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Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera)

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Abstract. Tipulomorpha (crane flies) comprise one of the largest subgroups of Diptera, but its phylogeny at different levels has been poorly explored. This study presents the most comprehensive cladistic analysis of the group ever made, with emphasis on the genera and subgenera of the subfamily Limnophilinae (Limoniidae), assumed to include some of the earliest lineages of Tipulomorpha *sensu stricto* and therefore important for the understanding of the early patterns in the evolution of the crane flies. Eighty-eight characters of the male imago were scored for 104 exemplar species. The most parsimonious trees were searched using implied weighting, in the framework of a sensitivity analysis with different values of k (2 to 6). The dataset based on the characters of adult male morphology showed high levels of homoplasy and yielded very incongruent and unstable phylogenetic results, which are very sensitive to changes in analytical parameters. In the preferred and most parsimonious phylogenetic hypothesis, the Pediciidae is the sister-group of all other Tipulomorpha *sensu stricto*. The results indicate the paraphyly of the Limoniidae with respect to the Cylindrotomidae and Tipulidae, which are considered sister-groups. The Limoniidae subfamilies Limnophilinae, Limoniinae and Chioneinae are considered non-monophyletic. The study allowed a reconstruction of the possible ground plan condition of selected features of the adult male morphology of crane flies. The genera/subgenera *Epiphragma* (*Epiphragma*), *Acantholimnophila*, *Shannonomyia*, *Limnophila* (*Arctolimnophila*), *Eloeophila*, *Conosia*, *Polymera*, *Polymera* (*Polymerodes*), *Prionolabis*, *Eutonia*, *Phylidorea* (*Phylidorea*), *Metalimnophila*, *Gynoplistia* (*Cerozodia*), *Gynoplistia* (*Dirhipis*), *Nothophila*, *Pseudolimnophila* (*Pseudolimnophila*), *Pilaria* and *Ulomorpha* are considered monophyletic, but in general are defined by combinations of very homoplastic character states. Two Temperate Gondwanan clades, (*Tonnoirella* + (*Edwardsomyia* + (*Tinemyia* + (*Rhamphophila* + (*Nothophila*))))) and ((*Notholimnophila* + *Bergrothomyia*) + (*Mesolimnophila* + (*Chilelimnophila* + *Ctenolimnophila*))) are recovered. The genera *Limnophila, Neolimnomyia, Gynoplistia* (*sensu lato*) and *Hexatoma* (*sensu lato*) are considered non-monophyletic. The systematic position and some morphological characters of 'problematic' taxa, such as *Dactylolabis*, *Elephantomyia*, *Helius* and *Atarba* are discussed on the light of the proposed phylogeny and the analysis of the characters. Character states are richly illustrated. A detailed study of the morphology of the male genitalia is made, and several genera and species have the morphology of the male genitalia illustrated for the first time.

Additional keywords: comparative morphology, Cylindrotomidae, implied weighting, Limnophilinae, Limoniidae, Pediciidae, Tipulidae.

Introduction

The Tipulomorpha – crane flies – are one of the largest groups of the order Diptera, including over 15 000 extant species in approximately 500 genera and subgenera worldwide. Adults of this group are commonly found in moist forested areas near ponds and streams, but also occur in grasslands, cultivated fields, urban yards and even deserts. The immature stages of most species live in aquatic or semi aquatic habitats, but many species with terrestrial larvae are also known (Alexander and Byers 1981; Gelhaus 2005; De Jong *et al.* 2008).

There is a conflict in the classification of crane flies regarding the taxonomic ranks attributed to the higher taxa. According to one system of classification (e.g. Starý 1992; Oosterbroek 2008), which is the one followed in this paper, the Tipulomorpha includes four families: Tipulidae, Limoniidae, Pediciidae and Cylindrotomidae. An alternative classificatory scheme groups the crane flies into a single family, the Tipulidae *sensu lato*, with the taxa treated here as families ranked as subfamilies (Tipulinae, Limoniinae and Cylindrotominae) and tribe (Pediciini, subordinated to the subfamily Limoniinae) (e.g. Alexander and Alexander 1970, Gelhaus in press).

Following Hennig (1973), crane flies were usually grouped into one superfamily, the Tipuloidea, within the infraorder Tipulomorpha in the suborder Nematocera. In the latest classification of the Diptera (Amorim and Yeates 2006), with the abandonment of the paraphyletic Nematocera, the Tipulomorpha received the status of suborder. The systematic position of the dipteran family Trichoceridae (winter crane flies), which may belong to the Tipulomorpha as the sister-group of the other four families, or elsewhere, is still in dispute. In any case, as

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discussed in more detail below in this paper, the monophyly of the Tipulomorpha excluding Trichoceridae (i.e. the Tipulomorpha *sensu stricto*, including the families Tipulidae, Limoniidae, Pediciidae and Cylindrotomidae) is well established.

Tipulidae and Limoniidae are widely distributed groups, including approximately 4000 and 11 000 species respectively. Pediciidae, with little more than 400 species, is lacking only in the Afrotropical region. Cylindrotomidae, with 71 described species, occurs mainly in the Nearctic, Palearctic, Oriental and Australasian regions. This family is also lacking in the Afrotropical region, and is represented in the Neotropics by a single species, from Chile (Oosterbroek 2008).

Most recently, the families Psychotipidae and Archilimoniidae were included in the Tipulomorpha (Krzeminski and Krzeminska 2003). Originally erected by Shcherbakov *et al.* (1995) as a subfamily of Vladipteridae (a group originally included in the Diptera but now considered a subgroup of Mecoptera), Psychotipidae includes two extinct species in a single genus from the Triassic of Asia. Archilimoniidae was already erected as a subgroup of Tipulomorpha, and includes a single genus and species, *Archilimonia vogesiana* Krzeminski & Krzeminska, from the Triassic of France (Krzeminski and Krzeminska 2003).

Although it is one of the largest groups of lower Diptera in terms of the number of described species, the Tipulomorpha remains a vastly unknown group. The immature stages are known for at least one species in approximately 150 genera and subgenera, or less than one-third of the genera and subgenera included in the suborder, and this knowledge is almost exclusively restricted to taxa of the Northern Hemisphere (Oosterbroek and Theowald 1991). Virtually nothing is known about the biology of most species. Pritchard (1983) is still the most comprehensive account of several aspects of the biology of Tipulomorpha, including information on immature life style, life cycle and population dynamics, among others.

The phylogeny of Tipulomorpha, at different levels, has been a poorly explored issue. Early attempts to present the phylogenetic patterns of the group include Alexander (1920) and Savchenko (1966, *apud* Starý 1992), but studies using modern methods of inference are few. For the family Pediciidae, there are no published modern phylogenetic studies. A phylogenetic study of the genera included in the subfamily Stibadocerinae (Cylindrotomidae) was carried out by Ribeiro (in press). Most of the work conducted more recently deals with the phylogeny of subgroups of Tipulidae: Oosterbroek (1980) investigated the phylogenetic relationships of species in the genus *Nephrotoma*; Tangelder (1985, 1988) studied the phylogeny and biogeography of the Holarctic *dorsalis* species-group in *Nephrotoma*; Theowald (1984) studied the phylogeny and biogeography of *Tipula* (*sensu stricto*); a phylogenetic revision of the genus *Prionocera* was made by Brodo (1987); De Jong conducted phylogenetic studies with the genera *Elnoretta*, *Valdiviana* and *Euvaldiviana* (De Jong 1989), *Nephrotoma* (De Jong 1993) and subgroups of *Tipula* (De Jong 1994*a*, 1994*b*, 1995*a*, 1995*b*); Gelhaus (2005) studied the phylogeny and biogeography of *Tipula* (*Eremotipula*) and the relationships among related subgenera of *Tipula*. For the Limoniidae, the only phylogenetic studies so far conducted are those by Oosterbroek and Theowald (1991) and Starý (1992), which are discussed in detail in other part of this paper, and a phylogenetic revision of the Neotropical species of the genus *Styringomyia* (Ribeiro 2003).

According to the most recent classification (Starý 1992; Oosterbroek 2008), the extant genera of Limoniidae are grouped into four subfamilies, the Chioneinae (60 genera and 81 subgenera), Dactylolabidinae (1 genus, 4 subgenera), Limoniinae (34 genera, 73 subgenera) and Limnophilinae (52 genera, 57 subgenera).

Limoniidae fossils from the Upper Triassic of North America of approximately 208 million years in age are among the oldest known fossils of Diptera (Krzeminski 1992; Krzeminski and Krzeminska 2003; Blagoderov *et al.* 2007), and this family has an extensive fossil record with more than 300 species described for many different Mesozoic and Cenozoic deposits all over the world, especially Jurassic and Tertiary deposits of Asia and Europe (Evenhuis 1994). Many Mesozoic genera are not included in any of the four subfamilies of the classification given by Oosterbroek (2008) for the extant fauna: *Archilimonia* Krzeminski (Triassic) was placed in the subfamily Archilimoniinae; *Architipula* Handlirsch, *Metarchilimonia* Blagoderov, Grimaldi & Fraser, and *Mabelysia* Shcherbakov (all from the Triassic) were placed in the Architipulinae. The Jurassic genera *Eotipula* Handlirsch and *Eotipulina* Kalugina & Kovalev, and the Cretaceous genera *Cratotipula* Ribeiro & Martins-Neto and *Okrenomyia* Ribeiro & Krzeminski are included in the subfamily Eotipulinae. *Gnomusca*, a genus from the Triassic erected by Shcherbakov *et al.* (1995) and then positioned in the subfamily Gnomuscinae in the Limoniidae, was more recently transferred, though tentatively, to the Trichoceromorpha by Krzeminski and Krzeminska (2003).

Systematic position of Tipulomorpha within the Diptera, and the relationships among major Tipulomorphan lineages

Even though the monophyly of the Tipulomorpha *sensu stricto* seems relatively well corroborated, its position within the Diptera is one of the most conflicting aspects of Diptera phylogenetics. Hennig (1973, 1981), based mostly on the characters of wing venation, included Trichoceridae in the Tipulomorpha as the sister-group of the Tipulomorpha *sensu stricto*, and this clade – named Polyneura by Hennig, and referred to hereinafter as Tipulomorpha *sensu* Hennig – was considered the sister-group of the remaining Diptera (Oligoneura). Wood and Borkent (1989), in an analysis using the characters of the immature stages, also considered the Tipulomorpha *sensu stricto* as the sister-group of all other Diptera, but transferred the Trichoceridae to the Psychodomorpha. Krzeminski (1992), based on fossils only, considered the Tipulomorpha *sensu* Hennig as the sister-group of the Ptychopteromorpha (Ptychopteridae and Euptychopteridae). In a study by Oosterbroek and Courtney (1995), based on characters of the immature stages and adults, the monophyly of Tipulomorpha *sensu* Hennig was corroborated, but the clade appeared as the sister-group of the Anisopodidae + Brachycera. In the molecular study by Friedrich and Tautz (1997), the monophyly of Tipulomorpha *sensu stricto* was corroborated, but the study brought no further grounds to the understanding of the group's position within the Diptera owing to the low resolution within Diptera lineages. Krzeminski and Evenhuis (2000) and Krzeminski and Krzeminska (2003) considered Tipulomorpha *sensu* Hennig the sister-group of the 'Neoneura'

(Culicomorpha and Ptychopteromorpha) + 'Diarchineura' (Grauvogeliomorpha, Nadipteromorpha, Tanyderomorpha and Psychodomorpha). Yeates and Wiegmann (2005) constructed a supertree of dipteran relationships on which Trichoceridae belongs to the Psychodomorpha and Tipulomorpha *sensu stricto* is the sister-group of Brachycera. Blagoderov *et al.* (2007) investigated the phylogenetic relationships among early dipteran lineages based mostly on fossils, and again considered the Tipulomorpha as the sister-group to the rest of the Diptera. In the most recent phylogenetic study of the Lower Diptera using molecular data (Bertone *et al.* 2008), the sister-group relationship between Trichoceridae and Tipulomorpha *sensu stricto* is corroborated, but the position of this clade (the Tipulomorpha *sensu* Hennig) is equivocal and differs topologically under different analyses with different analytical parameters.

Although the systematic position of Tipulomorpha is controversial, the phylogenetic relationships among its major lineages are almost completely unknown. Hitherto, only two papers have particularly addressed this issue.

Starý (1992) proposed a cladogram (Fig. 1), based on the study of 11 characters of adult external morphology scored for eight terminal taxa. Trichoceridae is considered the sister-group of Tipulomorpha *sensu stricto*. Limoniidae is considered monophyletic and the sister-group of (Pediciidae + (Tipulidae + Cylindrotomidae)). Within the Limoniidae, Starý (1992) proposed the genus *Dactylolabis* as the sister-group of (Limnophilinae + (Chioneinae + Limoniinae)).

Oosterbroek and Theowald (1991), based on characters of larvae and pupae, investigated the phylogenetic relationships among 47 extant genera of the subfamilies Limnophilinae, Limoniinae and Chioneinae. Also, a phylogeny of the major lineages of Tipulomorpha *sensu stricto* was proposed, including 11 Limoniidae terminal taxa and the families Pediciidae, Tipulidae and Cylindrotomidae. The cladogram proposed by these authors for the relationships among the major lineages of Tipulomorpha is shown in Figure 2. The taxonomic sample used by Oosterbroek and Theowald (1991) is clearly too small considering the total number of taxa and the morphological diversity found within the Tipulomorpha. However, even this reduced sample was enough to raise interesting questions deserving further analysis. The study points to the non-monophyly of the Limoniidae and the subfamilies Limnophilinae, Limoniinae and Chioneinae. Evidence corroborates the sister-group relationships between Tipulidae and Cylindrotomidae, but the monophyly of the family Pediciidae is questioned.

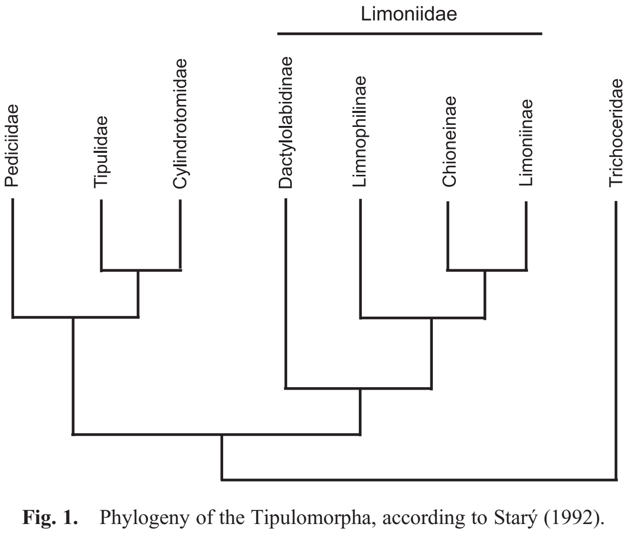


Fig. 1. Phylogeny of the Tipulomorpha, according to Starý (1992).

The Limnophilinae

> '*Leaving out of account for the moment the genera of the* Gynoplistia *group, the members of this tribe are exceedingly difficult to classify, because, although the numerous species exhibit an extensive range of structure, there are few obvious characters on which genera can be defined*' *(F. W. Edwards 1923).*

The subfamily Limnophilinae is traditionally defined by the following characters of the adult fly: three to four branches of R reaching the wing margin; vein sc-r situated distal to the level of the origin of Rs; tibial spurs present. The taxon has *Limnophila* Macquart, 1834 as the type genus and was originally proposed by Bigot (1854) as a family (Starý 1992, Sabrosky 1999). In Osten Sacken (1869), the sections Limnophilina and Anisomerina had genera now included in the Limnophilinae, such as *Limnophila*, *Epiphragma*, *Ulomorpha*, *Hexatoma*, *Cladolipes*, *Eriocera*, among others. Alexander (1912) started referring to the groups including these genera as Limnophilini and Anisomerini, tribes subordinated to the subfamily Limoniinae in the Tipulidae *sensu lato*. After Alexander (1914), Hexatomini was the name in usage. This was probably led by the recognition of *Hexatoma* as senior synonym of *Anisomera*. The names Limnophilini or Limnophilinae were never used in the classifications followed by C. P. Alexander since then. The necessity of using Limnophilini or Limonophilinae, instead of Hexatomini or Hexatominae, to conform to the nomenclatural principle of priority was pointed out by Starý (1992). This was followed by Oosterbroek (2008), who included in the subfamily approximately 52 genera and 57 subgenera.

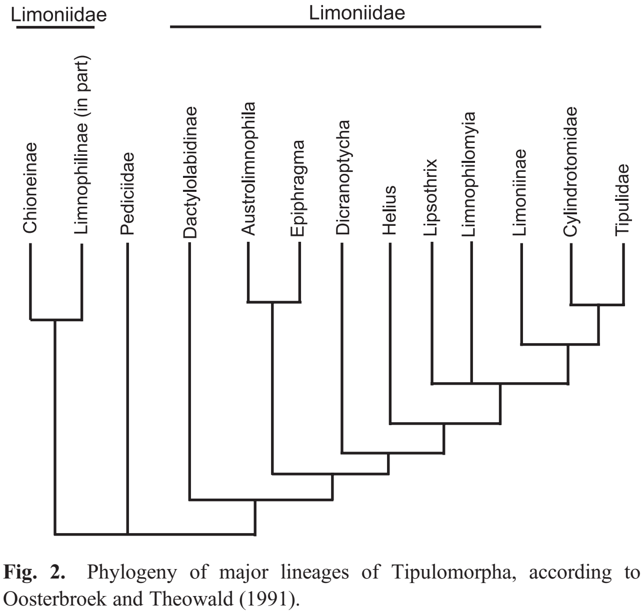


Fig. 2. Phylogeny of major lineages of Tipulomorpha, according to Oosterbroek and Theowald (1991).

The taxonomic characters defining the Limnophilinae are clearly a mix of plesiomorphies (for instance, the four branched radius and the presence of tibial spurs) and apomorphic characters for which the exact hierarchical distribution is unknown (for example, the presence of a three branched radius, which also occurs in genera belonging to other subfamilies). Given the heterogeneity of the subfamily, other characters that could be used to define it more satisfactorily are lacking. Indeed, being a non-monophyletic taxon, as demonstrated in Oosterbroek and Theowald (1991) and confirmed by this study, synapomorphies simply do not exist for it. It is owing to these facts that previous taxonomists trying to arrange its included genera into natural subgroups were faced with great difficulties. This is explicitly pointed out by F. Edwards in the excerpt cited above.

The main purpose of this paper is to investigate the early patterns of diversification of crane flies, through a phylogenetic analysis emphasising the groups included in the Limnophilinae, and using morphological characters of the adult male flies. Some particular presuppositions are explicitly used as the starting point for this study: (1) the subfamily Limnophilinae may be non-monophyletic; (2) the subfamily includes representatives of the earliest Tipulomorphan lineages; and (3) the roots of the families Tipulidae, Cylindrotomidae, and perhaps even the Pediciidae, are likely to be found among the Limnophilinae. Accordingly, an understanding of the early pattern of diversification and the relationships among these earliest Tipulomorphan lineages would require a more detailed analysis of this heterogeneous group. To test these hypotheses, the analysis focused on the interrelationships among the Limnophilinae genera and subgenera, but included a taxonomic sample of other Tipulomorpha subgroups that allowed the discussion of issues related to its higher-level phylogeny.

Material and methods

Ingroup taxonomic sampling

Ideally, for the purposes of the best possible phylogenetic estimation, the inclusion of all Limnophilinae genera and subgenera would be desirable. However, for practical reasons it was not possible. The type species of the genera and subgenera were included whenever appropriate specimens were available. Some genera had a proportionally higher percentage of subgenera included in the analysis, whereas others had just a few, or even a single, of its subgenera represented. This resulted in the monophyly of certain genera being more roughly tested than others. The large genus *Limnophila* was the one with the highest percentage of included subgenera (ca. 73%). In total, 81 species in 59 genera and subgenera were included in the analysis. This number corresponds to approximately 62% of the total number of recognised Limnophilinae genera and subgenera.

Outgroup taxonomic sampling

Given the uncertainties on the systematic position of Tipulomorpha within the Diptera, and the non-monophyly of the Limnophilinae, the issue on outgroup sampling acquires a special relevance for this study.

The order Mecoptera, or at least part of it, is traditionally considered the sister-group of the Diptera (for a recent revision of the subject, see Whiting 2005). Mecopterans clearly keep the plesiomorphic conditions of several characters modified along the evolution of the Diptera. Primary homology hypotheses can be easily established for several structures found in Mecoptera and Tipulomorpha, especially concerning the characters of the wing venation. For this reason, representatives of the Mecoptera were included in the outgroup. In the case of Tipulomorpha being the sister-group of the other Diptera, as pointed out by some studies, the inclusion of Mecoptera would be especially interesting. In case the Tipulomorpha is nested within a more derived clade within the Diptera, as advocated by some authors, the inclusion of other Diptera families could be useful for the proper determination of character polarity. Several similarities are shared between the Trichoceridae and the Tipulomorpha *sensu stricto*, and many authors have defended the sister-group relationship between them. For this reason, the Trichoceridae was included. Among all other still-extant dipteran families, the Tanyderidae is the one for which, concerning the characters of wing venation, the easiest comparisons can be made with the conditions found the Tipulomorpha and for this reason this family was also included. The family Pachyneuridae seems to keep some plesiomorphic features in the structures of head capsule, antenna, gonocoxite and gonostylus. To help with the proper polarisation of some characters within the Tipulomorpha, the genera *Pachyneura* and *Cramptonomyia* were also included in the data matrix.

To test the possible relationships of Limnophilinae subgroups with other Tipulomorpha families, exemplars from the families Pediciidae, Tipulidae and Cylindrotomidae were included in the analysis. Within the Tipulidae, taxa considered by Oosterbroek (1980) as belonging to early lineages (e.g. *Leptotarsus* and *Ptilogyna*) were chosen, as well as genera presumably belonging to more derived groups (*Zelandotipula* and *Tipula*). The included exemplars of the families Pediciidae and Cylindrotomidae were chosen solely on the basis of specimen availability.

There are a wide range of taxa belonging to the other Limoniidae subfamilies that may potentially be related to Limnophilinae subgroups. A comprehensive sampling within these subfamilies is out of the scope of this study. Only a few genera of the subfamilies Limoniinae and Chioneinae were sampled, and the Dactylolabidinae was represented in the analysis by two species of its single included genus, *Dactylolabis*. Many of the sampled taxa of the other subfamilies (e.g. *Dactylolabis*, *Atarba*, *Elephantomyia* and *Helius*) have been traditionally difficult to place. To test potential affinities of these problematic taxa with Limnophilinae subgroups, and track possible transformation series leading to their unique and distinguished morphological features, these taxa were included in the study.

In total, 104 outgroup and ingroup terminal taxa were included in the data matrix, corresponding to exemplars of 103 species. For one species (*Shannonomyia lenta*) another line was added in the matrix for a variant form. A list of the terminal taxa with their corresponding geographical distributions is given in Table 1.

Table 1. List of the terminal taxa and their geographic distributions

Asterisks indicate the type-species of genus or subgenus. Species in which the male terminalia are illustrated for the first time are shown in bold

Taxa	Distribution
Mecoptera	
Bittacus strigosus Hagen, 1861	Nearctic (USA)
Thyridates pintoi (Souza Lopes & Mangabeira, 1942)	Neotropical (Brazil)
Tanyderidae	
Protoplasa fitchii Osten Sacken, 1859	Nearctic (Canada, USA)
Pachyneuridae	
Cramptonomyia spenceri	Nearctic
Pachyneura sp.	
Trichoceridae	
Diazosma sp.	Nearctic (Canada)
Trichocera bimacula Walker, 1848	Nearctic (USA)
Cylindrotomidae	
Cylindrotoma distinctissima (Meigen, 1818)*	Palearctic
Liogma nodicornis (Osten Sacken, 1865)*	Nearctic (Canada, USA)
Phalacrocera tipulina Osten Sacken, 1865	Nearctic (Canada, USA)
Triogma trisulcata (Schummel, 1829)	Palearctic
Stibadocerella albitarsis (de Meijere, 1919)	Oriental (Sumatra, Borneo: Sarawak).
Pediciidae	
Malaisemyia manipurensis Alexander, 1964	Oriental (India)
Pedicia sp.	Nearctic (USA)
Tricyphona sp.	Nearctic (USA)
Tipulidae	
***Leptotarsus (Longurio) gymnocerus* (Alexander, 1938)**	Neotropical (Brazil)
Ptilogyna sp.	Neotropical (Brazil)
Tipula (Triplicitipula) aequalis Doane, 1901	Nearctic (USA)
Zelandotipula novarae (Schiner, 1868)	Australian (New Zealand)
Limoniinae	
Dicranomyia (Dicranomyia) monostromia (Tokunaga, 1930)	Palearctic (Japan, Honshu, Shikoku)
Elephantomyia (Elephantomyia) westwoodi* Osten Sacken, 1869	Nearctic (Canada, USA)
Helius sp.	Neotropical (Brazil)
Chioneinae	
Atarba (Atarba) picticornis Osten Sacken, 1869*	Nearctic (Canada, USA)
Rhabdomastix chilota Alexander, 1929	Neotropical (Chile)
Dactylolabidinae	
***Dactylolabis (Dactylolabis) cubitalis* (Osten Sacken, 1869)**	Nearctic (USA)
Dactylolabis (Dactylolabis) montana (Osten Sacken, 1860)*	Nearctic (Canada, USA)
Limnophilinae	
***Acantholimnophila bispina* (Alexander, 1922)**	Australian (New Zealand)
Acantholimnophila maorica* (Alexander, 1922)	Australian (New Zealand)
Austrolimnophila (Austrolimnophila) eutaeniata (Bigot, 1888)*	Neotropical (Argentina, Chile, Falkland)
Bergrothomyia diemenensis Alexander, 1928	Australian (Australia)
Chilelimnophila lyra (Alexander, 1952)*	Neotropical (Chile)
***Clydonodozus neavei* Alexander, 1920**	Afrotropical (Congo)
***Conosia angustissima* Alexander, 1927**	Afrotropical
Conosia irrorata* (Wiedemann, 1828)	Palearctic, Afrotropical, Oriental, Australian
***Ctenolimnophila (Campbellomyia) paulistae* Alexander, 1943**	Neotropical (Brazil)
Edwardsomyia chiloensis Alexander, 1929*	Neotropical (Chile)
Eloeophila aldrichi aldrichi (Alexander, 1927)	Nearctic (Canada, USA)
Eloeophila maculata* (Meigen, 1804)	Palearctic
***Eloeophila trimaculata* (Zetterstedt, 1838)**	Palearctic
Epiphragma (Epiphragma) fasciapenne (Say, 1823)	Nearctic (Canada, USA)
Epiphragma (Epiphragma) nigripleuralis Alexander, 1945	Neotropical (Brazil)
Euphylidorea niveitarsis (Osten Sacken, 1869)*	Nearctic (USA)
Eupilaria phoenosoma (Alexander, 1931)*	Oriental (Philippines)
***Eupilaria suavis* Alexander, 1949**	Oriental (India)
***Eutonia alleni* (Johnson, 1909)**	Nearctic (USA)
Eutonia barbipes* (Meigen, 1804)	Palearctic
Gynoplistia (Cerozodia) laticosta Alexander, 1930	Australian (New Zealand)
***Gynoplistia (Cerzodia) hemiptera hemiptera* (Alexander, 1922)**	Australian (New Zealand)

(*continued next page*)

Table 1. (*continued*)

Taxa	Distribution
Gynoplistia (Dirhipis) luteola Alexander, 1971	Neotropical (Chile)
***Gynoplistia (Dirhipis) striatipennis* Alexander, 1928**	Neotropical (Argentina, Chile)
***Gynoplistia (Gynoplistia) fimbriata* Alexander, 1920**	Australian (New Zealand)
Gynoplistia (Gynoplistia) fuscoplumbea Edwards, 1923	Australian (New Zealand)
Gynoplistia (Xenolimnophila) flindersi Alexander, 1931	Australian (Australia)
Hexatoma (Cladolipes) cisatlantica (Alexander, 1937)	Neotropical (Brazil)
Hexatoma (Eriocera) atroantica Alexander, 1947	Oriental (India)
***Hexatoma (Eriocera) austera* (Doane, 1900)**	Nearctic (Canada, USA)
***Hexatoma (Eriocera) bruneri* (Alexander, 1928)**	Neotropical (Cuba)
Hexatoma (Euhexatoma) triphragma* Alexander, 1936	Oriental (China, Hainan)
***Hexatoma (Hexatoma) microcera* Alexander, 1926**	Nearctic
Hexatoma (Parahexatoma) pauliani* Alexander, 1951	Afrotropical (Madagascar)
***Idioptera nearctica* (Alexander, 1966)**	Nearctic (Canada, USA)
Lecteria (Lecteria) sp.	Neotropical (Brazil)
Limnophila (Arctolimnophila) subcostata (Alexander, 1911)*	Nearctic (Canada, USA)
Limnophila (Atopolimnophila) laricicola Alexander, 1912*	Nearctic (Canada, USA)
Limnophila (Dendrolimnophila) shikokuensis Alexander, 1953	Palearctic (Japan)
Limnophila (Dicranophragma) fuscovaria* Osten Saken, 1860	Nearctic (Canada, USA)
Limnophila (Elporiomyia) nox* Alexander, 1921	Afrotropical (South Africa)
Limnophila (Hesperolimnophila) euxesta Alexander, 1924	Nearctic (USA)
Limnophila (Idiolimnophila) emmelina* Alexander, 1914	Nearctic (Canada, USA)
Limnophila (Indolimnophila) bituminosa Alexander, 1931	Oriental (Philippines)
Limnophila (Lasiomastix) macrocera* (Say, 1823)	Nearctic (Canada, USA)
Limnophila (Limnophila) pictipennis* (Meigen, 1818)	Palearctic
Limnophila (Nesolimnophila) luteifemorata Alexander, 1963	Afrotropical (Madagascar)
***Limnophila (Arctolimnophila) claggi* Alexander, 1931**	Nearctic (Canada, USA)
Limnophila (Arctolimnophila) subcostata*	Nearctic (Canada, USA)
Mesolimnophila lutea* (Philippi, 1866)	Neotropical (Chile)
Metalimnophila howesi* (Alexander, 1922)	Australian (New Zealand)
***Metalimnophila productella* Alexander, 1926**	Australian (New Zealand)
***Neolimnomyia (Brachylimnophila) nemoralis* (Meigen, 1818)**	Palearctic
Neolimnomyia (Neolimnomyia) filata (Walker, 1856)*	Palearctic
Notholimnophila exclusa* (Alexander, 1922)	Australian (New Zealand)
Nothophila fuscana* Edwards, 1922	Australian (New Zealand)
***Nothophila nebulosa* Edwards, 1922**	Australian (New Zealand)
Paralimnophila (Paralimnophila) leucophaeata (Skuse, 1890)*	Australian (Australia)
Paralimnophila (Paralimnophila) skusei (Hutton, 1902)	Australian (New Zealand)
***Phylidorea (Phylidorea) longicornis pietatis* (Alexander, 1950)**	Palearctic (Russia, Mongolia, North Korea)
Phylidorea (Phylidorea) umbrarum (Krogerus, 1937)	Palearctic, (Finland, Russia, North Korea)
***Pilaria discicollis* (Meigen, 1818)**	Palearctic
Pilaria meridiana* (Staeger, 1840)	Nearctic, Palearctic
Polymera (Polymera) niveitarsis Alexander, 1913	Neotropical
Polymera (Polymerodes) catharinae Alexander, 1931	Neotropical (Brazil)
Polymera (Polymerodes) evanescens Alexander, 1948	Neotropical (Brazil)
Polymera (Polymerodes) parishi* Alexander, 1920	Neotropical (Brazil, Paraguay)
Priolonabis rufibasis (Osten Sacken, 1860)*	Nearctic (Canada, USA)
Prionolabis walleyi (Alexander, 1929)	Nearctic (Canada, USA)
Prolimnophila areolata* (Osten Sacken, 1860)	Nearctic (Canada, USA)
Pseudolimnophila legitima Alexander, 1931	Oriental (Philippines)
Pseudolimnophila luteipennis (Osten Sacken, 1860)*	Nearctic (Canada, USA)
Rhamphophila sinistra (Hutton, 1900)*	Australian (New Zealand)
Shannonomyia (Shannonomyia) brevinervis Alexander, 1929	Neotropical (Chile)
Shannonomyia (Shannonomyia) lenta* (Osten Sacken, 1860)	Nearctic (Canada, USA)
Tinemyia margaritifera Hutton, 1900*	Australian (New Zealand)
Tonnoirella gemella* Alexander, 1928	Australian (Australia)
Ulomorpha pilosella* (Osten Sacken, 1860)	Nearctic (Canada, USA)
***Ulomorpha rogersella* Alexander, 1929**	Nearctic (USA)

This study is based mostly on the direct observation of specimens. For the following taxa, however, the data were scored from the literature: *Dicranomyia* (*Dicranomyia*) *monostromia* (described in detail in Tokunaga 1930); *Tipula* (*Triplicitipula*) *aequalis* (described in detail in Rees and Ferris 1939, as *Tipula reesi*); *Liogma nodicornis* and

Phalacrocera tipulina (Brodo 1967); *Cramptonomyia spenceri* (Wood 1981).

Studied collections and specimen preparation

Most of the specimens examined in this study belong to the Alexander Collection of Crane Flies, housed at the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). A few specimens were borrowed from the following institutions: The Natural History Museum, London, UK (BMNH); Iowa State University, Ames, USA (ISU); Zoologisch Museum, the Netherlands (ZMAN); Palacký University, Czech Republic (PU); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP) and Departamento de Biologia, FFCLRP, Universidade de São Paulo, Brazil (DBRP).

The studied specimens were dissected, photographed and illustrated. The resulting pictures and drawings constituted the base on which the characters were scored. The dissected parts of specimens were cleared with warmed KOH and mounted in non-permanent microscope slides with glycerol. While preparing the slides, special care was taken to avoid damaging the three-dimensional structure of the specimens. After study the dissected parts were transferred to microvials and pinned with their corresponding specimens. The selection of specimens was greatly biased by the availability of intact exemplars that could be dissected, mounted and observed following a standardised protocol.

The abbreviations used in the figures are as follows:

aed	aedeagus.
aed apod	aedeagus apodeme.
cgonst	clasper of gonostylus.
goncx	gonocoxite.
iInterb	interbase.
lp	lateral process of aedeagal sheath.
ped	pedicel.
pg	post-gena.
scp	scape.
t9	ninth tergite.

Character list and definitions

The character data matrix is shown in Table 2 (also see Accessory Publication on the *Invertebrate Systematics* website). The terminology for most characters follows McAlpine (1981). Many of the structures dealt with in this study did not have a terminological treatment in McAlpine (1981), and some terms were took from other sources or used here for the first time as specified in each case. The terminology adopted for the wing veins is shown in Figs 3 and 4. The adopted terminology and primary homology hypothesis for the gonostylar branches across the different crane fly families follow Ribeiro (2006). Many of the characters and character states defined below are of easy conceptualisation and, accordingly, are only verbally defined. In some cases, the understanding of the studied variation demands a more detailed examination of the accompanying illustrations. For a few characters, there are illustrations available in the literature that may be cited but not reproduced here. The figures indicated as exemplifying the character states may not necessarily denote the exact condition found in all the taxa interpreted as having such state (even within a single character state definition, some variation may occur between taxa), but may be more typical examples or those of easier visualisation.

Twelve characters of the list below (2, 3, 6, 11, 13, 14, 18, 19, 31, 35, 37 and 84) deal with proportions in the dimensions of different structures. In coding such characters, special care were taken to define states only after the taking of several measures and comparisons of the resultant ratios; in other words, after the observation of gaps in the distribution of measured features in the studied taxa.

In the following list of characters, the codes do not denote *a priori* decisions on polarity. Character polarities are defined in this study *a posteriori* with rooting using the outgroup method revised by Nixon and Carpenter (1993).

(*1*) *Ocelli:* 0-absent; 1-present.

(*2*) *Proportions of scape in lateral view*: (0) almost as long as high; (1) little longer than high (less than 3× longer than high); (2) much longer than high (ca. 3× longer than high or more).

(*3*) *Length of scape relative to the length of pedicel:* (0) up to 1.5× the length of pedicel; (1) between 1.6 and 3.5× the length of pedicel; (2) more than 3.5× the length of pedicel.

(*4*) *Number of flagellomeres:* (0) five; (1) six; (2) nine; (3) ten; (4) twelve; (5) thirteen; (6) fourteen; (7) fifteen; (8) sixteen; (9) twenty; (10) more than twenty.

(*5*) *Format of flagellomeres:* (0) ovoid (dorsal and ventral margins equally curved or near so); (1) tubular (dorsal and ventral margins almost straight); (2) constricted in the middle.

(*6*) *Proportions of flagellomeres:* (0) up to ca. 3× longer than broad; (1) more than 3× longer than broad.

(*7*) *First and second flagellomeres fused:* (0) absent; (1) present (Fig. 8, arrow).

(*8*) *Flagellomeres:* (0) non-pectinated; (1) slightly pectinated (only a small protuberance at the base of the flagellomere (Figs 5, 6); (2) strongly pectinated (Fig. 7).

(*9*) *Antenna:* (0) 'normal'; (1) plumose (with many long and thin verticils).

(*10*) *Compound eyes:* (0) with hairs between ommatidia; (1) bare.

(*11*) *Rostrum length:* (0) reduced (Fig. 9); (1) at most, little longer than the length of the head (Figs 10, 11, 14, 15); (2) long (Figs 12, 13); (3) very long (as in *Elephantomyia*).

(*12*) *Nasus:* (0) absent; (1) present.

(*13*) *Size of the area between the posterior margin of the eye and dorsoposterior margin of the occiput (Fig. 16, distance A) relative to the total length of the eye (Fig. 16, distance B):* (0) less than one half the length of the eye; (1) ca. one-half of the length of the eye; (2) between a little more than one-half and the total length of the eye.

(*14*) *Height of the head at the level of the occiput (Figs 11 and 15, distance A) relative to the maximum height of the head (Figs 11 and 15, distance B):* (0) similar or little less than the maximum height (Figs 14, 15); less than the maximum height (Fig. 11).

(*15*) *Anterodorsal region of the head:* (0) non-protuberant (Figs 11–15); (1) slightly protuberant; (2) very protuberant (Figs 9, 10).

(*16*) *Well defined horn-like protuberances at the anterodorsal margin of the head:* (0) absent; (1) present (Ribeiro and Amorim 2002: fig. 13).

Table 2. Data matrix for cladistic analysis (characters 1-44)

Inapplicable characters coded as '-' and missing data coded as '?'. Polymorphisms: 0/1 = A, 5/6 = B

Taxa	Characters								
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	88888888 12345678
Thyridates pintoi	1009110001	1001000010	00221?0100	2101300200	1021005201	02100-----	------00??	?????-----	------00
Bittacus strigosus	1009110001	1011000010	00221?0000	2101301200	1020005201	02100-----	------00??	?????-----	------00
Protoplasa fitchii	1006000000	1001100221	00220---10	2101300100	1000105001	11000-----	------0020	10??10----	------10
Pachyneura sp.	1007100001	10?1000??1	20000--001	?00131-101	0010002001	00000-----	------00??	???00-----	------00
Cramptonomyia	1005110001	10?1000??1	20110--101	101--00401	1020002001	00000-----	------0021	???00-----	------00
Trichocera bimacula	1006110000	1011100011	0022120101	0000102101	1010004201	10000-----	------0010	1000011000	-1011000
Diazosma sp.	1006110001	1011100011	0022130101	1000102101	1010004200	00000-----	------0?10	1000011000	-???0000
Malaisemyia manipurensis	0105000000	1021201221	00101-0000	-01--01102	1010013101	01000-----	------0010	0-10011100	-1121100
Tricyphona sp.	0115000000	1021001121	00201-0200	111--01003	1020002101	01000-----	------0020	10?000----	------00
Pedicia sp.	0105000001	1011201231	00201-0100	001--02102	1010101101	010???????	??????0010	0-10011100	-1121100
Stibadocerella albitarsis	0005110011	0011001011	2012???001	--0--1--03	1000103001	0000100003	00-0000010	0-10011000	-0001010
Cylindrotoma distinctissima	0006110001	1021001011	21221-1201	101--01101	1000102101	01000-----	------0020	0-10011000	-1001010
Triogma trisulcata	0116000001	1021001011	21121-1301	-01--1-103	1000103101	01100-----	------0010	0-10011000	-0011010
Liogma nodicornis	0006100001	10???????1	?1221-?201	--1--1--03	1000102101	0?100-----	------0020	0-00011000	-0111010
Phalacrocera tipulina	0216000001	10???????1	?12211?201	100-31-003	0000102101	0?100-----	------00?0	0-?0001?00	-0111010
Mesolimnophila lutea	0226000001	1021001211	0012130301	1100102102	1010003101	0200100003	00-0110010	0-10011000	-1011000
Lecteria (Lecteria) sp.	0216000001	1011001221	0022130201	2102102102	1000102100	0000100003	3100100?0	10?0011000	-0011000
Clydonodozus neavei	021?0A1001	001?001221	0012120301	2102102101	11?0103100	0001100203	00-0110000	10000110--	-1000000
Conosia irrorata	02140A1001	001?001321	0012121301	2102002301	11?0102100	0101100203	00-001000?	10000110--	-10-0000
Conosia angustissima	0213001001	001?001321	0012120301	1102002201	11?0102100	0001100203	00-0010000	10000110--	-10-0000
Bergrothomyia diemenensis	011?000001	2021001311	0012120211	0001101003	1010103101	0100100203	00-1110000	0-?0011?00	-???1000
Notholimnophila exclusa	0116000001	1020101221	0002100111	100121-002	1010103101	0200100203	00-1110010	0-10011000	-1021000
Gynoplistia (X) flindersi	0218000101	1011001121	00?2130201	1101101003	1000103101	0000100203	00-1110011	1000011000	-0021000
Gynoplistia (G) fuscoplumbea	0??7000201	10?1001??1	0012130301	2101101103	1000003101	0100100203	0101100011	0-10011100	-01?1000
Ctenolimnophila (C) paulistae	0106000001	0011001211	0012130301	110111-003	1020103101	0100100203	00-0110021	0-10011100	-1131000
Limnophila (D) fuscovaria	0116000001	1011101211	0012130301	1100103103	1010103101	0000100103	0100000020	1010011101	-1021000
Neolimnomyia (B) nemoralis	0116000001	1011001211	0012130201	1001103103	1010103101	0000100203	0100000010	1010011101	-1021000
Neolimnomyia (N) filata	0116000001	1021001111	0012130201	100111-003	1010103101	0000100003	00-0010010	0-1001112-	-1121000
Shannonomyia (S) lenta	0116000001	1011001321	0012130101	100111-002	1010103101	0100101002	0100000010	001101111-	21121000
Shannonomyia (S) lenta var.	0116000001	1011001321	0012110101	100111-002	1010103101	0100101002	0100000010	001101111-	21121000
Shannonomyia (S) brevinervis	0116000001	1021001211	0012100101	100120-003	1010103101	0100100002	0100000000	0-1101111-	21121000
Prolimnophila areolata	0116000001	1011001121	002-130201	0000102101	1010004101	0100100002	0100000020	1010011100	-1011000
Dactylolabis (D) montana	0216000001	1021001211	0012130301	0101103103	1010000101	0200100000	00-0000021	0-00011100	-1121000

(*continued next page*)

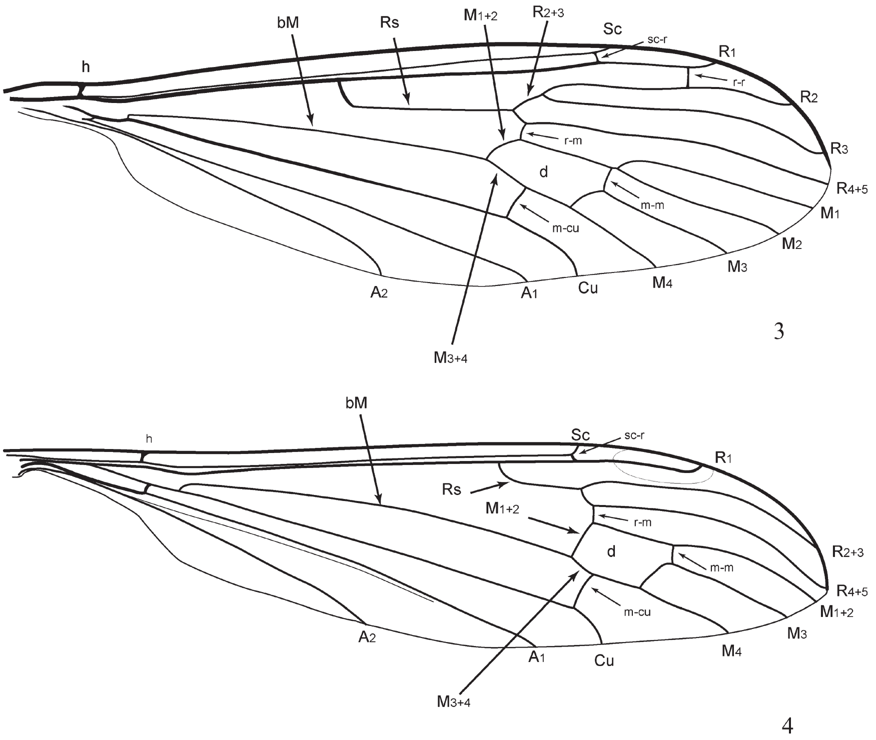
Table 2. (*continued*)

Taxa	Characters								
	0000000001	1111111112	2222222223	3333333334	444444445	5555555556	6666666667	7777777778	88888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Dactylolabis (D) cubitalis	0216000001	1021001221	0022130301	1101102103	1010002101	0200100000	00-0000001	0-00011100	-1131000
Epiphragma (E) fasciapenne	0215001001	1021001111	0012130211	1001103003	1011003101	0100100002	10-0000000	0-10111100	-0131000
Epiphragma (E) nigripleuralis	0216011001	1021001211	0022130311	1101101003	1011003101	0100100002	0100010000	0-10111100	-0011000
Acantolimnophila maorica	0106110001	101?001011	0022130301	1000102102	1010002101	0201100002	00-0000000	0-00111100	-013-000
Acantolimnophila bispina	0006110001	1011001011	0022130301	1000102102	1010002101	0201100002	00-0000010	0-0011111-	2012-000
Limnophila (A) subcostata	0116000001	1021111111	20121301A1	1001101002	1000103101	0100100203	0100000000	1000011000	-1011000
Lmnophila (A) claggi	0106000001	1021101011	2012130101	1001102103	1000103101	0100100203	0100000010	0-00011000	-1021000
Limnophila (A) laricicola	0116000001	1011001111	2012131101	1101102002	1000103101	0200100203	3100000021	0-00010000	-0001000
Atarba (A) picticornis	0006110001	1001101121	20020--001	011--1-103	1010101101	1100100203	0100010021	0-10000100	-003?000
Leptotarsus (L) gymnocerus	0112100001	1001201111	2012121101	0001201103	1000104101	0100100002	20-0001020	0---00----	-----000
Ptilogyna sp.	0225100201	1111001231	21-2111101	2101100002	1000104101	0100100003	0100001020	0---00----	-----000
Zelandotipula novorae	021???0001	1110101221	21-2121101	0001202103	1000103101	0110100000	00-0001021	0---00----	-----000
Tipula (T) aequalis	0214000001	1020101221	21-202?101	1001101102	1000104101	0110100010	30-0001?20	0---00----	-----000
Limnophila (E) nox	0116000001	1011101101	0002130201	A101103003	1000103101	0101100203	0100000000	1000011000	-0011000
Limnophila (I) bituminosa	0106000001	1011001?01	20120--201	1001103002	1020003101	0101100003	00-0000000	1010011000	-1121000
Helius sp.	0106000001	1011001231	20120--101	211--1-102	1010003100	0001100203	0100000021	1010011000	-0011000
Elephantomyia (E) westwoodi	0005001001	3021001131	20120--001	111--1-103	101000310?	0000100203	0100000021	0-10011000	-0011000
Eupilaria phoenosoma	0116000001	1011001111	1012120201	210111-103	1010102101	0210100203	00-0000000	1000011000	-0011000
Idioptera nearctica	0116110001	1021101011	2012120101	1101103002	1000113101	0100100203	00-0000000	10?0011000	-00?1000
Eloeophila maculata	011B000001	1011001321	0012120301	1101101102	1010113101	0100100203	20-0010000	0-00011000	-0011000
Eloeophila trimaculata	0106000001	1021001101	2012120201	2101102103	1010113101	0100100203	20-2110000	0-00011000	-0011000
Eloeophila aldrichi aldrichi	0106000001	1021001221	0012120201	1101102101	1010113101	0100100203	20-2010000	0-00011000	-0011000
Euphylidorea niveitarsis	0006110001	1011001111	0002130201	1101102103	1010103101	0000100001	0100000010	1000011000	-0011000
Limnophila (L) macrocera	0006110111	1011001011	2002130201	2101103102	1010103111	0100100203	00-0010000	1110011000	-0021000
Polymera (P) niveitarsis	0006110011	1001001121	0022130301	0000103002	0010002101	0000100203	2100000?1	0-?0010000	-1021000
Polymera (P) parishi	0005210011	1001001??1	0002120201	100011-002	0010001100	0000100203	20-0000000	0-10011100	-1021000
Polymera (P) catharinae	000??10011	1001001011	0002120201	000011-002	0010101100	0000100203	20-100000?	0-10010100	-1021000
Polymera (P) evanescens	0005210011	1001001111	0012130201	100011-002	0010102100	0000100203	20-1000010	0-?0011?00	-10?1000
Eupilaria suavis	0216000001	1011001111	1002120201	210211-103	1010103101	0000100203	10-0000000	1100011000	-0011000
Limnophila (D) shikokuensis	0106000001	101?001111	0002130201	000111-003	1010003101	0200101203	0100000010	1110011000	-1131000
Priolonabis rufibasis	0116000001	1020001011	0022130301	1101102003	1010103101	0100111002	10-2000011	0-?0011000	-1031000
Prionolabis walleyi	0116000001	102?0011?1	0012130211	1101103?03	1010103101	0100111002	10-20000??	0-?0011000	-????000
Limnophila (H) euxesta	0216000001	1020001101	2022130111	2101102002	A000102101	0000100203	30-0000000	1100011000	-0011000
Eutonia barbipes	0226000001	1020011221	0022130301	2101102102	1000103101	0000100213	---0000000	0-00011000	-0011000
Eutonia alleni	0226000001	1020011221	0022130301	2101102003	1000103101	0000100213	---0000000	0-00011000	-0011000

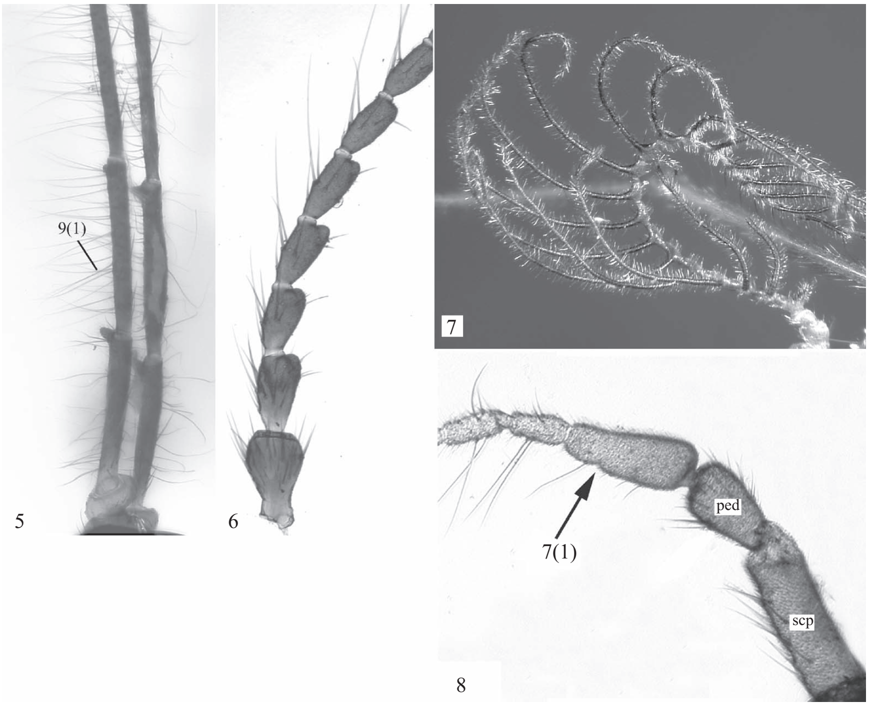
(*continued next page*)

Table 2. (*continued*)

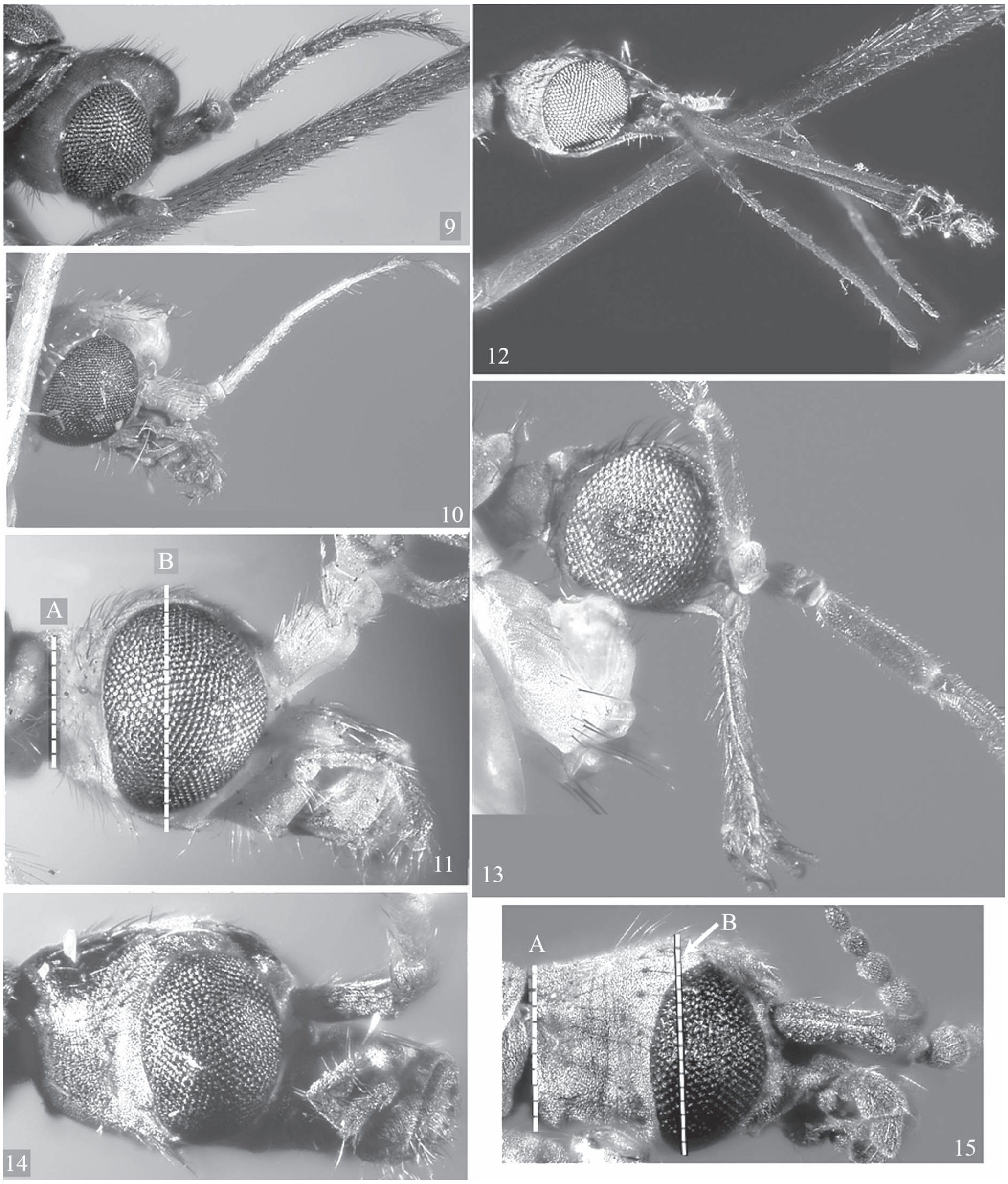
Taxa	Characters								
	0000000001	1111111112	2222222223	3333333334	444444445	5555555556	6666666667	7777777778	88888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Limnophila (N) luteifemorata	0116000001	1010001321	00121?0201	1001102103	1010003101	0100100003	20-0000110	0-00011100	-0121000
Limnophila (L) pictipennis	0226000001	10?0001??1	00120--201	1001103103	1010103101	0101100003	00-0000111	0-00011100	-0021000
Dicranomyia (D) monostromia	0214000001	1010000231	20001-0001	211--1-003	1000101100	0000100203	00-0000000	0-00011100	-0011000
Rhabdomastix chilota	0106110001	1010100121	?0020--101	100131-003	1010003100	1000100203	30-0010000	0-00011100	-0131000
Paralimnophila (P) skusei	0116110001	1011001221	0012130211	1102102102	1010101101	0100101203	0100000010	1000011000	-0001000
Chilelimnophila lyra	01060A0001	10210013?1	20120--301	1101103002	1010103101	0100100203	0110110010	1010011000	-0011000
Phylidorea (P) longicornis pietatis	0116010001	1021001111	2012131111	1101102002	1000003101	0000100203	10-0000011	1101011000	-0001000
Phylidorea (P) umbrarum	0117010001	1021001111	2012130111	1101102002	1000003101	0001100203	00-0010011	1001011000	-00?1000
Metalimnophila productella	0106110001	10110012?1	0012120101	1000103102	1010103101	0200100001	3110000010	1011011000	-1121000
Metalimnophila howesi	0106110001	1011001221	0012120101	1000102002	1010103101	0100100001	0110000010	10?1011000	-1011000
Paralimnophila (P) leucophaeata	010?110201	1011001211	0012130201	2102101102	1010103101	0100100203	20-0000000	1000011000	-0011000
Gynoplistia (C) hemiptera hemiptera	000A100201	1011101221	0012130201	2101101102	1000103101	0100100203	3110000010	0-10011100	-1131000
Gynoplistia (C) laticosta	000A100201	1011001211	0012130201	2101101102	1000103101	0100100203	3110000010	0-10011100	-1131000
Gynoplistia (G) fimbriata	0118000201	1011001211	0012131201	2101101103	1000103101	0000100203	3110000011	0-10011100	-0131000
Gynoplistia (D) luteola	000?100201	1011011211	0012131301	1001101102	1000103101	0100100203	30-0000010	0-1000----	-----001
Gynoplistia (D) striatipennis	0009000201	1011011211	0012131301	0001101101	1000103101	0100100203	30-0000010	0-1000----	-----001
Limnophila (I) emmelina	0115000001	1021001121	0012130101	210101-102	1000103101	0101101003	3111000011	0-00011100	-0011000
Austrolimnophila (A) eutaeniata	011?110001	1011001211	0022130311	1000101003	1010003101	0?00100003	10-10100??	????011?00	-????000
Tonnoirella gemella	0106000001	2011001211	0022130301	1001101102	1020002101	0200100003	00-1010010	0-00011000	-0121000
Edwardsomyia chiloensis	0116110001	2001001311	0022130301	1101101102	1020003101	0100100002	3110010010	0-00111000	-0011000
Tinemyia margaritifera	0106110001	3001001231	0022130311	1101102003	1020002101	0201100002	00-0000010	0-00011000	-0021000
Rhamphophila sinistra	0116110001	2011001321	0022130311	1001102102	1010001101	0000101002	10-0000010	1000011000	-0011000
Nothophila fuscana	01060A0001	0011001111	0022130301	0001102002	1010003111	0100101002	20-0000010	1000011100	-1121000
Nothophila nebulosa	01?60A0001	00110011?1	0022130201	0001102002	1010003111	0100101002	00-0000010	1100011100	-0021000
Hexatoma (E) austera	0110110001	1011101011	0012120201	210111-003	1000101101	0000100103	00-1000020	0-00011000	-0001000
Pseudolimnophila luteipennis	0216010001	1021001221	0012120311	2101101002	1010103101	0000100203	00-1000010	0-1001101-	210??000
Pseudolimnophila legitima	0216110001	1021001121	0012120201	2101103102	1010103101	0000100203	00-1000010	0-1001101-	210?1000
Hexatoma (E) triphragma	0121110001	1011201211	0022130201	2101102101	1000103101	0100100103	10-1000010	0-1001111-	21131000
Hexatoma (E) atroantica	0111110001	1001101321	1022121301	110011-103	1000103101	0000100103	10-1000020	0-1001101-	21021000
Pilaria meridiana	011B000001	101?001211	0002111301	100111-002	1010103101	0100100203	10-2000020	0-0001101-	200?1000
Pilaria discicollis	0116000001	1011001221	0002111301	1001102102	1000103101	0100100203	10-1000011	0-??01101-	200?1000
Ulomorpha pilosella	02160A0001	10210011?1	20020--201	000111-002	1000103111	0000100103	10-1000010	0-00011010	00011000
Ulomorpha rogersella	02160A0001	1021001121	20020--211	100101-002	1010103111	0000100103	10-1000010	0-00011010	00011000
Hexatoma (E) bruneri	0111110001	1011111221	0022120101	110121-103	1000102101	0000100003	10-1000020	0-1001101-	01011000
Hexatoma (P) pauliani	0111110001	101?111111	0012100201	110131--13	000010-101	0100100103	10-0000020	0-?001101-	11011000
Hexatoma (C) cisatlantica	0110110001	0011201121	00021-0201	001--1--12	000010-101	0000100203	00-0000020	0-10011000	-1021000
Hexatoma (H) microcera	0110110001	1011111011	0012100201	110131--12	000010-101	0000100203	10-0000020	0-1001101-	11011000



Figs 3, 4. Adopted wing vein homology system and terminology. 3, *Edwardsomyia chiloensis*. 4, *Elephantomyia* (*Elephantomyia*) *westwoodi*.



Figs 5–8. Morphological characters, antenna. 5, *Limnophila* (*Lasiomastix*) *macrocera*. 6, *Gynoplistia* (*Xenolimnophila*) *flindersi*. 7, *Gynoplistia* (*Cerozodia*) *hemiptera hemiptera*. 8, *Epiphragma* (*Epiphragma*) *fasciapenne*.



Figs 9–15. Morphological characters, head, lateral view. 9, *Hexatoma* (*Cladolipes*) *cisatlantica*. 10, *Hexatoma* (*Euhexatoma*) *triphragma*. 11, *Gynoplistia* (*Gynoplistia*) *fimbriata*. 12, *Tonnoirella gemella*. 13, *Edwardsomyia chiloensis*. 14, *Limnophila* (*Hesperolimnophila*) *euxesta*. 15, *Limnophila* (*Limnophila*) *pictipennis*.

(*17*) *Posterior region of the head (post-gena):* (0) separated medially by a membranous area (e.g. *Trichocera*; see Peterson 1916: fig. 78); (1) meeting medially, not separated by a membranous area (Figs 21–23).

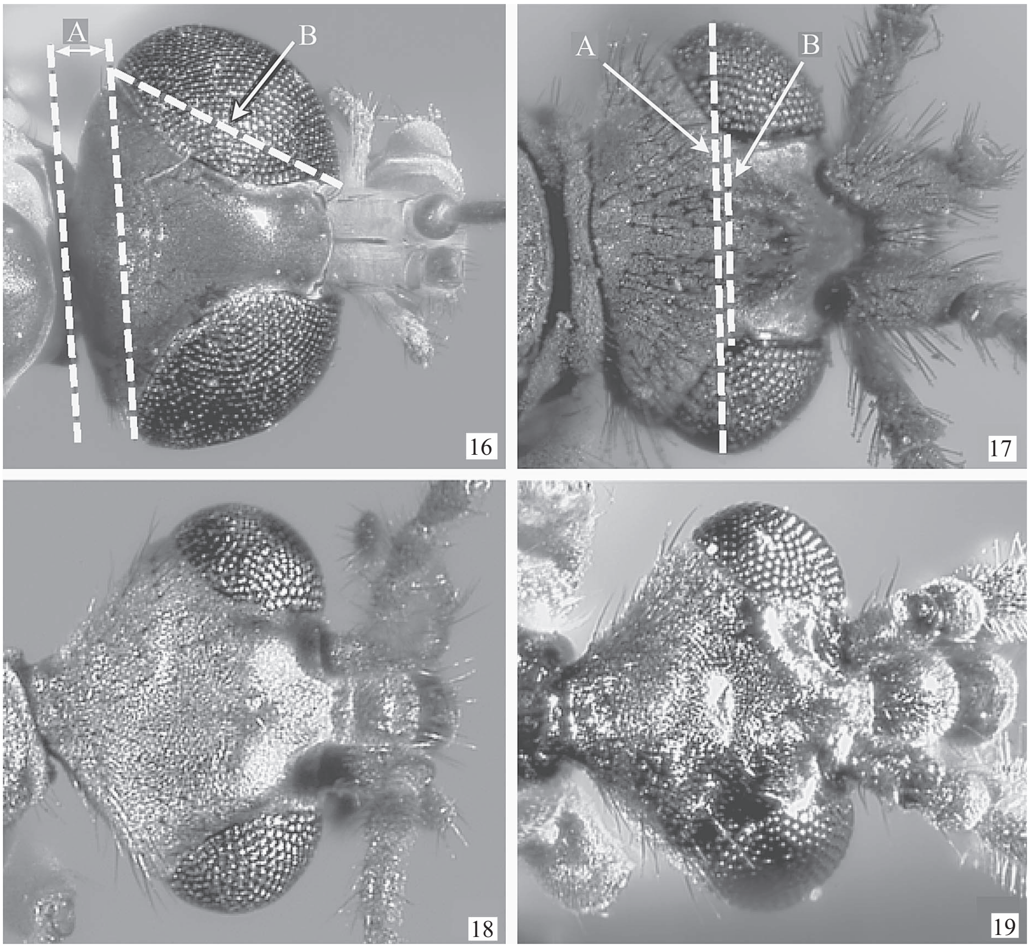
(*18*) *Ratio between the minimal ventral distance between the eyes (Figs 20 and 22, distance A) and the total ventral width of the head (Figs 20 and 22, distance B):* (0) greater than 0.35 (Fig. 20); (1) between ca. 0.2 and 0.35 (Fig. 21); (2) less than 0.2 (eyes still separated) (Fig. 22); (3) eyes meeting ventrally (Fig. 23).

(*19*) *Ratio between the distance among the eyes at the level of the head's dorsal transversal axis (Fig. 17, distance B) and total head width (Fig. 17, distance A):* (0) greater than 0.6; (1) between ca. 0.4 and 0.6; (2) between ca. 0.2 and 0.4; (3) less than 0.2.

(*20*) *Posterior wings transformed into halteres:* (0) absent; (1) present.

The presence of posterior wings transformed into halteres is a synapomorphy of the Diptera. This character was included to bring more stability at the base of the cladogram with the inclusion of representatives of Mecoptera in the outgroups.

(*21*) *Costal vein:* (0) circumbient; (1) interrupted or abruptly narrowed between R_2 and R_3; (2) interrupted or abruptly narrowed between R_3 and R_{4+5}.



Figs 16–19. Morphological characters, head, dorsal view. 16, *Hexatoma* (*Eriocera*) *atroantica*. 17, *Hexatoma* (*Eriocera*) *austera*. 18, *Limnophila* (*Arctolimnophila*) *subcostata*. 19, *Limnophila* (*Arctolimnophila*) *claggi*.

(*22*) *Apex of vein Sc:* (0) reaching the wing margin (Figs 25–29); (1) atrophied, not reaching the wing margin (Fig. 24).

(*23*) *Position of the apex of vein Sc relative to the first bifurcation of Rs:* (0) basal to the bifurcation of Rs (Fig. 26); (1) approximately at the level of the bifurcation of Rs (Fig. 27); (2) distal to the bifurcation of Rs (Figs 28, 29).

(*24*) *Position of the crossvein sc-r:* (0) basal to the origin of Rs; (1) approximately at the level of origin of Rs; (2) distal to the origin of Rs.

(*25*) *Crossvein r-r:* (0) absent (Fig. 27); (1) present (Figs 24–26, 28, 29).

(*26*) *Position of the crossvein r-r:* (0) basal to the bifurcation of R_{2+3} (Fig. 30); (1) very near or at the exact point of bifurcation of R_{2+3} (Figs 31, 35); (2) distal to the bifurcation of R_{2+3}, but more close to this point than to the mid-point of R_2 (Fig. 32); (3) more close to the mid-point of R_2 than to any other point (Fig. 33, 34).

(*27*) *Inclination of the crossvein r-r:* (0) more or less perpendicular to the wing longitudinal axis (Figs 30, 32, 33); (1) oblique to the wing longitudinal axis (Figs 24, 31, 34, 35).

(*28*) *Origin of Rs relative to the apexes of the veins A_2 and A_1:* (0) approximately at the level of the apex of A_1; (1) basal to the level of the apex of A_1 and distal to the level of the apex of A_2 (between A_1 and A_2); (2) approximately at the level of the apex of A_2; (3) basal to the level of the apex of A_2.

(*29*) *Projection (spur) near the base of vein Rs:* (0) absent; (1) present.

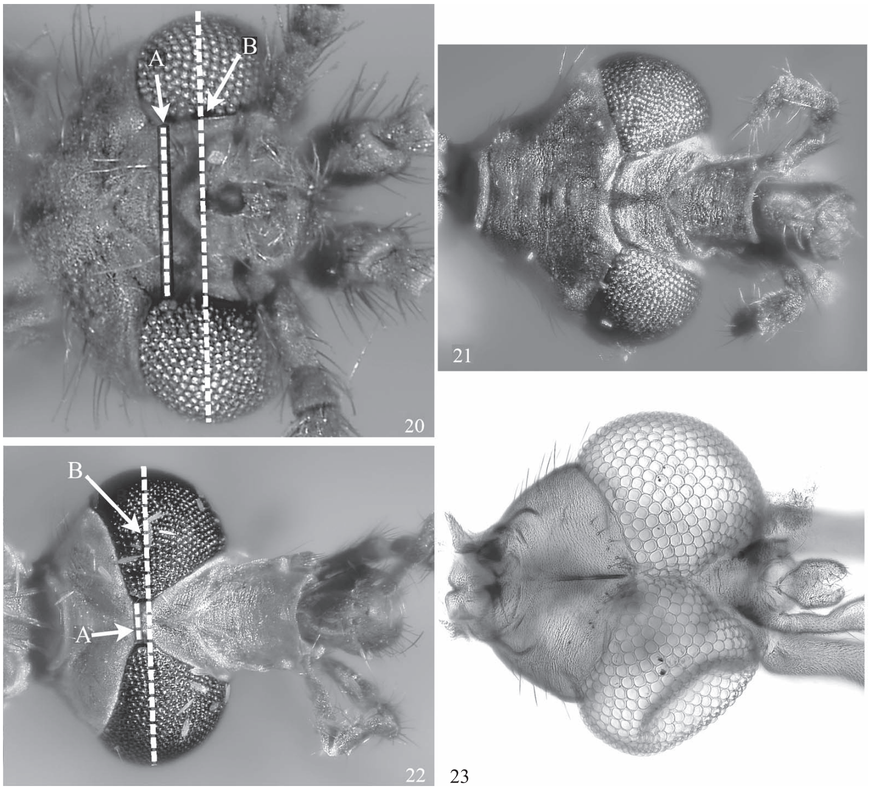
(*30*) *Veins R_4 and R_5:* (0) both reaching the wing margin; (1) fused into a single vein R_{4+5} reaching the wing margin.

(*31*) *Length of the section between the origin of vein R_{4+5} and the point of contact of R_{4+5} with r-m (Figs 36–39, white arrow):* (0) less than $\frac{1}{2}\times$ the length of r-m (Fig. 36); (1) between $\frac{1}{2}$ and $2\times$ the length of r-m (Figs 37–38); (2) longer than $2\times$ the length of r-m (Fig. 39).

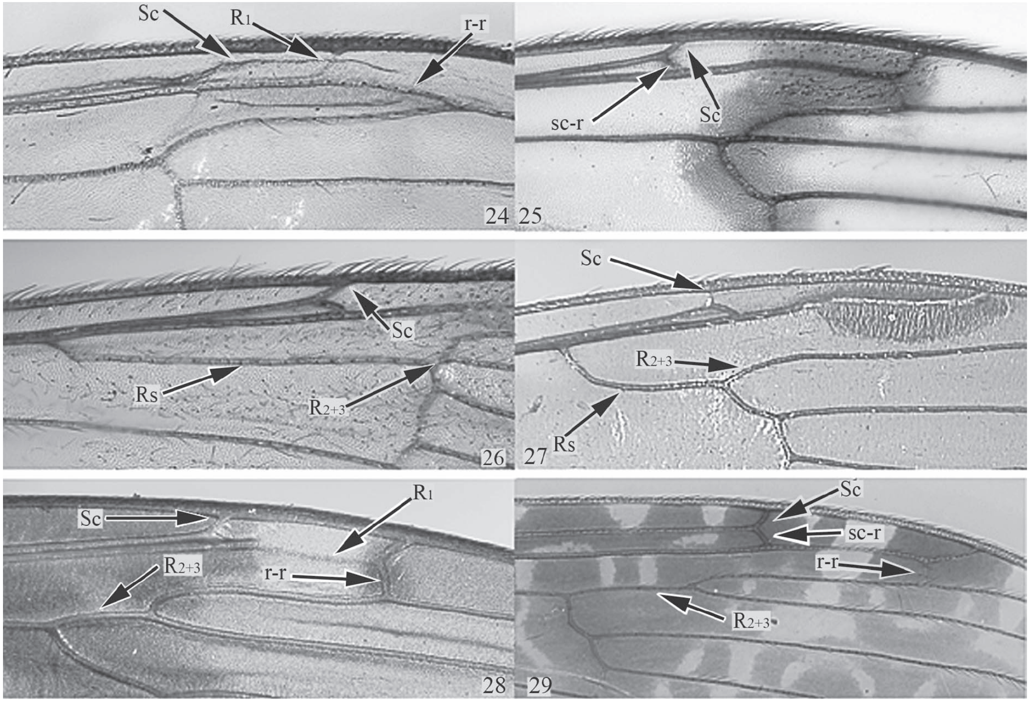
(*32*) *Straight line between the point of origin of R_{4+5} and the point of contact of r-m with M_{1+2} (Figs 36–39, white line between points A and B):* (0) not very inclined, sub-perpendicular to the wing longitudinal axis (Figs 36, 37); (1) very inclined relative to the wing longitudinal axis (origin of R_{4+5} situated well basal to the point of contact of r-m with M_{1+2}) (Figs 38, 39).

(*33*) *Vein R_{2+3}:* (0) bifurcated (cell r2 present) (Fig. 3); non-bifurcated (cell r2 absent) (Fig. 4).

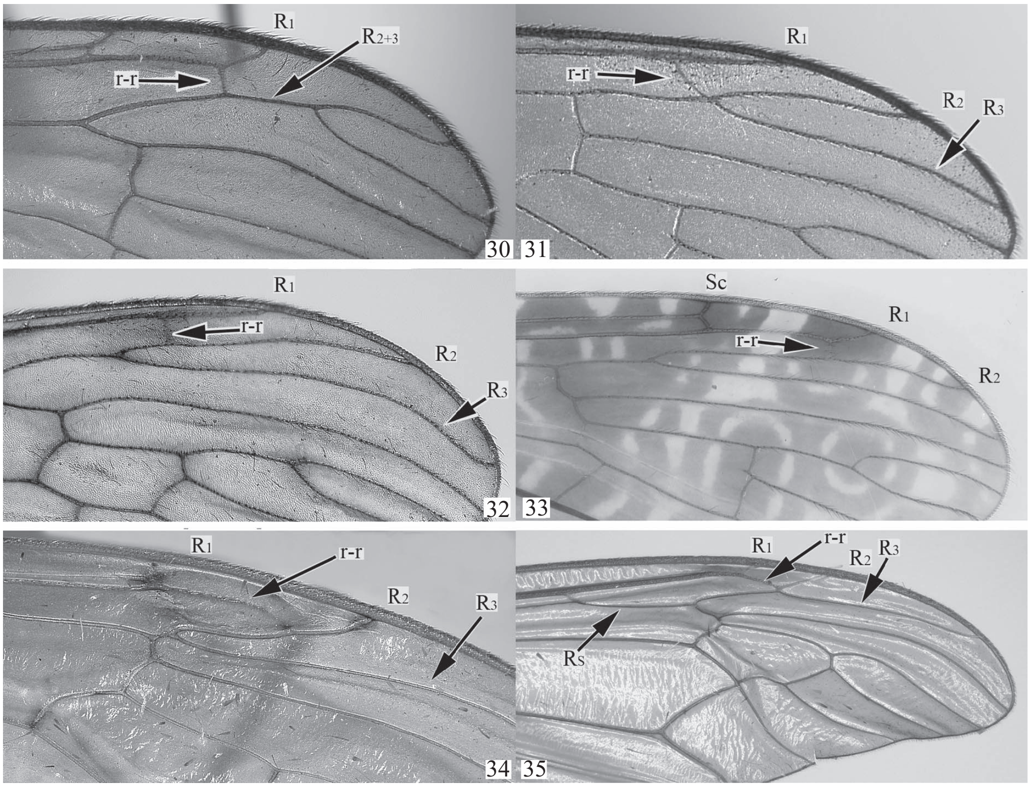
(*34*) *Veins R_2 and R_3:* (0) reaching the wing margin almost parallel to each other (Figs 40, 41); (1) gradually diverging from



Figs 20–23. Morphological characters, head, ventral view. 20, *Hexatoma* (*Eriocera*) *austera*. 21, *Limnophila* (*Hesperolimnophila*) *euxesta*. 22, *Gynoplistia* (*Cerozodia*) *laticosta*. 23, *Conosia angustissima*.



Figs 24–29. Morphological characters, wing. 24, *Cylindrotoma distinctissima*. 25, *Limnophila* (*Lasiomastix*) *macrocera*. 26, *Ulomorpha pilosella*. 27, *Elephantomyia* (*Elephantomyia*) *westwoodi*. 28, *Eutonia alleni*. 29, *Tinemyia margaritifera*.



Figs 30–35. Morphological characters, wing. 30, *Hexatoma* (*Parahexatoma*) *pauliani*. 31, *Pilaria discicollis*. 32, *Pseudolimnophila* (*Pseudolimnophila*) *luteipennis*. 33, *Tinemyia margaritifera*. 34, *Gynoplistia* (*Dirhipis*) *striatipennis*. 35, *Ptilogyna* sp. (Tipulidae).

each other as they approach and reach the wing margin (Figs 42, 45, 46, 47); (2) abruptly diverging from each other after running more or less in parallel (Figs 43, 44).

(*35*) *Petiole of cell r2:* (0) absent (bifurcation of R_{2+3} basal to the origin of R_{4+5}) (Figs 43, 45); (1) shorter than $\frac{1}{2}$ the length of R_3 (Figs 42, 44); (2) between ca. $\frac{1}{2}$ and the total length of R_3 (Fig. 46); (3) longer than the length of R_3 (Fig. 47).

(*36*) *Vein M_{1+2}:* (0) bifurcated (cell m1 present) (Figs 48–49); (1) non-bifurcated (cell m1 absent) (Figs 50–53).

(*37*) *Petiole of cell m1:* (0) absent (m-m linking M_3 to M_2) (Fig. 54); (1) shorter than $\frac{1}{2}$ the length of M_1 (Fig. 55); (2) between ca. $\frac{1}{2}$ and the total length of M_1 (Fig. 56); (3) longer than M_1 (Fig. 57).

(*38*) *Position of the crossvein r-m at the section between the first bifurcation of bM and the point of contact of M_{1+2} or M_1 with m-m:* (0) closer to the first bifurcation of bM than to the mid-point of the section (Fig. 58); (1) closer to the mid-point of the section than to either the first bifurcation of bM or point of contact with m-m (Fig. 59) ; (2) very close to or at the exact point of contact with m-m (Fig. 60); posterior to the point of contact with m-m (Fig. 61); (3) r-m linked to M_1.

(*39*) *Vein M_{3+4}:* (0) bifurcated (Figs 48–50); (1) non-bifurcated (Figs 51–53).

(*40*) *Section of M_{1+2} between its origin and point of contact with r-m:* (0) not very inclined, almost aligned with bM (Fig. 62); (1) inclined relative to bM, but describing a gentle curve (Fig. 63); (2) inclined relative to bM, describing an abrupt curve (Figs 64, 65); (3) abruptly inclined relative to bM and straight (Figs 66, 67).

(*41*) *Discal cell:* (0) absent (Figs 30, 36); (1) present (Figs 32–35).

(*42*) *Vein h:* (0) well defined and visible (Figs 71–74, 76); (1) faint (Fig. 75).

(*43*) *Position of vein h:* (0) closer to the point of bifurcation than to the origin of M+Cu (Figs 74, 76); (1) closer to the mid-point between the origin and bifurcation of M+Cu (Fig. 73); (2) closer to the origin of M+Cu. (Figs 71, 72).

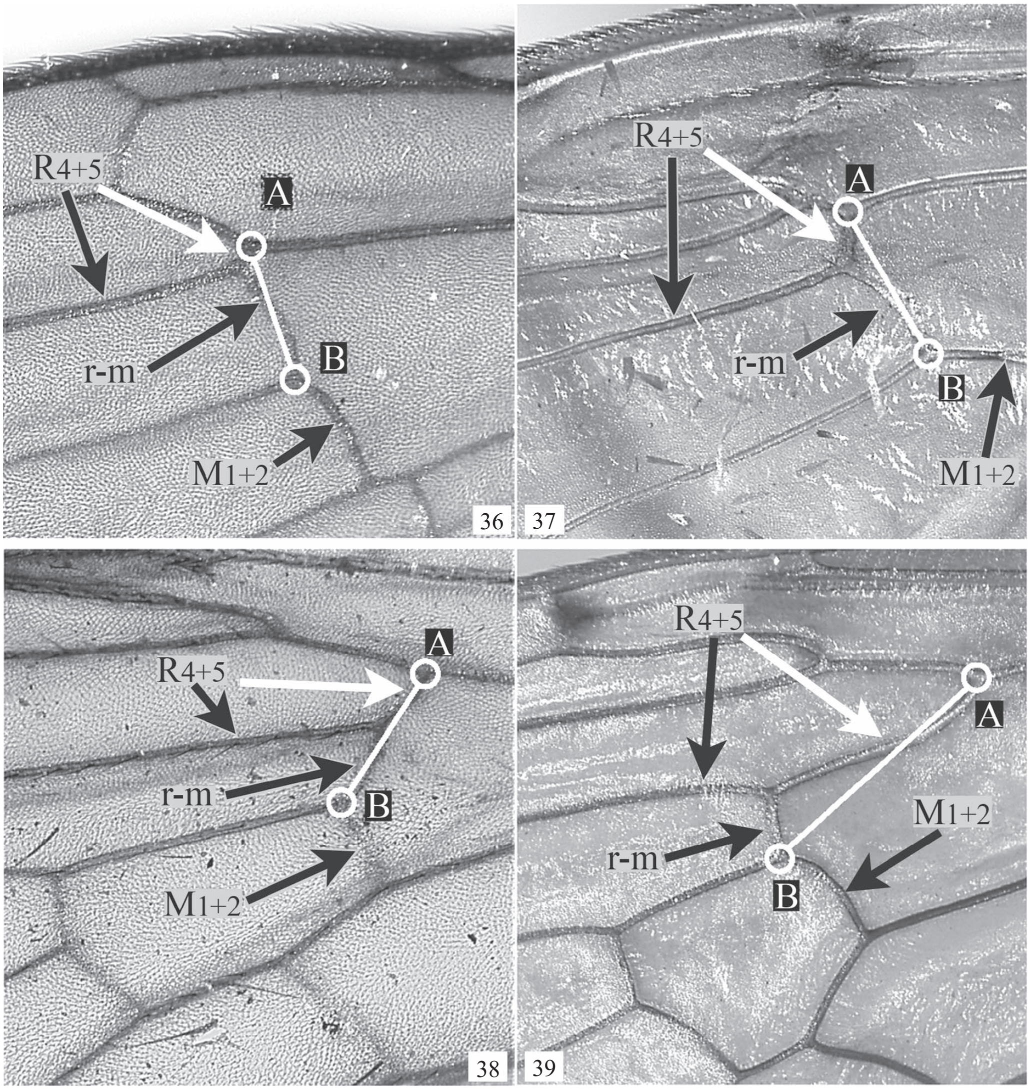
(*44*) *Additional crossvein at the distal half of cell Sc:* (0) absent; (1) present.

(*45*) *Intumescence between veins R and bM near the wing base (arculus):* (0) absent (Figs 71–73); (1) present (Figs 74–76, white arrow).

In some taxa, there is a link near the base of the wing between the veins R and bM. Edwards (1923, 1938) called this structure the arculus, sometimes referring to it as a vein. This structure can be more or less well defined, but seems to constitute an intumescence rather than a true crossvein.

(*46*) *Additional crossvein between M and Cu situated basally to m-cu:* (0) absent; (1) present.

(*47*) *Position of crossvein m-cu:* (0) attached basally to the point of the first bifurcation of to bM (Fig. 68); (1) attached to near



Figs 36–39. Morphological characters, wing. 36, *Hexatoma* (*Cladolipes*) *cisatlantica*. 37, *Gynoplistia* (*Dirhipis*) *striatipennis*. 38, *Prionolabis walleyi*. 39, *Eutonia barbipes*.

or just at the point of the first bifurcation of bM (Fig. 69); (2) situated distally to the first bifurcation of bM, but closer to this point than the mid-point of discal cell (m-cu attached to M$_{3+4}$) (Fig. 70). (3) situated more closely to the mid-point of discal cell than any of its extremities (m-cu attached to M$_{3+4}$) (Figs 64–67). (4) situated more closely to the bifurcation of M$_{3+4}$ than the mid-point of discal cell (attached to M$_{3+4}$) (Fig. 63); (5) attached to M$_4$ (Fig. 62).

(*48*) *Vein A$_2$:* (0) absent; (1) normally developed; (2) reduced.

Most commonly, the vein A$_2$ in Tipulomorpha is well developed, and its apex reach the wing margin well beyond the base of the wing. In Mecoptera and Trichoceridae, this vein is more reduced and in *Stibadocerella* (Cylindrotomidae) it is absent.

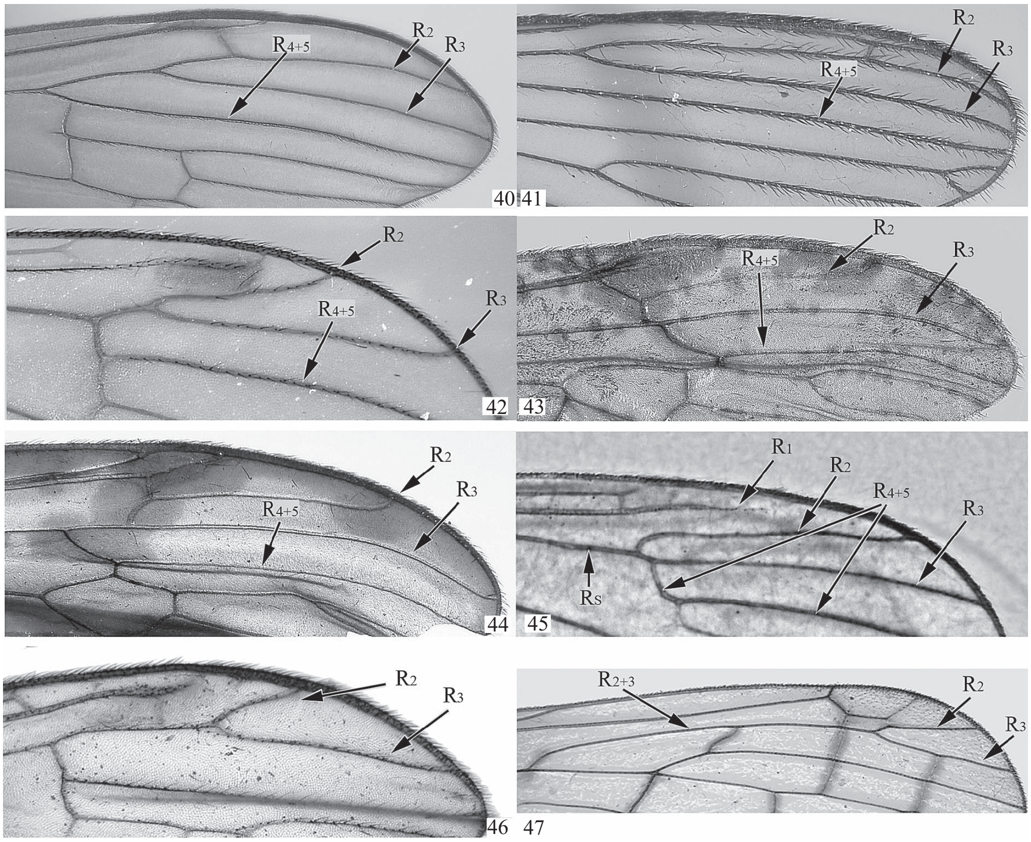
(*49*) *Macrotrichia in wing membrane:* (0) absent; (1) present over most of wing surface (Figs 26, 49, 64).

(*50*) *Tibial spurs:* (0) absent; (1) present.

(*51*) *Mesothoracic meron:* (0) not attached to the thorax; (1) attached to the thorax.

In the order Diptera, the meron is restricted to the mesothorax. However, mecopterans keep the more plesiomorphic condition of the thorax, in which a metathoracic meron is also present. In Mecoptera, the meron is well developed, but forms a distinct sclerite separated from the other thoracic sclerites by a thin membranous area. In most Tipulomorpha, the mesothoracic meron has been greatly reduced in size compared with Mecoptera, but are clearly separated from the pleural sclerites by a membrane. In *Protoplasa* (Tanyderidae), *Trichocera* (Trichoceridae) and some Limoniidae (e.g. *Atarba* and several Chioneinae) the mesothoracic meron is well attached to the other pleural sclerites.

(*52*) *Format of posterior margin of ninth tergite:* (0) forming no extensions; (1) forming extensions which are wider than long, as short horn-like extensions (Figs 83–86); (2) forming



Figs 40–47. Morphological characters, wing. 40, *Hexatoma* (*Eriocera*) *atroantica*. 41, *Polymera* (*Polymera*) *niveitarsis*. 42, *Limnophila* (*Arctolimnophila*) *claggi*. 43, *Conosia irrorata*. 44, *Clydonodozus neavei*. 45, *Limnophila* (*Idiolimnophila*) *emmelina*. 46, *Shannonomyia* (*Shannonomyia*) *brevinervis*. 47, *Bittacus strigosus* (Mecoptera).

extensions which are longer than wide, as long horn-like extensions (Figs 80, 96, 97).

(*53*) *Gonocoxite:* (0) cone-shaped, generally longer than high; (1) semi-globular, not much longer than high.

This character was first scored by Oosterbroek (1980), who compared the general shape of the gonocoxite of most Tipulidae, which is in general semi-globular and almost as long as high (Oosterbroek 1980: fig. 3), with that of most Limoniidae and some Tipulidae, which is more cone-shaped and much longer than high (Oosterbroek 1980: fig. 4).

(*54*) *Position of gonostylus in the gonocoxite:* (0) terminal; (1) subterminal (Figs 82–84, 108, 110).

(*55*) *Gonostylus:* (0) undivided (Figs 77–79); (1) divided into lobe of gonostylus and clasper of gonostylus (Fig. 80).

(*56*) *Lobe of gonostylus:* (0) non-bifurcated; (1) bifurcated (Fig. 117).

(*57*) *Lobe at the base of the lobe of gonostylus:* (0) absent; (1) present (Figs 116, 117, 123, 137–139).

(*58*) *Clasper of gonostylus:* (0) hairy; (1) slightly hairy (with minute hairs, generally at the base of the gonostylus); (2) glabrous.

(*59*) *Clasper of gonostylus:* (0) undivided; (1) well divided at its base into two parts (Figs 121, 122).

(*60*) *Clasper of gonostylus:* (0) weakly sclerotised, fleshy; (1) mostly weakly sclerotised, but with some sclerotisation of the very apex of the clasper (Fig. 112); (2) with the central region weakly sclerotised, but with a strong sclerotisation of the margins of the clasper; (3) strongly sclerotised in general.

(*61*) *Apex of the clasper of gonostylus:* (0) gradually narrowed; (1) abruptly narrowed (Figs 137, 143–146); (2) abruptly narrowed with a strong dilatation of the distal portion of the anterior margin (Figs 105–107, 129); (3) dilated (Figs 120, 128, 133).

(*62*) *Apex of the clasper of gonostylus:* (0) simple (Figs 82–84, 96–97); (1) bifid (Figs 81, 89, 90, 92–93).

(*63*) *Apical bifurcation of the clasper of gonostylus:* (0) little developed, tooth-like (Figs 81, 89, 90, 92, 93); (1) greatly developed, branch-like (Figs127, 128, 130, 131).

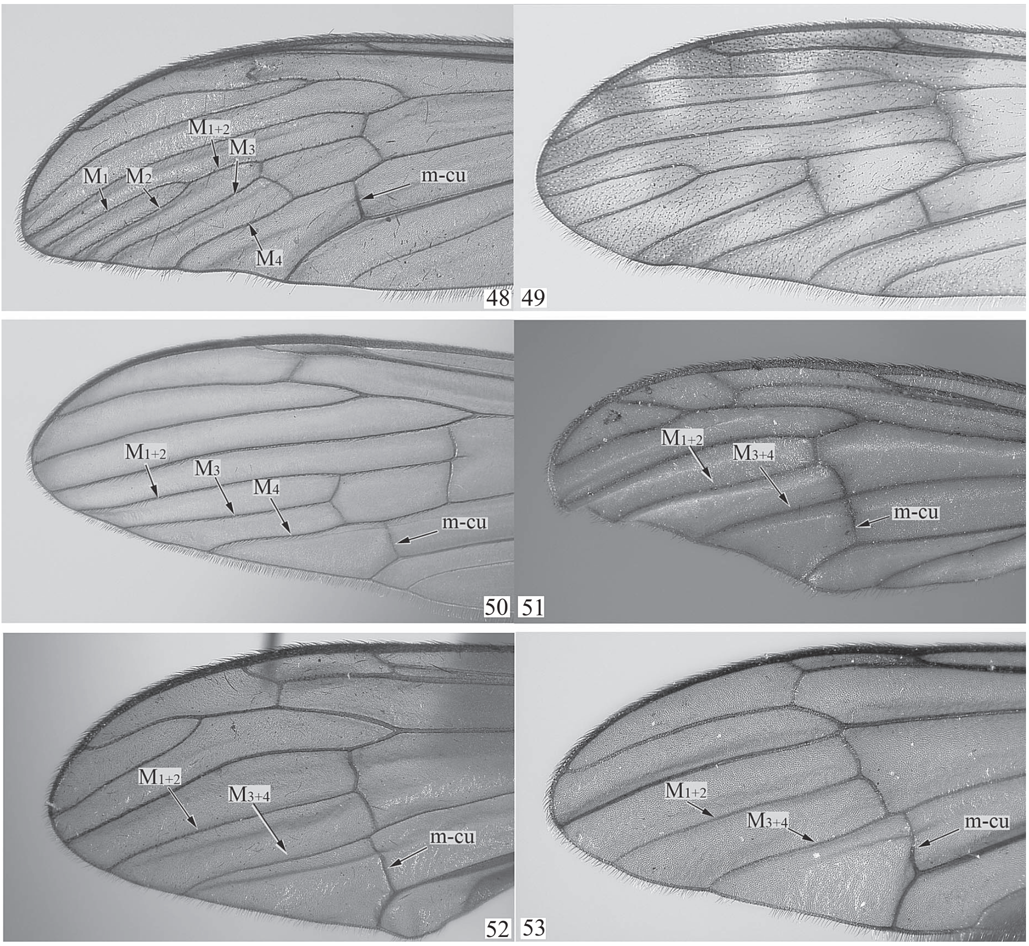
(*64*) *Distal portion of the anterior margin of the clasper of gonostylus:* (0) smooth; (1) slightly serrated (Figs 140, 141, 144–146); (2) strongly serrated (Figs 105–107, 117, 143).

(*65*) *Area between the anterior and posterior margins of the clasper of gonostylus:* (0) smooth; (1) serrated (Figs 105–107).

(*66*) *Posterior margin of the clasper of gonostylus:* (0) smooth; (1) serrated (Figs 105–107).

(*67*) *Trajectory described by the aedeagus in lateral view from its base to its apex:* (0) straight; (1) curved.

In most Tipulomorpha, the trajectory described by the aedeagus in lateral view, from its base to its apex, is basically



Figs 48–53. Morphological characters, wing. 48, *Pseudolimnophila* (*Pseudolimnophila*) *luteipennis*. 49, *Nothophila nebulosa*. 50, *Hexatoma* (*Eriocera*) *atroantica*. 51, *Hexatoma* (*Hexatoma*) *microcera*. 52, *Hexatoma* (*Parahexatoma*) *pauliani*. 53, *Hexatoma* (*Cladolipes*) *cisatlantica*.

a straight line. The aedeagus is simply projected porteriorly and, at most, is slightly curved. A typical condition is found, for example, in *Chilelimnophila* (Ribeiro 2007: fig. 12). In the Tipulidae, the situation is quite different. Instead of simply projecting itself porteriorly, the aedagus is projected anteriorly from its base, and forms a curved loop before directing posteriorly and reaching the posterior margin of the terminalia. A typical condition is found in many species of *Tipula* (De Jong 1994*b*: figs 3, 5, 89–91; De Jong 1995*a*: fig. 4).

(*68*) *Margins of the internal canal of the aedeagus:* (0) smooth; (1) rugged (Figs 191, 192).

(*69*) *Position of the anterior margin of the aedeagus apodeme (in dorsal view):* (0) well posterior to the level of the anterior margin of paramere (Figs 155–158, 168, 169, 171, 174, 178–180); (1) from not very anterior to more or less aligned with the anterior margin of paramere (Figs 151, 152, 159, 162, 164, 165); (2) well anterior to the level of the anterior margin of paramere (Figs 153, 160, 163, 167, 183, 184).

(*70*) *Width of the aedeagus apodeme relative to the width of the aedeagus:* (0) not much wider than the aedeagus; (1) much wider than the aedeagus (Figs 160, 175, 183, 184, 192).

(*71*) *Lateral processes of the aedeagal sheath:* (0) absent or little developed (Figs 152, 153, 154); (1) present and well developed (Figs 151, 155–158).

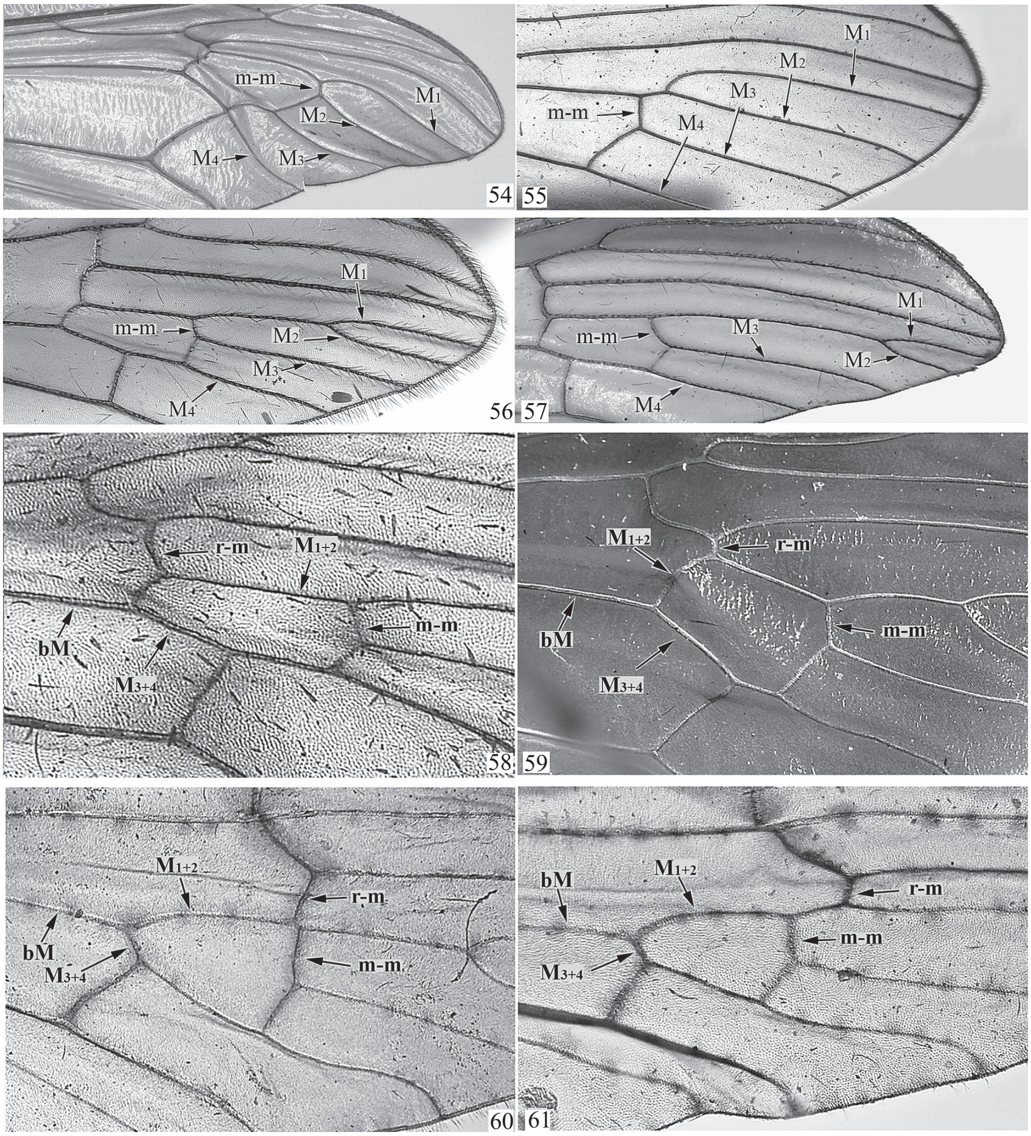
The aedeagal sheath is here defined as being the structure into which the aedeagus is inserted and that forms the ventral connection between the parameres. The degree of development of the aedeagal sheath is quite variable, and it may or may not bear lateral processes. These processes have sometimes been called gonapophyses by C. P. Alexander.

(*72*) *Lateral processes of aedeagal sheath:* (0) simple; (1) bifid (Figs 188, 189, 193, 212).

(*73*) *Position of the posterior extremity of the paramere relative to the lateral margin of the interbase:* (0) displaced medially relative to the lateral margin of the interbase (Figs 151, 155–158, 161, 173, 174); (1) more or less aligned with the lateral margin of the interbase (Figs 153, 154, 159, 160, 162–165).

(*74*) *Ventral region of the parameres:* (0) not laterally extended; (1) laterally extended (Figs 166, 198–201).

(*75*) *Area of the aedeagal sheath between the medial margin of paramere and lateral margin of aedeagus:* (0) relatively narrow; (1) widened (Figs 168–171).



Figs 54–61. Morphological characters, wing. 54, *Ptilogyna* sp. (Tipulidae). 55, *Tonnoirella gemella*. 56, *Metalimnophila howesi*. 57, *Neolimnomyia* (*Brachylimnophila*) *nemoralis*. 58, *Idioptera nearctica*. 59, *Gynoplistia* (*Cerozodia*) *hemiptera hemiptera*. 60, *Conosia angustissima*. 61, *Conosia irrorata*.

(*76*) *Interbase:* (0) absent or indistinguishable; (1) present, clearly noticeable.

The interbase is a conspicuous blade like structure present and clearly noticeable in some Trichoceridae, some Cylindrotomidae and most Limoniidae. It is situated dorsally and in general articulates laterally with the gonocoxite apodeme. Its form can be quite variable. In the Tipulidae, these paired structures seem to be absent, or at least not so clearly noticeable.

(*77*) *Interbase:* (0) non-individualised from the paramere; (1) individualised from the paramere.

In a few Limoniidae, as in *Gynoplistia* (*Dirhipis*) (Fig. 205), and *Limnophila* (*Atopolimnophila*) *laricicola* (Fig. 175), there are blade like structures in the same position of the interbases. However, these blades seem fused with the parameres so that their limits cannot be unequivocally distinguished.

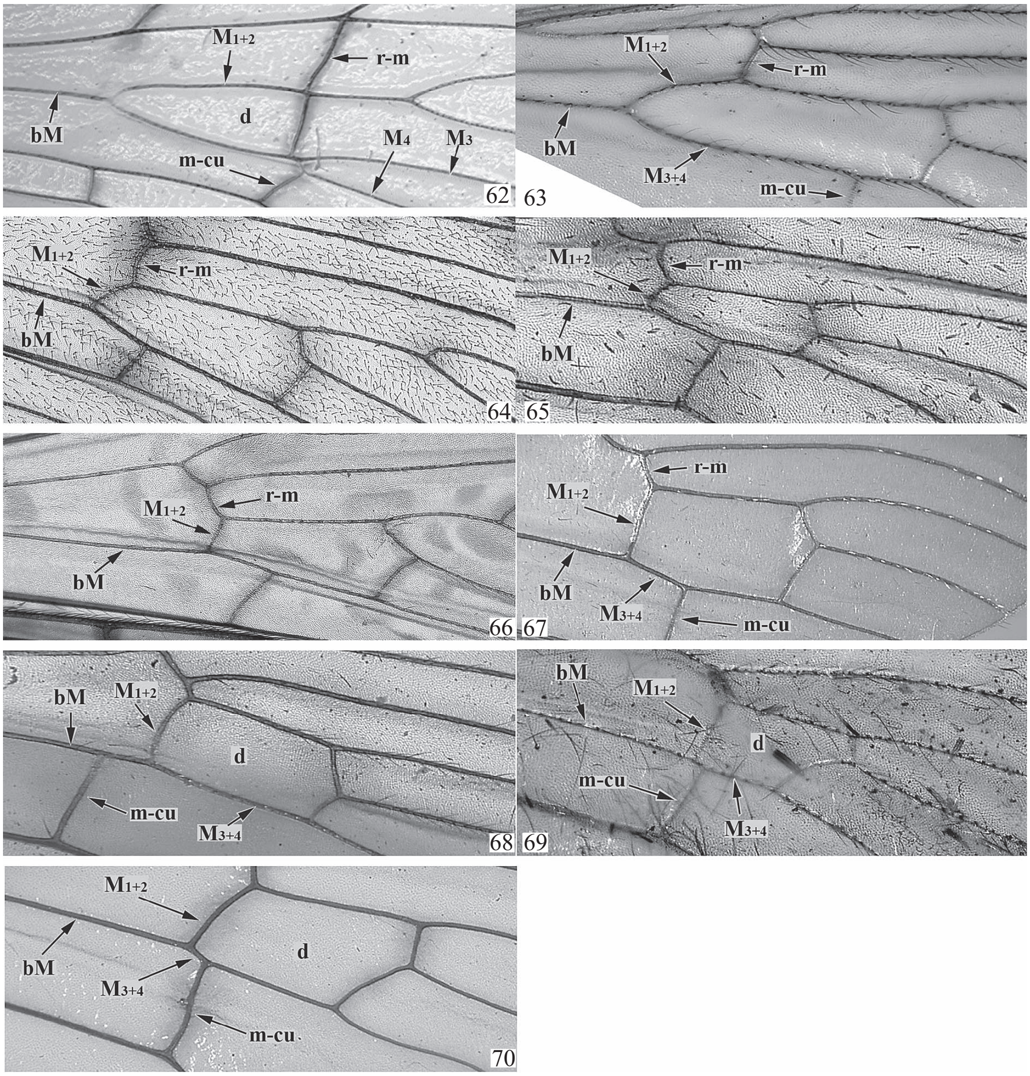
(*78*) *Interbase:* (0) fused medially (Figs 151, 153, 154–158, 159,161; (1) separated medially (Figs 160, 162, 163–172).

(*79*) *Distal portion of interbase:* (0) simple, without any branching; (1) two-branched (Figs 166, 214–221); (2) serrated (Fig. 165).

(*80*) *Distal portion of interbase:* (0) when simple, narrowed or dilated, but without a sub-apical constriction; (1) rounded and dilated after a sub-apical constriction (Figs 163, 164).

(*81*) *Interbase branches:* (0) similar in length (Figs 218, 219); (1) lateral branch longer than medial branch (Figs 220, 221, 223); (2) lateral branch shorter than medial branch (Figs 214–217).

(*82*) *Basolateral portion of interbase:* (0) forming a relatively long and robust extension generally clearly connected with the gonocoxite apodeme (Figs 81, 155, 168–171, 177–180,



Figs 62–70. Morphological characters, wing. 62, *Bittacus strigosus* (Mecoptera). 63, *Prolimnophila areolata*. 64, *Nothophila fuscana*. 65, *Idioptera nearctica*. 66, *Epiphragma* (*Epiphragma*) *nigripleuralis*. 67, *Elephantomyia* (*Elephantomyia*) *westwoodi*. 68, *Dactylolabis* (*Dactylolabis*) *montana*. 69, *Atarba* (*Atarba*) *picticornis*. 70, *Lecteria* (*Lecteria*) sp.

193–197); (1) not extended (Figs 151, 153, 154, 159, 160, 162–167).

(*83*) *Basomedial portion of interbase:* (0) forming an extension longer than wide; (1) not extended.

(*84*) *Ratio between the maximum length of interbase and its maximum width at the base:* (0) less than 1; (1) between ca. 1 and 1.5; (2) between 1.5 and 2.5; (3) greater than 2.5.

(*85*) *Main body of interbase:* (0) absent (only the base of interbase present) (Figs 156–158); (1) present.

The interbase most often articulates with the gonocoxite apodeme laterally (or lateroposteriorly) and with the paramere anteriorly. The region of the interbase between these two points of articulation normally forms the basal part (or base) of the interbase. The rest of the interbase forms its main body, i.e, the main part which is mostly blade-like and sometimes is very well developed. Typical examples are found, for example, in *Eupilaria*, *Idioptera* and *Eloeophila* (Figs 176–180). In the genera *Conosia* and *Clydonodozus* the interbase is quite modified, and the part defined here as its main body is lacking or not present in its most common configuration. In these genera, only the part corresponding to the base of the interbase seems to be present (Figs 156–158).

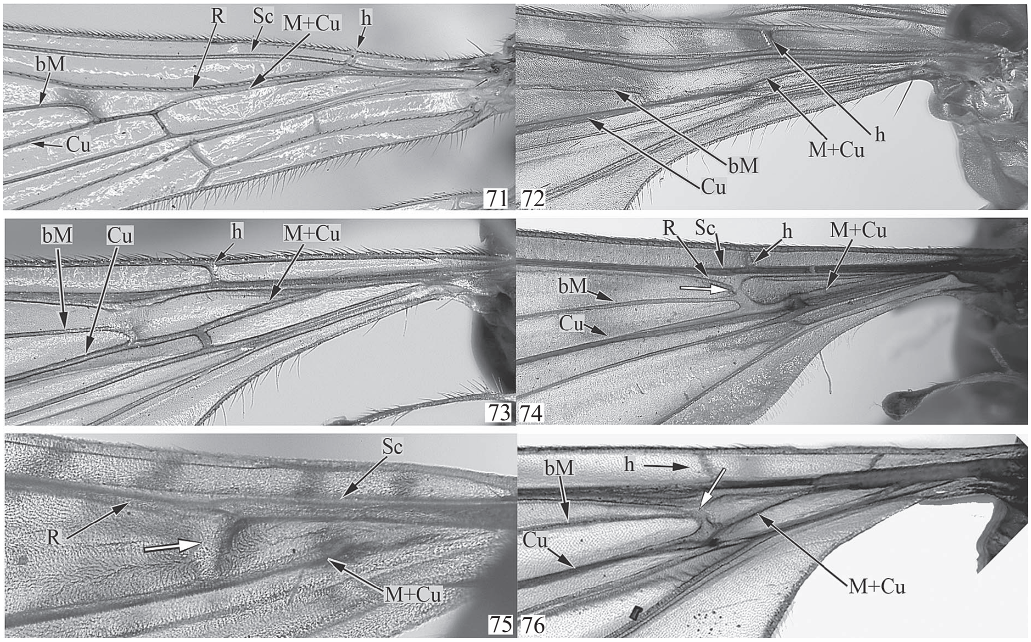
(*86*) *Interbase:* (0) not fused with the gonocoxite; (1) fused with the gonocoxite (Fig. 78).

(*87*) *Aedeagus:* (0) simple; (1) trifid (Fig. 153).

(*88*) *Lateral margins of the aedeagal sheath:* (0) smooth; (1) rough (Fig. 205).

Phylogenetic analysis

The phylogenetic analysis was made under the criterion of parsimony and the shortest trees were searched using implied weighting, which attributes different weights to characters



Figs 71–76. Morphological characters, wing. 71, *Bittacus strigosus* (Mecoptera). 72, *Tinemyia margaritifera*. 73, *Elephantomyia* (*Elephantomyia*) *westwoodi*. 74, *Hexatoma* (*Eriocera*) *bruneri*. 75, *Conosia irrorata*. 76, *Cylindrotoma distinctissima* (Cylindrotomidae).

together with tree construction (Goloboff 1993). In differentially weighted inferences, the topologies supported by the more congruent characters are preferred, at the expense of those supported by the more homoplastic characters. The strength of which the more homoplastic characters will be downweighted can be controlled during the implementation of implied weighting by changing the value of the weighting constant k. Lower values of k will downweigh more homoplastic characters more severely than relatively higher values. However, knowing beforehand which value of k should be used seems impossible. Also, it is a legitimate question if a single predetermined value of k is justifiable for every dataset. These limitations are inherent to the use of implied weighting. Given this, addressing the sensitivity of the data to different weighting schemes was preferred. Such analysis was done combining different values of k (from 2 to 6), evaluated independently through several different parsimony analyses (Table 3).

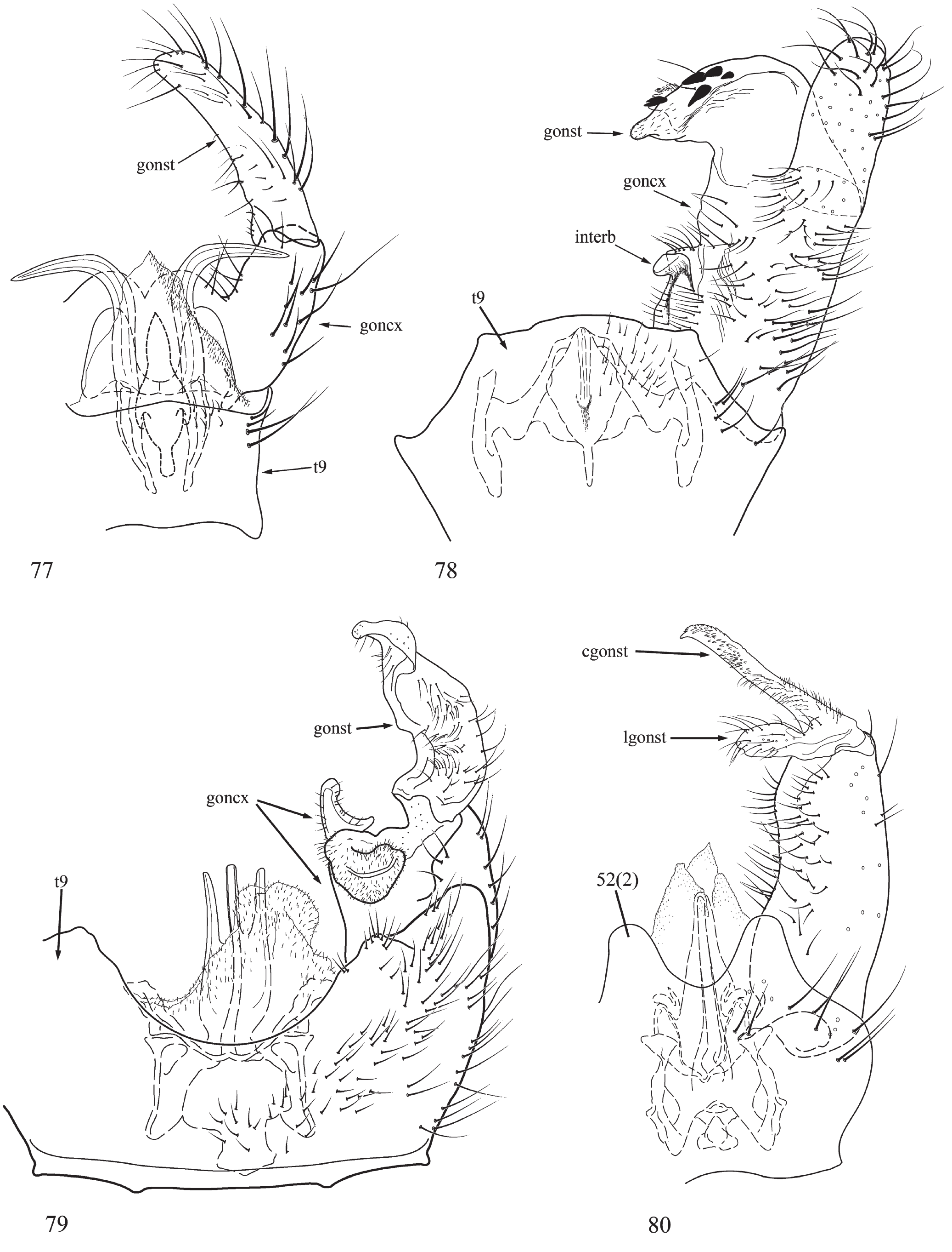
The sensitivity of the data to variation in the values of k was accessed through taxonomic congruence (or topological congruence), inferred from the resolution of the strict consensus trees. All analyses were performed in TNT version 1.1 for Windows (Goloboff *et al.* 2003), using heuristic searches with tree-bisection-reconnection (TBR) branch swapping, random stepwise addition sequence and 10 000 replicates holding up to 10 trees per replication. In all cases, characters were treated as unordered. Trees were rooted following the outgroup method revised by Nixon and Carpenter (1993).

Results and discussion

Homoplasy levels and clade stability

The external morphology of the adult male crane flies showed an extremely high level of homoplasy (see Table 4). Most of the nodes in the different cladograms obtained by the different analyses (details below) are supported by different combinations of homoplastic character states. The consistency index (*CI*) of the trees obtained by the various analyses range from 0.135 to 0.146 (Table 3). During the construction of the data matrix, several preliminary analyses and assessment of initial tree estimates allowed the rechecking, reinterpretation and correcting of some characters and states, and this process of reciprocal illumination eventually resulted in less ambiguity. However, the high level of homoplasy in the dataset is probably not an artifact derived from limitations in defining characters and states, but a real phenomenon. For other insect groups, recent phylogenetic studies based on morphological evidence have been faced with the same difficulties. For example, Belokobylskij *et al.* (2004) evaluated the relative performance of adult morphological characters, compared with character systems from larval morphology, for the reconstruction of phylogenetic relationships in braconid wasps (Hymenoptera). These authors concluded that the external characters of adults (male and female terminalia excluded) yielded the relatively more incongruent and poorly resolved results, mostly due to high levels of homoplasy. The consistency index found by Belokobylskij *et al.* (2004) for the best trees based on the adult external morphology was 0.139. The addition of characters from reproductive organs (terminalia) and larval characters helped to increase *CI* values, but the best trees found in the whole study still had a very low consistency index ($CI = 0.238$).

The sensitivity analysis has shown a great level of incongruence among the phylogenetic results obtained using different values of k. This high level of instability concerning the components of the various clades is undoubtedly a consequence of the high level of homoplasy. If the sensitivity of clades to changes in analytical parameters provides an insight



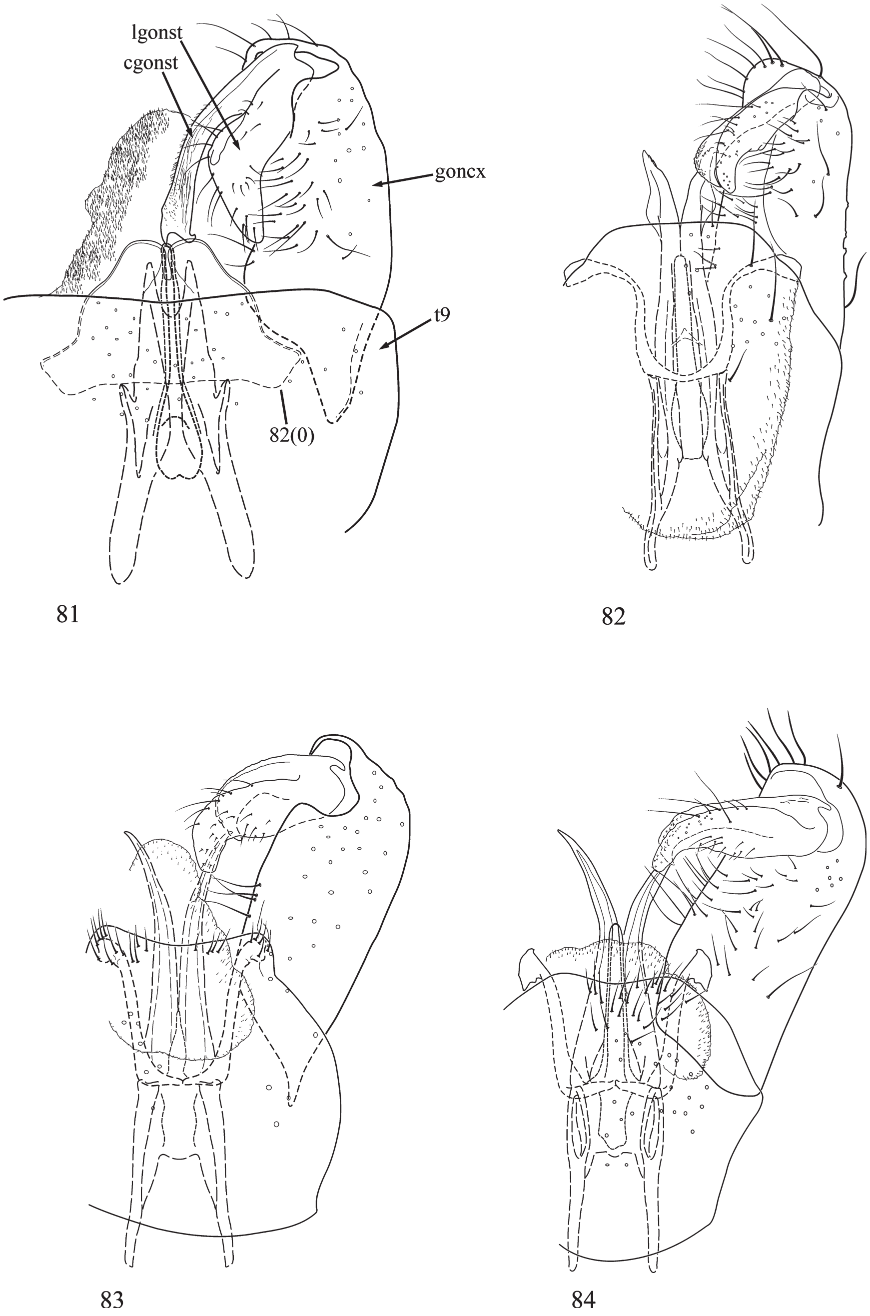
Figs 77–80. Morphological characters, male terminalia, dorsal view. 77, *Trichocera bimacula* (Trichoceridae). 78, *Malaisemyia manipurensis* (Pediciidae). 79, *Cylindrotoma distinctissima* (Cylindrotomidae). 80, *Mesolimnophila lutea*.

on the support of groups (Giribet 2003), then most of the clades recovered in the different analyses must be considered as having very weak support in general.

As a consequence of the basic premises used as the starting point for this research, the phylogenetic results obtained are greatly biased by a larger taxonomic sampling in the Limnophilinae compared with other Limoniidae subfamilies. However, the addition of more taxa from the other subfamilies is unlikely to increase *CI* values or reduce the level of incongruence in the overall results, as for the other groups not included in this study, the external adult morphology probably display the same level of homoplasy as in the included taxa.

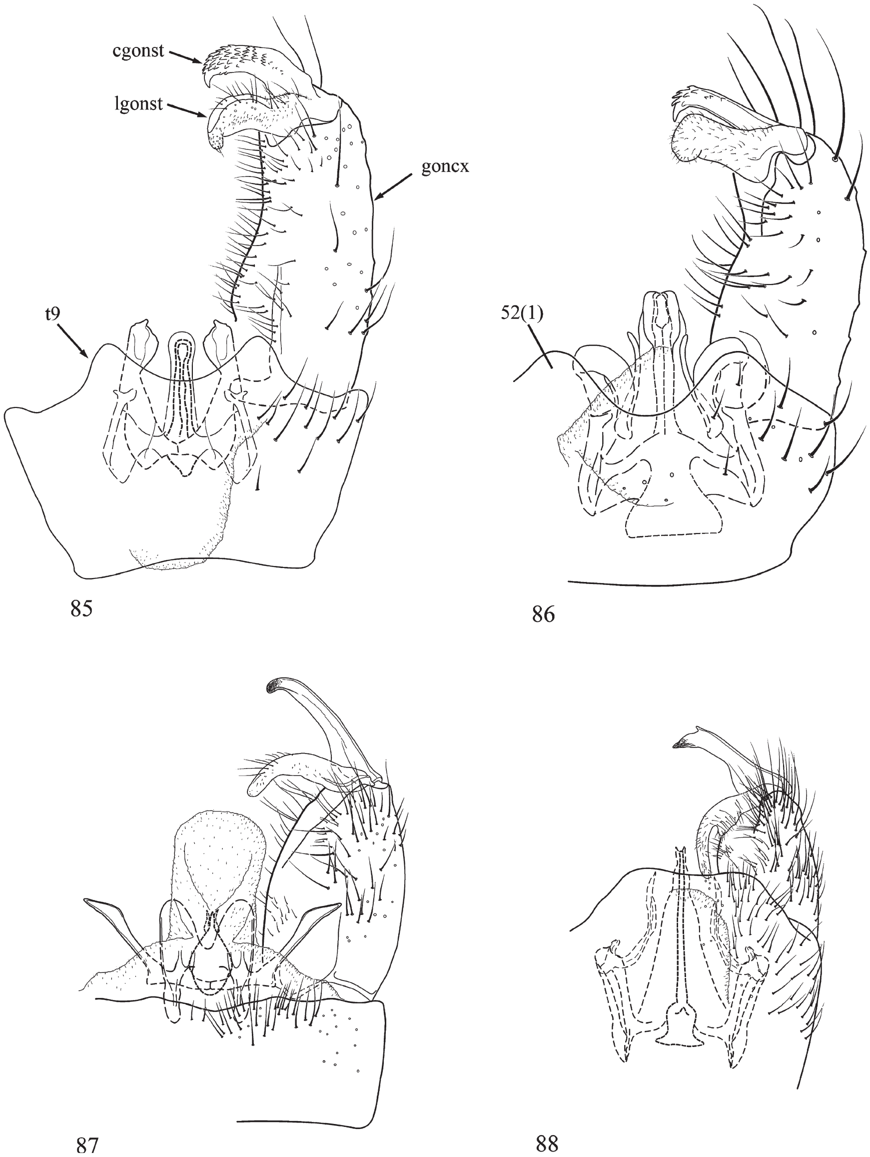
Higher-level relationships

Large and highly incongruent (complex) datasets often require the exploration and use of different tree search strategies in order



Figs 81–84. Morphological characters, male terminalia, dorsal view. 81, *Lecteria* (*Lecteria*) sp. 82, *Clydonodozus neavei*. 83, *Conosia irrorata*. 84, *Conosia angustissima*.

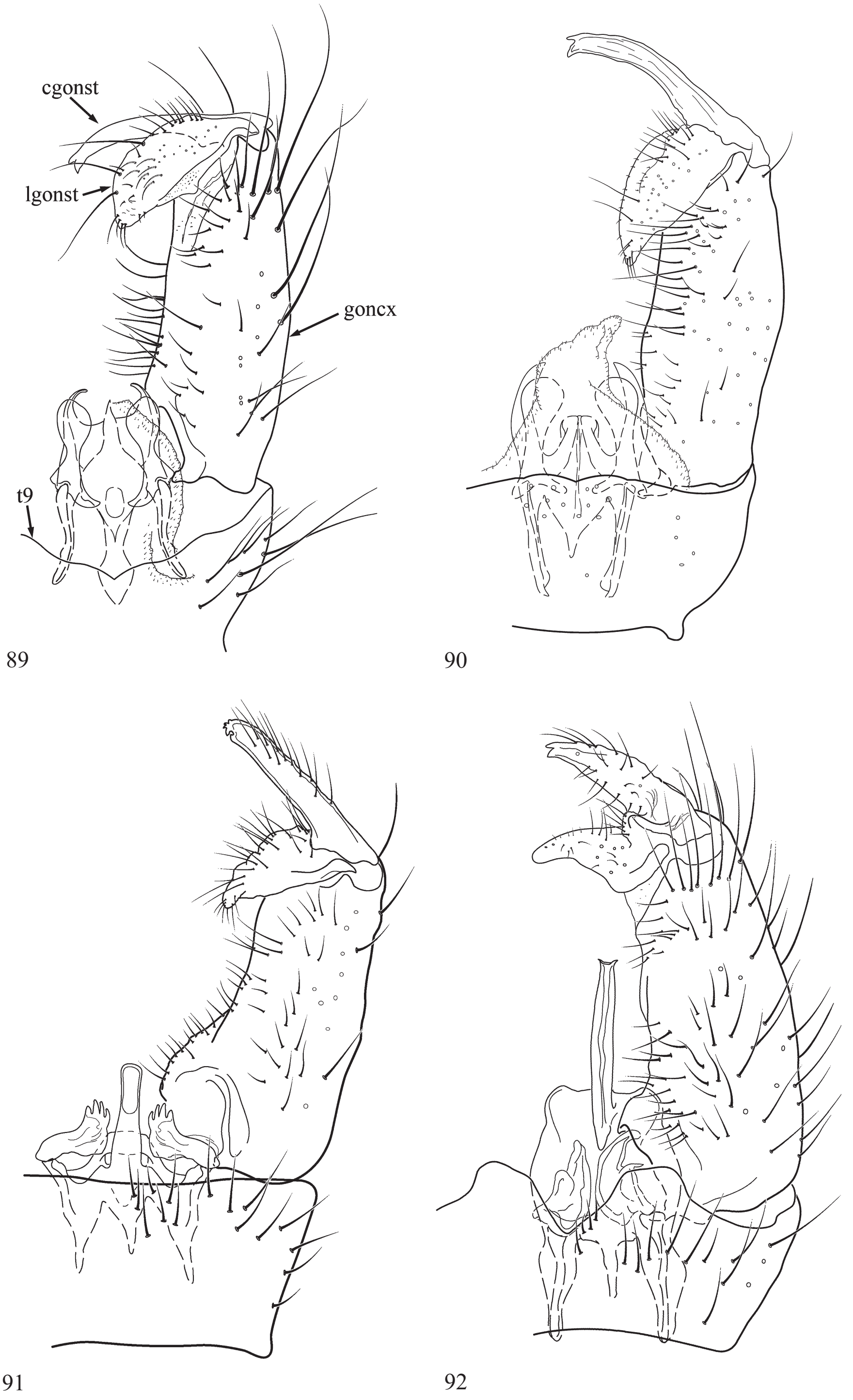
to maximise the possibility of finding a most parsimonious reconstruction using heuristic (non-exact) tree search algorithms, which are the only numerical tools available to deal with them. Understanding the full meaning of the results of phylogenetic analyses of datasets like the one analysed in this study can be greatly complicated by the fact that, usually, the results are not clear-cut solutions, but reflect the complex nature of the data which yielded them. In dealing with large and highly homoplastic datasets using heuristic search algorithms, the search for the best results can be greatly benefited by the use of the background knowledge provided by what we have learned from previous studies and other kinds of data. This knowledge can guide the exploration of the dataset in order to find an overall most parsimonious solution (or the best result based on some other preferred methodological criterion). Choosing the best alternative among highly conflicting results may also depend of some critical evaluation of the available evidences. This may require the critical reassessment of the data directly included in the study. Again, background knowledge can shed some light on this process.



Figs 85–88. Morphological characters, male terminalia, dorsal view. 85, *Notholimnophila exclusa*. 86, *Ctenolimnophila* (*Campbellomyia*) *paulistae*. 87, *Gynoplistia* (*Xenolimnophila*) *flindersi*. 88, *Gynoplistia* (*Gynoplistia*) *fuscoplumbea*.

As already discussed, the problem of the relationships among the genera and subgenera in any one of the largest subfamilies of Limoniidae cannot be separated from the big picture of crane fly phylogeny, given the likely paraphyly of these heterogeneous subfamilies, which can in fact include part of the other families. Moreover, testing the hypothesis that some of the earliest lineages of crane flies are included in the Limnophilinae required the inclusion of representatives of other Limoniidae subfamilies and Tipulomorpha families. Even though a stable hypothesis about higher-level relationships could not be achieved as the outcome of the present study, there are issues worthy of being addressed in the light of previous hypotheses, our current level of knowledge, and the results achieved here. Also, the general picture obtained for the family-level relationships – for which some background knowledge already exists as a result of previous studies – could guide the understanding, and helped choosing among the combination of analytical parameters leading to the best results at lower levels.

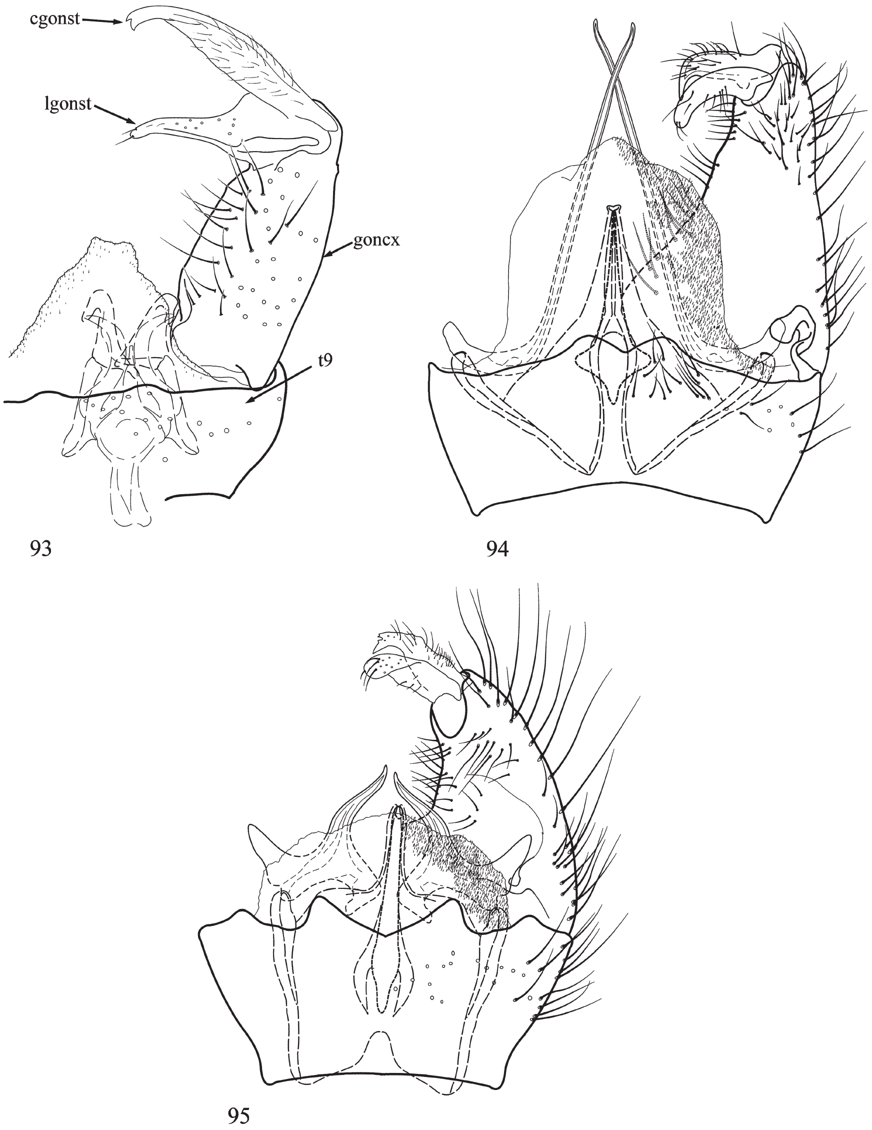
In order to explore different search strategies for finding the best general picture for both the family-level and lower-level relationships, the analytical protocol explained under 'Materials and methods' was used in three different circumstances. The reasoning and justifications of each situation are successively discussed bellow. A detailed discussion on the results obtained for the family-level, which includes a critical judgment of the evidences supporting the different results, is deemed here as an important step before the evaluation of the results at lower levels.



Figs 89–92. Morphological characters, male terminalia, dorsal view. 89, *Limnophila* (*Dicranophragma*) *fuscovaria*. 90, *Neolimnomyia* (*Brachylimnophila*) *nemoralis*. 91, *Neolimnomyia* (*Neolimnomyia*) *filata*. 92, *Shannonomyia* (*Shannonomyia*) *lenta*.

Entire matrix with no constraints of monophyly

An analysis of the complete data matrix was made without any constraints on the monophyly of any particular group. A synthesis of the results of the 5 analyses with different values of k (from 2 to 6) is shown in Table 3. Considering the topologies generated by each k value independently, a high degree of resolution is noted despite the enormous amount of homoplasy in the dataset. But a high degree of taxonomic incongruence is found when the results yielded by the different parameters are compared, as shown by the



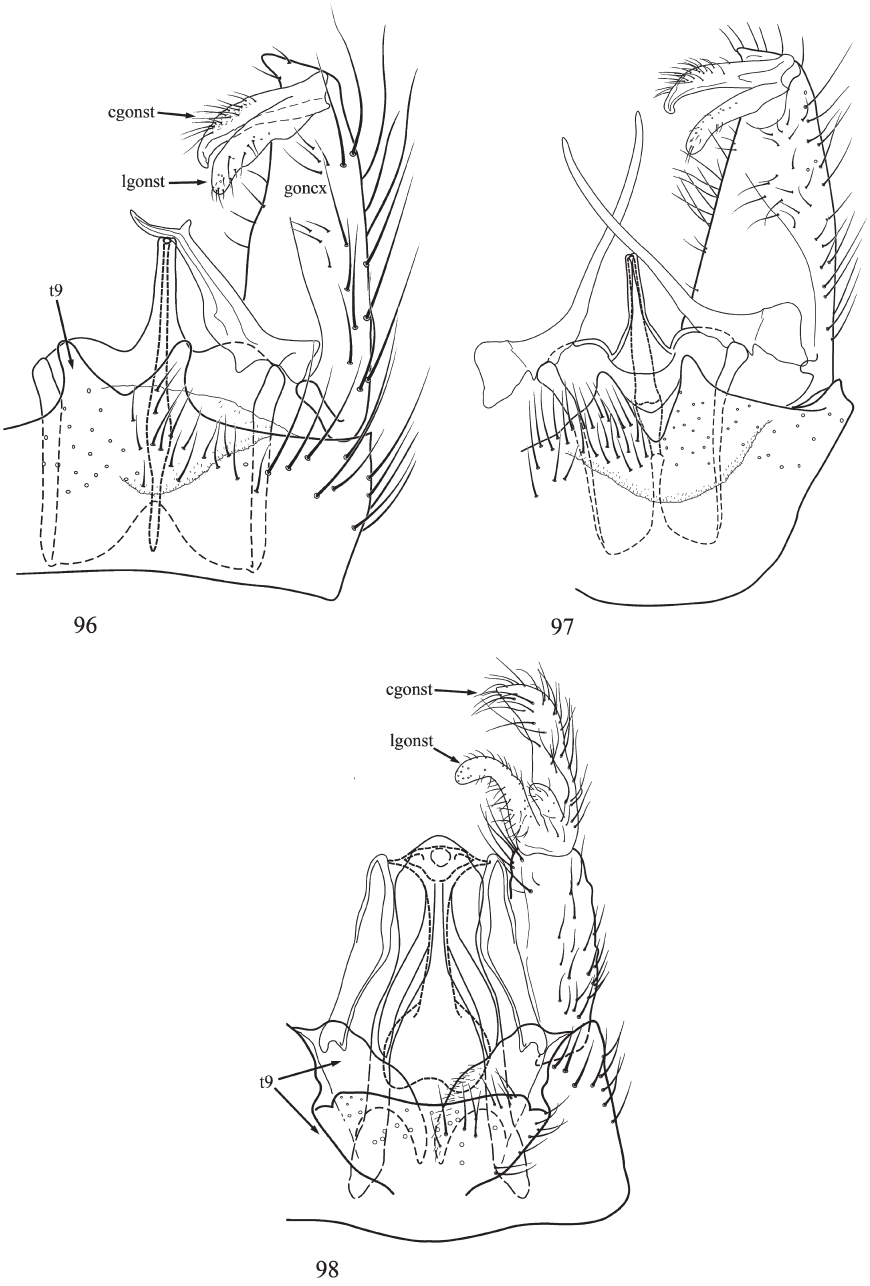
Figs 93–95. Morphological characters, male terminalia, dorsal view. 93, *Prolimnophila areolata*. 94, *Epiphragma* (*Epiphragma*) *fasciapenne*. 95, *Epiphragma* (*Epiphragma*) *nigripleuralis*.

low resolution of the strict consensus tree of the 9 topologies yielded by the 5 analyses (Fig. 224). In other words, although the dataset based on the morphology of the adult male crane flies can recover well solved topologies, at least when implied weighting is employed, it supports quite different and conflicting phylogenetic hypotheses.

According to Goloboff (1993), the fittest tree is the one which, in the face of character conflict, implies fewer steps for the less homoplastic characters and in tree searches using implied weights, the trees with the higher fitness should be preferred. Among the analyses dealt with in this section, that with k = 6 yielded the tree with the higher fitness.

Perhaps the most striking aspect of the results of the unconstrained analysis of the complete data matrix concerns the recovered relationships at family-level, which is quite distinct from the results of previous studies. As shown by the strict consensus tree of Fig. 224, all the analyses with different values of k pointed to the sister-group relationship of the Pediciidae with part of the Cylindrotomidae, and to the position of this clade as the sister-group of all other Tipulomorpha *sensu stricto*. The monophyly of the Cylindrotomidae is not recovered by these analyses, and *Stibadocerella* (subfamily Stibadocerinae) is always nested within the clade containing (*Limnophila* (*L.*) *macrocera* + *Polymera*).

The non-monophyly of the Cylindrotomidae as indicated by the unconstrained analysis of the complete data matrix is considered here as very unlikely. The Cylindrotomidae is the smallest family of crane flies. Its monophyly seems very well supported, among other things, by the trifid aedeagus (Character 87, state 1). This is an apomorphic character state not shared by any other crane fly subgroup outside the Cylindrotomidae

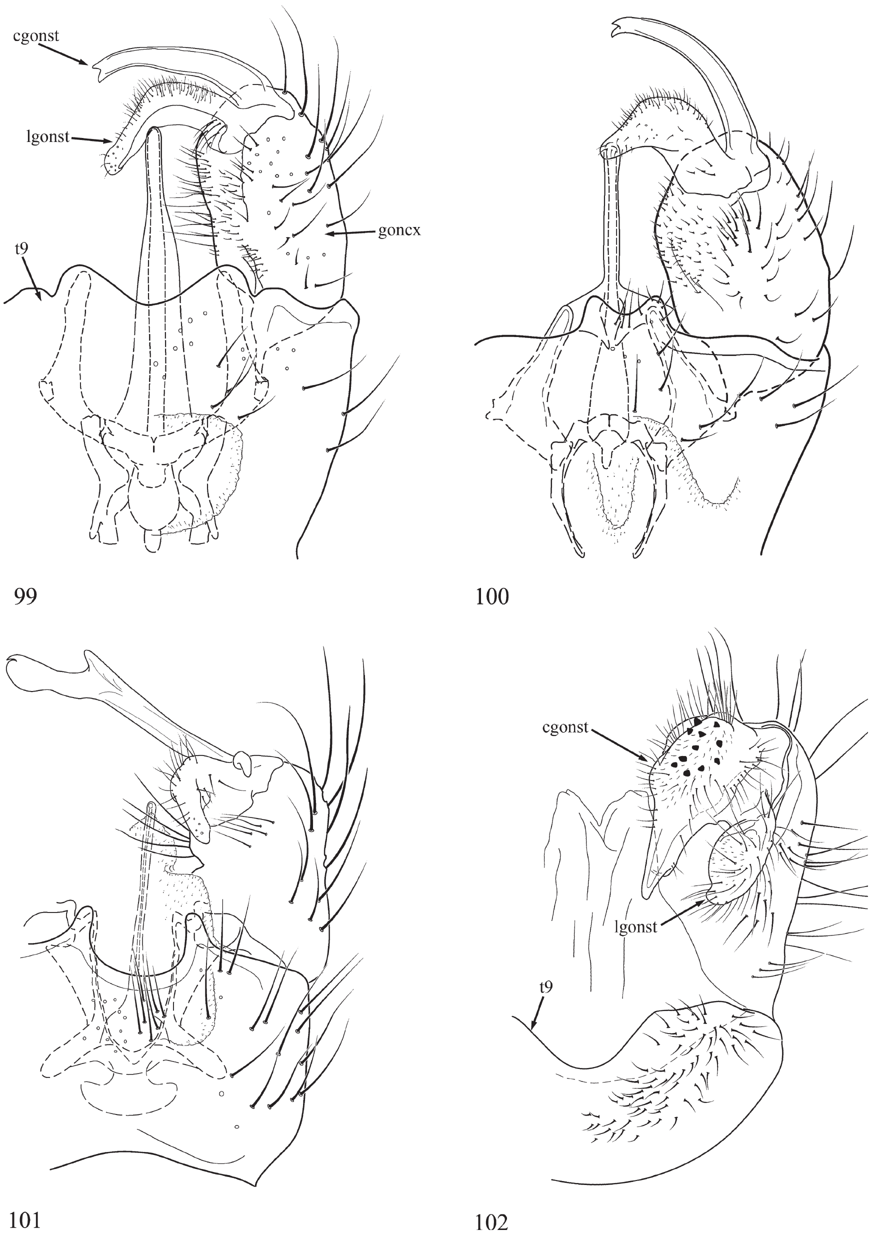


Figs 96–98. Morphological characters, male terminalia, dorsal view. 96, *Acantholimnophila bispina*. 97, *Acantholimnophila maorica*. 98, *Dactylolabis* (*Dactylolabis*) *cubitalis*.

(Ribeiro in press). The anomalous position of *Stibadocerella* can be explained by other reasons. Most probably, valuable characters for stabilising higher-level relationships are lacking in the data matrix. Alternatively, the trees found in these analyses may even not be the most parsimonious solutions for this dataset, since the use of a heuristic search strategy does not guarantee that a most parsimonious solution will be found. On the other hand, the several autapomorphic modifications in *Stibadocerella* (for instance, the loss of the second anal vein, presence of a plumose antenna, the reduction of the rostrum) are probably the cause of its unlikely position near *Polymera*.

Unconstrained analysis with *Stibadocerella* excluded

A second analysis was made, to test the effect of excluding *Stibadocerella* of the data matrix. A synthesis of the results is shown in Table 3. For equivalent values of k, the fitness of the trees was higher in the reduced matrix compared with the complete matrix. Again, the fittest tree was obtained with k = 6 (Fig. 225). Regarding the degree of taxonomic congruence, the exclusion of *Stibadocerella* had no effect at all, and the strict consensus of the 9 trees with different values of k has just the same topology as shown in Fig. 224 (except, of course, by the absence

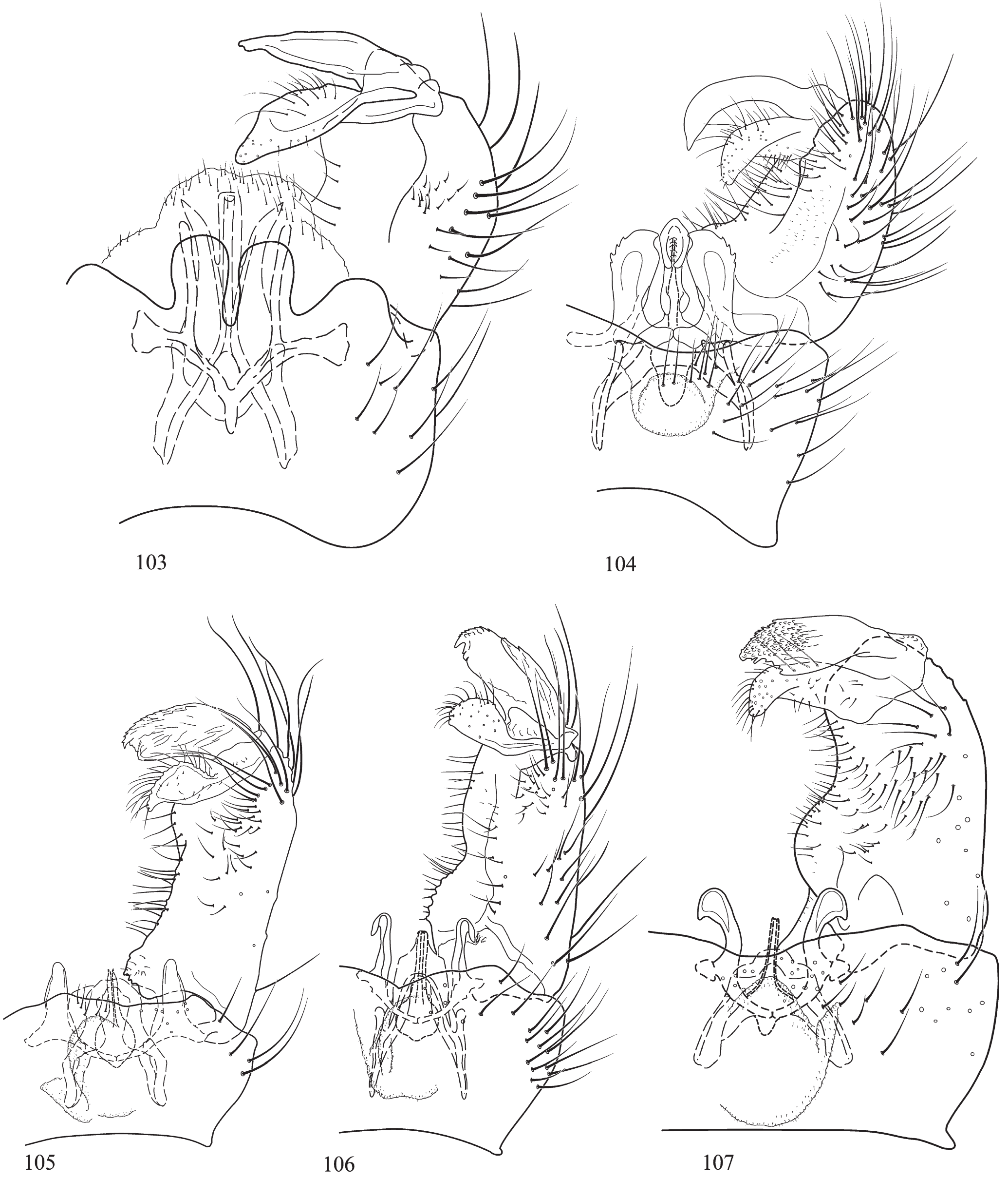


Figs 99–102. Morphological characters, male terminalia, dorsal view. 99, *Limnophila* (*Arctolimnophila*) *claggi*. 100, *Limnophila* (*Arctolimnophila*) *subcostata*. 101, *Limnophila* (*Atopolimnophila*) *laricicola*. 102, *Leptotarsus* (*Longurio*) *gymnocerus* (Tipulidae).

of the excluded taxon). Again, the Pediciidae and Cylindrotomidae are considered sister-groups and together form the sister taxa of all other Tipulomorpha *sensu stricto*.

The sister-group relationship between the Cylindrotomidae and Pediciidae must be evaluated cautiously and critically as this pattern seems to be biased by taxonomic and character sampling. There is a single apomorphic state supporting this clade, which is the loss of the cell r2 (Character 33, state 1). It seems beyond dispute that the plesiomorphic condition for the Tipulomorpha is a bifurcated vein R_{2+3} (with cell r2 present), but the loss of cell r2 may have occurred independently several times in different lineages. In at least one species of Pediciidae, *Tricyphona* (*Tricyphona*) *protea* (Alexander and Byers 1981: fig. 38), and some Cylindrotomidae, including *Phalacrocera tipulina* which is present in the data matrix (Brodo 1967: fig. 56), the vein R_{2+3} is bifurcated and the cell r2 is present. If the Pediciidae is indeed monophyletic, the morphology of the wing venation as found in *T. protea* may be similar to the condition found in the Pediciidae ground plan. Also, a bifurcated vein R_{2+3} is probably the plesiomorphic condition in Cylindrotomidae (Ribeiro in press). The loss of cell r2 could have happened independently in both families.

Regarding the family-level phylogeny of crane flies, *Stibadocerella* is a very important taxon as it brings

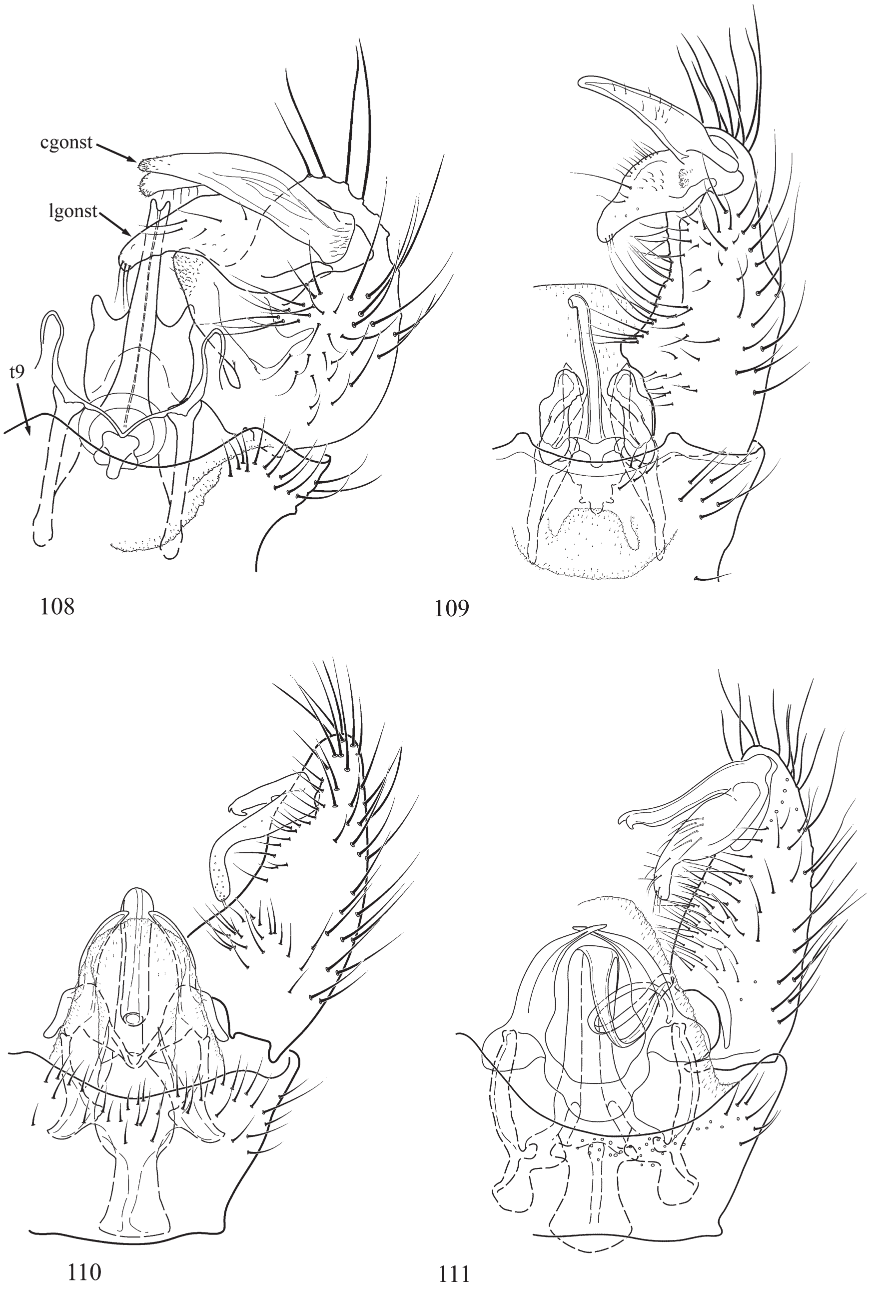


Figs 103–107. Morphological characters, male terminalia, dorsal view. 103, *Eupilaria phoenosoma*. 104, *Idioptera nearctica*. 105, *Eloeophila maculata*. 106, *Eloeophila aldrichi aldrichi*. 107, *Eloeophila trimaculata*.

information with important implications for the phylogenetic position of the Cylindrotomidae. In all known members of the subfamily Cylindrotominae, the gonostylus is undivided (Character 55, state 0). It has been a quite obscure question whether the simple gonostylus in Cylindrotominae is plesiomorphic or corresponds to a secondary loss of one of the gonostylar branches. *Stibadocerella*, together with some other Stibadocerinae genera such as *Stibadocerodes* and *Stibadocera*, all keep a branched gonostylus, strongly suggesting that this condition is plesiomorphic for the Cylindrotomidae. Given such evidences, it seems that the position occupied by the Cylindrotomidae as the sister-group of the Pediciidae and outside the clade containing the bulk of Tipulomorpha is misleading.

Entire matrix with Cylindrotomidae monophyly constrained

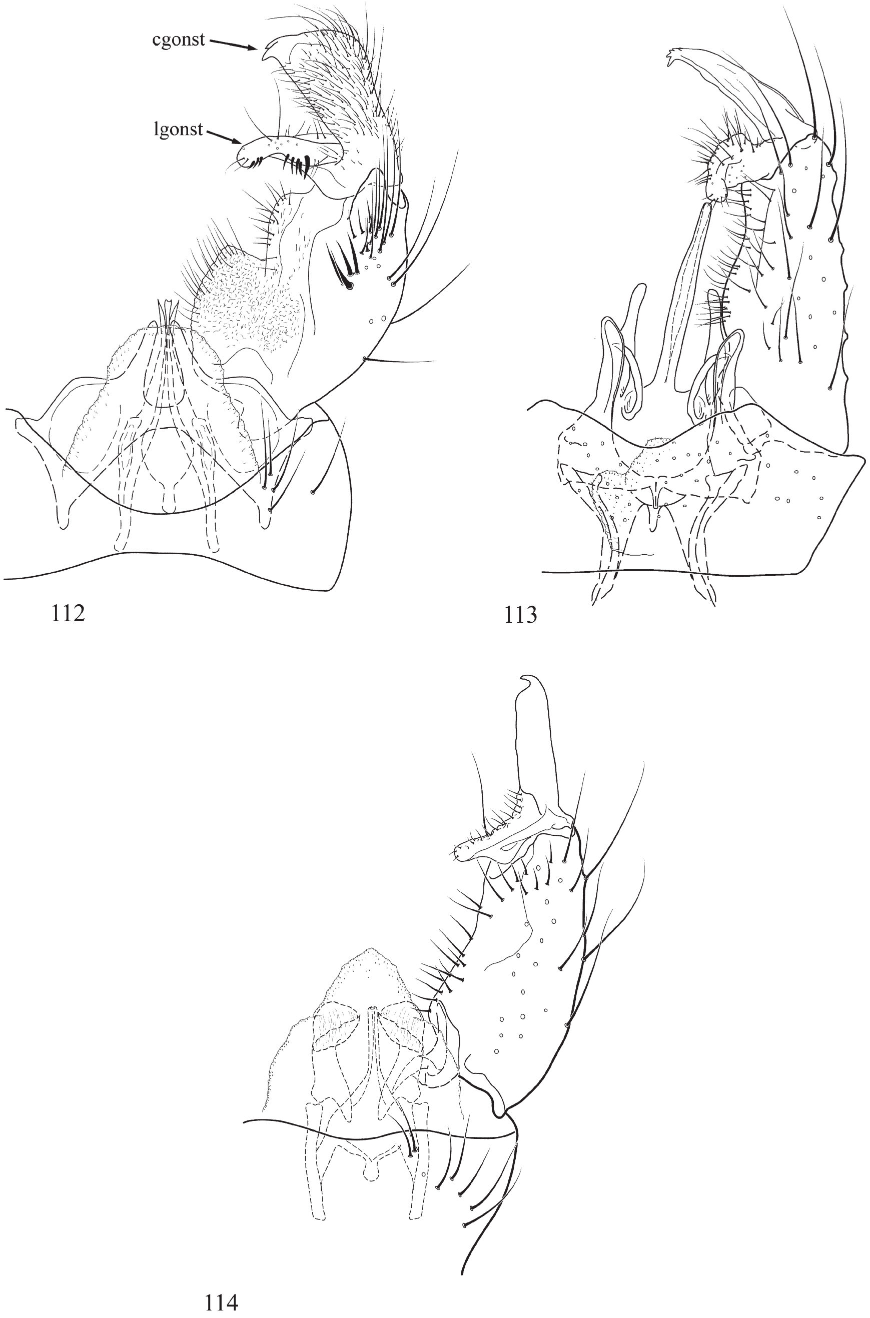
A third set of analyses was conducted, in which all taxa were included but the monophyly of the Cylindrotomidae was constrained. A synthesis of the results is shown in Table 3. For the values of k = 2, 3, and 4, the fitness of the trees yielded by the constrained analyses were little lower than that of the other analyses. For k = 5, the fitness was higher in the constrained analysis. For k = 6, the constrained analysis yielded trees less fit than that provided by the other analyses with the same value. However, considering only the 5 analyses of the constrained set, the fittest tree was provided by k = 6 (Figs 227–229). For k = 6, the constrained analysis (which also includes all taxa) yielded a most parsimonious solution than the unconstrained analysis of the



Figs 108–111. Morphological characters, male terminalia, dorsal view. 108, *Limnophila* (*Elporiomyia*) *nox*. 109, *Limnophila* (*Indolimnophila*) *bituminosa*. 110, *Helius* sp. 111, *Elephantomyia* (*Elephantomyia*) *westwoodi*.

complete matrix, which is 13 steps longer (see Table 3). This is an important result. The failure of the unconstrained analysis to find a most parsimonious solution is probably related to the poor performance of the heuristic search algorithm in face of the highly homoplastic and complex dataset, which obviously impose great difficulties for the calculation of a most parsimonious solution. Constraining the monophlyly of the Cylindrotomidae greatly reduced the number of possible trees, helping the tree search algorithm finding a more parsimonious tree. This exemplifies the need of exploring different tree search strategies when dealing with highly incongruent datasets. It also shows how effectively our background knowledge can guide exploring alternative tree search strategies, which can eventually help us finding an overall solution which is better on the light of well accepted methodological criteria (in this case, parsimony).

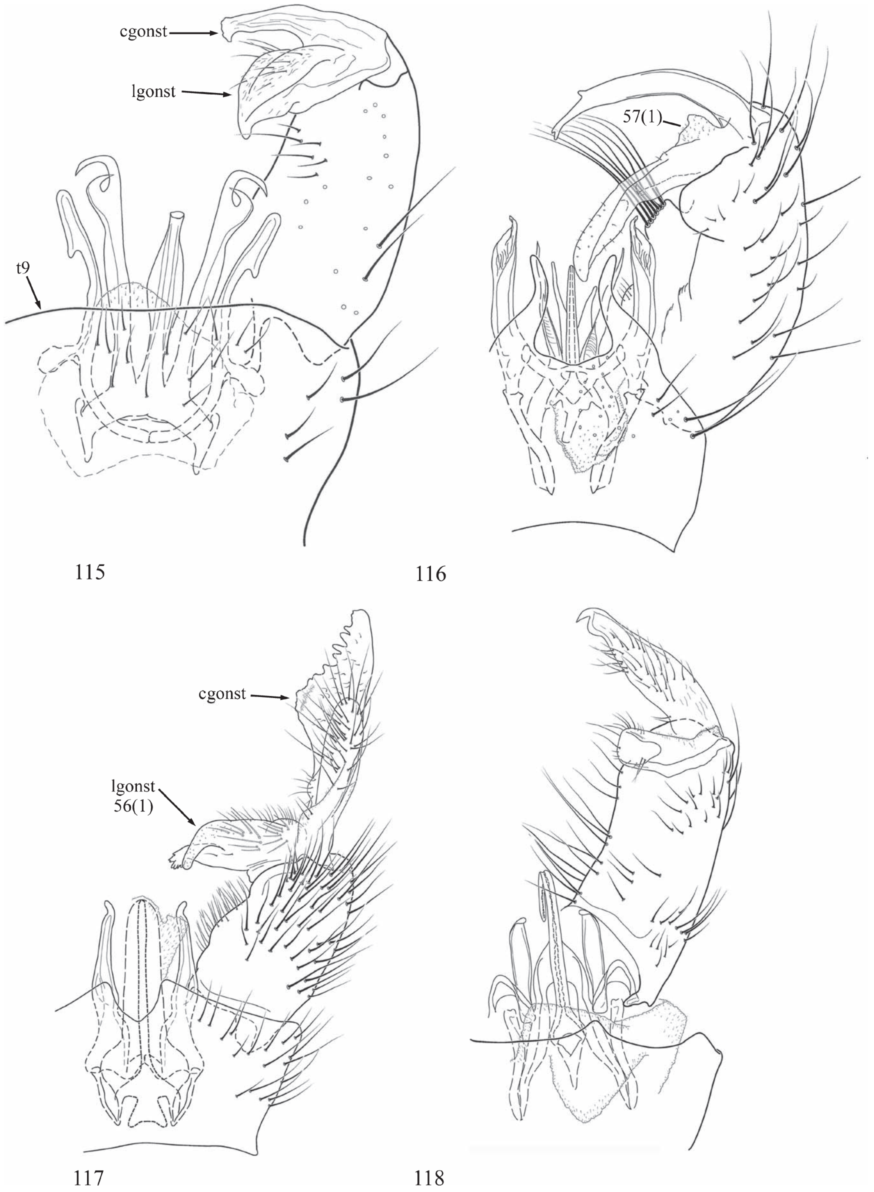
Constraining the monophyly of the Cylindrotomidae had little effect on the degree of congruence between the results yielded by different values of k, as shown in the strict consensus tree of Fig. 226.



Figs 112–114. Morphological characters, male terminalia, dorsal view. 112, *Euphylidorea niveitarsis*. 113, *Limnophila* (*Lasiomastix*) *macrocera*. 114, *Polymera* (*Polymerodes*) *parishi*.

In the fittest tree of the constrained analysis, the Pediciidae is the sister-group of all other Tipulomorpha *sensu stricto*. It has been suggested (e.g. Starý 1992; Ribeiro 2006) that a branched gonostylus is present in the Tipulomorphan ground plan. This view is challenged by the results of the constrained analysis. The results favor the interpretation that the single unbranched gonostylus as found in the Pediciidae is due not to the secondary loss of one of the gonostylar branches, but by keeping the original condition of a single gonostylus inherited from the Diptera ground plan. However, the Limoniidae is considered as paraphyletic with respect to the Cylindrotomidae and Tipulidae, and the unbranched gonostylus in part of the Cylindrotomidae is considered as secondary.

In the constrained analysis, Tipulidae and Cylindrotomidae are considered sister-groups, in accordance with Oosterbroek and Theowald (1991) and Starý (1992). Starý (1992) based this conclusion on two characters. The first one is called 'reticulation of radial veins'. What is termed 'reticulation of radial veins' by Starý (1992), is coded here as a single character (Character 27) describing the variation in the



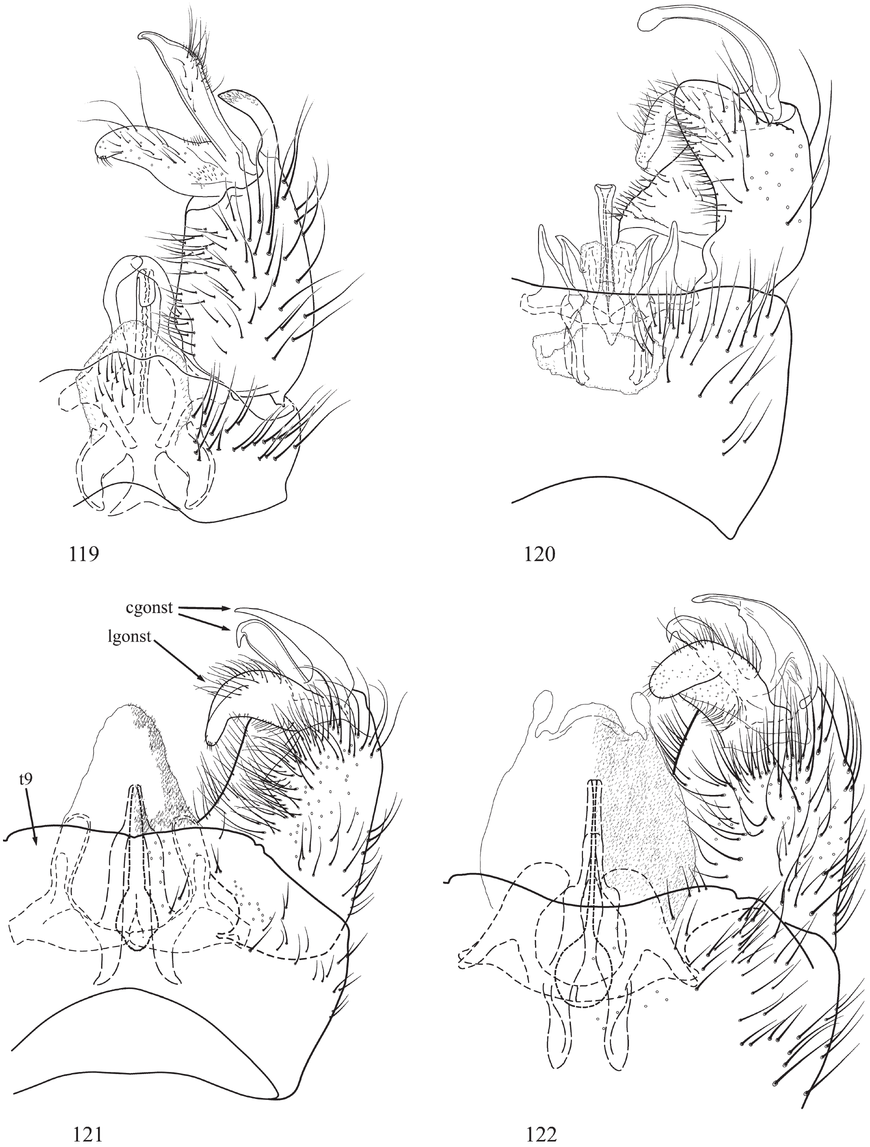
115 116 117 118

Figs 115–118. Morphological characters, male terminalia, dorsal view. 115, *Eupilaria suavis*. 116, *Limnophila* (*Dendrolimnophila*) *shikokuensis*. 117, *Prionolabis rufibasis*. 118, *Limnophila* (*Nesolimnophila*) *luteifemorata*.

inclination of the cross-vein r-r. The plesiomorphic condition for the Tipulomorpha is the vein r-r more or less perpendicular to the longitudinal axis of the wing (Character 27, state 0). Starý (1992) considered the inclined vein r-r (termed by him R_2) a synapomorphy of the (Tipulidae + Cylindrotomidae), but observed that the condition also occurs in certain genera within the Limoniidae. In the tree shown in Figs 227–229, the apomorphic condition of this character is not a synapomorphy of (Tipulidae + Cylindrotomidae), but of the clade (*Limnophila* (*Atopolimnophila*) *laricicola* + (Tipulidae + Cylindrotomidae)). The apomorphic state is also present in (*Gynoplistia* (*G.*) *fimbriata* + (*Gynoplistia* (*Dirhipis*))) and (*Hexatoma* (E.) *atroantica* + (*Pilaria*)).

Another synapomorphy mentioned by Starý (1992) in support of the (Tipulidae + Cylindrotomidae) clade is the posterior fusion of the stipites. This character was not included in this analysis. However, Starý (1992) noted that such fusion of the stipites occur not only in the Tipulidae and Cylindrotomidae, but also in other genera within the Limnophilinae, Chioneinae and Limoniinae.

Oosterbroek and Theowald (1991) presented evidence for the sister-group relationship between the Tipulidae and Cylindrotomidae derived from immature stage morphology. A detailed account of these characters is presented by Oosterbroek and Theowald (1991) under characters 20–23 and will not be repeated here. It must be noted, however, that information on immature stages are available for a very



Figs 119–122. Morphological characters, male terminalia, dorsal view. 119, *Limnophila* (*Limnophila*) *pictipennis*. 120, *Limnophila* (*Hesperolimnophila*) *euxesta*. 121, *Eutonia alleni*. 122, *Eutonia barbipes*.

limited number of taxa, and a quite different picture may be revealed when the distribution of immature characters across the Tipulomorpha becomes better known.

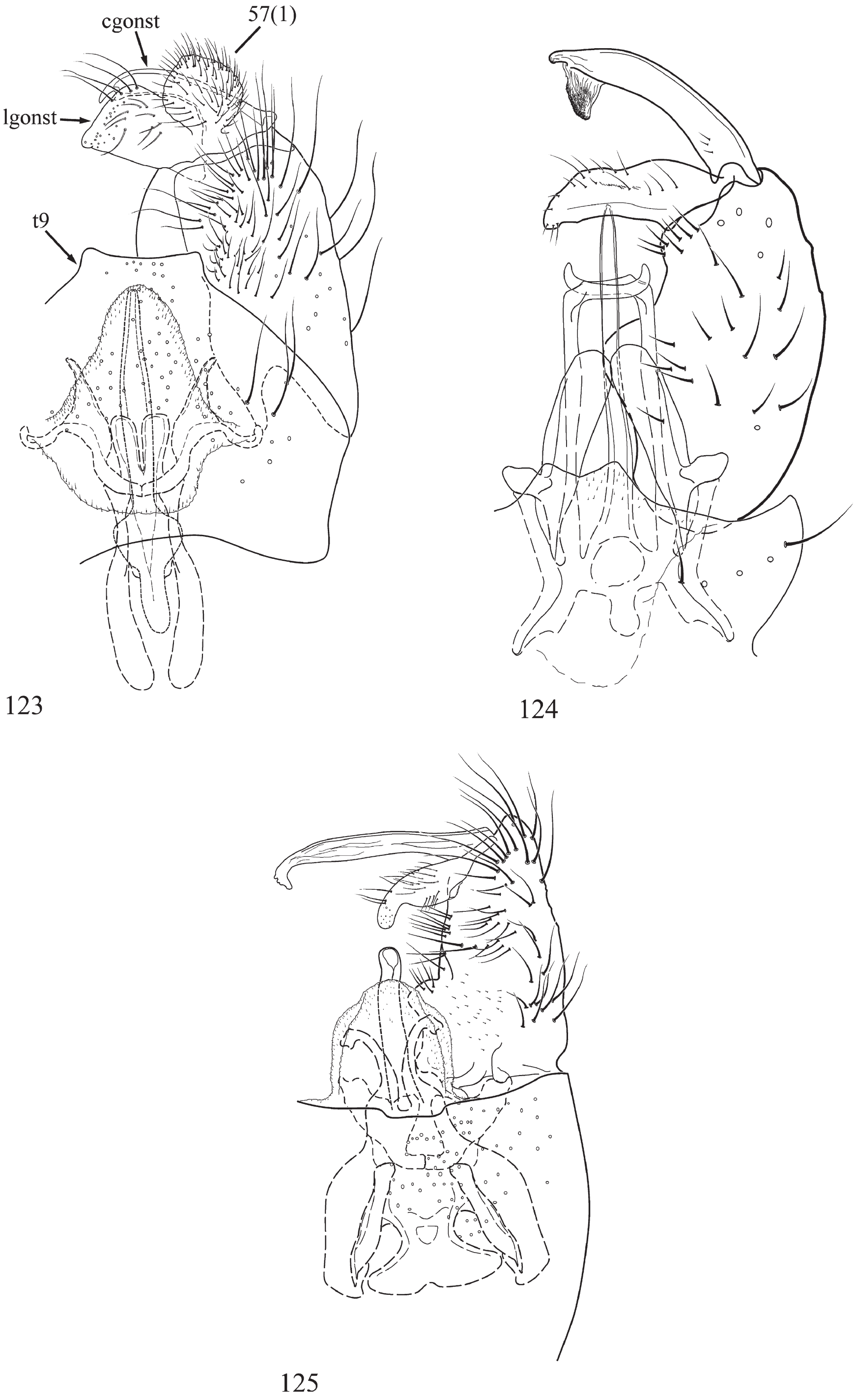
Regarding family-level relationships, the fittest tree of the constrained analysis ($k = 6$) shown in Figs 227–229 is more congruent with previous studies using adult morphology (Starý 1992) as well as with the evidences provided by the characters of immature stages (Oosterbroek and Theowald 1991). It is also a more parsimonious solution than the fittest tree ($k = 6$) of the unconstrained analysis of the entire data. Therefore, it is considered here as a better phylogenetic hypothesis than any of the trees yielded by the other analyses. The topology at the genus/subgenus level as revealed by this analysis is also considered as the preferred hypothesis. The following discussions are mostly based on this tree (generally referred to as the preferred tree), although some reference to the results of the other analyses are eventually made along the text.

Monophyly of Tipulomorpha sensu stricto

The monophyly of the Tipulomorpha *sensu stricto* is recovered by all the analyses with different parameters. The synapomorphic characters of the group, as shown in the preferred topology, will be discussed here.

The ocelli are absent (Character 1, state 0) in all known members of the Tipulomorpha *sensu stricto*, and this character supports the monophyly of the group in the preferred tree.

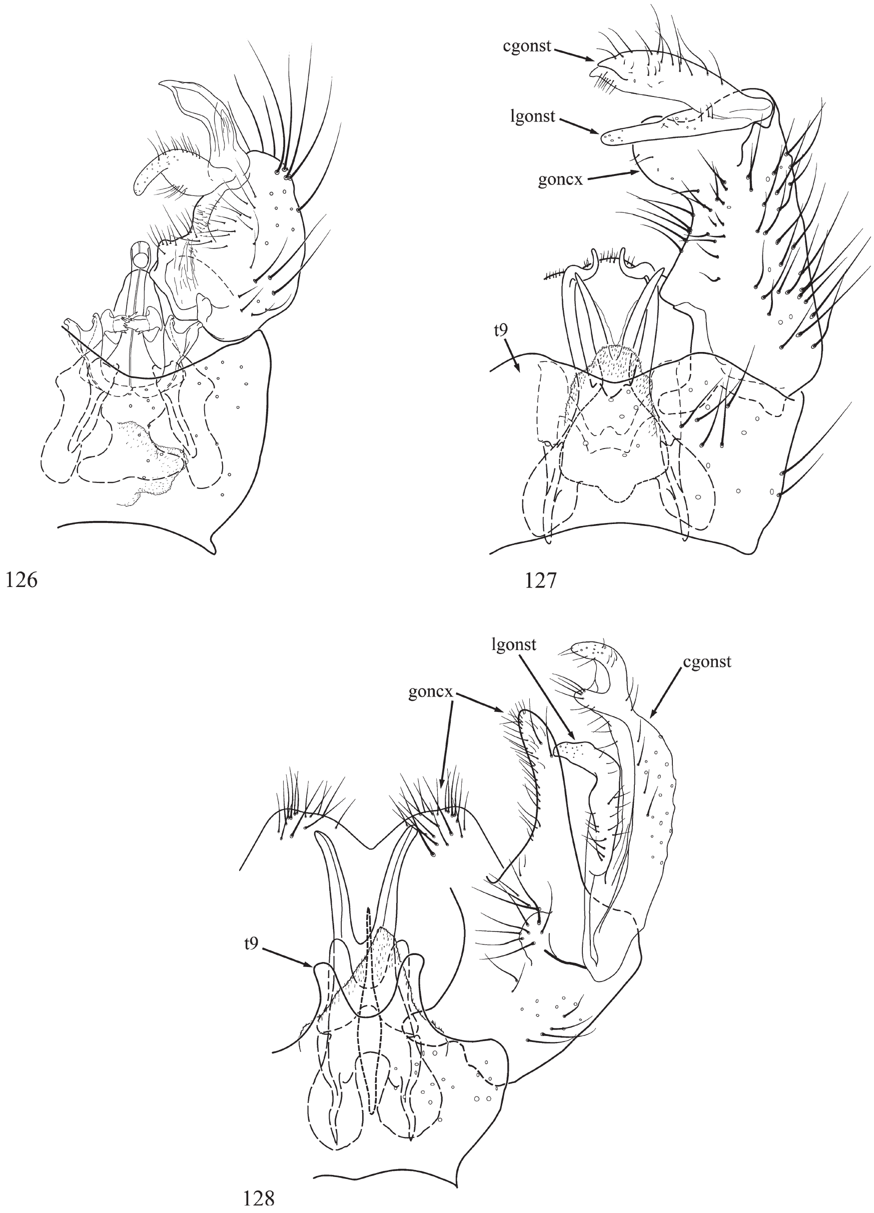
The characters of the antenna are among the most homoplastic of the entire dataset. The transformation of the scape, from almost as long as high (Character 2, state 0) to a little longer than high (Character 2, state 1) is considered an unambiguous



Figs 123–125. Morphological characters, male terminalia, dorsal view. 123, *Paralimnophila* (*Paralimnophila*) *skusei*. 124, *Chilelimnophila lyra*. 125, *Phylidorea* (*Phylidorea*) *umbrarum*.

synapomophy of the Tipulomorpha *sensu stricto* in the preferred tree. However, this character is very homoplastic, and its transformations in higher nodes of the tree are almost always ambiguous.

The transformation of the shape of the flagellomeres, from tubular to ovoid (Character 5, from state 1 to 0) is also considered an unambiguous transformation at level of the Tipulomorpha ground plan. Mecopterans and most of the non-Tipulomorphan outgroups included in the analysis (the exception is the tanyderid *Protoplasa fitchii*) have tubular flagellomeres. Indeed, it is quite possible that tubular flagellomeres are plesiomorphic for the Diptera. However, the distribution of this character in the tree is problematic and subjected to many reversals and independent acquisitions.



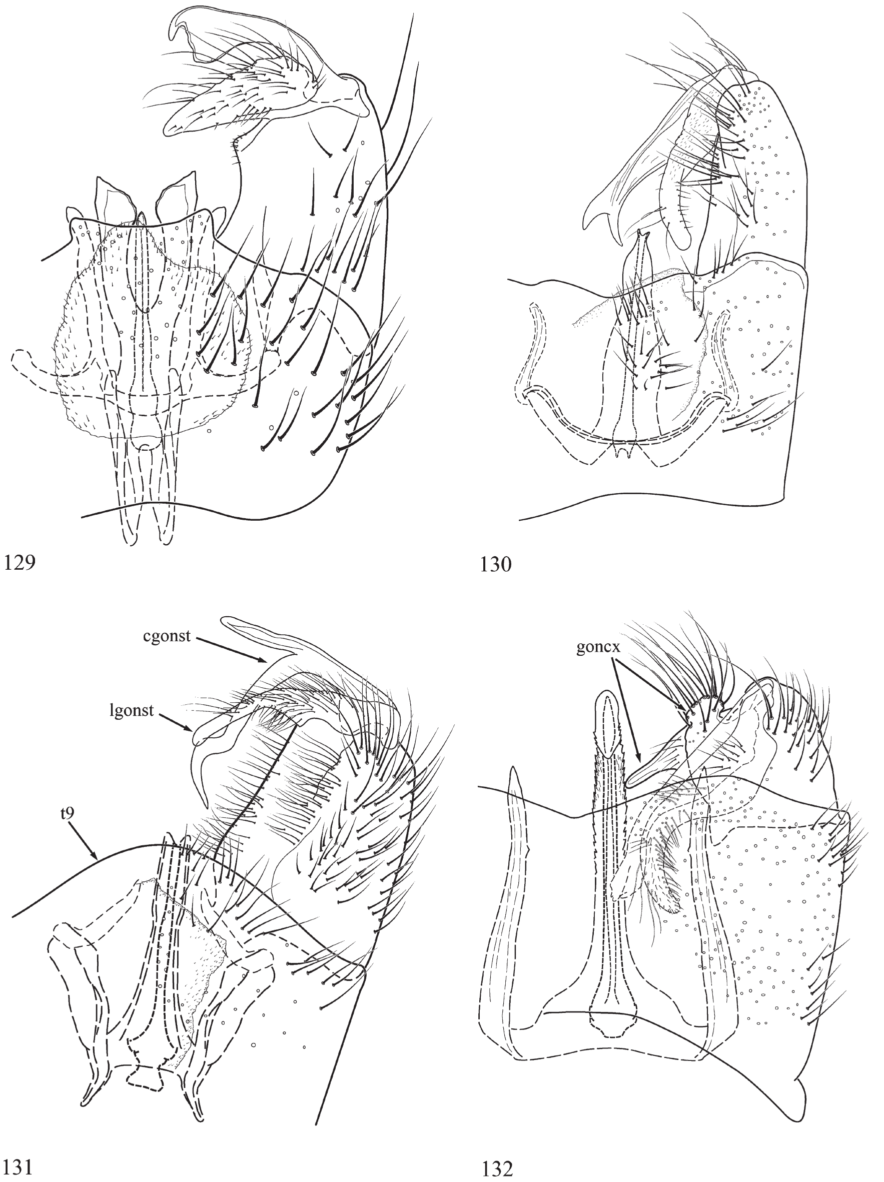
Figs 126–128. Morphological characters, male terminalia, dorsal view. 126, *Phylidorea* (*Phylidorea*) *longicornis pietatis*. 127, *Metalimnophila howesi*. 128, *Metalimnophila productella*.

In Mecoptera, most Lower Diptera, and in all non-Tipulomorphan outgroups of the analysis, the medial margins of the post-gena does not meet medially so that the posterior region of the head capsule (ventrally positioned in Tipulomorpha) is separated by a membranous area (Character 17, state 0). There is little doubt that this condition is plesiomorphic for the Diptera, and this state is pointed as the plesiomorphic condition at the root of the preferred tree. A change from a membranous (Character 17, state 0) to a non-membranous condition of the posterior part of the head (Character 17, state 1), due to the closing of the medial margins of the post-gena, is indicated to have occurred at the very base of the Tipulomorpha *sensu stricto*, with a reversal in the (*Dicranomyia* + *Rhabdomastix*) clade.

The second anal vein (vein A_2) is well developed in the Tipulomorpha *sensu stricto*. This vein was secondarily lost in the Cylindrotomidae genus *Stibadocerella* (Ribeiro in press). The Mecoptera and Trichoceridae both have a more reduced vein A_2 (Saigusa 2006), suggesting that the well develop vein A_2 is likely to correspond to a synapomorphy for the Tipulomorpha *sensu stricto*, as indicated by the preferred tree.

A posteriori calculation of selected Tipulomorphan ground plan features

The study of the distribution of the characters in the preferred tree allows the *a posteriori* reconstruction of the possible ground plan



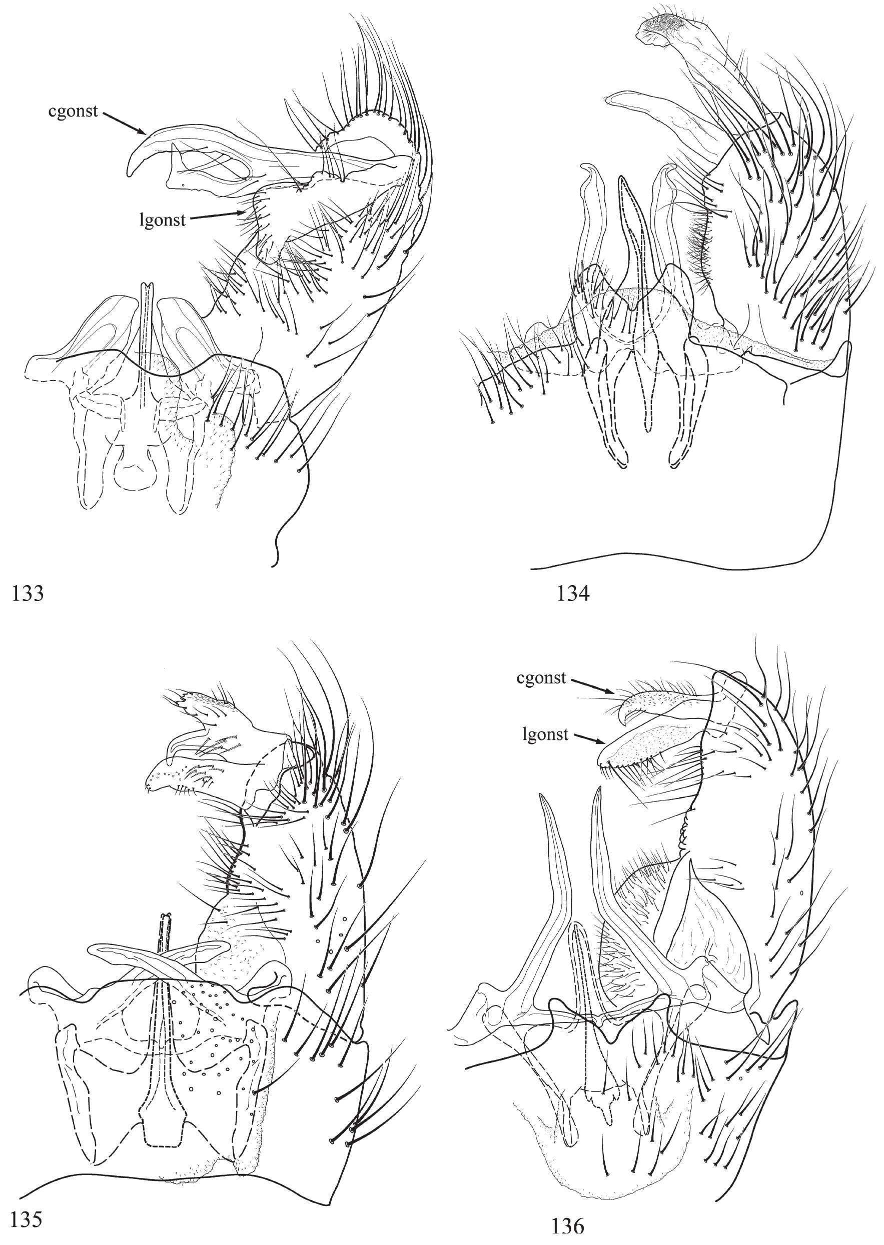
Figs 129–132. Morphological characters, male terminalia, dorsal view. 129, *Paralimnophila* (*Paralimnophila*) *leuchophaeata*. 130, *Gynoplistia* (*Cerozodia*) *hemiptera hemiptera*. 131, *Gynoplistia* (*Gynoplistia*) *fimbriata*. 132, *Gynoplistia* (*Dirhipis*) *striatipennis*.

condition of several Tipulomorphan features. This ground plan reconstruction must include the synapomorphic states already discussed in the previous section. However, there are other features that, although not synapomorphic, are likely to be present in the last common ancestor of the Tipulomorpha *sensu stricto*, as plesiomorphies inherited from previous nodes. Describing the Tipulomorphan ground plan in this wider sense may have a high heuristic value. It can be instructive for future research seeking to identify problems of homology and evolutionary trends in the morphology of crane flies, as well as resolving relationships within groups at lower levels of universality. An explicit formulation of the ground plan conditions of several features in Tipulomorpha may also be useful for studies seeking the understanding of the phylogenetic position of the group within the Diptera.

Mostly unambiguous state transformations are considered, but comments may also be made on characters of ambiguous optimisation.

Head and appendages

The antenna has fourteen flagellomeres (Character 4, state 6). The general aspect of the verticils makes the antenna looks ‘normal’, not plumose (Character 9, state 0). Each flagellomere is ovoid (Character 5, state 0) and probably not much longer than broad (Character 6, state 0). The scape is a little

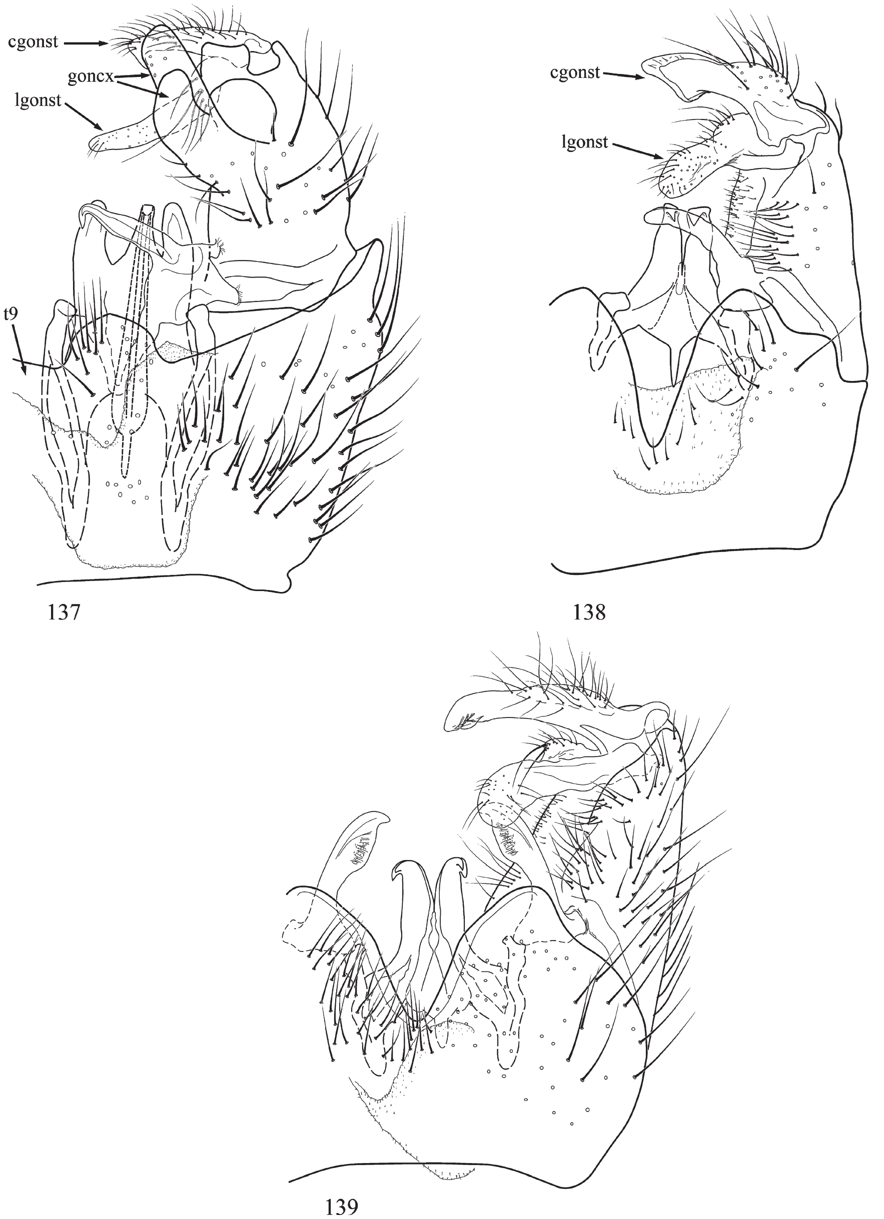


Figs 133–136. Morphological characters, male terminalia, dorsal view. 133, *Limnophila* (*Idiolimnophila*) *emmelina*. 134. *Tonnoirella gemella*. 135, *Edwardsomyia chiloensis*. 136, *Tinemyia margaritifera*.

longer than high (Character 2, state 1), and no longer than 1.5x the length of the pedicel (Character 3, state 0). The eyes are bare (Character 10, state 1). The anterodorsal region of the head lacks any kind of protuberance (Character 15, state 0; Character 16, state 0). The medial margins of the compound eyes are widely separated dorsally (Character 19, state 1). In the posterior region of the head, the medial margins of the post-gena meet medially, so that this region is not separated by a membrane (Character 17, state 0). The rostrum length is at most a little longer than the length of the head (Character 11, state 1).

Wing and thorax

The costal vein is circumbient (Character 21, state 0). The apex of the vein Sc reaches the wing margin (Character 22, state 0) in a point distal to the bifurcation of Rs (Character 23, state 2). The cross-vein sc-r is present and also positioned distal to the origin of Rs (Character 24, state 2). The cross-vein r-r is present (Character 25, state 1), situated closer to the mid-point of vein R_2 than to any other point (Character 26, state 3), and its inclination is more or less perpendicular to the longitudinal axis of the wing (Character



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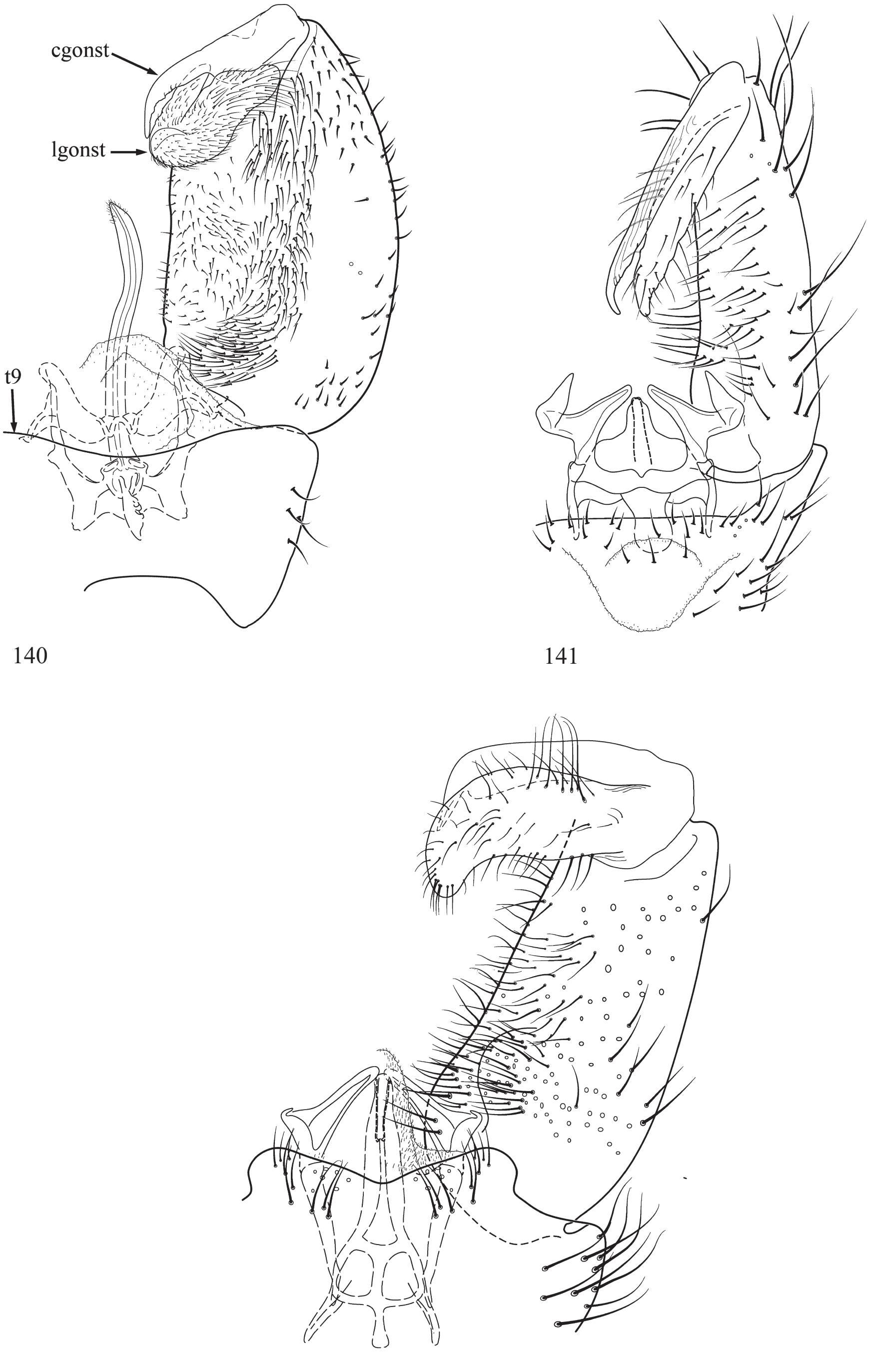
Figs 137–139. Morphological characters, male terminalia, dorsal view. 137, *Rhamphophila sinistra*. 138, *Nothophila fuscana*. 139, *Nothophila nebulosa*.

27, state 0). The exact point of origin of Rs relative to the apex of veins A_1 and A_2 (Character 28) is uncertain, but surely there is no spur or projection near the base of Rs (Character 29, state 0). The vein R_{2+3} is bifurcated (Character 33, state 0), and R_2 and R_3 both reach the wing margin and run more or less in parallel or only gradually diverging from each other (Character 34, state 0 or 1). The petiole of cell R_2 (vein R_{2+3}) is short, more precisely, shorter than $\frac{1}{2}$ the length of vein R_3 (Character 35, state 1). The vein M_{1+2} is bifurcated (Character 36, state 0) and the length of the petiole of cell m_1 is between $\frac{1}{2}$ and the total length of vein M_1 (Character 37, state 2). The vein M_{3+4} is bifurcated (Character 39, state 0). The discal cell is present (Character 41, state 0). The vein h is well defined and visible (Character 42, state 0). The arculus is absent (Character 45, state 0). The position of the cross-vein m-cu (Character 47) is quite uncertain. The vein A_2 is well developed (Character 48, state 1). There are no macrotrichia in the wing membrane (Character 49: state 0). The tibial spurs are present (Character 50, state 1). The meron is detached from the other thoracic sclerites (Character 51, state 0).

Male terminalia

The gonocoxite is cone-shaped, longer than high (Character 53, state 0), and bears an apical (terminal) gonostylus (Character 54, state 0). The gonostylus is undivided (Character 55, state 0), the divided gonostylus being a synapomorphy of the



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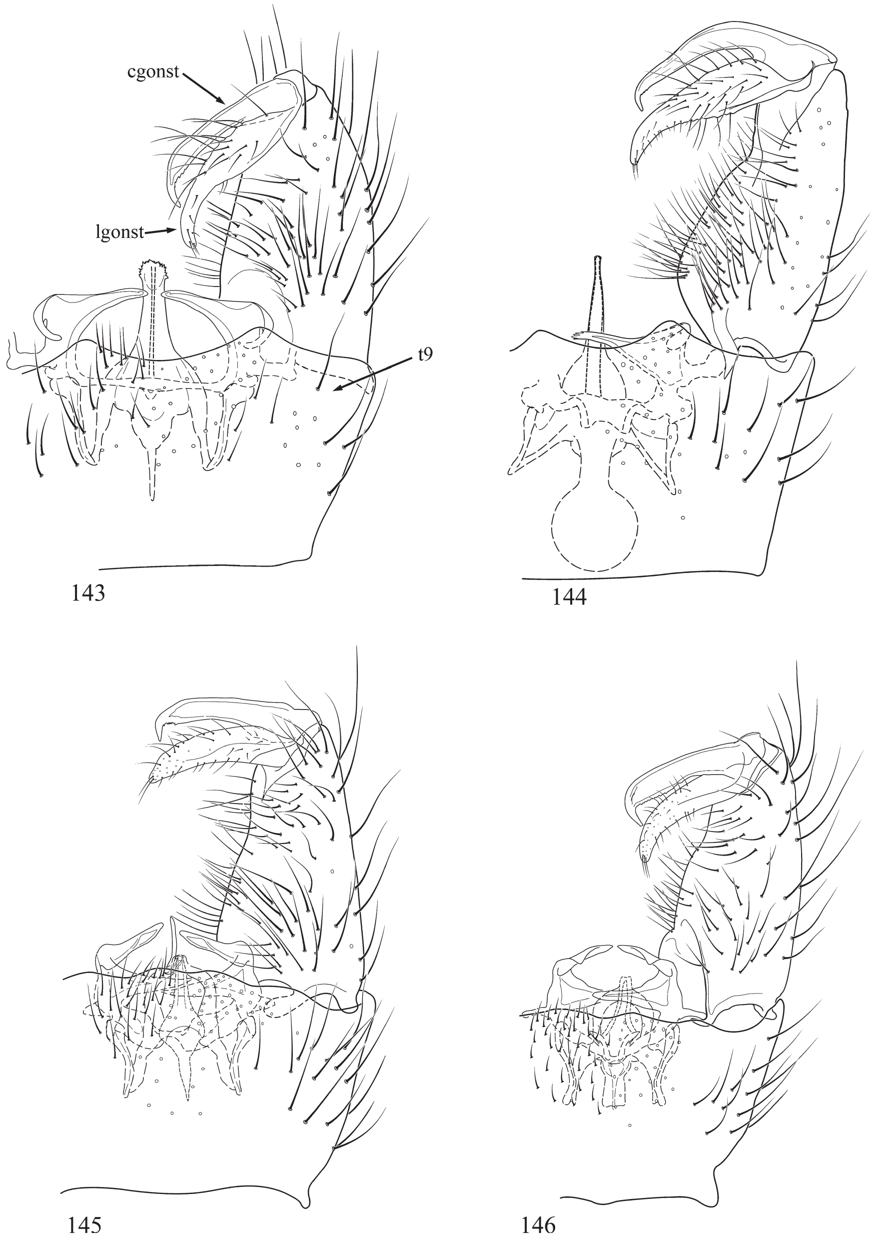
Figs 140–142. Morphological characters, male terminalia, dorsal view. 140, *Hexatoma* (*Eriocera*) *austera*. 141, *Pseudolimnophila legitima*. 142, *Hexatoma* (*Euhexatoma*) *triphragma*.

Tipulomorpha except Pediciidae. The aedeagus describes a straight (or nearly straight) trajectory from its base to its apex (Character 67, state 0), and its internal margins are smooth (Character 68, state 0). The aedeagus apodeme is not much larger than the aedeagus itself (Character 70, state 0). The lateral processes of the aedeagal sheath are likely to be present, well developed (Character 71, state 0), and simple, not bifid (Character 72, state 0). The area of the aedeagal sheath between the lateral margin of the aedeagus and the medial margin of the paramere is relatively narrow (Character 75, state 0). The interbases are present, clearly noticeable (Character 76, state 1). The interbases do not have lateral extensions (Character 82, state 1). They articulate with the parameres but are not fused with them, so looking like

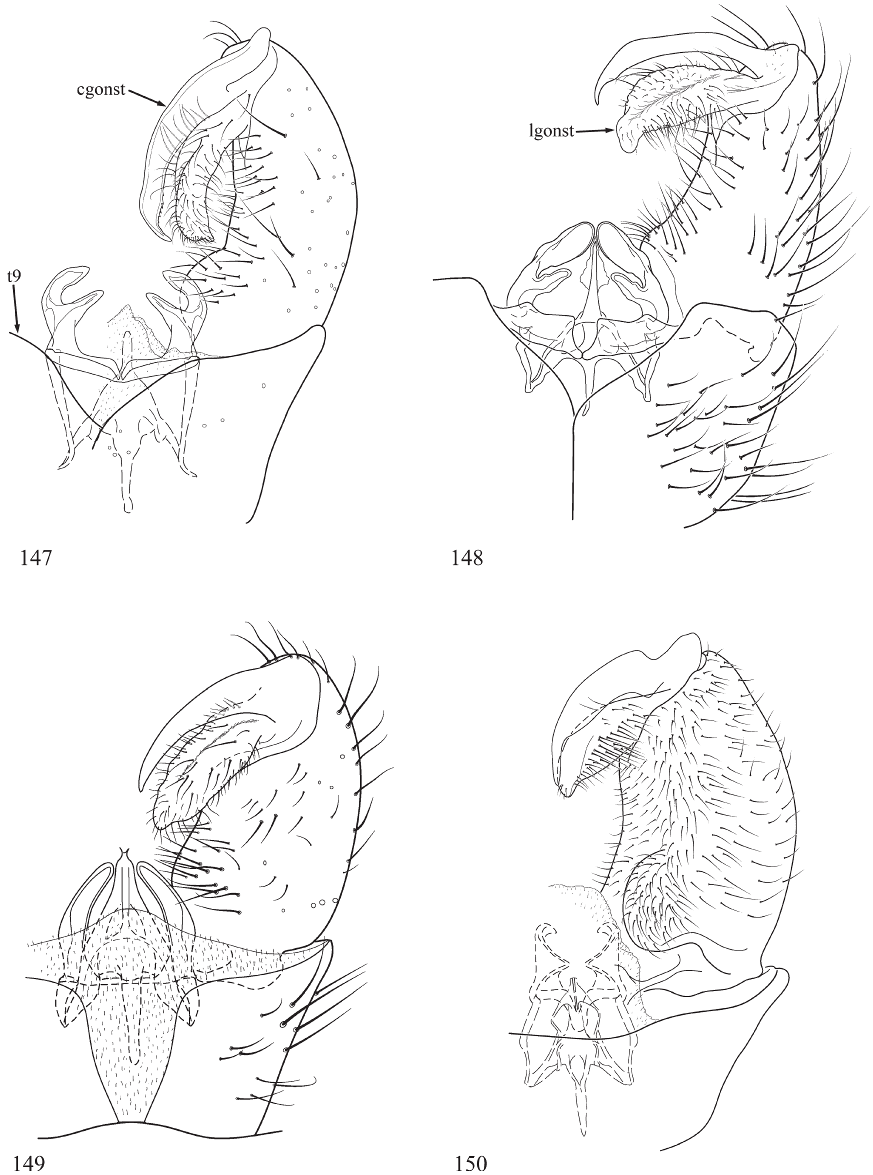


Figs 143–146. Morphological characters, male terminalia, dorsal view. 143, *Pilaria meridiana*. 144, *Pilaria discicollis*. 145, *Ulomorpha pilosella*. 146, *Ulomorpha rogersella*.

individualised blade-like structures (Character 77, state 1). Whether the interbases are fused medially or lay as separate blades (Character 78) is uncertain. However, in *Trichocera*, the large blade-like structure (Figs 77 and 151) considered here as homologous with the interbase of the Tipulomorpha *sensu stricto* is fused medially, suggesting this condition as the one present at the level of the Tipulomorphan ground plan. The evolution of this character is subjected some level of homoplasy, but in most cases there is a transformation from the fused state (Character 78, state 0) to the separated state (Character 78, state 1), which thus seems to be apomorphic. The distal part of the interbase is simple, without any branching (Character 79, state 0). The basolateral portions of the interbase seem to be non-extended (Character 82, state 1), but the subsequent evolution of this character is somewhat confusing and subjected to several independent reversals. The precise length of the interbase, as compared with its width (Character 84), cannot be unequivocally known on the basis of distribution of this character but seems to be intermediary between the states 1 and 2 (see section on character definitions). The aedeagus is simple, not trifid (Character 87, state 0).

Lower-level relationships

This section highlights several aspects of the phylogenetic relationships of Tipulomorpha bellow the family-level. The

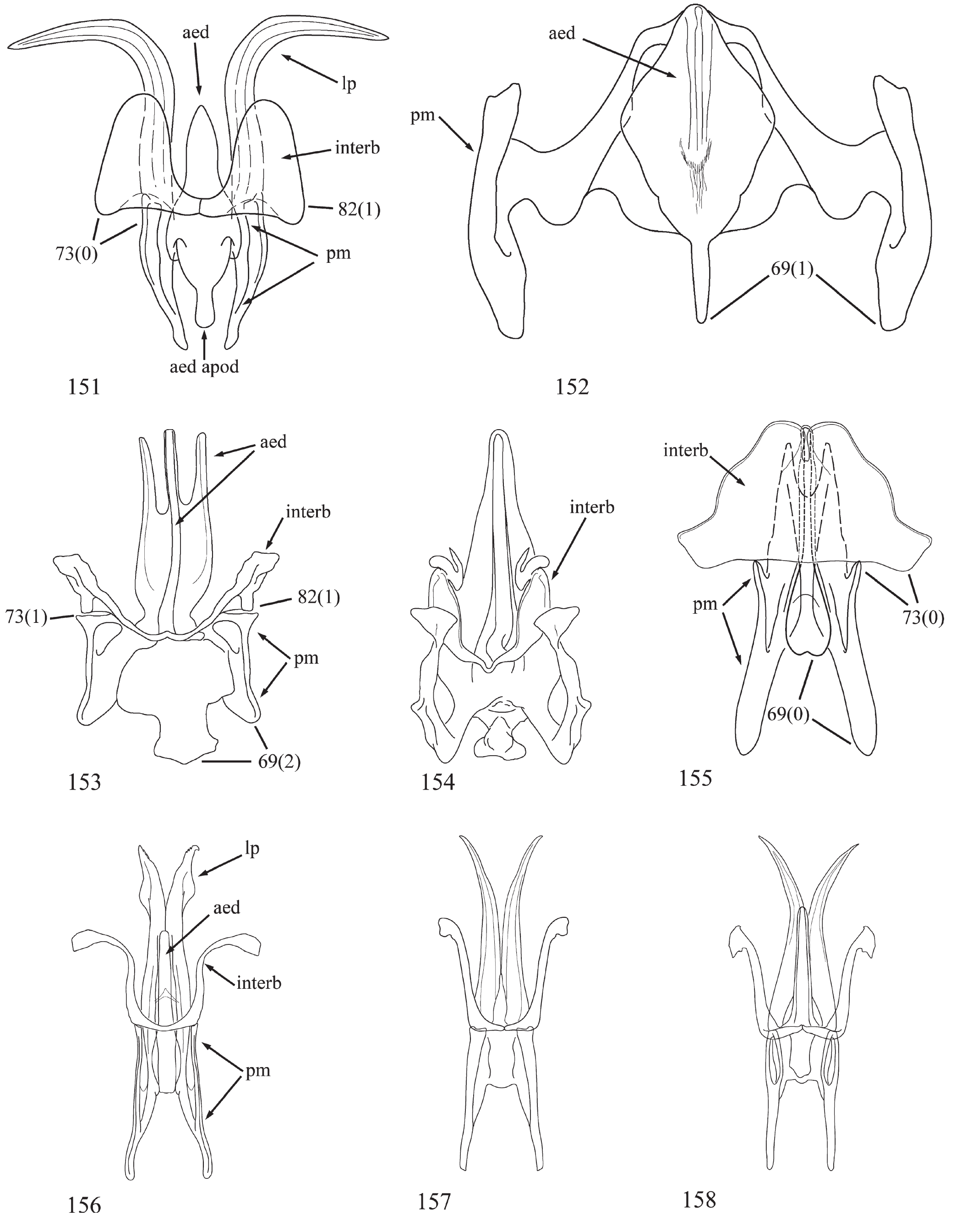


Figs 147–150. Morphological characters, male terminalia, dorsal view. 147, *Hexatoma* (*Eriocera*) *bruneri*. 148, *Hexatoma* (*Parahexatoma*) *pauliani*. 149, *Hexatoma* (*Cladolipes*) *cisatlantica*. 150, *Hexatoma* (*Hexatoma*) *microcera*.

section will not describe in detail all the differences in clade composition and character transformations between the various trees recovered by the different analyses. Even a node-by-node discussion of the preferred tree will not be undertaken here. Such a discussion would naturally be quite lengthy, and given the great instability of the overall phylogenetic results and uncertainties on the composition of the clades of intermediate levels of generality (i.e. between the genera/subgenera and family-levels) the utility of such a treatment would be doubtful. Instead, the discussion will focus on selected problems (namely, the monophyly *versus* paraphyly of the Limnophilinae and some of its included genera/subgenera), selected clades (groups with special biogeographical interest or supported by relatively more robust evidences) and the position of 'problematic' taxa. The reader interested in the characters supporting every node of the preferred tree can access this information directly from Figs 227–229.

Limnophilinae monophyly: immature stages *versus* adult characters

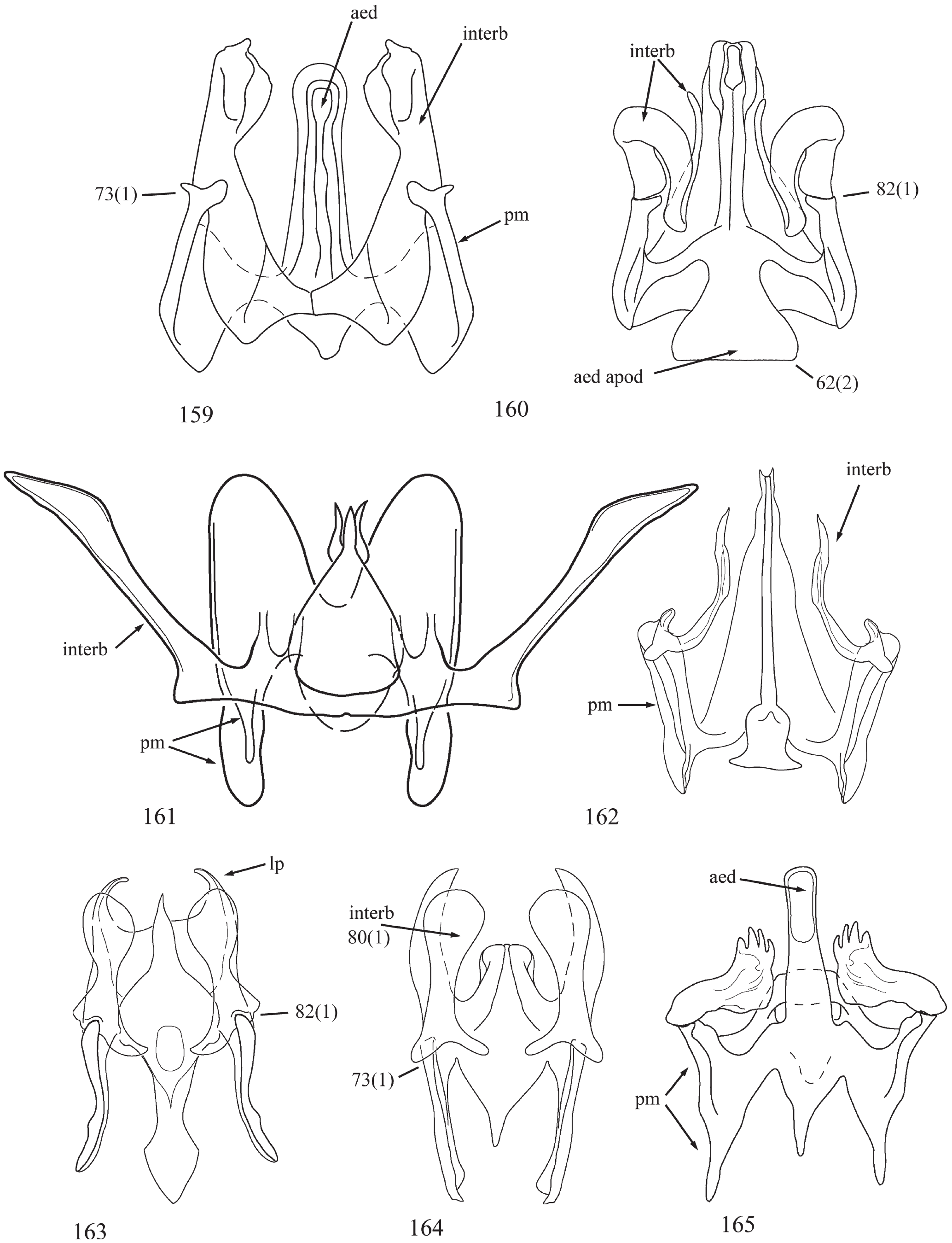
According to the present study, the Limnophilinae is paraphyletic with respect to the subfamilies Dactylolabidinae, Limoniinae, part of the Chioneinae, and the families Tipulidae and Cylindrotomidae. None of the different analyses supported a monophyletic Limnophilinae. Most of the adult features traditionally used to define the subfamily (e.g. four branched radius; vein sc-r situated distal to the level of the origin of Rs;



Figs 151–158. Morphological characters, male terminalia, internal structures, dorsal view. 151, *Trichocera bimacula* (Trichoceridae). 152, *Malaisemyia manipurensis* (Pediciidae). 153, *Cylindrotoma distinctissima* (Cylindrotomidae). 154, *Mesolimnophila lutea*. 155, *Lecteria (Lecteria)* sp. 156, *Clydonodozus neavei*. 157, *Conosia irrorata*. 158, *Conosia angustissima*.

presence of tibial spurs) are present in the Tipulomorphan ground plan.

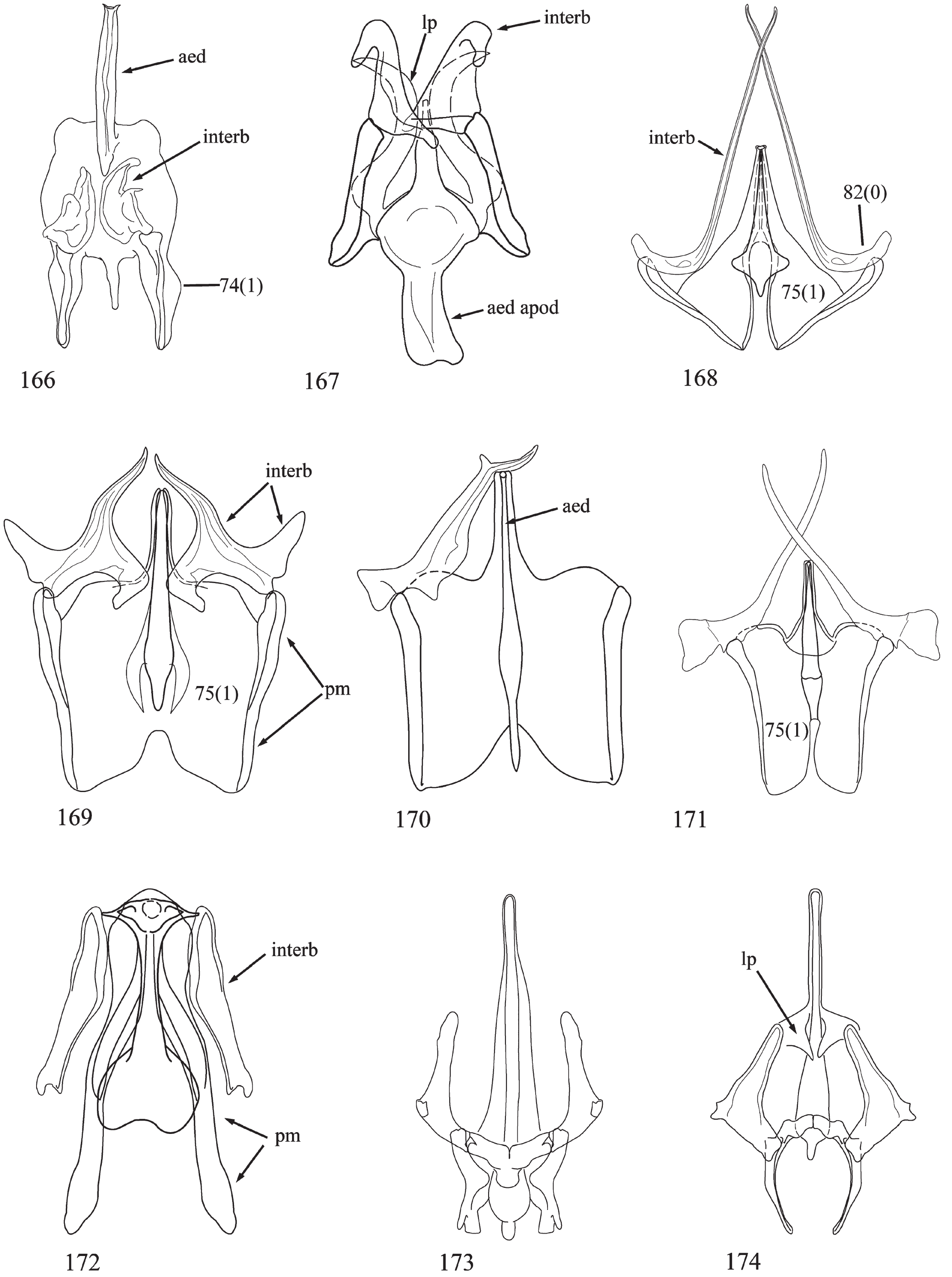
Even though the paraphyly of the Limnophilinae as a whole is also indicated by the study of Oosterbroek and Theowald (1991) based on the characters of immature stages, these authors proposed a clade including twelve Limnophilinae genera (*Pseudolimnophila*, *Pilaria*, *Ulomorpha*, *Polymera*, *Phylidorea*, *Euphylidorea*, *Eloeophila*, *Hexatoma*, *Limnophila*, *Neolimnomyia*, *Conosia* and *Eutonia*) (Oosterbroek and Theowald 1991: fig. 6). The genus *Paradelphomyia* is tentatively placed as the sister-group of this clade, and the whole group could be regarded as a monophyletic Limnophilinae (Hexatominae in their terminology) in a more restricted sense. The relationships of most genera included in this Limnophilinae *sensu stricto* as proposed by Oosterbroek and Theowald (1991) are quite distinct of the results obtained in the



Figs 159–165. Morphological characters, male terminalia, internal structures, dorsal view. 159, *Notholimnophila exclusa*. 160, *Ctenolimnophila* (*Campbellomyia*) *paulistae*. 161, *Gynoplistia* (*Xenolimnophila*) *flindersi*. 162, *Gynoplistia* (*Gynoplistia*) *fuscoplumbea*. 163, *Limnophila* (*Dicranophragma*) *fuscovaria*. 164, *Neolimnomyia* (*Brachylimnophila*) *nemoralis*. 165, *Neolimnomyia* (*Neolimnomyia*) *filata*.

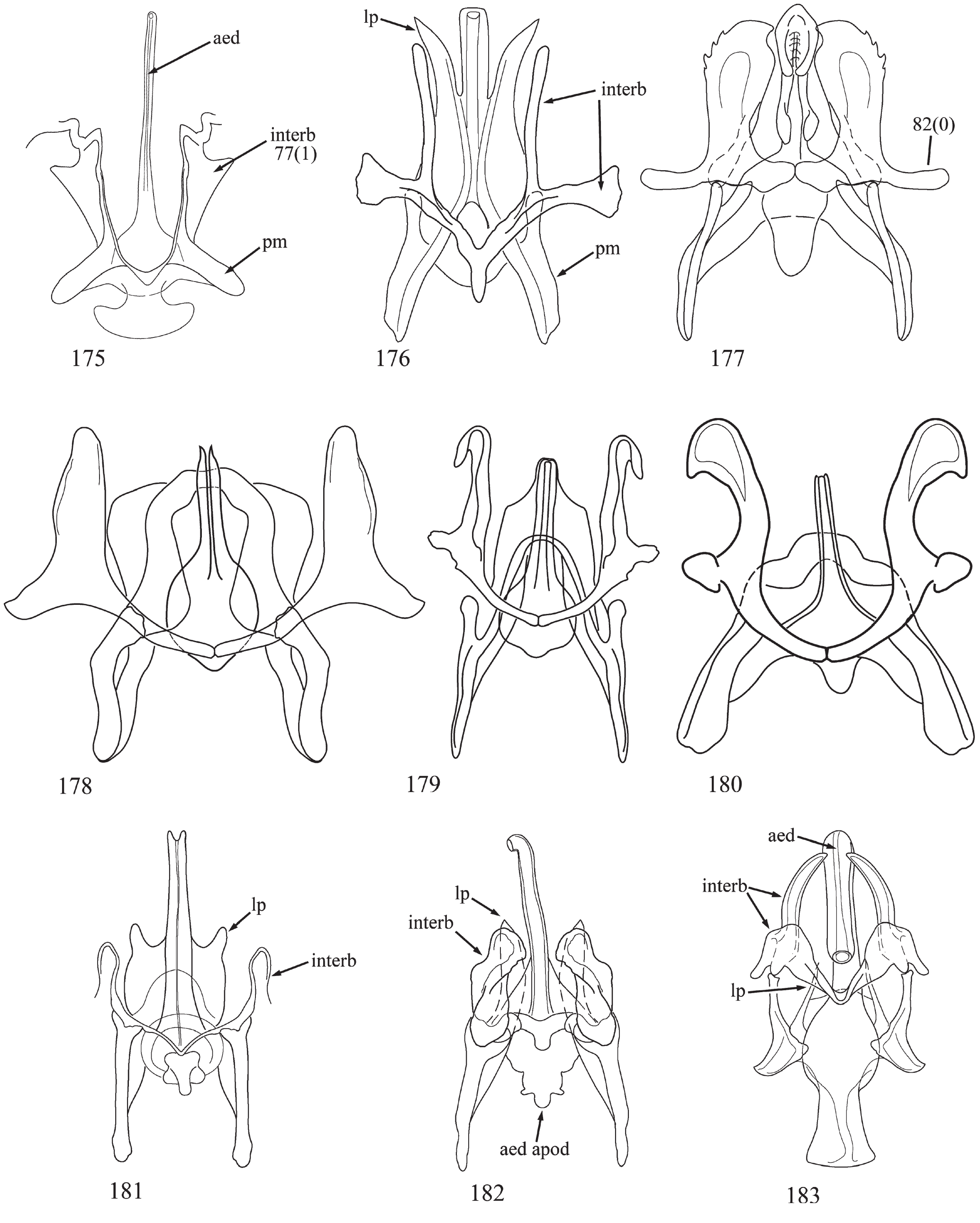
present study. This great discrepancy calls for a more detailed evaluation of the evidences used by Oosterbroek and Theowald (1991) to establish the relationships among the genera included in the clade.

According to Oosterbroek and Theowald (1991), in the genera included in this Limnophilinae *sensu stricto*, the spiracular field of the larva normally has four elongated flattened lobes, with the ventral ones the longest. However, Oosterbroek and Theowald (1991) are skeptical in considering this condition a synapomorphy of this clade, given the presence of a similar state in genera belonging to the subfamily Chioneinae. No further clear evidence is given by Oosterbroek and Theowald (1991) to support the monophyly of this Limnophilinae *sensu stricto* including *Paradelphomyia.*



Figs 166–174. Morphological characters, male terminalia, internal structures, dorsal view. 166, *Shannonomyia* (*Shannonomyia*) *lenta*. 167, *Prolimnophila areolata*. 168, *Epiphragma* (*Epiphragma*) *fasciapenne*. 169, *Epiphragma* (*Epiphragma*) *nigripleuralis*. 170, *Acantholimnophila bispina*. 171, *Acantholimnophila maorica*. 172, *Dactylolabis* (*Dactylolabis*) *cubitalis*. 173, *Limnophila* (*Arctolimnophila*) *claggi*. 174, *Limnophila* (*Arctolimnophila*) *subcostata*.

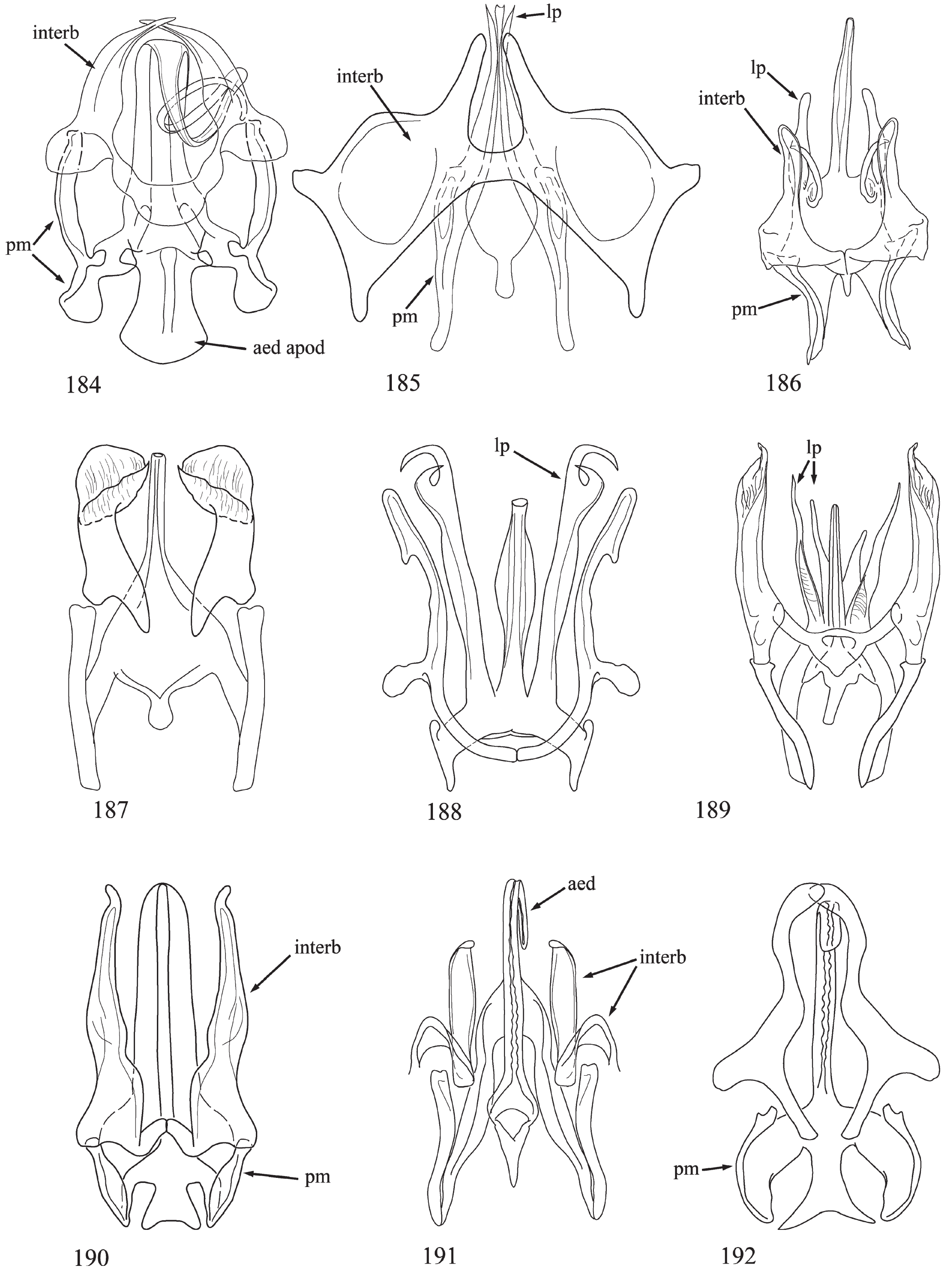
Many of the other characters used to define the relationships within the higher nodes in this clade are also problematical. Many of such characters are quite variable or either unknown in many of the included genera. In other cases, the characters are also present in several taxa outside the clade. These problems are explicitly pointed out by Oosterbroek and Theowald (1991) in their descriptions of these characters. With the same kind of skepticisms presented by Oosterbroek and Theowald (1991) regarding the monophyly of the entire group (including *Paradelphomyia*), one may consider that the evidences on the



Figs 175–183. Morphological characters, male terminalia, internal structures, dorsal view. 175, *Limnophila* (*Atopolimnophila*) *laricicola*. 176, *Eupilaria phoenosoma*. 177, *Idioptera nearctica*. 178, *Eloeophila maculata*. 179, *Eloeophila aldrichi aldrichi*. 180, *Eloeophila trimaculata*. 181, *Limnophila* (*Elporiomyia*) *nox*. 182, *Limnophila* (*Indolimnophila*) *bituminosa*. 183, *Helius* sp.

monophyly of many of the higher nodes of the clade, on the basis of immature stage characters, are also very weak.

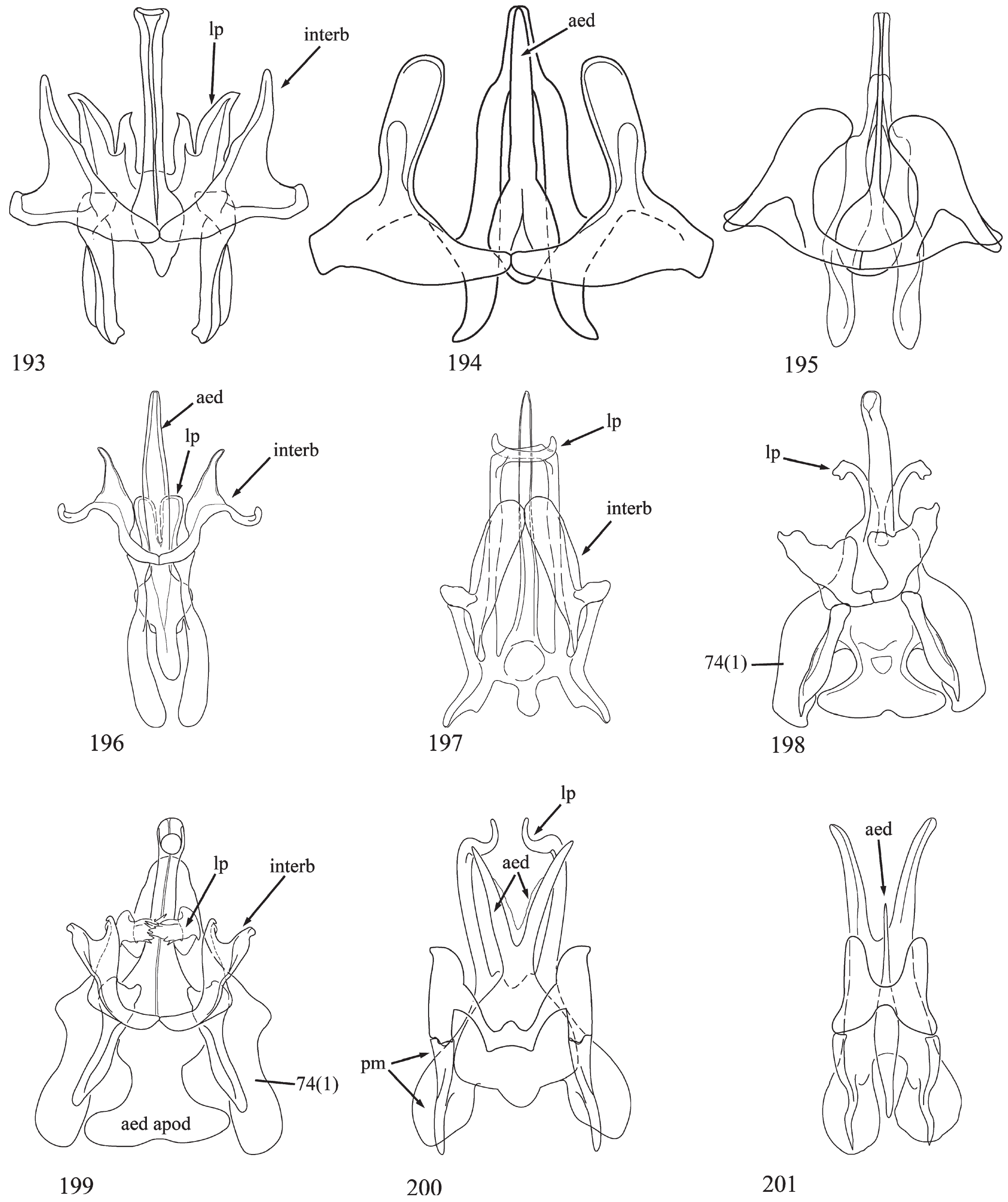
A more general aspect of the study by Oosterbroek and Theowald (1991) makes it difficult a straightforward comparison of their results with those obtained here on the basis of adult characters. The overall analysis employed by Oosterbroek and Theowald (1991) is not quantitative, but largely qualitative. There is no data matrix, which makes it quite difficult to access the distribution of the characters in the taxa, and there is no guarantee that the overall phylogenetic results presented there would be the most parsimonious if the evidences were reunited in a data matrix and analysed using modern methods and tree search algorithms. There is undoubtedly certain level of homoplasy in the characters of the immature stages as discussed by Oosterbroek and Theowald (1991) in their detailed description of the characters. But we do not know how these data would behave, and how congruent with each other they would be in a numerical, quantitative analysis.



Figs 184–192. Morphological characters, male terminalia, internal structures, dorsal view. 184, *Elephantomyia* (*Elephantomyia*) *westwoodi*. 185, *Euphylidorea niveitarsis*. 186, *Limnophila* (*Lasiomastix*) *macrocera*. 187, *Polymera* (*Polymerodes*) *parishi*. 188, *Eupilaria suavis*. 189, *Limnophila* (*Dendrolimnophila*) *shikokuensis*. 190, *Prionolabis rufibasis*. 191, *Limnophila* (*Nesolimnophila*) *luteifemorata*. 192, *Limnophila* (*Limnophila*) *pictipennis*.

Monophyletic genera and subgenera

Among the Limnophilinae genera or subgenera for which more than one species were included in the analysis, several are monophyletic according to the preferred tree. This section will mostly discuss the characters supporting the monophyly of these groups, even though the relationships of some of these genera with other genera may also be considered here. The discussion will focus on the more robust (less homoplastic) characters. Even though less robust characters may also be mentioned, in general

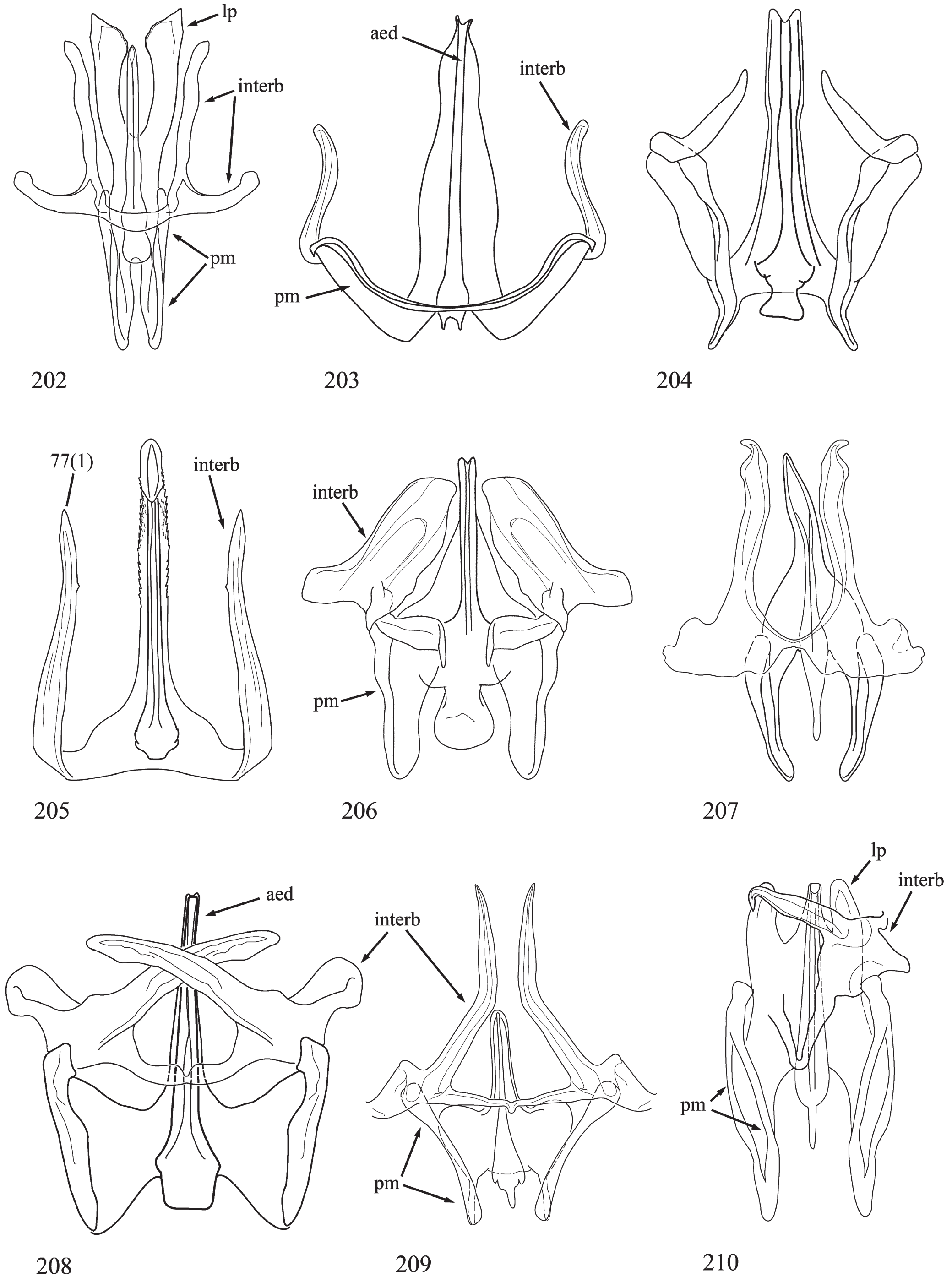


Figs 193–201. Morphological characters, male terminalia, internal structures, dorsal view. *Limnophila* (*Hesperolimnophila*) *euxesta*. 194, *Eutonia alleni*. 195, *Eutonia barbipes*. 196, *Paralimnophila* (*Paralimnophla*) *skusei*. 197, *Chilelimnophila lyra*. 198, *Phylidorea* (*Phylidorea*) *umbrarum*. 199, *Phylidorea* (*Phylidorea*) *longicornis pietatis*. 200, *Metalimnophila howesi*. 201, *Metalimnophila productella*.

they are not described in detail but only cited. In the discussion that follows, the term *unambiguous* refers to states unambiguously optimised as synapomorphies at the level of the discussed nodes of the tree, and not necessarily to non-homoplatic characters (which can also be labeled *unambiguous* in this other sense). A complete description of the unambiguously optimised synapomorphies of all clades is given in Figs 227–229. All information about the diversity and geographical distributions of the discussed groups were taken from Oosterbroek (2008).

Epiphragma (Epiphragma) *and* Acantholimnophila

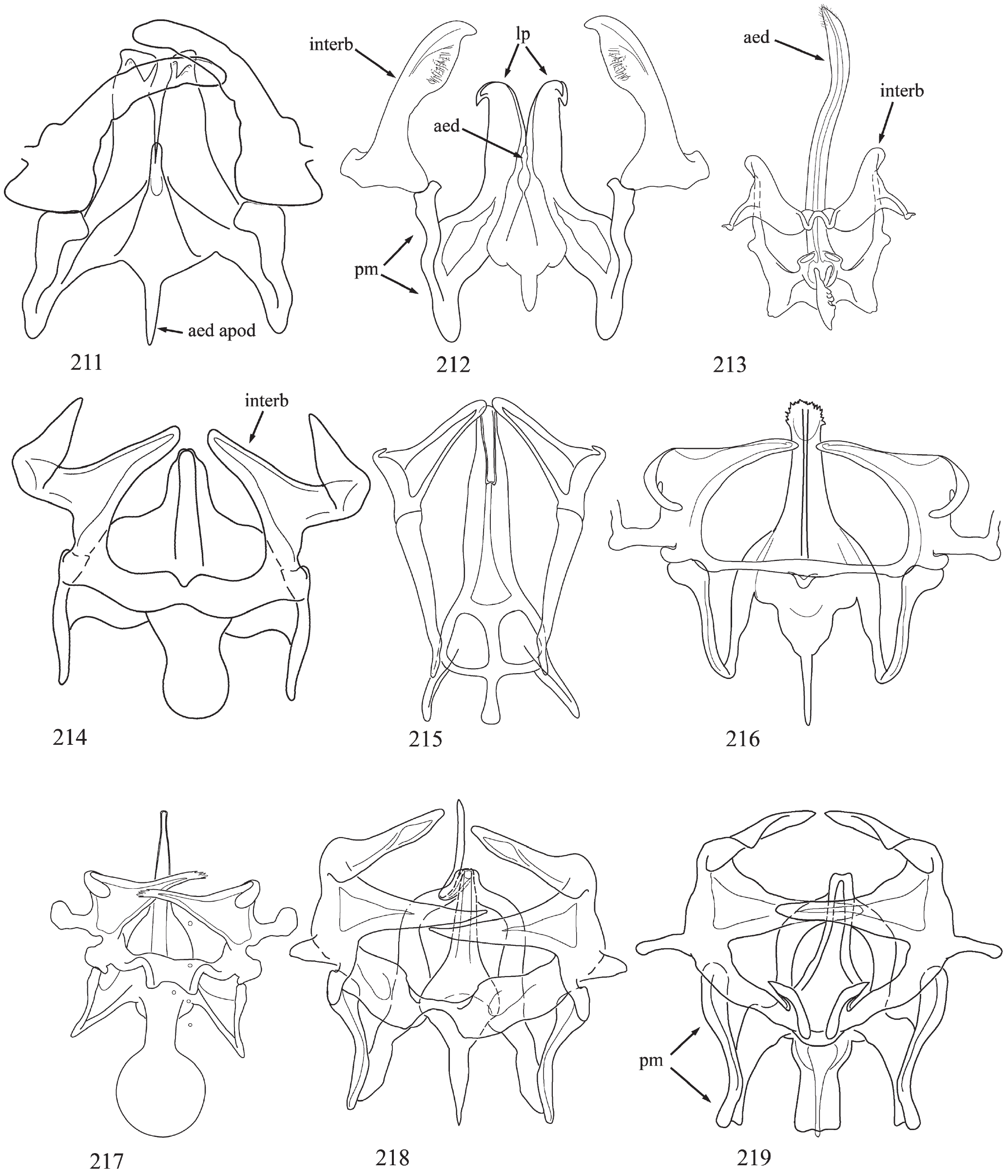
Epiphragma is a large genus with four subgenera and over 150 species. The group is present worldwide except for the Afrotropical region. Only two species of the subgenus *E.* (*Epiphragma*) were included in the analysis. The monophyly of the subgenus is corroborated in the preferred tree by four unambiguous synapomorphies. Two of these (characters 29 and 38) are quite homoplastic. The other two characters, however, seem to be good synapomorphic diagnostic



Figs 202–210. Morphological characters, male terminalia, internal structures, dorsal view. 202, *Paralimnophila* (*Paralimnophila*) *leuchophaeata*. 203, *Gynoplistia* (*Cerozodia*) *hemiptera hemiptera*. 204, *Gynoplistia* (*Gynoplistia*) *fimbriata*. 205, *Gynoplistia* (*Dirhipis*) *striatipennis*. 206, *Limnophila* (*Idiolimnophila*) *emmelina*. 207, *Tonnoirella gemella*. 208, *Edwardsomyia chiloensis*. 209, *Tinemyia margaritifera*. 210, *Rhamphophila sinistra*.

features: the first and second flagellomeres are fused (Character 7, state 1) and there is an additional cross-vein at the distal half of cell Sc (Character 44, state 1). The fusion of the first and second flagellomeres (Character 7) is subjected to certain level of homoplasy within the Tipulomorpha *sensu stricto*, occurring also in the (*Conosia* + *Clydonodosus*) clade and in *Elephantomyia*, but the apomorphic state of Character 44 seems to be exclusive of *Epiphragma* within the Tipulomorpha.

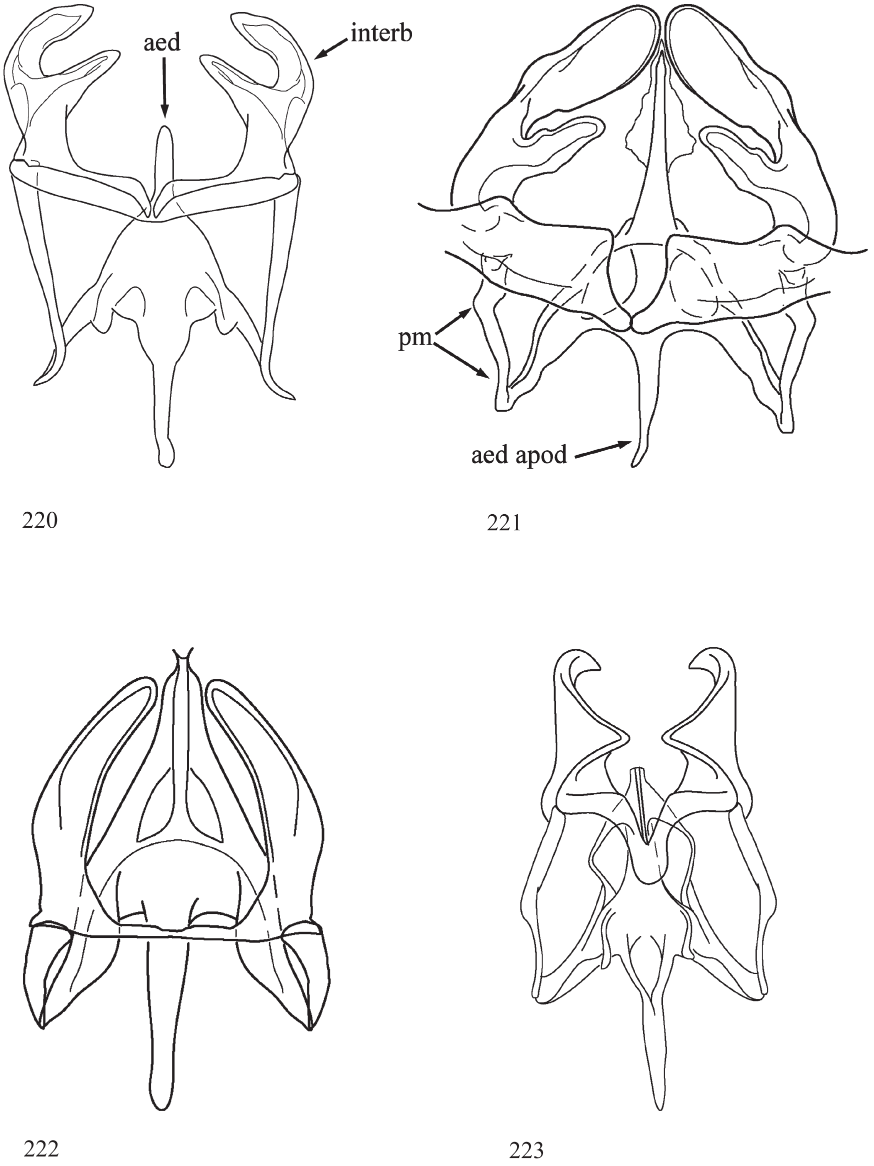
Alexander (1924) erected the genus *Acantholimnophila* to include two species restricted to New Zealand and previously described as *Limnophila* species. The group is largely unknown, with the only published data previously available being the



Figs 211–219. Morphological characters, male terminalia, internal structures, dorsal view. 211, *Nothophila fuscana*. 212, *Nothophila nebulosa*. 213, *Hexatoma* (*Eriocera*) *austera*. 214, *Pseudolimnophila legitima*. 215, *Hexatoma* (*Euhexatoma*) *triphragma*. 216, *Pilaria meridiana*. 217, *Pilaria discicollis*. 218, *Ulomorpha pilosella*. 219, *Ulomorpha rogersella*.

original descriptions (Alexander 1922) and a short characterisation of the genus (Alexander 1924). The two species of the genus, *A. maorica* and *A. bispina*, were included in this study, and their male terminalia are here illustrated for the first time. The monophyly of the genus is indicated in the preferred tree, but is not always recovered by other analyses. A straightforward definition of this genus on the basis of unequivocally apomorphic states is problematical on the basis of the characters scored in this study. Some of the unambiguous synapomorphies supporting its monophyly in the preferred tree are very homoplastic (Characters 5, 18 and 40). Others are interpreted as secondary reversals to conditions similar to that present in the Tipulomorphan ground plan and future analyses may indicate that they are actually symplesiomorphies. For example, the scape and pedicel are similar in length (Character 3, state 0) and the veins R_2 and R_3 reach the wing margin almost parallel to each other (Character 34, state 0). However, both species share a quite long antenna, a subterminal gonostylus (Character 54, state 1), and the overall morphology of the male genitalia is very similar in both taxa, including the acute apex of the conocoxite (Figs 96–97).

Alexander (1924) suggested a close proximity between *Epiphragma* and *Acantholimnophila* on the basis of similarities of the interbases in both genera. The present study



Figs 220–223. Morphological characters, male terminalia, internal structures, dorsal view. 220, *Hexatoma* (*Eriocera*) *bruneri*. 221, *Hexatoma* (*Parahexatoma*) *pauliani*. 222, *Hexatoma* (*Cladolipes*) *cisatlantica*. 223, *Hexatoma* (*Hexatoma*) *microcera*.

corroborates this conclusion, and *Epiphragma* and *Acantholimnophila* appear as sister-groups in the preferred tree and in the fittest tree yielded by the analysis of the reduced matrix. The sister-group relationship between *Epiphragma* and *Acantholimnophila* is supported by two unambiguous synapomorphies in the preferred tree: the great expansion of the aedeagal sheath between the medial margin of paramere and lateral margin of aedeagus (Character 75, state 1) and the extended lateral margins of the interbases, which occur in a very similar way in both genera (Figs 94–97). Actually, the general aspect of the male genitalia is extremely similar in *Epiphragma* and *Acantholimnophila*, and may include potential informative characters not scored in the present study.

Alexander (1924) also suggested a close proximity of *Epiphragma* with *Tinemyia*, *Tonnoirella*, and *Edwardsomyia*, but this pattern is not corroborated here.

Shannonomyia

Shannonomyia is a large genus with two subgenera and 4 Nearctic and 102 Neotropical species. This study included only two species of the typical subgenus, the Neotropical *S. brevinervis* and the Nearctic *S. lenta* (the type species of the genus). The included species of *Shannonomyia* appear forming a clade in all the analyses performed in this study. Only two unambiguous synapomorphies support the monophyly of the group, even

Table 3. Synthesis of the 15 analyses under different weighting schemes, different options regarding the inclusion/exclusion of taxa and different constraints of monophyly

	Unconstrained analysis of complete matrix				
	k = 2	k = 3	k = 4	k = 5	k = 6
Number of trees	1	3	1	3	1
Fit	35.16	39.67	43.23	46.15	48.65
Tree length	1066	1031	1019	1015	1002
CI	0.135	0.140	0.141	0.142	0.144
	Unconstrained analysis with *Stibadocerella* excluded				
	k = 2	k = 3	k = 4	k = 5	k = 6
Number of trees	1	3	1	3	1
Fit	35.70	40.12	43.64	46.52	49.00
Tree length	1046	1021	1008	1004	984
CI	0.137	0.141	0.142	0.143	0.146
	Analysis of complete matrix with the monophyly of Cylindrotomidae constrained				
	k = 2	k = 3	k = 4	k = 5	k = 6
Number of trees	5	1	3	3	1
Fit	34.97	39.48	43.02	46.96	48.49
Tree length	1064	1041	1034	1017	989
CI	0.135	0.138	0.139	0.142	0.145

though they are among the less homoplastic of the whole dataset. In both the included species, the ventral region of the parameres are extended laterally (Character 74, state 1) and the distal portion of the interbase is bifid. Gelhaus (in press) comments on the difficulties in defining the limits of the genus, and maybe these apomorphic character states can be useful in providing a better definition based on apomorphic shared features.

Limnophila (Arctolimnophila)

Alexander (1966) erected *Arctolimnophila* as a subgenus of *Limnophila* to include two species previously described under the genera *Phylidorea* (*Phylidorea subcostata*) and *Limnophila* (*Limnophila claggi*). Both species were included in the present study and appear forming a clade of sister species in the preferred tree. However, the two unambiguous synapomorphies supporting this clade (Character 13, state 2 and Character 15, state 1) are both subjected to substantial levels of homoplasy (28 and 19 steps, respectively) and the clade is not recovered by all the analyses. The overall morphology of both species, including details of wing venation and male genitalia (Figs 99–100) are quite similar and it seems very likely that the taxon is indeed monophyletic. Most probably the status of *Arctolimnophila* should be raised to the genus level, especially considering the likely paraphyly of the large genus *Limnophila* (discussed below in this paper).

Eloeophila

Eloeophila comprises 91 described species. The group is absent in the Neotropical and Australasian regions. Three species of this genus were included in the present study, including the type species of the genus, *E. maculata*. All the different analyses performed pointed to the monophyly of the group. Its unambiguous synapomorphies include the apex of the clasper of gonostylus abruptly narrowed (Character 61, state 1), the posterior margin of the clasper of gonostylus serrated (Character 66, state 1) and the absence of the lateral processes of the aedeagal sheath (Character 71, state 0).

All the analyses pointed to the sister-group relationship between *Eloeophila* and *Idioptera*, the synapomorphy of this clade being the presence of an additional cross-vein between M and Cu situated basally to m-cu (Character 46, state 1). However, as pointed out by Edwards (1938), this additional cross-vein may be absent in one of both wings of some *Eloeophila* specimens.

Conosia

Conosia comprises 11 species distributed mostly in the Afrotropics, but present also in the Palearctic, Oriental and Australasian regions. The genus is very easily recognisable by the general aspect of its wing venation (Alexander 1963: fig. 17) including the peculiar shape of the radial sector and discal cell (Fig. 43). The rostrum and month parts are greatly reduced, the palpomeres are partially fused and the eyes meet ventrally (Fig. 23). The unambiguous synapomorphies supporting its monophyly include the condition of the eyes just mentioned (Character 18, state 3), the absence of the petiole of cell r2 (Character 35, state 0), and the smooth area between the anterior and posterior margins of the clasper of gonostylus (Character 65, state 0), which is here interpreted as a secondary reversal from a serrated condition.

All the performed analyses pointed to the genus *Clydonodozus* as the sister-group of *Conosia*. *Clydonodozus* is also a small group including 24 species. Alexander (1956) already recognised the close proximity between both groups. The unambiguous synapomorphies of the (*Conosia* + *Clydonodozus*) clade include the fusion of the first and second flagellomeres (Character 7, state 1); reduction of the rostrum (Character 11, state 0); the cross-vein r-r situated distal to the point of bifurcation

Table 4. Character diagnostics of tree in Figures 227–229

Character	Number of steps	*CI*	*RI*	Character	Number of steps	*CI*	*RI*	Character	Number of steps	*CI*	*RI*
1	1	1.000	1.000	31	32	0.063	0.250	61	23	0.130	0.459
2	20	0.100	0.600	32	23	0.043	0.532	62	18	0.056	0.393
3	24	0.083	0.511	33	7	0.143	0.455	63	1	1.000	1.000
4	25	0.360	0.333	34	13	0.154	0.450	64	9	0.222	0.667
5	22	0.091	0.474	35	12	0.250	0.357	65	4	0.250	0.667
6	17	0.059	0.568	36	16	0.063	0.500	66	12	0.083	0.450
7	3	0.333	0.600	37	25	0.120	0.405	67	1	1.000	1.000
8	5	0.400	0.625	38	31	0.129	0.357	68	1	1.000	1.000
9	2	0.500	0.800	39	1	1.000	1.000	69	24	0.083	0.551
10	3	0.333	0.333	40	34	0.088	0.426	70	14	0.071	0.278
11	9	0.333	0.455	41	4	0.250	0.625	71	17	0.059	0.500
12	2	0.500	0.000	42	1	1.000	1.000	72	3	0.333	0.600
13	28	0.071	0.381	43	20	0.100	0.609	73	15	0.067	0.641
14	3	0.333	0.800	44	2	0.500	0.500	74	2	0.500	0.833
15	19	0.105	0.227	45	14	0.071	0.606	75	3	0.333	0.600
16	5	0.200	0.429	46	2	0.500	0.750	76	6	0.167	0.545
17	2	0.500	0.875	47	28	0.179	0.281	77	4	0.250	0.000
18	38	0.079	0.364	48	3	0.667	0.833	78	12	0.083	0.633
19	31	0.097	0.333	49	3	0.333	0.500	79	5	0.400	0.786
20	1	1.000	1.000	50	5	0.200	0.600	80	1	1.000	1.000
21	13	0.154	0.593	51	4	0.250	0.000	81	2	1.000	1.000
22	2	0.500	0.833	52	32	0.063	0.400	82	15	0.067	0.650
23	26	0.077	0.478	53	4	0.250	0.571	83	17	0.059	0.360
24	4	0.500	0.500	54	8	0.125	0.364	84	31	0.097	0.349
25	7	0.143	0.500	55	2	0.500	0.917	85	2	0.500	0.667
26	19	0.158	0.448	56	1	1.000	1.000	86	1	1.000	1.00
27	5	0.200	0.692	57	5	0.200	0.556	87	2	0.500	0.800
28	34	0.088	0.492	58	16	0.125	0.650	88	1	1.000	1.00
29	12	0.083	0.214	59	2	0.500	0.500				
30	3	0.333	0.600	60	8	0.375	0.750				

of R_{2+3}, but closer to this point than to the mid-point of R_2 (Character 26, state 2); the vein Rs originating in a point basal to the level of the apex of vein A_2 (Character 28, state 3); humeral vein (vein h) faint (Character 42, state 1); the gonostylus subterminal in position (Character 54, state 1); the posterior margin of the clasper of gonostylus serrated (Character 66, state 1); the basolateral portion of the interbase not extended (Character 82, state 1); and the loss of the main body of the interbase (Character 85, state 0).

In the preferred tree, the sister-group of the (*Conosia* + *Clydonodozus*) clade is *Lecteria*. The genus *Lecteria* includes 23 Neotropical, 18 Afrotropical and 1 Oriental species. The genus was considered very difficult to place by Alexander (1948*a*, 1956) but Alexander (1969) briefly commented on the close affinities among *Lecteria*, *Conosia* and *Clydonodozus*. The close proximity of *Lecteria* with the (*Conosia* + *Clydonodozus*) clade is recovered either by the fittest tree of the analysis of the reduced matrix and the preferred tree, on the basis of the following unambiguous synapomorphies: the very narrow distance, ventrally, between the lateral margins of the eyes (Character 18, state 2); veins R_2 and R_3 abruptly diverging from each other after running more or less in parallel (Character 34, state 2); and the loss of the tibial spurs (Character 50, state 0).

Polymera

The genus *Polymera* has two recognised subgenera. The typical subgenus comprises 65 species in the Nearctic, Palearctic, Oriental and Neotropical regions, the latest including the great majority (50) of the species. The subgenus *P*. (*Polymerodes*) is restricted to the Neotropics and includes 8 described species only. The monophyly of the genus, though not recovered by all the performed analyses, appear in the unconstrained analyses of the complete matrix (Fig. 224), in the fittest tree of the unconstrained analysis of the reduced matrix (Fig. 225), and in the preferred tree (Figs 227–229). All but one (the loss of the discal cell; Character 41, state 0) of the unambiguous synapomorphies of the genus in the preferred tree are very homoplastic (Character 13, state 0; Character 32, state 0; Character 34, state 0; Character 38, state 0; Character 61, state 2; Character 71, state 0 and Character 82, state 1), but this combination of characters is unique. The monophyly of the subgenus *P*. (*Polymerodes*) is also based on the combination of very homoplastic characters, the least of which being the loss of the tibial spurs (Character 50, state 1).

Prionolabis

Prionolabis includes over 70 species in the Holarctic and Oriental regions. Two Nearctic species, *P. rufibasis* (the type of the genus) and *P. walley* were included in the study, and always appear forming a clade on the basis of several unambiguous synapomorphies (Fig. 228). Three of them are not very homoplastic in general and deserve mention here: the lobe of gonostylus is bifurcated (Character 56, state 1; a character state unique to the studied species of the genus); the clasper of the gonostylus has its central region weakly sclerotised, but is strongly sclerotised at its margins (Character 60, state2); the distal part of the clasper of gonostylus is strongly serrated (Character 64, state 2).

Eutonia

Eutonia is a small genus of 6 Nearctic and Palearctic species. Two species, *E. barbipes* (the type of the genus) and *E. alleni* were included in this study and they form a clade in all the analyses performed here. In the preferred tree, the unambiguous synapomorphies of *Eutonia* are the great development of the scape relative to the length of the pedicel (Character 3, state 2), the small, but well defined horn-like protuberances in the head (Character 16, state 1), the eyes meeting ventrally (Character 18, state 2), and the clasper of gonostylus well divided at its base into two parts (Character 59, state 1). This last feature is unique to this genus within the Limoniidae genera included in the study, and even though a subdivision of the clasper of gonostylus also occurs in the tipulid species *Tipula reesi* used as an outgroup, these two occurrences are obviously not homologous.

Phylidorea (Phylidorea)

Phylidorea includes three subgenera and over 40 Palearctic species. This study included two species of the typical subgenus, *P. umbrarum* and *P. longicornis pietatis*. The monophyly of this group is recovered in the fittest tree of the unconstrained analysis of the reduced matrix (Fig. 225) and in the preferred tree, but is not recovered by all the analyses. Nine unambiguous synapomorphies support the clade with the two representatives of the genus in the preferred tree, but all are very homoplastic features or appear as secondary reversals to conditions similar to that of the ground plan: the flagellomeres are ovoid (as in the ground plan; Character 5, state 0); the area between the posterior margin of the eyes and the dorsoposterior margin of the occiput is greatly developed (Character13, state 2); the minimal ventral distance between the eyes is very similar in both species (Character 18, state 1); the costal vein is interrupted between R_3 and R_{4+5} (Character 21, state 2); the base of vein Rs has a spur or projection (Character 29, state 1); the vein h is situated closer to the point of bifurcation than to the origin of M+Cu (Character 43, state 0); the arculus is absent (as in the ground plan; Character 45, state 0); the posterior margin of the ninth tergite lacks extensions (Character 52, state 0); the aedeagus apodeme is very wide compared with width of the aedeagus (Character 70, state 1).

Metalimnophila

Metalimnophila is a group of 21 nominal species restricted to New Zealand. The entire male terminalia of this genus is illustrated here for the first time for the two species included in this study, *M. howesi* (the type of the genus, Figs 127 and 200) and *M. productella* (Figs 128 and 201). The two included species of *Metalimnophila* form a clade in all the analyses performed in this study. In the preferred tree, many synapomorphies support its monophyly. However, several of such character states are conditions similar to that of early nodes or even the ground plan, optimised in the tree as secondary reversals at the level of this genus: pedicel almost as long as high (Character 3, state 0); the position of the cross-vein r-r (Character 26, state 2); veins R_2 and R_3 reaching the margin almost parallel to each other (Character 34, state 0); clasper of gonostylus hairy (Character 58, state 0); the basolateral portion of the interbase not extended (Character 82, state 1). Future studies may indicate that these character states are actually plesiomorphic features shared by members of the group. Other synapomorphic features, which are homoplastic outside the clade but are not treated as reversals, include details of the wing venation (Character 32, state 0), and the clasper of gonostylus mostly weakly sclerotised, but with some sclerotisation at its apex (Character 60, state 1).

A clade including *Phylidorea* and *Metalimnophila* as sister-groups appear in both the fittest tree of the unconstrained analysis of the reduced matrix (Fig. 225) and in the preferred tree, here with two unambiguous synapomorphies supporting it: the origin of Rs situated between the level of the apexes of veins A_1 and A_2 (Character 28, state1), and the ventral margins of the parameres extended laterally (Character 74, state 1). It is noteworthy that a similar lateral expansion of the ventral margins of the parameres occurs only in *Shannonomyia* (Fig. 166), but in a much lesser extent.

Gynoplistia (Cerozodia) *and* Gynoplistia (Dirhipis)

Gynoplistia is a diverse genus (over 300 species included) subdivided into four subgenera, mostly distributed in southern temperate regions of the world (Southern South America, New Zealand and Australia). Three species of the typical subgenus are also known from the Oriental region (Indonesia: Sulawesi).

Representatives of the four recognised subgenera were included in this study, but the monophyly of the genus is almost always not recovered by the different analyses performed here. However, a clade containing part of the typical subgenus, and the monophyletic subgenera *G.* (*Cerozodia*) and *G.* (*Dirhipis*) is often recovered, as in the fittest tree of the unconstrained analysis of the reduced matrix (Fig. 225) and in the preferred tree (Fig. 229). This clade is supported in the preferred tree by a combination of several unambiguous, but very homoplastic synapomorphies.

The monophyly of the subgenus *G.* (*Cerozodia*) is recovered by all the performed analyses, but in the preferred tree there is a single unambiguous synapomorphy in support of it, which is the secondary loss of the extension of the basolateral portion of the interbase (Character 82, state 2). In this particular case, the interbase is not even connected with the gonocoxite apodeme and this condition is unusual. In the species of *G.* (*Cerozodia*) examined, the general aspect of the male genitalia is quite similar, including potential characters not scored in the study. For example, the lobe of gonostylus is quite long and narrow in both species and the apex of the clasper is enlarged and bifid in a similar and characteristic way (Fig. 130).

The monophyly of *G.* (*Dirhipis*) is also recovered by all the analyses performed, and in the preferred tree there are several unambiguous synapomorphies supporting it, including some of the less homoplastic characters of the whole dataset: the well defined horn-like protuberances in the head (Character 16, state 1), the indistinguishing interbases (Character 76, state 0), and the rough appearance of the lateral margins of the aedeagal sheath (Character 88, state 1), which is unique, among the terminal taxa included in this study, to the species of this subgenus.

Nothophila

The genus *Nothophila* includes two species from New Zealand. The two species, *N. fuscana* and *N. exclusa*, were included in this study, and appear forming a clade in most of the performed analyses. In the preferred tree, the synapomorphic features of the genus include the reduction of the length of the rostrum (Character 11, state 0), the presence of macrotrichia over most of the surface of the wing (Character 49, state 1) and the interbases separated medially (Character 78, state 1). As in the ground plan, the flagellomeres are ovoid in both species (Character 5, state 0) but this is considered a secondary reversal at the level of this genus. The male genitalia of the included species of *Nothophila* are illustrated here for the first time (Figs 138, 139, 211, 212).

Pseudolimnophila (Pseudolimnophila)

Pseudolimnophila is a large genus with over 80 included species. There are two subgenera, the typical subgenus, which is absent only in the Australasian region, and the Afrotropical subgenus *P.* (*Calolimnophila*). Two species of the typical subgenus were included in this study, the Nearctic *P. luteipennis* (the type species of the genus) and the Oriental *P. legitima*. The two species form a clade in all the analyses performed, even though a single unambiguous synapomorphy supports its monophyly in the preferred tree, which is the great development of the length of the scape in comparison with its height (Character 2, state 2).

Pilaria

The widespread genus *Pilaria* is represented in this study by two species, *P. meridiana* (the type of the genus) and *P. discicollis*. These taxa form a clade in all the performed analyses. In the preferred tree, several unambiguous synapomorphies support the monophyly of the group, but these form a combination of mostly very homoplastic features (Fig. 229). The antenna has ovoid flagellomeres as in the ground plan (Character 5, state 0), but this character is optimised as secondary reversal at this level.

Ulomorpha

Ulomorpha is a small genus with 10 described species in the Nearctic and Palearctic regions. Two Nearctic species, *U. rogersella* and *U. pilosella* (the type species of the genus) were included in this study and they form a clade in all the performed analyses. A relatively long list of ten unambiguous synapomorphies supports its monophyly in the preferred tree. However, as in many other clades recovered in this study, most of these characters are subjected to high levels of homoplasy, the relatively more robust being the loss of the cross-vein r-r (Character 25, state 0) and the presence of macrotrichia over most of the surface of the wing (Character 49, state 1).

Pseudolimnophila + Ulomorpha + Pilaria + Hexatoma (sensu lato)

A clade recovered in the preferred tree including the genera *Pseudolimnophila*, *Hexatoma* (*sensu lato*), *Pilaria* and *Ulomorpha* deserves special mention here. Even though there is a single unambiguous synapomorphy supporting this clade, it is one of the less homoplastic characters of the whole dataset. In most of the terminal taxa included in this clade the interbase is bifid (Character 79, state 1). This character state occurs outside this clade only in *Shannonomyia* (Fig. 166) and *Acantholimnophila* (as an autapomorphy of the species *A. bispina*; Fig. 170). However, while the expression of this character state in the included species of this clade is quite similar among them (for example, compare Figs 214, 216–220), it is very dissimilar to the condition found in *Shannonomyia* and *Acantholimnophila*. This particular bifid condition of the interbase (Character 79, state 1) is thus considered as a relatively robust character supporting the close relationship between *Pseudolimnophila*, *Hexatoma* (*sensu lato*), *Pilaria* and *Ulomorpha*, even though some additional transformation and even a reversion to a non-bifid condition (Character 79, state 0) must be assumed to have occurred in some of the higher branches of the clade, as for example in *Hexatoma* (*Cladolipes*) *cisatlantica* (Figs 149, 222).

Temperate Gondwanan clades

Exploring the biogeographical implications of the phylogenetic results presented here is well beyond the scope of this study. However, at least two clades recovered in the study include poorly diverse groups of restricted distributions in southern parts of the globe, in disjunct temperate areas of Southern South America, New Zealand and Australia. This section highlights the results obtained for these Temperate Gondwanan clades.

One of such clades includes the genera (*Tonnoirella* + (*Edwardsomyia* + (*Tinemyia* + (*Rhamphophila* + (*Nothophila*))))). This clade is recovered in the preferred tree, as well as in the fittest tree of the analysis of the reduced matrix (Fig. 225).

Tonnoirella has one species (with two subspecies) from Tasmania. *Edwardsomyia* includes a single species from South Chile. *Tinemyia* is also monotypic and restricted to New Zealand. *Rhamphophila* and *Nothophila* include, respectively, three and two species from New Zealand.

Alexander (1928, 1929, 1948*a*) considered the genera *Tonnoirella*, *Tinemyia*, *Rhamphophila*, and *Edwardsomyia* as closely related to each other on the basis of the elongate rostrum and, indeed, the most robust evidence supporting this clade is the increase of the length of the rostrum (Character 11, state 2) which reaches its maximum in *Tinemyia* (Character 11, state 3), but suffers a reversal (to state 0) in *Nothophila*. According to the phylogenetic picture adopted herein, the evolution of the length of the rostrum is also subjected to a certain level of homoplasy outside this clade. An elongated rostrum also evolved independently in *Bergrothomyia* and *Elephantomyia*, and the reduction of the rostrum occurred in *Hexatoma* (*Cladolipes*),

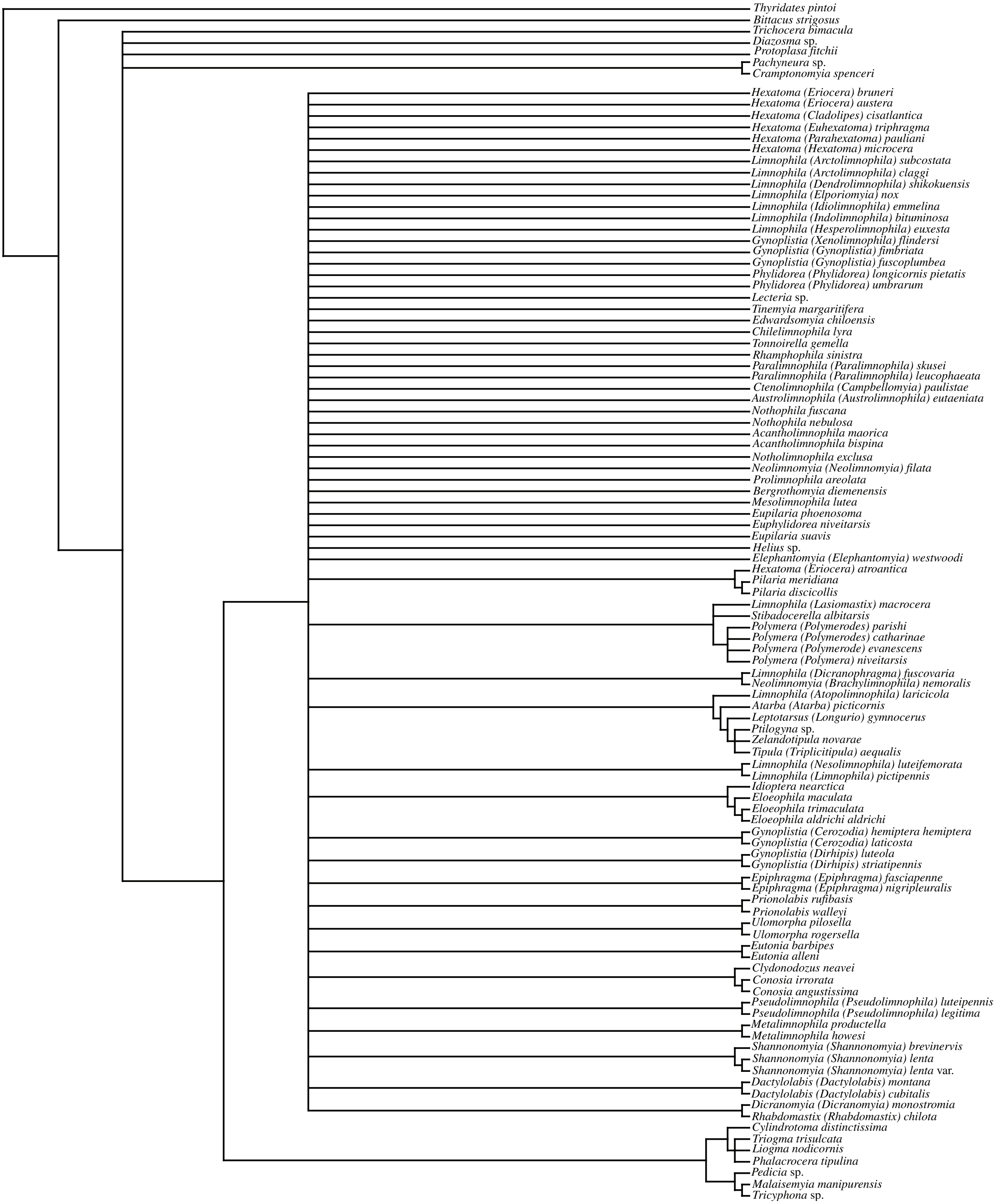


Fig. 224. Unconstrained analyis of the complete matrix. Strict consensus tree of all the nine topologies yielded by the five analyses with k ranging from 2 to 6.

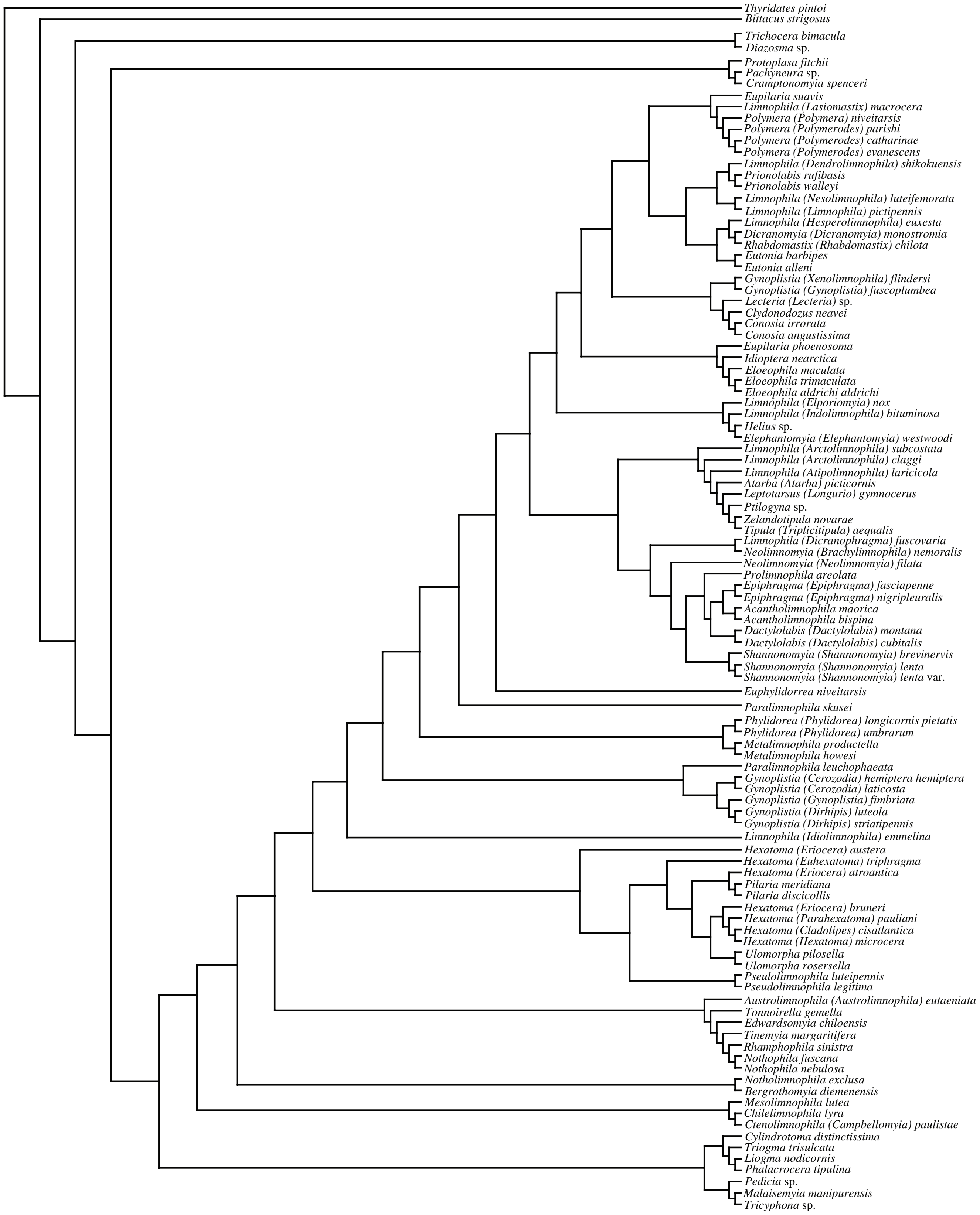


Fig. 225. Unconstrained analysis with *Stibadocerella* excluded. Fittest tree (k = 6).

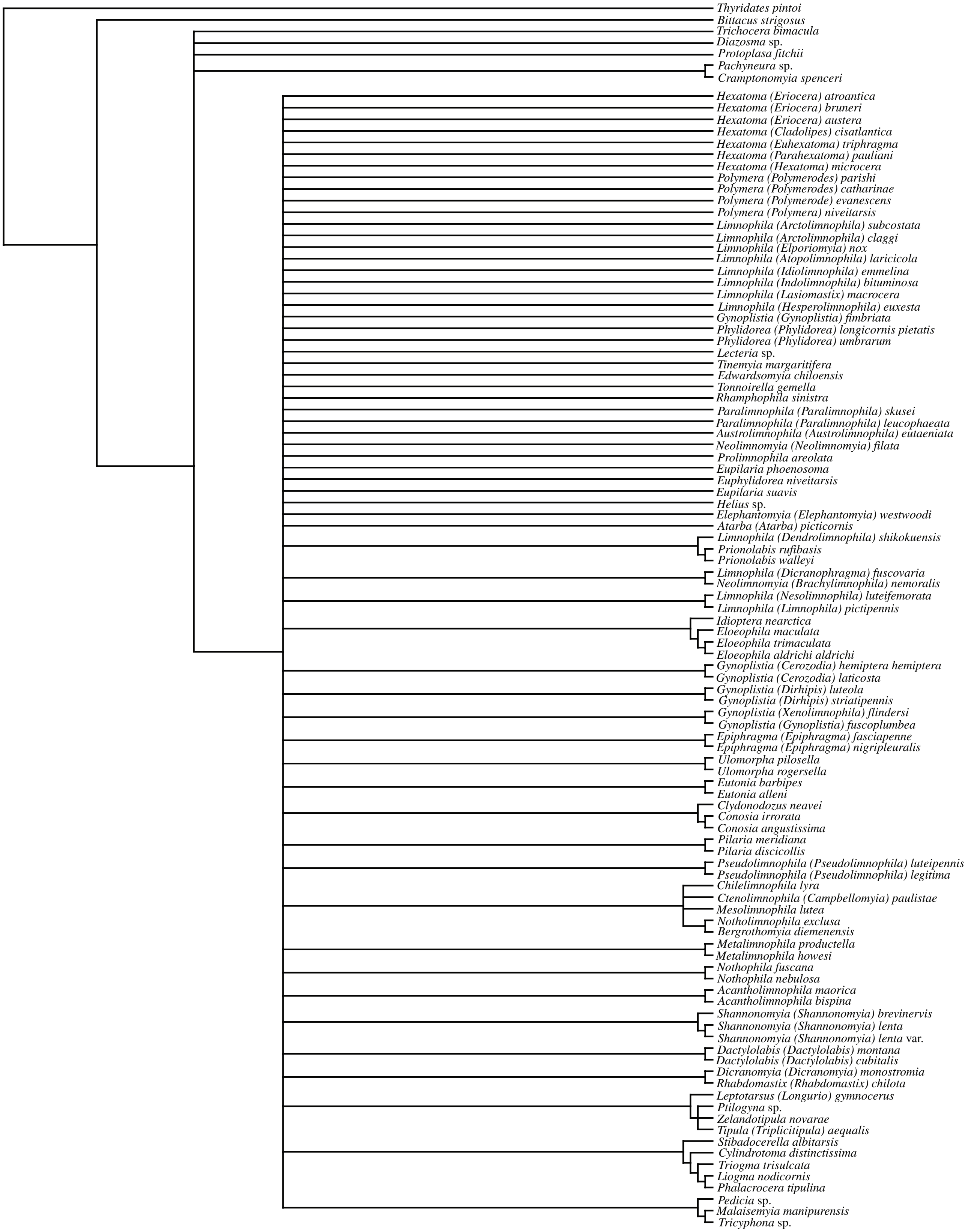
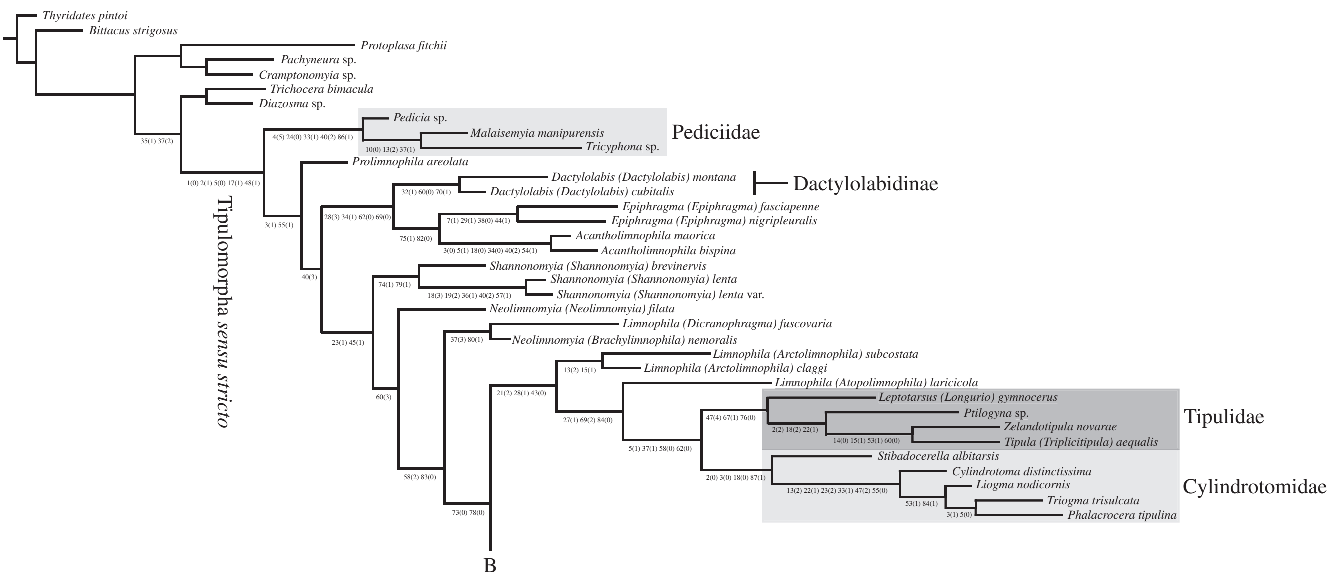


Fig. 226. Analysis of the complete matrix with the monophyly of Cylindrotomidae constrained. Strict consensus tree of all the nine topologies yielded by the 5 analyses with k ranging from 2 to 6.

Ctenolimnophila and at the base of the (*Conosia* + *Clydonodozus*) clade.

Another clade including taxa of restricted distributions in now disjunct Temperate Gondwanan areas include ((*Notholimnophila* + *Bergrothomyia*) + (*Mesolimnophila* + (*Chilelimnophila* + *Ctenolimnophila*))). *Notholimnophila* is monotypic and known exclusively from New Zealand. The male genitalia of its only included species, *N. exclusa*, is illustrated here for the first time (Fig. 85). *Bergrothomyia* include three species restricted to Australia (New South Wales, Victoria and Tasmania). The Neotropical genera *Mesolimnophila* and *Chilelimnophila* are also monotypic and endemic to South Chile. A detailed redescription of *Chilelimnophila* is provided by Ribeiro (2007). *Ctenolimnophila* includes three subgenera, and is a more widespread genus. Although the bulk of the group is from New Zealand, it is also present in the Neotropical and Afrotropical Regions. One Neotropical species of the subgenus *C.* (*Campbellomyia*) was included in this study.

The most robust unambiguous synapomorphy of the ((*Notholimnophila* + *Bergrothomyia*) + (*Mesolimnophila* +



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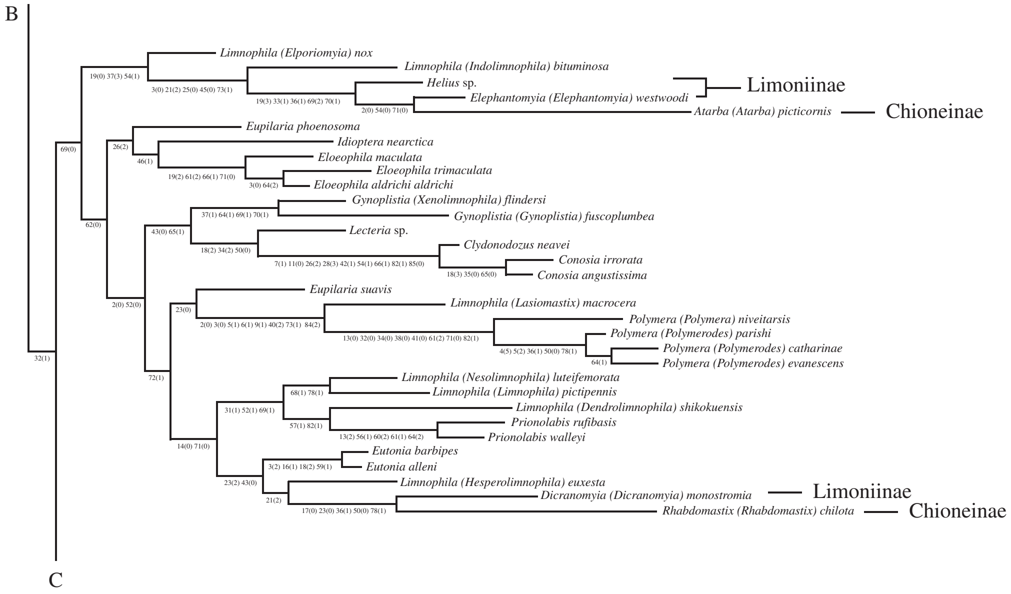

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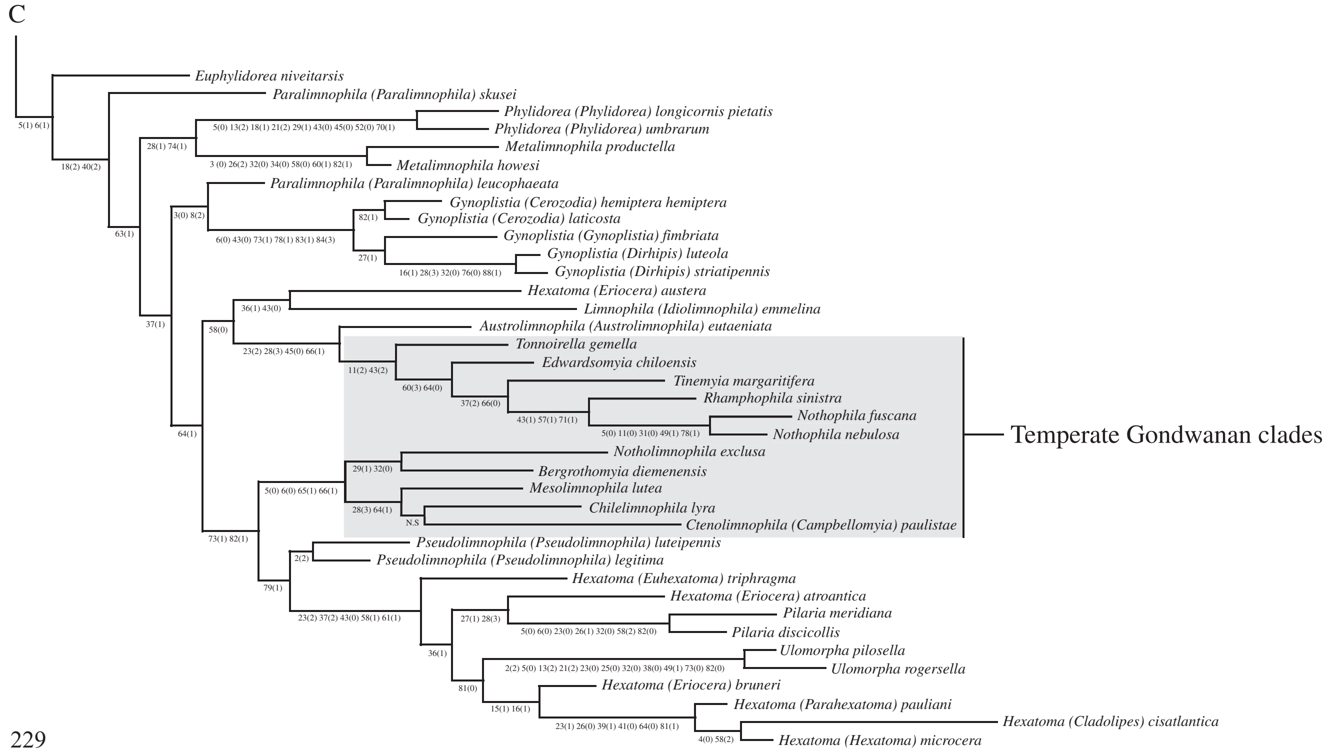
Figs 227–229. Analysis of the complete matrix with the monophyly of Cylindrotomidae constrained. Fittest tree (k = 6; length = 989; *CI* = 0.145) and preferred phylogenetic hypothesis. Branch lengths are proportional to the number of transformations (synapomorphies and autapomorphies). Autapomorphic transformations are omitted. The abbreviation N.S. at the base of the (*Chilelimnophila* + *Ctenolimnophila*) clade means no unequivocal apomorphic character support.



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Figs 227–229. (*continuted*)

(*Chilelimnophila* + *Ctenolimnophila*))) clade in the preferred tree is the area between the anterior and posterior margins of the clasper of gonostylus serrated (Character 65, state 1) (Figs 80, 85, 124).

The sister-group relationship between *Notholimnophila* and *Bergrothomyia* is supported in the preferred tree by two characters of wing venation, the less homoplastic of which is the presence of a spur or projection near the base of vein Rs (Character 29, state 1).

The monophyly of the clade including (*Mesolimnophila* + (*Chilelimnophila* + *Ctenolimnophila*))) is supported in the preferred tree by two unambiguous synapomorphies, the relatively more robust being the distal portion of the anterior margin of the clasper of gonostylus slightly serrated (Character 64, state 1). The recovered sister-group relationship between *Chilelimnophila* and *Ctenolimnophila* is particularly fragile, for there is no unambiguous synapomorphies supporting this pattern in the preferred tree.

Non-monophyletic genera and subgenera

Several genera and subgenera traditionally recognised appear as non-monophyletic according to the present study.

Neolimnomyia includes over 30 species in the Palearctic, Nearctic and Afrotropical regions and three subgenera. Two subgenera, the typical subgenus and *N.* (*Brachylimnophila*), were incuded in the study. The monophyly of the genus is not recovered by any of the performed analyses, and the position of *N.* (*Neolimnomyia*) *filata* is quite variable. However, a clade formed by (*Neolimnomyia* (*Brachylimnophila*) *nemoralis* + *Limnophila* (*Dicranophragma*) *fuscovaria*) is always recovered. The unambiguous synapomorphies of this clade are the petiole of cell m1 longer than vein M_1 (Character 37, state 3) and the distal part of the interbase rounded and dilated after a sub-apical constriction (Character 80, state 1). The general morphology of the male genitalia in both species (Figs 89, 90, 163, 164) is very similar. It may include potential apomorphic characters not scored in this study, but several of the similarities shared by both taxa are plesiomorphies, such as the well developed lateral processes of the aedeagal sheath. Additionally, both taxa share long macrotrichia along the wing veins, but this character was not scored in this study, so its status as a possible synapomorphy is unknown. Only a more detailed revision of the included species of *L.* (*Dicranophragma*) and *Neolimnomyia* will be able to define generic and subgeneric limits more satisfactorily.

Limnophila, with 15 subgenera and over 200 species worldwide, is one of the largest genera within the Tipulomorpha. Eleven subgenera of *Limnophila* were included in the present study. The heterogeneity and artificiality of *Limnophila* has been previously recognised by Alexander (e.g. Alexander 1924, 1929) and several taxa now included in other genera were previously described as *Limnophila* species. All the trees obtained by this study has pointed to the paraphyly of this genus.

Gynoplistia is a diverse genus with over 300 species and four subgenera. The group is mostly distributed in southern temperate regions of the world (Southern South America, New Zealand and

Australia), but three species of the typical subgenus are also known from the Oriental region. Representatives of the four recognised subgenera were included in this study. The genus *Gynoplistia* is considered as non-monophyletic in most of the different analyses performed here. In the preferred tree, part of the typical subgenus form a clade with the subgenus *G.* (*Xenolimnophila*) (Fig. 228), while other part is well included in the clade containing the subgenera *G.* (*Cerozodia*) and *G.* (*Dirhipis*) (Fig. 229).

Hexatoma includes six subgenera, of which only *H.* (*Coreozelia*) is not included in this study. *Hexatoma* is one of the largest genera of the Diptera with over 600 species and is present in all biogeographical regions. The non-monophyly of *Hexatoma* is demonstrated in this study by all the analyses performed, and in the preferred tree, the genera *Pseudolimnophila*, *Ulomorpha* and *Pilaria* are nested within it. The non-monophyly of the large and morphologically diverse subgenus *H.* (*Eriocera*) is also demonstrated. The subgenera *H.* (*Cladolipes*), *H.* (*Hexatoma*) and *H.* (*Parahexatoma*), however, are morphologically well defined groups, and appear forming a clade in the fittest trees of all the different analyses. The monophyly of this clade in the preferred tree is supported by several unambiguous synapomorphies, the most robust (least homoplastic) of which being the non-bifurcated vein M_{3+4} (Character 39, state 1), the loss of the discal cell (Character 41, state 0), the distal portion of the anterior margin of the clasper of gonostylus smooth (Character 64, state 0) as a reversal evolved from a serrated condition, and the lateral branch of the interbase longer than the medial branch (Character 81, state 1; inapplicable in *Cladolipes*). The absence of the discal cell shared by these groups was already pointed out by Ribeiro (2005) as a possible indication of their close relationships. The position of each subgenus can change, however, depending on the set of parameters considered. In the preferred tree, their interrelationships are (*Parahexatoma* + (*Cladolipes* + *Hexatoma sensu stricto.*)). The sister-group relationship between *H.* (*Cladolipes*) and *H.* (*Hexatoma*) is corroborated in the preferred tree by two unambiguous synapomorphies: the further reduction in the number of flagellomeres from 6 to 5 (Character 4, state 0) and the clasper of gonostylus glabrous (Character 58, state 2), evolved from a slightly hairy gonostylus (i.e. gonostylus with minute hairs, normally at its base: Character 58, state 2).

A few considerations of some 'problematic' taxa

This study included representatives of some taxa that have been traditionally difficult to place. The inclusion of these taxa was mainly designed to test their possible affinities of members of the Limnophilinae. However, since the phylogenetic results obtained in this study are very instable in general, fixing their systematic position more confidently could not yet be attained. Nevertheless, the character analysis does provide a glimpse of the evolutionary transformations leading to some of the distinguished morphological features of these taxa.

Dactylolabis

Dactylolabis includes four subgenera, and is the only genus of the subfamily Dactylolabidinae (Oosterbroek 2008). Traditionally, *Dactylolabis* was part of the Limnophilinae. Starý (1992) raised its status to subfamily, based on the result of his phylogenetic study (Fig. 1) in which *Dactylolabis* is the sister-group to the other Limoniidae.

The unusual morphological features of *Dactylolabis* refer mostly to the structure of the male genitalia, including the fleshy gonostylus (Fig. 98), uncommon within the Limoniidae. In the context of the present study, this genus does not form a very long branch, with only three unambiguous synapomorphies supporting its monophyly in the preferred tree (Fig. 227).

Starý (1992) considered the strong sclerotisation of the so called outer gonostylus a synapomorphy of the Limoniidae except *Dactylolabis*. The outer gonostylus of the Limoniidae corresponds to what is referred to in this paper as the clasper of gonostylus (for a detailed discussion on the homology problems related to the terms inner and outer gonostyli, and the reasoning for adopting a new terminology, see Ribeiro 2006). The relative degree of sclerotisation of this structure is quite variable within the Limoniidae, and this character is coded here as including four character states (Character 60, states 0–3). The present study indicates that a strongly sclerotised clasper of gonostylus is most likely plesiomorphic for the Tipulomorpha except Pediciidae. For all taxa in which a less sclerotised clasper is present, as for instance *Dactylolabis*, *Metalimnophila* and *Euphylidorea*, the phylogeny favors the interpretation that such conditions are due to a secondary modification of the plesiomorphic condition.

Elephantomyia, Helius *and* Atarba

The systematic position of the genus *Elephantomyia* has been traditionally problematic. An examination of the different opinions on this issue is given by Ribeiro and Amorim (2002).

The unusual features of this genus include the greatly elongated rostrum (Character 11, state 3), which bears the month parts at its tip, and the reduced radial sector, which is composed of only two elements reaching the wing margin, R_{2+3} and R_{4+5}.

Alexander (1948*b*) was probably the first author to suggest the close proximity between *Elephantomyia* and *Helius*, on the basis of the lengthened rostrum, shared between *Elephantomyia* and some *Helius* species, and the overall similarities in the male genitalia in both genera. This view was reinforced by other authors, such as Savchenko (1983), and Ribeiro and Amorim (2002). Although not recovered by most of the analyses, the sister-group relationship between *Elephantomyia* and *Helius* is supported by the analysis of the reduced matrix (Fig. 225). In the preferred tree, however, *Atarba* is the sister-group of *Elephantomyia* in the clade (*Helius* + (*Elephantomyia* + *Atarba*)).

The unambiguous synapomorphies supporting this clade in the preferred tree are the narrow distance, dorsally, between the eyes (Character 19, state 3), the vein R_{2+3} non-bifurcated (Character 33, state 1), vein M_{1+2} non-bifurcated (Character 36, state 1), the anterior margin of the aedeagus apodeme situated well anterior to the level of the anterior margin of paramere (Character 69, state 2) and the aedeagus apodeme much wider than the aedeagus (Character 70, state 1).

The genus *Atarba* can occur in different places of the cladogram depending on the analytical parameters considered. For instance, *Atarba* appears as the sister-group of the Tipulidae in all the unconstrained analyses of the complete matrix (see consensus tree of Fig. 224). The sister-group relationship between *Atarba* and *Elephantomyia* in the preferred tree is supported by three unambiguous synapomorphies: scape almost as long as high in lateral view (Character 2, state 0), the terminal gonostylus (Character 54, state 0; as in the ground plan, but interpreted as a reversal from a subterminal gonostylus), and the well developed lateral processes of the aedeagal sheath (Character 71, state 1; as in the ground plan, but again interpreted as a reversal).

The position of *Atarba* as sister-group of *Elephantomyia* in the preferred tree is considered here as very unlikely. One of the characters supporting this grouping (Character 2) is very homoplastic (20 steps in the preferred tree). The terminal gonostylus (Character 54, state 0) is likely the plesiomorphic condition for Tipulomorpha. Several *Elephantomyia* species have a subterminal gonostylus, but many have a terminal gonostylus, which is probably plesiomorphic for the genus. In any case, this character is quite variable within the genus. The presence of well developed lateral processes of the aedeagal sheath is also plesiomorphic. This character has only 8 steps in the preferred tree, and in all other nodes its transformation involves the loss of the lateral processes (a change from state 0 to 1). The only place in the preferred tree where a reversal of this character occurs (from 1 to 0) is at the base of the (*Elephantomyia* + *Atarba*) clade.

In *Atarba*, as in many other Chioneinae genera, the mesothoracic meron is attached to the other sclerites of the thorax (Character 51, state 1). Crampton (1925) considered this condition as the key character in defining the Chioneinae (in his paper, Eriopterini), and it seems more likely, on the basis of this character, that *Atarba* is more closely related to some Chioneinae subgroup than to any of the Limnophilinae genera included in this study. However, the fusion of the mesothoracic meron to the other thoracic sclerites had evolved independently in other families, as in Trichoceridae (*Trichocera*) and Tanyderidae (*Protoplasa*).

Final comments

> '. . .*people who inquire without first stating the difficulties are like those who do not know where to go; besides, a man does not otherwise know even whether he has found what he is looking for or not; for the end is not clear to such a man, while to him who has first discussed the difficulties it is clear.*'
>
> Aristotle, Metaphysics. Quoted in Edward Grant: A history of Natural Philosophy, from the ancient world to the nineteenth century. Cambridge University Press 2007, p. 46.

This study was mainly designed to solve relationships among the genera and subgenera of the Limnophilinae, and to illuminate their possible affinities with other crane fly lineages, in particular the families Pediciidae, Tipulidae and Cylindrotomidae, bringing some light to the understanding of the early patterns of diversification of the Tipulomorpha *sensu stricto*. But still, this is the most comprehensive cladistic analysis of the Tipulomorpha ever made, and only the second study to infer the group's phylogeny using the characters of imago. In many respects, the results conflict with the previous studies by Oosterbroek and Theowald (1991) and Starý (1992). This is no surprise, however, given the enormous difference in taxonomic sampling, which is much larger here than in the previous studies. Prior to this paper, the largest phylogenetic study of the Tipulomorpha was that by Oosterbroek and Theowald (1991), based on characters of immature stages, but the largely qualitative approach of that study contrasts with the quantitative (numerical) approach adopted here, making it difficult a straightforward comparison between the results obtained in each study. However, the background knowledge generated by previous studies, in particular concerning the family-level relationships, was very useful in guiding the tree-search strategies employed here in order to find the combination of analytical parameters leading to a most parsimonious solution. It also helped the interpretation and evaluation of the highly conflicting results.

This study brings no simple, definitive conclusions about the lower or higher-level relationships of crane flies, and this is due to many reasons. The dataset based on Tipulomorphan external adult male morphology is extremely homoplastic and this explains the disagreements among the results yielded by different analytical parameters. However, the results obtained here must be used as working hypotheses on which future studies can be based, even though a more complete and stable picture of the lower and higher-level phylogeny of the Tipulomorpha will still demand several years of investigations.

This study began with the specific premises that the Limnophilinae included some of the earliest lineages of Tipulomorpha, and that the understanding of the early patterns of crane fly diversification would necessarily depend on a closer view of this heterogeneous group. In part, these premises held true. But a much larger taxonomic sampling is necessary, not only to include other Limnophilinae genera and subgenera, but also more taxa of the subfamilies Chioneinae and Limoniinae. An increased taxonomic sample will undoubtedly influence our understanding of the early pattern of diversification in the Tipulomorpha.

A larger character sampling is also necessary. No information was scored from the females and thoracic morphology was virtually neglected by this study. A detailed study of thoracic sclerites may reveal characters that could help to stabilise relationships within clades of intermediate levels of generality.

The implications of this study to the phylogenetic classification of the Tipulomorpha transcend different levels. It indicates that several genera and subgenera, including some of the most diverse such as *Limnophila* and *Hexatoma*, are not monophyletic. Raising the status of some subgenera to the genus level will be a natural advancement, but this would require further studies including a more representative sampling of the taxa under consideration.

If Cylindrotomidae, Pediciidae and Tipulidae are to be considered as distinct families, several new families must be erected for subgroups of Limoniidae. However, proposing a new classification for the Tipulomorpha on the basis of the results presented here would be too precipitate.

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Appendix 1. List of examined specimens (ingroup and outgroup) in alphabetical order of genus and subgenus

Label information in italics. Information of different labels separated by '/'. Added notes within brakets. Depositaries within square brakets. Each entry is a different specimen

Mecoptera
Bittacus strigosus Hagen, 1861. Male. *N.Y.: Tompkins Co. Ithaca – Six Mile Creek just above Van Natta's Dam/Bittacus strigosus Hagen, 1861, Det. RGBeard 1968.* [MZSP]
Thyridates pintoi (Souza Lopes & Mangabeira, 1942). Male. *Barra do Tapirapé, Mato Grosso, Brasil, XI. 1964, B. malkin col./B. pintoi*. [MZSP]

Tanyderidae
Protoplasa fitchii Osten Sacken, 1859. Male. *Baddeck, N.S., 2.vii.1936/Protoplasa fitchii Det. H. J. Teskey 1988.* [DBRP]

Trichoceridae
Diazosma sp. Male. *Vancouver, B.C. 20.v.30, N. Leech/Trichoceridae, Diazosma* sp. [USNM]
Trichocera bimacula Walker, 1848. Male. *Atlanta, Ca. XI-17 1975, H. D. Pratt/Trichocera bimacula Det. H. D. Pratt, 1975.* [USNM]
Trichocera bimacula Walker, 1848. Male. *Atlanta, Ca. XI-28 1975, H. D. Pratt/Trichocera bimacula Walker Det. H. D. Pratt, 1975/Light trap* [USNM]

Cylindrotomidae
Cylindrotoma distinctissima (Meigen, 1818). Male. *FRANCE 06, 23km N SOSPEL, 14.VI.1997, 1500M, pine forest. P. Oosterbroek & C. Hatveld.* [ZMAN]
Cylindrotoma distinctissima (Meigen, 1818). Male. *FRANCE 06, 23km N SOSPEL, 14.VI.1997, 1500M, pine forest. P. Oosterbroek & C. Hatveld.* [ZMAN]
Stibadocerella albitarsis (de Meijere, 1919). Male. *SARAWAK: Mt. Dulit, 4.000ft. Moss forest, 25.x.1932./Oxford Univ. Exp. B.M.Hobby & A.W.Moore., B.M.1933-254.* (Specimen identified by F.W Edwards at no specified date). [BMNH]
Triogma trisulcata (Schummel, 1829). Male. *DE WIEDEN Ov., 4km Z Wanneperveen, Sphagnum tnilveen en moerasbos, 24 IV 1995, P. Oosterbroek.* [ZMAN]
Triogma trisulcata (Schummel, 1829). Male. *DE WIEDEN Ov., 4km Z Wanneperveen, Sphagnum tnilveen en moerasbos, 24 IV 1995, P. Oosterbroek.* [ZMAN]

Pediciidae
Malaisemyia manipurensis Alexander, 1964. Male. Paratype. *INDIA – ASSAN, MANIPUR, FERNAND SCHIMID/Sirhoi Kashong, 6000, VI-6. 60.* [USNM]
Malaisemyia manipurensis Alexander, 1964. Male. Paratype. *INDIA – ASSAN, MANIPUR, FERNAND SCHIMID /Hkayam Boum, 7500, VI-13. 60.* [USNM]
Pedicia sp. Male. *Pedicia (P) margarita. Det. M. J. Petersen, 2002.* [ISU]
Tricyphona calcar. Male. *USA: NC: Havwood Co., Great Smoky Mtns. NP. Swallow Fork Tr. 960m, 35°43′N 83°09′E, coll. MJ.Petersen, 12-May-05.* [ISU]
Tricyphona calcar. Male. *USA: NC: Havwood Co., Great Smoky Mtns. NP. Swallow Fork Tr. 960m, 35°43′N 83°09′E, coll. MJ.Petersen, 12-May-05.* [ISU]

Tipulidae
Leptotarsus (Longurio) gymnocerus (Alexander, 1938). Male. Paratype. *Marambaia, S. Brazil, 1100m, X II-2. 35. Zikan/Macromastix gymnocera.* [USNM]
Leptotarsus (Longurio) gymnocerus (Alexander, 1938). Male. Paratype. *Marambaia, S. Brazil, 1100m, X II-2. 35. Zikan./Macromastix gymnocera.* [USNM]
Ptilogyna sp. Male. *Brasil, SP. Salesópolis, E. B. Boracéia, Ponte Rio Claro, 14-xii-2003. G. C. Ribeiro/Ptilogyna* sp. *Det. G. C. Ribeiro, 2005.* [DBRP]
Ptilogyna sp. Male. *Brasil, SP. Salesópolis, E. B. Boracéia, Ponte Rio Claro, 14-16 xii-2003, luz. G. C. Ribeiro/Ptilogyna* sp. *Det. G. C. Ribeiro, 2005.* [DBRP]
Zelandotipula novarae (Schiner, 1868). Male. *NEW ZEALAND: Auckland, Mataitai Clevedon, 19 March, 1931. Pritchard.* [USNM]
Zelandotipula novarae (Schiner, 1868). Male. *NEW ZEALAND: Auckland, St. Heliers, 27 Oct. 1930, A. T. Pyaoft/Zelandotipula novorae (Schiner). det Alexander, 33.* [USNM]

Limoniinae
Elephantomyia (Elephantomyia) westwoodi Osten Sacken, 1869. Male. *Lost River, NH, July, 1931, A. L. Melander/ALMelander Collection 1961/Elephantomyia westwodi O. S. Det. C. P. Alexander.* [USNM]
Elephantomyia (Elephantomyia) westwoodi Osten Sacken, 1869. Male. *White Mts, NH, Dolly Copp, 15 Jully '31, Alexander/ALMelander Collection 1961/ Elephantomyia westwoodi O. S. Det. C. P. Alexander.* [USNM]
Helius sp. Male. *Brasil, SP, 30/x/2000, P. E. Intervales, 'Roda d'água', Puçá, Ribeiro, G. C. col.* [DBRP]

Chioneinae
Atarba picticornis Osten Sacken. *2E Helock For., Gatlinburg, Tenn, G3MNP 4000, NE, Sweeps 29 Jun '47, R. H. Whittaker/Atarba picticornis O. S., Det. C. P. Alexander, 1950.* [USNM]
Atarba picticornis Osten Sacken. Male. *Belchertown, Mass., 900', VI-17, '33, F. K. Show/Atarba picticornis O. S., Det. C. P. Alexander, 1933.* [USNM]
Atarba picticornis Osten Sacken. Male. *Falls Church, Va., Rolmes Run, 5-IX-1960, W. W. Wirth, ligth trap.* [USNM]
Rhabdomastix chilota Alexander, 1929. Male. *Chile, Chiloe I. Chaiten, II-5/8, 54. Peña/Rhabdomastix chilota Det. C. P. Alexander, 1968.* [MZSP]

Dactylolabidinae
Dactylolabis (Dactylolabis) cubitalis (Osten Sacken, 1869). Male. *Knoxville, Tenn. Apr. 21, 38, A. C. Cale/Dactylolabis cubitalis (O. S.), Det. C. P. Alexander, 1940.*
Dactylolabis (Dactylolabis) cubitalis (Osten Sacken, 1869). Male. *Beebe Lake, Ithaka, N.Y., V. 28. II/Dactylolabis cubitalis (O. S.), Det. C. P. Alexander, 1925.*
Dactylolabis (Dactylolabis) montana (Osten Sacken, 1860). Male. *New Richmond, S. Gaspe, Que., VII – I, '31, Alexander/Dactylolabis montana (O.S.), Det. C. P. Alexander, 1931.* [USNM]
Dactylolabis (Dactylolabis) montana (Osten Sacken, 1860). Male. *Niagra Glen, Ont., I-VI- 1926, G. S. Walley/Dactylolabis montana (O. S.), Det. C. P. Alexander, 1926.* [USNM]

Limnophilinae
Acantholimnophila bispina (Alexander, 1922). Male. *Rewanvi, New Zealand, II – 15 '23, T. R. Harris/Acantholimnophila bispina (Al.), Det. C. P. Alexander, 1923.* [USNM]
Acantholimnophila maorica (Alexander, 1922). Male. Paratype. *Dunedin, N. Z., Nov. 26, 1921, Geo Howes.* [USNM]
Acantholimnophila maorica (Alexander, 1922). Male. Paratype. *Dunedin, N. Z., Nov. 26, 1921, Geo Howes.* [USNM]

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Acantholimnophila maorica (Alexander, 1922). Male. Paratype. *Dunedin, N. Z., Nov. 26, 1921, Geo Howes.* [USNM]

Austrolimnophila eutaeniata (Bigot, 1888). Male. *Cayutue, S. Chile, V-18 '39, Wolffhügel/Austrolimnophila eutaeniata (Bigot), Det. C. P. Alexander.* [USNM]

Bergrothomyia diemenensis Alexander, 1928 Male. Paratype. *G. H. Hardy, Zeehan, Feb. 1924.* [USNM]

Bergrothomyia diemenensis Alexander, 1928 Male. Paratype. *G. H. Hardy, Zeehan, Feb. 1924.* [USNM]

Chilelimnophila lyra (Alexander, 1952). Male. *Chile, Curacautin, Rio Blanco, 15–29 January, 1959/Chielimnophila lyra (Alexander), Det. G. C. Ribeiro, 2004.* [USNM]

Chilelimnophila lyra (Alexander, 1952). Male. *Chile, Curacautin, Rio Blanco, 15–29 January, 1959/Chielimnophila lyra (Alexander), Det. G. C. Ribeiro, 2004.* [USNM]

Clydonodozus neavei Alexander, 1920. Male. *Lubumbashi, KatangaBCgo, 11, 45S. 27, 40E., Jan. 8, 1921/Mich. Bequaert Coll./Clydonodozus neavei Alex. Det. C. P. Alexander, 1922.* [USNM]

Conosia angustissima (Alexander, 1927). Male. Paratype. *Fernando Poo, Umbeg. v. Moca, 8.11.61, W. Hartwig leg.* [USNM]

Conosia angustissima (Alexander, 1927). Male. Paratype. *Fernando Poo, Umbeg. v. Moca, 14.11.61, W. Hartwig leg.* [USNM]

Conosia irrorata (Wiedemann, 1828). Male. *Madagascar, Rogez Dist., 900m, VII-1946, Lamberton/Conosia irrorata (Wd), Det. C. P. Alexander, 1953.* [USNM]

Conosia irrorata (Wiedemann, 1828). Male. *Madagascar, Rogez Dist., 900m, VII-1946, Lamberton/Conosia irrorata (Wd), Det. C. P. Alexander, 1953.* [USNM]

Ctenolimnophila paulitae Alexander, 1943. Male. *Brasilien, Nova Teutonia, 27°11′B 52°23′L, X-3-1944, Fritz Plaumann/Ctenolimnophila paulitae Al., Det. C. P. Alexander, 1967.* [USNM]

Ctenolimnophila paulitae Alexander, 1943. Male. *Brasilien, Nova Teutonia, 27°11′B 52°23′L, X-16-1944, Fritz Plaumann/Ctenolimnophila paulitae Al., Det. C. P. Alexander, 1967.* [USNM]

Edwardsomyia chiloensis Alexander, 1929. Male. Paratype. *Ancud, Chile, Dec. 18, '26, Shannon.* [USNM]

Edwardsomyia chiloensis Alexander, 1929. Male. *S. Chile, Chiloe I. Aucar, I-6/15. 52, Peña/Edwardsomyia chiloensis Al. Det. C. P. Alexander, 1953.* [USNM]

Eloeophila aldrichi aldrichi (Alexander, 1927). Male. Paratype. *Banff, Alta., 30.VII.1922, C. B. D. Garrett.* [USNM]

Eloeophila aldrichi aldrichi (Alexander, 1927). Male. *Wash, Mt Baker, Silver Fir Cp., 1800, VIII-13, 47, Alexander/Limnophila aldrichi Al. Det. C. P. Alexander.* [USNM]

Eloeophila maculata (Meigen, 1804). Male. *Silkeborg, 3. 8.* (??)/*Ephelia marmorata Meig.* [USNM]

Eloeophila maculata (Meigen, 1804). Male. *Eph. Marmorata Mg./Denmark, Est. Call, Staeger.* [USNM]

Eloeophila maculata (Meigen, 1804). Male. *Hagl/Sweden/Ephelia marmorata Mg.* [USNM]

Eloeophila trimaculata (Zetterstedt, 1838). Male. *MORAVIA, 4. 7. 1968, Pradea B. Opava, J. Starý leg./L. (Eloeophila) trimacula (Zett.)*, *J. Starý det. 1971.* [USNM]

Epiphragma (Epiphragma) fasciapenne (Say, 1823). Male. *Glen Echo Md, May 14 1922/JRMalloch, Collector.* [USNM]

Epiphragma (Epiphragma) fasciapenne (Say, 1823). Male. *Peekskill NY, 11 June 1927, A. L. Melander/A. L. Melander Collection 1961/ Ephiphragma fascipennis (Say). Det. C. P. Alexander 1946.* [USNM]

Epiphragma (Epiphragma) nigripleuralis Alexander. Male. Paratype. *N. Teutonia, Brazil, Oct. 17 '35, Plaumann.* [USNM]

Epiphragma (Epiphragma) nigripleuralis Alexander. Male. Paratype. *N. Teutonia, Brazil, Oct. 17 '35, Plaumann.* [USNM]

Euphylidorea niveitarsis (Osten Sacken, 1869). Male. Paratype. *Cinchona, S. India, Anamalai Hills, 4000-5000ft. IX-2 1946. P. Susai Nathan*. [USNM]

Euphylidorea niveitarsis (Osten Sacken, 1869). Male. Paratype. *Cinchona, S. India, Anamalai Hills, 4000-5000ft. IX-2 1946. P. Susai Nathan*. [USNM]

Euphylidorea niveitarsis (Osten Sacken, 1869). Male. Paratype. *Cinchona, S. India, Anamalai Hills, 4000-5000ft. IX-2 1946. P. Susai Nathan*. [USNM]

Eupilaria phoenosoma (Alexander, 1931). Male. Paratype. *Ube, PI, Feb. 11, '30, Rivera/Pilaria phoenosoma.* [USNM]

Eupilaria phoenosoma (Alexander, 1931). Male. Paratype. *Ube, PI, Feb. 11, '30, Rivera/Pilaria phoenosoma.* [USNM]

Eupilaria phoenosoma (Alexander, 1931). Male. Paratype. *Ube, PI, Feb. 11, '30, Rivera/Pilaria phoenosoma.* [USNM]

Eupilaria phoenosoma (Alexander, 1931). Male. Paratype. *Ube, PI, Mar.3, '30, McGregor/Pilaria phoenosoma.* [USNM]

Eupilaria suavis Alexander, 1949 (USNM 273-276)

Eutonia alleni (Johnson, 1909). Male. *Brookview, N. Y., VI-21, '23, Alexander/Limnophila alleni John, Det. C. P. Alexander, 1935.* [USNM]

Eutonia alleni (Johnson, 1909). Male. *Great Falls, May, 23. 18 VA/W L Mc Atee, Collector/Limnophila alleni John, Det. C. P. Alexander.* [USNM]

Eutonia barbipes (Meigen, 1804). Male. *Hilversum, deMeijere, VI. II./Eutonia barbipes Mg.* [USNM]

Eutonia barbipes (Meigen, 1804). Male. *Moravia 14. 6. 1970, Moravicani, J. Starý leg./L. (Eutonia) barbipes (Meig.), J. Starý det. 1971.* [USNM]

Gynoplistia (Cerozodia) hemiptera hemiptera (Alexander, 1922). Male. Paratype. *Mt. Ruapehu, N. Z., Alpine Zone, January 1921, M. N. Watt.* [USNM]

Gynoplistia (Cerozodia) hemiptera hemiptera (Alexander, 1922). Male. *Ohakune, to, hurt on Ruapeliu, New Zealand, 3000–4500 ft. Jan. 12, 1923, T. R. Harris./Cerozodia hudsoni Ed. var. hemiptera Al. Det. C. P. Alexander, 1923.* [USNM]

Gynoplistia (Cerozodia) laticosta Alexander, 1930. Male. Holotype. *Glenorchy, N. Zeal., 2500 ft., Jan- 1, 25, F. S. Oliver.* [USNM]

Gynoplistia (Cerozodia) laticosta Alexander, 1930. Male. Paratype. *Glenorchy, N. Zeal., 2500 ft., Jan- 1, 25, F. S. Oliver.* [USNM]

Gynoplistia (Dirhipis) luteola Alexander, 1971. Male. *Chile, Osorno, Pucatrihue, Feb. 5, '68*, *Salgado en Peña./Gynoplistia luteola Al. Det. C. P. Alexander, 1968.* [USNM]

Gynoplistia (Dirhipis) striatipennis Alexander, 1971. Male. *Puerto Varas, S. Chile, Jan. '33* (1933), *L. Read./Gynoplistia striatipennis Al. Det. C. P. Alexander, 1933.* [USNM]

Gynoplistia (Dirhipis) striatipennis Alexander, 1971. Male. *Chile, Malleco, Nahualbuta*, *Cabreria, 1100 m, I.* (January) *9/15 '77* (1977)*, Luis Pena./ Gynoplistia striatipennis Al. Det. C. P. Alexander.* [USNM]

Gynoplistia (Gynoplistia) fimbriata Alexander, 1920. Male. *Ohakune, N. Z., Alt. 2060 ft., Nov. 16 1921, T. R. Harris/Gynoplistia fimbriata Alex. Det. C. P. Alexander, 1923.* [USNM]

Gynoplistia (Gynoplistia) fimbriata Alexander, 1920. Male. *Ohakune, N. Z., Alt. 2060 ft., Dec. 9 1922, T. R. Harris/Gynoplistia fimbriata Al. Det. C. P. Alexander, 1923.* [USNM]

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Gynoplistia (Gynoplistia) fuscoplumbea Edwards, 1923. Male. *Ohakune, N. Z., Alt. 2060 ft., Oct. 309 1921, T. R. Harris*/*Gynoplistia fuscoplumbea Edw. Det. C. P. Alexander, 1922.* [USNM]

Gynoplistia (Xenolimnophila) flindersi Alexander, 1931. Male. *Beech Forest, Vic., 11–19 Jan. 1932, F. E. Wilson./Gynoplistia flindersi Al. Det. C. P. Alexander, 1932.* [USNM]

Gynoplistia (Xenolimnophila) flindersi Alexander, 1931. Male. Paratype. *Flinders Isl., Tas., Miss. Wood.* [USNM]

Hexatoma (Cladolipes) cisatlantica Alexander, 1937. Male. Holotype. *Brasilien, Nova Teutonia, Fritz Plaumann.* [USNM]

Hexatoma (Eriocera) atroantica Alexander, 1957. Male. Paratype. *S. India Anamalai Hills, Cinchona, 3500*, *V-1956, S. Nathan.* [USNM]

Hexatoma (Eriocera) austera (Doane, 1900). Male. Paratype. (No information on locality) *ALMelander Collection 1961.* [USNM]

Hexatoma (Eriocera) bruneri (Alexander, 1928). Paratype. *Jarahuenca, Oriente, Cuba, VII-15, '27, S. C. Bruner.* [USNM]

Hexatoma (Euhexatoma) triphragma Alexander, 1936. Male. Holotype. *Liamui Hainan,429 met. VII-31, 35* (1935)*, Gressitt.* [USNM]

Hexatoma (Hexatoma) microcera Alexander, 1926. Male. Paratype. *Amer. Bor. Alte Sammlung.* [USNM]

Hexatoma (Parahexatoma) pauliani Alexander, 1951. Male. Paratype. *Madagascar, Mont Tsaratanana, 1300 m, Oct. 49*, *Paulian.* [USNM]

Idioptera nearctica (Alexander, 1966). Male. Paratype. *Aklavik, N. W. T., July 15 1931, Bryant, Lot. 249.* [USNM]

Idioptera nearctica (Alexander, 1966). Male. Paratype. *Aklavik, N. W. T., July 8 1931, Bryant, Lot. 245.* [USNM]

Lecteria (Lecteria) sp. Male. *Pará, Braz., Apr. 1930. H. C. Davis*/*Lecteria armillaris (F), Det. C. P. Alexander, 1935.* [USNM]

Lecteria (Lecteria) sp. Male. *San Carlos, Costa Rica*/*Coll. Schild & Burgdorf*/*Lecteria armillaris Fabr.*/ *Det. C. P. Alexander, 1912.* [USNM]

Limnophila (Arctolimnophila) claggi Alexander, 1931. Male. Holotype. *Bobtail Cr. Grand Co., Col. 11000, VII-20 '29, C. F. Clagg.* [USNM]

Limnophila (Arctolimnophila) claggi Alexander, 1931. Male. *Mt. Ranier, Wash. 4700 ft., Jul. 11, 1940, H. & M. Townes/Limnophila claggi Alex., Det. C. P. Alexander, 1942.* [USNM]

Limnophila (Arctolimnophila) subcostata (Alexander, 1911). Male. Holotype. *Coy Glen, Inthaca, NY, May 21, 1911.* [USNM]

Limnophila (Arctolimnophila) subcostata (Alexander, 1911). Male. Paratype. *Coy Glen, Inthaca, NY, May 21, 1911.* [USNM]

Limnophila (Atopolimnophila) laricicola Alexander, 1912. Male. Holotype. *Canada Lake, Fulton Co., n.4., 1550 ft, June 20, 1911, (Alexander).* [USNM]

Limnophila (Atopolimnophila) laricicola Alexander, 1912. Male. *Stowe, Vt., June 20, '27, Alxander*/*Limnophila laricicola Al., Det. C. P. Alexander, 1927.* [USNM]

Limnophila (Atopolimnophila) laricicola Alexander, 1912. Male. *Stowe, Vt., June 20, '27, Alxander*/*Limnophila laricicola Al., Det. C. P. Alexander, 1927.* [USNM]

Limnophila (Dendrolimnophila) shikokuensis Alexander, 1953. Male. Holotype. *Japan, Sikoku, Nisigawa, Yanase, 600m, V-4 – 51, Issiki-Ito.* [USNM]

Limnophila (Dendrolimnophila) shikokuensis Alexander, 1953. Male. Paratype. *Japan, Sikoku* (not Shikoku)*, Nisigawa, Yanase, 600m, V-4 – 51, Issiki-Ito.* [USNM]

Limnophila (Dicranophragma) fuscovaria Osten Sacken, 1860. Male. *WEST VIRGINIA: Pendleton County, Seneca Rocks, 3Jul. 1983, black light, G. F. & J. F. Hevel.* [USNM]

Limnophila (Dicranophragma) fuscovaria Osten Sacken, 1860. Male. *Jackson Co., Fla., Marianna, IV – 13 – 1928, J. S. Rogers/Limnophila fuscovaria O. S., Det. J. S. Rogers 1930.* [USNM]

Limnophila (Elporiomyia) nox Alexander, 1921. *Witte River, Wellington, 1500 ft./Limnophila nox Al., Det. C. P. Alexander, 1923.* [USNM]

Limnophila (Elporiomyia) nox Alexander, 1921. *Witte River, Wellington, 1500 ft./Limnophila nox Alex., Det. C. P. Alexander, 1923.* [USNM]

Limnophila (Hesperolimnophila) euxesta Alexander, 1924. Male. Holotype. *Longmire Springs, Wash., June, 1917/H. G. Dyar, Coll.* [USNM]

Limnophila (Idiolimnophila) emmelina Alexander, 1914. Male. Holotype. *Great Falls, Fairfax 60; Va., April 20, '13, Fredk Knab.* [USNM]

Limnophila (Indolimnophila) bituminosa. Alexander, 1931. Male. Paratype. *MtApo, Phil. Is, 8000 ft., Sept. 19, 1930, C. F. Clagg*. [USNM]

Limnophila (Indolimnophila) bituminosa. Alexander, 1931. Male. Paratype. *MtApo, Phil. Is., 8000 ft., Sept. 19' 30, C. F. Clagg.* [USNM]

Limnophila (Indolimnophila) bituminosa. Alexander, 1931. Male. Paratype. *MtApo, Phil. Is., 8-9300 ft., Sept. 18' 30, C. F. Clagg.* [USNM]

Limnophila (Lasiomastix) macrocera (Say, 1823) Male. *Hensler's Wd., Hanover, 9 Md; VI-16'21, Alexander*/*Limnophila macrocera (Say), Det. C. P. Alexander, 1925*. [USNM]

Limnophila (Lasiomastix) macrocera (Say, 1823) Male. *Hensler's Wd., Hanover, Md; June 16'21, Alexander*/*Limnophila macrocera (Say), Det. C. P. Alexander, 1925*. [USNM]

Limnophila (Nesolimnophila) luteifemorata Alexander, 1963. Male. Paratype. *Madagascar, Maroantsetra, Ambodivoangy, Mar-'52, Paulian.* [USNM]

Limnophila pictipennis Meigen, 1818. Male. *Berlin, Grunewld., 8-97* (August 1897?)/*Limnophila pictipennis Det. Oldenberg.* [USNM]

Limnophila pictipennis Meigen, 1818. Male. *Riedel, Ürdingen*/*Poecilostola pictipennis Mg., det. M. P. Riedel.* [USNM]

Limnophila (Nesolimnophila) luteifemorata Alexander, 1963. Male Paratype. *Madagascar, Rogez Dist., 900m, Dec. 1946., Lamberton.* [USNM]

Mesolimnophila lutea (Philippi, 1865). Male. *Ancud, Chiloe, Id., Chile, Dec. 18, 1926. R. C. Shannon/Polymoria lutea Ph. Det. C. P. Alexander, 1928.* [USNM]

Mesolimnophila lutea (Philippi, 1865). Male. *Ancud, Chiloe, Id., Chile, Dec. 18, 1926. R. C. Shannon/Polymoria lutea Ph. Det. C. P. Alexander, 1928.* [USNM]

Mesolimnophila lutea (Philippi, 1865). Male. *Chile, Chiloe I. Dalcahue, Feb. 1954, Peña/Mesolimnophila lutea (Ph.). Det. C. P. Alexander, 1968.* [USNM]

Mesolimnophila lutea (Philippi, 1865). Male. *Chile, Chiloe I. Dalcahue, Feb. 1954, Peña/Mesolimnophila lutea (Ph.). Det. C. P. Alexander, 1968.* [USNM]

Metalimnophila howesi (Alexander, 1922). Male. Paratype. *Dunedin, N. Z., November 26, 1921, Geo. Howes.* [USNM]

Metalimnophila howesi (Alexander, 1922). Male. *Raetihi Hill, Ohakune, N. Z. 2800 ft. Nov. 30, '23, T. R. Harris/Limnophila howesi (Al.), Det. C. P. Alexander, 1924.* [USNM]

Metalimnophila howesi (Alexander, 1922). Male. *Ohakune, N. Z. Alt. 2060 ft. Nov. 14, 1922. T. R. Harris/Limnophila howesi Al. Det. C. P. Alexander, 1923.* [USNM]

Metalimnophila productella Alexander, 1926. Male. Paratype. *Dunedin, N. Z., November 26, 1921, Geo. Howes.* [USNM]

Metalimnophila productella Alexander, 1926. Male. Paratype. *Dunedin, N. Z., November 26, 1921, Geo. Howes.* [USNM]

Metalimnophila productella Alexander, 1926. Male. Paratype. *Dunedin, N. Z., November 26, 1921, Geo. Howes.* [USNM]

Neolimnomyia (Brachylimnophila) nemoralis (Meigen, 1818). Male. *Entrèves, Mt. de la Saxe, 1250m–1300m, 22-VII-1962.* [ZMAN]

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Appendix 1. (*continued*)

Neolimnomyia (Brachylimnophila) nemoralis (Meigen, 1818). Male. *Entrèves, Mt. de la Saxe, 1250m–1300m, 22-VII-1962.* [ZMAN]

Neolimnomyia (Neolimnomyia) filata (Walker, 1856). Male. *CZ: MORAVIA. 5. 6. 1997. Libavá env. Stará Voda, J. Stary, leg. (6271)/Neolimnomyia (s. str.) filata (Walker), J. Starý det. 2005.* [PU]

Notholimnophila exclusa (Alexander, 1922) . Male. *Ohakune, N. Z. alt. 2060 ft., Dec. 10, 1922, T. R. Harris/Limnophila exclusa Al., Det. C. P. Alexander, 1923.* [USNM]

Nothophila fuscana Edwards, 1922. Male. *Mt. Gray, N3, Canterbury* (New Zealand Adm. Region)*, 2000 ft, march 19, '22, J. W. Campbell/Nothophila fuscana (Ed), Det. C. P. Alexander, 1923.* [USNM]

Nothophila fuscana Edwards, 1922. Male. *New Zealand, No. Auckland, Swanson, Wilfred Long/Nothophila fuscana Ed. Det. C. P. Alexander, 1950.* [USNM]

Nothophila nebulosa Edwards, 1922. Male. *New Zealand, No. Auckland, Swanson, Wilfred Long/Nothophila nebulosa (Ed.), Det. C. P. Alexander, 1951.* [USNM]

Nothophila nebulosa Edwards, 1922. Male. *Wiltons Bush, Wellington. N. Z. Apr. 20, 1922, G. V. Hudson/COMPARED WITH TYPE MATERIAL, Nothophila nebulosa (Edw.), Det. Hudson 1922.* [USNM]

Nothophila nebulosa Edwards, 1922. Male. *Wiltons Bush, Wellington. N. Z. Apr. 20, 1922, G. V. Hudson/COMPARED WITH TYPE MATERIAL, Nothophila nebulosa (Edw.), Det. Hudson 1922.* [USNM]

Pachyneura sp. Male. *Japan, Hokkaido, Daisetsuzan Nt Pk, Yukomanpetsu 1100m, 2.VII.86. M. Wood.* [DBRP]

Paralimnophila englishae (Alexander). Male. Paratype. *Buckmaster's Crossing, Yass, N. S. W., Nov. 22, '33, K. English.* [USNM] [obs: synonym of *leuchophaeata* (Skuse, 1890)]

Paralimnophila englishae (Alexander, 1937). Male. Paratype. *Buckmaster's Crossing, Yass, N. S. W., Nov. 22, '33, K. English.* [USNM] [obs: synonym of *leuchophaeata* (Skuse, 1890)]

Paralimnophila skusei (Hutton, 1902). Male. *NEW ZEALAND: Auckland, Mercer Waikato, 19–25 March 1931, Pritchard.* [USNM]

Paralimnophila skusei (Hutton, 1902). Male. *Ohakune, N. Z., Alt. 2060 ft., Oct. 7, 1921. T. R. Harris/Limnophila skusei Hutt., Det. C. P. Alexander, 1922.* [USNM]

Paralimnophila skusei (Hutton, 1902). Male. *Ross, N. Z. Westland, Feb. 19, '13, T. R. Harris/Limnophila skusei Hutt., Det. C. P. Alexander, 1923.* [USNM]

Phylidorea (Phylidorea) longicornis pietatis (Alexander, 1950). Male. Holotype. *North Korea, Kankio Nando, Puksu Pyaksan/Alt. 500 ft., August 21, 1939, A. Yankovsky.* [USNM]

Phylidorea (Phylidorea) longicornis pietatis (Alexander, 1950). Male. Paratype. *North Korera, Kankio Nando, Puksu Pyaksan/Alt. 500 ft., August 21, 1939, A. Yankovsky.* [USNM]

Phylidorea (Phylidorea) megapygia (Alexander, 1938). Male. Paratype. *Chonsani, Paiktusan, N. Corea, 3500, VII-15, 37* (July 15, 1937)*, Yankovsky.* [Obs: junior synonym of *umbrarum* (Krogerus, 1937)]. [USNM]

Pilaria discicollis (Meigen, 1818). Male. *Hitchin, Herts, 5. VII, 1918, F. W. Edwards, 1919-63/Pilaria discicollis Mg., F. W. Edwards. Det. 1920.* [USNM]

Pilaria discicollis (Meigen, 1818). Male. Letchworth, Herts, VI, 1917, F. W. Edwards, 1919-63/*Pilaria discicollis Mg., F. W. Edwards. Det. 1920.* [USNM]

Pilaria meridiana (Staeger, 1840). Male. *Bozeman Mont, July 12, 1917/Collection DrHGDyar/Pilaria osborni (Al.), Det. C. P. Alexander, 1921.* [USNM 194]

Pilaria meridiana (Staeger, 1840). Male. *Czechoslovakia, Moravia, Moravicany, Sept. 2, 1972, J. Starý/Pilaria meridiana (Staeger), det. Starý.* [USNM]

Polymera (Polymera) niveitarsis Alexander, 1913. Male. Holotype. *Bocas d Toro*, *28 Sept. 03, Pan, POsterhount Collector*. [USNM]

Polymera (Polymera) niveitarsis Alexander, 1913. Male. Paratype. *Igarape Assu, Para, Brazil, Jan. 1912, H. S. Parish.* [USNM]

Polymera (Polymerodes) catharinae Alexander, 1931. Male. Holotype. *Jaraguá, Sta. Catarina, Brazil, Aug. 24 '29*, *F. Schade.* [USNM]

Polymera (Polymerodes) evanescens Alexander, 1948. Male. Holotype. *Brasilien, Nova Teutonia, 27° 11' B.52° 23' L., Fritz Plaumann, X-3-1944.* [USNM]

Polymera (Polymerodes) parishi Alexander, 1920. Male. Holotype. *Manaos, Brazil, Nov. 4, 1919, H. S. Prish.* [USNM]

Polymera (Polymerodes) parishi Alexander, 1920. Male. *Villarica, Paraguay, Feb. 18. '35. F. Schade.* [USNM]

Prionolabis rufibasis (Osten Sacken, 1860). Male. *Brookview, N.Y., VI-7 '23, Alexander/Limnophila rufibasis O. S., Det. C. P. Alexander.* [USNM]

Prionolabis rufibasis (Osten Sacken, 1860). Male. *Howley PENN, 30 May, '37, ALMelander/Limnophila rufibasis O. S., Det. C. P. Alexander, 1946.* [USNM]

Prionolabis rufibasis (Osten Sacken, 1860). Male. *Maywood Va, Alexandria Co, Apr. 27. 1919*/W. L. *Mc Atee Collector/Limnophila rufibasis O. S., Det. C. P. Alexander, 1919.* [USNM]

Prionolabis walleyi (Alexander, 1929). Male. *Smoky Mts., Tenn., Alt. 6400 ft. VII – 16 1939, Mss. J. Huff/Limnophila walleyi Al., Det. C. P. Alexander.* [USNM]

Prolimnophila areolata (Osten Sacken, 1860). Male. *Burke falls, Ont. 9.vii.1926, F.P.Ide/Limnophila areolata O.S., Det. C. P. Alexander, 1927.* [USNM]

Prolimnophila areolata (Osten Sacken, 1860). Male. *Woodworths Lake, Fulton Co. NY, Alexander/Limnophila areolata O.S. Det. C. P. Alexander, 1925.* [USNM]

Prolimnophila areolata (Osten Sacken, 1860). Male. *Hyattsville, 9.v.13 Md/Fredk Knab Collector/Limnophila areolata O. S.* [USNM]

Pseudolimnophila legitima Alexander, 1931. Male. Paratype. *Mt Apo, Phil Is, 6500 ft, Sep. 14 '30, C. F. Clagg.* [USNM]

Pseudolimnophila legitima Alexander, 1931. Male. Paratype. *Mt Apo, Phil Is, 6500 ft, Sep. 14 '30, C. F. Clagg.* [USNM]

Pseudolimnophila luteipennis (Osten Sacken, 1860). Male. *Orono, Me, 10 June '13/Pseudolimnophila luteipennis (O. S.), Det. C. P. Alexander, 1925.* [USNM]

Pseudolimnophila luteipennis (Osten Sacken, 1860). Male. *Spartanburg Co. S. Car., April 7, 1961./Limnophila luteipennis O. S.* [USNM]

Rhamphophilla sinistra (Hutton, 1900). Male. *Ohakune, N. Z., alt. 2060 ft., Dec. 10, 1922. T. R. Harris/Rhamphophilla sinistra (Hutt), Det. C. P. Alexander, 1923.* [USNM]

Rhamphophilla sinistra (Hutton, 1900). Male. *Ohakune, N. Z., alt. 2060 ft., Dec. 31, 1922. T. R. Harris/Rhamphophilla sinistra (Hutt), Det. C. P. Alexander, 1922.* [USNM]

Shannonomyia (Shannonomyia) brevinervis Alexander, 1929. Male. *Chile, Osorno, Pucatrihue, Apr. 10-12 '68, Peña/Shannonomyia brevinervis Al. Det. C. P. Alexander.* [USNM]

Shannonomyia (Shannonomyia) brevinervis Alexander, 1929. Male. *Chile Chiloe I. Chepu, iv-4/6 '68. Peña/Shannonomyia brevinervis Al. Det. C. P. Alexander.* [USNM]

Shannonomyia (Shannonomyia) brevinervis Alexander, 1929. Male. *Chile Chiloe I. Chepu, iv-4/6 '68. Peña/Shannonomyia brevinervis Al. Det. C. P. Alexander.* [USNM]

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Appendix 1. (*continued*)

Shannonomyia (Shannonomyia) lenta (Osten Sacken, 1860). Male. *Woodworths Lake, Fulton Co. NY, Alexander/Pilaria lenta (O.S), Det. C. P. Alexander, 1925.* [USNM]

Shannonomyia (Shannonomyia) lenta (Osten Sacken, 1860). Male. *Woodworths Lake, Fulton Co. NY, Alexander/Pilaria lenta (O.S), Det. C. P. Alexander, 1925.* [USNM]

Shannonomyia (Shannonomyia) lenta (Osten Sacken, 1860). Male. *Woodworths Lake, Fulton Co. NY, Alexander/Pilaria lenta (O.S), Det. C. P. Alexander, 1925.* [USNM]

Tinemyia margaritifera Hutton, 1900. Male. *Raetihi Hill, Ohakune, N3, Summit, XI-20, 1923, T. R. Harris.* [USNM]

Tinemyia margaritifera Hutton, 1900. Male. *Tinemyia margaritifera Hutt. Det. C. P. Alexander, 1924.* [USNM]

Tonnoirella gemela Alexander, 1928. Male. Paratype. *Tasm. Mt Field, 21 Dec. 1922, A. Tonnoir.* [USNM]

Tonnoirella gemela Alexander, 1928. Male. Paratype. *Tasm. Mt Field, 18 Dec. 1922, A. Tonnoir.* [USNM]

Ulomorpha pilosella (Osten Sacken, 1860). Male. *Cincinatus, N.Y., July 20, 19*(??)*, C. P. Alexander/Ulomorpha piloella O. S., Det. C. P. Alexander, 1925.* [USNM]

Ulomorpha pilosella (Osten Sacken, 1860). Male. *Cincinatus, N.Y., July 20, 19*(??)*, C. P. Alexander/Ulomorpha piloella O. S., Det. C. P. Alexander, 1925.* [USNM]

Ulomorpha pilosella (Osten Sacken, 1860). Male. *Orono ME., 12 June '13./Ulomorpha pilosella O. S., Det. C. P. Alexander, 1925.* [USNM]

Ulomorpha rogersella Alexander, 1929. Male. *Neel Gap, Ga., 5-22-46, P. W. Fattig/Ulomorpha rogersella Al., Det. C. P. Alexander, 1947.* [USNM]

Ulomorpha rogersella Alexander, 1929. Male. Paratype. *Jackson Co., Fla. Marianna, IV. 13. 1928., J. S. Rogers.* [USNM]

Ulomorpha rogersella Alexander, 1929. Male. *Smoky Mts., N. C., Alt. 5860 ft. VI-II, 1939, C. P. Alexander/Ulomorpha regersella Al., Det. C. P. Alexander, 1940.* [USNM]