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Family groups of Diopsoidea and Nerioidea (Diptera: Schizophora)—Definition, history and relationships

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Abstract

The Acalyptratae are a diverse, heterogenous assemblage of dozens of families of "higher flies" in the Schizophora (Diptera). There are ten acalyptrate superfamilies, two of which are reviewed and redefined here at the family-group level: Diopsoidea and Nerioidea. The superfamily Diopsoidea includes seven families: Diopsidae (two subfamilies and two tribes), Gobryidae, Megamerinidae, Nothybidae, Psilidae (three subfamilies), Somatiidae and Syringogastridae. The superfamily Nerioidea also includes seven families: Cypselosomatidae, Fergusoninidae, Micropezidae (five subfamilies), Neriidae, Pseudopomyzidae, Tanypezidae and Strongylophthalmyiidae. All 14 families are redescribed, figured and keyed, including notes on subordinate family-level groups. Homologies for external and genitalic characters are established, and the superfamilies and their family-level groups are discussed. A morphological phylogenetic analysis is provided, including representatives from all family-level groups in both ingroup superfamilies, as well as twelve outgroup taxa from five other acalyptrate superfamilies. Both superfamilies were supported as monophyletic, although both the Diopsoidea and its basal branches were supported by highly homoplasious characters and are here only tentatively accepted; a relationship between Diopsidae, Syringogastridae and Megamerinidae is strongly supported. Nerioidea is a well-defined group divided into three lineages, including one containing Pseudopomyzidae, Cypselosomatidae and Fergusoninidae, the latter of which was previously considered to be related to the family Agromyzidae (Opomyzoidea). Diopsoidea and Nerioidea were not found to be related.

Key words: Diptera, Nerioidea, Diopsoidea, phylogeny, Acalyptratae, redefinition, family groups

Introduction

The Acalyptratae (Schizophora) includes nearly half of all dipteran families (see Pape *et al.* (2011)) and is weakly supported as monophyletic. The general consensus is that it is almost certainly an artificial clustering of families rendered paraphyletic by the calyptrate flies. Ten superfamilies are recognized: Carnoidea, Conopoidea, Diopsoidea, Ephydryoidea, Lauxanioidea, Nerioidea, Opomyzoidea, Sciomyzoidea, Sphaeroceroidea and Tephritoidea. The family Conopidae is the sole member of the superfamily Conopoidea, and while there is molecular evidence to treat it as Sciomyzoidea (Wiegmann *et al.,* 2011), support is relatively weak. Sister-group relationships between many families are uncertain, and the definition of many families themselves have undergone considerable change—see J.F. McAlpine (1989) and Yeates *et al.* (2007). The reason for this instability may be that many acalyptrate lineages trace their origins to a burst of speciation in the recovery period following the K-T extinction event 66mya (Wiegmann *et al*. 2011; Lambkin *et al*., 2013), leaving little time for complex synapomorphies to develop to provide evidence of common ancestry. Many of these lineages are also now highly specialized and derived in biology, morphology and genetics (sometimes quite remarkably so), confusing analyses by producing an abundance of homoplasy, and either modifying or erasing potentially useful synapomorphies.

The composition of superfamilies is in flux, but some have been relatively stable in recent decades and may in fact be natural groupings, Ephydroidea and Tephritoidea among them. Other superfamilies are proving to be artificial assemblages, including the former Opomyzoidea; this superfamily was dismantled by Winkler *et al.* (2010), although Roháček (2006) provided modest morphological support for Anthomyzidae + Opomyzidae. Family-level relationships among the acalyptrates were constructed in detail by Griffiths (1972) and Hennig (1958), but the superfamilies were mostly presented as an unresolved polytomy within Schizophora, with Hennig admitting that many families could not even be reliably placed to superfamily. A superfamily classification was presented by J.F. McAlpine (1989) using a select subset of characters that also supported a monophyletic Acalyptratae. Much work clearly remains to be done until a stable family-level classification is produced for the acalyptrates, but ongoing studies are providing small steps towards this goal by testing and developing hypotheses.

The present work is a continuation of these studies, focusing on the superfamilies Diopsoidea and Nerioidea. These superfamilies are treated here together because several families have shifted between the two, especially Tanypezidae and Strongylophthalmyiidae, and J.F. McAlpine (1989) argued for a sister group relationship between them.

The Diopsoidea consists of seven families that are each highly distinctive: **Diopsidae** (Figs 143–190, 405–410), or the "stalk-eyed flies", is a mostly saprophagous group that includes some phytophages and an occasional pest on rice crops; **Gobryidae** (Figs 67–70, 82–97, 402), or "hinge flies", is a small, bizarre, monogeneric Australasian family with a straight abdomen that can be sharply angled upwards; **Megamerinidae** (Figs 98–123, 403) is a small family of black, large-bodied Palaearctic/Oriental species; **Nothybidae** (Figs 50–64, 399–400) is small, monogeneric, Australasian/Southeast Asian in distribution and one of the few fly families assumed to give birth to larvae; **Psilidae** (Figs 1–48, 395–398) is relatively widespread and diverse, containing over 300 species including the carrot rust fly; **Somatiidae** (Figs 65–66, 71–80, 401) is a small, monogeneric, Neotropical family of stout, yellow and black species; **Syringogastridae** (Figs 124–142, 404) is a small, monogeneric family of Neotropical ant-mimics.

The Nerioidea also includes seven families: **Cypselosomatidae** (Figs 205–232, 413–414) is an Australasian group extending north to Nepal that is known from rotting fruit, latrines and bat dung; **Fergusoninidae** (Figs 191–204, 411), below associated with nerioid families for the first time but historically allied to the opomyzoid family Agromyzidae ("leaf mining flies"), is a family of unusual bright yellow flies that form galls on Myrtaceae that exhibit the only known only instance of mutualism between flies and nematodes; **Micropezidae** (Figs 312–394, 421–422), or "stilt-legged flies", is the most diverse family of either Nerioidea or Diopsoidea with about 700 species in five subfamilies, is similarly long-bodied but more delicate in form compared to Neriidae, and while some larvae are are predaceous or agricultural pests, most are found in decay, primarily in plant tissue; **Neriidae** (Figs 291–311, 412), or "cactus flies", is a widespread and diverse group of long, straight and sometimes spiny species found in necrotic plant tissue; **Strongylophthalmyiidae** (Figs 262, 274–290, 417–418), or "hardwood flies", is a relatively diverse family that occurrs primarily from east to southeast Asia and is associated with dead wood; **Tanypezidae** (Figs 257–261, 263–271, 419–420), or "stretched-foot flies", is a less diverse, mostly New World family that is most speciose in the tropics and also associated with dead wood; **Pseudopomyzidae** (Figs 233–256, 415–416) is a widespread and relatively genus-rich family mostly associated with decaying plant matter. One fossil genus of uncertain placement is known from Baltic amber (*Cypselosomatites succini* Hennig).

The present study is divided into several sections. First, a discussion of morphology is provided to establish homology across families and to highlight relevant structures, especially those of the genitalia, which have been treated inconsistently in the literature. Second, a key is provided for the diopsoid and nerioid family groups. Third, each family in these groups is redescribed with relevant notes on their constituent subfamilies and tribes, with illustrations and photographs given; families are listed alphabetically within the subfamily (Diopsoidea first) and figures presented according to phylogenetic relationship to more easily compare homologous structures. Fourth, the superfamilies and their family-level groups are discussed in a historical context, following their treatment in the literature and tracing their limits. Fifth, a phylogenetic analysis using morphological characters is provided to i) test the monophyly of the Diopsoidea and Nerioidea, ii) test the hypothesized sister-group relationship between the Diopsoidea and Nerioidea, iii) determine the relationships of the family-level groups within these superfamilies.

The composition and relationships of the diopsoid tribes are not tested here as these are convincingly established elsewhere (see discussion below) and their inclusion would be redundant. Subfamily relationships within the Micropezidae and Neriidae are also not examined, as this is outside the scope of the present study and resolving this complex issue will first require a large investment in genus-level revisionary work.

Multiple representatives from each family-group are examined, with the exception of Belobackenbardiinae, two subfamilies of Micropezidae (Eurybatinae and the monotypic Calycopteryginae) and the tribes of Diopsinae. Exemplars from twelve outgroup families in five superfamilies were included in the analysis: Agromyzidae, Anthomyzidae, Aulacigastridae, Clusiidae, Neurochaetidae, Opomyzidae, Odiniidae ("Opomyzoidea"), Chyromyiidae (Sphaeroceroidea), Curtonotidae (Ephydroidea), Lauxaniidae (Lauxanioidea), Lonchaeidae and Piophilidae (Tephritoidea).

The present study is confined to adult specimens, with immature stages treated as outside of the scope of this project, although relevant published sources on these stages are provided in the individual family sections. While it is recognized that all stages may reveal features both diagnostic and phylogenetically informative, as well-illustrated by Meier & Hilger (2000), this approach was taken for two reasons. The first is that adult Schizophora are much more character rich than immatures, especially when considering the male genitalia. Furthermore, adult specimens of the taxa under consideration are readily accessible in collections, while immature stages are uncommon or entirely unknown for most.

Quantitative phylogenetic analyses have already been published to resolve the internal structure of a number of families considered here, but the present study is one of the few to apply this technique across the diopsoid and nerioid families. Wiegmann *et al.* (2011) provided a phylogeny of the Diptera using mitochondrial and nuclear genes combined with morphological data across an impressive sampling of the dipteran families. The morphological data were treated in detail later in Lambkin *et al.*'s (2013) companion analysis. Marshall *et al.* (2010) provided an analysis including a broad representation of both Syringogastridae and Diopsidae.

Materials and methods

Pinned adult specimens were examined from the following collections: Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, Canada (CNC); University of Guelph Insect Collection, Guelph, Canada (DEBU); KwaZulu-Natal Museum, Pietermaritzburg, South Africa (NMSA); National Museum of Natural History, Washington, D.C., USA (USNM). Amber-preserved specimens of extinct taxa were examined from The Hoffeins Collection, Hamburg, Germany (CCHH). Only a single female is known of the genus *Nartshukia*, the female holotype of *N. musiva* Shatalkin; this specimen is deposited in the Zoological Museum, Moscow (ZMUM), and was examined via photographs that were originally published in Lonsdale (2013).

Abdomens of dissected specimens were prepared washing in ethanol after the soft tissue was dissolved in hot Lactic Acid. Genitalia are stored in glycerin in microvials pinned with the specimen. Genitalia were observed and illustrated using a Nikon Optiphot compound microscope with an attached camera lucida. Figures of internal genitalia are enlarged for clarity of finer structures.

The character matrix was initially developed in DELTA (Dallwitz *et al*., 2000) but completed in Mesquite (Maddison & Maddison, 2018). Phylogenetic analysis was performed using TNT ver. 1.1 (Goloboff *et al*., 2003), using a heuristic search with swapping algorithm tree bisection reconnection (TBR), saving 1000 trees per replication. Trees were figured using Winclada (Nixon, 2002) with ACCTRAN optimization. The taxa used in the analysis are listed below in the Material Examined section; characters and characters states are listed in Appendix 1. The matrix used for the analysis contains 61 taxa and 323 characters (Appendix 2).

Material Examined

DIOPSOIDEA

Diopsidae

Centrioncinae

•*Centrioncus decoronotus* Feijen

KENYA. East Kenya, Meru District, Upper Imenti Forest, vii.1973, E. Balyetagara, CNC731580-731582 (2♂ 1♀, CNC).

• *Centrioncus sanorum* (Feijen)

SOUTH AFRICA. KwaZulu-Natal: 75 km west-southwest of Estcourt, Cathedral Peaks Forest Station, Rainbow Gorge, Podocarp Forest, 1500m, 10–18.xii.1979, S. & J. Peck, dung trap, CNC731604-731609 (3♂ 2♀, CNC), 7–31.xii.1979, CNC731606 (1♀, CNC), Cape, Grahamstown, 750m, southern forest, 8.i.1986, W.R. Mason, CNC731611, CNC731600-731603 (2♂ 3♀, CNC).

Diopsinae

Diopsini

•*Diasemopsis aethiopica* (Rondani)

NIGERIA. Kaouna, 4.v.1962, D.C. Eidt, light trap, CNC731588 (1♀, CNC). **TANZANIA**. Same, 15.v.1962, CNC731587 (1♀, CNC). **TOGO**. Alavagno, 23.x.1978, P.T. Dang, CNC731589 (1♂, CNC), 25.x.1978, CNC731590, CNC731591 (1♂ 1♀, CNC).

Sphryacephalini

•*Sphyracephala subbifasciata* Fitch

CANADA. Ontario: Chatterton, 25.vii.1956, John C. Martin, John C. Martin Collection, CNC731617 (1♂, CNC), Maynooth, 8.x.1951, J.F. McAlpine, CNC731619 (1♀, CNC), Ottawa, 4.x.1951, J.F. McAlpine, CNC731612, CNC731613 (2♂, CNC), Simcoe, 23.vi.1939, G.E. Shewell, CNC731616 (1♂, CNC), Spencerville, 21.x.1937, G.H. Hammond, CNC731614 (1♂, CNC), Quebec: Kazubazua, 6–10.vi.1927, W.J. Brown, CNC731615 (1♀, CNC), Mount St. Marie Low, 548m, 20.ix.1965, J.R. Vockeroth, CNC731618 (1♀, CNC).

Incertae sedis

•*Prosphyracephala succini* (Loew)

Baltic amber: 1380-2 (1♀?, CCHH), 1380-3 (1?, CCHH), 1380-5 (1♂, CCHH).

Gobryidae

•*Gobrya* sp. 1

PHILIPPINES. Laguna, Los Baños, Mt. Makiling, trail, 14°8′46″N, 121°13′50″E, 300–500m, 20–30.iii.2010, S.A. Marshall, debu00332502, debu00332503 (1♂ 1♀, DEBU). VIETNAM. Catcat, Sapa District, 22°19′26.64″N, 103°48′30.64″E, 18.viii.2011, S.A. Marshall (5♂ 4♀, DEBU).

•*Gobrya* sp. 2

MALAYSIA. Pahang: Kuala Tahan, Taman Negara National Park, 200m, Rainforest, 21.vi.1990, J. Heraty, CNC728154 (1♂, CNC), Johor Endau Rompin National Park, 2°37′12″N 103°21′0″E, 120–300m, 28–31.v.2013, E. Jendek & O. Sausa, CNC728155 (♂, CNC), Perak, Belum-Temenggor: Pulau Banding (15km env), 5°33′5″N 101°20′33″E, 300 to 400m, 27.iii–14.iv.2015, E. Jendek & O. Sausa, CNC440214 (1♂, CNC).

Megamerinidae

•*Megamerina dolium* (Fabricius)

UNITED KINGDOM. **England**: Oxford, vi.1954, J.R. Vockeroth, CNC731543 (1♂, CNC). **CHINA.** Heilongjiang, Fengling State Nature Res., Yichun, 48°5′N, 129°58′E, mixed Pinus/deciduous forest, 28.vi–10.vii.2000, P. Shivonen, debu0015015 (1♀, DEBU).

•*Palaeotanypeza spinosa* Meunier

Baltic amber: 1656-1 (1♀, CCHH), 1656-2 (1♂, CCHH), 1656-3 (1♀, CCHH), 1811-6 (1♀, CCHH).

•*Texara* sp.

JAPAN. Iwate: Mount Hayachine, 400m, 19.vii.1989, Makihara & Sharkey, CNC731546-731552 (5♂ 2♀, CNC), 25.vii.1989, CNC731553-731555 (2♂ 1♀, CNC).

Nothybidae

• *Nothybus biguttatus* Wulp

INDONESIA. West Java: Tjipanas, 1524–3048m, 8.viii.1965, J.E. Lukavsky, CNC481374, CNC481375 (1♂ 1♀, CNC). [also see Lonsdale & Marshall (2016)]

•*Nothybus triguttatus* Bezzi

PHILIPPINES. Palawan: Eran Pt., 8km SW Tarumpitago Pt., at light, 31.xii.1959–4.i.1960, L.W. Quate, CNC481389 (1♀, CNC), Mindanao Lanao, Butig Mts., 24km NE of Butig, 1080m, jungle along stream, 21.vi.1958, H.E. Milliron, CNC481388 (1♂, CNC), Mt. Lobi,1000′, viii.1945, Leyte (1♂, USNM). [also see Lonsdale& Marshall (2016)]

Psilidae

Belobackenbardiinae

•*Belobackenbardia cornicula* Shatalkin

SOUTH AFRICA. Mariepskop, TVL, 2430DB, c. 1500m, 8.iv.1964, E.H., NMSA-DIP71789, NMSA-DIP71788 (1♂ 1♀ paratypes, NMSA).

Chylizinae

•*Chyliza leguminicola* Melander

CANADA. British Columbia: Horseshoe Bay, 0–91m, 25.v.1961, J.R. Vockeroth, CNC731539, CNC731540 (1♂ 1♀, CNC), Vancouver, Point Grey, 49°16′12.74″N 123°13′13.64″W, 15.v.1973, J.R. Vockeroth, CNC731538 (1♂, CNC).

•*Chyliza notata* Loew

CANADA. British Columbia: Mission City, 4.vii.1953, W.R.M. Mason, CNC731537 (1♀, CNC), Ontario: Ottawa, 26.v.1958, J.R. Vockeroth, CNC731532,CNC731533 (1♂,1♀, CNC), 27.v.1958, CNC731534 (1♂, CNC), 28.vi.1952, J.F. McAlpine, newly cut Manitoba Maple, CNC731535 (1♀, CNC). **USA.** North Carolina: Highlands, 914m, vi.1957, W.R.M. Mason, Horse Cove, CNC731536 (1♂, CNC).

Psilinae

•*Loxocera cylindrica* Say

CANADA. Newfoundland and Labrador: St. John's, Agriculture Exp. Station, 47°30′54.11″N 52°47′3.24″W, 26.vii.1967, J.F. McAlpine, CNC731521 (1♂, CNC), Ontario: Gananoque, 13.vii.1941, G.S. Walley, CNC731520 (1♂, CNC), Penetang, 2.viii.1956, J.G. Chillcott, CNC731525 (1♀, CNC). **USA.** Iowa: Ames, 9.vii.1947, A.R. Brooks, CNC731523,CNC731524 (1♂ 1♀, CNC), Tennessee: Great Smoky Mountains National Park, 1584m, 29.v.1957, J.R. Vockeroth, Indian Gap, CNC731522 (1♂, CNC).

•*Psila hennigi* (Thompson & Pont)

CANADA. British Columbia: Agassiz, v.1947, R. Glendenning, CNC731527, CNC731528 (2♂, CNC), Armstrong, 22.ix.1954, J.H. McLeod, Wong Jones, CNC731530 (1♂, CNC), Qualicum, 15.vi.1955, G.E. Shewell, CNC731529 (1♀, CNC), Victoria, 7.x.1953, M.D. Noble, CNC731531 (1♀, CNC), Ontario: Ottawa, 45°25′28.02″N 75°42′4.50″W, 12.vi.1958, J.R. Vockeroth, CNC731526 (1♀, CNC).

Incertae sedis

•*Electrochyliza succini* Hennig

Baltic amber: 836-1 (1♂, CCHH), 836-5 (1♀, CCHH), 1675-3 (1♀, CCHH), 1736-8 (1♀, CCHH), 1763-11 (1♂, CCHH).

Somatiidae

•*Somatia schildi* Steyskal

MEXICO. Veracruz, Estacion Biologica Los Tuxlas, ca. 15km N of Catemaco, 15–17.ix.1987, A.L. Norrbom, feeding on underside of leaves of broadleafed plant, evening (1730) (1♂ 1♀, USNM).

•*Somatia aestiva* (Fabricius)

ECUADOR. Napo: Napo River, Coca, 250m, 25–30.iv.1965, L. Pena, CNC731569 (1♀, CNC), v.1965, CNC731568 (1♀, CNC), Napo River, 250m, 12–30.iv.1965, L. Pena, CNC731566 (1♀, CNC), **TRINIDAD.** Manzanilla, x.1959, CNC731567 (1♂, CNC), Saugre-Grande, x.1959, CNC731562-731565 (1♂ 3♀, CNC).

Syringogastridae

•*Syringogaster rufa* Cresson

COSTA RICA. Heredia: 5.5 km south of Puerto Viejo, 4–5.iii.1991, B.J. Sinclair, CNC731560 (1♂, CNC), Corcovado National Park, Trails Near San Pedrillo Ranger Station, 8°37′0″N 83°44′0″W, 13.viii.2001, J. & A. Skevington, CNC731559 (1♂, CNC), Osa Pen. Corcovado National Park, Near San Pedrillo Ranger Station, 8°37′0″N 83°44′0″W, 12–15.viii.2001, J.M. Cumming, CNC731558 (1♂, CNC), Surrubres, Kertesz, CNC731557 (1♀, CNC). **PANAMA**. Barro Colorado Island, viii.1938, F.M. Hull, CNC731561 (1♂, CNC).

•*Syringogaster atricalyx* Marshall

BOLIVIA. La Paz, Heath River Wildlife Centre, ~21km SSW Puerto Heath, 12°40′S, 68°42′W, 29.iv–12.v.2007, S.M. Paiero, debu00303033-debu00303037 (3♂ 2♀ paratypes, DEBU). **ECUADOR.** Napo: Jatun Sacha Res., 6km E Misahualli, 450m, 1°4′S, 77°37′W, on foliage, 30.iv–8.v.2002, M. Buck, debu0018260 (1♀ paratype, DEBU). **PERU.** Madre de Dios, Los Amigos Biol. Stn., treefall pans, 6–10.vi.2006, Paiero&Klymko, debu00273026, debu00273029 (2♂ paratypes, DEBU).

NERIOIDEA

Cypselosomatidae

•*Clisa australis* (McAlpine)

AUSTRALIA. New South Wales: Dorrigo National Park, Subtropical rainforest, 22–23.x.1980, D.J. Bickel, CNC731437-731440 (2♂ 2♀, CNC).

•*Formicosepsis* sp. nr. *biseta*

PHILIPPINES. Laguna, University of Philippines, Los Baños, 14°9′52″N, 121°14′16″E, along river, 1.iv.2010, S.A.&S.N. Marshall, debu00320919-debu00320923, debu00321007, debu00320973 (4♂ 4♀, DEBU).

Fergusoninidae

•*Fergusonina turneri* Taylor

AUSTRALIA. Queensland/New South Wales, 2000–2003, S.A Wineriter, G.R. Buckingham & J.A. Lollis, Lab-Reared: USA: Florida: Alachua County: Gainesville: FDACS ex *Melaleuca quinquenervia,* CNC731374-731378 (2♂ 3♀, CNC).

•*Fergusonina* sp.

PHILIPPINES. Surigao del Sur Bislia, 9.i.1987, L.V. Tablon, Ex gall on *Eucalyptus deglupta* flower bud, CNC731379-731384 (4♂ 2♀, CNC).

Micropezidae

Calycopteryginae

•*Calycopteryx moseleyi* Eaton

Kerguelen Island, 6.v.1952, A. LaRue (1♀, USNM), 22–23.iii.1952, CNC731366 (1♂, CNC), 6.v.1952, CNC731364, CNC731365 (1♂ 1♀, CNC), [label data incorrect, listed as Canada] CNC731367 (1♀, CNC).

Calobatinae

•*Compsobata mima* (Hennig)

USA. Colorado: Mount Evans, Doolittle Ranch, 2987m, 23.vii.1961, B.H. Poole, CNC731343 (1♂, CNC), 3.viii.1961, CNC731344 (1♂, CNC), 9.vii.1961, W.R.M. Mason, CNC731342 (1♀, CNC), Mount Evans, Echo Lake, 182m, 11.viii.1961, C.H. Mann, CNC731346 (1♀, CNC), Nederland, 3 miles north, 2590m, marshy stream margin, 2.vii.1961, J.G. Chillcott, CNC731345 (1♀, CNC), State Bridge, near Bond, 2133m, 24–25.vi.1961, B.H. Poole, CNC731347 (1♂, CNC).

•*Cnodacophora nasoni* (Cresson)

CANADA. British Columbia: Lac La Hache, 15.vii.1973, H.J. Teskey, CNC731348, CNC731349 (1♂ 1♀, CNC), Lac Le Jeune, 27.vi.1973, H.J. Teskey, CNC731352 (1♀, CNC), Sawmill Lake, Telegraph Creek, 335m, 2.vii.1960, R. Pilfrey, *Carex*, grass, Equisetum beside lake, CNC731353 (1♂, CNC), Summit Lake, Alaska Highway, Mile 392, 1371m, 11–14.vii.1959, E.E. MacDougall, CNC731350 (1♀, CNC), 21.vii.1959, R.E. Leech, CNC731351 (1♂, CNC).

Eurybatinae

•*Metopochetus terminalis* (Walker)

AUSTRALIA. New South Wales: National Park, 10.x.1959, D.K. McAlpine, CNC731368 (2♂, CNC), 19.xi.1960, CNC731369 (2♀, CNC).

Micropezinae

•*Cryogonus formicarius* (Rondani)

CHILE. Santiago, El Canelo, 29.xi.1954, L.E. Pena, CNC731371, CNC731372 (1♂ 1♀, CNC), x.1952, CNC731373 (1♀, CNC), 23.xi.1954, CNC731370 (1♂, CNC).

•*Micropeza* sp.

BOLIVIA. Cochabamba: 26.i.1976, L.E. Pena, CNC731335-731339 (4♂ 1♀, CNC), Salancachi Sucre, 2600m, 23.ii.1976, L.E. Pena, CNC731340,CNC731341 (1♂ 1♀, CNC).

Taeniapterinae

•*Grallipeza mellea* (Williston)

ST. VINCENT. Majora, W.I., Malaise trap, summer 1972, CNC731360- 731362 (2♂ 1♀, CNC), Richmond Val., 25.viii.1978, Malaise trap, CNC731363 (1♀, CNC).

•*Taeniaptera tibialis* (Macquart)

BOLIVIA. Santa Cruz: xi.1969, in palm, CNC731358, CNC731359 (1♂ 1♀, CNC). **PERU**. Madre de Dios: Avispas, 400m, 10–20.ix.1962, L. Pena, CNC731357 (1♂, CNC), 20–30.ix.1962, CNC731354-731356 (3♀, CNC).

Neriidae

•*Chaetonerius* sp.

NIGERIA. Ibadan, 10.ix.1962, D.C. Eidt, Malaise trap, CNC731468 (1♀, CNC), 10.vii.1962, CNC731465, CNC731466 (1♂ 1♀, CNC), 9.ix.1962, CNC731467 (1♀, CNC), 9.viii.1962, CNC731464 (1♀, CNC).

•*Gymnonerius fuscus* (Wiedemann)

SRI LANKA. Central Province: Katugastota, Kahalla, 487m, 29.viii.1967, P.B. Karunaratne, CNC731460, CNC731461 (1♂ 1♀, CNC), 24.viii.1967, CNC731458 (1♀, CNC), Western Province: Kohuwala, 4m, 6.x.1966, P.B. Karunaratne, CNC731462, CNC731463 (1♂ 1♀, CNC), Nugegoda, 19.viii.1967, P.B. Karunaratne, CNC731459 (1♂, CNC).

•*Odontoloxozus longicornis* (Coquillett)

MEXICO. Durango: 5 miles west of Durango, 1981m, 11.viii.1964, J.F. McAlpine, CNC731455 (1♂, CNC), Sinaloa: Concordia, 274m, 7.vii.1964, W.R.M. Mason, CNC731457 (1♀, CNC). **USA.** Arizona: Tucson, 28.iii.1967, D.M. Wood, CNC731453, CNC731454 (1♂ 1♀, CNC), Texas: Chisos Basin, Big Bend National Park, 11.v.1959, Howden & Becker, CNC731456 (1♂, CNC).

•*Telostylinus* sp.

SRI LANKA. Western Province: Kohuwala, 4m, 6.x.1966, P.B. Karunaratne, CNC731449-731452 (3♂ 1♀, CNC).

Pseudopomyzidae

•*Eopseudopomyza kuehnei* Hennig

Baltic amber: 688-1 (1♀, CCHH), 688-6 (1♂, CCHH), 688-8 (1♀, CCHH), 692-2 (1♂, CCHH), 696-1 (1♂, CCHH), 696-3 (1♀, CCHH), 696-7 (1♂, CCHH).

•*Heloclusia imperfecta* Malloch

CHILE. Aysén: Puerto Cisnes, 44°45′0″S 72°40′0″W, 16–28.ii.1961, Pena, CNC731412 (1♂, CNC).

•*Latheticomyia infumata* Wheeler

BOLIVIA. La Paz: Chulumani, Apa Apa Reserve, 2000m, 16°21′15″S, 67°30′21″W, dung baits, 1.iv.2001, S.A. Marshall, debu00190446 (1♂, DEBU), La Paz: Caranavi, ca. 10km NW, road to ENTEL tower, 1400m, 15°46′35″S, 67°35′48″W, dung pans, 13.iv.2001, S.A. Marshall, debu00189595, debu00189991-00189993, debu00189996, debu00190019, debu00190029 (3♂ 4♀, DEBU). **COSTA RICA.** Puntarenas: Las Alturas Bio. Stn., 8°57′N, 82°58′W, tree fall, 2000m, 12.viii.1995, S.A. Marshall (1♀, DEBU), San José: Zurqui de Moravia, 10°3′N, 84°1′W, 1600m, vii.1992, P. Hanson, debu00241759 (2♀, DEBU). **VENEZUELA.** Mérida: La Azulita, 20km SE, ULA Biol. Res., La Carbonera, 2300m, podocarp forest, Malaise, 28.vi–3.viii.1989, S.&J. Peck, debu00152787, debu00152788 (2♀, DEBU).

•*Pseudopomyza* (*P.*) *antipoda* Harrison

NEW ZEALAND. Campbell Island, Air Nets, Beeman Camp, 27.i.1962, K.P. Rennell, CNC731413 (1♀, CNC).

• ***Pseudopomyza* (*Rhinopomyzella*) *nigrimana* (Hennig)**

JAMAICA. 1219m, 10.vii.1966, Howden & Becker, Hardwar Gap, CNC731447, CNC731448 (1♂ 1♀, CNC), 25.vii.1966, CNC731445, CNC731446 (1♂ 1♀, CNC).

Strongylophthalmyiidae

•***Nartshukia musiva* Shatalkin**

VIETNAM. Hanoi: 70 km NW Hanoi, Ba Vi, 400m, forest, 22.xi.1990, Narchuk (1♀holotype, ZMUM) [only photos examined].

•***Strongylophthalmyia angustipennis* Melander**

CANADA. Manitoba: Erickson, 1 mile south, 10 miles east, 29.vii.1984, W.E. Ralley, CNC731396 (1♂, CNC), New Brunswick: Kent County, Bouctouche, Irving Eco Centre & dunes, 46°31′54″N 64°41′32″W, 5.viii.2011, O. Lonsdale, CNC731395 (1♀, CNC), Ontario: S.S. Marie, Birchwood Park, mixed forest, 26.vii.1986, K.N. Barber, CNC731390 (1♂, CNC), solid maple log, 27.vii.1986, with mites, CNC731391 (1♂, CNC), mixed forest, 5.vii.1986, CNC731392 (1♂, CNC). **USA.** Arizona: 10 miles northwest of Flagstaff San Francisco Mountains, 2895m, spruce-fir-aspen meadow, 18–24.vii.1979, S.&J. Peck, Malaise trap, CNC731393, CNC731394 (2♀, CNC).

Tanypezidae

•***Neotanypeza claripennis* (Schiner)**

ECUADOR. Pichincha: Tandapi, 1300–1700m, 21.vi.1965, L. Pena, CNC731408 (1♂, CNC), Rio Palenque, 0°35′0″S 70°22′0″W, 150m, 22–26.ii.1976, G.E. Shewell, CNC731409,CNC731410 (1♂,1♀, CNC). **MEXICO**. Chiapas: 20 miles north of Huixtla, 3.vi.1969, W.R.M. Mason, CNC731407 (1♂, CNC), Veracruz: Catemaco, 335m, 16–18.vi.1969, W.R.M. Mason, CNC731411 (1♀, CNC).

•***Tanypeza longimana* Fallén**

CANADA. British Columbia: Kleanza Creek, 14.vii.1960, G.E. Shewell, CNC731402, CNC731403 (1♂ 1♀, CNC), Ontario: Iroquois Falls, *Populus-Picea* wood, rich undergrowth, 22.vi.1987, J.R. Vockeroth, CNC731406 (1♀, CNC), S. March, 8.viii.1962, J.R. Vockeroth, CNC731404 (1♂, CNC), Quebec: Gatineau County, Masham Township, 45°38′39.53″N 76°0′50.49″W, 15.vii.1974, D.M. Wood, CNC731401 (1♂, CNC), Kam County, Park Reserve, 8.vii.1957, G.E. Shewell, CNC731405 (1♀, CNC).

Genus incertae sedis

•***Cypselosomatites succini* Hennig**

Baltic amber: 1285-2 (1♂, CCHH), 1285-3 (1♂ 1♀, CCHH), 1285-4 (1♀, CCHH), 1763-1 (1♀, CCHH).

Outgroups

Agromyzidae

•***Agromyza albipennis* Meigen**

CANADA. Newfoundland & Labrador: St. John's, Agric. Exp. Sta., 12.vii.1967, J.F. McAlpine (1♂, CNC), 15.vii.1967 (1♀, CNC), Yukon: Dempster Highway, mi. 51, 18–27.vii.1973, G.&M. Wood (1♂, CNC). **USA**. Alaska: Umiat, 12.viii.1959, H. Madge (1♂, CNC).

Anthomyzidae

•***Stiphrosoma humerale* Roháček & Barber**

CANADA. British Columbia: Creston, 8.ix.1947, D.B. Waddell, CNC731481 (1♂ paratype, CNC), Vernon, 12.vii.1937, D.B. Waddell, WC, CNC731484 (1♂, CNC), Nova Scotia: Meat Cove, 47°1′35.56″N 60°33′34.42″W, among grass roots, 10.vii.1983, J.R. Vockeroth, CNC731483 (1♀ paratype, CNC). **USA**. North Carolina: Mount Mitchell, 12.viii.1957, L.A. Kelton, CNC731482 (1♀ paratype, CNC).

Aulacigastridae

•***Aulacigaster leucopeza* (Meigen)**

CANADA. Ontario: Ottawa, 10.v.1952, J.F. McAlpine, bleeding elm, CNC731508 (1♂, CNC), Ottawa 20.iv.1955, J.R. Vockeroth, CNC731511 (1♀, CNC). **USA.** Illinois: Champaign, 14.x.1956, J.F. McAlpine, at bleeding elm, CNC731509, CNC731510 (2♂, CNC).

Chyromyidae

•***Chyromya flava* (Linnaeus)**

CANADA. Ontario: Ottawa, 22.vi.1952, J.F. McAlpine, at robin dung on *Acer negundo*, CNC731494-731496 (2♂ 1♀, CNC), Quebec: Abbotsford, vi.1936, Shewell, CNC731497 (1♀, CNC).

Clusiidae

• *Sobarocephala latifrons* (Loew)

CANADA. New Brunswick: Kouchibouguac N.P., 46°49′59.01″N 64°55′11″W, 30.vii–8.viii.2013, O. Lonsdale, CNC316794 (1♀, CNC), Ontario: Hilton Falls Cons. Area, 43°30′22″N 79°57′47.01″W, 25.vii.2015, O. Lonsdale, CNC461956, CNC461981 (2♀, CNC), Milton, 7161 Appleby Line, 43°28′19″N 79°54′40″W, 23–25.vii.2015, O. Lonsdale, CNC461764 (1♀, CNC), Quebec: Wakefield, 45°38′25.99″N 75°55′45.24″W, 26.vi.1946, G.E. Shewell, CNC884094, CNC91448 (1♂ 1♀, CNC). **USA.** North Carolina: Highlands, Horse Cove Bog., 35°2′41.21″N 83°10′20.87″W, 914m, 18.vii.1957, J.G. Chillcott, CNC884089 (1♂, CNC).

Curtonotidae

•*Curtonotum helvum* (Loew)

CANADA. Manitoba: Bald Head Hills, 13 miles north of Glenboro, 9.viii.1958, R.L. Hurley, CNC731512-731515 (2♂ 2♀, CNC).

Lauxaniidae

•*Minettia flaveola* (Coquillett)

USA. California: Contra Costale, Marsh Creek, 29.x.1936, G.E. Bohart, CNC731516 (1♂, CNC), Eldorado County, fallen leaf, 1981m, 3 miles south of flowery meadow, 13.vii.1961, J.G. Chillcott, CNC731519 (1♀, CNC), Eldorado County, 2286m, 13.vii.1961, B.H. Poole, CNC731517 (1♀, CNC),Whittier, 26.vii.1923, A.J. Basinger, CNC731518 (1♀, CNC).

Lonchaeidae

•*Lonchaea polita* (Say)

CANADA. Ontario: Ottawa, 29.vii.1938, G.E. Shewell, CNC731498, CNC731499 (2♂, CNC). **USA.** Maryland: Laurel, 25.v.1965, Malaise trap, CNC731500, CNC731501 (2♀, CNC).

Neurochaetidae

•*Neurochaeta inversa* McAlpine

AUSTRALIA. New South Wales: Brinerville near Bellingen, iv.1977, H.G. Cogger & E. Cameron, CNC731418-731420 (1♂ 2♀ paratypes, CNC).

Odiniidae

•*Neoalticomerus seamansi* Shewell

CANADA. Alberta: Burmis, 17.xii.1963, *Pinus flexilis* (Log) Reared 62A2144 84, CNC731417 (1♀, CNC), Lethbridge, 49°41′36″N 112°50′30″W, 18.vii.1963, CNC731414, CNC731415 (1♂ 1♀, CNC), Ontario: Finch, 28.vii.1977, CNC731416 (1♂, CNC).

Opomyzidae

•*Geomyza tripunctata* Fallén

CANADA. Ontario: Ottawa, near Uplands Airport, 45°19′9.25″N 75°40′9.04″W, 22.v.1990, J.M. Cumming, CNC731490 (1♀, CNC), Ottawa, 45°25'28.02"N 75°42'4.50"W, damp second growth *Acer-Betula* wood, 22.vii.1991, J.R. Vockeroth, CNC731489 (1♀, CNC). **SPAIN**. San Sebastien, 7.vii.1960, J.R. Vockeroth, CNC731491-731493 (3♂, CNC).

Piophilidae

•*Piophila bipunctatus* (Fallén)

USA. New Mexico: Catron County, 6 miles south of Luna, 2438m, pond, pine forest, 9–14.vii.1979, S. & J. Peck, Malaise trap, CNC731421-731424 (2♂ 2♀, CNC).

Terminology & Homology

Terminology for external and female genitalic morphology follows that in Cumming & Wood (2017), the recent "standard" presented in the Manual of Afrotropical Diptera. Relevant external structures are labeled in Figs 1– 3, 5, 18, 242, 243 and 396–398. Terminology for male genitalic structures follows that in Cumming *et al.* (1995) and Sinclair *et al.* (2013); structures relevant for Diopsoidea and Nerioidea are discussed below due to their application below in the phylogenetic analysis and in the redefinition of family groups.

The identity of genitalic structures across much of Diptera has been thoroughly investigated and is now well-understood for "lower" Diptera in which many of the ancestral sclerites are still present and well-defined—see Cumming & Wood (2017) and the references therein. In contrast, sclerite homology of male Schizophora is less commonly addressed, making the consistent application of terms difficult for many families, especially since many Schizophora exhibit a reduction and fusion of structures that obscures their origin and identity. Broad taxonomic sampling across the schizophoran families here, however, has allowed for more confident character homologization to compliment the above sources.

The male abdomen is divided into the **preabdomen**, which is usually simple consists of segments 1–5 in male Cyclorrhapha, and the terminalia (or "postabdomen"), which is modified for copulation. The **terminalia** is segments 6–10 in male Cyclorrhapha and consists of the hypopygium (these are the genitalia proper or the "postgenital segments" of McAlpine (1981)) and the adjacent modified segments ("pregenital segments" of McAlpine (1981)) that comprise segments 6–8. Segments anterior to tergite 6 are also modified in some taxa such as Micropezidae, where sternite 5 is produced into a conspicuous "genital fork".

Tergite 6 is sometimes similar to tergite 5, but in some taxa, including many Diopsoidea and Nerioidea, it is reduced to absent, fused to sternite 8, or slightly enlarged. **Sternite 6** (S6) is ventral to ventral/left lateral; it may be simple, unattached to other sclerites and symmetrical to nearly symmetrical, but it is usually associated or fused to the posterior modified region and asymmetrical, further reflecting circumversion of the terminalia that is usually more dramatically exhibited in the 7th and 8th segments (see discussion in McAlpine (1981)). Segments 7 and 8 are reduced to a left lateral **sternite 7** (S7) and a left lateral to dorsal **sternite 8** (S8) ("pregenital sclerite" of Buck & Marshall (2006b)) that are fused with their suture sometimes inconspicuous. When the sternites form a complete ring around the abdomen, it may be referred to as an "annulus".

What cannot be established at the present is if S8 retains any vestige of tergite 7 (T7) or any other sclerites, as indisputable intermediate stages of fusion cannot be identified, although exemplars of almost all eremoneuran families have been examined in dissection or as illustrations in the literature where available. Ignorance of the homology of the pregenital sclerites of higher flies has led to widespread inconsistency in terminology, not just across publications, but within them. This includes several consecutive chapters of the *Manual of Nearctic Diptera*, where Steyskal's (1987b) interpretation recognizes the dorsal sclerite as S8, with T7 absent; Knutson (1987) interprets this sclerite as syntergosternite 8; Steyskal (1987c) recognizes syntergosternite 7+8; and Vockeroth (1987) accepts a separate T7 and T8, apparently following Griffiths (1972). Similar to Vockeroth (1987), additional sclerites in the lateral membrane anterior to the genitalia are usually interpreted as T7, but these may prove to be secondarily derived structures, as already appears to be the case for the structure identified as T7 in Lonsdale & Marshall (2008) based on subsequent phylogenetic study.

One pair of additional novel structures preceding the hypopygium are the **supernumerary sclerites** of Neriidae (Fig. 301) and Micropezidae (Fig. 335). These are sclerotized sections of the membrane anterior to S7.

T9 forms the **epandrium**, which in acalyptrates is rounded, dorsal and dome-shaped, enclosing the internal components, and ventrally meeting the surstyli and cerci. One pair of **cerci** flank the anus ventrally, and are setose, usually lobate and sometimes partially fused; a transverse band below the cerci in Somatiidae is derived from sclerotization of the membrane. There is usually one pair of **surstyli** ("outer telomere" of Feijen (1983)), articulated with, or fused to, the distolateral margin of the epandrium. The **subepandrial sclerite** (also called "sternite 10") is often plate-like and closely associated with the interior surface of the epandrium and surstylar base to form a point of articulation between these and remaining internal components of the genitalia, often via dorsolateral arms of the hypandrium; a lobe of the subepandrial sclerite was incorrectly termed "inner telomere" by Feijen (1983), and "cerci" by Taylor (2004). The cerci, surstyli, epandrium and the subepandrial sclerite are here referred to here as the "external components of the genitalia"; these form an outer containing capsule for the inner structures that have sometimes been termed the "hypandrial complex" (eg. Galinskaya & Ovtshinnikova (2015); Lonsdale & Marshall (2010)).

In cleared acalyptrate specimens, the internal components of the genitalia often appear as a closely knit complex of structures that are attached to, but distinct from, the external components. S9 forms the **hypandrium**, which is sometimes visible externally in part; in *Nothybus*, it is conspicuous and plate-like, presenting as part of the external components; setae are sometimes present, as in most Diopsoidea and Nerioidea. The hypandrium is U-shaped if the paired dorsolateral "arms" are separate, but it forms a ring if they are fused; some Psilidae have a medial portion of the hypandrium removed as a floating ventral plate, with the phallapodeme assuming its original position to form a “phallapodemic plate” (see Figs 38–39). The **phallapodeme** articulates with the phallus and is usually rod-like or carinate; the hypandrium may act against the phallapodeme as a fulcrum, or the two may be fused; the bifurcated base was termed the “phallapodemic arms” by Buck & Marshall (2006a, b). There is one pair of **postgonites** positioned adjacent to the base of the phallapodeme and basiphallus, being internal relative to the position of the pregonites; in acalyptrates it is usually band-like and sometimes setose. There is one pair of **pregonites** that are outer-lateral, usually lobate and setose, and sometimes articulating with or fused to the lateral margin of the hypandrium; it was called sclerite “x” by Griffiths (1972), “paramere” and “suspensor” by McAlpine & Shatalkin (1998), “aedaegal mantle” by Taylor (2004), “ventral arm of paramere” by McAlpine & Shatalkin (1998), and “postgonite” by Buck & Marshall (2006a, b) and Lonsdale (2013). In Nerioidea, the pregonite is unusual in being very long, narrow and fused to the inner margin of the hypandrium.

The components of the phallus are sometimes fused into a single structure or further subdivided, but it is usually ancestrally divided into the **basiphallus** and **distiphallus**. The basiphallus articulates with the phallapodeme and surrounds the ejaculatory duct before its insertion into the distiphallus; the basiphallus is less commonly segmented, but in some non-related families, such as Agromyzidae, it is divided into a basal ring (“phallophore”) and one pair of apical plates that usually flank, but do not fully surround the duct.

Cumming & Wood (2017) describe the epiphallus as a lobe produced from the surface of the basiphallus, but notes that the term has been applied to analogous structures elsewhere. This has recently been applied by Lonsdale (2013) to a structure that Cumming & Wood (2017) correctly define as the **phallic plate** (=sclerite “y” of Griffiths (1972) and ”caudal process of transandrium” of Roháček & Barber (2016)); this structure occurs in Nerioidea aside from Fergusoninidae, and is normally immobile and fused to the hypandrium, but is free and segmented in Tanypezidae and Strongylophthalmyiidae.

The single **ejaculatory apodeme** consists of a distal blade (often fan-shaped) with a short stem that connects to a subspherical **sperm pump**. A sclerotized band on the pump may predominate and/or extend onto the base of the duct.

Key to the family groups of Diopsoidea and Nerioidea

1 . Face well-sclerotized. Antenna usually deflexed to strongly elbowed with pedicel sometimes cap-like; if antenna porrect to slightly deflexed then either fore (Diopsidae; Fig. 144) or hind femur (Megamerinidae; Fig. 105) entirely swollen. Veins R_{2+3} and R_{4+5} subparallel to very slightly convergent apically (Fig. 397). Katepisternal seta absent and ocelli positioned near vertex. Anal cell comparable in size to subcostal cell, usually only slightly smaller (Fig. 398). 0–1 notopleural setae, or 2 setae displaced posteriorly (Somatiidae; Fig. 77). Pregonite various, but never band-like and fused to hypandrium; when present, postgonite separate from pregonite and flanking sides of basiphallus (Figs 108–109). Phallic plate never present. Male cercus usually resting in large perianal region bearing anus posteriorly (positioned apically in Megamerinidae). Phallus usually compact and complex with medial break, sometimes basal section longer and apparently straight (Megamerinidae; Fig. 108); sometimes long, coiled, unbroken (Nothybidae). Female segment 7 usually with short, discrete tergite and sternite (Fig. 62), but tergite and sternite sometimes fused (Figs 65, 69); partial weak connections between T7 and S7 seen in some such as Diopsidae, but with large membranous areas also (Fig. 178); terminalia visible externally at rest. Female sternite 10 never with internal process . . . . **DIOPSOIDEA** … 2

\- Face usually weakly sclerotized, at least ventromedially (sclerotized in Fergusoninidae). Antenna usually porrect to slightly deflexed (elbowed in Tanypezidae), not cap-like, and femora never entirely swollen (but sometimes with medial bulge). Veins R_{2+3} and R_{4+5} usually convergent (Fig. 412); if parallel (Fig. 411), then either katepisternal seta present (Fergusoninidae, Pseudopomyzidae) or ocelli shifted anteriorly towards center of frons (some Micropezidae, *Strongylophthalmyia*; Fig. 277). Anal cell usually much smaller than subcostal cell (size comparable in some Micropezidae, *Formicosepsis*; Fig. 414). 1–2 notopleural setae, never displaced posteriorly. Male cercus usually conspicuously distal to margin of epandrium (not Fergusoninidae, Tanypezidae, Strongylophthalmyiidae) (Figs 217, 218). Phallic plate usually present (absent in Fergusoninidae) (Fig. 222). Pregonite long, band-like, base fused to inner ventromedial margin of hypandrium; apex ending in similar, but smaller pregonite (Figs 221–222). Phallus usually elongate and narrow, sometimes rod-like, sometimes with swollen terminal structure. Female segment 7 fused into thickened oviscape that is longer than wide and contains telescoped terminalia at rest (Figs 223–224). Female sternite 10 usually with rod-like internal process (Fig. 228). . . . .**NERIOIDEA** … 12

2 . Either fore (Fig. 131) or hind femur swollen (Fig. 125) and with stout ventral spines. Abdomen often long and narrow basally, appearing petiolate (stouter in some Diopsidae). 3

\- All femora slender, without spines. Abdomen not petiolate. 8

3 . Halter knob brown (Figs 82–83). Dark portions of body with blue iridescence. Head with slight dorsoventral compression, buccal cavity deeply recessed posteroventrally (Fig. 85). Pedicel cap-like with deep dorsal seam forming triangular emargination. Frons width not more than ¼ width of head (Fig. 86). Inner vertical seta present. Narrow pit below anterior spiracle. Leg with swollen femur not bearing ridged tibia. Abdomen straight, sometimes strongly angled upwards when preserved. Male genitalia

strongly asymmetrical (Figs 89–97); phallus minute, not readily distinguishable amongst globular internal genitalia. . . . . **Gobryidae**

- Halter knob white. Without iridescence. Head not compressed, buccal cavity ventral to anteroventral. Pedicel various, but if cap-like and with dorsal seam, then seam not split (Syringogastridae; Fig. 126). Frons width more than ¼ head width. Inner vertical seta usually absent (present in some Megamerinidae). Pleuron smooth below anterior spiracle, without pit. Leg with swollen femur bearing tibia with one pair of ridges that sometimes fuse. Abdomen normally not held straight and angled upwards. Male genitalia apparently symmetrical, although phallus often twisted and asymmetrical; phallus longer, well-developed. 4

4 . Head with (Diopsinae; Fig. 145) or without eye stalks (Centrioncinae; Fig. 132). Fore femur swollen (Fig. 131) (hind femur uncommonly also swollen); femoral glands absent. Apical scutellar seta on long process (Fig. 130, arrow). Katatergite swollen, sometimes with spine. Vein bm-m absent (Figs 405–410). . . . . **Diopsidae** … 5

- Eyes never stalked. Hind femur swollen (Fig. 125); femoral glands opening in small ventral pits on at least fore and mid legs on posteroventral surface (Figs 103, 129). Apical scutellar seta either not raised (Megamerinidae) or on minute protuberance (Syringogastridae). Katatergite surface shallowly rounded. Vein bm-m present (Figs 403, 404).. 7

5 . Eyes normal, not displaced laterally on stalks (Figs 130–133). Face well-developed, flat. Arista pubescent. Katatergite rounded. Vein CuA relatively straight (Figs 405, 406). Vein CuA+CuP reaching wing margin. Mid tibia with one ventroapical seta. Surstylus narrow and trilobed, articulating with epandrium (Figs 155–157). Male cercus L-shaped. . . . . **Centrioncinae**

- Eyes displaced laterally on stalks (Figs 145, 151). Face medially compressed into sulcus. Arista glabrous. Katatergite with spine. Vein CuA strongly curved with posterodistal angle reduced (Figs 407–410). Vein CuA+CuP not reaching wing margin. Mid tibia with two ventroapical setae. Surstylus shape not as above, fused to epandrium (Figs 160–162, 169–171). Male cercus linear. . . . . **Diopsinae** … 6

6 . Eye stalks always longer than width of remaining medial section of frons (Figs 149–152). Alula absent (Figs 408–410). CuA+CuP absent past anal cell. Sometimes either genovertical plate developed ventrally into “teeth”, or spine present over wing base. . . . . **Diopsini**

- Eye stalks sometimes reduced, narrower than or comparable to width of remaining medial section of frons (Figs 143–147). Alula reduced to well-developed (Fig. 407). CuA+CuP apically developed. Genovertical plate without “teeth”; spine never present over wing base. . . . . **Sphyracephalini**

7 . Large-bodied, length usually exceeding 8 mm (Figs 98–105). Black with antenna, face and most of legs pale. Antenna porrect, pedicel linear, without seam; arista short plumose to pubescent. Frons projecting and tapering anteriorly with one pair of oblique lateromedial folds; frons with one pair of dark velvety patches lateromedially and with single silvery patch behind ocelli. Face compressed into medial carina. Inner vertical present. One fronto-orbital seta sometimes present. Apical scutellar seta not raised. Precoxal bridge absent. Subcosta complete (Fig. 403). Wing faintly infuscated. Ridges on hind tibia fused. Only tergites 1–2 fused. Female terminalia elongate, telescoping, directed apically (Figs 119–122). Male sternite 8 and epandrium elongate; cercus arising apically from epandrium (Figs 110–113). Hypandrium and phallus narrow, elongate, with apex of phallus flagellate (Figs 108–109, 116–117). . . . . **Megamerinidae**

- Smaller-bodied, length 4–6 mm (Figs 124–129). Colour various, usually yellow to brown. Antenna elbowed, pedicel cap-like and with seam; arista plumose. Frons flat, not folded, without velvety patches. Face flat, well-developed. Inner vertical absent. Fronto-orbital setae absent. Apical scutellar seta on minute protuberance. Precoxal bridge present. Subcosta incomplete (Fig. 404). Wing patterned. Ridges on hind tibia separate. Tergites 1–3(4) fused. Female terminalia very short, shielded ventrally under apex of abdomen (Figs 140–141). Male sternite 8 band-like, epandrium small; cercus sunken deep within perianal region on epandrium (Figs 134–136). Hypandrium and phallus broad, not elongate, phallus thicker, sometimes short, minutely spinulose (Figs 138–139).. . . . . **Syringogastridae**

8 . Frons with three blackish velvety patches. Subscutellum very large, reaching or exceeding apex of scutellum. Thorax with presutural scutum elongate, head displaced from base of fore coxae. Precoxal bridge present, very large; postmetacoxal bridge absent. Single notopleural seta on rounded setulose tubercle. Costa unbroken. Basal cells very small, restricted to very base of wing; radial and medial veins entirely straight and divergent along length; cell bm open anterodistally.. . . . . **Nothybidae**

- Frons without velvety patches. Subscutellum small. Thorax not elongate. Precoxal bridge absent; postmetacoxal bridge present (Somatiidae, Chylizinae) or absent. Notopleural seta(e) not raised on process. Costa with subcostal break. Basal cells well-developed, exceeding basal ¼ of wing; radial and medial veins not as above, at least partially convergent or bent at some point along length; cell bm closed. 9

9 . Very stout, 3.5–5.2mm long, with broad, domed, downturned abdomen; black and bright yellow (Figs 71–77). Face flat, slightly concave. Ocelli at vertex, without intervening space. Arista bipectinate. Scutellum swollen with minute tubercles at base of setae. Subcosta complete, well-developed along length; vein R_1 not arched (Fig. 401). One vertical sometimes present; fronto-orbitals absent; postocellars convergent; vibrissa small; two notopleurals closely spaced posteriorly; anepisternal present; mid tibia with 3 distoventral setae. No grooves extending from anterior spiracle. Tergites 1 and 2 with suture complete, raised and with minute crenulations along posteromedial surface (Fig. 77, arrow). Male and female terminalia concealed under apex of abdomen. Female tergite and sternite 7 fused, segments posterior to segment 7 external (Fig. 65). Surstyli asymmetrical (Fig. 80). Phallus long and ribbon-like. . . . . **Somatiidae**

- Elongate, 3–12mm long, with abdomen long and often narrow; colour variable, usually not as above (Figs 1–18, 47–48). Face flat, often with sharply angled ventral plate marked with transverse striations (Fig. 3, arrow). Setose space present between ocelli and vertex. Arista pubescent to short plumose. Scutellum neither swollen nor tuberculate. Subcosta continuing to costa at near right angle as hyaline weakening in membrane; vein R_1 slightly (Fig. 395) to broadly arched apically (Figs 396–398). Two or three vertical setae present; one or two fronto-orbitals sometimes present; postocellars divergent when present; vibrissa absent; only 1 notopleural posteriorly; anepisternal absent; mid tibia with one or two ventroapical setae. Lateral margins of anterior spiracle confluent with two grooves that sometimes coalesce in a pit. Tergites 1 and 2 fused, but suture not as above. Male and female terminalia pointed distally, not concealed. Female tergite and sternite 7 separate, containing posterior telescoped segments (Figs 41–43). Surstyli symmetrical when present (Figs 19–22, 28–29). Phallus small, rod-like (Fig. 38) to globular (Figs 25, 31). . . . . **Psilidae** … 10

10 . Katatergite strongly bulging (Fig. 5). Postmetacoxal bridge present. Cell r1 past vein sc more strongly bulging, widest slightly after base or only tapering apically (Fig. 396). Anal cell much shorter than cell bm. Hind femur sometimes with small, microtrichose ovate pit ventroapically. Usually three pairs of vertical setae, uncommonly two. Usually two or three pairs of scutellar setae. Back of head strongly concave dorsally, usually forming a sharp angle with vertex. **Chylizinae**

\- Katatergite slightly swollen (Fig. 17). Postmetacoxal bridge absent. Cell r1 past vein sc widest at base (Figs 395, 397, 398), only shallowly bulging. Anal cell only slightly shorter than cell bm. Hind femur never with ventroapical pit, but sometimes with patch of short pile (most *Loxocera*, Psilinae). Usually two pairs of vertical setae, uncommonly three. One or two pairs of scutellar setae. Back of head gently curved, slightly swollen to slightly concave. 11

11 . Head more ovate in lateral view (Fig. 13). Postgena with short, dense patch of setulae (difficult to see without oblique light). Anal lobe of wing reduced (Fig. 395). Surstylus present (Figs 19–22). . . . . **Belobackenbardiinae**

\- Face strongly receding anteroventrally, making head subtriangular in lateral view (Figs 17–18). Postgena with regular, sparse setulae. Anal lobe of wing developed (Figs 397–398). Surstylus absent (Figs 33–36). . . . . **Psilinae**

12 . Vibrissa present (Fig. 242). Small-bodied, 1.5–5.5mm, but usually less than 3.0mm. Subcostal vein incomplete (Fig. 415). Fore femur with posteroventral spine-like setae (Figs 194, 206, 207, 237, 241); hind femur with large distal seta. Epandrium usually with one pair of outstanding dorsal setae (Figs 195, 217, 244); sternite 8 sometimes with one pair of similar setae (Figs 216–217). 13

\- Vibrissa absent. Body usually longer than 5.0mm, but sometimes as small as 2.0mm (some Strongylophthalmyiidae). Subcostal vein incomplete (Strongylophthalmyiidae; Fig. 418) or complete (Fig. 411). Femoral setae not as above. Epandrium and sternite 8 without outstanding setae. 15

13 . Legs very short; mostly bright yellow with limited dark pattern (Figs 191–194). Head relatively short, anteriorly flattened; lunule large, exposed; face fully sclerotized. Postocellar setae immediately adjacent to ocellar tubercle. Presutural acrostical setae absent; scapular setae absent. Anepisternal seta present. Greater ampulla absent. **Fergusoninidae**

\- Legs well-developed, sometimes slender; body darkly coloured. Head not flattened anteriorly, lunule concealed or barely visible; face membranous, at least ventromedially. Postocellar setae distant from ocelli and laterally displaced. Presutural acrostical and/or scapular setae sometimes present (Fig. 243). Anepisternal seta absent. Greater ampulla present. 14

14 . Interfrontal seta present (Fig. 209), sometimes minute to absent. Three fronto-orbitals, proclinate with posterior seta reclinate (Figs 205–215). Postocellar setae divergent. 0–6 pairs of acrostichal setae, with at least 1 presutural pair when present. Scapular setae absent. One or two scutellar setae with apical pair on tuberculate swelling (sometimes indistinct). If katepisternal seta present, then small and setula-like. Katepisternum bulging with dorsal margin sharply angled inwards (Figs 206, 215). Fore femur with row of stout anteroventral spines that may also appear on mid and hind femora (Fig. 207). Fore femur with one outstanding posteroventral seta subapically. Mid tibia with medial setae. Veins R$_{4+5}$ and M$_1$ convergent (Figs 413–414). Ultimate section of vein M$_4$ usually absent (very short if present) and posterodistal corner of cell dm rounded (apex of M$_4$ bowed if more angulate). Outstanding seta always present on male sternite 8 and epandrium (Figs 216–218). . . . . **Cypselosomatidae**

\- Interfrontal seta absent. Usually three fronto-orbitals (sometimes two or four), relcinate to lateroclinate (Figs 233–243). Postocellar setae convergent. Acrostichal setae absent, present in one or two pairs, or present in single anteromedial series that may extend presuturally. Scapular setae sometimes present (absent to reduced in *Pseudopomyza*). Two to five scutellars, tubercles absent. One or two well-developed katepisternal setae, uncommonly none. Katepisternum surface flatter than above. Femora without spines. Fore femur with series of strong posteroventral setae (Fig. 237). Mid tibia almost always without medial setae. Veins R$_{4+5}$ and M$_1$ subparallel (Figs 415–416). Ultimate section of vein M$_4$ present and posterodistal corner of cell dm angulate. Outstanding seta sometimes absent from male sternite 8 (Fig. 244) and sometimes also epandrium. . . . . . . **Pseudopomyzidae**

15 . Occiput with long, dense pile. Precoxal bridge present (Fig. 279). Presutural intra-alar sometimes present (Figs 257–258). Anepisternal usually present (absent in *Nartshukia*; Fig. 262). Katepisternal absent. Calypter lobate. Halter stalk with series of setulae that may be minute, pale and inconspicuous (Strongylophthalmyiidae). Surstylus fused to epandrium (Fig. 281). Male cercus sunken past distal margin of epandrium. Male supernumerary sclerites absent. Two spermathecae (Fig. 272) with one sometimes reduced (Fig. 290). 16

\- Occiput with normal, sparse setulae; sometimes longer and denser (eg. Calobatinae), but not as above. Precoxal bridge usually absent (present in some Neriidae). Presutural intra-alar absent (Figs 316–317, 326–327, 329). Anepisternal absent. Katepisternal usually present (absent in some Neriidae). Calypter linear. Halter stalk bare. Surstylus articulating with epandrium (Figs 341–343) or absent (Figs 349–352). Male cercus emerging from distal margin of epandrium. Male supernumerary sclerites present, tucked underneath epandrium (Figs 301, 335). Three or four spermathecae (Figs 311, 375, 394). 17

16 . Head globose and approximately as high as long (Figs 262, 274–280). Frons shining, without raised disc behind tubercle. Clypeus band-like. Occiput shining with pile yellow. Outer vertical seta present. Lateral scutellar seta absent. Thorax long and narrow, without silvery tomentose stripes. Subcosta incomplete. Subcostal break present. Vein R$_1$ bare. Veins R$_{4+5}$ and M$_1$ usually parallel apically (Fig. 418) but convergent in *Nartshukia* (Fig. 417). Vein CuA slightly bent. Halter stalk with basal setulae that are pale and minute. Greater ampulla absent. Tergite 2 without outstanding lateral setae. Sternite 2 entire (Fig. 286). Male sternite 8 not tomentose. Epandrium and surstylus without setulae, only strong setae, and surface with "pebbled" texture (Figs 281–283). Female tergite and sternite 7 fused, with sternite 7 narrowly divided (Fig. 286) (unknown for *Nartshukia*). . . . . **Strongylophthalmyiidae**

\- Head higher than long and back of head flat (Figs 257–261). Frons extensively tomentose and velvety with tomentose disk-like shelf behind tubercle. Anterior margin of clypeus broad. Occiput tomentose with pile white. Outer vertical seta absent. Lateral scutellar seta present. Thorax stout and broad with silvery tomentose stripes. Subcosta complete (Figs 419–420). Subcostal break absent. Vein R$_1$ setulose. Veins R$_{4+5}$ and M$_1$ strongly converging to apex. Vein CuA strongly curved. Halter stalk with dark setulae. Greater ampulla present. Tergite 2 with long, stout anterolateral setae. Sternite 2 usually divided transversely near anterior margin. Male sternite 8 silvery tomentose (Figs 263–265). Epandrium and surstylus with setulae and not textured as above. Female tergite and sternite 7 separate and strongly divided longitudinally (Figs 269–270). . . . . Tanypezidae

17 . Antenna porrect, straight, usually long; arista apical to dorsoapical; pedicel large with pointed extension on inner surface that extends into first flagellomere (Figs 291–297). Dorsum of face and frons projecting anteriorly, and at least one fronto-orbital seta present. Setae and setulae reduced, with remaining setae often dark, short, erect and sometimes spinose (at least on fore femur and coxa). Postocellar setae convergent. Vibrissa small if present. One katepisternal present or absent. Scutellum slightly convex to flat. Mid coxae approximate. Setulae on legs in straight rows that are sometimes on raised ridges. Vein CuA rounded (Fig. 412). Alula and anal lobe well-developed or slightly reduced. Male sternite 5 simple, plate-like (Fig. 298). Phallus never with bulb (Figs 303–304). . . . . Neriidae

\- Antenna porrect to slightly downturned or elbowed, never held straight out; arista dorsobasal to dorsomedial; pedicel small, distal margin sometimes with shallow angle, but never as above (Figs 312–333). If dorsum of face and frons projecting anteriorly, then fronto-orbital setae absent (Micropezinae; Fig. 321)). Setae and setulae normal, never spinose. Postocellar setae usually divergent when present, uncommonly convergent. Vibrissa absent. At least 1–3 katepisternals present. Scutellum rounded (reduced in apterous species). Mid coxae strongly separated by intervening process of mesosternum. Setulae on legs irregular in distribution. Vein CuA straight (Figs 421–422). Alula and anal lobe reduced. Male sternite 5 usually with forked process (Figs 334, 336). Phallus often with swollen bulb (Fig. 340). . . . . Micropezidae … 18

18 . Mid and hind tibiae with setae restricted to apex if present. Hind tarsus more than half length of hind tibia. Postocellar setae usually absent (Figs 312–316, 330–333).. 19

\- Mid and hind tibiae with series of outstanding dorsal setae along length (Fig. 323). Hind tarsus less than half length of hind tibia. Postocellar setae usually present (Fig. 325) (absent some Taeniapterinae). 20

19 . First flagellomere longer than wide and longer than pedicel (Figs 312–316). Eye large; gena narrow and band-like. Fore coxae contiguous at rest. Scutellum, wing and halter well-developed. Setae and setulae large and obvious. Body pruinose with glabrous regions, and with contrasting bright and dark sclerites. Two postsutural supra-alar setae. Male genital fork large, well-developed, protruding from surface of abdomen (Figs 313, 334, 336).. . . . . **Calobatinae**

\- First flagellomere small and rounded, as long as pedicel (Figs 328–333). Eye reduced; gena more than half height of eye. Fore coxae not touching. Scutellum, wing and halter vestigial. Setae and setulae highly reduced. Body dull pruinose, and dark brown with orange regions. Postsutural supra-alar setae absent. Male genital fork reduced, flattened, not raised from surface of abdomen (Fig. 367). . . . . **Calycopteryginae**

20 . Fronto-orbital setae absent (Figs 317–321). Frons with shining ridge directed between bases of vertical setae or towards outer vertical. Face compressed into medial sulcus. Head elongate, dorsum of face and frons projecting anteriorly, postgena and occiput produced as broad space behind eye (seen laterally). Cells bm and dm confluent (vein bm-m absent) (Fig. 422). Distal vein of anal cell (CuA) perpendicular to anal vein CuA+CuP. Anterodorsal region of pleuron more extensively fused to scutum, strongly curving inwards, largely obliterating postpronotum and making anterior spiracle more visible dorsally. Anteromedial margin of pronotum forming wide, slightly raised, transverse collar. Fore coxa length twice width. Tibiae never grooved. Body generally dark brown to black with some banding on legs. . . . . **Micropezinae**

\- Frontal-orbital setae present (only absent in the stalk-eyed *Anaeropsis*). Frons without shining ridge as above. Face flat. Head usually globular to high, not elongated as above, and with space behind eye usually an band-like (viewed laterally). Cells bm and dm usually divided by vein bm-m, which is uncommonly atrophied. Distal vein of anal cell (CuA) at least slightly angled (not perfectly perpendicular to anal vein CuA+CuP), but sometimes very conspicuously angled so as to produce a long, triangular anal cell (some Taeniapterinae). Pleuron and scutum distinct, postpronotum modestly developed, anterior spiracle laterally positioned. Anterior margin of pronotum not developed as above. Fore coxa length exceeding twice width. One or more tibiae sometimes grooved. Colour various, usually paler or more strongly patterned than above. 21

21 . Ocelli usually displaced anteriorly towards center of frons (Fig. 325). Katepisternum with many setae arranged into one or two vertical “fans “ (Figs 323, 326). Subscutellum strongly reduced. Postmetacoxal bridge absent. Anal cell sometimes short but sometimes very elongate and subtriangular, longer than remaining apical section of CuA+CuP. Surstylus absent, epandrium sometimes slightly to strongly compressed laterally (Figs 349–352). . . . . **Taeniapterinae**

\- Ocelli close to vertex. Katepisternum with five or fewer setae that may or may not be arranged in a vertical series (Fig. 327). Subscutellum developed, sometimes enlarged. Postmetacoxal bridge sometimes present. Anal cell neither elongate nor strongly angled. Surstylus present, epandrium broadly rounded (Figs 356–357).. . . . . **Eurybatinae** … 22

22 . Back of head without tubercle. Hind tibia with bare dorsoapical region flanked on one side by series of small, suberect setae. Axillary fascicle absent. . . . . **Eurybatini**

\- Back of head with bulging tubercle above foramen. Hind tibia with dorsoapical region evenly setulose. Axillary fascicle present in winged species (*Badisis* apterous).. . . . . **Metopochetini**

Family Descriptions—Superfamily Diopsoidea

Diopsidae Billberg, 1820

(Figs 143–190, 405–410)

Type genus: *Diopsis* Linnaeus 1775: 5, by Billberg, 1820: 115 [as "Diopsides"]. **Type species of genus:** *Diopsis ichneumonea* Linnaeus, 1775: 5, by monotypy.

At least 170 species in 13 genera are known (Meier & Hilger, 2000; Meier & Baker, 2002). Most are restricted to the Afrotropical Region, but many also occur in the Oriental Region. No species are found in the Neotropics, and very few occur in the Palaearctic and Australian Regions (Papp, Földvári & Paulovics, 1997; Feijen, 1989). The two New World species, found in North America east of the Rockies, are treated in Feijen (1989), who also provides a synopsis of the world genera. Revisions of genera are ongoing, with several new species recently described (eg. Feijen & Feijen, 2012, 2013).

Centrioncinae consists of the single genus *Centrioncus*, containing 22 described species from montane afrotropical forests. Due to their characteristic distribution, Feijen adopted the common name of "Afromontane forest flies". Species include Speiser's 1910 genotype (*C. prodiopsis* Speiser), one species more recently described by DeMeyer (2004), and 20 species described by Feijen (1983) in his thorough revision of the "Centrionicidae". Feijen (1983) also included in this family his new genus *Teloglabrus*, which McAlpine (1997b) recommended treating as a junior synonym of *Centrioncus*.

While the subfamily is largely defined on genitalic features (Feijen, 1983) impractical for diagnosis, it is readily characterized by having many of the synapomorphies of the Diopsidae with the conspicuous absence of eye stalks (Figs 130–133): a scutellum with long apical spines (Fig. 130, arrow), a bulbous katatergite (but without a spine), tarsi with dark "sawlines" lengthwise along the tarsomeres (Fig. 131), absence of bm-m (Fig. 405), a porrect antenna, raptorial fore legs, and only one outer vertical and one fronto-orbital seta.

The readily identifiable **Diopsinae** includes *Prospyracephala* and the tribes Diopsini and Sphyracephalini. It was defined by Hennig (1965) as having eye stalks with the antennae approximate to the separated eye margins (Figs 143–152), one spine on a bulbous katatergite, a glabrous arista, an elongate cell *cu*a (except *Prosphyracephala*) (Figs 407–410), veins M_4 and CuA+CuP not extending to the wing margin, absence of the supra-alar and notopleural setae, loss of the tubercles on the hind femur, and usually an additonal subapical seta on the mid tibia. *Prospyracephala* is known from *P. breviata* (Meunier) from Baltic amber; *P. succini* (Loew), recovered from early Oligocene Baltic, Miocene Saxon and Eocene Rovno amber (Feijen, 1989; Schumann, 1994; Perkovsky *et al.*, 2015); *P. kerneggeri* Kotrba, from Baltic amber (Kotrba, 2009); the tentatively placed *P. rubiensis* Lewis, from shale deposits in Montana (late Oligocene); and one unnamed specimen from oil-shale sediments in France (lower Oligocene) (Lutz, 1985). The only other known fossil Diopsidae are several specimens of *Diopsis* listed in Handlirch (1906–1908), and while Hennig (1965) believed these to also likely represent *Prospyracephala*, this is yet to be verified.

The tribe **Sphyracephalini** consists largely of *Sphyracephala* species (Figs 143–147, 160–168), which unlike most other Diopsinae, has relatively short eye stalks, and extends from the Old World tropics and subtropics into the north temperate Regions, including two species in North America (Feijen, 1989). Clarification of tribal boundaries was provided by Kotrba & Balke (2006), who found strong support for inclusion of the malagasy *Cladodiopsis* Séguy in Sphyracephalini using morphologial and molecular data.

The **Diopsini** is a diverse tribe encompassing most diopsid genera. It is defined by reduced segmentation of the arista, absence of CuA+CuP past cell *cu*a (Figs 408–410), fusion of tergites 3 and sometimes 4 to syntergite 1+2, a reduced male S8 (Fig. 170), reduced scutellar setae, reduction of the alula and anal lobe, and often much longer eye stalks (Figs 148–152) (Meier & Hilger, 2000; Kotrba, 2004). Ten genera were recognized in Feijen (1989), but Meier & Baker (2002) synonymized (or reinstated the previous synonymies of) *Cyrtodiopsis* with *Teleopsis*, and *Trichodiopsis* and *Chaetodiopsis* with *Diasemopsis*. Additional studies will very likely produce additional generic redefinitions.

Treatments of Diopsidae in the literature include regional catalogues by Sabrosky (1965a), Feijen (1989) [Nearctic], Hennig (1941c) [Palaearctic], Steyskal (1977f) [Oriental], Evenhuis (1989e) [Australian] and Cogan & Shillito (1980) [Afrotropics]. A World catalogue was developed by Steyskal (1972). Other major taxonomic works include Shillito (1940), who revised the family at the genus level, Shillito (1971), who reviewed the diopsid genera and attempted a reconstruction of phylogeny, and Feijen (1984, 1989), who listed the diopsoid genera and reviewed the family (*sensu* Feijen (1983)). Feijen (1989) also presents the most recent genus key, as well as an extensive synopsis of morphology and a synopsis of the group's treatment in the literature. Shillito (1960, 1976) assembled a bibliography of major works on the family. A more recent summary of studies in taxonomy and organismal biology is provided in Meier & Hilger (2000) and Meier & Baker (2002), who also developed diopsid phylogenetics considerably via numerical analyses. Phylogenetics of the family was additionally treated in Baker *et al.* (2001), Baker & Wilkinson (2001), Kotrba (2004) and Kotrba & Balke (2006). Kotrba (1995) investigated the female terminalia of select Diopsini and provided a summary of similar works on the subject.

Biology. Species are often found in rather wet, humid and shady areas, often on low foliage, especially near streams, with the adults feeding on liquefied plant and animal material, and larvae being mostly saprophagous or facultatively phytophagous, associating with plants with existing primary damage (Oosterbroek, 1998, Meier & Hilger, 2000; Marshall, 2012). A few are obligate phytophages, including those species of agricultural relevance (Meier & Hilger, 2000), and while several African grass-feeding species are regularly found stem-boring on crops such as sugar cane and maize, only the rice-feeding *Diopsis longicornis* Macquart is known to be pestiferous (Feijen, 1989).

A summary of feeding strategies is presented in Ferrar (1987), a discussion of agricultural impact and life history is provided in Feijen (1989), and literature pertaining to host use and life history are summarized in Shillito (1960, 1974). Adults are weak fliers and sometimes known to be gregarious (Feijen, 1989).

The unusual eye stalks of this family has made it an attractive subject for ethologists and evolutionary biologists. A thorough summary of varied aspects of diopsid behaviour was provided in Feijen (1989), including descriptions of agonistic, precopulatory and copulatory behaviour, as well as the defence of territories through display and sometimes physical combat. Much attention has been given to the origin of increased eye span, male agonistic behaviour, female sexual selection and inherited fitness. As eye stalk length can be correlated to fitness, they provide exaggerated intraspecific signals linked to success in female sexual selection and better assessment of body size between rival males; this signalling is useful in resolving male contests because both time and the physical investment required for battle are costly (Panhuis & Wilkinson, 1999), although the degree to which this is true remains uncertain (Brandt & Swallow, 2009). While eyespan is usually directly correlated to body length, dimorphism—wherein male eyespan increases geometrically with body length (Burkhardt *et al*., 1994)—has evolved at least four times in the family (Baker & Wilkinson, 2001).

Immature stages. The egg, larval instars and puparia of Sphyracephalini and Diopsini are described and illustrated in Feijen (1989). Descriptions of immature stages are also documented in Descamps (1957), and eggs are thoroughly documented for most genera in Meier & Hilger (2000).

Adult Diagnosis. Stout-bodied and often heavily sclerotized flies, with representatives of the Diopsinae characterized by eye stalks in both sexes, which unlike other stalk-eyed flies (some Tephritidae, Drosophilidae, etc.), have the antenna removed to the end of the stalks near the eye margin (Figs 145, 151). Body length 3.0–12.0mm; eye span 1.5–17.0mm. Antenna porrect; pedicel without dorsal seam; arista inserted dorsoapically (not dorsobasally) and with vestiture very short to absent. Vibrissa, postocellar and inner vertical setae absent; ocellar seta minute and setula-like if present; one fronto-orbital. Face well-sclerotized; Diopsinae with face almost to entirely absent, compressed into facial sulcus (Fig. 145). Apical scutellar seta on long, thin process (arrow, Fig. 130), lateral seta absent; katatergite with bulging "callus" produced apically into long spine in Diopsinae. Precoxal bridge present to absent; postmetacoxal bridge present. Fore coxa lengthened and fore femur enlarged with ventral rows of spines (Figs 131, 144); hind femur slender with posteroventral row of spines; tarsal "sawlines" present on mid and hind legs (see Fig. 131; McAlpine (1997b: fig. 40)). Vein bm-m absent; costa unbroken; subcosta complete (Figs 405–410).

Adult Definition. Colour black to brown or reddish, sometimes with yellow and/or white patches (Figs 130–152). Body length 3.0–12.0mm; eye span 1.5–17.0mm (greater in males if species sexually dimorphic).

Chaetotaxy: 1 outer vertical; 0–1 fronto-orbital (sometimes reduced when present) [=inner vertical in Diopsinae of Feijen (1983, 1989)]; *Diopsina draconigena* Feijen apparently with small orbital and 4 pairs of fronto-orbitals [not examined, possibly enlarged setulae]; minute setula-like ocellar sometimes present; 0 postocellar; pedicel in Diopsinae with apical ring of setulae (sometimes reduced) including one larger dorsal and ventral setula. 0 anterior notopleural, 0–1 posterior notopleural; 0–1 posterior supra-alar on shallow to pronounced supra-alar carina (slightly inset from level of notopleural in Centrioncinae, more medially displaced in Diopsinae); 1 posterior intra-alar; 0–1 postsutural dorsocentral; 0–1 lateral scutellar, 0–1 apical scutellar; 0 setae on pleuron. Body usually covered with minute setulae, sometimes providing a grey or silvery sheen; Diopsinae often also with much longer setulae (sparse to dense) across body, appearing as thin and often paler setae, and/or with patches of body surface partially to entirely glabrous, or with glabrous pattern; *Diopsis* and *Eurydiopsis* sometimes with thoracic setae absent excluding apical scutellar and intra-alar. Mid tibia with relatively small ventral subapical seta that is stronger and duplicated in Diopsinae.

Head. Antenna porrect, relatively short with first flagellomere subovate; pedicel without dorsal seam; arista inserted dorsoapically to dorsomedially (not dorsobasally); arista pubescent (Centrioncinae) to glabrous (Diopsinae). Fronto-orbital sometimes arising from tubercle. Face well-sclerotized; Diopsinae with face almost entirely absent, compressed into facial sulcus (sometimes obliterated) resulting from meeting of genal/parafacial plates along midline (Fig. 145) (small portion of face sometimes evident dorsally where sulcus meets ptilinal suture); Diopsini sometimes with genovertical plate produced into anteroventral "peristomal teeth". Buccal cavity relatively broad. Ptilinum well-developed. Eye with anteromedial ommatidia enlarged. Diopsinae with eyes and antennae removed to ends of stalks that may exceed body length, with sexual dimorphism evident in some species. Ocelli slightly raised, appearing closer to centre of frons in species with eye stalks where frons is broadly rounded. Clypeus broadly rounded and sometimes projecting; palpus slender and subcylindrical to slightly compressed laterally; labium with sides rounded, with broad distal emargination and with one pair of pronounced setae. Back of head with small process above foramen magnum that in Diopsinae is slightly elongate and dorsoapically produced, articulating with bulbous dorsal concavity on pronotal collar (Fig. 147).

Thorax. Stout, well sclerotized and convex. Proepisternum shifted dorsally, displacing postpronotum posteriorly. Scutum narrowing anteriorly and sharply narrowing posteriorly, particularly in Diopsinae, leaving margin above wing base pronounced; vertical posterolateral section of scutum beside scutellum sometimes enlarged, displacing disc of scutum anteriorly. Anteromedial section of pronotum produced as pronotal collar; forming slight dorsomedial extension in Centrioncinae (Figs 130–131); larger in Diopsinae, incorporating some or all of proepisternum, sometimes very pronounced and elongate, with proepisterna enlarged and meeting, or nearly meeting dorsomedially (Figs 149–150). Precoxal bridge present or absent; some Diopsinae with membrane surrounding prosternum slightly sclerotized or forming semi-discrete plate; prosternum setose; postmetacoxal bridge present. Transverse suture (visible on lateral 1/3 of scutum) and margin of postpronotum clearly delimited by glabrous groove. Scutum with thin carina over wing base (bearing seta in Centrioncinae) that is produced into spine medially in some Diopsini. Anepisternum with vertical posterodorsal and ventromedial grooves that sometimes meet medially; Diopsinae with katepisternum and meron fused with suture sometimes reduced to almost entirely absent; coxopleural streak absent. Greater ampulla broad, shallow. Katatergite with bulging "callus" sometimes produced as a spine. Metasternum not extending between hind coxae and not attached to postmetacoxal bridge, which is straight along ventral margin. Metathorax with cylindrical extension meeting abdomen. Scutellum broadly attached to scutum with reinforced dorsal and ventral ridges extending laterally along scutal margin; apical scutellar setae on spines that are narrow and subcylindrical (Centrioncinae, Sphyracephalini and some Diopsini) to elongate conical (some Diopsini, with setae sometimes absent).

Wing. (Figs 405–410) Wing relatively narrow, with anal lobe and alula sometimes reduced or absent (Diopsinae), wing rarely reduced; clear to variably infuscated or otherwise patterned with spots or bands. Vein bm-m absent; costa unbroken, extending to M_1; subcosta complete. Veins R_{4+5} and M_1 subparallel to slightly converging. Vein CuA+CuP reaching wing margin (Centrioncinae), short (Sphyracephalini) or absent (Diopsini). Cell *cu*a relatively narrow in Diopsinae, becoming elongate in Diopsini; vein CuA long and straight in Centrioncinae, narrow and rounded in Diopsinae. Calypter hairs of moderate length, not long. Wings sometimes relatively weakly developed; *Diopsina draconigena* brachypterous.

Legs. Fore coxa elongate; fore femur swollen (Fig. 131) (narrower in some Diopsini (Fig. 150), particularly *Diopsis*) with two distoventral rows of spinous setae (rows long to very short); Diopsinae with spines on fore femur sometimes accompanied by 2 (less commonly 1) pronounced rows of longer spinous setae; hind femur sometimes also swollen (*Eosiopsis* Feijen). Hind femur with short row of much smaller posterodistal tubercles in Centrioncinae. Femoral glands absent. Fore tibia with double ventral scalloped ridge that is often black and heavily sclerotized, and sometimes slightly curved to match contour of enlarged femur; Centrioncinae with fore tibial brush discrete, pale, visibly contasting surrounding dark setae. Fore tarsi usually shorter than fore tibia. Mid and hind tarsi with "sawlines" (Fig. 131) that are sometimes reduced in *Sphyracephala*.

Abdomen. Abdomen narrowed basally, sometimes distinctly clavate or petiolate. Spiracles 1–7 usually in membrane below tergite, sometimes with spiracle 1 enclosed in tergite and sometimes female spiracle 7 enclosed in tergite (Fig. 178); male with last pair of spiracles enclosed in pregenital sclerites, or just anterior to them (Figs 153–154). Syntergite normally consisting of tergites 1 and 2, but sometimes also 3(4), with sutures variably evident. Sternite 1 well-developed, wider than long (Fig. 154); posteromedial margin of S1 with dark, thin transverse sclerotized band, often separated from sternite as separate, floating sclerite. Sternites 2 and 3 largest.

Female abdomen. (Figs 177–190) Terminalia relatively short and broad, not telescoped or forming oviscape, but sometimes more abruptly narrowed past segment 6; sometimes deflexed apically. S7 and T7 usually united anterolaterally; S7 sometimes transversely divided with posterior section sometimes lost, or sometimes posterior and (less frquently) anterior section also divided longitudinally. T8 and S8 longitudinally divided, but sometimes halves of sclerite secondarily joined medially; S2–5 rarely with similar division. S10 short, variable in shape, setose. Cerci separate, variable in shape, with several setae. Non-sclerotized internal organs described in Kumar (1978) and Kumar & Nutsugah (1976). Usually three spermathecae on two long ducts, with one pair joined near apex of single duct; Diopsinae sometimes only one spermatheca on each duct; shape of spermatheca "egg-shaped" to more elongate and subcylindrical, with base often narrower and surface often rough, tuberculate, or with subconical projections; apex sometimes invaginated or duct telescoped within spermatheca; surface sometimes also with "[t]iny satellites, linked with fine filaments" (Feijen, 1989); spermatheca and apex of duct pigmented. Ventral receptacle short with apical clustering of small sacs, sometimes forming dome confluent with genital chamber. Diopsinae with vaginal sclerite confluent with genital chamber wall, usually circular or ovate, and sometimes accompanied by additional separate distal semicircular band.

Male abdomen. (Figs 153–176) Sternites entire, with S6 divided longitudinally and moderately to highly reduced in Diopsinae; S5 also uncommonly divided. Tergite 6 usually short with setae along posterior margin. Sternite 7 band-like and fused to S8; Centrioncinae with ventral band reaching right margin of S8, which is large, dome-like and symmetrical (Figs 153–154). Epandrium and surstyli well-developed; surstyli converging and fused to epandrium in Diopsinae (Fig. 160); Centrioncinae with surstylus narrow and trilobed, with long spines on anterodistal branch and short tubercles on posterodistal branch (Figs 155–157). Cerci narrow, separate; Centrioncinae with cerci large and L-shaped, covering enlarged ventral lobe of subepandrial sclerite (Fig. 157). Subepandrial sclerite usually simple, curved and plate-like (Figs 162, 169), but Centrioncinae with one pair of enlarged setose ventral lobes with broad, setose distal section (Fig. 156). Phallapodeme narrow distally and with medial extension fused to hypandrium. Hypandrium broad and plate-like laterally with distal and medial setae (medial setae on lobe in Centrioncinae, surrounding by weakened/broken section of hypandrium; Fig. 158); "arms" of hypandrium short, not fused dorsally. In Centrioncinae, pregonite large, setose and lobate (Figs 158–159); in Diopsinae, pregonite narrow, linear; apex setose in Diopsini (Figs 173–174), with long, parallel tubercles in *Sphyracephala* (Figs 165–166). Postgonite absent. Basiphallus U-shaped, elongate, sometimes asymmetrical. Epiphallus sometimes present as minutely spinulose membrane. Distiphallus with flat basal section (forked or longitudinally divided in Diopsinae) and complex, forked apical section with one pair of membranous "wings" (spinulose in Diopsinae) and dark medial sclerite; membranous region from base of basiphallus to posterior surface of distiphallus variably sclerotized, often thick and complex, acting as a supporting structure (Figs 168, 176). Ejaculatory apodeme with linear or fan-shaped blade with darker base sometimes with subbasal "flagellum" (Fig. 172); sperm pump with cup- or ring-shaped sclerotization.

Gobryidae McAlpine, 1997

(Figs 67–70, 82–97, 402)

Type genus: *Gobrya* Walker 1860: 166, by McAlpine (1997a: 182). **Type species of genus:** *Gobrya bacchoides* Walker, 1860: 167, by monotypy.

The family Gobryidae is one of the most recently described families of flies. They were termed "hinge flies" by McAlpine (1997b) because of the characteristic articulation of the narrow, straight abdomen with the thorax, which is also seen to a lesser degree in the Megamerinidae, the family in which there were once placed. Gobryidae consists of at least eight species in the single genus *Gobrya* (McAlpine, 1997b), although only five are described. Species occur in the Oriental Region and adjoining parts of the Australian Region. There is no key to species. Species were catalogued as Megamerinidae in Steyskal (1977e) [Oriental] and Evenhuis (1989b) [Australian].

Biology. The biology of *Gobrya* is unknown, although specimens have been collected on foliage or near the margin of lowland rainforests (D.K. McAlpine, 1997b).

Immature stages. Unknown.

Adult Diagnosis. Colour dark brown (including halter knob), slightly iridescent, with antenna, mouthparts and parts of legs white to yellow; body surface mostly glossy (Figs 82–88). Body length 3.5–8.0mm. Antenna elbowed, first flagellomere elongate; pedicel with dorsal suture; arista sparsely long plumose, with rays becoming shorter apically and sparser ventrally to base. Head short and broad, nearly twice width of thorax; face convex and well sclerotized with mouthparts ventral and receded; frons and dorsum of ptilinal suture narrow (lateral arms nearly absent). Cephalic chaetotaxy reduced to two verticals, with vibrissa, fronto-orbitals, postocellar and ocellar setae absent. Thoracic chaetotaxy reduced to notopleural (one), two supra-alars, and apical scutellar (on slight tubercle). Broad precoxal and postmetacoxal bridges present, although postmetacoxal bridge sometimes membranous medially. Hind femur long and stout with two ventral rows of spines. Abdomen petiolate, straight and narrow with apex slightly widened. Wing with anal lobe and alula strongly reduced; costa unbroken; subcosta complete; R_{4+5} and M_1 slightly convergent (Fig. 402). Male external terminalia globular and asymmetrical (Figs 89–97).

Adult Definition. Colour dark brown (including halter knob and sometimes base), slightly bluish iridescent on darkly pigmented sections, and with antenna, mouthparts and parts of legs white to yellow (Figs 82–88). Body length 3.5–8.0mm.

Chaetotaxy: 1 inner vertical; 1 outer vertical; 0 fronto-orbital; 0 ocellar; 0 postocellar; vibrissa absent. Face and gena irregularly and sparsely setulose. Postoccipital setae present dorsolaterally. 0 presutural intra-alar; 0 postpronotal; 0–1 anterior notopleural, 1 posterior notopleural; 0–1 posterior supra-alar; 0 posterior intra-alar; 0 dorsocentrals; 0 acrostichals; 1 apical scutellar (on small tubercle); 0 proepisternal; 0 anepisternal; 0 katepisternal (sometimes with dense setulae ventrally). Body mostly glossy and bare with very short microtomentum present on head, notum, limited portions of abdomen, and pre- and postmetacoxal bridges; setulose on prosternum (posteriorly and laterally), posterior margin of anepisternum, behind posterior thoracic spiracle, katepisternum, notum and gena; parafacial and lateral margin of frons with single row of erect setulae; pedicel with several ventromedial and one dorsal seta. Mid tibia with ventroapical seta. Hind tibia sometimes with one or two distinct anterodistal setae. Hind basitarsomere with longer basal hairs and bare elongate anterobasal recess.

Head. Antenna elbowed, bases approximate; pedicel rounded, with wide, deep seam to dorsum, dividing smaller outer surface from broader, convex inner surface; first flagellomere elongate, narrower than pedicel; arista unsegmented and sparsely long plumose, with rays becoming shorter apically and sparser ventrally to base (Fig. 85). Head short and broad, nearly twice width of thorax; frons narrow (slightly more than half width of eye), smooth, flat, horizontal and slightly constricted posteriorly, with ocellar triangle not evident; orbital plate not delimited, but evident as short, pale posteromedial region that tapers at both ends (Fig. 86); ocelli at vertex; ptilinal suture very short, without long lateral arms. Back of head concave dorsomedially and with setulose bulge above foramen. Lunule absent. Face strongly convex ventrally (similar to Psilidae but broadly rounded) and fused to parafacial (suture sometimes evident in part); face and parafacial sometimes strongly swollen laterally, forming medial groove; gena broad, not distinct from face, and both it and venter of postgena mostly sunken beneath head and facing ventrally; buccal cavity ovate, relatively small, sharply delimited; clypeus longer than wide, rounded with apex pointed; mouthparts reduced.

Thorax. Thorax elongate and narrow, without pronotal “neck”, but with shallow medial and lateral carinae displacing cervical sclerites. Precoxal bridge present; bulging laterally, with medial groove, posterior surface raised (Fig. 84); prosternum velvety, relatively broad, setose laterally; postmetacoxal bridge high if present. Proepisternum broad, bulging anterodorsally, sometimes fused to postpronotum. Suture between katepisternum and anepisternum only present for a short distance posteriorly, partially evident anteriorly as darker line. Suture between katatergite and anepimeron sunken; posteromedial margin of mediotergite extended as lobe that meets longer band-like anteromedial extension of T1. Greater ampulla present. Anterior thoracic spiracle laterally compressed, ventrally with groove terminating in small, deep pit (similar to some Psilidae); tubercle present below posterior spiracle. Broad membranous space separating anepisternum and anepimeron.

Wing. (Fig. 402) Wing slender; anal lobe and alula strongly reduced; apically infuscated. Calypter linear, with several long hairs. Cells bm and *cu*a (slightly shorter) ending approximately at apex of Sc; cells *cu*a and bm, and adjoining wing margin, without microsetulae. Cell dm narrow, slightly wider apically. Costa unbroken; subcosta complete; R_{4+5} and M_1 slightly convergent. M_4 ending before wing margin, CuA+CuP ending closer to margin.

Legs. Hind femur long, slightly swollen (Fig. 83). Femora ventrally with paired rows of thickened setae that may appear spine-like (sometimes reduced to base); spines darker and larger on the more posterior legs; fore and mid femora with rows of usually 4–6 spinose setae (smaller and fewer on posterior row), and hind femur with 3–6 spinulose setae on anterior row and 8–12 on tubercles on posterior row.

Abdomen. Abdomen straight, narrow (narrowest medially on segment 2), petiolate with apex slightly clavate. T1 and S1 broadly emarginated anteriorly to provide membranous space that folds to meet thorax when abdomen angled. T1 completely fused to T2, lateral margins evident (Fig. 89); S1 with reduced setation; T1+2 nearly as long as remining pregenitalic segments; T3 and S3 slightly longer than wide, tergites and sternites 4–6 wider than long, becoming progressively shorter posterioly. Spiracles 1–5 in membrane, spiracles 6 and 7 enclosed by tergite.

Female genitalia. (Figs 67–70) T6 and S6 fused with suture not evident. Segments 7, 8 and 10 very short with sclerites broad; S8 bare in material examined; T10 larger than S10. Cerci very short and broad. Spermathecae 1 + 2, with paired spermathecae on short stalks; spermathecae and apical section of ducts pigmented; spermathecae with sparse, minute pits.

Male genitalia. (Figs 89–97) T6 fused to S8, which is nearly symmetrical; S6 and S7 absent, with pregenital sclerites membranous ventrally. Terminalia past T8 strongly asymmetrical; components of internal genitalia of tentative homology. Phallapodeme present (not absent, as stated in McAlpine (1997)). Epandrium subspherical, atrophied on left side, oblique; right anteroventral corner produced. Left surstylus small, pale, subrectangular; right surstylus larger, darker, bulbous. Subepandrial sclerite small, near ventral margin of epandrium and with one pair of small separate sclerites. Hypandrium bare, with medial bridge weakly sclerotized, flat and minutely setose; arms meeting dorsally; approximately U-shaped with right side strongly elaborated into several different posterior lobes and thin anterior carina. Phallapodeme short, carinate. Postgonite absent. Right pregonite absent; left pregonite (perhaps further elaboration of hypandrium?) flat, short and with more sclerotized margin. Epiphallus absent. Distiphallus short, stout, narrowest at base, and with cylindrical subbasal process with apical hairs; basiphallus produced as long left lateral lobe. Ejaculatory apodeme with broad, pale blade, and short thin stalk with narrow base; sperm pump cup-shaped with dark basal ring.

Megamerinidae Hendel, 1913

(Figs 98–123, 403)

Type genus: *Megamerina* Rondani 1861: 10 [new name for *Lissa* Meigen 1826: 370, preoccupied by Leach (1815) (Decapoda)], by Hendel (1913: 90). **Type species of genus:** *Ocyptera dolium* Fabricius, 1805: 315, by automatic designation [type species for *Lissa* Meigen (*Chliza loxocerina* Fallén, 1820 =*Ocyptera dolium*) by monotypy].

Megamerinidae, as it is presently defined, is a small and morphologically conserved family mostly consisting of *Texara* species (at least 14 species) that are found mainly in the Oriental Region, but also in the Palaearctic. The remaining two monotypic genera are the Palaearctic *Megamerina,* and the Chinese (Hubei, Sichuan and Zheijang Provinces) *Protexara* Yang [not examined]. Present generic limits are heavily reliant on the development of the fronto-orbital seta, being either strong (*Texara*), weak (*Protexara*) or absent (*Megamerina*). *Protexara* is further characterized by several small spines on the fore and mid femora, and the male cercus and surstylus are broadest basally (Yang, 1996), but the male terminalia are otherwise reminiscent of *Megamerina* (Figs 106–109) and may prove to belong in that genus. The phallus of *Texara* is distinct (Figs 116–117), including one pair of terminal corkscrew-like filaments.

The Megamerinidae was last treated by McAlpine (1997a), who discussed the history and relationships of the family, Krivosheina *et al.* (1996), who provided a key to Russian species, and Yang (1996), who treated the Chinese fauna. Xue and Chao (1998) treated the Megamerinidae of China, describing five new species. Steyskal (1977e) provided a catalogue for Oriental species, and Nartshuk (1984) provided one for Palaearctic species.

Hennig's (1965) concept of Megamerinidae also included the monotypic *Palaeotanypeza* Meunier from Baltic amber (upper Eocene?), which was originally described as Tanypezidae (Meunier, 1917). The genus was only tentatively maintained as Megamerinidae by D.K. McAlpine (1997a) and J.F. McAlpine (1989), but examination of both sexes for the present study strongly support placement in Megamerinidae. It is clearly distinct from the more slender living taxa, however, whose mostly narrowed legs, longer petiolate abdomen and smaller head with elongate antenna exaggerate the thicker portions of the body, including the hind femur. Dimensions of the fossil taxon (see Hoffeins & Tschirnhaus (2009: figs 7–9)) are closer to other generalized acalyptrates in some respects, although the hind femur is about as thick as that of modern megamerinids. J.F. McAlpine (1989) suggested separate subfamilial rank for the genus, and while possibly justified, seems unnecessary.

Biology. Larvae of Palaearctic *Texara* and *Megamerina* have been found to be predaceous on other fly larvae under the bark of fallen deciduous trees (willow, poplar, oak and especially aspen) and in decaying vegetation (Krivosheina & Krivosheina, 1997), agreeing with Hennig's (1943) earlier assumptions. Adult specimens have been collected in damp meadows, various mixed and deciduous forests, undergrowth, and on rotting wood and cut aspen (Roháček, 2016).

Immature stages. Descriptions and illustrations of the third instar larva and puparium of *M. dolium* (Fabricius) were provided by Krivosheina & Mamaev (1967) and Hennig (1943), respectively. Ferrar (1989) summarized knowledge on larvae and puparia known at the time. Krivosheina & Krivosheina (1997) redescribed the larva of *M. dolium*, described the larva of *T. savolaineni* (Frey), and described the larva and puparium of *T. stackelbergi* Krivosheina, Krivosheina & Nartschuk.

Adult Diagnosis (extant genera). Relatively large, long, slender and heavily-built (Figs 98–105). Body length usually 8.0–18.0mm. Colour black with antenna, face, halter and most of legs white to yellow; setae black to white, setulae white; wings slightly infumated. Antenna porrect; pedicel without dorsal seam; arista short-plumose. Head subspherical in profile; face narrowed into thin medial carina; frons projecting and tapering anteriorly with one pair of oblique lateromedial folds; frons with one pair of dark velvety lateromedial patches and single silvery patch behind ocelli. Vibrissa, postocellar, and sometimes ocellar seta absent. Postpronotal absent. Enlarged hind femur with two rows of spines ventrally; hind tibia curved and with double sclerotized ridge on venter fused along most of length; all femora with row of glands both posteroventrally and anteroventrally (only posteroventral on fore and mid femora in Syringogastridae). Fronto-orbital seta present or absent. Precoxal bridge absent; postmetacoxal bridge present; thorax produced at narrow point of attachment to abdomen. Costa unbroken; sc complete (Fig. 403).

Adult Definition (extant genera). Relatively large and slender, heavily-built and well sclerotized (Figs 98–105). Body length usually 8.0–18.0mm. Colour black with antenna, face, halter and most of legs white to yellow; setae black (major setae) to white, setulae yellowish-white. Scutum minutely punctate at base of setulae.

Chaetotaxy: 1 inner vertical; 1 outer vertical; 0 (*Megamerina*) or 1 weak (*Protexara*) or well-developed (*Texara*) fronto-orbital; 0 ocellar; 0 postocellar; vibrissa absent. 0 presutural intra-alar; 0 postpronotal; 1 posterior notopleural; 2 posterior supra-alar; 0 posterior intra-alar; 0–1 dorsocentrals; 0 acrostichals; 1 apical scutellar (lateral seta absent); 0 proepisternal; 0 anepisternal; 0 katepisternal. Pedicel with dense dark setulae. Frons with irregular lateral row of proclinate to lateroclinate setulae; face, parafacial, gena with dense white pubescence forming narrow band around eye to dorsum of occiput; sparse hairs on face continuing as shorter series of denser hairs on venter of gena; frons with one pair of brownish-purple lateromedial velvety patches. Occiput and back of head with long white (often weak and curled) to black (straighter) pile that are not differentiated into separate postoccular setae. Thorax and legs with dense to sparse white setulae, except on postalar wall (microtomentose) metanotum (microtomentose to partially bare on anatergite and posterior half of katatergite) and pleuron behind wing base and below postpronotum; proepisternum otherwise with patch of short, dense, isolated (usually white) hairs that extends onto anterolateral surface of fore coxa; notal setulae with pattern of "partings", most noticeably between dorsocentral rows, with setulae directed inwards along a single line postsuturally, and along two parallel lines presuturally (Fig. 98). Fore tibia with white setulae dense (Fig. 99). Mid tibia with ventroapical seta. Pregenitalic abdominal tergites with longer setae laterally, especially along posterior margin of T1, and sometimes to a lesser degree along posterior margins of other pregenitalic tergites; posterior setae on S1 also longer.

Head. Antenna porrect, pedicel without dorsal seam, sometimes inner-distal margin slightly angulate; first flagellomere discoid with apical margin sometimes slightly truncated; arista white, short plumose to pubescent. Anterior margin of frons with two medial folds extending back from ptilinal suture (i.e. ptilinal suture H-shaped) that raises medial section of frons ("medial frontal lobe" of McAlpine (1997a)); produced anteriorly (conspicuous when viewed laterally) with sides broadly rounded to cover dorsolateral margins of face and parafacial (Figs 101–102). Lunule present, medially grooved, horizontal with anterior section curved down between antennal bases (Fig. 100). Sides of face converging medially, enclosing centre of face within carinate sulcus (continuous with groove on lunule); sulcus split ventrally at epistoma (usually narrow, but wider than high in *Megamerina*). Clypeus rounded, anterior section subrectangular and sometimes shallowly notched. Back of head broadly rounded, vertex slightly shifted forward; with pronounced microsetulose lobe above foramen and teardrop-shaped silvery tomentose patch reaching ocellar tubercle.

Thorax. Proepisternum shifted dorsally, fused to posteriorly displaced postpronotum. Transverse suture vestigial medially, at midpoint of scutum; supra-alar carina shallow; postalar wall sharply angled downwards with margin slightly carinate. Scutellum and subscutellum small, shallow. Greater ampulla present. Katepisternum and meron fused (suture evident as minute pit over mid coxa); anepisternum deeply receding below postpronotum. Coxopleural streak present. Metathorax with cylindrical extension meeting abdomen; sharply and deeply recessed above spiracle. Metasternum extending between hind coxae as pointed process, not reaching postmetacoxal bridge. Precoxal bridge absent; prosternum arrowhead-shaped; presternum small, spindle-shaped, duplicated; subcervical sclerite floating, linear; postmetacoxal bridge present, high; membrane around prosternum and hind coxae slightly sclerotized, scaled.

Wing. (Fig. 403) M_4 and CuA+CuP reaching wing margin. Cell br bulging into dm. Cell *cu*a short and CuA straight. Anal cell and most of cell bm bare. Veins R_{4+5} and M_1 subparallel, slightly converging apically. Costa unbroken; sc complete, ending far from apex of R_1. Calypter hairs moderately long.

Legs. Hind femur strongly swollen (Figs 98–99) with two rows of spines (usually 12–14) ventrally; hind tibia curved (curve corresponding to shape of swollen femur) and with one pair of sclerotized ridges ventrally that may be fused along most of length. Fore and mid femora also slightly swollen medially, but not nearly as extensively as hind femur; with 3–4 small ventral spines in *Protexara*. All femora with row of glands both posteroventrally and anteroventrally (Fig. 103) with surrounding pigment orange. Tarsomeres with strong ventroapical setae; fore and mid basitarsomeres with long ventral hairs.

Abdomen. T1 and S1 broadly emarginated anteriorly to provide membranous space that folds to meet thorax when abdomen angled (Fig. 119). Segments longer than wide. Sternites 1–5 weakly sclerotized marginally; S1 with dark, transverse posteromedial sclerotization; S2 with one pair of internal, anterolateral hooks. Spiracles 1–6 in membrane. At least T2 (sometimes also T3 and T4) with pair of silvery posterolateral patches (Fig. 99).

Male genitalia. (Figs 106–117) Right spiracle 7 present, in membrane. Tergite 6 divided into two, small, narrow dorsal strips. S7 separate or partially fused to right anterolateral margin of S8. S6 bare, narrow, adjacent to S7. S8 large, elongate, tapering apically. Epandrium tapering basally and with thickly sclerotized distal margin. Cercus subtriangular, usually widest apically, with pointed tubercle-like setae on inner surface. Surstylus movable, strongly incurved, with inner patches of basal and apical tubercles. Subepandrial sclerite V-shaped with two ventral setae on each side. Hypandrium elongate, arms meeting posterodorsally; distally fused to short anteroventral extensions of phallapodeme that continue slightly distal of hypandrial margin; distal half of hypandrium weakly sclerotized excluding narrow margin, thin texturing and one pair of floating, setose sclerites. Pregonite apically spinulose and with comb of short, stout setae, directed anteriorly, perpendicular to postgonite. Postgonite dark, rod or ribbon-like, confluent with base of pregonite and extending to phallapodeme. Basiphallus small, fused to distiphallus. Epiphallus sometimes present. Distiphallus with long, straight base composed of two parallel ribbons that bend ventrally at apex; apically with thick spinulose process on right side (“scabrous process” of McAlpine (1997a)), and with dark sclerite(s) and filamentous processes (“terminal filaments” of McAlpine (1997a)) on left side; some filaments modified into double corkscrew in *Texara* (Figs 116–117). Ejaculatory apodeme with large, stout stem ending in short, clear blade with supporting ribs; stem and blade rotated 90° relative to insertion of duct; stem with stout medial carina above duct; sperm pump with paired marginal sclerotized bands.

Female genitalia. (Figs 118–123) T6 and S6 widest before midpoint, closely associated but not fused. T7 and S7 fused into long, thin tube enclosing spiracles. T8 and S8 weakly sclerotized, separate, and with numerous longitudinal grooves. T10 and S10 small, narrow and minutely grooved; T10 with lateral fold. Cercus length more than twice width, slightly incurved, broadly rounded apically. Membrane between segments 5–8 long, and segments past segment 5 long and thin, allowing for most of these to telescope. Spermatheca slightly elongate with pointed apex, surface sparsely covered with minute divots; spermatheca and apex of duct pigmented.

Variation—Paleotanypeza (fossil). (Tschirnhaus & Hoffeins, 2009: figs 7–9) As described above, except as follows. Body length approximately 8.8–9.5mm; one female (with elongate ovipositor extended) 18.0mm long. Single well-developed fronto-orbital present; one dorsocentral seta (slightly shorter than scutellar seta); small lateral hairs on face slightly shorter, but present; cannot verify if frons with lateral velvety patches; silvery tomentose patch behind ocelli not present; “partings” of setulae not evident on notum. First flagellomere subcircular; pedicel length less than half height, with angulate projection modestly developed on inner surface and shallowly developed on outer surface; arista bare; cannot verify presence of medial groove on lunule; face not sunken laterally beside parafacial; clypeus not notched anteromedially; without microsetulose lobe above foramen; back of head “normally” rounded. Thorax without proepisternum shifted dorsally; postalar wall not sharply angled or carinate; katepisternum and meron not fused; typically acalyptrate in dimensions, without severely narrowed or recessed regions. Swollen hind femur not as evident as all legs are well-developed, not narrowed; fore femur with ventrodistal rows of spines as on hind leg, two anterior and three posterior spines on male and 5 anterior and 7 posterior spines (1 and 3 shorter) on female; hind tibia not curved, without sclerotized ridges; hind tibia with ventroapical seta towards anterior surface;

male hind tibia with row of black setulae on ventrobasal half. Abdomen thicker at base, not elongate or narrowed; cannot verify position or presence of spiracles; silvery regions on abdomen restricted to tergite 1 (patches broad, posterolateral, narrowly connecting) and tergite 4 (broad lateral stripe). Female segments 6–10 extremely elongate with extensive intersegmental space; T6 and S6 well-developed, segments 7–10 indistinctly sclerotized. Male tergite 6 not visible, but similarly small if present; cercus broad and bilobed apically, with additional floating mediobasal sclerotized patch; surstylus apically broad with margin straight, distomarginal tubercles densely arranged in comb-like line (reminder of tubercles on inner face not visible if present).

Nothybidae Aczél, 1955

(Figs 50–64, 399–400)

Type genus: *Nothybus* Rondani 1875: 439, by Aczél (1955c: 2). **Type species of genus:** *Nothybus longithorax* Rondani, 1875: 439 [=*N. longicollis* Walker, 1856: 135] by monotypy.

The small family Nothybidae contains the single genus *Nothybus*, which occurs throughout much of the Oriental Region including India, as well as Papua New Guinea and Nepal. Mention of specimens from the Solomon Islands in Evenhuis (1989f) cannot be verified. Nothybidae was recently revised by Lonsdale & Marshall (2016), who described and imaged the larva, and recognized and figured 11 species, three of which were newly described. A twelfth species described by Galinskaya & Shatalkin (2017) on the basis of a single female appears to be conspecific with *N. longicollis*.

Biology. Little is known of the biology of *Nothybus*. D.K. McAlpine (1974) noted hovering in a Malaysian male of *N. lineifer* Enderlein (as *N. decorus* Meijere) that when captured, hovered over the author's arm and "struck it rapidly two or three times with the abdomen as if attempting to sting or lay eggs", and when at rest, held its wings slightly raised over the abdomen with the anal lobes touching and the costal margin slightly raised. When at rest, this male waved its fore legs "reminiscent of the family Micropezidae". Similar behaviour in Chinese and Vietnamese specimens was noted in Paiero & Marshall (2014) and Lonsdale & Marshall (2016), with specimens waving forelegs in the manner of incheumonid antennae, and patrolling leaf surfaces in patches of filtered sunlight along forest streams and paths. Paiero & Marshall (2014) discussed some behaviour of *N. sumatranus* Enderlein, where both sexes were observed standing or slowly walking on leaf surfaces, or slowly flying between leaves; courtship behaviour was described and photographed, wherein the male deposited oral fluids on the leaf surface as part of a nuptial gift, which is otherwise unknown among diopsoids. Similar behaviour was also observed for *N. longicollis* (Lonsdale & Marshall, 2016). Specimens have been collected in numerous forest types, often near water (McAlpine, 1974; Lonsdale & Marshall, 2016).

Species are likely viviparous, with McAlpine (1989) recovering a larva from the enlarged oviduct of a *N. longicollis* female, and Meier *et al.* (1999) noting simultaneous facultative viviparity in *N. kempi* (Brunetti), with mature eggs in the ovaries. A single larva was recovered by Lonsdale & Marshall (2016) from the abdomen of a *N. longicollis* female.

Immature stages. The larva of *N. longicollis* was photographed and described by Lonsdale & Marshall (2016).

Adult Diagnosis. Relatively large-bodied, long-legged, slender and elongate, with anterior portion of thorax moderately to strongly produced, far removed from fore coxae; body length 5.5–15.0mm (Figs 49–55). Subscutellum large and subconical, reaching or exceeding apex of scutellum. Colour often orange to brown or partly black with abdomen darker, and with variable striping of pigment or iridescence on head and thorax; head with three dark velvety patches. First flagellomere slightly to distinctly angled, narrow, twice as long as wide; pedicel with dorsal seam. Precoxal bridge present, postmetacoxal bridge absent. Vibrissa, ocellar, postocellar, postpronotal, anterior notopleural and katepisternal setae absent. Two strong pairs of scutellar setae; 1 notopleural, 1 dorsocentral and 1 anepisternal. Wing with alula and anal lobe nearly absent (Figs 399–400); radial and medial veins divergent; patterning often distinct and elaborate; cell cua and bm very short, with cell bm open anterodistally; cell br open; upper calypter margin pubescent; costa unbroken; sc complete. Female tergite and sternite 7 separate, not forming oviscape.

Adult Definition [from Lonsdale & Marshall (2016)]. Body length 5.5–15.0mm.

Colour: (Figs 49–55) Setae mostly or entirely black. Usually yellowish-orange in base colour with mottling or ill-defined stripes, abdomen often darker; sometimes dark brown with smaller orange patches. Most of thorax and abdomen with light greyish to thicker black pruinosity; at least tergite 5 with black velvety patch. First flagellomere usually black apically, face usually with dark brown to black spot often flanked or surrounded by silvery tomentosity. Frons with three black velvety patches including one comma-shaped pair anterolaterally and one rounded/subquadrate patch behind ocelli. Thorax always with purplish-white pruinose iridescent stripes that are most prominent on postpronotum. Apices of femora, tibiae and tarsi usually dark; fore tarsus white, at least at base. Wing often lightly infuscated past dm-m, sometimes with discrete infuscated bands around veins, and often with darker pigment marginally; usually with transverse brown band extending from M_4 to costa at level of dm-m, past which is clouded region often enclosing two or three clear and strongly iridescent spots in cells r_{2+3}, r_{4+5} and m_1. Halter white to yellow, base usually partially brown, knob sometimes faintly brownish.

Chaetotaxy: 1 inner vertical; 1 outer vertical; 2 reclinate fronto-orbitals (anterior slightly inset); 0 ocellars; 0 postocellars; vibrissa absent. 0 presutural intra-alars; 0 postpronotals; 1 notopleural (anterior seta absent); 1 posterior supra-alar; 1 postalar; 0 posterior intra-alars; 1 dorsocentral; 0 acrostichals; 1 lateral scutellar, 1 apical scutellar; 0 proepisternals; 1 anepisternal; 0 katepisternals. Weak lateral row of postocular setae. Mid coxa with strong lateral seta. Mid tibia with 1 strong ventroapical seta. Pedicel with one large dorsal and several enlarged ventral setae; dorsal half of face, parafacial and anterolateral region of frons minutely setulose (Fig. 49); prementum one pair of short and long setae. Thoracic setulae in relatively consistent, characteristic pattern of rows (Fig. 51). Tibiae and tarsi with setulae in rows with dense ventrobasal patch on basitarsomeres.

Head. Suborbicular, ocelli apparently near midpoint of head. Antenna angled with pedicel cap-like and with dorsal seam, arista bipectinate; first flagellomere slightly longer than wide. Face well sclerotized, convex; often with dark brown to dark yellow protrusion/tubercle ventromedially. Gena and postgena very narrow. Clypeus large, produced; labium widest distally; palpus narrow. Head with broad post-ocellar concavity and bulge above foramen.

Thorax. Extended anteriorly, displaced from base of fore coxa (pronounced in *N. longicollis*); postpronotum elongate. Posterolateral corner of notopleuron with small tubercle at base of seta. Scutellum relatively long, flat dorsally and laterally. Subscutellum conical, larger than scutellum (Figs 50–51, 53). Posterodorsal margin of katepisternum abruptly recessed. Proepisternum extending into lobed plate anteriorly. Katepisternum and meron partially fused. Greater ampulla absent. Coxopleural streak sometimes visible. Precoxal bridge present, very large and broad, fused to teardrop-shaped prosternum; postmetacoxal bridge absent. Spiracles broadly ovate, fringed with short hairs.

Wing. (Figs 399–400) Length 5.0–10.4mm. Alula and anal lobe vestigial. Costa unbroken. Vein sc complete. CuA+CuP reaching wing margin when present. Cell *cu*a and bm short. Cell br open. Cell bm open anterodistally. Basal cells and cell *cu*a without microtrichia. Radial and medial veins divergent. M_4 reaching wing margin. CuA slightly curved. Upper calypter linear, pubescent; lower calypter vestigial.

Legs. Long and slender; tarsus elongate, similar in length to tibia. Hind basitarsus with slight basal swelling, similar to Tanypezidae.

Abdomen. Relatively stout, subcylindrical, slightly constricted at base and gradually tapeed apically. Pregenitalic sternites long and narrow, except sternite 1 wider than long, and sternite 6 relatively short. Spiracles 1–6 in membrane, male 6th spiracles associated with weakly sclerotized margin of tergite 6; 7th spiracle sometimes absent.

Male genitalia. (Figs 56–61) Sternite 7 membranous, very short. Sternite 8 dorsal, tapered laterally, symmetrical. Cercus finger-like or relatively broad, often flat or slightly raised, subconical in *N. longicollis*. Surstylus long and slender to small and rounded; usually at least partially fused to epandrium (free in *N. longicollis*). Subepandrial sclerite with curved medial plate extending ventrally to fuse to inner surface of surstylus. Hypandrium with broad, densely setose lateral plates, usually broadly connected medially to phallapodeme (separate in *N. longicollis*). Pregonite well-developed, setose, pointed, textured; this structure is here interpreted as the pregonite because of its external articulation with the hypandrium and chaetotaxy, although its position relative to the base of the phallapodeme suggests that it could instead be the postgonite, which is currently interpreted as absent. Basiphallus subcylindrical with ring-like base, fused to distiphallus, extending posteriorly as reticulate and ill-defined epiphallus. Distiphallus long, flat and ribbon-like with one pair of dark bands extending at least to midpoint; apex often with one pair of clear tubules. Ejaculatory apodeme with clear blade; stalk well-developed with minute cylindrical perforations and asymmetrical base usually enclosing narrow fossa; sperm sac membranous.

Female genitalia. (Figs 62–64) T7 and S7 separate. Female terminal segments relatively short, wider than long;

T8 sometimes longitudinally divided basally; S8 sometimes entirely divided; T10 and S10 small, subtriangular. Two small black spherical spermathecae on separate long, unpigmented, distally narrowed ducts that arise on short common duct or process of bursa copulatrix. Ventral receptacle with transversely wrinkled stem expanding into bent, sometimes pigmented apical lobe with small membranous sac emerging subapically.

Psilidae Macquart, 1835

(Figs 1–48, 395–398)

Type genus: *Psila* Meigen 1803: 278, by Macquart (1835: 416) [as Psilomydae after unjustifiable name change of *Psila* to *Psilomyia* by Latreille (1929); Loxoceridae proposed in same paper (p. 372)]. **Type species of genus:** *Musca fimetaria* Linnaeus 1761: 458, by subsequent designation [Westwood 1840: 146].

The Psilidae are a group of mostly north temperate flies with 335 described species in three subfamilies globally (Shatalkin & Merz, 2010). One common name applied to the family is "rust fly", because the larva of *Psila hennigi* (known until recently as *Psila rosae* (Fabricius)) produced rust-like traces and decay in the root of its hosts, including carrot, parsnip and turnip. Adult Psilidae have a thick coat of long, dense setulae that emerge from pits, and the shape of the face (Figs 3, 18) and the absence of the precoxal bridge are also quite characteristic, as is the shape of the wing and its venation, including the peculiar curvature of vein R_1 past the subcostal break (Figs 395–398), the latter of which is quite evident in the fossil *Electrochyliza*. Early family and genus-level treatments of this species-rich group include Capelle (1953), Frey (1925a, 1955), Hennig (1941b), Johnson (1920) and Melander (1920). More recently, the Old World fauna has been revised by Iwasa (1989, 1991, 1994), Shatalkin (1983, 1986, 1989, 1998a, 1998b) and Wang & Yang (1996); the New World fauna was treated by Buck & Marshall (2006a, 2006b). Regional catalogues are provided in Shewell (1965) [Nearctic], Soós (1984d) [Palaearctic], Cogan (1977, 1980b) [Oriental, Afrotropical], Evenhuis (1989d) [Australian] and Prado (1975) [Neotropical]. The fauna of all Regions requires revision.

The subfamily **Psilinae** (Figs 6–9, 17–18) is mostly north temperate in distribution, and includes 216 species (Shatalkin & Merz, 2010). While it occurs in all biogeographic regions, the few known Neotropical species are restricted to Central America from Mexico to Costa Rica (Buck, 2010). The subfamily is split between *Psila* and *Loxocera*, which were redefined by Buck & Marshall (2006a, 2006b) using adult external, adult genitalic and egg morphological characters. Buck (2010) mentions that six subgenera are recognized in *Psila* s.l., with the monophyly of some of these subordinate taxa still to be properly established—*Psila* Meigen s.s., *Asiopsila* Shatalkin, *Psilosoma* Zetterstedt, *Freyopsila* Shatalkin, *Synaphopsila* Hendel and *Xenopsila* Buck. *Afropsila* Shatalkin, *Chamaepsila* Hendel, *Oxypsila* Frey and *Tetrapsila* Frey should also be included among these. Three subgenera were included in *Loxocera* s.l.—*Loxocera* Meigen s.s., *Tropeopsila* Shatalkin and *Imantimyia* Frey. Groups requiring special consideration include the Afrotropical *Loxocerosoma* Verbeke with three species, likely considered to be synonymous with *Loxocera* (Buck & Marshall, 2006b), and the monotypic *Loxochyliza* Verbeke from Nepal, which is presently unplaced (see Shatalkin (1998)). The east Palaearctic *Tropeopsila* Shatalkin (two species) is presently treated as a subgenus of *Loxocera*, but Buck & Marshall (2006b) consider its position in need of verification.

Chylizinae (Figs 1–5) includes the single genus *Chyliza*, with 118 described species (Shatalkin, 2014). The genus is global in distribution, and the only psilid known from South America (Buck, 2010), but it is best represented in the Australian and Afrotropical Regions (Shatalkin, 1998a). Subgenera have been proposed for the genus, but Shatalkin (1998) is followed here in considering these as likely synonyms because they are based on few and likely homoplastic characters that likely do not reflect natural groupings. As an alternative to the existing subgenus system, Shatalkin (1998) provided a preliminary three-group subdivision of the genus based on colour. Future considerations of genus subdivision should be based on the results of a more thorough phylogenetic analysis.

Belobackenbardiinae (Figs 10–18) contains three species in the South African genus *Belobackenbardia* Shatalkin. Shatalkin (2002) considered the most ancestral lineage of Psilidae, and defined it in part by a brush of short white hair on the postgena (not close to eye margin as similar hairs in *Chyliza*; also found in some *Loxocera*), a basally bushier arista, and a relatively large epandrium fused to large, apically bilobed surstyli; one pair of large dorsal epandrial processes occur in most species. An additional synapomorphy proposed by Shatalkin (2002) is a long, curved phallus, but this is here interpreted as the pregonite, with the actual phallus ventromedial to these structures, being small and mostly membranous. There are likely additional synapomorphies of the male genitalia, but only a single species was examined for this study and the genitalia of the other species are not figured in the literature.

The only accepted fossil Psilidae is *Electrochyliza* Hennig*,* which contains the single species *E. succini* Hennig (Eocene/Oligocene Baltic amber), although at least one other species of *Electrochyliza* is present in the Hoffeins collection. The visible external male genitalia bear a resemblance to those of Psilinae, but not much more can be inferred at present. The monotypic *Psilites* Heer (Miocene compression fossil, Croatia) [not examined] was excluded from the family by Gentilini *et al.* (2006), who suggested that it might actually be a tephritoid. An unidentified *Psila* species was mentioned by Schöberlin (1888) (Miocene compression fossil, Switzerland), and unidentified Psilidae in amber are mentioned in Tschirnhaus & Hoffeins (2009).

Biology. Adults of Nearctic Psilidae are often found on foliage and sometimes fallen wood in closed woods, and Old World species are found in dense vegetation in regions that experience high rainfall, including areas of high elevation (Cogan, 1977). An unidentified *Loxocera* has been observed feeding on insects, likely scavenging (S.A. Marshall, pers. comm.).

Larvae are known to be primary feeders on living plants in stems, roots, bulbs and under the bark of thin twigs on trees (Shatalkin & Merz, 2010). *Psila s.l.* species develop in the stems and roots of a variety of grasses and other herbaceous plants, including the carrot rust fly (*Psila hennigi* (Thompson & Pont); Figs 17–18, 47), which can be a significant pest of umbelliferous crops such as carrot and celery (Degen *et al.,* 1999; John *et al.* 2001; Collier & Finch, 2009). Originally Palaearctic in distribution, the carrot rust fly is now known in Canada, the United States, Cuba, South Africa and New Zealand (CABI, 1992; Botha *et al.,* 2001). *Psila fimentaria* (L.) is known from *Carex*. Monocots serve as hosts for the larvae of the less commonly encountered *Loxocera*, including *Carex* (Valley *et al.,* 1969), *Juncus* (Chandler, 1975b; Ferrar, 1987), *Digitaria* (Capelle, 1953) and possibly *Luzula* (Chandler, 1975b), which may have driven the development of the laterally compressed ovipositor characteristic of that genus (Buck, 2010).

Larvae of north temperate *Chyliza* are known to feed on living trees and herbs (Chandler, 1975b; Ferrar, 1987) in at least 10 plant families (Sueyoshi, 2013), and Capelle (1953) found larvae in rotting wood. *Chyliza notata* has been observed ovipositing on fresh tree wounds where the larvae tunnel into the living tissue; pupation occurs just under the bark (Ferrar, 1987). *Chyliza leptogaster* (Panzer) has been recovered from deciduous trees and is known to cause phloem necroses; *C. annulipes* Macquart is found in conifers and are associated with wounds. *Chyliza* have also been found under the bark of trees housing buprestids (Gates *et al.,* 2006), with initial introduction in trees apparently occurring through existing wounds in the plant (Lyneborg, 1987). Sugiura & Yamazaki (2006) found larvae of *Chyliza* in galls induced by Cecidomyiidae species, Yamazaki & Sugiura (2008) found *C. splendida* in *Wisteria* galls induced by bacteria, and in some cases the psilid larvae appear to have induced the gall itself (Chandler, 1975b; Ferrar, 1987). Precopulatory, copulatory and oviposition behaviour of *Chyliza vittata* on a leafless orchid (*Gastroda elata*) was described by Sugiura (2016), but other orchids are also known to serve as hosts where the larva feeds internally on leaves, stems and underground tissue (Suetsugu, 2016).

Immature stages. Psiline larval morphology was described for two *Loxocera* in Meijere (1941, 1945), and the eggs of *Loxocera* and *Psila* species were thoroughly described in Buck & Marshall (2006a, 2006b). Illustrations and descriptions of immature stages of Chylizinae and Psilinae are also available in Ferrar (1987), who provides references to original sources in the literature.

Adult Diagnosis. Medium-sized, often narrow-bodied; dorsum with shallow to deep pits at base of setae and setulae, at least on notum. Orange to yellow with brown to black pattern, or predominantly dark. Antenna elbowed; pedicel with dorsal seam; first flagellomere slightly to very elongate. Face usually with angled ventromedial plate with transverse striations; sometimes strongly receding ventrally (very broadly so in some Psilinae); ocelli slightly shifted anteriorly, distant from postocellar; ocellar tubercle and space anterior to postocellars with patch of setulae. Vibrissa absent; ocellar seta usually very long when present. Anterior spiracle in ovate depression with grooves sometimes forming a pit (Fig. 17); thorax covered with long, dense setulae (also *Somatia*, Megamerinidae), at least dorsally but sometimes also laterally and ventrally. Cell br narrowed on distal section (Figs 395–398); costa with subcostal break; subcosta continuing to costa at near right angle as hyaline weakening in membrane; similar to Opomyzidae, vein R_1 distal to subcostal insertion usually long and slightly to more broadly arched (exaggerated in Chylzinae (Fig. 396), narrow and straight in Belobackenbardiinae).

Adult Definition. Medium-sized, often narrow-bodied flies (Figs 1–18, 47–48); body length 3.0–12.0mm. Surface well-sclerotized with shallow to deep pits (sometimes forming transverse striations) dorsally at base of setae and setulae, at least on notum. Orange to yellow with brown to black pattern, or predominantly dark with halter often pale (knob rarely dark); arista black to white.

Chaetotaxy: 1 inner vertical; 1–2 outer verticals; 0–2 fronto-orbitals; 0–1 ocellar (often very long when present, potentially extending to eye margin); 0–1 postocellar (divergent); vibrissa absent. Pedicel often densely setulose, sometimes with longer marginal seta(e) dorsally and ventrally. Frontal vitta with numerous scattered rows of setulae, often inclinate and/or proclinate medially and anteriorly, continuing posteriorly onto occiput and postgena, dense in Chylizinae (Fig. 4); vitta sometimes velvety; ocellar tubercle setulose, separated from postovertical by similarly setulose patch; parafacial and/or sides of face microtomentose; venter of gena and parafacial with row of setulae. 0 presutural intra-alar; 0–1 postpronotal; 0 anterior notopleural; 0–1 posterior notopleural; 2 posterior supra-alar; 0 posterior intra-alar; 1–4 dorsocentrals; 0–1 acrostichals; 2–3 scutellars (uncommonly 1 or 4); 0 proepisternal; 0 anepisternal; 0 katepisternal. Body largely covered with dense, short setulae; proepisternum with patch of white microtrichia (restricted to ventral margin or extending to encompass ventral half of sclerite, and sometimes extending to spiracle; absent in Belobackenbardiinae); setulae on scutum with partings and crowns that are distinct as in Megamerinidae (Chylizinae (Fig. 1)) or inconspicuous to absent; pleuron sparsely setulose posterior to wing base, mostly densely setulose anterior to wing base with bare patches, sometimes with conspicuously downturned patch of setulae along venter of anepisternum. Scutellum bare to sparsely setulose or microtomentose; remainder of metanotum microtomentose to setulose, with katatergite most conspicuously and densely haired and mediotergite sometimes bare. Mid tibia with one distinct ventroapical seta, sometimes accompanied by additional smaller seta; hind tibia sometimes with ventroapical seta.

Head. Antenna elbowed (Fig. 5); pedicel with dorsal seam; arista pubescent to short plumose, rarely flattened, inserted subbasally to medially; first flagellomere slightly (Fig. 5) to considerably elongate (Fig. 6), length rarely less than 1.5 times width but sometimes exceeding seven times width; scape and pedicel sometimes also slightly elongate. Frons setulose with ocellar triangle bare and elongate (sometimes attaining anterior margin); ocelli slightly shifted anteriorly, divided from postocellar by setulose patch. Face usually with angled ventral plate impressed with slight to deep transverse striations; facial plate most distinct and projecting in Chylizinae (Fig. 3), sometimes short to absent in *Psila* (Fig. 18) and absent in *Loxocera* (Fig. 8), but transverse striations still faintly evident; face gradually or abruptly receding ventrally in Psilinae, making head subtriangular in lateral view (Fig. 17). Clypeus well-developed, nearly flat and plate like with anterior margin truncated or with medial emargination; palpus varying from small and subcylindrical to large and laterally compressed; labium with short setulae densely to sparsely arranged or restricted to ventral margin.

Thorax. Katatergite slightly (Psilinae; Fig. 17), modestly (*Electrochyliza*, Belobackenbardiinae; Fig. 12) or strongly (Chylizinae; Fig. 5) bulging. Precoxal bridge absent; postmetacoxal bridge absent or present (Chylizinae). Prosternum small, weakly sclerotized and bilobed, with narrow, lightly sclerotized strip running anterior to sclerites; posterior surface raised. Spiracles subcircular, setulose; posterior spiracle angled dorsally; one or two grooves extending ventrally from anterior spiracle, sometimes ending in a pit. Metanotum with small, laterally directed dorsolateral lobes meeting abdomen.

Wing. (Figs 395–398) Clear to lightly infuscated or with slight patterning, often along veins. Anal lobe and alula well-developed, sometimes slightly reduced. Cell br narrowed on distal section; costa with subcostal break; subcosta usually continuing to costa at near right angle as hyaline weakening in membrane, and sc cell past this break elongate and usually at least faintly arched, but strongly bulging in Chylizinae (less pronounced than state seen in Opomyzidae); in Belobackenbardia (Fig. 395), cell sc straight and sharply narrowing apically, and subcostal vein abutting vein R_1 on distal half (perhaps fused), indistinct apically where it is only distinct as hyaline weakening cutting across much shallower sc cell. Veins R_{4+5} and M_1 subparallel; M_1 strongly arched in some Psilinae (Figs 7, 398). Cells bm and cu*p* reaching, or nearly reaching, level of apex of R_s, with cell *cu*a slightly (Psilinae) to substantially (Chylizinae) shorter. Vein CuA straight. M_4 and CuA+CuP not reaching wing margin. Upper calypter with hairs long to moderate in length.

Legs. Hind femur of *Loxocera* usually with patch of ventral subapical pile, Chylizinae usually with small, microtrichose ovate pit.

Abdomen. Tergites and sternites separate, sternites not narrowed. Setae pronounced posterolaterally on tergites. Sternite 1 bare or nearly so. Spiracles 1–7 in membrane, 7th embedded in tergite in Belobackenbardiinae; 7th spiracle sometimes absent in male.

Male genitalia. (Figs 19–39) S6 separate, symmetrical, sometimes with posteromedial emargination that may nearly divide sclerite. S8 dorsal, sometimes bare, reduced (Psilinae) to absent (Belobackenbardiinae, Chylizinae); sometimes fused to T6; sometimes with additional vestiges laterally that (in part) may represent S7 (positioned left laterally in other families). Epandrium and surstylus largely immobile, strongly secured to membrane laterally. Epandrium broad, shallow. Cerci simple, sometimes fused. Surstylus present or absent (Psilinae). Subepandrial sclerite absent (Chylizinae, some Psilinae) or composed of two flat, separate lobes (large and basally confluent in Belobackenbardiinae). Hypandrium well-developed, with several medial setae (except Belobackenbardiinae); sometimes with posterolateral apodeme (Chylizinae); arms usually fused posterodorsally. Some Psilidae with medial portion of hypandrium removed as floating ventral plate (Figs 33–34), with phallapodeme assuming its original position to form "phallapodemic plate" (see Figs 38–39); phallapodeme otherwise rod-like, sometimes folded longitudinally (Belobackenbardiinae; Fig. 24), sometimes widened near base (Chylizinae; Fig. 31), sometimes fused to remainder of hypandrium to form broad, flat plate that may be flat, folded, curved, T-shaped or bifurcate (Psilinae; Fig. 38). Pregonite thin and band-like (Chylizinae; Fig. 31) to large and lobe-like (Belobackenbardiinae (Fig. 25), Psilinae (Fig. 38)); sometimes absent. Postgonite absent. Epiphallus absent. Phallus composed of fused basiphallus and distiphallus; shape flat and linear, bifid, pouch-like or globose; sometimes fused to base of phallapodeme. Ejaculatory apodeme very small with duct sometimes extremely widened.

Female genitalia. (Figs 40–46) Membrane between segments 7 and 8 long, narrow, only short and unmodified in Belobackenbardiinae (Figs 41–43). Except for Belobackenbardiinae, segments 8 and 10 narrow, telescoped within segment 7 at rest, with minute longitudinal grooves; these segments usually distinct from each other, with segment 8 longer and sclerites sometimes divided longitudinally; S8 and T8 mostly undifferentiated; Belobackenbardiinae with S8 narrow and T8 high, laterally compressed. *Loxocera* abdomen variably modified apically, including lateral compression past segment 6. Cerci short, separate to mostly fused, subcylindrical to compressed; sometimes fused to T10; lateral peg-like sensillae absent in *Electrochyliza,* Belobackenbardiinae and some Psilinae. Internal components weakly sclerotized and unpigmented (base partially so in Belobackenbardiinae on spermatheca (duct?) and accessory glands); Belobackenbardiinae (Fig. 44) with spermathecae and ducts represented by short narrow, basally pigmented tubules, ventral receptacle perhaps represented by cluster of subspherical swellings apically; Chylizinae (Fig. 46) with spermathecae sac-like, distal section of duct wider with basal grooves, and ventral receptacle (or accessory gland?) flagellar with filamentous apical tubule; Psilinae (Fig. 45) genitalia of uncertain homology, with spermathecae perhaps reduced to apical swellings on widened genital chamber, and ventral receptacle not evident.

Variation—Electrochyliza (fossil). Differs from other Psilidae as follows: frons with minute longitudinal wrinkles following angle of ocellar triangle, which does not attain anterior margin; ventral facial plate, semicircular, height ¼ medial width, with two transverse striations; M_1 shallowly arched; longitudinal grooves on ovipositor apparently absent.The following structures could not be observed: thoracic sternites, postabdominal spiracles, surstylus and male and female internal genitalia.

Somatiidae Hendel, 1935

(Figs 65–66, 71–80, 401)

Type genus: *Somatia* Schiner 1868: 245, by Hendel (1935: 56). **Type species of genus:** *Somatia xanthomelas* Schiner, 1868: 246 [=*Tephritis aestiva* Fabricius, 1805: 318], by original designation.

Somatiidae is a small family of seven morphologically similar Neotropical species in the single genus *Somatia,* with only *S. aestiva* (F.) encountered with relative frequency. The genus was first keyed and then catalogued by Steyskal (1968c, 1970a), and later reviewed by Lonsdale & McAlpine (2010).

Biology. Marshall (2006) first observed adult *Somatia* feeding on a dead caterpillar. Species have also been observed at the extrafloral nectaries of several plants. Carvalho-Filho (2017) found numerous specimens feeding on the underside of *Solanum stramonifolium* Jacq. (Solanaceae) leaves, as well as one specimen "licking the calyx" of *Pleonotoma jasminifolia* (Kunth) Miers (Bignoniaceae). The author speculated that extra-floral nectaries may explain the presence of *Somatia* specimens on other plants mentioned in the literature, including legumes (Marshall, 2012). Hespenheide (1985) also noted that *Somatia* "are common visitors at extrafloral nectaries of other plants", and Grimaldi (2016) found *Somatia* at nectaries of *Passiflora* (Passifloraceae).

Immature stages. Unknown.

Adult Diagnosis. Relatively small to medium-sized yellow and black species with stout thorax and broad, downturned abdomen. Antenna elbowed, first flagellomere elongate; pedicel with dorsal seam; arista bipectinate. Frons produced anteriorly as flat, widening plate. Outer vertical, fronto-orbital, ocellar and sometimes inner vertical setae absent; vibrissa small; postocellars convergent (divergent in other Diopsoidea). Postpronotal, proepisternal and katepisternal setae absent; notal setulae long and dense; one dorsocentral, one prescutellar acrostichal and one anepisternal seta; 2–3 pairs of scutellar setae on small tubercles; notopleural setae both closely set posteriorly. Mid tibia with three ventroapical setae. Back of head with strong dorsal semicircular carina and pronotum produced as short "neck". Transverse suture complete. Suture between T1 and T2 medially crenulated. Precoxal bridge absent, postmetacoxal bridge present. Wing with alula and anal lobe weak; cells bm and cup long; costa with sc break; sc complete.

Adult Definition. Relatively small to medium-sized flies with a stout, bulging thorax and narrow "neck" (=pronotal collar) (Figs 71–77); body length 3.5–5.2mm. Colour mostly yellow with contrasting black pattern, but *S. lanei* Papavero mostly dark; setae and setulae yellow with setae sometimes darker and abdominal setulae on brown pattern sometimes also darker.

Chaetotaxy: 0–1 inner vertical; 0 outer vertical; 0 fronto-orbital; 0 ocellar; 1 postocellar (convergent); vibrissa small. 0 presutural intra-alars; 0 postpronotal; 2 posterior notopleurals (likely representing anterior and posterior setae); 2 posterior supra-alar (one sometimes duplicated on one or both sides); 1 posterior intra-alar; 1 dorsocentral; 1 acrostichal; 2–3 scutellars on minute tubercle; 0 proepisternal; 1 anepisternal; 0 katepisternal. Pedicel with small marginal setae including longer dorsal and ventral seta; frons densely setulose laterally (inclinate inner row and erect outer row, becoming more scattered anteriorly and posteriorly) and with broad, shining medial region; postocular setae short and in single row laterally, becoming longer, more numerous and scattered dorsally; back of head with longer ventromarginal setae. Setulae long, straight and dense on scutum and abdominal tergites, sometimes difficult to distinguish from short setae; scutellum with similar setulae that are paler, denser and shorter; pleuron with short to long erect setulae mostly restricted to anepisternum and katepisternum; posterior spiracle with several outstanding setae near posterior margin. Body glabrous with microsetulae restricted to metanotum and portions of pleuron, including katepimeron. Fore tibia sometimes with slightly pronounced ventroapical setula; mid tibia with three ventroapical setae.

Head. Antenna elbowed, first flagellomere flat and relatively broad, length more than twice width (extending to lower margin of face); pedicel with dorsal seam; arista bipectinate. Frons produced anteriorly as flat widening plate covering base of antenna; ocelli near vertex. Face with shallow, wide ridge below antennal bases. Back of head flat above foramen with prominent semicircular carina (setulose dorsomedially). Clypeus broad, well-developed; palpus subcylindrical; labium with long apical processes and one or two pairs of subapical setae.

Thorax. Large and bulging, including scutellum; with narrow pronotal collar; lateral corners of scutellum extended along margin of scutum as carinae. Transverse suture complete. Greater ampulla absent. Presternum vestigial. Anterior spiracle slit-like, oblique, in crease between bulging anepisternum and postpronotum. Katatergite flat. Metathorax with narrow, shallow subcylindrical extension meeting abdomen. Coxopleural streak present. Precoxal bridge absent; prosternum broad, flat along raised posterior margin and with shallow anteromedial point; postmetacoxal bridge high, well-developed.

Wing. (Fig. 401) Wing slightly narrowed with anal lobe and alula reduced. Basal stripe, variably developed medial stripe and anterior and anterodistal margins dark brown. R_{2+3} and M_1 convergent apically. Apical section of M_4 present or absent; M_4 and CuA+CuP not reaching wing margin. Cells bm and cup long, exceeding apex of R_s; costa with sc break; sc complete. Calypter almost linear, hairs of moderate length.

Legs. Slender, shifted forward, with apices of coxae approximate; base of elongate fore coxa dorsally removed to ventrolateral margin of collar.

Abdomen. Dorsum broadly dome-like with T2 largest; terminalia short, stout, much narrower and held under apex of abdomen; sternites much narrower, forming narrow medial line. T1 and T2 fused with suture complete, raised and with minute crenulations along posteromedial surface (Fig. 77, arrow). T2 with broad anterolateral bulge. Spiracles 1–6 in membrane; 7th spiracle in tergite (Fig. 78). Following description of terminalia based on dissections of *S. aestiva*.

Male genitalia. (Figs 78–80) S6 offset, nearly symmetrical. S7+8 dorsal, band-like, encompassing spiracles, slightly longer on left side. Epandrium semicircular and band-like, lateral margins meeting bases of asymmetrical surstyli that are sinuate and ventrally approximate (left surstylus treated as "postgonite" in Lonsdale & McAlpine (2010)). Cerci broad, meeting medially, appearing as ventral setose bands on inflated, membranous perianal region; sclerotized band in membrane below cerci. Hypandrium, epiphallus, and gonites absent. Phallapodeme free within abdomen, articulating with fused basiphallus + distiphallus. Distiphallus, long, black, ribbon-like, partially coiled and exposed. Ejaculatory apodeme large with fan-like blade grading into basally narrow stem; sperm pump with large membranous fringe encompassing base of apodeme.

Female genitalia. (Figs 65–66) T7 and S7 fused into stout oviscape enclosing spiracles. T8 short and wide, wrapping around segment laterally; S8 subrectangular, wider than long. T10, S10 and cercus short, wide and broadly rounded. Spermatheca slightly more than two times longer than wide, subcylindrical with rounded ends, dark pigment and numerous minute papillae; ducts relatively short, not pigmented apically. Ventral receptacle short, flagellate.

Syringogastridae Prado, 1969

(Figs 124–142, 404)

Type genus: *Syringogaster* Cresson 1912: 392, by Prado (1969: 1). **Type species of genus:** *Syringogaster rufa* Cresson, 1912: 393, by original designation.

Syringogastridae is a small, well-defined family of 22 extant and two fossil species in the genus *Syringogaster* that was last revised by Marshall *et al.* (2009). Marshall *et al.* (2009) described 11 new species and divided the genus into four species groups following a phylogenetic analysis, with one of these groups consisting of the two known fossil species discovered in Dominican amber. Species are found throughout the Neotropics, with *S. subnearctica* Feijen narrowly extending into Nearctic Mexico.

Biology. Most species are found below 800m (but rarely up to 1400m) in lowland tropical forests, often on or underneath large leaves. Adults are uncommonly encountered but they can be abundant locally, sometimes as multi-species assemblages; while most are found singly, they sometimes occur in large groups, possibly representing mating aggregations (Marshall *et al.,* 2009; Marshall & Buck, 2010). Adults have been attracted to sprayed maple syrup solutions and collected at extra-floral nectaries (Marshall *et al.,* 2009). “Bubbling” behaviour between mating pairs been observed, and females in mating aggregations were seen with swollen abdomens that were perhaps filled with honeydew (Marshall *et al.,* 2009). Large numbers of one species were collected on “low, lush vegetation flanking a sea-level path”, and other specimens have been collected in primary forest, secondary forest, a garden, a swampy area at a forest edge, on foliage and “on pendulous *Heliconia* inflorescences” (Marshall *et al.*, 2009). Adults resemble pale to dark ants, a similarity exaggerated by their wing shape and pattern; field observations report very accurate ant-like walking behaviour (Papavero, 1964; Marshall *et al.*, 2009; Marshall & Buck, 2010). Larvae and puparia are unknown, but eggs of *S. atricalyx* (photographed) and *S. lopesi* are described in Marshall *et al.* (2009), and the egg of an unidentified species is briefly described in Meier & Baker (2002).

Immature stages. Unknown.

Adult Diagnosis. Small, slender, ant-like (Figs 124–128); wing length 4.0–6.0mm. Colour yellow to dark brown or partially patterned. Inner verticals, fronto-orbitals, postocellars, vibrissae and most thoracic setae absent, excluding apical scutellar and posterior supra-alar. Antenna elbowed with first flagellomere slightly elongate; pedicel with dorsal seam. Back of head with supracervical collar and anterior portion of pronotum produced into short “neck”. Thorax mostly smooth; with sharp humeral and supra-alar carinae; posterior spiracle with surrounding ridge and processes. Precoxal bridge present; postmetacoxal bridge present; thorax produced at narrow point of attachment to abdomen. Enlarged hind femur with two rows of spines ventrally; hind tibia curved and with double sclerotized ridge ventrally (separate, not united as in Megamerinidae); fore and mid femora with row of glands posteroventrally (Fig. 129); mid and hind tarsi with “sawlines” (Fig. 125). Wing variably patterned; alula absent; upper calypter margin pubescent, not long-haired; sc incomplete; costa unbroken (Fig. 404). Abdomen petiolate with segments 1–3(4) fused; external terminalia small, on underside of abdomen.

Adult Definition. Wing length 4.0–6.0mm. Ant-like, with form accentuated by slender petiolate abdomen and narrow patterned wings closely appressed to body (Figs 124–128). Colour yellow or reddish-orange with brownish to dark brown pattern, sometimes mostly dark and/or with light yellow to white legs.

Chaetotaxy: 0 inner vertical; 1 outer vertical; 0 fronto-orbitals; 0–1 ocellar (short to very long); 0 postocellars; vibrissa absent, but vibrissal angle sometimes with prominent setae. 0 presutural intra-alars; 0 postpronotals; 0 anterior notopleurals; 0–1 small, setula-like posterior notopleural; 1 posterior supra-alar (on minute tubercle); 0 posterior intra-alars; 0 dorsocentrals; 0 acrostichals; 1 scutellar (on minute tubercle); 0 proepisternals; 0 anepisternals; 0 katepisternals. Parafacial and pedicel without outstanding setae. Back of head microsetulose. Metanotum and dorsal regions of pleuron microsetulose (remainder of pleuron glabrous); pleuron with scattered thin setae that are concentrated anteroventrally and on metapleuron, and on femora and abdomen. Posterior spiracle with dense setulae and several golden hair-like setae. Fore femur with anteroventral row of 2–12 small, stout pointed spinules, and sometimes with single posteroventral spinule; distal posteroventral margin also with rows of gland openings (Fig. 129). Hind femur with with both anteroventral and posteroventral rows of 4–15 spinules. Fore tibia with short brush of densely clustered pale setulae. Mid tibia with small ventroapical seta. Mid and hind tarsi with "sawlines" (longitudinal rows of dark, flattened setae; Fig. 125)—present on anterior and posterior surfaces of basal 3–4 tarsomeres on mid and hind legs, excluding posterior surface of hind basitarsomere.

Head. Head partially globose with back of head mostly to partially flat. Antenna elbowed; pedicel with dorsal seam; first flagellomere elongate (2–3 times longer than wide), flat, dorsally carinate; arista sparsely short plumose (possibly bipectinate). Ocellar triangle glabrous or tomentose, nearly attaining anterior margin of frons; orbital plate not differentiated; remainder of frons matte and minutely setulose with setulae sometimes slightly longer anteromedially (never appearing as interfrontals); ocelli separated from vertex by area approximately as long as tubercle. Face narrow; microscales occurring at least medially; gena shallow; parafacial narrow, tomentose. Clypeus large, prominent; palpus narrow, subcylindrical. Back of head with short collar derived from semicircular carina with dorsomedial patch of microsetulae. Anterior ommatidia enlarged.

Thorax. Pronotal collar present, meeting corresponding process on back of head. Proepisternum shifted dorsally, displacing postpronotum posteriorly. Scutum with humeral and supra-alar carinae; notopleural and anepisternal junction sometimes also with carina ("notopleural carina"); scutum slightly bulging lateral to dorsocentral rows, sometimes obvious as one pair of flat ovate notopleural and supra-alar pads. Katatergite flat. Precoxal bridge present with suture between prosternum and proepisternum absent, setulose laterally, surface raised; postmetacoxal bridge present, fused to metasternum between hind coxae. Scutellum small, short, preceded by deep anterior and lateral grooves; subscutellum vestigial to absent. Greater ampulla absent. Metanotum with high, narrow cylindrical process meeting abdomen. Posterior spiracle prominent; flanked ventrally by bilobed ridge and anteriorly by two processes separated by circular notch.

Wing. (Fig. 404) Narrow, slender, wth alula and anal lobe highly reduced. Patterned with three coalescing transverse bands, or dark with three clear transverse spots. Vein bm-m absent or faint. CuA straight to shallowly rounded. Cell *cu*a exceeding bm by usually more than length of CuA+CuP. M_4 not reaching wing margin; CuA+CuP sometimes absent or reaching wing margin as weak vein or fold. Costa unbroken; sc incomplete, sometimes partially coalescing with R_1. Calypter reduced with short to medium-length hairs.

Legs. Legs slender with hind femur swollen; hind tibia correspondingly curved and stout with two ventral rows of black sclerotized ridges (separate, not fused), apically with shallow triangular process. Fore coxa broadly separated from mid coxa, inserted ventrolateral to shallow collar. Fore and mid femora with posteroventral row of gland openings; glands clustered in circular pits (often along distinctly raised surface), with ducts long, narrow and with slightly widened apical chamber (Fig. 129).

Abdomen. Abdomen petiolate, widest past T3 and narrowed at pregenital segments, under which the terminalia is partially to mostly hidden (Figs 140–141); T3 and sometimes also T4 fused to syntergite T1+2, suture past T1 and sometimes T2 absent. Sternites much narrower than tergites, sometimes weakly sclerotized and mostly indistinct aside from presence of setae; wider than long past segment 4; S1 with very small, dark transverse posterolateral ridge. Spiracle 1 in margin of tergite, spiracles 2–4 in membrane, spiracles 5–7 variable.

Male genitalia. (Figs 134–139) S6 of variable shape, sometimes reduced or medially divided. S8 short, bandlike, fused to narrower, ventral S7, essentially symmetrical, enclosing 7th spiracles. Epandrial sides often subparallel medially and sometimes with one pair of marginal dorsolateral lobes. Cerci small but well-developed, usually fused along most of length. Surstylus movable, usually more than half length of epandrium, often rounded apically, sometimes narrow. Subepandrial sclerite reduced to one pair of small lateral sclerites connected by broad membrane. Hypandrium with arms joined posterodorsally and anterior bridge usually complete; setose with pronounced ventrobasal lobe. Phallapodeme well-developed, slightly carinate apically; usually separate from hypandrium, with slender processes ("phallic guides") reaching hypandrium. Pregonite lobate, setulose, articulating with hypandrium. Postgonite dark, rod-like, extending from base of phallapodeme to pregonite. Basiphallus large, wedge-shaped. Epiphallus absent. Distiphallus broad with apex sac-like, twisted and spinulose; with one pair of ventral bands. Ejaculatory apodeme with pale blade sometimes reduced, stem sometimes with medial setula-like structures; sperm pump shallow, venter with ill-defined sclerotization sometimes cup-like, sometimes extending to base of duct.

Female genitalia. (Figs 140–142) T7 and T8 short, wide. T10 and S10 simple, short. Terminal segments short, barely telescoping. Cercus narrow, relatively long and thin. Spermathecae telescoped and transversely wrinkled, in two pairs on long duct with short apical branches (paired bodies close, contiguous or fused); spermatheca and apex of duct pigmented. Ventral receptacle short, sac-like. Apex of genital chamber with lightly sclerotized dome ("vaginal plate" in Marshall *et al*. (2009)) arched over shallow lateroventral elaborations of membrane.

Family Descriptions—Superfamily Nerioidea

Cypselosomatidae Hendel, 1931

(Figs 205–232, 413–414)

Type genus: *Cypselosoma* Hendel 1913: 105, by Hendel (1931: 5). **Type species of genus:** *Cypselosoma gephyrae* Hendel, 1913: 105, by original designation.

Cypselosomatidae inlcudes 13 species of small-bodied flies in three extant genera—*Clisa* McAlpine (2 species), *Cypselosoma* (2 species) and *Formicosepsis* (9 species). Species are known from Australia, Lord Howe Island (*Clisa*), Nepal (*Cypselosoma*) and Southeast Asia (*Cypselosoma*, *Formicosepsis*) to Taiwan (*Formicosepsis*). The monotypic fossil genus *Cypselosomatites* Hennig was described for Cypselosomatidae (Hennig, 1965), but later moved to Micropezidae by D.K. McAlpine (1998b).

D.K. McAlpine (1966) reviewed and keyed the two cypselosomatid genera known at the time, and later briefly treated the family for description of his new genus *Clisa* (D.K. McAlpine, 1993). His 1966 paper also contrasted the Cypselosomatidae to the Neriidae and Micropezidae, compared the species of *Cypselosoma*, and provided thorough notes on the cave-dwelling *Clisa australis* (as *Cypselsoma australe*). Cypselosomatidae was catalogued in the Oriental and Australian Regions by Steyskal (1977a) and Mathis (1989a), respectively. The two species of of *Cypselosoma* are differentiated by Shatalkin (2014). *Formicosepsis* was last revised in Andersson (1976), who divided the six species known at the time into two subgenera (*Formicosepsis* Meijere s.s. and *Lycosepsis* Enderlein), mostly on the basis of an apical tooth on the scutellum and fore femoral spines in *Lycosepsis*; *Formicosepsis* s.s. was split into two species groups. Papp *et al.* (2006) described three Thai species for *Formicosepsis* and *Lycosepsis*, but did not provide an explanation as to why the two genera were given equal generic standing. Recognition of *Lycosepsis* is probably unwarranted, at least as a full genus, considering both the small number of described species and the uncertain monophyly of both groups.

Biology. Adults, puparia and larvae of the Australian *Clisa australis* (McAlpine) were discovered by D.K. McAlpine (1966) in a high-humidity section of a cave hosting a colony of the bat *Miniopterus schreibersi* (Kuhl). Larvae were found in dung piles on the cave floor, and dung was recovered from the larval gut; adults were observed on and above the cave floor, with specimens sometimes observed copulating on the dung. Specimens have also been recovered over latrines at the edge of forest reserves (D.K. McAlpine, 1993), providing a similar "enclosed, humid environment". *Clisa disneyi* McAlpine was collected on Lord Howe Island in a "stunted, mossy rainforest on the summit of Mount Gower". Larvae of a *Cypselosoma* species tentatively identified as *C. gephryae*, some of which formed puparia, were recorded on rotting banana plants by Curran (1931). *Formicosepsis* species have been found at elevations above 900m near streams in ravines, sometimes near tea plantations (Andersson, 1976), on foliage in rainforests (D.K. McAlpine, 1998a) and on a cut banana stem (Marshall, 2012); specimens have also been cultured on dung (S. Marshall, pers. comm.). Malaise trap samples from Thailand suggest that *Formicosepsis* can sometimes be locally abundant and collected in pans baited with dung.

Immature stages. Puparia and third instar larvae of the Australian *Clisa australis* were described by McAlpine (1966).

Adult Diagnosis. *Cypselosoma* (Figs 205–210) and *Clisa* relatively compact; *Formicosepsis* (Figs 211–215) more ant-like, somewhat resembling Strongylophthalmyiidae but with head sleeker and wing narrower; 2.5–5.0mm long. Face membranous, at least ventromedially. Interfrontal present (Fig. 209) (likely homologous with anterior fronto-orbital), sometimes minute to absent; 3 latero- to anteroclinate fronto-orbitals; postocellars divergent, removed from ocellar tubercle; vibrissa present. 4–6 dorsocentrals, with 1–2 smaller setae along dorsocentral line anteriorly; 0–6 acrostichal setae, with at least 1 presutural when present. Pleuron only with proepisternal seta and sometimes one or two very small katepisternals. Katepisternum bulging with dorsal margin sharply angled inwards (white region in Fig. 206). Femora usually with distinct ventroapical spines; mid tibia with numerous setae. Vein bm-m absent; ultimate section of M_4 usually absent (short in some *Cypselsoma*) and posterodistal corner of cell dm rounded (angulate in *Cypselsoma*, but with apex of M bowed); veins R_{4+5} and M_1 converging; costa with sc break; vein sc ending freely in subcostal cell (Figs 413–414).

Adult Definition. Body length 2.5–5.0mm. Colour mostly brown to black, often with yellow and white or brownish patches, mostly on head, legs, anterior surface of thorax and dorsum of katepisternum; halter brown to light brown with apex of knob brownish to white. Body relatively small; compact in *Cypselosoma* (Figs 205–210) and *Clisa*; very slender and ant-like in *Formicosepsis* (Figs 211–215).

Chaetotaxy: 1 inner vertical; 1 outer vertical; 3 fronto-orbitals (proclinate with posterior seta reclinate); 1 ocellar; 1 postocellar (divergent to subparallel, relatively large); 1 interfrontal (smaller than fronto-orbitals and hair-like to inconspicuous in *Formicosepsis*, but nearly as large as anterior fronto-orbital in *Cypselosoma* (Fig. 209); likely homologous with fronto-orbital); vibrissa present; back of head sometimes with additional paravertical seta dorsolaterally (Fig. 208); pedicel with line of marginal setae including one large dorsal; several small weak genals, 1 subgenal (possibly enlarged posterior genal setula); postoculars in single line, sometimes setula-like or only present dorsally (*Cypselosoma*); labium usually with one large basal pair of setae and at least one apical pair. 1 presutural intra-alar; 0–2 postpronotals; 2 notopleurals; 2 posterior supra-alars; 0 posterior intra-alars; 4, 5 (*Formicosepsis, Clisa disneyi*) or 6 dorsocentrals (*Cypselosoma* and *Clisa australis*), including at least one presutural, and *Clisa* and *Cypselosoma* with one or two smaller setae in front of anterior dorsocentral; 6 acrostichal setae in *Cypselosoma*, 1 or 2 presutural to sutural pairs in *Clisa,* and 0–6 finer pairs in *Formicosepsis*; 1 apical scutellar on small tubercle; lateral scutellar smaller than apical if present, sometimes setula-like, sometimes shifted medially; 1 proepisternal (reduced to absent in *Formicosepsis*); 0 anepisternals; 0 katepisternals (if 1 or 2 present, then very small and setula-like); prosternum bare. Fore femur with row of stout anteroventral spines, and with at least 1 long, stout, posteriorly directed seta subapically (Fig. 207); mid and hind femora often with 2–5 spine-like anteromedial and anteroventral setae distally (length variable), often on distinct tubercle (*Formicosepsis* with only 0–2 spines); hind femur usually with anteroventral of spines distally with one or two of these enlarged (*Formicosepsis* also with row of similar posteroventral spines that are sometimes indistinct to absent, and sometimes lacking anteroventral setae). Fore tibial brush discrete, pale, contrasting surrounding dark setulae (Fig. 214). Mid tibia with medial setae dorsally and posteriorly (sometimes reduced to only 1–3 on one or both sides in *Formicosepsis*); ventrally with one to several medial setae; apically with at least one distinct anteroventral seta, but sometimes also with several additional small to moderately sized setae around margin.

Head. Antenna porrect to slightly elbowed; first flagellomere discoid; arista bare, inserted basally to submedially. Frons truncated along anterior margin and slightly projecting, slightly narrowing anteriorly; pilose medially, sometimes excluding part or all of ocellar triangle; notum (except *Cypselosoma*) and frontal vitta with fine to coarse microsculpturing; ocellar triangle shining, elongate with margins usually indistinct; ocelli shifted anteriorly, removed from postocellars. Ommatidia slightly larger anteromedially in some *Formicosepsis*. Face membranous (sometimes only weakly sclerotized), excluding well-sclerotized dorsolateral or lateral regions. Gena usually shining and bulging, more than 1/3 eye height, but reduced to narrow strip in *Formicosepsis*; postgena and occiput well-developed, sometimes broad. Back of head with semicircular carina that is produced into small dorsomedial lobe in *Formicosepsis*. Clypeus large, broadly rounded; palpus subcylindrical.

Thorax. Notum entirely microsetulose to glossy, or with fine pruinose pattern (some *Formicosepsis*); pleuron smooth, mostly glossy with setulae and pruinosity largely restricted to venter of katepisternum. Greater ampulla present. Coxopleural streak usually weak to absent; posterior margin of anepisternum grooved; katepisternum and meron fused; katepisternum bulging with dorsal 1/3 directed inwards, forming broad "shelf" (note white area in Fig. 206) (similar but much shallower shelf seen in some Neriidae); dorsal katepisternal suture short, ending in broad proepisternum. *Formicosepsis* with developed pronotal collar, and anterodorsal margin of katepisternum and postpronotum wrapping around scutum; thorax and abdomen, long, slender and exhibiting extensive fusion of sclerites. Precoxal and postmetacoxal bridges absent. Prosternum fused to anteroventral margin of fused katepisterna, with discrete bulge between base of widely separated coxae and anteromedial fossa. Presternum sometimes reduced. Scutellum flat to convex, sometimes relatively short; some *Formicosepsis* with upturned apical spine.

Wing. (Figs 413–414) Clear to lightly infuscated, or clouded with clear bands. Anal lobe and alula well-developed (*Clisa*, *Cypselosoma*) or strongly reduced (*Formicosepsis*). Vein R_{2+3} closely following costa along length; veins R_{4+5} and M_1 converging. Vein bm-m absent. Vein r-m sometimes oblique; sometimes short. Cell *cu*a short, but sometimes nearly reaching level of subcostal vein apex. Ultimate section of vein M_4 usually absent (short in *Cypselsoma*) and posterodistal corner of cell dm rounded (angulate in *Cypselsoma*, but with apex of M_4 bowed). Vein CuA slightly rounded to straight. Costa with sc break (sometimes indistinct); vein sc ending freely in subcostal cell. Calypter hairs short.

Legs. Legs slender; femora slender to relatively stout; hind tibia sometimes slightly compressed laterally. Mid tibia swollen in *Cypselosoma*.

Abdomen. Spiracles 1–6 in membrane, 7th spiracle enclosed by sclerite (Figs 217, 223, 230). *Formicosepsis* with T3 fused to T1+2. Pregenitalic sternites slightly longer or shorter than wide; S1 particularly short in *Clisa* and *Cypselosoma*; sternites of *Formicosepsis* considerably narrower with midline bare.

Male genitalia. (Figs 216–222) Terminalia essentially symmetrical. S6 with reduced setation; overlapping and partially articulating with S7. S7 ventral, fused with S8 to form complete ring. S8 large, dome-like, with dorsomedial surface pronounced and posterolateral margins with small emargination; with one pair of large, stout setae. Subepandrial sclerite flat, V-shaped, with apical seta. Epandrium shallow and narrow, usually with one pair of larger posterodorsal setae. Cerci narrow, fused via membrane, distal to margin of epandrium. Surstylus as long as cercus, narrow. Hypandrium, narrow, arms fused. Phallic plate very long, narrow, unbroken. Phallapodeme rod-like, without extensions to hypandrium; base deviated and plate-like. Postgonite narrow, band-like, and meeting each other at or near point of fusion to hypandrium. Postgonite short, band-like, with small setose apical bulb; base textured, meeting apex of postgonite. Epiphallus absent. Distiphallus flat and rod-like, sometimes with membranous apical flagellum. Ejaculatory apodeme stout base grading into short, weakly sclerotized and asymmetrical blade; sperm pump clear.

Female genitalia. (Figs 223–232) T7 and S7 fused into complete oviscape that is widest subbasally and strongly tapered apically; 7th spiracles ventrolateral. Remaining terminalia very narrow, entirely telescoped within oviscape. T8 and S8 divided longitudinally, roughly textured with tooth-like denticles that are also found along intersegmental membrane to segment 10. T10 with two apical setae; S10 with few apical setae and numerous empty sockets extending along most of length onto short internal process with apical disc. Cerci short, approximate and minutely setose. Genital chamber sometimes with weakly sclerotized transverse folds. Ventral receptacle linear, and narrow to relatively broad. 2 clear or pigmented spermathecae; shape sac- or rod-like, with one sometimes atrophied; duct long and thin, or short, flat and folded.

Fergusoninidae Tonnoir, 1937

(Figs 191–204, 411)

Type genus: *Fergusonina* Malloch 1924: 337, by Tonnoir (1937: 129) [as subfamily “Fergusoninae”]. **Type species of genus:** *Fergusonina microcera* Malloch, 1924: 338, by original designation.

Fergusoninidae has 40 described species in the genus *Fergusonina* (Purcell *et al.,* 2016), but Scheffer *et al.* (2017) identified 85 “putative species” in their study, and there are potentially upwards of hundreds of additional species awaiting discovery (Scheffer *et al.,* 2004; Purcell *et al.*, 2013). Species can be difficult to differentiate, with diagnosis often depending on minutae of the male and female genitalia—see Taylor (2004). Molecular sequence data are currently being used to delimit and refine species boundaries and relationships for the *Melaleuca*-feeding *Fergusonina* (Scheffer *et al*., 2004). Purcell *et al.* (2016) developed a phylogeny correlating the structure of the sclerotized larval dorsal shield to gall type, and also supported the use of host and larval morphology in diagnosis. An updated molecular phylogeny of the family utilizing multiple and protein-coding genes is being developed (Purcell *et al*., 2016; S. Scheffer, pers. comm.).

The family is Australasian in distribution, with species known from Australia, India, Papua New Guinea, the Philippines and New Zealand (Harris, 1982; Taylor *et al.,* 2007). The last keys to species were provided by Tonnoir (1937), who recognized 20 species at the time, and by Taylor (2004), who keyed species associated *Melaleuca*. A catalogue to Australian species was provided by Evenhuis (1989g). The complete mitochondrial genome of *Fergusonina taylori* Nelson & Yeates was published by Nelson, Cameron & Yeates (2011).

Biology. All species of *Fergusonina* for which biology is known are gall-feeders in the living tissue of Myrtaceae and are involved in an obligate mutualistic association with nematodes in the genus *Fergusobia* Currie (Tylenchida: Neotylenchidae). This represents the only recorded mutualism between flies and nematodes. This relationship was first discovered by Morgan (1933) and then described by Currie (1937) for taxa reared from *Eucalyptus*.

Eucalyptus species are host for most known *Fergusonina*, but flies have also been reared from over 65 species of *Melaleuca*, *Leptospermum, Sygyzium* and *Metrosideros* (Purcell *et al.*, 2013; Scheffer *et al.*, 2017). Females select ovipositions sites in areas of new growth, specifically in the developing buds of shoots, inflorescences, flowers, leaves or stems of the host plant, and the number, location and morphology of the resultant galls appear to be characteristic for each *Fergusonina/Fergusobia* pair (Currie, 1937; Giblin-Davis *et al.*, 2003; Purcell *et al.*, 2015). As a result, while multiple species pairs may be found on the same host plant, the galls of each are usually visually distinct (Taylor, 2004). Galls may house a single larva ("unilocular") or many larvae ("multilocular"), each in its own locule (Purcell *et al.*, 2015). Ye *et al.* (2007) reported galls containing tens to hundreds of larvae. Larvae in multilocular galls may have been laid by one or more females (Purcell *et al.,* 2015). As many as four species of fly can be found on a single host species, and one species of fly may be found on one or more species of host plant, usually within the same host subgenus, but sometimes in more distantly related hosts if those hosts are sympatric, possibly as a result of the availability of novel host choice via artificial plantings (Purcell *et al.*, 2017).

Overall host associations largely appear to be conservative, with all species restricted to a single host genus in Scheffer *et al.* (2017), who analyzed fergusoninid phylogeny with respect to host usage and gall type. The authors found 73% of species on only a single host species, but they noted that this was a likely underestimate of monophagy in the group. Other studies found host usage among broad-leaved *Melaleuca*-feeders to be similarly conservative, where flies showed fidelity to only one or two host species (Taylor, 2004; Scheffer *et al.*, 2004). This is in contrast to the similarly plant-feeding Agromyzidae, whose relatively high levels of monophagy are likely only a result of limited sampling and likely to decrease substantially given further study.

There are 42 species of *Fergusobia* presently described (Davies *et al.,* 2010, 2016). The nematode-fly pairing is an exclusive relationship between one species of nematode and one species of fly (Davies & Giblin-Davis, 2004), although the occurrence of multiple species pairings on the same host plant, and sometimes the same individual plant, allows for the theoretical possibility of the horizontal transfer of nematodes between fly species (Purcell *et al.*, 2015). Close patterns of co-evolution between the nematode, fly and host plant are evident, at least in some clades (Davies & Giblin-Davis, 2004; Taylor *et al.*, 2005; Nelson *et al.*, 2011a, b), but much remains to be discovered of these complex relationships.

Adult female *Fergusonina* carry *Fergusobia* nematodes within their abdomens, the juveniles of which are deposited with fly eggs during oviposition on or near undifferentiated meristematic host plant tissue. The juvenile nematodes are the first to feed on the plant, inducing gall formation before the hatching of the fly egg (Giblin-Davis *et al.*, 2001). The gall is maintained by the fly and provides shelter and a food source for the fly and nematode alike, which feed on hypertrophied plant cells and secretions in the chamber it excavates (Giblin-Davis *et al.*, 2003).

As summarized in Purcell *et al.* (2015), the nematodes that are deposited on the host plant during oviposition develop into at least one generation of parthenogenetic females, which eventually lay eggs that become diploid females and males (the latter are also potentially haploid), producing the sexual, or amphimictic generation. The mated females of this generation are the preparasitic stage that invades the third instar of the fly larva, subsequently moulting without the development of a new cuticle. These female nematodes become fully parasitic, losing the stylet and digestive tract, and develop epidermal microvilli to absorb fly haemolymph. The eggs of this parasitic female hatch and move into the female host's oviduct to be deposited with the next generation fly eggs in new plant tissue, completing the cycle (Currie, 1937; Giblin-Davis *et al.*, 2001). No male flies have ever been found with these nematodes present. Further details on life cycle, host specificity and diversity of *Fergusobia* nematodes are discussed in Davies *et al*. (2016), following a series of articles with nematode descriptions in Davies *et al*. (2014). A summary of *Fergusonina/Fergusobia* species associations, host associations and gall types, as influenced by fly oviposition placement and timing, were provided by Nelson *et al*. (2014).

Due to host specificity of the fly/nematode pair, *Fergusonina turneri* Taylor (paired with the nematode *Fergusobia quinquenerviae* Davies & Giblin-Davis) were released as part of efforts to control *Melaleuca quinquenervia* in Florida, where the plant is considered an invasive weed and a severe threat to everglade ecosystems (Pratt *et al.,* 2013). Control efforts were considered unsuccessful, as viable populations did not establish following release events in 2005 and 2006.

Immature stages. The egg and all larval instars of *Fergusonina nicholsoni* Tonnoir were described by Currie (1937), who also discussed the third instars of 17 additional species. The third instar of *F. syzygii* Harris was described by Harris (1982). Hennig (1958) described the puparium and enclosed third instar of *F. tillyardi* Tonnoir. The egg of *F. turneri* was figured by Taylor (2004). Additional descriptions and/or photos and illustrations of the distinctive larvae of fergusoninid species are provided in Harris (1982), Taylor (2004), Taylor & Davies (2010), Nelson *et al.* (2011), Purcell *et al.* (2016, 2017) and the references therein. Most fergusoninid larvae have a species-specific "dorsal shield" of sclerotized spicules, bands or combs extending from the mesothorax to abdominal segment 7; both the larva and puparium have a comb-like plate between abdominal segments 1 and 2.

Adult Diagnosis. Very small, compact, mostly bright yellow flies with blackish patches, mostly black setae, and a strong, often black ovipositor (Fig. 194). Head characteristically broad and flattened anteriorly (Fig. 193), with small ventral face and antenna, and large parafacial and lunule. Setae sometimes not much larger than surrounding setulae; vibrissa present, 1–3 lateroclinate fronto-orbitals, 0–2 prescutellar acrostichals and 1–3 dorsocentrals near posterior margin of scutum. Veins R_{4+5} and M_1 subparallel (Fig. 411). Costa with humeral break and sometimes with subcostal weakening; subcostal vein abbreviated, ending in R_1.

Adult Definition. Colour yellow with characteristic pattern of black pigmentation dorsally, including spot on ocellar tubercle, one to three pairs of stripes on scutum (sometimes very reduced), frequently black ovipositor, and extensive to reduced pigmentation on abdomen (Figs 191, 192, 194). Setae mostly black. Body length 1.6–2.8mm.

Chaetotaxy: 1 inner vertical; 1 outer vertical (sometimes long); 2–3 fronto-orbitals (lateroclinate); 1 ocellar; 1 postocellar (divergent to subparallel); vibrissa short. Frons with numerous scattered setulae that continue along parafacial in single row, usually also continuing onto gena and postgena, with some of these scattered and sometimes forming a relatively linear series under eye. 1 presutural intra-alar (uncommonly 2); 1 postpronotal; 2 notopleurals; 2 postsutural supra-alar; 1 postsutural intra-alar; 2–3 dorsocentrals (postioned posteriorly on scutum); 0–2 acrostichals (postioned posteriorly on scutum); 2–3 scutellars; 0 proepisternal; 1 anepisternal; 1 katepisternal (sometimes also with additional shorter seta). Setae sometimes not much larger than surrounding setulae. Body micropruinose. Fore femur with several outstanding dorsal and posteroventral setae, both angled posteriorly, and with long, thin ventrobasal seta (sometimes also on mid leg); hind femur usually with 1 outstanding anteroventral seta subapically, but sometimes with 2 or more; mid tibia with ventroapical seta.

Head. (Fig. 193) Antenna small, porrect, held against face within shallow cavity; pedicel with dorsal seam absent; first flagellomere small, rounded; arista pubescent, with dorsobasal insertion. Lunule very large; frons strongly curved downwards anteriorly to meet face; ocellar tubercle near vertex. Face well sclerotized, small; with medial carina that is sometimes partially expanded over antenna. Gena approximately half height of eye. Clypeus rounded; palpus subcylindrical; labium short and tapered apically with one small pair of setae.

Thorax. Precoxal and postmetacoxal bridges absent. Prosternum narrow, subrectangular with anterior width slightly greater. Greater ampulla absent. Scutellum flat to slightly convex dorsally, sometimes with surface wrinkled. Subscutellum present, small or slightly enlarged. Coxopleural streak absent.

Wing. (Fig. 411) Clear to greyish. Veins R_{4+5} and M_1 subparallel. Costa extending to M_1, but often quite weak after R_{2+3} and sometimes apparently terminating at R_{4+5} (Taylor, 2004). Medial and cross-veins sometimes weak, with dm-m sometimes incomplete or absent. M_4 ending at or near wing margin; CuA+CuP ending before wing margin. Vein bm-m incomplete to absent. Costa with humeral break, but sometimes also with subcostal weakening; subcostal vein abbreviated, ending in R_1. Cells *cu*p and bm very small. Calypter hairs moderately long.

Legs. Slender, short. Tarsomeres relatively short, with terminal 4 segments not longer than wide.

Abdomen. Sternites 1–4 small, sometimes desclerotized with chaetotaxy reduced, including bare S1; at least S5 with one pair of dominant lateral setae (Fig. 201). Spiracles 1–5 in membrane below tergites; 6th spiracle in membrane anterior to segment in females, and 7th spiracle enclosed anterolaterally in T7 on posteriorly angled tubercle; male 6th spiracle anterior to epandrium in membrane laterally and left 7th spiracle present near 6th. T3 sometimes incomplete on left side, tapering to a point and with "orphaned" spiracle on that side adjacent to 4th spiracle (Fig. 201).

Male genitalia. (Figs 195–200) Pregenital sclerites reduced to thin dorsal strip (possibly only remnant of S8) that may be completely membranous; essentially symmetrical. Epandrium with one or two pairs of dominant setae; ventral margin somewhat narrowed, approximating base of surstyli. Subepandrial sclerite mostly flat, weakly sclerotized and plate-like with deep ventromedial desclerotization and one pair of thick, sclerotized ventral lobes with irregular vertical row of short setae. Cerci small, lobate, largely fused. Surstylus small, lobate, curved in cross-section with anterior margins directed medially. Hypandrium broad, essentially planar with arms lateral; setae in concealed cluster at base of pregonite. Phallic plate absent. Phallapodeme flat, carinate, with one pair of anteromedial processes meeting inner-medial surface of hypandrium; broadly arched or U-shaped in profile. Pregonite long, band-like, fused to inner-medial surface of hypandrium, with scattered small setae along length. Postgonite short with pointed tooth-like apex; position apical to, and largely contiguous with postgonite; with short setae and empty sockets. Phallus (basiphallus+distiphallus) small, clear, tubular, with oblique ovate opening not reaching distal margin of postgonite; ventrobasal margin shortly before opening contiguous with phallapodeme base. Ejaculatory apodeme very small, globular, on very short, but relatively wide duct that barely exceeds arch of pregonite.

Female genitalia. (Figs 201–204) T6 and S6 completely fused into medially bulging sclerotized tube with few posteromedial and ventromedial setae sometimes arranged in transverse series, and larger row of larger setae completely encircling segment posteriorly; partially retracted into segment 5. T7 and S7 fused into oviscape with sutures sometimes still visible; segments distal to oviscape retracted. S8 and T8 divided medially, band-like and minutely textured. Segment 10 reduced to "internal process" of S10, which forms long, narrow, well-sclerotized stylet. Intersegmental membrane after segment 8 very elongate, basally with anteriorly directed spicules. Spermathecae (2) present (described for the first time here but noted as present in Taylor (2004)); flattened, pigmented, with shape subcircular to subtriangular, with short apical stem supporting small, dark apical bulb; ducts clear, short, fused before union with genital chamber. Ventral receptacle approximately as long as spermatheca, subcylindrical with shallow transverse wrinkles before wider subapical collar and rounded apical cap.

Micropezidae Loew, 1862

(Figs 312–394, 421–422)

Type genus: *Micropeza* Meigen 1803: 276, in Loew (1862: 38) [see Sabrosky (1999) for discussion]. **Type species of genus:** *Musca corrigiolata* Linnaeus, 1767: 995, by monotypy.

Micropezidae is the most diverse family of Nerioidea with about 700 described species (Marshall, 2012) and it is certain that many more await discovered based on the productivity of recent revisionary work. Species occur globally except for Antarctica and New Zealand, with most diversity to be found in tropical regions. Five subfamilies are presently accepted within a monophyletic Micropezidae—Calycopteryginae, Calobatinae, Eurybatinae, Micropezinae and Taeniapterinae—reflecting the most recent classification of D.K. McAlpine (1975, 1998).

Micropezidae are relatively elongate and gracile, with long, narrow legs, and sometimes colourful patterning. While these aspects are modestly developed in Calobatinae, which is more typically acalyptrate in appearance, they can be exceptionally exaggerated in the other subfamilies, especially in the length of the mid and hind legs, which may far exceed the length of the body (see Marshall (2016: fig. 43, 2017: fig. 97)). A number of species mimic Hymenoptera, especially Ichneumonidae, and lineages in several subfamilies have independently converged on ant-mimicry (see Marshall (2016: figs 40, 41), sometimes including the development of a petiolate and sometimes nodular abdomen. The latter is well-illustrated in the apterous Australian *Badisis ambulans* McAlpine (Eurybatinae).

Wing loss is also seen in *Calycopteryx moseleyi* Eaton (Figs 328–333), the sole member of the subfamily **Calycopteryginae**, where vestiges of the wing and halter are still evident. This species, restricted to the Kergulen and Heard Islands in the south Indian Ocean, is adapted to life on windswept islands, and is atypically drab, robust and stout.

The more "modestly" proportioned subfamily **Calobatinae** (Figs 312–316) differs from other Micropezidae in lacking strong dorsal setae on the mid and hind tibiae, in having stronger apical tibial setae, more evenly distributed setae on the katepisternum, and wider abdominal sternites. The subfamily is Holarctic in distribution.

Members of the distinct subfamily **Micropezinae** (Figs 317–321) are exceptionally narrow, gracile and dark in appearance. The head is also elongate, cross-vein bm-m is absent, and there are no fronto-orbital setae. Most species occur in the diverse *Micropeza*, which is mostly Neotropical but also Holarctic in distribution, but three species are also known from *Cryogonus* Cresson, restricted to Chile and Argentina. The west Palaearctic *Micropeza corrigiolata* has been discovered in Canada (Hoebecke & Wheeler, 1994) and South Africa (Barraclough, 1996), where it was likely introduced via agricultural trade since the larvae are known to occur in the root nodules of commercially important legumes.

The subfamily **Eurybatinae** is almost entirely Oriental and Australian in distribution, but one monotypic genus is known from Costa Rica (Marshall, 2002), and one is known from Mauritius and Réunion (Barraclough, 1992a). One genus of Eurybatinae is so far known only from males, *Anaeropsis* Bigot; it is the only stalk-eyed nerioid and the only non-micropezine without fronto-orbitals (see D.K. McAlpine (1975)). The monophyly of the subfamily is "rather weakly supported" (D.K. McAlpine, 1998), and ongoing research suggests that its tribes Metopochetini (Fig. 327) and Eurybatini should be treated as separate subfamilies (Jackson *et al*., in manuscript; Yusof & Marshall, in manuscript).

Taeniapterinae (Figs 322–326) is the most diverse subfamily of Micropezidae in terms of both genera and species. It is found in all biogeographic regions with highest diversity in the Neotropics. The subfamily is characterized by a fan-like clustering of setae posteriorly on the katepisternum, sometimes anteriorly shifted ocelli, sometimes a laterally compressed epandrium, a lack of surstyli, elongate fore coxae (also Eurybatinae) and sometimes a pointed anal cell (also Eurybatinae) that can be exceptionaly long in some species (D.K. McAlpine, 1998).

Regional catalogues of Micropezidae are available in Steyskal (1965b) [Americas north of Mexico]; Aczél (1949c) [Neotropical Region]; Steyskal (1968a) [Americas south of USA]; Marshall *et al.* (2016) [Colombia]; Soós (1984a) [Palaearctic Region]; Steyskal (1980b) [Afrotropical Region]; Steyskal (1977c) [Oriental Region]; Evenhuis (1989a) [Australasia/Oceaniania]. The North American fauna has been treated or summarized by Cresson (1938), Merritt (1971, 1972), Merritt & James (1973), Merritt & Peterson (1976) and Steyskal (1987a). Treatments of the Palaearctic fauna have been provided by Czerny (1930a), Greve & Nielsen (1991), Roháček & Barták (1990) and Ozerov (1987). In the last few decades, work on the Afrotropical fauna include genus and regional revisions by Barraclough (1992b, 1993c, 1996) and Marshall (2014, 2017, 2019). Treatments of the Australasian fauna were provided by Steyskal (1947, 1952), who reviewed some species from the Solomon Islands and described Australasian specimens deposited in the USNM. Aczél (1959) treated the Micropezidae of Micronesia. D.K. McAlpine reclassified the family-level groups of Micropezidae and reviewed the Australasian Eurybatinae (D.K. McAlpine, 1975), and later revised the fauna of Australia (D.K. McAlpine, 1998). Li *et al.* (2015) revised the Oriental *Cothornobata*. Early works on the Neotropical fauna include Cresson (1930), Hennig (1934b, 1935a, b) and Aczél (1949b, 1951). Contemporary revisionary work of Neotropical taxa is being primarily developed by S.A. Marshall and colleagues: Marshall (2002, 2004a, b, 2010, 2011, 2013, 2014, 2015, 2016), Marshall & Jackson (2014), Ferro & Marshall (2018).

Fossils of five species in four genera of Micropezidae are listed in Evenhuis (1997): *Calobata rottensis* (Statz) [compression fossil, Oligocene, Germany]; *Micropeza prompta* Meunier [Copal fossil, Tanzania, Pleistocene / Holocene]; *Rainieria* sp. [amber, Dominican Republic, Oligocene/Miocene]; *Electrobata myrmecia* Hennig [amber, Baltic Region, Eocene / Oligocene]; *E. tertiaria* (Meunier) [amber, Baltic Region, Eocene / Oligocene]. D.K. McAlpine (1998) suggested that both named *Electrobata* species might be best treated within different genera, which would certainly seem warranted based on their divergence in chaetotaxy, venation and sclerite shape. Evenhuis (1997) further notes that other, possibly undescribed species are mentioned in the literature from Baltic amber, Chiapas amber and Sicilian amber, and a specimen of Micropezidae in Dominican amber is figured in Grimaldi & Engel (2005). An additional "*Electrobata* spec." from Baltic amber was examined in Hennig (1967). Tschirnhaus & Hoffeins (2009) also list additional taxa from Baltic amber that they did not formally describe, but included in a key to Baltic Amber Acalyptratae.

One fossil genus and species was previously recognized for Cypselosomatidae—*Cypselosomatites succini* Hennig. The species was described from Baltic amber by Hennig (1965), who considered it basal to the remainder of the family. D.K. McAlpine (1966) noted that the species more closely approached Micropezidae in morphology, but no reclassification was proposed until a later date when he formally treated it as Micropezidae (D.K. McAlpine, 1998).

Biology. Adults of Micropezidae are often encountered on horizontal surfaces such as low foliage and logs, usually in sunspots, and sometimes near moving or standing water, including temporary pools (Merritt & James, 1973; Roháček & Barták, 1990; Marshall, 2010, 2012). Many species occur at a variety of elevations, mostly lowlands, but some species and genera are found only at high-altitudes, including Neotropical *Mesoconius* (see Marshall (2015)). North temperate species mostly occur in moist wooded areas, but also meadows, marshes and grasses along water (Merritt & James, 1973; Roháček & Barták, 1990; Roháček, 2012b); *Micropeza corrigiolata* has been collected off of grass and vegetation in moist, shaded areas, and in meadows and fields containing legumes (Barraclough, 1996; Hoebeke & Wheeler, 1994). In Australia, species of *Metopochetus* were mostly collected in rainforests, similar to Australian *Cothornobata* and *Crepidochetus*, as well as on standing *Eucalyptus* trees and saplings (D.K. McAlpine, 1998). *Mimegralla australica* Hennig appears to prefer disturbed habitats (D.K. McAlpine, 1998). Neotropical species are known from numerous habitats, including rainforests, edges and disturbed habitats such as cacao plantations, but also native forests (Marshall, 2010, 2013). Some taxa appear to require pristine habitats that have had little to no disturbance, such as *Mesoconius*, which is particularly restricted in its habitat requirements (Marshall, 2010). South African taeniapterines occur in sunlit areas, open woodlands, disturbed areas including suburban areas or cultivated gardens, and cool, shaded, humid forests, sometimes at edges (Barraclough, 1996).

Adults can be locally abundant on carrion, artificial honeydew and decaying fruit (Barraclough, 1996; Marshall, 2010, 2012, 2013), but also on ripe or damaged fruit (Oosetrbrook, 1998). *Mimegralla albimana* Doleschall was considered an opportunistic feeder on a decomposing pig carcass (Chin *et al*., 2011). Many taxa are also very frequently found at mammal or bird dung, sometimes in large numbers (Merritt & James, 1973; Marshall, 2010, 2012), and small dung baits of are a reliable means of collection, although some taxa do not appear to be attracted to this substrate, including *Tenthes* Cresson, *Metasphen* Frey and some *Grallipeza* (Taeniapterinae) (Marshall, 2010, 2013). Feeding on insects is known in some adult Micropezidae, especially Calobatinae, which may be at least facultatively predaceous (Marshall, 2012), with observations of specimens feeding on aphids and small, mostly nematocerous Diptera (Colyer & Hammond, 1968). *Taeniaptera lasciva* (Fab.) is noted as being a predator on adult *Diatraea saccharalis* (Fab.), the sugarcane moth borer (Bennett & Alam, 1985).

Mimicry of Hymenoptera appears to be common among Micropezidae, modeling species of Formicidae, Ichneumonidae and sometimes Pompilidae (Marshall, 2010). While the benefits of ant-mimicry are well documented and known to have evolved independently at least 70 times (Mclver & Stonedahl, 1993), the relative benefits of parasitoid mimicry are yet to be determined, although it would appear to be sufficient given the number of presumed mimics, especially within Taeniapterinae. Many Ichneumonidae, including Ophioninae and Tryphoninae, are capable of stinging, with some being quite painful, and species of several subfamilies are known to release a pungent, possibly protective odour when disturbed (Quicke, 2013). These and other Ichneumonidae are also capable of using their ovipositor to keep distance from an enemy and may engage in aggressive behaviour such as biting. Mimics of Ichneumonidae have entirely to partially bright white fore tarsi and are typically found on foliage or usually hori-ozontal bark (Berg, 1947), waving one or both extended fore legs in front of them, with these legs having the movement and appearance of the model's antennae (Hennig, 1935b; Barraclough, 1996; D.K. McAlpine, 1998; Marshall, 2010). Individuals of one of these mimics, *Ptilosphen viriolatus* Enderlein, were observed in "sleeping aggregations", wherein sleeping individuals faced the petiole, and slowly and continuously waved their fore legs in a manner similar to that seen while awake (Ortiz, 2001). Barraclough (1996) noted this leg-waiving was sometimes seen between individuals of the same species, although the role of this behaviour and their sex was not determined.

Courtship behaviour appears to have an important role in reproduction. Behaviour of the ant mimic *Cardiacephala arthriticus* (Wiedemann) was recorded by Wheeler (1924) in detail, wherein a male on the top of a large leaf fended off rival males and engaged females to convince them to mate. Females appeared to chase away males until the males convinced them to mate by presenting regurgitated fluid as a gift while "dancing". The provision of fluid gifts and other courtship activities continued until mating was completed. Marshall (2012) noted that the oral exchange of fluids is also common in *Taeniaptera* and photographed such a transfer between a pair of *T. trivittata* Macquart. Barraclough (1996) theorized that similar exchanges of nuptial gifts would be present in those Taeniapterinae with lateral swellings anteriorly in the male pleural membrane such as *Mimegralla*. He suggested that the swellings had a glandular function similar to that seen in Tephritidae, where the swollen structures were associated with trophallaxis during courtship. Conversely, the author noted an alternative interpretation by D.K. McAlpine, who thought that the swellings were instead "evaporative areas associated with the release of a pheromone". Other components of taeniapterine copulatory behaviour may involve "kissing" behaviour, not necessarily associated with the exchange of nuptial gifts, along with "stilting and stroking" actions (Marshall, 2012). Female display to attract a mate was observed in the taeniapterine *Ptilosphen tetrastigma* (Schiner), where a white banded abdomen and positioning of banded white forelegs were used (Marshall, 2012).

Oviposition in wood has been recorded for a number of Taeniapterinae and Eurybatinae, where eggs may be laid in cracks or irregularities in the wood or bark surface, sometimes including the openings of beetle burrows (Marshall, 2012). A male *Grammicomyia* Bigot was observed on a patch of fallen wood that was suitable for oviposition, where he waited for a female to arrive while defending the patch from other males (Marshall, 2012).

Much remains to be discovered of micropezid larval life history, but individuals appear to be generalist saprophages in a variety of habitats, with a preference for moist, rotting plant matter, most often including wood (with a minority in roots), grass and fruit, but also dung. Calobatinae have been reared from heaps of decaying vegetation, including grass (Teskey, 1972; Ferrar, 1987), and Russian *Calobatella petonella* (L.), which is known to overwinter in the soil, was reared from sewage tanks and pig dung (Lobanov, 1960).

In Eurybatinae, Li *et al*. (2015) suggested that larval development in rotting wood was likely widespread, noting that females from five genera were observed ovipositing on that substrate, including taxa photographed by Marshall (2012). Larvae of the unusual *Badisis ambulans* develop at the bottom of the cup leaves of *Cephalotus follicularis* (the Albany pitcher plant) (Yeates, 1992; Marshall, 2012), but this host specialization appears to be atypical for the family (D.K. McAlpine 1998). The likely ant model of *B. ambulans* has been observed on the same host plant (D.K. McAlpine, 1998).

In Taeniapterinae, larvae are mostly known from varied rotting media, especially plants: decaying vegetative material for *Mimegralla coeruleifrons* (Hennig, 1936c); decaying sugar cane cuttings for *Taeniaptera lasciva* (Cresson, 1938); the surrounding pulp of *Metroxylon sagu* (true Sago palm) seeds for *M. albimana striatosafciata* (Berg, 1947); decaying fruit of *Myrianthus arborea* for *M. gowdeyi* (Frey) and the palm tree *Borassus flabellifera* for *M. respondens* (Walker) (Verbeke, 1951). Albuquerque (1972) was able to rear *Scipopus belzebul* (Schiner) under lab conditions from rotting banana and human feces. Rotten wood in trees, sometimes noticeably attacked by fungus, has served as substrate for numerous species: rotting *Liriodendron tulipfera* for *Calobatina geometroides* (Cresson) (Wallace, 1969); rotting wood of *Erythrina caffra* for *Cephalosphen conifrons* (Bigot) (Hennig, 1936c); standing, rotting *Ulmus americana* suffering fungal attack for *Rainieria brunneipes* (Cresson) (Steyskal, 1942); beneath the bark of dead trees for *M. a. albimana* (Bohart & Gressitt, 1951) and *M. albimana striatosafciata* (Enderlein) (Berg, 1947); dead banana wood for *M. albimana galbula* (Bohart & Gressitt, 1951), *T. lasciva* (Fab.), *T. annulata* (Fab.) and *Plocoscelus conifer* (Hendel) (Fischer, 1932). Adult occurrence of *Rainieria calceata* (Fallén) on fallen *Fagus* sp. (beech) was tentatively taken as an indicator of larval habitat by Chandler (1975a). Numerous species in other genera have also been observed ovipositing in a variety of decaying plant material, including wood, rotting stems and *Typha* stems (see Marshall (2010, 2012)).

Species of *Mimegralla* (Taeniapterinae) are also known to be primary invaders of live plants. *Mimegralla coeruleifrons* (Macquart)—otherwise known as the "rhizome fly"—attacks ginger (*Zingiber officinale*) (Steyskal, 1964) and turmeric (*Curcuma longa*), tunneling in the outer and inner regions of the rhizome (Ghorpade *et al.*, 1988). The host plant experiences yellowing and drying of the leaves and the main shoot, and is opened to invasion by a number of disease-causing fungi and nematodes (Ghorpade *et al.*, 1988). Steyskal (1964) noted that records cited by Hennig (1952a, b) on *Curcuma* sp. (wild arrowroot) may also be *M. coeruleifrons*, and that other larvae found in North America on intercepted ginger from China were possibly *Mimegralla*, perhaps *M. albimana galbula* (Osten Sacken).

In Micropezinae, the sometimes pestiferous *Micropeza corrigiolata* might breed in compost heaps (Chinery, 1986), but larvae are known to occur on live legumes, specifically, in the fresh root nodules of *Pisum arvense* L., *Medicago sativa* L. and *Trifolium pratense* L.; the nodule is hollowed out from the inside leaving an empty shell, after which the larva burrows 30 cm into the soil to overwinter (Müller, 1957).

Calycopteryx mosleyi (Calycopteryginae) eggs were found on and under leaves on *Pringlea antiscorbutica* R. Br. ("Kergulen cabbage"). Larvae were found mining shallow pits in the roots of the plant, and were recovered among numerous other substrates, including under stones, other vegetation including *Azorella* sp., and the soil under decomposing animal matter, including the carcass of a "sea elephant" (presumably the Southern elephant seal, *Mirounga leonine* (Linnaeus)); puparia were recovered from moss and rotting seaweed (Womersley, 1937). Ferrar (1987) suggested that this relatively broad diet may not necessarily include *P. antiscorbutica*, which is absent from one island upon which the fly occurs.

Immature stages. Most descriptions of immature stages of Micropezidae are listed in Ferrar (1987), with references to published data on Calobatinae, Micropezinae, Taeniapterinae and Calycopteryginae. Third instar larvae and puparia of *Badisis ambulans* (Eurybatinae) were additionally described by Yeates (1992). Marshall (2013) figured larvae of *Grallipeza spinuliger* (Cresson).

Adult Diagnosis. Medium to large-sized flies; very slender and long-legged, especially mid and hind legs, with the fore legs shorter (Figs 312–333). Body length 5.0–21.0mm. Colour variable, often with banded legs including white segments on fore tarsus; wing variable, clear to cloudy, often banded. Ocellar seta and vibrissa absent. Usually one or two posteriorly positioned dorsocentrals, sometimes zero or up to six. Anepisternal, postpronotal and lateral scutellar setae absent. Katepisternal seta present, positioned posteriorly, often duplicated, triplicated or multiplicated (Figs 323, 326). Mid and hind tibiae usually with linear dorsal series of setae (absent in Calobatinae and *Calycopteryx*). Antenna slightly elbowed with length of first flagellomere usually one to two times width. Scutellum generally small, rounded. Wing and halter rarely vestigial to absent (*Calycopteryx* (Fig. 330–331), *Badisis*); relatively narrow with alula and anal lobe reduced (Figs 421–422); veins R_{4+5} and M_1 convergent apically, sometimes fused for short distance; costa unbroken; sc complete; anal cell with distal vein (CuA) straight. Males usually with forked process on sternite 5 (Fig. 336); phallus usually with complex "phallic bulb", sometimes with terminal flagella(e). Female with segment 7 forming large oviscape within which terminal segments are telescoped (Fig. 319).

Adult Definition. Medium to large-sized flies; body length 5.0–21.0mm. Very slender and usually very long-legged, especially mid and hind legs (possibly far exceeding body length), with fore legs shorter (Figs 312–333); shorter-legged in some, including Calobatinae and apterous species. Colour variable, black to pale yellow, often conspicuously patterned with banded legs, including white segments on fore tarsus; sometimes with iridescence or pruinose to silvery tomentose pattern; wing variable, clear to cloudy, often banded. Abdominal membrane sometimes patterned with setulae and/or pigment, continuing pattern on sclerites. Mostly pruinose; often with shiny patches, mostly on head and pleuron.

Chaetotaxy: 0–1 inner vertical; 0–1 outer vertical; usually 1–3 fronto-orbitals, but sometimes 0 (Micropezinae, *Anaeropsis*) or as many as 6; 0–1 small ocellar; 0–1 postocellar (slightly divergent to convergent); vibrissa absent. 0 presutural intra-alar; 0 postpronotal; 1–2 notopeurals (only anterior sometimes reduced to absent); 2 postsutural supra-alar (0 *Calycopteryx*, 1 *Badisis*); 0 postsutural intra-alar, uncommonly 1 generally small seta; usually 1 or 2 dorsocentrals, uncommonly 0 or up to 6 extending onto presutural scutum; 0 acrostichal; 1 scutellar (apical only, but sometimes also with strong discal or marginal setulae); 0–1 proepisternal (small to large), but sometimes ventral margin above fore coxa instead with series of setae; 0 anepisternal, but sometimes with posteromedial scattering of enlarged setulae; at least 1–3 katepisternals (uncommonly 1), but few Eurybatinae with up to 5 setae arranged vertically, and all Taeniapterinae with many setae mostly arranged into one or two thick vertical "fans" and sometimes also with medial or posterior scattering of enlarged setulae. Sometimes 1 or more small "suprahumeral" setae (Marshall 2013) on anterior margin of scutum medial to postpronotum. Face and frons variably setulose. Anterior margin of clypeus with distinct setae in *Hoplocheiloma* Cresson. Prosternum setose or bare. Fore femur sometimes with two rows of strong ventral setae; mid and hind femora sometimes with one or more outstanding dorsal setae. Dorsal or ventral apical setae on tibiae inconspicuous if present, never much longer than setulae, more commonly with multiple setae along margin that may be displaced laterally but sometimes with single outstanding medial seta; apex of fore tibia uncommonly with ventral seta. Mid and hind tibiae sometimes (not Calobatinae or Calycopteryginae) with dorsal row of setae (Fig. 323) that may be duplicated, staggered or scattered.

Head. Antenna shallowly to strongly deflexed. Pedicel and scape small; pedicel sometimes with outer-dorsal notch. First flagellomere rounded, sometimes tapering apically; uncommonly shorter than wide, usually more elongate with length not more than twice width. Arista inserted subbasally (appearing more apical on shortened antenna of *Calycopteryx*); usually bare, pubescent or short to long plumose, sometimes with longer rays; rays usually shorter or absent distally. Eye usually large, rendering gena, postgena and parafacial very narrow when viewed in profile (not *Calycopteryx*). Orbital plate usually well-developed and wide, delimiting long orbital vitta; shining, silvery tomentose or pruinose, but if pruinose, then sometimes not distinguishable; width of vitta variable, sometimes tapering at one or both ends, or ending in a point anteriorly (i.e. orbital plates meeting), sometimes sunken or swollen medially; frons usually rounded, sometimes prominently so, but sometimes flattened or somewhat concave; anterior margin of frons sometimes raised and partially curled laterally; frons, dorsum of face and parafacial sometimes moderately to strongly projecting; vertex sometimes evident as an angle, but often broadly rounded, apparently displacing posterior region of frons onto back of head. Ocellar tubercle flat or rounded, positioned near vertex or shifted anteriorly, sometimes slightly past centre of frons. Marshall (2011) follows Cresson (1930) in dividing the posterolateral region of the frons into two sections; the lateral "paracephalon", which bears the outer vertical seta, and the medial "epicephalon", which bears the inner vertical seta. Lunule concealed to narrowly visible. Face soft, at least less sclerotized ventrally, with adjacent sclerotized margin of face and parafacial sometimes approximate or meeting medially, reducing softer medial section to narrow band or carina (similar to Megamerinidae); sclerotized dorsal region of face usually prominent to raised or subcarinate medially; face sometimes very short with buccal cavity extending dorsally towards ventrally angled frons (especially in ant-like species); antennal bases meeting medially or separated, sometimes divided by more than width of scape. Back of head shallowly rounded, sometimes narrowly produced to meet thorax, sometimes with bulge above foramen. Clypeus well-developed, sometimes recessed, sometimes very large, broad and prominent. Palpus narrow and cylindrical to broad and flattened, sometimes not much longer than wide.

Thorax. High, often narrow, notum shallowly to strongly rounded; anteroventral region around fore coxae sometimes recessed, and katepisternum and/or postsutural region sometimes bulging with posterior margin recessed. Transverse suture at or behind midpoint of scutum, mostly or entirely complete; presutural thorax sometimes pronounced, with anteromedial region of scutum long, bulging and sometimes overhanging pronotum, and with notopleuron elongate and pointed posterolaterally. Pronotum sometimes extended anteriorly to form narrow "neck". Postpronotum various, either small and rounded, bulging, obliterated or narrow and elongate. Scutellum short, rounded, sometimes angled dorsally; reduced in apterous species. Subscutellum variable, usually moderately developed to narrow and linear or absent; sometimes swollen and bulging (some Eurybatinae), rarely conical and larger than scutellum as in Nothybidae (*Nestima*). Metanotum sometimes reduced (Micropezinae) or atrophied (*Calycopteryx*), usually well-developed and high with katatergite swollen; sometimes strongly swollen with conical protuberance in some *Mesoconius*. Precoxal bridge absent. Postmetacoxal bridge present in some Eurybatinae. Prosternum variable; sometimes divided into anterior presternum and posterior basisternum; base of prosternum (or basisternum) sometimes fused to anteromedial margin of katepisternum. Male metasternum sometimes with posteriorly directed process approximating ends of genital fork (some Calobatinae).

Wing. (Figs 421–422) Wing relatively narrow with alula and anal lobe reduced. Vein R_1 terminating proximal to end of Sc or further beyond. Vein R_{2+3} sometimes relatively short. Veins R_{4+5} and M_1 convergent apically, sometimes fused for short distance; costa unbroken; sc complete; anal cell with distal vein (CuA) straight, rarely slightly sinuate; CuA sometimes much longer than terminal section of CuA+CuP (some Taeniapterinae). Basal and anal cells sometimes bare in part. "Axillary fascicle" (comb of setae on upper margin of upper calypter particular to Micropezidae) usually present. Haltere well-developed to very slender and gracile with small knob. Wing and haltere uncommonly vestigial (*Calycopteryx*) to absent (*Badisis*).

Legs. Hind and mid femora sometimes with abrupt swelling. Hind femur sometimes flattened and grooved. Tibiae (usually hind, or mid and hind, less commonly also fore tibia) uncommonly flattened, sometimes conspicuously so, and with longitudinal groove for at least part of its length on one or both sides (some Eurybatini, Taeniapterinae); fore tibia grooved only in some Taeniapterinae. Fore tarsus sometimes much shorter than fore tibia; apical male fore tarsomeres uncommonly modified (eg. some *Mesoconius*); fourth tarsomere slightly to much shorter than fifth tarsomere.

Abdomen. Typically long and slender. Anterior two segments sometimes narrow and elongate, giving abdomen petiolate appearance; if petiolate, syntergite 1+2 sometimes also appearing "nodular", similar to ants (eg. *Badisis*). Sternite 1 usually evidently subtriangular to trapezoidal with anterior margin widest (Fig. 352); sternites 2–4 sometimes narrow to linear with anterior margin of sternite 2 wider. Abdomen past segment 6 usually strongly downturned and sometimes conspicuously glabrous and smooth. Abdominal membrane sometimes patterned with setulae or pigment, reflecting pattern on sclerites; male lateral membrane at segment 2 or 2–3 (but rarely 4—see Marshall (2014)) sometimes with swollen or inflatable "pleural sac"; abdomen sometimes swollen ventromedially. Spiracles 1–6 in membrane, spiracle 7 enclosed (sometimes in membrane in males).

Male genitalia. (Figs 334–370) S5 with bifid "genital fork" (Figs 334, 336) that is sometimes reduced (eg. *Calycopteryx*; Fig. 367) or absent (eg. some Taeniapterinae and Micropezinae); fork sometimes with short basal stalk or weakly to entirely divided at base. S6 separate from S7; S6 sometimes with process that extends between arms of genital fork (some Calobatinae; Fig. 313); S6 sometimes simple and plate-like with shape subtriangular to trapezoidal (Fig. 352), but strongly modified in some species, with narrow, sclerotized apodeme anteriorly that continues as two or three thickened ribs along plate-like posterior section (Fig. 336). S7 and S8 often entirely or mostly bare, with anterior margin more heavily sclerotized; S8 broad, dorsal, partially fused to S7 anterolaterally, leaving a broad to inconspicuous suture or cleft between the two sclerites posteriorly; S7 left lateral, sometimes extending ventrally. Membrane extending anteriorly from S7 and S8 with one or two floating supernumerary sclerites (Fig. 335) that are folded internally (also found in Neriidae). Subepandrial sclerite setose ventrolaterally, more weakly sclerotized medially, sometimes divided into halves that are joined dorsally or entirely divided. Epandrium setose with apex shallowly constricted, sometimes with anterodorsal margin produced, sometimes narrow and elongate. Cerci well-developed, separate, setose. Surstylus shape variable, usually short; sometimes absent (Taeniapterinae; Figs 349–352). Hypandrium bare, narrow; arms fused to elongate phallic plate that may be variably divided into two bands (Figs 340, 353–354). Pregonite long, band-like, minutely setose (but see Marshall (2019)); base fused to inner ventromedial surface of hypandrium. Postgonite shorter, band-like, sometimes partially fused to pregonite; apex usually swollen and outwardly directed; sometimes asymmetrical (some Taeniapterinae). Phallapodeme long, rod-like with apex slightly to strongly enlarged; sometimes with paired ventromedial process weakly to completely fused to inner surface of hypandrium. Epiphallus absent. Basiphallus small, ring- or U-shaped; rarely enlarged. Distiphallus long, rod-like with basal shaft, “phallic bulb”, and sometimes one or two apical flagellae; dorsum of shaft sometimes membranous; venter sclerotized, usually plate-like and sometimes medially split into two parallel bands; phallic bulb usually complex, uncommonly absent (Marshall, 2017), sometimes elongate with apical swelling (see Marshall (2014: fig. 7)). Ejaculatory apodeme usually large and stout, with short stem and broad, fan-like blade; sometimes reduced (eg. Barraclough (1996: fig. 14), Marshall (2002)); sperm pump shallow, wide, ventrally sclerotized and sometimes lobate and/or minutely spinulose.

Female genitalia. (Figs 371–394) Female segment 7 forming large, heavily sclerotized oviscape that encloses telescoped terminal segments at rest; sometimes variably compressed, medially bent, or basally and/or apically swollen; suture between tergite and sternite sometimes evident as a vestige anteriorly and posteriorly. Spiracle 7 enclosed within fused S7 and T7 anteriorly, but partially exposed to weakly sclerotized region if suture present anteriorly. Membranous region between segments 7 and 8 narrow, elongate, minutely wrinkled longitudinally. S8–10 and T8–10 small, narrow, apically setose. Internal rod-like process produced from S10 reduced to absent. Cercus small, rounded, setose. Normally three spermathecae (solitary spermatheca on one duct, paired spermathecae apically branching from second duct); four spermathecae in at least some Micropezinae (Freidberg, 1984) and Taeniapterinae (S.A. Marshall, pers. comm.); McAlpine (1996) discussed Dufour’s (1851) finding of two spermathecae in *Compsobata cothurnata* (Panzer) [=*Compsobata cibaria* (L.)], but a female dissected for the present study showed three spermathecae. Spermathecae pigmented, surface usually with subtle to conspicuous wrinkles, pits or protuberances; shape variable, usually spherical to ovate; length uncommonly more than twice width, with one or both ends somewhat invaginated; solitary spermatheca sometimes atrophied or differing in shape. Two spermathecal ducts, apex sometimes pigmented; surface sometimes minutely wrinkled and/or ornamented with outgrowths. Ventral receptacle highly variable, normally small, rounded to mushroom-shaped, sometimes pigmented or enlarged.

Variation—Cypselosomatites (*incertae sedis* in Nerioidea). Large-bodied species with relatively “typical” acalyptrate dimensions, but somewhat reminiscent of extant Micropezidae, with scutellum small, rounded and slightly upturned, with mid and hind legs slightly elongate (fore basitarsomere longer than half length of fore tibia) and mid coxae separated. *Cypselosomatites* similar to some Micropezidae as follows: two strong vertically arranged setae on katepisternum, two dorsocentrals, one outer and one inner vertical, no proepisternal, prosternum setose, fore tibia without apical setae; ocellar tubercle flat, near midpoint of frons; antennae separated by width of scape; postpronotum small and rounded; katatergite small. Differing from Micropezidae as follows: antenna porrect, arista bare; four fronto-orbitals, posterior seta displaced posteriorly, nearly level with inner vertical seta and as far from that seta as inner vertical is from outer vertical; ocellars small, proclinate; lateral scutellar present, nearly as long as small posterior intra-alar; legs without outstanding setae except for ventroapical seta on mid and hind tibiae (slightly offset from midline); alula and anal lobe well-developed; CuA rounded. Subcostal break absent in examined specimens, not present, as noted by Hennig (1965). Due to cloudiness in the amber surrounding the examined specimens, many regions are not visible, including the postcoxal region, the thoracic sternites, and most of the abdomen including the spiracles and male genitalia; it cannot be determined if a genital fork is present, but if it is present, then it is very small.

Neriidae Westwood, 1840

(Figs 291–311, 412)

Type genus: *Nerius* Fabricius 1805: 264, by Westwood (1840: 588). **Type species of genus:** *Nerius pilifer* Fabricius, 1805, by subsequent designation [Coquillett 1910: 575].

The Neriidae is a relatively small family of almost global distribution with over 110 species in more than 19 genera (Sepúlveda *et al.*, 2013a) that are primarily tropical in distribution, with most species found in the Neotropical Region. Species often develop as immatures in decaying vegetable matter, including a Nearctic *Odontoloxozus* that is found in necrotic cactus tissue, giving rise to the common name “cactus flies”.

The widespread subfamily Neriinae is defined by prominent antennal bases formed by an enlarged and medially divided lunule. The Old World subfamily Telostylinae is characterized by an ancestral form of antennal insertion, leading some to suspect that it represents a paraphylic group from which the Neriinae arose (Pitkin, 1989; Buck, 2010). A closer, quantitative analysis of the phylogenetic relationships between neriid genera was performed by

Koch *et al.* (2014), who used a combination of discrete and continuous morphological characters to dismantle support for all historically defining characters of the subfamilies and genus groups, finding these to support artificial groupings; the family itself was strongly supported as monophyletic and the previous assumption of an Oriental origin for the family (Aczél, 1954b) was supported. Since Koch *et al.* (2014) did not provide an alternative system of classification and their phylogeny does not support any simple subdivision of the family, it is not recommended that any be imposed until a more extensive analysis of global taxa is performed, followed by correlation of useful diagnostic characters to natural groups. The doctoral thesis of Pereira-Colavite (2013) is a preliminary step in this direction, but this requires publication and verification. The monophyly of genera should also ideally be examined following revision, as recently done for *Glyphidops* Enderlein (Sepúlveda *et al.*, 2014) and the smaller genera *Cerantichir* Enderlein (Sepúlveda *et al.*, 2013a), *Eoneria* Aczél (Sepúlveda *et al.*, 2013b) and *Longina* Wiedemann (Buck & Marshall, 2004), which are now much more thoroughly understood.

The New World fauna was revised by Aczél (1961) and discussed in Buck (2010). The much smaller Palaearctic fauna was treated in Czerny (1930b, 1932) and Hendel (1932). Aczél (1954b, 1955a, 1959) treated portions of the fauna of Southeast Asia and Oceania. Afrotropical species are treated in Aczél (1954c, 1954d, 1955b) and Barraclough (1993a, b). The only thorough investigation of the World Neriidae was provided by Hennig (1937), who wrote a key to genera and reapproached the classification and zoogeography of the family. Species limits in two Nearctic *Odontoloxozus* established using molecular data are discussed in Pfeiler *et al.* (2013). *Telostylinus angusticollis* is used as a model organism in experimental biology, as summarized in Kopps *et al.* (2013), who provided genetic sequence data and developed microsatellite markers. Regional species catalogues are provided in Steyskal (1965c) [Nearctic], Czerny (1930b), Soós (1984b) [Palaearctic], Steyskal (1977b) [Oriental], Pitkin (1989) [Australian], Steyskal (1980a) [Afrotropical], and Aczél (1949c), Steyskal (1968b) and Sepúlveda & Carvalho (2016) [Neotropical].

Biology. Larvae are known to breed in decaying vegetable matter, often fruit, but specimens are sometimes found in rotting tree bark (including *Carica* and *Dysoxylum*), wood that has only recently begun to decay (Eberhard, 1998), stems (Oosterbrook, 1989; Pitkin, 1989) and beetle borings from wood (Preston-Mafham, 2001). Other species occur in injured or diseased tree tissue (Buck, 2010), including the New World *Odontoloxozus*, which occurs on necrotic cactus (Ryckman & Olsen, 1963). Larval breeding spots interpreted as favourable oviposition sites by females of some species are guarded by males, with some males also guarding females following copulation and during oviposition (Mangan, 1979; Preston-Mafham, 2001). Adults feed on sap, the excretions of rotten trees, fruit, and other decaying matter including carrion and dung (Buck, 2010; Dufek *et al.,* 2014), and can be collected in fruit-fly traps (Aczél, 1961). *Telostylinus lineolatus* (Wiedemann) was considered an opportunistic feeder on a decomposing pig carcass (Chin *et al.,* 2011). Immature stages of *O. longicornis* were described by Olsen & Ryckman (1963) and Steyskal (1965), and immature stages and the development of larvae of *Glyphidops flavifrons* (Bigot) were described by Mondragón & Cironza (2016).

Immature stages. Immature stages of Neriidae are best known for *Odontoloxozus longicornis*, with Olsen & Ryckman (1963) detailing the egg, larvae and puparium, the first of which has a characteristic elongate anterior filament that projects through the host epidermis (Olsen & Ryckman, 1963: figs 1, 19). Berg (1947) further detailed the third instar larva and puparium of *Telostylinus lineolatus*. Managan & Baldwin (1986) examined the larvae of *O. pachycericola* Managan & Baldwin, *O. longicornis,* and their hybrids, from which polytene chromosomes were extracted and analyzed.

Adult Diagnosis. Body length 5.0–15.0mm. Body long and slender, accentuated by lengthened head, anteriorly pointed and often elongate antenna with apical arista, and straight, horizontally held abdomen; more heavily sclerotized and spinose than similar families such as Micropezidae. Legs long and slender, sometimes stout; femora usually originating relatively close to each other under midpoint of body. Usually conspicuously vittate and sometimes with glabrous spots at base of setae. Setae and setulae reduced, with remaining setae often dark, short, erect and sometimes stout to spinose; thickened setae usually present at least on fore femur or coxa, but sometimes also on remaining coxae and femora, pleuron and subgena. Ocellars absent; postocellars convergent and distant from anteriorly removed ocellar tubercle. Vibrissa-like seta often small if present. Thoracic chaetotaxy reduced, but with at least 1 dorsocentral, 1 posterior notopleural and 1 apical scutellar. Face mostly to entirely membranous; projecting, not distinct from lunule. "Antennal base" sometimes appearing as additional antennal segment. Pedicel with angulate extension on inner-distal margin (Fig. 294). Precoxal bridge sometimes present. Subcostal break or weakening usually absent; subcosta complete (Fig. 412). Veins R_{4+5} and M_1 convergent. Female with segment 7 forming large ovipositor that encloses terminal segments at rest (Figs 306–307); male with epandrium long, narrow and usually constricted medially (Figs 299–302).

Adult Definition. Body long and slender, with form accentuated by often elongate head and antenna, apical arista, and abdomen that is held straight and horizontally; body appearing more heavily sclerotized and spinose than similar families such as Micropezidae. Colour usually brown to yellow or reddish; often conspicuously vittate, particularly on head, notum, pleuron and abdomen; sometimes with spots at base of setae; halter white with knob and parts of base sometimes brown; arista often white. Usually microtomentose with legs, ovipositor and portions of head shining to subshining, sometimes in addition to pattern of glabrous spots on thorax and abdomen; face, lunule and frons (at least around tubercle) velvety; parafacial often silvery. Body length 5.0–15.0mm.

Chaetotaxy: 1 inner vertical (sometimes indistinct); 0–1 outer vertical (sometimes small and indistinct); 1–5 fronto-orbitals (erect); 0 ocellars; 1 postocellar (convergent, sometimes subparallel when short, not moved anteriorly with ocelli, leaving intervening gap); sometimes small vibrissa-like seta present on genal margin near posterior margin of eye. 1–0 dark, stout subgenal setae, but gena, subgena and occiput also with scattered dark and/or pale, fine setae, particularly at posteroventral angle, where it may be dense. Back of head with one pair of discrete setulose patches above foramen (also some Pseudopomyzidae). Postoccipital setae weak, scattered, sometimes with 1 to several dark outstanding setae dorsally or laterally. 0 presutural intra-alars; 0–1 postpronotal; 1–2 notopleurals (anterior seta reduced to absent); 2 posterior supra-alars; 0 posterior intra-alars; 1, 2, 5 or 6 dorsocentrals; 0 acrostichals; 1–2 scutellars (lateral seta often reduced if present and positioned dorsally); 0–1 proepisternal (sometimes fine and inconspicuous if present, and usually on shallow to conspicuous ridge); 0 anepisternals; 0–1 katepisternal. Setae usually short and stout, setulae usually reduced to absent; at least some setae on fore femur or fore coxa spinose or thickened; spinose setae sometimes also present on remaining coxae and femora, pleuron and subgena; females with fewer spinose setae that are mostly or only present on legs. Femora sometimes with two ventral rows of spinose setae, sometimes on tubercles, becoming less distinct basally and/or with posterior row reduced; femora sometimes with several thicker dorsal setae. Legs with straight rows of setulae that are often along ridges (pronounced on tibiae); fore tibia with one dorsoapical and sometimes one ventroapical seta; mid and hind tibiae with at least one outstanding ventroapical seta, and often with small or moderately developed dorsoapical seta. Pregenitalic sternites with reduced setation, particularly along midline.

Head. Antenna porrect, sometimes laterally compressed, usually elongate and narrow; scape sometimes with transverse dorsomedial groove; pedicel with pronounced extension on inner-distal margin; first flagellomere longer than wide, infrequently as enlarged as pedicel or scape, apex usually pointed but sometimes rounded, truncated or angulate; arista apical to dorsoapical with hairs pubescent to absent. Antenna sometimes separated from frontal vitta by "antennal bases" (Fig. 293) that possibly originate from lunule; "antennal bases" are small to large and bulbous, are separate or confluent dorsomedially, and may smoothly meet parafacial laterally or be divided from it by suture. Face membranous, sometimes with dorsolateral margin sclerotized; face and parafacial elongate, projecting. Frontal vitta sunken medially; anterior margin straight to pointed. Orbital plate sometimes with short, truncated apodeme projecting internally (Fig 296) (only verified for *Gymnonerius fuscus* Wiedemann and *Telostylinus* sp.). Occiput and postgena elongate and distinct when viewed laterally, with occiput never exceeding length of eye; if back of head produced and bulging, then anterior margin of thorax similarly bulging to form truncated abutment. Mouthparts often long and narrow; palpus narrow, flat/compressed; labium with distal processes well-developed, usually with one pair of stout basomedial setae and one pair of finer apical setae.

Thorax. Often elongate due to lengthening of presutural thorax; proepisternum relatively large. Transverse suture sometimes complete. Scutellum with dorsum slightly convex to flat, sometimes grooved. Anterior spiracle often above sunken recess encompassing discrete bulge. Katatergite bulging. Prosternum usually narrow and linear, sometimes wide and plate-like, sometimes partially bilobed anterior to coxae; some taxa (including *Nerius* and *Loxozus*) with especially broad prosternum reaching (and sometimes fused to) incurved proepisternum, forming precoxal bridge. Postmetacoxal bridge absent.

Wing. (Fig. 412) Usually clear to slightly clouded, or with more discrete clouding either apically, anteriorly, or along veins; often with general yellow to brown tint that becomes darker anterodistally. Sometimes dm-m or radial and medial veins shallowly sinuate. CuA+CuP not reaching wing margin; M_4 reaching wing margin. Vein bm-m sometimes weak or atrophied. Radial and medial veins, and dm-m, sometimes with supernumerary veins. Alula and anal lobe well-developed, but wing sometimes relatively slender. Subcostal break or weakening usually absent; subcosta complete. Calypter broadly lobate with hairs long.

Legs. Long and slender, with fore coxa and sometimes also femora and tibiae thickened. All femora usually originating relatively close together under midpoint of body. Tarsus sometimes longer than tibia.

Abdomen. Held straight and parallel to ground; sometimes relatively short. Pregenitalic sternites narrow with S1 transverse, narrow (Fig. 306). Spiracles 1–6 in membrane; female 7th spiracles ventromedial in small membranous pocket in oviscape (fused T7 and S7); both male 7th spiracles absent. Terminalia relatively uniform across species.

Male genitalia. (Figs 298–305) S6 short, symmetrical. S7 fused to downturned S8 left laterally. One pair of supernumerary sclerites in membrane anteroventral to S7+8. Subepandrial sclerite deeply divided, weakly sclerotized medially; setose distolaterally. Epandrium elongate and narrow, almost always constricted medially. Cerci narrow, lobate, united along much of length by membrane. Surstylus small, finger-like. Internal genitalia, excluding basiphallus and postgonite, elongate and narrow. Hypandrium divided ventrally, inner-ventral surface fused to long, band-like pregonite; hypandrial arms meeting dorsally, fused to long, narrow phallic plate. Postgonite short, band-like, apically swollen and setose. Phallapodeme separate from hypandrium, base flat. Epiphallus absent. Basiphallus small, fused to distiphallus. Distiphallus long, narrow, tubular and mostly membranous with one pair of parallel ventral ribbons; often with elongate membranous flagellum (removed in figure). Ejaculatory apodeme with stem stout, blade weakly sclerotized; sperm pump membranous.

Female genitalia. (Figs 306–311) T7 and S7 fused into oviscape; elongate, widest subbasally and narrowing apically, slightly compressed dorsoventrally. T8 and S8 divided medially, minutely textured and band-like. Segment 10 small; 2 apical setae on T10, 4 apical setae on S10; S10 with internal apodeme that has small sockets along length and apical swelling. Cerci relatively short, rounded, approximate and minutely setose. 1+2 or 2+2 spermathecae (Buck & Marshall, 2004), clear, with wide ducts. Ventral receptacle small, sac-like, sometimes indiscrete.

Pseudopomyzidae McAlpine, 1966

(Figs 233–256, 415–416)

Type genus: *Pseudopomyza* Strobl 1893: 284, by McAlpine, 1966: 683. **Type species of genus:** *Pseudopomyza nitidissima* Strobl, 1893: 284 [=*Opomyza atrimana* Meigen, 1830: 106], by monotypy.

The Pseudopomyzidae incudes the following extant taxa: *Heloclusia* Malloch (Chile; 1 species; Figs 233–236), *Latheticomyia* Wheeler (Nearctic and Neotropical; 7 species, with at least two more undescribed in Central America (Buck & McAlpine, 2010; Marques & Rafael, 2016); Figs 238–241), *Polypathomyia* Krivosheina (eastern Palaearctic; 1 species), *Pseudopomyzella* Hennig (Neotropical; 1 species), *Pseudopomyza* Strobl (all regions except Afrotropics; 11 species, with at least several more undescribed in the Neotropical Region (Buck & McAlpine, 2010) and Thailand (Merz, 2006); Fig. 242–243), *Tenuia* Malloch (Palaearctic and Oriental; 2 species). One fossil genus is known from Baltic amber that includes two species: *Eopseudopomyza kuehni* Hennig and *E. szadziewskii* Hoffeins & Woźnica; specimens identified as "Pseudopomyzidae sp." are listed in Tschirnhaus & Hoffeins (2009).

Keys to World genera were provided in the family treatments of Hennig (1969) and Krivosheina (1979). The New World and Palaearctic genera are keyed and discussed in Buck & McAlpine (2010), and McAlpine & Shatalkin (1998), respectively. *Pseudopomyza* and its constituent subgenera were treated in McAlpine (1994), who recognized *Pseudopomyza*, *Rhinopomyzella*, and the new subgenera *Apops* McAlpine and *Dete* McAlpine; *Macalpinella* Papp was also included as a subgenus by Buck & McAlpine (2010). McAlpine (1996) redefined the family and proposed three tentative genus groups: "Group 1" (*Latheticomyia, Tenuia*), "Group 2" (*Heloclusia, Polypathomyia*, *Pseudopomyza*) and "Group 3" (*Pseudopomyzella* and *Eopseudopomyza*).

The species of Pseudopomyzidae were catalogued regionally in Krivosheina (1984b) [Palaearctic], Vockeroth (1977) [Oriental], Mathis (1989b) [Australian] and Prado (1984) [Neotropical, as part of Cypselosomatidae]. Wheeler (1956) and Marques & Rafael (2016) provide keys to the species of *Latheticomyia*; New World *Pseudopomyza* are keyed by Hennig (1969) and New Zealand species by Harrison (1976). The two fossil species of *Eopseudopomyza* are keyed by Hoffeins & Woźnica (2013).

Biology. Species are generally considered to be uncommon or rare, having "potentially narrow ecological requirements" (McAlpine & Shatalkin, 1998), but *Pseudopomyza* (see below) and *Rhinopomyzella* can sometimes be abundant. Adults have been found in forests, and similar to many Cypselosomatidae, may occur at higher elevations (McAlpine & Shatalkin, 1998). Frey (1952) observed adult *Pseudopomyza atrimana* swarming over recently fallen logs and Roháček (2012a) found this species *en masse* on heaps of rotting grass cuttings where mating was observed to take place. Roháček (2012a, b) also thoroughly summarized habitat associations for this species in the literature, including other occurrences of adults on fallen wood and rotting substrates, as well as on flowers and recently cut stumps or logs of deciduous trees, and he noted the spring emergence of adults that may have developed on rotting vegetation. Larvae of *Polypathomyia stackelbergi* Krivosheina have been found under bark (including roots) of rotting deciduous trees such as *Maackia*, *Phellodendron*, *Kalopanax* and oak (Krivosheina, 1979, 1984b; McAlpine & Shatalkin, 1998). *Tenuia* is known from localities with osier and has been seen on willow sap (see McAlpine & Shatalkin (1998)). Neotropical species are attracted to decaying vegetation, particularly fallen trees, and have been observed around kitchen compost. Some *Latheticomyia*, particularly the males, are also attracted to dung baits, especially when the bait is positioned near logs or moss near streams (Marshall, in Buck & McAlpine, 2010), and *Latheticomyia* have been recovered from banana-baited *Drosophila* traps (Wheeler, 1956). In New Zealand, *Pseudopomyza brevis* (Harrison) was found under plant litter and dead sea birds, and *P. brevicaudata* (Harrison) was found in a fowl yard (Harrison, 1976). Large numbers of *Polypathomyia stackelbergi* are known to swarm around small vertebrate carcasses (McAlpine & Shatalkin, 1998).

Immature stages. No immature stages have been described.

Adult Diagnosis. Small to medium sized flies, 1.5–5.5mm long, colour mostly brown, sometimes similar in appearance to some Cypselosomatidae and Sphaeroceridae (particularly Limosininae and Copromyzinae, which also lack an anepisternal seta) (Figs 233–236); *Latheticomyia* (Figs 238–241) is reminiscent of small pruinose Neriidae. Postocellars convergent, distant from ocellar tubercle; usually 3 fronto-orbitals (reclinate to lateroclinate); usually one pair of paraverticals; vibrissae present. At least 4 dorsocentrals; usually 1–4 pairs of transverse "scapular" setae near anterior margin of scutum; sometimes with paired prescutellar acrostichals, sometimes with single medial series of sutural acrostichals (*Pseudopomyza*); anepisternals usually absent; 1–2 katepisternals, uncommonly 0. Wing with subcostal break and also humeral break or weakening (Figs 415–416). Femora with slender ventrobasal seta (sometimes absent from hind leg); fore femur with several long posteroventral setae (posteriorly directed) and with posterodorsal row of similar long setae; hind femur with large anterodorsal seta past midpoint.

Adult Definition. Relatively small-bodied and compact. Body length 1.5–5.5mm. Colour mostly brown with yellow to white regions, mostly on head and legs, but sometimes with dark pattern on head or mostly yellow (Figs 233–236); *Latheticomyia* with broad white to yellowish stripes (Figs 238–241). Mesonotum and frons (excluding orbital plate) usually pruinose to matte, but sometimes glossy; pleuron lightly pruinose to glossy.

Chaetotaxy: 1 inner vertical; 1 outer vertical; usually 3 fronto-orbitals (reclinate to lateroclinate, anterior pair sometimes reduced; only two pairs in some *Pseudopomyza*, 4 in *Pseudopomyzella*); 1 ocellar (long); 1 postocellar (convergent); dorsomedial seta(e) behind ocellar tubercle usually enlarged as paraverticals; vibrissa present (Fig. 242). Pedicel with at least one marginal row of setae, including one large dorsal and sometimes several large ventrals. Frons with scattered setulae. Face bare or dorsally setulose (sometimes only indistinctly so in *Pseudopomyza* and *Heloclusia*). Postoccipital setae usually in distinct row, at least dorsally; sometimes additional smaller and/or scattered setae laterally. Gena with setulae usually minute, linear to scattered, but sometimes with one outstanding medial seta that may appear as duplicated vibrissa. 2–3 subgenal setae with anterior seta sometimes positioned anteriorly on gena. Labium with 1 strong medial and 1–2 strong distal setae. 1 presutural intra-alar (absent in some *Pseudopomyza*); 1 postpronotal; 2 notopleurals; 2 posterior supra-alars; 2 posterior intra-alars (smaller seta at posterior margin sometimes setula-like); 4–5 dorsocentrals (at least one presutural); acrostichals sometimes absent (*Latheticomyia*, *Polypathomyia*, *Heloclusia*), sometimes present as one or two prescutellar pairs, and *Pseudopomyza* with single medial sutural to presutural row of one to several setae (Fig. 243); 2–5 scutellars (decreasing in length anteriorly, rarely all short; apical scutellar seta uncommonly on minute tubercle (*Pseudopomyzella*)); 1 proepisternal (sometimes on shallow tubercle); anepisternum usually bare, rarely setulose with outstanding seta (*Pseudopomyzella*); 1–2 katepisternals, uncommonly 0 (some *Pseudopomyza*). 1–4 pairs of transverse scapular setae across anterior margin of scutum (absent or with one reduced pair in some *Pseudopomyza*). Scutellum sometimes setulose dorsally and marginally. Prosternum bare. Femora with slender ventrobasal seta that is sometimes absent from hind leg; fore femur with several long posteroventral setae (posteriorly directed), and with posterodorsal row of similar long setae; hind femur with large anterodorsal seta past midpoint (sometimes reduced, eg. *Latheticomyia*). Mid tibia with ventroapical seta, and fore or hind tibia sometimes with similar seta. *Heloclusia* relatively hirsute, with legs and venter of pleuron long setulose, and with stout setae on femora and tibiae. Fore basitarsus with longer ventrobasal setae.

Head. Antenna porrect; first flagellomere discoid or slightly truncated to shallowly pointed; arista short pubescent, sometimes elongate, inserted on first flagellomere apically to subapically. Frons flat to sunken medially, sometimes convex; ocelli shifted anteriorly, leaving narrow gap between tubercle and postocellar. Face partially membranous, at least ventromedially, distinct from surrounding sclerotized regions; sometimes with variably developed facial carina or bulge below antennal bases. Gena shining and bulging, ususally at least 1/3 height of eye to almost one-half height, but sometimes as shallow as 1/9 height (eg. some *Latheticomyia*). Clypeus narrow to relatively thick, U-shaped with anterior margin sometimes slightly truncated; palpus subcylindrical to slightly compressed or spatulate.

Thorax. Precoxal and postmetacoxal bridges absent. Prosternum very narrow, linear. Greater ampulla shallow. Coxopleural streak usually weak to absent. Dorsal katepisternal suture meeting complete proepimeral suture at right angle or near right angle.

Wing. (Figs 415–416) Clear to infuscated. Costa with sc break; also with humeral weakening (eg. *Latheticomyia*) that usually produces a break (eg. *Pseudopomyza*); costal margin sometimes spinulose (*Tenuia*, *Heloclusia, Polypathomyia*); vein sc complete or ending freely in subcostal cell very close to terminus of vein R_1. Veins R_{4+5} and M_1 subparallel. M_4 usually not reaching wing margin; CuA+CuP not reaching wing margin. Vein bm-m usually absent, but sometimes partially developed or complete. CuA sometimes atrophied to absent. *Pseudopomyza brevis* brachypterous.

Legs. Legs slender, relatively short. Fore basitarsomere with anteroventral process in *Polypathomyia*; some male *Latheticomyia* with similar lobate process on inner surface.

Abdomen. Sternites shorter or longer than wide, often bare medially, sometimes desclerotized along midline. Spiracles 1–6 sometimes in membrane, sometimes associated with tergal margin or enclosed; 7th spiracles usually enclosed by sclerites.

Male genitalia. (Figs 244–249) Terminalia essentially symmetrical, but sometimes with phallus strikingly asymmetrical (eg. Fig. 248). S6 separate, symmetrical, variably modified (eg. overlapping S7 and S8 in *Pseudopomyza*, or produced as forked process in *Tenuia*). S7 and S8 forming complete or nearly complete sclerotized ring, with S8 large mostly dorsal and dome-like, often with one pair of large, stout dorsal setae; slightly asymmetrical. Subepandrial sclerite flat, U-shaped with apical setae. Epandrium relatively narrow with slight basal constriction and usually with one pair of dominant posterodorsal setae; dominant setae sometimes absent from S8, or both S8 and epandrium. Cerci narrow, connected along length via membrane, but *Tenuia* and *Polypathomyia* with apices broad and fused. Surstylus narrow, sometimes bent, curled or clavate; sometimes with small spine-like setae apically. Hypandrium with arms joined dorsally, fused to phallic plate that reaches basiphallus. Phallapodeme separate from hypandrium, rod-like. Pregonite long, band-like, with minute setae (reduced in *Tenuia*); end of pregonite reaching band-like postgonite that is swollen and setose apically. Epiphallus absent. Basiphallus separate from distiphallus, often cylindrical, sometimes elongate. Distiphallus often elongate and rod-like along most of length, sometimes curved; phallus short, sometimes asymmetrical. Ejaculatory apodeme well-developed to small, widening apically.

Female genitalia. (Figs 250–256) T7 and S7 fused into stout oviscape with suture at least partially evident; widest subbasally, strongly narrowing apically; sometimes with paired ventrobasal bulges; spiracles sublateral, sometimes within membranous fissure reaching intersegmental membrane. T8 and S8 divided, roughly textured with tooth-like denticles that are also found along intersegmental membrane to segment 10. T10 with two apical setae; S10 with four apical setae and numerous sockets extending along short, narrow internal process with apical disc. Cercus short, rounded, approximate, minutely setose. Ventral receptacle with stalk and apical bulb. Two spermathecae, sometimes asymmetrical; on relatively short membranous duct.

Strongylophthalmyiidae Hendel, 1917

(Figs 262, 274–290, 417–418)

Type genus: *Strongylophthalmyia* Heller 1902: 226 [n. n. *Strongylophthalmus* Hendel, preoccupied by Motschoulsky, 1860], by Hendel 1917: 37 [incorrect original spelling ("Strongylophthalmyinae"), corrected to Strongylophthalmyiinae in Brues & Melander (1932: 340)]. **Type species of genus:** *Chyliza ustulata* Zetterstedt, 1847, by automatic designation [type species for *Strongylophthalmus*].

The family Strongylophthalmyiidae, or "hardwood flies", is known from a single Vietnamese female of *Nartshukia* Shatalkin (Shatalkin, 1993, 1994), and 87 species of *Strongylophthalmyia* (Evenhuis, 2016; Galinskaya & Shatalkin, 2018), although there are certainly dozens more undescribed, with Evenhuis (2016) estimating approximately 150 species. Many *Strongylophthalmyia* are distributed in the eastern Palaearctic Region, but most occur in the Orient. Two species occur in the Nearctic and several species extend into, or are endemic to, the Australian Region including mainland Australia, but this Region's fauna remains undescribed. The family is unknown from the Neotropics, Europe and Africa, with the two described Afrotropical species transferred to the family Clusiidae by Barraclough (2000). The family shows a relatively clean east/west division with its sister-family Tanypezidae, which is primarily New World in distribution (Lonsdale, 2013).

Within *Strongylophthalmyia,* Shatalkin (1996) described two species groups that he recognized were not monophyletic and did not encompass most species in the genus. One group was defined by long, thin processes on the epandrium (*S. crinata* group) and one was defined by a dorsal process on the male first flagellomere (*S. punctata* group). Evenhuis (2016) placed almost all species in four provisionally accepted species groups (pending phylogenetic analysis): the *S. punctata* group (including the *S. punctata* and *S. coarcta* subgroups), the *S. crinata* group, the *S. ustulata* group and the *S. fascipennis* group.

The two Nearctic species were thoroughly revised by Barber (2006). The Old World species were treated in a series of small regional treatments in Frey (1955), Steyskal (1971a), Krivosheina (1981, 1999), Shatalkin (1981, 1993, 1996), Iwasa (1992, 1998), Iwasa & Evenhuis (2014), Yang & Wang (1992, 1996), Papp *et al.* (2006) and Galinskaya & Shatalkin (2016, 2018). Evenhuis (2016) has initiated a series of comprehensive reviews of the World *Strongylophthalmyia*, including a discussion of life history and a summary of historical study; a key to species groups and species is also included, but the importance of male-specific characters for diagnosis severely limits abilities to identify females. Regional catalogues include Shewell (1965) [Nearctic], Krivosheina (1984a), Palaczyk *et al.* (2013) [Palaearctic], Steyskal (1977d) [Oriental] and Evenhuis (1989c) [Australian]. A checklist of World species was provided by Iwasa & Evenhuis (2014), and a World catalogue is expected upon completion of the present series of revisions by Evenhuis (Evenhuis, pers. comm.).

Biology. Adults of *Strongylophthalmyia* are often found in forests on foliage, fallen tree trunks and stumps (Shatalkin, 1994). Unidentified species have been observed in Australia on *Alocasia* foliage, and in New Guinea on banana foliage exhibiting ant-like behaviour (Evenhuis, 1989c). *Strongylophthalmyia crinata* is also known to be drawn in large numbers to freshly cut stumps (Shatalkin, 1994), and individuals have also been observed on "bleeds" in trees infected with pathogeneic fungi (Barber, 2006) and near streams and waterfalls (Papp *et al.*, 2006).

Copulation may occur on dead wood, as observed for *S. pengellyi* (Barber, 2006), but it also occus on foliage, as seen in *S. angustipennis* (Marshall, 2006; Evenhuis, 2016), *S. crinata* and *S. raricornis* (copulation described in detail in Shatalkin (1994)). Females have been observed ovipositing, or attempting to oviposit, on fallen trees and in holes bored in wood by beetles, possibly scolytids, with age, texture, and fungal associations of the dead wood possibly influencing site selection (Barber, 2006; Palacztk *et al.*, 2013; Evenhuis, 2016). Larvae of north temperate species have been reared from the inner layers of bark within rotting aspen, birch and elm, where mature or nearly mature larvae likely overwinter, with puparia recovered from the outer layers (Krivosheina, 1981, 1984a; Barber, 2006). Nothing is known of the biology of *Nartshukia.*

Immature stages. The egg of *S. angustipennis* was photographed and described in Lonsdale (2013), and larvae were described in Barber (2006). The larva and puparium of *S. ustulata* were described by Mamaev *et al.* (1977) and Rotheray & Robertson (1998), respectively.

Adult Diagnosis. Relatively slender, gracile, somewhat ant-like. Head globose with broad concavity above foramen, not compressed as seen in *Formicosepsis* (Cypselosomatidae). Antenna decumbent with first flagellomere slightly longer than wide (sometimes enlarged, bifid or with dorsal process), arista short pubescent to bare. Mostly brown to black with sometimes contrastingly pale setulae (Figs 262, 274–280). Ocellar seta well-developed, sometimes very long; postocellars divergent, often proclinate. Vibrissa absent. 2–3 small fronto-orbitals with anterior seta shorter. Usually 1 or 2 dorsocentrals, but sometimes up to 7. Usually 1 anepisternal (0 in *Nartshukia*). 0 katepisternals. Lateral scutellar seta reduced to absent. Precoxal bridge large and well-developed (Fig. 279); postmetacoxal bridge absent. R_{4+5} usually parallel to M_1, rarely converging. Costal break present; subcosta usually incomplete, sometimes faintly extending to costa.

Adult Definition. Generally ant-like in form, with small, slender body and narrow legs (Figs 262, 274–280). Colour black to brown, with pale setulae in some, and often with paler or yellow areas on head, thorax and legs; thorax sometimes with bluish iridescence; halter white with stem sometimes darker and knob sometimes dark. Body sometimes with conspicuous microtexturing on notum (similar to Cypselosomatidae) and microstriations on frons; microtexturing sometimes also on clypeus, and less frequently on pleuron and abdomen. Body length 2.0–7.5mm.

Chaetotaxy: Setae mostly fine and difficult to differentiate from long setulae. Setae mostly dark, setulae mostly yellowish and often long; setulae sometimes relatively dense but often reduced on head and thorax, sometimes excluding anepisternum and venter of katepisternum; body usually glabrous and smooth, sometimes with thin micropilosity. 1 inner vertical; 1 outer vertical; 2–3 fronto-orbitals (reclinate to slightly lateroclinate, anterior seta shorter); 1 ocellar (usually long, but sometimes shorter than postocellar); 1 postocellar (divergent, removed from ocelli, erect to proclinate in *Strongylophthalmyia*); vibrissa absent; usually numerous genal setae extending dorsally along tomentose parafacial (absent in *Nartshukia*). Scape with scattered marginal setae and one dominant dorsal seta; pedicel with dominant dorsal seta that may be elongate; first flagellomere often densely pilose. Frons with sparse row of lateral setulae and anterior margin with one to several pairs of minute to relatively well-developed setae; postgena covered with long pale pile; postocular setae mostly short and scattered, with dorsal setae (lateral only) in series. 0–1 presutural intra-alar; 0–1 postpronotal (weak if present); 1–2 notopleurals; 1–2 posterior supra-alar (sometimes reduced); 0 posterior intra-alars; usually 1 dorsocentral, sometimes 2–3, uncommonly 4 to 7 (anterior setae reduced with at least one presutural); 0 acrostichals (reduced pair uncommonly present); 1–2 scutellars (lateral pair weak if present); 0 or 1 (*Nartshukia*) proepisternal; 1 or 0 (*Nartshukia*) anepisternals; 0 katepisternals. One pair of small scapular setae anteriorly on scutum in *S. splendida* Yang & Wang (Galinskaya & Shatalkin, 2016). Halter stalk with series of pale setae. Male fore femur sometimes with dark stout setae dorsally, sometimes in two rows, but sometimes only 1 seta ventromedially; mid tibia with ventroapical seta; male femora sometimes with longer ventrobasal seta. Abdomen with longer setae laterally and posteriorly. Epandrium, surstylus and sternites 7 and 8 bare, with “pebbled” texture.

Head. Antenna decumbent; first flagellomere often discoid, slightly longer than wide (difference sometimes negligible), sometimes enlarged and ovate or unusually shaped (eg. bifid or with small to very large process resembling thickened arista); arista short pubescent to bare, length sometimes reduced to half length of first flagellomere. Head globose, slightly wider than thorax and slightly longer than high, with postgena and occiput bulging; back of head with medial concavity, excluding rounded shelf above foramen. Frons with minute, shallow striations; narrowing anteriorly and sometimes slightly projecting over antennal base; ocellar triangle narrow to relatively wide, usually indistinct, not attaining anterior margin. Ocelli removed from postocellar setae, usually situated near midpoint of frons (*Strongylophthalmyia*), but sometimes close to vertex (*Nartshukia*). Anteromedial ommatidia slightly enlarged. Parafacial and sometimes anterior margin of orbital plate slightly produced lateral to antennal base, with parafacial sometimes shallowly carinate; parafacial and gena with silvery tomentose band extending to posteromedial margin of eye. Gena very shallow, less than 1/10 height of eye. Face sclerotized dorsolaterally; with narrow medial membranous space widening to buccal cavity; face/parafacial sometimes reduced in height, and usually at least slightly compressed laterally due to convergence of eyes (more extreme cases similar in appearance to Megamerinidae, which may also have dense silvery pilosity on parafacial); shallow facial carina developed in *Nartshukia*. Male clypeus band-like, subquadrate, sometimes membranous and appearing absent; female clypeus thick, bulbous, sometimes very large and plate-like, projecting or deeply recessed; palpus subcylindrical; male palpus sometimes compressed, leaf-like, pediculate, clavate or with small process, sometimes with several scale-like setae; labium short, bulging laterally, with long setae.

Thorax. Relatively narrow with presutural regions slightly lengthened, removing fore coxa anteriorly. Transverse suture sometimes nearly complete. Notopleuron mostly sunken. Scutellum small, rounded or with sides and apex straighter. Greater ampulla absent. Coxopleural streak present. Katatergite narrow, sometimes bulging. Precoxal bridge present, broad; sutures between postpronotum, proepisternum (bulging) and prosternum indistinct (Fig. 279); postmetacoxal bridge absent.

Wing. Clear, clouded, with faded spot or band(s); wing interference patterns discussed in Evenhuis (2016). Alula small and anal lobe well-developed or slightly narrowed. Veins R_{4+5} and M_1 convergent (*Nartshukia, S. curvinervis* Frey; Fig. 417) or parallel to very slightly convergent (most *Strongylophthalmyia;* Fig. 418); M_1 often arched in *Strongylophthalmyia*, similar to some Psilidae. M_4 and CuA+CuP not reaching wing margin, but sometimes very closely approaching it. Vein CuA slightly bent (*Strongylophthalmyia*) or straight (*Nartshukia*). Costal break present; subcosta usually incomplete, sometimes faintly extending to costa. Calypter broadly lobate, hairs long.

Legs. Slender, fore legs up to half length of other legs. Male fore leg sometimes with secondary sexual characters—fore tibiae and basitarsomeres bent, flattened or deviated, apparently for clasping purposes while mating (see Barber (2006)), setae sometimes pattered or thickened and clustered, sometimes with short spicules; mid basitarsus sometimes modified. Hind trochanter and/or femur base uncommonly with one or two inner-basal processes; hind basitarsus sometimes with scale-like setae (both sexes).

Abdomen. Slender, tapering (Fig. 286). Sternites less setose, partially desclerotized along midline to S7 in females and S5 in males. Spiracles 1–6 in membrane below tergite. 7th spiracle absent. Membrane with relatively long, shaggy microtrichia. Pregenitalic sclerites subrectangular, mostly longer than wide with S1 broader and shorter; sternites smaller, less sclerotized to membranous.

Male genitalia. (Figs 281–285) S6 well-defined, ventral to left lateral, apically setose, well sclerotized along distal and left lateral margins, incorporated into elongate pregenital band mostly composed of large dorsal S8. Surstylus fused to epandrium, narrow when apparent, sometimes apically ribbon-like (*S. crinita* group); inner-distal surface with short, stout setae. Epandrium sometimes basally constricted, sometimes with long, thin, sometimes branched ventral process. Subepandrial sclerite composed of one pair of flat, bare adjoining plates. Cerci narrow, sometimes elongate, fused along length (mostly via membrane). Hypandrium arched with narrow ventromedial bridge and single ventral seta on each lobe; with ventromedial process that is sometimes apically bifid (interpreted as postgonite by Barber (2006)). Phallapodeme long, rod-like, with one pair of processes that widen to point of fusion with hypandrium. Pregonite very long, narrow and band-like, with apex slightly swollen and setose; base fused to inner surface of hypandrium. Postgonite absent. Phallic plate divided into two articulating sclerites. Epiphallus absent. Distiphallus narrow and extremely long (“globular” in *S. thaii* Papp (Papp *et al*., 2006)), with sclerotized bands and apical “glans”, usually unsegmented, membrane minutely trichose. Ejaculatory apodeme sometimes small, narrow to finger-like with subbasal swelling.

Female genitalia. (Figs 286–290) Segment 6 broad medially, tapered at base; margins of T6 and S6 sometimes meeting but not fused. T7 and S7 completely fused on basal ¾ to form slightly narrowing sclerotized tube, with lateral and dorsomedial emarginations, and with linear ventromedial weakening or sulcus; distal ¼ of segment essentially membranous with ring of marginal setae. Segments 7 and 8 separated by extremely long intersegmental space. T8 and S8 medially divided into two pairs of sclerotized bands; line of setae on ventral bands. S10 and T10 relatively elongate and well-developed, with long, narrow internal process emerging as apodeme from S10. Cerci moderately long, curved in cross section, fused along most of length via membrane. Segments 7–10 mostly retractile, forming slender ovipositor. Genital chamber with folded vaginal sclerite. Ventral receptacle transverse, reniform, with surface corrugated to lobate. 2 spermathecae, one atrophied or absent, the other short, broad and telescoped, with minute transverse wrinkles; ducts fused near base.

Tanypezidae Rondani, 1856

(Figs 257–261, 263–271, 419–420)

Type genus: *Tanypeza* Fallén 1820: 4, by Rondani 1856: 114 (as Tanypezina). **Type species of genus:** *Tanypeza longimana* Fallén, 1820: 4, by monotypy.

The “stretched-foot flies” (Tschirnhaus, 2008) is an almost entirely New World family with two genera: *Tanypeza*, which contains the Nearctic *T. picticornis* Knab & Shannon and the Holarctic *T. longimana,* and *Neotanypeza* Hendel, which contains 25 extant Neotropical species, although there are certainly additional species yet to be discovered. One fossil species is known, *N. dominicana* Lonsdale & Apigian, from Dominican amber dated to 17–20mbp (Lonsdale & Apigian, 2010).

The family is relatively large-bodied and distinctive, making them easily recognized in the field, but species are uniform in appearance and homoplasy appears to be widespread. As such, the delimitation of species boundaries has proven difficult and additional study is required. The species of *Tanypeza* were keyed by Steyskal (1965) and the species of *Neotanypeza* by Lonsdale (2013), following earlier treatments by Hennig (1936a) and Enderlein (1936). A catalogue of World species was provided by Lonsdale (2014).

Since species currently treated as Tanypezidae exhibit strong physical uniformity, almost all were initially described as *Tanypeza*, subgenera of *Tanypeza*, or genera only weakly differentiated from *Tanypeza*. Only *Neotanypeza ornatipes* (Bigot) was initially classified elsewhere, described in the micropezid genus *Taeniaptera*. In an attempt to segregate the modest variation presented by Neotropical species, Hendel (1903) erected the genus *Neotanypeza*, and Enderlein (1913, 1936) erected the genera *Scipopeza*, *Tripolphopeza*, *Tritanypeza* and *Polphopeza*. *Polphopeza* was synonymized with *Neotanypeza* by Hennig (1936a) but resurrected by Enderlein (1936) that same year. Lonsdale (2013) found that the Tanypezidae split quite easily between a north temperate *Tanypeza* and a Neotropical *Neotanypeza*, and since the internal structure of the latter did not lend itself to further subdivision, all of Enderlein’s genera were treated as synonyms of *Neotanypeza*.

Biology. Roháček (1998, 2016) collected European *Tanypeza longimana* adults in low vegetation in humid deciduous woods, often near running water. Collections were often at low altitudes in floodplains or submontane regions. Chandler (1975a) speculated that, like *Strongylophthalmyia*, the larvae of Tanypezidae live in rotting wood and are at least partially saprophagous, and Roháček (2016) collected adults in a trap set over rotting wood. This speculation was partially supported by Foote (1970), who was able to raise larvae derived from a gravid female of *T. longimana* to the third instar on decayed watermelon rind. Nothing is known of the biology of Neotropical species.

Immature stages. Eggs of *Tanypeza longimana* and *Neotanypeza elegans* (Wiedemann) were photographed and described by Lonsdale (2103). Descriptions of the three larval instars of *T. longimana* were provided by Foote (1970). The puparium is unknown.

Adult Diagnosis. Relatively large flies, 5.0–12.1mm in length, with stout thorax and long, slender legs (Figs 257–261). Mostly black with legs, antenna and face often yellow in part, but parts of thorax and abdomen sometimes also pale; silvery tomentose stripes on thorax, occiput, parafacial and frons; vertex with flat, circular, variably tomentose "ocellar disc" separating ocelli from back of head; frontal vitta velvety black to dark purple. Head higher than long, hemispherical. Antenna elbowed with first flagellomere usually broad and approximately two times longer than wide. Postgena with long white hairs. Vibrissa, outer vertical, acrostichal, proepisternal and katepisternal setae absent; ocellar seta small. Greater ampulla present. Veins R_{4+5} and M_1 converging; subcosta complete; costa unbroken; vein R_1 setulose dorsally (Figs 419–420).

Adult Definition. Body length 5.0–12.1mm. Colour predominantly dark brown to black, with legs partially yellow (more so towards base), and antenna and face (with lateral stripes) often yellow to pale yellow or white in part; additional sections of thorax and abdomen less commonly yellow; head, thorax and male S8 with silvery tomentose stripes; halter white.

Chaetotaxy: 1 inner vertical; 0 outer verticals; 0–2 fronto-orbitals (reclinate, anterior seta smaller if present); 1 ocellar (small to minute); 1 postocellar (divergent, very small in extant *Neotanypeza*); vibrissa absent. Pedicel with dominant dorsal seta. Orbital setulae minute, in single row. Gena with row of short, dense setulae. Postgena with dense long white hairs. Subgenal setae distinct. Postocculars small, dark, blending into pale scattered pile laterally; sometimes with one or two postocculars shifted ventromedially as small, thin paraverticals. 0–1 presutural intra-alar; 0–1 postpronotal; 2 notopleurals; 2 posterior supra-alars; 0–1 posterior intra-alar; 1–3 dorsocentrals (postsutural); 0 acrostichals; 2 scutellars; 0 proepisternals (sometimes with outstanding setula that resembles proepisternal); 1 anepisternal, usually also with additional elongate setae along posterior margin that are often thinner and shorter; 0 katepisternals. Vein R_1 setulose dorsally. Halter stalk with series of small black dorsal setulae. Pleuron with long, pale, sparse pile, with longest hairs on anepimeron; with large shining to subshining regions. Mid tibia with ventroapical seta; sometimes with slightly pronounced setulae around antero- or posterolateral margins. *Tanypeza* males with stout back setae anteromedially on hind trochanter and posterobasally on hind femur. *Neotanypeza* with slightly pronounced setae along posteroventral margin of femora that are only darker and slightly pronounced on fore femur; apicodorsal surface of fore femur and posteromedial surface of mid femur sometimes with strong setae; mid tibia sometimes with slightly darker, thickened posteromedial setulae. T2 with long, stout anterolateral setae.

Head. Large with back relatively flat, abruptly meeting vertex. Antenna elbowed with first flagellomere usually broad and more than two times longer than wide; arista short plumose to pubescent, subbasal; bases of antennae approximated. Frons usually black to dark purple and velvety; strongly narrowed in male; postgena, gena and parafacial silvery tomentose, with silvery band extending along lateral margin of frons to varying extents; frons and face microstriate. Ocelli separated from posterior margin of frons by variably tomentose, circular "ocellar disc" (Fig. 260). Face membranous (slightly more heavily sclerotized dorsally and along antennal grooves), bulging dorsomedially but mostly flat and grading smoothly into buccal cavity. Lunule narrow, small. Gena very narrow, short, shifted anteriorly and angled dorsally, bringing forward posterior genal angle; parafacial and gena with series of slightly longer pale hairs. Foramen large, nearly ⅓ width of back of head and almost reaching large buccal cavity. Clypeus relatively narrow with margins subparallel and anterior margin rounded, recessed within buccal cavity; palpus broadly ovate and laterally compressed.

Thorax. Relatively large and stout; with silvery tomentose stripes, including one from notopleuron to meron or katepisternum (Figs 257–261); *Tanypeza* with less distinct medial stripe on scutum. Katatergite relatively narrow and bulging. Greater ampulla present. Katepisternum with deep recess anterior to meron. Precoxal bridge well-developed, broad, with suture between proepisternum and postpronotum evident; postmetacoxal bridge present, with medial suture or gap in *Tanypeza*.

Wing. (Figs 419–420) Clear to variously pigmented, often with apical or anterodistal infuscation. Veins R_{4+5} and M_1 converging apically. Calypter broad and lobe-like with marginal hairs long; lower calypter densely haired, "fuzzy". Vein CuA strongly bowed. M_4 reaching wing margin, sometimes as fold; CuA+CuP not reaching wing margin. Costa unbroken; subcosta complete.

Legs. Legs long and slender. Mid tibia with several small ventroapical setae. Hind tibia deviated subbasally in extant *Neotanypeza*. Hind basitarsus with ventrobasal protuberance that is shallow in *Tanypeza* and pronounced in *Neotanypeza*. Mid and hind tarsi with stout ventrolateral setae.

Abdomen. Spiracles in membrane below tergite; male 7th spiracle ventral, lateral to inner-distal margin of S8 (Fig. 264). T2 with stout anterolateral setae. Sternites narrow with S1 broader; S2 sometimes entire, but usually with anterior margin divided into separate, transverse sclerite, with adjoining margins of both sclerites doubly emarginate.

Male genitalia. (Figs 263–268) S6 subrectangular, usually asymmetrical, shifted towards S7; partially desclerotized with dark shining band on left lateral margin. Fusion of S7 and S8 extensive; both often with reduced chaetotaxy. S8 silvery tomentose. Surstylus completely fused to epandrium with suture absent; *Neotanypeza* with stout, pointed inner-distal setae that are also often found on outer-posterior surface. Cerci well-developed, narrow, fused along most of length. Subepandrial sclerite composed of one pair of narrow, ventrally converging plates. Hypandrium with halves separate ventrally (*Tanypeza*) or with weak to well-developed anteroventral bridge; setae few or absent; arms usually separate. Phallic plate composed of two articulating sclerites that fold flat over each other. Phallapodeme long, rod-like, sometimes with one pair of anteromedial processes fused to inner surface of hypandrium. Pregonite long, narrow, band-like, with apex slightly swollen and setose and base curved to fuse to inner surface of hypandrium. Postgonite absent. Epiphallus absent. Basiphallus small, fused to distiphallus. Distiphallus of *Tanypeza* long, straight, partially membranous with ventral sclerotized bands and apical "glans"; distiphallus of *Neotanypeza* flat and rod-like, short to relatively long, usually with at least lateral margins sclerotized, and uncommonly with medial break. Ejaculatory apodeme small, finger-like.

Female genitalia. (Figs 269–271) Tergites and sternites separate. Segments 7–10 forming slender ovipositor that mostly retracts within segment 6, which is widest anterior to midpoint; with long intersegmental regions that are minutely trichose basally between segments 6 and 7 and segments 7 and 8. S7, S8, T7 and T8 divided medially, forming narrow bands, with reduced setae on segment 8. T10 and S10 tapered apically, with reduced setae; S10 with long internal process. Cerci moderately long, curved in cross-section, connected along length by membrane and fused along distoventral margin. Ventral receptacle composed of small dome over series of vesicles. Spermathecae spherical and pigmented, surface minutely papillose; ducts moderately long and clear.

Historical treatment of the diopsoid family groups

Gobryidae, Megamerinidae, Syringogastridae & Nothybidae. Hendel (1913) used his new subfamily Megamerininae to encompass taxa that would eventually coalesce into our present concepts of Megamerinidae, Gobryidae and Syringogastridae. Hendel's (1913) grouping was followed by Bezzi (1913), who apparently coordinated his classifications with Hendel via correspondence (see McAlpine (1997a)), and by Enderlein (1920), Frey (1928), Curran (1934), Hennig (1941d) and Brues *et al.* (1954), although *Syringogaster* and *Gobrya* were not addressed together by Frey, Curran and Hennig because of the geographic scope of their works. Cresson (1912) first classified *Syringogaster* as Psilidae, and Walker (1860) described *Gobrya* as "Psilides", a group he also used to hold *Megamerina* (Walker, 1853). Hennig (1958, 1965, 1973) maintained Hendel's system, although he was clearly aware how distinct the gobryid and syringogastrid genera were from *Texara* and *Megamerina*.

Hendel (1916) raised Megamerinidae to full family rank and hypothesized relationships with other Acalyptratae, placing it in his Sepsidariae (Megamerinidae, Sepsidae, Diopsidae). Associations with Sepsidae were also previously considered by Schiner (1862) and Wulp (1896), who treated *Megamerina* (or *Lissa*) as Sepsinae, Schiner (1864) erected Anomalae in the Sepsinae to encompass *Lissa* and *Rhynchaea* Zetterstedt (Piophilidae), and Becker (1905) used a concept of Sepsidae that included *Lissa*, *Scotimyza* (Ephydridae) and genera of Piophilidae. Enderlein (1920) treated Megamerininae as a subfamily of Sepsidae. Frey (1921) grouped Diopsidae and Megamerinidae in his large "Sciomyzaeformes" of 42 families, which also notably included Sepsidae and Piophilidae. Lindner (1925) associated Diopsidae and Megamerinidae with Sepsidae.

Rondani (1874) included *Megamerina* and genera of Sepsidae and Micropezidae in his Tanypezinae. This group was previously called "Tanipezina" and included *Tanypeza* (as "*Tanipeza*") and varied tephritoid genera. Tanypezinae would also eventually include his new genus *Nothybus* (Rondani, 1875), whose large body and long legs would destine it for frequent comparison to Tanypezidae and Micropezidae. Rondani's classification was followed by Bigot (1886a, b), who called the higher group Tanypezidi and noted that he could not confidently place *Gobrya* to family.

Osten-Sacken (1882) treated *Nothybus* as Micropezidae ("Tylidae" at the time) with *Anaeropsis* and *Nestima*, and Wulp (1896) considered *Gobrya* and *Nothybus* to belong to Calobatinae, which also included *Seraca* Walker (syn. *Sophira* Walker: Tephritidae) and genera now belonging to Micropezidae s.l. and Neriidae. Bigot's (1892) Calobatidae was similar to Wulp's concept, including in it *Nothybus*, *Texara*, *Cephalia* Meigen (Ulidiidae), *Nerius*, *Macrotoma* Laporte (syn. *Longina* Wiedemann) (Neriidae), and six micropezid genera. Meijere's (1908, 1911) usage of Calobatinae was restricted to *Gobrya* and several neriid and micropezid s.l. genera, but was later expanded to include some tephritoid taxa and *Texara dioctrioides* Walker (Meijere, 1918). Enderlein's Calobatinae (1922) included *Nothybus*, *Gobrya,* and most Micropezidae s.l. except for Micropezinae and Neriinae. Cresson (1912) maintained *Nothybus* in Micropezidae in the subfamily Neriinae.

Frey (1927) considered *Nothybus* to be closer to Tanypezidae than Micropezidae and erected the new family Nothybidae for it. The family was recognized by all subsequent authors, including Aczél (1955c), who strangely titled his paper "Nothybidae, a new family of Diptera".

Syringogaster was moved from Megamerinidae to its own family Syringogastridae by Prado (1969), who also tentatively included *Megamerina fulvida* Bigot, which is now considered Richardiidae (Marshall *et al*., 2009). Placement of *Gobrya* in Megamerinidae was maintained by Steyskal (1977e), J.F. McAlpine (1989) and Evenhuis (1989b). Colless & McAlpine (1970) considered the position of *Gobrya* tentative, suggesting a possible relationship with *Syringogaster*, but they later moved it to Nothybidae (D.K. McAlpine, 1982; Colless & McAlpine, 1991). *Gobrya* was only actually treated as Syringogastridae by Ferrar (1987), although no support for this placement was provided. Gobryidae was eventually erected for *Gobrya* by D.K. McAlpine (1997b).

Somatiidae. The type species of *Somatia, S. aestiva*, was long considered to be Tephritoidea. It was originally described as *Tephritis* Latreille by Fabricius (1805) in the Trypetidae (=Tephritidae), which was followed by subsequent authors including Wiedemann (1830a), who treated it as *Trypeta*. Loew may have considered it Richardiidae, as suggested by Enderlein (1927) who had access to his manuscript notes, and Steyskal (1958) was amenable to an association between *Somatia* and this family. Hennig (1958) similarly considered a possible relationship with Richardiidae, but also Heleomyzidae. Curran (1934) placed *Somatia* in the Psilidae along with *Strongylophthalmyia*. Hendel (1935) provided *Somatia* its own family, where it has remained despite Griffiths' (1972) argument for placement in Periscelididae as the subfamily Somatiinae, which was later found to lack support by J.F. McAlpine (1989) and D.K. McAlpine (1997b).

Psilidae. Most Psilidae are divided between two subfamilies that have been quite stable over the last 150 years aside from nomenclatural changes (see Sabrosky (1999)), dividing the monogeneric Chylizinae from most remaining genus groups in the Psilinae. Hennig (1965) considered psilids to all belong to the subfamily Psilinae, within which was the uplaced fossil *Electrochyliza* and the tribes Chylizini and Psilini; this tribal system was only followed by Prado (1975). Belobackenbardiinae was recently described for the small South African genus *Belobackenbardia* (Shatalkin, 2002).

The family group Psilidae originates with Macquart's (1835) Psilomydae, based on *Psilomyia* Latreille, an unnecessary replacement name for *Psila*. This was proven incorrect and Walker (1853) used the original name *Psila* as root for the family name "Psilides". Psilomydae originally included a diversity of taxa: *Orygma* Meigen (Sepsidae), *Trigonometopus* Macquart (Lauxaniidae), *Eurina* Meigen, *Platycephala* (Chloropidae) *Psilomyia* (Psilidae), *Pyrgota* Wiedemann (Pyrgotidae), *Otites* Latreille, *Tetanops* Fallén and *Dorycera* Meigen (Ulidiidae).

Macquart (1835) also erected the family Loxoceridae for *Loxocera* and *Platystyla* Macquart (now a synonym of *Loxocera* s.s. (Buck & Marshall, 2006b)), placing it separately from Psilomydae in his Loxocerides, which encompassed the families Loxoceridae, Opomyzidae, Scatomyzidae (=Scathophagidae) and Palomydae. The family Palomydae is mostly Sciomyzidae, but it was historically used by Robineau-Desvoidy (1830) for *Loxocera* (Sabrosky, 1999). While Loxoceridae and Psilidae are both available names for the family, Psilidae is preferentially used by contemporary authors. Macquart's system was followed by Blanchard (1840) and Lioy (1864, 1895), the latter of whom treated the family groups as Loxoceriti and Psilomyti (later "Psilomyiti") in the tribe Acalypteridi. Westwood (1840) would use Loxocerides to contain *Chyliza*, *Psilomyia*, *Loxocera* and *Lissa* (=*Megamerina*).

Walker (1853) treated Loxoceridae as a synonym of Psilides, and included *Psila, Chyliza, Loxocera*, *Micropeza* (but not *Calobata*, which was considered Sepsides), *Tetanura*, *Piophila* Fallén and *Lissa*. Walker (1856) later included *Nerius* and *Texara* in Psilides, and then in his review of the fauna of Celebes (=Sulawesi), included *Seraca* (Tephritidae), *Psila, Micropeza, Coenurgia* Walker*, Nerius, Texara* and *Gobrya* (Walker, 1860). The name Psilides was also used by Dahlbom (1853) for a group of genera in the Diapriidae (Hymenoptera) that is now treated as the tribe Psilini; the name was based on *Psilus* Panzer and could compete for priority. Sabrosky (1999) noted that "Agassiz (1846: 312) emended Dahlbom's Psilides to Psiloidae".

Prior to Macquart (1835), Fallén (1820) included the psilid genera *Chyliza* and *Loxocera* in his Opomyzides, which also included *Calobata*, *Tanypeza*, *Tetanura* (Sciomyzidae), *Opomyza* Fallén (Opomyzidae) and *Scatophaga* Fabricius (Scathophagidae), the latter of which included species of *Psila* at the time. Zetterstedt's (1838) incarnation of Opomyzides grouped *Loxocera* with *Calobata, Micropeza, Opomyza*, *Colobaea* Zetterstedt (Sciomyzidae) and *Scatophaga*. Zetterstedt (1847, 1849, 1860) would later include *Tanypeza*, *Tetanura* and *Chyliza* in the Opomyzides, as Fallén did. Latreille (1825) used Dolichocerae to contain *Loxocera, Lauxania* (Lauxaniidae)*, Sepedon* Latreille and *Tetanocera* Dumeril (Sciomyzidae).

Rondani (1856) erected the group Chilizina—later renamed Chylizinae (Rondani, 1876)—within the family Agromyzidae to encompass genera that now fall within the present-day boundaries of Psilidae: *Pachilomera* Rondani (=*Psilosoma* Zetterstedt)*, Loxocera, Psila, Platystyla, Megachetum* Rondani (=*Chyliza* Fallen) and *Chyliza*. Bigot (1887) accepted this placement within Agromyzidae, but used the subfamilies Psilinae and Chilizinae [sic]. Bigot (1892) subsequently separated the genera *Chyliza* and *Psila* in the families Chylisidae [sic] and Psilomydae, respectively.

The family name Psilidae was first used by Loew (1861a, b), and then by Osten-Sacken (1862) to encompass the genera *Loxocera*, *Psila* and *Chyliza*. Some would continue to use the group as a subfamily, such as Meijere (1914) and Schiner (1862), who included *Loxocera, Platystyla* (=*Loxocera*)*, Chyliza, Psila* and *Psilosoma*. Williston (1908) used a relatively modern concept of Psilidae that only otherwise included *Megamerina,* and Cresson (1912) added his new genus *Syringogaster* to it. *Megamerina* was soon thereafter removed from Psilidae by Hendel (1916), taking *Syringogaster* and *Gobrya* with it (see above), but other genera still found their way into Psilidae. One of these was *Somatia*, which was placed there by Curran in 1934, only to be removed a year later when given its own family by Hendel (1935). The Chilean *Schizostomyia* Malloch was originally described as Psilidae, but was removed by Hennig (1971) to the Anthomyzoidea; McAlpine (1989) later treated *Schizostomyia* as an uplaced genus in Asteioinea related to *Paraleucopis* Malloch and *Mallochianamyia* Santos-Neto (as "*Gayomyia* Malloch", a preoccupied name in Hemerobiidae).

Strongylophthalmyia was extensively treated as Psilidae historically and was originally described in that family by Hendel (1902) as "*Strongylophthalmus*". *Strongylophthalmyia* and would also appear as Psilidae in Becker (1905), who also included *Lamprophthalma* Portschinsky (Platystomatidae), and in Frey (1928) and Hennig (1941d). The genus *Labropsila* Meijere, now a junior synonym of *Strongylophthalmyia*, was also described as Psilinae by Meijere (1914).

DIOPSIDAE. A thorough historical account of Diopsidae is provided in Feijen (1989), which is briefly summarized here with some additional information as it relates to family boundaries. Historical associations between all lineages of stalk-eyed flies occur throughout the literature, beginning with Latreille's (1809) clustering of *Achias* (Platystomatidae) and *Diopsis* in Muscides, although Fallén (1810) would soon thereafter remove *Achias* to his Syrphici and *Diopsis* to his Ortalides, the latter of which also included *Sepedon*, *Tephritis*, *Sepsis* Fallén and *Micropeza*. This placement of *Diopsis* in Ortalides was followed by Dalman (1817, 1820), who found similarities to taxa elsewhere in Fallén's classification and would later (Dalman, 1823) recommended a separate family group for *Achias* and *Diopsis*. Latreille's (1825) classification maintained *Diopsis* and *Achais* separately, and he sent *Diopsis* into his Scathophilae with seven genera from six currently recognized families. A subsequent classification (Latreille, 1829) placed *Diopsis* in Carpomyzae with a different, but similarly diverse set of taxa, including genera of Micropezidae, Sepsidae and Tephritoidea, among others. Similarities were drawn between *Diopsis* and *Achias* by Say (1828) when he described *Sphyracephala* for the Nearctic *Diopsis brevicornis* Say, seeing it as an intermediate between the two. Wiedemann (1830b) treated *Plagiocephalus* Wiedemann (Ulidiidae) and *Zygotrica* Wiedemann [=*Zygothrica* Wiedemann, Drosophilidae] (including *Z. robusta* Bigot, now Platystomatidae) as subgenera of *Achias*, which was followed by Gray (1832), who may have also implicitly included the stalk-eyed *Sphyracephala*. Westwood (1848) treated *Diopsis*, *Sphyracephala* and *Achias* in the muscid section Athericera.

Macquart (1835) considered *Achias* Muscidae and *Diopsis* Sepsidae, and Desmarest (1860) similarly maintained *Diopsis* in his Sepsitae. Macquart (1843) later noted that the sepsid placement was for convenience only, and then removed *Diopsis* to his tribe "Diopsideae, Nob." (*nobis* =ours). He was likely unaware that a family group name had already been provided for this genus. The first family group named for *Diopsis* was actually Billberg's (1820) Diopsides, which included *Diopsis*, *Achias*, *Calobata* and *Loxocera*. Walker (1856) also provided his own family group name for *Diopsis*, his subfamily "Diopsides Walk.", which was kept separate from *Achias* in the subfamily "Achiides Walk.". The presently accepted family spelling Diopsidae was provided first by Bigot (1852), who included in it the genera *Diopsis* and *Sphyracephala,* and then by Osten-Sacken (1862).

Westwood (1837) revised *Diopsis* and noted that while the antennae were laterally displaced in this genus, they were positioned centrally on the head in other genera with eye stalks. This character was acknowledged by subsequent authors and utilized prominently in keys. Rondani (1873) temporarily moved *Diopsis* to Tanypezinae, but he then (Rondani, 1875) grouped the stalk-eyed flies he was aware of in Diopsidinae: *Diopsis*, *Diasemopsis*, *Hexechopsis* Rondani (=*Sphyracephala*), *Sphyracephala*, *Teleopsis*, *Zygocephala* Rondani (=*Sphyracephala*), *Plagiocephala* Macquart (Ulidiidae), *Zygothrica* and *Achias*. Bigot (1880) treated these as Diopsidae, and also included the stalk-eyed micropezid *Anaeropsis* Bigot.

A classification eventually approximating a modern concept of the family was used by Loew (1873), Osten-Sacken (1881, 1882) and Wulp (1896), who restricted the family to include only those species with the antennae positioned distally on the eye stalks, referring *Achias* to Ortalinae, *Anaeropsis* to Calobatinae and *Zygothrica* to Drosophilinae. Most authors would continue treating the group as a subfamily until after Meijere (1916).

The narrowed boundaries of Diopsidae were again expanded when Shillito (1950) recognized that *Centrioncus* Speiser belonged to the family. This placement was followed by subsequent authors, including Hennig (1965), who provided cladistic support for the new family concept and later (Hennig, 1965) erected the subfamily Centrioncinae for *Centrioncus*. Hennig (1965), whose family group system is followed here, placed all remaining genera in Diopsinae, which was divided into the tribes Diopsini and Sphyracephalini, and his new fossil "ancestral group" *Prosphyracephala* Hennig. Shillito (1971) and Cogan & Shillito (1980) raised the two tribes to the level of subfamily. Feijen (1983, 1989) later treated Centrioncinae as a separate family, considering it to be more closely related to Syringogastridae, but this was not supported in later studies (McAlpine, 1997b; Meier & Hilger, 2000; Kotrba, 2004). A lack of outgroup exemplars likely contributed to Feijen's analytical issues, as only idealized ingroup family-level representatives were considered for the phylogeny.

Since 2000, reaffirmation of *Centrioncus* as Diopsidae was provided in a new wave of quantitative numerical studies incorporating molecular and morphological characters, sometimes in combination, although these were largely or entirely applicable only to Diopsidae and its constituent family-level groupings, but Syringogastridae was sometimes also included. Meier & Hilger's (2000) morphological analyses, which incorporated adult and egg morphology, convincingly recovered a Diopsidae inclusive of *Centrioncus*. Meier & Hilger (2000) additionally provided characters supporting Gobryidae as sister to Diopsidae + Syringogastridae. Marshall *et al.* (2010) added molecular data for species of *Syringogaster* to the data sets of Baker *et al.* (2001) and Kotrba & Balke (2006) in their analysis of Syringogastridae, recovering both families as monophyletic and *Centrioncus* as sister to the remaining Diopsidae; the authors also suggested that Megamerinidae was sister to Diopsidae + Syringogastridae.

Centrioncus was originally described as Sepsidae by Speiser (1910) for a species he saw as intermediate between Diopsidae and Sepsidae, recognizing the general diopsid body plan past the absence of eye stalks. While maintained as Sepsidae, this placement was not accepted by Frey (1925b) or Duda (1925), the latter of whom considered it closer to Diopsidae, but also suggested a relationship with Chloropidae.

DIOPSOIDEA. Modern superfamily concepts including the diopsoid families slowly emerged from contributions by authors such as Hendel (1916), who grouped these taxa in his "Sepsoidea", the subdivisions within which were eventually given names (Hendel, 1922): Sepsidariae (Megamerinidae, Sepsidae, Diopsidae), Piophilariae (Piophilidae and its synonym Thyreophoridae) and Psilariae (Psilidae). Along similar lines, Lindner (1925) also grouped Diopsidae, Megamerinidae and Sepsidae, and Frey (1921) grouped Diopsidae, Megamerinidae and Psilidae in his large Sciomyzaeformes, notably alongside Sepsidae, and separate from Micropezidae and Neriidae in the Conopiformes and Tanypezidae in the Ortalidiformes. Hennig (1941d) grouped Megamerinidae, Diopsidae, Psilidae, Sepsidae, Sciomyzidae and Piophilidae in the Sciomyzidea. Other authors in the middle of the century prior to the works of Hennig continued affiliations with Sepsidae (see Feijen (1989)), including Brues *et al.* (1954), who used Sepsoidea to include Sepsidae, Piophilidae, Thyreophoridae, Megamerinidae, Diopsidae and Psilidae; Nothybidae would be grouped with Tylidae, Neriidae and Tanypezidae in Tyloidea. Crampton (1944b) was unusual in clustering Diopsidae with Lauxaniidae and Chamaemyiidae in his Lauxanioidea.

The original name for the superfamily in present use is Nothyboidea, which originated in the classification of Aczel (1954a). He erected the superfamily for *Nothybus*, segregated it from the remaining Schizophora who were assumed to be more closely related due to asymmetry of the male postabdomen. The symmetry in *Nothybus* is now assumed to be secondarily derived, as is the symmetry or near symmetry of the postabdomen seen in other Acalyptratae—see McAlpine (1997b), Buck & Marshall (2006c), Huber *et al*. (2007).

Disagreeing with Aczel's classification, Nothyboidea was repurposed by Hennig (1958) into a larger acalyptrate superfamily that has been recognized by most subsequent authors, at least in part. Hennig included in it Megamerinidae (including Syringogastridae), Nothybidae, Diopsidae, Psilidae, Tanypezidae and Strongylophthalmyiidae; *Somatia* was thought to have a possible relationship with Richardiidae or Helomyzidae. One of the unusual characteristics of Hennig's (1958) Nothyboidea compared to other superfamilies was that it was not supported by synapomorphy, but was conceived of primarily through exclusion from other equivalent groups. Hennig (1965) was later sure of the monophyly of the superfamily, however, and considered Diopsidae and Megamerinidae to be closest to Nothybidae on the basis of a reduction of cephalic chaetotaxy; this lineage in turn was seen as possibly related to Psilidae on the basis of an absence of two thoracic setae—the anterior notopleural and the inner postalar.

Hennig's (1958) discovery of a relationship between Tanypezidae and Strongylophthalmyiidae was important, breaking long-standing historical associations between *Tanypeza* with Micropezidae, and *Strongylophthalmyia* with Psilidae. D.K. McAlpine (1997b) recognized numerous parallels between these two families and Nerioidea, but still only went so far as to leave them (as Tanypezidae s.l.) *incertae sedis* in Schizophora.

The most radical subsequent departure from Hennig's system was by Griffiths (1972), who used Nothyboidea to include Nothybidae, Psilidae, Teratomyzidae and Periscelididae, with Somatiidae included as a subfamily of the latter. The presence of a single post-alar seta and several male genitalic characters were provided as support, although the genitalic characters were either of uncertain interpretation (arc of movement of phallus, supposed fusion of phallapodeme to body wall) or occur frequently elsewhere in the Acalyptratae (reduction of sternites 6–8), including in those families he removed from the Nothyboidea. The families removed were placed in three other prefamilies: Sciomyzoinea (Megamerinidae plus 8 other families); Diopsioinea (Diopsidae+Syringogastridae); and Tanypezoinea (Tanypezidae including Strongylophthalmyiidae, Heteromyzidae). Griffiths' groupings were reiterated in Steyskal's (1974) discussion of dipteran classification, but the prefamily names were standardized to Diopsoidea, Tanypezoidea and Sciomyzoidea, which were later adopted by Hackman & Väisänen (1985). The superfamily name "Tanypezoidea" was used in the Afrotropical Diptera catalogue in the sense of Hennig's Nothyboidea, including Diopsidae, Tanypezidae and Psilidae (Crosskey, 1980), and in D.K. McAlpine's (1982) discussion of New Guinea Diptera, including Tanypezidae, Nothybidae, Diopsidae and Psilidae. Aczél's earlier (1949a) use of "Tanypezidiformes" refers to placement of Tanypezidae in a clade with Micropezidae and Neriidae, discussed below. Most of Griffiths' system was later abandoned and largely dismantled by J.F. McAlpine (1989) and D.K. McAlpine (1985, 1997b), although the relationship between Diopsidae and Syringogastridae has proven resilient.

When J.F. McAlpine (1989) discussed the phylogeny of the Muscomorpha, he returned to Hennig's interpretations, maintaining Strongylophthalmyiidae as sister to Tanypezidae, *Centrioncus* as a genus within Diopsidae and Somatiidae as sister to Psilidae (suggested by Hennig (1973)). He also treated Diopsidae as sister to Syringogastridae + Megamerinidae (including *Gobrya* and *Palaeotanypeza*). Conversely, D.K. McAlpine (1997b) considered a relationship between Megamerinidae and Syringogastridae "too improbable for further consideration", preferring to place the former in Nerioidea.

J.F. McAlpine (1989) divided the superfamily into two groups. "Group 1" consisted of Tanypezidae + Strongylophthalmyiidae, which was interpreted as more generalized than "group 2", which contained the remaining families. Steyskal's (1974) name "Diopsoidea" was used for the superfamily because Billberg's (1820) "Diopsides" was the oldest family group name available. J.F. McAlpine (1989) defined the Diopsoidea largely in contrast to the more robustly defined Nerioidea, and treated both as sister superfamilies on the basis of four weak characters doubted by D.K. McAlpine (1997b). He further characterized the Diopsoidea by sexual dimorphism of head and loss of the katepisternal seta, which were interpreted as plesiomorphic.

D.K. McAlpine thoroughly revisited concepts of Diopsoidea and Nerioidea in two papers more specifically examining the definition and placement of Megamerinidae (McAlpine, 1997a) and *Gobrya* (McAlpine, 1997b), the former of which he used to doubtfully encompass *Palaeotanypeza*, and the latter of which he erected a new family for. In contrast to previous authors, D.K. McAlpine (1997a) provisionally treated Somatiidae and Tanypezidae (including Strongylophthalmyiidae) as Diopsoidea, but later (1997b) considered both of them unplaced in Schizophora. Regarding Megamerinidae, D.K. McAlpine (1997a) deconstructed J.F. McAlpine's (1989) evidence supporting a relationship with either Diopsidae or Syringogastridae. He instead treated Megamerinidae as Nerioidea, returning to his earlier (D.K. McAlpine, 1966) suggestion that the family "should… probably be placed near the Micropezidae". Rohdendorf (1964, 1974, 1977) was also unable to place Somatiidae, isolating it in his Somatiidea/Somatioidea. He found no clear evidence of relationships to families in his revised Diopsoidea, and outlined likely or potential convergence in characters and composite structures that could potentially ally them with other Schizophora. He did note, however, that the least improbable placement of Tanypezidae was within Nerioidea.

D.K. McAlpine (1997b) provided varied and detailed evidence to support a potential relationship between Nothybidae and Psilidae, but also between Nothybidae and Gobryidae and possibly even Nothybidae and Curtonotidae (Ephydroidea). He eventually left Psilidae, Nothybidae and Gobryidae as unplaced in the superfamily. He further strongly supported the group Diopsoinea within Diopsoidea, albeit in a definition strongly revised from that initially provided by Griffiths (1972). Examining the Diopsoidea itself, D.K. McAlpine (1997b) rejected support for the group as it was defined by J.F. McAlpine (1989), instead providing a set of 18 characters representing likely groundplan states of the superfamily. By his own admission, no synapomorphies were presented that would support its monophyly, just as there were none originally present in Hennig (1958), or even in J.F. McAlpine (1989), as synapomorphies provided by the latter do not stand up to scrutiny. This did not appear to matter much in the case of his own hypothesis, however, as he discussed at length how rigorously supported characters are not always available and that "one should not feel forced to produce a solution to the relationships of every taxon", and that "it is therefore possible that a group of families may be or may approximate to a monophyletic group without providing clearly indicated groundplan autapomorphies". He believed his concept of Diopsoidea represented such a group.

Historical treatment of the nerioid family groups

FERGUSONINIDAE. *Fergusonina* was originally treated as Agromyzidae (Malloch, 1924, 1925, 1932), when Tonnoir (1937) placed in its own subfamily "Fergusoninae". The monogeneric subfamily was later provided family-level status as Fergusoninidae by Hennig (1958), following the subfamily spelling "Fergusonininae" used by D.K. McAlpine (1958). Associations with the Agromyzidae have persisted since *Fergusonina* was removed to its own family, and Colless & D.K. McAlpine (1970) were open to the possibility that *Fergusonina* was a specialized agromyzid. Hennig (1973) was uncertain of this agromyzid association, however, and Griffiths (1972) found "no morphological ground for such a classification" and left it as *incertae sedis* in the Schizophora.

J.F. McAlpine (1989) supported a sister-family relationship between Agromyzidae and Fergusoninidae in his Opomyzoidea, suprafamily Agromyzoinea, which also included the Odiniidae. He provided numerous characters in support of this relationship, but reevaluation reveals most of these to be either misinterpreted or of dubious polarity and almost certainly plesiomorphic. Some of the remaining characters, such as atrophy of the male pregenitalic sclerites, may be a result of convergence due to reduction in body size, which is regularly seen in other diminutive Schizophora. The only complex characters of note listed by J.F. McAlpine (1989) in support of a sister-family relationship between Agromyzidae and Fergusoninidae are those of the female terminalia, which are likely subject to convergence in form due to similarity in function, as discussed below in the phylogenetic analysis.

The family has never previously been allied to the nerioid families, although J.F. McAlpine (1989) noted of the phallapodeme that the "transversely flared distal (anterior) end is strangely reminiscent of similar conditions in certain Cypselosomatidae", as is the strong pair of setae near the base of the epandrium.

CYPSELOSOMATIDAE AND PSEUDOPOMYZIDAE. *Cypselosoma* was originally described by Hendel (1913) as being allied to the family Cypselidae (=Sphaeroceridae), and he later included it there in its own subfamily, Cypselosominae (Hendel, 1931). Brues *et al.* (1954) later corrected the subfamily name to Cypselosomatinae. *Lipotherina* Meijere, a junior synonym of *Cypselosoma*, was also described as Borboridae (=Sphaeroceridae). Duda (1938) preferred not to divide the Sphaeroceridae into subfamilies, but in an earlier paper he differentiated several genera lacking the characteristic modified hind basitarsomere as "Borboridae spuriae": *Colocasiomyia* Meijere (Drosophilidae), *Cypselosoma* (Cypselosomatidae), *Fiebrigella* Duda (Chloropidae), *Platyborborus* Meijere (=*Colocasiomyia,* Drosophilidae) and *Therina* Meigen (Sphaeroceridae?).

Prior to its association with *Cypselosoma*, *Formicosepsis* was described as Sepsidae, with a similarity to Megamerinidae noted. Duda (1925), followed by Malloch (1928), removed it to *incertae sedis*. The genus *Lycosepsis*, variably treated as a synonym (Duda, 1925), subgenus (Anderson, 1976) or sister-genus (Papp, 2006) of *Formicosepsis*, was also described by Enderlein (1920) as Sepsidae. Hennig (1941a, 1941d) treated both *Cypselosoma* and *Formicosepsis* as Tylidae (subfamily Trepidariinae in Hennig (1941d)), but he later moved both genera to Clusiidae (Hennig, 1948) and then back to Tylidae (Hennig, 1952a). Hennig (1958) finally recognized Cypselosomatinae and raised it to full family rank as Cypselosomatidae, including *Cypselosoma* and *Formicosepsis*. Rohdendorf (1964) used the misspelled subfamily name Formicosepsidinae as a *nomen nudum* (see Steyskal (1999)). D.K. McAlpine (1993) added the third and last described genus to the family—*Clisa*.

Within Pseudopomyzidae, the unusual and varied appearance of included genera has contributed to a complex history of classification—*Pseudopomyza* was originally considered to be Drosophilidae by Strobl (1893) and then Milichiidae (as a subfamily in the Agromyzidae) by Hendel (1902) and Brues *et al.* (1954). Malloch (1926) originally treated *Tenuia* Malloch as Opomyzidae, and he (Malloch, 1933a, b) originally considered *Protoborborus* Malloch and *Heloclusia* Malloch to be Heleomyzidae, which is understandable considering their bristly exterior. The unusual *Latheticomyia* was unplaced to family by Wheeler (1956) when first described.

The name Pseudopomyzidae was first published by Frey (1941) as a *nomen nudum* (Sabrosky, 1999), simply providing the name in a checklist without description. D.K. McAlpine (1966) later officially designated the family in his treatment of the Cypselosomatidae, and established its placement in the Nerioidea, including in it the genera *Pseudopomyza* and *Heloclusia*. Additional genera, either new or previously classified elsewhere, were added to the family by Hennig (1969, 1971), Steyskal (1970b), Krivosheina (1979), D.K. McAlpine (1994) and Papp (2005).

Krivosheina (1979) later used *Latheticomyia* as the nominal genus for the new subfamily Latheticomyiinae (including *Latheticomyia, Polypathomyia* and possibly *Tenuia*), separating it from a redefined Pseudopomyzinae (including *Pseudopomyza*, as the genera *Pseudopomyza* and *Rhinopomyzella*) and the unplaced genera *Heloclusia* and *Pseudopomyzella*. Although these subfamilies were never adopted by the community, they may eventually be of use if classification is re-approached in a phylogenetic context. The family group name Latheticomyiidae was once used as a *nomen nudum* (Commonwealth Institute of Entomology, 1958).

D.K. McAlpine's (1966) inclusion of Pseudopomyzidae in the Nerioidea (as "Micropezoidea") would initiate thorough conversations on phylogenetics and classification, as further analysis by authors such as Hennig (1971) and Griffiths (1972) provided additional morphological characters, especially of the male genitalia, that supported basal placement of the cypselosomatid and pseudopomyzid genera in the superfamily. Griffiths (1972) treated the Pseudopomyzidae as a subfamily in an enlarged Cypselosomatidae, believing that the latter rendered the former paraphyletic. He discussed that within these families, those genera with enlarged setae on the male external postabdomen formed a single lineage, with those pseudopomyzids missing these being basal. This subfamily classification was maintained by some, including Harrison (1976), Nartshuk (1977), Rohdendorf (1977), Prado (1984), J.F. McAlpine (1987, 1989) and Carvalho-Filho & Esposito (2011). Andersson (1976) did not directly deal with the Pseudopomyzidae, but he did not find this subfamily system "convincing because of the convergence and parallelism which commonly affects these characters", and provided characters supporting monophyly of the family. Krivosheina (1979) later mirrored this sentiment and provided a separate set of defining characters. Most other authors—including D.K. McAlpine (1966, 1978, 1993, 1996), Hennig (1971), Krivosheina (1979), Shatalkin (1995) and D.K. McAlpine & Shatalkin (1996)—weakly to strongly agreed that the two families were monophyletic and rejected Griffiths' (1972) subfamily hypothesis, although they could not establish whether their observed similarity was due to the sharing of synapomorphies or synplesiomorphies and tentatively retained them as separate basal entities in the superfamily. D.K. McAlpine (1996) provided characters in support of a monophyletic Pseudopomyzidae that was maintained by D.K. McAlpine & Shatalkin (1998), who noted that paraphyly of the family was "out of the question". Separation of the two families has been maintained by most authors, including Hennig (1969), Steyskal (1970b), Vockeroth (1977), Papp (2005), Merz (1997), Papp *et al.* (2006), Buck & McAlpine (2010), Marshall (2012), Roháček (2012b), Palaczyk *et al.* (2013) and Marques & Rafael (2016).

TANYPEZIDAE AND STRONGYLOPHTHALMYIIDAE. Upon description of the genus, Fallén (1820) included *Tanypeza* in his Opomyzides, which also included psilid genera, *Tetanura*, *Opomyza* and *Scatophaga*. Zetterstedt's (1838) subsequent usage of Opomyzides initially included families now in Psilidae, Micropezidae, Opomyzidae, Sciomyzidae and Scathophagidae, but he later also followed Westwood (1840) in treating *Tanypeza* as Opomyzides (Zetterstedt

1847, 1849, 1860). Macquart (1835) repurposed Latreille's (1829) Leptopoditae to group *Tanypeza* with genera from Neriidae, Micropezidae and Richardiidae. Continued association of *Tanypeza* with Micropezidae was continued by Osten-Sacken (1882), Williston (1896), Aldrich (1905), Williston (1908) (while noting that *Tanypeza* represented a different family) and Johnson (1925). Brauer (1880) differed in his consideration of *Tanypeza*, including it in the predominantly calyptrate group Schizometopa, which was separate from the predominantly acalyptrate group Holometopa.

The family name Tanypezidae originated with Rondani's (1865) "Tanypezina", which included *Tanypeza* (as "*Tanipeza*") and a range of genera now considered Ulidiidae, Megamerinidae, Micropezidae and Sepsidae. The group was soon thereafter modified to Tanypezinae by Schiner (1862), who narrowed the group to *Tanypeza*, *Tetanura* (Sciomyzidae) and some Micropezidae. Rondani (1873) temporarily used Tanypezinae to hold *Diopsis* (he removed it to Diopsinae in 1875) and later used a similarly flexible version of Tanypezinae to include genera now treated as Micropezidae, Sepsidae (Rondani, 1874) and Nothybidae (Rondani, 1875). First usage of the name Tanypezidae was by Bigot (1880), who did not specifically discuss included genera, although he would later (Bigot, 1886) follow a broad classification similar to that of Rondani. Boundaries of the family continued to fluctuate until Hendel (1903) isolated *Tanypeza* in a much narrowed Tanypezidae. A departure from this narrowed concept was made by Enderlein (1913), who included *Myrmecomyia* Robineau-Desvoidy (=*Cephalia* Meigen, Ulidiidae) and *Tetradiscus* Bigot (=*Chyliza* Fallén, Psilidae) in Tanypezidae, but these would be removed by Hennig (1936a).

Regarding the family Strongylophthalmyiidae, *Strongylophthalmyia* and its junior synonym *Labropsila* Meijere were initially described as Psilidae (or "Psilinae"), as was the family group itself when it was erected by Hendel (1917) as the subfamily "Strongylophthalmyinae". Correction of the spelling of the subfamily name to Strongylophthalmyiinae was given by Brues & Melander (1932). Treatment of *Strongylophthalmyia* as Psilidae was continued by authors including Becker (1905), Meijere (1914), Frey (1928) and Hennig (1941d). Shewell (1965) and Cole & Schlinger (1969) were the last to maintain this system after Hennig (1958) provided full family rank for Strongylophthalmyiidae following recognition of a sister-group relationship with Tanypezidae.

NERIIDAE. The family name Neriidae originated with Westwood's (1840) "Neriades", which took the more familiar form "Neriinae" in Hendel (1903), and "Neriidae" in Hendel (1916). The synonym Longinidi was used by Bigot (1858) (originally "Longinidii" (Bigot, 1852)) (Sabrosky, 1999).

Neriinae was included as a subfamily of Micropezidae (or "Tylidae") by Hendel (1903), Cresson (1912), Enderlein (1922), Hennig (1936, 1941) and Aczél (1949c). In his treatment of Micropezidae, Enderlein (1922) used the neriine tribes Neriini and Telostylini, which would also be utilized by Hennig (1936b) and Aczél (1949c) as subordinate micropezid groups. When Neriidae was treated as a full family, most authors beginning with Czerny (1932) repurposed the two tribes as the subfamilies Neriinae and Telostylinae, although Aczél (1951, 1954a, b, 1961) maintained them as tribes. Aczél (1961) further split Neriini into the *Eoneria* and *Nerius* genus groups. Neriidae was treated as a full family by Hendel (1916, 1922, 1932), Frey (1927), Czerny (1930a, 1932), Cresson (1930), Curran (1934), Aczél (1949b) and Hennig (1950), as well as by all subsequent authors.

A close relationship between *Nerius* and Micropezidae has been widely recognized historically. Osten-Sacken (1882), Williston (1896, 1908) and Brues & Melander (1915) followed previous authors in including neriid genera in a broad concept of Micropezidae, that prior to 1900, also variably included a number of genera from other families such as *Nothybus* and *Tanypeza* (see above). Wulp (1896), Bigot (1892) and Meijere (1908, 1911, 1916, 1918) treated the higher family group as Calobatinae or Calobatidae, and also used it to contain genera now placed in several different families. Prior to these authors, neriid and micropezid genera were clustered together in the group Thelidomydae by Robineau-Desvoidy (1826, 1830), in Latreille's (1829) Leptopoditae by Macquart (1835) with *Tanypeza* and *Setellia* (Richardiidae), in a widened concept of Psilides by Walker (1856, 1860) (see above), and in Bigot's (1866a) diverse Tanypezidi.

MICROPEZIDAE.

A) Family-group names

The history of classification and nomenclature of micropezid taxa has been relatively convoluted, but most authors now follow D.K. McAlpine (1975) in recognizing five subfamilies: Calobatinae, Calycopteryginae, Eurybatinae, Micropezinae and Taeniapterinae. Eurybatinae is in turn divided into the tribes Eurybatini and Metopochetini.

The family name occurs as Tylidae throughout much of the literature after the type genus *Tylos* Meigen,

1800. The name was first used as Tylinae by Hendel (1910), and Tylidae by Bezzi (1914). The name *Tylos* was suppressed in favour of *Micropeza* Meigen 1803 by the Commission, however, citing laws of priority and homonomy (ICZN, 1955). Meigen's (1800) pamphlet providing the name *Tylos* was also later suppressed (IZCN, 1963), which had the further effect of suppressing the name *Trepidaria* Meigen, 1800, the type genus for the subfamily Trepidariinae. Trepidariinae was erected by Czerny (1930a) and raised to the level of family by Crampton (1944b) and Hennig (1958). The next available name for *Trepidaria* was *Calobata* Meigen, 1803, resulting in the family group name Calobatinae, which was already in use at both the family (Bigot, 1892; Curran, 1934) and subfamily levels (Meijere, 1916; Enderlein, 1922; Frey, 1927, 1958; Cresson, 1930).

Sabrosky (1999) noted a complication wherein the name Calobatidae, erected in 1853 by Bigot, had priority over Micropezidae, which occurred first under the spelling "Micropezitae" in Desmarest (1860), and then the following year as Micropezidae in Loew (1861a). Fixation of the name Micropezidae "could only be resolved, if desired, by action of the Commission", although the action might prove unnecessary if Calobatidae is ever supported as a family separate from Micropezidae, as suggested by Hennig (1965, 1967, 1969, 1973).

The subfamily Taeniapterinae, erected by Cresson (1930) also appears under other names in the literature. One of these names is Czerny's (1930a) Rainieriinae, after *Rainieria* Rondani, which appeared in print only a few days prior to the Cresson's paper naming Taeniapterinae after *Taeniaptera* Macquart (see Sabrosky (1999)). Both of these are preceded by Frey's (1927) Tanypodinae for the genus *Tanipoda* Rondani, an unnecessary replacement name for *Rainiera*. The subfamily name follows the misspelling of the genus name as it appears in Schiner (1864)—"*Tanypoda*". Frey (1958) later mentions the name Tanypodidae in a sentence noting an association between it and the families Neriidae, Micropezidae and Nothybidae, while still treating Taeniapterinae as a valid subfamily in Micropezidae.

B) Family boundaries

Higher taxa including micropezid genera originally encompassed other long-legged diopsoid and (primarily) nerioid families. These include Zetterstedt's (1838) Opomyzides (discussed above); Latreille's (1825) Carpomyzae, which clustered *Micropeza* with *Dictya* Meigen (Sciomyzidae) and the tephritoid *Platystoma* Meigen*, Tephritis* and *Dacus* Fabricius; and Latreille's (1825) Gonocephalae, which grouped *Calobata* and *Nerius* with *Otites* (Ulidiidae) and *Oscinis* Latreille (Chloropidae). Latreille's (1829) Leptopoditae was used by Macquart (1835) to cluster *Tanypeza* with *Setellia* Robineau-Desvoidy (Richardiidae), and micropezid and neriid genera. Robineau-Desvoidy's (1830) Phytomydae was divided into the tribes Myodinae and Thelidomydae, the latter of which included the micropezid genera *Calobata*, *Micropeza*, *Neria* and *Phantasma* (=*Micropeza*), and the sepsid genera *Nemopoda*, *Themira* and *Saltella*. Walker (1856) divided micropezid genera between Sepsides (*Calobata*, *Nothybus longicollis* (as *Cardiacephala* Macquart)) and Psilides (*Micropeza*, *Nerius*). Rondani's (1874) concept of Tanypezinae added micropezid and sepsid genera to a group he (Rondani, 1856) already used to include *Tanypeza*, *Megamerina* and some Tephritoidea. This broad concept was built upon by Rondani (1875), who included *Nothybus* in Tanypezinae, and then by Bigot (1886a, b), who called the group Tanypezidi. Schiner's (1862) Tanypezinae was much narrower, clustering *Tanypeza* and *Tetanura* (Sciomyzidae) with the genera of Micropezidae.

Desmarest's (1860) Micropezitae followed Macquart's (1835) classification, including *Micropeza*, *Calobata*, *Taeniaptera*, *Nerius*, *Longina*, *Tanypeza* and *Setellia* (spelled "*Sepellia*"). Osten-Sacken (1882) retained *Tanypeza* in the family, but noted that it "can hardly be considered a Micropezid", and it was soon thereafter removed to its own family by Hendel (1903).

Most authors would recognize a modern version of Micropezidae s.l. after the beginning of the 20th century as Neriidae was removed as a subordinate family group and other genera such as *Tanypeza* and *Nothybus* were removed to their own families. Some authors, however, continued to recognize Neriinae as a subfamily (Enderlein, 1922) or treated the micropezid subfamiles as full families (Curran, 1934; Aczél, 1954b; Hennig, 1958, 1965. 1973; Shtakel'berg, 1988).

Explicit definition of family groups initially developed either through diagnoses or keys, through general characterization of the family and its constituent taxa (as in Cresson (1930), Hennig (1934a, 1935a, b), Aczél (1951), Merritt & Peterson (1976) and D.K. McAlpine (1975, 1996), among many others), or through characterization of the constituent parts of Micropezoidea s.s. (see Hennig (1958)). More explicit definition appeared in Czerny (1930), Steyskal (1987a), J.F. McAlpine (1989), Marshall (2010), and the genitalic descriptions of Griffiths (1972). The most thorough treatment was in D.K. McAlpine's (1998) revision of the Australian Micropezidae, where a diagnosis for the family was provided, and hypothesized groundplan states and autapomorphies for family groups were listed to develop the subfamilial and tribal phylogeny originally provided in McAlpine (1975).

C) Subfamily boundaries

The neriid genera were often included in the family (under Micropezidae or various equivalent family-group names) up until Meijere (1916), after which, Hendel (1916) removed them to their own family, but they were again treated as the micropezid subfamily or tribe Neriinae/Neriini by Enderlein (1922), Hennig (1936b, 1941a) and Aczél (1949c). Composition of the neriid family group quite consistent through time, contrasting those subfamilies now considered true Micropezidae, which fluctuated widely in name and content.

A relatively modern concept of Micropezidae began to form under Enderlein (1922), who recognized three subfamilies: Neriinae; a Micropezinae that included *Micropeza* and other genera now included as its synonyms or subgenera; and Calobatinae, which clustered the remaining micropezid genera with *Nothybus* and *Gobrya.* This narrow definition of Micropezinae was to be maintained by most subsequent authors, but Calobatinae (=Trepidariinae) would be frequently subdivided. Frey (1927) began by dividing the Calobatinae in to a narrow Calobatinae including *Calobata*, *Calobatella* and *Paracalobata* and a large Tanypodinae (=Taeniapterinae, =Rainieriinae) that also included genera now considered to be Eurybatinae (*Calycopteryx* was excluded from the classification). A variant of Tanypodinae/ Taeniapterinae was maintained in many later classifications with the exception of Curran (1934) and Shtakel'berg (1988a, b), who recognized a narrow Micropezidae (equal to Micropezinae *sensu* Enderlein) and a large Calobatidae.

Division of Calobatinae occurred when Frey (1958) split the subfamily into the tribes Calobatini and Eurybatini. Calobatini would be briefly mentioned in Cresson (1930) as a tribe of Micropezidae, but its boundaries were not elaborated upon. Frey's (1958) tribal system would be followed by Hennig (1965), who recognized the families Micropezidae, Taeniapteridae and Calobatidae, and included *Calycopteryx* in the Eurybatini; he noted that Calobatidae might be paraphyletic. In earlier papers, Hennig recognized a family-level Taeniapteridae and a Tylidae that was split into either Tylinae and Trepidariinae (Hennig, 1950), Micropezidae and Trepidariidae (Hennig, 1958), or Micropezidae and Calobatidae (Hennig, 1973). Hennig (1958) considered *Calycopteryx* to be Trepidariinae before he recognized Eurybatini, although this can be inferred at an earlier date (Hennig, 1936b) in his mention of the Kerguelen Islands where the genus is endemic. No other authors (aside from the possible *lapsus* in Aczél (1954b)) would divide the Micropezidae into separate families as such.

A subfamily-level Eurybatinae was recognized in D.K. McAlpine's (1975) landmark reclassification of Micropezidae, where he divided the subfamily into the monogeneric Metopochetini and the larger Eurybatini. He also erected the subfamily Calycopteryginae for *Calycopteryx*, which he considered sister to the remaining Micropezidae, although the highly derived morphology of this odd wingless genus makes McAlpine's use of external features for phylogenetic placement questionable.

Subdivision of the Taeniapterinae into two tribes—Taeniapterini and Rainieriini—would be made by Steyskal (1947). This system was only otherwise be adopted by Aczél (1951, 1959), who used the name Grallipezini instead of Rainieriini in 1951. The analysis of Jackson *et al.* (2015) recovered a paraphyletic Rainieriini, and ongoing research suggests that neither tribe adequately reflects natural groupings in the subfamily (S.A. Marshall, pers. comm.), so divisions below Taeniapterinae will not be recognized for the current study. Hennig (1936b, 1952a) split the Tylidae into the Taeniapterinae and Tylinae, the latter of which was further divided into Tylini and Trepidariini. Aczél (1954b), perhaps in error, treated Calobatidae as a synonym of Taeniapteridae. Albuquerque (1989) added one subtribe—Cardiacephalina—to the Taeniapterini, which does not appear to be supported (Ferro & Marshall, 2018).

NERIOIDEA. Modern concepts of Nerioidea developed from a number of separate threads that converged over the last century. This frequently involved the narrowing of family concepts, and the expulsion of other long-legged, narrow (sometimes ant-like) or large-bodied taxa only superficially similar to Tanypezidae or Micropezidae, including *Nothybus*, Sepsidae and some Tephritoidea. Conversely, consideration of larger suites of characters, often complex and genitalic in nature, allowed for the inclusion "atypical" taxa. These included Hennig's (1941d, 1952a) placement of *Cypselosoma* and *Formicosepsis* in Tylidae, Hennig's (1958) support for a relationship between Strongylophthalmyiidae and Tanypezidae, and D.K. McAlpine's (1966), Hennig's (1958, 1965, 1969) and Griffiths' (1972) refined concepts of Cypselosomatidae and Pseudopomyzidae.

TABLE 1. Classification of subfamilies of Micropezidae, as well as some commonly allied family groups in select publications.

AUTHOR	YEAR	Micropezinae	Calycopteryginae	Eurybatinae	Calobatinae	Taeniapterinae	Neriidae	Nothybidae	Tanypezidae
Demarest	1860	Micropezitae			Micropezitae	Micropezitae	Micropezitae		Micropezitae
Osten-Sacken	1882	Micropezidae		Micropezidae	Micropezidae	Micropezidae	Micropezidae	Micropezidae	Micropezidae
Bigot	1892				Calobatidae	Calobatidae	Calobatidae	Calobatidae	
Wulp	1896	Calobatinae		Calobatinae	Calobatinae	Calobatinae	Calobatinae	Calobatinae	
Hendel	1903	Micropezinae			Micropezinae	Micropezinae	**Neriinae***	Micropezinae (as "*Nothybius*")	**Tanypezinae**
Hendel	1910	Tylinae			Tylinae				
Cresson	1912	Micropezinae					Neriinae	Neriinae	
Bezzi	1914	Tylidae		Tylidae	Tylidae	Tylidae	Tylidae		
Hendel	1916	Tylidae					Neriidae*		
Meijere	1916a, b				Calobatinae		Calobatinae		Ortalinae
Enderlein	1922	Micropezinae	Calobatinae	Calobatinae	Calobatinae	Calobatinae	Neriinae	Calobatinae	
Hendel	1922	Tylidae					Neriidae*		Tanypezidae
Frey	1927	Micropezinae		Tanypodinae	Calobatinae	Tanypodinae	**Neriidae***	**Nothybidae***	**Tanypezidae**
Cresson	1930	Micropezinae			Micropezinae (Calobatini)	Taeniapterinae	Neriidae*		
Czerny	1930	Tylinae			Trepidariinae	Rainieriinae	Neriidae*		
Czerny	1932	Tylinae		Rainieriinae		Rainieriinae	Neriidae*		
Hendel	1932	Tylinae			Tylinae	Rainieriinae	Neriidae*		Tanypezidae
Curran	1934	**Micropezidae***			Calobatidae*	**Calobatidae***	Neriidae*		Tanypezidae
Hennig	1934, 1935	Tylinae		Trepidariinae	Trepidariinae	Taeniapterinae			
Hennig	1936b	Tylinae (Tylini)	Tylinae (Trepidariini)	Tylinae (Trepidariini)	Tylinae (Trepidariini)	Taeniapterinae	Neriinae		
Hennig	1938	Tylinae		Trepidariinae	Trepidariinae	Taeniapterinae			
Hennig	1941	Tylinae			Trepidariinae	Taeniapterinae	Neriinae		

...Continued on the next page

TABLE 1. (Continued)

AUTHOR	YEAR	Micropezinae	Calycopteryginae	Eurybatinae	Calobatinae	Taeniapterinae	Neriidae	Nothybidae	Tanypezidae
Steyskal	1947	Micropezinae		Trepidariinae	Trepidariinae	Taeniapterini+Rainieriini			Tanypezidae
Aczél	1949a, b	Tylinae			Trepidariinae	Taeniapterinae	Neriidae*		
Aczél	1949b	Tylinae			Trepidariinae	Taeniapterinae			
Aczél	1949c	Tylinae			Trepidariinae	Taeniapterinae	Neriinae		
Hennig	1950	Tylinae			Trepidariinae	**Taeniapteridae***	Neriidae*		
Aczél	1951	Tylinae			Trepidariinae	Taeniapterini+Grallipezini	Neriidae*		Tanypezidae
Hennig	1952	Tylinae (Tylini)	Tylinae (Trepidariini)	Tylinae (Trepidariini)	Tylinae (Trepidariini)	Taeniapterinae	Neriinae		
Steyskal	1952	Tylinae		Trepidariinae	Trepidariinae	Taeniapterinae			
Aczél	1954b	**Tylidae***			Taeniapteridae	**Taeniapteridae***	Neriidae*		Tanypezidae
Frey	1958	Micropezinae		Calobatinae (Eurybatini)	Calobatinae (Calobatini)	Taeniapterinae		Nothybidae*	
Hennig	1958	**Micropezidae***	**Trepariidae***	**Trepariidae***	**Trepariidae***	**Taeniapteridae***	Neriidae*		Tanypezidae
Aczél	1959	Micropezinae (Micropezini)		Micropezinae (Trepidariini)	Micropezinae (Trepidariini)	Taeniapterini+Rainieriini	Neriidae*		
Hennig	1965	**Micropezidae***	**Calobatidae*** (Eurybatini)	**Calobatidae** (Eurybatini)	**Calobatidae*** (Calobatini)	**Taeniapteridae***	Neriidae*		Tanypezidae
McAlpine, D.K.	1966	Micropezinae				Taeniapterinae	Neriidae*		
Hennig	1967				Calobatidae*				
Hennig	1969				Calobatidae*				
Hennig	1973	**Micropezidae***	**Calobatidae***	**Calobatidae***	**Calobatidae***	**Taeniapteridae***	Neriidae*		Tanypezidae
McAlpine, D.K.	1975	Micropezinae	Calycopteryginae	Eurybatinae (Eurybatini + Metopochetini)	Calobatinae	Taeniapterinae	Neriidae*		
Shtakel'berg	1988	**Micropezidae***			**Calobatidae***	**Calobatidae***			Tanypezidae
McAlpine, J.F.	1989	Micropezinae	Calycopteryginae	Eurybatinae	Calobatinae	Taeniapterinae	Neriidae*		Tanypezidae

After removing Neriidae as a subordinate group of Micropezidae, Hendel (1916) continued to recognize a close association between the two families by maintaining them in the higher group Tyloidea (or "Tyloïdea"). He (Hendel, 1922) placed them in the Tephritomorphae as sister to Tephritoidea, which included Tanypezidae, the tephritoid families, Agromyzidae and Lonchaeidae. Hendel's Tephritoidea reflects Frey's (1921) Ortalidiformes of the previous year, but Hendel did not accept Frey's Conopiformes, which grouped Neriidae, Micropezidae, Conopidae, Chloropidae and Milichiidae. Hendel's Tyloidea was used by Hennig (1937), although he would briefly return to treating Neriidae as a subfamily of Tylidae (Hennig, 1941, 1952a) in the group Trypetides. Tyloidea would only otherwise be maintained by Brues *et al*. (1954) to group Tylidae, Neriidae, Tanypezidae and Nothybidae.

Crampton (1944a) used the superfamily Calobatoidea for Micropezidae, Calobatidae and Neriidae, utilizing questionable interpretations of the male pregenitalic sclerites to infer phylogeny. Micropezidae was suggested to be ancestral to Calyptratae (similar to Clusiidae), and the superfamily itself was thought to be an "isolated, primitive group… [d]escended from the Pipunculidae or the Platypezidae".

Aczél (1949a) maintained the relationship between Neriidae and Micropezidae, and considered Tanypezidae to be sister to this pair in a group he called the Tanypezidiformes. In Aczél's classification, which was quantified in a later work (Aczél, 1951), Tanypezidiformes was thought to develop from "primitive Ortalidiformes" and was now sister to "recent Ortalidiformes".

In 1958, Hennig used the new superfamily Micropezoidea to cluster the families Taeniapteridae, Micropezidae, Trepidariidae and Neriidae, whose arrangement was based on a long series of external and genitalic characters. Cypselosomatidae would be allied to these families as part of a wider Micropezoidea s.l. Hennig (1965, 1973) maintained this system with Trepidariidae called Calobatidae.

D.K. McAlpine (1966) disagreed with Hennig's justification for raising the micropezid subfamilies to full family rank and reduced them once again to subfamilies of Micropezidae. He maintained Hennig's Micropezoidea, however, and added to it the families Pseudopomyzidae and Megamerinidae (treated as Diopsoidea by other authors—see above). While some parallels were drawn between Pseudopomyzidae and Micropezoidea, especially Cypselosomatidae, detailed justification for the inclusion of these families would be left to later studies.

Hennig's 1958 study additionally established a relationship between Tanypezidae and Strongylophthalmyiidae that would be maintained by all subsequent authors. J.F. McAlpine (1989), Griffiths (1972) and D.K. McAlpine (1997a, b), however, preferred to include *Strongylophthalmyia* in an enlarged Tanypezidae, and Cogan (1980a) and Korneyev (1999) recognized Tanypezinae and Strongylophthalmyiinae as subfamilies of Tanypezidae. Lonsdale (2013) supported a sister-group relationship between the two taxa, but preferred to maintain them as separate families because both were more strongly supported as monophyletic and a united family was impractical for diagnosis. Thirteen primarily genitalic synapomorphies for this family pair were listed by Lonsdale (2013), some of which are here found to be more widely shared with other Nerioidea.

Contrary to previous classifications, Hennig (1958) did not ally Tanypezidae with either nerioid or tephritoid families, but instead preferred basal placement in a repurposed Nothyboidea that included Psilidae, Diopsidae, Nothybidae and Megamerinidae. This classification was followed in a number of subsequent catalogues and by J.F. McAlpine (1989), who provided redefinition of the included families. In the introduction to the *Manual of Nearctic Diptera* (J.F. McAlpine *et al.*, 1981), J.F. McAlpine renamed the two superfamilies Diopsoidea and Nerioidea after the oldest included family group names. In J.F. McAlpine's system, Tanypezidae + Strongylophthalmyiidae was a generalized basal lineage of Diopsoidea that he called "group 1"; the nerioid families were presented as Micropezidae s.l. and Neriidae+Cypselosomatidae (incl. Pseudopomyzidae). D.K. McAlpine (1997a) could not confidently assign Tanypezidae (including Strongylophthalmyiidae) to a superfamily; he first treated Tanypezidae and Somatiidae as Diopsoidea, but then relegated them to *incertae sedis* within Schizophora (D.K. McAlpine, 1997b).

J.F. McAlpine (1989) additionally provided weak justification for a sister-group relationship between Nerioidea and Diopsoidea. Similarly, Rohdendorf (1964, 1974, 1977) earlier used his superfamily Psilidea/Psiloidea to group the families in both of these superfamilies, excluding Somatiidae: Cypselosomatidae (including Pseudopomyzidae), Neriidae, Micropezidae, Tanypezidae (including Strongylophthalmyiidae), Psilidae, Megamerinidae (*Gobrya* not mentioned), Diopsidae (including Syringogastridae), Nothybidae and Periscelididae (including Teratomyzidae).

An alternate classification by Griffiths (1972) placed Tanypezidae (including Strongylophthalmyiidae) and Heteromyzidae in the prefamily Tanypezoinea. This system was reiterated in Steyskal's (1974) discussion of dipteran classification (as "Tanypezoidea"), but it was never adopted and subsequently disproven (see discussion above). Griffiths' (1972) Micropezoinea and "Micropezidae family-group" were equivalent to Hennig's (1958) Micropezoidea s.l. and s.s., respectively, with the modification of including Pseudopomyzidae in Cypselosomatidae. Griffiths rejected D.K. McAlpine's (1966) association of Megamerinidae with the micropezoid families, instead placing it in his prefamily Sciomyzoinea.

One of the more recent attempts to clarify nerioid relationships was provided by D.K. McAlpine (1996), who focused on characterization of the family Pseudopomyzidae and re-examination of the evidence provided by previous authors in support of nerioid classification. D.K. McAlpine's characterization of the superfamily was made incidentally or indirectly throughout his study as he discussed the possible plesiomorphic or synapomorphic condition of characters found in the individual nerioid families; characters were polarized in part using the Heleomyzoidea as an outgroup. Following his earlier work (D.K. McAlpine, 1966), he continued to include Pseudopomyzidae, Cypselosomatidae, Megamerinidae, Neriidae and Micropezidae s.l. in the superfamily. Mention was made of a possible relationship between Micropezidae and Cypselosomatidae.

Some support for nerioid family group relationships was provided by Wiegmann *et al.* (2011), who utilized molecular sequence data to reconstruct dipteran phylogeny. While there was generally poor resolution across the Schizophora outside the Ephydroidea and some of the Tephritoidea and Calyptratae, there was good bootstrap support for Tanypezidae + Strongylophthalmyiidae, and the other sequenced nerioid families (Micropezidae, Neriidae, Cypselosomatidae) were recovered together with <80% bootstrap support. Marshall's (2012) general review of Diptera classification lists the diopsoid families as Tanypezidae, Strongylophthalmyiidae, Diopsidae, Psilidae, Syringogastridae, Megamerinidae, Nothybidae, Somatiidae and Gobryidae, and the nerioid families as Micropezidae, Neriidae, Cypselosomatidae and Pseudopomyzidae.

PHYLOGENETIC ANALYSIS

Analysis of the matrix produced 3 trees 1306 steps in length; numerous characters were found to be largely homoplastic, with the phylogeny presenting a consistency index (CI) of 0.27 and a retention index (RI) of 0.69. Despite this homoplasy, relationships between taxa were mostly consistent and the family groups tested were always recovered as monophyletic. Ingroup variation was seen in placement of the micropezid subfamilies, which were not tested for here.

The following discussion will exclude mention of specific characters if highly homoplastic unless their occurrence is relevant, but the entire set of optimized characters is shown in Figs 424–425. The strict consensus tree is presented in Fig. 423.

A) Superfamily support and outgroups (Fig. 424)

i) Nerioidea. There was strong support for a monophyletic Nerioidea, and for family-group relationships within the superfamily. The superfamily was supported by a number of seemingly reliable synapomorphies: (23) postocellars removed from ocelli (also Chyromyidae, Anthomyidae, Psilidae); (29) face membranous in part (also Piophilidae, Chyromyidae, Anthomyzidae, Opomyzidae, reversed Fergusoninidae); (45) labium with 2 pairs of erect and one distal pair of lateroclinate setae; (228) female S10 and T10 with setae terminal only (also Agromyzidae, Aulacigastridae); (230) female sternite 10 with internal rod-like process (also Curtonotidae, reduced in some families, especially Micropezidae); (297) pregonite band-like, fused to inner surface of hypandrium; (298) postgonite originating at or near apex of pregonite; (303) phallic plate present (broken and articulated in Strongylophthalmyiidae + Tanypezidae, reversed Fergusoninidae).

Other likely synapomorphies or groundplan states of Nerioidea include the following, although these are not specifically listed as such since they are also found in Lonchaeidae, which was recovered as the superfamily's sister-group: (219) tergite and sternite 7 fused into a cylinder (also Agromyzidae); (289) phallapodeme with one pair of anteromedial processes extending to meet hypandrium (frequently reversed). Most Nerioidea also exhibit the following: (229) female tergite and sternite 10 with a maximum of 2 and 4 setae (respectively); (227) female terminalia telescoped (common elsewhere); (284) hypandrium bare (common elsewhere). There is no support for a relationship of Nerioidea with Diopsoidea, and while the latter two character states are common to both, these are commonly paralleled and likely homoplastic.

While Lonchaeidae was recovered as sister to Nerioidea it is likely an artifact of the analysis. Supporting characters appear homoplastic, especially when considering recovery of Piophilidae elsewhere in the tree, as the inclusion of Lonchaeidae and Piophilidae in Tephritoidea is well accepted—see Korneyev (1999) and Han & Ro (2016).

ii) Diopsoidea. Diopsoidea was recovered as monophyletic, but the evidence provided was weak, or at the very least easily subject to alternate interpretation. Supporting characters are likely homoplastic, being either reversed in constituent families, or simple reductive characters prone to loss. Many of these reductive characters involve the loss of setae, which are easily paralleled; they are also likely linked and therefore not strong independent indicators of shared evolutionary history.

A number of other similarly homoplastic characters support the basal placement of Psilidae, Nothybidae, Somatiidae and Gobryidae in the superfamily. Despite this ambiguous support, there is no evidence for their exclusion, so they are here tentatively maintained in the broader traditional boundaries of the superfamily. Excluding these, there is a core group of three families that is well-supported by complex synapomorphies: Megamerinidae, Diopsidae and Syringogastridae, the last two of which were previously grouped in the prefamily Diopsoinea (Griffiths, 1972; D.K. McAlpine, 1997b).

Characters supporting Diopsoidea include: (5) pedicel with dorsal seam (expanded in Gobryidae, lost in Megamerinidae and Diopsidae); (7) first flagellomere elongate (found frequently elsewhere, reversed in Megamerinidae and Diopsidae); (59) vibrissa lost (reversed Somatiidae, independently derived in Nerioidea, Lauxaniidae and Lonchaeidae); (78) proepisternal seta absent (also lost in Anthomyzidae and several lineages of Nerioidea); (87) anterior notopleural seta absent (recovered Gobryidae, also lost several times in Nerioidea); (135) katepisternal seta absent (also lost several times in Nerioidea); (173) alula reduced (highly homoplastic and sometimes subject to interpretation); (174) basal costal setae absent (recovered in Nothybidae, paralleled frequently elsewhere); (203) large body size (reversed in some, paralleled in Nerioidea); (249) male genitalic and pregenitalic sclerites almost symmetrical (due to reduction and possibly not homologous across diopsoid families, as opposed to the more complex state seen in Cypselosomatidae and Pseudopomyzidae; also Agromyzidae).

Similar to the support provided for Diopsoidea and its basal lineages, there is relatively voluminous support for diopsoid outgroups that is also reductive in nature, highly homoplastic and likely unreliable. The most distant outgroups consist of three families of Lauxanioidea, Ephydroidea and Sphaeroceroidea, which belong superfamilies that exhibit at least modest stability in the literature (see McAlpine (1989), Roháček *et al.* (2001) and Yeates *et al.* (2007)), and it is relatively safe to assume that the proposed character support is due to plesiomorphy or convergence.

The families recovered as most closely related to Diopsoidea are members of the deconstructed "Opomyzoidea". These relationships were supported by a number of homoplasious characters including: (8) antenna deflexed (except Aulacigastridae, reversed in Megamerinidae and Diopsidae); (35) lunule hidden (reversed Megamerinidae); (288) hypandrial arms fused posterobasally; (300) postgonite lost (not shared with Anthomyzidae+Opomyzidae and most core diopsoid families); loss of numerous of setae including the (63) postocellar (recovered Anthomyzidae, Psilidae, Somatiidae), (77) proepisternal (except Anthomyzidae), (79) prescutellar acrostichal (recovered Psilidae, Somatiidae), (90) presutural intra-alar (except Opomyzidae, Neurochaetidae), (93) postsutural intra-alar (recovered Opomyzidae, Somatiidae), (103) anepisternal (recovered Opomyzidae, Somatiidae) and (174) basal costal setae (except Neurochaetidae, Anthomyzidae). The immediate sister-group to Diopsoidea is Neurochaetidae, but this relationship is suspect as it only shares characters reversed in many diopsoid lineages: (11) arista bipectinate (reversed in Psilidae and Diopsidae); (21) ocellar triangle long (not evident in Gobryidae and Diopsidae); (76) presternum reduced (only shared with Somatiidae, Syringogastridae and some Diopsidae); (80) a single dorsocentral (reversed in Gobryidae and most core diopsoid families); (305) fusion of basiphallus to distiphallus (reversed Gobryidae and Diopsidae).

B) Nerioidea—Family group relationships

The Nerioidea can be divided into three well-supported family groups.

i) Fergusoninidae, Cypselosomatidae & Pseudopomyzidae. The most significant characters supporting this lineage are (51) a high gena, (59) vibrissa present, (143) a posteroventral row of spine-like setae on the fore femur, (149) a large distal seta on the hind femur, (176) a costal break (reversed Cypselosomatidae and some Pseudopomyzidae), (177) an incomplete subcosta (also Strongylophthalmyiidae), (191) reduction of vein bm-m, (226) longitudinal division of female sternite 8, which is band-like and densely textured, (227) complete retraction of the female terminalia, (249) symmetry of the male genitalic and pregenitalic sclerites (complex in Cypselosomatidae and Pseudopomyzidae, possibly convergent due to reduction in Fergusoninidae) and (258) one pair of outstanding dorsal setae on the epandrium (reversed in some).

There is strong support for a monophyletic Cypselosomatidae, and while there is quantitatively less for Pseudopomyzidae, evidence for its monophyly is convincing, contradicting the hypothesis that it is rendered paraphyletic by Cypselosomatidae. Pseudopomyzidae is supported as follows: (65) postocellars convergent (also Neriidae); (74) prosternum linear (also Neriidae and Micropezinae); (141) fore femur with row of relatively long, thick posterodorsal setae; (175) costal break preceded by at least 2 outstanding setae; (286) ventral distolateral margins of hypandrium carinate.

Fergusoninidae is basal in the group, sister to Cypselosomatidae+Pseudopomyzidae. The latter species pair is supported by numerous synapomorphies, including the following: (50) gena shining and bulging (reversed in some taxa); (56) paraverticals present (lost in *Formicosepsis*); (79) presutural acrostichal setae present (sometimes absent); (80) at least three dorsocentrals present; (81) presutural scutum with dorsocentral and scapular setae (sometimes absent); (103) anepisternal seta lost (frequently paralleled elsewhere); (104) greater ampulla present (frequently found elsewhere); (217) female sternite 1 wide, short; (246) male sternites 6 and 7 overlapping and articulating; (248) male sternites 7 and 8 forming complete circular "annulus"; (256) male sternite 8 with one pair of outstanding setae similar to those on the epandrium (reversed in some Pseudopomyzidae); (262) male spiracle 7 enclosed in tergite; (275) cercus positioned distally on epandrium; (290) phallapodeme modified at intersection with pregonite.

This is the first time Fergusoninidae has been considered to be closely related to a nerioid family instead of the Agromyzidae. If phytophagy of larvae within living plant tissue originated independently in the two lineages, however, similarity in form could be explained as convergence due to similarity in function. In both families the female postabdomen is specialized for the oviposition of eggs either within that tissue directly or the enclosed spaces thereupon: the terminal segments of the abdomen are narrow and elongate, the sclerites are widely separated by elongate membranous regions, and segment 7 forms a dark oviscape stabilized by a dorsomedial keel that projects anteriorly into segment 6. The ovipositor of *Fergusonina* is quite different in overall structure, however, as noted by Tonnoir (1937), with T6 and S6 large and fused, and the external terminalia past segment 7 largely reduced to a piercing stylet. The fergusoninid female abdomen past segment 6 is similar to other Nerioidea, however, with modifications associated with oviposition in living plant tissue (not softer, decayed tissue) easily accounting for the differences observed. The Agromyzidae and Fergusoninidae both also share a reduction of the male pregenitalic sclerites (sternites 6–8), but this is also likely convergent due to a reduction in body size—a necessity when developing in extremely small spaces; similar reductions are also seen in other diminutive acalyptrate Diptera. The primary male genitalic structures are widely dissimilar in detail between Agromyzidae and Fergusoninidae, however, mirroring dissimilarity in overall external morphology and genetic sequence data. Conversely, similarities between Fergusoninidae, Pseudopomyzidae and Cypselosomatidae are striking when specimens are compared in detail, especially when recognizing leg chaetotaxy, the enlarged dorsal epandrial setae, and the typical nerioid hypandrium, pregonite and postgonite.

ii) Tanypezidae & Strongylophthalmyiidae. Strong support for a relationship between Tanypezidae and Strongylophthalmyiidae is unsurprising as it has been long accepted by authors. The present results differ slightly from Lonsdale's 2013 most recent analysis, however, as broader taxonomic sampling of the two superfamilies in which these families have been historically placed has allowed for reconsideration and repolarization of many of the characters used to unite them. The monophyly of this lineage within Nerioidea is supported as follows: (8) first flagellomere elbowed (also Micropezidae, some Cypselosomatidae); (21) ocellar triangle elongate but not reaching anterior margin of frons; (73) precoxal bridge present; (77) proepisternal seta absent (paralleled frequently elsewhere); (107) katatergite narrow and bulging; (122) subalar sclerite bent, not straight; (132) katepisternum with deep recess anterior to meron; (169) halter with series of setae on stalk (pale in Strongylophthalmyiidae and dark in Tanypezidae); (171) upper calypter hairs long; (224) female 7th spiracles free from tergite; (231) female cerci curved in cross-section and largely to completely fused; (269) surstylus fused to epandrium (found in several lineages elsewhere, including some Fergusoninidae and Micropezidae); (278) subepandrial sclerite bare (also some Micropezidae); (284) one hypandrial seta recovered; (288) hypandrial arms free, not fused dorsally (also Fergusoninidae); (300) postgonite lost; (303) phallic plate composed of two folding, articulating sclerites; (311) distiphallus with spinulose membrane and apical "glans" or acrophallus (reversed in some Tanypezidae).

A relationship with the family group containing Neriidae is weakly supported by the following: (59) loss of vibrissa (character polarity uncertain); (79) acrostichal seta lost (paralleled frequently elsewhere); (177) basal costa setae lost (recovered in some taxa); (184) R_{4+5} and M_1 convergent (also Cypselosomatidae, reversed in *Strongylophthalmyia*); (203) large body size; (310) elongate and laterally sclerotized distiphallus (reversed in some).

iii) Micropezidae, Neriidae & *Cypselosomatites*. The fossil *Cypselosomatites* was recovered as sister to Micropezidae in the analysis on the basis of (135, 136) multiple vertically arranged katepisternal setae; the remaining characters are homoplastic or not visible on the fossil (either concealed or genitalic). If *Cypselosomatites* is included as the basal-most branch of an enlarged Micropezidae (not promulgated here), this arrangement of katepisternal setae is the only character useful for family diagnosis and therefore not desirable as there are lineages in which one or more of these setae are reduced or obscured by surrounding setulae (some Calobatinae), or where the ancestral state of a single seta is recovered (some Micropezinae).

The family group can be defined by the following characters (noting that genitalic character states are unknown for *Cypselosomatites*): (60) ocellars reduced (not *Cypselosomatites*); (78, 90, 103) postpronotal, presutural intra-alar and anepisternal setae absent; (187) M_4 reaching wing margin; (225) female segment 8 longitudinally striated (also some Diopsoidea); (236) at least three spermathecae (uncommonly reversed); (251) male sternites 7 and 8 deeply divided along adjoining margins (not fused or connected along thickened margin); (263) one or two supernumerary sclerites present; (275) male cercus positioned past epandrium, not sunken within it; (285) hypandrium with membranous anteroventral attachment to pregenital sclerites and epandrium.

Within Micropezidae, while the relationships between the subfamilies were not tested, the monophyly of the family was, and it appears to be quite robustly supported by the following: (8) first flagellomere deflexed; (76) presternum very large; (95) lateral scutellar setae lost (also highly reduced in Neriidae); (138) mid coxae separated medially by process of mesonotum (not visible in available *Cypselosomatites*); (164) hind ventroapical tibial seta absent; (188) vein CuA straight (not sinuate); (207) suture between tergites 1 and 2 obliterated; (230) internal process of female sternite 10 highly reduced; (240) spermathecal duct apically pigmented (reversed in some subfamilies); (241) male sternite 5 with genital fork developed (secondarily reduced or lost in some); (245) male sternite 6 medially produced with anteromedial and anterolateral sclerotized bands; (265) anteroventral corner of epandrium with narrow process (articulates with hypandrium); distiphallus (308) segmented and (316) with distal bulb (lost in some lineages); This evidence would contradict the hypothesis that the family is paraphyletic with respect to Neriidae.

C) Diopsoidea—Family group relationships (Fig. 425)

i) Diopsoidea. Basal branches in the superfamily are supported by highly homoplastic characters that are either of uncertain polarity, or are reversed, usually in two or more constituent families.

Psilidae was recovered as the basal-most offshoot of the superfamily, with the remainder definied by the following: (21) ocellar triangle attaining anterior margin of frons (triangle not evident in Gobryidae and Diopsidae); (23) postocellars and ocelli approximate, not widely spaced (possibly of reversed polarity); (60) ocellar setae reduced (reversed in some Megamerinidae and Syringogastridae); (101) scutellum and subscutellum fused (reversed in some Megamerinidae and Gobryidae); (175) costa unbroken (subcostal break present in Somatiidae); (177) subcosta complete (possibly of reversed polarity); (187) M_4 reaching wing margin (reversed in some lineages); (201) microtrichia on basal wing cells absent (reversed in the core diopsoid families); (320) ejaculatory apodeme large, well-developed (likely of reversed polarity).

The subfamilies of Psilidae were all recovered as distinct and well-supported. While only a single representative of Belobackenbardiinae was available for the analysis, there is nothing to suggest from the original species descriptions that the monophyly of this group is suspect. Belobackenbardiinae is supported as basal in the family, sister to a lineage comprised of the *Electrochyliza* (extinct, unplaced to subfamily) and Chylizinae+Psilinae. This lineage excluding Belobackenbardiinae is characterized by the following: (32) angled, transversely striated ventral plate on face; (63, 79, 173) recovery of the postocellar and prescutellar acrostichal setae and a better developed alula (reversed in some); (194) subcostal cell bulging past insertion of subcostal vein, lengthening distal curved section of subcostal vein; (224) female 7th spiracles free from tergite; (227) female terminalia more strongly retracted; (284) at least two hypandrial setae. While the polarity of many of these characters is uncertain, the structure of the face and subcostal cell and vein would appear to be reliable. Chylizinae and Psilinae are best supported as monophyletic on the basis of: (41) clypeus notched (frequently reversed); (47) parafacial with outstanding setulae; (48) parafacial glossy (without microtomentum); (105) anepimeron setulose (reversed in some); (119) proepisternum with patch of short, dense, isolated and usually white hairs; (128) anterior half of pleuron and sometimes postpronotum with long pile (reversed in some); (213) sternite 2 divided transversely (reversed in some, similar state seen in Tanypezidae); (225) female segment 8 minutely and longitudinally striated (also seen in Megamerinidae and the Neriidae family group).

Further excluding Nothybidae, the remaining diopsoids are united by: (55) strong semicircular carina above foramen magnum (reversed in Gobryidae, forming complete circle in Diopsinae); (67) fronto-orbital setae reduced to 1 or 0; (96) tubercle present at base of apical scutellar setae (absent Megamerinidae, likely homologous with the long scutellar spines of Diopsidae); (114) postmetacoxal bridge present (absent in some Gobryidae); (115) cylindrical extension produced from metathorax to meet abdomen (reversed in Gobryidae); (128) thorax with long pile (reversed Gobryidae and Diopsidae); (249) recovered asymmetry of male postabdomen (again reversed in Megamerinidae and Diopsidae); (262) male spiracle 7 enclosed in tergite (reversed in Megamerinidae and Diopsinae); (268) asymmetry of surstyli (reversed in Megamerinidae, Syringogastridae and Diopsidae); (294) pregonite lost (recovered in Megamerinidae, Syringogastridae and Diopsidae, likely of reversed polarity).

The remaining taxa, Gobryidae and the core families Megamerinidae, Syringogastridae and Diopsidae, are supported by the following characters but, while they are somewhat more convincingly united compared to the remaining basal taxa, their putative synapomporphies are still rich in homoplasy: (20) ocellar triangle indistinct (reversed in Syringogastridae); (47) parafacial with setae (reversed Diopsinae); (75) prosternum setose laterally (also setulose medially in Diopsinae); (80) dorsocentral setae absent (reversed in Megamerinidae and some Diopsidae); (91) anterior supra-alar seta absent (reversed Megamerinidae and Centrioncinae); (95) lateral scutellar setae absent (also some Nerioidea); (101) subscutellum free from scutellum (reversed in Syringogastride and Diopsidae); (104) greater ampulla present (reversed Syringogastridae); (105) anepimeron setulose (reversed in some Gobryidae); (121) subalar sclerite incorporated into anepimeron (reversed in Megamerinidae); (142, 143) fore femur with anteroventral and posteroventral rows of spine-like setae (reversed in Megamerinidae and Syringogastridae); (146) hind leg with anteroventral and posteroventral rows of spine-like setae (anteroventral row lost in Centrioncinae and both rows lost in Diopsinae); (147) hind femur strongly thickened (reversed in Diopsidae); (156) tibial setae with scale-like base; (188) CuA shallowly rounded (straight in Syringogastridae); (204) abdomen petiolate (except *Paleotanypeza*); (207) suture between tergites 1 and 2 obliterated; (214) anterior margin of female sternite 1 deeply recessed (reversed Syringogastridae and Diopsidae); (236) more than two spermathecae (reversed Megamerinidae and some Diopsidae); (240) apex of spermathecal ducts pigmented.

ii) Megamerinidae, Syringogastridae & Diopsidae. These three families form a robustly supported clade defined by external and genitalic synapomorphies. While many of these characters are frequently reversed in one or more lineages, the full suite of characters taken together makes a convincing argument for the monophyly of this lineage. Characters include: (5) dorsal seam of pedicel lost (recovered in Syringogastridae); (7) first flagellomere discoid (elongate in Syringogastridae); (8) first flagellomere porrect (elbowed in Syringogastridae); (106) suture between katepisternum and meron absent or tightly joined and smooth (except *Paleotanypeza* and Centrioncinae); (112) metasternum extending between hind coxae (reversed in Diopsidae); (117, 118) proepisternum shifted dorsally, displacing postpronotum; (134) katepisternum produced dorsally past ventral quarter of anepisternum (reversed in *Paleotanypeza* and some Syringogastridae); (150) femoral glands present (all femora on both antero- and posteroventral surfaces in Megamerinidae, fore and mid femora on posteroventral surface in Syringogastridae, lost in Diopsidae); (173) alula well-developed (reduced in Syringogastridae and some Diopsidae); (183) vein R_{2+3} short, meeting costa before or at half distance between wing apex and apex of CuA+CuP (reversed in Diopsinae); (195) cell br bulging into cell dm (reversed in Diopsinae); (201) basal wing cells microtrichose; (211) sternite 1 with dark submarginal transverse ridge that sometimes separates from remainder of sclerite; (249 male pregenitalic sclerites symmetrical (reversed Syringogastridae); (272) inner surface of surstylus with spine-like setae (also Nothybidae, reversed in some Syringogastridae and Diopsidae); (284) at least two hypandrial setae, with setae dense in Diopsinae; (294, 300) pregonite and postgonite recovered (polarity of characters likely reversed); (302) postgonite dark, narrow and pointed ventrally (reversed Centrioncinae); (308) distiphallus complex, divided into strongly differentiated basal and apical sclerites and (310) at least basally with lateral sclerotized bands (reversed Diopsidae); (318) at least part of distiphallus membrane spinulose (reversed Centrioncinae and some Syringogastridae).

Within this family group, Syringogastridae and Diopsidae are clustered on the following (in part): (57) pronotal collar developed; (69) inner vertical seta lost; (86) supra-alar ridge developed; (101) scutellum and subscutellum fused; (107) katatergite flat; (165) mid and hind tarsi with "sawlines"; (197) anal cell shorter; (217) female sternite 6 wide, short; (224) female 7th spiracle free from tergite; (237) spermathecae at least partially telescoped; (248) male pregenitalic sclerites forming complete "annulus" (reversed in Diopsinae); (252) male sternite 8 bare; (295) pregonite articulating with hypandrium; (317) distiphallus sac-like, membranous and heavily spinulose.

Conclusions

The present findings support both Diopsoidea and Nerioidea as monophyletic, with Diopsoidea consisting of Psilidae, Nothybidae, Somatiidae, Gobryidae, Megamerinidae, Syringogastridae and Diopsidae, and Nerioidea consisting of Fergusoninidae, Cypselosomatidae, Pseudopomyzidae, Strongylophthalmyiidae, Tanypezidae, Neriidae, Micropezidae and the fossil genus *Cypselomomatites*. While outgroup affiliations are uncertain, the two are not appear to be related.

There is ambiguous support associating Diopsoidea with some of the former Opomyzoidea, but this is likely due to homoplasy, with many characters being readily paralleled or lost. Most of these supportive characters are reductions in chaetotaxy and should be of weaker predictive value if they are linked, which would logically appear to be the case.

Similarly weak or homoplastic characters unite the basal Diopsoidea and further analysis is required for substantiation. Despite a lack of unambiguous, complex synapomorphic support for the superfamily and for the position of the basal four families, these relationships are nonetheless tentatively accepted here in the absence of convincing alternative hypotheses. Conversely, the superfamily contains a core group of familes that are strongly supported as monophyletic: Megamerinidae, Syringogastridae and Diopsidae. Within Psilidae, Shatalkin's (2002) referral of *Belobackenbardia* to its own subfamily Belobackenbardiinae is supported, as it was recovered separate from the rest of the family, made up of the fossil *Electrochyliza* and the sister subfamilies Psilinae+Chylizinae.

Nerioidea was much more convincingly recovered as monophyletic and is readily divided into three family groups. These relationships are well-defined and mostly unsurprising since they have much precedent in the literature, but the relationship between Fergusoninidae and the lineage of Cypselosomatidae + Pseudopomyzidae is novel. Fergusoninidae was closely associated with, or included in the "opomyzoid" family Agromyzidae since its original description, but the evidence previously provided to support this relationship is most likely due to convergence, driven in part by larval feeding in living plant tissue. This larval habit is unusual in the Diopsoidea and Nerioidea, as most taxa occur on decaying tissue (especially plant tissue), but there are some exceptions that are primary invaders of plants. These include some Micropezidae such as *Micropeza corrigiolata* and the "rhizome fly" *Mimegralla coeruleifrons*, a few stem-boring Diopsidae including *Diopsis longicornis* on rice, and most Psilidae including the carrot rust fly *Psila hennigi*. The fossil genus *Cypselosomatites* is supported as the sister group to Micropezidae, partially reflecting the findings of D.K. McAlpine (1966, 1998).

All family-level groups tested for were recovered as monophyletic. These included a modestly supported Pseudopomyzidae, which some considered paraphyletic with respect to Cypselosomatidae, and a strongly supported Micropezidae, which some considered paraphyletic with respect to Neriidae (see discussions above).

With these families redescribed and a tentative phylogeny presented, it is hoped that additional work on these taxa can be facilitated, allowing for deeper understanding of these widespread, specialized and sometimes diverse groups, with sister-group relationships and character polarities better established. These should in turn help answer questions that could not be resolved here, including the internal structure of Neriidae and Micropezidae, and of course, the arrangement of the basal diopsoid branches. While a number of novel characters and family group relationships were newly or better established here, it was unsurprisingly reaffirmed that Diopsoidea, similar to many other acalyptrate groupings, is a heterogenous assemblage of unusual families that are as uniquely derived as they are resistant to phylogenetic reconstruction beyond a core group. The difference between backbone support on the phylogeny and support for individual families is in high contrast.

In lineages such as Schizophora that have experienced rapid diversification, it is uncommon for single characters providing solid proof of ancestry to present themselves, and increased volumes of data may not necessarily provide better resolution. In the present study, the data strengthened support for relatively well-known lineages and helped resolve a number of other relationships, but little more was accomplished for some groups that have historically resisted association. Among these groups, homology remains difficult to establish and homoplasy is rampant. Parallel molecular work has also accomplished much in the resolution of dipteran phylogenetics by providing additional and much larger data sets, but many results similarly involve reaffirmation of what was either suspected or modestly supported previously, and polytomies and weakly supported branches still abound.

To remedy this situation, it is recommended that family- and genus-level treatments of the acalyptrate families are continued. The present study would not have been possible without access to such studies already present in the literature, primarily in the form of systematic revisions and reviews. These in-depth studies reveal global variation across both taxa and characters in more detail than is possible in single phylogenetic works such as this, and they can begin to develop well-informed hypotheses of ancestry that utilize more numerous ingroup taxa, or perhaps even all known species. The broader context provided by these studies allows for closer comparison of taxa and more convincing homologization of characters, the discovery of new synapomorphic features, and the better characterization and diagnosis of taxa in opposition to their closest and most morphologically similar relatives. When examining the historical literature, this approach of working from the bottom up has proven to be the most reliable and productive way to recover relationships efficiently, and when combined with species description, also simultaneously provides much needed alpha-level taxonomic work.

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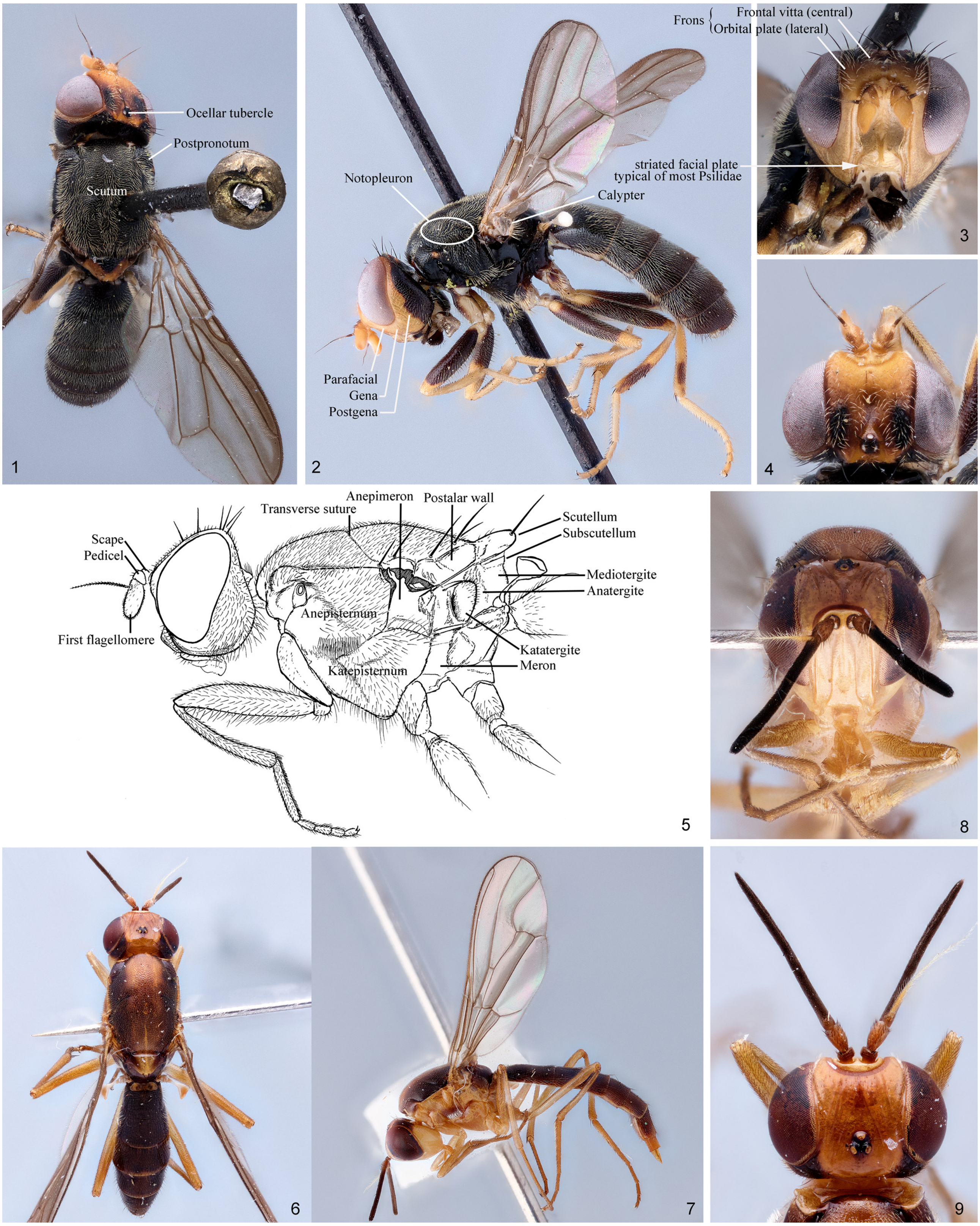
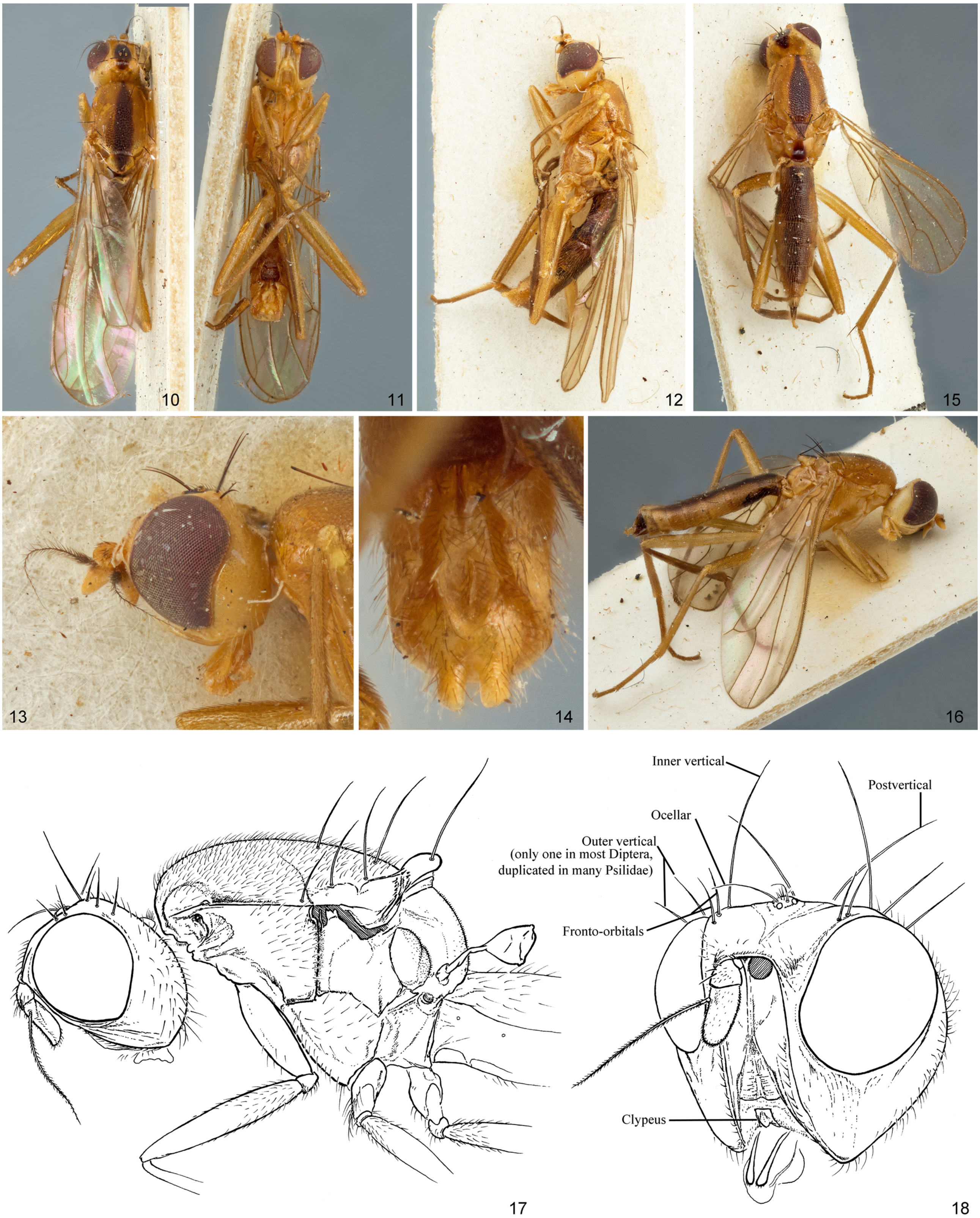
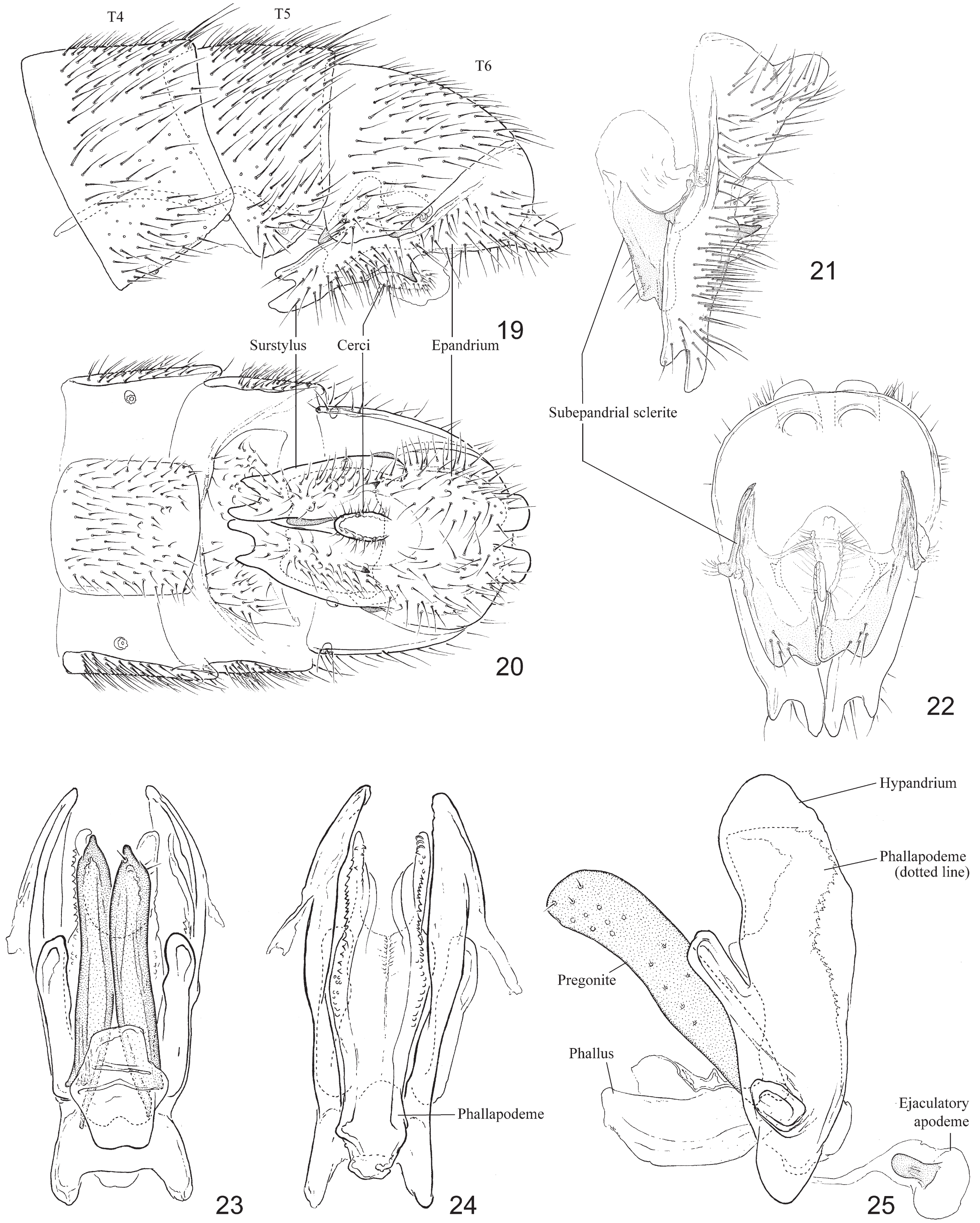


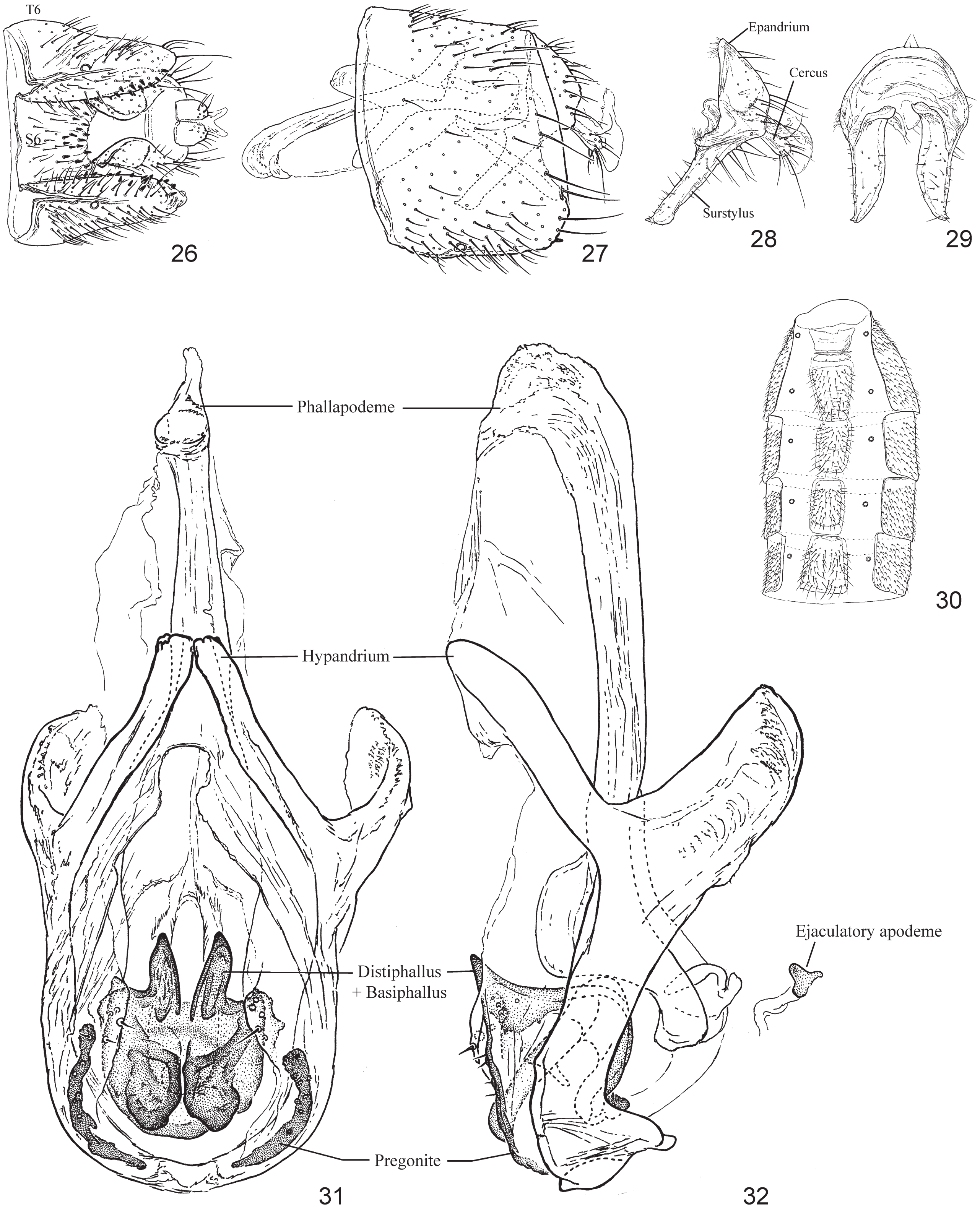
FIGURES 1–9. Figs 1–4: *Chyliza leguminicola* Melander (Psilidae); 1: dorsal; 2: lateral; 3: head, anterior; 4: head, dorsal. Fig. 5: *Chyliza erudita* Melander, lateral. Figs 6–9: *Loxocera* sp.; 6: dorsal; 7: lateral; 8: head, anterior; 9: head, dorsal.



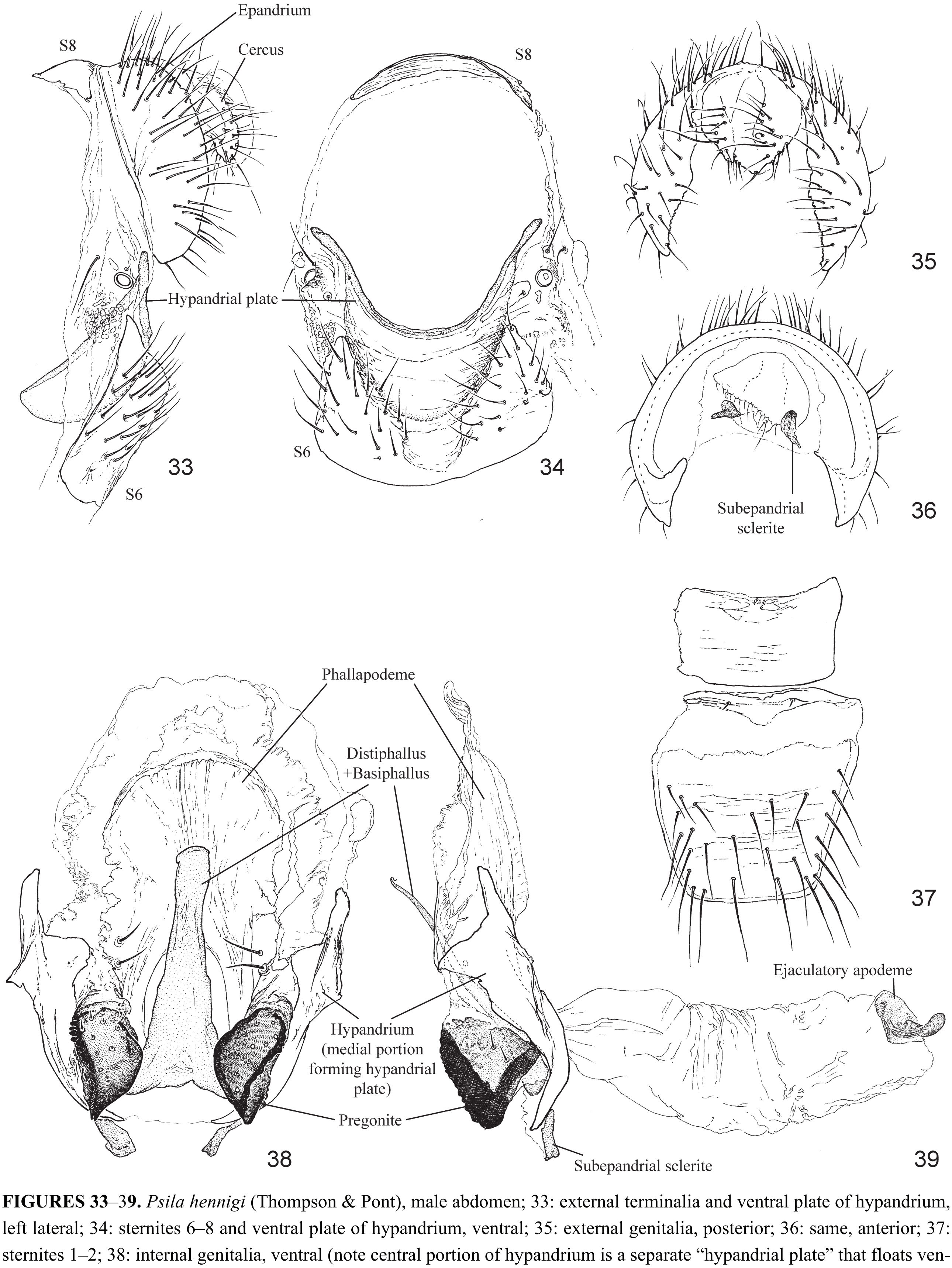
FIGURES 10–18. Figs 10–16: *Belobackenbardia cornicula* Shatalkin (Psilidae), paratypes; 10: male dorsal; 11: male ventral; 12: male lateral; 13: male head, lateral; 14: male terminalia, ventral; 15: female dorsal; 16: female lateral. Figs 17–18: *Psila hennigi* (Thompson & Pont) (Psilidae); 17: lateral; 18: head.



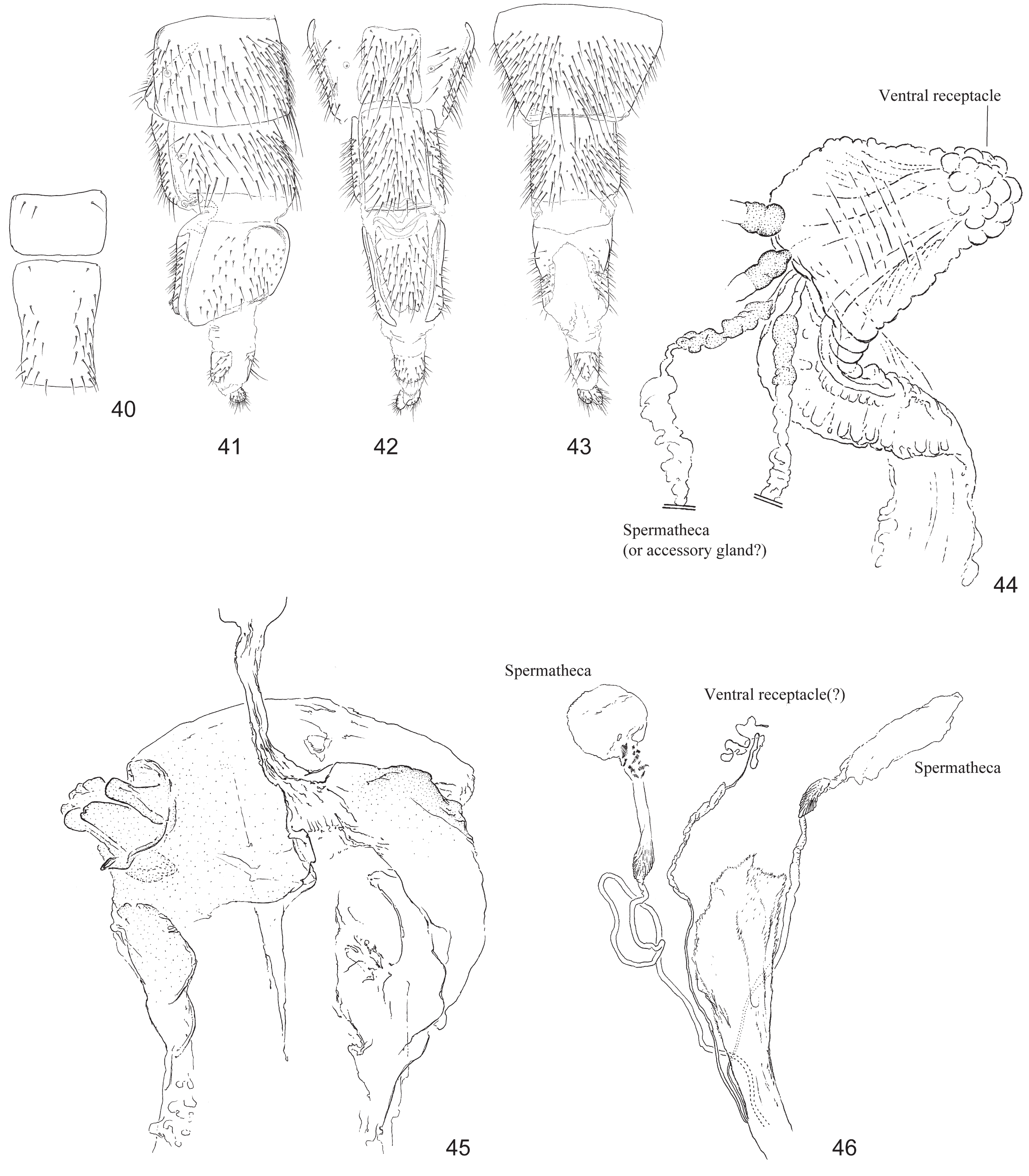
FIGURES 19–25. Figs 19–25: *Belobackenbardia cornicula* Shatalkin, paratype, male abdomen; 19: segment 4 to genitalia, lateral; 20: same, ventral; 21: external genitalia, lateral; 22: same, anterior; 23: internal genitalia, ventral; 24: same, dorsal; 25: same, left lateral.



FIGURES 26–32. Figs 26–32: *Chyliza notata* Loew (Psilidae), male abdomen; 26: segment 6 to genitalia, ventral; 27: same, lateral; 28: external genitalia, lateral; 29: same, anterior; 30: segments 1–5, ventral; 31: internal genitalia, ventral; 32: same, left lateral.

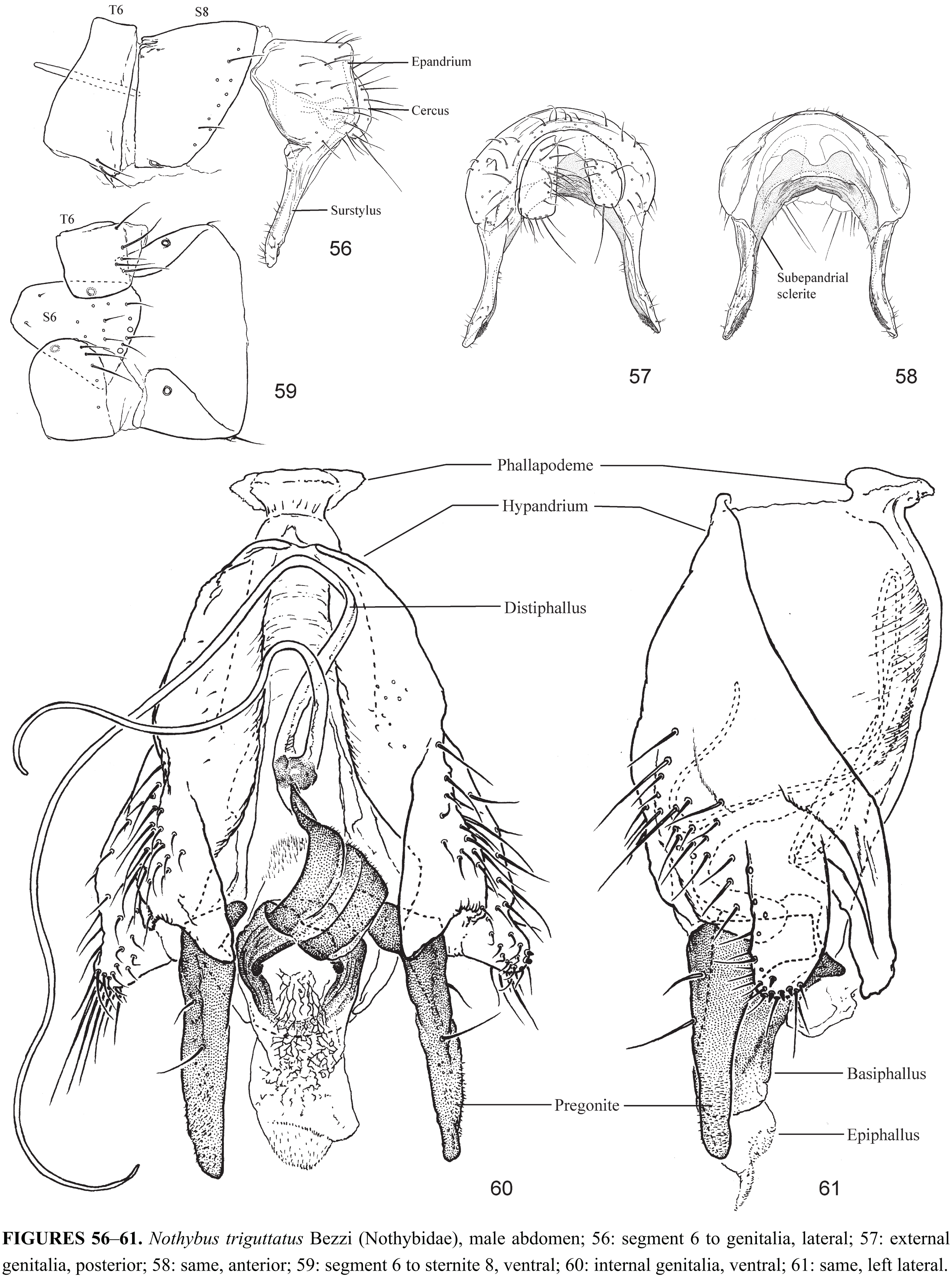


FIGURES 33–**39.** *Psila hennigi* (Thompson & Pont), male abdomen; 33: external terminalia and ventral plate of hypandrium, left lateral; 34: sternites 6–8 and ventral plate of hypandrium, ventral; 35: external genitalia, posterior; 36: same, anterior; 37: sternites 1–2; 38: internal genitalia, ventral (note central portion of hypandrium is a separate "hypandrial plate" that floats ventrally next to S6; the phallapodeme is partially fused to the remaining lateral arms of the hypandrium); 39: same, left lateral.

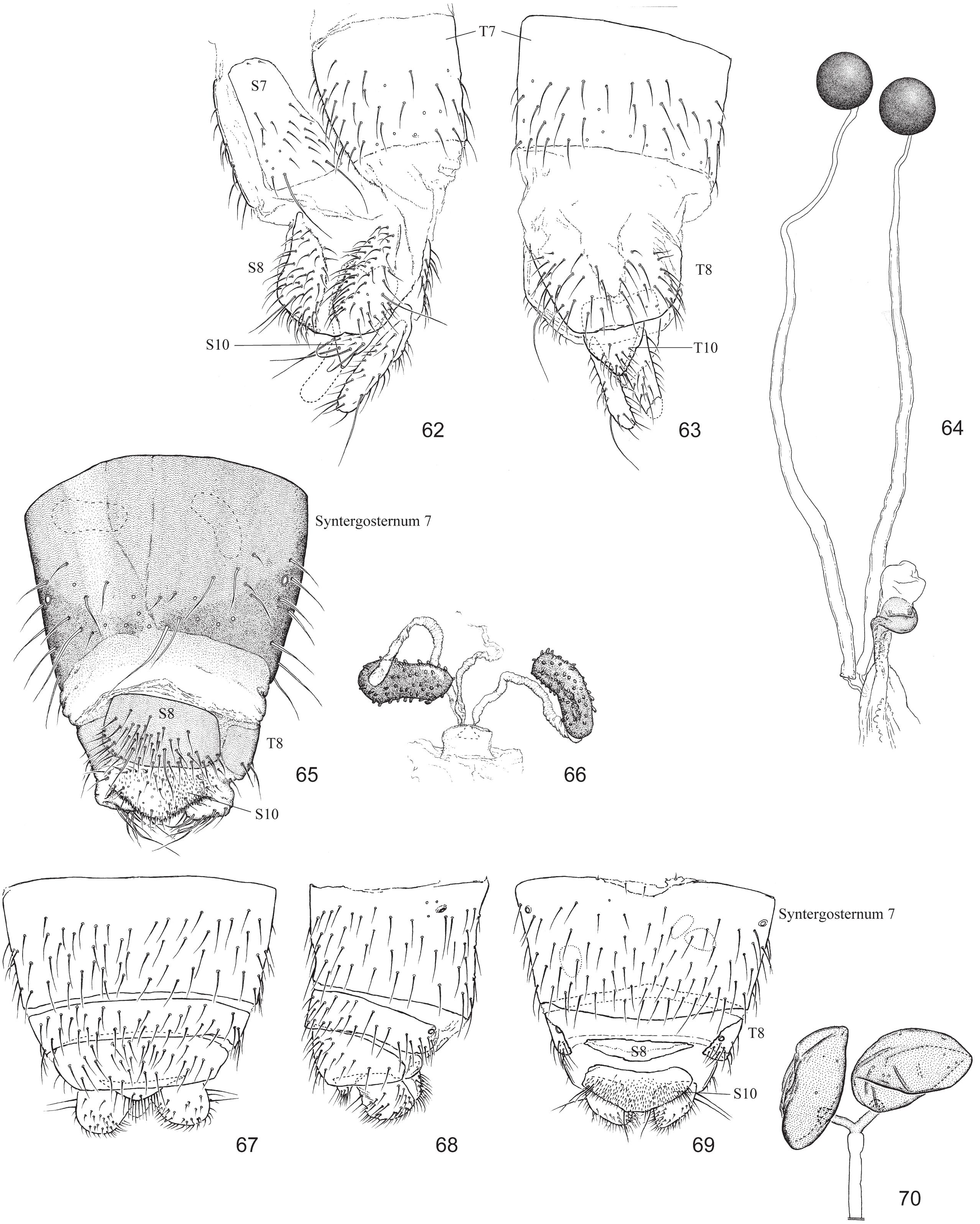


FIGURES 40–46. Fig 40: *Loxocera collaris* Loew (Psilidae), female sternites 1–2. Figs 41–44: *Belobackenbardia cornicula* Shatalkin, paratype female abdomen; 41: sternite 6 to cerci, left lateral; 42: same, ventral; 43: same, dorsal; 44: internal genitalia. Fig. 45: *Loxocera cylindrica* Say, female internal genitalia. Fig. 46: *Chyliza notata* Loew, female internal genitalia.

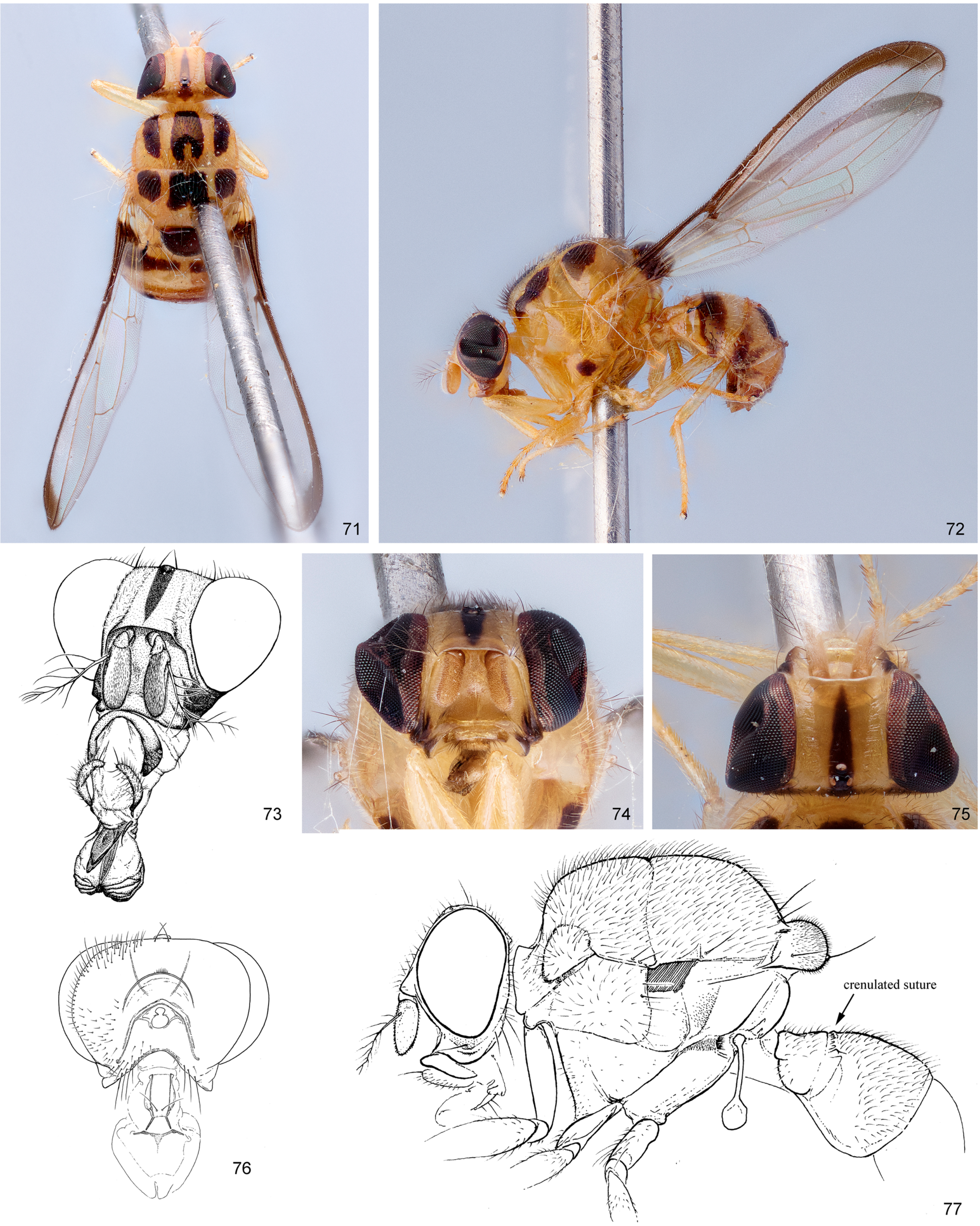
FIGURES 47–55. Fig. 47: *Psila hennigi* (Thompson & Pont), ex lab culture. Fig. 48: *Chyliza* sp., Ontario, Canada. Figs 49–53: *Nothybus longicollis* (Walker) (Nothybidae); 49: head, anterior; 50: lateral; 51: dorsal; 52: ventral; 53: holotype male. Fig. 54: *Nothybus sumatranus* Enderlein. Fig. 55: *Nothybus absens* Lonsdale & Marshall, holotype, male.



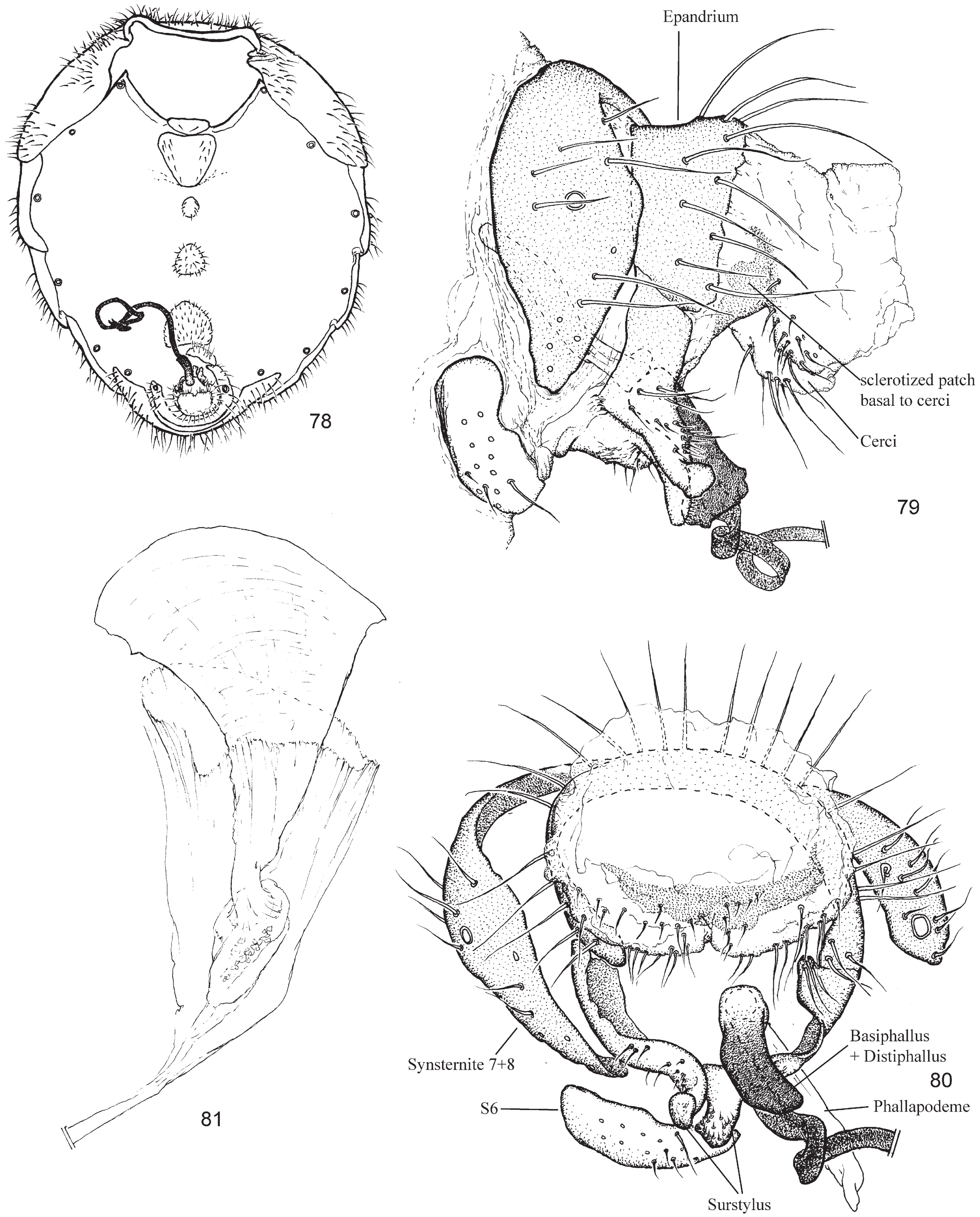
FIGURES 56–61. *Nothybus triguttatus* Bezzi (Nothybidae), male abdomen; 56: segment 6 to genitalia, lateral; 57: external genitalia, posterior; 58: same, anterior; 59: segment 6 to sternite 8, ventral; 60: internal genitalia, ventral; 61: same, left lateral.



FIGURES 62–70. Figs 62–64: *Nothybus biguttatus* Wulp (Nothybidae), female abdomen; 62: segment 7 to cercus, ventral; 63: same, dorsal; 64: internal genitalia. Figs 65–66: *Somatia aestiva* (Fabricius), female abdomen; 65: segment 7 to cerci; 66: internal genitalia. Figs 67–70: *Gobrya* sp., female abdomen; 67: segment 6 to cerci, dorsal; 68: same, right lateral; 69: same, ventral; 70: spermathecae.

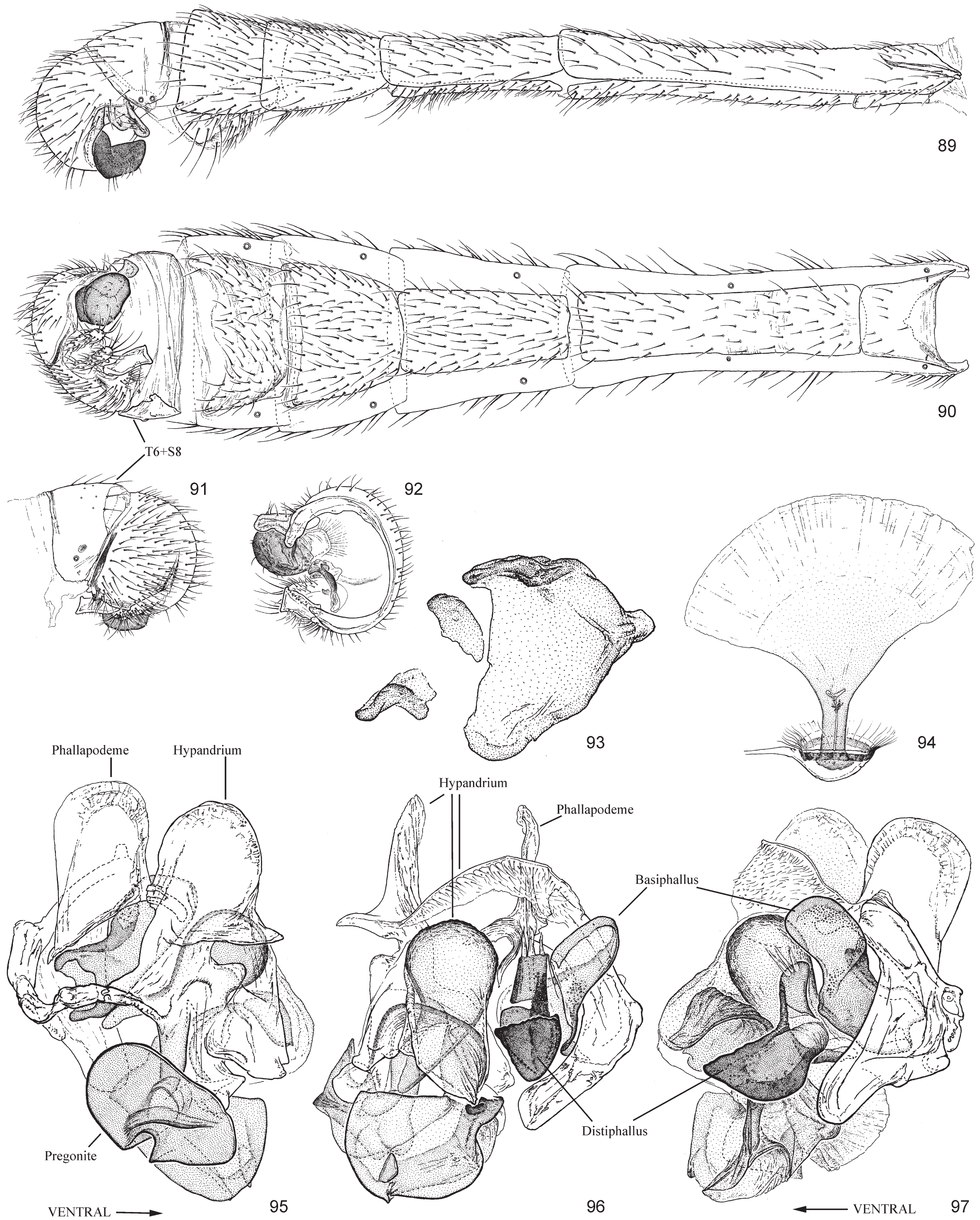


FIGURES 71–77. *Somatia aestiva* (Fabricius) (Somatiidae); 71: female dorsal; 72: same, lateral; 73: head, anterolateral; 74: female head, anterior; 75: same, dorsal; 76: head, posterior; 77: lateral.

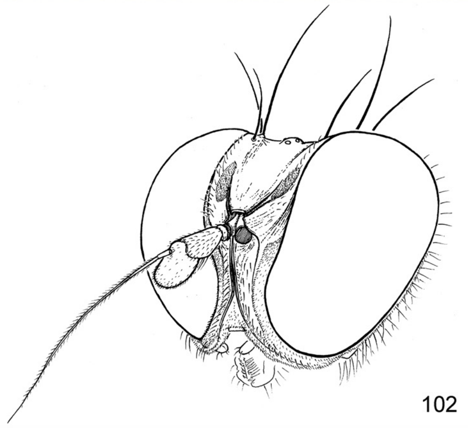


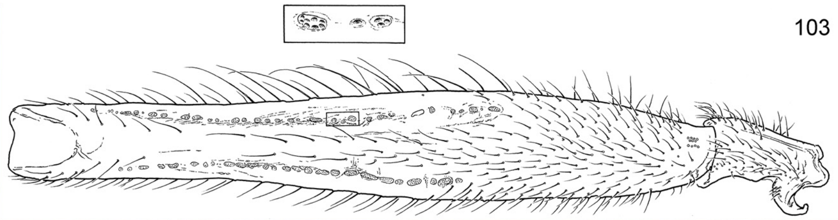
FIGURES 78–81. *Somatia aestiva* (Fabricius) (Somatiidae), male abdomen; 78: ventral; 79: terminalia, left lateral; 80: same, posterior; 81: ejaculatory apodeme.

FIGURES 82–88. *Gobrya* sp. (Gobryidae); 82: female, dorsal; 83: same, lateral; 84: male, ventral; 85: female head, anterior; 86: same, dorsal; 87: male, Seram, Indonesia; 88: male, Sarawak, Malaysia.

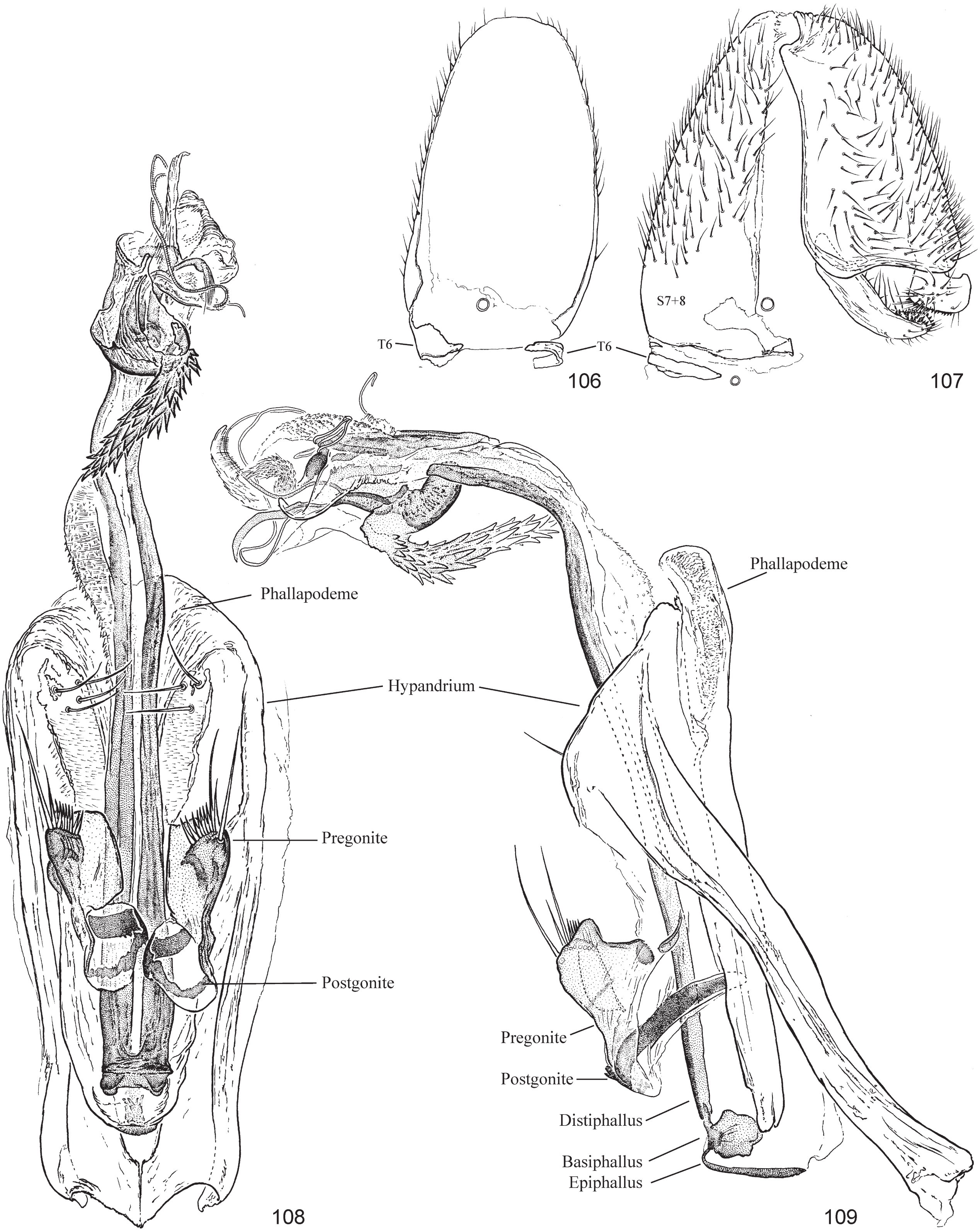


FIGURES 89–97. *Gobrya* sp. (Gobryidae), male abdomen; 89: right lateral; 90: ventral (right surstylus shaded); 91: terminalia, left lateral; 92: external genitalia, anterior (right surstylus and subepandrial sclerite shaded); 93: enlarged detail of subepandrial sclerite; 94: ejaculatory apodeme; 95: internal genitalia, right lateral; 96: same, ventral; 97: same, left lateral.

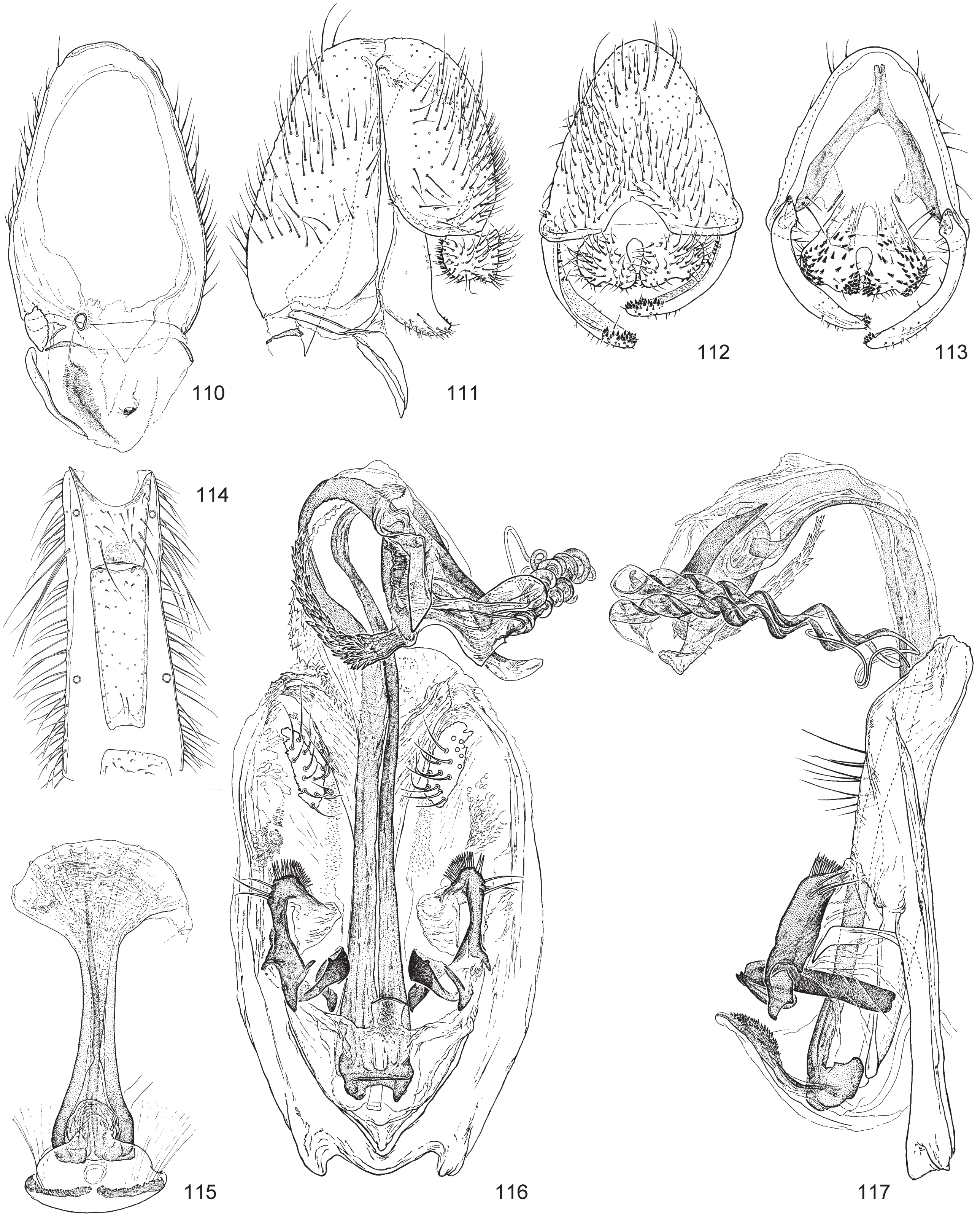




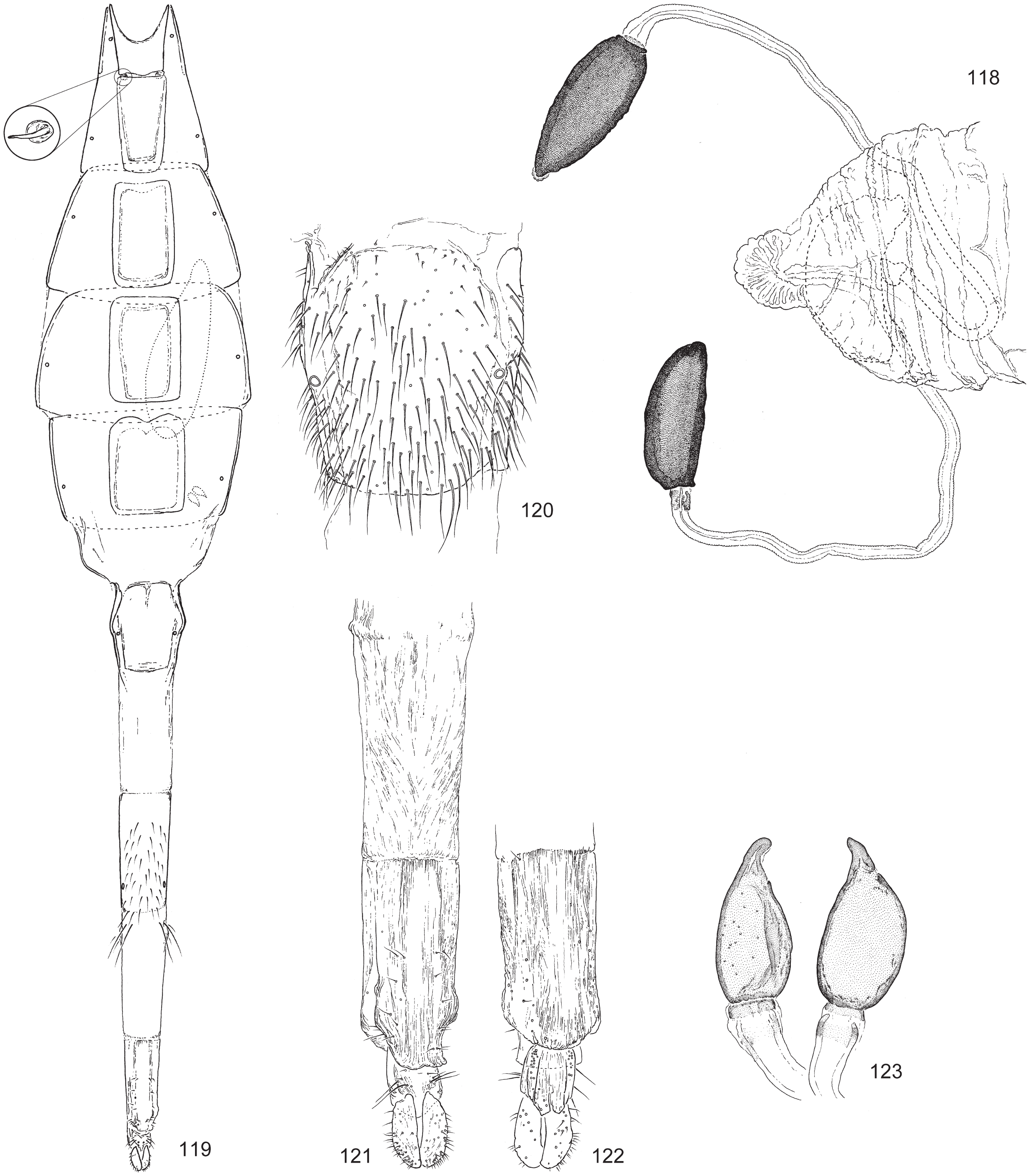
FIGURES 98–105. *Texara* sp. (Megamerinidae); 98: male, dorsal; 99: same, lateral; 100: male head, anterior; 101: same, dorsal; 102: same, anterolateral; 103: fore femur, ventral, with detail of gland openings; 104: male and female copulating, Vietnam; 105: male, Singapore.



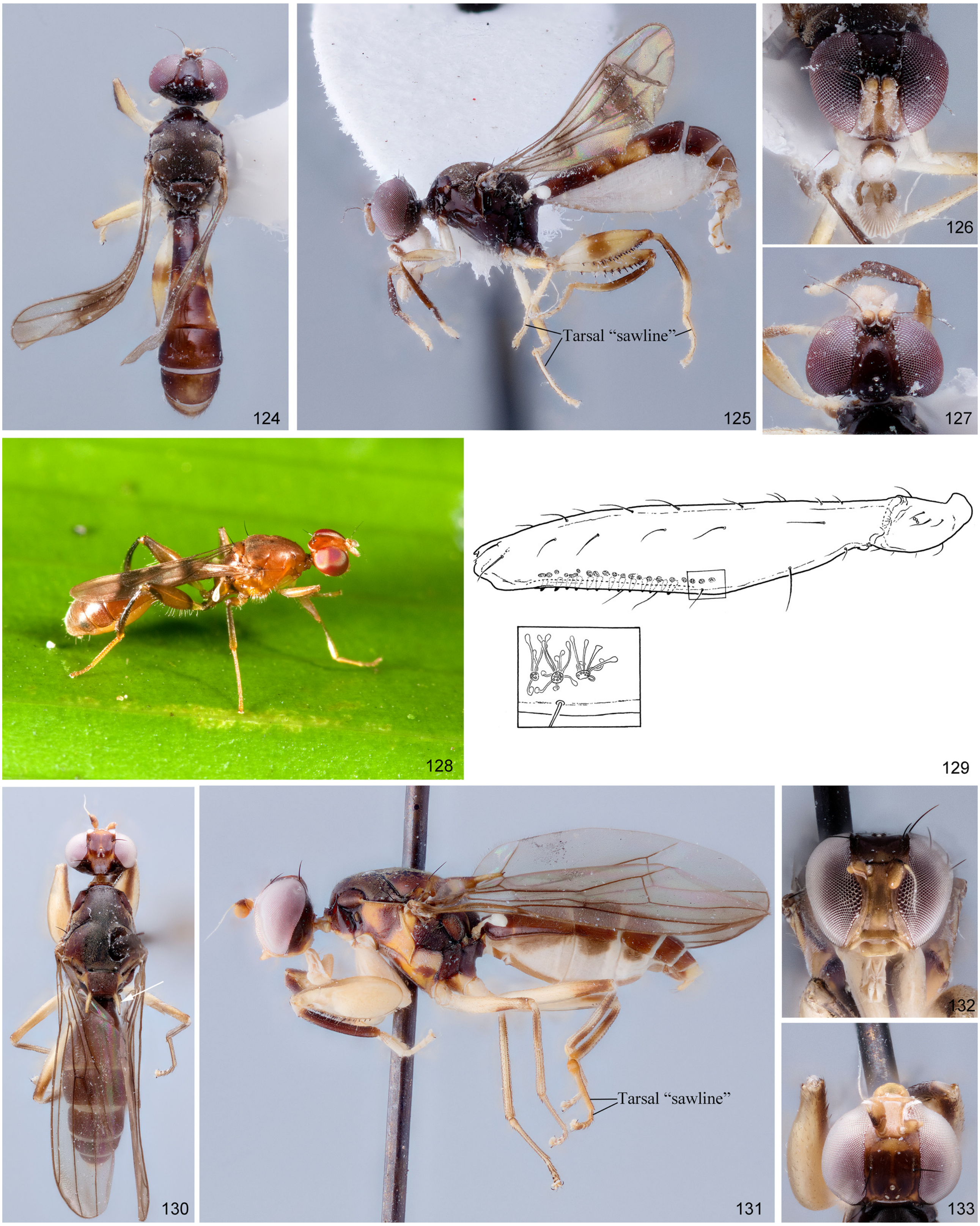
FIGURES 106–109. *Megamerina dolium* (Fabricius) (Megamerinidae), male terminalia; 106: sternites 6–8, ventral; 107: terminalia, left lateral; 108: internal genitalia, ventral; 109: same, left lateral.



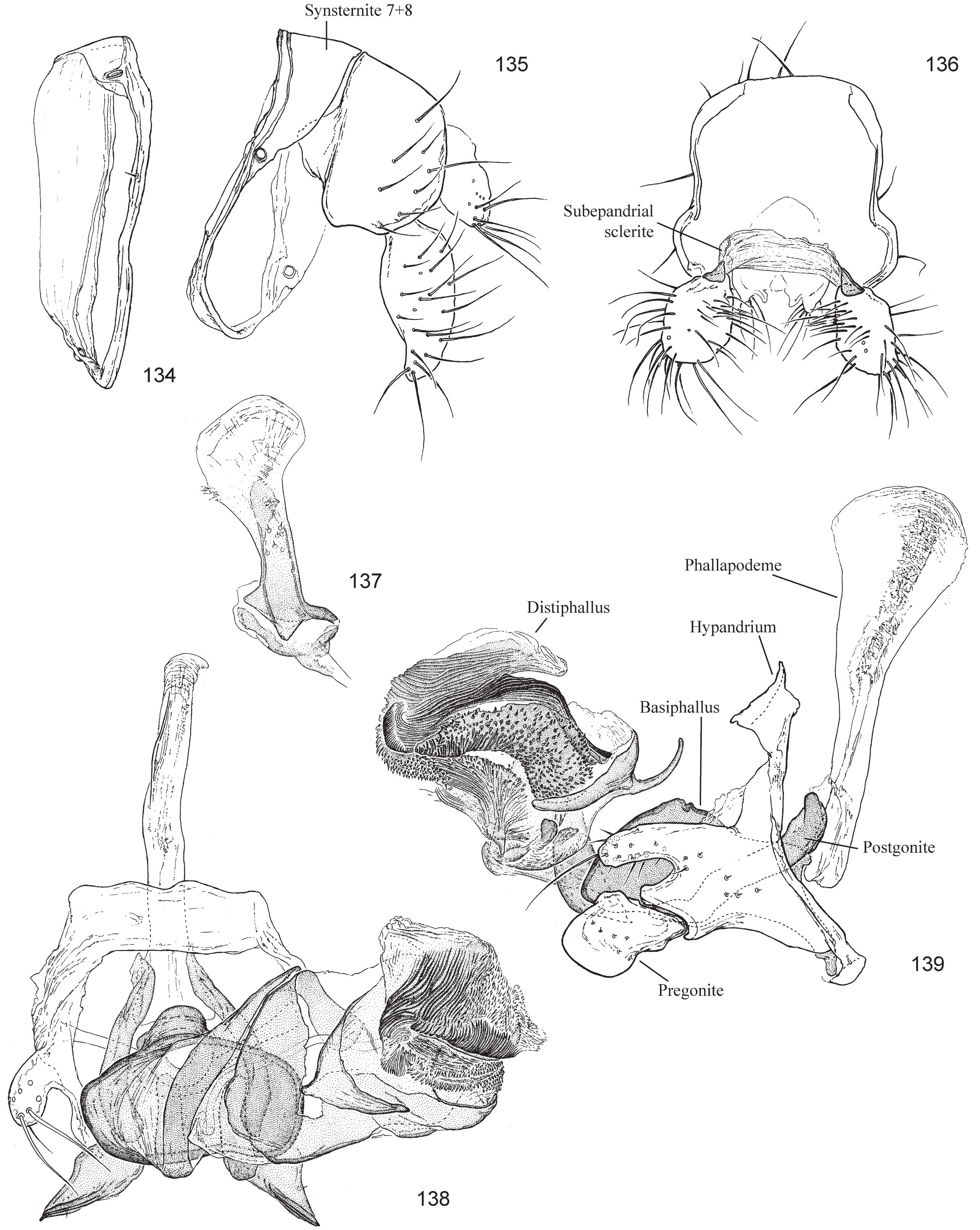
FIGURES 110–117. *Texara* sp. (Megamerinidae), male abdomen; 110: sternites 6–8, ventral; 111: terminalia, left lateral; 112: external genitalia, posterior; 113: same, anterior; 114: sternites 1–2, ventral; 115: ejaculatory apodeme; 116: internal genitalia, ventral; 117: same, left lateral.



FIGURES 118–123. Fig. 118: *Megamerina dolium* (Fabricius) (Megamerinidae), female internal genitalia. Figs 119–123: *Texara* sp., female abdomen; 119: ventral; 120: segment 6, dorsal; 121: segment 8 to cerci, ventral; 122: same, dorsal; 123: spermathecae.



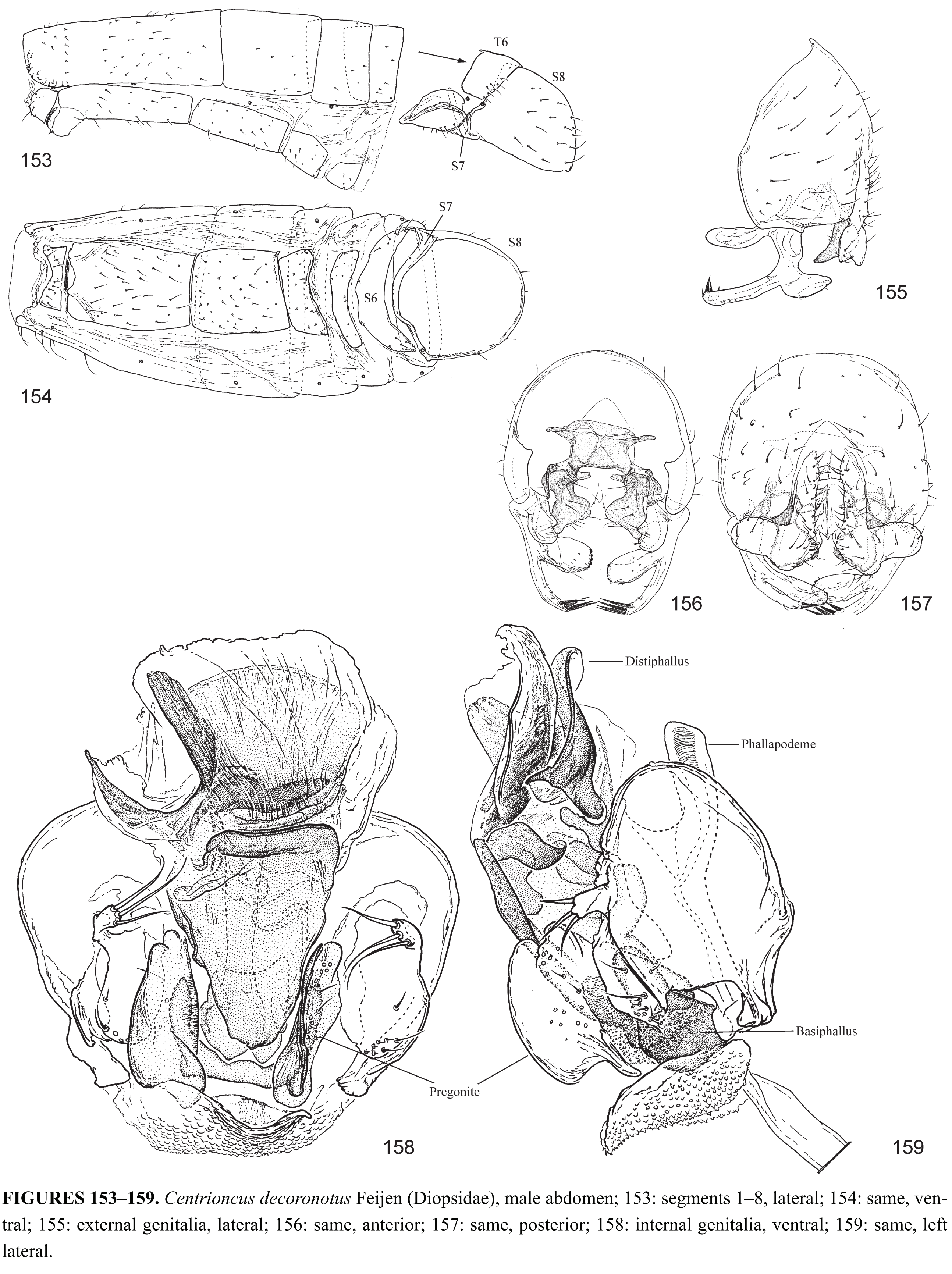
FIGURES 124–133. Figs 124–127: *Syringogaster atricalyx* Marshall & Buck (Syringogastridae), male paratype; 124: dorsal; 125: lateral; 126: head anterior; 127: head dorsal. Fig. 128: *Syringogaster* sp., Ecuador. Fig. 129: *S. atricalyx*, fore femur, ventral, with detail of glands including internal structure. Figs 130–133: *Centrioncus* sp., female; 130: dorsal; 131: lateral; 132: head anterior; 133: head dorsal.



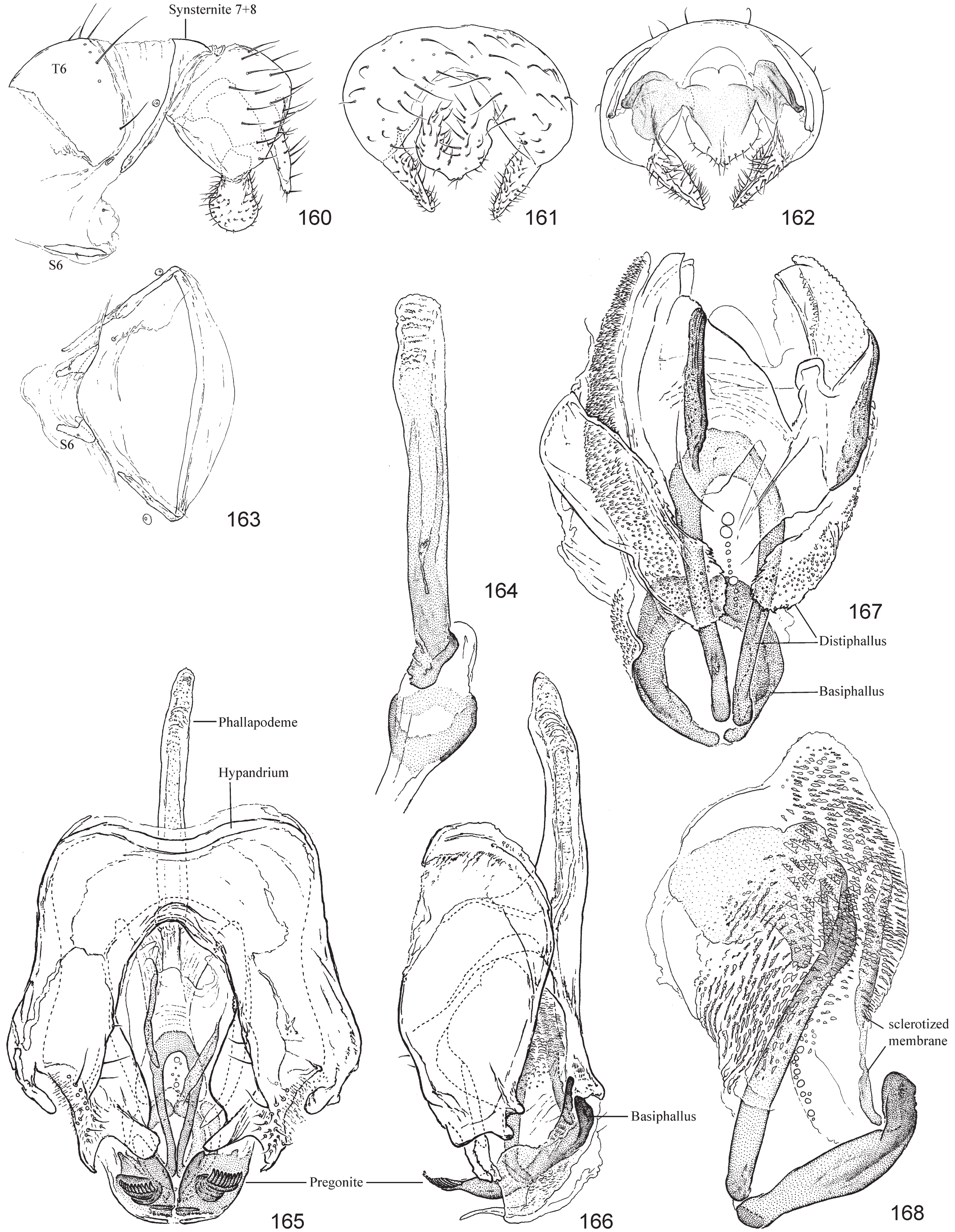
FIGURES 134–139. *Syringogaster atricalyx* Marshall & Buck (Syringogastridae), male paratype, terminalia; 134: sternites 6–8, ventral; 135: same, left lateral; 136: external genitalia, anterior; 137: ejaculatory apodeme; 138: internal genitalia, ventral; 139: same, left lateral.

FIGURES 140–142. *Syringogaster atricalyx* Marshall & Buck (Syringogastridae), female paratype, abdomen; 140: ventral; 141: lateral; 142: internal genitalia.

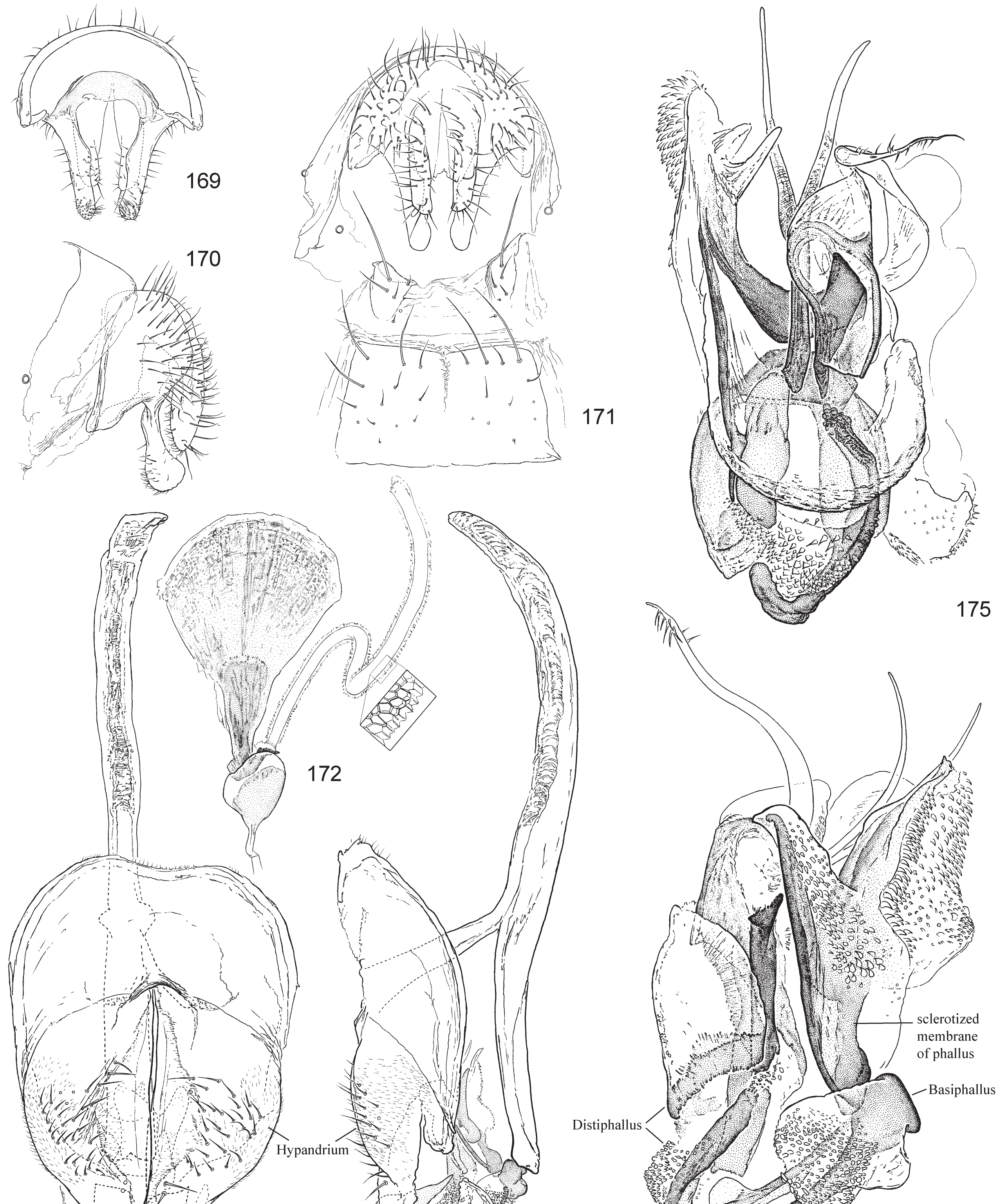
FIGURES 143–152. Figs 143–147: *Sphyracephala subbifasciata* Fitch, male (Diopsidae); 143: dorsal; 144: lateral; 145: head, anterior; 146: head, dorsal; 147: head, posterior. Fig. 148: *Teleopsis sykesii* (Westwood) (Diopsidae), India. Figs 149–152: *Eurydiopsis* sp. (Diopsidae), female; 149: dorsal; 150: lateral; 151: head, anterior; 152: head, dorsal.



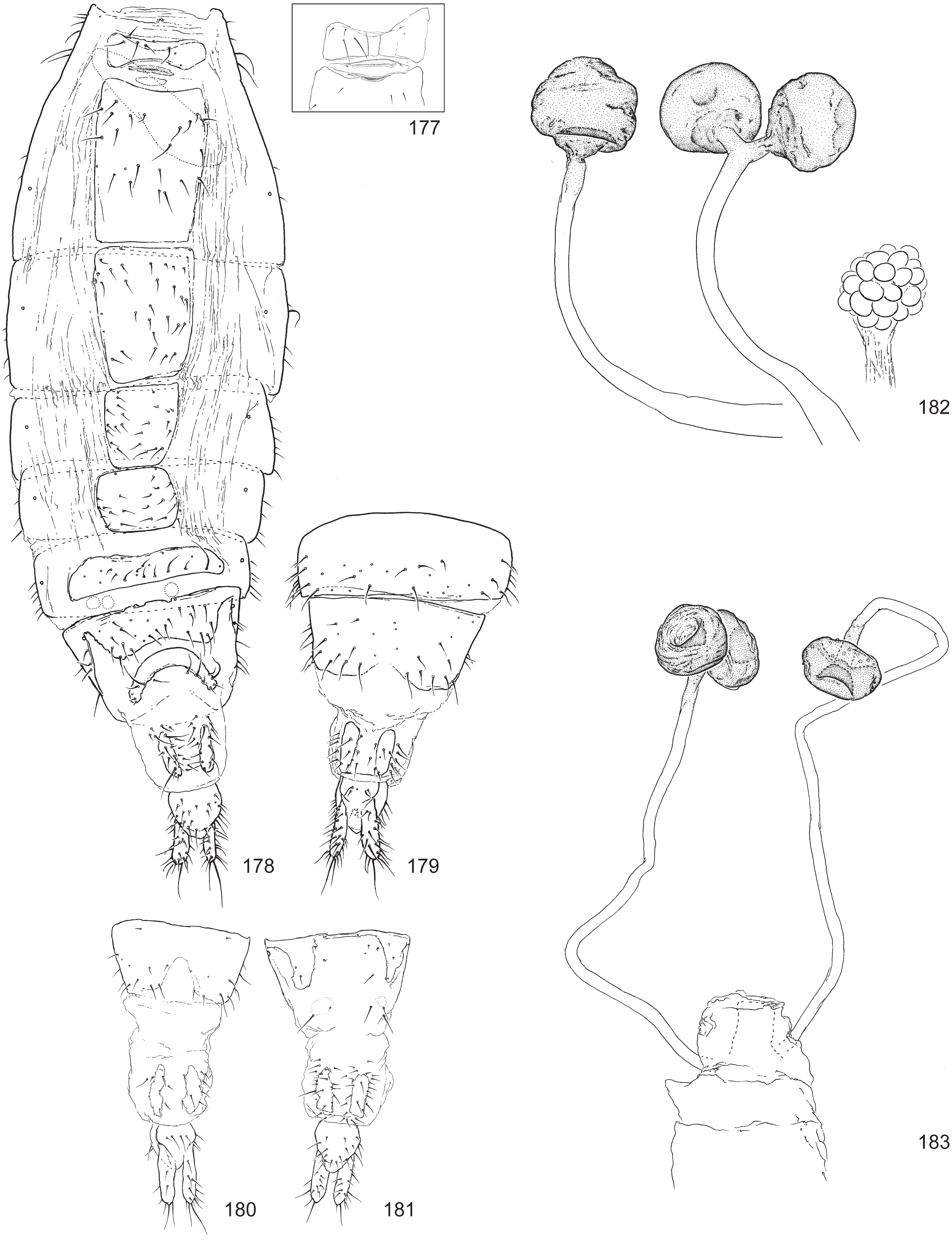
FIGURES 153–159. *Centrioncus decoronotus* Feijen (Diopsidae), male abdomen; 153: segments 1–8, lateral; 154: same, ventral; 155: external genitalia, lateral; 156: same, anterior; 157: same, posterior; 158: internal genitalia, ventral; 159: same, left lateral.



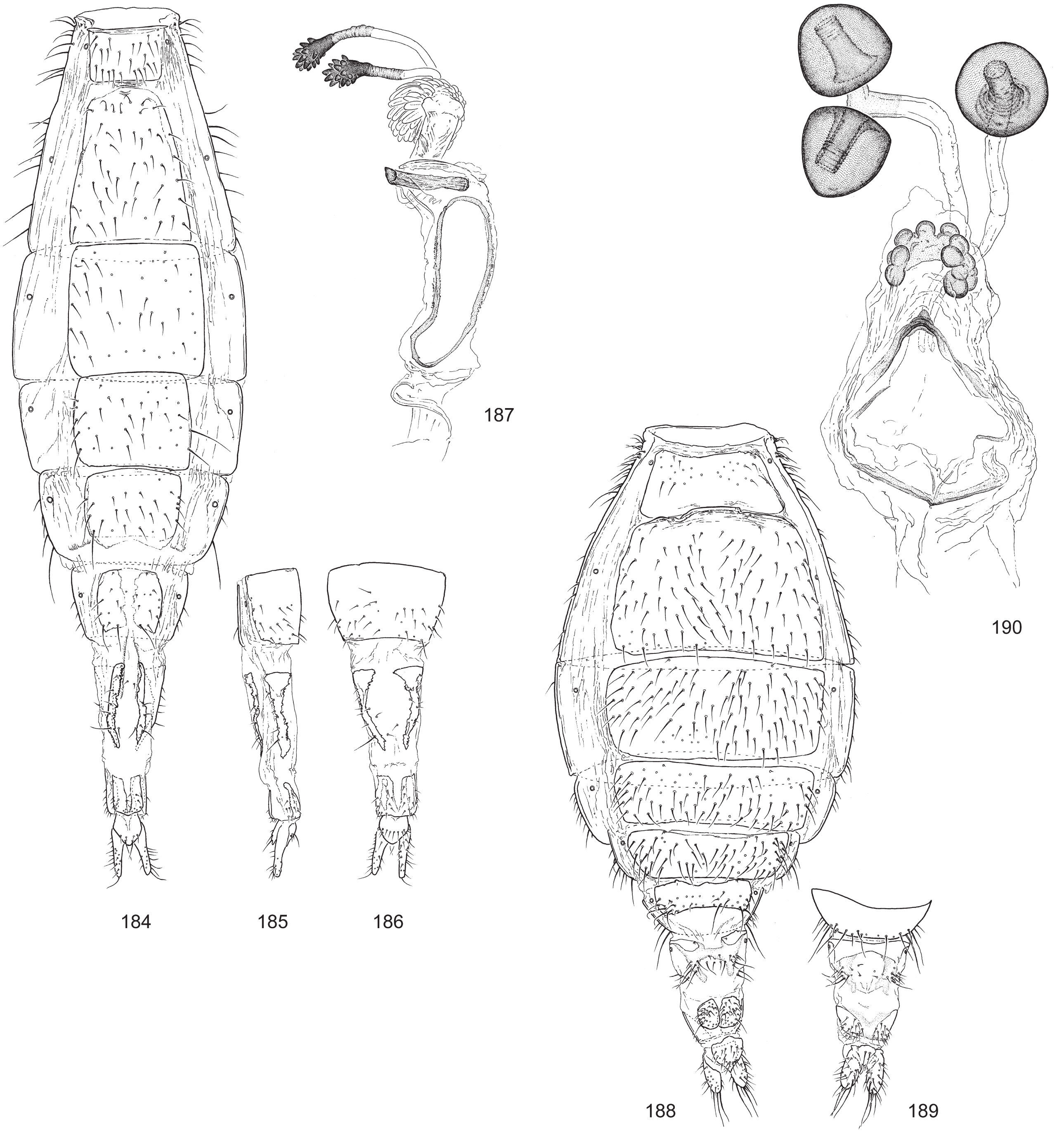
FIGURES 160–168. *Sphyracephala subbifasciata* Fitch (Diopsidae), male abdomen; 160: segment 6 to genitalia, lateral; 161: external genitalia, posterior; 162: same, anterior; 163: sternites 6–8, ventral; 164: ejaculatory apodeme; 165: internal genitalia, ventral; 166: same, left lateral; 167: detail of phallus, ventral; 168: same, left lateral.



FIGURES 169–176. *Diasemopsis aethiopica* (Rondani) (Diopsidae), male abdomen; 169: external genitalia, anterior; 170: terminalia, lateral; 171: sternite 5 and terminalia, ventral; 172: ejaculatory apodeme; 173: internal genitalia, ventral; 174: same, left lateral; 175: detail of phallus, ventral; 176: same, left lateral.

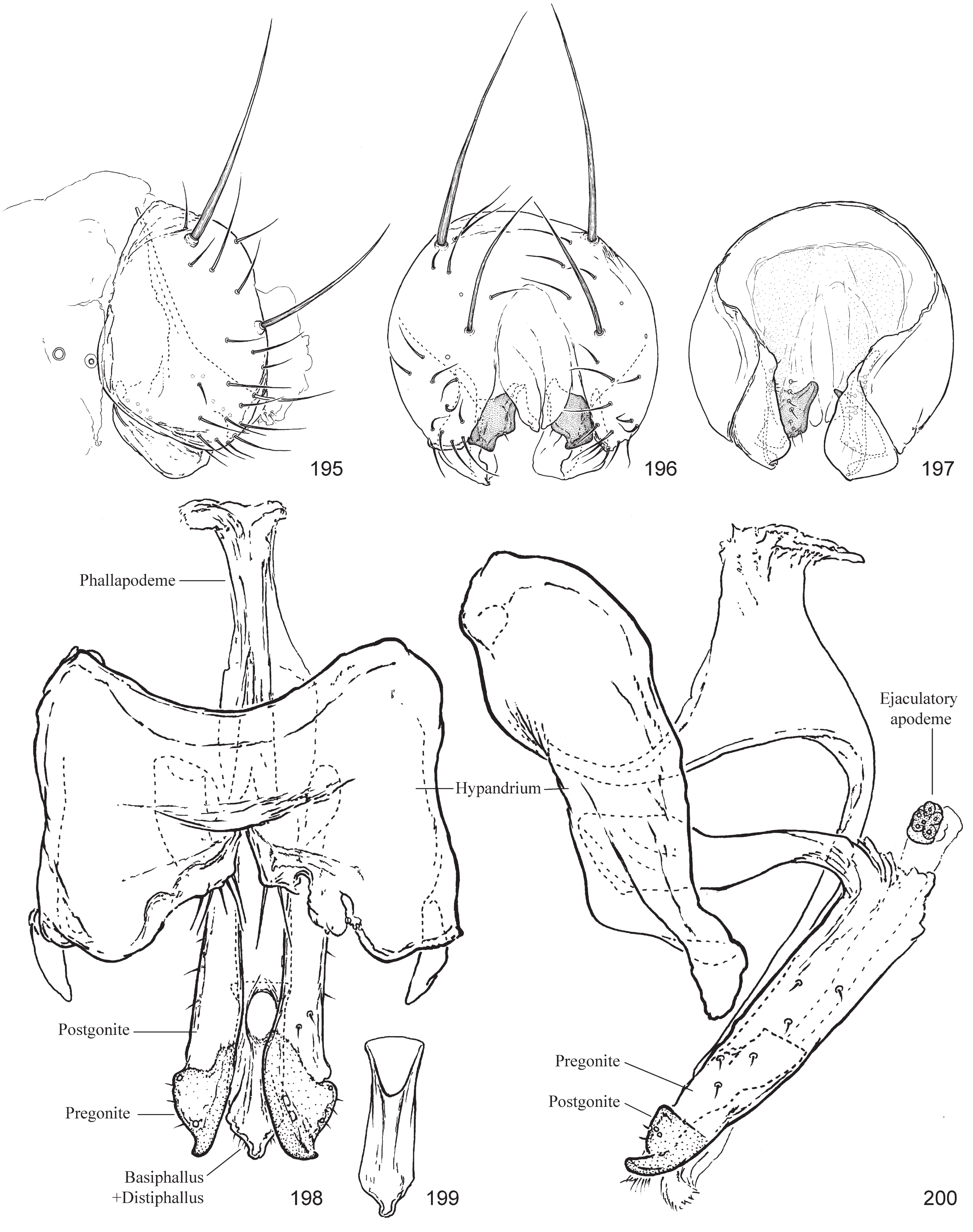


FIGURES 177–183. Fig. 177: *Centrioncus* sp. (Diopsidae), sternites 1–2. Figs 178–179: *Centrioncus* sp., female abdomen; 178: ventral; 179: segment 6 to cerci, dorsal. Figs 180–181: *Centrioncus* sp., female segment 7 to cerci; 180: dorsal; 181: ventral. Figs 182–183: female internal genitalia; 182: *Centrioncus* sp.; 183: *Centrioncus* sp.

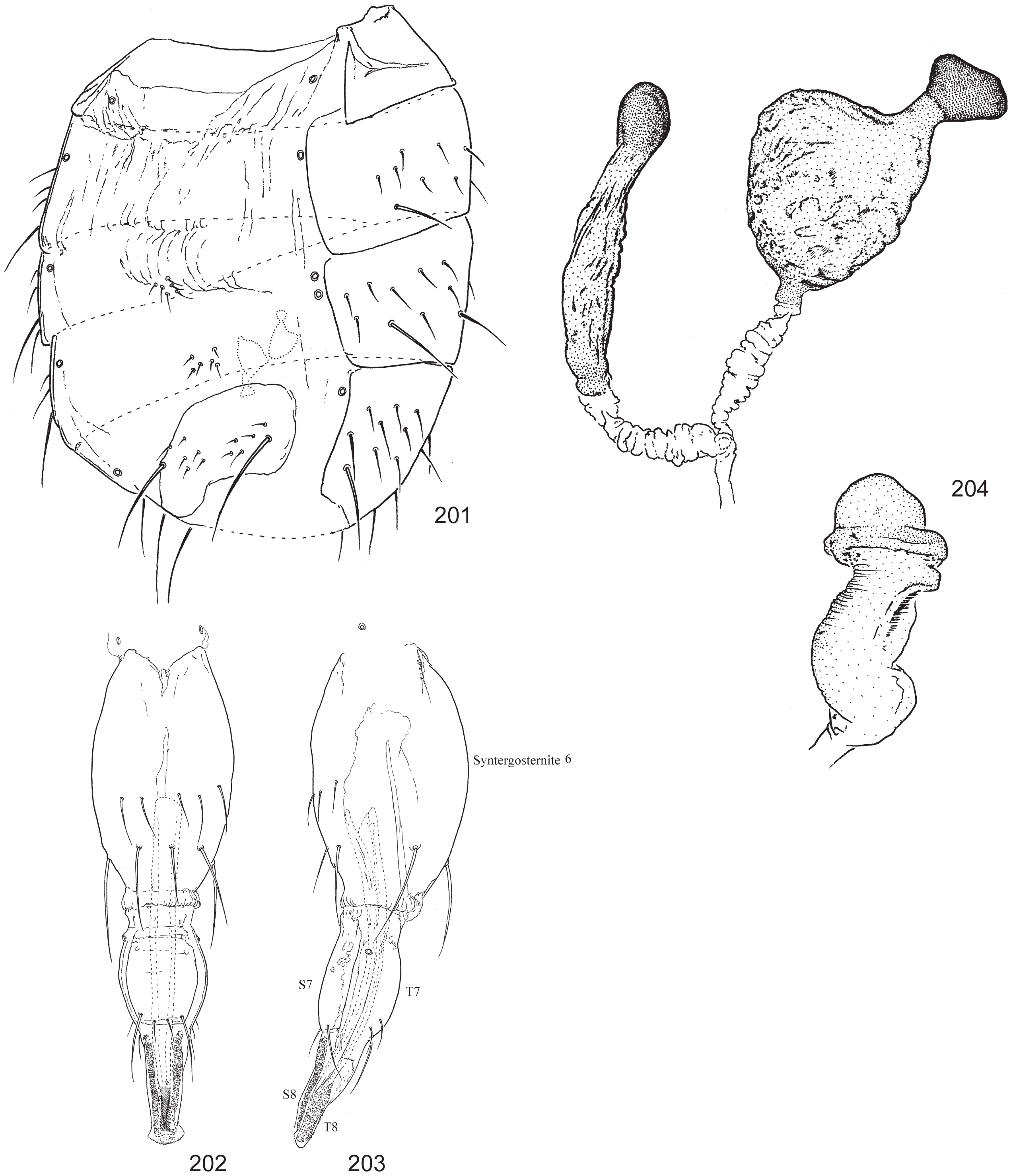


FIGURES 184–190. Figs 184–187: *Diasemopsis aethiopica* (Rondani) (Diopsidae), female abdomen; 184: ventral; 185: segment 6 to cerci, lateral; 186: same, dorsal; 187: internal genitalia. Figs 188–190: *Sphyracephala subbifasciata* Fitch (Diopsidae), female abdomen; 188: ventral; 189: segment 6 to cerci, dorsal; 190: internal genitalia.

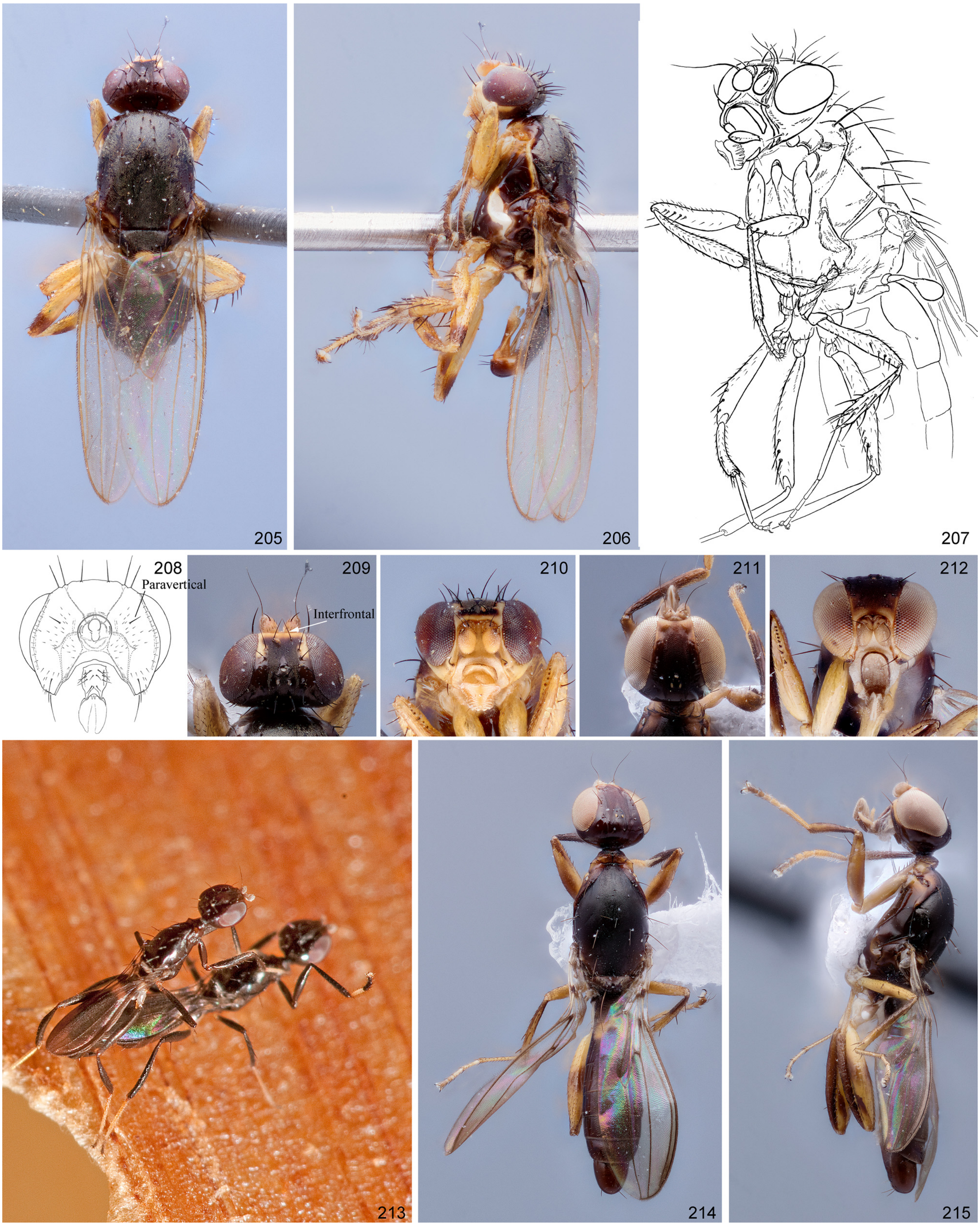
FIGURES 191–194. *Fergusonina* spp. (Fergusoninidae); 191: male dorsal; 192: male lateral; 193: head, anterolateral; 194: female lateral.



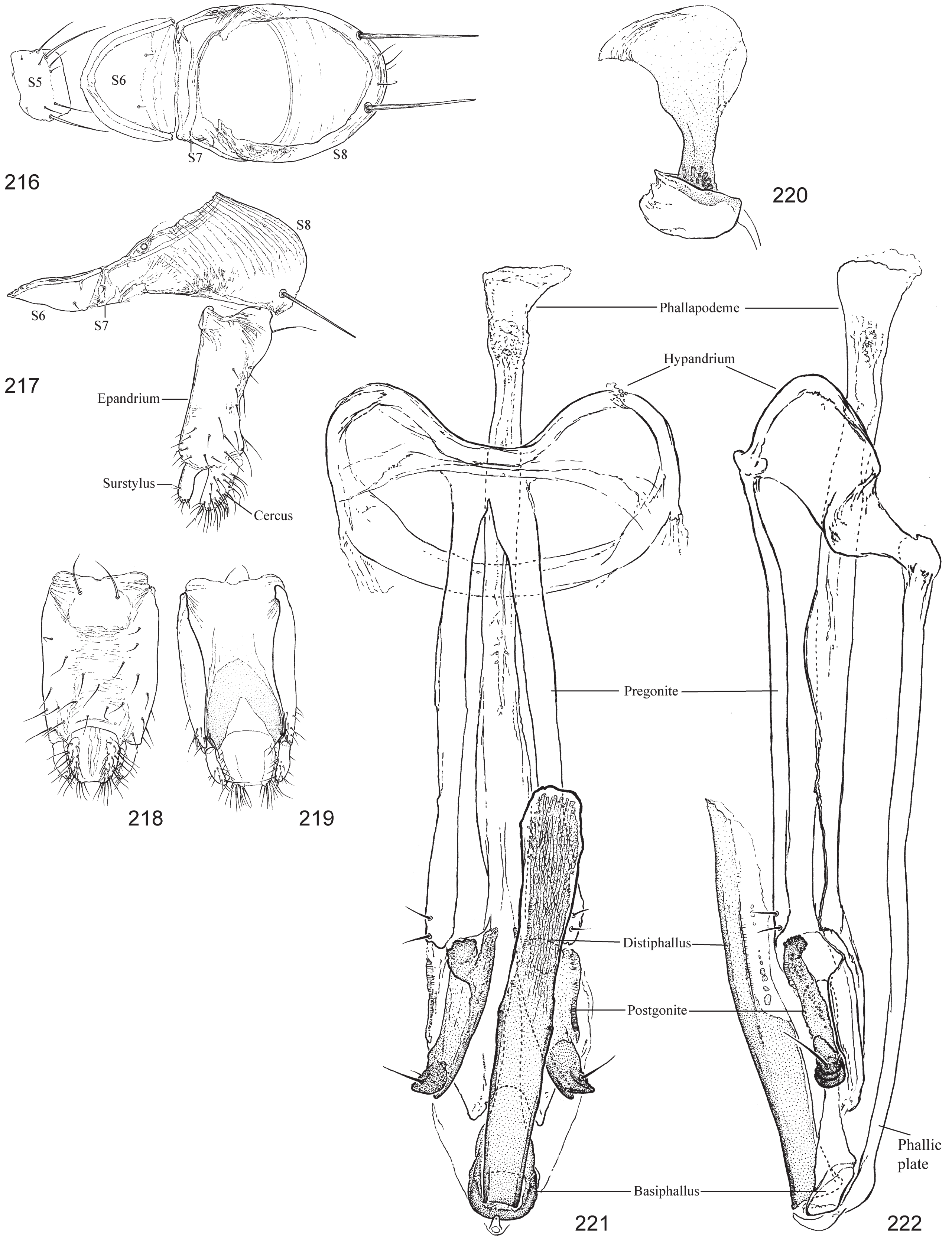
FIGURES 195–200. *Fergusonina* sp. (Fergusoninidae), male terminalia; 195: left lateral; 196: external genitalia, posterior; 197: same, anterior; 198: internal genitalia, ventral; 199: detail of phallus; 200: internal genitalia, left lateral.



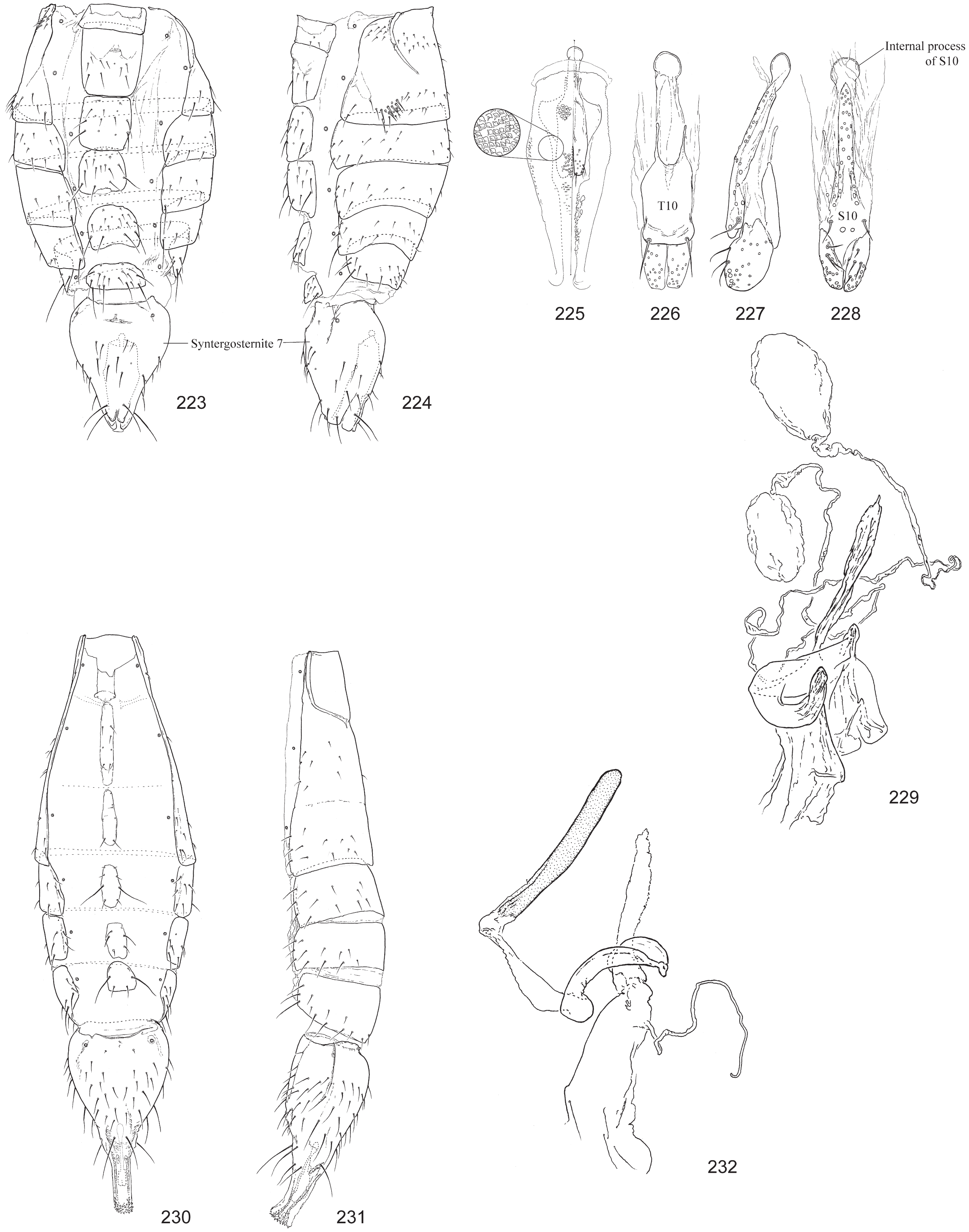
FIGURES 201–204. *Fergusonina* sp. (Fergusoninidae), female; 201: segments 1–5, ventral; 202: segments 6–cerci, ventral; 203: same, lateral; 204: internal genitalia.



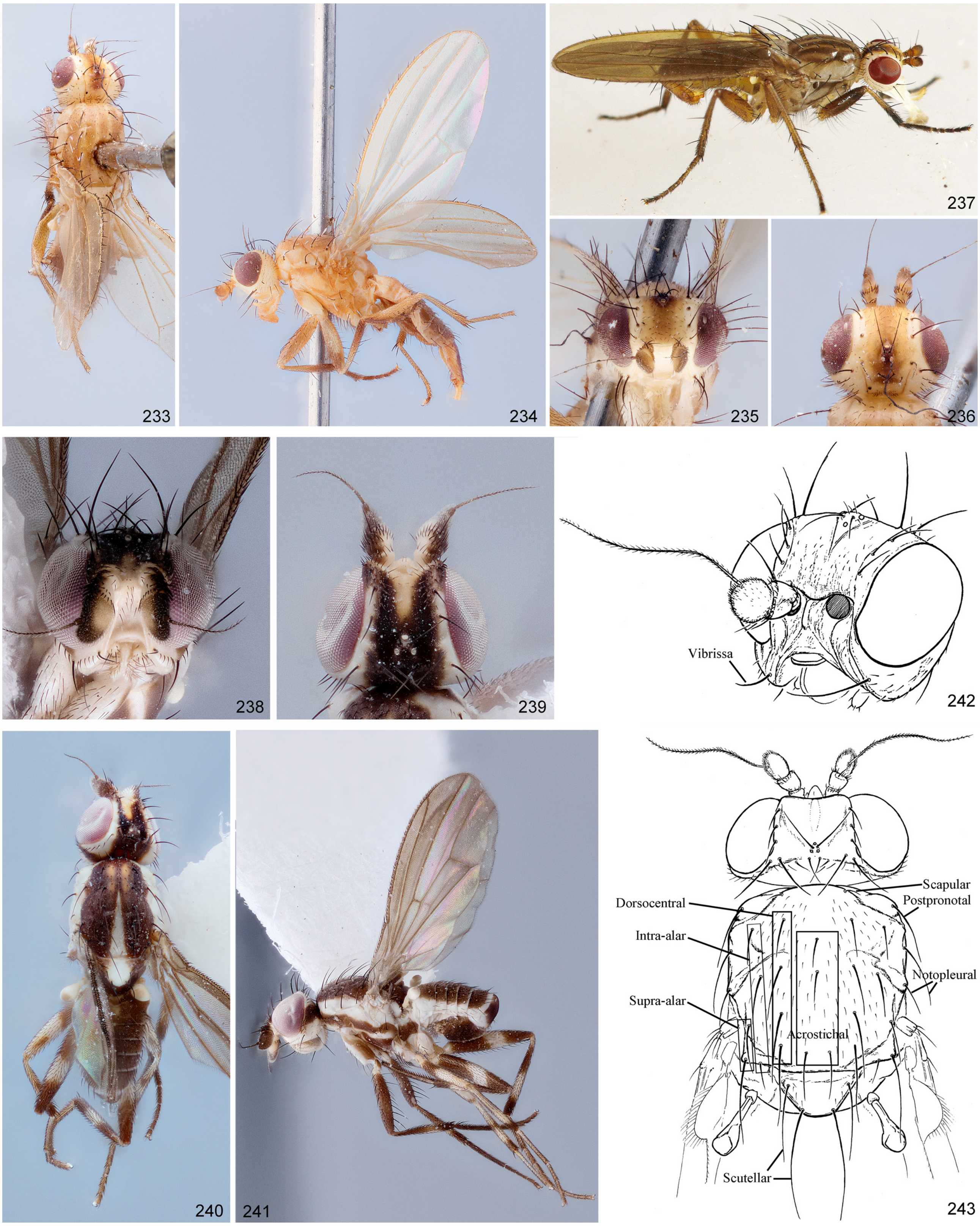
FIGURES 205–215. *Cypselosoma gephyrae* Hendel (Cypselosomatidae), male; 205: dorsal; 206: lateral; 207: ventrolateral; 208: head, posterior; 209: head, dorsal; 210: head, anterior. Figs 211–212: *Formicosepsis biseta* (Papp) (Cypselosomatidae), male head; 211: dorsal; 212: anterior. Fig. 213: *Formicosepsis* sp., male and female copulating, Philippines. Figs 214–215: *F. biseta*, male: 214: dorsal; 215: lateral.



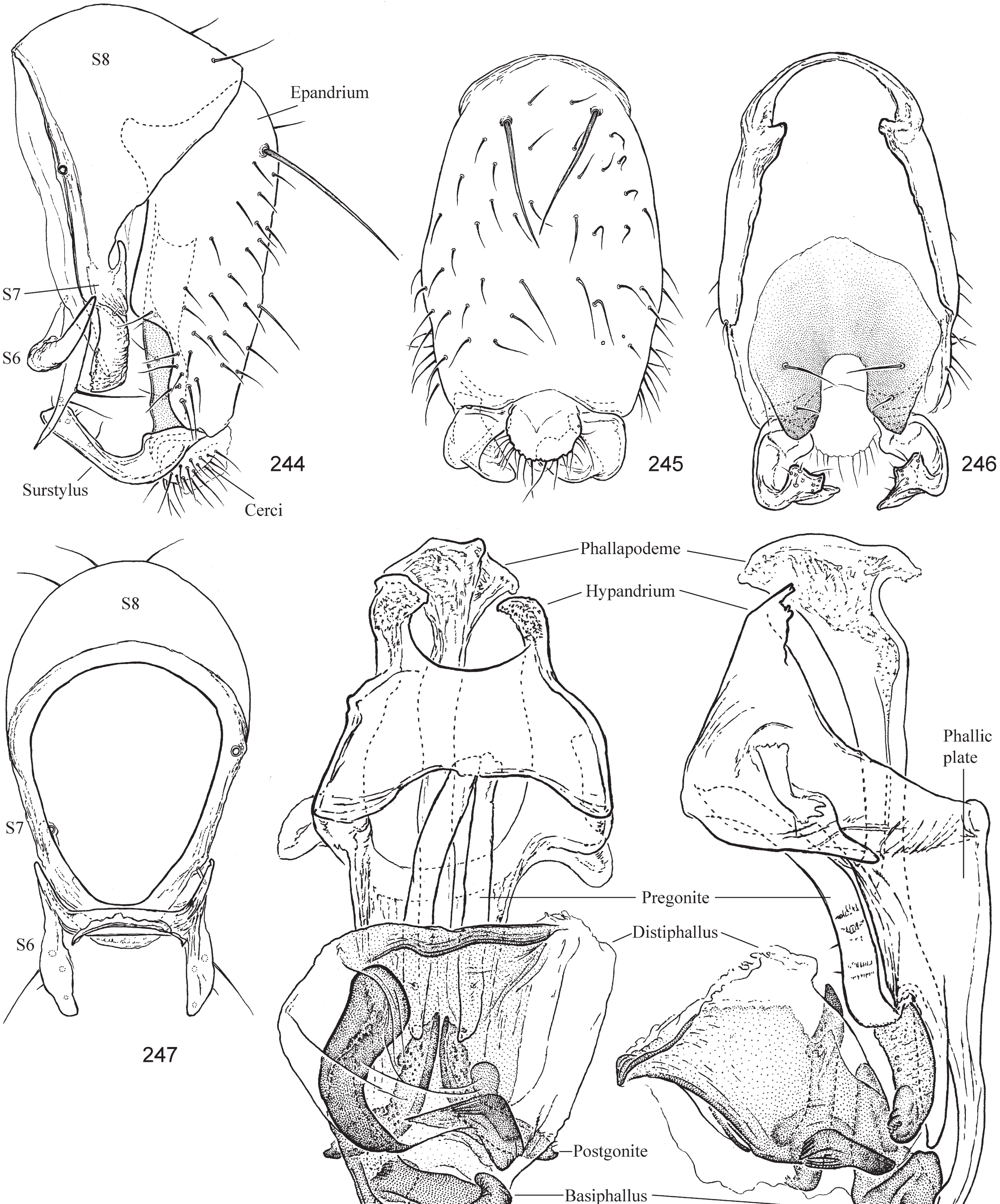
FIGURES 216–222. *Clisa australis* (McAlpine) (Cypselosomatidae), male terminalia; 216: sternites 6–8, ventral; 217: sternite 6 and segment 7 to cerci, lateral; 218: external genitalia, posterior; 219: same, anterior; 220: ejaculatory apodeme; 221: internal genitalia, ventral; 222: same, left lateral.



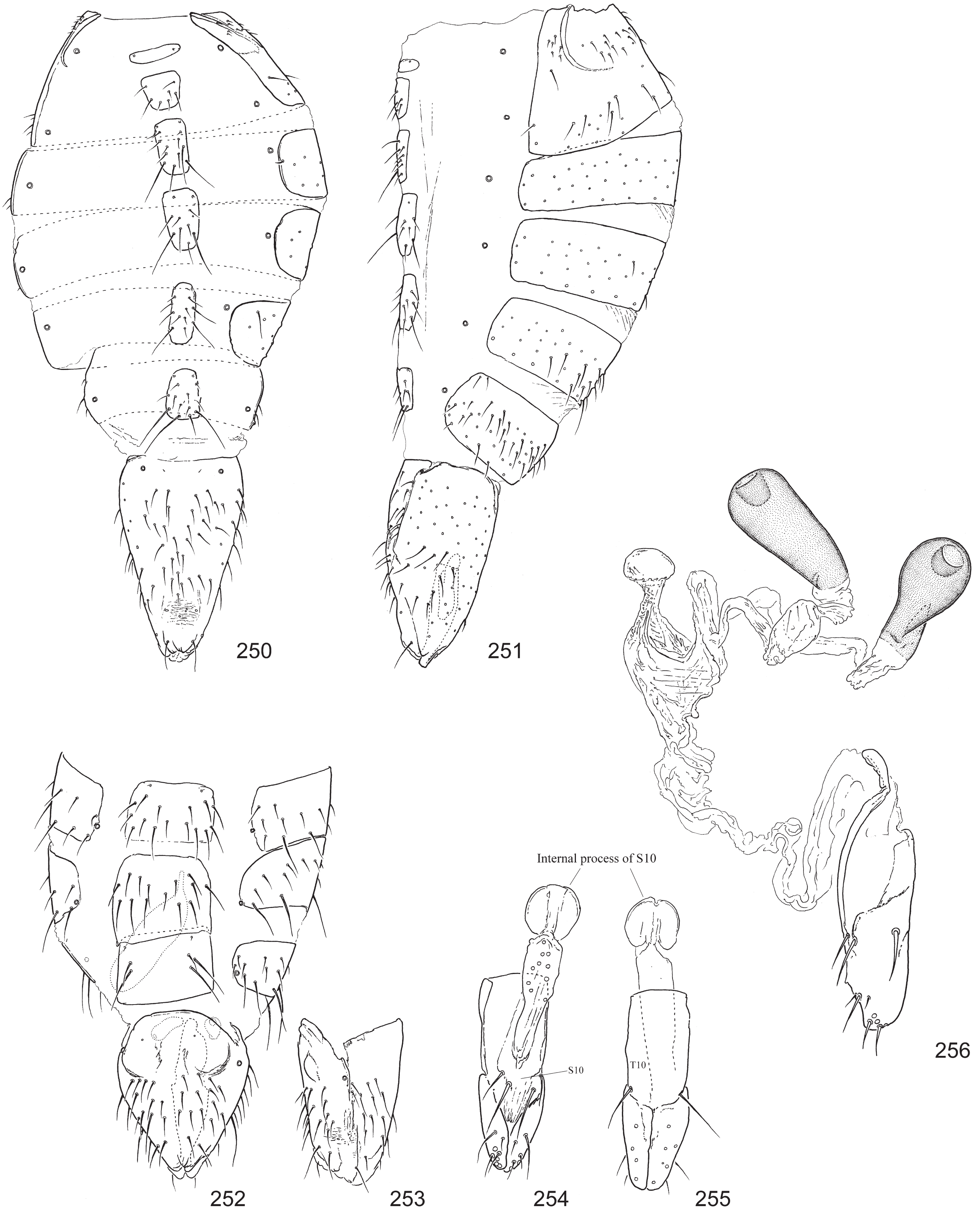
FIGURES 223–232. *Cypselosoma gephyrae* Hendel (Cypselosomatidae), female abdomen; 223: ventral (terminalia retracted); 224: lateral; 225: detail of retracted terminalia; 226: segment 10 and cerci, dorsal; 227: same, lateral; 228: same, ventral; 229: internal genitalia. Figs 230–232: *Formicosepsis* sp., female abdomen; 230: ventral (terminalia retracted); 231: same, lateral; 232: internal genitalia.



FIGURES 233–243. Figs 233–237: *Heloclusia imperfecta* Malloch (Pseudopomyzidae); 233: female dorsal; 234: same, lateral; 235: head anterior; 236: head dorsal; 237: male, Chile. Figs 238–241: *Latheticomyia* sp. (Pseudopomyzidae), male; 238: head, anterior; 239: head, dorsal; 240: dorsal; 241: lateral. Fig. 242: *Pseudopomyza atrimana* (Meigen) (Pseudopomyzidae), head anterior. Fig. 243: *Pseudopomyza* (*Rhinopomyzella*) sp., dorsal.

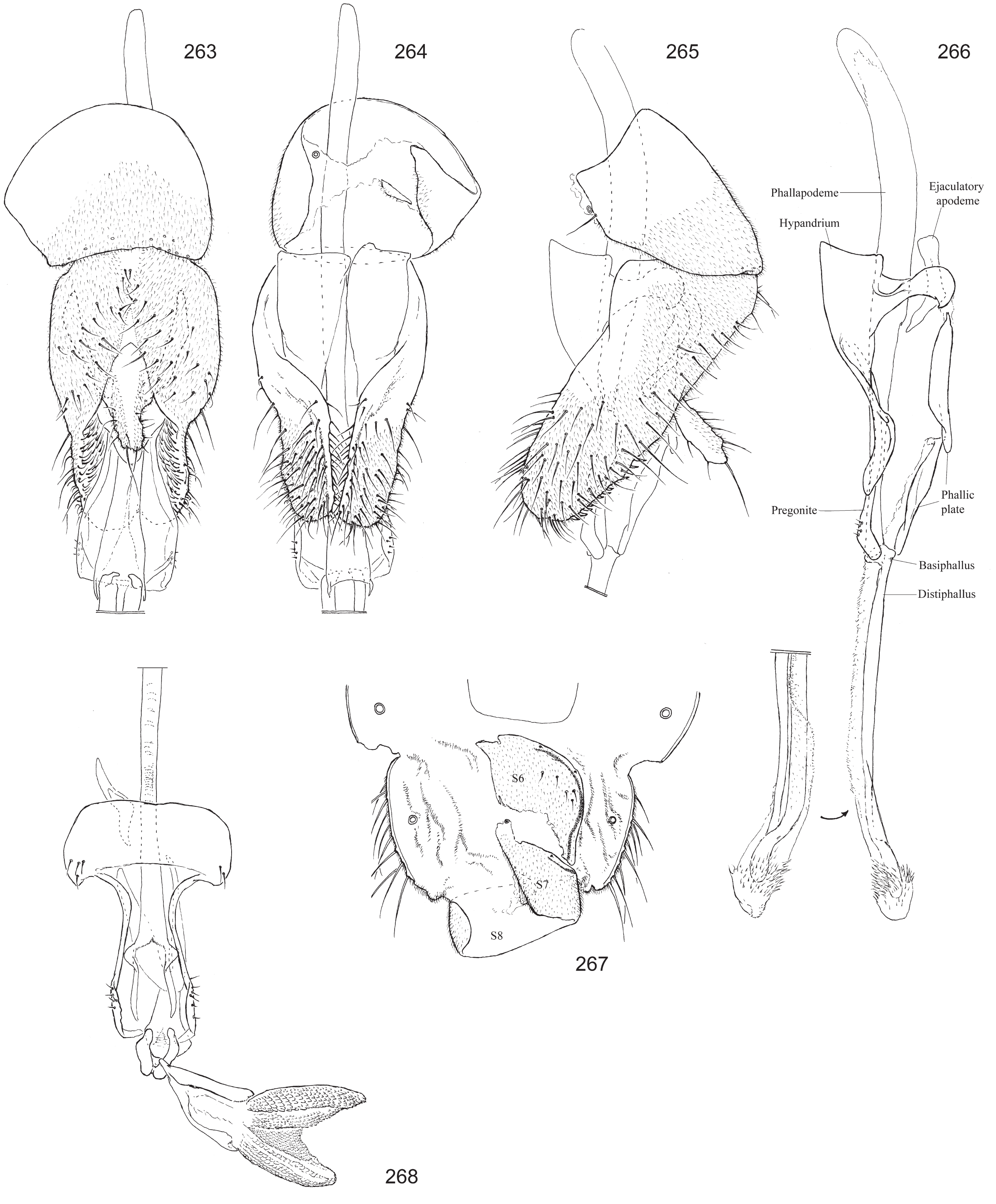


FIGURES 244–249. *Pseudopomyza atrimana* (Meigen) (Pseudopomyzidae), male terminalia; 244: lateral; 245: external genitalia, posterior; 246: same, anterior; 247: sternites 6–8, ventral; 248: internal genitalia, ventral; 249: same, left lateral.

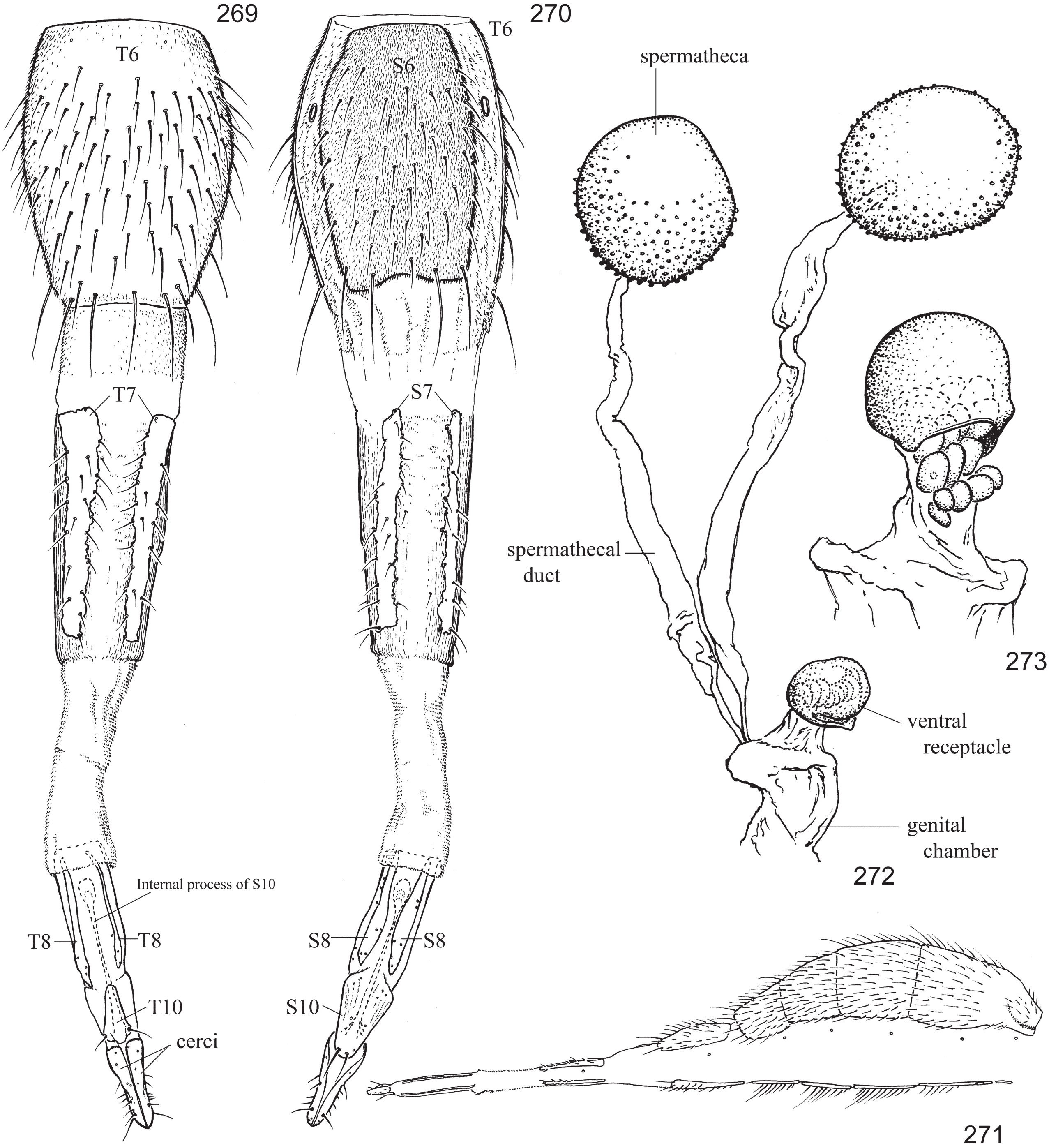


FIGURES 250–256. Figs 250–251: *Latheticomyia* sp. (Pseudopomyzidae), female abdomen; 250: ventral; 251: lateral. Figs 252–256: *Pseudopomyza atrimana* (Meigen) (Pseudopomyzidae), female abdomen; 252: segments 4 to cerci (terminalia retracted), ventral; 253: segment 7, lateral; 254: segment 10 and cerci, ventral; 255: same, dorsal; 256: internal genitalia.

FIGURES 257–262. Figs 257–260: *Neotanypeza claripennis* Schiner (Tanypezidae), female; 257: dorsal; 258: lateral; 259: head, anterior; 260: head, dorsal. Fig. 261: *Neotanypeza* sp., female, Peru. Fig. 262: *Nartshukia musiva* Shatalkin (Strongylophthalmyiidae), female holotype.



FIGURES 263–268. Figs 263–267: *Tanypeza longimana* Fallén (Tanypezidae), male abdomen; 263: terminalia, posterior; 264: same, anterior; 265: same, lateral; 266: internal genitalia, with rotated view of phallus apex inset; 267: apex of segment 5 to sternite 8, ventral. Fig. 268: *Neotanypeza rutila* (Wulp) (Tanypezidae), male internal genitalia, ventral.



FIGURES 269–273. Figs 269–272: *Neotanypeza elegans* (Wiedemann) (Tanypezidae), female abdomen; 269: segment 6 to cerci, dorsal; 270: same, ventral; 271: abdomen, lateral; 272: internal genitalia. Fig. 273: *Tanypeza longimana* Fallén (Tanypezidae), ventral receptacle.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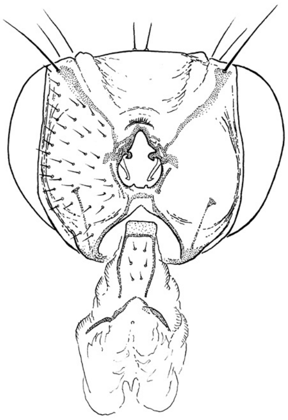
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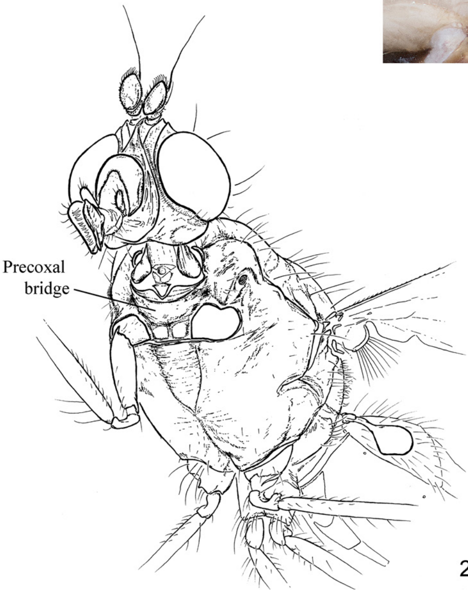

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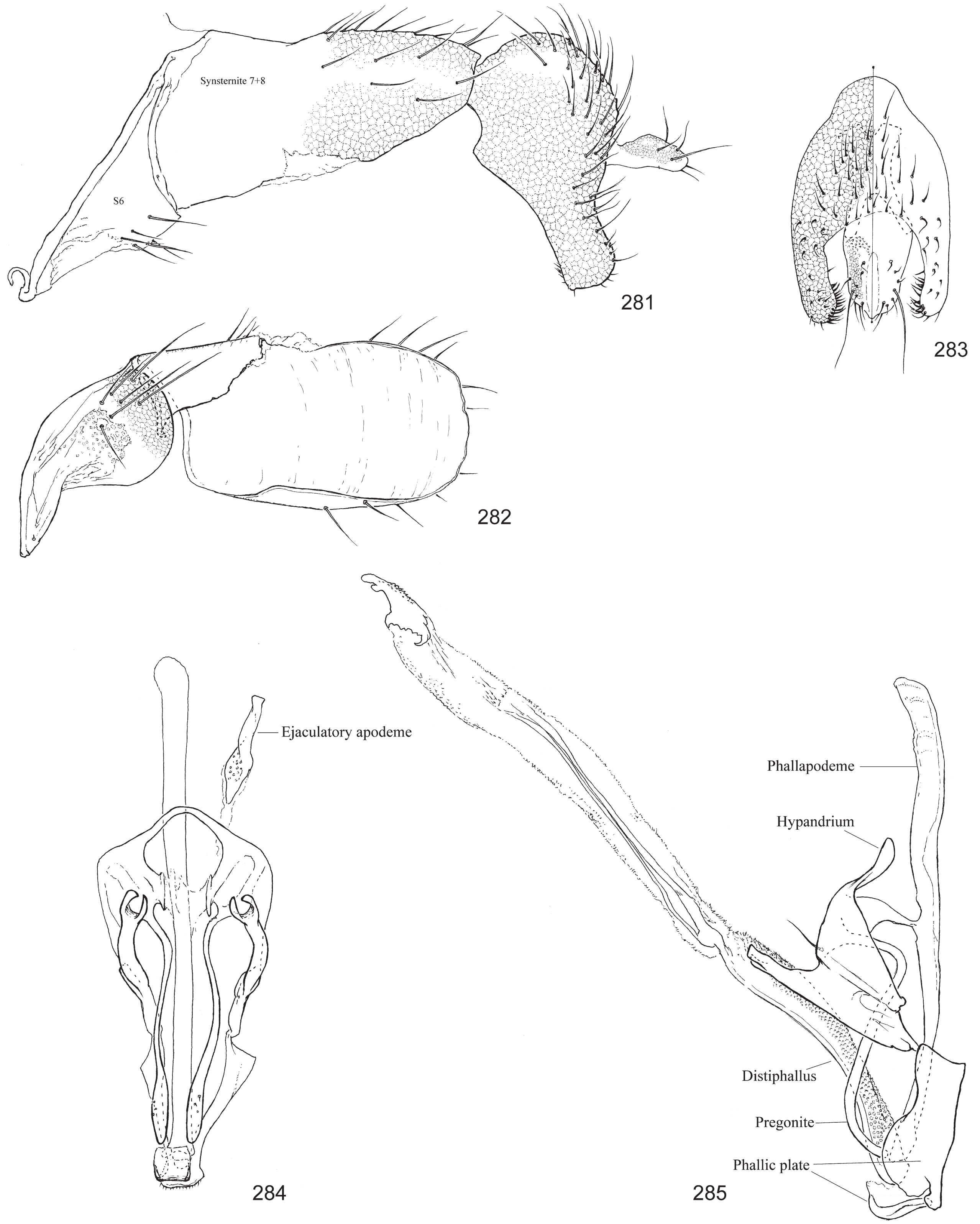
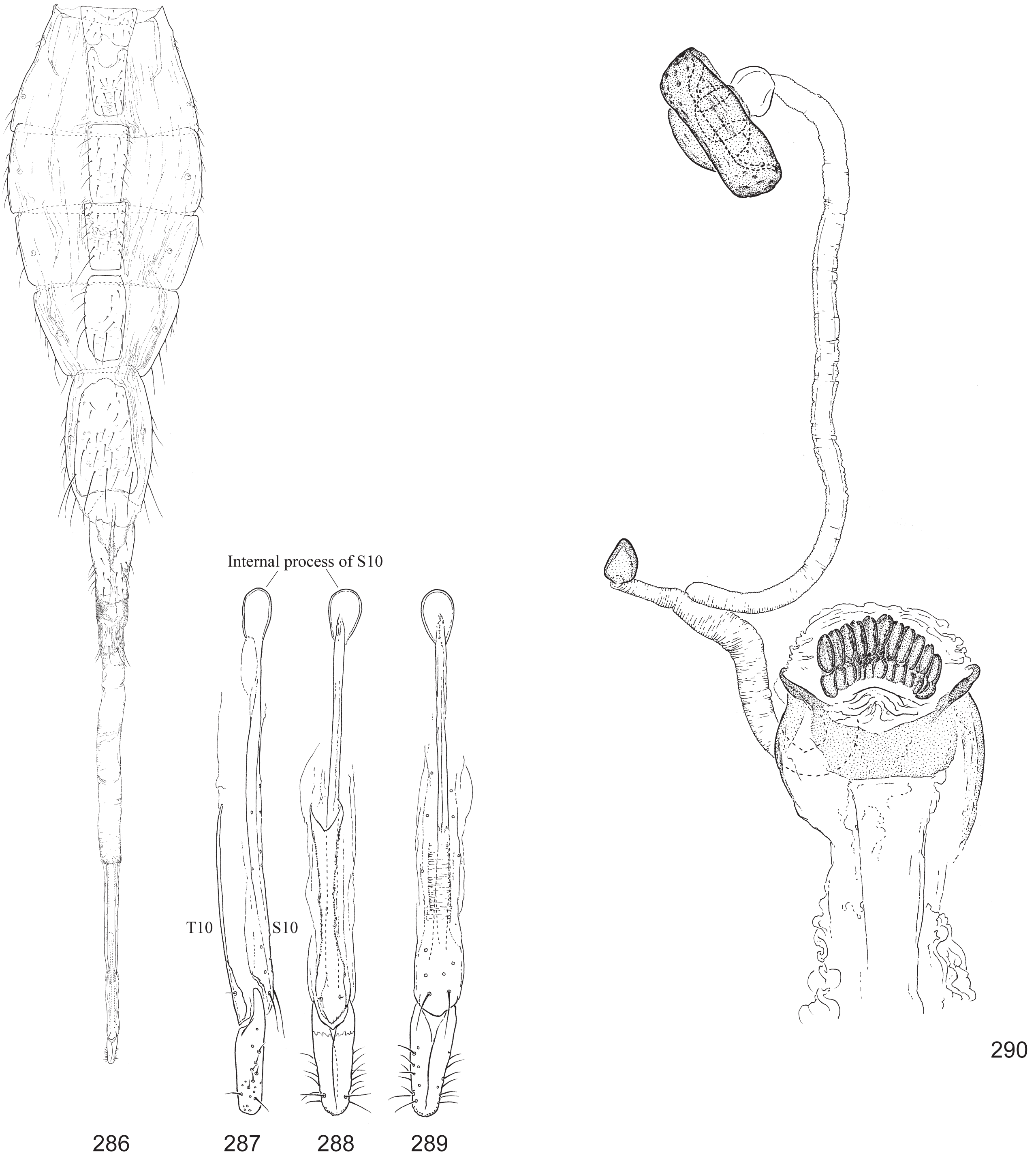
FIGURES 274–280. Figs 274–278: *Strongylophthalmyia angustipennis* Melander (Strongylophthalmyiidae), male; 274: dorsal; 275: lateral; 276: head anterior; 277: head, dorsal; 278: head, posterior. Fig. 279: *Strongylophthalmyia* sp., anteroventral. Fig. 280: *Strongylophthalmyia* sp., Vietnam.



FIGURES 281–285. *Strongylophthalmyia angustipennis* Melander (Strongylophthalmyiidae), male terminalia; 281: lateral; 282: sternites 6–8, ventral; 283: external genitalia, posterior; 284: internal genitalia (phallus removed), ventral; 285: internal genitalia, left lateral.



FIGURES 286–290. *Strongylophthalmyia angustipennis* Melander (Strongylophthalmyiidae), female abdomen; 286: ventral; 287: segment 10 and cerci, lateral; 288: same, dorsal; 289: same, ventral; 290: internal genitalia.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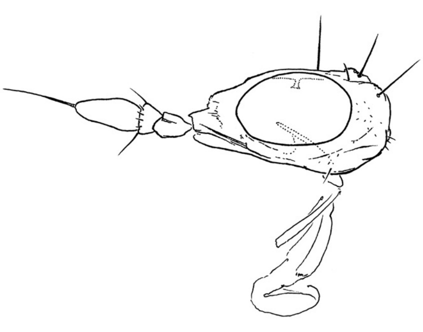
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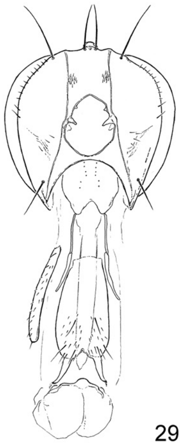
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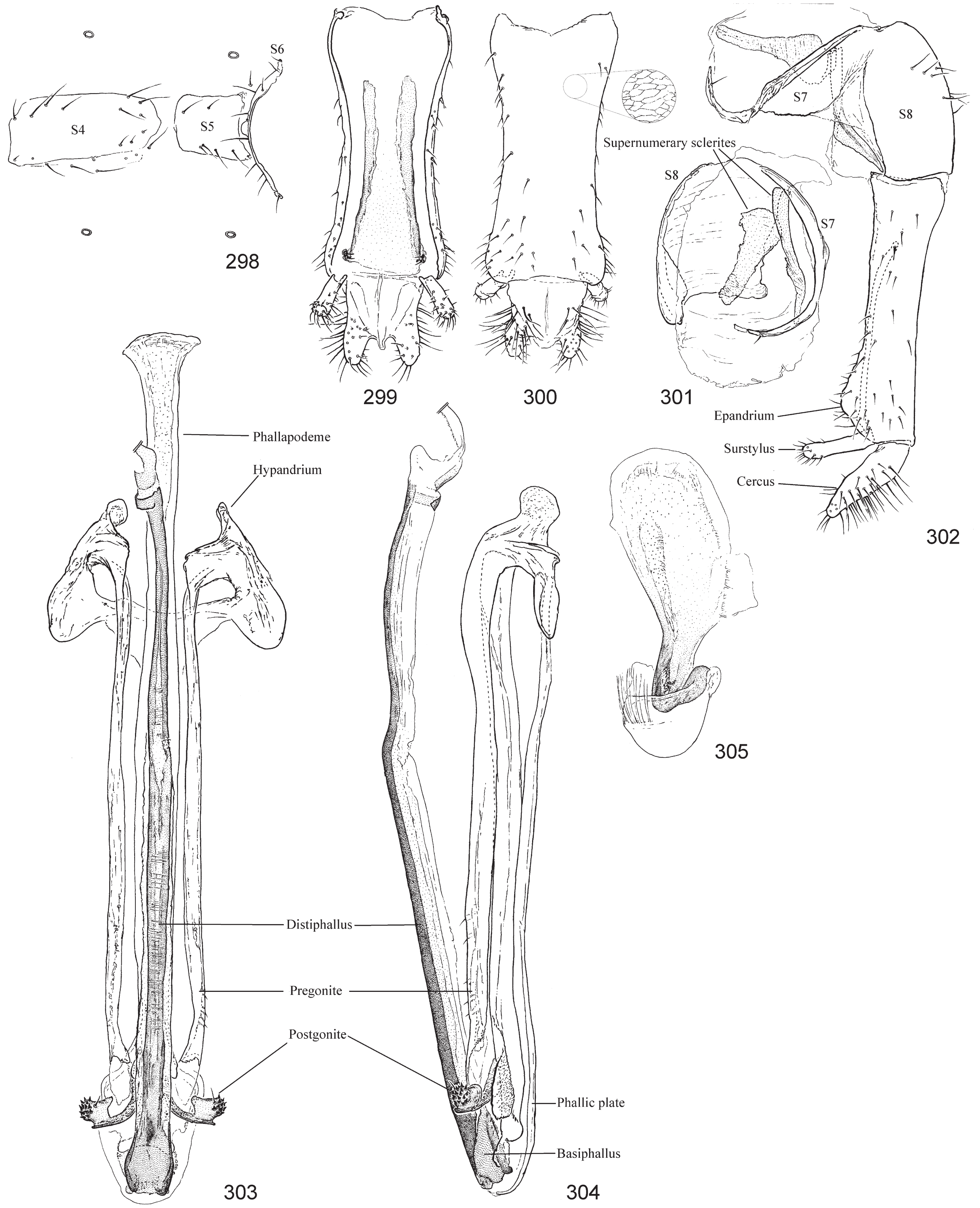
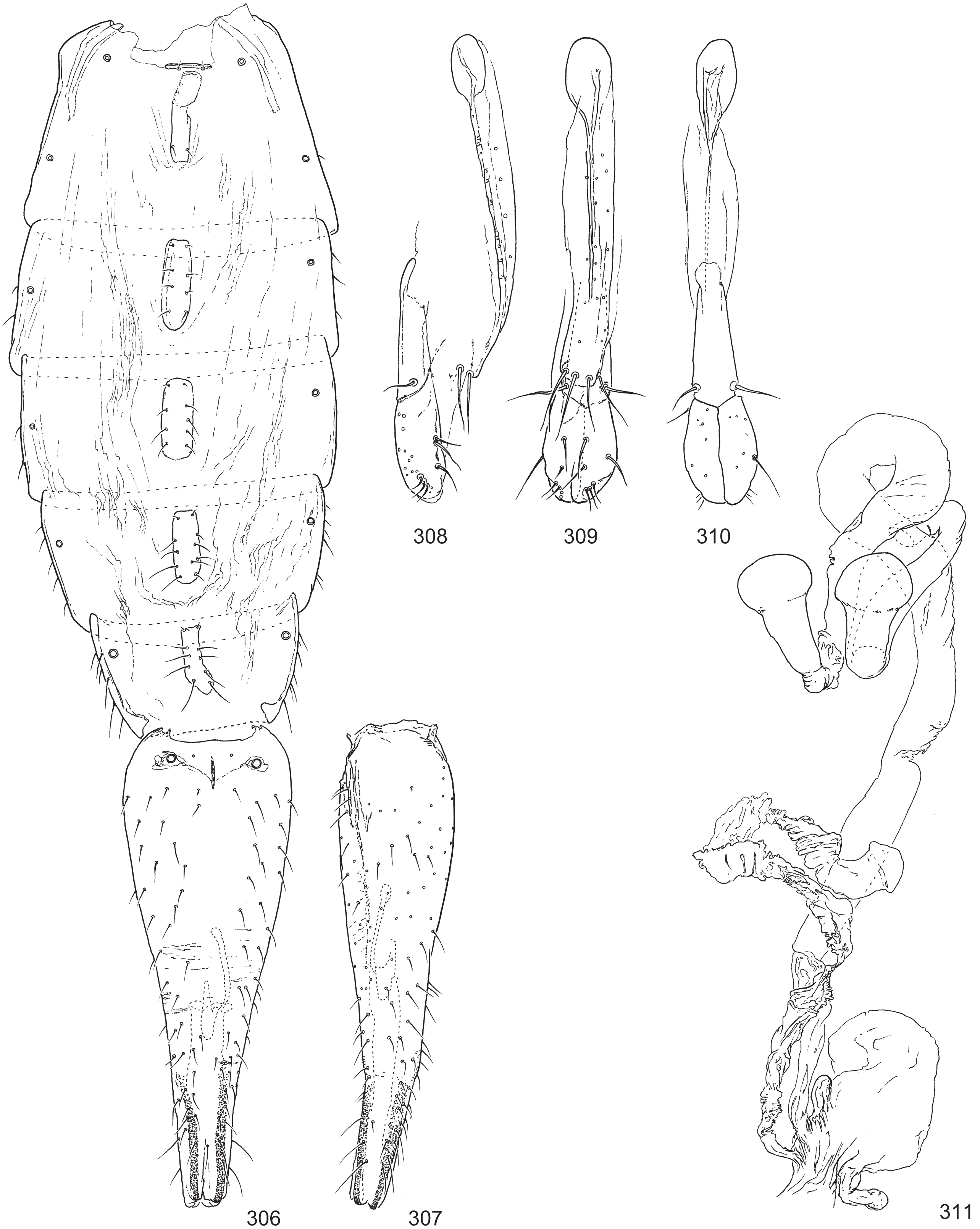
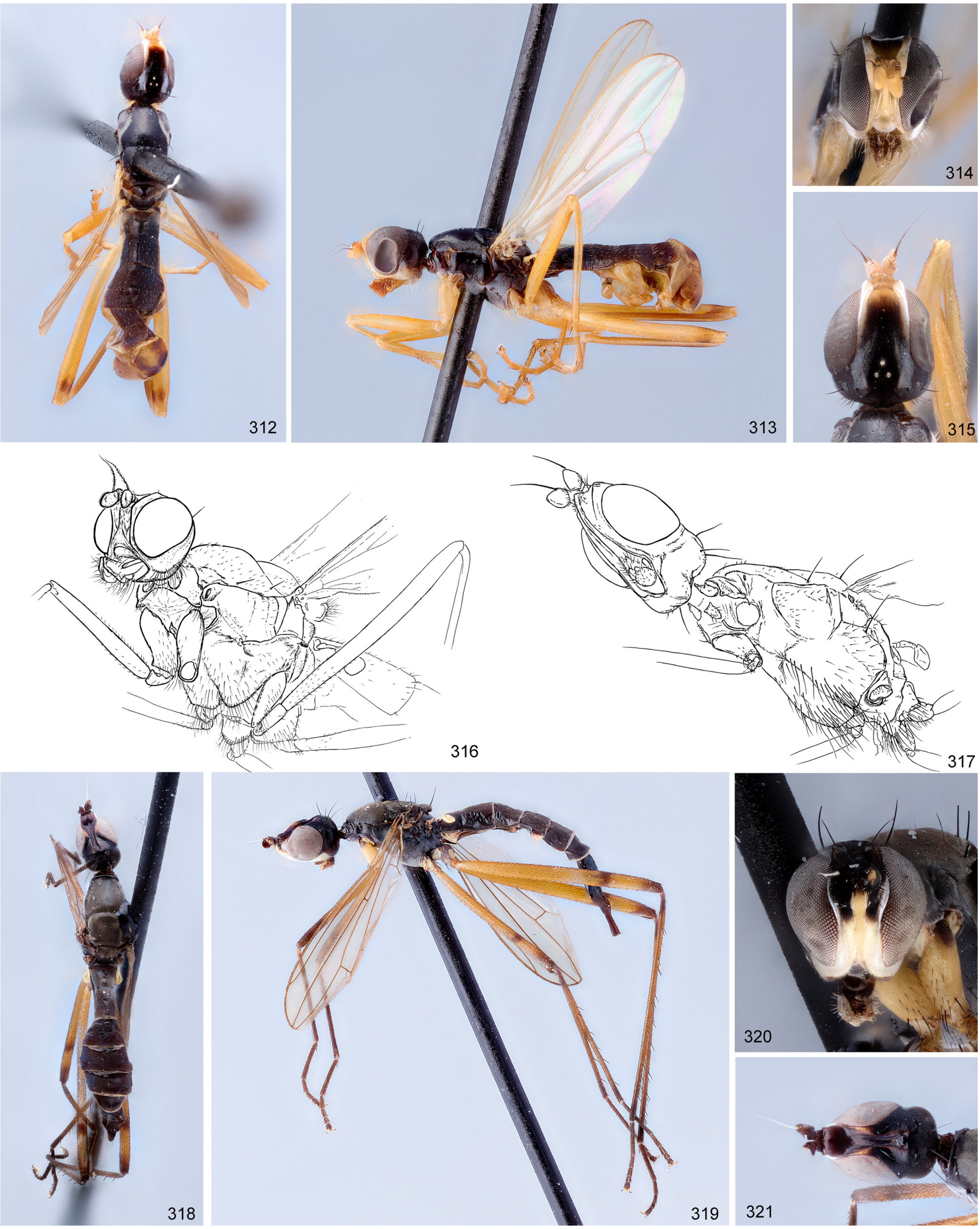
FIGURES 291–297. Figs 291–294: *Odontoloxozus peruanus* Hennig (Neriidae), male; 291: dorsal; 292: lateral; 293: head, dorsal; 294: head, anterior. Fig. 295: cf. *Chaetonerius* sp. (Neriidae), Seram, Indonesia. Figs 296–297: *Telostylinus* sp. (Neriidae); 296: lateral (note process arising from inner surface of orbital plate); 297: posterior.



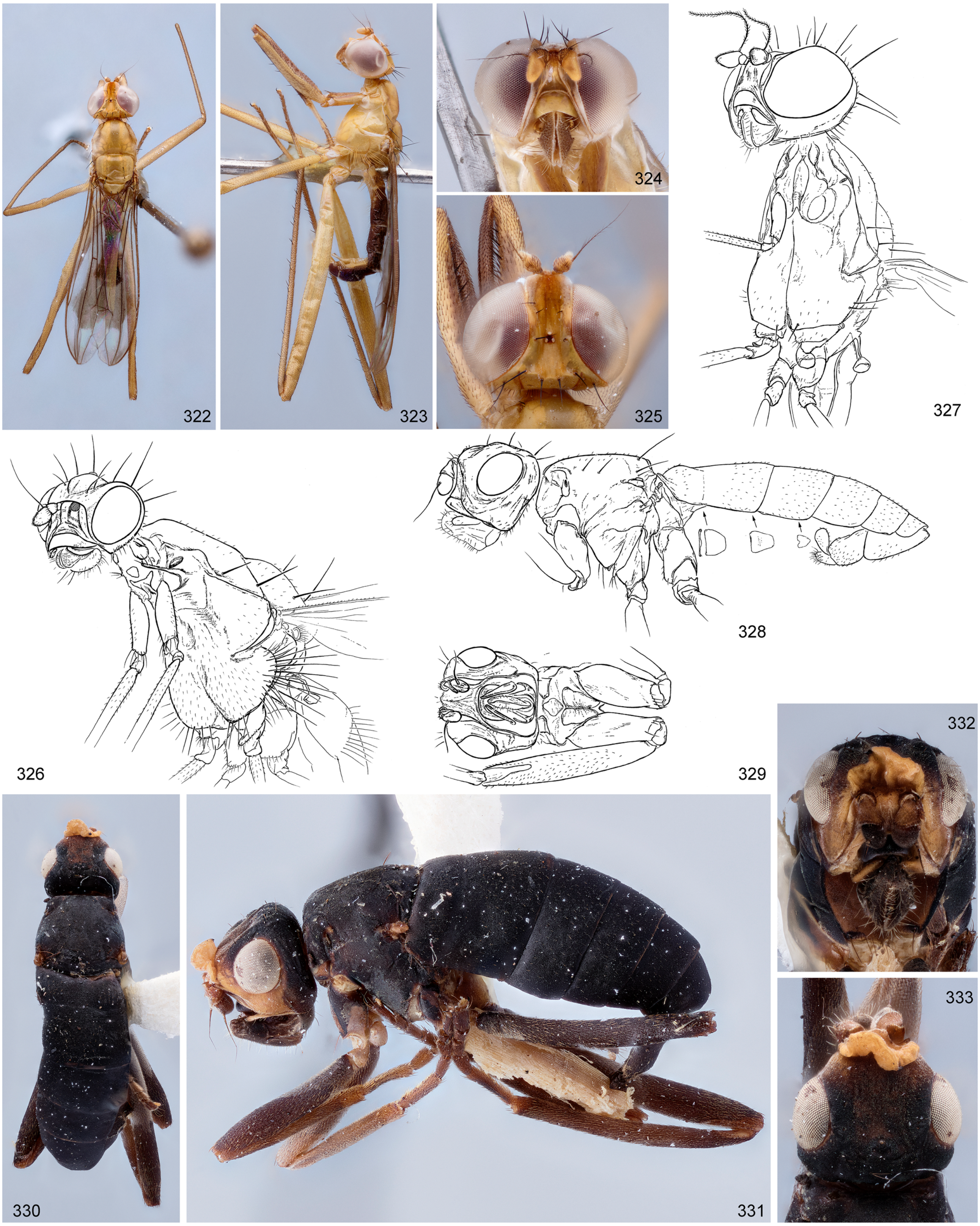
FIGURES 298–305. *Odontoloxozus longicornis* (Coquillett) (Neriidae), male abdomen; 298: sternites 4–6, ventral; 299: external genitalia, anterior; 300: same, posterior (with detail of texture); 301: sternites 7–8, anterior; 302: terminalia, lateral; 303: internal genitalia, ventral; 304: same, left lateral; 305: ejaculatory apodeme.



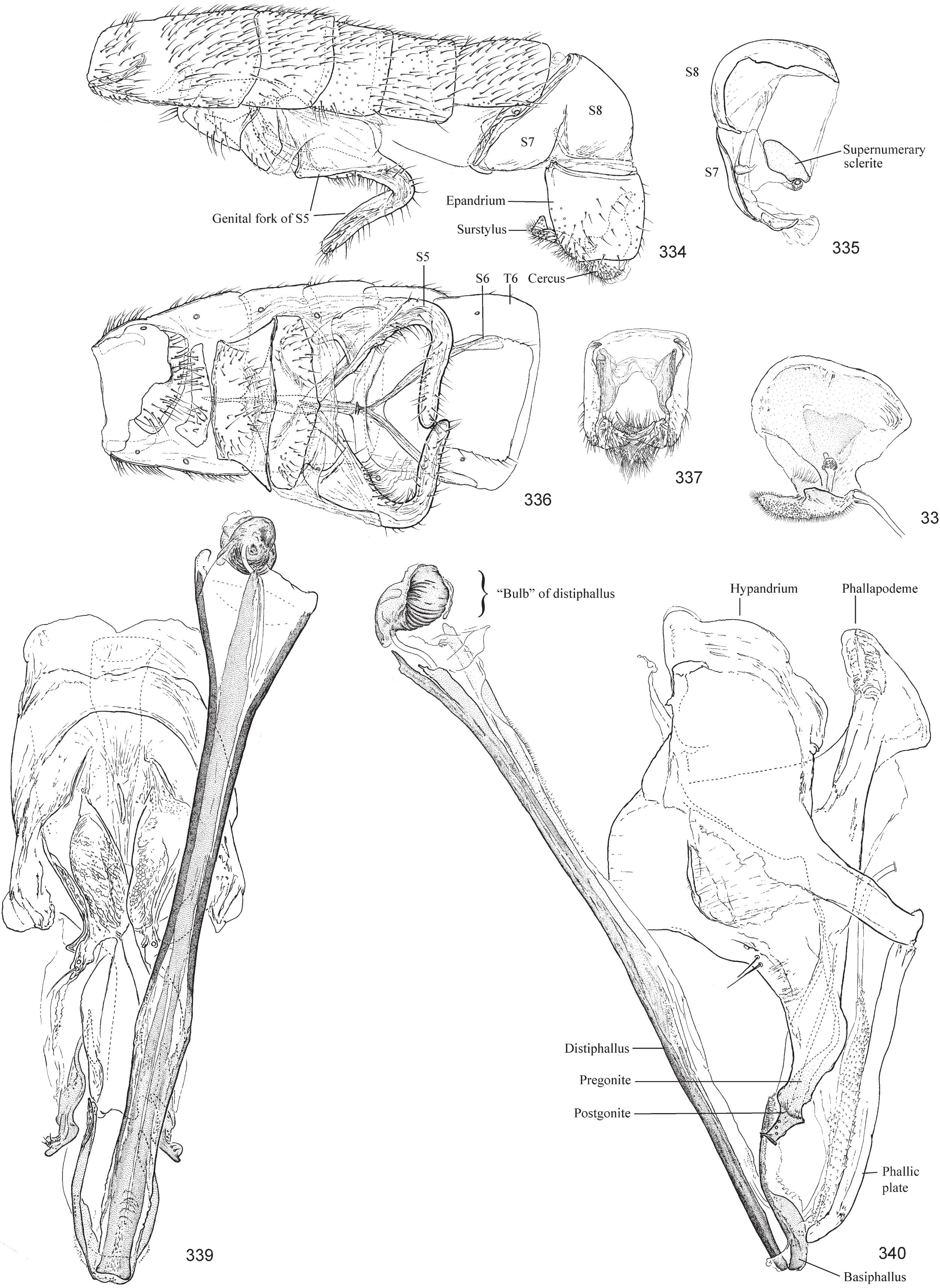
FIGURES 306–311. Figs 306–310: *Telostylinus* sp. (Neriidae), female abdomen; 306: ventral (terminalia retracted); 307: segment 7 to cerci ((terminalia retracted), lateral; 308: segment 10 and cerci, lateral; 309: same, ventral; 310: same, dorsal. Fig. 311: *Odontoloxozus longicornis* (Coquillett) (Neriidae), female internal genitalia.



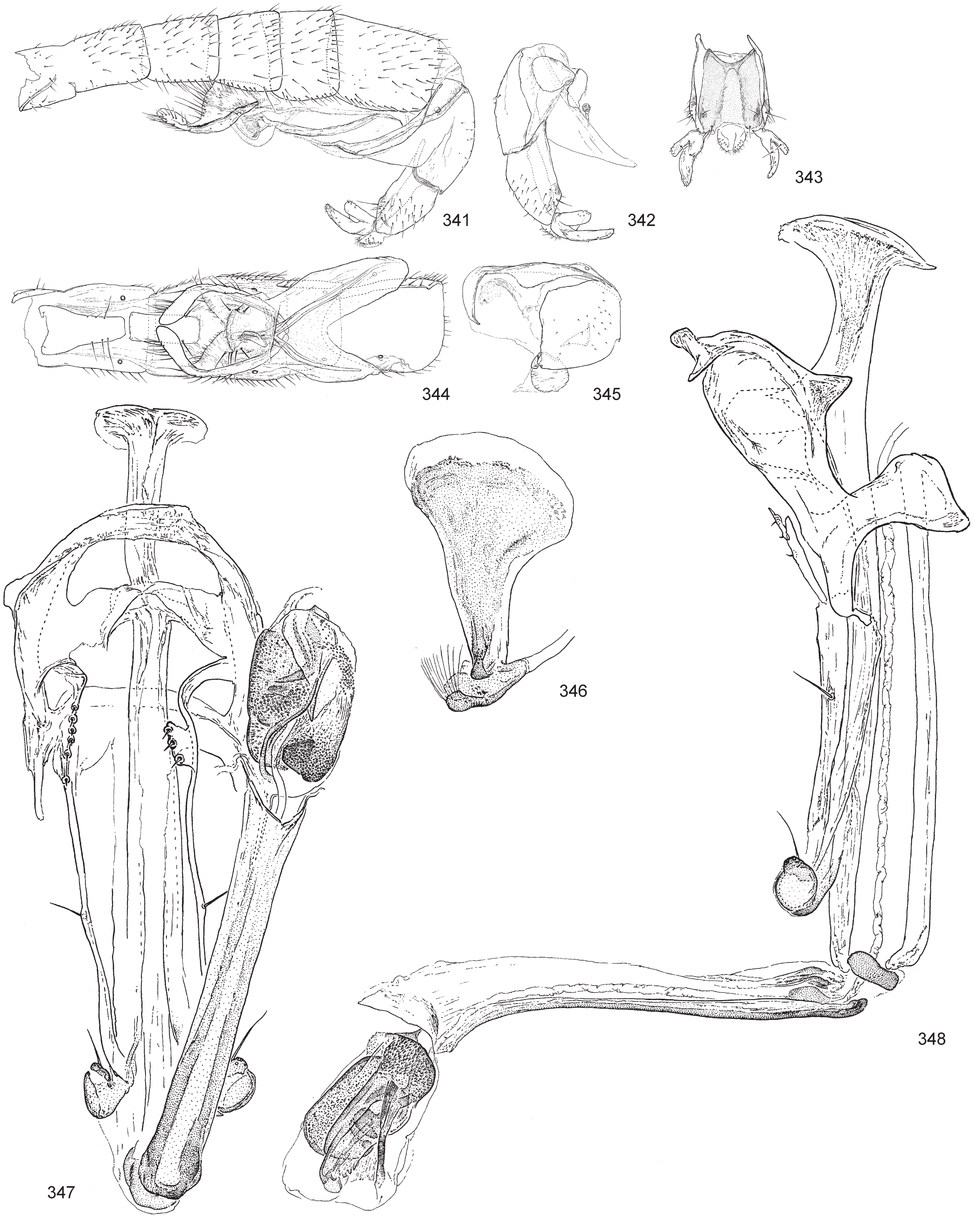
FIGURES 312–321. Figs 312–315: *Calobata pallipes* Say (Micropezidae), male; 312: dorsal; 313: lateral; 314: head anterior; 315: head, dorsal. Fig. 316: *Compsobata mima* (Hennig) (Micropezidae). Fig. 317: *Micropeza lineata* van Duzee (Micropezidae). Figs 318–321: *Micropeza* sp. (Micropezidae), female; 318: dorsal; 319: lateral; 320: head anterior; 321: head dorsal.



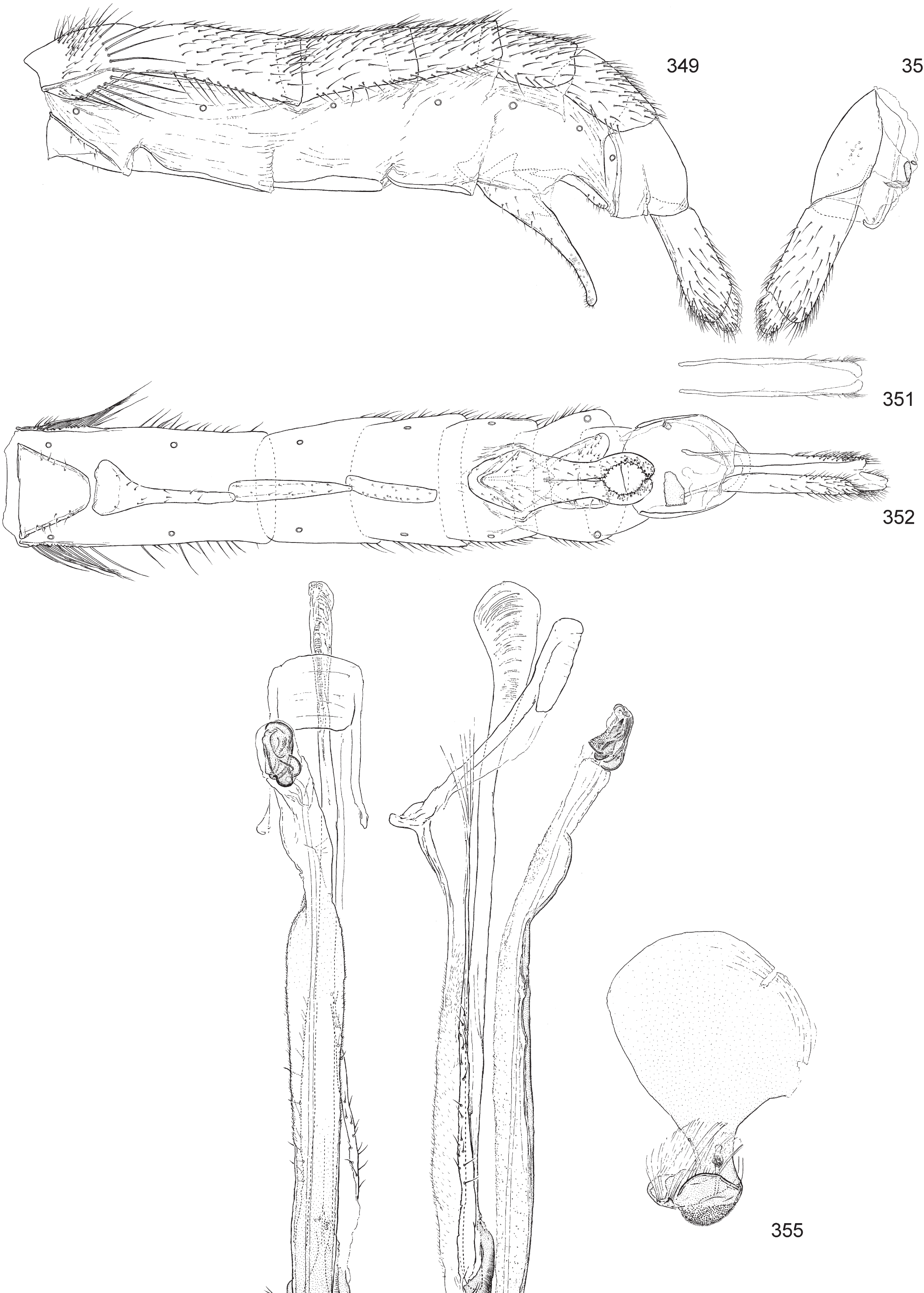
FIGURES 322–333. Figs 322–325: *Grallipeza mellea* Williston (Micropezidae), male; 322: dorsal; 323: lateral; 324: head anterior; 325: head dorsal. Fig. 326: *Raineria* sp. (Micropezidae). Fig. 327: *Metopochetus* sp. (Micropezidae). Figs 328–333: *Calycopteryx mosleyi* Eaton (Micropezidae); 328: male lateral; 329: male ventral; 330: female dorsal; 331: female lateral; 332: head anterior; 333: head dorsal.



FIGURES 334–340. *Cnodacophora nasoni* (Cresson) (Micropezidae), male abdomen; 334: lateral; 335: sternites 7–8, anterior; 336: segments 1–6, ventral; 337: external genitalia, anterior; 338: ejaculatory apodeme; 339: internal genitalia, ventral; 340: same, left lateral.

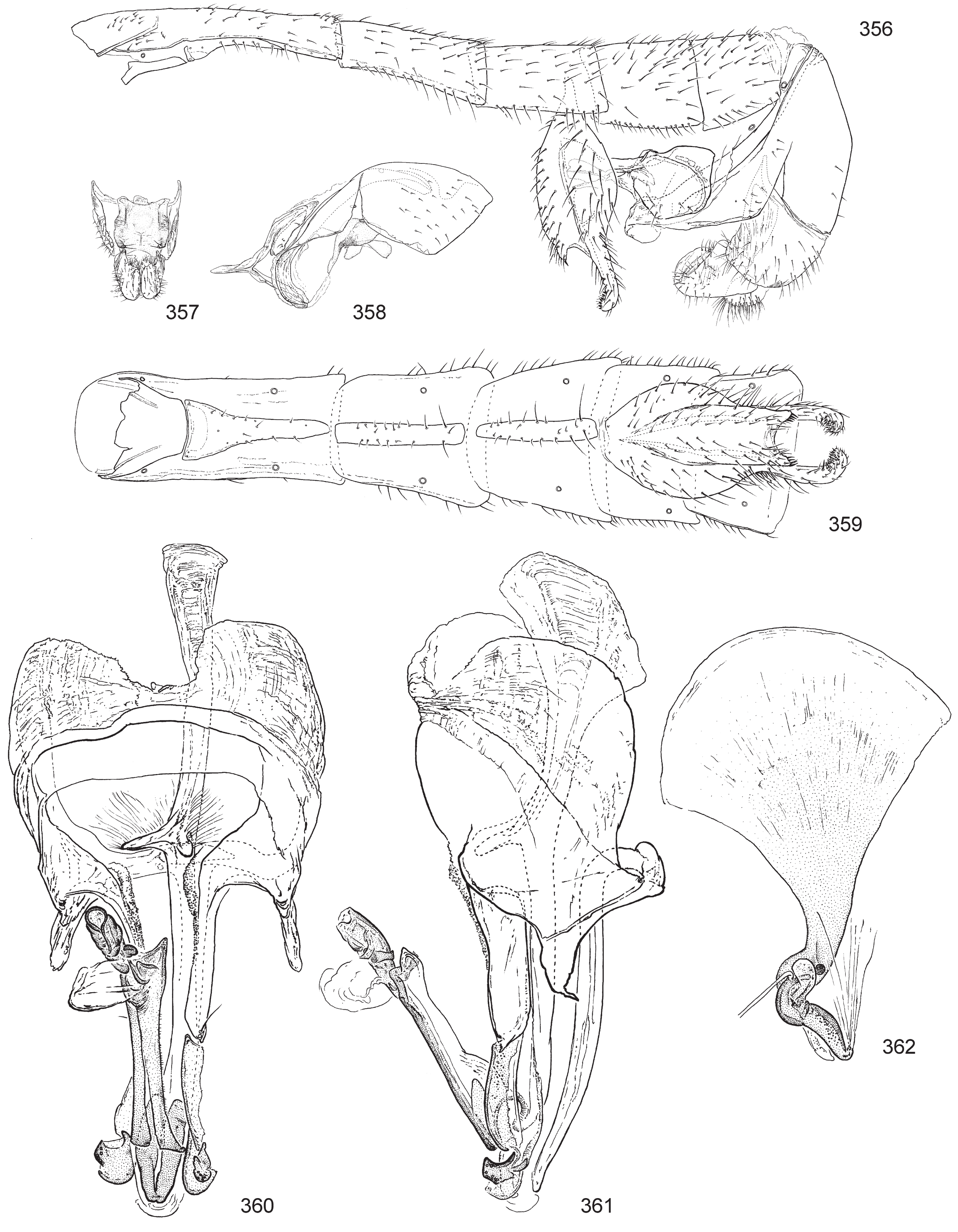


FIGURES 341–348. *Cryogonus formicarius* (Rondani) (Micropezidae), male abdomen; 341: left lateral; 342: terminalia, right lateral; 343: external genitalia, anterior; 344: segments 1(partial)–6, ventral; 345: sternites 7–8, ventral; 346: ejaculatory apodeme; 347: internal genitalia, ventral; 348: same, left lateral.

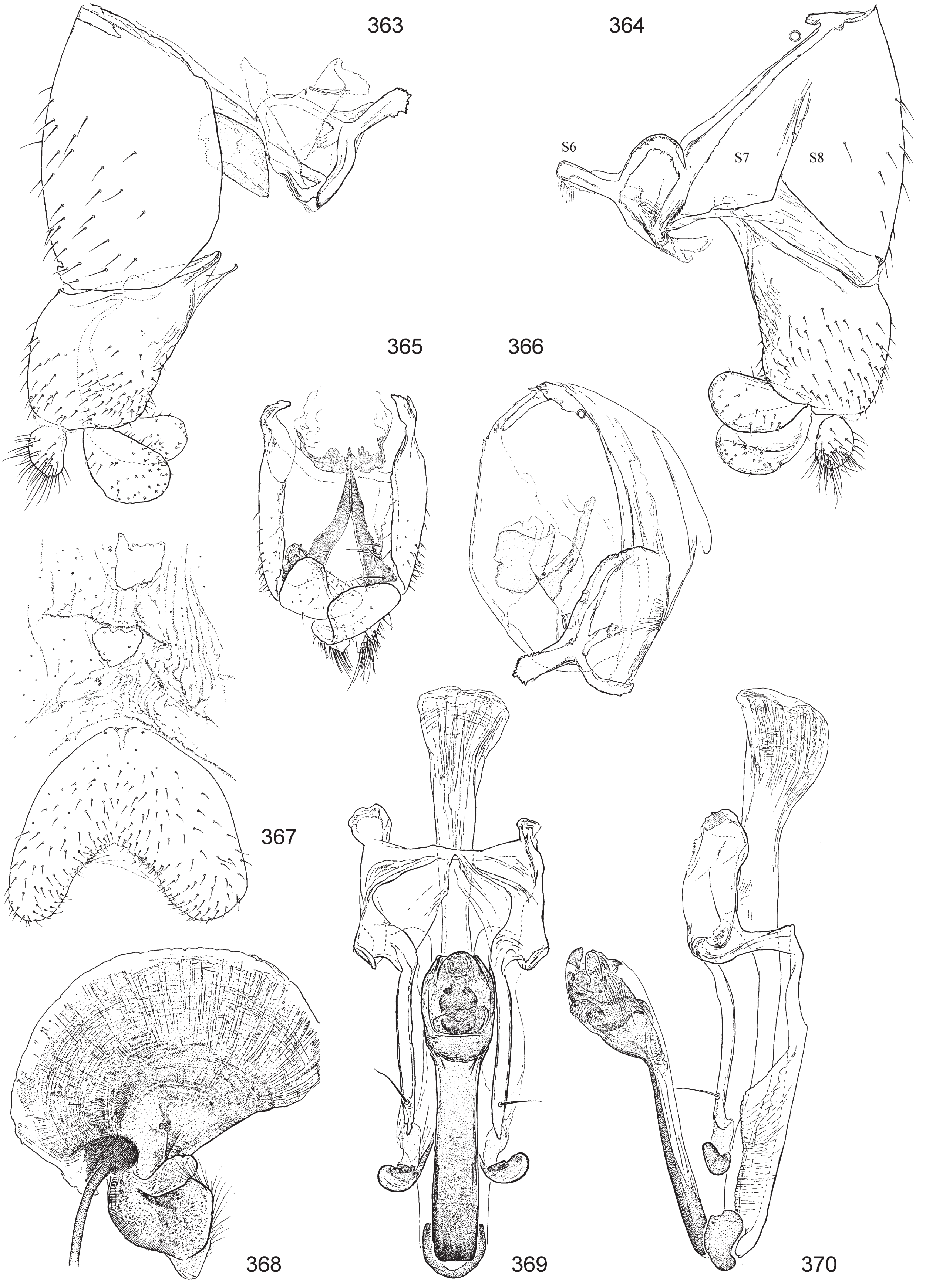


FIGURES 349–355. *Grallipeza mellea* Williston (Micropezidae), male abdomen; 349: left lateral; 350: terminalia, right lateral; 351: subepandrial sclerite; 352: abdomen, ventral; 353: internal genitalia, ventral; 354: same, right lateral; 355: ejaculatory

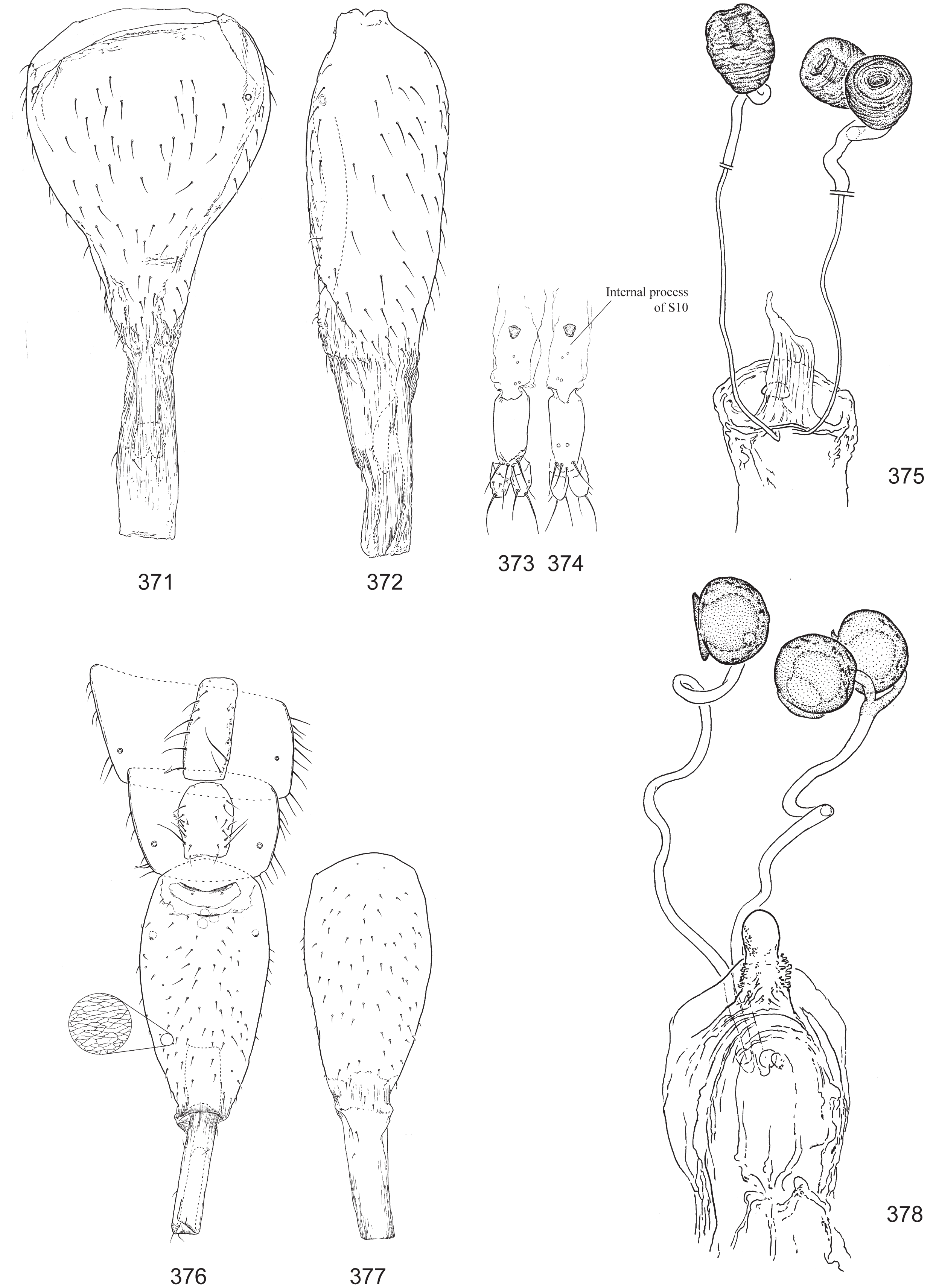
apodeme.



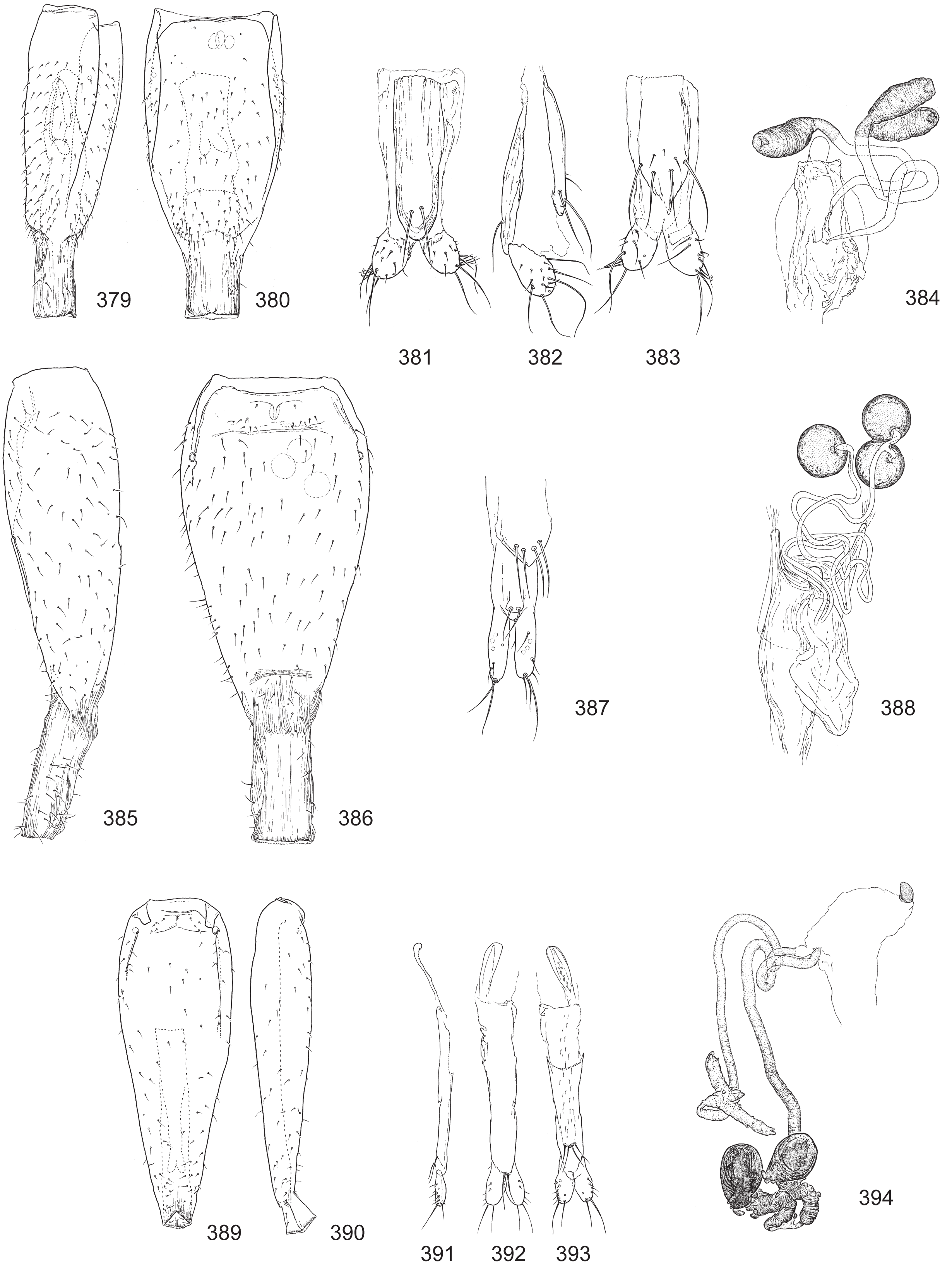
FIGURES 356–362. *Metopochetus* sp. (Micropezidae), male abdomen; 356: lateral; 357: external genitalia, anterior; 358: sternites 6–8, ventral; 359: segments 1–6, ventral; 360: internal genitalia, ventral; 361: same, left lateral; 362: ejaculatory apodeme.



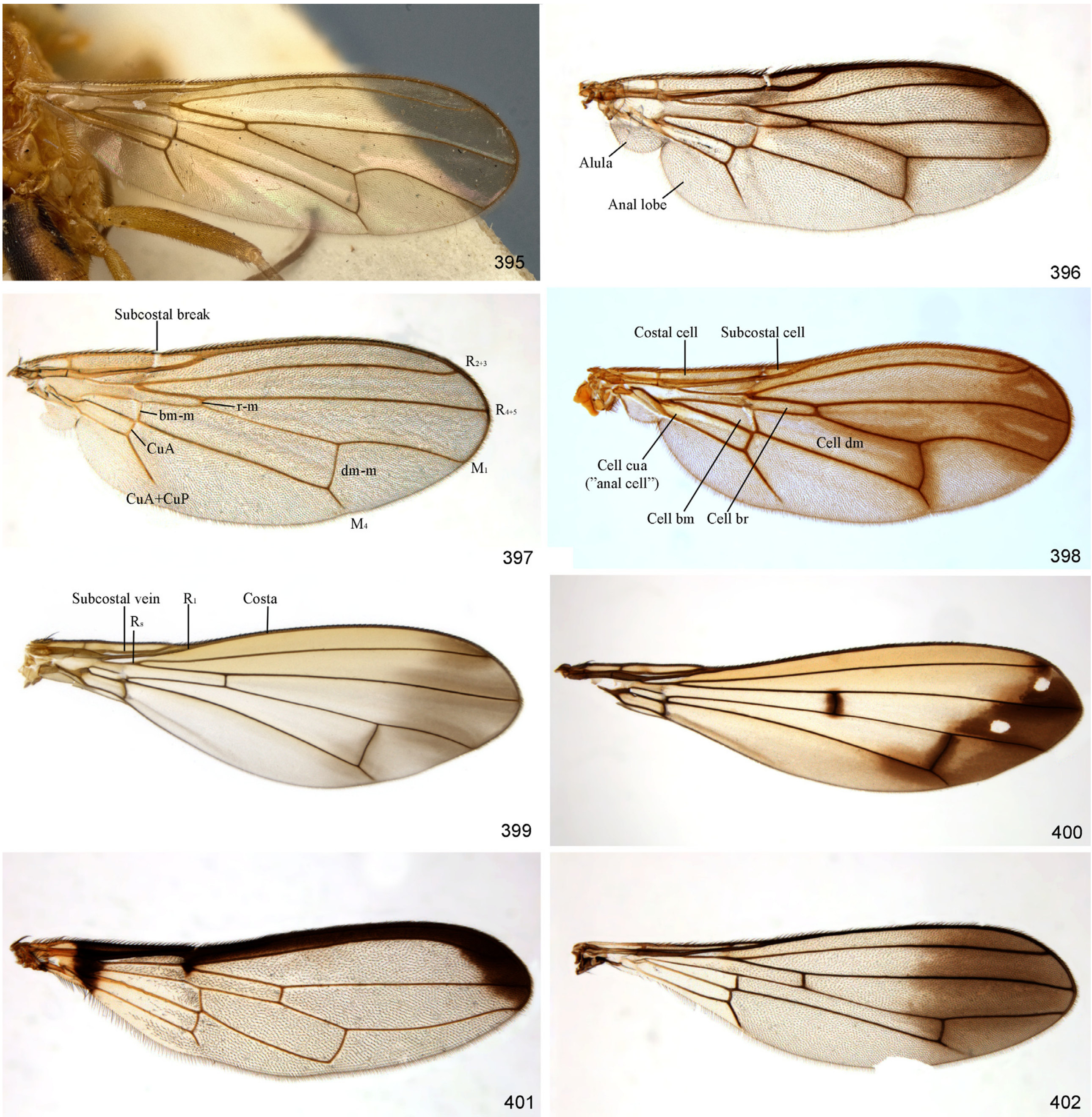
FIGURES 363–370. *Calycopteryx mosley*i Eaton (Micropezidae), male abdomen; 363: terminalia, right lateral; 364: same, left lateral; 365: external genitalia, anterior; 366: sternites 6–8, ventral; 367: sternites 3–5; 368: ejaculatory apodeme; 369: internal genitalia, ventral; 370: same, left lateral.



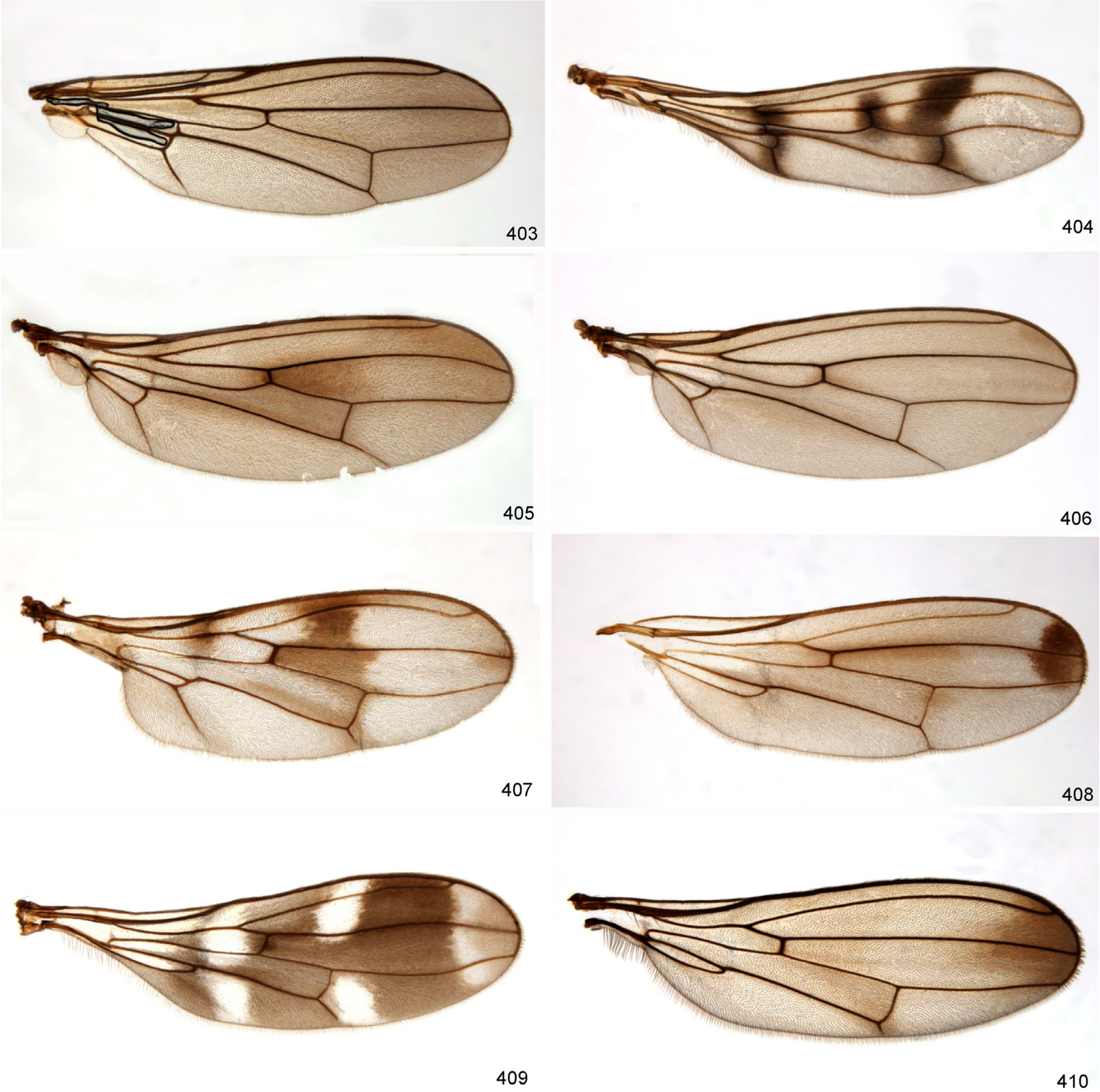
FIGURES 371–378. *Cnodacophora nasoni* (Cresson) (Micropezidae), female abdomen; 371: segment 7 to cerci (terminalia retracted); 372: same, lateral; 373: segment 10 and cerci, ventral; 374: same, dorsal; 375: internal genitalia. Figs 376–378: *Cryogonus formicarius* (Rondani) (Micropezidae), female abdomen; 376: segments 5 to cerci (terminalia retracted), with detail of texture; 377: segment 7 to cerci, dorsal; 378: internal genitalia.



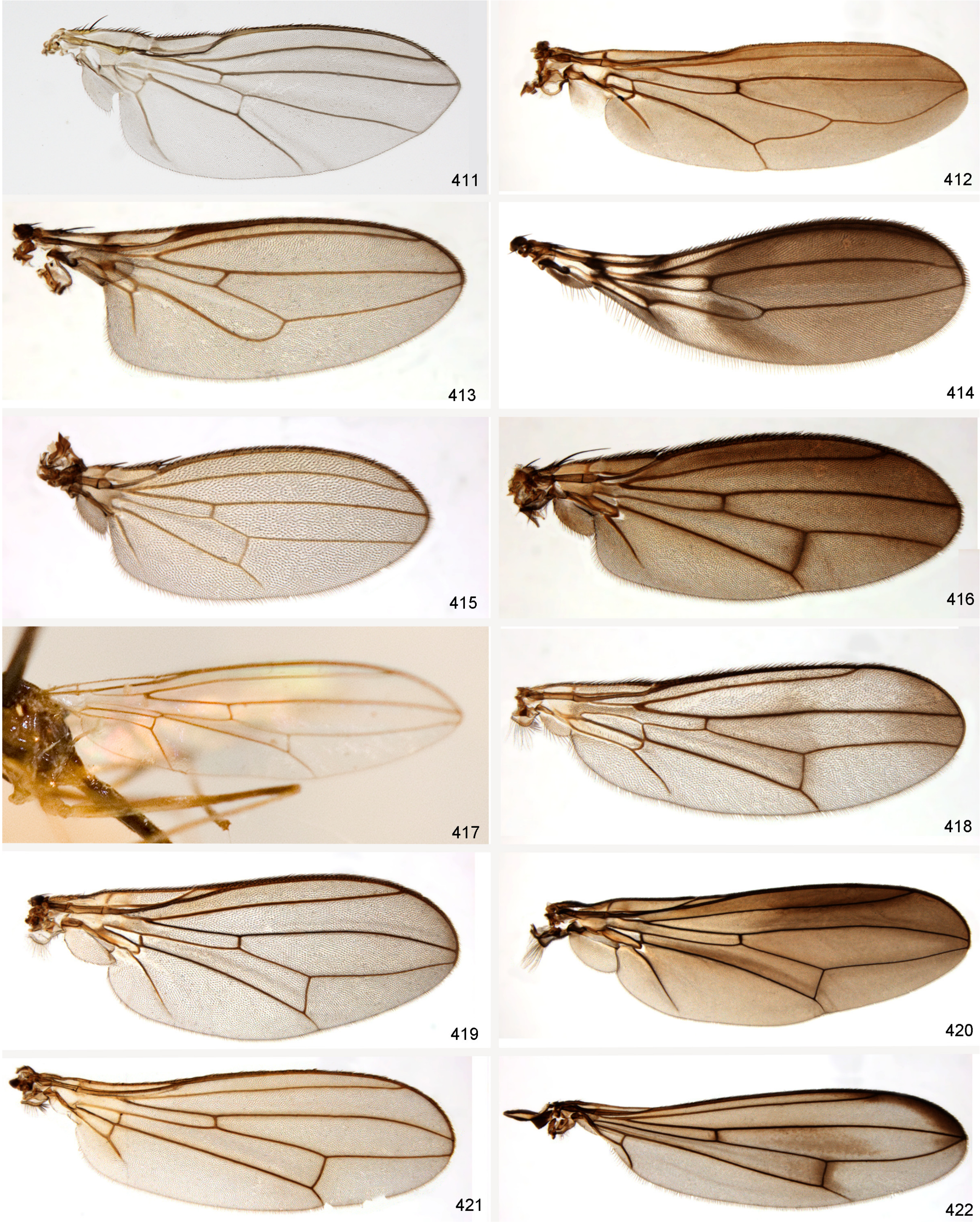
FIGURES 379–394. Figs 379–384: *Calycopteryx mosleyi* Eaton (Micropezidae), female abdomen; 379: segment 7 to cerci (terminalia retracted), lateral; 380: same, ventral; 381: segment 10 and cerci, dorsal; 382: same, lateral; 383: same, ventral; 384: internal genitalia. Figs 385–388: *Metopochetus* sp. (Micropezidae), female abdomen; 385: segment 7 to cerci (terminalia retracted), lateral; 386: same, ventral; 387: segment 10 and cerci, ventral; 388: internal genitalia. Figs 389–394: *Grallipeza mellea* Williston (Micropezidae), female abdomen; 389: segment 7 to cerci (terminalia retracted), ventral; 390: same, lateral; 391: segment 10 and cerci, lateral; 392: same, dorsal; 393: same, ventral; 394: internal genitalia.



FIGURES 395–402. Wings; 395: *Belobackenbardia cornicula* Shatalkin (Psilidae), female paratype; 396: *Chyliza notata* Loew (Psilidae); 397: *Psila hennigi* (Thompson & Pont) (Psilidae); 398: *Loxocera cylindrica* Say (Psilidae); 399: *Nothybus longicollis* (Walker) (Nothybidae); 400: *N. biguttatus* Wulp; 401: *Somatia aestiva* (Fabricius) (Somatiidae); 402: *Gobrya* sp. (Gobryidae).



FIGURES 403–410. Wings; 403: *Texara* sp. (Megamerinidae); 404: *Syringogaster rufa* Cresson (Syringogastridae); 405: *Centrioncus decoronotus* Feijen (Diopsidae); 406: C*entrioncus sanorum* (Feijen) (Diopsidae); 407: *Sphyracephala subbifasciata* Fitch (Diopsidae); 408: *Diopsis* sp. (Diopsidae); 409: *Teleopsis* sp. (Diopsidae); 410: *Diasemopsis aethiopica* (Rondani) (Diopsidae).



FIGURES 411–422. Wings: **411:** *Fergusonina* sp. (Fergusoninidae); **412:** *Odontoloxozus longicornis* (Coquillett) (Neriidae); **413:** *Clisa australis* (McAlpine) (Cypselosomatidae); **414:** *Formicosepsis* sp. (Cypselosomatidae); **415:** *Pseudopomyza* (*Rhinopomyzella*) *nigrimana* Hennig (Pseudopomyzidae); **416:** *Latheticomyia* sp. (Pseudopomyzidae); **417:** *Nartshukia musiva* Shatalkin, holotype (Strongylophthalmyiidae); **418:** *Strongylophthalmyia angustipennis* Melander (Strongylophthalmyiidae); **419:** *Tanypeza longimana* Fallén (Tanypezidae); **420:** *Neotanypeza marshalli* Lonsdale (Tanypezidae); **421:** *Compsobata mima* (Hennig) (Micropezidae); **422:** *Micropeza* sp. (Micropezidae).

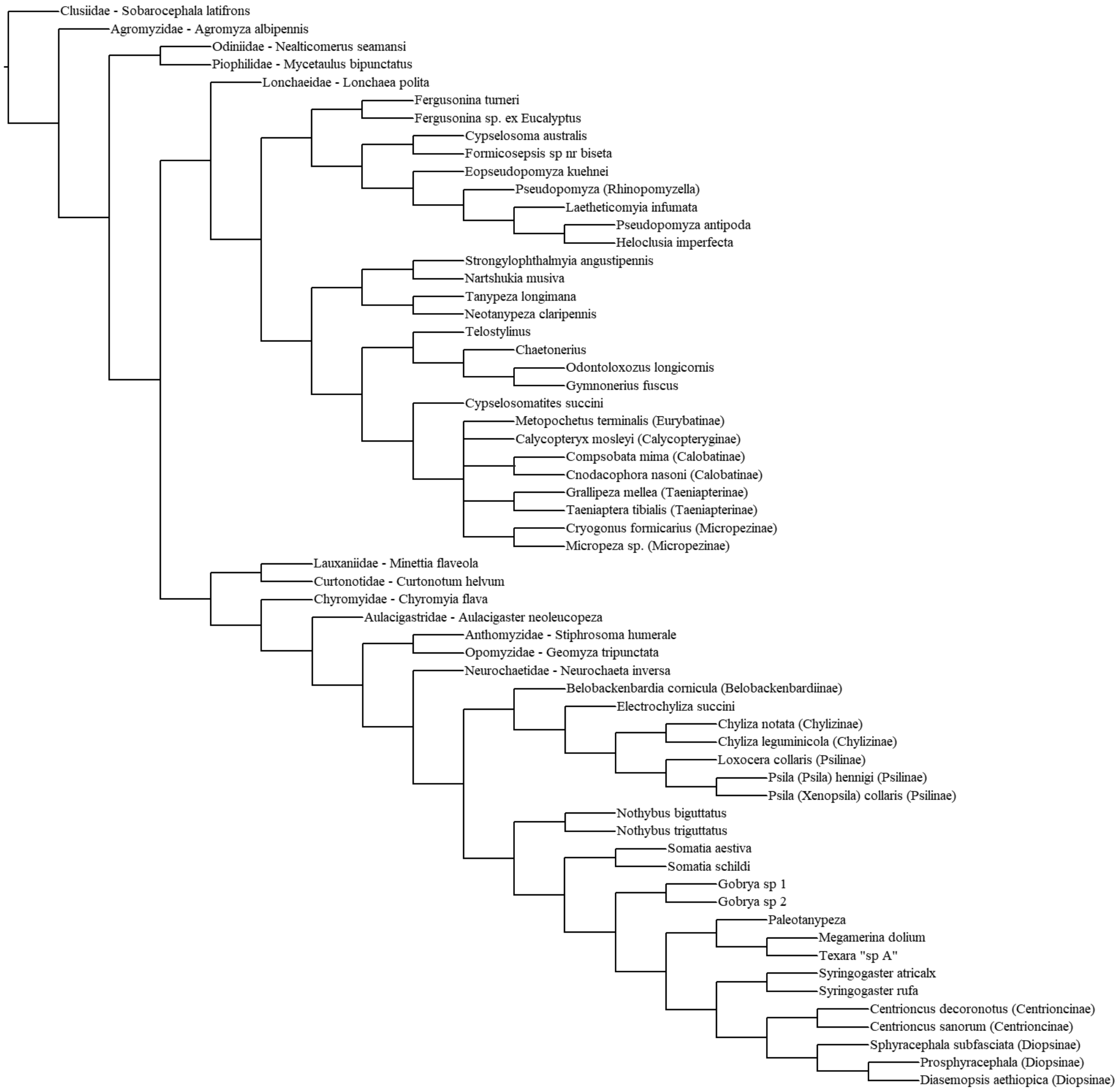


FIGURE 423. Strict consensus of three trees produced from the phylogenetic analysis.

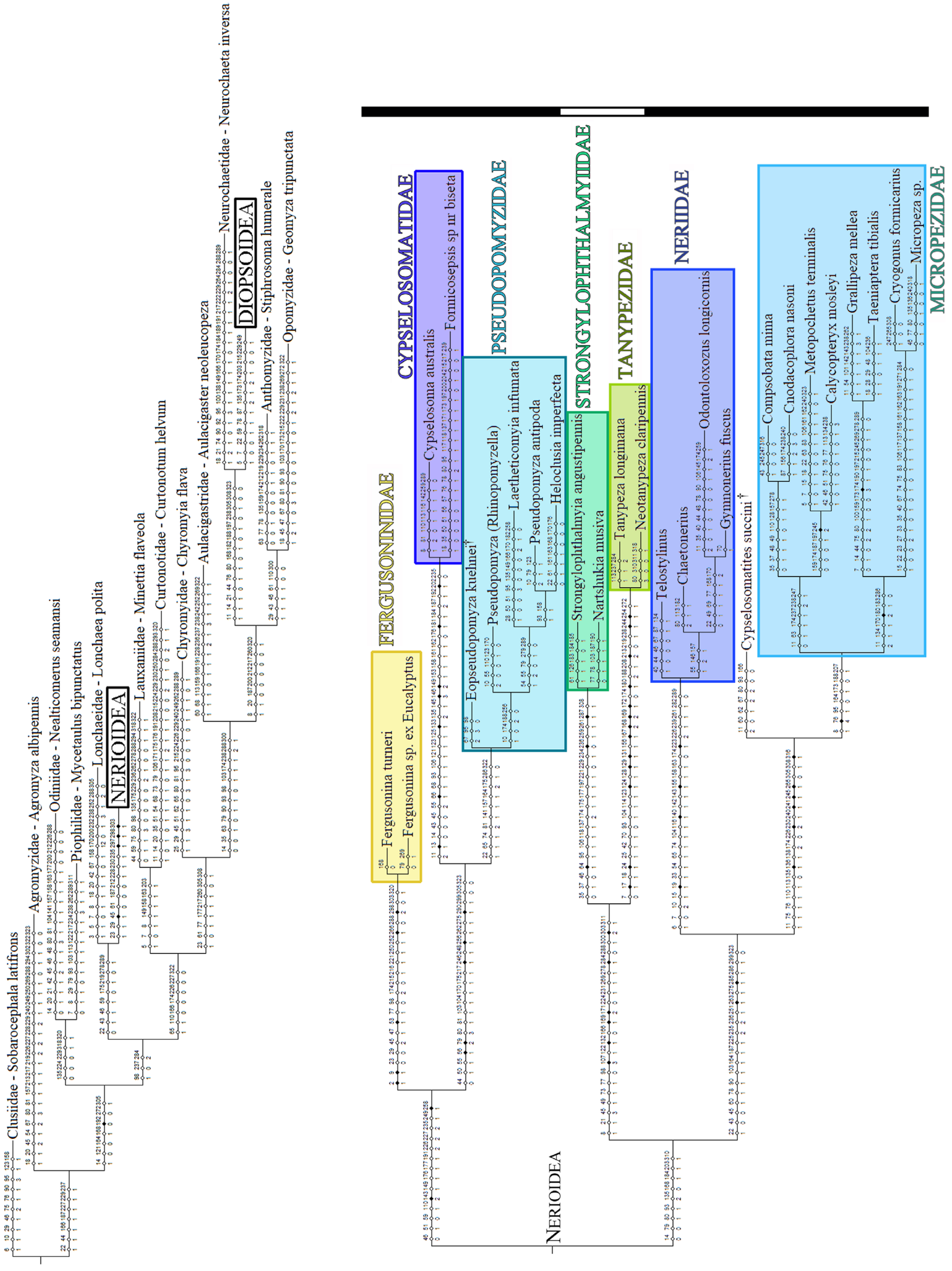


FIGURE 424. One of three most parsimonious trees produced from the phylogenetic analysis, detailing outgroups and families of Nerioidea. Diopsoidea represented by single operational taxonomic unit.

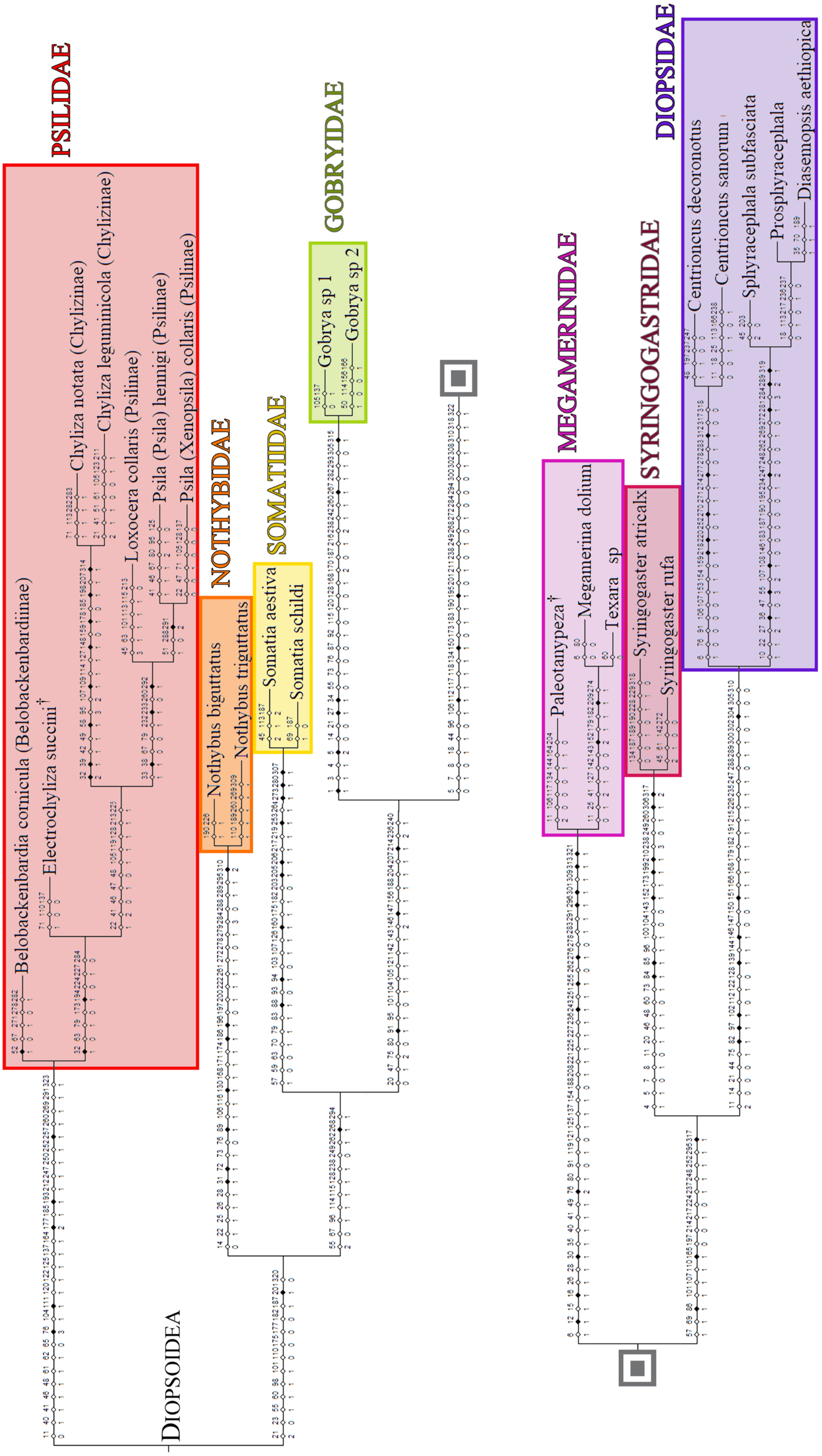


FIGURE 425. Detailed families of Diopsoidea from selected most parsimonious tree.

APPENDIX 1. Characters used in the phylogenetic analysis. The following characters were treated as ordered: 3-6, 8-9, 12-13, 15-17, 19-20, 23-27, 29-34, 36, 38-42, 49-50, 52-56, 58, 60-64, 68-74, 77-78, 80-82, 84-94, 96-97, 99-103, 105-109, 111-112, 114-121, 123-127, 129-134, 136-145, 147-148, 151-156, 159-162, 165-169, 173, 175-176, 178-181, 185-186, 189, 191-194, 195-196, 198-199, 201-202, 204-207, 209-214, 216-228, 230, 232-234, 239, 241-247, 249-252, 254-256, 258-270, 272-274, 276-318, 320-322.

1. Body colour
0 Not iridescent if dark
1 If with extensive dark regions, these blue iridescent

2. Body colour
0 Variably pigmented, but not entirely bright yellow
1 Entirely bright yellow, sometimes with limited darker pattern

3. Halter colour
0 Pale, sometimes faintly brownish or base brown
1 Knob brown

4. Pedicel
0 Cylindrical to bent or angled
1 Cap-like

5. Pedicel—dorsal seam
0 Absent
1 Present, linear
2 Present, split to form wide triangular opening

6. Pedicel—inner triangular extension
0 Absent
1 Present

7. First flagellomere
0 Elongate
1 Discoid

8. First flagellomere
0 Porrect
1 Deflexed

9. First flagellomere
0 Well-developed, projecting
1 Reduced, concealed in pits medially

10. Arista—insertion
0 Dorsobasal
1 Dorsoapical
2 Apical

11. Arista—vestiture
0 Pubescent to short plumose
1 Bipectinate
2 Bare

12. Frons—Sharp groove between orbits and frontal vitta
0 Absent
1 Present

13. Frons—texture
0 Smooth; pilosity variable
1 Minutely textured and pilose

14. Frons

0 Bare, or nearly so; sometimes pilose to velvety; sometimes with anterior or lateral setulae
1 With numerous evenly scattered setulae, at least on orbital plate

15. Frons

0 Relatively flat medially, level with orbital plate
1 Sunken medially

16. Frons

0 Sometimes produced, not folded anteromedially
1 Produced anteriorly AND with one pair of anteromedial folds

17. Frons—width

0 Equal in both sexes
1 Strongly narrowed in male

18. Orbital plate

0 Inner margin not visible; sometimes indicated by pattern of pilosity
1 Discreet

19. Orbital plate, internal surface

0 Without apodeme
1 With long, subrectangular apodeme

20. Ocellar triangle

0 Not well differentiated from surrounding frons, or reduced to tubercle
1 Visible

21. Ocellar triangle

0 Short, less than 2/3 length of frons, or not visible
1 2/3 length of frons
2 Attaining anterior margin of frons (or nearly so)

22. Ocellar triangle—vestiture

0 Shining (sometimes excluding tubercle)
1 With pubescence

23. Ocellar tubercle

0 Adjacent to postocellars
1 Removed anteriorly and separate from postocellars

24. Ocellar disc

0 Absent
1 Present

25. Vestiture patch—post-ocellar

0 Absent
1 Present

26. Vestiture patch—frons, lateromedial (1 pair)

0 Absent
1 Present

27. Face—width

0 Normal
1 “Gobryidae-type” (wide, bulging, strongly recessed ventrally)
2 Recessed and concealed by prominent parafacials

28. Face—vestiture

0 Bare
1 Haired

29. Face—sclerotization

0 Well sclerotized
1 Membranous or soft, at least ventromedially

30. Face—medial sulcus

0 Absent

1 Present (due to meeting of antennal grooves)

31. Face—ventromedial protrusion with dark spot

0 Absent
1 Present

32. Face—angled, ventromedial plate with transverse striations

0 Absent
1 Present
2 Present, and strongly projecting

33. Face and parafacial

0 Vertical, or nearly so; rounded in *Gobrya*
1 Projecting anterodorsally and receding ventrally

34. Ptilinal suture

0 Well developed
1 Narrow, without descending lateral arms

35. Lunule

0 Hidden
1 Exposed

36. Eye stalks

0 Absent
1 Strongly developed

37. Head—shape

0 Without the below combination of characters
1 Orbicular; back of head concave above foramen and bulging laterally

38. Head—shape in profile

0 Ovate to semicircular, flat posteriorly or otherwise, but not triangular as below
1 Subtriangular and higher than long

39. Buccal cavity

0 Bare to short-pilose
1 Long-haired, with anterior marginal hairs prominent

40. Clypeus

0 Rounded, sometimes upcurved anteriorly
1 Flattened, sometimes with anterior margin truncated

41. Clypeus—anterior margin

0 Rounded
1 Truncated
2 Notched

42. Palpus

0 Not considerably higher than wide
1 High, laterally flattened; ovate to spatulate

43. Labellum—transverse posterobasal sclerite

0 Well developed, discreet
1 Absent

44. Labium—distal paired processes

0 Well developed
1 Reduced

45. Labium—pairs of large setae

0 2 or more, and not arranged as below
1 3, with 2 pairs erect and one distal pair lateroclinate
2 1
3 0

46. Parafacial—silvery pubescence

0 Absent

1 Present

47. Parafacial—vestiture

0 Bare

1 With scattered medial setae

48. Postgena—silvery pubescence

0 Absent

1 Present

49. Occiput—long, white setae

0 Absent

1 Present

50. Gena

0 Variably pilose and straight or shallowly rounded

1 Shining and bulging

51. Gena height

0 Less than 1/3 eye height

1 At least 1/3 eye height

52. Postgena—ovate, medial patch of microsetulae

0 Absent

1 Present

53. Head shape

0 More rounded in profile anteriorly

1 Anteriorly flattened

54. Back of head

0 Bare or variable setulose, but not as below

1 With one pair of discreet dorsomedial patches of setae

55. Back of head—carina above foramen

0 Absent

1 Present, dorsal

2 Present, strongly semicircular

3 Complete, circular

56. Back of head—setae

0 Setulose only, or with scattered setae

1 With additional outstanding setae ("paraverticals")

57. Pronotal collar

0 Receding medially

1 Well developed medially

58. Back of head

0 Largely free from thorax; easily viewed

1 Strongly appressed to thorax

59. Vibrissa

0 Present

1 Absent

60. Ocellar setae

0 Present

1 Absent, or not larger than setulae

61. Ocellar setae—length

0 Short; not reaching eye margin

1 Long; extending past inner margin of eye if directed laterally

62. Patch of scattered setulae behind ocellar tubercle

0 Absent

1 Present

63. Postocellar seta

0 Present
1 Absent

64. Postocellar setae
0 Reclinate or absent
1 Proclinate

65. Postocellar seta
0 Divergent to subparallel
1 Convergent

66. Interfrontal seta
0 Absent
1 Present

67. Fronto-orbital seta(s)
0 0 or 1
1 2 or 3
2 4 or more

68. Fronto-orbital setae
0 Various, but not as below
1 Posterior seta reclinate and anterior seta(s) proclinate

69. Inner vertical seta
0 Present
1 Absent

70. Outer vertical seta
0 Present
1 Absent

71. Outer vertical seta
0 Single or absent
1 Duplicated

72. Thorax
0 Unmodified or slightly produced medially
1 Extremely elongate presuturally

73. Precoxal bridge
0 Absent
1 Present

74. Prosternum
0 Various, but not thin and linear
1 Linear

75. Prosternum
0 Bare
1 Setose
2 Setose laterally only

76. Presternum
0 Present
1 Absent or vestigial
2 Duplicated anteriorly
3 Weakly sclerotized, elongate, confluent with prosternum
4 Very large

77. Proepisternal seta
0 Present
1 Absent

78. Postpronotal seta
0 Present
1 Absent

79. Acrostichal seta

0 Absent

1 Present, prescutellar

2 Present, presutural to sutural

80. Dorsocentral seta(s), postsutural

0 0

1 1

2 2

3 3 or 4

81. Dorsocentral seta(s), presutural

0 Absent

1 Present

2 Present, in addition to one or two smaller anterior "scapular setae"

82. Scutum

0 Not as below

1 Border of postpronotum and lateral section of transverse suture grooved and shining

83. Scutum—transverse suture

0 Well developed, incomplete medially

1 Nearly absent

84. Humeral carina

0 Absent

1 Present

85. Postpronotal ridge

0 Absent

1 Present

86. Supra-alar ridge

0 Absent

1 Present

87. Notopleural seta, anterior

0 Present

1 Absent

88. Notopleural seta, anterior

0 Absent or positioned anteriorly

1 Shifted posteriorly, appearing as duplicated posterior notopleural

89. Posterior notopleural seta

0 Base not on raised surface

1 On tubercle

90. Presutural intra-alar seta

0 Present

1 Absent

91. Anterior supra-alar seta

0 Present

1 Absent

92. Posterior supra-alar seta

0 Present

1 Absent

93. Posterior intra-alar seta

0 Present

1 Absent

94. Scutum and scutellum

0 Without bulging appearance

1 Large and bulging

95. Scutellum setae, pairs

0 0
1 1
2 2
3 3 or more

96. Tubercle at base of apical scutellar seta

0 Absent
1 Present

97. Scutellum, spines

0 Absent
1 Present

98. Scutellum

0 Bare
1 Setulose

99. Subscutellum

0 Not enlarged as below
1 Subconical, larger than scutellum

100. Subscutellum

0 Well developed
1 Reduced, linear

101. Subscutellum

0 Separated from scutellum by membrane
1 Contiguous with scutellum

102. Anepisternum, posterior ventral sulcus

0 Absent
1 Present

103. Anepisternal seta

0 Present
1 Absent

104. Anepimeron, greater ampulla

0 Absent
1 Present

105. Anepimeron (excluding subalar sclerite)

0 Bare
1 Setulose

106. Suture between katepisternum and meron

0 Present
1 Absent, or smooth if still visible

107. Katatergite

0 Convex
1 Flat
2 Strongly bulging
3 Bulging, but very narrow (like longitudinal section of cylinder)

108. Katatergite—spine

0 Absent
1 Present

109. Katatergite

0 Bare or with short hairs
1 Long-haired

110. Coxopleural streak

0 Present
1 Absent

111. Anterior thoracic spiracle
0 Not sunken as below
1 In ovate depression

112. Metasternum
0 Not produced between hind coxae
1 Extending between hind coxae as a thin process

113. Metasternum
0 Bare
1 Setulose

114. Postmetacoxal bridge
0 Absent
1 Present

115. Metathorax, cylindrical extension
0 Absent
1 Present

116. Proepisternum
0 Higher than long (seen laterally), or small and slightly longer than high
1 Large, anteriorly projecting and longer than high

117. Proepisternum
0 Unmodified
1 Displacing postpronotum posteriorly

118. Proepisternum
0 Not produced dorsally, normal
1 Produced dorsally past anterior spiracle

119. Proepisternum—patch of short, dense, isolated (usually white) hairs
0 Absent
1 Present

120. Anterior spiracle
0 Not grooved, not above pit
1 With grooves ventrally that usually end in a pit

121. Subalar sclerite
0 Present, well-developed
1 Minute to absent, largely incorporated into anepimeron

122. Subalar sclerite
0 Linear, or only very shallowly curved
1 V or U-shaped

123. Subalar sclerite
0 Convex
1 Flat

124. Meron, pilose anteromedial emargination
0 Absent
1 Present

125. Scutum—texture
0 Relatively smooth, sometimes glossy
1 Minutely textured

126. Notal setulae
0 Short, weakly curved and (often) dark
1 Long, erect and yellow

127. Notal setulae
0 Erect, generally curved posteriorly
1 With “partings” and “crowns”

128. Thorax—long pile

0 Absent
1 Present on anterior half of pleuron and sometimes postpronotum

129. Thorax—transverse silvery tomentose stripes
0 Absent
1 Present

130. Purple iridescent pruinosity on thorax
0 Absent
1 Present

131. Meron, posterior margin
0 Pilose or bare, not reflective
1 Silvery tomentose

132. Katepisternum
0 Posterior margin normal, elevated
1 With deep recess anterior to meron

133. Katepisternum
0 Evenly rounded
1 With broad dorsal “shelf”

134. Katepisternum
0 Not produced
1 Produced dorsally past ventral 1/4 of anepisternum

135. Katepisternal seta number
0 2 or more
1 1
2 0

136. Katepisternal setae—arrangement
0 Horizontal or oblique if present; or only 0-1 setae present
1 Vertical

137. Postpronotum & proepisternum
0 Separate
1 Fused

138. Mid coxae
0 Approximate
1 Separated medially by process of mesonotum

139. Fore femur
0 Slender, narrow
1 Thickened

140. Fore coxa, male
0 Setulose to setose, but never with spines
1 With stout spines

141. Fore femur—row of relatively long and thick posterodorsal setae
0 Absent
1 Present

142. Fore femur, anteroventral row of spine-like setae
0 Absent
1 Present

143. Fore femur, posteroventral row of spine-like setae
0 Absent
1 Present
2 Present but few, long, posteriorly directed

144. Fore femur, antero- and posteroventral row of thickened setae accompanying spines
0 Absent
1 Present

145. Mid femur—anteromedial to -distal spines
0 Absent
1 Present

146. Hind femur, rows of spine-like setae
0 Absent
1 Posteroventral row
2 Antero- and posteroventral rows
3 Anteroventral, few in number, long and angled anteriorly

147. Hind femur
0 Slender, unmodified
1 Thickened, raptorial in appearance

148. Hind femur
0 Without wide ventral pit
1 With ovate, pilose distoventral pit

149. Hind femur, large seta past midpoint
0 Absent
1 Present, dorsal
2 Present, ventral

150. Femoral glands—fore femur
0 Absent
1 Present

151. Fore tibia, ventral ridge
0 Absent
1 Present

152. Hind tibia, one pair of ventral ridges
0 Absent
1 Present
2 Present, with ridges united

153. Fore tibial brush
0 Well-developed, normal; sometimes reduced to absent
1 Discreet, pale, visibly contasting surrounding dark setae

154. Fore tibia
0 Long pale ventral hairs absent
1 With discreet patch of long, pale hairs distoventrally

155. Tibiae—rows of setulae
0 Setulae not on raised rows
1 On raised rows, making tibia angled (not rounded) in cross-section

156. Tibiae—setae
0 Unmodified
1 Some setae arising from small dark tubercles bearing apical scale-like process

157. Fore tibia, ventroapical seta
0 Absent
1 Present

158. Mid tibia, dorsoapical seta
0 Absent
1 Present

159. Mid tibia—ventroapical seta
0 Absent
1 Present, but if more, then not as below

160. Mid tibial setae
0 Various, but not as below
1 Reduced to three strong ventroapical setae

161. Mid tibia
0 Two or fewer setae on basal half
1 Three large setae on basal half
162. Mid tibia
0 Fewer than 6 dorsal setae
1 More than 6 dorsal setae
163. Hind tibia, dorsoapical seta
0 Absent
1 Present
164. Hind tibia, ventroapical seta
0 Absent
1 Present
165. Mid and hind basitarsus—"sawlines"
0 Absent
1 Present
166. Fore basotarsomere
0 More than half length of fore tibia
1 Less than, or equal to, half length fore tibia
167. Hind basitarsus, ventrobasal process
0 Absent
1 Present
168. Mid basotarsomere
0 With scattered setulae
1 Bare along ventral midline
2 With small spine-like setae posteriorly
169. Halter
0 Stalk bare
1 Stalk with series of pale setae
2 Stalk with series of short black setae
170. Halter; dark pigmentation
0 Absent; entirely white
1 Present on stalk
2 Present on knob
171. Upper calypter, hairs
0 Moderately long to short
1 Pubescent
2 Very long
172. Lower calypter
0 Short-haired, pubescent
1 Densely haired (“furry”)
173. Alula
0 Well developed
1 Reduced to absent
174. Basal costal setae
0 2
1 1
2 0
3 3
175. Costa, subcostal break or weakening
0 Absent
1 Present
2 Present, preceded by at least 2 outstanding setae

176. Costa—humeral break or weakening

0 Absent
1 Present

177. Subcosta

0 Complete, ending in costa
1 Abbreviated, ending freely in cell sc or fused to vein R1
2 Continuing to costa at near right angle apically as weakening in membrane

178. Cell sc past subcostal vein

0 Shorter than length of cell br past vein bm-cu
1 Longer than length of cell br past vein bm-cu

179. Vein Rs

0 Ending close to level of anal cell
1 Ending far past level of anal cell

180. Vein R1

0 Bare dorsally
1 Setulose dorsally
2 With 2 or 3 setulae (Micropezinae; Taeniapterinae)

181. Vein R2+3

0 Usually diverging from costa slightly past base; not close to costa
1 Entirely parallel to costa (until apex), as close to costa as vein Rs

182. Vein R2+3

0 Apex relatively straight, not curved to meet costa
1 Apex curved to meet costa

183. Vein R2+3

0 Long, meeting costa after half of distance between wing apex and end of A1+CuA2
1 Short, meeting costa before or at half of distance between wing apex and end of A1+CuA2

184. R4+5 and M1

0 Parallel, or ony one vein slightly angled
1 Convergent

185. Distal section of vein M1

0 Straight
1 Evenly arched posteriorly

186. Radial and medial veins

0 Convergent to parallel, at least in part along length, usually at crossveins
1 Entirely diverging from base

187. M4

0 Ending before wing margin
1 Reaching margin of wing
2 Absent

188. CuA

0 Straight
1 Shallowly rounded
2 Strongly rounded

189. CuA+CuP

0 Present
1 Absent

190. CuA+CuP

0 Ending before wing margin
1 Reaching wing margin

191. Crossvein bm-cu

0 Present
1 Absent

192. Vein dm-m

0 On distal half of wing

1 Near midpoint of wing or more basal

193. Vein r-m and distal half of cell br

0 Relatively wide

1 Considerably narrower than anal cell

194. Subcostal cell past insertion (or projected insertion) of Sc

0 Sides converging

1 Sides parallel or diverging at base

195. Cell br

0 Posterodistal margin straight

1 Posterodistal bulging into cell dm

196. Cell bm

0 Vein M unbroken in anterior corner

1 Anterior corner on vein M open

197. Anal cell (cua)

0 Short, less than 12% wing length

1 Long, at least 12% length of wing

198. Anal cell (cua)

0 Vein bm-cu and CuA nearly level or bm-cu absent

1 Distance between bm-cu and CuA nearly as long as CuA2

199. M4Cell cup

0 Not much longer than cell bm, or cell bm or cua absent

1 Length exceeding cell bm by more than length of CuA

200. Anal cell (cua) size

0 Comparable in size to subcostal cell

1 Much smaller than subcostal cell

201. Basal wing cells

0 Evenly trichose

1 Without microtrichae, at least on basal half

202. Cell dm—posterodistal corner

0 Angulate

1 Rounded

203. Body length

0 Less than 4mm

1 More than 4mm

204. Abdomen—shape petiolate

0 No

1 Yes, with terminalia tucked under apex

205. Abdomen shape

0 Narrower, usually directed posteriorly

1 Broad, dome-like, downturned

206. Tergites 1 and 2—suture

0 Shallow, sometimes indistinct medially

1 Deep, obvious, lined with small punctures

207. Tergites 1 and 2—suture

0 Evident, at least laterally as a groove or dark line

1 Entirely absent

208. Tergite 2

0 Anterolateral setae not strongly differentiated

1 With stout anterolateral setae

209. Tergite 2
- 0 Without reflective patches as below
- 1 With one pair of posterolateral reflective patches

210. Tergite 2 fused to tergite 3
- 0 No
- 1 Yes

211. Sternite 1
- 0 Without transverse ridge
- 1 With dark submarginal transverse ridge, sometimes separated from remainder of sclerite

212. Sternite 1
- 0 Setose
- 1 Bare

213. Anterior margin of sternite 2
- 0 Not transversely divided (sometimes partially divided)
- 1 With short, wide separate sclerite
- 2 Adjoining margins of divided sternite 2 doubly emarginate

214. Female sternite 1
- 0 Anterior margin straight
- 1 Anterior margin deeply recessed

215. Female sternite 1
- 0 Length equal or greater to width
- 1 Wider than long

216. Female segment 6
- 0 Tergite and sternites separate
- 1 Tergite and sternite fused, forming complete tube
- 2 Tergite and sternite only fused at base, forming thin band; divided posteriorly

217. Female sternite 6
- 0 Elongate or nearly square; sometimes fused to tergite
- 1 Wide and short

218. Female sternite 7
- 0 Entire or longitudinally divided
- 1 Transversely divided

219. Female segment 7
- 0 Tergite and sternite separate, or only fused in part; not forming complete tube
- 1 Tergite and sternite entirely fused into complete cylinder

220. Female segment 7
- 0 Tergite and sternite not fused as below
- 1 Tergite and sternite fused at base only to form thin ring

221. Female segments 7 and 8
- 0 Separated by membranous region equal to or shorter than length of segment 8
- 1 Separated by membranous region far exceeding length of segment 8

222. Spiracles—7th segment
- 0 Present
- 1 Absent

223. Female 7th spiracles
- 0 Lateral
- 1 Ventromedial

224. Female 7th spiracles
- 0 Within membranous space
- 1 Enclosed in tergite

225. Female segment 8
- 0 Smooth, or minutely spinulose

1 Minutely and longitudinally striated

226. Female sternite 8

0 Entire

1 Longitudinally divided

2 Longitudinally divided, band-like and densely textured with minute sclerotizations

227. Female segments 8–10

0 Visible externally, extruded

1 Segment 10 and cerci partially retracted within oviscape (segment 8 at least partially visible)

2 Segment 8 to cerci retracted within oviscape

228. Female segment 10

0 Setae extending to midpoint or base of sclerite

1 Setae terminal only

229. Female tergite 10 and sternite 10

0 With more than two and four setae

1 At most with 2 and 4 setae, respectively

2 Various, but neither of the above

230. Female sternite 10

0 Without internal process

1 With long, internally-directed and often apically-widened "internal process"

2 Internal process reduced, largely fused with membrane basal to sternite

231. Female cerci, shape

0 Ovate in cross-section, or not as below

1 Curved in cross-section and largely (or completely) fused

232. Female cerci—peg-like sensillae

0 Absent

1 Present

233. Spermathecae & ventral receptacle

0 Well developed

1 Atrophied, largely incorporated into genital chamber

234. Vaginal sclerite

0 Absent

1 Present

235. Ventral receptacle

0 Simple, sac-like

1 Composed of a cluster of domelike or spherical chambers

2 A small round chamber on a short (to absent), weakly sclerotized stalk, sometimes absorbed

236. Spermathecae, number

0 1

1 2

2 3 or 4

237. Spermathecae

0 Not telescoped

1 Telescoped, at least shallowly at one end

238. Spermatheca

0 Surface smooth

1 Surface papillose

2 Surface with minute divots

3 Transversely wrinkled

239. Spermathecal ducts

0 Narrow

1 Nearly as wide as spermathecae

240. Spermathecal duct adjoining spermatheca
0 Clear
1 Pigmented
241. Male sternite 5
0 Flat
1 Bilobed and slightly to strongly produced
242. Male tergite 6
0 Separate from sternite 8
1 Fused to sternite 8
243. Male tergite 6
0 Not divided as below
1 Divided into 2 small strips
244. Male sternite 6
0 Evenly sclerotized medially
1 With dark, shining, left lateral sclerotized band
245. Male sternite 6
0 Not produced medially
1 Medially produced with anteromedial and anterolateral sclerotized bands
2 Medially produced with medial, anteromedial and anterolateral sclerotized bands; broad and stout ("eurybatine-like")
246. Male sternite 6
0 Not as below
1 Overlapping and articulating with sternite 7
247. Male sternite 6
0 Entire
1 Posterior margin deeply cleft to entirely divided
2 Entirely divided and strongly reduced
248. Male sternite 7
0 Incomplete ventrally, "annulus" membranous in part
1 Forming complete ventral band
249. Male external genitalic and pregenitalic sclerites
0 Asymmetrical
1 Symmetrical, or nearly so (excluding spiracles)
250. Male sternites 7&8
0 Well developed
1 Largely atrophied; reduced to thin dorsal strip
251. Male sternites 7&8
0 Extensively fused, or not as below
1 Deeply divided along adjoining margins
252. Male sternite 8
0 Setose
1 Bare
253. Male sternite 8
0 Various, but not as below
1 Narrow and band-like, enclosing spiracles on either side, with sternites 6 and 7 not visible
254. Male sternite 8
0 Not reflective
1 Silvery tomentose
255. Male sternite 8
0 Not enlarged as below
1 Dorsally elongate, large; dominating much smaller pregenitalic segments
256. Male sternite 8—one pair of very large dorsal setae
0 Absent

1 Present

257. Epandrium

0 freely moving

1 immobile

258. Epandrium—one pair of very large dorsal setae

0 Absent

1 Present

259. Epandrium, surstylus, sternites 7 and 8—texture

0 Setulose, without texture as below

1 Bare, with skin-like or “pebbled” texture

260. Male right spiracle 6

0 Partially to entirely free in membrane

1 Enclosed by sclerite

261. Male spiracle 7

0 Present

1 Absent

262. Male spiracle 7

0 At least partially contiguous with membrane

1 Enclosed in tergite

263. Male supernumary sclerites

0 Absent

1 Present (1 or 2), enclosed within sternites 7&8

264. Epandrium

0 Dome-like

1 Flat, band-like

265. Epandrium, anterolateral corner

0 Not produced

1 Produced as thin extension

266. Epandrium, distal margin

0 Broad

1 Constricted, surstyli approximated

267. Epandrium asymmetrical

0 No

1 Yes

268. Surstyli asymmetrical

0 No

1 Yes

269. Surstylus

0 Separate from epandrium; distinct

1 Fused to epandrium; sometimes entirely absent

270. Surstylus

0 Entire, sometimes split apically

1 3-lobed

271. Surstylus

0 Apical margin entire

1 Apically bilobed

272. Inner surface of surstylus

0 Setose or bare

1 With setae and stouter spine-like setae

273. Male cerci

0 Discreet

1 Flat; floating on surface of membranous terminal sac (Somatia-like)

274. Male cerci

0 Narrow

1 Very broad and truncated apically

275. Male cercus

0 Lying in perianal region medially on epandrium, but sometimes more apically

1 Apical on epandrium with perianal region indistinct or reduced

276. Inner surface of male cerci

0 Setose or bare

1 With setae and tubercle-like setae

277. Subepandrial sclerite

0 Not modified as below

1 With broad setose apical lobe

278. Subepandrial sclerite

0 Setose

1 Bare

279. Subepandrial sclerite

0 Without elongate, tuberculate ventral processes

1 With elongate ventral extensions similar to surstyli; apically tuberculate; sometimes fused to surstylus

280. Hypandrium

0 Present

1 Absent

281. Hypandrium

0 Not enclosing phallus

1 Enclosing phallus

282. Hypandrium

0 Halves meeting ventromedially

1 Divided ventromedially

283. Hypandrium

0 Various, but not as below

1 With discreet floating sclerotized and setose plate

284. Hypandrium—seta number

0 Two or more

1 One

2 None

3 Densely setose medially

285. Anterior margin of hypandrium

0 Attachment to external components through dorsal "arms"

1 With strong anteroventral membranous attachment to annulus and epandrium (Neriidae+Micropezidae)

286. Hypandrium, anterolateral margin

0 Not produced

1 Produced, usually as a thin carina

287. Hypandrium—large anterior, bifid process

0 Absent

1 Present

288. Hypandrial arms

0 Separate

1 Fused dorsally, forming complete ring (Neroidea)

2 Fused, forming complete ring, with point of attachment shifted posteriorly (most Diopsoidea)

289. Phallapodeme

0 Phallapodeme free from hypandrium anteriorly, but often articulating

1 With one pair of anteromedial processes extending to meet hypandrium

2 Hypandrium weak and recessed distal to point of fusion

290. Phallapodeme
0 Base smooth and relatively straight
1 Notched or otherwise widened at point of fusion with pregonite
291. Phallapodeme
0 Not forming phallapodemic plate; bare
1 Widened, forming narrow phallapodemic plate
2 Fused to hypandrial arms to form broad phallapodemic plate; remainder of hypandrium free
292. Phallapodeme
0 Bare
1 Setose
293. Phallapodeme
0 Rod-like; if not rod-like, then not as below
1 Strongly reduced, carinate with length barely more than height (Gobrya-like)
294. Pregonite
0 Present
1 Absent
295. Pregonite
0 Free, or otherwise fused, sometimes absent
1 Articulating with hypandrium
296. Pregonite
0 Various, but not as below
1 Lobate, angled anteriorly and with apical cluster of spines
297. Pregonite
0 Not band-like as described below
1 Band-like, fused to inner surface of hypandrium
298. Postgonite
0 Free, or otherwise fused, sometimes absent
1 Originating near apex of pregonite
2 Fused to apex of pregonite, small and subtriangular
299. Postgonite
0 Plate-like, lobate or absent
1 With band-like base and thicker apical section
300. Postgonite
0 Present
1 Absent
301. Postgonite
0 Not clearly perpendicular to pregonite
1 Perpendicular to pregonite
302. Postgonite
0 Various, but not as below
1 Dark, narrow and pointed ventrally
303. Phallic plate
0 Absent
1 Present, fused to hypandrium, unbroken
2 Present, divided into two moveable plates
304. Membranous dorsal region on phallus
0 Various, but not as below
1 Forming U-shaped supporting structure dorsal to distiphallus
305. Basiphallus
0 Separate from distiphallus
1 Fused to distiphallus, or not evident (possibly absent)

306. Basiphallus

0 Various, but not as below

1 Greatly enlarged and wedge-shaped

307. Distiphallus

0 Not ribbon-like; not visible when not in use

1 Very long, black and ribbon-like; permanently extruded from abdomen

308. Distiphallus

0 Entire

1 Divided into strongly differentiated basal and apical sclerites

309. Distiphallus

0 Without apical flagellae

1 With thin apical flagellae, sometimes forming large coils

310. Distiphallus

0 Various, but not as below

1 Longer than hypandrium and thickly sclerotized laterally (ie. 2 parallel bands)

2 Double-banded and apically bifurcated

311. Distiphallus

0 Membrane sometimes spinulose, but apical glans never present

1 With spinulose membrane and apical "glans" or acrophallus

312. Distiphallus

0 Various, but not as below

1 "Centrioncus-type" structure—broad, flat, overlapping and relatively short; right lateral process

313. Distiphallus

0 Without scabrous process

1 With spinulose apical process lying transversely ("scabrous process" of McAlpine)

314. Distiphallus

0 Various, but not globular

1 Globular, lobed, Chyliza-type

315. Distiphallus—short anterobasal tubule

0 Absent

1 Present

316. Bulb of distiphallus

0 Absent

1 Present

317. Distiphallus

0 Bare if sac-like, or not as below

1 Sac-like, membranous and heavily spinulose

2 Sac-like, spinulose and with subapical "horn"

318. Distiphallus membrane

0 Smooth or haired

1 Spinulose

319. Distiphallus membrane

0 Not modified as below

1 Membrane from base of basiphallus to dorsal surface of distiphallus sclerotized as complex supportive structure

320. Ejaculatory apodeme

0 Well developed

1 Minute, atrophied

321. Ejaculatory apodeme

0 Without carina

1 With pronounced posterior carina

322. Ejaculatory duct

0 Relatively long

1 Short, with ejaculatory apodeme directly adjacent to remainder of hypandrial complex

323. Ejaculatory apodeme—sperm pump

0 Present

1 Absent

APPENDIX 2. Character matrix used in the analysis.

‘Clusiidae—Sobarocephala latifrons’ 0000011001000000000000000000100000100000000001000000000000001000001000000021001200000000010000300000000000000000000000001010000000000010000000000000000000000011000010000000001100000000000001000100000001000000000001001000000001010000000001000000000000000000000000000000000001000001000000000100000000000000000000000000000?0011

‘Agromyzidae—Agromyza albipennis’ 00000010000000000101010000000000001000000001200000000100000010000020000000000013100000000000002000000000000000000000000010?000000000001000000000000000000001010000101000000011000000000000110001000000010000000000011010101000010221200000011001000000001100000000000000000100100000100000000000000010000000100000000000000?0000

‘Anthomyzidae—Stiphrosoma humerale’ 0000001100000000000101100000100000000000001101000000000000001000101000000000010200000000010010200000000100000000000000000000000000000000000000000000000000000000000000000000100000001010000000000100000000000000000000000100100010000100000000010101000000000000000000000010000000000000001000002000200000000000000000000010000000001?1001

‘Opomyzidae—Geomyza tripunctata’ 0000001100000000010101?000001000000000000001121100000000000001010?000000000001003100000000000002000000000000000000000000000000000000000100000000000000000000001000000001010011101000000000001000000000000000000000000000000000001??00002010000102000??00000000000000000000000100100000100000200020000000000000000000010000000000?1011

‘Odiniidae—Nealticomerus seamansi’ 00000010000000000000111?0000000000010000001012101000000000000100000100000000000131000000000000020000000010000000000000000000000000000000000100000000000000111000100101000001101000000000110000000000000000000000000010000000000010000000?1100000000000000000000000000000000000000010000000000000000000000000010000000000001?1???

‘Chyromyidae—Chyromyia flava’ 000000100000010000?0011010001000001000000??300000100000000001000010000000?101310000000000000300100000000000100000000000000000000000100000000000000000000000100000000100000010100000000011000000000001000000000001000010000000010000000001000100000000100000000010100000000000000001000002000010000000000000000000010000000000?0001

‘Neurochaetidae—Neurochaeta inversa’ 000000110010010001?121?0000000000000000000??00000000000000000010?01000000101100100000000000110300001001000000100000000000000000000000010010000000?0001000000000100000010001000001010000101000?10100000??00000000000000000101000001??000020000001000000000000000000000000?0100000000000000010000000000100000000?001??0?10000000000000?1000

‘Aulacigastridae—Aulacigaster neoleucopeza’ 000000100000000000?001?0000000000000000000??0000000000000001001??01100000000100200000000010010200000000100000010010000000000000000000001000000000000000000000000000000101000001101?000000001100100000000100000000000100101000000100011000000?2130001000000000100000001??000000100000000010000020002000000000?001??0?00010000000000?0011

‘Piophilidae—Mycetaulus bipunctatus’ 000000010000010000?0010000001000001000000001000000000000000010000010000000000002000000000000102000000010000000001000000001000000000000000000000000000000000000001000000101000001100000000000011000000000001000000000001001010000000001100000010113000??00000000000000000010000000000000001000000000110000000000000000100000100000001?1011

‘Lonchaeidae—Lonchaea polita’ 001010010000010001?1000000000000000100000001?10100000000000001010000000000000000012000000000000002001000000000000000000000000000000000000001000000000000000000000001100000010 10(12)0001000000000000011000000000000000000000000100100010000101101001000103000??0000000010000000000000000000000000000000020002100000000000000000000000000000?0011

‘Lauxaniidae—Minettia flaveola’ 000010010000010000?001000000000000010000000?00000000000000001010001010000000100013000000000000002000000000000001000000000000000000000000000000000000000010000000011000100001000000000000000000110000000000010010000000010010000000010000000000002000000000000000000000000100000000000000000000200000000010000000000100000000000001?0011

‘Curtonotidae—Curtonotum helvum’ 000010010010000000?101000000000000000000000001000000100100000001000101
100001000000200000000000000200100000001000100000000000000000000000010000000000000100000000110001000001
00100021000000000001100100000000100100001000100000000000000000210000010?00000000000100000000000000000000
000000001000000000200001000000000000100000000000000?1001

‘Chyliza notata (Chylizinae)’ 0000100100000010000011110000000002000000112100001010000000011011000010001000
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210001000000000001100110000100010000110000000000001010000000000100?000000010110100001001000000000100000000
10001100002001000000000100001000000000100000001001

‘Chyliza leguminicola (Chylizinae)’ 000010010000010000?121100000000020000001111000010101000000011001000010
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00000100000?000200100000000100001000000000100000001001

‘Loxocera collaris (Psilinae)’ 00001001000000100000111100000000011000010120003010000000000010111000000000000
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02000010010000000011001000001000000000100000000000001010000110?1?0??000000?01?010000100?00000000100000000
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‘Psila (Psila) hennigi (Psilinae)’ 000010010000010000?11110000000001100001011000011000100000000101100001000000
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‘Psila (Xenopsila) collaris (Psilinae)’ 000010010000010000?11010000000001100001012000000000100000000101100000
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‘Belobackenbardia cornicula (Belobackenbardiinae) ’00001001000001000?110100000000000000000110000101000100
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Electrochyliza_succini 000010010000010000?11010000000010000000110??0101000000?00010110000100010000??111
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Nothybus_triguttatus 000010010010000000?121?0110100100000000000000000000000001000110010?010000110001101
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Somatia_aestiva 0000100100100100000120000000000000000000000002000000000201001000010000100000111110010
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?000001?????1????1010000000000000000

Somatia_schildi 00001001001001000??120000000000000000000000000000000000002010010000100011000001111100010
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?000001?????1????1010000000000000000

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1000000000100010110010000001010000000100000000000202010100000000000000000010100001100000000010001020002
000011000000100000000000000100000000

Gobrya_sp_2 1011200100100000000?00000001000000100000000?000100100000000011001??0000000102011000000000000111101101000011100000000000000110000000000000200000011002100000000000100000010102001200000000000010000000010001011001000000101000000?????????????????01000000000000000001010000110000000001000102000200001100000100000000000000001000000000

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Megamerina_dolium 000000100001011101?020?0110101000010000120?100101000002000110010?000000000221100000000100100101001000011110000010110111000001011000001201000000002100102010100100000000000000020000100110001001000010100000110011101001000000100110100000000010001001000001010001000000000000000010101000000010000200100001000011001001110010000100110

‘Texara «sp A»’ 0000011000010111010020?0110101000010000120010010100000200010001 0?000000000221101000000100100101001000011110000010110111000001011000001201000000002100102010100100000000000000020000100110001001000010100000110011101001000000100110100000000010001001000001010001000000000000000000101010000000100002001000010000110010011100100001 00110

Paleotanypeza 00000110002101110 1?020?00?010100001000011 0??0010100?0020001100 10?000000000?211010000001001001010010000111000000 0?011001100000100100000020100001110210010001010010000100000000020000000001000100100001010000010001100?0010000001???1010??00????????00?0000010?00010000????0000000?10001???

‘Centrioncus decoronotus (Centrioncinae)’ 000001100020000001?000?000000000000000000000000011000000201011001 0?0001000000101100010001100100101011001111100001000110110011000000000000120001001110100001011010000000001101000000200001001100011011000101000001100100010001011010000010000000001200010000000110000000000000100000001110100100000010000010000001000010001000100010000000000010

‘Centrioncus sanorum (Centrioncinae)’ 0000011000000000000?000?01000000000000000000000001000000002010110010?0001000000101100010001100100101011001111100001001110110011000000000000120001001110100001011010000000001001000002000010011000110110001000000001100100010001011010000010000000012110100000011100000000000000100000001110100100000010000010000001000010001000100010000000000010

‘Prosphyracephala (Diopsinae)’ 000000100120000000?00??00020000000001000000???00000000?3010110010?000100000??11000100011001101010110011111121010??1101100110000000000000120001001110000000?0?00?00100000?10100??020000100100000100100000000000110010 00??00??????????????????????????0???

‘Sphyracephala subfasciata (Diopsinae)’ 0000001001200000010001?00020000000001000000000200000000030101100 10?000100000111100010001100110101011001111112101000110110011000000000000012000100111000000010000100100000110100000200001001000000100100000000000000100100010001010000000010000000112100100000020100100000000000000000010000000001001003000020000010000100010001000000000 1110010

‘Diasemopsis aethiopica (Diopsinae)’ 000000100120000000?001?0002000000001100000000000000000003010110010?00011000011110001000110011010101100111111210100111011001100000000000001200010011100000001000010010000001101000002000010010000001101000000000000110010001000100000000000010000000111000100000002010010000000000000000010000000010010030000200000100001000100010000000001110010

Tanypeza_longimana 00000001000000001100101110001000001000000011131001000000000010000000100100100010010000000000000020000000010030000001100000000111000110110020000000000000000000000100100000000122021000000010001000200000000000100100001000020100000000001111110001111000000100000000010000000000000000100100000001000002000010000000 1?0100201000011000000000011

Neotanypeza_claripennis 000000010000000011001011100010000010000000111310010000000000100000001001001000100300000000000000200000000100300000001000000001110001101100200000000000000000000001001000000001220210000000100010002000000000000100100001000020100000000001111110001101000000100000000010000000000000010010000010000010000100000001?01002010000000000000100011

Strongylophthalmyia_angustipennis 000000110000000000001010000010000000100000113000100000000010100100100000100010010000000000001010000000000130000000000100010001000001002010000000000000000000000100000000010200210100000101001000000000100100100000000000100010100?01110110011000000000000000000000000101000000010000000010000010010100000001?01002010010110000000000011

Nartshukia_musiva 0000001?00000000?0?????00000100000001000?0???00010000???0010000?0010000010??01010000000000???010000001?0??00?00?00001?00??00000000?0020?000000000000?00000000?00000000??02?021010000001001101000000100100100???0?????0??

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‘Cryogonus formicarius (Micropezinae)’ 00000011002000100000000000020100010000001000101000000000000011000000000000104010100100000010010100100001001000100100010000000000000000101110000000000000000000110111001000100120000020011001000100000000100100010000000100010000110111200002200011000101000100000000000010000000100010000000001001100000001110001 00?00010000010000010

‘Micropeza sp. (Micropezinae)’ 000000110020001000?00000002010001000000100010000000000000011000000000000 010411000010000001001010010000100100010010001000000000000000011011000000000000000000001101110010001001200000200110010001000000000100100010000000100010000110111200002200001000100000100000000000010100000100010000000000100110000000111???100001010000010100010

‘Metopochetus terminalis (Eurybatinae)’ 000010010000001001?0001000000100000100000000010100000?000000110000001000000001401010010000001001010010000100100010010000000000000000000000010100000000000000000000000110001000000100000000000100000000000010010010001000000010001000011011120000221200100020100010000000000001010000000001000000002110110000000111000100001010000010000011

‘Calycopteryx mosleyi (Calycopteryginae)’ 0000001100000000000?00110000010000010000001010000000100000001(0 1)0010?010000000000110100000000010010?00?0??01000000100000000000???000000000010101000000000000000000000000000000100?????????????????????????????0???10001000000001000100001101112000022130110002010001000000000000101000000000010000000021101100000001110001000010100000100000 10

‘Compsobata mima (Calobatinae)’ 000000110000000000000011000001000000010000011010110000000000110010?01000000014010100000000010010100100001000000000100000000000000001000000(0 1)101000000000000000000010100000010000000110000000000100100000000000010010001000000010001000011011120000221201100000000010000000000001010000000000100100000211011000000011100010000101000000000000?0

‘Cnodacophora nasoni (Calobatinae)’ 000000110000000000?0011000001000000010000001010110000000000110010?010000000140101000000100100101001000010000000001000000000000000100000001010000000000000000001101000000100000012000000000100100000000000010010001000000010001000011011120000221300100010100010000000000?1?100000000010010000002110110000000111000 1?0001?10000010000010

‘Grallipeza mellea (Taeniapterinae)’ 000000010010010000?001100000100000100000000001000000010000110000001000000002401020000000001001010010110100000010010000000000000000000101010001100000000000000000000001000(1 2)00030000020011001001000000100100100010000000000001000011011120000220301100000000010000000000011010001000001001000000210010000000001110001000010100000100000 10

‘Taeniaptera tibialis (Taeniapterinae)’ 000000010020010001?0011000010000001000000000101000000000001100000010000000240102000000000100101001010011000000100100000000000000000000001010100000000000000000000000000001000?000300000200110010010000001001001000100000000000010000110111200002100011000000000100000000000010100010000010010000002100100000000111000100001010000010000010

Odontoloxozus_longicornis_ 000001000220001000?0001000000100010000000100000101100001??0011000010101000010010010000000000000010200100001101000000000100000000000000000000200001011012000000001011100011010102000200000000010011000000000000100100000000000100010001112111100002200100000000000100000001010100000000000100000010211010000000011100010100001000000000000 10

Telostylinus 00000100020000100010011000001000101000010000000000000010?0011000010000000010001010000001 0010010(1 2)00100001100000000000010000000000000000001200001011000000000000100110001101000000000000000000100110000000000010010000000000001000100011121111000022001000000000000100000000010100000000000010000001021101000000000111000101000010000000000010

Gymnonerius_fuscus 000001000200001000100010000010001010000000010100100001100011000010101100010 0?101000000000100102001000011000000000001000000000000000000200001011002000000001011100011010102000000000000100110000000000010010000000000010001000111211110000220010000000000010000000001010000000000010000001021101000000001110001010000100000000000010

Chaetonerius 00000100020000100 0?0011000000100010100000000101000000001?0001100001010000000100010200000000010010200100001100000000100100000000000000000002000010110020000000010111000110100000000000000001010011000000000001001000000000001000100011121111000022001000000000001000000000101000000000001000000102110100000000111000101000010000000000010

Fergusonina_turneri 010000101000010000000000000000000001000000011201000101000000000000001000000???1012000000000000020000000000000010000000000000000000000000100000002000001000000000100000010000000201100000000001001000000000100000000000000010010100102 2?11000021000000000000?10100000100000001000000000000000020000100000001200000010000000000000001011

Fergusonina_sp._ex_Eucalyptus 0100001010000 10000?0000000000000000100000 00??2010001010?000000000001000000???10020000000000000020000000000000010000000000000000000000000100000002000001000000000100000010100000201100000000000100100000000100000000000000010010100102 2?11000021000000000000?101000001000000010010000000000000020000100000000120000001000000000000001011

Cypselosoma_australis 000000110020100000000010000010000010000000000000011000210000000001110000000000232000000000000102001000011010000001001000010101000000001020000000120130020001000011011000101 0(1 2)00011010001001002100110000000101000000000000010101000010221110000010000000001011000000101100100000000000001000000002000101000000111000100000000000000000010

Formicosepsis_sp_nr_biseta 000000100020100001?000100000010000000000000000000000000201000000001110000000101221000000000000101001000011010001000000110010101000000010201 00?0020130020001000011011000101 0(1 2)1011101000100100210011000010000101000000000000000100001022111000000100100000010110000000101000100000000000001000000000200011100000001110001000000000000000000?0

Eopseudopomyza_kuehnei_ 000000100000010000?0011000000100000100000000010?00001(0 1)000?1000000000102000000???0023200000000000000300000001100000 10??00000000000000000000000(0 1)0000010200000100000001010000101010(1 2)000121100000000000100100 00?000?00000000000?001010100?????2?????????????00000?0??0000001010????000000???001???

‘Pseudopomyza (Rhinopomyzella)’ 000000100200010000000110000010000010000000101000011000010000000010100000010000232000000000000002001000011000000000000000000001000000000001000001020000010000000101000010101000000211000000000?0010000?000?00000000000000101010000102211100002100000000010110000000010001000000000?00010000000002010111000000011100010000000000000000????

Laetheticomyia_infumata 000000100100010000000110000110000010000000101000000001210000000001010000001000003200000000000000300100001100000100000000000000000000000000001020000000000000101000010001020000211000010000020010000000010000000000000001010100001022111000021000000000101100000000000010000000000001000100002010101000000111000100000000000000000000

Pseudopomyza_antipoda 000000100200010000?00110000001000001000000 0???000011001?1000000000101000000 1??0013200000000000010200100001100000100000000000010000000000010000?10200000100000001110000101010(1 2)00002110000000000?0010000000001000000000???0???

Heloclusia_imperfecta 000000100100010000?0001000000100000100000000101000011001?100001000101000000100000320000000000001020010000110000010000000000000000000000010000010200000100000001110101101000000002010000000000200100000000100000000000000????????????????????????????000????????00?0010?????????0?????????????????0???????????????????????????????????