PHYLOGENY OF THE TRIBE ELACHIPTERINI (DIPTERA: CHLOROPIDAE)

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ABSTRACT

The phylogenetic relationships of the tribe Elachipterini were investigated based on the examination of 75 species from most zoogeographical realms except the Australasian realm. Sixty-eight exemplar species were included in a cladistic analysis based on 77 morphological characters of adult specimens. Nine genera are recognized in the Elachipterini: *Allomedeia* **gen. nov.,** *Alombus* Becker, *Anatrichus* Loew, *Ceratobarys,* Coquillett, *Disciphus* Becker, *Elachiptera* Macquart, *Goniaspis* Duda, *Melanochaeta* Bezzi and *Sepsidoscinis* Hendel. *Myrmecosepsis* Kertesz is synonymised with *Anatrichus*, and *Togeciphus* Nishijima and *Cyrtomomyia* Becker are synonymised with *Elachiptera*. Twenty new combinations are established. A key to genera of the tribe Elachipterini is provided. Redescriptions of the genera are included. The new genus *Allomedeia* is described, including the description of the type species, *Allomedeia xanthotes* **sp. nov.**

RÉSUMÉ

Une étude phylogénétique de la tribut des Elachipterini, incluant 75 espèces provenant de la majorité des régions biogéographiques, ainsi qu'une analyse cladistique, basée sur 77 caractères morphologiques des adultes de 68 espèces examplaires, ont été réalisées. Neuf genres appartenant à cette tribut sont reconnus : *Allomedeia* **gen. nov.,** *Alombus* Becker, *Anatrichus* Loew, *Ceratobarys* Coquillett, *Disciphus* Becker, *Elachiptera* Macquart, *Goniaspis* Duda, *Melanochaeta* Bezzi and *Sepsidoscinis* Hendel. De plus, 20 nouvelles combinaisons au niveau générique sont établies. Trois genres sont synonymizé : *Myrmecosepsis* Kertesz avec *Anatrichus* et *Togeciphus* Nishijima et *Cyrtomomyia* Becker avec *Elachiptera*. Une clé d'identification des genres est présenté. La révision de tous les genres sont inclus. Le nouveau genre *Allomedeia* est decris, inlcuant une description de l'espèce type, *Allomedeia xanthotes* **sp. nov**.

1. INTRODUCTION AND LITERATURE REVIEW

1.1. Diversity of Diptera and Chloropidae

Diptera (true flies) is one of the most diverse orders of insects, with more than 152,000 species described worldwide in 162 families (Evenhuis et al. 2007). The range of size (less than 1 mm to several cm), colors and body form is extraordinary. Diptera are dominant in virtually all terrestrial habitats and in many aquatic environments (Grootaert 2008, Pape 2008) where they occupy a broad range of ecological roles and are often significant contributors to food webs and ecosystem function (Pape 2008). Their evolutionary diversity is as rich as their ecological diversity, with a wide array of morphology, mating systems, and life histories (Evenhuis 2008, Kirk-Spriggs and Stuckenberg 2008).

Diptera are traditionally divided into two major groups: a basal, paraphyletic "Nematocera" and a monophyletic suborder Brachycera. There are several monophyletic subgroups within Brachycera, including the morphologically well-supported Schizophora which is, in turn, divided into the monophyletic Calyptratae and the Acalyptratae, which may not be monophyletic (Woodley et al. 2009). The Acalyptratae includes almost half the recognized families of Diptera and about 20% of the known species (Woodley et al 2009).

The family Chloropidae is one of the most species rich and ecologically diverse families of acalyptrate Diptera (Sabrosky 1987). It is comprised of approximately 2800 described species within 160 recognized genera (Evenhuis et al. 2007). Because of their abundance in grassy habitats, they are commonly known as grass flies (Nartshuk 1983, Sabrosky 1987). However, they are a cosmopolitan group with a nearly worldwide

distribution (except Antarctica), inhabiting areas ranging from riparian habitats and tropical forest canopies to bare mountain summits and deserts, as well as agricultural fields and urban landscapes (Nartshuk 1994).

1.2. Defining Characteristics of Chloropidae

Adult members of this family are small to medium flies ranging in size from 1 to 7 mm in length (Andersson 1977). They are highly variable morphologically, but the family as a whole has several autapomorphies including reduced chaetotaxy on the head and thorax, a clearly delineated frontal triangle and a vertical propleural carina. The wing venation is also characteristic, with crossvein bm-cu and cell cu*p* absent and a distinct kink or flexure in vein CuA_1 (Andersson 1977, Buck 2006). The color and texture of chloropids are very variable. Adults range from yellow to completely black, often with distinctive patterns on the head, thorax and/or abdomen. Many are also extensively textured, especially on the thorax and abdomen.

Chloropid larvae are white to cream colored, usually cylindrical, tapering anteriorly and rounded posteriorly; however, exact shapes vary depending on their ecological habits (Ferrar 1987). Phytophagous stem borers, some secondary invaders of plants damaged by other insects (such as some species of *Elachiptera* Macquart) (Sabrosky 1987, Beaulieu and Wheeler 2002) and predators of stem mining larvae, such as *Anatrichus* Loew (Wongsiri et al. 1974), are slender, elongate cylindrical maggots that taper anteriorly. Gall forming chloropid species tend not to be as elongated (McAlpine 1989). Chloropid larvae usually have ventral transverse spines along their bodies, which vary between species and the anterior spiracles are fan shaped with 4 to 17 papillae

(Deeming 1981, Ferrar 1987); the posterior spiracles are distinct in both puparia and larvae as cylindrical processes projecting directly from the body with oval spiracular slits with simple to branched interspiracular hairs (Sabrosky 1987).

1.3. Biology of Chloropidae

The Chloropidae are one of the most ecologically diverse families of Diptera (Ferrar 1987). As with most fly families, much of the research on habits of this family has been on the medically and agriculturally important species such as crop pests of grasses and cereals (Poaceae) (e.g., *Oscinella frit* (L.), *Meromyza* spp.). Several Chloropidae in addition to the well-known plant pest species are primary invaders of other herbaceous monocots (e.g., *Chlorops* spp. on Cyperaceae and Poaceae). Most are stem borers, but there are 23 known gall inducing species (e.g. *Lipara* spp. in *Phragmites* (Poaceae) and *Chlorops* spp. and *Eurina* spp. in several host plants) (Sabrosky 1987, De Bruyn 2005). Species in some genera such as *Tricimba* Lioy and *Gaurax* Loew are fungivorous (Bunyard and Foote 1990).

Several chloropid species in the genera *Hippelates* Loew, *Liohippelates* Duda and *Siphunculina* Rondani are also detrimental as a nuisance to humans and livestock, by feeding as adults on secretions from eyes, mouths, skin and wounds, often in large numbers (Ferrar 1987). Some of these species also act as disease vectors (Ferrar 1987, Sabrosky 1987).

Despite the focus on the groups mentioned above, the majority of chloropids are saprophagous. Several genera contain species that are secondary invaders of herbaceous monocots, living in decaying and macerated tissues of grasses, sedges, spike rushes and

skunk cabbage. Several species of *Elachiptera* have been reared from damaged plants (Brown 1956, Beaulieu and Wheeler 2002). Boppré and Pitkin (1998) found that chloropid species in multiple genera (*Melanochaeta* Bezzi, *Chlorops* Meigen, *Oscinella* Becker) are attracted to pyrrolizidine alkaloids (PAs), which are secondary plant metabolites secreted by certain types of recently damaged plants. There are also several species that are saprophagous on dead or dying animals; some species of *Olcella* Enderlein and *Conioscinella* Duda are attracted by volatile defensive and pheromonal compounds ((E)-2-hexenal, (E)-2-octenal and (E)-decenal) produced by spider prey, and presumably use these chemical cues to find injured insects to feed on (Aldrich & Barros 1995, Zhang & Aldrich 2004). Another species of *Conioscinella*, *C. hinkleyi* (Malloch), has been reared from dead horseshoe crabs and larval Lepidoptera (Norrbom 1983). Some species are inquilines in galls or in feeding galleries made by other insects or are nest associates of Hymenoptera. An unidentified species of *Fiebrigella* Duda eats the pollen provisions stored in nests cells of *Megalopta* spp. (Halictidae) bees (Smith et al. 2008) and a species of *Apotropina* Hendel has been reared from sand wasps (Sphecidae) in Australia (Evans & Matthews 1971).

A few species of Chloropidae are predaceous. *Anatrichus* species are predators on stem boring insects, especially those in rice (Ferrar 1987). Species of *Thaumatomyia* are larval predators of aphids (Homoptera: Phloeomyzidae) (Raspi 1996). The larvae of *Pseudogaurax* Malloch have been reared from the egg masses of *Nephila* Leach spiders, mantises and tussock moths (Ferrar 1987, Barnes et al. 1992). One genus is an especially spectacular parasite: the larvae of the Australian genus *Batrachomyia* Krefft are subcutaneous parasites of frogs (Ferrar 1987, Sabrosky 1987).

As adults, Chloropidae can be collected in a wide range of habitats including deserts, ocean beaches, wetlands, forests undergrowth and forest canopies, but are especially abundant in grassy areas. They are commonly associated with sedges, grasses, flowers and other vegetation (Sabrosky 1987).

1.4. Systematics and phylogeny of Chloropidae

The first described chloropid was a Palearctic species - *Oscinella frit* (Linnaeus 1758) and the major contributions to our knowledge of the Chloropidae were, at first, focused on the description of species of the western Palaearctic with great advances by Fallén (1820), Meigen (1803, 1826, 1830, 1838), Macquart (1835) and Rondani (1856) as well as in other regions of the world, by Loew (1845, 1860). The described diversity of the Chloropidae of other regions increased with Becker's worldwide monographs in the early 1900s (Becker 1910a, 1910b, 1911, 1912, 1913, 1914, 1916). This was soon followed by major contributions by Duda (1930, 1932-1933), Enderlein (1911a, 1911b) and Malloch (1913, 1914). Significant contributions in the mid to late 1900s included Andersson's (1977) taxonomic and phylogenetic studies of Old World Chloropidae, Kanmiya's (1983) systematic study of the Japanese fauna, Nartshuk's (1983, 1984a, 1984b, 1987) studies on evolutionary relationships and contribution to the Palaearctic catalogue and Sabrosky's (1984) world species checklist and contributions to Australasian and Oceanian, Nearctic and Afrotropical catalogs (Sabrosky 1965, 1980, 1987, 1989, Sabrosky & Paganelli 1984). Andersson (1977), Kanmiya (1983), Nartshuk (1983, 1987) and Sabrosky (1984) are particularly significant in that they provide the basis for the current tribal and subfamily classification of the family.

Currently, the Chloropidae is divided into three subfamilies: Siphonellopsinae, Chloropinae and Oscinellinae. Most authors consider Siphonellopsinae to be the sister group to the rest of the family (Andersson 1977, Kanmiya 1983, Nartshuk 1983). Andersson (1977) originally intended to conduct an explicit phylogenetic analysis of the family, but he perceived several problems with this and concluded that the family was not amenable to a cladistic analysis (Andersson 1977, 1979). Nevertheless, he summarized overall phylogenetic relationships within the family and concluded that Siphonellopsinae is the basal subfamily and the sister group to the Chloropinae-Oscinellinae clade.

1.4.1. Subfamily Siphonellopsinae

The Siphonellopsinae is the hypothesized sister group to Chloropinae plus Oscinellinae based on the retention of several plesiomorphic character states. This subfamily generally has more extensive bristling on the thorax, and the arrangement and orientation of cephalic setae is more similar to related families such as Milichiidae, than to other chloropids. The male genitalia are asymmetrical, which is also plesiomorphic (Buck 2006). The three genera placed in this subfamily (Sabrosky 1984): *Apotropina*, *Siphonellopsina* Andersson and *Siphonellopsis* Strobl have considerable variability in morphological characters and the generic limits are unclear.

1.4.2. Chloropinae-Oscinellinae Clade

The sister group to Siphonellopsinae is the Chloropinae-Oscinellinae clade. Is it considered monophyletic because of reduction of cephalic bristles, reduction of postpronotal bristles to one and characters associated with the male postabdomen:

symmetrical dorsal pregenital sclerite and loss of sternite 6 (T.A. Wheeler, pers. comm.). The monophyly of this clade, even though it is currently accepted, has not been tested. Changes may be required with further phylogenetic study.

1.4.2. Subfamily Chloropinae

The Chloropinae, sister group to the Oscinellinae, contains 66 genera in seven tribes (Sabrosky 1984). Its monophyly is defined based mainly on a wing character: the costal vein (C) only extending to near vein R_{4+5} (McAlpine 1989). There are some other potential apomorphies but these require a comprehensive phylogenetic analysis for confirmation. Members of this subfamily usually lack a tibial organ, are larger than average chloropids and often have yellow coloration with contrasting patterns on the thorax (Andersson 1977). Even though the monophyly of this subfamily is widely accepted, the relationships within it have not been adequately studied, and the limits of some genera are unclear and need to be re-evaluated (T.A. Wheeler, pers. comm.).

1.4.3. Subfamily Oscinellinae

The last, and largest, of the three subfamilies is the Oscinellinae. Members are in general small, 1-5mm, uniformly colored flies with the costal vein extending to vein M_{1+2} and, usually, the presence of a tibial organ. However, there is wide variation, especially in size and color (Andersson 1977, Kanmiya 1983). The oscinelline genus *Lipara* contains the largest chloropids described to date. In contrast, members of the Neotropical genus *Oscinicita* Wheeler are 1mm long. In addition to size, many other morphological features vary considerably. Overall color pattern, head shape, cephalic and thoracic

chaetotaxy, wing venation and male genitalia all differ between genera and between species within genera. The divergence in structure of, for example, the third antennal segment (small and round to extremely elongate and reniform) and arista (very thin and filiform to very wide and densely pubescent) makes scoring characters a challenge, especially given that homoplasy is common in Oscinellinae (Andersson 1979). The thorax varies in overall shape, square to elongate rectangular, and from flattened dorsally to very convex. The shape of the scutellum is often a good character to distinguish genera because it varies in shape from trapezoidal to semicircular to almost covering the whole abdomen; scutellar projections are well-developed in some oscinelline genera. Wing loss has evolved in some members of this subfamily and some lineages have evolved extreme character differences, such as dense fields of spines in place of bristles. Structures on the legs also vary; the femoral organ on the mid-femur varies in the number of modified bristles, in the placement of these bristles as well as in the presence of the entire structure, the hind tibial apical spur varies in size, color and location on the hind tibia. Color patterns and texture can vary widely within a genus, adding to the difficulty of using color patterns as character for phylogenetic analysis.

Four hypotheses have been proposed about the composition of tribes (or genus groups) within the Oscinellinae.

Andersson (1977) divided the Oscinellinae into two tribes: Rhodesiellini and Oscinellini, and further divided the Oscinellinae into genus groups. Rhodesiellini has six genera, and Oscinellini has 40 genera (although Andersson did not examine many New World genera) subdivided into nine genus groups: the *Javanoscinis*, *Elachiptera*, *Gaurax*, *Dicraeus*, *Lipara*, *Polyodaspis*, *Aphanotrigonum*, *Oscinella* and *Eribolus* groups. Other

authors (e.g., Nartshuk 1983, Sabrosky 1984) treated Andersson's genus groups as tribes. As noted previously, Andersson did not include an explicit phylogenetic analysis because he concluded that the phylogeny of the family could not be reconstructed given the amount of homoplasy within the family. His analysis was also restricted in the number of exemplar taxa; the study was based primarily on the Old World fauna and relatively few morphological characters were used.

Kanmiya (1983), in a systematic study of the Japanese Chloropidae, rearranged several of Andersson's genus groups; he also included genera and species that were not used in Andersson's study. Kanmiya transferred several genera from one genus group into another and erected several new genus groups. Like Andersson, Kanmiya's study was geographically limited. He examined only Japanese species and, although he did consider additional genera in his classification, it was not a phylogenetic study of the world fauna.

Nartshuk (1984) presented a dendrogram demonstrating the relationships within the subfamily Oscinellinae but her analysis was not explicitly based on the cladistic method. She treated the Siphonellopsinae as a separate family and restricted Chloropidae to Chloropinae and Oscinellinae, along with elevating the previous tribes Rhodesiellini and Hippelatini to subfamily level. Since it is the only study to date that has presented a phylogenetic tree of relationships within the Chloropidae, it has been used in the current study as a working hypothesis of chloropid phylogenetic relationships and has been used in selecting outgroup taxa.

Sabrosky (1984) compiled an unpublished, but widely distributed and cited, checklist of the Chloropidae of the world. He, like Nartshuk, elevated the genus groups to

tribes. However, he returned the Siphonellopsinae to subfamily status, and Rhodesiellini and Hippelatini to tribe status. He also questioned the tribal membership of several genera, and left a number of genera (especially New World genera) unplaced. However, because that work was only a checklist, no supporting characters for his classification were discussed and no reasons were given for these changes.

1.5. Tribe Elachipterini

Elachipterini has been considered a genus group (Andersson 1977, Kanmiya 1983) or tribe (Nartshuk 1983, Sabrosky 1984) of Oscinellinae.

Historically, membership of Elachipterini has been variable. Andersson (1977) defined the *Elachiptera* genus group as having upright or procurved, convergent or cruciate ocellar bristles, oval somewhat incised eyes, a broad postgena, oval or kidney-shaped third antennal segment often with a thickened arista with long dense pubescence, specialized structures on the scutellum, femoral organ with a group or 1 or 2 rows of warts, and a distinct tibial organ. He included seven genera in the group: *Elachiptera*, *Melanochaeta*, *Disciphus* Becker, *Cadrema* Walker, *Anatrichus*, *Myrmecosepsis* Kertesz and *Sepsidoscinis* Hendel.

Kanmiya (1983) accepted Andersson's definition of the tribe, but excluded *Myrmecosepsis* and *Sepsidoscinis* because of several apomorphic characters: compressed head, third antennal segment not oval or kidney shaped, ocellar bristles proclinate, inner vertical bristle distinct, long propleuron, mesonotum prolonged into a neck, scutellum oblong and elevated upwards distally, abdomen narrowed and elongate, sternites 1+2 absent, cercus discrete, and postgonite linear/oblong. He also excluded *Cadrema* from the

group because that genus has a spur on the hind tibia, upcurved bristles on dorsal edge of the sternopleuron, elongate conical scutellum, and oblong postgonites. Kanmiya included *Togeciphus* Nishijima in the group, but without justification.

Nartshuk (1983) disagreed with Kanmiya's removal of *Myrmecosepsis* and *Sepsidoscinis* but agreed with his assessment of *Cadrema*. She also removed *Melanochaeta* from the tribe. However, she did include two genera: *Alombus* Becker and *Cyrtomomyia* Becker, that were not included in the tribe by previous authors, probably because they are restricted to the Afrotropical realm.

Sabrosky (1984) agreed on most points with Nartshuk; however, he believed that *Melanochaeta* belonged within the tribe. He added the Nearctic genus *Ceratobarys* Coquillett to Elachipterini. Sabrosky also noted that the genus *Goniaspis* Duda, assigned by Nartshuk and others to the tribe Hippelatini, might belong either to Elachipterini or Botanobiini.

Ceratobarys has recently been synonymised with *Elachiptera* (Wheeler and Forest 2002) and Sabrosky's hypothesis on the placement *Goniaspis* in Elachipterini has been supported by morphological evidence (Mlynarek and Wheeler 2009). Thus, at the beginning of this study Elachipterini contained ten genera: *Alombus*, *Anatrichus*, *Cyrtomomyia*, *Disciphus*, *Elachiptera*, *Goniaspis*, *Melanochaeta*, *Myrmecosepsis*, *Sepsidoscinis* and *Togeciphus*.

Like most chloropids, little is known about the larval stages of Elachipterini. They are believed to be phytophagous feeding on various plants. However some larval stages of a few species of the Elachipterini have been documented. Multiple species of *Elachiptera* have been reared from injured plants (Beaulieu and Wheeler 2002). Ferrar

(1987) summarized other rearing records of *Elachiptera*. *Elachiptera bimaculata* (Loew) and *Elachiptera scrobiculata* (Strobl) have been reared from turnip and sorghum. Several other species have been reared as saprophagous secondary invaders of decaying plants: *E. cornuta* (Fallén) in cereal grasses; *E. costata* (Loew), *E. decipiens* (Loew) and *E. nigriceps* (Loew) from pine cones and skunk cabbage; *E. insignis* (Thomson) from decayed rice stems. The other studied larvae are members of *Anatrichus*. These are necrophagous or predaceous on rice pests or are found scavenging on dead caterpillars (Ferrar 1987).

1.6. Objectives

The main objective of this project was to conduct a phylogenetic analysis of the tribe Elachipterini using the cladistic method. Three existing, and competing, classifications were treated as hypotheses to be tested: Andersson's (1977) classification, Nartshuk's (1983) "phylogeny" and Sabrosky's (1984) checklist and classification.

The main objective was divided into three specific objectives in order to arrive at a revised classification of the tribe:

1. Test the monophyly of the tribe Elachipterini as currently recognized and, if necessary, redefine the limits of the tribe;

2. Test the monophyly of each of the included genera of Elachipterini and, if necessary, redefine generic limits to reflect their phylogenetic relationships;

3. Determine the phylogenetic relationships between genera assigned to the tribe.

2. MATERIALS AND METHODS

2.1. Source of specimens

Specimens from the following collections (with collection codons) were studied:

BMNH Department of Entomology, The Natural History Museum, London, United Kingdom.

CNC Canadian National Collection of Insects, Ottawa, ON, Canada

DEBU University of Guelph Insect Collection, Guelph, ON, Canada

INBC Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

LEM Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada.

NMSA Natal Museum, Pietermaritzburg, Kwa-Zulu Natal, South Africa.

USNM United States National Museum of Natural History, Washington, DC, USA.

A detailed list of material examined is provided following the generic descriptions. For each species examined, the geographic distribution, by realm, is given in square brackets as follows: **AT** - Afrotropical *sensu* Crosskey and White (1977); **AU** - Australasian/Oceanian *sensu* Evenhuis (1989); **NE** - Nearctic *sensu* Thompson (1999); **NT** - Neotropical *sensu* Thompson (1999); **OR** - Oriental *sensu* Delfinado and Hardy (1973); **PA** - Palearctic *sensu* Soós and Papp (1984).

2.2. Exemplar Species

The Elachipterini includes more than 165 described species (Sabrosky 1984, Appendix 3), and many undescribed species. Thus, given the scope of this project, it would be difficult and impractical to examine and include all of them in the analysis. Therefore, the exemplar approach was chosen for the study (Yeates 1995). The phylogenetic analysis included 68 ingroup exemplar species: 62 described species from all known genera of Elachipterini *sensu* Sabrosky (1984) and six undescribed species that were either assignable to known genera or that we determined should be included in Elachipterini based on the definition of the tribe *sensu* Andersson (1977) (Appendix 1). Exemplar species were treated as terminal taxa (Yeates 1995, Wiens 1998). Thirty additional species of Elachipterini were examined, but their characters were consistent with species already included in the analysis and therefore I decided to omit them from the phylogenetic analysis.

The type species of *Anatrichus, Elachiptera, Disciphus, Goniaspis, Melanochaeta, Myrmecosepsis, Togeciphus* and *Sepsidoscinis* were included as exemplars. Specimens of the type species of *Alombus* and *Cyrtomomyia* could not be obtained within the time frame of this project. However, other species were compared with the original descriptions of the type species and were considered appropriate representatives of those genera. For small genera, most of the species were examined but only a subset of these were included in the analysis. For genera with many species (e.g., *Elachiptera*, *Melanochaeta*), the type species, plus representatives of each species group and each zoogeographic realm in which the genus occurs were chosen based on Sabrosky (1984).

Seven outgroups from multiple tribes of Oscinellinae: *Hippelates plebejus* Loew and *Liohippelates pusio* (Loew) (tribe Hippelatini); *Cadrema pallida* (Loew) (tribe Botanobiini); *Oscinella frit* (tribe Oscinellini); *Eribolus nana* (Zetterstedt), *Oscinisoma alienum* (Becker) and *Rhopalopterum soror* (Macquart) (tribe Oscinisomatini), were used to root the tree and polarize characters (Maddison et al. 1984). The number of outgroups was high because the tribal level relationships of the Chloropidae are unresolved. I wanted to achieve the broadest range of representatives to test the potential monophyly and relationships of the Elachipterini.

2.3. Specimen Preparation

Male and female genitalia were prepared by removing the abdomens from specimens and clearing them in 85% lactic acid heated in a microwave oven for two to three intervals of 15 seconds, separated by a cooling period of one minute. Dissected abdomens were stored in glycerin in microvials pinned beneath the source specimens.

2.4. Characters and Terminology

A total of 77 characters was used for this analysis; 66 based on adult morphology and 11 on male genitalia (Appendix 2). Morphological terminology follows McAlpine (1981) for non-genitalic structures and Mlynarek and Wheeler (2008) for male genitalic structures.

2.5. Phylogenetic Analysis

For the parsimony analysis, a matrix (Appendix 1) was constructed using MacClade 4.08 (Maddison & Maddison 2005).

A heuristic search in TNT version 1.1 (Goloboff et al. 2008) using parsimony was performed using 1000 replicates, saving 100 trees per replicate. TBR (Tree Bisect Reconnect) branch swapping was used and branches were collapsed if maximum length was zero. The MaxTrees limit was set to 40000 trees.

Absolute Bremer support (Bremer 1994) and Bootstrap values (Felsenstein 1985) were calculated using TNT. For Bremer support values, a search for suboptimal trees with 1-20 additional steps was performed, after which the values were calculated. Bootstrap values were based on 1000 replicates using the same parameters as with the heuristic search.

2.6. Nomenclatural Changes and New Taxa

This thesis does not satisfy the criteria of publication as defined by Articles 8 and 9 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) and thus any nomenclatural changes or new taxa proposed in this thesis should not be considered valid for the purposes of zoological nomenclature until published in the scientific literature.

3. RESULTS AND DISCUSSION

3.1. Monophyly and Limits of Elachipterini

The analysis using TNT resulted in 288 equally parsimonious trees with a length of 486 steps, a consistency index of 0.22 and a retention index of 0.61. Bremer support (BrS) and Bootstrap values are plotted on the strict consensus cladogram (Fig. 1A, 1B). One of the 288 most parsimonious cladograms was selected as a basis for the classification of the tribe and character state changes are plotted on that tree (Figs 2-10).

The monophyly of the tribe Elachipterini is supported (BrS = 2 Fig. 1A) by seven characters; shiny ocellar tubercle (7:1), a reniform third antennal segment (16:1), a scutellum that is trapezoidal in dorsal view (30:1) and flattened dorsally (31:1), cerci that ventrally expand into a point (69:1), parallel sided surstyli (71:1) and triangular postgonites (72:1) (Fig. 2). Even though none of these characters is uniquely derived, the combination provides good support for the tribe.

Contrary to Kanmiya's (1983) hypothesis, *Sepsidoscinis* and *Myrmecosepsis* are members of Elachipterini. However, there is support for the suggestion by previous authors (Kanmiya 1983, Sabrosky 1984) that *Cadrema* should be removed from the tribe.

Two undescribed species (new species E and new species F) that were originally considered possible members of Elachipterini were consistently placed outside the tribe in analyses (Fig. 1A). The other four new species (A through D) were placed within Elachipterini and are discussed under the relevant genera.

3.2. Relationships within Elachipterini

3.2.1. Overall patterns of relationship

The tribe is divided into two main monophyletic groups, one containing *Allomedeia*, *Alombus*, *Anatrichus, Disciphus* and *Sepsidoscinis* (referred to as the *Anatrichus* clade); and one containing *Ceratobarys, Elachiptera*, *Goniaspis*, and *Melanochaeta* (referred to as the *Elachiptera* clade).

3.2.2. *Anatrichus* Clade

The monophyly of this clade is supported (BrS = 1, Fig. 1A, 2) by seven homoplasious characters: the arista more than twice as long as the height of the third antennal segment (17:1), the reduced ocellar bristles (23:1), the absence of the inner vertical bristles (25:1), the mesonotum longer than wide (27:1), absence of the postpronotal bristle (38:1), wing with a spotted pattern (53:2) and wing much longer than wide (55:1).

Disciphus is the basal member of the *Anatrichus* clade and is not closely related to *Elachiptera*, as previously hypothesized (Andersson 1977, Kanmiya 1983). It is supported (BrS = 4, Bootstrap = 52, Figs. 1A, 3) by one uniquely derived synapomorphy: one orbital bristle longer than the other orbital bristles (20:1), and three homoplasious characters: the interfrontal bristles on the inner margin of the frontal triangle (21:2), the pair of long apical tubercles on the scutellum (35:2), and the reduced cerci in lateral view (66:1). *Disciphus subelongatus* Kanmiya is not closely related to the other described species of *Disciphus*; it was nested within *Elachiptera* in the analysis.

The sister clade of *Disciphus* is comprised of *Allomedeia*, *Alombus*, *Anatrichus* and *Sepsidoscinis*. It is supported (BrS = 3 Fig. 1A, 2) by ocellar bristles shorter than postvertival bristles (24:1), a long pronotum (26:2), a pospronotum that is obviously longer than wide (28:1), second costal sector shorter than the third costal sector (56:2) and abdomen at least 1.5 times longer than the thorax (58:1).

Allomedeia is a weakly supported genus (BrS = 1, Figs. 1A, 4) defined by the margin of the frons diverging dorsally (3:1), subapical scutellar bristles absent (47:0), absence of a femoral organ (48:3), wings that are shaded at least along the veins (53:1) reduced anal angle (54:1), all bristles on cerci equal (68:1), the cerci fused medially (67:1), surstylus wide (70.1), parallel-sided (71.1) with a flattened tip (75:1), All species of *Allomedeia* are undescribed. Three of the species were included in the matrix (as new species B, C and D) and new species B is described below as the type species of *Allomedeia*. The remaining species will be described in a separate revision of the genus.

The remaining genera of the *Anatrichus* clade (*Alombus, Sepsidoscinis* and *Anatrichus*) form a strongly supported monophyletic clade (BrS = 8, Bootstrap = 60, Fig. 1A, 2) supported by 11 characters (1:2, 9:2, 10:1, 16:0, 26:1, 28:0, 30:2, 36:0, 37:1, 61:1, 62:1) including one uniquely derived synapomorphy, abdomen constricted at base (61:1, Fig. 27).

Alombus, is also a strongly supported monophyletic genus (BrS = 19, Bootstrap = 94 Figs. 1A, 2 & 5), probably partly due to several morphological changes associated with the loss of flight in this group. Ten characters (24:0, 31:0, 40:3, 43.1, 47:0, 52:2, 57:1, 59:1, 69:0, 74:1) support its monophyly including one that is uniquely derived, the absence of an anterior notopleural bristle (40:3). Four additional characters (53-56) were

plotted by TNT as state changes in the genus, but all are inapplicable wing characters that were coded as missing states. These have been omitted from the cladogram in Figs. 2 and 5.

The two remaining genera of the *Anatrichus* clade, *Sepsidoscinis* and *Anatrichus* are supported as a monophyletic group (BrS = 3 Figs. 1A, 6) by three characters (27:0, 48:3, 73:1).

Although *Sepsidoscinis* is a monotypic genus and is the well-supported sister group to *Anatrichus*, I have decided to retain as a separate genus to maintain stability with previous nomenclature. It is supported by 12 characters (3:1, 4:1, 12:2, 21:2, 22:1, 35:2, 36:2, 40:1, 44:1, 52:1, 67:1, 76:1) with one uniquely derived synapomorphy, a bi-lobed surstylus (76:1 Fig. 61, 62). An additional character state change (71:?) was plotted by TNT as an apomorphy for *Sepsidoscinis*, but that character state is inapplicable because of the highly modified surstylus in this genus (76.1) and the character state change was omitted from the cladogram (Figs. 2, 6).

The limits of *Anatrichus* have been expanded to include the species previously assigned to *Myrmecosepsis*. *Anatrichus* is supported (BrS = 3) by 16 characters (32:1, 35:0, 36:0, 39:3, 40:2, 41:1, 42:1, 44:2, 45:1, 53:0, 56:0, 59:2, 60:1, 63:1, 65:1, 75:2), of which seven are uniquely derived synapomorphies: the presence of many posterior and anterior notopleurals (39:3, 40:2), the modification of bristles into spines on the thorax (41:1, 44:2), the modification of the abdomen into one large sclerotized syntergite covering the entire length of the abdomen (59:2, 60:1) and the sternites divided into many pieces (65:1).

3.2.3. *Elachiptera* Clade

The monophyly of this clade is supported (BrS = 1, Fig. 1A, 2) by the possession of an arista that is less than twice the length of the third antennal segment (17:0), the rugose surface of the scutellum (33:1) and a well sclerotized hypandrium in lateral view (73:1).

Goniaspis comprises the basal lineage of this group. Its monophyly is supported (BrS = 4 Figs. 2, 7) by the presence of a short to long apical hind tibial spur (51:1) and the second costal sector that is as long as the third (56:1). Two of the ten described species in this genus were included in the analysis as well as an additional undescribed species (new species A) that was potentially referable to *Goniaspis*. That species is the sister group to the rest of the genus (Fig. 7).

The sister group to *Goniaspis* includes *Ceratobarys*, *Melanochaeta* and *Elachiptera*. Support is low (BrS = 1, Fig. 1A) and assumes many reversals; this is not surprising because homoplasy in the Chloropidae is very high. This clade of three genera is monophyletic based on the presence of a thin arista (18:1) that is heavily pubescent (19:1) and two orbital bristles that are longer than the rest (20:2).

The traditional limits of *Elachiptera* have changed as a result of this analysis (Figs. 1A, 1B), with the species previously assigned to *Elachiptera* divided into two monophyletic groups separated by a monophyletic *Melanochaeta*.

Although Wheeler and Forrest (2002) synonymized *Ceratobarys* with *Elachiptera*, I have reinstated it for the clade that forms the sister group to a monophyletic clade of *Melanochaeta* and *Elachiptera.* *Ceratobarys* is a weakly supported genus (BrS = 1, Figs. 1A, 2, 8) based on a dorsally elongated third antennal

segment (15:1), although this character state is independently derived in *Elachiptera*. Wheeler and Forrest (2002) synonymized *Ceratobarys* with *Elachiptera* based on the observation that the type species, *C. eulophus* Coquillett), was closely related to a group of yellow Neotropical species of *Elachiptera* with a trapezoidal scutellum. While these species are congeneric, the yellow species are all part of this clade, for which *Ceratobarys* is the oldest available name

Andersson (1977) considered *Melanochaeta* and *Elachiptera* closely related. This has been supported in this analysis (BrS = 1, Fig. 1B, 2) by two characters: shorter ocellar bristles than the postvertical bristles (24:1) and a round scutellum (30:0, Figs. 42, 51).

Melanochaeta is a monophyletic group supported (BrS = 3, Figs. 1B, 9) by four characters: the frontal triangle is shorter than three-quarters of the length of the frons (5:1), the dorsal posterior notopleural is reduced (31:0), the scutellum is convex dorsally (33:0) and smooth in appearance (39:2).

The greatest change in classification arising from this analysis is in the limits of *Elachiptera*. This genus is supported (BrS = 1, Fig. 1B) by a dorsally elongated third antennal segment (15:1) and the presence of 4 or more tubercles on the scutellum (36:2). As noted above, several species previously assigned to *Elachiptera* have been transferred to *Ceratobarys*. In addition, *Elachiptera* now includes all of the species that were previously placed in *Cyrtomomyia* and *Togeciphus*, as well as *Disciphus subelongatus*. *Cyrtomomyia* was treated as a subgenus of *Elachiptera* by Sabrosky (1951), because of many morphological similarities. However, he subsequently reinstated it as a genus (Sabrosky 1980). The four exemplar species of *Cyrtomomyia* are monophyletic, but nested well within *Elachiptera* along with *Disciphus subelongatus* (Figs. 1B, 10).

Consequently, *Cyrtomomyia* is considered a synonym of *Elachiptera*, and *D. subelongatus* is transferred from *Disciphus* to *Elachiptera*. The type species of *Togeciphus, T. katoi* Nishijima, was also nested well within *Elachiptera* (Figs. 1B, 10), and thus *Togeciphus* is synonymized with *Elachiptera*.

3.3. Revised classification of the Elachipterini

3.3.1. Tribe Elachipterini

Type genus: *Elachiptera* Macquart, 1835.

Included genera: *Allomedeia* gen. nov., *Alombus* Becker, 1914, *Anatrichus* Loew, 1860, *Ceratobarys* Coquillett, 1898, *Disciphus* Becker, 1911, *Elachiptera* Macquart, 1835, *Goniaspis* Duda, 1930, *Melanochaeta* Bezzi, 1895 and *Sepsidoscinis* Hendel, 1914.

Diagnosis

This tribe can be recognized by the following combination of characters: rounded vertex of the head, palpus with uneven setulation, third antennal segment reniform, a parallel sided surstylus, weakly sclerotized pregonite fused with postgonite, weakly sclerotized elongated basiphallus, a short membranous distiphallus, a simple phallapodeme and a sclerotized phallic guide. Although other characters define the group, they are lost in some genera or species within the tribe. Some species of Elachipterini are bizarre and instantly recognizable because of unique autapomorphies (e.g. Figs. 18, 24, 55).

3.3.2. Key to the genera of tribe Elachipterini

1. Wings present, longer than length of abdomen …….2

- Wings absent or short, shorter than length of abdomen……...8

2. Thorax with numerous straight spines (Figs. 24, 26); abdominal tergites 1, 2 and 3 fused and covering most of rest of abdomen (Fig. 27); arista thin (Fig. 25)……...*Anatrichus* (in part)

- Thorax without straight spines; abdomen usually unmodified, if modified, tergite 3 not fused not fused with tergites 1 and 2; arista thick or thin ……..3

3. Scutellum trapezoidal or triangular (Figs. 14, 32, 38, 47)……..…4

- Scutellum round (Fig. 26, 42, 51)……..…..7

4. Head with very strong, short vertical bristles (Fig. 11); eye large; face very narrow; femoral organ absent; abdomen narrow and elongate; male cerci fused medially (Fig. 15)……....*Allomedeia*

- Head with vertical bristles long but not exceptionally strong; eye smaller; face wide; femoral organ present; abdomen not unusually narrow or elongate; male cerci separated medially (Figs. 33, 39, 48)……..…5

5. Scutellar tubercles at least half as long as scutellum (Fig. 38); wing with a spotted pattern (Fig. 37)…….*Disciphus*

Scutellar tubercles absent or short, less than half as long as scutellum (Figs. 32, 47); wing clear or at most shaded along veins…….....6

6. Arista thick; third antennal segment elongated (Fig. 31); hind tibial spur usually absent (long in *C. eulophus* from southern Nearctic); surstylus thin in lateral view ……..……..*Ceratobarys*

- Arista thin; third antennal segment not elongated (Fig. 46); hind tibial spur present, usually longer than tibial diameter; surstylus wide in lateral view ……..….*Goniaspis*

7. Scutellum with 2-6 short to medium tubercles, rugose dorsally (Fig. 42); frontal triangle long, usually reaching anterior margin of frons……...*Elachiptera* (in part)

- Scutellum with no tubercles, smooth dorsally (Fig. 51); frontal triangle short, usually reaching at most to three-quarters of frons…….*Melanochaeta*

8. Wing and halteres short……...9

- Wing and halteres absent……...11

9. Thorax and scutellum with spine-like bristles (Figs. 24, 26)….*Anatrichus* (in part)

- Thorax and scutellum without spine-like bristles……..…10

10. Pronotum elongated (Fig. 56), head compressed in lateral view (Fig. 55); scutellum triangular with 4-5 long tubercles (Figs. 59-60); wing with a spotted pattern (Fig. 58)…….*Sepsidoscinis*

- Pronotum short, head not compressed; scutellum round with 4 tubercles (Fig. 42); wing clear ……...……..*Elachiptera* (in part)

11. Overall color black; reduced bristling, only one notopleural present…….*Alombus*

- Overall color yellow; spine-like bristles over thorax and scutellum …….*Anatrichus* (in part)

3.3.3. *Allomedeia* gen nov.

(Figs. 11-17)

Type species: *Allomedeia xanthotes* n.sp. (by present designation).

Diagnosis

Chloropidae, Oscinellinae, strong inner and outer postverticals, very elongate slender abdomen, small trapezoidal scutellum, wing with reduced anal angle, long slender arista and fused cerci in the males.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view (Fig. 11); frontal triangle shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, carina absent; first flagellomere reniform, higher than wide, arista longer than width of frons, and slender to wide at base (Fig. 12); proboscis and palpus short and sometimes thin.

Scutum square, as wide as long; thoracic chaetotaxy: 1 anterior, 1 posterior notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum flat dorsally, trapezoidal, usually wider than long (Fig. 14); 1 pair apical scutellar bristles on very small to very long tubercles, 1 or 2 pairs of lateral scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, second

costal sector equal to or shorter than third costal sector, distance between crossvein r-m and dm-cu 2.4 times length of dm-cu, anal angle reduced; alula small, much longer than wide (Fig. 13); veins pale to darekned; halter white. Legs long and slender; male femoral organ absent; small, apical ventral spur on mid tibia; hind tibial spur absent; tibial organ linear, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites very slender, with sparse setae, lateral abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, barely higher than long in lateral view (Fig. 16) and wider than high in posterior view (Fig. 15); surstylus simple, clavate or quadrate; hypandrium open posteriorly (Fig. 17); cercus fused medially with other cercus, triangular, projecting posteroventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Allomedeia is restricted to the Afrotropical realm, from central Africa to South Africa.

Phylogenetic Relationships

Allomedeia is a member of the *Anatrichus* clade, sister group to *Alombus*, *Sepsidoscinis* and *Anatrichus*. All these genera are restricted to the Old World tropics.

Remarks

The structure of the male genitalia, especially the fused cerci, is a strong defining character for this group. Although medially fused male cerci is probably an apomorphy for the subfamily Chloropinae, it is an unusual character in oscinellines.

Etymology

The name is derived from the Greek *Allo* (different) and *Medos* (genitals), referring to the unusual shape of the male genitalia. The gender of the name is feminine.

Material examined

Allomedeia xanthotes sp. n., [**AT**]: 1 ♂, 4 ♀♀, 1 sex unknown (NMSA).

Allomedeia sp. 2, [**AT**]: 3 ♂♂, 8 ♀♀ (NMSA).

Allomedeia sp. 3, [**AT**]: 2 ♂♂, 3 ♀♀, 1 sex unknown (CNC).

***Allomedeia xanthotes* sp. n.**

(Figs. 11-17)

Diagnosis: Oscinelline with antennal segment thin at base, a very shiny thorax, a black postpronotum and a yellow scutellum with no tubercles.

Description: Total length 2.8-3.2mm. Overall colour black; frontal triangle black sometimes anteriorly paler, shining, 0.8-0.85 times length of frons; ocellar tubercle black, shining; frons yellow, darkening anteriorly; cephalic setae dark, 4 fronto-orbital setae

weakly developed, interfrontal setulae along margin of frontal triangle and fronto-orbital setulae sparse, weak; gena black, shiny, microtomentose anteriorly, 0.06 times eye height; face yellow, scape and pedicel yellow, first flagellomere yellow, darker on dorsal edge, first flagellomere reniform, arista black, yellow basally, pubescence sparse and weak (Fig. 12); clypeus, palpus and proboscis yellow.

Scutum black, shiny except for pollinose pre-scutellar region, scutum longer than wide; scutellum yellow, paler than scutum, trapezoidal (Fig. 14), 1.5 to 1.75 times as wide as long, microtomentose; apical scutellar bristles strong, on small tubercles on upper margin of scutellum, lateral scutellar bristles unrecognizable from surrounding setea. Legs yellow, femora distally brown; femoral organ absent, tibial organ linear, pale, occupying middle fifth of hind tibia. Wing with pale brown infuscations between R_{4+5} and M_{1+2}; veins darkened (Fig. 13); ratio of costal sectors C1: C2: C3: C4 – 1: 1.5: 1.4: 0.4; halter pale yellow.

Abdomen same color as thorax (in some specimens paler medially), sparsely microtomentose; syntergite 1+2 uniformly sclerotized, twice as long as other tergites.

Male postabdomen (Figs. 15-17): small; epandrium slightly higher than long in lateral view, wider than high in posterior view, with several setae; surstylus 0.5 times the height of epandrium, round, with broadly rounded apex, surstylus with sparse setae; cercus fused, rectangular with rounded edges, cercus with long setae; distiphallus weakly sclerotized, straight, blunt ended.

Type Material: Holotype ♂: SOUTH AFRICA: Port St. Johns Dist: Coastal forest, E Cape Prov, 16-17.x.1959, B. & P. Stuckenberg (NMSA); Paratypes: same data as

holotype (1 sex unknown, NMSA); same data as holotype except, xi.1961 (1♀, NMSA); Port St Johns, B. & P. Stuckenberg, 20-25.xi.1961 (1♀, NMSA); Ngome forest between Vryheid & Nongoma, Natal, 11-12.iv.1960, B. & P. Stuckenberg (1♀, NMSA); Dhlinza forest, Eshowe, Zululand, 5-6.iv.1960, B. & P. Stuckenberg (1♀, NMSA).

Etymology: The species name is from the Greek *xanthos* (yellow), referring to the yellow color of the scutellum.

3.3.4. *Alombus* Becker, 1914

(Figs. 18-23)

Alombus Becker, 1914: 129. Type species: *Alombus politus* Becker, 1914.

Diagnosis

Chloropidae, Oscinellinae with wings and halteres completely lost. Very small, black, reduced bristling, one long posterior notopleural, very small scutellum, tergites 1+2 large and sclerotized.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view (Fig. 18); frontal triangle shining and bare; frons bare to microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate short postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size; eye sparsely and microscopically pubescent; gena narrow,

vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere round-reniform, higher than wide, arista longer than width of frons, and slender (Fig. 19); proboscis and palpus short, black.

Scutum as wide as long; thoracic chaetotaxy: 0 anterior, 1 posterior notopleural, 0 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum rounded dorsally, triangular, usually wider than long (Fig. 20); 1 pair apical long scutellar bristles, no or 1 pair of lateral scutellar bristles almost unrecognisable. Wing absent; halteres absent. Legs slender; male femoral organ present as two rows of 3-5 tubercles; small, apical ventral spur on mid tibia; hind tibial spur absent; tibial organ oval, sometimes very narrow, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly shiny, large; sternites small, with sparse setae, abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view and wider than high in posterior view; surstylus simple, clavate or quadrate; hypandrium closed posteriorly; cercus small, round, projecting ventrally (Figs. 21-23).

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Species of *Alombus* are restricted to the Afrotropical region, at high elevations in central Africa.

Phylogenetic Relationships

Alombus is most closely related to *Sepsidoscinis* and *Anatrichus* based on multiple characters: the head much longer than high in lateral view, a round third antennal segment, highly modified, triangular scutellum, and the constriction at the base of the abdomen.

Remarks

Alombus is a genus of very modified chloropids, especially because of the complete loss of wings. However, its monophyly and family placement have never been questioned.

Material examined

Alombus meruensis (Richards, 1955), [**AT**]: 1 ♂ (USNM).

Alombus seminitidus (Villeneuve, 1934), [**AT**]: 3 ♂♂, 3 ♀♀ (USNM).

3.3.5. *Anatrichus* Loew, 1860

(Figs. 24-30)

Anatrichus Loew, 1860: 97. Type species: *Anatrichus erinaceus* Loew, 1860.

Myrmecosepsis Kertesz, 1914: 244. Type species: *Myrmecosepsis hystrix* Kertesz, 1914 **new synonym.**

Echinia Paramonov, 1961: 97. Type species: *Echinia bisegmenta* Paramonov, 1961.

New combinations

Anatrichus hystrix (Kertesz, 1914) **comb. nov.** (*Myrmecosepsis*); *Anatrichus taprobane*

(Andersson, 1977) **comb. nov.** (*Myrmecosepsis*).

Diagnosis

Chloropidae, Oscinellinae with long spines on thorax and scutellum, abdominal tergites fused into one large dorsal plate and slender arista.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view (Fig. 24); frontal triangle shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere reniform, as long as wide, arista longer than width of frons, and slender (Fig. 25); proboscis and palpus short.

Scutum square, as wide as long; covered in spines, thoracic chaetotaxy: modified into spines, many anterior, many posterior notopleurals, many postsutural supra-alar bristle, many dorsocentral bristles; scutellum round to flat dorsally, triangular, rounded at tip, usually longer than wide, covered in spines (Fig. 26); many scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing present or absent, short or long, narrow, with or without markings, second costal sector longer than third costal sector when wings long, or shorter than third costal sector when wings reduced, distance between crossveins r-m and dm-cu 2-3 times length of dm-cu, anal angle reduced, alula

small, much longer than wide; veins pale (Figs. 24, 30); halter white. Legs long and slender; male femoral organ absent or present as two rows of 5 tubercles; small, apical ventral spur on mid tibia; hind tibial spur absent or present, usually apical; tibial organ oval, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites 1+2+3 fused into large plate covering the abdomen, setulose laterally, with textured base or dorsal region, tergites 4 and 5 very narrow, hidden under large fused tergite (Fig. 27); sternites divided into many small sclerotized regions, with sparse setae, abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view and wider than high in posterior view (Fig. 28); surstylus simple, parallel sided with a pointed tip (Fig. 29); hypandrium closed posteriorly; cercus wide, rectangular to triangular, projecting dorsoventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Anatrichus is mostly restricted to the Afrotropical and Oriental realms. *Anatrichus pygmaeus* has been introduced into Northern Australia (Paramonov 1961).

Phylogenetic Relationships

Anatrichus is the terminal group of the *Anatrichus* clade because of many highly derived

characters. It is the sister group to *Sepsidoscinis*.

Material examined

Anatrichus erinaceus Loew, 1860, [**AT**]: 17 ♂♂, 15 ♀♀, 2 sex unknown (CNC).

Anatrichus hystrix (Kertesz, 1914), [**OR**]: 1 ♂ (USNM).

Anatrichus pygmaeus Lamb, 1918, [**AU**, **OR**]: 5 ♂♂, 1 ♀ (LEM); 5 ♂♂, 7 ♀♀ (CNC); 2 ♂♂ (USNM).

Anatrichus taprobane (Andersson, 1977), [**OR**]: 1 ♀ (CNC); 3 ♂♂, 4 ♂♂ (USNM).

3.3.6. *Ceratobarys* Coquillett, 1898

(Figs. 31-34)

Ceratobarys Coquillett, 1898: 45. Type species *Hippelates eulophus.*

New combinations

Ceratobarys attenuata (Adams, 1908) **comb. nov.** (*Elachiptera*); *Ceratobarys cultrata* (Wheeler and Forrest, 2002) **comb. nov.** (*Elachiptera*); *Ceratobarys flavida* (Williston, 1896) **comb. nov.** (*Elachiptera*); *Ceratobarys melinifrons* (Mlynarek and Wheeler, 2008) **comb. nov.** (*Elachiptera*); *Ceratobarys fucosa* (Mlynarek and Wheeler, 2008) **comb. nov.** (*Elachiptera*); *Ceratobarys queposana* (Mlynarek and Wheeler, 2008) **comb. nov.** (*Elachiptera*); *Ceratobarys rubida* (Becker, 1912) **comb. nov.** (*Elachiptera*); *Ceratobarys sacculicornis* (Enderlein, 1911) **comb. nov.** (*Elachiptera*); *Ceratobarys willistoni* (Sabrosky, 1948) **comb. nov.** (*Elachiptera*).

Diagnosis

Chloropidae, Oscinellinae with a trapezoidal scutellum with 2 small tubercles, first flagellomere elongated dorsally, and thick arista.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view; frontal triangle long, shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on or slightly on inner margin of frontal triangle, fronto-orbital bristles reclinate, long, sometimes 2 slightly longer than the others; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere reniform, dorsal region elongate, higher than wide, arista longer than width of frons, and thick (Fig. 31); proboscis and palpus short.

Scutum rectangular, longer than wide; thoracic chaetotaxy: 1 anterior, 1 posterior notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum flat dorsally, trapezoidal, usually wider than long (Fig. 32); 1 pair apical scutellar bristles on small tubercles, 1 pair of lateral scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, usually clear (darkened in *C. fucosa*), second costal sector equal to or shorter than third costal sector, distance between crossvein r-m and dm-cu 2.5 - 3 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins pale or darkened; halter white. Legs long and slender; male femoral organ present as 1-3 rows of 3-5 tubercles; small, apical ventral spur on mid

tibia; hind tibial spur present or absent, usually apical, length variable; tibial organ oval, sometimes very narrow, 0.25 to 0.3 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites narrow, with sparse setae, abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view (Fig. 34) and wider than high in posterior view (Fig. 33); surstylus simple, very narrow; hypandrium closed posteriorly; pregonite fused with postgonite, weakly sclerotized; basiphallus elongate, weakly sclerotized; distiphallus short, membranous; phallapodeme simple; phallic guide sclerotized; cercus small, triangular, projecting dorsoventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Ceratobarys is restricted to the Neotropical region except for *C. eulophus* and *C. willistoni* from the southern Nearctic region.

Phylogenetic Relationships

Ceratobarys is most closely related to the *Melanochaeta* and *Elachiptera* clade.

Remarks

The genus was synonymized with *Elachiptera* by Wheeler and Forrest (2002) because the

type, and only included species (*C. eulophus*) was considered closely related to the other Neotropical *Elachiptera* with a yellow, trapezoidal scutellum. The only distinguishing character was the long hind tibial spur in *Ceratobarys* (small or absent in *Elachiptera*). Although my analysis confirmed that *C. eulophus* is congeneric with those Neotropical species, it is not congeneric with the type species of *Elachiptera*. Thus, I have reinstated *Ceratobarys* as the valid name for this mostly Neotropical clade.

Material examined

Ceratobarys attenuata (Adams, 1908), [**NT**]: 5 ♂♂, 5 ♀♀ (LEM); 3 ♀♀ (USNM).

Ceratobarys cultrata (Wheeler and Forrest, 2002), [**NT**]: 4 ♂♂, 5 ♀♀, 1 sex unknown paratypes (LEM).

Ceratobarys eulophus (Loew, 1872), [**NE**]: 7 ♂♂, 6 ♀♀ (LEM); 1 ♂, 1 ♀ (USNM).

Ceratobarys flavida (Williston, 1896), [**NT**]: 8 ♂♂, 11 ♀♀ (LEM).

Ceratobarys melinifrons (Mlynarek and Wheeler, 2008), [**NT**]: 2 ♂♂, 1♀ paratypes (USNM).

Ceratobarys fucosa (Mlynarek and Wheeler, 2008), [**NT**]: 2♀♀ (LEM); 2 ♂♂, 2 ♀♀ paratypes (USNM).

Ceratobarys queposana (Mlynarek and Wheeler, 2008), [**NT**]: 15 ♂♂, 11 ♀♀ paratypes (LEM).

Ceratobarys rubida (Becker, 1912), [**NT**]: 2 ♀♀ (LEM) 1 ♂, 1 ♀ (USNM) 1 ♂, 2 ♀♀ (CNC).

Ceratobarys sacculicornis (Enderlein, 1911), [**NT**]: 8 ♂♂, 5 ♀♀ (LEM); 2 ♂♂, 2 ♀♀ (CNC).

Ceratobarys willistoni (Sabrosky, 1948), [**NE**]: 1 ♂, 1 ♀ (LEM); 2 ♂♂ paratypes, 2 ♂♂, 1 ♀ (USNM).

3.3.7. *Disciphus* Becker, 1911

(Figs. 35-40)

Disciphus Becker, 1911: 98. Type species: *Disciphis peregrinus* Becker 1911.

Diagnosis: Chloropidae, Oscinellinae with a patterned wing, a trapezoidal scutellum with a pair of long tubercles and long slender arista.

Description: Chloropidae, Oscinellinae. Vertex of head rounded in lateral view (Fig. 35); frontal triangle shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on inner margin of frontal triangle, fronto-orbital bristles reclinate, one longer than others; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere reniform, higher than wide, arista longer than width of frons, and slender (Fig. 36); proboscis and palpus short.

Scutum square, as wide as long; thoracic chaetotaxy: 1 anterior, 1 posterior notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum flat dorsally, trapezoidal, usually wider than long, with a pair of very long scutellar tubercles (Fig. 38); 1 pair apical scutellar bristles, 1 pair of lateral scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, with a

pattern, second costal sector equal longer than third costal sector, distance between crossvein r-m and dm-cu 3.5 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins dark; halter white (Fig.37). Legs long and slender; male femoral organ present as 1-3 rows of 8-10 tubercles; small, apical ventral spur on mid tibia; hind tibial spur absent; tibial organ oval, sometimes very narrow, 0.2 to 0.25 times length of hind tibia.

Abdomen slender, abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites slender, with sparse setae, abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view (Fig. 40) and wider than high in posterior view (Fig. 39); surstylus simple, parallel sided; hypandrium open posteriorly; cercus small, rectangular, projecting posteroventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Disciphus is restricted to the Oriental realm. As previously defined, the distribution of *Disciphus* also included the Palearctic region (Japan). However, based on this study, the Japanese species (*Disciphus subelongatus*) has been transferred to *Elachiptera*.

Phylogenetic Relationships

Although Andersson (1977) assigned *Disciphus* to the *Elachiptera* genus group he

believed that it was closely related to *Elachiptera* and *Melanochaeta*. This analysis confirms that *Disciphus* belongs in Elachipterini, but is the basal genus of the *Anatrichus* clade.

Material examined

Disciphus alatus Becker, 1911, [**OR**]: 8 ♂♂, 2 ♀♀ (LEM).

Disciphus flavitarsis Duda, 1930, [**OR**]: 3 ♂♂ (LEM).

Disciphus peregrinus Becker, 1911, [**OR**]: 5 ♂♂ (LEM); 6 ♂♂, 2 ♀♀ (USNM).

3.3.8. *Elachiptera* Macquart, 1835

(Figs. 41-45)

Elachiptera Macquart, 1835: 621. Type species: *Chlorops brevipennis* Meigen (orig. des.).

Crassiseta von Roser, 1840: 63. Type species: *Oscinis cornuta* Fallen, 1820.

Pachychaeta Loew, 1845: 50. Type species: *Oscinis cornuta* Fallen, 1820.

Macrochetum Rondani, 1856: 127. Type species: *Oscinis cornuta* Fallen, 1820.

Myrmecomorpha Corti, 1909: 141. Type species: *Chlorops brevipennis* Meigen, 1830.

Cyrtomomyia Becker, 1913: 166. Type species: *Cyrtomomyia pulchra* Becker 1913 **new synonym.**

Doliomyia Johannsen 1924: 89. Type species: *Melanochaeta longiventris* Johannsen, 1924.

Neoelachiptera Séguy 1938: 360. Type species: *Neoelachiptera lerouxi* Séguy, 1938

Chaetaspis Nishijima 1954: 84. Type species: *Chaetaspis katoi* Nishijima, 1954 (Preocc.

Bollman, 1887).

Togeciphus Nishijima 1955: 53. Type species: *Chaetaspis katoi* Nishijima, 1954 (replacement name for *Chaetaspis* Nishijima). **new synonym.**

New combinations

Elachiptera ensifer (Sabrosky, 1951) **comb. nov.** (*Cyrtomomyia*); *Elachiptera katoi* (Nishijima, 1955) **comb. nov.** (*Togeciphus*); *Elachiptera maculinervis* (Becker, 1910) **comb. nov.** (*Cyrtomomyia*); *Elachiptera punctulata* (Becker, 1912) **comb. nov.** (*Cyrtomomyia*); *Elachiptera subelongatus* (Kanmiya, 1983) **comb. nov.** (*Disciphus*); *Elachiptera tuberculata* (Adams, 1905) **comb. nov.** (*Cyrtomomyia*).

Diagnosis

Chloropidae, Oscinellinae with a reniform 3rd antennal segment slightly elongated dorsally, a thick arista and a flat, rugose, round scutellum with many tubercles.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view; frontal triangle shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size to 2 longer than the other; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first

flagellomere reniform, higher than wide, arista longer than width of frons, and slender (Fig. 41); proboscis and palpus short.

Scutum square to longer than wide; thoracic chaetotaxy: 1 anterior, 1 posterior notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum flat dorsally, round, usually wider than long, usually rugose (Fig. 42); 1 pair apical scutellar bristles on tubercles, 1 or 2 pairs of lateral scutellar bristles on tubercles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, clear or with some markings, second costal sector equal to or shorter than third costal sector, distance between crossvein r-m and dm-cu 2.4 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins pale; halter white. Legs long and slender; male femoral organ present as 1-3 rows of 3-5 tubercles; small, apical ventral spur on mid tibia; hind tibial spur usually absent or short and apical; tibial organ oval, sometimes very narrow, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites slender, with sparse setae, abdominal membrane not sclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view (Fig. 44) and wider than high in posterior view (Fig. 43); surstylus simple, clavate or quadrate; hypandrium open posteriorly (Fig. 45); cercus small, triangular, projecting dorsoventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Elachiptera is widespread in the Nearctic, Palearctic, Afrotropical regions.

Phylogenetic Relationships

Elachiptera is the sister group to *Melanochaeta* based on scutellum shape.

Remarks

All Neotropical species previously assigned to *Elachiptera* are now in *Ceratobarys*.

Material examined

Elachiptera angusta Sabrosky, 1948, [**NE**]: 5 ♂♂, 4 ♀♀ (LEM).

Elachiptera aquila Wheeler, 2003, [**NE**]: 1 ♂♂, 6 ♀♀ paratypes (LEM); 1 ♂, 1 ♀ (LEM).

Elachiptera bimaculata (Loew, 1845), [**PA**]: 1 ♀ (LEM); 5 ♂♂, 4 ♀♀ (CNC); 5 ♂♂, 3 ♀♀ (USNM).

Elachiptera brevipennis (Meigen, 1830), [**PA**]: 2 ♂♂, 6 ♀♀ (USNM).

Elachiptera cornuta (Fallen, 1820), [**PA**]: 4 ♂♂, 6 ♀♀ (LEM); 1 ♂ (CNC); 4 ♂♂, 4 ♀♀ (USNM).

Elachiptera costata (Loew, 1863), [**NE**]: 30 ♂♂, 44 ♀♀ (LEM).

Elachiptera decipiens (Loew, 1863), [**NE**]: 6 ♂♂, 7 ♀♀ (LEM).

Elachiptera diastema Collin, 1946, [**PA**]: 16 ♂♂, 13 ♀♀ (CNC).

Elachiptera ensifer Sabrosky, 1951, [**AT**]: 2 ♂♂, 5 ♀♀ (USNM).

Elachiptera erythropleura Sabrosky, 1948, [**NE**]: 4 ♂♂, 5 ♀♀ (LEM).

Elachiptera flaviceps Sabrosky, 1948, [**NE**]: 11 ♂♂, 4 ♀♀ (LEM).

Elachiptera formosa (Loew, 1863), [**NE**]: 5 ♂♂, 3 ♀♀ (USNM).

Elachiptera insignis (Thomson, 1869), [**PA**]: 2 ♂♂ (LEM); 4 ♂♂, 2 ♀♀ (USNM).

Elachiptera katoi (Nishijima, 1954), [**PA**]: 9 ♂♂, 2 ♀♀ (USNM).

Elachiptera longiventris (Johannsen, 1924), [**NE**]: 1 ♀ paratype, 2 ♀♀ (USNM).

Elachiptera megaspis (Loew, 1858), [**PA**]: 7 ♂♂, 7 ♀♀, 1 sex unknown (LEM); 24 ♂♂, 18 ♀♀ (CNC); 5 ♂♂, 4 ♀♀ (USNM).

Elachiptera molybdeana Séguy, 1957, [**AT**]: 1 ♂, 2 ♀♀ (USNM).

Elachiptera nigriceps (Loew, 1863), [**NE**]: 36 ♂♂, 35 ♀♀ (LEM).

Elachiptera occipitalis Becker, 1910, [**AT**]: 1 ♂, 2 ♀♀ (LEM); 1 ♀ (CNC); 3 ♂♂, 5 ♀♀ (USNM).

Elachiptera pechumani Sabrosky, 1948, [**NE**]: 3 ♂♂, 8 ♀♀ (LEM); 14 ♂♂, 7 ♀♀, 1 sex unknown (CNC).

Elachiptera penita (Adams, 1908), [**NE**]: 22 ♂♂, 24 ♀♀ (LEM); 3 ♂♂, 1 ♀ (USNM).

Elachiptera punctulata Becker, 1912, [**AT**]: 2 ♂♂, 1 ♀ (NATAL).

Elachiptera subelongatus (Kanmiya, 1983), [**PA**]: 2 ♂♂, 2 ♀♀ (LEM); 1 ♂ paratype (USNM).

Elachiptera tanganyikae Sabrosky, 1965, [**AT**]: 1 ♂ paratype, 1 ♀ paratype (USNM).

Elachiptera tarda (Adams, 1905), [**AT**]: 2 ♂♂, 3 ♀♀ (BMNH).

Elachiptera tuberculata (Adams, 1905), [**AT**]: 3 ♂♂ (USNM).

Elachiptera tuberculifera (Corti, 1909), [**PA**]: 1 ♂ (LEM); 3 ♂♂ (CNC); 3 ♂♂, 2 ♀♀ (USNM).

Elachiptera vittata Sabrosky, 1948, [**NE**]: 9 ♂♂, 20 ♀♀ (LEM); 13 ♂♂, 12 ♀♀ (CNC).

3.3.9. *Goniaspis* Duda, 1930

(Figs. 46-49)

Goniaspis Duda, 1930: 59. Type species: *Cadrema rubra* Becker, 1916 (subs. des. by Duda 1931: 165).

Paleoenderleiniella Duda, 1930: 57. Type species: *Cadrema rubra* Becker, 1916 (subs. des. by Sabrosky 1941b: 761)

Diagnosis

Chloropidae, Oscinellinae with an apicoventral, hind-tibial spur, trapezoidal scutellum and long slender arista.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view; frontal triangle shining and bare; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere reniform, higher than wide, arista longer than width of frons, and slender (Fig. 46); proboscis and palpus short.

Scutum square, as wide as long; thoracic chaetotaxy: 1 anterior, 1 posterior notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum usually flat dorsally, trapezoidal, usually wider than long (Fig. 47); 1 pair apical scutellar bristles on

small tubercles, 1 or 2 pairs of lateral scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, with no markings, second costal sector equal to or shorter than third costal sector, distance between crossvein r-m and dm-cu 2.4 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins pale; halter white. Legs long and slender; male femoral organ present as two rows of 3-5 tubercles; small, apical ventral spur on mid tibia; hind tibial spur present, usually apical, length usually more than twice diameter of hind tibia; tibial organ oval, sometimes very narrow, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites slender, with sparse setae, abdominal membrane desclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view (Fig. 49) and wider than high in posterior view (Fig. 48); surstylus simple, clavate or quadrate; hypandrium closed posteriorly; cercus small, triangular, projecting posteroventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Species of *Goniaspis* have been recorded only from the Neotropical region including the Caribbean.

Phylogenetic Relationships

Goniaspis is the basal genus of the *Elachiptera* clade, and the sister group to the clade containing *Ceratobarys*, *Melanochaeta* and *Elachiptera.* This supports Sabrosky's (1984) and Mlynarek and Wheeler's (2009) suggestion that this genus is a member of Elachipterini and not Hippelatini.

Remarks

Goniaspis has recently been revised (Mlynarek and Wheeler 2009). As a result of this analysis, the generic limits have expanded to include an undescribed Puerto Rican species with a short hind tibial spur.

Material examined

Goniaspis rubra (Becker, 1916), [**NT**]: 6 ♂♂, 4 ♀♀ (CNC); 4 ♂♂, 9 ♀♀ (USNM).

Goniaspis truncata (Malloch, 1913), [**NT**]: 1 ♂, 2 ♀♀ (LEM); 1 ♀ holotype, 1 ♂ paratype, 2 ♀♀ paratypes, 13 ♂♂, 11 ♀♀ (USNM); 1 ♂, 1 ♀ (DEBU).

Goniaspis equalis (Williston, 1896), [**NT**]: 1 ♀ (LEM); 2 ♂♂ syntypes, 1♀ syntype (BMNH).

Goniaspis lucia Mlynarek and Wheeler 2009, [**NT**]: 27 ♂♂, 9 ♀ paratypes (LEM).

Goniaspis n. sp., [**NT**]: 6 ♂♂, 2 ♀♀ (USNM).

3.3.10. *Melanochaeta* Bezzi, 1906

(Figs. 50-54)

Pachychoeta Bezzi, 1895: 72 (preocc. by Bigot, 1857). Type species: *Elachiptera atterima* Strobl, 1880 = *capreolus* (Haliday, 1838)

Melanochaeta Bezzi, 1906: 50 (replacement name for *Pachychoeta* Bezzi 1895). Type species: *Elachiptera atterima* Strobl, 1880 = *capreolus* (Haliday, 1838)

Pachychaeta , error or emend.

Pachychaetina Hendel, 1907: 98 (unnecessary replacement name for *Pachychoeta* Bezzi, 1895.) Type species: *Oscinis capreolus* Haliday, 1838

Lasiochaeta Corti, 1909: 147. Type species: *Elachiptera pubescens* Thalhammer, 1898

Diagnosis

Chloropidae, Oscinellinae with round and smooth scutellum, a reniform third antennal segment, slender to thick arista with heavy pubescence and two fronto-orbital bristles longer than the others.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view; frontal triangle shining, bare to pollinose; frons microtomentose; cephalic chaetotaxy: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, 2 longer than others; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct; face flat, wide, carina absent; first flagellomere reniform, higher than wide, arista longer than width of frons, slender to flat and wide, always heavily pubescent (Fig. 50); proboscis short, palpus short to longer.

Scutum square, as wide as long; thoracic chaetotaxy: 1 anterior, 2 posterior notopleurals (upper posterior sometimes weak), 1 postsutural supra-alar bristle, 1

dorsocentral bristle; scutellum rounded dorsally, round, wider than long (Fig. 51); 1 pair apical scutellar bristles, 1 pairs of lateral scutellar bristles; thoracic pleurites bare except for a row of setulae on katepisternum. Wing long, narrow, with no markings, second costal sector equal to third costal sector, distance between crossvein r-m and dm-cu 2-4 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins pale; halter white. Legs long and slender; male femoral organ present as 1-3 rows of 4-6 tubercles; small, apical ventral spur on mid tibia; hind tibial spur absent; tibial organ oval, sometimes very narrow, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites setulose laterally and with sparse setae posteriorly, mostly microtomentose; sternites slender, with sparse setae, abdominal membrane not sclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view and wider than high in posterior view (Fig. 52); surstylus simple, narrow, parallel sided (Fig. 53); hypandrium closed posteriorly (Fig. 54); cercus small, triangular, projecting posteroventrally.

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

Melanochaeta is distributed in the Palearctic, Afrotropical, Oriental and Nearctic realms, with highest species richness in the Afrotropical and Palearctic realms.

Phylogenetic Relationships

Melanochaeta is most closely related to *Elachiptera* based on cephalic bristling and shape of the scutellum.

Material examined

Melanochaeta atricornis (Adams, 1905), [**AT**]: 2 ♂♂, 7 ♀♀ (USNM).

Melanochaeta capreolus (Haliday, 1838), [**PA**]: 4 ♂♂, 8 ♀♀ (USNM).

Melanochaeta dubia (Lamb, 1918), [**AT**]: 5 ♂♂, 3 ♀♀ (USNM).

Melanochaeta eunota (Loew, 1872), [**NE**]: 3 ♂♂, 3 ♀♀ (LEM).

Melanochaeta flavifrontata (Becker, 1903), [**AT, PA**]: 1 ♂, 8 ♀♀ (LEM); 1 ♂ (CNC); 4 ♂♂, 4 ♀♀ (USNM).

Melanochaeta freyi (Duda, 1934), [**AT**]: 2 ♂♂, 3 ♀♀ (USNM).

Melanochaeta indistincta (Becker, 1911), [**OR**]: 5 ♂♂, 1 ♀ (USNM).

Melanochaeta kaw Sabrosky, 1948, [**NE**]: 1 ♂ paratype, 2 ♀♀ paratypes, 4 ♂♂, 1 sex unknown (USNM).

Melanochaeta lindbergi (Sabrosky, 1957), [**AT**]: 4 ♂♂ paratypes, 4 ♀♀ paratypes (USNM).

Melanochaeta pubescens (Thalhammer, 1896), [**PA**]: 17 ♂♂, 7 ♀♀ (LEM); 10 ♂♂, 1 ♀ (CNC); 3 ♂♂, 1 ♀ (USNM).

Melanochaeta scapularis (Adams, 1905), [**AT**]: 14 ♂♂, 17 ♀♀ (LEM); 10 ♂♂, 14 ♀♀ (CNC).

Melanochaeta umbrosa (Becker, 1924), [**OR**]: 3 ♂♂, 2 ♀♀ (USNM).

Melanochaeta vulgaris (Adams, 1905), [**AT**]: 5 ♂♂ 12 ♀♀ (LEM); 2 ♂♂, 1 ♀ (CNC).

3.3.11. *Sepsidoscinis* Hendel, 1914

(Figs. 55-62)

Sepsidoscinis Hendel, 1914: 247. Type species: *Sepsidoscinis maculipennis* Hendel, 1914.

Diagnosis

Chloropidae, Oscinellinae with a laterally compressed head, an elongated postpronotum, contracted abdomen at base, triangular scutellum with long tubercles, short, patterned wings and long slender arista.

Description

Chloropidae, Oscinellinae. Vertex of head rounded in lateral view, head compressed in lateral view (Fig. 55); frontal triangle shining and bare; frons shining; cephalic chaetotaxy reduced: long peristomal bristles, cruciate postocellar bristles, cruciate short ocellar bristles, long outer vertical bristles, interfrontal bristles long and on margin of frontal triangle, fronto-orbital bristles reclinate, of equal size; eye sparsely and microscopically pubescent; gena narrow, vibrissal angle rounded, indistinct, vibrissa with 2 similar bristles; face flat, wide, carina absent; first flagellomere reniform, as long as wide, arista longer than width of frons, and slender (Fig. 57); proboscis and palpus short.

Scutum widening posteriorly (Fig. 56), as wide as long; thoracic chaetotaxy: 1 anterior, 1 posterior weak notopleurals, 1 postsutural supra-alar bristle, 1 dorsocentral bristle; scutellum dorsally flat dorsally, creating 45º angle with scutum, giving impression of a triangular point, usually wider than long (Figs. 55, 59-60); 1 pair apical scutellar

bristles, 1 or 2 pairs of lateral scutellar bristles on long tubercles (Figs. 59-60); thoracic pleurites bare except for a row of setulae on katepisternum. Wing short, narrow, with a wide spot at center (Fig. 58), second costal sector equal to or shorter than third costal sector, distance between crossvein r-m and dm-cu 2.4 times length of dm-cu, anal angle reduced, alula small, much longer than wide; veins pale; halter white. Legs long and slender; male femoral organ absent; small, apical ventral spur on mid tibia; hind tibial spur absent; tibial organ narrow, 0.2 to 0.25 times length of hind tibia.

Abdominal tergites shiny, tergites 1+2 very narrow dorsally, tergite 3 enlarged (Fig. 56); sternites slender, with sparse setae, abdominal membrane not sclerotized; male spiracles 3-5 in membrane near lateral margin of tergite.

Male postabdomen: pregenital sclerites narrow; spiracles 6 and 7 in membrane ventral to lateral margin of dorsal sclerite; epandrium rounded, usually higher than long in lateral view (Fig. 62) and wider than high in posterior view (Fig. 61); surstylus bi-lobed, upper lobe clavate, lower lobe ending in pointed tip; hypandrium open posteriorly; cercus fused with two projections, thin, projecting posteroventrally (Fig. 61).

Female terminalia not modified, cerci separate, round, setulose.

Geographic distribution

This monotypic genus is restricted to the Oriental realm in southern China, Nepal, India, Sri Lanka, Indonesia and Vietnam.

Phylogenetic Relationships

Sepsidoscinis is the sister group to *Anatrichus*.

Remarks

Although *Sepsidoscinis* is a monotypic genus and is closely related to *Anatrichus.* I have decided to retain it as a separate genus for ease of recognition and nomenclatural stability.

Material examined

Sepsidoscinis maculipennis (Hendel, 1914), [**OR**]: 1 ♂, 1 ♀ (LEM); 1 ♀ (CNC); 3 ♂♂, 7 ♀♀, 1 sex unknown (USNM).

4. CONCLUSION AND RECOMMENDATIONS FOR FUTURE WORK

Andersson (1977) came to the conclusion that the chloropids are not amenable to the cladistic method, because of extensive homoplasy in the characters that are generally used for defining genera in the family (e.g., antennal shape, wing venation, patterns of color and texture). He suggested that the chloropids may have evolved too recently for phylogenetic analysis to reveal clear patterns of relationship (Andersson 1977, 1979). However, Andersson's analysis was done by hand and was based on too few exemplar species and characters to be able to see clear evolutionary patterns. By accepting that many characters are homoplasious and by coding enough characters and species as exemplars, it was possible in this study to conduct a phylogenetic analysis and construct a well-supported hypothesis on the evolutionary relationships of a widespread and species-rich subgroup of Chloropidae.

This thesis represents an important contribution to the systematics of the Chloropidae, because it includes the first phylogenetically based hypothesis of generic relationships for any tribe of chloropids.

Although the phylogenetic analysis supported the monophyly of several recognized genera of Elachipterini, it has necessitated changes in the classification of the tribe. The analysis demonstrated support for the monophyly of the tribe and many of the genera as previously recognized: *Melanochaeta*, *Goniaspis*, *Alombus*, *Sepsidoscinis* and *Disciphus*. Three genera have been synonymised: *Cyrtomomyia*, *Togeciphus* and *Myrmecosepsis*. The limits to the remaining genera have been redefined, with *Ceratobarys* resurrected as a valid genus and one new genus, *Allomedeia*, described. The limits of *Elachiptera* have been changed significantly in order to make the genus

monophyletic. A revised checklist of all the species of Elachipterini is presented in Appendix 3.

The phylogeny also illustrates some interesting biogeographical patterns within the tribe. The *Anatrichus* clade is restricted to the Old World tropics, with *Disciphus* and *Sepsidoscinis* restricted to the Oriental region, *Alombus* and *Allomedeia* endemic to the Afrotropical region, and *Anatrichus* shared by both realms, and introduced to Australia. The *Elachiptera* clade is more widespread, but the two basal genera, *Goniaspis* and *Ceratobarys*, are primarily Neotropical. *Melanochaeta* and *Elachiptera* are each found in multiple realms, primarily Holarctic and Afrotropical, and reconstructing their geographic history would require comprehensive revisions of those genera.

Although this analysis is a major step forward in the understanding of relationships within the Chloropidae, it should be stressed that this is a preliminary hypothesis that should be tested in future studies. Several potential tests of this hypothesis, or expansions of this project should be considered:

1. Testing the phylogeny of the Elachipterini through the addition of exemplar species, and confirming the generic placement of those species. This would be especially relevant for the as yet unplaced species of "*Elachiptera*" listed in Appendix 3.
2. Testing the phylogeny of the Elachipterini through the use of different character sets, such as molecular sequence data or morphometric analysis. The use of additional life stages would require the collection of larvae of many more species, and is probably premature at present.

3. Worldwide revisions of the genera of Elachipterini based on the revised generic definitions. Although *Goniaspis* has recently been revised (Mlynarek and Wheeler 2009), most other genera are in need of species descriptions, species-level phylogenetic analyses, and revised keys to species.
    a. At this point in time, revising *Elachiptera* would be valuable. This analysis has changed the limits of *Elachiptera* and, as mentioned previously, there remain several unplaced "*Elachiptera*" species (Appendix 3).
    b. Revising *Anatrichus* would also be relevant. Throughout this study, many examined specimens are not consistent with any described species. Since the species are important in pest management in rice production, proper identification of *Anatrichus* species is necessary.
4. Expanding the matrix to include additional tribes and genera of the subfamily Oscinellinae, in order to provide a framework for phylogeny of the Chloropidae.
5. Studying in more detail the biogeographical patterns of the Elachipterini and hypothesizing on the origins and dispersal of the tribe and included genera, especially the widespread genera *Elachiptera* and *Melanochaeta*.

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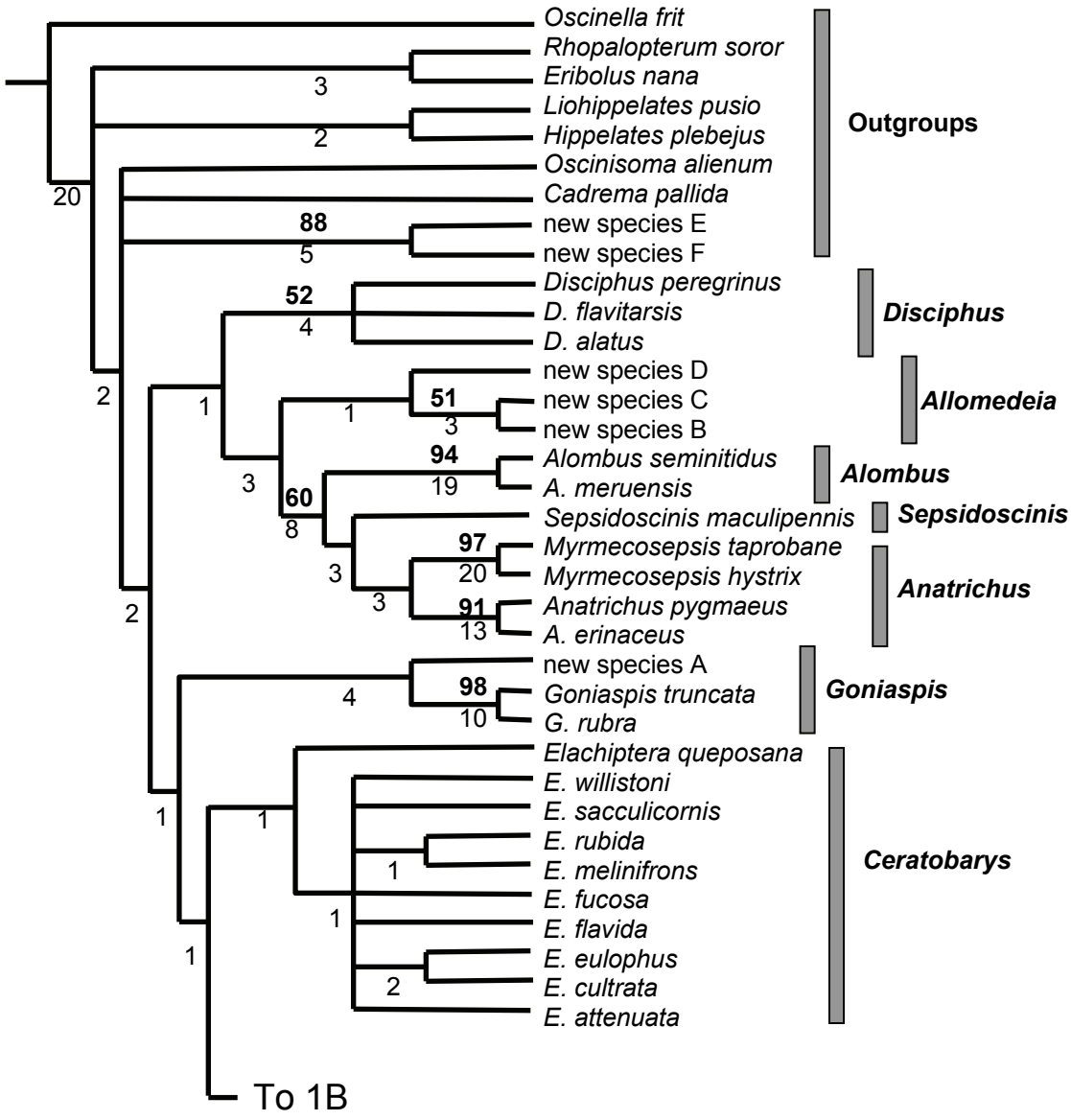


Fig. 1A. Strict consensus tree of 288 most parsimonious trees showing relationships of Elachipterini (basal portion). Bremer support values are below the branches, bootstrap values are in bold above the branches. Species are shown in their generic assignments prior to this study; new generic limits are indicated by gray bars.

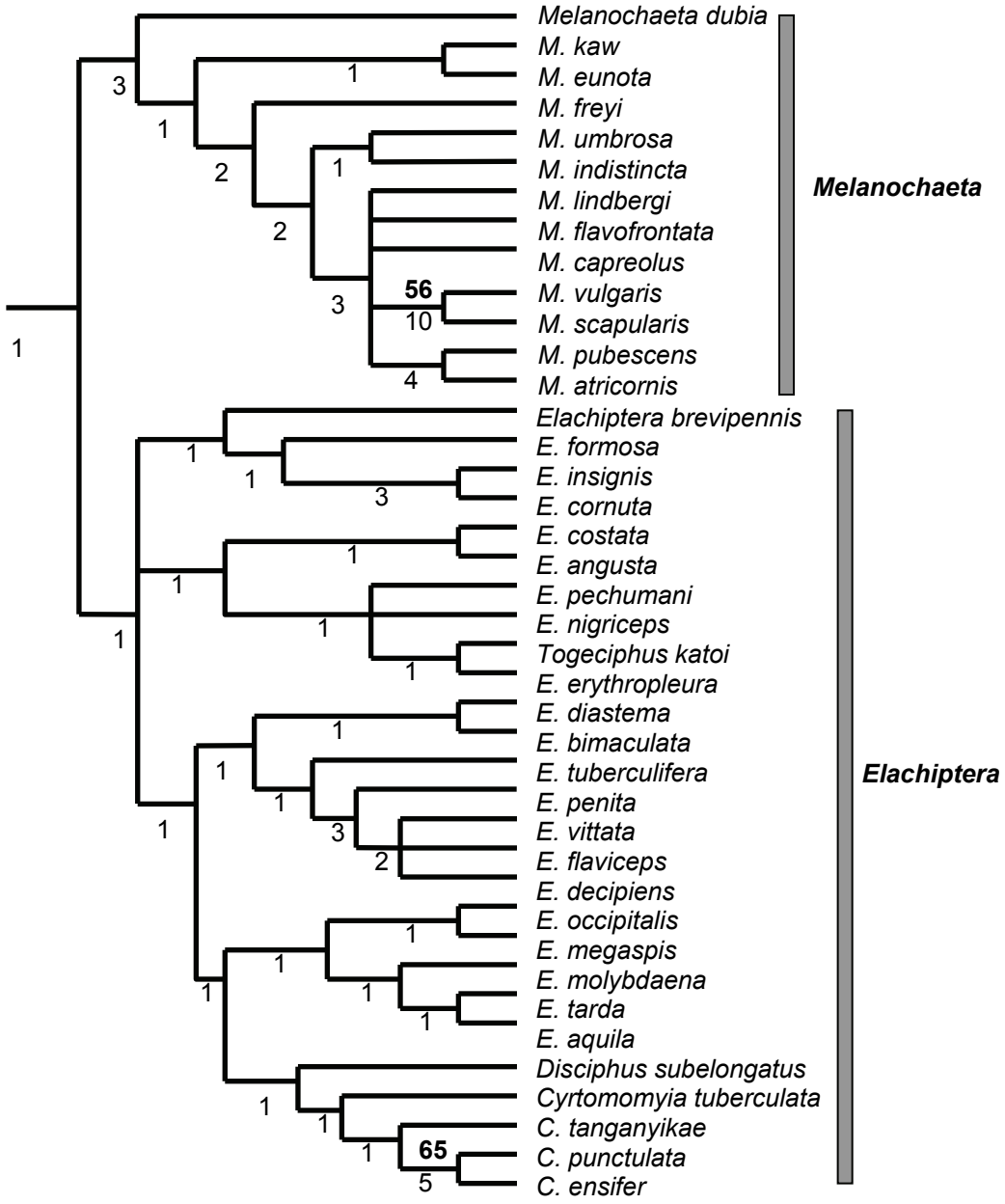


Fig. 1B. Strict consensus tree of 288 most parsimonious trees showing relationships of Elachipterini (apical portion). Bremer support values are below the branches, bootstrap values are in bold above the branches. Species are shown in their generic assignments prior to this study; new generic limits are indicated by gray bars.

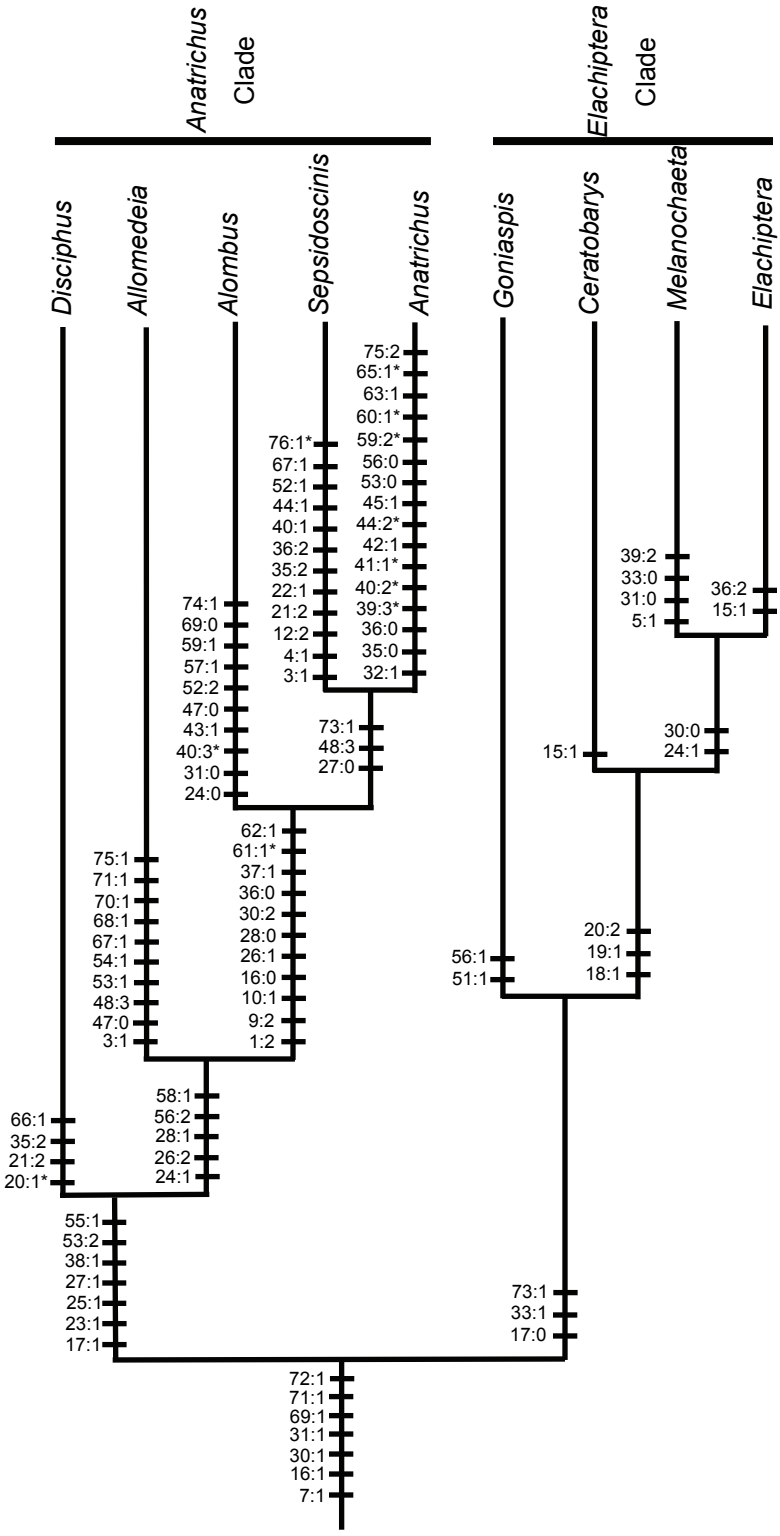


Fig. 2. One of 288 most parsimonious trees showing generic relationships of the Tribe Elachipterini. Black bars – homoplasious character states; asterisks – uniquely derived character states.

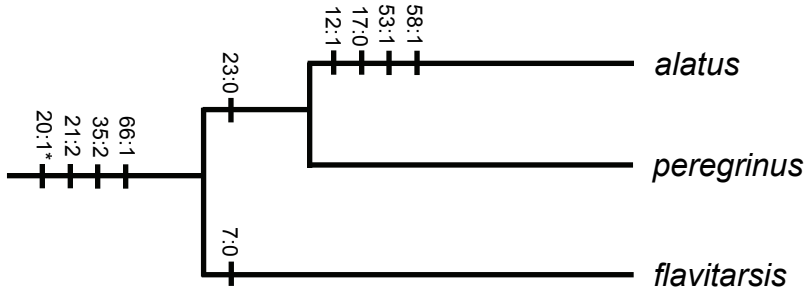


Fig. 3. One of 288 most parsimonious trees showing relationships of the *Anatrichus* clade (*Disciphus*). Black bars – homoplasious character states; asterix – uniquely derived character states.

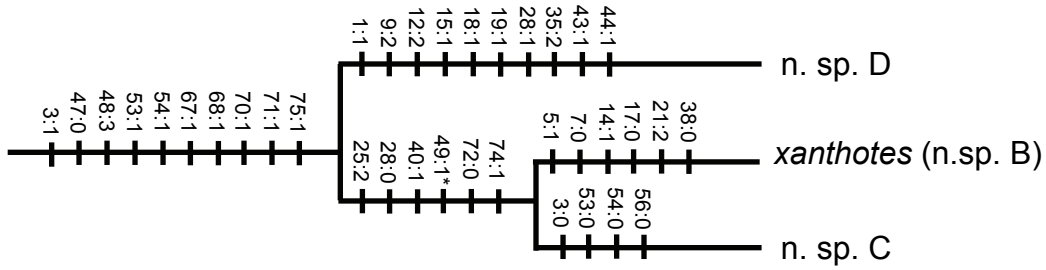


Fig. 4. One of 288 most parsimonious trees showing relationships of the *Anatrichus* clade (*Allomedeia*). Black bars – homoplasious character states; asterix – uniquely derived characters states.

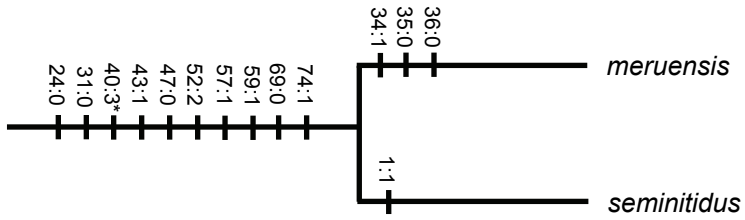


Fig. 5. One of 288 most parsimonious trees showing relationships of the *Anatrichus* clade (*Alombus*). Black bars – homoplasious character states; asterix – uniquely derived character states.

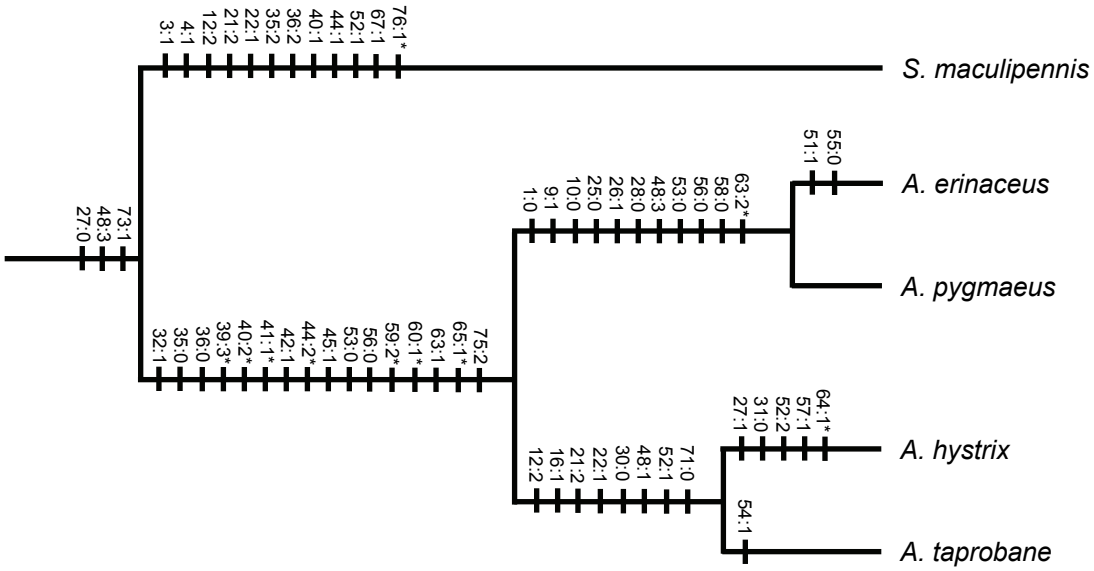


Fig. 6. One of 288 most parsimonious trees showing relationships of the *Anatrichus* clade (*Anatrichus and Sepsidoscinis*). Black bars – homoplasious character states; asterix – uniquely derived character states.

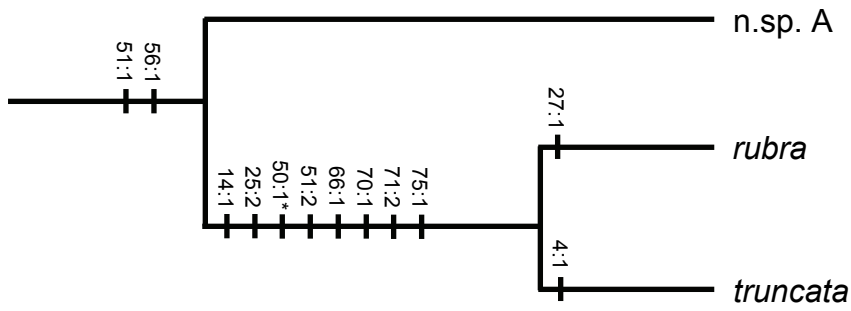


Fig. 7. One of 288 most parsimonious trees showing relationships of the *Elachiptera* clade (*Goniaspis*). Black bars – homoplasious character states.

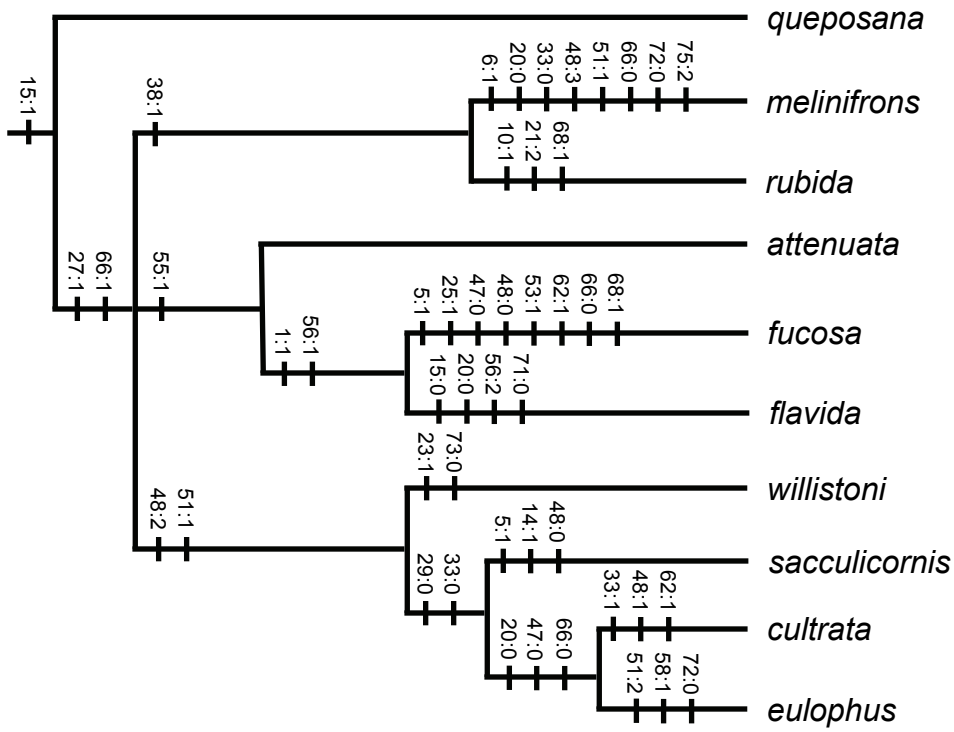


Fig. 8. One of 288 most parsimonious trees showing relationships of the *Elachiptera* clade (*Ceratobarys*). Black bars – homoplasious character states.

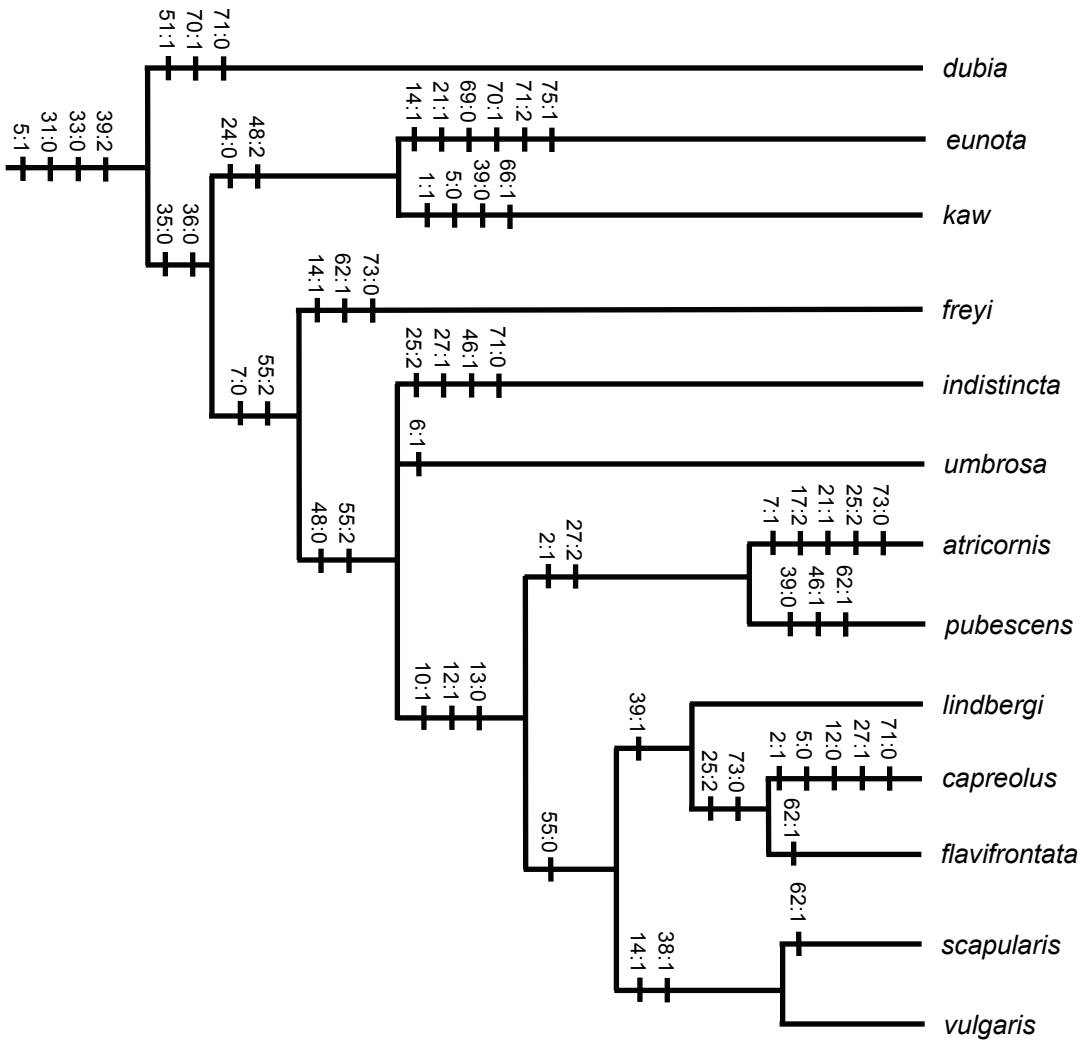


Fig. 9. One of 288 most parsimonious trees showing relationships of the *Elachiptera* clade (*Melanochaeta*). Black bars – homoplasious character states.

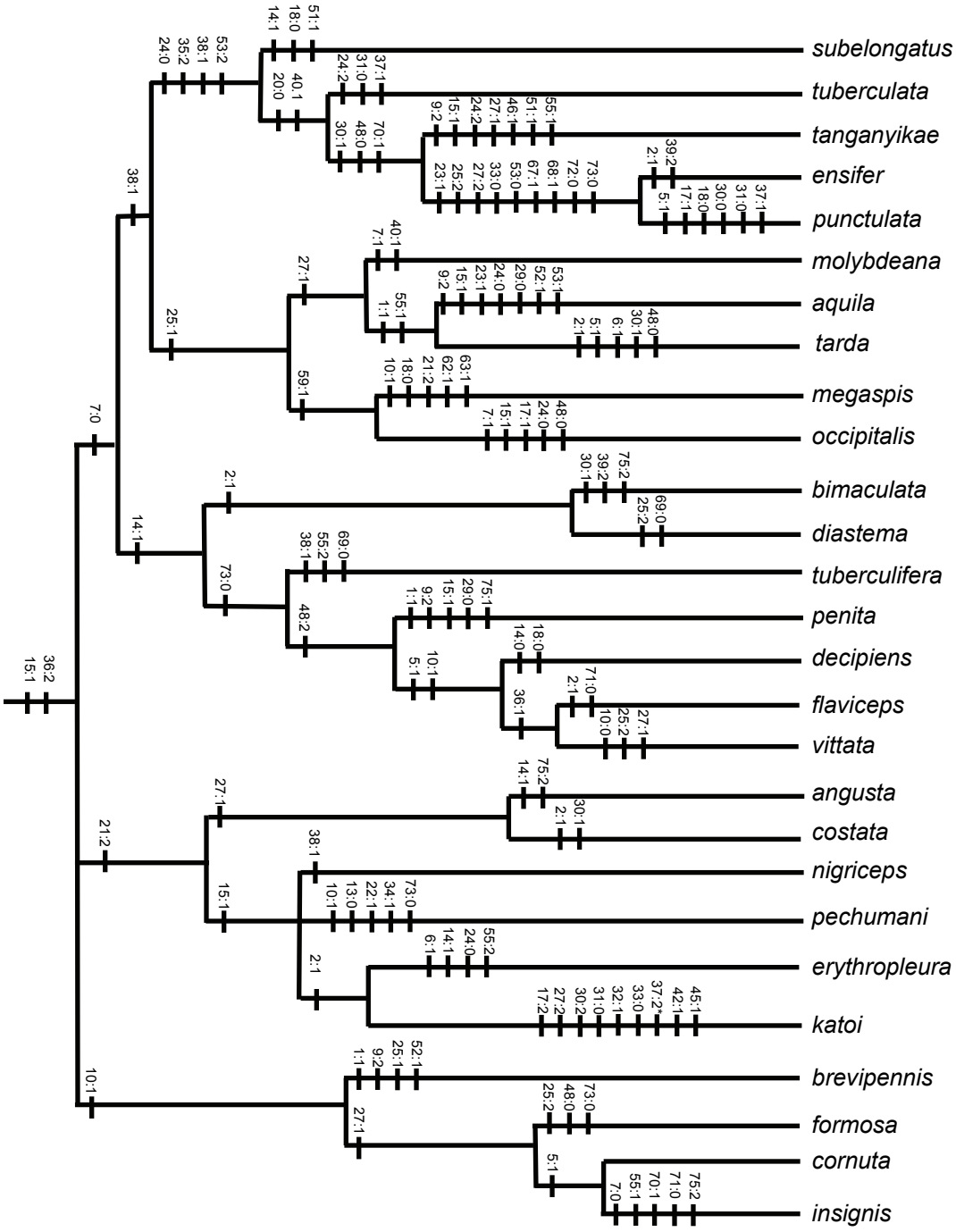
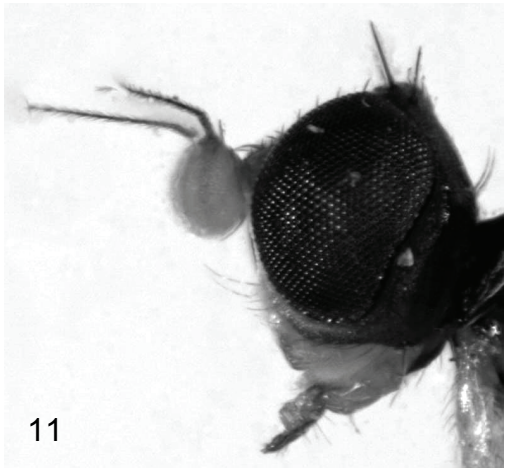
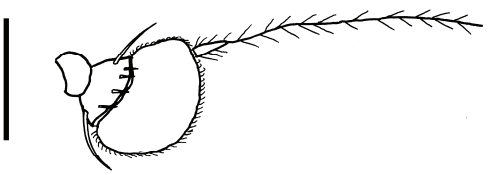
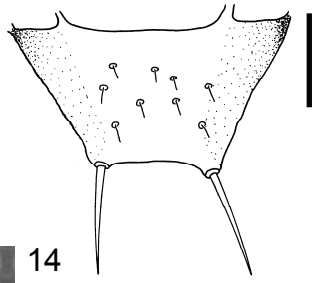
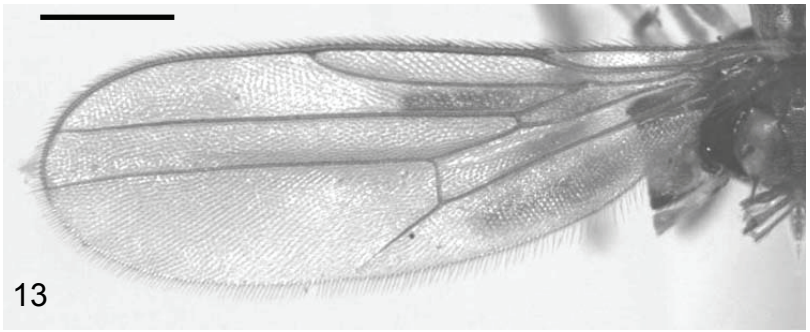


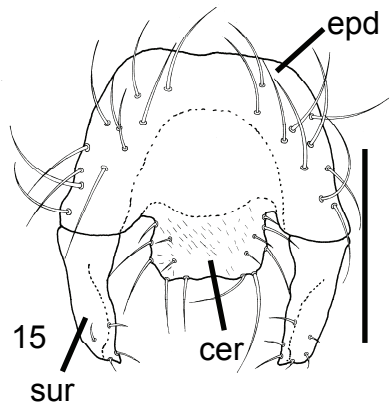
Fig. 10. One of 288 most parsimonious trees showing relationships of the *Elachiptera* clade *(Elachiptera).* Black bars – homoplasious character states; asterisks – uniquely derived character states.

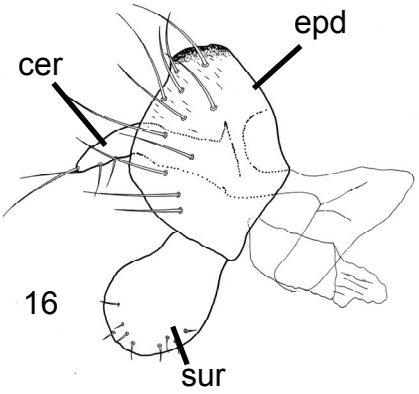


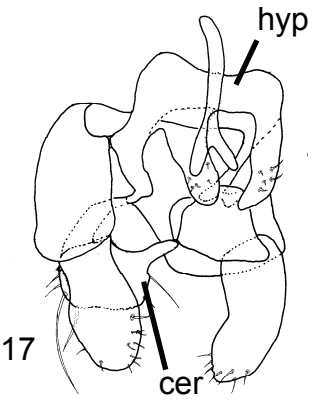




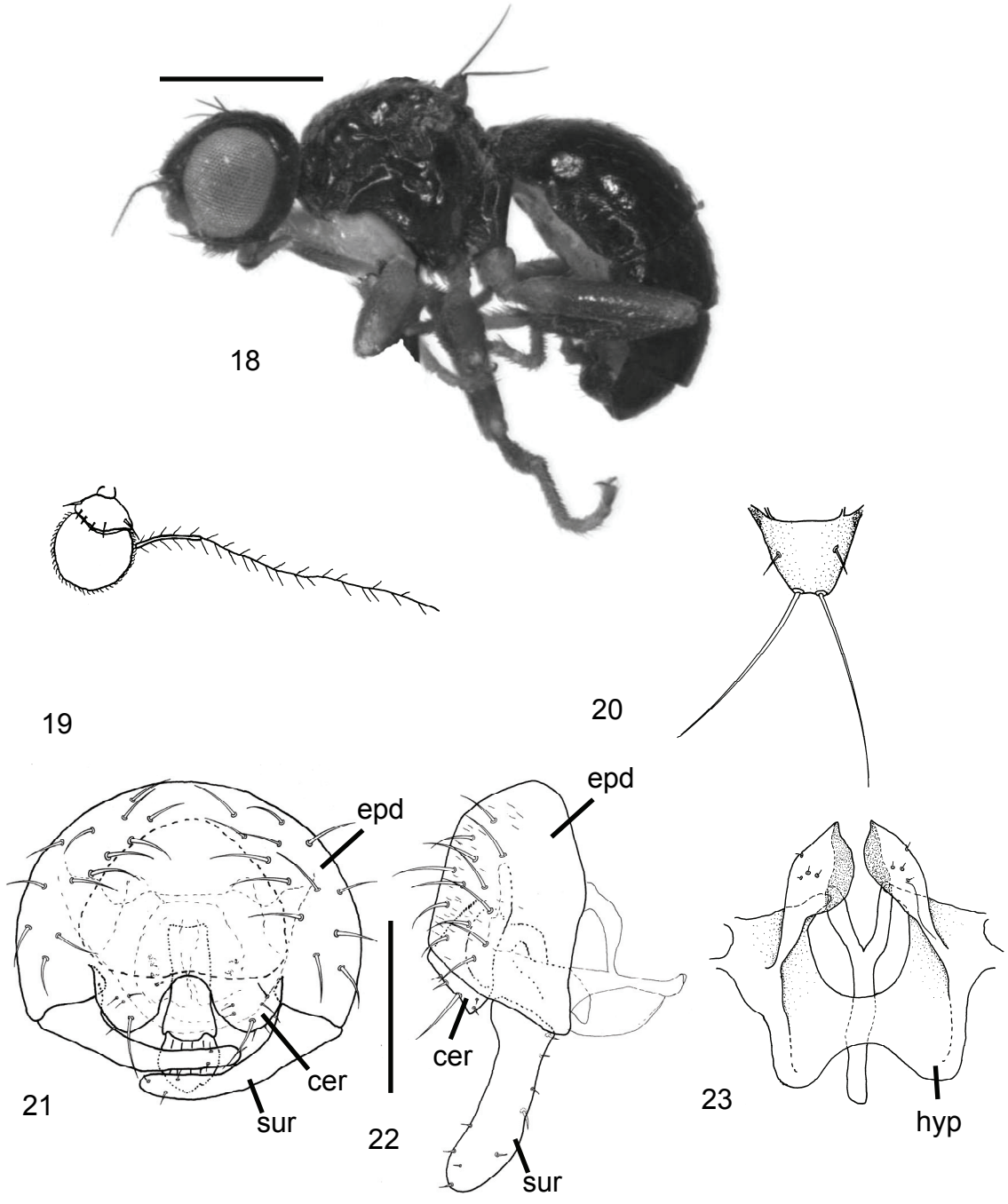




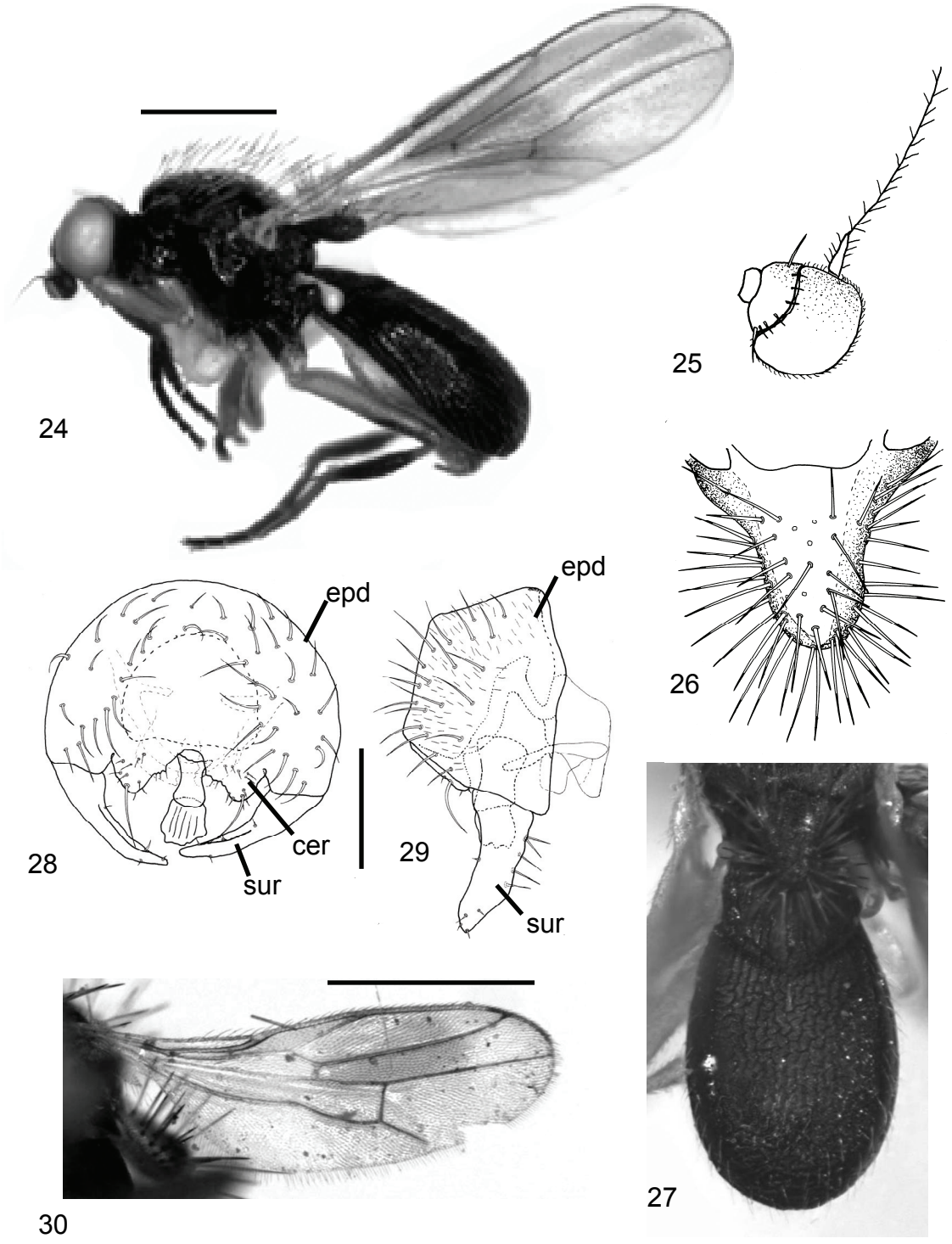




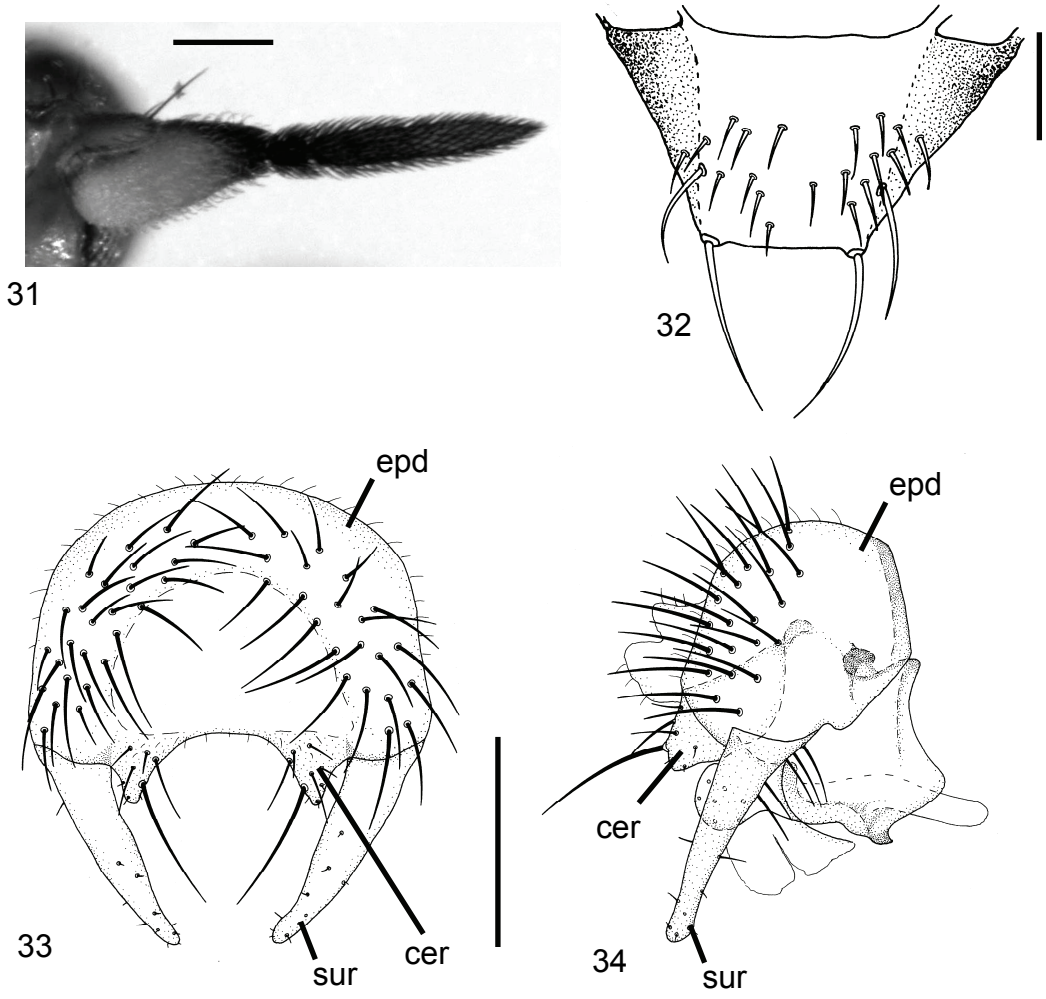
Figs. 11-17. *Allomedeia xanthotes*. 11. Head, lateral; 12. Antenna; 13. Wing; 14. Scutellum, dorsal; 15. Male genitalia, posterior; 16. Male genitalia, lateral; 17. Male genitalia, ventrolateral. Abbreviations: cer – cerci; epd – epandrium; hyp – hypandrium; sur - surstylus. Scale bars figs. 11 & 13 = 0.5mm; fig. 14-16 = 0.1mm



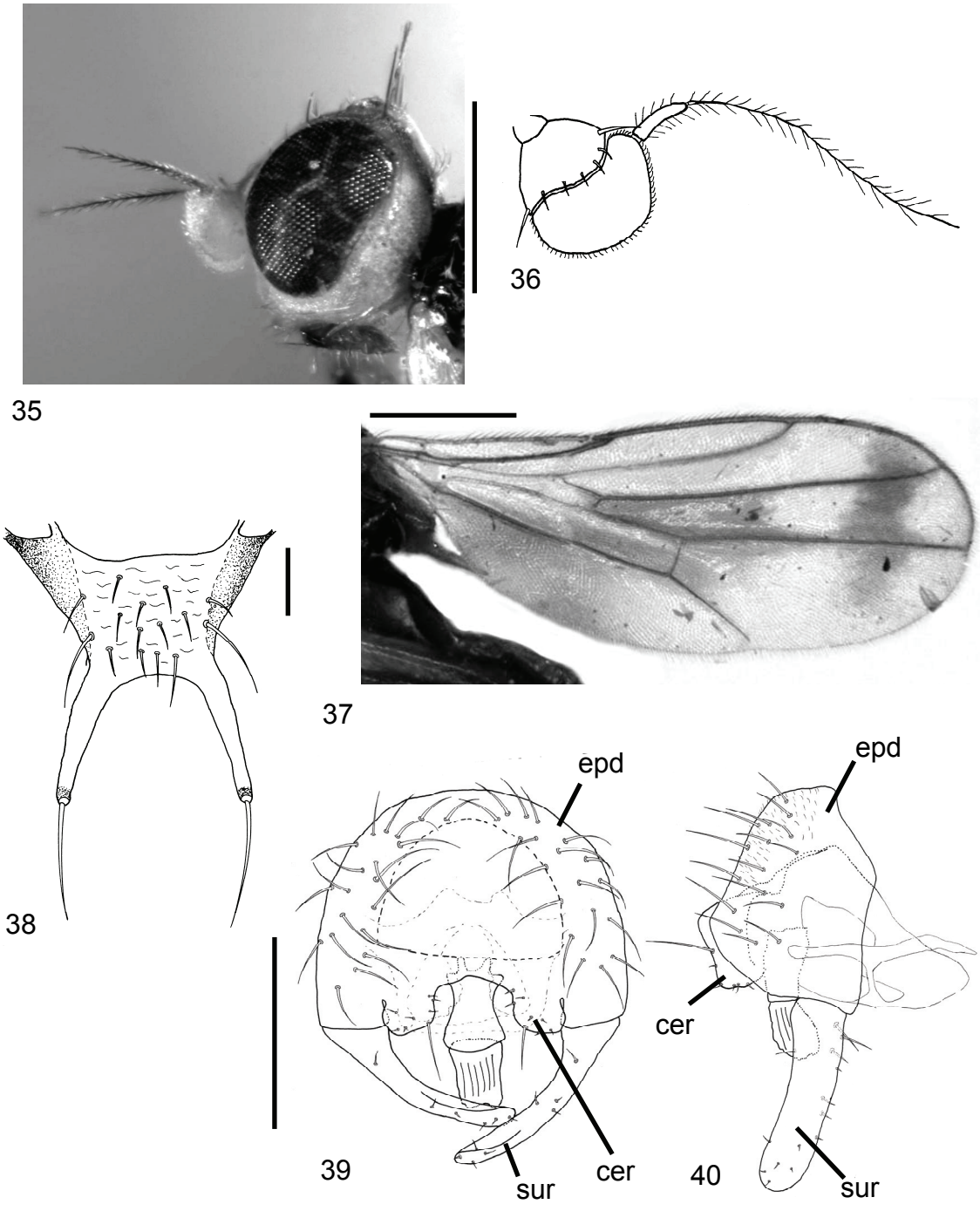
Figs. 18-23. *Alombus seminitidus*. 18. Habitus, lateral; 19. Antenna; 20. Scutellum, dorsal; 21. Male genitalia, posterior; 22. Male genitalia, lateral; 23. Male genitalia, ventral. Abbreviations: cer – cerci; epd – epandrium; hyp – hypandrium; sur - surstylus. Scale bars fig. 18 = 0.5mm; fig. 21-22 = 0.1mm



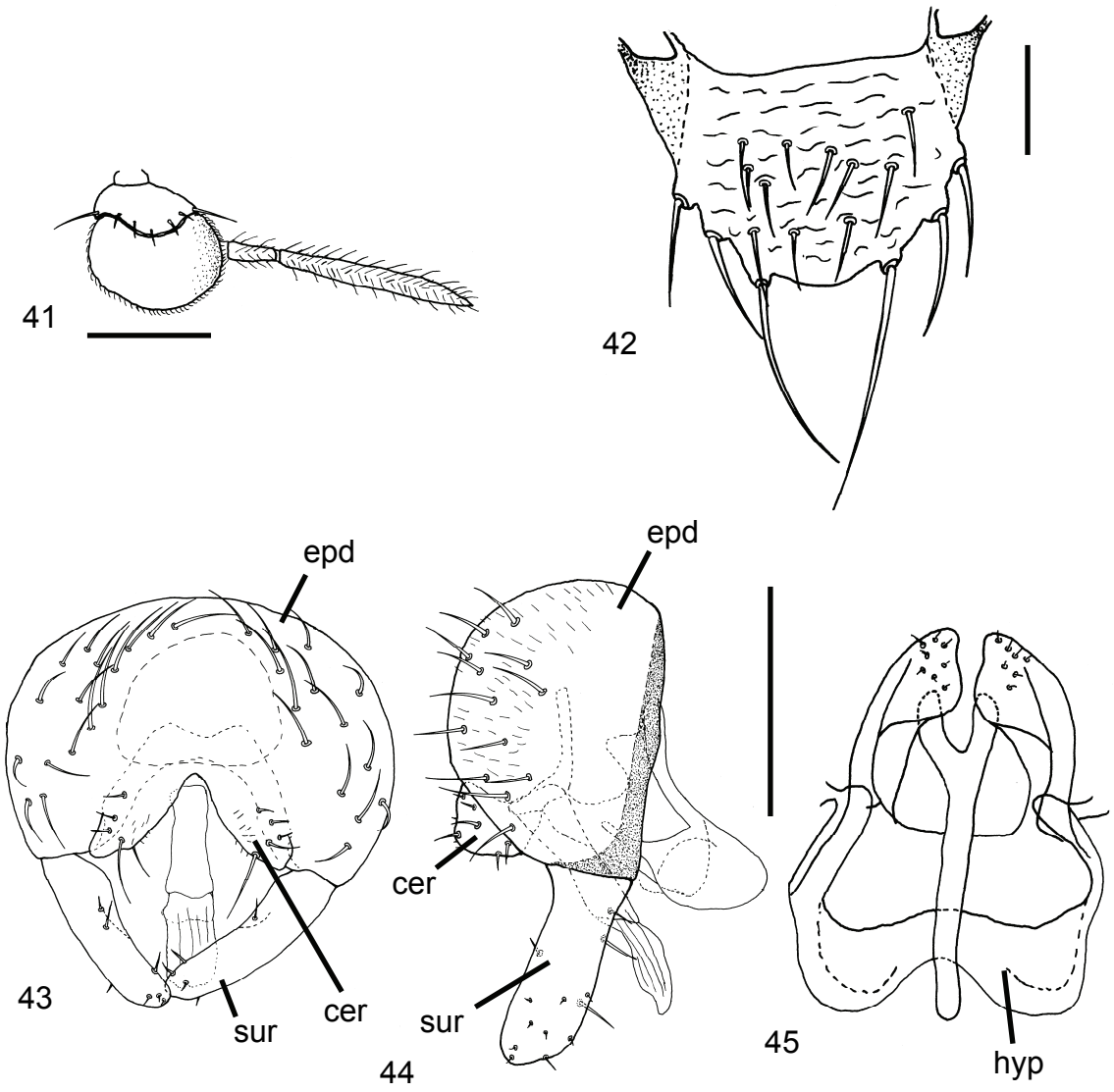
Figs. 24-30. *Anatrichus* species. 24-27. *Anatrichus pygmaeus* 24. Habitus, lateral; 25. Antenna; 26. Scutellum, dorsal; 27. Abdomen, dorsal; 28-30. *Anatrichus taprobane* 28. Male genitalia, posterior; 29. Male genitalia, lateral; 30. Wing. Abbreviations: cer- cerci; epd – epandrium; sur - surstylus. Scale bars figs. 24 & 30 = 0.5mm; fig. 28-29 = 0.1mm



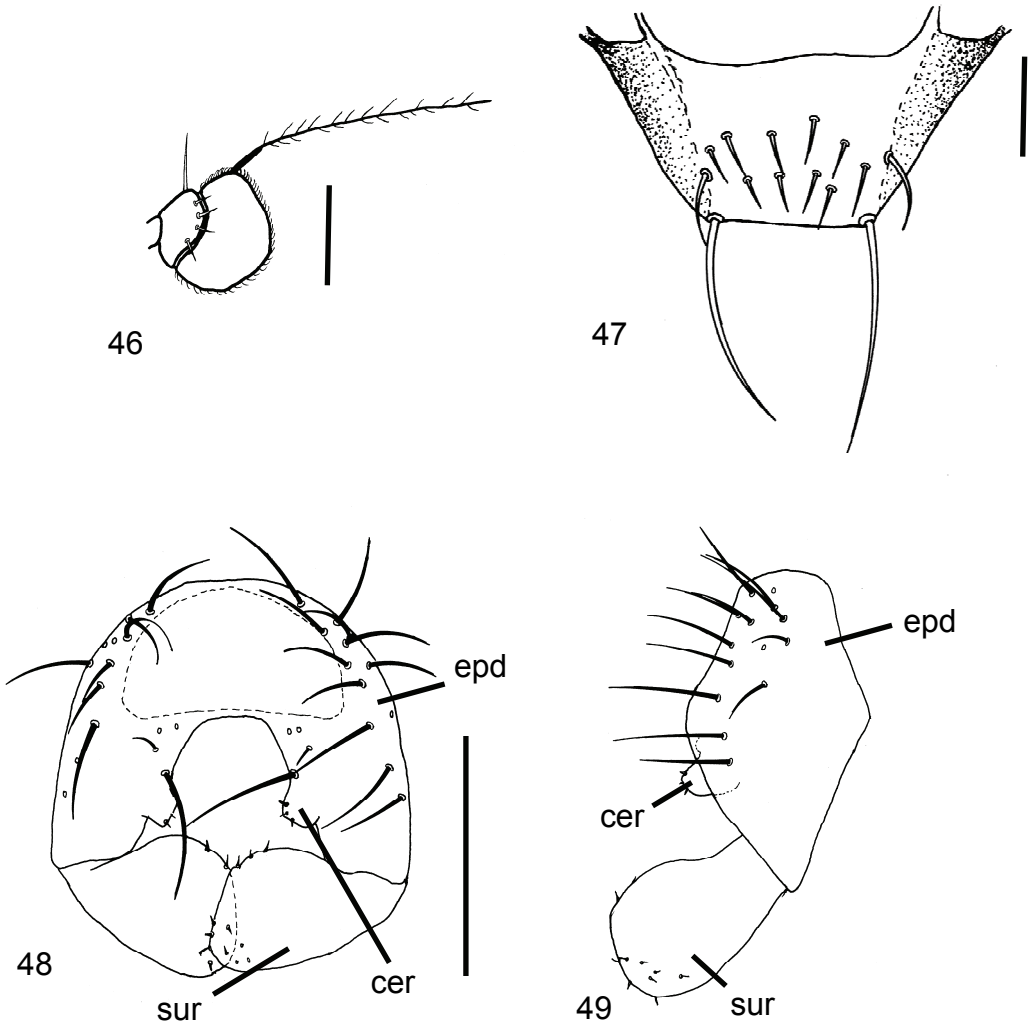
Figs. 31-34. *Ceratobarys eulophus*. 31. Antenna; 32. Scutellum, dorsal; 33. Male genitalia, posterior; 34. Male genitalia, lateral. (33-34 reproduced with permission from Wheeler and Forrest 2002). Abbreviations: cer – cerci; epd – epandrium; sur - surstylus. Scale bars = 0.1mm



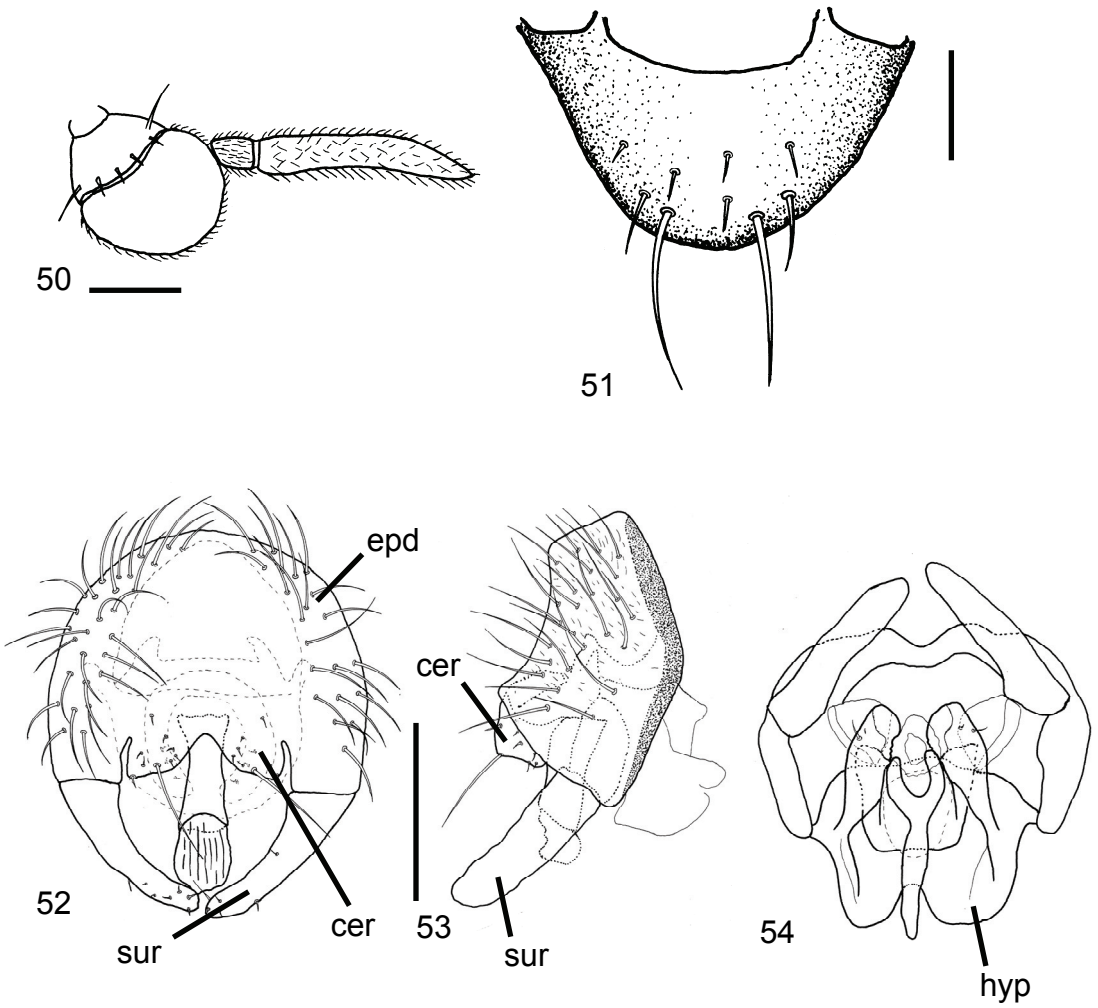
Figs. 35-40. *Disciphus peregrinus*. 35. Head, lateral; 36. Antenna; 37. Wing; 38. Scutellum, dorsal; 39. Male genitalia, posterior; 40. Male genitalia, lateral. Abbreviations: cer – cerci; epd – epandrium; sur - surstylus. Scale bars figs. 35 & 37 = 0.5mm; fig. 38-39 = 0.1mm



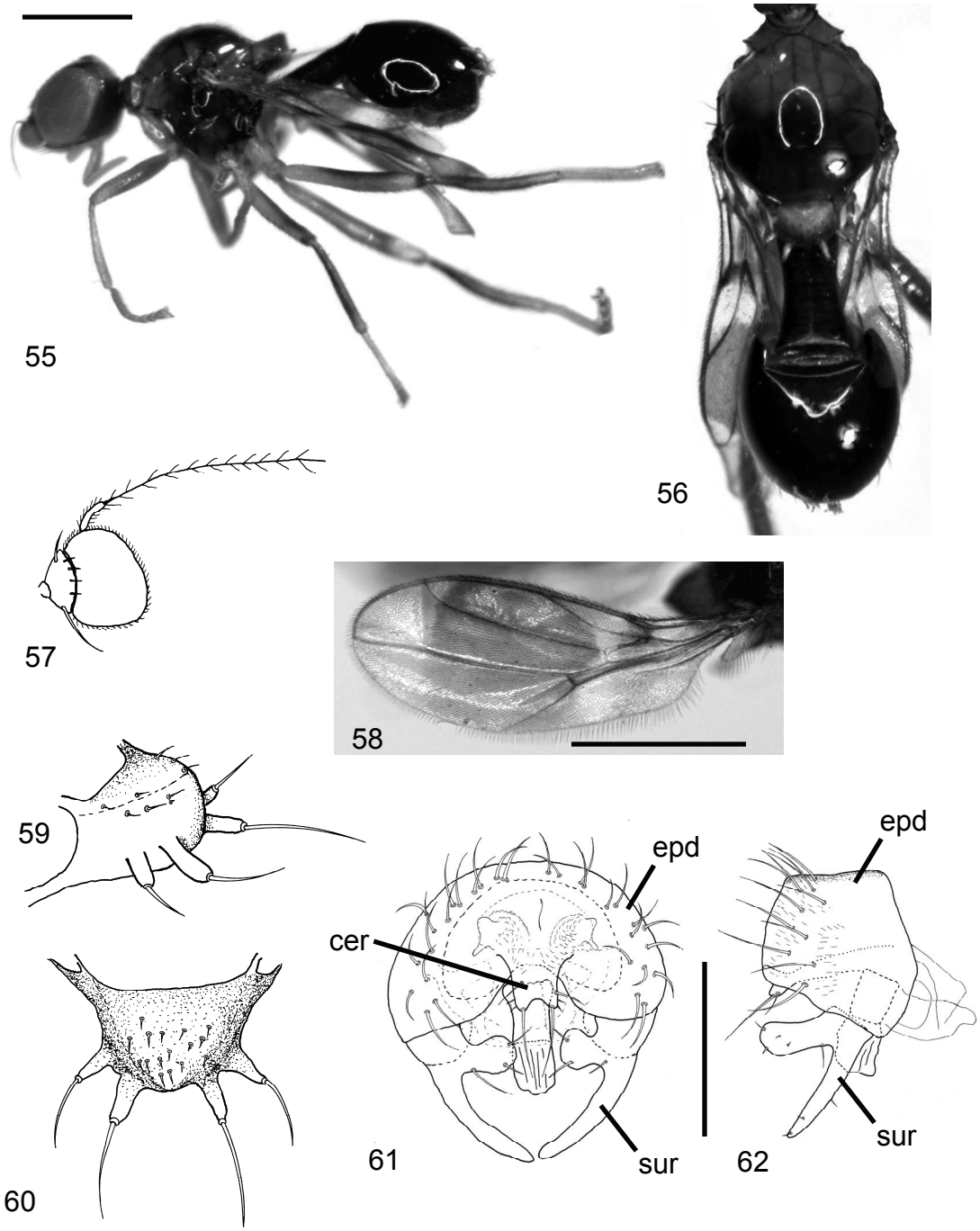
Figs. 41-45. *Elachiptera brevipennis*. 41. Antenna; 42. Scutellum, dorsal; 43. Male genitalia, posterior; 44. Male genitalia, lateral; 45. Male genitalia, ventral. Abbreviations: cer – cerci; epd – epandrium; hyp – hypandrium; sur - surstylus. Scale bars = 0.1mm



Figs. 46-49. *Goniaspis rubra*. 46. Antenna; 47. Scutellum, dorsal; 48. Male genitalia, posterior; 49. Male genitalia, lateral. (48-49 reproduced with permission from Mlynarek and Wheeler 2009). Abbreviations: cer – cerci; epd – epandrium; sur - surstylus. Scale bars = 0.1mm



Figs. 50-54. *Melanochaeta* species. 50-51. *Melanochaeta capreolus* 50. Antenna; 51. Scutellum, dorsal; 52-54. *Melanochaeta atricornis* 52. Male genitalia, posterior; 53. Male genitalia, lateral; 54. Male genitalia, ventral. Abbreviations: cer – cerci; epd – epandrium; hyp – hypandrium; sur - surstylus. Scale bars = 0.1mm



Figs. 55-62. *Sepsidoscinis maculipennis*. 55. Habitus, lateral; 56. Thorax and abdomen, dorsal; 57. Antenna; 58. Wing; 59. Scutellum, dorsolateral; 60. Scutellum, dorsal; 61. Male genitalia, posterior; 62. Male genitalia, lateral. Abbreviations: cer – cerci; epd – epandrium; sur - surstylus. Scale bars figs. 55 & 58 = 0.5mm; figs 61-62 = 0.1mm

Appendix 1. Character state matrix for Elachipterini. Taxon names are in their previously accepted combinations. Missing and inapplicable data are indicated by "?".

	1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	777777 123456
INGROUP TAXA								
Alombus meruensis Richards	2000001121	0000001000	0?10121112	000100?103	0010000100	02????1110	1100000000	110100
Alombus seminitidus Villeneuve	1000001121	0000001000	0010121112	0000111103	0010000100	02????1110	1100000000	110100
Anatrichus erinaceus Loew	0000001110	0000001000	0011010012	1100001132	1102101300	1000000021	1120100010	111020
Anatrichus pygmaeus Lamb	0000001110	0000001000	0011010012	1100001132	1102101300	0000100021	1120100010	111020
Cyrtomomyia ensifer (Sabrosky)	0100000110	0000010110	0010212011	1000220121	0000001?00	0000000000	0000001111	100000
C. punctulata (Becker)	0000100110	0000011010	0010212010	0000221101	0000001000	0000000000	0000001111	100000
C. tanganyikae (Sabrosky)	0000000120	0000110110	0002011011	1010220101	0000011000	1020100000	0000000011	111000
C. tuberculata (Adams)	0000000110	0000010110	0002010010	0010221101	0000001100	0020000000	0000000010	111000
Disciphus alatus Becker	0000001110	0100010001	2000111011	1000210100	0000001100	0010100100	0000010010	110000
D. flavitarsis Duda	0000000110	0000011001	2010111011	1000210100	0000001100	0020100000	0000010010	110000
D. peregrinus Becker	0000001110	0000011001	2000111011	1000210100	0000001100	0020100000	0000010010	110000
D. subelongatus Kanmiya	0000000110	0001010012	0000010010	1010220100	0000001100	1020000000	0000000010	111000
Elachiptera angusta Sabrosky	0000001110	0001010112	2001011010	1010120000	0000001100	0000000000	0000000010	111020
E. aquila Wheeler	1000000120	0000110112	0010111010	1010120100	0000001100	0110100000	0000000010	111000
E. attenuata (Adams)	0000001110	0000110112	0000011011	1010110000	0000001100	0000100000	0000010010	111000
E. bimaculata (Loew)	0100000110	0001010112	0001010011	1010120020	0000001100	0000000000	0000000010	111020
E. brevipennis (Meigen)	1000001121	0000010112	0001110010	1010120000	0000001100	0100000000	0000000010	111000
E cornuta (Fállen)	0000101111	0000010112	0001011010	1010120000	0000001100	0000000000	0000000010	111000
E. costata (Loew)	0100001110	0000010112	2001011011	1010120000	0000001100	0000000000	0000000010	111000
E. cultrata Wheeler & Forrest	0000001110	0000110110	0000011001	1010110000	0000000100	1000000000	0100000010	111000
E. decipiens (Loew)	0000100111	0000010012	0001010010	1010120000	0000001200	0000000000	0000000010	110000
E. diastema Collin	0100000110	0001010112	0001210010	1010120000	0000001100	0000000000	0000000000	111000
E erythropleura Sabrosky	0100011110	0001110112	2000010010	1010120000	0000001100	0000200000	0000000010	111000
E. eulophus (Loew)	0000001110	0000110110	0000011001	1000110000	0000000200	2000000100	0000000010	101000
E. flaviceps Sabrosky	0100100111	0001010112	0001010010	1010110000	0000001200	0000000000	0000000010	010000
E. flavida Williston	1000001110	0000010110	0000011011	1010110000	0000001100	0000120000	0000010010	011000
E. formosa (Loew)	0000001111	0000010112	0001211010	1010120000	0000001000	0000000000	0000000010	110000
E. fucosa Mlynarek & Wheeler	1000101110	0000110112	0000111011	1010110000	0000000000	0010110000	0100000110	111000
E. insignis (Thomson)	0000100111	0000010112	0001011010	1010120000	0000001100	0000100000	0000000011	011020

E. megaspis (Loew)	0000000111	0000010012	2001110010	1010120100	0000001100	0000000010	0110000010	111000
E. melinifrons Mlynarek&Wheeler	0000011110	0000110110	0000011011	1000110100	0000001300	1000000000	0000000010	101020
E. molybdaena Śeguy	0000001110	0000010112	0001111010	1010120101	0000001100	0000000000	0000000010	111000
E. nigriceps (Loew)	0000001110	0000110112	2001010010	1010120100	0000001100	0000000000	0000000010	111000
E. occipitalis Becker	0000001110	0000111112	0000110010	1010120100	0000001000	0000000010	0000000010	111000
E. pechumani Sabrosky	0000001111	0010110112	2101010010	1011120000	0000001100	0000000000	0000000010	110000
E. penita (Adams)	1000000120	0001110112	0001010000	1010120000	0000001200	0000000000	0000000010	110010
E. queposana Mlynarek&Wheeler	0000001110	0000110112	0000010011	1010110000	0000001100	0000000000	0000000010	111000
E. rubida Becker	0000001111	0000110112	2000011011	1010110100	0000001100	0000000000	0000010110	111000
E. sacculicornis (Enderlein)	0000101110	0001110112	0000011001	1000110000	0000001000	1000000000	0000010010	111000
E. tarda (Adams)	1100110110	0000010112	0001111011	1010120100	0000001000	0000100000	0000000010	111000
E. tuberculifera (Corti)	0000000110	0001010112	0001010010	1010120100	0000001100	0000200000	0000000000	110000
E. vittata Sabrosky	0000100110	0001010112	0001211010	1010110000	0000001200	0000000000	0000000010	110000
E. willistoni Sabrosky	0000001110	0000110112	0010011011	1010110000	0000001200	1000000000	0000010010	110000
Goniaspis rubra (Becker)	0000001110	0001010000	0000211011	1010110000	0000001101	2000010000	0000010011	111010
G. truncata (Malloch)	0001001110	0001010000	0000210011	1010110000	0000001101	2000010000	0000010011	111010
Melanochaeta atricornis (Adams)	0100101111	0110012112	1001212010	0000000020	0000001000	0000200000	0000000010	110000
M. capreolus (Haliday)	0100000111	0010010112	0001211010	0000000010	0000001000	0000000000	0000000010	010000
M. dubia (Lamb)	0000101110	0000010112	0001010010	0000110020	0000001100	1000000000	0100000011	011000
M. eunota (Loew)	0000101110	0001010112	1000010010	0000000020	0000001200	0000000000	0000000001	111010
M. flavofrontata (Becker)	0000100111	0110010112	0001210010	0000000010	0000001000	0000000000	0100000010	110000
M. freyi (Duda)	0000100110	0001010112	0001010010	0000000020	0000001100	0000000000	0100000010	110000
M. indistincta (Becker)	0000100110	0000010112	0001211010	0000000020	0000011000	0000200000	0000000010	011000
M. kaw Sabrosky	1000001110	0000010112	0000010010	0000000000	0000001200	0000000000	0100010010	111000
M. lindbergi (Sabrosky)	0000100111	0110010112	0001010010	0000000010	0000001000	0000000000	0000000010	111000
M. pubescens (Thalhammer)	0100100111	0110010112	0001012010	0000000000	0000011000	0000200000	0100000010	111000
M. scapularis (Adams)	0000100111	0111010112	0001010010	0000000120	0000001000	0000000000	0100000010	111000
M. umbrosa (Becker)	0000110110	0000010112	0001010010	0000000020	0000001000	0000200000	0000000010	111000
M. vulgaris (Adams)	0000100111	0111010112	0001010010	0000000120	0000001000	0000000000	0000000010	111000
Myrmecosepsis hystrix Kertesz	2000001121	0200011000	2111121110	010000?132	1102101100	02????1121	1111100010	011020
M. taprobane Andersson	2000001121	0200011000	211?120110	110000?132	1102101100	0121120121	1110100010	011020
Myrmecosepsis n. sp.	2000001121	0200011000	2111121110	100000?132	1102101100	02????1121	1111100010	010020
Sepsidoscinis maculipennis Hendel	2011001121	0200001000	2111120112	1000221101	0001001300	0120120100	1100001010	?11001
Togeciphus katoi Nishijima	0100001110	0000112112	2001012012	0100122000	0100101100	0000000000	0000000010	111000
new species E	0001001110	0000011000	2000010010	0011121020	0000001200	0000020000	0000000010	010000
new species F	0001000110	0000011000	2000010011	0010111020	0000001200	0000000000	0000000010	010000
new species A	0000001110	0000010000	0000010011	1010110000	0000001100	1000010000	0000000010	111000

new species D	1010001120	0200111110	0011121111	1000210100	0011000300	0001120100	0000001111	110010
new species B	0010100110	0001010000	2011221011	1000110001	0000000310	0011120100	0000001111	100110
new species C	0000001110	0000011000	0011221011	1000110101	0000000310	0020100100	0000001111	100110
OUTGROUP TAXA								
Hippelates plebejus Loew	0001110000	1012002000	0000000000	0000000010	0000010000	2000200000	0000010011	001020
Liohippelates pusio (Loew)	0001101000	0012000000	0000000000	0011000010	0000001000	2000200000	0000000000	101000
Cadrema pallida (Loew)	0100001100	0001012000	1000001010	1010110010	0000001000	2000000000	0000000001	000000
Oscinella frit (Linneaus)	0000000010	0011000000	0000002010	0000000010	0000000001	0000000000	0000000001	000020
Eribolus nana (Zetterstedt)	1000010120	0000000002	0000000000	1000000000	0000000100	0000000100	0000000000	101000
Oscinisoma alienum (Becker)	2000100120	0000001002	0000010000	0010110000	0000001100	0000000000	0000010000	010020
Rhopolopterum soror (Macquart)	1001100010	0000000000	0001000000	0000000000	0000000000	0000100100	0000010000	100000

Appendix 2: Adult morphological characters used in the analysis of phylogenetic relationships of Elachipterini. 0 – plesiomorphic state; 1, 2, 3 – apomorphic states

1 – Head height: higher than long in lateral view (0); as high as long (1); obviously longer than high (2)

2 – Frons, length: longer than wide (0); as long as wide (1); wider than long (2)

3 – Frons, shape: dorsally converging (0); dorsally diverging (1); sides parallel (2)

4 – Frontal triangle, margins: concave (0); straight (1)

5 – Frontal triangle, length: reaching anterior margin of frons (0); at most three quarters frons length (1).

6 – Frontal triangle, texture: pollinose (0); shiny (1)

7 – Ocellar tubercle, texture: pollinose (0); shiny (1)

8 – Vertex, lateral view: flattened (0); rounded (1)

9 – Postgena, width: 0.25-0.4 times length of short axis of eye (0); 0.1-0.2 times length of short axis of eye (1); at least 0.5 times length of short axis of eye (2)

10 – Palpus, shape: narrowing to tip in lateral view (0); parallel sided, ending bluntly (1)

11 – Palpus, dorsal surface: round (0); flattened dorsally (1)

12 – Palpus, length: distinct but at most as long as clypeus (0); more than length of clypeus (1); very small,inconspicuous (2)

13 – Palpus setae, length: all equivalent (0); a few longer setae (1)

14 – Carina: absent (0); present, only half the length of face (1); full length of face (2)

15 – Third antennal segment, dorsal shape: round (0); elongate (1)

16 – Third antennal segment, shape: round (0); reniform (1)

17 – Arista, size: 1.5-2.0 times height of third antennal segment (0); 2.5-3.5 times height of third antennal segment (1); 0.5-1.0 times height of third antennal segment (2)

18 – Arista, thickness at base: thin (0); thick (1)

19 – Arista, pubescence: sparse (0); heavy (1)

20 – Orbital bristles, size: all equivalent (0); one stronger than others (1); two or more orbitals stronger than others (2)

21 – Interfrontal bristles, position on frontal triangle: outside margin (0); at the margin (1); inside margin (2)

22 – Ocellar bristles, orientation: erect (0); proclinate (1)

23 – Ocellar bristles, size: as long as other head bristles (0); ocellar bristles reduced, almost absent (1)

24 – Ocellar bristles, length: as long as post-vertical bristles (0); shorter than post-vertical bristles (1); longer than post-vertical bristles (2)

25 – Inner vertical bristles: present, shorter than outer verticals (0); absent (1); present, as long as outer verticals (2)

26 – Pronotum, size: short, not noticeable in dorsal view (0); noticeable but short (1); long, conspicuous (2)

27 – Mesonotum, shape: as long as wide (0); longer than wide (1); wider than long (2)

28 – Postpronotum, size: wider than long (0); elongated, obviously longer than wide (1)

29 – Scutellum, angle: same plane as mesonotum (0); angled in a different plane than mesonotum (1)

30 – Scutellum, shape in dorsal view: rounded (0); trapezoidal (1); triangular (2)

31 – Scutellum, shape in lateral view: convex dorsally (0); flat dorsally (1)

32 – Scutellum, size: wider at base than long (0); longer than wide at base (1)

33 – Scutellum, texture of dorsal surface: smooth (0); rugose (1)

34 – Scutellum, pollinosity: pollinose (0); shiny (1)

35 – Scutellar tubercles, size: absent (0); present and short, less than half the length of scutellum (1); present and long, more than half of the length of scutellum (2)

36 – Tubercles, number: zero (0); two (1); 4 or more (2)

37 – Tubercles, position on scutellum: dorsal margin (0); ventral to dorsal margin (1); on ventral margin and below (2)

38 – Postpronotal bristle: present (0); absent (1)

39 – Dorsal posterior notopleural: absent (0); present and large (1); present but reduced, at most half the size of ventral notopleural (2); many (3)

40 – Anterior notopleural: present (0); reduced, at most half the size of posterior notopleural (1); many (2)

41 – Thoracic spines: absent (0); present (1)

42 – Scutellar spines: absent (0); present (1)

43 – Postsutural dorsocentral bristle: present (0); absent (1)

44 – Postsutural intra-alar bristle: one (0); absent (1); many (2)

45 – Postsutural supraalar bristle: absent (0); present (1)

46 – Thoracic pleura, texture: shiny (0); pollinose (1)

47 – Subapical scutellar bristles: absent (0); present, at least half the length of apical scutellar bristles (1)

48 – Femoral organ, shape: one row (0); two rows (1); a patch, 3 or more rows (2); absent (3)

49 – Tibial organ setae, position: in a row (0); irregularly aligned or in a clump (1)

50 – Tibial organ, shape: linear (0); round/oval (1)

51 – Hind tibial spur: absent (0); short, less than diameter of tibia (1); long, more than diameter of tibia (2)

52 – Wing, size: longer than abdomen (0); shorter than abdomen (1); wings absent (2)

53 – Wing, color: clear (0); shaded along veins (1); patterned at center (2)

54 – Wing, anal angle: distinctly developed and broad (0); anal angle reduced, almost 180° (1)

55 – Wing width to length ratio: 40/100 (0); 35/100 (1); 45/100 (2)

56 – Costal sectors, size: C2 longer than C3 (0); C2 as long as C3 (1); C2 shorter than C3 (2)

57 – Halteres: present (0); absent (1)

58 – Abdomen, size: as long as mesonotum (0); 1.5-2 times longer than mesonotum (1)

59 – Tergites 1+2, size: less than half the length of abdomen (0); more than half the length of abdomen but not covering it completely (1); one large sclerite covering abdomen (2)

60 – Tergites 1+2: separated from other tergites (0); fused with tergite 3 (1)

61 – Abdomen, width at base: wide at base, all tergites the same width (0); constricted at base, basal tergites narrower than others (1)

62 – Tergites 1+2, sclerotization: membranous medially posteroventral to scutellum (0); fully sclerotized (1)

63 – Abdomen, texture: smooth (0); rugose, textured basally (1) rugose and textured over entire length (2)

64 – Abdomen, bristling: no modified bristles (0); spines instead of bristles (1)

65 – Abominal sternites: single plate (0); broken into many small pieces (1)

66 – Cerci, size: broad in posterior view (0); small in posterior view (1)

67 – Cerci, fusion: separated by anal membrane (0); fused (1)

68 – Cerci, bristling: one bristle on cerci four times longer than the rest (0); all bristles equivalent (1)

69 – Cerci, shape: evenly round (0); uneven, contracting into point ventrally (1)

70 – Surstylus, size: three to five times as long as wide in lateral view (0); at most two times as long as wide in lateral view (1)

71 – Surstylus, shape: triangular in lateral view (0); parallel sided (1)

72 – Postgonites, shape: linear, round (0); triangular (1)

73 – Hypandrium, size: delicate in lateral view (0); massive in lateral view (1)

74 – Arms of hypandrium: not branched and regular (0); branched (1)

75 – Surstylus tip: round (0); flattened (1); pointed (2)

76 – Surstylus, shape: single lobe (0); double lobe (1)

Appendix 3. Revised Checklist of the Elachipterini.

Genus *ALLOMEDEIA* gen. nov.

Allomedeia gen. nov. Type species: *A. xanthotes* n. sp. (by present designation)

xanthotes n. sp., [**AT**]

Genus *ALOMBUS* Becker

Alombus Becker, 1914. Type species: *A. politus* Becker

constrictus Richards, 1955, [**AT**]

dasypus Richards, 1955, [**AT**]

echinatus Richards, 1955, [**AT**]

fuscipes Richards, 1962, [**AT**]

leleupi Richards, 1955, [**AT**]

meruensis Richards, 1962, [**AT**]

pachytarsis Richards, 1955, [**AT**]

politoides Richards, 1965, [**AT**]

politus Becker, 1914, [**AT**]

scutellatus Villeneuve, 1934, [**AT**]

seminitidus Villeneuve, 1934, [**AT**]

Genus *ANATRICHUS* Loew

Anatrichus Loew, 1860. Type species: *A. erinaceus* Loew.

Myrmecosepsis Kertesz, 1914. Type species: *M. hystrix* Kertesz.

Echinia Paramanov, 1961. Type species: *E. bisegmenta* Paramanov.

erinaceus Loew, 1860, [**AT**]

hystrix (Kertesz, 1914) (*Myrmecosepsis*) , [**OR**]

pygmaeus Lamb, 1918, [**AU, OR**]

taprobane (Andersson, 1977) (*Myrmecosepsis*) , [**OR**]

Genus *CERATOBARYS* Coquillett

Ceratobarys Coquillett, 1898. Type species: *Hippelates eulophus* Loew.

attenuata (Adams, 1908) (*Crassiseta*) , [**NT**]

coniotrigona (Duda, 1933) (*Elachiptera*) , [**NT**]

cultrata (Wheeler & Forrest, 2002) (*Elachiptera*) , [**NT**]

eulophus (Loew, 1872) (*Hippelates*) , [**NE**]

flavida (Williston, 1896) (*Elachiptera*) , [**NT**]

fucosa (Mlynarek & Wheeler, 2008) (*Elachiptera*) , [**NT**]

melinifrons (Mlynarek & Wheeler, 2008) (*Elachiptera*) , [**NT**]

pollinosa Sabrosky, 1938, [**NT**]

queposana (Mlynarek & Wheeler 2008) (*Elachiptera*) , [**NT**]

rubida (Becker, 1912) (*Elachiptera*) , [**NT**]

sacculicornis (Enderlein, 1911) (*Gampsocera)* , [**NT**]

willistoni (Sabrosky, 1948) (*Elachiptera*) , [**NE**]

Genus *DISCIPHUS* Becker

Disciphus Becker, 1911. Type species: *D. peregrinus* Becker.

alatus Becker, 1911, [**OR**]

flavitarsis Duda, 1930, [**OR**]

peregrinus Becker, 1911, [**OR**]

Genus *ELACHIPTERA* Macquart

Elachiptera Macquart, 1835. Type species: *Chlorops brevipennis* Meigen.

Crassiseta von Roser, 1840. Type species: *Oscinis cornuta* Fallen.

Pachychaeta Loew, 1845. Type species: *Oscinis cornuta* Fallen.

Macrochetum Rondani, 1856. Type species: *Oscinis cornuta* Fallen.

Myrmecomorpha Corti, 1909. Type species: *Chlorops brevipennis* Meigen.

Cyrtomomyia Becker, 1913. Type species: *C. pulchra* Becker

Doliomyia Johannsen, 1924.Type species: *Melanochaeta longiventris* Johannsen.

Neoelachiptera Séguy, 1938. Type species: *N. lerouxi* Séguy

Togeciphus Nishijima, 1955. Type species: *Chaetaspis katoi* Nishijma.

angusta Sabrosky, 1948, [**NE**]

angustifrons Sabrosky, 1948, [**NE**]

angustistylum Sabrosky 1948, [**NE**]

aquila Wheeler, 2003, [**NE**]

biculiminata Nishijima, 1956, [**PA**]

bimaculata (Loew, 1845) (*Crassiseta*) , [**PA**]

brevipennis (Meigen, 1830) , [**PA**]

californica Sabrosky, 1948, [**NE**]

conjuncta (Adams, 1905) (*Crassiseta*) , [**AT**]

cornuta (Fallen, 1820) , [**PA**]

costata (Loew, 1863) , [**NE**]

decipiens (Loew, 1863) , [**NE**]

diastema Collin, 1946, [**PA**]

ensifer Sabrosky, 1951, [**AT**]

ericius (Kanmiya, 1983) (*Togeciphus*) , [**PA**]

erythropleura Sabrosky, 1948, [**NE**]

flaviceps Sabrosky, 1948, [**NE**]

formosa (Loew, 1863) (*Crassiseta*) , [**NE**]

graeca Becker, 1910, [**PA**]

insignis (Thomson, 1869) (*Crassiseta*) , [**PA**]

japonica Nishijima, 1956, [**PA**]

katoi (Nishijima, 1954) (*Chaetaspis*) , [**PA**]

knowltoni Sabrosky, 1948, [**NE**]

lerouxi (Séguy, 1938) (*Neoelachiptera*) , [**AT**]

longiventris (Johannsen, 1924) (*Melanochaeta*) , [**NE**]

maculinervis Becker, 1910, [**AT**]

maculipennis Sabrosky, 1951, [**AT**]

megaspis (Loew, 1858) (*Crassiseta*) , [**PA**]

minima Kanmiya, 1983, [**PA**]

molybdeana Séguy, 1957, [**AT**]

nigriceps (Loew, 1863) (*Crassiseta*) , [**PA**]

occipitalis Becker, 1910, [**AT**]

pechumani Sabrosky, 1948, [**NE**]

penita (Adams, 1908) (*Crassiseta*) , [**NE**]

pulchra (Becker, 1913) (*Cyrtomomyia*) , [**AT**]

punctulata Becker, 1912, [**AT**]

sibirica (Loew, 1858)(*Crassiseta*) , [**PA**]

simplicipes Becker, 1910, [**AT**]

subelongatus (Kanmiya, 1983) (*Disciphus*) , [**PA**]

tanganyikae Sabrosky, 1965, [**AT**]

tarda (Adams, 1905) (*Crassiseta*) , [**AT**]

tau Sabrosky, 1948, [**NE**]

tecta Becker, 1916, [**AT**]

triangularis Becker, 1912, [**AT**]

tuberculata (Adams, 1905) (*Crassiseta*) , [**AT**]

tuberculifera (Corti, 1909) (*Crassiseta*) , [**PA**]

ugandae Sabrosky, 1951, [**AT**]

uniseta Collin, 1939, [**PA**]

vittata Sabrosky, 1948, [**NE**]

Genus *GONIASPIS* Duda

Goniaspis Duda, 1930. Type species: *Cadrema rubra* Becker.

Palaeoenderleiniella Duda, 1930. Type species: *Cadrema rubra* Becker.

equalis (Williston, 1896) (*Hippelates*), [**NT**]

lucia Mlynarek & Wheeler, 2009, [**NT**]

lurida Mlynarek & Wheeler, 2009, [**NT**]

obscurata Duda, 1930, [**NT**]

opaca Mlynarek & Wheeler, 2009, [**NT**]

rubra (Becker, 1916) (*Cadrema*) , [**NT**]

scutellaris (Williston, 1896) (*Hippelates*) , [**NT**]

subequalis (Malloch, 1913) (*Hippelates*) , [**NT**]

truncata (Malloch, 1913) (*Hippelates*) , [**NT**]

versicolor Mlynarek & Wheeler, 2009, [**NT**]

Genus *MELANOCHAETA* Bezzi

Pachychoeta Bezzi, 1895 (as subgenus of *Crassiseta*). Type species: *Elachiptera aterrima* Strobl (Preocc. Bigot)

Melanochaeta Bezzi, 1906. Type species: *Elachiptera aterrima* Strobl. (replacement name for *Pachychoeta* Bezzi)

Pachychaetina Hendel, 1907. Type species: *Elachiptera aterimma* Strobl. (unnecessary replacement name for *Pachychoeta Bezzi*)

Lasiochaeta Corti, 1909. Type species: *Elachiptera pubescens* Thalhammer.

atricornis (Adams, 1905) (*Crassiseta*) , [**AT**]

basilaris (Adams, 1905) (*Oscinis*) , [**AT**]

bengalensis (Cherian, 1975) (*Elachiptera*) , [**OR**]

capreolus (Haliday, 1838) (*Oscinis*) , [**PA**]

comoroensis (Sabrosky, 1979) (*Elachiptera*) , [**AT**]

diabolus Becker, 1913, [**AT**]

dubia (Lamb, 1918) (*Elachiptera*) , [**AT**]

eunota (Loew, 1872) (*Crassiseta*) , [**NE**]

flavofrontata (Becker, 1903) (*Crassiseta*) , [**AT**, **PA**]

freyi (Duda, 1934) (*Elachiptera*) , [**AT**]

indistincta (Becker, 1911) (*Gampsocera*) , [**OR**]

kaw Sabrosky, 1948, [**NE**]

lindbergi (Sabrosky, 1957) (*Elachiptera*) , [**AT**]

luteopilosa (Cherian, 1975) (*Elachiptera*) , [**OR**]

melampus Becker, 1912, [**NE**]

nigripalpis (Becker, 1912) (*Oscinella*) , [**AT**]

nigritibiella (Becker, 1910) (*Oscinella*) , [**AT**]

opaca (Duda, 1932) (*Elachiptera*) , [**NE**]

palmata (Loew, 1852) (*Crassiseta*) , [**AT**]

pilosula Becker, 1910, [**AT**]

pubescens (Thalhammer, 1896) (*Elachiptera*) , [P**A**]

scapularis (Adams, 1905) (*Crassiseta*) , [**AT**]

umbrosa (Becker, 1924) (*Elachiptera*) , [**OR**]

vulgaris (Adams, 1905) (*Crassiseta*) , [**AT**]

Genus *SEPSIDOSCINIS* Hendel

Sepsidoscinis Hendel, 1914. Type species: *S. maculipennis* Hendel

maculipennis Hendel, 1914, [**OR**]

Genus *ELACHIPTERA* sensu Sabrosky 1984

(Species not examined and information in literature not adequate to assign to a genus)

assamensis Cherian, 1975, [**OR**]

austriaca Duda, 1932, [**PA**]

breviscutellata Nartshuk, 1964, [**PA**]

dubiosa (Becker, 1916) , [**NT**]

edwardsi Sabrosky, 1951, [**AT**]

indica Cherian, 1975, [**OR**]

lenis Collin, 1949, [**AT**]

lividipennis Duda, 1934, [**AT**]

lyrica Sabrosky, 1977, [**AT**]

melaena (Becker, 1912) (*Melanochaeta*) , [**NT**]

octoseta Cherian, 1975, [**OR**]

orizea Séguy, 1949, [**PA**]

popovi Nartshuk, 1962, [**PA**]

rubrolimbata Duda, 1930, [**NT**]

rufescens (Walker, 1871) (*Oscinis*) , [**AT**]

ruficollis (Frey, 1918) (*Melanochaeta*) , [**NT**]

rufifrons Duda, 1932, [**PA**]

scrobiculata (Strobl, 1900) , [**PA**]

striatifrons Peterfi, 1965, [**PA**]

sublineata (Becker, 1912) (*Melanochaeta*) , [**NT**]

submediterranea Beschovski, 1980, [**PA**]

unimaculata Becker, 1913, [**AT**]

viator Nartshuk, 1971, [**PA**