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Abstract

A phylogenetic analysis of the Mycetophiliformia (= Sciaroidea) was performed to determine the relationships among its families and to place the following genera of uncertain position in the system: *Heterotricha, Ohakunea, Colonomyia, Freemanomyia, Rhynchoheterotricha, Chiletricha, Afrotricha, Anisotricha, Kenyatricha, Nepaletricha, Sciarosoma, Sciaropota, Insulatricha, Cabamofa, Rogambara,* and *Starkomyia. Eratomyia* **n. gen.** is described based on a new species from Ecuador. *Colonomyia brasiliana* **sp.n.** and *Colonomyia freemani* **sp.n.** are described respectively from southern Brazil and Chile. The male of *Cabamofa mira* Jaschhof is described for the first time. A total of 64 terminal taxa and 137 transformation series (with 202 characters) were included in the data matrix, with a number of new features from thoracic morphology. Willi Hennig's 1973 system for the higher Bibionomorpha was adopted using the name Mycetophiliformia for the Sciaroidea. The Mycetophiliformia are monophyletic. The family Cecidomyiidae appears as the sister group of the remaining Mycetophiliformia, followed by the Sciaridae. In the preferred topology, the Rangomaramidae appear as the group sister of a clade consisting of (Ditomyiidae + Bolitophilidae + Diadocidiidae + Keroplatidae) and of (Lygistorrhinidae + Mycetophilidae). The topology within the Rangomaramidae is (Chiletrichinae **subfam. n.** (Heterotrichinae **subfam. n.** ((Rangomaraminae + Ohakuneinae **subfam. n.**)))). The Chiletrichinae include the genera *Kenyatricha, Rhynchoheterotricha, Insulatricha, Chiletricha,* and *Eratomyia* **n. gen.** Heterotrichinae and Rangomaraminae are monotypic. The subfamily Ohakuneinae includes *Ohakunea, Colonomyia, Cabamofa,* and *Rogambara.* The positions of *Freemanomyia, Loicia, Taxicnemis, Sciaropota, Starkomyia, Anisotricha, Nepaletricha,* and *Sciarosoma* are considered. *Afrotricha* might belong to the Sciaridae. The similarities used by many authors to gather the Sciaridae and Mycetophilidae in a clade are shown to be a combination of plesiomorphies and homoplasies.

Key words: Diptera, phylogeny, Bibionomorpha, Mycetophiliformia, Sciaroidea

Introduction

Amorim & Yeates (2006) revised the classification of the ealier groups of Diptera, formally eliminating the "Nematocera" and ranking its infraorders as suborders, among which are the Bibionomorpha. It is well accepted that most families of the Bibionomorpha together form a monophyletic group consisting of the Pachyneuridae, Bibionidae, Cecidomyiidae, Sciaridae, Rangomaramidae, Ditomyiidae, Bolitophilidae, Diadocidiidae, Keroplatidae, Lygistorrhinidae, and Mycetophilidae. The inclusion in this group of the Anisopodidae *s. l.*, however, has been more questionable. Some authors, such as Tuomikoski (1961), have proposed a separate clade, the Anisopodomorpha, for the family. Wood & Borkent (1989) interpreted some similarities in the mouthparts of the larvae to be shared, derived features with the Psychodidae and other families in the Psychodomorpha, whereas Woodley (1989) and Oosterbroek & Courtney (1995) accepted the family as the sister group of the Brachycera. The Scatopsoidea earlier were considered by Hennig (1973) to belong to the Bibionomorpha, and the Axymyiidae have been included in the group by most authors, but have been transferred to a separate taxon Axymyiomorpha. Whatever the included families, however, the monophyly of the group has never been clearly demonstrated. This paper addresses the relationships within a less inclusive sample of clades, usually referred to by Hennig (1954, 1973) as the Mycetophiliformia, or as the Sciaroidea by more recent authors (e.g., Wood & Borkent 1989, Chandler 2002, Hippa & Vilkamaa 2005, Jaschhof *et al.* 2005, Hippa & Vilkamaa 2006, Jaschhof 2006).

Unusual genera and relationships among the Mycetophiliformia

The phylogenetic relationships among families of the Mycetophiliformia have remained unsolved, despite the large recent effort after many decades of relatively minor interest on the subject. Not only is there conflict about the position of the Sciaridae and Cecidomyiidae in relation to other families of the group (Bolitophilidae, Ditomyiidae, Diadocidiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae, and Rangomaramidae),

but also several genera have never been given a stable position in the system, including *Heterotricha* Loew, *Ohakunea* Tonnoir & Edwards, *Freemanomyia* Jaschhof, and others.

Heterotricha, originally known from a Baltic amber fossil species, was associated by Meunier (1904) with the Sciaridae, but was seen as more closely related to the Diadocidiidae by Tonnoir & Edwards (1927), Tonnoir (1929), Hennig (1954), Colless (1963), and Papavero (1977). On the contrary, Edwards (1925), Frey (1942), Freeman (1951, 1960), and Shaw (1953) followed Meunier (1904), placing the genus in the Sciaridae. Hennig (1973) included *Heterotricha* followed by a question mark in the Sciaridae. A New Zealand species was later added to the genus by Tonnoir & Edwards (1927), and southern South American species were added by Edwards (1933) and Freeman (1951); Chandler (2002) described a species from southern Europe. *Rhynchoheterotricha* was later described based on a single species from South Africa by Freeman (1960), who thought the genus to be closely related to *Heterotricha*.

The position of *Freemanomyia* (= *Pterogymnus* Freeman) also has been unclear. Freeman (1951) originally placed the genus in the Diadocidiidae, a move apparently accepted by Colless (1963). Hennig (1954) raised the question of whether the genus was related to the Bolitophilidae, but later Hennig (1973) still included the genus in the Diadocidiidae, maintaining the position as doubtful. Papavero (1977) cited Hennig's (1973) doubts, but kept the genus in the Diadocidiidae.

Ohakunea was described by Tonnoir & Edwards (1927), based on a single species from New Zealand, and it was placed in the Sciaridae. Later, Freeman (1951) described a second species from Chile, and Colless (1963) described a third from Australia. These two authors, plus Frey (1942) and Shaw (1953), accepted the placement of the genus, by Tonnoir & Edwards (1927), with the sciarids. Hennig (1973) kept *Ohakunea* in the Sciaridae, but a question mark follows the genus name in his paper. Jaschhof & Hippa (2003) reviewed *Ohakunea*, added two new species from Papua New Guinea, and showed that its association with the Sciaridae would be mistaken, proposing that the genus belongs to another clade in the Mycetophiliformia.

Colless (1963) described *Colonomyia* as closely related to *Ohakunea*, based on one species from Australia and one from Chile. Although Colless (1963) left both genera in the Sciaridae, he stressed that they had some important similarities with some groups of Mycetophilidae *s. l.* Two additional species from Chile and southern Argentina were added to *Colonomyia* by Matile & Duret (1994), and Hippa & Jaschhof (2004) revised the genus and added one new species from Costa Rica and another from Papua New Guinea.

In a large revision, Chandler (2002) created new genera for most of the species previously placed in *Heterotricha* — *Chiletricha* for southern South American species, *Afrotricha* for an Afrotropical species, and *Anisotricha* for a New Zealand species — and created new genera for previously undescribed species — *Kenyatricha* for an Afrotropical species, and *Nepaletricha*, *Sciarosoma*, and *Sciaropota* for Palearctic species. Jaschhof (2004a) described three new species from New Zealand in *Insulatricha*, a genus associated with the *Heterotricha* group, though he did not assign the genus to any family. *Sciarosoma* was redescribed in detail by Jaschhof *et al.* (2005).

Jaschhof & Didham (2002) described the genus *Rangomarama*, based on five new species from New Zealand. They considered *Rangomarama* the sister group of (Cecidomyiidae + Sciaridae) and ranked the taxon as a separate family, the Rangomaramidae. In his description of *Starkomyia*, Jaschhof (2004c) considered the genus to be connected to a clade including the Sciaridae, Cecidomyiidae, Rangomaramidae, and the groups *Heterotricha* and *Ohakunea*.

Hippa & Vilkamaa (2005, 2006) placed *Rangomarama* as a subfamily of the Sciaridae in the most recent systematic considerations of this group. *Sciarotricha*, described by Hippa & Vilkamaa (2005), conforms to a typical sciarid, even though possibly close to the beginning of the diversification of the family. Jaschhof (2005) more recently described the genera *Cabamofa* and *Rogambara* from Costa Rica, based on a single species each, and associated both genera with *Ohakunea*.

The question of the position of these "*Heterotrichia* group" of genera is only part of a larger problem, i.e., of properly establishing the relationships between major Mycetophiliformia clades. Hennig (1954, 1973)

accepted the Sciaridae as the sister group of (Lygistorrhinidae + Mycetophilidae), largely based on the basalization of the cubital fork and the shift of the transverse veins r-m and m-cu to a longitudinal position in the wing. In his system, Bolitophilidae, Ditomyiidae, Diadocidiidae, and Keroplatidae would have originated earlier than the separation between Sciaridae and Mycetophilidae.

Wood & Borkent's (1989) reconstruction of the relationships among lower dipterans resulted in a new arrangement for the Bibionomorpha. They modified Hennig's (1954) concept of the Mycetophiliformia, transferring the Scatopsoidea to the Psychodomorpha and, for the first time, moving the Sciaridae to a position closer to the origin of the clade, sister group to the Cecidomyiidae (Fig. 1), a position later also suggested by Blaschke-Berthold (1994).

In his large study of the Keroplatidae, Matile (1990) followed Hennig's (1973) more traditional view of the relationships between Sciaridae and (Lygistorrhinidae + Mycetophilidae *s. s.*), accepting Diadocidiidae and Keroplatidae as sister families (Fig. 2).

In Chandler's (2002) overall consideration of the phylogeny of the Mycetophiliformia, (*Ohakunea* + *Colonomyia*) compose a monophyletic group with a clade including Sciaridae, *Heterotricha*, *Chiletricha*, and most other orphan genera. This entire group would be the closest clade of (Mycetophilidae *s. s.* + Lygistorrhinidae + *Freemanomyia*). To a certain extent, this system agrees with that of Hennig (1973). More to the base are Bolitophilidae, and then the Keroplatidae and Diadocidiidae in a polytomy with the Ditomyiidae, and the Cecidomyiidae sister to the remainder of the group (Fig. 3).

Blagoderov & Grimaldi's (2004) study of Cretaceous amber sciaroids has a partially solved phylogeny for Mesozoic genera and recent families. In their scheme of wing evolution, *Heterotricha*, *Pterogymnus*, and related Mesozoic genera are associated with the Bolitophilidae.

Jaschhof & Didham (2002) followed Wood & Borkent (1989), associating the Sciaridae and Cecidomyiidae in a clade. Their family Rangomaramidae appears as the sister group of the Cecidomyiidae (Fig. 4), but they did not address the question of the other higher Mycetophiliformia clades. Jaschhof & Hippa (2003) accepted that *Ohakunea* would deserve a family-level clade in the Mycetophiliformia, but not directly connected to the Sciaridae. In his discussion of *Starkomyia*, Jaschhof (2004c) proposed a monophyletic group composed of the Sciaridae, Cecidomyiidae, Rangomaramidae, and genera of the groups *Heterotricha* and *Ohakunea*.

Hippa & Vilkamaa (2005, 2006) proposed phylogenies for the Mycetophiliformia, with a system quite different from that of Chandler (2002). The cladograms obtained for the relationships between the major clades in their first analysis with and without Mesozoic fossils (Hippa & Vilkamaa, 2005) are quite different. In the analysis with only recent groups, (Keroplatidae + Ditomyiidae) would compose the sister group of the remaining Mycetophiliformia, followed in sequence by Bolitophilidae, Diadocidiidae, a clade with *Heterotricha* and *Ohakunea*, another clade with *Chiletricha* and related genera, and then Cecidomyiidae, (*Sciaropota* + Lygistorrhinidae + Mycetophilidae), and (*Sciarosoma* + *Sciarotricha* + *Rangomarama* + Sciaridae) (Fig. 5). When fossils were added, the Cecidomyiidae have a position closer to the origin of the group, followed by a pair of larger clades: one of them embracing *Heterotricha*, *Chiletricha*, and related genera, together with Bolitophilidae, Diadocidiidae, Ditomyiidae, and Keroplatidae, and the other including *Ohakunea* and Mycetophilidae as sister groups, together with *Sciarosoma*, *Sciarotricha*, *Rangomarama*, and Sciaridae (Fig. 6). In their review of their own data with additional taxa included (Hippa & Vilkamaa 2006), some differences appeared. Cecids are still sister to the rest of the clade, followed in sequence by the Ditomyiidae, Diadocidiidae, Keroplatidae, Bolitophilidae, and a clade including Sciaridae, Mycetophilidae, Lygistorrhinidae, *Rangomarama*, and this set of genera of uncertain position. In this clade, *Starkomyia* is sister to the remainder of the group, to which follow *Heterotricha* and *Afrotricha* in a clade, *Chiletricha* and related genera, *Ohakunea* and *Colonomyia*, and Mycetophilidae and Lygistorrhinidae as the sister groups of the Sciaridae including *Rangomarama*.

All these phylogenies can be summarized in two main proposals. One places the Sciaridae close to the Mycetophilidae, and the other moves the Sciaridae to the base of the group, usually in a clade also bearing the

Cecidomyiidae.

Most recent phylogenetic studies for the Mycetophiliformia follow to some extent a cladistic argumentation, but they have strong limitations in terms of taxa sampling and the number of characters used, especially if we consider the complexity of the problem under scrutiny. The widest analysis made to date is that of Hippa & Vilkamaa (2006), with 45 terminal taxa and 78 characters, but the differences between their own (Hippa & Vilkamaa, 2005, 2006) cladograms (with and without fossils, and adding more taxa in 2006) show the difficulty of the problem. In any case, the consensus between the systems proposed for the Mycetophiliformia by Hennig (1973), Matile (1990), Jaschhof & Didham (2002), Chandler (2002), and Hippa & Vilkamaa (2005, 2006) is not much more than a fundamental polytomy. Perhaps the only well accepted clade is (Lygistorrhinidae + Mycetophilidae).

In this paper, we describe two new Neotropical species of *Colonomyia*, a new genus close to *Chiletricha*, and the previously unknown male of *Cabamofa*; illustrate many of the groups involved; and perform a large study of the relationships within the group. The study of the relationships includes a rather ample ingroup and outgroup taxon sampling, and a new array of characters, including thoracic pleural sclerite features, that proved to be especially informative. We also consider the impact of methodological decisions on the phylogenetic analysis and on the final topology.

The purposes of this study are twofold. One is to obtain a phylogeny of the group and to solve the problem of the genera of uncertain position at the family level within the higher Bibionomorpha. The other is to give a better basis for rooting phylogenetic studies within families. In other words, studies of generic relationships within families are affected by decisions about outgroups sampled, which depends on our view about the degree of proximity between outgroup clades. The Sciaridae phylogeny obtained by Vilkamaa & Hippa (2004), for example, seems to have been strongly affected by their choices of outgroups. In their topology, sciarid genera with a longer cubital stem and macrotrichia on the wing membrane, which may be plesiomorphic features, are at the top of the cladogram. This could change simply with an alternative sample of outgroups. Two other examples are Söli's (1997) and Tozoni's (1998) studies of the Mycetophilidae relationships, which were affected by their decisions about the position of the Sciaridae, and Matile's (1990) view of the position of the Sciaridae in his study of Keroplatidae phylogeny.

Finally, the proper placement of the diverse Mycetophiliformia Mesozoic fossils in a sound phylogeny – a task not undertaken here – would show the actual degree of diversification of the Bibionomorpha in the Jurassic, and the impact of the apparently large faunal change due to extinction at the J-K border, an effort initiated by Blagoderov & Grimaldi (2004) and Hippa & Vilkamaa (2005).

Material

An adequate protocol of phylogenetic analysis must deal with problems of correct rooting, level of homoplasy between ingroups and outgroups, level of homoplasy within the ingroup, and correct optimization at the base of clades with considerable within-clade variation. The choice of ingroup and outgroup species, therefore, is not a trivial task. Two main strategies were followed here to avoid these pitfalls: (1) the inclusion of species belonging to all Bibionomorpha families outside the Mycetophiliformia, as well as species outside the Bibionomorpha, and (2) the inclusion of a higher number of representatives of larger families, e.g., cecids, sciarids, mycetophilids, keroplatids, and ditomyiids. Selection of material within each family was done to avoid species belonging to the same subclades, allowing character optimization at the base of the family of features that are actually general to the family. The number of species examined in this study is much larger than that listed in Table 1, which allowed a better understanding of the evolution of characters within each family.

TABLE 1. List of terminal taxa in the numerical analysis of the Mycetophiliformia and outgroups.

Limoniidae
    1. *Edwardsomyia*
Trichoceridae
    2. *Trichocera*
Anisopodoidea
    3. *Olbiogaster*
    4. *Austrogaster*
Pachyneuridae
    5. *Cramptonomyia*
Bibionidae
    6. *Hesperinus*
    7. *Penthetria*
    8. *Plecia*
Cecidomyiidae
    9. *Catotricha*
    10. *Lestremia*
    11. *Porricondyla*
    12. *Asphondylia*
Sciaridae
    13. *Trichomegalosphys*
    14. *Apelmocreagris*
    15. *Bradysia*
Rangomaramidae
    16. *Ohakunea*
    17. *Colonomyia* sp.
    18. *Colonomyia brasiliana*, n. sp.
    19. *Cabamofa*
    21. *Heterotricha*
    22. *Kenyatricha*
    23. *Rhynchoheterotricha*
    24. *Insulatricha*
    25. *Chiletricha*
    26. *Eratomyia*
    27. *Rangomarama*
Bolitophilidae
    28. *Bolitophila*
Keroplatidae
    29. *Arachnocampa*
    30. *Paleoplatyura*
    31. *Macrocera*
    32. *Platyura*
    33. *Keroplatus*
    34. *Orfelia*

Ditomyiidae
    35. *Symmerus*
    36. *Australosymmerus*
    37. *Melosymmerus*
    38. *Nervijuncta*
    39. *Ditomyia*
Diadocidiidae
    39. *Diadocidia*
Lygistorrhinidae
    40. *Probolaeus*
Mycetophilidae
    41. *Drepanocercus*
    42. *Paratinia*
    43. *Coelosia*
    44. *Boletina*
    45. *Tetragoneura*
    46. *Dziedzickia*
    47. *Megalopelma*
    48. *Neoempheria*
    49. *Monoclona*
    50. *Acnemia*
    51. *Leia*
    52. *Manota*
    53. *Trichonta*
    54. *Rymosia*
Genera of uncertain family assignment
    55. *Taxicnemis*
    56. *Sciarosoma*
    57. *Sciaropota*
    58. *Afrotricha*
    59. *Anisotricha*
    60. *Nepaletricha*
    61. *Freemanomyia*
    62. *Starkomyia*
    63. *Loicia*

The Anisopodidae have been added here as one of the outgroups in relation to the Mycetophiliformia. The test of the monophyly of the Bibionomorpha, however, was not one of the goals of this paper, even though some thoracic features supported the inclusion of the family within the suborder. A more sound examination of this problem would demand a higher number of outgroups external to the suborder, here limited to two species. The Scatopsidae, on the other hand, have been indicated as not belonging to the Bibionomorpha by Wood & Borkent (1989), Amorim (1994), and Amorim & Grimaldi (2006). It is not a member of the Myceto-

philiformia and was not included here, even as an outgroup.

Characters were scored from the specimens available and checked from the literature whenever possible. The main literature sources were Tonnoir & Edwards (1927), Shaw (1948, 1953), Freeman (1951), Shaw & Shaw (1951), Saigusa (1973), Munroe (1974), Wood & Borkent (1989), Matile (1990), Amorim (1993), Blaschke-Berthold (1994), Gagné (1994), Amorim *et al.* (1996), Söli (1997), Jaschhof (1998, 2000, 2004a, b, c, 2005), Tozoni (1998), Pinto & Amorim (2000), Chandler (2002), Jaschhof & Didham (2002), and Blago-derov & Grimaldi (2004).

This study was based on about 150 specimens pinned, on slides, and in alcohol (Appendix 1). Many of the specimens were slide-mounted and drawn in detail. All original drawings were made after dissection, clearing, and mounting parts on permanent slides. All drawings are rescaled to the same size to facilitate comparisons. The list of 64 terminal taxa formally included in the data matrix is in Table 1. Information for most terminal taxa comes directly from species. The only exception is *Probolaeus*, in which the wing features are too apomorphic in this genus (with a large number of inapplicable conditions); therefore, wing characters from *Palaeognoriste*, which preserve some features lost in more advanced lygistorrhinids, were merged with the matrix. Also, immature characters (when available) were generalized at the family level, except for the Rangomaramidae. Terminology follows that of McAlpine (1981), except for some wing veins, which follows that of Colless & McAlpine (1991). The material studied was kindly loaned from the following institutions, to which we are deeply thankful:

AMNH	USA, State of New York, New York, American Museum of Natural History
NHM	United Kingdom, London, The Natural History Museum
BPBM	USA, Hawaii, Honolulu, Bernice P. Bishop Museum
CNC	Canada, Ontario, Ottawa, Canadian National Collection of Insects
MNHN	France, Paris, Muséum National d'Histoire Naturelle
MZSP	Brazil, State of São Paulo, São Paulo, Museu de Zoologia da Universidade de São Paulo
NMNH	USA, Washington, D.C., National Museum of Natural History
NHMO	Norway, Oslo, University of Oslo, Natural History Museum

Abbreviations used in the figures are as follows:

aed ap	=aedeagal apodeme
anp	= antepronotum
ans	= anepisternum
ans h	= anepisternum height
Ce	= cercus
ces	= cervical sclerite
cxI–III	= coxa I–III
ej ap	= ejaculatory apodeme
emI–III	= epimeron I–III
emII w	= epimeron II width
esI–III	= episternum I–III
esIII w	= epsternum III width
Gc	= gonocoxite
gc br	= gonocoxal bridge
gon ap	= gonocoxal apodeme
Gs	= gonostylus
hal	= halter

kts	= katepisternum
ltI	= laterotergite
ltI h	= laterotergite height
ltI w	= laterotergite width
mdt	= mediotergite
mdt h	= mediotergite height
MeII	= meron II
mtn	= metanotum
mtn	= metanotum
pnp	= posterior notal phragma
ptIII	= pleurotrochantin III
scl	= scutellum
sct	= scutum
SI	= Sternite I
SIX	= Sternite IX
TI	= Tergite I
TVIII–X	= Tergite VIII–X
trI	= trochanter I

Methods

"Characters" actually correspond to complex hypotheses themselves, and as such must be tested, something frequently overlooked in cladistic literature. The data matrix presented here was constructed in a number of rounds, with checking and rechecking of the original hypotheses of primary homology and coding. In other words, intermediary topologies highlight character incongruence and allow the correction of mistakes in hypotheses of primary homology, coding limits, mistyping, and misobservations. Denying this process would correspond to the acceptance of original ignorance as the best hypothesis over which numerical analyses are performed. Moreover, true homoplasy and missing data demand a careful handling of the numerical step of the matrix analysis. Different algorithms deal differently with characters, often resulting in significant differences in the final topology. The analysis protocol in this study was designed to highlight the impact of the different parsimony algorithms and missing data for the results. The sequence of numerical runs performed is listed in Table 2. Most runs were made with 50 replicates, but the Goloboff k = 3 option was run with 1 million replicates (Goloboff 1993). Numerical analyses of the data matrix were run in PAUP version 4.0b10 (Swofford 2003). The runs with 1 million replicates were done at the Bioportal at the University of Oslo (http://www.bioportal.uio.no/). Character distribution was checked using McClade 4.0 PPC. Trees were designed using TreeView and drawn using Adobe Illustrator.

Finally, another question concerns the relationships within each of the more diverse families, namely the Ditomyiidae, Keroplatidae, and Mycetophilidae. The focus of our study is the position of the genera *Heterotricha*, *Ohakunea*, and allies, and the relationships among the Mycetophiliformia families. Larger species sampling in larger bibionomorph families was necessary to solve this problem, but in principle, mycetophilid phylogeny was not the goal of our study. Hence, most of the phylogenetic signal at the intergeneric level in these families corresponds to homoplasies in relation to features also originating elsewhere. Even though there was some effort to obtain information for intrafamilial relationships from the literature, genera in these families were, in large degree, gathered by plastic features, in such a way that the detailed results are not reliable. For example, Söli (1997) and Tozoni (1998) point to a position of the Sciophilinae close to the origin of the Mycetophilidae, which does not appear here. Also, it is apparent from Munroe's (1974) paper that *Sym-*

merus is connected to *Melosymmerus* and *Australosymmerus*, not to *Ditomyia* and *Nervijuncta*. This would not be relevant in our study, were it not that the relative position of the genera within each family is implied in different optimizations of features at the base of the family. Indeed, the exclusion of a single genus of these families from the data matrix resulted in topology changes at higher levels in the Mycetophiliformia phylogeny. Even though future studies might use a more extensive sampling of Keroplatidae and Mycetophilidae (see below), we believe that the sample used here was adequate to obtain stable results for interfamilial relationships.

TABLE 2. Different options used (algorithms, sets of characters, and sets of terminals) in the parsimony analyses performed using the data matrix for the Mycetophiliformia.

1. Entire matrix, unweighted 50 replicates (Fig. 44)
2. Character and taxon reduced matrix, unweighted 1 million replicates (characters 16 and 17 removed) (Fig. 45)
3. Entire matrix, successive weighting (Fig. 46)
4. Character and taxon reduced matrix, successive weighting (Fig. 47)
5. Character reduced matrix, Goloboff k = 3, 50 replicates (Fig. 48)
6. Character and taxon reduced matrix, Goloboff k = 1, 50 replicates (Fig. 49)
7. Character and taxon reduced matrix, Goloboff k = 2, 50 replicates (Fig. 50)
8. Character and taxon reduced matrix, Goloboff k = 3, 1 million replicates (Fig. 51)
9. Character and taxon reduced matrix, Goloboff k = 4, 50 replicates (Fig. 52)
10. Character and taxon reduced matrix, Goloboff k = 5, 50 replicates (Fig. 53)
11. Character and taxon reduced matrix, Goloboff k = 6, 50 replicates (Fig. 54)
12. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Freemanomyia* added (Fig. 55)
13. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Loicia* added (Fig. 56)
14. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Taxicnemis* added (Fig. 57)
15. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Afrotricha* added (Fig. 58)
16. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Anisotricha* added (Fig. 59)
17. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Nepaletricha* added (Fig. 60)
18. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Sciarosoma* added (Fig. 61)
19. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Sciaropota* added (Fig. 62)
20. Character and taxon reduced matrix, Goloboff k = 3, 50 replicates, *Starkomyia* added (Fig. 63)

New taxa and redescriptions

Rangomaramidae Jaschhof & Didham, 2002

Rangomaramidae Jaschhof & Didham, 2002

Type genus. *Rangomarama* Jaschhof & Didham, 2002: 45, by original designation

Diagnosis. Thorax elongate, mesepimeron high and slender, sometimes completely absent ventrally, laterotergite only slightly projected, mediotergite high, slightly curved. R_4 always absent, m-cu connecting CuA basally in wing, first CuA sector about half to one tenth second sector, m-cu sometimes incomplete, tb (M_{1+2}/M_{3+4}) always longitudinal.

Description. Colour usually brown, shining or dull, sometimes with yellowish areas. Body size 1.7–6.0 mm, wing length 2.0–5.5 mm. Usually 3 ocelli, sometimes lateral ocelli displaced toward margin, but never really in contact with eye, ocelli absent in *Rogambara* and *Cabamofa*, eye-bridge absent or incomplete in most genera, complete only in *Rogambara* and *Cabamofa*. Antenna with 14 flagellomeres, first article usually 1.5 times second flagellomere, with setae haphazardly distributed. Maxillary palpus with palpiger plus 4 palpomeres, last segment much longer than preceding in the Chiletrichinae, *Ohakunea*, and *Colonomyia*. Thorax

elongate, as in other higher Mycetophiliformia families. Primary anapleural suture and midpleural pit present, katepisternum not particularly developed. Anepisternal and katepisternal setae absent, with few exceptions. Mesopleurotrochantin absent. Mesepimeron high, slender, or completely absent ventrally due to fusion of katepisternum and laterotergite. Mesepimeral setae only in *Eratomyia*, n. gen. Laterotergite convex posteriorly, projected into the mediotergite, slightly projected laterally, dorsal margin only just reaching pleural membrane by approximation between mesepimeron and mediotergite, setae present only in *Heterotricha*. Mediotergite high, slightly curved, completely bare. Metepisternum not particularly developed, nor reduced, postnotal phragma not particularly reduced. Segment 8 well developed, only slightly shorter than preceding segments. Coxae elongated, tibial spurs 1:2:2, tibial spurs not as developed as in ditomyiids or most mycetophilids. Front tibia with differentiated area and regular row of setae, with exception of *Chiletricha*. Wing elongated, sometimes setae on membrane present or absent. Sc incomplete in the family, with possible exception of *Rangomarama*. Base of Rs oblique or transverse, very elongate only in *Rangomarama*, r-m transverse or slightly oblique backwards, longitudinal (in line with second sector of Rs) and particularly developed in Ohakuneinae, nearly absent in *Heterotricha* and absent in *Rangomarama*. R_4 always absent, R_1 reaching C before middle of wing only in *Colonomyia* and *Rogambara*. M_{1+2} forking usually beyond half of wing, medial fork long in *Heterotricha*, *Ohakunea*, and *Colonomyia*. Most genera with m-cu reaching CuA typically close to base of wing, with tb (M_{1+2}/M_{3+4}; see discussion below) longitudinal. First sector of CuA usually short, longer only in *Eratomyia*, n. gen. A_1 always incomplete, absent in *Colonomyia*, *Cabamofa*, and *Rogambara*. Abdomen more slender at base than mesally, but not as slender as in keroplatids and mycetophilids. Male gonocoxite, gonostyle, tergite 9, and cercus variable. In females, first cercomere shorter in *Heterotricha* and *Chiletricha*, and longer in *Rangomarama*. Two sclerotized spermathecae present in all genera for which information is available.

Discussion. Rangomaramidae until now included only the type genus. In the analysis herein performed, *Chiletricha*, *Ohakunea*, *Heterotricha*, and related genera compose a monophyletic group with *Rangomarama* within the Mycetophiliformia. Chiletrichinae and Ohakuneinae form robust smaller monophyletic clades. In the preferred topology, *Heterotricha* is in a monophyletic group including these two clades and *Rangomarama*. Even though there is still some instability, there is phylogenetic signal that allows familial assignment to all these genera that were orphans within the system. A number of other genera might also fit in the clade, but because of missing data, we preferred to keep their inclusion in the family still pending. These genera include *Anisotricha*, *Nepaletricha*, *Freemanomyia*, *Sciarosoma*, and *Sciaropota*.

Key for Identification of the Genera of Rangomaramidae

1. r-m longitudinal, in line with second sector of Rs (Ohakuneinae, **subfam. n.**) 2
-   r-m transverse or oblique 5
2. First sector of Rs visible 3
-   First sector of Rs entirely missing 4
3. M_{1+2} complete .... (Costa Rica) *Rogambara* Jaschhof
-   M_{1+2} incomplete at base .... (Costa Rica) *Cabamofa* Jaschhof
4. Rs originating before half of wing; base of M_4 complete ....
    .... (Australia, Costa Rica, Chile, Brazil) *Colonomyia* Colless
-   Rs originating beyond distal half of the wing; base of M_4 incomplete ....
    .... New Zealand, Australia, Papua New Guinea, Chile) *Ohakunea* Edwards
5. First sector of Rs short; r-m present.. 6
-   First sector of Rs long; r-m absent, tb much longer than m-cu ....
    .... Rangomaraminae (New Zealand) *Rangomarama* Jaschhof & Didham

6. R_5 running very close to C, first sector of Rs tiny, transverse, r-m scarcely visible; medial fork long, M_1 and M_2 diverging before middle of wing. Tergite 9 devoid of distal projections bearing strong spines .... Heterotrichinae, **subfam. n.** (Europe and Japan, Baltic amber) *Heterotricha* Loew
- R_5 not close to C, first sector of Rs normally developed, oblique forward, r-m produced, at least slightly oblique backwards; medial fork short, M_1 and M_2 diverging beyond middle of wing. Tergite 9 bearing 1 or 2 pairs of distal projections with strong spines (Chiletrichinae, **subfam. n.**) 7
7. Proboscis long, maxillary palpus displaced to apex .... (South Africa) *Rhynchoheterotricha* Freeman
- Proboscis short, normal 8
8. M_{1+2}/M_{3+4} longer than m-cu .... (Kenya) *Kenyatricha* Chandler
- M_{1+2}/M_{3+4} shorter than m-cu 9
9. Rs originating before basal third of wing; R_1 reaching C about at middle of wing; M_1 and M_2 continuously diverging ....(New Zealand) *Insulatricha* Jaschhof
- Rs originating beyond basal third of wing; R_1 reaching C at distal third of wing; M_1 not gradually diverging 10
10. m-cu reaching CuA very basally, basal cell slender ....(Chile, southern Brazil) *Chiletricha* Chandler
- m-cu reaching CuA more distally, basal cell wide .... (Ecuador) *Eratomyia* n. gen.

Heterotrichinae, subfam. n.

Type genus. *Heterotricha* Loew, here designated

Diagnosis. As for the genus *sensu* Chandler (2002).

Description. Three ocelli present, lateral ocelli separated by about their diameter from eye margin. Eyes at most slightly emarginate, eye bridge absent, eyes practically bare. Laterotergite setouse, other pleura bare, except for prothoracic sclerites. Midpleural pit present. R_5 running very close to C, first sector of Rs tiny, transverse, r-m scarcely visible; medial fork long, M_1 and M_2 diverging before middle of wing. Wing membrane largely covered with macrotrichia. Male tergite 9 devoid of distal projections bearing strong spines found in Chiletrichinae. Gonostylus simple. Female cerci 2 segmented, first segment shorter than second; no sclerotized spermathececae.

Chiletrichinae, subfam. n.

Type genus. *Chiletricha* Chandler, here designated

Diagnosis. First flagellomere more than 1.5 times succeeding flagellomeres. Medial fork relatively short, M_1 and M_2 diverging beyond middle of wing; r-m oblique backwards. Male tergite 9 with 1 or 2 pairs of projections, each with number of short, black spines.

Description. Three ocelli present, median one usually slightly more ventral than lateral ones, lateral ocelli apart from eye margin. Eyes at most slightly emarginate, eye bridge absent. Basal flagellomere typically elongate, more than 1.5 times succeeding flagellomeres, setae haphazardly distributed. Clypeus short, except in 1 species of *Rhynchoheterotricha*, in which it is as long as front tibia. Maxillary palpus with palpiger plus 4 palpomeres, distal article longer than preceding ones (in *Rhynchoheterotricha* and *Kenyatricha* unknown). Proepimeron triangular. Primary anapleural suture present. Mesepimeron elongate, quite straight, high, slender at ventral end. Laterotergite rounded posteriorly. R_5 long, R_1 shorter only in *Insulatricha*, first sector of Rs short, oblique forward, r-m short (except in *Eratomyia*, **gen. n.**), oblique backwards. Medial fork short, M_1 and M_2 diverging beyond middle of wing, tb (M_{1+2}/M_{3+4}) longitudinal, at most slightly longer than m-cu. A_1

present, incomplete. Male tergite 9 with 1 or 2 pairs of distal projections, each with group of strong spines, a unique feature within Bibionomorpha.

   Genera included: *Chiletricha*, *Eratomyia*, *Insulatricha*, *Rhynchoheterotricha*, and *Kenyatricha*. *Anisotricha* and *Nepaletricha* should be placed here tentatively, although this is pending a reexamination of their species.

Eratomyia, n. gen.
(Figs. 7–15)

Type species. *Eratomyia magnifica* sp. n., here designated

   Diagnosis. First sector of m-cu longer than in other genera of subfamily, m-cu reaching CuA more distally. M_{1+2}/M_{3+4} shorter than m-cu, r-m long. Tergites 1-4 and 6 shining brown, tergite 5 yellow. Midpleural pit absent.

   Etymology. The species name is feminine, from the Greek *eratos*, lovely, meaning a lovely fly.

   Comments. This genus, which is known only from the type species, from Ecuador, appears in the phylogenetic analysis (below) as the sister group of *Chiletricha*, which is known from Chile, southern Argentina, and southern Brazil. It differs from the *Chiletricha* species in wing features, with a much wider basal cell, R_5 separated from C, and M_4 originating from CuA not as basally in the wing (Figs. 10, 16). Mouthparts are fairly similar (Figs. 7, 17). In the thorax, the mesepimeron of *Eratomyia* is more slender on its ventral half, whereas the laterotergite is slightly larger (Figs. 8, 18). Tergite 9 has strong spines on a pair of distal projections (Fig. 12–15), as also seen in *Chiletricha* (Fig. 19), *Rhynchoheterotricha*, and *Insulatricha*, and the gonocoxites have a pair of unique digitiform projections bearing setae and a pair of spines.

Eratomyia magnifica, sp. n.

Diagnosis. As for the genus.

   Material examined. Holotype, ♂, ECUADOR, Quito-Baiza, E. Papallactam, 2,900m, 12–15 II 1971, L.G Peña col. (MZSP).

   Description. Total length, 5.58 mm. Wing length, 4.80 mm. Terminalia length, 0.22 mm.

   Male. Head (Fig. 7). Scape yellow. Antenna dark brown, 1st flagellomere 1.5 times longer than 2nd flagellomere; 4th flagellomere 4.4 times longer than wide, densely setose (both flagella broken). Frons light brown with some setae. Palpi yellow, except darker segment 1, very long, twice length of head, palpiger plus 4 palpomeres, last segment 1.5 longer than penultimate. Labella yellow. Stipes long, shining yellow. Occiput dark brown. **Thorax** (Fig. 8). Scutum shining blackish brown, with pair of rows of dorsocentral setae. Scutellum blackish brown. Pleural sclerites shining blackish brown, except for katepisternum, covered with silvery pruinescence, and brownish episternum II. Halter brownish yellow, base longer than scape. Episternum I not particularly developed. Epimeron I triangular. Anepisternum bare, anepisternal cleft deep, suture reaching primary anapleural suture. Katepisternum with pair of setae dorsally. Suture between katepisternum and laterotergite nearly vertical. Midpleural pit absent. Mesepimeron long, with 9 setae, suture extending from dorsal margin. Suture between laterotergite and mediotergite deeply concave. Mediotergite high, only slightly curved. Metepisternum well developed, metepimeron discernible. Mesopleurotrochantin apparently absent, a small, triangular sclerite present at contact between katepisternum, mesepimeron, and anterodorsal extension apparently not homologous. **Legs.** Coxae long, brownish yellow at base, trochanters brownish, femora yellow, long, tibiae ocher-brown, tarsi brown. Spurs 1-2-2. Tibia 1 with spur on inner ventral apex, and modified area at inner apex bearing regular row of setae (Fig. 9). Meron clearly present on coxa II, in format similar to that

in some limoniids and in pachyneurids. **Wing** (Fig. 10)**.** Sc incomplete, reaching basal third of wing. R_1 long, reaching C beyond distal third. R_5 reaching C close to wing apex, running quite apart from R_1. r-m long, slightly longer than first sector of Rs. Medial fork short, M_{1+2} separating from M_{3+4} beyond half of wing. Basal cell wide, m-cu and M_{1+2} / M_{3+4} quite separated from base of R; m-cu long, gently curved. A_1 incomplete, absent on distal third, anal lobe reduced. **Abdomen.** Tergites 1–4 and 6 dark shining brown, tergite 5 yellow. Tergites wide, sternite narrow. **Terminalia** (Figs 11–15)**.** Terminalia black. Segment 8 normally developed. Sternite 9 triangular, laterally fused to gonocoxite to form synsternogonocoxite. Gonocoxites not projected beyond gonostyles, pair of digitiform processes arising inward distally, bearing some setae and pair of spines. Gonostyles more or less digitiform, directed inward, setose (without spines), with short tooth at apex. Aedeagus present with apodeme proximally and tegmen-like structure distally. Gonocoxal bridge well developed dorsal to aedeagus. Tergite 9 with pair of well-developed distal projections and deep mesal incision almost reaching anterior margin; projections with about 16 black spines. Tergite 10 present, weakly sclerotized, apparently fused to cerci (or with ear-like distal projections laterally).

Female. Unknown.

Etymology. The species name comes from the Latin word *magnificus*, meaning magnificent or splendid.

Ohakuneinae, subfam. n.

Type genus. *Ohakunea* Tonnoir & Edwards, 1927, here designated

Diagnosis. r-m perfectly longitudinal, "cubital fork" (separation between M_4 and CuA) strongly displaced to base of wing, M_4 hardly complete at base.

Genera included: *Ohakunea, Colonomyia, Cabamofa*, and *Rogambara*, corresponding to the *Ohakunea* group of Jaschhof (2005).

Colonomyia Colless

Colonomyia Colless, 1963: 305

Type species. *Colonomyia albicaulis* Colless, 1963: 305, by original designation

Diagnosis. First sector of Rs very short, transverse. R_1 short, reaching C just before middle of wing. Apex of M_{1+2} and base of medial fork very faint or absent. Base of M_4 also very weak. M_{1+2}/M_{3+4} longitudinal, aligned with r-m and second sector of Rs; r-m completely longitudinal, longer than R_1. M_4 connecting directly to CuA, very close to base of wing or complete at very base. Katepisternum in contact with laterotergite, obliterating ventral half of mesepisternum. Meron absent. Gonocoxites fused to each other mesally along considerable length; gonostyle digitiform, with wide base and slender apex; ejaculatory apodeme quite long.

Colonomyia brasiliana, sp. n.
(Figs. 20, 21)

Diagnosis. *Colonomyia brasiliana* differs from the other species of the genus by the long area of connection between the gonocoxites mesally, and the extension of the enlarged area of the gonostyle.

Material examined. Holotype (on permanent slide mount), ♂, BRAZIL, State of São Paulo, Salesópolis (Boracea), 14.viii.1947, E. Rabello & Trav. F. Paratypes, 3 ♂♂, same data as holotype, but viii.1949, Lane & Coher col. (MZSP); 1 ♂, same data as holotype, but viii.1947, J. Lane col. (MZSP).

Description. Total length, 2.24 mm. Wing length, 2.30 mm. Terminalia length, 0.24 mm; Gc length mesally, 0.12 mm; Gs length, 0.16 mm; aedeagus length, 0.18 mm. **Male. Colour.** Antenna brown. Palpus light brown. Frons and occiput brown. Scutum and scutellum shining brown, lighter at borders. Pronotum, proepisternum, and proepimeron yellow-brown. Anepisternum brown, katepisternum brown, light brown on ventral third; mesepimeron, laterotergite, and mediotergite brown; metepisternum light brown. Pedicel of halter yellow, capitulum brown. Coxae and femora yellow-brown, fore femur darker; tibiae and tarsi light brown, darker to apex. Segment 1 light brown, segments 2–8 brown. Terminalia brown. **Head.** Scape, pedicellus, and flagellum brown, scape and pedicellus with few setae, pedicellus almost round. Antenna with 14 flagellomeres, first flagellomere 1.5 times length of second flagellomere; fourth flagellomere 3.2 longer than width; flagellomeres of apical half of antenna with distal neck. Frons brown. Palpus short, not longer than head, with 4 palpomeres, last segments about 1.5 times longer than preceding one; third segment without sensilla. Labella short, with few setulae at apex. Ocelli almost in line. **Thorax.** Some few, fine setae on postpronotum and proepisternum, no setae on remaining pleural sclerites. Scattered weak setae on mesonotum, with row of longer acrostichal setae; many small scutellar bristles and about 4 longer setae; irregular row of 5 or 6 stronger supra-alar and 2 prescutellar setae. Proepimeron long and slender distally. Anapleural suture very weak. Mesepimeron nearly absent at ventral third, katepisternum apparently fused to laterotergite. Laterotergite slightly projected outward on ventral half; mediotergite high, slightly curved; postnotal phragma short, ventrad to mediotergite, not projected into abdomen. Row of 4 or 5 setae at distal half of pedicel of halter. **Wing.** Macrotrichia on both faces of wing membrane and on dorsal face of all wing veins. Sc incomplete, short, sc-r absent. R_1 relatively short, reaching C slightly beyond middle of wing. First sector of Rs very short, perfectly transverse, close to basal third of wing; R_5 running quite close to C, abruptly approaching margin at wing apex; C produced beyond R_5, nearly reaching M_1. r-m perfectly longitudinal, very long. Medial fork very weak, nearly vanishing. M_4 detached from CuA at the base, CuA strongly curved to margin at distal fourth. A_1 not traceable. **Legs.** Tibial spurs 1:2:2, spurs thin, about as long as width of tibiae at apex, mid and hind spurs of equal length. Apex of front tibia with modified area bearing regular row of thin setae, plus some scattered setulae. Strong tooth basally on tarsal claws. First tarsomere more than twice length of second tarsomere of all legs. No regular row of setae distally on mid and hind legs. **Abdomen.** Sternite and tergite 1 light brown, 2–8 brown, terminalia brown. **Terminalia.** Gonocoxites fused to each other mesally, with mesal suture, distally projected laterally; syngonocoxite well developed. Gonostyle digitiform apically, slightly curved, wide at basal two thirds, slender apically, with fine, long scattered setae at basal two thirds. T9 wide and short, well sclerotized. T10 present, weakly sclerotized, with cerci lobose.

Female. Unknown

Etymology. The species name refers to the geographical origin of the examined material, Brazil.

Comments. This species diverges from other species of the genus especially in features of the male terminalia. It shares with *Colonomyia borea* Hippa & Jaschhof, 2004 the long connection between the gonocoxites mesally, but the wide part of the gonostyle basally is more extensive in *C. brasiliana*, sp. n.

Colonomyia freemani, **sp. n.**
(Figs. 22–27)

Diagnosis. This species differs from other *Colonomyia* species by the slender syngonocoxite and the short enlarged base of the gonostyle.

Material examined. Holotype, ♂, CHILE, Dalcahue, I. Chiloé, iv.1968, L. E. Peña col. Paratypes, 8 ♂♂, 4 ♀♀, same data as holotype; 4 ♂♂, 1 ♀ same data, but ii.1962; 1 male, Osorno, Pucatrihue, ii.1967, L. E. Peña col. (MZSP).

Description. Male. Total length, 2.30 mm. Wing length, 2.66 mm. Terminalia length, 0.22 mm; Gc length mesally, 0.06 mm; Gs length, 0.135 mm; aedeagus length, 0.13 mm. **Female.** Total length, 2.30 mm. Wing

length, 2.40 mm. **Male. Colour.** Antenna brown. Palpus light brown. Frons and occiput dark brown. Scutum and scutellum dull dark brown, lighter at anterolateral borders. Pronotum, proepisternum, and proepimeron yellow-brown. Katepisternum brown on dorsal two thirds, yellow on ventral third. Anepisternum, mesepimeron, laterotergite and mediotergite brown; metepisternum yellow. Pedicel of halter yellow, capitulum brown. Coxae and femora yellow-brown, tibiae and tarsi light brown, darker to apex. Segment 1 yellow-brown, segments 2–8 brown. Terminalia brown. **Head.** Scape and pedicellus with few setae, pedicellus almost round. Antenna with 14 flagellomeres with fine, scattered setae, first flagellomeres 1.3 times length of second flagellomere; 4th flagellomere 4.8 longer than width. Last segment 1.5 times longer 3rd segment. Frons brown, with scattered setae. Palpus short, not longer than head, 4 segments of about same length, with some few scattered setae, no sensorial pit. Third segment without sensorial pit. Cardo-stipes elongated, weakly sclerotized, with 2 setae. Ocelli almost in line, separated from each other by width of ocellus. Eye bridge incomplete, separated by twice width of ocellus. **Thorax.** Some few, fine setae on postpronotum and proepisternum, no setae on remaining pleural sclerites. Scattered weak setae on mesonotum with row of longer acrostichal setae; many small scutellar bristles, with about 4 longer setae. Irregular row of 5 or 6 stronger supra-alar setae; 2 prescutellar setae. Proepimeron long and slender. Anapleural suture absent. Mesepimeron nearly absent at ventral third, katepisternum apparently fused to laterotergite. Laterotergite slightly bulging, mediotergite high, only slightly curved at ventral third; postnotal phragma short, ventrad to mediotergite, not projecting into the abdomen. Row of 5 or 6 setae at pedicel of halter. **Legs.** Tibial spurs 1:2:2, spurs thin, about as long as width of tibiae at apex, mid and hind spurs of equal length. Apex of front tibia with modified area bearing regular row of setae. Strong tooth basally on tarsal claws. First tarsomere more than twice length of second tarsomere of all legs. No regular row of setae distally on mid and hind legs. **Wing.** Sc incomplete, quite short, sc-r not present. R_1 relatively short, reaching C not much beyond middle of wing. First sector of Rs very short, perfectly transverse, close to basal third of wing; R_5 running quite close to C, abruptly approaching margin at apex; C produced much beyond R_5, nearly reaching M_1. r-m perfectly longitudinal, very long. Medial fork weak, nearly vanishing. M_4 detached from CuA at base, CuA strongly curved to margin at distal fourth. A_1 not traceable. **Abdomen.** Segments 1–8 well sclerotized, with scattered setae on tergites and sclerites; segment 8 produced, tergite more sclerotized than sternite, not too short. **Terminalia.** Gonocoxites fused to each other mesally, forming mesal suture, projecting distally at sides; syngonocoxite short. Gonostyle digitiform, curved, wide at basal half, slender at distal half; long, fine scattered setae at basal two thirds. T9 wide and short, well sclerotized. T10 present, weakly sclerotized, with short, lobose cerci.

Female. As for male. Body length, 2.16 mm. Wing length, 2.66 mm.

Etymology. This species is named after Paul Freeman, English entomologist who made an important contribution to the description and understanding of the diversity of a number of dipteran groups, including the fauna of southern Argentina and Chile.

Comments. The general digitiform shape of the gonostyle of *C. freemani* is quite similar to that of *C. borea* and *C. brasiliana*, but with the enlarged base shorter. The gonocoxites, however, are fused along a short extension, which is shared in the Neotropical species of the genus perhaps only with *C. magellanica* Matile & Duret. It differs from *C. magellanica* by the shape of the gonostyle, with a short distal projection.

Colonomyia **sp.**
(Figs. 28–31)

Material examined. ♀, ARGENTINA, Rio Negro, Nov1926, R&E Shannon, Porto Blest, xii.2.26; ♀, CHILE, 49°S. Puerto Edén, Isla Wellington, 28-XI-1958. 1300 ft., Royal Society Chilean exped. 1959 (NHM).

Description. Male. Unknown. **Female.** Total length, 3.16 mm. Wing length, 3.28–3.52 mm. **Head.**

Scape, pedicellus, and flagellum dark brown, flagellomere, long, 4.0 times width, and densely setose (both flagella broken). Frons light brown with some setae. Palpus yellow, except darker segment 1, very long, twice length of head, last segment 1.75 times longer than penultimate. Labella yellow. Stipes long, shining yellow. Occiput dark brown. **Thorax.** Shining blackish brown with pair of rows of dc setae. Scutellum blackish brown. Pleural sclerites shining blackish brown, except katepisternum covered with silvery pruinescence, and brownish episternum II. Halter brownish yellow. Coxae long, brownish yellow at base, trochanters brownish, femora yellow, long, tibiae ochre-brown, tarsi brown. Tibia 1 with spur on inner ventral apex, and unmodified area on apex with row of setae. **Abdomen.** Tergites 1–4 and 6 dark shining brown, tergite 5 yellow. Tergite 1 large, sternites narrow, not visible on dry specimen. Genitalia black.

Comments. These two females seem to be conspecific and present some differences in relation to the remaining specimens of *Colonomyia*. The female terminalia resemble those of *C. magellanica* (Hippa & Jaschhof 2004, Fig. 20), possibly due to plesiomorphy. The specimens are considerably larger than all remaining species of the genus, with more than 3.0 mm total length and wing length, whereas all other Neotropical species vary from 1.9 to 2.8 mm. Differences in a number of features between *Colonomyia* sp. and the remaining species of the genus resulted in topologies in the phylogenetic analysis in which the species fits either with the remaining specimens of *Colonomyia* or closer to *Ohakunea*. Knowledge of the male is needed before drawing further conclusions.

Ohakunea **Tonnoir & Edwards**

Ohakunea Tonnoir & Edwards, 1927: 799
Type species. *O. bicolor* Edwards, 1927: 799

Ohakunea chilensis **Freeman**
(Figs. 32–37)

The species has been redescribed recently by Jaschhof & Hippa (2003), and no additions are necessary. We illustrate here some aspects of the species important for character analysis.

Material examined. 1 ♂, S. CHILE, Llanquihue prov., Casa Pangue, F. & M. Edwards, 4–10.xii.1926, B.M. 1927, Paul Freeman det.; 2 ♂♂, CHILE, Dalcahue, I. Chiloé, i.1962, L. E. Peña col., Det. D. S. Amorim 1983; 1 ♀, same data, but iv.1968, L. E. Peña col., Det. D. S. Amorim 1983 (MZSP).

Cabamofa **Jaschhof**

Cabamofa Jaschhof, 2006: 328
Type species. *Cabamofa mira* Jaschhof

Cabamofa mira **Jaschhof**
(Figs. 38–47)

Material examined. 1 ♂, COSTA RICA, Turrialba, Nov. 1922, Pab. Schild, A.L. Melander Collection 1961, D.S. Amorim, det. (NMNH).

The original description of the species is sufficiently detailed. Illustration of some structures helps the phylogenetic discussion (Figs. 38–43). The male terminalia are described and illustrated here for the first time (Figs. 44–47).

Male terminalia. The gonocoxites are fused mesally along a considerable distance and they do not

project distally beyond the distal margin of this syngonocoxite plate (Fig. 44). The gonostyle is trifid, with a digitiform projection more distally and an additional more basal projection that widens to the end; fine setae cover the gonostyle (Fig. 45). The ejaculatory apodeme extends a short distance distally as a flat sclerite, bifid at the apex. The aedeagus forms a wide plate behind the ejaculatory apodeme, the aedeagal apodemes forming a pair of basal, lateral projections (Fig. 46). Tergite 9 is well developed, with some spines on the distal corners and scattered setae; tergite 10 is membranous and apparently fused distally to the lobose cerci (Fig. 47).

Sciaroidea Billberg

Sciaraedes Billberg, 1820: 121
Sciaridae Skuse, 1888: 22, 24
Sciaroidea McAlpine *et al.*, 1981: 2; Wood & Borkent, 1989: 1351

Families included: Sciaridae.
  Diagnosis. As for the family Sciaridae.
  Comments. The position of the family is sister to all other Mycetophiliformia families except the Cecidomyiidae. Because of the need for superfamily names for clades gathering groups of families (e.g., Keroplatoidea and Mycetophiloidea), the superfamily rank is restricted to the Sciaridae; and Hennig's name, Mycetophiliformia, for this higher clade in the Bibionomorpha is recovered. Moreover, one of the reasons for the name Sciaroidea being applied to the Mycetophiliformia by McAlpine (1981) was the acceptance of Mycetophilidae *s. l.*, in which many smaller clades appeared as subfamilies.

Keroplatoidea Rondani

Ceroplatina Rondani, 1856: 40, 191
Keroplatidae Tuomikoski, 1966: 255

Families included: Ditomyiidae, Bolitophilidae, Diadocidiidae, Keroplatidae.
  Description. Flagellomeres cylindrical or flattened, 14 segmented in all families except ditomyiids; maxillary palpus with palpiger and 4 or fewere palpomeres; with few exceptions, 3 ocelli present, close to each other. Mesepimeron high and slender, sometimes absent ventrally by fusion of laterotergito to katepisternum; laterotergite at least slightly protruded, in some groups highly projected outward; mediotergite plesiomorphically high and slightly curved, secondarily folded in some keroplatids. R_4, when present, originating more apically in wing, almost always connecting C, only exceptionally R_1, as in some species of *Bolitophila*; r-m, when present, nearly transverse (secondary condition); cell r5 usually wide; medial fork usually long; bM typically absent, with exception of *Bolitophila*, *Arachnocampa*, and few keroplatids, as *Palaeoplatyura*; m-cu connecting more distally to CuA, except in *Bolitophila*; A_1 plesiomorphically complete, incomplete in few groups.
  Comments. The set of families within the Keroplatoidea have the "cubital fork" (actually, the connection of m-cu to CuA) displaced secondarily to a distal position – different from the condition in the remaining families of Mycetophiliformia, such as the Sciaridae, Cecidomyiidae, and Rangomaramidae, which have a very basal "cubital fork". The condition in the Mycetophilidae is nonhomologous, with a secondary distal fusion of M_4 to CuA. This clade appears in all analyses performed here, as well as in one of the reconstructions of Hippa & Vilkamaa (2005).

Mycetophiloidea Newman

Mycetophilites Newman, 1834: 379, 386
Mycetophilidae Macquart, 1838: 76
Mycetophiloidea Malloch, 1917: 182, 246

Families included: Lygistorrhinidae, Mycetophilidae.

Description. Flagellomeres cylindrical or flattened, 14 segmented, with few exceptions. Maxillary palpus with palpiger and 4 or fewer palpomeres; 3 ocelli usually present, sometimes 2, 1, or no ocelli present, lateral ocelli often displaced to margin, contacting eye margin. Mesepimeron slender, sometimes absent ventrally by fusion of laterotergite to katepisternum; laterotergite protruded, in some groups reduced in size and strongly projected outward; mediotergite shorter and curved, in some cases very reduced in height. R_4, if present, transverse, connecting to R_1; r-m oblique or longitudinal (secondary condition), more or less elongated; cell r5 usually slender; medial fork long or short; true m-cu seldom present, as in *Loicia*, usually connection of M_4 to CuA secondary, more distally in wing; A_1 always incomplete. Abdomen with basal constriction, more evident than in Keroplatoidea; segment 8 very short.

Comments. The Mycetophiloidea include only the Lygistorrhinidae and Mycetophilidae. *Lygistorrhina* and *Probolaeus* are apomorphic within the lygistorrhinids, with many wing veins incomplete, but some more plesiomorphic genera, such as the fossil *Archaeognoriste* (Blagoderov & Grimaldi 2004), have more complete wing venation. Most Mycetophilidae have a distal, secondary fusion of M_4 to CuA. Some mycetophilid genera, such as *Loicia*, are particularly plesiomorphic, with M_4 extending to the base of the wing, where it meets bM, which extends into a short true m-cu. It is beyond the scope of our study to investigate the position of these genera in relation to the Lygistorrhinidae and the remainder of the Mycetophilidae genera, although this is a question to be examined in future studies.

Character analysis

The data matrix is in Table 3, and the topologies of the different runs of the matrix (described in Table 1) are in Figs. 48–67. The topology accepted here corresponds to analysis 8 in Table 3. Figure 68 has that topology, with all characters of unique origin placed on their respective nodes. Homoplasies referring to characters 1–67 are placed at the top of the terminal taxa line clades in Fig. 68, whereas homoplasies of characters 68–126 are in Fig. 69. Comparative drawings of the head, thorax, and wings are in Figs. 118–203.

Details about the level of origin, hypotheses of primary homology, coding, multiple origin, reversion, ACCTRAN and DELTRAN options, and alternative interpretations of secondary homology with more steps are considered in the discussion of characters below.

1. Ocelli: 0. present; **1.** middle reduced; **2.** absent

The ocelli have been lost many times in the evolution of the Diptera. In the Bibionomorpha, the loss of the median ocellus is seen in some mycetophilid genera and in some keroplatids (e.g., some *Keroplatus* species). The ocelli are completely lost four times, twice within the Cecidomyiidae and once in the clade (*Rogambara* + *Cabamofa*) and within the keroplatid subfamily Sciarokeroplatinae (Papp & Sevcik 2005).

2. Median ocellus: 0. normal; **1.** sunken

A sunken ocellus is known only in *Megalopelma* (Mycetophilidae).

3. Lateral ocelli: 0. at apex of head; **1.** in contact with or very close to eye

TABLE 3. Complete Sciaroidea data matrix used in the study, with 65 terminal taxa and 137 characters.

```
                    00000 00001 11111 11112 22222 22223 33333 33334 44444 44445 55555 55556 66666 66667 77777 77778 88888 88889 99999 99990 00000 00001 11111 11112 22222 22223 33333 33
                    12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67
Edwardsomyia        2--00 00000 10000 0?010 ?0010 10010 00011 00120 00000 ?0000 00001 00000 00001 --001 00000 00000 10-0- -010- 0000? 1-0?? ?0010 ????? 0?0?0 1000- 1?--- ----- 33
Trichocera          00000 01000 10000 0?010 00000 10011 11110 0000? ????? ?0000 00100 ?0000 00001 --000 00000 10001 -0-10- 00000 00000 1-000 01110 02???- 10??? ?000- 10??? ????? 67
Olbiogaster         00000 00000 0?010 01000 00100 00000 11110 10011 10011 ?0000 00100 01110 00011 --000 00001 10001 --000 00000 00000 1-000 11110 00030 20000 13000 ----- ----- ??
Sylvicola           00000 00100 00100 00100 00100 00000 01110 10011 10011 ?0000 01010 02110 00011 --000 00001 10001 --000 00001 00000 01110 11111 00000 07101 0000- 00000 00000 00
Cramptonomyia       00000 00100 00000 00?20 00100 00000 10000 00011 01000 02000 01000 1-110 00011 03000 00001 10100 -1100 00001 00000 11111 10000 00030 20000 13000 00000 00000 00
Hesperinus          00000 01300 00000 00110 10000 00011 11011 01000 01010 01000 10011 ?0000 10001 10001 01000 1-100 00001 00000 00000 11111 11111 11011 10010 07000 00000 00000 00
Penthetria          00000 01310 00000 ??110 11011 10011 11010 01010 01010 01000 00000 01000 101-0 10001 01000 1-100 00001 00000 00000 1-011 10010 00100 03100 00001 00000 00000 10
Plecia              00001 ?1410 00000 00110 ?0000 11011 11010 10011 1?010 01000 10001 01000 101-0 10001 010-- 1-0?? ????? ?0000 00000 1-0?? 11110 01100 01100 0000? 10000 00000 10
Catotricha          2?-0? ??21? ????? ??2?? ?2021 ?1021 11110 010-0 00100 01111 1-200 0101- 101-1 --200 00022 -1-10 3-0-- 01110 0000? ?-011 0???? ?2?00? 0???? ?000- 12000 00110 01
Lestremia           00001 00510 00000 00010 ?1021 01010 11110 010-1 01111 01111 1-210 0101- 101-1 -300 00022 -1-1- 3-0-- 1--10 01011 ?-011 00000 07110 0012? 10000 02000 00110 01
Porricondyla        20-01 00010 07010 00010 11021 01010 11110 01?-1 01111 01111 1-212 --1122 1-20 -1122 00022 -1-1- 3-0-- 1--10 01011 0--0 00110 02160 1?10- 12000 02000 00110 01
Asphondylia         20-01 00200 03000 00101 10111 11110 11110 10011 10011 10011 1-100 111-1 1-20 -1-102 -00022 -1-10 3-010 0-110 1-011 0-010 00110 02100 00000 0000- 00000 00001 00
Apelmocreagris      00001 00100 01000 00130 10111 11110 11100 10011 10011 10011 1-100 111-1 1-02 2101- 00022 -1-11 3-010 0-110 1-011 1-010 00110 00100 00000 00000 02000 00001 00
Trichomegalosphys   00001 00100 01000 00130 11010 10011 11100 11100 11100 0201- 1-200 111-1 1-02 2102- 00022 -1-11 3-010 0-010 1-011 1-010 11110 00100 00000 02000 00001 00
Bradysia            00001 00100 01000 00130 11010 10110 11110 10110 10110 10110 1-200 101-1 1-02 2101- 00022 -1-11 3-010 0-110 1-011 1-011 11110 00001 00100 00001 11000 11000 00
Diadocidia          00000 01100 00000 00150 10011 01110 11110 10010 10010 1-010 1-010 101-1 -000 0101- 00022 -1-10 0-001 00000 00000 00001 04100 00000 11001 11000 00
Ditomyia            00001 01010 01010 00160 00111 01110 11111 01110 01110 10011 1-001 -101- 2-001 -00022 -1-00 2-001 00000 11110 00001 01100 20002 02001 10000 00
Nervijuncta         00001 01010 01010 10160 00111 01110 11111 11111 01110 10011 1-110 -101- 2-001 -101- 10022 -1-00 2-001 00010 01111 00001 01100 20140 2?-?? ?2--- ----- -0
Symmerus            00000 00120 00110 ??150 00111 11021 11111 2?110 ?1110 01011 1-000 0101- 2-000 -101- 00022 -1-00 2-001 00000 10001 02110 01110 00002 02001 10000 00
Australosymmerus    00000 00120 00010 10150 00121 11110 11111 1?110 ?1110 11011 1-000 0101- 1-000 0101- ?1110 -1-00 0-001 00000 11001 02110 01110 03100 20002 02001 00
Melosymmerus        00000 10120 00110 10150 00121 01101 11111 1?110 01110 11011 1-010 0121- 00012 -00022 -1-00 0-001 00000 11011 01110 00100 02110 20002 02--- ----- -0
Bolitophila         00100 10000 00000 00130 10000 00011 11111 00011 00010 11000 11000 1?000 12?00 00012 -121- 0101- 00100 01111 10011 11011 00110 20100 00100 10000 00
Arachnocampa        00000 01100 ??120 ??150 ?2120 01100 01111 01100 02110 2?110 0001 -000 01201 0002- -1210 00001 00100 1-011 20100 11011 01111 00150 02??? ?2??? ?1001 11000 00
Paleoplatyura       00000 ??200 ?2?50 2?011 2112? ?11?? ?2?20 20110 01?20 ?2110 01200 00022 -1210 10001 1-0?? ?2120 11111 1-021 ?2??? 22??? 01001 11000 00
Macrocera           00000 00100 00000 01150 11212 01101 11110 10110 01110 00011 02110 01010 1111- -12-- --111 -1-- 00022 --121 10000 01010 1-010 11111 10001 01001 11000 00
Orfelia             00000 00100 00000 01150 11212 11101 11110 00110 00110 01010 01010 01010 1111- -12-- -021 -1-10 00022 -1-10 00000 01111 1-010 11111 00110 05100 00000 1?001 11000 00
Platyura            00000 00?00 01000 ?1150 10011 11101 11100 00110 01010 02011 0-01-0 1211- -021 -1210 1-001 00000 11111 1-011 01110 0?1?0 0???? ?2?00 11000 00
Keroplatus          2-000 00100 03--0 11150 10011 11101 11000 00110 0?200 01011 1-011 1211- -12-- 1-001 1-10 3-010 1-0?? ?2120 11111 1-011 00110 0?1?0 ?2??0 11000 00
Rhynchoheterotricha 0?000 ?11?? 1?20? ?1150 00011 07?11 11210 10112 ?21?? ?2110 1-001 1211- -12-- 1-001 1-10 3-010 1-0?? ?2??? ?2??? 22??? 01110 0?1?0 0500- 12001 11000 00
Kenyatricha         00000 ?11?? 0?20? ?212? 1?21?? ?21?? 11110 10110 1?220 ?2?20 00011 -000 1102- -000 3-010 0002? ?2??? ????? 00010 0?221 0---- -?--- -?--- --
Insulatricha        00000 02100 00100 ??150 00111 11110 10110 20011 1-010 1101- -000 1101- -000 3-010 02000 00010 00011 00121 ?---- -?--- --
Chiletricha         00000 01100 00100 10140 10011 11110 11100 00011 01000 01000 1102- -000 3-010 00010 00011 05111 01001 01--- -?--- --
Eratomyia           00000 01?00 01200 10150 01010 01110 11100 00110 1-000 1112- -002 3-010 10011 00210 40111 ?---- -?--- --
```

TABLE 3 (continued).

Rangomarama	00000	01100	00000	1?150	1001?	111?0	01111	11110	10120	1??-0	10010	22100	101-1	--000	1101-	00022	-1-00	3-010	01110	1-0??	?????	?????	10110	00100	00002	01---	--
Heterotricha	00000	00100	00000	??240	10011	11110	0?111	11100	1?11?	??200	01011	?1100	111-1	--000	1121-	00022	-1-10	3-010	01110	00022	?00??	2?120	00?00	00011	0?---	--
Ohakunea	00000	22100	00100	00050	10011	11110	01111	11100	1011?	?1011	?1011	1-0-1	--1-1	--002	2102-	10122	-1-1-	3-01-	11110	00010	010-1	00110	17100	0100-	1?---	--
Colonomyia sp.	00000	00100	00160	00160	10011	11110	01111	11110	10100	1-200	12011	1-200	111-1	--102	2102-	10122	-1-1-	3-01-	11110	00011	11111	00010	06100	01002	0?---	--
C. brasiliana, sp.n.	00000	00100	00000	00160	10011	11110	01?11	11110	10110	10100	12011	1-200	111-1	--102	2102-	10122	-1-1-	3-01-	11110	00011	11111	10010	12?20	01002	0?---	--
Cabamofa mira	20-01	00100	00010	00160	10011	11100	01111	11110	00110	10100	00011	1-0-2	--1-1	--000	211--	10222	-1-10	3-010	11110	1-010	01011	10010	06100	0100-	11---	--
Rogambara	2--01	07100	00000	02060	10011	11110	01101	11110	10140	1?1?0	02011	1-111	111-1	--000	-112-	10122	-1-10	3-010	01110	1-0??	?????	2?120	06100	0100-	11---	--
Probolaeus	00000	00100	12--0	11150	00011	11212	11111	11100	10131	11010	02010	1-110	111-1	--100	110--	00222	-1-1-	2-01-	1-110	0-1-1	-11-2	01110	00100	00002	0?001	10000	00
Taxicnemis	0?00?	0?2??	0????	?????	?????	11111	1?2??	?2??0	?011?	?011?	02011	1-010	101-0	--010	1102-	00022	-1-1-	3-01-	11110	0007?	0-1-1	2?120	01200	0---	-?---	--
Loicia	??70?	?????	?????	?????	?????	?????0	?????	?????0	?211?	?????0	00010	01000	111-0	02000	1101-	00022	-1-10	3-010	00110	0007?	?????	????0	0?2??	??-??	?????	??
Freemanomyia	0?000	?11??	00?0?	?21??	?????	11?10	0?211	????0	1011?	02010	01000	111-0	01000	101-0	1101-	00022	-1-10	3-010	01110	0-0??	?????	????0	20100	0---	-?---	--
Starkomyia	00010	07100	00200	??750	10011	11110	01111	11110	10111	17?70	01000	111-0	02000	101-0	1101-	00022	-1-10	3-010	01110	07000	00011	07110	00100	0---	-?---	--
Drepanocercus	00010	00100	00010	01150	10011	11210	01111	10110	10110	10010	01000	111-0	02001	1121-	00012	-1-1-	3-010	0-110	01010	00010	01010	11002	??????	2000?	0?001	10000	00
Paratinia	00110	00100	01150	10011	11211	11110	10110	10110	10010	01000	111-0	02001	1101-	00022	-1-11	3-010	0-010	01110	11002	01??	????0	01110	2100?	21001	10000	00
Coelosia	00000	00101	00001	01150	10111	11211	11111	11110	10110	1-000	01000	111-1	--002	1120-	00022	-1-11	3-000	0-010	01110	11012	01110	01110	00100	0100?	01001	10000	00
Boletina	00000	00101	01150	10011	11211	11111	11110	10010	10010	01000	111-1	--001	1120-	00022	-1-11	3-000	0-010	01110	11012	01110	00100	01110	00100	01001	10000	00
Tetragoneura	10101	00021	01150	10011	11211	11111	11110	12011	0-021	111-0	02002	1101-	00022	-1-11	3-000	0-010	1-0-0	11110	10002	02100	01110	02000	01001	10000	00
Dziedzickia	10000	10101	11150	10011	11211	11111	11100	11010	0-000	101-0	02101	1120-	00022	-1-11	3-000	0-010	1-010	01110	10002	0000-	01110	10700	01001	10000	00
Megalopelma	01000	12101	01150	10011	11211	11111	11100	10010	00000	111-0	02100	1120-	00022	-1-11	3-000	0-010	00000	00110	00120	0012?	2000?	0012?	21001	10000	00
Neoempheria	10101	01101	01151	10011	01211	11211	11110	10011	10010	101-0	02100	1101-	00022	-1-11	3-000	1-011	11110	10012	01110	00100	00120	01001	10000	00
Monoclona	1-000	10101	11151	10011	11211	11111	11000	10010	00000	111-1	--100	1120-	00022	3-000	--10	00000	01110	10012	10100	0???	?1001	10000	00
Acnemia	00000	10101	11151	10011	11211	11111	11000	10010	01110	111-1	--100	1120-	00022	3-----	--10	00100	01110	10012	01100	0????	?1001	10000	00
Leia	00100	10101	11151	10011	11211	11111	11100	01010	0-020	111-1	--102	1100-	00022	-1-11	3-000	0-010	1-010	01111	30100	00002	01001	10000	00
Manota	00000	10101	00021	011-1	10011	11312	11100	11010	02011	1-211	111-1	-102	11---	20122	-1-11	3-010	0-011	1-0-0	0-110	-0012	30100	30100	01001	10000	00
Trichonta	00100	10111	11141	10011	13311	11100	10110	01011	1-000	111-1	--001	1120-	00022	-1-11	3-000	0-012	1-010	01110	0012?	04100	0000?	21001	10000	00
Rymosia	10100	10101	11151	10011	13311	11110	11000	01011	1-000	111-1	--001	1120-	00022	-1-11	3-020	1-0-0	01110	11112	01110	00100	00002	01001	10000	00
Sciarosoma	00000	?11??	0?00?	0015?	00011	11110	0??11	11110	10011	1-000	111-1	--001	2101-	00022	-1-10	3-010	01110	0???	?????	2?120	04140	0-----	-?---	--
Sciaropota	00000	?11??	0?00?	?????	00011	11110	0??11	11110	????0	10011	1-110	1101-	00022	-1-10	3-010	01110	0???	?????	2?120	04100	0-----	-?---	--
Afrotricha	00000	?11??	0????	?????	0?211	01?11	11110	1?11?	?????0	1-010	1101-	00022	-1-10	3-010	01110	0???	?????	2?120	00100	0-----	-?---	--
Antisotricha	00000	01100	00100	?2120	10011	11111	0??11	11110	10110	11010	101-1	--100	0102-	00022	-1-10	3-010	01110	00000	0000?	??120	05100	00002	01---	--
Nepaletricha	00000	?11??	0?70?	?????	11111	0?211	11110	12?1?	?????0	1-010	101-1	--000	0102-	00022	-1-10	3-010	01110	0007?	?	??120	05100	0-----	-?---	--

There is some variation in the precise position of the lateral ocelli, especially within the Mycetophilidae and the Keroplatidae. It is difficult to apply coding consistently for conditions intermediate between the most plesiomorphic (all three ocelli close together in an ocellar triangle) and the most apomorphic condition, with the lateral ocelli touching the eye margin. The most apomorphic condition in our study occurs in different mycetophilid genera. Additional states can be used in a study of mycetophilid phylogeny.

4. Cleft between median occellus and eye: 0. absent; **1.** present

This condition was indicated by Söli (1997) as a synapomorphy for (*Drepanocercus* + *Paratinia*), but in our analysis it was insufficient to sustain this small monophyletic group, with *Drepanocercus* in most trees appearing as the sister group of the Mycetophiloidea. This means that the character is homoplastic.

5. Eye-bridge: 0. absent (dichoptic); **1.** present, complete (completely holoptic)

A complete eye-bridge in the Bibionomorpha is independently acquired in *Plecia*, Cecidomyiidae, Sciaridae, *Nervijuncta*, and (*Cabamofa* + *Rogambara*). A number of intermediary conditions of incomplete eye-bridges can be seen in different higher Mycetophiliformia genera, but they are difficult to code and consistently apply in the analysis, so they were not included here.

6. Pedicel: 0. with short setae; **1.** with strong/long setae; **2.** without setae

Well-developed antennal pedicellar setae is a feature shared by most, but not all mycetophilid genera (Söli 1997). *Ohakunea* and one of the species of *Colonomyia* have no setae on the pedicel.

7. Antennal basal flagellomere: 0. same size as, or slightly longer, than other flagellomeres; **1.** 1.5 times longer than succeeding flagellomeres

The relative size of the scape, pedicel, and flagellomeres vary in different dipteran groups. Equal size of flagellomeres seems to be the plesiomorphic condition. The problem of the number of character states and of coding limits applies here. Different codings were tried, resulting in differences in the tree topology. Many mycetophilids, keroplatids, ditomyiids, and others have a long first flagellomere, but it does not reach 1.5 times the length of the second flagellomere. As the character is coded here, it is apomorphic in all Bibionidae, all Chiletrichinae, *Colonomyia*, *Rangomarama*, Ditomyiinae, *Bolitophila*, *Diadocidia*, and *Arachnocampa*, indicating many cases of independent development of the apomorphic condition. The condition in higher keroplatids seems to be secondary, because Bolitophilidae, Diadocidiidae, and *Arachnocampa* are apomorphic. The condition at the base of the Rangomaramidae is equivocal, but DELTRAN seems preferable here, with different acquisitions of the apomorphic conditions.

8. Flagellum: 0. 15 flagellomeres or more; **1.** 14 flagellomeres; **2.** 12 flagellomeres; **3.** 10 flagellomeres; **4.** 9 flagellomeres; **5.** 6 flagellomeres

The number of flagellomeres in the Diptera groundplan, according to Hennig (1973), is 14, as seen in most limoniids, including *Edwardsomyia*, and in many bibionomorphs. This condition is considerably stable in the Mycetophiliformia. A flagellum with 15 flagellomeres is seen, for example, in *Trichocera*. This condition in the Bibionomorpha is present only due to secondary acquisition, as in the Porricondylinae and in the Ditomyiidae. The last flagellomere in ditomyiids is actually very small and is a subdivision of the last flagellomere of other sciaroids. Gradual reduction of the number of flagellomeres is seen in Bibionidae and cecids. A high number of flagellomeres is seen in some higher cecid genera not sampled here.

9. Distribution of flagellomere setae: 0. haphazard; **1.** encircling rows; **2.** reduced in number

Plesiomorphically, flagellomere setae are irregularly distributed. Regular whorls of setae are independently acquired in different dipteran groups. Within the Bibionomorpha, they occur in bibionids, cecids (even

though there is secondary loss in the family), *Trichonta*, and Ditomyiinae, whereas the Symmerinae have a reduced number of setae.

10. Prementum: 0. distinct; **1.** reduced

A reduced prementum has been shown by Söli (1997) to be a synapomorphy gathering most mycetophilids (i.e., excluding *Drepanocercus* and *Paratinia*). This character is important to give structure to the internal relationships of the mycetophilids.

11. Clypeus: 0. normal, short; **1.** strongly projected to form proboscis

Within the limits of this study, an elongated proboscis is independently derived in *Rhynchoheterotricha* and lygistorrhinids, and to a lesser degree in *Bolitophila*. Other Mycetophiliformia genera, such as *Rhynchosciara* (Sciaridae), *Macrorrhyncha* (Keroplatidae), and *Gnoriste* (Mycetophilidae), also have independent development of a proboscis, but do not appear here as terminal taxa.

12. Maxillary palpus including palpiger plus: 0. 4 palpomeres; **1.** 3 palpomeres; **2.** 2 palpomeres; **3.** 1 palpomere

The number of maxillary palpal segments varies considerably within the families, and wildly in some, such as cecids. In the Bibionomorpha, a reduction from the condition of palpiger plus four articles to three articles occurs at the base of the Sciaridae, of the Ditomyiinae, of the Keroplatini, and independently in the genera *Paratinia*, *Neoempheria*, and *Trichonta*, and in several other Mycetophilinae not included here (Rindal & Søli 1997). Reduction directly to three articles occurs in the Lygistorrhinidae and to two segments in *Asphondylia* and *Keroplatus*. In the Lygistorrhinidae, there are further reductions, but this most plesiomorphic condition can be seen, for example, in the fossil genus *Archaeognoriste* described by Blagoderov & Grimaldi (2004) from Myanmar amber. The fact that there is no secondary homology between the apomorphic condition in different bibionomorph groups shows that there are probably different means by which the apomorphic condition is acquired, for example, by loss of the palpiger or by fusion of different segments.

13. Last palpomere: 0. at most 1.5 times length of preceding palpomere; **1.** longer than 1.5 times preceding palpomere

A longer last segment appeared at different times in Bibionomorpha evolution – in *Sylvicola*, within the Chiletrichinae, in the (*Ohakunea* + *Colonomyia*) clade, and twice in the Ditomyiidae. In the Mycetophilidae, most genera are apomorphic, but not *Drepanocercus*, *Paratinia*, and *Manota*. The condition in *Manota* is probably a reversion, whereas in the other two genera, it might be plesiomorphic. Additional conditions (of even longer and shorter last palpomeres) have been examined, but added more noise than stability to the analysis. *Rhynchoheterotricha* and *Kenyatricha* are not known for this feature.

14. Third palpomere: 0. as wide as other palpomeres; **1.** enlarged, at least twice size of other palpomeres; **2.** produced beyond 4th palpomere

The original third segment in many dipterans bears a sensorial pit with modified sensilla, and in most groups it is only slightly wider than other palpomeres. A particular development of the third segment is a synapomorphy of the Ditomyiidae, with a parallel origin in *Drepanocercus* and *Cabamofa*. This condition is also seen in *Cordyla* (Mycetophilidae), but this genus was not included in our study. A third segment projected beyond the base of the fourth segment occurs independently in the mycetophilid genera *Tetragoneura* and *Manota*.

15. Prescutum: 0. distinct; **1.** not seperable from presutural area

Söli (1997) indicated that the prescutum not separable from the presutural area is a synapomorphy for

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most mycetophilids, excluding genera such as *Paratinia* and *Drepanocercus*. This feature gives structure to the base of the Mycetophilidae and avoids the collapse of some higher genera to the base of the group, based on secondary losses.

16. Basisternite: 0. bare; **1.** with setae

17. Episternum I and basisternite: 0. fused; **1.** separate sclerites

These two characters were excluded from most runs in the analysis because they are difficult to verify and, hence, not reliable in the present data matrix, even though they are potentially informative. There are basisternite setae in *Chiletricha* and *Eratomyia*, as well as in different keroplatoid and mycetophiloid genera. Two main Bibionomorpha clades seem to present the episternum separate from the basisternite: the (Lygistor-rhinidae + Mycetophilidae) and the (Bolitophilidae + Diadocidiidae + Keroplatidae), with the Ditomyiidae plesiomorphic. *Trichocera* and *Olbiogaster* also have episternum I and the basisternite separate.

18. Episternum I: 0. bare; **1.** with group of setae

A bare episternum I is apparently plesiomorphic in Diptera, and proepisternal setae might be synapomor-phic for the Bibionomorpha. Secondary losses occur in the Cecidomyiidae, *Ohakunea*, and *Rogambara*.

19. Ratio of width of metepisternum (esIII w) at ventral end and mesepimeron ventral width (emII w): 0. 0.6–1.0; **1.** 1.1–1.4; **2.** 1.6–2.2; **3.** 2.5–2.6; **4.** 2.8–3.5; **5.** 4.0–6.0; **6.** katepisternum fused to laterotergite, mesepimeron not reaching ventral end of pleura (Figs. 70–76)

In the evolution of the Bibionomorpha, there was a long sequence of reduction of the width of the ventral end of the mesepimeron. The condition seen in the limoniid *Edwardsomyia* is the same as in bibionids and cecids, but the condition in *Trichocera* is apparently even more plesiomorphic and also present in the Aniso-podoidea. The mesepimeron in the Sciaridae is slightly more slender (state 4) than in cecids (state 3), whereas in most keroplatoids and mycetophiloids, the ventral half of the sclerite is reduced to a very slender strip (state 5), excluding the Sciaridae from a higher position in the Mycetophiliformia. The fusion of the katepisternum and the laterotergite (state 6) is seen in the Ditomyiinae and most Ohakuneinae, resulting in the mesepimeron being restricted to a dorsal, more or less triangular sclerite. In *Bolitophila*, *Arachnocampa*, *Chiletricha*, *Het-erotricha*, and *Trichonta*, the mesepimeron is more plesiomorphic than in most remaining members of the clade, corresponding to independent reversals. In *Trichonta*, this reduction is related to other distortions of the thoracic shape, with modification of the size of the metepisternum and the mesepimeron. The shape of the mesepimeron is constant within the families, which makes this an important feature pointing to the mono-phyly of all Mycetophiliformia except the Cecidomyiidae, and of all Mycetophiliformia except cecids and sciarids.

20. Primary anapleural suture: 0. present; **1.** absent

The loss of the primary anapleural suture appears in the cladogram as a single occurrence within the Myc-etophilidae. However, in Tozoni's (1998) and Söli's (1999) mycetophilid phylogenies, this is clearly a homoplasy between the Sciophilinae and higher mycetophilid genera, meaning that there is insufficient infor-mation here to correctly reconstruct the mycetophilid phylogeny. Correct optimization at the Mycetophilidae groundplan would show the primary anapleural suture present.

21. Midpleural pit: 0. absent; **1.** present

The midpleural pit is absent in *Edwardsomyia*, *Trichocera*, and in the Anisopodoidea, and the presence of a midpleural pit gathers most Bibionomorpha families in a single clade. There are secondary independent losses of this character in *Porricondyla*, lygistorrhinids, *Bolitophila*, and ditomyiids. In some groups, it is not

easy to determine whether or not the pit is present. Hippa & Vilkamaa (2005: 126) pointed out a number of intermediate conditions in the group.

22. Ventral half of mesepimeron: 0. straight or slightly inclined over katepisternum; **1.** strongly inclined

A marked inclination of the mesepimeron over the katepisternum is typical of the Sciaridae. A strong inclination is also seen in *Asphondylia*, but the shape of the sclerite is different.

23. Anterodorsal end of metepisternum: 0. fused to laterotergite or mesepimeron; **1.** reaching katepisternum (Figs. 77, 78)

In all Ditomyiidae genera, the dorsal end of the metepisternum reaches the katepisternum. A similar condition is seen in *Coelosia*.

24. Total height of laterotergite and mediotergite (md h): 0. equal to or smaller than anepisternum height (an h); **1.** higher than anepisternum (Figs. 79, 80)

A high laterotergite and mediotergite is another feature indicating the monophyly of all Mycetophiliformia except the Cecidomyiidae. This feature is constant within the families. Adding more states increases information but reduces the consistency index, because in some groups there is a parallel development of the anepisternum height. The apparent apomorphic condition in *Edwardsomyia* is due to a relative reduction of the anepisternum size, not to the development of the laterotergite, as seen in sciaroids.

25. Medio-posterior border of laterotergite: 0. straight, only gently concave; **1.** concave, projecting into mediotergite (Figs. 81, 82)

The limit between the laterotergite and the mediotergite in most non-brachyceran dipterans is typically straight. In the higher Mycetophiliformia, the laterotergite is concave posteriorly, projected into the mediotergite. This is another condition that is stable in most families and indicates that the Sciaridae do not belong in a higher position in the Mycetophiliformia phylogeny.

26. Area of laterotergite delimited by anterior margin and a line between anteroventral and anterodorsal angles: 0. large; **1.** narrow (Figs. 83, 84)

This is another relatively constant feature within families of the entire Bibionomorpha. This character is apomorphic in all higher sciaroids (except *Neoempheria*), and plesiomorphic in all sciarids and cecids. The reversion in *Neoempheria* is due to a secondary change in the shape of the thorax.

27. Dorsal margin of laterotergite: 0. largely in contact with membranous area below wing; **1.** laterotergite scarcely reaching dorsal margin of pleura (mediotergite displacing anterodorsal margin anteriorly)

The laterotergite plesiomorphically has a large contact dorsally with the membrane laterad to the scutum. In all Rangomaramidae, Keroplatoidea, and Mycetophiloidea, there is an approximation of the posterodorsal end of the mesepimeron and the anterodorsal end of the mediotergite, reducing (in some cases eliminating) the contact between the laterotergite and the membrane ventrad to the mesoscutum.

28. Laterotergite laterally: 0. flat; **1.** slightly projected outwards; **2.** produced over episternum III, with spiracle not in same plane as laterotergite; **3.** bulging, with projection covering posterior spiracle (Figs. 88–90)

The laterotergite is flat in most dipteran families. This condition is observable in all non-mycetophiliform bibionomorph families, including cecids and sciarids. In rangomaramids, ditomyiids, *Bolitophila*, *Diadocidia*, and *Arachnocampa*, a slightly projected laterotergite is seen. This laterotergite is independently modified twice, in most keroplatids and in the (Lygistorrhinidae + Mycetophilidae) clade, in which the laterotergite is strongly projected over the posterior spiracle. There is a condition even more modified in higher myceto-

philids and in some keroplatids. The condition in the Sciaridae is plesiomorphic, indicating a sister-group condition in relation to all Mycetophiliformia except cecids. This character was discussed by Shaw & Shaw (1948), and Söli (1997). In the coding of Hippa & Vilkamaa (2005), the character is apomorphic for the keroplatoids and mycetophiloids (including *Freemanomyia*), but it was not sufficient to gather these two clades in their analysis.

29. Laterotergite: 0. height versus width approximately equal; **1.** height at least 1.2 times laterotergite width (Figs. 91, 92)

This feature is a measure of the shape of the laterotergite, not its size relative to other sclerites. It is synapomorphic for all Mycetophiliformia except the Cecidomyiidae. There is a reversion in *Cabamofa*.

30. Mediotergite posteriorly: 0. nearly straight or slightly projecting in profile; **1.** curved in profile; **2.** nearly folded midway to tergite I (Figs. 93–96)

The shape of the mediotergite in profile shows important variation within the Bibionomorpha. More than three steps can be established, but other intermediary conditions would be difficult to code. The Ditomyiidae and *Drepanocercus* are plesiomorphic for this character, with a nearly straight mediotergite. The sister-group condition between Ditomyiidae and (Bolitophilidae + Diadocidiidae + Keroplatidae) and between *Drepanocercus* and the (Lygistorrhinidae + Mycetophilidae) clade implies two parallel acquisitions of the first apomorphic state. A strongly arched mediotergite is independently acquired in a clade including most keroplatids, in Lygistorrhinidae, and in *Manota*.

31. Ventral end of mediotergite: 0. just below dorsal end; **1.** displaced anteriorly

In most keroplatids, lygistorrhinids and most mycetophilids, the arched mediotergite has a displacement of the postnotal phragma to a more anterior position. *Drepanocercus* is plesiomorphic for this feature. This feature has been illustrated by Jaschhof (2004c).

32. Meron: 0. produced; **1.** not detectable

Some confusion exists in the literature about the meron within the Bibionomorpha. A meron attached to the mesocoxa is plesiomorphic in Diptera (also present, e.g., in the Mecoptera) and in the Bibionomorpha is preserved in the Anisopodoidea, Pachyneuridae, Bibionidae, and most Cecidomyiidae. Within the Mycetophiliformia, the meron is entirely absent in most genera, but is present in the Chiletrichinae and in Bolitophilidae. The shortest tree would point to the loss of the meron as a synapomorphy of the Sciaridae+, with secondary independent reacquisitions in Chiletrichinae and Bolitophilidae. This seems quite unexpected, because the shape of the meron in both families is typical and does not appear to be a *de novo* development.

33. Mesopleurotrochantin: 0. present and well developed; **1.** absent

The loss of the mesopleurotrochantin occurred many times in Diptera. Within the Bibionomorpha it may have occurred only once, at the base of the Mycetophiliformia. In the sciarid *Apelmocreagris* and in *Bolitophila*, there is a sclerite that could be homologous to the pleurotrochantin. If this is correct, there would be two reacquisitions. Actually, the pleurotrochantin might have moved its position to closer to the mesosternum, so it would not have been lost. In this case, the reversals would be more feasible, in the sense that they would not be *de novo* origins of the sclerite.

34. Setae on anepisternum: 0. absent; **1.** present

The anepisternum seems to be devoid of setae at the base of the Bibionomorpha. Anepisternal setae appeared many times in the evolution of the group, the most important ones, in terms of gathering terminal clades, at the base of the Symmerinae (which does not appear here as monophyletic) and at the base of the

(Macrocerinae + Keroplatinae).

35. Setae on dorsal posterior corner of katepisternum: 0. present; **1.** absent

Katepisternal setae seem to be present at the base of the Bibionomorpha, because they are present in anisopodoids, pachyneurids, and bibionids. Hence, the loss of these setae would be a synapomorphy of the Mycetophiliformia, with reacquisitions in isolated genera.

36. Setae on mesepimeron: 0. absent; **1.** present

The presence of epimeral setae is apomorphic and occurs in the Anisopodoidea, in *Asphondylia*, and in *Eratomyia*.

37. Setae on metepimeron: 0. absent; **1.** present

Metepimeral setae in the Bibionomorpha, to our knowledge, occur only in *Cramptonomyia*.

38. Setae on metepisternum: 0. present; **1.** absent

Evolution of metepisternal setae is very plastic. They are apparently absent in the Bibionomorpha groundplan, but secondarily appear in different isolated groups.

39. Setae on laterotergite: 0. present; **1.** absent

Laterotergite setae are present in *Cramptonomyia*, *Arachnocampa*, *Keroplatus*, *Ohakunea*, *Heterotricha*, and many mycetophilid genera. In most cases, this feature corresponds to independent acquisitions. The topology for the relationships within the higher Mycetophilidae obtained here is unrealistic, so the evolution of this character within the family is of little meaning.

40. Setae on antepronotum: 0. absent; **1.** present

Antepronotal setae are rare in the Bibionomorpha, being present only in *Drepanocercus* and the Ditomyiidae.

41. Setae on postpronotum: 0. absent; **1.** present

Postpronotal setae are acquired on different occasions in the evolution of the Bibionomorpha. The character gathers terminal taxa only in the Keroplatinae and in the (*Chiletricha* + *Eratomyia*) clade.

42. Postnotal phragma: 0. reduced or only reaching segment of abdomen; **1.** extending close to distal end of segment of abdomen

There is variation in the extension of the postnotal phragma in different groups of Diptera, and is particularly remarkable in the Scatopsidae. Jaschhof (2004c) has shown the considerable variation in the shape of the postnotal phragma within the Mycetophiliformia, but it is not easy to code the conditions found. In the cecids, there is a considerable development of the postnotal phragma, which is synapomorphic for the family. A similar condition is found in *Hesperinus*. Intermediary states are widespread.

43. Hind coxae height / width rate: 0. smaller than 2.0; **1.** larger than 2.0

This is a classical character of higher Bibionomorpha, a synapomorphy shared by the entire Mycetophiliformia except cecids. More states can be established, but additional coding generated considerable noise. In the complete analysis of Hippa & Vilkamaa (2005), the conclusions are the same.

44. Tibial spurs: 0. present 2-2-2; **1.** present 1-2-2; **2.** absent (Cecidomyiidae, Rangomaramidae Scatopsidae); **3.** present 1-1-2; **4.** present 1-1-1

The 1:2:2 condition of tibial spurs would be a clear synapomorphy for Diptera (modified from the 2:2:2 condition of earlier levels of the mecopteroid phylogeny), but the Tipulidae *s. s.* show the plesiomorphic condition. This problem cannot be properly addressed here, but there is no doubt that 1:2:2 is the plesiomorphic condition in Bibionomorpha. The 1:1:2 state is seen only in *Probolaeus*, whereas the 1:1:1 condition is exclusive of *Rogambara*. Complete loss of tibial spurs is known in cecids and *Rangomarama*. The set of characters considered here shows no direct evidence of relationship between the Cecidomyiidae and Rangomaramidae, so the loss of tibial spurs appears to have happened twice in the evolution of the Mycetophiliformia. Apparently, at least some *Rangomarama* have reduced tibial spurs. We ran a modified data matrix but there were no changes in the topology, since it would appear as an autapomorphy of the genus.

45. Row of setae at apex of tibia I: 0. present; **1.** not visible as arc or regular row of setae

A regular row of elongated setae at the apex of the fore tibia is absent in the Bibionomorpha groundplan, but is commonly present in the Mycetophiliformia except for the cecids. In the Sciaridae, the row of setae is typically known in genera around *Bradysia*, but other genera of the family are devoid of these setae. All higher members of the Mycetophiliformia (with a few cases of secondary loss) have this row of apical front tibial setae, pointing to a single origin at the base of the Sciaridae+ clade.

46. Apex of tibia I: 0. without differentiated area; **1.** with differentiated, membranous area

A differentiated area at the apex of the front tibia is widespread in the Mycetophiliformia, with the exception of the Cecidomyiidae and some isolated genera. A single origin with different losses is more parsimonious, separating cecids from the rest of the Mycetophiliformia.

47. Apical row of seta on tibia II: 0. present; **1.** absent

A regular row of apical setae on the mid tibia is known in a few Mycetophiliformia clades, and is independently derived in the Ohakuneinae, *Keroplatus*, *Nervijuncta*, and *Neoempheria*.

48. Apex of tibia III: 0. with normal setae; **1.** row of developed setae

A regular row of apical setae on the hind tibia is found more often in the Mycetophiliformia than are the mid tibia apical setae. The origin of the character is still equivocal. Because these combs of setae are not identical in shape, there could be five or six independent origins.

49. Length of mid tibial spurs: 0. short, up to 1.5 times tibia width; **1.** long, at least twice tibia apical width

Long tibial spurs is another classic feature of higher Bibionomorpha. The apomorphic condition is seen in *Hesperinus*, *Diadocidia*, *Orfelia*, all Ditomyiidae, and the (Lygistorrhinidae + Mycetophilidae) clade, indicating five independent acquisitions. Some higher Mycetophiliformia genera have mid tibial spurs shorter than 1.5 times the tibial apex length (and, hence, must be coded as plesiomorphic), but they are much longer than the condition seen in bibionids and sciarids. Hence, two states actually reflect quite poorly the evolution of the size of the spurs in the higher Bibionomorpha.

50. First tarsomere: 0. about as long as second; **1.** greatly shortened

A shortened first tarsomere is typical of higher cecids.

51. Tarsal claws: 0. simple; **1.** toothed

The plesiomorphic condition of tarsal claws is simple, toothed claws appearing many times. Toothed tarsal claws appear as a synapomorphy of the (Keroplatoidea + Mycetophiloidea) clade, and also appear in *Rangomarama* and *Colonomyia*. Secondary losses of claw teeth seem perfectly feasible and have occurred many times. The shape of the claws is not identical in all groups where they appear, corroborating the idea of homoplasy.

52. Costa: 0. produced beyond apex of R_5; **1.** ending at apex of R_5; **2.** almost reaching M_1

A short extension of C beyond the apex of R_5 is plesiomorphic in the Bibionomorpha, from which both apomorphic, opposite conditions originated, nearly reaching M_1 or ending at R_5. Both changes are very plastic.

53. Costa: 0. interrupted at or just beyond R_5; **1.** continuing around wing

In cecids and in *Trichocera*, there is a sclerotization along the wing margin beyond the apex of C. This usually has been referred to as an extension of C, but is most certainly incorrect. The texture of the sclerotization is different from that of wing veins and there is a clear interruption after C, just before this wing margin sclerotization. Moreover, the condition in the Cecidomyiidae is isolated from that of *Trichocera* or the Brachycera, so nonhomology is far more parsimonious.

54. Subcosta reaching C: 0. between distal third and middle of wing; **1.** at basal half of wing

A long Sc, reaching the apical third of the wing, is known in different ancient families of Diptera. In the groups sampled here, it can be seen in *Edwardsomyia* and *Trichocera*, as well as in the Pachyneuridae and Bibionidae, within the Bibionomorpha. The plesiomorphic condition is also present in *Catotricha*. A DELTRAN interpretation would favour the origin of the apomorphic condition at the base of the Anisopodoidea, within the cecids, and at the base of the Sciaridae+ clade.

55. Subcosta: 0. complete; **1.** incomplete

A complete Sc is obviously plesiomorphic, an incomplete Sc occurring many times in Diptera evolution. In the Bibionomorpha, it occurs in cecids, at the base of the clades Sciaridae, Chiletrichinae, Heterotrichinae, and Ditomyiidae, and in different groups within the Mycetophilidae. Optimization is equivocal at the base of the Mycetophiliformia, but multiple reductions are more acceptable than multiple reversions. Reference to "sc ending in C" or "Sc ending in R_1" is often seen in the literature, but is incorrect. Sc1 ending in C is plesiomorphic, whereas Sc ending in R_1 is an incomplete Sc1 with Sc2 present.

56. Sc2: 0. present; **1.** absent or very weak

Sc2 is a small vein in the Diptera wing groundplan, lost many times within different clades. High incongruence implies a very low weight in the analysis, so this character is probably not interfering in the final topology. The plasticity of the vein adds to the difficulty to observe it in groups in which the vein is extremely weak, so this character is difficult to code. There are possibly some cases in which the vein has been overlooked in the literature. The smallest number of steps for this character indicates loss followed by "secondary production" of the vein in some groups, which would be unexpected.

57. Sc2: 0. reaching R_1 close to apex of Sc; **1.** at about half of Sc; **2.** basally at Sc

If the mere existence of Sc2 is difficult to determine (character 56), understanding details of its evolution is even more difficult. The character is inapplicable to most Mycetophiliformia. The plesiomorphic condition, at least in the Bibionomorpha, seems to be of Sc2 connecting with R_1 mesally in Sc. Strong basalization of Sc occurs in *Olbiogaster*, *Cramptonomyia*, *Arachnocampa*, *Platyura*, and *Rangomarama*. A secondary displacement of Sc2 to the apex occurs only in mycetophilids. More than these three conditions can be established, but plasticity generates even more incongruence.

58. R_1 reaching C: 0. beyond distal third; **1.** between middle of wing and distal third; **2.** more basal than middle of wing

A long R_1, reaching the margin at the distal third of the wing, is plesiomorphic and seen in most bibiono-

morph genera. Displacement of R_1 towards the base of the wing occurs independently at the base of the Aniso-podoidea, in the Lestremiinae+, in all Sciaridae, and in isolated higher clades.

59. Origin of Rs: 0. between basal third and middle of wing; **1.** before basal third; **2.** more apical than middle of wing

There is some variation concerning the position of the radial fork into R_1 and Rs. The plesiomorphic condition, seen in earlier dipteran families, is between the basal third and middle of the wing. There is basalization of this fork in different clades, a relevant apomorphic feature shared by keroplatids and *Arachnocampa*, but not enough to keep these clades together in this analysis. Displacement of the radial fork to the apex is typical of some mycetophilids. In Tozoni's (1998) study, this feature gathers *Tetragoneura* and most Leiinae, but the phylogenetic signal in our study is not enough to keep the Leiinae genera together. There is some variation within the range of the plesiomorphic conditions, but more than three states could not be meaningfully coded here.

60. Base of Rs: 0. present; **1.** faint; **2.** absent

There are a few cases in which the base of Rs (i.e., the basal connection between R_1 and the longitudinal portion of the vein beyond r-m) is weak or lost. This condition occurs within the higher cecids, more than once in the mycetophilids, in the keroplatids, and more than once within the Ohakuneinae.

61. First sector of Rs: 0. more than 2.5 times width of medial fork at apex; **1.** less than 2.0 times medial fork width

A long base of Rs (from origin to r-m) is plesiomorphic in the Bibionomorpha, a condition also shared with other dipteran families. A shortening of the basal sector of Rs is a synapomorphy of (Bibioniformia + Mycetophiliformia).

62. Position of first sector of Rs: 0. longitudinal or oblique; **1.** transverse or nearly transverse

Changes related to the base of Rs were one of the most important features to link sciarids, lygistorrhinids, and mycetophilids, as accepted by Hennig (1954, 1973), Matile (1990), Chandler (2002, character 4), and Hippa & Vilkamaa (2005, character 34). A rather longitudinal or oblique first sector of Rs is plesiomorphic, and is found in most bibionomorphs. A short and transverse base of Rs is found in all Sciaridae, *Heterotricha*, Ohakuneinae, Lygistorrhinidae, and in some Mycetophilidae. This is one of the characters that may suggest a connection of *Heterotricha* and *Ohakunea* with the Sciaridae, as well as the connection between Sciaridae and Mycetophilidae, shown here to be homoplastic. Many mycetophilid genera actually have a short, but not truly transverse first sector of Rs, as in sciarids and, for example, *Ohakunea*. In the most parsimonious tree, this feature links *Heterotricha* and the Ohakuneinae.

63. R_2: 0. present; **1.** absent

Within the range of this analysis, the loss of R_2 occurs a single time, at the base of the Bibionidae+.

64. R_2: 0. forked; **1.** simple

A forked R_2 is known in a few recent non-brachyceran dipterans, as well as in some Triassic fossils (Krzeminsky & Krzeminska 2003). In this analysis, a simple R_2 appears as a synapomorphy of the Bibionomorpha, but is due to sampling. *Pachyneura* has a forked R_2, a condition lost at the base of the Anisopodoidea, in the Cramptonomyiinae, and in the Bibionidae+.

65. Fork of R_{4+5}: 0. present; **1.** absent

As demonstrated by Amorim (1993), R_2 is present in the Anisopodoidea and R_4 is missing, whereas in the

(Bibionidae + Mycetophiliformia) R_2 is lost (see character 63) and R_4 is preserved in many groups – an interpretation also accepted by Chandler (2002). The loss of R_4 has occurred so repeatedly that strict parsimony (especially with a limited sample of variation within the families) points to a sequence of loss, reacquisition, and secondary losses. No recent sciarids have R_4, which is also absent in *Rangomarama*, the Ohakuneinae, *Heterotricha*, the Chiletrichinae *Diadocidia*, the Lygistorrhinidae, some Bolitophilidae, and some Mycetophilidae. In the Keroplatidae, R_4 is present in most of the family, but is missing in *Arachnocampa* and a few other genera, such as *Chiasmoneura*. "Reacquisition" of R_4 would link all higher members of the Mycetophiliformia, but it seems more feasible to accept a slightly higher number of steps of losses, than a shorter solution implying in many, *de novo* productions of R_4 with the same shape and at the same position. Jaschhof & Hippa (2003, Fig. 11) interpret the crossvein in *Ohakunea* as R_4. This is unlikely. We examined our specimens in detail and do not see any evidence of a "true base of Rs" more basally in the wing. Moreover, *Colonomyia* suggests a displacement of the base of Rs to the apex, so we see no reason to accept the transverse vein in *Ohakunea* as a secondary production of R_4. We checked our interpretation, changing the data matrix to code this vein as proposed by Jaschhof & Hippa (2003), but there was no shift in the placement of the genus.

66. Second section of Rs (from r-m to origin of R_4): 0. equal to or shorter than twice width of medial fork at apex; **1.** more than twice medial fork width

A more basal position of the origin of R_4 seems to be plesiomorphic, as seen in ealier bibionomorphs families and in other dipteran suborders. The absence of R_4 in most families makes this character rather difficult to interpret. A shift of the origin of R_4 to the apex probably occurred at the base of the Bibionidae+. Hence, the condition of R_4 more basal (in many cases, transverse) in mycetophilids and in the ditomyiid *Nervjuncta* would be secondary. Intermediate conditions in mycetophilids are difficult to code, but a higher number of states could be informative in a study of the Mycetophilidae phylogeny.

67. R_4: 0. long, reaching C distally in wing; **1.** shorter, reaching C close to R_1; **2.** fused to R_1 apically; **3.** fused to R_2

R_4 fused to C distally in the wing is undoubtedly plesiomorphic in the Bibionomorpha. Most Mycetophiliformia lack R_4, so the interpretation of the evolution of the vein is not easy. A displacement of the apex of R_4 more to the base, close to R_1, appears as a synapomorphy of (Bolitophilidae + Keroplatidae). A fusion of R_4 to R_1 is seen in part of *Bolitophila*, in some keroplatids, and in the entire (Lygistorrhinidae + Mycetophilidae) clade. A transverse vein between R_5 and R_2 is seen in the Cramptonomyiinae (*Cramptonomyia*, *Haruka*, and *Pergratospes*) within the Pachyneuridae, but is absent in *Pachyneura*. This could be either R_4 or a secondary r-r vein.

68. R_5: 0. long, reaching margin at wing apex or just before (smaller than M_1-M_2 distance); **1.** shorter, reaching C between 1.0 and 2.0 M_1-M_2 distance from apex; **2.** very short, reaching C more than twice M_1-M_2 distance; **3.** beyond wing apex

Changes in the position where R_5 reaches the margin occur quite often. A displacement of the apex of R_5 to a more posterior position in the wing (state 3) occurs at the base of the Cecidomyiidae and in (*Australosymmerus* + *Melosymmerus*). A reduction of the extension of R_5 occurs many times, as in the cecid Lestremiinae, at the base of the Sciaridae, in most keroplatids, thrice in the Ohakuneinae, in the Lygistorrhinidae, and on different occasions within the Mycetophilidae. States can be subdivided without much gain of phylogenetic information.

69. r-m: 0. present; **1.** fusion of M_{1+2} and Rs obliterating r-m

A fusion between the base of M_{1+2} and Rs, obliterating r-m, occurs within the Mycetophiliformia only in *Rogambara*, in the Ditomyiinae, and in most, but not all Keroplatidae.

70. r-m: 0. shorter than C-Sc distance; **1.** 1.0–2.0 times C-Sc distance; **2.** 2.5 times longer than C-Sc distance

The r-m is a relatively short, transverse vein between Rs and M_{1+2}. An elongated r-m occurs in cases in which r-m keeps its transverse condition (as in Bibionidae), but more often in cases in which r-m is directed obliquely backwards (as in *Rhynchoheterotricha* and some mycetophilids) or longitudinally (as in Sciaridae and most Ohakuneinae). State 1 is synapomorphic for the Mycetophiliformia, followed by secondary changes.

71. r-m: 0. transverse to wing length; **1.** directed obliquely backwards; **2.** longitudinal

Matile (1990, character 8) used this feature to link the Sciaridae, Lygistorrhinidae, and Mycetophilidae. In Hippa & Vilkamaa (2005, character 38), it joins the Sciaridae to *Rangomarama*, *Sciarosoma*, and the Archizelmiridae. Even though there is some instability concerning the position of some of the Mycetophiliformia clades, no single tree was obtained in this study in which sciarids, rangomaramids and/or the mycetophiloids compose a monophyletic group. The displacement of the cubital fork to the base of the wing in some cases, but not all, is followed by the displacement of r-m to an oblique or a longitudinal position. The shift of the typically transverse r-m to an oblique condition is synapomorphic for the Mycetophiliformia. A truly longitudinal r-m is known in the group only in part of the Cecidomyiidae, in all the Sciaridae, in the Ohakuneinae, and a few mycetophilid genera, such as *Manota*. A transverse r-m is seen in *Kenyatricha*, *Melosymmerus*, *Diadocidia*, and *Palaeoplatyura*; therefore, in these genera this condition would be due to reversions. Most keroplatids have a fusion between M_{1+2} and the base of Rs (character 70), so r-m is obliterated and, hence, not comparable.

72. Posterior (medial, cubital, and anal) wing veins: 0. normally sclerotized; **1.** faint

Typically, sclerotized medial and cubital veins in the Bibionomorpha are seen only in the Anisopodoidea and in the Pachyneuridae. In all Bibionidae and in the Mycetophiliformia, variable degrees of reduction occur in the sclerotization of these veins.

73. M_{1+2} forking: 0. between half of wing and distal third; **1.** beyond distal third; **2.** before half of wing

Determination of the Diptera groundplan condition is not easy for this feature. A medial fork between the middle of the wing and the distal third seems to be the plesiomorphic condition in the Bibionomorpha. Displacement of the medial fork toward the apex occurred in *Eratomyia* and in (*Cabamofa* + *Rogambara*). A longer medial fork is known in *Melosymmerus*, keroplatids, and in different mycetophilid genera. Additional intermediary conditions may be informative but are difficult to code.

74. First sector of M_{1+2} (from bM to r-m): 0. 1.0 times r-m length; **1.** 0.5–1.0 times r-m length; **2.** 0.1–0.5 times r-m length; **3.** nearly absent, bm-cu nearly in line with r-m

This character is inapplicable in most Mycetophiliformia, not because of the absence of the base of M_{1+2}, but because bM is lost in many groups, making it impossible to determine where M_{1+2} ends and where M_{3+4} begins. Within the group, bM has been confirmed only in *Arachnocampa*, *Bolitophila*, and *Diadocidia* (very short) (character 79). The condition of a long first sector of M_{1+2} in relation to r-m length is plesiomorphic, as seen, for example, in *Olbiogaster* and *Hesperinus*. A relatively short M_{1+2} first sector is seen in *Cramptonomyia* and *Arachnocampa*.

75. Second section of M_{1+2} (from r-m to fork): 0. smaller than 1.5 times medial fork width at apex; **1.** 2.0–3.0 times medial fork width; **2.** more than 3.0 times distance of medial fork width

The second section of M_{1+2} is plesiomorphically short at the base of the Bibionomorpha, becoming longer in the Pachyneuridae and at the base of the Mycetophiliformia. An even longer M_{1+2} second section appears in the Ohakuneinae and at the base of the Chiletrichinae. Reversions are seen in the Bolitophilidae, Keroplatidae, and distinct Mycetophilidae genera.

76. Base of medial fork: 0. well produced; **1.** scarcely produced; **2.** absent

A weak base of the medial fork is seen in the Ohakuneinae and in *Nervijuncta*. *Manota* and *Porricondyla* have completely lost the base of the medial fork; in *Porricondyla* the entire medial fork is absent.

77. Medial fork: 0. present; **1.** absent

Absence of the medial fork is typical of higher cecids.

78. M_{1+2}: 0. well produced; **1.** only distal stalk present

A reduction of M_{1+2} is known only in *Cabamofa* and *Probolaeus*.

79. bM: 0. present; **1.** weak; **2.** absent

A fold in the basal cell of the wing has been interpreted as bM many times in the literature. Within the Mycetophiliformia, a true vein at that position is only recognizable in *Bolitophila* (weak) and *Arachnocampa*. A weak spur is seen in *Diadocidia*. *Cramptonomyia* also has a weak bM, but in the Bibionidae it is well sclerotized. The loss of bM seems to have occurred at the base of the Mycetophiliformia. If the reacquisition is unique, there would be a secondary loss in the (Diadocidiidae + Keroplatidae). A number of parallel losses could be hypothesized, but it implies more steps (cecids, sciarids, rangomaramids, mycetophiloids, ditomyiids, and keroplatids). The hypothesis that in the Cecidomyiidae and Sciaridae the connection between M_{1+2} and CuA has a different origin (Fig. 118) than that of other Mycetophiliformia supports the hypothesis that the condition seen in Bolitophilidae and *Arachnocampa* is truly plesiomorphic.

80. M_3: 0. well sclerotized; **1.** more faint than other posterior veins; **2.** absent

A well sclerotized M_3 is absent in the Bibionomorpha. A weak M_3 is found in the Anisopodoidea and Pachyneuridae, whereas in the Bibionidae and Mycetophiliformia, M_3 is absent.

81. m-cu: 0. connected to M_4, with short first sector ("bm-cu" of literature) of M_4 present; **1.** connected to M_{3+4}, with no first sector of M_4

Interpreting CuA_1 of the literature (Hennig 1973, McAlpine 1981) as M_4 (Colless & McAlpine 1991, Krzeminsky & Krzeminska 2003) demands a reinterpretation of the evolution of m-cu. A true m-cu (in this interpretation) corresponds to what is usually referred to as the first sector of CuA_1; the first sector of M_4 here corresponds to bm-cu of authors, and M_4 beyond m-cu here corresponds to the distal section of CuA_1. Colless & McAlpine (1991) propose a groundplan for the dipteran wing in which m-cu joins M_{3+4} basal to its fork. This condition is seen here in the limoniid *Edwardsomyia*, in *Trichocera*, and in *Cramptonomyia*. Hence, the m-cu connected directly to M_4, seen in the Anisopodoidea, would be apomorphic.

82. m-m: 0. present; **1.** absent

The loss of m-m in the Bibionomorpha occurs at the same level as the loss of M_3, as a synapomorphy of the Bibionidae+.

83. First sector of M_4 (= bm-cu): 0. longer than medial fork width at apex; **1.** between 0.5 and 1.0 times medial fork width; **2.** smaller than 1/3 of medial fork width

The shift of the M_{3+4} fork from a distal position to a more basal position is a synapomorphy of the Bibionomorpha. This corresponds to a shift from a long first sector of M_{3+4} to a shorter one. The loss of bM makes the character inapplicable, because the precise limit between M_{1+2} and M_{3+4} cannot be verified. In *Bolitophila* and *Arachnocampa*, the probable secondary bM creates a very short first sector of M_{3+4} (which would be non-homologous).

84. Width of basal radial (br) + basal medial (bm) combined cells (from base of R to CuA): 0. larger than medial fork width at apex; **1.** smaller than medial fork width

There is considerable variation in the size of the br + bm combined cells within the Mycetophiliformia. When bM is present, the basal radial and medial cells are usually large. The loss of bM is followed by a reduction in the width of the br + bm cells, which is synapomorphic for the entire Mycetophiliformia. Consequently, the conditions found in *Rangomarama* and Ditomyiidae must be seen as reversions. A number of intermediary conditions can be added in the future.

85. m-cu: 0. present, connecting M_{3+4} to CuA; **1.** absent, with distal part of M_4 connecting directly to CuA and base of M_4 in line with M_{3+4} to base of CuA

Higher Bibionomorpha groups have m-cu reaching CuA more basally at the wing (basalization of the "cubital fork"). With the loss of bM at the base of the Mycetophiliformia, the first sector of M_{1+2} becomes continuous with the first sector of M_{3+4}, which connects to m-cu. In most groups, a shift in position occurs, such that the base of M_4 goes from transverse, as in the Anisopodoidea or Bibionidae, to longitudinal, as in the cecid *Catotricha*, but there is still a distinct m-cu. However, in the Sciaridae and Mycetophilidae, this M_{1+2}/M_{3+4} longitudinal vein continues with m-cu right to CuA, M_4 becoming attached to CuA without a basal connection with the rest of the medial sector. The most probable explanation for the condition found in the Sciaridae and Mycetophilidae is that M_4 was broken basally, with a secondary connection with CuA more distally. Evidence of this can be seen in some cecids that also lost the base of M_4, where a basal spur can be verified, as well as in *Drepanocercus* and *Paratinia* (Fig. 173).

86. First sector of M_{3+4}: 0. transverse; **1.** inclined forward; **2.** inclined backward; **3.** longitudinal

The first sector of M_{3+4} is inclined forward in the Diptera groundplan, as seen in *Edwardsomyia*, *Trichocera*, and the Anisopodoidea, with M_{1+2} forking obliquely toward the anterior margin. *Cramptonomyia* already has M_{1+2} aligned with bM, the first sector of M_{3+4} forking transversely, a condition preserved plesiomorphically only in the Bibionidae. With the exception of some taxa in the Keroplatoidea, all remaining Mycetophiliformia have a longitudinal first sector of M_{3+4}, so this is a synapomorphy for the group. This situation forces the interpretation that the shift of the base of origin of M_{3+4} to a transverse position in *Bolitophila*, *Arachnocampa*, *Diadocidia*, keroplatids, *Australosymmerus*, and *Melosymmerus* is a reversion. This secondary condition in these keroplatoid groups is also obvious for other characters, such as the m-cu reaching CuA (the shorter "cubital fork").

87. Length of M_{1+2}: 0. reaching beyond basal 1/3 of wing; **1.** ending before basal 1/3

The long first sector M_{1+2} in *Bolitophila* is a unique feature because it is the result of r-m keeping its original position mesally in the wing and the displacement of the basal fork of M_{1+2} and M_{3+4} to a basal position.

88. First sector of M_{3+4}: 0. recognizable; **1.** base of M_{3+4} fused to CuA, with typical first sector not recognizable

The loss of bM at the base of the Mycetophiliformia was followed by a number of other changes in the

position of related veins, such as the first sector of M_{1+2}, M_{3+4}, m-cu, r-m, and others. Some of these veins acquired a composite nature, with parts coming from different veins, of which the limits became unrecognizable. This condition means that Hennig's (1954) use of "tb" for the posterior cross-vein in these groups is a better alternative than naming it as only one of these veins (e.g., M_{3+4}). A major change in the evolution of some groups of Mycetophiliformia is the connection of M_4 or M_{3+4} directly to CuA, without an m-cu cross-vein. This condition is typical of all sciarids and all mycetophilids except *Loicia*. *Drepanocercus* has a long "cubital fork", but there is no m-cu. The most parsimonious interpretation of the set of characters studied here shows that the Sciaridae originate close to the base of the Mycetophiliformia. Consequently, direct connection of M_4 to CuA without an intertwining m-cu would be homoplastic between the Sciaridae and the Mycetophilidae. The plesiomorphic condition is seen in *Loicia* and other genera such as *Taxicnemis*, *Starkomyia*, and *Freemanomyia*. None of the known Lygistorrhinidae genera, including *Palaeognoriste*, are comparable for this character.

89. Ratio of first sector of CuA (basal to m-cu) / to second sector of CuA (from m-cu to margin): 0. 5.5–2.0; **1.** 1.9–1.1; **2.** 1.0–0.7; **3.** 0.6–0.1; **4.** smaller than 0.1

This feature corresponds to the "length of the cubital fork" in usual nomenclature. The point at which m-cu reaches CuA is distal in the wing at the base of the Diptera, as seen in *Edwardsomyia*, *Trichocera*, and *Cramptonomyia* (state 0), the first sector of CuA being much longer than the second sector. The condition in the Anisopodoidea (state 1), in which the first sector is only slightly longer than the second, is more apomorphic than in the Pachyneuridae. A more apomorphic condition (state 2) is shared by the Bibionidae and Mycetophiliformia. At the base of this latter group, the feature is equivocal because of a secondary reduction in higher cecids, but state 2 should be the groundplan condition. This state is preserved in the Ditomyiidae, *Arachnocampa*, other keroplatids, and some mycetophilids. *Diadocidia* and most mycetophild genera have a more plesiomorphic condition, whereas most sciarids are more apomorphic. *Bolitophila* and most rangomaramids show state 3, whereas the Ohakuneinae, *Kenyatricha*, *Drepanocercus*, and *Catotricha* have a very short first sector of CuA (state 4). We assume here that m-cu closer to the wing margin ("short cubital fork", state 3) is synapomorphic for all Mycetophiliformia except cecids and sciarids. Thus, the condition in groups such as ditomyiids, keroplatids, *Diadocidia*, and most mycetophilids would be secondary. The important implication here is that the similarity in this feature between the rangomaramids, many Jurassic Mycetophiliformia, *Bolitophila*, *Starkomyia*, *Loicia*, *Freemanomyia*, and others would be symplesiomorphic. The condition in most mycetophilids, cecids, and sciarids in this case would be the result of a fusion of M_4 to CuA in a more distal position, with the loss of m-cu and part of M_{3+4}. This condition is seen in *Drepanocercus* and *Paratinia*.

90. Shape of m-cu basally: 0. curved; **1.** with basal angle

These two states are not precise definitions of the conditions found. In different ancient genera of mycetophiliforms with basalization of m-cu, M_{3+4} runs parallel to CuA up to about the middle of wing. Such a condition is lost in the groups with displacement of m-cu back to a more apical position, such as *Diadocidia*, keroplatids, and ditomyiids. Because *Bolitophila* is plesiomorphic, it would have appeared twice in the topology obtained.

91. Connection of m-cu to CuA: 0. produced; **1.** interrupted

In some groups of Mycetophiliformia, the base of M_4 and m-cu are lacking and not reaching CuA. This condition typically occurs in the Cecidomyiidae except *Catotricha*, Ohakuneinae, and Lygistorrhinidae. Some mycetophilid genera show M_4 interrupted basally, with a secondary connection of M_4 to CuA, so the incomplete base of M_4 could be a shared derived feature between the Lygistorrhinidae and the Mycetophilidae, absent only in those genera with m-cu clearly present, such as in *Starkomyia*, *Freemanomyia*, *Loicia*.

92. m-cu: 0. oblique; **1.** longitudinal

An oblique true m-cu is the plesiomorphic condition found in, for example, *Edwardsomyia*, *Trichocera*, and earlier Bibionomorpha families. A longitudinal m-cu is synapomorphic for the Mycetophiliformia. This condition is clear in *Catotricha*, Rangomaramidae, *Loicia*, *Starkomyia*, and *Freemanomyia*. The condition in other cecids, sciarids, and mycetophilids – with M_{1+2} and M_{3+4} in line, connected to CuA more basally – seems actually to be derived from a wing venation with m-cu longitudinal. The condition seen in the Keroplatoidea, hence, would be the result of a reversion, as discussed for character 89.

93. Shape of M_4 basally: 0. strongly diverging from CuA from very base; **1.** parallel to CuA along its basal 1/3

This feature is part of the process of basalization of m-cu. In *Catotricha*, most sciarids, rangomaramids and genera such as *Bolitophila*, *Arachnocampa*, those of the lygistorrhinids, and *Loicia*, m-cu connects CuA basally at the wing, so M_4 is parallel to CuA along a considerable extension. This condition indicates this feature to be synapomorphic for the Mycetophiliformia. The condition in the Diadocidiidae, Keroplatidae, and Ditomyiidae would be secondary, with m-cu moving back to the apex. In mycetophilids and higher cecids (as discussed under character 89), a fusion of part M_4 to CuA occurred, so there is no true m-cu. *Bolitophila* and *Arachnocampa* are plesiomorphic for this feature, so that in the Keroplatoidea, this distal connection of m-cu to CuA in an oblique position would have appeared twice – in the Ditomyiidae, and in *Diadocidia* and most keroplatids.

94. A_1: 0. complete; **1.** incomplete, or absent

An incomplete A_1 occurs some dozen times in the evolution of the dipterans. Within the Bibionomorpha, A_1 is complete in the non-Mycetophiliformia families and in most ditomyiids, *Bolitophila*, *Diadocidia*, and most keroplatids. The most parsimonious interpretation would point to a reduction at the base of the Mycetophiliformia, with a secondary extension of A_1 to the wing margin in the clade Ditomyiidae+. The less parsimonious option would involve the loss of A_1 five times – in the Cecidomyiidae, Sciaridae, Rangomaramidae, Mycetophilidae, and *Nervijuncta*.

95. Wing microtrichia: 0. irregularly arranged; **1.** at least partially regularly arranged; **2.** regularly arranged

Regularly arranged microtrichia over the wing membrane is a unique synapomorphy of the (Manotinae + Mycetophilinae) clade within the mycetophilids. The second step is exclusive of Mycetophilinae.

96. Macrotrichia on wing membrane: 0. present; **1.** absent

This character is relatively difficult to interpret and is highly plastic. Whatever the groundplan condition in Diptera, the number of steps would be high. Apparently, bare wings would be plesiomorphic in the Bibionomorpha, with macrotrichia appearing over the membrane in *Sylvicola*, Pachyneuridae, cecids, some sciarids, thrice in the Rangomaramidae, Diadocidiidae, Ditomyiidae, and at least once within the Sciophilinae (Mycetophilidae) (not seen in the topology obtained here because of the unreliable inner mycetophilid phylogeny).

97. Macrotrichia on wing membrane: 0. straight; **1.** curved

Curved macrotrichia are known in *Ohakunea* and some cecids.

98. Microtrichia on wing membrane: 0. present; **1.** absent

Southern hemisphere Symmerinae (*Australosymmerus* and *Melosymmerus*) and some Sciophilinae secondarily lost the microtrichia over the wing membrane.

99. Ventral setae on distal half of Sc: 0. present; **1.** absent

100. Ventral setae on R_1: 0. present; **1.** absent

101. Ventral setae on R_5: 0. present; **1.** absent

102. Ventral setae on M_{1+2}: 0. present; **1.** absent

103. Ventral setae on M_1: 0. present; **1.** absent

104. Ventral setae on A_1: 0. present; **1.** absent

105. Dorsal setae distally on Sc: 0. present; **1.** absent

106. Dorsal setae on M: 0. present; **1.** absent

107. Dorsal setae on base of M_1 and M_2: 0. present; **1.** absent

108. Dorsal setae on cubital veins: 0. present; **1.** absent

109. Dorsal setae on A_1: 0. present; **1.** absent

Characters 99–109 concern the macrotrichia on wing veins. Optimization points to the presence of macrotrichia as plesiomorphic in most, but not all cases. The number of steps is almost always high, with reversions occurring many times.

110. Insertion of abdomen: 0. wide; **1.** slender; **2.** waist

A waist at the base of the abdomen is a typical key feature of mycetophilids that also is present in lygistorrhinids. The condition in the Keroplatoidea is intermediate.

111. Abdominal segment 1: 0. as developed as segment 2; **1.** 2/3 to 1/3 of segment 1

A relatively reduced segment 1 is known in the Ohakuneinae.

112. Male segment 8: 0. about 1/2 to 1/3 of segment 7; **1.** very short.

A reduced length of segment 8 is known in the Lygistorrhinidae and Mycetophilidae, even though intermediary conditions (and homoplasies) occur in other higher members of the Mycetophiliformia.

113. Male sternite 9 (hypandrium): 0. produced as separate sclerite; **1.** fused to gonocoxites, resulting in synsternogonocoxite; **2.** projected between gonocoxites

No Bibionomorpha has a completely independent sternite 9; the sclerite is always fused laterally to the gonocoxites. The shape of sternite 9, when still recognizable, varies considerably, but in *Insulatricha*, *Chiletricha*, and *Eratomyia* there is a projection between the gonocoxites, a condition similar to that seen in *Symmerus*.

114. Male sternite 9: 0. well defined; **1.** reduced to slender strip

Sternite 9 reduced to a strip is synapomorphic for the Mycetophiliformia, with some secondary development in *Arachnocampa* and the Ditomyiinae.

115. Male sperm pump: 0. absent as sclerotized plate; **1.** present

A sclerotized sperm pump is known in limoniids, *Valeseguya*, scatopsids, and canthyloscelids (Amorim & Grimaldi 2006), outside the Bibionomorpha, and may correspond to a Diptera groundplan condition. Within the Bibionomorpha, it is known in the Anisopodoidea as a plesiomorphy, its loss being synapomorphic for the rest of the group. *Leia* has an unusual secondary sclerotization of the sperm pump.

116. Male gonocoxite: 0. not projected beyond gonostyle (Gs); **1.** with distal projections ventrally; **2.** with dorsal projections; **3.** with lateral extensions beyond base of Gs; **4.** with digitiform inner subdistal projection

The shape of the gonocoxite varies considerably among the Mycetophiliformia. Different apomorphic modifications were stated here, but they do not gather any of the terminal taxa.

117. Male gonostyle: 0. straight, simple; **1.** with subapical projection; **2.** swollen; **3.** strongly arched; **4.** strongly bifid; **5.** bifid, with basal projection short; **6.** club shaped and digitiform apically; **7.** sigmoid

The shape of the gonostyle varies even more wildly. Six conditions were proposed here, in addition to the simple, digitiform, plesiomorphic state. Synapomorphies show the monophyly of the Ohakuneinae (state 6) and of a clade within the Keroplatidae (state 5).

118. Aedeagus: 0. present as tubular sclerite; **1.** present as flattened sclerite

A tubular, typical aedeagus is absent in all Bibionomorpha except the Anisopodoidea. There are a number of other modifications, such as the presence of a tegmen, but insufficient knowledge, as pointed out by Hippa & Vilkamaa (2005), would lead to a defective phylogenetic signal, so they were not used here.

119. Male T9: 0. rectangular; **1.** with pair of posterior digitiform projections; **2.** with 2 pairs of posterior projections; **3.** reduced; **4.** short and wide; **5.** divided into pair of lobes; **6.** with 2 distal lobes; **7.** with pair of spinose dorsolateral lobes

Some variation occurs in the shape of tergite 9, which is rectangular in its plesiomorphic condition. The presence of projected posterior lobes (one or two pairs) with a tuft of spines (character 120) is unique in the Chiletrichinae. We are not sure whether or not these are the "cleft enlarged setae" of Jaschhof & Didham (2002) or the "megasetae" of Hippa & Vilkamaa (2005), seen in one species of *Rangomarama*. These setae are absent in most bibionomorph families.

120. Male T9: 0. posterior lobes absent or with normal setae; **1.** posterior lobes spinose

This is a synapomorphy of the Chiletrichinae.

121. Male cerci: 0. normally developed and present as a lobe; **1.** reduced or absent; **2.** very developed

Reduced or absent cerci are known in some cecids within the Bibionomorpha. In *Olbiogaster* (e.g., Peterson 1981, Fig. 16) and in the Ditomyiidae (Munroe 1974, Figs. 1a, c), on the other hand, there is a secondary development of the cerci, which assume quite large proportions in the male terminalia.

122. Female sternite 8: 0. normal; **1.** short

A reduced female sternite 8 is known in *Chiletricha* and the Ohakuneinae.

123. Female terminalia: 0. normal; **1.** needle-like

Needle-like female terminalia are a shared feature of higher Cecidomyiinae.

124. Female tergite 10 and first cercomere (Ce1): 0. with normal setae; **1.** with long macrotrichia

Developed setae on the female tergite 10 and first cercus article are known in *Heterotricha*.

125. Female Ce1: 0. slightly longer than Ce2; **1.** shorter than Ce2; **2.** twice as long as Ce2

The relative lengths of the first and second articles of the female cercus vary considerably among the Bibionomorpha. A shorter first cercomere is seen in the Bibionidae, *Heterotricha*, *Chiletricha*, and *Arachnocampa*. A longer distal cercomere is known in *Rangomarama*, the Ditomyiidae, and the Mycetophiloidea. *Drepanocercus* has a plesiomorphic condition, which is partially responsible for branching earlier than the Lygistorrhinidae in the clade.

126. Female Ce2: 0. present; **1.** absent

Loss of the female distal cercomere is fairly common among dipteran groups and appears many times within the Bibionomorpha.

127. Sclerotized spermathecae: 0. 3; **1.** 2; **2.** 0; **3.** 1

The evolution of the number of spermathecae is interesting in different dipteran clades. In the Bibionomorpha, the plesiomorphic condition is the presence of three sclerotized spermathecae. Some cecids, sciarids, and ditomyiids have no sclerotized spermathecae, whereas the rest of the Mycetophiliformia have two sclerotized spermathecae, even though in many cases the literature information is doubtful. In this scenario, strict optimization would point to a loss of sclerotization at the base of the Mycetophiliformia, with reacquisition in the higher families, followed by an additional loss in the Ditomyiidae, which is an odd interpretation. One additional step seems more feasible, with independent losses, the condition in the rest of the Mycetophiliformia being plesiomorphic.

The next 10 characters refer to immature features proposed in the literature. In contrast to the previous characters, here we generalize features for families or genera in which there have been some larvae or pupae described. The Rangomaramidae, *Catotricha*, *Apelmocreagris*, *Nervijuncta*, *Australosymmerus*, and *Symmerus* appear as noncomparable. Hence, there is some risk of false generalizations for some of the features included.

128. Larval antenna: 0. short; **1.** developed

129. Larval mandible: 0. normal; **1.** flattened

These two characters are autapomorphic for the Bolitophilidae.

130. Larval maxillary palpus: 0. normally developed; **1.** reduced (Matile 1990)

131. Larval clypeofrontal apodeme: 0. short; **1.** extended (Matile 1990)

Reduced mouthparts and an extended clypeofrontal apodeme are proposed by Matile (1990, pages 367 and following) as larval synapomorphies gathering the Lygistorrhinidae and Mycetophilidae.

132. Larval abdominal stigma VII: 0. present; **1.** absent (Matile 1997)

The loss of the larval abdominal stigma VII was proposed by Matile (1997) to be a synapomorphy uniting *Diadocidia* and the Keroplatidae.

133. Larval head capsule and mouthparts: 0. complete and of normal size; **1.** minute, reduced to a tiny cone at the anterior end of the larva, with stylet-like mandibles

134. Larval cardo: 0. free from anterior margin of head capsule; **1.** fused with, or closely appressed to, ante-

rior margin of head capsule

A reduced larval head capsule and mouthparts, with the cardo fused to the anterior margin of the head, is typical within the Bibionomorpha of the Cecidomyiidae.

135. Larval postgenal lobes: 0. more or less meeting midventrally to form hypostomal brigde; **1.** meeting in two places to enclose pyriform membranous area

Postgenal lobes meeting in two places is synapomorphic for the Sciaridae.

136. Larval intersegmental fissures: 0. each continous around body; **1.** not continuous laterally

Interrupted intersegmental fissures is synapomorphic for the Bibionidae.

137. Larvae sternal spatula: 0. absent; **1.** present;

The sternal spatula is a unique apomorphy of the cecid larvae.

Species sampling, character coding, algorithm, and tree topologies

This is the widest study ever made of the phylogenetic relationships within the higher Bibionomorpha. It includes 64 terminal taxa representing all bibionomorph families and two non-bibionomorph clades, and encloses a considerable sample of genera within the more diversified Mycetophiliformia families. Taking the Mycetophiliformia as the ingroup, we sampled eight species belonging to five families inserted in the phylogeny of the Bibionomorpha at successively more basal levels. The matrix includes 137 transformation series, with a total of 202 characters. All Mycetophiliformia genera of difficult placement were primarily included in the data matrix and the complete sample of families allows real tests about the placement of these genera in the system. More diverse families had a larger number of species sampled: Mycetophilidae with 14 species, Keroplatidae with 6 species, and Ditomyiidae with 5 species. Nevertheless, we intend to show the points of weakness of the analysis, making it easier to recognize the more robust hypotheses.

Subtle decisions in cladistic studies frequently imply relevant differences in the topological outcomes. Alhough we may use the term "parsimony" to refer to the simplest hypotheses, given a data matrix and an algorithm, there may be significant incongruence between the MPTs obtained using the same database under different decisions in the analysis protocol. This concerns different aspects of the method:

(1)   given a hypothesis to be tested, what are the major ingroup clades included in the analysis;
(2)   the number of sampled taxa belonging to each of the larger ingroup clades;
(3)   the position of these sampled taxa within their clades;
(4)   the major outgroup clades included in the analysis;
(5)   the number of sampled species belonging to each of the outgroup clades;
(6)   the position of these sampled outgroup species within their clades;
(7)   the total number of characters in the matrix;
(8)   decisions about primary homology;
(9)   decisions about coding, especially of multistate characters;
(10)   decisions about the parsimony algorithms used (not to mention the use of non-parsimony methods).

Some of these points seem more obvious, such as the clades to be included in an analysis if we want a given hypothesis to be tested. There are pitfalls and many cases of false tests of monophyly in the literature. Most of the other of these points, however, are largely neglected. Sampling is a major issue. Larger ingroup

and outgroup sampling is indispensable for studies at higher levels of analysis when there is a considerable degree of homoplasy. In this study, when sampling was not comprehensive enough, the inclusion or exclusion of a single species or of a single character in the data matrix produced different results in the topology.

There is a large degree of incongruence between the Mycetophiliformia proposed in the literature (Hennig 1973, Wood & Borkent 1989, Matile 1990, Chandler 2002, Jaschhof & Didham 2002, Blagoderov & Grimaldi 2004, Hippa & Vilkamaa 2005). Most previous studies of the Mycetophiliformia seem to have been affected by the number of families sampled (avoiding adequate tests), the number of outgroups sampled (avoiding adequate rooting), the number of species belonging to larger families, and the number of overall characters. Even though one or two outgroups sampled might be enough to unequivocally root characters at the top of the ingroup topology, in these cases the phylogenetic signal is often insufficient to properly solve the relationships at the base of the ingroup, especially when there are homoplasies between ingroup and outgroup species (which frequently is the case). Larger outgroup sampling (in terms of total number of species and total number of levels sampled) mitigates the effect of homoplasies over the character optimization at the base of the ingroup and, hence, generates more robust hypotheses of relationships at the base of the ingroup.

Larger species sampling within ingroup major clades is also indispensable. Cecidomyiids, sciarids, keroplatids, and mycetophilids are particularly diversified groups. Despite the focus of the study on the interfamilial relationships, the results are affected by the number (and the position) of the species belonging to each family. In the case of the Mycetophilidae, for example, with only one or two species of Mycetophilinae or Leiinae, optimization would produce a distorted reconstruction of the groundplan of the family and, hence, affect the position of the family. Because of the extensive homoplasy in the group, such as the presence or absence of macrotrichia over the wing membrane and veins, loss of veins, and shifts and fusions of veins, undersampling of species within families implies a high risk of gathering clades based on interfamily homoplasies. This problem might have been responsible for some of the differences found in the literature concerning the position of, for example, the Sciaridae in the Mycetophiliformia phylogeny.

Finally, coding and primary homology are difficult subjects. In preliminary runs of the matrix, recoding of a single character (in the sense of changing the number of steps) and recoding of a single species (in the sense of changing a doubtful condition of a character in a species) was enough to change the position of some larger clades in the tree. This does not mean that characters with low CI are bad. Consistency of the data (i.e., nested congruent characters) is, in most cases, enough to make these characters especially useful as sources of information at higher levels in the cladogram. Moreover, *a posteriori* weighting is particularly efficient in recognizing characters for which there is no secondary homology, and reduces their influence over the final topology. Missing data have their own effect on the overall numerical analysis and have to be handled with proper care. In our understanding, insufficient sampling of "intragroup" species (in the case of this analysis, genera within families such as Keroplatidae and Mycetophilidae) and insufficient characters for these inner levels is responsible for some of the instability in our results.

Mycetophiliformia major clade relationships

In our study, the unweighted analysis, as expected, allowed many possible topologies of equal length, resulting in a less informative consensus (Fig. 44). The unweighted analysis of the entire matrix produced 1114 trees of equal length in a heuristic analysis (Fig. 44), while the unweighted analysis of the character- and taxon-reduced matrix resulted in 61 trees of 657 steps (Fig. 97). *A posteriori* weighting methods downweight the more incongruent characters, giving the congruent characters a greater influence on the final topology (Figs. 45–61).

Despite the differences among the trees obtained, all topologies agree about some important clades. One of the most important is the sister-group relationship between the Cecidomyiidae and the rest of the Myceto-

philiformia. No single topology obtained under any of the 20 protocols indicates the Cecidomyiidae and the Sciaridae as sister groups, as proposed by Wood & Borkent (1989) and Blaschke-Berthold (1994), or as closely related groups (Jaschhof & Didham 2002). In our study, four characters of unique origin and seven other characters with homoplastic history in the group point to the monophyly of all Mycetophiliformia except cecids. This conclusion is corroborated by the analysis of Hippa & Vilkamaa (2005) with recent and fossil groups (Fig. 6), but not their analysis with only recent groups (Fig. 5).

Another consistent clade in the entire analysis includes all Mycetophiliformia except cecids and sciarids. This clade was suggested for the first time by Wood & Borkent (1989), in conflict with the opinions of, for example, Hennig (1954, 1973), Matile (1990), and Chandler (2002), who accepted a more direct connection between the Sciaridae and the (Lygistorrhinidae + Mycetophilidae) clade. The characters here gathering all higher Mycetophiliformia except the Cecidomyiidae and Sciaridae include mainly thoracic sclerites. Five characters of unique origin in the Bibionomorpha, plus two other homoplasies, sustain the monophyly of the group. Thoracic morphology shows an impressive stability in the evolution of the group, with relatively constant patterns within families, despite existing variation among families; that is, these features are not too plastic and are thus ideal as a phylogenetic signal. At the base of the Bibionomorpha, the thorax is shorter in height, with a wide ventral end of the mesepimeron, the mediotergite is short and straight, and the laterotergite is flat. There is little question that cecids and sciarids are plesiomorphic for these features. The Rangomaramidae and other Mycetophiliformia families are much more elongate midges, with a slender mesepimeron (which is absent ventrally in different groups) and a long mediotergite.

There is good Bremer support for the monophyly of the Anisopodiformia, Bibionidae, Cecidomyiidae, Sciaridae, Ohakuneinae, Ditomyiidae, and Keroplatidae except *Arachnocampa* (Fig. 97). The monophyly of the Bibionomorpha (although there is not an exhaustive sampling of non-Bibionomorpha species) has good support, as well as the monophyly of all Bibionomorpha except the Anisopodiformia. The monophyly of the Mycetophiliformia and of all Mycetophiliformia except Cecidomyiidae has high Bremer support, and the support for the monophyly of all Mycetophiliformia except Cecidomyiidae and Sciaridae is good.

Actually, the earlier placement of the Sciaridae close to the Mycetophilidae now is shown to be due to a mixture of homoplasy, plesiomorphy, and errors of primary homology of wing features. Figures 98–117 show a detailed study of vein homology, using colours for different vein sectors. Despite some superficial similarities, generically referred to in the literature as "basalization of the cubital fork", the means of achieving the final condition in different major clades were actually not the same (Fig. 118). This seems to be due to the use, in older literature, of too apomorphic species to generate the interpretation of primary homology, resulting in wrong hypotheses. In the Cecidomyiidae, the "cubital fork" can be seen only in *Catotricha*. However, the shape of this "CuA" basally, when compared to bibionids and anisopodids, shows that the long, longitudinal vein basally is bM, not of M_4 (= CuA_1), followed by bM_{1+2}. In other words, at the base of the Cecidomyiidae, m-cu was lost, followed, in higher levels of cecid evolution, by the loss of the base of M_{3+4} and, later, by the fusion of M_4 to CuA, resulting in an apparent "cubital fork in a distal position in the wing". In the Sciaridae, the process is entirely different. There is no problem in recognizing that r-m is longitudinal, followed by bM_{1+2} and bM, but the connection of M_4 to bM is entirely lost and M_4 connects directly to CuA distally. In most Rangomaramidae, the condition is similar to that of early clades of the Keroplatoidea and Mycetophiloidea (e.g., *Bolitophila* and *Loicia*), as well as many Jurassic fossils of the Mycetophiliformia. The base of M (bM) is absent and there is a continuous line along bM_{1+2}, M_{3+4}, and bM_4 connected to m-cu, in a longitudinal position. Even this generalized condition presents variation, with r-m transverse or longitudinal. The condition in mycetophilids is still different. *Loicia* species actually show that the base of M_4 is lost by a fusion of M_4 to CuA. Hence, the longitudinal vein in the Sciaridae corresponds to bM + bM_{1+2}, whereas in the Mycetophilidae, bM is lost and the vein corresponds to (m-cu + bM_4 + bM_{3+4} + bM_{1+2}) (compare, e.g., with the condition in *Loicia*, Fig. 163). Thoracic features corroborate this view, with sciarids more plesiomorphic than the

Rangomaramidae in relation to the condition seen in the Mycetophiloidea and the Keroplatoidea (Figs. 165–168).

The monophyly of the clade including Lygistorrhinidae and Mycetophilidae is supported in all trees obtained, but the monophyly of the Mycetophilidae is not clear. In many trees, *Drepanocercus* and *Loicia* (see below) are placed in the tree in a more basal position than the lygistorrhinids, although some of the reconstructions point to a monophyletic Mycetophilidae.

A solid clade in our study is composed of the families Ditomyiidae, Bolitophilidae, Diadocidiidae, and Keroplatidae – the Keroplatoidea. Even though the relationships between these families within the clade are still not well supported, this set of families consistently appeared as a monophyletic group within the higher Mycetophiliformia. This result is new in relation to all published papers on higher Bibionomorpha relationships. That this clade appears in all analysis options indicates that the hypothesis should be considered carefully in future studies. Within the clade, there are still doubts about the position of *Arachnocampa*, which in most trees appears ealier than *Diadocidia*. Most topologies show the Ditomyiidae originated earlier than the Bolitophilidae within the Keroplatoidea. The monophyly of the Keroplatoidea would be entirely unexpected were it not for the study of Hippa & Vilkamaa (2005) (Fig. 6), in which this clade is also present. The relationships among the families in their results differ from those obtained here, but the composition is the same. This clade appears in their study in the topology including a higher number of terminal taxa, with the presence of the fossil genera. The subfamilial status given to *Sciarokeroplatus*, recently described by Papp & Sevcik (2005), is questionable and does not affect the optimization of characters to the base of the Keroplatidae.

The question of the relationships of the genera around *Heterotricha* and *Ohakunea* demands more work, but there is considerable advance. In the topology accepted here (Figs. 64, 65), the Rangomaramidae come out as a clade that includes most of these genera of uncertain position (Figs. 53, 54, 59, 61). When this group is not monophyletic, it is mostly due to the displacement of *Heterotricha* to the (Lygistorrhinidae + Mycetophilidae) clade (Figs. 45, 47–51, 56–58, 63), but also to the displacement of *Rangomarama* to the Keroplatoidea (Fig. 62), or to the division of the clade into two main parts (Figs. 55, 60). Despite the doubts about *Rangomarama* and *Heterotricha*, two smaller clades are consistent in the entire analysis — the Chiletrichinae (including *Kenyatricha*, *Rhynchoheterotricha*, *Insulatricha*, *Chiletricha*, and *Eratomyia* n. gen.) and the Ohakuneinae (including *Ohakunea*, *Colonomyia*, *Cabamofa*, and *Rogambara*). The Chiletrichinae also appear as a clade in both analyses of Hippa & Vilkamaa (2005), in one case with *Heterotricha* and *Afrotricha*, and in another case as an isolated group. Hippa & Vilkamaa (2005) did not include either *Rogambara* or *Cabamofa* in their study. *Ohakunea* and *Colonomyia*, however, appeared as a monophyletic group.

The relationships between the higher Mycetophiliformia clades – Rangomaramidae, Keroplatoidea, and Mycetophiloidea – are still a subject of concern. In the topology accepted here, Keroplatoidea and Mycetophiloidea are sister groups. In many of the topologies, however, the Rangomaramidae appear as the sister group of the Mycetophiloidea; still another alternative shows the Rangomaramidae paraphyletic in relation to the (Keroplatoidea + Mycetophiloidea) clade. Considering the entire set of characters involved, we prefer the topology with Keroplatoidea and Mycetophiloidea as sister groups. This discussion, however, does not affect the hypothesis of the monophyly of these three main clades, but only their relative positions. Finally, a subsequent study will have to deal with the number of extinct Mesozoic genera and families that are related to the Mycetophiliformia, described, for example, by Rohdendorf (1962, 1991), Blagoderov (1993), Blagoderov & Grimaldi (2004), and Grimaldi *et al.* (2006). Such a study not only would give more robustness to the analysis itself, but also would help to attribute age to the clades, with implications for biogeography and evolution of the group over the world.

More detailed comments are made below about each genus of the Rangomaramidae and some other genera of intriguing position.

Heterotricha. Chandler (2002) kept in this genus only four species, three of which are known from Baltic amber, and one of which is recent with a Palearctic distribution. No *Heterotricha* species were examined in

this study. Whenever the entire Rangomaramidae appeared together in this analysis, *Heterotricha* did not fit directly in the Chiletrichinae, demonstrating that Chandler's (2002) decision of breaking the original *Heterotricha* into many genera was correct. The backward base of Rs in *Heterotricha* and nearly absent r-m is unique in the Mycetophiliformia; m-cu joins CuA in a basal position, which is also an apomorphy, but that does not help place *Heterotricha* in the system. The position of R_5 close to C finds some similarity with *Chiletricha*, but is not enough *per se* to gather these two clades. In many of the topologies, the genus is separated from the rest of the Rangomaramidae, joining the Mycetophiloidea; this situation shall be considered in future studies, although it might be an effect of missing data.

Rangomarama. This genus (for which no specimens were examined in this study) includes five species restricted to New Zealand. *Rangomarama* was associated with the Cecidomyiidae by Jaschhof & Didham (2002), based on the absence of tibial spurs. In the study of Hippa & Vilkamaa (2005), it appears as the sister group of the Sciaridae or of (Sciaridae + Archizelmiridae). In most trees obtained here, *Rangomarama* fits in a clade with the Chiletrichinae and the Ohakuneinae. In the few cases where the genus does not fit in these two clades, it appears in the polytomy at the base of the higher Mycetophiliformia (Fig. 44), and in one case as the sister group of the Keroplatoidea (Fig. 45). The thoracic morphology of the species of the genus, based on what can be inferred from the original description, does not exhibit the typical plesiomorphic condition in the Sciaridae and Cecidomyiidae. This is well corroborated by the wing venation, showing the pattern seen in most rangomaramids, early keroplatoid clades, and mycetophiloids, with an aligned m-cu with $M_4 + M_{3+4} + bM_{1+2}$, m-cu connecting CuA very basally. The long base of Rs is autapomorphic and is not informative about the position of the genus. The position of the genus in the system should still be taken carefully. Placing *Rangomarama* in a subfamily of its own reduces name changes in case of adjustments of the topology.

Ohakunea. This genus is circumantarctic in distribution, with one species in Chile, one in New Zealand, one in Australia, and two in Papua New Guinea. *Ohakunea* came together with *Colonomyia*, *Rogambara*, and *Cabamofa* to form a clade in all topologies. Its position within the Ohakuneinae, however, remains doubtful. In the unweighted analysis (Fig. 44), it is in a polytomy at the base of the Ohakuneinae. In some topologies (Figs. 45, 48, 53, 54, 56, 58, 60, 61), it appears as the sister group of (*Cabamofa* + *Rogambara*) or as sister to the rest of the Ohakuneinae (Fig. 47). In most analyses, however, *Ohakunea* is the sister group of one of the species of *Colonomyia*. Even though in the wing venation of the genus, the medial veins are nearly unsclerotized, the pattern is typical of the rangomaramids, with the displacement of the origin of m-cu even more to the base of the wing. The interpretation of Jaschhof & Hippa (2003) of the presence of R_4 distally seems equivocal. *Colonomyia* has the base of Rs clearly displaced to the apex and this feature is synapomorphic for the subfamily. R_4 is lost in the clade because the base of the Rangomaramidae and the examination of *Ohakunea chilensis* showed no evidence of a true Rs more basally in the wing. In the trees of Hippa & Vilkamaa (2005), it came together with *Colonomyia* as the sister group of (*Afrotricha* + *Heterotricha*) in the analysis of only extant taxa and in a clade with the Mycetophiloidea in the analysis that included fossils.

Colonomyia. Colonomyia is represented here with two species, and the genus is paraphyletic in the preferred tree (Fig. 68), but not in the tree from the unweighted analysis (Fig. 44). The genus is probably monophyletic, but a more detailed comparison between the Australasian and the Neotropical species is desirable.

Chiletricha, Rhynchoheterotricha, Kenyatricha, Insulatricha, and Eratomyia. The Chiletrichinae, comprising these five genera, are monophyletic in all topologies obtained except in the unweighted analysis (Fig. 44). *Chiletricha* is restricted to southern South America, with seven species in Chile and southern Argentina, and one species in southern Brazil. *Rhynchoheterotricha* includes a single species from South Africa. *Kenyatricha* includes two species from East African mountains. *Eratomyia* is known from one specimen from Ecuador. *Kenyatricha* and *Rhynchoheterotricha* alternate as the sister clade of the remainder of the Chiletrichinae. *Insulatricha*, with three species in New Zealand, always appears as the sister group of (*Chiletricha* + *Eratomyia*).

Afrotricha. When included in the analysis, *Afrotricha* (with a single species from Africa) appears either as

the sister group of the Sciaridae (Figs. 44, 46, 58) or of the Mycetophiloidea. Chandler's (2002) representation of the thorax shows a wide mesepimeron, but the wing feature is not typical of sciarids, with r-m oblique (not longitudinal) and m-cu present, in line with $bM_4 + M_{3+4} + M_{1+2}$, typical of higher Mycetophiliformia. Until reexamination, the genus should be considered *incertae sedis* in the group.

Anisotricha and *Nepaletricha.* Both these genera are generalized in relation to the wing pattern of the rangomaramids. *Anisotricha* now includes two species from New Zealand, whereas *Nepaletricha* has a single Palearctic species. *Anisotricha* and *Nepaletricha* fit within the Rangomaramidae when included in the analysis, but their precise positions in the group demand additional information. In most trees (Figs. 46, 48), they fit in the Okanuneinae, but in one case (Fig. 60), *Nepaletricha* appeared as the sister genus of *Rangomarama*. In the topologies of Hippa & Vilkamaa (2005), both genera would fit in the Chiletrichinae. The wing venation of both genera is rather conservative, with a transverse, short r-m; a short, oblique base of Rs; and a long, longitudinal $m\text{-}cu + M_4 + M_{3+4} + bM_{1+2}$. *Anisotricha similis* has some stronger setae on a pair of short projections of T9, but not as typical as in the other Chiletrichinae; *A. novaezealandia* and *Nepaletricha* have no distinctly modified setae, so their placement with other Chiletrichinae seems doubtful. Their association with the Rangomaramidae is clear, but their subfamilial assignment is still uncertain.

Sciarosoma. This genus has a single species from northern Europe. The position of this genus varies widely in the different analyses. In two cases, *Sciarosoma* joins the Keroplatoidea (Figs. 46, 48), and in one case, is in the Ohakuneinae (Fig. 61). We disagree with the conclusions of Hippa & Vilkamaa (2005), who assign *Sciarosoma* to the Sciaridae as a separate subfamily, thus agreeing with Jaschhof *et al.* (2005). The wing venation follows the rangomaramid general pattern, with m-cu present and slightly long and r-m absent (i.e., not longitudinal). The thorax is also apomorphic for features shared with the higher Mycetophiliformia. Our understanding is that the genus cannot be placed in any family before reexamination, but a placement close to the Keroplatoidea would not be surprising. The redescription of the genus based on additional specimens by Jaschhof *et al.* (2005) was published after the numerical analyses performed in this study were ready, but some are useful. Some of the features they redescribed, for example, the bipartite gonostyle or the five-articled maxillary palpus, correspond to autapomorphies or plesiomorphies that do not help solve the problem of its position within the system. However, the "quite bulging" laterotergite indicates that, despite the longitudinal r-m in the wing, *Sciarosoma* will fit somewhere in the (Rangomaramidae + Keroplatoidea + Mycetophiloidea) clade in the Mycetophiliformia, not connected to the Sciaridae, as proposed by Hippa & Vilkamaa (2005).

Sciaropota. *Sciaropota*, presently including a single Japanese species, appeared in our study connected to the Mycetophiloidea (Fig. 63), to the Keroplatoidea (Fig. 46), or at an even ealier position within the higher Mycetophiliformia (Fig. 48). The mesepimeron is unusually wide at the basal end, but it is not inclined over the katepisternum, as in sciarids or cecids. Also, the wing venation follows the general pattern of the higher clades of the Mycetophiliformia. In both analyses of Hippa & Vilkamaa (2005), it came out associated with the Mycetophiloidea. Based on our analysis, we suggest it should not yet be assigned to any family-level taxon.

Freemanomyia. *Freemanomyia* is known from a single southern Neotropical species, which retains R_4. In our analyses, it appeared as the sister group of the Rangomaramidae (Fig. 55), of *Rangomarama* (Fig. 48), or of the Mycetophiloidea (Figs. 44, 46). The genus is connected to the higher Mycetophiliformia. The basal cell is very wide, Rs originates distally, r-m is well developed and oblique in position, Sc is complete, and R_4 is produced and attached to R_1. Even though relatively plesiomorphic, some of these features are typical of the Mycetophiloidea. In Chandler's (2002) reconstruction, the genus (as *Pterogymnus*) also appeared as the sister group of (Lygistorrhinidae + Mycetophilidae), whereas in the analysis of Hippa & Vilkamaa (2005), it is the sister group of the Lygistorrhinidae in a clade that also includes the Mycetophilidae. It seems reasonable that the genus belongs to the Mycetophiloidea, sister to the remainder of the clade.

Taxicnemis. *Taxicnemis*, known from two New Zealand species, appeared in our study either connected to

the Mycetophiloidea (Figs. 46, 57) or to the Ohakuneinae (Fig. 48). Detailed examination of the type species is desirable, although the wing venation gives some clues. The genus is definitely not associated with any higher mycetophilid clade, because it does not have M_4 fused to CuA distally in the wing. R_4 present and connected to R_1 and a long *tb* could suggest placement in the Mycetophilidae in an early position. *Taxicnemis* was not included in the study of Hippa & Vilkamaa (2005), and Chandler (2002) probably considered it a true mycetophilid.

Loicia. *Loicia*, an interesting genus with a single Canadian species, has m-cu connecting CuA and M_4, a plesiomorphic condition not seen in other true mycetophilids. The genus appeared in our analysis as the sister group of (Rangomaramidae + Mycetophiloidea) (Fig. 56) and within the Mycetophiloidea (Figs. 44, 46). The genus might compose a clade with *Freemanomyia*, *Starkomyia*, and *Taxicnemis* at the base of the Mycetophiloidea.

Starkomyia. *Starkomyia*, a genus of one species recently described from New Zealand, appeared in all of our analyses as an early clade within the Mycetophiloidea. This result disagrees from the original proposition by Jaschhof (2004c), who raised a number of hypotheses and concluded that the genus is the sister group of a clade including the Cecidomyiidae, the Sciaridae, and the groups *Heterotricha* and *Ohakunea*. *Starkomyia* has a long and slender mesepimeron, a well-developed and apically slender laterotergite, and a high mediotergite, suggesting that it does not connect to the cecids and sciarids. Wing venation corroborates its position with the more advanced Mycetophiliformia, with a basal connection of m-cu to CuA and a very short bCuA. The presence of R_4 is plesiomorphic, but its connection to R_1 is more typical of the Mycetophiloidea. A position of the genus as the sister group of the rest of this clade, as indicated by the results here, seems reasonable.

Sciarotricha. This genus is presently restricted to a single Afrotropical species and was not included in our study. The original description is very detailed, and we can verify that the wing venation agrees with that of the Sciaridae (Hippa & Vilkamaa 2005, Fig. 5D). The thoracic sclerites also show no deviation from the typical shape of the sciarid plates, so there is no reason to question the decision of Hippa & Vilkamaa (2005) to include the genus in the Sciaridae.

A phylogenetic classification of the Mycetophiliformia

A detailed discussion about the evolution of characters in a group such as the Mycetophiliformia demands communication about a much larger number of inclusive taxa in the classification. We tried to attribute names for a number of the more important inclusive taxa appearing in the phylogeny, minimizing the creation of new taxa. The use of Hennig's (1954) concept of Mycetophiliformia (which corresponds to the 'Sciaroidea' in the sense of most papers recently published about the group) made this task easier, the superfamily being restricted to one step below in the classification. Hence, new taxa were necessary only for larger clades within the Rangomaramidae. The Keroplatoidea appears as an important clade here, uniting ditomyiids, bolitophilids, diadocidiids, and keroplatids.

Mycetophiliformia
    Cecidomyioidea
        Cecidomyiidae
    Sciaroidea
        Sciaridae
    Rangomaramoidea
        Rangomaramidae
            Chiletrichinae, **subfam. n.** – *Rhynchoheterotricha*, *Kenyatricha*, *Insulatricha*, *Chiletricha*, *Eratomyia* **gen. n.**, *Anisotricha, Nepaletricha*

Rangomaraminae – *Rangomarama*
Heterotrichinae, **subfam. n.** – *Heterotricha*
Ohakuneinae, **subfam. n.** – *Ohakunea, Colonomyia, Cabamofa, Rogambara*
Keroplatoidea
Ditomyiidae
Bolitophilidae
Diadocidiidae
Keroplatidae
Mycetophiloidea
Lygistorrhinidae
Mycetophilidae

Genera *incertae sedis* within the Mycetophiliformia: *Taxicnemis, Sciarosoma, Sciaropota, Afrotricha, Freemanomyia, Starkomyia, Loicia*

Acknowledgements

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Appendix 1. List of examined specimens

Limoniidae

Edwardsomyia chiloensis Alexander, 1929 – male, S. CHILE, Chiloe I., Aucar, I - 6/15.1952, Peña / Det. C.P. Alexander

Trichoceridae

Trichocera columbiana Alexander, 1927 – male, CANADA, N.W.T., Muskox L., 64°42'N, 108° 10'W, ecological data g: 12-VIII- 1953, B. Chilkott, col., Det: Ch. Dahl 1966, F.R.B.: Winnipeg 2–5, females

Trichocera columbiana Alexander, 1927 – female, CANADA, N.W.T. Resolute Bay, Cornwallis Is., 5 VII 1949, E.H.N. Smith col., Det: Ch. Dahl 1966, CNC

Anisopodoidea

Sylvicola cf. *annulifer* (Edwards, 1923) – male, BRAZIL, State of Amazonas, Rio Javari, Estirão do Equador, XI. 1979, M. Alvarenga col., Det D.S. Amorim 1983

Olbiogaster alvarengai Tonzoni, 1993 – **Holotype**, male, BRAZIL, State of São Paulo, Teodoro Sampaio, Mailase trap, XI 1977, M. Alvarenga col.

Mycetobia limanda Stone, 1966 – male, USA, Oregon, N. Plains, Washingon Co., 19 May 1963, K. Goeden, along stream, USNM No. 68116

Mycetobia divergens (Walker, 1856) – Det D.S. Amorim

Olbiogaster sp. – male, BOLIVIA, Dept., Beni, Rio Mamora, Approx. 5 km. NW, Mouth of Rio Grande, VIII-3-4-1965, J.K. Bouseman col.

Olbiogaster sackeni Edwards, 1915 – male, BRAZIL, State of Bahia, Itabuna, Reserva Ecologica CEPEC, Mata, Light trap, 07-07. X. 1985, Paulo S. Terra col.

Olbiogaster marinonii Tozoni, 1993 – **Paratype**, BRAZIL, State of Paraná, Fênix, Reserva Est. – ITCF, 06. X. 1985, PROFAUPAR, Malaise trap

Cramptonomyiidae

Cramptonomyia spenceri Alexander, 1931 – male, CANADA, Point grey, Vancouver B.C., 20 – III 1973, J. R. Vockeroth, CNC

Cramptonomyia spenceri Alexander, 1931 – female, CANADA, Point grey, Vancouver B.C., 20 – III 1973, J. R. Vockeroth, CNC, Layer of eggs

Pachyneura fasciata Zetterstedt, 1838 – male, JAPAN, Hokkaido, Daisetsuzan Nt Pk, Yukomanpetsu 1100m, 2. VII.86 M. Wood, CNC

Bibionidae

Hesperinus sp. – male, USA, Lake Creek Camp, Park Co. Wyo. 13 mi, SE. Cooke city Mont., July 23,1953 6900 ft., F., P. & B. Rindge, Collected on NSF, Grant G 9037

Plecia sp. – CONGO, Ruercu, S.W. Mikeno, Belg. March 10. 1927, 9500 ft.

Plecia sp. – BRAZIL, State of São Paulo, José do Barreiro, (Serra da Bocaina) - 1650 m, Malaise trap, XI. 1967, M. Alvarenga col.

Bibio sp. – USA, Montana, S. Coscaron, Collector, Hamilton, Ravalli, Co. June 20, 1964

Cecidomyiidae

Porricondylinae sp. – 4 spp., CHILE, Dalcahue, I. Chiloé, IV.1968, L. E. Peña col.

Porricondylinae sp. – 2 spp. , BRAZIL, State of Santa Catarina, Nova Teutônia, 27º11' B. 52º23'L., Fritz Plaumann, 300–500 m, VIII 1971

Lestremia sp. – 7, females, BRAZIL, State of Santa Catarina, Nova Teutonia, 27º11' B. 52º23'L., Fritz Plaumann, 300–500 m, VIII 1971

Lestremia sp. – 7, females, BRAZIL, State of Santa Catarina, Nova Teutonia, VIII 1967, Fritz Plaumann col.

Sciaridae

Trichomegalophsys sp. – BRAZIL, State of Amazonas, Rio Javari, Estirão do Equador, XI. 1979, M. Alvarenga col., Det. D. S. Amorim

Trichomegalophsys sp. – BRAZIL, State of Paraná, Porto Alcidia, Forattini col., VII-54

Zygoneura sp. – BRAZIL, State of Bahia, J.A Winder, TL 1973.51, Bishop Museum

Bradysia sp. – BRAZIL, State of Bahia, Emergence trap on Cacao leaf litter, 1970–72, J.A. Winder, TL. 1973.51, Bishop Museum

Pseudosciara sp. – BRAZIL, State of Bahia, TL 1972, Bishop Museum

Rangomaramidae

Eratomyia magnifica, n.sp. – **Holotype**. ECUADOR, Quito-Baiza, E. Papallacta, 2.900m, 12–15.ii.1971, L.G Peña col.

Chiletricha marginata Edwards, 1940 – BRAZIL, State of São Paulo, Campos do Jordão, viii.1949, J. Lane col., J. Lane det.

Chiletricha seminuda Freeman, 1951 – CHILE, Dalcahue, I. Chiloé, IV.1968, L. E. Peña col., N. Papavero det.

Chiletricha seminuda Freeman, 1951 – CHILE, Dalcahue, I. Chiloé, iv.1968, L. E. Peña col., D.S. Amorim det,

Chiletricha seminuda Freeman, 1951 – CHILE, Terra Del Fuego, Pto. Percy, 17. xii. 1960, L. E. Pena col., D. S. Amorim det.

Chiletricha seminuda Freeman, 1951 – 1 male, S. CHILE, Llanquihue prov., Casa Pangue, F. & M. Edwards, 12–13.xii.1926, B.M. 1927, Paul Freeman det.

Ohakunea chilensis Freeman, 1951 – 2 males, CHILE, Dalcahue, I. Chiloé, i.1962, L. E. Peña col., Det. D. S. Amorim 1983

Ohakunea chilensis Freeman, 1951 – female, CHILE, Dalcahue, I. Chiloé, iv.1968, L. E. Peña col., Det. D. S. Amorim 1983

Ohakunea chilensis Freeman, 1951 – male, S. CHILE, Llanquihue prov., Casa Pangue, F. & M. Edwards, 4–10.xii.1926, B.M. 1927, Paul Freeman det.

Colonomyia freemani, n. sp. – Holotype, male, 7 male and 4 female paratypes, CHILE, Dalcahue, I. Chiloé, iv.1968, L. E. Peña col.

Colonomyia freemani, n. sp. – 4 male and 1 female paratypes, CHILE, Dalcahue, I. Chiloé, ii.1962, L. E. Peña col.

Colonomyia freemani, n. sp. – 1 male paratype, CHILE, Osorno, Pucatrihue, ii.1967, L. E. Peña col.

Colonomyia brasiliensis, n. sp. – **Holotype**, male, 1 male **paratype**, BRAZIL, State of São Paulo, Salesópolis (Boracea), 14.viii.1947, E. Rabelle & Trav. F.

Colonomyia brasiliensis, n. sp. – 2 male **paratypes**, BRAZIL, State of São Paulo, Salesópolis (Boracea), viii.1949, Lane & Coher col.

Colonomyia sp. – BRAZIL, State of Mato Grosso, Chapada dos Guimarães, POLONOROESTE, Malaise trap, 03–06.march.1983, Exp. Dep. Zool. UFPR

Colonomyia sp. – female, ARGENTINA, Rio Negro, Nov 1926, R&E Shannon, Porto Blest, xii.2.26

Colonomyia sp. – female, CHILE, 49ºS. Puerto Edén, Isla Wellington, 28-XI-1958. 1300 ft., Royal society Chilean exped. 1959

Cabamofa mira Jaschhof, 2005 – male, COSTA RICA, Turrialba, Nov. 1922, Pab. Schild, A.L. Melander Collection 1961, D.S. Amorim, det.

Diadocidiidae

Diadocidia valida Mik, 1874 – male, NORWAY, EIS19, VE, Borre: Veggfjell, Mal. Trap. July 1997, Leg. L. O. Hansen

Diadocidia (*A.*) sp. – female, NORWAY, EIS28, AK, AAs: AArungen, Syverud, 23 Oct. – 19.ix. 2003, E. Rindal leg., UTMWGS8432VNNM988180

Diadocidia (*D.*) sp. – CHILE, Dalcahue I. Chiloé, IV.1968, L. E. Peña col.

Diadocidia (*A.*) sp. – BRAZIL, State of Amazonas, Rio Javari, Estirão do Equador, XI. 1979, M. Alvarenga col., Det. D. S. Amorim 1983

Ditomyiidae

Ditomyia fasciata (Meigen, 1818) – 2 males, ENGLAND, Gerrard's Cross, Bucks, P.A. Buxton, Oct. 1951, From *Polyporus picipes*, det. D. D. Munroe

Ditomyia sp. – male, USA, Ardmore, Pa. V-5-12, GMGreene collector

Symmerus akikoae Saigusa, 1973 – male, NE BURMA, Kambaiti 7000 ft, May 9, 1934, R. Malaise trap, Det. D. S. Amorim

Australosymmerus bivittatus (Freeman, 1951) – 2 males, CHILE, Osorno Province, P.N Puyehue, 600 m, Ag. Calientes to 2kmS, 10–22 February 1979, D. & M. Davis, & B. Akerbergs, Det. D. S. Amorim 1985

Australosymmerus bivittatus (Freeman, 1951) – male, CHILE, Casa Pangue, Llanquihue, Dec 1926, R & E Shannon, Det. D. S. amorim 1985

Australosymmerus (*Melosymmerus*) *bisetosus* (Edwards, 1940) – 5 males, BRAZIL, State of Santa Catarina, Nova Teutonia, 27°11' B. 52°23'L., Fritz Plaumann, 20.11.1938, Det. John Lane 1951

Nervijuncta nigrescens Marshall, 1896 – male, NEW ZEALAND, Raetihi Hill., 3000 ft. XI. 1923, T.R Harris, B.M. 1924-22

Nervijuncta wakefieldi (Edwards, 1921) – male, NEW ZEALAND, Governor's Bay, 30. XI 1922, J. F. Tapley, B.M. 1923-424

Bolitophilidae

Bolitophila (*C.*) sp. 2 – 1 female, NORWAY, EIS 41, HOI, Eidsfjord, Simadalen, Tveit, 6 IX – 18 X 2003, Leg. E. Rindal, 23VWGS84MN006086

Bolitophila (*C.*) sp. – 1 male, NORWAY, EIS 41, HOI, Eidsfjord, Simadalen, Tveit, 1 May – 12 June 2004, Leg. E. Rindal & T. Darup, 23VWGS84MN006086,

Bolitophila sp. – 1 male, USA, Lake Vahn, IDA, 9 June 1918, A.L. Melander, A.L. Melander collection 1961

Keroplatidae

Arachnocampa luminosa (Skuse, 1891) – female, NEW ZEALAND, Waitomo Grotto, Waitomo 129 NH, S. Auckland VI – 29–65, F. Jones & M. Steptoe.

Platyura sp. – 1 female, BRAZIL, State of Paraná, Curitiba, Capão da Imbuia, Malaise trap, 02–09. VI 1979, A.F. Yamamoto col.

Isoneuromyia sp. – male, BRAZIL, State of Minas Gerais, Águas Vermelhas 800m, Malaise trap, XII.1983, M. Alvarenga col.

Neoplatyura sp. – female, BRAZIL, State of Paraná, Curitiba, Capão da Imbuia, Malaise trap, 02–09. VI 1979, A.F. Yamamoto col.

Platyroptilon sp. – BRAZIL, State of Amazonas, Rio Javari, Estirão do Equador, XI. 1979, M. Alvarenga col., Det D. S. Amorim 1983

Lygistorrhinidae

Probolaeus sp. 1 – male, BRAZIL, State of Paraná, Antonina, Res. Sapitanduva, IX 86, Malaise trap, Profaupar.

Probolaeus sp. 2 – male, 2 females, BRAZIL, State of Paraná, Telêmaco Borba, Res. Samuel Klabin, Malaise trap, 15. IX 1986, Profaupar

Mycetophilidae

Paratinia sciarina Mik, 1874 – 1 male, 1 female, NORWAY, Luster, Jolesdalen, Øyastrondi, 20.08–11.09.1988, G. Söli leg.

Drepanocercus spinistylus Soli, 1993 – 1 male, NORWAY, Luster, Jolesdalen, Øyastrondi, 20.08–11.09.1988, G. Söli leg.

Sciophila sp. – male, BRAZIL, State of Paraná, Guarapuava, Águas de Santa Clara, Malaise trap, 15.IX.1986, Profaupar

Cluzobra sp. – male, BRAZIL, State of Paraná, Jundiaí do Sul, Faz. Monte Verde, Malaise trap, 29.IX.86, Profaupar

Megalopelma sp. – male, BRAZIL, State of Paraná, Jundiaí do Sul, Faz. Monte Verde, Malaise trap, 08.IX.86, Profaupar

Eudicrana sp. – male BRAZIL, State of Pará, Altamira, Arn. Intercepgão, 08–22. IV. 1986, (MPEG) N. Degallier col.

Allocotocera sp. – 1 male, BRAZIL, State of Paraná, S. Jose dos Pinhais, Serra mar, BR 277, km 54, Malaise trap, 24.XI. 1986, Profaupar

Monoclona sp. – male, BRAZIL, State of Paraná, Guarapuava, Águas de Santa Clara, Malaise trap, 15.IX.1986, Profaupar

Synapha sp. – 3 males, 3 females, BRAZIL, State of Paraná, Telêmaco Borba, Res. Samuel Klabin, Malaise trap, 10. XI 1986, Profaupar

Coelosia sp. – female, NORWAY, EIS 46, HES, ELVERUM: Starmoen NR, 11 June – 29 July 2004, L.O. Hansen & E. Rindal, 32VWGS84PN46244907, Malaise trap S.

Dziedzickia sp. – male, 1 female, BRAZIL, State of Paraná, Telêmaco Borba, Res. Samuel Klabin, Malaise trap, X 1986, Profaupar

Mycomya sp. – male, BRAZIL, State of Paraná, Guarapuava, Águas de Santa Clara, Malaise trap, 15.IX.1986, Profaupar

Neoempheria sp. – 1 male, 3 females, (Fazenda Caruaru), 900ms - VI. 1972, J. Lima col.

Leia sp. – male, BRAZIL, State of Paraná, Curitiba, Capão da Imbuia, Mata-Malaise trap, 02–09. VI 1979, A.F. Yama-moto

Leia sp. 2 – male, BRAZIL, State of Paraná, Curitiba, Capão da Imbuia, Malaise trap, 02–09. VI 1979, A.F. Yamamoto col.

Leia sp. – male, BRAZIL, State of Paraná, Jundiaí do Sul, Faz. Monte Verde, Profaupar 29.IX.86, Malaise (1.3)

Megophthalmidia sp. – 2 males, 3 females, BRAZIL, State of Pernambuco, Caruaru, Fazenda Caruaru – 900 m, VI. 1972, J. Lima col.

Tetragoneura sp. – 3 males, 3 females, BRAZIL, State of Pernambuco, Caruaru, Fazenda Caruaru – 900 m, Malaise trap, VI. 1972, J. Lima col.

Tetragoneura sp. – female, BRAZIL, State of Paraná, Jundiaí do Sul, Faz. Monte Verde, Profaupar 29.IX.86, Malaise (1.3)

Manota sp. – 1 male, 1 female, BRAZIL, State of Paraná, Ponta Gossa (V. Velha) Res. Iapar, Br 376, Profaupar 08.XIII.86, Malaise

Manota sp. – male, BRAZIL, State of Rondônia, Vilhena, (Chapada dos Parecis), XI. 1973, Roppa & Alwarenga col.

Manota sp. – male, BRAZIL, State of São Paulo, Riberão Preto, Campus Universitário-USP, 18–21.III.1994, Malaise trap

Mycetophila sp. – BRAZIL, State of Paraná, Antonina, Res. Sapitanduva, 23. II 87, Malaise trap, Profaupar

Rymosia sp. – 2 males, 2 females, BRAZIL, State of Paraná, S. Jose dos Pinhais, BR 277, km 54, Torre Telepar, Malaise trap, VII. 1984, J.A. Rafael col.

Trichonta sp. – 2 males, BRAZIL, RO, Vilhena, Cerrado, Malaise trap, 17.X.1986, C. Elias col.
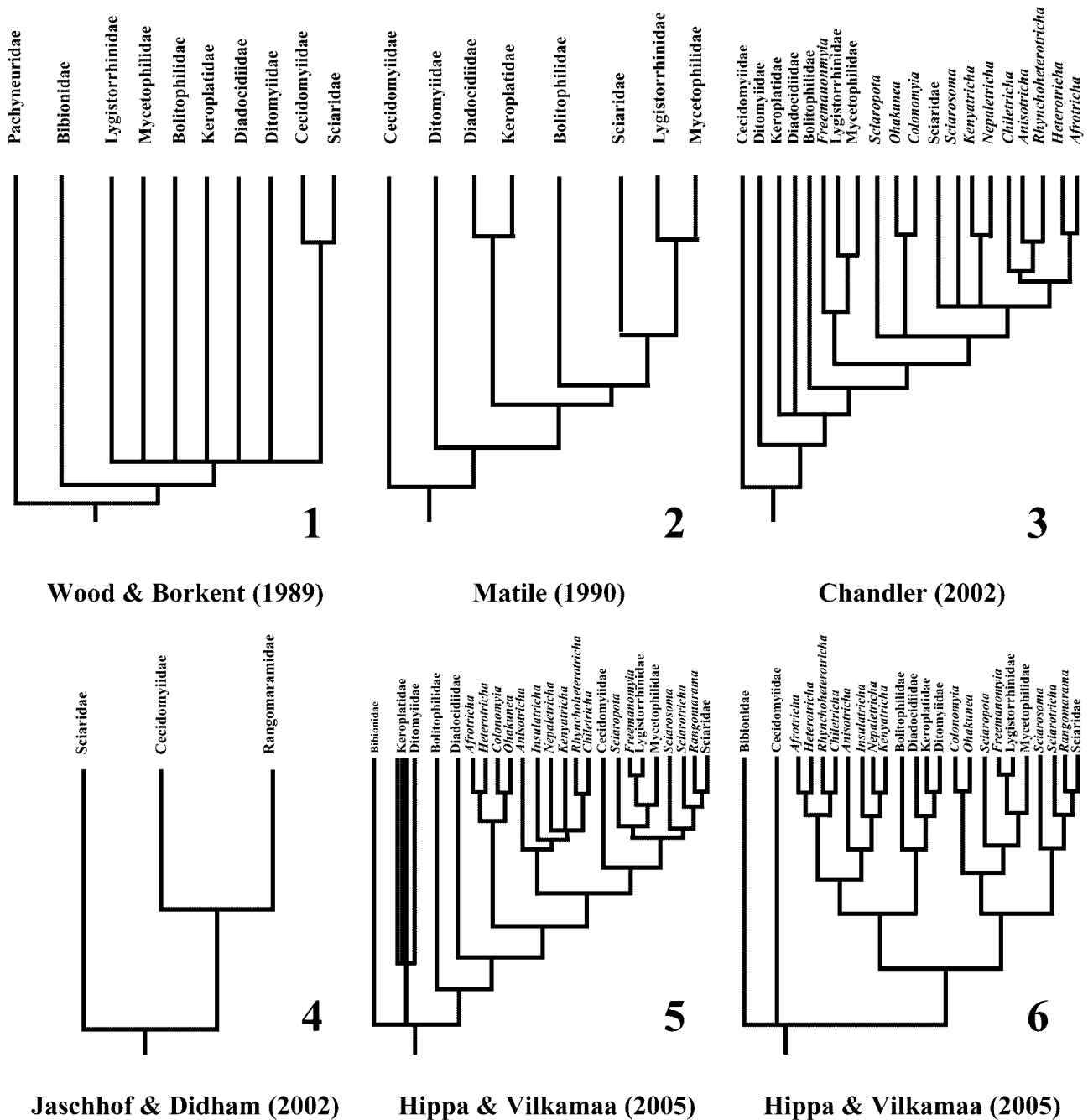
FIGURES 1–6. Phylogenetic relationships proposed for the Bibionomorpha major clades. **1.** Proposal of Wood & Borkent (1989), with the exclusion of the Anisopodiformia. **2.** Matile's (1990) analysis of the Mycetophiliformia. **3.** Chandler's (2002) study, with the inclusion of the genera of difficult placement within the Mycetophiliformia. **4.** The relationships proposed by Jaschhof & Didham (2002) for Sciaridae, Cecidomyiidae, and Rangomaramidae. **5.** Relationships proposed by Hippa & Vilkamaa (2005) for the Mycetophiliformia, including only recent taxa. **6.** Same, including fossil taxa (not shown).
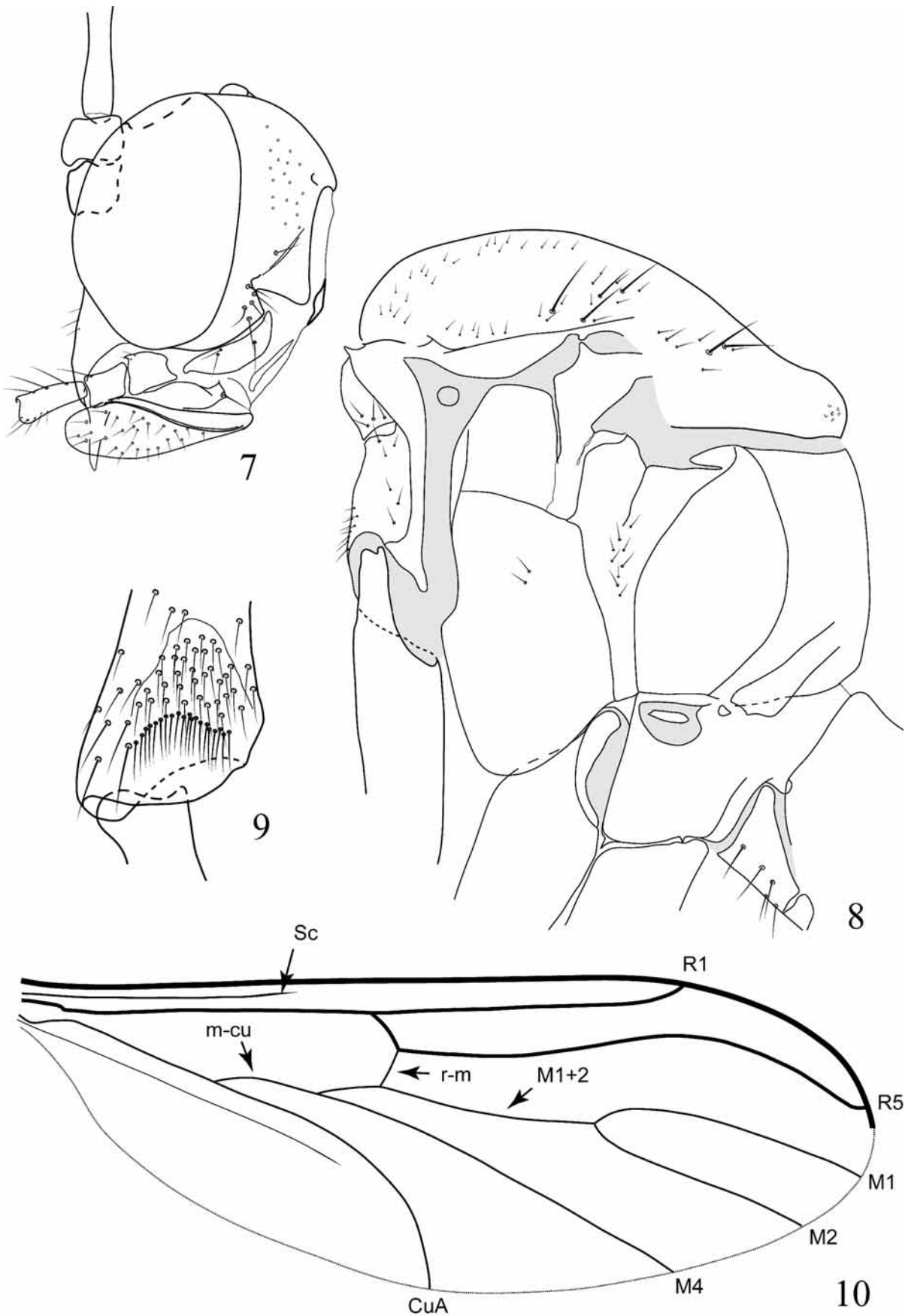
FIGURES 7–10. *Eratomyia magnifica*, **sp. n. 7.** Head (apical maxillary palpal segments not represented), lateral view. **8.** Thorax. **9.** Front tibial apex, inner view. **10.** Wing.
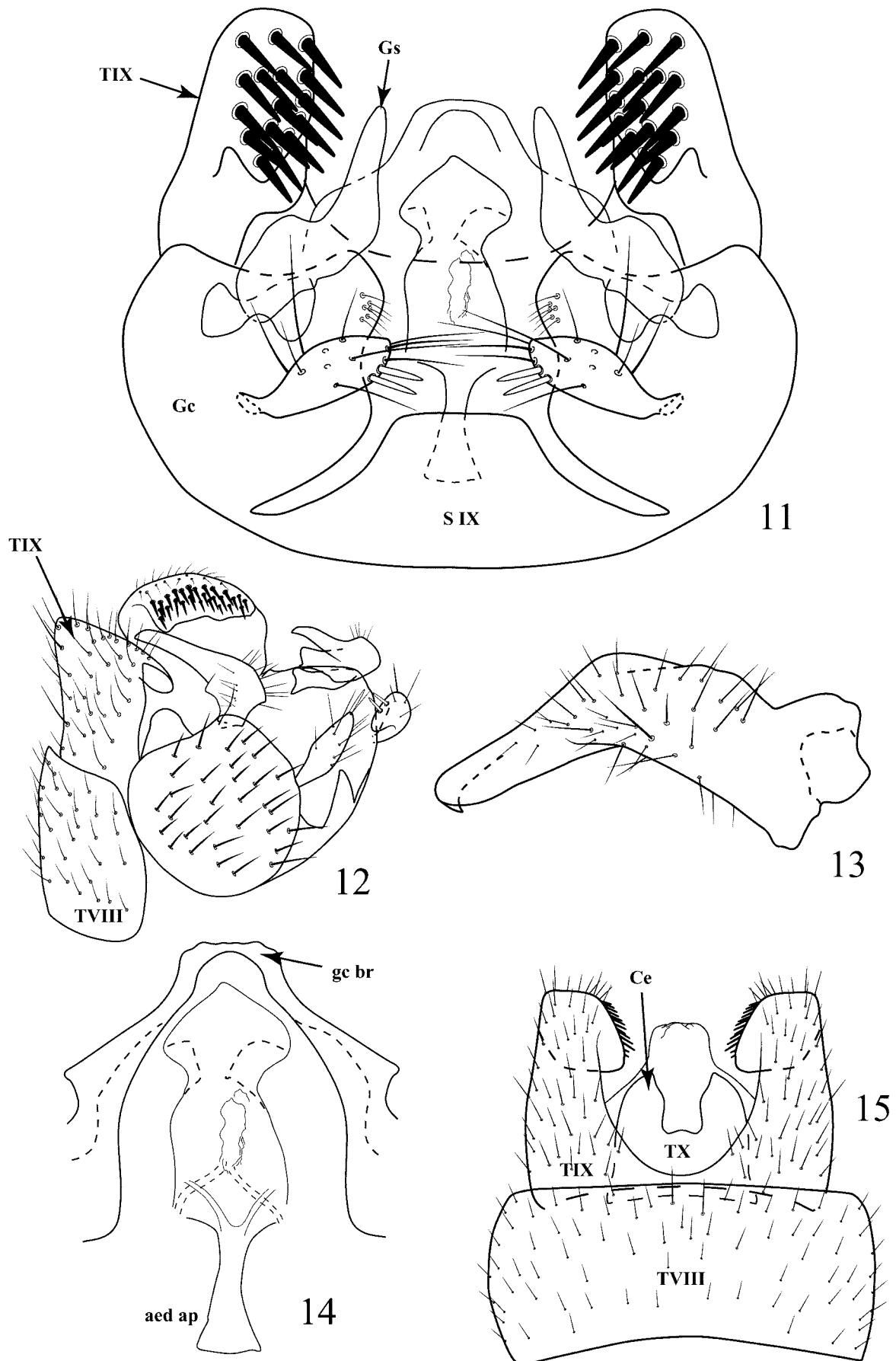
FIGURES 11–15. *Eratomyia magnifica*, **sp. n. 11.** Male terminalia, posterior view. **12.** Male terminalia, lateral view. **13.** Gonostyle, external view. **14.** Aedeagus and gonocoxal bridge. **15.** Tergites VIII–X and cerci, posterior view.
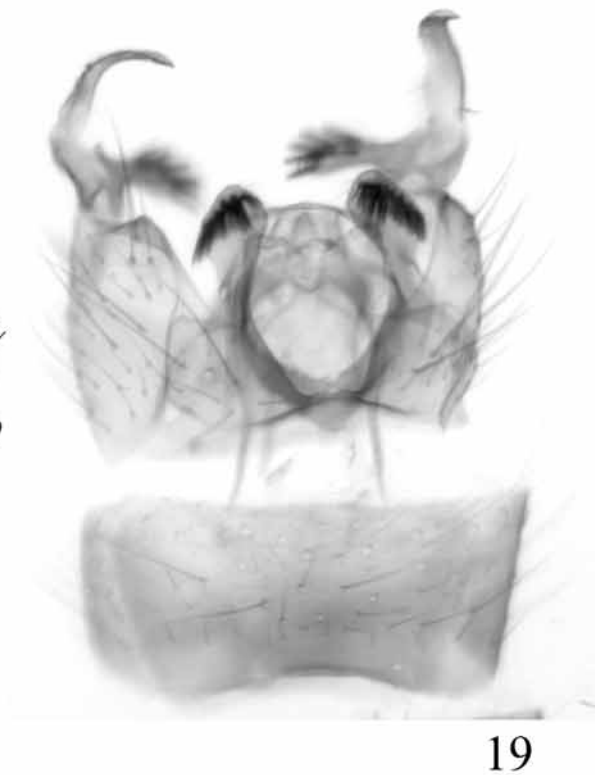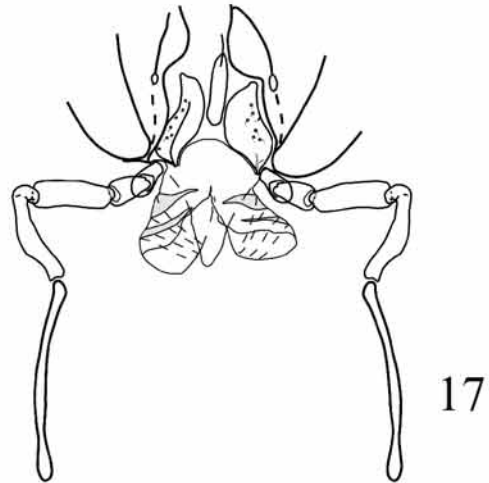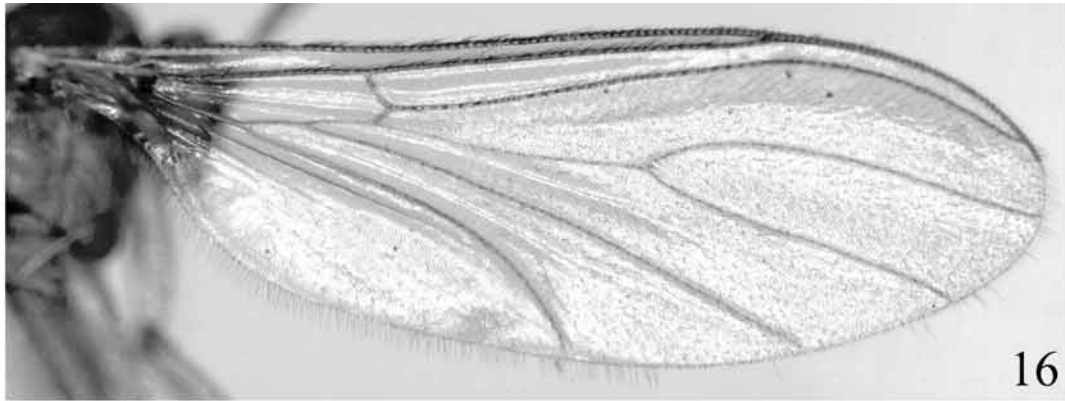
FIGURES 16–19. *Chiletricha*. **16, 17.** *Chiletricha seminuda* (Freeman). **16.** Wing. **17.** Mouthparts, posterior view. **18, 19.** *Chiletricha marginata* (Edwards). **18.** Thorax. **19.** Male terminalia, dorsal view.
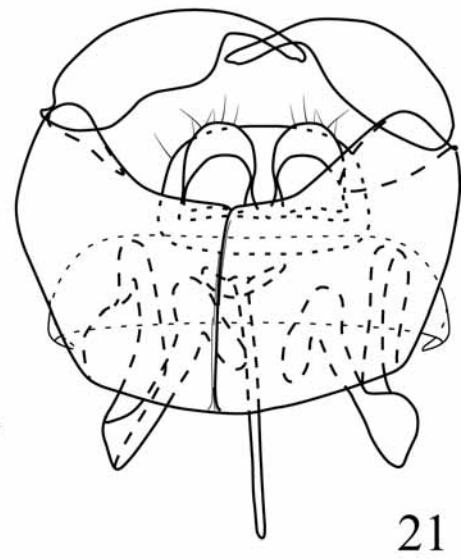
FIGURES 20–21. *Colonomyia brasiliana*, **sp. n. 20.** Thorax. **21.** Male terminalia.
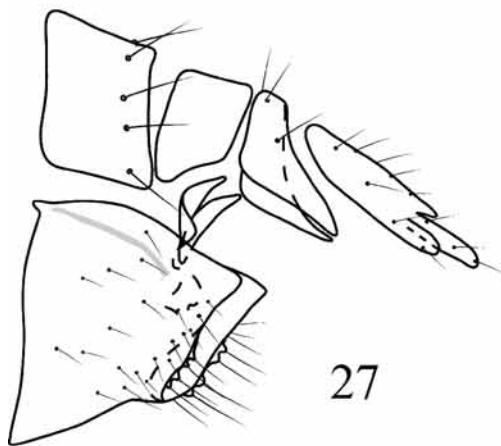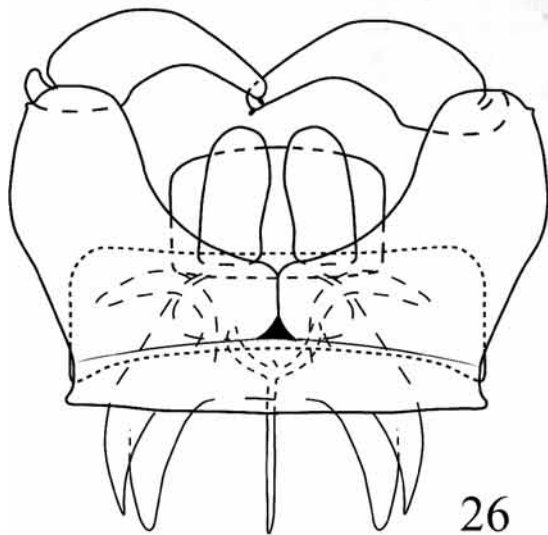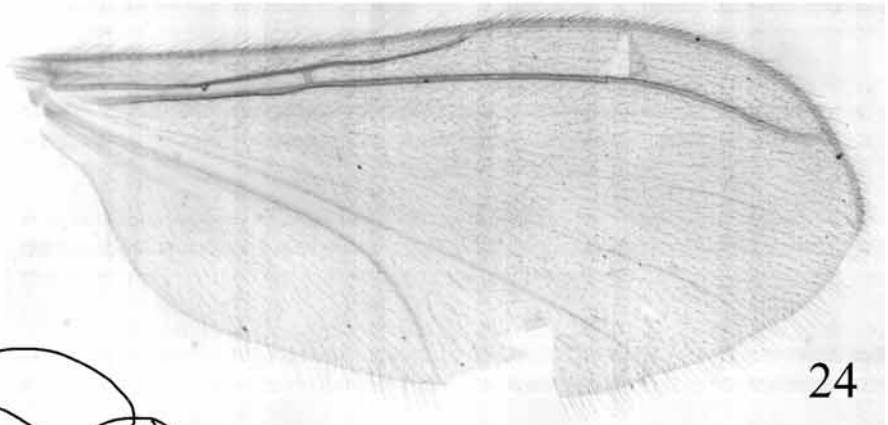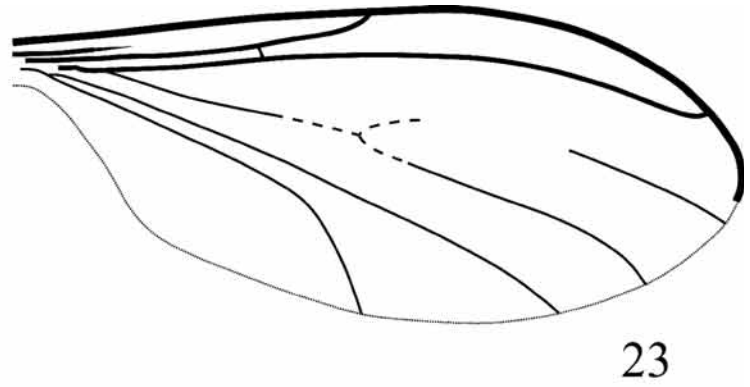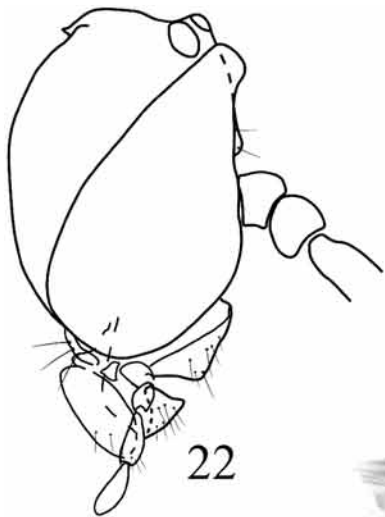
FIGURES 22–27. *Colonomyia freemani*, **sp. n. 22.** Head, lateral view. **23, 24.** Wing. **25.** Thorax. **26.** Male terminalia, ventral view. **27.** Female terminalia, lateral view.

R1
R5
M1+2
M4
CuA
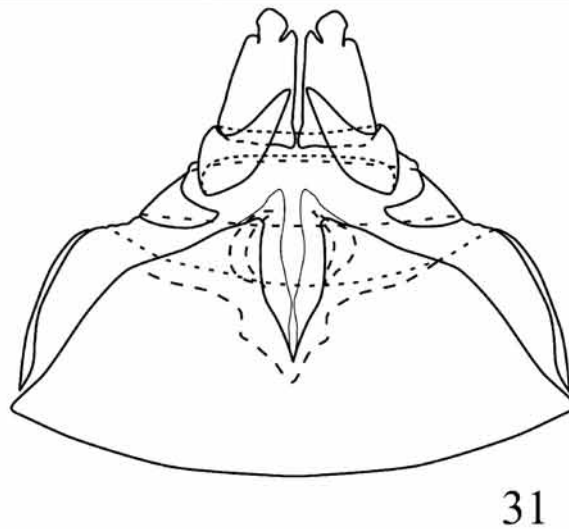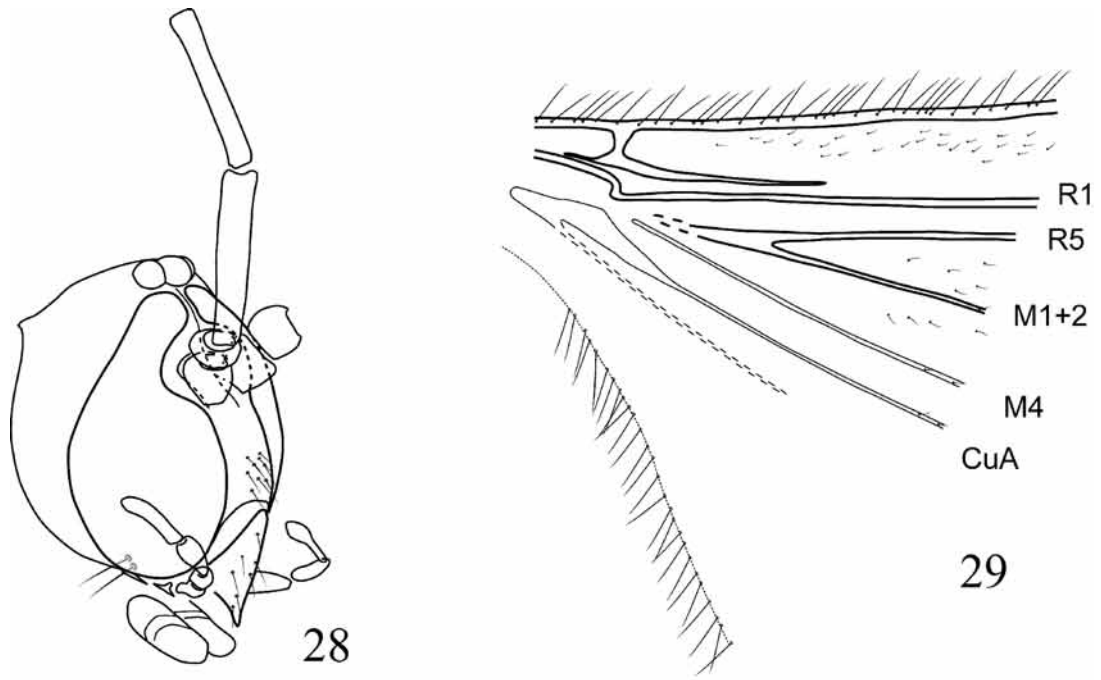
FIGURES 28–31. *Colonomyia* sp. **28.** Head, frontolateral view. **29.** Base of wing. **30.** Wing. **31.** Female terminalia, ventral view.
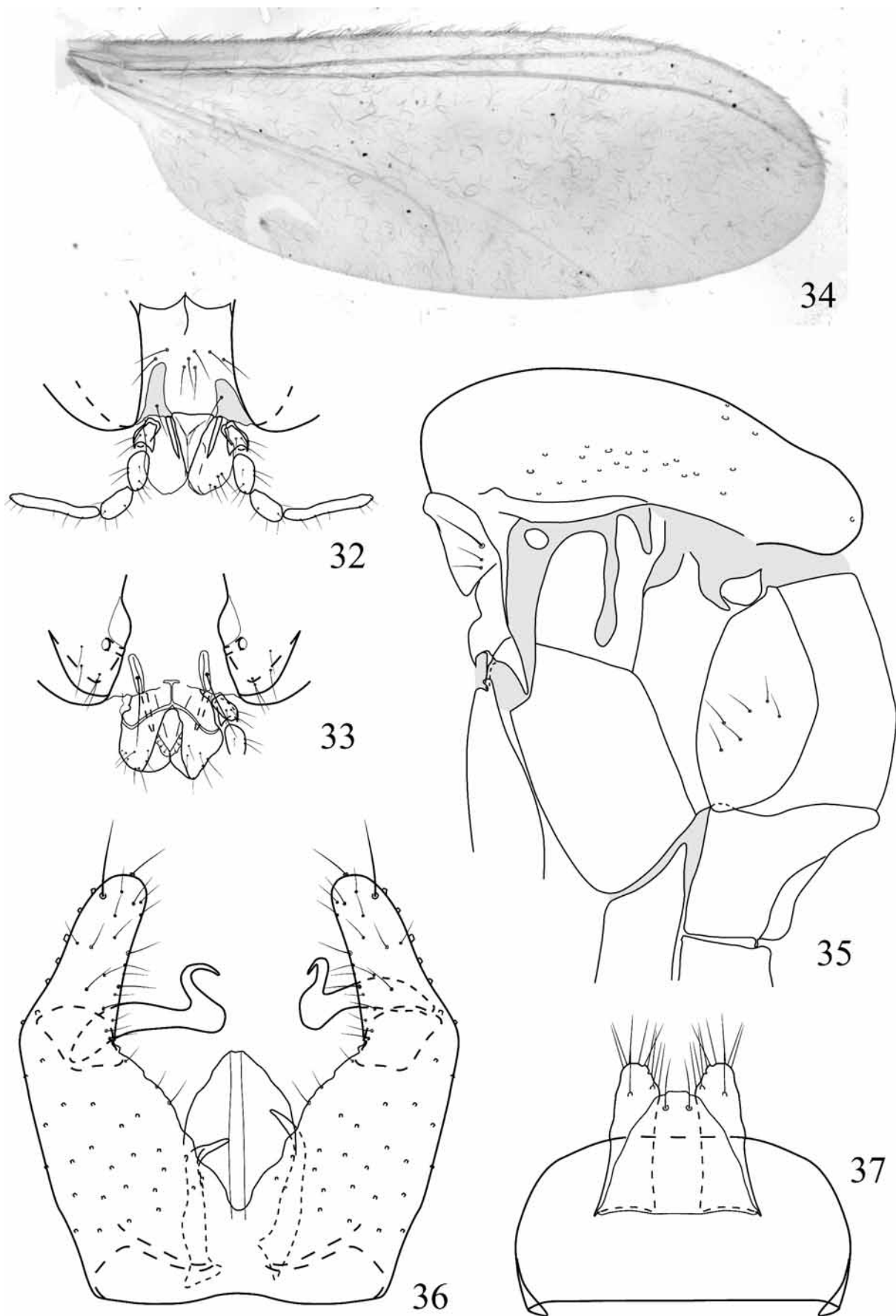
FIGURES 32–37. *Ohakunea chilensis* Freeman. **32.** Head, frontal view. **33.** Head, posterior view. **34.** Wing. **35.** Thorax. **36.** Male terminalia, ventral view. **37.** Tergites IX and X and cerci, ventral view.
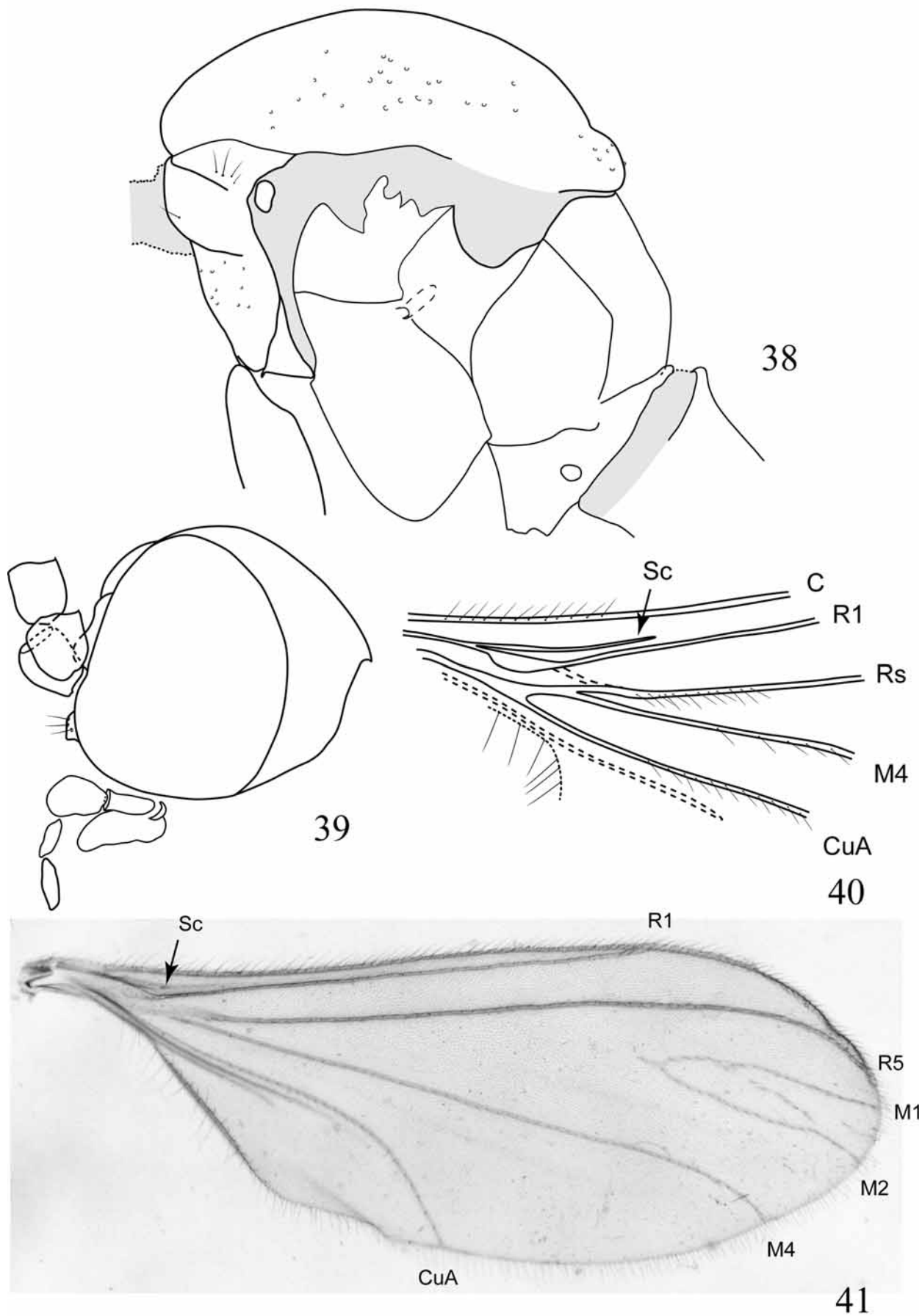
FIGURES 38–41. *Cabamofa mira* Jaschhof, male. **38.** Thorax. **39.** Head, lateral view. **40.** Base of wing. **41.** Wing.
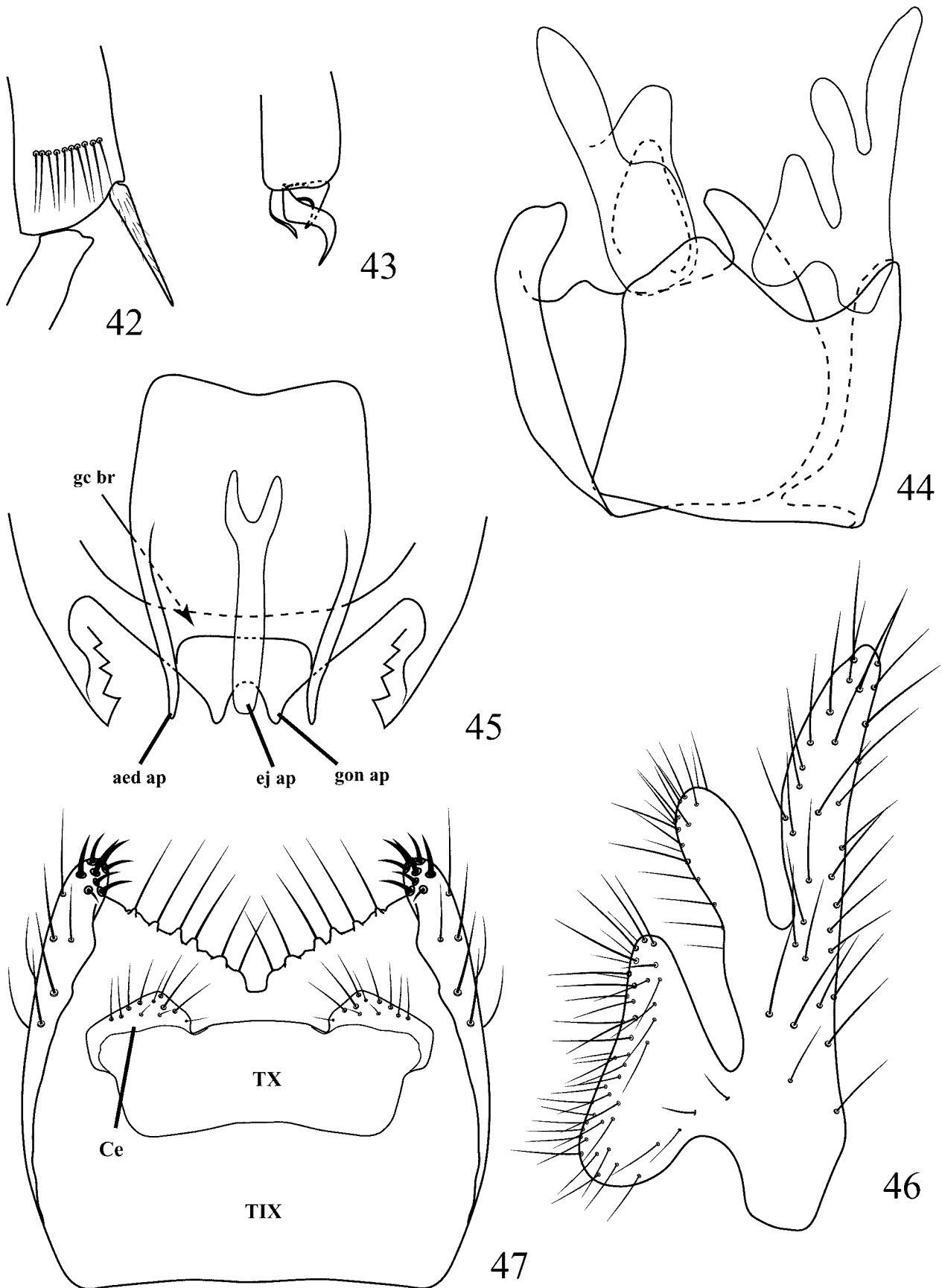
FIGURES 42–47. *Cabamofa mira* Jaschhof, male. **42.** Front tibial apex, inner view. **43.** Tarsal claw. **44.** Male terminalia, lateral view. **45.** Gonostyle. **46.** Gonocoxal apodeme and aedeagus, ventral view. **47.** Tergites IX and X and cerci, ventral view.
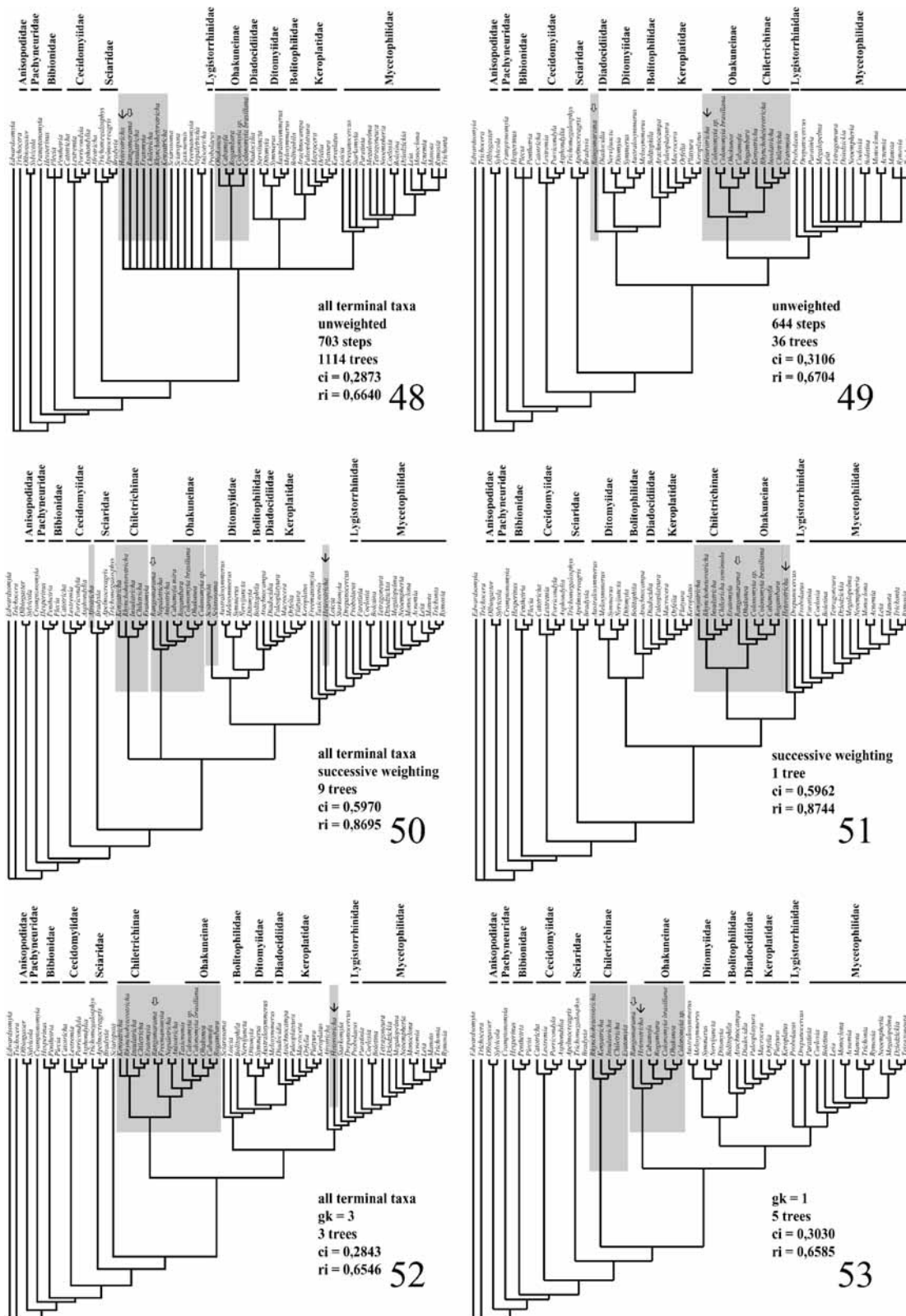
FIGURES 48–53. Topology obtained from the analysis of the data matrix under different algorithms and options. **48.** Equal weight, complete matrix. **49.** Equal weight, reduced matrix (terminal taxa with high number of missing data excluded). **50.** Successive weighting, complete matrix. **51.** Successive weighting, reduced matrix. **52.** Goloboff parsimony, reduced matrix, gk = 0. **53.** Goloboff parsimony, reduced matrix, gk = 1. Shadings correspond to the genera in each topology that fit in the Rangomaramidae in the classification accepted here. ? shows the position of *Rangomarama* and ? shows the position of *Heterotricha* in each topology.
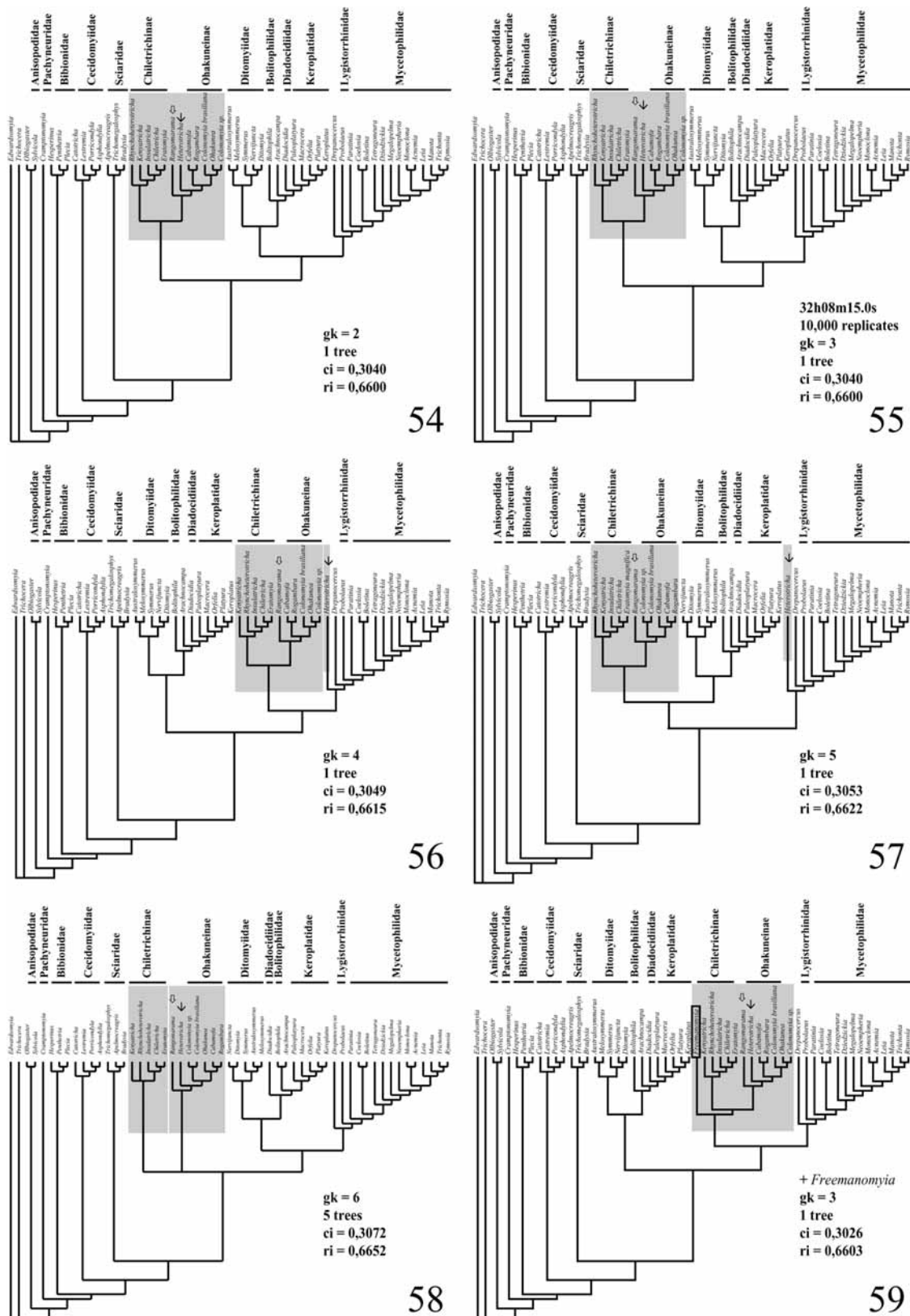
FIGURES 54–59. Topology obtained from the analysis of the data matrix under different algorithms and options. **54.** Goloboff parsimony, reduced matrix, gk = 2. **55.** Goloboff parsimony, reduced matrix, gk = 3. **56.** Goloboff parsimony, reduced matrix, gk = 4. **57.** Goloboff parsimony, reduced matrix, gk = 5. **58.** Goloboff parsimony, reduced matrix, gk = 6. **59.** Goloboff parsimony, reduced matrix + *Freemanomyia*, gk = 3. Shadings correspond to the genera in each topology that fit in the Rangomaramidae in the classification accepted here. ? shows the position of *Rangomarama* and ? shows the position of *Heterotricha* in each topology.
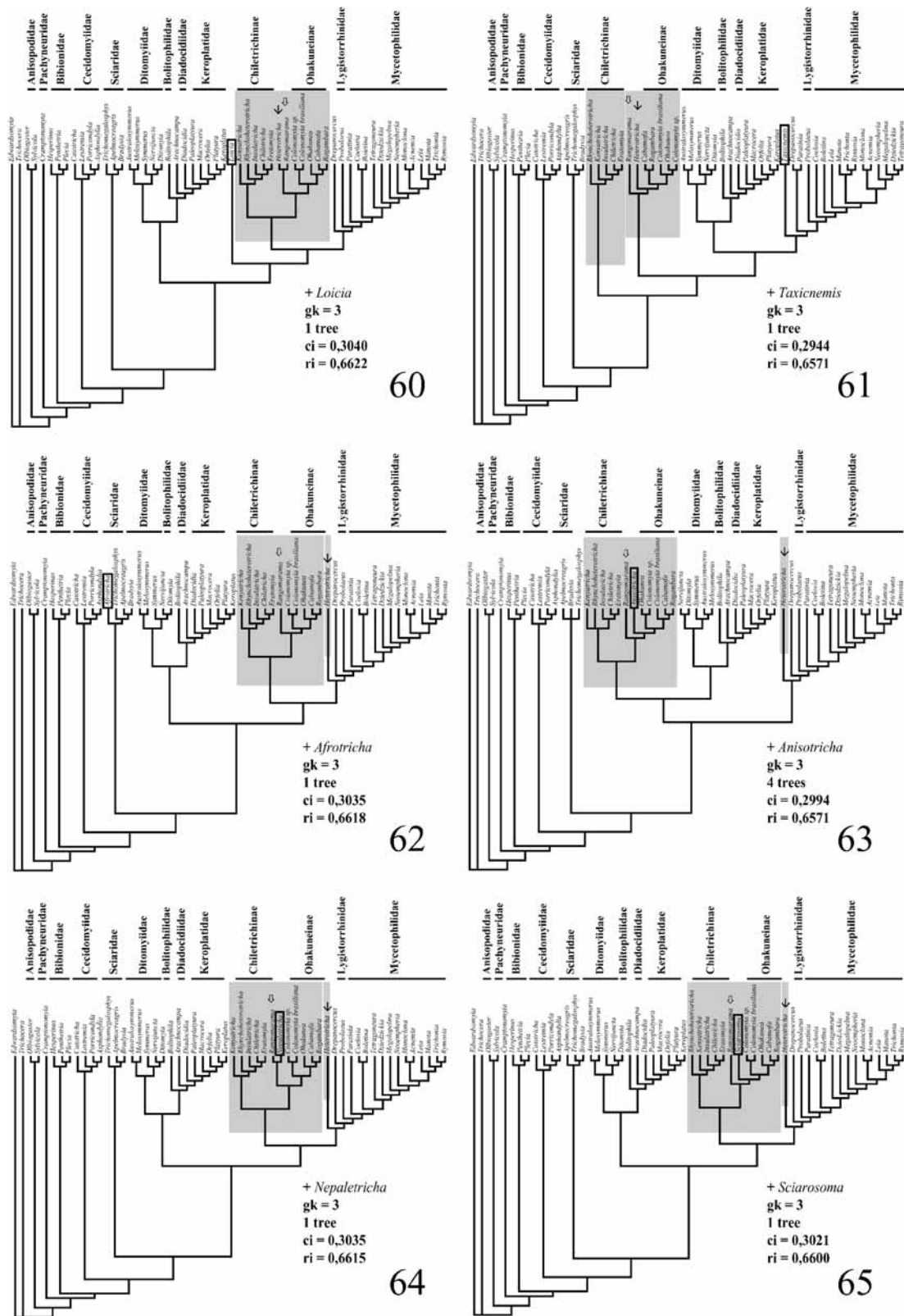
FIGURES 60–65. Topology obtained from the analysis of the data matrix under different algorithms and options. **60.** Goloboff parsimony, reduced matrix + *Loicia*, gk = 3. **61.** Goloboff parsimony, reduced matrix + *Taxicnemis*, gk = 3. **62.** Goloboff parsimony, reduced matrix + *Afrotricha*, gk = 3. **63.** Goloboff parsimony, reduced matrix + *Anisotricha*, gk = 3. **64.** Goloboff parsimony, reduced matrix + *Nepaletricha*, gk = 3. **65.** Goloboff parsimony, reduced matrix + *Sciarosoma*, gk = 3. Shadings correspond to the genera in each topology that fit in the Rangomaramidae in the classification accepted here. ? shows the position of *Rangomarama* and ? shows the position of *Heterotricha* in each topology.
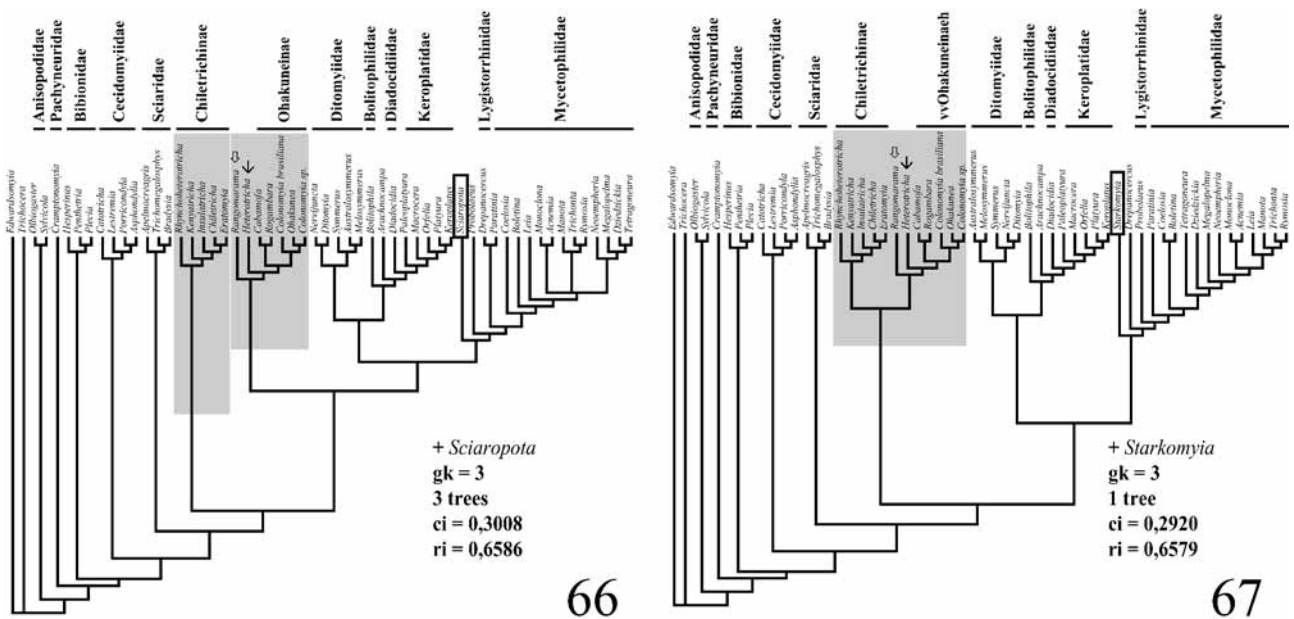
FIGURES 66, 67. Topology obtained from the analysis of the data matrix under different algorithms and options. **66.** Goloboff parsimony, reduced matrix + *Sciaropota*, gk = 3. **67.** Goloboff parsimony, reduced matrix + *Starkomyia*, gk = 3. Shadings correspond to the genera in each topology that fit in the Rangomaramidae in the classification accepted here. ? shows the position of *Rangomarama* and ? shows the position of *Heterotricha* in each topology.
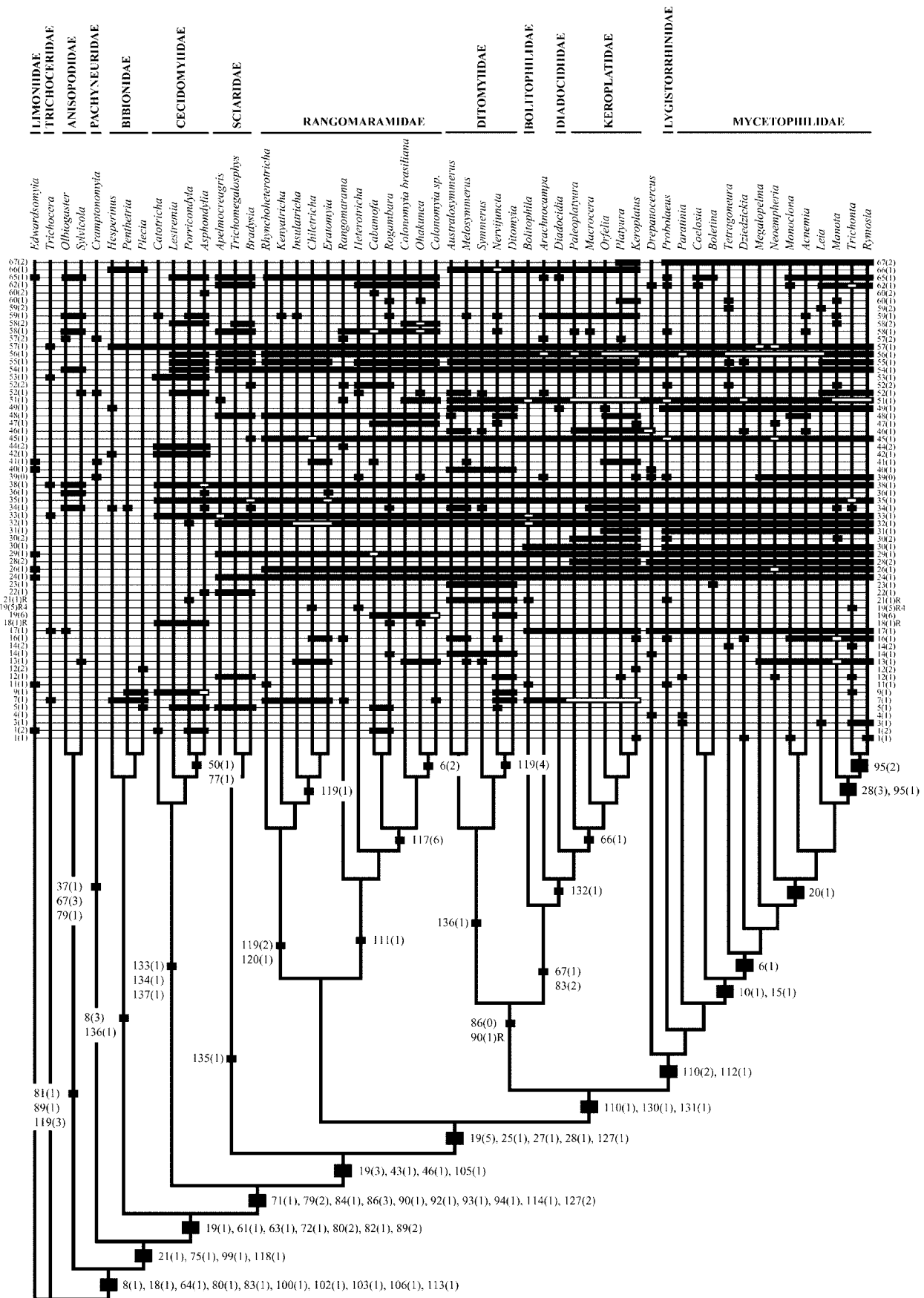
FIGURE 68. Cladogram obtained with gk = 3. Characters of unique origin at the nodes and characters of multiple origin (1–67) at top; autapomorphies not included.
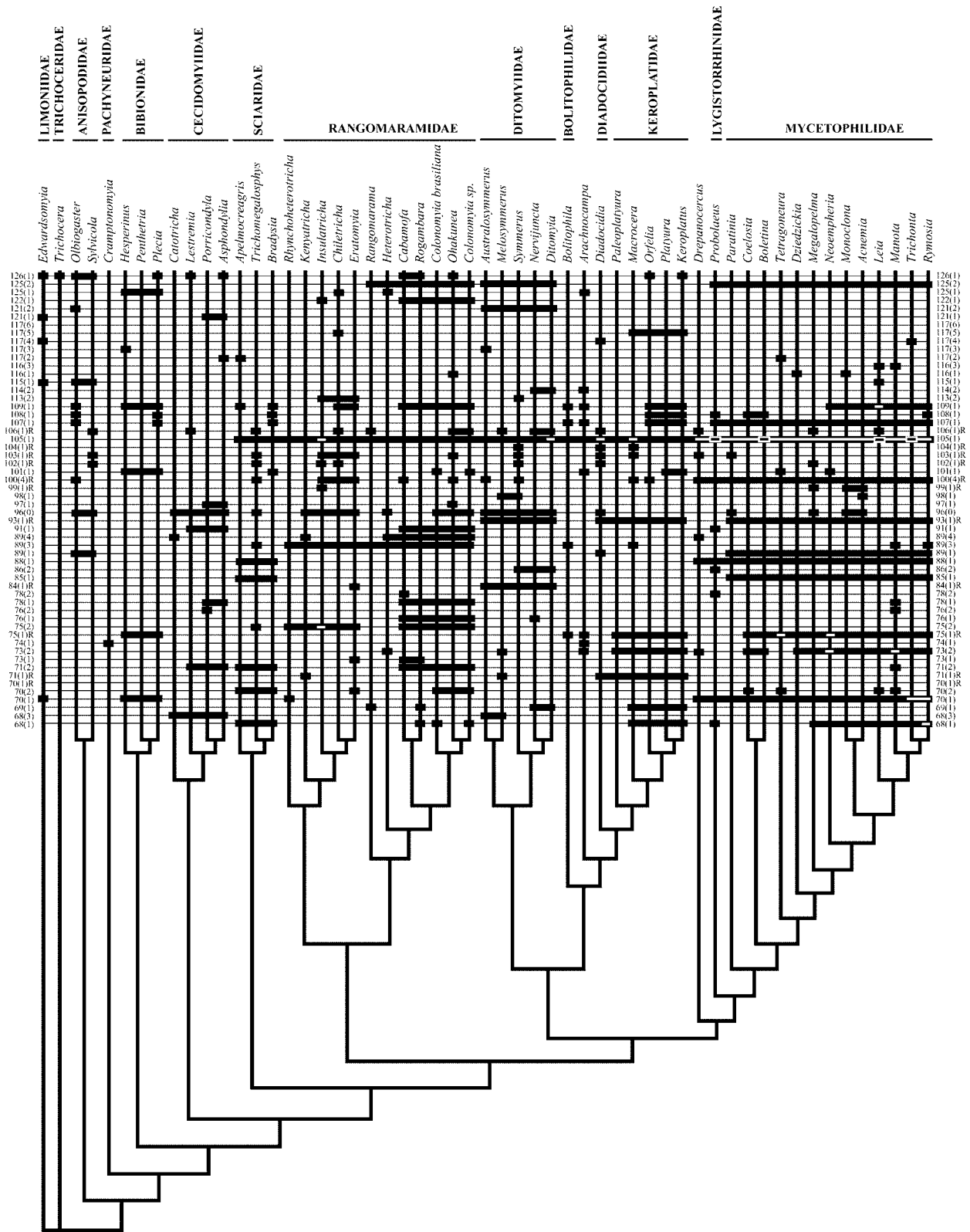
FIGURE 69. Cladogram obtained with gk = 3. Characters of multiple origin (68–126) at top; autapomorphies not included.
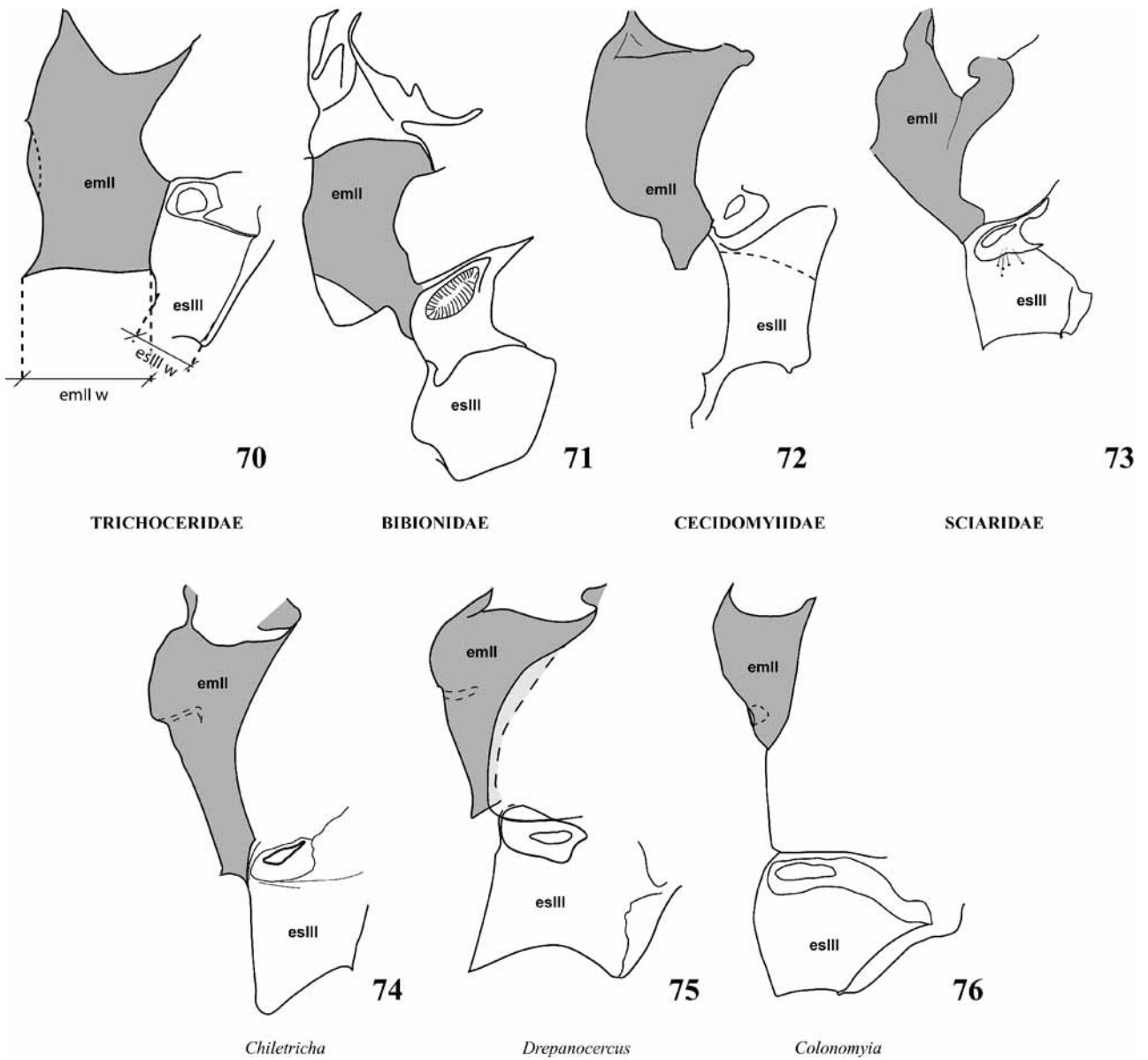
FIGURES 70–76. Different states of character 19. **70.** *Trichocera*. **71.** *Hesperinus*. **72.** *Asphondylia*. **73.** *Trichomegalosphys*. **74.** *Chiletricha*. **75.** *Drepanocercus*. **76.** *Colonomyia*.
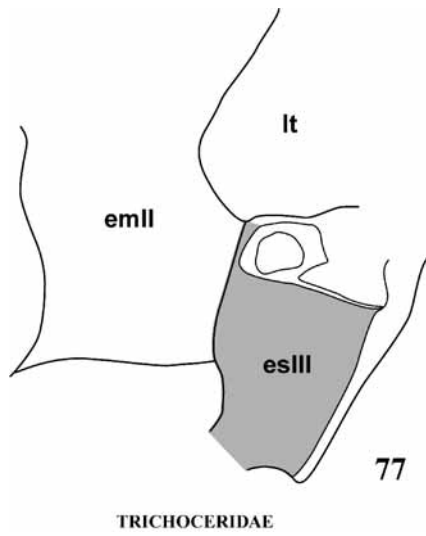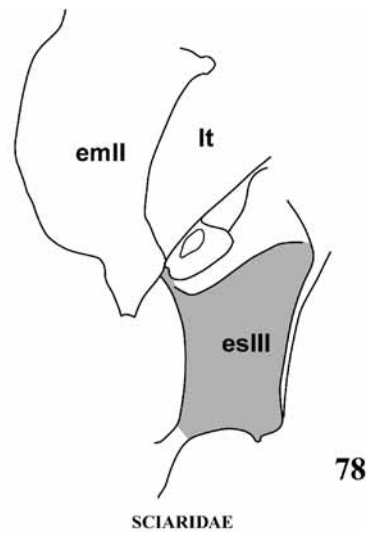
FIGURES 77, 78. Different states of character 23. **77.** *Trichocera.* **78.** *Trichomegalosphys.*
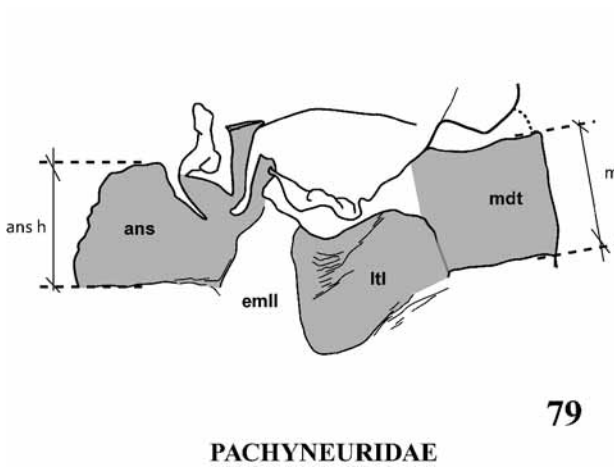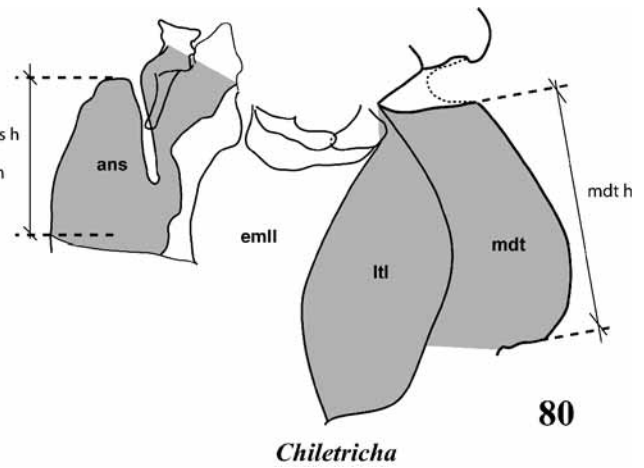
FIGURES 79, 80. Different states of character 24. **79.** *Pachyneura.* **80.** *Chiletricha.*
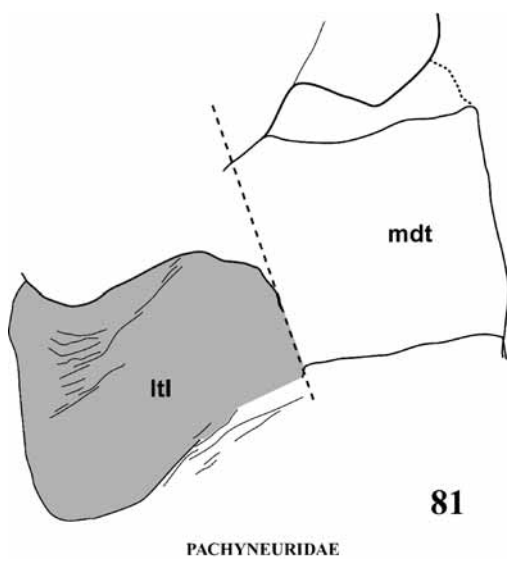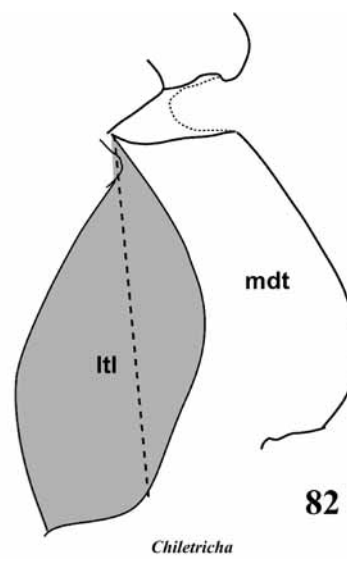
FIGURES 81, 82. Different states of character 25. **81.** *Pachyneura.* **82.** *Chiletricha.*
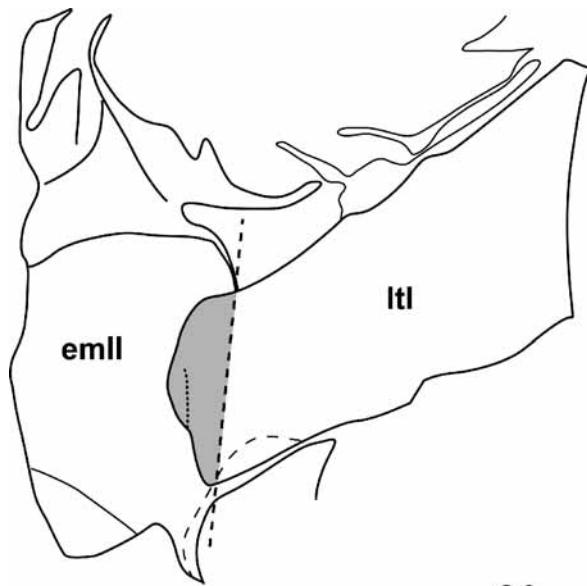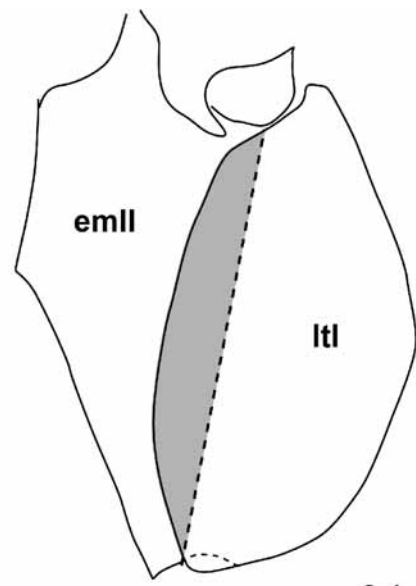
FIGURES 83, 84. Different states of character 26. **83.** *Hesperinus*. **84.** *Ohakunea*.
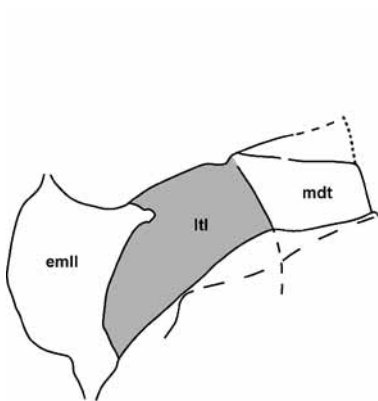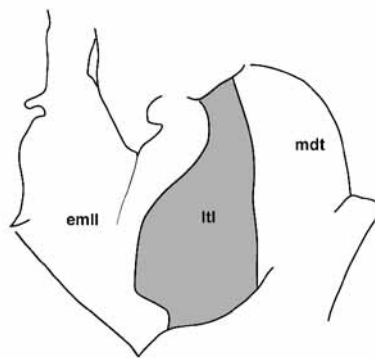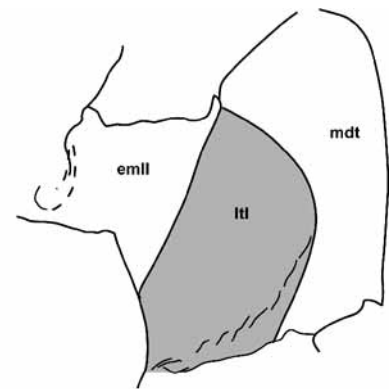
FIGURES 85–87. Different states of character 27. **85.** *Asphondylia*. **86.** *Trichomegalosphys*. **87.** *Ditomyia*.
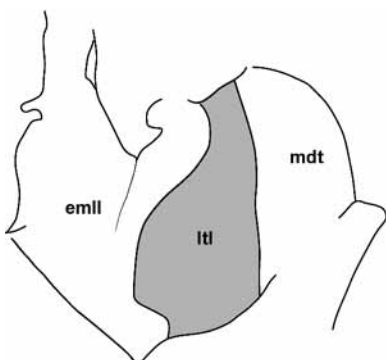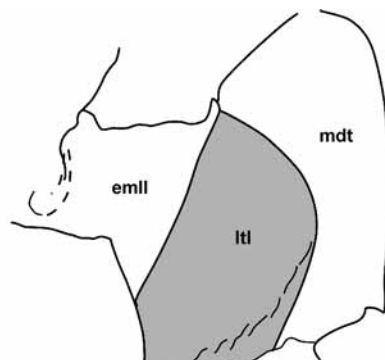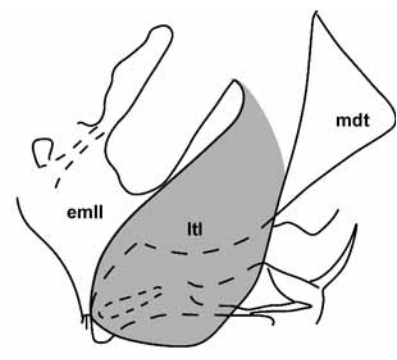
FIGURES 88–90. Different states of character 28. **88.** *Trichomegalosphys*. **89.** *Ditomyia*. **90.** *Platyroptilon*.
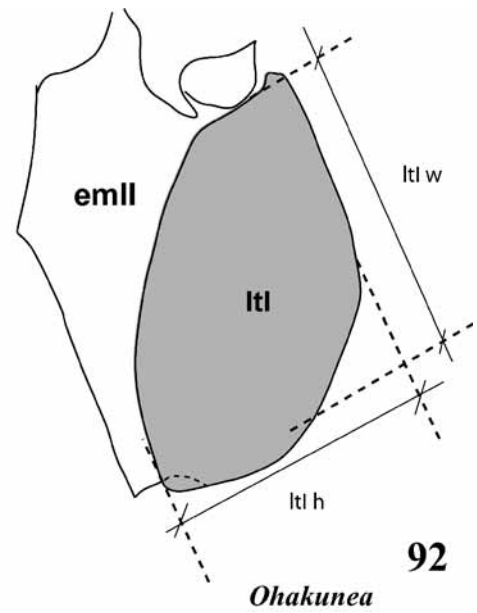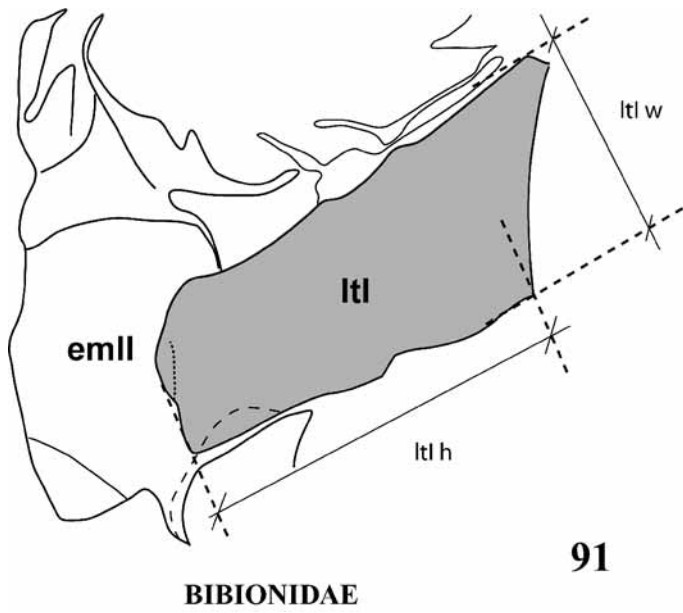
FIGURES 91, 92. Different states of character 29. **91.** *Hesperinus*. **92.** *Ohakunea*.
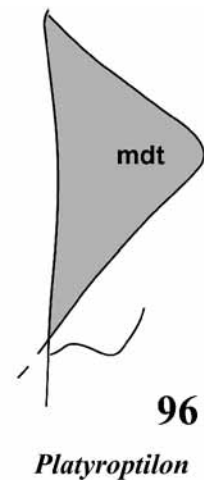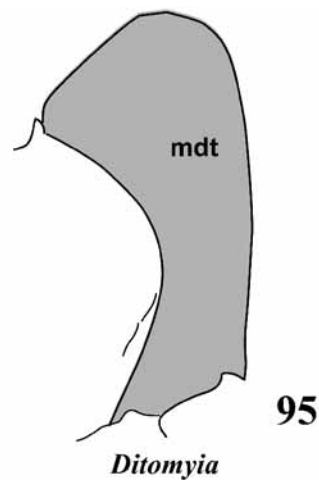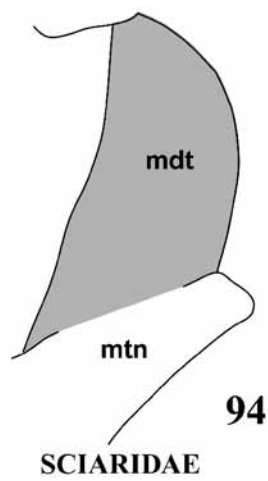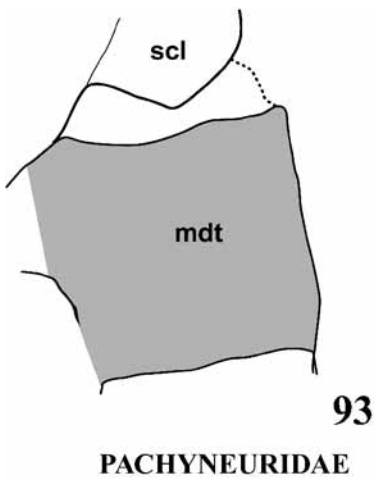
FIGURES 93–96. Different states of character 30. **93.** *Pachyneura*. **94.** *Trichomegalosphys*. **95.** *Ditomyia*. **96.** *Platyroptilon*.
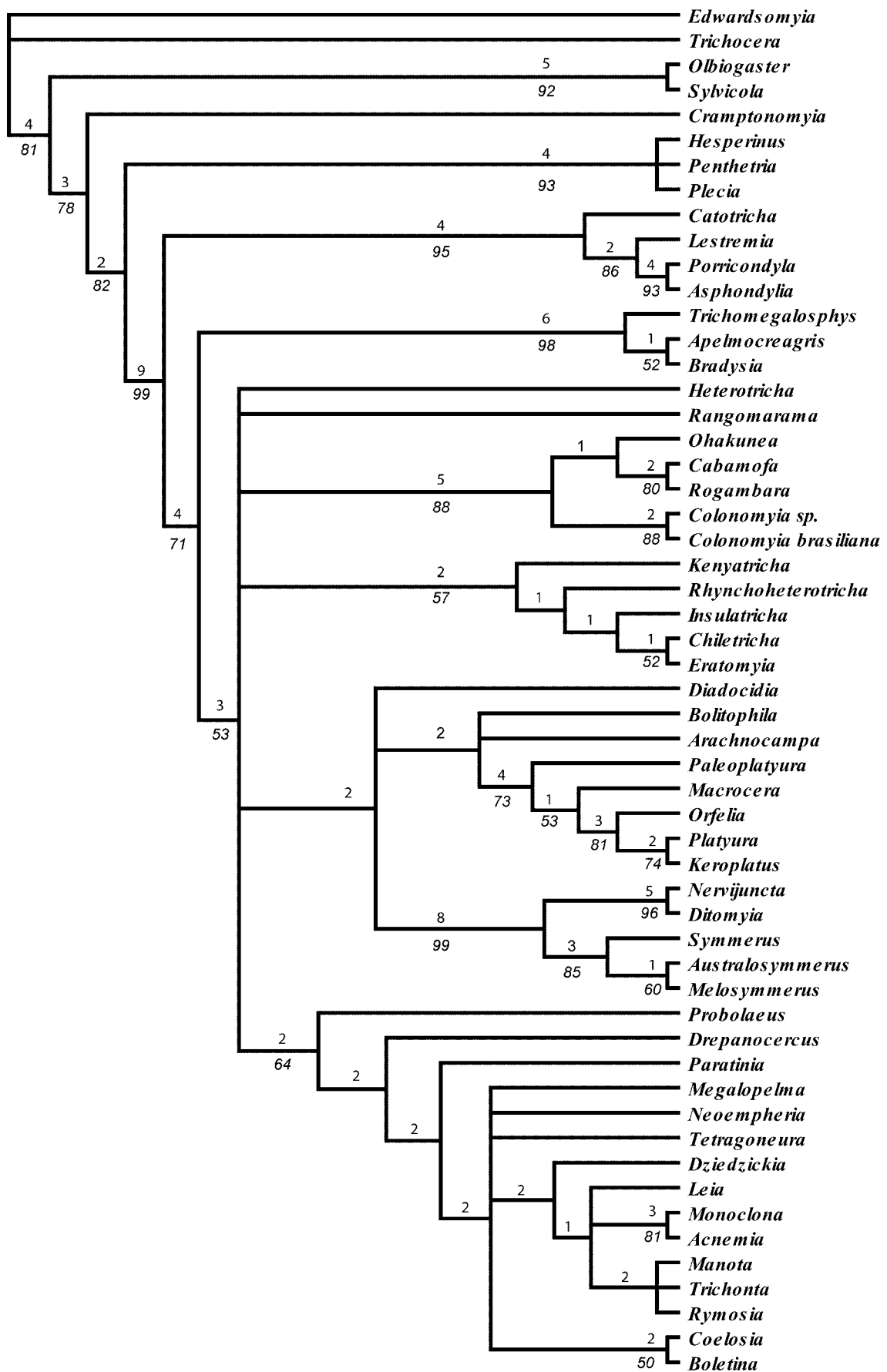
FIGURE 97. Bremer support (above nodes) and bootstrap values (below nodes) (based on 100 replicates) on nodes of tree obtained using equal weight parsimony analysis with 1,000,000 replicates.
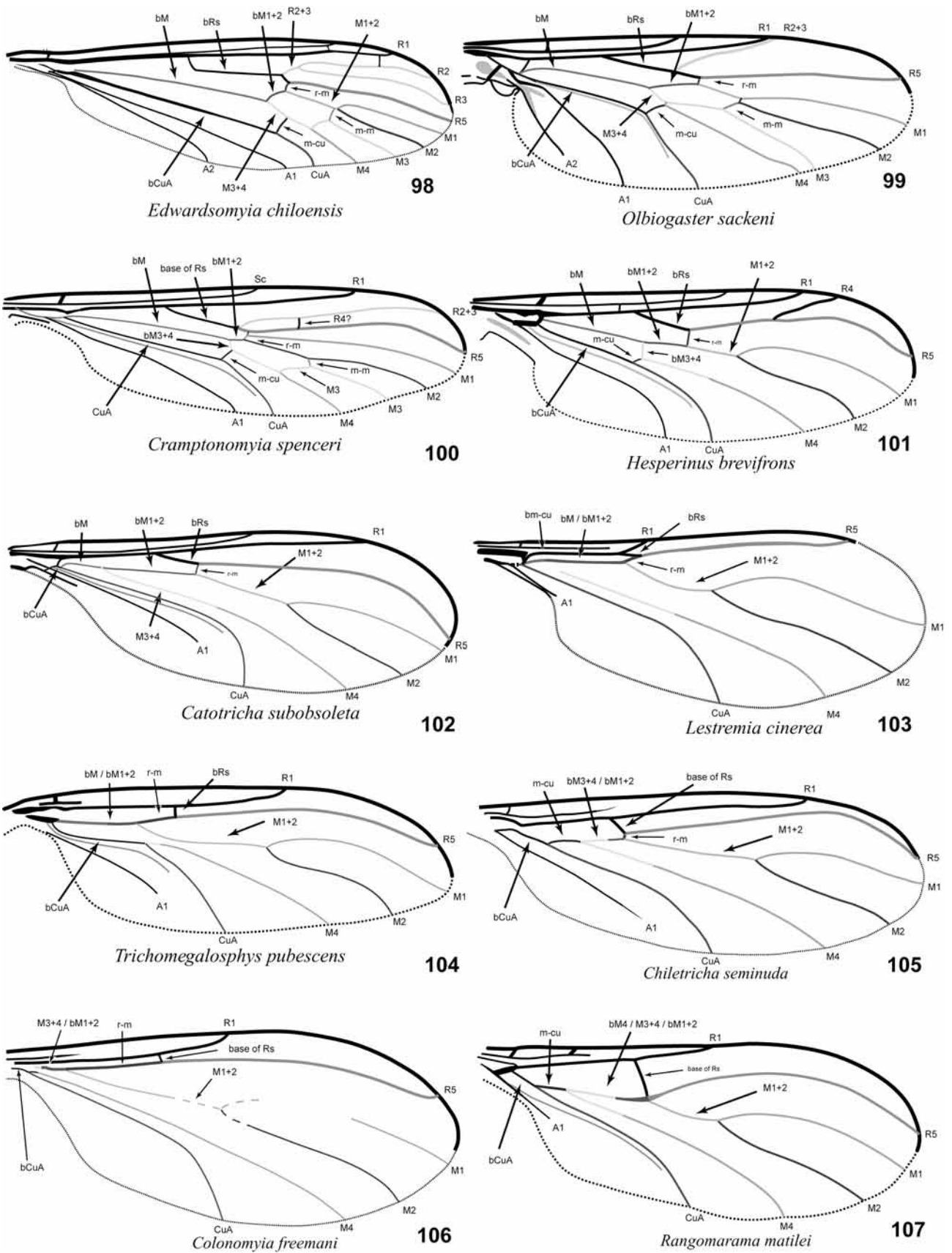
FIGURES 98–107. A study of wing vein homology using different colours for distinct sections of most veins. **98.** *Edwarsomyia.* **99.** *Olbiogaster.* **100.** *Cramptonomyia.* **101.** *Hesperinus.* **102.** *Catotricha.* **103.** *Lestremia.* **104.** *Trichomegalosphys.* **105.** *Chiletricha.* **106.** *Colonomyia.* **107.** *Rangomarama.*
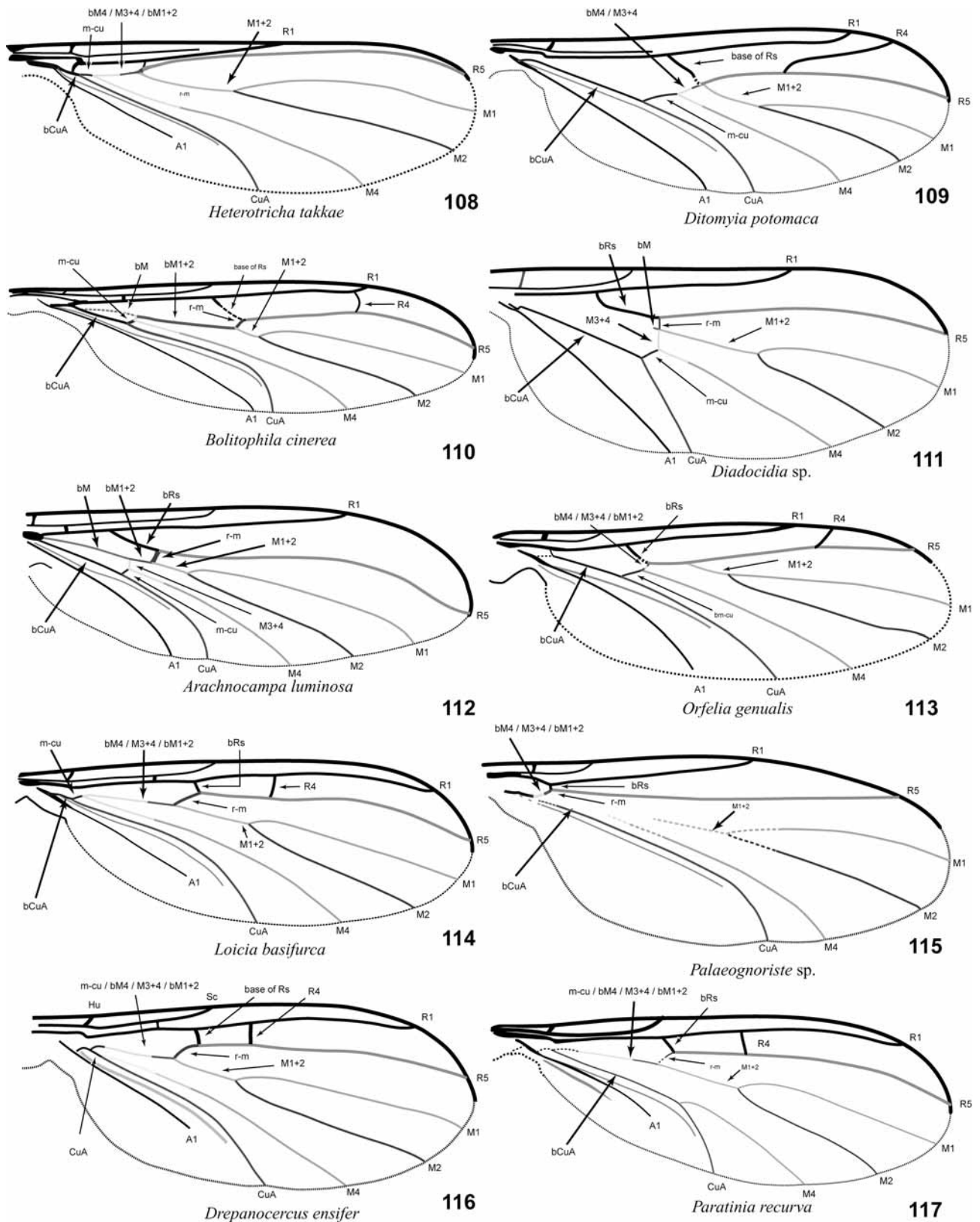
FIGURES 108–117. A study of wing vein homology using different colours for distinct sections of most veins. **108.** *Heterotricha.* **109.** *Ditomyia.* **110.** *Bolitophila.* **111.** *Diadocidia.* **112.** *Arachnocampa.* **113.** *Orfelia.* **114.** *Loicia.* **115.** *Palaeognoriste.* **116.** *Drepanocercus.* **117.** *Paratinia.*
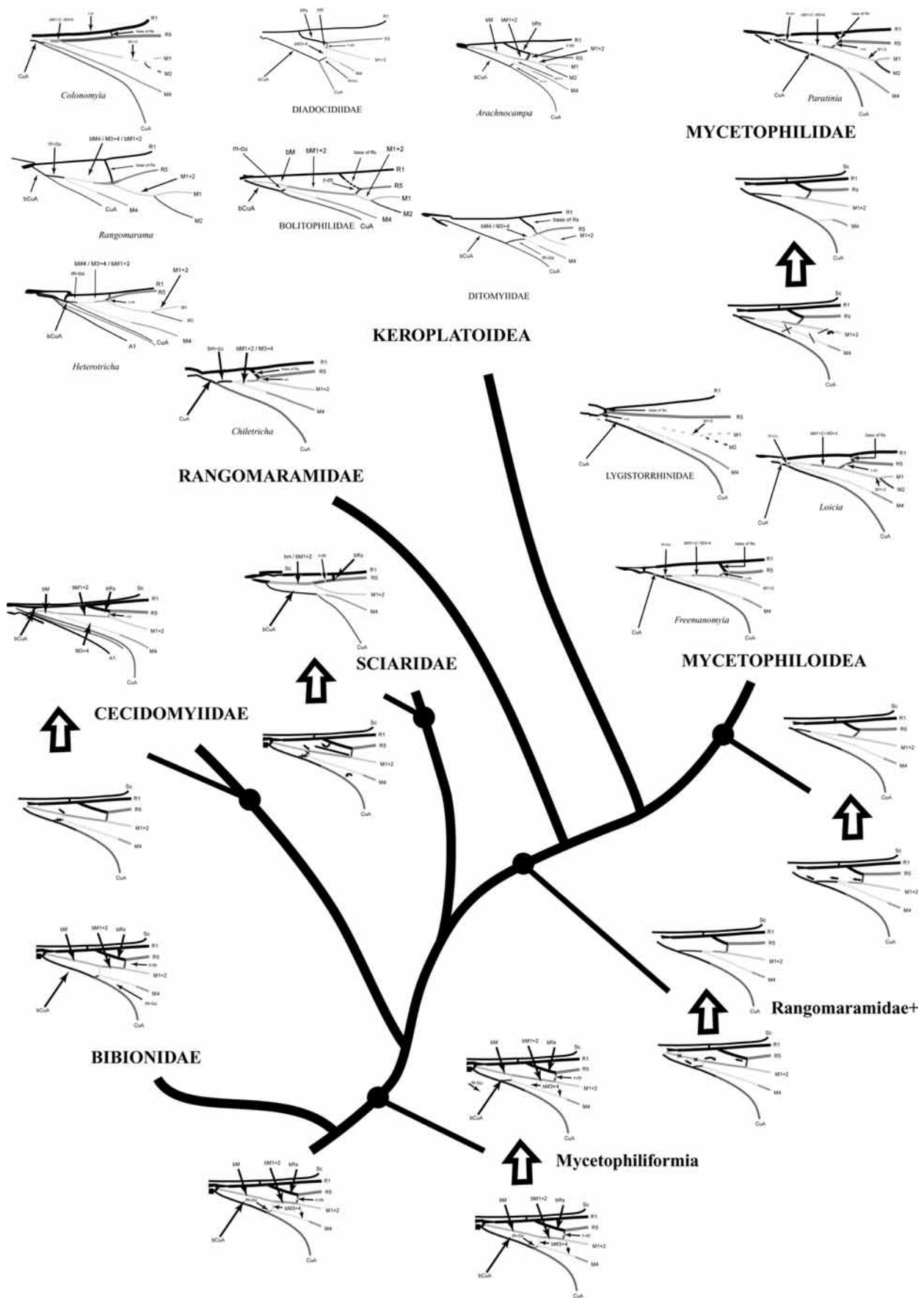
FIGURE 118. Main changes in the wing venation along the evolution of the Mycetophiliformia.
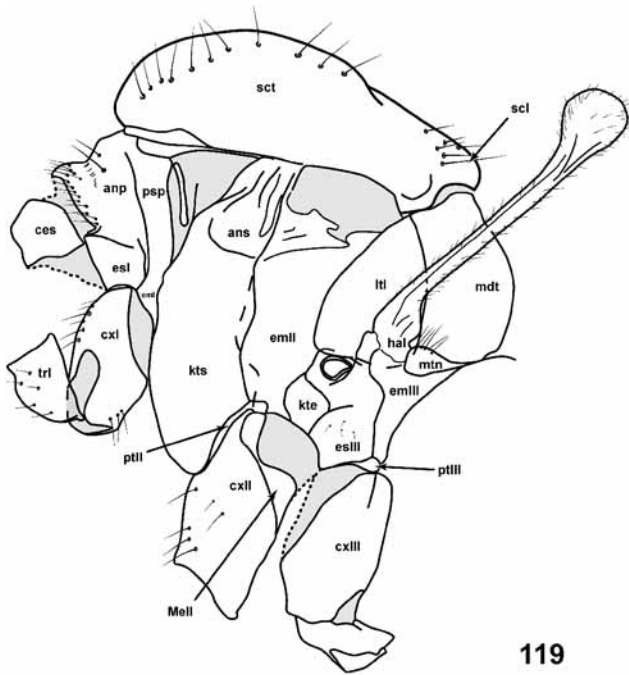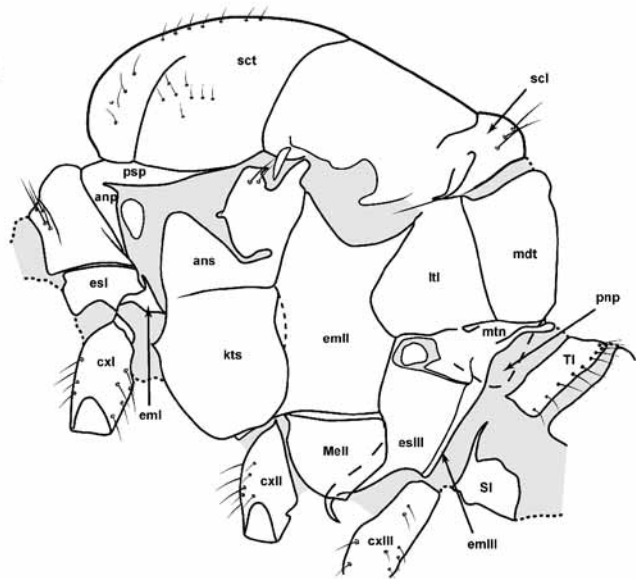
FIGURES 119–122. Thoracic pleural sclerites. **119.** *Edwardsomyia chiloensis*. **120.** *Trichocera columbiana*. **121.** *Olbiogaster sackeni*. **122.** *Pachyneura fasciata*.
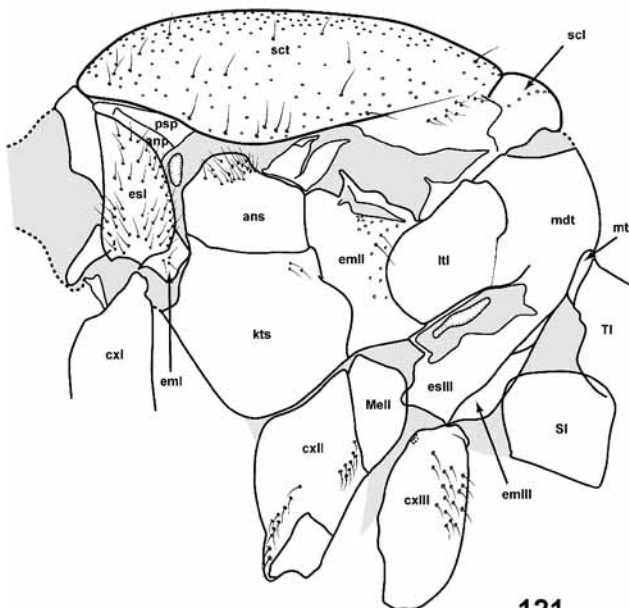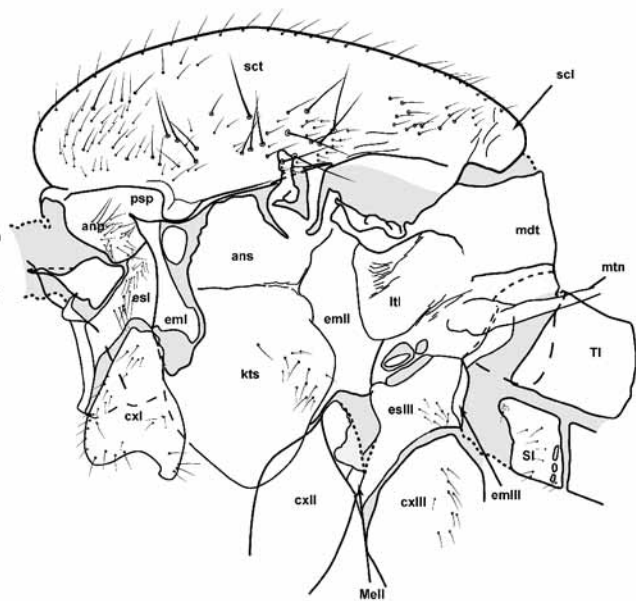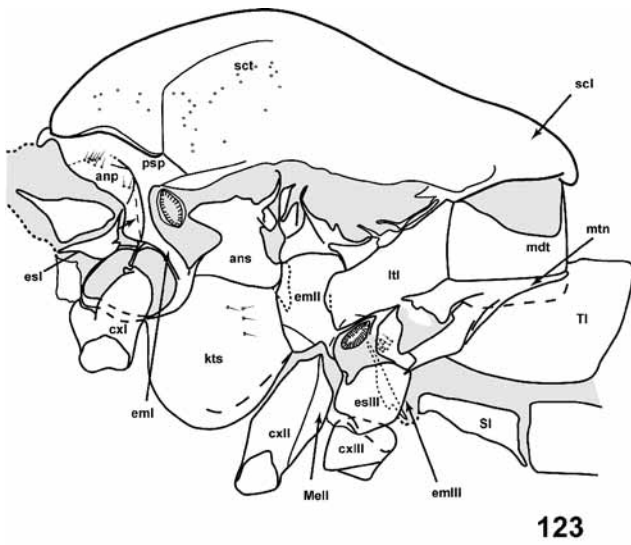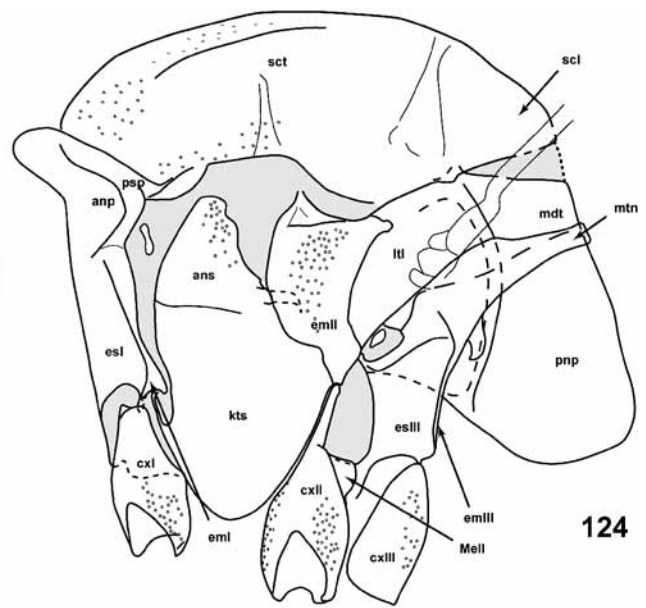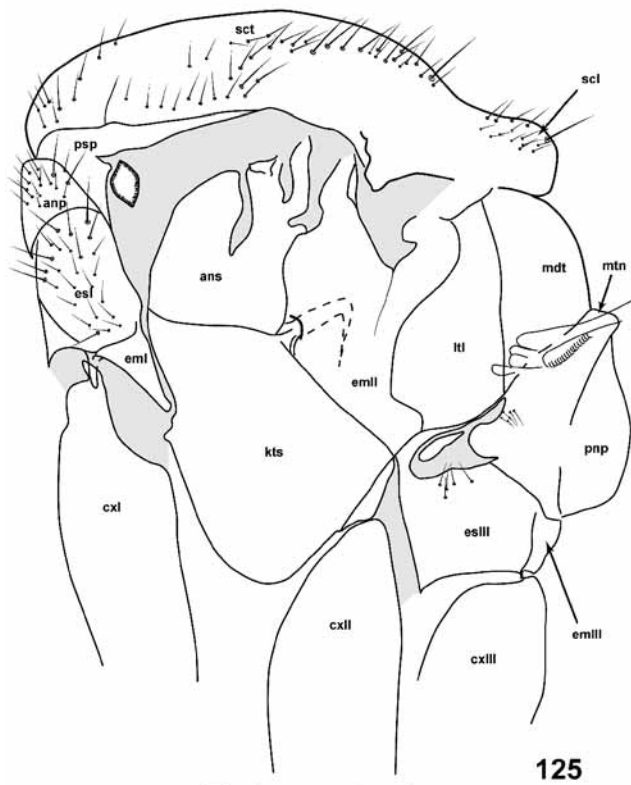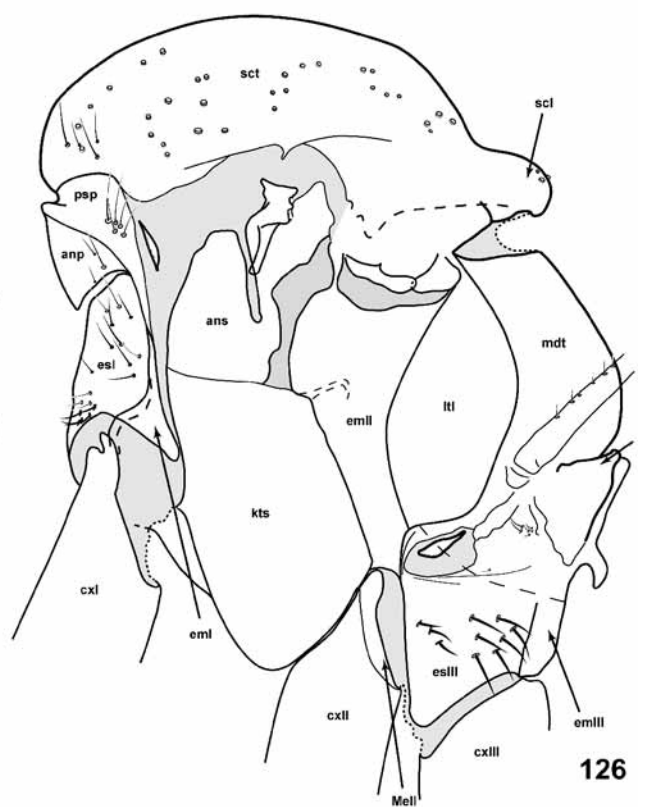
FIGURES 123–126. Thoracic pleural sclerites. **123.** *Hesperinus* sp. **124.** *Asphondylia* sp. **125.** *Trichomegalosphys* sp. **126.** *Chiletricha marginata*.
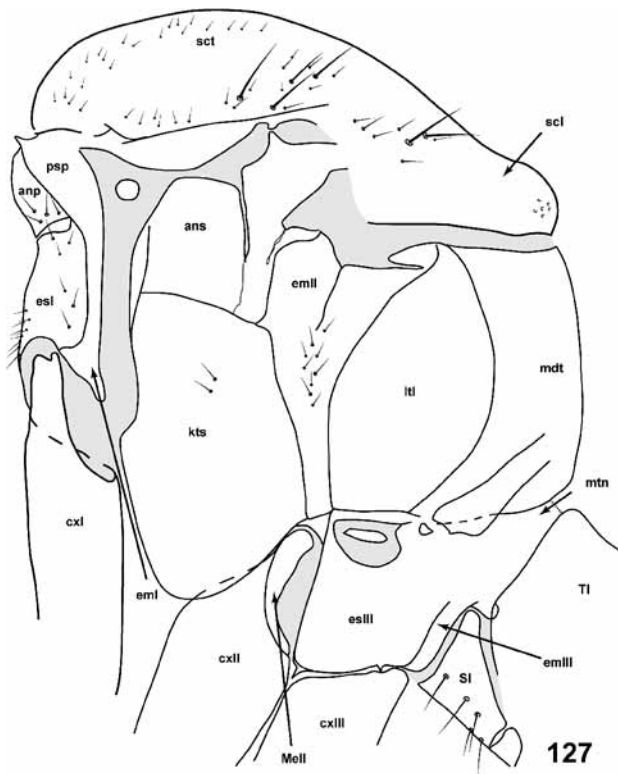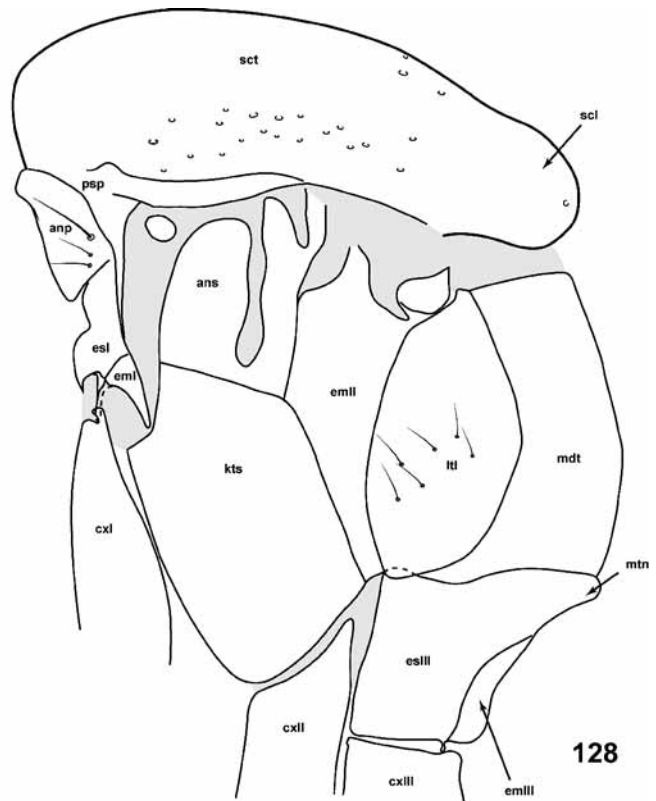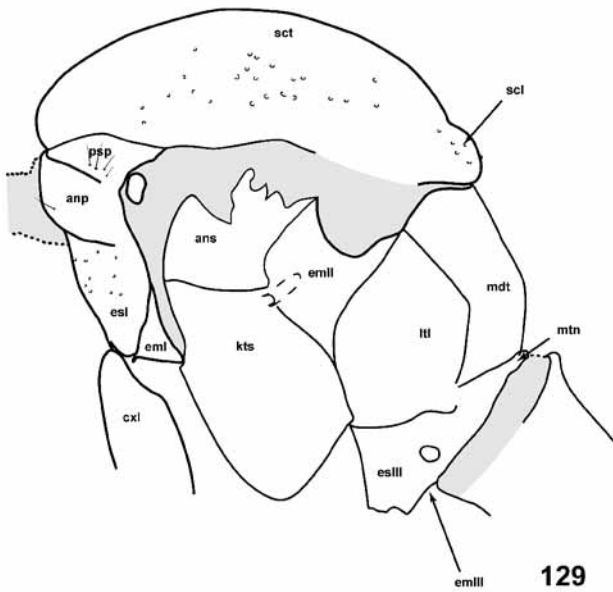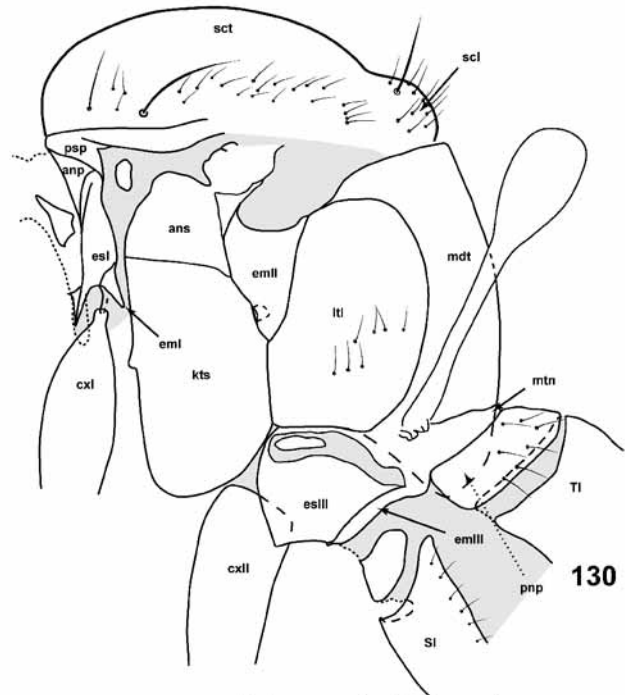
FIGURES 127–130. Thoracic pleural sclerites. **127.** *Eratomyia magnifica*, **gen. n., sp. n. 128.** *Ohakunea chilensis.* **129.** *Cabamofa mira.* **130.** *Colonomyia freemani*, n. sp.
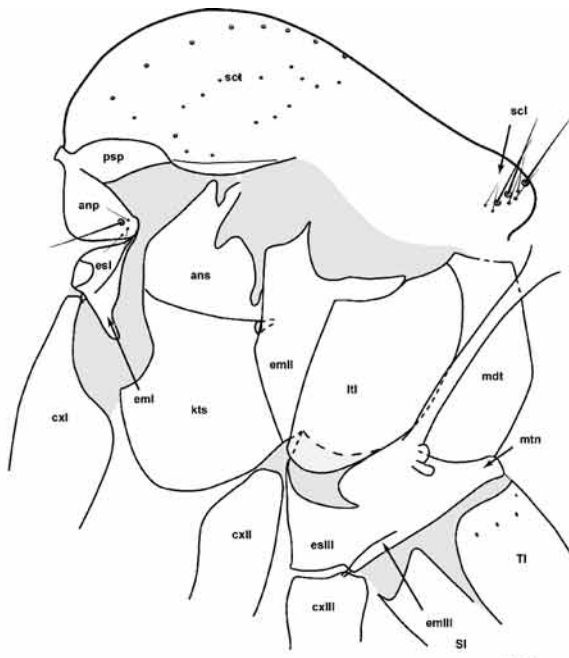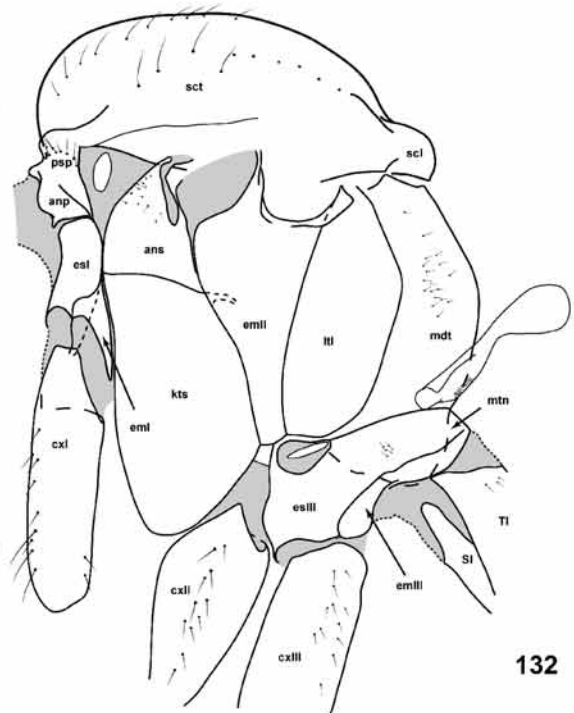
FIGURES 131–134. Thoracic pleural sclerites. **131.** *Diadocidia* sp. **132.** *Bolitophila* sp. **133.** *Arachnocampa luminosa* (modified from Matile 1990). **134.** *Platyroptilon* sp.
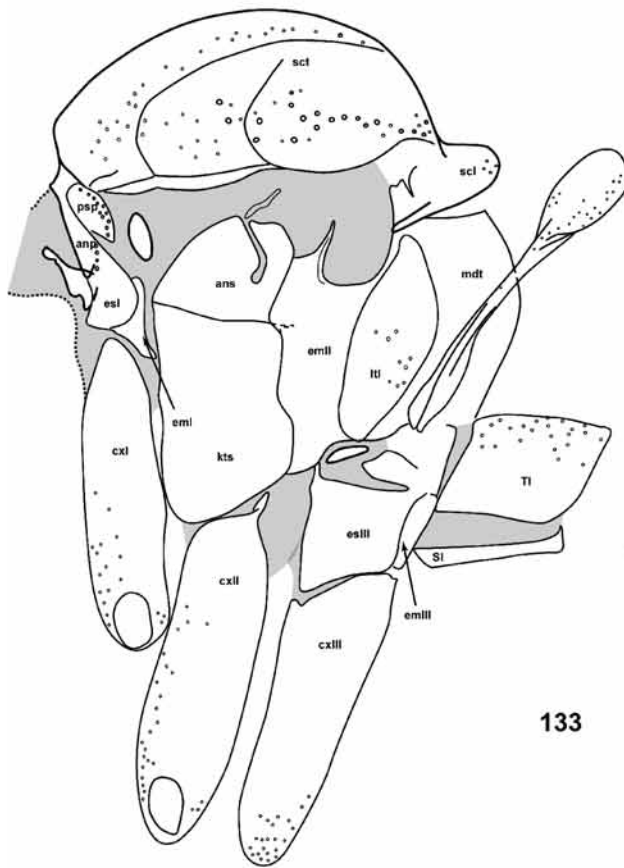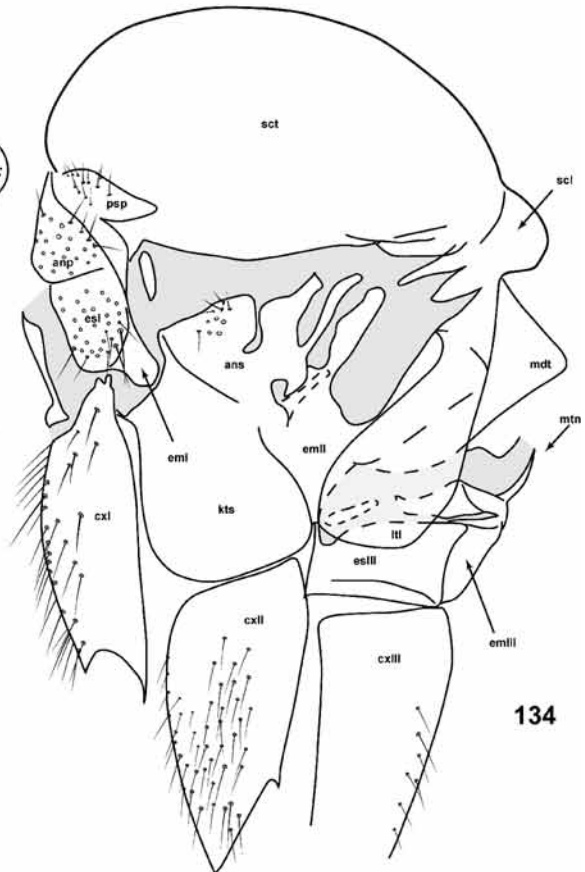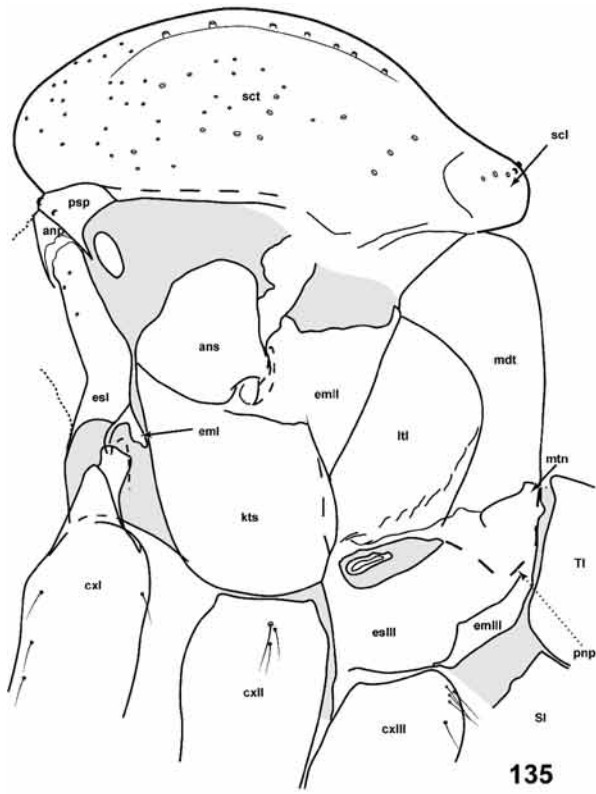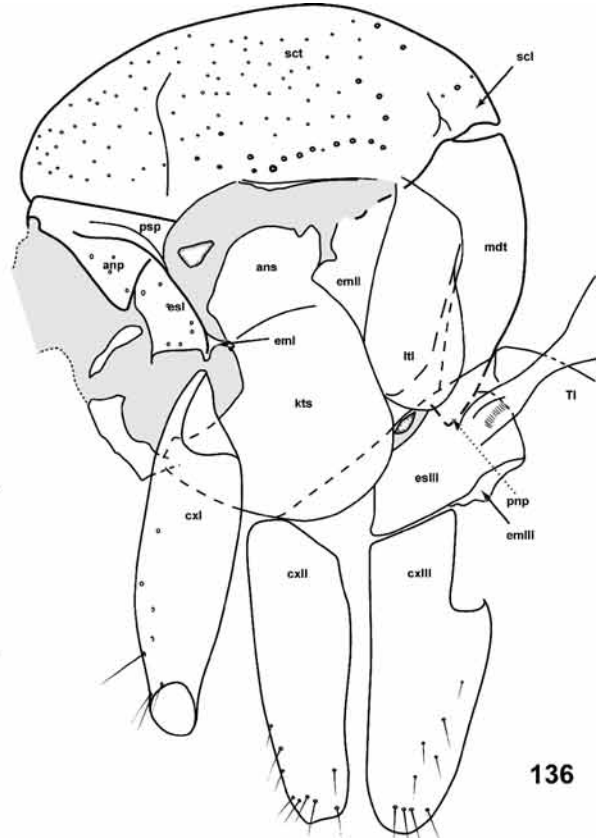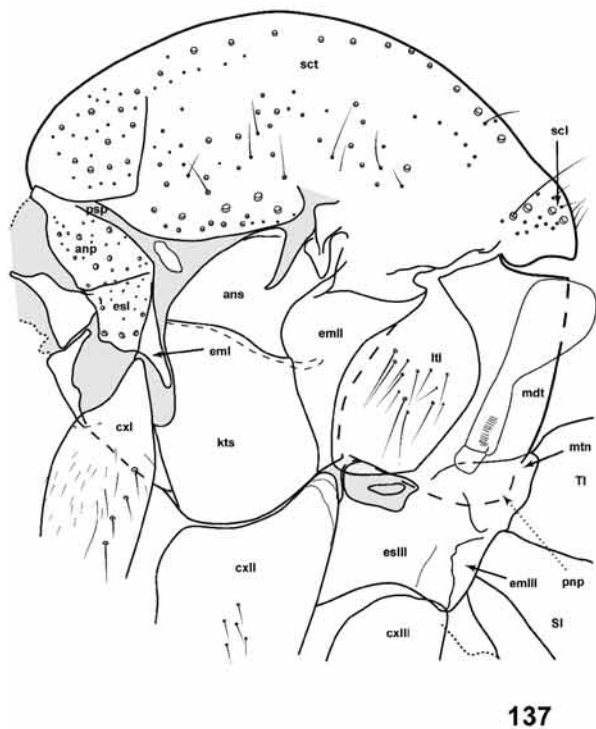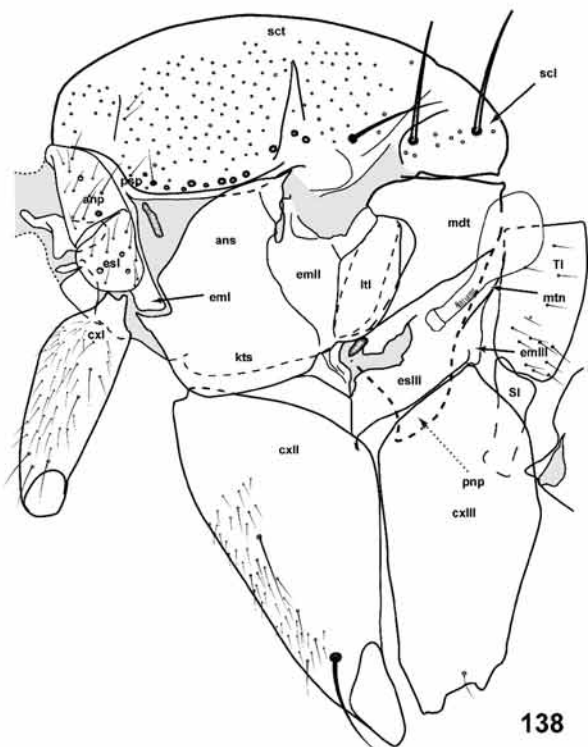
FIGURES 135–138. Thoracic pleural sclerites. **135.** *Ditomyia fasciata*. **136.** *Probolaeus* sp. **137.** *Drepanocercus spinistylus*. **138.** *Procycloneura paranaensis*.
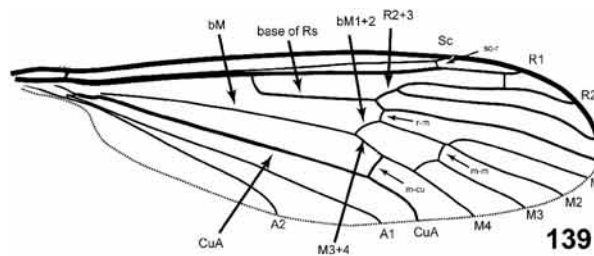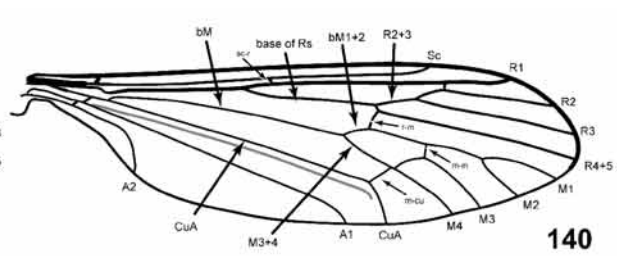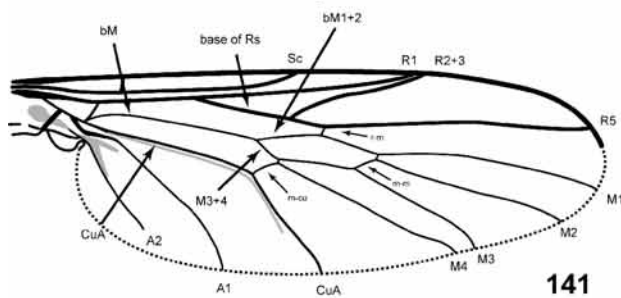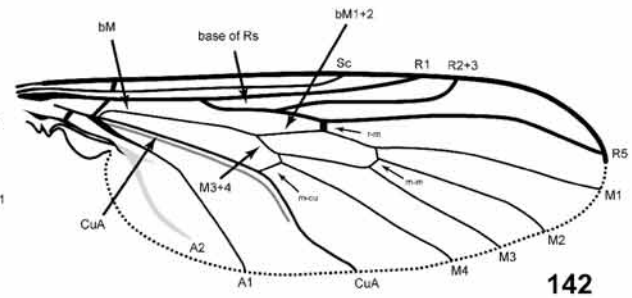
FIGURES 139–148. Wings. **139.** *Edwardsomyia chiloensis*. **140.** *Trichocera garretti*. **141.** *Olbiogaster sackeni*. **142.** *Sylvicola fenestralis*. **143.** *Cramptonomyia spenceri*. **144.** *Hesperinus brevifrons*. **145.** *Plecia americana*. **146.** *Catotricha subobsoleta*. **147.** *Lestremia cinerea*. **148.** *Trichomegalosphys pubescens*.
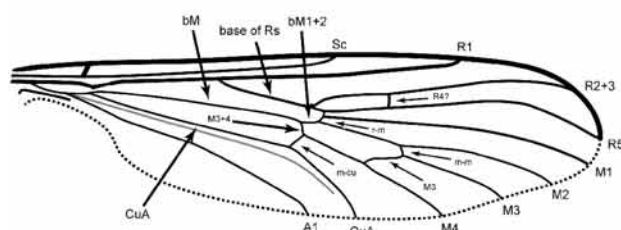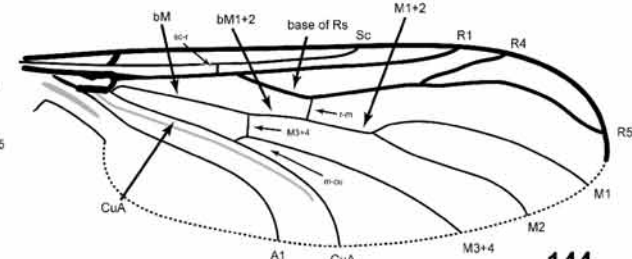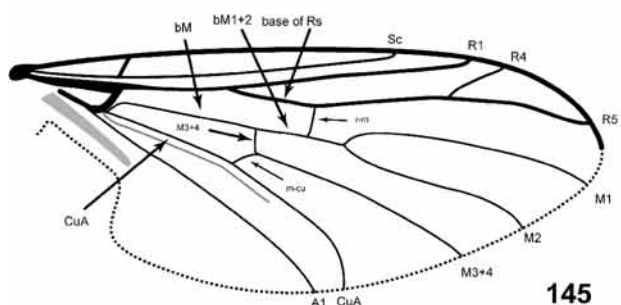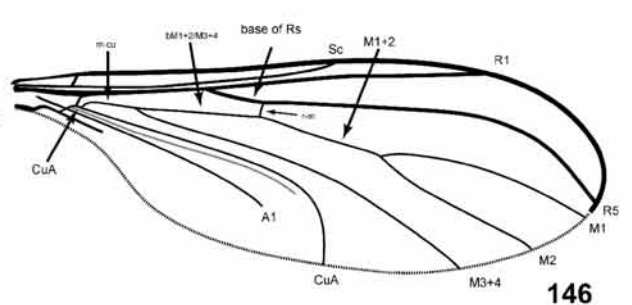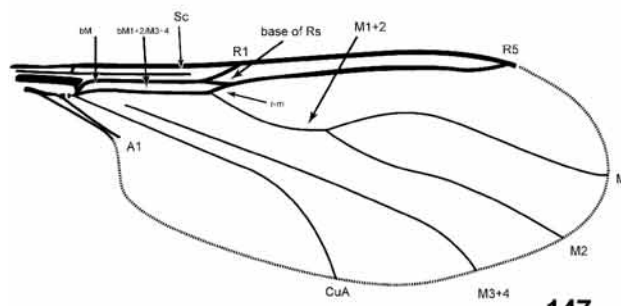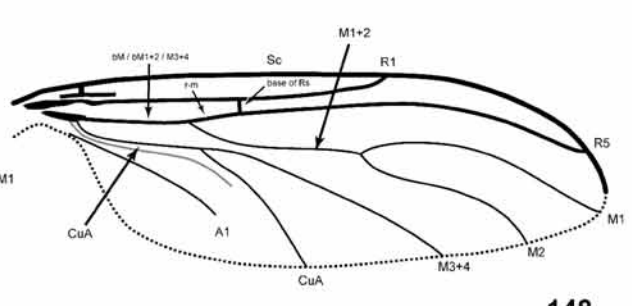
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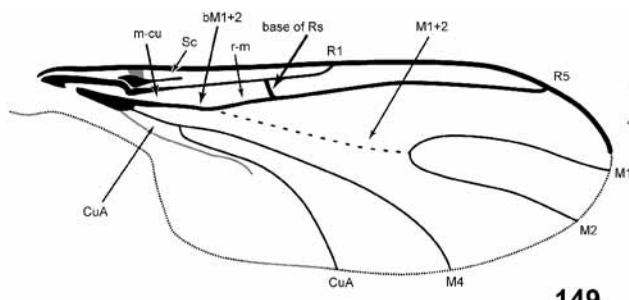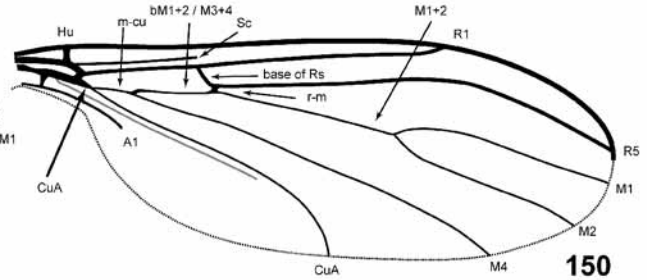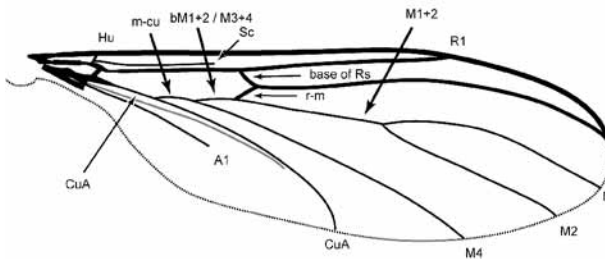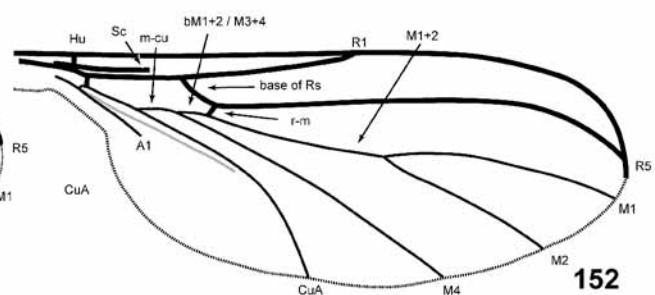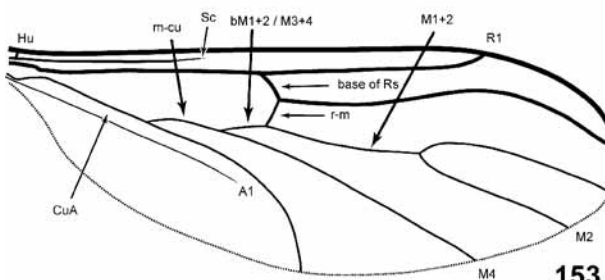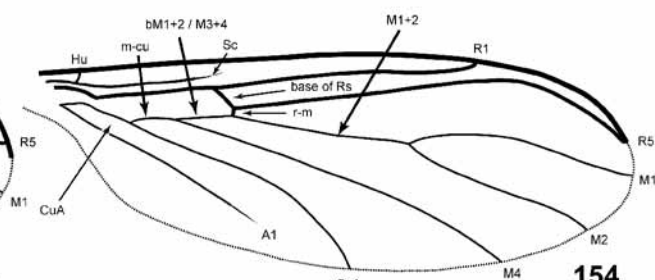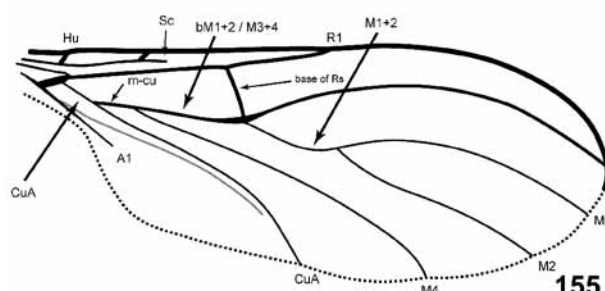
FIGURES 149–156. Wings. **149.** *Bradysia* sp. **150.** *Kenyatricha elgon.* **151.** *Rhynchoheterotricha stuckenbergae.* **152.** *Insulatricha hippai.* **153.** *Eratomyia magnifica*, **gen. n.**, **sp. n. 154.** *Chiletricha seminuda.* **155.** *Rangomarama matilei.* **156.** *Heterotricha takkae.*
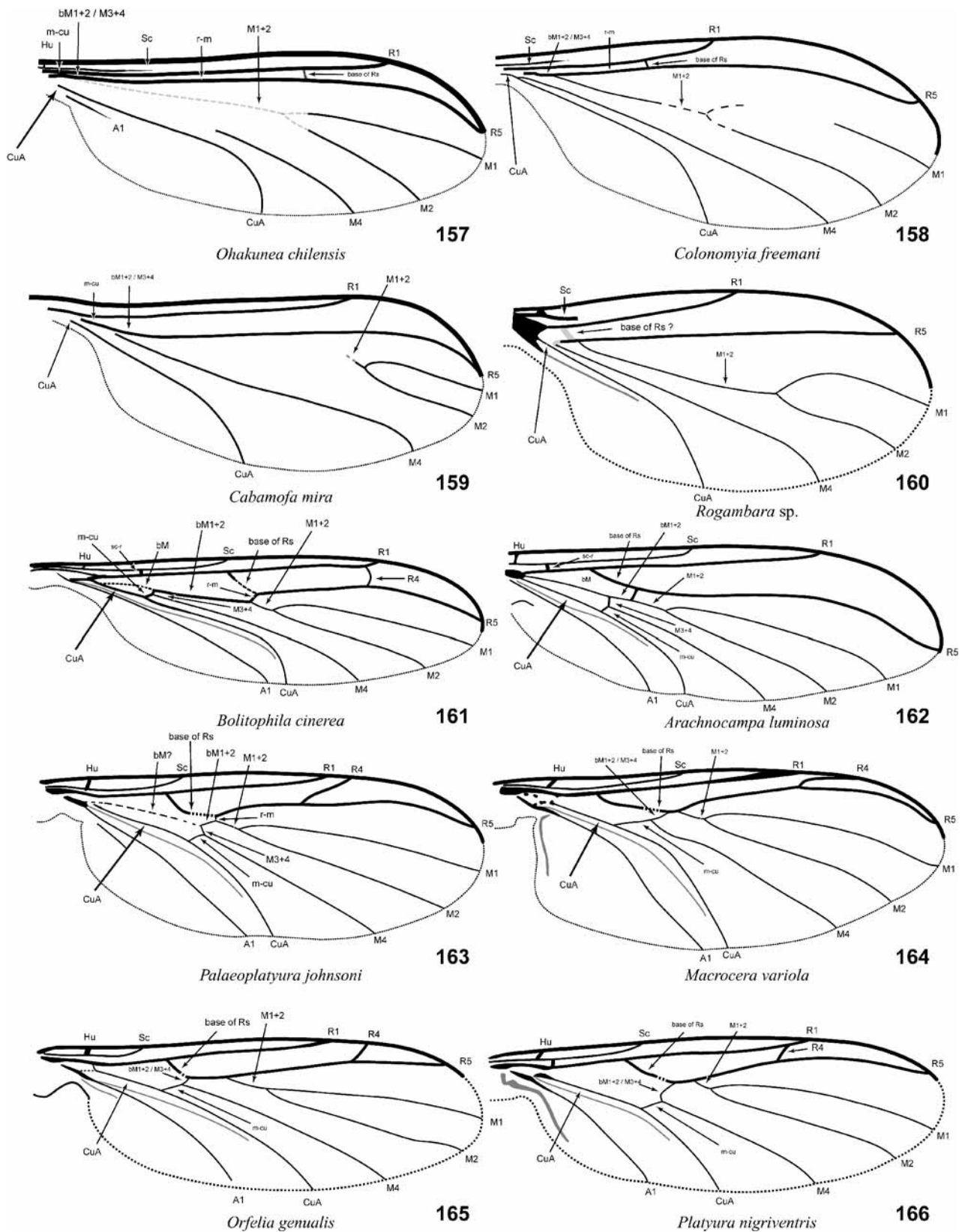
FIGURES 157–166. Wings. **157.** *Ohakunea chilensis*. **158.** *Colonomyia freemani*. **159.** *Cabamofa mira*. **160.** *Rogambara* sp. **161.** *Bolitophila cinerea*. **162.** *Arachnocampa luminosa*. **163.** *Palaeoplatyura johnsoni*. **164.** *Macrocera variola*. **165.** *Orfelia genualis*. **166.** *Platyura nigriventris*.
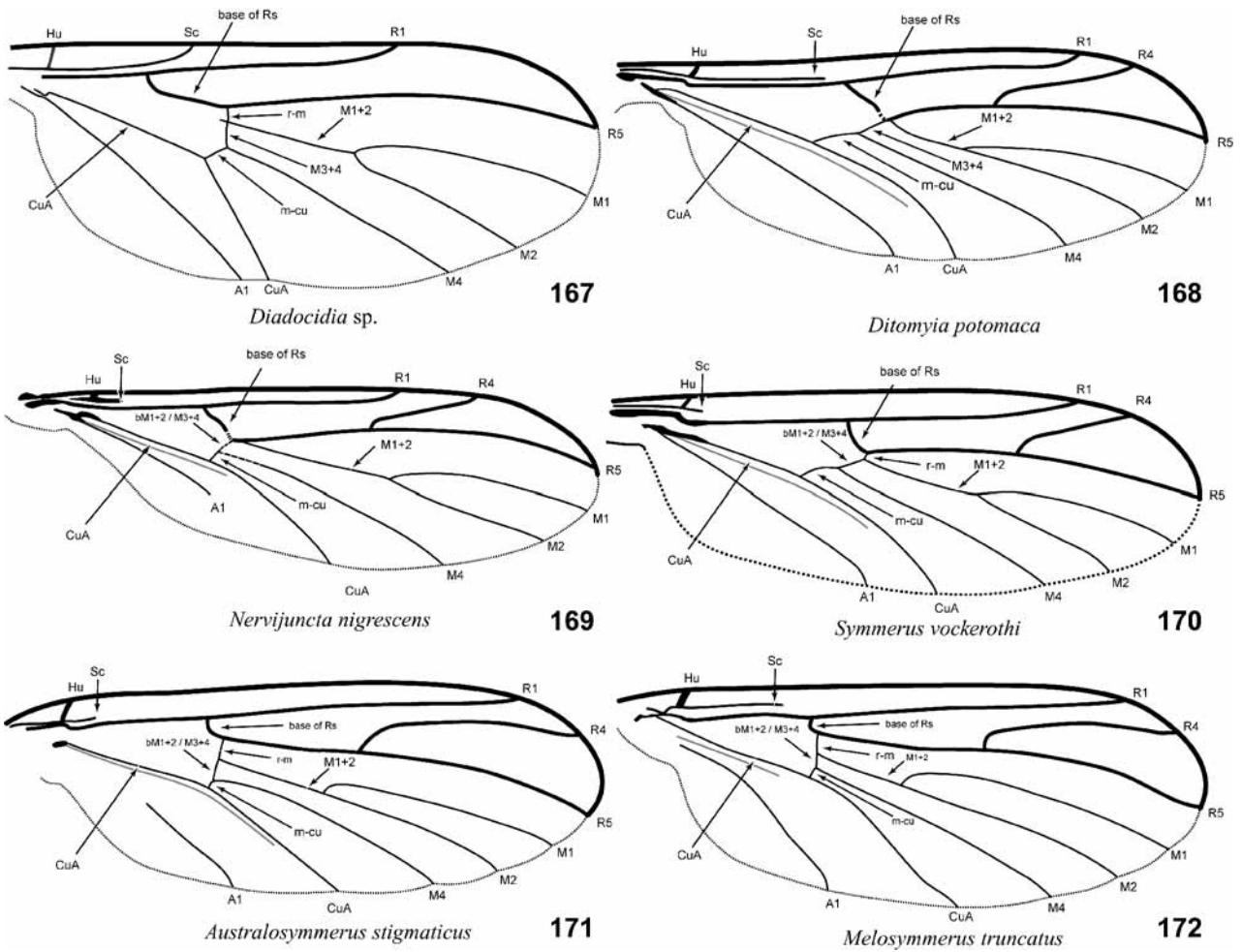
FIGURES 167–172. Wings. **167.** *Diadocidia* sp. **168.** *Ditomyia potomaca*. **169.** *Nervijuncta nigrescens*. **170.** *Symmerus vockerothi*. **171.** *Australosymmerus stigmaticus*. **172.** *Melosymmerus truncatus*.
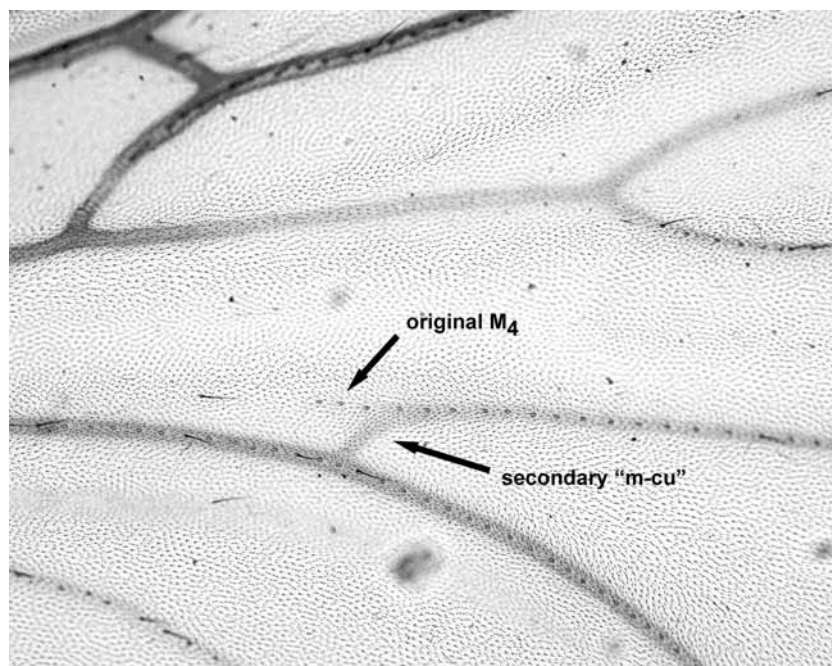
FIGURES 173. Detail of the base of the wing of *Paratinia sciarosoma*, with the extension of M_4 basally to the secondary contact between M_4 and CuA_1.
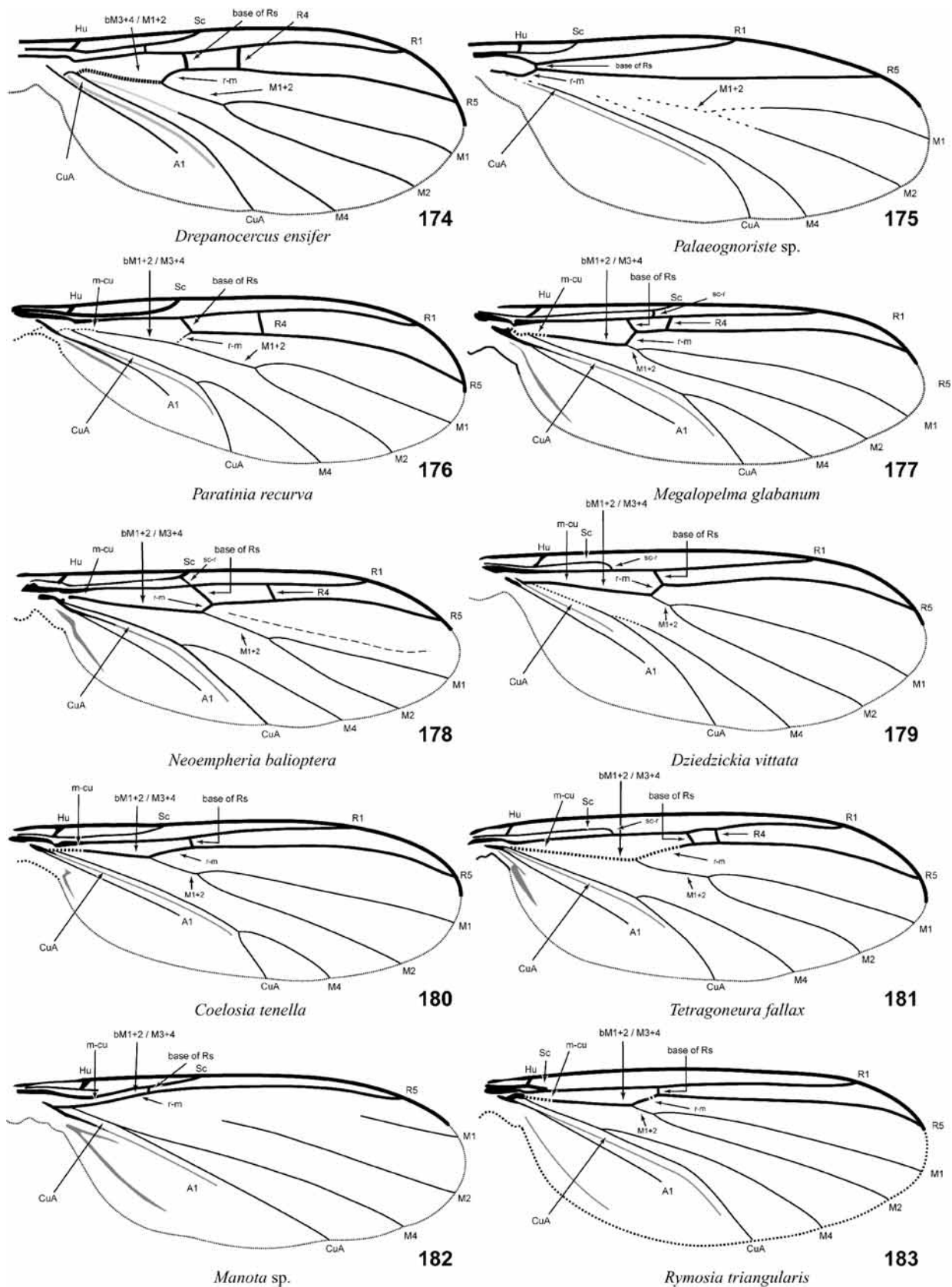
FIGURES 174–183. Wings. **174.** *Drepanocercus ensifer.* **175.** *Palaeognoriste* sp. **176.** *Paratinia recurva.* **177.** *Megalopelma glabanum.* **178.** *Neoempheria balioptera.* **179.** *Dziedzickia vittata.* **180.** *Coelosia tenella.* **181.** *Tetragoneura fallax.* **182.** *Manota* sp. **183.** *Rymosia triangularis.*
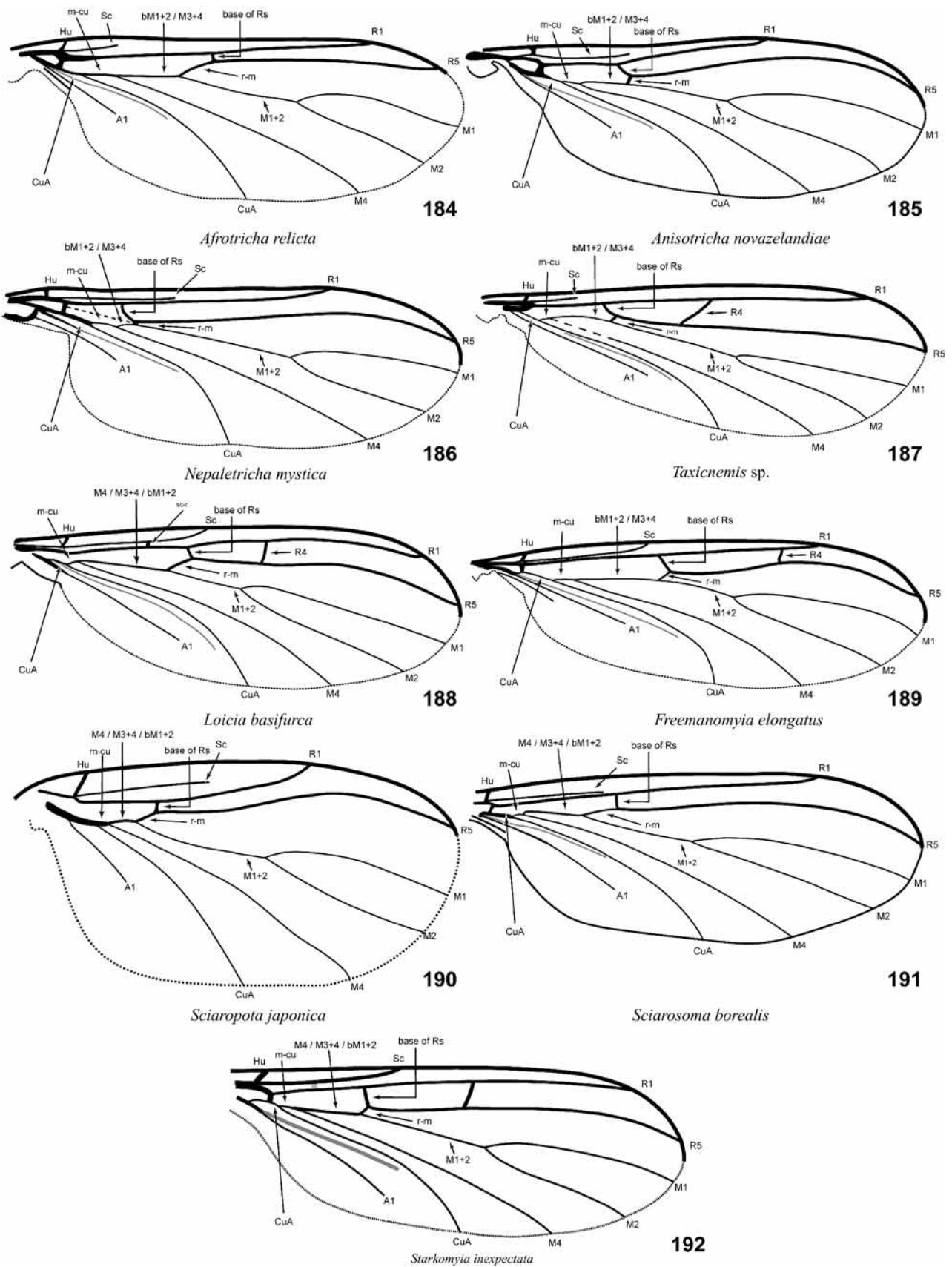
FIGURES 184–192. Wings. **184.** *Afrotricha relicta.* **185.** *Anisotricha novazealandiae.* **186.** *Nepaletricha mystica.* **187.** *Taxicnemis* sp. **188.** *Loicia basifurca.* **189.** *Freemanomyia elongatus.* **190.** *Sciaropota japonica.* **191.** *Sciarosoma borealis.* **192.** *Starkomyia inexpectata.*
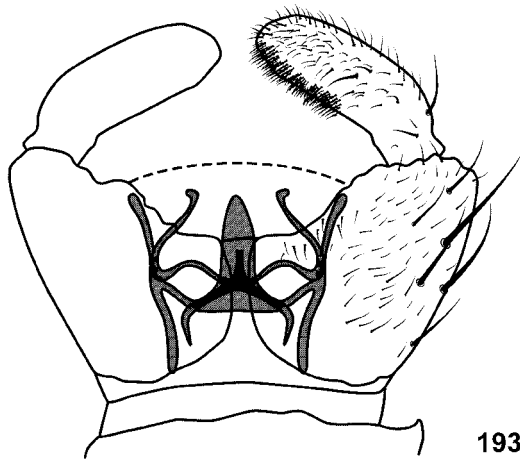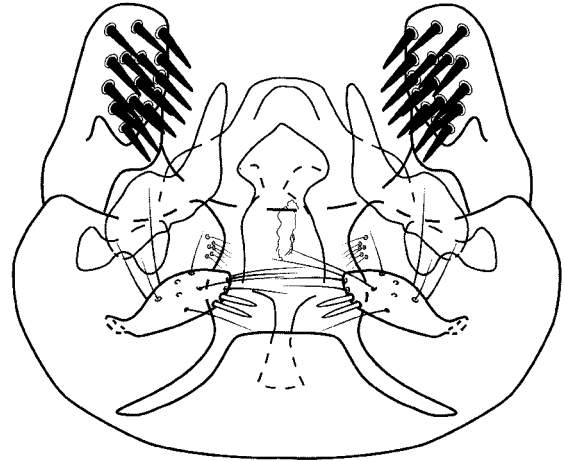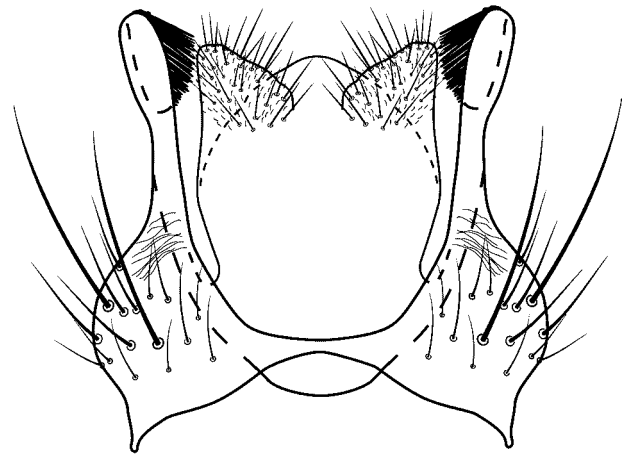
FIGURES 193–198. Male terminalia. 193. *Cramptonomyia spenceri*. 194. *Eratomyia magnifica*, **gen. n.**, **sp. n.** 195. *Chiletricha marginata*. 196. *Colonomyia brasiliana*, n. sp. 197. *Diadocidia* sp. 198. *Nervijuncta wakefeldi*.
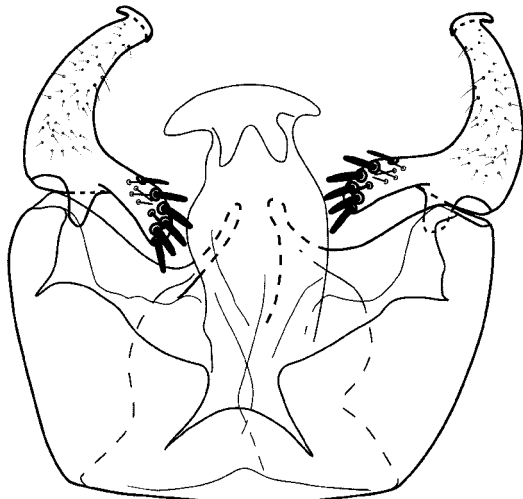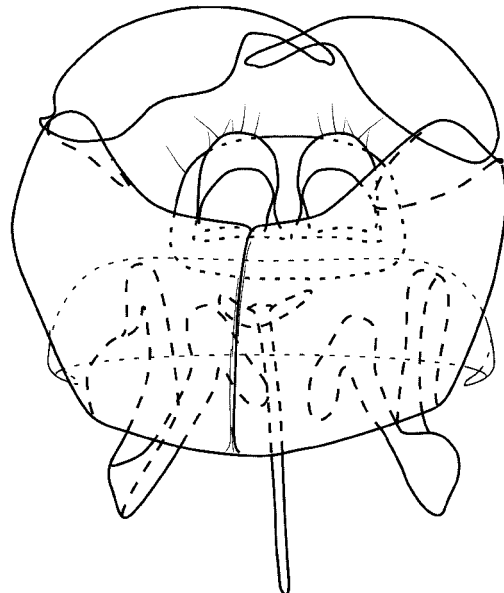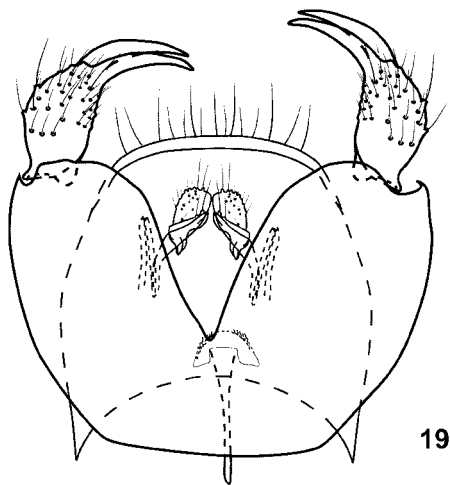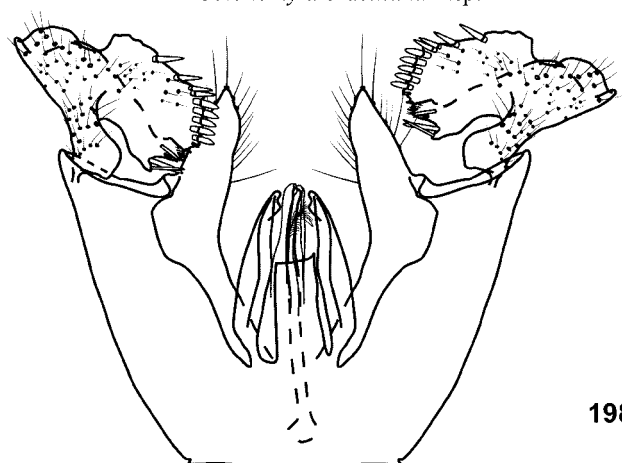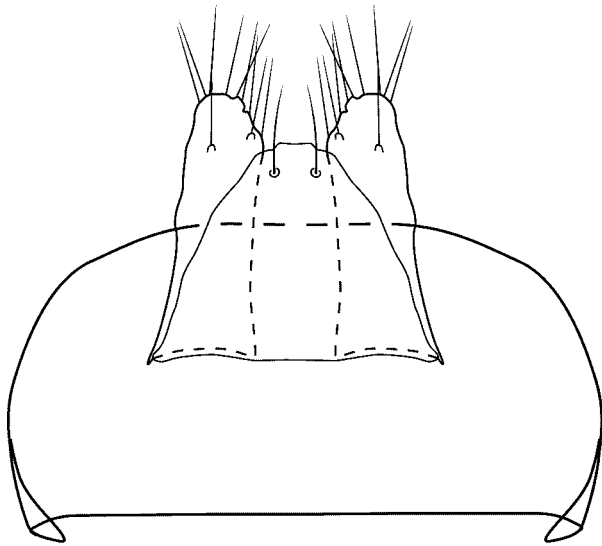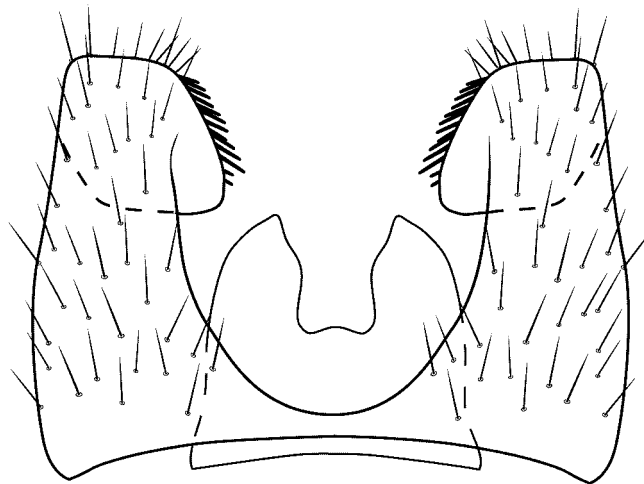
Ohakunea chilensis Freeman **199**

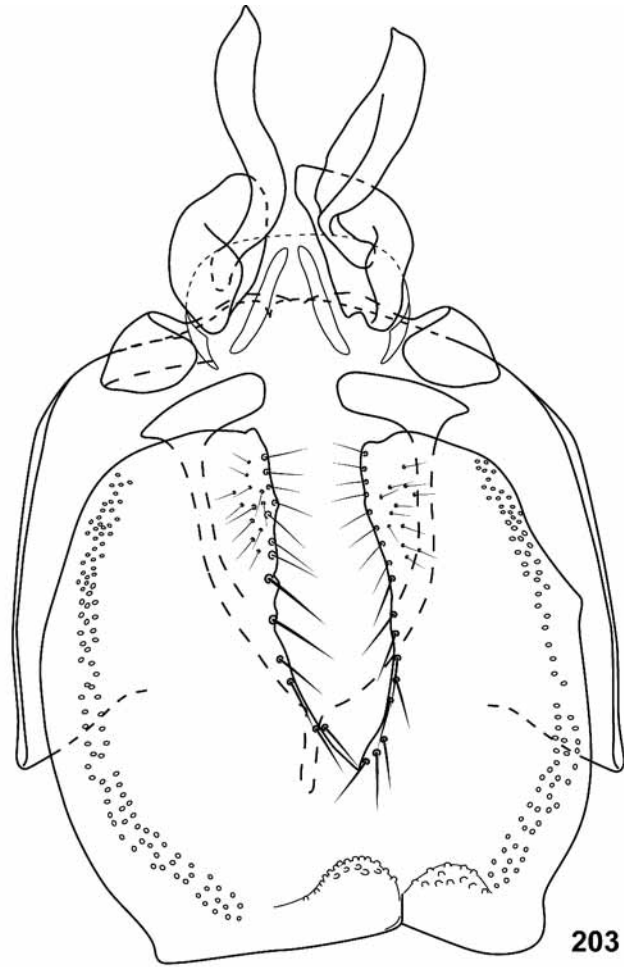*Chiletricha marginata* Edwards **200**

201

Eratomyia magnifica, n.sp.

FIGURES 199–201. Male terminalia tergites IX–X/cercus. **199.** *Ohakunea chilensis*. **200.** *Chiletricha marginata*. **201.** *Eratomyia magnifica*, **gen. n.**, **sp. n.**

Colonomyia freemani, n.sp.

Chiletricha seminuda Freeman

FIGURES 202–203. Female terminalia. 202. *Colonomyia freemani*, **sp. n.** 203. *Chiletricha marginata.*