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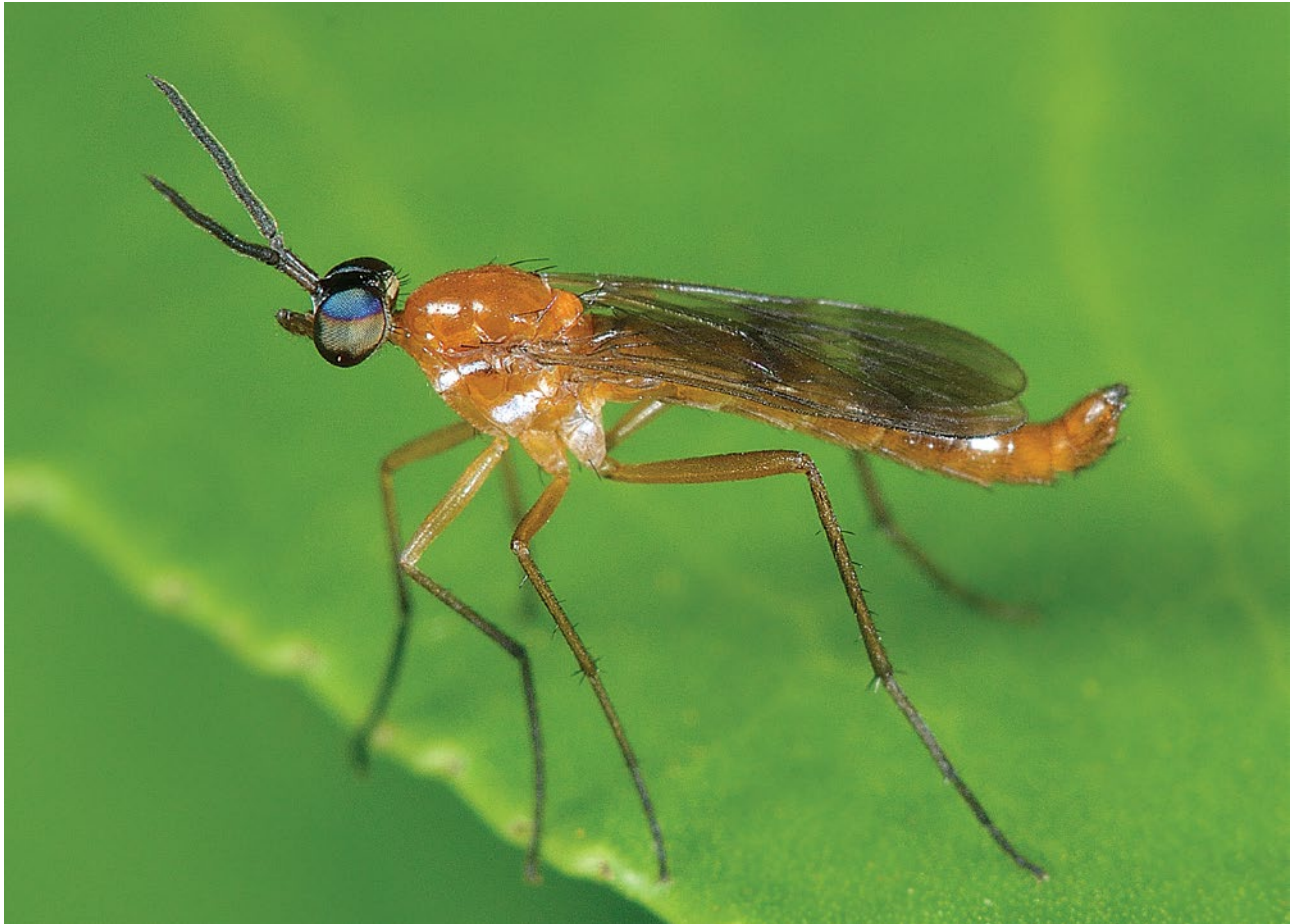
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## THEREVIDAE

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  $M_1$ – $M_3$ .

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 infusate, 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).



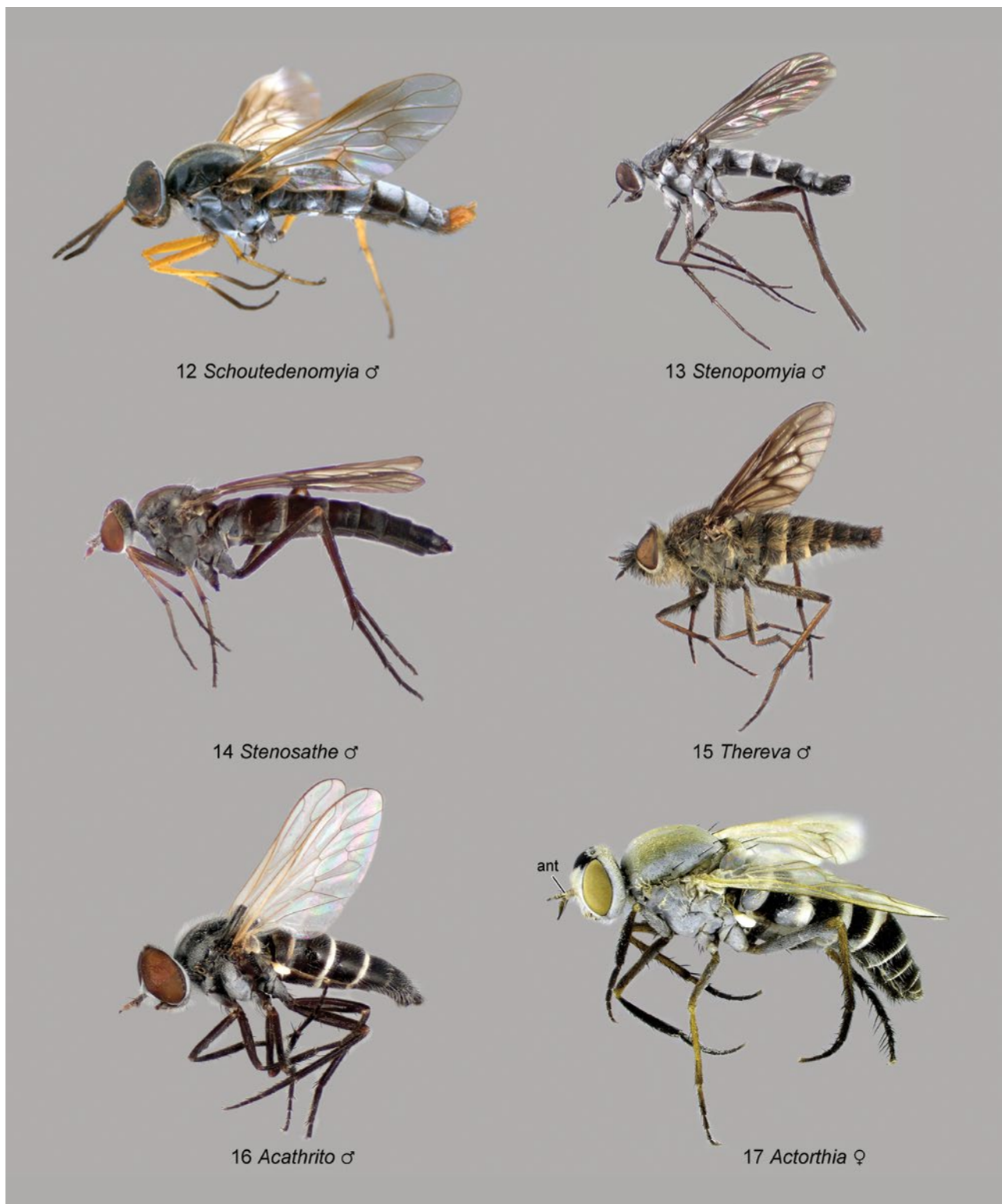
**Figs 49.2–5.** Photographs of living Afrotropical Therevidae: (2) *Acathrito lindneri* Lyneborg (South Africa); (3) *Xestomyza lugubris* Wiedemann (South Africa); (4) *Irwiniella tomentosa* (Becker) (Namibia); (5) *Stenopomyia angulata* Lyneborg (Madagascar). Photographs © S.A. Marshall.





**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) *Neotherrevella* 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 1954a). 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 (1954a, 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).

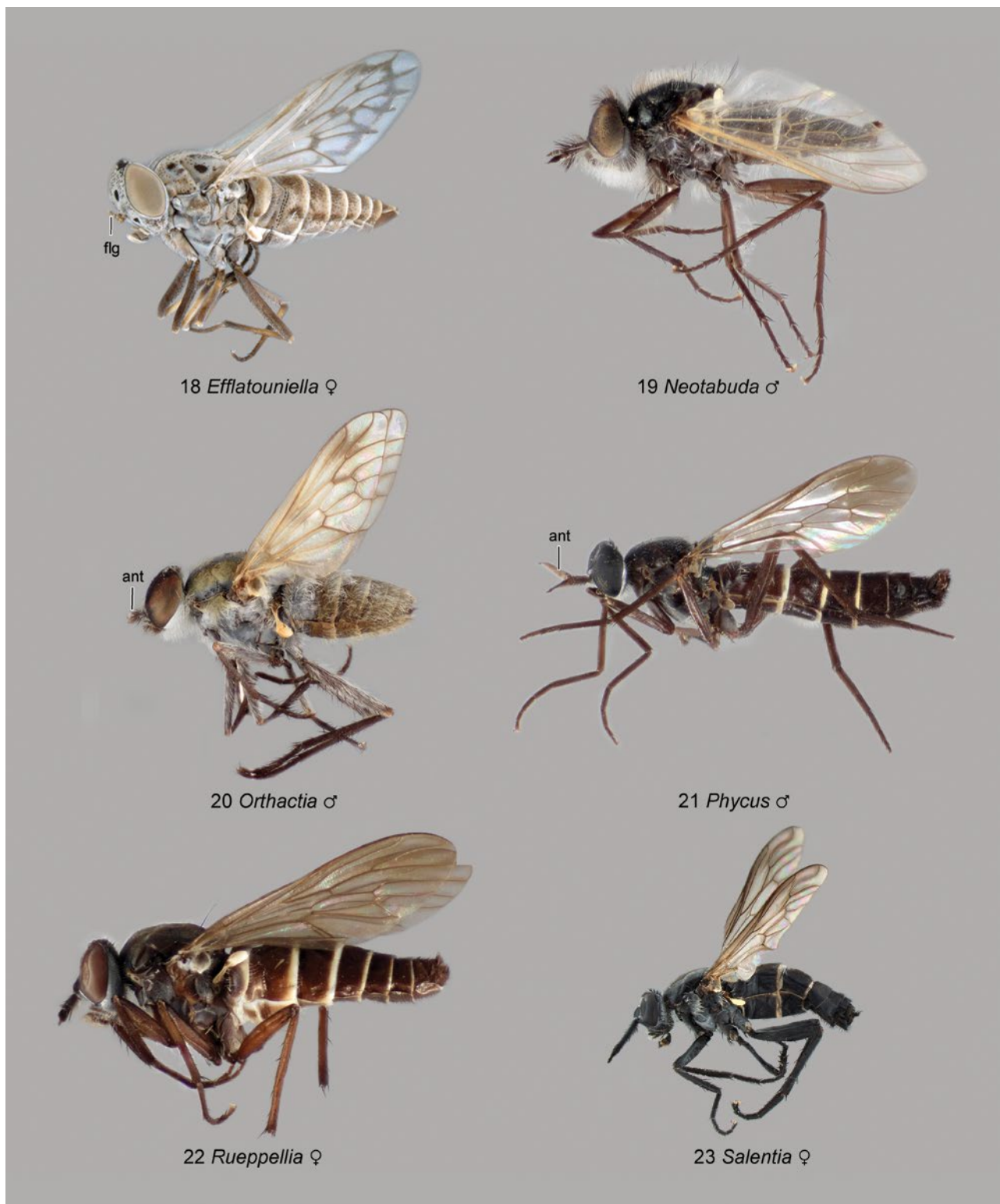
Adults appear to only imbibe water and a few taxa may feed on plant nectar or exudates from trees. Isaac (1925), as well as some early authors (Lundbeck 1908: 133; Williston 1908: 205), have stated that adults prey on other insects, but these observations have never been verified and remain highly doubtful (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 sphecoid wasps, such as *Crabro* F. (Kurczewski 2003), *Oxybelus* Latreille (Matthews & Matthews 2005; Peckham *et al.* 1973) and *Bembix* F. (Hauser & Irwin 2003; Kimsey *et al.* 1981).

## Economic significance

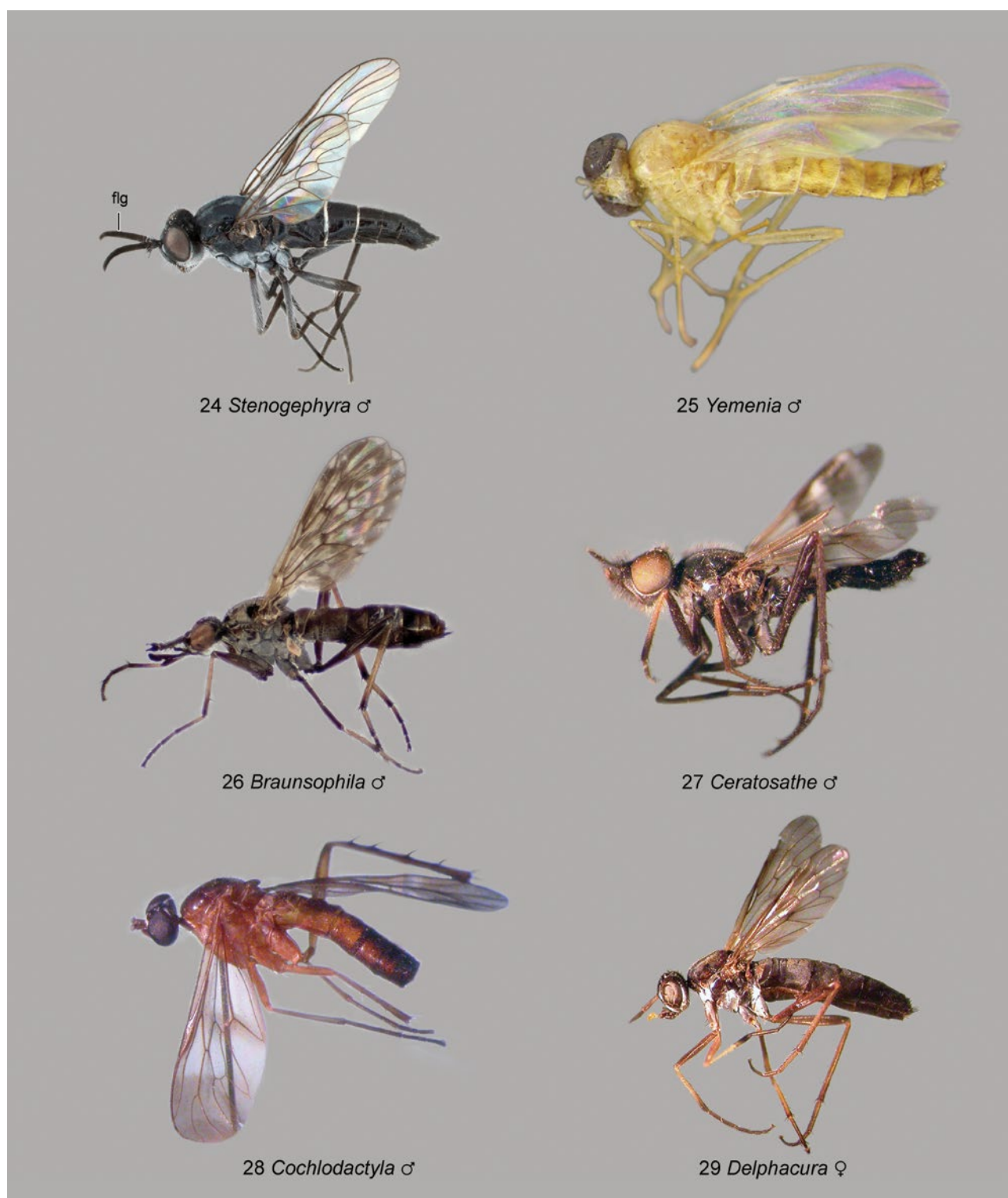
Early records reported that therevid larvae may be pests on cereal crops (Klein 1918), but this was soon refuted (Goetze 1932; Müller 1920). Predatory larvae are in fact beneficial in agricultural and forestry ecosystems, attacking a wide variety of pest insect larvae (e.g., Pinkham & Oseto 1987, 1988; 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 therevid 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 1976a, 1980b: 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.* 2013a, 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 (*Acatritho* Lyneborg, *Actorthia*, *Neotabuda* Kröber, *Orthactia* Kröber, *Rueppellia* Wiedemann, *Salentia*) and the Old and

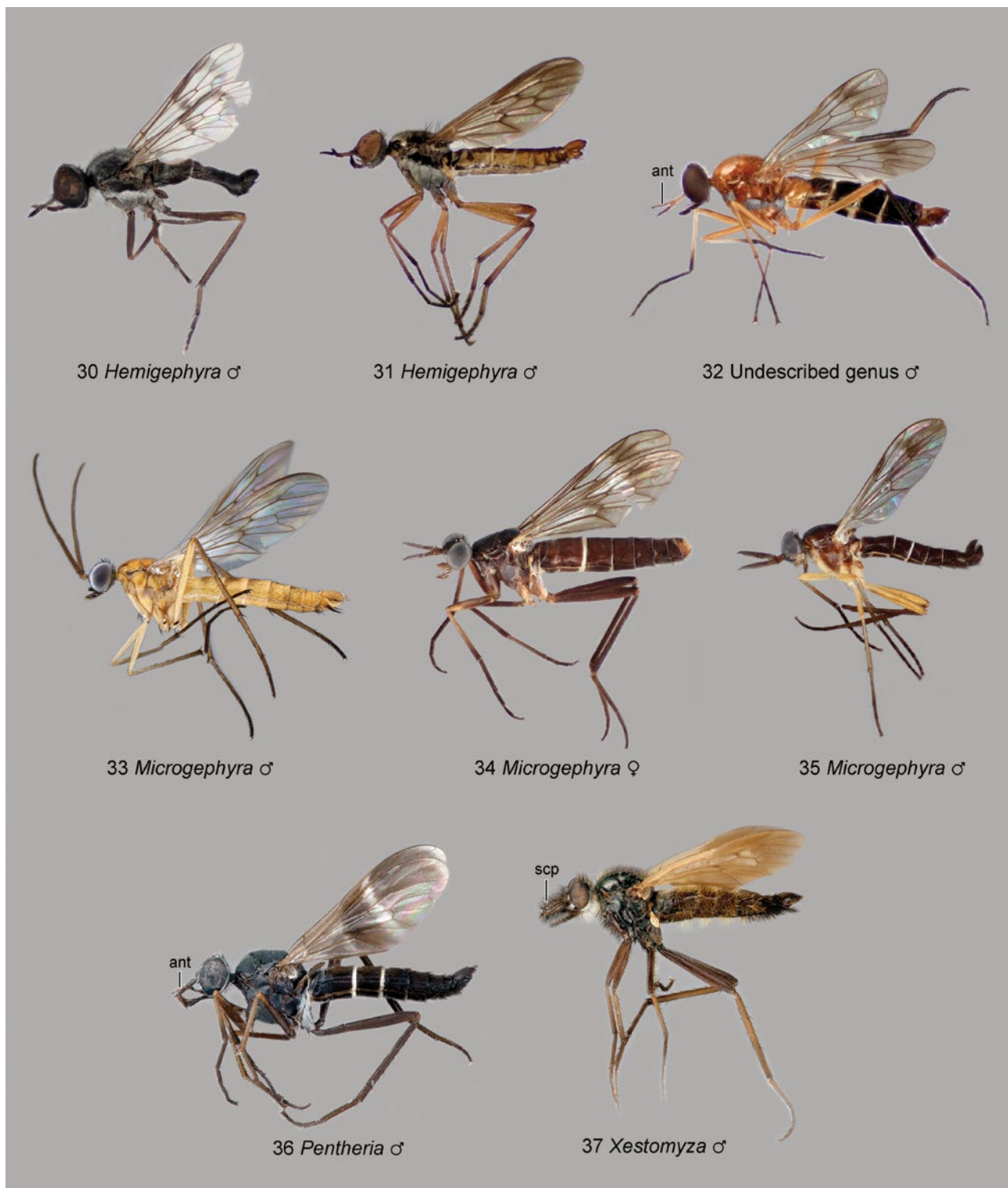
New World *Phycus* genus-group (Afrotropical genera: *Phycus*, *Stenogephyra* Lyneborg). Xestomyzinae is divided into the New World *Henicomys* Coquillett genus-group (single genus *Henicomys*) and the *Xestomyza* genus-group, which only occurs in the Afrotropical Region and includes all other genera.

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, *Kroeberella* Hauser (all from Baltic Amber) and *Palaeopherochera* Hauser (Florissant) (Hauser 2007; Hauser & Irwin 2005a). 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 (*Henicomys*) 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 2005a).

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, *Pseudotherava* 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 (Cyclotellini) 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 (1912a–f, 1913a–c), followed shortly thereafter by his work on the world Therevidae (Kröber 1913d: 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 1976a) 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, 1976b) 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, 1976b) 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, 1978c, 1980a, 1987, 1988, 1989b). 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 infusate . . . . . 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  $\frac{1}{3}$  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  $\frac{1}{3}$  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  $10 \times$  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  $5 \times$  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 *Irwinella* 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) . . . . . *Irwinella* 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) . . . . . *Schoutedenumyia* 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

***Acatritho* 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. *Acatritho* (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 (1989b), 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.

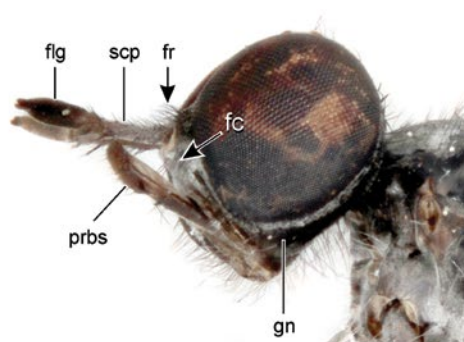
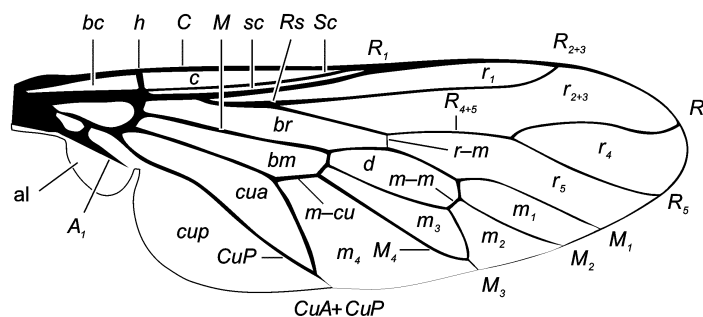
***Braunsophila* Kröber** (Xestomyzinae). An endemic genus of four described species confined to South Africa. *Braunsophila* (Fig. 26) includes small (length: 4.5–5.0 mm), brown species with maculate wings (Fig. 61), the proboscis is longer than the head and the male eyes are dichoptic. This genus is 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 (1976b).

***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 (1976a). *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 *Pseudotherava* 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 (1976a) 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 (1976a) 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 pseudo-segment, 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 (1976a).

***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.

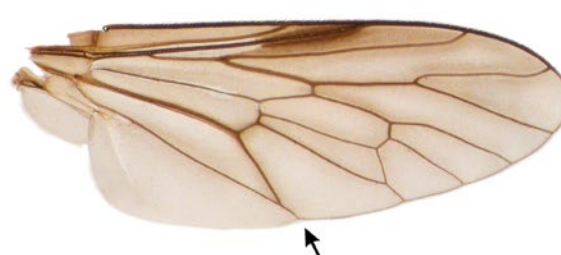
***Cochlodactyla* Lyneborg** (Xestomyzinae). An endemic monotypic genus, with the single described species, *C. munroi* Lyneborg, 1972 (Figs 28, 63), described from the Eastern Cape Province, South Africa. This rare species is characterised by its orange colour, the dichoptic male eyes, the short proboscis



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 (1976a). *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 (1976a) 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* Ségué, *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.

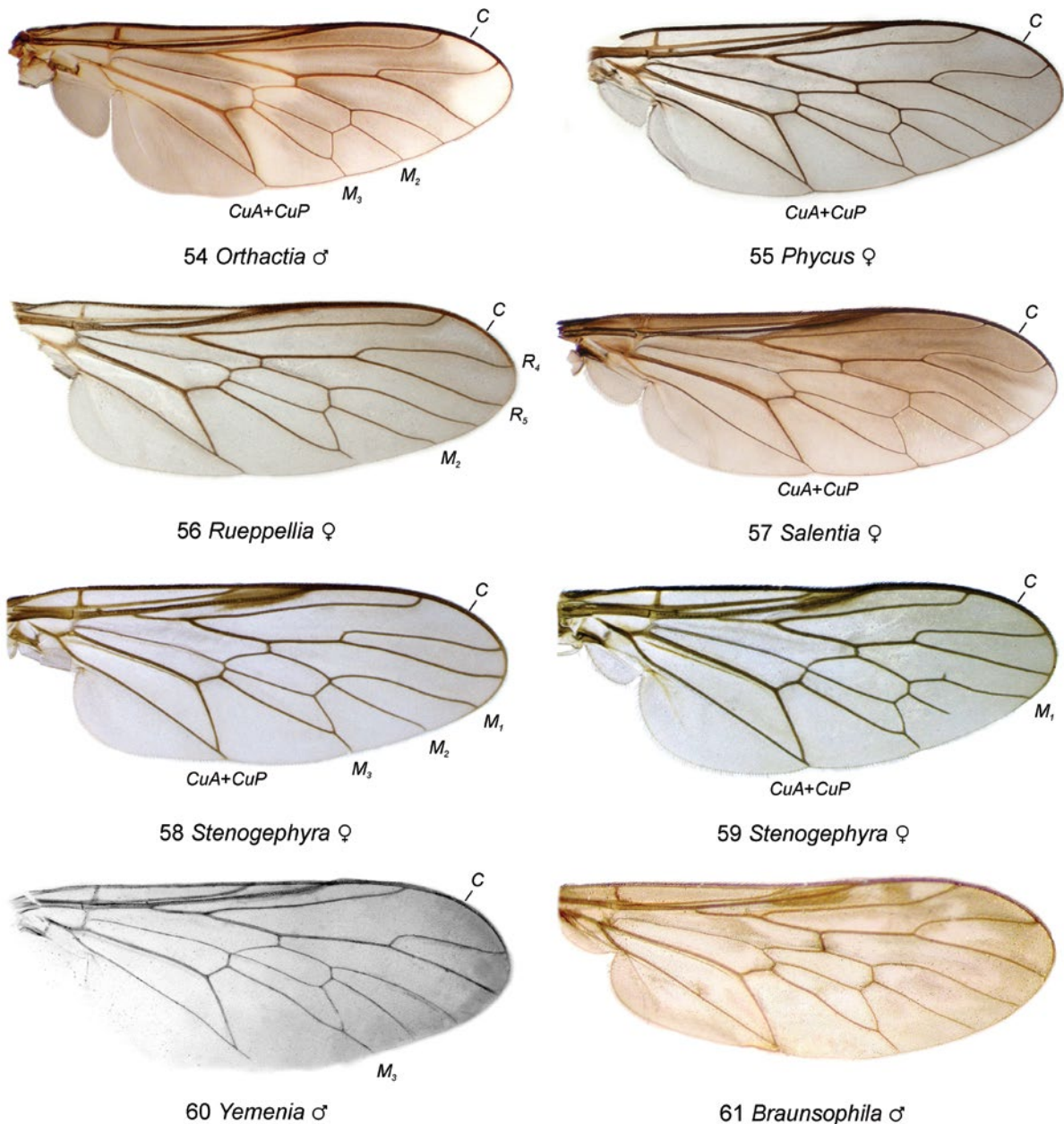
***Microgephyra* Lyneborg** (Xestomyzinae). An endemic genus of 14 described species occurring in southern parts of the continental Afrotropics and Madagascar (Hauser & Irwin 2005b; Lyneborg 1972). *Microgephyra* (Figs 1, 33–35) are small- to large-sized species (length: 4–10 mm), often black or brown, 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 *Irwinia*. It is, therefore, likely that *Neophycus* is a synonym of *Irwinia* 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. Lynneborg (1980a) last revised the genus. *Neotabuda* (Fig. 19) are

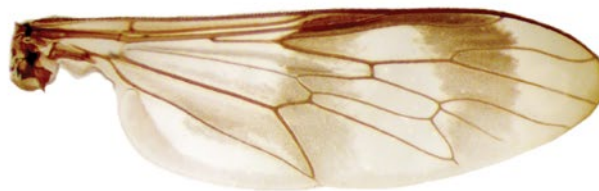


**Figs 49.54–61.** Wings of Therevidae (dorsal views): (54) *Orthactia* sp. ♂; (55) *Phycus niger* (Kröber) ♀; (56) *Rueppellia* sp. ♀; (57) *Salentia* sp. ♀; (58) *Stenogephyra dianeae* Webb & Hauser ♀; (59) *S. janiceae* Webb & Hauser ♀; (60) *Yemenia flavus* (Lynneborg) ♂; (61) *Braunsophila* sp. ♂.

Abbreviations: C – costal vein; CuA+CuP – anterior branch of cubital vein + posterior branch of cubital vein; M<sub>1</sub> – first branch of media; M<sub>2</sub> – second branch of media; M<sub>3</sub> – third branch of media; R<sub>4</sub> – upper branch of third branch of radius; R<sub>5</sub> – 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 (1980a).

***Neotherevella* Lyneborg** (Therevinae). A genus of four described species, occurring disparately in the Afrotropical and Palearctic 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 1976a, 1978b). 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 (1976a) 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 Afro-

tropical 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 (1978c).



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*<sub>1</sub> – first branch of media; *R*<sub>4</sub> – upper branch of third branch of radius; *R*<sub>5</sub> – lower branch of third branch of radius.



***Pseudotherewa* 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 *Irwinella* and *Thereva*. *Pseudotherewa* (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). *Pseudotherewa* 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 *Pseudotherewa* the face is much narrower. The genus is closely related to the *Acantotherewa*, *Acrosathe* and *Irwinella* and is ascribed to the *Pandivirilia* genus-group. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lyneborg (1976a).

***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 (1989a). *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.

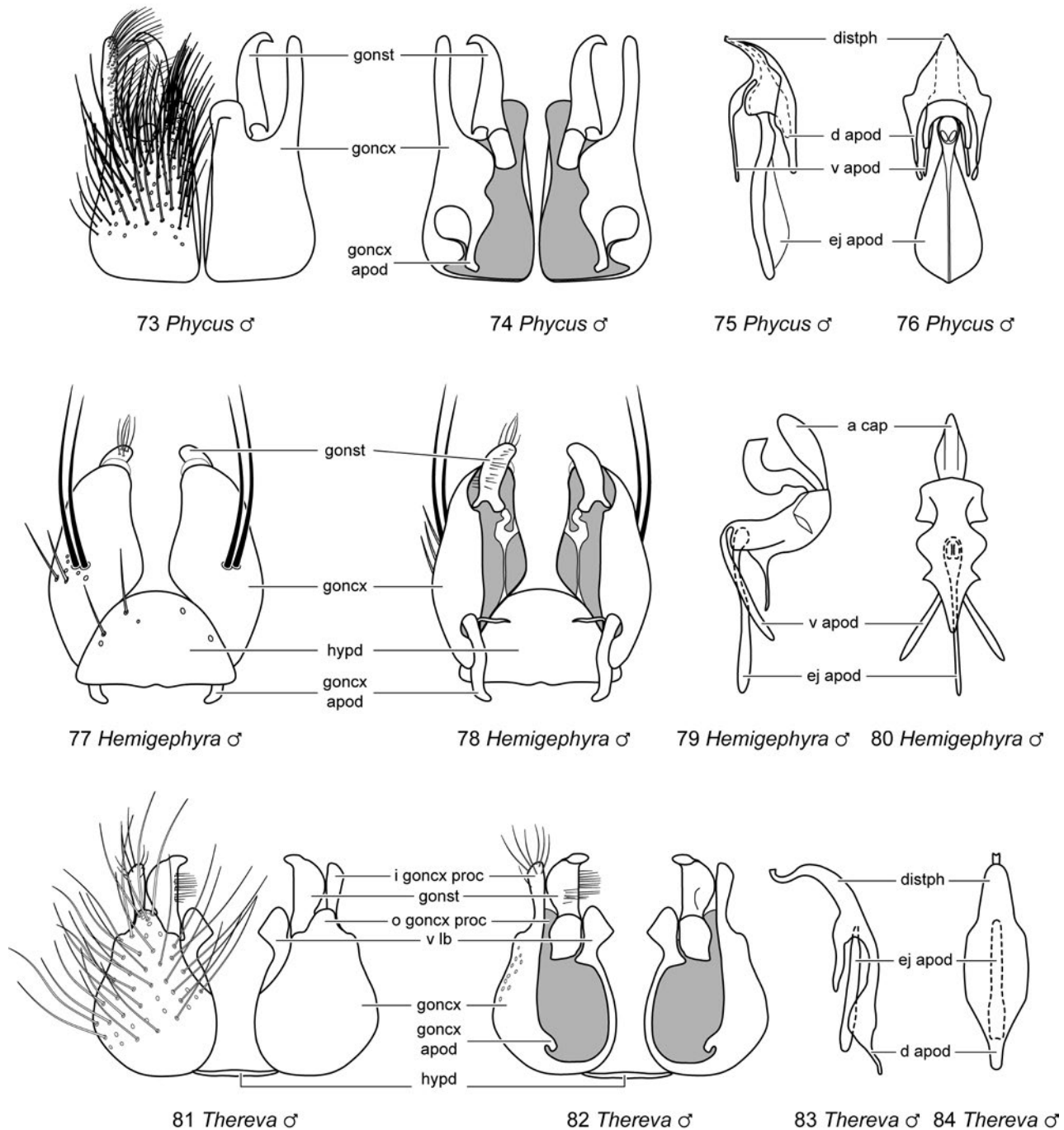
***Schoutedenomyia* Kröber** (Therevinae). A rarely encountered genus of 15 described species, widely distributed throughout the Afrotropical, Oriental and Palaearctic (Mediterranean) Regions. Several undescribed species are also represented in collections from the Oriental Region (Lyneborg 1976a, 1978a, 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 1976a). 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 (1976a) provided an identification key to Afrotropical species and later described two additional species (Lyneborg 1978a).

***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 (1976a) 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 (1976a).

***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 (1976a), 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 terminal 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 (1976a).

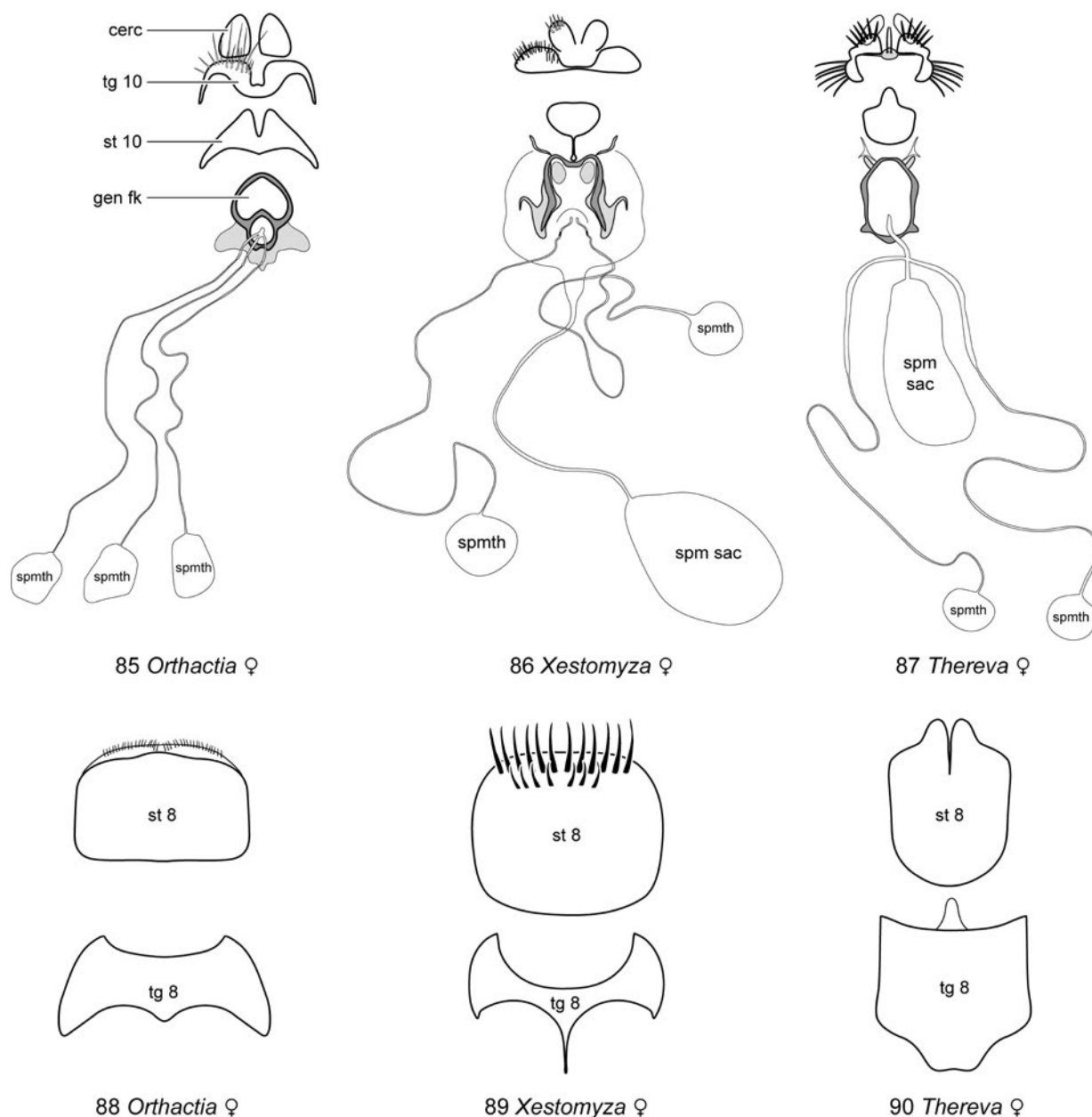


**Figs 49.73–84.** Male terminalia of Therevidae: (73) male terminalia of *Phycus* sp., ventral view; (74) same, dorsal view; (75) aedeagal complex of *Phycus* sp., lateral view; (76) same, dorsal view; (77) male terminalia of *Hemigephyra braunsi* (Kröber), ventral view; (78) same, dorsal view; (79) 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



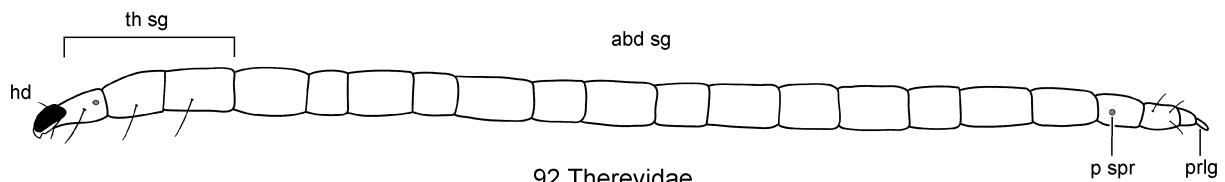
**Figs 49.85–90.** Female terminalia, sternites and tergites of Therevinae: (85) terminalia of *Orthactia* sp., dorsal view; (86) same, *Xestomyza lugubris* Wiedemann; (87) same, *Thereva* sp.; (88) sternite 8 (above), ventral view and tergites 8 (below), dorsal view of *Orthactia* sp.; (89), same, *Xestomyza lugubris* Wiedemann; (90) same, *Thereva* sp.

Abbreviations: cerc – cercus; gen fk – genital fork; spm sac – spermathecal sac; spmth – spermatheca; st – sternite; tg – tergite.

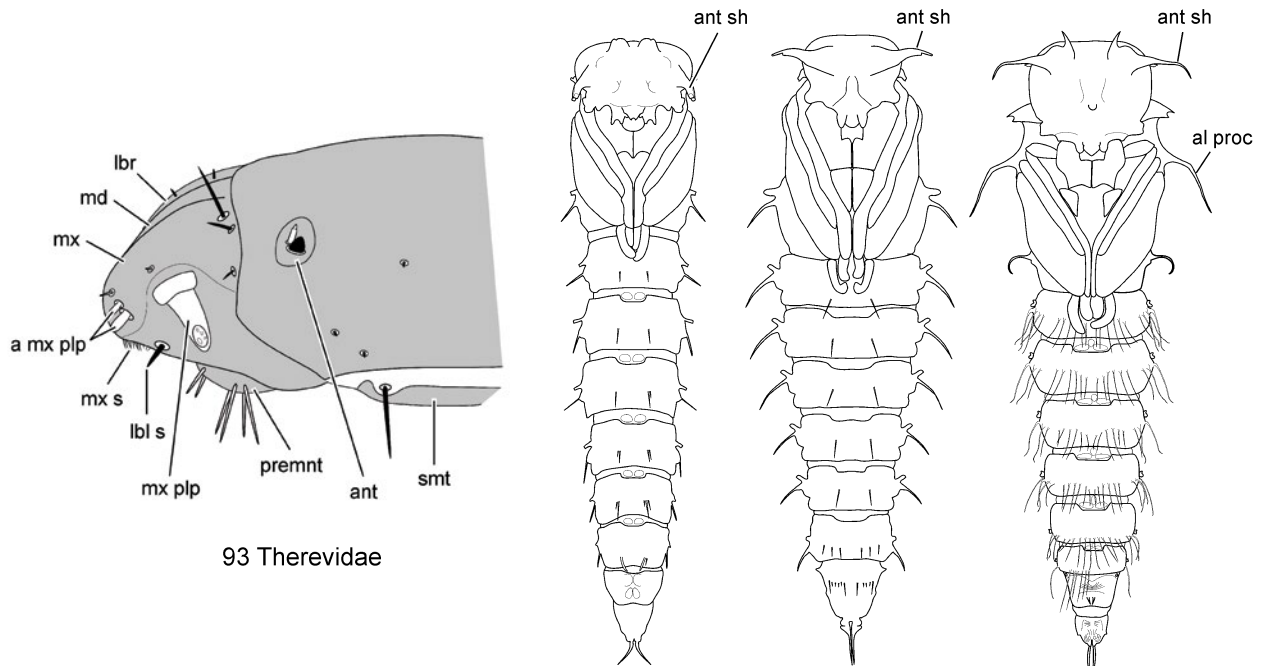




91 Therevidae



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 *Irwinella*, 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 *Euphyicus*. Biology and immature stages remain unknown. An identification key to Afrotropical species was provided by Lynneborg (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* Lynneborg, 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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