malawi and Zambia), East Africa (Burundi, Eritrea, Ethiopia, Kenya, Rwanda, Sudan, Tanzania and Uganda), West Africa (Burkina Faso, Côte d'Ivoire, Gambia, Ghana, Guinea, Liberia, Mali, Nigeria, Senegal, Sierra Leone and Togo) and the Indian Ocean islands (Madagascar) (Dikow 2003). The genus inhabits grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch at the tips of grass, shrubs, bushes and trees (Fig. 42). Oviposition takes place through random egg-dropping. Some biological information was provided by Cuthbertson (1939). Other useful references include Londt (2010*b*, 2012*a*). Dikow (2003) provided an identification key to the 55 Afrotropical species.



145 *Emphysomera* ♂

146 *Emphysomera* ♂

147 *Euscelidia* ♂

148 *Euscelidia* ♂

149 *Gonioscelis* ♂

150 *Gonioscelis* ♂

Figs 48.145–150. Habitus photographs of Asilidae: (145) *Emphysomera pallidapex* (Bigot), dorsal view ♂; (146) same, lateral view; (147) *Euscelidia procula* (Walker), dorsal view ♂; (148) same, lateral view; (149) *Gonioscelis* sp., dorsal view ♂; (150) same, lateral view.

Abbreviations: al – alula; C – costal vein; fc – face; fem – femur; m_3 – third medial cell; pprn – postpronotum; r_1 – first radial cell; r_4 – fourth radial cell; r_5 – fifth radial cell; sctl – scutellum; styl – stylus; tg – tergite.

Fishermyia **Londt** (Stenopogoninae)**.** An endemic monotypic genus, with the single large-sized species, *F. stuckenbergi* Londt, 2012, confined to the Indian Ocean islands (Madagascar) (Londt 2012*b*). The species inhabits arid spiny woodland habitats and adults perch on the ground. Oviposition takes place in sand or soil.

Gerrolasius **Hermann** (Laphriinae)**.** An endemic genus of three small species, *G. hermanni* Londt, 1988, *G. meridionalis* Hermann, 1920 and *G. oldroydi* Londt, 1988, confined to Southern Africa (Botswana, Mozambique and South Africa) and East Africa (Somalia) (Londt 1988*b*). The genus inhabits grassland and savanna habitats and adults perch at the tips of grass. Oviposition takes place through random egg-dropping. Londt (1988*b*) provided an identification key to the three species.

Gibbasilus **Londt** (Asilinae)**.** An endemic genus of six medium-sized species confined to Southern Africa (South Africa). The genus was described by Londt (1986*a*) and was later reviewed by Londt (1990*b*, 2016). The genus inhabits Fynbos habitats and adults perch at the tips of shrubs and bushes. Oviposition takes place on or in vegetation. Londt (2016) provided an identification key to the six species.

Goneccalypsis **Hermann** (Laphriinae)**.** A genus of four small-sized species (Fig. 28) occurring in the Afrotropical and Oriental Regions. Two species occur in the Afrotropics, *G. argenteoviridis* (Hermann, 1907) and *G. montanus* Londt, 1982, confined to Southern Africa (Lesotho and South Africa) (Londt 1982*a*). The genus inhabits grassland (incl. montane grassland) and savanna habitats and adults perch at the tips of grass. Oviposition probably takes place through random egg-dropping. Londt (1982*a*) provided an identification key to the two Afrotropical species.

Gongromyia **Londt** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *G. bulla* Londt, 2002, confined to Southern Africa (South Africa) (Londt 2002*b*). The species probably inhabits grassland habitats and adults perch within and at the tips of grass. Oviposition probably takes place in or on vegetation.

Gonioscelis **Schiner** (Stenopogoninae)**.** An endemic genus of 40 medium-sized species (Figs 52, 149, 150), widely distributed throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Cameroon, Chad, Democratic Republic of Congo, Malawi, Republic of Congo and Zambia), East Africa (Burundi, Eritrea, Ethiopia, Kenya, Tanzania and Uganda) and West Africa (Gambia and Ghana) (Londt 2004*c*). The genus inhabits grassland, Fynbos, savanna and woodland habitats and adults perch on the ground or on rocks and at the tips of grass, shrubs and bushes (Fig. 52). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1936, 1938, 1939). Other useful references include Engel (1926), Londt (2010*b*), Oldroyd (1970, 1974), Ricardo (1925), Tomasovic (2009) and Tomasovic & Constant (2013). Londt (2004*c*) provided an identification key to the 40 Afrotropical species.

Habropogon **Loew** (Brachyrhopalinae)**.** A genus of 43 small-sized species (Figs 20, 151, 152, 256–258), occurring in the Afrotropical and Palaearctic Regions. Ten species are recorded from the Afrotropics, with a disjunct distribution in sub-Saharan Africa, recorded from Southern Africa (Namibia and South Africa), the southern Arabian Peninsula (United Arab Emirates and Yemen) and West Africa (Gambia) (Londt 2000*b*). The genus inhabits grassland and savanna habitats and adults perch on the ground or on low vegetation (Fig. 20). Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011), Kirk-Spriggs & McGregor (2009) and Londt (1981*a*, 1999*a*, 2000*b*, 2010*b*, 2012*a*). Londt (2000*b*) provided the most recent identification key to Afrotropical species, but see Bosák & Hradský (2011: 731) for two additional species.

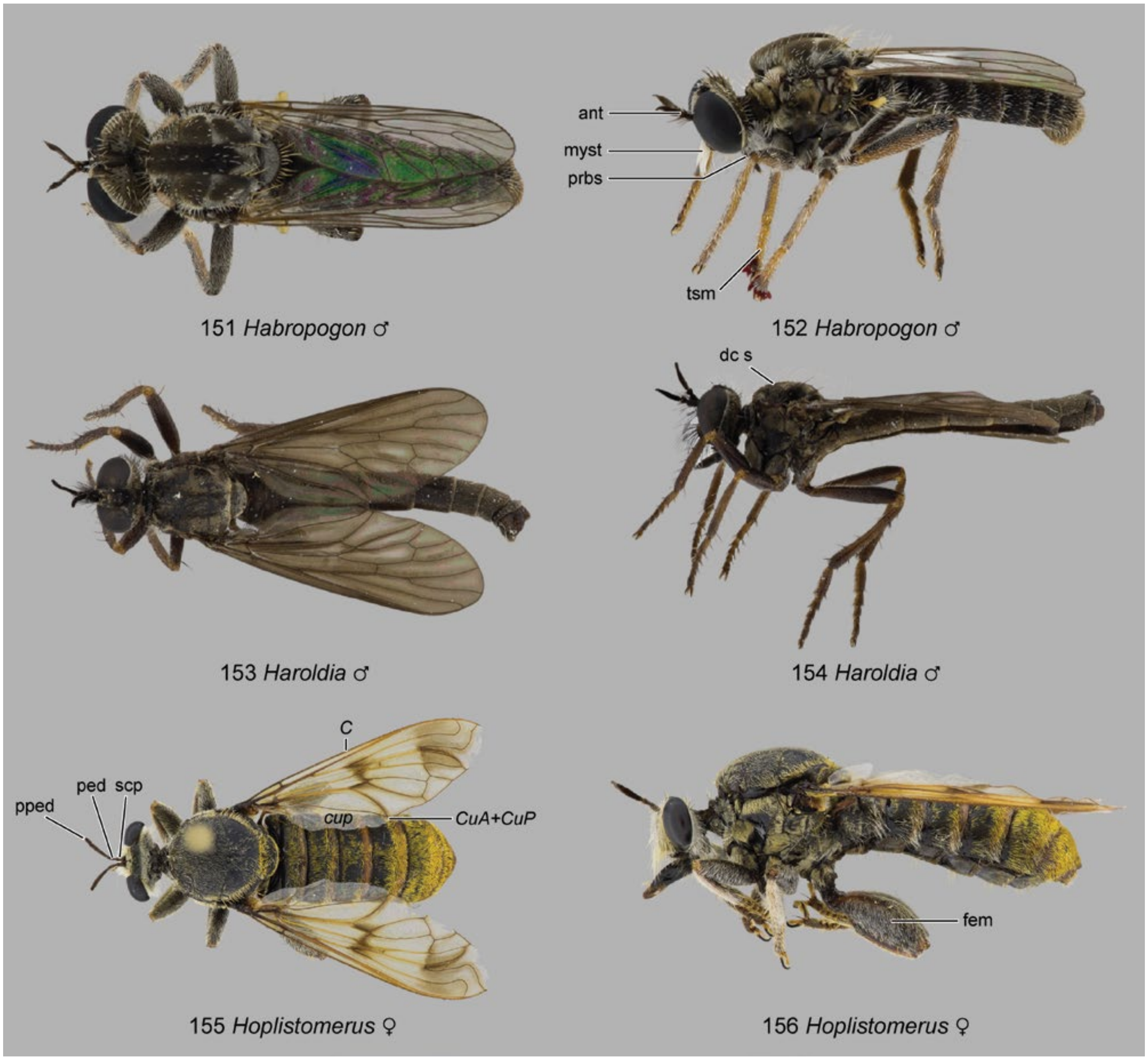
Haroldia **Londt** (Stenopogoninae)**.** An endemic genus of two small species (Figs 153, 154), *H. oldroydi* Londt, 1999 and *H. trivialis* (Oldroyd, 1974), confined to Southern Africa (South Africa) (Londt 1999*d*). The genus inhabits Fynbos and Succulent-Karoo habitats and adults perch on the ground (coastal sand dunes and beaches). Oviposition takes place in sand or soil. Other useful references include Oldroyd (1974). Londt (1999*d*) provided an identification key to the two species.

Heligmonevra **Bigot** (Asilinae)**.** A genus of 61 medium-sized species occurring in the Afrotropical, Australasian and Oriental Regions. Twenty-four species are recorded from the Afrotropics, being widespread throughout the region, including Southern Africa (Namibia), Central Africa (Bioko Is. (Equatorial Guinea), Cameroon, Democratic Republic of Congo, Gabon, Malawi and Republic of Congo), East Africa (Eritrea, Kenya, Tanzania (incl. Zanzibar Is.)), West Africa (Côte d'Ivoire, Gambia and Ghana) and the Indian Ocean islands (Madagascar and Seychelles). The genus inhabits forest, savanna and woodland habitats and adults perch within grass. Oviposition probably takes place on or in vegetation. Martin (1964) reviewed the Malagasy fauna (13 species) and other useful references include Engel (1927), Londt (2002*b*, 2010*b*, 2012*a*) and Tomasovic & Dekoninck (2014). No identification key to Afrotropical fauna is currently available.

Hermannomyia **Oldroyd** (Brachyrhopalinae)**.** An endemic genus of three medium-sized species, *H. engeli* (Hull, 1962), *H. oldroydi* Londt, 1981 and *H. ukazi* Londt & Copeland, 2013, confined to Southern Africa (Lesotho, South Africa and Zimbabwe) and East Africa (Kenya). The genus inhabits grassland, savanna and woodland habitats and adults perch on the ground. Oviposition takes place in sand or soil. The genus was reviewed by Londt (1981*a*) and Londt & Copeland (2013) and other useful references include Oldroyd (1974). Londt & Copeland (2013) provided an identification key to the three species.

Hippomachus **Engel** (Asilinae)**.** A near endemic genus of ten medium-sized species, occurring in the Afrotropical and Palaearctic Regions. Nine species occur in the Afrotropics that are widespread in sub-Saharan Africa, recorded from Southern Africa (Namibia, South Africa and Zimbabwe), Central Africa (Angola and Central African Republic), East Africa (Djibouti and Kenya) and West Africa (Gambia) (Londt 1983*b*, 1985*a*, 2010*b*). The genus inhabits savanna and woodland habitats and adults perch within trees. Oviposition takes place on or in vegetation. Londt (1983*b*) provided the most recent identification key to Afrotropical species, but see Londt (1985*a*, 2010*b*) for two additional species.

Hoplistomerus **Macquart** (Laphriinae)**.** An endemic genus of 11 medium- to large-sized species (Figs 29, 83, 155, 156, 267, 268), widely distributed throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Chad, Democratic Republic of Congo, Malawi and Zambia), East Africa (Ethiopia, Kenya, Somalia, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (Yemen) and West Africa (Gambia, Ghana, Guinea, Mali, Mauritania, Niger, Nigeria and Senegal) (Londt 2007*b*). *Hoplistomerus nobilis* was accidentally introduced into the Neotropical Region (Costa Rica) (Fisher 2009: 622). The genus mainly inhabits grassland and savanna habitats and adults perch on the ground or on stones (Fig. 29). Oviposition probably takes place in decomposing vegetable matter (including dung). The genus feeds almost exclusively on dung-frequenting beetles (Coleoptera: Scarabaeidae)



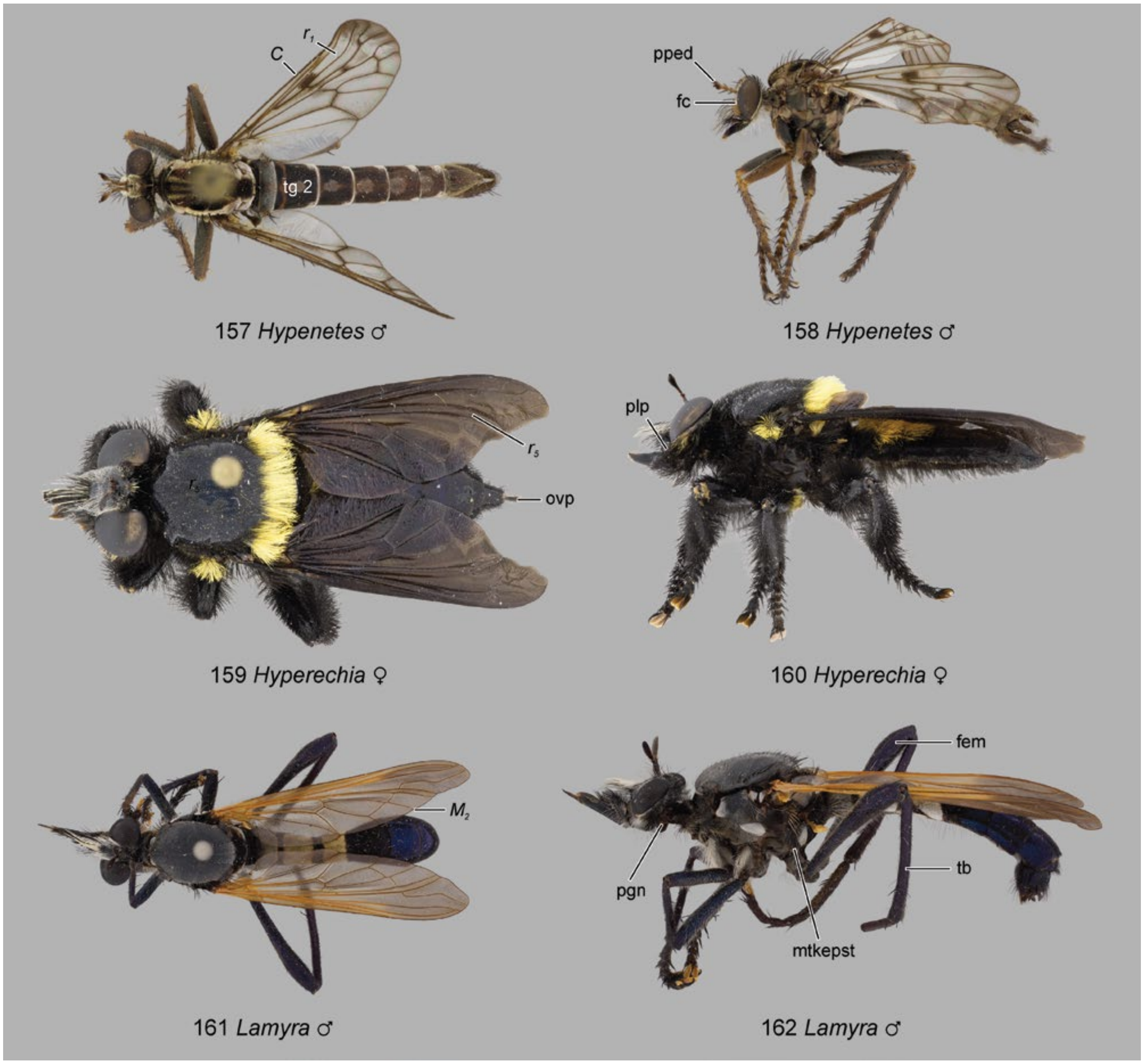
151 *Habropogon* ♂ 152 *Habropogon* ♂ 153 *Haroldia* ♂ 154 *Haroldia* ♂ 155 *Hoplistomerus* ♀ 156 *Hoplistomerus* ♀

Figs 48.151–156. Habitus photographs of Asilidae: (151) *Habropogon capensis* Londt, dorsal view ♂; (152) same, lateral view; (153) *Haroldia trivialis* (Oldroyd), dorsal view ♂; (154) same, lateral view; (155) *Hoplistomerus nobilis* Loew, dorsal view ♀; (156) same, lateral view.

Abbreviations: ant – antenna; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *cup* – posterior cubital cell; dc s – dorsocentral seta; fem – femur; myst – mystax; ped – pedicel; pped – postpedicel; prbs – proboscis; scp – scape; tsm – tarsomeres.

and some biological information was provided by Cuthbertson (1933, 1936, 1939). Other useful references include Londt (2010*b*, 2012*a*) and Oldroyd (1940, 1970, 1974). An identification key to the 11 species is provided by Londt 2007*b*.

Hoplopheromerus **Becker** (Asilinae)**.** A genus of ten large-sized species, occurring in the Afrotropical, Oriental and Palaearctic Regions. Five species occur in the Afrotropics that are fairly widespread throughout sub-Saharan Africa, including Central Africa (Democratic Republic of Congo) and West Africa (Burkina Faso, Côte d'Ivoire, Guinea and Nigeria). The genus inhabits forest habitats and adults perch within trees. Oviposition takes place on or in vegetation. *Curvirostris* and *Hoplopheromerus* key out together in the above identification key and these genera are potentially synonymous, with *Hoplopheromerus* then having priority. Other useful references include Londt (2002*b*). Tsacas & Oldroyd (1967) provided the most recent identification key to the five Afrotropical species.

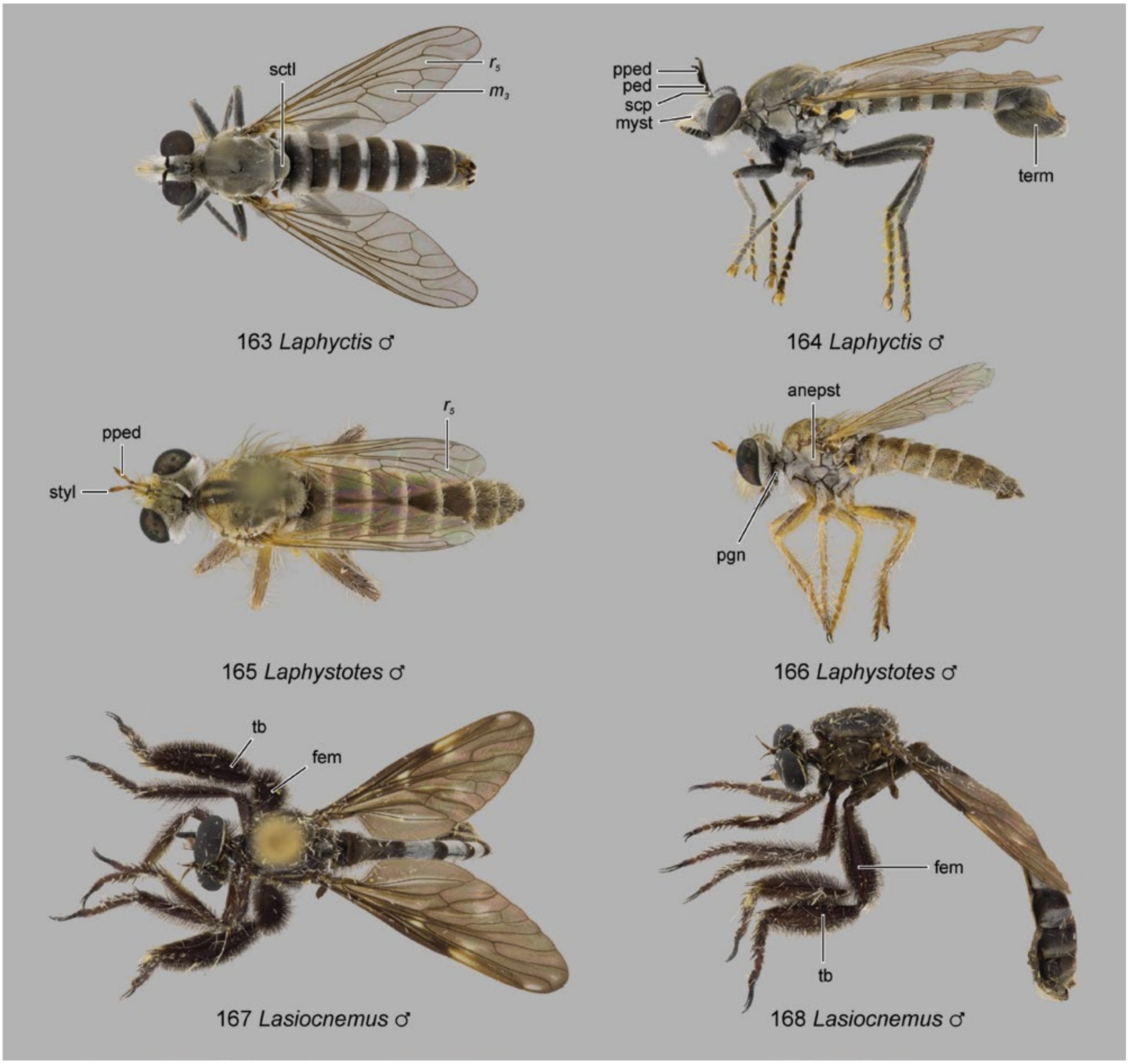


Figs 48.157–162. Habitus photographs of Asilidae: (157) *Hypenetes stigmatias* Loew, dorsal view ♂; (158) same, lateral view; (159) *Hyperechia nigripennis* (Wiedemann), dorsal view ♀; (160) same, lateral view; (161) *Lamyra gulo* (Loew), dorsal view ♂; (162) same, lateral view.

Abbreviations: *C* – costal vein; fc – face; fem – femur; M_2 – second branch of media; mtkepst – metakatepisternum; ovp – ovipositor; pgn – postgena; plp – palpus; pped – postpedicel; r_1 – first radial cell; r_5 – fifth radial cell; tb – tibia; tg – tergite.

Hynirhynchus **Lindner** (Brachyrhopalinae)**.** An endemic genus of two small- to medium-sized species, *H. pantherinus* (Bigot, 1879) and *H. zebra* Lindner, 1955, recorded from East Africa (Kenya and Tanzania) and West Africa (Gambia and Senegal) (Londt 1992*a*). Little is known regarding the biology of the genus, but it probably inhabits grassland, savanna and woodland habitats and adults probably perch on the ground or on river banks. Oviposition takes place in sand or soil. Other useful references include Lindner (1955) and Londt (2010*b*). Londt (1992*a*) provided an identification key to the two species.

Hypenetes **Loew** (Tillobromatinae)**.** An endemic genus of 21 small- to large-sized species (Figs 61, 157, 158, 303–306), confined to Southern Africa (South Africa) (Londt 1985*b*). The genus inhabits grassland, Fynbos and savanna habitats and adults perch on the ground, on beaches, rocks, or the tips of grass (Fig. 61). Oviposition takes place in sand or soil. Other



163 *Laphyctis* ♂

164 *Laphyctis* ♂

165 *Laphystotes* ♂

166 *Laphystotes* ♂

167 *Lasiocnemus* ♂

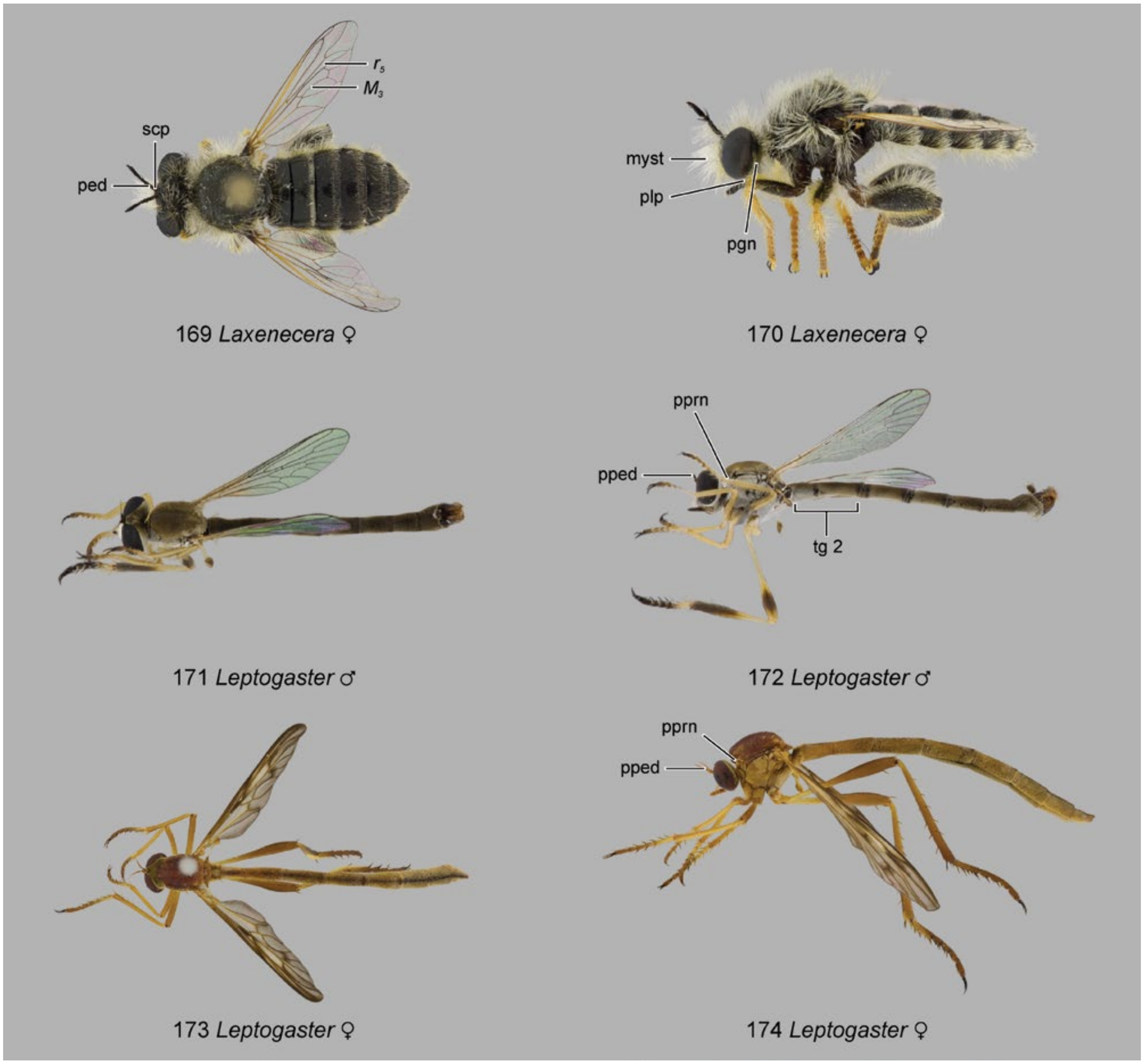
168 *Lasiocnemus* ♂

Figs 48.163–168. Habitus photographs of Asilidae: (163) *Laphyctis* sp., dorsal view ♂; (164) same, lateral view; (165) *Laphystotes ariel* Londt, dorsal view ♂; (166) same, lateral view; (167) *Lasiocnemus lugens* Loew, dorsal view ♂; (168) same, lateral view.

Abbreviations: anepst – anepisternum; fem – femur; m_3 – third medial cell; myst – mystax; ped – pedicel; pgn – postgena; pped – postpedicel; r_5 – fifth radial cell; scp – scape; sctl – scutellum; styl – stylus; tb – tibia; term – terminalia.

useful references include Oldroyd (1974). Londt (1985*b*) provided an identification key to the 21 species.

Hyperechia **Schiner** (Laphriinae)**.** A genus of 17 large-sized, carpenter bee (*Xylocopa* Latreille species; Apidae) mimicking flies (Figs 159, 160), occurring in the Afrotropical and Oriental Regions, in need of modern revision. Fourteen species occur in the Afrotropics, which are fairly widespread throughout the region, recorded from Southern Africa (Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Cameroon, Democratic Republic of Congo and Malawi), East Africa (Kenya and Tanzania (incl. Zanzibar)), West Africa (Guinea and Senegal) and the Indian Ocean islands (Madagascar). The genus inhabits forest and woodland habitats and adults perch within trees. Oviposition takes place on or in vegetation (wood). Some biological information was provided by Cuthbertson (1934) and Poulton (1925) who also illustrated the immature stages. Other useful references include Enderlein (1930), Grünberg (1907),



169 *Laxenecera* ♀ 170 *Laxenecera* ♀

171 *Leptogaster* ♂ 172 *Leptogaster* ♂

173 *Leptogaster* ♀ 174 *Leptogaster* ♀

Figs 48.169–174. Habitus photographs of Asilidae: (169) *Laxenecera mollis* (Loew), dorsal view ♀; (170) same, lateral view; (171) *Leptogaster aganniphe* Janssens, dorsal view ♂; (172) same, lateral view; (173) *L. carotenoides* Tomasovic, dorsal view ♀; (174) same, lateral view.

Abbreviations: M_3 – third branch of media; myst – mystax; ped – pedicel; pgn – postgena; plp – palpus; pped – postpedicel; pprn – postpronotum; r_5 – fifth radial cell; scp – scape; tg – tergite.

Londt (2010*b*) and Oldroyd (1970, 1974). Oldroyd (1970, 1974) provided the most recent identification keys to part of the Afrotropical fauna.

Irwinomyia **Londt** (Brachyrhopalinae)**.** An endemic genus of two small-sized species, *I. argentea* Londt, 1994 and *I. aurea* Londt, 1994, confined to Southern Africa (Namibia) (Londt 1994*b*). The biology of the genus is poorly known, but species inhabit grassland, savanna and semi-desert habitats and adults perch on the ground or possibly within and/or at the tips of grass. Oviposition takes place in sand or soil. Londt (1994*b*) provided an identification key to the two species.

Ischiolobos **Londt** (Brachyrhopalinae)**.** An endemic genus of four small-sized species, confined to Southern Africa (Lesotho and South Africa) and East Africa (Tanzania) (Londt 2005*b*). The genus inhabits grassland, Fynbos and savanna habitats and adults perch on the ground or within grass. Oviposition takes place in sand or soil. Other useful references include Lindner (1955). Londt (2005*b*) provided an identification key to the four species.

Juxtasilus **Londt** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *J. capensis* (Londt, 1979), confined to Southern Africa (South Africa) (Londt 2005*a*). The species inhabits Fynbos and semi-desert habitats and adults probably perch within and/or at the tips of shrubs and bushes. Oviposition takes place on or in vegetation.

Katharma **Oldroyd** (Laphriinae)**.** An endemic monotypic genus, with the single large-sized species, *K. sanguinaria* Oldroyd, 1960, confined to the Indian Ocean islands (Madagascar) (Oldroyd 1960*a*). The biology of the species remains unknown, but it probably inhabits forest habitats and adults perch within trees. The oviposition strategy is unknown, but probably takes place on or in vegetation. Other useful references include Tomasovic (2014).

Katharmacercus **Tomasovic** (Laphriinae)**.** An endemic genus of two large-sized species, *K. flagellata* (Oldroyd, 1960) and *K. matilei* (Menier & Tsacas, 2001), confined to the Indian Ocean islands (Madagascar) (Tomasovic 2014). The biology of the genus remains unknown, but species probably inhabit forest habitats and adults perch within shrubs and bushes. The oviposition strategy is unknown, but probably takes place on or in vegetation. Other useful references include Menier & Tsacas (2001). No identification key to the species is currently available.

Labarus **Londt** (Asilinae)**.** An endemic monotypic genus, with the single small-sized species, *L. ignota* Londt, 2005 (Figs 237–239, 252, 253), confined to Southern Africa (South Africa) (Londt 2005a). The species inhabits Fynbos habitats and adults probably perch within and/or at the tips of shrubs and bushes. Oviposition takes place on or in vegetation.

Lamyra **Loew** (Laphriinae)**.** A genus of four large- to very large-sized, wasp-like species (Figs 30, 161, 162, 269–271). The genus is endemic to the Afrotropical Region, although one species, *L. vorax* Loew, 1858, extends into Israel and Saudi Arabia in the Palaearctic Region (Dikow & Londt 2000*a*). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo, Malawi and Zambia), East Africa (Djibouti, Ethiopia, Kenya, Somalia, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (United Arab Emirates and Yemen; the photograph provided in Fig. 30 also represents a new record for Oman) and West Africa (Burkina Faso, Gambia, Ghana, Mauritania and Niger). The genus inhabits savanna and woodland habitats and adults perch at the tips of shrubs, bushes and trees (Fig. 30). The oviposition strategy remains unknown, but probably takes place on or in vegetation (wood). Some biological information was provided by Bosák & Hradský (2011: 714) and Cuthbertson (1938). Other useful references include Bosák & Hradský (2011), Kirk-Spriggs & McGregor (2009), Londt (2010*b*) and Oldroyd (1974). Dikow & Londt (2000*a*) provided an identification key to the four species.

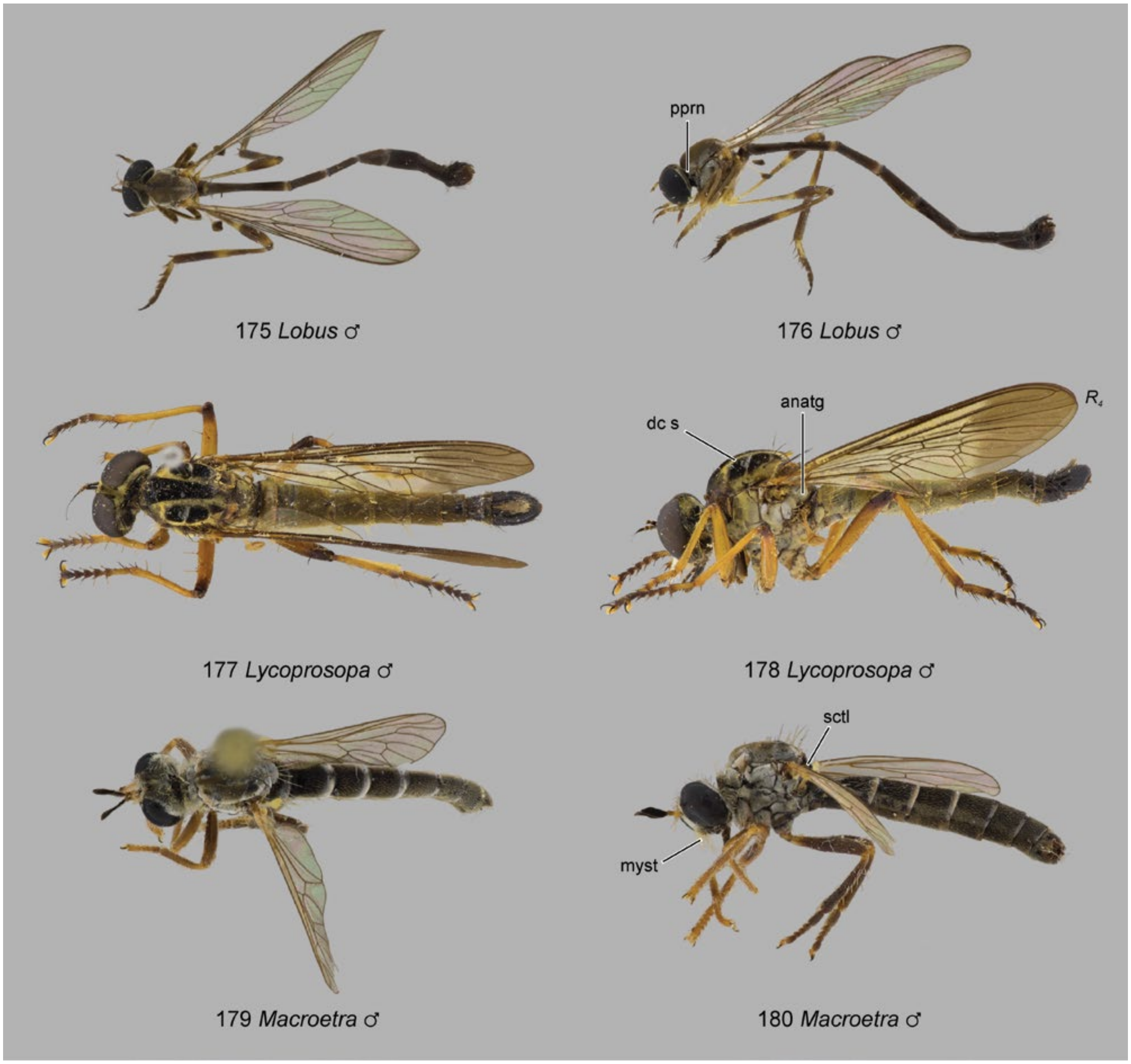
Laphyctis **Loew** (Laphriinae)**.** An endemic genus of two medium-sized, wasp-like species (Figs 31, 163, 164), *L. gigantella* (Loew, 1852) and *L. orichalcea* (Lindner, 1973), requiring modern revision, recorded from Southern Africa (Mozambique, Namibia, South Africa and Zimbabwe) and East Africa (Kenya). The genus apparently inhabits savanna and semi-desert habitats and adults perch on the ground (Fig. 31). The oviposition strategy remains unknown, but probably takes place on or in sand or soil. Other useful references include Lindner (1973) and Oldroyd (1974), who dealt with species under the name *Laphystia*; later transferred to *Laphyctis* by Londt (1988*b*). No identification key is currently available.

Laphystotes **Oldroyd** (Laphriinae). An endemic genus of two small-sized species (Figs 165, 166, 272–274), *L. albicans* (Engel, 1932) and *L. ariel* Londt, 2004, confined to Southern Africa (Namibia, South Africa and Zimbabwe) (Londt 2004*a*). The genus inhabits savanna habitats and adults perch on the ground. Oviposition probably takes place in sand or soil. Other useful references include Oldroyd (1974). Londt (2004*a*) provided an identification key to the two species.

Lasiocnemus **Loew** (Leptogastrinae)**.** An endemic genus of eight small- to large-sized species (Figs 167, 168, 278–280), reviewed by Dikow (2007). The genus is widely distributed throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Namibia, Mozambique, South Africa, Swaziland and Zimbabwe), Central Africa (Cameroon, Democratic Republic of Congo, Malawi and Zambia), East Africa (Kenya, Somalia and Tanzania) and West Africa (Côte d'Ivoire, Nigeria and Senegal) (Dikow 2007). There are also unpublished records from Ethiopia. The genus inhabits grassland, savanna and woodland habitats and adults perch at the tips of grass. Oviposition takes place through random egg-dropping. Other useful references include Janssens (1952). Dikow (2007) provided an identification key to the eight species.

Laxenecera **Macquart** (Laphriinae)**.** A large genus of 32 small- to large-sized, bee-like species (Figs 32, 169, 170), requiring modern revision. The genus occurs in the Afrotropical and Oriental Regions, with highest diversity in the Afrotropics, with 29 species. The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo, Gabon, Malawi and Zambia), East Africa (Burundi, Ethiopia, Kenya, Somalia, Tanzania and Uganda), the southern Arabian Peninsula (recorded from "Arabia") and West Africa (Côte d'Ivoire, Gambia, Nigeria, Senegal and Sierra Leone). The genus inhabits grassland and savanna habitats and adults perch within and at the tips of grass (Fig. 32). The oviposition strategy is unknown, but may involve oviposition in or on vegetation. Some biological information was provided by Cuthbertson (1937, 1938). Other useful references include Londt (2010*b*, 2012*a*), Oldroyd (1970, 1974), Tomasovic (2008*a*) and Tomasovic & Constant (2013). Oldroyd (1974) provided the most recent identification key to Southern African species.

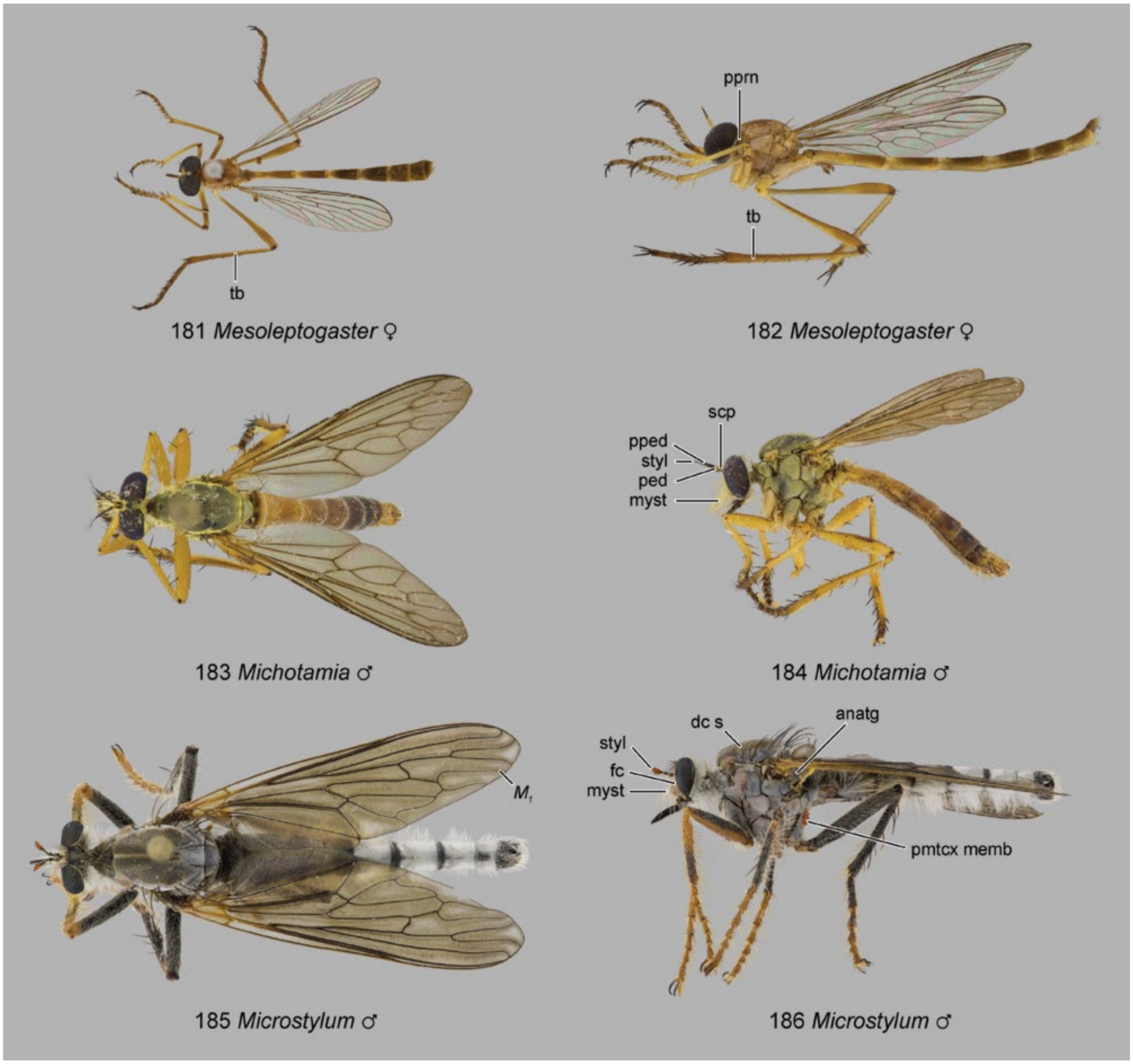
Leptogaster **Meigen** (Leptogastrinae)**.** A very large genus of 204 small- to medium-sized species (Figs 43, 171–174), occurring in all zoogeographical regions, except Antarctica, with 55 species in the Afrotropics. The genus is in need of



Figs 48.175–180. Habitus photographs of Asilidae: (175) *Lobus* sp., dorsal view ♂; (176) same, lateral view; (177) *Lycoprosopa atrimaculata* (Hobby), dorsal view ♂; (178) same, lateral view; (179) *Macroetra damara* Londt, dorsal view ♂; (180) same, lateral view.

Abbreviations: anatg – anatergite; dc s – dorsocentral seta; myst – mystax; pprn – postpronotum; R_4 – upper branch of third branch of radius; sctl – scutellum.

modern revision as it is currently paraphyletic, with the Afrotropical species not representing *Leptogaster sensu stricto* (T. Dikow, unpubl.). Oldroyd (1980: 357) catalogued the fauna and the study of *Leptogaster* type specimens reveals that many of these require transfer to existing genera, including *Lobus* and *Mesoleptogaster* (see below), reducing the total number of *Leptogaster* species from 74 to 55 (T. Dikow, unpubl.). The genus is widespread throughout the Afrotropics, recorded from Southern Africa (South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo), East Africa (Burundi, Rwanda, Somalia, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (United Arab Emirates and Socotra Is. (Yemen)), West Africa (Côte d'Ivoire and Gambia) and the Indian Ocean islands (Madagascar). There are also unpublished records from Botswana, Eritrea, Ethiopia, Lesotho, Mali, Namibia and Seychelles. The genus inhabits grassland, savanna

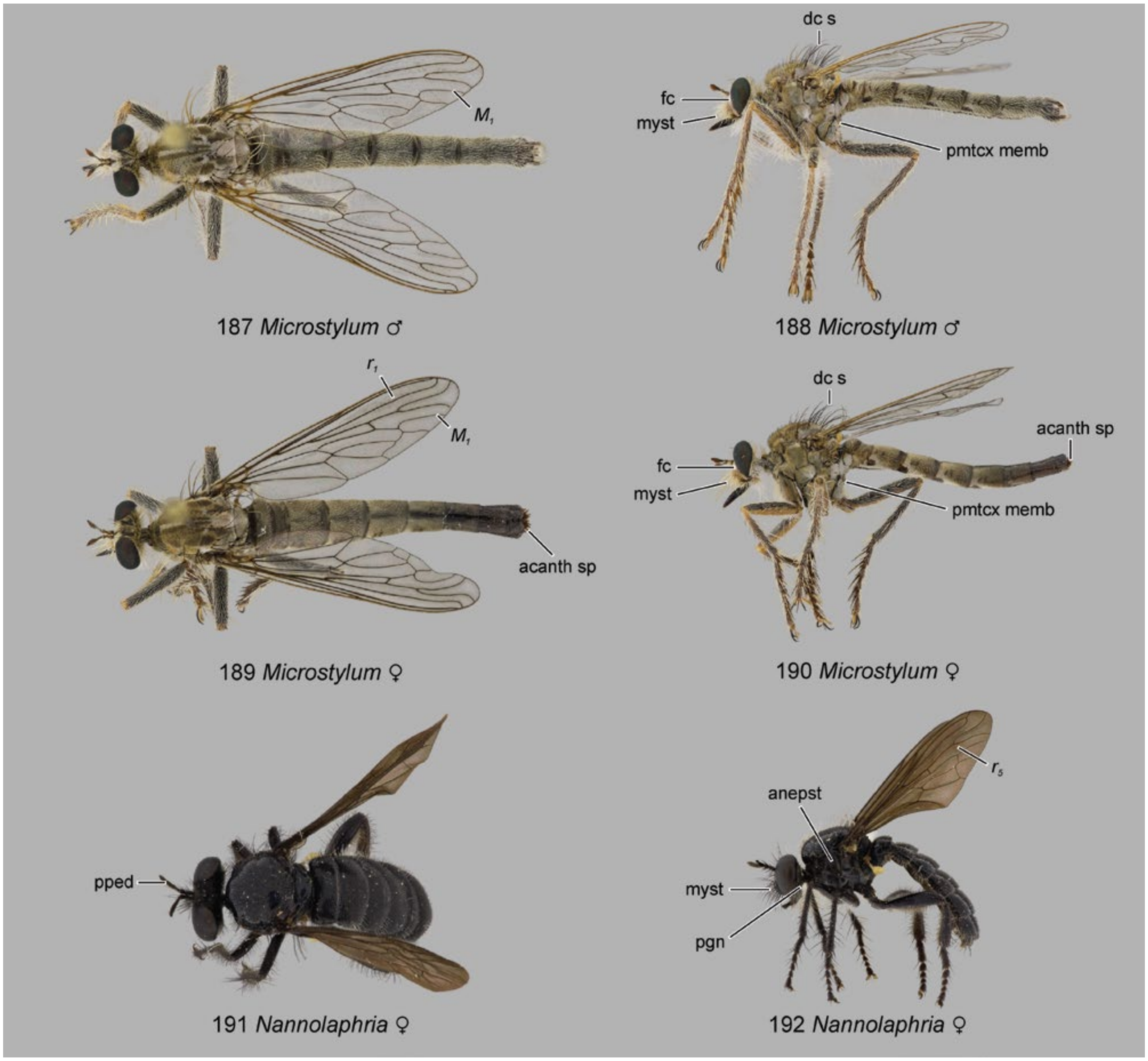


Figs 48.181–186. Habitus photographs of Asilidae: (181) *Mesoleptogaster* sp., dorsal view ♀; (182) same, lateral view; (183) *Michotamia fuscifemorata* Joseph & Parui, dorsal view ♂ (non-Afrotropical); (184) same, lateral view; (185) *Microstylum* sp., dorsal view ♂; (186) same, lateral view.

Abbreviations: anatg – anatergite; dc s – dorsocentral seta; fc – face; M_1 – first branch of media; myst – mystax; ped – pedicel; pmtcx memb – postmetacoxal membrane; pped – postpedicel; pprn – postpronotum; scp – scape; styl – stylus; tb – tibia.

and woodland habitats and adults perch within grass (Fig. 43). Oviposition takes place through random egg-dropping. Other useful references include Bosák & Hradský (2011), Janssens (1953, 1954, 1955, 1957), Londt (2010*b*), Martin (1964) and Oldroyd (1970). No identification key to Afrotropical fauna is currently available.

Lobus **Martin** (Leptogastrinae)**.** A genus of 31 small- to medium-sized species (Figs 44, 175, 176), occurring in the Afrotropical, Oriental and Palaearctic Regions, with 17 species in the Afrotropics (Martin 1972). Although seven species were catalogued by Oldroyd (1980: 359), there are numerous additional species in the Afrotropics. The study of type specimens has indicated that 11 species should be assigned to the genus and unidentified material has also revealed additional undescribed species (T. Dikow, unpubl.). The genus is fairly widely distributed, recorded from Central Africa (Democratic Republic of Congo), East Africa (Ethiopia, Eritrea, Kenya, Rwanda and



187 *Microstylum* ♂

188 *Microstylum* ♂

189 *Microstylum* ♀

190 *Microstylum* ♀

191 *Nannolaphria* ♀

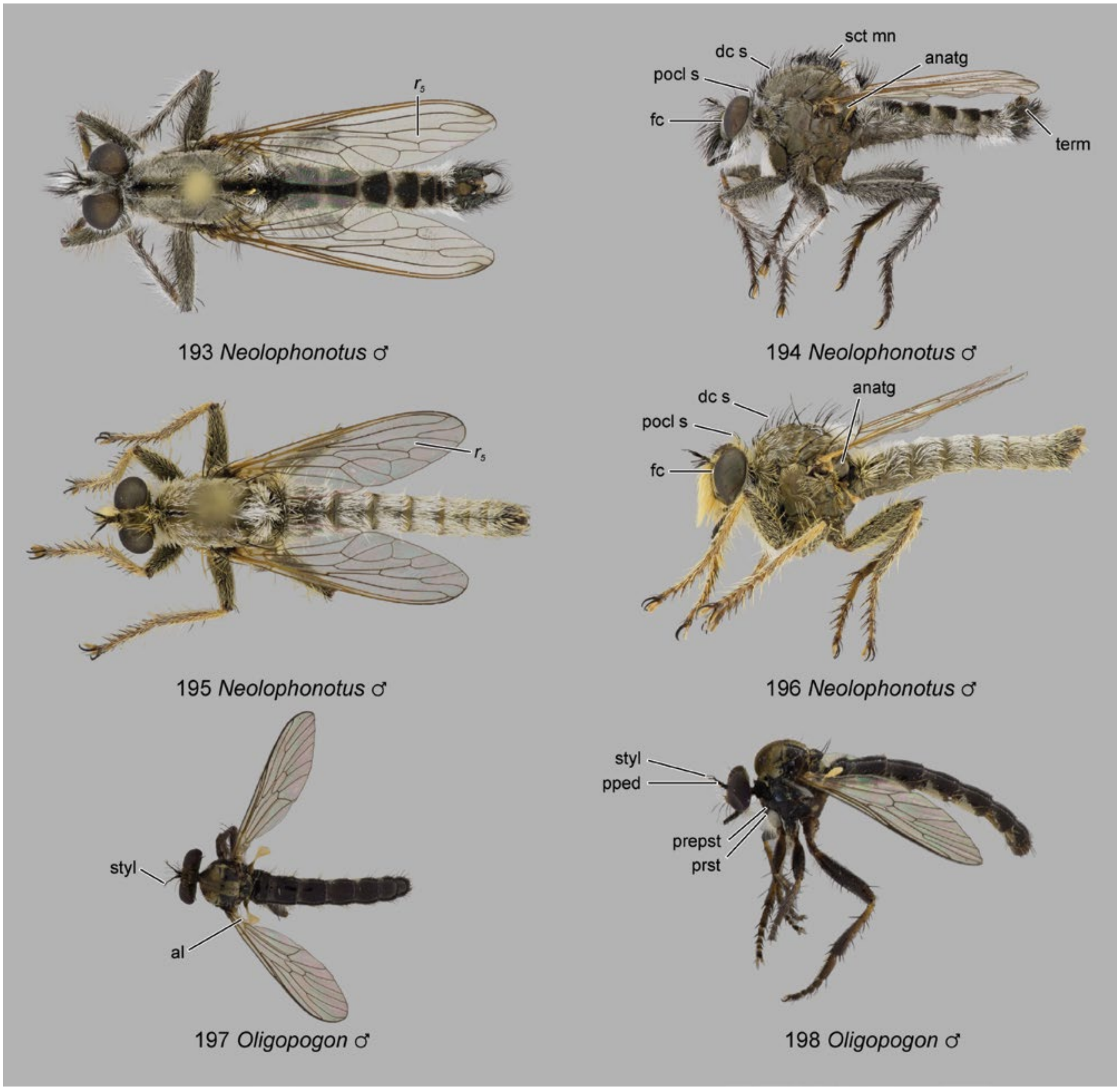
192 *Nannolaphria* ♀

Figs 48.187–192. Habitus photographs of Asilidae: (187) *Microstylum* sp., dorsal view ♂; (188) same, lateral view; (189) same, dorsal view ♀; (190) same, lateral view; (191) *Nannolaphria nigra* Londt, dorsal view ♀; (192) same, lateral view.

Abbreviations: acanth sp – acanthophorite spine; anepst – anepisternum; dc s – dorsocentral seta; fc – face; M_1 – first branch of media; myst – mystax; pgn – postgena; pmtcx memb – postmetacoxal membrane; pped – postpedicel; r_1 – first radial cell; r_5 – fifth radial cell.

Somalia) and West Africa (Liberia). There are also unpublished records from Angola, Benin, Cameroon, Central African Republic, Ghana, Guinea-Bissau, Madagascar, Namibia, Nigeria, South Africa, Tanzania, Uganda and Zambia. Recorded localities indicate that the genus inhabits forest or woodland habitats and adults probably perch at the tips of shrubs, bushes and trees (Fig. 44). Oviposition probably takes place through random egg-dropping. Other useful references include Tomasovic (2013) and Tomasovic & De Bakker (2010). No identification key to Afrotropical species is currently available.

***Loewinella* Hermann** (Laphriinae)**.** A genus of nine small-sized species, occurring in the Afrotropical and Palaearctic Regions, with six species in the Afrotropics (Londt 1982*a*).



193 *Neolophonotus* ♂

194 *Neolophonotus* ♂

195 *Neolophonotus* ♂

196 *Neolophonotus* ♂

197 *Oligopogon* ♂

198 *Oligopogon* ♂

Figs 48.193–198. Habitus photographs of Asilidae: (193) *Neolophonotus bimaculatus* Londt, dorsal view ♂; (194) same, lateral view; (195) *N. chionthrix* Hull, dorsal view ♂; (196) same, lateral view; (197) *Oligopogon penicillatus* Loew, dorsal view ♂; (198) same, lateral view.

Abbreviations: al – alula; anatg – anatergite; dc s – dorsocentral seta; fc – face; pocl s – postocular seta; pped – postpedicel; prepst – proepisternum; prst – prosternum; r_5 – fifth radial cell; sct mn – scutal mane; styl – stylus; term – terminalia.

The genus is widespread in the Afrotropics, recorded from Southern Africa (Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo), West Africa (Côte d'Ivoire, Niger and Nigeria) and the Indian Ocean islands (Madagascar). The genus inhabits grassland, savanna and woodland habitats and adults perch at the tips of grass. Oviposition probably takes place through random egg-dropping. Londt (1982*a*) provided an identification key to the six Afrotropical species.

***Longibeccus* Scarbrough** (Ommatiinae)**.** An endemic genus of two medium- to large-sized species (Figs 284–286, 290, 291), *L. fuscovittatus* (Ricardo, 1900) and *L. imperator* (Oldroyd, 1939), widely distributed throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, South Africa and Zimbabwe), Central Africa (Angola, Chad and Democratic Republic of Congo), East Africa (Ethiopia, Kenya, Sudan and Uganda) and West Africa (Côte d'Ivoire, Ghana and Nigeria) (Scarbrough 2010). The genus inhabits savanna and woodland habitats and adults probably perch within grass, shrubs and bushes. Oviposition probably takes place through random egg-dropping. Scarbrough (2010) provided an identification key to the two species.

***Lycoprosopa* Hull** (Asilinae)**.** An endemic genus of two large-sized species (Figs 177, 178), *L. atrimaculata* (Hobby, 1934) and *L. dioctriaeformis* (Macquart, 1846), requiring modern revision. The genus is confined to the Indian Ocean islands (Madagascar and Mauritius). The genus probably inhabits forest habitats and adults probably perch within and/or at the tips of trees. Oviposition takes place on or in vegetation. Other useful references include Hobby (1934), Hull (1962) and Londt (2005*a*). No identification key to the two species is currently available.

***Lycostommyia* Oldroyd** (Tillobromatinae)**.** An endemic genus of six medium-sized species, confined to Southern Africa (Namibia and South Africa) (Londt 1992*a*). The genus inhabits Fynbos, grassland, savanna, semi-desert and woodland habitats and adults perch on the ground or on rocks. Oviposition takes place in sand or soil. Other useful references include Hermann (1907) and Oldroyd (1974). Londt (1992*a*) provided an identification key to the six species.

***Machimus* Loew** (Asilinae)**.** A genus of 187 medium-sized species, occurring in the Afrotropical, Nearctic, Oriental, Palaearctic and possibly Neotropical Regions, but requiring modern revision. Thirteen species occur in the Afrotropics, confined to Central Africa (Democratic Republic of Congo and Malawi) and East Africa (Ethiopia, Kenya, Tanzania (incl. Zanzibar Is.) and Uganda). The genus probably inhabits savanna and woodland habitats and adults perch on the ground (Efflatoun 1934, 1937) and within shrubs and bushes. Oviposition takes place on or in vegetation. Some biological information was provided (as *Tolmerus*) by Cuthbertson (1935, 1936). Other useful references include Londt (2002*b*) and Tomasovic (2013, 2014). No identification key to Afrotropical species is currently available.

***Macroetra* Londt** (Brachyrhopalinae)**.** An endemic genus of three small-sized species (Figs 179, 180), *M. angola* Londt, 1994, *M. cera* Londt, 1994 and *M. damara* Londt, 1994, recorded from Southern Africa (Namibia and South Africa) and Central Africa (Angola) (Londt 1994*b*). The genus inhabits grassland and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (1994*b*) provided an identification key to the three species.

***Megadrillus* Bigot** (Asilinae)**.** An endemic genus of two medium-sized species, *M. brevipennis* (Macquart, 1838) and *M. heteronevrus* (Macquart, 1838), transferred to *Neolophonotus* and reviewed by Londt (1987*b*), but subsequently resurrected by Londt (2004*b*). The genus is confined to Southern Africa (South Africa) and inhabits Fynbos habitats and adults perch on the ground or on stones. Oviposition takes place in sand or soil. Species can be identified by reference to Londt (1987*b*).

***Melouromyia* Londt** (Asilinae)**.** An endemic genus of two medium-sized species (Fig. 9), *M. diaphorus* Londt, 2002 and *M. natalensis* (Ricardo, 1919), recorded from Southern Africa (Botswana, Mozambique, South Africa, Swaziland and Zimbabwe) and Central Africa (Malawi) (Londt 2002*b*). The genus inhabits forest, savanna and woodland habitats and adults perch within and at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation. Londt (2002*b*) provided an identification key to the two species.

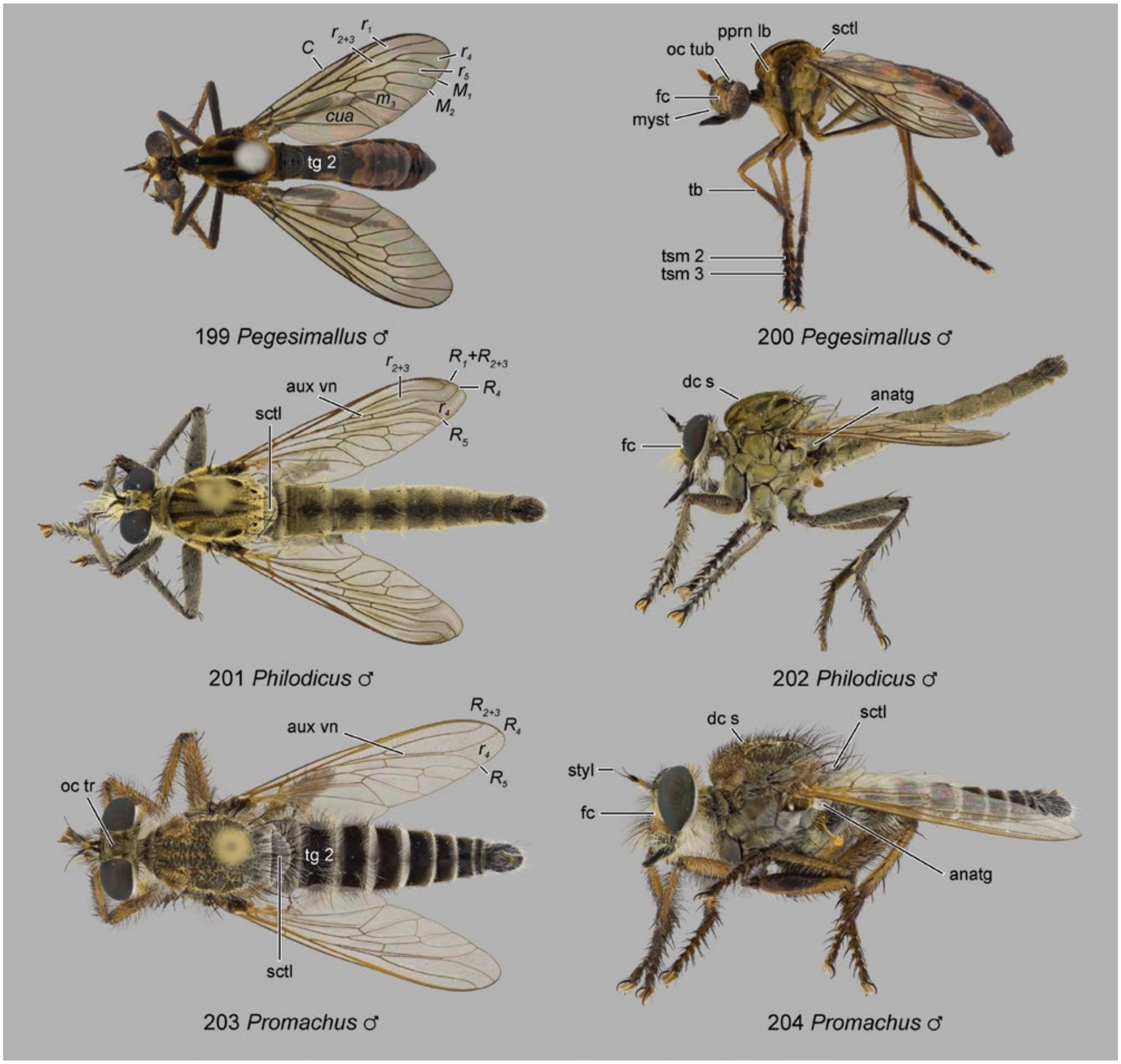
***Metommatius* Hull** (Ommatiinae)**.** A genus of three medium-sized species, *M. planatus* (Scarbrough & Marascia, 2000), *M. politus* (Scarbrough & Marascia, 2000) and *M. pulchellus* (Bromley, 1936), occurring in the Afrotropical and Palaearctic Regions (Scarbrough & Marascia 2000). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Malawi), East Africa (Kenya and Tanzania) and West Africa (Ghana). The genus inhabits savanna and woodland habitats and adults perch at the tips of grass, shrubs, bushes and trees. Oviposition takes place through random egg-dropping. Scarbrough (2010) published an identification key to the three species.

***Mesoleptogaster* Frey** (Leptogastrinae)**.** A genus of 30 medium-sized species (Figs 45, 181, 182), occurring in the Afrotropical, Oceanian, Oriental and Palaearctic Regions. Five species occur in the Afrotropics. Hull (1962) accepted Frey's subgenus and combined *Leptogaster madagascariensis* Frey, 1937 with *Mesoleptogaster*, which was not followed by Oldroyd (1980: 357). The genus was, however, accepted by Geller-Grimm (2004) and Lehr (1988*a*: 270). This species, along with four other *Leptogaster* species and additional undescribed species requires to be combined with *Mesoleptogaster*, based on the study of type specimens of *Leptogaster* (T. Dikow, unpubl.). *Mesoleptogaster* is a fairly widely distributed genus, with unpublished records from Central Africa (Angola, Cameroon and Democratic Republic of Congo), East Africa (Ethiopia and Tanzania), the Indian Ocean islands (Madagascar), Southern Africa (Mozambique and South Africa) and West Africa (Ghana, Mali and Nigeria). The biology remains unknown. Recorded localities suggest that the genus inhabits forest or woodland habitats and adults probably perch at the tips of shrubs, bushes and trees (Fig. 45). Oviposition probably takes place through random egg-dropping. No identification key to Afrotropical species is currently available.

***Michotamia* Macquart** (Ommatiinae)**.** A genus of 34 large-sized species (Figs 183, 184), occurring in the Afrotropical, Australasian and Oriental Regions, with the single species, *M. coarctata* (Macquart, 1855), recorded from the Afrotropics

(Scarbrough 2010), confined to the Indian Ocean islands (Madagascar). The biology remains unknown, but the genus probably inhabits forest habitats with adults perching at the tips of shrubs, bushes, or trees. Oviposition probably takes place through random egg-dropping.

***Microphontes* Londt** (Brachyrhopalinae)**.** An endemic genus of three small-sized species, *M. megoura* Londt, 1994, *M. safra* Londt, 1994 and *M. whittingtoni* Londt, 1994, confined to Southern Africa (Namibia and South Africa) (Londt 1994*b*). The genus inhabits Fynbos and grassland habitats and adults perch

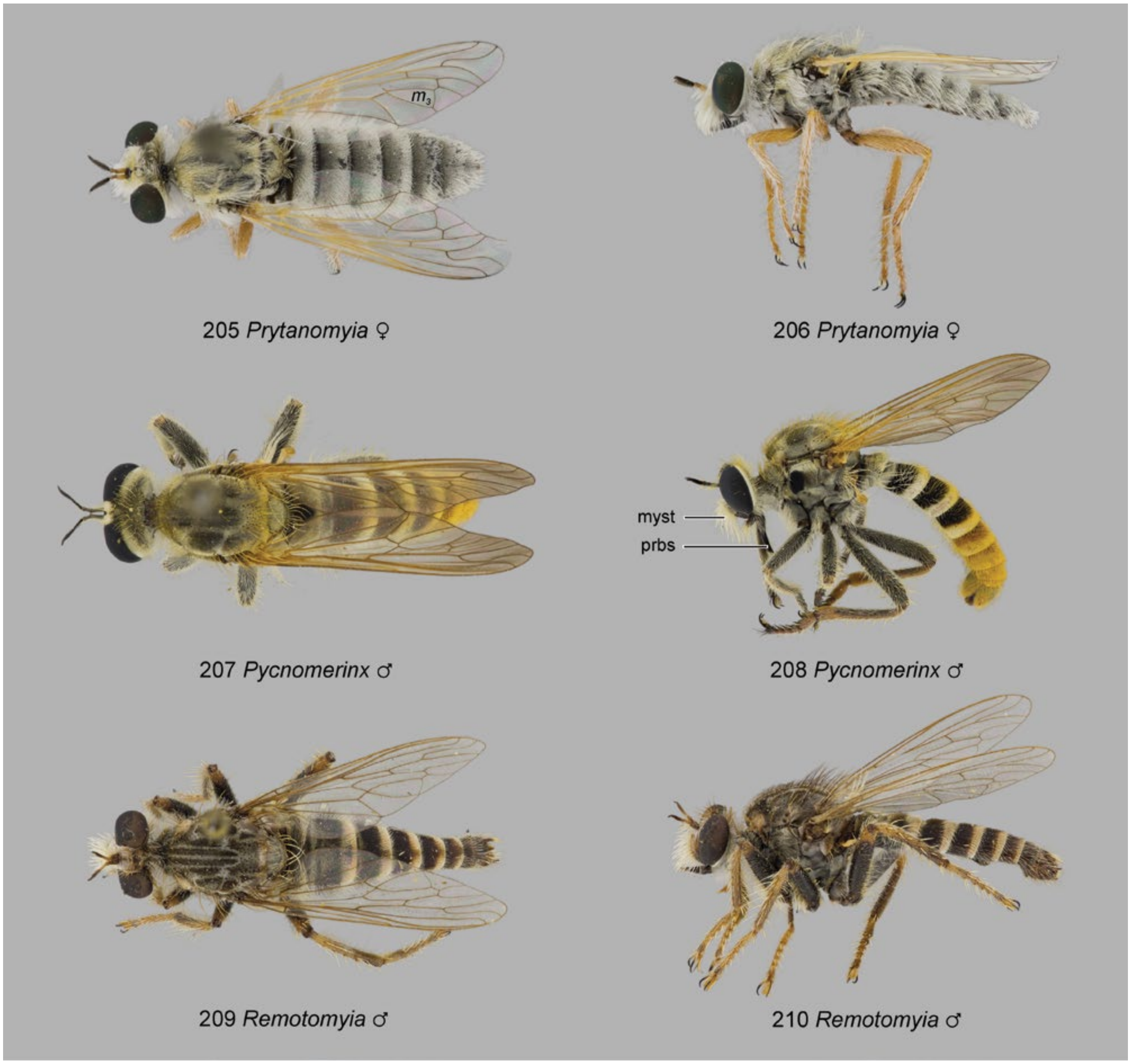


Figs 48.199–204. Habitus photographs of Asilidae: (199) *Pegesimallus calvifrons* Londt, dorsal view ♂; (200) same, lateral view; (201) *Philodicus fraterculus* (Walker), dorsal view ♂; (202) same, lateral view; (203) *Promachus amastrus* (Walker), dorsal view ♂; (204) same, lateral view.

Abbreviations: anatg – anatergite; aux vn – auxiliary vein; *C* – costal vein; *cua* – anterior cubital cell; dc s – dorsocentral seta; fc – face; M_1 – first branch of media; M_2 – second branch of media; m_3 – third medial cell; myst – mystax; oc tr – ocellar triangle; oc tub – ocellar tubercle; pprn lb – postpronotal lobe; r_1 – first radial cell; R_1+R_{2+3} – anterior branch of radius + second branch of radius; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; sctl – scutellum; styl – stylus; tb – tibia; tg – tergite; tsm – tarsomere.

on the ground. Oviposition takes place in sand or soil. Londt (1994*b*) provided an identification key to the three species.

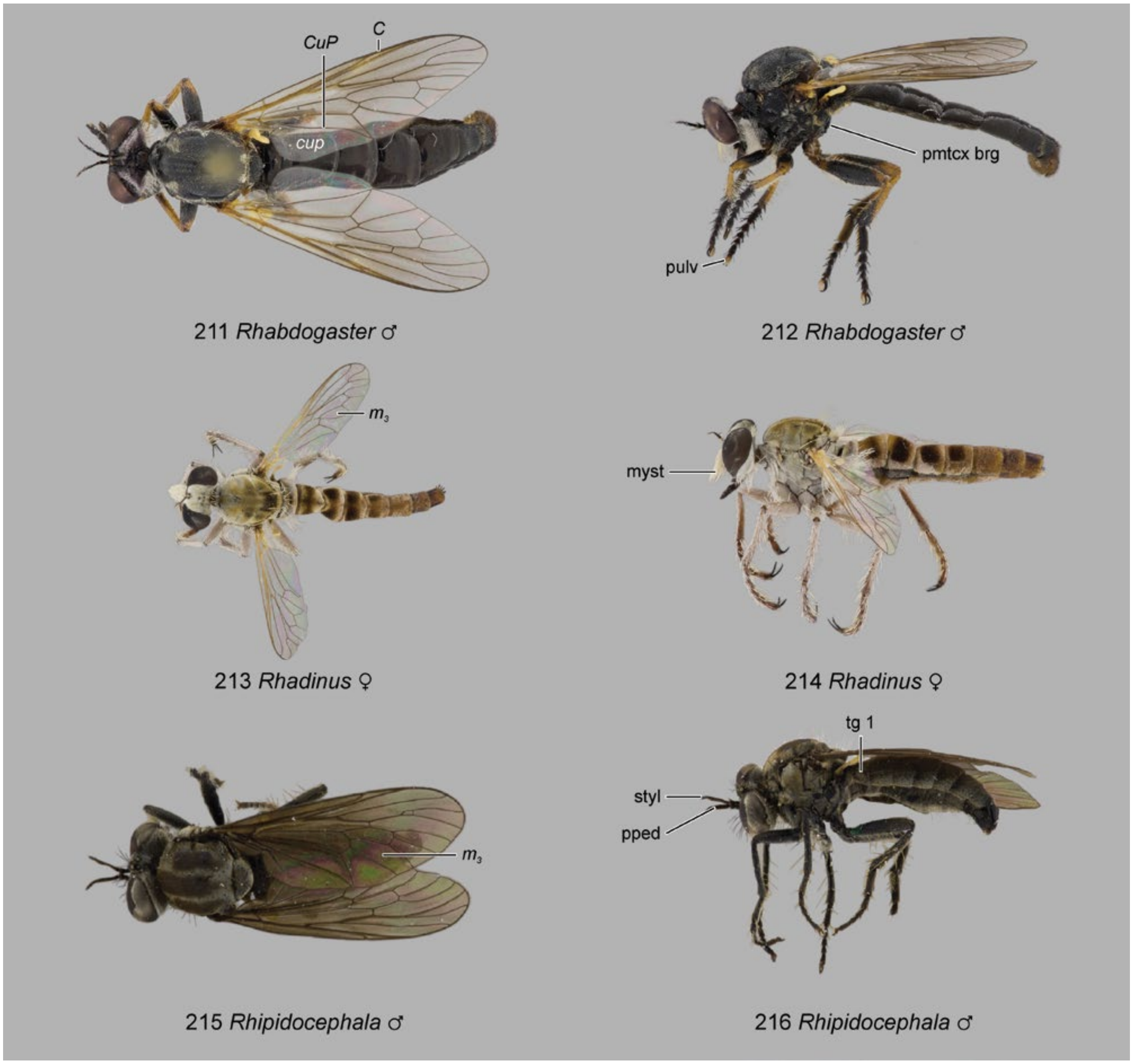
***Microstylum* Macquart** (Stenopogoninae)**.** A very large genus of 138 large- to very large-sized species (Figs 53–55, 74, 185–190), occurring in the Afrotropical, Nearctic, Neotropical (E. Fisher, pers. comm. 2017), Oriental and Palaearctic Regions, while Geller-Grimm (2004) questioned records from the Australasian Region. The genus requires modern revision, with many undescribed species known from Madagascar alone (E. Fisher, pers. comm. 2017). Seventy-nine species occur in the Afrotropics, but 50 valid names are catalogued and species remain in need of modern taxonomic treatment. The genus is widespread throughout the Afrotropics, recorded from Southern Africa (Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Chad, Democratic Republic of Congo, Gabon, Malawi and Zambia), East Africa (Kenya, Sudan and Tanzania), West Africa (Gambia, Nigeria and



Figs 48.205–210. Habitus photographs of Asilidae: (205) *Prytanomyia kochi* (Lindner), dorsal view ♀; (206) same, lateral view; (207) *Pycnomerinx* sp., dorsal view ♂; (208) same, lateral view; (209) *Remotomyia longipalpus* Londt, dorsal view ♂; (210) same, lateral view.

Abbreviations: m_3 – third medial cell; myst – mystax; prbs – proboscis.

Senegal) and the Indian Ocean islands (Madagascar). The genus inhabits forest, Fynbos, grassland, savanna and woodland habitats and adults perch on the ground, on rocks, or at the tips of grass, shrubs or bushes (Figs 53–55). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1933, 1937, 1939). The Malagasy fauna has received useful taxonomic treatments through the work of Bromley (1927), who described seven new species and keyed 11 of the 15 then known and Bromley (1931), who added a further five new species. Bromley (1942), Engel (1932), Oldroyd (1960*a*) and Timon-David (1952) together added a further nine species to the fauna, Timon-David (1952) producing another identification key to species, which Oldroyd (1960*a*) updated. Malagasy *Microstylum* are among the largest known Afrotropical Asilidae and a specimen of *Microstylum magnum* Bromley, 1927 in Muséum national d'Histoire naturelle, Paris, France, has a body length of 65 mm and a wing length of 40 mm (E. Fisher, pers. comm. 2017). Other useful references



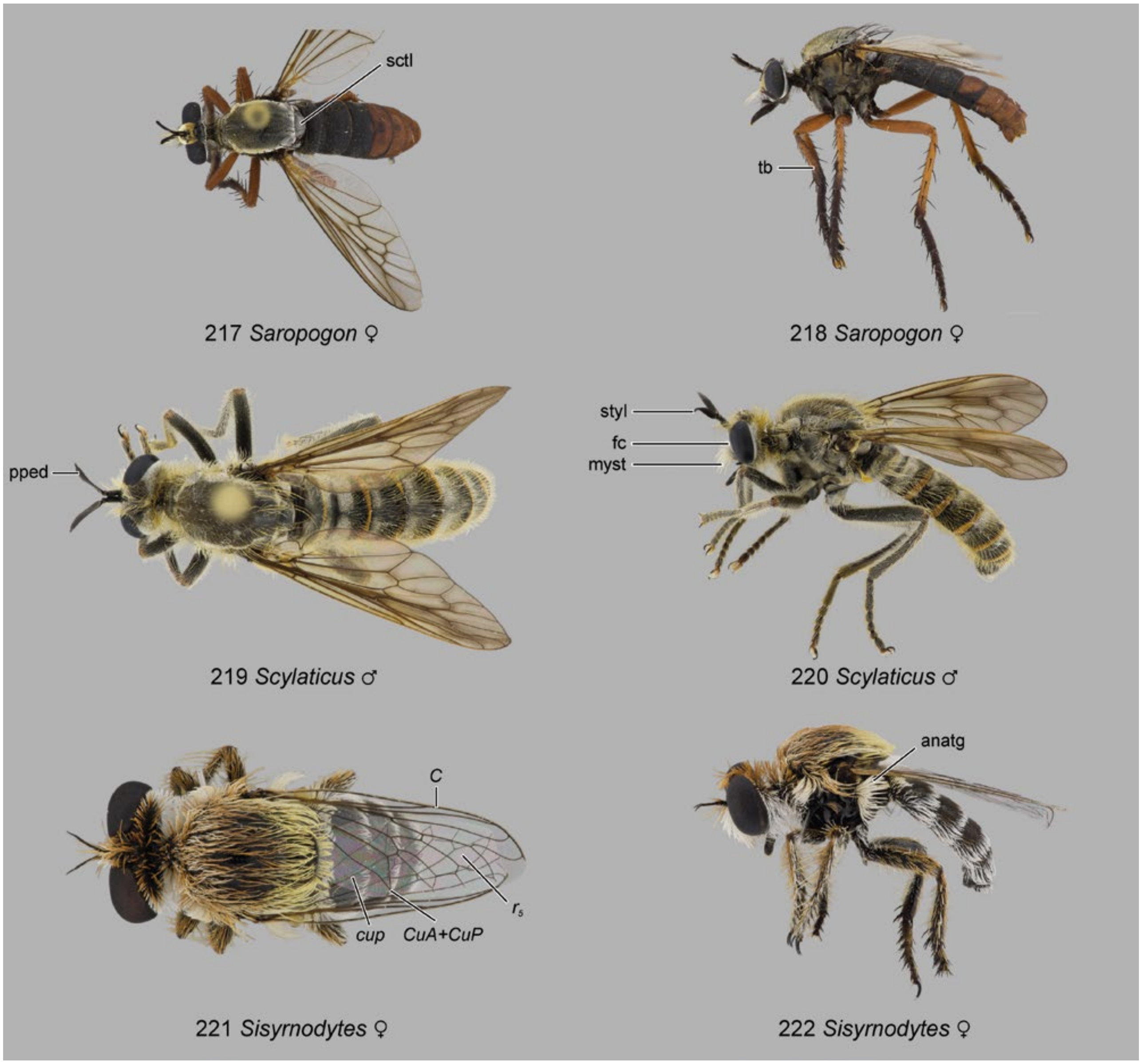
Figs 48.211–216. Habitus photographs of Asilidae: (211) *Rhabdogaster* sp., dorsal view ♂; (212) same, lateral view; (213) *Rhadinus tewfiki* Efflatoun, dorsal view ♀; (214) same, lateral view; (215) *Rhipidocephala* sp., dorsal view ♂; (216) same, lateral view.

Abbreviations: *C* – costal vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; m_3 – third medial cell; myst – mystax; pmtcx brg – postmetacoxal bridge; pped – postpedicel; pulv – pulvillus; styl – stylus; tg – tergite.

include Engel's (1932) key to the species he was familiar with, Bromley (1947) and Oldroyd (1970). No single identification key to Afrotropical species is currently available.

Millenarius **Londt** (Asilinae)**.** An endemic genus of four medium-sized species (Figs 240–242, 318, 319), described by Londt (2005*a*) and later reviewed by Londt (2014*a*). The genus is confined to Southern Africa (South Africa) and inhabits grassland habitats and adults perch within or at the tips of grass. Oviposition takes place on or in vegetation, with the eggs pasted between leaves (Londt & Harris 1987). Londt (2014*a*) provided an identification key to the four species.

Nannolaphria **Londt** (Laphriinae)**.** An endemic monotypic genus, with the single medium-sized species, *N. niger* Londt, 1977 (Figs 191, 192), confined to Southern Africa (South Africa)



217 *Saropogon* ♀

218 *Saropogon* ♀

219 *Scylaticus* ♂

220 *Scylaticus* ♂

221 *Sisyrnodytes* ♀

222 *Sisyrnodytes* ♀

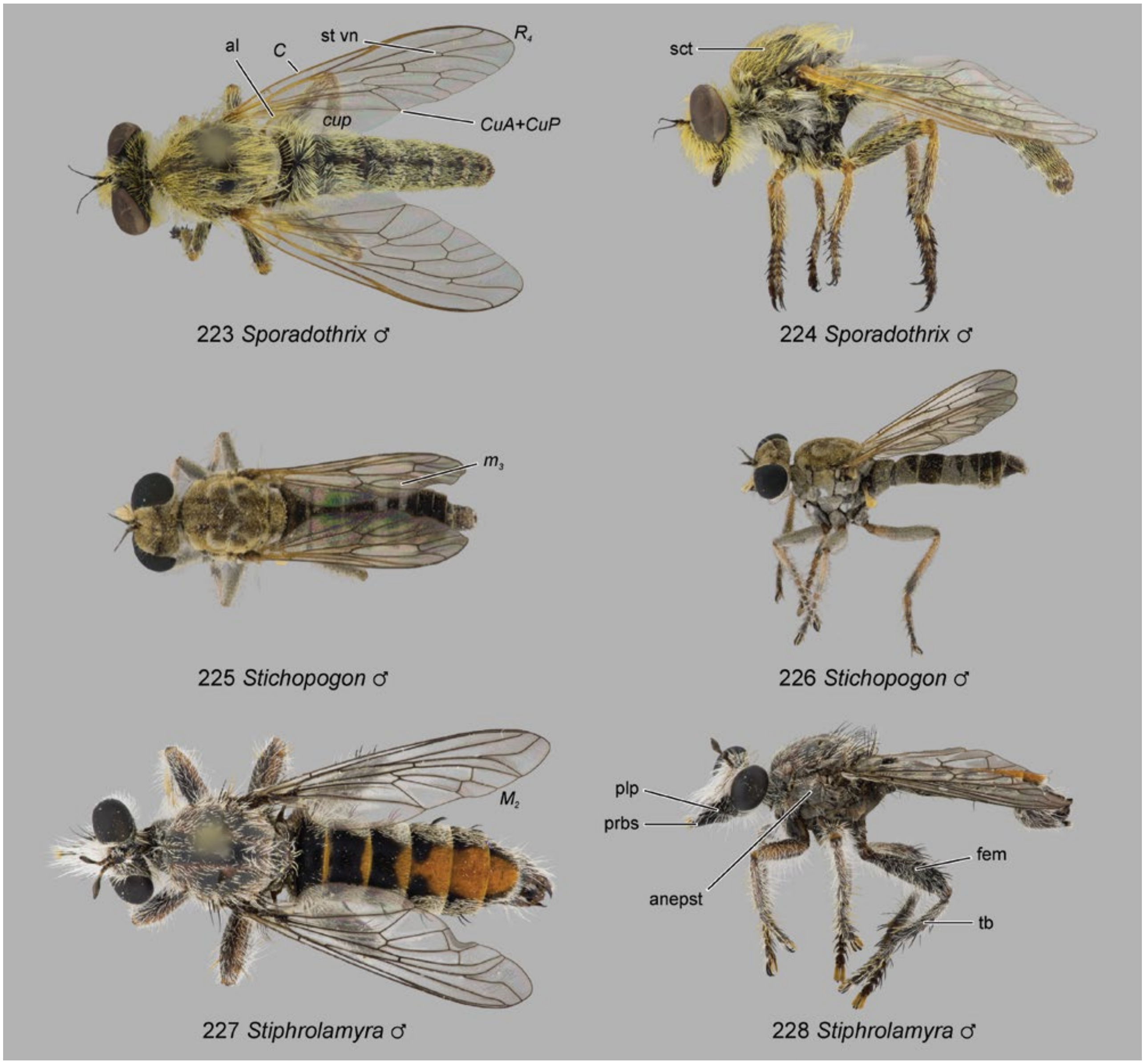
Figs 48.217–222. Habitus photographs of Asilidae: (217) *Saropogon zinidi* Londt, dorsal view ♀; (218) same, lateral view; (219) *Scylaticus costalis* (Wiedemann), dorsal view ♂; (220) same, lateral view; (221) *Sisyrnodytes subater* Oldroyd, dorsal view ♀; (222) same, lateral view.

Abbreviations: anatg – anatergite; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *cup* – posterior cubital cell; fc – face; myst – mystax; pped – postpedicel; r_5 – fifth radial cell; sctl – scutellum; styl – stylus; tb – tibia.

(Londt 1977, 2015a). The species inhabits forest habitats and adults perch at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation.

Nanoculcita **Londt & Copeland** (Stichopogoninae)**.** An endemic monotypic genus, with the single medium-sized species, *N. kenya* Londt & Copeland, 2017, confined to Eastern Africa (Kenya) (Londt & Copeland 2017). The species inhabits sandy areas in open forest and woodland habitats and adults perch on the ground, or on riverbanks and beaches. Oviposition takes place in sand or soil.

Neolophonotus **Engel** (Asilinae)**.** A near endemic genus of 256 medium- to large-sized species (Figs 10–12, 75, 193–196, 243–245), 254 of which occur in the Afrotropical Region, with two species extending into Egypt in the Palaearctic.



223 *Sporadothrix* ♂ 224 *Sporadothrix* ♂
225 *Stichopogon* ♂ 226 *Stichopogon* ♂
227 *Stiphrolamyra* ♂ 228 *Stiphrolamyra* ♂

Figs 48.223–228. Habitus photographs of Asilidae: (223) *Sporadothrix gracilis* Hermann, dorsal view ♂; (224) same, lateral view; (225) *Stichopogon hermanni* Bezzi, dorsal view ♂; (226) same, lateral view; (227) *Stiphrolamyra diaxantha* (Hermann), dorsal view ♂; (228) same, lateral view.

Abbreviations: al – alula; anepst – anepisternum; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *cup* – posterior cubital cell; fem – femur; M_2 – second branch of media; m_3 – third medial cell; plp – palpus; prbs – proboscis; R_4 – upper branch of third branch of radius; sct – scutum; st vn – stump vein; tb – tibia.

Neolophonotus is one of the most speciose genera globally and is divided into five species-groups, based on overall morphological similarity. The genus was reviewed by Londt (1985*d*, 1986*b*, 1987*b*, 1988*a*), who subsequently added a few additional species (Londt 1990*a*) and is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo, Malawi and Zambia), East Africa (Eritrea, Ethiopia, Kenya, Somalia, Tanzania and Uganda) and the southern Arabian Peninsula (United Arab Emirates). The genus inhabits, grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch on the ground, on beaches, rocks and stones, in riparian habitats or at the tips of grass, shrubs, bushes and trees (Figs 10–12). Oviposition takes place in sand or soil, or on or in vegetation (*N. suillus* species-group). Some biological information was provided by Cuthbertson (1936, 1937, 1938, 1939, some as *Lophopeltis* Engel). Other useful references include Bosák & Hradský (2011), Engel (1927), Londt (2004*b*), Tomasovic (2009) and Tomasovic & Constant (2013). Londt (1985*d*, 1986*b*, 1987*b*, 1988*a*, 1990*a*) provided the most recent identification keys to Afrotropical species, but see also *Megadrillus* (Londt 2004*b*).

***Notiolaphria* Londt** (Laphriinae)**.** An endemic genus of six medium-sized species (Figs 33, 34), described by Londt (1977) and reviewed by Londt (2015*a*). The genus is recorded from Southern Africa (Mozambique and Zimbabwe), Central Africa (Malawi), East Africa (Burundi, Kenya, Tanzania and Uganda) and the Indian Ocean islands (Comoros, Madagascar, Mauritius and Réunion Is.) (Londt 2015*a*). The genus inhabits forest habitats and adults perch on fallen trees (E. Fisher, pers. comm. 2017), but have also been photographed on exposed leaves (Figs 33, 34). Oviposition probably takes place on or in vegetation. Londt (2015*a*) provided an identification key to the six species.

***Notomochtherus* Londt** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *N. brevicauda* Londt, 2002, confined to Southern Africa (South Africa) (Londt 2002*b*). The species probably inhabits Fynbos and grassland habitats and adults perch within grass. The oviposition strategy remains unknown as females are unknown.

***Nusa* Walker** (Laphriinae)**.** A genus of 30 medium-sized species (Fig. 35), occurring in the Afrotropical, Oriental and Palaearctic Regions, with three species in the Afrotropics, *N. eos* Londt, 2006, *N. infumata* (Loew, 1851) and *N. ingwavuma* Oldroyd, 1974 (Londt 2006*a*). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo, Malawi and Zambia), East Africa (Ethiopia, Kenya, Somalia, Sudan, Tanzania (incl. Zanzibar Is.) and Uganda), the southern Arabian Peninsula (Socotra Is. (Yemen)) and West Africa (Gambia, Ghana and Mali). The genus inhabits grassland and savanna habitats and adults perch on the ground and on stones (Fig. 35). Oviposition probably takes place in sand or soil. Some biological information was provided by Cuthbertson (1939, under the synonym *Dasythrix* Loew). Other useful references include Londt (2010*b*) and Oldroyd (1970, 1974). Londt (2006*a*) provided an identification key to the three Afrotropical species.

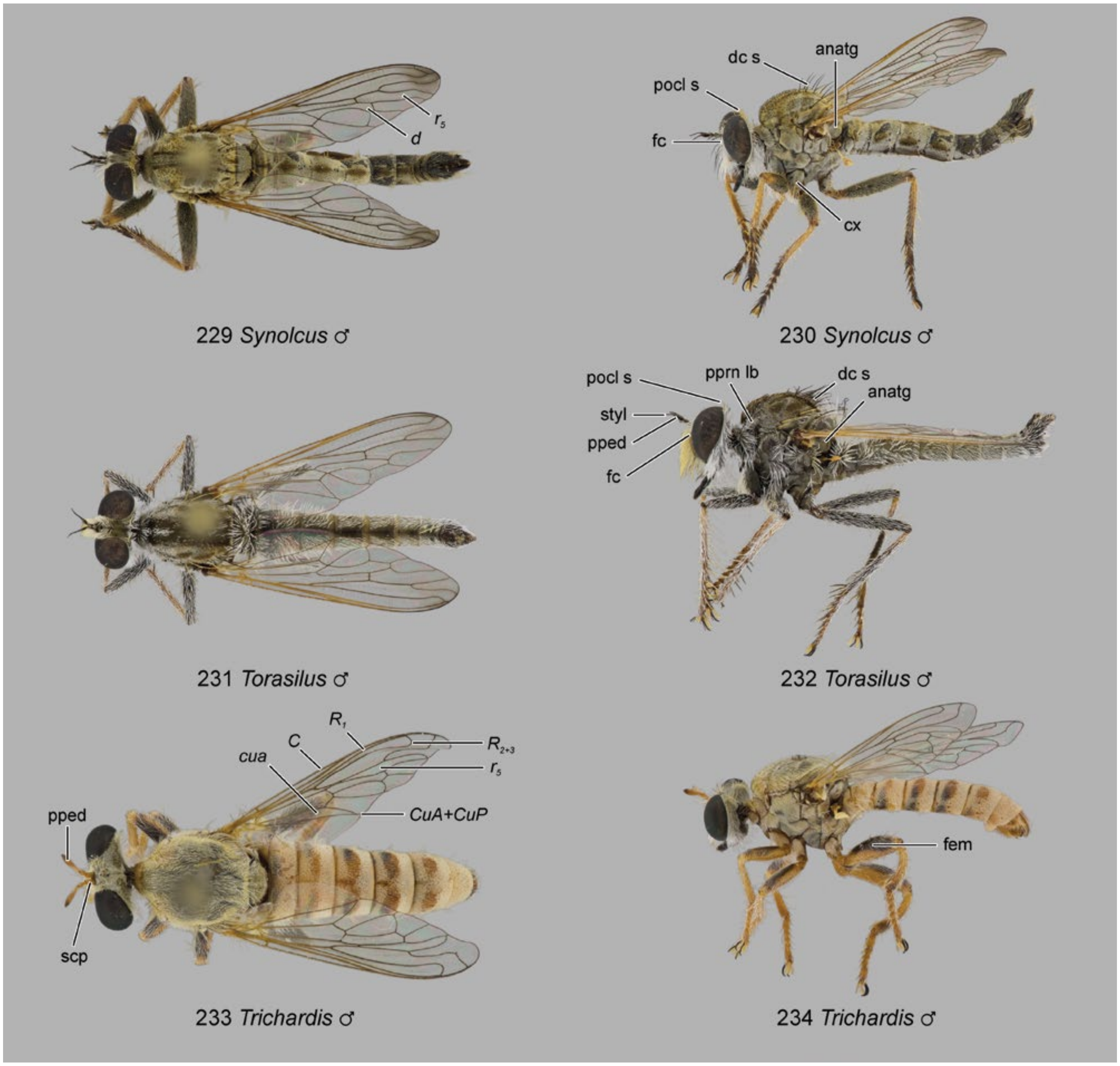
***Oligopogon* Loew** (*incertae sedis*)**.** A genus of 35 small-sized species (Figs 24, 197, 198), occurring in the Afrotropical and Palaearctic Regions, with 29 species in the Afrotropics (Londt 2014*b*). The taxonomic position of the genus remains uncertain. Oldroyd (1980: 370) placed it together with genera he listed as Trigonomiminae; Geller-Grimm (2004) listed it under the subfamily Stenopogoninae; and Dikow (2009*a*) considered the genus as *incertae sedis*. The genus has its highest species diversity in the Afrotropics, where it is widespread throughout the region, recorded from Southern Africa (Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Democratic Republic of Congo, Malawi and Zambia), East Africa (Burundi, Kenya, Sudan and Tanzania), West Africa (Côte d'Ivoire, Gambia, Ghana, Nigeria and Senegal) and the Indian Ocean islands (Madagascar) (Londt 2014*b*). The genus inhabits forest (margins), grassland and savanna habitats and adults perch on the ground, within or at the tips of grass, shrubs, bushes and trees (Fig. 24). Oviposition probably takes place in sand or soil. Other useful references include Geller-Grimm & Hradský (2003), Londt (2010*b*, 2012*a*), Oldroyd (1970, 1974) and Tomasovic & De Bakker (2010). Londt (2014*b*) provided an identification key to the 29 Afrotropical species.

***Ommatius* Wiedemann** (Ommatiinae)**.** A very large genus of *ca* 250 medium- to large-sized species (Figs 47, 48, 287–289), occurring in the Afrotropical, Australasian, Nearctic, Neotropical and Palaearctic Regions, with 70 species in the Afrotropics. The genus requires modern revision. The Malagasy fauna was studied by Oldroyd (1960*b*) who described four new species and later reviewed by Martin (1964), who added a further 20 species and provided an identification key. The 41 species occurring in sub-Saharan Africa still require modern revision, despite Scarbrough (2002, 2003, 2010) and Scarbrough *et al*. (2003) having described 19 species in recent years. The genus is widespread throughout the Afrotropics, recorded from Southern Africa (Mozambique, South Africa and Zimbabwe), Central Africa (Angola, Cameroon, Chad, Democratic Republic of Congo, Malawi, Republic of Congo and Zambia), East Africa (Burundi, Ethiopia, Kenya, Rwanda, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (United Arab Emirates and Yemen (incl. Socotra Is. and Abd al Kuri Is.)), West Africa (Côte d'Ivoire, Gambia, Ghana, Guinea, Niger, Nigeria and Senegal) and the Indian Ocean islands (Comoros, Madagascar and Mauritius). The genus inhabits grassland, savanna and woodland habitats and adults perch within grass and at the tips of shrubs, bushes and trees (Figs 47, 48). Oviposition takes place through random egg-dropping. Some biological information was provided by Cuthbertson (1933, 1934, 1936, 1937, 1938, 1939). Other useful references include Bromley (1936, 1942), Londt (2010*b*, 2012*a*), Oldroyd (1960*b*, 1968, 1970, 1974) and Tomasovic (2009). No single identification key to Afrotropical species is currently available.

***Ontomyia* Dikow & Londt** (Stenopogoninae)**.** An endemic monotypic genus, with the single medium-sized species, *O. ricardoi* (Londt, 1985) (Figs 295–297), confined to Southern Africa (Namibia) (Dikow & Londt 2000*b*). The species inhabits grassland, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil.

***Oratostylum* Ricardo** (Stenopogoninae)**.** An endemic genus of three medium-sized species, *O. crenum* Dikow & Londt, 2000, *O. lepidum* Ricardo, 1925 and *O. zebra* Dikow & Londt, 2000, confined to Southern Africa (Botswana, Namibia, South Africa and Zimbabwe) (Dikow & Londt 2000*b*). The genus inhabits grassland and savanna habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Ricardo (1925). Dikow & Londt (2000*b*) provided an identification key to the three species.

Orthogonis **Hermann** (Laphriinae)**.** A genus of 15 medium-sized species, occurring in the Afrotropical, Australasian, Nearctic and Oriental Regions, with the single Afrotropical species, *O. madagascarensis* Bromley, 1942, confined to the Indian Ocean islands (Madagascar) (Bromley 1942). The biology remains unknown, but the species probably inhabits forest



Figs 48.229–234. Habitus photographs of Asilidae: (229) *Synolcus acrobaptus* (Wiedemann), dorsal view ♂; (230) same, lateral view; (231) *Torasilus solus* Londt, dorsal view ♂; (232) same, lateral view; (233) *Trichardis picta* Hermann, dorsal view ♂; (234) same, lateral view.

Abbreviations: anatg – anatergite; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; cx – coxa; *d* – discal cell; dc s – dorsocentral seta; fc – face; fem – femur; pocl s – postocular seta; pped – postpedicel; pprn lb – postpronotal lobe; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; r_5 – fifth radial cell; scp – scape; styl – stylus.

habitats and adults probably perch within or at the tips of shrubs, bushes and trees. The oviposition strategy is unknown, but probably takes place on or in vegetation. Other useful references include Hull (1962).

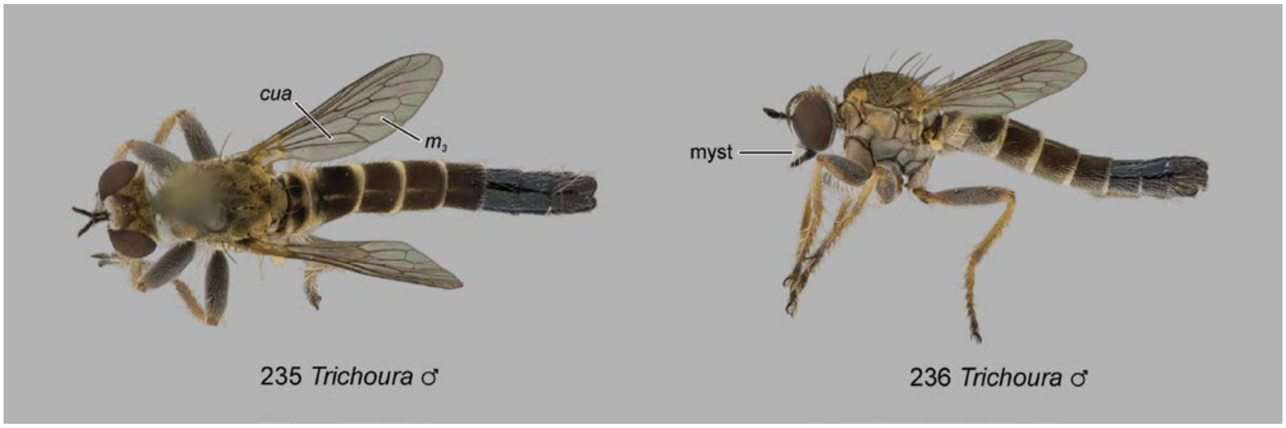
***Oxynoton* Janssens** (Brachyrhopalinae)**.** An endemic genus of two small- to medium-sized species, *O. arnaudi* Oldroyd, 1974 and *O. francoisi* Janssens, 1951, recorded from Southern Africa (Zimbabwe), Central Africa (Chad, Democratic Republic of Congo and Zambia) and East Africa (Burundi, Kenya, Rwanda and Tanzania) (Londt 1996). Oldroyd (1980: 371) listed the genus in the tribe Xenomyzini (Trigonomiminae), but Londt (1996) included it to the subfamily Stenopogoninae. It is here included in the subfamily Brachyrhopalinae. The biology and immature stages remain unknown, but the genus probably inhabits savanna habitats and adults probably perch on the ground and within and at the tips of grass. Oviposition takes place in sand or soil. Londt (1996) provided an identification key to the two species.

***Pedomyia* Londt** (Brachyrhopalinae)**.** An endemic genus of nine small-sized, bee-like species, confined to Southern Africa (Namibia and South Africa) (Londt 1994*b*). The genus inhabits grassland, Fynbos, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Londt (1994*b*) provided an identification key to the nine species.

***Pegesimallus* Loew** (Dasypogoninae)**.** A large genus of 51 small- to large-sized species (Figs 21–23, 76, 199, 200, 262, 263), occurring in the Afrotropical, Oriental and Palaearctic Regions, with 46 species in the Afrotropics (Londt 1980*b*). The genus is widespread, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Cameroon, Central African Republic, Democratic Republic of Congo, Gabon, Malawi and Zambia), East Africa (Burundi, Kenya, Somalia, Sudan, Tanzania and Uganda), West Africa (Benin, Burkina Faso, Côte d'Ivoire, Gambia, Guinea, Nigeria, Senegal and Sierra Leone) and the Indian Ocean islands (Madagascar). The genus inhabits forest, savanna and woodland habitats and adults perch on the ground, within grass or within and at the tips of shrubs and bushes (Figs 21–23). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1936, 1938, as *Neolaparus* Williston). Other useful references include Bromley (1936), Londt (2010*b*, 2012*a*) and Tomasovic (2008*b*). Londt (1980*b*) provided an identification key to the 46 Afrotropical species.

***Perasis* Hermann** (Laphriinae)**.** A genus of ten medium-sized species, occurring in the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. Two species occur in the Afrotropics, *P. carpenteri* Oldroyd, 1970 and *P. transvaalensis* Ricardo, 1925 (Londt 2007*a*). The genus is fairly widespread in sub-Saharan Africa, recorded from Southern Africa (South Africa) and East Africa (Burundi and Uganda). Lehr (1988*a*: 211) further records *P. arabicus* (Macquart, 1838) from the southern Arabian Peninsula (Yemen), but no specimens from the Afrotropical part of the Arabian Peninsula were studied by Londt (1999*b*, 2007*a*). The genus inhabits grassland and savanna habitats and adults perch on the ground. Oviposition probably takes place in sand or soil. Other useful references include Londt (1999*b*), Oldroyd (1970) and Ricardo (1925). Londt (2007*a*) provided an identification key to the two Afrotropical species.

***Philodicus* Loew** (Asilinae)**.** A genus of 50 large-sized species (Figs 13, 201, 202, 246–248) requiring modern revision, occurring in the Afrotropical, possibly Australasian, Oriental and Palaearctic Regions, with 23 species in the Afrotropics (Blasdale 1957). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Namibia, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo and Malawi), East Africa (Kenya, Somalia, Sudan and Uganda), the southern Arabian Peninsula (Yemen) and West Africa (Benin, Côte d'Ivoire, Gambia, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone and Togo). The genus probably inhabits grassland (usually in the vicinity of fresh or saline water), savanna and woodland habitats and adults perch on the ground or on beaches and river banks and at the tips of grass, shrubs and bushes (Fig. 13). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1937, 1938, 1939).



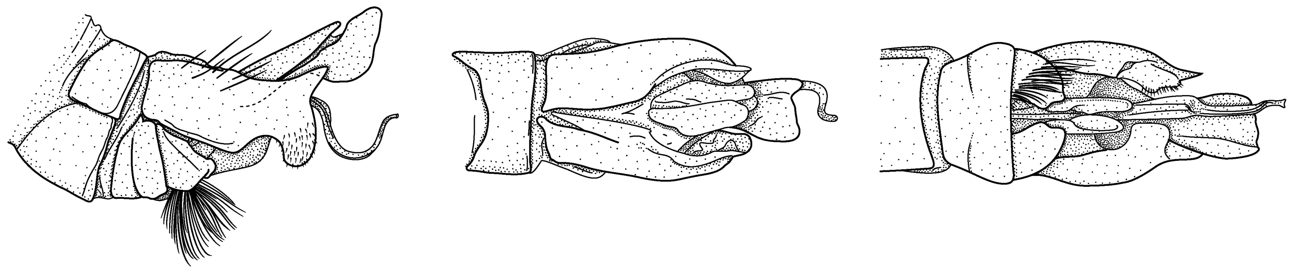
Figs 48.235–236. Habitus photographs of Asilidae: (235) *Trichoura tankwa* Londt, dorsal view ♂; (236) same, lateral view.

Abbreviations: *cua* – anterior cubital cell; m_3 – third medial cell; myst – mystax.

Other useful references include Londt (1978, 2005*a*, 2010*b*, 2012*a*, 2015*b*) and Tomasovic (2012*a*). Blasdale (1957) and Londt (2015*b*) provided the most recent identification keys to Afrotropical species.

***Pilophoneus* Londt** (Laphriinae)**.** An endemic genus of two medium-sized, bee-like species, *P. analogos* Londt, 2014 and *P. krugeri* (Oldroyd, 1974), described by Londt (1988*b*) and later reviewed by Londt (2014*d*). The genus is recorded in sub-Saharan Africa from Southern Africa (South Africa), Central Africa (Zambia) and East Africa (Tanzania). The genus inhabits grassland and savanna habitats and adults probably perch within and/or at the tips of grass. The oviposition strategy remains unknown, but may involve inserting eggs into dead wood. Other useful references include Oldroyd (1974). Londt (2014*d*) provided an identification key to the two species.

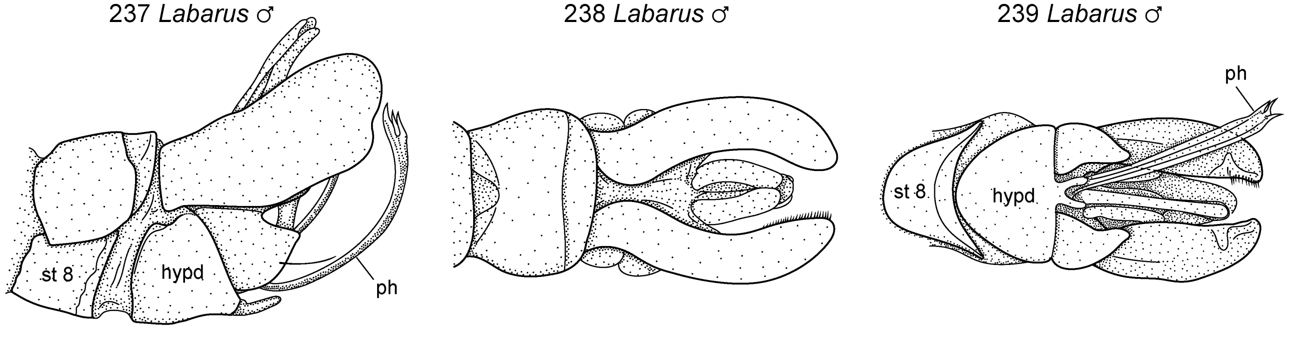
***Proagonistes* Loew** (Laphriinae)**.** A large endemic genus of 22 large- to very large-sized, pompilid-mimicking species (Figs 36, 37) reviewed by Bromley (1930, 1933), but requiring modern revision. The genus is widely distributed throughout sub-Saharan Africa, recorded from Southern Africa (Mozambique, South Africa and Zimbabwe), Central Africa (Cameroon, Democratic Republic of Congo, Gabon, Malawi and Republic of Congo), East Africa (Kenya, Tanzania and Uganda), West Africa (Côte d'Ivoire, Ghana, Guinea, Nigeria and Sierra Leone), the Indian Ocean islands (Madagascar) and the Atlantic Ocean islands (São Tomé and Príncipe). The genus inhabits forest and woodland habitats and adults perch within shrubs, bushes and trees (Figs 36, 37). Other useful references include Oldroyd (1970), Tomasovic (2010) and Tomasovic & Kwandjo (2007). Oviposition probably takes place on or in vegetation. Oldroyd (1970) provided the most recent identification key to the 22 Afrotropical species.



237 *Labarus* ♂

238 *Labarus* ♂

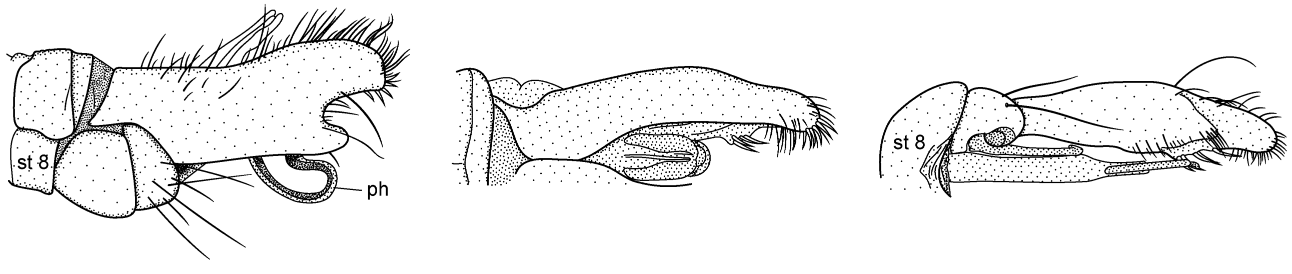
239 *Labarus* ♂



240 *Millenarius* ♂

241 *Millenarius* ♂

242 *Millenarius* ♂



243 *Neolophonotus* ♂

244 *Neolophonotus* ♂

245 *Neolophonotus* ♂

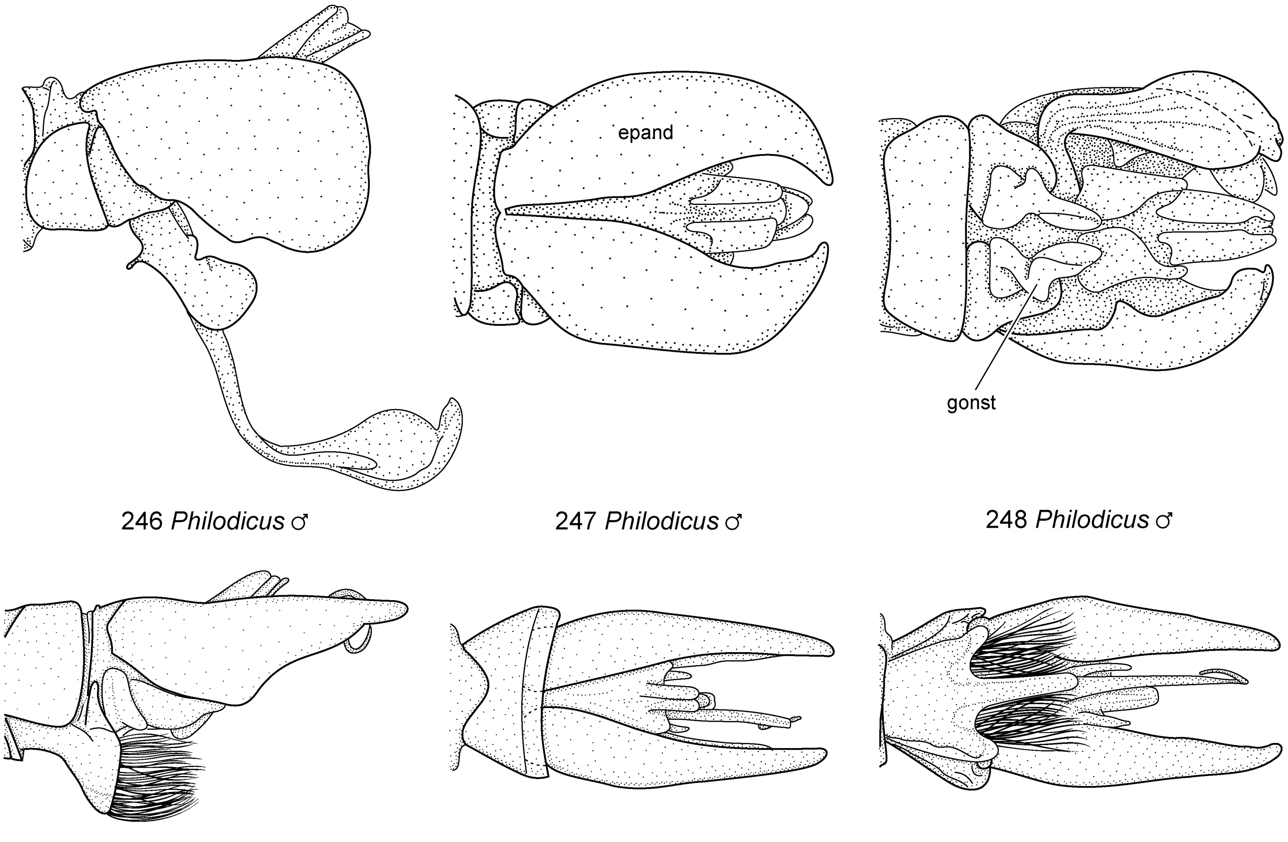
Figs 48.237–245. Male terminalia of Asilidae (Asilinae): (237) *Labarus ignota* Londt, lateral view; (238) same, dorsal view; (239) same, ventral view; (240) *Millenarius graminosus* Londt, lateral view; (241) same, dorsal view; (242) same, ventral view; (243) *Neolophonotus boa* Londt, lateral view; (244) same, dorsal view; (245) same, ventral view. Figs 237–239 (after Londt 2005*a*, figs 36–38), Figs 240–242 (after Londt 2005*a*, figs 44–46), Figs 243–245 (after Londt 1988*a*, figs 56–58).

Abbreviations: hypd – hypandrium; ph – phallus; st – sternite.

***Promachus* Loew** (Asilinae)**.** A very large genus of 230 medium- to large-sized species (Figs 1, 14–16, 77, 84, 203, 204), occurring in all zoogeographical regions, except Antarctica, but requiring modern revision. While Geller-Grimm (2004) placed *Bactria* Meigen in synonymy with *Promachus*, the taxonomic position of these genera has not been adequately resolved, as *Bactria* is the older name (Londt 2005*a*). Ninety-eight species occur in the Afrotropics, being widespread throughout the Afrotropics, recorded from Southern Africa (Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola, Bioko Is. (Equatorial Guinea), Cameroon, Democratic Republic of Congo, Gabon, Malawi, Republic of Congo and Zambia), East Africa (Ethiopia, Kenya, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (United Arab Emirates and Socotra Is. (Yemen)), West Africa (Benin, Côte d'Ivoire, Gambia, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone and Togo) and the Indian Ocean islands (Madagascar). The genus inhabits forest, grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch on stones, within grass or at the tips of shrubs and bushes (Figs 1, 14–16). Oviposition takes place on or in vegetation. Some biological information was provided by Cuthbertson (1934, 1935, 1937, 1938, 1939, some as *Bactria*). Other useful references include Bosák & Hradský (2011), Bromley (1931), Londt (2010*b*), Oldroyd (1974) and Tomasovic (2012*b*, 2014). No identification key to Afrotropical species is currently available.

***Prytanomyia* Özdikmen** (Laphriinae). An endemic monotypic genus, with the single small-sized species, *P. kochi* (Lindner, 1973) (Figs 38, 78, 205, 206), described by Oldroyd (1974, as *Prytania*). The species is confined to Southern Africa (Namibia) and Central Africa (Angola) and inhabits desert habitats and adults perch on the ground or on beaches (Fig. 38). Oviposition probably takes place in sand or soil. The genus was reviewed by Londt & Dikow (2017).

***Pycnomerinx* Hull** (Stenopogoninae)**.** An endemic genus of three medium-sized, wasp-like species, *P. cogani* Oldroyd, 1974, *P. gweta* Oldroyd, 1974 and *P. rhodesii* (Ricardo, 1925) (Figs 207, 208), confined to Southern Africa (Botswana, Namibia and Zimbabwe) (Londt 1990*c*), with unpublished records from Mozambique. The genus inhabits grassland and savanna habitats and adults perch on the ground or at the tips of grass. Oviposition takes place in sand or soil. Other useful



246 *Philodicus* ♂ 247 *Philodicus* ♂ 248 *Philodicus* ♂

249 *Synolcus* ♂ 250 *Synolcus* ♂ 251 *Synolcus* ♂

Figs 48.246–251. Male terminalia of Asilidae (Asilinae): (246) *Philodicus tenuipes* Loew, lateral view; (247) same, dorsal view; (248) same, ventral view; (249) *Synolcus acrobaptus* (Wiedemann), lateral view; (250) same, dorsal view; (251) same, ventral view. Figs 246–248 (after Londt 2015*b*, figs 21–23), Figs 249–251 (after Londt 2012*d*, figs 14–16).

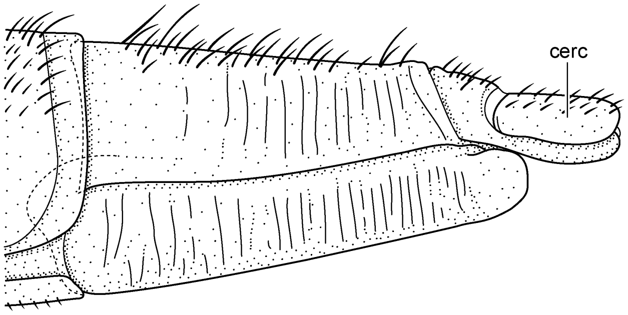
Abbreviations: epand – epandrium; gonst – gonostylus.

references include Oldroyd (1974). Londt (1990*c*) provided an identification key to the three species.

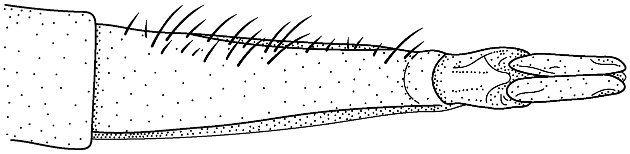
Pygommatius **Scarbrough & Marascia** (Ommatiinae)**.** A genus of 39 medium-sized species, occurring in the Afrotropical and Oriental Regions, with 25 species in the Afrotropics. Originally described by Scarbrough & Marascia (2003), as a subgenus of *Ommatius*, the group was elevated to generic rank by Scarbrough & Hill (2005). The genus is widespread, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Cameroon, Central African Republic, Chad, Democratic Republic of Congo, Gabon, Malawi, Republic of Congo and Zambia), East Africa (Ethiopia, Kenya, Tanzania and Uganda), West Africa (Benin, Côte d'Ivoire, Gambia, Ghana, Guinea, Mali, Nigeria and Sierra Leone) and the Indian Ocean islands (Madagascar) (Scarbrough & Marascia 2003). The genus inhabits grassland, savanna and woodland habitats and adults perch at the tips of grass, shrubs, bushes and trees. Oviposition takes place through random egg-dropping. Other useful references include Londt (2010*b*, 2012*a*) and Scarbrough (2010). Scarbrough & Marascia (2003) provided an identification key to the 25 Afrotropical species.

Remotomyia **Londt** (Stenopogoninae)**.** An endemic genus of four medium- to large-sized species (Figs 209, 210), confined to Southern Africa (Botswana, Namibia, South Africa and Zimbabwe) (Londt 1983*c*). The genus inhabits grassland, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Dikow & Londt (2000*b*) and Hull (1967). Dikow & Londt (2000*b*) provided an identification key to the four species.

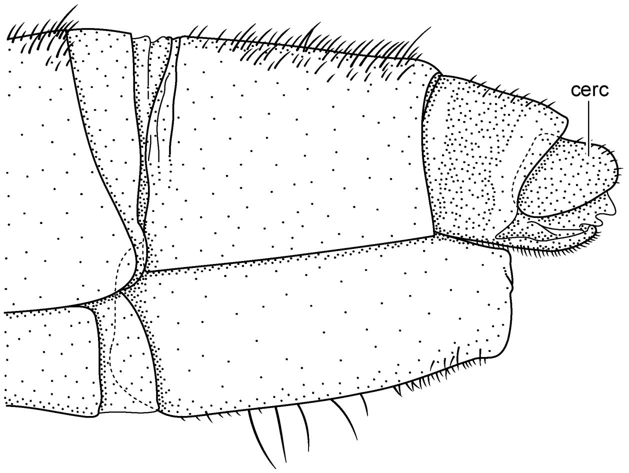
Rhabdogaster **Loew** (Brachyrhopalinae)**.** A near endemic genus of 39 small- to medium-sized species (Figs 211, 212, 259–261), with *R. cinerascens* (Wulp, 1899) extending into Saudi Arabia (Londt 2006*c*) and Iran (Lehr 1988*a*: 226) in the Palaearctic (Londt 2006*c*). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), Central Africa (Angola, Democratic Republic of



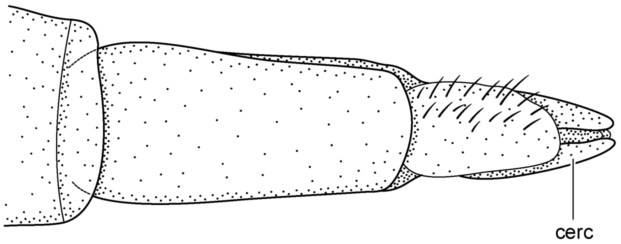
252 *Labarus* ♀



253 *Labarus* ♀



254 *Millenarius* ♀



255 *Millenarius* ♀

Figs 48.252–255. Female ovipositors of Asilidae (Asilinae): (252) *Labarus ignota* Londt, lateral view; (253) same, dorsal view; (254) *Millenarius graminosus* Londt, lateral view; (255) same, dorsal view. Figs 252, 253 (after Londt 2005*a*, figs 41, 42), Figs 254, 255 (after Londt 2005*a*, figs 49, 50).

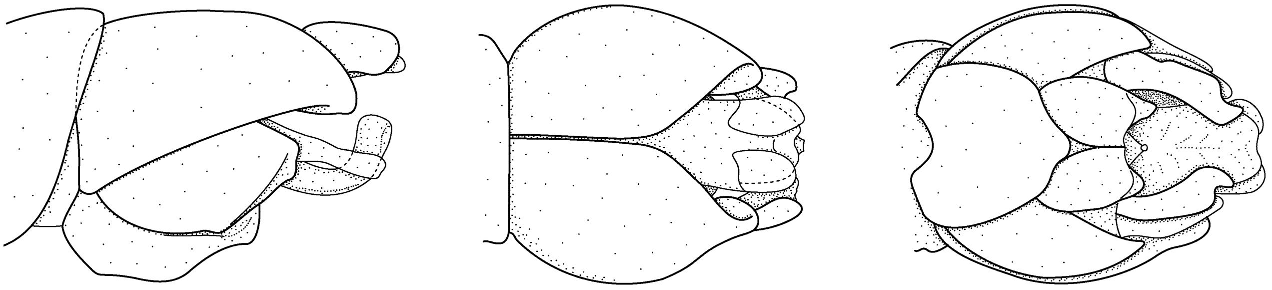
Abbreviation: cerc – cercus.

Congo and Zambia), East Africa (Eritrea, Kenya, Sudan, Tanzania and Uganda), the southern Arabian Peninsula (Yemen and Oman) and West Africa (Côte d'Ivoire and Gambia) (Londt 2006*c*). The genus inhabits grassland, Fynbos, savanna and woodland habitats and adults perch on the ground and at the tips of grass. Oviposition takes place in sand or soil. Other useful references include Londt (1993*b*, 2010*b*) and Tomasovic & Constant (2013). Londt (2006*c*) provided an identification key to the 39 Afrotropical species.

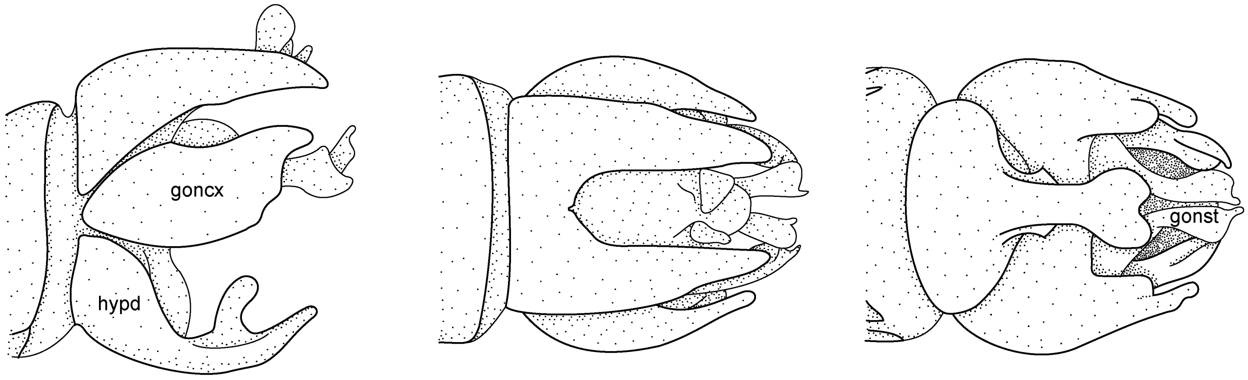
Rhacholaemus **Hermann** (Stenopogoninae)**.** An endemic genus of nine small- to medium-sized species confined to Southern Africa (Namibia and South Africa) (Londt 1999*d*). The genus inhabits grassland, Fynbos, savanna and semi-desert habitats and adults perch on the ground. Oviposition takes place in sand or soil. Other useful references include Oldroyd (1974). Londt (1999*d*) provided an identification key to the nine species.

Rhadinus **Loew** (Stichopogoninae)**.** A genus of ten small-sized, bee-like species (Figs 57, 213, 214), occurring in the Afrotropical and Palaearctic Regions, which requires modern revision. Four species occur in the Afrotropics, confined to East Africa (Sudan) and the southern Arabian Peninsula (United Arab Emirates and Yemen (incl. Socotra Is.)), with unpublished records from Djibouti. The biology of the genus is poorly known, but species probably inhabit semi-desert habitats and adults probably perch on the ground or on beaches and river banks. Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011), Efflatoun (1934, 1937) and Geller-Grimm (2002). No identification key to Afrotropical species is currently available.

Rhipidocephala **Hermann** (Trigonomiminae)**.** An endemic genus of 26 small-sized species (Figs 64, 65, 215, 216), reviewed by Oldroyd (1966), but requiring modern revision. Geller-Grimm (2004) and Lehr (1988*a*: 214) recorded the genus as questionable from the Palaearctic parts of the Arabian Peninsula. The genus is widespread, recorded from Southern Africa (Botswana, Lesotho, Mozambique, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo), East Africa (Burundi, Ethiopia, Kenya, Somalia and Tanzania), the southern Arabian Peninsula (Yemen), West Africa (Gambia, Ghana and Nigeria) and the Indian Ocean islands (Madagascar) (Oldroyd 1966). The genus inhabits grassland, Fynbos, savanna and woodland habitats and adults perch at the tips of grass or within shrubs and bushes (Figs 64, 65). Oviposition takes place through random egg-dropping. Some biological information was provided by Cuthbertson (1935). Oldroyd (1966) provided the most recent identification key to the 26 species.



256 *Habropogon* ♂ 257 *Habropogon* ♂ 258 *Habropogon* ♂



259 *Rhabdogaster* ♂ 260 *Rhabdogaster* ♂ 261 *Rhabdogaster* ♂

Figs 48.256–261. Male terminalia of Asilidae (Brachyrhopalinae): (256) *Habropogon capensis* Londt, lateral view; (257) same, dorsal view; (258) same, ventral view; (259) *Rhabdogaster eremia* Londt, lateral view; (260) same, dorsal view; (261) same, ventral view. Figs 256–258 (after Londt 2000*b*, figs 28–30), Figs 259–261 (after Londt 2006*c*, figs 21–23).

Abbreviations: goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium.

***Robertomyia* Londt** (Asilinae)**.** An endemic genus of two medium- to large-sized species, *R. lavignei* Londt, 1990 and *R. snowi* Londt, 2010, described by Londt (1990*a*) and later reviewed by Londt (2010*b*). The genus is recorded from East Africa (Somalia) and West Africa (Gambia), with an unpublished record from Kenya. The genus probably inhabits savanna and woodland habitats and adults probably perch at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation. Londt (2010*b*) provided an identification key to the two species.

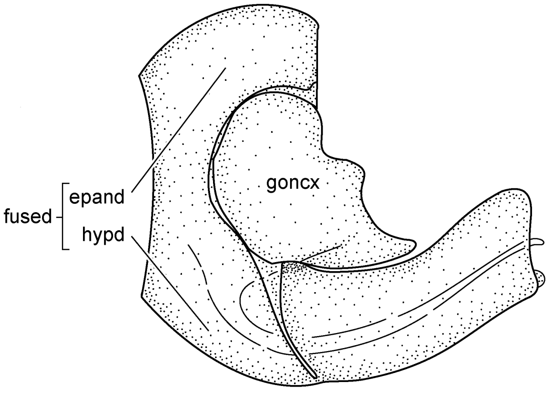
***Saropogon* Loew** (Dasypogoninae)**.** A genus of 135 small- to medium-sized species (Figs 217, 218), occurring in all zoogeographical regions, except Antarctica. Ten species occur in the Afrotropics, confined to East Africa (Eritrea, Ethiopia, Kenya, Sudan and Tanzania), the southern Arabian Peninsula (Oman, United Arab Emirates and Yemen) and West Africa (Mali, Mauritania, Niger and Senegal) (Londt 1997). The genus apparently inhabits grassland, savanna and semi-desert habitats and adults probably perch on the ground or on low vegetation. Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011) and Londt (2010*b*). Londt (1997) provided the most recent identification key to the 10 sub-Saharan species, but see Bosák & Hradský (2011) for the Arabian Peninsula fauna.

***Schildia* Aldrich** (Leptogastrinae)**.** A genus of ten small-sized species (Figs 281–283), occurring in the Afrotropical, Neotropical and Oriental Regions, with a single Afrotropical species, *S. adina* Dikow & Bayless, 2009, confined to the Indian Ocean islands (Madagascar) (Dikow & Bayless 2009). While many extralimital species inhabit forest habitats, *S. adina* purportedly inhabits "xeric shrub lands" and adults probably perch at the tips of shrubs, bushes and trees. The oviposition strategy probably involves random egg-dropping. Dikow & Bayless (2009) provided an identification key to the world fauna.

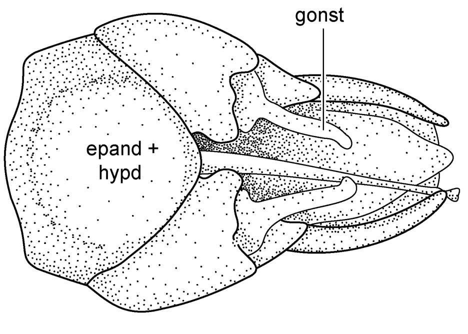
***Scylaticus* Loew** (Stenopogoninae)**.** A genus of 48 small- to large-sized, bee- or wasp-like species (Figs 56, 219, 220), occurring in the Afrotropical, Neotropical, Oriental and Palaearctic Regions, with 36 species in the Afrotropics (Londt 1992*c*). The genus is distributed mainly in Southern Africa, but is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Lesotho, Namibia, South Africa and Zimbabwe), Central Africa (Malawi and Zambia), East Africa (Kenya), West Africa (Gambia) and the southern Arabian Peninsula (United Arab Emirates) (Londt 1992*c*). The genus inhabits grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch on the ground or at the tips of shrubs and bushes (Fig. 56). Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011), Engel (1932), Londt (2010*b*) and Tomasovic & Constant (2013). Londt (1992*c*) provided an identification key to the 36 Afrotropical species.

***Sisyrnodytes* Loew** (Willistonininae)**.** A genus of 18 small- to medium-sized, bee-like species (Figs 67, 79, 221, 222, 310, 311), occurring in the Afrotropical and Palaearctic Regions, with 16 species in the Afrotropics (Londt 2009*a*). The genus is widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Malawi and Zambia), East Africa (Eritrea, Kenya and Tanzania), the southern Arabian Peninsula (United Arab Emirates and Yemen) and West Africa (Benin, Gambia, Mauritania, Niger and Nigeria) (Londt 2009*a*). The genus inhabits grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch on the ground or on stones and rocks (Fig. 67). Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011) and Oldroyd (1957). Londt (2009*a*) provided an identification key to the 16 Afrotropical species.

***Smeryngolaphria* Hermann** (Laphriinae)**.** A genus of 10 small- to medium-sized species, occurring in the Afrotropical and Oriental Regions. Three species occur in the Afrotropics, *S. bicolorala* Tomasovic, 2003, *S. pallida* Bromley, 1935 and *S. bromleyi* Londt, 1989, reviewed by Londt (1989*b*) with further revision required. The genus is fairly widespread throughout the Afrotropics, recorded from Central Africa (Democratic



262 *Pegasimallus* ♂



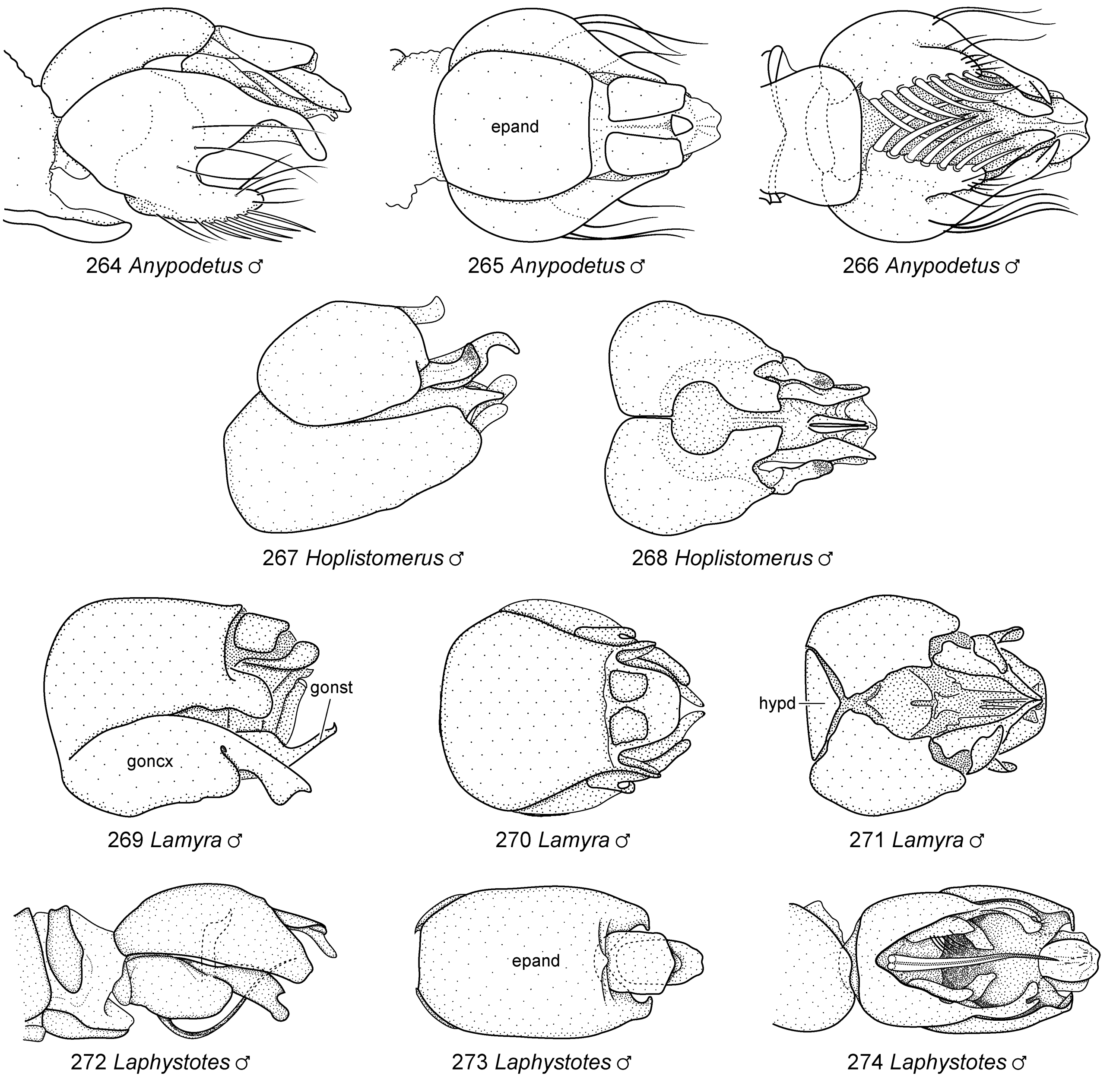
263 *Pegasimallus* ♂

Figs 48.262–263. Male terminalia of Asilidae (Dasypogoninae): (262) *Pegesimallus laticornis* (Loew), lateral view; (263) same, ventral view. Figs 262, 263 (after Londt 1980*b*, figs 53, 54).

Abbreviations: epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium.

Republic of Congo), West Africa (Nigeria) and the Indian Ocean islands (Madagascar) (Londt 1989*b*). The biology of the genus remains unknown, but species probably inhabit forest habitats and adults probably perch within trees. Oviposition probably takes place on or in vegetation. Other useful references include Tomasovic (2003). Londt (1989*b*) provided the most recent identification key to Afrotropical species, but see Tomasovic (2003) for an additional species.

***Sphagomyia* Londt** (Asilinae)**.** An endemic genus of three small-sized species, *S. botswana* Londt, 2002, *S. gambia* Londt, 2012 and *S. kenya* Londt, 2002, described by Londt (2002*b*)



264 *Anypodetus* ♂ 265 *Anypodetus* ♂ 266 *Anypodetus* ♂
267 *Hoplistomerus* ♂ 268 *Hoplistomerus* ♂
269 *Lamyra* ♂ 270 *Lamyra* ♂ 271 *Lamyra* ♂
272 *Laphystotes* ♂ 273 *Laphystotes* ♂ 274 *Laphystotes* ♂

Figs 48.264–274. Male terminalia of Asilidae (Laphriinae): (264) *Anypodetus leucothrix* Londt, lateral view; (265) same, dorsal view; (266) same, ventral view; (267) *Hoplistomerus nobilis* Loew, lateral view; (268) same, ventral view; (269) *Lamyra gulo* (Loew), lateral view; (270) same, dorsal view; (271) same, ventral view; (272) *Laphystotes ariel* Londt, lateral view; (273) same, dorsal view; (274) same, ventral view. Figs 264–266 (after Londt 2000*a*, figs 19–21), Figs 267, 268 (after Londt 2007*b*, figs 21, 23), Figs 269–271 (after Dikow & Londt 2000, figs 4–6), Figs 272–274 (after Londt 2004*a*, figs 17–19).

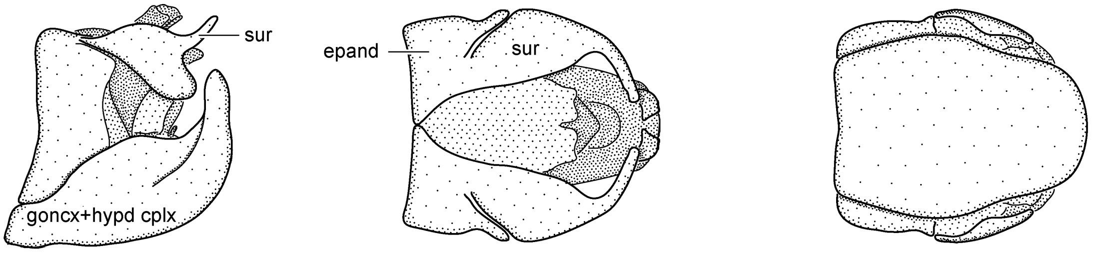
Abbreviations: epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium.

and reviewed by Londt (2012*a*). Species are recorded from Southern Africa (Botswana and South Africa), East Africa (Kenya) and West Africa (Gambia). The genus inhabits savanna and woodland habitats and adults probably perch within shrubs and bushes. Oviposition probably takes place on or in vegetation. Londt (2012*a*) provided an identification key to the three species.

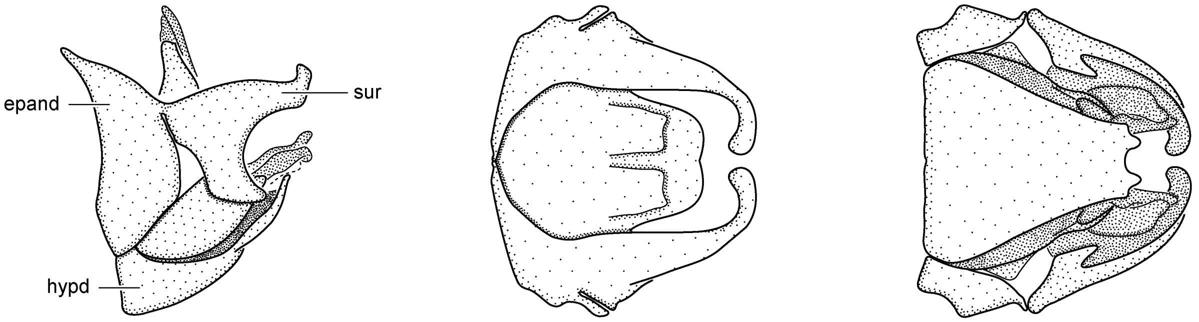
Sporadothrix **Hermann** (Willistonininae)**.** An endemic monotypic genus, with the single medium-sized species, *S. gracilis* Hermann, 1907 (Figs 80, 223, 224), confined to Southern Africa (Botswana, Namibia and South Africa) (Londt 2010*c*). The species inhabits grassland, savanna and semi-desert habitats and adults perch on the ground or within grass. Oviposition takes place in sand or soil.

Stenopogon **Loew** (Stenopogoninae)**.** A large genus of 170 medium-sized species, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions, that is in need of modern revision. Only two species occur in the Afrotropics, *S. coxalis* (Becker, 1922) and *S. lehri* Londt, 1999, that were reviewed by Londt (1999*d*, 2002*a*) and are confined to East Africa (Kenya, Somalia and Sudan). The biology of the genus remains unknown, but species probably inhabit grassland, savanna and semi-desert habitats and adults perch on the ground or on low vegetation. Oviposition takes place in sand or soil. No identification key to Afrotropical species is currently available.

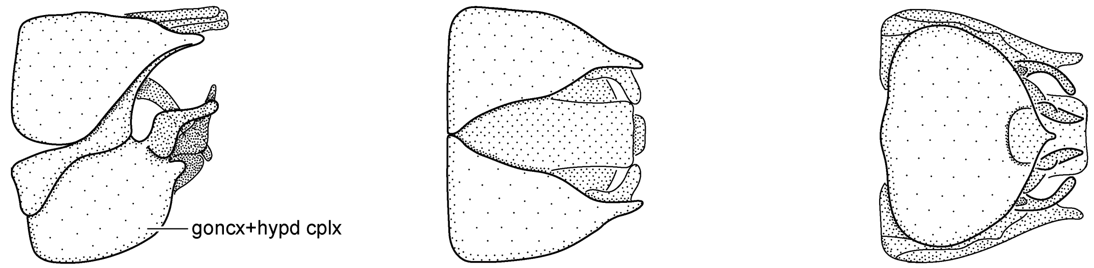
Stichopogon **Loew** (Stichopogoninae)**.** A large genus of 102 small-sized species (Figs 58–60, 81, 225, 226, 301, 302), occurring in all zoogeographical regions, except Antarctica.



275 *Euscelidia* ♂ 276 *Euscelidia* ♂ 277 *Euscelidia* ♂



278 *Lasiocnemus* ♂ 279 *Lasiocnemus* ♂ 280 *Lasiocnemus* ♂

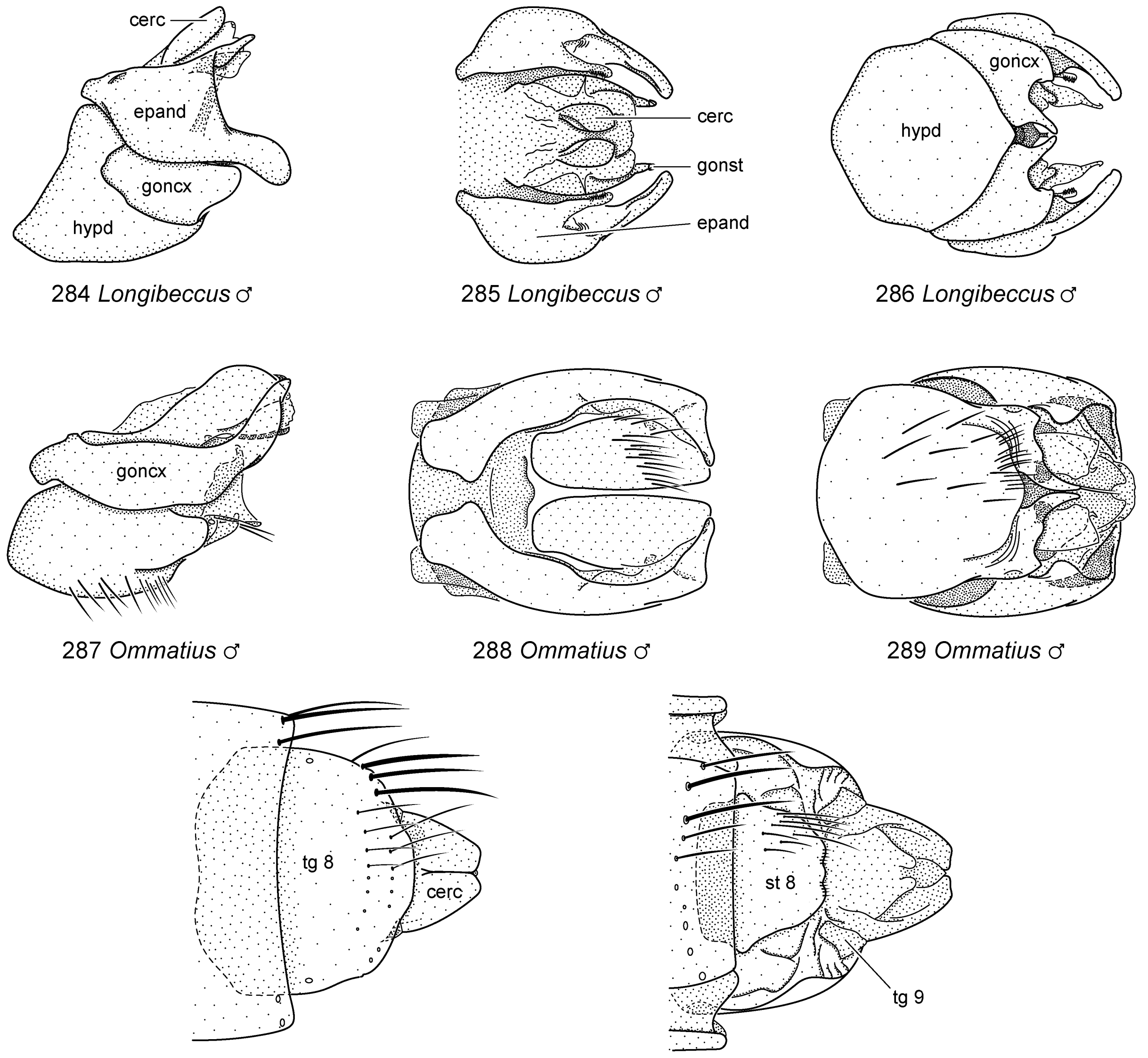


281 *Schildia* ♂ 282 *Schildia* ♂ 283 *Schildia* ♂

Figs 48.275–283. Male terminalia of Asilidae (Leptogastrinae): (275) *Euscelidia ochricornis* (Loew), lateral view; (276) same, dorsal view; (277) same, ventral view; (278) *Lasiocnemus londti* Dikow, lateral view; (279) same, dorsal view; (280) same, ventral view; (281) *Schildia adina* Dikow & Bayless, lateral view; (282) same, dorsal view; (283) same, ventral view. Figs 275–277 (after Dikow 2003, fig. 23), Figs 278–280 (after Dikow 2007, figs 5–7), Figs 281–283 (after Dikow & Bayless 2009, figs 13–15).

Abbreviations: epand – epandrium; goncx+hypd cplx – gonocoxal + hypandrial complex; hypd – hypandrium; sur – surstylus.

Seventeen species occur in the Afrotropics (Londt 1979*b*), that are widespread throughout the region, recorded from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Angola and Democratic Republic of Congo), East Africa (Ethiopia and Sudan), the southern Arabian Peninsula (United Arab Emirates and Yemen (incl. Socotra Is.)), West Africa (Gambia, Mauritania and Niger) and the Indian Ocean islands (Madagascar). The genus inhabits grassland, Fynbos, savanna and semi-desert habitats and adults perch on the ground, or on beaches and river banks (Figs 58–60). Oviposition takes place in sand or soil. Some biological information was provided by Cuthbertson (1938). Other useful references include Bosák & Hradský (2011), Efflatoun (1934, 1937), Howarth (2006), Londt (2010*b*), Oldroyd (1970, 1974) and Séguy (1955). Londt (1979*b*) provided the most recent identification key to eight Afrotropical species, but see the recent addition of the southern Arabian Peninsula fauna by Bosák & Hradský (2011: 746).



284 *Longibeccus* ♂ 285 *Longibeccus* ♂ 286 *Longibeccus* ♂

287 *Ommatius* ♂ 288 *Ommatius* ♂ 289 *Ommatius* ♂

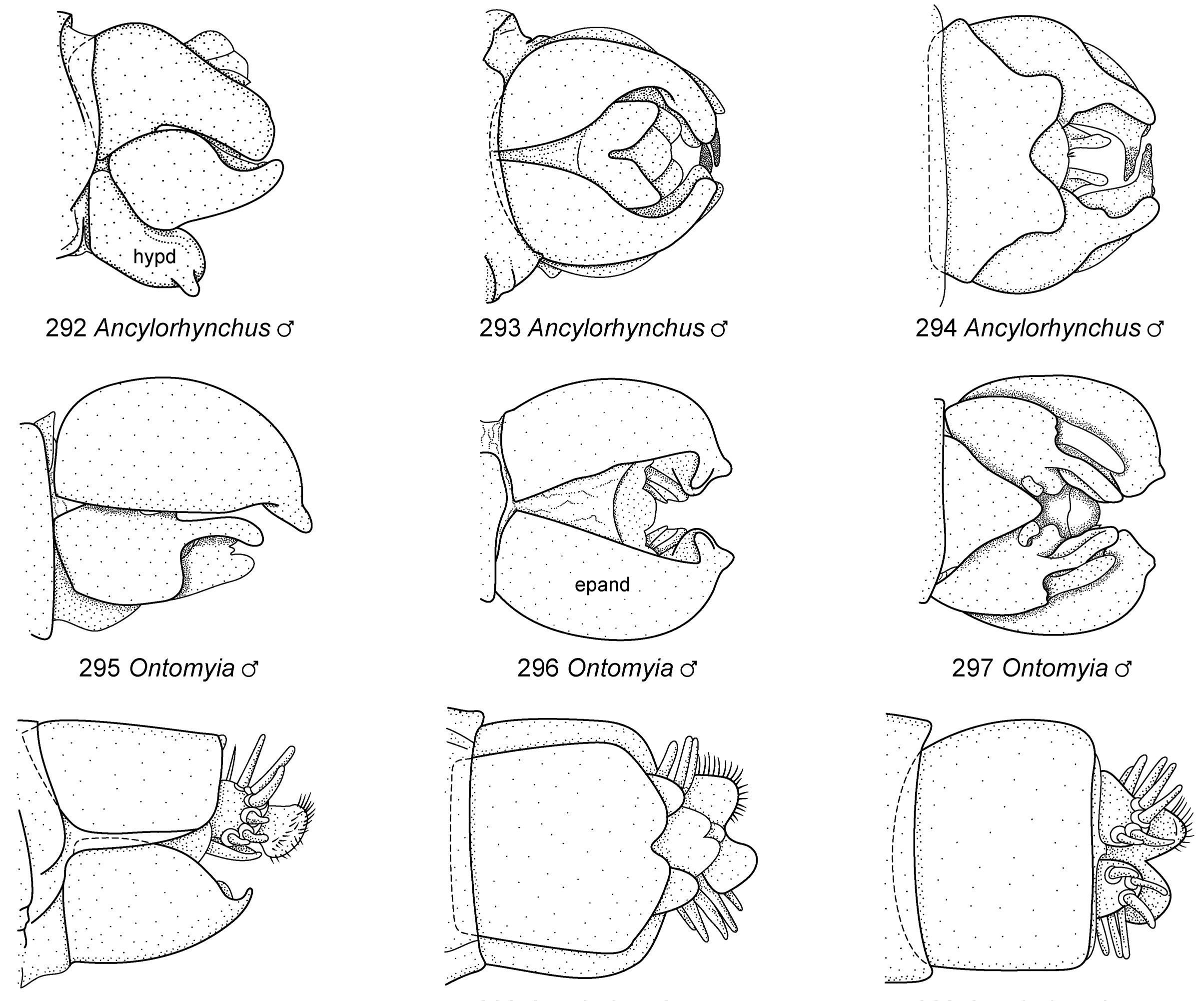
290 *Longibeccus* ♀ 291 *Longibeccus* ♀

Figs 48.284–291. Male and female terminalia of Asilidae (Ommatiinae): (284) male terminalia of *Longibeccus fuscovittatus* (Ricardo), lateral view; (285) same, dorsal view; (286) same, ventral view; (287) same, *Ommatius neotenellus* Bromley, lateral view; (288) same, dorsal view; (289) same, ventral view; (290) female terminalia of *L. fuscovittatus*, dorsal view; (291) same, ventral view. Figs 284–291 (after Scarbrough 2010, figs 31–33, 74–76, 37, 38, respectively).

Abbreviations: cerc – cercus; epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; st – sternite; tg – tergite.

Stiphrolamyra **Engel** (Laphriinae)**.** A genus of 15 small- to large-sized, wasp-like species (Figs 39, 82, 227, 228), occurring in the Afrotropical and Palaearctic Regions. Ten species occur in the Afrotropics (Londt 1983*a*), that are widespread throughout sub-Saharan Africa, recorded from Southern Africa (Botswana, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Democratic Republic of Congo), East Africa (Kenya and Uganda) and the southern Arabian Peninsula (United Arab Emirates and Yemen). The genus inhabits arid biomes, including grassland, savanna and semi-desert habitats and adults perch on rocks or at the tips of shrubs and bushes (Fig. 39). Oviposition probably takes place through random egg-dropping. Other useful references include Bosák & Hradský (2011), Kirk-Spriggs & McGregor (2009), Oldroyd (1974) and Theodor (1980). Londt (1983*a*) provided the most recent identification key to the eight Southern African species.

Storthyngomerus **Hermann** (Laphriinae)**.** An endemic genus of five wasp-like species, distributed throughout the Afrotropics, recorded from Southern Africa (Botswana, Mozambique, South Africa and Zimbabwe), Central Africa (Cameroon, Democratic Republic of Congo, Gabon and Malawi), East Africa (Kenya, Tanzania and Uganda), West Africa (Côte d'Ivoire, Gambia, Ghana, Guinea, Liberia, Nigeria and Sierra Leone) and the Indian Ocean islands (Madagascar) (Londt 1998*b*). The genus inhabits forest habitats and adults perch at the tips of shrubs, bushes and trees. Oviposition probably takes



292 *Ancylorhynchus* ♂
293 *Ancylorhynchus* ♂
294 *Ancylorhynchus* ♂
295 *Ontomyia* ♂
296 *Ontomyia* ♂
297 *Ontomyia* ♂
298 *Ancylorhynchus* ♀
299 *Ancylorhynchus* ♀
300 *Ancylorhynchus* ♀

Figs 48.292–300. Male and female terminalia of Asilidae (Stenopogoninae): (292) male terminalia of *Ancylorhynchus cruciger* (Loew), lateral view; (293) same, dorsal view; (294) same, ventral view; (295) same, *Ontomyia ricardoi* (Londt), lateral view; (296) same, dorsal view; (297) same, ventral view; (298) female terminalia of *A. cruciger*, lateral view; (299) same, ventral view; (300) same, dorsal view. Figs 292–294, 298–300 (after Londt 2011, figs 61–66), Figs 295–297 (after Dikow & Londt 2000, figs 2–4).

Abbreviations: epand – epandrium; hypd – hypandrium.

place on or in vegetation. Other useful references include Londt (2010*b*) and Oldroyd (1970, 1974). Londt (1998*b*) provided an identification key to the five species.

Synolcus **Loew** (Asilinae)**.** An endemic genus of 13 medium- to large-sized species (Figs 17, 229, 230, 249–251), reviewed by Londt (1980*a*, 1990*b*, 2012*d*) and recorded from Southern Africa (Namibia and South Africa) and Central Africa (Malawi). The genus inhabits forest, savanna, semi-desert and woodland habitats and adults perch on the ground or within shrubs, bushes and trees (Fig. 17). Oviposition takes place on or in vegetation. Londt (2012*d*) provided an identification key to the thirteen species.

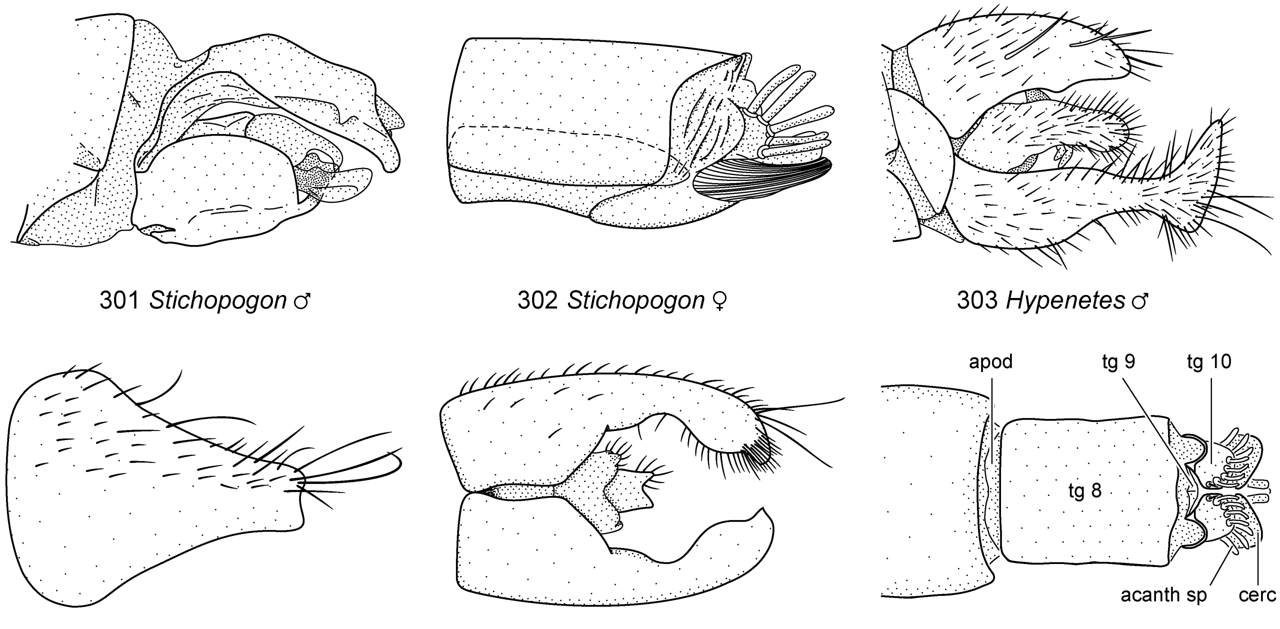
Systropalpus **Hull** (Laphriinae)**.** An endemic monotypic genus, with the single large-sized species, *S. aurivulpes* Hull, 1962, confined to East Africa (Ethiopia). The biology remains unknown, but the species probably inhabits forest or woodland habitats and adults probably perch within trees. Oviposition probably takes place on or in vegetation.

Teratopomyia **Oldroyd** (Brachyrhopalinae)**.** An endemic monotypic genus, with the single medium-sized, wasp-like species, *T. cyaneus* (F., 1781), confined to Southern Africa (Lesotho and South Africa) (Londt 2009*b*). The species inhabits Fynbos and savanna habitats and adults perch on the ground or at the tips of grass, shrubs and bushes. Oviposition takes place in sand or soil.

Thallosia **Oldroyd** (Ommatiinae)**.** An endemic monotypic genus, with the single medium-sized species, *T. congoicola* Oldroyd, 1970, confined to Central Africa (Democratic Republic of Congo) and West Africa (Gambia). The species inhabits savanna and woodland habitats and adults probably perch within grass or at the tips of shrubs, bushes and trees. Oviposition probably takes place through random egg-dropping. Other useful references include Londt (2010*b*) and Scarbrough (2010).

Tolmerus **Loew** (Asilinae)**.** A genus of 73 medium- to large-sized species, occurring in the Afrotropical, Nearctic and Palaearctic Regions and requiring modern revision. Three species occur in the Afrotropics, *T. socotrae* Geller-Grimm, 2002, *T. unicus* (Becker, 1910) and *T. wraniki* Geller-Grimm, 2002, confined to the southern Arabian Peninsula (Yemen (incl. Socotra Is.)). The status of the genus requires clarification. Oldroyd (1980: 339) listed *Tolmerus* as a synonym of *Machimus*, but Geller-Grimm (2002) recorded three species of *Tolmerus* from Socotra Is. (Yemen) and Geller-Grimm (2004) listed *Tolmerus* as a distinct genus. The genus probably inhabits savanna habitats and adults probably perch within shrubs and bushes. Oviposition probably takes place on or in vegetation. No identification key to Afrotropical species is currently available, but detailed descriptions are provided by Geller-Grimm (2002).

Torasilus **Londt** (Asilinae)**.** An endemic monotypic genus, with the single large-sized species, *T. solus* Londt, 2005 (Figs


301 *Stichopogon* ♂ 302 *Stichopogon* ♀ 303 *Hypenetes* ♂
304 *Hypenetes* ♂ 305 *Hypenetes* ♂ 306 *Hypenetes* ♀

Figs 48.301–306. Male and female terminalia of Asilidae (Stichopogoninae and Tillobromatinae): (301) male terminalia of *Stichopogon punctum* Loew, lateral view; (302) same, female terminalia, lateral view; (303) male terminalia of *Hypenetes stigmatias* Loew, lateral view; (304) same, male hypandrium, ventral view; (305) same, dorsal view; (306) female terminalia of *H. stigmatias*, dorsal view. Figs 301, 302 (after Londt 1979*b*, figs 27, 35), Figs 303–305 (after Londt 1985*b*, figs 77–79), Fig. 306 (after Dikow 2009*a*, fig. 87).

Abbreviations: acanth sp – acanthophorite spine; apod – apodeme; cerc – cercus; tg – tergite.

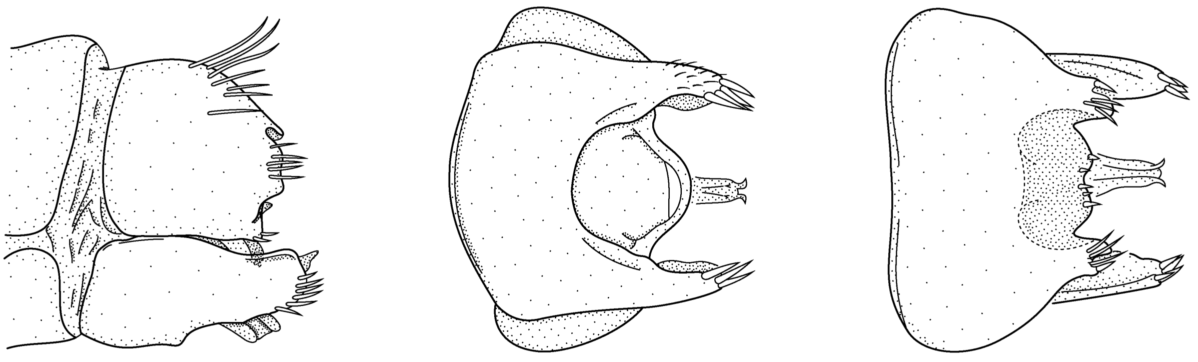
231, 232), confined to Southern Africa (Namibia). The species inhabits desert and semi-desert habitats and adults perch on the ground. Oviposition probably takes place on or in vegetation.

***Trichardis* Hermann** (Laphriinae)**.** A genus of 28 small- to medium-sized, bee-like species (Figs 40, 41, 233, 234), occurring in the Afrotropical and Palaearctic Regions. Twenty-five species occur in the Afrotropics (Londt 2008*b*), that are widespread throughout sub-Saharan Africa, reported from Southern Africa (Botswana, Lesotho, Mozambique, Namibia, South Africa and Zimbabwe), Central Africa (Chad, Democratic Republic of Congo and Malawi), East Africa (Eritrea, Ethiopia, Kenya, Somalia and Tanzania), the southern Arabian Peninsula (United Arab Emirates and Yemen (incl. Socotra Is. and Abd al Kuri Is.)) and West Africa (Burkina Faso, Côte d'Ivoire, Gambia, Mali, Niger, Nigeria and Senegal). There are also unpublished records from Djibouti. The genus inhabits grassland, Fynbos, savanna, semi-desert and woodland habitats and adults perch on the ground and on stones. Oviposition takes place in sand or soil. Other useful references include Bosák & Hradský (2011), Bosák *et al*. (2014), Geller-Grimm (2002), Londt (2010*b*) and Oldroyd (1974). Londt (2008*b*) provided an identification key to 25 Afrotropical species.

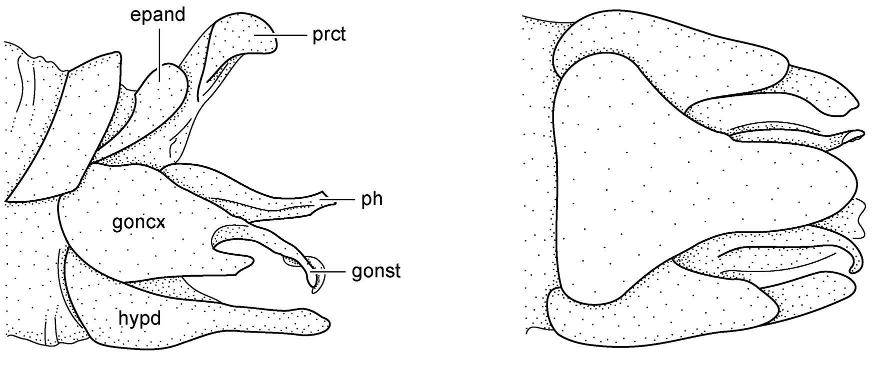
***Trichoura* Londt** (Willistonininae)**.** An endemic genus of seven small-sized species (Figs 68, 235, 236), confined to Southern Africa (South Africa). The genus was described by Londt (1994*b*) and reviewed by Londt & Dikow (2016). Species inhabit grassland, savanna and semi-desert habitats and adults perch on the ground or on low vegetation (Fig. 68). Oviposition takes place in sand or soil. Londt & Dikow (2016) provided an identification key to the seven species.

***Tsacasiella* Lehr** (Asilinae)**.** An endemic genus of eight medium- to large-sized species reviewed by Tsacas (1969), who described most of the species in *Neomochtherus* and Londt (2002*b*). The genus is recorded from Southern Africa (Botswana, Namibia and Zimbabwe), Central Africa (Democratic Republic of Congo, Malawi and Zambia) and East Africa (Kenya and Rwanda). The genus inhabits forest, savanna and woodland habitats and adults perch within grass, shrubs and bushes. Oviposition probably takes place on or in vegetation. Londt (2002*b*) provided an identification key to the eight species.

***Tuberconspicus* Tomasovic** (Asilinae)**.** An endemic monotypic genus, with the single medium-sized species, *T. aethiopicus* Tomasovic, 2014, confined to East Africa (Ethiopia) (Tomasovic 2014). The species is morphologically similar to



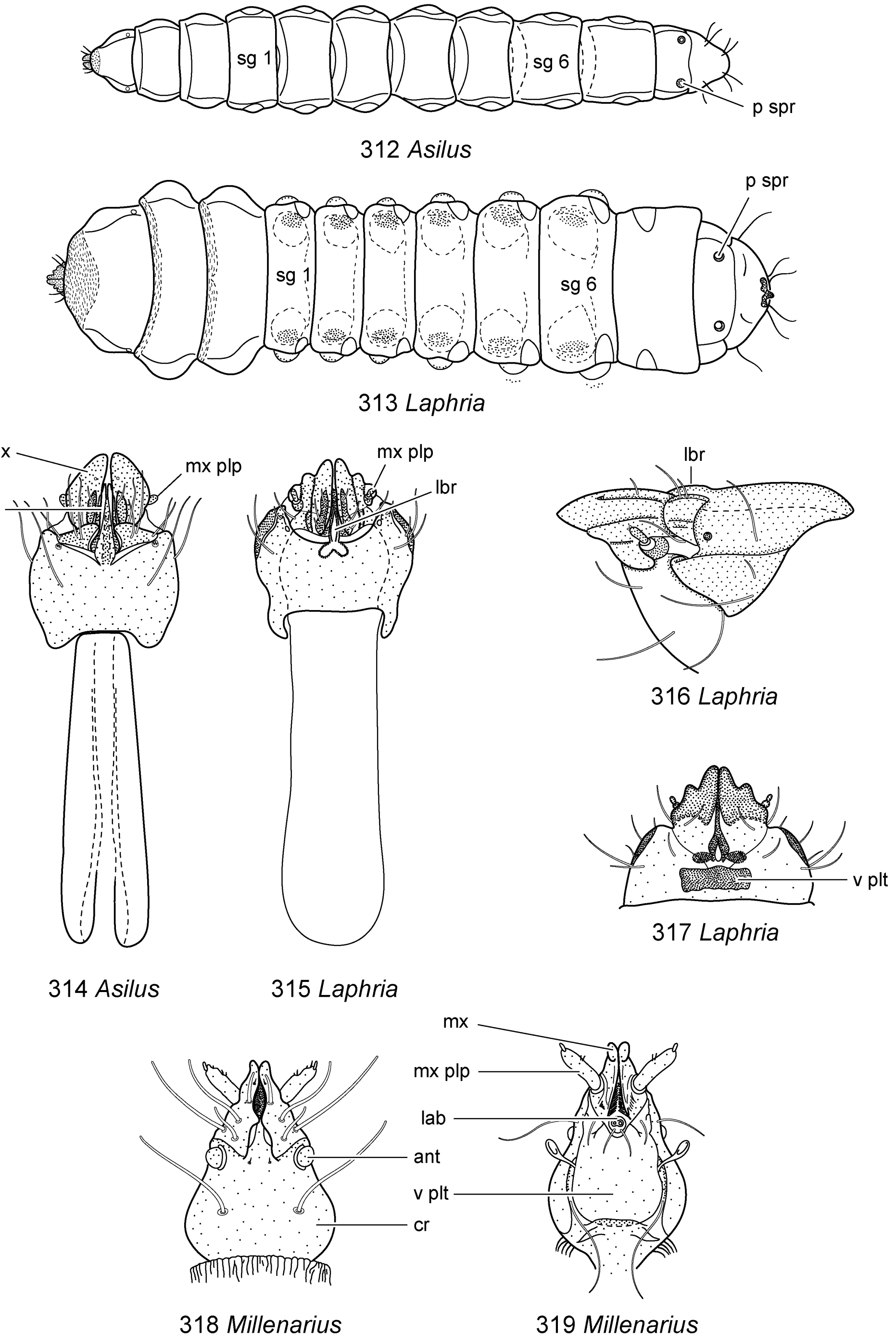
307 *Damalis* ♂ 308 *Damalis* ♂ 309 *Damalis* ♂



310 *Sisyrnodytes* ♂ 311 *Sisyrnodytes* ♂

Figs 48.307–311. Male terminalia of Asilidae (Trigonomiminae and Willistonininae): (307) *Damalis neavei* Londt, lateral view; (308) same, dorsal view; (309) same, ventral view; (310) *Sisyrnodytes apicalis* Oldroyd, lateral view; (311) same, ventral view. Figs 307–309 (after Londt 1989*a*, figs 118–120), Figs 310, 311 (after Londt 2009*a*, figs 8, 9).

Abbreviations: epand – epandrium; goncx – gonocoxite; gonst – gonostylus; hypd – hypandrium; ph – phallus; prct – proctiger.



312 *Asilus*

313 *Laphria*

314 *Asilus*

315 *Laphria*

316 *Laphria*

317 *Laphria*

318 *Millenarius*

319 *Millenarius*

Figs 48.312–319. Larval features of Asilidae: (312) larval habitus of *Asilus crabroniformis* L., dorsal view (non-Afrotropical); (313) same, *Laphria gibbosa* L., dorsal view (non-Afrotropical); (314) head capsule and rod of *A. crabroniformis*, dorsal view; (315) same, *L. gibbosa*, dorsal view; (316) same, head capsule, lateral view; (317) same, ventral view; (318) head capsule of *Millenarius dichaetus* Hull, dorsal view; (319) same, ventral view. Figs 312–317 (after Melin 1923, figs 171, 160, 172, 131–133), Figs 318, 319 (after Londt & Harris 1987, figs 6, 7).

Abbreviations: ant – antenna; cr – cranium; lab – labium; lbr – labrum; md – mandible; mx – maxilla; mx plp – maxillary palpus; p spr – posterior spiracle; sg – segment; v plt – ventral plate.

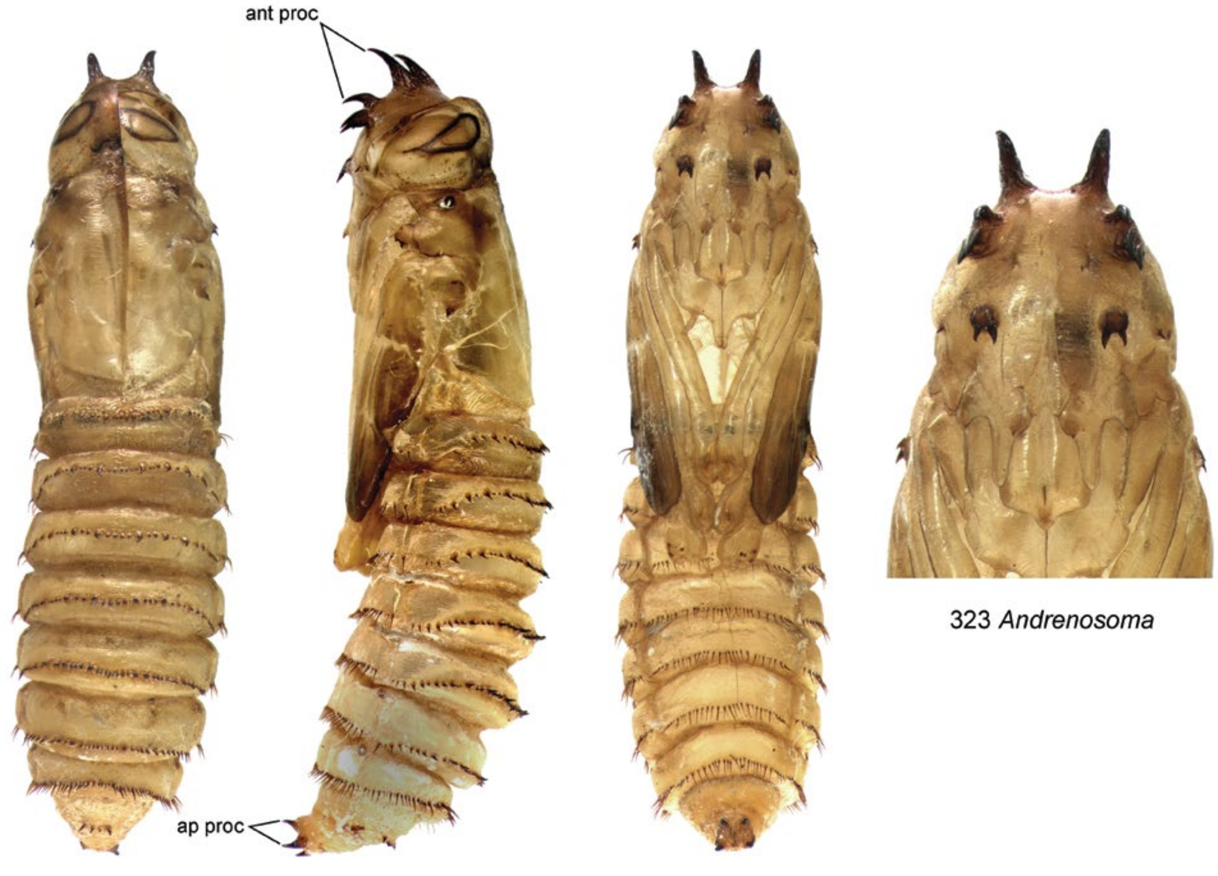
species of the diverse genus *Promachus*. The habitat and ecology of the species remain unknown.

Turkmenomyia **Paramonov** (Stichopogoninae)**.** A genus of four small-sized species, occurring in the Afrotropical and Palaearctic Regions. A single species, *T. paramonovi* Bosák & Hradský, 2011, occurs in the Afrotropics, confined to the southern Arabian Peninsula (United Arab Emirates) (Bosák & Hradský 2011: 751). *Turkmenomyia* has been treated as a synonym of *Eremodromus* Zimin (Geller-Grimm 2004; Lehr 1979) and was reinstated to full generic status for Palaearctic species (Bosák & Hradský 2011: 751). The biology of the species remains unknown, but is probably similar to *Stichopogon*, inhabiting semi-desert habitats and adults perching on the ground. Oviposition takes place in sand or soil.

Valiraptor **Londt** (Asilinae)**.** An endemic genus of four medium- to large-sized species (Londt 2002*b*), confined to Southern Africa (Namibia and South Africa). The genus inhabits forest, grassland, savanna and woodland habitats and adults probably perch within grass, shrubs and bushes. Oviposition takes place on or in vegetation. Londt (2002*b*) provided an identification key to the four species.

Wadipogon **Bosák & Hradský** (Brachyrhopalinae)**.** A genus of three small-sized species, occurring in the Afrotropical and Palaearctic Regions. The genus is primarily distributed in Egypt, with two species in the Afrotropics, *W. pulchrum* (Efflatoun, 1937) and *W. szpilai* Bosák & Hradský, 2011, confined to the southern Arabian Peninsula (United Arab Emirates) (Bosák & Hradský 2011: 739). The biology remains unknown, but the genus probably inhabits semi-desert habitats and adults probably perch on the ground. Oviposition takes place in sand or soil. Other useful references include Efflatoun (1937). No identification key to Afrotropical species is currently available.

Zelamyia **Londt** (Asilinae)**.** An endemic monotypic genus, with the single small-sized species, *Z. alyctus* Londt, 2005, confined to Southern Africa (South Africa) (Londt 2005*a*). The genus inhabits Fynbos habitats and adults probably perch within and/or at the tips of shrubs and bushes. Oviposition probably takes place on or in vegetation.



320 *Andrenosoma* 321 *Andrenosoma* 322 *Andrenosoma* 323 *Andrenosoma*

Figs 48.320–323. Pupal features of Asilidae: (320) pupal habitus of *Andrenosoma cruentum* (McAtee), dorsal view (non-Afrotropical); (321) same, lateral view; (322) same, ventral view; (323) same, detail of anterior section, ventral view. Figs 320–323 (photographs © J. Barnes).

Abbreviations: ant proc – antennal process; ap proc – apical process.

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THEREVIDAE

49

(Stiletto Flies)

Martin Hauser, Shaun L. Winterton, Ashley H. Kirk-Spriggs and Kevin C. Holston

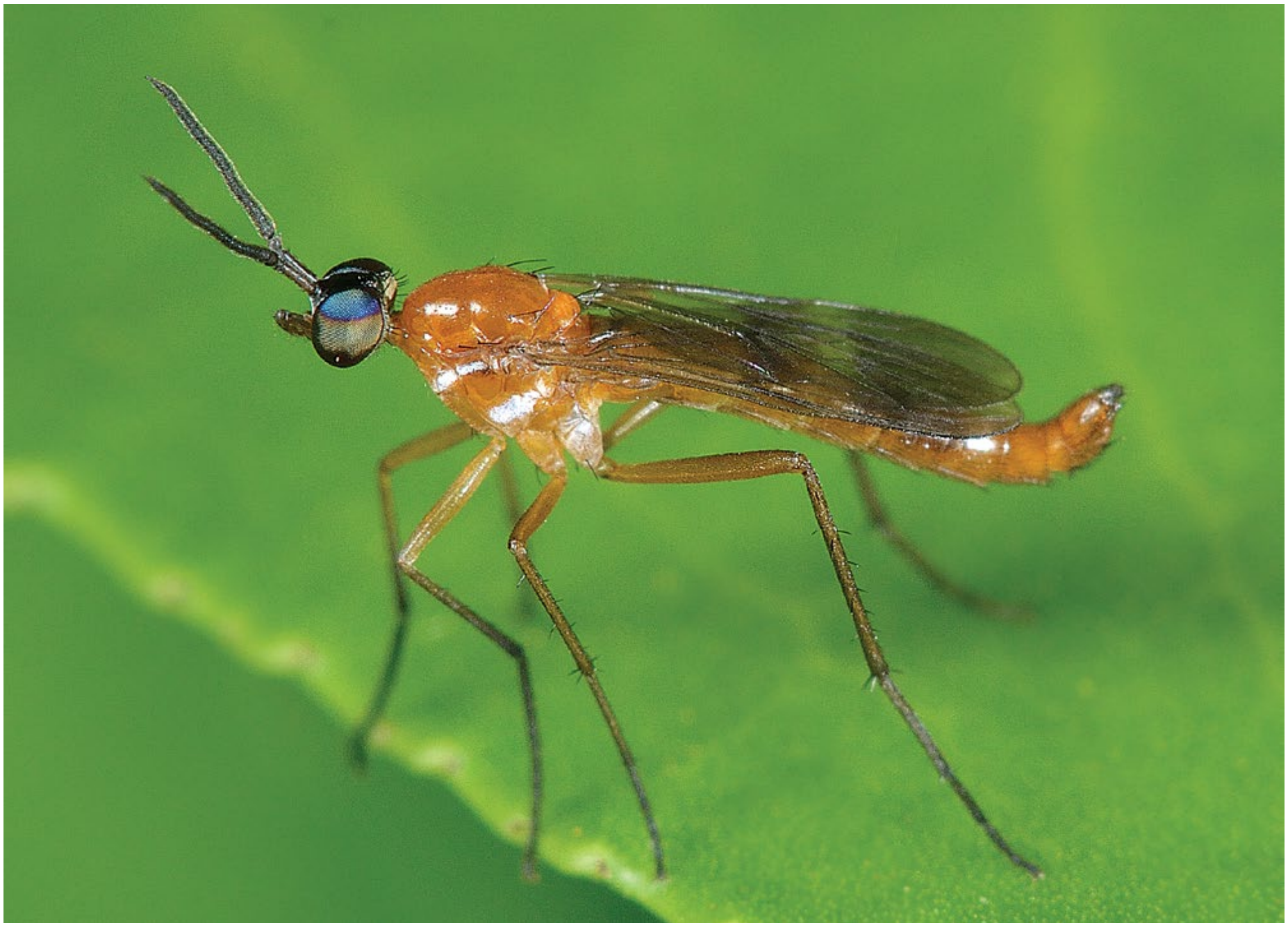

Fig. 49.1. Male of *Microgephyra stuckenbergi* Lyneborg (South Africa) (photograph © S.A. Marshall).

Diagnosis

Small- to large-sized flies (body length: 3–15 mm), with slender to moderately thick body, often tapering gradually towards posterior end (Figs 1–37); colouration mainly black, through grey and brown to earth tones, sometimes red and orange, rarely with silver pubescence; body often clothed to varying degrees in long setae, as well as pubescence from silver to white, gold or earth colours; pubescence may be absent with bare regions displaying ground colouration, especially on head (often polished) and abdomen, creating species-specific patterns.

Head with male eyes usually holoptic (with few exceptions, e.g., *Phycus* Walker), invariably dichoptic in females; eye usually bare (with few exceptions, e.g., *Braunsophila* Kröber); antenna with scape often elongate, sometimes enlarged; pedicel often as long as wide; flagellum with 2–3 flagellomeres and usually a short apical arista (e.g., Figs 24, 37, 38).

Thorax with macrosetae black to white. Wing venation exhibits little overall variation (Figs 39–72); costal vein (C) may be circumambient (e.g., Figs 40–48) or ending between veins M_1 and *CuA* (e.g., Figs 49–72); vein R_4 often sinuous (Fig. 45), diverging from vein R_5; discal cell (*d*) elongate, with veins M_1–M_3

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1183–1208.

originating apically; veins M_1 and M_2 usually reaching wing margin; cell m_3 often closed (Fig. 45), but (especially in higher Therevidae) open (Fig. 46); *r–m* crossvein invariably present (Fig. 39); wing membrane mostly hyaline or infuscate, sometimes with fasciae or irregular patterns (Figs 43, 69), often with dark suffusion along veins, especially crossveins (Fig. 48). Legs (*e.g.*, Figs 1–37) slender, never enlarged, tibia and femora frequently with macrosetae, sometimes lateral spines on tarsi elongated for digging in sand; a knob on the anteromedial part of the hind coxa (often referred as "hind coxal knob") typically present (exceptions include *Actorthia* Kröber and some *Neotherevella* Lyneborg).

Abdomen with 8 pregenital segments, sometimes clothed in silver pubescence, with setal pile usually longer in male; male terminalia (Figs 73–84) moderately complex, unrotated; gonostylus (Figs 73, 74, 77, 78, 81, 82) articulated subapically, armature variable, sometimes with enlarged spines; articulated inner gonocoxal process (Figs 81, 82) rarely present in Afrotropical genera; epandrium not divided medially; parameral sheath tube-like around endophallus with dorsal and/or ventral apodemes variously shaped; hypandrium (Figs 77, 78, 81, 82) absent to well-developed, sometimes fused with gonocoxites; female terminalia (Figs 85–90) with two sets of acanthophorite macrosetae on tergite 10 (higher Therevidae) (Fig. 87), sometimes reduced (Phycusinae) (Fig. 85) or with digging macrosetae on sternite 8 (Xestomyzinae) (Fig. 89); internal complement and arrangement of spermathecae with spermathecal sac variable among subfamilies: in Xestomyzinae 2 spermathecae and spermathecal sac present (Fig. 86) and joined separately with roof of bursa copulatrix (surrounded by genital fork); in Therevinae spermathecal ducts merge with spermathecal sac duct in common duct joining roof of bursa copulatrix (Fig. 87); in Phycusinae, spermathecal sac absent and 3 spermathecae merge in common duct before joining roof of bursa copulatrix (Fig. 85); genital fork in Therevinae forming single closed ring (Fig. 87), in Xestomyzinae U-shaped (Fig. 86) and in Phycusinae composed of 2 ring structures (Fig. 85); sternite 10 in Therevinae oval-shaped with single, medial, posterior protrusion (Fig. 87), in Phycusinae triangular with medial, posterior insertion (Fig. 85) and in Xestomyzinae oval-shaped, with thin anterior protrusion in contact with posterior margin of genital fork (Fig. 86).


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Figs 49.2–5. Photographs of living Afrotropical Therevidae: (2) *Acathrito lindneri* Lyneborg (South Africa); (3) *Xestomyza lugubris* Wiedemann (South Africa); (4) *Irwiniella tomentosa* (Becker) (Namibia); (5) *Stenopomyia angulata* Lyneborg (Madagascar). Photographs © S.A. Marshall.

6 *Caenophthalmus* ♂

7 *Hoplosathe* ♂

8 *Irwiniella* ♂

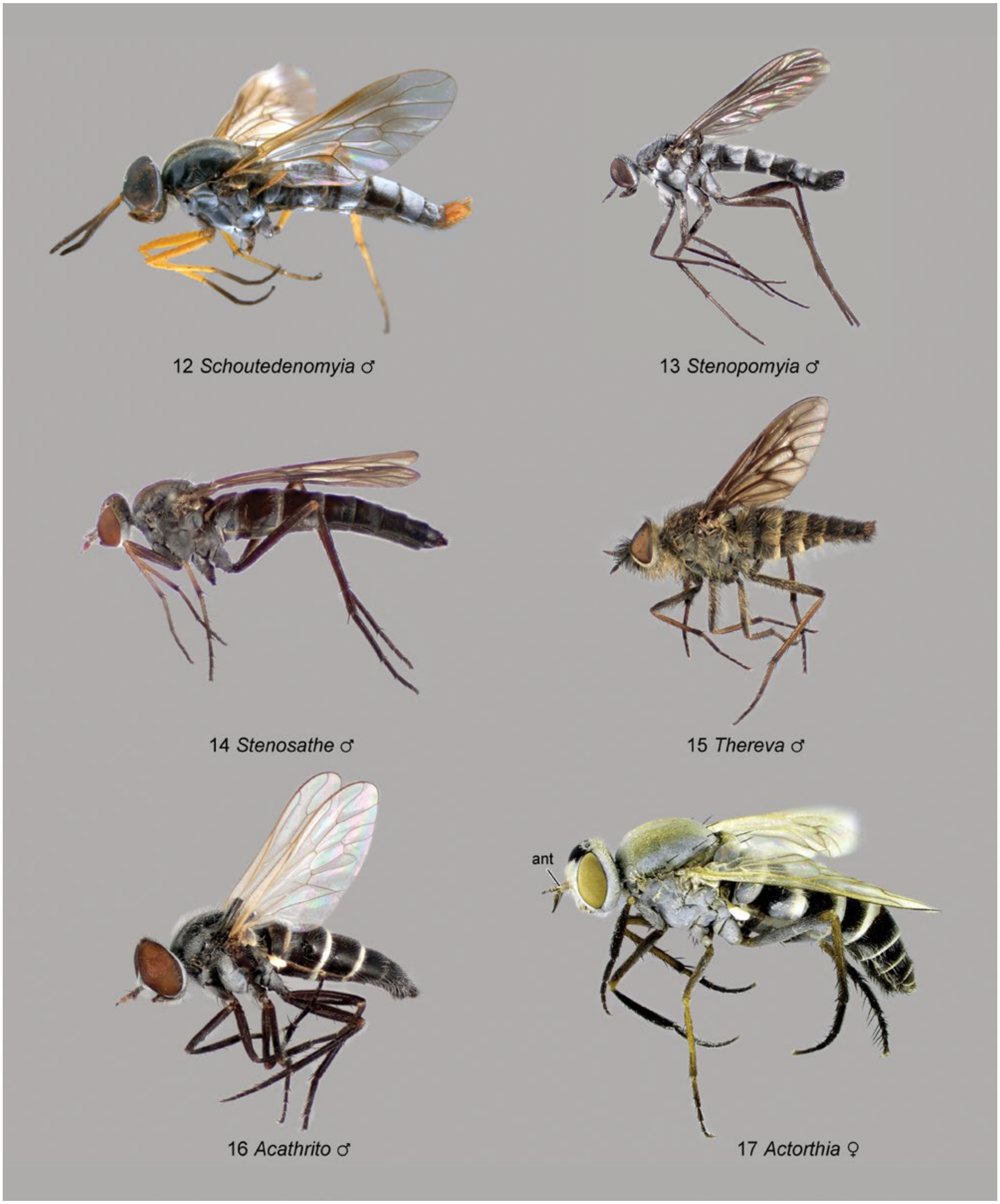
9 *Neophycus* ♂

10 *Neotherevella* ♂

11 *Pseudothereva* ♂

Figs 49.6–11. Habitus of Therevidae (lateral views): (6) *Caenophthalmus* sp. ♂; (7) *Hoplosathe brevistyla* Lyneborg & Zaitzev ♂; (8) *Irwiniella* sp. ♂; (9) *Neophycus antennatus* Kröber ♂; (10) *Neotherevella* sp. ♂; (11) *Pseudothereva* sp. ♂.

Abbreviation: ant – antenna.



Figs 49.12–17. Habitus of Therevidae (lateral views): (12) *Schoutedenomyia* sp. ♂; (13) *Stenopomyia* sp. ♂; (14) *Stenosathe* sp. ♀; (15) *Thereva seminitida stuckenbergi* Lyneborg ♂; (16) *Acathrito* sp. ♂; (17) *Actorthia lacteipennis* (Becker) ♀.

Abbreviation: ant – antenna.

Therevidae are not very distinctive flies, exhibiting many generalised characteristics and may superficially resemble families such as Athericidae (see Chapter 38), Bombyliidae (see Chapter 45) and Rhagionidae (see Chapter 37). Therevids can be readily differentiated from these families by the presence of the 2- or 3-segmented antennal flagellum, the unrotated male terminalia and the absence of the pulvilliform mediolobus on the tarsi.

Biology and immature stages

Very little is known regarding the biology and immature stages of stiletto flies and most observations are anecdotal, although some general characteristics are apparent. Useful summaries of biology are provided by Cole (1923), Gaimari & Webb (2009: 634) and Irwin & Lyneborg (1981). Most observations of immature stages are based on Holarctic species (*e.g.*, Collinge 1909; Hildebrand 1952; Keil 2005; Lundbeck 1908; Malloch 1915, 1917), with the notable exceptions of Engel & Cuthbertson (1938) and Irwin (1972, 1976, 2001), who provided detailed observations on biology and immature stages from Namibia, South Africa and Zimbabwe, English (1950) who contributed to knowledge of the Australian fauna and Bhatia (1936) and Isaac (1925), who contributed to the Oriental (Indian) fauna.

Oviposition takes place into the substrate; a process aided by the acanthophorite spines on the tip of the female abdomen (Agapophytinae and Therevinae), the enlarged digging setae on sternite 8 (Xestomyzinae) (Fig. 89), or the hind legs (Phycusinae) (Irwin 1976). Immature stages are mainly encountered in sand, loose soil, in or under leaf litter and sometimes in the mulch of dead trees, as well as in burrows of rodents and reptiles (Webb 2009), in dung and in fungi (Kurina 1994; Scholtz 1849). Larvae can be found relatively easily by sifting sand, loose soil and other substrates (Fig. 91). Larvae move rapidly in a snake-like fashion, leveraging sections of the body laterally against the substrate, contrary to most dipteran larvae, that exhibit a worm-like, peristaltic movement. Larvae appear to be opportunistic predators on a wide variety of arthropod prey (*e.g.*, Collinge 1909; Gepp & Klausnitzer 2005; Owen 1993; Příhoda 1952). Cannibalism is frequently reported, and the fact that many species are found in the same soil sample, raises questions as to how larvae avoid competition, although some studies suggest microhabitat preferences (Keil 2005) and habitat partitioning (Holston 2005). Pupae (Figs 94–96) are often clothed in sand particles, which appear to be "glued" to the cuticle and may serve as camouflage and/or protection. Although the pupal stage is often no longer than two weeks in duration, pupae are capable of movement and wriggle away when disturbed. Pupae migrate close to the soil surface shortly prior to eclosion and exuviae can often be found protruding from surrounding substrate surfaces.

Larvae (Figs 91–93) are pale brown to white in colour, with a black to brown, strongly sclerotised head capsule. The body exhibits a distinct secondary segmentation of the abdominal segments, giving the appearance of 17 abdominal segments (Hennig 1952: 60) (Fig. 92). This rather unique trait is shared with larvae of the family Scenopinidae. Therevidae larvae differ, however, in the shape of the metacephalic rod, which is spatulate at the posterior end in Therevidae, but parallel-sided in Scenopinidae (Fig. 91) (Brauns 1954*a*). Segment 8 has the posterior spiracle, but it is not clear if segment 8 is also divided and if the divisions following the segment with the spiracle belong to abdominal segment 9 (Hennig 1952: 60). The larval respiratory system is amphipneustic, with an anterior spiracle on thoracic segment 1. A single, long seta is present on each side of thoracic segments 1–3 and three pairs of shorter setae are present on the segment posterior to segment 8; larvae are otherwise devoid of setae. The head morphology presented in Fig. 93 is mainly based on English (1950) and Irwin (1972), as well as on electron micrographs.

The pupa (Figs 94–96) is of the exarate type and morphology can determine both sex and subfamily placement. In Phycusinae the antennal sheath is at a 45° angle from the long axis of the body (Fig. 94), while in all other subfamilies it is at 90° (Figs 95, 96). Therevinae possess a large alar process (Fig. 96), which is absent in the other subfamilies (Figs 94, 95). There are no known differences between Xestomyzinae (Fig. 95) and Agapophytinae pupae, but few pupae are known for these two subfamilies. Subfamily identification of therevid pupae is possible, however, as these two last mentioned subfamilies are not distributed in the same zoogeographical regions. The immature morphology of larvae and pupae are described by Bhatia (1936), Brauns (1954*a*, *b*), De Meijere (1916), English (1950), Hauser & Irwin (2003), Hennig (1952: 61 and citations therein), Irwin (1972) and Irwin & Yeates (1995).

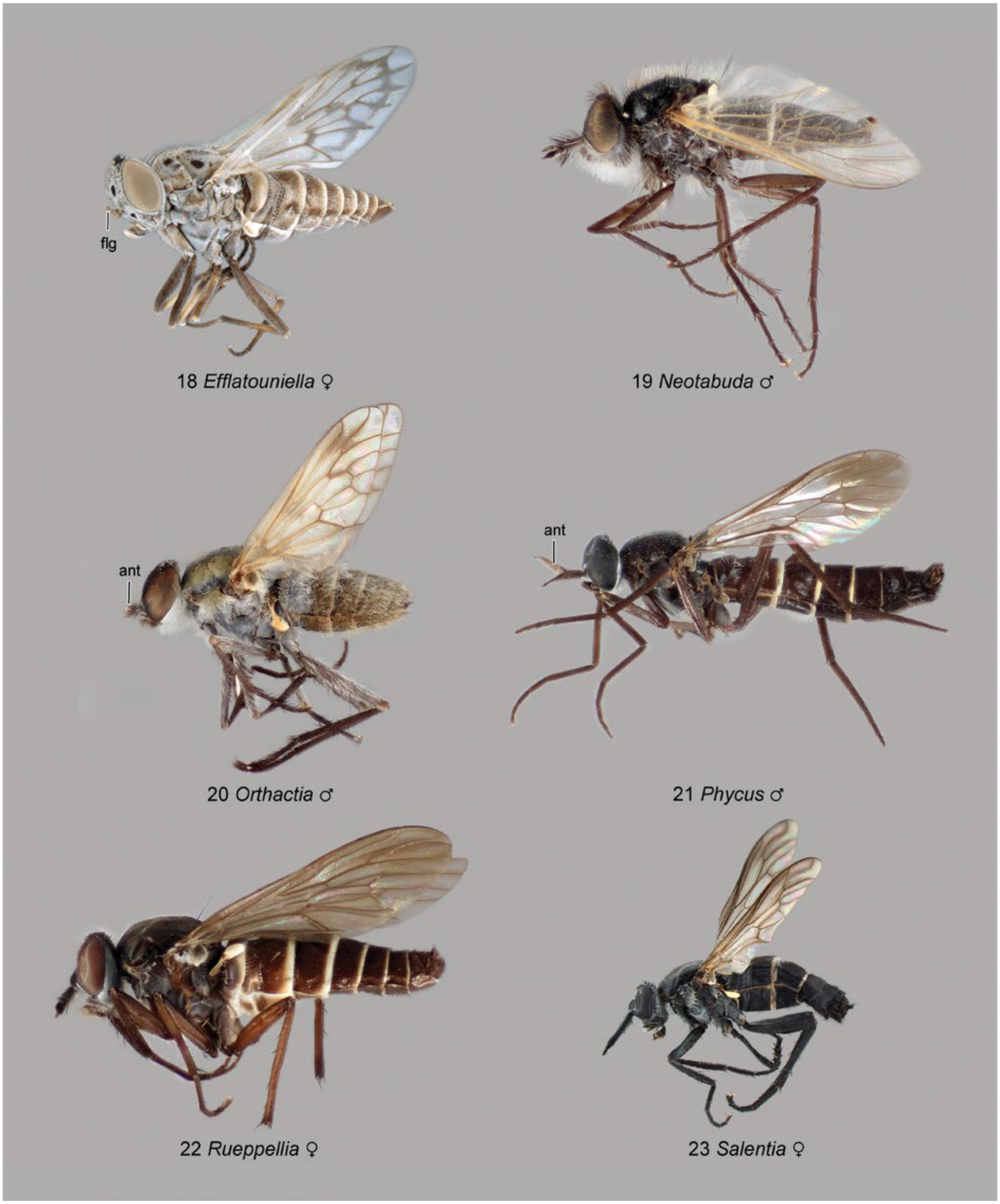
Adults are diurnal, but despite this are not frequently collected. The most efficient collecting method is the use of Malaise traps (see Chapter 2) intersecting flight paths along forest edges, or in dry *wadis*, especially when there is a small amount of water beneath the trap. In xeric environments standing water, damp soil, or urine are major attractants for these flies, while in more mesic environments adults are less concentrated and more difficult to locate. There are indications that some species are pyrophilous and are attracted to forest fires (Klocke *et al*. 2011). Some species form male mating swarms, or loose mating leks along stretches of open sand, above isolated shrubs, on tree trunks or in tree foliage (Gaimari & Webb 2009; Winterton & Irwin 2001).

Adults appear to only imbibe water and a few taxa may feed on plant nectar or exudates from trees. Isaac (1925), as well as some early authors (Lundbeck 1908: 133; Williston 1908: 205), have stated that adults prey on other insects, but these observations have never been verified and remain highly doubtful (see below), considering the rather soft mouthparts of adult flies.

The only parasites reared from Therevidae are bombyliid flies (English 1950; Irwin & Yeates 1995). Noticeable are the absence of hymenopteran larval parasites (Lundbeck 1908). Adult therevid flies fall prey to Asilidae and sphecid wasps, such as *Crabro* F. (Kurczewski 2003), *Oxybelus* Latreille (Mathews & Matthews 2005; Peckham *et al*. 1973) and *Bembix* F. (Hauser & Irwin 2003; Kimsey *et al*. 1981).

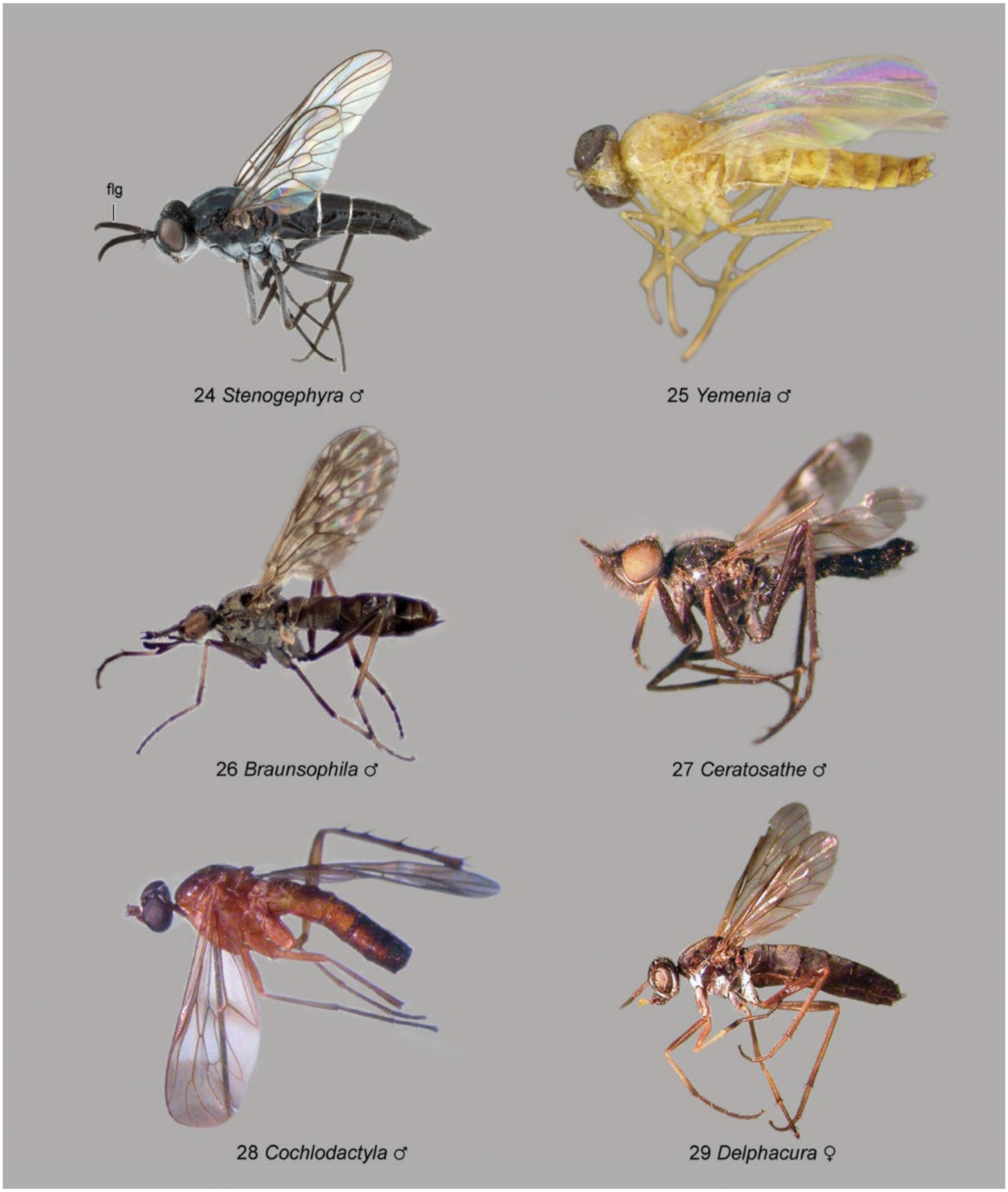
Economic significance

Early records reported that therevid larvae may be pests on cereal crops (Klein 1918), but this was soon refuted (Goetze 1932; Müller 1920). Predatory larvae are in fact beneficial in agricultural and forestry ecosystems, attacking a wide variety of pest insect larvae (*e.g.*, Pinkham & Oseto 1987, 1988; Příhoda



Figs 49.18–23. Habitus of Therevidae (lateral views): (18) *Efflatouniella* sp. ♀; (19) *Neotabuda* sp. ♂; (20) *Orthactia* sp. ♂; (21) *Phycus* sp. ♂; (22) *Rueppellia* sp. ♀; (23) *Salentia* sp. ♀.

Abbreviations: ant – antenna; flg – flagellum.



Figs 49.24–29. Habitus of Therevidae (lateral views): (24) *Stenogephyra dianeae* Webb & Hauser ♂; (25) *Yemenia flavus* (Lyneborg) ♂; (26) *Braunsophila* sp. ♂; (27) *Ceratosathe tridactyla* Lyneborg ♂; (28) *Cochlodactyla munroi* Lyneborg ♂; (29) *Delphacura mosselensis* Lyneborg ♀.

Abbreviation: flg – flagellum.

1952; Smith & Johnson 1989). The magnitude of their impact is poorly understood, but it is likely that they are more important predators in arid climates with sandy soil, than in more temperate or tropical regions. In a few instances, adult Therevidae are known to visit flowers, but because this is a very rare event, they are not likely to play a significant role as pollinators.

Classification

Therevidae are ascribed to the superfamily Asiloidea and are sister-group to the Scenopinidae, with which they share the unique morphological feature of secondary abdominal segmentation of the larvae (Yeates *et al*. 2003, 2006). Although the larvae of non-Afrotropical Apsilocephalidae and Evocoidae are not known, these two families are considered most closely related to Therevidae and Scenopinidae. Until recently, Apsilocephalidae was treated as a subordinate group within the Therevidae (Irwin & Lyneborg 1981). In recent phylogenies of these four therevoid families, based on molecular and morphological data (Winterton & Ware 2015; Winterton *et al*. 2016), all families were recovered as monophyletic, the sister-group relationship between Scenopinidae and Therevidae was well-supported, and this clade was supported as the sister-group to Evocoidae + Apsilocephalidae.

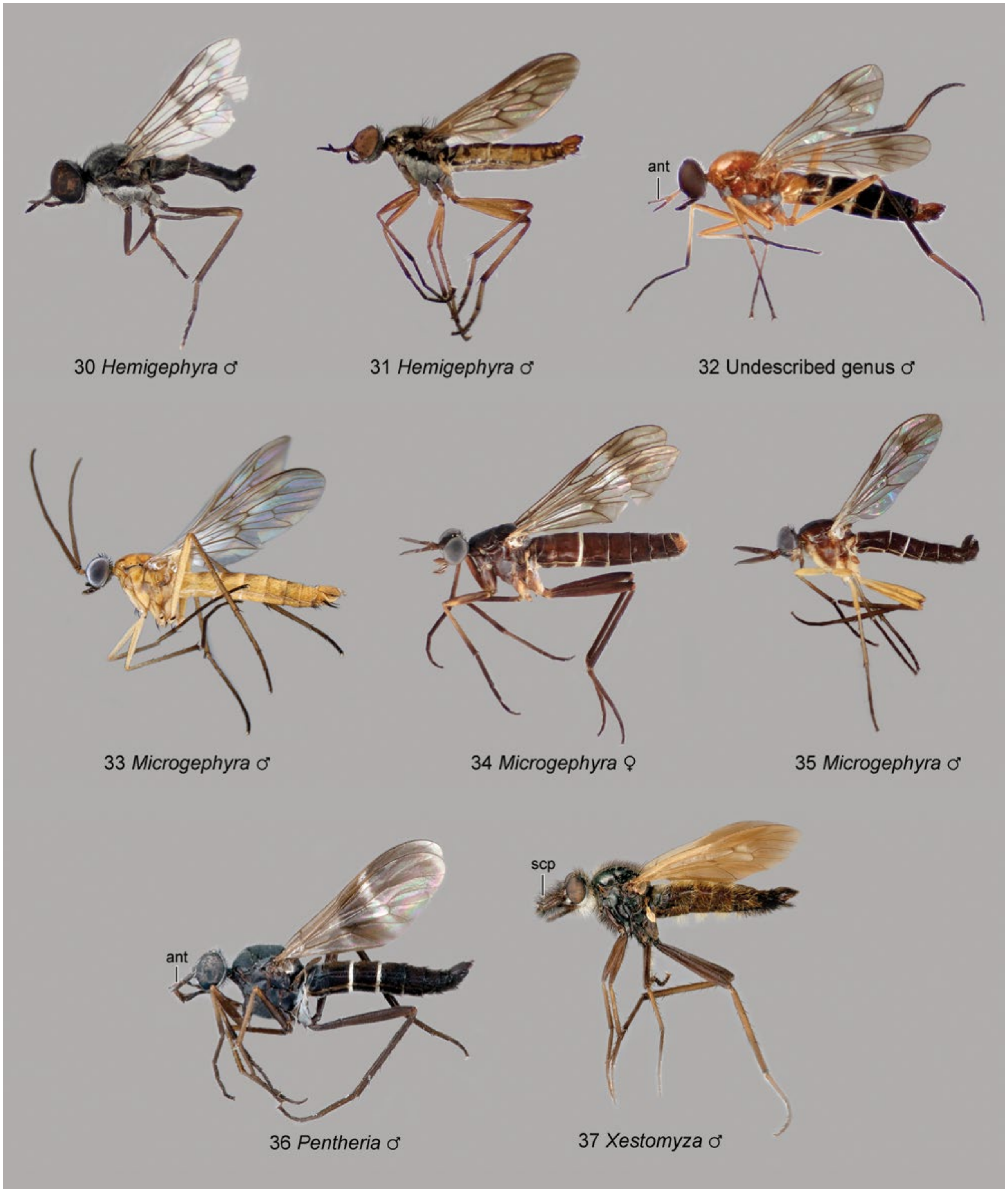
Approximately 1,170 species of Therevidae have been described globally, although many undescribed species have been examined in collections by the writers during recent taxonomic studies. The subfamily classification has improved enormously during the past few decades and four subfamilies and one tribe are now recognised. Lyneborg (1972) provided the initial modern diagnosis for the mainly Afrotropical *Xestomyza* Wiedemann genus-group and characterised it as a tribe together with Phycusini in the subfamily Phycusinae (Lyneborg 1976*a*, 1980*b*: 316, 1983). Irwin & Lyneborg (1981) only recognised two subfamilies of Therevidae (Therevinae and Phycinae), in their revision of Nearctic stiletto flies, although Irwin & Webb (1992) also recognised Xestomyzinae as a third subfamily. In the Australasian Region two additional, largely endemic groups, the informal *Taenogera* Kröber genus-group (Winterton *et al*. 1999) and the subfamily Agapophytinae (Winterton *et al*. 2001) were recognised until Winterton (2011) and Winterton & Ware (2015) extended the circumscription of the Agapophytinae to include the *Taenogera* genus-group. Xestomyzinae and Phycusinae are also recognised in modern taxonomic revisions of their included genera (Hauser 2007, 2012; Winterton *et al*. 2012). Note, the stem (Phyc-) of the previously used subfamily name Phycinae (which was a junior homonym of a fish family-group name), was replaced by Phycus- resulting in Phycusinae following a proposal to the International Commission of Zoological Nomenclature (Gaimari *et al*. 2013*a*, *b*; International Commission of Zoological Nomenclature 2015). Although the four subfamilies have always been well characterised, phylogenetic relationships among the subfamilies have remained unclear. Winterton *et al*. (2016) found strong support that the Phycusinae are sister-group to the remaining subfamilies and that Xestomyzinae is sister-group to the clade of Therevinae + Agapophytinae. The Phycusinae can be divided into two groups: the Old World *Salentia* Costa genus-group (*Acathrito* Lyneborg, *Actorthia*, *Neotabuda* Kröber, *Orthactia* Kröber, *Rueppellia* Wiedemann, *Salentia*) and the Old and New World *Phycus* genus-group (Afrotropical genera: *Phycus*, *Stenogephyra* Lyneborg). Xestomyzinae is divided into the New World *Henicomyia* Coquillett genus-group (single genus *Henicomyia*) and the *Xestomyza* genus-group, which only occurs in the Afrotropical Region and includes all other genera.

Fifteen genera and more than 130 described species of Phycusinae are described globally, of which six genera and 57 species occur in the Afrotropical Region. Phycusinae is found in all major zoogeographical regions, except Australasia, but greatest species diversity occurs in the Afrotropics, with the genera *Neotabuda*, *Orthactia* and *Stenogephyra* endemic to the region. Four fossil genera of Phycusinae are known: *Dasystethos* Hauser, *Glaesorthactia* Hennig, *Kroeberiella* Hauser (all from Baltic Amber) and *Palaeopherocera* Hauser (Florissant) (Hauser 2007; Hauser & Irwin 2005*a*). Phycusinae is characterised by a number of features, including reduction of the acanthophorite spines, the presence of abdominal spiracles in the tergites (not in the membrane), presence of a sensory pit at the tip of the palpus, the antennal sheath of the pupa set at a 45° angle to the body axis, the spermathecal ducts unite to form a common duct before entering the bursa copulatrix, absence of a spermathecal sac and a sclerotised bar separating the anterior and posterior parts of the genital fork. With the reduction of acanthophorite spines, which are used to facilitate penetration of the abdomen into soil or sand, this subfamily instead uses the hind legs to dig a small pit into which a single egg is deposited (Irwin 1976). Each female therevid lays between 25 and 50 eggs (M. Irwin, pers. comm. 2016).

Xestomyzinae is a smaller subfamily with 10 genera and 46 species globally, which mainly occurs in the Afrotropical Region, with nine genera and 40 species, all of which are endemic to the region. Only one genus (*Henicomyia*) occurs in the New World. Adults typically have banded wings and bear a superficial resemblance to species of Agapophytinae. The costal vein invariably ends at vein M_2. Synapomorphies for this well characterised subfamily are the modified digging macrosetae of the female eighth sternite, a sclerotised ring at the base of the spermathecal duct, spermathecal ducts entering the genital fork membrane separately from the spermathecal sac and posteriorly rounded male sternite 10, with a long anterior extension. Fossil Xestomyzinae have been found in Baltic and Mexican Ambers, which indicates that this group was much more widely distributed, at least during the Eocene (Hauser 2007; Hauser & Irwin 2005*a*).

Agapophytinae is restricted to the Australasian Region and the Southern Cone of South America, with more than 230 species in 28 genera, with a significant number of undescribed species. The subfamily is diverse in the Australasian Region (Winterton *et al*. 2001), but is absent from the Afrotropics.

Therevinae is a virtually cosmopolitan subfamily that is dominant with respect to species diversity in most zoogeographical regions, except Antarctica and Australia, with respect to species diversity. Of the 71 genera with almost 800 species globally, the Afrotropical Region has relatively few genera and species. Nine genera and 66 species occur in the Afrotropics, of which three genera (*Caenophthalmus* Kröber, *Pseudothereva* Lyneborg and *Stenopomyia* Lyneborg) are endemic to the region. Therevinae are characterised by lanceolate setae on the hind femora and spermathecal ducts joining to the spermathecal sac duct before



Figs 49.30–37. Habitus of Therevidae (lateral views): (30) *Hemigephyra atra* Lyneborg ♂; (31) *H. braunsi* (Kröber) ♂; (32) Undescribed genus ♂; (33) *Microgephyra* sp. ♂; (34) *Microgephyra* sp. ♀; (35) *Microgephyra* sp. ♂; (36) *Pentheria* sp. ♂; (37) *Xestomyza lugubris* Wiedemann ♂.

Abbreviations: ant – antenna; scp – scape.

entering the bursa copulatrix. This subfamily has been divided into several informal genus-groups, based on the presence of additional characters, such as setal pile on various sclerites and varied structures of the male terminalia (Holston *et al*. 2007). Therevinae is the only subfamily in which a tribe (Cyclotelini) is currently recognised (Gaimari & Irwin 2000), although no species in this tribe occur in the Afrotropics.

Identification

The first comprehensive revision of Afrotropical Therevidae was the work of Kröber (1912*a*–*f*, 1913*a*–*c*), followed shortly thereafter by his work on the world Therevidae (Kröber 1913*d*: 6), both of which are now largely out of date. Useful identification keys to Afrotropical Therevidae that include many of the described species cover the Xestomyzinae (Lyneborg 1972), Therevinae (Lyneborg 1976*a*) and Phycusinae (Winterton *et al*. 2012). Lyneborg (1972) published an identification key to the Xestomyzinae that distinguishes species rather than genera and it remains difficult to produce a key for Afrotropical genera. Lyneborg (1972, 1976*b*) admitted that some genera may not be monophyletic, noting that diagnostic characters were difficult to establish for several genera with wide geographic distributions and higher species diversity. Lyneborg (1972, 1976*b*) asserted that even some of his new genera (*e.g.*, *Microgephyra*) were based on "plesiomorphous" characters and are likely "paraphyletic", but was also explicit in associating these genera with what he considered closely related taxa. Lyneborg did not publish a key to the genera of Afrotropical Phycusinae, but he revised most genera in several publications (*e.g.*, Lyneborg 1972, 1978*c*, 1980*a*, 1987, 1988, 1989*b*). Winterton *et al*. (2012) provided a key to Palaearctic genera of Phycusinae, describing a new genus from Egypt.

Adult Therevidae are usually direct-pinned in the field and smaller specimens micro-pinned for later double-mounting (see Chapter 2).

Key to genera of Afrotropical Therevidae

1. Hind tibia without lanceolate-like setae adjacent to setula-like setae; costal wing vein (*C*) not circumambient, ending between veins R_4 and *CuA* (*e.g.*, Figs 50, 52); scutellum with 0–1 pair of macrosetae 2

– Hind tibia with lanceolate-like setae adjacent to setula-like setae; costal wing vein (*C*) circumambient (*e.g.*, Figs 40–45); scutellum with 2 pairs of macrosetae (THEREVINAE) 23

2. Wing vein R_1 bare; costal vein (*C*) invariably ending at vein M_2; wing membrane often with 2 darker longitudinal fascia, rarely hyaline (*Xestomyza* and *Microgephyra latipennis* Lyneborg, 1976) (Fig. 72), or maculated (*Braunsophila*) (Fig. 61), or wing reduced (*Lyneborgia* Irwin); palpus without apical pit; female sternite 8 with strong macrosetae (Fig. 89); 2 membranous spermathecae present, with 1 spermathecal sac (Fig. 86) (XESTOMYZINAE) 3

– Wing vein R_1 setulose dorsally; costal vein (*C*) ending at veins M_1, M_2, M_3, or *CuA*; wing membrane usually without longitudinal fascia, being clear or with anterior or apical infuscation (*e.g.*, Figs 50, 52, 53, 55–60); palpus without apical pit; female sternite 8 without strong macrosetae (Fig. 85); 3 membranous spermathecae present, without spermathecal sac (Fig. 85) (PHYCUSINAE) 13

3. Face and gena with numerous conspicuous setae (shorter in *Hemigephyra atra* Lyneborg, 1972, Fig. 38) 4

– Face and gena bare, without setae 7

4. Antennal scape enlarged, much thicker than pedicel (Figs 3, 37); male eyes dichoptic . . . . *Xestomyza* Wiedemann

– Antennal scape subequal in width to pedicel (*e.g.*, Fig. 38); male eyes holoptic or dichoptic 5

5. Proboscis as long as, or shorter than head (Fig. 38); male eyes holoptic . . . . *Hemigephyra* Lyneborg [in part; *H. atra*]

– Proboscis much longer than head (Fig. 26); male eyes holoptic or dichoptic (*e.g.*, Fig. 24) 6

6. Wing membrane maculate (Fig. 26); scutellum disk without velvety black patch; male eyes dichoptic . . . . *Braunsophila* Kröber

– Wing membrane with 3 brown fasciae (Fig. 62); scutellum disk with velvety black patch; male eyes holoptic . . . . *Ceratosathe* Lyneborg

7. Antenna ventrally directed (Fig. 36); wing membrane with 2 dark fasciae (except in *P. obscura* Kröber) (Figs 36, 71), apical fascia much broader than basal (*Cochlodactyla* Lyneborg with apical wing fascia broader (Fig. 63), but then antenna parallel to body axis) . . . . *Pentheria* Kröber

– Antenna horizontally directed (*e.g.*, Fig. 31) and parallel to body axis (in some specimens of *Delphacura* antenna ventrally directed, but wing without fascia); wing membrane without fasciae (*e.g.*, Fig. 66), or if with 2 dark fasciae, then these subequal (*e.g.*, Fig. 69) (except in *Cochlodactyla* with broader apical wing fascia (Fig. 63)) 8

8. Scutellum without setae; thorax with 1 notopleural macroseta; female wing vestigial. . . . .*Lyneborgia* Irwin

– Scutellum with 1 pair of setae; thorax with 2 notopleural macrosetae (except in Undescribed genus, with only 1); female wing normal (except in *Cochlodactyla* (Fig. 63)). 9

9. Thorax with 1 notopleural seta; length of wing enclosed by veins R_4 and R_5 2 × as large as enclosed wing margin between veins R_5 and M_1 (Fig. 70); only apical part of wing membrane infuscate . . . . Undescribed genus

– Thorax with 2 notopleural setae; length of wing enclosed by veins R_4 and R_5 only slightly larger than enclosed wing margin between veins R_5 and M_1 (e.g., Fig. 66) (except *Cochlodactyla* (Fig. 63)); wing membrane either with 2 fasciae, hyaline, or mottled 10

10. Antennal scape setose along medial surface; wing membrane darkened, crossveins with weak, darker infuscation (Fig. 66); female head with postocular area enlarged, cushion-shaped . . . . *Hemigephyra* Lyneborg [in part; *H. braunsi* (Kröber, 1931)]

– Antennal scape bare on medial surface; wing membrane either with 2 fasciae, hyaline, or mottled (*e.g.*, Figs 63, 65, 67, 68); female head with postocular area not enlarged 11

11. Wing with 2 dark fasciae, the more apical entirely covering distal ⅓ of wing (Fig. 63); wing with dorsal surface of costal vein (*C*) with scattered setulae . . . . *Cochlodactyla* Lyneborg

– Wing with or without fasciae, if fasciae present, then the more apical one never entirely covering distal ⅓ of wing; wing with dorsal surface of costal vein (*C*) with 2 rows of setulae 12

12. Thorax with > 5 short dorsocentral setae (dc); antennal sockets not protruding; scape 4 × as long as pedicel . . . . *Delphacura* Lyneborg

– Thorax with 0–2 long dorsocentral setae (dc); antennal sockets protruding; scape at most 3 × as long as pedicel . . . .*Microgephyra* Lyneborg

13. Wing with costal vein (*C*) ending at vein *CuA+CuP* (*e.g.*, Figs 50, 54, 55, 57) 14

– Wing with costal vein (*C*) ending before vein *CuA+CuP*, at veins R_4, R_5, M_1, M_2 or M_3 (*e.g.*, Figs 52, 56, 59). 19

14. Mid coxa setulose on posterior surface; antennal scape often elongated or thickened (Arabian Peninsula) . . . .*Salentia* Costa

– Mid coxa bare on posterior surface; antennal scape modified or unmodified (Arabian Peninsula and sub-Saharan Africa). 15

15. Antenna significantly longer than head (viewed laterally) (Fig. 21); palpus 2-segmented; male eyes dichoptic . . . .*Phycus* Walker

– Antenna shorter than or as long as head (viewed laterally) (*e.g.*, Fig. 17); palpus 1-segmented; male eyes usually holoptic, rarely dichoptic 16

16. Hind coxal knob absent; male terminalia with lateral extension on gonocoxite. . . . . . *Actorthia* Kröber

– Hind coxal knob present; male terminalia without lateral extension on gonocoxite 17

17. Thorax with prosternal depression setose; without dorsocentral setae; metanepisternum setose; scutellum disk velvet black, often with modified bundles of setae; male terminalia with gonocoxites fused; hypandrium fused to gonocoxites; hind tarsi with long lateral setae; wing membrane often maculated (Fig. 54); antennal flagellomere 2-segmented (sub-Saharan Africa) . . . .*Orthactia* Kröber

– Thorax with prosternal depression bare; often with 1 or 2 pairs of dorsocentral setae; metanepisternum bare; scutellum disk never velvet black, often silver dusted, never with modified setae; male terminalia with gonocoxites separated; hypandrium separate from gonocoxites; hind tarsi without long lateral setae; wing membrane maculate or hyaline (*e.g.*, Figs 51–53); antennal flagellomere 2- or 3-segmented (sub-Saharan Africa & Arabian Peninsula). 18

18. Small-sized (length: 2.8–4.5 mm), light coloured species; wing membrane often with pattern (Figs 18, 51); antennal scape not thickened, or longer than remainder of antenna, only with fine, sparse short setae; flagellomere 2-segmented (Arabian Peninsula & Namibia) . . . . *Efflatouniella* Kröber [in part]

– Small- to medium-sized (length: 3–10 mm), black species; wing membrane hyaline, without markings (Figs 19, 53); antennal scape modified, sometimes thicker (in females) and often longer than remainder of antenna, with dense, thick long setae; flagellomere 3-segmented (southern Africa). . . . .*Neotabuda* Kröber

19. Antennal flagellomere 1 longer than head (in lateral view) (Fig. 24); costal wing vein (*C*) ending at vein M_1 (Figs 58, 59); thorax with prosternal depression bare; male eyes dichoptic; male terminalia with gonocoxites separated . . . . *Stenogephyra* Lyneborg

– Antennal flagellomere 1 much shorter than head (in lateral view) (Fig. 18); costal wing vein (*C*) ending at veins R_4, R_5, M_1, M_2 or M_3 (*e.g.*, Figs 49, 52, 56, 60); thorax with prosternal depression setose, rarely bare; male eyes holoptic; male terminalia with gonocoxites fused, rarely separated 20

20. Costal wing vein (*C*) ending at veins R_4 or R_5 (Fig. 52); male terminalia with gonocoxites separated. . . . . *Efflatouniella* Kröber [in part]

– Costal wing vein (*C*) ending at veins M_1, M_2 or M_3 (*e.g.*, Figs 56, 60); male terminalia with gonocoxites separated or fused 21

21. Costal wing vein (*C*) ending at vein M_3 (Fig. 60); male eyes dichoptic; male terminalia with gonocoxites separated (endemic to Yemen) . . . . *Yemenia* Koçak & Kemal

– Costal wing vein (*C*) ending at veins M_1 or M_2 (*e.g.*, Figs 49, 56); male eyes holoptic; male terminalia with gonocoxites fused (widespread) 22

22. Wing veins R_4 and R_5 convergent (Fig. 56); male terminalia with gonocoxite without lateral extension . . . . *Rueppellia* Wiedemann

– Wing veins R_4 and R_5 divergent (Fig. 49); male terminalia with gonocoxite with lateral extension . . . . *Acathrito* Lyneborg

23. Mid coxa with distinct setal pile on posterior surface (more distinct in male) 24

– Mid coxa without pile on posterior surface. 29

24. Antennal scape elongate, at least 10 × as long as wide (Fig. 9); flagellum white with terminal style, as long as or longer than head; head with parafacial pile absent . . . . *Neophycus* Kröber

– Antennal shape shorter, typically no more than 5 × as long as wide (*e.g.*, Figs 6, 11, 15); flagellum not as above, never white; head with parafacial pile present or absent 25

25. Head with parafacial setal pile often extensive 26

– Head without parafacial pile (rarely present in some species of *Irwiniella* Lyneborg) 28

26. Antennal flagellum with basal segment-like constriction; female eye often reduced in size, narrowed . . . . *Caenophthalmus* Kröber

– Antennal flagellum without basal constriction; female eye not greatly reduced in size or narrowed . . . 27

27. Female head with frons broadly bare, without callosities; distance between eyes in both sexes at ventral margin less than height of head . . . . *Pseudothereva* Lyneborg

– Female head with frons pubescent, frequently with bare callosity dorsally; distance between eyes in both sexes at ventral margin greater than height of head . . . . *Thereva* Latreille

28. Body frequently densely clothed in silver-white to bronze lanceolate setae (Fig. 10); body size relatively small (length: 7.0–8.0 mm); head height typically equal to length in profile; entire frons silver pubescent, female with 2 large black pubescent maculae dorsally . . . . *Neotherevella* Lyneborg

– Body with or without dense covering of elongate pile, but setae never lanceolate (Fig. 8); body size variable (length: 5.5–12.0 mm); head typically higher than long in profile; lower frons silver pubescent, upper frons brown pubescent (especially in female) . . . . *Irwiniella* Lyneborg

29. Prosternum with setal pile medially; wing membrane strongly banded (Figs 7, 41); head and body clothed in dense yellow-grey pubescence . . . . *Hoplosathe* Lyneborg & Zaitzev

– Prosternum typically bare (rarely pilose medially in *Stenosathe* Lyneborg); wing membrane usually hyaline, invariably without strong fasciae (*e.g.*, Figs 45–47); head and body without dense pubescence 30

30. Palpus apparently 2-segmented (usually); tibial macrosetae relatively small (particularly on fore and mid legs); male terminalia with distiphallus greatly elongate and curved ventrally (continental Afrotropics) . . . . *Schoutedenomyia* Kröber

– Palpus clearly 1-segmented; tibial macrosetae regularly sized; male terminalia with distiphallus typically short (rarely longer) and only slightly curved ventrally (Madagascar and continental Afrotropics) 31

31. Male eye facets uniformly sized, inner lower margin of eye slightly divergent; male and female frons patterned with black brown and grey pubescence; prosternum in both sexes bare along medial furrow, pile only present laterally; male terminalia with epandrium usually highly modified, with expanded posterolateral margin; parameral sheath with dorsal apodeme relatively broad (endemic to Madagascar) . . . . *Stenopomyia* Lyneborg

– Male eye facets larger dorsally, inner lower margin of eye more divergent; male and female frons pubescence uniform grey or brown, not patterned; thorax in both sexes with prosternum pilose on entire surface; male terminalia with epandrium unmodified; parameral sheath with dorsal apodeme very narrow (continental Afrotropics) . . . . *Stenosathe* Lyneborg

Synopsis of the fauna

***Acathrito* Lyneborg** (Phycusinae)**.** A genus of nine described (and several undescribed) species, occurring in the Afrotropical, Oriental and Palaearctic Regions, west from the Canary Is., south through Angola to South Africa, to Kenya and Tanzania, north into Egypt and the Arabian Peninsula, north to Turkmenistan, as well as in the western part of India south to Sri Lanka. Six described species are known from the Afrotropics. *Acathrito* (Figs 2, 16) are medium-sized (length: 5–7 mm), grey-black species characterised by holoptic males, with antennae shorter than the head and fused gonocoxites, that are also fused with the hypandrium and have posterolateral extensions. The costal vein (*C*) ends at vein M_2 (Figs 39, 49). It is remarkable that most specimens have been collected in coastal regions and that there are several endemic species on oceanic islands (Canary Is., Socotra Is. (Yemen) and Sri Lanka). Biology and immature stages otherwise remain unknown. Afrotropical species were revised and keyed by Lyneborg (1989*b*), but this work does not include the South African species *A. basalis* (Loew, 1858), which was recently transferred to this genus by Badrawy & Mohammad (2011).

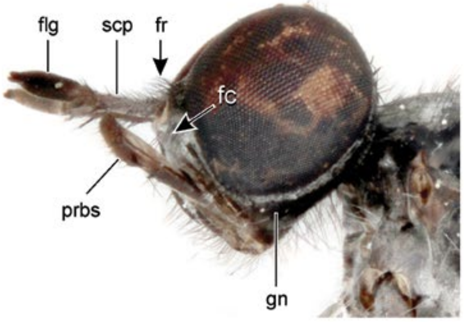
***Actorthia* Kröber** (Phycusinae)**.** A genus of 13 described species occurring in the north-eastern Afrotropical and southern Palaearctic desert regions, from Mauritania eastwards through Egypt and the Middle East to the deserts of Central Asia and Mongolia. Three species are known from the Afrotropics: *A. canescens* (Surcouf, 1921) from Djibouti; *A. lacteipennis* Becker, 1913 from United Arab Emirates; and *A. spinicornis* (Séguy, 1953) from Mauritania. *Actorthia* (Fig. 17) are medium-sized (length: 5.0–7.5 mm), black to orange species, often clothed in silver setulae and pubescence and females often have elongate digging spines on the hind tarsi, very similar to *Orthactia*. The costal wing vein (*C*) ends at vein *CuA+CuP* (Fig. 50). The taxonomy of this genus is in disarray, as most species were described in different genera (one even in the Tabanidae), resulting in several synonyms, but at the same time there appears to be high diversity, with many undescribed species in poorly collected desert regions (Hauser 2017). Biology and immature stages remain unknown. An identification key to Afrotropical species is unavailable.

***Braunsophila* Kröber** (Xestomyzinae)**.** An endemic genus of four described species confined to South Africa. *Braunsophila* (Fig. 26) includes small (length: 4.5–5.0 mm), brown species with maculate wings (Fig. 61), the proboscis is longer than the head and the male eyes are dichoptic. This genus is closely related to *Ceratosathe* and *Xestomyza*, all having relatively long mouthparts and are more setose than most species of Xestomyzinae. Most specimens have been found close to the coast between June and September. Biology and immature stages are otherwise unknown. An identification key to the four species was provided by Lyneborg (1976*b*).

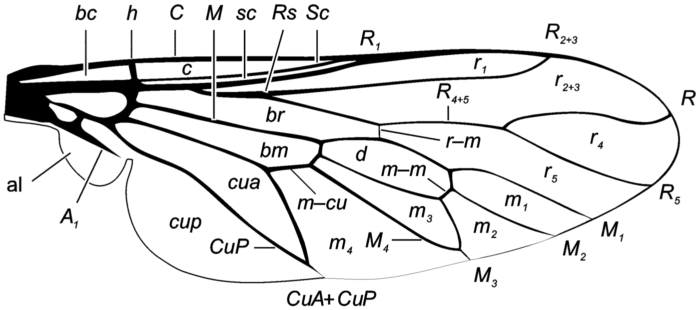
***Caenophthalmus* Kröber** (Therevinae)**.** An endemic genus of eight described species restricted to coastal dunes of the Cape Province, South Africa. The most recent revision of the genus is that of Lyneborg (1976*a*). *Caenophthalmus* is placed in the *Thereva* genus-group, including genera such as *Baryphora* Loew, *Cionophora* Egger and *Euphycus* Kröber (Holston *et al*. 2007; Webb 2005). The genus is most closely related to *Pseudothereva* and *Thereva*, with similar dense setal pile on the body, including dense parafacial setae. Females of many species are unique among stiletto flies in having greatly reduced eyes, which are narrowed and occupy a relatively small proportion of the head. *Caenophthalmus* (Figs 6, 40) is characterised by the constricted base of the antennal flagellum, giving the appearance of an additional segment. Lyneborg (1976*a*) proposed the *T. turneri* species-group (*i.e.*, *Thereva curticornis* Kröber, 1912, *T. globulicornis* Lyneborg, 1976 and *T. turneri* Lyneborg, 1976), as the likely sister-group to *Caenophthalmus* and these species were transferred to *Caenophthalmus* by Winterton *et al*. (2016). Lyneborg (1976*a*) discussed the series of characteristics supporting a sister-group relationship between the *turneri* species-group and *Caenophthalmus*, including constriction of the base of the flagellum into a pseudosegment, the well-sclerotised subepandrial sclerite and the emarginate anterior margin of the dorsal apodeme of the parameral sheath. Similarly, Holston *et al*. (2007) and Winterton *et al*. (2016) demonstrated the polyphyly of *Thereva* in phylogenetic analyses based on DNA sequence data, which supported inclusion of the *turneri* species-group species within *Caenophthalmus*. Species of *Caenophthalmus* occur in coastal and inland dune systems of the Cape Province, South Africa. While the narrowed female eyes of some species are a distinctive feature by which Kröber originally defined the genus, the basally constricted antennal flagellum is a more reliable synapomorphy of the genus. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg (1976*a*).

***Ceratosathe* Lyneborg** (Xestomyzinae)**.** An endemic monotypic genus, with the single described species, *C. tridactyla* Lyneborg, 1972 (Fig. 27), recorded only from the Western Cape Province, South Africa (Lyneborg 1972). This medium-sized (length: 5.2–7.8 mm) black species is characterised by the proboscis being longer than the head, the 2-segmented antennal flagellum, the scutellum disk with a velvet black patch and the mid coxa with setae posteriorly. The holoptic male eyes and the banded wings (Fig. 62) differentiate this genus from the closely related *Braunsophila*. All available specimens of *C. tridactyla* were collected between October and January. Biology and immature stages are otherwise unknown.

***Cochlodactyla* Lyneborg** (Xestomyzinae)**.** An endemic monotypic genus, with the single described species, *C. munroi* Lyneborg, 1972 (Figs 28, 63), described from the Eastern Cape Province, South Africa. This rare species is characterised by its orange colour, the dichoptic male eyes, the short proboscis



38 *Hemigephyra* ♂



39 *Acathrito* ♂

40 *Caenophthalmus* ♂

41 *Hoplosathe* ♀

42 *Irwiniella* ♂

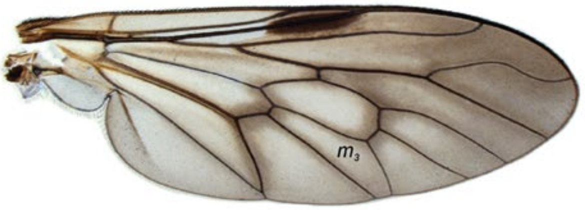
43 *Neotherevella* ♂

44 *Pseudothereva* ♂

45 *Schoutedenomyia* ♂

Figs 49.38–45. Head and wings of Therevidae: (38) head of *Hemigephyra atra* Lyneborg, lateral view ♂ (arrows indicate setulae on face and frons); (39) wing of *Acathrito basalis* (Loew), dorsal view ♂; (40) same, *Caenophthalmus gracilis* Lyneborg ♂; (41) same, *Hoplosathe brevistyla* Lyneborg & Zaitzev ♀; (42) same, *Irwiniella* sp. ♂; (43) same, *Neotherevella* sp. ♂; (44) same, *Pseudothereva parviseta* Lyneborg ♂; (45) same; *Schoutedenomyia* sp. ♂.

Abbreviations: A_1 – first branch of anal vein; al – alula; *bc* – basal costal cell; *bm* – basal medial cell; *br* – basal radial cell; *c* – costal cell; *C* – costal vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; flg – flagellum; fc – face; fr – frons; gn – gena; *h* – humeral crossvein; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; prbs – proboscis; R_1 – anterior branch of radius; r_1 – first radial cell; r_{2+3} – second + third radial cell; R_{2+3} – second branch of radius; r_4 – fourth radial cell; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein; scp – scape.

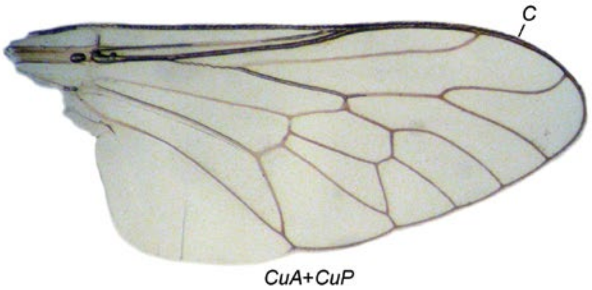


46 *Stenopomyia* ♂

47 *Stenosathe* ♀

48 *Thereva* ♂

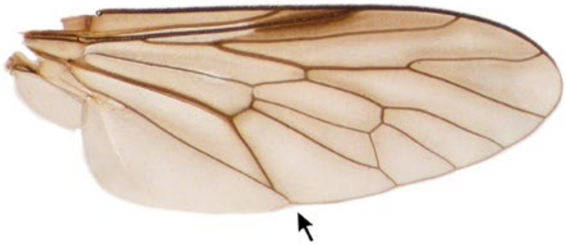
49 *Acathrito* ♂



50 *Actorthia* ♀

51 *Efflatouniella* ♀

52 *Efflatouniella* ♀



53 *Neotabuda* ♀

Figs 49. 46–53. Wings of Therevidae (dorsal views): (46) *Stenopomyia* sp. ♂; (47) *Stenosathe* sp. ♀; (48) *Thereva seminitida stuckenbergi* Lyneborg ♂; (49) *Acathrito* sp. ♂; (50) *Actorthia lacteipennis* (Becker) ♀; (51) *Efflatouniella sinatica* Mohammad & Badrawy ♀; (52) *Efflatouniella* sp. ♀; (53) *Neotabuda* sp. ♀ (arrow indicates extent of costal vein).

Abbreviations: *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_1 – first branch of media; m_3 – third medial cell; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

and the 2-segmented flagellum (Lyneborg 1972). The type specimen was collected in November. Biology and immature stages are otherwise unknown.

***Delphacura* Lyneborg** (Xestomyzinae)**.** An endemic monotypic genus, with the single described species, *D. mosselensis* Lyneborg, 1972 (Fig. 29), described from the Western Cape Province, South Africa. This rarely collected species is characterised by having the head with only a few setae, the antennal flagellum 3-segmented and the male eyes holoptic. The wing (Fig. 64) is also unmarked, which is unusual for species in the subfamily Xestomyzinae. Adults have been collected from January to March. Biology and immature stages are otherwise unknown.

***Efflatouniella* Kröber** (Phycusinae)**.** A genus of four species occurring in the Afrotropical, Oriental and Palaearctic Regions, from Egypt through the Middle East and the Arabian Peninsula to Central Asia. Two species, one described, *E. sinatica* Mohammad & Badrawy, 2011 and one described by Hauser (2017), occur in United Arab Emirates and Yemen in the Arabian Peninsula (Fig. 18) and an undescribed species is known from Namibia (Hauser, in prep.). The genus was revised recently by Mohammad & Badrawy (2011) and Hauser (2017). Species of the genus represent the smallest Therevidae at only 2.8–4.5 mm in length. With the frontally compressed head, the black velvet marking on the frons of most species and the strangely marked wings (Figs 51, 52) with the costal vein (*C*) ending at veins R_5 or *CuA+CuP*, their relationships to other Phycusinae remain unclear. Species of the genus occur in desert regions and generally prefer sandy soils. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Hauser (2017).

***Hemigephyra* Lyneborg** (Xestomyzinae)**.** An endemic genus of two species, *H. atra* Lyneborg, 1976 (Fig. 30) and *H. braunsi* (Kröber, 1931) (Fig. 31), from South Africa and Zimbabwe, respectively (Lyneborg 1972). Lyneborg (1972) mentioned the possibility that the two species may not belong to the same genus and are likely unrelated. These two species may be placed in separate genera in the future. *Hemigephyra* are medium-sized (length: 5.0–6.8 mm), black or brownish flies. Males are holoptic, the proboscis is as long as or longer than the head, the antennal flagellum is 2-segmented (Fig. 38) and the velvet black patch on the scutellum disk is present in *H. atra* and absent in *H. braunsi*. See Figs 77–80 for an example of the male terminalia of this genus. Adults have been collected from September to February and in April. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg (1972).

***Hoplosathe* Lyneborg & Zaitzev** (Therevinae)**.** This distinctive genus of 10 described species occurs throughout the Palaearctic Region from Morocco to China. Lyneborg & Zaitzev (1980) described the genus and the majority of species. Lui & Yang (2013) described two additional species from China, one of which was synonymised by Hauser (2017). *Hoplosathe brevistyla* Lyneborg & Zaitzev, 1980 (Fig. 7) is the only species with a distribution extending into the north-eastern part of the Afrotropical Region (*i.e.*, United Arab Emirates) (Hauser 2017). This genus is easily distinguished by the strongly marked wings (Figs 7, 41), extensive greyish pubescence on the head and body, the presence of setal pile medially on the prosternum, a bare posterior surface of the mid coxa and a post-spiracular patch of setae on the metanepisternum. *Hoplosathe* is placed in the *Pandivirilia* genus-group. Species of the genus prefer desert environments. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg & Zaitzev (1980).

***Irwiniella* Lyneborg** (Therevinae)**.** A species-rich genus of 40 described species that is widely distributed throughout the Afrotropical Region and the rest of the Old World, except Australia, New Zealand and Western Europe. Fourteen species occur in the Afrotropics, with the most recent revision that of Lyneborg (1976*a*). *Irwiniella* (Figs 4, 8, 42) is a frequent representative of the fauna of numerous islands throughout the Atlantic, Indian and Pacific Oceans, more so than any other therevine genus. Lyneborg (1976*a*) erected the genus based on Afrotropical species, but defining the genus based on apomorphic characters is problematic, as many characters used to differentiate the genus are likely plesiomorphies. Most species are further characterised by brown pubescence on the upper frons in both sexes and usually a posterolateral process on the parameral sheath. *Irwiniella* is closely related to *Acantothereva* Séguy, *Acrosathe* Irwin & Lyneborg and *Pseudothereva* Lyneborg and is placed in the *Pandivirilia* genus-group (Holston *et al.* 2007). The genus is in need of systematic revision to identify the potentially numerous synonyms and new species, especially throughout the Oriental and Oceanian Regions. The genus is often associated with dune systems (Lyneborg 1986). Biology and immature stages are otherwise unknown. An identification key to Afrotropical species is unavailable.

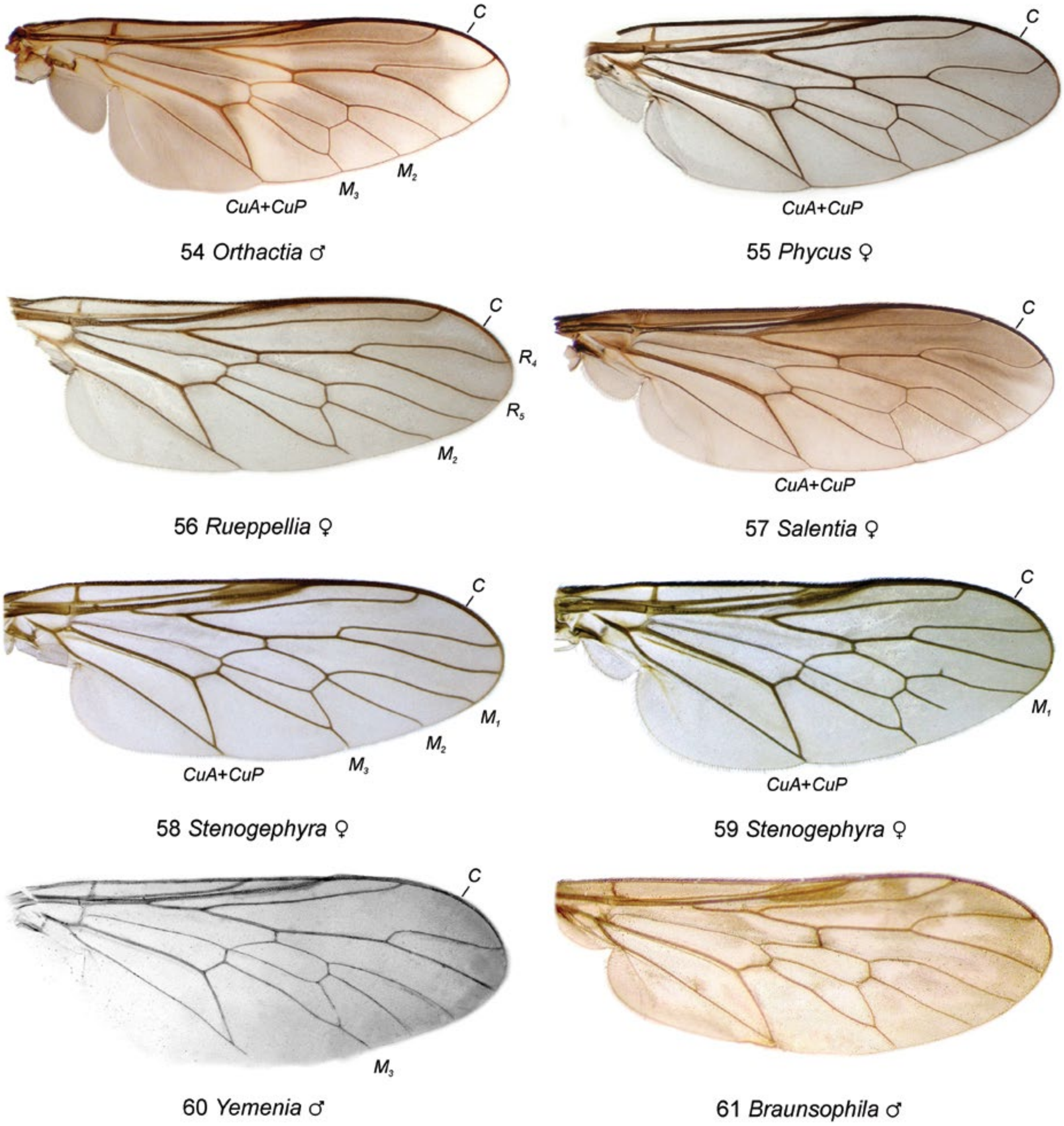
***Lyneborgia* Irwin** (Xestomyzinae)**.** An endemic genus of two described species, *L. ammodyta* Irwin, 1973 and *L. stenoptera* Irwin, 1973, confined to South Africa. The brachypterous females of this very rare genus are unique amongst Therevidae. *Lyneborgia* are medium- to large-sized flies (length: 5.5–9 mm) and all information regarding the genus was summarised by Irwin (1973). Biology and immature stages were described by Irwin (1973), who also provided an identification key.

***Microgephyra* Lyneborg** (Xestomyzinae)**.** An endemic genus of 14 described species occurring in southern parts of the continental Afrotropics and Madagascar (Hauser & Irwin 2005*b*; Lyneborg 1972). *Microgephyra* (Figs 1, 33–35) are small- to large-sized species (length: 4–10 mm), often black or brown, sometimes reddish orange in colour, the head lacks long setae and most species have dichoptic eyes in males. The wing can be clear, banded or mottled (Figs 67–69). The genus is likely not monophyletic and may be split up in the future. At least one undescribed species is known from Madagascar. Biology and immature stages are known for two species of *Microgephyra* described by Irwin (1972) and an identification key to part of the Afrotropical species was provided by Lyneborg (1972).

***Neophycus* Kröber** (Therevinae)**.** An endemic monotypic genus, with the single described species, *N. antennatus* Kröber, 1931 (Fig. 9), known only from two male specimens from Cameroon and Nigeria. The genus is defined solely on apparent autapomorphies, such as the greatly elongate antennal scape with a short whitish flagellum and slightly narrowed wings, but otherwise fits well within the concept of *Irwiniella*.

The male terminalia of both genera are very similar and *Neophycus* exhibits the typical distinctive setal and pubescence patterns found in *Irwiniella*. It is, therefore, likely that *Neophycus* is a synonym of *Irwiniella* and simply an aberrant species of the latter. Biology and immature stages remain unknown

Neotabuda **Kröber** (Phycusinae)**.** An endemic genus of 20 described species with greatest diversity in South Africa, but with records from Botswana, Mozambique and Namibia. At least two additional undescribed species are known. Lyneborg (1980*a*) last revised the genus. *Neotabuda* (Fig. 19) are



54 *Orthactia* ♂

55 *Phycus* ♀

56 *Rueppellia* ♀

57 *Salentia* ♀

58 *Stenogephyra* ♀

59 *Stenogephyra* ♀

60 *Yemenia* ♂

61 *Braunsophila* ♂

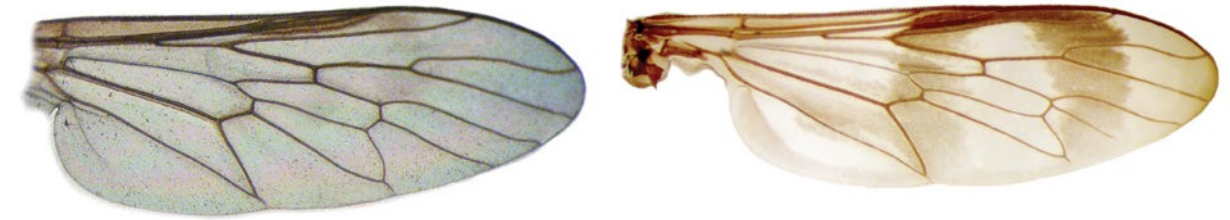
Figs 49.54–61. Wings of Therevidae (dorsal views): (54) *Orthactia* sp. ♂; (55) *Phycus niger* (Kröber) ♀; (56) *Rueppellia* sp. ♀; (57) *Salentia* sp. ♀; (58) *Stenogephyra dianeae* Webb & Hauser ♀; (59) *S. janiceae* Webb & Hauser ♀; (60) *Yemenia flavus* (Lyneborg) ♂; (61) *Braunsophila* sp. ♂.

Abbreviations: *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_1 – first branch of media; M_2 – second branch of media; M_3 – third branch of media; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

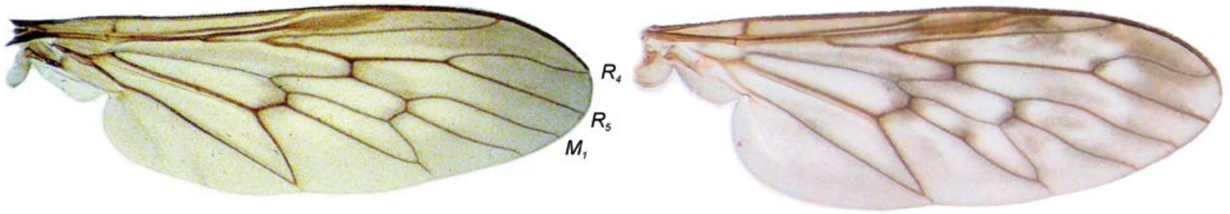
small- to medium-sized (length: 3.6–10.0 mm), broad, blackish species, with the costal wing vein (*C*) ending at vein *CuA+CuP* (Fig. 53). The male eyes are mostly holoptic, rarely separated by a distance narrower than the ocellar tubercle, the eyes of a few species have long, dense setae, the antennal scape is often thicker than the pedicel and the gonocoxites are separated. Most known specimens were reared from larvae and further rearing efforts will surely raise the number of new species. The collecting records indicate activity in every month, except April and May. An identification key to Afrotropical species was provided by Lyneborg (1980*a*).

***Neotherevella* Lyneborg** (Therevinae)**.** A genus of four described species, occurring disparately in the Afrotropical and Palaearctic Regions. Two species occur in the Afrotropics: *N. macularis* (Wiedemann, 1828), recorded from Mauritania, Morocco and Sudan and *N. arenaria* (Lyneborg, 1976), recorded from Namibia (Lyneborg 1976*a*, 1978*b*). This genus is diagnosed by the body being clothed in an extensive whitish-grey pubescence, admixed with a dense pile of elongate lanceolate setae, the parafacial setae are absent and setal pile is present on the posterior surface of the mid coxa. Females of *Neotherevella* have a characteristic broad frons, clothed in whitish grey

62 *Ceratosathe* ♂ 63 *Cochlodactyla* ♂



64 *Delphacura* ♀ 65 *Hemigephyra* ♂



66 *Hemigephyra* ♂ 67 *Microgephyra* ♂

68 *Microgephyra* ♀ 69 *Microgephyra* ♂

Figs 49.62–69. Wings of Therevidae (dorsal views): (62) *Ceratosathe tridactyla* Lyneborg ♂; (63) *Cochlodactyla munroi* Lyneborg ♂; (64) *Delphacura mosselensis* Lyneborg ♀; (65) *Hemigephyra atra* Lyneborg ♂; (66) *H. braunsi* (Kröber) ♂; (67) *Microgephyra chrysothorax* Hauser ♂; (68) *M. latipennis* Lyneborg ♀; (69) *M. elegans* Hauser ♂.

Abbreviations: *C* – costal vein; M_1 – first branch of media; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

pubescence, with two large black maculae. Males lack this feature and have a very narrow frons, except for the Palaearctic species *N. kozlovi* Zaitzev, 1971. See Fig. 43 for an example of the wing of the genus. All species in the genus appear to be associated with sandy dune systems and have greatly elongated tibial and tarsal macrosetae, as has been reported previously in *Orthactia* by Lyneborg (1988). Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg (1976*a*) under the name *Neothereva* Kröber.

***Orthactia* Kröber** (Phycusinae)**.** An endemic genus with seven described species recorded from Namibia and South Africa. *Orthactia* (Fig. 20) are medium-sized (length: 6.2–8.2 mm), rather colourful species, with a mixture of black, brown to orange and white and the wing membrane has colourful irregular patterns. The costal vein (*C*) ends at vein *CuA+CuP* (Fig. 54). The antennae are much shorter than the head (Fig. 20) and the gonocoxites are fused with each other and to the hypandrium. Adults are active from September to March, but better sampling may reveal a flight period during the entire year. Species-specific modifications of setae on the scutellum into tufts and combs are remarkable and rather unique in this family. Both sexes have long spines on the tarsi, which may facilitate walking on sand of dunes and/or digging in sand, which is their preferred substrate. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg (1988).

***Pentheria* Kröber** (Xestomyzinae)**.** An endemic genus of ten described species, occurring in the southern parts of the Afrotropical Region. *Pentheria* (Fig. 36) are amongst the larger Xestomyzinae (length: 6–12.3 mm) and can be differentiated by the antenna being ventrally directed and not on the same axis as the body, the wing membrane (Fig. 71) nearly always has two fascia (of which the apical one is the broadest). The scutellum has a velvet patch and the antennal flagellum is 3-segmented. The identification of females to species is often problematic, while males can be easily identified by reference to characters of the male terminalia. Adults have been collected from September to January. The biology and immature stages of only one species is known (Irwin 1972). Only eight of the ten described species were included in the identification key of Lyneborg (1972) and this should be used with caution, as several undescribed species are known.

***Phycus* Walker** (Phycusinae)**.** A widely distributed genus of 25 described species, occurring in all zoogeographical regions, except the Australasian Region and Antarctica. Thirteen species are recorded from the Afrotropical Region, which has the greatest diversity of species globally. *Phycus* (Fig. 21) are medium- to large-sized (length: 5.4–11.4 mm) species, often black to light brown in colour and easily separable from other phycusine flies by the dichoptic male eyes, the long antennae and the 2-segmented palpus. The costal vein (*C*) ends at vein *CuA+CuP* (Fig. 55). An example of the male terminalia is illustrated in Figs 73–76. Species of *Phycus* occur in savanna and afforested habitats and appear to be more adapted to forest-like habitats than most other Afrotropical Phycusinae. Biology and immature stages are otherwise unknown. An identification key to Afrotropical species was provided by Lyneborg (1978*c*).

70 Undescribed genus ♂

71 *Pentheria* ♂

72 *Xestomyza* ♂

Figs 49.70–72. Wings of Therevidae (dorsal views): (70) Undescribed genus ♂; (71) *Pentheria* sp. ♂; (72) *Xestomyza lugubris* Wiedemann ♂.

Abbreviations: M_1 – first branch of media; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

Pseudothereva **Lyneborg** (Therevinae)**.** An endemic genus of four described species, recorded from Ethiopia, Kenya and South Africa. Males are only known for two species, *P. aethiopica* (Bezzi, 1906) from Ethiopia and *P. parviseta* Lyneborg, 1976 from South Africa, so the concept of the genus is currently not especially stable, compared to the morphologically similar, yet highly variable genera *Irwiniella* and *Thereva*. *Pseudothereva* (Fig. 11) can be differentiated from other Afrotropical genera based on the following characters: dense pile present on the parafacial, the posterior surface of the mid coxae and the prosternal furrow and wing cell m_3 is closed and short-petiolate (except in *P. parviseta*) (Fig. 44). *Pseudothereva* is very similar in appearance to *Thereva*, but can be differentiated based on head shape; in *Thereva* the face width is equal to, or greater than, head height, while in *Pseudothereva* the face is much narrower. The genus is closely related to the *Acantothereva*, *Acrosathe* and *Irwiniella* and is ascribed to the *Pandivirilia* genus-group. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lyneborg (1976*a*).

Rueppellia **Wiedemann** (Phycusinae)**.** A genus of five described species occurring in the Afrotropical and Palaearctic Regions, with a rather unique distribution pattern. Two described species, *R. keiseri* Lyneborg, 1989 and *R. multisetosa* Lyneborg, 1989 and at least five undescribed species are endemic to Madagascar, none occur in sub-Saharan Africa and one species, *R. semiflava* Wiedemann, 1830, occurs in Oman, United Arab Emirates, Yemen, Egypt and Israel. The two other species are distributed from North Africa to central Asia (Badrawy & Mohammad 2011; Hauser 2017). The Malagasy species were described by Lyneborg (1989*a*). *Rueppellia* (Fig. 22) are small- to medium-sized (length: 5–6 mm) black to brown species, characterised by the convergent R_4 and R_5 wing veins, the costal vein (C) ends at vein M_2 (Fig. 56), the holoptic eyes of males and gonocoxites that are fused to each other and the hypandrium. Biology and immature stages remain unknown. An identification key to Afrotropical species is unavailable.

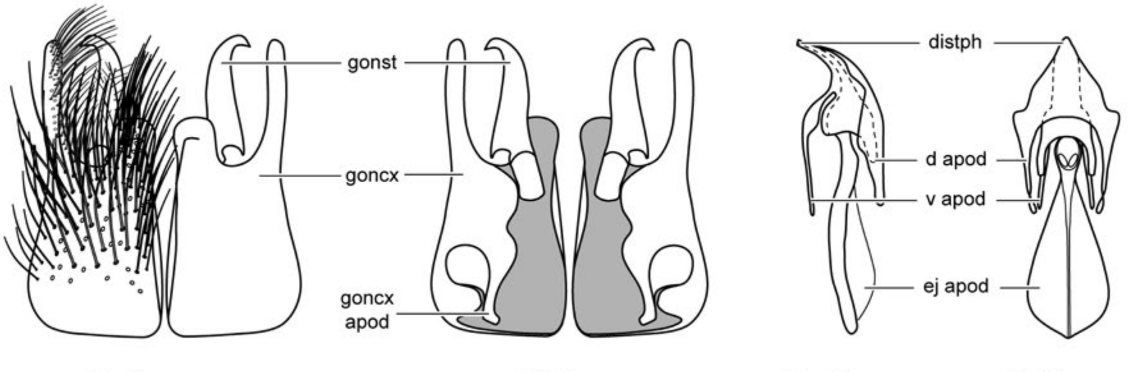
Salentia **Costa** (Phycusinae)**.** A predominantly Palaearctic genus of 11 described species, occurring from Morocco through the Mediterranean, into the Middle East (Egypt, Israel) through Iran to Central Asia (Kazakhstan) and south to Yemen, where one unidentified species enters the Afrotropical Region. There is no current revision of this genus. Zaitzev (1977) published a key to Palaearctic species, but failed to include several previously described species. *Salentia* (Fig. 23) are medium-sized (length: 6–9 mm), black, slender species with holoptic males, the antenna is often longer than the head, and/or the scape is significantly enlarged. The flagellum is 3-segmented and the proboscis is shorter than the head. The costal vein (C) ends at vein *CuA+CuP* (Fig. 57). Biology and immature stages remain unknown. An identification key to Afrotropical species is unavailable.

Schoutedenomyia **Kröber** (Therevinae)**.** A rarely encountered genus of 15 described species, widely distributed throughout the Afrotropical, Oriental and Palaearctic (Mediterranean) Regions. Several undescribed species are also represented in collections from the Oriental Region (Lyneborg 1976*a*, 1978*a*, 1986). *Schoutedenomyia* (Fig. 12) is readily differentiated by the lack of pilosity on the head and body, wing cell m_3 is typically petiolate (Fig. 45), the dististylus is narrowly elongate and by the macrosetae on the fore tibia, which is distinctly reduced in size. While many stiletto flies exhibit an association with coastal habitats, *Schoutedenomyia* appears to be more associated with freshwater riparian habitats (Lyneborg 1976*a*). The genus is superficially similar to the New World genus *Cerocatus* Rondani (= *Cyclotelus* Walker), but is more closely related to *Stenopomyia* and the Oriental genus *Megapalla* Lyneborg, based on both morphological (Lyneborg 2001) and molecular data (Holston *et al*. 2007). Biology and immature stages remain unknown. Lyneborg (1976*a*) provided an identification key to Afrotropical species and later described two additional species (Lyneborg 1978*a*).

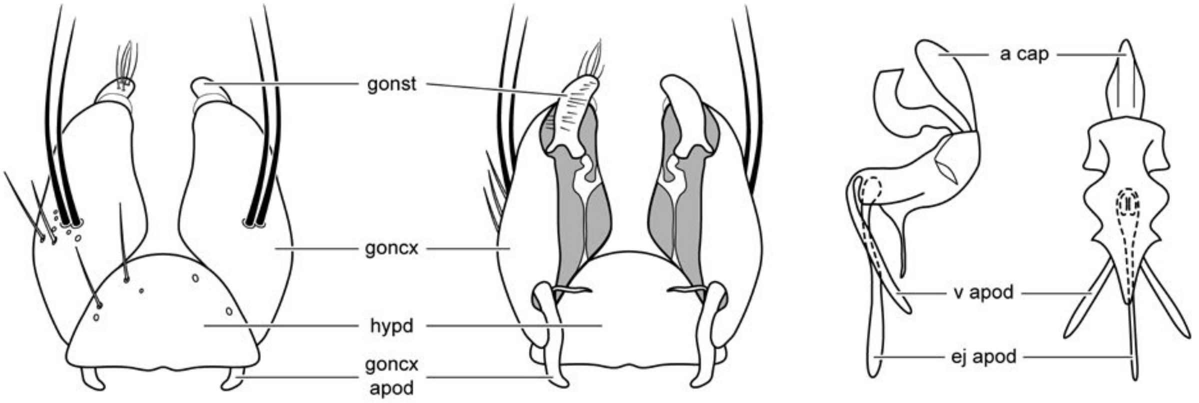
Stenogephyra **Lyneborg** (Phycusinae)**.** An endemic genus of seven described species confined to Namibia and South Africa. *Stenogephyra* (Fig. 24) are small (length: 3.5–5 mm) species, with very long antennae resembling small *Phycus* spp., but are actually not closely related, contrary to what Lyneborg (1987: 472) stated when describing the genus. The costal vein (C) ends at veins M_1 or M_2, at or distinctly before the wing margin (Figs 58, 59). Living adults of at least one species have bluish eyes. The long acanthophorite spines are unusual as these are usually strongly reduced in this subfamily. Irwin (2001) published information on flight periodicity of *Stenogephyra* in Namibia. The pupa of the genus is known (Fig. 88) and also described in Webb & Hauser (2011). An identification key to Afrotropical species was provided by Webb & Hauser (2011).

Stenopomyia **Lyneborg** (Therevinae)**.** An endemic genus of 13 described species confined to Madagascar. Undoubtedly, additional species are yet to be discovered. Lyneborg (1976*a*) revised the genus and described the majority of species. *Stenopomyia* adults (Figs 5, 13) are relatively slender and elegant, with sparse pile covering. The genus is characterised by the absence of setal pile on the prosternum, posterior surface of the mid coxa and frons, the uniformly sized male eye facets, wing cell m_3 open (Fig. 46) and the distinctively enlarged epandrium. This genus is ascribed to the *Thereva* genus-group and a sister-group relationship between *Stenopomyia* and *Schoutedenomyia* is supported by molecular data (Holston *et al*. 2007). The antennal scape length and width of the frons in the male are highly variable in this genus. *Stenopomyia* is divided into two species-groups (*S. keiseri* Lyneborg, 1976 and *S. variegata* (Bigot, 1859) species-groups), based largely on frontal dimensions and scape length. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lyneborg (1976*a*).

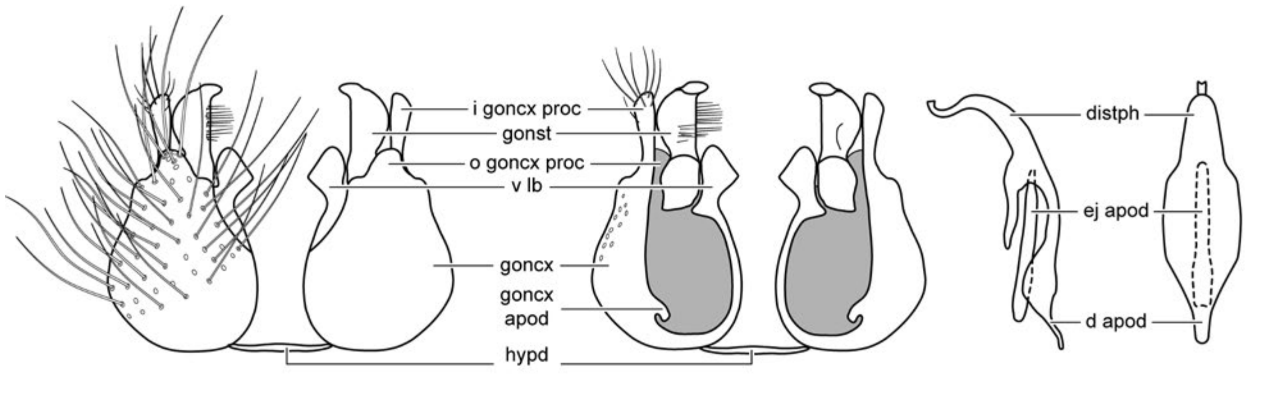
Stenosathe **Lyneborg** (Therevinae)**.** A genus of three species occurring in the Afrotropical and Oriental Regions. *Stenosathe* (Fig. 14) was originally erected to accommodate two southern African species by Lyneborg (1976*a*), with *S. brachycera* (Loew, 1858) described from South Africa and *S. pilosa* Lyneborg, 1976 described from Zimbabwe. A central Asian species, *Psilocephala pulchra* Kröber, 1912, was subsequently transferred to the genus by Lyneborg (1986). Closely related to *Stenopomyia*, this genus lacks the apomorphic terminalic features characteristic of the Malagasy genus. Consequently, this genus is defined largely on plesiomorphic characters and may not represent a monophyletic group. See Fig. 47 for an example of the wing of the genus. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lyneborg (1976*a*).



73 *Phycus* ♂ 74 *Phycus* ♂ 75 *Phycus* ♂ 76 *Phycus* ♂



77 *Hemigephyra* ♂ 78 *Hemigephyra* ♂ 79 *Hemigephyra* ♂ 80 *Hemigephyra* ♂

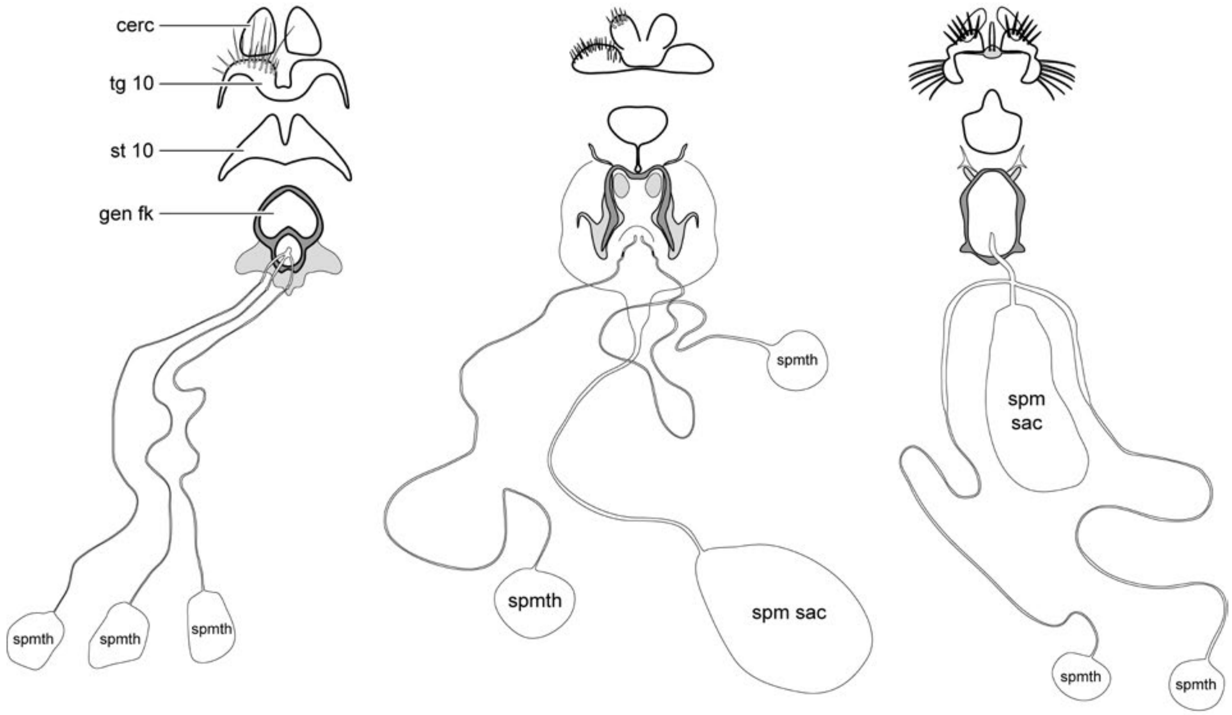


81 *Thereva* ♂ 82 *Thereva* ♂ 83 *Thereva* ♂ 84 *Thereva* ♂

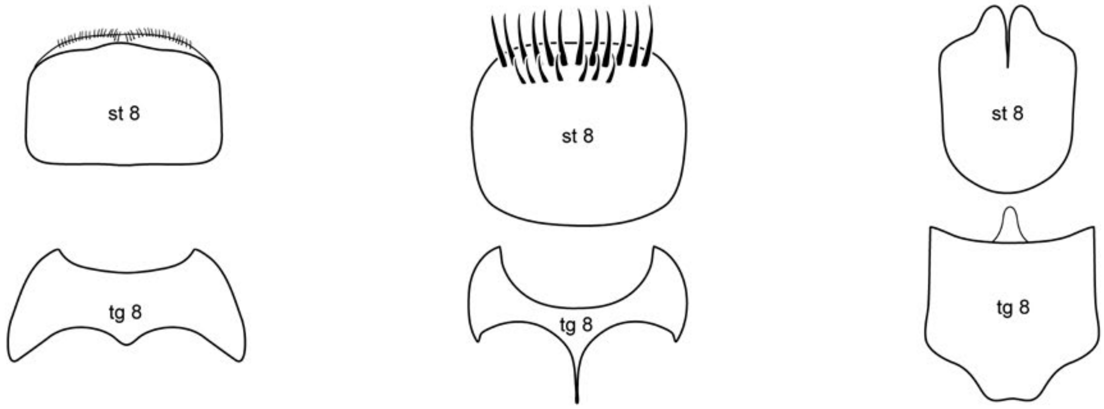
Figs 49.73–84. Male terminalia of Therevidae: (73) male terminalia of *Phycus* sp., ventral view; (74) same, dorsal view; (75) aedeagal complex of *Phycus* sp., lateral view; (76) same, dorsal view; (77) male terminalia of *Hemigephyra braunsi* (Kröber), ventral view; (78) same, dorsal view; (79) aedeagal complex of *H. braunsi*, lateral view; (80) same, dorsal view; (81) male terminalia of *Thereva seminitida stuckenbergi* Lyneborg, ventral view; (82) same, dorsal view; (83) aedeagal complex of *T. seminitida stuckenbergi*, lateral view; (84) same, dorsal view.

Abbreviations: a cap – apical cap; d apod – dorsal apodeme; distph – distiphallus; ej apod – ejaculatory apodeme; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; i goncx proc – inner gonocoxal process; o goncx proc – outer gonocoxal process; v apod – ventral apodeme; v lb – ventral lobe.

***Thereva* Latreille** (Therevinae)**.** The most species-rich genus of stiletto flies, with 185 described species. The genus occurs in all zoogeographical regions, except the Australasian and Neotropical Regions and Antarctica, with most in the Holarctic. Only the Nearctic fauna has been recently and adequately revised (Holston & Irwin 2005). Eight species are recorded from the Afrotropical Region. Lyneborg (1976a) revised the Afrotropical fauna and divided the genus into two species-groups: the *T. seminitida* Becker, 1909 and *T. nobilitata* (F., 1775) species-groups. A third group – the *T. turneri* Lyneborg, 1976 species-group was transferred to the genus *Caenophthalmus* (Winterton *et al.* 2016). A distinctive feature that differentiates *Thereva* from other Afrotropical genera is the face (Fig. 15), which is densely pilose and very wide relative to head height. The prosternal furrow and posterior surface of the mid coxa are also densely pilose and females frequently have glossy



85 *Orthactia* ♀ 86 *Xestomyza* ♀ 87 *Thereva* ♀

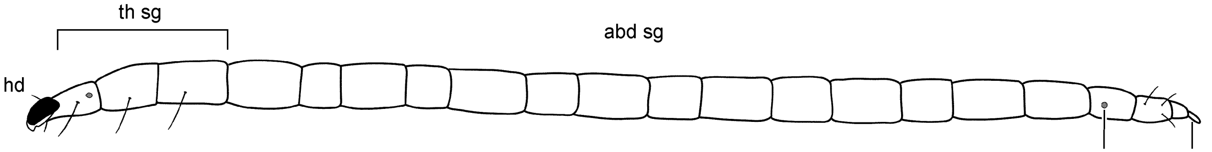


88 *Orthactia* ♀ 89 *Xestomyza* ♀ 90 *Thereva* ♀

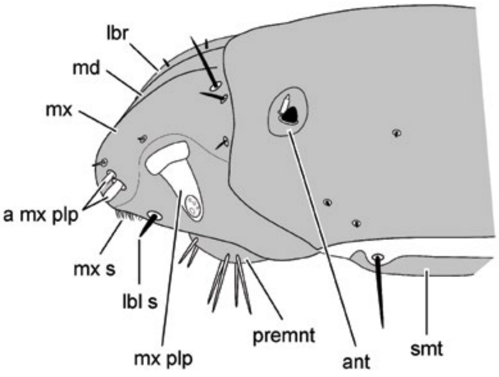
Figs 49.85–90. Female terminalia, sternites and tergites of Therevidae: (85) terminalia of *Orthactia* sp., dorsal view; (86) same, *Xestomyza lugubris* Wiedemann; (87) same, *Thereva* sp.; (88) sternite 8 (above), ventral view and tergites 8 (below), dorsal view of *Orthactia* sp.; (89), same, *Xestomyza lugubris* Wiedemann; (90) same, *Thereva* sp.

Abbreviations: cerc – cercus; gen fk – genital fork; spm sac – spermathecal sac; spmth – spermatheca; st – sternite; tg – tergite.

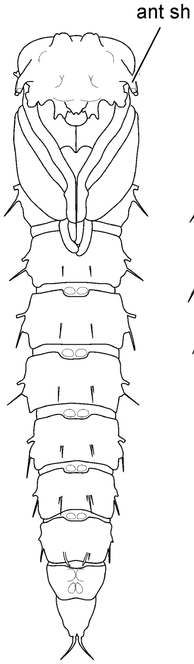
91 Therevidae



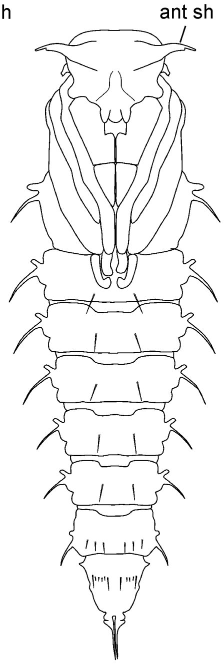
92 Therevidae



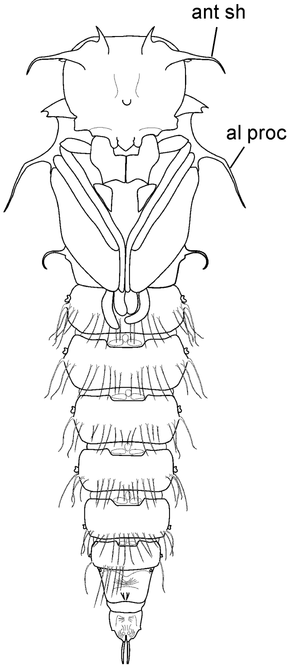
93 Therevidae



94 *Stenogephyra* (Phycinae)



95 *Microgephyra* (Xestomyzinae)



96 *Ammonaios* (Therevinae)

Figs 49.91–96. Larvae and pupae of Therevidae: (91) photograph of larval habitus of Therevidae larva, dorsal view (United Arab Emirates); (92) larval habitus of Therevidae, lateral view (indicating secondary segmentation); (93) larval head capsule of Therevidae, lateral view; (94) pupal habitus of *Stenogephyra* sp., ventral view; (95) same, *Microgephyra* sp., ventral view; (96) same, *Ammonaios* sp., ventral view (non-Afrotropical). Fig. 91 (photograph M. Hauser), Fig. 93 (after Irwin 1972, figs 4, 5 & English 1950, fig. 2, combined), Fig. 94 (after Webb & Hauser 2011, fig. 41), Fig. 95 (after Irwin 1972, figs 8, 9, 14, combined), Fig. 96 (after Hauser & Irwin 2003, fig. 35).

Abbreviations: a mx plp – anterior maxillary palpus; abd sg – abdominal segments; al proc – alar process; ant – antenna; ant sh – antennal sheath; hd – head; lbl s – labellar seta; lbr – labrum; md – mandible; mx – maxilla; mx plp – maxillary palpus; mx s – maxillary setae; mtceph rd – metacephalic rod; p spr – posterior spiracle; premnt – prementum; prlg – proleg; smt – submentum; th sg – thoracic segments.

callosities on the frons, either single or paired. See Fig. 48 for an example of the wing of the genus and Figs 81–84 for the male terminalia. In contrast to *Irwiniella*, which is frequently found on oceanic islands, *Thereva* is known from relatively few islands and is noticeably absent from Madagascar. This genus is ascribed to the *Thereva* genus-group and is closely related to the genera *Baryphora*, *Caenophthalmus*, *Cionophora* and *Euphycus*. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lyneborg (1976a).

Undescribed genus (Xestomyzinae)**.** This new genus (Figs 32, 70) is known from three species occurring in Botswana, Kenya and South Africa respectively. This genus extends the range of African Xestomyzinae significantly farther northwards. Biology and immature stages remain unknown.

***Xestomyza* Wiedemann** (Xestomyzinae)**.** An endemic genus of two described species, *X. lugubris* Wiedemann, 1820 and *X. stuckenbergi* Hauser, 2012, plus one undescribed species, all confined to South Africa. *Xestomyza* (Figs 3, 37) are medium- to large-sized (length: 7–11.5 mm), grey to black species, characterised by the enlarged flagellomere 1, the setulose face, dichoptic male eyes, the antenna and proboscis longer than the head and the scutellum without a velvet macula. The costal vein (*C*) ends at vein M_2 (Fig. 72). Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Hauser (2012).

***Yemenia* Koçak & Kemal** (Phycusinae)**.** An endemic monotypic genus, with the single species originally described as *Araeopus flavus* Lyneborg, 1983 (Fig. 25), based on four males collected in North Yemen in April. As the genus name was preoccupied, Koçak & Kemal (2009) erected the genus *Yemenia* to contain it, without examining specimens of the species. No additional specimens of this enigmatic genus have been collected subsequently. *Yemenia* are small (length: 4.5 mm), yellow-brownish species, with dichoptic males, the costal wing vein (*C*) ends at vein M_2 (Fig. 60) and the gonocoxites are separated. Biology and immature stages remain unknown.

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SCENOPINIDAE 50

(Window Flies)

Shaun L. Winterton and Stephen D. Gaimari

Fig. 50.1. Female of *Scenopinus* sp. (South Africa) (photograph © S.A. Marshall).

Diagnosis

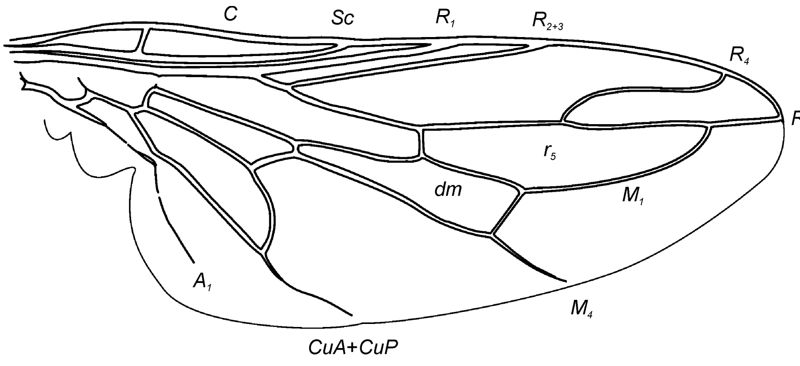
The family Scenopinidae can be diagnosed as follows (modified after Woodley 2009: 650):

Small- to medium-sized flies (body length: 1.5–9.0 mm), usually shiny black, grey-brown to yellowish tan, sometimes with distinct yellow and white markings, body frequently overlain with dense grey or brown pubescence (Fig. 1). Body shape either short and broad, or slender and elongate.

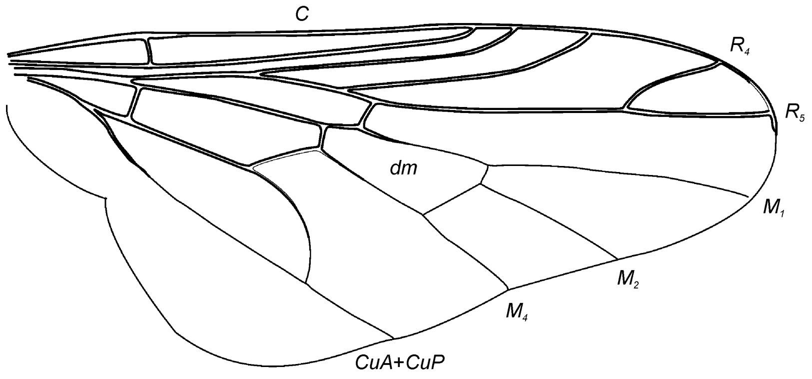
Head (Figs 5, 6) with eyes holoptic (males) to widely separated (females); occiput lacking macrosetae (or rarely minute); antenna usually shorter than head length (rarely longer), with flagellum apparently composed of a single article with apical or subapical stylus; mouthparts absent or present, very short to longer than head length, with labellum fleshy.

Thorax with macrosetae rarely present (some Proratinae). Scutellum rounded. Wing membrane hyaline, or milky white translucent (usually only in male), caused by minute covering of microtrichia, rarely with infuscate brown markings; costal vein (C) extending around wing margin (in non-Afrotropical Caenotinae), or ending at wing apex (Proratinae and Scenopininae); vein M_1 complete to wing margin (Caenotinae, Proratinae and Scenopininae: Scenopinini) (Figs 3, 4), or anteriorly-directed and joining vein R_5, rendering cell r_5 petiolate (Scenopininae: Metatrichini) (Fig. 2); vein M_3 rarely present (Caenotinae), while vein M_2 present only in Proratinae (Fig. 3) and Caenotinae; vein M_4 at least partially fused with vein M_3, to arise from posterior margin of discal medial cell (*dm*); length of vein M_4 variable, ranging from highly abbreviated, to complete to wing margin. Legs with few macrosetae, usually only at apices of tibiae and tarsal segments; tibial spurs absent; hind

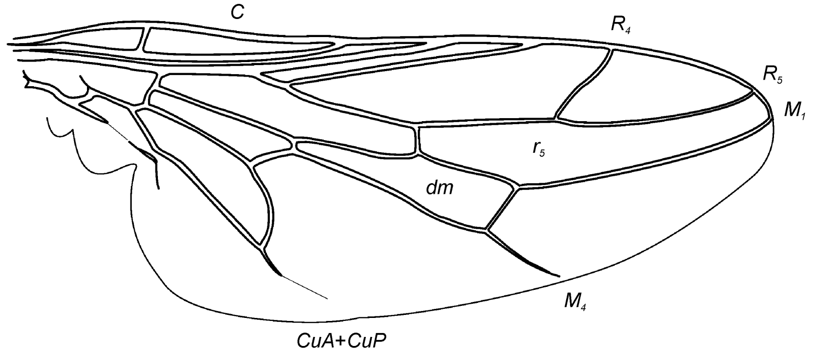
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1209–1219.



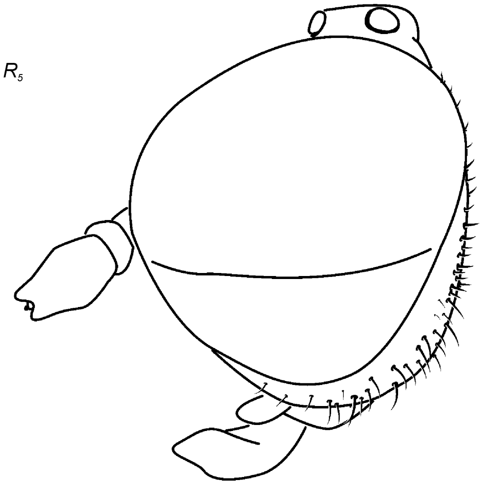
2 *Propebrevitrichia*



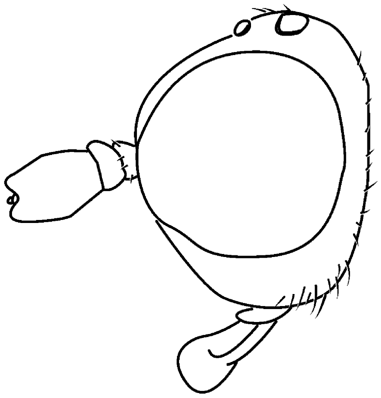
3 *Cyrtosathe*



4 *Prepseudatrichia*



5 *Propebrevitrichia* ♂



6 *Propebrevitrichia* ♀

Figs 50.2–6. Wings and heads of Scenopinidae: (2) wing of *Propebrevitrichia* sp.; (3) same, *Cyrtosathe kirkspriggsi* Winterton & Metz; (4) same, *Prepseudatrichia* sp.; (5) male head of *Propebrevitrichia serowensis* Winterton, lateral view; (6) same, female. Fig 3 (after Winterton & Metz 2005, fig. 2), Figs 2, 5–6 (after Winterton 2005, figs 1C, 1E).

Abbreviations: A_1 – first branch of anal vein; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; r_5 – fifth radial cell; R_5 – lower branch of third branch of radius.

coxal knob present (some Caenotinae and Proratinae), or absent (Scenopininae).

Abdominal tergite 2 with medial patch of specialised sensory setae, shape of setae and patch variable, either single patch or medially divided into 2 patches (Figs 17–19); male terminalia rotated 180° (Scenopininae), or not rotated (Caenotinae and Proratinae); male terminalia with tergite and sternite 8 either separate, or fused laterally, forming a narrow ring-like synsclerite (Scenopinini); phallus with distiphallus bifid or trifid (Scenopinini), lateral accessory lobes associated with basiphallus present (Scenopininae) (Figs 10–12), or absent (Fig. 15); gonocoxal apodeme length variable, if phallus greatly elongate anteriorly into abdominal cavity, then gonocoxal apodeme also greatly elongate to accommodate muscle attachments (Figs 14, 15); gonocoxite well-developed, but reduced in Scenopininae; gonostylus variably developed, often reduced; hypandrium either a well-developed single sclerite (Caenotinae and Proratinae) (Fig. 14), or reduced as paired sclerites (Scenopininae) (Fig. 8), sometimes with extensive setal comb; epandrium medially divided into 2 lamellae, enlarged in Scenopininae to enclose remaining terminalia; female terminalia with acanthophorite spines present or absent; 2 spermathecae, sclerotised (Caenotinae and Scenopininae) (Fig. 13) or membranous (Proratinae) (Fig. 16); spermathecal sac present; spermathecal ducts either joining directly to roof of bursa, or joining to spermathecal sac duct (Caenotinae). Metz *et al*. (2002) described the functional morphology of terminalia while *in copula* for a species of *Prorates* Melander.

Scenopinidae are distinctive flies, but may superficially resemble families, such as Empididae (see Chapter 51), Bombyliidae (see Chapter 45), Therevidae (see Chapter 49) and Mythicomyiidae (see Chapter 44). Scenopinids can be readily differentiated from all of these families by the presence of the sensory setal patch on abdominal tergite 2 and the male terminalia, with lateral aedeagal lobes and the medially divided epandrium.

Biology and immature stages

While found in a variety of habitats, Scenopinidae diversity is greatest in arid regions. Larval scenopinids are elongate, fossorial generalist predators of arthropods in sandy, friable soils and leaf litter, although larvae are known from habitats as diverse as termite mounds, bat guano, beehives, vertebrate nests and burrows, galleries of wood-boring insects, including the boreholes of timber pests and stored products (Dobson 1999; Gnaspini 1989; Kelsey 1969, 1970*a*, *b*, 1981a: 526, *b*, 1989: 350; Rahman *et al*. 1981; Yao & Lo 1992; Yucel 1988).

Adult scenopinids are nectar- and honeydew-feeders and are often collected by sweeping flowers and foliage (Kelsey 1975, 1981*a*). Males of a few Afrotropical species are known to form swarms, especially in the genera *Scenopinus* Latreille and *Propebrevitrichia* Kelsey (Kelsey 1976; unpubl. data). Adults of a few species are regularly collected on windows inside human dwellings, due to their predation as larvae on pests associated with human activities (Cole 1923; Kelsey 1969; Melander 1950).

Larvae of Scenopinidae are typically vermiform, smooth-bodied and pale coloured (Fig. 20). The head capsule is well-developed, with the elongate metacephalic rod narrowed apically and the abdomen secondarily segmented (Woodley 1989: 1386). The respiratory system is amphipneustic, with an anterior pair of spiracles located posteriorly on the first thoracic segment and the posterior pair located posteriorly on the apparent antepenultimate segment (Krivosheina 1997). The pupa (Figs 21–24) is elongate and lacks prominent spines and processes, the antennal sheath is anterolaterally directed and the wing sheath length is variable relative to the lengths of the leg sheaths. The abdomen is equipped with rows of spines on each segment, with spine-like processes more numerous and elongate in fossorial species. Wood-boring genera of the tribe Metatrichini have short spines, with ribbed inter-segmental membranes (Fig. 23) and there is an additional row of abdominal spines in the tribe Scenopinini (Fig. 24).

Different types of niche occupation and specialised prey usage appear restricted to particular genera and may be phylogenetically informative. One group of genera, comprising non-Afrotropical *Belosta* Hardy, *Prepseudatrichia* Kelsey, *Pseudatrichia* Osten Sacken, non-Afrotropical *Stenomphrale* Kröber and non-Afrotropical *Neopseudatrichia* Kelsey, appear to be specialised predators of wood-boring insects (*e.g*., beetle larvae). Adults of this group of genera have morphological adaptations for exiting narrow confines of galleries, including elongate body shape, smooth cuticle and compressed head. Reconstructing a phylogeny of Scenopinidae based on morphology and molecular data, Winterton & Ware (2015) showed that this group of genera is not monophyletic and that this type of life history, along with the associated morphological adaptations, evolved at least twice in the family, once in Metatrichini in a clade comprising *Belosta*, *Pseudatrichia*, *Stenomphrale* and *Neopseudatrichia*, and independently in Scenopinini with *Prepseudatrichia*.

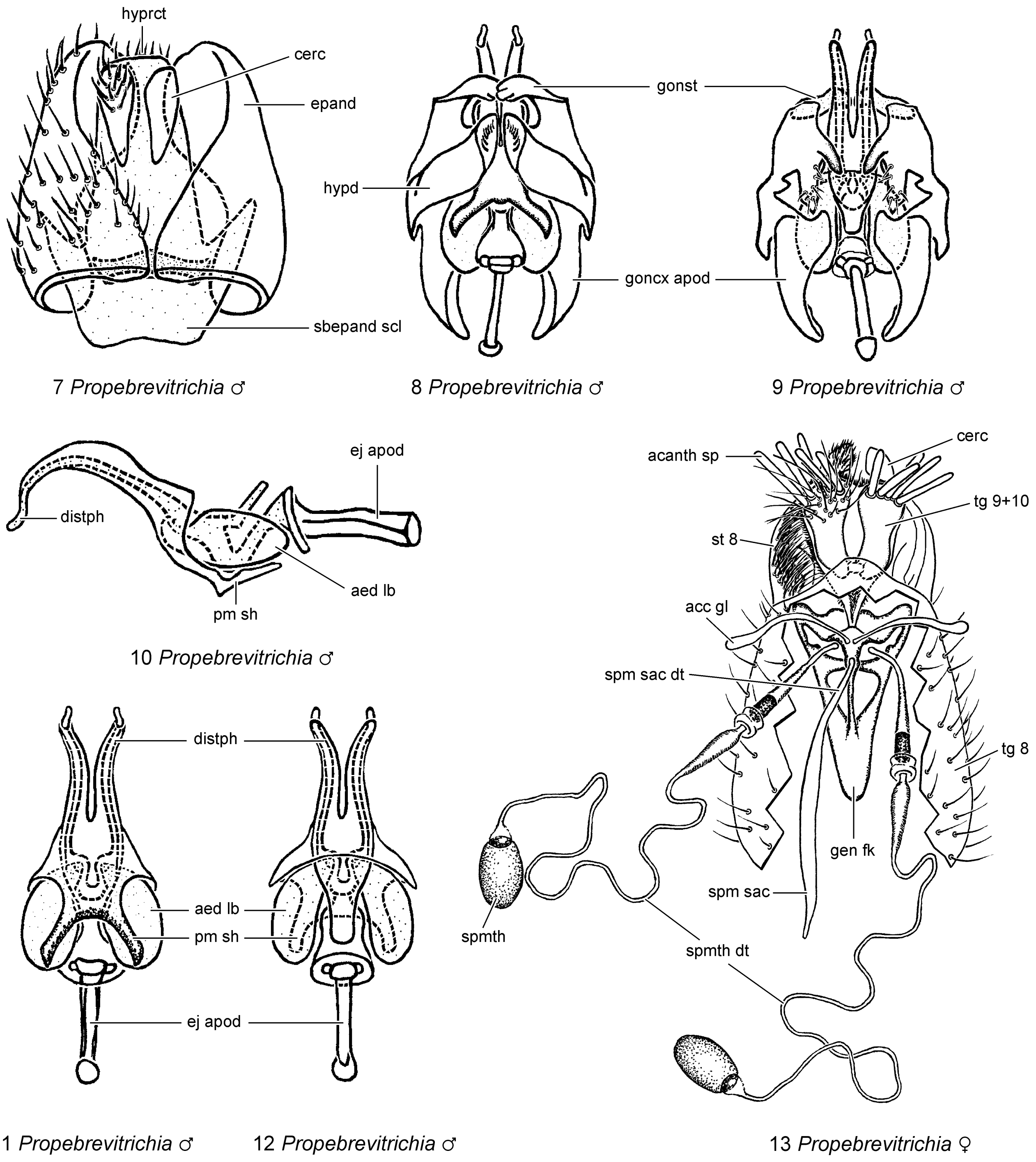
Economic significance

An exceptional case of human urogenital myiasis is recorded for a larva of *Scenopinus* (Thompson *et al*. 1970). The two cosmopolitan species, *Scenopinus fenestralis* (L., 1758) and *S. glabrifrons* Meigen, 1824, are both at least partly associated with human dwellings, being predators of carpet beetles of the genus *Anthrenus* Schaeffer (Dermestidae).

Classification

Scenopinidae are asiloid flies placed in a group of four families (known as the therevoid clade), that also contain Therevidae and non-Afrotropical Apsilocephalidae and Evocoidae. The sister-group relationship between Therevidae and Scenopinidae has been long accepted, but their relationship to Apsilocephalidae and Evocoidae has remained obscure, compounded by the suggested possible paraphyly of Therevidae by Scenopinidae (*e.g*., Woodley 1989: 1386, 2009: 650). In the phylogeny of the therevoid clade by Winterton & Ware (2015), all families were found to be monophyletic, with strong support for the sister-group relationship between Scenopinidae and Therevidae, in a clade sister to Evocoidae as sister to Apsilocephalidae.

Scenopinidae were traditionally defined around what is now regarded as the subfamily Scenopininae, until Yeates (1992)

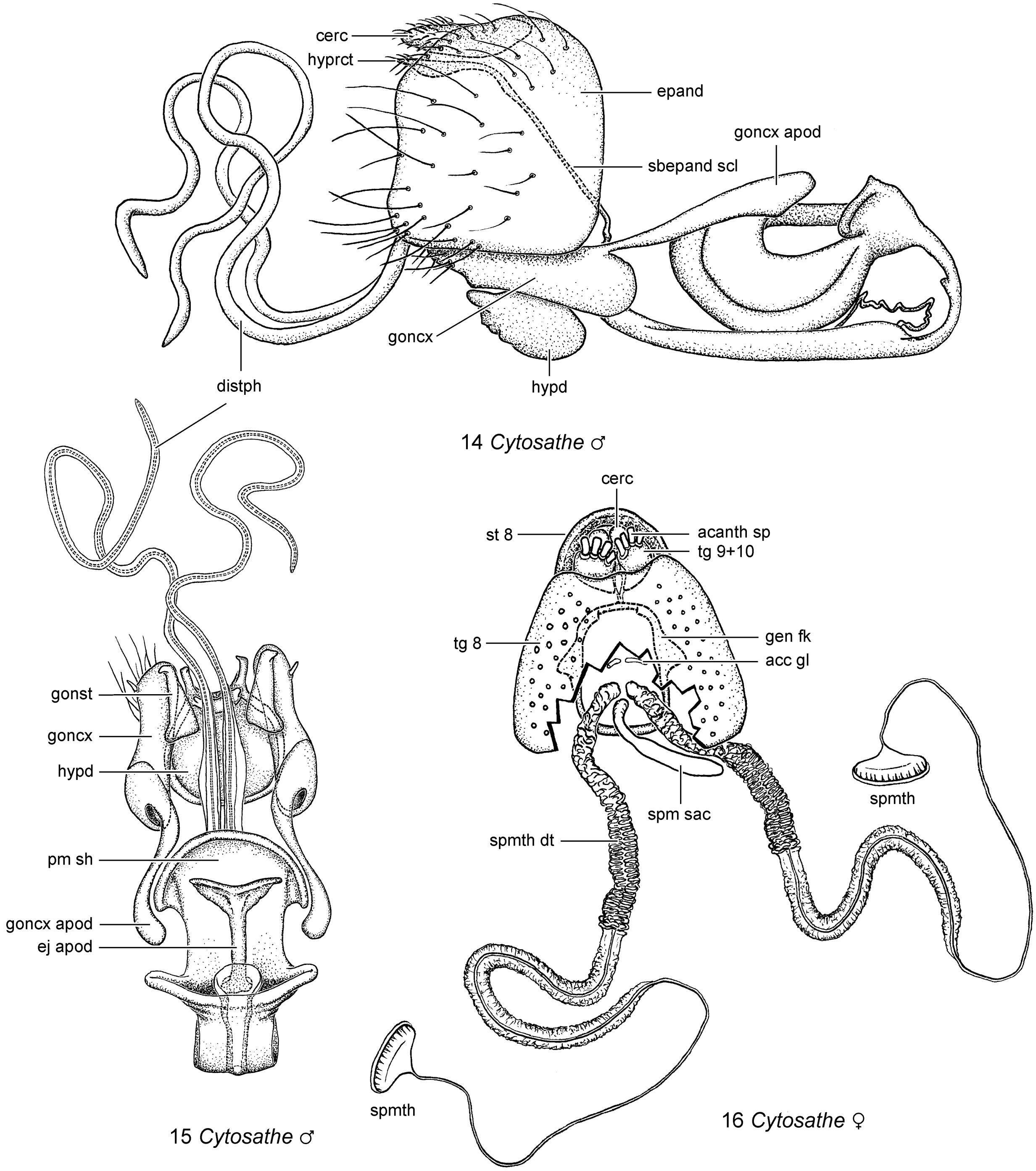

7 *Propebrevitrichia* ♂ 8 *Propebrevitrichia* ♂ 9 *Propebrevitrichia* ♂

10 *Propebrevitrichia* ♂

11 *Propebrevitrichia* ♂ 12 *Propebrevitrichia* ♂ 13 *Propebrevitrichia* ♀

Figs 50.7–13. Male and female terminalia of Scenopinidae (Scenopininae): (7) epandrium and associated structures of *Propebrevitrichia serowensis* Winterton, dorsal view; (8) same, genitalic, ventral view; (9) same, dorsal view; (10) same, aedeagus, lateral view; (11) same, ventral view; (12) same, dorsal view; (13) same, female terminalia, dorsal view (tergite 8 cut away to indicate internal structures). Figs 7–13 (after Winterton 2005, figs 2A–C, 2G, 2E, 2F, 3A, respectively).

Abbreviations: acanth sp – acanthophorite spine; acc gl – accessory gland; aed lb – aedeagal lobe; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; gen fk – genital fork; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; pm sh – parameral sheath; sbepand scl – subepandrial sclerite; spm sac – sperm sac; spm sac dt – sperm sac duct; spmth – spermatheca; spmth dt – spermathecal duct; st – sternite; tg – tergite.



Figs 50.14–16. Male and female terminalia of Scenopinidae (Proratinae): (14) male genitalic capsule of *Cyrtosathe kirkspriggsi* Winterton & Metz, lateral view; (15) same, genitalic capsule (part), dorsal view; (16) same, female terminalia (tergite 8 cut away to indicate internal structures), dorsal view. Figs 14–16 (after Winterton & Metz 2005, figs 3C, 3E, 4C).

Abbreviations: acanth sp – acanthophorite spine; acc gl – accessory gland; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; epand – epandrium; gen fk – genital fork; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; pm sh – parameral sheath; sbepand scl – subepandrial sclerite; spm sac – sperm sac; spmth – spermatheca; spmth dt – spermathecal duct; st – sternite; tg – tergite.

expanded the concept of the family, by transferring the enigmatic genera *Caenotus* Cole, *Prorates*, *Alloxytropus* Bezzi and *Caenotoides* Hall from Bombyliidae to Scenopinidae and proposed a classification based on three subfamilies: Caenotinae, Proratinae and Scenopininae. In a phylogenetic study, Winterton & Ware (2015) also recovered these subfamilies as monophyletic. Only two subfamilies, Proratinae and Scenopininae, occur in the Afrotropical Region. The subfamily Caenotinae, with the single genus *Caenotus*, occurs only in the Nearctic Region and part of Neotropical Mexico (Metz 2003). Proratinae comprises six genera with *ca* 20 species, being mostly New World in distribution. In the Old World the predominantly Palaearctic genus *Alloxytropus* is represented by two species in northern Africa and the Middle East, while a single monotypic Afrotropical genus, *Cyrtosathe* Winterton & Metz, is known only from Namibia.

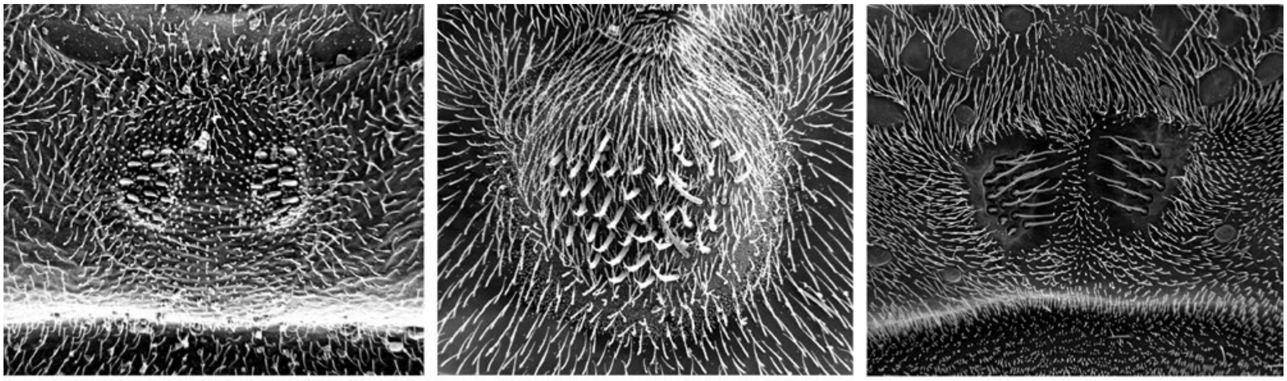
Scenopininae are by far the largest group in the family, with 17 genera and at least 387 species. Besides the single proratine species, all known Afrotropical scenopinids belong to Scenopininae. There are five genera that are endemic to the New World (*Belosta*, *Brevitrichia* Hardy, *Heteromphrale* Kröber, *Irwiniana* Kelsey and *Pseudatrichia*), with a total of 108 species. Australia has four endemic genera (*Neopseudatrichia*, *Paramonova* Kelsey, *Paratrichia* Kelsey and *Riekiella* Paramonov) with 50 species. Although the Palaearctic Region (including North Africa) has 74 endemic species, most of these are in the virtually cosmopolitan genus *Scenopinus*, but 11 species are in four endemic genera (*Kelseyana* Winterton & Gharali, *Iranotrichia* Winterton & Gharali, *Pseudomphrale* Kröber and *Stenomphrale*). The only endemic Afrotropical genus is *Propebrevitrichia* with 15 species. The remaining genera are more widespread, with only *Scenopinus* and *Metatrichia* Coquillett being found in all zoogeographical regions, except Antarctica. The genera *Prepseudatrichia* and *Seguyia* Kelsey are strictly Old World, both being found in the Afrotropical, Oriental and Palaearctic Regions.

Based on phylogenetic results, Winterton & Ware (2015) divided the subfamily Scenopininae into two tribes, Metatrichini and Scenopinini. Scenopinini comprises the genera *Prepseudatrichia*, *Seguyia* and *Scenopinus* and is defined based on the following characteristics: wing vein R_4 anteriorly directed towards the wing margin well before the wing apex and is relatively short and straight; female acanthophorite spines absent; male terminalia with tergite and sternite 8 fused laterally, forming a narrow ring-like synsclerite (Nagatomi *et al*. 1994, figs 1–5); and basiphallus bulbous and recurved towards the hypandrium. All remaining genera in the family are placed in Metatrichini with monophyly of this clade supported by synapomorphies, such as wing vein M_1 (as M_{1+2}) fused to vein R_5 and the female spermathecal duct valves well-developed.

The genus *Scenopinus* is by far the largest in the family, with 194 valid scenopinine species. The genus is not divided into subgenera, but there are four more or less distinct species-groups: the *S. albicinctus*-group (78 species), *S. brevicornis*-group (32), *S. fenestralis*-group (32) and *S. velutinus*-group (52). The *S. velutinus*-group includes only New World species, plus the two species found on the Pacific oceanic islands of Fiji and Hawaii. Except for the two virtually cosmopolitan species, *S. fenestralis* and *S. glabrifrons*, the *S. fenestralis*-group is found primarily in the Palaearctic and Oriental Regions; one endemic species in recorded from Namibia (Kelsey 1976). The *S. albicinctus*-group is strictly Old World, with 23 species in the Afrotropics and all 30 species of *Scenopinus* in Australia belong to this group. Half of the diversity of the *S. brevicornis*-group is in the Afrotropics, with the remainder in the Palaearctic (including one species apparently introduced from the Afrotropics) and one from Asia (Kelsey 1969, 1973*b*).

Identification

Identification of scenopinid species can be difficult for most genera, as the external morphology of species in many genera is rather homogeneous, often despite dramatic differences in male terminalic structures. This is often compounded by poor character choice in the various identification keys provided by Kelsey (enumerated below) and the fact that 150 of the described species have female primary types, which typically represents the only known specimen. Male terminalia are usually critical for proper species differentiation in this family and unassociated females may be difficult to identify with confidence. Often, the keys of Kelsey include separate keys


17 *Metatrichia* 18 *Seguyia* 19 *Scenopinus*

Figs 50.17–19. Scanning electron micrographs of setal patches on tergite 2 of Scenopinidae (dorsal views): (17) *Metatrichia* sp.; (18) *Seguyia* sp.; (19) *Scenopinus* sp.

to males and females. The landmark work on Scenopinidae is that of Kelsey (1969), which includes identification keys to all genera and species of the world known at that time, representing about half of the currently known fauna. Later, Kelsey produced several papers that dealt with the Afrotropical fauna, including keys and a review of species in particular areas. For example, the scenopinids of Africa south of the Equator were treated by Kelsey (1971, 1976) and Nigeria by Kelsey (1984). Ebejer (2009) recently described two new species of *Scenopinus* from the United Arab Emirates. Kelsey's works on the genus *Scenopinus* delineated four species-groups. Winterton & Ware (2015) suggested that these species-groups are likely paraphyletic and the characters used originally by Kelsey (1969) to define them, such as flagellum length and epandrium/hypandrium shape, are not consistent across groups. Consequently, placement of most species described by Kelsey (and other authors) in any species-group of *Scenopinus* is somewhat arbitrary, with numerous intermediate forms. Identification according to species-groups in *Scenopinus* should, therefore, be undertaken with caution and should always be qualified with consultation of type specimens and figures of the male terminalia. The below identification key is largely based on Winterton & Gharali (2011), with some modifications.

Scenopinidae are usually micro-pinned in the field for later double-mounting. Alternatively, specimens can be preserved in ethanol for later critical-point-drying and point-mounting (see Chapter 2).

Key to genera of Afrotropical Scenopinidae

1. Wing with 3 veins originating posteriorly from discal medial cell (*dm*) (*i.e.*, veins M_1, M_2 and M_4) (*e.g.*, Fig. 3); male terminalia unrotated, with phallus and gonocoxal apodemes greatly elongate, much longer than genitalic capsule (*e.g.*, Fig. 14) (PRORATINAE) 2

– Wing with 2 veins originating posteriorly from discal medial cell (*dm*) (*i.e.*, veins M_1 and M_4) (*e.g.*, Figs 2, 4); male terminalia rotated 180°, with phallus and gonocoxal apodemes relatively short, rarely protruding anteriorly from genitalic capsule; phallus extending anteriorly and not folded on itself (e.g., Figs 7–12) (SCENOPININAE) 3

2. Abdominal tergite 2 setal patch rounded, with very slight medial separation into two hemispheres; female tergite 8 with erect, elongate setae arranged in ring-like pattern; male aedeagus folded dorsally onto itself, so that ejaculatory apodeme projects posteriorly (Figs 14, 15) . . . . *Cyrtosathe* Winterton & Metz

– Abdominal tergite 2 setal patch distinctly undivided; female tergite 8 without erect, elongate setae; male aedeagus extending anteriorly and not folded on itself. . . . . *Alloxytropus* Bezzi

3. Wing vein M_1 fused to vein R_5 before wing margin (cell r_5 closed, petiolate) (e.g., Fig. 2) (METATRICHINI) 4

– Wing vein M_1 separate from vein R_5 to wing margin (cell r_5 open) (e.g., Fig. 4) (SCENOPININI). 5

4. Robust bodied flies, with broad, flat abdomen in both sexes; sexes of approximately equal size; male terminalia with epandrium short, not entirely enclosing terminalia; female terminalia with sternite 8 not elongate and lacking acanthophorite spines . . . . *Metatrichia* Coquillett

– Relatively delicate flies, with narrow tapered abdomen, particularly in female; abdomen much longer in female, displaying distinct sexual size dimorphism; male terminalia (Figs 7–12) with epandrium long, enclosing terminalia; female terminalia (Fig. 13) with elongate sternite 8 and acanthophorite spines . . . . *Propebrevitrichia* Kelsey

5. Wing vein M_4 terminating just beyond discal medial cell (*dm*) far from wing margin; female terminalia with sternite 8 with comb-like band of elongate setae . . . . *Seguyia* Kelsey

– Wing vein M_{3+4} reaching, or terminating just prior to, posterior wing margin; female terminalia with sternite 8 without distinct comb-like band of elongate setae. 6

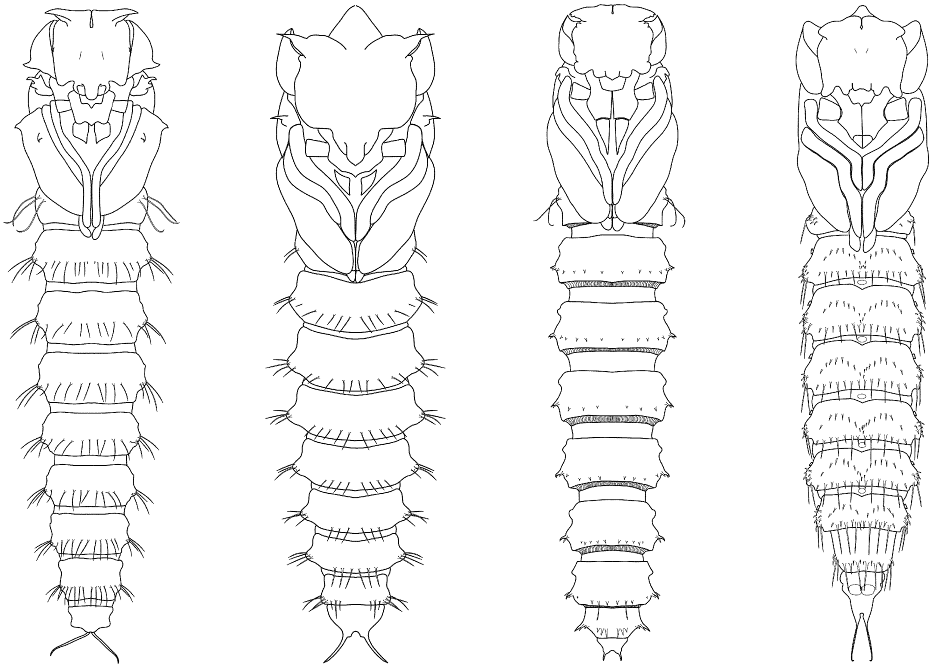
6. Head length generally longer than height (sometimes subequal); body elongate; abdomen elongate and cylindrical . . . . *Prepseudatrichia* Kelsey

– Head length generally shorter than height; body relatively short; abdomen wide . . . . *Scenopinus* Latreille

Synopsis of the fauna

Kelsey (1980) recorded 60 species in five genera for the Afrotropical Region, *i.e.*, *Metatrichia*, *Prepseudatrichia*, *Propebrevitrichia*, *Scenopinus* and *Seguyia*. Two genera of Proratinae have also been recently added to the fauna and the total number of species known from the region is 68. Identification keys to the world genera were provided by Kelsey (1969) and more recently by Winterton & Gharali (2011). Genera not treated here, but found in neighbouring parts of the Palaearctic Region include: *Iranotrichia*, *Kelseyana* and *Stenomphrale*. *Scenopinus* is by far the dominant genus in the region, accounting for over half the known species. The next most species-rich genus is the endemic *Propebrevitrichia*, from southern Africa, followed by *Metatrichia*, *Seguyia* and *Prepseudatrichia*, each with three species.

20 *Scenopinus*



21 *Brevitrichia* 22 *Metatrichia* 23 *Pseudatrichia* 24 *Scenopinus*

Figs 50.20–24. Larvae and pupae of Scenopinidae: (20) larvae of *Scenopinus* sp., dorsal view; (21) pupa of *Brevitrichia* sp., ventral view; (22) same, *Metatrichia* sp.; (23) same, *Pseudatrichia* sp.; (24) same, *Scenopinus fenestralis* L. Fig. 20 (photograph © C. Eiseman), Figs 21–24 (courtesy M. Hauser).

***Alloxytropus* Bezzi** (Proratinae)**.** A genus of five species distributed mainly throughout the Palaearctic Region, although *A. anomalus* Bezzi, 1925 is a commonly encountered species in Egypt and Israel, extending into Sudan, Oman and the United Arab Emirates (Ebejer 2009; Winterton & Kerr 2006;). *Alloxytropus* can be distinguished from *Cyrtosathe*, based on the shape of the male and female terminalia, wing venation characters and the shape of the abdominal tergite 2 setal patch. The distinction between *Alloxytropus* and *Prorates* is unclear and these two genera have been considered synonymous by some authors. Winterton & Ware (2015) demonstrated that *Prorates* was likely paraphyletic relative to both *Acaenotus* Nagtomi & Yanagida and *Alloxytropus* and the status of these genera requires further clarification. The biology and immature stages remain unknown.

***Cyrtosathe* Winterton & Metz** (Proratinae)**.** This endemic, monotypic proratine genus represents the only non-scenopinine genus in the Afrotropics. The single species, *C. kirkspriggsi* Winterton & Metz, 2005 (Figs 3, 14–16), was collected using Malaise and pitfall traps at two localities in south-western Namibia (Winterton & Metz 2005), in the Succulent-karoo biome, *ca* 75 km from the coast. Exhibiting an intermediate set of characteristics that precluded ready placement into any subfamily when originally described; it was initially left as *incertae sedis* in the family (Winterton & Metz 2005). Winterton & Ware (2015) subsequently found that *Cyrtosathe* was the sister to all other Proratinae, supporting the hypothesis of an Afrotropical origin of the subfamily. *Cyrtosathe* can be distinguished from other Afrotropical scenopinid genera by the wing (Fig. 3) having three veins originating posteriorly on the discal medial cell (*dm*) (*i.e.*, veins M_1, M_2 and M_4), the male terminalia (Figs 14, 15) are not rotated, with the phallus and gonocoxal apodemes greatly elongate (much longer than the genitalic capsule) and the phallus being folded dorsally onto itself, so the ejaculatory apodeme projects posteriorly. No undescribed species are currently known. The biology and immature stages remain unknown.

***Metatrichia* Coquillett** (Scenopininae: Metatrichini)**.** A genus of 17 described species occurring in all zoogeographical regions, except Antarctica, none of which occur in more than one region. The Palaearctic Region, with six species, has the greatest concentration of species for this genus (Krivosheina & Krivosheina 1999). In the Afrotropical Region, there are three described species: *M. lophyrosoma* (Speiser, 1920), from southern Africa; *M. nigeriana* Kelsey, 1984, from Nigeria; and *M. stevensoni* (Bezzi, 1925), from Namibia through Kenya. The identification key of Kelsey (1971) covers the species south of the Equator and the diagnosis in Kelsey (1984) serves to separate the Nigerian species from the other two. Species of this genus can be distinguished from other window fly genera (except for the Palaearctic genus *Pseudomphrale*, which may be synonymous), by the wing cell r_5 being closed and petiolate (*i.e.*, veins M_1 and R_5 merge before the wing margin), the relatively large and robust body size, the abdomen being broadly flattened and blunt apically in both sexes, the body frequently being clothed in white scale-like setae, the male hypandrium being short and formed as paired spatulate sclerites, the ejaculatory apodeme being broadly spatulate and the female terminalia lacking acanthophorite spines (Winterton & Woodley 2009). *Metatrichia* is closely related to *Iranotrichia*, *Kelseyana* and *Pseudomphrale* (Winterton & Gharali 2011; Winterton & Ware 2015). The biology and immature stages remain unknown.

***Prepseudatrichia* Kelsey** (Scenopininae: Scenopinini)**.** An Old World genus of four described species occurring in the Afrotropical, Oriental and Palaearctic Regions. Three species occur in the Afrotropics: *P. mateui* Kelsey, 1969, described from Algeria, Chad, Mali and Nigeria (Kelsey 1981*b*, 1984); *P. stenogaster* (Séguy, 1931), from Mozambique; and *P. violacea* Kelsey, 1969, from Chad. Winterton (2011) provides an identification key, modified from Kelsey (1969), noting that the females are unknown for some species and the males for others. Figures and descriptions are found in Kelsey (1969), Krivosheina (1980) and Winterton (2011). *Prepseudatrichia* is the sister genus to *Scenopinus* (Winterton & Ware 2015). *Prepseudatrichia* can be differentiated from all other scenopinid genera based on the elongate glossy black body with an elongate and cylindrical abdomen, the head being longer than or subequal to the height, the wing vein M_1 being separate from vein R_5 to the wing margin (cell r_5 open) (Fig. 4), the male terminalia having a well-developed hypandrium (paired sclerites subtriangular in shape and weakly sclerotised), the trifid distiphallus and the phallus extending anteriorly into the body cavity with well-developed lateral lobes and the female abdomen lacking acanthophorite spines. Species of this genus are specialist predators on wood-boring beetles, with adults reared from beetle galleries in *Acacia* (Fabaceae), *Ferula* (Apiaceae) and *Sterculia* (Malvaceae) trees (Kelsey 1969, 1971; Krivosheina 1980).

***Propebrevitrichia* Kelsey** (Scenopininae: Metatrichini)**.** An endemic genus of 15 described species. Kelsey (1969, 1971) described the first three species from South Africa, followed by a comprehensive study of the genus (Kelsey 1976) providing descriptions and illustrations for 11 new species and identification keys to all species, eight being from South Africa and six from Namibia. Winterton (2005) added a species from Botswana, noting where it keys out in the key of Kelsey (1976), and how to differentiate it from that species. *Propebrevitrichia* is restricted to the southern-most parts of the Afrotropics and is a basal representative of Metatrichini, a tribe dominated by genera typically endemic to Southern Hemisphere continents (Kelsey 1973*b*; Winterton & Ware 2015). Species of this genus can be recognised by being relatively delicate flies, with a narrow tapered abdomen (females) with the head profile being higher than long (Figs 5, 6), wing vein M_1 being fused with vein R_5 before the wing margin to form a closed and petiolate cell r_5 (Fig. 2), female sternite 8 being only slightly longer than tergite 8, and sternite 8 being rounded apically and not lobed and with distinctive acanthophorite spines present (Fig. 13). Most species of the genus have been collected in close association with sandy areas, including dunes, sandy plains and riverbanks and numerous species have been reared from larvae (Kelsey 1969, 1973*a*, 1976, 1984). Adult males of *P. canuta* Kelsey, 1976, and an undescribed species, have been observed to swarm at the summits of coastal vegetated dunes (Kelsey 1976; unpubl. data). There are several new species of this genus known from South Africa.

***Scenopinus* Latreille** (Scenopininae: Scenopinini)**.** A virtually cosmopolitan genus of 195 described species, occurring in all zoogeographical regions, except Antarctica. The genus is divided into four species-groups, three of which occur in the Afrotropics, collectively with 41 described species. A major problem with the various identification keys to species currently available is that species exhibit significant sexual dimorphism and separate keys are provided for males and females. This is problematic when most species are only known from a single sex. There are no comprehensive keys to Afrotropical species of *Scenopinus*, even when considering species-groups, so multiple published works invariably need to be consulted. Identification must begin by consulting Kelsey (1969, 1971), supplemented by reference to the later works of Kelsey. Species of this genus can be distinguished from other scenopinid genera by the relatively short body length, the head length being shorter than the height and wing vein M_1 being separate from vein R_5 to the wing margin (cell r_5 open), M_4 reaching the wing margin, the distiphallus is trifid and lateral aedeagal lobes typically enlarged. Kelsey (1969) defined the four species-groups based principally on differences in the antennal flagellum and body size and the shape and size of the hypandrium (misinterpreted as additional lobes of the epandrium). The status of these species-groups is questionable, as three of the four are not monophyletic, and characteristics defining each being highly variable and subjective (Winterton & Ware 2015). There is significant overlap in the scenopinid fauna of the continental Afrotropics and Madagascar, with many species being found in both. There are also many undescribed species of this genus in collections originating from Madagascar. For the *S. albicinctus*-group, *sensu* Kelsey (1969), new species are described in Kelsey (1973*a*, 1976, 1984). In addition, Kelsey (1971) constructed a *de novo* identification key to the species occurring south of the Equator, which potentially eliminates some Afrotropical species from consideration. Kelsey (1984) treated the three species from Nigeria, one of which, *S. ikoyianus* Kelsey, 1984, was known only from the male. The species of this group are widespread in the Afrotropics. Three species are known from Madagascar, while one is from nearby Seychelles. In the continental Afrotropics, species are known mostly from eastern Africa, from Ethiopia south to South Africa, but with a few species occurring as far west as Cameroon, Mali and Nigeria. The biology of this group is diverse, with the following examples of larval biology: *S. bouvieri* (Séguy, 1920) was reared from the nest of a pigeon (Kelsey 1969); *S. inquelinus* (Séguy, 1931) was reared from the fungus *Polyporus* (Polyporaceae), presumably a predator in that system (Kelsey 1969); *S. zambianus* Kelsey, 1973 was reared from larvae among leaf debris in a sandy wash in *Brachystegia* woodlands (Kelsey 1973*a*); several species are associated with sand dune systems, being reared from larvae (Kelsey 1976). For extralimital species, others have been reared from nests of rodents and as predators of store-product pests (Kelsey 1969). For the *S. brevicornis*-group, the key of Kelsey (1969) covers most of the species in the region, although Kelsey (1971) treated the species south of the Equator, including one new species, *S. stuckenbergi* Kelsey, 1971. The key of Kelsey (1984) covers only the two species described therein, namely: *S. cornesi* Kelsey, 1984 and *S. kontagoranus* Kelsey, 1984, from Nigeria. Three species occur in Madagascar, together with one from Seychelles. Two species occur in Nigeria, two in South Africa and one in Eritrea. For the *S. fenestralis*-group, the keys in Kelsey (1971, 1976) cover the two cosmopolitan species, *S. fenestralis* and *S. glabrifrons* and a third endemic species, *S. namibensis* Kelsey, 1976. *Scenopinus namibensis* is known to form male swarms in open shady areas (Kelsey 1976).

***Seguyia* Kelsey** (Scenopininae: Scenopinini)**.** A genus of six described species restricted to parts of the Old World. One species is Palaearctic (Egypt), two occur in South-east Asia (India and Thailand) and the remaining three are Afrotropical. *Seguyia deemingi* Kelsey, 1984, is known from northern Nigeria, while *S. galactica* (Séguy, 1938) and *S. turneri* Kelsey, 1969 occur in Kenya and South Africa, respectively. *Seguyia* is the sister genus to *Scenopinus* + *Prepseudatrichia*. *Seguyia* can be differentiated from other scenopinid genera by wing vein M_1 being separate from vein R_5 to the wing margin (cell r_5 open), vein M_4 is short or absent beyond the discal cell and the female sternite 8 having a comb-like band of elongate setae. The identification key of Kelsey (1971) (as *Seguyella* Kelsey) is the most recent, but only includes the two species known at that time, descriptions and illustrations of which are found in Kelsey (1969). Although Kelsey (1984) published a key that includes the Nigerian species of the genus, this does not include the other two species, so the works need to be used in combination. The three Afrotropical species are known from diverse habitat types, ranging from savanna (*S. deemingi*), montane (*S. galactica*) and coastal Mediterranean (*S. turneri*) biomes. The biology and immature stages remain unknown.

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EMPIDIDAE 51

(Empidid Dance Flies or Balloon Flies)

Bradley J. Sinclair and Christophe Daugeron

Fig. 51.1. Mating pair of *Empis glandis* Smith, with nuptial gift (South Africa) (photograph C. d'Haese).

Diagnosis

Adults small- to medium-sized flies (body length: 1–12 mm); darkish to light in colour, rarely metallic green (Figs 1–10).

Head variously shaped, never large and usually narrower than thorax; compound eye generally large, male holoptic, or dichoptic and female dichoptic (Figs 26, 28–31, 34–37); antenna with stylus setulose; pedicel without thumb-like conus; postpedicel variously shaped; stylus short to elongate, usually comprised of 2 articles, usually arising apically, or subdorsally, from postpedicel, occasionally appearing arista-like; apex of stylus usually bearing sensillum; mouthparts with proboscis short and fleshy, to extremely elongate and slender (Figs 34, 35); labrum usually armed at apex with paired epipharyngeal blades (Fig. 37); palpus 1-segmented; labellum bearing

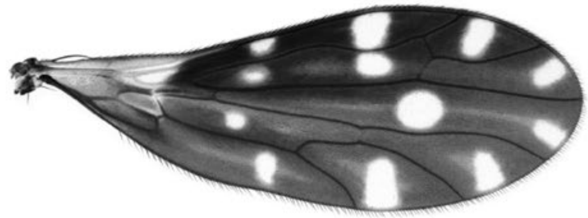
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1221–1235.

pseudotracheae (absent in Afrotropical Empidini); chaetotaxy of head limited, pair of ocellar setae usually present, vertical setae present, or absent.

Thorax usually rectangular in dorsal outline, sometimes extended anteriorly; disk of thorax virtually flat, to greatly arched and dome-like; chaetotaxy of thorax including notopleural, dorsocentral and scutellar setae, with various other dorsal setae present; laterotergite with, or without, setae (Fig. 33). Wing of varied shape and size, sometimes broadened, rarely reduced, or absent; alula and anal lobe often lacking; colour, hyaline to infuscate and maculate; venation relatively complete, rarely markedly reduced, sometimes sexually dimorphic; cell *cua* closed, very rarely absent, never reaching wing margin; outer cell *cua* shape truncate, rounded, or recurved (Figs 11–23). Legs varied in length, thickness and armature; sometimes sexually dimorphic, with rows of pinnate setae in females and clasping, or glandular, structures in males; often 1 pair with raptorial modifications; empodium usually setiform, pulvilliform in some aquatic groups.

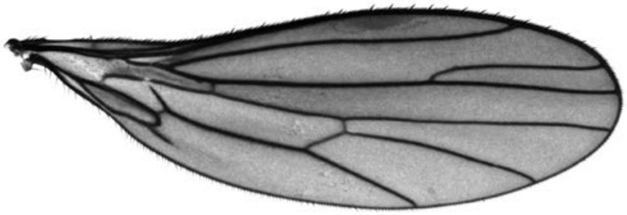
Abdomen subcylindrical, usually elongate, sometimes short; some tergites with abdominal plaques laterally; some Empidini with eversible pleural sacs in females and occasionally in males (e.g., *E. glandis* Smith, 1969); male terminalia very rarely rotated, usually symmetrical; ejaculatory apodeme usually lever-like, articulated ventrally against base of phallus (Cumming *et al*. 1995; Sinclair 2000: 67); female terminalia without acanthophorites; 1 spermatheca present internally, usually sclerotised and pigmented.

Figs 51.2–10. Photographs of living Afrotropical Empididae (all South African): (2, 3) *Afrodromia* spp.; (4) *Clinocera* sp.; (5) *Atrichopleura* sp.; (6) male of *Empis glandis* Smith "stealing" nectar from flowers of *Lobelia* (?) sp.; (7) *Hilarempis* sp.; (8) *Afrodromia* sp.; (9) *Empis* sp.; (10) *Kowarzia capicola* (Smith). Figs 2–5, 7–10 (photographs © S.A. Marshall), Fig. 6 (photograph C. Daugeron).

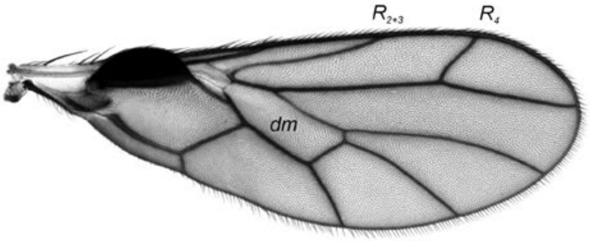


11 *Dolichocephala*

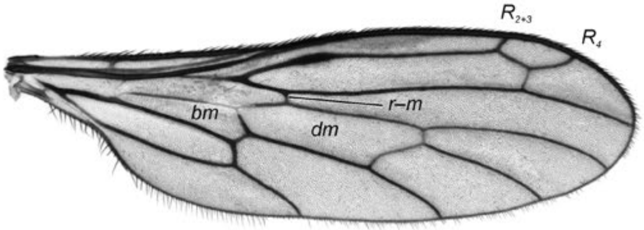
12 *Clinocera*



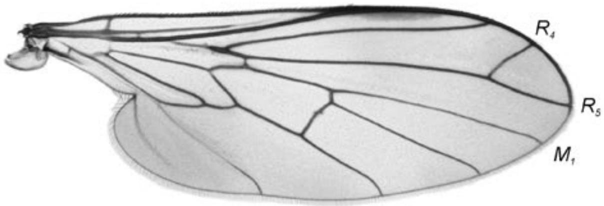
13 *Kowarzia*



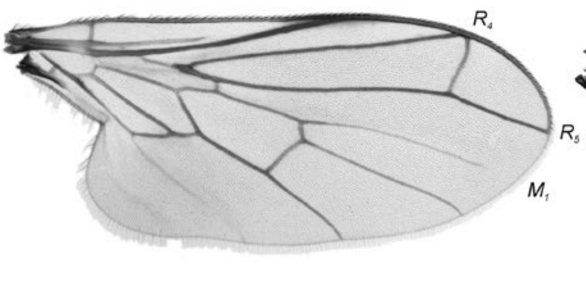
14 *Drymodromia*



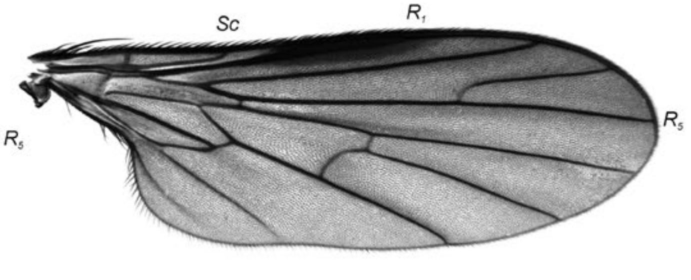
15 *Afrodromia*



16 *Empis verae*



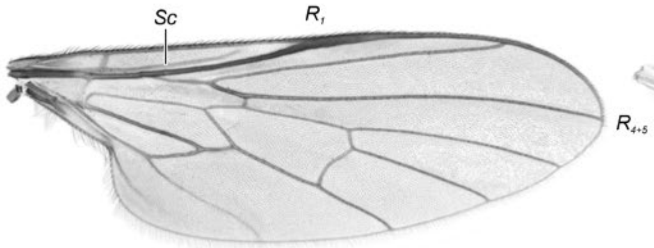
17 *Empis vetula*



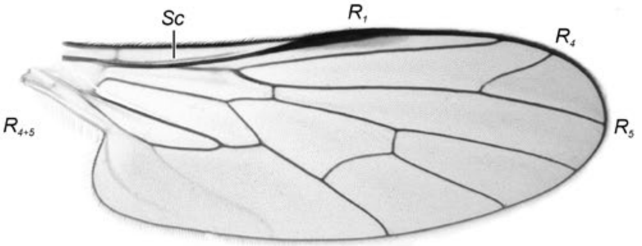
18 *Hilara*

Figs 51.11–18. Wings of Empididae (dorsal views): (11) *Dolichocephala duodecempunctata* Smith; (12) *Clinocera* sp.; (13) *Kowarzia capicola* (Smith); (14) *Drymodromia similis* Smith; (15) *Afrodromia concolor* Smith; (16) *Empis verae* Smith; (17) *E. vetula* Smith; (18) *Hilara* sp.

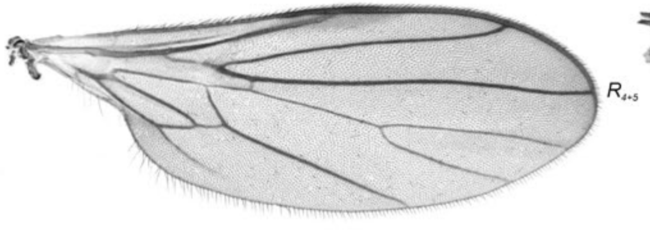
Abbreviations: *bm* – basal medial cell; *dm* – discal medial cell; M_1 – first branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcostal vein.



19 *Atrichopleura*

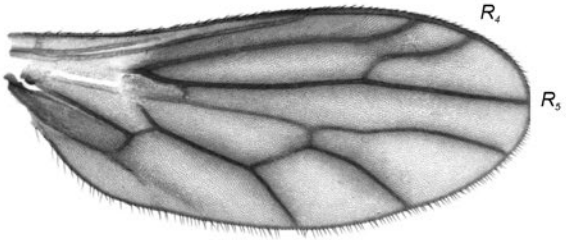


20 *Hilarempis*

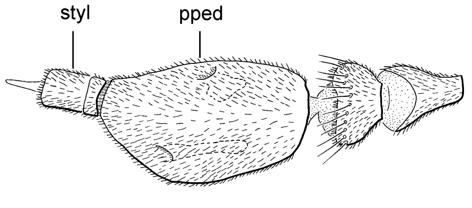


21 *Edenophorus*

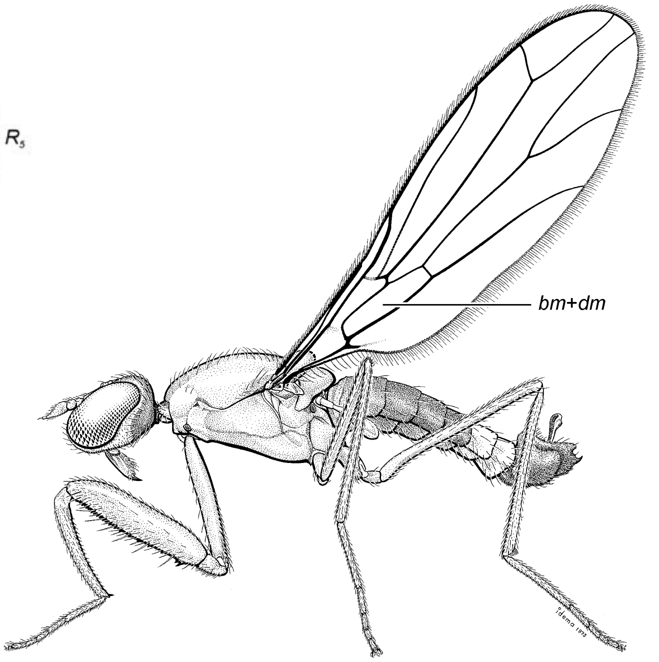
22 *Hormopeza*



23 Undescribed Genus



24 *Hormopeza*



25 *Hemerodromia*

Figs 51.19–25. Wings, antenna and habitus of Empididae: (19) wing of, *Atrichopleura* sp. dorsal view; (20) same, *Hilarempis breviseta* Smith; (21) same, *Edenophorus hiemalis* Sinclair; (22) same, *Hormopeza senator* Melander (non-Afrotropical); (23) same, Undescribed genus; (24) antenna of *H. senator*, lateral view; (25) habitus of *Hemerodromia oratoria* (Fallén), lateral view (non-Afrotropical). Fig. 24 (after Sinclair & Cumming 2006, fig. 8), Fig. 25 (Steyskal & Knutson 1981, fig. 2).

Abbreviations: *bm+dm* – basal medial cell + discal medial cell; pped – postpedicel; R_1 – anterior branch of radius; R_4 – upper branch of third branch of radius; R_{4+5} – third branch of radius; R_5 – lower branch of third branch of radius; *Sc* – subcostal vein; styl – stylus.

Empididae can generally be differentiated from similar Brachystomatidae (see Chapter 53), Hybotidae (see Chapter 52) and Dolichopodidae (*sensu lato*) (see Chapter 56), in having a setulose scape, the radial wing vein often branched, dichoptic females, the laterotergite setulose, or bare, the female abdomen telescoping and lacking acanthophorites and the male terminalia rarely asymmetrical and usually unrotated.

Biology and immature stages

The Empididae represent a large group of primarily predaceous flies. Two subfamilies, Clinocerinae and Hemerodromiinae, are considered to be entirely predaceous (Chvála 1976; Daugeron 1997: 168; Sinclair 1995a), with clinocerines either capturing prey on the ground or water surface, but also capable of catching prey in flight (Downes & Smith 1969). The flower-visiting habit is considered synapomorphic for the subfamily Empidinae and predation is only conserved during the mating period in most groups (Chvála 1976; Daugeron 1997: 171). Although flower-visiting behaviour is common in the tribe Empidini, it is less frequent in the tribe Hilarini (Plant 2004). The prey of *Hilara* Meigen often consists of dead insects scavenged from the water surface, where adults form large swarms or aggregations (Plant 2004).

Larvae of Empididae are predaceous on arthropods and are found in moist soil and aquatic habitats. Our knowledge of the immature stages of the Empididae is largely based on aquatic genera of Hemerodromiinae and Clinocerinae (Figs 41, 43) and none have been described from the Afrotropical Region. Truly aquatic larvae are apneustic (incl. *Roederiodes* Coquillett; see Sinclair & Harkrider 2004) and usually bear distinct abdominal prolegs (Fig. 41). Larvae of the Empidinae are amphipneustic and lack prolegs (Fig. 42) (Dyte 1967). As in all other empidoid larvae, the mandible comprises at least four components, with additional components present in Hemerodromiinae and Clinocerinae (Dyte 1967; Sinclair 1992). The pupae of Hemerodromiinae are unique among empidoids in possessing elongate filamentous spiracular gills on the prothorax and the first seven abdominal segments (Fig. 44). Empididae are not known to spin a cocoon prior to pupation (Dyte 1967).

Dance flies (Empidinae) are well known for their mating behaviour, including complex swarms with nuptial gifts transferred by males to females (Chvála 1976; Cumming 1994) (*e.g.*, Fig. 1). Although in such cases mate choice is the prerogative of females and hence conforms to current models of mate selection in insects (Thornhill & Alcock 1983: 73), sex-role-reversed mate selection is also common and appears to correlate with the presence of secondary sexual characteristics in females (Cumming 1994; Daugeron *et al*. 2009). Depending on the species, nuptial gifts include prey, various types of inedible objects, or secreted balloons (Chvála 1976; Sinclair *et al*. 2013). Among the tribe Hilarini, nuptial gifts are often wrapped in silk produced by specialised cells on the male fore tarsus (Sutherland *et al*. 2007; Young & Merritt 2003).

The feeding and mating behaviours of *Empis glandis* were recently observed in South Africa (C. Daugeron, pers. obs.). Mating behaviour is typical of the Empidinae, with swarming and prey presentation (Fig. 1). In this species females generally rest on branches, awaiting male swarm formation. As soon as males commence swarming, females take flight and enter the swarm to mate and receive prey. Both sexes were also observed feeding on nectar, but in this case flies collect nectar by probing through the petals at the base of the flower (Fig. 6). This is the first known example among species of empidines to exhibit a "cheating" behaviour, where nectar is obtained without entering the flower and, therefore, contact with pollen-carrying structures is avoided.

Economic significance

No species of economic importance are currently known, although predation on certain families of biting flies has been observed (Downes 1970; Sinclair & Harkrider 2004; Werner & Pont 2003). The occurrence of immature stages of Clinocerinae and Hemerodromiinae (or simply identified as Empididae), in aquatic macroinvertebrate surveys contribute to assessments of water quality (*e.g*., Hilsenhoff 1988; Jones *et al*. 1981; Kazanci & Dügel 2000; Maue & Springer 2008). Empididae are often among the most important pollinators (Larson *et al*. 2001) in temperate areas (Dzhambazov & Teneva 2002; Lindgaard Hansen & Molau 1994; Patt *et al*. 1989) and Arctic regions (Kevan 1972) and alpine environments (Lefebvre *et al*. 2014).

Classification

The Empidoidea are a monophyletic lineage that is sister-group to the Cyclorrhapha (Collins & Wiegmann 2002; Cumming *et al*. 1995; Sinclair & Cumming 2006). Chvála (1983) first divided the Empidoidea into five families, although recognition of the precise limits of his included families remained debated (Cumming 1989; Cumming *et al*. 1995; Woodley 1989: 1389). On the basis of a morphological cladistic analysis, Sinclair & Cumming (2006) also justified division of the Empidoidea into families, namely the Atelestidae, Brachystomatidae, Dolichopodidae (including Microphorinae and Parathalassiinae), Empididae and Hybotidae. Molecular analyses recover four families, with Empididae more broadly defined to include the brachystomatids (Moulton & Wiegmann 2007). Despite these opposing conclusions, the more restrictive concept of the Empididae is recognised in this chapter, defined on a suite of characters (wing vein R_{4+5} generally branched; prosternum forming precoxal bridge; laterotergite usually setulose; and female terminalia normally with simple cerci). *Oreogeton* Schiner and *Homalocnemis* Philippi were considered *incertae sedis* within the Empidoidea by Sinclair & Cumming (2006), but are now recognised as Oreogetonidae and Homalocnemidae, respectively (Pape *et al*. 2011).

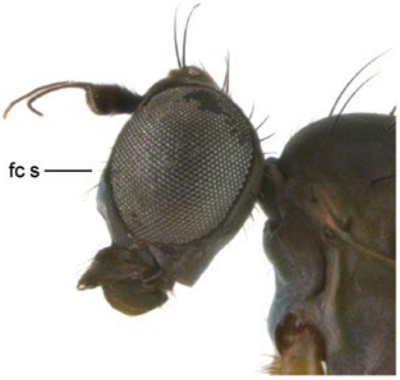
The Empididae comprise 73 genera worldwide, classified in four subfamilies, four tribes and three unplaced genera or genus-groups (Sinclair 2016; Sinclair & Cumming 2006). Seventeen genera occur in the Afrotropical Region, with six genera assigned to the Empidinae (incl. Empidini and Hilarini), three assigned to Hemerodromiinae, six assigned to Clinocerinae, one assigned to Ragadinae and one undescribed genus that is currently unassigned. The following account provides a brief overview of each subfamily and tribe that occurs in the region.

26 *Afroclinocera*

27 *Afroclinocera*

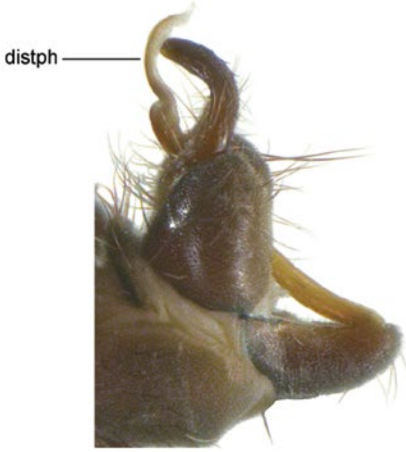
28 *Roederiodes*

29 *Dolichocephala*



30 *Kowarzia*

31 *Wiedemannia*

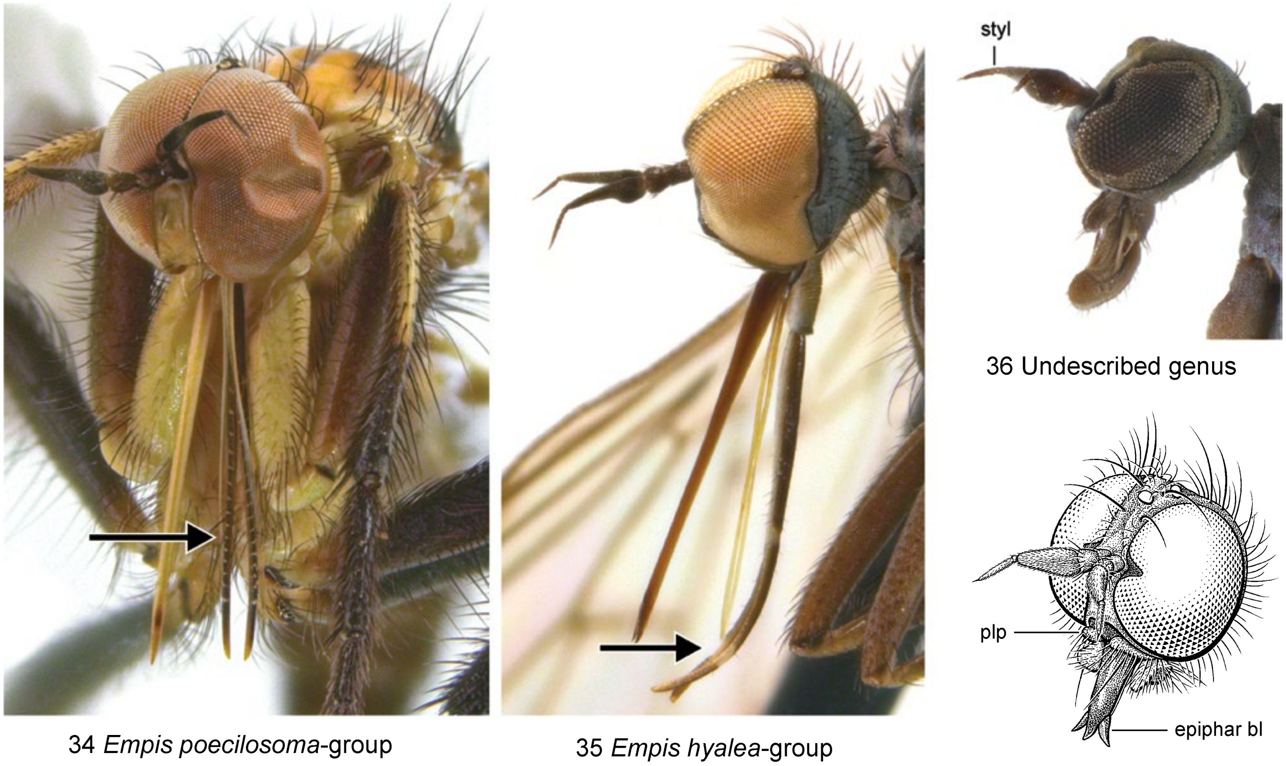


32 *Kowarzia*

33 *Empis poecilosoma*-group

Figs 51.26–33. Heads, hind leg, male terminalia and head and thorax of Empididae (Clinocerinae and Empidini) (all lateral views): (26) head of *Afroclinocera obesa* Sinclair; (27) same, hind leg; (28) head of *Roederiodes bifidus* Sinclair; (29) same, *Dolichocephala duodecempunctata* Smith; (30) same, *Kowarzia capicola* (Smith); (31) same, *Wiedemannia edendalensis* Smith; (32) male terminalia of *K. capicola*; (33) head and thorax of *Empis poecilosoma*-group (arrow indicating postsutural supra-alar macula).

Abbreviations: distph – distiphallus; fc s – facial setae; lbr – labrum; ltg – laterotergite.

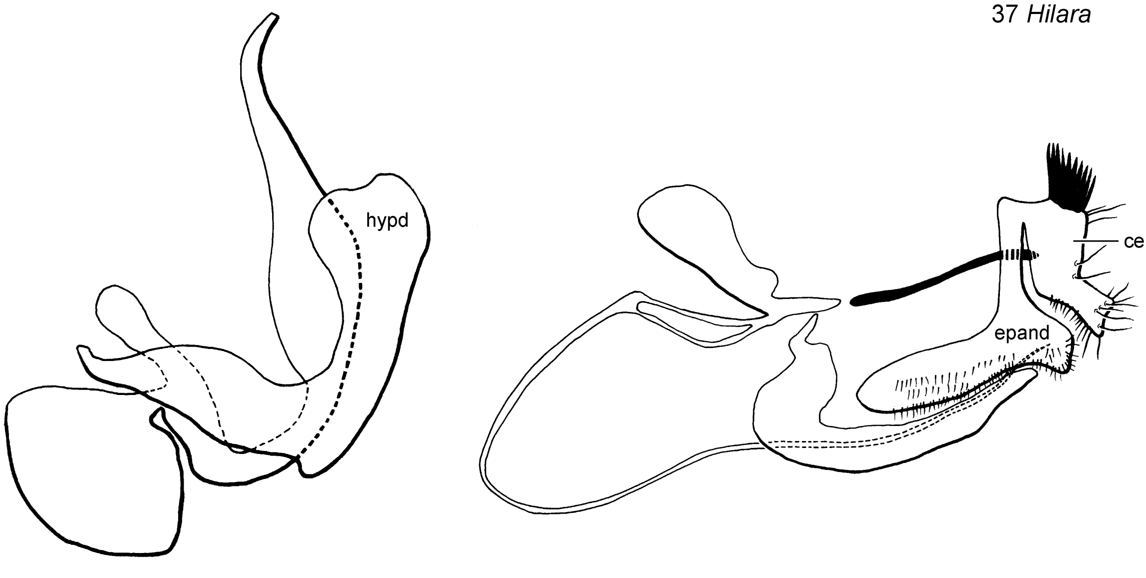


34 *Empis poecilosoma*-group

35 *Empis hyalea*-group

36 Undescribed genus

37 *Hilara*



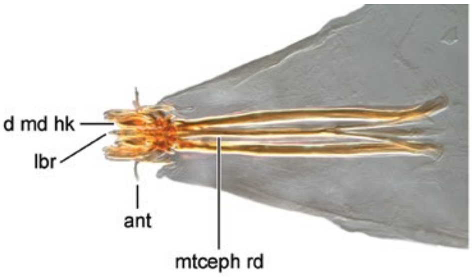
38 *Empis bivittata*-group ♂

39 *Empis namwamba*-group ♂

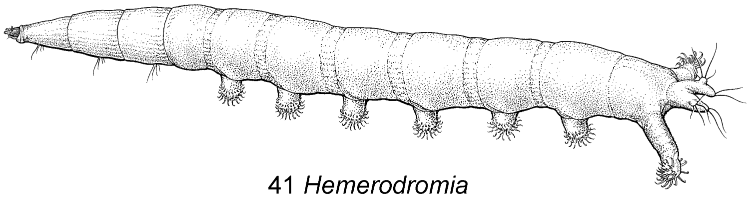
Figs 51.34–39. Heads and male terminalia of Empididae: (34) head of *Empis poecilosoma*-group, anterior view (arrow indicates annulations); (35) same, *Empis hyalea*-group, lateral view (arrow indicates desclerotised zone on labellum) (non-Afrotropical); (36) head of Undescribed genus, lateral view; (37) same, *Hilara femorata* Loew, oblique view (non-Afrotropical); (38) male terminalia of *Empis bivittata*-group, lateral view; (39) same, *Empis namwamba*-group. Fig. 37 (Steyskal & Knutson 1981, fig. 40), Figs 38, 39 (after Daugeron & Grootaert 2003, figs 2A, 4A).

Abbreviations: cerc – cercus; epand – epandrium; epiphar bl – epipharyngeal blade; hypd – hypandrium; plp – palpus; styl – stylus.

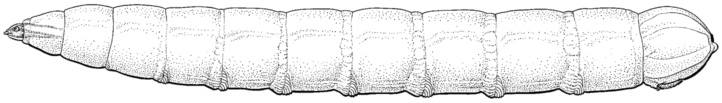
Clinocerinae are a well-established subfamily and one of the major groups of predaceous Diptera directly associated with running water, or lotic habitats. The subfamily is most common in the Nearctic and Palaearctic Regions and significantly less so at lower latitudes and south of the Equator (Sinclair 2008: 1). In the Afrotropical Region the Clinocerinae are recorded from temperate areas, with adults frequenting rocky streams. They are generally most efficiently collected by hand-collecting over suitable habitats. The main characters used to recognise the subfamily are the presence of stout costal setae, the sucker-like labellum and pulvilliform empodium (Sinclair 1995*a*). The included genera are well defined



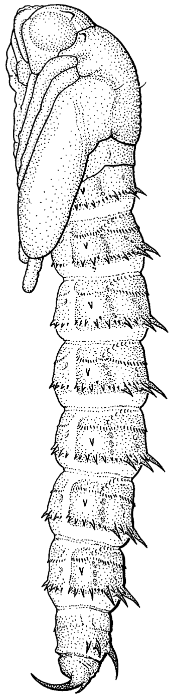
40 *Hemerodromia*



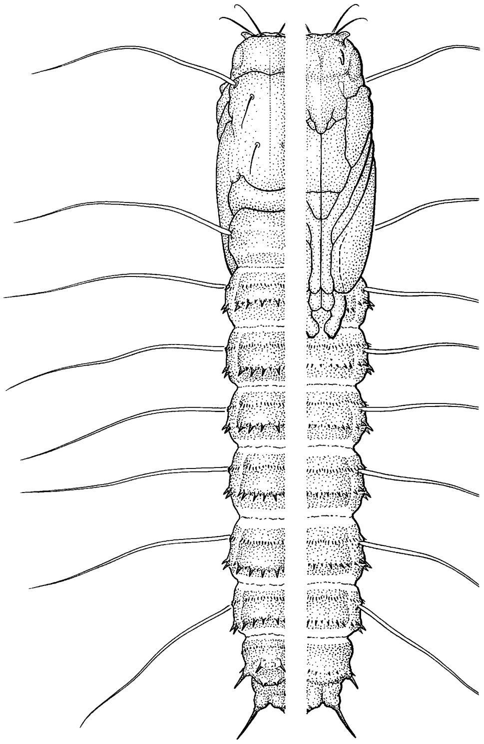
41 *Hemerodromia*



42 Empidini



43 *Clinocera*



44 *Hemerodromia*

Figs 51.40–44. Immature stages of Empididae: (40) larval head capsule of *Hemerodromia* sp., dorsal view (non-Afrotropical); (41) larva of *Hemerodromia* sp., oblique view (non-Afrotropical); (42) larva of Empidini, lateral view (non-Afrotropical); (43) pupa of *Clinocera stagnalis* (Haliday), lateral view (non-Afrotropical); (44) dorsal (left) and ventral (right) views of pupa of Hemerodromiinae (non-Afrotropical). Figs 41–44 (Steyskal & Knutson 1981, figs 56, 57, 61, 62).

Abbreviations: ant – antenna; d md hk – dorsal mandibular hook; lbr – labrum; mtceph rd – metacephalic rod.

and generic phylogenetic relationships have been analysed (Sinclair 1995*a*).

Hemerodromiinae are one of the most distinctive subfamilies, characterised by raptorial fore legs, fore and mid coxae well-separated and fore femur bearing at least a single ventral row of stout setae (Plant 2011*a*; Sinclair & Cumming 2006). The subfamily is found virtually worldwide and primarily occurs in damp, shaded temperate and tropical forests. The phylogenetic relationships of the Hemerodromiinae have been analysed and the subfamily is divided into two tribes, with two genera unassigned to tribe (see below under "Synopsis of the fauna") (Plant 2011*a*). The tribe Chelipodini are characterised by presence of setae on the laterotergite, unbranched wing vein R_{4+5} and complex male cerci. The tribe Hemerodromiini are characterised by elongation of the thorax, loss of strong dorsocentral setae and absence of wing cell *cua*, with at most only vein *CuA* remaining (Plant 2011*a*).

The Empidinae are defined by a suite of characters, including the strongly upcurved palpus, wing generally broad, non-raptorial fore legs and presence of a precoxal bridge. The subfamily is divided into two tribes, the Empidini and Hilarini. The Empidini primarily occur in the Holarctic Realm, with only certain groups extending into lower latitudes and south of the Equator. This lineage is poorly defined and undoubtedly paraphyletic, distinguished from the Hilarini by a setulose laterotergite, enlarged male cerci and the costal wing vein ending, or weakened, beyond the radial vein (Sinclair & Cumming 2006). The more widely distributed Hilarini is clearly defined by a bare laterotergite, costa circumambient, wing vein R_1 thickened at the costal vein and male tarsomere 1 often enlarged (Sinclair & Cumming 2006).

The Ragadinae was recently elevated to subfamilial level, characterised by the recurved labrum and apical epipharyngeal comb (Sinclair 2016). Although this lineage is found virtually worldwide, only a single species is known from the Afrotropical Region. The included genera are well defined and the phylogenetic relationships of the genus-group have been analysed (Sinclair 1999*c*).

Identification

Knowledge of Afrotropical Empididae is based primarily on Garrett Jones (1940) and Smith (1969), with the Clinocerinae updated by Sinclair (1999*b*). Afrotropical genera can be partially identified using the identification keys in Smith (1969) and Sinclair (1999*b*) for the Clinocerinae.

Empididae are best collected into alcohol, critical-point-dried and then glued to pins (see Chapter 2).

Key to genera of Afrotropical Empididae

1\. Eye with dense ommatrichia (*e.g.*, Figs 29, 31); labellum usually sucker-like (*e.g.*, Figs 26, 29–31), or gena and proboscis greatly enlarged and lengthened (*e.g.*, Fig. 28) (CLINOCERINAE) 2

– Eye bare, lacking ommatrichia (*e.g.*, Figs 34, 35); labellum rarely sucker-like; gena not enlarged and proboscis variable in structure 9

2\. Wing reduced to slender filament or narrow blade 3

– Wing present and well-developed. 4

3\. Neck arising high on occiput; head slender and tapered towards narrow mouthparts (Fig. 29). . . . . *Dolichocephala* Macquart [in part]

– Neck arising near centre of occiput; head broad with broad mouthparts (Fig. 31) . . . . *Wiedemannia* Zetterstedt [in part]

4\. Labrum long, equal to height of head, base swollen (Fig. 26); thorax with acrostichal setae long, ¼ length of dorsocentral setae; legs with long setae, 1–2 × width of leg segment; hind femur of male inflated (Fig. 27) . . . .*Afroclinocera* Sinclair

– Labrum usually short, *ca* ¼ height of head (*e.g.*, Figs 29–31); if labrum long, base not swollen (*e.g.*, Fig. 28); thorax with acrostichal setae greatly reduced or absent; legs lacking long and stout setae; hind femur of male not inflated 5

5\. Proboscis (including labrum) as long as head; labrum long and slender; labellum narrow not sucker-like (Fig. 28) . . . . *Roederiodes* Coquillett

– Proboscis less than ½ height of head; labrum subtriangular; labellum sucker-like (*e.g.*, Figs 29–31) 6

6\. Neck arising high on occiput, from near vertex of head (Fig. 29); wing usually with white irrorations (Fig. 11) . . . . *Dolichocephala* Macquart [in part]

– Neck arising near centre of occiput, or level with centre of eye (*e.g.*, Figs 30, 31); wing lacking white maculae or irrorations; if present (*e.g.*, Figs 4, 12) head rounded and neck inserted opposite centre of eye 7

7\. Head with lower margin of face lacking notch, or deep concave notch above mouthparts; male terminalia with phallus with or without apical filament; wing with or without several white maculae (Fig. 12). . . . . *Clinocera* Meigen

– Head with lower margin of face with notch or deep cleft (*e.g.*, Fig. 31); male terminalia with phallus bearing articulated apical filament, or distiphallus (*e.g.*, Fig. 32); wing without maculae (*e.g.*, Fig. 13) 8

8. Face with setulae along inner margin of eye (Fig. 30) . . . . *Kowarzia* Mik

– Face without setulae along inner margin of eye (Fig. 31). . . . . *Wiedemannia* Zetterstedt [in part]

9. Fore coxa at least ⅔ length of fore femur; fore femur with 1 or 2 rows of black, peg-like setae ventrally; fore femur width 2–3 × that of fore tibia (*e.g.*, Fig. 25); in doubtful cases wing veins R_{2+3} and R_4 connected by auxiliary crossvein (*e.g.*, Fig. 15) (HEMERODROMIINAE) 10

– Fore coxa less than ½ length of fore femur; fore femur without black, peg-like setae ventrally; fore femur width usually less than 2 × that of fore tibia; wing veins R_{2+3} and R_4 not connected by auxiliary crossvein (*e.g.*, Figs 16–23) 12

10. Wing with discal medial cell (*dm*) fused with cell *bm*; crossvein *bm–m* absent (Fig. 25) . . . . *Hemerodromia* Meigen

– Wing with discal medial cell (*dm*) not fused to cell *bm*; crossvein *bm–m* present (*e.g.*, Figs 14, 15) . . 11

11. Wing with crossvein *r–m* absent, so that upper margin of discal medial cell (*dm*) formed by base of vein R_{4+5}; vein R_4 not joined to vein R_{2+3} by auxiliary crossvein (Fig. 14). . . . . *Drymodromia* Becker

– Wing with crossvein *r–m* present; vein R_4 joined to vein R_{2+3} by auxiliary crossvein (Fig. 15). . . . . *Afrodromia* Smith

12. Thorax with laterotergite with group of dark or pale setae (Fig. 33); wing vein R_{4+5} usually forked, angle greater than 45°; often with vein M_1 and occasionally vein M_2 not reaching wing margin (Figs 16, 17) (EMPIDINAE: EMPIDINI) . . . . *Empis* L. 13

– Thorax with laterotergite bare; wing vein R_{4+5} unforked, or forked at angle less than 45°; veins M_1 and M_2 invariably extending to wing margin (*e.g.*, Figs 18–23) 19

13. Labium bearing annulations, bare (*e.g.*, Fig. 34, arrowed); thorax with proepisternum bare; female spermatheca unsclerotised 14

– Labium lacking annulations (*e.g.*, Fig. 35), with short setae, or apparently bare (only some minute bristly setulae); thorax with proepisternum with at least 1 seta; female spermatheca spherical, well-sclerotised 17

14. Proboscis very long, with labrum at least 3.5–4 × head height; eyes of male at least feebly dichoptic, never holoptic, upper ommatidia not enlarged; female abdomen metallic or at least very shiny . . . . *Empis* (*Disneyempis* Smith)

– Proboscis shorter, labrum less than 3 × head height; eyes of male generally holoptic, with upper ommatidia enlarged (Fig. 34); females abdomen not metallic . . . .(*Empis* (*Coptophlebia*) complex of subgenera) 15

15. Antenna with terminal articles aristiform; male terminalia with cercus fused laterally with epandrial lamella (Fig. 39) . . . . *Empis* (*Coptophlebia*) *namwamba*-group

– Antenna with terminal articles styliform; male terminalia with cercus not fused laterally with epandrial lamella. 16

16. Thorax with scutum with black macula at base of wing in front of posteriormost postsutural supra-alar seta (Fig. 33); male terminalia with hypandrium apically divided into tongue-like projections; male postabdomen unmodified . . . . *Empis* (*Coptophlebia*) *poecilosoma*-group

– Thorax with scutum brownish or blackish, without black macula at base of wing; male terminalia with hypandrium not divided into tongue-like projections; male postabdomen invariably considerably modified. . . . . *Empis* (*Coptophlebia*) *chrysocera*-group

17. Labella with desclerotised zone at mid point (Fig. 35); male terminalia with epandrium unpaired . . . . *Empis* (*Coptophlebia*) *hyalea*-group

– Labella without desclerotised zone; male terminalia with epandrium paired 18

18. Male terminalia with sternite 8 desclerotised medially; hypandrium not lengthened, not bifid apically . . . . *Empis* (*Empis*) *setitarsus*-group

– Male terminalia with sternite 8 normally sclerotised; hypandrium massive, upright in apical ½, apically bifid (Fig. 38) . . . . *Empis* (*Coptophlebia*) *bivittata*-group

19. Palpus arched forward beneath head (*e.g.*, Fig. 37); if palpus straight, then postpedicel greatly elongate; wing vein R_1 distinctly dilated before joining costal vein (C) (*e.g.*, Figs 18–20) (EMPIDINAE: HILARINI) 20

– Palpus straight, projecting obliquely or parallel to proboscis; wing vein R_1 not dilated before joining costal vein (*C*) (*e.g.*, Figs 21–23) 23

20. Wing vein *Sc* complete, reaching costal vein (*C*) (*e.g.*, Fig. 18) 21

– Wing vein *Sc* evanescent apically, not reaching costal vein (*C*) (*e.g.*, Figs 19, 20) 22

21. Antennal postpedicel generally short, distinctly tapered, shorter than proboscis; stylus at least ⅓ length of postpedicel (Fig. 37) . . . . *Hilara* Meigen

– Antennal postpedicel greatly elongate, filiform; stylus very short in comparison to postpedicel . . . . *Afroempis* Smith

22. Wing vein R_{4+5} unbranched (Fig. 19) . . . . *Atrichopleura* Bezzi

– Wing vein R_{4+5} branched (Fig. 20) . . . . *Hilarempis* Bezzi

23. Wing vein R_{4+5} unbranched (Fig. 21) (EMPIDINAE [in part]) . . . . *Edenophorus* Smith

– Wing vein R_{4+5} branched (*e.g.*, Figs 22, 23). 24

24. Antennal postpedicel broad, not greatly tapered apically; stylus with 2 articles: with cylindrical basal article and apical spine-like sensillum (Fig. 24); wing broad, with well-developed anal lobe; veins very pale; wing membrane with sparse microtrichia, with some bare areas (Fig. 22) (RAGADINAE) . . . . *Hormopeza* Zetterstedt

– Antennal postpedicel elongate and tapered; stylus with 3 articles: first article short, ring-like, second article 3–4 × longer than wide; apical article peg-like (Fig. 36); wing narrow, anal lobe undeveloped; veins dark and membrane infuscate, clothed in dense microtrichia, lacking bare patches (Fig. 23) (unassigned to subfamily) . . . . Undescribed genus

Synopsis of the fauna

Seventeen genera of Empididae are recorded from the Afrotropics, six of which are endemic to the region and four of which were identified subsequent to Smith's (1969) southern Africa monograph. Other modern identification keys available for Afrotropical genera are indicated in the below sections. The moderately diverse empidid fauna known from Madagascar is entirely undescribed. The undescribed species mentioned below were identified from collections of the American Museum of Natural History (New York, USA), California Academy of Sciences (San Francisco, USA), Canadian National Collection of Insects (Ottawa, Canada), Zoological Museum (Copenhagen, Denmark), KwaZulu-Natal Museum (Pietermaritzburg, South Africa), National Museum of Namibia (Windhoek, Namibia) and the National Museum (Bloemfontein, South Africa).

***Afroempis* Smith** (Empidinae: Hilarini)**.** An endemic monotypic South African genus based on two specimens from the Eastern Cape Province (Smith 1969). The type species, *A. stuckenbergi* Smith, 1969, is a distinctive species, with a greatly elongated antennal postpedicel (longer than tibia). The male terminalia appear to be typical of the Hilarini, with elongate and upright postgonites. The biology of this species and immature stages remain unknown.

***Afrodromia* Smith** (Hemerodromiinae)**.** An endemic genus of 13 described species all confined to southern Africa (Smith 1969) (see *Drymodromia* below). The genus, which is unassigned to tribe, is distinguished from *Drymodromia* by presence of the *r–m* crossvein and an auxiliary crossvein between wing veins R_4 and R_{2+3}. Smith (1969) identified several additional species, but the specimens were in too poor condition for formal description and several new species based on subsequent collections have been identified. The biology of this genus and immature stages remain unknown.

***Afroclinocera* Sinclair** (Clinocerinae)**.** An endemic genus based on two species from KwaZulu-Natal Province, South Africa. The genus is distinguished from other clinocerine genera by the complete subcostal vein; the elongate arista-like stylus; and the inflated male hind femur (Sinclair 1999*b*). *Afroclinocera obesa* Sinclair, 1999, was collected at the base of a small waterfall, observed skating, or gliding on calm pools, with all legs in contact with the waters' surface (Sinclair 1999*b*). Sinclair (1999*b*) provided an identification key to species. The immature stages remain unknown.

***Atrichopleura* Bezzi** (Empidinae: Hilarini)**.** A genus of 28 described species, occurring in the Afrotropical, Australasian and Neotropical Regions. In the Afrotropics the genus is known to occur only in South Africa, with two described species (Smith 1969), although many additional species remain to be identified. The genus is poorly defined and is virtually identical to *Hilara* or *Hilarempis*, but with an unbranched radial wing vein. As currently defined, *Atrichopleura* is a Southern Hemisphere genus (Câmara *et al*. 2013), with an incomplete *Sc* vein in Neotropical and Afrotropical species; whereas *Sc* is complete in Australian (+ New Caledonia) species. *Atrichopleura compitalis* Collin, 1928, from New Zealand, is incorrectly assigned to *Atrichopleura* and a new genus needs to be erected to accommodate this species (Sinclair 2011). The biology and immature stages remain unknown.

***Clinocera* Meigen** (Clinocerinae)**.** A genus of 109 described species, occurring in all zoogeographical regions, except Antarctica. The three known described South African species of *Clinocera* are assigned to the *C. tripunctata*-group, which is endemic to the Afrotropics (Sinclair 1999*b*). The phylogenetic relationships of this group to the remaining *Clinocera* species-groups remain weak (Sinclair 2008: 212). In addition, two undescribed species from South Africa and three undescribed species from Madagascar have been identified. Elsewhere in the Afrotropics, the Holarctic species, *C. stagnalis* (Haliday, 1833) is known from United Arab Emirates (Plant 2009) and an undescribed species is known from Tanzania, also assigned to the *C. stagnalis*-group. This undescribed species is very similar to the former species, but the legs are entirely pale and there is an auxiliary crossvein between wing veins R_{2+3} and R_4. *Clinocera* is distinguished from other clinocerines by the absence of a lower facial notch; the male cercal plate with long setae evenly distributed; and the facial setulae usually absent (Sinclair 1995*a*). The immature stages of *Clinocera* are aquatic, occurring primarily in seepages and small headwater streams (Sinclair 2008: 6). Sinclair (1999*b*) provided an identification key to South African species.

***Dolichocephala* Macquart** (Clinocerinae)**.** A genus of some 50 described species occurring in all zoogeographical regions, except Antarctica (Sinclair 1995*a*; Sinclair & MacDonald 2012). *Dolichocephala* is distinguished generally by the elongate head; the high attachment of head to thorax; and the setae of the male cercal plate confined to a small apical prominence (Sinclair 1995*a*). There are 11 described species of *Dolichocephala* known from East and South Africa. Two reduced winged species known from high elevations in Uganda (Garrett Jones 1940), were originally assigned to two monotypic genera (*Fur* Garrett Jones and *Obstinocephala* Garrett Jones), but were later synonymised with *Dolichocephala* by Sinclair (1995*a*). Three undescribed species are known from Madagascar and one is known from Kenya. Specimens of *Dolichocephala* are often collected on damp slopes along trails and seepage habitats (Sinclair & MacDonald 2012). The immature stages have been collected in aquatic vegetation in seepage, or madicolous habitats (Vaillant 1953*a*). Identification keys to Afrotropical species were provided by Garrett Jones (1940) and Smith (1969).

***Drymodromia* Becker** (Hemerodromiinae)**.** An endemic genus of 16 described species recorded from East and South Africa (Garrett Jones 1940; Smith 1969; Wagner & Andersen 1995). Together with *Afrodromia*, these genera are sister-group to the remaining Hemerodromiinae and currently unassigned to tribe (Plant 2011*a*). *Drymodromia* has a shortened discal medial (*dm*) wing cell; lacks an *r–m* crossvein; and vein *CuA+CuP* reaches the wing margin (Smith 1969). The biology and immature stages remain unknown.

***Edenophorus* Smith** (Empidinae)**.** An endemic South African genus, originally described on the basis of a single female specimen (Smith 1969). *Edenophorus* was redefined with the discovery of male specimens and now includes seven species (Sinclair 2002). *Edenophorus* is included in the subfamily Empidinae, but currently is best left unassigned to tribe. The genus is characterised by the anteriorly positioned proboscis; straight palpus; unbranched radial (R_{4+5}) vein; and pair of postpronotal setae (Sinclair 2002). The apparent highly localised occurrence of this genus, being active during the winter months and its phylogenetic position, suggest that the genus should be classified as a Gondwanan element (Sinclair 2002, 2003). Sinclair (2002) provided an identification key to species. The biology and immature stages remain unknown.

***Empis* L.** (Empidinae: Empidini)**.** This is a heterogeneous genus of *ca* 800 species mainly occurring in the Holarctic where it is considerably diversified. A subgeneric classification based on the Palaearctic fauna was established by Bezzi (1909), but it is hardly applicable to other regions of the world. All known Afrotropical species of the tribe Empidini, including those with unbranched wing vein R_{4+5}, belong to this genus. In the Afrotropics, *Empis* is currently divided in three subgenera: *E.* (*Disneyempis* Smith), *Empis sensu stricto* and *E.* (*Coptophlebia* Bezzi). *Empis* (*Coptophlebia*) includes all *Empis sensu stricto*-like species, with wing vein M_1 abbreviated; however, this subgenus should be only recognised for a group of Holarctic and Oriental species (Daugeron & Grootaert 2003). Although a complete review of the taxonomy of the Empidinae is yet to be completed, some species of *E.* (*Coptophlebia*) were recently transferred to the subgenus *Empis sensu stricto* and the remaining *E.* (*Coptophlebia*) spp. tentatively retained in this subgenus (Daugeron & Grootaert 2003). Seven monophyletic groups are recognised within Afrotropical Empidini (Daugeron 2000, 2001; Daugeron & Grootaert 2003), that include 69 known species. The seven groups include the subgenera *E.* (*Disneyempis*) (five species), *Empis sensu stricto* represented by the *E. setitarsus*-group (24 species) and four *E.* (*Coptophlebia*) species-groups – *E.* (*C.*) *namwamba* (14 species), *E.* (*C.*) *chrysocera* (10 species), *E.* (*C.*) *bivittata* (13 species), *E.* (*C.*) *poecilosoma* (three undescribed species from Namibia and Madagascar) and *E.* (*C.*) *hyalea* (three species; see Daugeron & Grootaert 2005). The *E.* (*C.*) *hyalea*-group is cosmopolitan (except Antarctica) and the *E.* (*C.*) *poecilosoma*-group has representatives in the Oriental Region, whereas the remaining groups are Afrotropical endemics. Identification keys to South African species of *Empis sensu stricto* and *E.* (*Coptophlebia*) were proposed by Smith (1969); additional keys were recently published to all species of *E.* (*Disneyempis*) and the *E. chrysocera*- and *E. setitarsus*-groups (Daugeron 2000, 2001; Daugeron & Grootaert 2003). Immature stages of *Empis* occur in woodland soil and leaf litter (Smith 1969). Adults prey mainly upon flying insects and are frequent flower-visitors

***Hemerodromia* Meigen** (Hemerodromiinae: Hemerodromiini)**.** A genus of some 145 described species, occurring in all zoogeographical regions, except Antarctica (Plant *et al.* 2012*a*). Despite regional variations in morphology, the genus appears to be well-founded (Plant & Sinclair 2008). There are 21 described Afrotropical species known from southern and East Africa (Plant *et al.* 2012*a*; Smith 1980: 439). Several additional undescribed species are known from Madagascar and across western Africa (A.R. Plant, pers. comm. 2014). Although wing cell *cua* is absent in most *Hemerodromia*, vein *CuA* is present in several South African species, but otherwise these species fit the generic diagnosis, which includes a shortened stylus; forked radial (R_{4+5}) and medial (M_{1+2}) veins; fusion of discal medial (*dm*) cell with *bm* cell; and absence of stigma and humeral crossvein (Plant 2011*b*; Plant *et al.* 2012*a*). The immature stages of *Hemerodromia* are aquatic, occurring in streams and rivers (Vaillant 1953*b*).

***Hilara* Meigen** (Empidinae: Hilarini)**.** A genus of *ca* 400 described species, occurring in all zoogeographical regions, except Antarctica. Within the tribe Hilarini, *Hilara* is characterised by a complete wing vein *Sc*. Sixteen species are known from the Afrotropical Region, most of which are described from South Africa, but the genus is further known from Ethiopia, Kenya, Madagascar, Tanzania and United Arab Emirates. An identification key to the South African species was provided by Smith (1969). Larvae occur in woodland soils, leaf litter and wood. Males often skim over water seeking prey trapped in the surface film. Males use the prey in courtship as nuptial gifts, sometimes wrapping prey in silk produced by the fore leg basal tarsomere (Smith 1969).

Hilarempis **Bezzi** (Empidinae: Hilarini)**.** A genus of 110 described species, occurring primarily in the Southern Hemisphere (Yang *et al*. 2007: 238). The genus includes *Hilara*-like flies with wing vein *Sc* abbreviated. Afrotropical *Hilarempis* can also be distinguished from species of *Hilara* by the presence of setula-like setae on the anepisternum. The genus includes 32 species from South Africa, Tanzania and Zimbabwe and many species remain to be described. An identification key to all known Afrotropical species was proposed by Smith (1969). The genus is also present in Latin America, Australia and New Zealand. The behaviour of *Hilarempis dasytibia* Smith, 1969, was recently observed (C. Daugeron, pers. obs.) and exhibits typical hilarine behaviour, in which males swarm over streams, apparently seeking prey, or dead insects floating on the surface of the water. The immature stages remain unknown.

Hormopeza **Zetterstedt** (Ragadinae)**.** A genus of 12 described species, primarily occurring in the Northern Hemisphere, with additional records from Australia, Brazil, South Africa and Thailand (Daugeron 1999; Plant *et al*. 2012*b*; Sinclair 1995*b*). In the Afrotropical Region, one species is recorded from Pietermaritzburg, South Africa (Sinclair 1995*b*) and a recently collected specimen from near Harrisburg, South Africa. *Hormopeza* is distinguished by the very broad antennal postpedicel, with cylindrical stylus; broad wings; V-shaped *R*-fork and pale veins. Species of *Hormopeza* are known as "empidid smoke flies", due to their attraction to wood smoke and smoke impregnated clothing and possibly breeding in recently burned trees and logs (Sinclair & Cumming 2006). The immature stages remain unknown.

Kowarzia **Mik** (Clinocerinae)**.** An Old World genus of 35 described species. In the Afrotropical Region the genus is represented by a species complex that extends from southern Europe to South Africa. Many species in this complex are based on small series, exhibiting slight differences in curvature of the clasping cercus of the male terminalia and body colouration (Sinclair 1999*b*). One species of *Kowarzia* is known from South Africa and three are described from East Africa (Sinclair 1999*b*; Smith 1969). Undescribed species, or populations, are also known from Malawi and Madagascar. All species appear to belong to the *K. plectrum* species-group, on the basis of the shape of the clasping cercus and are related to European species (Sinclair 1999*b*; Wagner & Andersen 1995). The genus is distinguished by a row of facial setulae along the inner margin of each eye; and small lower facial notch. The immature stages of *Kowarzia* are aquatic, occurring in seepages and small streams (Vaillant 1952).

Roederiodes **Coquillett** (Clinocerinae)**.** A genus of 19 described species, primarily occurring in the Northern Hemisphere. In the Afrotropical Region it is known from one species from Tanzania (Wagner & Andersen 1995), one species from South Africa (Sinclair 1999*b*) and an undescribed species from Kenya. *Roederiodes* is characterised by a long slender labrum and labium (Sinclair 1995*a*). The immature stages occur in rocky streams and rivers (Sinclair & Harkrider 2004), with adults alighting very close to the waters' surface, often on the underside of emergent rocks.

Undescribed genus (Unassigned to subfamily)**.** This undescribed genus possibly belongs to the subfamily Clinocerinae, but is known from only three specimens, all in poor condition. These specimens originate from the Western Cape Province of South Africa, collected in the Knersvlakte of southern Namaqualand. The genus is distinguished by the narrow and infuscate clinocerine-like wings and dark veins. The biology and immature stages remain unknown.

Wiedemannia **Zetterstedt** (Clinocerinae)**.** A genus of *ca* 115 described species, occurring in all zoogeographical regions, except the Neotropics and Antarctica. Afrotropical *Wiedemannia* comprises eight described species from East and southern Africa (Sinclair 1999*a*, *b*) and two undescribed species from Malawi and Tanzania, respectively. The Afrotropical species comprise a monophyletic group, possibly related to European species (Sinclair 1999*b*). This clinocerine genus is distinguished by a distinct facial carina, or notch, on the lower margin of the face; wide gena; and the acrostichal setae often well-developed. All life stages of *Wiedemannia* are primarily confined to cool streams.

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HYBOTIDAE 52

(Hybotid Dance Flies)

Bradley J. Sinclair and Jeffrey M. Cumming

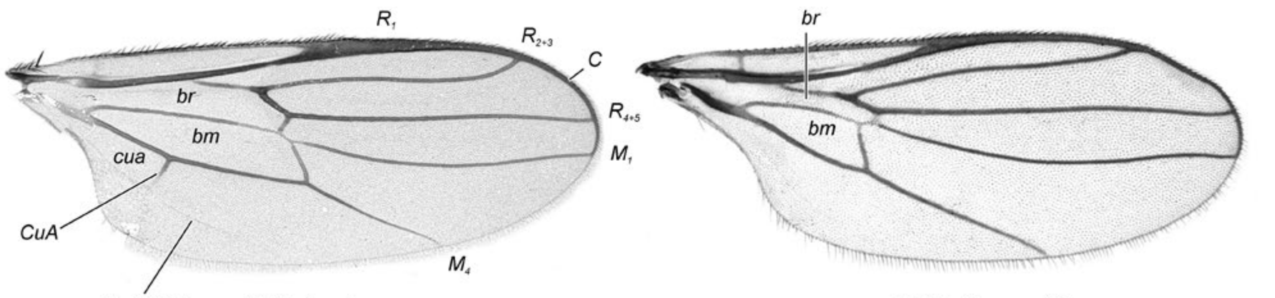
Fig. 52.1. Female of *Crossopalpus aenescens* (Wiedemann) (Tanzania) (photograph © S.A. Marshall).

Diagnosis

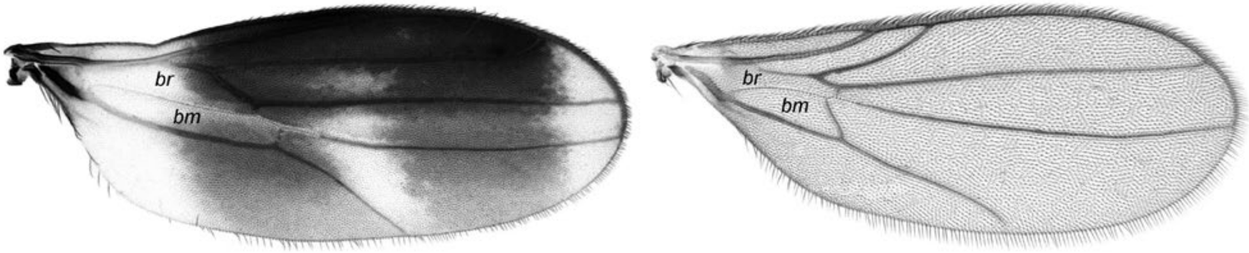
Adults small- to medium-sized flies (body length: 1.0–10.0 mm); darkish to light in colour (Fig. 1), subshiny, rarely metallic green.

Head variously shaped, never large and usually narrower than thorax; compound eye generally large, holoptic in males and dichoptic in females, or dichoptic in both sexes (females holoptic in Hybotinae) (Figs 26–32), sometimes with ommatrichia; antenna with scape devoid of setae; pedicel lacking thumb-like conus; postpedicel (first flagellomere) variously shaped; stylus short, to elongate, usually comprised of 2 articles, apical or situated more dorsally and appearing arista-like (Figs 13–16); proboscis short to elongate; labrum usually armed with epipharyngeal blades at apex; palpus 1-segmented, with

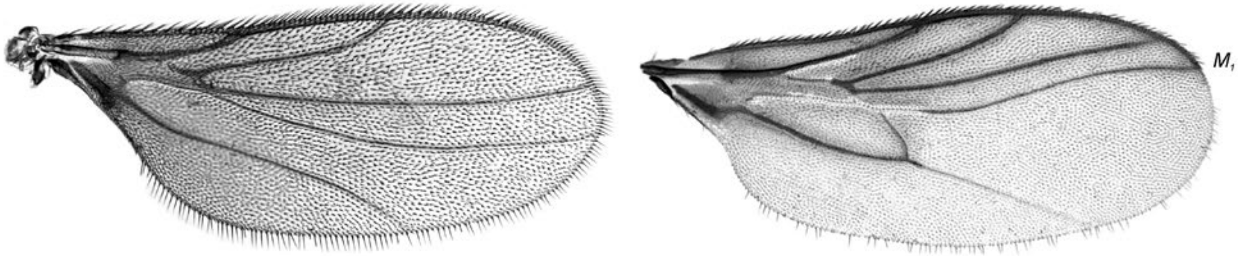
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1237–1249.



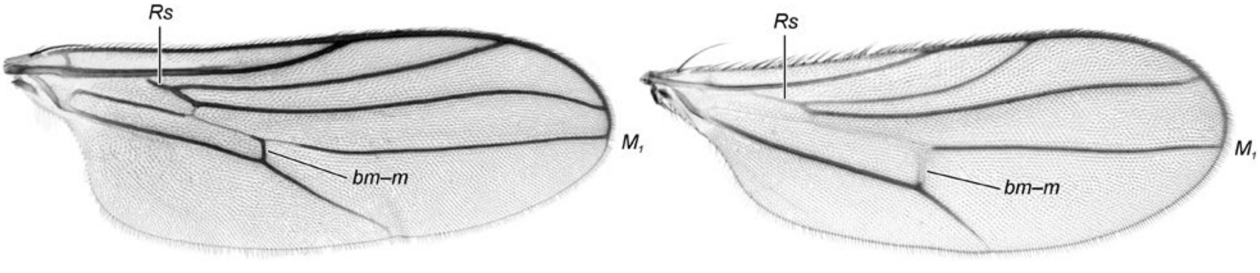
2 *Platypalpus* 3 "*Tachyempis*"



4 *Tachydromia* 5 *Chersodromia*



6 Undescribed Genus A 7 Undescribed Genus B



8 *Crossopalpus* 9 *Elaphropeza*

Figs 52.2–9. Wings of Hybotidae (dorsal views): (2) *Platypalpus* sp. (non-Afrotropical); (3) "*Tachyempis*" sp.; (4) *Tachydromia calcarata* (Strobl) (non-Afrotropical); (5) *Chersodromia* sp.; (6) Undescribed genus A; (7) Undescribed genus B; (8) *Crossopalpus aenescens* (Wiedemann); (9) *Elaphropeza secunda* (Smith). Fig. 6 (photograph A. Stark).

Abbreviations: *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *Rs* – radial sector.

sclerotised basal plate, or palpifer; lacinia absent, stipes fused to labial paraphyses; labellum with, or without, pseudotracheae; chaetotaxy of head limited, 1–2 pairs of ocellar setae usually present, vertical setae present, or absent.

Thorax usually rectangular in dorsal outline, sometimes extended anteriorly; disk of thorax virtually flat, to greatly arched and dome-like; chaetotaxy of thorax including notopleural setae and scutellar setae, with various other dorsal setae present; prothorax isolated, not fused to proepisternum, or fused to form precoxal bridge; laterotergite bare. Wing (Figs 2–10, 17–24) of varied shape and size, sometimes broadened, rarely reduced (Tachydromiinae: *Stilpon* Loew); alula and anal lobe often lacking, or reduced; colour hyaline to infuscate; costal vein (C) ending at, or near, vein R_{4+5}, or veins M_1/M_{1+2}; vein R_{4+5} unbranched; discal medial (*dm*) cell present (Figs 17–24), or absent (Figs 2–10) (Tachydromiinae); 2 or 3 veins emitted from discal medial cell; cell *cua* never reaching wing margin, or sometimes absent (many Tachydromiinae). Legs varied in length, thickness and armature; rarely sexually dimorphic, without clasping structures in males, often mid or hind pair with raptorial modifications (Fig. 11); base of fore tibia with anteroventral gland (Fig. 25); empodium usually setiform.

Abdomen subcylindrical, usually elongate, sometimes short; some tergites with abdominal plaques laterally; abdominal glands and modified sclerites often present in males (rarely females) of tribe Drapetidini (= Drapetini); male terminalia, sometimes including sclerites of segment 8 (*e.g.*, Drapetidini), rotated, or twisted 45°–90° to the right (barely rotated 45° in *Trichinomyia* Tuomikoski), usually asymmetrical; gonocoxal apodeme confined to anterior margin of hypandrium, lacking process; ejaculatory apodeme lever-like, articulated ventrally against base of phallus, or fused with phallus; female terminalia without acanthophorites; 1 unpigmented spermatheca present internally.

Hybotids can be differentiated from all other Empidoidea by the presence of a palpifer, or small sclerite, at the base of the palpus; presence of a fore tibial gland (Fig. 25); and male terminalia that are rotated to the right and are usually partially asymmetrical. Some Mythicomyiidae (see Chapter 44), that have an unbranched wing vein R_{4+5} may also be confused with Hybotidae, but these micro bee flies generally have a longer cell *cua*, that attains, or virtually attains, the wing margin.

Biology and immature stages

The species classified here in the Hybotidae represent a large group of predaceous flies, including a few flower visiting taxa. Adults are often found in various forest habitats, on tree trunks, fallen logs, leaves and aquatic vegetation, although some taxa are associated with more open areas, such as fields, marshes, coastal zones, mangroves and beaches (Collin 1961: 42, 53, 61; Grootaert & Shamshev 2012).

The Hybotinae (including *Bicellaria* Macquart (absent in Afrotropics)), capture their prey in flight, whereas the Tachydromiinae capture prey on substrates (Chvála 1983). Several genera of Oedaleinae (*Allanthalia* Melander, *Anthalia* Zetterstedt and *Euthyneura* Macquart) (Chvála 1983), are flower visitors, with pollen-feeding confirmed at least for the genus *Anthalia* (Downes & Smith 1969).

The immature stages of Hybotidae are poorly known. Larvae are generally found in moist soil, rotten wood, dung, or coastal habitats and also appear to be predaceous on various arthropods, particularly other dipterous larvae (Cumming & Cooper 1993; Cumming & Sinclair 2009: 654). As is the case with other empidoid larvae, they possess a slightly sclerotised cranium with two slender metacephalic rods lying above two tentorial arms (Fig. 36). Hybotid larvae possess an amphipneustic respiratory system, lack abdominal prolegs and usually have a rounded terminal segment, with a small caudal lobe (Dyte 1967; Steyskal & Knutson 1981: 608). The larva of the Holarctic species *Chersodromia arenaria* (Haliday, 1833) (Fig. 35), however, possesses three setulose caudal lobes (Marshall 1979). Hybotid pupae, as far as is known, have either short or moderately long (Fig. 34), prothoracic respiratory organs (Dyte 1967) and are found in cocoons spun by the larva (but, see Cumming & Cooper 1993: 95).

Mating has been transferred to the ground, or on vegetation in the Hybotidae, although hovering individuals, or swarming males, are known in most groups (Chvála 1983). The significance of the large aerial male aggregations observed in *Bicellaria* is unknown, although Chvála (1980) considered these aggregations to be "relict swarms".

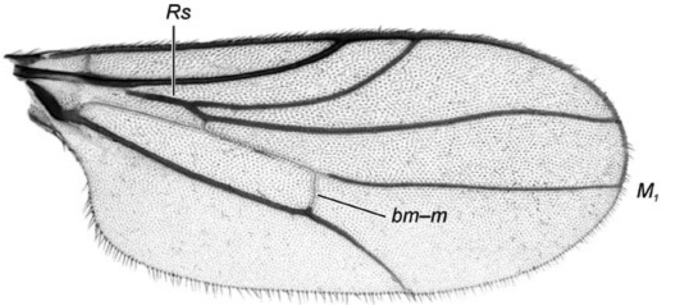
Economic significance

The Hybotidae are mostly predaceous flies and a few studies have recognised the economic importance of the group. Species of *Platypalpus* Macquart, in particular, have been identified as important natural control agents of numerous pests in agricultural and forestry situations, especially those of Diptera pests of cereal crops (Cumming & Cooper 1993; Stark 1994; Stark & Wetzel 1987).

Classification

The Hybotidae are consistently recovered as strongly monophyletic in phylogenetic analyses and are one of at least five recognised families of Empidoidea (Chvála 1983; Moulton & Wiegmann 2007; Sinclair & Cumming 2006). The Ocydromiinae *sensu lato*, Hybotinae and Tachydromiinae have been recognised as closely related since Melander (1928), and together were clearly defined by Tuomikoski (1966). Synapomorphies uniting the family include: presence of a palpifer, or external sclerite, between palpus and stipes (Sinclair & Cumming 2006, fig. 75); base of fore tibia with gland opening anteroventrally (Fig. 25); apex of antenna usually bearing slender seta-like apical sensillum; wing vein R_{4+5} unbranched; and gonocoxal apodeme of male terminalia reduced and lacking anterior process (Sinclair & Cumming 2006).

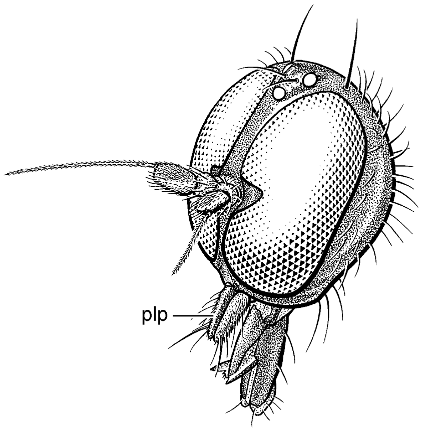
The Hybotidae comprises 64 genera worldwide, classified in five subfamilies, five tribes and one unplaced genus (Sinclair & Cumming 2006). There are 19 described and two undescribed genera that occur in the Afrotropical Region, with nine genera assigned to the Hybotinae, one assigned to the Ocydromiinae, ten assigned to the Tachydromiinae and one genus currently unassigned to subfamily. The following account gives a brief overview of each subfamily and tribe that occurs in the region.



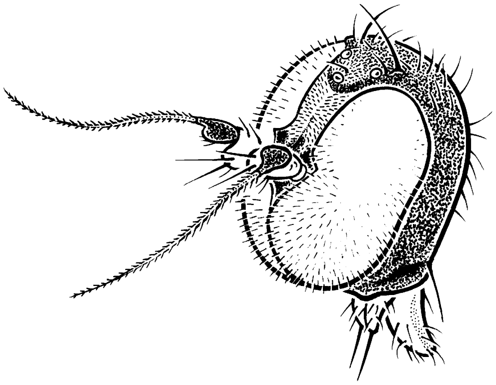
10 *Drapetis*

11 *Platypalpus*

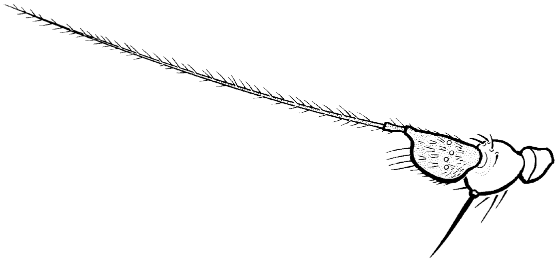
12 *Tachydromia*



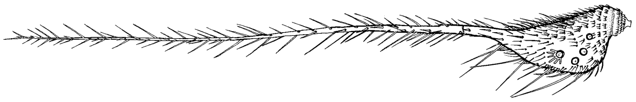
13 *Tachydromia*



14 *Stilpon*



15 *Stilpon*



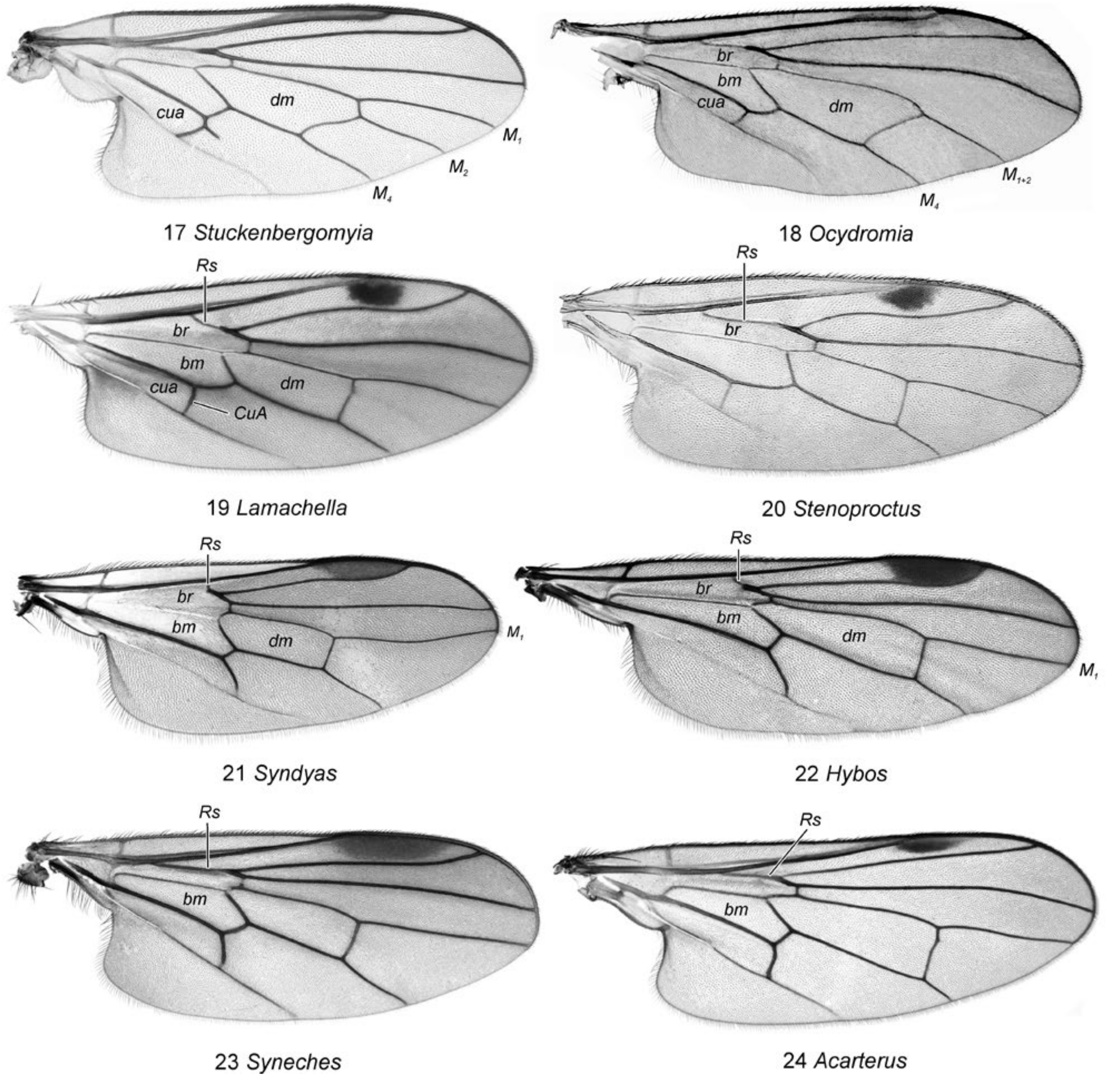
16 Undescribed Genus A

Figs 52.10–16. Wing, leg, thorax, heads and antennae of Hybotidae: (10) wing of *Drapetis* sp., dorsal view; (11) mid leg of *Platypalpus* sp., anterior view; (12) thorax of *Tachydromia calcanea* (Meigen), dorsal view (non-Afrotropical); (13) head of *Tachydromia maculipennis* Walker, anterolateral view (non-Afrotropical); (14) same, *Stilpon curvipes* Melander (non-Afrotropical); (15) antenna of *S. vockerothi* Cumming, lateral view (non-Afrotropical); (16) same, Undescribed genus A. Fig. 13 (Steyskal & Knutson 1981, fig. 11), Figs 14, 15 (Cumming & Cooper 1992, figs 1, 3); Fig. 16 (courtesy A. Stark).

Abbreviations: *bm–m* – basal medial crossvein; M_1 – first branch of media; plp – palpus; pprn lb – postpronotal lobe; *Rs* – radial sector.

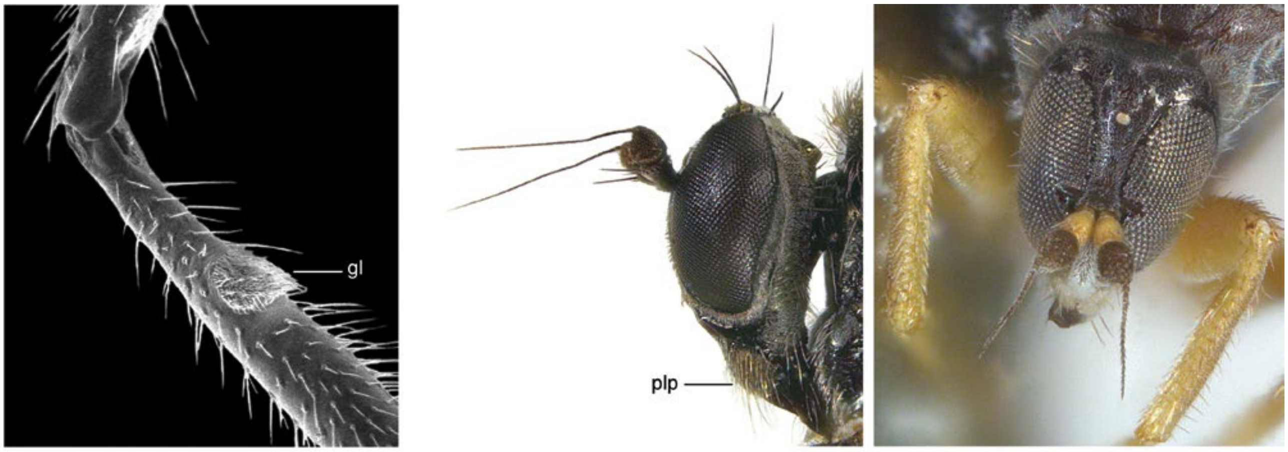
The Hybotinae are a readily recognised subfamily, characterised by: holoptic females (in most genera); proboscis often stout and projecting obliquely; wing broad with two veins emitted from wing cell *dm*; and prosternum isolated and separated from proepisternum (Sinclair & Cumming 2006). The subfamily is divided into two tribes, with only the Hybotini occurring in the Afrotropics. The genera of the Hybotini were placed into several groups by Sinclair (1996), but no phylogenetic analysis of the tribe has yet been published.

The Tachydromiinae are one of the most readily recognisable lineages in the Empidoidea, characterised by: wing without



Figs 52.17–24. Wings of Hybotidae (dorsal view): (17) *Stuckenbergomyia* sp.; (18) *Ocydromia* sp. (non-Afrotropical); (19) *Lamachella* sp.; (20) *Stenoproctus unipunctatus* Loew; (21) *Syndyas* sp.; (22) *Hybos* sp.; (23) *Syneches* sp.; (24) *Acarterus londti* Sinclair. Figs 18, 20 (Sinclair & Cumming 2006, figs 382, 386).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *dm* – discal medial cell; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; *Rs* – radial sector.



25 *Ocydromia* 26 *Crossopalpus* 27 "*Tachyempis*"

28 *Euhybus* 29 *Hybos* 30 *Syneches*

31 *Acarterus* 32 *Afrohybos* 33 *Afrohybos*

Figs 52.25–33. Heads and legs of Hybotidae: (25) stereoscan micrograph of base of fore tibia of *Ocydromia glabricola* (Fallén), anteroventral view (non-Afrotropical); (26) head of *Crossopalpus aenescens* (Wiedemann), lateral view; (27) same, "*Tachyempis*" sp., anterodorsal view; (28) same, *Euhybus* sp., lateral view; (29) same, *Hybos* sp.; (30) same, *Syneches* sp.; (31) same, *Acarterus londti* Sinclair; (32) same, *Afrohybos* sp.; (33) hind tarsus of *Afrohybos* sp. Fig. 25 (Sinclair & Cumming 2006, fig. 414).

Abbreviations: gl – gland; plp – palpus.

pterostigma, vein M_2 and cell *dm*; and absence of pseudotracheae (Sinclair & Cumming 2006). The Tachydromiinae are tiny, to small, predatory flies, often observed running on leaves, tree trunks, logs and amongst leaf litter, in habitats ranging from tropical forests, to dry sandy beaches (Grootaert & Shamshev 2012). Two of three tribes occur in the Afrotropics, with the Tachydromiini defined by the presence of a precoxal bridge. The Drapetidini are defined by eyes with ommatrichia and loss of wing vein *CuA* and a free tergite 10 in females (Sinclair & Cumming 2006).

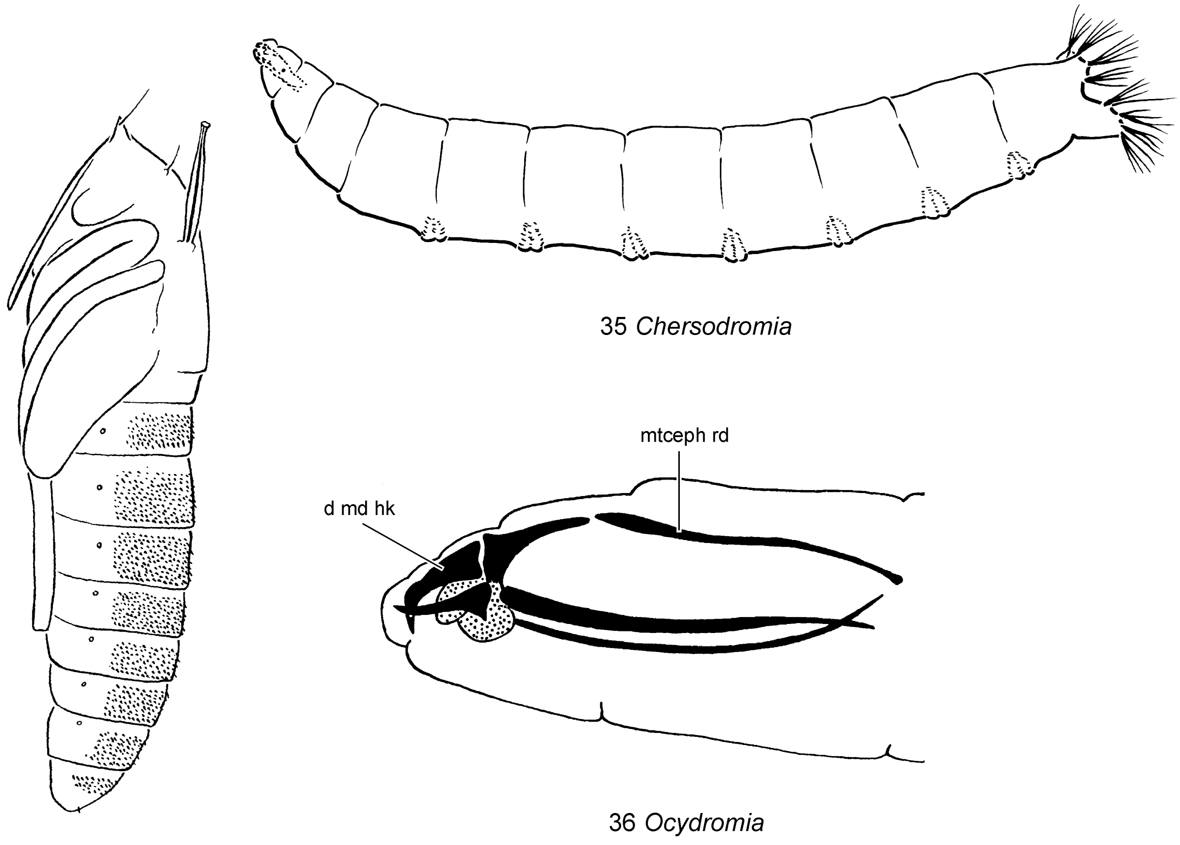
The Ocydromiinae were redefined by Sinclair & Cumming (2000), characterised by the following features: wing cell *cua* with truncate apex (except some non-Afrotropical *Apterodromia* Oldroyd); two or three veins emitted from cell *dm*; proboscis short; male terminalia asymmetrical; phallus biarticulated; postgonites absent; and surstyli fully articulated (Sinclair & Cumming 2006).

Stuckenbergomyia Smith was removed from the Ocydromiinae, but its subfamilial assignment remains unknown (Sinclair & Cumming 2006). It is likely that this lineage represents a new subfamily. Further details are outlined below, under the "Synopsis of the fauna" section.

Identification

Our knowledge of Afrotropical Hybotidae remains rather limited to date. Only a few species level treatments are available for South Africa (Sinclair 1996; Smith 1969), East Africa (Garrett Jones 1940), Democratic Republic of Congo (Grootaert & Shamshev 2013*a*, 2014) and Sierra Leone (Raffone 1994, 2012). The relatively diverse hybotid fauna from Madagascar remains completely undescribed, except for two species of *Elaphropeza* Macquart (Shamshev & Grootaert 2009) and the widespread species *Crossopalpus aenescens* (Wiedemann, 1830) (Cumming & Sinclair 2014).

The identification key provided below compliments the keys in Smith (1969) and Sinclair (1996), but with the addition of several newly identified genera from the Afrotropical Region. Hybotidae are best collected into alcohol, critical-point-dried and then glued to pins (see Chapter 2).



35 *Chersodromia*

36 *Ocydromia*

34 *Drapetis*

Figs 52.34–36. Immature stages of Hybotidae: (34) pupa of *Drapetis* sp., lateral view (non-Afrotropical); (35) larva of *Chersodromia arenaria* (Haliday), lateral view (non-Afrotropical); (36) head of first-instar larva of *Ocydromia glabricola* (Fallén), lateral view (non-Afrotropical). Fig. 34 (after Malloch 1917, fig. 7), Fig. 35 (after Marshall 1979, fig. 12), Fig 36 (after Hobby & Smith 1962, fig. 2).

Abbreviations: d md hk – dorsal mandibular hook; mtceph rd – metacephalic rod.

Key to genera of Afrotropical Hybotidae

1. Wings present 2

– Wings greatly shortened, shorter than abdomen (TACHYDROMIINAE [in part]) . . . .*Stilpon* Loew [in part]

2. Wing cell *dm* absent (*e.g.*, Figs 2–10) (TACHYDROMIINAE [in part]) 3

– Wing cell *dm* present (*e.g.*, Figs 17–24) 12

3. Wing cell *cua* more or less formed, with vein *CuA* distinct and vein *CuA+CuP* present, although sometimes faint (Fig. 2); mid femur thickest, armed with rows of spine-like setae and longer bristle-like setae ventrally (Fig. 11); mid tibia sometimes ending in sharp spur . . . . *Platypalpus* Macquart

– Wing cell *cua* absent, without veins *CuA* or *CuA+CuP*, trace of vein *CuA+CuP* sometimes apparent (*e.g.*, Figs 3–10); mid femur not thicker than fore femur, rarely armed ventrally; mid tibia not spurred. 4

4. Head with eyes bare; palpus narrow (*e.g.*, Fig. 13); thorax with postpronotal lobe distinctly differentiated, large and sometimes elongated (*e.g.*, Fig. 12) 5

– Head with eyes with tiny ommatrichia (*e.g.*, Fig. 14); palpus oval, usually broad (*e.g.*, Fig. 26); thorax with postpronotal lobe not distinctly differentiated, small and indistinct 6

5. Wing cell *br* equal to or slightly longer than cell *bm* at apex (Fig. 3); thorax with mesonotum only slightly longer than broad, with postpronotal lobe subquadrate; wing membrane hyaline to slightly infuscate (Fig. 3) . . . . *"Tachyempis" sensu* Smith

– Wing cell *br* distinctly shorter than cell *bm* at apex (Fig. 4); thorax with mesonotum much longer than broad, with postpronotal lobe elongate (Fig. 12); wing membrane usually maculate with crossbands or maculae (Fig. 4) . . . . *Tachydromia* Meigen

6. Wing with cell *br* equal to, or longer than, cell *bm* at apex (Fig. 5) . . . . *Chersodromia* Walker

– Wing with cell *br* distinctly shorter than cell *bm* at apex (*e.g.*, Figs 7–10), or cell *bm* absent (*e.g.*, Fig. 6). 7

7. Wing cell *bm* absent (Fig. 6); antennal arista-like stylus in terminal position (Fig. 16) . . . . [Undescribed genus A]

– Wing cell *bm* present (*e.g.*, Figs 7–10); antennal arista-like stylus variable (*e.g.*, Figs 15, 26) 8

8. Wing vein M_1 meeting costal vein (*C*) anterior or prior to wing apex (Fig. 7) . . . . [Undescribed genus B]

– Wing vein M_1 meeting costal vein (*C*) posterior to or at wing apex (*e.g.*, Figs 8–10) 9

9. Head with margins of frons virtually parallel, widely separated above antennae, at most only slightly diverging dorsally (Fig. 14); eyes contiguous on face; antenna with dorsoapical arista-like stylus; postpedicel short and round (Fig. 15); abdominal tergites without squamiform setae; male terminalia with 1 slender internal apodeme . . . . *Stilpon* Loew [in part]

– Head with margins of frons clearly diverging dorsally, closely-spaced, or virtually contiguous above antennae; eyes at least narrowly separated on face; antenna with terminal, or subterminal arista-like stylus (*e.g.*, Fig. 26); postpedicel short-oval or lanceolate or conical; some abdominal tergites usually with squamiform setae laterally; male terminalia with 2 slender internal apodemes (rarely 1 apodeme in some *Elaphropeza*) 10

10. Head with gena distinctly developed below eye (Fig. 26); wing vein *Rs* short, as short as or shorter than *bm–m* crossvein (Fig. 8); antennal pedicel with distinct ventral seta (Fig. 26) . . . . . *Crossopalpus* Bigot

– Head with gena scarcely extended below eye; wing vein *Rs* long, longer than *bm–m* crossvein (*e.g.*, Figs 9, 10); antennal pedicel usually lacking distinct ventral seta 11

11. Thorax with anepisternum bare; head with occiput convex; antennal postpedicel conical to lanceolate; hind tibia usually with long anterodorsal setae; body often with yellowish markings . . . .*Elaphropeza* Macquart

– Thorax with anepisternum possessing some scattered setulae, at least dorsally; head with occiput somewhat flattened; antennal postpedicel usually more oval (as in Fig. 26); hind tibia without long anterodorsal setae; body dark brown to black . . . . *Drapetis* Meigen

12. Three wing veins emitted from cell *dm* reaching wing margin (Fig. 17); cell *cua* emitting short spur vein; antenna with stylus stout, short, subequal to length of pedicel (*incertae sedis* in Hybotidae) . . . . *Stuckenbergomyia* Smith

– Two wing veins emitted from cell *dm* reaching wing margin (*e.g.*, Figs 18–24); cell *cua* not emitting spur vein; antennal stylus arista-like, usually subequal to, or longer than, postpedicel 13

13. Cell *cua* of wing shorter than cell *bm,* truncate (*e.g.*, Figs 19, 20); distance from apex of cell *cua* to apex of cell *bm* usually longer than length of vein *CuA* 14

– Cell *cua* of wing as long as or longer than cell *bm*, with apex (*CuA*) usually arched to meet vein *CuA+CuP* at acute angle (*e.g.*, Figs 21–23); if cell *cua* truncate (*e.g.*, Fig. 24), then distance from apex of cell *cua* to cell *bm* shorter than length of vein *CuA* (HYBOTINAE [in part]) 17

14. Pterostigma of wing elongate, distant from straight vein R_{2+3} (Fig. 18); crossvein *dm–m* oblique, arched to posterior margin of wing; antennal postpedicel ovate, with supra-terminal arista-like stylus (OCYDROMIINAE). . . . . *Ocydromia* Meigen

– Pterostigma of wing short, oval, with vein R_{2+3} arched beneath (*e.g.*, Figs 19, 20); crossvein *dm–m* usually straight, not arched to posterior margin of wing; antennal postpedicel rounded or tapered apically, with terminal stylus (HYBOTINAE [in part]). 15

15. Eye pubescent, with short ommatrichia; hind femur slender. . . . . *Chillcottomyia* Saigusa

– Eye bare; hind femur swollen. 16

16. Wing vein *Rs* arising distal to middle of cell *bm* (Fig. 19). . . . . *Lamachella* Melander

– Wing vein *Rs* arising basal to middle of cell *bm* (Fig. 20). . . . . *Stenoproctus* Loew

17. Wing vein *Rs* short, arising distal to middle of cell *bm* (*e.g.*, Figs 21, 22) 18

– Wing vein *Rs* long, arising basal to middle of cell *bm* (*e.g.*, Figs 23, 24). 20

18. Proboscis and palpus short, to moderately projecting, not extending beyond face; labellum not constricted for piercing, with pseudotracheae (Fig. 28) . . . . *Euhybus* Coquillett

– Proboscis elongate and projecting; palpus prominent, extending beyond face; labellum constricted for piercing, without pseudotracheae (*e.g.*, Fig. 29) 19

19. Basal section of wing vein *M* markedly weakened; cell *br* broader than cell *bm*; cell *dm* usually much shorter than last section of vein M_1 (Fig. 21); costal and basal cells often with bare sections lacking microtrichia . . . . *Syndyas* Loew

– Wing vein *M* strong basally, or only slightly weakened; cell *br* not broader than cell *bm*; cell *dm* usually subequal in length, or longer than last section of vein M_1 (Fig. 22); costal and basal cells lacking bare sections, entirely clothed in microtrichia . . . .*Hybos* Meigen

20. Antennal postpedicel short ovate; labellum rigid lacking pseudotracheae; eyes flattened above . . . . *Syneches* Walker

– Antennal postpedicel conical; labellum developed with pseudotracheae; eyes rounded, not flattened above 21

21. Proboscis short, fleshy (Fig. 32); hind tarsomere 1 swollen, nearly twice width of fore tarsomere 1 (Fig. 33). . . . . *Afrohybos* Smith

– Proboscis often long and rigid, (Fig. 31); hind tarsomere 1 slender, only slightly broader than fore tarsomere 1 . . . . *Acarterus* Loew

Synopsis of the fauna

This review is based primarily on Smith (1969, 1980) and previously unstudied material from the Albany Museum (Grahamstown, South Africa); American Museum of Natural History (New York, USA); California Academy of Sciences (San Francisco, USA); Canadian National Collection of Insects (Ottawa, Canada); Carnegie Museum of Natural History (Pittsburgh, USA); KwaZulu-Natal Museum (Pietermaritzburg, South Africa); National Museum of Namibia (Windhoek, Namibia); National Museum, Bloemfontein (South Africa) and National Museum of Natural History (Washington, D.C., USA).

***Acarterus* Loew** (Hybotinae)**.** An endemic southern African genus that includes eight described and at least five, or six, undescribed species (Sinclair 1996, 2003). Adults have been collected in grasslands, low shrubs and macchia vegetation. The long, slender, rigid proboscis of most species suggests that they may visit flowers, presumably consuming nectar (since no pollen has been observed in the gut of dissected specimens). *Acarterus* is distinguished from other hybotine genera by its slender proboscis and truncate wing cell *cua*, equal in length to cell *bm* (Sinclair 1996). An identification key to species was provided by Sinclair (1996).

***Afrohybos* Smith** (Hybotinae)**.** An endemic southern African genus. The original generic concept was based on a highly autapomorphic male. The generic concept is expanded here, to include the "undescribed genus" identified in Sinclair (1996). At least six undescribed species are known, and the genus is in need of revision (Sinclair 2003). All species of *Afrohybos* share an expanded hind first tarsomere and a short, fleshy proboscis.

The biology remains unknown and no identification keys to Afrotropical species are currently available.

***Chersodromia* Walker** (Tachydromiinae: Drapetidini)**.** This genus is confined primarily to marine shorelines with nearly 70 described species occurring in all zoogeographical regions, except Antarctica (Grootaert & Shamshev 2012; Sinclair & Cumming 2013). *Chersodromia* is distinguished from other tachydromiine genera by its virtually equal length basal wing cells (*br* and *bm*), bristly legs (particularly on the tibiae), broad gena and usually widely separated eyes. Within the Afrotropical Region, a described species is known from the coast of Seychelles (Raffone 1987) and another is known from primary forest habitat in Democratic Republic of Congo (Grootaert & Shamshev 2013*b*). The species from the Congo belongs to a specialised forest-dwelling group of *Chersodromia* (*i.e.*, *C. flavicaput*-group), known outside the Afrotropical Region from South-east Asia and New Guinea (Grootaert & Shamshev 2012; Grootaert *et al*. 2007). Two undescribed species belonging to the *C. flavicaput*-group have also been collected from montane rainforests in Madagascar. The habits and biology of the genus are not well documented, although adults are known to be highly predaceous (Chvála 1975). Larvae of the Holarctic seashore species *C. arenaria* (Fig. 35) inhabit decaying wrack, where they appear to prey on wrack-feeding sphaerocerid fly larvae belonging to the genus *Thoracochaeta* Duda (Marshall 1979). Grootaert & Shamshev (2013*b*) provided morphological differences that distinguish the two described species of Afrotropical *Chersodromia*.

***Chillcottomyia* Saigusa** (Hybotinae)**.** This genus was erected for a group of *Stenoproctus*-like flies, with slender hind femora, pubescent eyes and highly asymmetrical male terminalia (Saigusa 1986). *Chillcottomyia* illustrates an Afrotropical/Oriental biogeographical linkage, with species recorded from China, Japan, Nepal, Philippines and Taiwan (Saigusa 1986; Sinclair 2003; Yang & Grootaert 2006). In the Afrotropical Region a single species is known from South Africa (Sinclair 1996, 2003; Smith 1969) and an undescribed species is known from Madagascar. The biology of the genus remains unknown.

***Crossopalpus* Bigot** (Tachydromiinae: Drapetidini)**.** This genus currently includes 84 described species (Grootaert & Shamshev 2013*a*, 2014) distributed in all zoogeographical regions, except Antarctica. Nineteen species have been described from the continental Afrotropical Region, with many additional species expected to be discovered. One species, *C. aenescens*, is extremely widespread, having been recorded from the Arabian Peninsula to southern Africa, including Madagascar (Cumming & Sinclair 2014). In addition to the record above, at least five additional undescribed species are known to occur in Madagascar. *Crossopalpus* is very similar to the tachydromiine genera *Drapetis* and *Elaphropeza*, but can be most easily distinguished by a more extensive gena and shortened *Rs* wing vein. Adults of *Crossopalpus* are predaceous and are encountered in various habitats depending on the species, including forests, fields, marshes and coastal zones (Chvála 1975). Some species have been reared from dung, where they are probably preying on small flies (Chvála 1975; Smith 1969). Raffone (1994) provided an identification key to the Afrotropical species of *Crossopalpus* that was later modified by Grootaert & Shamshev (2013a) by adding a new species. The key, however, does not include *C. subaenescens* Collin, 1960, which occurs as far south as Yemen and Sudan in the Afrotropical Region (Chvála & Kovalev 1989).

***Drapetis* Meigen** (Tachydromiinae: Drapetidini)**.** This genus includes over 80 described species occurring in all zoogeographical regions, except Antarctica, with nine known from the Afrotropical Region (Grootaert & Shamshev 2013*a*, 2014). Numerous additional species await description, including at least six from Madagascar. *Drapetis* is most similar to the tachydromiine genus *Elaphropeza*, but is most easily distinguished by the presence of a few scattered setulae on the anepisternum of *Drapetis*, as opposed to a completely bare anepisternum in *Elaphropeza*. Adults of *Drapetis* are predaceous and are encountered in various habitats (Rogers 1983; Whittington 1993). Some species have been reared from rotten tree stumps (Smith 1969). Grootaert & Shamshev (2014) provided the most recent identification key to described Afrotropical species.

***Elaphropeza* Macquart** (Tachydromiinae: Drapetidini)**.** Almost 225 described species are classified in this mainly circumtropical genus (Grootaert & Shamshev 2013*a*, 2014), recorded from all zoogeographical regions, except Antarctica. Fifty-one described species of *Elaphropeza* are currently known from the Afrotropical Region (Grootaert & Shamshev 2014), including two from Madagascar (Shamshev & Grootaert 2009). This is probably only a small proportion of the actual diversity of the region, as recent sampling has revealed numerous additional undescribed species (Grootaert & Shamshev 2013*a*, 2014). Adults of *Elaphropeza* occur on ground vegetation and the leaves of bushes and trees (Chvála 1975). The Palaearctic species, *E. ephippiata* (Fallén, 1815), has been reared from woodland soil (Smith 1969). An identification key to the 30 species of *Elaphropeza* recorded from Democratic Republic of Congo was provided by Grootaert & Shamshev (2014).

***Euhybus* Coquillett** (Hybotinae)**.** This is a primarily New World genus, with six additional described species known from southern China, Taiwan and Tibet (Liu *et al*. 2011; Wang *et al*. 2013). Undescribed species are known from Fiji, Israel and Nepal (Sinclair, unpubl.). Within the Afrotropical Region, this genus is known on the basis of at least two undescribed species from Madagascar and one undescribed species from Zimbabwe. The generic concept of this taxon needs to be re-evaluated on a world basis, to include proper differentiation from *Neohybos* Ale-Rocha & Carvalho and *Smithybos* Ale-Rocha, which are currently confined to the New World. Although there are no reports on biology, adults are assumed to be predaceous.

***Hybos* Meigen** (Hybotinae)**.** There are more than 200 described species occurring in all zoogeographical regions, except Antarctica, with the greatest diversity found in Asia, predominantly in the eastern Oriental Region (Plant 2013). Only two species are described in the Afrotropical Region, from Kenya and South Africa (Smith 1969), with an undescribed species also known from Tanzania. This is likely indicative of low species diversity in the continental Afrotropics. In contrast, more than ten species have been identified from a small sample of *Hybos* from Madagascar. The genus is characterised by a stout and rigid proboscis, eyes narrowly separated on the face and convergent wing veins R_{4+5} and M_1. Adults are predators, usually observed alighting on leaf tips and attack flying insects (Chvála 1983). Smith (1969) provided an identification key to Afrotropical species.

***Lamachella* Melander** (Hybotinae)**.** Four described species are recorded from Cameroon, South Africa and Uganda (Smith 1969). A fifth species was unexpectedly discovered in Germany, reared from a rotting tree trunk of *Tilia* (Malvaceae) (Chvála & Stark 1997). This genus appears most closely related to *Stenoproctus* on the basis of a short wing cell *cua*, but differs by a shortened vein *Rs* arising beyond the middle of cell *bm*. Smith (1969) provided an identification key to Afrotropical species.

***Ocydromia* Meigen** (Ocydromiinae)**.** This genus is primarily known from the Nearctic and Palaearctic Regions, and also occurs in Burma, India and East and South Africa (Yang *et al*. 2007: 333). Despite being widespread, only nine described species are known, although the Nearctic fauna still requires revision. Two species are described from the Afrotropical Region (Smith 1969). The genus is characterised by a broad wing cell *dm* emitting two veins, ovate postpedicel with supraterminal arista-like stylus, simple legs (lacking distinct setae), and narrowly dichoptic females. Species of *Ocydromia* have been reared from dung and females are viviparous (Hobby & Smith 1962). Smith (1969) provided an identification key to Afrotropical species.

***Platypalpus* Macquart** (Tachydromiinae: Tachydromiini)**.** This is the largest genus of Hybotidae, with approximately 550 described species recorded from all zoogeographical regions, except Antarctica, although nearly 75% of these species are known from the Palaearctic and Nearctic Regions (Grootaert & Shamshev 2012). Currently, 28 species have been described from the continental Afrotropics, usually from areas of higher elevation, or more northern latitudes (Smith 1980: 432). The genus is not yet recorded from Madagascar, but at least six undescribed species are known to occur there. *Platypalpus* is a distinctive tachydromiine genus characterised by raptorial mid legs, with thickened armed mid femora and presence of a nearly complete cell *cua* on the wing. Adults are encountered in various habitats running over surfaces of leaves on bushes and trees, or amongst ground vegetation in search of small insect prey (Chvála 1975). Parthenogenesis is probably a common reproductive mode in *Platypalpus*, where males of several species are extremely rare or unknown, and it has been demonstrated in at least one species (Cumming & Cooper 1993). Immature stages of *Platypalpus* are poorly known with a report of a larva reared from under moss (Smith 1969). Larvae of three species were obtained by Cumming & Cooper (1993) and observed to be predaceous on small Diptera larvae. Identification keys to the described species of *Platypalpus* recorded from East Africa and South Africa were provided by Smith (1967) and Smith (1969), respectively.

***Stenoproctus* Loew** (Hybotinae)**.** An endemic genus, known from East and southern Africa (Smith 1969). There are 14 described species and numerous additional species that remain unstudied. Species definitions require re-evaluation, given that males and females appear to differ in wing shading and body colouration and several species are based solely on females. *Stenoproctus* is characterised by a short wing cell *cua* and elongate vein *Rs* arising proximal, or basal to, the middle of cell *bm*. The habits and biology of this genus remain unknown. Identification keys are available for South African (Smith 1969) and East African species (Garrett Jones 1940).

***Stilpon* Loew** (Tachydromiinae: Drapetidini)**.** About 60 extant species of *Stilpon* are known, occurring in the Afrotropical, Nearctic, Oriental and Palaearctic Regions (Grootaert & Shamshev 2012, 2013*a*). Only four described species occur in the Afrotropics, recorded from Democratic Republic of Congo, Sierra Leone and South Africa (Grootaert & Shamshev 2013*a*). Additional species have been collected elsewhere in the region, including at least four undescribed species from Madagascar. *Stilpon obscuripes* Adams, 1905 from Zimbabwe, was transferred to *Crossopalpus* by Cumming & Cooper (1992) and synonymised with *C. aenescens* by Cumming & Sinclair (2014). *Stilpon* can be distinguished from other related drapetidine genera (Tachydromiinae), by the linear, to sublinear, frons; small rounded postpedicel, with dorsoapical arista-like stylus; shortened wing cell *br*; and large male terminalia, with a single slender internal apodeme. Adults are predaceous and are found in low-lying vegetation zones in various open habitats, including grasslands, marshes and bogs, understory vegetation in open riparian woodlands, and coastal areas (Cumming & Cooper 1992). No identification keys to Afrotropical species are currently available.

***Stuckenbergomyia* Smith** (Hybotidae: *incertae sedis*)**.** A genus endemic to southern Africa, with two described species. Undescribed species are also known from Zimbabwe (Smith 1969, as *Stuckenbergia*), Namibia (Sinclair 2003) and the Western Cape Province of South Africa. *Stuckenbergomyia* is a rarely collected genus, originally assigned to the subfamily Ocydromiinae (Smith 1969), but is currently considered *incertae sedis* within the Hybotidae (Sinclair & Cumming 2006). The genus is characterised by a stout antennal stylus, three complete wing veins emitted from cell *dm* and a short spur vein, that extends from cell *cua*. Species of *Stuckenbergomyia* are believed to occur in dry montane grasslands (Smith 1969) and the form of the mouthparts suggests that they are flower visitors. Smith (1969) provided an identification key to species.

***Syndyas* Loew** (Hybotinae)**.** This genus occurs in all zoogeographical regions, except Antarctica, with 37 described species (Grootaert & Shamshev 2013*a*; Shamshev & Grootaert 2012), as well as undescribed species from northern Australia (Sinclair unpubl.). *Syndyas* is most speciose in the Afrotropics with 15 described species from Democratic Republic of Congo, East and southern Africa (Grootaert & Shamshev 2013*a*; Smith 1969). An undescribed species is also known from Madagascar and numerous additional Afrotropical species are expected. Unfortunately, many Afrotropical species are poorly defined and several are based solely on females. Additional collections and study of this genus are required. *Syndyas* is a distinctive genus, with the basal section of wing vein *M* markedly weakened, cell *br* broader than cell *bm*, and the costal and basal cells usually with bare sections lacking microtrichia. In North America, several species are primarily known only from *Sphagnum* (Sphagnidae) bogs (Teskey & Chillcott 1977) and adults are predaceous (Chvála 1983). Identification keys to Afrotropical species are available in Garrett Jones (1940), Grootaert & Shamshev (2013*a*) and Smith (1969).

***Syneches* Walker** (Hybotinae)**.** This genus was redefined to include a number of related genera, or subgenera (including *Parahybos iridipennis* Kertész, 1899, from Seychelles, see Grootaert *et al*. 2009: 164) (Sinclair 2011). Consequently, approximately 175 described species are now included in this genus, which occurs in all zoogeographical regions, except Antarctica (Grootaert & Shamshev 2013*a*). *Syneches* is one of the better known hybotid genera occurring in the Afrotropics, with 19 species described from across the region (Grootaert & Shamshev 2013*a*). Several new continental species have been identified, as well as almost 20 undescribed species from Madagascar. The genus is characterised by an elongate *Rs* wing vein, short ovate postpedicel, rigid labellum lacking pseudotracheae and eyes that are flattened above. Adults of *Syneches* are predaceous and are commonly encountered in grassland areas and forest edges (Wilder 1974). Identification keys to Afrotropical species were provided by Garrett Jones (1940) and Smith (1969).

***Tachydromia* Meigen** (Tachydromiinae: Tachydromiini)**.** This genus currently contains 118 described species distributed in all zoogeographical regions, except Antarctica, including five species from the Afrotropical Region (Grootaert *et al.* 2015). Afrotropical species are known from Democratic Republic of Congo, Ethiopia, Lesotho, South Africa and Uganda. *Tachydromia* is a genus of small ant-like flies that normally possess banded or maculate wings. Species can be distinguished from other Tachydromiinae by a dichoptic head (in both sexes) with bare eyes, virtually parallel-sided frons, narrow palpus, slender thorax, with large differentiated postpronotal lobes and the wing without cell *cua*. Adults of *Tachydromia* are predaceous and run rapidly on vertical and horizontal surfaces to catch their prey (Chvála 1975). Nothing is known about the immature stages of the genus. Grootaert *et al.* (2015) provided an identification key to described Afrotropical species.

***"Tachyempis" sensu* Smith** (Tachydromiinae: Tachydromiini)**.** *Tachyempis* Melander currently contains 21 described New World species (Yang *et al*. 2007: 443) and two described species from southern Africa included by Melander (1928) and Smith (1969). The Afrotropical species differ significantly from the New World species in their longer mouthparts, with narrower palpus, less dorsally divergent frons (Fig. 27) and wing cell *br* slightly longer than cell *bm*. These two species are probably not congeneric with New World *Tachyempis* and appear to be more closely related to *Tachydromia*. Smith (1969) mentions a third undescribed species of this group from South Africa, and another undescribed species has been collected in Madagascar. The biology of the group remains unknown. Smith (1969) provided an identification key to the two described Afrotropical species.

Undescribed genus A (Tachydromiinae: Drapetidini)**.** This undescribed genus is currently known from Cameroon (A. Stark, pers. comm. 2014), Democratic Republic of Congo (Grootaert & Shamshev 2013a) and South Africa (I.V. Shamshev, pers. comm. 2014). Species in this genus are very small tachydromiine flies, about 1 mm in length that have distinctive venation lacking wing cell *bm*.

Undescribed genus B (Tachydromiinae: Drapetidini)**.** An undescribed genus that is currently represented by a single species from South Africa. This genus is most easily distinguished from other tachydromiine genera by the anteriorly directed wing vein M_1 that parallels vein R_{4+5}.

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BRACHYSTOMATIDAE 53

(Brachystomatid Dance Flies)

Bradley J. Sinclair

Fig. 53.1. Male of *Apalocnemis* sp. (non-Afrotropical) (photograph © S.A. Marshall).

Diagnosis

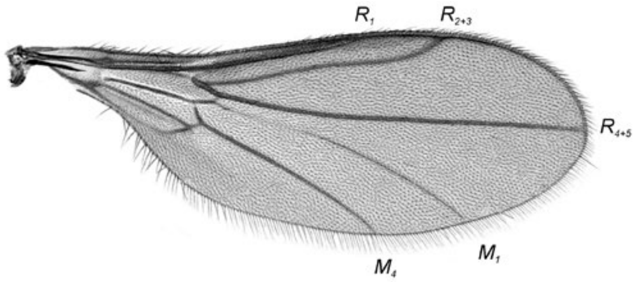
Adults small to medium-sized flies (wing length: 1.5–10.0 mm); darkish to light in colour (Fig. 1).

Head variously shaped, never large and usually narrower than thorax; compound eyes generally large, males often holoptic (Fig. 1) with females dichoptic (Figs 8, 9), or eyes closely approximated in both sexes, or males and females dichoptic; antenna with scape bearing numerous setae; pedicel with thumb-like conus, inserted into postpedicel (Ceratomerinae), or conus absent (Trichopezinae and Brachystomatinae); postpedicel variously shaped (Figs 3, 8, 9); stylus ranging from absent to elongate, usually comprised of 2 articles, situated apically on postpedicel, appearing arista-like, or rather stout; proboscis short to elongate; labrum armed at apex

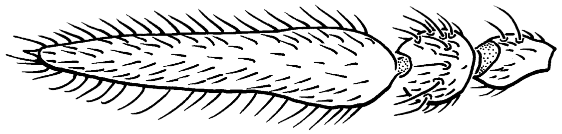
Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1251–1256.

with epipharyngeal blades; palpus 1-segmented, projecting obliquely, not strongly arched; chaetotaxy of head limited, pair of ocellar setae usually present, vertical setae present and weakly differentiated from postocular setae, or absent.

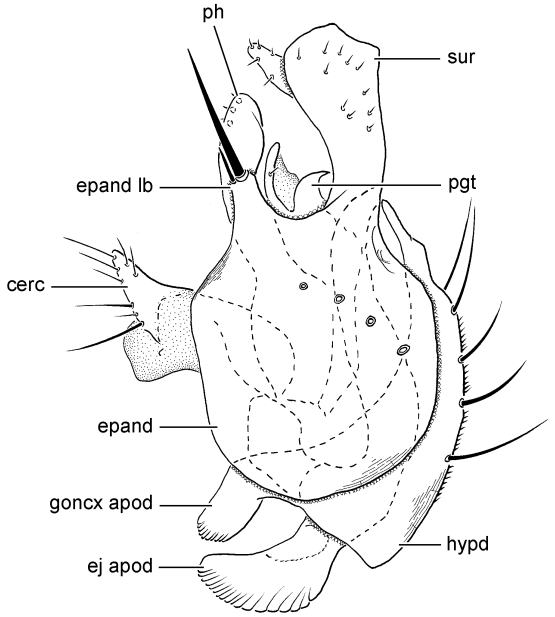
Thorax usually rectangular in dorsal outline sometimes extended anteriorly; disk of thorax virtually flat to strongly arched; chaetotaxy of thorax includes notopleural setae and scutellar setae, with various other dorsal setae present and usually well-developed; prosternum separate from, or fused to proepisternum; laterotergite bare or setulose. Wings of varied shape and size, sometimes broadened, rarely reduced; alula and anal lobe often lacking; colour hyaline to infuscate (Figs 2, 6, 7); venation generally uniform, relatively complete; radial vein (R_{4+5}) branched, or unbranched; discal medial (*dm*) cell present, rarely absent; cell *cua* closed, never reaching wing margin, rarely absent (most Ceratomerinae); cell *cua* shorter than vein *CuA+CuP*, or longer (Brachystomatinae), usually subequal to length of cell *bm*, rarely longer. Legs varied in length, thickness and armature; sometimes sexually dimorphic with modified setae and lobes in males; empodium usually setiform, pulvilliform in some aquatic groups.



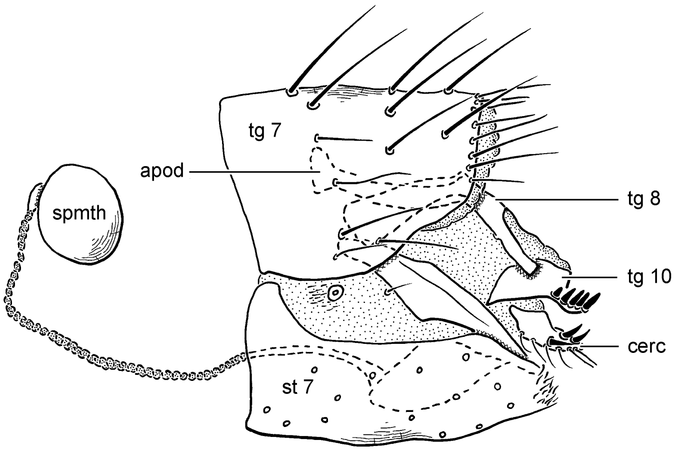
2 *Afropeza*



3 *Afropeza*



4 *Afropeza* ♂



5 *Afropeza* ♀

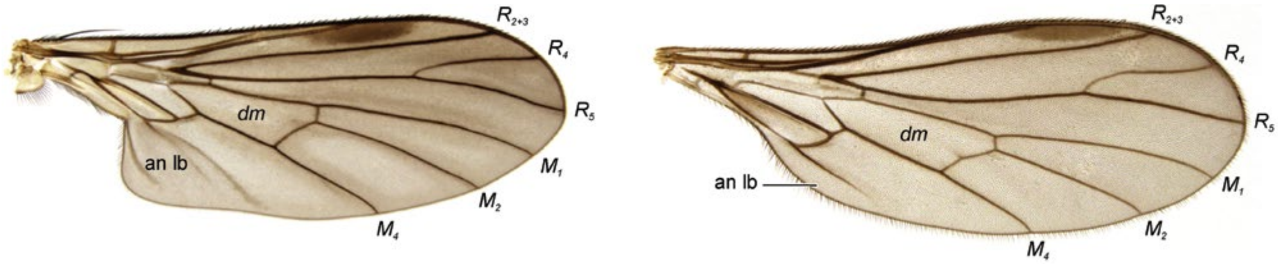
Figs 53.2–5. Wing, antenna and male and female terminalia of Brachystomatidae: (2) wing of *Afropeza* sp., dorsal view; (3) antenna of *A. silvatica* Sinclair & Shamshev, lateral view; (4) same, male terminalia, lateral view; (5) same, female terminalia, lateral view. Figs 3–5 (Sinclair & Shamshev 2012, figs 2, 7, 9).

Abbreviations: apod – apodeme; cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epand lb – epandrial lobe; goncx apod – gonocoxal apodeme; hypd – hypandrium; M_1 – first branch of media; M_4 – fourth branch of media; pgt – postgonite; ph – phallus; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; spmth – spermatheca; st – sternite; sur – surstylus; tg – tergite.

Abdomen subcylindrical, usually elongate, some tergites with distinct abdominal plaques laterally; male terminalia unrotated, usually symmetrical (Fig. 4), rarely asymmetrical (some genera of *Trichopeza*-group); ejaculatory apodeme often plate-like, narrowly fused to base of phallus (Sinclair & Cumming 2006); female terminalia with acanthophorites, sometimes reduced; tergite 8 often with internal apodeme; 1 spermatheca internally (Fig. 5).

Brachystomatid flies are difficult to characterise, being more readily distinguished on the basis of subfamilies or generic groupings. The family can generally be differentiated from similar empidoids by the circumambient costa and truncate female abdomen, bearing acanthophorites and upright, well-sclerotised cerci. Only Dolichopodidae *sensu lato* (see Chapter 56), usually bear distinct acanthophorites, but these usually have metallic body colouration unlike brachystomatids. In addition, in dolichopodids vein *Rs* originates at or near level of crossvein *h* and crossvein *r–m* is situated in the basal ¼ of wing, unlike brachystomatids, which have vein *Rs* originating well distal to level of crossvein *h* and crossvein *r–m* is distal to basal ¼ of the wing. Male brachystomatids usually have the ejaculatory apodeme plate-like and fused to base of phallus. Within the Brachystomatidae, the pedicel with conus is inserted into the postpedicel in the Ceratomerinae, and cell *cua* is generally longer than cell *bm* in most Brachystomatinae. The Trichopezinae includes species which usually possess a distinct median apodeme, projecting anteriorly from tergite 8 in the female terminalia (Sinclair & Cumming 2006).

In the Afrotropical Region, the Brachystomatidae are distinguished from other Empidoidea by the following combination of characters: females dichoptic, or eyes narrowly separated; palpus projecting obliquely, not strongly curved; laterotergite bare; costa circumambient, although sometimes reduced beyond vein R_{4+5}; vein R_1 not swollen before joining



6 *Apalocnemis*

7 *Rubistella*

8 *Apalocnemis* ♀

9 *Rubistella* ♀

Figs 53.6–9. Wings and heads of Brachystomatidae: (6) wing of *Apalocnemis* sp., dorsal view (non-Afrotropical); (7) same, *Rubistella* sp.; (8) head of *Apalocnemis* sp., lateral view ♀; (9) same, *Rubistella* sp. ♀.

Abbreviations: an lb – anal lobe; *dm* – discal medial cell; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius.

costa; fore legs not raptorial; and female abdomen truncate, bearing acanthophorites.

Biology and immature stages

Adults are encountered in various forest habitats from tropical to alpine/boreal zones. Species of *Heleodromia* Haliday have frequently been collected along the banks of rivers and streams, on rocks near waterfalls, or on moist soil of forest floors and tundra (Sinclair *et al*. 2011). *Apalocnemis* Philippi has been collected on riparian rocks in streams and small rivers in eastern Australia and New Zealand (pers. obs.). The non-Afrotropical species *Apalocnemis maura* Collin, 1933, has been observed forming dense swarms at 0–1.5 m over small streams in wet forests in Chile (A.R. Plant, pers. comm. 2014). *Niphogenia* Melander has generally been collected about rills formed from melting snow drifts in mountains of western North America (Melander 1928; pers. obs.).

Most species of the Brachystomatidae are presumably predaceous flies, with a species-group of *Ceratomerus* Philippi from New Zealand (Sinclair 2003*a*) and Chilean species of *Apalocnemis* (A.R. Plant, pers. comm. 2014) observed on flowers. Direct-feeding observations are rare in this family. In the Trichopezinae, adults of *Niphogenia eucera* Melander, 1927 (non-Afrotropical) have been observed feeding on insect larvae (Wilder 1981) and the non-Afrotropical species *Trichopeza longicornis* (Meigen, 1822) has been observed feeding on small midges held by the fore legs (Ulrich 1981). Adults of *Ceratomerus ordinatus* Hardy, 1930 (non-Afrotropical) were observed feeding, or scavenging, on conspecific flies that were freshly squashed on emergent rocks along a river (Sinclair 2003*a*).

The immature stages are unknown for all genera of Brachystomatidae, but are assumed to be similar to the general empidoid form outlined in Steyskal & Knutson (1981: 622).

Economic significance

No species of economic importance are currently known.

Classification

On the basis of a morphological cladistic analysis, Sinclair & Cumming (2006) divided the superfamily Empidoidea into five families: the Atelestidae, Brachystomatidae, Dolichopodidae, Empididae and Hybotidae. The monophyly of the Brachystomatidae is supported by fusion of the ejaculatory apodeme to the phallus, female tergite 7 usually with a posterior fringe of setae and female cerci held upright (Fig. 5) (Sinclair & Cumming 2006). In contrast, the familial level classification of the Brachystomatidae, and specifically, the monophyly of the subfamily Trichopezinae has received weak, or no support in molecular phylogenetic studies (Collins & Wiegmann 2002; Moulton & Wiegmann 2007). Despite these opposing conclusions, the expanded concept of the Brachystomatidae, as characterised by Sinclair & Cumming (2006) to include the Ceratomerinae and Trichopezinae, is generally accepted by Empidoidea systematists. The family was included in a review of European Diptera families (Oosterbroek 2006: 117) and was also recognised in the familial level classification of the Diptera (Pape *et al*. 2011).

The Brachystomatidae comprise 22 genera worldwide, classified in three subfamilies. Three genera occur in the Afrotropical Region, all assigned to the subfamily Trichopezinae. The Trichopezinae are a heterogeneous group, distinguished from other empidoid subfamilies by the truncate female abdomen, which usually bears an internal median apodeme arising from the anterior margin of tergite 8 (Sinclair 1995). Among Afrotropical genera, *Apalocnemis* is assigned to the *Heterophlebus*-group, whereas *Rubistella* Garrett Jones and *Afropeza* Sinclair & Shamshev remain unassigned to any of the four included genus-groups (Sinclair & Cumming 2006).

The subfamily Ceratomerinae (non-Afrotropical) is defined by the distinctive antennal conus, a finger-like projection from the pedicel that inserts into the postpedicel, and absence of cell *cua* (except *Glyphidopeza* Sinclair). The subfamily includes three genera, confined to South America, Australia and New Zealand (Sinclair 2010). The taxa are common in temperate forests and along cool streams, where they are most easily collected using yellow pan traps. Sinclair (2010) analysed the phylogenetic relationships of the genera and species-groups and discussed provisional biogeographic patterns.

The subfamily Brachystomatinae (non-Afrotropical) is defined on the basis of a coiled spermatheca, H-shaped maxilla and articulated male cerci (Sinclair & Cumming 2006). The three assigned genera are largely confined to the Northern Hemisphere, with a single species recorded from northern Thailand in the Oriental Region (Plant 2010).

Identification

Knowledge of species of Afrotropical Brachystomatidae is based primarily on Garrett Jones (1940), Sinclair & Shamshev (2012), Smith (1967, 1969) and Wagner & Andersen (1995).

The key to subfamilies of Empididae in Smith (1969) is outdated, given the new subfamily concepts, and subsequent description of numerous new genera. The key to genera of Brachystomatidae included in this chapter represents the first for the Afrotropical Region. Brachystomatidae are best collected into alcohol, critical-point-dried and then glued to pins (see Chapter 2).

Key to genera of Afrotropical Brachystomatidae

1. Wing with discal medial cell (*dm*) absent; veins M_{1+2} (= M_1) and R_{4+5} simple (Fig. 2) . . . . *Afropeza* Sinclair & Shamshev

– Wing with discal medial cell (*dm*) present; vein M_{1+2} forked; vein R_{4+5} usually forked (e.g., Figs 6, 7) 2

2. Wing with broad anal lobe, axillary angle virtually at right angles; radial fork V-shaped (Figs 1, 6); males holoptic; thoracic setae stout and distinct. . . . . *Apalocnemis* Philippi
– Wing with narrow anal lobe; radial fork bell-shaped or vein R_{4+5} simple (Fig. 7); male eyes closely approximated, or more widely separated; thoracic setae fine and inconspicuous . . . . . *Rubistella* Garrett Jones

Synopsis of the fauna

Three genera and 14 described species of Brachystomatidae are recorded from the Afrotropical Region, from East Africa and southern Africa. The family is only well characterised from East Africa and southern Africa (South Africa). The occurrence of species of this family in other parts of Africa remains unknown.

***Afropeza* Sinclair & Shamshev** (Trichopezinae)**.** An endemic genus restricted to South Africa, comprising three described species (Sinclair & Shamshev 2012). A possible additional species is known from the Western Cape Province, South Africa. *Afropeza* is readily identified by the following: eyes closely approximate on frons in both sexes; absence of discal medial cell; and unbranched vein M_{1+2} greatly weakened, especially subbasally. The phylogenetic relationships of *Afropeza* to other genera of Trichopezinae remain unknown. An identification key to species of *Afropeza* is provided by Sinclair & Shamshev (2012).

***Apalocnemis* Philippi** (Trichopezinae)**.** A genus of 28 described species worldwide, occurring mainly in the Australasian and Neotropical Regions (Cumming & Sinclair 2009: 666; Rafael & Sinclair 2012). The genus is broadly defined (males holoptic; wing with radial fork long and V-shaped; vein *Sc* weakened apically) and requires a worldwide revision to clearly establish its monophyly. The Afrotropical record of *Apalocnemis* is an undescribed species, based on a single female specimen collected during winter from the Karkloof mountain range of KwaZulu-Natal Province, South Africa (Sinclair 2003*b*). The African species is characterised by an elongate postpedicel, lacking a distinct stylus and short female proboscis (Fig. 8). The generic assignment of the African species remains tentative.

***Rubistella* Garrett Jones** (Trichopezinae)**.** An endemic genus with eleven species known from East and southern Africa. Three undescribed species have been identified from South Africa. *Rubistella* is characterised by slender wings (anal lobe not developed), male eyes distinctly separated above the antennae and short mouthparts (Fig. 9) (Smith 1969). Identification keys to described species are provided by Garrett Jones (1940) and Smith (1969).

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ATELESTIDAE 54

(Atelestid Dance Flies)

Bradley J. Sinclair

Fig. 54.1. Female of *Alavesia daura* Sinclair & Kirk-Spriggs (Namibia) (Sinclair & Kirk-Spriggs 2010, fig. 1).

Diagnosis

Small sized flies (wing length: 1.9–2.2 mm); darkish to light in colour. Males holoptic (except *Alavesia* Waters & Arillo), with upper facets enlarged; broadly dichoptic in females.

Head (Fig. 1) with antennae inserted below, or submedially (viewed in profile); scape bare; postpedicel short-ovate to elongate-lanceolate (Fig. 3); arista-like stylus with 1 or 2 short basal segments; proboscis obliquely directed forward; labrum of variable length, rounded apically, lacking epipharyngeal blades; palpus 1-segmented, elongate; pseudotracheae usually present; chaetotaxy of head reduced, pair of ocellar setae usually present, vertical setae present or absent.

Thorax (Fig. 1) usually slightly arched; prosternum small, separate from proepisternum; acrostichal and dorsocentral setae separated; laterotergite glabrous. Wing (Fig. 2) with

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well-developed axillary angle and alula variably developed; costal vein (*C*) ending at, or slightly beyond vein M_1; vein *Sc* incomplete; vein R_{4+5} unbranched; first branch of media unforked (M_1), if forked (*Meghyperus* Loew), then veins branch beyond discal medial (*dm*) cell; cell *dm* present or absent; cell *cua* large, at least as large as basal cells, or longer, cell closed, never reaching wing margin; vein *CuA+CuP* extending to wing margin. Legs short, lacking modified setae; hind tibia sometimes dilated; fore tibia lacking ventrobasal gland.

Abdomen subcylindrical, some tergites with abdominal plaques laterally; tergite 8 narrower than preceding sclerites; male terminalia (Figs 4, 5) symmetrical, unrotated; hypandrium short, with elongate gonocoxal apodemes; ventral apodemes and postgonites present or absent; surstylus apical or subapical; female terminalia (Figs 6, 7), with tergite 10 absent; 1 spermatheca present with spherical receptacle.

Atelestids are generally differentiated from other Empidoidea by their distinctive wing venation, either cell *dm* greatly reduced with arching medial veins (Fig. 2), or lacking cell *dm*, or vein M_{1+2} forked beyond cell *dm* (see Chvála 1983, figs 561, 562). In the Afrotropical Region, the Atelestidae are readily distinguished from other Empidoidea by their unique wing venation and elongate, lanceolate postpedicel (Figs 1, 3).

Biology and immature stages

The immature stages are not known for any genera of Atelestidae and little information is available on adult behaviour. All adults of Atelestidae lack epipharyngeal blades and are assumed to be obligate flower-visitors (Sinclair & Kirk-Spriggs 2010). Among the five extant genera, however, only *Acarteroptera* Collin has been observed feeding on flowers and pollen grains have been reported in the abdomen (Cumming & Sinclair 2008: 1148; Sinclair & Cumming 2006). Aerial swarming has been observed for two species of *Atelestus* Walker, but mating has not been observed (Chvála 1983).

In the Afrotropics, extant species of *Alavesia* are known only from the Brandberg massif, Namibia, collected in Malaise traps set over riverbeds on the upland plateau. The specimens were collected following periods of prolonged precipitation, which likely triggered adult flight activity. The Brandberg has been highlighted as a Gondwanan refugium for relict species or "living fossils" (Sinclair & Kirk-Spriggs 2010).

Economic significance

No species of economic importance are currently known.

Classification

The atelestine family group was erected by Hennig (1970) for a group of three genera, namely *Acarteroptera*, *Atelestus*, and *Meghyperus*. Chvála (1983) elevated this group to family status, which was initially regarded as the sister-group to the Cyclorrhapha (Chvála 1983; Wiegmann *et al*. 1993). Currently, the Atelestidae is one of five families assigned to the superfamily Empidoidea, a monophyletic lineage, considered to be the sister-group to the Cyclorrhapha (Cumming *et al*. 1995; Collins & Wiegmann 2002; Sinclair & Cumming 2006). The Atelestidae is either regarded as the sister-group to the remaining Empidoidea (Collins & Wiegmann 2002; Moulton & Wiegmann 2007), or the sister to the Hybotidae (Sinclair & Cumming 2006).

The genus *Nemedina* Chandler was provisionally assigned to the Empidoidea, initially of uncertain subfamilial status, but was later transferred to the atelestid family group (Sinclair & Shamshev 2003). *Nemedina* is currently assigned to the subfamily Nemedininae (Sinclair & Cumming 2006), which also includes five Cretaceous amber genera (Grimaldi & Cumming 1999). The Nemedininae is defined by its unique venation, in which the apex of cell *br* is modified through the inclusion of a short vertical *Rs* vein and recurrent *r–m* crossvein, with radial and medial veins closely approximated (Sinclair & Cumming 2006). Species of *Nemedina* occur in the Palaearctic Region.

The genus *Alavesia* was originally based solely on fossil species from Early to Late Cretaceous ambers of Spain and Burma (Grimaldi *et al*. 2002; Peñalver & Arillo 2007). With the discovery of extant species in southern Africa, *Alavesia* was transferred to the Atelestidae and assigned to the subfamily Atelestinae (Sinclair & Kirk-Spriggs 2010), which also includes the Cretaceous amber genus *Atelestites* Grimaldi & Cumming. Among atelestid genera, only *Alavesia* is recorded from the Afrotropical Region (Sinclair & Kirk-Spriggs 2010). The Atelestinae are defined by the presence of a three-articled stylus (Fig. 3) (secondarily lost presumably in some *Meghyperus* and *Atelestus*), the presence of paired ventral apodemes, surstylus subapical and female postabdomen retracted into segment 4 or 5.

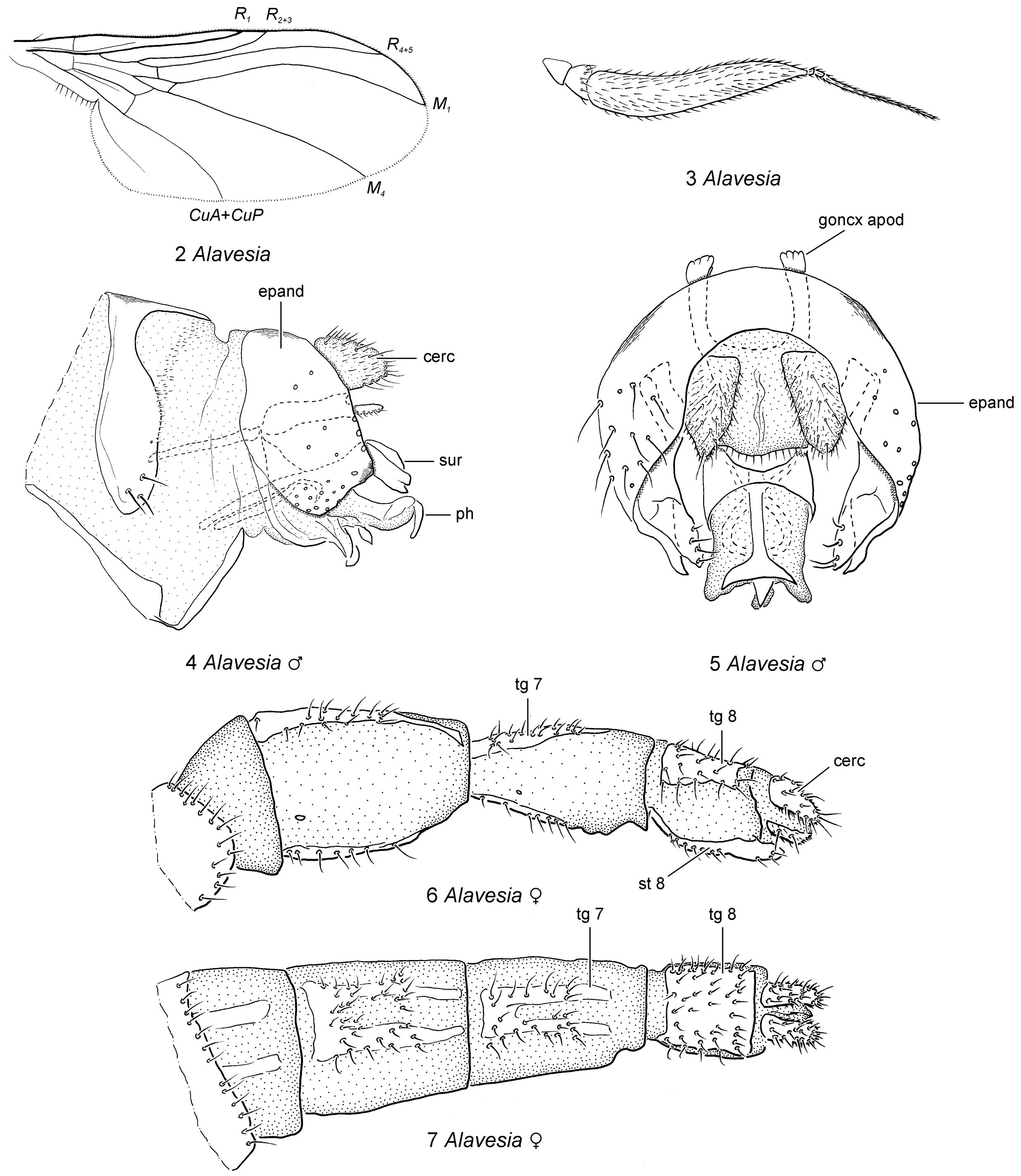
Identification

Keys to genera and species of Atelestidae of the western Palaearctic Region were presented by Chvála (1983). *Alavesia* was unknown from Africa at the time of Smith's (1969) monograph of Empididae *sensu lato*. The family level key in this *Manual* is the first Afrotropical key in which this family is identified. Sinclair & Cumming (2006) included the Atelestidae in their key to families and genus-groups of the Empidoidea.

Synopsis of the fauna

Only a single genus is known from the Afrotropical Region. The family remains poorly known, based on only four adult specimens collected from Namibia.

***Alavesia* Waters & Arillo** (Atelestinae)**.** The only two extant species of this genus are recorded from the upland plateau (1750 m) of the Brandberg massif in Namibia (Sinclair & Kirk-Spriggs 2010). *Alavesia* is differentiated from all other empidoid genera by the diminutive wing cell *dm*, veins M_1 and M_4 longer than ½ length of wing, postpedicel of the antenna long and lanceolate and the antennal stylus 3-segmented (Figs 2, 3).



2 *Alavesia*

3 *Alavesia*

4 *Alavesia* ♂

5 *Alavesia* ♂

6 *Alavesia* ♀

7 *Alavesia* ♀

Figs 54.2–7. Wing, antenna and male and female terminalia of Atelestidae: (2) wing of *Alavesia daura* Sinclair & Kirk-Spriggs, dorsal view; (3) male antenna of *A. brandbergensis* Sinclair & Kirk-Spriggs, lateral view; (4) male terminalia of *A. brandbergensis*, lateral view; (5) same, dorsal view; (6) female terminalia of *A. daura*, lateral view; (7) same, dorsal view. Figs 2, 4–7 (Sinclair & Kirk-Spriggs 2010, figs 3, 4).

Abbreviations: cerc – cercus; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; epand – epandrium; goncx apod – goncoxal apodeme; M_1 – first branch of media; M_4 – fourth branch of media; ph – phallus; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; st – sternite; sur – surstylus; tg – tergite.

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HOMALOCNEMIDAE 55

(Homalocnemid Dance Flies)

Bradley J. Sinclair

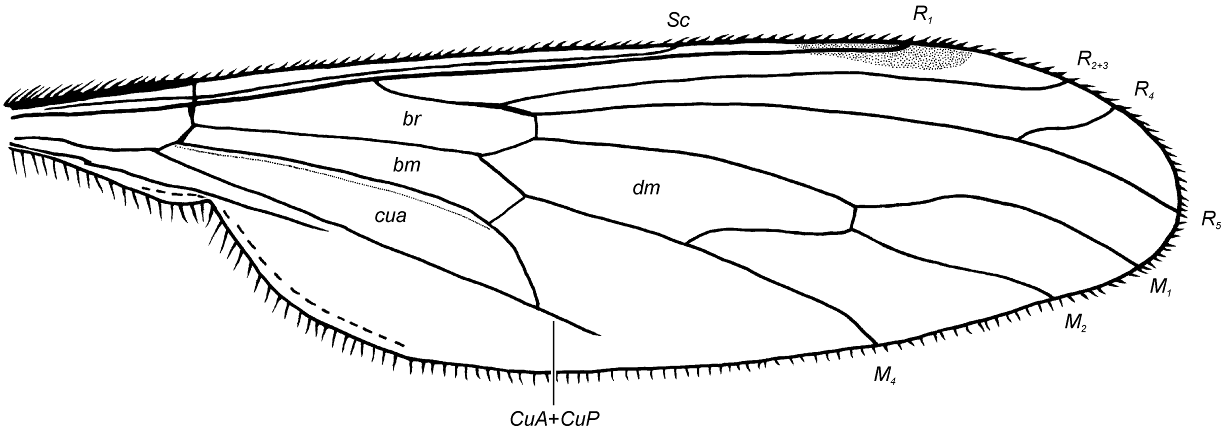
Fig. 55.1. Female of *Homalocnemis perspicua* (Hutton) (non-Afrotropical) (Kirk-Spriggs & Stuckenberg 2009, fig. 6.2).

Diagnosis

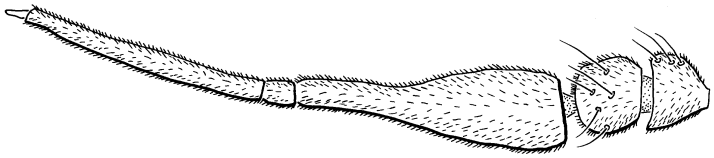
Medium-sized flies (wing length: 5–8.5 mm); darkish in colour.

Head large, wider than height, narrower than thorax (Fig. 1); compound eye large, encompassing entire lateral surface of head; males and females with eyes closely approximated on frons for long distance, upper facets enlarged; ocellar triangle prominent, elevated above eyes; antenna with postpedicel elongate; stylus elongate, cylindrical, not tapered, comprised of 2 articles, bearing apical peg-like receptor (Fig. 3); proboscis thick, tubular, projecting horizontally slightly beyond head; labrum lacking epipharyngeal blades; palpus 1-segmented, arched, closely appressed to concave face; chaetotaxy of head limited to pair of ocellar and occipital setae.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1261–1264.

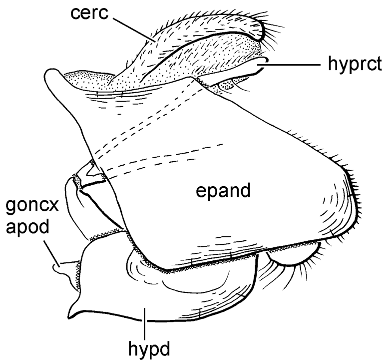


2 *Homalocnemis*

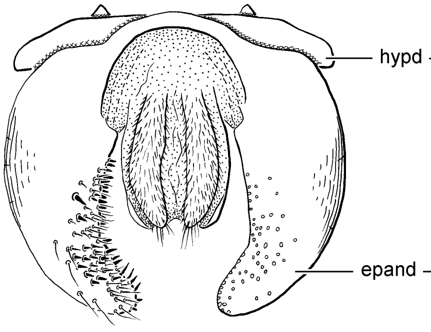


3 *Homalocnemis*

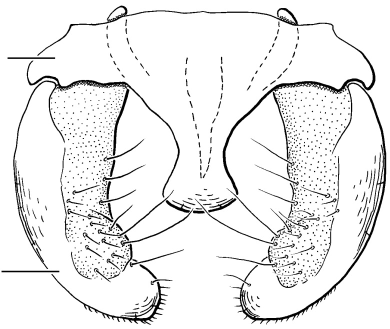
4 *Homalocnemis*



5 *Homalocnemis*



6 *Homalocnemis*



7 *Homalocnemis*

Figs 55.2–7. Wing, antenna, mid leg and male terminalia of Homalocnemidae: (2) wing of *Homalocnemis namibiensis* Chvála, dorsal view; (3) antenna of *H. adelensis* (Miller), lateral view (non-Afrotropical); (4) mid leg of *H. perspicua* (Hutton), oblique lateral view (non-Afrotropical); (5) male terminalia of *H. adelensis*, lateral view (non-Afrotropical); (6) same, dorsal view; (7) same, ventral view. Fig. 2 (after Chvála 1991, fig. 1), Fig. 3 (after Sinclair & Cumming 2006, fig. 5), Figs 5–7 (after Sinclair & Cumming 2006, figs 262, 263, 265).

Abbreviations: *bm* – basal medial cell; *br* – basal radial cell; cerc – cercus; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; epand – epandrium; goncx apod – gonocoxal apodeme; hypd – hypandrium; hyprt – hypoproct; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; *Sc* – subcostal vein.

Thorax distinctly humped, or arched; prosternum fused to proepisternum; laterotergite bare; chaetotaxy of thorax includes notopleural setae and scutellar setae, with various other dorsal setae present. Wing elongate, with anal lobe well-developed; alula reduced; stigma elongate and distinct; venation complete (Fig. 2); costa circumambient; vein *Sc* complete; vein R_{4+5} branched; vein M_1 distinctly sinuous; cell *cua* longer than basal cells *bm* and *br*, lower angle acute; vein *CuA+CuP* reaching wing margin, or abruptly ending before wing margin. Legs with erect setae; mid femur swollen, raptorial with geniculate tibia (Figs 1, 4); empodium setiform.

Abdomen subcylindrical, elongate, tergites with abdominal plaques laterally and dorsoanteriorly; male terminalia (Figs 5–7) unrotated, epandrium U-shaped, surstyli absent, hypandrium fused with phallus to form rigid intromittent organ; female terminalia without acanthophorites; cercus thinly sclerotised; 1 elongate spermatheca present internally.

Homalocnemids can generally be differentiated from other Empidoidea by their distinctive wing venation (Fig. 2), with elongate cell *cua* and branched vein R_{4+5}, broad head, with large eyes and raptorial mid legs (Fig. 4).

Biology and immature stages

In the Afrotropics, only a single specimen of *Homalocnemis* Philippi has been collected, recorded from the humid coastal fog zone of Namibia (Chvála 1991). In southern South America and New Zealand, species are known from humid temperate forests (pers. obs.), with additional collection records from near waterfalls, lakes or small pools (Collin 1928: 57). In New Zealand a concentration (approximately 5–10 individuals) of a *Homalocnemis* sp. were observed resting on, or flying near, the terminal branches of small bushes and fronds of ferns in the shrub layer, in moderately closed-canopy forest, at an elevation of *ca* 500 m. This behaviour does not represent swarming and such flights may be hunting forays (superficially similar to loose aggregations of some hunting *Hybos* spp.; A.R. Plant, pers. obs. 2014). *Homalocnemis adelensis* (Miller, 1913) has been recorded along sea-beaches, flying over pools in New Zealand (Collin 1928: 57). In Namibia the single specimen was collected on a flowering succulent growing between the desert dunes and the beach. This genus is thought to be a survivor of a Namibian mid-Tertiary woodland fauna (Kirk-Spriggs & Stuckenberg 2009: 161).

Little else is known regarding the biology and behaviour of the genus. Feeding habits have not been reported, but presumably adults are predaceous, based on the morphology of the mouthparts (Sinclair & Cumming 2006, fig. 54) and the mid legs. The mid femora are swollen (Fig. 4) in both sexes and it is likely they are used to secure prey. The immature stages are unknown.

Economic significance

No species of economic importance are currently known.

Classification

Homalocnemis has been assigned to its own subfamily, the Homalocneminae (Collin 1928), the subfamily Brachystomatinae (Chvála 1983; Melander 1928: 11; Smith 1989: 388), the subfamily Hybotinae (Collin 1933: 8), or considered *incertae sedis* within the Empidoidea and the sister-group to the remaining Empidoidea, exclusive of the *Iteaphila*-group and *Oreogeton* Schiner (Sinclair & Cumming 2006). As the Empidoidea are now recognised as comprising at least five families, the last mentioned phylogenetic position (*i.e.*, sister-group to the remaining empidoids), has led to the recognition of the family Homalocnemidae (Pape *et al*. 2011). No molecular phylogenetic studies have included samples of *Homalocnemis*.

The family is small, with only one genus and seven described species, recorded from Chile, Namibia and New Zealand (Sinclair & Cumming 2006). No additional undescribed species are currently known.

Identification

Homalocnemis was unknown from the Afrotropical Region at the time of Smith's (1969) monograph of the Empididae *sensu lato*. The familial level key in this *Manual* is the first Afrotropical key in which this family is identified. The *Homalocnemis* genus-group is included in the family and genus-group key to the Empidoidea (Sinclair & Cumming 2006). Homalocnemidae are best pinned fresh in the field or micro-pinned fresh in the field for later double-mounting (see Chapter 2).

Synopsis of the fauna

This family is poorly studied due to the scarcity of available collections. Our current knowledge of the Afrotropical fauna is based on a single female specimen.

Homalocnemis **Philippi.** A single species, *H. namibiensis* Chvála, 1991, is recorded from the coastal region of Namibia (Chvála 1991). The genus is characterised by the elongate wing cell *cua*; broadly divergent radial fork; and swollen mid femur.

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DOLICHOPODIDAE 56

(Long-legged Dance Flies)

Igor Ya. Grichanov and Scott E. Brooks

Fig. 56.1. Female of *Cemocarus* sp. (South Africa) (photograph © S.A. Marshall).

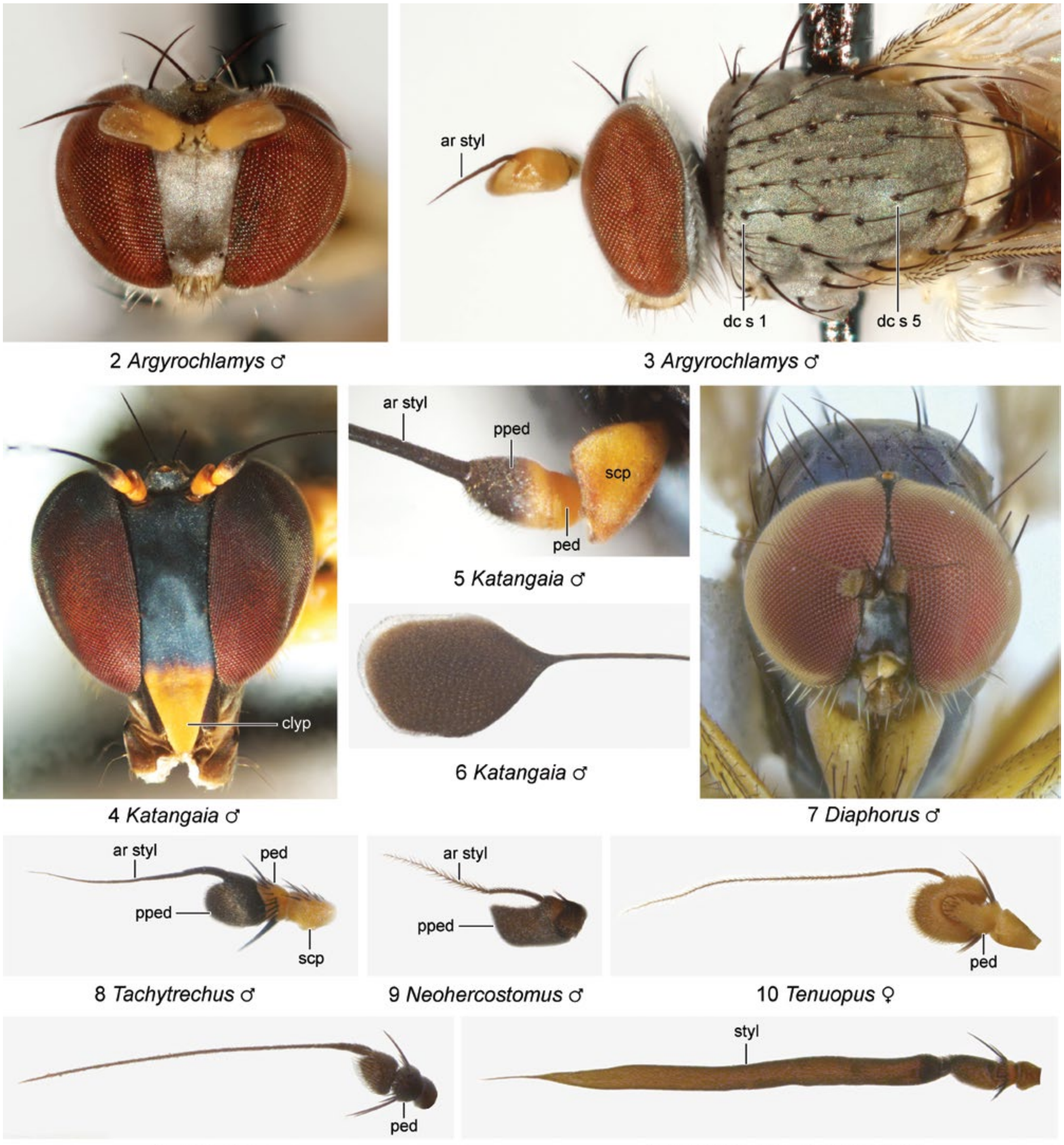
Diagnosis

The family Dolichopodidae comprising the traditional Dolichopodidae and the basal microphorine and parathalassiine genera, may be diagnosed as follows:

Small- to medium-sized flies (body length: 0.8–9.0 mm), with slender build (Figs 1, 232–237); wing with vein *Rs* originating at, or near level of humeral crossvein (*h*), shortened basal cells (less than ½ length of cell *dm*), with crossvein *r–m* in the basal ¼ of wing (*e.g.*, Figs 63, 79); male terminalia rotated and lateroflexed forward below the preceding abdominal segments, with pregenital segments partially twisted, or rotated, and several additional characters of the hypopygium (Sinclair & Cumming 2006). The microphorine and parathalassiine genera are small (1–3 mm) non-metallic, shiny whitish, or greyish pruinose to dark coloured flies, with costal vein (C) circumambient, crossvein *bm–m* present and cell *dm* emitting 3 branches (*i.e.*, veins M_1, M_2, M_4) (Figs 63, 64). The Dolichopodidae exclusive of the microphorine and parathalassiine genera (*i.e.*, the traditional Dolichopodidae), can be diagnosed by the following additional characters: costal vein (C) ending at, or before vein M_1, subcostal vein (*Sc*) very short and ending in vein R_1, cell *dm* emitting 2 veins (M_1 and M_4), and crossvein *bm–m* absent (cells *bm* and *dm* confluent) (*e.g.*, Fig. 65).

Adults often with metallic colouration, characteristically blue-green with bronze reflections, sometimes brown to black,

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. *Suricata* 5. South African National Biodiversity Institute, Pretoria; pp. 1265–1320.



2 *Argyrochlamys* ♂

3 *Argyrochlamys* ♂

4 *Katangaia* ♂

5 *Katangaia* ♂

6 *Katangaia* ♂

7 *Diaphorus* ♂

8 *Tachytrechus* ♂

9 *Neohercostomus* ♂

10 *Tenuopus* ♀

11 *Bickeliolus* ♂

12 *Chrysosoma* (*Kalocheta*) ♀

Figs 56.2–12. Heads and antennae of Dolichopodidae: (2) head of *Argyrochlamys impudicus* Lamb, anterior view ♂; (3) same, head and thorax, dorsal view (head rotated 90° showing left lateral aspect); (4) head of *Katangaia tanzaniensis* Grichanov, anterior view ♂; (5) same, antenna, lateral view; (6) same, antennal arista-like stylus (apex), lateral view; (7) head of *Diaphorus* sp., anterior view ♂; (8) antenna of *Tachytrechus tessellatus* (Macquart), lateral view ♂; (9) same, *Neohercostomus duviardi* (Couturier), lateral view ♂; (10) same, *Tenuopus* sp. ♀; (11) same, *Bickeliolus* sp. ♂; (12) same, *Chrysosoma* (*Kalocheta*) sp. ♀. Figs 2, 3 (courtesy M. Tkoc), Figs 4–6 (after Grichanov 2012e, figs 3–5).

Abbreviations: ar styl – arista-like stylus; clyp – clypeus; dc s – dorsocentral seta; ped – pedicel; pped – postpedicel; scp – scape; styl – stylus.

greyish, or yellow (Figs 232–237). Males often adorned with secondary sexual characters on head (especially antennae, mouthparts), legs, wings and abdomen. These secondary sexual characters often exhibit parallel development in unrelated groups and include flag-like flattening of the arista-like stylus and tarsomeres, strongly-modified setae and cuticular projections, prolongation and deformation of leg segments, orientated silvery tomentum, maculation and deformation of wings (Bickel 2009: 672).

Head more or less hemispherical, with sparse setation, rarely with fronto-orbital setae; compound eye occupying most of head in lateral view (Figs 1, 3, 13–16, 18, 19), rarely holoptic on frons (males of *Diaphorus* Meigen, *Schistostoma* Becker, Figs 7, 24), usually clothed in ommatrichia, but sometimes bare (*Medetera* Fischer von Waldheim, *Schistostoma*); antenna generally inserted on upper ⅓ of head, rarely below middle (male *Diaphorus*); stylus arista-like, usually comprised of 2 articles, 1 article in parathalassiines (Figs 31, 32) and in males of some species with modified antennae; proboscis developed as pair of laterally crushing labellar lobes, each with six, usually modified pseudotracheae (Sato 1991) on inner surface; Dolichopodidae *sensu stricto* with stout, pointed epipharyngeal blades (utilised in tearing the bodies of their prey) and elongated epipharyngeal apodeme projecting vertically into head.

Thorax usually with chaetotaxy well-differentiated (Figs 3, 228). Legs usually long and slender and often with reduced setation, male legs often adorned with male secondary sexual characters, including peculiarities in pubescence and chaetotaxy, and/or elongation, compression, or deformation of tarsi, tibiae, or femora. Wing (Figs 63–145) with reduced venation, M_2 usually absent, except in microphorines (Fig. 63), parathalassiines (Fig. 64), most Sciapodinae (Figs 121–131, 133–135), some *Dolichopus* Latreille (Fig. 79) and *Lichtwardtia* Enderlein (= *Dolichopus ziczac*-group *sensu* Brooks 2005) (Fig. 82); anal vein (*CuA+CuP*) abbreviated, or fold-like, not reaching wing margin.

Abdomen long and slender (*Neurigona* Rondani, Sciapodinae), to short (*Hydrophorus* Fallén), preabdomen more or less conical, narrowing apically; male usually with six symmetrical preabdominal segments, segment 7 usually modified into stalk, or hypopygial peduncle (weakly sclerotised to membranous in *Pseudohercostomus* Stackelberg), segment 8 (*e.g.*, Figs 149–151, 154, 158, 160, 194, 208) reduced to cap-like sternite covering left lateral, or sometimes basal epandrial foramen (*e.g.*, Figs 153, 190, 208); male terminalia (Figs 149–157, 159–219) rotated 90° to 180° to right and lateroflexed an additional 180° to right, hypopygium either largely encapsulated in pocket formed by abdominal sternites 5 and 6 (*e.g.*, Figs 149, 151), free but sessile (*i.e.*, exposed, but situated close to tip of abdomen on short segment 7, *e.g.*, Fig. 208), or pedunculate on stalk-like segment 7 and projecting forward beneath preabdomen (*e.g.*, Fig. 160); female preabdomen usually comprised of 5 segments with apical segments usually retracted into segment 5, sometimes (some microphorines and parathalassiines), with apical segments retracted into segment 6; female terminalia variously with dorsoapical spines, setae, or papillae, or in *Thrypticus* Gerstaecker, modified into sclerotised knife-shaped ovipositor adapted for piercing plant tissues (Fig. 147).

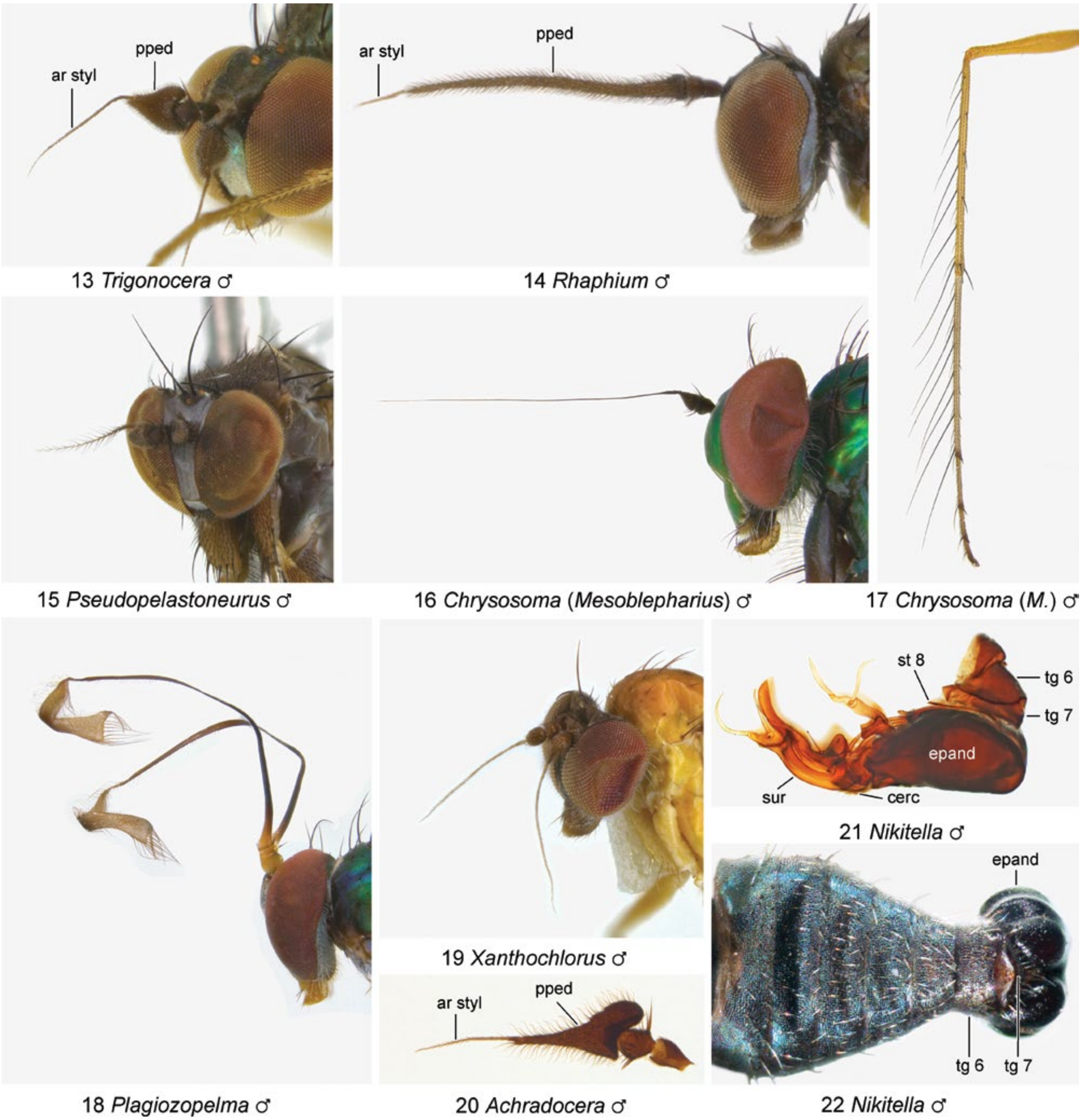
Most dolichopodids can be easily recognised by their reduced wing venation, long legs, usually with sparse setation, large compound eyes with males and females usually dichoptic, antennal stylus arista-like, labellate mouthparts, metallic thoracic colouration (Bickel 2009: 672) and male terminalia rotated and lateroflexed to the right. The basal microphorine and parathalassiine genera are non-metallic and have more complex wing venation (cell *dm* emitting three branches instead of two) and may be confused with other groups of Empidoidea at first glance. Some Clinocerinae (Empididae) (see Chapter 51), show a superficial resemblance to dolichopodids, but these almost always have wing vein R_{4+5} branched and the male terminalia are unrotated. Species of some acalyptrate families (with metallic body colouration) show a superficial resemblance to dolichopodids, but these all have a ptilinal suture, and often also possess fronto-orbital setae, genae and/or a plumose arista (Bickel 2009: 672).

Biology and immature stages

Information on the immature stages of Dolichopodidae is sparse (Robinson & Vockeroth 1981, for summary and larval key), and nothing is known about the immature stages of Afrotropical species. Larvae (Figs 224, 227) are whitish, slender, tapered anteriorly, with a 4-component mandible and apically expanded metacephalic rods (Fig. 225), creeping welts on abdominal segments 1–7, and terminal abdominal segment bearing several lobes. Pupae (Fig. 226) are characterised by a pair of long, dorsal prothoracic spiracles (Dyte 1967*b*; Robinson & Vockeroth 1981: 627).

Larvae occur in mud, damp soil, leaf litter, moss, algal mats, decaying marine algae, sap wounds, under bark, in tree hole debris, within plant tissues, and on inter-tidal rocks (Dyte 1959; Poulding 1998, 2011). Before pupation the final instar spins a protective cocoon incorporating soil particles and other environmental debris, which encapsulates the pupa, except for the tips of the prothoracic spiracles, which protrude from a small aperture (Dyte 1959). Little is known about the biology of the immature stages of dolichopodids. Most larvae are thought to be predators, or scavengers, except for *Thrypticus* which are phytophagous stem-miners in grasses, sedges and rushes (Dyte 1959; Poulding 1998).

Adults are abundant in warm moist environments, including stream and lake margins, forests, salt marshes, seashores and freshwater seepages. They occur on sand, damp ground, grass, leaves, tree trunks, river rocks and on other surfaces, usually near water. Adults are predaceous, feeding primarily on small, soft-bodied arthropods and annelids. Ulrich (2005) provided an exhaustive review of literature data on predation by adult Dolichopodidae and found that the larvae and adults of Diptera are the most frequently observed prey (especially Chironomidae and Culicidae, but see comments by Ulrich 2005), followed by Homoptera, Collembola, mites and Thysanoptera. Other documented prey items include annelids, cladocerans, amphipods, small myriapods, odonate eggs, termites, psocopterans, beetle larvae (*i.e.*, Curculionidae and Scolytidae), early instar caterpillars, dead and wounded arthropods and amphibian embryos (references in Ulrich 2005). Although the adults of some dolichopodids (*e.g.*, *Hydrophorus* Fallén, *Scellus* Loew, *Hydatostega* Phillipi, *Thinophilus* Wahlberg, *Aphrosylus* Haliday) are known to use their fore legs to hold and manipulate their prey, most grab prey directly with their flexible labellar



13 *Trigonocera* ♂

14 *Rhaphium* ♂

15 *Pseudopelastoneurus* ♂

16 *Chrysosoma* (*Mesoblepharius*) ♂

17 *Chrysosoma* (*M.*) ♂

18 *Plagiozopelma* ♂

19 *Xanthochlorus* ♂

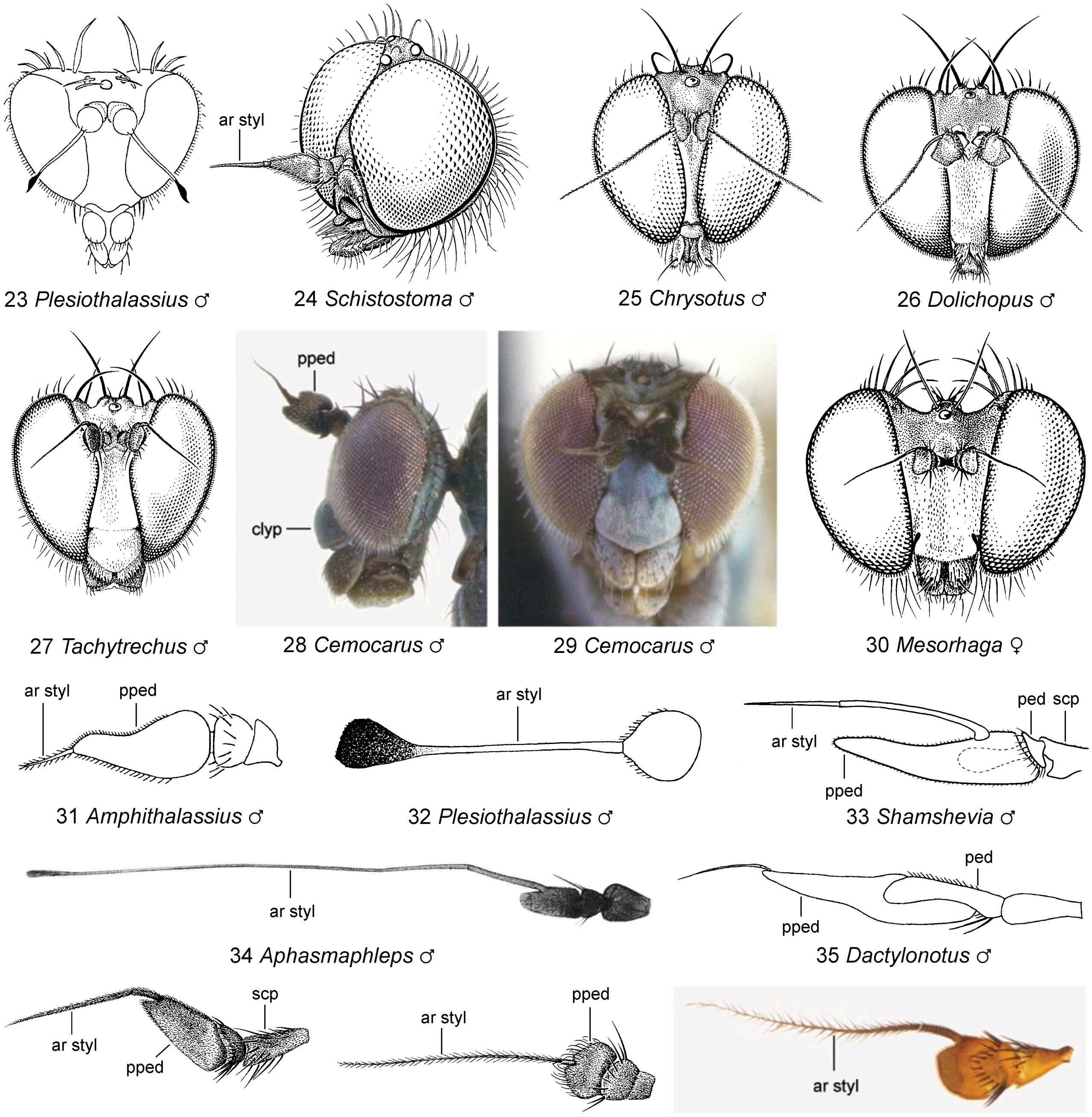
20 *Achradocera* ♂

21 *Nikitella* ♂

22 *Nikitella* ♂

Figs 56.13–22. Heads, antennae, leg, abdomen and male terminalia of Dolichopodidae: (13) head of *Trigonocera rivosa* Becker, anterolateral view ♂; (14) same, *Rhaphium* sp., lateral view ♂; (15) same, *Pseudopelastoneurus diversifemur* (Parent), anterolateral view ♂; (16) same, *Chrysosoma* (*Mesoblepharius*) sp., lateral view ♂; (17) mid leg of *Chrysosoma* (*Mesoblepharius*) sp., anterodorsal view ♂; (18) head of *Plagiozopelma bequaerti* (Curran), lateral view ♂; (19) same, *Xanthochlorus kustovi* Grichanov, anterolateral view ♂; (20) antenna of *Achradocera africana* Parent, lateral view ♂; (21) male terminalia of *Nikitella vikhrevi* Grichanov, left lateral view; (22) abdomen and male terminalia of *N. vikhrevi*, dorsal view. Figs 21, 22 (after Grichanov 2011*a*, figs 8, 9).

Abbreviations: ar styl – arista-like stylus; cerc – cercus; epand – epandrium; pped – postpedicel; st – sternite; sur – surstylus; tg – tergite.



23 *Plesiothalassius* ♂ 24 *Schistostoma* ♂ 25 *Chrysotus* ♂ 26 *Dolichopus* ♂

27 *Tachytrechus* ♂ 28 *Cemocarus* ♂ 29 *Cemocarus* ♂ 30 *Mesorhaga* ♀

31 *Amphithalassius* ♂ 32 *Plesiothalassius* ♂ 33 *Shamshevia* ♂

34 *Aphasmaphleps* ♂ 35 *Dactylonotus* ♂

36 *Argyra* ♂ 37 *Chrysotus* ♂ 38 *Apelastoneurus* ♂

Figs 56.23–38. Heads and antennae of Dolichopodidae: (23) head of *Plesiothalassius capensis* (Smith), anterior view ♂; (24) same, *Schistostoma yakimensis* (Melander) (non-Afrotropical), anterolateral view ♂; (25) same, *Chrysotus pallipes* Loew (non-Afrotropical), anterior view ♂; (26) same, *Dolichopus cuprinus* Wiedemann (non-Afrotropical) ♂; (27) same, *Tachytrechus vorax* Loew (non-Afrotropical) ♂; (28) same, *Cemocarus* sp., lateral view ♂; (29) same, anterior view ♂; (30) same, *Mesorhaga pallidicornis* Van Duzee (non-Afrotropical) ♀; (31) antenna of *Amphithalassius piricornis* Ulrich, lateral view ♂; (32) antenna (postpedicel and arista-like stylus) of *Plesiothalassius capensis* ♂; (33) same, *Shamshevia hoanibensis* Grichanov ♂; (34) same, *Aphasmaphleps paulyi* Capellari & Grichanov ♂; (35) same, *Dactylonotus rudebecki* Vanschuytbroeck ♂; (36) same, *Argyra currani* Van Duzee (non-Afrotropical) ♂; (37) same, *Chrysotus pallipes* ♂; (38) same, *Apelastoneurus ineditus* (Parent) ♂. Figs 23, 31, 32 (after Ulrich 1991, figs 2, 24, 4, respectively), Fig. 24 (Steyskal & Knutson 1981, fig. 38), Figs 25, 26, 27, 30, 36, 37 (Robinson & Vockeroth 1981, figs 6, 4, 8, 2, 14, 13, respectively), Fig. 34 (after Capellari & Grichanov 2012, fig. 5), Fig. 35 (after Grichanov 1998*b*, fig. 2).

Abbreviations: ar styl – arista-like stylus; clyp – clypeus; ped – pedicel; pped – postpedicel; scp – scape.

lobes. Prey items are punctured with the epipharyngeal blades, masticated and the liquids and liquefied contents sucked up through the labellar pseudotracheae (Ulrich 2005 and references cited therein). In addition to feeding on live prey, many adult dolichopodids have also been observed taking up honeydew (Ulrich 2005) and some are known to be anthophilous and feed on nectar (Pollet *et al*. 2010 and references cited therein).

As discussed by Bickel (2009: 672), adult male dolichopodids are known for their elaborate secondary sexual characters, which presumably facilitate species recognition during courtship. In general, males have a range of diagnostic male secondary sexual characters and/or terminalia characters, while females of closely related species are often inseparable morphologically. Many adult dolichopodids exhibit complex mating behaviour. Males of many dolichopodines engage in mating dances which usually involve wing displays, or displays of secondary sexual characteristics. Males of some species establish territories which they defend from conspecific males and other intruders (Lunau 1992). Some *Hydrophorus* males engage in mate guarding and hold the female with their fore legs following copulation, thus preventing other males from mating with her (Dyte 1988).

Economic significance

Dolichopodids are important and ubiquitous natural enemies of pests in a variety of habitats. Several genera have been reported as predators on the immatures and emerging adults of mosquitoes, including the *Anopheles gambiae* Giles complex, the most important vectors of malaria in sub-Saharan Africa (Service 1971, 1973; Ulrich 2005). The larvae of several species of the genus *Medetera* are well-documented and effective predators of developing scolytid beetles within their galleries under tree bark (Bickel 1985 and references therein).

Dolichopodids also play an important role in agroecosystems and have been recorded in considerable numbers in orchards, vineyards, crops of cotton, grains and vegetables, where they are presumed to help regulate populations of phytophagous pests (Brunel *et al*. 1989; Duviard 1973; Grichanov 1990; Rathman *et al*. 1988).

Several Neotropical species of the phytophagous genus *Thrypticus* have been reared from the petioles and stems of water hyacinth. These species have potential as biocontrol agents of this New World aquatic plant which is an invasive weed in the waterways of Asia, Australasia and Africa (Bickel & Hernández 2004).

A number of studies (*e.g.*, Gelbič & Olejníček 2011 and references cited therein; Pollet 2001) demonstrate that dolichopodids have very specific habitat requirements and react quickly to environmental changes, making them potentially useful as bioindicators for site quality assessment and conservation purposes.

Classification

Dolichopodidae is one of seven families within the superfamily Empidoidea of the Eremoneura. The other six empidoid families are the Atelestidae, Brachystomatidae, Empididae, Homalocnemidae, Hybotidae and Oreogetonidae (non-Afrotropical) (Sinclair & Cumming 2006; Pape *et al*. 2011). Recently, the limits of the Dolichopodidae have been expanded to include the microphorine and parathalassine genera, which were previously classified within the traditional Empididae or in a separate family Microphoridae (Chvála 1983). In the classification proposed by Sinclair & Cumming (2006), this expanded concept of the Dolichopodidae is referred to as Dolichopodidae *sensu lato*, whereas the subfamilies exclusive of Microphorinae and Parathalassiinae are referred to as Dolichopodidae *sensu stricto* and is equivalent to the traditional concept of Dolichopodidae. Grichanov (2011*d*) proposed the epifamily rank Dolichopodoidae, which is equivalent to Sinclair & Cumming's (2006) Dolichopodidae *sensu lato*.

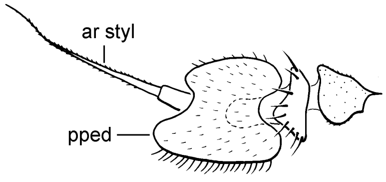
Numerous subfamily classifications have been proposed for the Dolichopodidae (*e.g.*, Becker 1917–1918; Negrobov 1986; Robinson 1970; Ulrich 1981; Yang *et al*. 2006: 3). As noted by Bickel (2009: 672), most of the currently recognised subfamilies are largely based on the Palaearctic fauna and many of these (*e.g.*, Diaphorinae, Hydrophorinae, Rhaphiinae and Sympycninae), tend to break down when applied to the super-diverse tropical and southern temperate faunas outside the Holarctic Realm.

Twelve dolichopodid subfamilies are currently recognised in the Afrotropical Region (Grichanov 2011*d*). Grichanov (2011*d*) provided an identification key to the subfamilies of Dolichopodidae that occur in the Afrotropical Region, as well as separate generic keys for each subfamily.

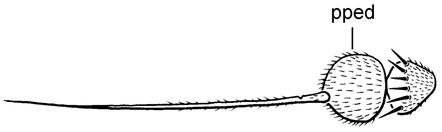
Microphorinae (= Microphoridae *sensu* Grichanov 2011*d*), is a small group of basal dolichopodids of which only three species of the genus *Schistostoma* are known to occur in the Afrotropical Region (Shamshev & Sinclair 2006). Adults are small (1–3 mm) non-metallic, greyish flies, with antennal arista-like stylus 2-articled, male eyes holoptic (Fig. 24), wing with costal vein (C) circumambient, crossvein *bm–m* complete, cell *dm* emitting 3 branches (Fig. 63). *Schistostoma* typically inhabit sandy biotopes, or stream margins.

Parathalassiinae is a small group of basal dolichopodids that are primarily associated with sea coasts. The Afrotropical fauna includes eight species and two genera, *Amphithalassius* Ulrich and *Plesiothalassius* Ulrich, from sandy coastal habitats of South Africa (Ulrich 1991). Adults are small (1–3 mm) non-metallic, whitish, or greyish pruinose flies with antennal arista-like stylus one-articled (Figs 31, 32), wing with costal vein (C) circumambient, crossvein *bm–m* virtually complete, but not usually joining vein M_1 and cell *dm* emitting three branches (Fig. 64).

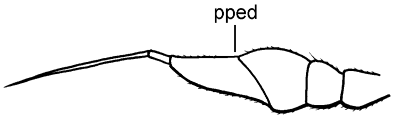
Diaphorinae is one of the most diverse subfamilies of Dolichopodidae, but its boundaries are not precisely defined (Capellari & Grichanov 2012). The subfamily is usually recognised by the arista-like stylus subapical, or inserted in apical incision (rarely basidorsal), thorax with posterior mesonotum usually not flattened, mid and hind femora each lacking anterior preapical seta, wing veins R_{4+5} and M_1 subparallel, or diverging distad of *dm–m* crossvein and lateral seta of hind coxa usually in basal quarter. Diaphorines occur in a variety of habitats and some genera (*e.g.*, *Chrysotus* Meigen and *Diaphorus*) are active on soil and vegetation in dry, to very wet



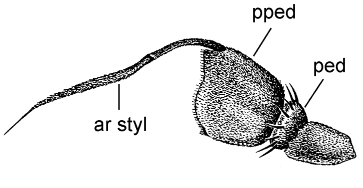
39 *Cemocarus* ♂



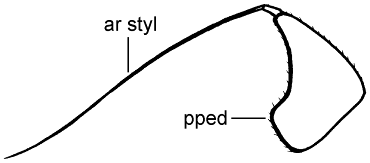
40 *Cymatopus* ♂



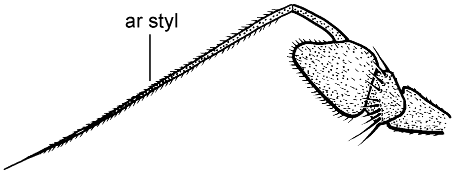
41 *Epithalassius* ♂



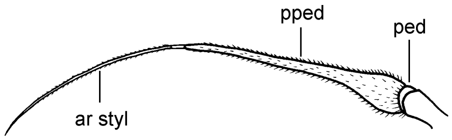
42 *Hydrophorus* ♂



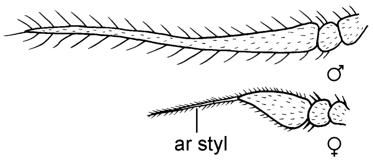
43 *Machaerium* ♂



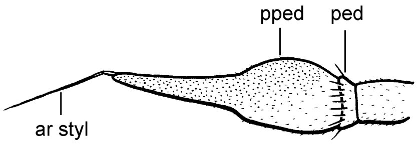
44 *Orthoceratium* ♂



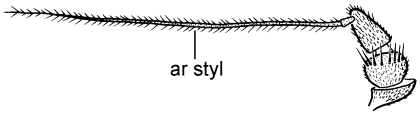
45 *Euxiphocerus* ♂



46 *Grootaertia*

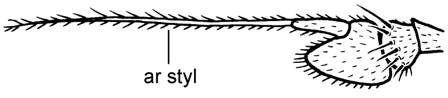


47 *Systenus* ♂

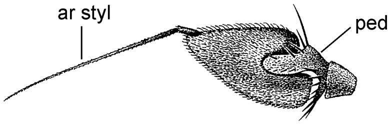


48 *Paramedetera* ♀

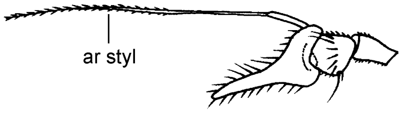
49 *Micromorphus* ♂



50 *Peloropeodes* ♂



51 *Syntormon* ♂



52 *Telmaturgus* ♂

Figs 56.39–52. Antennae (lateral views, unless otherwise stated) of Dolichopodidae: (39) *Cemocarus griseatus* (Curran) ♂; (40) *Cymatopus stuckenbergi* Grootaert & Grichanov ♂; (41) *Epithalassius susmani* Grichanov ♂ (non-Afrotropical); (42) *Hydrophorus intentus* Aldrich (non-Afrotropical) ♂; (43) postpedicel and arista-like stylus of *Machaerium thinophilum* (Loew) ♂; (44) *Orthoceratium lacustre* (Scopoli) ♂; (45) *Euxiphocerus disjunctus* Grichanov ♂; (46) *Grootaertia skorpionensis* Grichanov, Kirk-Spriggs & Grootaert ♂ (above), ♀ (below); (47) *Systenus africanus* Grichanov ♂; (48) *Paramedetera papuensis* Grootaert & Meuffels (non-Afrotropical) (dorsal view) ♀; (49) *Micromorphus maraisi* Grichanov ♂; (50) *Peloropeodes tsacasi* Grichanov ♂; (51) *Syntormon tricoloripes* Curran (non-Afrotropical) ♂; (52) *Telmaturgus mastigomyoformis* (Grichanov) ♂. Fig. 39 (after Meuffels & Grootaert 1984, fig. 7c), Fig. 40 (after Grootaert & Grichanov 2008, fig. 3), Fig. 41 (after Grichanov 2008*a*, fig. 11), Figs 42, 51 (Robinson & Vockeroth 1981, figs 20, 18, respectively), Fig. 43 (after Masolva & Negrobov 2006, fig. 12), Fig. 44 (after Grichanov *et al*. 2011, fig. 104), Fig. 45 (after Grichanov 2009*b*, fig. 2), Fig. 46 (after Grichanov *et al*. 2006, figs 1, 2), Fig. 47 (after Grichanov & Mostovski 2009*b*, fig. 2), Fig. 48 (after Meuffels & Grootaert 1997, fig. 3), Figs 49, 50 (after Grichanov 2000*c*, figs 27, 25, respectively), Fig. 52 (after Grichanov 2008*c*, fig. 42).

Abbreviations: ar styl – arista-like stylus; ped – pedicel; pped – postpedicel.

places, whereas others (*e.g.*, *Asyndetus* Loew), are common in littoral habitats (Pollet & Brooks 2008: 2238). The Afrotropical diaphorine fauna includes *ca* 75 species.

Dolichopodinae is the most diverse subfamily of Dolichopodidae and in the Afrotropics comprises *ca* 25% of the known dolichopodid fauna, with *ca* 180 described species (Grichanov 2004: 3, 2011*b*). Dolichopodines are found in a variety of habitats, ranging from salt marshes and pond margins to humid forests, or sandy beaches. The subfamily is easily recognised by the dorsally setose antennal scape (Fig. 8), mid and hind femora each with strong anterior preapical seta, male terminalia usually large, pedunculate and projecting forward beneath abdomen, and thorax with posterior mesonotum not flattened (Brooks 2005).

Hydrophorinae is a large and widespread subfamily that comprises a relatively small proportion of the known Afrotropical Dolichopodidae, with *ca* 55 described species (Grichanov 1997*e*). As a group, the subfamily is not easily diagnosed and is likely paraphyletic. The "aphrosyline" representatives (Fig. 1) have the body and legs clothed in dense grey tomentum, thorax with mesonotum usually flattened in posterior quarter, antennal postpedicel often ovate and conical, with apical arista-like stylus and mouthparts with palpus often enlarged (Bickel 2009: 675). The other hydrophorine genera can be recognised by the head with large pair of postvertical setae that are off-set from the postorbital setae, ventral postorbital setae becoming a field of fine pale setulae across the ventral postcranium and wing crossvein *dm–m* equal to, or longer than, distal section of vein M_4 (Bickel 2009: 681). Hydrophorines are among the most hygrophilous dolichopodids and several genera are restricted to rocky seashores (*e.g.*, "aphrosylines"), whereas others prefer sandy to muddy beaches (*e.g.*, *Machaerium* Haliday, *Thinophilus* Wahlberg), vertical seeps (*e.g.*, *Liancalus* Loew), or standing water (*e.g.*, *Hydrophorus*) (Pollet & Brooks 2008: 2238).

Medeterinae is a large virtually cosmopolitan subfamily of dolichopodids that includes *ca* 90 described Afrotropical species (Grichanov 1999*a*, 2000*b*, 2011*a*). Many medeterines are arboreal and rest on tree trunks, or other vertical surfaces. Over one-third of described Afrotropical species are included in the widespread and diverse genus *Medetera*. The larvae of many species of *Medetera* live in the galleries of bark beetles and are predaceous on developing beetle larvae. *Thrypticus* larvae are unique among dolichopodids as phytophagous leaf-miners in monocotyledons (Pollet & Brooks 2008: 2239). Species of the subfamily are distinguished by the head with distinctly concave occiput, the thorax with flattened posterior mesonotum, mid and hind femora each lacking anterior preapical seta and male terminalia usually large and pedunculate with segment 7 setose.

Neurigoninae are typically slender long-legged flies, with thorax and abdomen often mainly yellow. As with medeterines, they are often encountered on tree trunks. The subfamily is usually recognised by the thorax with flattened posterior mesonotum, mid and hind femora each lacking anterior preapical seta, antennal arista-like stylus dorsal, or subapical, male terminalia large and pedunculate, supported on a bare segment 7 and female terminalia with acanthophorite setae. The subfamily is not well-represented in the Afrotropical Region and is known only from female specimens from Central Africa and Seychelles, suspected to be *Neurigona* (Grichanov 2010*c*). The unusual endemic Afrotropical genus *Tenuopus* Curran, has historically been assigned to the Neurigoninae, but the genus has several atypical characters (*e.g.*, posterior mesonotum not flattened, mid and hind femora each usually with strong anterior preapical seta), suggesting that it should be excluded from the subfamily (Naglis 2001).

Peloropeodinae is a poorly defined group that includes many genera that were previously placed in the Sympycninae. The subfamily is recognised by the thorax with flattened posterior mesonotum, mid and hind femora each with anterior preapical seta, male tergite 6 and segment 7 bare, male terminalia usually large and pedunculate. There are *ca* 25 known species of peloropeodines in the Afrotropics.

Rhaphiinae is one of the more historically unstable dolichopodid subfamilies. The subfamily is not well-represented in the Afrotropical Region and comprises 15 described species in the genus *Rhaphium* Meigen (Grichanov 1995*a*, 2001).

Sciapodinae are among the largest and most conspicuous dolichopodids in the tropics and are frequently found sun-basking in the lower canopy or the higher herb vegetation (Pollet & Brooks 2008: 2239). Sciapodines comprise *ca* 30% of the known Afrotropical dolichopodid fauna, with over 230 described species (Grichanov 1998*g*, 1999*b*, 2000*b*, 2003). The genera *Amblypsilopus* Bigot and *Chrysosoma* Guérin-Méneville are particularly diverse in the Afrotropics, with over 50 described species in each. The subfamily is easily recognised by their slender habitus, head with strongly excavated vertex (Fig. 30) and branched wing vein M_{1+2} (Figs 121–135), although this last mentioned feature has been secondarily lost in *Mesorhaga* Schiner and some species of *Amblypsilopus* (Bickel 1994).

Sympycninae is one of the largest dolichopodid subfamilies, but the group is very poorly defined, with uncertain limits and is likely paraphyletic. Species of the subfamily are usually recognised by the following characters: head with postvertical setae (if present) near vertex and in-line with postorbital setae, thorax with posterior mesonotum not flattened, mid and hind femora each with strong anterior preapical seta, wing veins R_{4+5} and M_1 usually subparallel and crossvein *dm–m* usually shorter than distal section of vein M_4, and male abdominal segment 7 usually weakly-developed, with hypopygium encapsulated. Most Sympycninae are distinctly hygrophilous and occur in very wet and often shaded habitats, from salt marshes to peat moors and high altitude montane habitats (Pollet & Brooks 2008: 2239). There are over 70 described species of Sympycninae in the Afrotropical Region.

Xanthochlorinae is an enigmatic subfamily that includes the single, forest-inhabiting genus *Xanthochlorus* Loew. The subfamily is distinguished by the mainly yellow body, thorax with prescutellar depression present, mid and hind femora lacking anterior preapical setae, male abdominal tergum 6 setulose, female abdomen blunt-tipped with segments 6–7 exposed and setulose and female terminalia with acanthophorite setae. One species is known from the Afrotropical Region (Grichanov 2010*i*).

Identification

Important early works on Afrotropical Dolichopodidae include Becker (1923), who provided the first review of the family in the region and Parent (1929), who provided a checklist and identification keys to the genera and species known at that time. Other important early contributions include the works of C.H. Curran and P. Vanschuytbroeck. For a complete listing of references for these authors see Smith *et al*. (1980: 889).

Dyte & Smith (1980) catalogued the Afrotropical Dolichopodidae and listed 513 species in 51 genera. Since then, *ca* 355 species have been added, and approximately 100 previously recorded species have been either relegated to synonymy, or excluded from the region as a result of corrected misidentifications, bringing the total number of recognised species to *ca* 770. Currently, 90 genera are recognised in the region (Grichanov 2010*h*, 2011*d*; Grichanov *et al.* 2014; Naglis 2014). Key references for the Afrotropical microphorine and parathalassiine fauna include Ulrich (1991) and Shamshev & Sinclair (2006). With the exception of a few papers (*e.g.*, Couturier 1978, 1985, 1986; Meuffels & Grootaert 1984, 2007, 2009; Negrobov & Kulibali 1983; Negrobov & Schumann 1990; Negrobov *et al*. 1981, 1982, 1987; Rampini 1982; Rampini & Munari 1987), the bulk of recent systematic studies on Afrotropical Dolichopodidae *sensu stricto* has been undertaken by the first author.

For the past two decades, the first author has been actively studying the Afrotropical dolichopodid fauna, resulting in the description of 21 new genera and over 320 new species and subspecies, as well as the production of a multitude of reviews and revisionary studies at both the generic and subfamilial levels. These works were recently summarised in Grichanov's (2011*d*) monograph. The following identification key and generic synopses builds on that work and treats all 90 dolichopodid genera known to occur in the Afrotropical Region.

In general, the below identification key will work better with male specimens, as many dolichopodid genera are largely characterised by male secondary sexual characters and/or by features of the male terminalia. Figures illustrating the male terminalia in lateral view are oriented as they appear on the intact specimen (rotated 180° and lateroflexed to the right), with the morphologically ventral surface of the terminalia facing up, dorsal surface down, anterior end facing right and posterior end facing left (except Figs 171, 194 and 208, in which the posterior end is directed downwards).

Larger specimens can be direct-pinned in the field and smaller specimens can be mounted on the side of a pin using a small dab of shellac glue on the right side of the thorax, or micro-pinned for later double-mounting. Air-drying smaller specimens may cause the heads to collapse and bodies to shrivel, however, so these are generally better initially preserved in 75% alcohol for later critical-point-drying and mounting (see Chapter 2).

Key to genera of Afrotropical Dolichopodidae

1\. Wing with *bm–m* crossvein; cell *dm* emitting 3 branches to wing margin (*i.e.*, veins M_1, M_2, M_4); costal vein (C) running around wing margin (*e.g.*, Figs 63, 64); body black in ground colour, with greyish pruinosity, or whitish pruinose 2

– Wing without *bm–m* crossvein (cells *bm* and *dm* confluent); cell *bm+dm* emitting 2 veins (M_1 and M_4), vein M_1 sometimes branched, or with stump-like vein M_2 at middle of distal section; costal vein (C) ending at vein M_1 (sometimes at tip of vein R_{2+3}) (*e.g.*, Figs 65–145); body generally metallic, or yellow, rarely greyish (DOLICHOPODIDAE *sensu stricto*) 4

2\. Antennal arista-like stylus 2-articled (Fig. 24); male eyes contiguous on frons (Fig. 24); wing with anal lobe well-developed (Fig. 63) (MICROPHORINAE) . . . . *Schistostoma* Becker

– Antennal arista-like stylus 1-articled (*e.g.*, Figs 31, 32); male eyes widely separated on frons (*e.g.*, Fig. 23); wing with anal lobe reduced (*e.g.*, Fig. 64) (PARATHALASSIINAE) 3

3\. Antennal postpedicel conical, or pear-shaped, tapering apicad (Fig. 31); head with face wide in both sexes, not narrowing in middle; postocular setae uni- to biseriate; thorax with prothoracic precoxal bridge partly developed; acrostichal setae uniserial at least posteriorly, sometimes reduced; female terminalia with tergite 8 not cleft . . . . *Amphithalassius* Ulrich

– Antennal postpedicel globular, or oval, broadly rounded at apex (Fig. 32); head with face moderately wide in both sexes, more or less narrowing in middle (Fig. 23); postocular setae multiseriate; thorax with prothorax without precoxal bridge; acrostichal setae paired and flanked by accessory setae; female terminalia with tergite 8 deeply cleft . . . . *Plesiothalassius* Ulrich

4\. Vertex of head strongly excavated on either side of ocellar tubercle (*e.g.*, Fig. 30), or if weakly excavated, then wing vein M_{1+2} distinctly branched, with vein M_2 present at least as a fold in membrane (*e.g.*, Figs 113, 121–131, 133–135) (vein M_2 absent in *Mesorhaga*, Fig. 132); thorax with mesonotum usually short, about as wide as long; posterior mesonotum not flattened; male terminalia with hypopygium exerted 5

– Vertex of head usually not excavated on either side of ocellar tubercle (*e.g.*, Figs 25–27) (excavated in some *Urodolichus* Lamb); wing vein M_{1+2} unbranched (*e.g.*, Fig. 80), or with vein M_2 present only as short stump vein (*e.g.*, Figs 79, 82); posterior mesonotum various; male terminalia with hypopygium various. 24

5. Head without vertical setae in both sexes; antennal pedicel forming short thumb-like projection on inner side of postpedicel (Fig. 10); abdominal segment 1 without tergal window; male terminalia with hypopygium mostly exerted, but with small segment 7; hypandrium strongly reduced (*incertae sedis*) . . . . *Tenuopus* Curran

– Head with vertical setae strong at least in females, often setula-like in males; antennal pedicel simple, without projection (*e.g.*, Fig. 11); abdominal segment 1 with tergal window anterodorsally (Bickel 1994, fig. 1a); male terminalia with hypopygium exerted and distinctly pedunculate; hypandrium usually well-developed and asymmetrical (reduced in *Condylostylus* Bigot) (SCIAPODINAE) 6

6. Mid and/or hind femora each with distinct anterior preapical seta (*e.g.*, Fig. 54) 7

– Femora without distinct anterior preapical seta (*e.g.*, Fig. 53) 9

7. Mid and hind femora each with anterior preapical seta; tarsi simple; thorax with proepisternum with more or less strong ventral setae . . . . *Bickelia* Grichanov

– Hind femur only with anterior preapical seta; some tarsomeres of at least fore tarsus often modified; thorax with proepisternum without strong ventral setae 8

8. Male terminalia with cercus with 1–2 variously ornamented ventral projections (basoventral projection slender and free) (Fig. 210) . . . . *Mascaromyia* Bickel [in part]

– Male terminalia with cercus without basoventral projections (Fig. 217) . . . . *Sciapus* Zeller

9. Wing vein M_2 absent, without fold, or indication on membrane (Fig. 132); antennal arista-like stylus usually dorsal; head with strong vertical seta in both sexes; clypeus adjacent to margin of eyes; thorax with dorsocentral setae strong in both sexes; male terminalia with hypopygium elongate and cylindrical (Fig. 216) . . . . *Mesorhaga* Schiner

– Wing vein M_2 present, even if as fold, or indication on membrane (*e.g.*, Figs 121, 123–131, 133, 134); other characters various 10

10. Scutellum with both pairs of scutellar setae long; antennal pedicel usually with long dorsal and ventral setae; arista-like stylus dorsal, or dorsoapical; wing membrane often with dark brown fascia (*e.g.*, Figs 126–128) 11

– Scutellum usually with 1 pair of strong setae, lateral pair of setae short, setula-like, or absent; other characters various 14

11. Male hind tibia anteriorly with distinct callus or areole in basal ½; male terminalia with hypandrium and phallus long and thick; surstylus and/or epandrial lobe well-developed (Fig. 215) . . . . . *Parentia* Hardy

– Male hind tibia without distinct callus or areole in basal ½; male terminalia with hypandrium, phallus, surstylus and epandrial lobe greatly reduced (Figs 211–213) . . . . *Condylostylus* Bigot 12

12. Head with frons with strong vertical seta arising from setulose mound; fore tibia with 1–2 long apicoventral setae . . . . *Condylostylus paricoxa* Parent species-group

– Head with frons with a strong vertical seta only, with at most 1 fine setula on small mound; fore tibia without long apicoventral seta 13

13. Male wing venation modified, apical part of vein M_{1+2} strongly curved towards posterior wing margin, vein M_1 virtually in line with stump vein M_2 (Fig. 128) . . . . *Condylostylus pateraeformis* Becker species-group

– Male wing venation unmodified (Fig. 126) . . . . *Condylostylus burgeoni* Parent species-group

14. Antennal arista-like stylus usually apical on triangular postpedicel, usually long and more than ½ body length in females; male arista-like stylus sometimes with apical flag (*e.g.*, Fig. 18); fore tibia often with long seta; wing with *dm–m* crossvein various (*e.g.*, Figs 124, 125, 130, 134) 15

– Antennal arista-like stylus usually distinctly dorsal on subrectangular postpedicel and rarely longer than head width (*e.g.*, Fig. 11), or if apical, or dorsoapical, then invariably with following characters: male antenna with arista-like stylus rarely with apical flag; tibial chaetotaxy often weak, especially in males; wing with *dm–m* crossvein usually straight (*e.g.*, Figs 121, 123, 129, 131) 20

15. Antennal postpedicel very long; head with vertical setae short, or absent in both sexes; frons and face narrow; wing with *dm–m* crossvein straight, or slightly convex (Fig. 130); thorax with acrostichal setae short and weak; pleura usually yellow; tibiae and first tarsomeres with strong setae in both sexes; male terminalia with cercus simple . . . . *Gigantosciapus* Grichanov

– Antennal postpedicel usually short; head with vertical setae, strong (at least in female), or setula-like; frons and face usually broad; wing with *dm–m* crossvein sinuous (*e.g.*, Fig. 124), or straight (*e.g.*, Fig. 121); thorax with acrostichal setae often long; other characters various 16

16. Wing with *dm–m* crossvein usually straight (Fig. 121); legs elongate, with a few major setae; male terminalia with cercus simple . . . . *Amblypsilopus* Bigot [in part]

– Wing with *dm–m* crossvein usually sinuous (*e.g.*, Figs 124, 125) (sometimes sinuation weak, *e.g.*, Fig. 134); tibiae often with major setae; male terminalia with cercus usually deeply forked. 17

17. Head with frons highly polished, metallic blue-green; male frons bare, or with single weak vertical seta only; male antennal scape often swollen and vase-shaped; pedicel usually with short ventral and dorsal setae (Fig. 18); fore coxa with either 3–7 strong lateral spine-like setae (stronger in females than males), or fore coxa with 3 strong black distolateral setae. . . . . *Plagiozopelma* Enderlein

– Head with vertex and frons usually with pruinosity, sometimes polished; male frons often with setulae on lateral slope; male antennal scape rarely swollen and vase-shaped; pedicel often with long ventral and dorsal setae; fore coxa without strong lateral spine-like setae . . . . . . *Chrysosoma* Guérin-Méneville 18

18. Male mid tarsomere 1 and tibia without long setae . . . . *Chrysosoma sensu stricto*

– Male mid tarsomere 1 (and usually mid tibia), with very long posterior, or posterodorsal setae (*e.g.*, Fig. 17). 19

19. Antenna in both sexes with stylus strongly flattened and strap-like, with setula-like apical part (Fig. 12) . . . . *Chrysosoma* (*Kalocheta* Becker)

– Antenna in both sexes with stylus simple, arista-like . . . . *Chrysosoma* (*Mesoblepharius* Bigot)

20. Male terminalia with cercus with distinctive sclerotised basal hook-shaped lobe (*e.g.*, Figs 218, 219); scutellum without lateral seta; male fore tarsomere 1 flattened, forming ventral cushion with dense pale pile 21

– Male terminalia with cercus without sclerotised basal hook-shaped lobe; other characters various . . . 22

21. Male head with strong vertical seta; thorax with acrostichal setae short, or absent; wing with alula usually reduced (Fig. 123); femora usually bare; male terminalia with cercus usually with apical brush of long setae (Fig. 219). . . . . *Bickeliolus* Grichanov

– Male head with group of setulae laterally on frons; thorax with 3 long acrostichal setae; wing with alula well-developed (Fig. 129); femora usually with long black ventral setulae; male terminalia with cercus with short, or long setae, but without apical brush (Fig. 218) . . . . *Ethiosciapus* Bickel

22. Head with face wide; thorax with 4 strong dorsocentral setae (anterior seta sometimes short); male fore tarsomere 1 slightly broadened, with ventral pile; male terminalia with hypopygium globular, with basal foramen, cercus with ventral lobe articulated at base (Fig. 214) . . . . *Dytomyia* Bickel

– Head with face narrow; thorax with dorsocentral setae various; male fore tarsomere 1 usually simple; male terminalia with hypopygium various, usually with lateral foramen 23

23. Head with vertical setae in males usually strongly reduced, or lateral frons with dense setulae; thorax of male usually with some anterior dorsocentral setae weak and setula-like; female fore femur rarely with strong basoventral setae; male terminalia with cercus usually simple . . . . *Amblypsilopus* Bigot [in part]

– Head with strong vertical setae, either in both sexes, or in females alone; proclinate vertical setae sometimes absent in males; thorax in both sexes with 4–5 dorsocentral setae, all strong; female fore femur often with stout basoventral setae; male terminalia with cercus usually with 2 strong ventral projections (Fig. 210) . . . . *Mascaromyia* Bickel [in part]

24. Head with clypeus beak-like, projecting below ventral eye margin; frons height extremely reduced, with base of antennae closely abutting ocellar triangle near vertex of head (Fig. 4); antennal arista-like stylus apical (Fig. 5) with thickened, or broad flag-like tip in males (Fig. 6); male terminalia with hypopygium large and pedunculate, with large cercus-bearing claw-like medial projection (Fig. 174) (*incertae sedis*) . . . . *Katangaia* Parent

– Head with clypeus variable, ventral margin truncate or rounded, ending before or projecting below ventral eye margin (*e.g.*, Figs 2, 7, 15, 25–29), but not usually beak-like; frons height not usually extremely reduced, antennae inserted lower on head (*e.g.*, Figs 2, 13, 15, 25–29); male terminalia with cercus not as above; other characters variable 25

25. Habitus bulky; wing veins R_{4+5} and M_1 divergent (Fig. 85); thorax with metepimeron wide; hind coxa with lateral seta at apex; mid and hind femora wide and compressed laterally, each with strong anterior preapical seta; all tibiae with strong setae; mid and hind tarsi with dense, closely-spaced transverse bands of short setae; female terminalia with hemitergites of tergite 10 densely clothed in acanthophorite spines (Fig. 148); male terminalia with abdominal segment 7 reduced (weakly sclerotised to membraneous); hypopygium (Fig. 175) encapsulated (*incertae sedis*) . . . . *Pseudohercostomus* Stackelberg

– Habitus various; wing veins R_{4+5} and M_1 usually subparallel or convergent (*e.g.*, Figs 65, 67, 69–84, 86–120, 136–144), sometimes divergent (*e.g.*, Fig. 68); mid and hind femora with, or without, strong anterior preapical seta; tibial chaetotaxy variable; mid and hind tarsi usually without closely-spaced transverse bands of short setae; female terminalia with hemitergites of tergite 10 not densely clothed in spines, usually bearing single transverse row of acanthophorite spines, or setae; male terminalia with abdominal segment 7 variable; hypopygium encapsulated or pedunculate; other characters differ. 26

26. Antennal scape with setae on dorsal surface (*e.g.*, Fig. 8); thorax with posterior mesonotum not flattened; mid and hind femora each with strong anterior preapical seta; all tibiae with strong setae; male terminalia with hypopygium (*e.g.*, Figs 159–170, 172, 173) usually large, supported on a well-developed peduncle-like segment 7 (e.g., Fig. 160) and projecting forward beneath preabdomen (hypopygium small with segment 7 short and largely hidden in *Pseudopelastoneurus* Grichanov, Fig. 171) (DOLICHOPODINAE) 27

– Antennal scape usually bare (some *Argyra* Macquart and *Syntormon* Loew spp. with setae on dorsal surface of scape); other features variable 43

27. Wing vein M_{1+2} with angular, seemingly broken, zigzag-shaped bend, with anteroproximal and posterodistal stump veins (Fig. 82); veins R_{4+5} and M_1 virtually parallel; hind tarsomere 1 with distinct dorsal seta (sometimes short) . . . . *Lichtwardtia* Enderlein (= *Dolichopus ziczac*-group *sensu* Brooks 2005)

– Wing vein M_{1+2} not as above (sometimes with M_2 stump vein); vein R_{4+5} and distal part of vein M_1 converging, or subparallel; hind tarsomere 1 with, or without, distinct dorsal setae 28

28. Hind tarsomere 1 with 1–3 strong dorsal setae; wing vein M_1 sigmoid at middle of distal part, sometimes with stump vein M_2 (Fig. 79) . . . .*Dolichopus* Latreille

– Hind tarsomere 1 lacking strong dorsal setae, rarely with 1–2 weak dorsal setae, slightly longer than diameter of tarsomere 1 (a few *Afrohercostomus* Grichanov spp.); wing vein M_1 various. 29

29. Head with face narrowed beneath antennae, somewhat widened towards clypeus (Fig. 27); antennal arista-like stylus short and bare; postpedicel usually short and suboval (Fig. 8); hind femur with series of strong anterodorsal setae in apical ½, preceding anterior preapical seta; wing vein M_1 usually with gentle anterior bend before middle of distal part, then running towards vein R_{4+5}, reaching costal vein (C) well before wing tip (Fig. 89) . . . .*Tachytrechus* Haliday

– Head with face regularly narrowed towards clypeus, or parallel-sided; antennal arista-like stylus often pubescent; postpedicel usually subtriangular, asymmetrical; hind femur usually without series of strong anterodorsal setae preceding anterior preapical seta; wing vein M_1 with anterior bend, or straight . . . 30

30. Wing vein M_1 virtually straight (*e.g.*, Figs 75, 77), or slightly convex anteriorly (e.g., Fig. 83); veins M_1 and R_{4+5} subparallel; if veins M_1 and R_{4+5} weakly convergent (some *Neohercostomus* Grichanov spp.), then male antennal postpedicel securiform, with basidorsal arista-like stylus (*e.g.*, Fig. 9) 31

– Wing vein M_1 with distinct anterior bend, curve or sinuation; veins M_1 and R_{4+5} distinctly convergent (e.g., Figs 76, 78, 80, 81, 84, 86–88); male antennal postpedicel not as above. 36

31. Antennal arista-like stylus bearing long pubescence; thoracic pleura with cluster of fine setulae anterior to posterior spiracle; thorax with 5 dorsocentral setae; male mid tarsomeres 1–4 often clear white; hind femur with anterior preapical seta positioned far from apex (0.6–0.7 length from base); wing membrane usually brown, often with pale transverse fascia just beyond *dm–m* crossvein (Fig. 77); male terminalia with hypopygium large; epandrium ovoid, longer than high, apicoventral epandrial lobe long and slender, with expanded apex; apex of postgonite narrow; hypandrium simple, narrow and trough-like; cercus small, simple with a few long setae on distal margin (Fig. 162) . . . . *Afropelastoneurus* Grichanov

– Antennal arista-like stylus with pubescence variable; thoracic pleura anterior to posterior spiracle with setulae absent or present; thorax with 5–6 dorsocentral setae; hind femur with anterior preapical seta usually near apex; wing not as above, evenly greyish to hyaline, apex sometimes with dark macula, or white margin in male; other characters various. 32

32. Thorax with distinct darkened area above notopleuron; 6 dorsocentral setae; male tarsomeres 3–5 usually flattened and slightly widened, often with silvery pile on one side (Fig. 59); male abdominal spiracle 7 enlarged (Fig. 158); male terminalia with hypopygium with hypandrium short, conical, fused to epandrium laterally; cercus subtriangular and usually pale (Fig. 159). . . . . *Afrohercostomus* Grichanov

– Thorax lacking darkened area above notopleuron; 5–6 dorsocentral setae; male hind tarsus unmodified; male abdominal spiracle 7 not enlarged; male terminalia with hypopygium not as above. 33

33. Male antennal postpedicel securiform, with basidorsal arista-like stylus (Fig. 9); mid tibia lacking strong ventral setae, at most with row of weak ventral setae; thorax with 5 dorsocentral setae . . . . *Neohercostomus* Grichanov 34

– Male antennal postpedicel subtriangular with mid-dorsal arista-like stylus, or elongate triangular with basidorsal arista-like stylus; mid tibia with at least 1 strong ventral seta; thorax with 5–6 dorsocentral setae 35

34. Head with ventral postocular setae black, or white; hind femur blackish, or brown at least in apical ⅓; male wing apex unmodified; male terminalia with hypopygium pedunculate, anteriorly directed in habitus; epandrium elongate, symmetrical; cercus usually narrow, often ornamented with processes, or bunches of long setae (Figs 166, 168). . . . . *Neohercostomus* (*Neohercostomus* Grichanov)

– Head with ventral postocular setae black; hind femur entirely yellow, or darkened at apex; male wing apex modified, membrane with dark macula, or white margin near tip of vein M_1; male terminalia with hypopygium sessile, ventrally directed in habitus; epandrium rounded, left and right epandrial lobes asymmetrical; male cercus small, suboval, without processes, or bunches of long setae (Fig. 167). . . . . *Neohercostomus* (*Subhercostomus* Grichanov)

35. Male antennal pedicel reduced; head with clypeus lacking pair of strong setae; thoracic pleura bare anterior to posterior spiracle; male terminalia with hypopygium with right and left basiventral epandrial lobes elongate and digitiform, with pointed knob-like tip, shifted ventrally and flanking hypandrium, forming a composite tripartite structure in ventral view (Brooks 2005, figs 32A–C); dorsal lobe of surstylus with preapical frayed seta (Brooks 2005, fig. 32B). . . . . *Sybistroma* Meigen [in part]

– Male antennal pedicel normally developed; head with clypeus bearing 1 pair of strong setae in both sexes (Fig. 231, indicated with arrow); thoracic pleura with cluster of fine setulae anterior to posterior spiracle; male terminalia with hypopygium not as above (see Grichanov *et al*. 2014, fig. 3) . . . . *Setihercostomus* Zhang & Yang

36. Body non-metallic; thorax grey pruinose (*e.g*., Fig. 3), mainly black, or yellow (sometimes with dark longitudinal fascia); abdomen dark grey-brown to partly or mostly yellow, with black dorsolateral maculae; thorax with 6 dorsocentral setae with fifth pair strongly off-set medially (*e.g*., Fig. 3), or 5 dorsocentral setae aligned in row; wing vein M_1 beyond *dm–m* crossvein with strong anterior bend and convergent with vein R_{4+5}; *dm–m* crossvein located near middle of wing length, or in basal ⅓ (*e.g*., Figs 78, 84); female terminalia (*e.g*., Fig. 146) with tergite 10 undivided, V-shaped, with acanthophorite spines encircling apex; tergite 8 with rod-like apicolateral projections that protrude from tip of abdomen. 37

– Body usually metallic; thorax with 5–6 dorsocentral setae, aligned, or with penultimate pair weakly off-set medially; wing venation variable; *dm–m* crossvein located near middle of wing length; female terminalia with tergite 10 divided medially, not V-shaped, hemitergites broad with transverse row of acanthophorite spines; tergite 8 lacking rod-like apicolateral projections 38

37. Head with frons distinctly wider than high and shorter than face; face broad in both sexes (Fig. 2); antennal arista-like stylus dorsal (Fig. 3) to apical; thorax densely grey pruinose, or yellow, with white pruinescence . . . . *Argyrochlamys* Lamb

– Head with frons about as wide as high and subequal to height of face; face of male very narrow (slightly wider in female); antennal arista-like stylus basidorsal; thorax yellow-orange with dark longitudinal fascia to mainly black. . . . . *Pseudargyrochlamys* Grichanov

38. Male antennal pedicel reduced, postpedicel subtriangular, slightly longer than high, arista-like stylus subapical, bare, basal article *ca* ⅓ length of distal article, black and evenly thickened, distal article dirty yellow basally, with white suboval apical lamella; male wing modified with thumb-like apical projection (Fig. 88); male fore tarsomeres 1–5 dorsoventrally flattened; male terminalia with hypopygium as in Fig. 172 . . . . *Sybistroma* Meigen [in part]; *S. bogoria* (Grichanov)

– Male antenna not as above; male wing without thumb-like apical projection; legs variable; male terminalia not as above; other characters differ 39

39. Wing vein M_1 with weak sinuous anterior bend at middle of distal part, weakly convergent, or subparallel to vein R_{4+5} at wing apex (Fig. 80); male fore tarsus modified, tarsomeres 3–5 usually with crest of dorsal setae, tarsomere 3 usually laterally flattened, tarsomeres 4 and 5 slender, or laterally flattened (Fig. 55); mid femur with 1 strong posterior preapical seta about even with anterior preapical seta; hind femur usually slender; male terminalia with hypopygium with basiventral epandrial lobes and hypandrium forming a complex of entangled asymmetrical lobes (Fig. 165) . . . . *Hercostomus* Loew

– Wing vein M_1 with distinct anterior bend in distal part, strongly convergent with vein R_{4+5}, or strongly sinuate and usually distinctly convergent with vein R_{4+5} (e.g., Figs 76, 81, 86, 87); hind femur often wide and laterally flattened; male terminalia with hypandrium free, not entangled with epandrial lobes; other characters various 40

40. Body colouration brownish; antennal arista-like stylus plumose, with dorsal and ventral setulae longer than lateral setulae (Fig. 15); thorax with acrostichal setae biserial, or quadriserial; fore and mid femora

yellow, hind femur mostly dark brown; hind tibia lacking strong ventral setae; wing vein M_1 with abrupt anterior bend just beyond middle of distal part, with gentle arc towards vein R_{4+5} (Fig. 87); male terminalia small, rounded and encapsulated (Fig. 171) . . . . *Pseudopelastoneurus* Grichanov

– Body usually metallic; antennal arista-like stylus with long, or short pubescence; thorax with acrostichal setae usually biserial, never quadriserial; femora differently coloured; hind tibia with, or without, strong ventral setae; wing vein M_1 various; male terminalia with hypopygium usually large and pedunculate; other characters various 41

41. Antennal arista-like stylus dorsal, usually at distal ⅔, or ¾ of postpedicel, with short pubescence; wing vein M_1 convex posteriad, with gentle curvation towards vein R_{4+5} at middle of distal part (Fig. 86); thorax usually with fine setulae on metepimeron; male fore or mid legs often ornamented; male terminalia with hypopygium (Fig. 170) large and dark coloured; epandrium trapezoidal, longer than high in lateral view, with shorter ventral side; apicoventral epandrial lobe expanded distally, often with 1–2 finely branched setae; cercus large and black, often with inner lobe, or fold-bearing brush of setulae . . . . *Pseudoparaclius* Grichanov

– Antennal arista-like stylus with pubescence short or long; wing with curvature of vein M_1 variable; male terminalia with hypopygium not as above; epandrium variously shaped, not trapezoidal; apicoventral epandrial lobe without 1–2 finely branched setae; other features variable 42

42. Antennal arista-like stylus short-pubescent, with setulae shorter than basal diameter of stylus; wing vein M_1 with abrupt right-angular anterior bend at distal ⅔, with deep arc towards vein R_{4+5} (Fig. 76); hind tibia without strong ventral setae, usually with row of very fine short setae; male terminalia with hypopygium (Fig. 161) with epandrium large, suboval, nearly 2 × as long as high; apicoventral epandrial lobe very small, not stick-shaped; hypandrium and phallus narrow and simple; postgonite and surstylus relatively short; surstylus with dorsal lobe distinctly broader than ventral lobe; cercus small, simple . . . . *Afroparaclius* Grichanov

– Antennal arista-like stylus usually long-pubescent (Fig. 38), with setulae at least 1.5–2.0 × longer than basal diameter of stylus; wing vein M_1 various, often gently curved, or sinuate, without abrupt right-angular anterior bend (Fig. 81); hind tibia usually with strong ventral setae, if absent then male terminalia with apicoventral epandrial lobe stick-shaped; hypopygium various; other characters various . . . . *Apelastoneurus* Grichanov

43. Labellum hook-shaped in lateral view, with long recurved, generally protruding hypopharynx (*e.g.*, Fig. 229); palpus large and triangular (HYDROPHORINAE [in part]) 44

– Labellum normal in lateral view, not hook-shaped, hypopharynx not recurved and protruding; palpus variable 45

44. Antennal postpedicel rounded basally, with narrow conical apex and apical arista-like stylus (Fig. 229); fore tibia at apex with distinct erect spine-like seta; male hind tarsomere 1 simple, without strong setae (north-western coastal Afrotropics) . . . . *Aphrosylus* Haliday

– Antennal postpedicel globular basally, with short conoid apex; arista-like stylus dorsal; fore tibia without spine-like seta at apex; male hind tarsomere 1 curved, with strong setae (Canary Is.) . . . . [*Teneriffa* Becker]

45. Thorax with proepimeron with ventral digitiform projection behind base of fore coxa (Fig. 230, indicated with arrow); males and often females with wing venation distorted and wing tip modified (Fig. 96); large gangly flies (HYDROPHORINAE [in part]) . . . . *Liancalus* Loew

– Thorax with proepimeron lacking ventral digitiform projection behind base of fore coxa; other characters various 46

46. Antennal postpedicel large, trapezoidal, with short arista-like stylus situated in dorsoapical excavation of postpedicel (Figs 28, 39); head with face wide (Fig. 29); clypeus prominent and bulging (Figs 1, 28); found on marine coasts (HYDROPHORINAE [in part]) . . . . *Cemocarus* Meuffels & Grootaert

– Antennal postpedicel and arista-like stylus not as above; other characters various. 47

47. Wing vein M_1 with two right angle bends in male, moderately sinuous in female; *dm–m* crossvein longer than apical part of vein M_4 (Fig. 98); thorax with 7 strong dorsocentral setae; posterior mesonotum flattened immediately anterior to scutellum; mid and hind femora each with strong anterior preapical seta; antenna with dorsal arista-like stylus (Fig. 44); male terminalia with hypopygium as in Fig. 180; large gangly flies (HYDROPHORINAE [in part]). . . . . *Orthoceratium* Schrank

– Wing vein M_1 without two right angle bends in male; other characters various 48

48. Thorax with posterior mesonotum distinctly flattened and slightly depressed, from ⅓–½ of surface, between dorsocentral setae and distinct from curved anterior mesonotum (*e.g.*, Fig. 228) (note: the

mesonotal depression may be bulged outwards and obscured in specimens that have been critically-point-dried) 49

– Thorax with posterior mesonotum not flattened, or at most, only slightly, or apparently flattened immediately anterior to scutellum 71

49. Mid and/or hind femora with distinct anterior, or anterodorsal preapical seta; wing veins R_{4+5} and M_1 subparallel (*e.g.*, Figs 115–119) (PELOROPEODINAE) 50

– Mid and hind femora bare of major anterior preapical seta; wing veins R_{4+5} and M_1 various 54

50. Thorax without acrostichal setae; scutellum with single pair of setae; male terminalia sessile (Fig. 198) . . . . *Micromorphus* Mik

– Thorax with acrostichal setae, although sometimes small; other characters various 51

51. Male head with face broad, slightly narrowed downward; face beneath antennae 2 × as wide as height of postpedicel; wing with *dm–m* crossvein very short, at least 5 × shorter than apical part of vein M_4, located at basal ⅓ of wing length (Fig. 116); male terminalia with surstylus L-shaped (Fig. 196), left dorsal surstylar arm shorter, or longer than right one . . . . *Meuffelsia* Grichanov

– Male head with face distinctly, or strongly narrowed downward; wing with *dm–m* crossvein at most 2–3 × shorter than apical part of vein M_4 (*e.g.*, Figs 115, 118, 119); male terminalia with surstylus not as above 52

52. Male claws symmetrical on fore tarsus; male mid coxa without apical spine of glued setae; abdomen longer than thorax; male terminalia with segment 7 short, or long . . . . *Griphophanes* Grootaert & Meuffels

– Male claws on fore tarsus symmetrical or asymmetrical; male mid coxa with or without apical spine of glued setae; abdomen as long as thorax; male terminalia with segment 7 short (*e.g.*, Fig. 194) 53

53. Antennal arista-like stylus dorsal (Fig. 50); male claws asymmetrical on fore tarsus (Fig. 56); male mid coxa usually with apical spine of glued setae . . . . *Peloropeodes* Wheeler

– Antennal arista-like stylus apical, or subapical, inserted in notch of postpedicel; male claws symmetrical on fore tarsus; male mid coxa without apical spine of glued setae . . . . *Nepalomyia* Hollis

54. Body and legs clothed in dense grey tomentum, usually obscuring cuticle; antennal postpedicel with apical arista-like stylus; head with postorbital setae strong, in single row dorsally, but as field of fine, pale setulae across ventral postcranium; found on marine coasts (HYDROPHORINAE [in part]) 55

– Body tomentum usually not dense with underlying cuticle visible; other characters various 56

55. Antennal postpedicel (Fig. 41) with distinct transverse ridge, appearing bisegmented, apical portion beyond ridge subtriangular; thorax with acrostichal setae; wing (Fig. 93) rather broad, with veins R_{4+5} and M_1 convergent; vein M_1 curved anteriorly reaching wing margin before wing apex; male terminalia with hypopygium with bilobate cercus (Fig. 179) . . . . *Epithalassius* Mik

– Antennal postpedicel without transverse ridge, rounded (Fig. 40), or subtriangular; thorax without acrostichal setae; wing (Fig. 92) relatively narrow with veins R_{4+5} and M_1 subparallel; vein M_1 more or less straight, reaching wing margin at wing apex; male terminalia with hypopygium with cercus single-lobed, strap-like (Fig. 178) . . . . *Cymatopus* Kertész

56. Antennal arista-like stylus usually dorsal; head with face with dense tomentosity; wing vein M_1 distinctly sinuate at middle of distal part, with pronounced flexion (*bosse alaire*) in membrane (Fig. 112); hind tarsomere 1 usually longer than tarsomere 2; male abdominal segments 4 and/or 5 sometimes with ventral modifications; male terminalia with hypopygium usually globular, on peduncle formed by short segment 7 and sometimes enfolded by preceding abdominal segments (NEURIGONINAE) . . . . *Neurigona* Rondani

– Antennal arista-like stylus usually apical, sometimes subapical, dorsal, or basidorsal; head with face often metallic; wing vein M_1 various (*e.g.*, Figs 72, 100–111, 144); hind tarsomere 1 usually much shorter than tarsomere 2; male abdominal segments 4 and 5 unmodified; male terminalia with hypopygium pedunculate, sessile, or encapsulated 57

57. Male antennal scape with long, pointed ventral process; antennal pedicel with long apical condyle or conus projecting into postpedicel; male postpedicel long and flat with pointed apex, arista-like stylus basidorsal with basal article longer than apical article (Fig. 33); wing with *dm–m* crossvein faint, located near wing base (Fig. 72) (DIAPHORINAE [in part]) . . . . *Shamshevia* Grichanov

– Antenna not as above, arista-like stylus usually apical, sometimes subapical, or dorsal; wing with *dm–m* crossvein well-developed, located well distal to wing base (*e.g.*, Figs 100–111, 144) 58

58. Antennal arista-like stylus dorsal; thorax with acrostichal setae absent; male wing often with posterior margin angular (Fig. 105); male abdominal tergite 1 with pair of dorsal bulb-like structures; female abdominal tergite 1 with several strong setae in place of bulb-like structures; male terminalia with cercus long and narrow (Fig. 187) (MEDETERINAE [in part]) . . . . *Craterophorus* Lamb

– Antennal arista-like stylus usually apical, sometimes subapical; thorax with acrostichal setae present, or absent; male wing with posterior margin rounded; abdominal tergite 1 without dorsal bulb-like structures, or strong setae; male terminalia with cercus variable. 59

59. Antenna sexually dimorphic; male postpedicel elongate; wing veins R_{4+5} and M_1 subapically bowed; distal sector of veins R_{4+5} and M_1 with flexion (*e.g.*, Figs 100–103); thorax with posterior pair of acrostichal setae often distinctly larger than preceding pair and off-set laterally; usually 6 strong dorsocentral setae; male terminalia with abdominal segment 7 with tergite and sternite distinct; epandrium and hypandrium immovably fused (*e.g.*, Figs 181–184); female terminalia with tergite 10 divided medially into 2 hemitergites, each bearing row of 4 spines (MEDETERINAE [in part]) 60

– Antenna usually similar in male and female, or sometimes dimorphic (e.g., Fig. 46); wing veins R_{4+5} and M_1 subparallel (*e.g.*, Figs 104, 106, 108, 144), or convergent (*e.g.*, Figs 107, 109–111); vein M_1 without flexion; thorax with acrostichal setae absent, or aligned in 2 rows; usually 5, or fewer dorsocentral setae; male terminalia with abdominal segment 7 with tergite and sternite seemingly fused, or sternite greatly reduced; hypandrium free and movable; female hemitergites usually without spines 63

60. Antennal pedicel reduced and very short (especially in males), with pair of long apicodorsal setae (⅔ length of scape) in both sexes; male postpedicel elongate-triangular, arista-like stylus longer than postpedicel; male fore tarsomeres 4 and 5 and claws distinctly modified; male abdominal sterna 4–6 well-sclerotised; segment 6 mostly concealed, bare; male terminalia with tergite 7 forming very narrow ring, enclosed within segment 6; hypopygium sessile, cercus over 2 × length of epandrium (Fig. 184) . . . . *Systenoneurus* Grichanov

– Antennal pedicel reduced, or unmodified, with only short setae (*e.g.*, Fig. 47); male postpedicel not regularly triangular; arista-like stylus usually shorter than postpedicel; male fore tarsus simple; all abdominal sterna membranous, or only weakly sclerotised in male; segment 6 exposed and setulose; male terminalia with segment 7 variously developed; hypopygium sessile, or pedunculate, cercus about equal, or shorter than epandrium (*e.g.*, Figs 181–183) 61

61. Body mainly black; antennal postpedicel elongate-ovoid, with rounded apex, flattened laterally, at most 2 × longer than high at base in male (as long as high in female); arista-like stylus subapical-dorsolateral; male terminalia with hypopygium (Fig. 181) pedunculate, with epandrium deeply emarginated laterally at middle, cercus with setulose digitiform apical lobe and long ventral process, hypandrium bilobate, phallus trilobate . . . . *Systenomorphus* Grichanov

– Body usually metallic green, or with distinct green, or bluish reflection; male antennal postpedicel long, at least 2.5 × longer than high at base, swollen at base and tapering apically; arista-like stylus apical, or strictly dorsoapical (*e.g.*, Figs 45, 47); male terminalia with hypopygium (*e.g.*, Figs 182, 183) either sessile, or pedunculate, cercus without setulose digitiform apical lobe and long ventral process, hypandrium and phallus simple. 62

62. Head with postocular setae flattened; male antennal pedicel greatly reduced; male postpedicel 5–6 × longer than high at base (Fig. 45); male terminalia with abdominal segment 7 short; hypopygium (Fig. 183) sessile . . . . *Euxiphocerus* Parent

– Head with postocular setae simple; male antennal pedicel not reduced; male postpedicel at most 3–4 × longer than high at base (Fig. 47); male terminalia with abdominal segment 7 long, forming peduncle for hypopygium . . . . *Systenus* Loew

63. Wing veins R_{4+5} and M_1 more or less parallel beyond *dm–m* crossvein (*e.g.*, Figs 104, 106, 108, 144) 64

– Wing veins R_{4+5} and M_1 distinctly curved and convergent beyond *dm–m* crossvein (*e.g.*, Figs 107, 109–111) (MEDETERINAE [in part]) 68

64. Body colouration usually bright metallic green; thorax with acrostichal setae; hind coxa with 2 lateral setae (MEDETERINAE [in part]) 65

– Body greenish black, brownish, or yellow, not bright metallic green; thorax without acrostichal setae; hind coxa with 1 lateral seta. 66

65. Female terminalia with ovipositor blade-like, sclerotised and narrow (Fig. 147); male terminalia with surstylus strongly deflexed dorsad, usually lying conformably with similarly deflexed, oblong-shaped cercus (Fig. 186) . . . . *Thrypticus* Gerstaecker

– Female terminalia with ovipositor soft; male terminalia with surstylus and cercus usually not deflexed dorsad (Fig. 185) . . . . *Corindia* Bickel

66. Body (except head) almost entirely yellow; thorax with 5 dorsocentral setae (additional weak anterior seta may be present); male terminalia with cercus C-shaped, with long, curved lateroventral lobe (XANTHOCHLORINAE) . . . . *Xanthochlorus* Loew

– Body black, greenish black, or partly yellow, with prominent dark markings; thorax with 4 strong dorsocentral setae (additional weak anterior seta may be present); male terminalia with cercus simple, without long, curved lateroventral lobe (*e.g.*, Figs 190, 191) (MEDETERINAE [in part]) 67

67. Antenna with arista-like stylus apicolateral (Fig. 48); distal sectors of wing veins R_{4+5} and M_1 straight and parallel (Fig. 108); male terminalia with abdominal segment 7 forming peduncle; hypopygium (Fig. 191) largely symmetrical; epandrial foramen basolateral; phallus without lateral lobes . . . . *Paramedetera* Grootaert & Meuffels

– Antenna with arista-like stylus apical (stylus fused with postpedicel in males of some species) (Fig. 46); distal sectors of wing veins R_{4+5} and M_1 parallel, weakly arched anteriorly (Fig. 106); male terminalia with abdominal segment 7 semicircular, narrow; hypopygium sessile, asymmetrical; epandrial foramen dorsolateral; phallus with large lateral lobes (Fig. 190) . . . . *Grootaertia* Grichanov

68. Wing vein M_1 bowed posteriorly beyond *dm–m* crossvein and slightly flexed just before apex (*e.g.*, Fig. 111), or straight; if vein M_1 straight, then male terminalia with cercus with articulated distal lobe (*e.g.*, Fig. 188) 69

– Wing vein M_1 bowed anteriorly beyond *dm–m* crossvein (*e.g.*, Figs 107, 109, 110), rarely straight; male terminalia with cercus lacking articulated distal lobe (*e.g.*, Figs 189, 192, 193) 70

69. Head with facial suture distinct at eye margins only; fore and mid femora with ventral spine-like setae; male terminalia (Figs 21, 22) with segment 7 and sternite 8 reduced; sternite 8 positioned medially over base of hypopygium; hypopygium symmetrical with epandrial foramen positioned basally; cercus simple . . . . *Nikitella* Grichanov

– Head with facial suture distinctly separating clypeus; mid and hind femora with, or without, distinctive ventral setae; male terminalia with segment 7 and sternite 8 normally developed; sternite 8 positioned over left side of hypopygium; hypopygium asymmetrical with epandrial foramen positioned left laterally; cercus with articulated distal lobe (Fig. 188) . . . . *Medeterella* Grichanov

70. Body usually shiny, weakly pruinescent; fore coxa with long anteroapical spine- or hook-like cluster of setae (shorter in females); at least fore and hind coxae yellow; male fore tarsus usually modified, with tarsomeres 1–4 slightly thickened and tarsomeres 1 and 3 with remarkable apical setae or processes . . . . *Dolichophorus* Lichtwardt

– Body rarely shiny; fore coxa with short anteroapical setae not forming spine or hook; all coxae dark, or only fore coxa yellow, rarely fore and hind coxae yellow; male fore tarsus differently modified, or simple . . . . *Medetera* Fischer von Waldheim (including *Saccopheronta* Becker & *Demetera* Grichanov)

71. Head with pair of large postvertical setae usually present on dorsal postcranium, out of line with postorbital series; postorbital setae strong, in single row dorsally, but as field of fine, pale setulae across ventral postcranium (*cf*. Fig. 230); male face usually wide; fronto-clypeal suture distinct, at least laterally; clypeus usually produced anteriorly; mouthparts with palpus usually large in both sexes and clothed in short setae; eye pubescent; wing with *dm–m* crossvein longer (*e.g.*, Figs 94, 95), or shorter (*e.g.*, Figs 97, 99), than distal section of vein M_4; abdomen often dorsoventrally flattened; male terminalia with hypopygium encapsulated at abdominal apex (HYDROPHORINAE [in part]) 72

– Head with postvertical setae, if present, usually near vertex and in line with postorbital series; postorbital setae usually as distinct row of setae on lower postcranium, even if pale coloured; male face often narrow with fronto-clypeal suture obscured; mouthparts with palpus usually small, although sometimes enlarged in males only; wing with *dm–m* crossvein usually shorter than distal section of vein M_4; abdomen usually ovate, rarely dorsoventrally flattened; other characters various 77

72. Antennal postpedicel broad basally, abruptly narrowed in distal ⅔, with arcuate ventral margin (Fig. 43); arista-like stylus apical . . . . *Machaerium* Haliday

– Antennal postpedicel not as above, usually short, slightly longer than high, with rounded apex; arista-like stylus usually dorsal or subapical 73

73. Antennal pedicel usually asymmetrical, projecting onto surface of postpedicel; postpedicel rounded, with dorsal arista-like stylus; wing with *dm–m* crossvein usually shorter than apical part of vein M_4 (*e.g.*, Fig. 99); thorax without acrostichal setae 74

– Antennal pedicel simple, not projecting onto surface of postpedicel (*e.g.*, Fig. 42); postpedicel shape variable, with subapical, or dorsal arista-like stylus; wing with *dm–m* crossvein usually longer than apical part of vein M_4 (*e.g.*, Figs 94, 95); thorax usually with acrostichal setae 75

74. Thorax with mesonotum with 4 dorsocentral setae; tibiae with short, or weak apical setae (Egypt; Oriental Region) . . . . [*Paralleloneurum* Becker]

– Thorax with mesonotum usually with 5, or more dorsocentral setae (rarely with 4); tibiae with strong apical setae (widespread Afrotropics) . . . . *Thinophilus* Wahlberg

75. Antennal postpedicel about as long as high, without apicoventral point; arista-like stylus subapical; thorax with mesonotum with small setae; 1 pair of dorsocentral setae; acrostichal setae in 2 rows (western Mediterranean) . . . . [*Anahydrophorus* Becker]

– Antennal postpedicel usually with apicoventral point (*e.g.*, Fig. 42); arista-like stylus subapical, or dorsal thorax with mesonotum with several strong dorsocentral setae; acrostichal setae in 1 row, rarely absent, or biseriate. 76

76. Thorax with anepimeron with seta, or tuft of fine setulae anterior to posterior spiracle . . . . *Hydatostega* Philippi

– Thorax with anepimeron bare anterior to posterior spiracle . . . . *Hydrophorus* Fallén

77. Antennal pedicel with finger-like projection overlapping postpedicel dorsally (Fig. 35); male terminalia with sternite 8 with strong projecting setae (Fig. 154) (*incertae sedis*) . . . . *Dactylonotus* Parent

– Antennal pedicel simple, without dorsal projection, or forming lateral projection on inside face of postpedicel; male terminalia with sternite 8 with, or without, strong projecting setae 78

78. Antennal postpedicel triangular, usually much longer than basal width; arista-like stylus strictly apical (Fig. 14); wing veins M_1 and R_{4+5} often slightly bowed in respect to each other (Fig. 120); male terminalia with hypopygium (Fig. 156) distinctive, surstylus large with apex structurally complex and multilobate, cercus often elongate (RHAPHIINAE) . . . . *Rhaphium* Meigen

– Antennal postpedicel not as above; arista-like stylus basidorsal to subapical (*e.g.*, Figs 13, 34, 36, 51, 52, 220, 221), or inserted in apical incision (*e.g.*, Fig. 37), if arista-like stylus apical (*i.e.*, *Achradocera* Becker, Fig. 20; some *Syntormon* spp.), then hind coxa with lateral seta positioned at base (*Achradocera*), or with antennal pedicel forming a thumb-like projection or conus into postpedicel on inside face (*Syntormon*, Fig. 51); male terminalia not as above, surstylus comprised of 1 or 2 relatively simple lobes (*e.g.*, Figs 150, 152, 153, 157, 197, 200–208); other characters various 79

79. Head usually ovate in anterior view, higher than wide; antenna usually set high on head, *ca* 0.25 height from vertex; mid and/or hind femora with distinct anterior preapical seta; fore tibia often with anterodorsal comb-like row of short setae on distal ½; lateral seta of hind coxa usually near middle; wing with anal angle often reduced, or lost (e.g., Figs 137, 140–142) (SYMPYCNINAE) 80

– Head rounder in anterior view, about as high as wide; antenna position variable, closer to middle of head (0.4–0.5 height from vertex); mid and hind femora without anterior preapical seta, or such apparent preapical setae weak, or indistinct from background field of setae; fore tibia without anterodorsal comb-like row of short setae on distal ½; lateral seta of hind coxa near middle, or in basal ¼; wing with anal angle variable, sometimes well-developed (*e.g.*, Figs 68, 71) 89

80. Antennal scape often with setulae above; pedicel, viewed on inside face, forming more or less long, thumb-like projection or conus into postpedicel (Fig. 51); arista-like stylus apical, or subapical; female face bulging, in lateral view projecting beyond curvature of eye; thorax with anepimeron anterior to posterior spiracle and metepimeron with fine pale setulae . . . . *Syntormon* Loew

– Antennal scape bare above; pedicel simple, vase-like, or globular, without thumb-like projection; arista-like stylus often distinctly dorsal; female face usually not bulging, conforming with curvature of eyes; thorax with anepimeron and metepimeron usually bare (metepimeron of *Campsicnemus* Haliday with fine setulae) 81

81. Head with face in both sexes narrowest near middle; thorax with metepimeron with fine setulae; fore tibia without anterodorsal row of short setae on distal ½; male fore and/or mid leg often strongly modified; abdomen broad, dorsoventrally flattened, often short . . . . *Campsicnemus* Haliday

– Head with face in both sexes parallel-sided, or gradually narrowed ventrally; thorax with metepimeron bare; abdomen usually cylindrical; other characters various 82

82. Thorax with acrostichal setae absent; legs with tarsomeres 2–5 regularly decreasing in length; other characters variable 83

– Thorax with at least a few distinct acrostichal setae, although sometimes small; male fore and hind legs often with tarsomeres 2–5 not regularly decreasing in length (*i.e.*, with 1 or more tarsomeres shortened) 84

83. Thorax with mesonotum often yellow, with 2 large black, or brown lateral maculae; wing vein R_{2+3} of male not swollen in basal portion (Fig. 140) . . . . *Sympycnus* Loew [Group I]

– Thorax with mesonotum regularly dark, without black, or brown lateral maculae; wing vein R_{2+3} of male sometimes swollen in basal portion (Fig. 138). . . . .*Nurteria* Dyte & Smith

84. Thorax with mesonotum with large matt-brown, or velvety black area above wing base; male tarsi unmodified; male terminalia with hypopygium as in Fig. 201. . . . . *Lamprochromus* Mik

– Thorax with mesonotum without matt-brown, or velvety black area above wing base; male tarsi often ornamented (*e.g.*, Figs 53, 57, 58, 62); male terminalia with hypopygium not as above 85

85. Female head with clypeus strongly bulging; thorax with mesonotum with 3 or 4 pairs of strong dorsocentral setae; male fore leg with some tarsomeres usually shortened, flattened, or ornamented with processes, spines, or remarkable setulae (Figs 57, 58); male hind leg with tarsomeres 2–5 regularly decreasing in length (Fig. 61); male hind tarsomere 1 often ornamented with remarkable setae, or setulae . . . . *Telmaturgus* Mik

– Female head with clypeus more or less flat, or slightly bulging; thorax with mesonotum with at least 5 pairs of strong dorsocentral setae; fore tarsomeres usually simple, or shortened, rarely ornamented with remarkable setulae; male hind leg with tarsomeres 2–5 either regularly decreasing in length, or with at least 1 tarsomere shortened (*e.g.*, Figs 53, 62); male hind tarsomere 1 rarely ornamented with remarkable setae, or setulae 86

86. Wing veins R_{4+5} and M_1 slightly diverging rather than parallel; crossvein *dm–m* perpendicular to long axis of wing, forming an acute angle with vein M_4; male with costal vein (*C*) thickened to vein R_1; head with 2 postvertical setae; male mid femur with ventral setae in basal part; hind tibia of male with strong ventral subapical seta; hind tarsomeres 2–5 regularly decreasing in length; male terminalia with epandrial foramen mostly mid dorsal (Fig. 208) . . . . *Teuchophorus* Loew

– Wing veins R_{4+5} and M_1 parallel; costal vein (*C*) of male not thickened; head with 1 postvertical seta; male terminalia with epandrial foramen mostly left basolateral; other characters various 87

87. Thorax with 5 pairs of strong dorsocentral setae; male hind leg with tarsomeres 1 and 2 shortened, tarsomere 2 often with elongate process (clidium) (Fig. 53), tarsomere 3 longer than 2, tarsomere 4 shorter than 3 . . . . *Chaetogonopteron* De Meijere

– Thorax usually with 6, rarely 5 pairs of strong dorsocentral setae; male hind leg with tarsomeres 1 and 2 not shortened, hind tarsomere 2 without elongate process 88

88. Thorax with proepisternum with fine setae; male mid leg usually simple, rarely some tarsomeres flattened; male hind tarsus with tarsomere 3 shorter than 2, often bearing 1 or more modified setae, tarsomere 4 usually longer and thinner than 3, often polished (Fig. 62); male wing without tuft of setae on margin of anal lobe (Fig. 140) . . . . *Sympycnus* [Group II]

– Thorax with proepisternum bare; male mid femur and tibia modified (Fig. 54); hind tarsomeres 2–5 regularly decreasing in length, simple; male wing usually with tuft of setae on margin of anal lobe (Fig. 139). . . . . *Olegonegrobovia* Grichanov

89. Body size < 2 mm; head with female clypeus with 4 projecting setae; thorax with acrostichal setae absent; lateral seta of hind coxa near middle; hind tarsomere 1 markedly shorter than hind tarsomere 2; wing veins R_{4+5} and M_1 subparallel (Fig. 114); vein M_1 more or less straight; male terminalia pedunculate, cercus ivory-white and subtriangular; postgonite prominent, often with several pedunculate setae (Fig. 197) (*incertae sedis*) . . . .*Acropsilus* Mik

– Body size variable, usually > 2 mm; head with female clypeus without projecting setae; thorax with acrostichal setae present, or absent; lateral seta of hind coxa usually in basal ¼; hind tarsomere 1 not markedly shorter than hind tarsomere 2; wing veins R_{4+5} and M_1 subparallel (*e.g.*, Figs 65, 67, 69, 70, 73), or divergent (*e.g.*, Fig. 68); vein M_1 more or less straight, or with distinct sinuation (*e.g.*, Fig. 74); male terminalia usually encapsulated (*e.g.*, Figs 149, 151), sometimes pedunculate (*Urodolichus*, Fig. 150) (DIAPHORINAE [in part] and *Urodolichus*). 90

90. Wing with costal vein (*C*) ending at vein R_{4+5} (*e.g.*, Fig. 68); vein M_1 discontinuous and weakened, with distal section often displaced; male antenna not elongated (*ca* ⅓ body length). 91

– Wing with costal vein (*C*) extending beyond vein R_{4+5} and usually ending at vein M_1, or sometimes ending between veins R_{4+5} and M_1 (*e.g.*, Figs 65–67, 69, 71, 73, 222, 223); vein M_1 continuous and usually strong; if vein M_1 evanescent (some *Aphasmaphleps* Grichanov spp., Fig. 66), then distal section of vein M_1 not displaced and antenna of male elongated (*ca* ¾ body length) (*e.g.*, Fig. 34). 92

91. Thorax with acrostichal setae; male terminalia with sternite 8 with strong projecting setae (as in Fig. 151). . . . . *Asyndetus* Loew

– Thorax without acrostichal setae, or microscopic; male terminalia with sternite 8 usually without strong setae . . . . *Cryptophleps* Lichtwardt

92. Wing with apical part of vein M_4 (*i.e.*, section beyond *dm–m* crossvein) > 7 × longer than *dm–m* crossvein (*e.g.*, Figs 66, 222, 223). 93

– Wing with apical part of vein M_4 usually < 4 × longer than *dm–m* crossvein (*e.g.*, Figs 65, 67, 69, 71, 73). 95

93. Male antennal arista-like stylus greatly elongated (Fig. 34); wing veins R_{4+5} and M_1 not shifted anteriad, with vein M_1 ending at wing apex (Fig. 66) . . . . *Aphasmaphleps* Grichanov

– Male antennal arista-like stylus not greatly elongated (*e.g.*, Figs 220, 221); wing veins R_{4+5} and M_1 shifted anteriad and closely approximated to costal vein (*C*), with vein M_1 ending before wing apex (*e.g.*, Figs 222, 223). 94

94. Male antennal arista-like stylus apicodorsal (Fig. 221); head with occiput concave; head without postvertical setae; thorax with acrostichal setae uniserial; scutellum with 1 pair of setae; hind coxa with 1 lateral seta . . . . *Emiratomyia* Naglis

– Male antennal arista-like stylus basidorsal (Fig. 220); head with occiput convex; head with postvertical setae; thorax with acrostichal setae absent; scutellum with 1 pair of strong setae and smaller pair of lateral setae; hind coxa with 2 lateral setae . . . . *Arabshamshevia* Naglis

95. Head with occiput concave; antennal postpedicel compressed laterally, blade-like to subtriangular (*Argyra*) (*e.g.*, Fig. 36), or rounded; arista-like stylus dorsal to dorsoapical 96

– Head with occiput convex, or flat; antennal postpedicel globular (*e.g.*, Fig. 37), reniform, conoid, or bud-like with indistinct apex, or postpedicel with apex abruptly drawn-out (*e.g.*, Fig. 13), or elongate and slender (*e.g.*, Fig. 20); arista-like stylus subapical or apical, rarely dorsal, sometimes inserted in apical incision 98

96. Hind coxa with external vertical row of 3–4 setae, decreasing in length ventrad; antennal scape with dorsal setae (Fig. 36) (scape bare in some Holarctic species). *Argyra* Macquart

– Hind coxa with 1 external seta in basal ¼; antennal scape bare 97

97. Antenna inserted at dorsal ¼ of head; antennal arista-like stylus dorsal; wing with distal section of vein M_1 with distinct sinuation near basal ⅓ (Fig. 74); male terminalia with segment 7 rather long (Fig. 150) (*incertae sedis*) . . . . *Urodolichus* Lamb

– Antennae inserted at middle of head; antennal arista-like stylus dorsoapical; wing with distal section of vein M_1 virtually straight; male terminalia with segment 7 short, hypopygium encapsulated (as in Fig. 149) (non-Afrotropical) . . . . [*Falbouria* Dyte]

98. Antennae inserted near middle of head; male eyes holoptic (*e.g.*, Fig. 7), or dichoptic, with frons and face broad (*e.g.*, Fig. 13); male terminalia with sternite 8 with strong projecting setae (*e.g.*, Fig. 151) 99

– Antennae inserted at dorsal ¼–⅓ of head; male dichoptic, with face strongly convergent beneath antennae (*e.g.*, Fig. 25), eyes sometimes contiguous; male terminalia with sternite 8 without strong projecting setae (*e.g.*, Fig. 149), rarely with short, thick setae. 101

99. Antennal pedicel forming a thumb-like inner condyle or conus, projecting into base of postpedicel (condyle smaller in female); male postpedicel large at base, with abruptly drawn-out apex (Fig. 13); female postpedicel smaller, with distinct pointed apex; thorax with 4th pair of dorsocentral setae shifted medially, 5th pair shifted laterally . . . . *Trigonocera* Becker

– Antennal pedicel not forming a thumb-like condyle or conus projecting into base of postpedicel; postpedicel rounded in both sexes, with indistinct pointed apex; thorax with dorsocentral setae in 2 regular rows 100

100. Male eyes holoptic (Fig. 7), or with eyes narrowly separated on frons; head rarely with frons broader than face; wing broadest in basal ¼ (Fig. 71). . . . . *Diaphorus* Meigen

– Male eyes dichoptic; head with frons broader than face; wing broadest medially (as in Fig. 69) (non-Afrotropical) . . . . [*Melanostolus* Kowarz]

101. Male antennal postpedicel with apical ½ very slender and drawn-out, bearing apical arista-like stylus (Fig. 20), lower postocular surface of male with numerous flattened pale setae. . . . . *Achradocera* Becker

– Male antennal postpedicel globular, reniform or conoid, with subapical arista-like stylus (Fig. 37); lower postocular surface with fine unmodified setae . . . . *Chrysotus* Meigen

Synopsis of the fauna

About 260 genera of Dolichopodidae are currently recognised in the world, of which 90 occur in the Afrotropical Region. About 7,700 species of Dolichopodidae have been described in the world fauna, of which *ca* 780 occur in the Afrotropics. Many additional Afrotropical species remain undescribed. Genera within square brackets in the above key are not treated below. These genera may be found to occur in the Afrotropics, but are currently unknown from the region.

***Achradocera* Becker** (Diaphorinae)**.** A genus of 17 described species, occurring in the Afrotropical, Australasian, Nearctic and Neotropical Regions. Four Afrotropical species have been described from Democratic Republic of Congo and South Africa. Capellari & Grichanov (2012) indicate, however, that these Afrotropical species probably do not belong in *Achradocera*. *Achradocera* has been classified as a subgenus of either *Chrysotus*, or *Diaphorus* in the past and is primarily distinguished by the male antennal postpedicel, with a slender apical projection, that bears an apical arista-like stylus (Fig. 20). There are currently no suitable identification keys to Afrotropical species.

***Acropsilus* Mik** (*Incertae sedis*)**.** This unusual genus of Old World dolichopodids has been variably placed in the subfamilies Diaphorinae, Peloropeodinae and Sympycninae, or as *incertae sedis* and includes 30 described species, occurring in the Afrotropical, Australasian, Oriental and Palaearctic Regions (Bickel 1998; Grichanov 1998*f*; Grichanov & Mostovski 2009*a*; Wang *et al*. 2007). Eight Afrotropical species have been described, but many more await description. *Acropsilus* is especially diverse in the moist Afrotropics. The Central African species, *Acropsilus brevitalus* (Parent, 1937), is also recorded from Israel (Grichanov 2011*d*). Adults are small (1–2 mm), mostly black, with dark setae on the head and thorax; the antennal arista-like stylus apical, or subapical; female head with clypeus with four projecting setae; thorax with posterior slope of mesonotum slightly flattened, but not depressed; acrostichal setae absent; wing veins R_{4+5} and M_1 subparallel (Fig. 114); hind tarsomere 1 distinctly shorter than tarsomere 2; and male terminalia with hypopygium (Fig. 197) with cercus usually ivory-white and subtriangular. Grichanov (1998*f*) provided an identification key to the seven Afrotropical species known at that time. Grichanov & Mostovski (2009*a*) subsequently synonymised the monotypic South African genus *Campsicnemoides* Curran with *Acropsilus*.

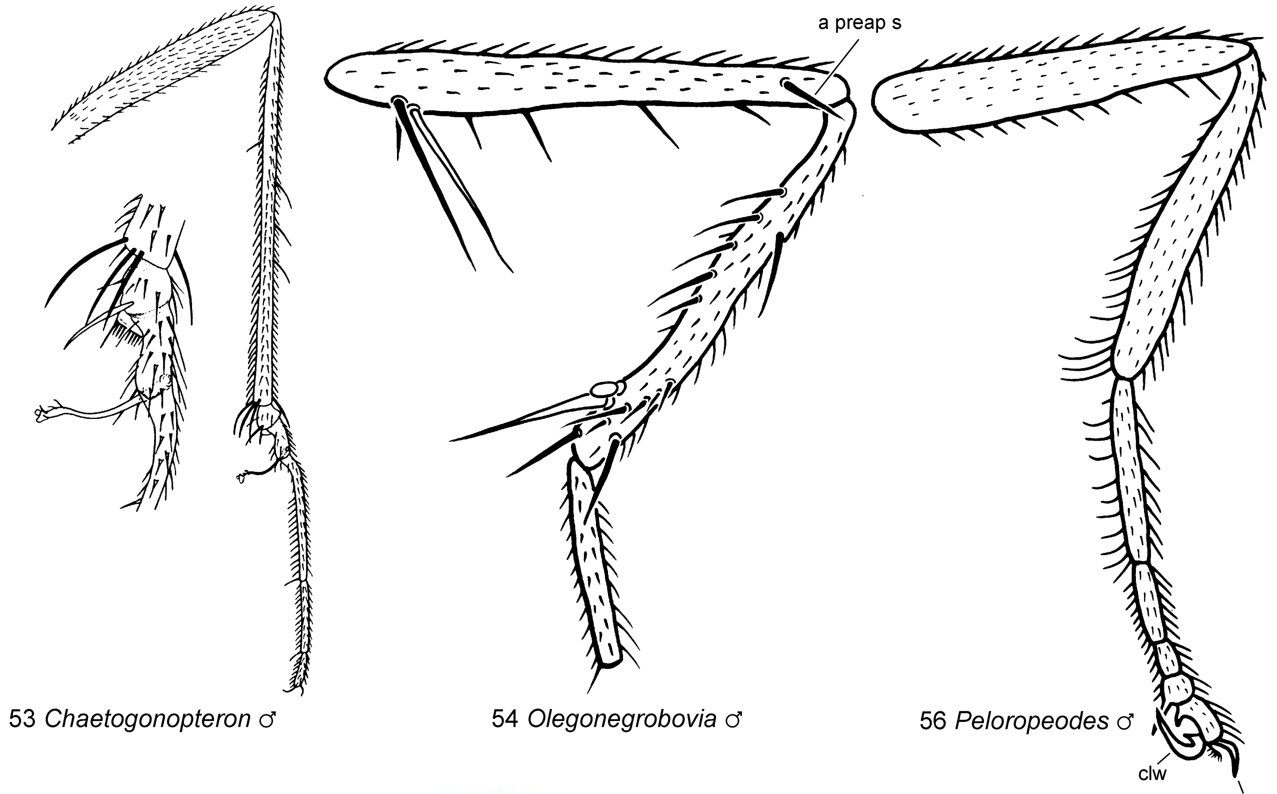
***Afrohercostomus* Grichanov** (Dolichopodinae)**.** An endemic Afrotropical genus of 15 described species, distributed from Ethiopia to South Africa (Grichanov 2010*g*), that comprises species previously included in Grichanov's (1999*c*) *Hercostomus* species-group I. Adults range from 3–6 mm and are distinguished by the following characters: wing vein M_1 virtually straight, or slightly convex anteriorly, subparallel, or slightly convergent with vein R_{4+5} (Fig. 75); thorax with mesonotum with darkened area above notopleuron; hind tarsomeres 3–5 of male usually flattened, with silvery pile on one side (Fig. 59); and male abdominal spiracle 7 enlarged (Fig. 158). See Fig. 159 for an example of the male terminalia of this genus. Grichanov (2010*g*) provided an identification key to known species.

***Afroparaclius* Grichanov** (Dolichopodinae)**.** An endemic Afrotropical genus established by Grichanov (2006*a*) for two species originally described in the genus *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 71; International Commission on Zoological Nomenclature 2004). The genus occurs in Burundi, Democratic Republic of Congo and Madagascar and both described species were included in an identification key compiled for *Paracleius* by Grichanov (2004: 184). Grichanov (2006*a*) indicated that *Afroparaclius* is probably paraphyletic. Adults are primarily distinguished by the antennal arista-like stylus, with short pubescence; wing with distal ⅓ of vein M_1 with right-angular, strongly arching anterior curvation towards vein R_{4+5} (Fig. 76) and characters of the male terminalia (Fig. 161) listed in the key.

***Afropelastoneurus* Grichanov** (Dolichopodinae)**.** An endemic Afrotropical genus established by Grichanov (2006*a*) for five species that were previously placed in *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 71; International Commission on Zoological Nomenclature 2004). The genus occurs in Democratic Republic of Congo and Equatorial Guinea (Bioko Is.) and the five described species were included in Grichanov's (2004: 184) identification key to *Paracleius*. One additional species from Democratic Republic of Congo awaits description. Adults are distinguished by the antennal arista-like stylus with long setulae; thorax with 5 dorsocentral setae; pleura with cluster of fine setulae anterior to posterior spiracle; wing membrane brown (usually with pale transverse fascia just beyond *dm–m* crossvein); wing veins R_{4+5} and M_1 straight and virtually parallel (Fig. 77); hind femur with anterior preapical seta far from apex (0.6–0.7 length from base); and characters of the male terminalia: hypandrium, phallus and cercus simple, postgonite narrow and simple, apicoventral epandrial lobe long and narrow with enlarged tip, surstylus short, sperm pump usually enlarged (Fig. 162). The genus appears to be closely related to *Gymnopternus* Loew.

***Amblypsilopus* Bigot** (Sciapodinae)**.** This poorly defined and probably polyphyletic genus includes *ca* 330 mainly tropical species and occurs in all zoogeographical regions, except Antarctica. Some 50 species are known from the continental Afrotropics and adjacent islands (Madagascar, Réunion Is. and Seychelles), of which some were previously placed in *Sciopolina* Curran and *Ethiosciapus* (Grichanov 2011*d*). An identification key to Afrotropical species was provided by Grichanov (1998*g*), but additional species were subsequently described by Grichanov (1999*b*, 2003) and several more await description. See Fig. 121 for an example of the wing of this genus.

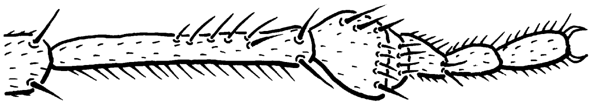
***Amphithalassius* Ulrich** (Parathalassiinae)**.** An endemic Afrotropical genus known only from coastal South Africa, that includes two described species (*A. piricornis* Ulrich, 1991 and *A. latus* Ulrich, 1991), plus three undescribed species (known only from females). Adults are small whitish pruinose flies distinguished by the following features: antenna with postpedicel conical and arista-like stylus 1-articled (Fig. 31); head with face wide in both sexes; thorax with prothoracic precoxal bridge incomplete; acrostichal setae uniserial; anterior mesonotal setae reduced; scutellum with 1 pair of setae; wing with *bm–m* crossvein present and cell *dm* emitting three branches; male terminalia with hypopygium compact; and female terminalia



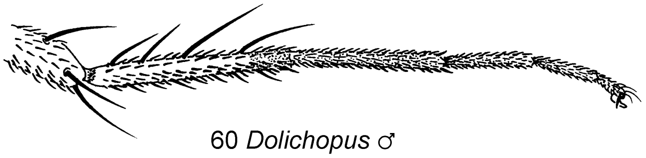
53 *Chaetogonopteron* ♂ 54 *Olegonegrobovia* ♂ 56 *Peloropeodes* ♂

55 *Hercostomus* ♂

57 *Telmaturgus* ♂



58 *Telmaturgus* ♂



60 *Dolichopus* ♂

59 *Afrohercostomus* ♂

61 *Telmaturgus* ♂

62 *Sympycnus* ♂

Figs 56.53–62. Legs of Dolichopodidae: (53) hind leg (above), basal tarsomeres (below) of *Chaetogonopteron araneipes* (Meuffels & Grootaert) (non-Afrotropical) ♂; (54) mid leg of *Olegonegrobovia couturieri* Grichanov (apical tarsomeres omitted) ♂; (55) fore tarsus of *Hercostomus* sp. ♂; (56) fore leg of *Peloropeodes matilei* Grichanov ♂; (57) fore tarsus of *Telmaturgus munroi* (Curran) ♂; (58) same, *Telmaturgus mastigomyoformis* (Grichanov) ♂; (59) hind tarsus of *Afrohercostomus blagoderovi* (Grichanov) ♂; (60) same, *Dolichopus cuprinus* Wiedemann (non-Afrotropical) ♂; (61) same, *T. munroi* ♂; (62) same, *Sympycnus discrepans* Parent ♂. Fig. 53 (after Meuffels & Grootaert 1987, figs 40, 41), Fig. 54 (after Grichanov 2000*c*, fig. 46), Fig. 56 (after Grichanov 2000*c*, fig. 37), Figs 58 (after Grichanov 2008*c*, fig. 43), Fig. 60 (Robinson & Vockeroth 1981, fig. 9).

Abbreviations: a preap s – anterior preapical seta; clw – claw.

with acanthophorite setae. Adults of *Amphithalassius* occur along sea coasts on dry sand, mostly dunes with sparse vegetation. Ulrich (1991) provided an identification key to known species.

***Apelastoneurus* Grichanov** (Dolichopodinae)**.** This genus was established by Grichanov (2006*a*) for 47 Afrotropical species that were previously placed in *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 71; International Commission on Zoological Nomenclature 2004). The genus is a poorly defined polyphyletic assemblage of species, usually with long pubescence on the antennal arista-like stylus (Fig. 38), wing with distal part of vein M_1 bent anteriorly and convergent with R_{4+5} (Fig. 81), and lacking the defining characters of the other dolichopodine genera. It is likely that many of the species placed in *Apelastoneurus* are related to Oriental, Australasian and New World species currently placed in *Paraclius* and *Pelastoneurus*. Species of *Apelastoneurus* are widely distributed within tropical Africa and on oceanic islands (Madagascar, Seychelles, St. Helena Is.) and were included in Grichanov's (2004: 184) identification key to *Paracleius*.

***Aphasmaphleps* Grichanov** (Diaphorinae)**.** This endemic Afrotropical genus includes four described species from the continental Afrotropics and Madagascar. Adults are small diaphorines characterised by the following characters: antennal pedicel not protruding into base of postpedicel; male antennal arista-like stylus elongate (basal segment of stylus similar in length to scape + pedicel, or longer) (Fig. 34); wing with *dm–m* crossvein positioned in basal ¼ (Fig. 66); vein M_1 ending at wing apex (sometimes evanescent); fore tarsus slightly thickened, with ventral pad of short white setulae, tarsomeres 4 and 5 with longer dorsal setae at apex, tarsomere 5 with enlarged pulvilli, claws absent; and male tergite 6 setulose. See Fig. 152 for an example of the male terminalia of this genus. *Aphasmaphleps* was described by Grichanov (2010*a*). Capellari & Grichanov (2012) described additional species and provided an identification key.

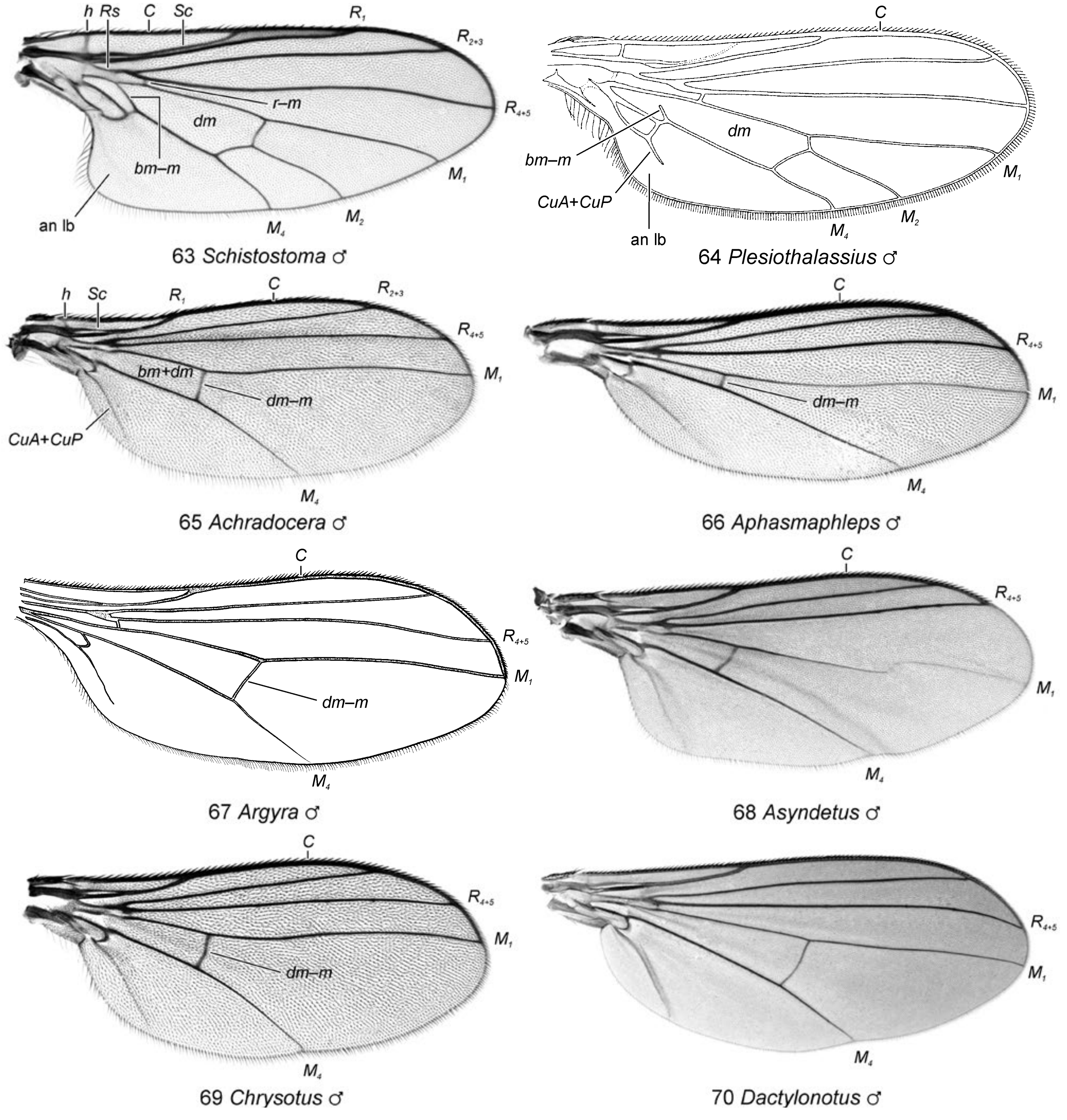
***Aphrosylus* Haliday** (Hydrophorinae)**.** This marine coastal genus of the "aphrosyline" group of genera includes 31 described species, most of which occur in the Mediterranean province. The Afrotropical fauna includes five described species, recorded from Cabo Verde, Senegal and Sierra Leone (Rampini 1982; Rampini & Munari 1987, identification key). The genus is distinguished by the following characters: antennal arista-like stylus apical; mouthparts with palpus large; hypopharynx projecting, hook-shaped and curved posteriorly (Fig. 229); fore tibia with distinct erect spinose apical seta; male hind tarsomere 1 simple, lacking strong seta. See Fig. 90 for an example of the wing of this genus and Fig. 176 for the male terminalia.

***Arabshamshevia* Naglis** (Diaphorinae)**.** This monotypic genus was established by Naglis (2014) for *A. ajbanensis* Naglis, 2014, from the United Arab Emirates. *Arabshamshevia* is only known from males and can be differentiated from other diaphorine genera by the following combination of characters: antennal scape with ventral projection; postpedicel elongated (3.7 × longer than high) and triangular with basidorsal arista-like stylus (Fig. 220); thorax with 5 dorsocentral setae, acrostichal setae absent; two pairs of scutellar setae; hind coxa bearing 2 lateral setae; wing with crossvein *dm–m* in basal ¼ of wing; wing veins R_{4+5} and M_1 displaced anteriad, vein M_1 with anterior bend near middle and joining costa anterior to wing apex (Fig. 222); body length less than 2 mm. *Arabshamshevia* is closely related to *Shamshevia* and *Emiratomyia*.

***Argyra* Macquart** (Diaphorinae)**.** This genus is largely Holarctic and Oriental and includes more than 110 described species. Grichanov (1998*e*) reviewed the Afrotropical fauna, which includes three described species and at least two additional undescribed species known from females only. Adults are medium-sized flies with the following characters: head with occiput concave; antenna (Fig. 36) with postpedicel laterally compressed (blade-like to subtriangular with distinct apex), arista-like stylus dorsal to dorsoapical; scape dorsally setose in some species; hind coxa with external vertical row of 3–4 setae, decreasing in length ventrally. See Fig. 67 for an example of the wing of this genus and Fig. 153 for the male terminalia. Grichanov (1998*e*) provided an identification key to described Afrotropical species.

***Argyrochlamys* Lamb** (Dolichopodinae)**.** This Old World genus includes six Afrotropical species from coastal habitats in Angola, Ghana, Sudan, Djibouti, Eritrea, Oman, Tanzania, Seychelles and Mauritius. *Argyrochlamys impudicus* Lamb, 1922, also occurs in the Palaearctic Region (Iran) and Oriental Region (Sri Lanka, Chagos Archipelago). *Argyrochlamys cavicola* (Parent, 1929) has also been recorded from the southern Palaearctic (Egypt). Adults (Fig. 236) are medium-sized, non-metallic, dark grey to yellowish, with the following characters: head with frons and face broad (Fig. 2); thorax with 6 dorsocentral setae, fifth pair usually strongly off-set medially (Fig. 3); wing vein M_1 beyond *dm–m* crossvein, with strong anterior bend (Fig. 78); hind tarsomere 1 of male with elongate comma-shaped posterobasal projection; female terminalia with protruding rod-like extensions of tergite 8 (Fig. 146). See Fig. 163 for an example of the male terminalia of this genus. *Argyrochlamys*, along with the closely related genera *Pseudargyrochlamys* and *Phoomyia* Naglis & Grootaert comprise a distinctive lineage of palaeotropical coastal dolichopodines, characterised by their uniquely modified female terminalia (Naglis *et al*. 2013). Species of *Argyrochlamys* and *Phoomyia* are restricted to sandy ocean beaches and are sometimes collected in ghost crab burrows (*Ocypode* Weber); however their ecological role within these burrows is currently unknown (Grichanov 2004: 15; Naglis *et al*. 2013). An identification key to species was provided by Grichanov (2010*b*).

***Asyndetus* Loew** (Diaphorinae)**.** This virtually cosmopolitan genus includes more than 100 species from all zoogeographical regions of the world, except Antarctica. The Afrotropical fauna comprises 14 species, including two doubtful species described from females. *Asyndetus* can be easily recognised by their distinctive wing venation, with the costal vein (C) ending at vein R_{4+5} and vein M_1 broken (Fig. 68), in combination with a parallel-sided face and clypeus in both sexes and acrostichal setae present. The closely related genus *Cryptophleps* has similar wing venation, but has the thorax with acrostichal setae microscopic or absent. *Asyndetus* may be common in littoral habitats, including arid coasts (Bickel & Sinclair 1997) and some species of the genus are rather abundant in African collections. Grichanov (2013*a*: 41) provided an identification key to Afrotropical species.



63 *Schistostoma* ♂

64 *Plesiothalassius* ♂

65 *Achradocera* ♂

66 *Aphasmaphleps* ♂

67 *Argyra* ♂

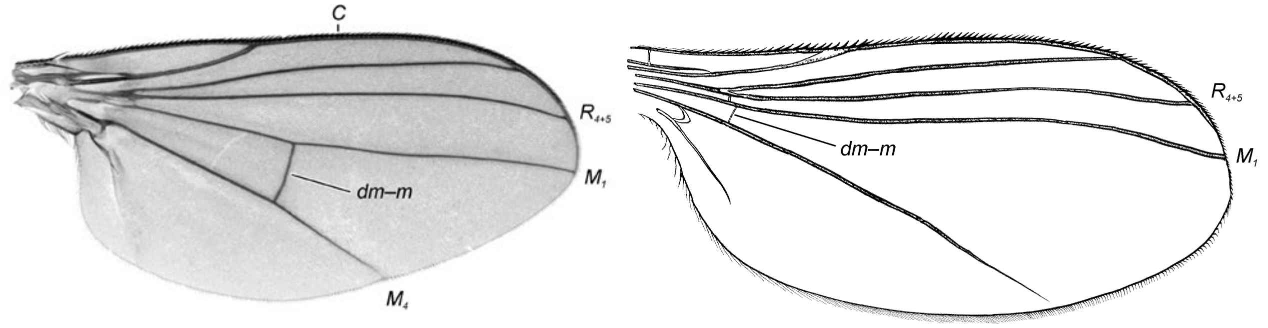
68 *Asyndetus* ♂

69 *Chrysotus* ♂

70 *Dactylonotus* ♂

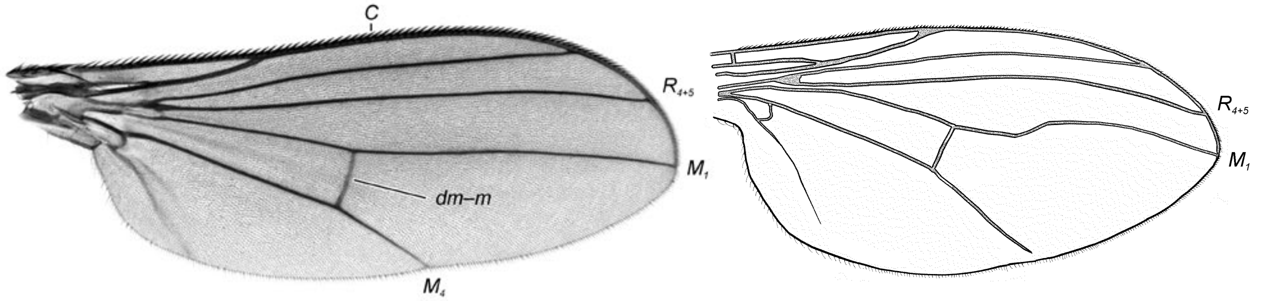
Figs 56.63–70. Wings of Dolichopodidae (dorsal views; all ♂): (63) *Schistostoma* sp.; (64) *Plesiothalassius capensis* (Smith); (65) *Achradocera africana* Parent; (66) *Aphasmaphleps bandia* Grichanov; (67) *Argyra* sp.; (68) *Asyndetus* sp.; (69) *Chrysotus* sp.; (70) *Dactylonotus* sp. Fig. 64 (after Ulrich 1991, fig. 6).

Abbreviations: an lb – anal lobe; *bm+dm* – basal medial cell + discal medial cell; *bm–m* – basal–medial crossvein; *C* – costal vein; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm* – discal medial cell; *dm–m* – discal medial crossvein; *h* – humeral crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Rs* – radial sector; *Sc* – subcosta.



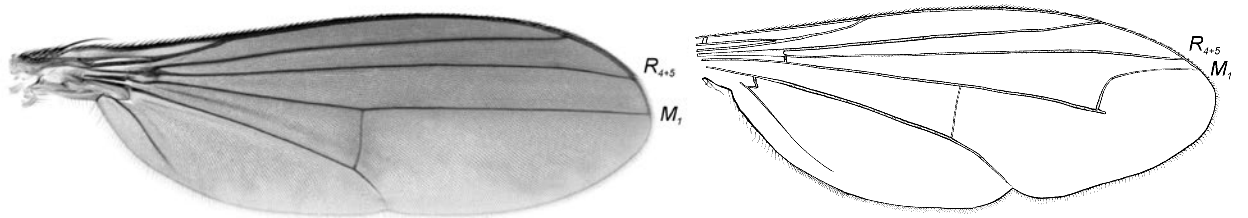
71 *Diaphorus* ♂

72 *Shamshevia* ♂



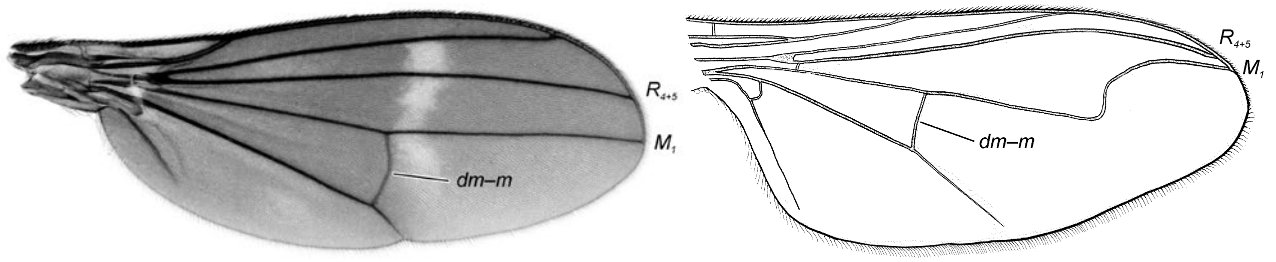
73 *Trigonocera* ♂

74 *Urodolichus* ♂



75 *Afrohercostomus* ♂

76 *Afroparaclius* ♂



77 *Afropelastoneurus* ♀

78 *Argyrochlamys* ♂

Figs 56.71–78. Wings of Dolichopodidae (dorsal views): (71) *Diaphorus* sp. ♂; (72) *Shamshevia hoanibensis* Grichanov ♂; (73) *Trigonocera munroi* (Curran) ♂; (74) *Urodolichus lambi* Grichanov ♂; (75) *Afrohercostomus blagoderovi* (Grichanov) ♂; (76) *Afroparaclius thompsoni* (Grichanov) ♂; (77) *Afropelastoneurus* sp. ♀; (78) *Argyrochlamys impudicus* Lamb ♂.

Abbreviations: *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{4+5} – third branch of radius.

Bickelia **Grichanov** (Sciapodinae)**.** This monotypic genus is easily distinguished from other Sciapodinae by the following characters: head with narrow tomentose face and frons; vertical setae present in both sexes; thorax with 2 fine ventral propleural setae; wing vein M_{1+2} branched (Fig. 122); and mid and hind femora each with anterior preapical seta. See Fig. 209 for an example of the male terminalia of this genus. *Bickelia parallela* (Macquart, 1842) is known from Mauritius, Seychelles and the Chagos Archipelago (Grichanov 1996*b*, 2003).

Bickeliolus **Grichanov** (Sciapodinae)**.** This genus (originally a subgenus of *Ethiosciapus*), includes seven species from the continental Afrotropical Region, Madagascar and Seychelles (Grichanov 1996*e*, 2011*d*). *Bickeliolus* differs from *Ethiosciapus* in the following respects: head with strong vertical seta on male frons; femora usually bare; thorax with acrostichal setae short, or absent; wing with alula usually reduced (Fig. 123); and male terminalia with cercus usually with apical brush of long setulae (Fig. 219). See Fig. 11 for an example of the antenna of this genus. Grichanov (2011*d*) recently transferred *Mascaromyia gerlachi* Meuffels & Grootaert, 2007, to *Bickeliolus*. An identification key to species was provided by Grichanov (1998*g*).

Campsicnemus **Haliday** (Sympycninae)**.** This genus numbers *ca* 300 species, with an extremely high diversity of endemic species in the Hawaiian Islands and French Polynesia (Goodman *et al*. 2014). *Campsicnemus* has been recorded from all zoogeographical regions, except the Neotropical Region and Antarctica. The Afrotropical fauna includes three described species from the continental Afrotropics and four species from St. Helena Is., including the European species *C. magius* (Loew, 1845), which has apparently been introduced to the island (Grichanov 2012*c*). Previous records of the Palaearctic species *C. armatus* (Zetterstedt, 1849) and *C. atlanticus* Dyte, 1980, from St. Helena Is. are based on misidentifications. Adults are tiny to medium-sized flies; head with face narrowed at middle; antennal arista-like stylus dorsal; thorax usually with 4, rarely 5 dorsocentral setae; acrostichal setae absent, or uniserial; wing veins R_{4+5} and M_1 more or less parallel (Fig. 136); male legs usually modified and ornamented, rarely simple; female abdomen flattened dorsoventrally. See Fig. 200 for an example of the male terminalia of this genus. Grichanov (1998*c*) provided an identification key to Afrotropical species and more recently (Grichanov 2012*c*), provided a key to species from the Atlantic Ocean islands, including St. Helena Is. Specimens of *Campsicnemus* are rare in African collections.

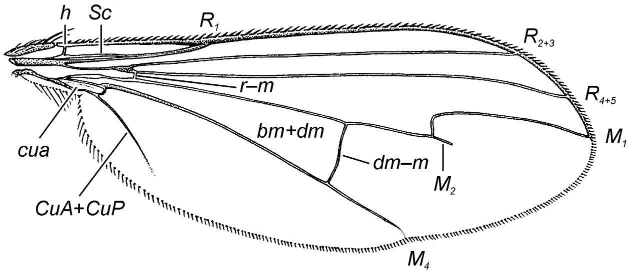
Cemocarus **Meuffels & Grootaert** (Hydrophorinae)**.** This endemic Afrotropical genus (Fig. 1) is known from coastal habitats in South Africa and Namibia and includes two described species (Grichanov 1997*e*; Meuffels & Grootaert 1984), as well as several additional undescribed species. The genus is part of the "aphrosyline" group of Hydrophorinae and is distinguished by the possession of a trapezoidal antennal postpedicel with subapical arista-like stylus in dorsoapical excavation (Figs 28, 39); head with wide face (Fig. 29); and a prominent bulging clypeus (Fig. 28). See Fig. 91 for an example of the wing of this genus and Fig. 177 for the male terminalia. There is no suitable identification key available for Afrotropical species.

Chaetogonopteron **De Meijere** (Sympycninae)**.** This genus comprises over 80 described species mainly from the Oriental and Australasian Regions. The Afrotropical Region includes the single variable species *C. nectarophagum* (Curran, 1924), which is widely distributed in the continental Afrotropics, adjacent islands and also extending into the southern Palaearctic and western Oriental Region (Grichanov 2006*b*). Four species were recorded from Seychelles by Meuffels & Grootaert (2007: 50; 2009: 155); however, three of these have since been transferred to *Sympycnus* Loew (Grichanov 2008*c*), and the other species is probably a synonym of *C. nectarophagum*. Adult males of *Chaetogonopteron* have the two basal segments of the hind tarsus greatly shortened, with tarsomere 2 often bearing an elongate process (clidium) (Fig. 53). See Fig. 137 for an example of the wing of this genus. Females cannot readily be separated from those of *Sympycnus* (Meuffels & Grootaert 1997). *Chaetogonopteron sobrium* (Meunier, 1910) is known from rather recent Zanzibaran copal (Pleistocene/Holocene) (Grichanov 2008*b*). Grichanov (2008*c*) provided a key to species-groups of Afrotropical *Sympycnus* and *Chaetogonopteron* and Meuffels & Grootaert (2009: 154) included *C. nectarophagum* (= *C. albipes* Lamb, 1926) in their key to the Sympycninae of Seychelles.

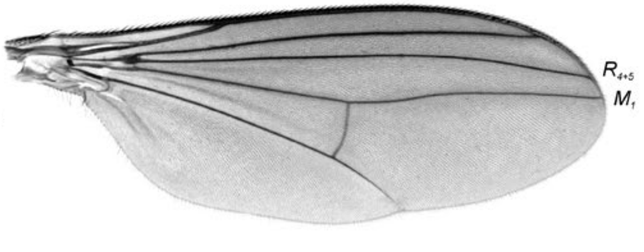
Chrysosoma **Guérin-Méneville** (Sciapodinae)**.** There are over 240 described species of *Chrysosoma* (most inhabiting the Old World tropics), of which 66 occur in the Afrotropical Region. The genus includes some of the largest sciapodines. Grichanov (1995*c*, 1999*b*) recognised three subgenera in the Afrotropics: *Chrysosoma sensu stricto*, *C.* (*Kalocheta* Becker) and *C.* (*Mesoblepharius* Bigot). *Chrysosoma* (*Kalocheta*) and *C.* (*Mesoblepharius*) appear to be confined to tropical Africa and are distinguished from the nominotypical subgenus by the series of long setae on tarsomere 1 of the male mid leg that usually extends onto the mid tibia (Fig. 17). *Chrysosoma* (*Kalocheta*) is further characterised by the flattened strap-like antennal stylus present in both sexes (Fig. 12). See Fig. 16 for an example of the head of this genus, Figs 124, 125 for the wing, and Fig. 233 for a photograph of a living specimen. An identification key to Afrotropical species was provided by Grichanov (1998*g*).

Chrysotus **Meigen** (Diaphorinae)**.** This virtually cosmopolitan genus includes some 350 species and is essentially a holding group for a large number of small-sized diaphorines. The Afrotropical fauna includes 16 described species (Grichanov 2011*d*), but undoubtedly more remain to be discovered. *Chrysotus* is close to *Achradocera*, but differs in the following respects: male antennal postpedicel globular (Fig. 37), reniform, or conoid, with long subapical arista-like stylus; lower postocular surface with fine unmodified setae. See Fig. 25 for an example of the head of this genus, Fig. 69 for the wing and Fig. 149 for the male terminalia. There is no suitable identification key available for Afrotropical species.

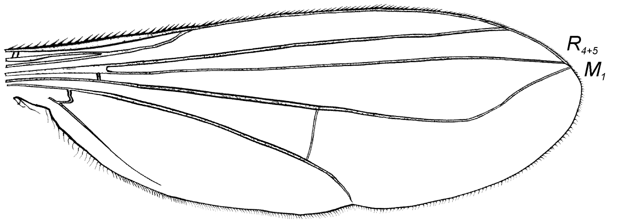
Condylostylus **Bigot** (Sciapodinae)**.** This mainly pantropical genus includes some 260 described species (excluding *ca* 30 doubtful names); of which most occur in the Neotropical Region. The Afrotropical fauna was studied by Grichanov (1996*d*, 1998*g*, 1999*b*, 2000*b*, 2003, 2010*e*) and includes 21 species (excluding those transferred to *Parentia*), which have been subdivided into three species-groups: the *C. paricoxa*-group, the *C. pateraeformis*-group and the *C. burgeoni*-group (= *Aldabromyia* Meuffels & Grootaert). The *C. pateraeformis*-group appears to be confined to the Afrotropical Region. Adults (Fig. 232) can be recognised by the following combination of



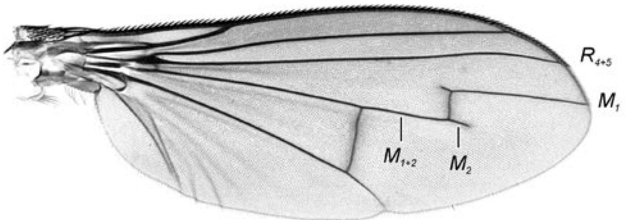
79 *Dolichopus* ♂



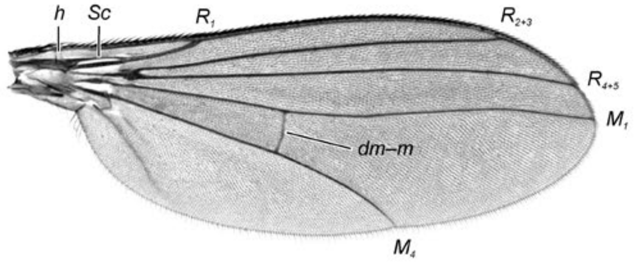
80 *Hercostomus* ♂



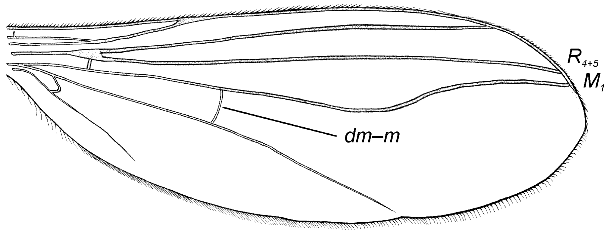
81 *Apelastoneurus* ♂



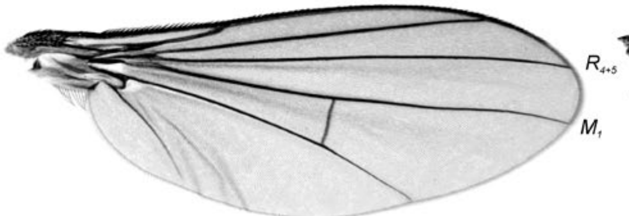
82 *Lichtwardtia* ♂



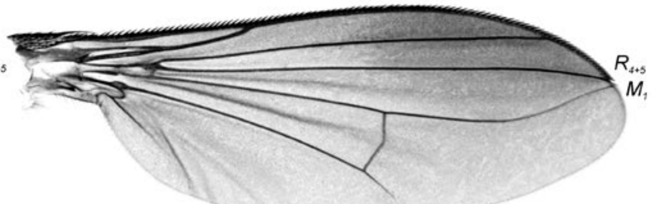
83 *Neohercostomus* ♂



84 *Pseudargyrochlamys* ♂



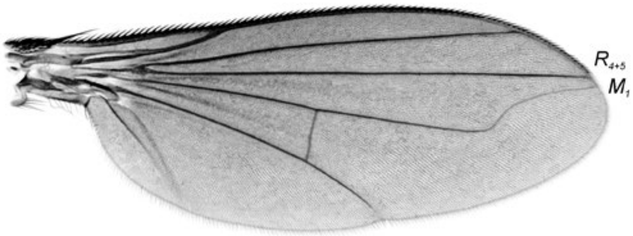
85 *Pseudohercostomus* ♀



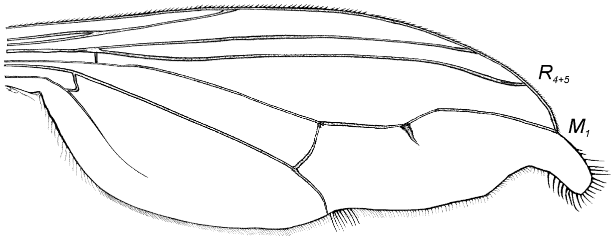
86 *Pseudoparaclius* ♀

Figs 56.79–86. Wings of Dolichopodidae (dorsal views): (79) *Dolichopus cuprinus* Wiedemann (non-Afrotropical) ♂; (80) *Hercostomus* sp. ♂; (81) *Apelastoneurus gabonensis* (Grichanov) ♂; (82) *Lichtwardtia* sp. ♂; (83) *Neohercostomus duviardi* (Couturier) ♂; (84) *Pseudargyrochlamys barracloughi* (Grichanov) ♂; (85) *Pseudohercostomus* sp. ♀; (86) *Pseudoparaclius* sp. ♀. Fig. 79 (Robinson & Vockeroth 1981, fig. 23).

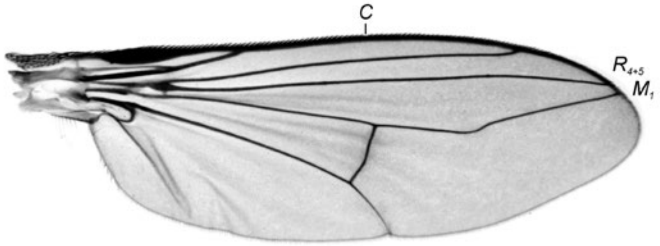
Abbreviations: *bm+dm* – basal medial cell + discal medial cell; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *dm–m* – discal medial crossvein; *h* – humeral crossvein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein; *Sc* – subcosta.



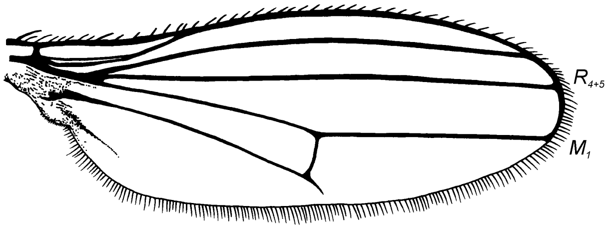
87 *Pseudopelastoneurus* ♂



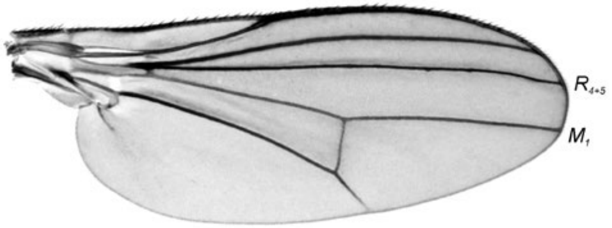
88 *Sybistroma* ♂



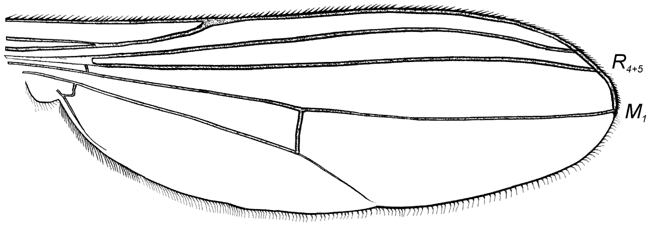
89 *Tachytrechus* ♂



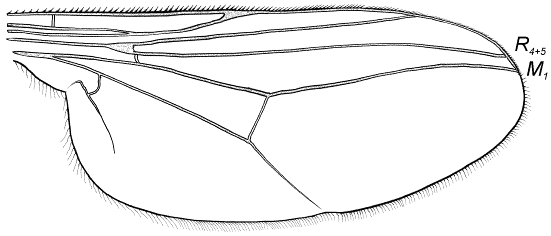
90 *Aphrosylus* ♂



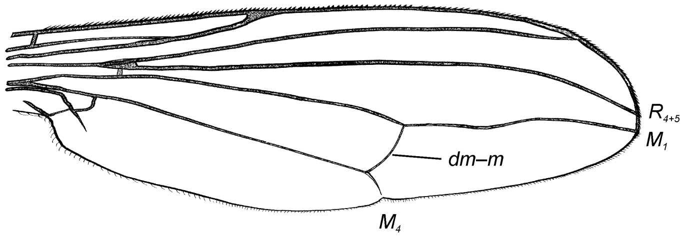
91 *Cemocarus* ♂



92 *Cymatopus* ♂



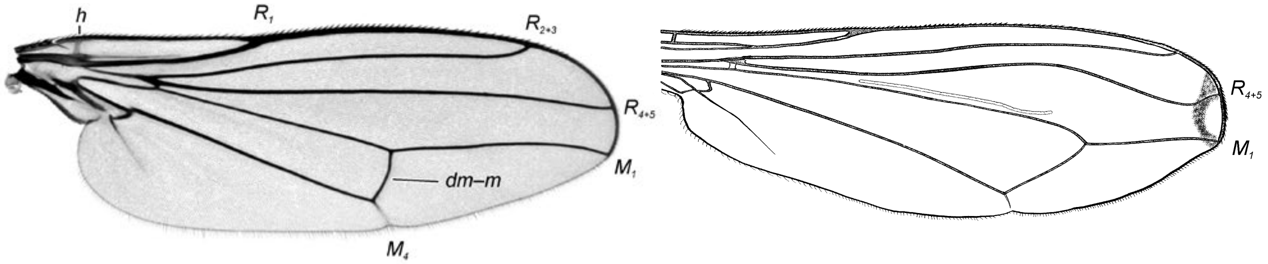
93 *Epithalassius* ♂



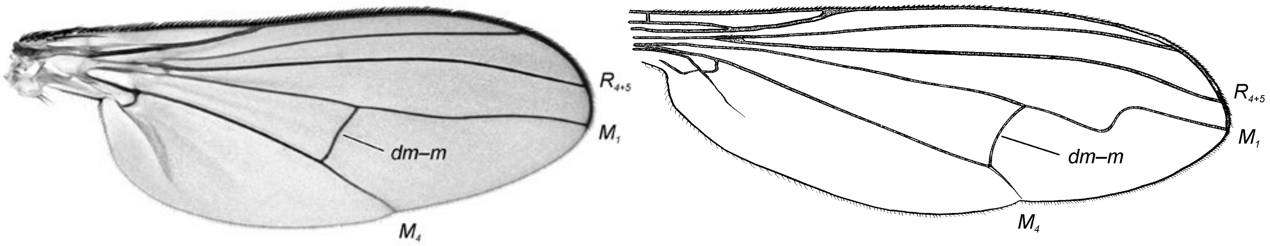
94 *Hydatostega* ♂

Figs 56.87–94. Wings of Dolichopodidae (dorsal views): (87) *Pseudopelastoneurus diversifemur* (Parent) ♂; (88) *Sybistroma bogoria* (Grichanov) ♂; (89) *Tachytrechus tessellatus* (Macquart) ♂; (90) *Aphrosylus gioiellae* Rampini & Munari ♂; (91) *Cemocarus* sp. ♂; (92) *Cymatopus madagascarensis* Grichanov ♂; (93) *Epithalassius corsicanus* Becker ♂; (94) *Hydatostega christopherseni* (Frey) ♂. Fig. 90 (after Rampini & Munari 1987, fig. 3).

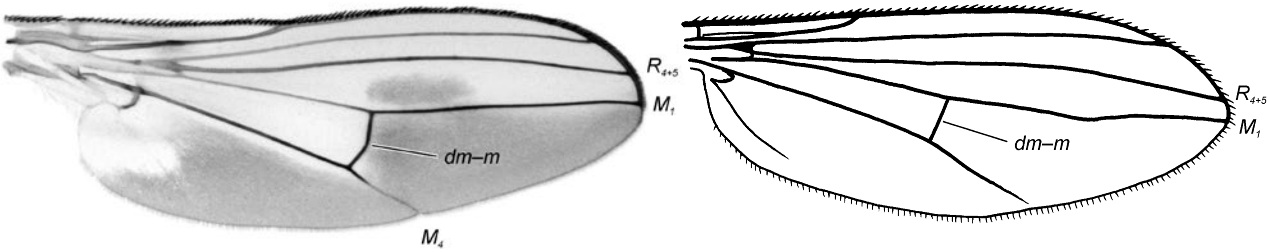
Abbreviations: *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_{4+5} – third branch of radius.



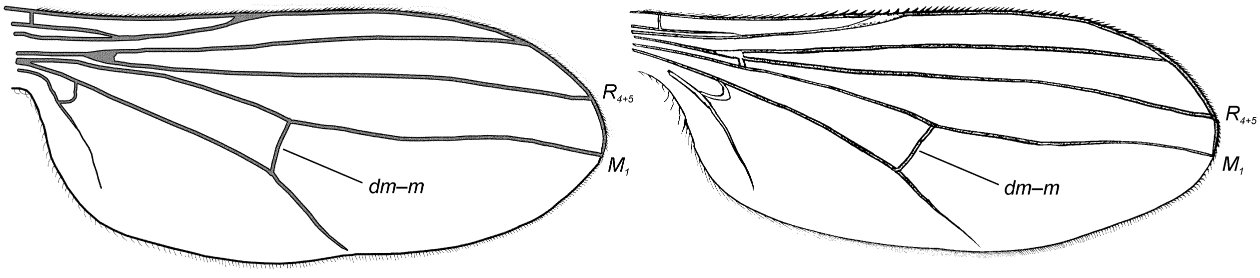
95 *Hydrophorus* ♂ 96 *Liancalus* ♂



97 *Machaerium* ♀ 98 *Orthoceratium* ♂



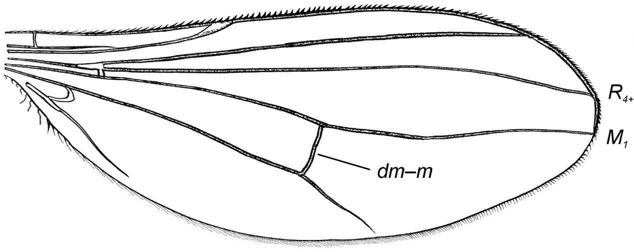
99 *Thinophilus* ♀ 100 *Systenus* ♂



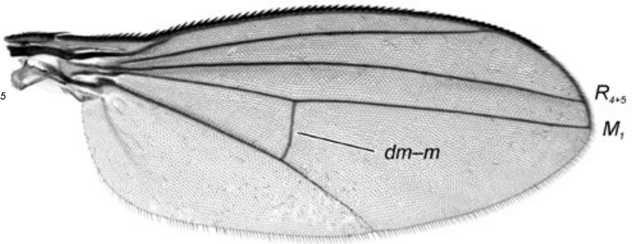
101 *Euxiphocerus* ♂ 102 *Systenomorphus* ♂

Figs 56.95–102. Wings of Dolichopodidae (dorsal views): (95) *Hydrophorus* sp. ♂; (96) *Liancalus peringueyi* Curran ♂; (97) *Machaerium maritimae* Haliday (non-Afrotropical) ♀; (98) *Orthoceratium lacustre* (Scopoli) ♂; (99) *Thinophilus* sp. ♀; (100) *Systenus africanus* Grichanov ♂; (101) *Euxiphocerus disjunctus* Grichanov ♂; (102) *Systenomorphus katyushae* Grichanov ♂. Fig. 100 (after Grichanov & Mostovski 2009*b*, fig. 3).

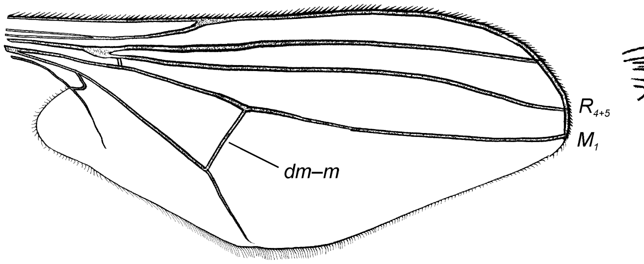
Abbreviations: *dm–m* – discal medial crossvein; *h* – humeral crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.



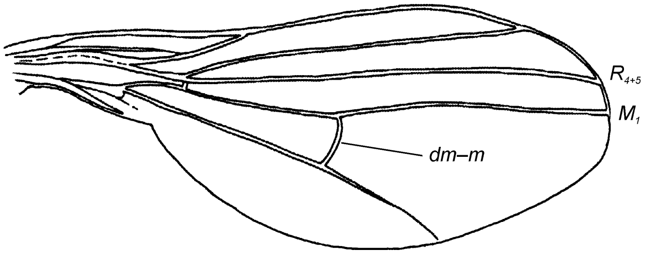
103 *Systenoneurus* ♂



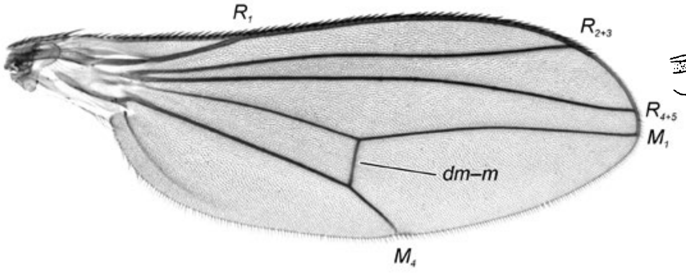
104 *Thrypticus* ♂



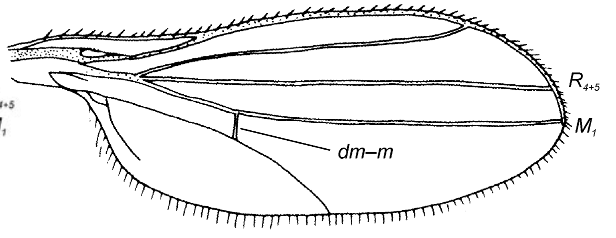
105 *Craterophorus* ♂



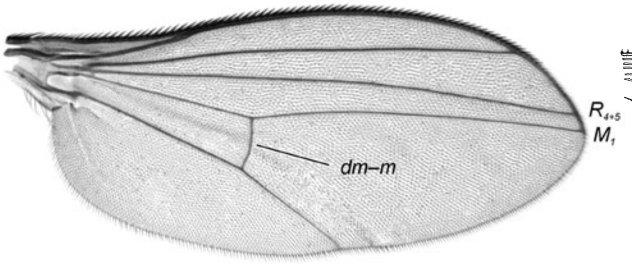
106 *Grootaertia* ♂



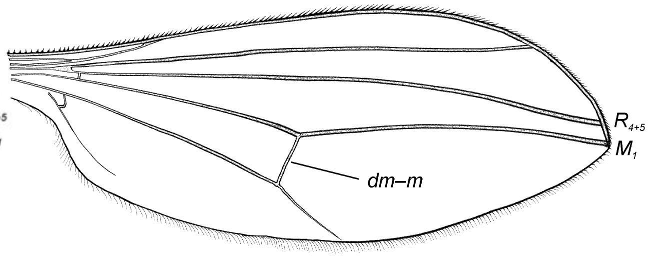
107 *Medetera* ♂



108 *Paramedetera* ♀



109 *Saccopheronta* ♂

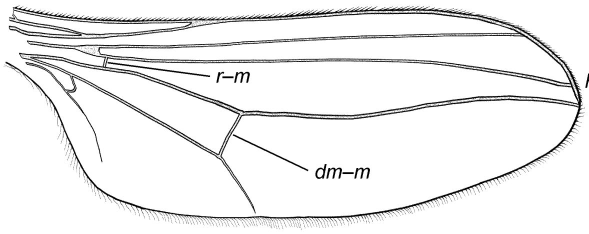


110 *Dolichophorus* ♂

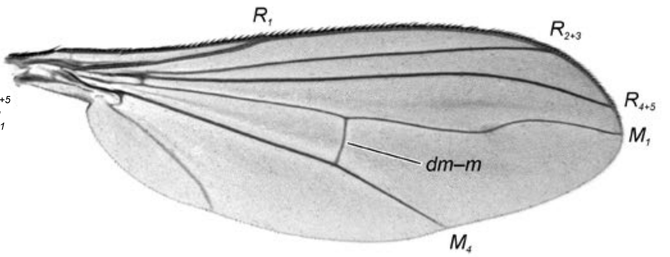
Figs 56.103–110. Wings of Dolichopodidae (dorsal views): (103) *Systenoneurus ovechkinae* Grichanov ♂; (104) *Thrypticus* sp. ♂; (105) *Craterophorus mirus* Lamb ♂; (106) *Grootaertia skorpionensis* Grichanov, Kirk-Spriggs & Grootaert ♂; (107) *Medetera* sp. ♂; (108) *Paramedetera papuensis* Grootaert & Meuffels ♀; (109) *Saccopheronta* sp. ♂; (110) *Dolichophorus friedmani* Grichanov ♂. Fig. 106 (after Grichanov *et al*. 2006, fig. 3), Fig. 108 (after Grootaert & Meuffels 1997*a*, fig. 4).

Abbreviations: *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

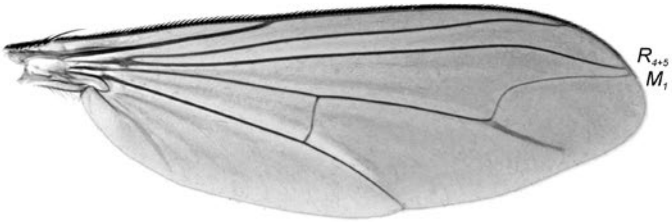
characters: head with frons of both sexes with raised setulose mound bearing strong vertical seta; antennal arista-like stylus dorsal to dorsoapical; pedicel with long dorsal and ventral setae; femora lacking anterior preapical seta; male hind tibia without callus; wing (Figs 126–128), often with dark brown fasciae; vein M_2 present even as a fold; vein M_1 beyond M_2, usually sharply recurved basally; 2 pairs of long scutellar setae; male terminalia with hypopygium (Figs 211–213) often rather small. An identification key to Afrotropical species of *Condylostylus* was provided by Grichanov (1998*g*). Grichanov (1999*b*, 2010e) subsequently published identification keys to the *C. pateraeformis*-group and *C. paricoxa*-group, respectively.



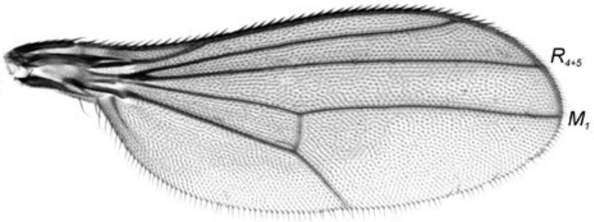
111 *Nikitella* ♂



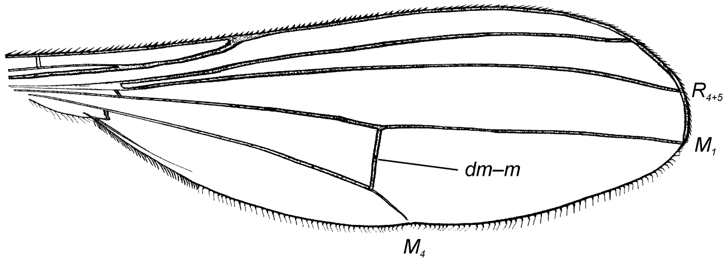
112 *Neurigona* ♀



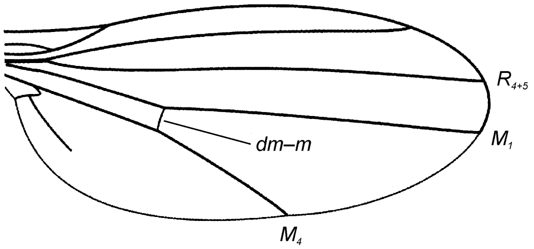
113 *Tenuopus* ♀



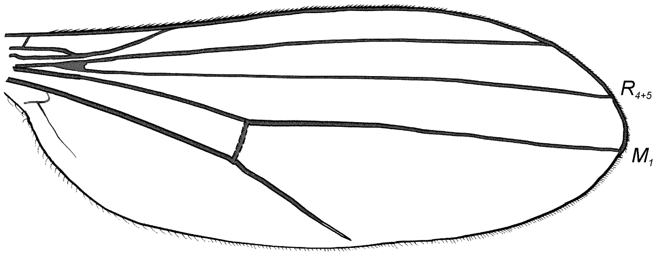
114 *Acropsilus* ♂



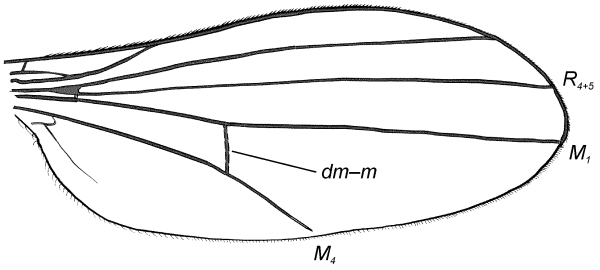
115 *Griphophanes* ♂



116 *Meuffelsia* ♂



117 *Micromorphus* ♂



118 *Nepalomyia* ♂

Figs 56.111–118. Wings of Dolichopodidae (dorsal views): (111) *Nikitella vikhrevi* Grichanov ♂; (112) *Neurigona quadrifasciata* (F.) (non-Afrotropical) ♀; (113) *Tenuopus* sp. ♀; (114) *Acropsilus* sp. ♂; (115) *Griphophanes garambaensis* Grichanov ♂; (116) *Meuffelsia erasmusorum* Grichanov ♂; (117) *Micromorphus aristalis* (Curran) ♂; (118) *Nepalomyia kotrbae* Grichanov ♂. Fig. 116 (after Grichanov & Mostovski 2008, fig. 3).

Abbreviations: *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; *r–m* – radial–medial crossvein.

***Corindia* Bickel** (Medeterinae)**.** This genus includes 12 species described from Australasia (Bickel 1986, 2014), four species described from the savanna belt of tropical Africa (Grichanov 1998*h*, 2000*b*) and many undescribed species in the New World (Bickel 2009: 691). *Corindia* is closely related to the stem-mining genus *Thrypticus*, differing in the structure of the female ovipositor which is cylindrical, rather than blade-like and sclerotised and the male surstylus and cercus which are usually not dorsally deflexed (Fig. 185). An identification key to Afrotropical species was provided by Grichanov (1998*h*).

***Craterophorus* Lamb** (Medeterinae)**.** This genus is endemic to the western Indian Ocean island States of Madagascar, Mauritius and Seychelles and includes five described species. Males are distinguished by the first abdominal tergite bearing a pair of dorsal bulbous structures (Lamb 1922, fig. 16b); male terminalia with hypopygium with long narrow cerci (Fig. 187); and wing often with posterior margin angular (Fig. 105). Females lack the bulbous structures on the first abdominal tergite, but have several strong setae in the same location. An identification key to known species was provided by Grichanov (1998*i*).

***Cryptophleps* Lichtwardt** (Diaphorinae)**.** This Old World genus comprises 23 species, of which four occur in the Afrotropical Region (Grichanov 2015). Species of *Cryptophleps* occur in a variety of habitats, including tropical coastal mudflats, mangroves, rainforests and temperate woodlands (Bickel 2005). *Cryptophleps* is closely related to *Asyndetus*, based on their similar wing venation (compare Fig. 68), with the costal vein (C) ending at vein R_{4+5}, and vein M_1 broken (see synopsis of *Asyndetus* above). Grichanov (2015) provided a key to Afrotropical and Palaearctic species.

***Cymatopus* Kertész** (Hydrophorinae)**.** This genus includes 22 mostly Australasian and Oriental species, with several species also described from the Neotropical and Afrotropical Regions. The Afrotropical species, *C. stuckenbergi* Grootaert & Grichanov, 2008, was described from Madagascar and belongs to the *C. longipilus* species-group, characterised by non-raptorial fore legs and ornamented hind legs (Grootaert & Grichanov 2008). The other known Afrotropical species, *C. madagascarensis* Grichanov, 2012, was described from the same locality as *C. stuckenbergi*, but belongs to the nominotypical *C. tibialis* species-group, with ornamented fore legs (Grichanov 2012*g*). The genus inhabits rocky sea shores and is part of the “aphrosyline” group of Hydrophorinae. Species of *Cymatopus* are similar to those of *Cemocarus*, but differ in the possession of a rounded, or conoid antennal postpedicel, with an apical arista-like stylus (Fig. 40). See Fig. 92 for an example of the wing of this genus and Fig. 178 for the male terminalia.

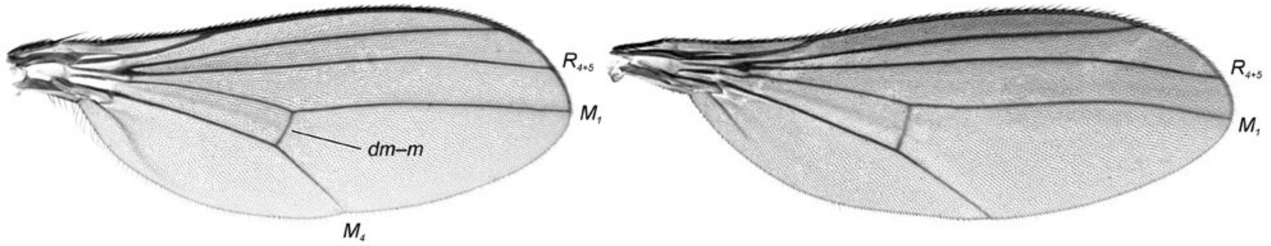
***Dactylonotus* Parent** (*Incertae sedis*)**.** This genus comprises seven described species, including one from New Zealand and six from southern Africa. Grichanov (1998*b*) provided an identification key to species; but since then *D. meuffelsi* Grichanov, 1998, has been synonymised with *D. rudebecki* Vanschuytbroeck, 1960 and *D. univittatus* (Loew, 1858) was transferred to *Dactylonotus* from *Neurigona* (Grichanov 2000*a*). More recently, Grichanov (2016) described two additional species from South Africa and provided an identification key to Afrotropical species. The genus can be recognised by the finger-like projection or conus of the antennal pedicel, which overlaps the postpedicel dorsally (Fig. 35); mid and hind femora with an anterior preapical seta; and male sternite 8 with strong projecting setae (Fig. 154). See Fig. 70 for an example of the wing of this genus.

***Diaphorus* Meigen** (Diaphorinae)**.** This virtually cosmopolitan genus includes some 260 described species and occurs in all zoogeographical regions, except Antarctica. The Afrotropical fauna includes 20 described species and several species await description. Adults are small- to medium-sized diaphorines with the following characters: male eyes contiguous (Fig. 7), or narrowly separated on frons; head with face rather wide and parallel-sided; antennal postpedicel rather small and short, usually wider than long; arista-like stylus with very short basal segment; thorax with acrostichal setae biseriate; wing usually somewhat wedge-shaped, with greatest width before middle (Fig. 71); male segment 8 with 4–8 strong setae (Fig. 151). *Diaphorus alsiosus* (Meunier, 1910) was described from rather recent Zanzibaran copal (Pleistocene/Holocene) (Grichanov 2008*b*). Grichanov (2012*f*) provided an identification key to seven species of the *Diaphorus nigricans*-group, which differs distinctly from other Afrotropical *Diaphorus* in the following combination of characters: usually small species (2–3 mm); eyes contiguous, or strongly convergent above antennae; head with face broad; mouthparts with palpus black-brown; femora mostly black-brown, with extreme apices often yellow; and abdomen entirely dark, usually black-green. There are no suitable identification keys to the entire Afrotropical fauna.

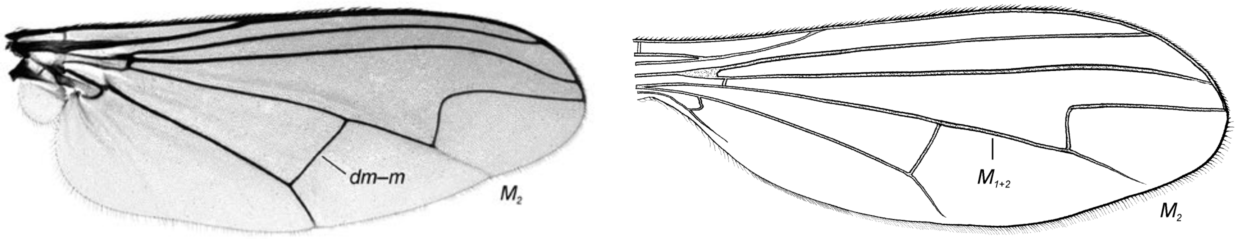
***Dolichophorus* Lichtwardt** (Medeterinae)**.** This distinctive genus includes three Palaearctic species and three Afrotropical species (Côte d’Ivoire, Democratic Republic of Congo, Madagascar; Sierra Leone, Tanzania). *Medetera hamata* Parent, 1936 (Democratic Republic of Congo) and the Oriental species, *M. maai* Bickel (Malaysia), are also probably referable to *Dolichophorus*. The genus is recognised by the fore coxa with a long spine-like, or hook-like, cluster of setae in both sexes. See Fig. 110 for an example of the wing of this genus and Fig. 189 for the male terminalia. An identification key to the six known species was provided by Grichanov (2009*a*).

***Dolichopus* Latreille** (Dolichopodinae)**.** Six species of Afrotropical *Dolichopus* were listed by Dyte & Smith (1980: 450). Of these, three were subsequently transferred to other genera, and the rest were excluded from the fauna of the region by Grichanov (2004: 18). In the same work, Grichanov also described one new endemic Afrotropical species and recorded three Palaearctic species of *Dolichopus* from the Afrotropical Region for the first time. Brooks (2005) synonymised *Lichtwardtia* with *Dolichopus*, but this has not been followed in subsequent works treating the Afrotropical fauna, which have continued to recognise *Lichtwardtia* as a separate genus, despite rendering *Dolichopus* paraphyletic as a result. *Dolichopus* exclusive of *Lichtwardtia* (including some 640 described species worldwide) are distinguished from other dolichopodines by the following characters: wing vein M_1 with sigmoidal bend and lacking anteroproximal stump vein (Fig. 79); hind leg with tarsomere 1 with 1–3 strong dorsal setae (Fig. 60); thorax with pleuron anterior to posterior spiracle with tuft of fine setulae. See Fig. 26 for an example of the head of this genus and Fig. 160 for the male terminalia. An identification key to known Afrotropical species was published by Grichanov (2004: 178).

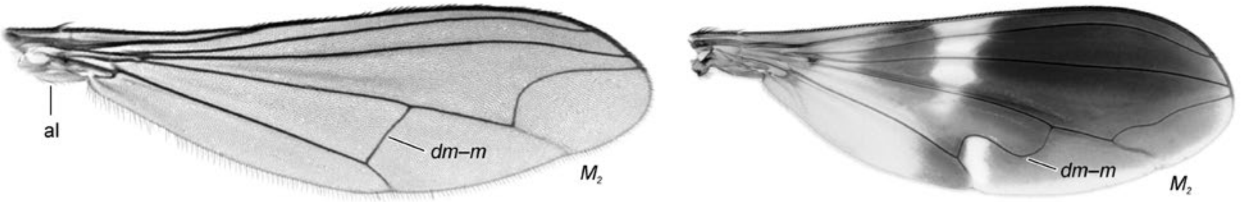
***Dytomyia* Bickel** (Sciapodinae)**.** This genus includes five species from Australia and New Guinea and five species from Madagascar (Grichanov 1998*g*, 1999*b*, 2003). Adults can be distinguished by the following characters: head with vertex not strongly excavated; vertical seta strong in both sexes; face and clypeus broad in both sexes; thorax with 4 strong dorsocentral setae in both sexes; lateral scutellar setae absent; female fore femur with 3–4 short pale basoventral setae; male fore tarsomere 1 swollen, with dense pale pile; male hind tibia sometimes with irregular swelling, or callus at near middle; male terminalia with cercus (Fig. 214) with short ventral lobe articulated at base (Bickel 1994). An identification key to Afrotropical species was provided by Grichanov (1998*g*), but does not include the more recently transferred species *D. lutescens* (Vanschuytbroeck, 1952).


119 *Peloropeodes* ♂

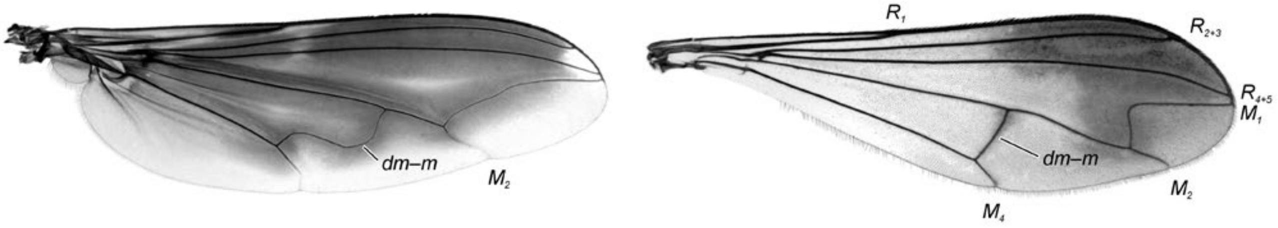
120 *Rhaphium* ♂


121 *Amblypsilopus* ♂

122 *Bickelia* ♂


123 *Bickeliolus* ♂

124 *Chrysosoma* (*Kalocheta*) ♀

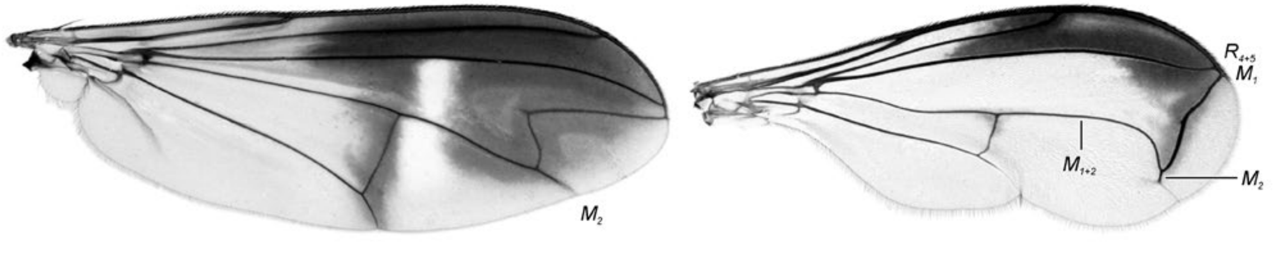

125 *Chrysosoma* (*Mesoblepharius*) ♂

126 *Condylostylus burgeoni*-group ♂

Figs 56.119–126. Wings of Dolichopodidae (dorsal views): (119) *Peloropeodes* sp. ♂; (120) *Rhaphium currani* (Parent) ♂; (121) *Amblypsilopus* sp. ♂; (122) *Bickelia parallela* (Macquart) ♂; (123) *Bickeliolus* sp. ♂; (124) *Chrysosoma* (*Kalocheta*) sp. ♀; (125) *C.* (*Mesoblepharius*) sp. ♂; (126) *Condylostylus* sp. (*burgeoni* Parent species-group) ♂.

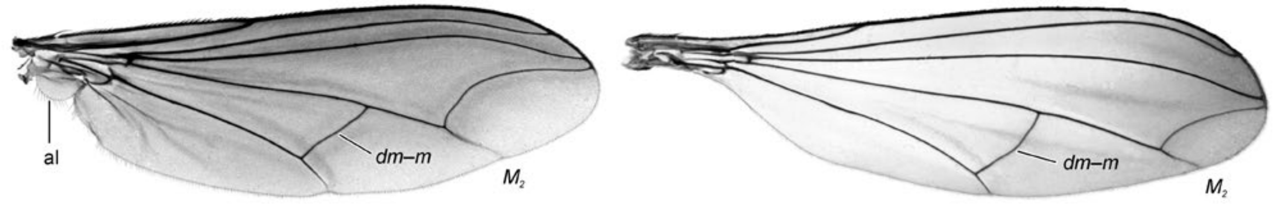
Abbreviations: al – alula; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

Emiratomyia **Naglis** (Diaphorinae)**.** This monotypic genus was established by Naglis (2014) for *E. arabica* Naglis, 2014 from the United Arab Emirates. *Emiratomyia* can be differentiated from other diaphorine genera by the following combination of characters: head with occiput concave, postvertical setae absent; male antennal postpedicel triangular (1.5 × longer than high), with apicodorsal arista-like stylus (Fig. 221); thorax with 4 dorsocentral setae, uniserial acrostichal setae, 1 pair of scutellar setae; hind coxa bearing 1 lateral seta; male fore leg with tarsomere 5 bearing single claw; male mid leg with tarsomeres modified; wing (Fig. 223) with crossvein *dm–m* in basal ¼ of wing; wing veins R_{4+5} and M_1 subparallel, displaced anteriad, vein M_1 lacking anterior bend near middle, joining costa anterior to wing apex; body length



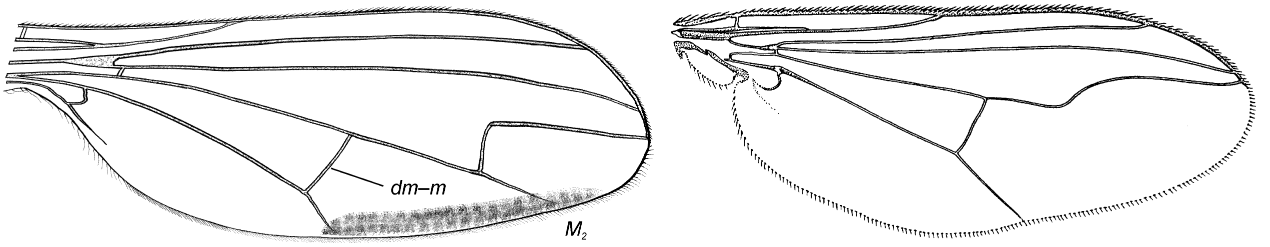
127 *Condylostylus paricoxa*-group ♂

128 *Condylostylus pateraeformis*-group ♂



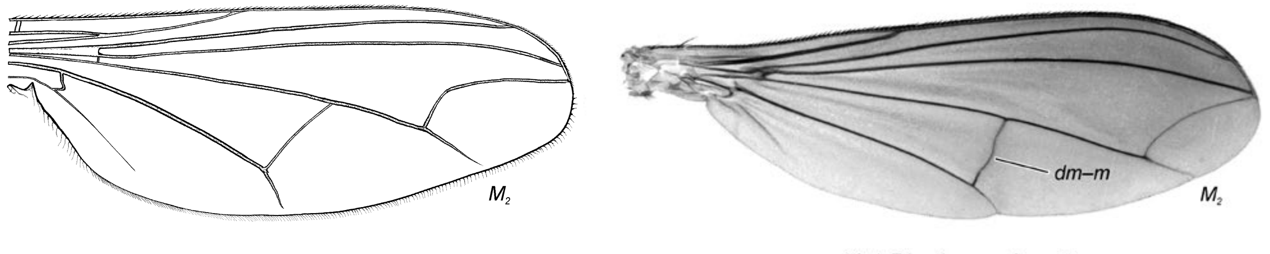
129 *Ethiosciapus* ♂

130 *Gigantosciapus* ♀



131 *Mascaromyia* ♂

132 *Mesorhaga* ♀



133 *Parentia* ♂

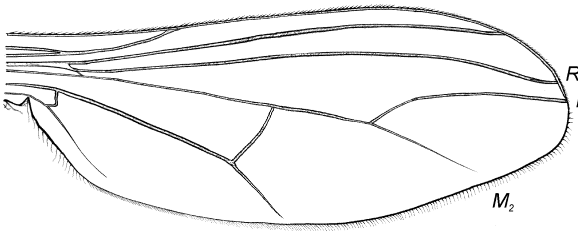
134 *Plagiozopelma* ♀

Figs 56.127–134. Wings of Dolichopodidae (dorsal views): (127) *Condylostylus* sp. (*paricoxa* Parent species-group) ♂; (128) *Condylostylus* sp. (*pateraeformis* Becker species-group) ♂; (129) *Ethiosciapus* sp. ♂; (130) *Gigantosciapus* sp. ♀; (131) *Mascaromyia leptogaster* (Thomson) ♂; (132) *Mesorhaga pallidicornis* Van Duzee (non-Afrotropical) ♀; (133) *Parentia* sp. ♂; (134) *Plagiozopelma* sp. ♀.

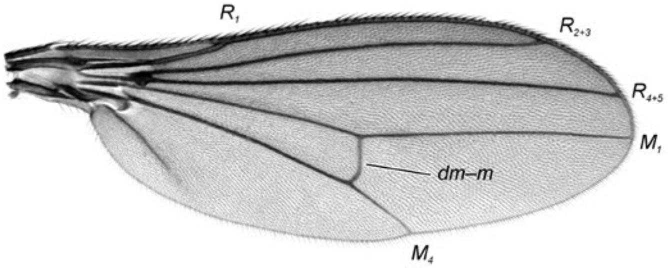
Abbreviations: al – alula; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_{1+2} – fused first and second branch of media; M_2 – second branch of media; R_{4+5} – third branch of radius.

less than 2 mm. *Emiratomyia* is closely related to *Shamshevia* and *Arabshamshevia*.

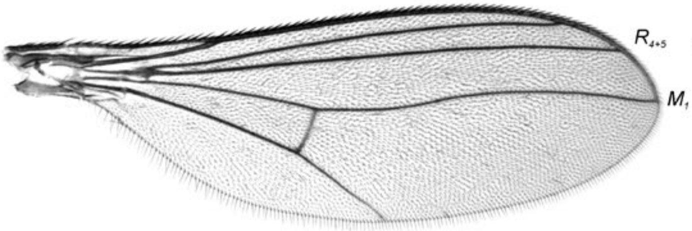
Epithalassius **Mik** (Hydrophorinae)**.** This genus is mainly Mediterranean and includes seven species which inhabit sandy beaches along sea coasts. Adults are recognised by their distinctive antennal postpedicel (Fig. 41); wing venation (Fig. 93); and male terminalia with bilobate cercus (Fig. 179). Two species are recorded from the Afrotropics, *E. corsicanus* Becker, 1910, from the coast of St. Helena Is., and *E. africus* Parent, 1930, from an inland locality near Brazzaville, Republic of Congo. The latter species, which is known only from the damaged female holotype, is doubtfully included in the genus. An identification key to known species was provided by Grichanov (2008a).



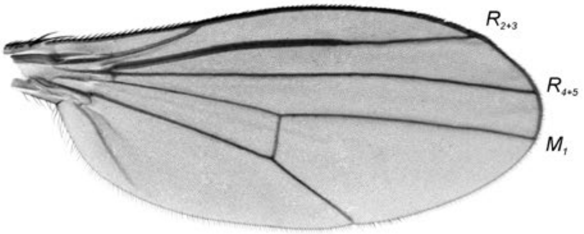
135 *Sciapus* ♂



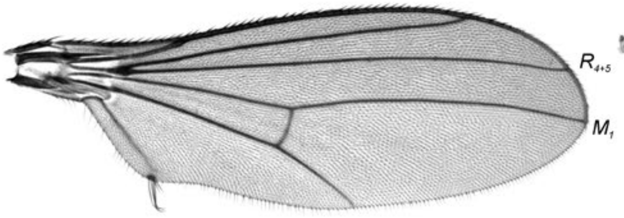
136 *Campsicnemus* ♂



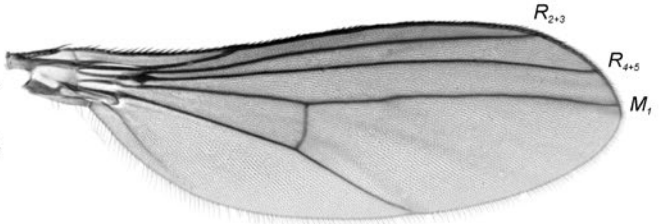
137 *Chaetogonopteron* ♂



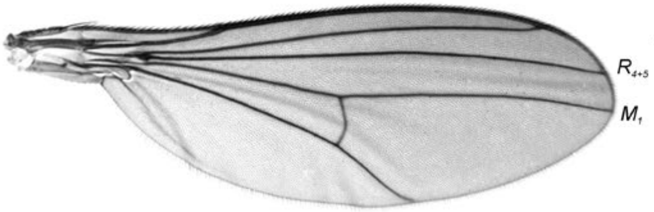
138 *Nurteria* ♂



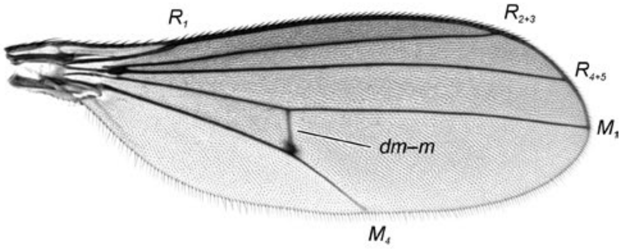
139 *Olegonegrobovia* ♂



140 *Sympycnus* ♂



141 *Syntormon* ♂



142 *Telmaturgus* ♂

Figs 56.135–142. Wings of Dolichopodidae (dorsal views): (135) *Sciapus endrodyi* Grichanov ♂; (136) *Campsicnemus* sp. ♂; (137) *Chaetogonopteron nectarophagum* (Curran) ♂; (138) *Nurteria* sp. ♂; (139) *Olegonegrobovia* sp. ♂; (140) *Sympycnus discrepans* Parent ♂; (141) *Syntormon* sp. ♂; (142) *Telmaturgus munroi* (Curran) ♂.

Abbreviations: *dm–m* – discal medial crossvein; M_1 – first branch of media; M_2 – second branch of media; M_4 – fourth branch of media; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius.

***Ethiosciapus* Bickel** (Sciapodinae)**.** This endemic Afrotropical genus includes nine species from the continental Afrotropics, Comores, Madagascar, Seychelles and St. Helena Is. Species of *Ethiosciapus* are distinguished by the distinctive male terminalia with basal hook on the cercus (Fig. 218); thorax lacking lateral scutellar seta; and tarsomere 1 of male fore leg flattened, with ventral pile (Bickel 1994). See Fig. 129 for an example of the wing of this genus. *Ethiosciapus* is closely related to *Bickeliolus* (see above). An identification key to Afrotropical species was provided by Grichanov (1998*g*).

***Euxiphocerus* Parent** (Medeterinae)**.** An endemic Afrotropical genus with three described species, recorded from Democratic Republic of Congo, Kenya, Namibia and South Africa (Grichanov 2009*b*). *Euxiphocerus* is close to *Systenus*, but can be distinguished by the head with flattened postocular setae; male antenna with reduced pedicel and elongate postpedicel (5–6 × longer than high) (Fig. 45); male terminalia with short abdominal segment 7; and hypopygium sessile (Fig. 183). See Fig. 101 for an example of the wing of this genus. An identification key was provided by Grichanov (2009*b*).

***Gigantosciapus* Grichanov** (Sciapodinae)**.** Thirteen species of this endemic Afrotropical genus occur in the humid tropics of continental Africa (Grichanov 1997*b*, 1998*g*). Adults are large lanky flies (body length up to 14 mm, antenna length up to 5 mm), distinguished by the following combination of characters: antennal postpedicel long, usually with long apical arista-like stylus; head with vertical setae, or setulae absent in both sexes; frons and face narrow; thorax with acrostichal setae weak and short; scutellum usually with 1 pair of strong setae; wing (Fig. 130) with vein M_2 present; *dm–m* crossvein often sinuous; anal area of wing reduced; femora without strong anterior preapical seta; all tibiae and first tarsomeres with strong setae in both sexes; male terminalia with cercus simple. An identification key was provided by Grichanov (1998*g*).

***Griphophanes* Grootaert & Meuffels** (Peloropeodinae)**.** This poorly defined genus includes 15 Oriental species (Grootaert & Meuffels 1997*b*; Naglis & Grootaert 2012) and two Afrotropical species, from the savannas of Democratic Republic of Congo (Grichanov 2010*d*). The Afrotropical *Griphophanes* are similar to *Peloropeodes*, but lack the male secondary sexual characters of that genus (*i.e.*, asymmetrical claws on fore tarsus, spine-like setal cluster on mid coxa). See Fig. 115 for an example of the wing of this genus and Fig. 195 for the male terminalia. Grichanov (2010*d*) provided a key to Afrotropical species.

***Grootaertia* Grichanov** (Medeterinae)**.** This endemic Afrotropical genus of small-sized medeterines comprises seven described species from Namibia and South Africa (Grichanov 1999*a*, 2000*b*; Grichanov *et al*. 2006) and at least one undescribed South African species. The genus is close to *Paramedetera*, but is distinguished by the following features: antennal arista-like stylus apical (Fig. 46); distal sectors of wing veins R_{4+5} and M_1 weakly arched anteriorly (Fig. 106); male terminalia with segment 7 semicircular, narrow, not forming peduncle; hypopygium (Fig. 190) sessile, asymmetrical; hypandrial lobes absent; phallus with large lateral lobes; female terminalia with tergite 10 undivided medially and bearing acanthophorite setae. An identification key was provided by Grichanov *et al*. (2006).

***Hercostomus* Loew** (Dolichopodinae)**.** Some 470 species of *Hercostomus* have been described worldwide from all zoogeographical regions, except Antarctica. The genus, as currently defined, is a polyphyletic assemblage (Brooks 2005). Grichanov (1999*c*, 2004: 23) treated the Afrotropical fauna and recognised three species-groups, of which groups I and III have since been established as the genera *Afrohercostomus* and *Neohercostomus*, respectively (Grichanov 2010*g*, 2011*b*). Grichanov's (1999*c*, 2004: 24) species-group II corresponds to *Hercostomus sensu stricto* (*i.e.*, the *H. longiventris* lineage *sensu* Brooks 2005) and includes some 20 described species which can be identified using Grichanov's (2004: 178) identification key to *Hercostomus sensu lato*. Afrotropical species of *Hercostomus sensu stricto* can be recognised by the following combination of characters: wing vein M_1 beyond *dm–m* crossvein with weak sinuous anterior bend (Fig. 80); male fore tarsus with tarsomere 3 usually compressed, with elongate setulae dorsally, with tarsomeres 4 and/or 5 also often modified (Fig. 55); mid and hind tarsi simple; mid femur with 1 strong posterior preapical seta about even with anterior preapical seta; male terminalia with hypopygium with basiventral epandrial lobes and hypandrium forming a complex of entangled asymmetrical lobes (Fig. 165).

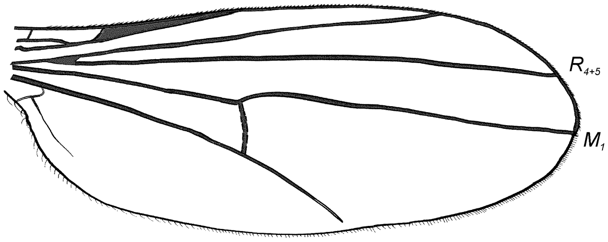
***Hydatostega* Philippi** (Hydrophorinae)**.** This genus includes eight New World species and three Afrotropical species. The Afrotropical species are restricted to the Tristan da Cunha Is. group and the genus is apparently absent from continental Africa (Grichanov 2005). *Hydatostega* is similar to *Hydrophorus*, but can be distinguished by the possession of a tuft of long setulae on the anepimeron of the thorax anterior to the posterior spiracle. See Fig. 94 for an example of the wing of this genus. Adults of *Hydatostega* are typically associated with standing water and are able to skate on the surface (like many *Hydrophorus*). Grichanov (2005) provided a key to the species from Tristan da Cunha Is.

***Hydrophorus* Fallén** (Hydrophorinae)**.** This primarily Holarctic genus occurs in all zoogeographical regions, except Antarctica and includes 115 described species. Twelve species are known from the Afrotropical Region, but many of these are unrecognisable, or are based on doubtful records (Grichanov 1997e). Adults are medium- to large-sized dolichopodids, with the following combination of characters: antennal postpedicel short with apico-ventral incision (Fig. 42); head with distinct gena; scutellum usually with 2 pairs of setae; thorax with anepimeron bare anterior to the posterior spiracle; wing crossvein *dm–m* longer than distal section of vein M_4 (Fig. 95); fore femur distinctly swollen and spinose ventrally; and fore tibia with row of ventral setae. Adults are typically associated with standing water and many species are known to skate on the water surface. Grichanov (1997e) provided the most recent identification key to species from continental Africa.

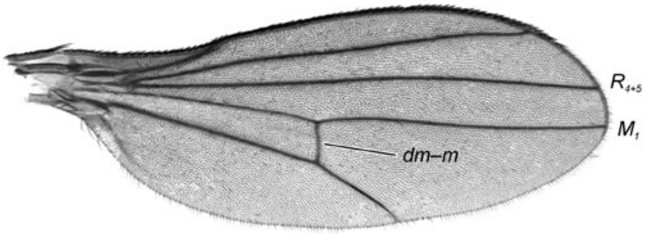
***Katangaia* Parent** (*Incertae sedis*)**.** A genus endemic to the continental Afrotropical Region (Democratic Republic of Congo, Ethiopia, Malawi and Tanzania), including four described species, reviewed and keyed by Grichanov (2012e). *Katangaia* resembles *Tachytrechus*, particularly in the structure of the clypeus, which is beak-like and projects below the lower eye margin (Fig. 4). The genus is further distinguished by the following features: antenna (Figs 5, 6) with apical arista-like stylus (with a thickened, or broad, flag-like tip in males), scape with short dorsal setulae; and large pedunculate male terminalia with claw-like medial projections on cercus (Fig. 174). See Fig. 145 for an example of the wing of this genus. The subfamily placement of *Katangaia* is somewhat contentious. The genus was described in the Rhaphiinae, but has since been placed either in the Dolichopodinae, or considered *incertae sedis* within the traditional Dolichopodidae (Brooks 2005; Grichanov 2012e).

***Lamprochromus* Mik** (Sympycninae)**.** This genus comprises 13 described species, including three from the Nearctic Region, nine from the Palaearctic Region and one, *L. belousovi* (Grichanov, 2008) (Fig. 201), from the Afrotropical Region (Democratic Republic of Congo). Adults are small, with a matt-brown, or velvety black area above the wing base and the thorax with 3 or 4 pairs of dorsocentral setae. *Lamprochromus belousovi* was included in the identification keys to Afrotropical *Sympycnus* (Grichanov 2008c) and *Telmaturgus* (Grichanov 2011c).

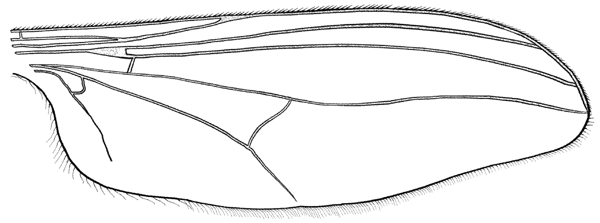
***Liancalus* Loew** (Hydrophorinae)**.** This genus includes 21 described species and is known from all zoogeographical regions, except Antarctica and Australasia. Five species have been described from the Afrotropics (Democratic Republic of Congo, Ethiopia, South Africa and Uganda). Adults of the genus are large gangly flies (Fig. 235), characterised by the thorax with a unique ventral digitiform projection on the proepimeron behind base of fore coxa (Fig. 230, indicated with arrow). The wing tip and venation of males are strongly modified and wing



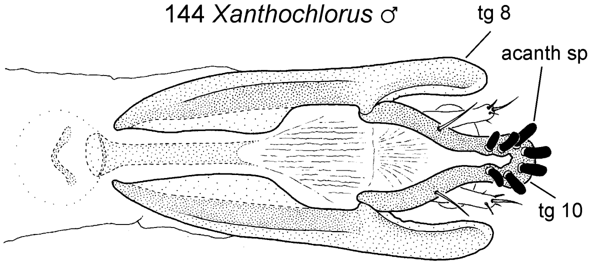
143 *Teuchophorus* ♂



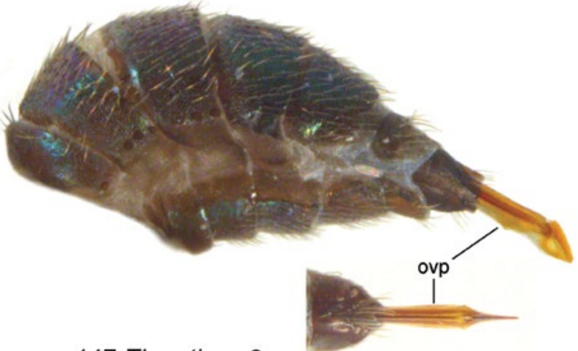
144 *Xanthochlorus* ♂



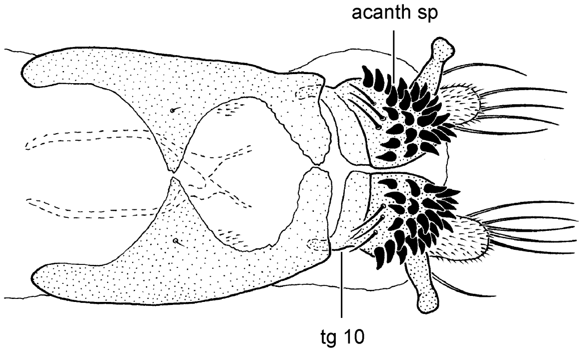
145 *Katangaia* ♂



146 *Argyrochlamys* ♀



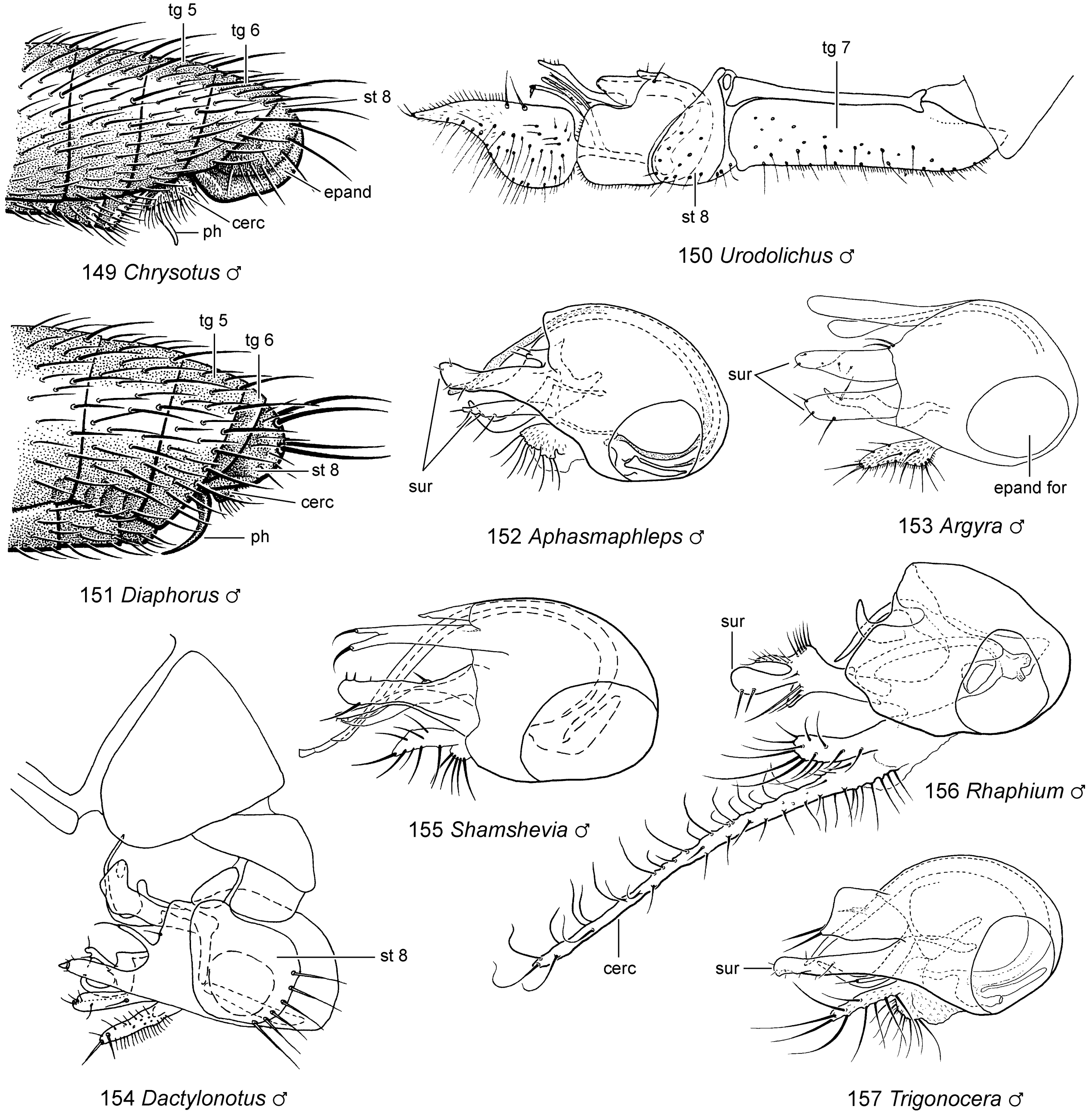
147 *Thrypticus* ♀



148 *Pseudohercostomus* ♀

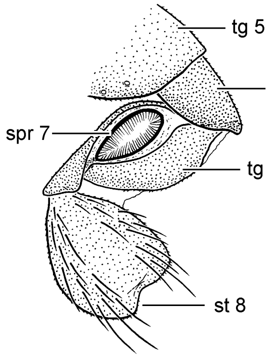
Figs 56.143–148. Wings and female terminalia of Dolichopodidae: (143) wing of *Teuchophorus caprivi* Grichanov, dorsal view ♂; (144) same, *Xanthochlorus kustovi* Grichanov ♂; (145) same, *Katangaia tanzaniensis* Grichanov ♂; (146) female terminalia of *Argyrochlamys impudicus* Lamb, dorsal view; (147) female abdomen of *Thrypticus willistoni* (Wheeler), lateral view (above), dorsal view of apex (below) (non-Afrotropical); (148) female terminalia of *Pseudohercostomus echinatus* Stackelberg, dorsal view. Figs 146, 148 (after Brooks 2005, figs 6D, 38E).

Abbreviations: acanth sp – acanthophorite spine; *dm–m* – discal medial crossvein; M_1 – first branch of media; ovp – ovipositor; R_{4+5} – third branch of radius; tg – tergite.

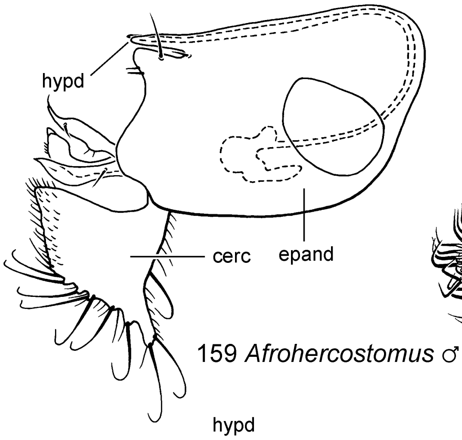


Figs 56.149–157. Male terminalia of Dolichopodidae (Diaphorinae, Rhaphiinae and *incertae sedis*) (lateral views): (149) *Chrysotus choricus* Wheeler (non-Afrotropical); (150) *Urodolichus lambi* Grichanov; (151) *Diaphorus gibbosus* Van Duzee (non-Afrotropical); (152) *Aphasmaphleps bickeli* Capellari & Grichanov; (153) *Argyra kireichuki* Grichanov; (154) *Dactylonotus univittatus* (Loew); (155) *Shamshevia hoanibensis* Grichanov; (156) *Rhaphium currani* (Parent); (157) *Trigonocera rivosa* Becker. Figs 149, 151 (Robinson & Vockeroth 1981, figs 36, 39), Fig. 150 (after Grichanov 1998*a*, fig. 1), Fig. 152 (after Capellari & Grichanov 2012, fig. 12), Fig. 153 (after Grichanov 1998*e*, fig. 2), Fig. 154 (after Grichanov 2000*a*, fig. 3), Fig. 155 (after Grichanov 2012*a*, fig. 5).

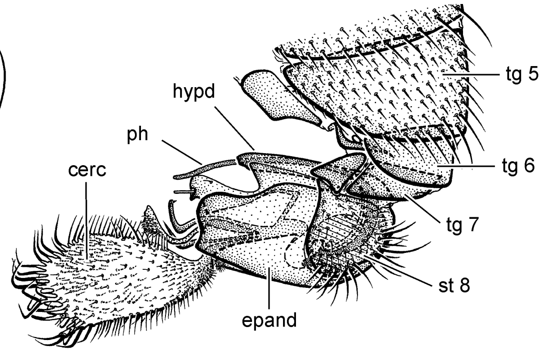
Abbreviations: cerc – cercus; epand – epandrium; epand for – epandrial foramen; ph – phallus; st – sternite; sur – surstylus; tg – tergite.



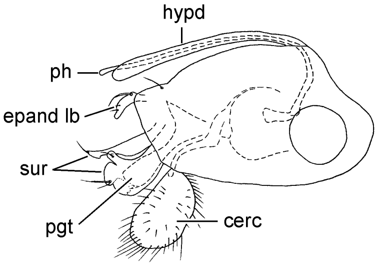
158 *Afrohercostomus* ♂



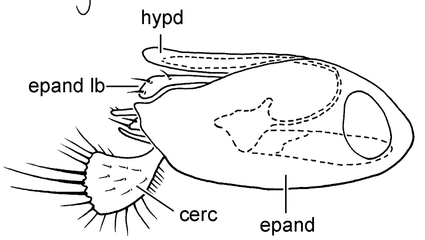
159 *Afrohercostomus* ♂



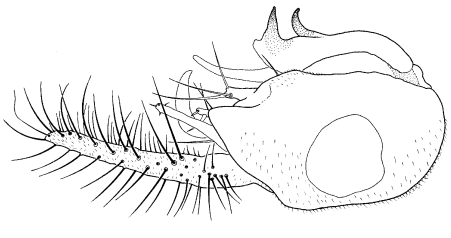
160 *Dolichopus* ♂



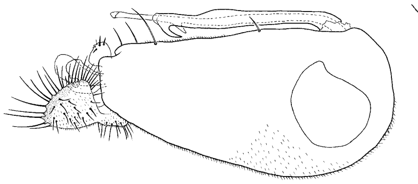
161 *Afroparaclius* ♂



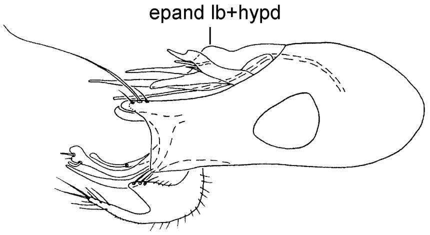
162 *Afropelastoneurus* ♂



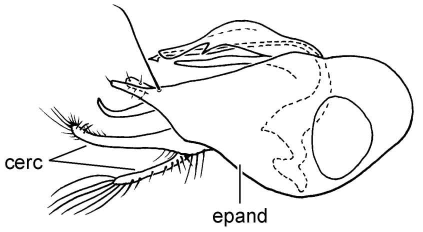
163 *Argyrochlamys* ♂



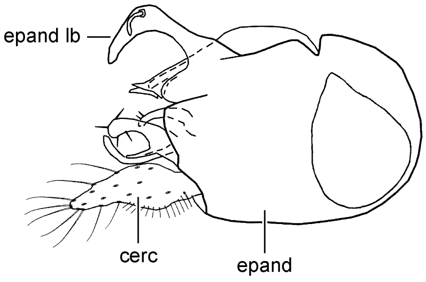
164 *Lichtwardtia* ♂



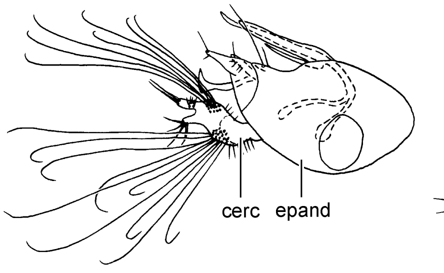
165 *Hercostomus* ♂



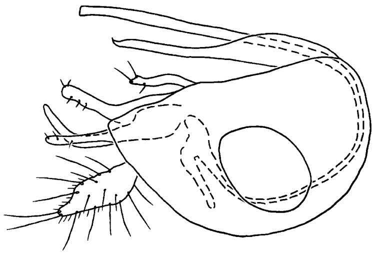
166 *Neohercostomus* ♂



167 *Neohercostomus* ♂



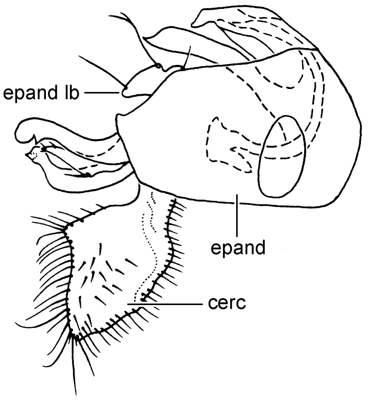
168 *Neohercostomus* ♂



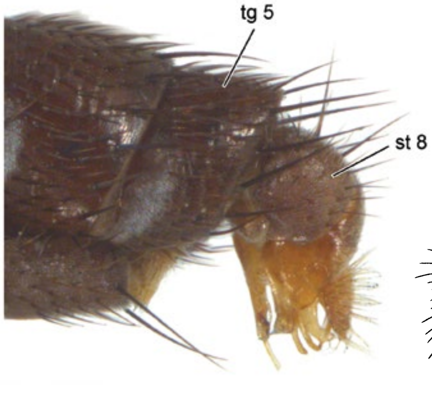
169 *Pseudargyrochlamys* ♂

Figs 56.158–169. Male terminalia of Dolichopodidae (Dolichopodinae) (lateral views): (158) abdominal segments 5–8 of *Afrohercostomus blagoderovi* (Grichanov); (159) *Afrohercostomus afer* (Rondani); (160) *Dolichopus brevipennis* Meigen (non-Afrotropical); (161) *Afroparaclius thompsoni* (Grichanov); (162) *Afropelastoneurus martius* (Grichanov); (163) *Argyrochlamys impudicus* Lamb; (164) *Lichtwardtia* sp. (non-Afrotropical); (165) *Hercostomus selikhovkini* Grichanov; (166) *Neohercostomus strictilamellatus* (Parent); (167) *N. manningi* Grichanov; (168) *N. itineris* (Grichanov); (169) *Pseudargyrochlamys michaeli* (Grichanov). Figs 159, 161, 162, 168, 169 (after Grichanov 2004, figs 10, 118, 91, 26, 93, respectively), Figs 165, 166 (after Grichanov 1999*c*, figs 11, 20), Fig. 160 (after McAlpine 1981, fig. 128), Figs 163, 164 (after Brooks 2005, figs 6A, 10A), Fig. 168 (after Grichanov 2011*b*, fig. 22).

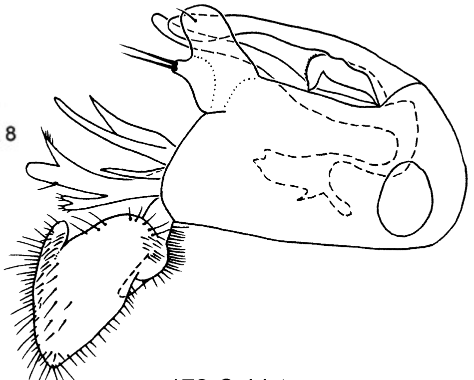
Abbreviations: cerc – cercus; epand – epandrium; epand lb – epandrial lobe; hypd – hypandrium; pgt – postgonite; ph – phallus; spr – spiracle; st – sternite; sur – surstylus; tg – tergite.



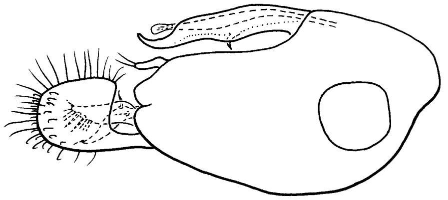
170 *Pseudoparaclius* ♂



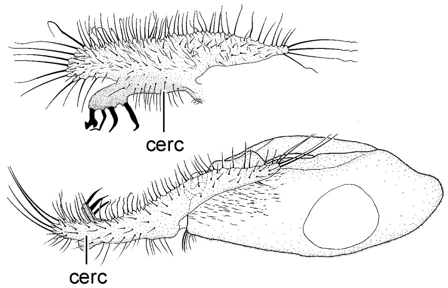
171 *Pseudopelastoneurus* ♂



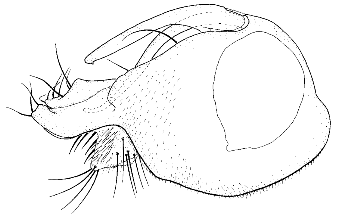
172 *Sybistroma* ♂



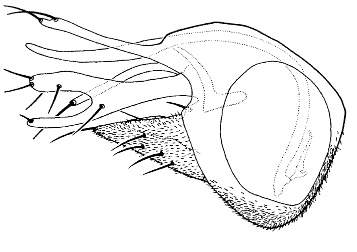
173 *Tachytrechus* ♂



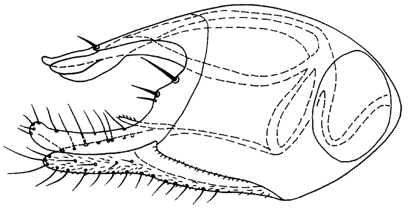
174 *Katangaia* ♂



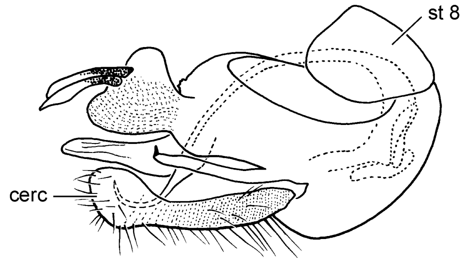
175 *Pseudohercostomus* ♂



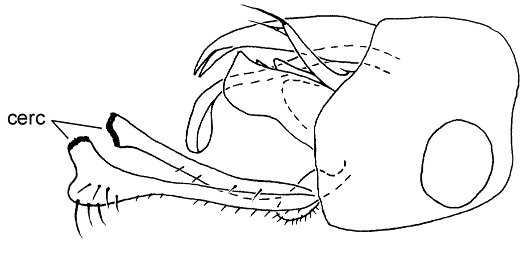
176 *Aphrosylus* ♂



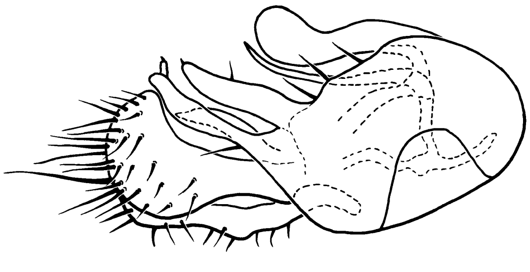
177 *Cemocarus* ♂



178 *Cymatopus* ♂



179 *Epithalassius* ♂



180 *Orthoceratium* ♂

Figs 56.170–180. Male terminalia of Dolichopodidae (Dolichopodinae, Hydrophorinae and *incertae sedis*) (lateral views): (170) *Pseudoparaclius brincki* (Vanschuytbroeck); (171) *Pseudopelastoneurus diversifemur* (Parent); (172) *Sybistroma bogoria* (Grichanov); (173) *Tachytrechus brittoni* Grichanov; (174) *Katangaia longifacies* Parent (including cercus in dorsal view, above); (175) *Pseudohercostomus echinatus* Stackelberg; (176) *Aphrosylus giordanii* Rampini & Munari; (177) *Cemocarus stuckenbergi* Grichanov; (178) *Cymatopus stuckenbergi* Grootaert & Grichanov; (179) *Epithalassius corsicanus* Becker; (180) *Orthoceratium lacustre* (Scopoli). Figs 170, 172 (after Grichanov 2004, figs 55, 40, respectively), Fig. 173 (after Grichanov 1998*d*, fig. 1), Figs 174, 175 (after Brooks 2005, figs 37A, 38A), Fig. 176 (after Rampini & Munari 1987, fig. 2), Fig. 177 (after Grichanov 1997*e*, fig. 8), Fig. 178 (after Grootaert & Grichanov 2008, fig. 8), Fig. 179 (after Grichanov 2008*a*, fig. 13), Fig. 180 (after Negrobov 1978, fig. 1331).

Abbreviations: cerc – cercus; epand – epandrium; epand lb – epandrial lobe; st – sternite; tg – tergite.

venation of females is also often modified (Fig. 96). *Liancalus* typically occur on wet rocks in vertical seepages, or near waterfalls. An identification key to Afrotropical species was provided by Dyte (1967*a*). Negrobov *et al*. (1987) subsequently described an additional species, *L. dytei* Negrobov, Grootaert & Coulibaly, 1987, from Democratic Republic of Congo.

Lichtwardtia **Enderlein** (Dolichopodinae)**.** The continued recognition of the genus *Lichtwardtia* renders the large, widespread genus *Dolichopus* paraphyletic. Brooks (2005) relegated *Lichtwardtia* to a species-group of *Dolichopus* (*i.e.*, the *Dolichopus ziczac*-group); however, this synonymy has not generally been followed by subsequent authors treating Afrotropical and Oriental species of this distinct lineage. Species of this group are easily recognised by the angular, seemingly broken, zigzag-shaped bend in wing vein M_{1+2}, with anteroproximal and posterodistal stump veins (Fig. 82). See Fig. 164 for an example of the male terminalia of this genus and Fig. 237 for a photograph of a living specimen. This group, with 22 included species, is restricted to the Old World tropics and Australia and is most diverse in the Afrotropics with 17 described (Grichanov 1998*k*, 2004: 54) and several undescribed species. An identification key to Afrotropical species was provided by Grichanov (2004: 182).

Machaerium **Haliday** (Hydrophorinae)**.** This genus includes three western Palaearctic species, of which the Mediterranean species *M. thinophilum* (Loew, 1857) also occurs in the Afrotropics (Tanzania) (Grichanov 2011*d*). Adults are medium-sized hydrophorines with the antennal postpedicel bulbous at base and abruptly narrowed distally, with acute apex, bearing an apical arista-like stylus (Fig. 43). See Fig. 97 for an example of the wing of this genus. Maslova & Negrobov (2006) provided a redescription of *M. thinophilum* and an identification key to known species.

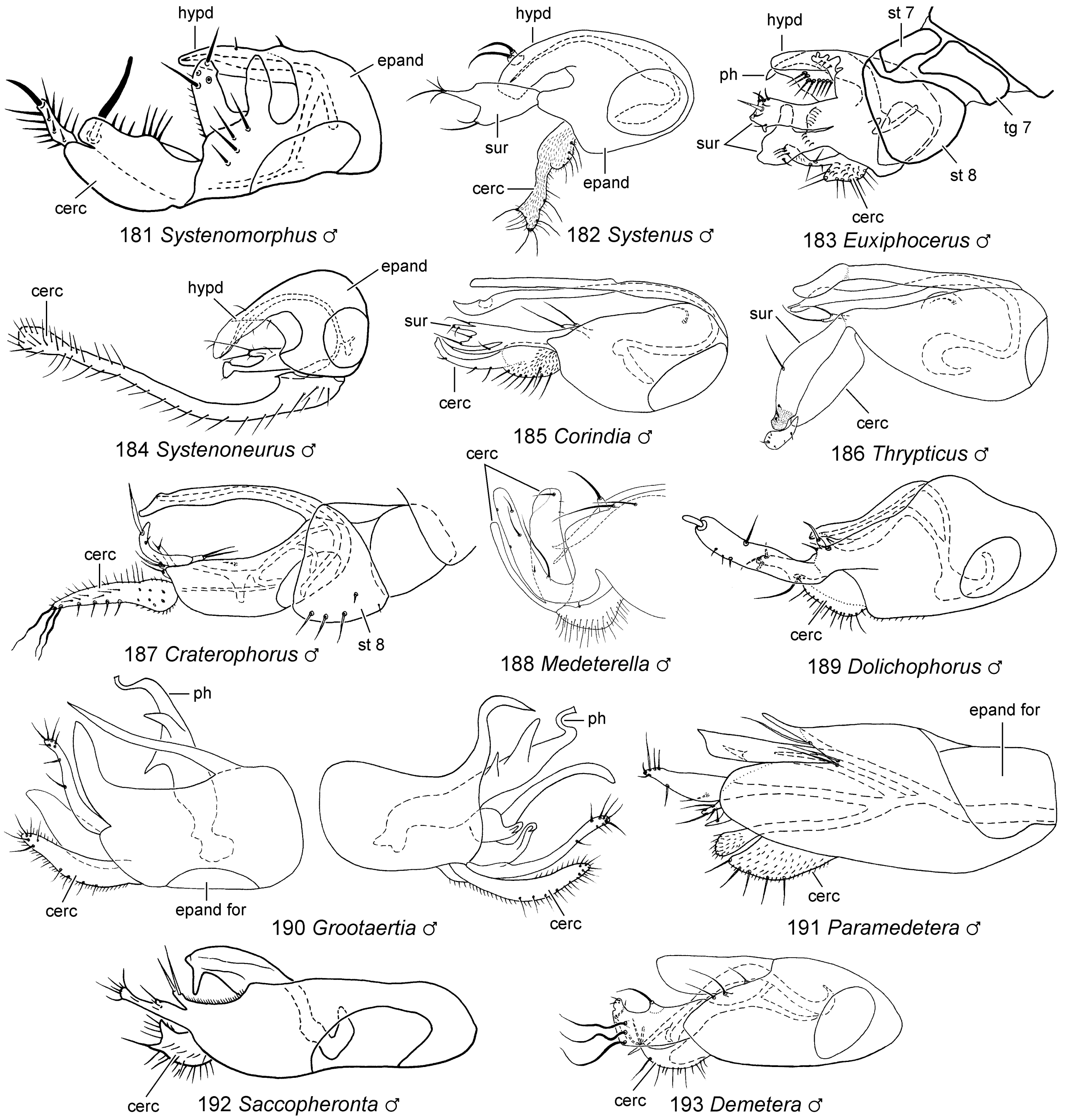
Mascaromyia **Bickel** (Sciapodinae)**.** This poorly defined Afrotropical genus includes 29 described species confined to the western Indian Ocean islands of the Chagos Archipelago, Mauritius (including Rodriguez Is.), Réunion Is. and Seychelles (Grichanov 1996*a*, 2003; Meuffels & Grootaert 2007). Adults are rather small, delicate sciapodines with elongate yellow legs. The genus is very similar to *Sciapus* and can only be confidently separated on the basis of male terminalia (Fig. 210). See Fig. 131 for an example of the wing of this genus. An identification key was provided by Grichanov (2003), but several undescribed species have subsequently been discovered.

Medetera **Fischer von Waldheim (including *Saccopheronta* Becker and *Demetera* Grichanov)** (Medeterinae)**.** The genus *Medetera sensu stricto* includes over 330 described species, of which 34 are known from the Afrotropical Region. Adults are typically found on tree trunks and larvae of many species are predators of scolytid bark beetles. Adults are tiny to medium-sized dolichopodids (1.2–5 mm), distinguished by the following combination of characters: fore coxa with short anteroapical setae not forming spine, or hook; coxae usually dark, or only fore coxa yellow; male anterior tarsus usually simple, rarely with elongate setulae; body rarely shiny; wing veins R_{4+5} and M_1 usually strongly convergent (Fig. 107). See Fig. 228 for an example of the head and thorax of this genus. An identification key to the Afrotropical species of *Medetera* was provided by Grichanov (1999*a*), although several additional species were subsequently described by Grichanov (2000*b*). *Saccopheronta* Becker is a pantropical genus comprised of almost 50 described species, including 14 from the Afrotropical Region (Grichanov 1997*c*, 1999*a*). The genus has been synonymised with *Medetera* and is equivalent to the *Medetera aberrans* Wheeler species-group (Bickel 1985, 1987, 2009: 691); however, this synonymy has not been followed in the Afrotropical dolichopodid literature. *Saccopheronta* is characterised by the following features: head with face and clypeus usually pruinose; thorax with field of setulae across anterior mesonotum; male fore leg with tarsomeres 2 and 3 thickened or flattened; wing (Fig. 109) with crossvein *dm–m* as long, or longer than maximum distance between veins R_{4+5} and M_1 (this feature also occurs in some species of *Medetera*); male terminalia with epandrium cylindrical, elongate, more than 2 × as long as high; epandrial foramen dorsolateral in position (Fig. 192). An identification key to Afrotropical species of *Saccopheronta* was provided by Grichanov (1999*a*). The genus *Demetera* Grichanov comprises eight Old World tropical and Australasian species and is equivalent to the *Medetera melanesiana* Bickel species-group (Bickel 1987; Grichanov 2009*a*, 2011*a*). The Afrotropical fauna includes the single species *D. demeteri* (Grichanov, 1997), from Ethiopia (Grichanov 1997*c*) (Fig. 193). *Demetera* is close to *Saccopheronta*, but is distinguished by the following characters: head with face and clypeus shiny blue-violet, without pruinosity; male fore leg unmodified; male terminalia with epandrium dorsoventrally flattened; epandrial foramen usually basal in position.

Medeterella **Grichanov** (Medeterinae)**.** This genus comprises nine described species, from the Afrotropical, Australasian and Oriental Regions, that were formerly placed in the *Medetera salomonis* Parent species-group (Bickel 1987; Grichanov 1997*f*, 2011*a*). *Medeterella* is similar to *Nikitella*, but is distinguished by the distinctive male terminalia with the cercus with articulated apical lobe (Fig. 188). *Medeterella pospelovi* (Grichanov, 1997) from Ghana is the only known Afrotropical species.

Mesorhaga **Schiner** (Sciapodinae)**.** This distinctive genus includes *ca* 100 described species and is known from all zoogeographical regions, except Antarctica. The Afrotropical fauna includes seven species. *Mesorhaga* are distinguished from other sciapodines primarily by the complete absence of wing vein M_2 (Fig. 132) and the male terminalia with distinctive elongate, cylindrical hypopygium (Fig. 216). See Fig. 30 for an example of the head of this genus. An identification key to Afrotropical species was provided by Grichanov (1998*g*), but two additional species have subsequently been described (Grichanov 1999*b*, 2000*b*).

Meuffelsia **Grichanov** (Peloropeodinae)**.** An endemic genus confined to South Africa with two described species (Grichanov & Mostovski 2008). *Meuffelsia* are small (< 2 mm) nondescript peloropeodines close to *Micromorphus* and *Peloropeodes*, with *dm–m* crossvein in basal third of wing and very short (at least 5 × shorter than apical part of vein M_4) (Fig. 116); thorax with acrostichal setae biserial; legs simple without modified setae, or claws; male terminalia with surstylus asymmetrical, with left dorsal arm shorter, or longer than right one and ventral arms subequal in length and directed ventrad (Fig. 196). The described species occur in mesic riparian habitats (Grichanov & Mostovski 2008).



Figs 56.181–193. Male terminalia of Dolichopodidae (Medeterinae) (lateral views): (181) *Systenomorphus katyushae* Grichanov; (182) *Systenus africanus* Grichanov; (183) *Euxiphocerus wulfi* Parent; (184) *Systenoneurus ovechkinae* Grichanov; (185) *Corindia verschureni* Grichanov; (186) *Thrypticus mironovi* Grichanov; (187) *Craterophorus currani* Grichanov; (188) *Medeterella pospelovi* (Grichanov); (189) *Dolichophorus luteoscutatus* (Parent); (190) *Grootaertia skorpionensis* Grichanov, Kirk-Spriggs & Grootaert (left and right lateral); (191) *Paramedetera sierraleonensis* Grichanov; (192) *Saccopheronta glabra* Negrobov, Vanschuytbroeck & Grichanov; (193) *Demetera demeteri* (Grichanov). Figs 181, 184 (after Grichanov 2010*f*, figs 9, 11), Fig. 182 (after Grichanov & Mostovski 2009*b*, fig. 4), Fig. 183 (after Grichanov 2009*b*, fig. 1), Fig. 185 (after Grichanov 1998*h*, fig. 1), Fig. 186 (after Grichanov 1998*j*, fig. 5), Fig. 187 (after Grichanov 1998*i*, fig. 1), Figs 188, 189 (after Grichanov 1997*f*, figs 8, 9), Fig. 190 (after Grichanov *et al*. 2006, figs 4, 5), Fig. 191 (after Grichanov 1999a, fig. 16); Fig. 192 (after Negrobov *et al*. 1981, fig. 8), Fig. 193 (after Grichanov 1997*c*, fig. 1).

Abbreviations: cerc – cercus; epand – epandrium; epand for – epandrial foramen; hypd – hypandrium; ph – phallus; st – sternite; sur – surstylus; tg – tergite.

Micromorphus **Mik** (Peloropeodinae)**.** A genus of 30 described species occurring in all zoogeographical regions, except the Australasian/Oceanian Regions and Antarctica. The Afrotropical fauna includes five described species (Grichanov 2013*c*; Grichanov & Mostovski 2009*a*), from southern Africa, Ethiopia, Kenya and Uganda. *Micromorphus* are small-sized peloropeodines, with antennal arista-like stylus dorsal (Fig. 49); thorax with acrostichal setae absent; posterior mesonotum flattened; scutellum bearing only 1 pair of setae; hind femur bearing true subapical seta; male hind leg with tarsomere 1 lacking upcurved basal spur; wing crossvein *dm–m* rather short (at least 4 × shorter than apical part of vein M_4) (Fig. 117); and male terminalia with hypopygium sessile (Fig. 198). An identification key to Afrotropical species was provided by Grichanov (2013*c*).

Neohercostomus **Grichanov** (Dolichopodinae)**.** This endemic Afrotropical genus includes 21 species from the continental Afrotropics (Grichanov 2011*b*) and comprises species previously included in Grichanov's (1999*c*, 2004: 24) *Hercostomus* species-group III. The genus is distinguished from *Hercostomus sensu stricto* and *Afrohercostomus*, primarily by the securiform male antennal postpedicel and pubescent basidorsal arista-like stylus (Fig. 9). See Fig. 83 for an example of the wing of this genus and Figs 166–168 for the male terminalia. Grichanov (2011*b*) recognised two subgenera: *Neohercostomus sensu stricto* and *N*. (*Subhercostomus* Grichanov), the latter of which includes three South African species with the wing apex modified. An identification key to species was provided by Grichanov (2011*b*).

Nepalomyia **Hollis** (Peloropeodinae)**.** This predominantly Oriental genus comprises nearly 80 described species, including four from the Nearctic Region and two each from the Palaearctic and Afrotropical Regions (Grichanov 2010*d*; Grootaert 2013). Grichanov (2010*d*) described two species from Réunion Is., and several additional undescribed species are known from Mauritius. The genus has not been recorded from continental Africa. The Afrotropical species of *Nepalomyia* are similar to those of the closely related genus *Peloropeodes*, but can be distinguished by the following characters: antennal arista-like stylus apical (often arising in an apical excavation of the postpedicel), or subapical; male fore tarsus with claws unmodified and symmetrical; male mid coxa lacking apical spine of glued setae. See Fig. 118 for an example of the wing of this genus and Fig. 199 for the male terminalia. There is no suitable identification key available for Afrotropical species.

Neurigona **Rondani** (Neurigoninae)**.** This genus includes over 150 described species with records from all zoogeographical regions, except Antarctica. The records from the Afrotropics (Central Africa and Seychelles), are based on unidentified females (Grichanov 2010*c*). The collection of male specimens is required to confirm the presence of this genus in the Afrotropical Region. See Fig. 112 for an example of the wing of this genus.

Nikitella **Grichanov** (Medeterinae)**.** This monotypic Afrotropical genus was established for *Nikitella vikhrevi* Grichanov, 2011, from Senegal (Grichanov 2011*a*). The genus resembles *Medeterella*, but with segments 7 and 8 of the male terminalia greatly reduced; hypopygium entirely symmetrical with foramen positioned basally; and cercus simple (Figs 21, 22). See Fig. 111 for an example of the wing of this genus.

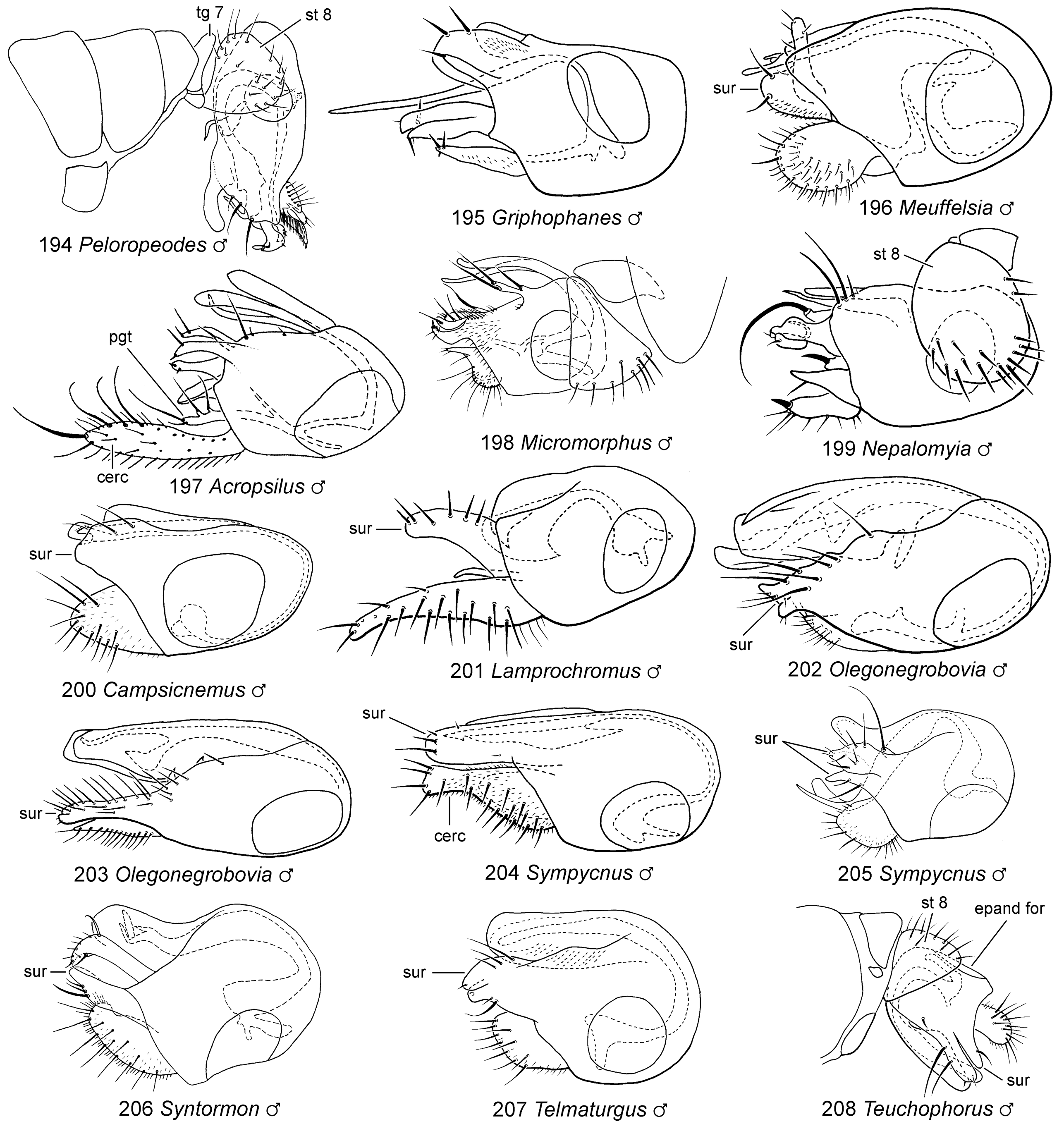
Nurteria **Dyte & Smith** (Sympycninae)**.** This endemic Afrotropical genus, with three included species from South Africa and Democratic Republic of Congo, was originally assigned to the Diaphorinae (Parent 1934), but apparently belongs in the Sympycninae (Capellari & Grichanov 2012; Ulrich 1981). Several undescribed species of the genus from southern Africa await description. Adults are small-sized, dull brownish dolichopodids, the head with frons and face broad in both sexes; mid and hind femora with an anterior preapical seta; thorax with acrostichal setae absent; males sometimes with base of wing vein R_{2+3} swollen (Fig. 138). There is no suitable identification key available for the genus.

Olegonegrobovia **Grichanov** (Sympycninae)**.** This genus is currently known only from the Afrotropical Region and includes six described species (Grichanov 1995*b*, 1996*c*, 2000*c*), as well as several undescribed ones. Some Oriental species currently placed in *Teuchophorus* probably belong in *Olegonegrobovia*. Meuffels & Grootaert (2004) synonymised *Olegonegrobovia* with *Teuchophorus*, but this was not adopted by Grichanov & Mostovski (2008). See Grichanov (2000*c*) for a detailed list of characters separating these two genera. Species of *Olegonegrobovia* are distinguished from other sympycnines by the possession of a comb of long setae on the anal margin of the male wing in almost all species (Fig. 139), and the thorax with a bare proepisternum. The male mid leg is modified in all described species (similar to many species of *Campsicnemus*) (Fig. 54). See Figs 202, 203 for examples of the male terminalia of this genus. There is no suitable identification key available for Afrotropical species.

Orthoceratium **Schrank** (Hydrophorinae)**.** Two species of this genus are known from the western Palaearctic, of which *O. lacustre* (Scopoli, 1763) is also recorded from Tanzania (Grichanov 1997*e*). Adults are large and resemble *Liancalus*, but possess a distinctive sinuous bend in wing vein M_1 (Fig. 98), and the thorax lacks a ventral projection on the proepimeron. See Fig. 44 for an example of the antenna of this genus and Fig. 180 for the male terminalia. Negrobov (1979) provided redescriptions of both species.

Paramedetera **Grootaert & Meuffels** (Medeterinae)**.** This genus of small-sized medeterines includes 15 Oriental species and one Afrotropical species (*P. sierraleonensis* Grichanov, 1999) from Sierra Leone (Grichanov 1999*a*; Grootaert & Meuffels 1997*a*). *Paramedetera* is close to *Grootaertia*, and can be distinguished from other medeterine genera by the following characters: antennal arista-like stylus apicolateral (Fig. 48); thorax with acrostichal setae absent; wing veins R_{4+5} and M_1 parallel and straight in distal section (Fig. 108); male terminalia with abdominal segment 7 forming peduncle; hypopygium symmetrical, foramen basolateral, hypandrial lobes present and phallus without lateral lobes (Fig. 191). Female *Paramedetera* have unmelanised areas on the abdominal terga, which are useful in species recognition (Grootaert & Meuffels 1997*a*).

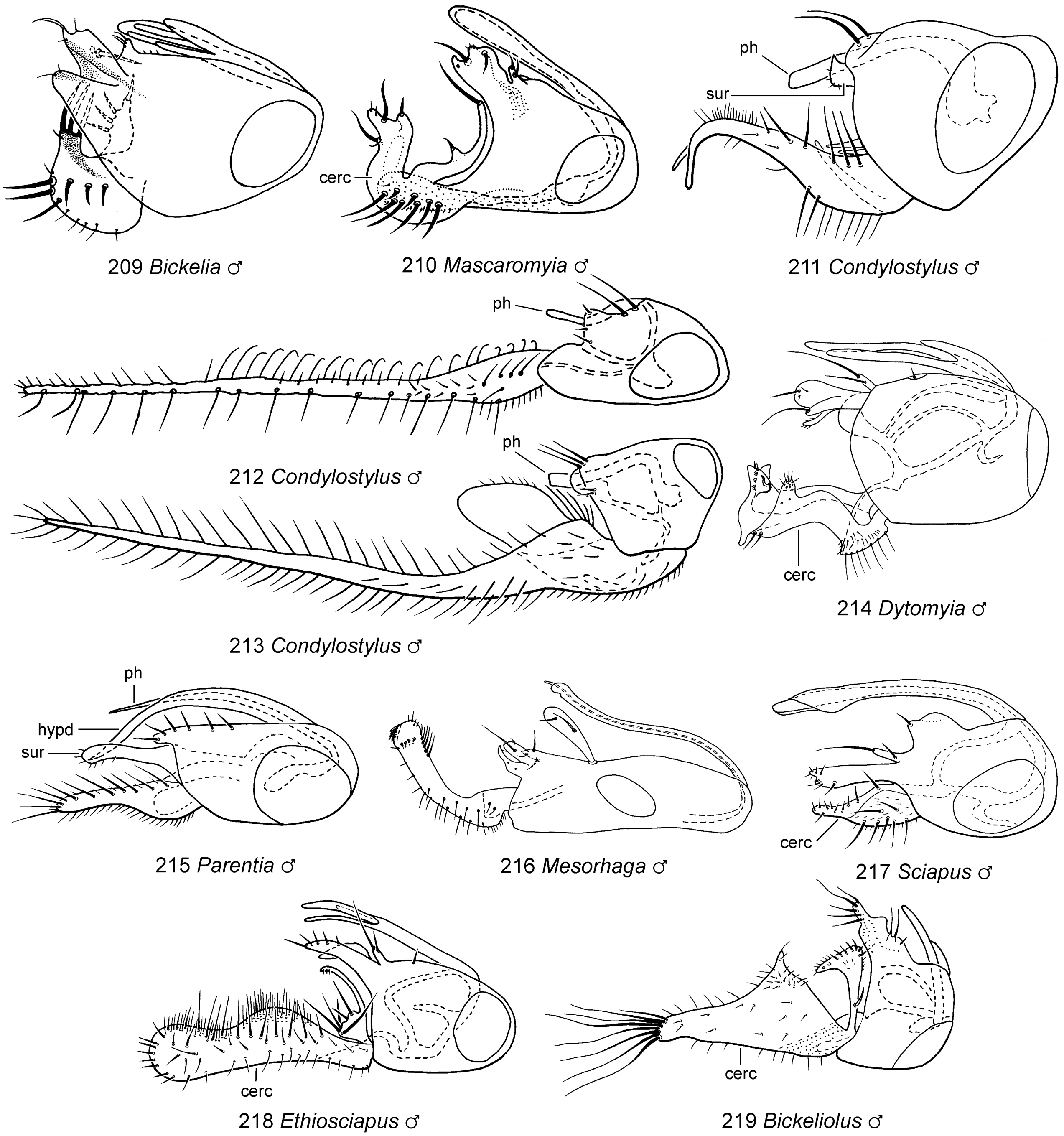
Parentia **Hardy** (Sciapodinae)**.** This primarily Australasian genus of Sciapodinae comprises over 70 species. Five species from southern Africa (Grichanov 1999*b*, 2000*b*) have been placed in *Parentia*; however, further studies are required to ascertain if they are indeed congeneric with the Australasian species. Adults can be identified by the following characters: wing vein R_1 elongate in male, vein M_2 arcuate (Fig. 133); head with



194 *Peloropeodes* ♂; 195 *Griphophanes* ♂; 196 *Meuffelsia* ♂; 197 *Acropsilus* ♂; 198 *Micromorphus* ♂; 199 *Nepalomyia* ♂; 200 *Campsicnemus* ♂; 201 *Lamprochromus* ♂; 202 *Olegonegrobovia* ♂; 203 *Olegonegrobovia* ♂; 204 *Sympycnus* ♂; 205 *Sympycnus* ♂; 206 *Syntormon* ♂; 207 *Telmaturgus* ♂; 208 *Teuchophorus* ♂

Figs 56.194–208. Male terminalia of Dolichopodidae (Peloropeodinae, Sympycninae and *incertae sedis*) (lateral views): (194) *Peloropeodes decembris* Grichanov; (195) *Griphophanes garambaensis* Grichanov; (196) *Meuffelsia erasmusorum* Grichanov; (197) *Acropsilus brevitalus* (Parent); (198) *Micromorphus maraisi* Grichanov; (199) *Nepalomyia kotrbae* Grichanov; (200) *Campsicnemus yangi* Grichanov; (201) *Lamprochromus belousovi* (Grichanov); (202) *Olegonegrobovia couturieri* Grichanov; (203) *O. daugeroni* Grichanov; (204) *Sympycnus ambalamanakana* Grichanov; (205) *S. kakamega* Grichanov; (206) *Syntormon fuscipes* (von Roser); (207) *Telmaturgus mastigomyoformis* (Grichanov); (208) *Teuchophorus caprivi* Grichanov. Figs 194, 198, 202, 203, 208 (after Grichanov 2000*c*, figs 6, 13, 21, 20, 14, respectively), Figs 195, 199 (after Grichanov 2010*d*, figs 14, 22), Fig. 196 (after Grichanov & Mostovski 2008, fig. 5), Fig. 197 (after Grichanov 1998*f*, fig. 2), Fig. 200 (after Grichanov 1998*c*, fig. 8), Figs 201, 204, 205, 207 (after Grichanov 2008*c*, figs 35, 9, 5, 41, respectively), Fig. 206 (after Grichanov 2001, fig. 1).

Abbreviations: cerc – cercus; epand for – epandrial foramen; pgt – postgonite; st – sternite; sur – surstylus; tg – tergite.



209 *Bickelia* ♂

210 *Mascaromyia* ♂

211 *Condylostylus* ♂

212 *Condylostylus* ♂

213 *Condylostylus* ♂

214 *Dytomyia* ♂

215 *Parentia* ♂

216 *Mesorhaga* ♂

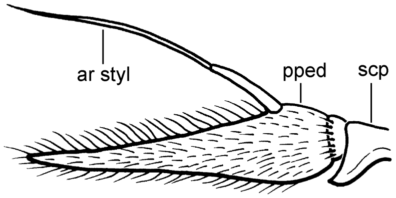
217 *Sciapus* ♂

218 *Ethiosciapus* ♂

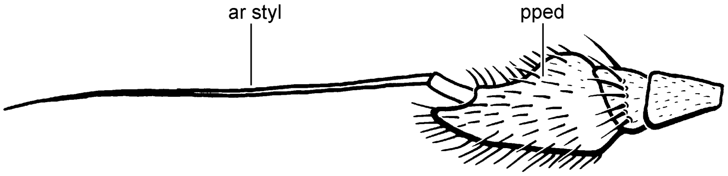
219 *Bickeliolus* ♂

Figs 56.209–219. Male terminalia of Dolichopodidae (Sciapodinae) (lateral views): (209) *Bickelia parallela* (Macquart); (210) *Mascaromyia leptogaster* (Thomson); (211) *Condylostylus pseudoparicoxa* Grichanov; (212) *C. burgeoni* Parent; (213) *C. patereaformis* Becker; (214) *Dytomyia deconickae* Grichanov; (215) *Parentia substenurus* Grichanov; (216) *Mesorhaga demeyeri* Grichanov; (217) *Sciapus endrodyi* Grichanov; (218) *Ethiosciapus finitimus* (Parent); (219) *Bickeliolus maslovae* (Grichanov). Fig. 209 (after Grichanov 1996*b*, fig. 2), Fig. 210 (after Grichanov 1996*a*, fig. 4), Figs 211, 213, 215 (after Grichanov 1999*b*, figs 6, 5, 8, respectively), Figs 212, 214, 216, 218 (after Grichanov 1998*g*, figs 9, 4, 1, 14, respectively), Fig. 217 (after Grichanov 1997*a*, fig. 2), Fig. 219 (after Grichanov 1996*e*, fig. 1).

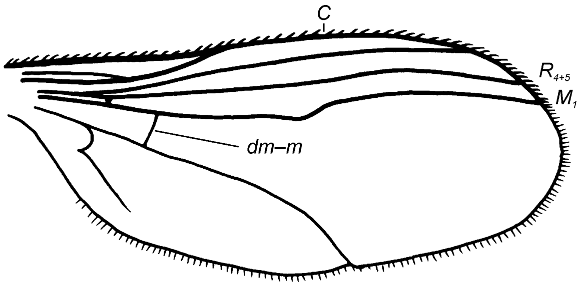
Abbreviations: cerc – cercus; hypd – hypandrium; ph – phallus; sur – surstylus.



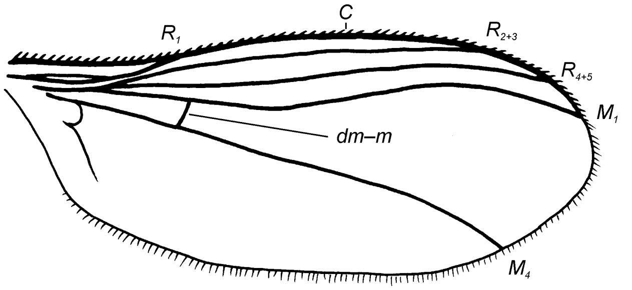
220 *Arabshamshevia* ♂



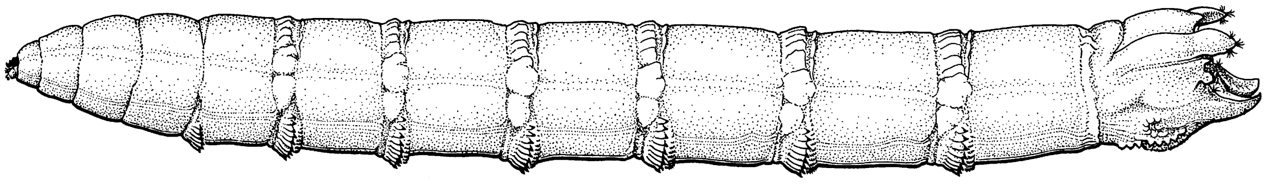
221 *Emiratomyia* ♂



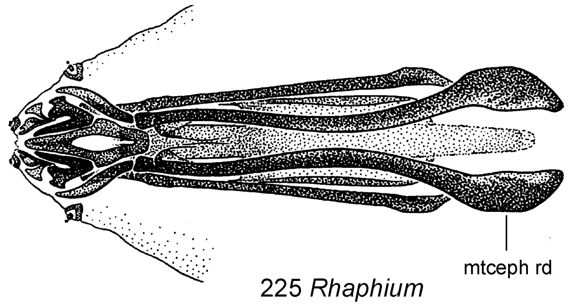
222 *Arabshamshevia* ♂



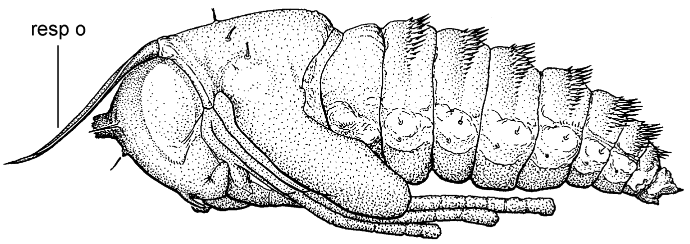
223 *Emiratomyia* ♂



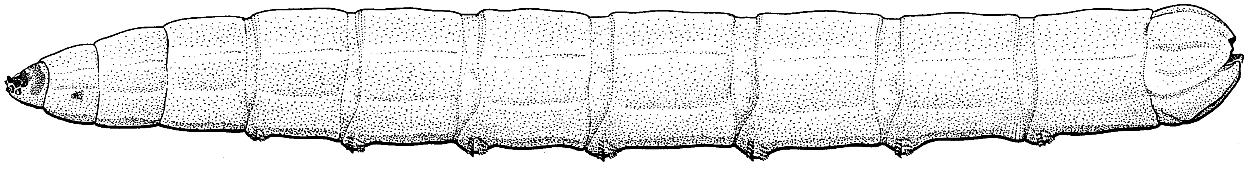
224 *Rhaphium*



225 *Rhaphium*



226 *Rhaphium*



227 *Medetera*

Figs 56.220–227. Antennae, wings and immature stages of Dolichopodidae: (220) antenna of *Arabshamshevia ajbanensis* Naglis, lateral view ♂; (221) same, *Emiratomyia arabica* Naglis; (222) wing of *A. ajbanensis*, dorsal view ♂; (223) same, *E. arabica* Naglis; (224) larval habitus of *Rhaphium campestre* Curran (non-Afrotropical), dorsolateral view; (225) larval cephaloskeleton of *R. slossonae* (Johnson) (non-Afrotropical), dorsal view; (226) pupal habitus of *R. slossonae*, lateral view; (227) larval habitus of *Medetera* sp. (non-Afrotropical), dorsolateral view. Figs 220–223 (after Naglis 2014, figs 8, 1, 9, 3, respectively), Figs 224–227 (Robinson & Vockeroth 1981, figs 40–42, 44, respectively).

Abbreviations: ar styl – arista-like stylus; *C* – costal vein; *dm–m* – discal medial crossvein; M_1 – first branch of media; M_4 – fourth branch of media; mtceph rd – metacephalic rod; pped – postpedicel; R_1 – anterior branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; resp o – respiratory organ; scp – scape.

clypeus semicircular; male hind tarsomeres 3–5 pad-like; male hind tibia with swollen callus; and male terminalia with cercus usually with ventral projection (Bickel 1994). *Parentia* occur along creeks and in wet forests, but also in arid to semi-arid habitats well away from water (Bickel 1994). See Fig. 215 for an example of the male terminalia of one of the Afrotropical species placed in this genus. Currently, there is no suitable identification key to Afrotropical species.

Peloropeodes **Wheeler** (Peloropeodinae)**.** This genus comprises 29 described species from the Afrotropical, Nearctic, Neotropical and Palaearctic Regions. The Afrotropical fauna includes five described species and at least two additional undescribed species from Madagascar and South Africa (Grichanov 2000*c*; Grichanov & Mostovski 2009*a*). The genus is recognised by the antenna with arista-like stylus dorsal (Fig. 50) and by the short blunt male abdomen. Males of the known Afrotropical species also have the fore leg with asymmetrical claws (Fig. 56) and mid leg with coxa bearing an apical spine of glued setae; however, these male secondary sexual characters are known to be absent in some Neotropical *Peloropeodes* (Bickel 2009: 680). See Fig. 119 for an example of the wing of this genus and Fig. 194 for the male terminalia. Currently, there is no suitable identification key to Afrotropical species.

Plagiozopelma **Enderlein** (Sciapodinae)**.** This genus of Sciapodinae comprises over 100 mainly Old World tropical species, including 17 from the Afrotropics. *Plagiozopelma* is close to *Chrysosoma*, but differs in the following characters: head with frons highly polished metallic blue-green; male frons bare, or with 1 weak vertical seta only; male antennal scape often swollen and vase-shaped; fore coxa with either 3–7 strong lateral spine-like setae (stronger in females than males), or 3 strong black distolateral setae. Males of the *P. bequaerti* (Curran) species-group are distinguished by the thickened and ornamented antennal arista-like stylus of males (Bickel 1994) (Fig. 18). See Fig. 134 for an example of the wing of this genus. An identification key to Afrotropical species was provided by Grichanov (1998*g*).

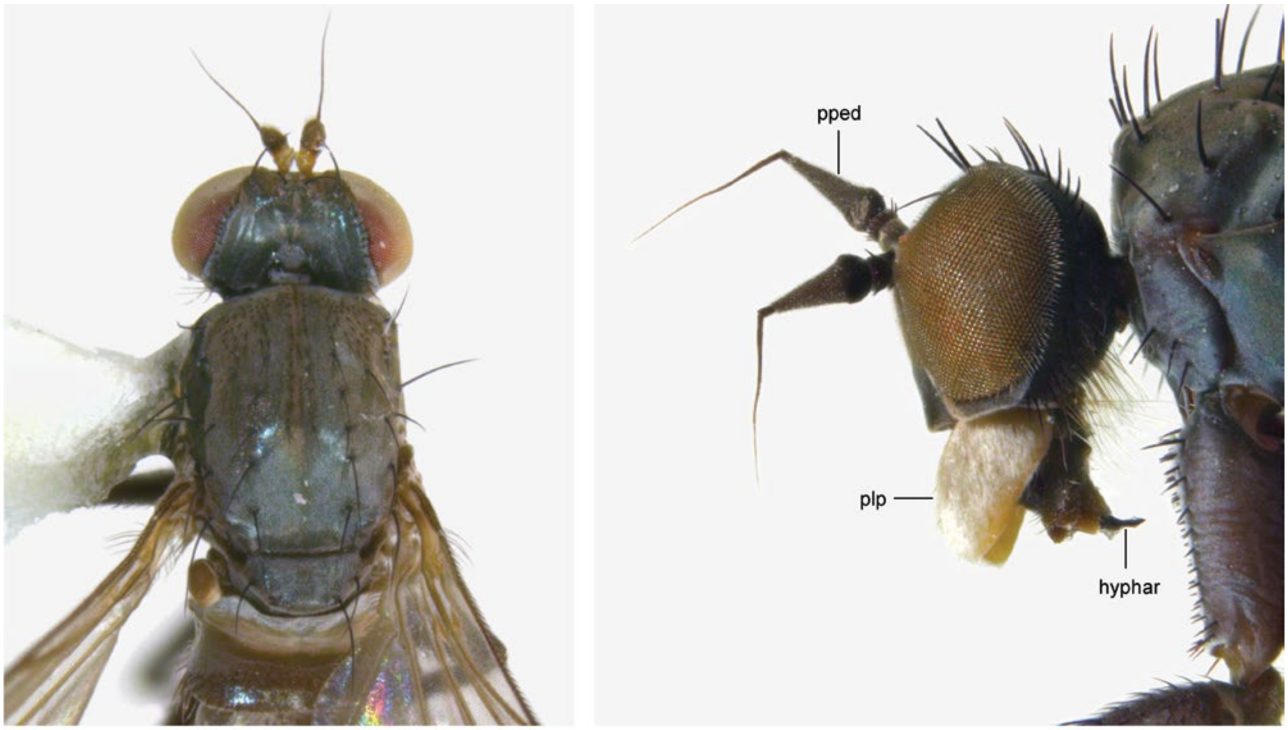
Plesiothalassius **Ulrich** (Parathalassiinae)**.** This endemic genus is known only from sandy sea coasts of South Africa and includes three described species (see Ulrich 1991 for identification key). Adults are small greyish white pruinose flies, with antennal postpedicel globular, or oval and broadly rounded at apex, and arista-like stylus 1-articled (Fig. 32); head with face moderately wide in both sexes (Fig. 23), more or less narrowing at middle; thorax with prothoracic precoxal bridge entirely lacking; acrostichal setae paired and flanked by accessory setae; scutellum with 1 pair of setae; wing with *bm–m* crossvein present, cell *dm* emitting three branches (Fig. 64); male terminalia with hypopygium compact; and female terminalia with acanthophorite setae, tergite 8 deeply cleft. Adults of *Plesiothalassius* occur along sea coasts on dry sand, mostly dunes with sparse vegetation.

Pseudargyrochlamys **Grichanov** (Dolichopodinae)**.** This endemic Afrotropical genus was established by Grichanov (2006*a*) for four South African species that were previously placed in *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 71; International Commission on Zoological Nomenclature 2004). The species are included in the identification key to *Paracleius* provided by Grichanov (2004: 184). Two of the species are associated with coastal dunes, whereas the other two were collected in forest and open woodland habitats surrounding the Kosi Bay estuary. The genus closely resembles the Old World genus *Argyrochlamys* and the Oriental genus *Phoomyia*, but has the head with face very narrow (slightly wider in females) and frons about as wide as high and subequal to face height. See Fig. 84 for an example of the wing of this genus and Fig. 169 for the male terminalia.

Pseudohercostomus **Stackelberg** (*Incertae sedis*)**.** Stackelberg (1931) erected this genus for the enigmatic Oriental species *P. echinatus* Stackelberg. Negrobov (1988) described a second species from Chile; however, the type is apparently lost and the description is inadequate to determine if the species is indeed correctly assigned to *Pseudohercostomus*. Yang & Grootaert (1999) subsequently added a third species from Oriental China. Possible undescribed species of *Pseudohercostomus* have been recorded from the Australasian Region (Brooks 2005) and from the Afrotropics (Madagascar and Malawi) (Dyte & Smith 1980: 453). Grichanov (2004: 102) recorded *P. echinatus* from Democratic Republic of Congo (as *Paracleius echinatus*) and indicated that the records from Madagascar and Malawi may refer to that species. The genus is recognised by its bulky habitus, thorax with wide metepimeron, wing veins R_{4+5} and M_1 slightly divergent (Fig. 85); hind coxa with extreme apical position of the lateral seta; male terminalia with segment 7 reduced and hypopygium (Fig. 175) encapsulated; and the distinctive female terminalia, with tergite 10 densely clothed in spines (Fig. 148). Stackelberg (1931) placed *Pseudohercostomus* in the Dolichopodinae; however, Brooks (2005) considered the genus *incertae sedis* within the Dolichopodidae *sensu stricto*.

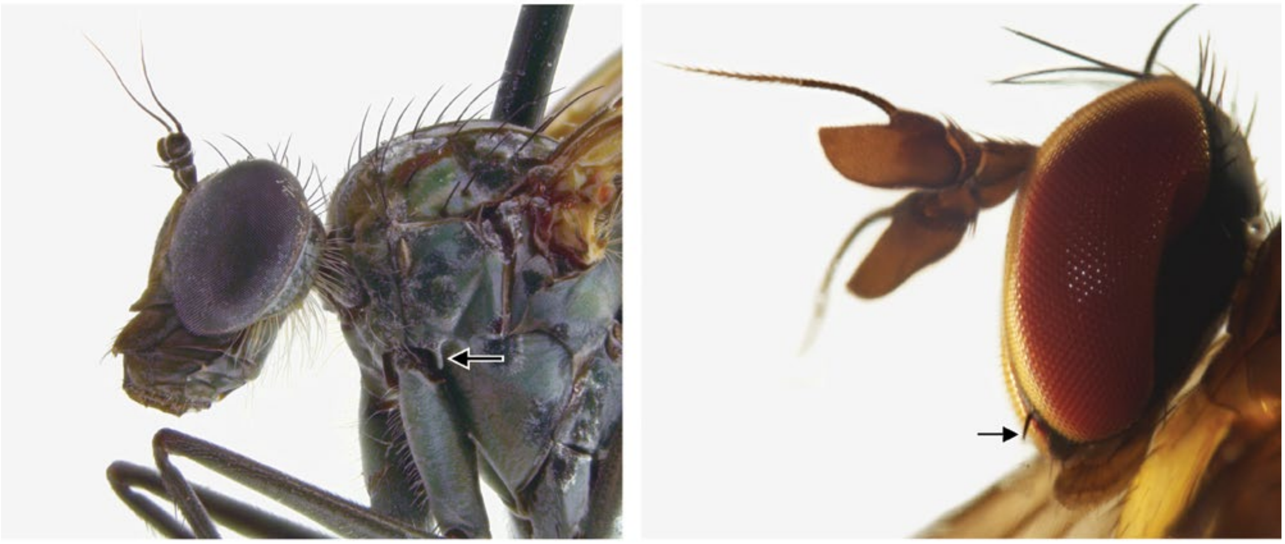
Pseudoparaclius **Grichanov** (Dolichopodinae)**.** This genus was established by Grichanov (2006*a*), for a group of Afrotropical species that were previously placed in *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 71; International Commission on Zoological Nomenclature 2004). The genus is widely distributed within the continental Afrotropics and includes 15 described species and at least two additional undescribed species. Kaae *et al*. (2015) provided a key to the known Afrotropical species. The writers have also examined species from the Palaearctic, Oriental and Australasian Regions which are referable to *Pseudoparaclius*, but are either undescribed or currently assigned to *Paraclius*. Adults are distinguished by the dorsally positioned antennal arista-like stylus with short pubescence; wing vein M_1 convex posteriad, with gentle curvation towards vein R_{4+5} at middle of distal part and joining costal vein (*C*) well before wing apex (Fig. 86); thorax usually with fine setulae on the metepimeron; and several characters of the male terminalia (Fig. 170).

Pseudopelastoneurus **Grichanov** (Dolichopodinae)**.** This endemic Afrotropical genus was established by Grichanov (2006*a*) for two species that were previously placed in *Paracleius* Bigot (now a suppressed senior synonym of *Pelastoneurus* Loew) (Brooks *et al*. 2002; Grichanov 2004: 17; International Commission on Zoological Nomenclature 2004). The genus is distributed from Sierra Leone in the west to Kenya in the east and Angola in the south. Adults are distinguished by the antennal arista-like stylus with long setulae (Fig. 15); wing vein



228 *Medetera* ♂

229 *Aphrosylus* ♂



230 *Liancalus* ♂

231 *Setihercostomus* ♂

Figs 56.228–231. Heads and thoraces of Dolichopodidae: (228) head and thorax of *Medetera signaticornis* Loew (non-Afrotropical), dorsal view ♂; (229) head of *Aphrosylus celtiber* Haliday (non-Afrotropical), lateral view ♂; (230) head and thorax of *Liancalus peringueyi* Curran, lateral view ♂ (arrow indicates projection of proepimeron); (231) head of *Setihercostomus scharffi* (Grichanov), lateral view ♂ (arrow indicates clypeal seta).

Abbreviations: hyphar – hypopharynx; plp – palpus; pped – postpedicel.

M_1 with strong anterior bend towards vein R_{4+5}, forming gentle arc and becoming subparallel to vein R_{4+5} apically (Fig. 87); male abdominal segments 6 and 7 reduced and male terminalia (Fig. 171) with hypopygium small, rounded and encapsulated. Both included species, *P. diversipes* (Parent, 1934) and *P. diversifemur* (Parent, 1935), were originally described in *Pelastoneurus* and are included in Grichanov's (2004: 184) identification key to *Paracleius*.

***Rhaphium* Meigen** (Rhaphiinae)**.** This genus includes *ca* 200 species, most of which occur in the Holarctic Realm. The Afrotropical fauna includes 15 species. Adults range in body size (1.5–5.7 mm), but most Afrotropical species are small (Fig. 234). The genus is easily recognised in the Afrotropical Region by the possession of a triangular and usually elongate antennal postpedicel, with apical arista-like stylus (Fig. 14). See Fig. 120 for an example of the wing of this genus and Fig. 156 for the male terminalia. An identification key to Afrotropical species was provided by Grichanov (1995*a*), although some synonyms were later established (Grichanov 2001).

***Schistostoma* Becker** (Microphorinae)**.** This genus includes 15 species from the Palaearctic Region, at least nine from the Nearctic Region (most of which require transfer from *Microphor*) and four described species from the Afrotropical Region, including one species from United Arab Emirates (Gatt 2014) and three species from the southern Afrotropical Region (Shamshev & Sinclair 2006). One additional undescribed Afrotropical species is known from KwaZulu-Natal Province, South Africa. Species of this genus are quite small, greyish flies inhabiting sandy biotopes, or stream margins and are characterised by the following features: antenna with arista-like stylus 2-articled (Fig. 24); wing with *bm–m* crossvein present, cell *dm* emitting three branches (Fig. 63); scutellum with 1–2 pairs of setae; male terminalia with hypandrial prolongation; and female terminalia with tergite 10 divided and bearing acanthophorite spines (Shamshev & Sinclair 2006). All known Afrotropical species are part of the *S. albopiliosum* (Becker) species-group, which is characterised by pubescent eyes; a modified male mid leg; and male terminalia with a shortened hypandrial lobe fused to the epandrium basally (Shamshev & Sinclair 2006). An identification key to the *S. albopiliosum* (Becker) species-group was provided by Shamshev & Sinclair (2006).

***Sciapus* Zeller** (Sciapodinae)**.** This genus has been recorded from all zoogeographical regions, except Antarctica and contains *ca* 75 species, over 65 of which occur in the Palaearctic Region. The Afrotropical fauna includes two species, *S. endrodyi* Grichanov, 1997 (Figs 135, 217), from Ghana, Gabon and Sierra Leone (Grichanov 1997*a*, 2011*d*, *e*, 2012*f*), and *S. adumbratus* Becker, 1902 from Oman, the United Arab Emirates and the southern Palaearctic Region (Grichanov & Negrobov 2014). Species of *Sciapus* are distinguished by the distinctive anterior preapical seta on hind femur in both sexes, and the group of 3–6 strong ventral setae on female fore femur (Bickel 1994).

***Setihercostomus* Zhang & Yang** (Dolichopodinae)**.** A genus of five described species occurring in the Afrotropical, Oriental and Palaearctic Regions (Pollet 2009; Yang *et al*. 2011; Zhang & Yang 2005). The Afrotropical fauna includes a single described species, *Setihercostomus scharffi* (Grichanov, 1999), from Tanzania (Grichanov *et al*. 2014), which was included in Grichanov's (2004: 182) key to *Hercostomus*. The genus is distinguished from other dolichopodines by the following characters: head with clypeus bearing 1 pair of strong setae in both sexes (Fig. 231, indicated with arrow); thoracic pleura with cluster of fine setulae anterior to posterior spiracle; wing with veins M_1 and R_{4+5} subparallel; male terminalia with cercus large and thick, virtually as long as epandrium. *Setihercostomus* is closely related to *Gymnopternus*.

***Shamshevia* Grichanov** (Diaphorinae)**.** This unusual genus of small-sized diaphorines includes the Afrotropical species *S. hoanibensis* Grichanov, 2012, from Namibia and the Oriental species *S. reshchikovi* Grichanov, 2012, from India (Grichanov 2012*a*, *b*, *d*). The genus is distinguished by the following characters: antennal pedicel with long apical condyle projecting into postpedicel; male antenna (Fig. 33) with postpedicel enlarged, arista-like stylus basidorsal, with basal article longer than apical article; wing (Fig. 72) with crossvein *dm–m* located near wing base; and posterior portion of mesonotum flattened. See Fig. 155 for an example of the male terminalia of this genus. An identification key to the two known species was provided by Grichanov (2012*d*). A third, undescribed species is known from Madagascar.

***Sybistroma* Meigen** (Dolichopodinae)**.** This genus contains *ca* 55 described species mainly from the Oriental and Palaearctic Regions. Most males of *Sybistroma* can be distinguished by their modified antenna (reduced pedicel, postpedicel sometimes enlarged, arista-like stylus often with 1, or more lamellae) and male terminalia (tripartite arrangement of basiventral lobes and hypandrium in ventral view). Males lacking modified antennae are distinguished by the possession of elongate setulose apicoventral epandrial lobes (Brooks 2005, figs 30A, 31A). Females of *Sybistroma* cannot readily be distinguished from those of *Hercostomus*. A single Afrotropical species, *S. bogoria* (Grichanov, 2004) (Figs 88, 172), has been described from Kenya (Grichanov 2004: 69, as *Ludovicius*). A second, undescribed species is known from Uganda.

***Sympycnus* Loew** (Sympycninae)**.** This poorly defined, virtually cosmopolitan genus comprises *ca* 270 described species and occurs in all zoogeographical regions, except Antarctica. There are no known synapomorphies characterising *Sympycnus*. As such, the genus is recognised by the absence of characters which define the other sympycnine genera. In his review of the Afrotropical *Sympycnus*, Grichanov (2008*c*) recognised three species-groups, of which the species in Group III were subsequently transferred to *Telmaturgus* (Grichanov 2011*c*). The Afrotropical fauna currently includes 28 described species, which can be identified using the identification key provided by Grichanov (2008*c*). See Fig. 140 for an example of the wing of this genus, Figs 204, 205 for the male terminalia and Fig. 62 for the hind tarsus of species Group II *sensu* Grichanov (2008*c*).

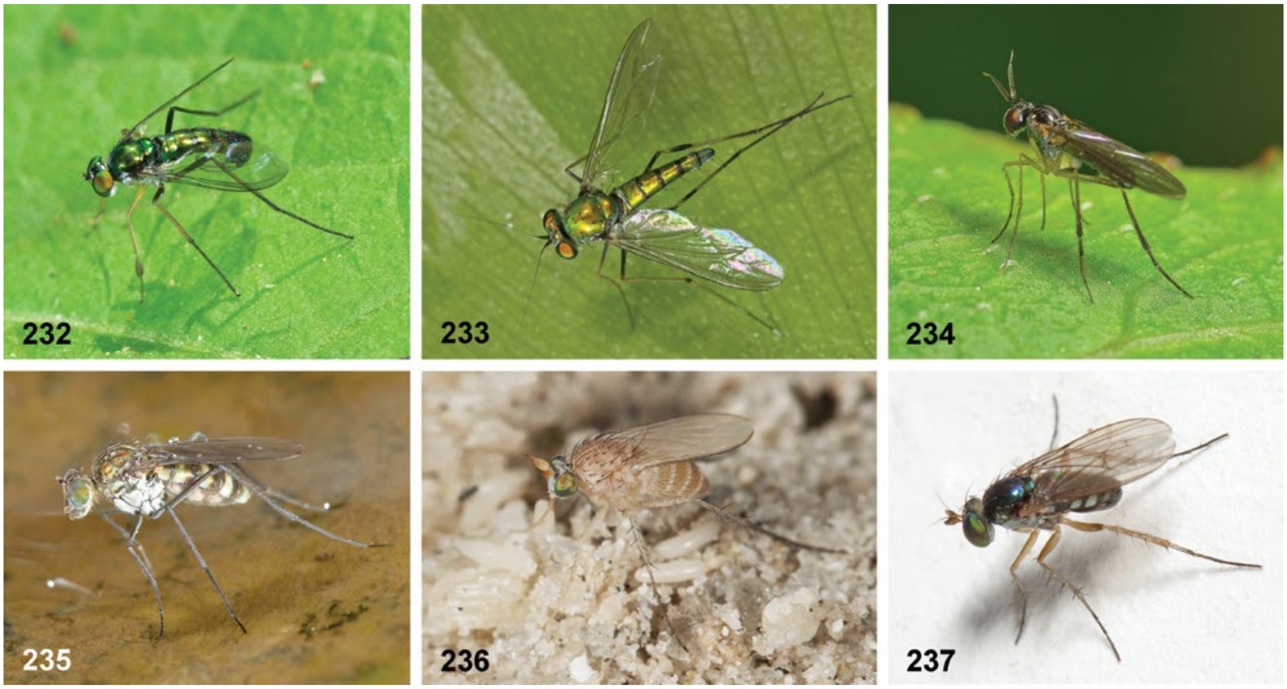
***Syntormon* Loew** (Sympycninae)**.** This virtually cosmopolitan genus occurs in all zoogeographical regions, except Antarctica, with *ca* 110 described species, 14 of which occur in the Afrotropical Region. Species of *Syntormon* are distinguished by their distinctive antennae, with the pedicel bearing a medial thumb-like process or conus, which projects onto the mediobasal surface of the postpedicel (Fig. 51). See Fig. 141 for an example of the wing of this genus and Fig. 206 for the male terminalia. An identification key to Afrotropical species was provided by Grichanov (2001).

***Systenomorphus* Grichanov** (Medeterinae)**.** This monotypic Afrotropical genus was established by Grichanov (2010*f*) for *S. katyushae* Grichanov (Figs 102, 181) from South Africa. *Systenomorphus* is closely related to *Euxiphocerus*, *Systenoneurus* and *Systenus*, but can be differentiated from these genera by the ovoid antennal postpedicel, with rounded apex (at most 2 × as long as basal height), short subapical-dorsolateral arista-like stylus, head with flattened postocular setae, blackish body, and characters of the male terminalia.

***Systenoneurus* Grichanov** (Medeterinae)**.** This monotypic Afrotropical genus was established by Grichanov (2010*f*) for *S. ovechkinae* Grichanov (Figs 103, 184) from Madagascar. *Systenoneurus* is closely related to *Euxiphocerus*, *Systenomorphus* and *Systenus*, but can be differentiated from these genera by the reduced antennal pedicel with 2 long apicodorsal setae; triangular male postpedicel (2 × as long as basal height); subapical-dorsolateral arista-like stylus (longer than postpedicel); head with simple postocular setae; male fore leg with modified apical tarsomere and claws; brownish black body; and characters of the male terminalia.

***Systenus* Loew** (Medeterinae)**.** This genus includes more than 30 described species and is known from all zoogeographical regions, except Antarctica. Larvae of *Systenus* are found in moist tree holes, decaying wood and sap runs. Adults range from 2–3 mm and are distinguished by the following characters: male antenna (Fig. 47) with pedicel not reduced, postpedicel elongate, swollen basally and tapering apically, arista-like stylus apical, or dorsoapical; head with postocular setae simple; distal sectors of veins R_{4+5} and M_1 with flexion (Fig. 100); thorax with posterior pair of acrostichal setae distinctly larger than preceding pair and off-set laterally; 6 strong dorsocentral setae present; male abdominal segment 7 forming elongate peduncle. See Fig. 182 for an example of the male terminalia of this genus. The Afrotropical fauna includes one described species, *S. africanus* Grichanov, 2009 (Grichanov & Mostovski 2009*b*) and at least one additional undescribed species. An identification key to the world species and species-groups was compiled by Grichanov & Mostovski (2009*b*).

***Tachytrechus* Haliday** (Dolichopodinae)**.** This virtually cosmopolitan genus occurs in all zoogeographical regions, except Antarctica, with over 150 described species, the majority of which occur in the New World, especially the Neotropics. The Afrotropical fauna includes 15 species (Grichanov 1998*d*, 2004: 170), found across the continent in riparian habitats and marshes, as well as beaches and coastal dunes. Species of *Tachytrechus* are distinguished by the following characters: head with face (Fig. 27) narrowed beneath antennae and widened towards clypeus; clypeus extending to, or beyond, lower eye margin; hind femur with several strong anterodorsal setae in apical ½ in addition to true anterior preapical seta; antennal postpedicel usually short and suboval and arista-like stylus short and bare (Fig. 8); wing vein M_1 usually with gentle curvation before middle of distal part, then running towards vein R_{4+5}, reaching costal vein (C) well before apex of wing (Fig. 89). See Fig. 173 for an example of the male terminalia of this genus. An identification key to Afrotropical species was provided by Grichanov (2004: 190).



Figs 56.232–237. Photographs of living Afrotropical Dolichopodidae: (232) *Condylostylus imitans* Curran (South Africa); (233) *Chrysosoma* sp. (Tanzania); (234) *Rhaphium currani* (Parent) (South Africa); (235) *Liancalus peringueyi* Curran (South Africa); (236) *Argyrochlamys marshalli* Grichanov (Tanzania); (237) *Lichtwardtia* (= *Dolichopus ziczac*-group) sp. (Tanzania). Photographs © S.A. Marshall.

Telmaturgus **Mik** (Sympycninae)**.** This genus of Sympycninae comprises 20 species with representatives in all zoogeographical regions, except Antarctica and Australasia (Grichanov 2011*c*; Runyon 2012). The Afrotropical fauna includes 11 species, most of which were previously placed in *Sympycnus* (Grichanov 2008*c*, Group III). The genus is fairly widely distributed across the continental Afrotropics and also occurs on Madagascar and Mauritius. Adults are small (*ca* 2 mm) and can be distinguished from other sympycnine genera, by the following combination of characters: thorax with 3 or 4 pairs of strong dorsocentral setae; male fore tarsomeres usually modified (Figs 57, 58); hind tarsomeres 2–4 regularly decreasing in length (Fig. 61); female head with clypeus strongly bulging. See Fig. 52 for an example of the antenna of this genus, Fig. 142 for the wing and Fig. 207 for the male terminalia. An identification key to Afrotropical species was provided by Grichanov (2011*c*).

Tenuopus **Curran** (*Incertae sedis*)**.** This genus is endemic to the continental Afrotropical Region, with 13 described species. Adults are distinguished by the head with the strongly excavated vertex on either side of the ocellar tubercle (similar to Sciapodinae); vertical setae absent; antennal pedicel forming short thumb-like projection or conus on inner side of postpedicel (Fig. 10); and wing with vein M_2 present only as a fold in membrane (Fig. 113). The general habitus and male terminalia of *Tenuopus* suggest placement in the Neurigoninae, but unlike neurigonines, species of *Tenuopus* have the thorax with the posterior mesonotum convex and the mid and hind femora usually each with anterior preapical seta. Grichanov (2000*a*) provided an identification key to species.

Teuchophorus **Loew** (Sympycninae)**.** This genus comprises *ca* 120 described species and is known from all zoogeographical regions, except Antarctica and the Neotropics. Most of the species occur in the Oriental and Australasian Regions and one species, *T. caprivi* Grichanov, 2000 (Figs 143, 208), is known from the Afrotropical Region (Namibia) (Grichanov 2000*c*). Meuffels & Grootaert (2004) synonymised the Afrotropical genus *Olegonegrobovia* with *Teuchophorus*, but the former is recognised as a valid genus here (see generic heading *Olegonegrobovia* above). Adults are small sympycnines with wing veins R_{4+5} and M_1 slightly diverging (rather than parallel), with crossvein *dm–m* perpendicular to long axis of the wing, forming an acute angle with vein M_4 and male wing often with costal vein (C) thickened to vein R_1. *Teuchophorus* adults are typically found on muddy and sandy patches along small forest streams and also in mangrove habitats (Grootaert 2006).

Thinophilus **Wahlberg** (Hydrophorinae)**.** This virtually cosmopolitan genus occurs in all zoogeographical regions, except Antarctica and includes over 120 described species, of which 22 occur in the Afrotropical Region, mostly in coastal habitats. Adults of *Thinophilus* are small to large flies with short rounded antennal pedicel, bearing a usually dorsal arista-like stylus; thorax with acrostichal setae absent; 4–6 dorsocentral setae present; scutellum with 2 or 4 strong setae; and tibia usually with strong setae. See Fig. 99 for an example of the wing of this genus. Grichanov (1997*d*) provided an identification key to *Thinophilus*, including Afrotropical and Palaearctic species.

Thrypticus **Gerstaecker** (Medeterinae)**.** This distinctive and virtually cosmopolitan genus occurs in all zoogeographical regions, except Antarctica and comprises *ca* 90 described species, including seven from the Afrotropical Region. Adults are small and usually bright metallic green, with the female terminalia with ovipositor sclerotised and blade-like for oviposition into plant tissues (Fig. 147), and male terminalia with surstylus strongly deflexed dorsally, usually lying with similarly deflexed, oblong-shaped cercus (Fig. 186). See Fig. 104 for an example of the wing of this genus. *Thrypticus* larvae are phytophagous stem-miners of aquatic and semi-aquatic monocotyledonous plants. Grichanov (1998*j*, 1999*a*) provided an identification key to Afrotropical species and one additional species was subsequently described by Grichanov (2000*b*).

Trigonocera **Becker** (Diaphorinae)**.** This genus comprises nine Old World species, including four from the Afrotropical Region (Grichanov 2013*b*). *Trigonocera rivosa* Becker, 1902, has been recorded from Botswana, Cabo Verde, Namibia, Senegal and Zambia in the Afrotropical Region; Egypt and Israel in the Palaearctic Region; and Thailand and Taiwan in the Oriental Region. Adults are small- to medium-sized diaphorines, with the head with frons and face wide; face almost parallel-sided; male antennal postpedicel with abruptly drawn-out apex; arista-like stylus apical, or slightly subapical (Fig. 13); male sternite 8 with strong projecting setae. They occur on vegetation around pools, in marshy meadows at riversides within savanna and forest ecoregions. See Fig. 73 for an example of the wing of this genus and Fig. 157 for the male terminalia. An identification key to world species was compiled by Grichanov (2013*b*).

Urodolichus **Lamb** (*Incertae sedis*)**.** This genus includes five Afrotropical species (Seychelles and Madagascar), one Oriental species (Sri Lanka) and one Australasian species (Papua New Guinea). Adults are medium-sized dolichopodids with the following combination of characters: antenna short, positioned at upper ¼ of head, arista-like stylus dorsal; thorax with mesonotum with biseriate acrostichal setae, lacking flattened posterior area; hind femur lacking true anterior preapical seta; hind coxa with exterior seta at basal ¼, hind tarsomere 1 much shorter than tarsomere 2; wing vein M_1 beyond crossvein *dm–m*, usually with distinct sinuation near basal ⅓ (Fig. 74); and male segment 7 rather long (Fig. 150). An identification key to Afrotropical species was provided by Grichanov (1998*a*).

Xanthochlorus **Loew** (Xanthochlorinae)**.** This enigmatic genus includes 15 described species from the Palaearctic Region, one from the Nearctic Region and one (*X. kustovi* Grichanov, 2010) (Figs 19, 144) from the Afrotropical Region (Madagascar) (Grichanov 2010*i*). The genus can be distinguished by the following combination of characters: thorax and abdomen yellow, or brownish; thorax with prescutellar depression present; wing veins R_{2+3} and M_1 virtually straight and parallel beyond crossvein *dm–m*; mid and hind femora lacking anterior preapical seta; male abdominal tergum 6 setulose; female abdominal segments 6 and 7 exposed (not retractable), setulose; and female terminalia lacking acanthophorite spines.

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TAXONOMIC INDEX TO VOLUME 2

Ashley H. Kirk-Spriggs

This index is restricted to the taxonomic names associated with Diptera that appear in Volume 2 of this *Manual*. Similar names of plants and animals other than Diptera are excluded. Bibliographical references are not indexed. Non-Afrotropical taxon names are also listed.

Taxonomic names are provided for all taxonomic ranks below order level (*i.e.*, series, subfamilies, superfamilies, tribes, genera, subgenera, species and subspecies). Other major divisions, such as lower Brachycera and orthorrhaphous Brachycera, are also indexed. Family name citations are only indexed for the first page of each family chapter (underlined), but all references to family names in other chapters are indexed separately. In the case of "Undescribed genera", as cited in the text, these are listed followed by the respective family name in parenthesis.

Taxonomic names of ranks above genus level are provided in upper case *regular* font and genus, species and subspecies names in *italic* font (including synonyms). If a text citation, illustration and/or family key citation appear on the same page, the page number is repeated in the order in which they appear. Authors' names are provided for genus, species and subspecies names and in such cases these names are followed by the names of the genera to which they are assigned. Subgeneric names are indexed in the same way as generic names and subspecific names in the same way as specific names. *Boldface* page numbers indicate where genus names appear in the identification keys; *underlined* page numbers indicate where a genus name appears in the "Synopsis of the fauna" section of each family chapter; *italicised* numbers indicate the location of illustrations of these taxa.

A complete index of taxonomic names of Diptera is included in Volume 4.

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True flies, or **Diptera**, constitute one of the largest orders of insects in the biosphere, with over 160,000 described species worldwide, more than 20,000 of which occur in the Afrotropical Region. They are as diverse morphologically and biologically as they are numerous and many groups have evolved spectacular structural adaptations that are commensurate with their environment and biology. During their long evolutionary history, virtually every terrestrial niche has been occupied by the Diptera, making them one of the most successful groups of organisms on Earth. Many have co-evolved in association with other organisms and become highly specialised parasites or parasitoids of a range of disparate groups of plants and animals. Whether focusing on their systematics, biology, biogeography, conservation, or the more applied aspects, the Diptera remain a fascinating and intriguing group. This four volume book, a collaboration of **over 90 international experts** on Diptera, is the first-ever synopsis of the **108 families** of flies known from the Afrotropical Region and includes discussions on biology and immature stages, economic importance, classification, identification to the genus level, as well as a synopsis of each genus. This work provides the basics for understanding the diversity of a major order of insects in a large tropical and sub-tropical region and is the first such synopsis of its kind for any major insect order occurring in the Afrotropics.

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