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**The morphology, higher-level phylogeny and classification
of the Empidoidea (Diptera)**

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The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera)

BRADLEY J. SINCLAIR¹ & JEFFREY M. CUMMING²

¹ *Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany.*

E-mail: b.sinclair.zfmk@uni-bonn.de

² *Invertebrate Biodiversity, Agriculture and Agri-Food Canada, C.E.F., Ottawa, ON, Canada K1A 0C6.*

E-mail: cummingjm@agr.gc.ca

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Abstract

A cladistic analysis of the Empidoidea and basal lineages of the Cyclorrhapha, based on morphological characters, confirms the monophyly of both groups as well as that of the Eremoneura. The resulting final trees are used to revise the classification of the Empidoidea to include the following five families: Empididae, Hybotidae, Atelestidae (including Nemedinae **n. subfam.**), Brachystomatidae **rev. stat.** (comprising the subfamilies Brachystomatinae, Ceratomerinae and Trichopezinae), and Dolichopodidae *s.lat.* The family Microphoridae is not recognized, and the Microphorinae and Parathalassiinae are assigned to the Dolichopodidae *s.lat.* The Dolichopodidae *s.str.* includes 15 subfamilies that were previously recognized within the family. Within the Empidoidea we found support for Atelestidae as the sister group to the Hybotidae and for the monophyly of Parathalassiinae + Dolichopodidae *s.str.* The Empididae remains poorly defined and the genera *Homalocnemis* Philippi, *Iteaphila* Zetterstedt, *Anthepiscopus* Becker, and *Oreogeton* Schiner are classified as *incertae sedis* within the Empidoidea. In addition, the following higher taxa are proposed: Symballophthalmini **n. tribe**, Bicellariini **n. tribe**, Oedaleinae **rev. stat.**, and Trichininae **rev. stat.**, which are all assigned to the Hybotidae. The genus *Sematopoda* Collin is tentatively assigned to Trichopezinae, and *Xanthodromia* Saigusa is transferred from Hemerodromiinae to Brachystomatinae.

All morphological characters are extensively discussed and illustrated, including details of the antennae, mouthparts, internal thoracic structures, wings, and male and female terminalia. In addition, a key to families and unplaced genus groups of the Empidoidea is provided. Feeding habits are also discussed in terms of the empidoid ground plan condition.

Key words: dance flies, long-legged flies, Empidoidea, Empididae, Hybotidae, Atelestidae, Brachystomatidae, Dolichopodidae, phylogeny, cladistics, morphology, genitalia, mouthparts, new subfamily, new tribes

Introduction

An estimated 11,400 species are described in the Empidoidea, making it among the largest of higher categories of Diptera (Thompson 2005). Fossils with empidoid-like venation are known from the upper Jurassic (Mostovski 1999), with the empidoid subfamilies present by the early Cretaceous (Grimaldi 1999; Grimaldi & Cumming 1999). In fact, the Empidoidea are among the best known lineages from the Cretaceous (Grimaldi 1999). Divergence time estimates for the Empidoidea range between 144–163 MYA (Wiegmann *et al.* 2003). They occur worldwide (except Antarctica), with certain lineages being particularly abundant or more diverse in temperate latitudes. For example, we have identified several “empidoid hotspots” (exclusive of Dolichopodidae *s.str.*) based on total number of described endemic genera, among which are included, New Zealand (13 endemic genera), South Africa (9), southern South America (11) and western North America (9).

The tremendous species diversity of the Empidoidea corresponds to an enormous morphological or structural diversity (Figs. 417–424), especially in the male genitalia. The

modifications range from symmetrical, unrotated, relatively simple genitalia (somewhat similar to asiloids) to asymmetrical and rotated (with secondary fusion of various sclerites) and occasionally secondary symmetry, which has often caused confusion and difficulties in determining homology. This wonderful and complex genitalic diversity was a major impetus for our earlier studies on male genitalia (Sinclair *et al.* 1994; Cumming *et al.* 1995). There are also extensive female and male (primarily) secondary sexual characters found on all body parts, particularly on the legs. In addition, there is a tremendous range in size, from the very large *Empis (Planempis) pan* Frey (wing length nearly 12 mm) to the tiny genus *Enlinia* Aldrich (wing length 0.8 mm: see Robinson 1969).

Empidoids breed in a variety of habitats, including running water (e.g., Wagner & Gathmann 1996), tidal zones, decaying wood (e.g., Meyer 2005), and moist soil. Adults are predators or flower visitors (feeding on nectar and/or pollen) and nearly all known larvae are predators (except *Thrypticus* Gerstäcker, secondarily phytophagous in stems of monocots). Investigations on the potential impact of predaceous empidoids acting as biocontrol agents on agricultural pests are only in the initial stages (see Cumming & Cooper 1993 and Stark 1994, for review of literature). Some empidoids are major predators of Simuliidae in both adult and larval stages (Werner & Pont 2003; Sinclair & Harkrider 2004).

The Empidoidea are also widely known, among biologists, for their elaborate mating displays and swarming behavior (hence the common name, dance flies, or sometimes balloon flies). Members of the Empidinae are particularly interesting because males transfer nuptial gifts comprising small insects, or other objects to females during mating (Cumming 1994). Studies on the function, evolution, and selection of mating systems have been investigated in a number of species of Empidinae (e.g., Newkirk 1970; Svensson & Petersson 1987; Sivinski & Petersson 1997; Preston-Mafham 1999; Funk & Tallamy 2000). In contrast to these aerial mating swarms, the Dolichopodidae *s.str.*, or long-legged flies, court and mate on the ground, accompanied by various forms of signalling (e.g., enlarged, brightly colored palpi, antennal flags, modified tarsal segments, wing waving) (Sivinski 1997; Zimmer *et al.* 2003).

Large gaps in the taxonomic knowledge of the Empidoidea remain for most regions of the world, especially in the Southern Hemisphere. There has been little work in southern South America since Collin (1933) and knowledge of the central African empidoid fauna (i.e., Empididae, Hybotidae), in particular, is very poor. But even in areas such as North America, many modern revisions have resulted in more than double the number of previously described species (e.g., Cumming & Cooper 1992; Sinclair 1994; MacDonald 1998; Pollet & Cumming 1998). In contrast, the knowledge of the phenology and distribution of the empidoid fauna is very well documented in Britain (Collin 1961; Assis Fonseca 1978; Plant 2003, 2004), France (Parent 1938) and Scandinavia (Chvála 1975, 1983, 1994, 2005).

Studies on the higher classification and phylogeny of the Empidoidea are herein reviewed (see Historical Review of the Phylogeny of the Empidoidea). During the past few years, there have been attempts to establish a stable phylogeny using molecular characters (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004), whereas the only published quantitative phylogeny using morphological characters is somewhat outdated and several characters are of questionable homology (Wiegmann *et al.* 1993; see below). Our interest in the higher classification of the Empidoidea arose during earlier revisionary studies on the Clinocerinae and Tachydromiinae, two highly distinctive lineages. We realized that our understanding of relationships was greatly hampered by inadequate knowledge of the relationships between lineages. In addition, the problems in the homologies in the male terminalia between these two disparate groups resulted in a great loss of potential characters vital in the reconstruction of phylogenies.

The Empidoidea are a pivotal group situated phylogenetically between the lower and higher Diptera. Consequently a thorough understanding of the relationships and morphology of this lineage is vital in determining ground plan conditions in the higher flies or Cyclorrhapha. To address this priority the aims of this study are three fold. Firstly, to provide concrete evidence for the monophyly of generic and family groupings of the Empidoidea, through the introduction of new morphological characters and homologies that have not been previously examined. For this reason, many of the character state descriptions are accompanied by lengthy discussions of form, structure and variation among taxa. Secondly, to provide a framework for the recognition of lower groupings such as subfamilies and tribes. Thirdly, to provide a comprehensive and highly illustrated review of empidoid adult morphology. We expect that the extensive illustrations will serve as an atlas for our empidoid colleagues in their continued investigations of this diverse group. This study does not directly address the higher classification of the Dolichopodidae *s.str.*, due to the complexities and size of this group. However, we hope that the ground plan trends established here will assist with future studies on this complex and highly diverse empidoid family.

Materials and Methods

Materials

This study is based on material borrowed from or deposited into the following institutions: Biosystematics Laboratory, Kyushu University, Fukuoka, Japan (BLKU), Canadian National Collection of Insects, Ottawa, Canada (CNC); Natal Museum, Pietermaritzburg, South Africa (NMSA); United States National Museum of Natural History (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

All dissections were made in glycerin and tissues cleared using hot 85% lactic acid. Wherever possible, entire specimens were cleared to facilitate observations of all

structures in glycerin under high magnification using a compound microscope. Some extremely pale structures (e.g., spermathecae) were stained using Delafields Haematoxylin. Due to the insufficient availability of alcohol preserved material for many exemplars, only morphological characters associated with sclerotized structures were analysed, rather than muscle, soft tissue, or molecular characters.

Terms used for adult structures primarily follow those of McAlpine (1981), except for the antenna where terms of Stuckenberg (1999) are used. Homologies of the male terminalia follow those of Cumming *et al.* (1995) and Sinclair (1996, 2000a). Larval terms follow those of Courtney *et al.* (2000).

Cladistic analysis

One hundred and twenty-two characters were included in the cladistic analysis, including 79 binary characters and 43 multistate characters. All characters were treated as unordered with multistate characters considered as non-additive, and all characters were equally weighted initially. Exemplar-level autapomorphies were not included in the analysis. Characters were scored for 57 ingroup exemplar genera, representing 64 species, belonging to the Eremoneura (see below under Taxon Sampling and Table 1). Character polarity was determined by rooting the tree with four asiloid outgroups, which together were constrained to be paraphyletic in relation to the ingroup.

Parsimony analysis of the character state matrix (Table 2) was performed using the program PAUP* version 4.0b10 (Swofford 2002). A heuristic search with stepwise addition was implemented to find the most parsimonious trees using random addition sequence of taxa, tree-bisection-reconnection (TBR) branch swapping and 1000 random replications. *A posteriori* character weighting was implemented using successive approximations according to the rescaled consistency index (RC).

Cladogram estimates (or statistics) such as consistency index (CI), retention index (RI) and rescaled consistency index (RC) were used to assess the fit of data to the cladograms. Branch support for each clade supported in all of the equally parsimonious trees (BrS) (Bremer 1994), was calculated with the program TreeRot version 2c (Sorenson 1999) by constraining the number of trees saved per replicate (for 20 replications) to 1000 for each node. Branch support indicates the number of extra steps from the most parsimonious solution at which a clade fails to be resolved in the consensus cladogram, as successively longer cladograms are examined (Skevington & Yeates 2001). Character evolution, character state distributions and alternative tree topologies were examined using the program MacClade 4 (Maddison & Maddison 2003).

Taxon sampling

Until recently, most empidooid subfamily definitions and phylogenies have been based primarily on Northern Hemisphere taxa, with little if any knowledge of Southern Hemisphere taxa incorporated. We have attempted to examine all genera wherever

possible and use these taxa to test currently accepted subfamily definitions and phylogenies. We believe that this previous northern bias has prevented workers from clearly establishing ground plan trends for the major empidoid lineages.

In contrast to our previous analyses of the Brachycera (Sinclair 1992; Sinclair *et al.* 1994; Cumming *et al.* 1995) we have changed from an intuitive to an exemplar method for determining ground plan states for higher taxa (see Yeates 1996). Although in some cases terminal taxa represent more than one species (e.g., *Hormopeza*, *Nemedina*) as opposed to single species advocated by Yeates (1996), this methodology should facilitate verification and testing by other researchers. For the analysis, normally two generic exemplars were selected from all currently accepted empidoid family-group taxa, one from what we consider the most primitive genus of each lineage (if no phylogeny is available) and the other from a genus assumed to be more distantly related on the basis of specialized genitalia, wing venation, etc. Groupings such as the plesiomorphic Oreogetoninae and Ocydromiinae *sensu* Chvála (1976, 1983, respectively) were divided into genus groups and exemplars were chosen from each. In this way, all genus groups were represented in the analysis. The choice of exemplars is discussed more fully below and is primarily the result of direct examination of all genera within each higher-level category wherever possible, accumulated over a fifteen-year survey. In most cases, the immature stages are unknown for a particular exemplar, and consequently another congeneric species was chosen in order to score these characters. In addition, exemplars from all the basal lineages of the Cyclorrhapha were included to test the monophyly of the Empidoidea versus paraphyly in relation to the Cyclorrhapha, as well as to test homoplasy of each character throughout the Eremoneura.

A complete list of exemplars is given in Table 1. Only the genus is listed in the resultant trees for spatial and visual reasons.

Asiloidea

The monophyly of this lineage remains largely unsupported or based on weak evidence (see Sinclair *et al.* 1994; Yeates 1994, 2002), especially if Eremoneura is included in the analysis. In fact, apomorphic trends within the Therevidae + Scenopinidae lineage or even the Hilarimorphidae point to a possible relationship with Eremoneura (Cumming *et al.* 1995; Yeates 2002). Exemplars from three families within the traditional Asiloidea were chosen based on Sinclair *et al.* (1994), Cumming *et al.* (1995), and Yeates (1994, 2002) and include the following taxa:

Asilidae

A species of *Diogmites* Loew of the subfamily Dasygogoninae was selected as an exemplar. This subfamily is considered the most basal clade of the Asilidae because of the presence of acanthophorites (Adisoemarto & Wood 1975). The male genitalia of *Diogmites* is considered representative of the ground plan condition of the family (Sinclair *et al.* 1994).

Therevidae

This family has traditionally been divided into two subfamilies, Therevinae and Phycinae (Irwin & Lyneborg 1981; Yang *et al.* 2000), although recently Winterton *et al.* (2001) added a third subfamily, Agapophytinae. A species of *Thereva* Latreille was chosen as an exemplar of the family. A species of this genus was also selected as one of three therevid exemplars in the phylogenetic analysis of the Asiloidea by Yeates (1994).

Hilarimorphidae

This family includes the nominal genus *Hilarimorpha* Schiner and *Apystomyia* Melander, which was recently included by Yeates (1994). Both genera were assigned by Sinclair *et al.* (1994) as *incertae sedis* within the Therevidae + Scenopinidae clade, but they appear to be closely related on the basis of similarities in the form of the gonostylus. Alternatively, Yeates (1994) considered the Hilarimorphidae as the sister group of the Bombyliidae, but later (2002) proposed it as the sister group to the Eremoneura. A species of *Hilarimorpha* was selected as an exemplar in this study. Wiegmann *et al.* (1993) included both genera of the Hilarimorphidae in their analysis of the Empidoidea because of many supposedly empidoid-like features.

Scenopinidae

The definition of this family was recently expanded to include the Proratinae, formerly of the Bombyliidae (Yeates 1992). *Caenotus* Cole retains many plesiomorphic features and consequently a species of this genus was selected as an exemplar of the Scenopinidae.

Empidoidea

Oreogetoninae

This subfamily is a polyphyletic collection of genera, first formally recognized by Chvála (1976), and is undoubtedly paraphyletic in relation to other empidoid subfamilies. All included genera in this group were sorted into the seven generic groupings listed below and each was scored separately in order to assess their position within the Empidoidea. We have attempted to refrain from referring to this subfamily throughout the remainder of this paper.

Brochella Melander is a monotypic genus known from far western North America. Its very odd and unique head, antenna, and male terminalia (Figs. 14, 64, 290–292) have inhibited confident subfamily assignment of this taxon. Based on mouthpart morphology, this species is predicted to be a flower visitor.

Hesperempis Melander group (including *Dryodromia* Rondani and *Toreus* Melander) represents another flower-feeding lineage. *Hesperempis* and *Toreus* are both Nearctic genera, whereas *Dryodromia* is confined to Europe.

Homalocnemis Philippi is a relict Gondwanan genus, recorded from Namibia, southern South America, and New Zealand. It is a large-sized and presumably predaceous

empidoid, with long wings and raptorial midlegs. Again the unusual structure of the male genitalia (Figs. 262–265) has obscured its subfamily assignment.

Hormopeza Zetterstedt is the most basal member of a small genus group that includes *Ragas* Walker, *Dipsomyia* Bezzi, *Zanclotus* Wilder, and *Hydropeza* Sinclair (referred to as the *Ragas* group by Sinclair 1999). *Hormopeza* is primarily found in the Northern Hemisphere (with records from South Africa, Brazil, and Australia) and has often been used as a representative of the ground plan condition of the Empidoidea. The male genitalia, especially the epandrium has attracted much attention and contrasting interpretations. Representatives of *Hormopeza*, as well as *Ragas* and *Zanclotus* were included in the analysis. *Ragas* occurs in the Palearctic and western Nearctic Regions (Sinclair 2001) and *Zanclotus* is confined to the western Nearctic (Sinclair 1999).

The coding for *Hormopeza* was based on two exemplar species because of a shortage of identified material resulting from poor knowledge of the Nearctic fauna and the need for a thorough revision of the Holarctic species.

Iteaphila Zetterstedt group (including *Anthepiscopopus* Becker) is a flower-feeding lineage with simplified mouthparts.

Oreogeton Schiner is restricted to the northern hemisphere (see Sinclair 1995a) and like other genera of the problematic Oreogetoninae, its male genitalia are unique (Figs. 268, 269), such that similarities and relationships to other empidoid genera remain uncertain.

Philetus Melander is a poorly known genus that includes two western North American species.

Hemerodromiinae

This very distinctive lineage of empidids with raptorial forelegs is divided into two tribes, Chelipodini and Hemerodromiini (Steyskal & Knutson 1981). *Chelipodozus* Collin of the Neotropical Region was selected to represent the Chelipodini and *Chelifera* Macquart was selected to represent the Hemerodromiini. The latter tribe is quite derived in terms of venation, pleural sclerites and mouthparts, yet males retain apparently plesiomorphic terminalia that appear very similar to those of the Empidini.

Clinocerinae

The subfamily Clinocerinae was reviewed by Sinclair (1995a) and a phylogenetic analysis was presented for all world genera. The subfamily can be separated into two main divisions, with a paraphyletic basal group of genera that are restricted primarily to the Southern Hemisphere and a large monophyletic group, including all derived genera, that is probably Laurasian in origin. The recently described primitive South African genus, *Afroclinocera* Sinclair (sister genus to *Proagomyia* Collin), was chosen to represent the ground plan condition, while *Clinocera* Meigen, which includes features that are clearly apomorphic compared to the ground plan condition, was selected from the derived group

of genera. This latter genus and the related genus, *Wiedemannia* Zetterstedt, have often been used in phylogenetic studies (e.g., Wiegmann *et al.* 1993) as sole representatives of this subfamily, but their derived features appear to have contributed to some confusion in the relationships of this lineage. Southern hemisphere genera generally appear much more informative in elucidating phylogenetic relationships.

Empidinae

Exemplars were chosen from the two major tribes, Empidini and Hilarini, and were chosen from three additional genera not currently assigned to a tribe. *Edenophorus* Smith is an endemic South African genus with seven described species (Sinclair 2002). *Empidadelpha* Collin is a Southern Hemisphere *Empis*-like genus with many undescribed Chilean and Australian species. The terminalia of *Empidadelpha* retain many plesiomorphic features not found in Northern Hemisphere species of Empidini *s.str.* *Sphicosa* Philippi is another apparent primitive genus that displays features of both Empidinae tribes. Representatives of these three taxa were also included in the analysis.

Nemedina group

The genus *Nemedina* Chandler is currently unassigned in the Empidoidea, but it appears to belong to an ancient lineage with many extinct genera (Grimaldi & Cumming 1999; Sinclair & Arnaud 2001). Given this ancient history and diversity, this lineage is much impoverished today. A recently discovered and described species of *Nemedina* facilitated inclusion of this taxon in the analysis (Sinclair & Shamshev 2003), as well as the discovery of males of the type species (Sinclair & Papp 2004).

Atelestinae

Exemplars of the three genera of the Atelestinae (i.e., *Acarteroptera* Collin, *Atelestus* Walker and *Meghyperus* Loew) were included in this analysis. The assignment of this lineage has been both problematic and controversial and thus it was thought that all variation within the lineage should be included rather than relying on a single taxon. An unpublished revision of this subfamily (Wiegmann 1989) assisted in determining appropriate taxa.

Ocydromiinae

This traditional paraphyletic subfamily was broken down into five monophyletic units following Sinclair & Cumming (1998). The Oedaleini is Holarctic in distribution, characterized by a stout postpedicel (first flagellomere), reduced arista-like style, and secondary fusion of the female cercus to tergite 10. A species of *Oedalea* Meigen represented this group in the analysis. The Ocydromiini is worldwide in distribution, recently redefined by Sinclair & Cumming (2000), and characterized by the following apomorphies: phallus biarticulated, and ventral apodemes and postgonites absent.

Exemplars of *Ocydromia* Meigen and *Neotrichina* Sinclair & Cumming were selected from this tribe for the analysis. *Trichinomyia* Tuomikoski, *Trichina* Meigen, and *Bicellaria* Macquart were treated by Chvála (1983) in the tribe Trichinini, but the monophyly of this group remains in doubt. Consequently, exemplars of each genus were included in the analysis. The first two genera are often considered among the most primitive of the hybotids. For purposes of discussion, we will avoid referring to the entire group using the subfamily ending, but rather refer to it simply as the ocydromiines.

Tachydromiinae

This subfamily is clearly monophyletic and is distributed worldwide. Exemplars were selected on the basis of the phylogenetic relationships presented by Chvála (1975, fig. 35) and unpublished data from studies by JMC. *Symballophthalmus* Becker was selected as the most plesiomorphic representative of the Tachydromiinae. The subfamily has generally been divided into two tribes, the Tachydromiini and Drapetini. *Platypalpus* Macquart was selected from the former tribe, whereas *Austrodromia* Collin was selected from the latter tribe.

Hybotinae

This subfamily is divided into four generic groupings, but inter-relationships among the groups remain unresolved (Sinclair 1996). Exemplars of the Hybotinae were chosen on the basis of data presented by Sinclair (1996). *Acarterus* Loew, which is isolated from more derived hybotine genera by its wing venation and mouthparts, was selected as a basal representative of the subfamily. *Stenoproctus* Loew was chosen as a representative of the *Stenoproctus* group, which is characterized by a shortened cell *cup* with a truncate apex. *Hybos* Meigen was selected as a representative of the more derived taxa of Hybotinae that possess a characteristic short-ovate first flagellomere.

Trichopezinae

This lineage was recently redefined to include taxa characterized by a large, laterally compressed apodeme arising on the anterior margin of the female eighth tergite (Sinclair 1995a). The subfamily can be separated into two groups by the presence or absence of holoptic male eyes. The form of the male cercus with its stout inner face possibly unites the genus group with holoptic males (includes: *Gloma* Meigen, *Heterophlebus* Philippi, *Apalocnemus* Philippi, and *Hyperperacera* Collin). *Heterophlebus*, which is confined to the Southern Hemisphere (i.e., South America and Australia), was selected as an exemplar of this clade on the basis of a large number of plesiomorphic features, including the form of the antennae, mouthparts and female terminalia. *Niphogenia* Melander was chosen as the representative of a small subgroup (including *Ceratempis* Melander), which display similarities with *Oreogeton* on the basis of their male terminalia. *Sabroskyella* Wilder was chosen as a representative of a complex of derived genera (including *Trichopeza* Rondani), which possess asymmetrical male terminalia and a long filamentous phallus.

Ceratomerinae

This subfamily is confined to the Southern Hemisphere on former Gondwanan landmasses. It is estimated to comprise more than 65 species among three described and several undescribed genera (Sinclair 1998, 2003a, unpubl. data). The distinctive conus projecting from the pedicel into the postpedicel is a well-accepted synapomorphy for the entire group (Sinclair 1997, 2003a). *Glyphidopeza* Sinclair appears to be the most basal lineage in the Ceratomerinae, retaining several plesiomorphic characters; for example, presence of pseudotracheae, a cell cup, and cell dm emitting three veins distally. All remaining ceratomerines lack these features and are characterized by a petiolate M_{1+2} (Sinclair 1997). Among these remaining taxa, *Icasma* Collin and the *Ceratomerus mediocris* group clearly have highly derived features in wing venation, male terminalia and abdominal sclerotization (Collin 1933; Sinclair 1997). Within *Ceratomerus* Philippi, the Australian and Chilean species appear the least modified. A species from both *Glyphidopeza* and *Ceratomerus* were chosen as exemplars, on the basis of a preliminary phylogenetic analysis of the subfamily (Sinclair 1998).

Brachystomatinae

This is a small subfamily with two known genera, *Anomalempis* Melander and *Brachystoma* Meigen. We chose to include both genera as exemplars, especially since the type genus is characterized by a number of apparent autapomorphies, including very narrow wings, which have been used in previous analyses to support proposed higher-level relationships and classifications. The Brachystomatinae is clearly monophyletic on the basis of L-shaped stipes and long, coiled spermathecae (Sinclair 1995a). Species of *Anomalempis* retain many plesiomorphies compared with those of *Brachystoma*, including features such as holoptic males and broad wings.

Microphorinae

Although the included genera are of similar form, the monophyly of this subfamily and the two recognized tribes, Microphorini and Parathalassiini, remains in doubt. Cumming & Brooks (2002) analysed the relationships of all extant and fossil genera in an effort to elucidate the basal classification of the Dolichopodidae *s.lat.* The microphorines as a whole are generally accepted as most closely related to the Dolichopodidae *s.str.* (Colless 1963; Hennig 1971; Chvála 1986), with possibly only the Parathalassiini representing the sister group to this large and specious family (Chvála 1988, Ulrich 2003). Consequently, five of seven described extant genera of the Microphorinae were included in the analysis with the hope of establishing ground plan features of both this lineage and the Dolichopodidae. For the purposes of discussion, we will avoid referring to these groups using subfamily and tribal endings, but rather refer simply to microphorids for the entire subfamily, microphorines for *Microphor* Macquart and *Schistostoma* Becker, and parathalassiines for the remaining extant genera.

Dolichopodidae

This family is very diverse and includes approximately 6900 species among some 245 genera (Grichanov 2006). Despite the family's large size, the Dolichopodidae are remarkably uniform in general appearance (especially compared to other empidoidea) and together are clearly defined by a large number of apomorphies including internal configuration of mouthparts, asymmetry of the male terminalia, presence of a genital foramen and sclerotized anal papillae. Exemplars were chosen from the subfamilies Sciapodinae (i.e., *Heteropsilopus* Bigot), Dolichopodinae [i.e., *Dolichopus* Latreille (*D. ziczac* Wiedemann group, formerly assigned to *Lichtwardtia* Enderlein, see Brooks 2005a)], and Sympycninae (i.e., *Sympycnus* Loew). The Sciapodinae are generally accepted as one of the most basal lineages (Negrobov 1986), because of a number of plesiomorphic features (Bickel 1994). However, several ground plan apomorphies remain disputed. Exemplars from the Dolichopodinae and Sympycninae were also included, because they exhibit the pedunculate and encapsulate dolichopodid genital forms, respectively.

Lower Cyclorrhapha

A broad selection of taxa was considered the best way to treat diversity in the basal lineages of the Cyclorrhapha. Homoplasy is very common within the Empidoidea and Cyclorrhapha and emphasis on a single lineage could bias the analysis. The choice of exemplars was based on the phylogeny of Cumming *et al.* (1995) and a molecular phylogeny of the lower Cyclorrhapha published by Collins & Wiegmann (2002b).

Opetiidae

The Opetiidae comprises the single extant genus *Opetia* Meigen, which was included as an exemplar. Cumming *et al.* (1995) considered it the most basal family of Cyclorrhapha because of the lack of a phallapodeme, antenna with a two-articled arista, acrostichals and dorsocentral setae undifferentiated, and costa circumambient. Although basal, this small aberrant family clearly belongs to the Cyclorrhapha because of the separated sperm pump, rotated (circumverted) male genitalia, and lack of abdominal plaques (Cumming *et al.*, 1995). Collins & Wiegmann (2002b) found support for a sister group relationship between the Opetiidae and Lonchopteridae, whereas Moulton & Wiegmann (2004) considered Opetiidae most closely related to Platypezidae.

Platypezidae

Microsania Zetterstedt of the subfamily Microsaniinae and *Agathomyia* Verrall of Callomyiinae (= Platypezininae) were chosen as exemplars. The monophyly of the family has not yet been proven satisfactorily (Chandler & Shatalkin 1998; Chandler 2001), however uniserial acrostichal setulae and an expanded male hind tarsus have been suggested as possible synapomorphies (Cumming *et al.* 1995). It is clearly a very primitive

family with the retention of male aerial swarming, male eyes in contact dorsally with enlarged facets, the lack of a well-developed condyle (conus) on the antennal pedicel, and the pupal respiratory organ not projecting through the puparium (Cumming *et al.* 1995; Chandler & Shatalkin 1998).

Lonchopteridae

This family is generally thought to comprise the single genus *Lonchoptera* Meigen, but several groupings are possible based on male genital structures. We chose *Lonchoptera uniseta* Curran as the exemplar of the Lonchopteridae based on the plesiomorphic form of the male terminalia, especially the hypandrium, which is sclerotized ventrally and not enclosed within the epandrium, and the presence of enlarged postgonites (as in Syrphidae).

Phoridae

The family Sciadoceridae has recently been relegated to subfamily status within the very speciose family Phoridae (Disney 2001), but this lineage remains one of the more primitive members of this family (Brown 1992; Cumming *et al.* 1995). The single extant species of *Sciadocera* White was selected as the exemplar for the entire lineage.

Syrphidae

Three subfamilies are generally recognized in this family: Microdontinae, Syrphinae, and Eristalinae. The former subfamily is often considered the most basal lineage (Thompson 1969), but see Skevington & Yeates (2000) and Ståhls *et al.* (2003) for a discussion of Syrphidae phylogeny. However, we chose an exemplar from the Syrphinae, i.e., *Syrphus ribesii* (L.), because of the retention of a more generalized form of the male terminalia. The Microdontinae lack a phallapodeme and articulated postgonites and this is considered autapomorphic for the subfamily (Cumming *et al.* 1995).

Schizophoran Cyclorrhapha

Anthomyiidae

The anthomyiid, *Strobilomyia* Michelsen was selected as a relatively generalized representative of the Calyptratae, which is considered one of the basal lineages of the exceptionally diverse Schizophora (McAlpine 1989).

Monophyly of the Eremoneura

Together the Cyclorrhapha and Empidoidea form a well-supported monophyletic lineage known as the Eremoneura (Griffiths 1972; Cumming & Sinclair 1990; Sinclair 1992; Wiegmann *et al.* 1993; Cumming *et al.* 1995; Yeates & Wiegmann 1999). This lineage is supported on the basis of the following characters: larval maxilla reduced to elongate, primarily membranous lobe; larval prementohypopharyngeal apparatus “V”-shaped; three

larval instars; one-segmented maxillary palpus; cell cup closed apically; wing vein M with only two branches; female abdominal tergite 9 lost; epandrium deeply emarginate; hypandrium and gonocoxites fused; lateral ejaculatory processes lost; subepandrial membrane completely sclerotized and divided laterally into pair of bacilliform sclerites, gonostyli absent; postgonites present (see discussion in Cumming *et al.* 1995 and characters 98 and 99 below).

Historical Review of the Phylogeny of the Empidoidea

Smith (1969) and Chvála (1983) provided historical reviews of the systematic position of the Empidoidea and “subfamily” divisions, and this will not be repeated here. It is the phylogenetic relationships within this superfamily that is of most interest in this study and there has been a long, rich history. The major publications and proposals are briefly reviewed in this section.

Hardy (1954) was the first to publish a branching diagram expressing the interrelationships of the subfamilies of the Empididae. The Hybotinae was linked with Empididae *s.str.* (+ Hemerodromiinae + Ceratomerinae) distant from Ocydromiinae and Tachydromiinae. His analysis was based on the consideration of wing venation. The former group apparently retains a concave M_1 and the latter group retains a convex M_1 . The configuration of these veins was re-analysed and discussed by Tuomikoski (1966). Hardy (1962) later expanded his ideas on relationships to include male terminalia, discussing hypothetical ancestral configuration and several trends. He gathered his data from Australian genera, comparing relationships of the Empididae, Platypezidae, Clinocerinae, and Lonchopteridae.

Bährmann (1960) presented evidence for the monophyly of the Hybotinae, Tachydromiinae and Ocydromiinae in contrast to Hardy (1954). However, no evidence was proposed for the monophyly of the Empidinae, Hemerodromiinae (+ Clinocerinae + Brachystomatinae) and Ceratomerinae.

Krystoph (1961) presented a broad, detailed survey of the structure of adult mouthparts of the Empididae. He presented evidence supporting the monophyly of the Hybotinae, Tachydromiinae and Ocydromiinae, and clearly stated that he considered the Hybotinae as the most derived lineage of this group in contrast to Bährmann (1960). In addition, Krystoph (1961) suggested that *Atelestus* (= *Platycnema* Zetterstedt) should be assigned to the Platypezidae (= clythiids) and that the Ocydromiinae may be paraphyletic in relation to the Tachydromiinae.

Collin dominated the taxonomy of the Empididae in the first half of the last century, especially on the basis of his New Zealand (Collin 1928), South American (Collin 1933) and British (Collin 1961) empidid revisions. These enormous efforts remain some of the most important and landmark works in the Empididae. Unfortunately, he often confounded

phylogenetic relationships by retaining genera within lineages, primarily for convenience, that he clearly believed were unrelated. This often caused confusion among subsequent researchers. The classification used by Collin (1961) has been discussed previously (see Tuomikoski 1966).

Colless (1963) provided the first strong arguments for the close relationship between the microphorids and Dolichopodidae, emphasizing the similarities of the male and female terminalia. At the time, the microphorine genera were either assigned to the Empidinae or Hybotinae.

Tuomikoski (1966) clearly listed and discussed the synapomorphies characterizing the ocydromioid or hybotid group of subfamilies. He clearly presented evidence of the paraphyletic Ocydromiinae and attempted to subdivide the subfamily into smaller monophyletic units. In addition, Tuomikoski (1966) clearly defined the Hybotinae and Tachydromiinae, their assigned genera, and also provided evidence for monophyletic subgroups. This is one of the most clearly expressed and supported discussions on empidoid phylogeny so far published.

Smith (1969) briefly, yet efficiently reviewed the history of subfamily groupings, and building on the ideas of previous workers presented a composite dendrogram of the phylogenetic relationships within the Empididae. He depicted the Empidinae, *Oreogeton* group, Ceratomerinae, Hemerodromiinae, Clinocerinae, and Brachystomatinae as evolving from a primitive *Oreogeton* type.

In two fossil empidid papers, Hennig (1970, 1971) reviewed and clearly presented the first distinct cladogram with a modest character set. He discussed the affinities of the microphorine and parathalassiine genera with the Dolichopodidae and the systematic position of several Cretaceous and Baltic amber specimens. In addition, Hennig (1970) recognized two new subfamilies: Microphorinae and Atelestinae, of which the latter was considered most closely related to the Ocydromioinea *s.str.* (= hybotid group of subfamilies). He also placed the remaining empidoids in the Empidoinea subfamily group, which he considered the sister group to the Ocydromioinea *s.lat.* subfamily group.

Chvála (1976) formally proposed the subfamily Oreogetoninae. It was a plesiomorphic assemblage of relatively primitive genera that did not readily fit into any other lineage. Previously this group had been informally referred to as the *Oreogeton* group (see Tuomikoski 1966).

Chvála (1981) presented the first cladogram that included all lineages of the Empidoidea (first depiction of 11 lineages) illustrating the position of fossils and the time of probable first appearance of each lineage. He considered the Atelestinae as the sister group to the hybotid group of subfamilies. In addition, he strongly hinted at the monophyletic origin of the Microphorinae and Dolichopodidae.

Chvála (1983) expanded on his previous paper and subdivided the traditional Empididae into four families: Empididae (including Empidinae, Oreogetoninae, Hemerodromiinae, Clinocerinae, Brachystomatinae), Hybotidae, Atelestidae and

Microphoridae. His reclassification brought together a variety of characters, including those of wing venation, adult mouthparts and genitalia. However, the taxa he examined were primarily from the Holarctic region and omitted several key southern hemisphere taxa. Chvála's monograph has strongly influenced recent empidoidean workers. His classification has been reviewed and critiqued by Griffiths (1983), Woodley (1989), Cumming (1989) and Sinclair (1995a).

In his analysis of the orthorrhaphous Brachycera, Woodley (1989) proposed two character states that supported the monophyly of the Empidoidea. Reviewing opposing arguments concerning the relationships of the Empidoidea, Woodley (1989) concluded that based on the strength of conflicting evidence, Chvála's hypothesis that the Cyclorrhapha arose from within the Empidoidea as the sister group to the Atelestidae, was very unlikely. He also was of the opinion that the hypothesis of Chvála (1983) would cause undue nomenclatural changes that should be deferred until the phylogenetic relationships among the groups were better understood.

In a survey of the homologies of the larval mandible in the Brachycera, Sinclair (1992) hypothesized that a mandible subdivided into four components was synapomorphic for the Empidoidea. However, the immature stages remain unknown for several significant lineages including the Atelestinae. Griffiths (1994) disputed the homologies of the empidoidean mandible and considered it maxillary in origin. He was strongly influenced by blastoderm fate map studies, which appeared to indicate that the larval mouthhooks in Cyclorrhapha arose from the maxillary lobe (Jürgens *et al.* 1986). However, it is also apparent that the various lobes of the blastoderm of *Drosophila* Fallén are extremely complex and difficult to interpret. For example, both the pharyngeal filter and ventral cornu are also indicated in these fate map studies as derivatives of the mandibular lobe area (Cumming *et al.* 1995). A review of the origins of the mouthhooks is presented in Courtney *et al.* (2000).

The analysis of Wiegmann *et al.* (1993) primarily investigated the origin of the Cyclorrhapha using alternative male genitalic hypotheses. This was the first computer-generated parsimony analysis. They concluded that the Cyclorrhapha probably arose from within the Empidoidea near the Atelestidae, while the relationships among the remaining major lineages appeared relatively unchanged from Chvála's interpretation. Unfortunately this analysis has several weaknesses and misinterpretations that we believe greatly weaken their conclusions concerning the relationships among the major lineages. For example: (1) homoplasy was underestimated for several characters (such as pseudotracheae and pubescent eyes) (see Sinclair 1995a; Cumming *et al.* 1995); (2) character state scoring for taxa was sometimes in error (e.g., presence of wing veins and spermathecae, and length of cells); (3) the outgroups used to represent the Asiloidea are considered by us to represent highly derived, atypical taxa (*Hilarimorpha*, *Apystomyia* and *Caenotus*) and the use of these outgroup taxa alone biased polarity decisions; (4) the interpretation of epandrial homologies was a mixture of periandrial and epandrial interpretations and was not strictly

that of Hennig and McAlpine (particularly that of *Hormopeza* and the controversial presence of a small epandrium).

Sinclair (1995a) redefined and elevated the Trichopezinae to subfamily rank. This redefinition was the result of the transfer of genera from four separate lineages. This grouping had been strongly hinted by previous workers, especially Collin (1933, 1961). This subfamily was considered most closely related to the Ceratomerinae and Brachystomatinae and together this clade was suggested to be the sister group of the Microphorinae + Dolichopodidae. This proposed phylogeny strongly conflicted with the phylogenetic and family classification of Chvála (1983). Although providing a strong argument for this new classification, it was based on a limited character set, which avoided problems created by additional homoplasious characters.

The study of Cumming *et al.* (1995) was primarily based on an analysis of male genitalic homologies and their phylogenetic implications. Evidence was first presented at the Second International Congress of Dipterology (Cumming & Sinclair 1990), but these ideas underwent substantial modification and refinement prior to the final publication. The major purpose of this investigation was to accurately describe the homologies of the male terminalia as observed through outgroup comparisons (drawing on studies of the lower Brachycera by Sinclair *et al.* 1994). This resulted in a revised epandrial hypothesis of male genitalic homologies and rejection of Griffiths (1972) periandrial hypothesis. At the time they hypothesized that the loss of gonostyli in the male terminalia of Empidoidea was synapomorphic, but gonostyli are now considered absent in all Eremoneura (see Sinclair 2000a). Shatalkin (1995) also presented an analysis of male genitalic homologies and presented evidence supporting the epandrial hypothesis. In particular, Shatalkin (1995) noted structures in male empidooids, termed gonopods, which generally are homologous to postgonites as defined in the present work.

Zatwarnicki (1996) presented a cladogram of the higher classification of the Orthogenya (= Empidoidea), based on a re-interpretation of the male hypopygium ("hinge hypothesis"). This hypothesis reversed the polarity of several of the characters in Chvála (1983), but largely supported Chvála's five family division of the superfamily. Zatwarnicki was critical of Woodley (1989) and Cumming *et al.* (1995) for not accepting Chvála's family classification.

Grimaldi & Cumming (1999) described ten new fossil genera assigned to the Empidoidea from Cretaceous ambers. They discussed the phylogenetic significance of these fossils, which were superimposed along with a geological time scale on the cladogram from Cumming *et al.* (1995).

Collins & Wiegmann (2002a) provided the first molecular analysis of the higher-level relationships of the Empidoidea. They stated that their data supported Chvála's five family classification, but also the monophyly of the Empidoidea with Atelestidae as the basal lineage. Their data also supported the monophyly of the Microphoridae + Dolichopodidae. There is little doubt about the monophyly of the atelestines and the separation from the

remaining empidoids was very well supported in their study. However, most of their other conclusions do not have strong bootstrap values or significant support in our opinion. The Microphoridae monophyly received little support with bootstrap values all below 50%, so we do not agree with their conclusion that Chvála's five family concept was entirely supported. It is curious that the morphologically well-supported Microphoridae + Dolichopodidae clade, received what we consider quite low bootstrap values in their combined analysis (60–70%). Also surprising is that the morphologically well-supported Hybotidae received relatively low bootstrap values in the combined analysis of only between 71–80%. Their taxon sampling for a rigorous molecular analysis appears to have been too small and much higher bootstrap values (+90%) would add to more confidence in their conclusions. Although a good first step, which will undoubtedly form the basis for future molecular analyses, much remains to be tested.

A second molecular study of the Eremoneura by Moulton & Wiegmann (2004) investigated mostly the phylogenetic utility of the nuclear coding gene CAD (rudimentary). This gene strongly supported the monophyly of the Empidoidea, Atelestidae, Empidoidea exclusive of Atelestidae, Hybotidae and Microphoridae + Dolichopodidae. Unfortunately taxon sampling was too sparse to adequately assess the relationships of the Trichopezinae, Hemerodromiinae and oreogetonine genera.

Yang & Yang (2004) attempted to analyse the higher classification of the Empididae *s.lat.* and concluded that the group was monophyletic in relation to the Dolichopodidae. However, the characters they used to support this conclusion (their characters 2, 3) are in fact ground plan apomorphies of the Eremoneura (see Cumming *et al.* 1995). Assigning the Microphorinae as the sister group to the Hybotinae clade entirely on the basis of asymmetrical genitalia (their character 4) shows a complete misunderstanding of the distinct differences of this feature in both lineages (see below).

In recent years, the assignment of the microphorids to the Dolichopodidae has become more widely accepted (e.g., Ulrich 2003; Shamshev & Grootaert 2005). To reflect this assignment, Ulrich (2003, 2004) reduced the Dolichopodidae of authors to the rank of subfamily (Dolichopodinae), and the rank of the conventional subfamilies to tribes. It remains to be seen however, whether this classification will become widely accepted among dolichopodid specialists.

Description of Characters in Cladistic Analysis

All characters scored for the cladistic analysis are listed, described and discussed below. The analysis is based on 114 adult characters and eight characters of the immature stages. Along with several new characters, we attempted to incorporate all traditional characters in the analysis, including those of Hennig (1970, 1971), Ulrich (1971), Chvála (1983), Cumming *et al.* (1995), although our definitions of certain characters may differ somewhat. Ten mostly traditional characters were excluded from the analysis for reasons

discussed below under the section: Characters not included in the cladistic analysis. The data matrix derived from this character analysis is presented in Table 2. Character distributions are discussed in relation to the figures of the cladograms (Trees 1–6). The following discussion of character states and distributions utilizes the higher taxonomic groups outlined in the Taxon Sampling section (e.g., Dolichopodidae refers to the traditional definition of the family), and not the revised classification introduced in later sections of this paper.

Adult stage

Head

1. *Male eye contiguity*. Holoptic (0); dichoptic (1).

Empidids are known for their large mating swarms in which males locate and capture females in flight (Downes 1969). The male eyes in such taxa are enlarged dorsally above the antennae so that they meet on the frons. This condition, termed holoptic, is common in Diptera and considered the plesiomorphic condition. Females normally have the eyes widely separated or the dichoptic condition. The dichoptic male condition occurs very often in the empidoidea, especially in groups that have lost the swarming habit secondarily; e.g., Clinocerinae, Hemerodromiinae, most Tachydromiinae. But not all swarming empidids have holoptic males, as found in taxa such as *Hilara* Meigen (Fig. 96). Although highly homoplasious, we have retained this character in the analysis as it has traditionally been used to support some relationships; e.g., parathalassiines + Dolichopodidae (Hennig 1971; Chvála 1983). Within the Dolichopodidae, the holoptic male condition also occurs in some Diaphorinae (Robinson & Vockeroth 1981, fig. 48.7).

2. *Eye pubescence*. Bare (0); eye with dense ommatrichia (1).

The eyes are normally bare macroscopically, but under high magnification scattered setulae or ommatrichia (Colless & McAlpine 1991) are occasionally present between facets of the compound eye. Dense ommatrichia, easily observed under low power is considered a derived condition and found in several groups, presumably independently. These groups include parathalassiines, Dolichopodidae, Clinocerinae (Fig. 409), Drapetini, *Chillcottomyia* Saigusa, *Aboccaputa* Plant, and *Apterodromia* Oldroyd. Although homoplasious, this character has also been used as evidence of the close relationship of the parathalassiines and Dolichopodidae (Hennig 1971; Chvála 1983).

3. *Female eye contiguity*. Separated on frons (0); closely approximated or holoptic on frons and facets enlarged (1).

The eyes of female Empidoidea are normally widely separated on the frons (dichoptic). In the Hybotinae, female eyes are closely approximated to holoptic on the

frons, with the facets usually enlarged. The only exception to holoptic females among the hybotines is the genus *Lamachella* Melander (eyes are narrowly separated). Female eyes are also closely approximated in the genus *Homalocnemis* and the upper facets are enlarged.

Females are also holoptic and facets enlarged in the genera *Bicellaria* and *Hoplocyrtoma* Melander. It is probable that these two genera represent the sister group to the Hybotinae. *Leptocyrtoma* Saigusa, which is also assigned to the *Bicellaria*-group, is dichoptic in both sexes, possibly secondarily. In addition to morphological similarities, the mating habits are also similar in the *Bicellaria*-group and Hybotinae, where “hunting” rather than mating swarms are formed (Chvála 1976). It is believed that the holoptic condition evolved to facilitate capturing and hunting flying insects from below (Chvála 1976). The similarities of the male terminalia of *Bicellaria* and *Lamachella*, specifically the form of the phallus, also supports this sister group relationship.

The closely approximated eyes in *Symballophthalmus* are not enlarged dorsally and enlarged facets are only confined to the anterior margin, and consequently not considered homologous and scored 0.

4. *Face*. Concave, depressed below eyes (at least in male) (0); flat, level with eyes (1).

The entire face is concave below the level of the eyes in basal Cyclorrhapha (Opetiidae and Platypezidae), Therevidae, and Scenopinidae. The face also appears less sclerotized than in taxa where the face is flat and level with the eye. Often the depression is filled by the retracted mouthparts. A flat face level with the eyes, at least on the upper half below the antennae is common within the Empidoidea except in the traditional basal lineages or most primitive genera. In some hybotids (e.g., *Stenoproctus*) the face is greatly sunken due to modification of the mouthparts, but the face is flat and level with the eyes just below the antennae, and scored 1.

5. *Scape vestiture*. Setae present (0); setae absent (1).

In the lower Brachycera, the scape is largely visible, bearing numerous setae (Fig. 2). A bare, reduced scape is known in the Atelestinae, *Nemedina*, hybotid lineages, microphorids, and many Dolichopodidae (Figs. 19–31, 38–42). Tuomikoski (1966) used this character in support of his Ocydromiinae group of subfamilies. The presence of setae was used as a key character of the Dolichopodinae (Brooks 2005a, character 1.1).

Although quite short and inconspicuous, the scape of *Hilarimorpha* bears several distinct setae (Fig. 3).

6. *Scape length*. Equal to or slightly longer than pedicel (0); more than twice as long as pedicel (1).

In Asiloidea (Yeates 1994) and Empidoidea, the length of the scape is normally 1–2 times its width (Figs. 2–9), but can be quite variable in Dolichopodidae (see Robinson &

Vockeroth 1981). In the apomorphic state, the scape of Ceratomerinae is distinctly lengthened, more than twice its width (Fig. 35). The greatly lengthened and outstretched antennae are immediately noticeable in live specimens of this subfamily (Fig. 423).

7. *Conus*. Absent (0); inserted laterally (1); inserted medially (2).

The base of the postpedicel (first flagellomere) is normally narrowed and inserted into an apical invagination of the pedicel (Figs. 37, 39) (Disney 1988). In the advanced condition, a narrow, thumb-like condyle or conus from the pedicel is inserted into the base of the postpedicel. The apex of the conus possesses a ring-like orifice, which enables the antennal nerve to run to the arista (Disney 1988). The presence of a conus in Empidoidea has likely evolved independently in the subfamily Ceratomerinae (Figs. 34–35) and several dolichopodid genera (e.g., *Dolichopus* (Fig. 43), *Tachytrechus* Haliday and *Syntormon* Loew). A similar feature is present in almost all Cyclorrhapha (Figs. 49–51), except Platypezidae and Opetiidae (Figs. 45–48) but the condition in Ceratomerinae is most certainly due to convergence (Hennig 1976; Disney 1988; McAlpine 1989; Cumming *et al.* 1995, character W). The form of the conus was coded as two advanced states, those with the conus inserted laterally being scored as 1 (Ceratomerinae), and those with the conus inserted medially (*Dolichopus* and Cyclorrhapha) being scored as 2.

Apparently a reduced conus is present in the Platypezid *Lindneromyia argyrogyna* (de Meijere) (Disney 1988, listed under *Plesioclythia* Kessel & Maggioncalda). As Disney (1988) points out, further investigation is required, especially whether congeneric species also possess a conus.

8. *Apical mechanoreceptor (segment 10 or flagellomere 8)*. Hyaline, peg-like (0); absent (1); long slender, bristle-like (2).

At the apex of the antennal style in Empidoidea, there is a small, bare, peg-like process (Figs. 4–13). This apical component has recently been identified as flagellomere 8 (segment 10) in an analysis by Stuckenberg (1999), and it is believed to function as a mechanoreceptor. Chvála (1983, p. 20) considered this apical component a third article of the stylus, whereas Yeates (1994, character 7) referred to this feature as the “style” of the antennal flagellum and not as an additional antennomere. The differentiation of flagellomere 8 into a hyaline, peg-like form is common among asiloids and empidooids. Flagellomere 8 is completely fused into a single postpedicel in *Brochella* (Fig. 14) and *Sabroskyella* (Fig. 37), and scored 1. The apical mechanoreceptor is normally absent in groups bearing a well-defined arista, including Dolichopodidae (Figs. 43–44) and all Cyclorrhapha (Figs. 45–51; Saigusa, 1963, figs. 2c–e). Exceptions to this condition include most hybotines (Figs. 21–23, 27–30), where a lengthened, bristle-like apical style is present and scored 2.

No clear separation of the apical flagellomere was seen in *Empis* L., *Sphicosa*, *Empidadelpha*, or *Philetus* (Figs. 9–12), however a distinct bare peg-like apex was

observed in cleared specimens under high magnification. A similar partial reduction was observed also in *Anomalempis* and *Heterophlebus* (Figs. 33, 36) and scored 0. This reduction of flagellomere 8 also can be observed in the figures of Chvála (1983, figs. 6–9). The phylogenetic significance of the reduction of the terminal flagellomere should be investigated further in these lineages.

9. *Articulation beyond postpedicel (excluding apical receptor)*. Zero (0); one (1); two (2); three (3).

Reduction in the number of free flagellar articles is common in the Brachycera, with at most four present in the ground plan of the Muscomorpha (*sensu* Woodley 1989). Stuckenberg (1999) described the pattern and evolution of the flagellomeres in the Vermileonidae, where the apical stylus (flagellomeres 7 and 8) is retained in all species. The number of intermediate flagellomeres is variable and sometimes only partially fused. The apical flagellomeres are modified into a mechanoreceptor, while the compound flagellar base (postpedicel) functions as a chemoreceptor (Stuckenberg 1999).

A two-articled stylus (excluding apical receptor) was observed in Therevidae (Fig. 1) and *Caenotus* (Fig. 2), whereas a one-articled stylus is present in *Hilarimorpha* (Fig. 3). In Empidoidea, the number of flagellomeres of the stylus varies from zero to three.

An apical stylus is absent in *Sabroskyella* (Trichopezinae), *Chelifera* (Hemerodromiinae) (Fig. 15), and some male *Ceratomerus*. A single articled stylus is found in all parathalassiine genera, including *Microphorella* Becker (Fig. 40), *Parathalassius* Mik (Fig. 41) (Hennig 1971; Chvála 1983), *Plesiothalassius* Ulrich, *Amphithalassius* Ulrich (Fig. 42) (Ulrich 1991), and *Thalassophorus* Saigusa (Saigusa 1986). On the basis of this character, the parathalassiines also include extinct genera such as *Cretomicrophorus* Negrobov, *Archichrysotus* Negrobov, and *Retinitus* Negrobov (Grimaldi & Cumming 1999; Cumming & Brooks 2002). As emphasized by Ulrich (1991), this character appears to be subject to homoplasy and hence should be interpreted with caution.

A three-articled arista is generally viewed as a synapomorphy of the Cyclorrhapha, exclusive of Opetiidae (Cumming *et al.* 1995). There are a few Empidoidea with a three-articled arista-like stylus, but these are obvious convergences as the empidoid ground plan is undoubtedly two-articled as concluded by Grimaldi & Cumming (1999). Some Atelestinae (Figs. 19–20) appear to have a similar configuration to the Cyclorrhapha, but the presence of the hyaline apical receptor demonstrates that these states are not homologous. Grimaldi & Cumming (1999) tested the ramifications of either three aristomeres or two aristomeres (3-articled vs. 2-articled arista) as being derived within the Cyclorrhapha, but both alternatives were equally parsimonious. A detailed morphological comparative study of the eremoneuran antenna is required.

10. *Arista/stylus position*. Apical (0); subapical or dorsal (1).

The arista-like stylus, scattered throughout the orthorrhaphous Brachycera and Empidoidea is usually positioned apically on the postpedicel. Within the Empidoidea, a subapical or dorsal arista-like stylus is found in *Ocydromia* (Fig. 24) and some Tachydromiinae (Steyskal & Knutson 1981). Bickel (1994, p. 17) viewed a dorsoapical arista-like stylus as plesiomorphic for the Sciapodinae, where the apical arista-like stylus of many (mostly male) taxa was viewed as secondarily derived, and hence a dorsoapical stylus (Figs. 43–44) was considered synapomorphic for the Dolichopodidae. In this analysis *Heteropsilopus* was scored as 1, on the basis of the form of the female antenna, where the male stylus is greatly lengthened. The arista is apical in the basal families of the Cyclorrhapha (Figs. 45–50) and presumably the ground plan condition.

11. *Form of antenna beyond postpedicel (excluding apical receptor)*. Tapering (0); cylindrical or tubular (nearly parallel-sided) (1).

The stylus is tapered apically in asiloids and most Empidoidea. In several primitive genera of the Empidoidea, the stylus is distinctly cylindrical or tubular and not tapered (Figs. 4–5, 8). This unique form is considered apomorphic and may indicate close relationships of some basal genera including *Iteaphila*, *Homalocnemis*, *Hesperempis*, and *Hormopeza*. However, the number of antennomeres fused within the postpedicel may differ among these taxa, suggesting that their similar shape may be due to convergence.

12. *Clypeal ridge*. Oblique and narrow (0); perpendicular and broad (1).

The clypeal ridge of lower Brachycera and basal Empidoidea arises obliquely from the clypeus (Figs. 52–85; Peterson 1916; Snodgrass 1943). In Dolichopodidae and parathalassiines, the clypeal ridge is positioned at nearly right angles with the clypeus and strongly fused together (Figs. 86–90). This fusion greatly affects the convexity and flexibility of the clypeus (see also Ulrich 1991).

13. *Clypeal ridge position*. Articulated with labrofulcral articulation point (0); distinctly removed from labrofulcral articulation point (1).

Among the basal lineages of the Empidoidea, the clypeal ridge is articulated with the labrum and cibarium at the labrofulcral articulation point (Figs. 54–67). Krystoph (1961) believed that separation of the clypeal ridge (referred to as the torma) from this articulation point was a distinctive synapomorphy of the ocydromiines + Hybotinae + Tachydromiinae. However, difficulties in coding were found when a thin layer of cuticle extends to the point of articulation, while the stout clypeal ridge remains visible but separated. Consequently, we have redefined the character state as the clypeal ridge being distinctly and widely separated from the labrofulcral point of articulation. The derived condition has likely evolved independently in the microphorids + Dolichopodidae (85–90), Hybotinae (Figs. 74–76), and Cyclorrhapha (Figs. 92, 94–95).

Krystoph (1961) interpreted this structure as the torma, in contrast to Snodgrass (1943) who demonstrated that on the basis of muscles, this ridge is clearly derived from the clypeus and not from the lateral basal processes of the labrum or tormae. This interpretation of the clypeal ridge was followed by Bletchly (1954, as anterior arch of the fulcrum) and McAlpine (1981) and is followed here.

14. *Female labrum*. Straight, not thickened (0); recurved, stout (1).

The labrum is straight and somewhat slender in most Empidoidea and lower Brachycera. A stout, recurved labrum occurs in females of *Hormopeza* (Fig. 57), both sexes of *Ragas* and related genera (Sinclair 1999; Sinclair & Saigusa 2001).

15. *Apex of labrum*. Pointed, straight (0); truncate, rounded in lateral view (1).

Most outgroup taxa and empidooids possess a narrow, pointed labrum (e.g., Fig. 54), and in empidooids it is associated with impaling prey. In the derived condition, the tip of the labrum arches ventrally (or posteriorly) and appears truncate laterally. This form is observed primarily in flower feeding groups (Figs. 55, 62) and also in the *Ragas* group (Fig. 57).

The apex of the labrum appears truncate in the asilid *Diogmites* (Fig. 52), likely a reflection of the minor role the labrum plays during feeding in this family.

16. *Epipharyngeal blades*. Absent (0); one or more pairs of lateral blades (1); blades very stout and sharply pointed (2); blades immovable, partially fused (3).

Most adult Empidoidea are considered predators of flying insects, using both a long, piercing labrum and hypopharynx (Laurence 1953). The ventral wall of the labrum is commonly referred to as the epipharynx and most adults possess one or more pairs of apical prongs or what Bletchly (1954) termed the epipharyngeal blades (= epipharyngeal armature, sclerites, prongs) flanking a median pointed labral tip (Figs. 57–63, 65–67). The blades are covered by an extension of the labrum, forming a dorsal sheath and medially forming an inner keel separating the blades (Bletchly 1954). The ventral margin often bares rows of peg-like sensilla (Fig. 66). No muscles are directly inserted onto the blades, but they are rotated through contraction of the labrum-epipharyngeal muscles. These muscles cause the labrum to press against the base of the blades, which then rotate outwards (Snodgrass 1922). These sharp blades form efficient piercing and masticating organs, used to enlarge the wound by cutting and scraping, similar to prestomal teeth of some calyptrates (Bletchly 1954).

The epipharyngeal blades have become heavily sclerotized and sharply pointed in Dolichopodidae (Fig. 89; Cregan 1941; Satô 1991) and is viewed as autapomorphic for the family (Woodley 1989, character 37). Several genera of the hybotid lineage (e.g., *Bicellaria* and *Neotrichina*) possess long, slender blades (Figs. 72, 74). Although distinctive, they appear to be highly variable among related genera and no consistent pattern was observed to facilitate accurate scoring of an additional character state.

17. *Apex of epipharynx beneath tip of labrum*. Unmodified (0); median comb of dorsally (or anteriorly) curved setae (1).

The presence of a small comb of setae beneath the apex of the labrum characterizes the *Ragas* group (including *Hormopeza*, *Dipsomyia*, *Hydropeza*, and *Zanclotus*) (Fig. 57; Sinclair 1999). As far as known, such a modification is absent in other empidooids.

18. *Epipharyngeal carina* (or apodeme). Absent (0); present (1); lengthened and projecting vertically into head (2).

A small carina or apodeme arising dorsally from the epipharyngeal wall (lower surface of labrum) is present at least on the proximal end near the base of the mouthparts (Figs. 57–59, 63, 67, 71–74, 85–90; Krystoph 1961, figs. 3,4). It is lacking in lower Cyclorrhapha and orthorrhaphous Brachycera (Figs. 52–53, 91–95) and possibly secondarily reduced in some flower visiting empidoids (Figs. 55, 62, 64, 69). The labrum-epipharyngeal muscle is inserted onto this apodeme.

The adult mouthparts of Dolichopodidae are also characterized by an enlarged carina, projecting vertically into the head capsule and scored as state 2 (Figs. 89–90; Peterson 1916, fig. 528; Cregan 1941; McAlpine 1981, fig. 2.51; Satô 1991). This character state is apparently widely distributed within the Dolichopodidae, including the subfamily Sciapodinae.

19. *Stipes form*. Straight, lacking branch (0); lateral branch of stipes extending posteriorly around prementum and fused to opposite pair (1).

The stipes is a straight rod and not branched in most Empidoidea. In the Brachystomatinae, the stipes is L-shaped, with the lateral branch projecting medially around the prementum to fuse to the branch of the opposite stipes (Figs. 80, 121; Chvála 1983, fig. 23). This configuration is also found in the genus *Dipsomyia* Bezzi (Sinclair 1999) and at least some *Sphicosa* (Fig. 118).

20. *Lacinia*. Blade-like, shorter than labrum generally (0); absent, stipes connected to paraphyses (1).

The stipes and a long lacinia are freely projecting in orthorrhaphous Brachycera (Figs. 52–53), many Empidoidea (Figs. 114–117, 122), Platypezidae (Fig. 109), and Lonchopteridae (Figs. 93). The fusion of the stipes to the labial paraphyses (loss of a “free” lacinia) is found in all ocydromiines, Hybotinae, and Tachydromiinae (Figs. 75, 78; Krystoph 1961). The loss of “free” lacinia is also observed in the parathalassiines + Dolichopodidae (Figs. 131–134) (including *Thalassophorus*, *Plesiothalassius*, and *Amphithalassius*) (Ulrich 1991). The stipes is connected to a free lacinia in the microphorines (Fig. 129; Chvála 1983). Among the lower Cyclorrhapha, the lacinia is apparently absent in *Sciadocera* White.

See Sinclair (1995a, character 2) for a discussion of the fusion of the lacinia with the labial paraphyses in Clinocerinae (Fig. 125), which is not considered homologous to the condition in the hybotid lineage. The lacinia in *Proagomyia* (Clinocerinae) is partially fused to the paraphyses, while free in *Afroclinocera*, and a similar partially fused condition was observed in *Schistostoma* and scored as 0. The condition in *Opetia* could not be determined due to the limited material and relative size, although it was scored as 0 in Wiegmann *et al.* (1993).

21. *Palpal segments*. Two segments (0); one segment (1).

The plesiomorphic number of palpal segments is two in asiloids (Fig. 52; Woodley 1989; Sinclair *et al.* 1994; Yeates 1994, 2002) and reduction to a single segment has occurred independently in several families. In Eremoneura, the number of segments is stabilized and reduced to one and is viewed as a ground plan apomorphy of the lineage (Figs. 68, 92–95; McAlpine 1989: 1414; Cumming *et al.* 1995). The apparent basal segment of the two-segmented palpus observed in some Phoridae (see Brown 1995) is actually a palpifer (Cumming & Wood in press) (see character 24 below).

22. *Palpal orientation*. Arched (0); straight, projecting obliquely (1); strongly curved, C-shaped (2).

The palpus is curved upwards and appressed to the clypeus in asiloids and also in the following Cyclorrhapha: *Sciadocera* (Fig. 94), *Microsania*, *Callomyia* Meigen, *Agathomyia*, *Calotarsa* Townsend, *Lonchoptera* (Fig. 93) and *Opetia*. This condition is also found in several empidoid genera including: *Dryodromia*, *Hormopeza*, *Oreogeton*, *Homalocnemis*, and *Heterophlebus*. Straight palpi, projecting obliquely are present in most empidoids (Figs. 75, 124). The highly curved or C-shaped palpus (character state 2) of Hilarini and most Empidini are likely a secondary modification (Figs. 59–60, 96).

23. *Palpal length*. Long (0); short, approximately 2–3 times as long as broad (1).

The palpus is more than three times as long as broad in many asiloids and basal empidoids (Figs. 52–53, 65, 68, 72, 75). A short palpus, less than three times as long as broad is primarily limited to some genera of the hybotid lineage, parathalassiines and Dolichopodidae (Figs. 87, 89).

24. *Palpus attachment*. Connected directly to stipes (0); palpus separate from stipes, connected to an external sclerite or palpifer (1).

In most Empidoidea, the base of the palpus is membranously attached to the lacinia (Figs. 68, 114–117). In contrast, the base of the palpus in ocydromiines, Hybotinae, and Tachydromiinae is attached to a small sclerotized palpifer (Figs. 70–72, 75, 78, 120; Krystoph 1961). This character state is unique to these empidoid groups and is a well-documented synapomorphy (Krystoph 1961; Tuomikoski 1966; Hennig 1971; Chvála

1983). A palpifer has also arisen independently in some Phoridae (referred to in phorid literature as the basal segment of a two-segmented palpus, see character 21 above) (Cumming & Wood in press).

25. *Position of labellum*. Held obliquely to mentum (0); held at right angles to mentum (1).

The labellum is held obliquely to the premental plate in the basal lineages of the Empidoidea (Figs. 72, 75, 122–123; Krystoph 1961). In Clinocerinae, the labellum is held at right angles to the premental plate (Figs. 124–125; Sinclair 1995a). This character state is synapomorphic for the subfamily. A similar development is found in some Dolichopodidae.

26. *Pseudotracheae*. More than 6 (0); 6 or less (1); absent (2).

It appears that 10 or more pseudotracheae are normally present in Empidoidea and lower Brachycera (Fig. 122), although absent in *Caenotus* and *Diogmites*. Pseudotracheae are lost numerous times in the Empidoidea including within the Clinocerinae (Figs. 124–125; Sinclair 1995a), Hemerodromiinae (Fig. 65), and Hybotinae. The absence of pseudotracheae in Tachydromiinae (Fig. 78; Krystoph 1961) is likely a synapomorphy for the subfamily (Cumming unpubl. data).

There are only six pseudotracheae in all parathalassiines and Dolichopodidae (Figs. 131–135; Satô 1991) (also found in a few other empidoid genera), which is proposed herein as a new synapomorphy supporting the monophyly of this clade.

27. *Pseudotracheal form*. Rings (0); geminate (1); thin lines (2).

Pseudotracheae are normally in the form of a canal of small rings. In all parathalassiines and Dolichopodidae examined, the pseudotracheae are highly modified, termed geminately sclerotized (Figs. 131–133, 135; Robinson 1970; Satô 1991). This form is quite widespread in the Dolichopodidae. Geminate pseudotracheae are herein also proposed as a new synapomorphy, strongly supporting the monophyly of the parathalassiines + Dolichopodidae clade.

The form of the pseudotracheae is potentially useful in studies of the higher classification of the Dolichopodidae. For example, the pseudotracheae of the Sciapodinae are uniquely modified, appearing as a pair of narrow double lines (Fig. 134; Satô 1991, figs. 10a,b), scored here as character state 2.

Thorax

28. *Transverse ventrocervical sclerite*. Absent (0); present (1).

An unpaired, thinly sclerotized transverse sclerite, known as the anterior ventrocervical sclerite is present in the ventral neck membrane of microphorids and Dolichopodidae (Figs. 144–146; Ulrich 1971, 1984, 1990; Marina 1985). A similar weakly

sclerotized sclerite is present in some Clinocerinae (Fig. 136; Chvála 1988), presumably independently. Often the ventral neck membrane bears dense microtrichia and appears to look like a narrow sclerite at certain angles.

29. *Prothoracic presternum shape*. Ventral portion narrow (0); ventral portion broad (1).

The plesiomorphic form of the presternum is considered to be either rounded or an inverted pear shape (Figs. 137–139, 142–143; Yeates 1994, character 75). In many taxa of the hybotid lineages, there is a single oval sclerite (Figs. 140–141), and in some cases below this sclerite is a narrow, pale vertical stripe of pigmentation. Often the presternum is weakly sclerotized and very difficult to confidently interpret. Ulrich (1990) considered the broad ventral portion of the presternum as a synapomorphy of parathalassiines + Dolichopodidae (Figs. 144–146), with the plesiomorphic condition present in the microphorines.

30. *Prosternum*. Separate between fore coxae (0); fused to proepisternum forming a precoxal bridge (1).

The Empidoidea has been traditionally divided into two groups, those with a small, isolated prosternum and those with an enlarged prosternum, fused laterally with the proepisternum. Recently this character has been used extensively in phylogenetic analyses (e.g., Chvála 1983; Wiegmann *et al.* 1993). This feature is often referred to as the precoxal bridge and appears to be quite homoplasious in the Empidoidea. Presence of the precoxal bridge is generally considered apomorphic in the Asiloidea (Yeates 1994). Some problems in coding occur when the prosternum is narrowly fused to the proepisternum (see Ulrich 1991), thus definition of a precoxal bridge is restricted to a broadly fused sclerite above the fore coxae, excluding such taxa as *Sciadocera*.

31. *Dorsal mesepimeral pocket*. Absent (0); present (1).

An endoskeletal ridge in the dorsal mesepimeron, running a semicircular course, forms a characteristic pocket (Fig. 149; Ulrich 1971, 1994). It either forms a complete or incomplete pocket with the laterotergite. Often semicircular external sutures between the postnotum and dorsal epimeron can predict the presence of the pocket. This character is widespread in the Empididae *s.str.*, Ceratomerinae and Trichopezinae.

Daugeron (1997) included an additional state (incomplete pocket) in his analysis of feeding behaviors. He proposed that an incomplete pocket was a synapomorphy of the Empidinae. This additional coding was not followed here.

32. *Intersegmental ridge between meso- and metapleuron*. Single pocket (0); two pockets (1).

The intersegmental ridge crosses the transepimeral suture, turning to form a single pocket, opening caudad. This plesiomorphic condition is found in microphorines (not

parathalassiines) and most other Empidoidea. In the parathalassiines and Dolichopodidae, two endoskeletal pockets are formed on either side of the transepimeral ridge, opening anteriorly (Ulrich 1971, 1984, 1990). Two endoskeletal pockets are also found in many Cyclorrhapha.

33. *Metepisternum*. Broad (0); narrowed ventrally; intersegmental suture converging towards metacoxal condyle (1); intersegmental suture strongly curved dividing metepisternum into two sclerites (2); dorsal and ventral sclerites of metepisternum widely separated by coming together of intersegmental suture and metapleural suture for some distance (3).

Normally the metepisternum is broad, similar in size to the mesepisternum, with the intersegmental suture running somewhat parallel to the metapleural suture. In all Empidoidea studied, the intersegmental suture runs convergently towards the metapleural suture and metacoxal condyle. Consequently in several Empidoidea the resulting metepisternum is much narrowed ventrally compared to outgroup taxa (scored state 1). The intersegmental suture normally fades out prior to reaching the condyle, but by extending the line the direction could be estimated.

In many taxa, the intersegmental suture arches towards the metapleural suture and divides the metepisternum into two components or sclerites. In *Nemedina* the sclerites are divided, but not separated (scored state 2). In all remaining empidoid taxa, the metepisternum is completely divided into two sclerites by the fusion or running together of the intersegmental and metapleural sutures for some distance (scored state 3) (see Ulrich 1971, p. 41: character b). This fusion can be quite great, such that the two sclerites are distantly separated as in some tachydromiines (Ulrich 1971, figs. 9,10).

34. *Lower metapleural arm*. Simple extension of pleural ridge (0); long, narrow, rod-shaped extension (1).

The lower metapleural ridge is primitively a simple extension for the attachment of the pleurosternal muscles (Figs. 147–148; Ulrich 1971, 1984). In microphorids and Dolichopodidae, this ridge is in the form of a narrow rod-shaped arm (Figs. 150–151; Ulrich 1971, 1984, 1990). A narrow lower metapleural arm also occurs in some Cyclorrhapha.

35. *Upper metapleural arm*. Broad lamellar extension (0); rod-shaped (1).

In most Empidoidea including *Microphor* and *Schistostoma*, the upper metapleural arm lies in the same plane as the pleural ridge, forming a broad lamellar extension (Ulrich 1971, 1984). In the modified condition, a rod-shaped arm extends longitudinally with its tip directed caudally (Figs. 150–151; Ulrich 1971, 1990). The latter condition is found in all parathalassiines and Dolichopodidae.

36. *Metasternal furca*. Sternal apophysis (paired furcal arm) with anteriorly directed projection and occasionally with dorsoposterior tip also developed (0); apophysis with posteroventrally directed tip (1); apophysis rod-shaped, lacking apical projections (2).

The metasternal apophysis serves as the point of attachment for the ventral longitudinal and pleurosternal muscles (Ulrich 1971, 1984, 1990). In the primitive state, it is thinly produced anteriorly and often also a thin posterodorsal arm is present (Figs. 152–161, 182–186). In this condition the longitudinal muscle and pleurosternal muscles are widely separated. In state 1, the posterior arm of the furca is directed distinctly ventrally and was proposed as a synapomorphy of the parathalassiines + Dolichopodidae (Figs. 177–181; Ulrich 1990). In state 2, the anterior and posterior arms of the furca are absent, and the furca appears simply rod-shaped. The latter state is present in the microphorines (*Microphor* and *Schistostoma*), *Nemedina*, and the hybotid lineages, although possibly secondarily modified in some Tachydromiinae (Figs. 162–169).

37. *Laterotergite vestiture*. Bare (0); setose (1).

A bare laterotergite is probably a ground plan character of the Eremoneura. In character state 1, the laterotergite bears a patch of setae or a few bristle-like setae distinct from any surrounding pubescence or setulae (Wiegmann *et al.* 1993). This sclerite is hairy in *Thereva* and *Syrphus* Fabricius, but it is clothed in long silky hairs that also cover most of the thorax and therefore it was scored as 0.

A bare laterotergite is used extensively to distinguish most Hilarini from the Empidini and many other sets of genera from each other (e.g., see Collin 1928, 1933; Smith 1969; Steyskal & Knutson 1981). As shown by Bickel (1996a), this character may vary within genera and is subject to much homoplasy within the Empidoidea. In orthorrhaphous Brachycera, Yeates (1994) considered a bare laterotergite as the apomorphic condition.

38. *Scutal vestiture*. Acrostichals undifferentiated, not separated by distinct gap and/or size from dorsocentrals (0); acrostichals and dorsocentrals differentiated by gap and/or size (1).

The eremoneuran outgroup generally has undifferentiated scutal vestiture. The ground plan of the Eremoneura appears to have the acrostichals and dorsocentrals differentiated, at least separated by a distinct gap. Several taxa within the hybotid lineages were scored state 0 (e.g., *Oedalea*), but other members of the same lineage possess state 1. Possibly this character would prove more useful at the generic level.

39. *Acrostichals*. Biserial (or multi-serial) (0); uniserial (1); absent (2).

The variation in the number of rows of acrostichal setulae is variable within the Empidoidea and maybe best used in a generic or species level phylogenetic study. In the basal Cyclorrhapha, state 1 is often quoted as a ground plan synapomorphy of the Platypezidae (Cumming *et al.* 1995).

40. *Postalar vestiture*. Numerous (0); 1–2 bristles or absent (1).

As implied by Wiegmann *et al.* (1993), state 1 appears to be a ground plan feature of at least the Eremoneura. However, we have redefined this state as 1–2 bristles or absent, because of the variability within the Empidoidea.

Legs

41. *Preapical femoral bristles*. Absent (0); present (1).

The presence of preapical bristles on the mid and hind femora (both anterior and posterior) has been regarded as part of the ground plan of the Dolichopodidae (Bickel 1994, p. 19). However, preapical, anterior or posterior, femoral bristles are absent in most sciapodines and several other groups of Dolichopodidae. Preapical bristles have arisen independently on several occasions in the remaining Empidoidea.

42. *Forelegs*. Simple (0); raptorial (1).

Normally the fore femur is distinctively swollen with a tightly fitting tibia in all members of the Hemerodromiinae as newly defined herein. The genera *Sematopoda* Collin and *Xanthodromia* Saigusa, which lack raptorial forelegs, are no longer assigned to this subfamily (see Proposed Classification of the Empidoidea). A few other groups of Empidoidea (e.g., *Hilara femorata* Loew complex, *Apterodromia*) possess raptorial forelegs, but these are not of the same form as the raptorial legs found in the Hemerodromiinae.

43. *Vesture of fore femur*. Simple setae (0); ventral row of spine-like setae (1).

The ventral margin of the fore femur bears at least one row of short, spine-like setae and is found in all Hemerodromiinae as newly defined herein (see Proposed Classification of the Empidoidea). This condition is not homologous to that which occurs in Hydrophorinae, where only males have modified setae used in mate guarding (Dyte 1988). The foreleg chaetotaxy of male clinocerines is also often modified.

44. *Length of gap between fore and mid coxae*. Less than twice length of mid coxa (0); more than twice length of mid coxa (1).

The Hemerodromiinae comprise a distinctive subfamily, characterized by their raptorial forelegs. Associated with the modified legs is a distinct increased separation of the foreleg from the midleg. This gap is measured by comparing the length, in a horizontal line, between the fore and mid coxae (not the direct length of gap from socket to socket).

45. *Fore tibial anteroapical comb*. Absent (0); present (1).

The presence of an anteroapical comb of setae (Fig. 411) has been used to separate the Hilarini from the Empidini (see Bickel 1996a). The presence of this comb is quite

widespread within the Empidoidea and is presumably a ground plan feature of the superfamily, although it is lost secondarily numerous times. The comb appears to be lacking in asiloids and sporadic in basal Cyclorrhapha.

46. *Hind tibial posteroapical comb*. Absent (0); present (1).

As observed on the foreleg, a large posteroapical comb is present (Fig. 412) and most likely used in grooming of the wing and additional body parts. It should not be confused with a series of appressed combs often present on the apical half of the hind tibia. The comb is present in all Empidoidea and some Cyclorrhapha.

47. *Fore tibial gland*. Absent (0); present (1).

A gland near the base of the fore tibia (Figs. 413–414) is a well-documented synapomorphy of ocydromiines + Hybotinae + Tachydromiinae (Tuomikoski 1966; Smith 1969; Hennig 1971). The function of this gland remains unknown and various differences in structure have been discussed by Tuomikoski (1966) and Smith (1969). Unfortunately it is nearly impossible to observe in fossil amber specimens and is also difficult to see in some extant species.

48. *Male fore first tarsomere*. Slender (0); enlarged (1).

In the Hilarini the first tarsomere of the male foreleg is distinctly swollen (Fig. 410) in comparison to all remaining tarsomeres, including other legs. This swollen tarsomere, which houses silk producing glands (Eltringham 1928) that are used to wrap objects for nuptial gifts, is unique to this tribe. It remains to be shown whether all hilarine genera with this swollen first tarsomere produce silk. The tarsomere is quite variable in size and shape within the tribe. The ultrastructure of the silk glands has been recently studied in a species of *Hilarempis* Bezzi (Young & Merritt 2003).

Wing

49. *Costal bristle*. Absent (0); present (1).

In many Empidoidea, there is a long bristle near the base of the wing on the anterodorsal margin of the costa, just proximal to the slight weakening (Figs. 370, 394–396). This character has not been reported previously and the basal bristle appears to be absent in lower Brachycera. It is often long and stout as seen in such taxa as *Oreogeton* (Fig. 365), *Empidadelpha* (Fig. 370), Clinocerinae (Fig. 376), and Ceratomerinae (Fig. 394). The basal bristles are not considered homologous in *Agathomyia* and *Opetia* because they are situated on the outer margin of the costa, and hence scored as 0. *Microsania*, which possesses two basal bristles (i.e., one outer and the other on the inner margin), was scored as 1.

50. *Costal termination*. Circumambient (0); ending at or just beyond R_{4+5}/R_5 (1) ending at or near M_1/M_{1+2} (2); ending at R_1 (3).

In the basal lineages of the Asiloidea, *Protempis* Ussatchev [the earliest known Empidoidea (Chvála 1983), but see Grimaldi & Cumming (1999)], Clinocerinae, and most oregoetonine genera, the costa extends around the entire wing margin (Figs. 363–369, 373–376). Reduction of the costa to M_1 or R_{4+5} has been considered a synapomorphy for the ocydromiines + Hybotinae + Tachydromiinae + microphorids + Dolichopodidae and possibly also the Atelestinae (Figs. 377–390, 401–403; Hennig 1970, 1971; Chvála 1983; Wiegmann *et al.* 1993). In contrast, Cumming & Sinclair (1990), Sinclair & Cumming (1994) and Cumming *et al.* (1995) considered the reduction of the costa to M_1 to have evolved independently in the Atelestinae + ocydromiines + Hybotinae + Tachydromiinae and Dolichopodidae (costa circumambient in microphorids, Figs. 397–400).

The costa ends just beyond R_{4+5} or R_5 in the Empidini (Figs. 370–371). However, reduction or weakening of the costa posteriorly has presumably also evolved independently several times in several other empidoid genera (e.g., *Gloma*). The costa is also reduced in most Cyclorrhapha (Figs. 404–405, 407–408), except Opetiidae (Fig. 406) and Lonchopteridae (McAlpine 1989; Cumming *et al.* 1995).

Unfortunately, the coding of this character is not always straightforward. For example, in *Symbalophthalmus* the costa is practically circumambient, only weakened posteriorly (Fig. 388; Chvála 1975) and appears to simply fade away in *Hormopeza* (Fig. 366). In addition, as seen in fossils, the termination of the costa can be quite variable, making it difficult to draw conclusions (Grimaldi & Cumming 1999). Thus the apparent homoplasious nature of this character renders it very weak and possibly unreliable in phylogenetic analyses (at least at this level), especially given difficulties in assessing this character when the costa fades away gradually rather than ending abruptly. However, the character has been retained in the matrix to illustrate its homoplasious nature.

51. *Subcosta termination*. Complete, reaching costa (0); subcosta incomplete, ending just short of costa (1); reduced, never longer than half length of basal cells or ending opposite branching of Rs (2); recurved joining R_1 (3).

In outgroups and many empidids, the subcosta is complete, ending in the costa (Figs. 361–368). An evanescent or incomplete subcosta has likely evolved independently in the Hemerodromiinae (Fig. 375), Empidini (Figs. 370–371), and several genera of the Trichopezinae (Fig. 396) and Clinocerinae. An incomplete subcosta was considered by Hennig (1970, 1971) as synapomorphic for the ocydromiines + Hybotinae + Tachydromiinae + microphorids + Dolichopodidae and Atelestinae. However, the subcosta is complete in microphorines (Fig. 397), while the subcosta either ends opposite the branching of Rs or ends in R_1 in Dolichopodidae and parathalassiines (Figs. 398–403). Therefore, it is highly unlikely that the loss of the apex of the subcosta in the Atelestinae

(including *Nemedina*) and hybotid lineages (Figs. 377–390) is homologous with the condition in the parathalassiines and Dolichopodidae.

52. *Costal vestiture*. Simple setae (0); widely spaced, erect spine-like setae (1); single row of spine-like setae (2); double row of spine-like setae (3); single row of spine-like setae between rows of finer setae (4).

The anterior margin of the costa bears a pair of rows of simple, appressed setae among basal empidoidea and taxa of the hybotid lineages. In the Clinocerinae, there are widely spaced stout, erect setae intermixed with these rows of simple setae (Figs. 376, 415; Sinclair 1995a, 2000b). The presence of stout, modified costal setae is considered apomorphic for this subfamily and was first recognized by Hackman and Väisänen (1985). Stout costal setae also occur, presumably independently, in some Trichopezinae, including an undescribed western Nearctic genus closely related to *Apalocnemis*, and some Ceratomerinae. The microphorids are characterized by a single row of spine-like setae (Figs. 397–400), mainly developed apically (state 2), except *Thalassophorus* that appears to have a double row of spine-like setae. The Dolichopodidae (Figs. 401–403) and basal Cyclorrhapha (Figs. 404–407), including *Opetia* possess a double row of spine-like setae (state 3). Lonchopteridae possess an aberrant costal vestiture with a row of spine-like setae between a pair of rows of finer setae (state 4), somewhat similar to the condition in Clinocerinae (see Hackman & Väisänen 1985).

53. *Pterostigma*. Overlapping apex of R_1 (0); absent (1).

The loss of the pterostigma has occurred often in the Empidoidea, but appears to be a ground plan synapomorphy for each of the clades, parathalassiines + Dolichopodidae (Figs. 398–403) and Tachydromiinae (Figs. 388–390). Attempts were made to score the position of the pterostigma, but position appears to be more appropriate at a lower level, possibly useful in generic analyses of a tribe or subfamily (e.g., Ceratomerinae, Sinclair unpubl. data).

54. R_1 *thickness*. Uniform thickness throughout (0); swollen before joining costa (1).

Vein R_1 is swollen prior to reaching the costa in most species of the Hilarini (Figs. 368–369; Collin 1961; Bickel 1996a). It is a defining feature of this tribe and is considered to have independently evolved in some *Platypalpus* (Fig. 389).

55. R_s *origin*. Distal, distant from humeral crossvein (0); opposite or very near humeral crossvein (1).

Vein R_s originates distally or distant from the humeral crossvein in most empidoidea and asiloids (Figs. 361–370). As noted by Colless (1963), R_s originates nearly opposite the humeral crossvein in Cyclorrhapha (Figs. 404–408), microphorids, and Dolichopodidae (Figs. 397–403). Chvála (1983) listed it as a ground plan feature of his Microphoridae.

56. R_{4+5} type. Branched (0); unbranched (1).

In the ground plan of the Empidoidea including *Protempis*, R_{4+5} is branched (Figs. 363–376). Hennig (1970, 1971) and Chvála (1983) considered an unbranched R_{4+5} synapomorphic for ocydromiines + Hybotinae + Tachydromiinae + Atelestinae + microphorids + Dolichopodidae. However, it appears more likely that this character state has developed independently in the Atelestinae (including *Nemedina*) + Hybotinae lineage (Figs. 189, 377–390) and the microphorids + Dolichopodidae lineage (Figs. 397–403), because of the existence of several conflicting characters.

This character state has also been derived independently in the Cyclorrhapha (McAlpine 1989; Cumming *et al.* 1995), as well as in several empidoid genera including *Anthepiscopus*, *Asymphyloptera* Collin, *Oreothalia* Melander, *Chelipoda* Macquart, *Monodromia* Collin, *Edenophorus*, *Rhamphomyia* Meigen, *Atrichopleura* Bezzi, *Icasma*, *Anomalempis* and *Heleodromia*. Its apparent homoplasious nature generally renders this character unreliable in phylogenetic analyses of higher classification, but within lineages it may be useful (see Sinclair 1997).

57. M_1 type. Present (0); absent (1).

In the Platypezidae, the medial veins branch distal to cell dm, with M_1 strongly arched and M_2 straight, running directly to the wing margin and in-line with the basal section of vein M. Hence the loss of the arched vein in *Agathomyia* is assumed to be M_1 (Fig. 405; Chandler 1994). Only the base of M_1 is lost in *Microsania* (Fig. 404). M_1 is also lost in many Ocydromiini (Fig. 382; Sinclair & Cumming 2000) (see character 58 below).

58. M_2 type. Present (0); absent (1).

In the ground plan of Empidoidea, vein M is forked (M_1 and M_2). In the derived state, it is believed that M_2 is lost, resulting in two veins extending from cell dm (Figs. 385–390). Chvála (1983) proposed this character state as a synapomorphy of Hybotinae + Tachydromiinae. Reduction in the number of branches of the medial vein has probably occurred independently in several taxa, including *Atelestus*, *Acarteroptera* (Fig. 377), *Nemedina* (Fig. 189) and within the Dolichopodidae (Fig. 402).

In many Ocydromiini, the wing venation is similar (two veins emitted from cell dm), but this is the result of the loss of M_1 (Fig. 382; Tuomikoski 1966) and hence not homologous.

59. *Discal cell*. Cell dm present (0); cell dm absent, due to loss of dm–cu crossvein (1).

In most empidoids and outgroups, including *Protempis*, cell dm is present. In Tachydromiinae, cell dm is absent through loss of crossvein dm–cu (Figs. 388–390). It has also been lost probably independently in at least the *Bicellaria* group (Fig. 384), *Nemedina* (Fig. 189) *Atelestus*, *Cryptophleps* Lichtwardt (Dolichopodidae), and some basal Cyclorrhapha (Figs. 404, 406).

60. *Relative length of cell cup to apical portion of A₁*. Length of cell cup longer than apical portion of A₁ (0); length of cell cup equal to or shorter than apical portion of A₁ (1).

In Asiloidea, the cell cup (= anal cell) is very long, nearly obtaining the wing margin (Figs. 361–362). In contrast, the length of this cell is quite variable within the Empidoidea. Hennig (1970) considered a long anal cell as plesiomorphic for the Empidoidea, as seen in the fossil genera *Trichinites* Hennig and *Protempis*. Shortening of the anal cell may have occurred in the Empidoidea several times (Figs. 363, 365–376, 379–386) and the shortened, truncate form of the anal cell in many ocydromiines is possibly synapomorphic (Hennig 1970). Alternatively, a shortened anal cell can be optimised at the base of the Eremoneura with subsequent lengthenings of this cell hypothesized to have arisen independently in several taxa.

61. *Shape of CuA₂*. Straight (0); truncate (1); recurved (2); distinctly convex (3); absent (4).

The shape of CuA₂ or apex of the cell cup and its phylogenetic significance has been discussed extensively in Empidoidea phylogenetic studies (e.g., Wiegmann *et al.* 1993). In addition, both the shape and relative lengths have been used extensively in keys to genera (e.g., Collin 1961; Steyskal & Knutson 1981). Hennig (1970) considered the enlarged anal cell of *Hybos* as secondary (Fig. 387), whereas *Syneches* Walker retained the basic plan of the Hybotinae. Chvála (1983) extensively compared and discussed the significance of CuA₂. He considered the primitive anal cell to be highly arched, similar to the Brachystomatinae, Atelestinae, and Hybotinae. Wiegmann *et al.* (1993) provided the first attempt at precisely defining various character states, combined with the relative lengths of the cell cup.

Within the Empidoidea there are many types of curvatures, which we have attempted to score into four categories. We have chosen also to separate the relative length of the cell cup (see character 60 above) from its apical shape. In the lower Brachycera and basal Cyclorrhapha (Figs. 361–362, 405, 408), CuA₂ is straight, running directly to the wing margin and creating a pointed cell cup. This appears to be the plesiomorphic condition for Eremoneura.

62. *Relative lengths of basal and discal cells*. Basal cells greater than half the length of cell dm (0); basal cells shortened, less than half the length of cell dm (1).

This character was first analysed by Hennig (1971) as a synapomorphy of the microphorids and possibly Dolichopodidae (Figs. 397–403). Shorter basal cells (br and bm) relative to cell dm are also found independently in the Cyclorrhapha (Fig. 405). This character was scored as inapplicable whenever cell dm was absent due to the loss of crossvein dm-cu, except when the presence of a forked M₁₊₂ allowed a rough estimate of the position of crossvein dm-cu near the base of the fork. Since cells bm and dm are both absent in *Nemedina*, this character was also scored as inapplicable for this genus.

63. *Bm-cu crossvein*. Present, cells dm and bm separate (0); weakened, cells bm and dm partially united (1); absent, cells bm and dm fused (2).

The basal crossvein (bm-cu or t_b) is complete in both *Microphor* and *Schistostoma* (Fig. 397), whereas it is incomplete in all parathalassiines (Figs. 398–400), except *Thalassophorus* (Hennig 1971; Chvála 1983; Ulrich 1991). It is viewed as a reversal to the plesiomorphic condition in the latter genus (see Cumming & Brooks 2002). In Dolichopodidae, the basal crossvein is incomplete in most Sciapodinae (Fig. 401; Bickel 1994), whereas the crossvein is completely absent in all remaining subfamilies (Figs. 402–403). The functional importance of this reduction is unknown.

Fusion of these cells is hypothesized to have evolved independently in certain Cyclorrhapha. In the Ceratomerinae, cell bm and cell dm are separate, although cell bm is faint (Figs. 393–394; Sinclair 1997).

64. *A₁ termination*. Complete, reaching wing margin, even as a fold (0); incomplete, ending before wing margin (1); absent (2).

Hennig (1971) proposed this character as a synapomorphy of the microphorids. Wiegmann *et al.* (1993) further defined it for a broader analysis. The vein A_1 is complete in lower Brachycera (Figs. 361–362) and basal Cyclorrhapha (Figs. 404–408). Unfortunately, variation in the length of the A_1 is considerable in the Empidoidea and in many taxa it fades prior to the wing margin. State 0 is present in Atelestinae (Figs. 377–378), *Nemedina* (Fig. 189) and most hybotid lineages (Figs. 379, 384, 385).

65. *Anal lobe form*. Lobe acute to right angled, from alular incision to lobe apex (0); lobe obtuse, distinctly convex opposite cell cup (1); absent (2).

The degree of reduction of the anal lobe of the Empidoidea wing is considerable. As stated by Wiegmann *et al.* (1993), discrete states are difficult to recognize. This character is also highly variable, with various stages of anal lobe reduction even within genera. As defined here, a small, obtuse lobe is retained in many groups that have traditionally been considered to have narrow, parallel-sided wings; e.g., Clinocerinae and Brachystomatinae (Fig. 391). Due to the difficulty in scoring this character, it should be used with caution in interpretation of phylogenetic patterns.

66. *Alula type*. Developed, convex (0); reduced (1); absent (2).

The alula is well developed in orthorrhaphous Brachycera and some Empidoidea. In other Empidoidea, it is reduced in both broad and narrow winged taxa. A large alula is retained only in Atelestinae (Figs. 377–378), Sciapodinae (Fig. 401) (Dolichopodidae), and basal Cyclorrhapha (Figs. 404–405, 408). The alula is more convex in male *Microsania* than in females.

Abdomen

67. *Abdominal plaques*. Present (0); absent (1).

Abdominal plaques are circular patches on the sclerites, representing external remnants of attachment sites for muscles in the pupae of nematocerous Diptera and orthorrhaphous Brachycera (Fig. 416; Stoffolano *et al.* 1988). These plaques are absent in all Cyclorrhapha, which have an immobile pupa inside a puparium (character 121). Consequently plaques, which are present in all Empidoidea, including Atelestinae (Fig. 254), are an indirect indicator of the method of pupation. In many empidooids, abdominal plaques appear as a transverse row on the anterior margin of a tergite.

Unfortunately, the shiny cuticle seen in fossil empidooids that are preserved in amber makes observation of the plaques difficult, and their presence or absence remains to be clearly demonstrated.

68. *Apical female abdominal segments*. All segments exposed, gradually telescopic (0); segment 8–10 retracted (1); segments 7–10 retracted (2); segments 6–10 retracted (3); segments 5–10 retracted (4).

In non-acanthophorite bearing Empidoidea, the abdomen is normally gradually telescopic, with all segments exposed (Figs. 202). In Ceratomerinae, Trichopezinae, and Brachystomatinae, the apical two segments are retracted within segment 7 and scored as 1 (Figs. 230, 237). Retraction into segment 6 occurs in *Schistostoma* (Fig. 239), *Amphithalassius*, and *Plesiothalassius* (state 2), but is not clearly retracted in the latter two genera. However, in *Microphor* (Fig. 240), *Microphorella*, *Parathalassius* and Dolichopodidae (Figs. 240–241, 244, 246–247) the terminal segments are distinctly retracted into segment 5 and scored as 3.

In Cyclorrhapha, the terminal segments of *Sciadocera* are retracted into segment 6 (Fig. 250), but in many groups they are retracted into segment 5 (e.g., in *Syrphus* and *Strobilomyia*). The female terminalia in *Opetia* are highly modified, with the apical segments fused into a specialized ovipositor (Fig. 249). This ovipositor and segment 5 are retracted within segment 4 (Chandler 1998) and scored as 4.

69. *Tergite 7 of female*. Lacking fringe (0); dense fringe of setae along posterior margin (1).

In most Eremoneura as well as outgroup taxa, slender setae are distributed evenly on tergite 7 of the female abdomen, rather than along the posterior margin as a fringe. A fringe of slender setae along the posterior margin of tergite 7 (Sinclair 1995a, fig. 77) is present in Trichopezinae (Fig. 237), Brachystomatinae and Ceratomerinae. Although absent in several genera, this fringe appears to be part of the ground plan of each lineage. A fringe of setae is lacking in the microphorids (Fig. 239) and Dolichopodidae.

70. *Male tergite 7 vestiture*. Setose (0); bare or only a few scattered setae (1).

Tergite 7 is bare or with only a few scattered setulae in the microphorids and most Dolichopodidae (Figs. 255–258, 260–261). Presence of setae in *Heteropsilopus* (Fig. 259) and other Sciapodinae is probably a reversal, contrary to Bickel (1994) who suggested that the loss of these setae within Dolichopodidae is probably apomorphic. Additional abdominal tergites are often also bare, and presence or absence of setae (related to whether sclerite is withdrawn in abdomen) should be investigated further as a possible character in the higher classification of the Dolichopodidae. For example, tergite 6 is bare in Dolichopodinae and Peloropeodinae and was considered a synapomorphy of this clade by Brooks (2005a).

71. *Male tergite 8*. Broad, rectangular (0); slender (1); absent (2); U-shaped (3).

In Empidoidea, tergite 8 of the male abdomen ranges from a broad sclerite, nearly equal in length to tergite 7, to a slender, rectangular transverse band (Fig. 296) (Bährmann 1960). A slender tergite 8 is herein defined as less than one-half the length of sternite 8. Wiegmann *et al.* (1993) proposed a U-shaped tergite 8 as a possible synapomorphy of the Atelestinae (Fig. 254) and this is accepted here, despite somewhat similar shapes observed in some Tachydromiinae.

In the microphorids, three states were observed. A small square tergite 8 is retained in *Microphor* and *Schistostoma* (Figs. 255–256). In *Plesiothalassius* and *Amphithalassius* a slender tergite 8 is present, whereas the tergite is absent in *Microphorella* and *Parathalassius* (Figs. 257–258). In Dolichopodidae, tergite 8 is absent (Figs. 259–261) as it is in most Cyclorrhapha or greatly reduced (Ulrich 1974), although sometimes it is interpreted as fused with sternite 8 to form a syntergosternite.

72. *Male pregenital segments*. Unrotated and unmodified (only tergite 8) (0); segment 7 tubular (1); sternite 7 positioned laterally or lost (2); segments 7 and 8 twisted through to 180° (3).

In the basal Empidoidea, the male pregenital segments are relatively unmodified. Only tergite 8 is narrowed in some groups. In the microphorids, pregenital segments 5–8 are asymmetrical and twisted to the right (Figs. 255–258). Tergite and sternite 7 are strongly sclerotized and arched laterally. Sternite 7 is tightly fitted to the ventral margin of tergite 7, while sternite 8 is oval and posterolateral. The tubular and somewhat compressed condition of segment 7 forms a stalk or peduncle upon which the hypopygium is mounted (Figs. 255–260). This type of postabdomen has been termed the pedunculate form, and given its configuration in the microphorids, this form represents the ground plan condition of the Dolichopodidae, which is in agreement with Bickel (1994). The condition in *Sympycnus*, where the sclerites of segment 7 are reduced (Fig. 261), represents the retracted or encapsulated form and is scored as 2.

Advance state 3 occurs in the Cyclorrhapha where the first 180° of rotation of the male terminalia occurs between the sclerites of segment 7 and 8 (Griffiths 1972; Cumming *et al.* 1995).

73. *Rectal papillae*. Present but membranous (0); 4 sclerotized papillae present (1).

In most Brachycera there are four rectal papillae (see Woodley 1989: 1387). In Dolichopodidae, the papillae are stout and more strongly sclerotized, and remain visible following clearing of the abdominal tissues in hot lactic acid. They appear as four barrel-shaped structures (Fig. 246) located near segments 5–7 (see also McAlpine 1981, fig. 2.102).

Rectal papillae were also observed in the cleared abdomen of *Sciadocera*. They appeared only as sclerotized rings, likely independently derived and scored as 0.

74. *Spiracles (female)*. Seven pairs of spiracles present in segments 1–7 (0); five pairs present in segments 1–5 (1); four pairs present in segments 1–4 (2).

Only five pairs of spiracles are present in female Dolichopodidae, whereas seven are present in all microphorids. In the basal Cyclorrhapha, the female abdomen in Opetiidae possesses only four pairs of spiracles (state 3), likely resulting from the modifications of the terminal segments (Cumming *et al.* 1995).

Female terminalia

75. *Number of spermathecae*. Three (0); two (1); one (2).

The plesiomorphic number of spermathecae in Diptera is hypothesized to be three, and this number is found in most lower Brachycera and Cyclorrhapha (Woodley 1989; McAlpine 1989). There is a single spermatheca in Empidoidea, including the problematic genera *Atelestus*, *Meghyperus*, and *Nemedina* (Figs. 216–217; Chandler, 1981). In the literature it has been generally assumed that the spermatheca is absent in ocydromiines, Hybotinae, and Tachydromiinae (e.g., Hennig 1970), but a single unpigmented, membranous spermatheca has been observed in several tachydromiine genera (Figs. 228; Cumming & Cooper 1992; Sinclair 1995a) and a few other hybotid groups (e.g., *Apterodromia*, Sinclair & Cumming 2000). In this study, previously unobserved spermathecae were discovered using lactic acid and differential interference contrast microscopy (or Nomarski illumination) (Figs. 221, 224, 227).

In basal Cyclorrhapha, three darkly pigmented, oval spermathecae are present (Fig. 248). The spermathecae could not be found in *Lonchoptera unisetata*, but were observed in an undetermined species from Japan. Two sausage-shaped receptacles were observed on very long and often tightly coiled ducts (Fig. 252), similar to that observed and illustrated by de Meijere (1906). Prior to this study the spermathecae of Opetiidae were unknown. Using techniques described above upon specimens preserved in ethanol, a single, unpigmented spermatheca was observed for the first time in *Opetia* (Fig. 249).

76. *Spermathecal pigmentation*. Darkly pigmented (0); unpigmented (1).

Pigmented spermathecal receptacles are considered the plesiomorphic condition. Pigmented receptacles are found throughout the lower Brachycera (Yeates 1994), except Therevidae (exclusive of *Apsilocephala* Kröber) (Irwin 1976). An unpigmented spermatheca is found in the hybotid lineages, parathalassiines, and Dolichopodidae (Figs. 221, 228, 246–247).

77. *Spermathecal receptacle*. Spherical (0); tubular, lacking distinct sclerotized receptacle (1); coiled tube (2); elongate, separate from duct (3); sac-like (4).

In outgroups and many empidoids, the female spermatheca consists of a dark spherical receptacle at the apex of a long, straight duct (Figs. 194, 196, 199–200). In the hybotid lineages, parathalassiines and Dolichopodidae, the spermathecal receptacle appears as a greatly lengthened, tubular duct (state 1), lacking the clear divisions in other empidoids (Figs. 241–242, 244). Because of the delicate and unpigmented nature of the spermatheca in these groups, it is not generally observed in taxonomic studies.

Dufour (1851) observed in species of *Dolichopus*, an oval vesicle (termed “glande sébifique”) at the end of a long coiled duct. In freshly collected specimens of *Hercostomus* Loew, a mass of glandular cells was observed at the apex of a long duct (Fig. 245). A similar form was described by Sturtevant (1925). In *Plesiothalassius* there is a flattened, oval, weakly sclerotized, darkly pigmented terminal mass. In fact it can often be observed through the cuticle of undissected females. Also a similar form occurs in the Clinocerinae (Fig. 213), which possess a mass of tissue at the apex of a long tube (Sinclair 1994, 1995a). It is likely that this mass of terminal cells is glandular in function, providing nutrition for the sperm stored in the long duct. In all these cases the spermatheca was scored as 1, and the mass of tissue is probably present in a wide range of taxa.

The sac-like condition of the spermatheca in *Opetia* and *Platypalpus* is considered specialized and independently derived. In the Brachystomatinae, the spermathecal receptacle is reduced to a long, tightly coiled tube (Figs. 230–231), possibly unique for the subfamily and was scored as 2. The somewhat similarly shaped and modified spermatheca in *Clinocera* (Clinocerinae) (Fig. 213) is considered to be independently derived and non-homologous with the brachystomatine condition, because the spermatheca in more basal clinocerine genera is unmodified (Sinclair 1995a).

78. *Tergite 8 apodeme*. Lacking (0); large rod-shaped or laterally flattened apodeme present (1).

Trichopezinae are distinctively characterized by the presence of a large, laterally compressed, median apodeme extending from the anterior margin of tergite 8 of the female and projecting into segment 7 (Figs. 235–237; Sinclair 1995a). This synapomorphy provided evidence for Sinclair (1995a) to propose a new subfamily concept that required the re-assignment of many genera to the Trichopezinae from lineages that were previously

considered unrelated. Flattened, horizontal, lateral shelf-like plates observed in some ceratomerines, *Anomalempis*, and *Schistostoma* (Figs. 231, 234, 238) are not considered homologous.

79. *Tergite 8 form*. Entire (0); posterior margin with deep membranous cleft (1); sclerite completely divided medially (2).

Tergite 8 is a broad rectangular sclerite in the ground plan of the Empidoidea, based on outgroup comparison. The posterior margin of the female tergite is characterized by a deep, broad, membranous cleft in Trichopezinae, Brachystomatinae (Fig. 231), and Ceratomerinae (state 1). In state 2, tergite 8 is completely divided medially, although the division is often narrow compared to the broad cleft in state 1. State 2 is present in most microphorids (Figs. 239–241, 244) (except *Amphithalassius*, Fig. 243, and *Plesiothalassius*) and Dolichopodidae.

80. *Sclerites of segment 8*. Separated (0); articulated or fused (1).

Sternite 8 of the female is separated from tergite 8 by a wide pleural membrane in the Asiloidea, oreogetonines (Figs. 191, 195–196), Empidinae (Fig. 197, 202–203), Hemerodromiinae, Clinocerinae (Fig. 214), and the hybotid lineages (Figs. 219–229). In the modified condition, the anterodorsal margin of sternite 8 is articulated or fused to the anteroventral margin of tergite 8 (Figs. 230–232, 234–238, 242, 246–247; Sinclair 1995a). This condition is found in the Trichopezinae, Brachystomatinae, Ceratomerinae, microphorids and Dolichopodidae.

81. *Tergite 9*. Present (0); absent (1).

The loss of tergite 9 is an eremoneuran ground plan synapomorphy (Cumming *et al.*, 1995). As pointed out by Griffiths (1983), the segmental homology of the terminalia of *Trichopeza*, *Heleodromia*, *Brachystoma*, and *Schistostoma* was misinterpreted by Chvála (1983, figs. 78–83, 85, 86; 1987, figs. 17–21, 43–45). In Chvála's illustrations, tergite 9 is actually tergite 10, tergite 10 is the cercus, and what are labelled cerci are setose membranous swellings encircling the anus.

Tergite 9 appears fused to tergite 10 in *Thereva*, but separate plates are still discernable and thus this condition is not considered homologous with Eremoneura. Tergite 9 is also absent in Hilarimorphidae, but whether this has evolved independently is unknown.

82. *Acanthophorites*. Present, single row of large spines (0); present, single row of slender bristles (1); present, spine-like setae scattered on tergite (2); absent (3).

In many Asiloidea (*sensu* Woodley 1989), tergite 10 is divided into two lobes termed acanthophorites that are characterized by bearing spine-like setae. Although acanthophorites appear to have been lost frequently in the Asiloidea (e.g., Mythicomyiinae, *Hilarimorpha*, and some Scenopinidae), Sinclair *et al.* (1994) regarded

acanthophorites as synapomorphic for the Heterodactyla (Bombyliidae + Asiloidea + Eremoneura). In contrast, Yeates (2002) using ground plan apomorphies coded the Bombyliidae as lacking acanthophorites.

In the Empidoidea, the presence of acanthophorites is restricted to the Trichopezinae, Brachystomatinae, Ceratomerinae, microphorids, and Dolichopodidae (Figs. 230–232, 234–244). They are absent in the oreogetonines, Empidinae, Hemerodromiinae, Clinocerinae, Atelestinae, and the hybotid lineage. Acanthophorites are absent also in the ground plan of the Cyclorrhapha (Figs. 249–251).

Acanthophorites appear to be lacking in the fossil microphorine *Microphorites* Hennig. The female terminalia of this genus is apparently slender, uniformly tapered and lacking spines (Hennig 1971; Grimaldi & Cumming 1999). Unfortunately the exact condition of the setae and their pattern of insertion is unknown, although it could be similar to that observed in *Microphor*, *Amphithalassius*, and *Plesiothalassius* (Figs. 240, 243; Sinclair 1995a, see also Ulrich 1991), where the outstanding bristles arise in a distinct transverse row, scored here as state 1.

The acanthophorite form differs greatly in Ceratomerinae and Trichopezinae compared to that of other empidoids and asiloids. The sclerite bears a large number of small, spine-like setae concentrated along the median and posterior margins (Figs. 232, 234–237). This is in contrast to the outgroup condition, where the acanthophorite spines are aligned in a transverse posterior row.

The form of the acanthophorites, or modified setae, can also be quite variable in size and number among Dolichopodidae (Bickel 1985, 1994). Dolichopodid acanthophorites are adapted to oviposition behavior, microhabitat and substrate, and consequently are subject to considerable homoplasy (Bickel pers. comm.).

83. *Segment 10*. Tergite and sternite 10 separate (0); tergite 10 articulated with sternite 10 (1).

The Dolichopodidae and some microphorids are characterized by having tergite and sternite 10 articulated anteriorly, similar to the sclerites of segment 8 (Figs. 238, 246–247; see also Chvála 1987, fig. 44; Sinclair 1995a, fig. 73). The articulation is possibly secondarily lost in *Amphithalassius* (Fig. 242) and *Plesiothalassius*, where sternite 8 is lengthened. The strengthening of sternite 8 in the latter two genera may be due to oviposition behavior, which is possibly associated with reduction of the acanthophorite spines.

A similar, but probably convergent form is also present in Brachystomatinae (Figs. 230–231), however the sclerites appear fused.

84. *Tergite 10*. Divided medially (0); undivided (1); absent (2); fused to cercus (3).

The condition of tergite 10 varies considerably in the Empidoidea. Tergite 10 is divided medially in most outgroup taxa (see Yeates 1994), remaining narrowly fused or

complete dorsally so that the sclerite normally appears deeply cleft or broadly U-shaped. In several lineages, including many Cyclorrhapha, the sclerite is undivided or possibly fused medially to form a single dorsal sclerite (Figs. 208, 211), while it is entirely absent in a few groups such as the Drapetini (e.g., *Austrodromia*) (Cumming & Cooper 1992), *Nemedina* and the Atelestinae (Fig. 215, 218). Although it appears absent in *Iteaphila* (Fig. 192), tergite 10 can be distinguished at the base of the long, slender cercus. In Oedaleini, tergite 10 is also fused to the globular cercus (Fig. 222), but it can be distinguished in cleared specimens, as can the tergite of *Ocydromia*.

85. *Cercus form.* Lightly sclerotized (0); heavily sclerotized (1); absent (2).

The female cercus is a lightly sclerotized, setose lobe in the Asiloidea. In the traditional basal lineages of the Empidoidea, the female cercus is a slender, blunt, setose lobe. In state 1, the cercus is a heavily sclerotized (Figs. 230–231, 234–244, 246–247; Sinclair 1995a, figs. 72–78). This modification of the cercus is present in Trichopezinae, Brachystomatinae, Ceratomerinae, microphorids and Dolichopodidae. The lightly sclerotized cercus of *Amphithalassius* (Fig. 243) and *Plesiothalassius* is possibly the result of secondary modification. The cercus of *Glyphidopeza* is absent (Fig. 232), contrary to Sinclair (1997).

86. *Cercus vestiture.* Setulae, or slender setae (0); short, spine-like setae (1); few setae, apex prolonged and pointed (2); bearing several pairs of very long, slender setae (3).

The vestiture of the female cercus remains unmodified in most Empidoidea, except in acanthophorite groups (i.e., Trichopezinae, Brachystomatinae, Ceratomerinae, microphorids and Dolichopodidae). In these taxa, the apex of the cercus is tapered into a pointed, spine-like process (state 2, Figs. 230–231, 237–239, 241, 244, 247), except in Ceratomerinae (Fig. 234) where the cercus bears spine-like setae (state 1). The cercus is unmodified in the parathalassiine genera *Amphithalassius* (Fig. 243) and *Plesiothalassius*, presumably secondarily because of the enlarged sternite 8. Very long apical setae (state 3) are present in *Heteropsilopus* (Fig. 246) and *Microphor* (Fig. 240).

87. *Orientation of female cercus.* Horizontal (0); slightly to strongly arched dorsally (1).

Throughout the lower Brachycera and Empidoidea, the female cercus is held horizontally, bearing setulae. In the Trichopezinae, Brachystomatinae, and Ceratomerinae, the female cercus is held upright, bearing stout setae or spines similar to those on tergite 10 (Figs. 230–231, 236–237; Sinclair 1995a, figs. 72, 76, 78). The structure of the cercus suggests that it assists the acanthophorites (character 82 above) in oviposition. The highly modified cercus of this group has led to several misinterpretations in homology. The cercus is held horizontally in the microphorids and Dolichopodidae, the other lineage with acanthophorites.

Male terminalia

88. *Hypopygium symmetry*. Symmetrical (0); hybotid asymmetry, including clasping structures (1) microphorine asymmetry, including clasping structures (2); dolichopodid asymmetry, excluding clasping structures (3); *Sabroskyella* asymmetry (*Trichopeza* group) (4); *Sciadocera* asymmetry (5).

The male terminalia are symmetrical in outgroup taxa and many of the traditionally more basal Empidoidea, as well as the Atelestinae (Figs. 298, 302), a few hybotid genera (Fig. 304), and primitive Cyclorrhapha (Cumming *et al.* 1995). Nevertheless, asymmetry appears to have evolved independently within the Empidoidea on numerous occasions (e.g., *Trichopeza* group of genera in the Trichopezinae, Fig. 343).

In the Dolichopodidae, asymmetry in the epandrium is generally retained only at the hypopygial foramen (Figs. 353–354), while the remainder of the epandrium is symmetrical. However, not surprisingly exceptions are often found in empidoid genitalic features (e.g., see Brooks 2005a, figs 14C, 15D, 34C), including several examples of secondarily symmetrical forms in the dolichopodid groups Plagioneurinae and Babinellinae (Bickel 1987). This is in contrast to the hybotid lineages where both the hypandrium and apex of the epandrium are asymmetrical (Figs. 307–308, 311–315, 318–319, 321–327).

As clearly stated by Wiegmann *et al.* (1993), the asymmetry of the hybotids and microphorids (Figs. 344, 347–351) is independently derived and we have scored them as separate states. In addition, despite the similar method of rotation, the asymmetry of the microphorids is highly complex and we consider that it differs greatly from that seen in the Dolichopodidae. Consequently, both lineages were also scored separately.

Despite its general use in phylogenetic studies (e.g., Chvála 1983; Wiegmann *et al.* 1993), we do not necessarily view asymmetry as a ground plan feature of the hybotid lineages. The terminalia of *Trichinomyia* (Figs. 303–304) appear symmetrical, whereas the terminalia of *Bicellaria*, *Syneches*, *Lamachella* are almost symmetrical (see Tuomikoski 1966).

The asymmetrical male terminalia seen in *Sabroskyella* (i.e., *Trichopeza* group) and *Sciadocera* were both scored independently, because each condition is not considered homologous to any of the states defined above. In *Sabroskyella*, the terminalia are twisted to the left with the epandrium and hypandrium fused (Fig. 343), whereas in *Sciadocera* the hypopygium is enlarged on the left side, although the cerci remain symmetrical (Fig. 360; Cumming *et al.* 1995).

89. *Male terminalia rotation*. Unrotated (0); rotated between 45–90° (1); rotated between 90–180° and lateroflexed (2); circumversion, rotated 360° (3).

It is generally assumed that rotation and flexion of the male hypopygium occurs as an adaptation for mating and protection of the genitalia, and that this has evolved in numerous

ways in different groups of Diptera (McAlpine 1981). In primitive Brachycera and most lineages of Empidoidea, including Atelestinae, the male terminalia are unrotated. Genitalic rotation appears to be a derived feature, independently evolved in a number of families of Brachycera (McAlpine 1981; Yeates 1994). In all members of the microphorids and Dolichopodidae, the male terminalia are rotated to the right, beginning with the pregenital segments (at least segment 7) and including the hypopygium, to between 90–180° and then lateroflexed to the right (Ulrich 1974; McAlpine 1981; Cumming & Sinclair 1990; Cumming *et al.* 1995). As a result of this rotation, the hypopygium lies along the right side of the abdomen with the phallus and cerci directed anteriorly. The rotation also results in twisting of the reproductive tract and hind gut in a manner reminiscent of that observed in the Cyclorrhapha (Bährmann 1966, fig. 6, but see comments of Ulrich 1974; Irwin 1974, figs. 4,5). In the microphorids, sternite 8 remains mostly aligned to sternite 7, however the abdomen is distinctly twisted to the right (Figs. 255–258). In Dolichopodidae, sternite 8 is positioned on the left lateral side (Figs. 259–260; Crampton 1942).

The male terminalia of ocydromiines, Hybotinae, and Tachydromiinae are rotated between 45–90° to the right. Since the rotation does not include pregenital segments (segments 7 and 8), the similarities in the rotation of the male terminalia with those of the microphorids and Dolichopodidae are not considered homologous (Cumming *et al.* 1995).

In Cyclorrhapha (including *Opetia*—see Cumming *et al.* 1995, character 7), the hypopygium is permanently circumverted 360° through a dextral rotation, such that the internal ducts of the reproductive tract and postabdominal nervous system are looped around the hind gut (McAlpine 1981; Cumming *et al.* 1995, see characters 7, 31 for discussion).

90. *Hyandrium form*. Subrectangular to triangular (0); prolonged apically (1); apically bilobed (2); shortened (3).

The form of the hyandrium is generally variable among genera and species and few features can be used at this level of analysis. One feature that appears to be consistent is the apical lobes, where in the hybotid lineages there is a pair of characteristic lobes (state 2), variable in size and length (Figs. 307, 314, 316, 326). State 1 is found in the Dolichopodidae (Figs. 352–354), where the hyandrium is lengthened into a protective phallic guide or sheath (= opisthyandrium, *sensu* Ulrich 1974). The large single hyandrial process in the microphorine genus *Schistostoma* (Fig. 344) (coded as 1) is not considered homologous because it is not associated with the phallus, contrary to Chvála (1987, fig. 14, labelled OHY). The hyandrium of Atelestinae and *Nemedina* is greatly reduced in comparison to the epandrium (state 3) (Figs. 298–299), with the slender processes of the gonocoxal apodemes nearly subequal in length to the hyandrium.

91. *Hyandrium and epandrium fusion*. Separate or clearly distinguishable (0); broadly and indistinguishably fused (1).

The epandrium and hypandrium are either articulated or somewhat fused at a narrow point in primitive Empidoidea (Figs. 262, 266, 270, 274, 280). In *Schistostoma*, the hypandrium and epandrium are fused basally at a narrow point similar to some basal empidoid genera and scored as state 0 (Fig. 344). In *Brachystoma nigrimanus* Loew and *Sabroskyella*, complete fusion of the hypandrium and epandrium has occurred (Figs. 331, 343), both apparently independently from the clades discussed below.

The epandrium and anterior portion of the hypandrium are usually fused in Dolichopodidae (Ulrich 1974, 1976). The posterior portion of the hypandrium (= opisthypandrium *sensu* Ulrich 1974) is an unpaired median ventral process, with a grooved dorsal surface serving as a phallic guide (Ulrich 1974, 1976). In this study, we refer to this ventral process as simply the hypandrium and the entire capsule as the epandrium since no separation of the anterior hypandrial portion remains (Figs. 352–354). In some *Microphorella* one epandrial lamella is broadly fused along its ventral margin to the hypandrium (Fig. 348), but this has been scored as 0, since both hypandrium and epandrium are clearly distinguishable. A similar condition occurs in *Amphithalassius*. The epandrium and hypandrium are also almost entirely fused in *Microphorella merzi* Gatt and the recently described genus, *Eothalassius* Shamshev & Grootaert, forming a genital capsule very similar to that observed in dolichopodids (Gatt 2003; Ulrich 2004; Shamshev & Grootaert 2005).

92. *Hypandrium and phallus fusion*. Separate (0); fused into intromittent organ (1).

The genera *Homalocnemis* and *Brochella* display a number of similar features that may indicate a close relationship, including the apparent fusion of the hypandrium and phallus to form a rigid intromittent organ (Figs. 264–265, 291). Other features shared between these taxa include the lack of epipharyngeal blades, and abdomens that are very wide and flattened. At present, no single feature strongly suggests a sister group relationship and the above characters are possibly either plesiomorphic or independently derived.

93. *Hypandrium and gonocoxite*. Separate (0); fused (1).

The gonocoxites and hypandrium are separate structures in the lower Brachycera, with partial or complete fusion occurring independently in several lineages (Sinclair *et al.* 1994). Complete fusion occurs in the Eremoneura and is considered a ground plan apomorphy (Cumming *et al.* 1995). The gonocoxal component can still be identified by the presence of paired processes of the gonocoxal apodemes (see below) in many basal lineages of the Empidoidea.

94. *Gonocoxal apodeme*. Projecting as narrow process beyond hypandrium (0); confined to anterior margin of hypandrium, lacking narrow process (1).

In the outgroups and many traditional basal empidoids, a pair of short, truncate

processes of the gonocoxal apodemes (= basimere apodeme *sensu* Hennig 1976, fig. 28) arise anterodorsally from the hypandrium (Figs. 263, 266, 269, 271, 275, 280, 286, 337) (note: these processes are simply termed here the gonocoxal apodemes). Paired apodemes arising from the hypandrial bridge are homologous to the gonocoxal apodemes of lower Brachycera (Sinclair *et al.* 1994) and contrary to Griffiths (1994), are not synapomorphic for the Empidoidea. Reduction of these apodemes to the anterior margin, so that they do not project beyond the hypandrium, appears highly correlated with the development of permanent male genitalic rotation (Figs. 303, 309, 310, 313, 329; Cumming *et al.* 1995, character 8). Thus the reduction is presumed to have occurred independently in the hybotid lineages and microphorids + Dolichopodidae clade. Gonocoxal apodemes are also greatly reduced in the ground plan of the Cyclorrhapha (Cumming *et al.* 1995), which also exhibit permanent rotation of the male genitalia (see character 89 above).

There is a trend in *Hilara*-like genera for the gonocoxal apodemes to be positioned dorsally near the cercus (Fig. 286), highly reduced or even absent and not projecting from the hypandrium, as in some *Hilarempis* (Fig. 284). There appears to be a trend toward gradual reduction of the projecting apodemes in the Hilarini.

95. *Gonocoxal apodeme form*. Not lengthened (0), greatly lengthened and slender.

The lengthened gonocoxal apodemes of the Atelestinae and *Nemedina* (Figs. 298–299, 301) are unique among the Empidoidea (Cumming *et al.* 1995; Sinclair & Shamshev 2003). In the ground plan state, the apodemes are rather short, stout processes (see character 94 above).

96. *Phallapodeme*. Absent (0); present (1); lever-like (2).

The phallapodeme is an evolutionary novelty within the Cyclorrhapha, which appears to have developed initially as a longitudinal invagination of the hypandrium (Figs. 356–357) surrounding the base of the phallus (see Cumming *et al.* 1995, characters 19 and 28). A lever-like phallapodeme has been considered a synapomorphy of Syrphoidea + Schizophora, despite apparent homoplasy in Ironomyiidae and a few species of Lonchopteridae, such as *Lonchoptera uniseta* (Fig. 359; Cumming *et al.* 1995).

97. *Ventral apodeme*. Absent (0); paired (1); single (2).

From the inner walls of the postgonites (see characters 99 and 100 below) extend slender apodemes that lie parallel to the phallus and are normally fused medially forming a single rod beneath the phallus and ejaculatory apodeme (Sinclair 1996). Thus a V-shaped apodeme is present in many groups (Figs. 312, 316, 319–320, 322–323), homologous to the second apodeme observed in the hybotid lineages, including Tachydromiinae (Figs. 328–330; Cumming & Cooper 1992). A pair of ventral rods is present in the Atelestinae (Figs. 299–301) and possibly represents precursors to the single fused rod in the hybotids. The ventral apodeme is secondarily articulated with the phallus in Tachydromiinae, an

autapomorphy of this lineage (Cumming unpubl. data). The ventral apodeme is broad in Oedaleini and *Hoplocyrtoma*.

Within the hybotid lineages, ventral apodemes are absent in the Ocydromiini (Sinclair & Cumming 2000), *Trichinomyia*, and *Trichina*. In the latter genus, two apodemes are present (Fig. 306), however the homology of the dorsal rod remains uncertain. If it is homologous with the ventral apodeme, a V-shaped neck would be expected and it should also be ventral or beneath the ejaculatory apodeme. Nevertheless, it could be homologous if it is assumed that the postgonites and ventral apodeme are associated with the apex of the phallus as in Atelestinae, such that the apex of the phallus in this lineage is actually mostly derived from the postgonite. A ventral apodeme is absent in *Nemedina* (Sinclair & Shamshev 2003).

98. *Gonostylus*. Present (0); absent (1).

Gonostyli are considered absent in the eremoneuran ground plan. The loss of gonostyli was originally considered apomorphic for only the Empidoidea (Cumming & Sinclair 1990; Cumming *et al.* 1995). Through further analysis of basal Empidoid genera, postgonite precursors (see below, character 99) were discovered which are homologous in position and form to the “gonostyli” of basal Cyclorrhapha (Cumming & Sinclair 1996). Consequently, this character has been re-evaluated and gonostyli are now also considered absent in all Cyclorrhapha (see Sinclair 2000a).

99. *Postgonites*. Absent (0); lobes or processes from hypandrium, often encircling phallus (1); upright, anterior to phallus near base of subepandrial sclerite (2); articulated at base (3); projecting toward proctiger (4).

We originally believed that the paired processes located near the phallus were remnants of gonostyli, the primary clasping structures of the lower Diptera or possibly simply postgonites of unknown homology (Cumming *et al.* 1995). But following a greater survey of Southern Hemisphere genera, we have reconsidered their homology (Cumming & Sinclair 1996; Sinclair 2000a). This more recent interpretation is discussed in greater detail below.

These lobes are now interpreted as *de novo* structures in the ground plan of the Eremoneura, and following Chvála (1983) and Sinclair (1996, 2000a) we refer to these structures as postgonites. This term has been commonly used for homologous structures in the Cyclorrhapha, especially in calyptrates. The possible ground plan condition is best illustrated in *Hormopeza* (Fig. 271) and *Opetia* (Fig. 355). It can be described as a pair of lobes running along the upper margin of hypandrium from the base of the phallus, extending beyond the posterior margin of the hypandrium and often partially encircling the phallus (Cumming *et al.* 1995, fig. 16). These lobes are likely sensory in function. In *Hilara*, a single muscle has been described that originates from the ejaculatory apodeme and is inserted onto the postgonite (Fig. 286) (Trehen 1961, muscle 2).

From the ground plan condition, we have been able to score at least three derived forms. In all hilarine genera (Figs. 283, 285–286) (including *Thinempis* Bickel, *Hybomyia* Plant), the postgonites appear as digitiform processes (= gonapophyses *sensu* Collin 1961), arising either from the hypandrium or secondarily fused to the subepandrial sclerite, and extending dorsally near the proctiger (state 2). This form is also observed in *Sphicosa* (Fig. 278), but according to figures in Collin (1933, fig. 61d) the hypopygium of this genus appears to be polymorphic in form. Thus any conclusions on the relationships between *Sphicosa* (and *Clinorhampha* Collin) and Hilarini based on this character should remain tentative.

In basal Cyclorrhapha, the postgonites appear articulated basally (Fig. 359) (state 3) and rotate with movement of the phallus. The postgonites in calyptrates are also rotated outwards upon movement of the phallapodeme and phallus, and do not function as claspers. In calyptrates, a single muscle originating from the phallapodeme and inserted onto the postgonite, is found in Calliphoridae (Salzer 1968) but is considered absent in Sarcophagidae (Ovtshinnikova 1994).

Postgonites are absent in *Rhamphomyia s.lat.* and Northern Hemisphere and African *Empis s.lat.* (Fig. 280), possibly representing a synapomorphy of this clade. They are also absent in Ocydromiini, *Trichina*, *Trichinomyia*, *Atelestus*, *Nemedina*, and *Sciadocera*.

The postgonites of the microphorids and Dolichopodidae are often difficult to homologue. However, a V-shaped or forked sclerite, which Hennig (1976) termed the “gabel”, is sometimes present and can often be used as a landmark since it is inserted at the base of the postgonites (Fig. 351) (telomeres *sensu* Hennig 1976). In Cumming *et al.* (1995, fig. 14), the purple shaded V-shaped sclerite in *Microphor pilimanus* (Strobl) (Fig. 345) encases the base of the phallus and extends apically to insert onto the base of a complex pair of sclerites labelled conical appendage or postgonites. The postgonites in at least some species of *Microphor* appear to have some glandular function (Ulrich 1988). This paired sclerite is medial to the hypandrial arms that extend from the hypandrium to the base of the phallus in Dolichopodidae (Cumming *et al.* 1995, fig. 15). In Dolichopodinae, the encasing of the phallus is apparently lost and only the medially fused postgonites are present lying within the U-shaped hypandrial arms, prolonged into a distinct, separate lamella-like process (Fig. 352). This lobe extends beyond the base of the cercus (Brooks 2005a; Dorsalanhang or appendix dorsalis *sensu* Ulrich 1974; process of sternite 10 *sensu* McAlpine 1981, figs. 2.127, 2.128). In *Achalcus* Loew a long, cylindrical, rod-shaped postgonite (unpaired) is present and also extends to and beyond the cercus (Pollet & Cumming 1998, fig. 3). In Sciapodinae, the gabel and postgonites only extend to the base of the bacilliform sclerite, possibly secondarily reduced (Fig. 353; Cumming *et al.* 1995, fig. 15).

In Dolichopodidae, there appears to be two major configurations of the postgonites. In Dolichopodinae, Medeterinae, Neurigoninae and Diaphorinae, the postgonites are fused medially and appear as a single median structure extending beyond the surstylus and

epandrial lobes, closely associated with the proctiger (state 4; see *Tachytrechus* above). In contrast, a pair of sclerites in Sympycninae and Plagioneurinae extend around the base of the phallus and arch dorsally, parallel to the phallus (Fig. 354). This pair of sclerites extends dorsally in association with the narrow hypandrium forming a pair of tubular processes. It is assumed these processes are homologous to postgonites, although they are in a plesiomorphic position compared to other dolichopodids.

100. *Postgonite fusion*. Postgonite free from apex of hypandrium (0); right postgonite secondarily weakly fused to apex of hypandrium (1).

As stated above, the postgonites are primitively paired lobes flanking the phallus. In Oedaleini and Tachydromiinae, the right postgonite is secondarily fused to the apex of the right hypandrial prolongation (Figs. 313–314). Although less clear in the Tachydromiinae, the ventral apodeme functions as a landmark identifying the remnants of the postgonites (Figs. 328, 330). The left postgonite remains lateral to the phallus, while the right postgonite is essentially ventrolateral.

101. *Lateral ejaculatory process*. Present (0); absent (1); retracted (2).

Lateral ejaculatory processes (= lateral aedeagal apodeme *sensu* Yeates, 1994; external ejaculatory sclerites *sensu* Griffiths 1994, 1996) are considered a ground plan apomorphy of the Brachycera (Sinclair *et al.* 1994). These processes are retracted within the base of the phallus in several families of orthorrhaphous Brachycera, including Therevidae, and they are absent in *Hilarimorpha* and *Caenotus* (Sinclair *et al.* 1994). Lateral ejaculatory processes are absent also in the ground plan of the Eremoneura (Cumming *et al.* 1995).

A pair of lateral apodemes is present in *Iteaphila nitidula* Zetterstedt, but they are fused to the base of the phallus and are not found in other species of this genus. Consequently these apodemes are not considered homologous with lateral ejaculatory processes.

102. *Ejaculatory apodeme*. Piston-like (0); lever-like, articulated to base of phallus (1); rod-shaped (undifferentiated from phallus) and fused to base of phallus (2); plate-like and fused to base of phallus (3); separated from phallus by short to long ejaculatory duct (4); absent (5).

In the ground plan of the Brachycera, the ejaculatory apodeme performs like a piston, moving freely in and out of the base of the phallus (Sinclair *et al.* 1994). In the ground plan of the Empidoidea, the ejaculatory apodeme articulates ventrally with the phallus, moving lever-like (Figs. 271, 273, 277–280) (see discussion in Cumming *et al.* 1995 and Sinclair 2000a). This modification of the ejaculatory apodeme is considered synapomorphic for the Empidoidea.

From the ground plan condition described above, the ejaculatory apodeme is often fused to the base of the phallus. There are two apparently nonhomologous forms of this

fusion. In Atelestinae and the hybotid lineages, the ejaculatory apodeme is rod-shaped, undifferentiated from the base of the phallus (state 2) (Figs. 303, 312, 317, 320, 323–324; Cumming *et al.* 1995, figs. 10a, 12a). In state 3, the ejaculatory apodeme is plate-like and narrowly fused to the base of a wide, tubular phallus in Trichopezinae, Ceratomerinae, and Brachystomatinae (Figs. 331, 333, 341).

Separation of the ejaculatory apodeme from the base of the phallus characterizes the Cyclorrhapha, including Opetiidae (Figs. 355, 356, 360; Cumming *et al.* 1995). The ejaculatory apodeme is also somewhat separated in several clinocerine genera, for example, *Clinocera* (Fig. 293), *Kowarzia* Mik and *Wiedemannia* (Sinclair 1995a).

103. *Shape of phallus*. Straight (0); upwardly curved (1).

A slender, distally upcurved phallus was listed by Chvála (1983) as a synapomorphy of his Empididae and ground plan feature of the Eremoneura. However, in many empidoideid groups and asiloids the phallus is nearly straight. Wiegmann *et al.* (1993; character 45) also scored an upcurved phallus character as synapomorphic for the Empidinae, Ceratomerinae, Clinocerinae, Hemerodromiinae, and Brachystomatinae. The definition of this character as used in these previous analyses was too simplistic and difficult to score in the lower Brachycera. Consequently, we have refined this character and include only those groups where the phallus has a distinctive ventral dip near its base, prior to arching dorsally. Within the Empidoidea, several groups appear to be characterized by this distinctively shaped phallus, including Empidinae (Figs. 277–280, 282–283, 286), Hemerodromiinae (Fig. 287), parathalassiines (Fig. 346), and Dolichopodidae (Figs. 352–354).

104. *Apex of phallus*. Simple. (0); apex articulated, flexible (1); apex with hood-like cap (2); apex emitting mostly membranous distiphallus (3).

The phallus of all *Ocydromia*-like genera is biarticulated, possessing an apical articulated appendage (Fig. 309; Collin 1961, fig. 94) and this is considered synapomorphic for this lineage (Sinclair & Cumming 2000). A flexible apical filament or distiphallus also occurs in some derived genera of Clinocerinae (Fig. 293) (Sinclair 1995a). A phallus with a hood-like cap (state 2) occurs in the Oedaleinae (Fig. 312), Hybotini (Figs. 320, 323), *Hoplocyrtoma*, *Bicellaria* (Fig. 317), *Trichina* and *Trichinomyia* (Fig. 303) (Cumming *et al.* 1995, fig. 12a). In some Hybotini, the apical hood is inflated and expanded, often with additional lobes (Fig. 324). This character is possibly synapomorphic for the above taxa, exclusive of Tachydromiinae, which have the apex of the phallus secondarily modified as a simple tube (Fig. 328).

The final state (3) is a synapomorphy of *Hormopeza* and the remaining genera in the *Ragas* group (Sinclair 1999). All included genera in this group possess a mostly membranous distiphallus that arises from the apex of the phallus (Fig. 271).

105. *Epandrium*. Shallowly notched or posterior margin straight (0); epandrial lamellae

separated along midline (1); deeply emarginate, U-shaped with basal connection (2); deeply emarginate epandrium without basal connection, lamellae widely separated (3).

In Eremoneura, the epandrium is either deeply emarginate along its dorsoapical margin (Figs. 263, 268, 276, 302) or is further modified into apical clasping structures (Figs. 297, 339; surstyli, character 109 below), that are derived from lateral outgrowths of the epandrium (Cumming *et al.* 1995). This form of the epandrium (state 2) is associated with the clasping function of the tergite and is a ground plan synapomorphy for the Eremoneura. In the lower Brachycera, the epandrium is normally broadly rectangular, but often apically cleft in many asiloids (Sinclair *et al.* 1994). In addition, a completely divided or medially split epandrium (coded as 1) is found in a number of asiloids including Scenopinidae (e.g., *Caenotus*) (Yeates 1994). This is distinguished from state 3, where the epandrial lamellae are widely separated, indicating that the widely separate state is likely derived from the deeply emarginate form (state 2). Separate lamellae occur widely in a range of empidooids including the Empidinae (Figs. 280, 284–285) (exclusive of *Dryodromia*, *Hesperempis*, and *Philetus*), Hemerodromiinae, Ceratomerinae (Fig. 334), and parathalassiines (Fig. 347–449).

106. *Hypopygial foramen*. Absent (0); present (1).

The Dolichopodidae are characterized by the left lateral position of the hypopygial foramen (Figs. 352–354), which is the result of the encapsulation of the genitalia (also characteristic of the Dolichopodidae, see character 91) (Ulrich 1974, 1976). Sternite 8, which is positioned on the left lateral side, lies over the foramen (Fig. 259). Although this unique position is an autapomorphy of the family, it is secondarily positioned anteriorly in Babindellinae (Bickel 1987) and *Plagioneurus* Loew.

107. *Subepandrial membrane*. Membranous at least at base (0); completely sclerotized (1).

In Eremoneura, the intersegmental membrane, termed the subepandrial membrane is completely sclerotized along its length from the hypoproct to the base of the phallus (Cumming *et al.* 1995). This sclerite, referred to as the subepandrial sclerite is often divided laterally into a pair of slender processes, termed bacilliform sclerites (see character 108 below).

108. *Bacilliform sclerites*. Absent (0); present (1); fused with the hypandrium, separated from base of phallus (2).

As stated above, the subepandrial sclerite is divided laterally into a pair of slender processes that extend to the outer apical margins of the epandrium, or surstyli when present (Cumming *et al.* 1995). These processes, termed bacilliform sclerites, assist in the clasping action by abducting the surstyli or the outer apical margins of the epandrium (see Cumming *et al.* 1995, p. 125). Bacilliform sclerites are present in Eremoneura and Apsilocephalidae (Sinclair *et al.* 1994; Cumming *et al.* 1995).

In the ground plan of Eremoneura, the bacilliform and subepandrial sclerites articulate

with the base of the phallus (Figs. 270, 280, 284, 331) (Cumming & Sinclair 1990; Cumming *et al.* 1995). In microphorids and most Dolichopodidae, the bacilliform and subepandrial sclerites extend beyond the articulation point with the base of the phallus (point of articulation labelled “y” in Hennig 1976, fig. 26) and fuse with the hypandrium or hypandrial arm (Figs 345, 352–353). This apomorphic state, coded as 2, is unique among the Empidoidea.

109. *Surstylus*. Absent (0); differentiated from epandrium, weakly articulated (1); fully articulated with epandrium (2).

In the ground plan of the Empidoidea, the epandrium is the sole clasping structure. It is deeply U-shaped, with inner bacilliform sclerites projecting towards the apex of each epandrial lobe (Figs. 263, 268, 270). The concentration of clasping action to the apex of the epandrium has led to a great deal of individual evolution augmenting the clasping ability. In the Cyclorrhapha, surstyli are part of the ground plan of the lineage (Figs. 355–357, 360), while they appear to have evolved independently a number of times within the Empidoidea (Cumming *et al.* 1995). In several lineages, surstyli are very poorly differentiated from the apex of the epandrium, usually distinguished by the presence of a narrow weakening or lateral notch in the cuticle of the epandrium or represented by a narrow apical lobe (Figs. 325, 332, 334, 340). Fully articulated surstyli as seen in Cyclorrhapha occur rarely in the Empidoidea (e.g., *Trichina* Fig. 307, *Neotrichina* Fig. 308, *Ocydromia* Fig. 311, *Symballopthalmus* Fig. 327, left surstylus).

The articulated lobes of the epandrium observed in *Philetus* (Fig. 274), *Hesperempis* (Fig. 272), *Dryodromia* and *Toreus* (of which the latter three at least appear to be related) lack clearly identifiable inner connections to the subepandrial sclerite (i.e., bacilliform sclerites) and are consequently not considered homologous to surstyli.

110. *Surstylar position*. Absent or apical (0); subapical on inner margin of epandrium (1).

The surstylus has evolved as a clasping lobe at the apex of the epandrium (see character 109 above). In the Atelestinae, the surstylus occurs subapically, arising mid-laterally from the subepandrial sclerite (Fig. 302; Cumming *et al.* 1995, fig. 10c). The pair of subapical surstyli appears to be more tactile or sensory in function, rather than clasping, which in the Atelestinae is performed by the apex of the epandrial lamellae. Similarly positioned surstyli occur in *Ragas*, but they are extremely slender and freely projecting (Sinclair & Saigusa 2001, figs. 11, 13), and are undoubtedly independently derived.

111. *Proctiger form*. Simple divided cercus and hypoproct (0); cercus, hypoproct and subepandrial sclerite forming complex structure (1).

In the Empidinae, Hemerodromiinae, *Philetus*, and *Hesperempis* surstyli are not developed at the apex of the epandrium. Instead, the clasping function is replaced by the apex of the epandrium, a complex cercus (see Rafael & Cumming 2004, figs. 16–17), and

various lobes of the subepandrial sclerite (Figs. 274, 278). In some cases, the cercus completely takes over the clasping function, such as in *Empis borealis* L. and species of *Hemerodromia* Meigen (see character 114 below). In Hilarini though, the cerci are restricted to an area immediately surrounding the anus and are associated with a complex of lobes bordering the anterior margin of the epandrium (Figs. 283, 286).

112. *Cercus articulation*. Unarticulated (0); lobes closely approximated basally, appearing articulated with epandrium (1).

The base of the male cercus is largely membranous and broadly connected with epandrium in most Empidoidea, Asiloidea and basal lineages of the Cyclorrhapha (Sinclair *et al.* 1994; Cumming *et al.* 1995). In the Brachystomatinae, the cercus is well sclerotized, even basally, and terminates abruptly with its connection to the epandrium (Fig. 332). The unique attachment enables the cerci to appear somewhat articulated and move as a unit. This form of cercus occurs also in *Xanthodromia*.

113. *Cercus sclerotization*. Fleshy, thinly sclerotized, clothed in fine short setae (0); heavily sclerotized, robust, often with inner sensilla (1).

A fleshy, setose male cercus, which is not modified for clasping, occurs in most Empidoidea, Asiloidea, and the basal lineages of Cyclorrhapha (Sinclair *et al.* 1994; Cumming *et al.* 1995). A heavily sclerotized cercus, modified for clasping, was first proposed by Ulrich (1975) as a synapomorphy of the Empidinae + Hemerodromiinae (Figs. 280–281, 287–288). However, a simple cercus is also known within this clade, including the Hilarini and many *Chelipoda*-like genera. Although this character requires further examination and may be too simplistically defined, it may prove useful in a study of the higher classification of the Empidinae, since it is also absent in *Empidadelpha* and some *Sphicosa* (Figs. 278–279).

The clasping cercus of some taxa of Clinocerinae (Fig. 293) is not homologous with the clasping cercus in the above taxa. The cercus in Clinocerinae is unmodified in basal genera (Fig. 294) and the clasping component results from the subdivision of the true cercus (Sinclair 1995a). The genus *Proclinopyga* is a pivotal taxon in this respect, in that the cercus is only partially subdivided and clearly shows the true origins of the clasping component in higher Clinocerinae.

114. *Cercus position and orientation*. Posterodorsal, held somewhat horizontally or obliquely (0); dorsal, held horizontally (1); anterodorsal, held upright (2).

In an unrotated position, the cercus is primitively positioned dorsolaterally to the epandrium (Figs. 262, 266, 270, 274). In state 1, the cercus is held dorsally, lying on the top of the hypopygium. This condition occurs in some Empidini and some Hemerodromiinae (Figs. 280, 288). In state 2, the cercus is held upright in a near vertical position, primarily the result of the upturned hypopygium. This form characterizes the

terminalia of the Hilarini (Fig. 286), and some Clinocerinae (Fig. 293) and Chelipodini.

Immature stages

Characters based on immature stages were included, despite the unavailability of several critical empidoid and cyclorrhaphan groups, such as *Homalocnemis*, *Iteaphila*, Atelestinae and *Opetia*. Characters of the immature stages were scored based on the genus chosen as an exemplar. If the immature stages were unknown, the character was scored as a question mark (?).

115. *Final instar mandible*. Two components (0); single component (1); four to six components (2).

The larval mandible of lower Brachycera is subdivided into two components, a distal hook and basal sclerite. From this plesiomorphic condition, the derived condition of the larval mandible comprises four components: distal hook, two connecting sclerites and a ventral sclerite (Dyde 1967; Sinclair 1992, character 21). Despite limited knowledge about immature stages, a four-component mandible has been considered a synapomorphy of the Empidoidea (Sinclair 1992). The larvae of some Hemerodromiinae and Clinocerinae are further divided into six components (Vaillant 1952, 1953; Sinclair 1992). This hypothesis appears reasonable given that the larval mandible of several basal lineages (e.g., *Oreogeton*) as well as in more advanced groups (such as Tachydromiinae and Dolichopodidae) have been examined.

The mandible of final instar cyclorrhaphous larvae is composed of a single component (character state 1), presumably derived from the two-component mandible of lower Brachycera (Sinclair 1992).

Despite claims to the contrary (Griffiths 1994), we continue to view the mouthhooks of orthorrhaphous and cyclorrhaphous larvae as mandibular in origin. Griffiths (1994) proposed that either (a) the mandible is lost in all Brachycera or (b) the mandible is lost in Eremoneura. However, two morphological landmarks argue strongly in favour of the mandibular origin of the brachyceran mouthhooks. Firstly, there is a campaniform sensillum near the epicondyle on the adoral surface of the basal sclerite of the Brachyceran mouthhook. This sensillum is also observed in a similar position on the mandible of many nematoceros Diptera and the Nannochoristidae (Mecoptera) and led Sinclair (1992) to conclude that the presence of this sensillum on the mandible was likely a ground plan plesiomorphy of Diptera. Secondly, the number of apodemes arising on the mouthhooks supports their mandibular origin. In nematoceros Diptera, Mecoptera, and Siphonaptera, the maxilla possesses at most a single apodeme (Matsuda 1965). If the mouthhooks were maxillary in origin, then the three apodemes present in orthorrhaphous Brachycera (Courtney *et al.* 2000, figs. 62, 69, 70) would require the gain of two apodemes. Furthermore, if the mandibles were lost in Eremoneura, at least one additional muscular apodeme would have to be gained. On the basis of the above evidence, it is much more

parsimonious to consider that both mandibles and maxillary structures are present in the ground plan of the Brachycera.

The embryological evidence cited by Griffiths (1994) is far from convincing. It is true that embryological studies have shown that the mandibles are apparently derived from the maxillary area of the blastoderm of *Drosophila*. But as indicated by Cumming *et al.* (1995, character N), the mandibular anlage is extremely complex and difficult to interpret (e.g., both the pharyngeal filter and ventral cornu are also indicated as derivatives of the mandibular lobe area). This is presumably due to the involution and profound reorganization of the head region in cyclorrhaphan larvae (see Jürgens *et al.* 1986). It is possible that the mouthhooks are composite structures, where the apical portion is of maxillary origin (Courtney *et al.* 2000). An elegant review of the origins of the mouthhooks in Cyclorrhapha is presented in Courtney *et al.* (2000).

116. *Maxilla*. Sclerotized (0); elongate, primarily membranous (1).

In the lower Brachycera, the maxilla is composed of well-defined sclerites, articulated posteriorly with the basal mandibular sclerite. The maxilla of *Eremoneura* is an elongate, primarily membranous lobe, delimited at its base by the antenna (Sinclair 1992).

117. *Cephaloskeleton*. Absent (0); present (1).

The cephaloskeleton that characterizes the larvae of Cyclorrhapha (McAlpine 1989: 1403) is strikingly different from that seen in more primitive Diptera. Although the cephaloskeleton is undoubtedly formed from pre-existing structures, there are no distinct transformation series exhibited in families of the orthorrhaphous Brachycera that appear to lead to the modified condition seen in Cyclorrhapha.

118. *Invagination of head*. Not invaginated (0); invaginated to form an atrium (1).

Refer to Cumming *et al.* (1995, character M) and Courtney *et al.* (2000) for a brief discussion of this character of the Cyclorrhapha. Contrary to de Meijere (1900), the fused maxillae over retracted larval mouthparts in *Lonchoptera* appear to indicate the presence of an atrium in this group (Cumming *et al.* 1995).

119. *Ventral cibarial ridges*. Absent (0); present (1).

In the lower Brachycera and Empidoidea, larvae are mostly predaceous on invertebrates and lack cibarial ridges. In the ground plan of the Cyclorrhapha, ventral cibarial ridges function as sieves for concentrating suspended nutrients (McAlpine 1989). See Sinclair (1992, character 23) for further details.

120. *Shape of larval hypopharyngeal sclerite*. Rectangular (0); V-shaped (1).

The primitive rectangular condition occurs in the Tabanomorpha and Asiloidea, whereas a V-shaped hypopharyngeal sclerite (or intermediate sclerite *sensu* Courtney *et al.*

2000) homologised by the position of the salivary duct, is present in the Empidoidea and basal Cyclorrhapha (Sinclair 1992, character 20).

121. *Pupa*. Free (0); enclosed by hardened cuticle of the last instar larva (puparium) (1).

A hardened puparium is characteristic of the Cyclorrhapha and is presumably independently derived within the Stratiomyomorpha (McAlpine 1989; Sinclair 1992). Lack of abdominal plaques (see character 67 above) in *Opetia* is an indirect indicator that the unknown larva of this basal cyclorrhaphan group also pupates inside a puparium (although it has still been scored as a ?).

122. *Pupal respiratory organ*. Not projecting through puparium (0); projecting through puparium (1).

The respiratory organs project through the puparium in Cyclorrhapha, exclusive of Platypezidae (and probably Opetiidae). See Cumming *et al.* (1995, character X) for references.

Characters not included in cladistic analysis

Upper eye facets.

Enlarged upper facets are normally associated with holoptic males and scored as a derived character by Yeates (1994). In the Empidoidea, only a few taxa with holoptic males lack enlarged facets (e.g., *Hormopeza*, *Schistostoma*). Because three of four outgroup taxa include holoptic males with enlarged facets, the computer analysis assigned the enlarged condition as plesiomorphic. Given its link with the holoptic condition in the exemplars chosen, the facet size character was removed because in the analysis it essentially doubled the weight of the dichoptic condition.

Palpal sensory pit.

The sensory pit on the palpus was discussed by Yeates (1994). This pit occurs in a number of Empidoidea, including *Hormopeza* (Fig. 122; Tuomikoski 1960, fig. 1d), *Hilara* (Fig. 116), *Bicellaria* (Fig. 120) and *Microphorella* (Colless 1963, fig. 1d; Shamshev & Grootaert 2004). It appears to have been lost frequently among genera and perhaps species and is usually only visible in dissected, cleared heads. Thus it is considered highly homoplasious and not useful for higher classification analyses.

Apical flagellomeres shortened, much shorter than first flagellomere.

This character has been used to define the Oedaleini (Fig. 25; Tuomikoski 1966). Although a useful diagnostic character, it is unfortunately not universal outside the Palearctic Region. Some Nearctic species of *Anthalia* Zetterstedt are known to have much longer apical flagellomeres (see Steyskal & Knutson 1981, fig. 47.48). Consequently this character was not used in this analysis.

Antennae inserted high on face.

This character was used by Hennig (1971) and Wiegmann *et al.* (1993) in their higher classification analyses, but we found it to be too variable to be useful at this level. We agree with Ulrich (1991) that this character should be limited to analyses of a few lineages, where it may be of greater value.

Paraphyses connected ventrally by transverse bar (H-shaped)

The paraphyses of the labium are connected ventrally by a transverse bar or strut within the hybotid lineages (Krystoph 1961). This transverse strut occurs in *Hybos*, *Stenoproctus* and *Oedalea*, and appears to be membranous in *Bicellaria*. It is absent in *Platypalpus*, *Anthalia*, and *Euthyneura* Macquart (Krystoph 1961). This character requires further investigation in all genera, but given its inconsistent distribution, it may be more useful in generic level analyses.

Dorsocentrals reduced to row of distinct bristles

The reduction of the dorsocentral bristles to a row of 5–10 distinct bristles has occurred numerous times within the lower Diptera, and thus this character is viewed as highly homoplasious.

Anterodorsal and posterodorsal tibial bristles

The presence or absence of leg bristles is highly variable in such a diverse group as the Empidoidea. Although it is proposed as a ground plan feature of the Dolichopodidae (Bickel 1994), it is probably more useful below the family level.

Hind tibia clavate or expanded laterally

The hindlegs of some Atelestinae (Fig. 188), microphorines, and some hybotids are quite similar in form and resemble the hindlegs of some Platypezidae. As pointed out by Chvála (1983), they are likely to have evolved independently in each group. The inconsistent presence of this character within genera made it very difficult to code in an all taxon study. Wiegmann *et al.* (1983) used this and the following character in their analysis.

Hind first tarsomere enlarged, flattened, broader than mid first tarsomere.

This character was omitted from the analysis because of the following observations. (1) Often the male hind first tarsomere is more strongly expanded, although in females it remains enlarged compared to the mid first tarsomere. (2) The size of the expanded tarsus varies between species; see comments on *Acarteroptera* by Collin (1933, p. 34). (3) It is present in various forms in a great diversity of taxa including *Bicellaria*, *Heterophlebus*, *Homalocnemis*, *Schistostoma*, Atelestinae (Figs. 187–188), Platypezidae, *Microphor holosericeus* (Meigen) (but not *M. pilimanus*), *Syndyas* Loew, *Afrohybos* Smith. (4) Differences in the cross-sectional aspect require further comparison. Thus this character appears to be highly variable in form and subject to considerable homoplasy.

Acropod

The structure of the acropod has been investigated by Röder (1984, 1986). He interpreted the empodium as a median process of the unguitactor plate. This is however not homologous to the median lobe (or mediolobus) of lower orthorrhaphous Brachycera, where it is derived from the membranous area distal to the unguitactor plate, and hence should not be termed an empodium. The mediolobus is possibly plesiomorphic based on similar lobes in Anisopodidae and Bibionidae (Röder 1984), or it may be independently derived in the lower Brachycera, supporting the monophyly of the Homeodactyla (Stuckenberg 2001). In Mecoptera, this median lobe is termed the arolium and a homologous lobe is also present in the Tipulidae (Röder 1986). The mediolobus and arolium are probably homologous, although the ultrastructure of the ventral surface and shape of the lobe greatly differs (Beutel & Gorb 2001).

The structure of the pulvillus and empodium is quite variable in Empidoidea, but well worth investigation. A “pulvilliform” empodium has traditionally been used as a diagnostic character of the Clinocerinae (see Sinclair 1995a), but its interpretation and homology in other empidoids is problematic. There is great variation in the size of the empodium and length and density of its ventral setation. In addition, interpretation is only possible through detailed studies using scanning electron microscopy and slide-mounted material. Very few illustrations exist for the structures of the acropod in Empidoidea, e.g., Röder (1984, figs. 70–73) and Sinclair (2000b, figs. 3,4). Although the empodium of Ceratomerinae, some species of *Hilara*, some species of *Rhamphomyia* (e.g., *Megacyttarus* Bigot), and some genera of the Trichopezinae and the Dolichopodidae (e.g., *Liancalus* Loew) could also be interpreted as possessing “pulvilliform” empodium, this is simply based on the presence of ventral pubescence. Detailed descriptions are necessary for more accurate interpretation of homology among these groups.

In addition, the structure of the pulvillus itself is also variable, especially in Clinocerinae, where the ventral surface can be divided into a series of plate-like segments (Sinclair 2000b).

Results of the Cladistic Analysis

The parsimony analysis of the character state matrix (Table 2) using the program PAUP* (Swofford 2002) generated 1728 most parsimonious trees, each with a length = 574, CI = 0.34, CI excluding uninformative characters = 0.34, RI = 0.72, and RC = 0.24. The strict consensus of these 1728 most parsimonious trees is illustrated in Trees 1–2. *A posteriori* character weighting using successive approximations according to the rescaled consistency index (RC) produced a single tree, which was one of the 1728 most parsimonious cladograms (Trees 3–6).

Higher-level relationships

Eremoneura, Empidoidea, and Cyclorrhapha monophyly

The monophyly of the Eremoneura is reconfirmed (Trees 1,3), supported by the following uniquely derived character states (character number in brackets): shortened cell cup (60.1), gonostylus absent (98.1), presence of a completely sclerotized subepandrial sclerite (107.1), larval maxilla elongate and membranous (116.1), and V-shaped hypopharyngeal sclerite (120.1). This is not surprising given that some 13 convincing synapomorphies have been proposed for this lineage (see Yeates & Wiegmann 1999). Bremer support (3) was considered relatively high given the number of convergent characters that occur between the lower Cyclorrhapha and Empidoidea. Collins & Wiegmann (2002a) have also resolved a monophyletic Eremoneura, although bootstrap support was not high. Moulton & Wiegmann (2004) resolved the Eremoneura with robust support.

The monophyly of the Empidoidea is also reconfirmed (Trees 1–3), although Bremer support (1) was low. This lineage was supported on the basis of a four to six component final instar larval mandible (115.2). Additional homoplasious character states include: dorsal and ventral sclerites of the metepisternum well separated (33.3), fore tibial anteroapical comb present (45.1), hind tibia posteroapical comb present (46.1), CuA₂ recurved (61.2), alula reduced (66.1), single spermatheca (75.2), ejaculatory apodeme lever-like (102.1). Molecular studies range from moderate to robust support for the Empidoidea (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004).

As stated in recent molecular analyses (Collins & Wiegmann 2002a,b; Moulton & Wiegmann 2004), the monophyly of the Cyclorrhapha (Trees 1,3) is robustly supported (Bremer support = 8). Uniquely derived morphological synapomorphies include: abdominal plaques absent (67.1), male segments 7 and 8 twisted through to 180° (72.3), male terminalia circumverted (89.3), as well as several unique characters of the immature stages, namely single component larval mandible (115.1), presence of a cephaloskeleton (117.1), head invaginated to form atrium (118.1), ventral cibarial ridges present (119.1), and last larval instar forming a puparium (121.1).

Cyclorrhaphan relationships

Although cyclorrhaphan relationships are not the primary focus of this study, the analysis (Trees 1,3) generally supports the cladogram of the basal lineages of Cyclorrhapha depicted by Cumming *et al.* (1995), even though that analysis was based on a more limited set of characters. The current analysis still places Opetiidae as the most basal lineage of the Cyclorrhapha rather than as a member of (or the sister group to) the Platypezidae (McAlpine 1989; Zatwarnicki 1996; Moulton & Wiegmann 2004), or as the sister group of the Lonchopteridae (Collins & Wiegmann 2002b). As proposed by Cumming *et al.* (1995), a sister group relationship of Lonchopteridae with the Phoroidea (represented here by the single exemplar *Sciadocera*) continues to be supported (Bremer

support = 3), as is the relationship of this entire lineage with the Syrphoidea and Schizophora, represented by the exemplars *Syrphus* and *Strobilomyia* respectively (Bremer support = 2). Resolution of the relationships among these three major cyclorrhaphan clades (i.e., Lonchopteridae + Phoroidea, Syrphoidea, and Schizophora) will require more extensive taxon sampling and the addition of characters of greater relevance within Cyclorrhapha, particularly the very diverse Schizophora.

Empidoid relationships

This analysis resolves five families within the Empidoidea [i.e., Empididae, Atelestidae, Hybotidae, Brachystomatidae (see Proposed Classification of the Empidoidea), Dolichopodidae], with *Homalocnemis*, *Oreogeton* and the *Iteaphila* group assigned as *incertae sedis*. The phylogenetic relationships or family divisions proposed herein (Tree 2) are similar to Cumming *et al.* (1995), but differ significantly from those hypothesized by Chvála (1983, fig. 140), Wiegmann *et al.* (1993) and Collins & Wiegmann (2002a). The differences relate to the recognition of the Brachystomatidae and the transfer of several subfamilies from the Empididae. Representatives of the Brachystomatidae were not included in the study of Moulton & Wiegmann (2004).

The interfamilial relationships among the Empidoidea estimated in this study are only partially resolved and included a large basal polychotomy in the strict consensus tree (Trees 1,2). In the successively weighted tree there is greater resolution (Trees 3–6), allowing some tentative relationships to be estimated and discussed. The basal interrelationships were also not well supported by molecular data (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004) and further studies will be required to address these phylogenetic problems.

In this study, the Empidoidea exclusive of *Homalocnemis* and *Iteaphila* group (Trees 2,3) were supported on the basis of the following homoplasious character states: epipharyngeal blades present (16.1), epipharyngeal carina present (18.1), palpi straight (22.1), and costal bristle present (49.1). Only the presence of epipharyngeal blades is convincing. *Homalocnemis* is clearly predaceous, yet lacks these blades, which are found in all other known predaceous empidoids. The *Iteaphila* group are flower-visiting empidoids and the only other flower visitors that also lack blades are *Brochella* and Atelestidae (see Reflections on feeding habits and ground plan condition).

The Empididae + Brachystomatidae + Dolichopodidae + Atelestidae + Hybotidae clade, exclusive of the genus *Oreogeton* (Trees 2,3), is weakly supported on the basis of two homoplasious character states: face flat (4.1) and surstylus weakly articulated (109.1). Both characters are not very convincing and consequently *Oreogeton* remains a difficult genus to assign in the Empidoidea. Although the male terminalia is somewhat similar to *Niphogenia* and an undescribed clinocerine genus from New Zealand, perhaps these similarities are based on symplesiomorphies.

Support for the sister pairing (Empididae + (Brachystomatidae + Dolichopodidae)) is very weak with the characters mostly pertaining to the form of the wing and the condition of male eyes (Tree 3). The presence of a precoxal bridge (30.1) is somewhat homoplasious, with losses in *Philetus*, Microphorinae, and some other genera. Additional characters are required to confidently assess this relationship.

The family Empididae was not resolved in the consensus tree (Trees 1,2) and on the successively weighted tree (Tree 4) is only supported by the homoplasious character state, dorsal mesepimeral pocket present (31.1). This character state is also a synapomorphy of the Ceratomerinae + Trichopezinae clade (Tree 5). Further study specifically focused on the Empididae may help to better define this family.

The Brachystomatidae + Dolichopodidae clade (Trees 2,5) was supported by a number of characters, but with low Bremer support (1). This group is supported by a single uniquely derived character state, sclerites of female segment 8 articulated or fused (80.1). Sinclair (1995a) first proposed this unique arrangement of sclerites as a synapomorphy. Additional support for this clade is found in the following homoplasious character states: acanthophorites present, with spines arranged in a row (82.0, reversal), female cercus heavily sclerotized (85.1), and female cercus prolonged and pointed apically (86.2). The presence of acanthophorites at this level of the Empidoidea clearly indicates that their form is not homologous with those found in the Asiloidea. This sister pairing (Brachystomatidae + Dolichopodidae) was not resolved in the data set of Collins & Wiegmann (2002a).

The Dolichopodidae *s.lat.* are very strongly supported, with high Bremer support (10) (Trees 2,5). The close relationship of the microphorids with the dolichopodids has long been hypothesized (Colless 1963; Hennig 1971). This clade is also supported by most molecular data, usually with fairly high degree of confidence (Collins & Wiegmann 2003a). This grouping is supported by two uniquely derived character states: male terminalia rotated between 90–180° and lateroflexed (89.2) and bacilliform sclerites fused to hypandrium (108.2). In addition, the following are among the homoplasious character states supporting this group: apical antennal mechanoreceptor absent (8.1), clypeal ridge removed from labrofulcral articulation (13.1), lower metapleural arm long and narrow (34.1), R_s near humeral vein (55.1), basal cells shortened (62.1), apical female segments 6–10 retracted (68.3), male tergite 7 bare (70.1), male segment 7 tubular (72.1), female tergite and sternite 10 articulated (83.1), and male terminalia asymmetrical (88.2).

The Atelestidae and Hybotidae are resolved (Bremer support = 3) as sister groups in all of the equally parsimonious trees (Trees 1,2,6). This sister group relationship was also suggested by Hennig (1970, 1971) and Chvála (1981) and is supported by the following homoplasious character states: scape bare (5.1), costa ending near the first M vein (50.2), subcosta incomplete (51.1), R_{4+5} unbranched (56.1), CuA_2 truncate (61.1), postgonites absent (99.0), ejaculatory apodeme rod-shaped and continuous with phallus (102.2). Molecular analyses consistently assign the Atelestidae as the sister group to the remaining

Empidoidea (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004), but if the Atelestidae (including also *Nemedina*) are moved into this basal position with the program MacClade 4 (Maddison & Maddison 2003) using our character state matrix (Table 2), the cladogram tree length is increased by six extra steps (length = 580), which we regard as a considerable increase. In addition, the sister group of the Hybotidae remained uncertain in the molecular analyses of Collins & Wiegmann (2002a).

The morphological phylogenies of Chvála (1983) and Wiegmann *et al.* (1993) both hypothesized a sister group relationship between the Hybotidae and the Microphoridae + Dolichopodidae clade, based on characters we consider too generally defined, highly homoplasious, or incorrectly scored.

The Atelestidae, including the genus *Nemedina* (Trees 2,6), are resolved with strong Bremer support (3), as was suggested by Sinclair & Shamshev (2003) and Sinclair & Papp (2004). The family group is strongly supported on the basis of two unique character states: hypandrium shorted (90.3) and gonocoxal apodeme greatly lengthened and slender (95.1). Additional supporting character states include: absence of epipharyngeal blades (16.0), M_2 absent (58.1), and female tergite 10 absent (84.2).

The Hybotidae remain a robustly supported family with high Bremer support (5) (Trees 2,6). This family has been widely recognized by empidoid workers since Chvála (1983) and Chvála & Kovalev (1989). Uniquely derived character states include: presence of a palpifer (24.1), tibial gland present (47.1), and male terminalia rotated between 45–90° (89.1). Additional support also include: apical mechanoreceptor bristle-like (8.2), lacinia absent (20.1), metasternal apophysis rod-shaped (36.2), gonocoxal apodeme confined to anterior margin of hypandrium (94.1), and apex of phallus with hood-like cap (104.2).

Lower-level relationships in Empidoidea

The empidoid relationships below family-level are highlighted in this section. The proposed relationships in this study differ significantly from Chvála (1983), Wiegmann *et al.* (1993) and Collins & Wiegmann (2002a), especially concerning the clades included in the Empididae (see Collins & Wiegmann 2002a, for review). The differences stem not from conflicting views concerning morphological homologies as stated by Collins & Wiegmann (2002a), but from the inclusion of many new characters, especially of the female terminalia (where there is no homology controversy). We feel these new morphological characters greatly enhance our understanding of the phylogeny and evolution of the Empidoidea and will ultimately lead to greater acceptance by co-workers of the proposed empidoid relationships. Our confidence in these hypothesized relationships is further strengthened by the diverse taxon sample that we used in this study.

Empidid relationships

The relationships within the Empididae remain rather tentative and require urgent study. With the removal of the ceratomerines and brachystomatines as proposed by Sinclair (1995a) and Cumming & Sinclair (1995), only the subfamily Hemerodromiinae [foreleg held far forward, raptorial with ventral spines (42.1, 43.1, 44.1)], maintains any sort of robust support (Trees 2, 4). The Hemerodromiinae are assigned as the sister group to the Empidinae on the basis of an upcurved phallus (103.1) and epandrial lamellae widely separated (105.3). The latter character is especially convincing, occurring presumably convergently in Ceratomerinae and the parathalassiines. The Clinocerinae were the best-supported empidid subfamily in the study of Collins & Wiegmann (2002a), but are only weakly supported in this study. This subfamily is supported on the following homoplasious character states: pubescent eyes (2.1), labellum held at right angles (25.1), erect costal spines (52.1).

The Empididae are divided into two major clades in the successively weighted tree (Tree 4), on the basis of a new character state: the form of the proctiger (111.1), where the cercus, hypoproct and subepandrial sclerite combine to form complex clasping structures, replacing the surstylus. The Empidinae is weakly supported on the basis of the costa ending near R_{4+5}/R_5 (50.1) (reversal in Hilarini), female tergite 10 undivided (84.1), and male cercus weakly sclerotized (113.0). Within this subfamily, the Empidinae (exclusive of *Edenophorus*) are convincingly supported by strongly upcurved palpi (22.2). The Empidini are paraphyletic and must be redefined, whereas the Hilarini remain a distinct group and a robustly supported tribe (Bremer support = 4) primarily on the basis of an enlarged male fore basitarsomere (48.1) and R_1 thickened (54.1) (Trees 2,4).

The *Ragas* group is here placed in the Empididae, but this assignment requires further investigation. Formerly, Sinclair (1999) left this genus group unplaced in the Empidoidea. The assignment of the *Ragas* group, *Brochella*, and *Philetus* in the Empididae, and the *Iteaphila* group and *Oreogeton* as *incertae sedis* in Empidoidea, clearly demonstrates that the subfamily Oreogetoninae is a paraphyletic assemblage, justifying its lack of recognition. In addition, Collins & Wiegmann (2002a) did not recover a monophyletic Oreogetoninae in their combined analyses.

Brachystomatid relationships

All three subfamilies are resolved as monophyletic, although the Trichopezinae are indicated as paraphyletic in the consensus tree (Tree 2). Collins & Wiegmann (2002a) also frequently recovered this clade (although usually including *Hesperempis*) and felt confident that it represented a natural group, even though it had low bootstrap support.

The subfamily Brachystomatinae is well supported (Bremer support = 5) by two uniquely derived character states (Trees 2, 5): spermathecal receptacle coiled (77.2) and male cercus articulated to epandrium (112.1). An additional supporting character is an H-shaped stipes (19.1).

The Trichopezinae + Ceratomerinae are assigned as sister groups (Tree 5) on the basis of acanthophorite spines scattered over tergite 10 (82.2) and the presence of a dorsal mesepimeral pocket (31.1). The Ceratomerinae are well supported on the basis of an elongate scape (6.1), conus present (7.1), and epandrial lamellae not connected (105.3). The Trichopezinae were not resolved in the consensus tree (Tree 2) and remain one of the more weakly supported subfamilies, defined on the basis of a single derived character state (Tree 5), female tergite 8 with median apodeme (78.1). With further study this lineage may be found to be paraphyletic in relation to the Ceratomerinae.

Dolichopodid s.lat. relationships

The Microphoridae *sensu* Chvála (1983) are paraphyletic in relation to the Dolichopodidae *s.str.* and consequently no longer recognized. As a result, the concept of the dolichopodids has been expanded to formally include the subfamilies Microphorinae and Parathalassiinae (Trees 2, 5). The Microphorinae remains a very weak group, defined on several unconvincing character states, which include three reversals: holoptic males (1.0), prosternum separate (30.0), metasternal apophysis rod-shaped (36.2), and anal lobe acute (65.0). Since no parathalassiines were included in the analysis of Collins & Wiegmann (2002a), an accurate assessment of the monophyly of the Microphoridae *sensu* Chvála (1983) by them was not possible.

The Parathalassiinae and Dolichopodidae *s.str.* are clearly demonstrated as forming a monophyletic group (Trees 2,5), with high Bremer support (10), based on the following character states: clypeal ridge perpendicular and broad (12.1), lacinia absent (20.1), six pseudotracheae present (26.1), pseudotracheal form geminate (although modified within various groups) (27.1), prothoracic presternum enlarged ventrally (29.1), intersegmental ridge with two pockets (32.1), upper metapleural arm rod-shaped (35.1), and metasternal furca with posteroventrally directed tip (36.1). We consider the pseudotracheal characters, both first proposed by Sinclair & Cumming (1998), very convincing.

The Dolichopodidae *s.str.* are unquestionably a monophyletic lineage (Trees 2,5) with very high Bremer support (12), defined by a long list of apomorphies that include: epipharyngeal blades very stout and sharply pointed (16.2), epipharyngeal carina lengthened into head (18.2), costa ending near M_1/R_{1+2} (50.2), costa with double row of spine-like setae (52.3), sclerotized rectal papillae present (73.1), female with five pairs of abdominal spiracles (74.1), male hypopygium asymmetrical (88.3), hypandrium prolonged apically (90.1), hypandrium and epandrium broadly fused (91.1), and hypopygial foramen present (106.1).

Atelestid relationships

This family is divided into two subfamilies, Nemedinae and Atelestinae (Trees 2,6). The subfamily Nemedinae is a newly recognized clade, which includes a single extant genus, readily recognized by its unique, derived venation (see Proposed classification of

the Empidoidea). Additional characters include: metepisternum divided into two sclerites (33.2), metasternal apophysis rod-shaped (36.2), and cell dm absent (59.1).

The Atelestinae are a robustly supported group in most molecular data sets (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004). The subfamily is also well supported in this study on the basis a U-shaped male tergite 8 (71.3) and subapical surstyli (110.1).

Hybotid relationships

The relationships within the Hybotidae (Trees 2, 6) remain mostly uncertain and similar inconclusive results were also found by Collins & Wiegmann (2002a). The subfamily Trichiniinae requires further clarification concerning its monophyly, particularly since it is clearly paraphyletic in our results. The two genera are assigned together in this subfamily mostly for convenience. The genus *Trichinomyia* is hypothesized to be the sister group to the remaining Hybotidae on the basis of its symmetrical male hypopygium. All other exemplars included this analysis were considered to be either slightly to distinctly asymmetrical (88.1).

Following Sinclair & Cumming (2000), the newly refined Ocydromiinae forms a well-supported monophyletic group on the basis of a flexible, articulated apical phallus (104.1) and fully articulated surstyli (109.2). The presence of the bilobed hypandrium (90.2) characterizes the *Trichina* + ((Oedaleinae + Tachydromiinae) + Hybotinae) clade, although it is apparently secondarily absent in the Tachydromiinae. The presence of a single ventral apodeme (97.2) and presence of postgonites (99.1) supports the clade (Oedaleinae + Tachydromiinae) + Hybotinae (Tree 6). The Oedaleinae and Tachydromiinae are hypothesized as sister groups on the basis of the right postgonite fused to the hypandrium (100.1). Since only a single representative of the Oedaleinae was included in this study, we can't comment on the monophyly of this subfamily, although the fusion of tergite 10 with the female cercus (84.3) is likely synapomorphic. In molecular studies, this lineage appears to be robustly supported (Collins & Wiegmann 2002a). The subfamily Tachydromiinae is well-supported morphologically (Bremer support = 3), on the basis of the following homoplasious character states: pseudotracheae absent (26.2), pterostigma absent (53.1), M_2 absent (58.1), cell dm absent (59.1), hypandrium lacking apical lobes (90.0), and ejaculatory apodeme secondarily lever-like (102.1). The concept of the Hybotinae is herein expanded to include the new tribe Bicellariini, based on the presence of holoptic females with facets enlarged (3.1). The tribe Hybotini is defined on the basis of the clypeal ridge removed from the labrofulcral point of articulation (13.1) and M_2 absent (58.1).

Reflections on feeding habits and ground plan condition

Among adult flies of the lower Brachycera, only Asilidae and Empidoidea are predaceous. In Asilidae, the spear-like hypopharynx alone is used in piercing and paralyzing their prey

(Melin 1923; Adisoemarto & Wood 1975), whereas in the Empidoidea it is the labrum and the epipharyngeal blades that pierce the prey. The prey is often held by the legs in most Empidoidea, except in Dolichopodidae *s.str.*, which use the labella to grasp and hold the prey (Snodgrass 1922; Ulrich 2005). It is this contrasting method of feeding that has led to the conclusion that the predaceous habits in Asilidae and Empidoidea are not homologous and have evolved independently. The only presumably predaceous empidid that lacks epipharyngeal blades is *Homalocnemis* (Fig. 54).

The feeding habits of the Empidoidea were reviewed by Chvála (1983) and Daugeron (1997), and only some overlooked or new data will be mentioned here. Most empidoids appear to be predaceous, especially based on mouthpart morphology. Predatory habits have been reported in most lineages, including the Clinocerinae, Hemerodromiinae and Hybotinae. Stark (1994) reviewed the prey composition and hunting behavior of species of *Platypalpus* (Tachydromiinae). In the Trichopezinae, *Niphogenia eucera* Melander has been observed feeding on insect larvae (Wilder 1981) and *Trichopeza longicornis* (Meigen) has been observed feeding on small midges held by its forelegs (Ulrich 1981). Adults of *Ceratomerus ordinatus* Hardy were observed feeding or scavenging on conspecific flies that were freshly squashed on emergent rocks (Sinclair 2003a). Most members of the Ceratomerinae are considered predaceous, except for a species group from New Zealand that have been collected on flowers (Sinclair 2003a). The predatory habits of the Dolichopodidae *s.str.*, including an extensive list of prey, have recently been reviewed and compiled by Ulrich (2005). Among the Empidinae, a review of the feeding habits of *Hilara* has also recently been published (Plant 2004).

In addition to predaceous habits, flower visitors (pollen and/or nectar feeders) are common among the empidoids. Many species of *Empis*, *Rhamphomyia*, *Anthalia*, and *Euthyneura* are well-known flower visitors (Tuomikoski 1952; Downes & Smith 1969; Chvála 1994; Grimaldi 1999). Since epipharyngeal blades are present in all these genera, it is assumed that flower visiting is secondarily derived. In other empidoids (e.g., *Dryodromia*, *Hesperempis*), epipharyngeal blades appear secondarily fused medially and are non-functional (Fig. 100; Krystoph 1961: fig. 6). Although no direct feeding observations are available, epipharyngeal blades are also absent in Atelestinae and *Nemedina*, which suggests that members of this lineage are also flower visitors. In fact, pollen grains were observed by us in the abdomen of dissected specimens of *Acarteroptera recta* Collin and the microphorine, *Schistostoma armipes* (Melander). Blades are also absent in *Brochella* and the flower visiting genus *Iteaphila* (Figs. 55, 64, 98, 101; Krystoph 1961) and there is no indication of secondary fusion. The lack of blades in primitive taxa such as atelestines and *Iteaphila* may be evidence that flower visiting evolved much earlier in the Empidoidea than has previously been assumed.

Daugeron (1997) optimized feeding habits (predaceous or flower visitor) on the Empidoidea cladogram of Cumming *et al.* (1995). This showed that predation was plesiomorphic or ancestral in Empidoidea, with flower visiting apomorphic for the

Empidinae. At that time, the atelestines were scored as unknown, but flower visiting has been confirmed in at least some atelestines (see above). How would this now affect the result? If optimized on the cladogram of Moulton & Wiegmann (2004: fig. 8a) where the Atelestidae are the sister group to the remaining Empidoidea, flower visiting would be the ground plan condition for the superfamily. However, in the present study optimization of feeding habits on Trees 3–6 corroborates the long standing hypothesis that predation is ancestral in Empidoidea.

Proposed Classification of the Empidoidea

The classification of the Empidoidea is herein revised to reflect the more robust clades supported in our analysis. All new higher empidoid taxa are supported by the relationships shown in the strict consensus tree (Trees 1–2), as are the relationships of most higher taxa. Additional support for the relationships of the higher empidoid taxa is provided by the single tree obtained by successive approximations weighting (Trees 3–6). It is not our intention to review the previous history of the classification of the Empidoidea, as this has been already done most recently by Chvála (1983). All the following family-group names and datings have been taken from Sabrosky (1999) and checked against the original literature. In addition, all extant genera are listed for each higher taxon (except for the subfamilies in the Dolichopodidae *s.str.*), key diagnostic features are given, as well as general information of interest to specific clades. A summary of the proposed classification is presented in Table 3.

Use of the name Empidoidea

Ulrich (1996) has proposed that the superfamily name Empidoidea should be replaced by one reflecting a higher rank on an equal basis with its sister group, the Cyclorrhapha. As has been previously suggested, that name would have to be the unfamiliar designation Orthogenya, first coined by Brauer (1883) to group the “Empididae” with the Dolichopodidae. Despite its unfamiliarity, Griffiths (1972) stressed his preference for Orthogenya, because such names avoid suffices to generic names that must be changed whenever new research causes the relative rankings of groups to be revised. Unfortunately, these names for higher ranks (e.g., Polyneura, Oligoneura) have generally not been accepted, although this may largely reflect a lack of confidence in the definition of the groups that these names represent. However, this is certainly not the case concerning definition of the Empidoidea.

Alternatively, continued use of the name Empidoidea would maintain stability. The name Empidoidea is immediately recognizable to specialists and non-specialists alike, especially among students and general biologists. In addition, changing to Orthogenya could potentially encourage division of the group into lower rankings, including new

superfamilies. Currently, it is certainly not possible to subdivide the Orthogenya into superfamilies, given the uncertainty of the interfamilial relationships based on this study and molecular investigations. We consider it best at this time to maintain use of the term Empidoidea until the interfamilial relationships of the entire group are more clearly understood.

Classification of the Empidoidea

Incertae sedis within Empidoidea

The subfamily Oreoetoninae is a paraphyletic assemblage that is no longer recognized. Some of the former oreoetonine genera are included in the following three clades, which are assigned as *incertae sedis* within Empidoidea.

Homalocnemis Philippi—This genus includes seven species, which are presently confined to former Gondwanan landmasses, and recorded from the following countries: New Zealand, Chile and Namibia (Smith 1967, 1989; Chvála 1991). *Homalocnemis* is predaceous, but epipharyngeal blades are lacking, which suggests that this genus represents one of the most basal extant lineages of the Empidoidea. Collin (1928) assigned this genus to its own subfamily, Homalocneminae and later assigned it to the Brachystomatinae (e.g., Chvála 1983). Sinclair (1995a) subsequently removed *Homalocnemis* from the latter subfamily, but did not suggest an alternative assignment. The status of this genus remains unresolved at present.

Iteaphila group (includes: *Anthepiscopus* Becker and *Iteaphila* Zetterstedt)—This is a flower-feeding lineage that like *Homalocnemis* also lacks epipharyngeal blades. The group appears to include an additional undescribed genus from Australia (Sinclair & Cumming 2000, new genus 2).

Oreoeton Schiner—This is a Holarctic genus that includes some 12 described species. The immature stages of this genus are aquatic (Sommerman 1962). *Oreoeton* is placed as the most basal empidoid lineage that possesses epipharyngeal blades (character 16.1) in the single tree obtained by *a posteriori* character weighting using successive approximations (Tree 3).

Empididae

Empides Latreille, 1809: 189, 191. Type genus *Empis* Linnaeus, 1758.
Empididae Giebel, 1856: 206.

The definition of the Empididae in this study is more restrictive than in previous classifications. The family is recognized on the basis of the following suite of characters (see also below—Key to Families and unplaced Genus Groups of Empidoidea): Vein R_{4+5}

normally branched, prosternum enlarged forming precoxal bridge, laterotergite usually with setae, male terminalia often with clasping-like cerci or hypandrium laterally flattened or keel-like, female terminalia usually telescopic with simple cerci. No distinct apomorphy is known to define this diverse lineage and further studies on the relationships of all genera in this family are urgently required. This family includes the following generic groupings, tribes and subfamilies:

Incertae sedis within Empididae

Ragas group (includes: *Dipsomyia* Bezzi, *Hormopeza* Zetterstedt, *Hydropeza* Sinclair, *Ragas* Walker, and *Zanclotus* Wilder)—This genus group of predaceous empidoids was clearly defined by Sinclair (1999) and is mainly characterized by the recurved labrum and apical epipharyngeal comb. The single tree obtained by *a posteriori* character weighting using successive approximations, placed this lineage and *Brochella* in the Empididae as the sister group to the Clinocerinae (Tree 4) primarily on the basis of the presence of a dorsal mesepimeral pocket (character 31.1), reduction of antennomere 10 (character 8.1), and a slender male tergite 8 (character 71.1). However, because of the degree of homoplasy associated with the last two characters in particular, and until the relationships and definition of the entire Empididae are better resolved, the phylogenetic assignment of the *Ragas* group will continue to remain uncertain.

The postpedicel of *Hormopeza* possesses a pair of sensory pits (Fig. 8; Tuomikoski 1960, fig. 1e), which are also very similar in form to those observed in the platypezid genus *Microsania* (Fig. 47). Both genera are commonly known as smoke flies and it is assumed that these pits and inner glands are used in the detection of smoke. Large swarms of both taxa have been observed in smoke from wood fires (see Sinclair 1995b and Bickel 1996b for references). Swarms of *Hormopeza* usually consist of equal numbers of both sexes, whereas swarms of *Microsania* consist almost entirely of males.

It has always been assumed that these flies use smoke as an aggregating queue to concentrate both sexes in an area that has been burned over by fires. It is also assumed that certain fungi, which grow only on fire-scarred wood function as hosts for *Microsania* larvae (Kessel 1989: 180). But the immature stages of both taxa remain unknown. It is possible that the smoke from fires does function as an aggregating queue, but mostly to attract the flies to fresh oviposition sites as has been observed for long-horned beetles (Cerambycidae), where great numbers swarm about forest fighting crews battling fires in Ontario (Carney 1999). It is possible that *Hormopeza* and *Microsania* also oviposit into the freshly damaged trees. This is a breeding habitat that should be more fully explored.

Brochella Melander—This monotypic genus is an odd unique taxon that occurs in the Cascade Mountains of the western Nearctic Region. *Brochella* is possibly a flower visitor on the basis of its mouthpart morphology. The single tree obtained by *a posteriori* character weighting using successive approximations, placed this genus with the *Ragas* group in the Empididae, as the sister group to the Clinocerinae (Tree 4). However, the

phylogenetic assignment of *Brochella* will remain uncertain, until the relationships of the Empididae are better resolved.

Philetus Melander—This genus includes two species confined to western North America. Very little is known of this genus and most specimens have been sporadically collected. Recently, one species was collected in large numbers during a canopy study of wet temperate rainforests on Vancouver Island (BC, Canada; specimens in CNC).

Hesperempis group (includes: *Dryodromia* Rondani, *Hesperempis* Melander, and *Toreus* Melander)—This genus group represents another flower-feeding lineage and possibly also includes an undescribed Australian genus. The thoracic chaetotaxy is reduced in all genera, and the bristles are pale white to yellowish.

Empidinae

Schiner (1862: lii) was apparently the first author to recognise the subfamily Empidinae, and also the first to arrange the empidids into five subfamilies (from Chvála 1983: 54). This subfamily is defined by the following suite of characters: palpi normally strongly upcurved, broad wings (anal lobe usually developed), forelegs not raptorial, empodium usually bristleform. Cumming (1994) hypothesized that presentation of nuptial gifts to females by males, correlated with loss of hunting ability in females, might represent two additional synapomorphies of the Empidinae (or at least a portion of the subfamily), although mating behaviors of the more plesiomorphic genera, such as *Edenophorus*, *Empidadelpha* and *Sphicosa*, are presently unknown. The Empidinae includes the following tribes:

Empidini

Collin (1961: 326) was perhaps the first worker to separate the Empididae into two tribes. This tribe is presently undefined and undoubtedly paraphyletic and presently simply a dumping group for all genera not assigned to the Hilarini. This lineage is distinguished from Hilarini on the basis of a setose laterotergite, cercus enlarged and functioning as a clasping organ, costa usually ending at or just beyond R_{4+5} , vein R_1 of constant thickness and male tarsomere 1 of foreleg rarely enlarged (Bickel 1996a). The Empidini includes the following genera: *Clinorhampha* Collin, *Empidadelpha* Collin, *Empis* Linnaeus, *Hystriichonotus* Collin, *Lamprempis* Wheeler and Melander, *Macrostomus* Wiedemann, *Opeatocerata* Melander, *Porphyrochroa* Melander, *Rhamphella* Malloch, *Rhamphomyia* Meigen, and *Sphicosa* Philippi (Smith 1980; Chvála & Wagner 1989; Rafael & Cumming 2004).

Edenophorus Smith was originally assigned to the Microphorinae when male specimens were not known. It was later transferred to the Ocydromiinae (Chvála, 1981), but males still remained unknown. Ulrich (1994) believed it showed affinities to the Empididae *sensu* Chvála (1983). Male specimens were identified by Sinclair (2002), confirming its assignment to the Empidinae. However, on the basis of the absence of

strongly arched palpi, *Edenophorus* is excluded from the clade comprising *Empidadelpha*, Empidini and Hilarini (Sinclair 2002). It is tentatively assigned herein to the Empidini until a better definition or diagnosis of this tribe is made available.

Hilarini

Hilarini Collin, 1961: 326. Type genus *Hilara* Meigen, 1822.

The tribe is well defined on basis of laterotergite usually bare, cercus usually small and desclerotised, hypandrium usually forming a keel-like hood over the phallus along the posterior margin, costa usually circumambient, R_1 thickened before it joins the costa and male tarsomere 1 of foreleg enlarged (Bickel 1996a). The following genera are included in the Hilarini: *Afroempis* Smith, *Allochrotus* Collin, *Amictoides* Bezzi, *Aplomera* Macquart, *Atrichopleura* Bezzi, *Bandella* Bickel, *Cunomyia* Bickel, *Deuteronista* Philippi, *Gynatoma* Collin, *Hilara* Meigen, *Hilarempis* Bezzi, *Hilarigona* Collin, *Hybomyia* Plant, *Pasitrichotus* Collin, *Thinempis* Bickel, and *Trichohilara* Collin (Smith 1980; Cumming 1994; Bickel 1996a, 1998, 2002).

Bickel (1998) considered *Cunomyia* primitive with respect to other Hilarini on the basis of the form of its male cercus and postabdominal structure. The male eyes are separated on the frons in this genus and the upper facets are not enlarged. It is possibly closely related to *Bandella* (Bickel 2002). Members of the *Hilara flavipes* Meigen complex have holoptic males with the upper ommatidia enlarged and Chvála (1999) has considered this the ground plan state based on outgroup comparison with the Empidini. This head morphology is co-related to primitive unmodified small synorchesic swarms.

Hemerodromiinae

Hemerodromiinae Schiner, 1862: li, lii. Type genus *Hemerodromia* Meigen, 1822.

Hemerodromiinae Wheeler & Melander, 1901: 376.

This is one of the most distinctive empidoid subfamilies, characterized by raptorial forelegs well separated from the midlegs and the fore femur bearing at least a single ventral row of stout setae. Some genera possess aquatic larvae, with adults of many genera found on emergent rocks and riparian vegetation of streams and rivers. The larva of *Chelipoda* is terrestrial (Trehen 1969). The Hemerodromiinae is divided into two tribes.

Chelipodini

Chelipodini Hendel, 1936: 1929.

This tribe can be separated from Hemerodromiini on the basis of the long arista more than twice the length of the postpedicel, scutum with well-developed setae, laterotergite with setae and male terminalia reflexed over abdomen (MacDonald 1988). The following genera are included in the Chelipodini: *Afrodromia* Smith, *Chelipoda* Macquart, *Chelipodozus* Collin, *Drymodromia* Becker, *Monodromia* Collin, *Phyllodromia* Zetterstedt, and *Ptilophyllodromia* Bezzi (Smith 1967, 1975, 1980, 1989).

The genus *Cephalodromia* Becker is not an empidoid and is assigned to the Mythicomyiidae (Platypyginae) (see Greathead & Evenhuis 2001). However, the generic assignment of the Taiwan species, *C. pictipennis* Bezzi, requires examination, but it should probably be tentatively assigned to *Chelipoda* until the Chelipodini can be defined on a world basis.

Hemerodromiini

This tribe can be separated from Chelipodini on the basis of the short antennal style less than twice the length of the postpedicel, scutum lacking well developed setae, laterotergite bare and male terminalia erect or projecting posteriorly (MacDonald 1988). The following genera are included in the Hemerodromiini: *Chelifera* Macquart, *Cladodromia* Bezzi, *Colabris* Melander, *Doliodromia* Collin, *Hemerodromia* Meigen, *Metachela* Coquillett and *Neoplasta* Coquillett (Smith 1967, 1975, 1980, 1989).

Clinocerinae

Clinocerinae Collin, 1928: 2, 3, 59. Type genus *Clinocera* Meigen, 1803.

Clinoceratinae Melander, 1928: 10.

The Clinocerinae is a very well defined lineage and one of the few lineages where the phylogenetic relationships of the genera have been evaluated with modern techniques (Sinclair 1995a). A number of genera remain to be described from the Australasian region. The larval habitat of the majority of taxa is considered aquatic, normally streams and rivers with rocky substrates. The most primitive genera dominate the Southern Hemisphere. The subfamily can be identified by the stout, erect costal setae, sucker-like labellum, pulvilliform empodium, anal lobe of wing not developed and CuA₂ recurved at apex of cell cup (Sinclair 1995a). The following genera are included in the Clinocerinae: *Aclinocera* Yang & Yang, *Afroclinocera* Sinclair, *Asymphyloptera* Collin, *Bergenstammia* Mik, *Clinocera* Meigen, *Clinocerella* Engel, *Dolichocephala* Macquart, *Hypenella* Collin, *Kowarzia* Mik, *Oreothalia* Melander, *Phaeobalia* Mik, *Proagomyia* Collin, *Proclinopyga* Melander, *Rhyacodromia* Saigusa, *Roederiodes* Coquillett, *Trichoclinocera* Collin, and *Wiedemannia* Zetterstedt (Sinclair 1995a).

Atelestidae

Atelestinae Hennig, 1970: 1, 3, 5, 6. Type genus *Atelestus* Walker, 1837.

Atelestidae Chvála, 1983: 85, 228.

The definition of this family is expanded here to include the new subfamily, Nemedinae. In the Atelestidae, the epipharyngeal blades are absent, female tergite 10 is also absent and males possess distinctively long processes of the gonocoxal apodemes and a shortened hypandrium (Sinclair & Shamshev 2003). Barták (2000) first proposed the assignment of *Nemedina* to the Atelestidae. Molecular analyses consistently assign the Atelestidae as the

sister group to the remaining Empidoidea (Collins & Wiegmann 2002a; Moulton & Wiegmann 2004). The following two subfamilies are recognized.

Nemedinae n. subfam.

Type genus *Nemedina* Chandler, 1981.

This is an ancient lineage that is represented by a single extant genus and several extinct genera (Grimaldi & Cumming 1999). The venation of this new subfamily is unique in the Empidoidea, characterized by the apex of cell br modified through the inclusion of a short vertical Rs and recurrent r-m, with radial and medial veins closely approximated (Chandler 1981; Grimaldi & Cumming 1999; Sinclair & Arnaud 2001; Sinclair & Shamshev 2003). This distinctive venation also characterizes five extinct genera from Cretaceous ambers (Grimaldi & Cumming 1999). See the Taxon sampling section for further discussion.

Atelestinae

The Atelestinae are defined on the presence of the subapical surstyli and the U-shaped male tergite 8. The following extant genera are included in the Atelestinae: *Acarteroptera* Collin, *Atelestus* Walker, and *Meghyperus* Loew (Chvála 1983).

Hybotidae

Hybotinae Meigen, 1820: x. Type genus *Hybos* Meigen, 1803.

Hybotidae Macquart, 1827: 136.

This family has long been recognized and for many years has been formally used in publications, especially by European workers. Its monophyly is not in doubt, characterized by the presence of a palpifer, fore tibial gland, gonocoxal apodeme restricted to anterolateral margin of hypandrium (lacking process), apex of antenna often with long, slender seta-like receptor, laterotergite bare and R₄₊₅ unbranched. This family is divided into the following subfamilies and unplaced genera:

Incertae sedis within Hybotidae

Stuckenbergomyia Smith—This genus was originally assigned to the Ocydromiinae (Smith 1969), but its placement remains in doubt. There are four known species confined to southern Africa (Sinclair 2003b).

Trichininae rev. stat.

Trichinini Chvála, 1983: 112, 114. Type genus *Trichina* Meigen, 1830.

The subfamily Trichininae is here tentatively redefined to include only two genera, *Trichina* Meigen and *Trichinomyia* Tuomikoski. These genera are grouped together mostly for convenience and it is hoped that future analyses will resolve their assignment within

the Hybotidae. This subfamily is distinguished from the remaining Hybotidae mostly on the basis of symplesiomorphies: dichoptic females, antennal style about half as long or shorter than the postpedicel, cell dm emitting three veins, proboscis short and directed downwards, ventral apodeme (see discussion under character 99) and postgonites absent.

Ocydromiinae

Ocydrominae Schiner, 1862: lii, liii. Type genus *Ocydromia* Meigen, 1820.

Ocydromiinae Melander, 1908: 222.

This redefined lineage follows the definition of Sinclair & Cumming (2000), distinguished by the following characters: short cell cup with truncate apex, arista subapical or much longer than postpedicel, proboscis short and directed downwards or recurved, 2–3 veins emitted from cell dm, male terminalia asymmetrical and rotated through 90°, phallus biarticulated, ventral apodeme and postgonites absent and epandrium with pair of articulated surstyli. The Ocydromiinae is here restricted to include the following genera: *Abocziputa* Plant, *Apterodromia* Oldroyd, *Austropeza* Plant, *Chvalaea* Papp & Földvári, *Hoplopeza* Bezzi, *Leptodromia* Sinclair & Cumming, *Leptodromiella* Tuomikoski, *Leptopeza* Macquart, *Leptopezella* Sinclair & Cumming, *Neotrichina* Sinclair & Cumming, *Ocydromia* Meigen, *Oropezella* Collin, *Pseudoscelolabes* Collin, *Scelolabes* Philippi, and *Stylocydromia* Saigusa (Tuomikoski 1966; Chvála 1983; Saigusa 1986; Plant 1989; Sinclair & Cumming 2000; Papp & Földvári 2001).

Oedaleinae **rev. stat.**

Oedaleini Chvála, 1983: 112, 162. Type genus *Oedalea* Meigen, 1820.

In this lineage the female cercus is fused to tergite 10, female segment 8 is elongate, the apical antennal style is often greatly shortened (shorter than postpedicel), mouthparts directed obliquely forwards, cell cup truncate apically and three veins emitted from cell dm (Tuomikoski 1966; Chvála 1983). The Oedaleinae include the following genera: *Allanthalia* Melander, *Anthalia* Zetterstedt, *Euthyneura* Macquart and *Oedalea* (Chvála 1983; Chvála & Kovalev 1989).

Tachydromiinae

Tachydromiae Meigen, 1822: vii. Type genus *Tachydromia* Meigen, 1803.

This distinctive subfamily is generally characterized by the apomorphic loss of M_2 and cell dm (due to the loss of dm-cu crossvein), but the subfamily also lacks the wing pterostigma and pseudotracheae, as well as possessing secondary modifications of the hybotid male genitalic ground plan (i.e., phallus with simple apex and the ejaculatory apodeme not fused to phallus base). The subfamily is divided into three tribes, namely the new tribe Symballophthalmini, and the Tachydromiini and Drapetini (Chvála 1975; Cumming 1990; Cumming unpubl. data).

Symballophthalmini n. tribe

Type genus *Symballophthalmus* Becker, 1889.

This new tribe includes the single genus *Symballophthalmus* Becker, formerly assigned to the Tachydromiini. It is a distinctive group (defined on the basis of apically broadened apomorphic wings) that retains numerous plesiomorphies (e.g., holoptic males), which exclude it from the other two tribes.

Tachydromiini

In its new restricted sense, the Tachydromiini is defined by the following apomorphies: presence of a precoxal bridge and a weakened A₁. The tribe includes the following genera: *Ariasella* Gil, *Charadrodromia* Melander, *Dysaletria* Loew, *Pieltaenia* Arias, *Platypalpus* Macquart, *Tachydromia* Meigen, *Tachyempis* Melander, and *Tachypeza* Meigen (Chvála & Kovalev 1989; Cumming 1990).

Drapetini

Drapetini Collin, 1961: 26. Type genus *Drapetis* Meigen, 1822.

This tribe is diagnosed by the following apomorphies: eyes with ommatrichia, loss of CuA₁ and loss of tergite 10 in females (correlated with sternite 10 positioned below the cerci) (Cumming & Cooper 1992; Solórzano Kraemer *et al.* 2005; Cumming unpubl. data). The Drapetini includes the following genera: *Allodromia* Smith, *Atodrapetis* Plant, *Austrodrapetis* Smith, *Austrodromia* Collin, *Chaetodromia* Chillcott, *Chersodromia* Walker, *Crossopalpus* Bigot, *Dusmetina* Gil, *Drapetis* Meigen, *Elaphropeza* Macquart, *Isodrapetis* Collin, *Megagrapha* Melander, *Micrempis* Melander, *Nanodromia* Grootaert, *Ngaheremyia* Plant & Didham, *Pontodromia* Grootaert, *Sinodrapetis* Yang, Gaimari & Grootaert, and *Stilpon* Loew (Chvála & Kovalev 1989; Cumming 1990; Cumming & Cooper 1992; Grootaert 1994; Plant 1997; Yang *et al.* 2004; Plant & Didham 2006).

Hybotinae

Hybotinae Meigen, 1820: x. Type genus *Hybos* Meigen, 1803.

This subfamily has been expanded to include the *Bicellaria* group of genera as suggested by Sinclair & Cumming (2000). The Hybotinae are characterized by holoptic females (except *Lamachella* and *Leptocrytoma*), proboscis often heavily sclerotized and projecting obliquely or horizontally forwards, wings generally with well developed anal lobe, cell dm emitting two veins and prosternum isolated and separated from proepisternum (Smith 1969; Chvála 1983; Sinclair 1996). This subfamily is divided into two tribes:

Bicellariini n. tribe

Type genus *Bicellaria* Macquart, 1823.

The Bicellariini is a distinctive group, defined on the basis of their unique wing venation: cell dm absent and the branches of M evanescent near mid wing (bases of veins abbreviated). This new tribe includes three genera formerly assigned to the Ocydromiinae: *Bicellaria* Macquart, *Hoplocrytoma* Melander, *Leptocrytoma* Saigusa.

Hybotini

This tribe is defined on a suite of characters including: cell dm emitting two veins, cell cup often as long as or longer than cell bm, wing usually broad with developed anal lobe and hind femur often enlarged with long setae beneath. The genera of the Hybotini were divided into several groups by Sinclair (1996). The following genera are included in the Hybotinae: *Acarterus* Loew, *Afrohybos* Smith, *Chillcottomyia* Saigusa, *Ceratohybos* Bezzi, *Euhybus* Coquillett, *Hybos* Meigen, *Lactistomyia* Melander, *Lamachella* Melander, *Neohybos* Ale-Rocha & Carvalho, *Parahybos* Kertész, *Smithybos* Ale-Rocha, *Stenoproctus* Loew, *Syndyas* Loew, and *Syneches* Walker (Smith 1967, 1975, 1980; Saigusa 1986; Ale-Rocha 2000; Ale-Rocha & Carvalho 2003).

Brachystomatidae n. stat.

Brachystomatinae Melander, 1908: 202. Type genus *Brachystoma* Meigen, 1822.

The Brachystomatinae is elevated to family rank and expanded to include the Ceratomerinae and Trichopezinae on the basis of several synapomorphies including: ejaculatory apodeme plate-like and narrowly fused to base of phallus, female tergite 7 usually bearing fringe of setae along posterior margin and female cercus held upright. This family includes the following three subfamilies:

Trichopezinae

Trichopezini Vaillant, 1981: 353. Type genus *Trichopeza* Rondani, 1856.

Trichopezinae Sinclair & Cumming, 1994: 200; Sinclair, 1995a: 720.

The Trichopezinae is not as well defined as the other two subfamilies of the Brachystomatidae. It is a very heterogeneous group distinguished by an internal median apodeme, which is usually present projecting anteriorly from female tergite 8 (see Key to Families below for further diagnostic characters). This subfamily includes the following genera and groups: *Heleodromia* group (including *Heleodromia* Haliday and *Pseudoheleodromia* Wagner); *Heterophlebus* group (including *Apalocnemis* Philippi, *Gloma* Meigen, *Heterophlebus* Philippi); *Niphogenia* group (including *Ceratempis* Melander and *Niphogenia* Melander); *Trichopeza* group (including *Boreodromia* Coquillett, *Ephydrempis* Saigusa, *Sabroskyella* Wilder, and *Trichopeza* Rondani); and *Rubistella* Garrett Jones (Sinclair 1995a).

In addition, *Sematopoda* Collin is tentatively assigned to the Trichopezinae, but confident placement must await the discovery of congeneric females.

Ceratomerinae

Ceratomerinae Collin, 1928: 1, 3, 16. Type genus *Ceratomerus* Philippi, 1865.

This distinctive subfamily is characterized by long narrow wings (lacking anal lobe), dichoptic in both sexes, scape more than twice as long as pedicel with long dorsal and

ventral setae, pedicel with finger-like conus and postpedicel elongate, often strap-like (Sinclair 2003a). The following three genera are included in the Ceratomerinae: *Ceratomerus* Philippi, *Glyphidopeza* Sinclair, and *Icasma* Collin (Sinclair 1997).

Brachystomatinae

The Brachystomatinae is defined here primarily on the basis of a coiled spermatheca, H-shaped lacinia and articulated male cercus. The subfamily has traditionally included only two genera, *Anomalempis* Melander and *Brachystoma* Meigen. *Xanthodromia* Saigusa, which lacks the long cell cup that characterizes the other two genera, was originally assigned to the Hemerodromiinae by Saigusa (1986), but is here transferred to the Brachystomatinae because of the form of the spermatheca, lacinia and male cercus.

Dolichopodidae s.lat.

Dolichopodes Latreille, 1809: 239, 290. Type genus *Dolichopus* Latreille, 1797.

Dolichopodidae Agassiz, 1846: 128.

The definition of the Dolichopodidae is herein expanded to include all genera formerly assigned to the Microphoridae *sensu* Chvála. There is no doubt about the monophyly of this family and the inclusion of the microphorids in the Dolichopodidae has been accepted by several recent authors (e.g., Cumming & Sinclair 2000; Ulrich 2003, 2004; Gatt 2003; Shamshev & Grootaert 2005). The Dolichopodidae now includes the Microphorinae, Parathalassiinae and Dolichopodidae *s.str.* In its expanded sense the family is characterized by several features, including the Rs originating at or near level of crossvein h, the basal cells shortened (less than half length of cell dm) such that crossvein r-m occurs in the basal fourth of wing, the male terminalia rotated (lateroflexed) forward beneath the preceding segments with the pregenital segments partially twisted or rotated, and the male hypopygium with reduced gonocoxal apodemes as well as bacilliform (or subepandrial) sclerites that fuse with the hypandrium.

Microphorinae

Microphorinae Collin, 1960: 393. Type genus *Microphor* Macquart, 1827.

This subfamily includes two extant genera, *Microphor* Macquart and *Schistostoma* Becker (Cumming & Brooks 2002). The group is not clearly defined and is maintained here primarily for convenience, until the relationships of both included genera are more clearly resolved by future analyses. This subfamily includes those taxa with holoptic males, more than six unmodified pseudotracheae, broad wings (i.e., anal lobe developed), costa circumambient, and a two-articled arista or stylus.

Parathalassiinae

Parathalassiini Chvála, 1981: 230, 231. Type genus *Parathalassius* Mik, 1891.

The diagnostic features of this subfamily include a single-articled arista or stylus, antennae inserted high on head, dichoptic males, narrow wing (anal lobe not developed), and often crossvein bm-cu is incomplete (Cumming & Brooks 2002). The Parathalassiinae includes the following extant genera: *Amphithalassius* Ulrich, *Chimerothalassius* Shamshev & Grootaert, *Eothalassius* Shamshev & Grootaert, *Microphorella* Becker, *Parathalassius* Mik, *Plesiothalassius* Ulrich, and *Thalassophorus* Saigusa (Saigusa 1986; Chvála 1989; Ulrich 1991; Cumming & Brooks 2002; Shamshev & Grootaert 2002, 2005).

Dolichopodidae s.str.

The Dolichopodidae s.str. currently comprise 245 genera and some 6900 species worldwide (Grichanov 2006). Ulrich (2003) recognised this lineage at the rank of subfamily, because of the inclusion of the microphorids in the Dolichopodidae, and reduced the rank of the included conventional subfamilies to tribal level (without naming them). The group is very well defined on the basis of several synapomorphies associated with the antennae, mouthparts, wing, abdomen and male terminalia. The Dolichopodidae s.str. are most easily identified however, on the basis of their metallic or yellow body color, narrow wings, costa ending at M_1 , Sc very short ending in vein R_1 , cell dm emitting two veins, and cells bm and dm fused (Chvála 1983; Robinson & Vockeroth 1981). The following 15 subfamilies are currently recognized in the Dolichopodidae s.str.: Achalcinae, Babindellinae, Diaphorinae, Dolichopodinae, Enliniinae, Hydrophorinae, Medeterinae, Neurigoninae, Peloropeodinae, Plagioneurinae, Rhapsiinae, Sciapodinae, Stolidosomatinae, Sympycninae, and Xanthochlorinae (Bickel 1987; Pollet *et al.* 2004). A few authors have further subdivided certain dolichopodid subfamilies into tribes (e.g., Negrobov 1986 for Diaphorinae, Dolichopodinae, Hydrophorinae, Medeterinae, and Sympycninae; Naglis 2001, 2002a,b, 2003a,b for Neurigoninae). Brooks (2005b) has recently reviewed the various higher classification schemes that have been proposed for the Dolichopodidae s.str.

Key to the Families and Unplaced Genus Groups of Empidoidea

This key is modified from Chvála (1983) and Sinclair & Cumming (2000). For reduced winged and wingless specimens refer to regional keys (e.g., Sinclair & Cumming 2000; Cumming & Sinclair in press).

- 1 Vein R_{4+5} unbranched (Figs. 377–390, 397–403); prosternum usually small and separated from proepimeron (except most Dolichopodidae s.lat. and some Tachydromiinae); laterotergite always bare; costa ending at wing tip (except Microphorinae and Parathalassiinae); first antennal segment (scape) often lacking setae 2
- Vein R_{4+5} branched (Figs. 363–376, 392–396); if not, then either prosternum large and fused with proepimeron forming precoxal bridge and laterotergite usually with setae,

- or costa circumambient; first antennal segment (scape) usually bearing setae 4
- 2 Fore tibia lacking gland; Rs originating at or near level of crossvein h; crossvein r-m in basal fourth of wing (Figs. 397–403); male terminalia rotated forward beneath preceding segments with pregenital segments partially twisted or rotated
..... **Dolichopodidae s.lat.**
- Base of fore tibia usually with posteroventral gland; if not base of wing with alula (Atelestinae, Figs. 377–378) or r-m recurrent and apex of cell br with three veins closely approximated (Nemedinae, Fig. 189); Rs originating well distal to level of crossvein h; crossvein r-m distal to basal fourth of wing (Figs. 387–390); male terminalia often twisted to the right, but not involving pregenital segments 3
- 3 Base of fore tibia with posteroventral gland (Figs. 413–414); apex of antenna usually with lengthened, bristle-like style (Figs. 21–25, 27–28) **Hybotidae**
- Base of fore tibia lacking posteroventral gland; apex of antenna with thickened, peg-like style receptor (Figs. 19–20) or receptor absent on tip of arista-like style (Fig. 18)
..... **Atelestidae**
- 4 Labrum strongly recurved, especially in females; epipharyngeal comb usually present at apex of labrum (Fig. 57); if not, then fore coxa with erect stout spines
..... **Ragas group (Empididae)**
- Labrum straight not strongly recurved (Figs. 54–56, 58–67); epipharyngeal comb absent; fore coxa never with erect stout spines 5
- 5 R_1 and R_{4+5} on upper side and M vein underside with setae (Fig. 365); female abdomen pointed apically, lacking acanthophorites (Fig. 195) **Oreogeton**
- R_1 and R_{4+5} and M vein bare; if setae present, female abdomen truncate apically, bearing acanthophorites (Fig. 236) 6
- 6 Cell *cup* extending beyond cell *bm* (Fig. 364); mid femur strongly swollen; female abdomen pointed apically, lacking acanthophorites (Fig. 191) **Homalocnemis**
- Cell *cup* not extending beyond cell *bm* (Figs. 363, 368–376); if so, female abdomen truncate apically, bearing acanthophorites Fig. 231); mid femur rarely strongly swollen 7
- 7 Labrum lacking epipharyngeal blades (Figs. 55, 98) and projecting obliquely forward
..... **Iteaphila group**
- Labrum with epipharyngeal blades present and usually projecting ventrally (Figs. 58–60, 63–67, 79–84); if blades apparently absent or secondarily fused (*Hesperempis* group, Figs. 62, 100), then thoracic chaetotaxy very short and pale 8
- 8 Ejaculatory apodeme plate-like and narrowly fused to base of phallus (Figs. 331, 333 341). Second antennal segment with conus inserted into postpedicel (Ceratomerinae, Figs. 34–35); or cell *cup* longer than cell *bm* (most Brachystomatinae, Figs. 391–392); or some veins bearing setae (Trichopezinae, part—*Heterophlebus* group, Figs. 395); or epandrium and hypandrium fused (Trichopezinae, part—*Trichopeza* group, Fig. 343);

or postpedicel somewhat reniform, drooping, bearing a long dorso-terminal arista-like style (Trichopezinae, part—*Gloma*); or epandrium with hook-like terminal projection (Trichopezinae, part—*Niphogenia* group, Fig. 338); or hypandrium prolonged posteriorly, bowl-like (Trichopezinae, part – *Heleodromia* group). Female abdomen truncate, usually bearing acanthophorites (spinous tergite 10); female tergite and sternite 8 closely approximated, articulated or fused anterolaterally (Figs. 230–232, 234–237) ..

- **Brachystomatidae**
- Ejaculatory apodeme not fused to base of phallus (Figs. 277–280). Second antennal segment lacking conus; cell *cup* shorter or subequal to cell *bm* (Figs. 368–376); all veins usually bare (except *Trichoclinocera*—*Clinocerinae*); epandrium and hypandrium rarely fused (Figs. 280, 282, 293); postpedicel symmetrical with apical style (style absent in *Brochella*, Fig. 14); epandrium lacking hook-like terminal process. Female abdomen pointed apically, lacking spines on tergite 10 (Figs. 197, 203, 209, 214); if present, tergite and sternite 8 not articulated anterolaterally and usually widely separated **Empididae (part)**

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TABLE 1. Exemplar taxa scored in the analysis. The classification used follows the revised classification presented herein.

Taxon	Collection Locality
Asilidae	
<i>Diogmites</i> sp.	Sonoita, AZ, USA
Therevidae	
<i>Thereva duplicis</i> Coquillett	no data
Hilarimorphidae	
<i>Hilarimorpha</i> sp.	Winnipeg, MB, Canada
Scenopinidae	
<i>Caenotus hospes</i> Melander	Organ Pipe Park, AZ, USA
Empidoidea	
<i>incertae sedis</i>	
<i>Homalocnemis adelensis</i> (Miller)	Otira and Stewart Is., New Zealand
<i>Iteaphila nitidula</i> Zetterstedt	Terrace, BC, Sunwapta Pass, AB, Cape Breton Highlands National Park, NS, Canada
<i>Oreogeton heterogamus</i> Melander	Cape Breton Highlands National Park, NS, Canada
Empididae	
<i>incertae sedis</i>	
<i>Brochella monticola</i> Melander	Mt. Rainier, WA, USA
<i>Hesperempis mabelae</i> Melander	Mt. Evans, CO, USA
<i>Hormopeza senator</i> Melander	Jasper, AB, Canada
<i>Hormopeza</i> sp.	Jasper, AB, Canada
<i>Philetus memorandum</i> Melander	Carmanah Valley, BC, Canada
<i>Ragas unica</i> Walker	Berlin, Germany
<i>Zanclotus dioktes</i> Wilder	Sun Valley, ID, USA
Empidinae	
<i>Edenophorus simplex</i> Sinclair	Vanrhynsdorp, Western Cape Prov., South Africa
<i>Empidadelpha propria</i> Collin	Lake Moana and Glitterburn, New Zealand
<i>Empis borealis</i> L.	Vlkov, Bohemia, Czech Republic
<i>Hilara maura</i> (Fab.)	Kunice, Bohemia, Czech Republic
<i>Hilarempis facilis</i> Collin	Magellanes Natales, Chile
<i>Sphicosa</i> sp.	Mt. Buffalo National Park, VIC, Australia
Hemerodromiinae	
<i>Chelifera valida</i> Loew	Lac Maunoir and Hyndman Lake, NWT, Canada
<i>Chelipodozus cinereus</i> Collin	Chiloé Is., Chile
Clinocerinae	
<i>Afroclinocera obesa</i> Sinclair	Pietermaritzburg, Natal, South Africa
<i>Clinocera fuscipennis</i> Loew	Great Smoky Mtns, TN, USA
Atelestidae	
Atelestinae	
<i>Acarteroptera recta</i> Collin	Las Trancas, Chile

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TABLE 1 (continued)

Taxon	Collection Locality
<i>Atelestus pulicarius</i> (Fallén)	Radovesice—Kajba, Bohemia bov, Czech Republic Slindon, Sx., England
<i>Meghyperus</i> sp.	Snow Creek, CA, USA
Nemedininae	
<i>Nemedina almirabilis</i> Chandler	Melegmány, Hungary
<i>Nemedina zaitsevi</i> Sinclair & Shamshev	Ustyurt Plateau, Kazakhstan
Hybotidae	
Trichininae	
<i>Trichina clavipes</i> (Meigen)	Jizersé, Bohemia, Czech Republic Lappvik, Sweden
<i>Trichinomyia flavipes</i> (Zetterstedt)	Mirošovice, and Senohraby, Bohemia, Czech Republic
Oedaleinae	
<i>Oedalea lanceolata</i> Melander	Terrace, BC, Canada
Ocydromiinae	
<i>Neotrichina</i> sp.	Conguillio NP, Cautin, Chile
<i>Ocydromia glabricula</i> (Fallén)	Banff, AB, and Duncan, BC, Canada
Hybotinae	
<i>Acarterus unicolor</i> Loew	Sevenweekspoort, Cape Prov., Nieuwoudtville, Cape Prov., South Africa
<i>Bicellaria</i> spp.	Vancouver & Terrace, BC, Griffith, ON, Canada
<i>Hybos reversus</i> Walker	Old Chelsea, QC, Cape Breton Highlands National Park, NS, Canada
<i>Stenoproctus unipunctatus</i> Loew	Cape of Good Hope, Cape Prov., South Africa
Tachydromiinae	
<i>Austrodromia talaris</i> Collin	Los Coigues, Cautin, Chile
<i>Platypalpus agilis</i> (Meigen)	Newcastle-u-Lyme, Staffs., England
<i>Platypalpus</i> sp.	Kumamoto Pref., Japan
<i>Symbalophthalmus masoni</i> Chillcott	Mt. Desert Is., ME, USA
Brachystomatidae	
Brachystomatinae	
<i>Anomalempis archon</i> Melander	Dempster Hwy, YT, Canada
<i>Brachystoma nigrimanus</i> Loew	Blacksburg, VA, USA
<i>Brachystoma occidentale</i> Melander	Sidney, BC, Canada
Ceratomerinae	
<i>Ceratomerus paradoxus</i> Philippi	Chiloé Is., Chile
<i>Glyphidopeza fluviatilis</i> Sinclair	Mt. Richmond Forest Park, New Zealand
Trichopezinae	
<i>Heterophlebus versabilis</i> (Collin)	Natales, Magellanes, Chile
<i>Niphogenia eucera</i> Melander	Mt. Hood National Forest, OR, USA
<i>Sabroskyella rancheria</i> Wilder	Huntington Lake, CA, USA

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TABLE 1 (continued)

Taxon	Collection Locality
Dolichopodidae s.lat.	
Microphorinae	
<i>Microphor pilimanus</i> (Strobl)	Sierra Nevada, Spain
<i>Microphor</i> sp. (female)	Alpine Lake, CA, USA
<i>Schistostoma armipes</i> (Melander)	Mission City, BC, Canada
Parathalassiinae	
<i>Amphithalassius latus</i> Ulrich	Natures Valley, Cape Prov., South Africa
<i>Microphorella</i> sp.	Marys Peak and Silver Falls State Park, OR, USA
<i>Parathalassius aldrichi</i> Melander	Brooks Peninsula, BC, Canada
Dolichopodidae s.str.	
Sciapodinae	
<i>Heteropsilopus squamifer</i> Hardy	Kur-ring-gai Chase NP, NSW, Australia
Dolichopodinae	
<i>Dolichopus ziczac</i> Wiedemann group	Berry Springs, NT, Australia
Sympycninae	
<i>Sympycnus anomalipennis</i> Becker	Mt. Kaputar, NSW, Australia
Cyclorrhapha	
Opetiidae	
<i>Opetia anomalipennis</i> Saigusa	Kurusou-kyō, Yamaguchi Pref., Honshu, Japan
<i>Opetia nigra</i> Meigen	Easington, Yorkshire, UK
Platypezidae	
<i>Agathomyia</i> spp.	Banff, AB, Old Chelsea, QC, Canada
<i>Microsania</i> sp.	Parson, AK, USA
Lonchopteridae	
<i>Lonchoptera uniseta</i> Curran	Elkwater, AB, Canada
<i>Lonchoptera</i> sp.	Fukuoka, Japan
Phoridae	
<i>Sciadocerus rufomaculata</i> White	Blue Mtns, NSW, Australia
Syrphidae	
<i>Syrphus ribesii</i> (L.)	Picton and Ottawa, ON, Canada
Anthomyiidae	
<i>Strobilomyia neanthracina</i> Michelsen	Stittsville, ON, Smithers, BC, Canada

TABLE 2. Character state matrix for cladistic analysis (characters 1–60). Inapplicable characters are indicated by “-” and missing data are indicated by “?”.

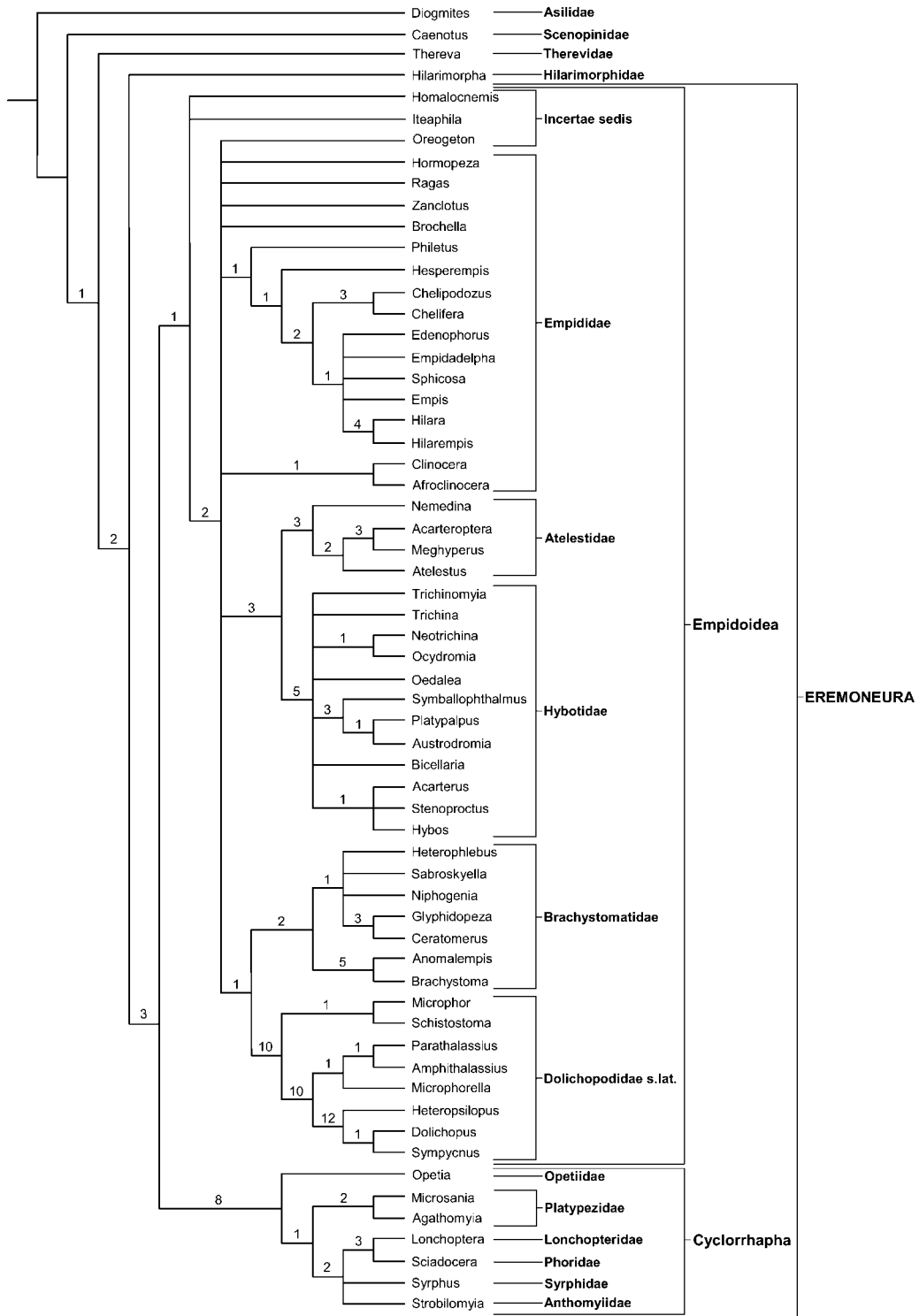
	1111111112	2222222223	3333333334	4444444445	5555555556	
	1234567890	1234567890	1234567890	1234567890	1234567890	
<i>Diogmites</i>	1001000000	-000100000	000002-000	0000001101	1000000000	0310000000
<i>Thereva</i>	0000010020	0000000000	1000000001	0000000001	0000000000	0300000000
<i>Hilarimorpha</i>	0000000010	0000000000	1000000000	0000000000	0000000000	0000000010
<i>Caenotus</i>	0000000020	0000000000	100002-000	0000000000	0000000000	0000000000
<i>Hormopeza</i>	0000100020	1001111100	1000000000	0010000101	0000110010	0000000001
<i>Ragas</i>	0001100020	1001111100	1100010000	1010000101	0000110000	0000000001
<i>Zanclotus</i>	1101000120	0001111100	110002-000	1010000101	0000110000	0000000001
<i>Oreogeton</i>	0000000020	0000110100	1000000100	1030001101	0000110010	0000000001
<i>Iteaphila</i>	0000000010	1000100000	1100000000	0030000101	0000110000	0000000001
<i>Homalocnemis</i>	0010000020	1000000000	1000000001	0010000100	0000110000	0000000000
<i>Brochella</i>	100100010-	-000100000	1100010001	1030001121	0000110000	0000000001
<i>Hesperempis</i>	1001000020	1000130000	1100000001	0030001100	0000010000	0000000001
<i>Philetus</i>	1001000020	0000010100	1100000100	1030000111	0000110010	0000000001
<i>Clinocera</i>	1101000120	0000030001	110012-101	1030001101	0000110010	0100000001
<i>Afroclinocera</i>	1101000220	0000010100	1100100001	1030001111	0000110010	0110000001
<i>Chelipodozus</i>	1001000110	0000010100	1100000??1	1?3???0121	0111110010	1000000001
<i>Chelifera</i>	1001000000	-000010100	110002-001	0030000101	0111110000	1000000001
<i>Edenophorus</i>	1001000020	0000010100	1100000001	1?3???0101	0000010011	1000010001
<i>Empidadelpha</i>	1001000020	0000010100	1200000001	1030001101	1000110011	1000000001
<i>Sphicosa</i>	0000000020	0000010110	1200010001	1030001101	0000110011	1000000001
<i>Empis</i>	0001010020	0000010100	1200000001	1030001101	0000010011	1000000001
<i>Hilara</i>	1001000020	0000010100	1200000001	1030000101	0000110110	0001000001
<i>Hilarempis</i>	1001000020	0000010100	1200000001	1030000101	0000110110	1001000001
<i>Nemedina</i>	0001100120	0000000000	1100000000	0020020101	0000110002	1000010111
<i>Acarteroptera</i>	0000100030	0000100000	1100010000	0010000101	0000010012	1000010101
<i>Meghyperus</i>	0000100030	0000100000	1100000000	0010000101	0000010012	1000010000
<i>Atelestus</i>	0000100020	0000000000	1100000000	0010000101	0000110012	1000010110
<i>Trichinomyia</i>	0001100220	0000010101	1111000000	0030020101	0000111012	1000010001
<i>Trichina</i>	0001100220	0000010101	1111000000	0030020101	0000111012	1000010001
<i>Neotrichina</i>	0001100220	0000010101	1111000000	0030020001	0000111012	1000010001
<i>Ocydromia</i>	0001100211	0000010101	1111000000	0030020101	0000111001	1000011001
<i>Oedalea</i>	0001100220	0000010101	1101000000	0030020001	0000111012	1000010001
<i>Symballophtalmus</i>	0001100120	0000010101	111102-000	0030020101	0000111012	1010010111
<i>Platypalpus</i>	1001100220	0000010101	111102-001	0030000101	0000111012	1011010111
<i>Austrodromia</i>	1101100220	0000010101	111102-000	0030020101	0000011012	1010010111
<i>Bicellaria</i>	0011100020	0000010101	1111000000	0030020101	0000111011	1000010011
<i>Acarterus</i>	0011100220	0010010101	1101000000	0030020101	0000111012	1000010101
<i>Stenoproctus</i>	0011100220	0010010101	1101000000	0030020101	0000111012	1000010101
<i>Hybos</i>	0011100220	0010010101	110102-000	0030020101	1000111002	1000010100
<i>Heterophlebus</i>	0001000020	0000010100	1000000001	1030001101	0000110011	0100000001
<i>Sabroskyella</i>	1101000100	-000010100	1100000001	1030000111	1000110010	1000000001
<i>Niphogenia</i>	1001010010	0000010101	1100000000	1030001111	0000110010	0000000001
<i>Anomalempis</i>	0001000020	0000010110	1100000001	0010000101	1000110000	0000010000
<i>Brachystoma</i>	1001000020	0000010110	1100000001	0030000101	0000110000	0000000000
<i>Glyphidopeza</i>	1001011220	0000010101	1100000001	1030000111	0000110010	0110000001
<i>Ceratomerus</i>	1001011220	0000010100	110002-001	1030000101	0000110010	0000000001
<i>Microphor</i>	0001100120	0010030000	1100000100	0031020101	0000110010	0200110001
<i>Schistostoma</i>	0001100120	0010010100	1100000100	0031020101	0000110010	0200110001
<i>Parathalassius</i>	1101100110	0110010101	1110011111	0131110101	0000110010	0210110001
<i>Microphorella</i>	1101100110	0110010101	1110011111	0131110101	0000110010	0210110001
<i>Amphithalassius</i>	1101100110	0110010101	1110011110	0131110111	0000110010	0210110001
<i>Heteropsilopus</i>	1101100121	0110020201	1110112111	0131110101	0000110002	2310110001
<i>Dolichopus</i>	1101002121	0110020201	1110111111	0131110101	1000110012	3310110001
<i>Sympycnus</i>	1101100121	0110020201	1110111111	0131110121	1000110012	3310110101
<i>Opetia</i>	0000000120	001000000?	1000000100	0000000001	0000000000	0300110011
<i>Microsania</i>	0000000130	0010000000	1000000000	0000000111	0000000013	0300110011
<i>Agathomyia</i>	0000000130	0010000000	1000000000	1000000111	0000000002	0300111000
<i>Lonchoptera</i>	1001002130	0000000000	1000000000	0100000121	1000110010	0410110011
<i>Sciadocera</i>	1001102131	0010000001	1000000100	1110000111	1000110011	3310110001
<i>Syrphus</i>	0001002121	0010000000	1000000000	0100000001	0000110001	0300010000
<i>Strobilomyia</i>	0001002131	0010000001	1100000000	0101000101	1000100002	0010110101

TABLE 2 (Continued). Character state matrix for cladistic analysis (characters 61–122).

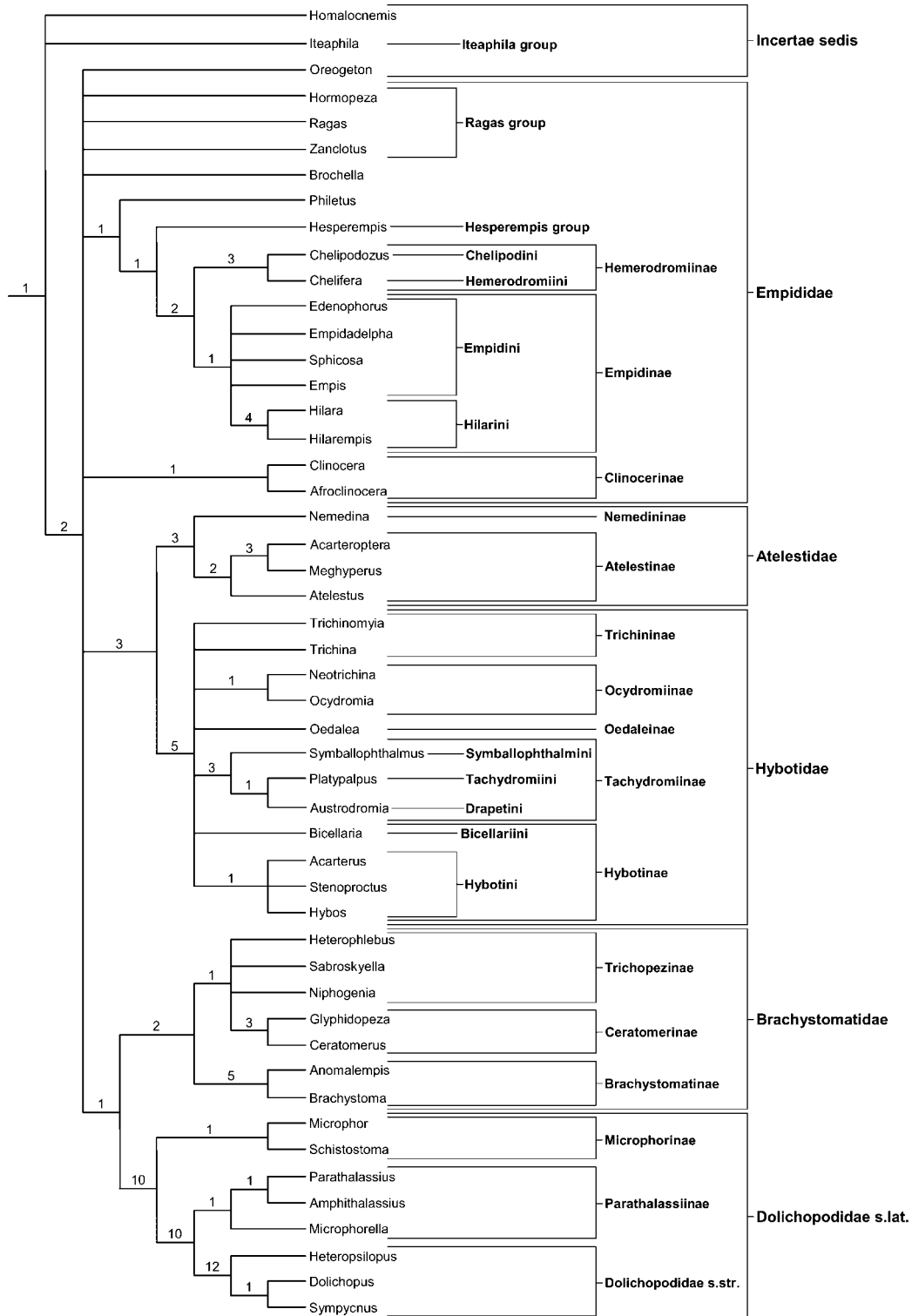
	1	1111111111	1111111111	11			
6666666667	7777777778	8888888889	9999999990	0000000001			
1234567890	1234567890	1234567890	1234567890	1234567890			
<i>Diogmites</i>	0000000000	0000000000	0000000000	0000000000	0000100000	0000000000	00
<i>Thereva</i>	0000000000	0000010000	0000000000	0000000000	2000000000	0000000000	00
<i>Hilarimorpha</i>	0000010000	0000003000	1301000000	0010000000	1000000000	0000??????	??
<i>Caenotus</i>	0000000000	0000100000	0000000000	0000000000	1000100000	0000??????	??
<i>Hormopeza</i>	1000020000	0000200000	1301000000	0010000110	1103201100	0000??????	??
<i>Ragas</i>	1001020000	1000200000	1301000000	0010000130	1103201111	0000??????	??
<i>Zanclotus</i>	2001120000	1000200000	1302000000	0010000130	1103201110	0000??????	??
<i>Oreogeton</i>	2000010000	0000200000	1300000000	0010000110	1100201100	0000210001	00
<i>Iteaphila</i>	2000010000	0000200000	1303000000	0010000110	1110201100	0000??????	??
<i>Homalocnemis</i>	3000010000	0000200000	1300000000	0110000110	1100201100	0000??????	??
<i>Brochella</i>	2001120000	1000???000	1301000000	0110000100	1500201110	0000??????	??
<i>Hesperempis</i>	1001120200	0000200000	1300000000	0011000110	1100201100	1012??????	??
<i>Philetus</i>	2001020000	0000214000	1300000000	0010000110	1100201100	1010??????	??
<i>Clinocera</i>	2001220000	1000201000	1300000000	0011000100	1400201110	0012210001	00
<i>Afroclinocera</i>	2001120000	1000200000	1301000000	0011000110	1100301110	0000??????	??
<i>Chelipodozus</i>	2001220000	1000200000	1301000000	0010000110	1110301100	1012??????	??
<i>Chelijera</i>	1001220000	0000200000	1300000000	0010000110	1110301100	1011210001	00
<i>Edenophorus</i>	2001120000	2000200??0	1301000000	0010000110	1110301100	1001??????	??
<i>Empidadelphina</i>	2001110000	0000200000	1301000000	0010000110	1110301100	1000??????	??
<i>Sphicosa</i>	2001010000	0000200000	1301000000	0010000120	1110301100	1002??????	??
<i>Empis</i>	2000010000	0000200000	1301000000	0010000100	1110301100	1011210001	00
<i>Hilara</i>	2000020000	1000200000	1301000000	0010000120	1110301100	1002210001	00
<i>Hilarempis</i>	2000020000	1000200000	1301000000	0011000120	1110301100	1002210001	00
<i>Nemedina</i>	1-00010000	1000200000	1302000003	0010100100	1103201110	0000??????	??
<i>Acarteroptera</i>	3000000000	3000200000	1302000003	0010101110	1200201111	0000??????	??
<i>Meghyperus</i>	3000000000	3000200000	1302000003	0010101110	1200201111	0000??????	??
<i>Atelestus</i>	3-00000000	3000200000	1302000003	0010100100	1200201111	0000??????	??
<i>Trichinomyia</i>	1000010000	0000???000	1300000010	0011000100	1202201110	0000??????	??
<i>Trichina</i>	1000010000	0000211000	1300000112	0011000100	1202201120	0000??????	??
<i>Neotrichina</i>	1000020000	0000???000	1300000110	0011000100	1201201120	0000??????	??
<i>Ocydromia</i>	1000020000	0000???000	1303000110	0011000100	1201201120	0000210001	00
<i>Oedalea</i>	1000010000	1000211000	1303000112	0011002111	1202201110	0000??????	??
<i>Symballopthalmus</i>	1-00120000	1000211000	1300000110	0011002111	1100201120	0000??????	??
<i>Platypalpus</i>	1-01120000	1000214000	1300000110	0011002111	1100201110	0000210001	00
<i>Austrodromia</i>	4-00120000	1000???000	1302000110	0011002111	1100201110	0000??????	??
<i>Bicellaria</i>	1000020000	0000211000	1300000112	0011002110	1202201110	0000??????	??
<i>Acarterus</i>	3000020000	1000211000	1300000112	0011002110	1202201110	0000??????	??
<i>Stenoproctus</i>	1000020000	1000???000	1300000112	0011002110	1202201110	0000??????	??
<i>Hybos</i>	3000020000	0000211000	1300000112	0011000110	1202201110	0000??????	??
<i>Heterophlebus</i>	2000010110	0000201111	1200121000	0010000110	1300201110	0000??????	??
<i>Sabroskyella</i>	2001120110	1000200111	1200121400	1011000100	1300201110	0002??????	??
<i>Niphogenia</i>	2001120110	1000201111	1201121000	0010000110	1300201110	0000??????	??
<i>Anomalempis</i>	2001020110	0000202011	1011121000	0010000110	1300201110	0100??????	??
<i>Brachystoma</i>	3001120110	1000202011	1011121000	1010000110	1300201100	0110??????	??
<i>Glyphidopeza</i>	2101220100	1000200011	12012--000	0011000110	1300301110	0000??????	??
<i>Ceratomerus</i>	4002220110	1000200011	1200111000	0010000110	1300301110	0000??????	??
<i>Microphor</i>	2101020301	0100200021	1110130220	0011000110	1100201210	0000??????	??
<i>Schistostoma</i>	2101020201	0100200021	1010120221	0011000110	1100201210	0000??????	??
<i>Parathalassius</i>	1111120301	2100211021	1010120220	0011000110	1110301210	0000??????	??
<i>Microphorella</i>	2111120301	2100211021	1010120220	0011000110	1110301210	0000??????	??
<i>Amphithalassius</i>	1111020201	1100211001	1100000220	0011000110	1110301210	0010??????	??
<i>Heteropsilopus</i>	2111100300	2111211021	1010130321	1011000140	1110211210	0000210001	00
<i>Dolichopus</i>	2121120301	2111211021	1010120321	1011000140	1110211210	0000210001	00
<i>Sympycnus</i>	2121120301	2211211021	1010120321	1011000110	1110211210	0000??????	?0
<i>Opetia</i>	0110001400	2302214000	130?000030	0011000110	1400201110	0000??????	??
<i>Microsania</i>	0-00001000	1300000000	1301000030	0011010130	1410201120	0000??????	??
<i>Agathomyia</i>	0101001000	1300000000	1301000030	0011010130	1500201120	0000111111	10
<i>Lonchoptera</i>	0100121000	2300113000	1301000030	0011020130	1400201100	0000111111	11
<i>Sciadocera</i>	0-10021200	2300111000	1301000530	0011010100	1400201120	0000111111	11
<i>Syrphus</i>	0000001300	2300000000	1300000030	0011020130	1400201120	0000111111	11
<i>Strobilomyia</i>	1100001300	2300000020	1301000030	0011020130	1400201120	0010111111	11

TABLE 3. Proposed classification of the Empidoidea.

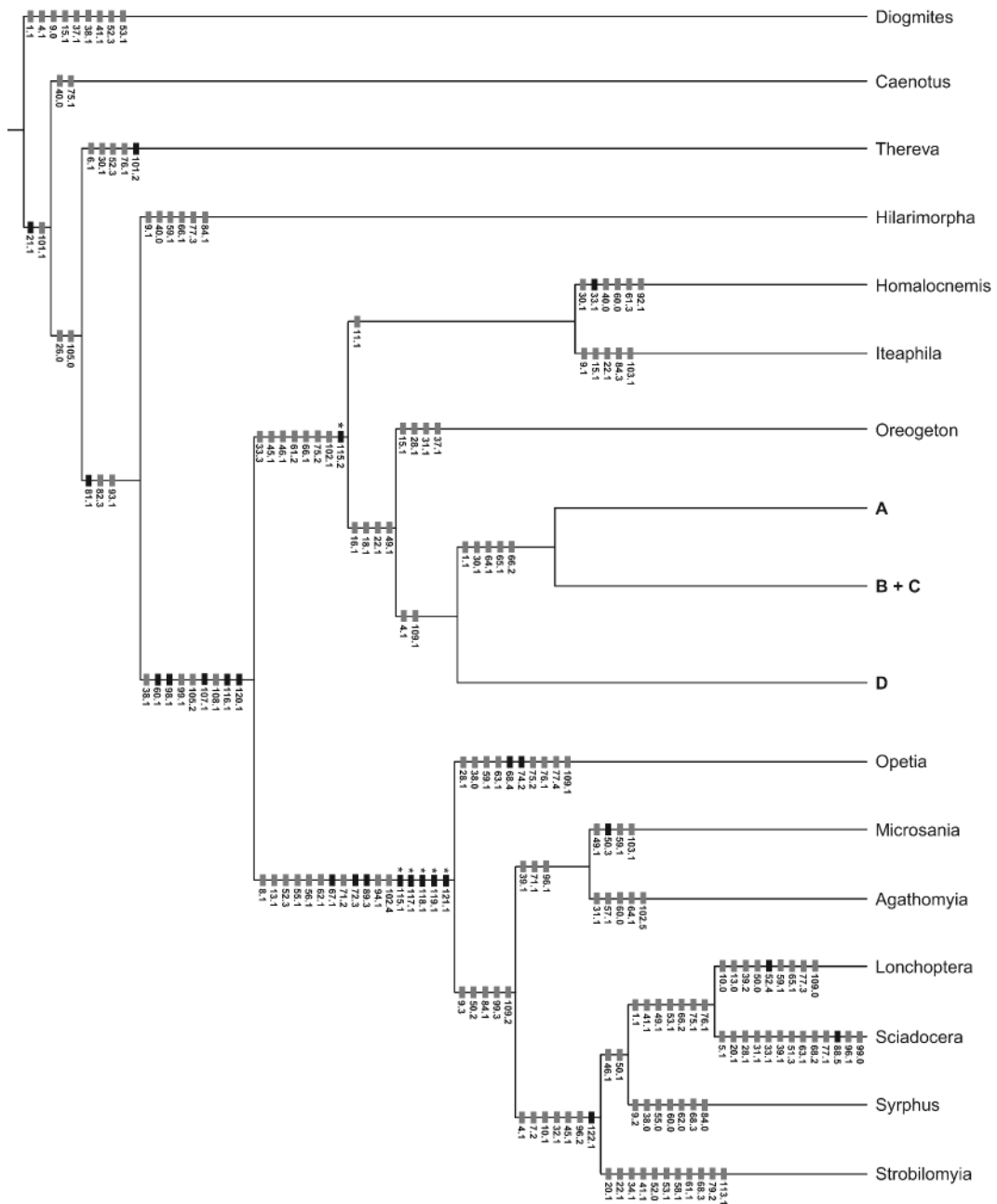
Empidoidea	
	<i>Incertae sedis (Homalocnemis, Iteaphila group, Oreogeton)</i>
Empididae	<i>Incertae sedis (Ragas group, Brochella, Philetus, Hesperempis group)</i>
	Hemerodromiinae
	Chelipodini
	Hemerodromiini
	Empidinae
	Empidini
	Hilarini
	Clinocerinae
Atelestidae	Nemedinae n. subfam.
	Atelestinae
Hybotidae	<i>Incertae sedis (Stuckenbergomyia)</i>
	Trichinae rev. stat.
	Ocydromiinae
	Oedaleinae rev. stat.
	Tachydromiinae
	Symballophthalmini n. tribe
	Tachydromiini
	Drapetini
	Hybotinae
	Bicellariini n. tribe
	Hybotini
Brachystomatidae rev. stat.	Trichopezinae
	Ceratomerinae
	Brachystomatinae
Dolichopodidae s.lat.	Microphorinae
	Parathalassiinae
	Dolichopodidae <i>s.str.</i>
	Achalcinae
	Babindellinae
	Diaphorinae
	Dolichopodinae
	Enliniinae
	Hydrophorinae
	Medeterinae
	Neurigoninae
	Peloropecodinae
	Plagioneurinae
	Rhaphiinae
	Sciapodinae
	Stolidosomatinae
	Sympycninae
	Xanthochlorinae



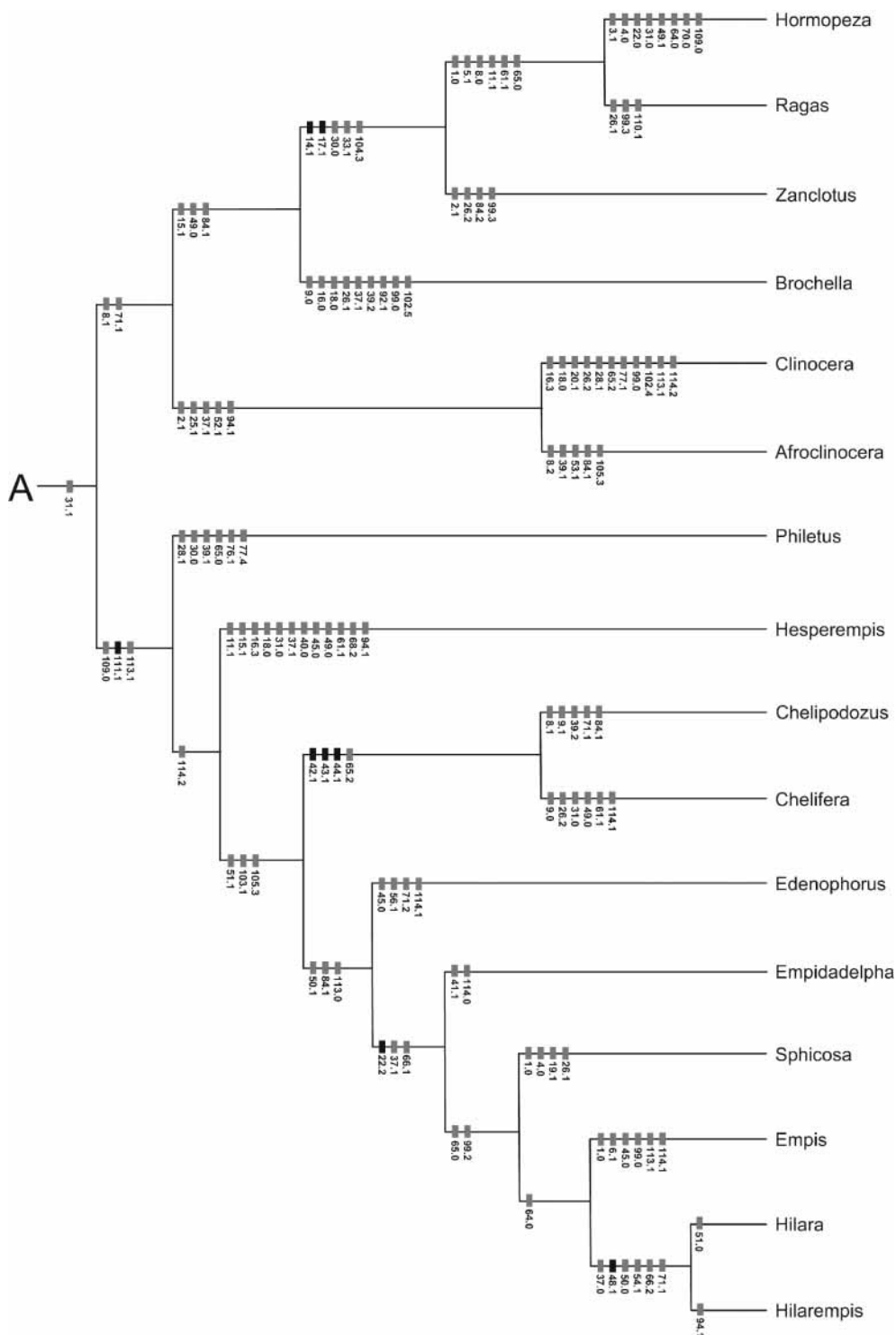
TREE 1. Strict consensus of the 1728 most parsimonious cladograms of the Eremoneura and outgroups produced by the analysis of the data matrix in Table 2. Proposed family limits are indicated by brackets on the right. Bremer support values are listed above each internode.



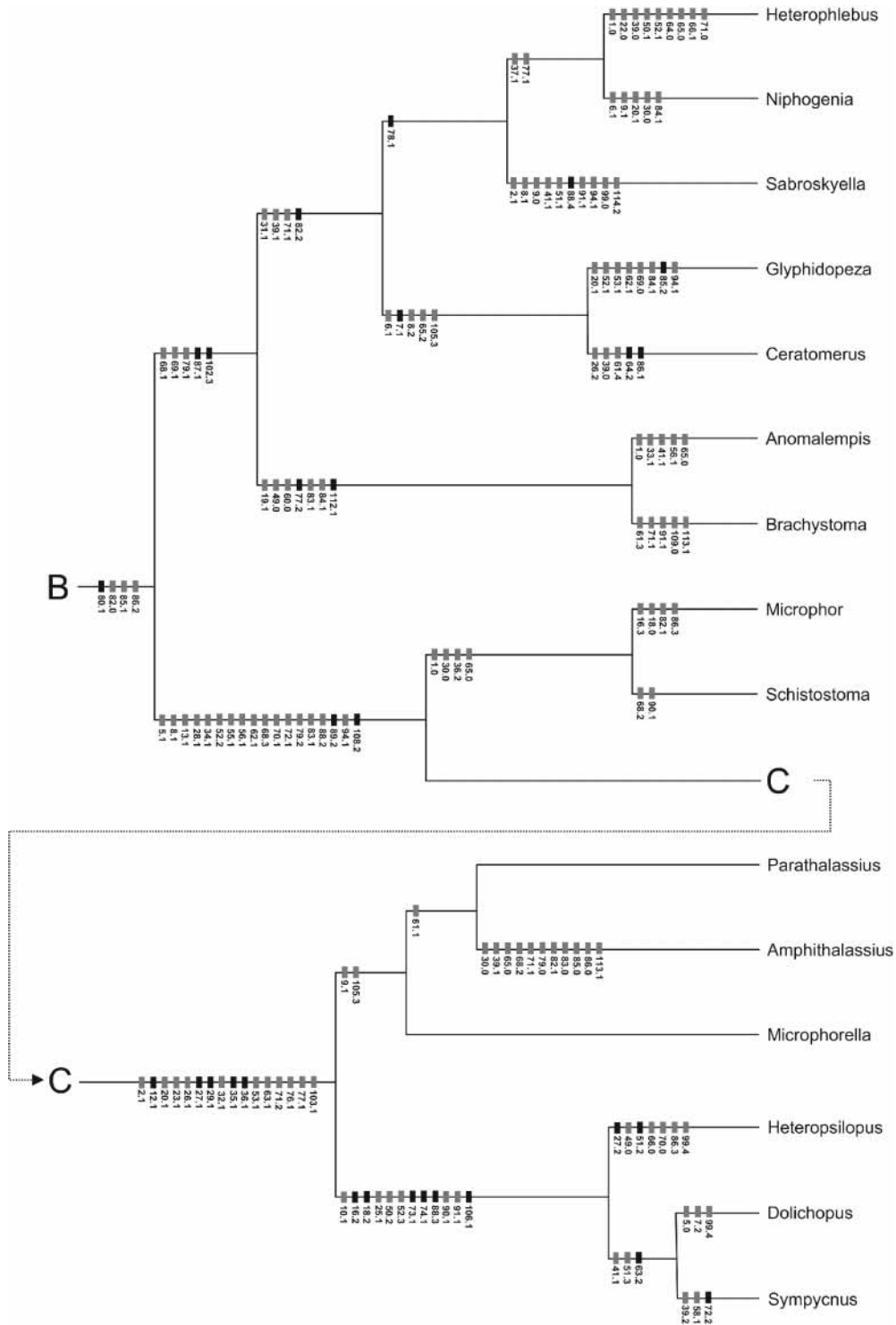
TREE 2. Empidoidea portion of the strict consensus of the 1728 most parsimonious cladograms produced by the analysis of the data matrix in Table 2. Proposed genus group, tribe, subfamily and family limits are indicated by brackets on the right. Bremer support values are listed above each internode.



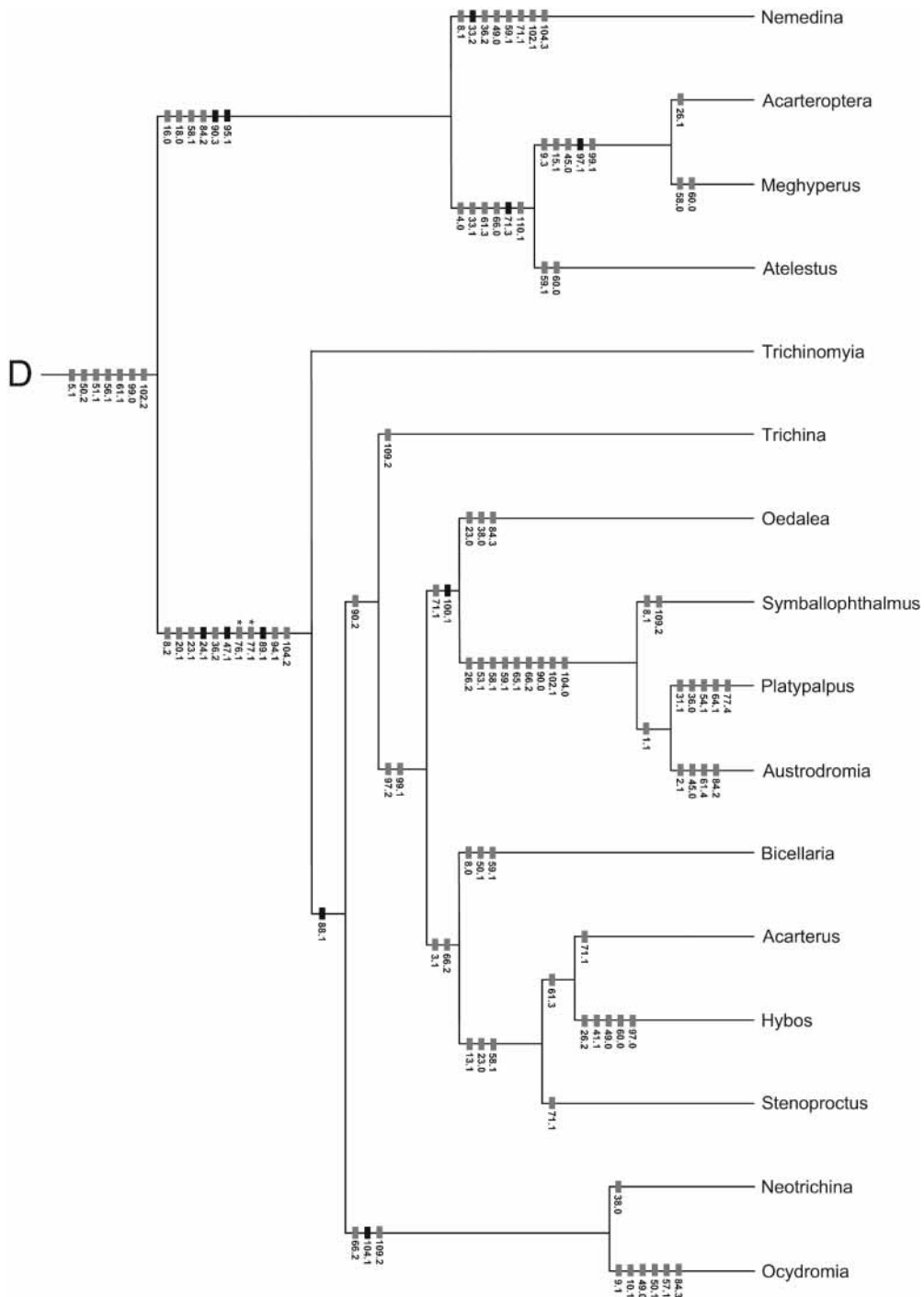
TREE 3. One of the 1728 most parsimonious cladograms of the Eremoneura and outgroups produced by the analysis of the data matrix in Table 2, and the single tree obtained by successive approximations weighting. Branches A-D continued in Trees 4-6. Character distribution shown by black hash marks for uniquely derived states and gray hash marks for homoplasious states (including subsequent transformations). * indicates that exact placement of state is equivocal due to missing data in basal lineage of supported clade.



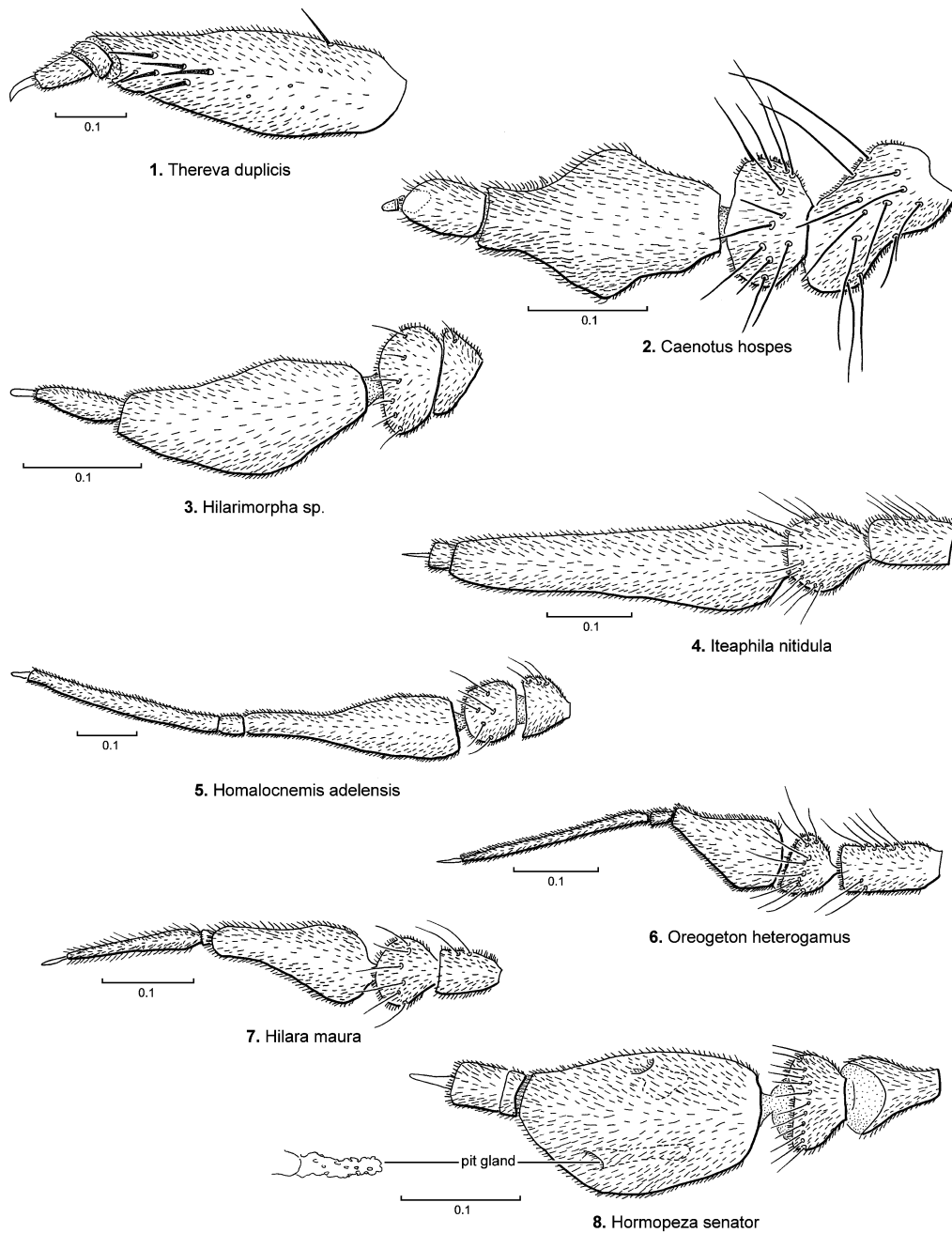
TREE 4. One of the 1728 most parsimonious cladograms produced by the analysis of the data matrix in Table 2, and the single tree obtained by successive approximations weighting (continued). The Empididae portion of the tree. Character distribution shown by black hash marks for uniquely derived states and gray hash marks for homoplasious states (including subsequent transformations).



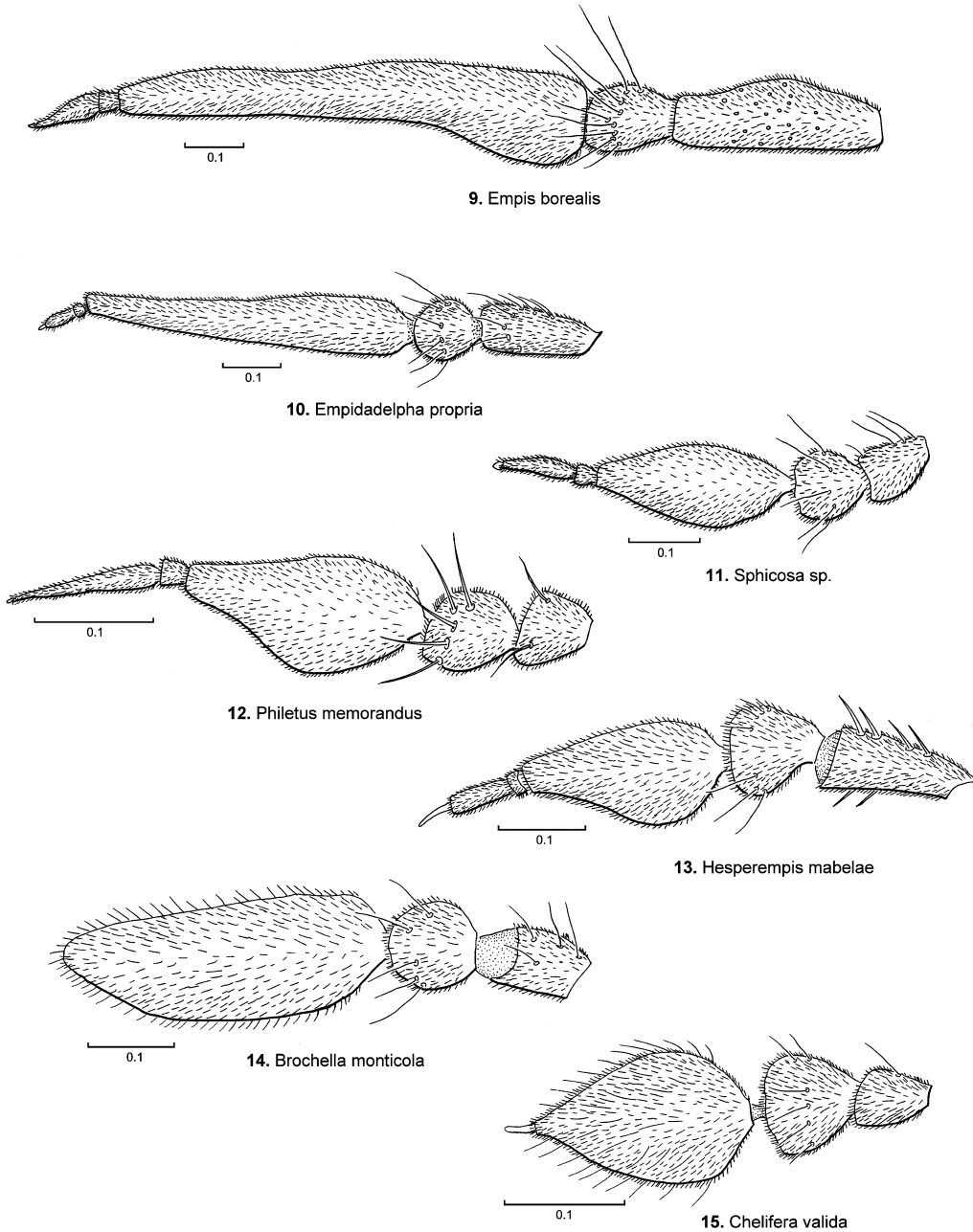
TREE 5. One of the 1728 most parsimonious cladograms produced by the analysis of the data matrix in Table 2, and the single tree obtained by successive approximations weighting (continued). The Brachystomatidae and Dolichopodidae portion of the tree. Character distribution shown by black hash marks for uniquely derived states and gray hash marks for homoplasious states (including subsequent transformations).



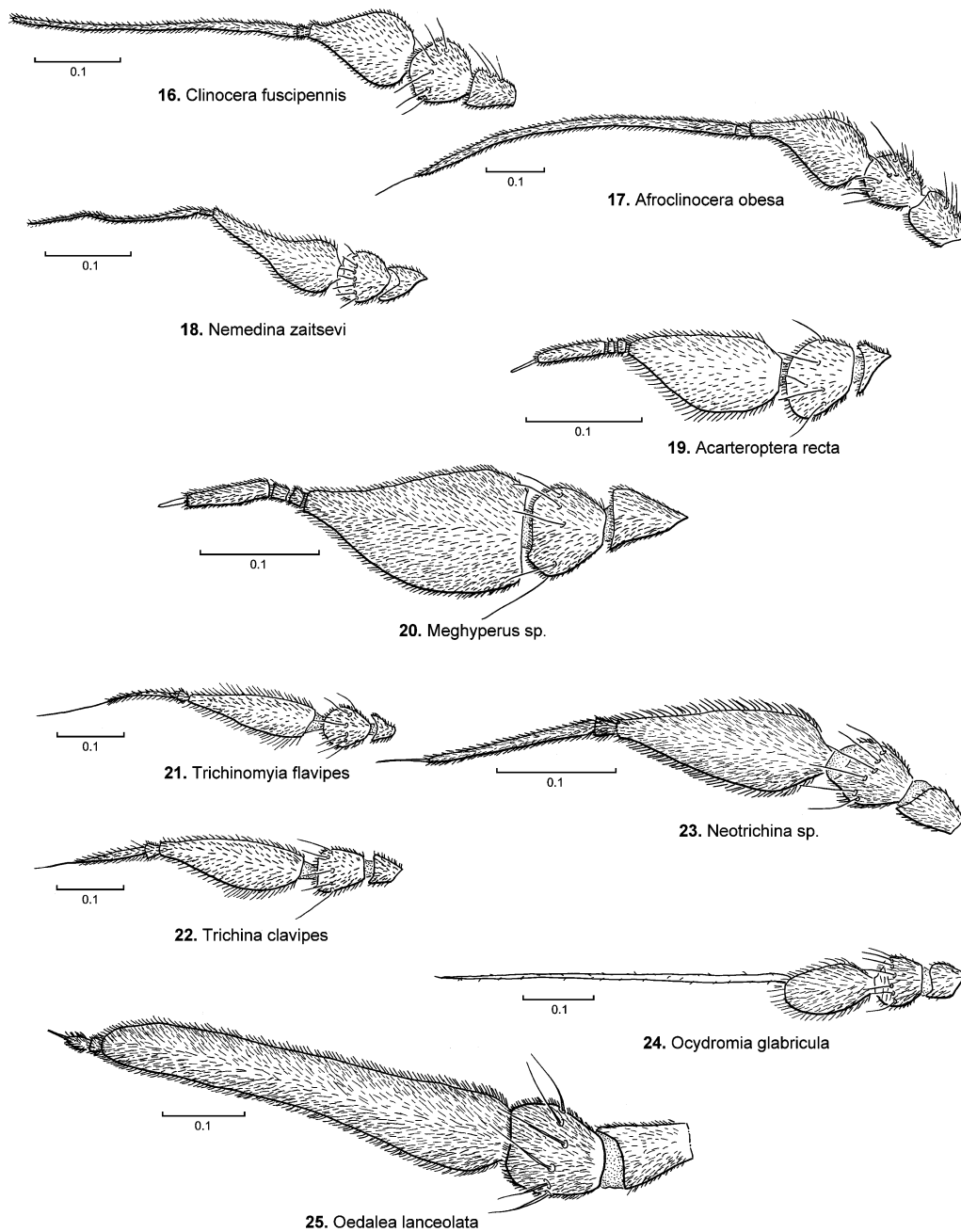
TREE 6. One of the 1728 most parsimonious cladograms produced by the analysis of the data matrix in Table 2, and the single tree obtained by successive approximations weighting (continued). The Atelestidae and Hybotidae portion of the tree. Character distribution shown by black hash marks for uniquely derived states and gray hash marks for homoplasious states (including subsequent transformations).



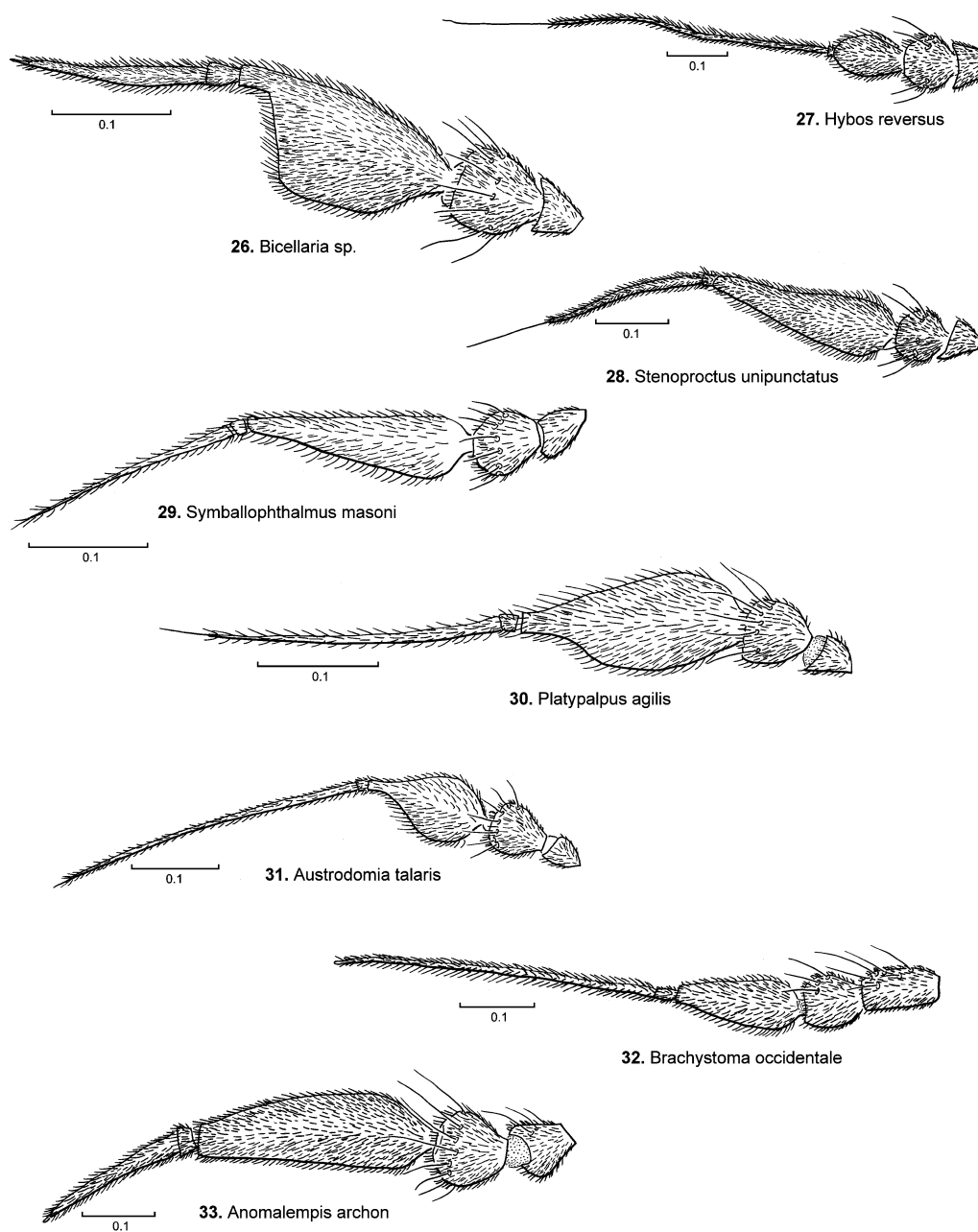
FIGURES 1–8. Antennae of Asiloidea and Empidoidea. **1.** Therevidae, *Thereva duplcis* Coquillett, scape and pedicel removed. **2.** Scenopinidae, *Caenotus hospes* Melander. **3.** Hilarimorphidae, *Hilarimorpha* sp. **4.** Empidoidea, *Iteaphila nitidula* Zetterstedt. **5.** Empidoidea, *Homalocnemis adelensis* (Miller). **6.** Empidoidea, *Oreogeton heterogamus* Melander. **7.** Empidoidea, *Hilara maura* (Fab.). **8.** Empidoidea, *Hormopeza senator* Melander, pit gland illustrated on left. Scale in mm.



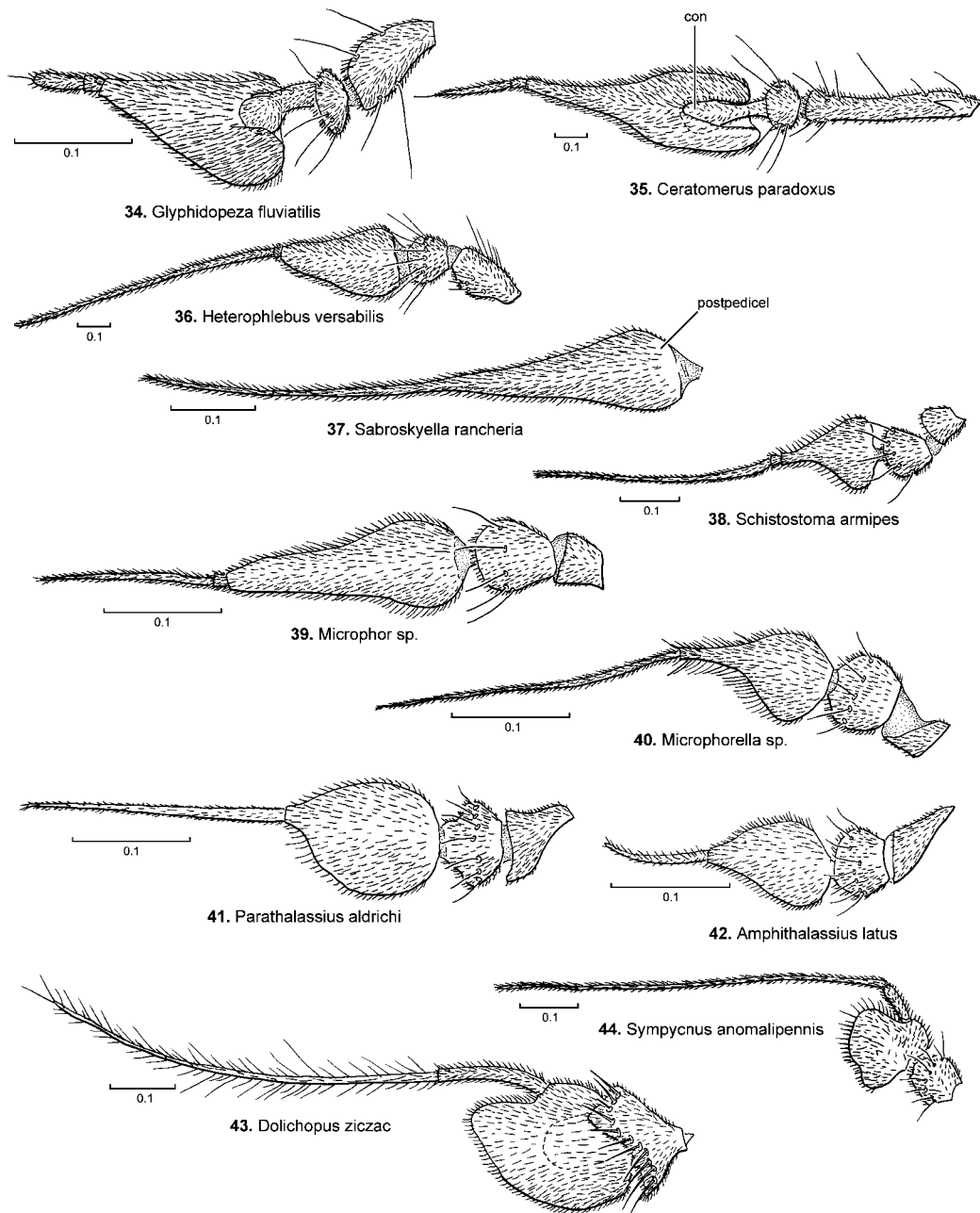
FIGURES 9–15. Antennae of Empidoidea. 9. *Empis borealis* L. 10. *Empidadelpha propria* Collin. 11. *Sphicosa* sp. 12. *Philetus memorandum* Melander. 13. *Hesperempis mabelae* Melander. 14. *Brochella monticola* Melander. 15. *Chelifera valida* Loew. Scale in mm.



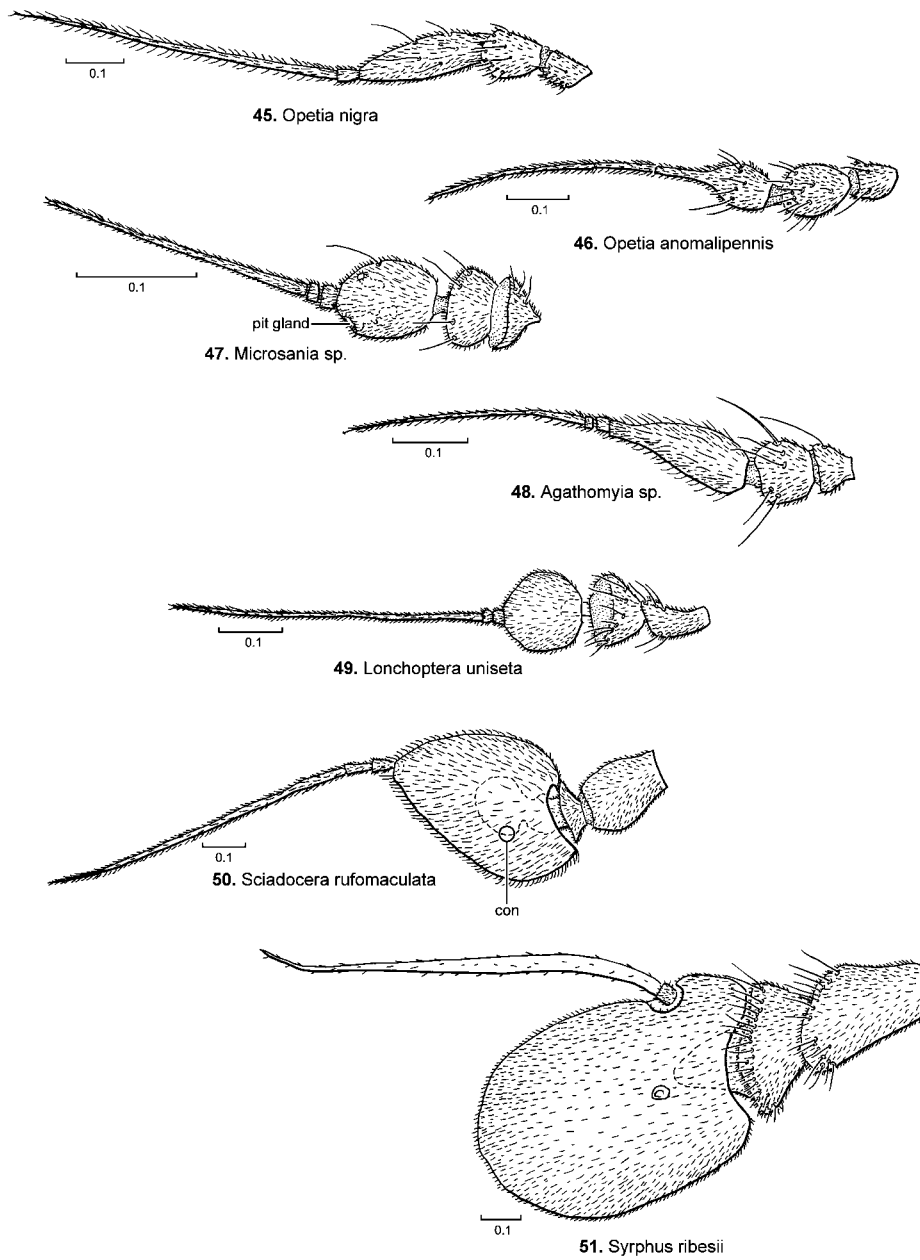
FIGURES 16–25. Antennae of Empidoidea. **16.** *Clinocera fuscipennis* Loew. **17.** *Afroclinocera obesa* Sinclair. **18.** *Nemedina zaitsevi* Sinclair & Shamshev. **19.** *Acarteroptera recta* Collin. **20.** *Meghyperus* sp. **21.** *Trichinomyia flavipes* (Zetterstedt). **22.** *Trichina clavipes* (Meigen). **23.** *Neotrichina* sp. **24.** *Ocydromia glabricula* (Fällén). **25.** *Oedalea lanceolata* Melander. Scale in mm.



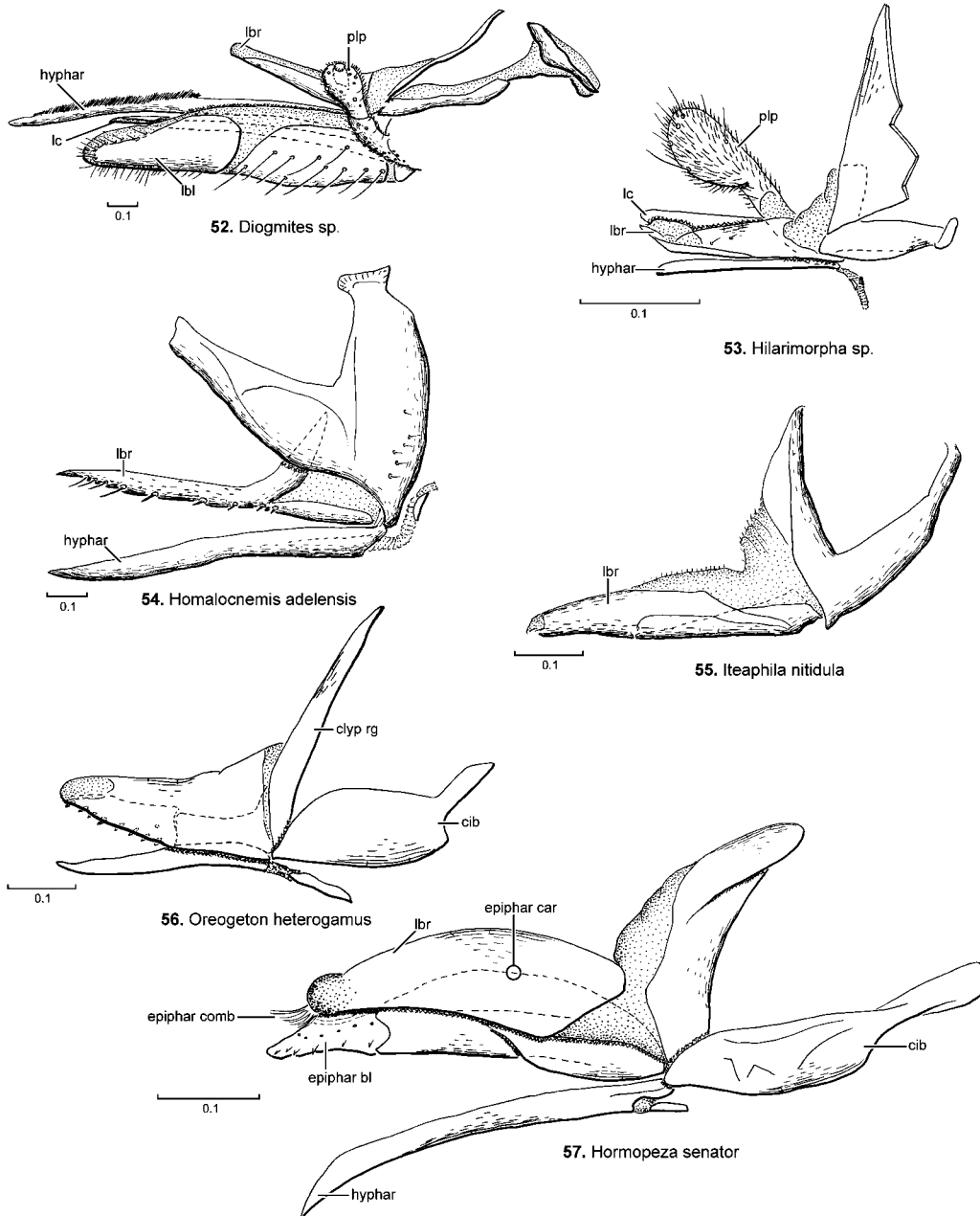
FIGURES 26–33. Antennae of Empidoidea. 26. *Bicellaria* sp. 27. *Hybos reversus* Walker. 28. *Stenoproctus unipunctatus* Loew. 29. *Symballophthalmus masoni* Chillcott. 30. *Platypalpus agilis* (Meigen). 31. *Austrodomia talaris* Collin. 32. *Brachystoma occidentale* Melander. 33. *Anomalempis archon* Melander. Scale in mm.



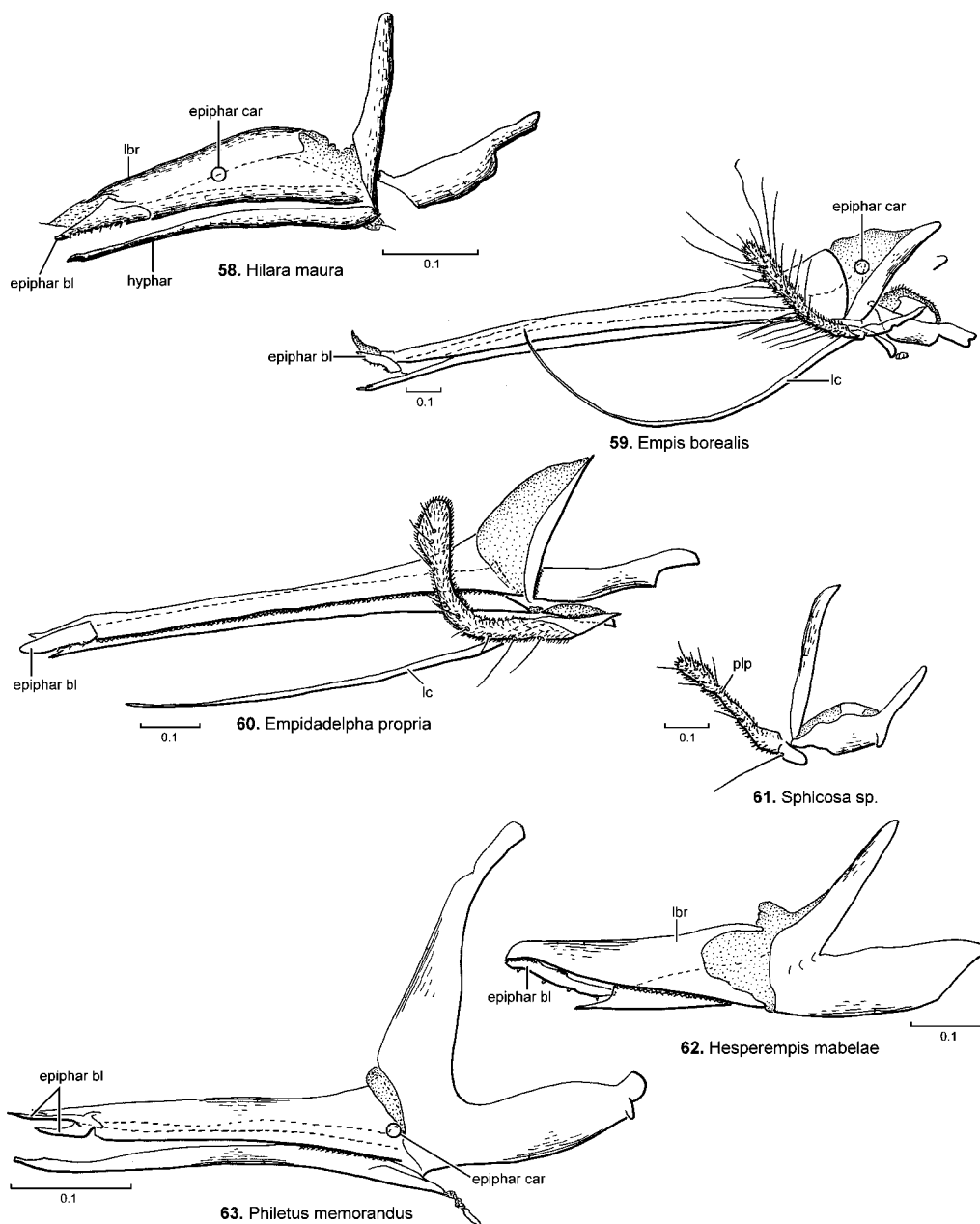
FIGURES 34–44. Antennae of Empidoidea. **34.** *Glyphidopeza fluviatilis* Sinclair. **35.** *Ceratomerus paradoxus* Philippi. **36.** *Heterophlebus versabilis* (Collin). **37.** *Sabroskyella rancheria* Wilder, scape and pedicel removed. **38.** *Schistostoma armipes* (Melander). **39.** *Microphor* sp. **40.** *Microphorella* sp. **41.** *Parathalassius aldrichi* Melander. **42.** *Amphithalassius latus* Ulrich. **43.** *Dolichopus ziczac* Wiedemann group, scape removed. **44.** *Sympycnus anomalipennis* Becker, scape removed. Abbreviation: con—conus. Scale in mm.



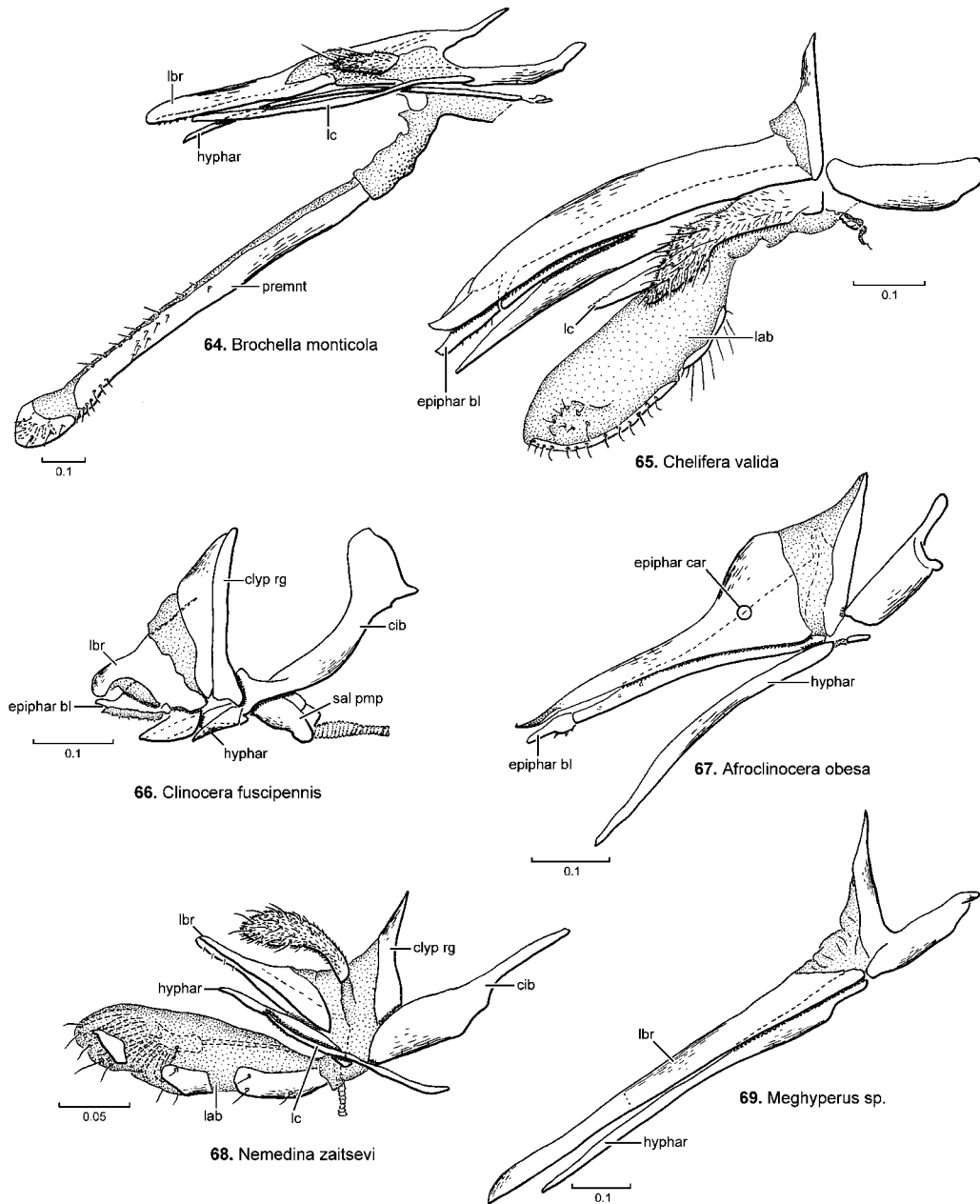
FIGURES 45–51. Antennae of Cyclorrhapha. **45.** *Opetia nigra* Meigen. **46.** *Opetia anomalipennis* Saigusa. **47.** *Microsania* sp. **48.** *Agathomyia* sp. **49.** *Lonchoptera unisetata* Curran. **50.** *Sciadocera rufomaculata* White. **51.** *Syrphus ribesii* (L.). Abbreviation: con—conus. Scale in mm.



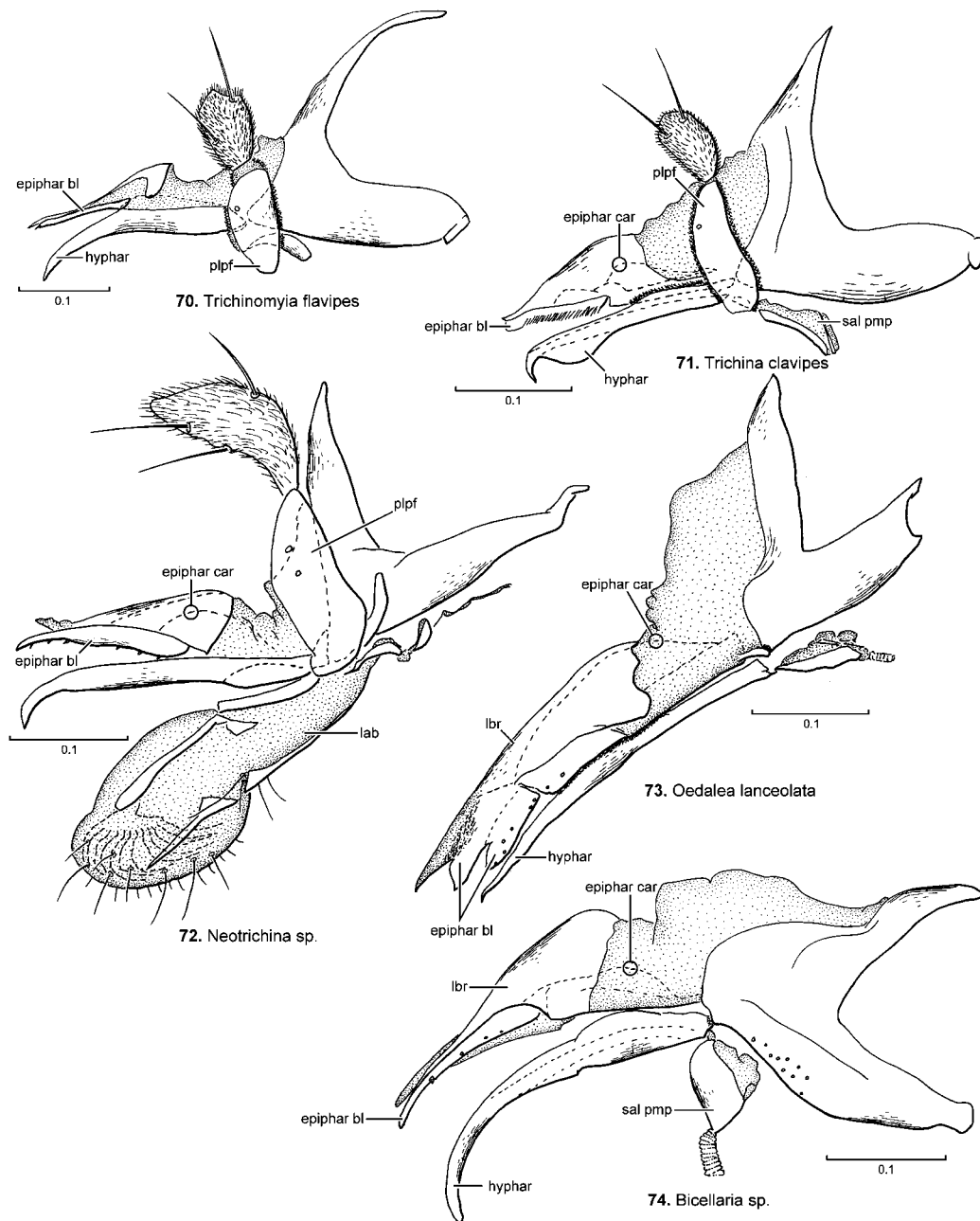
FIGURES 52–57. Mouthparts of Asiloidea and Empidoidea. **52.** Asilidae, *Diogmites* sp. **53.** Hilarimorphidae, *Hilarimorpha* sp., labium removed. **54.** Empidoidea, *Homalocnemis adelensis* (Miller), maxillae and labium removed. **55.** Empidoidea, *Iteaphila nitidula* Zetterstedt, labrum, cibarium and clypeal ridge. **56.** Empidoidea, *Oreogeton heterogamus* Melander, maxillae and labium removed. **57.** Empidoidea, *Hormopeza senator* Melander, maxillae and labium removed. Abbreviations: cib—cibarium, clyp rg—clypeal ridge, epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, epiphar comb—epipharyngeal comb, hyphar—hypopharynx, lbl—labellum, lbr—labrum, lc—lacinia, plp—palpus. Scale in mm.



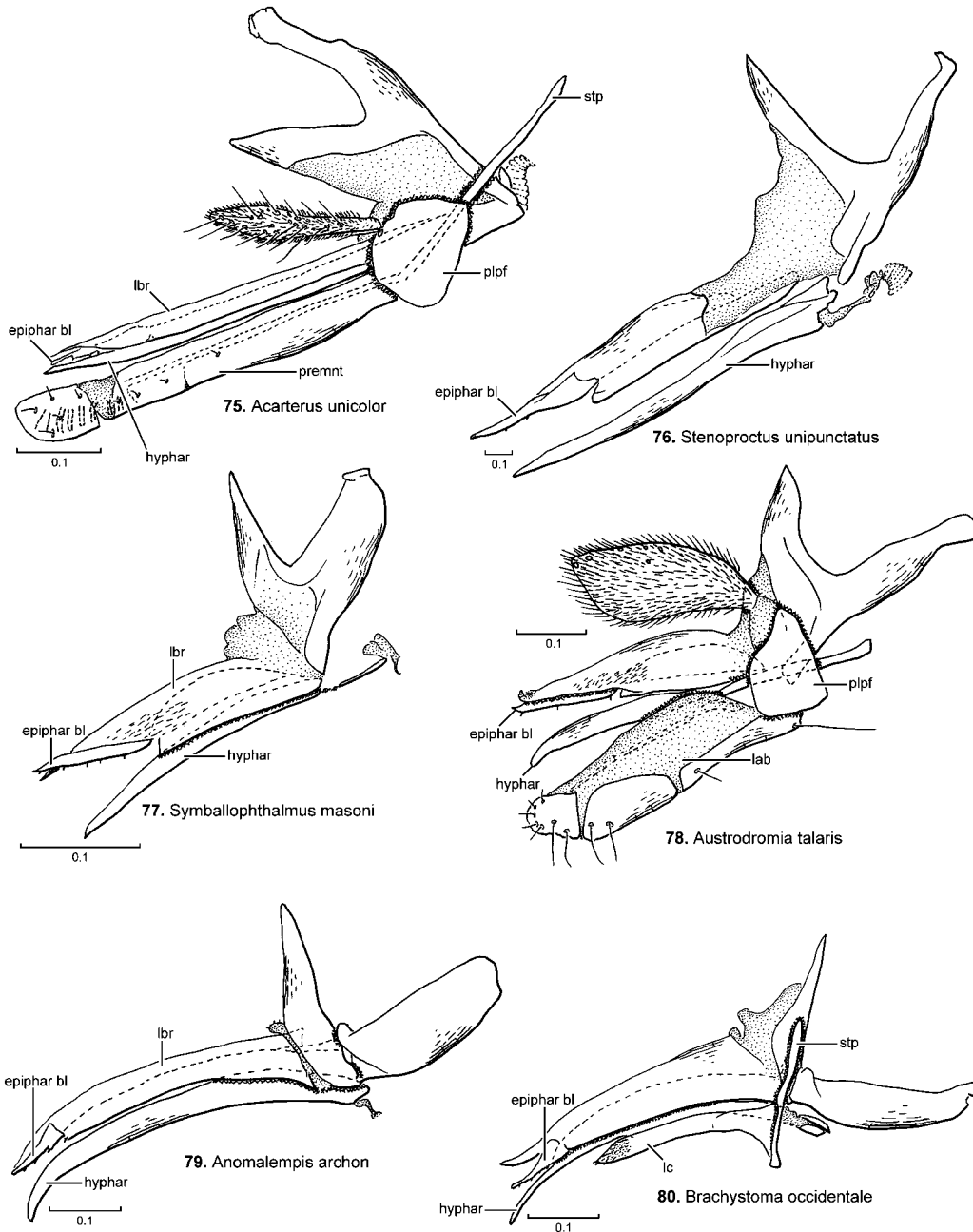
FIGURES 58–63. Mouthparts of Empidoidea. **58.** *Hilara maura* (Fab.), maxillae and labium removed. **59.** *Empis borealis* L., labium removed. **60.** *Empidadelpha propria* Collin, labium removed. **61.** *Spicosa* sp., palpus, clypeal ridge and cibarium. **62.** *Hesperempis mabelae* Melander, labrum, cibarium and clypeal ridge. **63.** *Philetus memorandum* Melander, maxillae and labium removed. Abbreviations: epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lbr—labrum, lc—lacinia, plp—palpus. Scale in mm.



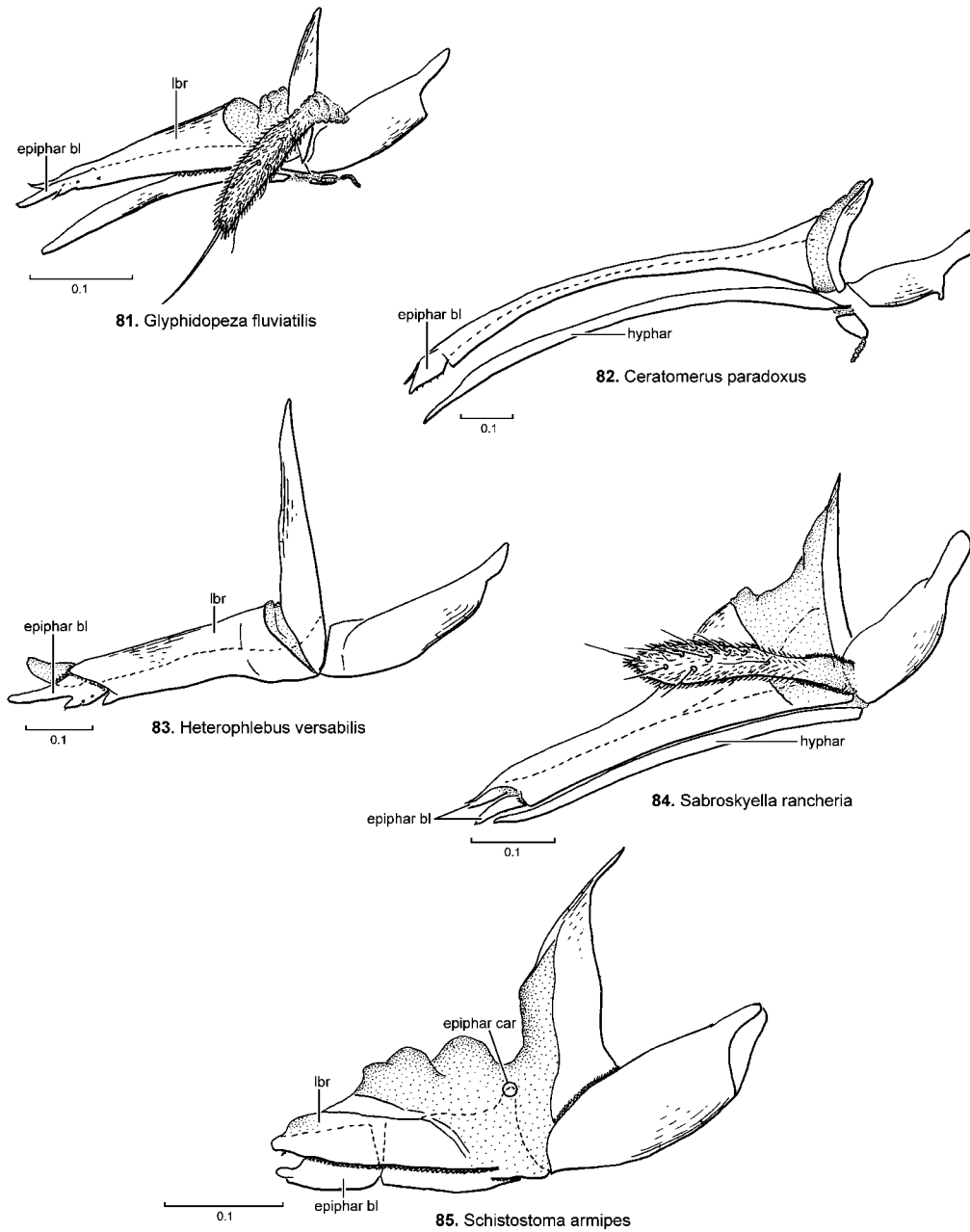
FIGURES 64–69. Mouthparts of Empidoidea. **64.** *Brochella monticola* Melander. **65.** *Chelifera valida* Loew. **66.** *Clinocera fuscipennis* Loew, maxillae and labium removed. **67.** *Afroclinocera obesa* Sinclair, maxillae and labium removed. **68.** *Nemedina zaitsevi* Sinclair & Shamshev. **69.** *Meghyperus* sp., maxillae and labium removed. Abbreviations: cib—cibarium, clyp rg—clypeal ridge, epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lab—labium, lbr—labrum, lc—lacinia, premnt—prementum, sal pmp—salivary pump. Scale in mm.



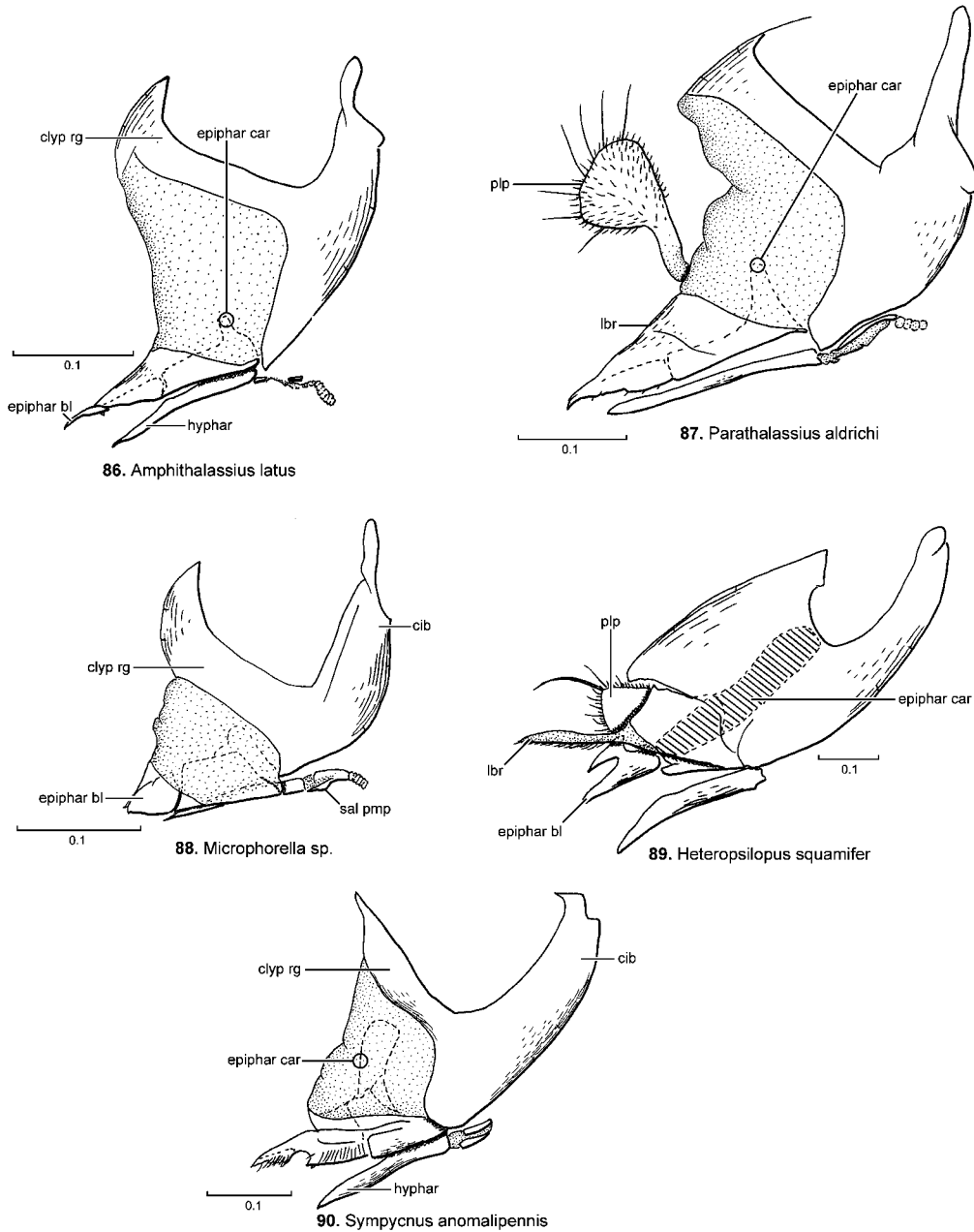
FIGURES 70–74. Mouthparts of Empidoidea. **70.** *Trichinomyia flavipes* (Zetterstedt), lacinia and labium removed. **71.** *Trichina clavipes* (Meigen), lacinia and labium removed. **72.** *Neotrichina* sp. **73.** *Oedalea lanceolata* Melander, maxillae and labium removed. **74.** *Bicellaria* sp., maxillae and labium removed. Abbreviations: epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lab—labium, lbr—labrum, plpf—palpifer, sal pmp—salivary pump. Scale in mm.



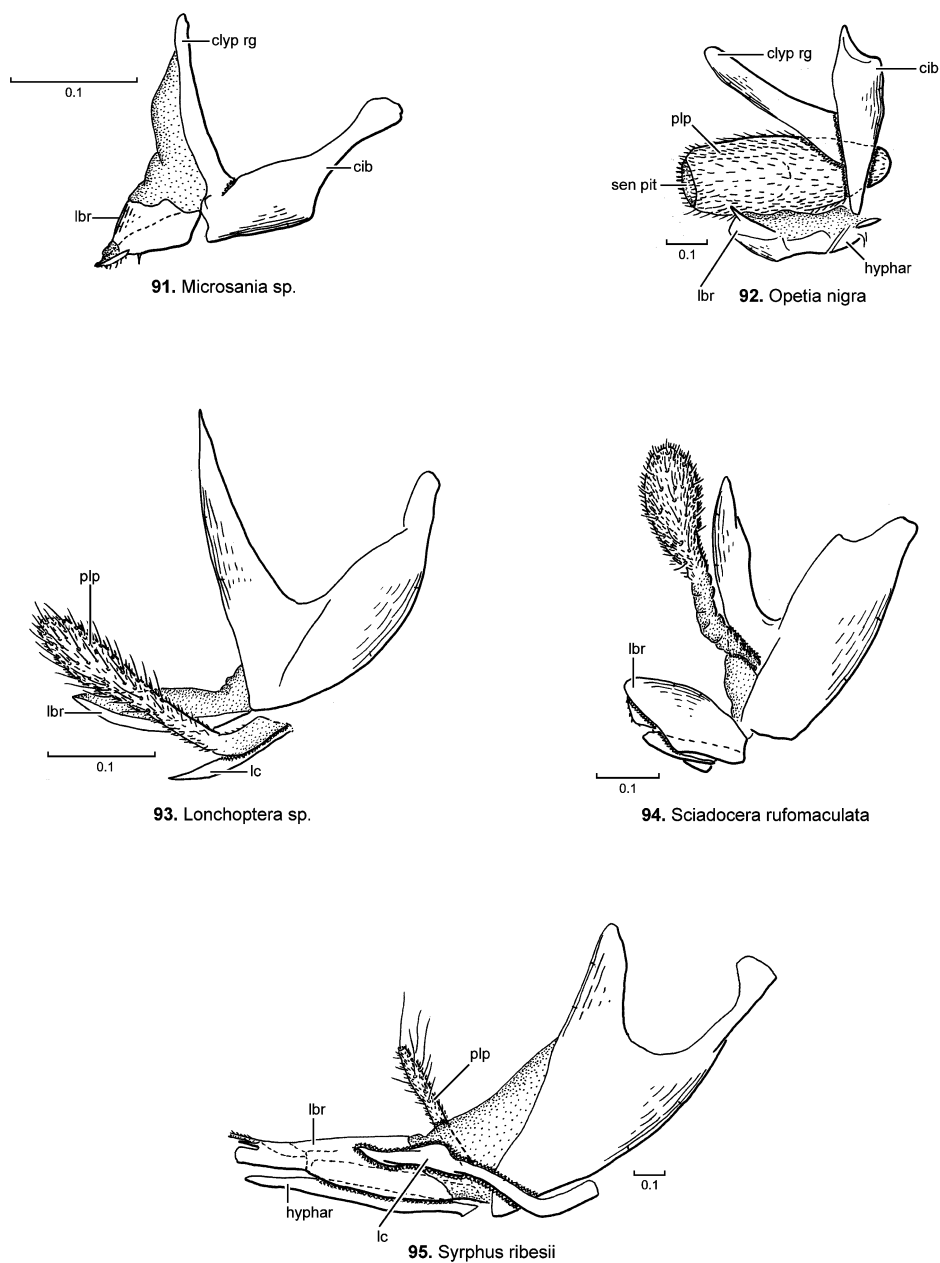
FIGURES 75–80. Mouthparts of Empidoidea. **75.** *Acarterus unicolor* Loew. **76.** *Stenoproctus unipunctatus* Loew, maxillae and labium removed. **77.** *Symballophthalmus masoni* Chillcott, maxillae and labium removed. **78.** *Austrodromia talaris* Collin. **79.** *Anomalempis achron* Melander, maxillae and labium removed. **80.** *Brachystoma occidentale* Melander, palpus and labium removed. Abbreviations: epiphar bl—epipharyngeal blade, hyphar—hypopharynx, lab—labium, lbr—labrum, lc—lacinia, plpf—palpifer, premnt—prementum, stp—stipes. Scale in mm.



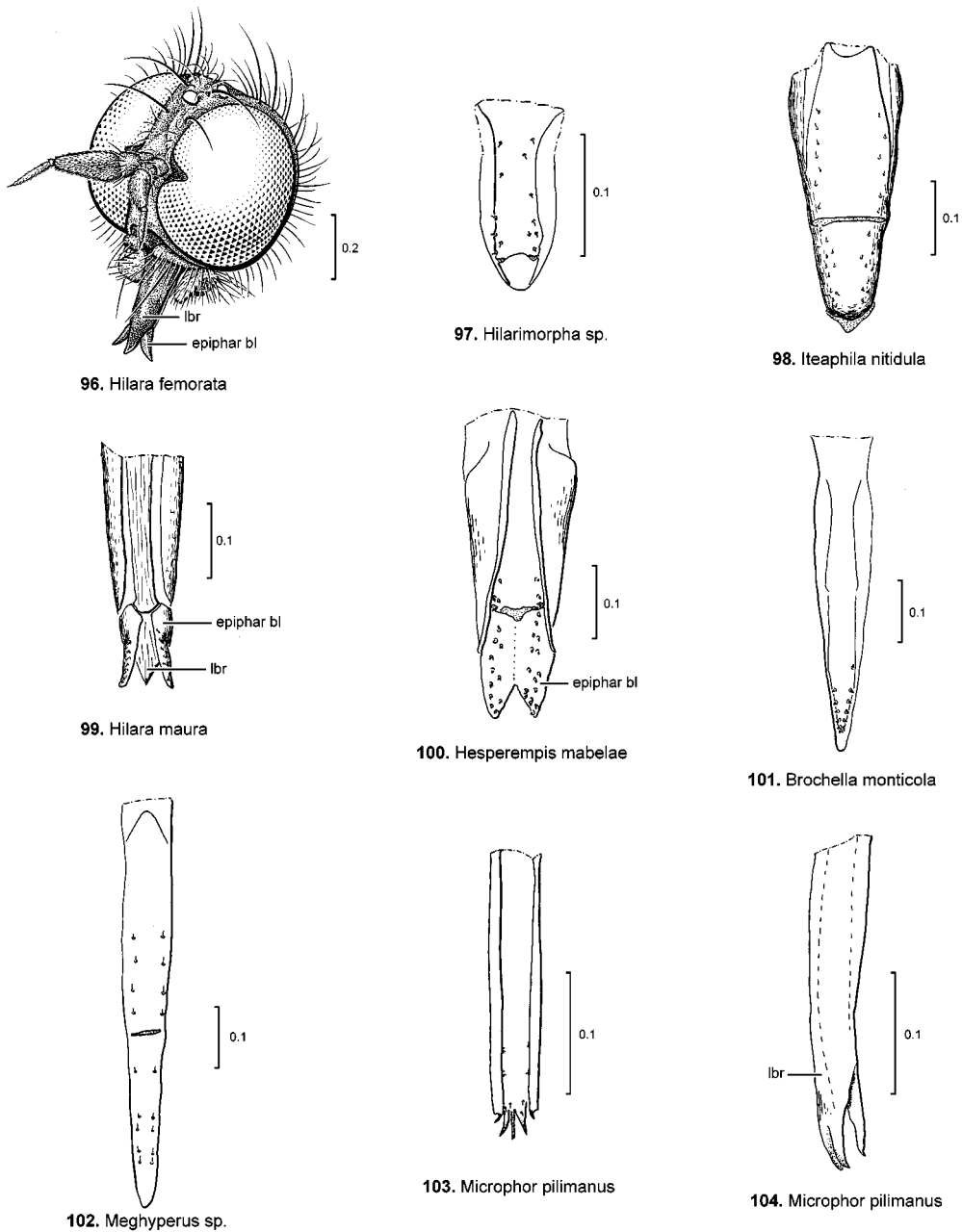
FIGURES 81–85. Mouthparts of Empidoidea. **81.** *Glyphidopeza fluviatilis* Sinclair, lacinia and labium removed. **82.** *Ceratomerus paradoxus* Philippi, maxillae and labium removed. **83.** *Heterophlebus versabilis* (Collin), hypopharynx, maxillae and labium removed. **84.** *Sabroskyella rancheria* Wilder, lacinia and labium removed. **85.** *Schistostoma armipes* (Melander), hypopharynx, maxillae and labium removed. Abbreviations: epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lbr—labrum. Scale in mm.



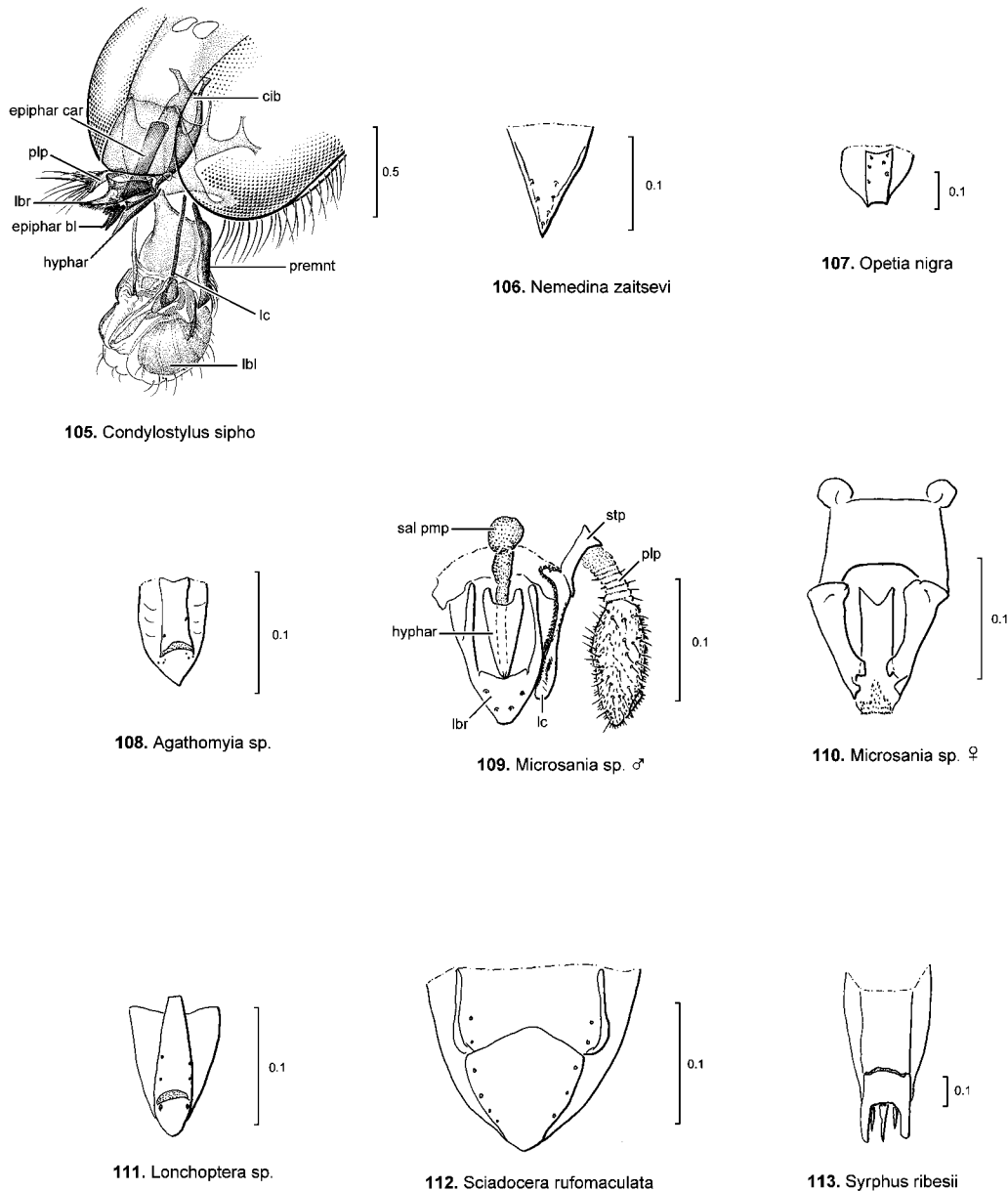
FIGURES 86–90. Mouthparts of Empidoidea. **86.** *Amphithalassius latus* Ulrich, maxillae and labium removed. **87.** *Parathalassius aldrichi* Melander, lacinia and labium removed. **88.** *Microphorella* sp., maxillae and labium removed. **89.** *Heteropsilopus squamifer* Hardy, lacinia and labium removed. **90.** *Sympycnus anomalipennis* Becker, maxillae and labium removed. Abbreviations: cib—cibarium, clyp rg—clypeal ridge, epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lbr—labrum, plp—palpus, sal pmp—salivary pump. Scale in mm.



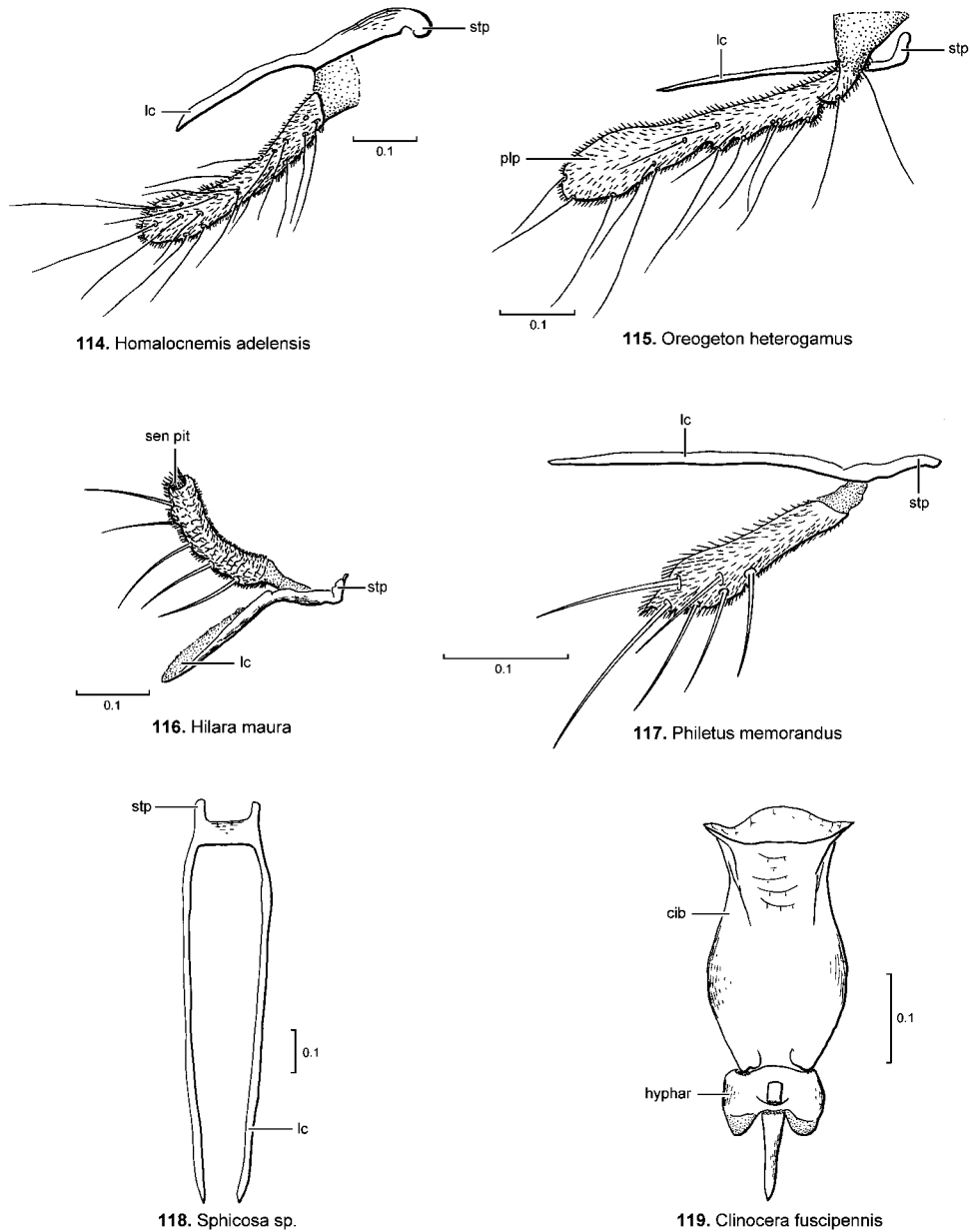
FIGURES 91–95. Mouthparts of Cyclorrhapha. **91.** *Microsania* sp., hypopharynx, maxillae and labium removed. **92.** *Opetia nigra* Meigen, lacinia and labium removed. **93.** *Lonchoptera* sp., labium removed. **94.** *Sciadocera rufomaculata* White, lacinia and labium removed. **95.** *Syrphus ribesii* (L.), labium removed. Abbreviations: cib—cibarium, clyp rg—clypeal ridge, hyphar—hypopharynx, lbr—labrum, lc—lacinia, plp—palpus, sen pit—sensory pit. Scale in mm.



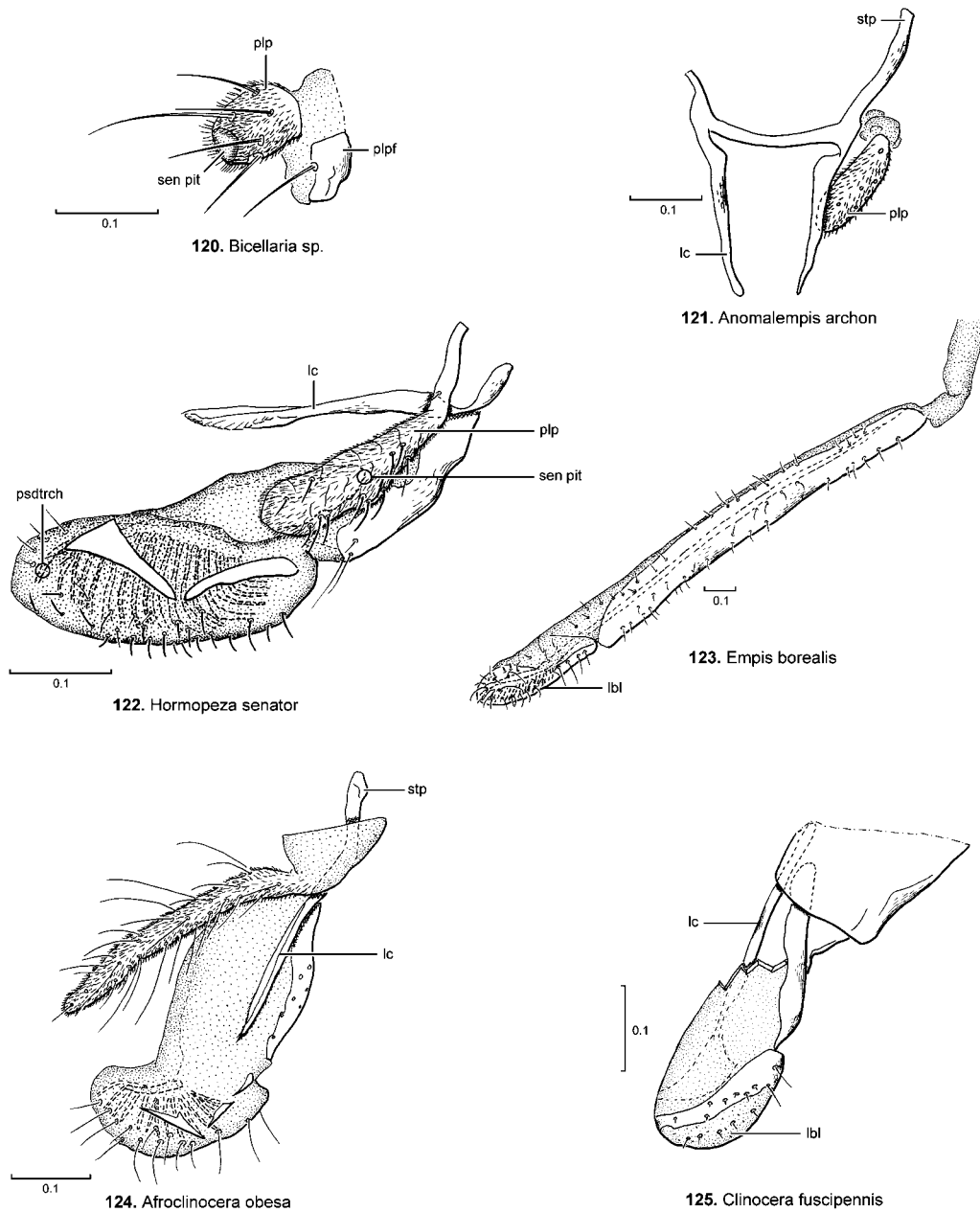
FIGURES 96–104. Labrum of Hilarimorphidae and Empidoidea. **96.** Empidoidea, *Hilara femorata* Loew (after Steyskal & Knutson 1981), head showing relationship of labrum. **97.** Hilarimorphidae, *Hilarimorpha* sp., ventral view. **98.** Empidoidea, *Iteaphila* sp., ventral view. **99.** Empidoidea, *Hilara maura* (Fab.), ventral view. **100.** Empidoidea, *Hesperempis mabelae* Melander, ventral view. **101.** Empidoidea, *Brochella monticola* Melander, ventral view. **102.** Empidoidea, *Meghyperus* sp., ventral view. **103–104.** Empidoidea, *Microphor pilimanus* (Strobl): **103.** ventral view. **104.** lateral view. Abbreviations: epihar bl—epipharyngeal blade, lbr—labrum. Scale in mm.



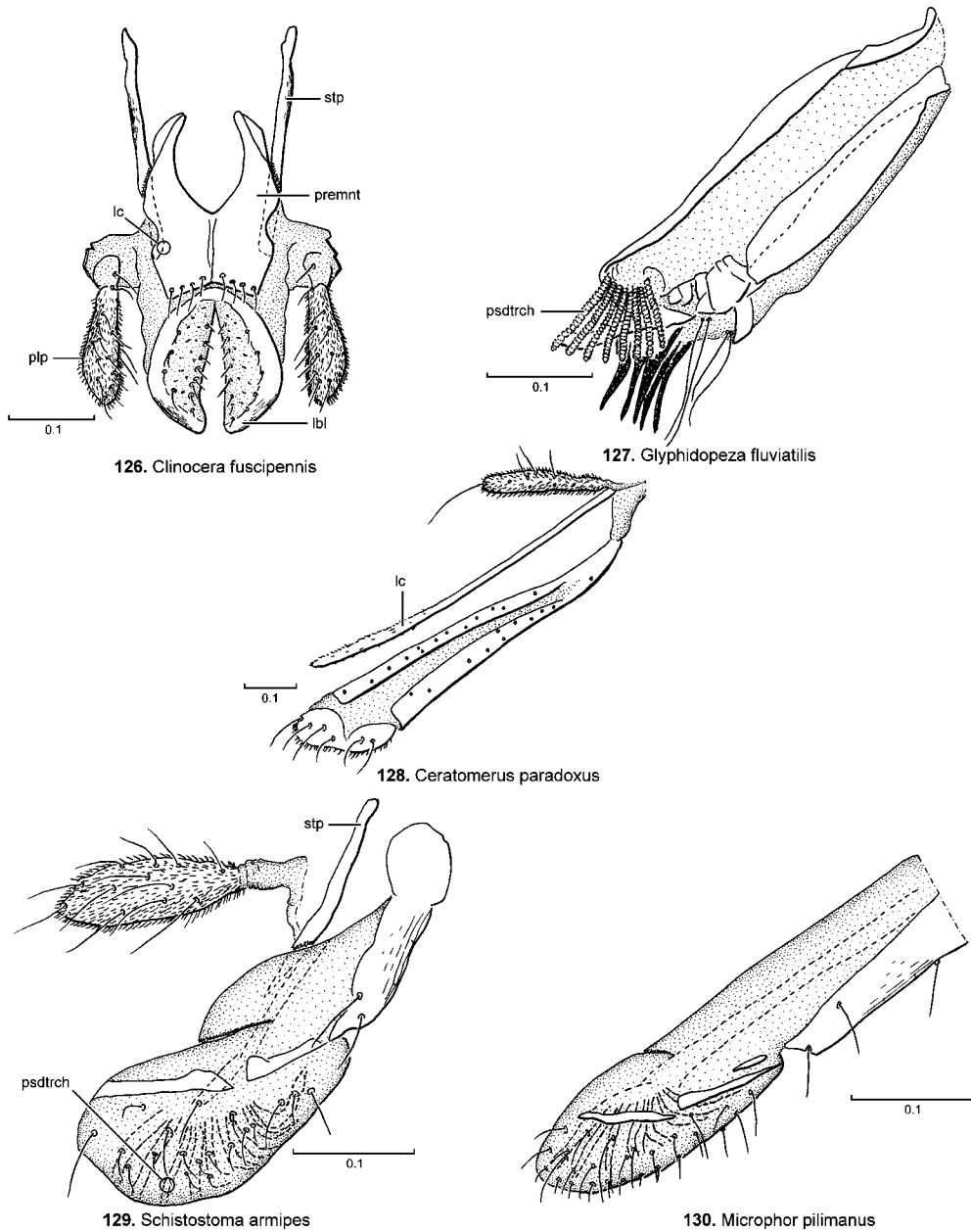
FIGURES 105–113. Labrum of Empidoidea and Cyclorrhapha. **105.** Empidoidea, *Condylostylus siphon* (Say) (after McAlpine 1981), head showing relationship of labrum. **106.** Empidoidea, *Nemedina zaitsevi* Sinclair & Shamshev, ventral view. **107.** Opetiidae, *Opetia nigra* Meigen, ventral view. **108.** Platypezidae, *Agathomyia* sp., ventral view. **109.** Platypezidae, *Microsania* sp., male, ventral view including hypopharynx and maxilla. **110.** Platypezidae, *Microsania* sp., female, ventral view. **111.** Lonchopteridae, *Lonchoptera* sp., ventral view. **112.** Sciadoceridae, *Sciadocera rufomaculata* White, ventral view. **113.** Syrphidae, *Syrphus ribesii* (L.), ventral view. Abbreviations: cib—cibarium, epiphar bl—epipharyngeal blade, epiphar car—epipharyngeal carina, hyphar—hypopharynx, lbl—labellum, lbr—labrum, lc—lacinia, plp—palpus, premnt—prementum, sal pmp—salivary pump, stp—stipes. Scale in mm.



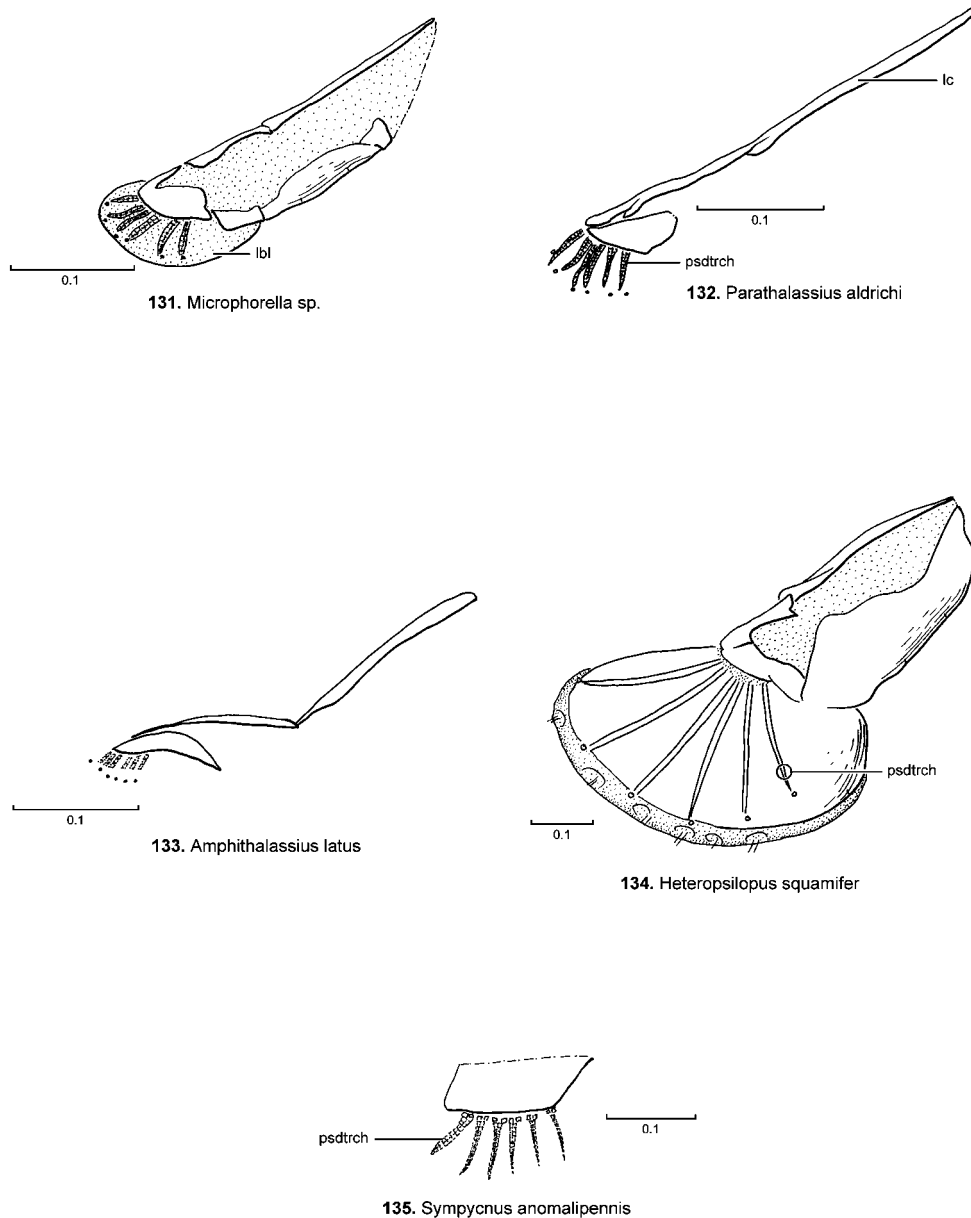
FIGURES 114–119. Mouthparts of Empidoidea. **114.** *Homalocnemis adelensis* (Miller), maxilla, lateral view. **115.** *Oreogeton heterogamus* Melander, maxilla, lateral view. **116.** *Hilara maura* (Fab.), maxilla, ventral view. **117.** *Philetus memorandum* Melander, maxilla, lateral view. **118.** *Sphicosa* sp., maxilla, palp removed, posterior view. **119.** *Clinocera fuscipennis* Loew, cibarium and hypopharynx, posterior view. Abbreviations: cib—cibarium, hyphar—hypopharynx, lc—lacinia, plp—palpus, sen pit—sensory pit, stp—stipes. Scale in mm.



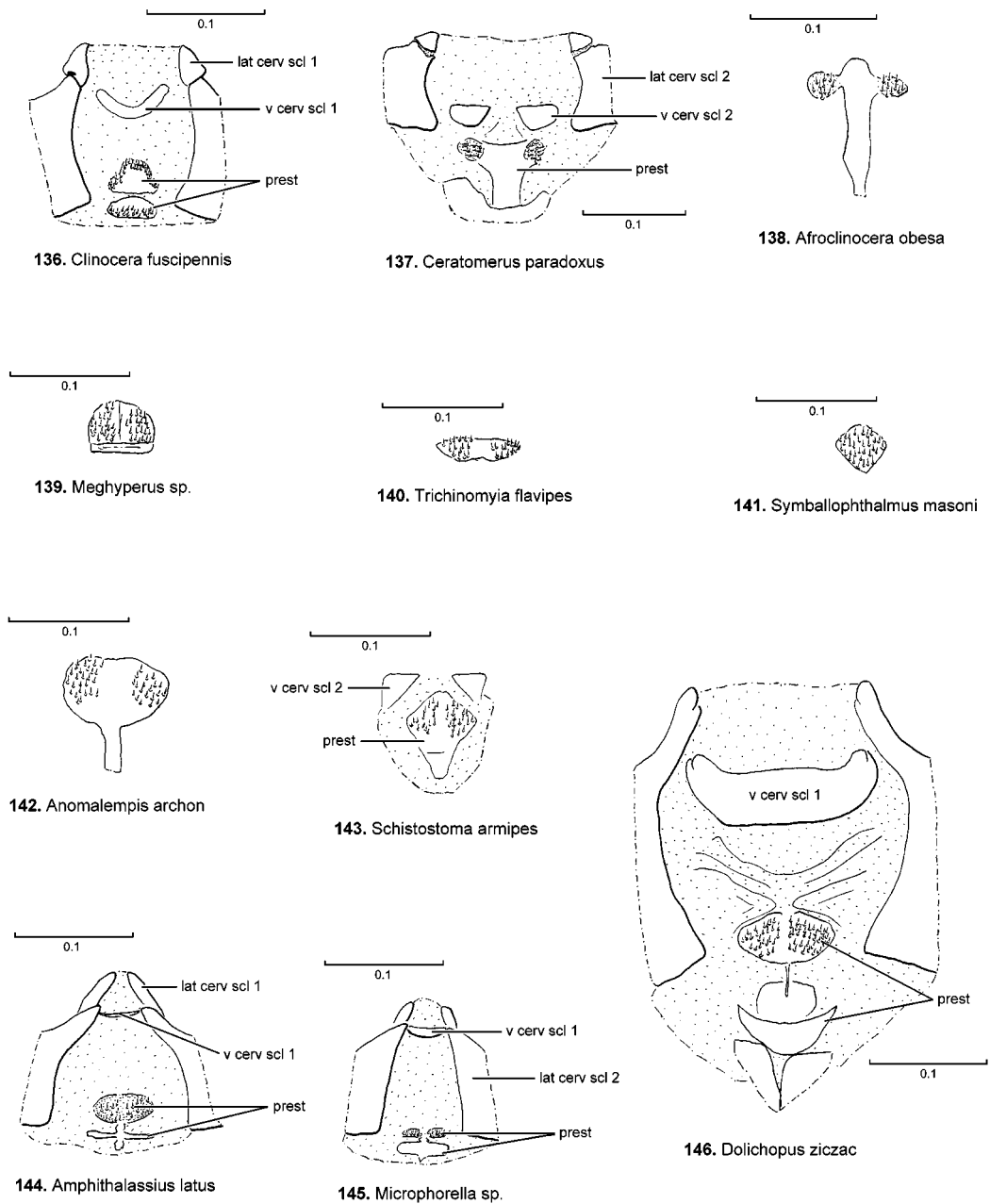
FIGURES 120–125. Mouthparts of Empidoidea. **120.** *Bicellaria* sp., palpus and palpifer, lateral view. **121.** *Anomalempis archon* Melander, maxilla, left palpus removed, posterior view. **122.** *Hormopeza senator* Melander, left maxilla and labium, lateral view. **123.** *Empis borealis* L., labium, lateral view. **124.** *Afroclinocera obesa* Sinclair, left maxilla and labium, lateral view. **125.** *Clinocera fuscipennis* Loew, lacinia and labium, lateral view. Abbreviations: lbl—labellum, lc—lacinia, plp—palpus, plpf—palpifer, psdtrch—pseudotrachea, sen pit—sensory pit, stp—stipes. Scale in mm.



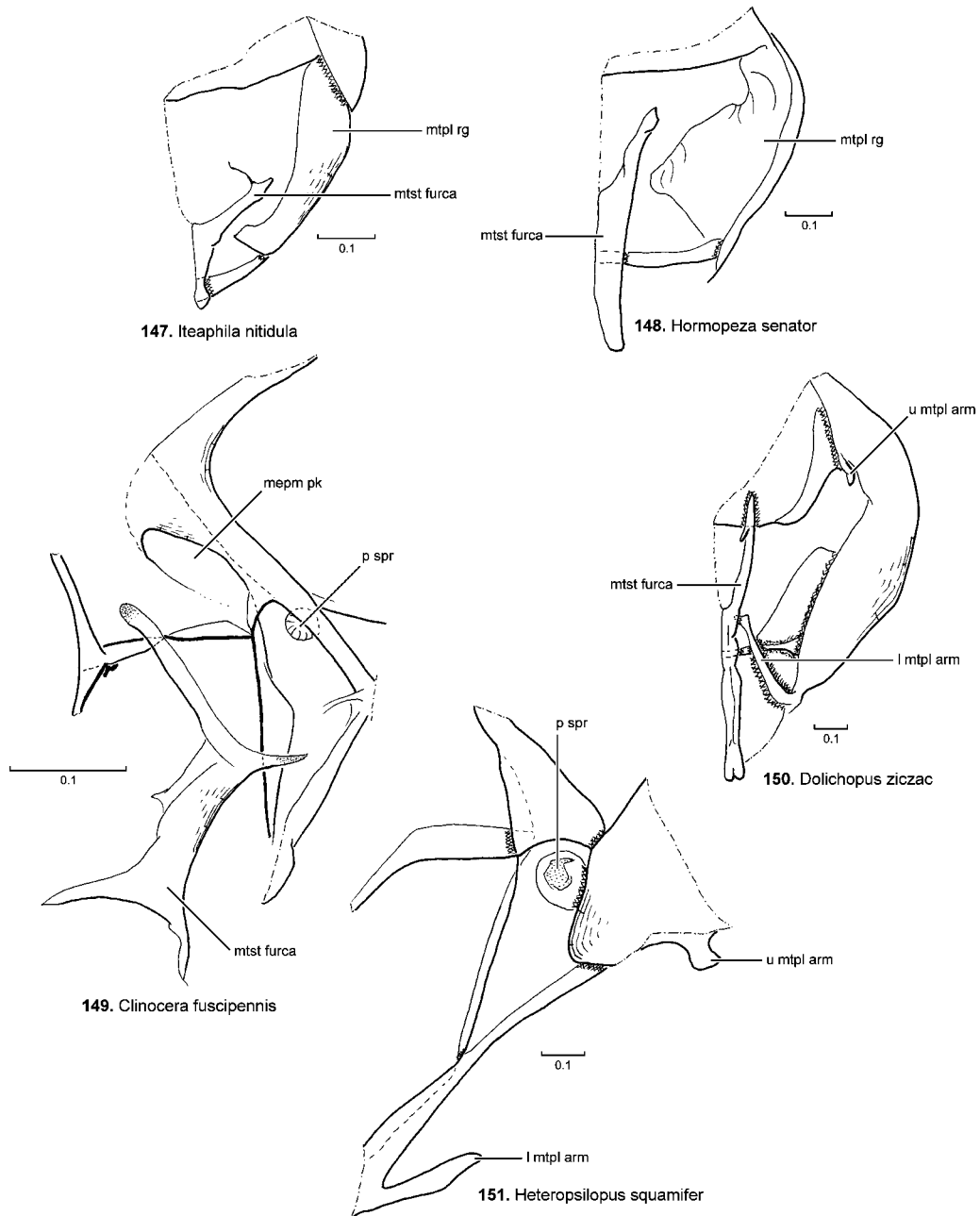
FIGURES 126–130. Mouthparts of Empidoidea. **126.** *Clinocera fuscipennis* Loew, maxilla and labium, posterior view. **127.** *Glyphidopeza fluviatilis* Sinclair, labium, inner view. **128.** *Ceratomerus paradoxus* Philippi, maxilla and labium, lateral view. **129.** *Schistostoma armipes* (Melander), maxilla and labium, lateral view. **130.** *Microphor pilimanus* (Strobl), labium, lateral view. Abbreviations: lbl—labellum, lc—lacinia, plp—palpus, premnt—prementum, psdtrch—pseudotrachea, stp—stipes. Scale in mm.



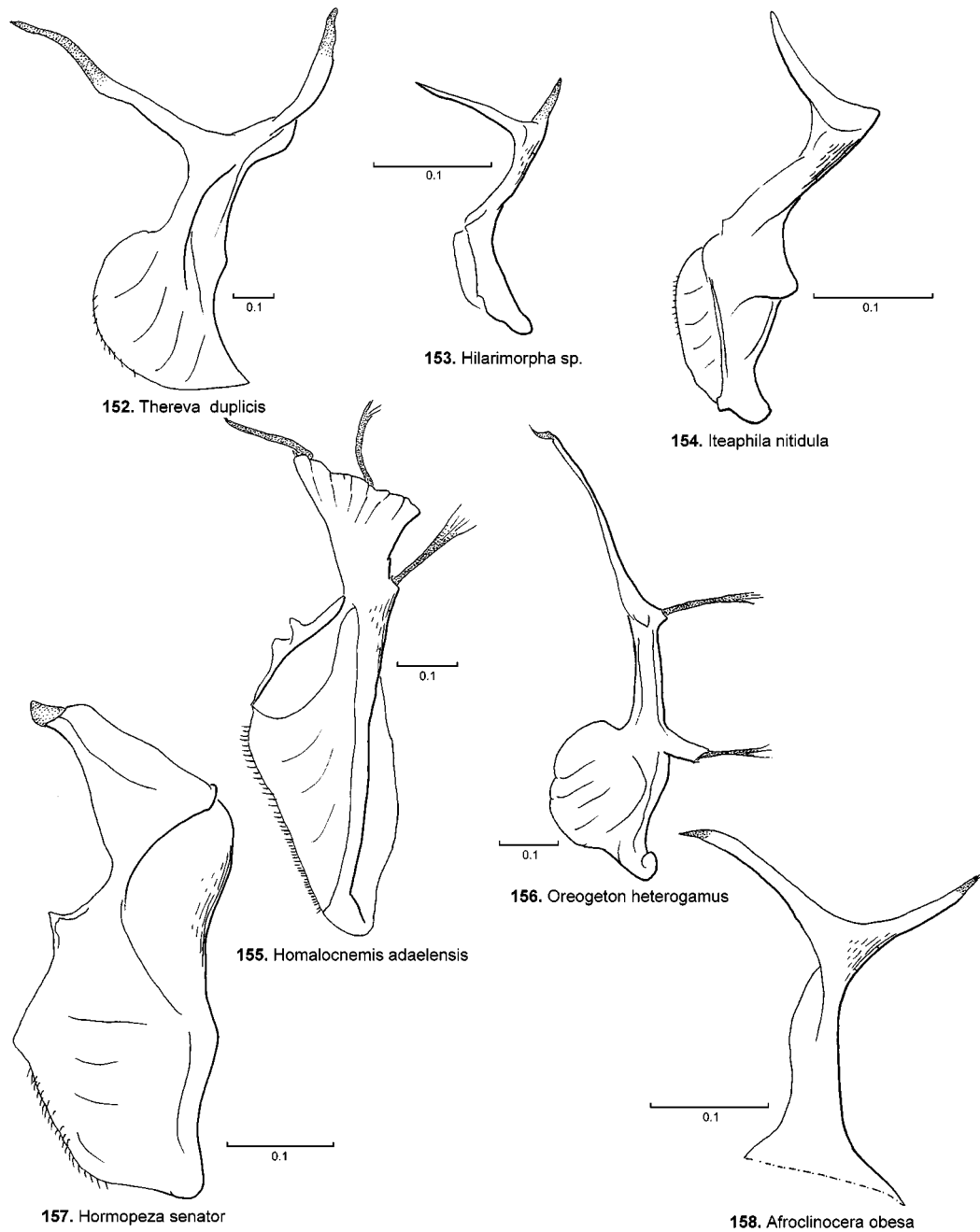
FIGURES 131–135. Mouthparts of Empidoidea. **131.** *Microphorella* sp., lacinia and labium, lateral view. **132.** *Parathalassius aldrichi* Melander, lacinia and labium, inner view. **133.** *Amphithalassius latus* Ulrich, lacinia and labium, inner view. **134.** *Heteropsilopus squamifer* Hardy, lacinia and labium, inner view. **135.** *Sympycnus anomalipennis* Becker, labellum, inner view. Abbreviations: lbl—labellum, lc—lacinia, psdtrch—pseudotrachea. Scale in mm.



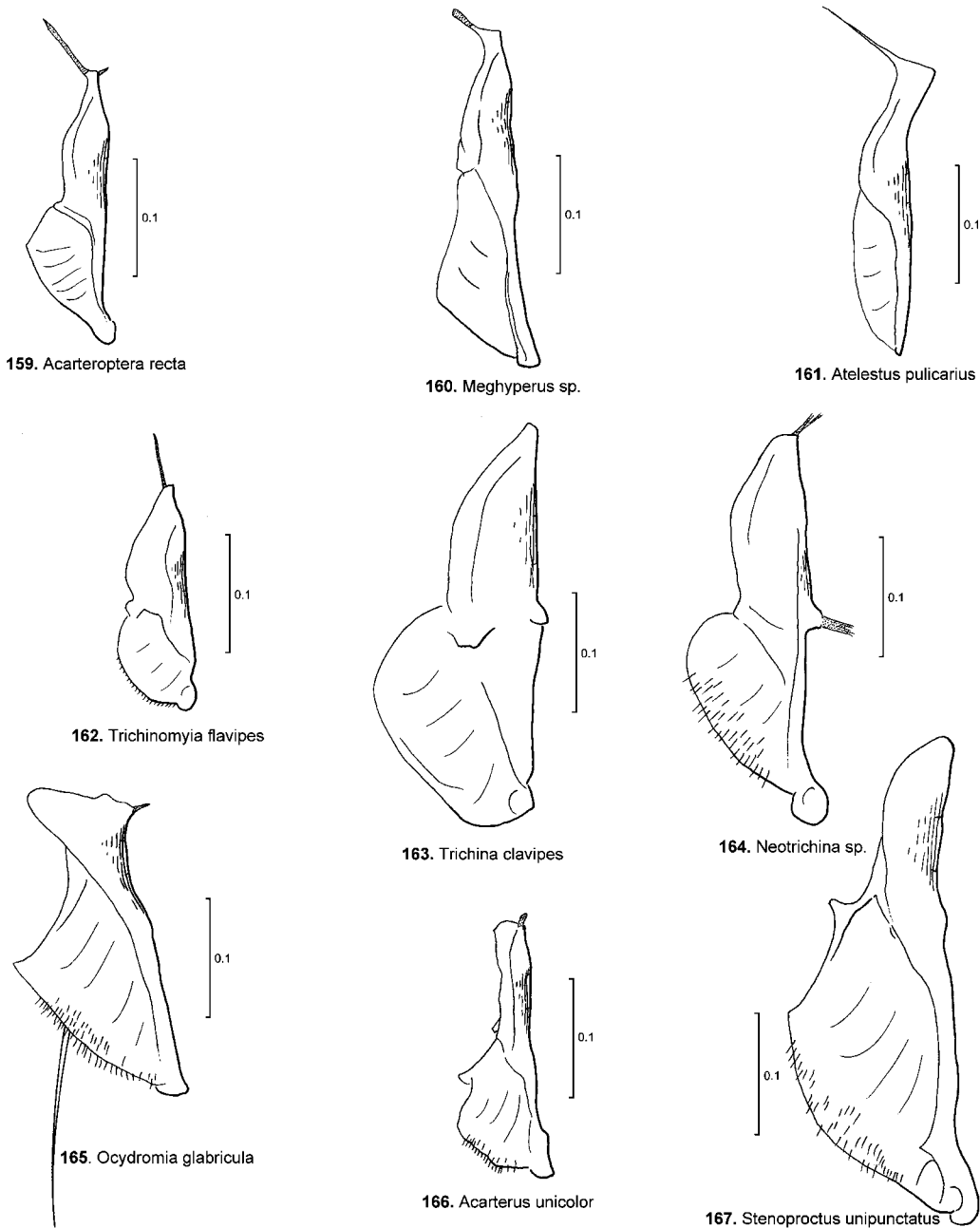
FIGURES 136–146. Prothoracic region of Empidoidea, anterior view. **136.** *Clinocera fuscipennis* Loew. **137.** *Ceratomerus paradoxus* Philippi. **138.** *Afroclinocera obesa* Sinclair, presternum **139.** *Meghyperus* sp., presternum. **140.** *Trichinomyia flavipes* (Zetterstedt), presternum. **141.** *Symballophthalmus masoni* Chillcott, presternum. **142.** *Anomalempis archon* Melander, presternum. **143.** *Schistostoma armipes* (Melander). **144.** *Amphithalassius latus* Ulrich. **145.** *Microphorella* sp. **146.** *Dolichopus ziczac* Wiedemann group. Abbreviations: lat cerv scl—lateral cervical sclerites 1 and 2, prest—presternum, v cerv scl—ventral cervical sclerites 1 and 2. Scale in mm.



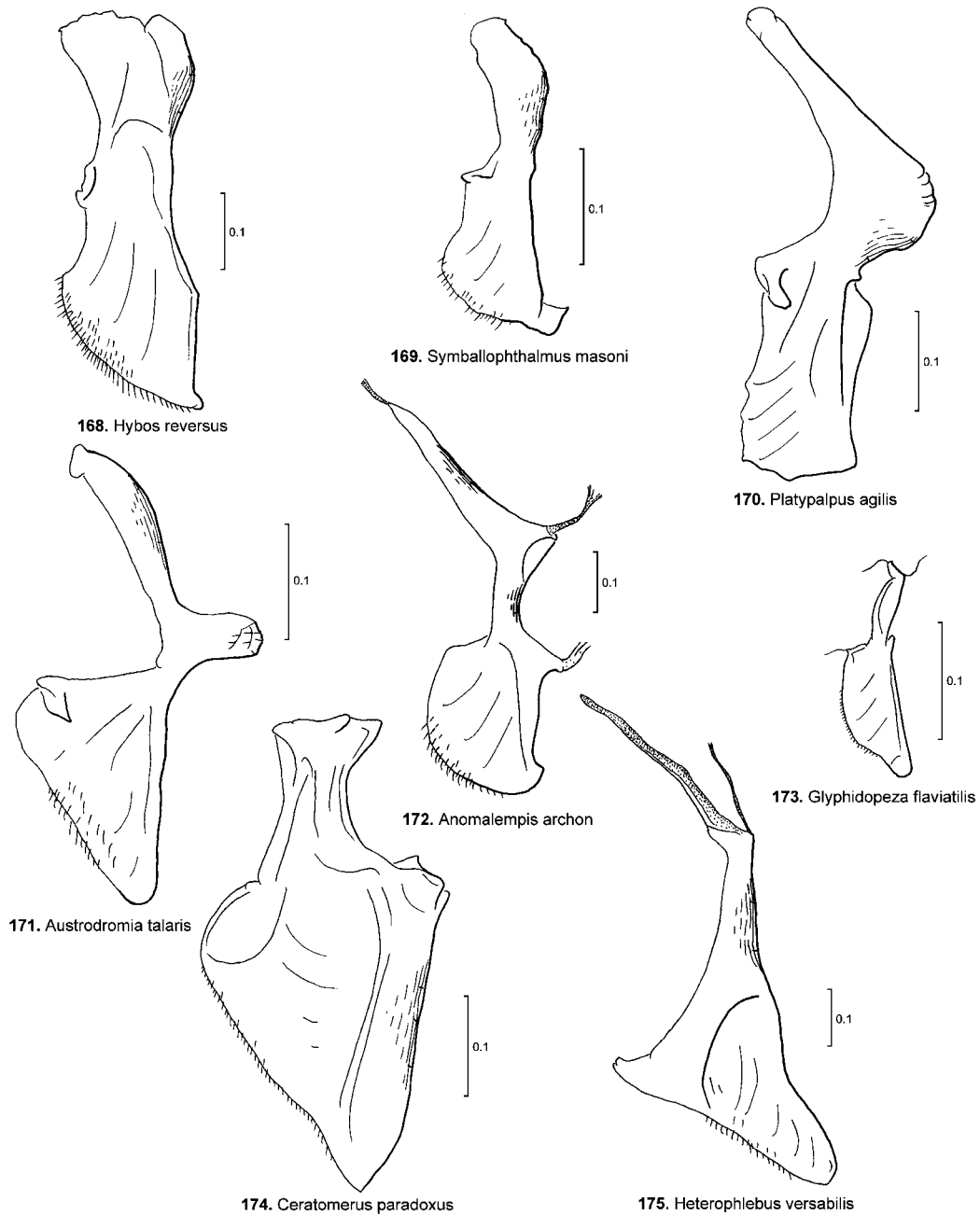
FIGURES 147–151. Internal thoracic skeleton of Empidoidea. **147.** *Iteaphila nitidula* Zetterstedt, metathorax, posterior view. **148.** *Hormopeza senator* Melander, metathorax, posterior view. **149.** *Clinocera fuscipennis* Loew, right posterior pleural region. **150.** *Dolichopus ziczac* Wiedemann group, metathorax, posterior view. **151.** *Heteropsilopus squamifer* Hardy, right posterior pleural region. Abbreviations: l mtpl arm—lower metapleural arm, mepm pk—mesepimeral pocket, mtpl rg—metapleural ridge, mtst furca—metasternal furca, p spr—posterior spiracle, u mtpl arm—upper metapleural arm. Scale in mm.



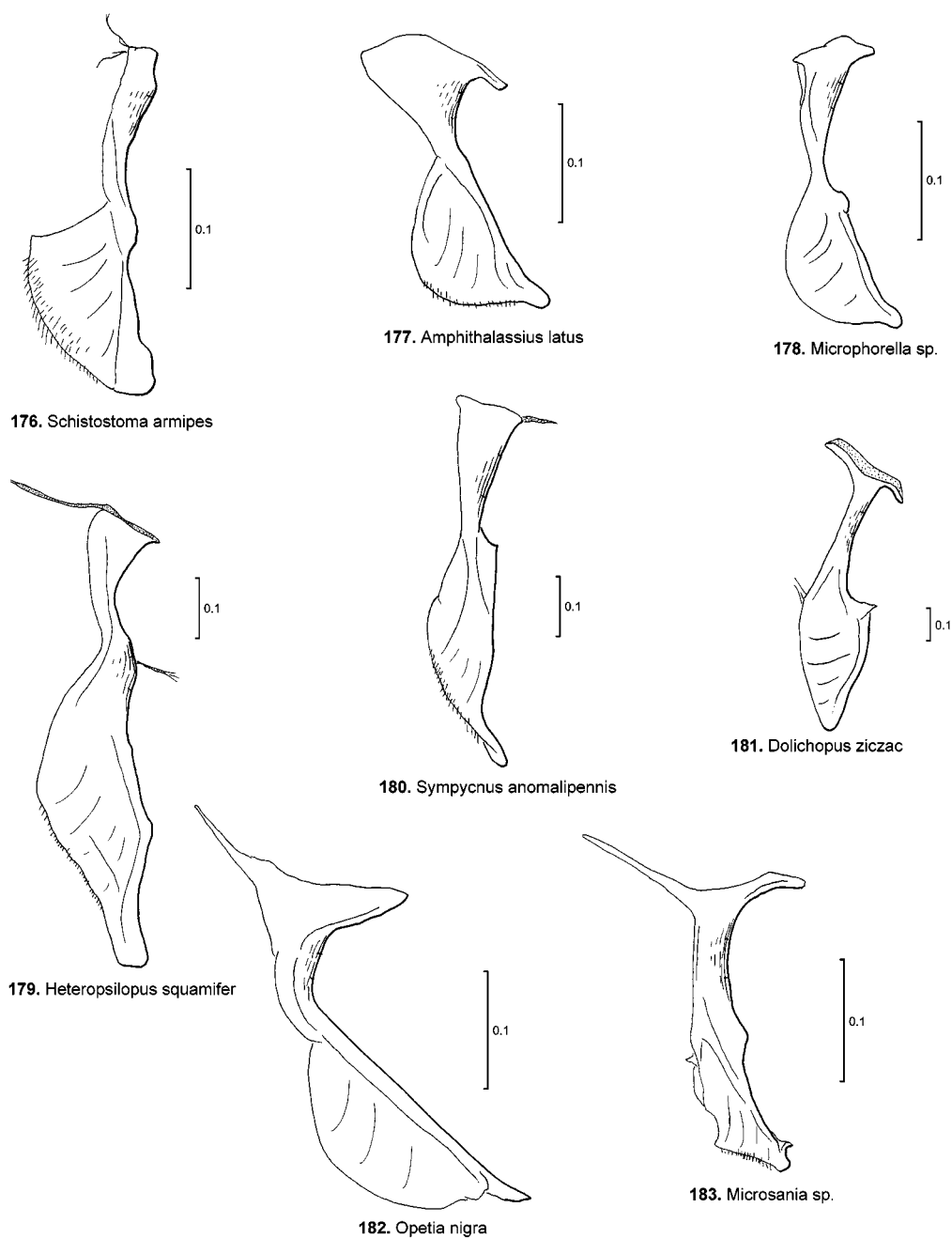
FIGURES 152–158. Metasternal furca of Asiloidea and Empidoidea, lateral view. **152.** Therevidae, *Thereva duplicis* Coquillett. **153.** Hilarimorphidae, *Hilarimorpha* sp. **154.** Empidoidea, *Iteaphila nitidula* Zetterstedt. **155.** Empidoidea, *Homalocnemis adaelensis* (Miller). **156.** Empidoidea, *Oreogeton heterogamus* Melander. **157.** Empidoidea, *Hormopeza senator* Melander. **158.** *Afroclinocera obesa* Sinclair. Scale in mm.



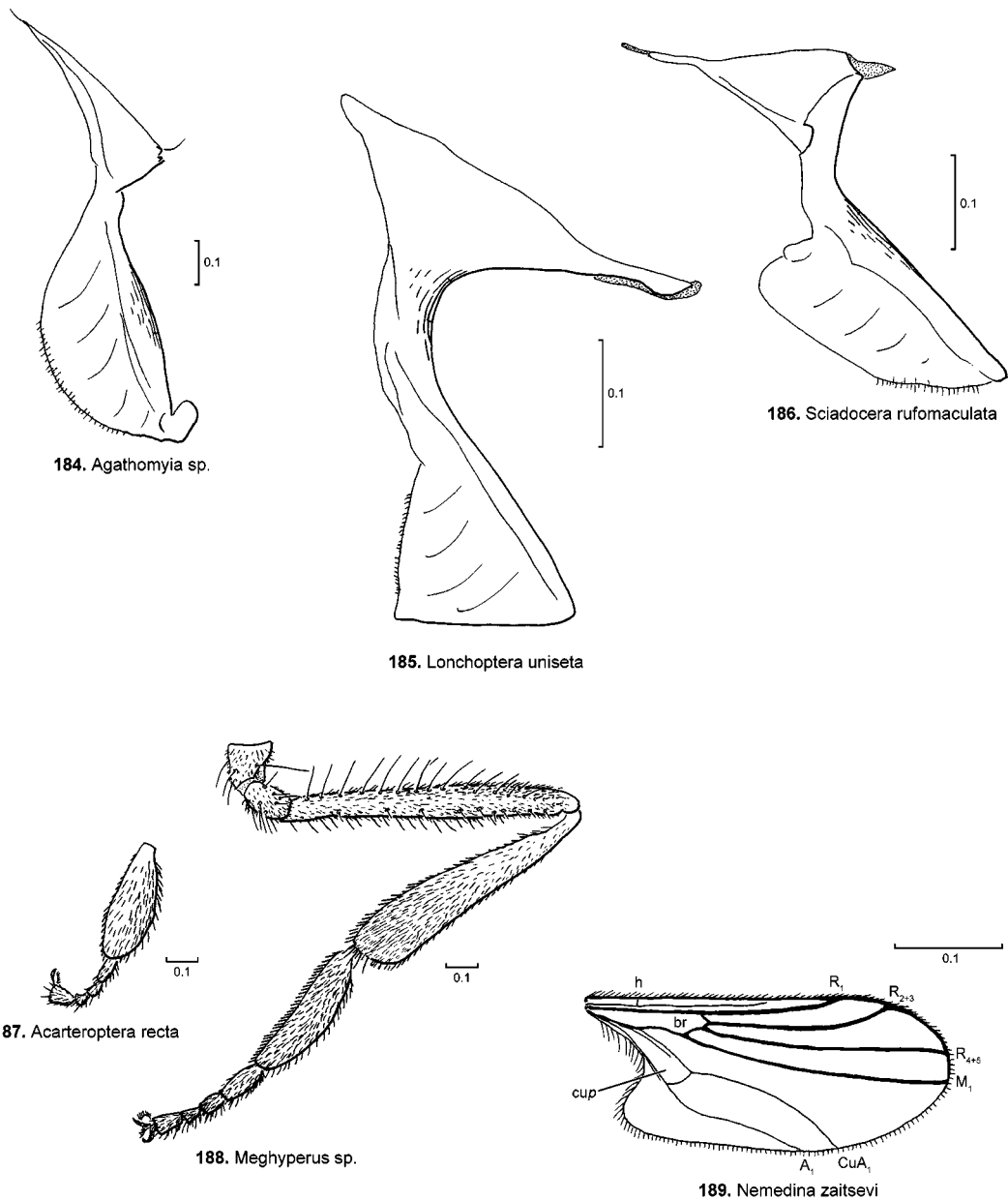
FIGURES 159–167. Metasternal furca of Empidoidea, lateral view. **159.** *Acarteroptera recta* Collin. **160.** *Meghyperus* sp. **161.** *Atelestus pulicarius* (Fallén). **162.** *Trichinomyia flavipes* (Zetterstedt). **163.** *Trichina clavipes* (Meigen). **164.** *Neotrichina* sp. **165.** *Ocydromia glabricola* (Fallén). **166.** *Acarterus unicolor* Loew. **167.** *Stenoproctus unipunctatus* Loew. Scale in mm.



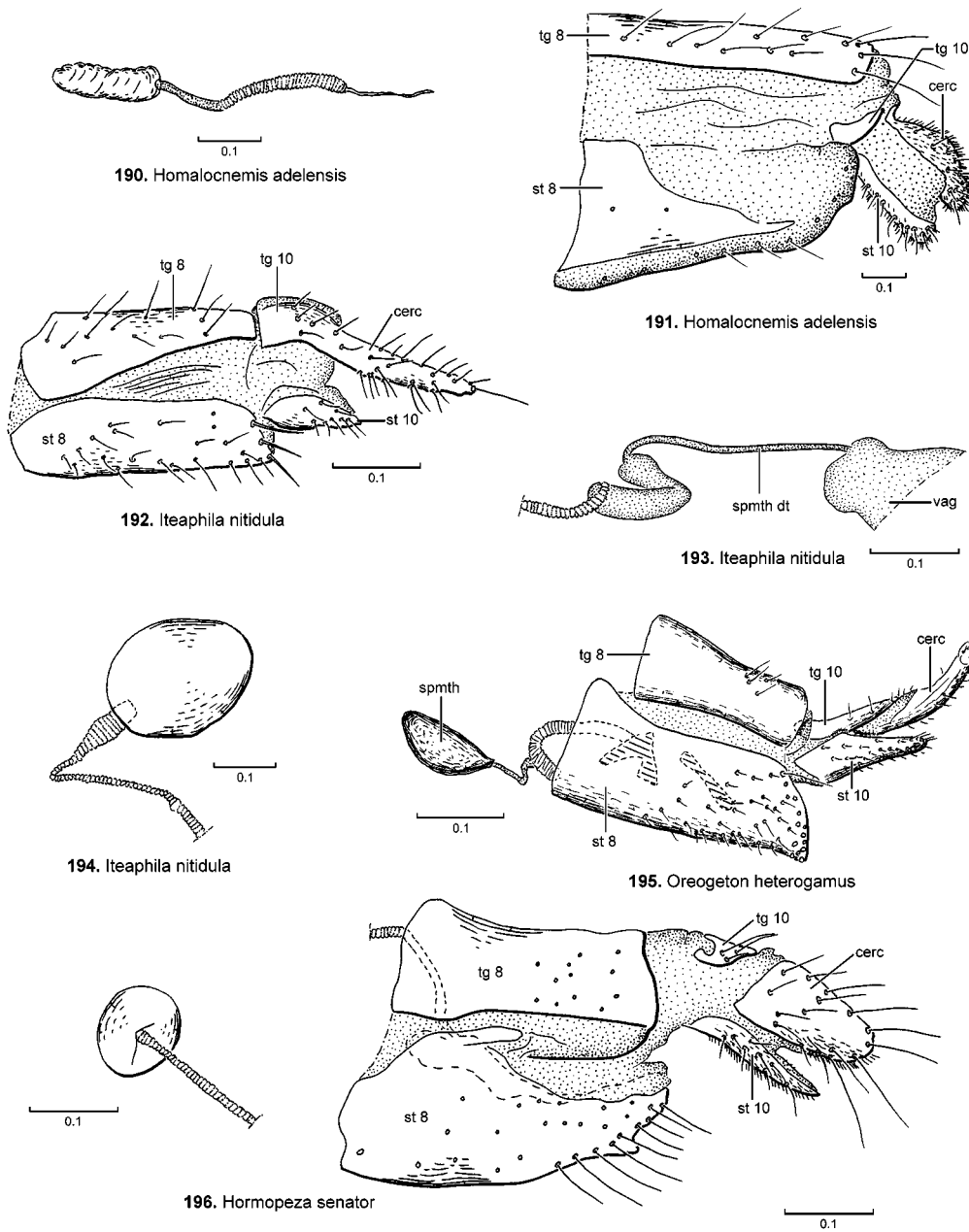
FIGURES 168–175. Metasternal furca of Empidoidea, lateral view. **168.** *Hybos reversus* Walker. **169.** *Symballophthalmus masoni* Chillcott. **170.** *Platypalpus agilis* (Meigen). **171.** *Austrodromia talaris* Collin. **172.** *Anomalempis archon* Melander. **173.** *Glyphidopeza fluviatilis* Sinclair, **174.** *Ceratomerus paradoxus* Philippi. **175.** *Heterophlebus versabilis* (Collin). Scale in mm.



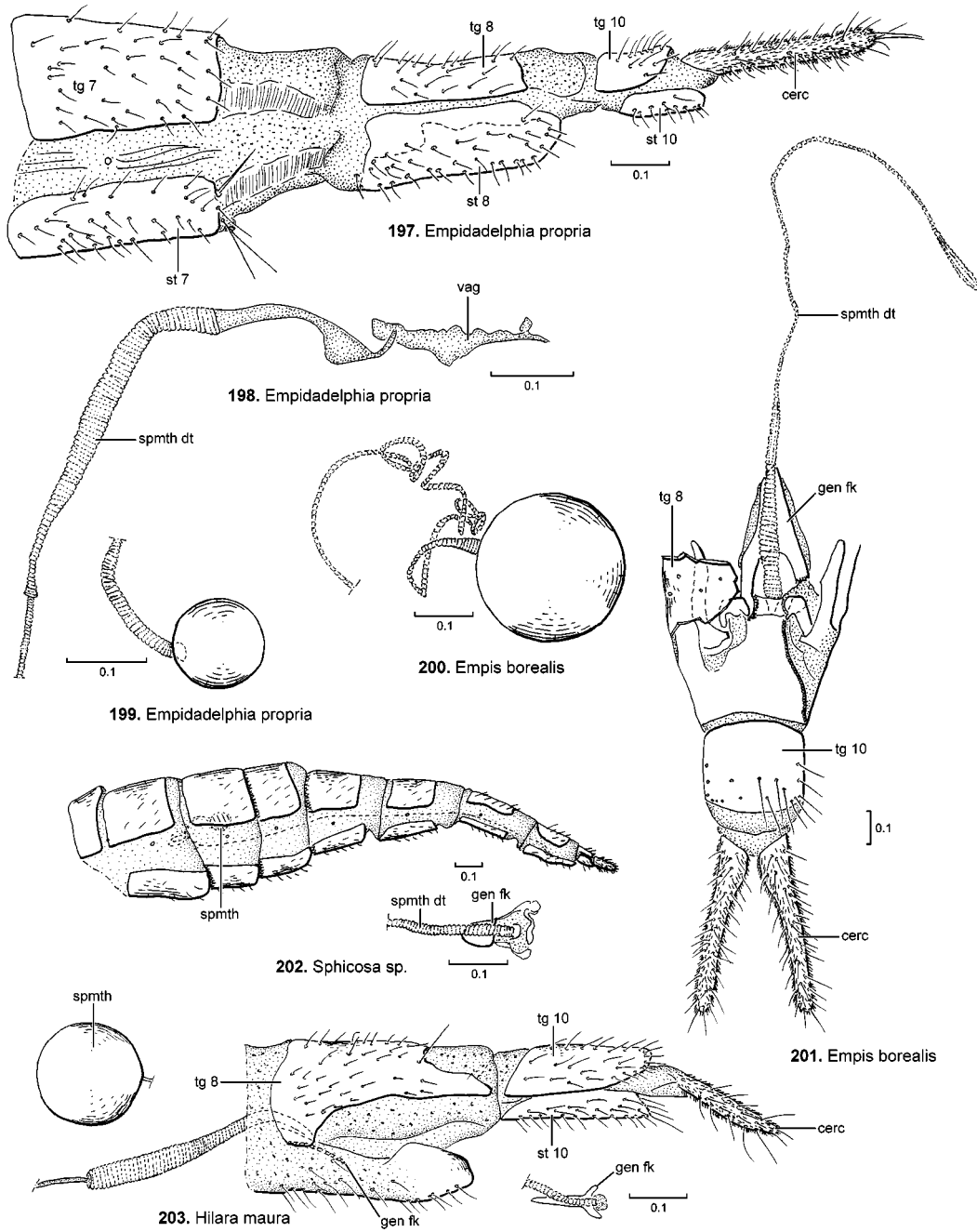
FIGURES 176–183. Metasternal furca of Empidoidea and Cyclorrhapha, lateral view. **176.** Empidoidea, *Schistostoma armipes* (Melander). **177.** Empidoidea, *Amphithalassius latus* Ulrich. **178.** Empidoidea, *Microphorella* sp. **179.** Empidoidea, *Heteropsilopus squamifer* Hardy. **180.** Empidoidea, *Sympycnus anomalipennis* Becker, **181.** Empidoidea, *Dolichopus ziczac* Wiedemann group. **182.** Opetiidae, *Opetia nigra* Meigen. **183.** Platypezidae, *Microsania* sp. Scale in mm.



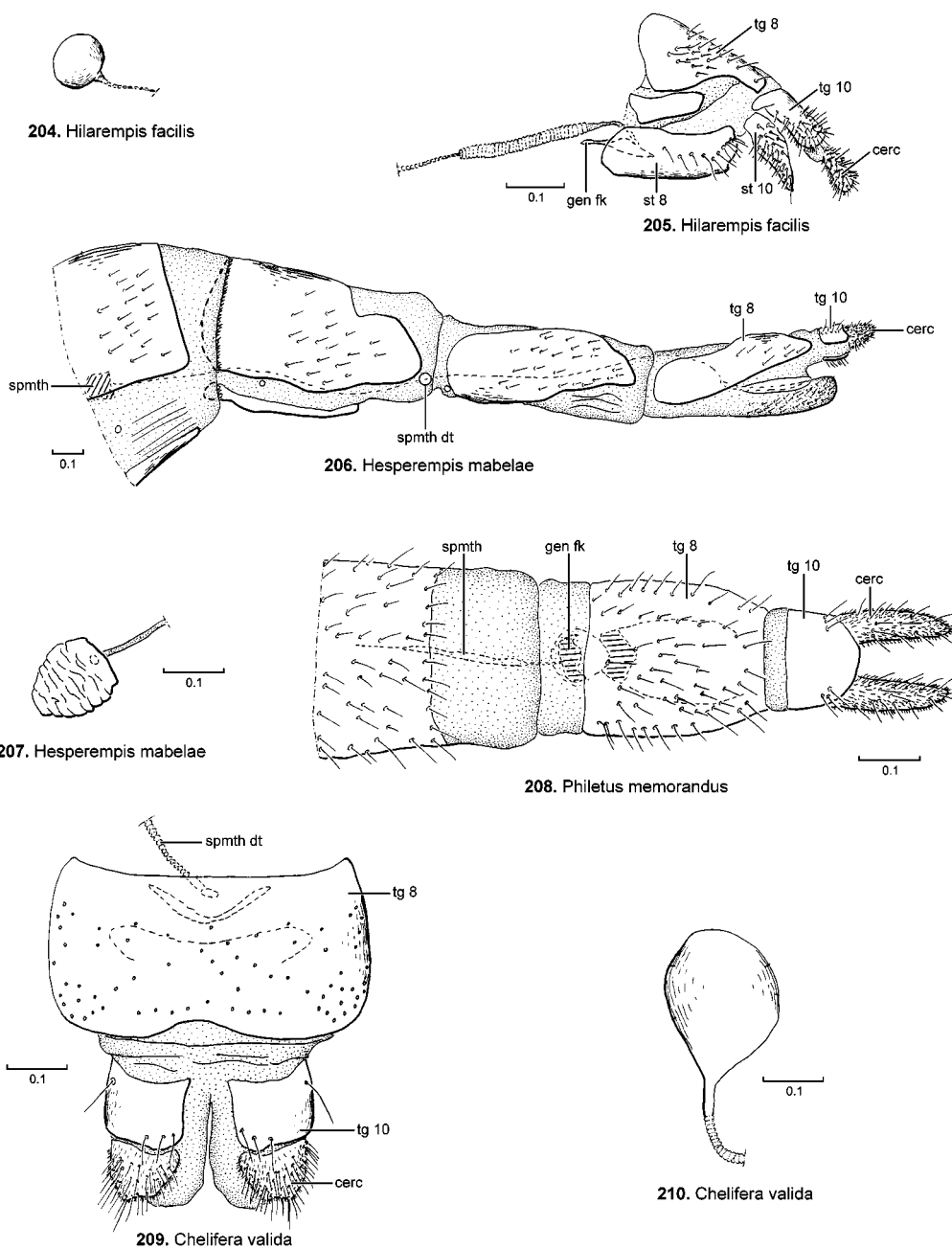
FIGURES 184–189. Thoracic structures of Empidoidea and Cyclorrhapha. **184.** Platypezidae, *Agathomyia* sp., metasternal furca, lateral view. **185.** Lonchopteridae, *Lonchoptera uniseta* Curran, metasternal furca, lateral view. **186.** Sciadoceridae, *Sciadocera rufomaculata* White, metasternal furca, lateral view. **187.** Empidoidea, *Acarteroptera recta* Collin, hind tarsus. **188.** Empidoidea, *Meghyperus* sp., hindleg. **189.** Empidoidea, *Nemedina zaitsevi* Sinclair & Shamshev, wing. Abbreviations: A_1 —anal vein, br—basal radial cell, CuA_1 —1st anterior branch of cubital vein, cup—posterior cubital (= anal) cell, h—humeral crossvein, M_1 —1st medial vein, R_1 —1st radial vein, R_{2+3} —2nd + 3rd radial vein, R_{4+5} —4th + 5th radial vein. Scale in mm.



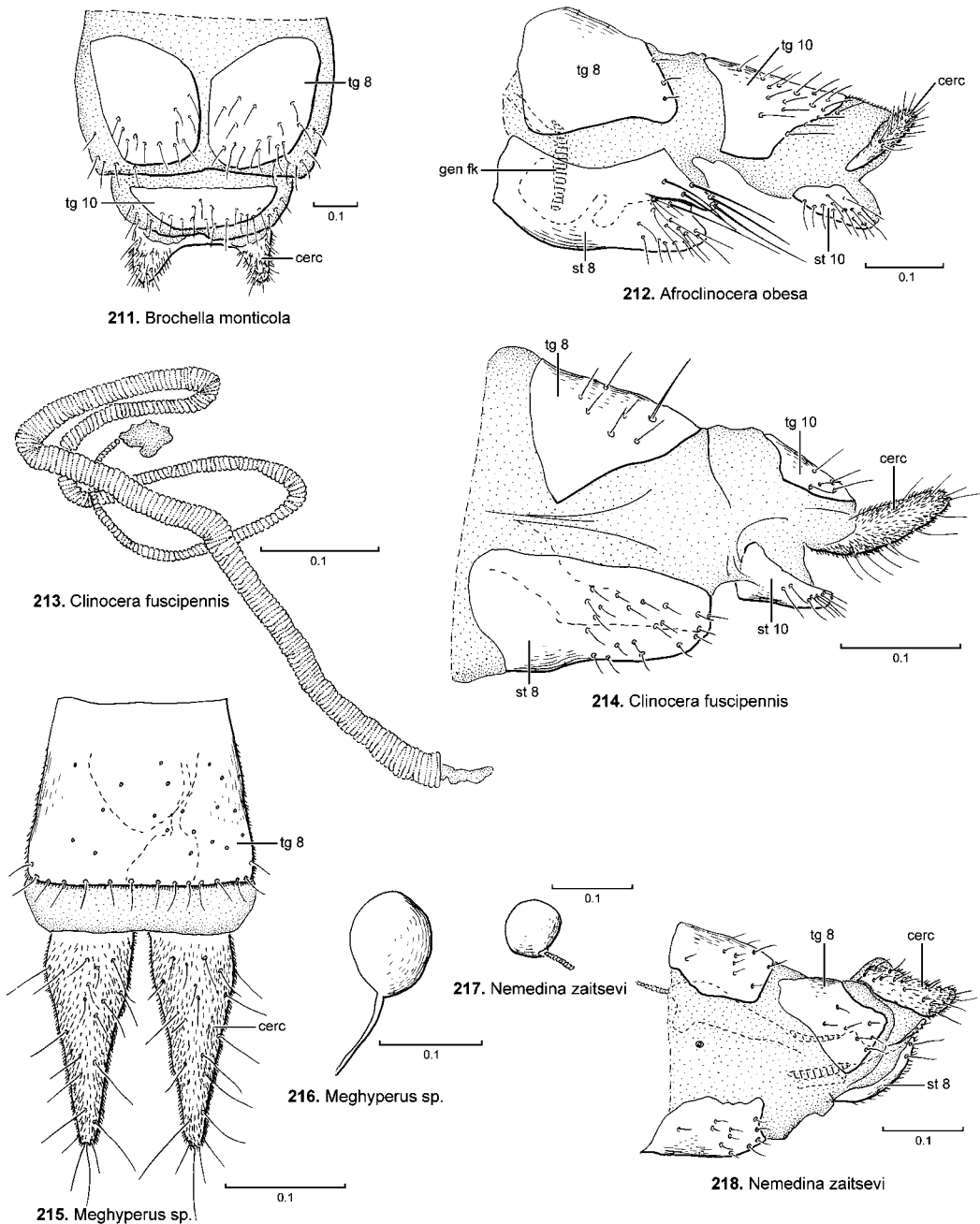
FIGURES 190–196. Female terminalia and spermathecae of Empidoidea, lateral view. **190.** *Homalocnemis adelensis* (Miller), spermatheca and duct. **191.** *Homalocnemis adelensis* (Miller). **192.** *Iteaphila nitidula* Zetterstedt. **193.** *Iteaphila nitidula* Zetterstedt, base of spermathecal duct. **194.** *Iteaphila nitidula* Zetterstedt, spermatheca and duct. **195.** *Oreogeton heterogamus* Melander. **196.** *Hormopeza senator* Melander, spermatheca on left side. Abbreviations: cerc—cercus, spmth—spermatheca, spmth dt—spermathecal duct, st—sternite 8 and 10, tg—tergite 8 and 10, vag—vagina. Scale in mm.



FIGURES 197–203. Female terminalia and spermathecae of Empidoidea. **197.** *Empidadelpha propria* Collin, postabdomen, lateral view. **198.** *Empidadelpha propria* Collin, spermathecal duct and vagina. **199.** *Empidadelpha propria* Collin, spermatheca and duct. **200.** *Empis borealis* L., spermatheca and duct. **201.** *Empis borealis* L., dorsal view. **202.** *Spicosa* sp., abdomen (lateral view), genital fork and base of spermathecal duct enlarged (dorsal view) below. **203.** *Hilara maura* (Fab.), spermatheca on left side, genital fork and base of spermathecal duct (dorsal view) below. Abbreviations: cerc—cercus, gen fk—genital fork, spmth—spermatheca, spmth dt—spermathecal duct, st—sternite 7, 8 and 10, tg—tergite 7, 8 and 10, vag—vagina. Scale in mm.



FIGURES 204–210. Female terminalia and spermathecae of Empidoidea. **204.** *Hilarempis facilis* Collin, spermatheca and duct. **205.** *Hilarempis facilis* Collin, lateral view with base of spermathecal duct. **206.** *Hesperempis mabelae* Melander, postabdomen, lateral view. **207.** *Hesperempis mabelae* Melander, spermatheca and duct. **208.** *Philetus memorandum* Melander, dorsal view. **209.** *Chelifera valida* Loew, dorsal view. **210.** *Chelifera valida* Loew, spermatheca and duct. Abbreviations: cerc—cercus, gen fk—genital fork, spmth—spermatheca, spmth dt—spermathecal duct, st—sternite 8 and 10, tg—tergite 8 and 10. Scale in mm.



FIGURES 211–218. Female terminalia and spermathecae of Empidoidea. **211.** *Brochella monticola* Melander, dorsal view. **212.** *Afroclinocera obesa* Sinclair, lateral view. **213.** *Clinocera fuscipennis* Loew, spermathecal duct. **214.** *Clinocera fuscipennis* Loew, lateral view. **215.** *Meghyperus* sp., dorsal view. **216.** *Meghyperus* sp., spermatheca and duct. **217.** *Nemedina zaitsevi* Sinclair & Shamshev, spermatheca and duct. **218.** *Nemedina zaitsevi* Sinclair & Shamshev, lateral view. Abbreviations: cerc—cercus, gen fk—genital fork, st—sternite 8 and 10, tg—tergite 8 and 10. Scale in mm.