AN ABSTRACT OF THE DISSERTATION OF

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Title: Evolution and Classification of Bibionidae (Diptera: Bibionomorpha).

Abstract approved:
Signature redacted for privacy.

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The family Bibionidae has a worldwide distribution and includes approximately 700 species in eight extant genera. Recent studies have not produced compelling evidence supporting Bibionidae as a monophyletic group or identified the sister group to bibionids. Therefore, the purpose of this study is to examine the classification and evolution of the family Bibionidae in a cladistic framework. The study has four primary objectives: 1) test the monophyly of the family; 2) determine the sister group of Bibionidae; 3) examine generic and subfamilial relationships within the family; and 4) provide a taxonomic revision of the extant and fossil genera of Bibionidae.

Cladistic methodology was employed and 212 morphological characters were developed from all life stages (adult, pupa, larva, and egg). Characters were coded as binary or multistate and considered equally weighted and unordered. A heuristic search with a multiple random taxon addition sequence was used and Bremer support values are provided to show relative branch support.

A strict consensus of 43 equal-length trees of 1,106 steps indicates that the family Bibionidae is monophyletic and is sister group to Pachyneuridae. All bibionid genera are supported as monophyletic except for *Bibio* and *Bibiodes* (monophyly of the latter genus was not examined because only one exemplar was included). Results indicate that the subfamilies Hesperininae and Bibioninae are monophyletic and Pleciinae is paraphyletic. The cladistic structure of the family is *Hesperinus* +

(*Penthetria* + (*Plecia* + (*Dilophus* + Bibionini))) and relationships between the four genera of tribe Bibionini are unresolved.

Eleven genera of Bibionidae are recognized in the generic revision; eight extant genera and three fossil genera. The three fossil genera, *Fushunoplecia* Hong, *Clothonopsis* Hong & Wang, and *Megeana* Meunier were not available for study and thus the status of these taxa and their placement within Bibionidae is unresolved. The extant genera are: *Hesperinus* Walker, *Penthetria* Meigen, *Plecia* Wiedemann, *Bibio* Geoffroy, *Bibiodes* Coquillett, *Bibionellus* Edwards, *Enicoscolus* Hardy, and *Dilophus* Meigen. A diagnosis and descriptions of all available life stages are provided for each of these genera. Additionally, several new generic synonyms are proposed. The fossil genus *Bibiopsis* Heer is treated as junior synonym of *Penthetria*. The fossil genus *Epiplecia* Giard and the extant subgenera *Heteroplecia* Hardy and *Pleciodes* Hardy are treated as junior synonyms of *Plecia*. The fossil genus *Lithosomyia* Carpenter is a junior synonym of *Bibio*, and the fossil genus *Bibiodites* Cockerell is a junior synonym of *Bibiodes*. Two genera previously included in the family Bibionidae are removed from the family. The fossil genus *Mesopleciella* Rohdendorf belongs in the extinct family Protopleciidae and the family placement of the fossil genus *Longicornia* could not be determined, but is not a bibionid.

Evolution and Classification of Bibionidae (Diptera: Bibionomorpha)

by
Scott J. Fitzgerald

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DEDICATION

Dedicated to my mom and dad who have always believed in me.

Evolution and Classification of Bibionidae (Diptera: Bibionomorpha)

INTRODUCTION

> "I have rarely come upon a scene of greater animation than a sheltered hollow in this wood presented. There was the undulating field, clad in waving grass and set about with the pale-hued springtime foliage of the white oaks; there were the flowering hawthorns; and there were the myriads of Bibios floating in the sunshine, streaming here and there like chaff before sudden gusts and swirls of air."
>
> – James G. Needham 1902

The insect order Diptera, or "true flies," is arguably the most poorly known of the larger insect orders and is of considerable medical, agricultural, and biological importance. Although the order is traditionally recognized as comprising the suborders Nematocera ("primitive flies") and Brachycera ("advanced flies"), data from numerous studies do not support "Nematocera" as a natural group (Krivosheina 1964, Hennig 1973, Amorim 1992, Oosterbroek & Courtney 1995, Michelsen 1996). A paraphyletic Nematocera, along with a renewed interest in the phylogeny of Diptera sparked by Wood & Borkent's (1989) landmark study, has resulted in considerable effort to reevaluate the major lineages of nematoceran flies in order to define monophyletic groups and identify the origin of the Brachycera. Within the nematoceran flies, part or all of the infraorder Bibionomorpha *sensu lato* is considered by many investigators as the likely sister group of Brachycera (Hennig 1973, Amorim 1992, Michelsen 1996, Leathers & Judd 2002). However, character homology, character variation, and lower-level relationships are poorly understood within Bibionomorpha and it has become clear that addressing these problems is critical to a re-evaluation of higher-level groups of Diptera (Woodley 1989).

The focus of this study is to produce a robust phylogeny of the family Bibionidae that will provide new insights into relationships within the infraorder Bibionomorpha and create a foundation for future investigators addressing the putative sister group to Brachycera. Bibionidae was chosen for study from among other Bibionomorpha for two reasons. Firstly, the family is not demonstrably monophyletic (Wood 1991, Amorim 1992, Oosterbroek & Courtney 1995). Secondly, some members of the family have a pair of lateral ejaculatory sclerites similar to those that are considered putative synapomorphies of the Brachycera; this has spurred a debate over the homology of these structures (Griffiths 1990, Sinclair *et al.* 1994). Thus far, no detailed morphological study has examined the distribution of these and other putative synapomorphies of Bibionidae and related families. Therefore, one aim of this study is to elucidate the distribution of characters within bibionids and test the putative homologies of these characters throughout infraorder Bibionomorpha via a parsimony framework.

Members of the family Bibionidae are common, yet somewhat atypical, nematoceran flies. Unlike most "primitive flies," which are fragile and gnat-like with elongate antennae, all bibionids except for species of *Hesperinus* Walker are rather robust with short compact antennae. They are small to moderately large flies (wing 2.0-15.0 mm long) and are black or bright orange and black. Adults are apparently nectivorous and are often seen on flowers. In temperate climates in the northern hemisphere bibionids are commonly known as "March flies" for their emergence in the early spring, though depending on latitude they can emerge any month of the year. Adults are usually very conspicuous as they emerge synchronously in huge numbers and often form dense mating aggregations. These huge emergences often attract attention, and some species of bibionids have received vernacular names such as "St. Marks's Fly" (*Bibio marci* L.) for its emergence around St. Mark's Day (April 25th) and "fever fly" (*Dilophus febrilis* L.) for the erroneous belief that this fly would swarm around the houses of fever-stricken people in Sweden (Freeman and Lane 1985).

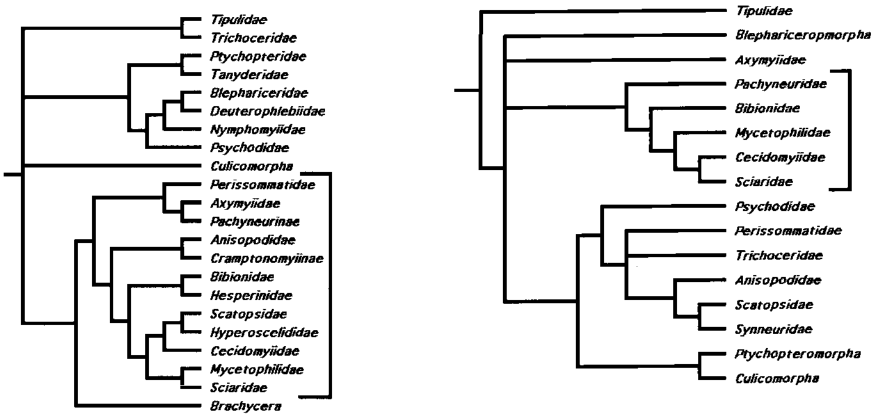
Although Bibionids have acquired a reputation for emerging in huge numbers, they are not one of the more species rich groups of nematoceran flies. Excluding polar regions, the family is found on all continents, but the group includes only about 700 extant species in eight genera. Despite being species poor, the classification of bibionids has been unstable and the boundaries of the family and its sister group remain unclear.

PAST AND PRESENT CLASSIFICATION

HIGHER LEVEL CLASSIFICATION - NEMATOCERA AND BIBIONOMORPHA

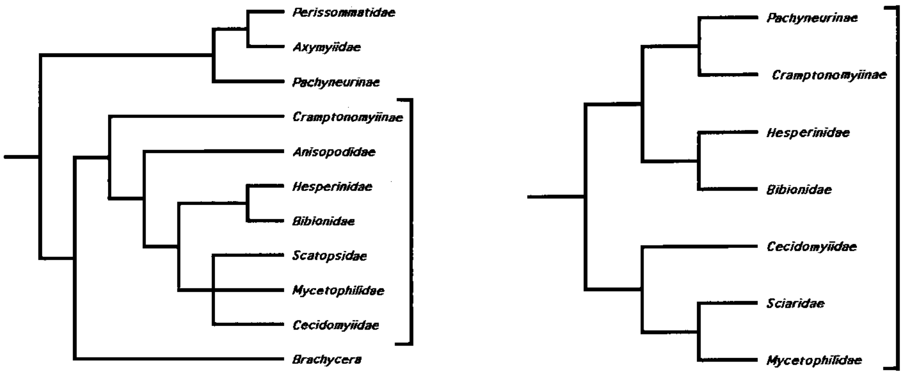
Nematoceran flies have been subdivided numerous ways, but are most recently divided into four, six, or seven infraorders, including minimally Ptychopteromorpha, Culicomorpha, Blephariceromorpha, and Bibionomorpha (Oosterbroek and Courtney 1995, Hennig 1973, Wood and Borkent 1989). Of these infraorders, both morphological and molecular data support Bibionomorpha (*sensu* Hennig 1954, 1973), or a component thereof (e.g. Anisopodidae), as sister group to the suborder Brachycera (Fig. 1a, c, f) (Rohdendorf 1946, Hennig 1968, 1973, 1981, Steyskal 1974, Hackman and Väisänen 1982, Krzeminski 1992, Amorim 1992, Michelsen 1996, Leathers & Judd 2002). However, the composition and classification of Bibionomorpha remains controversial (Wood and Borkent 1989, Wood 1991, Sinclair 1992, Oosterbroek and Courtney 1995, Yeates and Wiegmann 1999).

Infraorder Bibionomorpha (as "Bibiomorpha") was first erected by Hennig (1948). Later, Hennig (1954, 1973) proposed the first hypothesis of bibionomorph relationships and defined Bibionomorpha to include the taxa indicated in Fig. 1a. With the exception of additions or deletions of some of the smaller taxa, investigators over the next several decades generally agreed with Hennig's interpretation of Bibionomorpha (Rohdendorf 1964, Steyskal 1974, and Hackman and Väisänen 1982) until Wood and Borkent (1989) challenged his hypothesis. In contrast to Hennig's hypothesis which emphasized adult characters, Wood and Borkent (1989) reevaluated relationships within the Nematocera adding an extensive set of larval morphological characters. Their resulting hypothesis significantly modified Hennig's Bibionomorpha and redefined the group to include only the families in Fig. 1b. Subsequent studies tend to support either Hennig's (Amorim 1992, Michelsen 1996, and Friedrich &



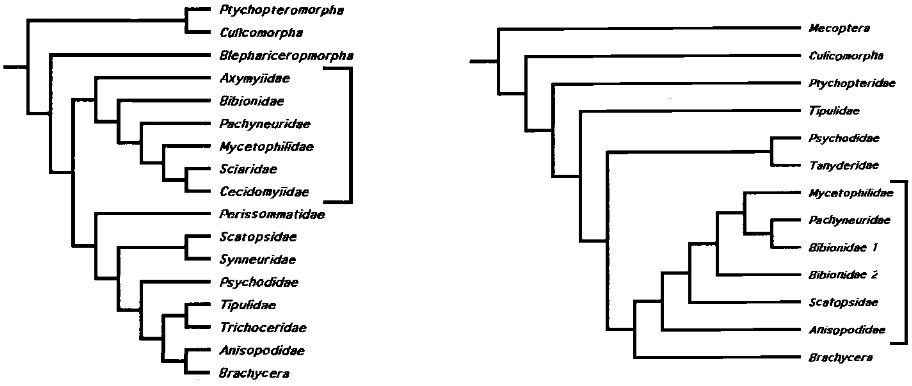
a - Hennig (1973)

b - Wood & Borkent (1989)



c - Amorim (1992)

d - Blaschke-Berthold (1994)



e - Oosterbroek & Courtney (1995)

f - Leathers & Judd (2002)

Figure 1, Interpretation of previous phylogenetic hypotheses of infraorder Bibionomorpha. Brackets indicate infraorder Bibionomorpha as defined by each author(s). Fossil taxa of Amorim (1992) have been excluded.

Tautz 1997) or Wood and Borkent's (Krivosheina 1988, Sinclair 1992, Blaschke-Berthold 1994, and Oosterbroek & Courtney 1995) hypothesis, but none of these studies have provided adequate evidence to establish monophyly of the infraorder. Despite the continuing debate over the membership of Bibionomorpha, investigators generally agree that Bibionomorpha includes at least the taxa Bibionidae, Pachyneuridae, and Sciaroidea (Mycetophilidae *s.l.* + Sciaridae + Cecidomyiidae).

PUTATIVE SISTER GROUPS OF BIBIONIDAE

Not surprisingly, the putative sister group to Bibionidae is disputed. At least five different clades have been proposed as the sister group to bibionids: Scatopsoidea + Sciaroidea (Hennig 1973, 1981, Amorim 1992; if fossil taxa are excluded), Scatopsoidea + Sciaroidea (excluding Bolitophilinae)(Rohdendorf 1964), Sciaroidea (Wood & Borkent 1989), Pachyneuridae (Griffiths 1990, Blaschke-Berthold 1994), and Pachyneuridae + Sciaroidea (Oosterbroek and Courtney 1995)(Fig. 1). In order to assess these sister group hypotheses, exemplars of Pachyneuridae, Scatopsoidea, Sciaroidea, and Axymyiidae (which was historically treated as a bibionid) need to be included in an analysis focusing on Bibionidae. A brief discussion of each of these groups is given below.

Pachyneuridae: The family Pachyneuridae has a Holarctic distribution and includes five species in four genera (Wood 1981a, Krivosheina 1997a, 2000). *Cramptonomyia spenceri* Alexander is the only species known from the Western Hemisphere and is endemic to the northwestern United States and southwestern Canada (Vockeroth 1974, Wood 1981a). The genus *Pachyneura* includes two species; *P. fasciata* Zetterstedt widely distributed in the Palearctic region and *P. oculata* Krivosheina and Mamaev known only from the Far East of Russia (Krivosheina 1997a). Lastly, *Haruka elegans* Okada is known from Japan and *Pergratospes holoptica* Krivosheina and Mamaev from eastern Siberia and Japan (Wood 1981a).

Classification of the family is controversial and both the familial boundaries and monophyly of the group are unresolved. For example, the genus *Pachyneura* has been placed in Mycetophilidae, Bibionidae, Pachyneuridae, and Tipulomorpha, as well as amalgamated with the families Hesperinidae and Axymyiidae (see discussion by Amorim 1992). Evidence for monophyly of Pachyneuridae is weak and some investigators suggest that the genera *Cramptonomyia*, *Haruka*, and *Pergratospes* should be treated as the distinct family Cramptonomyiidae, based on the shared presence of a number of adult and larval characters (Krivosheina and Mamaev 1970, Hennig 1973, Amorim 1992, Blaschke-Berthold 1994, and Krivosheina 1997a). No synapomorphies were found to support monophyly of Pachyneuridae by Amorim (1992) or Oosterbroek and Courtney (1995). However, Wood and Borkent (1989) suggested that the short, stout, apically setose gonostylus and hood-like epandrium are synapomorphies for the family. Furthermore, Blaschke-Berthold (1994) proposed three additional synapomorphies for the group: a pair of sclerotized plates of the larval prothorax, reduced anal lobe of the wing, and elongate adult legs. Unfortunately, the latter two characters lack precise homology statements and occur in numerous other groups of nematoceran flies.

There are several contradicting hypotheses of the sister group relationship to Pachyneuridae. Although Wood and Borkent (1989) provided no supporting evidence, they suggested that Pachyneuridae is sister group to the remainder of the Bibionomorpha (Fig 1b). Griffiths (1990) criticized Wood and Borkent's analysis, suggesting that Pachyneuridae and Bibionidae are monophyletic based on the structure of the larval labium and hypopharynx. Shortly thereafter, both Krivosheina (1991a) and Blaschke-Berthold (1994; Fig. 1d) supported Griffiths' assertion that Pachyneuridae is the sister group to Bibionidae. As part of an intensive study of the male terminalia of nematoceran flies, Wood (1991) reassessed his previous hypothesis (Wood & Borkent 1989) and stated that the loss of the ejaculatory apodeme (and hence the sperm pump) identifies Pachyneuridae as sister group to the remaining Bibionomorpha exclusive of Hesperinidae. However, Oosterbroek and Courtney

(1995) noted that the distribution of the sperm pump is not well understood in Bibionomorpha and that the structure is present in at least some Mycetophilidae (Matile 1990). Lastly, Oosterbroek and Courtney suggested Pachyneuridae is the sister group to Sciaroidea based on the pupal leg sheath not being superimposed and the presence of a sperm pump (Fig. 1e).

Larval pachyneurids bore in various kinds of rotten wood and adults emerge in winter or early spring (Krivosheina & Mamaev1970, Vockeroth 1974, Krivosheina 1997a, 2000).

Sciaroidea: This large group of over 11,200 described species includes the families Mycetophilidae *sensu lato* (4,500 spp.), Sciaridae (1,709 spp.) and Cecidomyiidae (5,000 spp.)(Söli et al. 2000, Menzel & Mohrig 1999, Gagné 1994). Monophyly of Sciaroidea has not been adequately demonstrated and the few synapomorphies which have been proposed (Wood & Borkent 1989, Blaschke-Berthold 1994, Oosterbroek & Courtney 1995, Matile 1990) are based on ground plan coding. Despite this, Sciaroidea is generally considered to be monophyletic and most of the debate over classification concerns the boundaries, rank, and relationship between subgroups within the superfamily, particularly regarding Mycetophilidae *s.l.* (Söli *et al.* 2000, Chandler 2002, Jaschhof & Didham 2002).

Mycetophilidae *s.l.*, commonly known as fungus gnats, are known from all continental areas and most oceanic islands (Vockeroth 1981). Classification of the group is controversial, particularly with regard to how many subfamilies or families should be recognized (e.g. Edwards 1925, 1941, Madwar 1937, Hennig 1948, 1973, Tuomikoski 1966a, 1966b, Matile 1980, 1989, 1990, Thompson 1989, Söli *et al.* 2000). Because of long standing tradition, most recent authors treat the Sciarinae (of Mycetophilidae) as the family Sciaridae (e.g. Winnertz 1867, Crampton 1925, Shaw 1948, Shaw and Shaw 1951, Steffan 1966, Vockeroth 1981, Wood and Borkent 1989, Blaschke-Berthold 1994) even though this classification may render mycetophilids paraphyletic (Vockeroth 1981, see Hennig 1954 as interpreted by Matile 1990: 365, and Wood and Borkent 1989: 1353). A tentative solution to this issue, and the classification that is followed here, is to treat the subfamilies of Mycetophilidae *s.l.* as separate families: Ditomyiidae, Diadocidiidae, Bolitophilidae, Keroplatidae, Lygistorrhinidae, and Mycetophilidae *sensu stricto* (e.g. Papavero 1977, 1978, Matile 1989, 1990, Thompson 1989, Blaschke-Berthold 1994, Zaitzev 1994, Söli et al. 2000).

Although sister group relationships within Sciaroidea are unclear, several studies consider Bibionidae (Wood and Borkent 1989), Pachyneuridae (Oosterbroek and Courtney 1995), or Bibionidae + Pachyneuridae (Blaschke-Berthold 1994), as the sister-group to Sciaroidea (Fig. 1). Both Keilin (1919b) and Madwar (1937) commented on the similarity of the structure of the larval labrum, maxilla, mandible, and spiracles of the mycetophiloid family Ditomyiidae to Bibionidae; and Matile (1990, 1997) considered Ditomyiidae to be the most primitive group of mycetophilids. The discussion of Ditomyiidae given by Wood and Borkent (1989) agrees with Madwar's (1937) assertion "that the Ditomyiinae may be found to occupy an intermediate position between the Mycetophilidae and Bibionidae." Furthermore, the bibionid genus *Hesperinus* was previously placed in Mycetophilidae *s.l.* (Johannsen 1909) and considered to be "clearly connected with primitive Mycetophilidae such as *Bolitophila*" (Edwards 1930). These hypotheses not only leave the sister group to Sciaroidea unclear, but challenge the monophyly of the taxon as well.

The biology of sciaroid larvae is very diverse. Many Cecidomyiidae are gall-makers while the remainder of the families have larvae which are primarily mycetophagous; boring into fleshy fungi, decaying wood (e.g. Ditomyiidae), and other substrates pervaded by fungi (Monroe 1974, Vockeroth 1981). There are many exceptions to this generalization such as some Keroplatidae which are predacious or even endoparasitic on terrestrial planarians (Hickman 1965, Matile 1990).

Scatopsoidea: This group includes the uncommonly collected family Canthyloscelidae (12 spp.), which has a bipolar distribution, and the more common family Scatopsidae (ca. 350 spp.) which is distributed worldwide (Haenni 1997a, 1997b). "There has been virtually no dispute that the Scatopsoidea constitutes a monophyletic group" (Amorim 2000) and the higher classification was recently reviewed and revised by Amorim (1982, 1994, 2000). However, until Enderlein's (1912) revision of the group, scatopsids were classified as a subfamily of Bibionidae and the two are still occasionally treated jointly in faunal and taxonomic works (e.g. Haenni 1985, D'Arcy-Burt & Chandler 1987).

Hypotheses of the sister group to Scatopsoidea include Cecidomyiidae (Hennig 1973), Anisopodidae (Wood & Borkent 1989), or some of the "higher Nematocera and Brachycera" (Oosterbroek & Courtney 1995). "[T]he strange similarity between the front tibiae of *Aspistes* (Scatopsidae) and those of the genus *Bibio* [Bibionidae], may indicate that the families are indeed sister groups" (Freeman and Lane 1985), but the strongly developed fossorial tibia in these two groups has also been suggested as a parallelism (Amorim 1982). Although there is little empirical evidence suggesting that Scatopsoidea is the sole sister clade to Bibionidae, Scatopsoidea + Sciaroidea (Hennig 1973, Amorim 1992)(Fig. 1a, c) or Scatopsoidea + Sciaroidea (excluding Bolitophilinae) (Rohdendorf 1964) have been hypothesized as putative sister groups to bibionids.

The larvae of scatopsids are saprophagous, living in decaying plants and fruits, though some are found in rotten wood and under tree bark (Haenni & Vaillant 1994). Larvae of Canthyloscelidae are saproxylobionts and are found in rotten wood and under the bark of various coniferous and deciduous trees (Mamaev and Krivosheina 1969, Teskey 1976, Haenni 1997a).

Axymyiidae: Axymyiidae is Holarctic in distribution and includes six described species in three genera (Wood 1981b, Mamaev and Krivosheina 1966, 1986, and Yang 1993). Systematic placement of the group has been controversial since even before the type-genus *Axymyia* was originally described by McAtee (1921b). Prior to the description of the adult stage, Alexander (1920) assigned the larvae to the family Tanyderidae. Since then, the genus has been placed in the families Bibionidae

(Coquillett 1909, Duda 1930, Enderlein 1936), Anisopodidae (Shannon 1921, Alexander 1942), Pachyneuridae (Edwards 1925b, 1928a, Séguy 1940, Hennig 1948, 1954, Alexander 1965), and Penthetriidae (cited by Mamaev & Krivosheina 1966). Rohdendorf (1946) elevated the group to family status, and Wood and Borkent (1989) proposed four larval, one pupal, and one adult synapomorphies to support monophyly of the group.

Although monophyly of Axymyiidae was well supported by Wood and Borkent (1989), its sister group relationship awaits detection. Hennig (1973) proposed that Axymyiidae + Pachyneuridae + Perissommatidae is the sister group to the remaining Bibionomorpha (Fig. 1a). Similarly, Amorim (1992) hypothesized that a clade, which includes Axymyiidae, *Pachyneura*, Perissommatidae, and several fossil taxa, is the sister group to Bibionomorpha + Brachycera (Fig. 1c). Considering that Wood and Borkent (1989) could find no justification supporting the previous placement of Axymyiidae in Bibionomorpha, they placed Axymyiidae (as infraorder Axymyiomorpha) in a polytomy with Blephariceromorpha, Bibionomorpha, and Psychodomorpha + Ptychopteromorpha + Culicomorpha (Fig. 1b). Oosterbroek and Courtney (1995) identified Axymyiidae as the sister group to the remaining Bibionomorpha based on the larval mandible moving in a horizontal plane, the larva with a fused torma, and adults with pulvilli and the costa not contiguous around the wing (Fig. 1e). Lastly, and in contrast to all these hypotheses which place Axymyiidae as sister group to, or as the most basal clade within Bibionomorpha, Mamaev & Krivosheina (1966) associated Axymyiidae with the Tipulomorpha based on the following larval characters: tracheal system amphipneustic, head capsule partly withdrawn into prothorax, head with pronounced dorsal emarginations on the posterior margin, and lateral plates of the head capsule fused on the ventral side.

Larval axymyiids are borers in wet rotten logs of various species of trees and are considered to be "ambrosia xylomycetophagous" or "symbiotically associated with wood-coloring fungi" (Krivosheina 1991b). Adults emerge and form mating swarms in winter or early spring (Krogstad 1959, Wood 1981b, Martinovsky and Rohácek 1993, Krivosheina 2000).

MONOPHYLY OF BIBIONIDAE

The family name Bibionidae dates back to Fleming (1821) when it first appeared in a supplement to the *Encyclopedia Britannica* (Sabrosky 1999). However, prior to the late 1930's the familial boundaries of "Bibionidae" were broad and included taxa now treated as separate families (scatopsids, canthyloscelids, pachyneurids, and axymyiids) (Williston 1896, 1908, Kertesz 1902, Lundstrom 1910, Duda 1930, Alexander 1931, Curran 1934, Enderlein 1936). Although these taxa were eventually removed, leaving the Bibionidae with eight genera and nearly 700 species, it remains unclear whether this restricted concept of the family constitutes a monophyletic group.

Monophyly of Bibionidae has been examined in several studies. Wood and Borkent (1989) suggested that the presence of laterally incontiguous intersegmental fissures of the larva is a synapomorphy for the group. However, two years later Wood (1991) reconsidered this hypothesis, suggesting that Bibionidae is paraphyletic based on the distribution of the sperm pump within Bibionomorpha and that the bibionid genus *Hesperinus* is sister group to the remainder of the infraorder. Blaschke-Berthold (1994) considered the ventral fusion of the gonocoxites and the antennae with less than fourteen flagellomeres as putative synapomorphies for Bibionidae. However, ventral fusion of the gonocoxites is present in most Sciaroidea as well as the pachyneurid genus *Pachyneura* (Wood 1991). Neither Amorim (1992) nor Oosterbroek and Courtney (1995) found synapomorphies supporting the family and the latter study concluded that "relationships within the Bibionoidea [=Bibionidae] are far from understood." Pinto and Amorim (2000) found thirteen synapomorphies for bibionids, but unfortunately a single hypothetical outgroup was used to root the tree. This approach artificially constrains the ingroup to be monophyletic and severely misrepresents the distribution of characters in putative sister groups. Further, a problem common to all these studies is the use of ground-plan coding to represent broad, diverse, taxonomic groups (i.e. families or genera).

CLASSIFICATION OF EXTANT BIBIONIDAE INTO SUBFAMILIES

As previously mentioned, the historical concept of Bibionidae was broad and included additional subfamilies, such as Scatopsinae and Pachyneurinae, which were eventually removed and given family status. In the following discussion these extralimital taxa will not be addressed. Rather, only the eight genera which are currently recognized as bibionids (Table 1) will be considered.

Because of D. Elmo Hardy's extensive taxonomic work on bibionids, the subfamilial classification proposed by Hardy and Takahashi (1960) is the classification that has been followed in most regional and systematic treatments. Initially however, Hardy (e.g. 1958b, 1959) followed the subfamilial classification presented in McAtee's (1921) revision of the Nearctic fauna which recognized two subfamilies (Pleciinae and Bibioninae) and treated the genus *Hesperinus* in the subfamily Pleciinae, along with *Plecia* and *Penthetria* (Table 1). The revised subfamilial classification proposed by Hardy and Takahashi (1960) includes elements of McAtee (1921), as well as of Hennig (1948; who noted the uncertain status of *Hesperinus*), yet is distinct from both (Table 1). Hardy and Takahashi's classification placed *Hesperinus* in the monogeneric subfamily Hesperininae (rather than Pleciinae), thus recognizing eight genera in the subfamilies Pleciinae, Hesperininae, and Bibioninae (Table 1). Unfortunately, Hardy's classification is based on the phenetic notion that two groups can be defined using the complementary states of a single character. However, as Farris (1971, 1977) pointed out, using complementary states of a single character to define groups is contradictory because only one of the two states represents a synapomorphy (the other is a plesiomorphy). For example, Hardy distinguished the subfamily Bibioninae by the unbranched Rs vein and presence of a fore-tibial spine and Pleciinae by the furcate Rs vein and the absence of a fore-tibial spine. Although this problem with Hardy's classification is best addressed within a cladistic framework, most studies challenging Hardy's classification have merely expressed a difference of opinion with regard to taxonomic rank (Table 1). For example, Hardy's subfamily Bibioninae is treated as the tribe Bibionini by Wood and Borkent (1989) or as the family Bibionidae in a restricted sense by Krivosheina (1986)(Table 1). Additionally, studies of adult characters by Rohdendorf (1964) and of immature stages by Krivosheina (1969) influenced some European and Russian investigators to recognize all of Hardy's subfamilies as separate families: Hesperinidae, Pleciidae, and Bibionidae (Krivosheina 1969, 1986, 1997b, Nartshuk 1990, 1994, 1995, 1998, Pecina 1998, Schumann 1992)(Table 1); though at least Hesperinidae had been proposed as a separate family far earlier by Hendel (1928,1936).

Table 1 - Classifications of Bibionidae as treated by McAtee (1921), Hardy and Takahashi (1960), Krivosheina (1986, 1997b), Wood and Borkent (1989), and Pinto and Amorim (2000). Taxon names in bold represent changes from the classification proposed by Hardy and Takahashi (1960).

McAtee 1921	**Hardy & Takahashi 1960**	**Krivosheina 1986, 1997b**	**Wood & Borkent 1989**	**Pinto & Amorim 2000**
Bibioninae	Bibioninae	Bibion**idae**	Bibioninae	Bibioninae
			Bibionini	
Bibio	*Bibio*	*Bibio*	*Bibio*	*Bibio*
Dilophus	*Dilophus*	*Dilophus*	*Dilophus*	*Dilophus*
Bibiodes	*Bibiodes*	*Bibiodes*	*Bibiodes*	*Bibiodes*
-	*Bibionellus*	?	*Bibionellus*	*Bibionellus*
-	*Enicoscolus*	?	*Enicoscolus*	*Enicoscolus*
Pleciinae	Pleciinae	Pleci**idae**	**Pleciini**	Pleciinae
Plecia	*Plecia*	*Plecia*	*Plecia*	*Plecia*
				Penthetriinae
Penthetria	*Penthetria*	*Penthetria*	*Penthetria*	*Penthetria*
-	Hesperininae	Hesperin**idae**	Hesperininae	Hesperininae
Hesperinus	*Hesperinus*	*Hesperinus*	*Hesperinus*	*Hesperinus*

Only two studies have examined subfamilial relationships within a cladistic framework. The analysis by Blaschke-Berthold (1994) was primarily focused on

Sciaroidea and only six species in four genera of Bibionidae were examined. With the exception of a difference in opinion of the rank of *Hesperinus*, her classification agreed with Hardy and Takahashi's (1960). In contrast, Pinto and Amorim (2000) examined all bibionid genera and proposed a subfamilial classification which disagreed with Hardy and Takahashi (1960)(Table 1). Results from their study indicate the subfamily Pleciinae is paraphyletic and the genus *Penthetria* Meigen is in the monotypic subfamily Penthetriinae rather than in Pleciinae. In agreement with Blaschke-Berthold (1994), Pinto and Amorim (2000) found synapomorphies supporting the monophyly of Hesperininae and Bibioninae.

GENERIC RELATIONSHIPS

Two cladistic studies have addressed relationships below the subfamily level. Skartveit & Willassen (1996) examined relationships within the subfamily Bibioninae and found the genus *Bibio* to be paraphyletic with respect to *Bibiodes* and *Bibionellus*. One weakness which could account for these results is limited taxon sampling; Skartveit & Willassen only examined the male of one species of each of the latter two genera, and characters for the other life stages (larvae and females) were unknown. Furthermore, exemplars of the bibionine genus *Enicoscolus* were not included. Despite these issues, their results suggested that the genus *Dilophus* is monophyletic and supported a clade including *Bibio*, *Bibiodes*, and *Bibionellus*. Furthermore, they noted that "the monophylies of the subfamily Pleciinae, and the genus *Penthetria* in particular, have not been demonstrated by convincing synapomorphies." Four years later, Pinto and Amorim (2000) provided the only phylogenetic hypothesis of generic relationships for the entire family. Similar to the findings of Skartveit & Willassen (1996), they stressed that they were not convinced that *Bibio* or *Plecia* are monophyletic and that the relationships within Bibioninae differed from alternatives by only a few steps (Pinto & Amorim 2000, D.S. Amorim pers. comm. 2002). It is noteworthy that when Pinto and Amorim's (2000) character data are treated as unordered, relationships within Bibioninae are completely unresolved (pers.

observation). In summary, at least three of the eight bibionid genera have not been demonstrated to be monophyletic, and relationships within the largest subfamily Bibioninae remain unclear.

BIBIONID BIOLOGY, DISTRIBUTION, & DIVERSIFICATION

BIOLOGY

As with many insects, most of the bibionid life cycle is spent in the larval stage. Larval bibionids live gregariously in the top layers of soil and leaf litter and are considered very important in soil formation because they degrade plant material and speed up humification processes (D'Aguilar & Bessard 1963, Karpachevsky *et al.* 1968, Gilyarov & Perel 1970, Szabo 1974, Pobozsny 1978, 1982, Vsevikidiva-Perel & Karpachevsky 1987, Hellrigl 1995, Frouz *et al.* 1999, Nováková & Frouz 1999). Larvae of only five of the eight genera are known (Pinto & Amorim 1996), but at present, larval habitats include soil, leaf and needle litter, decaying plant matter, rotten wood, and dung (Hardy 1945, Schremer 1958, Krivosheina & Mamaev 1967b, Teskey 1976, Portillo Rubio 1977, Hövemeyer 1998, Krivosheina 1998). Larvae are generally considered to be primarily phyto-saprophagous, feeding on leaf and needle litter and decaying organic matter (Hardy 1945, 1981). However, larvae are also frequently found feeding on the subterranean structures of live plants. Under these circumstances, larval bibionids are considered pests in both agricultural and urban settings where larvae feed on and damage cereal crops (barley, hops, oats, rye, and winter wheat), vegetable crops (asparagus, cabbage, cauliflower, celery, cucumber, lettuce, maize, peas, potato, rhubarb, strawberries, sugar beet, and tomato), ornamental flowers (anemones, chrysanthemums, roses, *Polyanthus*, and *Saxifraga*), nursery stock (ash, spruce, and larch seedlings), grass (grass seed fields, turf grass, lawns, golf courses, and pastures), and forage crops (alfalfa) (Hardy 1945, Freeman and Lane1985, D'Arcy-Burt and Blackshaw 1991). An excellent review of bibionids in agricultural systems is given by D'Arcy-Burt and Blackshaw (1991). Bibionids overwinter as larvae and avoid freezing by behaviors such as downward migration and feeding in large clusters (Todd & Block 1995), as well as by physiological adaptations such as unusually high super-cooling points (Sakagami *et al.* 1983). The habits of the larvae of *Hesperinus* differ markedly from those of other bibionids. *Hesperinus* larvae are xylophagous and are restricted to boring in the decaying wood of various deciduous trees (Krivosheina 1997b). Larvae of this genus are not considered pestiferous.

Last instar larvae of *Bibio* form individual cells in the soil in which they pupate (Hinton 1946, pers. obs.). Although pupae of *Bibio* are also occasionally found in rotten wood (Allen 1974, pers. obs.), this behavior is obligatory for the wood-boring genus *Hesperinus* (Krivosheina 1997b). The sexually dimorphic pupal stage lasts three to four weeks under natural conditions and as little as nine days in the laboratory (Kuitert 1975, Skartveit 1997). Bibionine adults eclose in their subterranean cells and dig to the surface with the aid of fossorial fore tibiae, while pupae of Pleciinae migrate to the soil surface prior to eclosion (Hinton 1946).

In the temperate region most adult bibionids emerge in early spring. However, some species emerge in late fall and others are apparently bivoltine (D'Arcy-Burt and Blackshaw 1992, Cherry 2000). Adults are usually conspicuous as they emerge synchronously in huge numbers and often form dense mating aggregations. Males form loose mating "swarms" and copulate immediately with females as they emerge from the soil. Members of *Plecia* Wiedemann, particularly *Plecia nearctica* Hardy, are known as "love bugs" or "honeymoon flies" (Hetrick 1970). This common name is derived from their habit of flying while still in copula; in which they may remain in for up to three days (Thompson 1975a, Thornhill 1976a). Adult love-bugs are considered a nuisance pest in Florida where they are attracted to automobile exhaust on roadways (Callahan and Denmark 1973, Whitesell 1974, Callahan et al. 1985). Large numbers of flies flying over roadways cause overheating of liquid-cooled engines by clogging radiators, reducing visibility, and marring automobile paint (Hetrick 1970, Denmark and Mead 1992). Furthermore, flies stick to wet paint on houses and buildings, which dictated a halt to the painting industry in Florida during May and September (Hetrick 1970). After mating, female bibionines dig a small chamber in the soil with their fossorial fore tibiae, lay a cluster of 44-4200 eggs, and die within the chamber (Girault 1905, Morris 1921, 1922, Skartveit 2002b). Unlike Bibioninae, females of *Plecia* do not dig a chamber, but lay eggs on the soil surface (Pinto and Amorim 1996). Adult bibionids are short-lived, and individuals only live between three days and a week (Hetrick 1970). They are often found on flowers and apparently feed on nectar or pollen, but also feed on honeydew and plant liquids associated with damage from other insect feeding (Engelhardt 1927, Sabrosky 1935, and D'Arcy-Burt and Blackshaw 1991). The report by Barraclough and Londt (1985) that "adults are herbivorous and feed predominantly as scavengers on decaying plant matter" is erroneous and was probably intended to describe the larval feeding habits. In contrast to *Plecia*, adults of some species of *Bibio* Geoffroy and *Dilophus* Meigen are beneficial to humans. These genera are considered important pollinators in orchards and are the exclusive pollinators of some species of Orchidaceae and Iridaceae (Lewis and Smith 1969, Johnson and Steiner 1994, P. Goldblatt per. comm.). Free (1993) suggested that certain Diptera, including the bibionid genera *Bibio* and *Dilophus*, are the most important pollinators of fruit trees apart from bees, but the relative importance of bibionids in this role has not been quantified (Freeman and Lane 1985). Bibionids are also an important food source for vertebrates. Due to the large numbers of adults and larvae frequently present, bibionids are often abundant in the diet of birds returning to nesting grounds during the spring migration (Pecina 1982, Freeman and Lane 1985). In contrast, adults of the genus *Hesperinus* are uncommon and little is known about the adult behavior or feeding habits (Krivosheina 1997b).

DISTRIBUTION & DIVERSIFICATION

Bibionids are small to medium-sized flies that achieve their greatest species diversity in the neotropics (Table 2). However, the problem with such a generalization is that patterns of species diversity vary greatly among genera. For example, in the New World, *Bibio* has thirty-two species in the United States, fifteen in Mexico, six in Central America, and six in South America; the number of species declines as one moves south in latitude. The opposite pattern is true for New World *Plecia* which has fifty-one species in South America and only two in the United States (Fitzgerald 2000). Additionally, bibionids may be locally endemic or widespread. Fitzgerald (2000) reported that 45% of the species recorded from Mexico are known only from that region, while some species are restricted to much smaller areas. For example, *Bibio criorhinus* Bellardi is known only from the Trans-Mexican Volcanic Belt (Fitzgerald 1997), a relatively small area which is considered a center of endemism for numerous plant and animal taxa (Ramamoorthy *et al.* 1993). A more extreme case of endemism is illustrated by the genus *Plecia*. Despite their ability to disperse (Hetrick 1970, Sharp et al. 1974, Thornhill 1976a, Buschman 1976), 91% of the *Plecia* species of the Caribbean islands and 83% of the species of Melanesia and Indonesia are endemic to a single island. In contrast, the opposite extreme is illustrated by widespread taxa, such as *Bibio brunnipes* (Fabricius), which has a circumpolar distribution (Fitzgerald & Skartveit 1997).

In addition to species-level patterns of diversity and endemicity an examination of the distribution of genera reveals larger scale biogeographic patterns (Table 2). The widespread genera *Bibio*, *Dilophus*, and *Plecia* are nearly cosmopolitan and are known from all continental areas except Antarctica, though *Plecia* is most diversified in the tropics. The small genus *Penthetria* is found in all zoogeographic regions except the Afrotropical and Australasian/Oceanic regions. The genus *Hesperinus* is Holarctic with one Nearctic and four Palearctic representatives. *Bibiodes*, also Holarctic, includes three species in western North America and one species in northern China. The genus *Bibionellus* is restricted to central South America (Argentina, Brazil, Bolivia; Pinto & Amorim 1997) and *Enicoscolus* is known only from a total of four species from Brazil, Mexico, New Guinea and northern Australia (Hardy 1961a, Fitzgerald 1997a).

Bibionidae is the best represented family in the fossil record of all Diptera, with over 345 species in nine genera (Evenhuis 1994, Nel 1994, Fitzgerald 1999, and unpublished data). The fossils are known from all zoogeographic regions and date back to the Upper Triassic (Carnian), approximately 225 million years ago (Evenhuis 1994). Although most of these species are represented only by compression fossils and are thus of limited value for studying a wide spectrum of characters, species discovered as amber inclusions are becoming more abundant and provide better character information for extinct forms (Evenhuis 1994, Waller *et al.* 2000, Fitzgerald & Grimaldi unpublished).

Table 2 - Number of bibionid species by genus and biogeographic region. Numbers in bold indicate exemplar sampling from each genus/region represented in the analysis. Subfamilial classification follows Pinto and Amorim (2000). Definitions of biogeographic regions follow regional Diptera catalogs (Bugledich 1999, Hardy 1966, 1973, 1980, 1983, 1989, Krivosheina, 1986, Krivosheina & Mamaev 1986). Species estimates are based on regional Diptera catalogs (cited above) and the following post-catalog works listed by region: Nearctic and Neotropical (Fitzgerald 1997a, b, c, 1998a, b, 2000, Fitzgerald & Skartveit 1997, Hardy 1953b, 1957, 1961a,1967b, Pinto & Amorim 1997, Sturm 1990), Palearctic (D'Arcy-Burt & Chandler 1987, Edwards 1928b, Fitzgerald & Skartveit 1997, Freeman & Lane 1985, Greve & Haenni 1994, Haenni & Báez 2001, Luo & Yang 1988b, Papp 1982, Skartveit 1993, Skartveit & Kaplan 1996, Yang & Luo 1987, 1988, 1989a, 1989b, Yang & Cheng 1997), Oriental (Luo & Yang 1988a), Australasian/Oceanic (Harrison 1990, Fitzgerald 2004).

Taxon	**Nearctic**	**Palearctic**	**Neotropical**	**Afrotropical**	**Oriental**	**Australasian/ Oceanic**	Total
Hesperininae							
Hesperinus	**1**	**4**	0	0	0	0	5
Pleciinae							
Plecia	**2**	**14**	**81**	**44**	**65**	**48**	254
Penthetriinae							
Penthetria	1	**14**	**6**	0	**12**	0	30
Bibioninae	**53**	**128**	**100**	29	**54**	**47**	411
Bibio	**32**	91	13	14	**39**	7	196
Dilophus	**18**	**36**	**80**	15	15	**41**	205
Bibionellus	0	0	**4**	0	0	0	4
Enicoscolus	0	0	**3**	0	0	1	4
Bibiodes	**3**	1	0	0	0	0	4
Total	57	160	187	73	131	97	698

MATERIALS & METHODS

TAXON SAMPLING

The goal of taxon sampling is to maximize taxonomic and biogeographic representation while capturing the spectrum of variation in the groups under study. Species-level exemplars were selected from across the current generic classification (Table 2) as well as from the putative species groups of *Plecia* identified by Hardy (1945, 1952a, 1953a, 1958a, 1968, 1969, 1982). Taxon sampling is increased in those groups that are not demonstrably monophyletic from previous studies or appear to be associated with "loose" diagnostic boundaries (e.g. Pleciinae; Pinto & Amorim 2000). All eight genera of Bibionidae are included (Table 3).

A broad sampling of outgroups is necessary to adequately test the monophyly of the family as well as to expand the usefulness of the results by developing homology hypotheses which can be applied across the infraorder. Outgroup selection is based on previous hypotheses and includes exemplars of Pachyneuridae, Ditomyiidae, Keroplatidae, Mycetophilidae *sensu stricto*, Sciaridae, Scatopsidae, Axymyiidae, Anisopodidae, Trichoceridae, Tipulidae, and Xylophagidae (Table 4)(Keilin 1919b, Madwar 1937, Hennig 1973, Wood & Borkent 1989, Woodley 1989, Griffiths 1990, Krivosheina 1991a, Amorim 1992, Sinclair *et al.* 1994, Blaschke-Berthold 1994, Oosterbroek & Courtney 1995, Michelsen 1996, Nagatomi 1996, Wiegmann *et al.* 2000, Leathers & Judd 2002).

Species exemplars are used rather than genus or family-level exemplars because use of the latter method requires ground-plan coding. Rather than coding the character states exactly as observed, ground-plan-coding requires making assumptions about the ground-plan character state for each group. This misrepresents the true diversity of character states within the taxon and is a highly subjective approach because a difference of opinion about ground-plan states can result in different classifications (Yeates 1995). Because species exemplars are being used, in the discussion of "CHARACTER HOMOLOGY AND VARIATION" a statement such as "absent

Table 3 – Exemplars of Bibionidae included in the analysis. Life stages for each exemplar species are indicated as available and scored in the analysis (+) or unavailable and not scored (-). Abbreviations for "Region" provided in Table 4.

Genus	**Species**	**Region**	**Male**	**Female**	**Pupa**	**Larva**
Hesperinus	*brevifrons* Walker	Nea	+	+	+	+
Hesperinus	*nigratus* Okada	Pal	+	+	-	-
Hesperinus	*cuspidistilus* Hardy & Tak.	Pal	+	-	-	-
Plecia	*lusca* Fitzgerald	Ao	+	+	-	-
Plecia	*amplipennis* Skuse	Ao	+	+	-	-
Plecia	*dimidiata* Macquart	Ao	+	+	-	-
Plecia	*aruensis* Edwards	Ao	+	+	-	-
Plecia	*erebea* Skuse	Ao	+	+	-	-
Plecia	*americana* Hardy	Neo/ne	+	+	-	-
Plecia	*nearctica* Hardy	Neo/ne	+	+	+	+
Plecia	*plagiata* Wiedemann	Neo	+	+	+	+
Plecia	*bicolor* Bellardi	Neo	+	+	-	-
Plecia	*ephippium* Speiser	Afr	+	+	-	-
Plecia	*zernyi* Hardy	Afr	+	+	-	-
Plecia	*freemani* Hardy	Afr	+	-	-	-
Plecia	*robusta* Hardy	Afr	+	-	-	-
Plecia	*paenerubescens* Hardy	afr	+	-	-	-
Plecia	*yabaensis* Hardy	afr	+	-	-	-
Plecia	*sinensis* Hardy	or	+	+	-	-
Plecia	*zamboanga* Hardy	or	+	+	-	-
Plecia	*mallochi* Hardy	or	+	+	-	+
Plecia	*imposter* Brunetti	or	+	+	-	-
Plecia	*hadrosoma* Hardy & Taka.	pal	+	+	-	-
Plecia	*thulinigra* Hardy	pal	+	+	-	+
Plecia	*nagatomii* Hardy & Taka.	pal	+	+	-	-
Penthetria	*nigrita* Perty	neo	+	+	-	-
Penthetria	*japonica* Wiedemann	pal	+	+	+	+
Penthetria	*funebris* Meigen	pal	+	+	+	+
Bibio	*albipennis* Say	nea	+	+	+	+
Bibio	*niggerrimus* Duda	or	+	+	-	-
Bibiodes	*aestivus* Melander	nea	+	+	-	-
Enicoscolus	*dolichocephalus* Hardy	nea/neo	-	+	-	-
Enicoscolus	*brachycephalus* Hardy	nea/neo	-	+	-	-
Bibionellus	?	neo	+	-	-	-
Bibionellus	*barettoi* Lane & Forattini	neo	+	+	-	-
Dilophus	*nigrostigma* Walker	ao	+	+	-	-
Dilophus	*serotinus* Loew	nea	+	+	-	-
Dilophus	*sayi* (Hardy)	neo/nea	+	+	+	+
Dilophus	*febrilis* (Linnaeus)	pal	+	+	+	+

Table 4 – Outgroup exemplars included in the analysis. Abbreviations used in the "Region" column: afr – Afrotropical, ao – Australasian/Oceanic, nea – Nearctic, neo – neotropical, or – Oriental, pal – Palearctic. Male, female, pupal, and larval life stages for each exemplar species are indicated as available and scored in the analysis (+) or unavailable and not scored (-).

Outgroup exemplars	**Region**	**Male**	**Female**	**Pupa**	**Larva**
Pachyneuridae					
Cramptonomyia spenceri Alexander	nea	+	+	+	+
Pachyneura fasciata Zetterstedt	pal	+	+	-	+
Haruka elegans Okada	pal	+	+	-	-
Ditomyiidae					
Symmerus coqulus Garrett	nea	+	+	+	+
Keroplatidae					
Keroplatus terminalis Coquillett	nea	+	+	+	+
Mycetophilidae s.s.					
Mycetophila favonica Chandler	nea	+	+	+	+
Bolitophilidae					
Bolitophila bucera Shaw	nea	+	+	+	+
Sciaridae					
Rhynchosciara americana (Wiedemann)	neo	+	+	+	+
Scatopsidae					
Scatopse notata (Linnaeus)	nea/pal	+	+	+	+
Arthria analis Kirby	nea	+	+	-	-
Anisopodidae					
Sylvicola fenestralis (Scopoli)	nea/pal	+	+	+	+
Sylvicola cinctus (Fabricius)	nea/pal	+	+	-	-
Mycetobia divergens Walker	nea	+	+	+	+
Axymyiidae					
Axymyia furcata McAtee	nea	+	+	+	+
n. gen. n. sp.	nea	+	+	+	+
Trichoceridae					
Trichocera tetonensis Alexander	nea	+	+	+	+
Tipulidae					
Ctenophora angustipennis Loew	nea	+	+	+	+
Xylophagidae					
Dialysis dispar Bigot	nea	+	+	-	-

from Axymyiidae and Scatopsidae" communicates that the character is absent from the exemplars examined and not necessarily that the character is absent from all species in these families.

SPECIES CONCEPTS

"Species" is the fundamental unit in organismal biology. Unfortunately, there is virtually no agreement on exactly what a species is (e.g. see Wheeler & Meier 2000, Avise 2000). Exemplars in this study are recognized as "species" and thus it is necessary to explain how these units have been diagnosed. The taxonomy of Bibionidae has been extensively treated by Hardy which provides an invaluable foundation for future work on bibionids (Hardy 1937, 1938, 1940, 1942a,b,c, 1945, 1948a,b, 1949a,b, 1950a,b,c, 1951a,b,c,d, 1952a,b,c,d, 1953a,b,c, 1956a, 1958a,b, 1959a,b, 1960a,b,c, 1961a,b,c, 1962a,b, 1965a,b,c, 1966, 1967a,b,c, 1968, 1969, 1971, 1973, 1980, 1982, 1989, Hardy & Takahashi 1960, Hardy & Delfinado 1969). It is unclear which of the twenty-two "species concepts" (Mayden 1997) was adhered to in the numerous taxonomic works that have been published on bibionids. However, in most recent works, starting about the time of Dr. Elmo Hardy's 1945 revision of the Nearctic fauna, species are operationally differentiated (at least in part) based on the structure of the male terminalia. This comes as no surprise since in some bibionid genera, such as *Penthetria*, the adult morphology is rather conservative and the male terminalia is one of the few sources of variability. The species concepts used here follow the following taxonomic works listed by family: Bibionidae (Fitzgerald 2004, Haenni 1982, Hardy 1937-1989 (see above), Hardy & Takahashi 1960, Harrison 1990, Krivosheina 1998, Krivosheina & Mamaev 1967a, Pinto & Amorim 1997); Pachyneuridae (Wood 1981a, Krivosheina 1997a, 2000); Ditomyiidae (Colless 1970, Monroe 1974); Keroplatidae (Matile 1990); Bolitophilidae (Shaw 1962); Mycetophilidae (Chandler 1993); Sciaridae (Breuer 1969, 1971); Scatopsidae (Cook 1957, 1965a); Anisopodidae (Pedersen 1968, Peterson 1981a, Pratt & Pratt 1980);

Axymyiidae (Wood 1981b); Trichoceridae (Pratt 2003); Tipulidae (Alexander 1967, Alexander & Byers 1981); and Xylophagidae (Webb 1978).

SPECIMENS

Over 5,000 specimens (mostly adult bibionids) were borrowed from numerous research and private collections specializing in material from all biogeographic regions. The following list includes persons and collections that loaned and donated material for study, and provides acronyms of collections where material has been deposited (collection acronyms follow Arnett, Samuelson, and Nishida (1993)). My deepest thanks to all these people and institutions for their help in making this study possible.

David Grimaldi, Tam Nguyen, American Museum of Natural History, New York (AMNH); Dan Bickel, Australian Museum, Sydney (AMSA); Don Colless, Australian National Insect Collection, Canberra (ANIC); Nigel Wyatt and John Chainey, The Natural History Museum, London (BMNH); Neal Evenhuis, and Keith Arakaki, Bernice P. Bishop Museum, Hawaii (BPBM); Richard W. Baumann, Monte L. Bean Life Science Museum, Brigham Young University, Utah (BYUC); Norman D. Penny and Keve J. Ribardo, California Academy of Sciences (CASC); Chen W. Young, The Carnegie Museum of Natural History, Pennsylvania (CMNH); D. Monty Wood, Jeff M. Cumming, and Harold Walther, Canadian National Collection of Insects, Ontario (CNCI); Boris C. Kondratieff and David Leatherman, C. P. Gillette Museum, Colorado State University (CSUC); Masahiro Ohara, Teruhiko Hironaga, and Kazunori Yoshizawa, Hokkaido University, Japan (EIHU); Cheryl B. Barr, Essig Museum of Entomology, Berkley, California (EMEC); Wilford J. Hanson, Utah State University, Logan (EMUS); Gary J. Steck and Robert E. Woodruff, Florida State Collection of Arthropods, Gainesville (FSCA); Manuel A. Zumbado, Instituto Nacional de Biodiversidad, Costa Rica (INBC); Don Webb and K.R. Zeiders, Illinois Natural History Survey Insect Collection (INHS); V.V. Ramamurthy, National Pusa

Collections, Indian Agriculture Research Institute (INPC); Patrick Grootaert, Royal Belgian Institute of Natural Sciences, Belgium (ISNB); Gregory W. Courtney, Iowa State University (ISUI); Koji Yasuda, National Institute for Agro-Environmental Sciences, Japan (ITLJ); Philip D. Perkins, Museum of Comparative Zoology, Harvard University, Massachusetts (MCZC); Loic Matile, Museum National d'Histoire Naturelle, Paris (MNHN); Marc De Meyer, Eliane De Coninck, and Mr. De Becker, Royal Museum for Central Africa, Belgium (MRAC); Brian R. Stuckenberg, David A. Barraclough, C. Conway, and Shayleen James, Natal Museum, South Africa (NMSA); Chang Man Yang, National University of Singapore (NMSC); Darlene Judd, Oregon State University, Corvallis (OSAC); Adrian Pont and Darren J. Mann, Hope Entomological Collections, Oxford (OXUM); Dalton de Souza Amorim, Universidade de São Paulo (RPSP); Robert W. Brooks, George W. Byers, and Elizabeth F. Smith, Snow Entomological Collections, University of Kansas, Lawrence (SEMC); Saul I. Frommer and Doug Yanega, University of California, Riverside, Entomological Research Collection (UCRC); Philip J. Clausen, University of Minnesota Insect Collection, St. Paul (UMSP); Atilano Contreras-Ramos, Coleccion Entomologica, Instituto de Biologia, Universidad Nacional Autonoma de Mexico (UNAM); F. Christian Thompson, National Museum of Natural History, Smithsonian Institution (USNM); Conrad Labandeira, Jann W. Thompson, and Mark Florence, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (USNM); Lita Greve Jensen, University of Bergen, Norway (ZMUB); Eliana Abdelhay, Universidade Federal do Rio de Janeiro; Ron Cherry, Everglades Research and Education Center, Florida; William G. Eberhart, University of Costa Rica; Jann Frouz, Institute of Soil Biology, Academy of Sciences of the Czech Republic; Geoff Hancock, University of Glasgow, Scotland; Martin Hauser and Kevin Holston, University of Illinois; Tim Mousseau, University of South Carolina; Will Reeves, Clemson University, South Carolina; O.P. Rupela and M. Sriveni, Natural Resources Management Program, ICRISAT, Patancheru, Hyderabad, India; Toyohei Saigusa, Kyushu University, Japan; Brad Sinclair, Zoologisches Forschungsinstitut und

Museum Alexander Koenig; John Skartveit, Department of Ecology & Conservation, SAC Ayr Campus, Scotland; Mitsuaki Sutou, Yokohama National University, Japan; Ann J. Stocker, Universidade de Sáo Paulo, Instituto de Biociências.

As with most families of Diptera, larval and pupal stages of Bibionidae are not well represented in museum collections. Larvae of only five of the eight genera are known and larvae of most Bibionidae are unknown at the species level (Table 3)(Pinto & Amorim 1996). Tables 2 and 3 summarize larval specimens which were available for study; most genera are represented, but usually only by one or two species from the Northern Hemisphere.

Unfortunately the larval specimens of several bibionid and pachyneurid species previously described in the literature have been either lost or destroyed and are reported as such here: larvae and pupae of *Plecia americana* Hardy which were reared by W.G. Bradley (Buschman 1976) were probably destroyed when the "collection burned and then was neglected for many years" (V. Moseley, Louisiana State Univ., pers. comm. 2002); larvae and pupae of *Plecia fulvicollis* (Fabricius)(Fletcher 1919: 58) were likely destroyed in an earthquake in 1934 (V.V. Ramamurthy (INPC), pers. comm. 2002); according to Marina G. Krivosheina (Moscow, pers. comm. 2001) the larval specimens of *Pachyneura oculata* Krivosheina and Mamaev (1972), *Hesperinus rohdendorfi* Krivosheina and Mamaev (1967a), *Plecia thulinigra* Hardy (Krivosheina 1972), and *Pergratospes holoptica* Krivosheina and Mamaev (1970) were "actively used during scientific [investigation] and [were] not kept up to the present time." Although it sounds as if the original specimens of the aforementioned taxa are no longer available from collections in Moscow (or St. Petersburg; E. Nartshuk pers. comm.), larval specimens determined by N.P. Krivosheina of the latter two species were available for study from CNCI and a dried out larval specimen of *H. rohdendorfi* was located at BPBM. Furthermore, recent studies of the larval retrocerebral endocrine complex in the larvae of *Plecia thulinigra* indicates that additional specimens of this taxon have been located or collected (Panov 1995).

COLLECTING & REARING

Collecting methods for adult bibionids included sweep-netting, malaise traps, black lights, and the use of anethole bait (D'Arcy-Burt & Blackshaw 1987, Cherry 1998). Black lights and malaise traps proved to be particularly successful. Considering that adequate adult material existed for study, most collecting effort was focused on immature stages.

Bibionid larvae were collected by digging and soil-sieving around plant roots and leaf litter in the vicinity of adult populations. Larval specimens were reared to allow association of life stages. Locating the gregarious immature stages is the most time-intensive part of the rearing process. Since adult emergence is synchronous, all life stages of bibionids are often present simultaneously at the beginning of the adult emergence period. Therefore, adults are used as the indicators of larval habitat and since the last larval skin is usually attached or adjacent to the posterior end of the pupa, all stages can then be associated.

Numerous species of both bibionids and outgroup taxa were collected as larvae or pupae in the field and reared to the adult stage. These taxa were reared in one quart, wide mouth, canning jars with fine mesh over the top (unless otherwise mentioned) and stored in an unheated building out of direct sunlight. In most cases the larval medium (e.g. soil, leaf litter) was placed directly in the jar without any other medium for pupation. For Sciaroidea (except Ditomyiidae and Keroplatidae) and *Trichocera* which infest fungi, field-picked fungal fruiting bodies were placed on about three inches of slightly moistened potting soil which larvae migrated into for pupation (modified from Buxton 1960). More specific natural history notes concerning larval habitat and development of individual taxa are provided in Appendix II – Rearing Notes.

HOMOLOGY

Central to the work of systematics is the concept of homology. Despite 160 years of conceptual (Hennig 1950), methodological (Kluge & Farris, 1969, Farris 1970) and technological (e.g. computers) advances since Owen (1843), and earlier Geoffroy (1818), who used the "principle of connections" and the "principle of composition" as the operational criteria to define homologous structures, systematists still recognize (or develop hypotheses about) homologous structures based on similar form, position, and connection (Remane 1952, Schuh 2000). These operational criteria are philosophically supported by Hennig's (1966: 121) "auxiliary principle" which states that structures in common between two taxa are not to be considered convergent *a priori* (i.e. they should be initially considered homologous until additional evidence suggests otherwise). The combination of these operational and philosophical criteria is the foundation for the approach to homology used in this study.

To ensure the repeatability of this study, it is critical that the hypotheses of homology developed here are transparent and thus open to criticism. Brower and Schawaroch (1996) presented an outline for assessing homology, and the ideas in the following summary are taken in part from their work. Firstly, a distinction between "character" and "character state" is necessary. A convenient way to conceptualize this distinction is that the character corresponds to the column of the data matrix being assembled and the character state corresponds to the value in each cell of the matrix (Brower & Schawaroch 1996). For example, based on operational criteria (i.e. similarity of form, position, and connection) the hind tibia of species A is tentatively considered to be homologous to the hind tibia of species B. This initial hypothesis of character homology is then treated as unproblematic background knowledge (Popper 1959, 1979) and acts as a foundation for a second hypothesis; a hypothesis of character state homology. The hypothesis of character state homology is based on the same operational criteria as the hypothesis of character homology. For example, species A and species B have the character "hind tibia" with the character state "swollen" whereas species C has the character "hind tibia" with the accompanying character state "not swollen;" the swollen state found in A and B is tentatively considered homologous. It is important to note that these statements about homology are only hypotheses and that these hypotheses must withstand the test of total character congruence before a hypothesis of homology as it is popularly defined, "due to common descent" (e.g. Simpson 1961), can be suggested (de Pinna 1991; primary versus secondary homology). Although hypotheses of character and character state homology are assumed in the cladistic analysis, they can be re-examined at any time if additional information, such as homoplasy indicated by character congruence, warrants re-examination (Hennig's (1966) "reciprocal illumination").

The above discussion provides only a general conceptual and methodological framework for the approach to homology used here. Details about how hypotheses of homology for individual characters and character states were determined are presented in the section on "CHARACTER HOMOLOGY AND VARIATION."

CHARACTER SYSTEMS

Many studies examining the classification and evolution of Diptera focus on a single character system from a single life stage; for example wing venation (Hennig 1954), male terminalia (Wood 1991), larval mouthparts (Sinclair 1992), and musculature of the prothorax (Michelsen 1996). Although these kinds of studies are critical in providing new information about these character systems and resolving the homology of structures, phylogenetic studies which emphasize characters from a single life stage or structure may support misleading arrangements of taxa (Rohlf 1963, Michener 1977, Roback & Moss 1978, Judd 1998). No study will ever include all character systems from all life stages. However, I have striven to provide a broad survey of traditional and novel morphological character systems from the adult, larval, and pupal stages. Admittedly, a large percentage of these morphological structures are external and future studies examining internal morphological, molecular, and behavioral characters would be of great value, particularly if they could be added to the dataset provided here.

When examining more than one "character system" in a single study there is some debate over whether these sets of characters should be analyzed simultaneously (total evidence approach; Kluge 1989, Brower 1996, Nixon & Carpenter 1996a, DeSalle & Brower 1997) or analyzed independently and only those sets found to yield congruent results later combined (e.g. Bull *et al.* 1993, Huelsenbeck *et al.* 1996). Although this debate includes numerous arguments that will not be expounded upon here, the two points which follow are ample justification for using the much less subjective "total evidence approach." Firstly, the delimitation of a "character system" is arbitrary. For example, the character system "male genitalia" could be broken down further into systems of "internal" versus "external," "sclerotized" versus "membranous," or "proctiger" versus "parameres" versus "sperm pump." Since the division of the characters into sets is arbitrary, analyzing each of these sets separately is also arbitrary. Secondly, the conscious decision to exclude some of the data after determining that they conflict with the other data is unacceptable in practice. If the notion that historical patterns can be resolved from character data is to be regarded as valid, then we must submit to the idea that no matter how many "bad" (homoplastic) data are added, these data are randomly distributed and will not "swamp out" the phylogenetic signal produced by the congruence of characters due to common ancestry (Farris 1983). Considering this, character data will be analyzed simultaneously (Chavarria & Carpenter 1994, Nixon & Carpenter 1996a, DeSalle & Brower 1997, Judd 1998, Gatesy *et al.* 1999).

CLADISTIC METHODS

Cladistic analyses are used to elucidate relationships and provide a framework for future studies. The analytical methods chosen are based on the philosophical stance that "extra background assumptions should be discarded, because they weaken the capacity of the empirical evidence to discriminate among competing theories"

(Brower 2000). Therefore, numerous *a priori* assumptions about the data (e.g. character weight, order, polarity, etc.) have been excluded. Characters are coded as multistate (Pimentel & Riggins 1987, Meier 1994) and binary. Characters are run as unordered and of equal weight, as this requires the fewest *ad hoc* hypotheses (Kluge & Farris 1969, Farris 1983, Kluge 1989, Brower *et al.* 1996) and allows novel hypotheses of character transformation to be examined. Because coding inapplicable character states as missing data may lead to unsupported nodes (Platnick *et al.* 1991), inapplicable states have been coded as autapomorphic and are referred to in the discussion of characters as scoring a taxon with an "inapplicable autapomorphy." Each alphanumeric value observed in the data matrix which is not defined as indicating a character state within the character in question represents an inapplicable autapomorphy. Furthermore, despite the problems associated with missing data (Platnick *et al.* 1991), immature stages are unknown for many taxa. Polymorphism for the purpose of this study is defined as different states of a character in a single taxon; such a taxon is coded as having both character states (e.g. "0 & 1") and is treated as a "polymorphism" in the PAUP analysis.

Ten thousand heuristic searches with random taxon addition sequence were used to help recover multiple tree islands if they occur (Maddison 1991). Tree bisection reconnection (TBR; Swofford & Olsen 1990) is preferred over other branch swapping options (NNI and SPR) in PAUP* 4.0b10(PPC) because it is both global in nature and yields more rearrangements than SPR (Goloboff 1996). Successive approximations weighting (SAW) using the rescaled consistency index could not be used to choose among equally parsimonious solutions (Farris 1969, 1989, Carpenter 1988) because SAW resulted in a longer tree not among the equally parsimonious solutions. Therefore, a strict consensus tree was used to summarize the multiple equally parsimonious cladograms (Nixon & Carpenter 1996b). Bremer support values (Bremer 1988, 1994) rather than bootstrap (Felsenstein 1985) or jackknife values (Lanyon 1985) were calculated to indicate the relative support of components on the tree. Despite the popularity of the latter methods, Bremer support values are preferred because bootstrapping is sensitive to autapomorphies (Carpenter 1996) and both of the latter methods rely on pseudo-replication using hypothetical data sets (i.e. data sets derived from your original data set via resampling with replacement of characters).

The network is rooted with *Ctenophora angustipennis* Loew (Tipulidae) because, unlike most other outgroup taxa included, no investigators consider the family Tipulidae as belonging to Bibionomorpha. Characters are optimized using ACCTRAN optimization.

PHYLOGENETIC RESULTS

The cladistic analysis resulted in 43 cladograms of 1,106 steps with a consistency index of 0.44 and a retention index of 0.67. A strict consensus tree was constructed from the 43 equal-length cladograms (Fig. 2). The tree is resolved except for generic relationships within Bibionini (node 24), some species-level relationships within *Plecia* (node 8), and Ditomyiidae is in an unresolved polytomy with the remainder of Sciaroidea (node 36) and the clade Bibionidae + Pachyneuridae (node 4). Character support for clades discussed below refers only to those characters that are unambiguously optimized on the tree (i.e. there is only a single most parsimonious optimization for this character). Node/clade numbers in the following discussion refer to the numbers indicated on the trees in figures 2 and 3. Although the strict consensus tree (Fig. 2) is the best summary of character data, and thus the relationships, mapping characters requires a fully resolved tree. Therefore, character state changes listed in the following discussion and in Appendix III are based on only one of the equal-length trees that was chosen at random (Fig. 3). Character changes are discussed only for branches that did not collapse in the strict consensus tree and are supported on all equally parsimonious cladograms (compare Figs. 2 & 3). In the following discussion unambiguous character support is listed in parentheses after each clade using the following format: the node #, followed by a colon, followed by the character number, followed by a colon, followed by the character state that supports that node/clade. Character state numbers which are underlined indicate that the character state is unique to the clade (i.e. perfectly consistent within this analysis). A complete list of character changes (both ambiguous and unambiguous) is reported in Appendix III. The character support listed below for each clade is intended only as a summary; a more detailed disussion of each of these characters is presented in the following section: "CHARACTER HOMOLOGY AND VARIATION." Bremer support values for clades are provided in figure 4.

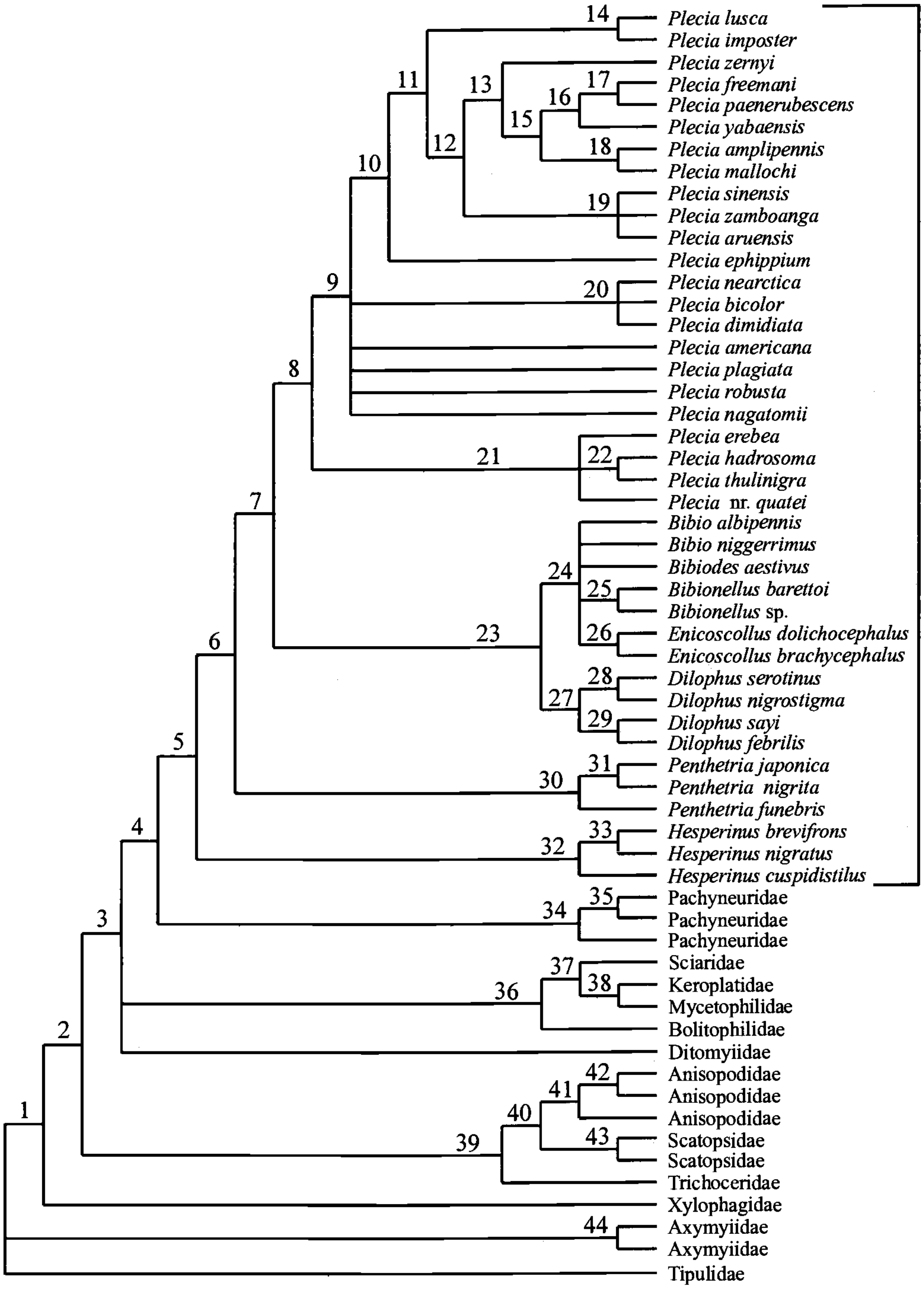


Figure 2. Strict consensus tree from 43 cladograms of 1,106 steps. Node numbers referred to in text. Bracket indicates family Bibionidae. Species names of outgoup exemplars replaced with family names (species names of outgroup exemplars are retained in Figs. 3 & 4).

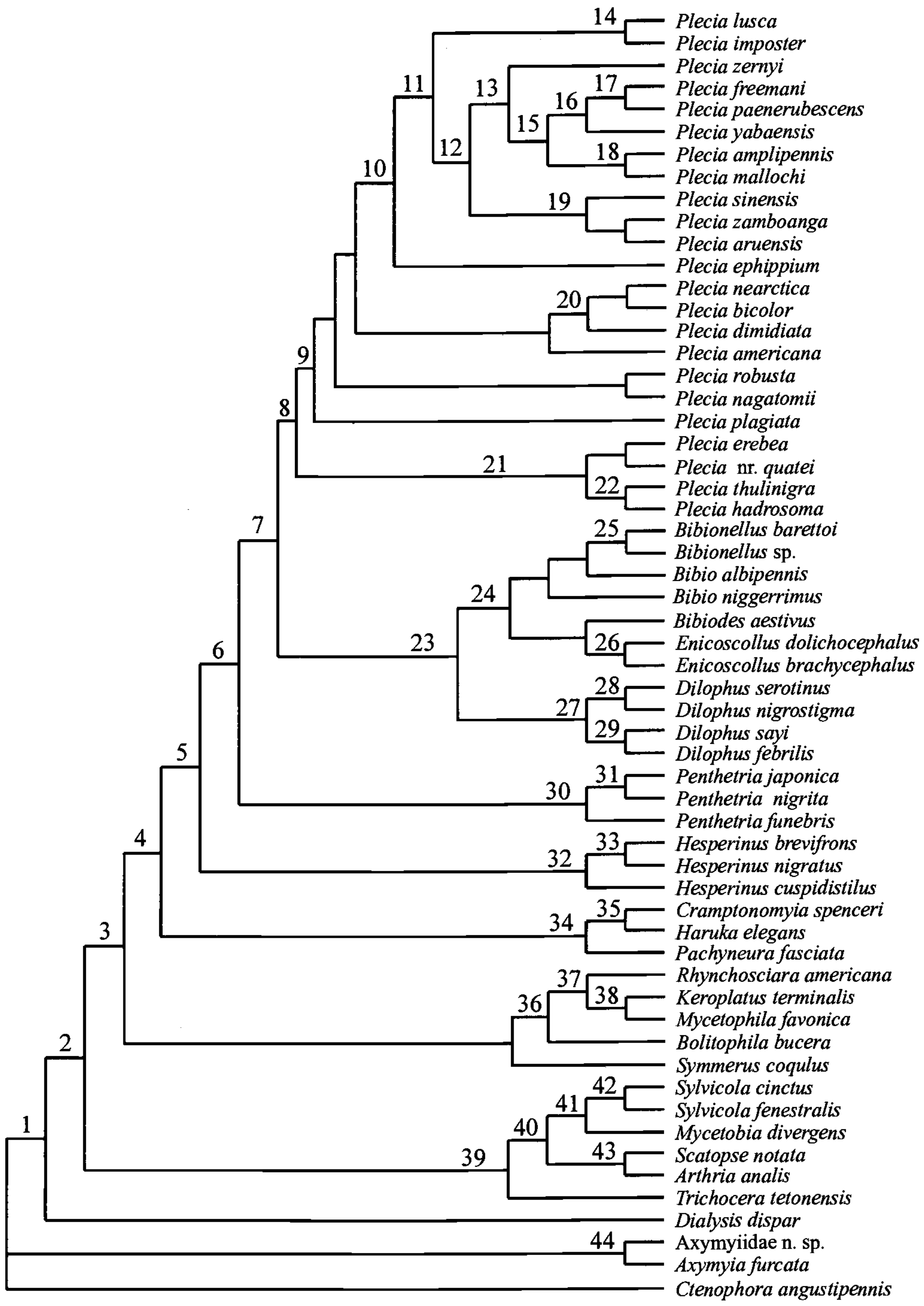


Figure 3. One of 43 cladograms of 1,106 steps. Node numbers are equivalent to those in figure 2 and are referred to in the text.

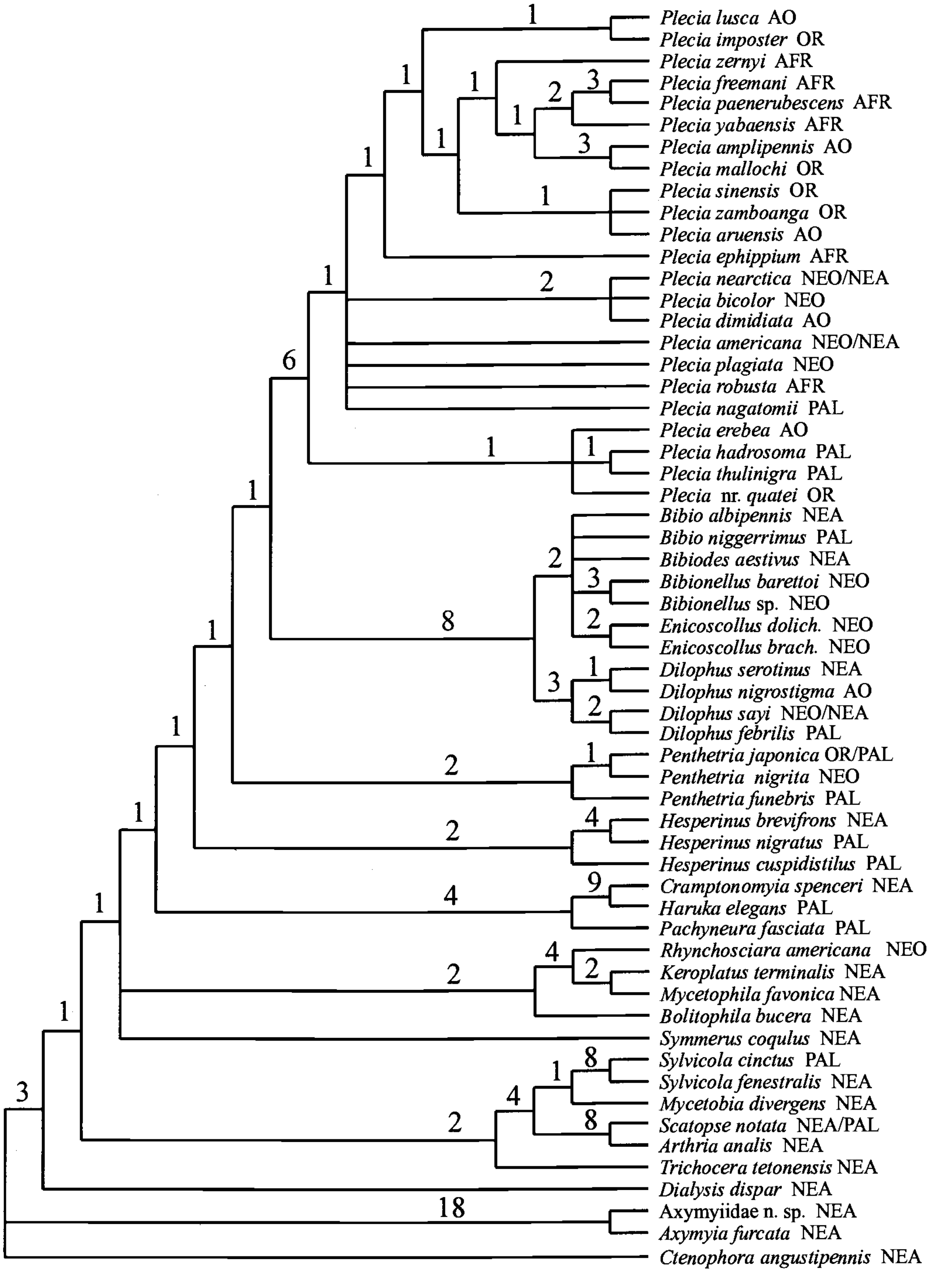


Figure 4. Bremer support. Strict consensus tree from 43 cladograms of 1,106 steps with CI = 0.44 and RI = 0.67. Bremer support values indicating relative branch support are listed above each branch. AFR = Afrotropical, AO = Australasian/Oceanic, NEA = Nearctic, NEO = Neotropical, OR = Oriental, PAL = Palearctic.

MONOPHYLY OF BIBIONIDAE AND ITS SISTER GROUP

The results indicate that Bibionidae is monophyletic and is sister group to Pachyneuridae (nodes 5 & 4, Fig. 2). The monophyly of Bibionidae, including the genus *Hesperinus*, is supported by eight adult and four larval characters (node 5: characters 10:5, 15:1, 26:0, 31:1, 67:1, 68:1, 79:1, 135:1, 149:1, 170:1, 171:1, 175:0). Although none of the twelve characters is unique to bibionids and some show considerable homoplasy in the analysis, character 149:1 (unaligned intersegmental fissures of larval abdomen (Fig. 28a; if)) is the most consistent because, besides Bibionidae, it is present only in *Scatopse* (Scatopsidae) and appears to be an independent development in the latter taxon. The presence of a complete postgenal bridge in the adult (15:1 (Fig. 6d; pgb)) has only two steps; it is present at the base of the tree in Tipulidae, Axymyiidae, and Xylophagidae, absent in Anisopodidae, Scatopsidae, Trichoceridae, Sciaroidea, and Pachyneuridae, and then present again in Bibionidae. The sensory cone of the larval antennae is sessile (170:1 (Fig. 31e-f; sc)) only in Bibionidae and some Sciaroidea (node 37). Additionally, presence of the larval postgenal bridge (171:1 (Fig. 30b; pgb)), absence of the presternum (26:0), and presence of a dorsoflexed hypopygium (135:1 (Fig. 5e)) support Bibionidae and show little homoplasy.

Fifteen characters support Pachyneuridae as the sister group to Bibionidae (node 4: 24:1, 28:1, 56:3, 73:0, 108:1, 140:1, <u>142:1</u>, 148:1, 152:1, 165:0, <u>166:1</u>, <u>172:1</u>, 177:1, <u>181:1</u>, 205:1) including the following four unique larval characters: larva with sclerotized cuticular scales (<u>142:1</u>), anterolateral margin of frontoclypeus developed into a strong spine (<u>166:1</u> (Fig. 31a; asf)), presence of ventral prothoracic sclerites (<u>172:1</u> (Fig. 28b; vps), and membranous labial area completely enclosed (<u>181:1</u> (Fig. 30b; mla). Additionally, the presence of unaligned intersegmental fissures between the meso- and metathorax of the larva (148:1 (Fig. 28a)) support this clade and are observed in only one exemplar (*Trichocera*) outside of Bibionidae + Pachyneuridae. Similarly, character 152:1 (mesothorax with three pseudosegments (Fig. 28a-b)) supports this clade, but is also present in *Trichocera* and a switch from three pseudosegments to two pseudosegments occurs in the clade *Plecia* + Bibioninae.

SUBFAMILIES OF BIBIONIDAE

Only two of the three traditional subfamilies of Bibionidae were found to be monophyletic, thus agreeing with the four-subfamily classification and phylogenetic hypothesis of subfamilies proposed by Pinto & Amorim (2000)(Table 1). The subfamily Bibioninae is supported as a monophyletic group by 20 unambiguous characters (node 23: 4:1, 16:0, 27:0, 28:0, 30:0, 31:0, 33:1, 44:1, 53:0, 56:1, 58:1, 60:2, 62:0, 67:0, 69:1, 96:1, 104:0, 108:0, 183:0, 207:1). Character state 44:1, presence of coeloconical sensillae on the inner surface of the tibia (Fig. 8f; cs), are unknown outside this subfamily. The lack of these sensillae in one species of Bibioninae (*Dilophus febrilis*) is most parsimoniously interpreted as a reversal. Additionally, the character states fore femora swollen (33:1 (Fig. 8e; fem)), spiracle 8 of male present (69:1 (Fig. 16b; sp8)), and vein R with transverse striations (58:1 (Fig. 14c insert)) are found only in Bibioninae and some Scatopsidae; the results imply they are independently developed in the latter taxon. Despite numerous characters supporting the subfamily, relationships within Bibioninae are not well resolved; a result which is undoubtedly related to the paraphyly of *Bibio* and missing data points for the unknown larvae of three of the five genera. This result is in agreement with the analysis by Skartveit & Willassen (1996) which indicated that *Bibio* may be paraphyletic with respect to some of the smaller genera. In this analysis, *Dilophus* is sister group to the remainder of the subfamily (tribe Bibionini of Pinto & Amorim 2000) which includes the genera *Bibio*, *Bibiodes*, *Bibionellus*, and *Enicoscolus*. The latter four genera are supported by four adult characters (node 24: 14:0, 36:1, 113:2, 115:1), including the apex of the fore tibia developed into a strong spine (36:1 (Fig. 8e; tsp)), which also occurs in Aspistinae (Scatopsidae). The subfamily Hesperininae, containing only the genus *Hesperinus*, is monophyletic and supported by the characters listed below for this genus. In contrast, the subfamily Pleciinae (*Plecia* + *Penthetria*) is paraphyletic and *Plecia* is supported as the sister group to subfamily Bibioninae by six characters (node 7: 10:7, 137:1, 160:0, 164:1, 167:0, 168:1). Three of these are larval characters, including the unique position of the posterior spiracles on the anterior margin of segment nine (160:0 (Fig. 29a)). *Penthetria* is supported as the sister group to *Plecia* + Bibioninae by twelve unambiguous characters (node 6: 1:1, 3:1, 11:1, 14:1, 41:1, 42:1, 46:1, 141:1, 150:1, 153:1, 158:1, 209:0), including the unique presence of fleshy tubercles on the larva (141:1 (Figs. 27a-b, 28c)). The unaligned, intersegmental fissures between segments 7 and 8 of the larva (150:1) is found only in this clade and *Bolitophila* (Bolitophilidae). Some additional characters that show some homoplasy within the anaysis that support this clade are the holoptic eye (1:1 (Fig. 5a-b)), male eye subdivided (3:1 (Figs. 5a, 6e)), antennal flagellomeres compressed (11:1 (Figs. 5a-b, 6b, 6e-f)), and pupal abdomen without rows of spinules (209:0).

GENERA OF BIBIONIDAE

All bibionid genera are monophyletic except for the genus *Bibio*, which is not supported as a monophyletic group. Additionally, monophyly of the genus *Bibiodes* can't be assessed since only one exemplar was included and thus monophyly of the genus was not examined. The genus *Plecia* is supported by eight unambiguous characters (node 8: 93:1, 94:1, 95:0, 113:1, 116:1, 126:0, 140:0, 163:0). Of these the anteriorly expanded dorsal bridge of the male terminalia (116:1 (Fig. 23a; db)) is unique to the genus, and the ovoid egg (140:0 (Fig. 26e)) is indicated as a reversal to the plesiomorphic condition from the sausage-shaped egg of other Bibionidae + Pachyneuridae. *Penthetria* is supported by four characters (node 30: 89:0, 126:1, 152:2, 205:0). None of these characters are unique to *Penthetria*, though character state 152:2 (larval mesothorax with two pseudosegments) is also found only in *Trichocera* (Trichoceridae). Initial observations on the number and position of fleshy tubercles in bibionid larvae (character not included in this analysis) suggests that an additional synapormophy for *Penthetria* may be the presence of only two tubercles in the posterior row of each abdominal segment. The genus *Enicoscolus* is supported by two adult characters (node 26: 49:1, 57:0) including costalization of the adult wing (49:1), which also occurs in Scatopsidae. *Bibionellus* is supported by six unambiguous characters (node 25: 34:1, 35:1, 90:2, 91:1, 92:2, 93:1). In addition to being diagnostic for the genus *Bibionellus*, the fore tibia with a ventral tubercle (35:1 (Fig. 8e)) and the fore femur with a ventral tubercle (34:1 (Fig. 8e)) are the most consistent of these six characters; the former character is unique to the genus and the presence of the latter character in the scatopsid genus *Arthira* is indicated here as convergent. Eight unambiguous characters (node 27: 5:1, 10:4, 22:1, 24:0, 37:1, 40:1, 46:0, 79:0) support the genus *Dilophus* including three unique adult characters: dorsum of the thorax with two rows of transverse spines (22:1 (Fig. 6a; tts)), fore tibia with an apical circlet of spines (37:1 (Fig. 8d; acs)), and fore tibia with medial spines (40:1 (Fig. 8d; ms)). *Hesperinus* is supported by three unambiguous characters (node 32: 12:1, 55:1, 76:0), including the unique apical dorsal development of the antennal flagellomere (12:1 (Fig. 5f; adat)).

SPECIES-LEVEL RELATIONSHIPS

Species-level relationships within *Plecia* are only partially resolved, but this is not surprising considering the small number of exemplars that were included from this large genus. Of the twenty-four unambiguous characters supporting species-level relationships within *Plecia*, nineteen are from the male terminalia and the other five adult characters are the number of antennal flagellomeres, color of the dorsum and katepisternum of the thorax, and shape of the hind tibia and basitarsus (10, 17, 19, 42, 46, 71, 76, 77, 80, 82, 83, 84, 87, 91, 92, 95 96, 97, 99, 109, 110, 114 117,126). It is likely that the topology of species-level relationships within *Plecia* will continue to change with the addition of new species.

OUTGROUPS, BIBIONOMORPHA, & HIGHER CLASSIFICATION

Although this study did not emphasize resolving relationships outside of Bibionidae, some outgroup and higher-level relationships are well supported and are summarized here.

PACHYNEURIDAE

Pachyneuridae, including the genus *Pachyneura*, is supported as a monophyletic group by seven unambiguous characters (node 34: 30:0, 43:1, 136:1, 143:1, 164:1, 173:2, 187:1) including one adult and three larval characters unique to the family: rotation of male terminalia with abdominal twist (136:1), larval thoracic segments ventrally enlarged (143:1 (Figs. 27d, 28b)), larval anterior tentorial arm fused to inner surface of cranium (173:2 (Fig. 30a)), and larval cardo subdivided (187:1 (Fig. 34)). The placement of the genus *Pachyneura* has been controversial because its wing venation is more similar to Axymyiidae than to other pachyneurids. Because of the similarity of the structure of the radial sector, it has been placed by some authors (Amorim 1992) in Axymyiomorpha with Axymyiidae. However, the wing venation of *Pachyneura* can be interpreted alternative ways. Despite scoring the wing venation of *Pachyneura* as homologous to that in axymyiids, total character congruence places *Pachyneura* within Pachyneuridae; this result suggests that the alternative interpretation of wing veins is more appropriate for this genus and that the similarity of the radial sector in Axymyiidae and *Pachyneura* is not homologus. See discussion of "THE RADIAL FIELD" in the section "CHARACTER HOMOLOGY AND VARIATION."

The pachyneurid subfamily Cramptonomyiinae, is supported by twelve unambiguous characters (node 35: 31:0, 54:1, 55:1, 59:1, 64:1, 88:0, 89:0, 96:1, 112:1, 113:2, 121:1, 122:2) including the unique presence of a radial cell (54:1 (Fig. 12b; br)). Additionally, the shaft of the ejaculatory apodeme is bifurcate (121:1 (Fig. 25; ea(s))), which in this analysis is also found in *Ctenophora* (Tipulidae).

SCIAROIDEA

Sciaroidea is not supported as a monophyletic group (Fig. 2; node 36 + Ditomyiidae). Bolitophilidae + (Sciaridae + (Keroplatidae + Mycetophilidae) is supported by eight unambiguous characters (node 36: 45:1, 159:1, 188:1, 189:1, 191:1, 192:1, 193:1, 196:1), including the larval synapomorphies: loss of the posterior spiracle (159:1), galeolacinia evenly serrate (191:1 (Fig. 33c-d; gl)), galeolacinia with lobe supporting palpifer (192:1 (Fig. 33c-d; lgl), galeolacinia tapered to a point (193:1 (Fig. 33c-d; apgl)), and palpifer + palpus a flat, oval plate (196:1 (Fig. 33c-d; mpf, mp)). This clade is in an unresolved polytomy with Ditomyiidae despite the inclusion of most of the characters from previous analyses that purport to unite all these taxa (Wood & Borkent 1989, Matile 1990, Blaschke-Bethold 1994, Oosterbroek & Courtney 1995). Sciaridae + (Keroplatidae + Mycetophilidae) is supported by eight unambiguous characters (node 37: 24:0, 60:2, 68:1, 74:1, 104:2, 169:2, 208:1, 209:0), including the unique presence of a silk pupal cocoon spun by the last instar larva (208:1). Additionally, the sensory cone of the larval antenna is plate-like (169:2) and the pupae lack rows of spinules on the abdominal segments (209:0), but these character states are also found in Bibionidae (exclusive of *Hesperinus*). Seven adult characters support Keroplatidae + Mycetophilidae (node 38: 25:0, 26:0, 70:1, 71:0, 72:0, 75:1, 87:1), but all show at least some homoplasy in the analysis.

BIBIONOMORPHA *SENSU STRICTO*

Bibionidae + Pachyneuridae is supported as the sister group of Sciaroidea by five unambiguous characters (node 3: 25:1, 82:0, 131:2, 157:1, 182:1), including presence of a precoxal bridge (25:1 (Fig. 7a; pcb)), aedeagal plate not tubular (131:2 (Fig. 25; ada)), larval abdominal spiracles 1-7 present (157:1 (Fig. 27a-e)), and tubercle of labial palp absent (182:1 (Fig. 33a, 34-38; lp)). This clade, Sciaroidea + (Bibionidae + Pachyneuridae), agrees with the hypothesis of relationship of Bibionomorpha *sensu stricto* proposed by Blaschke-Bethold (1994), except that here Sciaroidea is not supported as monophyletic. Furthermore, it supports the restricted concept of Bibionomorpha hypothesized by Wood & Borkent (1989), which includes only Bibionidae, Pachyneuridae, and Sciaroidea, because a broader definition of Bibionomorpha (i.e. one node more inclusive) would have to include not only Anisopodidae and Scatopsidae (as Hennig 1973, Amorim 1992), but also Trichoceridae (node 2).

NEODIPTERA & THE SISTER GROUP OF BRACHYCERA

Michelsen (1996) proposed the clade Neodiptera which includes the Brachycera + Bibionomorpha *sensu lato* (Hennig 1973) based on four characters of the adult prothorax and cervix. Neodiptera is not supported as a monophyletic group here due to the presence of Trichoceridae within the Neodipteran clade. Although only one of Michelsen's characters was included in this study (presence/absence of a precervical sclerite; 23 (Fig. 7a; pc)) it is worth noting that this character was down-weighted to zero in a successive approximations weighting analysis (SAW) using the rescaled consistency index (see discussion of SAW analysis below). The clade Trichoceridae + (Anisopodidae + Scatopsidae) is supported by fourteen unambiguous characters (node 39: 71:0, 104:2, 120:0, 127:0, 137:1, <u>147:1</u>, 188:1, 189:1, 197:1, <u>198:1</u>, <u>200:1</u>, <u>201:1</u>, <u>203:1</u>, <u>207:3</u>), including six unique larval characters: anus ventral (<u>147:1</u>), mandible vertically oriented (<u>198:1</u>), mandible with a sub-basal thumb of teeth (<u>200:1</u>), mandible with a line of weakness between base and apex (<u>201:1</u>), mandibular comb present (<u>203:1</u>), and premandible serrated and on outer edge of torma (<u>207:3</u>).

The clade Trichoceridae + (Anisopodidae + Scatopsidae) is supported as the sister group of Bibionomorpha *sensu stricto* by four unambiguous characters (node 2; 15:0, 67:0, 105:1, 119:0), including the absence of the adult postgenal bridge (15:0 (Fig. 6c; pgb)), and the epiproct undivided (105:1). The aforementioned clade is supported as the sister group of Brachycera (represented in this analysis by *Dialysis dispar* (family Xylophagidae); Fig. 2) by eight unambiguous characters (node 1: 24:2, 53:1, 79:0, 100:1, 102:0, 104:1, 107:1, 114:0). The most consistent of these characters is the presence of the dorsal sclerite (107:1 (Figs. 18a, 21a, 23-25; ds)) and the ventrolateral apodeme of the parameres (114:0 (Figs. 18a, 21a, 23-25; vla)), both of which are secondarily lost in Scatopsidae. Additionally, the clade is here supported by the presence of normally developed cerci (100:1 (Fig. 16a; cer)), which are secondarily lost in Trichoceridae. Undoubtedly these latter clades warrant further testing by the addition of more nematoceran exemplars, such as Blephariceridae and Psychodidae.

AXYMYIIDAE

Not surprisingly, the enigmatic family Axymyiidae is strongly supported as a monophyletic group by twenty-seven unambiguous characters (node 44: 3:1, 4:1, 5:1, 9:1, 20:1, 38:0, 56:2, 62:0, 75:2, 78:1, 92:2, 94:1, 95:1, 112:1, 113:5, 116:0, 123:0, 138:1, 139:2, 146:0, 154:0, 160:3, 164:2, 169:3, 170:2, 178:1, 199:2). More interestingly, its placement as the sister group of Bibionomorpha or as the most basal member of Bibionomorpha (Oosterbroek & Courtney 1995) is not supported here. Similarly, previous hypotheses that Axymyiidae is allied with Pachyneuridae or the genus *Pachyneura* are not supported (Hennig 1973, Amorim 1992).

COMPARISON OF RESULTS TO PREVIOUS STUDIES OF BIBIONIDAE

PINTO & AMORIM (2000)

The revised subfamilial classification proposed by Pinto & Amorim (2000)(Table 1) is supported by the present analysis. The present analysis also supports all generic relationships proposed by Pinto & Amorim except those within their tribe Bibionini (*Bibio*, *Bibionellus*, *Enicoscolus*, and *Bibiodes*). In the present analysis generic relationships within this tribe are unresolved, but in their analysis they are fully resolved. These differences are likely due to several variables. Their analysis is based on ground-plan coding at the rank of genus which artificially constrains each genus to be monophyletic. Because of this, their analysis cannot address the problem of whether or not *Bibio* is paraphyletic with respect to some of the smaller genera as suggested by Skartveit & Willassen (1996). Additionally, their characters are either weighted or ordered because a re-analyses of their data using an exhaustive search and treating the characters as equally-weighted and unordered does not result in any trees with the topology that they present (Pinto & Amorim 2000, Fig. 49). However, a strict consensus of the 3 equal-length trees recovered in the re-analysis of their data is consistent with the strict consensus tree found in the present analysis (Fig. 2, node 24): relationships within Bibionini are unresolved.

SKARTVEIT & WILLASSEN (1996)

The present analysis corroborates the findings of Skartveit & Willasen (1996) that *Bibio* is not supported as a monophyletic group. Their study suggests that some of the smaller genera within tribe Bibionini may have arisen within *Bibio*, but that further study was required to resolve this. The present analysis has not resolved this issue, probably because it suffers from similar shortcomings to Skartveit & Willassen (1996): missing data points for the unknown larval stages of three of the four genera of Bibionini. Acquisition of these larval stages, or fresh adult material for molecular analysis, may be the key to resolving relationships within this tribe. However, since the genera *Bibiodes*, *Bibionellus*, and *Enicoscolus* are very uncommonly collected, acquiring additional specimens of these genera will be difficult.

BLASCHKE-BERTHOLD (1994)

The present study corroborates the hypothesis proposed by Blaschke-Berthold (1994) that Bibionidae is monophyletic and is the sister group of Pachyneuridae, yet here it is founded on a largely different set of supporting characters. This discrepancy in character support is likely due to the fact that Blaschke-Berthold did not examine Pachyneuridae, four of the eight bibionid genera, and larval or pupal stages. Furthermore, the tree was not generated using a computer-based parsimony analysis and characters were ground-plan coded at the family level. Blaschke-Berthold (1994) considered the number of antennal flagellomeres reduced to ten segments and the gonocoxites medially fused, as synapomorphies of Bibionidae. The present analysis supports the first character as a synapormorphy of bibionids, but did not include the second character since the gonocoxites are medially fused in all the taxa examined here except *Cramptonomyia*. Three characters were considered synapormorphies of Pachyneuridae + Bibionidae by Blaschke-Berthold: larval antennae reduced into a plate, labial palps reduced, and prementum lying between hypopharyngeal sclerites. This analysis does not support any of these characters as evidence for the monophyly of this clade. Larval antennae reduced into a plate occurs in Bibionidae (except *Hesperinus*), and most Sciaroidea (except Bolitophilidae and Ditomyiidae), but not in Pachyneuridae. In the present analysis, the plate-like antenna ambiguously supports Bibionidae excluding *Hesperinus*. The reduced labial palps are here regarded as a synapomorphy of Bibionomorpha *sensu stricto*. Lastly, the prementum lying between the hypopharyngeal sclerites is not unique to Bibionidae + Pachyneuridae, but is the structure of the labium observed in nearly all of the taxa examined.

SUCCESSIVE APPROXIMATIONS WEIGHTING (SAW)

Successive approximations weighting (SAW) using the rescaled consistency index has been advocated as a method for choosing among numerous equal-length trees (Farris 1969, 1989, Carpenter 1988). However, in the present analysis SAW does not yield a tree that is among the forty-three equal-length trees, but yields a single, fully resolved tree that is five steps longer. Because this tree does not represent the best explanation of the character data accumulated here it is not presented. However, the SAW tree is consistent with the tree in figure 3 (a single, randomly chosen tree from the forty-three equal-length trees) with the following exceptions: 1) Sciaroidea is paraphyletic. Ditomyiidae is sister group to the remainder of Sciaroidea (node 36) + (Bibionidae + Pachyneuridae). 2) Relationships within Bibionini (node 24) are resolved as follows: (*Bibio albipennis* + (*Bibio niggerrimus* + *Enicoscolus*)) + (*Bibiodes* + *Bibionellus*). This result indicates that *Bibio* is paraphyletic with respect to *Enicoscolus*. 3) Species-level relationships within *Plecia* are significantly rearranged, but nodes 14, 13, 20, and 21 are present.

CHARACTER HOMOLOGY AND VARIATION

In the following section adult, larval and pupal characters are treated individually and the variation and homology of structures are discussed. Additionally, character states that provide unambiguous support are identified in connection with the node/clade that each one supports. Although some characters provide no unambiguous support in this analysis, this result does not indicate that the character is not phylogenetically informative, but simply indicates that it cannot be unambiguously optimized on the present topology (Fig. 3). This ambiguous optimization may be resolved with the future addition of missing data points for specific terminals currently coded as "?," as well as the addition of more taxa to make patterns of character distribution within diverse clades more clear.

Any alphanumeric value observed in the data matrix which is not defined as indicating a character state in the following character list should be considered an inapplicable autapomorphy (see "CLADISTIC METHODS "for discussion of this issue).

HEAD

1) Dorsal development of the male eye (CI: 0.28, RI: 0.68)

    dichoptic (0)
    broadly holoptic (1)
    eyebridge (2)

The male holoptic eye is considered an adaptation for swarming and locating mates during flight (McAlpine & Monroe 1968, Downes 1969, Zeil 1983b). For bibionids this hypothesis is supported by the observation that in the genus *Penthetria*, which typically has holoptic males, males of the species *P. funebris* Lund are both dichoptic and flightless (Skartveit & Willassen 1996). A similar condition is true for the genus *Hesperinus* in which dichoptic males apparently do not form mating swarms

(Krivosheina 1997b). In contrast, males of Trichoceridae form mating swarms, but are dichoptic. Because the holoptic condition may be correlated with the swarming habit, the phylogenetic informativeness of this character remains questionable (e.g. Wiegmann *et al.* 1993; character 1).

It is unclear whether the narrow eye-bridge observed in some families such as Psychodidae, Sciaridae, Scatopsidae, Canthyloscelidae, and some Mycetophilidae is homologous to the broadly holoptic eye observed in families such as Bibionidae, some Anisopodidae, Axymyiidae, and many Brachycera. However, considering that the difference between an "eye-bridge" and a "holoptic eye" is primarily one of relative width, both these conditions have been treated as two states of the same character here; "dorsal development of the male eye." Here, the male eye is considered holoptic if the eyes broadly meet dorsomedially (Fig. 5b) or are dorsomedially proximal less than the width of the ocellar tubercle, whereas those coded as dichoptic have the eyes separated by the frons a distance greater than or equal to the width of the antennae (Fig. 5e). The eye-bridge is a narrow, transverse, band that is similar to the broadly holoptic eye (Fig. 5d; eb).

Wood and Borkent (1989; character 33) considered the eye-bridge a synapomorphy of Sciaridae + Cecidomyiidae and the eye-bridge in Scatopsoidea to be an independent development. Due to the lack of *a priori* evidence suggesting otherwise, the eye-bridge in Sciaridae, Ditomyiidae, *Mycetobia*, and Scatopsidae is coded as homologous here. However, the sporadic distribution of the eye bridge in the strict consensus tree of the present analysis suggests that the eye bridge of Sciaroidea and Scatopsidae and even between different members of Sciaroidea may not be homologous, but since so few Scatopsoidea and Sciaroidea are included here, the taxon sampling is insufficient to make a definitive statement. Additionally, because the plesiomorphic state of this character is not clear, it is also difficult to interpret whether or not the eye bridge is simply a modification of the holoptic eye. The fact that the eye bridge also occurs in females, but the broadly holoptic eye never occurs in females suggests that the eye bridge is not simply a modification correlated with the more dorsal placement of the antennae in these taxa, but an independent development. The broadly holoptic eye (Fig. 5b) provides unambiguous support for node 6 (Bibionidae exclusive of *Hesperinus*).

2) Dorsal development of the female eye (CI: 0.25, RI: 0.25)
dichoptic (0)
eye bridge (1)

For exemplars examined here, males with an eye-bridge (Fig. 5d; eb) always have associated females with an eye-bridge while males with holoptic or dichoptic eyes have associated females that are dichoptic. Considering that the male and female conditions are not directly correlated, the dorsal development of the male and female eye are treated as independent characters. An eye bridge in females was observed in Scatopsidae, *Mycetobia*, Sciaridae, and *Symmerus*.

This character provides no unambiguous support in this analysis.

3) Male compound eye (CI: 0.22, RI: 0.81)
undivided (0)
divided (Fig. 5a, 6e) (1)

Male bibionids (except *Hesperinus*) have the compound eye subdivided into a dorsal and ventral region (Figs. 5a, 6e); the dorsal region with facets slightly larger than those of the ventral region. Usually there is a distinct line demarcating this division, but in some species there is no distinct division and change in facet size appears gradual. The dividing line is expressed either as an indentation or a thin sclerotized band which is free of facets. Although the ventral partition of the eye is usually slightly smaller, males of some taxa such as *Dilophus transvestis* Hardy (1968: 464) have a greatly enlarged ventral region and a correspondingly reduced dorsal region.

Zeil (1983bc) found that the dorsal region in male bibionids is responsible for tracking small moving objects, such as females, during flight, while the ventral partition is responsible for general flight control; this is probably also the case for other dipterans with a divided eye (Downes 1969). Within nematoceran flies, males of Axymyiidae, Perissommatidae, and some Simuliidae and Cecidomyiidae also have a subdivided compound eye (Colless 1962, Gagné 1981). Furthermore, the subdivided compound eye is found in members of most lower-brachyceran families such as Scenopinidae and Bombyliidae (Yeates 1994; character 10), Rhagionidae (James & Turner 1981), Stratiomyiidae (James 1981a), and Therevidae (Gaimari and Irwin 2000; character 7).

Related to the division of the compound eye, Pinto and Amorim (2000; characters 13 and 16) discuss the character: dorsal part of the eye with ommatidia which are equal to the ventral part, or ommatidia of the dorsal part larger than those in the ventral part (Fig. 6e). Although Downes (1969) reports that a few simuliids and one blepharicerid have the dorsal partition of the eye with smaller ommatidia, these taxa seem to be exceptional and at least the simuliids are thought to have this condition because they mate on the ground rather than in flight. Considering that no species were observed that have a divided eye in which the dorsal part of the eye does not have larger ommatidia, it is difficult to justify the two characters as independent. Therefore, the character on ommatidia size is not included here.

Despite three reversals in three species of *Plecia*, division of the compound eye unambiguously supports node 6 (Bibiondidae exclusive of *Hesperinus*) and Axymyiidae (node 44).

4) Triangular area of compound eye of male (CI: 0.66, RI: 0.88)

absent (0)

present (1)

When "present," the anterior, inner margin of the compound eye has a small, sclerotized, shining, triangular area devoid of facets (Fig. 6a; "ta"). This area is the anterior origin of the dividing line in those species with the eye divided into a dorsal and ventral partition. Although this triangular area was not observed in exemplars which do not have a divided eye, it is absent in some exemplars with a divided eye. A similar area is illustrated in the eyes of some taxa not examined here such as some Simuliidae (Peterson 1981b; Figs. 4-6) and the xylophagid genus *Rachicerus* (James 1981b; Fig. 4). This triangular area is present only in subfamily Bibioninae and Axymyiidae and unambiguously supports both these clades (nodes 23 & 44).

5) Female compound eye (CI: 0.25, RI: 0.66)
    undivided (0)
    divided (1)

Considering that there is no correlation between males with divided eyes and associated females with divided eyes (e.g. *Plecia* and *Penthetria* have males with divided eyes and females with undivided eyes), I treated the male and female conditions as independent.

The ventral partition of the male compound eye has previously been considered functionally equivalent (Zeil 1983a) and at least structurally and physiologically similar to the "undivided eye of females" (Dietrich 1909, Maher Ali 1957, Burkhardt & de la Motte 1972, Altner & Burkhardt 1981). However, the female eye is indistinctly divided in numerous bibionids as well as distinctly divided in females of Axymyiidae. The "indistinct" division is a slight, indented line dividing the eye in the same position as it is found in many males, but it is not as obvious as the division observed in males (Fig. 6a). Therefore, the ventral partition of the male eye and the entire female eye are not interpreted here as morphological homologs; rather, the whole eye is considered homologous between the sexes.

The divided female eye unambiguously supports Axymyiidae (node 44) and the genus *Dilophus* (node 27), though divided female eyes are also present in *Enicoscolus*, some *Bibio*, and some *Penthetria*.

6) Ocelli (CI: 0.50, RI: 0.00)
absent (0)
present (1)

The dorsal ocelli of male bibionids are presumed to aid in flight control and may work in cooperation with the ventral partition of the compound eye in horizon detection (Wunderer *et al.* 1988, Seifert *et al.* 1988). Nearly all bibionids have three ocelli which are closely set in a triangular arrangement on a poor to well-developed posteromedial tubercle (Fig. 5a, 6a; oc). However, the monotypic subgenus *Plecia* (*Heteroplecia*) Hardy (1950a), from New Guinea, as well as several *Plecia* species from New Caledonia (Fitzgerald 2004), lack the ocelli (as well as the ocular tubercle)(Fig. 6b). Within Bibionomorpha *s.l.* most Cecidomyiidae and the mycetophilids *Hesperodes* Coquillett and *Syndocosia* Speiser also lack ocelli (Gagné 1981, Vockeroth 1981). Oosterbroek and Courtney (1995; character 63) considered the presence of ocelli to be part of the Dipteran ground plan. Although the cladogram is rooted with *Ctenophora*, which like all tipulids lack ocelli, the absence of ocelli in these *Plecia* species is an independent loss of this structure. This character provides no unambiguous support in this analysis.

7) Arrangement of ocelli (CI: 0.50, RI: 0.50)
equilateral triangle (0)
isosceles triangle (1)

In Bibionidae and most outgroup taxa the ocelli are arranged in an equilateral triangle; a single most anteromedian ocellus and two slightly more posterolateral ocelli which are all approximately equidistant from each other (Fig. 6a; oc). However, Sciaroidea, *Arthria*, *Trichocera*, and *Pachyneura* have the ocelli arranged in the shape of an isosceles triangle; with the two posterolateral ocelli more widely separated (Fig. 5d). In some cases, such as *Bolitophila*, the isosceles triangle is so flattened that the ocelli are in an almost transverse line. *Mycetophila* has been scored as a "?" since the anteromedian ocellus is absent.

This character provides no unambiguous support in this analysis.

8) Anteromedian ocellus (CI: 0.80, RI: 0.50)

subequal in size to posterolateral ocelli (0)
reduced in size (1)
absent (2)

Bibionidae have the anteromedian ocellus subequal in size to the posterolateral ocelli (Fig. 6a; oc). However Sciaridae, *Keroplatus*, and *Symmerus* have the anteromedian ocellus reduced in size (Fig. 5d; amo) and in *Mycetophila* it is absent. The absence of only the anteromedian ocellus is not considered homologous to the absence of all ocelli observed in *Ctenophora* and some *Plecia*; these taxa have been scored as inapplicable for both this character as well as the previous character.

This character provides no unambiguous support in this analysis.

9) Stemmatic bulla tubercle (CI: 0.50, RI: 0.50)

absent (0)
present (1)

The stemmatic bulla is a small tubercle near the hind margin of the compound eye of some Chironomidae and Simuliidae and is assumed to be a remnant of the larval eye (McAlpine 1981a). Wood (1981b) noted a similar "swelling" in axmyiids. Based on the structure and position of the stemmatic bulla in the former families, it is interpreted here as homologous to the structure in axymyiids and *Sylvicola cinctus*. The bulla in axymyiids is much more strongly developed and in some species the tubercle appears to terminate in a single shining, glassy covering; these "lateral ocelli" were noted in some Palearctic axymyiids by Mamaev (1968) and Krivosheina (2000; Figs. 2, 4). This character unambiguously supports Axymyiidae (node 44).

10) Number antennal flagellomeres of male (CI: 0.50, RI: 0.64)

16 (0)
15 (1)
14 (2)
13 (3)
11 (4)
10 (5)
9 (6)
8 (7)
7 (8)
6 (9)
5 (A)
2 (B)

Pinto and Amorim (2000) include two characters on the number of male flagellomeres (characters 5 and 6). Both characters are based on ground plan coding and together include only the character states 7, 9, 10, and 14. However, this misrepresents the actual variation in flagellomere number in bibionids which ranges from four to twelve (Hardy 1968:463, Skartveit 1997). The number of flagellomeres recorded for brachyceran exemplars is two (the postpedicel and stylus) despite the fact that the postpedicel may represent the fusion of many flagellomeres (Stuckenberg 1999, Grimaldi *et al.* 2003). Considering that the distal antennal flagellomeres of

Trichocera are very difficult to differentiate, this taxon is coded as having 16 flagellomeres following Alexander (1981b) and Dahl and Krzeminska (1997).

The presence of 10 antennal segments provides unambiguous support for Bibionidae (node 5) despite numerous subsequent changes in flagellomere number within the taxon. Similarly, state 7 unambiguously supports nodes 7 and 15, and state 4 unambiguously supports node 27.

11) Longitudinal development of antennal flagellomeres of male (excluding apical segment) (CI: 0.14, RI: 0.50)

filiform; longer than broad (0)
compressed; broader than long to about as broad as long (1)

With the exception of *Hesperinus*, which has elongate filiform flagellomeres (Fig. 5e-f), rounded and strongly compressed antennal flagellomeres are characteristic of Bibionidae (Figs. 5a-b, 6b, 6e-f). Considering that the degree of compression of the antennal flagellomeres is actually a continuous character, coding taxa using the character states "longer than broad" versus "broader than long to about as broad as long" is probably arbitrary and thus, the character should be viewed with caution. Strongly compressed flagellomeres are also found in Scatopsidae and Canthyloscelidae (Cook 1981a and Peterson and Cook 1981). Additionally, the antennae of Axymyiidae, Keroplatidae, *Mycetobia*, *Haruka*, and Brachycera are coded as compressed, regardless of the possibility that the compressed condition in some of these groups may be the result of independent events (Pinto & Amorim 2000). The foliaceous condition observed in *Keroplatus* and the pectinate condition in *Ctenophora* are not coded as individual character states because these developments are structurally independent of the longitudinal development of the antennal flagellomeres.

The presence of compressed flagellomeres provided unambiguous support for node 6 (Bibionidae exclusive of *Hesperinus*).

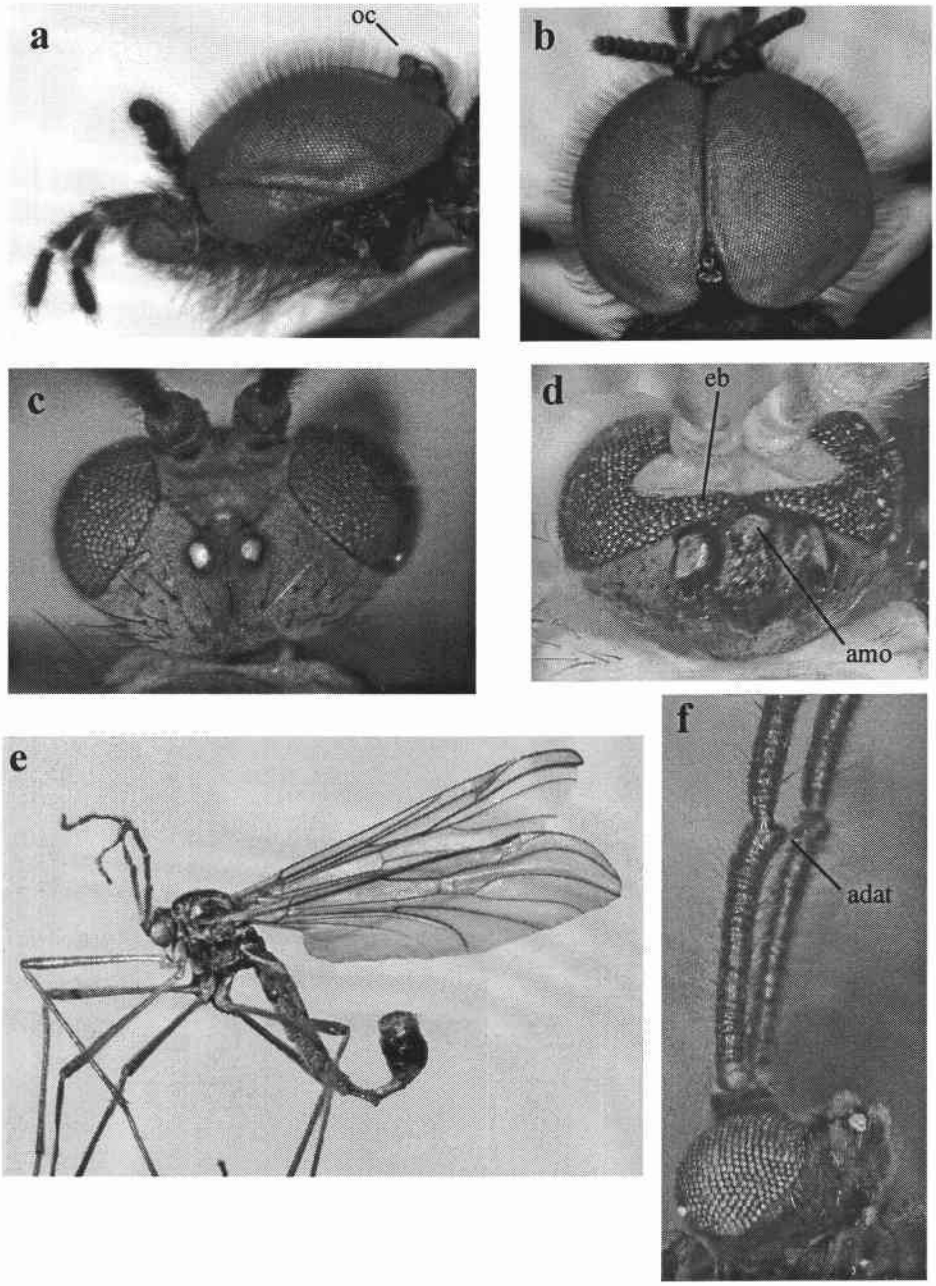


Figure 5. Adult head I. a-b, *Bibio niggerrimus* Duda (Bibionidae), male head. a, Lateral. b, Dorsal. c, *Cramptonomyia spenceri* Alexander (Pachyneuridae), male head, dorsal. d, *Symmerus coqulus* Garrett (Ditomyiidae), male head, dorsal. e, *Hesperinus brevifrons* Walker (Bibionidae), male habitus. f, *Hesperinus nigratus* Okada (Bibionidae), male head, lateral. Abbreviations: adat, apical dorsal antennal tubercle; amo, anteromedial ocellus; eb, eye bridge; oc, ocelli.

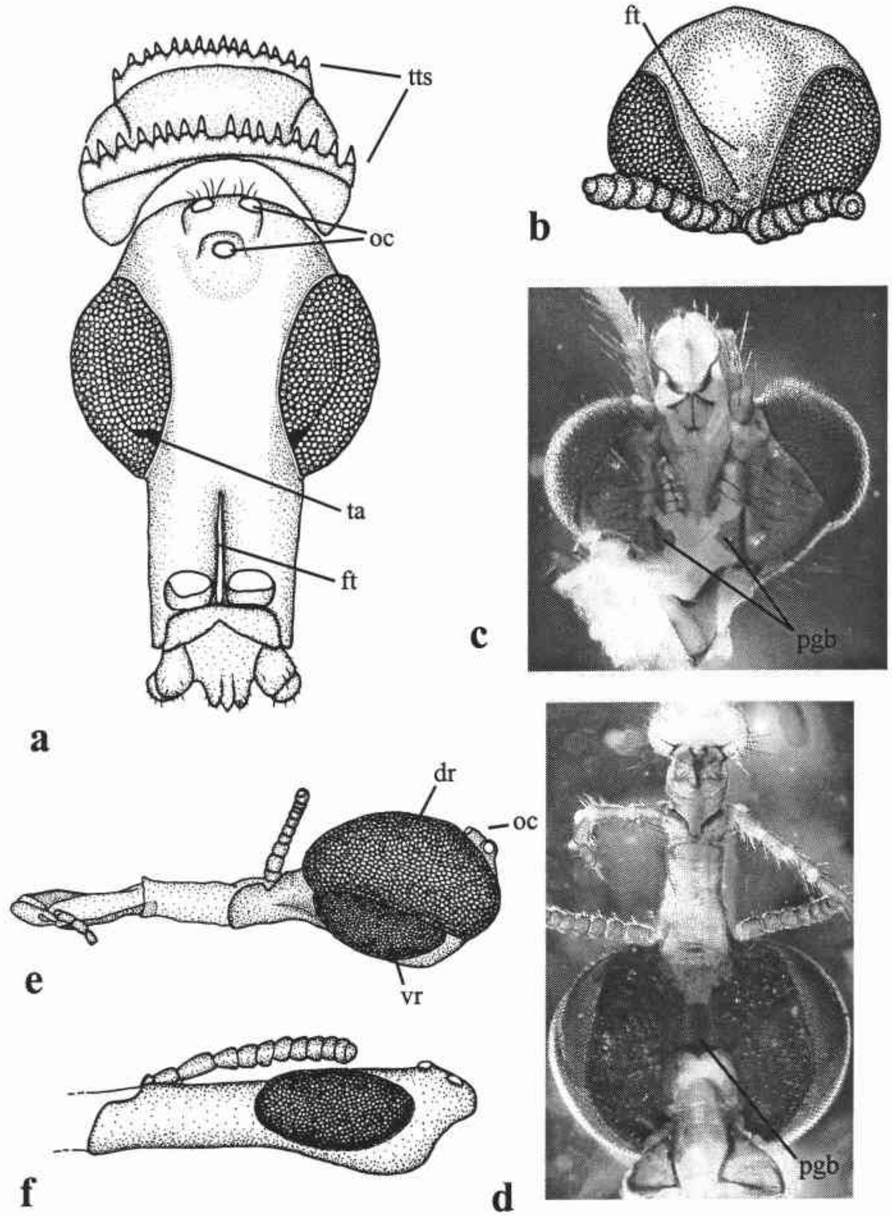


Figure 6, Adult head II. a, *Dilophus nigrostigma* Walker (Bibionidae), female head, dorsal. b, *Plecia lusca* Fitzgerald (Bibionidae), female head, dorsal. c, *Cramptonomyia spenceri* Alexander (Pachyneuridae), male head, ventral. d, *Plecia nearctica* Hardy (Bibionidae), male head, ventral. e-f, *Dilophus proxilus* Fitzgerald (Bibionidae), head. e, Male, lateral. f, Female, lateral. Abbreviations: dr, dorsal region of compound eye; ft, frontal tubercle; oc, ocelli; pgb, post genal bridge; ta, triangular area of compound eye; tts, transverse thoracic spines; vr, ventral region of compound eye.

12) Apical, dorsal surface of antennal flagellomeres of male (CI: 1.00, RI: 1.00)
    undeveloped (0)
    slightly produced (1)

Males of *Hesperinus* have the apical, dorsal surface of the antennal flagellomeres slightly developed giving antennae serrate appearance (Krivosheina 1997b). This apical, dorsal antennal tubercle (Fig. 5f; adat) is unique to the genus and provided unambiguous support for monophyly of the taxon (node 32).

13) Antennal length sexually dimorphic (CI: 0.25, RI: 0.25)
    male with much longer antennae (0)
    male and female antennae subequal (1)

This character takes into account the total length of the male flagellum relative to the length of the female flagellum (regardless of the number of flagellomeres in either). Vockeroth (1974) suggested that "the long male antennae may carry chemoreceptors which respond to a pheromone produced by the female," but "further observations are required to determine the reasons for the marked sexual dimorphism." Strongly, sexually dimorphic antennae are present in *Ctenophora*, *Cramptonomyia*, *Hesperinus*, and *Bolitophila*, in which females have antenna which are markedly shorter than in males even though the actual number of flagellomeres may be equal. Although some Bibioninae, *Plecia*, and *Penthetria* show sexual dimorphism in the number of antennal flagellomeres, it is typically the female which has extra segments (e.g. Hardy and Takahashi 1960) and the lengths of the male and female antennae are not markedly different.

Based on the strict consensus tree topology, sexual dimorphism in antennal length has arisen numerous times in unrelated groups and it did not unambiguously support any clade in this analysis.

14) Female head with frontal tubercle (CI: 0.12, RI: 0.61)
    absent (0)
    present (1)

The "frontal tubercle" is variable and may be a slightly swollen area, a distinct tubercle, or a longitudinal ridge which is located just posterior to the antennal sockets. Söli (1997) reported the presence of a frontal tubercle in Mycetophilidae *s.s.* Furthermore, the frontal tubercle (Fig. 6a-b; ft) is present in females of most exemplars of Bibionidae and Sciaroidea as well as some Anisopodidae.

Despite considerable homoplasy in this character, presence of a tubercle unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*), though the tubercle is secondarily lost in some Bibionini and unambiguously supports this clade (node 24).

15) Postgenal bridge (CI: 0.50, RI: 0.92)
    absent (0)
    present (1)

The postgenal bridge is the sclerotized ventral region of the head between the mouthparts and occipital foramen which is formed by fusion of the mesal margins of the postgenae (Peterson 1916). A membranous region is found ventromedially in those taxa without such a median fusion of the postgenae; in some taxa this membranous area was broad, while in others the mesal margins of the postgenae were adjacent, but not fused, leaving a narrow membranous region. A complete postgenal bridge was observed in Tipulidae, Bibionidae, and Xylophagidae (Fig. 6d; pgb). Taxa with the mesal margins adjacent, but not forming a complete bridge included Trichoceridae, Keroplatidae, *Arthria*, and Pachyneuridae (Fig. 6c; pgb).

The cladogram suggests the postgenal bridge of Bibionidae is an independent development than the bridge observed at the base of the tree in Tipulidae, Axymyiidae, and *Dialysis*. Absence of the postgenal bridge unambiguously supports node 2 (Bibionomorpha *sensu stricto* + (Trichoceridae + (Anisopodidae + Scatopsidae))). Likewise, the presence of an independently developed postgenal bridge supports Bibionidae (node 5).

THORAX

16) Vestiture of dorsum of thorax (CI: 0.12, RI: 0.66)
    not pruinose (0)
    pruinose (1)

Hardy (1945) uses this character (as "polished" versus "subopaque to gray dusted") to aid in diagnosing species of Neotropical *Plecia*. Several species of *Plecia* have most of the dorsum shining, but also have several thin, longitudinal, pruinose vittae. Although none of these taxa has been scored here, these pruinose stripes complicate the coding of this character and it is possible that the presence of stripes is best treated as a distinct character state.

Although this character shows considerable homoplasy, absence of pruinosity unambiguously supports Bibioninae (node 23).

17) Color of the dorsum of the thorax (male) (CI: 0.30, RI: 0.58)
    orange (0)
    brown to black (1)
    black anteriorly, orange posteriorly (2)

Hardy (1945) uses the color of the dorsum of the thorax and thoracic pleura to diagnose species of Bibionidae (in all genera except *Hesperinus*) and to help define species groups of *Plecia* (e.g. "entire dorsum rufous (bicolor group)" and "anterior portion of notum with a conspicuous black or dark brown area (collaris group)"). Although thoracic color seems to be rather consistent for many species of bibionids (pers. obs.), there are examples for which a single species may be black, orange, or bicolored such as *Plecia quadrivittata* Williston (Fitzgerald 1998a). Additionally, J. Skartveit (pers. comm.) observed that *Plecia ugandaensis* Hardy and *P. zernyi* Hardy may be either orange or black and that "this may be a rather variable character which is not useful for distinguishing species." Concerning the *Plecia decora* complex, Hardy (1968: 465) noted that "body coloration is apparently of no importance as a species group character." Considering that the variation of this color character is very poorly known it creates a problem with regard to scoring individuals; if only one color variation of a polymorphic taxon is examined, the data are misrepresentative of actual variability. Therefore, the color characters included here should be viewed with caution.

State 2 provides unambiguous support for node 17, but also occurs in other *Plecia* and *Penthetria*.

18) Color of the dorsum of thorax (female) (CI: 0.22, RI: 0.53)
orange (0)
brown to black (1)
black anteriorly, orange posteriorly (2)

Some female bibionids, particularly in the subfamily Bibioninae, have a differently colored thorax than that found in the corresponding male. Sexually dimorphic color of the thorax is absent in *Penthetria* and *Hesperinus*, but is at least represented by a few examples in *Plecia* (e.g. *P. rugosa* Hardy, *P. edwardsi* Hardy, and *P. rufimarginata* Hardy). Again, color variability is poorly documented and some species are known to be polymorphic with regard to thoracic color. However, the known polymorphic cases (see discussion of male thoracic color above) do not include any species which are sexually dimorphic for thoracic color, and examination of a series of specimens from a single collection of a known polymorphic taxon indicates that females are at least expressing the same polymorphic phenotype as the associated male.

This character provides no unambiguous support in this analysis.

19) Color of the male katepisternum (CI: 0.40, RI: 0.25)

entirely orange (0)
dorsally brown, ventrally orange (1)
brown to black (2)
dorsally yellow, ventrally brown (3)
dorsally brown, medially yellow, ventrally brown (4)

Some species of *Plecia* have an entirely orange thorax, while others have an orange dorsum and black pleura (e.g. Hardy 1945, 1982). Since the variability of the color of the thoracic pleura is unknown, this character should probably be interpreted with caution (as discussed for the previous character).

Character state 0 provides unambiguous support for node 18, though it also occurs in several other species of *Plecia* not included in this clade.

20) Dorsum of thorax with a pair of slightly depressed oval spots (CI: 1.00, RI: 1.00)

absent (0)
present (1)

Wood and Borkent (1989; character 25) considered the presence of these spots "apomorphic and unique to the Axymyiidae." These spots were observed in the two axymyiid exemplars here as well as *Axymyia japonica* Ishida. Additionally, Mamaev (1968) reported these structures in *Mesaxymyia stackelbergi* Mamaev. These oval spots have been illustrated by Wood (1981b; Fig. 1) and Krivosheina (2000; Fig. 5). Here the presence of these spots unambiguously supports Axymyiidae (node 44).

Figure 7, Adult thorax of Bibionidae. a-b, *Plecia nearctica* Hardy, thorax, lateral. c, *Bibio albipennis* Say, thorax lateral. d, *Plecia nearctica* Hardy, basisternum, ventral. e, *Bibio albipennis* Say, basisternum, ventral. Abbreviations: an, anterior notum; anepm, anepimeron; anepst, anepisternum; asp, anterior spiracle; bs, basisternum; bsl, basisternal lobe; cx1, coxa 1; cx2, coxa 2; cx3, coxa 3; dc, dorsocervical sclerites; dr, dorsal region of compound eye; epm, epimeron; eps, episternum; epsl, episternal lobe; kepst, katepisternum; lc, laterocervical sclerite; lt, laterotergite; mr, meron; mtkepst, metakatepisternum; nps, noto-pleural suture; pc, precervical sclerite; pcb, precoxal bridge; pgb, postgenal bridge; plrs, pleural suture; pn, posterior notum; pss, parapsidal sutures; tns, transnotal suture; vr, ventral region of compound eye.

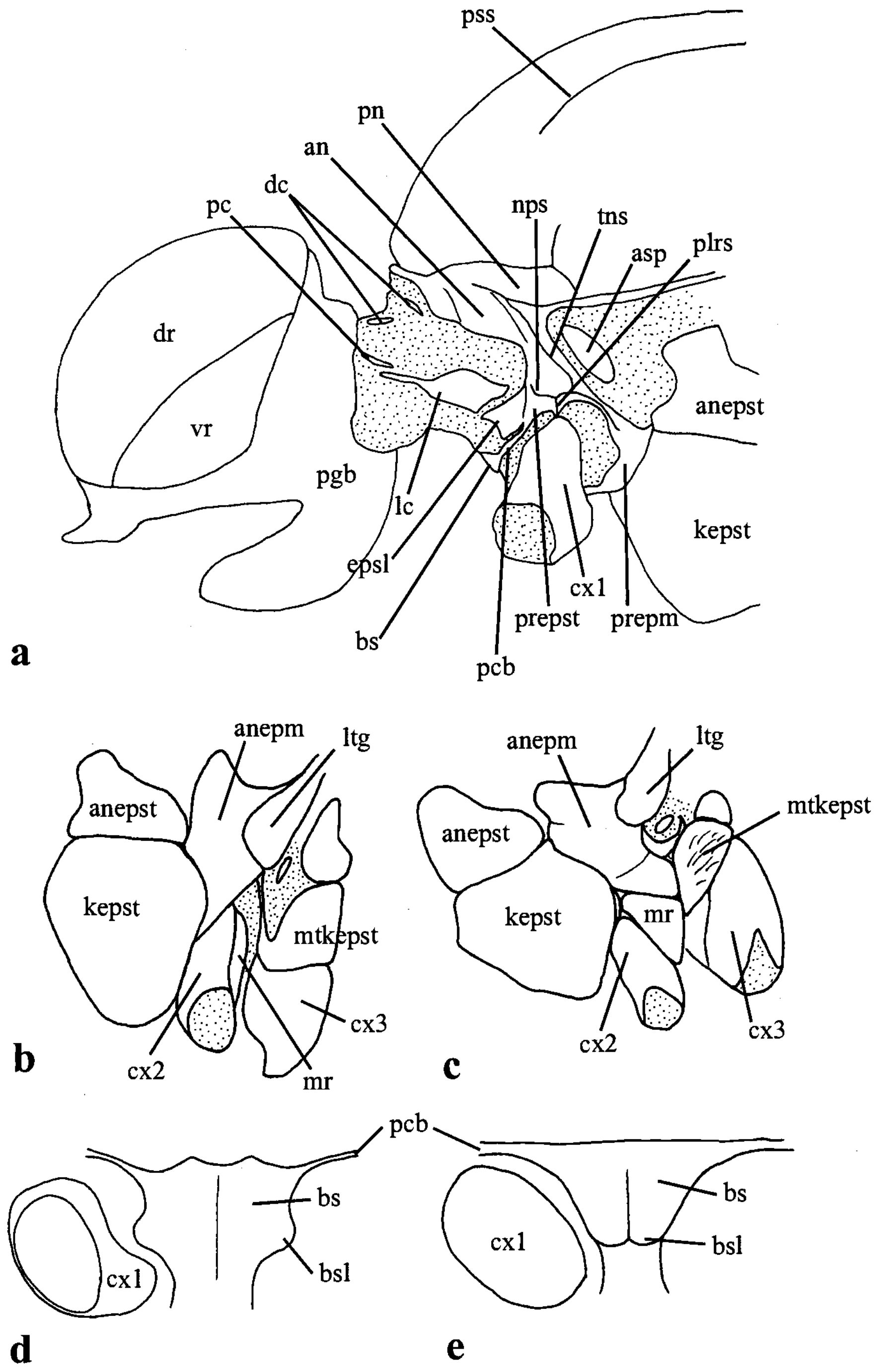


Figure 7, Adult thorax of Bibionidae.

21) Parapsidal sutures (CI: 1.00, RI: 1.00)

indistinct (0)
distinct (1)

Hardy and Takahashi (1960) use this character (as "mesonotal furrows") for distinguishing between species of *Plecia*. Although all bibionids have parapsidal sutures, in some species the sutures are present as distinct longitudinal grooves, while in others they are only vague longitudinal depressions. Distinct parapsidal sutures were observed here only in some *Plecia* (Fig. 7a; pss), though McAlpine (1981a) also reports that "strong" sutures are present in some Psychodidae.

The presence of distinct parapsidial sutures supports node 9 within *Plecia*.

22) Dorsum of thorax with two rows of transverse spines (CI: 1.00, RI: 1.00)

absent (0)
present (1)

The bibionid genus *Dilophus* has two transverse rows of anterodorsal thoracic spines (Fig. 6a; tts) which were not observed in any other taxon. The only other Bibionomorpha which have developments on the anterodorsal area of the thorax are Apistinae (Scatopsidae) which are characterized by an elevated U-shaped ridge rather than two rows of spines (Cook 1981a; Figs. 14-15). The condition observed in Apistinae is very different and is not considered homologous to the condition in *Dilophus*.

The presence of two rows of spines unambiguously supports monophyly of *Dilophus* (node 27)

23) Precervical sclerite (CI: 0.50, RI: 0.00)

absent (0)
present (1)

The terminology of the prothoracic and cervical sclerites follows Michelsen (1996). Michelsen (1996; character 1) suggested that the presence of a precervical sclerite, "a small, oblong sclerite attached by tough, flexible cuticle to the occipital condyle and a subapical area of the laterocervicale, respectively" (Fig. 7a; pc), is unique to Neodiptera. Unfortunately, this character is extremely difficult or impossible to examine in most pinned specimens, and removing heads from pinned specimens often destroys the area of interest. Thus, this character is scored only for those species which were represented by specimens in alcohol or pinned specimens which could be removed from the pin and softened in KOH. The precervical sclerite is absent in Tipulidae and Trichoceridae and the most parsimonious cladograms suggest that the absence of the precervical sclerite in Trichoceridae is an independent loss. This character provides no unambiguous support in this analysis.

24) Dorsocervical sclerite(s) (CI: 0.33, RI: 0.69)

one (0)
two (1)
absent (2)

When present, the dorsocervical sclerite(s) are found in the membranous laterodorsal part of the cervix. Dorsocervical sclerite(s) serve as the sclerotized attachment points for two muscles; the episterno (I)-dorsocervicalis (M1) and dorsocervico-laterocervicalis (M5) (Michelsen 1996). In addition to absence of the sclerite(s), two conditions of "presence" were observed. Firstly, the tipulid and axymyiids have a single, elongate, longitudinally oriented dorsocervical sclerite. Secondly, Pachyneuridae, Anisopodidae and Bibionidae (except *Dilophus*) have two smaller sclerites (Fig. 7a; dc). The more posterior of these two sclerites (posterior dorsocervical) is oblong, often transversely oriented, and sometimes hidden in a membranous fold under the anterior edge of the pronotum, while the more anterior sclerite (anterior dorsocervical) is often very close to the occipital foramen. Michelsen (1996) illustrated a single, elongate dorsocervical in *Axymyia furcata* McAtee and showed that it is the attachment point for muscles M1 and M5. Likewise, he showed that the paired dorsocervicals in *Sylvicola fuscatus* Fabricius are also the attachment point for both muscles; M1 attached to the anterior sclerite and M5 attached to the posterior sclerite. Considering the musculature, the single and paired dorsocervicals are interpreted as two states of the same character; since the difference between the two is possibly the result of a division of the single or a fusion of the paired sclerite(s). However, there is a possibility that the first character state (only a single sclerite) confounds two non-homologous conditions: a single elongate sclerite as well as the condition in which two smaller sclerites were present and one has been subsequently lost. For example, the bibionid genus *Dilophus* has only one dorsocervical sclerite, but it is small and located near the occipital foramen; it seems more likely that this is homologous to the more anterior of the two dorsocervicals seen in other bibionids (rather than the single elongate dorsocervical observed in axymyiids) and that the posterior dorsocervical has been lost. There is a similar questionable condition (a single sclerite, but considerably reduced in size compared to the tipulid and axymyiids) in some Sciaroidea and Xylophagidae as well as the scatopsid genus *Arthria*. Since the homology of the single dorsocervical sclerite is unclear (even musculature does not help because M5 is lacking in Bibionoidea and Sciaroidea (Michelsen 1996)), all those taxa with only a single sclerite have been coded as such. Despite the possibility that coding it this way may be confounding two conditions, at the present time it is impossible to recognize that these two conditions do in fact exist.

The presence of two dorsocervical sclerites unambiguously supports the clades Bibionidae + Pachyneuridae (node 4) and Anisopodidae (node 41). The presence of a single dorsocervical provides unambiguous support for *Dilophus* (node 27) and node 37 (part of Sciaroidea) and suggests that the presence of only a single small sclerite in *Dilophus* (previously discussed) is not homologous to the single large sclerite observed in Tipulidae and Axymyiidae or the single small sclerite of some Sciaroidea and *Arthria*. The absence of dorsocervicals unambiguously supports node 1, even though most of the taxa in this clade do not lack dorsocervicals. A less parsimonious, alternative explanation is that one large dorsocervical is plesiomorphic and a dorsocervical that is subdivided into two smaller sclerites is derived. The subsequent loss of one of these two smaller sclerites (as in *Dilophus*) represents another derived condition. This transition series suggests that the absence of dorsocervicals did not occur once at node 1 with new gains of dorsocervicals in Bibionidae + Pachyneuridae, Anisopodidae, some Sciaroidea, and some Scatopsoidea, but rather that the dorsocervicals have been independently lost in *Dialysis*, *Trichocera*, some Scatopsidae and some Sciaroidea. This would also explain the presence of one or two dorsocervicals in some Sciaroidea and Scatopsoidea.

25) Precoxal bridge (CI: 0.33, RI: 0.80)
absent (0)
present (1)

The precoxal bridge is a sclerotized fusion between part of the anterior margin of the proepisternum and the anterolateral margin of the basisternum forming a complete socket over the fore coxa (Fig. 7a; pcb). The bridge is absent in Tipulidae, Trichoceridae, Axymyiidae, Scatopsidae, Anisopodidae (except *Mycetobia*), *Mycetophila*, *Keroplatus*, and Xylophagidae, and present in the remainder of exemplars.

The presence of a precoxal bridge supports Sciaroidea + (Bibionidae + Pachyneuridae) (node 3), though it is secondarily lost in Keropolatidae and Mycetophilidae and unambiguously supports this clade (node 38).

26) Presternum (CI: 0.20, RI: 0.63)
absent (0)
present (1)

The presternum is a small sclerite located in the membrane anteromedial to the basisternum. The presternum is absent in Bibionidae (Fig. 7d-e), Scatopsidae, Ditomyiidae, Keroplatidae, Mycetophilidae, and *Ctenophora* and present in the remaining taxa. In Bolitophilidae the presternum is fused with the basisternum, but is still distinct as a small darker rectangular area; therefore, it is coded as present in this taxon. Although not present in *Ctenophora*, it apparently does occur in some tipulids (McAlpine 1981a; Fig. 2.64).

Absence of a presternum unambiguously supports Bibionidae (node 5), Keroplatidae + Mycetophilidae (node 38), and Scatopsidae (node 43).

27) Lobes of basisternum (CI: 0.14, RI: 0.73)

posterior (0)
lateral (1)

In the exemplars examined here, the posterior margin of the basisternum has two basic forms. In some taxa the basisternal lobe is at the extreme posterior end between the fore coxa (Fig. 7e; bsl), while in other taxa the lobes are in a more lateral position along the posterior margin of the basisternum (where they interact with a shallow emargination on the inner margin of the fore coxa)(Fig. 7d; bsl). Both states exist within Bibionidae.

This character has a rather sporadic distribution on the tree, but the presence of the lobes in the posterior position unambiguously supports Bibioninae (node 23).

28) Meron (CI: 0.40, RI: 0.85)

posterodorsally adjacent to surrounding sclerites (0)
posterodorsally surrounded by a membranous area (1)
absent (2)

Amorim *et al.* (1996) considered the structure of the meron in Bibionomorpha to be among the most primitive of Diptera due to the fusion of the sclerite to coxa II and its separation from the epimeron by a membranous area. Because of this and other characters, they tentatively suggest that Bibionomorpha may be the sister group to the remainder of the Diptera. In the present analysis, the character is focused on whether or not the meron fits tightly with the surrounding sclerites (Fig. 7c; mr) or is separated from surrounding sclerites by a posterodorsal membranous area (Fig. 7b; mr), but does not emphasize whether or not the meron is fused to coxa II.

The presence of a membranous area unambiguously supports Bibionidae + Pachyneuridae (node 4), though Bibioninae have a meron tightly fitting with surrounding sclerites which unambiguously supports this clade (node 23). The membranous area also occurs in Anisopodidae and Sciaridae and unambiguously supports Ansisopodidae (node 41).

29) Posterior margin of meron (CI: 0.33, RI: 0.55)
    not emarginate (0)
    medially emarginate (1)
    meron absent (2)

Many Bibionomorpha have the size of the meron reduced and its posterodorsal margin is surrounded by a membranous area (Fig. 7b; mr)(see previous character). Additionally, the posterior margin of the meron of some taxa has a distinct median or dorsomedian emargination (Crampton 1925, Figs. 26, 29). Both character states exist within Bibionidae. The meron is absent in *Mycetophila*.

This character provides no unambiguous support in this analysis.

30) Proepisternum (CI: 0.25, RI: 0.80)
    developed (0)
    greatly reduced (1)

The size of the proepisternum is reduced in Bibionidae except the subfamily Bibioninae. Such a reduction in size is quantified by whether or not the notopleural suture meets the transnontal suture below the ventral margin of the anterior spiracle (Fig. 7a; prepst) or meets it even with or dorsal to the dorsal margin of the anterior spiracle.

The strict consensus indicates that the reduced proepisternum is plesiomorphic with the well developed proepisternum independently developed and unambiguously supporting Bibioninae (node 23) and Pachyneuridae (node 34). A well developed proepisternum also occurs in Sciaridae and *Arthria*.

31) Membranous region between mediotergite and scutellum (CI: 0.18, RI: 0.60)
absent (0)
large (1)
a narrow strap (2)

In numerous species there is an elongate transverse membranous area between the posterior margin of the scutellum and the anterior margin of the mediotergite (the "aire sous-scutellaire" of Matile 1990; Fig. 20). This membranous area is sometimes absent (when the mediotergite and scutellum are abutted), present as a very narrow strip, or developed as a large crescent-shaped region.

There is considerable homoplasy in the distribution of this character. However, the presence of a large membranous area unambiguously supports Bibionidae (node 5) with reversal to both other conditions in Bibioninae. The loss of the membranous region unambiguously supports Cramptonomyiinae (node 35).

32) Laterotergite and katepisternum (CI: 1.00, RI: 1.00)
broadly separated by anepimeron (0)
touching or separated by only a very narrow strip of anepimeron (1)

Shaw (1948) and Shaw and Shaw (1951) noted that members of Mycetophilidae *sensu lato* have the laterotergite and katepisternum either touching or only narrowly separated due to a reduction in the size of the anepimeron (Shaw 1948, Figs. 1-7). *Keroplatus*, *Symmerus*, *Mycetophila*, *Bolitophila*, and Sciaridae have the laterotergite and katepisternum touching or narrowly separated by a thin strip of anepimeron (strip approximately less than half the width of the coxa). In all other examined taxa these sclerites are not touching or adjacent, but are broadly separated by the anepimeron (Fig. 7b-c).

Despite the presence of character state 1 only in Sciaroidea, this taxon is not supported here as a monophyletic group.

LEGS

33) Fore femur (CI: 0.50, RI: 0.90)

simple (0)
swollen (1)

Bibioninae and Aspistinae (Scatopsidae) have fore femora that are strongly swollen (Fig. 8e; fem). This may be related to the digging behavior of the males and females of some these taxa (see discussion of character 36; fore tibial spine).

The swollen femur unambiguously supports Bibioninae (node 23) and indicates that the swollen femur of *Arthria* is an independent development.

34) Fore femur with a ventral subapical tubercle (CI: 0.50, RI: 0.50)

absent (0)
present (1)

The ventral surface of the fore femur of the bibionid genus *Bibionellus* has a subapical tubercle covered with small denticles (Fig. 8e). This tubercle corresponds to a ventral, median tubercle on the fore tibia (Fig. 8e) and both tubercles are considered synapomorphic for the genus (Pinto & Amorim 1997; characters 4 and 5). Although slightly different in structure (lacking denticles, but with strong spine-like setae), the scatopsid genus *Arthria* also has a ventral tubercle on the fore femur, but lacks a corresponding tibial tubercle. Because there is no *a priori* evidence suggesting that the femoral tubercles arose independently, they are scored as homologous. Furthermore, considering the presence of corresponding tubercles in *Bibionellus* and only a single tubercle in *Arthria*, the femoral and tibial tubercles are considered independent and scored separately.

The presence of a ventral subapical tubercle on the fore femur and a median ventral tubercle on the fore tibia unambiguously support monophyly of the genus *Bibionellus* (25). The strict consensus topology indicates that the femoral tubercle in *Arthria* is an independent development.

35) Fore tibia with a ventral, median tubercle (CI: 1.00, RI: 1.00)

absent (0)
present (1)

See discussion of previous character.

36) Apex of fore tibia with dorsoapical edge developed into a strong spine (CI: 0.50, RI: 0.85)

absent (0)
present (1)

The bibionid genera *Bibio*, *Bibionellus*, *Bibiodes*, and *Enicoscolus* have the dorsoapical edge of the fore tibia elongated into a strong spine (Fig. 8a-c, e; tsp)(the "tibial mucron" of Pinto and Amorim 1996 and 2000; character 58). Girault (1905), observed females of *Bibio* using this spine for digging an egg laying chamber in the soil and both sexes dig with the fore tibia when emerging from the subterranean pupal chamber (pers. obs.). The scatopsid subfamily Aspistinae have a similar dorsoapical spine and "the subfamily is interesting because the leg structure with its spines is very suggestive of the family Bibionidae" (Freeman and Lane 1985). Amorim (1982: 48) explained the tibial spine in these two families as a parallelism. Although it may be a parallelism, considering the similar morphology and position of the spine, the structure is coded as homologous in the two taxa (thus avoideding an *a priori* determination of parallelism). Worthy of note is a fossil specimen of Elliidae (*Ellia colorissima* Krzeminska *et al.*) which Krzeminska *et al.* (1993) placed in the Axymyiomorpha based on its wing venation. A single foreleg of this species is preserved well enough for Krzeminska *et al.* (1993: 583, Fig. 2b) to observe an elongate apical spine on the fore tibia and an enlarged fore femora strikingly similar to the leg structure in some bibionids and scatopsids. All aforementioned taxa which have a dorsoapical spine on the fore tibia also have an enlarged fore femur. Without great imagination one might conclude that the characters "dorsoapical spine present" and "fore femora enlarged" are not independent; an enlarged and strongly musculated femur corresponding to the fossorial fore tibia. However, members of the bibionid genus *Dilophus* have an enlarged fore femur, but have an apical circlet of small spines (Fig. 8d; acs)(apparently derived from setae) that are not structurally homologous to the dorsoapical spine (an extension of the dorsal, apical edge of the tibia) even though functionally they serve the same purpose; Morris (1921) and Thornhill (1976b) observed females of several species of *Dilophus* digging with the fore tibia . It is possible that a digging behavior is directly correlated with the enlarged fore femora regardless of the fact that the apical development of the tibia in *Dilophus* and the remainder of Bibioninae is not homologous. Unfortunately, this behavioral character is unknown for other taxa with modified forelegs such as *Bibionellus* and *Enicoscolus* (Bibionidae) and Aspistinae (Scatopsidae). Further complicating the matter are the species of Canthyloscelidae (Scatopsoidea) which have a strongly swollen fore femur and no apical modification of the fore tibia. There are no observations of digging in the latter family, and the larvae are found in rotten wood rather than soil (Haenni 1997a). Pinto and Amorim (1996) considered the behavioral character "female digs cells on soil with apices of anterior tibia, where the eggs are placed" (character 1) to be autapomorphic for Bibioninae and noted that "the observations made in laboratory on two different species showed that *Plecia* does not present such behavior." A more complete understanding of the distribution of this behavioral character would be welcomed, but the character is not included here because its distribution is unknown for most of the included exemplars.

The strict consensus topology indicates that the fore tibial spine is an independent development in *Arthria* and Bibionini; the latter taxon is unambiguously supported by this character (node 24).

37) Apex of fore tibia with a circlet of strong spines (CI: 1.00, RI: 1.00)

absent (0)
present (1)

The presence of a circlet of articulated spines at the apex of the fore tibia (Fig. 8d; acs) is unique to *Dilophus* and, as with the unarticulated apical spine in other Bibioninae, they apparently aid the female in digging (Morris 1921, Thornhill 1976b). Pinto and Amorim (1996: 319) considered these spines to be "derivative of apical setae" which is a reasonable assumption; unlike the dorsoapical spine of other Bibioninae, they are not contiguous with the tibia, but are differentiated from the tibia and appear to arise from a socket.

The presence of an apical circlet of spines unambiguously supports *Dilophus* as a monophyletic group (node 27).

38) Number of fore tibial spur(s) (CI: 0.66, RI: 0.66)

absent (0)
one (1)
two (2)

Tibial spurs arise from the membrane between the tibia and first tarsomere. Most of the exemplar taxa, including Bibionidae, have a single fore tibial spur (Fig. 8a-c, e; tsr). Fore tibial spurs are absent from exemplar Scatopsidae and Axymyiidae, and are apparently absent from Cecidomyiidae (Wood & Borkent 1989; character 35), some Canthyloscelidae (Amorim 2000; character 13), some Lygistorrhinidae (Grimaldi & Blagoderov 2001), as well as some Orthorrhaphous Brachycera such as Pantophthalmidae, Stratiomyidae, and Xylomyidae (Woodley 1989; character 11). A pair of fore tibial spurs was observed here only in *Dialysis*. Regarding the loss of tibial spurs in Brachycera, Griffiths (1994) notes that "clearly caution is needed in interpreting absence of tibial spurs as a synapomorphy in view of the existence of independent reduction sequences."

The independent losses of fore tibial spines in Scatopsidae and Axymyiidae unambiguously support these clades (nodes 43 and 44).

39) Tibial organ (inner surface of fore tibia) (CI: 0.25, RI: 0.25)
absent (0)
present (1)

The "tibial organ" discussed here is not homologous to the "tibial organ" reported in the hind leg of some Chloropidae (McAlpine 1981a), but is homologous to the "anteroapical depressed area" (Vockeroth 1981), "patch of modified setae anteroapically" (Steffan 1981), and "tibialorgan" (Blaschke-Berthold 1994; character 33) on the ventral apex of the fore tibia of some Bibionomorpha. The structure of the tibial organ can be differentiated into two basic types; a single transverse row of setae (Fig. 9c-d; to), or numerous overlapping rows of setae set in an oval or triangular depression; the "comb" and "brush" respectively of Tuomikoski (1966b)(e.g. Steffan 1981; Figs. 24-29, Matile 1990; Figs. 1099-1103, Blaschke-Berthold 1994; Figs. 252-268, Söli 1997; Figs. 20A-E). An additional character state, which was not observed here, is the depressed area "extending up to five-sevenths length of tibia" (Söli *et al.*

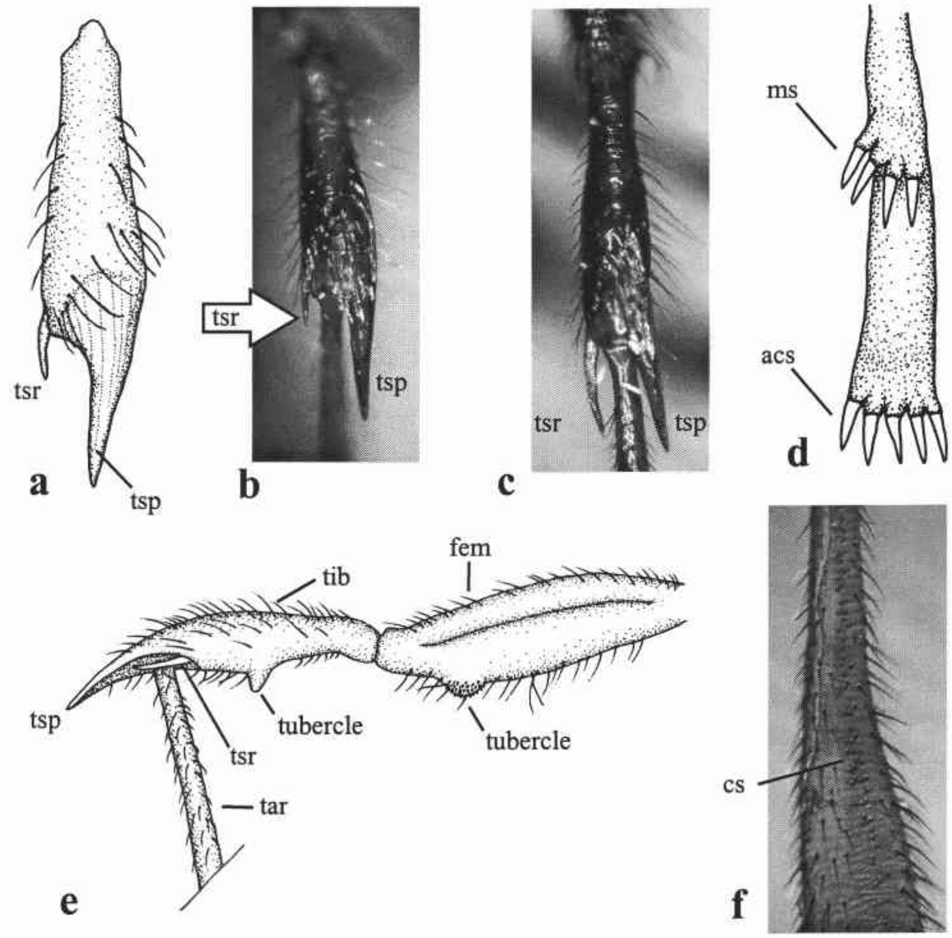


Figure 8, Legs I (Bibionidae). a, *Bibio illaudatus* Hardy, fore tibia, male. b, *Bibio xanthopus* Wied. fore tibia. c, *Bibio vestitus* Walker, fore tibia. d, *Dilophus proxilus* Fitzgerald, fore tibia, male. e, *Bibionellus* sp., fore leg, male. f, *Bibio brunnipes* (Fab.), hind tibia, inner surface, male. Abbreviations: acs, apical circlet of spines; cs, coeloconical sensillae; fem, femur; ms, medial spines; tar, tarsus; tib, tibia; tsp, tibial spine; tsr, tibial spur.

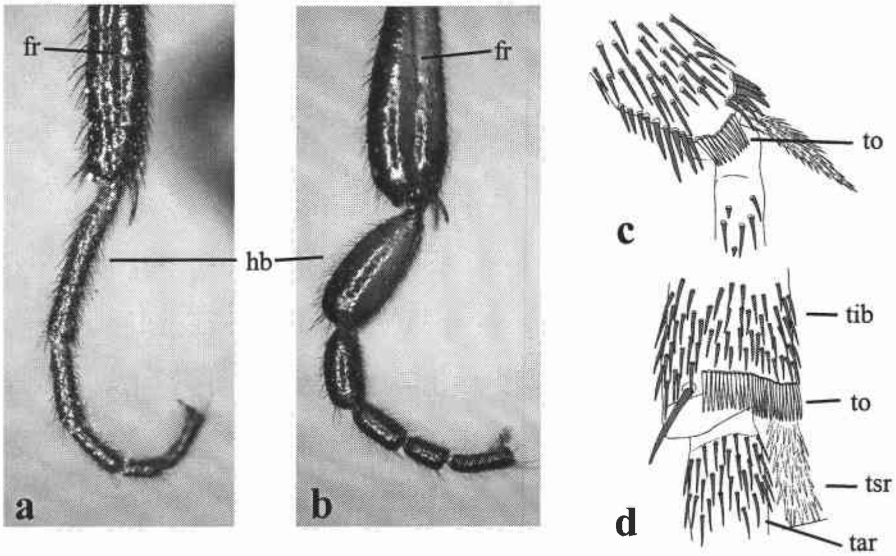


Figure 9, Legs II. a, *Bibio vestitus* Walker (Bibionidae), hind tibia/tarsi, male. b, *Bibio flukei* Hardy (Bibionidae), hind tibia/tarsi, male. c, *Sylvicola cinctus* (Fab.) (Anisopodidae), inner surface of fore tibia, male. d, *Symmerus coqulus* Garrett (Ditomyiidae), inner surface of fore tibia, male. Abbreviations: hb, hind basitarsus; fr, furrow; tar, tarsus; tib, tibia; to, tibial organ; tsr, tibial spur.

2000). Tuomikoski (1966b) suggested that the tibial organ "is probably used by the insect for cleaning the antennae and palpi" and it has since been shown to be associated with an underlying glandular plate (Blaschke-Berthold 1994, Figs. 269-271). Blaschke-Berthold (1994) considered the tibial organ a synapomorphy of the Mycetophilidae *s.l.* and Sciaridae because the structure was unknown outside this group, thus echoing Tuomikoski (1966b), who suggested that its presence in most Mycetophiloidea is "one of the best proofs of the monophyletic nature of the superfamily." However, Blaschke-Berthold (1994: character 45) notes that most Ditomyiidae do not have a tibial organ; she considers its absence in this group a secondary loss which is synapomorphic for the family. I observed a tibial organ in *Symmerus* (Ditomyiidae), Bolitophilidae, and *Sylvicola* (Anisopodidae). The tibial organ was absent in all other exemplar species including Keroplatidae and Sciaridae despite the fact that the structure occurs in numerous species of the latter families (Matile 1990, Steffan 1981, Freeman 1983, Menzel and Mohrig 1999). In *Symmerus*, *Bolitophila*, and *Sylvicola* the tibial organ lacked a depressed area, and was present as a simple subapical comb (Fig. 9c-d; to); Thompson (1975b; character 4) considers this condition to be the "primitive condition for all Mycetophiloidea." Only *Mycetophila favonica* had a tibial organ with a distinct depressed area.

The presence of a tibial organ did not support monophyly of any clade of Sciaroidea in this analysis, though this is possibly due to the limited taxon sampling from this diverse assemblage of flies.

40) Medial fore tibial spines (CI: 1.00, RI: 1.00)
absent (0)
present (1)

The fore tibia of the bibionid genus *Dilophus* has one or two sets of preapical dorsal spines which are identical in structure to those on the apex of the fore tibia (Fig. 8d; ms). It is likely that these spines aid in the digging behavior observed in this genus (see discussion of character: apex of fore tibia developed into a strong spine). These spines are unique to *Dilophus* and unambiguously support the genus as a monophyletic group (node 27).

41) Hind femur of male (CI: 0.16, RI: 0.73)
not clavate (0)
clavate (1)

Some Bibionidae have a median longitudinal furrow on the hind femur and/or tibia (Fig. 9a-b; fr); the "clavate" condition. Considering the variability of this character within bibionid genera it may not aid in resolving generic relationships, but it may have value at the level below genus.

Presence of a clavate femur unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*), though most of the species of *Plecia* examined do not have the clavate condition and this loss unambiguously supports node 10 within *Plecia*.

42) Hind tibia of male (CI: 0.12, RI: 0.66)
not clavate (0)
clavate (1)

See discussion of previous character. The clavate tibia unambiguously supports nodes 6 (Bibionidae exclusive of *Hesperinus*) and node 61 (within *Plecia*), though most of the species of *Plecia* examined do not have the clavate condition and this loss unambiguously supports node 10 within *Plecia*.

43) Hind tibia with two rows of dorsal setae (CI: 0.33, RI: 0.50)
absent (0)
present (1)

Although legs of Bibionidae lack macrosetae, many Sciaroidea and all Pachyneuridae have rows of macrosetae on various surfaces of the legs. The hind tibia of Pachyneuridae, Ditomyiidae, and *Mycetophila* have variously arranged setae including two rows of dorsal setae (Vockeroth 1981; Fig. 1); one anterodorsal and the second posterodorsal. The setae of the two rows are rather widely and evenly spaced and a particular seta may be paired with or somewhat offset from the seta of the adjacent row. Bolitophilidae has a single dorsal row of very closely spaced setae which is not considered homologous.

Although the analysis indicates that the rows of setae are not homologs in all these taxa, the presence of these setae in Pachyneuridae unambiguously supports this clade (node 34).

44) Inner surface of male hind tibia with coeloconical sensillae (CI: 0.50, RI: 0.85)
absent (0)
present (1)

Male (and most female) Bibioninae have a field of a few to several hundred coeloconical sensilla on the inner (or ventral) surface of the hind tibia (Fig. 8f; cs)(Skartveit 1997). The small, black, round sensilla are most easily observed if the tibia is illuminated from behind. The function of these sensillae is unknown, but this sensory region appears to be unique to the subfamily and unambiguously supports it as a monophyletic group (node 23).

45) Inner apex of hind tibia with an apical comb of setae (CI: 0.50, RI: 0.87)
absent (0)
present (1)

The apical comb of setae on the inner (or ventral) surface of the hind tibia occurs as a single row of either specialized pectinate or unmodified setae. Amorim and Tozoni

(1994; character 29) considered "apical pectinate bristles present on inner surface of hind tibia" a synapomorphy of Anisopodidae *s.s.* + Mycetobiidae (or Anisopodidae *s.l.* excluding Obliogastrinae), though it apparently also occurs in some Obliogastrinae (Peterson 1981a). Amorim (1982; Figs. 141,143 "cerdas apicais da tíbia") illustrated a posterior comb in several Scatopsidae, Matile (1990; Fig. 55 "peigne interne") observed a comb in some Keroplatidae, and Hutson *et al.* (1980) report a "tibial comb" in several genera of Mycetophilidae. Although the distribution of this character outside Bibionomorpha is not fully known, a similar structure is at least also reported in some Chironomidae (Oliver 1981; Figs. 59-62, 64-66) and Dixidae (Nowell 1951; Fig. 88d). A comb on the inner apex of the hind tibia is present in Anisopodidae, Scatopsidae, Keroplatidae, Sciaridae, Mycetophilidae, and Bolitophilidae.

Presence of a comb unambiguously supports two clades: Sciaroidea (except Ditomyiidae)(node 36) and Scatopsidae + Anisopodidae (node 40).

46) Male basitarsus (CI: 0.16, RI: 0.52)
slender elongate (0)
robust (1)
swollen (2)

The hind basitarsus of male Bibionidae ranges from slender to greatly swollen (Fig. 9a-b; hb). The function of the swollen condition is unknown, but as in other Diptera males which have unusually swollen hind tarsal segments (i.e. *Calotarsa* Townsend (Platypezidae)), it may play a part in sexual selection or aid in species recognition (Sivinski 1997, Chandler 2001). It is noteworthy that male bibionids (like *Calotarsa*) let the hind legs dangle below them while in flight. All three conditions (slender elongate, robust, and swollen) were observed in the bibionid genera *Plecia*, *Penthetria*, *Bibio* and *Dilophus*, while the remaining bibionid genera never exhibit the swollen condition.

Considering the variability of this character within genera it is surprising that the presence of a robust hind basitarsus unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*). Additionally, state 1 supports Scatopsidae (node 43), state 0 supports the genus *Dilophus* (node 27) and node 11 (a clade within *Plecia*), and state 2 supports node 17 within *Plecia*.

47) Pulvilli (CI: 0.16, RI: 0.00)
absent (0)
present (1)

The pulvilli are flap-like structures which are ventral to the claws and arise from the basipulvilli, a pair of tiny sclerites located at the lateral margins of the unguitractor plate on the ventral side of the fifth tarsomere (McAlpine 1981a; Fig. 75). Pulvilli are absent from Tipulomorpha and Psychodomorpha (Hennig 1973). They were observed in all exemplar taxa here except *Ctenophora*, *Symmerus*, *Mycetophila*, *Scatopse*, *Mycetobia*, and *Trichocera*. Dahl and Krzeminska (1997) report that pulvilli are present in Trichoceridae. However, pulvilli could not be found in the species of *Trichocera* examined here. In *Keroplatus* and *Sylvicola* the pulvilli are merely minute tufts of hairs which are difficult to observe (Matile 1990; Fig. 56), but are present. The pulvilli are "normally" developed (large and not difficult to observe) in the remaining taxa.

This character provides no unambiguous support in this analysis.

WING

As in other groups of insects, wing venation in flies is complicated by the vastly divergent hypotheses concerning the homology of veins, as well as the usage of different terminology by different investigators. The interpretation of wing veins in this study departs in various ways from the systems used in chapters of the Manual of Nearctic Diptera (e.g. Hardy 1981) and Colless and McAlpine (1991), because of an inclusion of structural and fossil evidence from studies cited below which post-date these works. This synthetic result provides a better hypothesis of the homology of wing veins in Bibionoidea, but additional evidence would be valuable in corroborating some of the ideas which, at present, rest on sometimes sparse evidence. The terminology used here is summarized in Table 5, which also provides a summary of how the same vein has been interpreted across different families by previous investigators.

Amorim (1992) provided a phylogenetic analysis of Bibionomorpha (including numerous fossils) based almost entirely on wing vein characters. Although he primarily uses terminology and homology following McAlpine (1981a), the venation for each family is not explicitly stated, and at least the recognition of bR4 in Cramptonomyiinae (Amorim 1992: 390) is in conflict with the views of McAlpine (1981b; Fig. 7). However, numerous characters here have been adopted or modified from his work and are discussed in light of his opinions and results.

Despite the heavy usage of wing veins in earlier classifications (e.g. Hennig 1954), Stark *et al.* (1999) found that in a survey of 100 publications on Diptera systematics "the average percentage of wing characters used in a study was approximately 16%, indicating that wing characters are not relied upon in an extreme fashion in dipteran systematics." These authors explain that the reason for this pattern is because "wing vein characters may be somewhat homoplasious at least in the Drosophilidae and may explain why systematists shy away from such characters." Although the actual amount of homoplasy present in wing vein characters is undetermined, in addition to real homoplasy (e.g. convergence), there is also perceived homoplasy which is the result of human error due to an investigators inability to confidently identify homologous veins across taxa. Considering this, despite a painstaking effort to identify homologs here, some of these hypotheses are undoubtedly ill-informed. The understanding of wing vein homology in Bibionoidea is incomplete and additional studies focusing on the radial field of *Pachyneura*, and the medial-cubital and anal fields of Bibionoidea would be very valuable.

Table 5 - Terminology and wing vein homology used by different investigators for various bibionomorph taxa. In the first column is the terminology for wing veins used here; "b" stands for "base of" (e.g. bR4 refers to the base of R4). Rows represent the equivalent vein or parts of veins as interpreted by different investigators for a particular family. A dash (-) indicates this vein or vein part is inapplicable for that taxon, and a question mark (?) indicates that it is unknown how that author interpreted the vein/vein part in question.

Terminology used here	Bibionidae Hardy (1981)	Pachyneuridae (Wood 1981a)	Anisopodidae (Peterson 1981a)	Mycetophilidae (Matile 1990)
C	C	C	C	C
Sc	Sc	Sc	Sc	Sc1
R1	R1	R1	R1	R1
R2+3	-	-	R2+3	-
bR2+3	?	base of R2+3	-	-
R(2+)3+4	-	R2+3	-	-
R4	R2+3	-	-	R4
bR4	base of R2+3	supnum. x-vein	-	-
R5	R4+5	R4+5	R4+5	R5
r-m	r-m	r-m	r-m	ta
M1	M1	M1	M1	M1
M2	M2	M2	M2	M2
M3	-	M3	M3	-
M4	-	CuA1	CuA1	-
M(3+)4	CuA1	-	-	M4
bM(3+)4	bm-cu	bm-cu	bm-cu	tb
d	-	Dm	D	-
m-m	bm-cu	m-m	m-m	-
m-cu	base CuA1	base CuA1	base CuA1	mcu
CuA	CuA2	CuA2	CuA2	Cu 1b
pseudo-vein	CuP	CuP	CuP	Cu 2
CuP	A1	A1	A1	A1
A1	A2	-	A2	A2

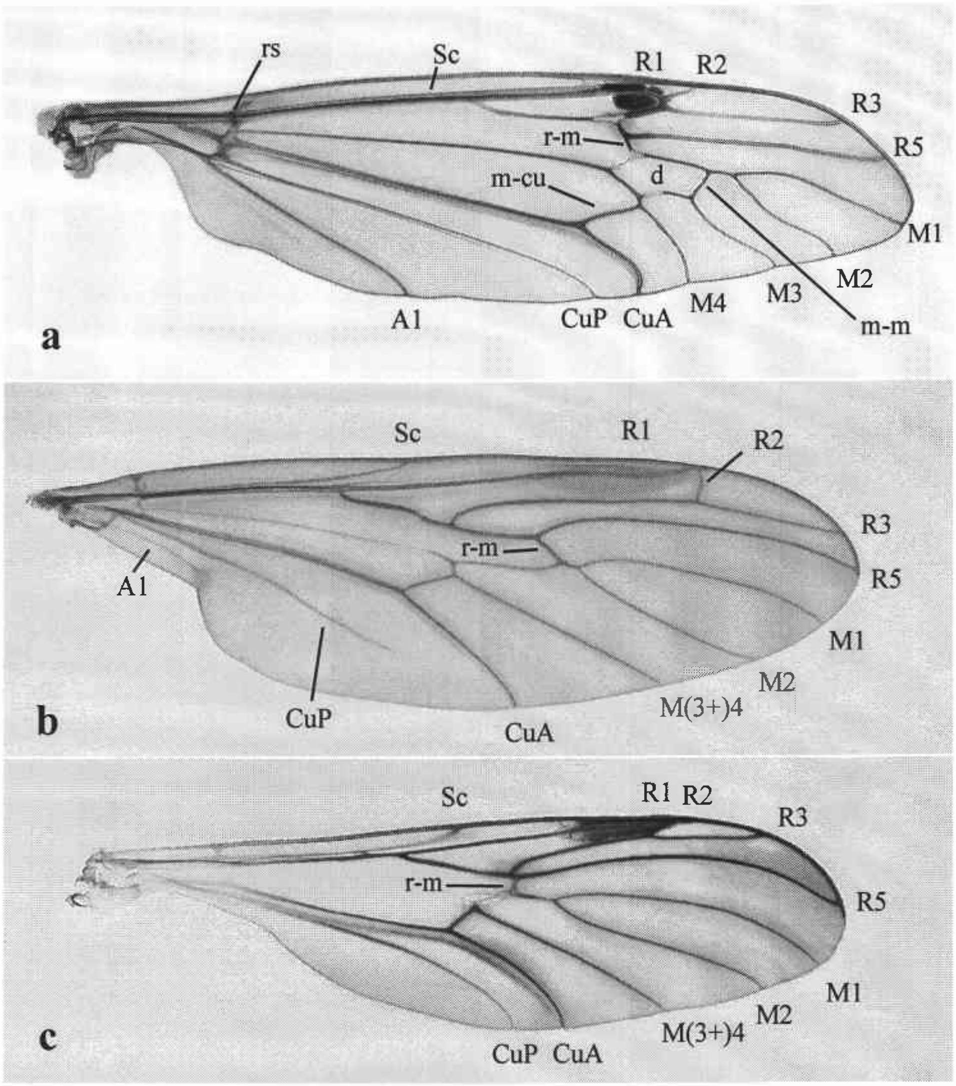


Figure 10, Wings I. a, *Ctenophora angustipennis* Loew (Tipulidae), male. b, Axymyiidae sp. (Oregon, USA), female. c, *Pachyneura fasciata* Zetterstedt (Pachyneuridae), male.

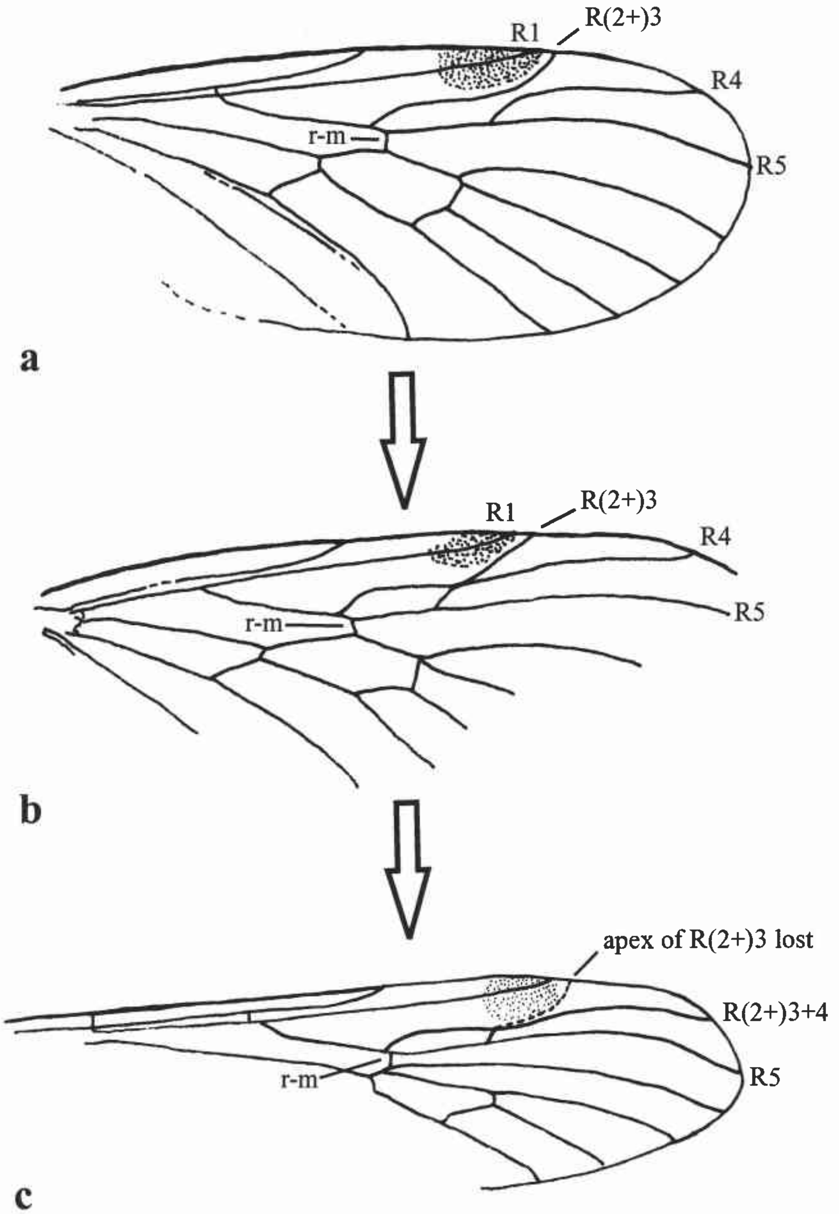


Figure 11, Possible transition series resulting in ventation of Cramptonomyiinae (Pachyneuridae). a, *Procramptonomyia* cf. *marianna* Krzeminski & Krzeminska (Procramptonomyiidae). b, *Procramptonomyia zigzagensis* Coram & Jarzembowski (Procramptonomyiidae). c, *Cramptonomyia spenceri* Alexander (Pachyneuridae). (Figs. a & b redrawn from Coram & Jarzembowski (1999)).

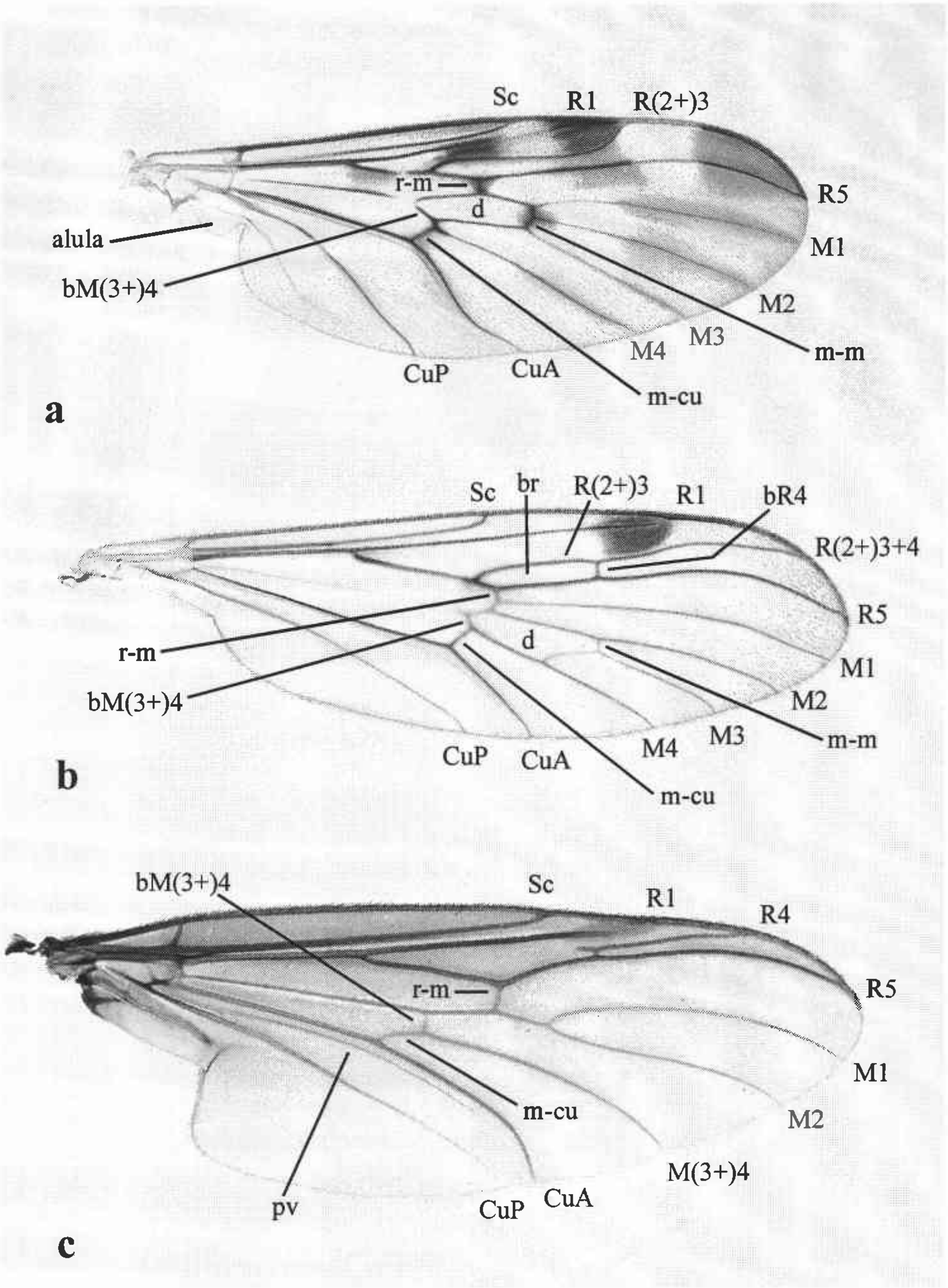


Figure 12, Wings II. a, *Sylvicola cinctus* (Fab.)(Anisopodidae), female. b, *Cramptonomyia spenceri* Alexander (Pachyneuridae), male. c, *Penthetria appendicula* Hardy (Bibionidae), male.

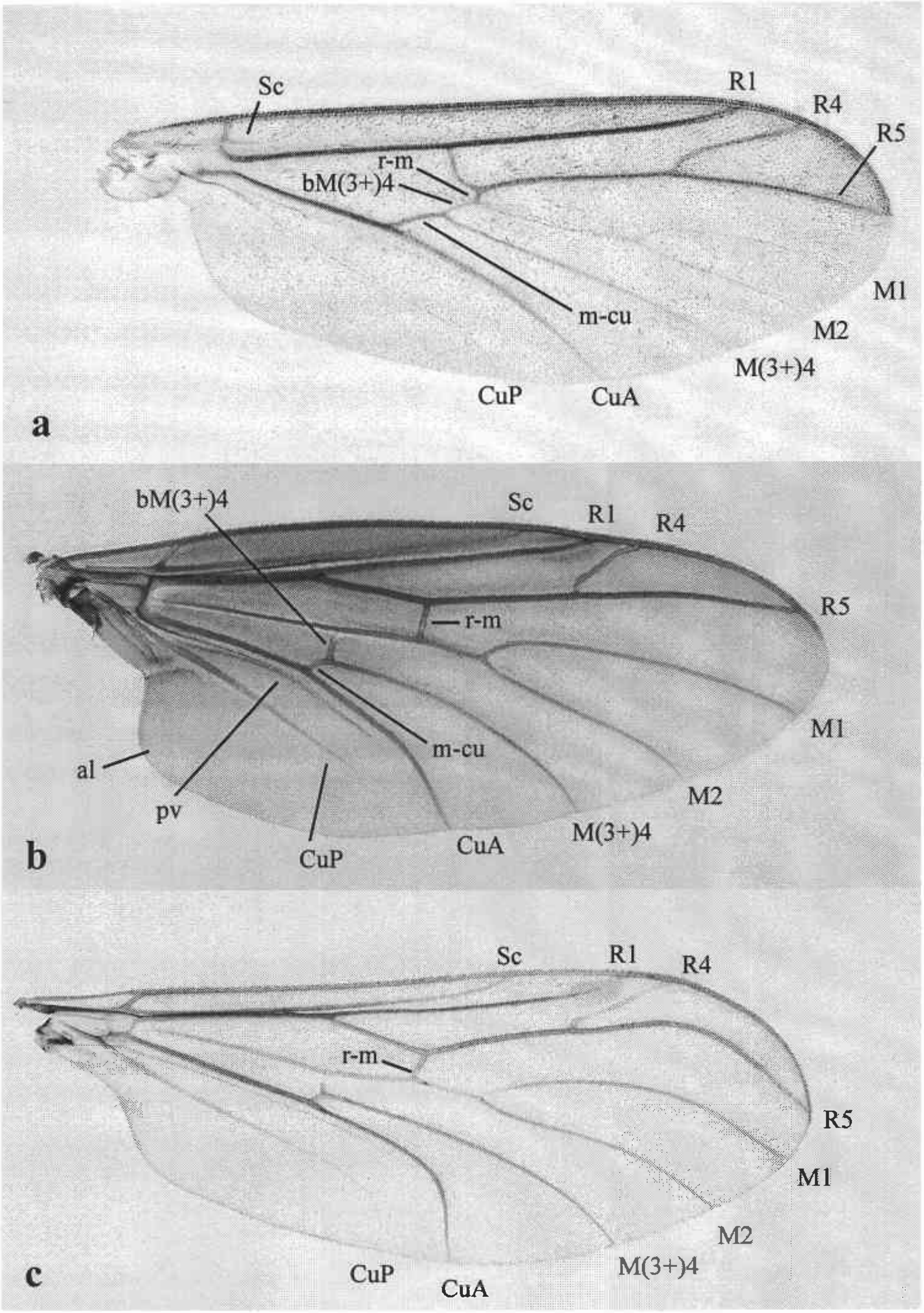


Figure 13, Wings III. a, *Symmerus coqulus* Garrett (Ditomyiidae), male. b, *Plecia nearctica* Hardy (Bibionidae), female. c, *Hesperinus cuspidistilus* Hardy & Takahashi (Bibionidae), male.

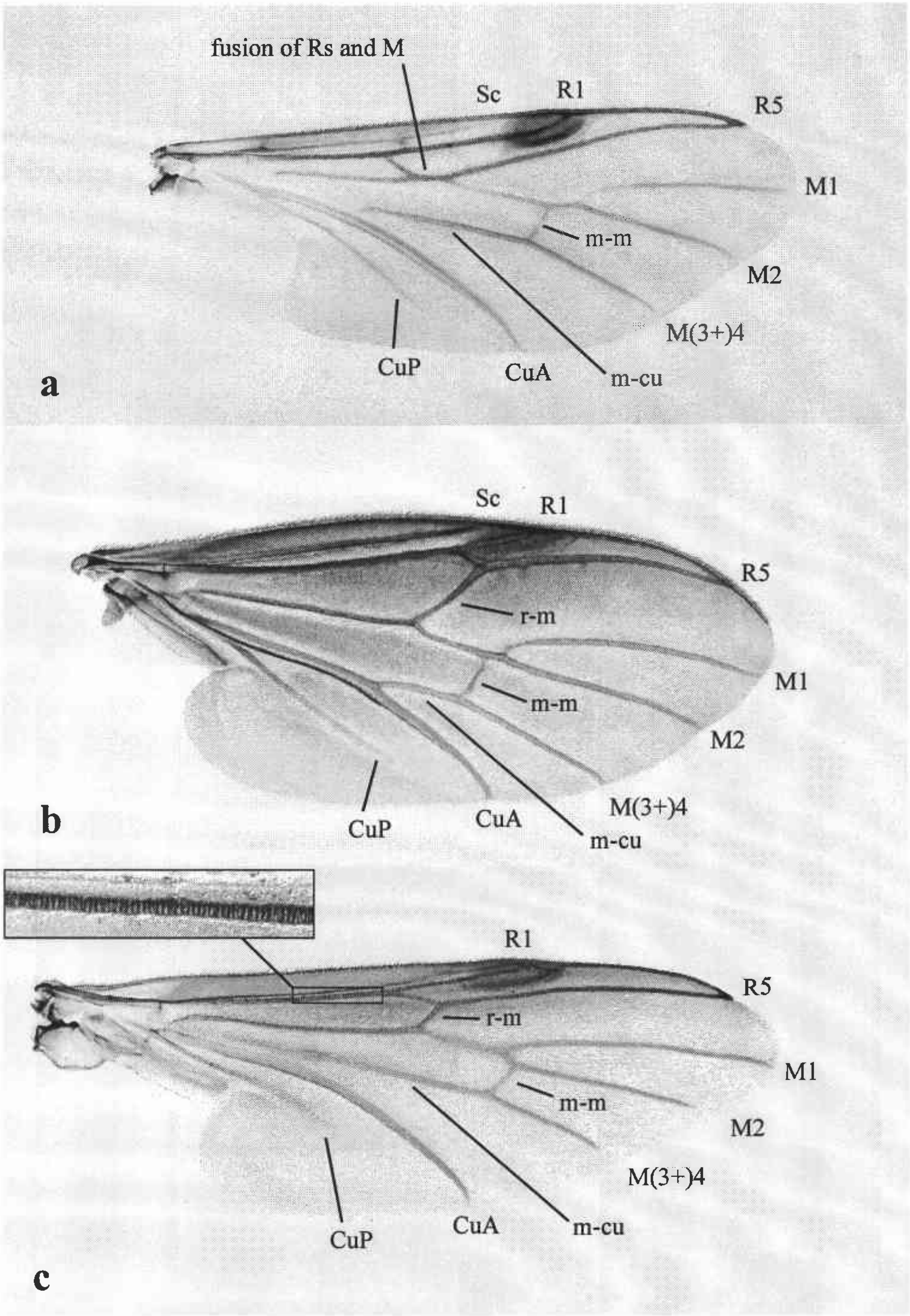


Figure 14, Wings IV. a, *Bibiodes aestivus* Melander (Bibionidae), male. b, *Dilophus sayi* (Hardy) (Bibionidae), female. c, *Bibio imitator* Walker (Bibionidae), male; insert showing transverse micostriations on radius.

48) Costa (CI: 0.33, RI: 0.00)

continuous around wing margin (0)
ending approximate to R5 (1)

A costal vein which ends at or shortly after R5 is considered by Hennig (1954: 290, 1973) to be a synapomorphy of Bibionomorpha. Amorim (1992; character 6) disagrees with Hennig stating that, "most basal groups of Brachycera do not present C clearly produced after M1," and he therefore considers the abbreviated costal vein a synapomorphy of a clade containing Axymyiomorpha, Bibionomorpha, and Brachycera. Here, C is continuous in Tipulidae (Fig. 10a), Trichoceridae, and Xylophagidae and it ends at, or shortly after, R5 in the remainder of taxa (Figs. 10a-b,12-14).

The continuous costa does not provide unambiguous support for any clade in this analysis.

49) Costa and radius shortened (CI: 0.50, RI: 0.66)

absent (0)
present (1)

Scatopsidae and the bibionid genus *Enicoscolus* have the costa and radius greatly shortened so that that these veins end on the leading edge of the wing well before the apex . The strict consensus topology indicates that this is an independent development in these two taxa and the costalized condition unambiguously supports both clades (nodes 26 and 43).

50) Vein Sc (CI: 0.14, RI: 0.53)

complete (0)
incomplete (1)

The subcosta may be complete (reaching the costa; Fig. 12) or incomplete (gradually disappearing before meeting the costa; Fig. 13a). A complete subcosta is present in most taxa and an incomplete subcosta is present in Ditomyiidae, most Bibioninae (except some *Dilophus*), Scatopsidae, Mycetophilidae, and Sciaridae. Amorim (1992; character 8) considered the incomplete subcosta to be a synapomorphy of Perissommatidae, but noted that the reduced condition "certainly appeared many dozens of times in Diptera."

Despite considerable homoplasy, the incomplete condition here unambiguously supports Scatopsidae (node 43)

THE RADIAL FIELD

Determining the homologies of the various branches of the radial sector in Bibionomorpha is a difficult problem. Current investigators generally agree that the dipteran ground plan includes four branches of the radial sector (Rs); R2, R3, R4, and R5, where R2 and R3 are paired and R4 and R5 are paired (McAlpine 1981a, Wootton & Ennos 1989, Colless & McAlpine 1991). Amorim (1992; character 20) argues that "in the basic plan of Diptera the first fork of Rs (R2+3/R4+5) is placed quite before r-m, whereas R4+5 apparently branches just before r-m. However, in most families in which R2+3 and R4 are present, the fork of R4+5 is clearly beyond r-m." He uses this positional evidence combined with patterns of fossil bibionomorphs, such as Protorhyphidae and *Eoplecia* Handlirsch that maintain both veins R(2+)3 and R4 (the former arising basal to and the latter arising distal to r-m (Fig. 11a)), as an argument for determining the homology of a single branch of Rs observed in most extant bibionomorphs. Although *Eoplecia* has been recently reinterpreted as having only a single branch of Rs (Ansorge & Krzeminski 1995), this finding does not affect Amorim's hypothesis because additional fossils such as Procramptonomyiidae also show this structure of R(2+)3 and R4 (Fig. 11a-b)(Coram & Jarzembowski 1999). If we use the criteria of position to determine the homology of the branches of Rs, the single branch of Rs basal to r-m in Anisopodidae is interpreted as R(2+)3 (Fig.12a) while the single branch of Rs distal to r-m in Bibionidae (*Plecia*, *Penthetria*, and *Hesperinus*) is interpreted as R4 (Figs. 13bc). The interpretation of the branches of Rs based on their position relative to r-m seems reasonable, but is confounded by the variation of the position and the structure of the first branch of Rs observed in Pachyneuridae (Cramptonomyiinae). Therefore the following discussion of the venation of this group is presented to help shed additional light upon the homology of the single branch of Rs in Bibionidae.

In Cramptonomyiinae the first branch of Rs can arise basal to r-m (*Cramptonomyia* (Fig. 12b)), even with r-m (*Haruka*), or distal to r-m (*Pergratospes*). However, because of the very unique structure of the first branch of Rs in this group we can be certain that it is the same vein in all three taxa (rather than R(2+)3 in the former and R4 in the latter). The unique condition of the branches of Rs in this group have been described as two elongate veins (R(2+)3 and R(4+)5) connected by a "supernumerary radial cross-vein" (Wood 1981a) or as R(2+)3 connected to R5 by a crossvein-like R4 (Hennig 1954, Amorim 1992). A modification of the latter interpretation is used here, where R4 is represented not only by the crossvein-like base, but is also the remainder of the vein distal to the crossvein. Evidence for this interpretation is based on the following fossil evidence. Coram and Jarzembowski (1999; Figs. 1-2) present a series of fossil Procramptonomyiidae which show R(2+)3 and R4 converging and adjacent in one wing, and in a second wing R(2+)3 and R4 converge and touch each other medially for a short distance (the authors note that in the latter case it was unclear whether the veins just touched or were actually fused for a short distance). This finding presents a very convincing transition series which can explain the unique venation of Cramptonomyiinae: R(2+)3 and R4 adjacent, R(2+)3 and R4 touching along a short length, fusion of the touching portions of these veins, and subsequent loss of the distal part of R(2+)3 (Fig. 11a-c)(Coram & Jarzembowski 1999). Without the aforementioned fossils one could argue that the "supernumerary cross-vein" could actually be R3 branching down from R2 rather than R4 branching up from R5. However, Shcherbakov *et al.* (1995) observed an aberrant specimen of

Haruka that has a short R2 present (ending in R1); this contradicts such an interpretation. The supernumerary cross-vein (of Wood 1981a) could also be interpreted as just a cross-vein, but I find the fossil evidence more compelling. If doubt of the identity of this vein persists for future investigators, additional evidence might be gained by an examination of the pupal wing sheath using the observation by Comstock and Needham (1898-1899) "that the principal veins are formed along the courses of tracheae, while in most cases the cross-veins have no tracheae within them."

Based on the above arguments, if we accept the interpretation for Pachyneuridae (Cramptonomyiinae) that the first branch of Rs is R(2+)3+4 (Figs. 11c, 12b) and that the base of this vein can be basal or distal to the r-m cross vein, it is difficult to interpret the first branch of Rs of the bibionid *Penthetria japonica* Wied., which is nearly identical in structure and position to *Pergratospes* (Cramptonomyiinae), as anything other than R(2+)3+4. In *Penthetria japonica* the first branch of Rs arises from R5 at a right angle even with or slightly distal to the r-m crossvein (Krivosheina & Krivosheina 1998) and then with another right angle, turns and runs nearly parallel to R5 (as in Fig. 12c). It differs only from *Pergratospes* in the absence of most of the base of R(2+)3, which could be arguably identified by the basally projecting stub vein in this and some other species of *Penthetria* (e.g. *P. appendiculata* Hardy (Hardy 1945), and *P. whipsawensis* Rice and "*Plecia*" *avus* (Handlirsch) (Rice 1959)). Again, if we accept this interpretation of the first branch of Rs in *Penthetria*, how do we interpret the first branch of Rs in the remainder of bibionids (many *Penthetria*, and all *Hesperinus* and *Plecia*) in which this branch originates at less of a right angle, lacks the stub vein, and is progressively more distal to r-m (Fig. 13b-c)? Hennig (1973), familiar with the above conditions in Cramptonomyiinae and *Penthetria*, suggested that the R(2+)3+4 interpretation may be preferable over an R4 designation for the first branch of Rs in bibionids. Although it is possible that the first branch of Rs in bibionids may be derived from a

Cramptonomyiinae-like condition, it is here interpreted that the first branch of Rs in Bibionidae is R4 rather than R(2+)3 or R(2+)3+4 for several reasons.

Firstly, as illustrated by Amorim (1992), strictly positional evidence suggests that this vein is R4 rather than R(2+)3. Despite the positional variation seen in Pachyneuridae, and the fact that R(2+)3 is clearly distal to the r-m crossvein in Ptychopteridae (Alexander 1981a) and fossil taxa such as Alinkidae and *Eomycetophila* (Krzeminski & Evenhuis 2000), most fossil Bibionomorpha with two branches of Rs have R(2+)3 basal to r-m and R4 distal to r-m (Fig. 11a-b)(Rohdendorf 1962, Amorim 1992, Blagoderov *et al.* 1993, Krzeminska *et al.* 1993, Coram & Jarzembowski 1999, Krzeminski & Evenhuis 2000). Furthermore, this arrangement is also true for most of the extant and fossil Orthorrhaphous Brachycera (e.g., Rohdendorf 1962, Kelsey 1969, James 1981, James & Turner 1981, Irwin & Lyneborg 1981, Grimaldi & Cumming 1999).

Secondly, an R4 designation based strictly on position is apparently corroborated by the uniquely structured vein in some *Penthetria* which has the appearance of being derived from a Cramptonomyiinae-like R(2+)3+4 condition (compare Figs. 12b-c). Although Hennig (1973) suggested that this vein may be best designated as R(2+)3+4 in bibionids, his position is probably based on the interpretation that R4 is represented only by the "transverse vein" (Hennig 1966: 142) between R(2+)3 and R5 rather than an interpretation that R4 is not only represented by this transverse vein (base of R4), but is also represented by the remainder of the longitudinal vein distal to it. Based on the fossil data presented by Coram and Jarzembowski (1999)(Fig. 12a-b) the latter interpretation is preferred here. In fossil Procramptonomyiidae which have R(2+)3 and R4 medially touching/fused for a short distance, R(2+)3 is represented by the base of the first branch of Rs up to about the junction with the crossvein-like base of R4 at which point the distal part of R(2+)3 is distinct and swings anteriorly where it reaches C (Fig. 11b). With this in mind, if we follow (R(2+)3 through Cramptonomyiinae to Bibionidae, R(2+)3 is eventually lost in its entirety; in Cramptonomyiinae the distal half of R(2+)3 is lost (Fig. 11a, 12b) and then in *Penthetria*, the basal half of R(2+)3 is lost (only identifiable as a small stump vein) leaving only R4 (unfused and distinct from R(2+)3 again)(Fig. 12c). It could be argued that some median part of R(2+)3 remains fused within R4, but this is unknowable and therefore designating this vein as R4 in Bibionidae (with the realization that the stump vein in *Penthetria* may represent the remnant of R(2+)3) seems reasonable and fits both the possible explanation for the unique structure of the wing in members of this genus as well as strictly positional evidence.

Although it does not detract from the positional evidence, arguing against a bibionid venation derived from a Cramptonomyiinae-like condition is the fact that a similar vein as that found in *Penthetria* (with the right angles and a stump vein) is found in various Rhagionidae *s.s.* (Stuckenberg 2001). In these taxa the vein distal to r-m is clearly R4 because it is the second branch of Rs, and R(2+)3 is present as a distinct and separate vein which originates basal to r-m (Stuckenberg 1965, e.g. Figs. 24 & 31, Nagatomi 1972, Fig. 2c, Yang & Nagatomi 1997, e.g. Figs.46, 71, 323). This suggests that at least in Rhagionidae *s.s.*, the stump vein associated with R4 is not the remnant of the base of R(2+)3. Although the presence of a similarly structured vein in Rhagionidae *s.s.* does not negate the possibility that the stump vein in *Penthetria* could be a remnant of R(2+)3, it does shed doubt on the significance of the stump vein observed in some members of this genus.

In summary, the primary criterion used here for determining the homology of branches of Rs in Bibionomorpha, following Amorim (1992), is the position of the vein basal or distal to r-m. Although most of the taxa were easily scored using this criterion, some taxa (such as Cramptonomyiinae mentioned above) were problematic and required reevaluation in light of additional evidence (e.g. fossils). The genus *Pachyneura* is also a problematic taxon and thus further discussion of how the branches of Rs were interpreted for this taxon is necessary.

The first branch of Rs in *Pachyneura* is very similar in structure to that of Axymyiidae (Fig. 10b-c). It is bifurcate in both taxa, but in *Pachyneura* it originates even with or distal to r-m and in Axymyiidae it originates basal to r-m. The first branch of Rs in axymyiids is interpreted as R2+3 based on positional evidence. This is not so easily determined in *Pachyneura* because the first branch of Rs is often even with or distal to r-m and thus should be designated as R4. However, since it is bifurcated, and R5 is already accounted for, it is then interpreted as R2+3 (as in axymyiids). Shcherbakov *et al.* (1995) suggest that the first branch of Rs in *Pachyneura* is R(2)+3+4 and was derived in a similar, but slightly different way, to the condition observed in Cramptonomyiinae; fusion of R(2+)3 and R4, but then loss of the base of R4 rather than the distal portion of R(2+)3. Hennig (1966) also designated the first branch of Rs in *Pachyneura* as R(2+)3+4, but provided no explanation. Since the structure of the radial sector in *Pachyneura* seems to be at the root of its controversial placement in Diptera (Bibionomorpha (Wood & Borkent 1989) versus Axymyiomorpha (Amorim 1992)), a conservative approach was used here regarding the interpretation of this branch which did not apply the transition series presented by Shcherbakov *et al.* (1995). Regardless of its potential validity, this transition series appears to be based on the preconceived notion that *Pachyneura* is allied with Cramptonomyiinae. The "capture of R4 by R2+3" hypothesis which Alexander (1927) presented for some Tipulidae, is slightly different than that presented by Shcherbakov *et al.* (1995) because it suggests a migration of R4 on to the R(2+)3 stem; but both hypotheses arrive at the same interpretation of these veins when applied to *Pachyneura*. However, the problem with applying Alexander's hypothesis is not one of preconceived notions of relationship, but the fact that if we apply "capture of R4 by R2+3" to *Pachyneura* we could just as easily apply it to Axymyiidae (e.g. Krzeminska *et al.* 1993). Although this does not seem initially to be a problem, it then follows that R3+4 is found basal to r-m in axymyiids which then places doubt upon a R(2+)3 designation of all other veins basal to r-m (e.g. in Anisopodidae).

Therefore, the first branch of Rs was designated as R2+3 in both Axymyiidae and *Pachyneura*. Regardless of the difficulty in interpreting the wing veins of these taxa and the possibility that they have been interpreted incorrectly, total character congruence should help to determine whether or not "the similarities in the wing venation between Axymyiidae and Pachyneuridae are due to symplesiomorphies and homoplasies" (Amorim 1992) or are synapomorphies.

The analysis indicates that *Pachyneura* forms a monophyletic group with other Pachyneuridae and that the wing veins of this taxon are probably best interpreted as R2+3+4 following the fossil transition series proposed by Shcherbakov *et al.* (1995) (see above discussion).

51) R3 (CI: 0.33, RI: 0.80)
absent (0)
present (1)

R3 was observed in Tipulidae, Trichoceridae, Pachyneuridae, Axymyiidae, Anisopodidae, and Xylophagidae (Figs. 10, 12a-b); and is absent in Bibionidae, Scatopsidae, and Sciaroidea (Figs. 12c, 13-14). Even though the distal half of R3 is lost in Cramptonomyiinae, the basal half is retained and thus is scored as present in this taxon. Considering that R3 is essentially absent in those species of *Penthetria* which apparently express a remnant of R3 only as a small stump vein (see "radial field" discussion above), R3 is scored as absent in these species. See "radial field" discussion of *Pachyneura* and Axymyiidae.

The analysis indicates that R3 has been lost a number of times and its loss provides unambiguous support only for Scatopsidae (node 43).

52) R2+3 (CI: 0.33, RI: 0.55)
absent (0)
bifurcate (1)
simple (2)

R2+3 is bifurcate (i.e. R2 present) in Tipulidae, Trichoceridae, *Pachyneura* (but see "radial field" discussion), and Axymyiidae (Fig. 10). An unbranched R(2+)3 was observed in Cramptonomyiinae, Anisopodidae, and Xylophagidae (Fig. 12a-b). Since R2+3 is absent in many taxa, whether or not R2+3 is bifurcate is an inapplicable character for these taxa. However, not enough alphanumeric symbols were available to score the inapplicable taxa as autapomorphic for this character, so they have been scored as absent both here and in the previous character.

This character provided no unambiguous support in this analysis.

53) R4 (CI: 0.16, RI: 0.76)
absent/fused with R5 (0)
present (1)

R4 is absent/fused with R5 in Anisopodidae, Scatopsidae, Bibioninae, Sciaridae, Axymyiidae, and *Ctenophora* (10a-b, 12a, 14). *Pachyneura* is coded as R4 absent, but see discussion of R2+3 designation above. Although R4 is typically present in the bibionid genus *Plecia* (Fig. 13b), I have examined an aberrant male specimen of *Plecia maura* Walker in which R4 is absent (CNCI).

The analysis indicates that the presence of R4 unambiguously supports node 1 and the subsequent secondary loss of R4 in Bibioninae and Anisopodidae + Scatopsidae provides unambiguous support for these clades (nodes 23 and 40).

54) Radial cell (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Despite the fact that McAlpine (1981a) uses a different interpretation of the radial sector than used here, he labels the radial cell formed in Cramptonomyiinae as cell br3 (basal radial cell, McAlpine 1981b; Fig. 7). This radial cell (Fig. 12b; br) is bounded by the branching of R(2+)3+4/R5 basally and the transverse section of R4 (bR4) distally. The cell is unique to Cramptonomyiinae and provides unambiguous support for this taxon (node 35)

55) Vein R5 (CI: 0.40, RI: 0.62)

relatively straight to gently posteriorly arched (0)
with obvious posteriorly directed arch near apex (1)
arching anteriorly (2)

This character is slightly modified from Amorim (1992; character 23). It is truly a continuous character, but is treated as discrete (relative degree of arch in apex of R5). Considering that Amorim (1992) observed the arch in only a subset of the taxa that that are coded as having an arch here, reflects on the subjectivity of determining the character states. Therefore, despite the fact that character state 1 unambiguously supports *Hesperinus* (node 32) and Cramptonomyiinae (node 35) this character should be viewed with caution. The anteriorly arching R5 was present only in Scatopsidae (node 43) and unambiguously supported this taxon.

56) R-m cross-vein ends in M1 (CI: 0.20, RI: 0.57)

r-m absent (0)
basal to its origin in Rs (1)
distal to its origin in Rs (2)
perpendicular to its origin in Rs (3)

This character is adopted and modified from Amorim's study (1992; character 24). The angle of r-m varied even within genera.

Character state 3 unambiguously supports node 4 (Bibionidae + Pachyneuridae) though it shows a subsequent change to state 1 in Bibioninae (node 23) which unambiguously supports this clade. Character state 2 unambiguously supports Axymyiidae (node 44). All these character states are present in taxa other than these supported clades.

57) Stem vein of R differentiated from distal portion via suture or break (CI: 0.14, RI: 0.33)

undifferentiated (0)
differentiated (1)

As part of the dipteran ground plan McAlpine (1981a) noted that the "base of R has a transverse suture-like constriction marking off the stem vein" (Fig. 10a; rs). This suture or break is not present in Trichoceridae, Pachyneuridae, Ditomyiidae, Keroplatidae, Xylophagidae, and the bibionid genera *Bibiodes* and *Enicoscolus*.

State 0 unambiguously supports the genus *Enicoscolus* though it also occurs in *Bibiodes* as well as a number of other taxa in the analysis.

58) base of R with transverse striations (CI: 0.50, RI: 0.91)

absent (0)
present (1)

The radial veins of the subfamily Bibioninae have minute transverse striations which are most easily observed when the wing is illuminated from behind (Fig. 14c insert). Amazingly, Cockerell (1915: 493) even noted this character from a bibionid compression fossil (*Bibiodites confluens* Cockerell) stating that "the strong veins, under a microscope, are seen to be transversely barred, exactly as in modern *Bibio*." Woodworth (1906: 44) explains that these "tracheoid markings" are found in numerous insect groups and are "due to excessive chitinization of the outer edges of the transverse folds of the layer of cells that in the pupa produce the veins" and that "the markings consist of thickenings of the cuticle which project on the convex side of the vein." Despite the wide distribution of these striations in various insect groups, they are apparently more prevalent in some groups than in others. In addition to bibionids, the presence of striations was also observed here only in the two examined Scatopsidae. Although the extent of its distribution within scatopsids is unknown, Amorim (1982; Figs. 109-110) illustrates striations also in *Arthria analis* (Kirby) and *Scatopse lapponica* Duda. Furthermore, similar striations apparently also occur in the base of the radial vein of some Sciaroidea (H. Hippa pers. comm. 2002).

The analysis indicated that the presence of transverse striations is an independent development in Bibioninae and Scatopsidae and unambiguously supports both these clades (nodes 23 and 43).

THE MEDIAL, CUBITAL, AND ANAL FIELDS

There are conflicting hypotheses concerning the medial and cubital fields of the dipteran wing. The Comstock-Needham interpretation recognizes three branches of M and two branches of Cu (followed by McAlpine 1981a), whereas the Alexander-Tillyard interpretation recognizes four branches of M and a single branch of Cu (followed by Colless and McAlpine 1991)(Byers 1989). Various investigators (e.g. Byers 1989, Wootton and Ennos 1989, and Shcherbakov *et al.* 1995) have since argued in support of the latter interpretation primarily because the unbranched CuA and four branches of M is the venation observed in most Mecoptera, including the Nannochoristidae (Willmann 1989). Hennig (1973) stated that investigators following this interpretation can find evidence in the cross-vein-like connection between M4 and CuA (the "distinctive" cubital fork of McAlpine 1981a) in taxa such as Tipuloidea (Fig. 10a) and Tanyderidae, but also noted that in Bibionomorpha (e.g. Sciaroidea) M4 would then be connected only with CuA and not with M. However, the loss of the base of M4 is the hypothesis followed here to explain the condition observed in Sciaroidea.

Following this interpretation, all Bibionidae have three branches of M (M1, M2, and M(3+)4) (Figs. 13a-b, 14) though some Australasian *Dilophus* have lost the stem and fork of M1+2 leaving only the unconnected distal ends of M1 and M2

(Fitzgerald 2004; Fig. 6). However, Bibionidae presents a special problem when trying to interpret the vein in question as M(3+)4 because the crossvein-like base of M(3+)4 (bM(3+)4) appears to migrate distally and thus act independently from the rest of M(3+)4 (compare Figs. 13b and 14c). For example, in *Plecia*, *Penthetria* and *Hesperinus* bM(3+)4 is found basal to r-m (Fig. 13b-c; bM(3+)4), while in Bibioninae a similar, but arguably not homologous, posterior crossvein is found quite distal to r-m (Fig. 14; m-m). These two transverse veins are considered homologs in recent works on Bibionidae (as bm-cu; Hardy 1981, Skartveit 1997) and the difference in position is presumably interpreted as a distal migration of the crossvein in Bibioninae. However, if we examine the positions of these two veins in other Bibionomorpha *sensu lato* with a more complete compliment of veins (e.g. Pachyneuridae and Anisopodidae), bM(3+)4 is basal to r-m and in alignment with a short m-cu, while crossvein m-m is always found distal to r-m and not closely associated with m-cu (Fig. 12a-b). If M3 coalesced with M4 and m-m is retained, then m-m bridges M2 and M(3+)4, rather than bridging M2 and M3. The condition observed in Bibioninae is interpreted as the absence of bM(3+)4 and the presence of m-m, while in the remainder of bibionids bM(3+)4 is present and m-m is absent. This interpretation is also suggested by Hennig (1973) and Shcherbakov *et al.* (1995).

The last point of discussion is the assignment of CuP and the subsequent number of anal veins. Wootton and Ennos (1989) considered Tillyard's Cu2 (CuP of McAlpine 1981a, Colless & McAlpine 1991) to be a secondary pseudo-vein, and the vein labeled A1 by these authors is then considered CuP, and A2 is A1. This arrangement was criticized by Krzeminski (1992), but the evidence presented by the former investigators is convincing and the wing veins in this study are treated accordingly. Therefore, as interpreted here, Bibionidae have a short A1 which does not reach beyond the small fold at the base of the anal lobe. Due to the complexity of the region, it is unclear whether or not A2 is present in Bibionidae. At least in some Bibioninae there is a short loop posterior to A1 which is connected distally to A1 (e.g. Hardy 1981, Fig. 10). Shcherbakov *et al.* (1995) illustrate a similar arrangement for

Bibioninae in which the longitudinal portion of A1 is absent, but the posterior "loop" is still present. Matile (1990; Fig. 34) treats both A1 and this "loop" as sclerites of the wing base in Mycetophilidae. It is beyond the scope of this study to resolve the homology of these veins/sclerites, but it is clear that additional work is needed on the anal area of the wing in order to establish the homology of these small and often obscure veins across Bibionomorpha.

59) Vein M with (CI: 0.20, RI: 0.33)
3 branches (0)
4 branches (1)

Four branches of M are present in Tipulidae, Trichoceridae, Pachyneuridae (except *Pachyneura*), Anisopodidae (except *Mycetobia*), and Xylophagidae (Figs. 10a, 12a-b), and three branches of M were observed in the remainder of the taxa (e.g. Fig. 13). In taxa with only three branches, it is apparently M3 (along with the discal cell) which is consistently lost or coalesced with M4. Amorim (1992; character 29) considered the loss of M3 synapomorphic for Bibionidae + Mycetophiliformia (Sciaroidea + Scatopsoidea).

State 1 unambiguously supports Cramptonomyiinae (node 35), though it also present in the other taxa mentioned above.

60) Base of M(3+)4 at junction of M (CI: 0.40, RI: 0.80)
basal to r-m/M junction (0)
base M(3+)4 absent (2)
even with r-m cross-vein (3)

The base of M(3+)4 is interpreted here as equivalent to the m-cu cross-vein of McAlpine (1981a); it is crossvein-like and leaves the stem of M basal to r-m in

Bibionidae (Fig. 13b; bM(3+)4) except for Bibioninae, in which it is absent (see discussion of medial-cubital field).

The analysis indicates that the loss of the base of M(3+)4 has occurred several times and unambiguously supports Bibioninae (node 23), Scatopsidae (node 43), and node 37 within Sciaroidea.

61) Cell cua (CI: 0.25, RI: 0.52)
not narrow distally (0)
narrow distally (1)
closed and petiolate (2)

The degree to which CuA arches posteriorly near the wing margin dictates the shape of the distal end of cell cua. If CuA is straight to slightly arched cua is not narrowed distally, but if it is more strongly arched the cell is tapered distally. The shape of the distal end of cua varies within genera of Bibionidae and may not be particularly informative above the species-group level. However, it has been included here because Hardy (1952a) erected the monotypic African subgenus *Plecia* (*Pleciodes*) based on the petiolate condition of cell cua in the species *ephippium* Speiser (Hardy 1952a; Fig. 1a). Considering that this species is otherwise unremarkable from other *Plecia* and the fact that the Australasian species *Plecia* (*Plecia*) *amplipennis* Skuse is polymorphic for this character state (distal end of cua narrowly open or closed and petiolate), the petiolate condition is probably best considered diagnostic for the species and not evidence for a distinct subgenus. Those taxa with CuP not reaching the wing margin have been scored as a "?" since it is unclear how the absent apex of CuP would affect the shape of cell cua in these taxa.

This character showed no unambiguous support in this analysis.

62) Vein CuP (CI: 0.20, RI: 0.75)
  not reaching wing margin (0)
  reaching wing margin (1)

CuP does not reach the wing margin in Bibioninae (node 23), Axymyiidae (node 44), and Scatopsidae (node 43) and provides unambiguous support for these clades. CuP also does not reach the wing margin in Mycetophilidae and Sciaridae.

63) A1 (CI: 0.50, RI: 0.00)
  reaching wing margin (0)
  not reaching wing margin (1)

A long anal vein which reaches the wing margin was observed only in Tipulidae (Fig. 10a) and Trichoceridae. This character provides no unambiguous support in this analysis.

64) Discal cell (CI: 0.20, RI: 0.33)
  absent (0)
  present (1)

McAlpine (1981a) recognized two different kinds of discal cells in flies; the true discal cell (d) and the discal medial cell (dm), which is different because "M3 disappears or combines with crossvein m-m" and "in this way cell m3 is eliminated and a new discal medial cell abuts directly on the cubital fork." Because of this distinction, the discal cell in Cramptonomyiinae (dm; Wood 1981a) and Anisopodidae (d; Peterson 1981a) are not considered to be homologous. However, when considering the presence of four branches of M, the difference between d and dm is insignificant and is merely a function of the branching point of M3+4; M3+4 branches basally in Anisopodidae so that d is posteriorly bounded mostly by M3 (Fig. 12a), whereas M3+4 branches distally in Cramptonomyiinae so that d is posteriorly bounded mostly by M3+4 (Fig. 12b). Therefore, the discal cells in these taxa are considered homologous here. A discal cell was observed in Tipulidae, Trichoceridae, Anisopodidae, Pachyneuridae (except *Pachyneura*), and Xylophagidae (Figs. 10a, 12a-b).

The presence of a discal cell unambiguously supports Cramptonomyiinae (node 35).

65) Alula (CI: 0.50, RI: 0.50)
absent (0)
present (1)

The alula "is usually absent or poorly developed in the Nematocera, except in the Anisopodidae, but is usually relatively large in the Brachycera" (McAlpine 1981a; Fig. 68). An alula was observed in Anisopodidae (except *Mycetobia*)(Fig. 12a) and a very weak alula observed in *Dialysis*. This character unambiguously supports node 42 (*Sylvicola*).

66) Wing with macrotrichia (CI: 0.33, RI: 0.33)
absent (0)
present (1)

Although the wing membrane of most taxa examined were covered with microtrichia, macrotrichia on the membrane was observed only in Anisopodidae, *Cramptonomyia*, and Ditomyiidae. This character unambiguously supports node 42 (*Sylvicola*).

67) Arculus (CI: 0.25, RI: 0.85)
absent (0)
present (1)

The arculus, also called MA by some authors, is a short transverse vein which stems between the bases of M and R near the level of the humeral crossvein. Its presence is considered part of the dipteran ground plan (McAlpine 1981a). Here it was absent in Pachyneuridae, Bibioninae, Sciaroidea, and Trichoceridae.

The absence/presence of the arculus is rather homoplastic. However, its absence unambiguously supports node 2 even though the vein is present in many of the taxa within this clade. Likewise, the presence of an arculus unambiguously supports Bibionidae (node 5) and a subsequent reversal to absence unambiguously supports Bibioninae (node 23).

68) Anal lobe of wing (CI: 0.12, RI: 0.30)
gently curved; not produced (0)
produced (1)

This character is really a continuous character with no adequate landmarks to help define character states. However, it is included here because the development of the proximal hind margin of the wing has been included in previous studies of Bibionomorpha (Amorim 1992; character 39) and the reduction of the anal lobe was considered a synapomorphy of Pachyneuridae by Blaschke-Berthold (1994; character 11). Because of the continuity between states 0 and 1, a "judgment" of the degree of development of the hind wing margin becomes necessary and, therefore, the subjectivity involved in this judgment make this character suspect. It is probably inappropriate to continue treating this character as discrete in future studies unless a more rigorous method of defining the states is developed.

Despite considerable homoplasy, the presence of a well developed anal lobe unambiguously supports Bibionidae (Fig. 13b; al), Anisopodidae + Scatopsidae, and node 37 within Sciaroidea.

ABDOMEN

69) Spiracle 8 of male (CI: 0.16, RI: 0.54)
absent (0)
present (1)

The eighth abdominal spiracle is present in females of numerous families of Diptera (including most Bibionidae), but is considered absent in males (McAlpine 1981a). Crampton (1942) stated that "seven pairs of spiracles are rather typical of the Diptera in general, and male Diptera apparently never have more than this number." Based on Crampton's work, Hennig (1973) considered seven spiracles in males a derived groundplan condition for the order. However, as noted by Blaschke-Berthold (1994), this hypothesis requires reevaluation because an eighth abdominal spiracle has been reported in males of several groups of flies including *Bibio* and *Dilophus* (Bibionidae) (Faucheux 1974, Blaschke-Berthold 1994), Aspistinae and Psectrosciarinae (Scatopsidae) (Cook 1965ab, Amorim & Haenni 1992), Canthyloscelidae (Haenni 1997a), *Machimus* and *Asilus* (Asilidae) (Reichardt 1929, Blaschke-Berthold 1994), and a number of genera of Therevidae (Winterton 2000, Winterton *et al.* 1999, 2000, 2001, and Winterton & Irwin 2001). Cook (1981b) also states that Chaoboridae have an abdomen with "eight simple pregenital segments, each bearing a pair of small spiracles," but an eighth spiracle is not present in male chaoborids (J. Ogawa pers. comm. 2003). Lastly, Young (1921) states that "*Chironomus ferrugineavitta*" has "at least seven and possibly eight abdominal spiracles, all in membrane," but this report has not been corroborated.

Based on Reichardt's illustration of the asilid *Machimus* (1929; Fig. 1) the eighth spiracle is lateral in position. Similarly, when an eighth spiracle is present in male therevids, it also maintains a lateral position, even though it may be located either in the pleural membrane or in the lateral edge of tergite eight (S.L. Winterton pers. comm. 2003). In contrast to this, Bibioninae, Canthyloscelidae, and the previously mentioned scatopsids have an eighth spiracle which is not found laterally in the pleural membrane between the eighth tergite and sternite, but it is found in a dorsal position between tergites eight and nine. In Bibioninae it is located in the membrane between tergites eight and nine (Fig. 16b; sp8) and is sometimes slightly enclosed by emarginations of the anterior margin of tergite 9 (epandrium). In *Arthria* (Scatopsidae) tergites 8 and 9 are fused and the spiracles are incorporated into the fused syntergite and are found on the transverse suture which marks the point of fusion. Similarly, the spiracles of other scatopsids and of Canthyloscelidae have also been incorporated into the surrounding tergites (often tergite 9) (Cook 1965ab, 1981a, Amorim & Haenni 1992, Haenni 1997a).

The morphology of the eighth spiracle of Bibioninae also differs from the preceding spiracles (1-7) because it is slightly larger and not flush with the membrane, but born on a small, fleshy, hump-like swelling of the membrane (Fig. 16b). The aperture of these membranous spiracles is difficult to confirm, but the membrane does appear to invaginate at the apex of the fleshy hump. An examination of adults of *Bibio albipennis* Say and *Bibio palliatus* McAtee revealed that the eighth spiracle is connected to trachea internally, which agrees with the study of the tracheal system in adults of *B. marci* L. by Faucheux (1974). The bibionids *Penthetria funebris*, *Plecia thulinigra* and *Plecia mallochi* have a pair of minute dark circular spots in the same position as the eighth spiracles of Bibioninae which, upon further investigation, revealed a minute fleshy hump not dissimilar in structure to the spiracle in *Bibio*, though an aperture was not observed. Based on their position and structure, they are undoubtedly homologous to the spiracles observed in *Bibio*, and an eighth spiracle in males of these genera has probably been overlooked because of its minute size. Although the size of these spiracles suggests that they are not functional, an internal examination of *P. mallochi* indicates that the trachea are attached at these points in a similar manner to *Bibio*.

Whitten (1955) illustrated that both the dorsal and lateral longitudinal trunks of the tracheal system of the larva of *Dilophus* end at, and attach to, the posterior spiracle. The same is true for larvae of the genus *Bibio* (pers. obs.). Examination of a mature pupa of *Bibio albipennis* in which the imago can be observed through the transparent pupal cuticle, indicates that the position of the adult spiracle eight is aligned with the posterior spiracles of the pupa and, by inference, also with the larvae, which have the posterior spiracles in a dorsolateral position on the anterior margin of segment nine. Considering the alignment of the spiracles in all three life stages, and the fact that the posterior spiracles serve as anchors for the main trunks of the tracheal system in both larvae and adults (Whitten 1955, Faucheux 1974), it is possible that the structures observed in adults of *Plecia* and *Penthetria* are not functioning spiracles but simply an external manifestation of the internal attachment points of these trunks. However, since it is difficult to determine whether or not a spiracle is "functional," an eighth spiracle (which is only found dorsally in the taxa studied here) is coded as present if there is any external indication of a structure.

The presence of spiracle 8 provides unambiguous support for Bibioninae despite the absence of this spiracle in *Bibiodes* and its presence in some *Plecia* and *Penthetria*.

70) Abdominal tergites of male (CI: 0.42, RI: 0.20)
concolorous (0)
dark basally, light distally (1)
light basally, dark distally (2)
light with a median dark stripe (3)

The abdominal tergites of bibionids are typically entirely black to dark brown. However the tergites of some other taxa, such as Pachyneuridae, are bicolored and are scored accordingly. State 1 unambiguously supports node 38, though it occurs in some Xylophagidae, Pachyneuridae, and Axymyiidae as well.

71) Anterior margin of abdominal tergites of male with plaques (CI: 0.10, RI: 0.43)

absent (0)

present (1)

Stoffolano *et al.* (1988) suggest that abdominal plaques are the site of attachment for muscles which are used by the pupa "for abdominal movements that assist in locomotion and for muscle action that assists the pharate adult in rupturing the pupal case." They considered the absence of these plaques in Muscomorpha a synapomorphy of the group. Although the presence/absence of abdominal plaques was informative at such a broad taxonomic scale, it is unclear whether or not the distribution of specific plaques, or areas with plaques, may be phylogenetically informative below the infraordinal level. Two characters are here developed by examining specific areas of the bibionid abdominal tergites which had plaques. The first area is the mediolateral portion of the tergites which sometimes have a single plaque present. The second area is the anterior edge of the tergites which sometimes have a transverse row of plaques along the edge giving it a serrated appearance. Both of these characters were found to vary even within a single genus.

Related to the presence/absence of a row of plaques on tergite two, is the position of the transverse row of plaques which, when present, is found either at the anterior margin, or in a more posterior position, giving the tergite the appearance of being subdivided. In some cases this more posterior transverse row is extensive enough that the tergite actually subdivides, and is separated by a very narrow strip of membrane. This subdivision may or may not be mirrored by the subdivision of sternite two which, according to Young (1921), subdivides more frequently than tergite two. Although not pursued further as a character in this study, the subdivision of tergite two is consistent within bibionid genera and may provide a source of character information which should be further investigated.

Abdominal plaques are most easily observed in either specimens preserved in alcohol or after the abdomen is softened in 10% KOH. This is particularly true of the plaques located near the anterior margin of the tergite which is typically hidden beneath the posterior margin of the preceding tergite, and must be telescopically pulled away from the preceding tergite for examination. The absence of plaques on the anterior margin of tergites provided unambiguous support for Trichoceridae + (Scatopsidae + Anisopodidae), though it showed a reversal in *Arthria* and considerable homoplasy elsewhere in the dataset.

72) Tergites of male with a mediolateral plaque (CI: 0.09, RI: 0.44)
absent (0)
present (1)

See previous character. Despite considerable homoplasy, absence of the mediolateral plaque unambiguously supports nodes 29 and 38.

MALE TERMINALIA

An excellent study of the structure and musculature of the male terminalia of Bibionomorpha (*sensu* Wood and Borkent 1989) was provided by Blaschke-Berthold (1994). In addition to exemplars of Sciaridae, Mycetophilidae *s. l.* and Cecidomyiidae, she examined six bibionid exemplars including representatives of the genera *Penthetria*, *Plecia*, *Bibio*, and *Dilophus*. Although the study is undoubtedly the best piece of descriptive work regarding terminalia of Bibionidae, it has several shortcomings. Firstly, as noted by Griffiths (1996), Blaschke-Berthold did not study the only other taxon within Bibionoidea, the small but controversial family Pachyneuridae. Secondly, the phylogenetic aspect of the study, although Hennigian in structure, lacks the empirical power and repeatability gained through both building a data matrix with species-level exemplars and using a computer algorithm to search for the best possible explanation for the observed character distribution. As it is not the goal to repeat the rigorous descriptive part of Blaschke-Berthold's work, this study builds on the foundation it provides by filling in taxonomic "holes" (e.g.

Pachyneuridae) as well as by providing alternative or refined ideas regarding the homology of structures based on new insights gained through outgroup comparison.

First a generalized description of the male terminalia of a bibionid is necessary as a foundation for the following more detailed discussion of structures: Externally, bibionids have a genital capsule which is consists of the dorsal epandrium (tergite nine)(Fig. 16a; ep), the fused gonocoxites laterally and ventrally, and the hypandrium (sternite nine) ventrally. The fusion of the gonocoxites and hypandrium into a single structure is then recognized as the "synsternogonocoxite" (Fig. 15a-b; sgx)(Pinto & Amorim 2000), though the hypandrium can be distinguished as a narrow, yet slightly thickened, transverse rim or strip along the anteroventral margin of the synsternogonocoxite (Fig. 15b; hp). Ventrally the posterior margin of the synsternogonocoxite is often medially emarginate with one or several pairs of short median lobes (Fig. 15b). Furthermore, the synsternogonocoxite often has a longitudinal, median, membranous, or slightly less sclerotized, patch or strip which may indicate the point of fusion between lateral gonocoxites. The anterolateral margin of the epandrium is sometimes narrowly fused to the synsternogonocoxite, forming a complete ring. The posterior margin of the epandrium is usually emarginate through which the apex of the cerci and proctiger is visible in dorsal view (Fig. 16a). Laterally the gonocoxites typically form a ring or pedicel in which the base of the gonostylus articulates. Laterally the gonocoxites of some taxa may be extended posteriorly above the socket into which the gonostylus articulates: here referred to as the lateral lobe of the gonocoxite (Fig. 15b; llg). The shape of the gonostylus is very diverse and ranges from short, simple, and digitate to sickle-like in most Bibioninae, but may be deeply bifurcate (e.g. *Bibiodes*) or more complex in *Plecia*.

Internally, the terminalia consists of an endophallus sandwiched between a ventral ejaculatory apodeme and the dorsal, medially fused parameres (Figs. 22-24). In some taxa, a collar-like aedeagus (*Hesperinus* (Fig. 22; ap)) or an aedeagal plate ("Endophallus-Platte" of Blaschke-Berthold 1994; *Dilophus*) are also present.

The males of the bibionid genus *Enicoscolus* are unknown, hence all male terminalia characters have been scored as "?" for this taxon.

Table 6 - Terminology and homology of the primary structures of the internal male terminalia. In the first column are the abbreviations and terminology used here. Rows provide a comparison of what I interpret to be homologous structures versus structures considered homologous by Blaschke-Berthold (1994). A dash (-) indicates this is inapplicable or absent for that taxon, and a question mark (?) indicates that I am unclear how Blaschke-Berthold interpreted the structure in that genus.

Terminology used here		Blaschke-Berthold (1994)					
		Bolitophila	*Mycetophila*	*Penthetria*	*Plecia*	*Dilophus*	*Bibio*
ap	aedeagal plate	-	-	-	-	EpPl	-
db	dorsal bridge	Db	-	Db	Db	-	-
ds	dorsal sclerite	Ds	dPl	Ds	Ds	Ds	Ds
ea	ejaculatory apodeme	Vsk	E	E	E	E	E
ed	ejaculatory duct	De	De	De	De	De	De
e	endophallus	Pu	Ded	Ep	Ep	Ep	Ep
ga	gonocoxal apodemes	?	GA	GA	GA	GA	GA
ma	median apodeme of paramere	meA	meA	meA	meA	-	-
pp	posterior process of paramere	Pa	lPw	-	lSp/dS	-	Pa/Pal
pt	phallotrema	Pt	Pt	Pt	Pt	Pt	Pt
vla	ventrolateral apodeme of paramere	caA	-	PlA	vSp	vLe	crA

Figure 15, Male terminalia of Bibionidae I. a, *Penthetria heteroptera* (Say), ventral. b, *Plecia imposter* Brunetti, ventral (left gonostylus removed). c-d, *Plecia imocellata* Fitzgerald. c, Ventral. d, Lateral. e-h, Epandrium, dorsal. e, *Plecia imocellata* Fitzgerald. f, *Penthetria heteroptera* (Say) g, *Plecia nitidipes* Edwards. h, *Plecia pellucida* Fitzgerald. Abbreviations: ds, dorsal sclerite; ec, epandrial cleft; ep, epandrium; gs, gonostylus; gxs, gonocoxal socket; hp, hypandrium; llg, lateral lobe gonocoxite; mel, median epandrial lobe(s); mls, median lobe synsternogonocoxite; pel, primary epandrial lobes; pl, paired lobes of synsternogonocoxite; sgx, synsternogonocoxite.

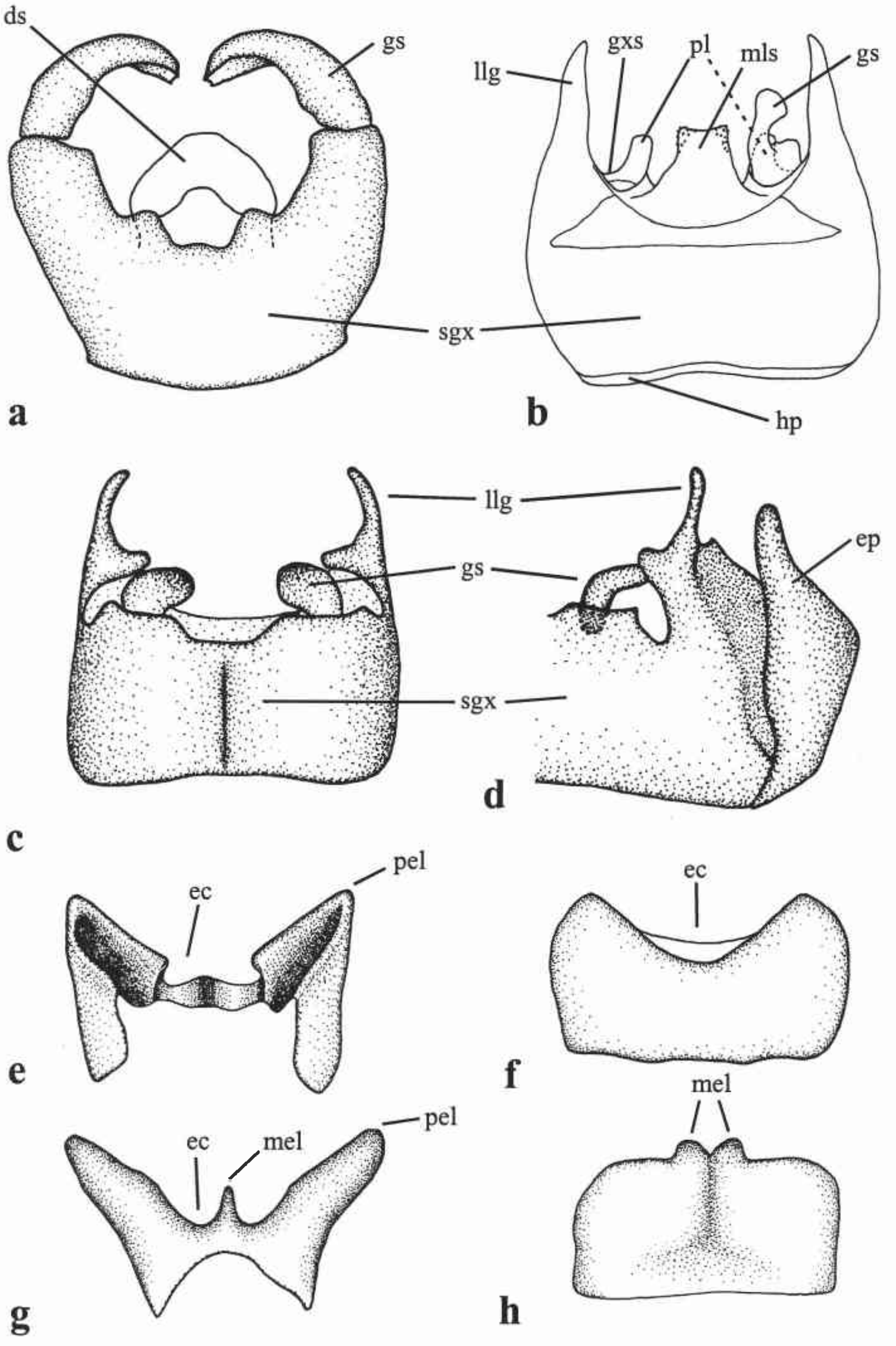


Figure 15, Male terminalia of Bibionidae I.

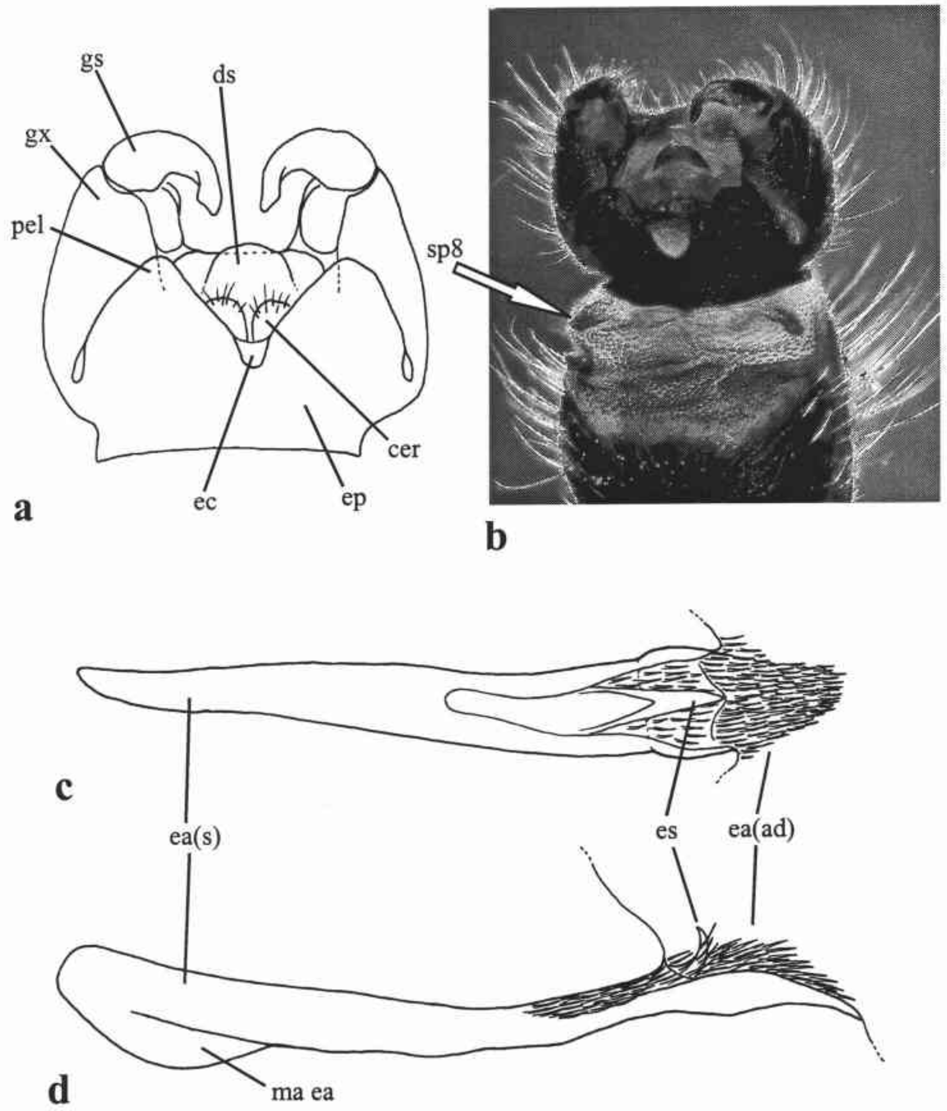


Figure 16, Male terminalia of Bibionidae II. a-b, *Bibio albipennis* Say, dorsal. c-d, *Dilophus sayi* (Hardy), ejaculatory apodeme. c, Dorsal. d, Lateral. Abbreviations: cer, cercus; ds, dorsal sclerite; ea(ad), apical differentiation of ejaculatory apodeme; ea(s), shaft of ejaculatory apodeme; ec, epandrial cleft; ep, epandrium; es, endoaedeagal spine; gs, gonostylus; gx, gonocoxite; ma ea, median apodeme of ejaculatory apodeme; pel, primary epandrial lobe; sp8, spiracle eight.

PRE-GENITAL SEGMENTS

73) Size of male tergite 8 (CI: 0.40, RI: 0.66)

normal size (0)
greatly reduced (1)
absent (2)

In all examined species of Bibionidae and Pachyneuridae, as well as *Ctenophora* (Tipulidae), tergite 8 is "normally developed" (not less than half the size of the preceding tergite 7) and is separated from sternite 8 by the pleural membrane. The eighth tergite of Axymyiidae is also separated from sternite 8 by the pleural membrane, but tergite 8 is much smaller. Further reduction of tergite 8 is seen in *Mycetobia divergens* in which tergite 8 is reduced to a small tongue of sclerite which protrudes from under the posterior edge of sternite 7 (the terminalia are rotated 180 degrees between segments 7 and 8). A greatly reduced tergite 8 was also observed in Ditomyiidae, Keroplatidae, Sciaridae, Mycetophilidae, Scatopsidae, Trichoceridae and Xylophagidae. Tergite eight is absent in *Scatopse.*

Presence of normally-sized tergite 8 provided unambiguous support for Bibionidae + Pachyneuridae (node 4) and *Sylvicola* (node 42).

74) Position of male tergite 8 (CI: 0.50, RI: 0.50)

external (0)
internal (1)
absent (2)

In a subset of the aforementioned taxa, which have a reduced tergite 8 (previous character) the tergite is found partially telescoped anteriorly underneath the previous tergite making it primarily "internal" and at least partially free of setae. An internal tergite 8 is present in *Arthria*, *Mycetobia*, Sciaridae, Mycetophilidae, and Keroplatidae. In *Mycetobia* tergite 8 is also narrowly fused to sternite 8 laterally, and the two sclerites form a narrow ring which just slightly overlaps the base of the gonocoxites and lies completely over the hypandrium.

State 1 provides unambiguous support for node 37 (clade within Sciaroidea).

75) Size of male sternite 8 (CI: 0.33, RI: 0.55)
normal (0)
reduced (1)
absent (2)

The reduction of the size of sternite 8 (compared to preceding tergites) can be independent of the reduction of tergite 8 since it was observed in taxa both with and without a reduced tergite 8. Sternite 8 was reduced in *Arthria*, Anisopodidae, Keroplatidae, Ditomyiidae, Mycetophilidae, and Xylophagidae. Sternite 8 is absent in *Scatopse* and Axymyiidae.

State 1 unambiguously supports nodes 38 (clade within Sciaroidea) and 40 (Anisopodidae + Scatopsidae). State 2 provided unambiguous support for Axymyiidae.

EPANDRIUM

Most of the characters of the epandrium included here are aimed at resolving relationships within species-groups of Bibionidae, particularly within the genus *Plecia*, and have been extracted from bibionid keys and developed from descriptions of species-groups provided by Hardy (e.g. 1945, 1968). Most of the characters focus on the shape of the posterior edge, which may be straight to deeply emarginate (epandrial cleft) and/or have various posteriorly or ventrally directed projections, which may be median, submedian, or lateral in position.

The epandrium is absent in *Sylvicola fenestralis*, but present as a very thin, hyaline transverse sclerotized strip in *Sylvicola cinctus*, which is fused to the anterolateral corners of the synsternogonocoxite. Therefore, in the former taxon, the epandrial characters have been scored as inapplicable autapomorphies.

76) Anterolateral edge of epandrium (CI: 0.18, RI: 0.50)
separate from hypandrium (0)
narrowly fused to hypandrium (1)

Wood (1991) considered a ring-like ninth segment (i.e. the epandrium laterally fused to the hypandrium) the groundplan for Diptera. Bibionidae exhibit both the fused (ring-like) and the not fused conditions, with the fused condition expressed as a very narrow union of the posterolateral margin of the epandrium with the anterior rim of the synsternogonocoxite (as in *Pachyneura* (Wood 1991; Fig. 7a)).

An epandrium separate from the hypandrium unambiguously supports *Hesperinus* (32) and node 13 within *Plecia*. Although all the examined Sciaroidea also have a separate epandrium and hypandrium this clade was not supported as monphyletic.

77) Inner edge of epandrium with pair of dense pad-like setal brushes (CI: 0.66, RI: 0.66)
absent (0)
present (1)

Some species of *Plecia* have a pair of dense pad-like brushes of setae on the inner surface of the epandrium. Hardy (1968) considered these "patches or dense coverings of closely-placed black hairs" which "are often flattened, scale-like and are usually branched at their tips as seen under high magnification" a character diagnostic of the *Plecia decora* complex of species (Hardy 1968; Fig. 44a).

Dense setal pads unambiguously supported node 15 within *Plecia* though there is a subsequent reversal at node 17 that unambiguously supports this clade. The clade supported by these setal pads does not agree with Hardy's (1968) concept of the primarily Australasian and Oriental *decora* complex because it here includes four African taxa. However, a broader survey of the species of *Plecia* is necessary to address this discrepancy.

78) Epandrium (CI: 0.66, RI: 0.50)
undivided (0)
divided (1)

In Axymyiidae and *Mycetobia* the epandrium is longitudinally medially divided into two parts (Wood 1991; Fig. 9b). The analysis indicates that the divided epandrium is an independent development in these two taxa and it unambiguously supports Axymyiidae (node 44).

79) Posterior edge of epandrium (CI: 0.25, RI: 0.50)
straight (0)
medially cleft (epandrial cleft) (1)
convex (2)

The shape of the epandrial cleft (Figs.16a, 15e-g; ec) has been used in diagnosing species of Bibionidae, particularly Bibioninae and *Plecia* (e.g. Hardy and Takahashi 1960). If the posterior edge of the epandrium is straight (0), the epandrial cleft is absent. Character state 2 (posterior edge slightly convex) is an autapomorphy for *Scatopse*.

Despite the fact that an epandrial cleft occurs in numerous other taxa outside Bibionidae and that numerous taxa within Bibionidae lack an epandrial cleft, the presence of an epandrial cleft unambiguously supports Bibionidae (node 5) in this analysis. Absence of an epandriual cleft unambiguously supports node 1 (Bibionomorpha *sensu lato* + Brachycera) and node 27 (*Dilophus*).

80) Shape of epandrial cleft (CI: 0.71, RI: 0.42)

V-shaped (0)
U-shaped (1)

A U versus V-shaped epandrial cleft is used to diagnose species of Bibionidae (e.g. Hardy 1945; *Penthetria*). The shape of the cleft is scored as a "?" in Axymyiidae and *Mycetobia* since the shape of the cleft is not observable due to the longitudinal division of the epandrium into two parts.

Within the genus *Plecia*, state 1 unambiguously supports node 12 and, state 0 unambiguously supports node 16.

81) Primary epandrial lobes (CI: 0.92, RI: 0.00)

broad (0)
acute, digitate (1)

The "primary epandrial lobes" are here defined as those lobes which are lateral portions of the posterior edge of the epandrium which become lobate as the result of a median epandrial cleft (Figs. 15e, 15g, 16a; pel). The apices of these lobes can be apically broadly flattened, rounded, or strongly developed into acute, digitate, or forcipate processes (Fig. 15e-h). Hardy (1968) used the shape of these lobes in helping to define some species groups of *Plecia*. Additionally, the shape of these lobes is diagnositic for some species of bibionids (e.g. Hardy 1945).

This character provides no unambiguous support in this analysis.

82) Epandrial cleft (CI: 0.78, RI: 0.25)

shallow (0)
deep (1)

The shape of the epandrial cleft has been previously used to distinguish species of Bibionidae by Hardy (e.g. 1945). Despite considerable homoplasy, state 0 supports Bibionomorpha *sensu stricto* (node 3) and state 1 supports node 9 within *Plecia*.

83) Median lobe(s) of posterior edge of epandrium (CI: 0.25, RI: 0.40)

absent (0)
present (1)

In the genus *Plecia* the posterior edge of the epandrium may be cleft or uncleft. Additionally, the posterior edge of the epandrium may have lobe(s) (other than the primary epandrial lobes) that vary in structure and position, and which have been used to help diagnose species (e.g. Hardy 1945). These lobes are designated as the "median epandrial lobes" (Fig. 15g-h) to differentiate them from the "primary epandrial lobes" (Fig. 15g; pel); the latter which are the result of an epandrial cleft. Median epandrial lobe(s) may be present with or without the presence of an epandrial cleft, but in both cases are medial or submedial in position. The lobe(s) are paired or unpaired, posteriorly or ventrally projecting, and dorsally to laterally flattened. The unpaired and paired conditions are considered homologous because many species with an unpaired lobe have the lobe with a median longitudinal "suture" or have the apex of the lobe slightly bifurcate, suggesting that the paired lobes fuse to become the unpaired lobe or vice versa. Although it is unclear whether or not it is derived from the median lobes, *Plecia robusta* has a median, shelf-like structure with spines; this taxon has been coded as a "?" for this character.

State unambiguously supports nodes 14 and 17 within genus *Plecia*.

84) Median epandrial lobe(s) (CI: 0.50, RI: 0.50)

absent (0)
ventrally directed (1)
posteriorly directed (2)
posteroventrally directed (3)

See discussion of previous character. There were not enough alphanumeric values available to score all the inapplicable taxa as autapomorphic. Therefore, the character state "absent" is included as a character state and scored again for those taxa which lack median epandrial lobes. However, since "absence" is plesiomorphic, scoring for the absence of this character twice has no bearing on the grouping of taxa.

State 2 unambiguously supports nodes 14 and 17 within *Plecia*.

85) Posterolateral edge of epandrium developed into a secondary lobe (CI: 0.28, RI: 0.16)

absent (0)
present (1)

An additional "kind" of epandrial lobe has been observed in some species of *Plecia*, which occurs on the outer posterolateral edge of the hind margin of the epandrium, lateral to the primary epandrial lobes. Here this lobe is termed the "secondary lobe" of the epandrium (e.g. see Hardy 1968, Fig. 17b).

This character provides no unambiguous support in this analysis.

86) Shape of epandrium (CI: 0.30, RI: 0.00)

wider than long (0)
longer than wide (1)
subquadrate (2)

Hardy (1968) uses the relative size of the epandrium to help define species-groups of *Plecia*. Although clearly continuous in nature, it is here treated as a discrete character. In order to account for body size a ratio has been adopted rather than merely measuring a single axis of the sclerite in each species.

This character provides no unambiguous support in this analysis.

87) Anterior edge of epandrium medially (CI: 0.15, RI: 0.45)
continuous (0)
emarginate (1)

In addition to the epandrial cleft on the posterior margin of the epandrium, the anterior edge of the epandrium is sometimes emarginated (Fig. 15e, g). In some cases, where a species has both the posterior and anterior edges emarginate, the epandrium can be medially reduced to a thin strap (Fig. 15e) or entirely divided medially (e.g. *Plecia apoxys* Fitzgerald 1998; Fig. 14). Since it is not always clear if a medially divided epandrium is the result of only a posterior epandrial cleft, only the result of a deep anterior emargination, or the combination of both, the presence or absence of a completely divided epandrium has been treated as a separate character (see above).

State 1 unambiguosly supports node 9 (clade within *Plecia*) and 38 (Keroplatidae + Mycetophilidae) and state 0 supports node 18 within *Plecia*.

HYPANDRIUM AND GONOCOXITES

88) Hypandrium ventrally (CI: 0.33, RI: 0.33)
not fused to gonocoxites (0)
fused to gonocoxites (1)

In the dipteran ground plan, the gonocoxites are considered to be ventromedially separate from each other and from the hypandrium (Wood 1991; Fig. 8). In Bibionidae the hypandrium (sternite nine) is always fused to the anterior margin of the ventromedially fused gonocoxites forming the "synsternogonocoxite" (Pinto & Amorim 2000), and is recognizable only as a narrow, often thickened, transverse rim or strip (Fig. 15b; hp). The hypandrium is ventrally fused to the anterior margin of the gonocoxites in all examined taxa except Cramptonomyiinae, *Trichocera*, and *Scatopse*. In the former two taxa, the hypandrium is distinctly separated by a membrane, and freely articulates with the anterior margin of the gonocoxites (Wood 1991; Figs. 6, 8). In *Scatopse* both the gonocoxites and hypandrium are internal and the gonocoxites seem to be present only laterally. The hypandrium has a ventromedian, posterior extension which ends in a jumble of asymmetric sclerites of uncertain origin and the hypandrium does not appear to be attached to the gonocoxites medioventrally. However, in *Scatopse* the hypandrium is laterally fused to the gonocoxites along a distinct seam and has been coded as such.

The separate hypandrium and gonocoxites unambiguously supports Cramptonomyiinae (node 35).

89) Hypandrium laterally (CI: 0.25, RI: 0.50)
not fused to gonocoxites (0)
fused to gonocoxites (1)

Although the hypandrium is ventrally fused with the gonocoxites in all Bibionidae, members of the genus *Penthetria*, and one species of *Dilophus*, were observed to have the lateral portion of the hypandrium (which wraps dorsally and is sometimes fused with the anterolateral edge of the epandrium) not fused to the gonocoxites and present laterally as a thin strap. Such an unfused condition was also observed in those taxa in which the hypandrium is also ventrally distinct; Cramptonomyiinae and *Trichocera*. See discussion of *Scatopse* in previous character.

The analysis indicates that a hypandrium that is laterally separate from the gonocoxites is independently developed in Cramptonomyiinae and *Penthetria*; this character state provides unambiguous support for both clades.

90) Paired lobes of the posteroventral margin of synsternogonocoxite (CI: 0.33, RI: 0.71)

absent (0)
on posterior margin synsternogonocoxite (1)
on gonocoxal socket (2)

Most *Plecia* have a pair of small digitate lobes which are found at the junction of where the gonocoxal socket (internal ring of gonocoxite which surrounds and forms a socket around the base of the gonostylus) meets, and is fused to, the posteroventral margin of the synsternogonocoxite (Fig. 15b; pl). In some species these lobes are essentially absent and present only as small humps, while in some taxa they are strongly developed digitate lobes. In some taxa these lobes are adjacent and median in position (e.g. *P. nearctica*), while in others they may be separated so that each lobe is more submedian in position (e.g. *P. zamboanga*). In some species the lobe is found in a more dorsal position along the rim of gonocoxite which forms the socket around the gonostylus (Fig. 15b; pl), and in some cases, such as *P. imposter* and *P. sinensis*, the gonostylus apparently works against this lobe when clasping. In *P. amplipennis* and *P. mallochi* the lobes are not distinct, but this area of the synsternogonocoxite/gonocoxal socket is well developed and fused to the gonostylus, apparently making the gonostyli immoveable. This well developed fused area is considered homologous with the lobe observed in other taxa because of its position (despite the fact that the fusion of structures makes a distinct lobe unrecognizable).

Presence of these lobes on the gonocoxal socket provides unambiguous support for node 11 within *Plecia* despite susequent changes to characters state 1 within this clade. Character state 1 also supports *Bibionellus* (node 25).

91) Paired lobes of the posteroventral margin of synsternogonocoxite (CI: 0.40, RI: 0.78)

lobes absent (0)
not fused to gonostylus (1)
fused to gonostylus (2)

See discussion of previous character. State 1 provides unambiguous support for node 11 within *Plecia* and node 25 (*Bibionellus*). Character state 2 unambiguously supports node 18 within *Plecia*.

92) Median lobe on posterior margin of synsternogonocoxite (CI: 0.33, RI: 0.42)

absent (0)
large (1)
small (2)

In addition to the paired lobes of the posteroventral margin of the synsternogonocoxite, some *Plecia* also have a well developed unpaired median lobe that is distinct in ventral view (Fig. 15b; mls). A heavily to very lightly sclerotized median lobe, which is large and visible in ventral view was found in several Oriental and Australasian/Oceanic species. A similar, much smaller, membranous to lightly sclerotized median lobe that is not visible in ventral view, was observed in several other species of *Plecia*. However, this character only includes median lobes which are developed to the extent that they are visible in ventral view. Additionally, the genus *Bibionellus* has a median lobe which is visible in ventral view, but smaller than those observed in *Plecia* (character state 2).

The presence of a small median lobe provides unambiguous support for *Bibionellus* (node 25) and Axymyiidae (node 44). Character state 1 supports node 18 within genus *Plecia*.

93) Gonocoxal socket (CI: 0.18, RI: 0.65)

incomplete (0)
a narrow ring (1)
an elongate tubular pedicel (2)

In Bibionidae, and most taxa examined here, the gonocoxite apically forms a socket into which the gonostylus is seated and articulates. This "gonocoxal socket" has several forms. In most bibionids the gonocoxites form an elongate tubular pedicel with an apical socket that positions the gonostylus considerably posterior to the posterior margin of the synsternogonocoxite (state 2 (Figs. 15a, 16a)). However, in the bibionid genus *Plecia*, the gonocoxal socket is a narrow ring which positions the gonostylus at the posterior margin of the synsternogonocoxite (state 1; Fig. 15b-d; gxs)). Three species of *Plecia* have an elongate tubular gonocoxal socket similar in structure to other bibionids: *P. lateralis* Hardy (extant; Mexico) *P. parisiensis* Gee *et al.* (Paris Basin amber; Gee *et al.* 2001) and *Plecia* sp. (Dominican amber; Fitzgerald and Grimaldi unpublished). A gonocoxal socket is absent (the inner wall not forming a closed ring) in Axymyiidae, *Sylvicola*, Scatopsidae, *Mycetophila*, Ditomyiidae, and *Plecia mallochi* Hardy.

Presence of a narrow, ring-like, gonocoxal socket provides unambiguous support for the genera *Plecia* (node 8) and *Bibionellus* (node 25). The incomplete gonocoxal socket unambiguously supports node 40 (Anisopodidae + Scatopsidae).

94) Lateral lobe of gonocoxite (CI: 0.14, RI: 0.68)

absent (0)
present (1)

Within Bibionidae the lateral lobe of the gonocoxite is present only in some species of *Plecia* (Fig. 15a-c; llg), and is defined as the lateral portion of the gonocoxite that extends posterior to the gonocoxal socket (in which the gonostylus articulates). The shape and position of the lateral lobe of the gonocoxite were used, among other characters, to delimit species groups of *Plecia* by Hardy (e.g. 1968). The presence of a lateral lobe in other taxa, such as Axymyiidae and *Arthria*, are probably convergent but are scored as homologs.

The analysis indicates that the lateral lobe in all these taxa is not homologous, but that the presence of a lateral lobe unambiguously supports the genus *Plecia* (node 8) even though there are several subsequent reversals within the genus. Additionally, the presence of an independently developed lateral lobe unambiguously supports Axymyiidae (node 44).

95) Position of lateral lobe of gonocoxite (CI: 0.27, RI: 0.52)
dorsal (0)
medial (1)
ventral (2)
lateral lobe absent (3)

See previous character. State 0 unambiguously supports *Plecia* (node 8), though there are numerous subsequent changes within the genus, including a change to state 2 that unambiguously supports node 14 within *Plecia*. State 1 provides unambiguous support for Axymyiidae.

96) Gonocoxal apodemes anterior to connection to paramere (CI: 0.27, RI: 0.71)
short and stub-like (0)
distinctly extended (1)
smoothly fused to paramere without stub or extension (2)
absent (3)

The proximodorsal margin of the gonocoxite is drawn out into an anteriorly projecting process, the gonocoxal apodeme, in most Nematocera (Wood 1991). It is an important landmark in the male genitalia because it identifies the attachment point of the parameres, which can be very diverse in structure (Figs. 22a, 24a, 25; ga) In Bibionidae the gonocoxal apodeme is either a short stub anterior to its connection to the paramere, smoothly fused to the paramere without any anteriorly directed stub, or anteriorly elongated. The elongated condition was observed in Bibioninae, Cramptonomyiinae, Keroplatidae, Sciaridae, and Xylophagidae (Figs. The gonocoxal apodemes are absent in Anisopodidae and Scatopsidae; in these taxa the parameres apparently "float" within the genital capsule.

The presence of elongate gonocoxal apodemes unambiguously supports Bibioninae (node 23) and Cramptonomyiinae (node 35). Additionally, within the genus *Plecia* state 2 supports node 12 and state 0 supports node 18.

97) Gonocoxal apodemes (CI: 0.33, RI: 0.33)
not fused to epandrium (0)
fused to epandrium (1)

Although the gonocoxal apodeme is normally not associated with the inner surface of the epandrium (see previous character), *Ctenophora*, *Mycetophila*, *Plecia amplipennis* and *P. mallochi* have a gonocoxal apodeme which is fused to both the inner surface of the epandrium and to the parameres.

State 1 unambiguously supports node 18 within *Plecia*.

98) Gonostylus with strong spines (CI: 0.50, RI: 0.85)
absent (0)
present (1)

The gonostylus of Bibionidae have normally developed setae, but are devoid of heavily sclerotized spicules or spines. A gonostylus with apical spicules/spines was observed in Pachyneuridae and Sciaroidea (e.g. see Wood 1981a, Fig. 4 and Steffan 1981, Figs. 20, 22).

This character provides no unambiguous support in this analysis.

99) Shape of gonostylus (CI: 1.00, RI: 1.00)
short, robust, simple, apically broadly rounded (0)
large, round base with abrupt constriction to apical digitate lobe (1)
L-shaped (2)
slender, digitate with a basal anterodorsally directed process (3)
basally laterally flattened, apically tapered (4)
very short with two small lobes (5)

The shape of the gonostylus is used in distinguishing species of bibionids. For most exemplars, no structural commonality between that species and additional species was observed. Thus, most of the taxa have been scored as autapomorphic for their specific gonostylus shape. However, there were sets of species which did seem to have a common theme regarding the shape of the gonostylus, and these character states are articulated above. Descriptions of each autapomorphic condition (all states in the matrix besides 1-5) are not included since these descriptions are of no particular value to the analysis and can be found in the original descriptions of these taxa. Furthermore, since there are not enough alphanumeric variables to score all the autapomorphic conditions, question marks ("?") are used in addition to all the available alphanumeric values; even though scoring those taxa with a "?" does not accurately represent the autapomorphic condition in the matrix/analysis.

The great variability in the shape of the gonostylus makes this character of little value for family level, but does provide some support for some species-groups and genera.

State 3 provides unambiguous support for node 13 within the genus *Plecia*.

PROCTIGER

100) Cerci (CI: 1.00, RI: 1.00)

absent (0)
normally developed (1)
minute (2)

Extremely minute cerci were observed in *Ctenophora,* though they are typically regarded as absent in tipulids (Sinclair 2000). Additionally, extremely minute cerci were also present in Axymyiidae; this interpretation of cerci of axymyiids differs from that of Wood (1981b) who states that the cerci of this family are "not reduced in size." Cerci are apparently absent in *Trichocera* (Hennig 1973), and could not be found in *Trichocera tetonensis*.

Node 1 is unambiguously supported by the presence of normally developed cerci with subsequent loss in Trichoceridae.

101) Cerci (CI: 1.00, RI: 1.00)

fleshy to lightly sclerotized (0)
strongly sclerotized (1)

The cerci of Bibionidae are short to slightly elongated, fleshy structures that are covered with setae (Fig. 16a; cer). Strongly sclerotized cerci are present only in Scatopsidae and presumably must aid in a clasping function. The structures interpreted here as cerci in scatopsids have been previously interpreted as either gonocoxites (Cook 1965a, Freeman & Lane 1985) or as cerci (Amorim 1982). Because the paired structures in question are in close association with the ventral margin of the proctiger (morphologically the dorsal margin, but the genitalia are rotated 180 degrees) and the posterior margin of the epandrium, they are interpreted as cerci in agreement with Amorim (1982). *Trichocera* is scored as inapplicable for this character since the cerci have been scored as absent in the previous character.

The presence of strongly sclerotized cerci unambiguously supports Scatopsidae (node 43).

102) Shape of the anal cone in ventral view (CI: 0.33, RI: 0.33)

mound-like (0)
tower-like (apically truncate) (1)
bowling-pin-shaped (2)
sword-shaped (3)
absent (4)

The anal cone is the membranous mound or cone-like structure which lies between the epiproct/cerci dorsally and the hypoproct ventrally and ends in the anus posteriorly. The shape of the anal cone as described here is in ventral view after the proctiger has been extracted from the genital capsule (often still attached to the epandrium). It varied among taxa from a basic mound-like or triangular shape to "tower-like" which is best described as apically (posteriorly) truncate with the apex sometimes slightly depressed medially. The bowling-pin-like anal cone has a median constriction and is narrowly rounded apically. Character state 3 is autapomorphic for Ditomyiidae. An anal cone was not observed in *Mycetobia* and is scored as absent in this taxon.

State 0 provides unambiguous support for node 1, though there are eleven subsequent changes within this clade including a change to state 1 that unambiguously supports node 33 within *Hesperinus*.

103) Hypoproct (CI: 0.25, RI: 0.55)

medially divided (0)
basally divided, apically fused (1)
entire (2)
absent (3)

The hypoproct (sternite 10; Wood 1991) was found in all taxa except Keroplatidae and *Mycetobia*. The hypoproct was scored as either medially divided (longitudinally), partially divided (anteriorly with a longitudinal cleft, but posteriorly with the halves still connected), or undivided (entire). All these character states were observed in Bibionidae.

This character provides no unambiguous support in this analysis.

104) Epiproct (CI: 0.28, RI: 0.75)
well developed (0)
reduced (1)
absent (2)

The epiproct (tergite 10; Wood 1991) of Bibionidae may be either well developed, reduced, or absent. As noted by Wood (1991) "there is scarcely any suggestion of tergite X in any dipteran" so here "well developed" is used in a relative sense when compared to an epiproct which is reduced to the point of almost being absent. State 0 refers to an epiproct that is large, sclerotized and distinct, state one to an epiproct that is reduced (may be sclerotized or membranous, but is minute), and state three to the absence of the sclerite.

A reduced epiproct unambiguously supports node 1, though it has been subsequently lost in several clades (nodes 39, 37, and 29) and undergone a reversal to "well-developed" in Bibioninae (node 23) and node 33 within *Hesperinus*.

105) Epiproct (CI: 0.68, RI: 0.58)
medially divided (0)
undivided (1)

In some species the epiproct is medially divided (longitudinally) into two sclerites. The divided condition was only seen in those taxa which are scored as having a well developed epiproct, probably because the "reduced" epiproct is too minute for such a division.

A medially undivided epiproct unambiguously supports node 2, though it has been subsequently divided in numerous taxa within this clade (including node 33 within *Hesperinus* which is supported by this change).

PARAMERES AND DORSAL BRIDGE

The term "parameres" as used here, does not imply that the structures labeled as such in these groups of Diptera are homologous to the parameres in other holometabolous insects (Griffiths 1981), but follows current terminology used in recent reviews of dipteran terminalia (McAlpine 1981a, Wood 1991, Sinclair 2000). The dipteran parameres are defined by Sinclair (2000) as "posteriorly directed rods or processes attached to the gonocoxal apodeme, and in many lineages are united medially to form a single sclerotized plate, dorsal to and usually arching over the aedeagus (Wood 1991)." This definition fits the general structure of the parameres observed in Bibionidae, but in order to develop characters which describe the often complicated three-dimensional structure of the parameres, additional terminology identifying individual "parts" of the parameres is necessary. Blaschke-Berthold (1994) subdivided the bibionid paramere into such smaller units and some of the terminology presented by Blaschke-Berthold has been adopted here. However, in several instances Blaschke-Berthold applies two or more terms to what is here interpreted as a homologous structure between taxa. Because of this disagreement concerning the homology of some structures, and the fact the work is in German, the terms have been translated, derived, and consolidated as deemed necessary (Table 6).

Blaschke-Berthold (1994) limits the use of the term paramere ("Parameren") to the tusk-like, paired lateral processes in *Bibio* (Bibionidae), *Bolitophila* (Bolitophilidae), and *Platyura* (Keroplatidae), and suggests that these processes may be homologous to the paired, tusk-like processes observed in taxa such as *Trichocera* (Trichoceridae). The median shield or plate-like sclerite observed in Bibionidae, and most Bibionomorpha, Blaschke-Berthold suggests is probably derived from a median fusion of something similar to the wing-like bases of the parameres found in *Trichocera*; she calls this fused median plate the "Dorsalsklerit" (dorsal sclerite). This investigator agrees with Blaschke-Berthold's suggestions of homology for the tusk-like processes (here termed "posterior processes of the paramere"(Figs. 18a, 24, 25; pp)) and the dorsal sclerite (Figs. 18, 21-25; ds) observed in Bibionomorpha and Trichoceridae. However, Blaschke-Berthold's (1994) restricted use of "parameres" for only the posterior processes is misleading because the dorsal sclerite often flows seamlessly into both the posterior processes and the ventrolateral apodemes. Therefore, "parameres" is used here to communicate the complex three dimensional structure that includes the dorsal sclerite (ds), median apodeme (ma), posterior processes (pp), and ventrolateral apodemes (vla)(Figs. 18, 21-25). Definitions of these structures will be discussed individually below.

106) Parameres (CI: 0.66, RI: 0.00)
separate (0)
medially fused (1)
absent (2)

The parameres may be either paired lateral structures or medially fused. In all taxa examined here except Scatopsidae and *Ctenophora*, the parameres are medially fused. Although Brodo (1987) states that parameres are absent in Tipulinae, a pair of lateral structures which arise from the gonocoxal apodemes in *Ctenophora* are here interpreted as parameres. In *Ctenophora* the gonocoxal apodeme arises from the dorsal inner surface of the gonocoxite and is partly fused with the inner surface of the epandrium. The gonocoxal apodeme ends in a short free stub and is fused just before the stub-like terminus to a small, differently colored sclerite which is here considered the paramere. The paramere is also ventrally fused to a thin sclerotized rim of gonocoxite which originates at the posterior margin of the synsternogonocoxite and projects dorsally. This rim is apparently homologous to the inner rim of the gonocoxal socket in which the gonostylus articulates. In *Scatopse* the parameres are represented only by a pair of gonostylus-like lobes which are not medially fused. In *Arthria* the parameres are absent; therefore this taxon is coded as inapplicable for the remainder of the characters concerning the parameres.

The parameres are medially fused in all the taxa except *Ctenophora* and Scatopsidae, yet this character does not provide unambiguous support for any nodes in this analysis.

Dorsal sclerite

107) Dorsal sclerite of the medially fused parameres (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Bibionidae, and most Bibionomorpha, have a median shield or plate-like sclerite which Blaschke-Berthold (1994) calls the "Dorsalsklerit" (dorsal sclerite)(Figs. 18a, 21a-25a; ds). Although Blaschke-Berthold stresses that a direct evolution from one group into the next is not being inferred, she suggests that the dorsal sclerite is probably derived from a median fusion of something similar to the wing-like bases of the parameres found in *Trichocera* (wing-like bases = lateral apodeme *sensu* Dahl and Krzeminska 1997; Fig. 35). A definition of the dorsal sclerite is necessary because it is clear that a median fusion of the parameres does not necessarily equate to the presence of a "dorsal sclerite." The plate-like dorsal sclerite is not only the most dorsal part of the medially fused parameres, it is also distinctly dorsal to the posterior processes and ventrolateral apodemes when viewed laterally (Fig. 24c). In cases where both the posterior processes and ventrolateral apodemes are difficult to distinguish or absent (e.g. in anisopodids), the dorsal sclerite can be recognized by the laterally compressed, flange or ridge-like, ventral, median apodeme (Fig.21a; ma) that occurs in many taxa. The wing-like bases of the parameres in *Trichocera* are spatially dorsal to both the posterior processes and ventrolateral apodemes and therefore fit the definition of the dorsal sclerite (Fig. 18d). Not all trichocerids have the parameres medially fused dorsally (Dahl & Krzeminska 1997; Figs. 22, 30). However, the species of *Trichocera* examined here, as well as those examined by Wood (1991; Fig. 6) and Ovtshinnikova (1994a; Fig. 10), have the wing-like bases of the paramere medially fused forming a triangular plate with the median area less thickly sclerotized (Fig. 18a). As did Ovtshinnikova (1994a; "dorsal aedeagal sheath"), this plate in trichocerids is interpreted as homologous to the dorsal sclerite in Bibionidae.

The dorsal sclerite is present in all taxa with medially fused parameres except for Axymyiidae. The median sclerotized area in axymyiids seems to be only a basal fusion of the posterior processes (as can be seen in *Trichocera*). It is interpreted this way in axymyiids because the medially fused area is in the same plane as, rather than dorsal to, the posterior processes (ventrolateral apodemes and median apodeme are absent in axymyiids). This conclusion is exemplified by *Axymyia japonica* Ishida in which the Y-shaped posterior processes are posteriorly distinct but become anteriorly fused, and join the dorsal bridge via a narrow longitudinal bar.

Presence of a dorsal sclerite unambiguously supports node 1, with a reversal in Scatopsidae.

108) Median apodeme of dorsal sclerite of paramere (CI: 0.58, RI: 0.66)
absent (0)
present as a well developed ridge (1)
only a suture (2)

The median apodeme of the paramere is a median, longitudinal, laterally flattened, and ventrally directed flange that runs along the ventral surface of the medially fused parameres and sometimes also extends along the ventral surface of the dorsal bridge (Fig. 21a; ma). Blaschke-Berthold (1994; 96, character 3: "Dorsalsklerit mit medialem

Apodem") suggested that the presence of a median apodeme is a synapomorphy of the bibionid clade *Plecia* + *Penthetria* (i.e. subfamily Pleciinae of some investigators). However, a median apodeme is also present in *Hesperinus*, Pachyneuridae, and Anisopodidae. Character state one is a single flange which is the condition found in most taxa. State two is the presence of a slight ridge-like line which represents the previous presence of such an apodeme. Though it is possible that this line is merely the line at which the paired parameres fused medially, such a line is not found in other taxa with medially fused parameres such as Bibioninae. In some species the median apodeme is posteriorly (*Plecia aruensis*) or anteriorly (*Haruka* and *Penthetria funebris*) bifurcated forming paired median ridges; the latter case is clearly imposed by the anterior emargination of the dorsal sclerite.

Blaschke-Berthold (1994: 14, 17) states that the median apodeme of some species of Bibionidae is the attachment point for muscle M3, which has its origin on either side of the median apodeme and attaches to the dorsal lip of the phallotrema, thus reducing the size of the lumen of the endophallus and widening the phallotrema when contracted. However, Ovtshinnikova (1994a) states that this muscle (as M30; see Blaschke-Berthold 1994, Table 2) has a different function in Bibionidae and also states that this muscle changes its point of attachment across different taxa resulting in greatly different functions in different taxa. In addition to providing the attachment for muscles, the median apodeme of some species acts as a piston which compresses the endophallus (*Bolitophila* (Blaschke-Berthold 1994: 39-40) and *Sylvicola* (Abul-Nasr 1950)). In *Sylvicola* the basiphallus is sandwiched between the ejaculatory apodeme and the rod-shaped, piston-like median apodeme of the paramere (Fig. 21a; ma) so that when two pairs of muscles (which stretch between the ejaculatory apodeme and the ventral surface of the dorsal sclerite) contract, the piston is driven into the basiphallus which is pinned against the plate-like apical portion of the ejaculatory apodeme.

Presence of a median apodeme unambiguously supports Bibionidae + Pachyneuridae (node 4). Subsequent changes in Bibioninae (node 23, state 0) and a clade within *Hesperinus* (node 33, state 2) unambiguously supports these clades.

109) Shape of dorsal sclerite of paramere (CI: 0.53, RI: 0.45)
broadly flattened (0)
narrow (1)
a thin transverse bar (2)

The dorsal sclerite of the paramere of most taxa is broad and shield-like (state 0)(Fig. 24a; ds). However, some members of the genus *Plecia* have the posterior portion of the dorsal sclerite forming a narrow longitudinal projection (state 1). Character state 2 is autapomorphic for *Plecia aruensis* which has the dorsal sclerite reduced to a very thin transverse bar resembling the structure of a dorsal bridge.

State 1 provides unambiguous support for nodes 15 and 20 within *Plecia.*

110) Posterior edge of dorsal sclerite folded ventrally into a dome-like hood (CI: 0.54, RI: 0.50)
absent (0)
present (1)

Pachyneura, *Hesperinus*, *Penthetria*, *Sylvicola*, *Bolitophila*, *Mycetophila*, and some *Dilophus* have the dorsal sclerite ventrally folded forming a dome-like hood (Figs. 15a, 21a, 22a; ds).

The analysis indicates that the dome-like posterior edge has developed independently numerous times and it provides unambiguous support only for node 87 within *Dilophus*.

111) Posterior edge of dorsal sclerite with horn-like lobes (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Plecia nearctica and *P. bicolor* have the posterior edge of the dorsal sclerite developed into a pair of elongate, horn-like lobes not observed in other exemplars (Fig.23a; ds).

This character provides no unambiguous support in this analysis.

Posterior processes

112) Posterior processes of the paramere (CI: 0.25, RI: 0.68)
absent (0)
present (1)

As mentioned in the section "PARAMERES," this investigator agrees with Blaschke-Berthold (1994) that the posterior processes of the paramere observed in some Bibionidae and Sciaroidea are homologous to the posterodorsally-directed tusk-like processes observed in Trichoceridae because they are identical in position relative to other parts of the terminalia, and are similar in structure. In both groups these processes are continuous with or narrowly separated from the ventrolateral apodemes and dorsal sclerite, but lie ventral to the dorsal sclerite and posterior to the ventrolateral apodemes (Fig. 24c). The posterior processes in Trichoceridae have been uncontroversially treated as part of the parameres (Wood 1991, Dahl & Krzeminska 1997), but the hollowed-out, channel-like dorsal groove in the trichocerid posterior process, as well as the fact that the bases of the processes are adjacent to each other and to the apex of the endophallus (Neumann 1958), suggest a possible function in transferring sperm. However, neither the histological study of trichocerid genitalia by Neumann (1958) nor personal observations found a connection between the endophallus and the channel-like grooves of the posterior processes in Trichoceridae. Lastly, the paired, posteriorly directed, laterally flattened processes in Axymyiidae are here interpreted as homologous to the posterior processes observed in trichocerids and the bibionomorphs listed in the following discussion.

Posterior processes of the paramere were observed here in *Trichocera*, Axymyiidae, *Bibio*, *Bibiodes*, *Bibionellus*, *Plecia*, Cramptonomyiinae, *Mycetophila*, and *Bolitophila* (Figs. 18a & d, 23-25; pp). Blaschke-Berthold (1994) did not consider the structures in *Plecia* to be homologous to the posterior processes found in *Bibio*, *Bolitophila*, and *Platyura* (Keroplatidae); she labeled the structures observed in *Plecia* as the "dorsale Spange" (dSp) or "laterale Spange" (lSp) (her Figs. 26-27) rather than "parameren" as in the other taxa (Table 6). However, both spatially and structurally, these paired, often apically acute structures, which lie slightly ventrolateral to the dorsal sclerite, are very similar to the posterior processes of the paramere in Bibioninae. Furthermore, the taxa that Blaschke-Berthold observed to have posterior processes (*Bibio*, *Bolitophila*, and *Platyura*) also have a closely associated muscle (M9) which runs from some point at the base of the posterior process to the ventral surface of the dorsal sclerite (her Figs. 60, 158, and 167). This is also the case for *Plecia*, in which M9 runs from the base of the processes in question to the median apodeme of the dorsal sclerite of the paramere (her Fig. 29). Therefore, in contrast to Blaschke-Berthold, these structures in *Plecia* are here interpreted as homologs to the posterior processes observed in the aforementioned taxa (Table 6)(Fig. 23; pp). An identical argument can be made for the genus *Mycetophila* which has a pair of posterior processes also with M9 stretching between the base of the process and the median apodeme of the paramere (treated as the "laterale Peniswand," "lPw," by Blaschke-Berthold 1994)(Table 6) . Ovtshinnikova (1994a) stated that M9 (as M39) occurs only in Bibioninae, but the study of genitalia of *Plecia* or Mycetophilidae was not included, and her finding is probably the result of incomplete taxon sampling. Blaschke-Berthold (1994; Table 1) lists the presence of M9 in six genera of Bibionomorpha.

This character shows some homoplasy in the data set, but the presence of posterior processes also provides unambiguous support for Cramptonomyiinae (node 35) and Axymyiidae (node 44).

113) Posterior processes of paramere (CI: 0.45, RI: 0.80)
absent (0)
scapula-like; basally enlarged apically tapered (1)
tusk like; a thin strap or rod which is not basally enlarged (2)
thin sheets (4)
large laterally compressed lobes (5)

The structure of the posterior processes in most taxa other than *Plecia* is rather uniform; a thin strap or rod which is tusk-like (Fig. 24a; pp). However, in *Plecia* the structure of the posterior processes is more diverse, and in many species, is anteriorly enlarged and scapula-like (Fig. 23c; pp). *Haruka* has a unique structure of the posterior processes because the apices of the processes have become fused to the posterior apex of the ejaculatory apodeme. In Axymyiidae the posterior processes are very large and laterally flattened lobes.

The scapula-like posterior processes (state 1) provide unambiguous support for the genus *Plecia* (node 8), though there are several reversals within the genus to alternative character states. The tusk-like posterior processes provide unambiguous support for Bibionini (node 24) and Cramptonomyiinae (node 35), though they are present in Bolitophilidae and Trichoceridae as well. Lastly, character state 5 unambiguously supports Axymyiidae (node 44).

Ventrolateral apodemes

114) Ventrolateral apodemes of paramere (CI: 0.42, RI: 0.63)
ventrolaterally distinct from dorsal sclerite (0)
incorporated/fused into ventrolateral walls of the dorsal sclerite (1)
absent (2)

The ventrolateral apodemes of the paramere are found in most of the taxa examined and typically arise from the ventral anterolateral edge of the dorsal sclerite, near the junction with the gonocoxal apodemes (18a&d, 21a, 22a, 23-25; vla). The ventrolateral apodeme serves, in part, as the attachment point for a muscle that stretches between this apodeme and the anterior end of the ejaculatory apodeme (M5 of Blaschke-Berthold 1994; M31 of Ovtshinnikova 1987, 1989, 1994a); the presence of this muscle provides evidence for the homology of the apodeme across the taxa. The ventrolateral apodemes are very diverse in structure, which range from a pair of short simple anteriorly or ventrally directed rods (e.g. *Cramptonomyia* (Fig. 25; vla)), to a pair of very elongate arms which arch ventrolaterally and in some cases have the apices ending at the ventrolateral edges of the phallotrema (e.g. *Plecia* (Fig. 23c; vla)). In some Orthorrhaphous Brachycera, the apices of the ventrolateral apodemes expand and fuse medioventrally, forming a unified plate that is ventral to the aedeagus (the "ventral plate" of Nagatomi (1984) or "ventral aedeagal plate" of Ovtshinnikova (1987)). The ventral plate may also occur as a pair of plates which arise from this plate-like expansion of the apices of the ventrolateral apodemes, but without a medioventral fusion of the plates into a unified plate. Nagatomi (1984) called these paired plates "interbases" but noted that they seemed to be homologous to the ventral plate in some genera of Orthorrhaphous Brachycera. The ventral plate(s) connection with the anterolateral margin of the dorsal sclerite, is lost in some taxa (e.g. *Dialysis*), so that the plate(s) is a completely separate sclerite. However, the homology of this plate with the ventrolateral apodemes is supported by the attachment of muscle M5 or M31 (as previously mentioned) which runs between this plate and the anterior apex of the ejaculatory apodeme (e.g. Ovtshinnikova 1987; Fig. 2). A structurally intermediate condition can be seen in Blephariceridae, in which the ventrolateral apodemes have fused to form a "ventral bridge" that still maintains its connection to the "tegmen" (dorsal sclerite) (Zwick 1977). Again, the ventral bridge in Blephariceridae is interpreted as homologous to the ventrolateral apodemes in other taxa based on the presence of muscle M31 (muscle 5 of Zwick 1977). A similar condition can be seen in some *Plecia*, in which the ventral-most portions of these apodemes have become enlarged and plate-like, but they are not medioventrally fused and the ventral apodemes still maintain their connection to the dorsal sclerite (Fig. 23c). The plate-like or lobate expansion of the ventrolateral apodeme is, not surprisingly, associated with the point of muscle attachment (e.g. in *Exeretonevra* Macquart (Xylophagidae), Palmer, Ovtshinnikova, & Yeates, 2000; Fig. 1c) and such an expansion can be found in some taxa even with comparatively short apodemes such as *Penthetria* (Blaschke-Berthold 1994; Fig. 7). It is possible that the ventral plate which was reported as an "aedeagal guide" in some taxa like *Cnephia* (Simuliidae), may also be homologous to the ventrolateral apodeme (e.g. Wood 1991, Figs. a-c, e, illustrates the aedeagal guide of *Cnephia* with similar structure and position to Brachycera and it even maintains a narrow dorsal connection to the parameres), but studies of the musculature of this taxon are necessary to help in determining the origin of this structure.

The ventrolateral apodeme is absent in Tipulidae, Axymyiidae, *Haruka*, and Scatopsidae (though in *Arthria* it is coded it as inapplicable since the parameres are absent in this taxon). In *Mycetobia* there are a pair of ventral and posteriorly directed arms, but because of their uncertain homology, they are scored as a "?." In *Haruka*, the dorsal edge of the dorsal sclerite is emarginated, dividing the dorsal sclerite into a pair of anteriorly (rather than ventrolaterally) directed lobes which may or may not be homologous to the ventrolateral apodemes. Because the ventrolateral apodeme is so short in *Cramptonomyia*, it is possible that in *Haruka* muscle M5 merely stretches between the ventrolateral rim of the dorsal sclerite and the ejaculatory apodeme and a distinct ventrolateral apodeme is absent. However, since there was no fresh material to examine the musculature in *Haruka*, this taxon is scored as a "?." In most of the examined taxa the ventrolateral apodeme is narrowly connected dorsally to the dorsal sclerite (except in *Dialysis* in which there is no connection) and ventrolaterally the ventrolateral apodeme is an arm, strap, or plate that is distinct from the dorsal sclerite (e.g. Fig. 24c). However, in *Penthetria*, *Hesperinus*, and in some *Dilophus*, the lateral and posterior edges of the dorsal sclerite are produced ventrolaterally (forming a hood), and are fused to the ventrolateral apodemes into a single, unified structure. In these taxa the ventrolateral apodeme is recognized by a seam or a thickened strap along the edge of the ventrolateral wall of the dorsal sclerite (Fig. 22a).

The presence of unfused ventrolateral apodemes (state 0) unambiguously supports node 1, though there are subsequent changes to alternative states within this clade, including a change to state 1 which unambiguously supports node 28 within *Dilophus*.

115) Apex of ventrolateral apodemes of paramere (CI: 0.57, RI: 0.53)
reaching posterior apex of ejaculatory apodeme (2)
not reaching posterior apex of ejaculatory apodeme (1)

See also discussion of ventrolateral apodeme in previous character. The ventrolateral apodemes of some taxa are short (Fig. 25), though many are more elongate and at least reach ventrolaterally to the ejaculatory apodeme when viewed laterally (Fig. 24c). However, in some taxa the apodemes also extend posteriorly and terminate near the posterior apex of the ejaculatory apodeme. In those taxa with a hood-like dorsal sclerite it was sometimes hard to discern (because of the ventrolateral fusion of the dorsal sclerite with the ventrolateral apodemes) whether or not the apodemes reached the apex of the ejaculatory apodeme, and these taxa have been scored as a "?."

State 1 provides unambiguous support for Bibionini (node 24).

Dorsal bridge

116) Dorsal bridge (CI: 0.25, RI: 0.80)
a narrow strap (0)
expanded apically (1)
absent (2)

The dorsal bridge is probably gonocoxal in origin and apparently represents a median fusion of the gonocoxal apodemes into a thin transverse bar. When present, the dorsal bridge of Bibionomorpha examined here is a narrow transverse bar fused to the anterior margin of the dorsal sclerite, though it can be differentiated from the dorsal sclerite by a thin transverse seam (Fig. 22a, 24a, 25; db). However, in some cases the two sclerites have either become unidentifiably fused (no seam) or there was no dorsal bridge to begin with; thus character state 2 ("absent") probably represents a composite state due to an inability to differentiate between these two fundamentally different conditions. A notable exception to "typical" structure of the dorsal bridge as a narrow transverse bar is the bibionid genus *Plecia* in which the dorsal bridge is anteriorly expanded into a shield-like plate (Fig. 23a; db). At least in some orthorrhaphous Brachycera the dorsal bridge is not fused to the dorsal sclerite, and is a separate sclerite displaced ventral to the dorsal bridge (Yeates 1994; character 113); this condition has not been observed here.

The expanded dorsal bridge unambiguously supports monophyly of the genus *Plecia* (node 8) and state 0 supports Axymyiidae (node 44).

117) Dorsal bridge (CI: 0.83, RI: 0.66)
contained within genital capsule (0)
hangs below anterior edge of epandrium (1)

In *Plecia* the dorsal bridge is expanded anteriorly into a shield-like plate similar to the dorsal sclerite (Fig. 23a; db). In some taxa the anterior expansion is so extensive that the sclerite protrudes into the abdomen beyond the anterior margin of the genital capsule (anterior to the anterior margins of the hypandrium and epandrium).

A reversal to state 0 unambiguously supports node 13 within *Plecia*.

Figure 17, Tipulidae and Axymyiidae, sperm pump. a, *Ctenophora angustipennis* Loew, sperm pump, lateral. b-c, Axymyiidae sp. (Oregon, USA), sperm pump. b, Lateral. c, Ventral. Abbreviations: ada, anteriorly directed apodemes of aedeagal plate; adm, adminiculum; ap, aedeagal plate; ea(ad), apical differentiation of ejaculatory apodeme; ea(s), shaft of ejaculatory apodeme; e(bp), endophallus (basiphallus); ed, ejaculatory duct; e(dp), endophallus (distiphallus); lea, lateral ejaculatory apodeme; pt, phallotrema.

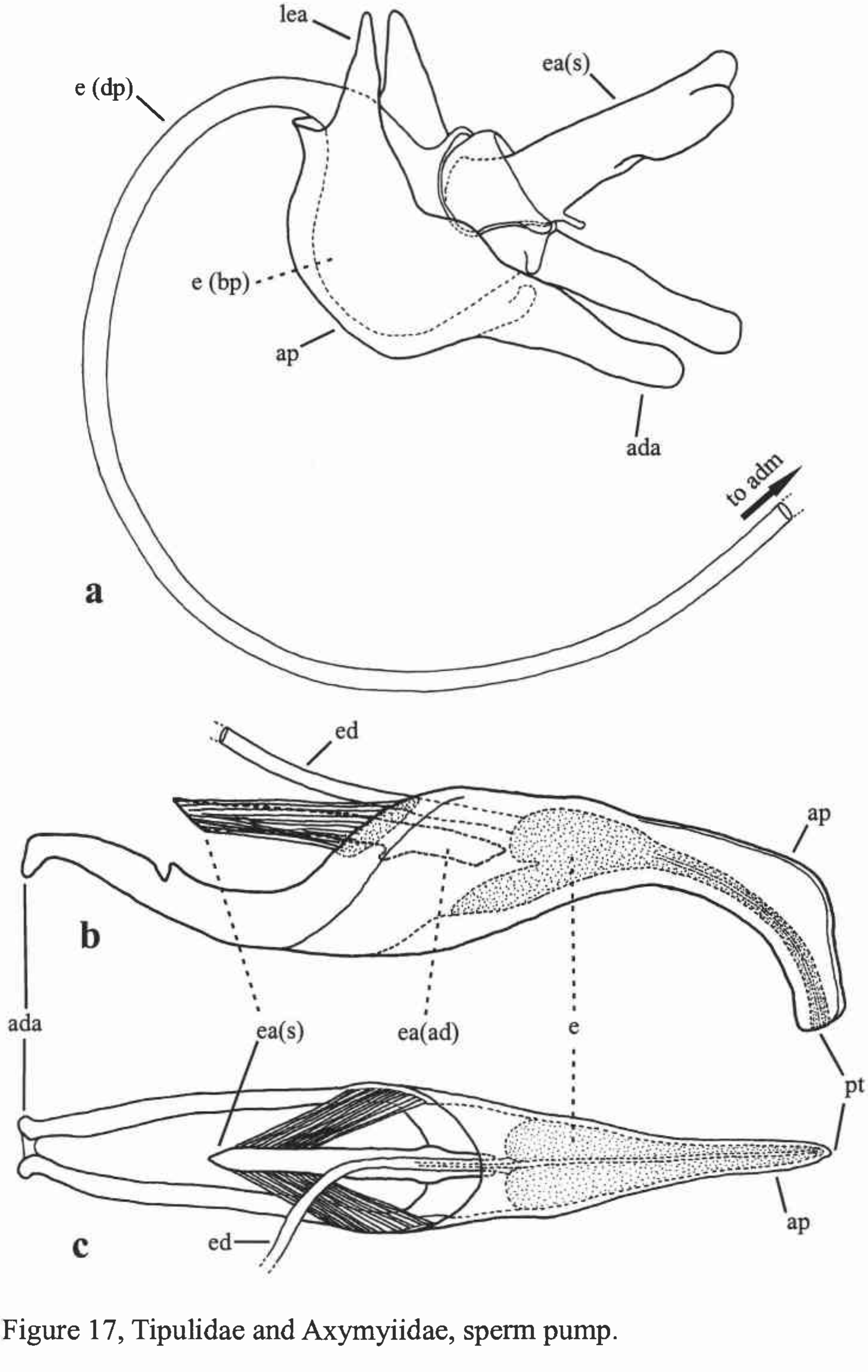


Figure 17, Tipulidae and Axymyiidae, sperm pump.

Figure 18, *Trichocera tetonensis* Alexander (Trichoceridae), male terminalia, internal. a, Parameres, doral. b, Sperm pump, lateral. c, Sperm pump, ventrolateral. d, Parameres and sperm pump, lateral. Abbreviations: ap, aedeagal plate; ds, dorsal sclerite; e, endophallus; ea, ejaculatory apodeme; ed, ejaculatory duct; ga, gonocoxal apodeme; lea, lateral ejaculatory apodemes; M32, muscle 32; pp, posterior processes of paramere; pt, phallotrema; vla; ventrolateral apodeme of paramere.

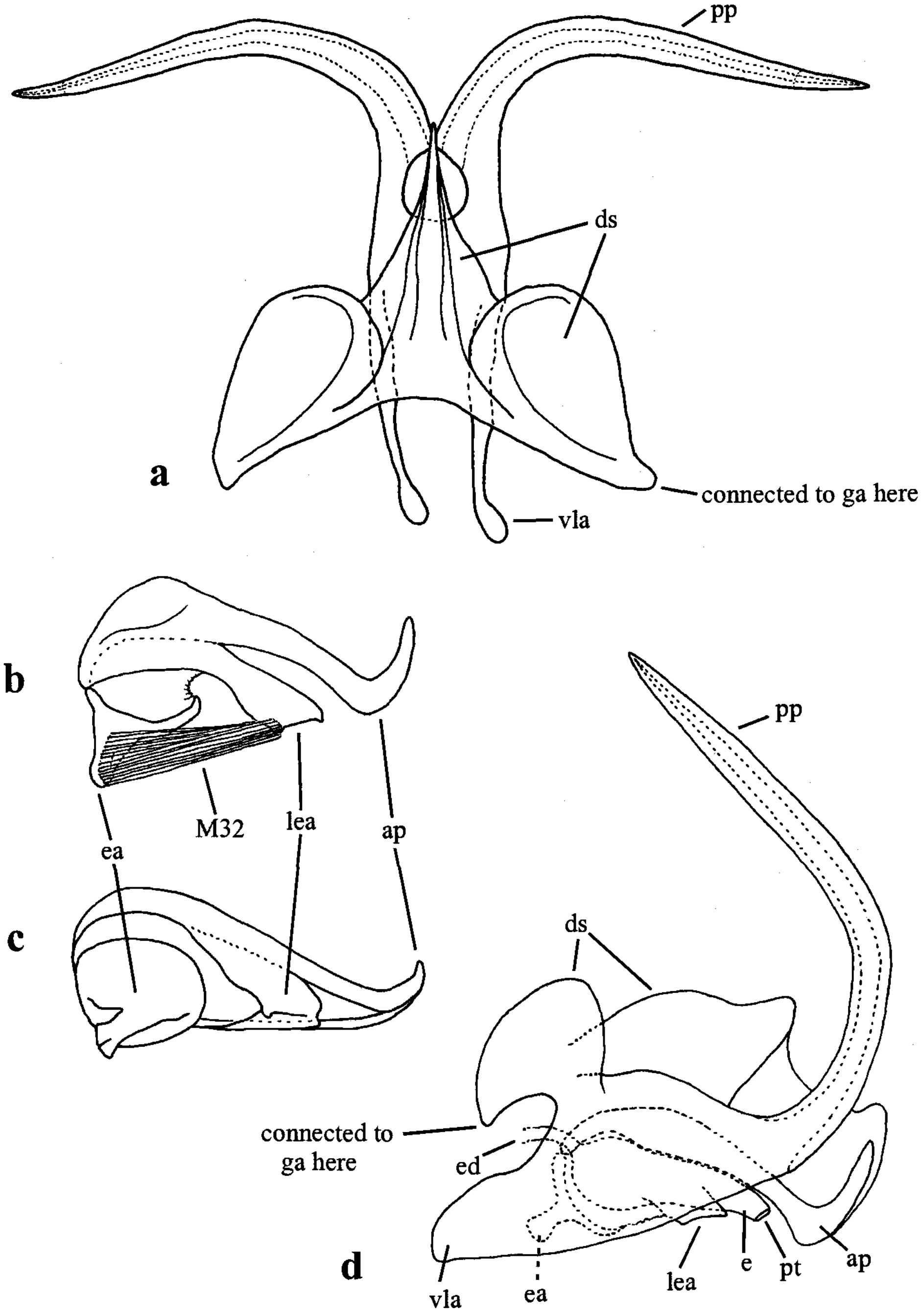


Figure 18, *Trichocera tetonensis* Alexander (Trichoceridae), male terminalia, internal.

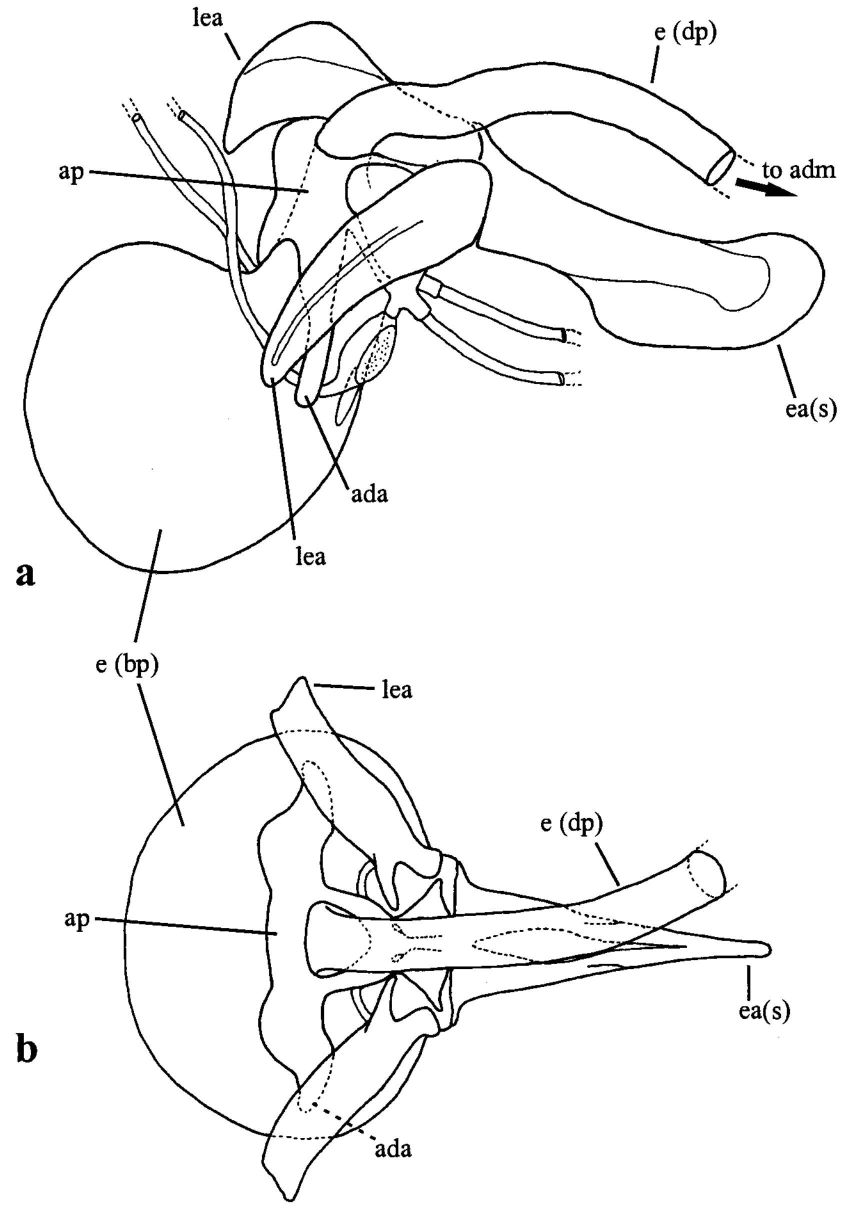


Figure 19, *Scatopse notata* (L.) (Scatopsidae), sperm pump. a, Lateral. b, Dorsal. Abbreviations: ada, anteriorly directed apodemes of aedeagal plate; adm, adminiculum; ap, aedeagal plate; ea(s), shaft of ejaculatory apodeme; e(bp), endophallus (basiphallus); e(dp), endophallus (distiphallus); lea, lateral ejaculatory apodemes.

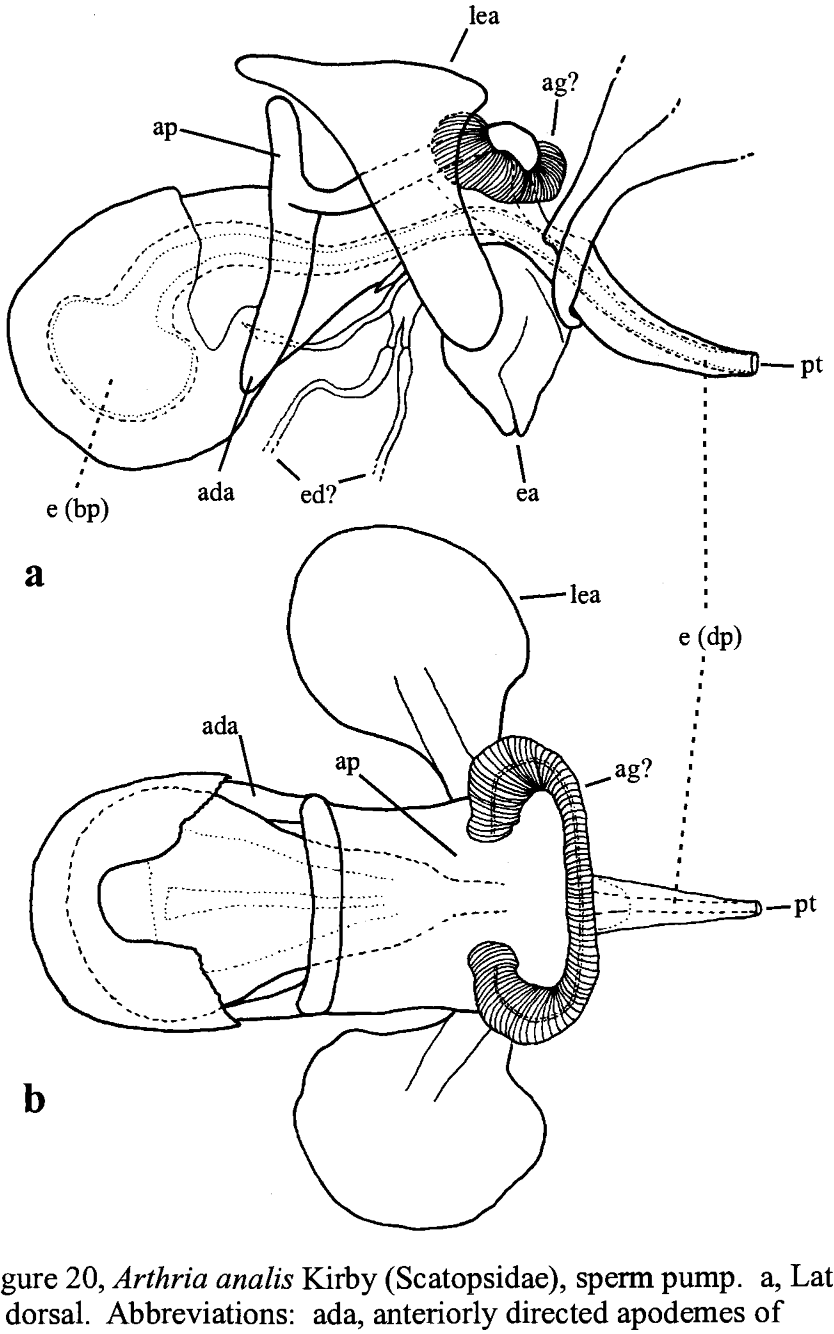


Figure 20, *Arthria analis* Kirby (Scatopsidae), sperm pump. a, Lateral. b, dorsal. Abbreviations: ada, anteriorly directed apodemes of aedeagal plate; ag, accessory glands; ap, aedeagal plate; ea, ejaculatory apodeme; e(bp), endophallus (basiphallus); ed, ejaculatory duct; e(dp), endophallus (distiphallus); lea, lateral ejaculatory apodemes; pt, phallotrema.

Figure 21, *Sylvicola cinctus* (Fab.) (Anisopodidae), male terminalia, internal. a, Parameres, sperm pump and adminiculum, lateral. b, Sperm pump, posteroventral. c, Sperm pump, lateral. Abbreviations: adm, adminiculum; ar, adminicular rods; ds, dorsal sclerite; ea, ejaculatory apodeme; e(bp), endophallus (basiphallus); ed, ejaculatory duct; e(dp), endophallus (distiphallus); gp, gonphyses; ma, median apodeme of paramere; ps, penis sac; pt, phallotrema; vla, ventrolateral apodemes of paramere.

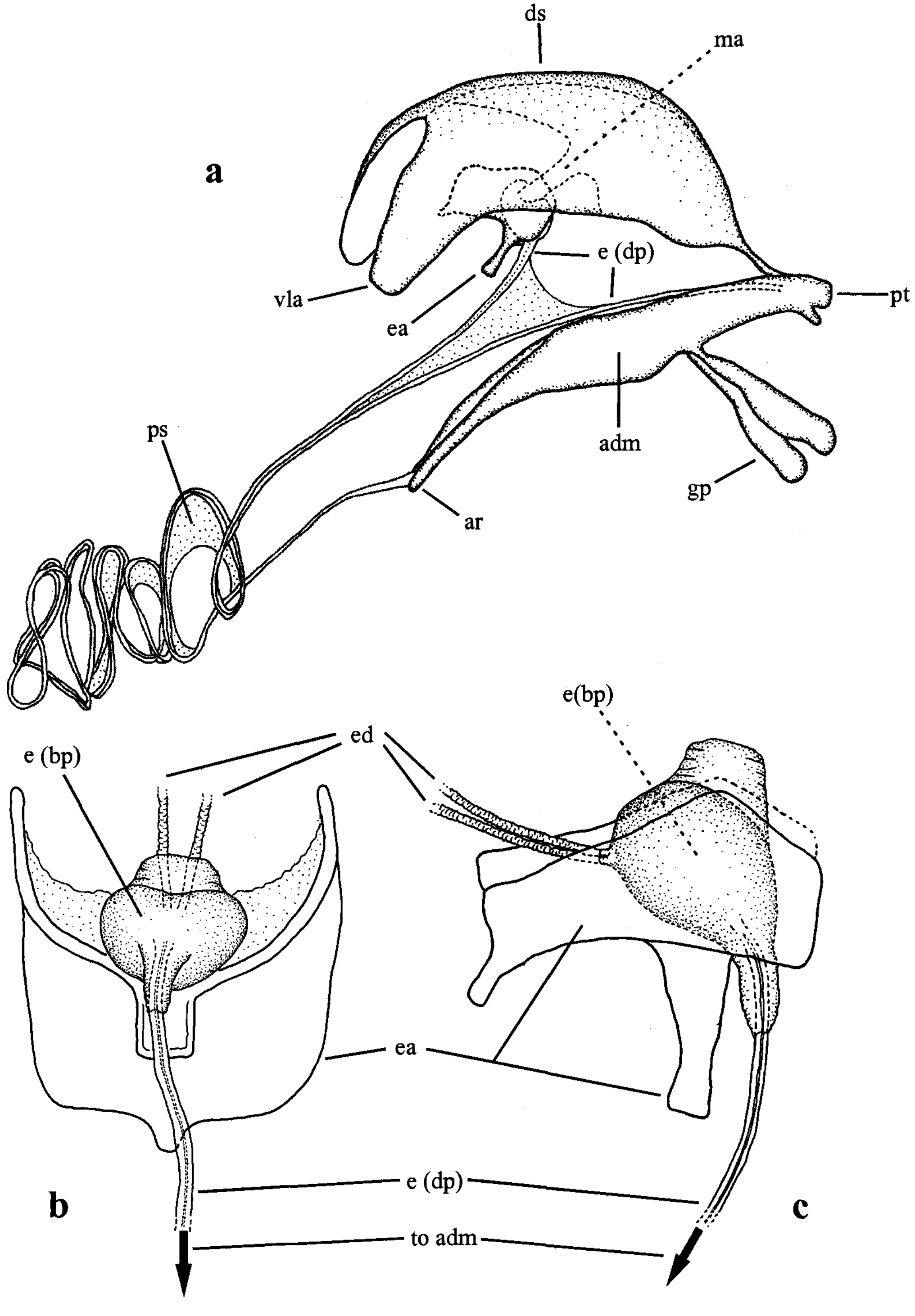


Figure 21, *Sylvicola cinctus* (Fab.) (Anisopodidae), male terminalia, internal.

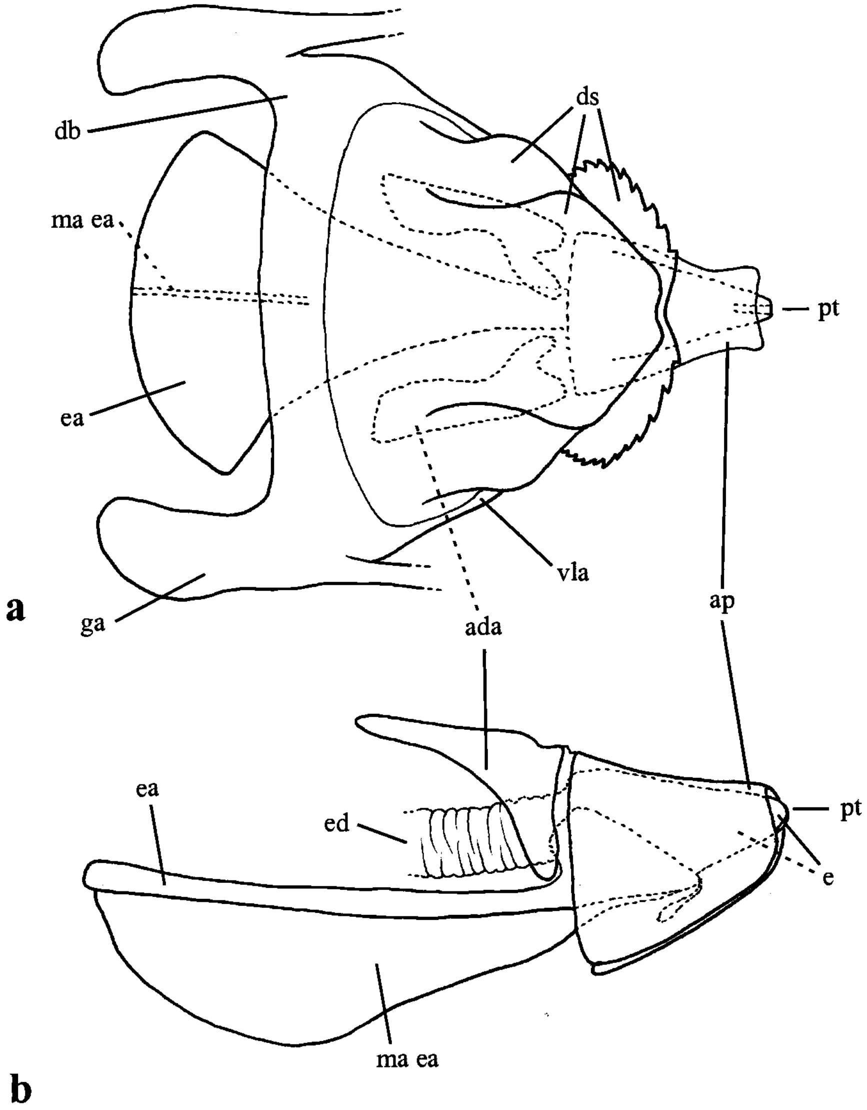


Figure 22, *Hesperinus brevifrons* Walker (Bibionidae), male terminalia, internal. a, Parameres and sperm pump, dorsal. b, Sperm pump, lateral. Abbreviations: ada, anteriorly directed apodemes of aedeagal plate; ap, aedeagal plate; db, dorsal bridge; ds, dorsal sclerite; e, endophallus; ea, ejaculatory apodeme; ed, ejaculatory duct; ga, gonocoxal apodeme; ma ea, median apodeme of ejaculatory apodeme; pt, phallotrema; vla; ventrolateral apodeme of paramere.

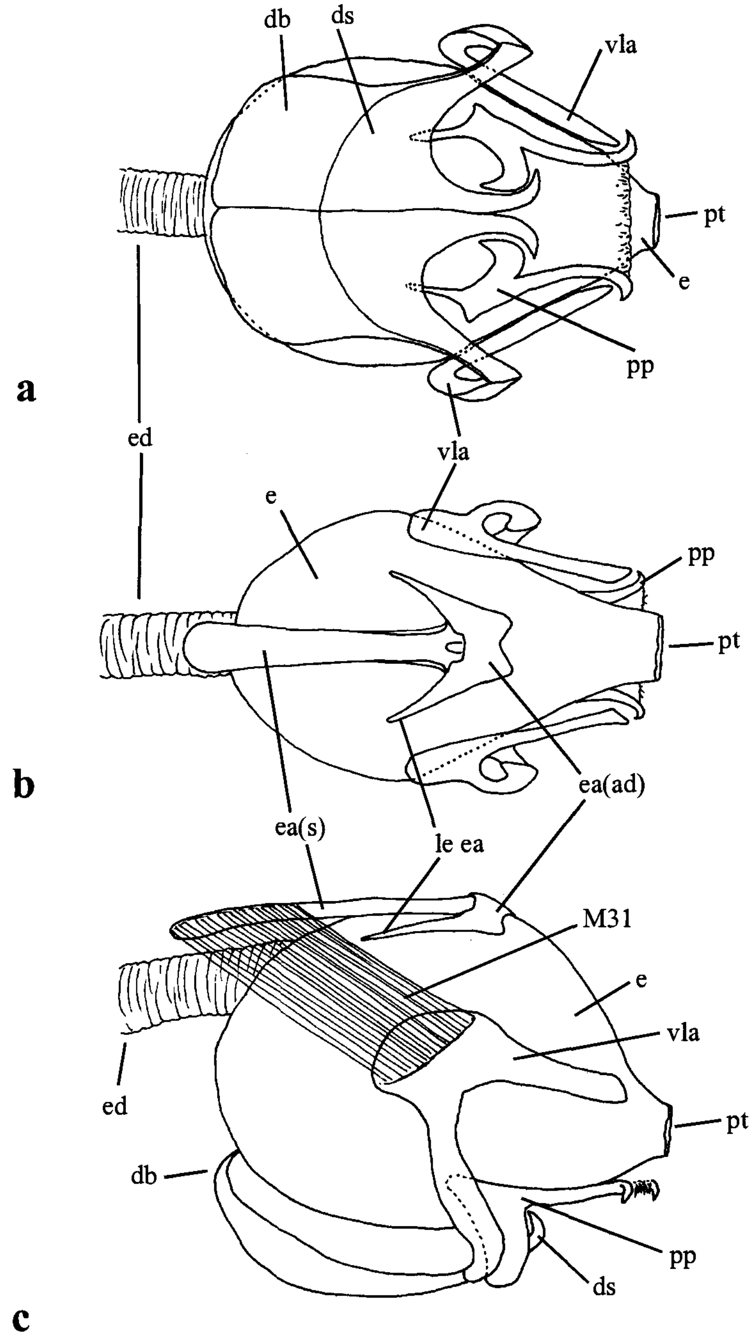


Figure 23, *Plecia nearctica* Hardy (Bibionidae), parameres and sperm pump. a, Dorsal. b, Ventral. c, Lateral. Abbreviations: db, dorsal bridge; ds, dorsal sclerite; e, endophallus; ea (ad), apical differentiation of ejaculatory apodeme; ea (s), shaft of ejaculatory apodeme; ed, ejaculatory duct; le ea, lateral extensions of ejaculatory apodeme; M31, muscle 31; pp, posterior processes of paramere; pt, phallotrema; vla, ventrolateral apodeme of paramere.

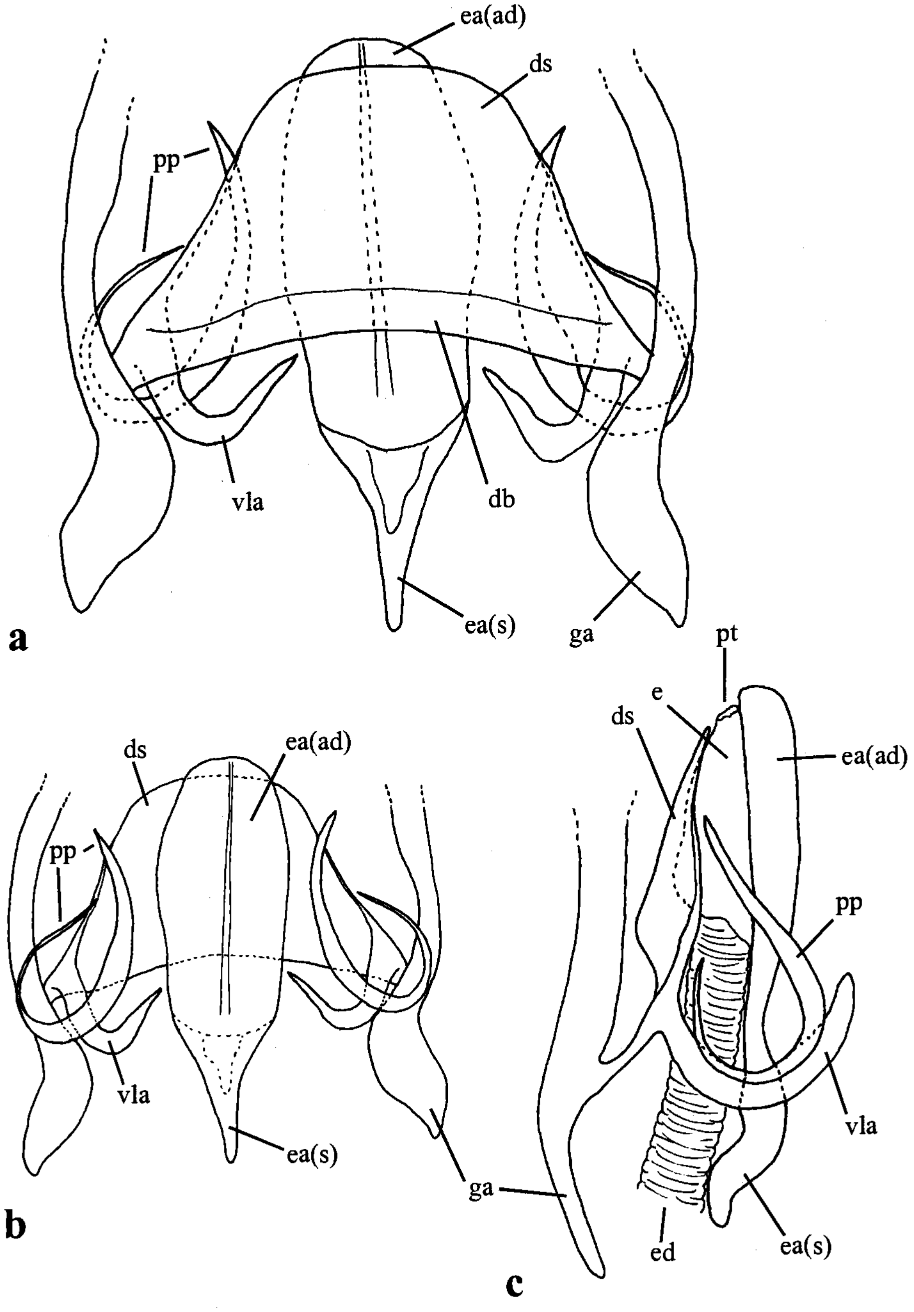


Figure 24, *Bibio albipennis* Say (Bibionidae), parameres and sperm pump. a, Dorsal, b, Ventral. c, Lateral. Abbreviations: db, dorsal bridge; ds, dorsal sclerite; e, endophallus; ea (ad), apical differentiation of ejaculatory apodeme; ea (s), shaft of ejaculatory apodeme; ed, ejaculatory duct; ga, gonocoxal apodeme; pp, posterior processes of paramere; pt, phallotrema; vla, ventrolateral apodeme of paramere.

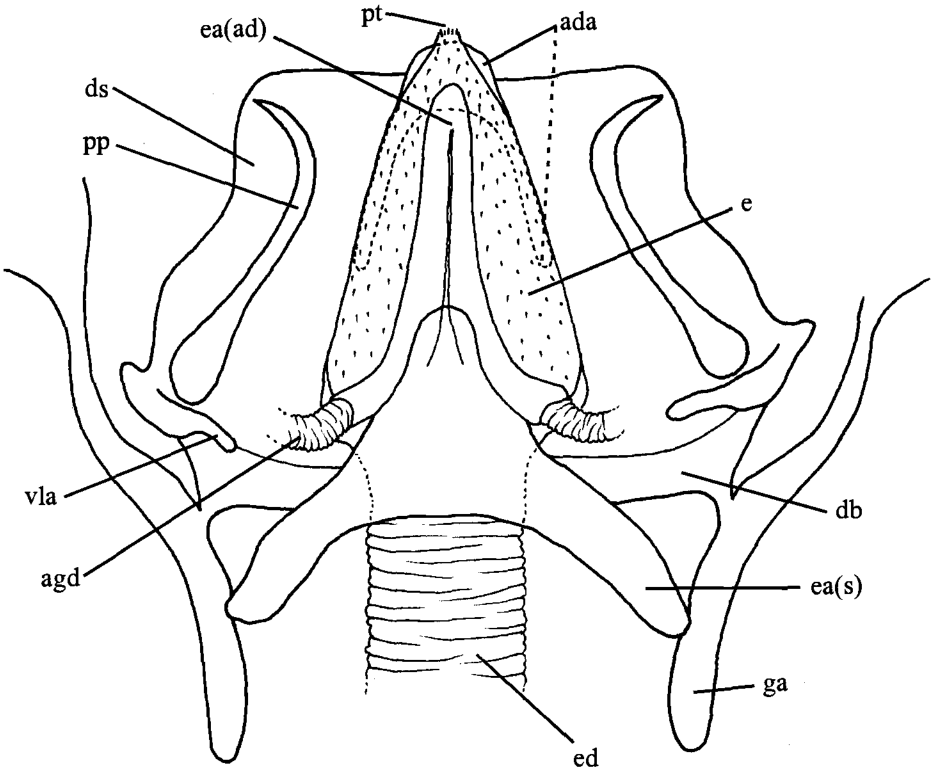


Figure 25, *Cramptonomyia spenceri* Alexander (Pachyneuridae), parameres and sperm pump, ventral. Abbreviations: ada, anteriorly directed apodemes of aedeagal plate; agd, accessory gland duct; db, dorsal bridge; ds, dorsal sclerite; e, endophallus; ea (ad), apical differentiation of ejaculatory apodeme; ea (s), shaft of ejaculatory apodeme; ed, ejaculatory duct; ga, gonocoxal apodeme; pp, posterior processes of paramere; pt, phallotrema; vla, ventrolateral apodeme of paramere.

SPERM PUMP

The sperm pump is composed of a conglomerate of structures and is considered part of the dipteran ground plan by Wood (1991). Sinclair *et al.* (1994: 409-410) provide a definition of the sperm pump for Orthorrhaphous Brachycera which is adequate in most respects to describe the structure of the pump observed in Bibionidae. However, the marked variation in the structure of the sperm pump and the inconsistent presence of all the structures associated with the pump across all the nematoceran taxa examined here requires additional discussion. As defined here the sperm pump includes at least the ejaculatory apodeme and endophallus (basiphallus + distiphallus), but often also includes at least some of the following structures depending upon the taxon: ejaculatory duct, lateral ejaculatory sclerites, aedeagus/aedeagal plate, and median apodeme of the paramere (see discussion of this structure under previous section concerning the "Dorsal sclerite"). These structures will be discussed individually below, but the basic structure of the pump is as follows.

The sperm pump is located at the junction of the endophallus and the ejaculatory duct, and is represented by an ejaculatory apodeme (Sinclair 2000). Either a paired or apparently unpaired ejaculatory duct, which begins at the vas deferens, enters the anterior portion of the endophallus (Fig. 23b, 24c). It is worthwhile to note that even in those taxa in which the ejaculatory duct appears to be unpaired (single), a cross-section of the duct indicates the existence of a median septum (*Plecia nearctica*, *Dilophus febrilis*, *Cramptonomyia spenceri* (pers. obs. and Trimble 1974; Fig. 1)), suggesting that the unpaired condition is likely the product of originally paired ducts that have become fused. The endophallus, especially the anterior portion, is almost always bounded on one side (often ventrally) by the ejaculatory apodeme, and on the other side (often dorsally) by all or part of the aedeagus/aedeagal plate (which may be plate-like, tubular, or subdivided into smaller sclerites; see discussion of aedeagus below)(Fig. 17a).

Wood (1991) reported that Bibionidae (except *Hesperinus*), Pachyneuridae, and Sciaroidea lacked an ejaculatory apodeme and hence a sperm pump, but Blaschke-Berthold (1994) showed that both the ejaculatory apodeme and a sperm pump are present in at least Bibionidae and Sciaroidea. The current investigation corroborates the latter study and also reports a sperm pump in Pachyneuridae and all outgroup taxa (Figs 17-25; ea). The homology of the individual parts of the sperm pump across all the taxa is established here based on position, structure, function, and musculature. Yet, the evolution of the dipteran sperm pump is complex and clearly requires additional study. Of particular value would be a study of the musculature in the nematoceran sperm pump. Such a study would greatly aid in confirming some of the tentative homologies suggested below regarding the aedeagal plate/aedeagus and its associated apodemes.

Ejaculatory apodeme

The ejaculatory apodeme is a sclerotized, unpaired rod or plate-like apodeme which serves as the attachment point for two to three pairs of muscles in nematocerous flies (Frommer 1963, Ovtshinnikova 1989, 1994a, Blaschke-Berthold 1994) and three pairs in Orthorrhaphous Brachycera (Ovtshinnikova 1987, 1989, 1994b, 2000, Palmer *et al.* 2000). Upon contraction, some of these muscles force the ejaculatory apodeme to compress the base of the endophallus in a piston or lever-like motion and help with the ejection of sperm or a spermatophore (Blaschke-Berthold 1994: 64, Sinclair *et al.* 1994, Sinclair 2000). These muscle pairs, particularly M31, which stretches between the ejaculatory apodeme and the ventrolateral apodeme of the paramere, is useful in establishing the homology of the ejaculatory apodeme and associated apodemes across taxa (Fig. 23c; M31).

The ejaculatory apodeme varies greatly in structure and position in relation to the other parts of the terminalia and some terminology is necessary to be able to discuss the different structure observed at opposite ends of the apodeme. The end of the apodeme which is the site of attachment for M31 (and sometimes M32) may be rod like (Fig. 24a), a ventrally flattened bar (Fig. 23b), a broad plate (Fig. 22a), laterally flattened, or bifurcate (Fig. 25). This end of the ejaculatory apodeme is anteriorly directed in most taxa and will be termed the "shaft" of the ejaculatory apodeme (Fig. 24a; ea(s)). The other end of the ejaculatory apodeme, which is posteriorly directed in most taxa, can be very different in structure than the shaft and will be termed the "apical differentiation" of the ejaculatory apodeme following Blaschke-Berthold (1994; "apikale Differenzierung des Ejakulator-Apodems")(Fig. 24a; ea(ad)). The apical differentiation may be narrower or broader than the shaft, but is always closely associated with the endophallus (Fig. 24; ea(ad)). In species with an apodeme operating in a piston-like motion, the apical differentiation is analogous to the head of the piston pressing against the base of the endophallus (Fig. 17b; ea(ad)); and in species that have an apodeme operating in a lever-like motion, the apical differentiation is the hinging-point that is usually attached to the wall of the endophallus by a membrane (Fig. 23c; ea(ad)). Blaschke-Berthold (1994; character 4) considered an ejaculatory apodeme that is differentiated into two parts synapomorphic for Bibionoidea + Mycetophiloidea. However, the ejaculatory apodeme of numerous taxa outside these groups (e.g. *Trichocera*, *Ctenophora*, Axymyiidae, and Anisopodidae) also have an ejaculatory apodeme with a two-part structure.

In some taxa, such as Axymyiidae and *Cramptonomyia*, the ejaculatory apodeme is also closely associated with the accessory glands. In these species a duct from each of two accessory glands attaches to the ejaculatory apodeme ventrally via a pair of sclerotized "spigots;" these spigots then lead into a duct(s?) that passes through the ejaculatory apodeme and empties into the endophallus (Fig. 25). Although a study of the accessory glands and their associated ducts has not been undertaken here, the fact that the accessory glands of bibionids are attached to the ejaculatory duct rather than passing through the ejaculatory apodeme (Blaschke-Berthold 1994, pers. obs.) suggests that a future study of these structures may provide additional character information.

118) Ejaculatory apodeme (CI: 0.25, RI: 0.62)

short (0)
elongate (1)

The ejaculatory apodeme is comparatively small in some species (e.g. *Sylvicola*, *Trichocera*, *Pachyneura*, and Axymyiidae (Figs. 18d, 21a; ea) while in other species, such as Bibionidae, the ejaculatory apodeme stretches approximately 3/4 of the length of the genital capsule (Fig. 24a-b).

This character provided no unambiguous support.

119) Shaft of ejaculatory apodeme with median apodeme (CI: 0.11, RI: 0.33)

absent (0)
present (1)

In some species, especially those that have a broadly dorsoventrally flattened ejaculatory apodeme (e.g. *Hesperinus brevifrons*), the ejaculatory apodeme has a longitudinal, laterally flattened, median flange, which helps support muscle attachment (Fig. 22a-b; ma ea). This flange is here termed the median apodeme of the ejaculatory apodeme and its presence gives the ejaculatory apodeme a T-shape when cross-sectioned.

This character is rather variable even at the generic level and showed considerable homoplasy within the analysis. Regardless, state 0 provides unambiguous support for node 2 and state 1 supports nodes 33 (clade within *Hesperinus*) and 108 (Scatopsidae).

120) Apex of the shaft of the ejaculatory apodeme (CI: 0.14, RI: 0.50)

rod-like (0)
dorsoventrally flattened (1)

Either a rod-like (roughly circular in cross-section) or a dorsoventrally flattened apex was observed here. This character does not include the change in the shape of the ejaculatory apodeme due to the presence of a median apodeme (see previous character). For example, *Hesperinus brevifrons* is coded as apex of shaft dorsoventrally flattened and median apodeme present.

A rod-like ejaculatory apodeme unambiguously supported Trichoceridae + (Anisopodidae + Scatopsidae) (node 39), though it is found in seven species representing various families outside this clade.

121) Apex of the shaft of the ejaculatory apodeme (CI: 0.50, RI: 0.50)
simple (0)
bifurcate (1)

The apex of the shaft of the ejaculatory apodeme in Cramptonomyiinae is bifurcated into two elongate arms (Fig. 25; ea(s)). Examination of muscle attachments confirms that this structure is homologous to the ejaculatory apodeme in other taxa because muscle M31 stretches from each arm of the bifurcated apex to the ventrolateral apodeme of the paramere. Though not as deeply bifurcate, a bifurcated ejaculatory apodeme was also observed in *Ctenophora*, and is reported in other Tipulidae as well (Jong 1993; Fig. 76).

The bifurcate ejaculatory apodeme unambiguously supports Cramptonomyiinae (node 35).

122) Apex of the shaft of the ejaculatory apodeme (CI: 0.11, RI: 0.28)
parallel-sided to slightly expanded anteriorly (0)
tapering anteriorly (1)
broadly expanded anteriorly (2)

The shape of the apex of the shaft the ejaculatory apodeme varies considerably even within genera. State 0 unambiguously supports node 11 within *Plecia* and state 1 supports Cramptonomyiinae (node 35).

123) Apex of apical differentiation of ejaculatory apodeme (CI: 0.50, RI: 0.50)
serrate (0)
smooth (1)

In axymyiids (pers. obs.) and *Pachyneura* (Wood 1991; Fig. 7c) the apical differentiation of the ejaculatory apodeme is minutely serrate, while in other taxa the serrations are absent. The apex of the ejaculatory apodeme of *Pachyneura* is external and the serrations probably come into contact with the female terminalia. In contrast, the apex of the ejaculatory apodeme of axymyiids is internal and the serrations appear to press against the base of the endophallus. Considering these differences it seems unlikely that the serrated condition is homolgous in both taxa, but it is tentatively coded as homologous until additional evidence suggests otherwise.

The analysis indicates that the serrated condition has arisen independently in these two taxa and it provides unambiguous support for Axymyiidae (node 44).

124) Endoaedeagal process (CI: 0.50, RI: 0.50)
absent (0)
present (1)

The presence of an endoaedeagal process is considered a synapomorphy of the Brachycera and "is lacking in the Nematocera" (Sinclair *et al.* 1994). *Dialysis*, the only brachyceran included in this analysis, has a large spine-like endoaedeagal process which projects into the apex of the endophallus. However, a similar, but considerably smaller, spine-like structure exists in the bibionid genus *Dilophus*. As in *Dialysis*, it projects from the apical differentiation of the ejaculatory apodeme into the sack-like endophallus (Fig. 16c-d; es). It seems unlikely that the structures in *Dilophus* and *Dialysis* are homologous, but they are coded as such until additional evidence suggests otherwise.

The analysis indicates that the endoaedeagal spine observed in Brachycera and *Dilophus* are not homologous.

125) Ejaculatory apodeme with lateral extensions supporting lateral rim of sperm sac (CI: 0.33, RI: 0.92)

absent (0)
present (1)

In *Plecia, Penthetria*, and *Bibionellus*, a pair of elongate structures, ranging from lightly sclerotized ribbons to more heavily sclerotized rods, extend from the apical differentiation of the ejaculatory apodeme and run along the edges of the endophallus (Fig. 23b; le ea). These lateral extensions of the ejaculatory apodeme may be elongate or present only as short nubs on the apical lateral edge of the apical differentiation.

This character did not provide any unambiguous support.

126) Lateral extensions of ejaculatory apodeme (CI: 0.25, RI: 0.77)

elongate (0)
short nubs (1)
absent (2)

See discussion of previous character. State 0 unambiguously supports *Plecia* (node 8), though there are subsequent changes to alternative states within the genus, including a change back to state 0 which unambiguously supports node 13. Additionally, state 1 provides unambiguous support for *Penthetria*.

127) Ejaculatory apodeme (CI: 0.33, RI: 0.60)
perpendicular to base of endophallus (0)
parallel to base of endophallus (1)

In some taxa the shaft of the ejaculatory apodeme rests perpendicular to the base of the endophallus or basiphallus so that if one were to extend an imaginary line following the plane of the ejaculatory apodeme, it would intersect the endophallus at a nearly right angle (Figs. 17a, 19a, 21c). In contrast, other taxa have the shaft of the ejaculatory apodeme sitting in such a position that if the above imaginary line were drawn it would not intersect the endophallus, but would run parallel to it (Fig. 23c, 24c). The fact that both character states have been observed in Tipulidae (Wood 1991; Figs. 2-5) suggests that the plane of the ejaculatory apodeme, relative to the base of the endophallus, may have changed multiple times independently and thus be subject to homoplasy.

The perpendicular ejaculatory apodeme unambiguously supports Trichoceridae + (Anisopodidae + Scatopsidae)(node 39), with a subsequent reversal in *Mycetobia.*

128) Apex of shaft of ejaculatory apodeme oriented (CI: 0.80, RI: 0.66)
dorsally (0)
anteriorly (1)
posteriorly (2)
anteroventrally (3)
ventrally (4)

The ejaculatory apodeme varies considerably in its relative position in the genital capsule and, as with the previous character, may be subject to homoplasy. Most of the taxa have the shaft facing anteriorly. The exceptions are *Scatopse*, *Mycetobia*, and *Bolitophila* which have the shaft facing posteriorly, *Arthria* ventrally (its apex is fused to the inner surface of the synsternogonocoxite), *Sylvicola* anteroventrally, and *Ctenophora* dorsally.

The posteriorly directed ejaculatory apodeme (state 2) unambiguously supports Anisopodidae + Scatopsidae (node 40), though *Sylviocla* changes to state 3 and *Arthria* to state 4.

Endophallus

The endophallus is the sack-like and/or tubular seminal duct which receives the contents of the ejaculatory duct(s) and accessory glands anteriorly and transports these products posteriorly through the secondary sexual opening(s): the phallotrema. Posteriorly, it is sometimes guided by a ventral "aedeagal guide" (Wood 1991; e.g. Fig. 5c-e), or a tubular or collar-like aedeagus.

The term "endophallus" has been used in more than one context in describing the seminal duct of Diptera, and therefore requires clarification. Bonhag (1951) labeled the seminal duct in Tabanidae as the endophallus. Sinclair (2000) states that the "endophallus" *sensu* Bonhag (1951) is equivalent to the "sperm sac," but later uses the term "endophallus" to communicate "a tubular extension of the sperm sac." To avoid further confusion of this term, and to have a term available for those taxa that do not have the seminal duct strongly differentiated into two parts, the term "endophallus" is here used in the broader sense to refer to the entire seminal duct. Many taxa have an endophallus that is pear-shaped (anteriorly broad, and gradually tapering posteriorly to the phallotrema(Fig. 23b; e)). In contrast, other taxa have the anterior portion of the endophallus sac- or bulb-like (Fig. 17a; e(bp) and strongly differentiated from a tubular or capillary-like posterior portion (Fig. 17a; e(dp)). In these taxa (e.g. *Ctenophora* and *Sylvicola*), two terms are used to communicate the marked subdivisions of the endophallus: a bulb-like anterior "basiphallus" ("sperm sac" of Sinclair 2000) and a tubular posterior "distiphallus" (used by Yeates 1994 as synonymous with the term "aedeagus" of previous authors). The distiphallus may be a single tube (e.g. *Ctenophora*, *Scatopse*), distally paired (*Mycetobia*), or tripartite (e.g. some Orthorrhaphous Brachycera (Yeates 1994), some Blephariceridae (Zwick 1977)).

There is considerable confusion regarding the difference between the aedeagus and the endophallus, particularly when a strongly differentiated distiphallus is present. Although the endophallus is membranous in most taxa, it is lightly to moderately sclerotized in some groups, particularly in those cases where the basiphallus and distiphallus are differentiated. For example, the endophallus of *Trichocera*, and Axymyiidae n. sp. is not strongly differentiated, but gradually tapers to a single opening (Figs. 17c, 18d; e). Likewise, in both taxa the endophallus is membranous and is enclosed and guided by a heavily sclerotized aedeagus (Figs. 17c, 18d; ap). Similarly the endophallus of *Hesperinus* is membranous and sack-like, and is apically enclosed by a sclerotized, collar-like aedeagus (Fig. 22; ap). In cases where the basiphallus and distiphallus are strongly differentiated, such as *Sylvicola, Mycetobia* and *Scatopse*, we also see a more moderately sclerotized endophallus. The distiphallus is endophallic in origin and is continuous with the basiphallus, whereas the aedeagus is a separate sclerite which (when present) partially or entirely encloses and guides the endophallus.

Although it is beyond the scope of this study, initial examination of some Blephariceridae suggests that the structure referred to as the "penis filaments" (Zwick 1977) or "aedeagus" (Courtney 2000; Fig. 22) is homologous to the distiphallus (i.e. endophallic in origin) rather than an aedeagus as defined above. In blephariceridis, this structure is continuous with the basiphallus ("vesica" Zwick 1977), and the capillary-like structure is more suggestive of the distiphallus of Anisopodidae (Fig. 21; e(dp)) than of the aedeagus of any of the aforementioned taxa. An almost identical structure to that of Blephariceridae is found in some Bombyliidae (Yeates 1994; Fig. 382-383), in which the distiphallus is also continuous with the basiphallus and the aedeagus is absent. However, a true aedeagus is clearly present in some Orthorrhaphous Brachycera, as can be observed in *Dialysis* which has a collar-like aedeagus that encloses and guides the largely membranous endophallus. An identical collar-like aedeagus is also found in the bibionid genus *Hesperinus* (Fig. 22; ap)(Sinclair 2000; Figs. 10-11, "aed").

129) Endophallus (CI: 0.50, RI: 0.80)

differentiated into distiphallus and basiphallus (0)
not differentiated (1)

See above discussion. *Ctenophora*, *Anisopodidae*, *Scatopsidae* have a strongly differentiated endophallus with a bulb-like basiphallus and a slender tubular distiphallus (Figs. 17a, 19a, 21a-b). The undifferentiated endophallus is sack-like and gradually tapered posteriorly (Fig. 18d, 23, 24c; e).

The differentiated endophallus unambiguously supports Anisopodidae + Scatopsidae (node 40).

130) Endophallus (CI: 1.00, RI: 1.00)

coiled (0)
linear (1)

The very elongate, capillary-like distiphallus of *Sylvicola* is uniquely coiled (Fig. 21a; e(dp)). Amorim and Tozoni (1994) consider this "coiled penis rod" as synapomorphic for *Sylvicola* and *Tonnoirina*, which they treat as the separate family Anisopodidae *sensu stricto*. A coiled distiphallus was here observed in only one other taxon, *Scatopse fuscipes* Meigen, but in this taxon the distiphallus does not coil anteriorly and then double-back on itself to form a paired coil which then extends posteriorly (as it does in *Sylvicola*). Consequently, the double coil observed in *Sylvicola* is not considered homologous with that observed in *S. fuscipes*.

The coiled distiphallus provides unambiguous support for node 42 (*Sylvicola*).

Aedeagus, adminiculum, and lateral ejaculatory sclerites

As previously mentioned under the discussion of the "Endophallus," the aedeagus is a distinct sclerite that is not to be confused with the endophallus/distiphallus. When the tubular aedeagus is present it is in close association with the endophallus and either encloses all of the endophallus or encloses only the apical portion for which it acts as a guide (e.g. Fig. 17b-c, 22; ap).

The following interpretation of the aedeagus requires additional study, but rests on the basic tenants of homology assessment which include similarity of position, structure, and function. Additional evidence was obtained by examining musculature. The aedeagus, as defined in the following discussion, is interpreted as homologous to the ventral plate of the sperm pump observed in tipulids such as *Ctenophora* and *Dolichopeza* (Fig. 17a; ap). Additionally, the lateral ejaculatory processes, which are considered synapomorphic of the Brachycera (Sinclair *et al.* 1994), are interpreted as originating from this sclerite (i.e. they are aedeagal in origin)(Fig. 17a; lea).

The basic structure of the sperm pump in nearly all the taxa examined here can be described as an endophallus sandwiched between an ejaculatory apodeme and another sclerite (Fig. 17). This second sclerite, despite its diverse structure, is homologous in all the included taxa based primarily on its position relative to other structures of the sperm pump. To make this homology assessment transparent, a discussion of the diversity of this sclerite (and associated sperm pumps) in multiple taxa is necessary. Nevertheless, the implied transition of structure does not necessarily represent an evolutionary transition series, but is merely an example of how intermediate forms connect dissimilar forms. The aedeagus and related structures are discussed in more detail in the following taxa:

Tipulidae: In *Ctenophora* and *Dolichopeza*, the sclerite opposite the ejaculatory apodeme, which is here termed the "aedeagal plate," is in the form of a plate that not only encloses the basiphallus on the surface opposite the ejaculatory apodeme, but also wraps around the lateral edges of the basiphallus (Fig. 17a; ap). In

Frommer's (1963) study of tipulid genitalia, this plate is called "the immovable apodemes of the semen pump." These immovable apodemes include a pair of elongate, posteriorly-oriented apodemes (Fig. 17a; ada), and a pair of short, broadly flattened, anteriorly-oriented apodemes (Fig. 17a; lea). Both pairs of apodemes serve in part as the attachment points for two pairs of muscles that operate the ejaculatory apodeme (Byers 1961, Frommer 1963, Ovtshinnikova 1980, pers. obs. in *Ctenophora*). The rotation of the sperm pump in these taxa is unusual, with the shaft of the ejaculatory apodeme facing dorsally, the aedeagal plate ventral, and the distiphallus running anteriorly and then looping ventrally under the sperm pump and running posteriorly (Fig. 17). However, if we rotate the sperm pump in these taxa so that the distiphallus points posteriorly, the aedeagal plate becomes dorsal, and the ejaculatory apodeme is in more of an anteroventral position, the components of this sperm pump easily translate into the components of the sperm pump in other tipulids such as *Hexatoma austere* or *Epiphragma*. It is likely that such a sagital rotation is nearly achieved in *Dolichopeza*, when the sperm pump rocks on the adminicular rods to extrude the distiphallus (Byers 1961). *Hexatoma austere* has a similarly structured dorsal aedeagal plate that covers the basiphallus, ventral ejaculatory apodeme, and posteriorly pointing distiphallus. The primary difference in structure between *Dolichopeza* and *Hexatoma* is that in *Hexatoma* the posteromedian portion of the aedeagal plate is formed into a long, slender, posteriorly-directed tube that ensheaths the distiphallus, and the strongly developed apodemes of the plate are absent. The same is true of the tipulid genus *Epiphragma*, except in this genus the strongly developed apodemes are maintained (Wood 1991; Fig. 2). The basic structure of the sperm pump is otherwise very similar in these taxa because the endophallus is bounded on one side by the aedeagus or aedeagal plate, and on the other side by the ejaculatory apodeme. The tipulid aedeagus is considered homologous to the tubular aedeagus observed in Axymyiidae, which also encloses the endophallus and has elongate anteriorly-directed apodemes (Fig. 17b-c).

Axymyiidae and Trichoceridae: Of the taxa studied here, only Axymyiidae, and *Trichocera* have a well developed tubular aedeagus which has not been reduced to a simple apical collar as seen in *Hesperinus* and *Dialysis*. In both axymyiids and *Trichocera* the membranous endophallus is enclosed by the sclerotized tubular aedeagus, but is clearly sandwiched between a more ventral ejaculatory apodeme and a more dorsal aedeagus. In both taxa the ejaculatory apodeme is in a more ventral plane than the endophallus based on the fact that the ejaculatory duct enters the base of the endophallus dorsal to the ejaculatory apodeme (Fig. 17b, 18d). Since the aedeagus is somewhat tubular it bounds both sides of the endophallus, but at least in axymyiids is a continuous surface only dorsally and does not completely meet midventrally; i.e. the tubular condition seems to be the product of a dorsal plate that has folded lateroventrally to enclose the endophallus. Furthermore, the axymyiid aedeagus has a pair of elongate anteriorly-directed apodemes which correspond to the apodemes discussed previously in Tipulidae (Fig. 17a-c; ada)("posterior immoveable apodemes" of Frommer 1963). These apodemes extend from the anterior ventrolateral edges of the aedeagus, which is where they would be expected to occur if the aedeagus were the product of a dorsal plate that has folded ventrolaterally. A similarly structured aedeagus has been observed in some Tipulidae such as *Epiphragma*, which has a tubular aedeagus that does not quite meet midventrally and is strikingly similar in structure to the aedeagus of axymyiids in lateral view (compare Figs. 2a and 9e of Wood 1991). In contrast, the aedeagus of *Trichocera* is not markedly tubular and does not have elongate anteriorly-directed apodemes. Yet, it does enclose the endophallus opposite the ejaculatory apodeme and does not have the structure characteristic of an adminiculum (see discussion of "Anisopodidae and *Scatopse*"); it is therefore considered homologous to the axymyiid aedeagus. Furthermore, both *Trichocera* and axymyiids have a muscle pair which stretches between the more ventral ejaculatory apodeme and the more dorsal aedeagus (Figs. 17b-c, 18b). This muscle pair may be homologous to the muscle pair observed stretching between the ejaculatory apodeme and the posteriorly-directed apodeme of the aedeagal plate in *Dolichopeza*, but establishing such a homology requires a broad study of the musculature in numerous nematocerous families. Ovtshinnikova (1994a) treats this muscle pair (M32) in *Trichocera* as homologous to the muscle pair that stretches between the ejaculatory apodeme and the "lateral ejaculatory processes" (Sinclair *et al.* 1994) of Orthorrhaphous Brachycera (Fig. 18b; M32). This is important because it suggests an aedeagal origin for these sclerites which will soon be discussed further.

Hesperinus and *Dialysis*: These two taxa are the only other species examined which have a tubular aedeagus. However, in both these species the aedeagus is reduced to a small aedeagal collar that guides the apex of the endophallus. This aedeagal collar is similar in structure to the apex of the axymyiid aedeagus because it is a continuous surface dorsally and does not completely meet midventrally (again giving the impression of a plate in which the lateral edges have been folded ventrally)(Fig. 22b; ap). In both *Hesperinus* and *Dialysis* there is a pair of sclerites which lie on the dorsal surface of the endophallus; these sclerites are called the the "lateral ejaculatory sclerites" when found in Orthorrhaphous Brachycera (Sinclair *et al.* 1993). Sinclair *et al.* (1993) noted that these structures in *Hesperinus* (Fig. 22; ada) "appear homologous to lateral ejaculatory processes in the Brachycera," but that "knowledge of the muscles of the sperm pump would greatly assist in determining the homology of these sclerites." A similar horseshoe-shaped sclerite is also found in *Cramptonomyia* (Fig. 25; ada) and *Pachyneura* and at least the former taxon has no muscle running from this sclerite to the ejaculatory apodeme which would suggest that this sclerite is at least not functionally homologous to the lateral ejaculatory sclerites of Brachycera. In pachyneurids this sclerite is more likely the remainder of the dorsal aedeagal plate which bears the rod-like, anteriorly-directed apodemes. As in *Scatopse* (discussed below) these apodemes have become reduced in size because they no longer serve as an attachment point for muscles which operate the ejaculatory apodeme (Fig. 19; ada). Due to a lack of specimens in alcohol, the musculature of *Hesperinus* has not been examined, but the sclerites in this taxon are considered homologous to the anteriorly directed apodemes of the aedeagal plate in

Pachyneuridae, Axymyiidae and Tipulidae for several reasons. The structure of these sclerites in both *Hesperinus* and Pachyneuridae are very similar and are identical in position; they lie on the dorsal surface of the endophallus, opposite the ventral ejaculatory apodeme that lie along the ventral surface of the endophallus. The slender horseshoe-shaped structure of this plate in *Cramptonomyia* (Fig. 25) is nearly identical to that found in *Hesperinus* species other than *H. brevifrons* which has a pair of sclerites that are medially divided and more strongly developed and flattened (Fig. 22; ada). Furthermore, in *Hesperinus* these sclerites are closely associated with the anterior margin of the aedeagal collar and are separated from it by a narrow transverse strip of membrane (Fig. 22; ada)(Sinclair 2000; Fig. 11). The sclerites are clearly associated with the aedeagal collar because they "tear off" with the aedeagal collar in dissections, which is not true of the lateral ejaculatory sclerites in *Dialysis*. Furthermore, the sclerites in *Hesperinus* are posteromedially adjacent so that together they form a horseshoe-shaped plate, with the elongate, lateral portions of the horseshoe extending anteriorly (Fig. 22) as do the anteriorly directed apodemes of the aedeagus of axymyiids and some tipulids (Fig.17; ada). Sinclair *et al.* (1994) noted the similarity between these sclerites in *Hesperinus* and the lateral ejaculatory processes in Orthorrhaphous Brachycera, but stated that "they do not appear to be associated with the anterior margin of the sperm sac and hence are not considered homologous." Indeed, despite the lack of much needed muscular evidence for *Hesperinus*, this investigator agrees with Sinclair *et al.* (1994) that the sclerites in *Hesperinus* are not homologs to the lateral ejaculatory sclerites in Orthorrhaphous Brachycera. The lateral ejaculatory sclerites of *Dialysis* will be discussed further under the section "Anisopodidae and *Scatopse*" below.

Anisopodidae and *Scatopse*: The tubular aedeagus is absent in these taxa, but is functionally replaced by an adminiculum, which is interpreted here as homologous to that found in tipulids. The term "aedeagal guide" is not used here because the structure is not a guide for the aedeagus (but rather for the distiphallus) and also because this term has been loosely used to describe numerous, and not necessarily homologous ventral structures in Diptera, which makes its usage somewhat problematic. The adminiculum in tipulids is an aedeagus-like structure that is fused to, and presumably originates from, the posteroventral margin of the ventrally fused gonocoxites. Similar to an aedeagus, the adminiculum acts as a guide for the endophallus and often has elongate anteriorly-oriented apodemes ("adminicular rods" of Byers 1961)(Fig. 21a; adm). However, the tipulid adminiculum differs in structure from the aedeagus as described above because it is a continuous surface ventrally, but dorsally it is a groove or channel rather than a closed tube. This is opposite the structure of the aedeagus observed in axymyiids, *Hesperinus*, and *Dialysis*, which are continuous dorsally and incompletely fused ventrally (Fig. 22b; ap). The adminiculum of *Sylvicola* has the groove or channel-like structure observed in tipulids and like the tipulid adminiculum, the thin membranous pouch or "penis sac" (Abul-Nasr 1950; "genital sac" of Rees & Ferris 1939), which holds the elongate distiphallus, is posteriorly attached to the adminicular rods (Byers 1961)(Fig. 21a; ps, ar). The adminiculum of *Mycetobia* and *Scatopse* is a complete tube but, like tipulids, is fused to the posterior margin of the gonocoxites and, besides guiding the apex of the distiphallus, does not otherwise seem to be associated with the sperm pump. Furthermore, as in tipulids, the adminiculum of *Sylvicola* and *Scatopse* is associated with a pair of lobate structures that are either fused to the ventral subapical surface of the adminiculum (*Sylvicola*) or are not fused, but cradle the apex of the adminiculum ventrally (*Scatopse*). These structures are termed gonopophyses in tipulids and are typically found in a fused condition (Fig. 21a; gp)(Byers 1961, Jong 1993).

Although the tubular aedeagus is absent in Anisopodidae and Scatopsidae, the homologous aedeagal plate, as observed in *Ctenophora* and *Dolichopeza*, is present (except in *Sylvicola*). As previously discussed, the aedeagal plate in *Ctenophora*, *Dolichopeza* and many other Tipulinae (Snodgrass 1904) is characterized by two pairs of apodemes; one broad and flattened pair, and one more rod-like, elongate pair. If the Tipulinae sperm pump is rotated to match the orientation of the pump in *Scatopse*, for example, which has a posteriorly facing ejaculatory apodeme, the homology of the apodemes of the aedeagal plate is apparent (compare Figs. 17a and19a). Both taxa have a basiphallus sandwiched between an ejaculatory apodeme on one side and a continuous plate (tipulids), or a subdivided plate (*Scatopse*), on the other side. In Tipulinae, the broad, flat apodemes arise at the same end of the plate where the distiphallus arises from the basiphallus (Fig. 17a; lea). This is also true for *Scatopse* except that these apodemes are detached from the remainder of the plate (Fig. 19a; lea), which still covers part of the surface of the basiphallus and has the additional pair of rod-like, anteriorly-directed apodemes as found in the tipulids (Fig. 19a; ap, ada). Unlike *Ctenophora* and *Dolichopeza*, in *Scatopse* these detached apodemes stick out at more of a right angle from the remainder of the plate, but such a lateral orientation of these apodemes has also been observed in other Tipulinae such as *Tipula bicornis* Forbes (Snodgrass 1904; Fig. 97). In *Ctenophora* and *Dolichopeza*, each of the two pairs of apodemes (Fig. 17a; lea, ada) of the aedeagal plate has a muscle pair which runs from the apodemes to the ejaculatory apodeme (Fig. 17a; ea(s))(Byers 1961, Frommer 1963, Ovtshinnikova 1980, pers. obs. in *Ctenophora*). In *Scatopse* only one muscle pair is retained, but like the tipulids it runs between the broad flat apodemes (Fig. 19a; lea) and the ejaculatory apodeme (pers. obs.). Corresponding to the lack of a second muscle pair in *Scatopse*, the elongate, rod-like apodemes (Fig. 19a; ada) are reduced in size and length in this taxon compared to those observed in the tipulids (Fig. 17a; ada). Ovtshinnikova (1989) labels the muscle pair running from the broad flat apodeme to the ejaculatory apodeme in *Tipula* as M10; a muscle which apparently disappears in the remainder of the Diptera she examined.

However, the detached apodemes present in *Scatopse* (Fig. 19; lea), and *Arthria* (Fig. 20; lea), are arguably not only homologous to the broad flat apodemes in Tipulinae (Fig. 17a; lea), but probably also to the "lateral ejaculatory processes" of Brachycera (Sinclair *et al.* 1993). Sinclair *et al.* (1993) noted the presence of these detached apodemes ("articulated paired processes") in the scatopsid *Aspistes*, but stated that "they do not appear to be associated with the anterior margin of the sperm sac and hence are not considered homologous" to the lateral ejaculatory sclerites in

Brachycera. Their conclusion is not followed here for several reasons. Despite the difference in position, in both scatopsids and most Orthorrhaphous Brachycera, these lateral ejaculatory sclerites are associated with the endophallus opposite the ejaculatory apodeme (Fig. 19b) and have a single muscle pair (M32 of Ovtshinnikova 1989) that stretches from the sclerites to the ejaculatory apodeme. A homologous interpretation of these sclerites also explains the fact that M32 stretches between the ejaculatory apodeme and the tubular aedeagus in *Trichocera* (Ovtshinnikova 1994a)(Fig. 18b), because the tubular aedeagus, the lateral ejaculatory processes, and the aedeagal plate of Tipulinae are here considered homologous. Furthermore, this interpretation would also account for the "disappearance" of Ovtshinnikova's M10, and "appearance" of M32; here these muscles are considered homologs.

Concerning the lateral ejaculatory sclerites, Sinclair *et al.* (1993) noted that "fused lateral processes arising from the base of the tubular aedeagus are found in the Tipulidae [e.g. *Liogma* Osten Sacken and *Dolichopeza* Curtis (Wood 1991, figs 3b, 5c)]," but that "these processes are not considered homologous to the lateral ejaculatory processes in the ground plan of the Brachycera, because they are not articulated and thus do not function to compress the sperm sac as they do in Brachycera." It is not clear which pair of apodemes Sinclair *et al.* are referring to, and only one of the two pairs of apodemes is here considered homologous to the lateral ejaculatory sclerites (the broad, flat, anteriorly-oriented apodeme opposite the slender elongate posteriorly-oriented apodeme in Wood (1991; Fig. 5e). However, if Sinclair *et al.* are referring to the broad apodemes, their analysis of the homology of these structures confounds character homology and character state homology. The difference between an articulated and a non-articulated apodeme constitutes a distinct character state but, it does not constitute a distinct character. Regardless of whether or not the broad, flat, apodemes are fused to the aedeagal plate (as in Tipulinae) or are detached (as in scatopsids and Orthorrhaphous Brachycera), if they have a homologous origin they should be treated as homologous structures with different states (where the character state describes the relative difference in structure).

Arthria: Although the scatopsid genus *Arthria* has an aedeagal plate and well developed lateral ejaculatory sclerites, it is unclear whether it has a tubular aedeagus, an adminiculum, or neither structure (Fig. 20). The distal portion of the endophallus of this taxon either lies within a conical sclerotized tube or is itself expanded into a conical sclerotized tube. The tubular structure in question is associated with the posterior edge of the aedeagal plate, but it is unclear whether or not it arises from the aedeagal plate. The tubular structure does not appear to be an adminiculum because it is not fused to the ventral margin of the fused gonocoxites, has no dorsal groove and no associated gonopophyses. The structure does not show similarity in structure to the tubular aedeagus of other taxa and it is possible that it is simply a thickening of the distal part of the distiphallus. Considering the uncertain homology of this structure it has been scored as a "?."

131) Posterior end of aedeagal plate (CI: 0.28, RI: 0.44)
not produced into a tubular aedeagus (0)
produced into a tubular or collar-like aedeagus (1)
absent (2)

Character state "0" is assigned to those taxa that have the posterior portion of the aedeagal plate present (identified by the broad flat apodemes) but not developed into a tubular aedeagus: *Ctenophora*, *Scatopse*, and *Mycetobia* (Fig. 17a, 19; ap). A tubular aedeagus was observed in axymyiids, *Trichocera*, *Hesperinus*, and *Dialysis* (Fig. 17b-c, 18c, 22; ap). The posterior part of the aedeagal plate is absent in the remainder of the taxa, even though some of these taxa retain the anterior part of the plate (i.e. the broad, flat apodemes and tubular aedeagus are absent, yet a plate with anteriorly directed apodemes is present, such as in pachyneurids (Fig. 25; ada)).

The absence of the posterior end of the aedeagal plate (state2) unambiguously supports Bibionomorpha *sensu stricto* (node 3), though there is a change to state 1 that supports node 33 within *Hesperinus* and a change to state 0 in Bolitophilidae.

132) Anteriorly-directed apodemes of aedeagal plate/aedeagus (CI: 0.25, RI: 0.70)
present (0)
absent (1)

Because of the unusual orientation of the sperm pump in Tipulinae (e.g. *Ctenophora*), the rod-like elongate apodemes of the aedeagal plate are posteriorly-directed (Fig. 17a; ada), whereas they are usually anteriorly-directed in most other taxa. In axymyiids these apodemes are present at the anterolateral edge of the tubular aedeagus (Fig. 17b-c; ada) while in taxa such as *Scatopse*, which have no tubular portion of the aedeagus, the anteriorly-directed apodemes are present at the anterolateral edge of a small saddle-shaped or U-shaped sclerite which covers part of the dorsal surface of the basiphallus (Fig. 19; ada). A similar U-shaped sclerite is present in pachyneurids and *Hesperinus* (Figs. 22, 25; ada). The anteriorly-directed apodemes are absent in Bibionidae (except *Hesperinus*), Sciaroidea, and *Sylvicola*. It is unclear whether or not these apodemes should be scored as present or absent in *Trichocera* and *Mycetobia* and these taxa have been scored as a "?."

This character did not provide any unambiguous support in this analysis.

133) Lateral ejaculatory sclerites (CI: 0.40, RI: 0.50)
immoveable (0)
articulated (1)
absent (2)

The lateral ejaculatory sclerites of Orthorrhaphous Brachycera are here considered homologous to the broad, flat, anteriorly directed apodemes found on the aedeagal plate of Tipulinae (Fig. 17a; lea)(see above discussion). The lateral ejaculatory sclerites are scored as immovable if they are fused to the aedeagal plate (as in *Ctenophora*), or if they are incorporated into the tubular aedeagus as in *Trichocera*, where muscle M32 stretches between the ejaculatory apodeme and a lobe of the aedeagus (Ovtshinnikova 1994a)(Fig. 18b-c; lea). A similar muscle was observed in axymyiids and therefore this taxon has also been scored as having "immovable" apodemes. Articulated apodemes were observed in Scatopsidae (Figs. 19-20; lea), *Bolitophila*, and *Dialysis*. These sclerites may also occur in *Mycetobia*, which has a large pair of processes which extend out laterally from the dorsal surface of the basiphallus. However, this taxon has been scored as a "?" since the sperm pump has undergone considerable fusion that makes determining the homology of the components difficult. Lateral ejaculatory sclerites are absent in the remainder of the taxa.

This character did not provide any unambiguous support in this analysis.

134) Adminiculum (CI: 0.33, RI: 0.50)
present (0)
absent (1)

An adminiculum is present in *Ctenophora*, *Scatopse*, and Anisopodidae (Fig. 21a; adm). It is absent in the remainder of taxa. The adminiculum in these groups is tentatively interpreted as homologous due to the similar structure and the presence of gonophyses (Fig. 21a; gp)(see above discussion).

The presence of an adminiculum unambiguously supports Anisopodidae + Scatopsidae (node 40).

ROTATION AND FLEXATION

135) Male hypopygium (CI: 0.50, RI: 0.85)
in same plane as abdomen (0)
dorsoflexed (1)

In most taxa examined, the hypopygium lies in the same plane as the rest of the abdomen. However, bibionids typically have the male hypopygium flexed dorsally (Fig. 5e). Although handling live specimens makes it clear that such a flexation is not permanent and the genitalia can be flexed into the same plane as the abdomen (pers. obs.), the dorsoflexation is maintained and quite consistent in preserved specimens. A slight dorsoflexation is also present in Axymyiidae, and some specimens of *Dialysis*.

The dorsoflexed hypopygium unambiguously supports Bibionidae (node 5).

136) Rotation of male hypopygium (CI: 0.33, RI: 0.50)
absent (0)
90-180 degree rotation with marked abdominal twist (1)
180 degree inversion without marked abdominal twist (2)

Rotation of the genitalia is known in many groups of flies (McAlpine 1981a) and Bibionidae facultatively rotate the abdomen 180 degrees to achieve copulation (pers. obs.). However, this kind of impermanent, behavioral rotation is not well documented for most of the groups under study. Thus, only an obligatory, permanent rotation of the genitalia will be considered here as this data can be interpreted from museum specimens. A 180 degree inversion was observed in Anisopodidae, some Scatopsidae, *Symmerus*, Keroplatidae, and Sciaridae. Although these taxa do not show any variation in the degree of rotation (i.e. all specimens have genitalia that is inverted 180 degrees), the genitalia of Pachyneuridae show some variation in the extent of rotation. The genitalia of *Cramptonomyia* is between 90 and 180 degrees rotated and the few males of *Pachyneura* and *Haruka* which were available for study have genitalia that is rotated approximately 90 degrees. In all three pachyneurid genera this rotation includes a marked longitudinal twisting of the abdomen starting as anterior as segment five. Despite the fact that a longitudinal twisting must occur in the abdomens of the previously mentioned non-pachyneurid taxa in order to achieve a 180 degree inversion of the genitalia, the abdomen appears entirely normal (not twisted) and the point of rotation is not easily determined. In contrast to this, the twist in the pachyneurid abdomen is a gradual twist which is easily followed from a dorsal to a ventral position. Since the rotation observed in pachyneurids seems slightly different in nature to that of the other taxa, they are assigned the separate character state "90-180 degree rotation with abdominal twist."

Character state 2 unambiguously supports Pachyneuridae (node 34).

FEMALE TERMINALIA & EGG

The "lock and key" hypothesis of insect genitalia describes a corresponding morphology or mechanical fit between the male and female genitalia which is considered partly responsible for reproductive isolation between different species (Shapiro & Porter 1989). Such a structural correspondence has been observed in some structures of the male and female genitalia of some Diptera. For example, in some species there is correspondence between the length of the male penis filaments and the length of female spermathecal ducts, or the number of functional penis filaments and the number of seminal receptacles (Zwick 1977: 10, Blaschke-Berthold 1994: 78, Ilango & Lane 2000). As noted by Farris (1983) "only independent lines of evidence should be used in evaluating genealogies," and therefore care should be taken to include either the male or female structure, but not both, if the structure appears to be correlated between the sexes. The characters of the female terminalia listed below do not have an obvious correlation with male characters included here and are tentatively considered independent.

Structures of the female terminalia have been shown to be informative in phylogenetic analyses of various groups of Diptera (e.g. Kotrba 1995 and references there) including Bibionidae (Pinto & Amorim 2000). However, most studies examining the female terminalia of bibionids examine only a few exemplars of the family and often fail to make a comparison between the structures of bibionids and putative sister groups such as Pachyneuridae (Iwata & Nagatomi 1979, 1981, Saether 1977, Pinto and Amorim 2000). Blaschke-Berthold (1994) provides the best overview of the female terminalia for bibionids as the study is in the context of other Bibionomorpha (though unfortunately lacking the Pachyneuridae) and attempts to provide a consistent use of terms and homology of structures across taxa. Although descriptions of female genitalia are here provided for all bibionid genera (see "Generic Revision"), the homology of several sclerites of the female genitalia remain uncertain and the variation in internal structure has yet to be adequately documented.

137) Female cerci (CI: 0.25, RI: 0.78)
two-segmented (0)
one-segmented (1)

Two segments is considered the primitive number of segments for the female cerci of Diptera (Fig. 26a; cer), though many groups of both nematoceran and brachyceran flies have only one segment (McAlpine 1981a, Nagatomi & Iwata 1976, 1978). A one-segmented cercus was observed in Tipulidae, Trichoceridae, Anisopodidae, Scatopsidae, Keroplatidae (though some keroplatid genera have a two-segmented cercus (Matile 1990)) and the bibionids *Bibio*, *Dilophus*, *Enicoscolus*, *Bibionellus*, *Bibiodes*, and *Plecia* (Fig. 26b-d; cer).

The one-segmented cercus unambiguously supports *Plecia* + Bibioninae (node 7) and Trichoceridae + (Anisopodidae + Scatopsidae)(node 39).

138) Female cerci with strong spine-like setae (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Strong spine-like setae were observed only on the apical segment of the cerci of Axymyiidae; this character unambiguously supports this taxon.

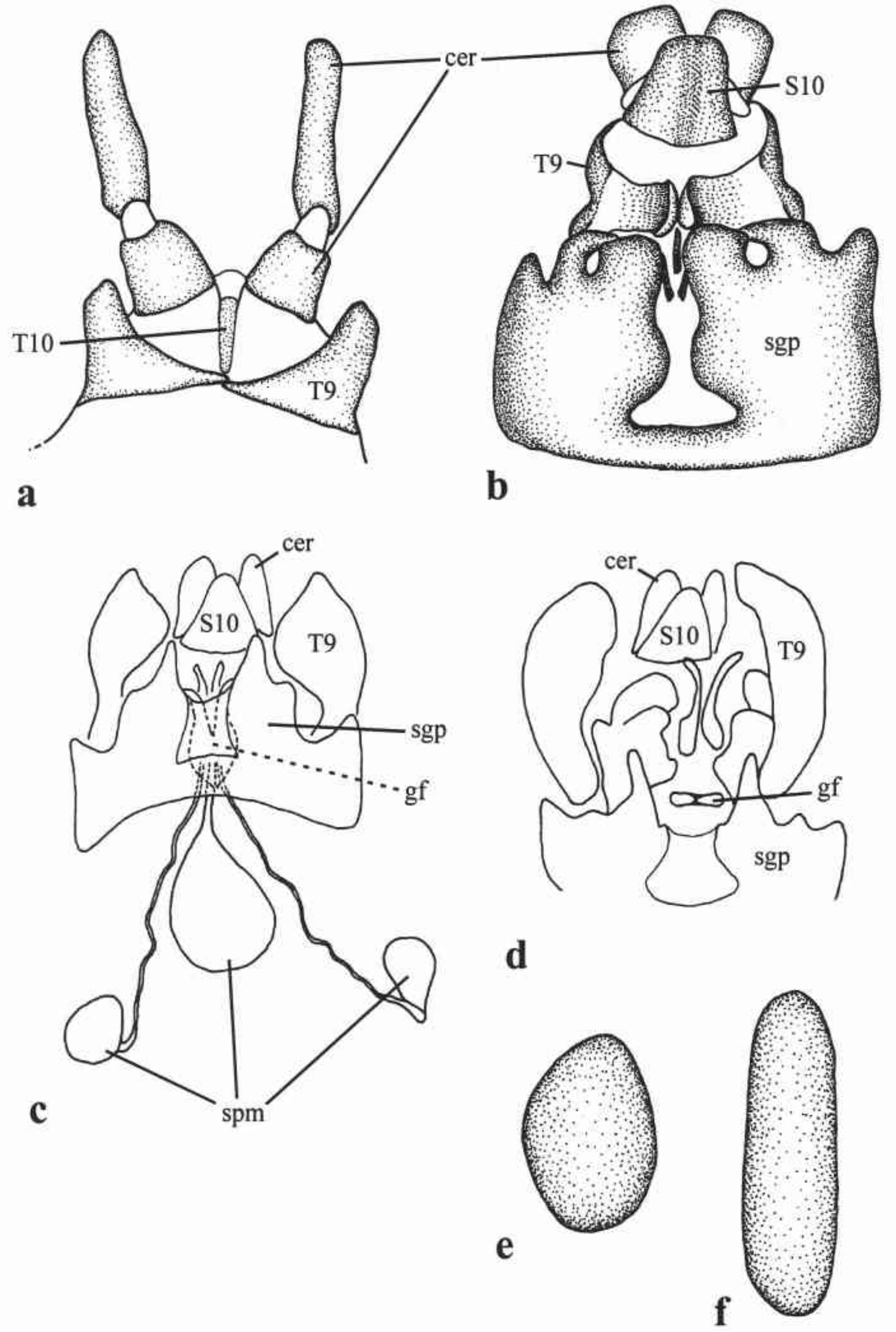


Figure 26, Female terminalia and eggs of Bibionidae. a, *Penthetria funebris* Meigen, dorsal. b, *Plecia evansi* Fitzgerald, ventral. c-d, *Plecia nearctica* Hardy. c, ventral. d, posteroventral. e, *Plecia nearctica* Hardy, egg. f, *Bibio albipennis* Say, egg. Abbreviations: cer, cercus; gf, genital fork; S10, sternite ten; sgp, subgenital plate; spm, spermatheca; T9, tergite nine; T10, tergite ten.

139) Number of spermathecae (CI: 0.40, RI: 0.72)

one (1)
two (2)
three (3)

Most taxa have one to three well-sclerotized to membranous, oval, capsule-like spermathecae. However, several taxa have a non-homologous spermathecal-sac-like structure which is derived from a spermatheca in some taxa and derived from a different structure in other taxa. For example, some species in the bibionid genus *Plecia* have three sclerotized, equally-sized, capsule-like spermathecae. In other species of *Plecia*, the median spermatheca is membranous and is subequal in size, slightly enlarged, or greatly enlarged into a membranous sac (Fig. 26c; spm). This median sac in *Plecia* is considered a bursa copulatrix by Leppla *et al.* (1975; Fig. 3). However, because of the intermediate forms seen across different species of *Plecia*, the membranous median sac in some *Plecia* is clearly derived from a sclerotized, capsule-like spermatheca. In contrast, taxa such as *Cramptonomyia* have a median membranous sac and three very delicate membranous spermathecae, suggesting that its median sac is not derived from a spermathecae (since all three spermathecae are present). Similar median, membranous, invaginations have been termed a "bursa copulatrix" in some Diptera though, as noted by Kotrba (2000), this term has been applied to various non-homologous structures and is a "general term for a pouch that receives the male genitalia, spermatophore or sperm during copulation." Byers (1961; Fig. 31) calls the median membranous sac in the tipulid *Dolichopeza* the "functional spermatheca." In *Dolichopeza*, this functional spermatheca is present in addition to a bursa copulatrix and three sclerotized, capsule-like spermathecae; leading one to conclude again that that in this taxon, the sac-like structure is not spermathecal in origin. A similar arrangement exists in the tipulid *Ctenophora* (pers. obs.) in which there is a common duct (bursa copulatrix of Byers 1961) leading from the genital opening anteriorly. From this bursa copulatrix the three spermathecal ducts branch off prior to the blind anterior apex of the bursa. This blind anterior apex of the bursa is considered the functional spermatheca (*sensu* Byers 1961). However, the structure of the "functional spermatheca" is very different from that of the other three spermathecae in both *Dolichopeza* and *Ctenophora* and thus the tipulid is coded as having three and not four spermathecae. In some Therevidae, there is a similar median membranous sac, or a series of membranous sacs (the "spermathecal sac" of Winterton *et al.* (1999)), but again this sac(s) is usually in addition to both a bursa copulatrix and three well developed spermathecae; though at least one therevid has only two capsule-like spermathecae and a median sac much like the bibionid *Plecia* (Winterton *et al.* 1999; Fig. 1B). *Symmerus* has two membranous spermathecae and a median membranous sac, but since no intermediate forms or other evidence suggest that the sac is spermathecal in origin, this taxon is coded as having two spermathecae.

Trichoceridae, Tipulidae, Xylophagidae, Pachyneuridae and Bibionidae (except *Bibionellus* which has only two) have three spermathecae. Sciaroidea and Axymyiidae have two, Anisopodidae has one to two, and Scatopsidae has one spermatheca(e).

The presence of two spermathecae provides unambiguous support for Axmyiidae, but not Sciaroidea which consistently has two spermathecae; Sciaroidea is not supported as a monophyletic group in this analysis. The presence of only one spermatheca unambiguously supports Anisopodidae + Scatopsidae (node 40), though *Mycetobia* has two spermathecae.

140) Egg (CI: 0.33, RI: 0.83)
robust, ovoid (0)
sausage-shaped (1)

Pinto & Amorim (1996) considered the ovoid-shaped egg of *Plecia* synapomorphic for the genus, though they noted that besides the sausage-shaped eggs of *Bibio* and *Dilophus* (Morris 1921, 1922) that egg shape was unknown for other genera. The abdomens of most female flies examined in this study were packed with eggs and during the course of examining internal structures of the female terminalia, egg shape was recorded. It is clear, based on the limited descriptions of eggs available in the literature, that egg shape may be very homoplastic. However, for the taxa examined here it was relatively consistent.

All genera of bibionids have elongate, sausage-shaped eggs (Fig. 26f) except *Plecia*, in which the eggs are ovoid (Fig. 26e), and *Bibionellus*, for which there were no eggs in the abdomen of the female examined. All non-bibionid groups examined had ovoid eggs, except for Pachyneuridae which also had sausage-shaped eggs (Vockeroth 1974; Fig. 5). The egg of *Axymyia furcata* is somewhat intermediate in shape and is coded as elongate.

Although the sculpturing of the chorion has not been utilized as a character here, it is noteworthy that both *Cramptonomyia* and *Haruka* have an egg with distinct longitudinal micro-ridges on the chorion (Vockeroth 1974; Fig. 5) which may be a synapomorphy for Cramptonomyiinae; the eggs of *Pachyneura* and Bibionidae are smooth.

The sausage-shaped egg unambiguously supports Bibionidae + Pachyneuridae (node 4) and a subsequent reversal to the ovoid egg provides unambiguous support for *Plecia* (node 8).

LARVA

Examination of larval structures can be critical to the understanding of phylogenetic relationships (e.g. van Emden 1957, Judd 1996, Palmer &Yeates 2000). Nevertheless, outside of numerous alpha-taxonomic studies (Morris 1917, 1921, 1922, Keilin 1919, Hennig 1948, Perraudin 1961, Brindle 1962, Krivosheina 1962, 1969, 1972, Skartveit 2002) the phylogenetic use of larval characters in Bibionidae has been explored in only a few studies (Skartveit & Willassen 1996, Pinto & Amorim 2000). With the possible exception of Krivosheina and Mamaev (1967b), there are no studies using comparative morphology to establish homology of larval structures both among bibionid genera, and between Bibionidae and putative sister groups, such as

Pachyneuridae. This is surprising since some of the few characters suggested as synapomorphies of Bibionidae are from the poorly studied larval stages (Wood & Borkent 1989, Skartveit & Willassen 1996), but it is also not so surprising when one considers the paucity of larval specimens available for study. Numerous larval characters were examined and are discussed below. However, the study of some character systems still remains incomplete. For example, despite some promising patterns which emerged during initial observations, an understanding of the chaetotaxy of the head and body was not completed during the course of this study and would be a valuable direction for future research.

BODY (GENERAL)

141) Body segments with rows of fleshy protuberances (CI: 1.00, RI: 1.00)
absent (0)
present (1)

The larvae of Bibionidae (except *Hesperinus*) are distinctive in that each body segment has distinct rows of fleshy protuberances (Figs. 27a-b, 28c). The protuberances are likely derived from setae because the number and pattern of protuberances is similar or identical to the number and pattern of setae observed in taxa without protuberances, such as *Hesperinus* and Pachyneuridae. Additionally, in those bibionids with fleshy protuberances, there is sometimes a combination of protuberances and setae where the total number adds up to the total number of setae observed in taxa without protuberances. For example, *Ctenophora*, *Pachyneura*, *Cramptonomyia*, and *Hesperinus* have two rows of setae per abdominal segment dorsally; an anterior row with 2 setae and a posterior row with 8 setae. *Dilophus febrilis* (L.) has an anterior row with zero setae/protuberances, and a posterior row with 6 setae and 2 protuberances. Likewise, the posterior row in *Bibio albipennis* Say has 8 protuberances. In addition to similar number and position of setae/protuberances, another source of evidence which suggests that the protuberances are derived from setae is the fact that first instar larvae of bibionids, such as *Dilophus febrilis*, lack protuberances but have a single row of 8 setae that arise from an enlarged conical base (Morris 1922; Fig. 1).

Because bibionids have protuberances as well as minute cuticular scales (see following character) that give the cuticle a fuzzy appearance, finding the very minute setae or remaining alveoli can be difficult. Therefore, rather than examining specific patterns of chaetotaxy, this character is here used to address only the presence or absence of fleshy protuberances. The presence of fleshy protuberances has previously been considered synapomorphic of bibionids exclusive of *Hesperinus* (Blaschke-Berthold 1994, character 21; Pinto & Amorim 2000, character 86). Anisopodidae, *Mycetophila*, *Bolitophila*, *Keroplatus*, *Symmerus*, Sciaridae, and Axymyiidae are entirely bare; they lack distinct rows of setae and/or protuberances.

The presence of fleshy tubercles on the larva provides unambiguous support for node 6 (Bibionidae exclusive of *Hesperinus*).

142) Sclerotized scales in cuticle (CI: 0.50, RI: 0.90)
absent (0)
present (1)

Bibionidae have extremely minute, sclerotized scales in the cuticle that are considered useful for specific identification of larvae (e.g. Brindle 1962, Skartveit 2002, Sutou 2002). The scales are flattened and, depending on the species, may be slender to broad and plate-like, and unadorned or possessing one to many sharp points. Because these scales cover most of the body surface, they are not considered homologous to the isolated patches of spinules present on the lobate creeping welts of some fly larvae. Cuticular scales are present in Bibionidae and Pachyneuridae and provide unambiguous support for this clade (node 4).

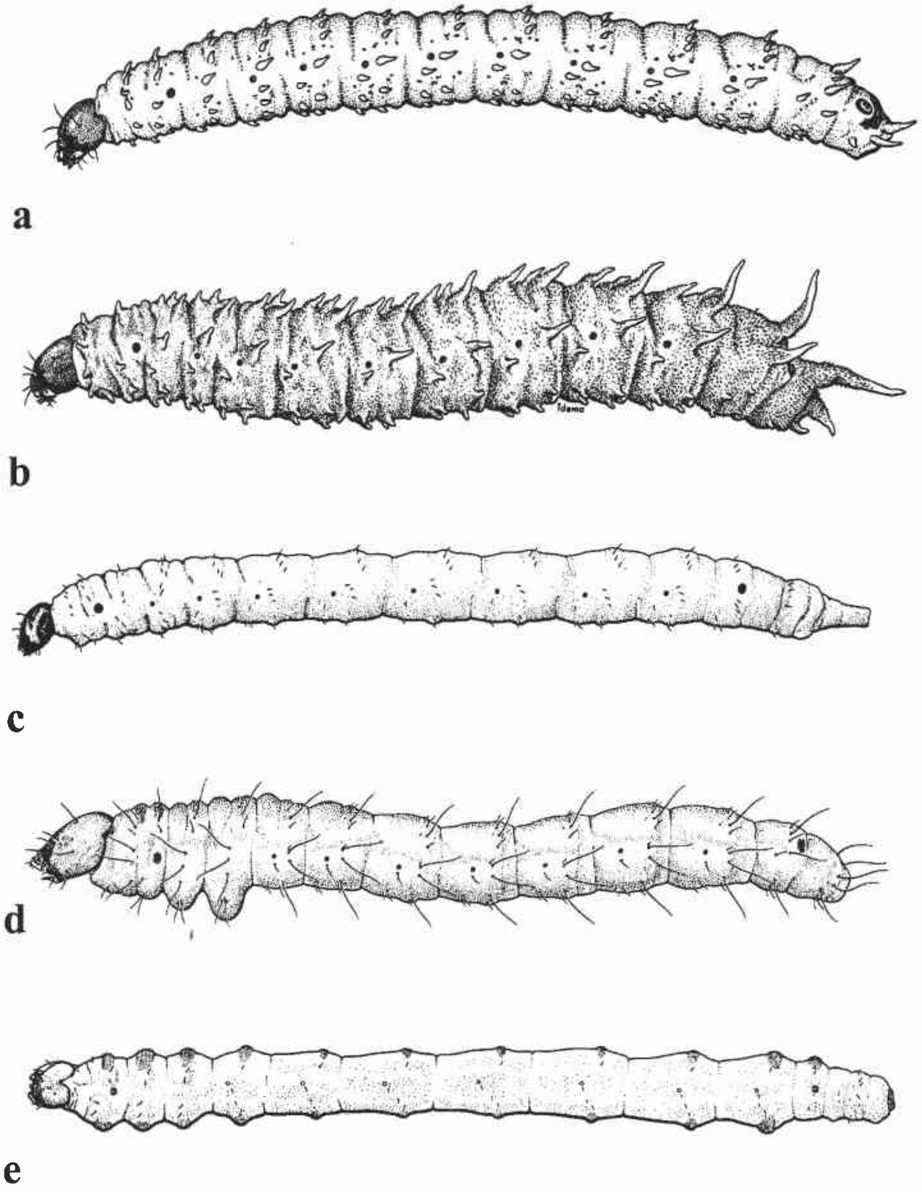


Figure 27, Larval habitus. a, *Bibio* sp. (Bibionidae) b, *Plecia nearctica* Hardy (Bibionidae). c, *Hesperinus rohdendorfi* Krivosheina & Mamaev (Bibionidae). d, *Cramptonomyia spenceri* Alexander (Pachyneuridae). e, *Symmerus coqulus* Garrett (Ditomyiidae). (Source: Manual of Nearctic Diptera - Volume 1, Fig. 12.5 (page 215); Figs. 13.12-13.14 (page 221), & Fig. 14.103 (page 244), Agriculture & Agri-Food Canada, 1981. Reproduced with permission of the Minister of Public Works and Government Services Canada, 2004).

Figure 28, Larva, general I. a, *Hesperinus brevifrons* Walker (Bibionidae), lateral; lines indicate position of intersegmental fissures and numbers indicate number of pseudosegments. b, *Cramptonomyia spenceri* Alexander (Pachyneuridae), lateral. c, *Plecia mallochi* Hardy (Bibionidae),ventral. Abbreviations: Ab1, abdominal segment one; Ab2, abdominal segment two; if, intersegmental fissures; pro, prothorax; mes, mesothorax; met, metathorax; metsp, metathoracic spiracle; sp, spiracle; vps, ventral prothoracic sclerites.

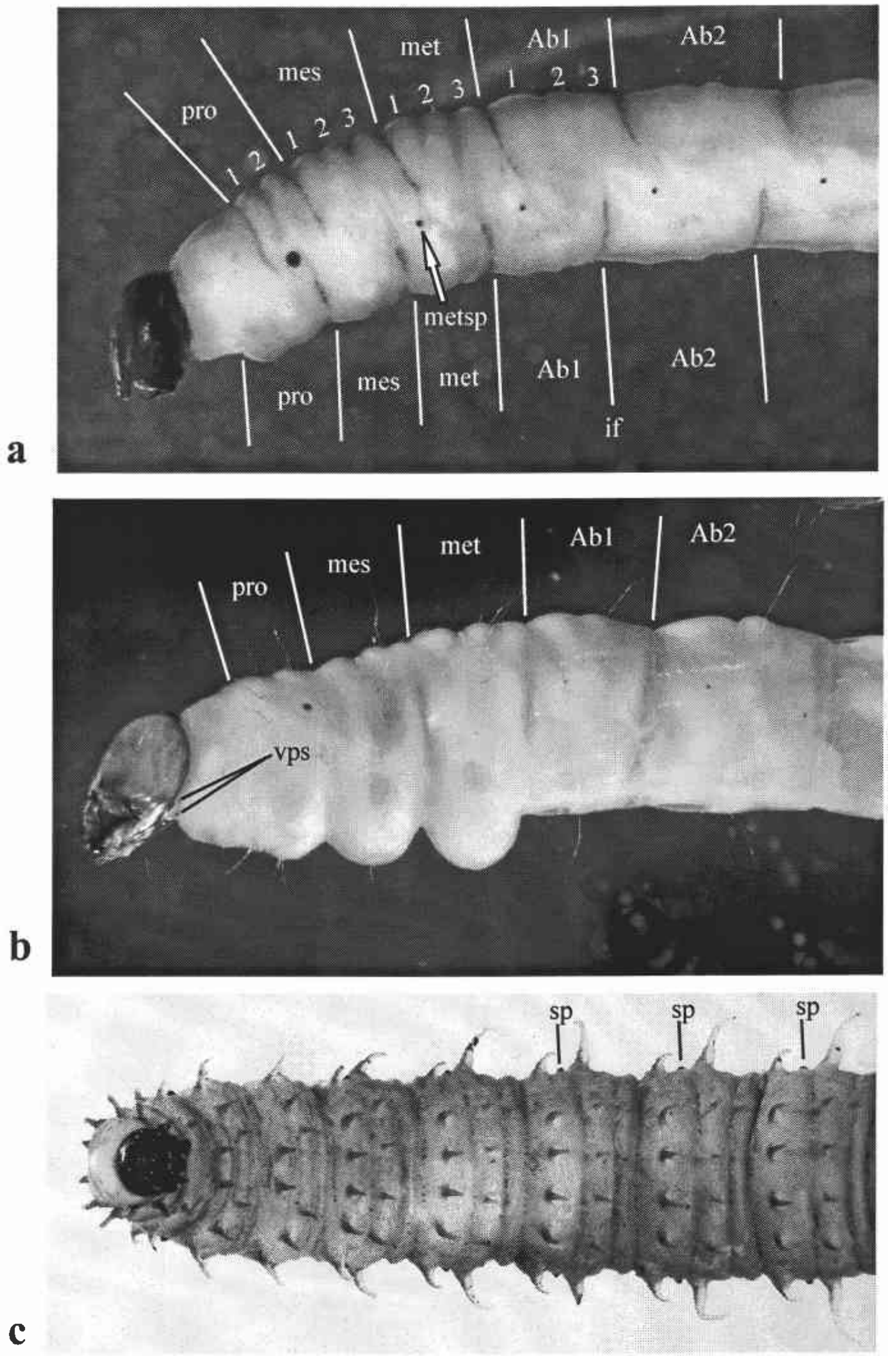


Figure 28, Larva, general I.

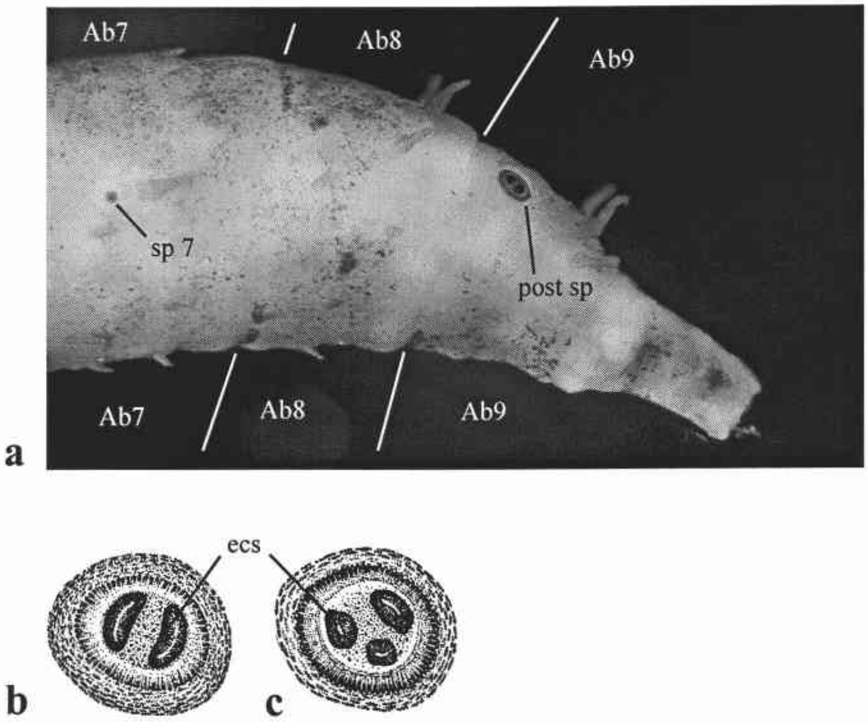


Figure 29, Larva, general II. a, *Bibio albipennis* Say (Bibionidae), lateral; lines indicate position of intersegmental fissures. b-c, Posterior spiracle. b, *Bibio* sp. (Bibionidae). c, *Dilophus* sp. (Bibionidae). Abbreviations: Ab7, abdominal segment seven; Ab8, abdominal segment eight; Ab9, abdominal segment nine; post sp, posterior spiracle; sp 7, spiracle seven; ecs, ecdysial scar. (Source of figs. b & c: Manual of Nearctic Diptera - Volume 1, Fig. 13.16-13.17 (page 221), Agriculture & Agri-Food Canada, 1981. Reproduced with permission of the Minister of Public Works and Government Services Canada, 2004).

143) Thoracic segments greatly enlarged ventrally (CI: 1.00, RI: 1.00)

absent (0)
present (1)

In larvae of Pachyneuridae, the thoracic segments are characteristically swollen and lobate ventrally; the prothorax is slightly swollen, the mesothorax is more swollen, and the metathorax is the most swollen, which creates a stair-step appearance (Figs. 27d, 28b). This character is also consistent in the pachyneurids *Pachyneura oculata* Krivosheina & Mamaev (1972; Plate 2, Fig. 1) and *Pergratospes holoptica* Krivosheina & Mamaev (Krivosheina 2000; Fig. 17) for which larvae were unavailable for study.

The ventrally enlarged thorax provides unambiguous support for Pachyneuridae (node 34).

144) Prothorax with lightly sclerotized plates dorsally (CI: 1.00, RI: -)

absent (0)
present (1)

Blaschke-Berthold (1994; character 12) suggested that the presence of sclerotized plate-like areas on the prothorax (Fig. 27d) are synapomorphic of Pachyneuridae, including the genus *Pachyneura*. Yet these plate-like sclerotizations were not here observed in *Pachyneura*. Although this character is autapomorphic for *Cramptonomyia* in this analysis, it also occurs in *Pergratospes* (pers. obs.) leading one to surmise that it may be synapomorphic for Cramptonomyiinae.

145) Ventral, flap-like tubercle (CI: 0.33, RI: 0.50)

absent (0)
present (1)

Plecia and *Penthetria* have a transverse, anteroposteriorly flattened, flap-like tubercle near the posteroventral margin of the head. The function of this flap-like tubercle is unknown. It is absent in *Plecia plagiata* Wiedemann.

This character did not provide any unambiguous support in this analysis.

146) Unretractable, elongate, sausage-link-like anal papillae (CI: 1.00, RI: 1.00)
present (0)
absent (1)

Anal papillae apparently provide an osmoregulatory function in aquatic and semi-aquatic larvae of nematoceran Diptera, but are absent from most terrestrial groups including Bibionomorpha, Anisopodidae and Scatopsidae (Courtney *et al.* 2000). Because anal papillae may be retractable, these structures can be difficult to identify in preserved specimens and, within Bibionomorpha, retractable papillae have been reported at least in *Keroplatus* and *Sciophila* (Matile 1990, Plachter 1979b, Courtney *et al.* 2000). Further complicating this character is that anal papillae range in structure from elongate and sausage-shaped to flat and pad-like. *Ctenophora* have what appears to be an anal "pad," and retracted papillae were not observed in preserved specimens of Trichoceridae or *Keroplatus*. Considering these difficulties, this character includes only anal papillae that are permanently extruded, elongate, and sausage-link-like. Such anal papillae are present only in Axymyiidae (Wood 1981b; Fig. 6) and unambiguously support this clade (node 44).

147) Anus (CI: 1.00, RI: 1.00)
terminal (0)
ventral (1)

As noted by Oosterbroek & Courtney (1995; character 47) the anus of most nematoceran larvae is posterior or posteroventral in position, and at the caudal end of the last abdominal segment. A ventrally positioned anus was observed in Anisopodidae, Scatopsidae, and *Trichocera* and unambiguously supports this clade (node 39).

SEGMENTATION

148) Intersegmental fissures separating meso- and metathorax (CI: 0.50, RI: 0.90)

aligned (0)
unaligned (1)

Wood & Borkent (1989; character 31) considered the laterally unaligned, intersegmental fissures a synapomorphy of Bibionidae. However, whether or not the dorsal and ventral intersegmental fissures are aligned laterally, varies depending upon which segment is examined. Therefore, their character is here subdivided into several characters by examining the intersegmental fissures between specific segments. The specific segments treated here were chosen because they show variation either within bibionids or between bibionids and outgroups.

The intersegmental fissures separating the meso- and metathorax are laterally unaligned in Bibionidae and Pachyneuridae (Fig. 28a) and unambiguously support this clade (node 4), though this character state is also found as an independent development in *Trichocera*.

149) Intersegmental fissures separating abdominal segments 1 and 2 (CI: 0.50, RI: 0.90)

aligned (0)
unaligned (1)

See discussion of previous character. The intersegmental fissures separating abdominal segments 1 and 2 are laterally unaligned in Bibionidae (Fig. 28a) and unambiguously support this clade (node 5), though this state is also found as an independent development in *Scatopse*.

150) Intersegmental fissures separating abdominal segments 7 and 8 (CI: 0.50, RI: 0.88)

aligned (0)
unaligned (1)

See discussion of previous character. The intersegmental fissures separating abdominal segments 7 and 8 are laterally unaligned in Bibionidae (except *Hesperinus*) and provide unambiguous support for this clade (node 6), though they are also found as an independent development in *Bolitophila*.

151) Prothorax dorsally (excluding pre-prothoracic segment) (CI: 0.40, RI: 0.70)

pseudosegments absent (0)
2 pseudosegments (1)
3 pseudosegments (2)

Numerous families of flies (such as Bibionidae, Anisopodidae, Psychodidae, and Trichoceridae) have 2 to 3 secondary subdivisions of some or all segments, and the number of subdivisions varies depending on which segment is examined. The number of pseudosegments of the prothorax, mesothorax, and third abdominal were examined because these segments show variation either within Bibionidae or between Bibionidae and outgroups.

Two pseudosegments of the prothorax were observed in *Cramptonomyia*, *Hesperinus*, *Penthetria*, *Dilophus*, and *Trichocera* (28a-b) and three pseudosegments were observed in *Plecia* and *Bibio*.

This character provides no unambiguous support in this analysis.

152) Mesothorax dorsally (CI: 0.66, RI: 0.90)

pseudosegments absent (0)
3 pseudosegments (1)
2 pseudosegments (2)

See discussion of previous character. Pachyneuridae, *Hesperinus*, *Bibio*, *Dilophus*, and *Plecia* have three pseudosegments (Fig. 28a-b); *Penthetria* and *Trichocera* have two.

The presence of 3 pseudosegments unambiguously supports Bibionidae + Pachyneuridae (node 4) and a change to 2 pseudosegments unambiguously supports the genus *Penthetria* (node 30).

153) Abdominal segment three (CI: 0.80, RI: 0.90)

pseudosegments absent (0)
3 pseudosegments (1)
2 unequal pseudosegments (2)
2 subequal pseudosegments (3)
6-8 pseudosegments (4)

See discussion of previous character. Bibionidae and *Trichocera* have three pseudosegments. The character state “2 pseudosegments” is broken down into 2 equal or 2 unequal pseudosegments because the unequally sized pseudosegments of anisopodids (one broad and one narrow ring (the “intercalary pseudosegment” of Teskey (1981)) did not appear to be homologous to the equally divided pseudosegments of *Ctenophora*. More numerous subdivisions (6-8 pseudosegments per segment) exist in the oligocheate-like larvae of Keroplatidae.

Three pseudosegments unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*) and two unequal pseudosegments unambiguously supports Anisopodidae (node 41).

154) Abdominal segment 9 (CI: 1.00, RI: 1.00)

absent (0)
present (1)

The actual number of segments of the larval stage can be difficult to interpret due to pseudosegmentation, weak intersegmental fissures, and apparent fusion of segments. Additionally, since most nematoceran flies have the posterior spiracles on segment eight, this pattern has apparently influenced hypotheses of pseudosegmentation when the posterior spiracles apparently occur on segment nine. For example, in all Bibionidae, segment nine is large and separated from segment eight by an obvious intersegmental fissure. The bibionid genera *Hesperinus* and *Penthetria* have the posterior spiracles positioned on the posterior edge of segment eight abutting the intersegmental fissure between segments eight and nine. In the genera *Bibio* and *Plecia*, the posterior spiracle is at the extreme anterior edge of segment nine abutting the intersegmental fissure between segments eight and nine. Presumably because of the common pattern of the posterior spiracle occurring on segment eight in most flies, it is suggested by some authors that perhaps what appears as segment nine in *Bibio* and *Plecia* is actually a subdivision of segment eight (e.g. Hennig 1948) regardless of the fact that the segmentation of larvae of all these genera is identical based on the intersegmental fissures and relative size of the terminal segment which bears the anus. It is this authors' opinion that such a hypothesis places too much importance on the location of the spiracle and that the posterior spiracles of *Bibio* and *Plecia* have shifted slightly in position from one side of the intersegmental fissure to the other (Fig. 29a).

Larval Anisopodidae also have an organization which complicates an understanding of their segmentation. Anisopodid abdominal segments are subdivided into two parts; a large segment and a narrow "intercalary pseudosegment" (Teskey 1981). However, if one counts the number of large segments in the genus *Mycetobia* (e.g. Krivosheina 1997c; Fig. 10) there are clearly nine segments and yet the posterior spiracles are terminal (at the very posterior tip of segment nine). This segmental pattern in anisopodids has been explained, presumably due to the location of the posterior spiracles, as eight real segments with the eighth segment variously subdivided (Peterson 1981a, Krivosheina 1997c, 1997d). Although it may require further study to clarify the number of segments in these taxa, segmentation here is based upon external evidence such as the position of intersegmental fissures (which tend to be deeper than fissures delineating pseudosegments) and features which are repeated on each abdominal segment (such as a row of setae). Oosterbroek & Courtney (1995) score Tipulidae, Trichoceridae, Anisopodidae, and Scatopsidae as having only eight segments. However, in all these taxa there appears to be nine segments, though the terminal segments are admittedly difficult to differentiate and in most cases much smaller than preceding segments; in *Trichocera* the eighth segment is partially telescoped into segment seven. The interpretation here of nine segments in *Trichocera* is in agreement with Dahl (1980) who states that Trichoceridae have nine segments if attention is paid to the fact that each segment bears a row of setae.

Based on the preceding analysis of segments, segment nine is absent only in Axymyiidae. This taxon has seven distinct abdominal segments plus an elongate respiratory siphon that may or may not correspond to segment eight. The reduced number of segments in Axymyiidae unambiguously supports this clade (node 44).

SPIRACLES

155) Prothoracic spiracle (CI: 0.50, RI: 0.00)

absent (0)

present (1)

As have many authors, Oosterbroek & Courtney (1995; character 49) address the arrangement of spiracles as large-scale patterns, using character states such as "polyneustic," "oligopneustic," and "apneustic." These large-scale patterns are here broken down into the presence/absence of specific spiracles in order to establish a more precise hypothesis of homology.

The prothoracic spiracle is present in all taxa except *Ctenophora* and (apparently) *Keroplatus*. However, Matile (1990) found a minute prothoracic spiracle in other species of Keroplatidae, including *Keroplatus*, using scanning electron microscopy. Therefore, despite the fact that the prothoracic spiracle in *Keroplatus* was not detected using light microscopy, it is scored as "present" following Matile (1990).

This character provides no unambiguous support in this analysis.

156) Metathoracic spiracle (CI: 0.50, RI: 0.90)

absent (0)
present (1)

Hinton (1947) states that the metathoracic spiracle is usually non-functional in most holometabolous insect larvae, but notes that Bibionidae and Siphonaptera are an exception. The present study does not take into account whether or not the metathoracic spiracle is functional, but merely whether or not it is present. A metathoracic spiracle was observed only in Bibionidae and *Pachyneura* (Fig. 28a); these are the only Diptera previously recorded as possessing ten spiracles (two thoracic and eight abdominal) (Teskey 1981).

This character provides no unambiguous support in this analysis.

157) Abdominal spiracles 1-7 (CI: 0.33, RI: 0.66)

absent (0)
present (1)

The presence/absence of abdominal spiracles 1-7 are apparently correlated and are thus treated together. They are present in Bibionidae, Pachyneuridae, Scatopsidae, and Sciaroidea (except *Keroplatus*)(Fig. 27).

The presence of spiracles 1-7 unambiguously supports Bibionomorpha *sensu stricto* (node 3), though they are secondarily lost in Keroplatidae and secondarily gained in *Scatopse*.

158) Thoracic and abdominal spiracles 1-7 (CI: 0.33, RI: 0.60)

flush with cuticle (0)
slightly elevated (1)

The thoracic and abdominal spiracles may be flush and approximately even with the cuticle or slightly elevated above the cuticle due to an elongated, tubular sclerotization (28c; sp). Although variation within individuals of the same species was not observed here, Bovien (1935) notes ecophenotypic plasticity in the degree of elongation of spiracles of *Scatopse* that was governed by the wetness of the larval habitat. Therefore, the phylogenetic utility of this character should be considered with this limitation in mind. An elevated spiracle is present in Bibionidae (except *Hesperinus* and *Bibio albipennis* Say), Scatopsidae, and some Sciaroidea.

Slightly elevated spiracles unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*).

159) Posterior spiracle (CI: 1.00, RI: 1.00)

present (0)
absent (1)

The posterior spiracle is absent in Sciaroidea except Ditomyiidae (Fig. 27e). This pattern was also noted by Wood & Borkent (1989: 1353) who suggest it as possible evidence of the paraphyly of Mycetophilidae *sensu lato*.

The absence of the posterior spiracle unambiguously supports Bolitophilidae + (Sciaridae + (Keroplatidae + Mycetophilidae))(node 36).

160) Position of posterior spiracle (CI: 0.87, RI: 0.88)

on anterior margin of segment 9 (0)
on segment 8 (1)
terminal on segment 9 (2)
at the apex of a respiratory siphon (3)

This character is intimately related to how the segmentation of the posterior abdomen is interpreted (see discussion of presence/absence of segment nine in section on "segmentation"). Most flies have the posterior spiracles positioned on segment eight (Teskey 1981). However, *Plecia* and *Bibio* have the posterior spiracles positioned on the anterior margin of segment nine (Fig. 29a). Anisopodidae and *Trichocera* have the posterior spiracle in a terminal position on what appears to be segment nine and are scored as "terminal." Axymyiidae have the posterior spiracle on an elongate, unretractable respiratory siphon, which may or may not correspond to segment eight.

The posterior spiracle on the anterior margin of segment 9 unambiguously supports *Plecia* + Bibioninae (node 7). The presence of the posterior spiracle on an elongate respiratory siphon unambiguously supports Axymyiidae (node 44).

161) Number of ecdysial scars of posterior spiracle (CI: 1.00, RI: 1.00)

1 ecdysial scar (0)
2 ecdysial scars (1)
3 ecdysial scars (2)

In most of the taxa examined, the structure of the posterior spiracle is summarized as a round or oval spiracular plate with a single, large, central, sclerotized ecdysial scar surrounded by the variously perforated spiracular opening: spiracle Type II of Keilin

(1944). The genera *Bibio* and *Dilophus* exhibit a modification of the Type II spiracle because the central ecdysial scar is subdivided into two scars in *Bibio* (Fig. 29a-b) and three scars in *Dilophus* (Fig. 29c)(Morris 1921, 1922). Although the different number of ecdysial scars is used to help differentiate the larval forms of these genera (e.g. Hardy 1981), Harrison (1983) noted that the larva of *Dilophus nigrostigma* (Walker) and *D. segnis* Hutton have only two scars, similar to the genus *Bibio*. Morris (1921) followed the larval development of *D. febrilis* (L.) and *D. femoratus* Meigen (as *D. albipennis* Meigen) and noted that the posterior spiracles of instars 1-2 had a single scar, instar 3 had two scars with one larger than the other, and the fourth (final) instar usually had three scars, though occasionally only two scars were present with one larger than the other (as in 3rd instar larvae). Therefore, it is possible that either the specimens studied by Harrison (1983) represented 3rd instar larvae or that the number of scars in 4th instar *Dilophus* is more variable than is currently appreciated. All the *Bibio* and *Dilophus* studied here had two and three scars respectively, while the remainder of bibionids had only a single ecdysial scar.

This character provides no unambiguous support in this analysis primarily due to the lack of available larval stages of Bibioninae examined here.

162) Position of ecdysial scar of posterior spiracle (CI: 1.00, RI: 1.00)

central (0)
lateral (1)

See discussion of previous character. Anisopodidae have a single ecdysial scar. Yet, unlike other taxa the scar is not central and surrounded by the functional opening of the spiracle, but is offset to the edge of the spiracle. Keilin & Tate (1940; Fig 80) also note this arrangement in the anisopodid genus *Obliogaster*. Taxa which lacked posterior spiracles are coded as inapplicable autapomorphies.

The lateral ecdysial scar unambiguously supported Anisopodidae (node 41).

HEAD (GENERAL)

163) Posterior margin of head (CI: 0.25, RI: 0.62)

partially embedded within larval cuticle (0)
entirely extruded (1)

In some taxa, the posterior margin of the head is partially embedded and covered by the anterior portion of the prothorax. This condition is exemplified by *Ctenophora* and Axymyiidae, though several taxa exhibited this condition to a lesser degree. All the following have an entirely extruded head capsule: Bibionidae (except *Plecia*), Pachyneuridae, Scatopsidae, Anisopodidae, Bolitophilidae, Sciaridae, Mycetophilidae, and Trichoceridae (Fig. 28a-b).

Character state 0 unambiguously supports the genus *Plecia* (node 8), though this character state is also found in four other exemplars outside of Bibionidae + Pachyneuridae.

164) Position of dorsal, posterolateral connection of prothorax to head (CI: 0.28, RI: 0.54)

absent (0)
on posterior margin of cranium along postoccipital carina (1)
on surface of cranium more anteriorly (2)

For some taxa, the posterolateral attachment point of the prothorax to the head is often marked by a thickened notch on the dorsolateral edge of the postoccipital carina ("échancrure des 'Latérialas'" of Perraudin (1961; Figs. 4 & 6) and "incision postérieure" of Matile (1990; Fig.154)). However, in some taxa this thickened notch is absent or is more anterior in position where it takes the form of a U-shaped or dark and thick oval region (e.g. *Symmerus* (Vockeroth 1981; Figs. 101, 103). Although this character may be related to the previous character, the states are not strictly correlated and thus it is treated independently. This character is variable within families, but consistent within genera.

Character state 1 unambiguously supports *Plecia* + Bibioninae (node 7) and Pachyneuridae (node 34). Character state 2 unambiguously supports Axymyiidae (node 44).

165) Ecdysial lines of posterior frontoclypeus (CI: 0.25, RI: 0.70)
meeting far from posterior margin of head (0)
meeting at posterior margin of head (1)

The cranium is dorsally separated into two main regions; the lateral genae and the median frontoclypeal apotome. These regions are separated by lines of weakness (the ecdysial lines) which form a U or V-shaped pattern on the head as they converge and meet, or nearly meet, posteriorly at the postoccipital carina (Fig. 31a; el). Conversely, the ecdysial lines of some taxa meet considerably anterior to the postoccipital carina, as observed in *Plecia*, *Penthetria*, *Hesperinus*, some *Dilophus*, some *Bibio*, Pachyneuridae, and *Scatopse*.

Character state 0 unambiguously supports Bibionidae + Pachyneuridae (node 4), though larvae of Bibioninae show a reversal to state 1.

166) Anterolateral margin of frontoclypeus (CI: 0.80, RI: 0.87)
undeveloped (0)
a large, anteroventrally-directed spine (1)
a small blunt knob (2)
a medially-bent spine (3)
a weak spine (4)

Bibionidae and Pachyneuridae have the anterolateral corners of the frontoclypeus developed into strong anteroventrally directed lobate spines (Fig. 31a;

asf)(Krivosheina & Mamaev 1967b; Fig. 4.4, 6.4, 13.4, 18.1, 20.1). This region is variously weakly developed or undeveloped in other taxa, but never strongly developed. States 3 and 4 are autapomorphic for *Scatopse* and *Mycetophila* respectively.

The strongly developed spine unambiguously supports Bibionidae + Pachyneuride (node 4).

167) Anteroventral stemmata (CI: 0.33, RI: 0.80)

absent (0)

present (1)

Two kinds of larval eyes, or stemmata, are present in the taxa studied here: the paired anteroventral stemmata and the paired dorsoposterior stemmata. Although most taxa have only one or the other kinds of stemmata, some Keroplatidae (Matile 1990; Fig. 127 (st d, st v)) and Bolitophilidae (pers. obs.) have both the anteroventral and dorsoposterior stemmata; which clearly indicates that the two are not a single homologous structure that has merely shifted in position depending upon the taxon. The anteroventral stemma is recognized by its position at the anterior edge of the gena near the dorsolateral mandibular articulation and ventral to the antenna (31c; avs). The anteroventral stemma is also characterized by a convex lense which, may or may not have underlying pigmented granules associated with it. Matile (1990: 94 and Fig. 133) states that the anteroventral stemma is also recognizable by an internal ring or ridge. The dorsal stemma differs from the anteroventral stemma because it is dorsoposterior to the antennae, lacks a convex lense, and is not internally manifest; it is simply a clear window in the cranium which usually has underlying, pigmented granules (Fig. 31a; dps).

Anteroventral stemmata are present in *Hesperinus*, *Penthetria*, Pachyneuridae, Sciaroidea, and *Trichocera*.

The absence of anteroventral stemmata unambiguously supports *Plecia* + Bibioninae (node 7), though they occur in numerous taxa near the base of the tree.

168) Dorsoposterior stemmata (CI: 0.33, RI: 0.80)

absent (0)
present (1)

See discussion of previous character. Dorsoposterior stemmata are present in *Bibio*, *Dilophus*, *Plecia*, Anisopodidae, and *Bolitophila* (Fig. 31a; dps). *Scatopse* has stemmata which are very slightly convex, but due to their posterodorsal position and the lack of an internal ring or ridge, they are interpreted as dorsoposterior stemmata.

The presence of dorsposterior stemmata unambiguously supports *Plecia* + Bibioninae (node7).

169) Antennal sensory cone (CI: 0.60, RI: 0.77)

conical (0)
large, globe-like (1)
plate-like (2)
minute, button-like (3)

The largest and most prominent antennal sensillum of the dipteran antennae is the apical sensory cone which is recognized in part by its size, position, and its multiporous structure (Nicastro *et al.* 1998), which makes it unique among the other antennal sensillae. The sensory cone has been described for most families, but under different names; for example, "sensory cone" (Nicastro *et al.* 1998; Fig. 1 a,c,e), "multiporous placoid sensillum" of Cecidomyiidae (Solinas *et al.* 1987), "ovoid distal segment" of Psychodidae (Pessoa *et al.* 2001), "cone-shaped sensillum" of Tipulidae (Baker et al. 2000; Fig. 2), "apical sensillum" of Tanyderidae (Anthon 1988), "aire préantennaire" of Bibionidae (Perraudin 1961; Fig. 4), and "antenne" of Keroplatidae

(Matile 1990; Fig. 155). Although the sensory cone is typically cone-shaped (much like a Christmas tree light bulb) it may be more elongate and sausage-shaped as in Scatopsidae (Haenni & Vaillant 1994; Fig. 2)), globe-shaped as in *Hesperinus* (Krivosheina & Mamaev 1967b; Fig. 18.1), or minute and button-like as in Anisopodidae and Axymyiidae (Krivosheina & Mamaev 1967b; Fig.62.2)(Fig. 31b-e; sc). Additionally, in Bibionidae (except *Hesperinus*) and most Sciaroidea (except Ditomyiidae, Bolitophilidae, and Cecidomyiidae) the sensory cone is not cone-like, but is a large flattened, round or oblong, slightly convex to slightly concave plate ("large pore plate" of Nicastro *et al.* 1998) which typically has a relatively small number of minute peg-like sensillae at its edge (Fig. 31f; sc). In addition to its varied structure, the sensory cone may be sessile on the cranium (Fig. 31e-f) or elevated by 1 to 2 sclerotized, cylindrical or ring-like antennal segments (Fig. 31b-d).

It is noteworthy that the apparently multi-segmented sensory cone observed in Cecidomyiidae and some Psychodidae appear to be the result of a fusion of the sensory cone with an adjacent sensillum whereby the adjacent sensillum becomes apical (e.g. Solinas *et al.* 1987, Fig. 1; Mukhopadhyay & Ghosh 2000, Fig. 3; Pessoa *et al.* 2001, Figs. 1 & 5-7). Likewise, it may be hypothesized that the multi-segmented apical sensillum in Bolitophilidae may have arisen this way. Compare, for example, Platchter's (1979b) Figs. 154 (*Symmerus*) and 156 (*Bolitophila*). *Symmerus* has a typical cone-shaped sensory cone with an adjacent bi-articulated sensillum that has a cylindrical basal segment and a peg-like apical segment. *Bolitophila* also has a cone-shaped sensory cone and a bi-articulated sensillum, but the bi-articulated sensillum arises from the apex of the sensory cone. Cecidomyiidae and Bolitophilidae are also the only Bibionomorpha with the sensory cone elevated on two antennal articles (a narrow basal ring followed by a more cylindrical segment); though Solinas *et al.* (1987) argue that the first ring in Cecidomyiidae is not a true antennomere.

The analysis indicates that the plate-like sensory cone in Bibionidae (except *Hesperinus*) and some Sciaroidea are independent developments. The plate-like sensory cone unambiguously supports node 37 (Sciaridae + (Keroplatidae +

Mycetophilidae)). However, due to the polytomy including Ditomyiidae and the remainder of Sciaroidea the plate-like sensory cone did not provide unambiguous support for Bibionidae (node 5). The minute, button-like sensory cone unambiguously supports Anisopodidae (node 41) and Axymyiidae (node 44).

170) Apical sensory cone of antenna (CI: 0.50, RI: 0.77)
elevated on one article (0)
sessile; not elevated (1)
elevated on two articles (2)

See discussion of previous character. In *Ctenophora*, Pachyneuridae, Ditomyiidae, Anisopodidae, Scatopsidae, and *Trichocera*, the sensory cone is elevated on one article (Fig. 31b-c), but in Axymyiidae and Bolitophilidae it is elevated on two articles (Fig. 31d). In Axymyiidae, the antennae are very minute, and the number of articles is difficult to discern. The apical article is slightly recessed in a cup-like rim that is separated from the cranium by a distinct seam, except for anteriorly where it appears to be fused to the cranium. This cup-like structure has tentatively interpreted as the basal of two antennal articles. In Bibionidae, Keroplatidae, Mycetophilidae, and Sciaridae, the sensory cone (as a plate) is not elevated on an article, but is sessile on the cranium/antennal socket (Fig. 31e-f).

In Pachyneuridae there is a single antennal article atop which sits the sensory cone and a number of smaller peg-like sensillae (Fig. 31c). However, this taxon also has a small ring-like base of the sensory cone that slightly elevates the sensory cone above the surrounding, apical, peg-like sensillae; this ring is not homologous to a second antennal article for two reasons. Firstly, in those taxa with two antennal articles, such as Bolitophilidae and Cecidomyiidae, the second antennal article has a conspicuous lateral sensillum (Madwar 1937, Fig. 77; Solinas *et al.* 1987, "dorsobasal sensillum"). This sensillum is present on the single antennal article of Pachyneuridae, Anisopodidae, Ditomyiidae, and Trichoceridae, confirming that the single article in these taxa is homologous to the second article of Bolitophilidae and Cecidomyiidae. Secondly, in taxa that have two antennal articles (e.g. Bolitophilidae, Tanyderidae, and Ptychopteridae) the second antennal article elevates all the apical antennal sensillae and not just the sensory cone (Madwar 1937, Fig. 77; Anthon 1988, Fig. 16; Anthon 1943a, Fig. 6). A ring-like base of the sensory cone, similar to the one observed here in Pachyneuridae, is also present in some Trichoceridae (Karandikar 1931).

Character state 1 unambiguously supports Bibionidae (node 5), though it is also found in some Sciaroidea (node 37). Additionally the presence of two articles unambiguously supports Axymyiidae (node 44).

171) Postgenal bridge (CI: 0.50, RI: 0.80)
incomplete (0)
complete (1)

The homology and origin of components of the ventral portion of the head capsule are controversial and beyond the scope of this discussion. The term "postgenal bridge" is adopted from Courtney *et al.* (2000) to describe the narrow bridge-like connection of the posterior margin of the ventral cranium in front of the occipital foramen (hypostomal bridge of Teskey 1981). The postgenal bridge is complete in Bibionidae, *Symmerus*, and *Trichocera* (Fig. 30b; pgb), and is polymorphic in *Pachyneura* (complete or slightly incomplete). Although the entire ventral portion of the head capsule of *Scatopse* and Axymyiidae is sclerotized, the margins of the genae are not posteriorly or ventromedially fused, but run parallel to each other; the median section between the inner margins of the genae are less heavily sclerotized and this median area is apparently of another origin. These taxa are scored as having an incomplete postgenal bridge.

A complete postgental bridge unambiguously supports Bibionidae (node 5).

Figure 30, Larval head. a, *Cramptonomyia spenceri* Alexander (Pachyneuridae), dorsal view; frontoclypeal apotome removed to show interior of cranium; white arrows indicate anterior tentorial arm fused to inner surface of cranium, black arrows indicate where arm is no longer fused. b, *Plecia nearctica* Hardy (Bibionidae), ventral (mandibles removed). Abbreviations: ata, anterior tentorial arm; cd, cardo; el, ecdysial lines of frontoclypeal apotome; epip, epipharynx; gl, galeolacinia; lb, laterobasal sclerite of palpifer; mand, mandible; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pgm, post genal bridge; pm, posterior mentum; prm, prementum.

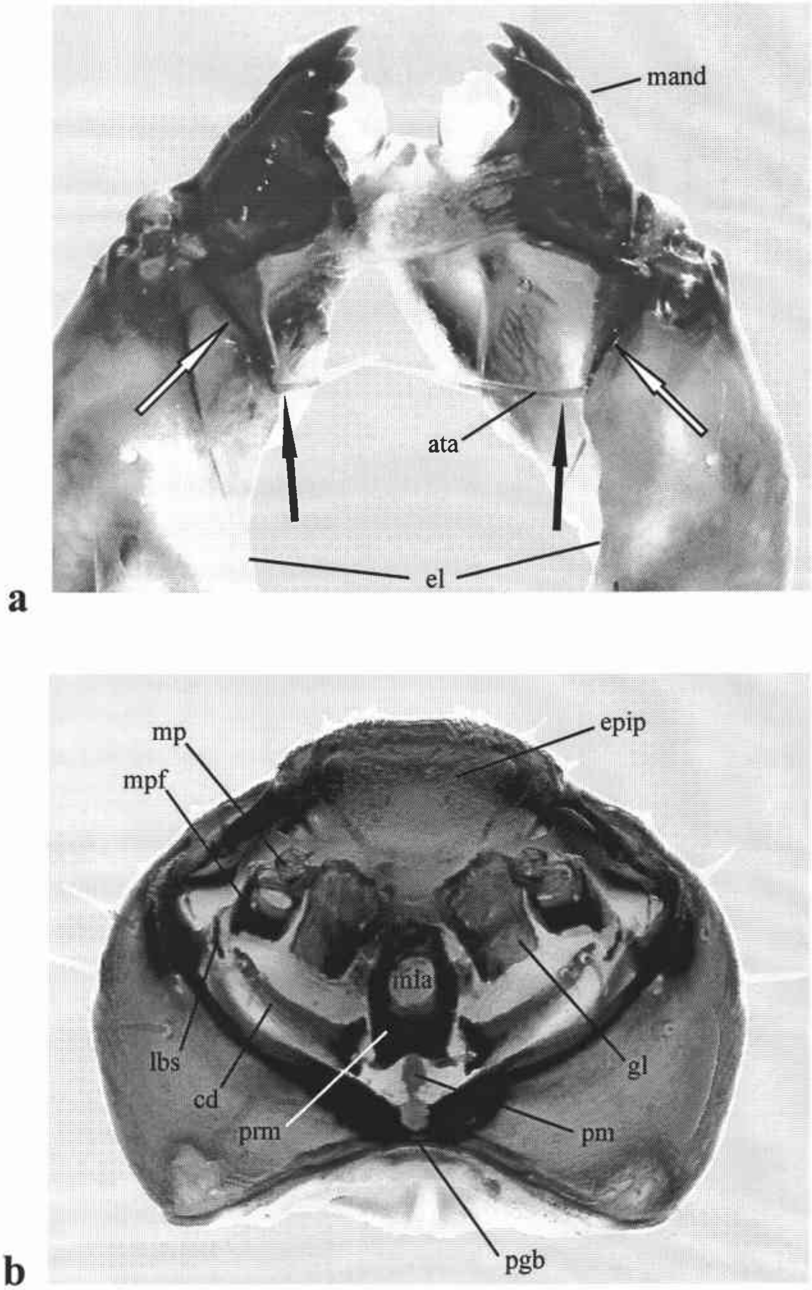


Figure 30, Larval head.

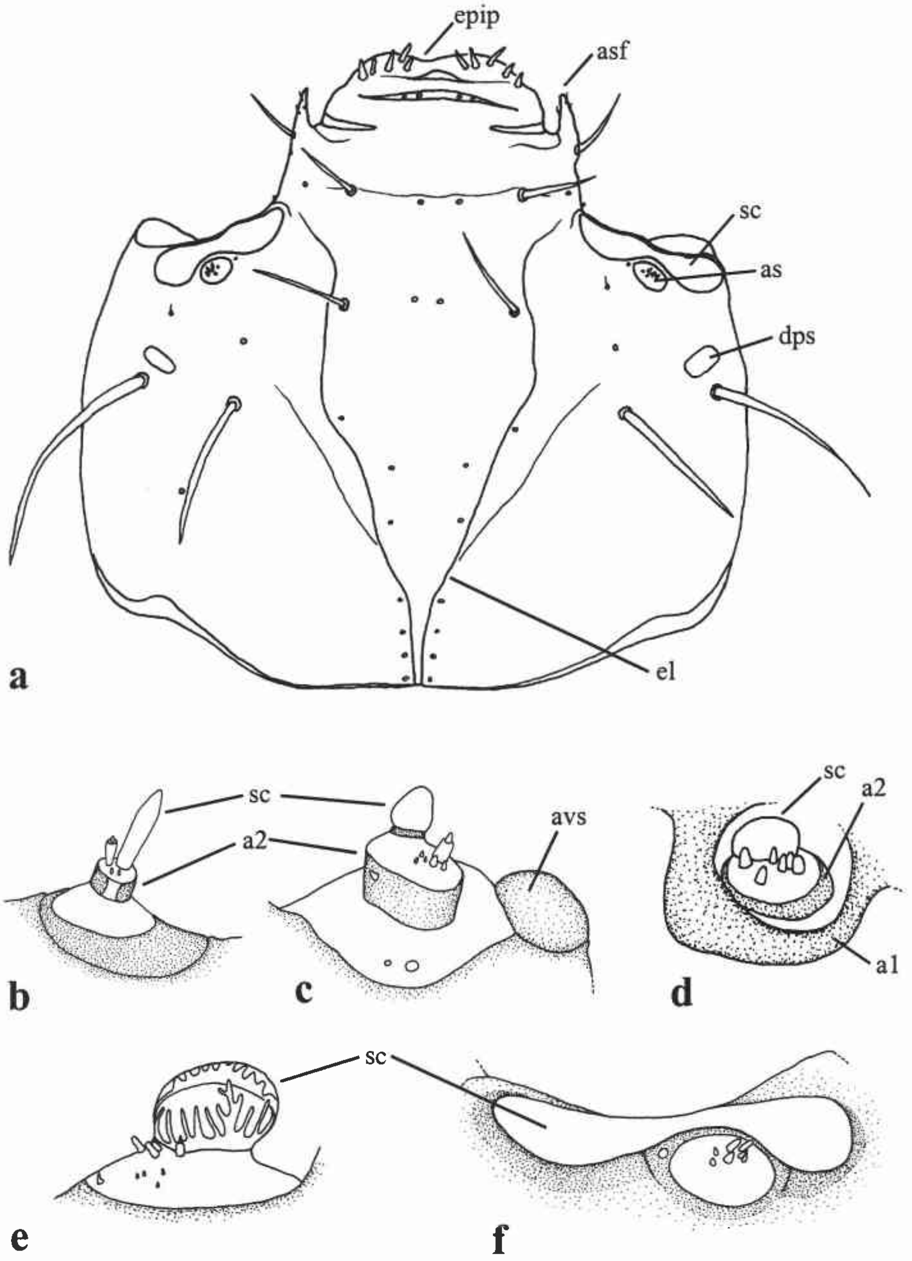


Figure 31, Larval head and antennae. a, *Bibio albipennis* Say (Bibionidae), head, dorsal. b-f, antennae. b, *Scatopse notata* (L.)(Scatopsidae). c, *Cramptonomyia spenceri* Alexander (Pachyneuridae). d, Axymyiidae new species. e, *Hesperinus brevifrons* Walker (Bibionidae). f, *Bibio albipennis* Say (Bibionidae). Abbreviations: a1, antennal article one; a2, antennal article two; as, antennal sensillae; asf, anterolateral spine of frontoclypeus; avs, anteroventral stemmata; dps, dorsoposterior stemmata; epip, epipharynx; sc, sensory cone.

172) Ventral prothoracic sclerites (CI: 1.00, RI: 1.00)

absent (0)

present (1)

Several small, irregular sclerites were detected in the cuticle on the ventral surface of the prothorax at the posteromedial margin of the head capsule of Bibionidae and Pachyneuridae (Fig. 28b; vps). Observation of these sclerites was occasionally hampered by folds in the cuticle that needed to be pulled taught before the sclerites were revealed. In the pachyneurid genus *Pergratospes*, there is a moderately-sized, subquadrate sclerite in this position, rather than the pair of minute sclerites in *Cramptonomyia*. The function of these sclerites is unknown, but they are here referred to as the "ventral prothoracic sclerites."

The presence of these sclerites unambiguously supports Bibionidae + Pachyneuridae (node 4).

173) Anterior tentorial arm (CI: 0.33, RI: 0.20)

absent (0)

free (1)

partially fused as a ridge to inner surface of cranium (2)

The anterior tentorial arm is part of the internal skeleton of the head. It arises as a rod-like bar from the anterior tentorial pit near the dorsal mandibular articulation and stretches, free of the cranium, posteroventrally, sometimes reaching the posterior tentorial arm. The anterior tentorial arm is well developed in taxa such as Anisopodidae (Teskey 1981; Fig. 5), but is weak and thread-like in most bibionids and absent in the bibionid *Plecia plagiata* Wiedemann. In Pachyneuridae, the anterior tentorial arms also arise at the anterior tentorial pits, but run posteromedially as a pair of ridges fused to the inner surface of the dorsal cranium until they reach the ecdysial lines separating the frontoclypeal apotome. At this point, the arms then become free of the cranium and run posteroventrally as thin rods (Fig. 30a). This condition is unique to Pachyneuridae and is not homologous to the short "dorsal arms" (outgrowths of the bases of the anterior tentorial arms) that were observed in *Obliogaster* (Anthon 1943a, as cited by Teskey 1981: 68), *Sylvicola*, *Mycetobia*, and *Trichocera* (pers. obs.). In these taxa the dorsal arms are present in addition to the elongate anterior tentorial arm. The dorsal arm of the anterior tentorial arm arises at the anterior end of the anterior tentorial arm, and runs posterolaterally a very short distance as a fused ridge on the inner dorsal surface of the cranium where it gradually disappears.

Character state 2 unambiguously supports Pachyneuridae (node 34).

174) Dorsal arm of anterior tentorial arm (CI: 0.50, RI: 0.50)

absent (0)
present (1)

See discussion of previous character. This character does not provide unambiguous support in this analysis because it is equally parsimonious to optimize the character as independent gains in Anisopodidae and Trichoceridae or as present in all the taxa in node 39 with a subsequent loss in Scatopsidae.

175) Posterior tentorial arm (CI: 0.25, RI: 0.62)

not forming a bridge (0)
forming a bridge (1)

Like the anterior tentorial arms, the posterior tentorial arms are part of the internal skeleton of the cranium. They arise from the posterior tentorial pits and in some taxa are medially fused, forming a bridge (Teskey 1981; Fig. 5, p tnt arm). A posterior tentorial bridge is present in Pachyneuridae, Anisopodidae, Trichoceridae, and Sciaroidea (except *Bolitophila*).

Absence of a posterior tentorial bridge unambiguously supports Bibionidae (node 5), though it is also absent in Tipulidae, Axymyiidae, *Scatopse*, and Bolitophilidae.

LABIUM, HYPOPHARYNX, AND ASSOCIATED STRUCTURES

The ventral portion of the head capsule, and in particular the structure and origin of the mentum, hypostoma, and labium, is controversial. Courtney *et al.* (2000) state that in most groups with a well-developed labium, including Bibionidae, "the submentum and mentum are fused into what is generally referred to as the postmentum, and other elements are collectively called the prementum." The only member of Bibionomorpha *s.l.* that exhibits all these structures is the anisopodid *Obliogaster*, which has a distinct submentum, mentum, and prementum (Anthon 1943a; Figs. 1 & 7). Each of these sclerites/regions as well as the hypopharynx and associated structures are discussed individually below.

Submentum: In *Obliogaster*, the submentum is a distinct subrectangular sclerite positioned between the anterior margin of the cranium and the posterior margin of the mentum (Anthon 1943a). Though it was not detected in any of the taxa examined here, from the figures provided by Anthon (1943b; Fig. 20) it appears that a submentum may also be present in the anisopodid *Mycetobia pallipes* Meigen.

Mentum: The mentum of *Obliogaster* includes a subrectangular posterior portion and a subrectangular, anteriorly toothed, anterior portion. The posterior portion of the mentum lies in the membrane between the anterior edge of the submentum and the posterior edge of the prementum and is demarcated from the toothed anterior portion of the mentum by a distinct, transverse indentation (Anthon 1943a; Figs. 1 & 7). The toothed anterior portion of the mentum, the hypostoma, lies exactly ventral to the prementum, obscuring the prementum in ventral view. Although a hypostoma is absent from the taxa examined here (except *Ctenophora*), the posterior portion of the mentum is present in numerous taxa as a sclerite which, as in *Obliogaster*, lies in the membrane at the posterior edge of the prementum. It is possible that the mentum and submentum are indistinguishably fused and form a synsclerite. However, such a fusion was not detected and consequently, the sclerite present between the posterior edge of the prementum and the anterior edge of the ventral cranium has been interpreted as the posterior mentum here (Fig. 30b; pm).

Prementum (labium): The prementum of *Obliogaster* has three primary parts: the labial palps, the glossa, and the "br" sclerite (Anthon 1943a). The paired labial palps are the most ventral structure of the prementum and are recognized as small circular tubercles bearing apical sensory papillae. The "brückenförmiger Teil des Praementums" (or "br" sclerite) of Anthon (1943a) and the glossa are closely associated sclerites. Anthon (1943a; Fig. 7) illustrates the br sclerite of *Obliogaster* as distinct from the closely appressed glossa by a seam; the br sclerite forms the approximate dorsal side, and the glossa forms the approximate ventral side, of the labium. The two sclerites are also distinct in *Mischoderus* (Tanyderidae)(Anthon1987; Fig. 23), where the glossa is minute and the br sclerite forms the larger sclerotized area just ventral to the salivary duct. With the exception of *Scatopse* (pers. obs.), a distinct br and glossa was not here observed. Thus, it is a question of whether these two sclerites are indistinguishably fused or if one or the other is absent in the other taxa examined. In taxa in which the sclerites are separate, the glossa is recognized by its tooth-like, lobate, anterolateral edges. Because such lobes are found throughout most of the taxa examined here (e.g. Fig. 35a-c, 38a; glos), the glossa is considered present, though one may still question whether or not the br sclerite is fused or absent. Since the individual recognition of these two sclerites is not possible here, the main sclerite of the labium, which is probably a synsclerite including the glossa and the br sclerite, will be referred to as the "labial synsclerite." The labial synsclerite of most taxa is an approximately upside-down-U-shaped sclerite (Fig. 34a; ls). The arms of the U face posteriorly and the rounded or truncate side of the U faces anteriorly. It may also be medially divided (anterior edge absent) so that it is essentially a pair of parallel, longitudinal rods, as is found in many Sciaroidea (Fig. 33b&d; ls). In many species the labial synsclerite has a tooth-like lobe on each anterolateral corner (glossa), though in some it has several lobes at each corner (e.g. *Symmerus* (Fig. 33a)) or is toothed along the entire anterior edge (e.g. *Ctenophora*). Typically the labial synsclerite comprises the anterior and lateral margins of the labium and anterolaterally encloses a ventromedial membranous area bearing the labial palps (Fig. 30b, 34a; mla).

Posterior labial sclerite: This sclerite is referred to simply as the labium by Madwar (1937) in most subgroups of Sciaroidea (though incorrectly labeled in the illustration of *Ctentrocnemis* (Fig. 64) in which his "labium" of other taxa is homologous to the pair of flattened oblong plates posteroventral to the "labium" labeled in the figure). However, his term is too vague to be very useful, so this sclerite will be referred to as the "posterior labial sclerite." The posterior labial sclerite is an arch-shaped or U-shaped sclerite that is associated with, and is typically found ventral to, the apex of the salivary duct. In some Ditomyiidae, the posterior end of the U-shaped sclerite is absent; this results in the subdivision of the sclerite into a pair of parallel plates (Madwar 1937; Fig. 64, and *Australosymmerus* (pers. obs.)). In *Ctenophora* and *Sylvicola*, this sclerite is a minute arch or U-shaped sclerite which, like the apex of the salivary duct, lies between the prementum and the hypopharynx (Figs. 32a, 35a; pls). In the ditomyiid *Symmerus*, it also lies directly ventral to the hypopharynx and dorsal to the prementum, but is a much larger U-shaped sclerite than observed in *Ctenophora* and *Sylvicola* (33a; pls). In the ditomyiid *Australosymmerus* Freeman, this sclerite is also well developed, but it is no longer dorsal to the prementum. Rather, it is more posterior in position so that here both the posterior labial sclerite and the prementum are in approximately the same plane. The development of the subquadrate labium observed in most Bibionidae and Pachyneuridae is then understood by examination of the bibionid *Hesperinus rohdendorfi* Krivosheina & Mamaev (1967b, Fig. 18.3; Krivosheina 1997, Fig. 16). In this taxon, the U-shaped labial synsclerite (with arms of U facing posteriorly) and the U-shaped posterior labial sclerite (with arms of U facing anteriorly) are in the same plane, and the arms of each U-shaped sclerite are nearly touching (as in Fig. 33d; *Bolitophila*). In *Pachyneura* the apices of the arms are fused, yet there remains a distinctly less sclerotized separation between the two sclerites (Fig. 34a). In other *Hesperinus* (Fig. 36a), as well as all other Bibionidae and Pachyneuridae, this fusion is complete, forming the rather unique subquadrate labium of these taxa (Figs. 36, 37a, 38a-b).

An identical fusion of the posterior labial sclerite with the labial synsclerite occurs in many species of Sciaroidea, except that in most Sciaroidea the labial synsclerite is represented by a pair of rods rather than an upside-down-U-shaped sclerite (Fig. 33b; ls). Additionally, many species of Sciaroidea have the labial synsclerite fused to sclerites of the hypopharynx. For these reasons, the sciaroid prementum is of a much different overall structure than that found in Bibionidae and Pachyneuridae, and has resulted in confusion concerning the homology of sclerites of the sciaroid labiohypopharynx. For example, Madwar (1937, Fig. 164) treats the labial synsclerite as part of the hypopharynx. Although the ventral labial sclerite of Sciaroidea is often recognized by a seam or slight separation between it and the labial synsclerite (Fig. 33b)(as described above in *Pachyneura*), in some cases it is smoothly fused to the labial synsclerite forming a U-shaped sclerite (where the arms of the U are homologous to the labial synsclerite, and the bottom of the U is homologous to the posterior labial sclerite). This U-shaped sclerite supports the posterior margin of the otherwise membranous prementum in some species of Sciaridae and Keroplatidae. It has been treated as the "sclérite prélabial" by Matile (1990; Figs. 137,138,162, 163, 193), but is here referred to as the "labial synsclerite + posterior labial sclerite." In some Sciaroidea (e.g. some *Mycetophila*, pers. obs.), the posterior labial sclerite is absent, resulting in an "open" posterior end of the prementum.

176) Toothed hypostoma (anterior mentum) (CI: 1.00, RI: -)

present (0)

absent (1)

See discussion of "Mentum." A hypostoma is present only in *Ctenophora* and is unknown from Bibionomorpha *sensu stricto*. This character provides no unambiguous support in this analysis.

177) Posterior mentum (CI: 0.50, RI: 0.87)
absent/indistinguishably fused (0)
present (1)

See discussion of "Mentum." The posterior mentum is present in Anisopodidae, Scatopsidae, Bibionidae, and Pachyneuridae. In Anisopodidae, *Cramptonomyia*, and the bibionids *Penthetria* and *Hesperinus*, it is a distinct rectangular sclerite which is not fused to surrounding sclerites (Figs. 32a, 34b, 36; pm). *Scatopse* has a transparent rectangular sclerite which posteriorly is appressed to the anterior margin of the head and separated from it by a seam. Anteriorly, it slightly overlaps the base of the prementum and is interpreted here as the mentum based upon its position. Teskey (1981; Fig. 5) and Anthon (1943b) did not find a mentum in *Sylvicola*. However, a mentum is present in the exemplar of this genus examined here, though it is only very weakly differentiated from the lightly sclerotized membrane on the ventral surface of the head. *Pachyneura*, and the bibionids *Plecia*, *Bibio*, and *Dilophus*, have a posterior mentum that is not distinct from surrounding sclerites; its anterior edge is fused to the posterior edge of the prementum and its posterior edge is fused to the anterior margin of the cranium, so that it appears as a narrow, longitudinal strap of sclerite supporting the prementum (Figs. 30b, 34a, 37a, 38a-b; pm). The remainder of the taxa have a mentum that is absent/indistinguishably fused with the ventral head capsule.

The presence of a mentum unambiguously supports Bibionidae + Pachyneuridae (node 4) and Anisopodidae + Scatopsidae (node 40).

Figure 32, Anisopodidae and Axymyiidae, larval mouthparts, ventral. a, *Sylvicola cinctus* (Fab.) (Anisopodidae), labium, hypopharynx, and maxilla. b-c, Axymyiidae sp. (Oregon, USA). b, Labiohypopharynx. c, Maxilla. Abbreviations: cd, cardo; gl, galeolacinia; hyp, hypopharynx; lp, labial palp; ls, labial synsclerite; mp, maxillary palp; mpf, maxillary palpifer; pls, posterior labial sclerite; pm, posterior mentum; sd, salivary duct; sr1, sensory region one; sr2, sensory region two.

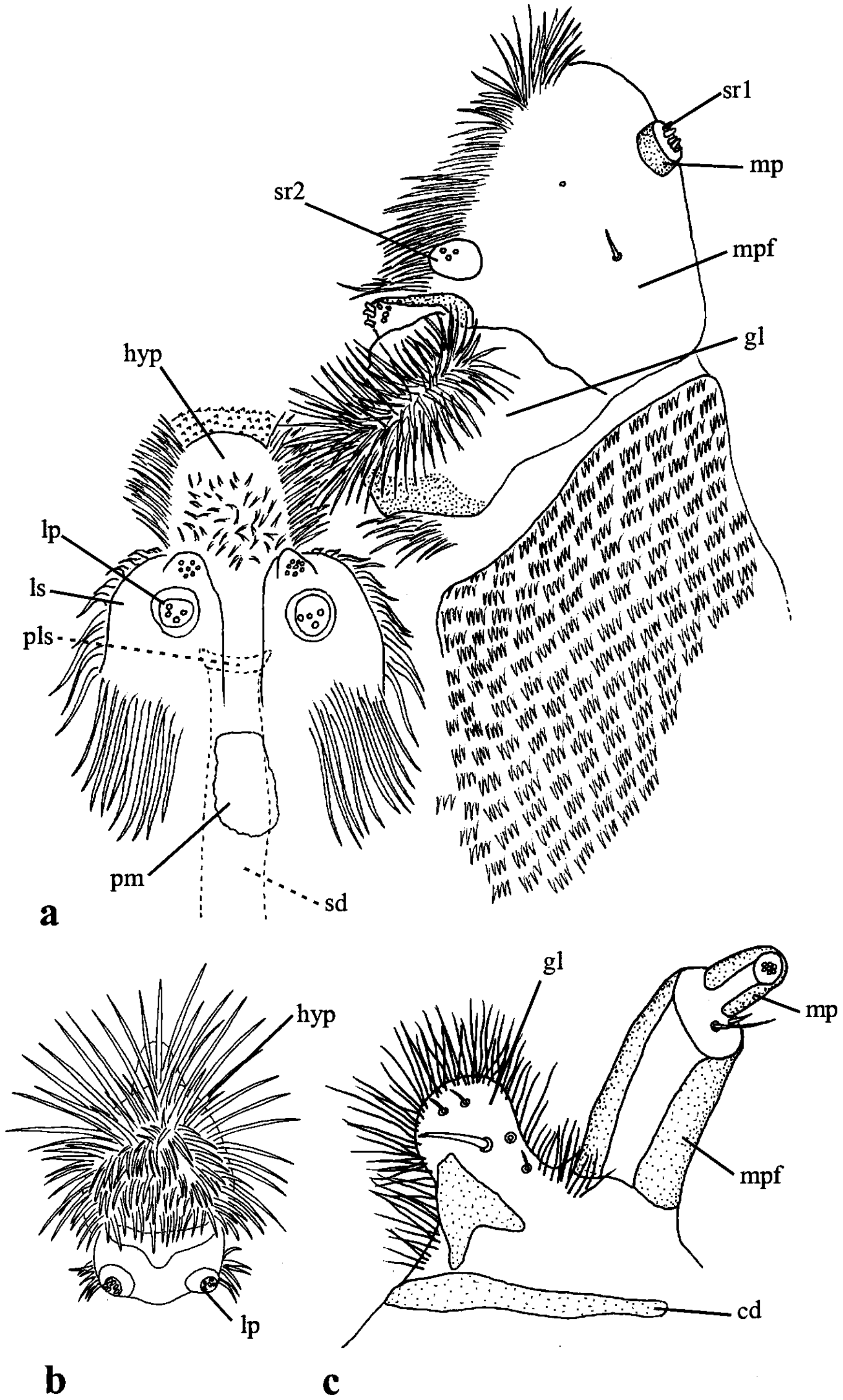


Figure 32, Anisopodidae and Axymyiidae, larval mouthparts, ventral.

Figure 33, Sciaroidea, larval mouthparts, ventral. a, *Symmerus coqulus* Garrett (Ditomyiidae), Labiohypopharynx and maxilla. b, *Rhynchosciara americana* (Wied.) (Sciaridae), labiohypopharynx. c, *Mycetophila favonica* Chandler (Mycetophilidae), maxilla. d, *Bolitophila bucera* Shaw (Bolitophilidae), labiohypopharynx and maxilla. Abbreviations: apgl, apical point of galeolacinia; cb, cibarial bar; cd, cardo; gl, galeolacinia; hs, hypopharyngeal sclerites; hyp, hypopharynx; lgl, laterobasal lobe of galeolacinia; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pls, posterior labial sclerite; sr1, sensory region one; sr2, sensory region two.

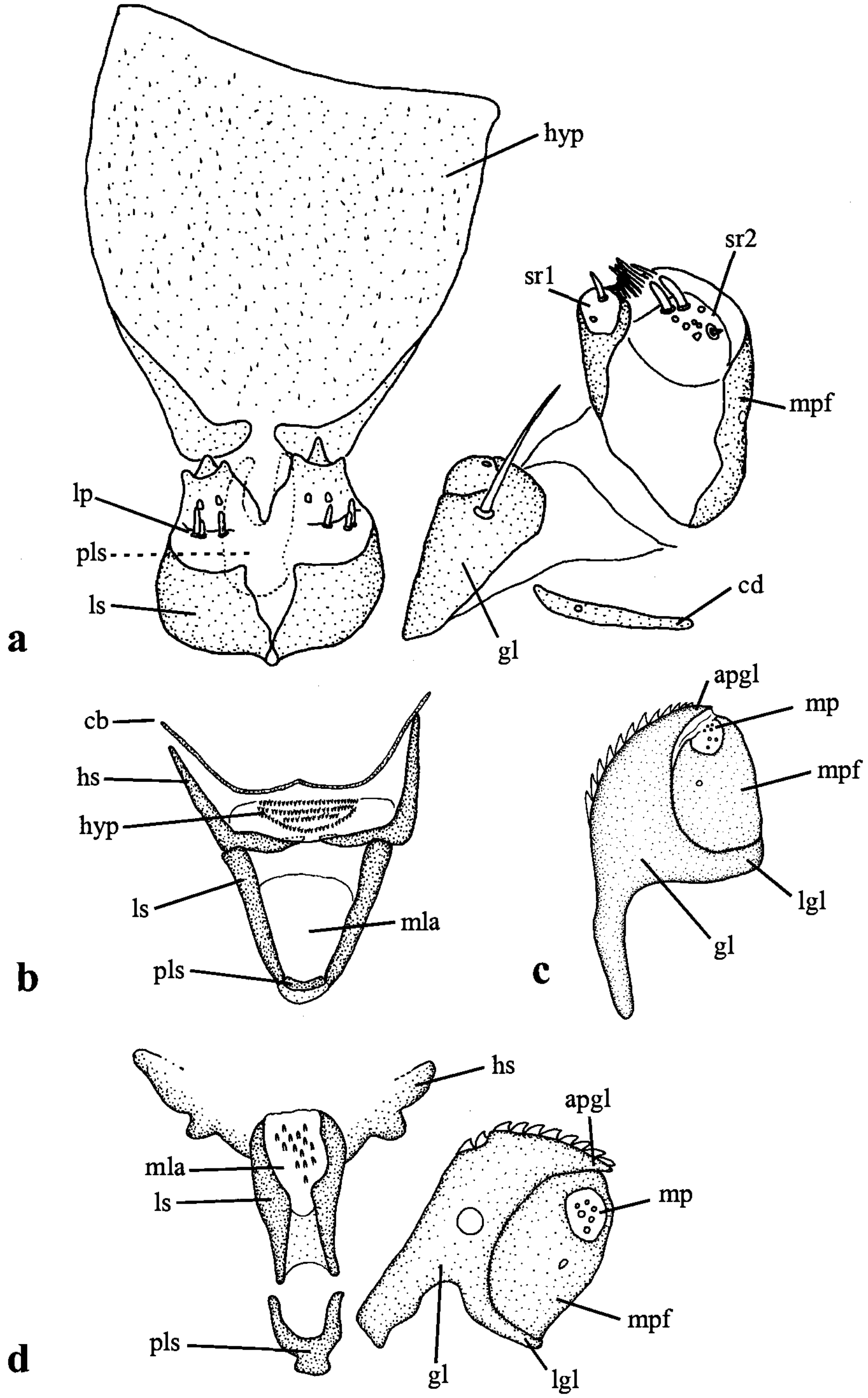


Figure 33, Sciaroidea, larval mouthparts, ventral.

Figure 34, Pachyneuridae, larval labium and maxilla, ventral. a, *Pachyneura fasciata* Zetterstedt. b, *Cramptonomyia spenceri* Alexander. Abbreviations: cd, cardo; cd1-4, setae 1, 2, 3 & 4 of the cardo; gl, galeolacinia; lbs, laterobasal sclerite of maxillary palpifer; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pls, posterior labial sclerite; pm, posterior mentum.

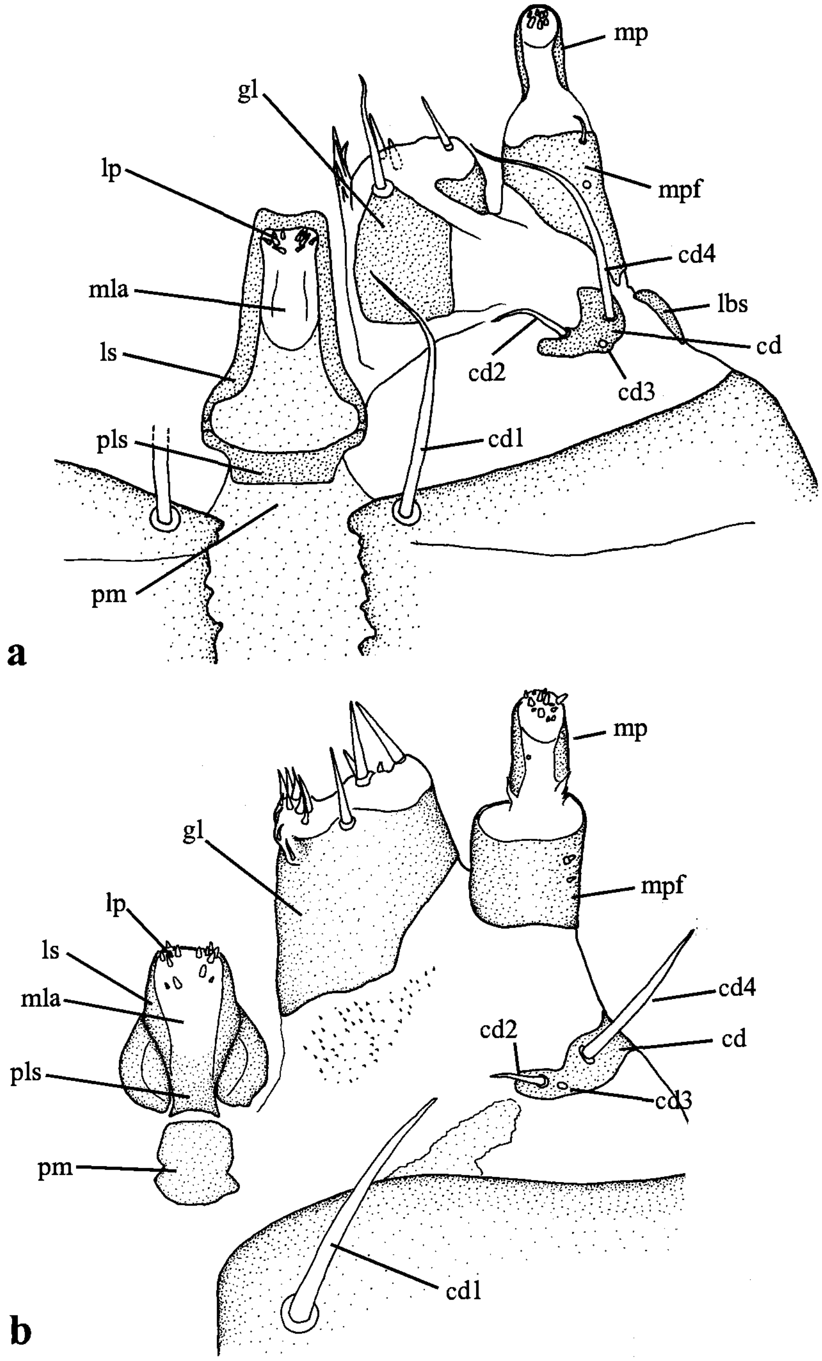


Figure 34, Pachyneuridae, larval labium and maxilla, ventral.

Figure 35, Larval labiohypopharynx. a, *Ctenophora angustipennis* Loew (Tipulidae), lateral. b-c, *Pachyneura fasciata* Zetterstedt (Pachyneuridae). b, Lateral. c, Dorsal. d, *Bibio albipennis* Say (Bibionidae), lateral. Abbreviations: cb, cibarial bar; glos, glossa; hs, hypopharyngeal sclerites; hyp, hypopharynx; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; pls, posterior labial sclerite.

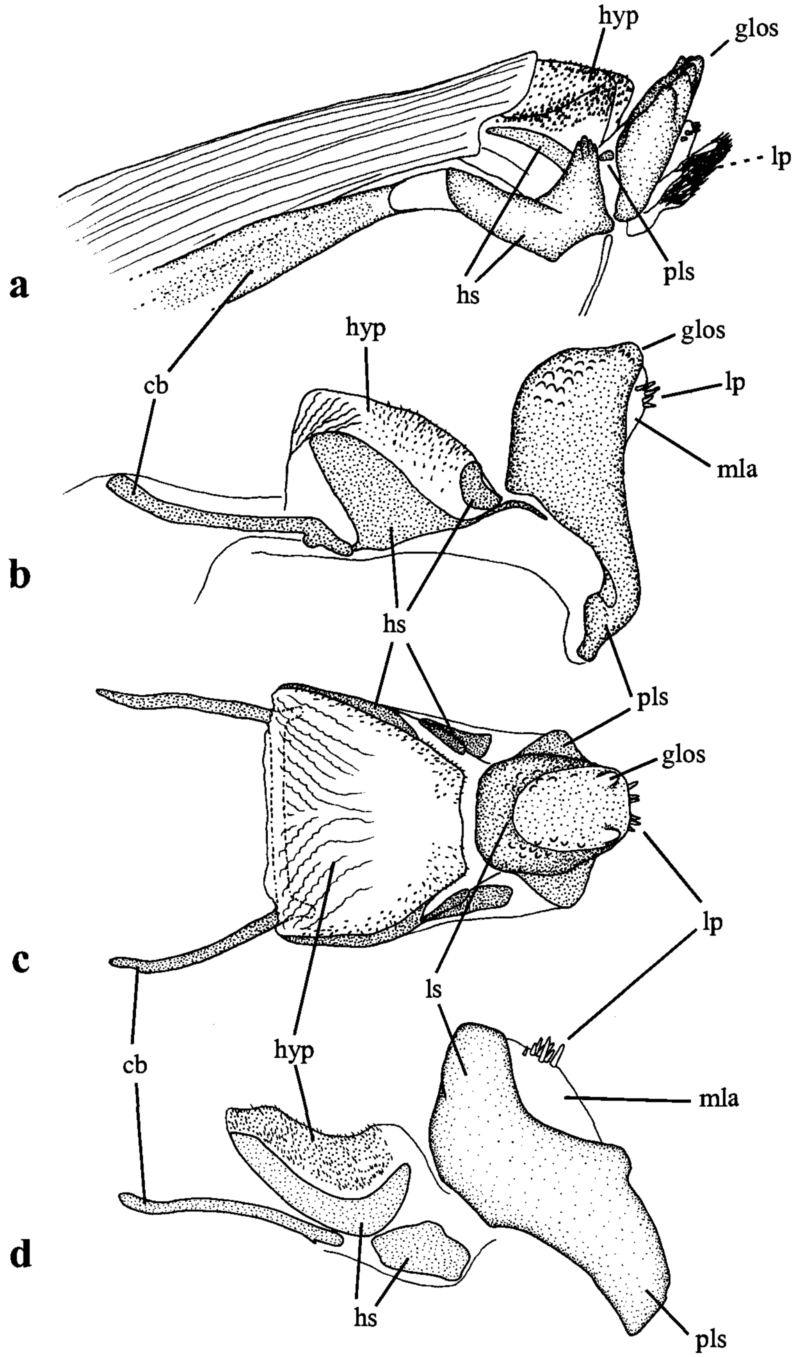


Figure 35, Larval labiohypopharynx.

Figure 36, *Hesperinus* and *Penthetria* (Bibionidae), larval labium and maxilla, ventral. a, *Hesperinus brevifrons* Walker. b-c, *Penthetria funebris* Meigen. b, Labium. c, Maxilla. Abbreviations: cd, cardo; cd1-4, setae 1, 2, 3 & 4 of the cardo; gl, galeolacinia; lbs, laterobasal lobe of maxillary palpifer; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pls, posterior labial sclerite; pm, posterior mentum.

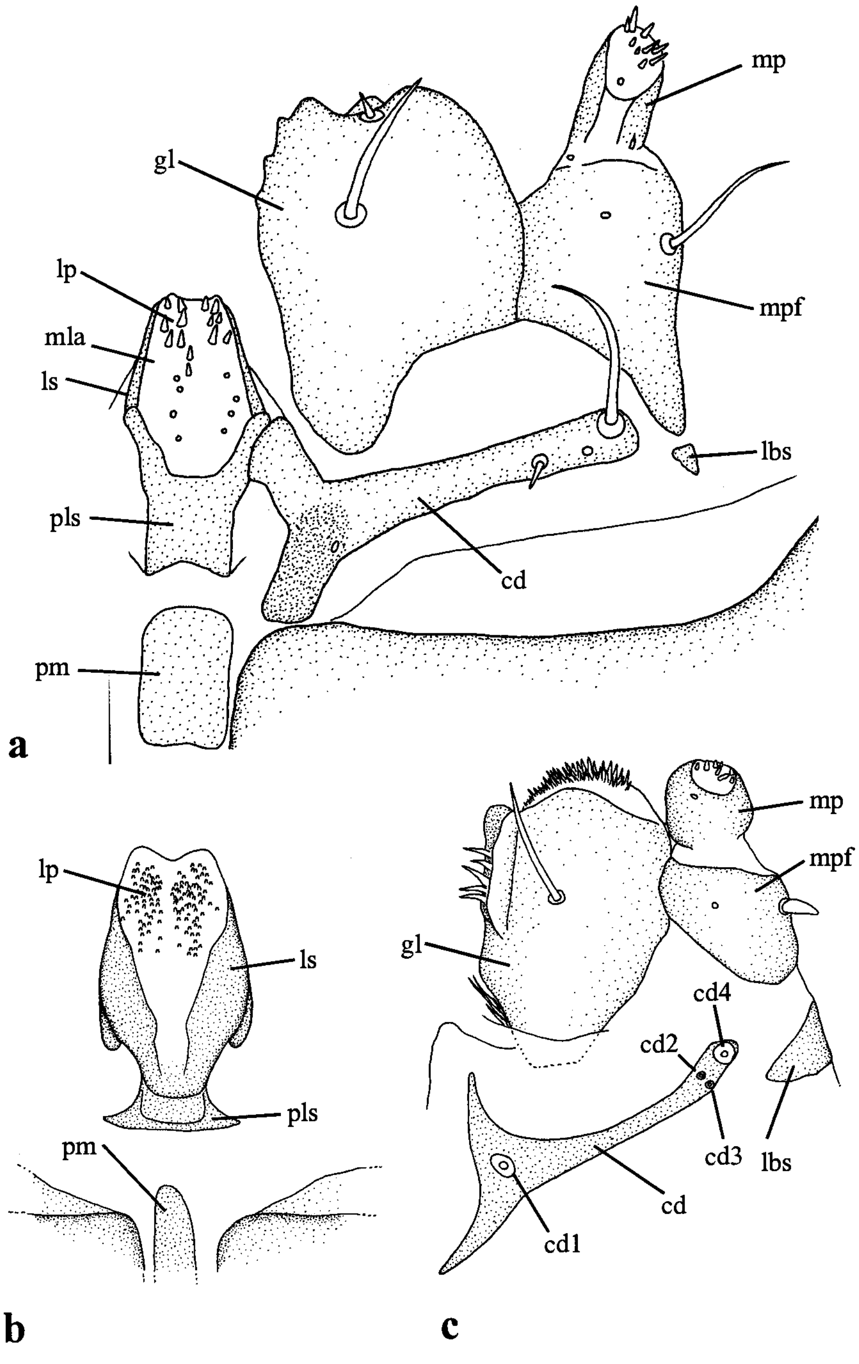


Figure 36, *Hesperinus* and *Penthetria* (Bibionidae), larval labium and maxilla, ventral.

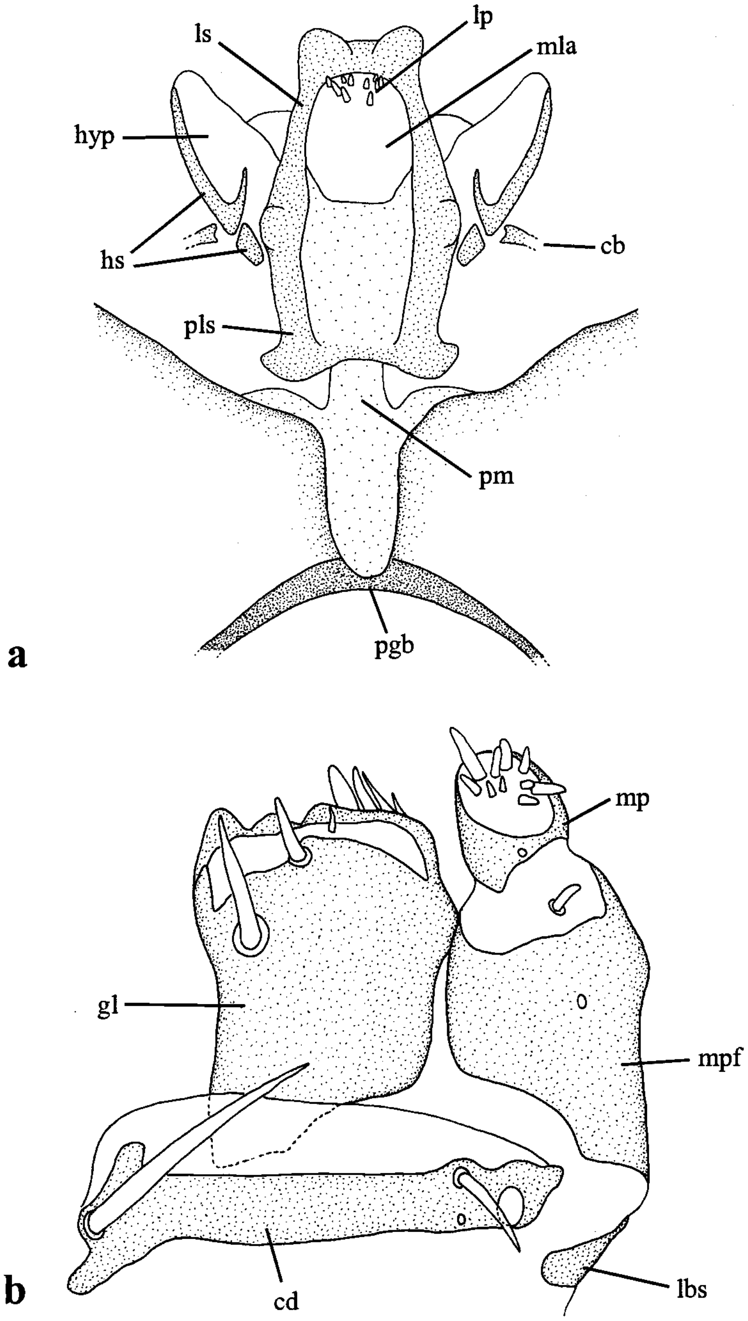


Figure 37, *Bibio albipennis* Say (Bibionidae), larval labiohypopharynx and maxilla, ventral. a, Labiohypopharynx. b, Maxilla. Abbreviations: cb, cibarial bar; cd, cardo; gl, galeolacinia; hs, hypopharyngeal sclerites; hyp, hypopharynx; lbs, laterobasal lobe of maxillary palpifer; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pgb, post genal bridge; pls, posterior labial sclerite; pm, posterior mentum.

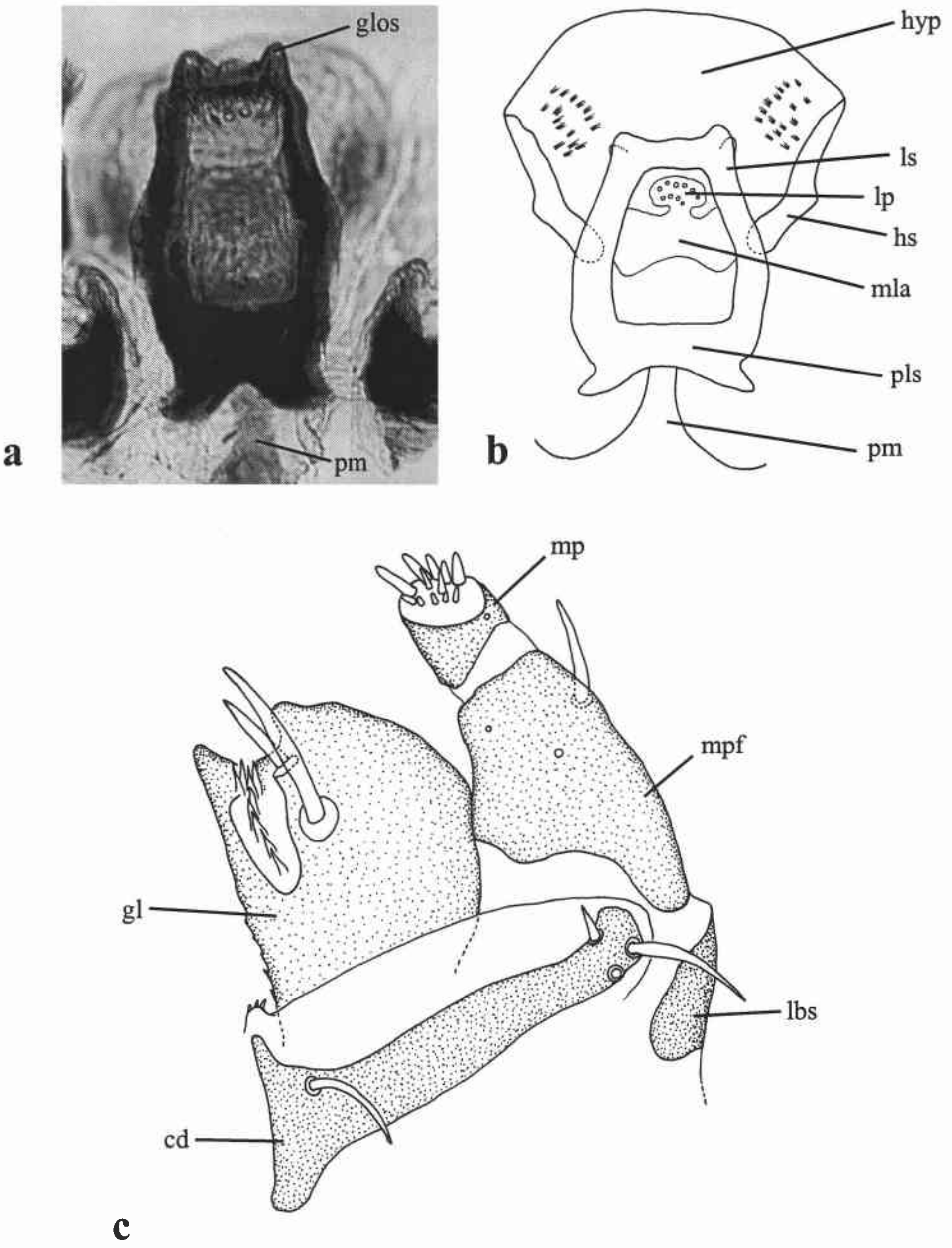


Figure 38, *Plecia* (Bibionidae), larval labiohypopharynx and maxilla, ventral. a, *P. thulinigra* Hardy, labiohypopharynx. b, *P. nearctica* Hardy, labiohypopharynx. c, *P. nearctica* Hardy, maxilla. Abbreviations: cd, cardo; gl, galeolacinia; glos, glossa; hs, hypopharyngeal sclerites; hyp, hypopharynx; lbs, laterobasal lobe of maxillary palpifer; lp, labial palp; ls, labial synsclerite; mla, membranous labial area; mp, maxillary palp; mpf, maxillary palpifer; pls, posterior labial sclerite; pm, posterior mentum.

178) Labial synsclerite (CI: 1.00, RI: 1.00)
present (0)
absent (1)

See discussion of "Prementum." The labial synsclerite is present in all taxa examined (Figs. 32a, 33-38; ls) except for Axymyiidae which has a membranous prementum (Fig. 32b). The absence of the labial synsclerite unambiguously supports Axymyiidae (node 44).

179) Posterior labial sclerite (CI: 0.40, RI: 0.57)
not fused to labial synsclerite (0)
fused to labial synsclerite (1)
absent (2)

See discussion of "Posterior labial sclerite" above. The posterior labial sclerite varies in its position relative to the labial synsclerite and may be either separate from or fused to the labial synsclerite. It is fused to the labial synsclerite in Bibionidae, Pachyneuridae, and Sciaroidea (Figs. 34-38; pls)(except Ditomyiidae and Bolitophilidae (Fig. 33a & d; pls)). In the exemplars of Sciaridae and Keroplatidae, the posterior labial sclerite is small and fused with the labial synsclerite into a U-shaped labial synsclerite + posterior labial sclerite (Fig. 33b; pls). Although its minute size and degree of fusion with the labial synsclerite can make the posterior labial sclerite difficult to observe in these taxa, it has been consistently observed in other species of these families (Madwar 1937; Figs. 120, 128, 141, and 152). The posterior labial sclerite is also very small in *Mycetophila*, but is fused to the posterior ends of the rod-like labial synsclerites. The posterior labial sclerite is minute and not fused with the labial synsclerite in *Ctenophora* and *Sylvicola* (Figs. 32a, 35a; pls) and is absent in Axymyiidae, Scatopsidae, *Mycetobia* and Trichoceridae.

This character provides no unambiguous support in this analysis.

180) Position of posterior labial sclerite (CI: 0.85, RI: 0.50)
ventral to prementum (0)
posterior to and in same plane as prementum (1)

See discussion of "Posterior labial sclerite." The posterior labial sclerite is ventral to the prementum in *Ctenophora*, *Sylvicola*, and *Symmerus* (Figs. 32a, 33a, 35a; pls); though Ditomyiidae is polymorphic for this character because some genera (e.g. *Symmerus*) have a sclerite that is ventral to the prementum and others (e.g. *Australosymmerus* (pers. obs.)) have one that is in the same plane as the prementum. The posterior labial sclerite is posterior to, and in the same plane as, the prementum in Bibionidae (Fig. 36), Pachyneuridae (Fig. 34), and Sciaroidea (Fig. Fig. 33b & d) (except *Symmerus*). The posterior labial sclerite is absent in the remainder of taxa.

This character provides no unambiguous support in this analysis.

181) Membranous labial area (CI: 1.00, RI: 1.00)
not enclosed (0)
enclosed by labial synsclerite and posterior labial sclerite (1)

See discussion of "Prementum" and "Posterior labial sclerite." In Bibionidae and Pachyneuridae, the labium has of unique structure. It is a subrectangular sclerotized frame formed by the upside-down-U-shaped labial synsclerite anteriorly and the posterior labial sclerite posteriorly (Fig. 34a; ls, pls). The "frame" formed by the fusion of these sclerites completely encloses a membranous area which bears a field of sensory papillae (labial palps) (Fig. 34a; mla, lp). Although some Sciaroidea, such as Sciaridae and Keroplatidae, also have a membranous area and a fusion of the labial synsclerite and posterior labial sclerite (Fig. 33b), the prementum of these taxa is very different because the labial synsclerite is a pair of rods (rather than upside-down-U-shaped sclerite), and the labial synsclerite is often fused with the pair of sclerites that support the hypopharynx (hypopharyngeal sclerites). In these taxa, either the membranous area is not entirely enclosed by a sclerotized frame (e.g. Matile 1990; Fig. 137), or part of the frame enclosing the membranous area includes the hypopharyngeal sclerites (Fig. 33b; hs, Matile 1990; Fig. 193).

Griffiths (1990) noted, presumably referring to this rather unique shape of the labium in bibionids and pachyneurids, that "the monophyly of the Pachyneuroidea + Bibionoidea is demonstrated by the synapomorphous structure of the larval labium and hypopharynx." Such a structure of the labium was here found only in these taxa, thus confirming Griffiths' assertion.

Character state 1 unambiguously supports Bibionidae + Pachyneuridae (node 4).

182) Tubercle of labial palps (CI: 1.00, RI: 1.00)

present (0)
absent (1)

The labial palps are located in a membranous area on the ventral surface of the prementum and are a pair of small tubercles bearing apical sensory papillae (Fig. 32a-b; lp). However, in Bibionidae, Pachyneuridae, and Sciaroidea the tubercles of the labial palps are absent and the palps are represented by two clusters of minute papillae or a more dispersed field of papillae (Figs. 34-38; lp). The papillae are not raised on a tubercle, but are still positioned in the membranous area which typically bears the labial palps and are here considered homologous to those papillae found at the apices of the tubercle-like labial palps of other taxa.

Absence of the tubercle of the labial palps unambiguously supports Sciaroidea + (Bibionidae + Pachyneuridae)(node 3).

183) Cibarial bar (CI: 0.50, RI: 0.75)

a pair of unconnected bars (0)
an open-ended-square-shaped bar (1)
a strongly sclerotized U or arch-shaped bar (2)
absent (3)

The cibarial bar is an elongate arch or U-shaped sclerite located at the posterodorsal margin of the hypopharynx (Figs. 33b, 35c; cb). Although the cibarial bar is typically considered to be only a single sclerite, when traced through a number of taxa the cibarial bar ranges from a pair of parallel rods to a strongly U-shaped or arched bar. This pattern was observed by Perraudin (1961) who noted the paired rods in Bibioninae and the U-shaped sclerite in Sciaridae and tenatively considered the two forms as homologous (1961, Figs.15 (bibionid) & 6 (sciarid); "bras oral" ("bo")). A pair of parallel, unconnected bars was observed in *Ctenophora*, *Trichocera*, and Bibioninae (Fig. 35a & d; cb). The ventral tips of these bars are connected by a transverse bar forming a single, square-ended-U-shaped sclerite in *Pachyneura* (Fig. 35b-c; cb); because the form of this cibarial bar appears structurally intermediate between the paired rods and the more uniform U-shaped bar it is assigned a separated character state. A strongly sclerotized U-shaped sclerite is observed in Axymyiidae, Anisopodidae, Scatopsidae, and Sciaroidea (except Ditomyiidae). The bibionids *Plecia*, *Penthetria*, and *Hesperinus*, the pachyneurid *Cramptonomyia*, and the ditomyiid *Symmerus* have no cibarial bar.

Character state 0 unambiguously supports Bibioninae (node 23).

184) Pharyngeal filter (CI: 0.50, RI: 0.80)

present (0)
absent (1)

The pharyngeal filter is a complex filtering structure which is located posterior to the cibarial bar (Anthon 1988, Fig. 23). The erratic distribution of this structure in Diptera has resulted in various hypotheses such as: multiple losses of the structure, and that it is not homologous in nematoceran and brachyceran flies (Oosterbroek & Courtney 1995; character 27, Courtney *et al.* 2000). A pharyngeal filter is present in Axymyiidae, Anisopodidae, Scatopsidae, and Trichoceridae. It is absent in all other taxa (Bibionomorpha *s.s.* and Tipulidae), though at least the tipulid genus *Ula* has a pharyngeal filter similar to that found in other nematoceran flies (Sinclair 1992).

This character provides no unambiguous support in this analysis.

CARDO AND MAXILLA

185) Ventral region of head posterior to maxilla with dense mat of appressed setae (CI: 0.50, RI: 0.00)

absent (0)
present (1)

Wood & Borkent (1989; character 44) noted the mat of appressed setae along the anteroventral edge of the cranium at the base of the maxilla in some members of their infraorder Psychodomorpha (Keilin & Tate 1940; Figs. 2, 16). Here a mat of setae was observed in *Sylvicola* (Fig. 32a) and *Trichocera,* but was absent in all other taxa including *Mycetobia* and *Scatopse.*

This character provides no unambiguous support in this analysis.

186) Shape of inner apex of cardo (CI: 0.50, RI: 0.75)

simple (0)
t-shaped (1)

The cardo is a slender transverse sclerite positioned in a membranous area between the posteroventral edge of the galeolacinia + palpifer and the anteroventral edge of the cranium (Fig. 30b). In those taxa with a well developed cardo, this sclerite bears three setae at the lateral apex of the sclerite and a single seta at the inner apex of the sclerite (Fig. 36c; cd1-cd4). The cardo may have the inner apex fused to the anteroventral margin of the cranium or have its entire length appressed against, or fused with the anteroventral margin of the cranium. Pachyneuridae have a cardo that is subdivided into two sclerites: a lateral portion bearing three setae (cd2-cd4) is in the membrane and a medial portion, recognized by the presence of a large seta (cd1), has become incorporated into the anteroventral, submedian part of the cranium (Fig. 34). *Cramptonomyia* has a broken, lightly sclerotized area between the subdivided portions which identifies the area that has been lost (Fig. 34b).

When the inner apex of the cardo is not fused to the anteroventral margin of the cranium it is simple (without lobes (Fig. 33a; cd)) or T-shaped (bearing an anteriorly directed lobe and a posteriorly directed lobe (Fig. 36; cd)). A T-shaped cardo was observed in Bibionidae and *Ctenophora*. In those taxa with the inner apex or all of the cardo fused to the anteroventral margin of the cranium, the structure of the inner apex is unknown and thus these taxa have been scored as a "?" (Scatopsidae, Anisopodidae, Pachyneuridae, *Bolitophila*, and *Mycetophila*). The remaining taxa have a simple cardo with an inner apex that is not lobate.

This character provides no unambiguous support in this analysis.

187) Cardo (CI: 1.00, RI: 1.00)

a single sclerite (0)
subdivided (1)

See discussion of previous character. A subdivided cardo was observed only in Pachyneuridae (Fig. 34). The remainder of taxa have the cardo as a simple transverse sclerite which is separate, appressed, or entirely fused to the anteroventral margin of the cranium.

The subdivided cardo unambiguously supports Pachyneuridae (node 34).

188) Entire length of cardo (CI: 0.50, RI: 0.85)
not appressed to anterior margin of head (0)
appressed (1)

See discussion of previous cardo characters. The cardo of Anisopodidae, Scatopsidae, Trichoceridae, *Keroplatus*, *Bolitophila*, and *Mycetophila* have a cardo that is closely appressed or partially to entirely fused to the anteroventral margin of the cranium (Fig. 32a). Other taxa have the cardo distinctly separated from the anterior margin of the head by a membranous area (Fig. 30b).

The appressed cardo provides unambiguous support for Sciaroidea (except Ditomyiidae)(node 36) and Trichoceridae + (Anisopodidae + Scatopsidae)(node 39).

189) Galeolacinia and palpifer + maxillary palp (CI: 0.50, RI: 0.85)
not appressed (0)
appressed (1)

In addition to the posterior cardo, the maxilla includes the more anteromedial galea and lacinia, which appear together as a single lobe in the taxa examined here (henceforth referred to as the "galeolacinia" (Fig. Fig. 30b; gl), and the more anterolateral palpifer, which bears a one-segmented maxillary palp (Fig. 37; mpf, mp). In most taxa the two lobes are adjacent basally, but otherwise there is a distinct gap between the galeolacinia and the palpifer. In contrast, these lobes are closely appressed and separated only by a seam in Anisopodidae, Scatopsidae, and Sciaroidea (except Ditomyiidae)(Fig. 32a).

Character state 1 provides unambiguous support for Sciaroidea (except Ditomyiidae)(node 36) and Trichoceridae + (Anisopodidae + Scatopsidae)(node 39).

190) Galeolacinia (CI: 0.50, RI: 0.80)

primarily sclerotized (0)
membranous (1)

In Tipulidae, Bibionidae, Pachyneuridae, and Sciaroidea the galeolacinia is primarily sclerotized and typically bears numerous spines or teeth at its apex (Figs. 33c-d, 34, 36-38; gl). The exception is Ditomyiidae which has a small, though still sclerotized, galeolacinia which does not bear apical teeth, but is smooth (Fig. 33a; gl). In Axymyiidae, Anisopodidae, Scatopsidae, and Trichoceridae the galeolacinia is primarily membranous and often bears numerous setae, but lacks apical teeth (Fig. 32a & c; gl) . A membranous maxilla was used as partial evidence by Wood & Borkent (1989; character 44) to support their infraorder Psychodomorpha.

This character provides no unambiguous support in this analysis.

191) Inner and anterior edge of galeolacinia (CI: 1.00, RI: 1.00)

not evenly serrate (0)
evenly serrate (1)

See discussion of previous character. The apex and inner edge of the galeolacinia of Sciaroidea (except Ditomyiidae) have a unique structure. Whereas all other taxa examined have either no teeth/spines or irregularly arranged teeth/spines, in Keroplatidae, Sciaridae, Mycetophilidae, and Bolitophilidae, the apical and inner surface of the galeolacinia is serrated with small, identical, evenly spaced teeth (Fig. 33c-d; gl). This serrate structure is relatively consistent in Sciaroidea (Madwar 1937, Plachter 1979b) with the notable exceptions being Ditomyiidae and Cecidomyiidae (Wood & Borkent 1989; 1353).

The serrated galeolacinia unambiguously supports node 36 within Sciaroidea.

192) Galeolacinia with lateral, posteroventral lobe supporting palpifer (CI: 1.00, RI: 1.00)

absent (0)
present (1)

In Sciaroidea (except Ditomyiidae), the outer, ventroposterior edge of the galeolacinia is developed into a point, shelf, or lobe which projects under the base of the palpifer and supports it. This is here referred to as the laterobasal lobe of the galeolacinia (Fig. 33c-d; lgl)

Character state 1 unambiguously supports node 36 within Sciaroidea.

193) Galeolacinia gradually anteriorly tapered to a single sclerotized point (CI: 1.00, RI: 1.00)

absent (0)
present (1)

The structure of the galeolacinia of Sciaroidea (except Ditomyiidae) is distinctive because it gradually tapers anteriorly to a point (Fig. 33c-d; apgl) rather than being broadly rounded or subquadrate as in other taxa examined (Fig. 36). In some sciaroids this pointed apex is exaggerated and extends over the apex of the maxillary palpus.

Character state 1 unambiguously supports node 36 within Sciaroidea.

194) Laterobasal sclerite of maxillary palpifer (CI: 0.50, RI: 0.90)

absent (0)
present (1)

At the lateral edge of the base of the maxillary palpifer there is a small sclerite in Bibionidae and *Pachyneura* here termed the "laterobasal sclerite of the maxillary palpifer" (Fig. 36; lbs). In *Pachyneura* this sclerite is more difficult to observe because it is not as heavily sclerotized as in Bibionidae and is somewhat transparent (Fig. 34; lbs). It was absent in the only other larva of Pachyneuridae dissected (*Cramptonomyia*). Although not observed in the Mycetophilidae studied here, this sclerite also occurs in various genera of Sciophilinae (Plachter 1979b; Figs. 2a (Sk), 28a, 29a, 30a, 32a, 33a, 34a). A posterior, lobate, extension of the lateral, basal portion of the palpifer was observed in *Ctenophora*. This lobe is in the same position as the laterobasal sclerite and is possibly homologous with it, but the distribution of both structures is too poorly known to make any firm statement concerning their homology at this time.

Although the presence of this sclerite is consistent within Bibionidae, this character provides no unambiguous support in this analysis because presence of the sclerite is polymorphic in Pachyneuridae and absent in all other taxa.

195) Maxillary palp (CI: 0.50, RI: 0.87)
well developed (0)
minute (1)

The lateral lobe of the maxilla typically has two parts: a basal segment (palpifer) and an apical, one-segmented, digitate palpus that bears apical peg-like sensillae (Fig. 37b). In some taxa, the palpifer and palp are fused to the degree that the lobes are difficult to distinguish and the palpus is recognized by a thin sclerotized ring, minute tubercle, or merely a cluster of apical, sensory, peg-like sensillae (Fig. 32a, 33a, 33c-d). Wood & Borkent (1989; character 45) considered the reduced palpus as partial evidence for their infraorder Psychodomorpha. Although the reduced palpus was observed in the psychodomorph taxa Anisopodidae, Scatopsidae, and Trichoceridae, it was also observed in all the exemplars of Sciaroidea. A reduced condition apparently also occurs in some Tipulidae and some Blephariceromorpha (Oosterbroek & Courtney 1995; character 26).

This character provides no unambiguous support in this analysis.

196) Palpifer + palpus a flattened oval plate (CI: 1.00, RI: 1.00)

absent (0)

present (1)

The palpifer + palpus of most taxa is either digitiform or in the form of a robust hump or lobe. However in Sciaroidea (except Ditomyiidae) the palpifer + palpus is a characteristically-shaped, flattened, oblong, oval plate that is closely associated with the outer edge of the galeolacinia (Fig. 33c-d; mpf, mp).

Character state 1 unambiguously supports node 36 within Sciaroidea.

197) Apex of maxillary palp (CI: 0.50, RI: 0.75)

single (0)

divided into 2 sensory regions (1)

The apex of the maxillary palp of most taxa is a single, round or oval, membranous region bearing peg-like sensillae (Fig. 34; mp). Yet in Anisopodidae, Scatopsidae, Trichoceridae and Ditomyiidae, the apex has two sensory regions which are defined by two sclerotized rings or, in some species, the two regions are on separate, small tubercles. These paired sensory regions were noted in Anisopodidae and Trichoceridae by Keilin & Tate (1940; Figs. 5, 25, 53) as sensory organs “a” and “b.” The sensory organ “b” in *Trichocera* is not as distinct as in *Sylvicola* and *Mycetobia* and is only tentatively coded here as present. In Anisopodidae and Trichoceridae the apex of the palpifer is rather large and the two sensory organs are widely separated (Fig. 32a; sr1, sr2). In contrast, the apex of the palpifer of *Scatopse* and *Symmerus* is narrow, yet both sensory organs are also present (33a; sr1, sr2). In these taxa the two sensory organs are separated by a pair of sclerotized rings or partial rings as was noted in Scatopsidae by Lyall (1929; Figs. 3, 4, 9).

The presence of two sensory regions unambiguously supports Trichoceridae + (Anisopodidae + Scatopsidae)(node 39), though it is also present in *Symmerus*.

MANDIBLE

198) Orientation of mandibles (CI: 1.00, RI: 1.00)

operating horizontally (0)
operating vertically (1)

The orientation of the mandibles, and their evolutionary shift from a horizontal, to an oblique, to a vertical orientation (or vice versa) has been considered in numerous studies (Wood & Borkent 1989, character 41; Sinclair 1992, characters 3 & 6; Oosterbroek & Courtney 1995, character18 & 19; Friedrich & Tautz 1997). The rotation of the mandible into a vertical plane is facilitated by a shift of the epicondyle to the tentorial phragma (Oosterbroek & Courtney; 1995). The movement of the position of the epicondyle aids in determining the homology of the position of the mandible, which can be anywhere between a horizontal and vertical orientation. A vertically oriented mandible was observed in Anisopodidae, Scatopsidae, and Trichoceridae. Although the vertical mandible is synapomorphic for these taxa here, the plesiomorphic condition is dubious since Tipulidae have members with both horizontally and vertically oriented mandibles (Oosterbroek & Theowald 1991).

The vertical orientation of the mandible unambiguously supports Trichoceridae + (Anisopodidae + Scatopsidae)(node 39). The larva of *Dialysis dispar* was not available for study, but like other Brachycera undoubtedly has vertically oriented mandibles. However, adult characters do not place *Dialysis* in a clade with the aforementioned taxa and artificially coding *Dialysis* with character state 1 has no effect on the topology.

199) Shape of apex of mandible (CI: 0.66, RI: 0.66)

scoop-shaped with teeth around edge of scoop (0)
laterally compressed into a thin, serrate edge (2)
apex a single, elongate point (3)

In most taxa, including Bibionidae, the sub-triangular mandible has a scoop-shaped apex with teeth distributed along the edge of the scoop (Fig. 30a; mand). In Keroplatidae, Bolitophilidae and Mycetophilidae, the mandible is strongly laterally compressed so that the apex is a thin, linear, edge bearing the teeth. The latter two taxa have mandibles resembling the edge of a circular-saw blade (a circular edge serrated with many small curved teeth); these mandibles have also been observed in other Bolitophilidae and Mycetophilidae (Plachter 1979b; Figs. 45b-48b, Madwar 1937). Axymyiidae have a robust mandible with a single, elongate, stout point at the apex (Krivosheina 2000; Fig. 30)(Wood & Borkent 1989; character 21).

Character state 3 unambiguously supports Axymyiidae. Additionally, the analysis indicates that character state 2 is either not homologus in all these taxa or Sciaridae has shown a reversal back to state 0.

200) Mandible with a sub-basal thumb of teeth (CI: 1.00, RI: 1.00)

absent (0)
present (1)

The presence of a sub-basal thumb-like projection curving toward the apex of the mandible was considered partial evidence for infraorder Psychodomorpha by Wood & Borkent (1989; character 42) though it apparently occurs in some Tipulidae as well (Oosterbroek & Courtney 1995; character 23). A sub-basal thumb was observed here in Anisopodidae, Trichoceridae, and Scatopsidae (Teskey 1981, Fig. 4) and unambiguously supports this clade (node 39)

201) Mandible with a line of weakness delineating apical portion (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Wood & Borkent (1989; character 43) considered the presence of a line of weakness separating the toothed apex of the mandible from the base of the mandible as partial evidence for their infraorder Psychodomorpha. A line of weakness also occurs in some Psychodidae and Ptychopteridae (Anthon 1943b), Blephariceridae and Deuterophlebiidae (Courtney 1991; character 4), and some Tipulidae (Oosterbroek & Theowald 1991). A line of weakness is also present separating an apical portion of the mandible in some Chaoboridae, though it is unclear whether this condition is homologous to that found in previously mentioned taxa (e.g. *Australomochlonyx* Freeman and *Mochlonyx* Loew; J. Ogawa, pers. comm. 2004). Here a mandible with the apex differentiated by a line of weakness was observed in Anisopodidae, Scatopsidae, and Trichoceridae (Teskey 1981, Fig. 4) and unambiguously supports this clade (node 39).

202) Prostheca (CI: 0.33, RI: 0.33)
absent (0)
present (1)

The presence of a prostheca, a brush or comb-like structure on the inner basal surface of the mandible (Teskey 1981, Fig. 3), is considered plesiomorphic in Diptera (Oosterbroek & Courtney, 1995; character 24). A prostheca was absent here in Anisopodidae, *Bolitophila*, and some species of Axymyiidae, though a small prostheca has been observed in the anisopodid *Obliogaster* (Anthon 1943a; Fig. 3), and here in the axymyiid *Axymyia furcata* McAtee.

Absence of a prostheca unambiguously supports Anisopodidae (node 41).

203) Mandibular comb (CI: 1.00, RI: 1.00)

absent (0)

present (1)

The mandible of numerous nematoceran taxa such as Culicomorpha, Ptychopteridae (Wood & Borkent 1989; character 4), and Psychodomorpha (Oosterbroek & Courtney, 1995; character 21), have a brush or comb of curved setae on the dorsal surface of the mandible. Here this structure, the "mandibular comb," was observed in Anisopodidae, Trichoceridae, and Scatopsidae (Teskey 1981, Fig. 4) and unambiguously supports this clade (node 39).

EPIPHARYNX AND ASSOCIATED STRUCTURES

204) Shape of epipharynx (CI: 0.33, RI: 0.66)

dorsoventrally flattened, subrectangular (0)

laterally compressed and triangular (1)

The epipharynx of most of the taxa examined is dorsoventrally flattened, subrectangular, and slightly bilobate (Fig. 30b; epip). A conical or wedge-shaped, anteroventrally pointed epipharynx (Wood & Borkent 1989, characters 38 & 20) was observed in Anisopodidae, Scatopsidae, Trichoceridae, Axymyiidae, and *Bolitophila*. Although, it was thought that this character may be related to the "closer approximation of the mandibles" in the Psychodomorpha (Wood & Borkent 1989), at least Axymyiidae and *Bolitophila* have horizontally orientated and not notably proximal mandibles. These characters are thus considered independent here. A wedge-shaped epipharynx is known in numerous other families including some Tipulidae.

This character provides no unambiguous support in this analysis.

205) Apex of labrum/epipharynx with strong spines (CI: 0.25, RI: 0.66)

absent (0)

present (1)

Ctenophora, Pachyneuridae, and Bibionidae (except *Penthetria* and *Plecia plagiata* Wied.) have strong spines along the apical edge of the labrum/epipharynx (Fig. 31a; epip).

Presence of strong spines unambiguously supports Bibionidae + Pachyneuridae (node 4), though a reversal in *Penthetria* unambiguously supports this genus (node 30).

206) Torma (CI: 0.50, RI: 0.85)

not fused to dorsal labral sclerite (0)

fused (1)

An "articulated" torma (a torma that is not fused to the dorsal labral sclerite), occurs in numerous lineages of nematoceran flies (Wood & Borkent 1989, character 40) and is considered part of the dipteran ground plan (Oosterbroek & Courtney 1995, character 12). Here a torma which wraps dorsolaterally and is fused to the dorsal labral sclerite was observed in Bibionidae, Pachyneuridae, and Sciaroidea (except Ditomyiidae). In Ditomyiidae the torma is wrapped dorsolaterally as in other Bibionomorpha *s.s.*, but it is not fused to the dorsal labral sclerite. Although this taxon represents the "not fused" condition and is coded as such, it is also an intermediate between a torma which ends laterally and is not fused to the dorsal labral sclerite (Anisopodidae, Scatopsidae, Trichoceridae, Axymyiidae, and Tipulidae) and a torma which wraps dorsolaterally and is fused to the dorsal labral sclerite. Oosterbroek & Courtney (1995; character 12) coded Axymyiidae as having a fused torma, but both exemplars of Axymyiidae examined here have the torma distinctly separated from the dorsal labral sclerite by a narrow membranous strip.

Because of the unresolved polytomy including Ditomyiidae and the remainder of Sciaroidea, this character provides no unambiguous support in this analysis despite the fact that character state 1 is consistent within Bibionidae + Pachyneuridae and Sciaroidea (except Ditomyiidae).

207) Premandible (CI: 0.50, RI: 0.72)
absent (0)
a simple unadorned sclerite (1)
on inner edge of torma, weakly sclerotized, with associated spines (2)
on outer edge of torma, heavily sclerotized, with serrated edge (3)

The premandible is a small sclerite associated with the labrum/epipharynx that articulates with the apex or sub-apex of the torma and usually bears a row of spines or teeth (Teskey 1981). The presence of a premandible or premandible-like-sclerite in numerous lineages has led to several hypotheses about the evolution of this structure (e.g. Wood & Borkent 1989, Sinclair 1992, Courtney 1991). However, despite its apparent presence in numerous Sciaroidea (Madwar 1937, Plachter 1979b, Krivosheina & Zaitsev 1980, Matile 1990) a true premandible is still considered absent in this lineage since "the specific homologies of these sclerites are unclear" (Oosterbroek & Courtney 1995). Here, any small round or subrectangular sclerite is interpreted as "the premandible" if it articulates with the apex or sub-apex of the torma. As noted by Wood & Borkent (1989; character 39) the premandible may be adorned (with spines/teeth) or unadorned (a simple sclerite without spines/teeth) and they considered the latter character state plesiomorphic.

Although previously considered as part of the apex of the torma in *Bibio* (Perraudin 1961; Fig. 8) a small unadorned premandible is present in the bibionids *Bibio*, *Dilophus*, some *Plecia* and some *Penthetria*, as well as Ditomyiidae (though some ditomyiids have a premandible with apical teeth (Krivosheina & Zaitsev 1980)). In addition to articulating with the apex of the torma, this unadorned sclerite is considered structurally homologous to the well developed and adorned premandible in Psychodomorpha because both sclerites act as the insertion point for the labial retractor muscle (Perraudin 1961). Although a hypothesis of character homology is thus warranted, some structural and slight positional differences in the premandible across these groups requires at least three character states; a very small unadorned premandible and two kinds of adorned premandibles. The unadorned premandible is a small, weakly sclerotized, subquadrate sclerite that lacks teeth or spines. In Anisopodidae, Trichoceridae, and Scatopsidae the premandible is associated with the lateral outer (or posterior) edge of the torma and is a heavily sclerotized sclerite with a serrated edge (Wood & Borkent 1989; Fig. 3). Structurally and positionally somewhat different is the premandible of Sciaroidea (except Ditomyiidae), which is associated with the inner (or anterior) apical edge of the torma (Matile 1990; Fig. 128). In these taxa the sclerite is weakly sclerotized and associated with a row of elongate spines which are separated from the edge of the sclerite by a gap or seam. The premandible is absent in Tipulidae, Axymyiidae, some *Plecia*, some *Penthetria*, *Hesperinus*, and Pachyneuridae.

Character state 1 unambiguously supports Bibioninae (node 23) and character state 3 unambiguously supports Trichoceridae + (Anisopodidae + Scatopsidae)(node 39).

PUPA

The pupal stages of most taxa examined here are unknown. However, in addition to the pupal stages borrowed from museum collections or reared, the following two taxa were scored, when possible, based on available illustrations or photographs of the pupal stage: *Pachyneura fasciata* (Krivosheina 1997a; Fig. 7), and *Haruka elegans* (Saigusa 1993).

208) Silk pupal cocoon spun by last instar larva (CI: 1.00, RI: 1.00)
absent (0)
present (1)

Matile (1997) states that silk secretion is ancestral for Sciaroidea and that larvae secrete silk for various purposes, including at least the building of the last instar cocoon in which the larvae pupate. He considers the lack of silk secretion in Ditomyiidae and Bolitophilidae to be an independent loss in these two groups. Here a silk pupal cocoon was observed in Keroplatidae, Mycetophilidae and Sciaridae. Although not personally observed in *Rhynchosciara americana*, this sciarid apparently spins a cocoon in the form of a "loose net" (E. Abdelhay pers. comm.). In agreement with Matile (1997), a silk cocoon was not observed in Ditomyiidae and Bolitophilidae. Plachter (1979a) illustrates the variety of webs and pupal cocoons spun by larvae of Sciaroidea.

Presence of a silk cocoon unambiguously supports node 37 indicating that silk secretion is not ancestral in Sciaroidea with secondary losses in Ditomyiidae and Bolitophilidae, but is a derived feature within Sciaroidea.

209) Abdominal tergites with a row of sclerotized spines/spinules (CI: 0.33, RI: 0.80)
absent (0)
present (1)

Plachter (1979c) reported two kinds of pupae in mycetophiloids; "the first type in which species pupate in the soil or in solid tubes in rotten wood or in fungi built by the larvae" that "are distinguished by spinulae covering the surface of the abdomen, segmental rows of spines, long hairs and the ability to bend their abdomen actively in order to move fore and back in the tube. The second type is always surrounded by a special web or cocoon in which the pupa is hanging or lying above the surface. These pupae posses a very smooth cuticle." Whereas Plachter's two types of pupae are distinguished by a variety of different (though perhaps related) characters, here the character is considerably more restricted and is defined as the presence or absence of rows of sclerotized spines/spinules on the abdominal tergites. Although *Plecia* and *Penthetria* carry-over fleshy lobes from the larval into the pupal stage, these are not considered homologous to the rows of sclerotized spines/spinules on the abdomen. Sclerotized spines/spinules are absent in Bibionidae (except the genus *Hesperinus*). Rows of spines/spinules are also absent in Keroplatidae and Mycetophilidae. Axymyiidae have rows of spines only on some abdominal segments, but have been coded as "spines present." *Scatopse* has semi-circular arrangements of modified setae (as is observed in the larval stage), that are not here considered homologous to the rows of spines observed in other taxa.

The absence of spinules unambiguously supports node 6 (Bibionidae exclusive of *Hesperinus*) and the silk-spinning Sciaroidea (node 37).

210) Fleshy lobes on abdomen (CI: 0.50, RI: 0.66)
absent (0)
present (1)

The presence of fleshy lobes on bibionid larvae is considered independent of this character because fleshy lobes are only carried over into the pupal stage in *Plecia* and *Penthetria* (Pinto & Amorim 1996, Figs. 21-23), but not in Bibioninae, which have a smooth pupal cuticle.

This character provides no unambiguous support in this analysis.

211) Leg sheaths (CI: 0.33, RI: 0.75)
superimposed (0)
parallel (1)

Oosterbroek & Courtney (1995) considered pupae with parallel (rather than superimposed) leg sheaths, a synapomorphy of Sciaroidea + Pachyneuridae, though they note that parallel leg sheaths occur in numerous other lineages of nematoceran flies. Parallel leg sheaths were observed here in Pachyneuridae, Sciaroidea and Tipulidae.

This character provides no unambiguous support in this analysis.

212) Respiratory horn (CI: 0.50, RI: 0.85)
present (0)
absent (1)

The anterior thoracic spiracle of Bibionidae, Pachyneuridae, and Sciaroidea (except Ditomyiidae) is more or less flush with the surface of the thorax or slightly elevated on a small protuberance. In Tipulidae, Anisopodidae, Scatopsidae, Trichoceridae, Axymyiidae, and Ditomyiidae, the anterior spiracle is associated with an elongate tube-like respiratory horn. Matile (1997) coded Bibionidae and Pachyneuridae as having large respiratory horns; this is incorrect.

This character provides no unambiguous support in this analysis.

GENERIC REVISION

The generic descriptions given below are based on the study of as many species as possible for each genus including a study of the D.E. Hardy Collection of World Bibionidae (BPBM); yet, it was not possible to examine all species in each genus. Furthermore, in only a small portion of these species was a more detailed study of the male and female terminalia undertaken. Consequently, though as accurate a picture as possible of the structural variation of each genus is here provided, the generic descriptions do not necessarily cover all the variation found in each of these genera and the descriptions will need to be modified in the future. This is especially true for the immature stages, which are known only from a handful of specimens. Larval descriptions are based upon last (or later) instars since the first instar larva is morphologically quite different and was not examined during the course of this study. The first instar larvae of several species are discussed in the following literature: *Plecia* (Pinto & Amorim 1996), *Bibio* (Morris 1917, 1921), and *Dilophus* (Morris 1922).

The generic boundaries are defined by synapomorphies in the phylogenetic analysis discussed in the previous sections. The study of specimens A new genus of fossil Bibionidae was hinted at in an abstract by Grimaldi *et al.* (2002), but no formal description was provided and this taxon was not examined in the present study. Those genera which are based solely on fossil forms are marked with an asterisk (*). The following works were critical in summarizing the nomenclature for the genera: Evenhuis (1994), Hardy (1959b, 1965a, 1966, 1973, 1980, 1983, 1989), Krivosheina (1986), Sabrosky (1999), and Thompson (2000).

Phylogenetically informative characters do not always provide the best diagnostic characters for easy recognition of a genus. Therefore, the diagnostic characters provided in the following diagnoses of each genus are often a combination of plesiomorphic and derived features and are not to be confused with the characters that support the monophyly of each genus. The phylogentically informative characters that define each genus have been summarized under the section "PHYLOGENETIC RESULTS" "GENERA OF BIBIONIDAE."

Eleven genera of Bibionidae are recognized here; eight extant genera and three fossil genera. The three fossil genera, *Fushunoplecia* Hong, *Clothonopsis* Hong & Wang, and *Megeana* Meunier were not available for study and thus the extact status of these taxa and their placement within Bibionidae is unresolved. The extant genera are: *Hesperinus* Walker, *Penthetria* Meigen, *Plecia* Wiedemann, *Bibio* Geoffroy, *Bibiodes* Coquillett, *Bibionellus* Edwards, *Enicoscolus* Hardy, and *Dilophus* Meigen. Several new generic synonyms are proposed. The fossil genus *Bibiopsis* Heer is treated as junior synonym of *Penthetria*. The fossil genus *Epiplecia* Giard and the extant subgenera *Heteroplecia* Hardy and *Pleciodes* Hardy are treated as junior synonyms of *Plecia*. The fossil genus *Lithosomyia* Carpenter is a junior synonym of *Bibio*, and the fossil genus *Bibiodites* Cockerell is a junior synonym of *Bibiodes*. Two genera previously included in the family Bibionidae (Evenhuis 1994) are removed from the family. The fossil genus *Mesopleciella* Rohdendorf belongs in the extinct family Protopleciidae and the family placement of the fossil genus *Longicornia* could not be determined.

FAMILY BIBIONIDAE

Genus *Hesperinus* Walker

Hesperinus Walker, 1848: 81. Type species: *Hesperinus brevifrons* Walker, 1848: 81 (by monotypy), [examined; BMNH].

Spodius Loew, 1858: 101. Type species: *Spodius imbecillus* Loew, 1858: 108 (by monotypy).

Diagnosis: Adults of *Hesperinus* are distinguished from other bibionids by the dichoptic eye of the male, and the elongate, filiform antennae (Fig. 5e-f). Larvae are distinguished by the absence of fleshy tubercles (Figs. 27c, 28a) and the globe-like, sensory cone of the antenna (Fig. 31e). Pupae are distinguished by the elongate antennal sheath and a transverse row of minute spinules on each abdominal segment.

Description: Adult: Small to medium-sized flies; 5.0-7.0 mm. Head: Head of both sexes dark brown, dorsoventrally compressed; in dorsal view slightly wider than long, oval-shaped. Both sexes with compound eye round or oval, strongly convex, dichoptic, and broadly separated by frons (Fig. 5e-f). Compound eye undivided, bare or with minute, stiff, hairs, ommatidia not varying in size or color. Triangular area devoid of ommatidia absent. Ocellar tubercle weakly developed, three ocelli arranged in a small, equilateral triangle. Female with or without minute tubercle just posterior to antennal sockets. Antenna light brown, set anteriorly along oral margin, with 10 flagellomeres. Flagellomeres longer than broad, filiform, cylindrical, with numerous short, stiff setae. Dorsoapical portion of each flagellomere of male slightly produced into a tubercle giving antennae a slight serrate appearance (Fig. 5f; adat). Despite an equal number of flagellomeres in both sexes, male antennae more elongate; approximately 1.75 times as long as in female. Sclerotized rostrum absent. Maxillary palps brown, with five segments; basal segment minute, third segment with dorsal, diagonal, sensory pit with dense, minute, specialized setae, and apical segment slender and more elongate than preceding palpomeres. Clypeus subquadrate, not elongate or folded under head. Posteroventrally, head with narrow, sclerotized bridge. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax dark brown to brown-black, opaque, smooth, with pruinescence, sometimes with grayish dorsocentral stripes. Parapsidal sutures subtle, not distinct as in some *Plecia*. Dorsum of thorax with dense, short, stiff hairs anteriorly, laterally, and in dorsocentral rows. Thoracic pleura brown and bare except for short setae on dorsal half of katepisternum. Legs: Coxa not quite reaching ventral margin of katepisternum in lateral view. Legs brown, usually darker distally, with dense, appressed, minute setae and very fine, minute, widely-spaced setae arising at nearly a right angle to surface of leg. Legs elongate compared to other Bibionidae (Fig. 5f). All femora not swollen; elongate, slender, subparallel, and only slightly enlarged apically. All tibia elongate, slender, subparallel. Apex of fore tibia unmodified, with single, minute spur. Apex of mid- and hind tibia with two slender, apically acute spurs approximately subequal in length. Inner surface of hind tibia without elongate field of small, round, black, specialized sensillae. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. Both sexes with hind basitarsus slender, elongate, never swollen. Wings: Halter light brown, lighter basally. Wing elongate, reaching back over abdomen; 6.0-8.0 mm (Fig. 13c). Wing evenly light brown fumose. Costal cell not darker than remainder of wing. Pterostigma oval, brown. Anterior wing veins slightly darker brown than posterior veins. Wing without macrotrichia, with microtrichia; microtrichia reaching wing margin. Anal lobe well developed, but not as strongly lobate as other Bibionidae. Costa ends just beyond R; reaching approximately 1/3 distance between R5 and M1. C and R not shortened or thickened as *Enicoscolus*. Subcosta elongate, complete. Radius without horizontal microstriations. Rs furcate; R2+3 absent, R4 present. R4 wavy, oblique, medium in length (longer than most *Plecia* and shorter than most *Penthetria*), ending in C. Radius with minute, evenly spaced setae. Apex of R5 distinctly arched posteriorly. R-m crossvein approximately 1/3 length of base Rs. Three branches of M present. Base M(3+)4 crossvein-like. M-m crossvein absent. CuA and CuP present, reaching wing margin. A1 very short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Brown, slender, elongate, with dense, short hairs. Male spiracles located in abdominal pleura, except spiracle eight absent. Male tergites and sternites 1-8 unmodified, female tergites 1-8 and sternites 1-7 unmodified (modified segments discussed with terminalia). Male terminalia: Terminalia slightly dorsoflexed, not rotated. Posterior margin tergite 9 (epandrium) medially, shallowly to deeply emarginated (epandrial cleft). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) typically broadly rounded, but may be slightly more narrow apically. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into a continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes slight seam. Posteromedian margin of synsternogonocoxite sometimes with a median hump or pair of humps which are membranous to lightly sclerotized. Gonocoxites forming a tubular pedicel in which the apical gonostyli articulate. Gonostylus usually of a rather simple shape; robust, curved, apically rounded to broadly U-shaped with 2-3 lobes, sometimes with patch of moderately strong, elongate, spine-like setae. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with setae. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of a complex three dimensional structure; dorsal sclerite and ventrolateral apodemes fused into an apically broadly rounded, dome-like structure (*H. brevifrons* Walker with minute spines apically). Dome-shaped paramere enclosing membranous, sac-like, endophallus. Endophallus cradled by more ventral ejaculatory apodeme (Fig. 22). Ejaculatory apodeme, simple, dorsoventrally flattened, and sometimes strongly expanded apically. Apical, collar-like aedeagus present. U-shaped or paired rod-like apodemes present (enclosed by paramere, dorsal to endophallus present). These apodemes are here considered homologous to one of two pairs of apodemes of the aedeagal plate (see discussion of sperm pump in section on adult character homology). Female terminalia: Tergite nine present, large. Tergite ten minute and sometimes subdivided into two small sclerites. Cerci two-segmented. Subgenital plate large, external, longitudinally subdivided and partially transversely subdivided. Genital fork present, but weakly developed (not absent as noted by Iwata & Nagatomi (1981)). In addition to genital fork, two minute pairs of sclerites present between posterior margin subgenital plate and anterior margin of sternite ten. Sternite 10 present, undivided. Three oval, sclerotized, capsule-like, spermathecae present; median spermathecae slightly larger. Elongate bursa copulatrix as in *Cramptonomyia* absent. **Immature**

stages: Only the larvae of *H. brevifrons* Walker and *H. rohdendorfi* Krivosheina & Mamaev are known. The larval and pupal stages of this genus have been recently summarized by Krivosheina (1997b). **Egg:** Elongate, sausage-shaped. **Larva:** Body white to cream-colored, elongate, cylindrical, slightly curved downwards in lateral view, with 3 thoracic and 9 abdominal segments (Figs. 27c, 28a). Body without fleshy tubercles found in other bibionids, but with transverse rows of short, black setae on each segment. Most abdominal segments ventrally with anterior row of 4 setae and posterior row of 6 setae, and dorsally with anterior row absent and posterior row of 8 setae. Each segment laterally, in the vicinity of the spiracle, with 4 setae. Cuticle with minute, sclerotized, spine-like scales. Thorax without lightly sclerotized plates and characteristic stair-step-like swollen areas observed in Pachyneuridae. Ventral flap-like tubercle on prothorax absent. Anus terminal, anal papillae apparently absent. Intersegmental fissures between meso- and metathorax unaligned, between abdominal segments 1 and 2 unaligned, and between abdominal segments 7 and 8 aligned. Dorsally the prothorax has 2 pseudosegments, mesothorax three pseudosegments, and most abdominal segments with three pseudosegments. Prothoracic and metathoracic spiracles present, flush with cuticle. Abdominal segments 1-8 with spiracles flush with cuticle; 1-7 lateral, 8 dorsolateral and larger than 1-7. The posterior spiracle (on posterior border of segment 8) round, with single, central ecdysial scar. Head densely sclerotized, black to dark brown, rounded, with setae. Ecdysial lines meeting in the form of a Y anterior to postoccipital carina. Anterolateral margin of frontoclypeus developed into a strong, anteroventrally directed spine. Labrum subrectangular with strong spines at apex of labrum/epipharynx. Anteroventral stemmata present, dorsoposterior stemmata absent. Antennae short, with globe-like antennal sensory cone with complex internal structure (Fig. 31e). Sensory cone not elevated on article, sessile in membranous antennal socket. Antennal socket with numerous, small setae near base of sensory cone, including a biarticulated sensilla. Postgenal bridge complete. Ventral prothoracic sclerites in cuticle at posterior, ventral margin of head capsule present. Anterior tentorial arm present, but weak, connected at anterior margin of head near mandibular articulation. Posterior tentorial bridge absent. Submentum apparently absent. Anterior mentum (hypostoma) absent, posterior mentum present as a median rectangular sclerite not fused to anteroventral margin of cranium or posterior margin of prementum (Fig. 36a). Labial synsclerite present, upside-down-U-shaped; each anterolateral margin with a small knob homologous to glossae. Posterior labial sclerite present, large, in same plane as (and usually fused to) labial synsclerite, though the sclerites are distinct via a seam or narrow membranous region. Tubercle of labial palps absent. Membranous labial area bearing field of papillae enclosed by subrectangular frame (formed by upside-down-U-shaped labial synsclerite and U-shaped posterior labial sclerite). Cibarial bar absent. Membranous, subquadrate hypopharynx covered with minute spines, supported by two pairs of hypopharyngeal sclerites. Pharyngeal filter absent. Cardo large, transverse, not closely appressed to anteroventral margin of cranium, T-shaped, inner apex of sclerite with an anteriorly directed lobe and a posteriorly directed lobe. Cardo with 4 setae (some represented only by alveoli) one seta at inner apex and a group of 3 at outer (lateral) apex. Inner, anterior lobe of cardo supporting prementum (Fig. 36a). Galeolacinia adjacent, but not closely appressed to palpifer. Galeolacinia primarily sclerotized ventrally, with numerous teeth and spines on inner edge, anteriorly, and on dorsal surface (Fig. 36a). Laterobasal sclerite of maxillary palpifer present. Palpifer sclerotized, tubular, bearing a one-segmented, cylindrical palpus. Palpus with only a single sensory region apically, bearing numerous, short, stout, peg-like setae. Mandible heavily sclerotized, subtriangular, with small number of short, stout, apical teeth. Mandible operating in horizontal plane, without line of weakness separating apical and basal portions, and lacking basal thumb of teeth. Prostheca present as tuft of long, parallel-sided setae. Mandibular comb absent. Epipharynx dorsoventrally flattened, slightly bilobate, with numerous small, inwardly directed spines plus 8 minute, peg-like setae. Torma wrapped dorsolaterally, fused and continuous with dorsal labrum. Premandible absent. **Pupa:** Elongate, slender, slightly tapering posteriorly. Head and thorax without distinct setae or spines. Respiratory horn absent;

anterior thoracic spiracle on slight tubercle. Abdomen without fleshy tubercles. Abdominal tergites with transverse rows of minute spinules. Leg sheaths superimposed. Pupa illustrated by Krivosheina (1997b).

Distribution: *Hesperinus* is Holarctic in distribution with five described species: 1 Nearctic and 4 Palearctic. Additionally, a female specimen from Malaysia was examined (NMSC) and there is also apparently an undescribed species from Japan (T. Saigusa pers. comm. 2000). No fossils of this genus are known (Fitzgerald 1999).

Genus *Penthetria* Meigen

Amasia Meigen, 1800: 20. Type species: *Crapitula motschulskii* Gimmerthal 1845: 330 (designated by Rohdendorf 1951: 65, Fig. 28B). Suppressed by I.C.Z.N., 1963: 339.

Penthetria Meigen, 1803: 264. Type species: *Penthetria funebris* Meigen, 1804: 104 (by monotypy in Meigen 1804: 104).

Threneste Wiedemann, 1830: 618. *Nomen nudum*.

Eupeitenus Macquart, 1838: 88 (also 1838: 84). Type species: *Penthetria atra* Macquart, 1834: 175 (by monotypy), [examined; BMNH].

Crapitula Gimmerthal, 1845: 330. Type species: *Crapitula motschulskii* Gimmerthal 1845: 330 (by monotypy).

**Protomyia* Heer, 1849: 231. Type species: *Protomyia lygaeoides* Heer, 1849: 232 (designated by Carpenter 1992: 414).

Bibiopsis* Heer, 1849: 228. Type species: *Bibiopsis cimicoides* Heer, 1849: 229 (designated by Carpenter 1992: 414). **New synonym.

**Mycetophaetus* Scudder, 1892: 20. Type species: *Mycetophaetus intermedius* Scudder, 1892: 20 (by monotypy), [examined; MCZC]. [Synonymized in Fitzgerald 1999].

Pleciomyia Brunetti, 1911: 269. Type species: *Penthetria melanaspis* Wiedemann, 1828: 72 (by monotypy).

Parapleciomyia Brunetti, 1912: 446. Type species: *Parapleciomyia carbonaria* Brunetti, 1912: 447 (by monotypy).

Nomenclatural notes: The genus *Bibiopsis* Heer is a fossil genus which was previously treated as a junior synonym of *Plecia* (Evenhuis 1994). However, Heer's (1849; Plate XV, Fig. 24b) illustration depicts R4 as elongate and subparallel to R5, rather than short and angled, which indicates that this taxon belongs to the genus *Penthetria*.

The fossil genus *Protomyia* was described by Heer (1849) and the genotype *Protomyia lygaeoides* Heer (1849) was later designated by Carpenter (1992). This genus is treated as a junior synonym of *Penthetria* by Evenhuis (1994). However, based on Heer's illustration of the genotype (1849; Tab. XVII, Fig. 1) it is unclear whether this taxon should be placed in the genus *Penthetria* because the orientation of vein R4; R4 is not subparallel as is typical for *Penthetria*, but arises at an angle from Rs as in *Plecia*. Since the illustration is very small and the accuracy questionable a study of the genotype would aid in resolving the placement of this genus. The genotype is not present with much of Heer's other material in the Eidenossische Technishe Hochschüle-Zentrum, Zürich (Milena Pika-Biolzi, pers. comm. 2004) or the Naturhistorisches Museum in Vienna (Ortwin Schultz, pers. comm. 2004).

Diagnosis: Adults of *Penthetria* are distinguished from other Bibionidae by the simple fore tibia, compact antennal flagellomeres, and vein R4 elongate and subparallel to R5 (Fig. 12c). The larva is distinguished by the presence of fleshy tubercles (each abdominal segement with two transverse rows of two tubercles each), the posterior spiracle on segment eight, and the mentum not fused to the anterior margin of the cranium or to the posterior margin of the labium (36b; pm). Pupae can be distinguished from all genera except *Plecia* by the presence of fleshy tubercles.

Description: **Adult:** Small to moderately large flies 4.0-11.0 mm. Head: Male head dorsoventrally compressed; in dorsal view slightly wider than long, oval-shaped. Male with almost entire dorsal surface of head occupied by broadly holoptic compound eye; except *P. funebris* Meigen compound eyes narrowly separated dorsally by longitudinal strip of frons approximately subequal in width to antennal flagellum. Male compound eye strongly divided into larger dorsal region and smaller ventral region; dorsal region usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by distinct longitudinal step (surface of dorsal region folds in toward surface of head to meet surface of the ventral region). Division not marked by narrow, longitudinal, shining, sclerotized band; smooth, triangular area devoid of ommatidia also absent. Female head dorsoventrally compressed, slightly wider than long. Female compound eye round or oval in shape, convex, dichoptic, and broadly separated by frons. Females also lack triangular area. Female compound eye with indistinct and slight longitudinal depression dividing compound eye, but lacking any difference in size of ommatidia or color between dorsal and ventral regions. Compound eye of both sexes bare or clothed with minute, stiff, or very elongate hairs. Ocellar tubercle well developed and prominent in males and moderately to weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle. Female with small tubercle or longitudinal ridge just posterior to antennal sockets. Male frons reduced to small, triangular region between anterior margin of compound eye and posterior margin of antennal sockets bearing minute tubercle or in *P. funebris* a minute pit. Sclerotized rostrum not produced, oral margin somewhat ventral in position. Antenna set anteriorly along oral margin, with 8-10 short, stout flagellomeres. Flagellomeres slightly broader than long, except most basal flagellomere about two times as long as subsequent flagellomere. Pedicel and flagellomeres with subapical ring of short setae and numerous dense, minute, appressed setae. Apical flagellomere slightly more elongate than preceding flagellomere, with rounded point apically. Head and antennae black to brown. Maxillary palps with five segments; basal segment minute, third segment thickened with dorsal, diagonal sensory pit with dense, minute, specialized setae; apical segment slender and most elongate of all palpomeres. Clypeus broader than long, never elongate. Ventrally, head entirely sclerotized. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax smooth, with thick pruinosity, usually opaque black, dark brown, anteriorly black and posteriorly orange, or rarely entirely orange as in *P. indica* (Brunetti). Parapsidal sutures subtle and not distinct as in some *Plecia*. Dorsum of thorax with dense, short, stiff hairs, to very elongate hairs, laterally, anteriorly, and in dorsocentral rows posteriorly. Thoracic pleura black to dark brown. Males with minute to moderately long hairs on metakatepisternum, and dorsal half of katepisternum. Anepisternum bare or with cluster of hairs at posterior margin. Meron, laterotergite, and mediotergite bare. Female thoracic pleura generally less hairy than male. Legs: Coxa short and not reaching ventral edge of katepisternum; reaching about half length of katepisternum in lateral view. Coxa usually with elongate hair. Legs black to dark brown. Fore femur relatively slender and more elongate; not short and swollen. Fore tibia elongate, slender, apex unmodified; outer edge not developed into strong spine. Fore tibia with a single, small spur. Middle legs unremarkable; with two apical tibial spurs. Hind legs with hind femur greatly swollen apically to more slender and only slightly enlarged apically. Hind tibia slender and nearly parallel-sided or slightly to greatly swollen apically. Inner surface of hind tibia without elongate field of small, round, black, specialized sensillae. Spurs of hind tibia slender, apically acute, subequal in length or ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. In males, hind tarsomeres vary in shape from slender, elongate, parallel-sided to slightly swollen and sausage-link-shaped. Female tarsomeres never swollen; slender to robust. Wing (Fig. 12c): Halter black. Wing 4.5-12.5 mm, elongate, reaching back over tip of abdomen; except brachypterous and distinctly shortened in males of *P. funebris*. Wing brown to blackish fumose. Costal cell often darker than remainder of wing in taxa with fumose wings. Wing color solid or with grade in intensity, but without distinct markings. Pterostigma oval, usually brown to black. Anterior wing veins typically darker than posterior veins. Wing without macrotrichia, with microtrichia. Anal lobe well developed. Costa ends at or just beyond R5; not shortened or thickened as *Enicoscolus*. Subcosta elongate, complete. Radius without horizontal microstriations. Rs furcate; R2+3 absent, R4 present. R4 relatively elongate and subparallel to slightly oblique to R5; base often arising at right angle to R5 then sharply bent in direction of wing tip. Base of R4 sometimes with sub-basal stump possibly representing remnant of R(2+)3 (e.g. *P. appendiculata* Hardy; Fig. 12c). R4 branches from R4+5 from slightly basal to, even with, or distinctly distal to r-m crossvein. Length of r-m crossvein much shorter than base of Rs. Rm meeting M1+2, or more distal in position and meeting only with branch of M1 (e.g. *P. japonica* Wiedemann; Hardy & Takahashi 1960, Fig. 2b). Three branches of M present. Base of M(3+)4 present and crossvein-like. M-m crossvein absent. CuA and CuP present, reaching wing margin, sometimes meeting distally forming closed cell cua. A1 short and weak; not extending beyond the small fold at the base of anal lobe. Abdomen: Black to dark brown with short to elongate hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles 1-7 located in lateral abdominal pleura, except spiracle eight, which is either absent or a remnant, if present, found dorsolaterally in membrane between tergites eight and nine (e.g. *P. funebris*). Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia: Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to deeply emarginated and nearly dividing tergite (epandrial cleft). Epandrial cleft U-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) typically broadly rounded, but sometimes forming narrow, rounded points apically. Anterior edge of epandrium sometimes shallowly to moderately medially emarginated. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into a continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes a slight seam. Posteromedian margin of synsternogonocoxite sometimes with median hump or pair of humps which are membranous to lightly sclerotized. Gonocoxites forming elongate, tubular pedicel in which the apical gonostyli articulate (Fig. 15a). Gonostylus usually of a rather simple shape; short, stout, robust, straight to very strongly anteriorly arched, gradually tapered to slightly expanded apically, apically broadly rounded to narrowly rounded or truncate, sometimes with an anterior spine. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of a complex three dimensional shape; dorsal sclerite and ventrolateral apodemes indistinguishably fused into a posteriorly broadly rounded, dome-like, hood. Ventral to parameres, membranous, sac-like, endophallus present which is cradled by more ventral ejaculatory apodeme. Ejaculatory apodeme, simple, dorsoventrally flattened. Aedeagus absent. Female terminalia: Tergite nine present as narrow, transverse strap, or subdivided into two sclerites; often strongly produced ventrolaterally. Tergite ten minute, longitudinally elongate. Cerci two-segmented (Fig. 26a). Subgenital plate large, longitudinally subdivided, with posterior margin lobate; inner margins of longitudinal cleft with minute, posteromedially-directed tubercle. Y-shaped genital fork present. In addition to genital fork, a minute pair of sclerites present between the posterior margin of the subgenital plate and the anterior margin of sternite ten. Sternite 10 present. Three rounded, sclerotized, capsule-like, spermathecae present. **Immature stages:** **Egg:** Elongate, sausage-shaped. **Larva:** Body gray, elongate, slightly dorsoventrally flattened, slightly curved downwards in lateral view, with 3 thoracic and 9 abdominal segments. Thorax and abdomen with transverse rows of elongate, fleshy tubercles on each segment both dorsally and ventrally. The number of tubercles in each row varies depending on the species, though thoracic segments tend to have fewer tubercles. Laterally, two tubercles present in vicinity of each abdominal spiracle except the posterior spiracle. Cuticle with dark brown to black, minute, sclerotized, spine-like scales. Thorax without lightly sclerotized plates and without characteristic stair-step-like swollen developments observed in Pachyneuridae. Ventral flap-like tubercle on prothorax present. Anus terminal, anal papillae apparently absent. Intersegmental fissures between meso- and metathorax, between abdominal segments 1 and 2, and between abdominal segments 7 and 8, unaligned. Dorsally, prothorax with 2 pseudosegments, mesothorax 2 pseudosegments, and most abdominal segments 3 pseudosegments. Prothoracic and metathoracic spiracles present. Abdominal segments 1-8 with spiracles; 1-7 lateral and 8 dorsolateral and larger than 1-7. All spiracles slightly protuberant, especially posterior spiracles. Posterior spiracle on posterior border of segment 8, round, with single, central, ecdysial scar. Head densely sclerotized, black to dark brown, rounded, somewhat dorsoventrally flattened, with setae. Head capable of being completely withdrawn into anterior portion of thorax. Ecdysial lines meeting in form of Y anterior to postoccipital carina. Anterolateral margin of frontoclypeus developed into strong, anteroventrally-directed spine. Labrum subrectangular without strong spines at apex of labrum/epipharynx. Anteroventral stemmata present, dorsoposterior stemmata absent. Antennae short, sensory cone in form of ovoid plate positioned within larger, round, antennal socket. Postgenal bridge complete. Ventral prothoracic sclerites in cuticle at posterior, ventral margin of head capsule present. Anterior tentorial arm present, weakly developed, connected at anterior margin of head near mandibular articulation. Posterior tentorial bridge absent. Submentum apparently absent or indistinguishably fused to ventral head capsule. Anterior mentum (hypostoma) absent, posterior mentum present as a narrow, longitudinal sclerite which is not fused to the anterior margin of the cranium or the posterior margin of the labium. Labial synsclerite present, upside-down-U-shaped; each anterolateral margin with small knob homologous to glossae. Posterior labial sclerite present, large, in same plane as, and smoothly fused to labial synsclerite; forming sclerotized frame completely enclosing membranous labial area. Tubercle of labial palps absent, membranous labial area bearing field of papillae. Cibarial bar absent. Membranous, hypopharynx with patches of minute spines, supported by two pairs of hypopharyngeal sclerites: each pair with one large sclerite and one minute sclerite. Pharyngeal filter absent. Cardo large, transverse, not closely appressed to anteroventral margin of cranium, T-shaped, with inner apex of sclerite with ab anteriorly directed lobe and a posteriorly directed lobe. Cardo with 4 setae (some represented only by alveoli); one seta at the inner apex and group of 3 at the outer (lateral) apex. Galeolacinia adjacent, but not closely appressed to palpifer. Galeolacinia primarily sclerotized ventrally with numerous teeth and spines on inner edge, apically, and on dorsal surface. Laterobasal sclerite of maxillary palpifer present. Palpifer sclerotized, tubular, bearing one-segmented cylindrical palpus. Palpus with single sensory region apically, bearing numerous short, stout, setae. Mandible heavily sclerotized, subtriangular, with small number of short, stout, apical teeth. Mandible operating in horizontal plane, without line of weakness separating apical and basal portions, and lacking basal thumb of teeth. Prostheca present. Mandibular comb absent. Epipharynx dorsoventrally flattened, slightly bilobate, with numerous small inwardly directed spines and small number of peg-like setae. Torma wrapped dorsolaterally, fused and continuous with dorsal labrum. Premandible absent. **Pupa:** Gray, leathery, sometimes enclosed within last larval skin. Head and thorax without distinct setae or spines. Respiratory horn absent; anterior thoracic spiracle on slight tubercle. Abdomen with fleshy tubercles, without sclerotized spines or setae. Abdominal tergites without transverse rows of minute spinules. Leg sheaths superimposed.

Distribution: *Penthetria* includes 30 species distributed worldwide except for the polar, Afrotropical, and Australasian/Oceanic regions (Table 2). Fossils are known from the Nearctic and Palearctic regions.

Genus *Plecia* Wiedemann

Plecia Wiedemann, 1828: 72. Type species: *Hirtea fulvicollis* Fabricius, 1805: 53 (designated by Blanchard 1840: 576).

Rhinoplecia Bellardi, 1859: 16 [also 1861: 216]. Type species: *Plecia rostrata* Bellardi, 1859: 15 (by monotypy).

Penthera Philippi, 1865: 639. Type species: *Penthera nigra* Philippi, 1865: 640 (by monotypy).

Epiplecia* Giard, 1879: 13. Type species: *Protomyia joannis* Oustalet, 1870: 143 (by monotypy). **New synonym.

Heteroplecia Hardy, 1950a: 75 (as subgenus of *Plecia* Wiedemann). Type species: *Plecia visenda* Hardy, 1950a: 75 (by monotypy); [examined; BMNH]. **New synonym.**

Pleciodes Hardy, 1952a: 76 (as subgenus of *Plecia* Wiedemann). Type species *Plecia ephippium* Speiser, 1909: 38 (designated by Hardy 1952a). **New synonym.**

**Lacibibio* Hong, *In* Hong *et al.* 1980: 47. Type species: *Lacibibio fushunensis* Hong, *In* Hong *et al.* 1980: 47-48 (original designation). [Synonymized by Zhang, 1989: 336; as *Plecia* sp.] [type in "China Geology Museum" (Wang Wenli, pers. comm. 2004)].

Nomenclatural notes: The genus *Epiplecia* Giard is a fossil genus (based on the species *Protomyia joannis* Oustalet) which was previously treated as a junior synonym of the genus *Penthetria* (Evenhuis 1994). However, Oustalet's illustration of this species (1870; plate VI, Fig. 4) shows that vein R4 is short and angled, rather than elongate and subparallel to R5, which indicates that this taxon belongs to the genus *Plecia*. A study of the genotype was not possible due to a pending study of Oustalet's species (A. Nel, pers. comm. 2003). Regardless, based on the illustration of this taxon it is treated here as a junior synonym of *Plecia*.

The subgenus *Pleciodes* was erected by Hardy (1952a) for the species *Plecia ephippium* Speiser based primarily on the presence of a closed cell cua. However, *P.*

ephippium differs in no other way from typical *Plecia*, and a closed cell cua is variably present or absent even within single species (e.g. *P. amplipennis* Skuse, pers. obs.). A variable cua is also present in *Penthetria japonica* Wiedemann, and this character may only be of specific importance in these genera. Therefore, *Plecia* (*Pleciodes*) is synonymized with *Plecia* (*Plecia*).

The subgenus *Plecia* (*Heteroplecia*) was erected for the single taxon *Plecia visenda* Hardy (1950a) based on the absence of ocelli and an ocellar tubercle. Later, Hardy (1968) stated that the lack of the ocelli and tubercle is probably only of specific importance and questioned whether *Heteroplecia* should be retained as a distinct subgenus. Fitzgerald (2004) added two taxa to the subgenus and also questioned the status of the subgenus. Although the relationship between species groups within *Plecia* is not well understood, the fact that *Plecia* (*Heteroplecia*) *lusca* Fitzgerald arises within the nominal subgenus in the phylogenetic analysis presented here requires that either the nominal subgenus be subdivided into smaller monophyletic groups or that the subgenus *Heteroplecia* should be synonymized with the nominal subgenus. Subdividing the nominal subgenus would be difficult based on the available characters and it seems more appropriate to synonymize the subgenus *Heteroplecia* with the nominal subgenus than to attempt to subdivide *Plecia* (*Plecia*). For these reasons, *Plecia* (*Heteroplecia*) is treated as a junior synonym of *Plecia* (*Plecia*).

Diagnosis: Adult *Plecia* are distinguished from other bibionids by the simple fore tibia, compact antennal flagellomeres (Fig. 6b), and vein R4 short and oblique with respect to R5 (Fig. 13b). Larvae are distinguished by the presence of fleshy tubercles (Figs. 27b, 28c), antennal sensory cone a flat oblong plate (as Fig. 31f; sc), mentum fused to anterior margin of cranium and posterior margin of labium (Fig. 30b; pm), and a single ecdysial scar of the posterior spiracle. The pupa can be distinguish from other bibionids except *Penthetria* by the presence of fleshy tubercles on the abdomen.

Description: **Adult:** Small to moderately large flies 3.0-13.0 mm. Head: Male head dorsoventrally compressed; in dorsal view slightly wider than long, oval-shaped. Male with almost entire dorsal surface of head occupied by broadly holoptic compound eye. Male compound eye undivided or indistinctly divided into larger dorsal region and smaller ventral region; dorsal region usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by subtle longitudinal indentation. Rarely division also marked by narrow, longitudinal, shining, sclerotized band. In males of species with undivided eye, size of ommatidia gradually decreases in size dorsally to ventrally. Triangular area between dorsal and ventral regions and frons absent in both sexes. Female head dorsoventrally compressed, oval and slightly wider than long to slightly longer than wide. Female compound eye round or oval in shape, convex, dichoptic, and broadly separated by frons (Fig. 6b). Female eye undivided. Compound eye of both sexes bare or clothed with minute, stiff, hairs. Ocellar tubercle well developed and prominent in males, weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle except for several species from New Guinea and New Caledonia which lack ocellar tubercle and ocelli (Hardy 1968, Fitzgerald 2004, Fig. 29). Female with small tubercle or longitudinal ridge just posterior to antennal sockets. Antenna set anteriorly along oral margin, with 6-9 short, stout flagellomeres; flagellomeres slightly broader than long. Females often with 1-2 flagellomeres more than male. First antennal flagellomere typically slightly more elongate than following flagellomeres. Sclerotized rostrum sometimes slightly produced anteriorly, often more produced in females. In those species with developed rostrum, antenna situated at anterodorsal edge of rostrum at oral margin. Pedicel and flagellomeres with subapical ring of short setae and numerous dense, minute, appressed setae. Apical flagellomere often smaller and button-like and apical flagellomeres sometimes difficult to differentiate due to apparent fusion. Head and antennae black to brown to orange. Maxillary palps with five segments; basal segment minute, third segment thickened with dorsal, diagonal sensory pit that has dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Clypeus + proboscis short to greatly elongated (ca. 1.5 times length of head) and capable of being folded beneath head (Fig. 6d). Ventrally head entirely sclerotized. Thorax (Fig. 7a-b, d): Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax usually black, brown, or orange, but sometimes gray or anteriorly black and posteriorly orange. Mesonotum smooth, shining or opaque, with or without thick pruinescence which may form longitudinal stripes, form a lateral ring around a median shining area, or cover entire dorsum. Parapsidal sutures subtle or as distinct grooves. Dorsum of thorax with dense, short, stiff hairs, to nearly bare. Thoracic pleura black, brown, or orange, sometimes strongly contrasting color of dorsum of thorax. Male with anepisternum, laterotergite, and meron bare. Metakatepisternum haired or bare, anepimeron with a few hairs or bare, and dorsal half of katepisternum haired. Female thoracic pleura generally less hairy than males; sclerites typically haired in males may have only a few minute, stiff hairs or be entirely bare. Legs: Coxa shorter than length of katepisternum; reaching about half way to ventral edge of katepisternum in lateral view. Coxa usually with elongate hair. Legs black or brown. Fore femur relatively slender, not swollen. Fore tibia not modified; without outer apex developed into strong spine. Fore tibia with single, minute spur. Middle legs unremarkable; with two apical tibial spurs. Hind legs with femur slender, slightly enlarged apically. Hind tibia slender, nearly parallel-sided to slightly swollen apically. Inner surface of hind tibia without elongate field of small, round, black, specialized sensillae. Spurs of hind tibia slender, apically acute, subequal in length or with ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. In males, hind tarsomeres vary in shape from slender, elongate, parallel-sided to slightly swollen and sausage-link-shaped. Female tarsomeres never swollen; slender to robust. Wings: Halter pale basally, dark distally or entirely dark. Wing elongate, reaching back over abdomen 3.5-15.0 mm (Fig. 13b). Wing hyaline to brown, black, gray, or orange fumose. Costal cell often darker than remainder of wing in taxa with fumose wings. Wing color usually solid or with grade in intensity (e.g.

becoming lighter posteriorly), rarely with distinct pattern of darkening along veins, or at wing tip, or with blotches. Pterostigma oval, brown to black and distinctly darker than wing membrane, or hyaline and apparently absent. Anterior wing veins typically darker than posterior veins; posterior veins hyaline, only slightly pigmented, or distinctly darker than membrane. Wing without macrotrichia, with microtrichia. Anal lobe well developed. Costa ending beyond R5, 1/5-1/2 distance between R5 and M1. Costa and R5 not shortened or thickened. Subcosta elongate, complete. Radius without horizontal microstriations. Rs furcate; R(2+)3 absent, R4 present, short, oblique, curved, straight, or with distinct basal bend. Length of r-m crossvein much shorter than base of Rs. Three branches of M present. Base of M(3+)4 present, crossvein-like. M-m crossvein absent. CuA and CuP present, reaching wing margin. Cell cua open, distally narrowed, closed at wing margin, or closed and petiolate. A1 very short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Brown to black with short to elongate, pale to dark hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles 1-7 located in lateral abdominal pleura, except spiracle eight, which is either absent or a remnant when present is found dorsolaterally in the membrane between tergites eight and nine (e.g. *P. thulinigra* Hardy, *P. mallochi* Hardy). Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia (Figs. 15b-d, e, g-h, 23): Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to deeply emarginated (epandrial cleft), sometimes dividing tergite completely or leaving only narrow, medial, transverse strap of sclerite connecting the two halves. Epandrial cleft sometimes with median or submedian lobe(s). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) broadly rounded, apically narrowed, or strongly forcipate. Anterior edge of epandrium sometimes medially emarginated. Inner surface of epandrium sometimes clothed with dense, black, scale-like setae (e.g. *P. trifida* Hardy (1968, Fig. 44a). Lateral gonocoxites + ventral sternite nine (hypandrium) fused into a continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes slight seam. Posteromedian margin of synsternogonocoxite sometimes with median hump or pair of humps which are small and membranous to very large and strongly sclerotized and that may bear additional lobes (e.g. *P. laffoonni* Hardy (1950a, Fig. 6a)). Laterally, gonocoxites often extending beyond gonostylus posteriorly forming digitate to flat, broad to narrow, apically acute or rounded lobe (lateral lobe of gonocoxite). Gonocoxites forming very narrow ring in which the apical gonostyli articulate. Gonostylus ventrolateral (more lateral in other bibionids). Shape of gonostylus highly variable; simple, digitate to complicated three-dimensional in structure with multiple lobes. Gonostyli sometimes fused to posterior margin of synsternogonocoxite or to each other via narrow, ventral band; in such cases gonostyli are apparently non-functional. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Dorsal bridge present, anteriorly expanded and shield-shaped. Ventral to proctiger are parameres of complex three dimensional shape, but with two main parts; dorsal sclerite and ventrolateral apodemes. Dorsal sclerite shield-like, posteriorly rounded, pointed, emarginate, or produced into two horn-like projections. Ventrolateral to dorsal sclerite, ventrolateral apodemes present and highly variable in shape; simple, bifurcate, tusk-like, flattened, or rod-like. Ventral to parameres, membranous, sac-like, endophallus present and cradled by more ventral ejaculatory apodeme. Ejaculatory apodeme, simple, dorsoventrally flattened. Aedeagus absent. Female terminalia: Tergite nine present, sometimes strongly developed ventrolaterally. Tergite ten minute, longitudinally elongate. Cerci one-segmented. Subgenital plate large and apparently transversely subdivided into two parts; a more anterior and external plate and a more posterior and internal plate. Anterior portion of subgenital plate partially longitudinally cleft or with plate entirely subdivided, posterior margin lobate; inner margins of longitudinal cleft with minute, posteromedially-directed tubercle. Posterior portion of subgenital plate longitudinally subdivided. Genital fork present. In addition to genital fork, a pair of small sclerites present between posterior margin of subgenital plate and anterior margin of sternite ten. Sternite ten present. Three spermathecae present. All spermathecae rounded, sclerotized, capsule-like and subequal in size, or sometimes median spermatheca membranous and subequal in size to membranous and greatly enlarged and sac-like. **Immature stages:** **Egg:** Ovoid, robust, light brownish when in abdomen, eventually turning black after being laid (Fig. 26e). **Larva:** Body white to cream-colored, elongate, cylindrical to slightly dorsoventrally flattened, slightly curved downwards in lateral view, with 3 thoracic and 9 abdominal segments (Figs. 27b, 28c). Thorax and abdomen with transverse rows of fleshy tubercles on each segment both dorsally and ventrally. Abdomen usually with two transverse rows of tubercles per segment, per side, though number of tubercles in each row varies between species. Thoracic segments tend to have fewer tubercles. For example, *Plecia nearctica* Hardy has prothorax ventrally with one row of two tubercles, meso- and metathorax each with anterior row of 2 and posterior row of 4, and each abdominal segment (except segment 9) each with two rows of 4. Dorsally the prothorax has single row of 2, and all other segments (except abdominal segments 8 and 9) have anterior row of two and posterior row of 4. Laterally, there are two tubercles in the vicinity of each spiracle except the posterior spiracle. Terminally there is a ring of 6 tubercles surrounding the anus (longest of all tubercles). Cuticle with dark brown, minute, sclerotized, spine-like scales. Thorax without lightly sclerotized plates and without characteristic stair-step-like swollen developments observed in Pachyneuridae. With or without ventral flap-like tubercle on prothorax. Anus terminal, anal papillae apparently absent. Intersegmental fissures between meso- and metathorax unaligned, between abdominal segments 1 and 2 unaligned, and between abdominal segments 7 and 8 unaligned. Dorsally prothorax with 3 pseudosegments, mesothorax 3 pseudosegments, and most abdominal segments 3 pseudosegments. Prothoracic and metathoracic spiracles present. Abdominal segments 1-8 with spiracles; 1-7 lateral and 8 dorsolateral and larger than 1-7. Posterior spiracle (on anterior border of segment 9) round, with single, central, ecdysial scar. Head densely sclerotized, black to dark brown, rounded, somewhat dorsoventrally flattened, with setae. Ecdysial lines meeting in form of Y anterior to postoccipital carina. Anterolateral margin of frontoclypeus developed into strong, anteroventrally-directed spine. Labrum subrectangular with strong spines at apex of labrum/epipharynx. Anteroventral stemmata absent, dorsoposterior stemmata present. Antennae short, sensory cone in form of elongate, ovoid-kidney-shaped, concave plate, bordering anterodorsal margin of cranium. Posteromedian margin of plate with small sclerotized tongue which bears minute antennal sensillae. Postgenal bridge complete. Ventral prothoracic sclerites in cuticle at posterior, ventral margin of head capsule present. Anterior tentorial arm usually present, but apparently absent in some species. When present, weak, connected at anterior margin of head near mandibular articulation. Posterior tentorial bridge absent. Submentum apparently absent. Anterior mentum (hypostoma) absent, posterior mentum present as narrow, longitudinal sclerite which is fused to anterior margin of cranium and posterior margin of labium (Fig. 38). Labial synsclerite present, upside-down-U-shaped; each anterolateral margin with a small knob homologous to glossae. Posterior labial sclerite present, large, in same plane as, and fused to labial synsclerite forming a wedge-shaped (broader posteriorly), sclerotized frame around membranous labial area. Tubercle-like labial palps absent (i.e. sensory setae not on elevated tubercle). Membranous labial area bearing field of papillae or two distinct clusters of papillae which are homologous to papillae typically elevated at apex of labial palp. Cibarial bar absent. Membranous hypopharynx with patches of minute spines and supported by single pair of hypopharyngeal sclerites (Fig. 38b). Pharyngeal filter absent. Cardo large, transverse, not closely appressed to anteroventral margin of cranium, T-shaped, with inner apex of sclerite with anteriorly directed lobe and posteriorly directed lobe. Cardo with 4 setae (some represented only by alveoli); one seta at inner apex and a group of 3 at outer (lateral) apex. Galeolacinia adjacent, but not closely appressed to palpifer. Galeolacinia primarily sclerotized ventrally with numerous teeth and spines on inner edge, apically, and on dorsal surface (Fig. 38c). Laterobasal sclerite of maxillary palpifer present. Palpifer sclerotized, tubular, bearing one-segmented cylindrical palpus. Palpus with single sensory region apically, bearing numerous short, stout, peg-like setae. Mandible heavily sclerotized, subtriangular, with small number of short, stout, apical teeth. Mandible operating in horizontal plane, without line of weakness separating apical and basal portions, and lacking basal thumb of teeth. Prostheca present. Mandibular comb absent. Epipharynx dorsoventrally flattened, slightly bilobate, with numerous small inwardly directed spines and small number of peg-like setae. Torma wrapped dorsolaterally, fused and continuous with dorsal labrum. Premandible absent. **Pupa:** Elongate, slender, white to cream colored, slightly tapering posteriorly. Head and thorax without distinct setae or spines. Respiratory horn absent; anterior thoracic spiracle on slight tubercle. Abdomen with small fleshy tubercles or ridges, but without spines or setae. Abdominal tergites without transverse rows of minute spinules. Leg sheaths superimposed. Pupa illustrated by Pinto and Amorim (1996).

Distribution: *Plecia* includes approximately 250 species and is distributed worldwide except for polar regions, though it is most diverse in the pantropics (Table 2). The genus is known from Nearctic, Palearctic, and Neotropical (as "Bibionidae?;" Grimaldi (1990)) compression fossils as well as from Canadian, Baltic, Mexican, Dominican, and lower Eocene (Paris Basin) ambers (Evenhuis 1994, Gee *et al.* 2001, Fitzgerald unpublished).

Genus *Bibio* Geoffroy

Bibio Geoffroy, 1762: 568. Type species: *Tipula hortulana* Linnaeus, 1758: 588 (designated by Latreille, 1810: 442 as "*Hirtea hortulta* Fabr."). Generic name validated by I.C.Z.N. 1957: 86, Opinion 441 and No 1050 on Official List of Generic Names in Zoology.

Pullata Harris, [1776]: 76. Type species: *Pullata funestus* Harris, [1776]: 77 (designated by Coquillett, 1910: 598).

Hirtea Fabricius, 1798: 551 (not Scopoli, 1763). No type designation.

Bibionus Rafinesque, 1815: 130 (unnecessary new replacement name for *Bibio* Geoffroy). Type species: *Tipula hortulana* Linnaeus, 1758 (automatic).

Dichaneurum Aymard, 1856: 42. *Nomen nudum.*

**Lithobibio* Beier, 1952: 133. Type species: *Lithobibio styriacus* Beier, 1952: 133 (by monotypy). [Synonymized with *Bibio* Geoffroy in Nel 1994].

**Mesomyia* Pongrácz, 1928: 174. Type species: *Bibio brevis* Heer, 1849: 225 (by monotypy). [Preoccupied by Macquart, 1850: 341].

Bibiophus Bollow, 1954: 209 and 211 (as subgenus of *Bibio* Geoffroy). Type species: *Bibio clavipes* Meigen, 1818: 317 (original designation). [Synonymized with *Bibio* Geoffroy in Hardy and Takahashi 1960].

Lithosomyia* Carpenter, 1986: 576 (new replacement name for *Mesomyia* Pongrácz). Type species: *Bibio brevis* Heer, 1849: 225 (automatic). **New synonym.

Discussion: Although the phylogenetic analysis in the previous sections did not support *Bibio* as a monophyletic group (Fig. 2), it is here retained as a distinct genus until further study can resolve generic relationships within tribe Bibionini (Fig. 2, node 24).

Nomenclatural notes: Hardy & Takahashi (1960) report that Bollow (1954) erected the subgenus *Bibio* (*Bibiophus*) for *B. clavipes* Meigen based in part on the fact that this species has six maxillary palpomeres. However, male and female specimens of *B. clavipes* examined here (Mongolia (BPBM)) had only five maxillary palpomeres. Following Hardy and Takahashi (1960), *Bibiophus* is treated as a synonym of *Bibio*.

The genus *Lithobibio* Beier was erected for a single fossil species with wing venation differing from typical bibionids by the two-branched Rs and four-branched M. Nel (1994) reexamined the genotype, found the venation had been misinterpreted by Beier, and correctly noted that the taxon has venation typical of the genus *Bibio* (no branches of Rs and three-branched M, base of Rs longer than r-m).

The fossil genus *Mesoymyia* Pongrácz (1928) was erected for a fossil specimen(s?) from Croatia that has a long stem of M and the presence of numerous crossveins in the medial field (Pongrácz 1928; Fig. 42d). Although the presence of numerous crossveins is unknown in the genus *Bibio*, the length of the stem of M is highly variable (see description of wing venation below) and not of generic importance. Strangely, rather than basing *Mesomyia* on the specimen that is illustrated, Pongrácz considers this specimen conspecific with the fossil species *Bibio brevis* Heer (1849), though he notes that he has not examined Heer's material and knows it only from the original description. The original description and illustrations of *Bibio brevis* (Heer 1849; Figs. 16a-16c) do not indicate any crossveins. *Bibio brevis* Heer is based on four specimens and one of these specimens was located at the Eidenossische Technishe Hochschüle-Zentrum, Zürich (Milena Pika-Biolzi, pers. comm. 2004) and borrowed for study; the other three were not located with Heer's material at the aforementioned institution or the Naturhistorisches Museum in Vienna (Ortwin Schultz, pers. comm. 2004). The single specimen that was borrowed has wing venation typical of *Bibio* and does not have various crossveins in the medial field, thus agreeing with Heer's placement of the specimen in this genus. Therefore, *Mesomyia* and its replacement name, *Lithosomyia* Carpenter (1986), are here treated as junior synonyms of *Bibio*. Since the specimen described and illustrated by Pongrácz has not been examined, it is possible that an additional genus of Bibionidae should be recognized based on this specimen, but using a new generic name and genotype.

Diagnosis: Adult *Bibio* are distinguished from other bibionids by the apex of the fore tibia developed into a strong spine (Fig. 8a-c), fore femur and tibia lacking ventral tubercles (see tubercles in Fig. 8e), veins Rs and M not fused for a short distance (see fused condition in Fig. 14a), vein R4 absent, and crossvein m-m present (Fig. 14c). Larvae are distinguished by the presence of short fleshy tubercles (Figs. 27a), antennal sensory cone a flat oblong plate (Fig. 31f; sc), mentum fused to anterior margin of cranium and posterior margin of labium (Fig. 37a; pm), and the presence of two ecdysial scars of the posterior spiracle. Pupae can be distinguished from *Plecia*, *Penthetria*, and *Hesperinus* by the absence of transverse rows of spinules and fleshy tubercles.

Description: Adult: Small to moderately large flies 3.0-14.0 mm. Head: Male head dorsoventrally compressed; in dorsal view slightly wider than long, oval-shaped. Male head with almost entire dorsal surface occupied by broadly holoptic compound eye (Fig. 5a-b). Male compound eye strongly divided into larger dorsal region and smaller ventral region; dorsal region usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by distinct longitudinal step (where surface of dorsal region folds in toward surface of head to meet surface of ventral region). The division also marked by narrow, longitudinal, shining, sclerotized band, which is usually partially to entirely devoid of ommatidia. Longitudinal band widest anteriorly where it forms a small, smooth, triangular area between dorsal and ventral regions and frons. Triangular area devoid of ommatidia. Female head also dorsoventrally compressed, but head shape ranges from oval and slightly wider than long to approximately two times as long as wide. Female compound eye round or oval in shape, strongly convex to somewhat flattened, dichoptic, and broadly separated by frons. Females usually have triangular area, but lack distinct division of compound eye. Females of many species with indistinct and slight longitudinal depression dividing compound eye, but lacking any difference in size of ommatidia or color between dorsal and ventral regions of eye. Compound eye of both sexes bare or clothed with minute, stiff, or very elongate hairs. Ocellar tubercle well developed and prominent in males and sometimes females, though typically only weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle. Female with or without small tubercle or longitudinal ridge just posterior to antennal sockets. Antenna set anteriorly along oral margin, with 5-9 short, stout flagellomeres; flagellomeres slightly broader than long to about as broad as long. Sclerotized rostrum sometimes slightly produced anteriorly, more produced in females. In those species with developed rostrum, antenna situated at anterodorsal edge of rostrum at oral margin. Pedicel and flagellomeres with subapical ring of short setae and numerous dense, minute, appressed setae. Apical flagellomere often smaller and button-like and apical flagellomeres sometimes difficult to differentiate due to apparent fusion. In some species apical flagellomeres slightly expanded and club-like (e.g. *Bibio longipalpus* Yang & Cheng 1997; Fig. 10). First antennal flagellomere typically slightly more elongate than subsequent flagellomeres. Head and antennae black to brown to orange. Maxillary palps with five segments; basal segment minute, third segment thickened with a dorsal, diagonal sensory pit with dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Clypeus + proboscis never greatly elongated. Ventrally head entirely sclerotized. Thorax (Fig. 7c, e): Precoxal bridge complete. Basisternum present, presternum absent (Fig. 7e). Dorsum of thorax black, brown, or orange, shining or opaque, smooth or minutely rugose (e.g. *B. tenebrosus* Coquillett; Hardy 1967a, Fig. 7f). Parapsidal sutures subtle, not distinct as in some *Plecia*. Dorsum of thorax with dense, short, stiff hairs, to very elongate hairs, to nearly bare. Thoracic pleura black, brown, or orange, sometimes strongly contrasting color of dorsum of thorax. Males with minute to moderately long hairs on anepisternum, metakatepisternum, and dorsal half of katepisternum. Anepimeron and meron haired or bare, laterotergite usually bare, but sometimes with only a few very minute, appressed hairs. Female thoracic pleura generally less hairy than in males; sclerites typically haired in males may have only a few minute, stiff hairs or be entirely bare (e.g. females of *B. turneri* Edwards with only a few hairs on anepisternum and the remainder of the thoracic pleura is bare). Legs: Coxa subequal to length of katepisternum; reaching ventral edge in lateral view. Coxa usually with elongate hair. Leg color highly variable; black, brown, orange, yellow, sometimes with femora and tibia of contrasting colors (e.g. femora orange, tibia black), sometimes with femur and/or tibia bicolored (light at base and darker distally). Fore femur moderately to strongly swollen, clavate. Fore femur sometimes with irregular rows of short stout setae ventrally (e.g. *B. aneuretus* Hardy & Takahashi 1960, Fig. 13b). *Bibio collaripes* Brunetti with large cluster of dense hair at base of fore femur (Hardy 1965b, Fig. 14). Fore femur and tibia shortened, but proportional. Fore tibia greatly modified; outer apex developed into strong spine which is typically apically acute (Fig. 8-a-c), but may be apically truncate as seen in lateral view (e.g. *B. tenebrosus* Coquillett; Hardy & Takahashi 1960, Fig. 31b). Fore tibia with single spur which is thicker than spurs on mid and hind tibia and variable in length; short and nearly rudimentary (e.g. *B. turneri* Hardy) to very elongate and subequal to length of tibial spine. Middle legs unremarkable; with two apical tibial spurs. Hind legs with hind femur greatly swollen apically to more slender and only slightly enlarged apically. Hind tibia slender and nearly parallel-sided to slightly swollen apically to greatly swollen apically (Fig. 9a-b). Inner surface of hind tibia with elongate field of small, round, black, specialized sensillae best observed when leg is illuminated from behind (Fig. 8f). Females often with fewer specialized sensillae than males and sometimes lacking specialized sensillae entirely. Spurs of hind tibia usually slender, apically acute, but may be flattened and apically rounded (e.g. *Bibio albipennis* Say) Hind tibial spurs subequal in length or ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. In males, hind tarsomeres vary in shape from short to elongate, parallel-sided to sausage-link-shaped, and slender to greatly swollen. Female tarsomeres never swollen; slender to robust. Wing (Fig. 14c): Halter pale or dark. Wing elongate, reaching back over abdomen; males 3.0 mm (*B. turneri* Edwards) to 10.5 mm (*B. tenebrosus* Coquillett) and females 3.5 mm to 15.5 mm. Wing hyaline to dark brown or black fumose, some species with whitish tinge (e.g. *B. albipennis* Say). Costal cell often darker than remainder of wing in taxa with colored wings. Wing color usually solid or with grade in intensity (e.g. becoming lighter posteriorly), rarely with spots on veins/crossveins (e.g. *B. scaurus* Hardy 1965c, Fig. 37). Pterostigma oval, usually brown to black and distinctly darker than wing membrane, but sometimes hyaline. Anterior wing veins typically darker than posterior veins; posterior veins hyaline, only slightly pigmented, or distinctly darker than membrane. Wing without macrotrichia, with microtrichia; microtrichia reaching wing margin or ending short of wing margin leaving narrow border along wing edge free of microtrichia (e.g. *B. pseudoclavipes* Hardy & Takahashi 1960, Fig. 27c). Anal lobe well developed. Costa ending at or just beyond R5; not shortened or thickened as *Enicoscolus*. Subcosta elongate, incomplete. Radius with horizontal microstriations (Fig. 14c insert). Rs simple; R2+3 and R4 absent. Length of r-m crossvein variable; shorter or more elongate than base of Rs. Three branches of M present. Stem of M variable in length; usually M furcates distinctly beyond r-m near position of m-m crossvein (e.g. *B. xanthopus* Wiedemann, Hardy 1981, Fig. 10) though M may furcate more basally almost at junction of M and r-m crossvein (e.g. *B. tenebrosus* Coquillett; Hardy & Takahashi 1960, Fig. 31d). M(3+)4 not connected to the remainder of M; base of M(3+)4 absent so that M(3+)4 appears continuous with m-cu crossvein. M-m crossvein present, often weak. CuA present, reaching wing margin, CuP short, not reaching margin. A1 very short and weak, not extending beyond small fold at base of anal lobe. Abdomen: Black, brown, or orange, usually with short to elongate, pale to dark hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles located in abdominal pleura, except spiracle eight, which is found dorsolaterally in the membrane between tergites eight and nine (Fig. 16b). Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia (Figs. 16a-b, 24): Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to deeply emarginated (epandrial cleft). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) typically broadly rounded, but may be slightly more narrow apically. Anterior edge of epandrium sometimes with lateral notches corresponding to position of spiracle eight. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes slight seam. Posteromedian margin of synsternogonocoxite sometimes with median hump or pair of humps which are membranous to lightly sclerotized. Gonocoxites forming tubular pedicel in which the apical gonostyli articulate. Gonostylus usually of a rather simple shape; round and robust basally, with short or elongate, digitate to gradually tapered, gently curved apical portion which may be apically round or acute. Some species with second (posterior) elongate lobe of gonostylus making gonostylus bifurcate as in *Bibiodes* (e.g. *Bibio nigriclavipes* Hardy & Takahashi, and *B. deceptus* Hardy & Takahashi 1960, Figs. 23b, 14d). Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of complex three dimensional shape, but with two main parts; dorsal sclerite and ventrolateral apodemes (Fig. 24a-b). Dorsal sclerite shield-like, posteriorly rounded. Ventral to dorsal sclerite, but protruding beyond posterior edge of dorsal sclerite a pair of tusk-like ventrolateral apodemes present. Ventral to parameres, membranous, sac-like, endophallus present and cradled by more ventral ejaculatory apodeme (Fig. 24c). Ejaculatory apodeme, simple, dorsoventrally flattened to rod-shaped or both (posteriorly flattened, anteriorly rod-shaped). Aedeagus absent. Female terminalia: Tergite nine present and well developed. Tergite ten narrow transverse strap. Cerci one-segmented. Subgenital plate large and apparently transversely subdivided into two plates; a more anterior and external plate and a more posterior and internal plate. Anterior portion of subgenital plate with posterior margin medially cleft and remainder of margin lobate. Posterior portion of subgenital plate longitudinally subdivided. Genital fork present. Sternite ten present. Three rounded, sclerotized, capsule-like, spermathecae present. **Immature stages:** **Egg:** Elongate, sausage-shaped, white (at least when first laid)(Fig. 26f). **Larva:** Body white, cream or yellowish-brown colored, elongate, cylindrical, sometimes slightly dorsoventrally flattened, slightly curved downwards in lateral view, with 3 thoracic and 9 abdominal segments (Fig.

27a). Thorax and abdomen with transverse rows of fleshy tubercles on each segment both dorsally and ventrally. Abdomen usually with two transverse rows per segment ventrally and one row per segment dorsally, though number of tubercles in each row varies depending on species. Thoracic segments tend to have fewer tubercles. Laterally, two tubercles present in vicinity of each spiracle except posterior spiracle. Terminally 4 tubercles surround anus; some of which are longest of all tubercles. Cuticle with dark brown, minute, sclerotized, scales which range in structure from spine-like, plate-like, or plate-like with a one or more points projecting from one side. Thorax without lightly sclerotized plates and without characteristic stair-step-like swollen developments observed in Pachyneuridae. Ventral flap-like tubercle of prothorax absent. Anus terminal, anal papillae apparently absent. Intersegmental fissures between meso- and metathorax, between abdominal segments 1 and 2, and between abdominal segments 7 and 8 unaligned. Dorsally prothorax with 3 pseudosegments, mesothorax 3 pseudosegments, and most abdominal segments 3 pseudosegments. Prothoracic and metathoracic spiracles present. Abdominal segments 1-8 with spiracles; 1-7 lateral and 8 dorsolateral and larger than 1-7. Posterior spiracle on anterior border of segment 9, round, with pair of central, crescent-shaped, ecdysial scars (Fig. 29a-b). Head not as heavily sclerotized as in non-bibionine bibionids, black to dark brown, rounded, somewhat dorsoventrally flattened, with setae. Ecdysial lines meeting in form of Y anterior to postoccipital carina or more V-shaped and either narrowly meeting or not meeting at postoccipital carina (Fig. 31a). Anterolateral margin of frontoclypeus developed into strong, anteroventrally-directed spine. Labrum subrectangular with strong spines at apex of labrum/epipharynx. Anteroventral stemmata absent, dorsoposterior stemmata present. Antennae short, sensory cone an elongate, ovoid, concave plate bordering anterodorsal margin of cranium (Fig. 31f). Posteromedian margin of plate with small, membranous, circular area which bears minute antennal sensillae. Postgenal bridge complete (Fig. 37a). Ventral prothoracic sclerites in cuticle at posterior, ventral margin of head capsule present. Anterior tentorial arm present, weak and thread-like, connected at anterior margin of head near mandibular articulation. Posterior tentorial bridge absent. Submentum apparently absent (or indistinguishably fused into ventral head capsule). Anterior mentum (hypostoma) absent, posterior mentum present as narrow, longitudinal sclerite fused to anterior margin of cranium and posterior margin of labium. Labial synsclerite present, upside-down-U-shaped, with each anterolateral margin with small knob homologous to glossae (Fig. 37b). Posterior labial sclerite present, large, in same plane as, and fused to labial synsclerite forming subrectangular, sclerotized frame around membranous labial area. Tubercle-like labial palps absent (i.e. no sensory setae on elevated tubercle). Membranous labial area bearing field of papillae. Cibarial bar present as two parallel rods. Membranous hypopharynx with minute spines, supported by two pairs of hypopharyngeal sclerites (Fig. 35d, 37a). Pharyngeal filter absent. Cardo large, transverse, not closely appressed to anteroventral margin of cranium, T-shaped, with inner apex of sclerite with anteriorly directed lobe and posteriorly directed lobe. Cardo with 4 setae (some represented only by alveoli) one seta at inner apex and group of 3 at outer (lateral) apex. Galeolacinia adjacent, but not closely appressed to palpifer. Galeolacinia primarily sclerotized ventrally with numerous teeth and spines on inner edge, apically, and on dorsal surface (Fig. 37b). Laterobasal sclerite of maxillary palpifer present. Palpifer sclerotized, tubular, bearing one-segmented cylindrical palpus. Palpus with only single sensory region apically, bearing numerous, short, stout, peg-like setae. Mandible heavily sclerotized, subtriangular, with small number of short, stout, apical teeth. Mandible operating in horizontal plane, without line of weakness separating apical and basal portions, and lacking basal thumb of teeth. Prostheca present, tuft-like. Mandibular comb absent. Epipharynx dorsoventrally flattened, slightly bilobate, with numerous small inwardly directed spines, and small number of peg-like setae. Torma wrapped dorsolaterally, fused and continuous with dorsal labrum. Premandible present; small, simple, unadorned, articulating with apex of torma. **Pupa:** Elongate, slender, white, cream, or gray, slightly tapering posteriorly. Sometimes partially enclosed within last larval skin. Head and thorax without distinct setae or spines. Respiratory horn absent;

anterior thoracic spiracle on slight tubercle. Abdomen without fleshy tubercles, spines, or setae. Leg sheaths superimposed. Pupa have been illustrated by numerous authors including Morris (1917, 1921) and Sutou (2002).

Distribution: Except for the polar regions, *Bibio* is distributed worldwide; yet it is most diverse in the Holarctic region (Table 2). Fossils of *Bibio* are known from the Nearctic, Palearctic, and Oriental regions.

Genus *Bibiodes* Coquillett

Bibiodes Coquillett 1904: 171. Type species: *Bibiodes halteralis* Coquillett, 1904: 171 (original designation)[examined; USNM].

Bibiodites* Cockerell, 1915: 493. Type species: *Bibiodites confluens* Cockerell, 1915: 493 (original designation)[examined; USNM]. **New synonym.

Nomenclatorial notes: *Bibiodites* was erected for the species *confluens* Cockerell which is known from a single compression fossil. Cockerell (1915) stated that this taxon "might be treated as a subgenus of *Bibiodes*, but it is less specialized than the modern flies." Although the fore tibial spurs of the holotype of *Bibiodites confluens* are not visible, the imprint of the body clearly places this taxon in the family Bibionidae. The anterior portion of one wing is well preserved and has the stem of Rs fused with the stem of M1+2 (obliterating crossvein r-m); venation that is diagnostic for the genus *Bibiodes*. Because no "less specialized" aspect of *Bibiodites* could be found, it is treated as a junior synonym of the *Bibiodes*.

Diagnosis: Adult *Bibiodes* are distinguished from other bibionids by the apex of the fore tibia developed into a strong spine (as Fig. 8b) and veins Rs and M fused for a short distance (Fig. 14a). Larvae are unknown. Pupae can be distinguished from *Plecia*, *Penthetria*, and *Hesperinus* by the absence of transverse rows of spinules.

Description: Adult: Small flies 3.0-4.0 mm. Head: Male head dorsoventrally compressed; in dorsal view slightly wider than long, oval-shaped. Male with almost entire dorsal surface of head occupied by broadly holoptic compound eye. Male compound eye strongly divided into larger dorsal region and smaller ventral region; dorsal region usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by distinct longitudinal step (where surface of dorsal region folds in toward surface of head to meet surface of ventral region). Division also marked by narrow, longitudinal, shining, sclerotized band, which is usually partially to entirely devoid of ommatidia. Longitudinal band widest anteriorly, forming small, smooth, triangular area between dorsal and ventral regions and frons. Triangular area devoid of ommatidia. Female head also dorsoventrally compressed, slightly longer than wide. Female compound eye oval, convex, dichoptic, and broadly separated by frons. Females have triangular area, but lack distinct or indistinct division of compound eye. Compound eye of both sexes with minute, stiff hairs. Ocellar tubercle well developed and prominent in males, weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle. Female without small tubercle or longitudinal ridge just posterior to antennal sockets. Sclerotized rostrum not produced. Antenna set anteriorly along oral margin, with 7-8 short, stout flagellomeres; flagellomeres slightly broader than long to about as broad as long. Pedicel and flagellomeres with subapical ring of short setae and numerous, dense, minute, appressed setae. Apical flagellomere often smaller and button-like and apical flagellomeres sometimes difficult to differentiate due to apparent fusion. First antennal flagellomere slightly more elongate than following flagellomeres. Head and antennae black to brown. Maxillary palps with five segments; basal segment minute, third segment thickened with a dorsal, diagonal sensory pit with dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Clypeus + proboscis never greatly elongated. Ventrally head entirely sclerotized. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax black, sub-shining, without pruinescence, smooth. Parapsidal sutures subtle and not distinct as in some *Plecia*. Dorsum of thorax with short to long hairs anteriorly, laterally, and in dorsocentral rows posteriorly. Thoracic pleura brown and mostly bare; male with some hairs on anepisternum, metakatepisternum, and dorsal half of katepisternum. Legs: Coxa subequal to length of katepisternum; reaching ventral edge in lateral view. Coxa usually with elongate hair. Leg color primarily brown with hind tibia and tarsi sometimes yellowish basally. Fore femur short, swollen, clavate with short to elongate hairs. Fore tibia greatly modified; outer apex developed into strong, apically acute spine. Fore tibia with single spur, thicker than spurs on mid and hind tibia and approximately 1/5-1/4 length of fore tibial spine. Middle legs unremarkable; with two apical tibial spurs. Hind legs with hind femur robust, slightly enlarged apically. Hind tibia slender and nearly parallel-sided to slightly swollen apically. Inner surface of hind tibia with elongate field of small, round, black, specialized sensillae which are best observed when leg is illuminated from behind. Spurs of hind tibia flattened, apically rounded, subequal in length or with ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. Male with hind tarsomeres elongate, robust to very slightly swollen. Female tarsomeres robust, not swollen. Wing (Fig. 14a): Halter pale. Wing elongate, reaching back over abdomen, 3.0-4.5 mm. Wing hyaline in male, slightly light brown fumose in female. Pterostigma oval, dark brown. Anterior wing veins brown, posterior veins hyaline to slightly pigmented. Wing without macrotrichia, with microtrichia. Anal lobe well developed. Costa ends at R5; not shortened or thickened as *Enicoscolus*. Subcosta elongate, but incomplete. Radius with horizontal microstriations. Rs simple; R2+3 and R4 absent. R-m crossvein absent; obliterated by short fusion of stem of M and Rs. Length of fusion variable; 1/3 length of Rs (*B. sinensis* Yang & Luo 1987, Fig. 4c) to approximately two times length of base of Rs. Three branches of M present. M furcates distinctly beyond r-m near position of m-m crossvein. M(3+)4 not connected to the remainder of M; base of M(3+)4 absent so that M(3+)4 appears continuous with m-cu crossvein. M-m crossvein present, often weak. CuA present, reaching wing margin, CuP short and not reaching margin. A1 short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Black to brown with short to elongate hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles located in abdominal pleura, except spiracle eight, which is found dorsolaterally in membrane between tergites eight and nine. Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia: Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to moderately emarginated (epandrial cleft). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) broadly rounded to slightly more narrowed apically. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes slight seam. Posteromedian margin of synsternogonocoxite sometimes with median hump. Gonocoxites forming tubular pedicel in which the apical gonostyli articulate. Gonostylus bifurcate; dorsal lobe shorter or subequal to ventral lobe, rounded, apically tapered. Ventral lobe flattened, sickle-shaped to more similar in shape to dorsal lobe. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of a complex three dimensional shape, but with two main parts; dorsal sclerite and ventrolateral apodemes. Dorsal sclerite shield-like, posteriorly rounded. Ventrolateral to dorsal sclerite, but protruding beyond posterior edge of dorsal sclerite, a pair of tusk-like ventrolateral apodemes present. Ventral to parameres, membranous, sac-like, endophallus present and cradled by more ventral ejaculatory apodeme. Ejaculatory apodeme, simple, dorsoventrally flattened. Aedeagus absent. Female terminalia: Tergite nine narrow. Tergite ten present; a weakly sclerotized, minute, transverse strap. Cerci one-segmented. Subgenital plate large, posterior margin medially cleft and remainder of margin lobate. Genital fork present. In addition to genital fork, a pair of small sclerites present between posterior margin of subgenital plate and anterior margin of sternite ten which may represent posterior division of subgenital plate observed in other Bibioninae. Sternite ten present. Three rounded, sclerotized, capsule-like, spermathecae present. **Immature stages:** **Egg:** White, elongate, sausage-shaped. **Larva:** Unknown. **Pupa:** Cream colored, smooth, bare. Respiratory horn absent. Abdomen without fleshy tubercles.

Distribution: *Bibiodes* includes four species: three from western North America and one from northern China (Table 2). Fossils of *Bibiodes* have been recorded from the western United States, England (as *Bibiodites*) and Sub-Saharan Africa (as "Bibionidae;" Rayner (1987)).

Genus *Bibionellus* Edwards

Bibionellus Edwards, 1935: 19. Type species *Bibionellus tibialis* Edwards, 1935: 19 (original designation).

Diagnosis: Adult *Bibionellus* are distinguished from other bibionids by the apex of the fore tibia developed into a strong spine (as Fig. 8b; tsp) and the fore femur and tibia with ventral tubercles (Fig. 8e). Larvae and pupae are unknown.

Description: **Adult:** Small flies approximately 4.0 mm long. Head: Male head dorsoventrally compressed; in dorsal view, slightly wider than long, oval-shaped. In males almost entire dorsal surface of head occupied by broadly holoptic compound eye. Male compound eye strongly divided into larger dorsal region and smaller ventral region; dorsal region usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by distinct longitudinal step (where surface of dorsal region folds in toward surface of head to meet surface of ventral region). Division also marked by narrow, longitudinal, shining, sclerotized band, which is usually partially to entirely devoid of ommatidia. Longitudinal band widest anteriorly where it forms a small, smooth, triangular area between dorsal and ventral regions and frons. Triangular area devoid of ommatidia. Female head dorsoventrally compressed, slightly longer than wide. Female compound eye oval, convex, dichoptic, broadly separated by frons. Female with triangular area present, but lacking distinct or indistinct division of compound eye. Compound eye of both sexes bare to sometimes with a few minute, stiff hairs. Ocellar tubercle well developed and prominent in males, weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle. Female without small tubercle or longitudinal ridge just posterior to antennal sockets. Antenna brown to black to orange, set anteriorly along oral margin, with 5-7 short, stout flagellomeres; flagellomeres slightly broader than long, except for first flagellomere slightly more elongate. Sclerotized rostrum not produced. Pedicel and flagellomeres with subapical ring of short setae and numerous, dense, minute, appressed setae. Apical flagellomere often small and button-like. Head black to brown to orange. Maxillary palps with five palpomeres (Pinto & Amorim (1997) state only four palpomeres present); basal segment minute, third segment thickened with dorsal, diagonal sensory pit with dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Clypeus + proboscis never greatly elongated. Ventrally, head entirely sclerotized. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax black to brown to orange, shining, without pruinosity, smooth. Parapsidal sutures subtle and not distinct as in some *Plecia*. Dorsum of thorax with short to moderately long hairs laterally and in dorsocentral rows. Thoracic pleura brown to orange. Male thoracic pleura bare except hairs on metakatepisternum. Legs: Coxa subequal to length of katepisternum; reaching ventral edge in lateral view. Legs brown, orange, or brown and yellow (e.g. basal 1/2 hind femur yellowish, distal 1/2 brown). Fore femur swollen, clavate. Fore femur and tibia shortened, but proportional. Fore femur subapicoventrally with a small, rounded, denticulate tubercle. Fore tibia greatly modified; outer apex developed into strong, apically acute, spine. Fore tibia with ventromedial tubercle corresponding to denticulate tubercle of femur. Fore tibia with single spur that is thicker than spurs on mid and hind tibia; spur short, approximately 1/4-1/5 length fore tibial spine. Middle legs unremarkable; with two apical tibial spurs. Hind femur swollen apically, clavate. Inner surface hind tibia with elongate field of small, round, black, specialized sensillae (best observed when leg illuminated from behind). Spurs of hind tibia slender, apically acute, ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. Male hind tarsomeres not swollen, but robust. Female hind basitarsomere slender, elongate. Wings: Halter pale basally, darker distally. Wing elongate, reaching back over abdomen 3.0-4.0 mm. Wing light brown to black fumose, costal cell darker. Pterostigma oval, brown. Anterior wing veins darker than posterior veins. Wing without macrotrichia, with microtrichia. Anal lobe well developed. Subcosta elongate, incomplete. Costa extending beyond R5 about half way between R5 and M1. Costa not shortened or thickened as *Enicoscolus*. Radius with horizontal microstriations. Rs simple; R2+3 and R4 absent. Length of r-m crossvein variable; shorter or more elongate than base of Rs. Three branches of M present. Stem of M variable in length; usually M furcates distinctly beyond r-m near position of m-m crossvein. M(3+)4 not connected to remainder of M; base of M(3+)4 absent so that M(3+)4 appears continuous with m-cu crossvein. M-m crossvein present, but often weak; attached to M either on stem near base of fork or on M2. CuA present, reaching wing margin, CuP short and not reaching margin. A1 very short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Brown to black with short hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles located in abdominal pleura, except spiracle eight, which is found dorsolaterally in membrane between tergites eight and nine. Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia: Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to moderately emarginated (epandrial cleft). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) broadly rounded. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into a continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable by only a narrow, strap-like thickening ventrally and sometimes slight seam. Posteromedian margin of synsternogonocoxite with median, sclerotized, tubercle and smaller, digitate, submedian tubercles ("mesossome" and "lateral projection of the mesossome" of Pinto & Amorim 1997, Figs. 31, 36, 42). Gonocoxites forming very narrow ring in which the apical gonostyli articulate. Gonostylus usually L or C-shaped, apically truncate. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of complex three dimensional shape, with two main parts; dorsal sclerite and ventrolateral apodemes. Dorsal sclerite shield-like, posteriorly rounded (translucent dorsal sclerite not illustrated in terminalia figures of Pinto & Amorim (1997)). Ventral to dorsal sclerite, but protruding beyond posterior edge of dorsal sclerite, pair of tusk-like ventrolateral apodemes present. Ventral to parameres, membranous, sac-like, endophallus present and cradled by more ventral ejaculatory apodeme. Ejaculatory apodeme, simple, dorsoventrally flattened. Aedeagus absent. Female terminalia: Tergite nine well developed, wrapped ventrolaterally into pair of small ventral lobes. Tergite ten absent. Cerci one-segmented. Subgenital plate large, shield-like, with posterior margin medially cleft and remainder of margin lobate. Inner margin of median cleft with pair of minute lobes. Genital fork present. Sternite ten present. Two oblong, spermathecae present that are appressed along their inner margins. Spermathecae mostly membranous except for small, lightly sclerotized hump at posterior apex of each one. **Immature stages: Egg:** Elongate sausage-shaped. **Larva & Pupa:** Unknown.

Distribution: *Bibionellus* is known from four species restricted to central South America (Argentina, Brazil, Bolivia; Pinto & Amorim 1997). No fossils of the genus are known.

Genus *Enicoscolus* Hardy

Enicoscolus Hardy, 1961a: 81. Type species: *Enicoscolus dolichocephalus* Hardy, 1961a: 81 (original designation) [examined; USNM].

Discussion: Only the female of this genus has been described in the literature. Amorim (pers. comm. 2002) stated that a male of this genus was recently found among unsorted material and is currently being described. As this male specimen was not available for study, the following description of the genus is based on females only.

Diagnosis: Adult *Enicoscolus* are distinguished from other bibionids by the apex of the fore tibia developed into a strong spine (Fig. 8a-c), fore femur and tibia lacking ventral tubercles (see tubercles in Fig. 8e), veins Rs and M not fused for a short distance (see fused condition in Fig. 14a), vein R4 absent, and crossvein m-m absent (see m-m present in Fig. 14c). Larvae and pupae are unknown.

Description: Adult (female only): Small flies 4.2-5.0 mm. Head dorsoventrally compressed, about as long as wide to approximately two times as long as wide. Compound eye oval, dichoptic, and broadly separated by frons. Triangular area devoid of ommatidia present at inner, anterior edge of compound eye, but distinct division of compound eye absent. Some species with indistinct and slight longitudinal depression dividing compound eye, but ommatidia of uniform size and color. Compound eye bare. Ocellar tubercle weakly developed, with three ocelli arranged in small, equilateral triangle. Without small tubercle or longitudinal ridge just posterior to antennal sockets. Antenna set anteriorly along oral margin, with 5-6 short, stout flagellomeres; flagellomeres slightly broader than long. Sclerotized rostrum sometimes slightly produced anteriorly. In those species with developed rostrum, antenna situated at anterodorsal edge of rostrum at oral margin. Pedicel and flagellomeres with subapical ring of short setae and numerous, dense, minute, appressed setae. Apical flagellomere often smaller and button-like and apical flagellomeres difficult to differentiate due to apparent fusion. Apical flagellomeres slightly expanded and club-like. First antennal flagellomere typically slightly more elongate than following flagellomeres. Head and antennae black to brown. Maxillary palps with five segments; basal segment minute, third segment thickened with dorsal, diagonal sensory pit with dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Clypeus + proboscis never greatly elongated. Ventrally head entirely sclerotized. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax black, brown, or orange, shining, smooth (not with minutely rugosity as in some *Bibio*). Parapsidal sutures subtle and not distinct as in some *Plecia*. Dorsum of thorax with dense, short, stiff hairs laterally, anteriorly, and forming dorsocentral rows posteriorly. Thoracic pleura orange, sometimes strongly contrasting color of dorsum of thorax. Thoracic pleura mostly bare, but with minute hairs on anepisternum. Legs: Coxa subequal to length of katepisternum; reaching ventral edge in lateral view. Legs black, brown, or orange. Fore femur strongly swollen, clavate. Fore femur and tibia shortened, but proportional. Fore tibia greatly modified; outer apex developed into strong, apically acute, spine. Fore tibia with a single minute spur which is much shorter than tibial spine and in some specimens difficult to find. Middle legs unremarkable; with two apical tibial spurs. Hind femur swollen with irregular rows of short, stiff hairs anteroventrally. Hind tibia slender and nearly parallel-sided. Inner surface of hind tibia without elongate field of small, round, black, specialized sensillae. Spurs of hind tibia usually flattened and apically rounded, subequal in length or ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. Hind tarsomeres slender, elongate, parallel-sided, to robust, but never swollen. Wing: Halter pale basally, dark distally. Wing elongate, reaching back over abdomen; 4.0-5.4 mm. Wing light brown fumose. Costal cell often darker than remainder of wing. Wing color solid, never with distinct markings. Pterostigma absent. Anterior wing veins darker than posterior veins; posterior veins only slightly pigmented. Wing without macrotrichia, with microtrichia; microtrichia reaching wing margin. Anal lobe well developed. Costa ending at or just beyond R5. Costa greatly shortened and thickened; reaching 2/3-3/4 length of wing. Subcosta elongate, incomplete. Radius with horizontal microstriations. Rs simple; R2+3 and R4 absent. Length of r-m crossvein longer than base of Rs. Three branches of M present; M1+2 forking just beyond r-m. M(3+)4 not connected to the remainder of M; base of M(3+)4 absent so that M(3+)4 appears continuous with m-cu crossvein. M-cu + M(3+)4 forking from junction with CuA near base of wing (ca. level of humeral crossvein). M-m crossvein absent. CuA present, reaching wing margin, CuP short and not reaching margin. A1 very short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Stout, dark brown with short pale hairs. Tergites 1-8 and sternites 1-7 unmodified. Abdominal pleura pleated. Female terminalia: Tergite nine present. Tergite ten present as a very minute, rounded, median sclerite or absent. Cerci one-segmented. Subgenital plate with posterior margin medially cleft and remainder of margin lobate. Anterior apex of median cleft of subgenital plate expanded into narrow, transverse, membranous, band making cleft an upside-down-T-shape. Genital fork present. Sternite ten present. Three rounded, sclerotized, capsule-like, spermathecae present. **Immature stages: Egg:** Elongate, sausage-shaped. **Larva & Pupa:** Unknown.

Distribution: *Enicoscolus* includes four species: two from Mexico, one from Brazil, and the fourth from northern Australia and New Guinea (Hardy 1961a, Fitzgerald 1997a). No fossils of this genus are known.

Genus *Dilophus* Meigen

Philia Meigen, 1800: 20. Type species: *Tipula febrilis* Linnaeus, 1758 (designated by Coquillett 1910: 588). Suppressed by I.C.Z.N., 1963: 339.

Dilophus Meigen, 1803: 264. Type species: *Tipula febrilis* Linnaeus, 1758 (designated by Latreille 1810: 442).

Acanthocnemis Blanchard 1852: 355. No type designation.

Cnemidoctenia Enderlein 1934: 181. Type species: *Dilophus crassicrus* Lundström, 1913: 394. [Synonymized by Hardy 1953b]

Dactylodiscia Enderlein 1934: 181. Type species: *Dilophus hiemalis* Becker, 1908: 59. [Synonymized by Hardy 1953b]

Tridicroctena Enderlein 1934: 181. Type species: *Dilophus africanus* Becker, 1903: 79. [Synonymized by Hardy 1953b]

Triploctenia Enderlein 1934: 181. Type species: *Dilophus tenuis* Meigen, 1818: 308. [Synonymized by Hardy 1953b].

Nomenclatural notes: Enderlein (1934) began subdividing the genus *Dilophus* based on the number of spines on the fore tibia, erecting the genera *Cnemidoctenia*, *Dactylodiscia*, *Tridicroctena*, and *Triploctenia*. As noted by Hardy (1953b), the fore tibial spines present good characters for specific diagnosis, but do not seem to indicate clear generic boundaries.

Diagnosis: Adult *Dilophus* are distinguished from other bibionids by the presence of two rows of transverse spines on the anterior dorsum of the thorax (Fig. 6a; tts), apex of the fore tibia with a circlet of spines (Fig. 8d; acs), and fore tibia with one or more sets of medial spines (Fig. 8d; ms). Larvae are distinguished by the presence of short fleshy tubercles (as in Fig. 27a), antennal sensory cone a flat oblong plate (as Fig. 31f; sc), mentum fused to anterior margin of cranium and posterior margin of labium (as Fig. 37a; pm), and the presence of three ecdysial scars of the posterior spiracle (Fig.

29c). Pupae can be distinguished from *Plecia*, *Penthetria*, and *Hesperinus* by the absence of transverse rows of spinules and fleshy tubercles.

Description: Adult: Small to medium-sized flies 2.0-8.0 mm. Head: Dorsoventrally compressed; in dorsal view, oval-shaped, slightly wider than long to very narrow and elongate (8.5 times as long as wide with most of this length accounted for by rostrum)(Fig. 6a, e-f). Male with almost entire dorsal surface of head occupied by broadly holoptic compound eye. Male compound eye distinctly to indistinctly divided into larger dorsal region and smaller ventral region (except in some species, such as *D. transvestis* Hardy (1968, Fig. 12a-b), in which dorsal region is much smaller than ventral region). Dorsal region of male compound eye usually lighter in color than ventral region and with larger ommatidia. Division between dorsal and ventral regions of compound eye distinguished by distinct longitudinal step or subtle indentation. Division also marked by narrow, longitudinal, shining, sclerotized band, which is usually partially to entirely devoid of ommatidia. Longitudinal band widest anteriorly where it forms a small, smooth, triangular area between dorsal and ventral regions and frons. Triangular area devoid of ommatidia. Female compound eye round or oval, convex, dichoptic, and broadly separated by frons. Females usually have triangular area, but lack distinct division of compound eye. Females of many species with indistinct and slight longitudinal depression dividing compound eye, but lacking any difference in size of ommatidia or color between dorsal and ventral regions of eye. Compound eye of both sexes bare or clothed with minute, stiff hairs. Ocellar tubercle weakly to well developed and prominent in males, typically only weakly developed in females. Both sexes with three ocelli arranged in small, equilateral triangle. Female with or without small tubercle or longitudinal ridge just posterior to antennal sockets. Antenna set anteriorly along oral margin, with 8-11 short, stout flagellomeres; flagellomeres slightly broader than long except first flagellomere typically slightly more elongate than following flagellomeres. Sclerotized rostrum absent to very strongly produced and elongated anteriorly; often more produced in females (Fig. 6e-f). Pedicel and flagellomeres with subapical ring of short setae in addition to numerous, dense, minute, appressed setae. Apical flagellomere often smaller and button-like and apical flagellomeres sometimes difficult to differentiate due to apparent fusion. Head and antennae black to brown to orange. Maxillary palps with five segments; basal segment minute, third segment thickened with dorsal, diagonal sensory pit with dense, minute, specialized setae, and apical segment slender and most elongate of all palpomeres. Mouthparts telescopic within sclerotized, tubular rostrum (Fig. 6e). Ventrally, head entirely sclerotized. Thorax: Precoxal bridge complete. Basisternum present, presternum absent. Dorsum of thorax black, brown, orange, or anteriorly black and posteriorly orange, smooth, sometimes with longitudinal dark stripes, shining or opaque, without pruinescence. Parapsidal sutures subtle and not distinct as in some *Plecia*. Dorsum of thorax with dense, short, stiff hairs, to very elongate hairs, to nearly bare; hairs often anteriorly, laterally, and in dorsocentral rows posteriorly. Mesonotum anteriorly with two transverse rows of strong, spine-like setae (mesonotal combs)(Fig. 6a; tts). Spines of mesonotal combs apically acute or blunt, each comb sometimes medially divided by small gap lacking spine-like setae. Some species (e.g. *D. acutidens* Edwards) with small longitudinal comb of several spine-like setae at each end of posterior or both mesonotal combs (Hardy & Delfinado 1969, Fig. 22c). Thoracic pleura black, brown, or orange, sometimes strongly contrasting color of dorsum of thorax. Male thoracic pleura bare or with only a few hairs; female generally less hairy than males. Legs: Coxa subequal to length of katepisternum, reaching ventral edge in lateral view. Coxa usually with short to elongate hair. Leg color highly variable; black, brown, orange, yellow, sometimes with femora and tibia of contrasting colors, sometimes with femur and/or tibia bicolored (e.g. light at base and darker distally). Fore femur moderately to strongly swollen, clavate. Fore femur and tibia shortened, but proportional. Fore tibia greatly modified; outer apex not developed into strong spine, but apex with crown of strong, spine-like setae which may be apically acute or blunt (Fig. 8d; acs). Distal 2/3 of fore tibia with 1-2 sets of primarily dorsal, spine-like setae (Fig. 8d; ms). Fore tibia with or without single, short spur which is thicker than spurs on mid and hind tibia. Middle legs unremarkable except in *D. multispinosus* Hardy, which has mid tibia with sub-apical ring of spine-like setae and longitudinal dorsal row of spine-like setae. Mid tibia with two apical spurs. Hind legs with hind femur greatly swollen apically to more slender and only slightly enlarged apically. Hind tibia slender and nearly parallel-sided to slightly swollen apically to greatly swollen apically. Inner surface of hind tibia with or without elongate field of small, round, black, specialized sensillae (best observed when leg is illuminated from behind). Females often with fewer specialized sensillae than males and sometimes lacking specialized sensillae entirely. Spurs of hind tibia slender, apically acute, subequal in length or with ventral spur slightly more elongate than dorsal spur. All legs with five tarsomeres, simple tarsal claws, pulvilli and pulvilliform empodia. In males, hind tarsomeres vary in shape from slender, elongate, parallel-sided to sausage-link-shaped, to greatly swollen. Female tarsomeres never swollen; slender to robust. Wing (Fig. 14b): Halter basally pale, distally dark or entirely dark. Wing elongate, reaching back over abdomen; 2.5-11.0 mm. Wing hyaline to dark brown or black fumose. Costal cell often darker than remainder of wing in taxa with fumose wings. Wing color usually solid or with grade in intensity (e.g. becoming lighter posteriorly), rarely with wing tip darkened or with blotches (e.g. *D. mcalpinei* Hardy (1982, Fig. 19a)). Pterostigma oval, usually brown to black and distinctly darker than wing membrane, but sometimes hyaline. Anterior wing veins typically darker than posterior veins; posterior veins hyaline, only slightly pigmented, or distinctly darker than membrane. Wing without macrotrichia, with microtrichia; microtrichia reaching wing margin or ending short of wing margin leaving narrow border along wing edge free of microtrichia (e.g. *D. multispinosus* Hardy). Anal lobe well developed. Costa ending distinctly beyond R5, often about 1/2 way between R5 and M1; not shortened or thickened as *Enicoscolus*. Subcosta elongate, incomplete or complete. Radius with horizontal microstriations and with or without minute evenly-spaced setae. Rs simple; R2+3 and R4 absent. Length of r-m crossvein 2-3 times longer than base of Rs. Three branches of M present. Stem of M present or absent;

when absent, M1 and M2 often not connected and only present distally (e.g. *D. tuthilli* (Hardy)(Harrison 1990, Fig. 22)). M(3+)4 not connected to the remainder of M; base of M(3+)4 absent so that M(3+)4 appears continuous with m-cu crossvein. M-m crossvein present or absent. CuA present, reaching wing margin, CuP short and not reaching margin. A1 very short and weak; not extending beyond small fold at base of anal lobe. Abdomen: Black to brown, usually with short to elongate, pale to dark hairs. Male abdomen elongate, gradually tapered posteriorly; female abdomen much stouter. Male spiracles located in abdominal pleura, except spiracle eight, which is found dorsolaterally in membrane between tergites eight and nine. Males with tergites and sternites 1-8 unmodified, females with tergites 1-8 and sternites 1-7 unmodified. Male terminalia: Terminalia slightly dorsoflexed, not rotated. Posterior margin of tergite 9 (epandrium) medially, shallowly to deeply emarginated (epandrial cleft). Epandrial cleft usually U or V-shaped; resulting lobate sides of posterior edge of epandrium (epandrial lobes) typically broadly rounded, but may be slightly more narrow apically. Anterior edge of epandrium sometimes with lateral notches corresponding to position of spiracle eight. Lateral gonocoxites + ventral sternite nine (hypandrium) fused into a continuous genital capsule (synsternogonocoxite). Hypandrium distinguishable only by narrow, strap-like thickening ventrally and sometimes a slight seam. Posteromedian margin of synsternogonocoxite sometimes with median hump or pair of humps which are membranous to lightly sclerotized. Gonocoxites forming tubular pedicel in which apical gonostyli articulate. Gonostylus usually of rather simple shape; round and robust basally, with short or elongate, digitate to gradually tapered, gently curved, apical portion which may be round or acute apically. Proctiger present ventral to epandrium; cerci normally protruding through epandrial cleft. Tergite and sternite ten (epiproct and hypoproct respectively) present. Cerci rounded, flap-like, fleshy, with hairs. Gonocoxal apodeme present, fused to parameres. Ventral to proctiger are parameres of complex three dimensional shape, but with two main parts; dorsal sclerite and ventrolateral apodemes. Dorsal sclerite shield-like, posteriorly rounded or posteromedially emarginate. Ventrolateral to dorsal sclerite, pair of plate or strap-like ventrolateral apodemes present or absent (fused indistinguishably with dorsal sclerite). Subquadrate aedeagal plate present and ventral to posterior edge of dorsal sclerite; lacking apodemes. Ventral to parameres and aedeagal plate, membranous, sac-like, endophallus present that is cradled by more ventral ejaculatory apodeme. Ejaculatory apodeme simple, dorsoventrally flattened or rod-like (Fig. 16c-d). Tubular aedeagus absent. Female terminalia: Tergite nine present and well developed. Tergite ten absent or minute. Cerci one-segmented. Subgenital plate large and apparently transversely subdivided into two plates; a more anterior and external plate and a more posterior and internal plate. Anterior portion of subgenital plate with posterior margin medially cleft and remainder of margin lobate. Posterior portion of subgenital plate longitudinally subdivided. Genital fork present. Sternite ten present. Three rounded, sclerotized, capsule-like, spermathecae present.

Immature stages: **Egg:** Elongate, sausage-shaped, white (at least when first laid).

Larva: Body white, cream or yellowish-brown colored, elongate, cylindrical, sometimes slightly dorsoventrally flattened, slightly curved downwards in lateral view, with 3 thoracic and 9 abdominal segments. Thorax and abdomen with transverse rows of small fleshy tubercles on each segment both dorsally and ventrally. The number of tubercles in each row varies depending on the species, though thoracic segments tend to have fewer tubercles. Cuticle with minute, sclerotized, scales which range in structure from spine-like, plate-like, or plate-like with one to many points projecting from one side. Thorax without lightly sclerotized plates and without characteristic stair-step-like swollen developments observed in Pachyneuridae. Ventral flap-like tubercle on prothorax absent. Anus terminal, anal papillae apparently absent. Intersegmental fissures between meso- and metathorax, between abdominal segments 1 and 2, and between abdominal segments 7 and 8, unaligned. Dorsally prothorax with 2 pseudosegments, mesothorax 3 pseudosegments, and most abdominal segments 3 pseudosegments. Prothoracic and metathoracic spiracles present. Abdominal segments 1-8 with spiracles; 1-7 lateral and 8 dorsolateral and larger than 1-7. Posterior spiracle (on anterior border of segment 9) round, with 2-3 central ecdysial scars; when only 2 scars present, they are not of equal size, but one is two times as large as the other. Head not as heavily sclerotized as in non-bibionine bibionids, black to dark brown, rounded, somewhat dorsoventrally flattened, with setae. Ecdysial lines meeting in form of Y anterior to postoccipital carina or more V-shaped and meeting or narrowly not meeting at postoccipital carina. Anterolateral margin of frontoclypeus developed into strong, anteroventrally-directed spine. Labrum subrectangular with strong spines at apex of labrum/epipharynx. Anteroventral stemmata absent, dorsoposterior stemmata present. Antennae short, sensory cone in form of elongate, ovoid, concave plate bordering anterodorsal margin of cranium. Posteromedian margin of plate with small, membranous, circular area which bears minute antennal sensillae. Postgenal bridge complete. Ventral prothoracic sclerites in cuticle at posterior, ventral margin of head capsule present. Anterior tentorial arm present, weak and thread-like, connected at anterior margin of head near mandibular articulation. Posterior tentorial bridge absent. Submentum apparently absent (or indistinguishably fused into ventral head capsule). Anterior mentum (hypostoma) absent, posterior mentum present as narrow, longitudinal sclerite fused to anterior margin of cranium and posterior margin of labium. Labial synsclerite present, upside-down-U-shaped, with each anterolateral margin with small knob homologous to glossae. Posterior labial sclerite large, in same plane as, and fused to, labial synsclerite (forming subrectangular, sclerotized frame around membranous labial area). Tubercle-like labial palps absent (i.e. sensory setae not on elevated tubercle). Membranous labial area bearing field of papillae. Cibarial bar present as two parallel rods. Membranous hypopharynx with minute spines, supported by two pairs of hypopharyngeal sclerites. Pharyngeal filter absent. Cardo large, transverse, not closely appressed to anteroventral margin of cranium, T-shaped, with inner apex of sclerite with anteriorly directed lobe and posteriorly directed lobe. Cardo with 4 setae (some represented only by alveoli) one seta at inner apex and group of 3 at outer (lateral) apex. Galeolacinia adjacent, but not closely appressed to palpifer. Galeolacinia primarily sclerotized ventrally with numerous teeth and spines on inner edge, apically, and on dorsal surface. Laterobasal sclerite of maxillary palpifer present. Palpifer sclerotized, tubular, bearing one-segmented, cylindrical palpus. Palpus with only single sensory region apically, bearing numerous, short, stout, setae. Mandible heavily sclerotized, subtriangular, with small number of short, stout, apical teeth. Mandible operating in horizontal plane, without line of weakness separating apical and basal portions, and lacking basal thumb of teeth. Prostheca present. Mandibular comb absent. Epipharynx dorsoventrally flattened, slightly bilobate, with numerous, small, inwardly directed spines and small number of peg-like setae. Torma wrapped dorsolaterally, fused and continuous with dorsal labrum. Premandible present, small, simple, unadorned, articulating with apex of torma. **Pupa:** Elongate, slender, white to cream colored, slightly tapering posteriorly. Head and thorax without distinct setae or spines. Respiratory horn absent; anterior thoracic spiracle on slight tubercle. Abdomen without fleshy tubercles, spines, or setae. Leg sheaths superimposed. Pupa illustrated by Morris (1922).

Distribution: *Dilophus* includes approximately 205 extant species and, except for the polar regions, is distributed world wide (Table 2). The genus is known from several Palearctic compression fossils, Dominican and Baltic ambers, and the compression fossil of a larva from New Zealand (Evenhuis 1994, Waller *et al.* 2000).

Genus **Fushunoplecia* Hong

****Fushunoplecia*** Hong, 2002: 221. Type species: *Fushunoplecia eocenica* Hong, 2002: 221-4 (original designation).

Discussion: Hong (2002) described *Fushunoplecia* from a single female in Chinese amber. The illustration of the wing venation provided by Hong (2002) shows five branches of M which is very unlikely. Inspection of the color microphotographs provided by Hong (2002) suggests that two of the branches of M appear to be folds in the wing rather than actual veins, but without examination of the genotype it is difficult to get an accurate picture of the wing venation of this taxon. The general gestalt of the specimen is vaguely similar to a bibionid, but this interpretation would require considerable morphological novelty to embellish a bibionid with five branches of M, a long, strong A2 vein which reaches the wing margin, an abdomen with at least ten large abdominal segments, and only a single tibial spur on the mid and hind legs. The genotype was not available for study, and consequently its placement cannot be further clarified here. According to Wang Wenli (Beijing Nat. Hist. Mus., pers. comm. 2004) the genotype is housed at the "China Zoology Museum."

Genus ******Clothonopsis*** Hong & Wang**

****Clothonopsis*** Hong & Wang, 1987: 258. Type species: *Clothonopsis miocenica* Hong & Wang, 1987: 258 (original designation).

Discussion: The genus *Clothonopsis* was originally described in the insect order Embioptera by Hong & Wang (1987) based on a single compression fossil. Zhang (1993) and Zhang *et al.* (1994) showed that the specimen is not an embiopteran and suggested that it probably belongs to the genus *Plecia* of the Bibionidae. However, based upon the illustration of the wing venation provided by Hong & Wang (1987) R4 is absent, whereas in *Plecia* it is present. The genotype is housed at the Beijing Natural History Museum, but is not available for study (Wang Wenli, pers. comm. 2004). Consequently, the placement of this taxon remains unresolved.

Genus **Megeana* Meunier

Megeana Meunier, 1899: 175. Type species: *Megeana hardyi* Evenhuis, 1994: 127 (designated by Evenhuis, 1994: 127).

Discussion: This genus is represented by a single specimen from Baltic amber that was first described by Meunier (1899) in his study of Loew's amber collection. Meunier (1899) lists the genus as "Megeana, Löw" with two question marks and he notes in a footnote (1899: 175) that he could not find a bibliographic record for the genus. Considering this, it seems a likely possibility that Loew had a manuscript name associated with the specimen that was never published; thus, the generic name became validated by Meunier's (1899) description and illustration. Since no specific name was given by Meunier for the type of the genus, Evenhuis (1994) provided the specific epithet *hardyi*.

Based on Meunier's illustration (1899; Fig. 20) the wing veins are bibionid-like except the structure of M(3+)4 which is unusual. However, if it is a bibionid, the antennae are short, apex of the fore tibia unmodified, and R4 elongate and subparallel, making this taxon most similar to the genus *Penthetria*. Although a study of the genotype is necessary to clarify the placement and identity of this taxon, the location of the genotype is currently unknown. It was not found with Meunier's other material at the Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen (H. Jahnke, pers. comm. 2004), or the State Museum of Natural History (previously the Dzieduszycki Museum) Lvov, Poland (R. Godunko, pers. comm. 2004). Additionally, it was not found with Loew's material in Göttingen, the Paläontologisches Museum, Humbolt-Universität, Berlin (E. Pietrzeniuk, pers. comm. 2000), or The Natural History Museum, London (A. Ross, pers. comm. 2004).

GENERA REMOVED FROM BIBIONIDAE

Genus **Mesopleciella* Rohdendorf

***Mesopleciella** Rohdendorf, 1946: 43. Type species: *Mesopleciella minor* Rohdendorf, 1946: 43 (original designation).

Discussion: *Mesopleciella* was treated as part of the family Bibionidae by Evenhuis (1994). However, in *Mesopleciella* the subcosta is shortened and the m-cu crossvein spans the base of M(3+)4 and CuA so that the basal portion of M(3+)4 is minute. These characters place *Mesopleciella* in the extinct family Protopleciidae that is defined as having a shortened subcosta and a single oblique branch of Rs that terminates near the end of R1 (Rohdendorf 1962: 479 and Carpenter, 1992: 414). Rohdendorf (1962) treated Protopleciidae as part of Bibionoidea and Shcherbakov *et al.* (1995: 110) treated Protopleciidae as part of Mycetophilidae *sensu lato* within Sciaroidea. Characters of the wing venation of Protopleciidae are found in both superfamilies, but the combination of a shortened subcosta and the presence of R4 is not found in Bibionidae (*Enicoscolus* has a short Sc, but lacks R4). The venation of Protopleciidae seems to have more in common with sciaroid taxa such as the family Keroplatidae, which may have both a short subcosta and R4 present and ending near the end of R1 (e.g. *Paleoplatyura* Meunier; Vockeroth 1981, Fig. 19). However, since the venation alone may be insufficient evidence to place this group, and the familial characters which define Protopleciidae are not unique, its status as a family is dubious and its relationship to other taxa remains unknown. Blagoderov's (1996) revision of Protopleciidae is adhered to, which treats the group as a distinct family and includes the genus *Mesopleciella*.

Genus ***_Longicornia_ Hong**

Longicornia Hong, 2002: 161. Type species: *Longicornia tenuis* Hong, 2002: 162-4 (original designation).

Discussion: Hong (2002) described *Longicornia* in the family Hesperinidae (=Hesperininae of Bibionidae) based on a single specimen in Chinese amber. The three-branched radial sector, hemispherical pedicel, antenna with 27 flagellomeres, and paired fore-tibial spurs illustrated by Hong suggests that this taxon is not a bibionid. Strangely, Hong (2002) compares *Longicornia* to Dixidae rather than to the genus *Hesperinus* or other bibionids. Although some of the above mentioned character states may suggest that the taxon should be placed in Culicomorpha, its extremely long antennae are more suggestive of Trichoptera than Diptera. The genotype, which is apparently housed in the "China Geology Museum" (Wang Wenli, pers. comm. 2004), needs to be examined to clarify the position of this taxon and was unavailable for study during the course of this work.

CONCLUSION

A strict consensus of 43 equal-length trees of 1,106 steps indicates that family Bibionidae is monophyletic and supported by twelve unambiguous characters. Fifteen unambiguous characters support Pachyneuridae as the sister group to Bibionidae, including four characters unique to the clade. All bibionid genera are unambiguously supported as monophyletic except for *Bibio* and *Bibiodes* (monophyly of the latter genus was not examined because only one exemplar was included). Additionally, results indicate that the subfamilies Hesperininae and Bibioninae are monophyletic and Pleciinae is paraphyletic. This finding supports the four-subfamily classification proposed by Pinto and Amorim (2000)(Table 1). The cladistic structure of the family is *Hesperinus* + (*Penthetria* + (*Plecia* + (*Dilophus* + Bibionini))) with relationships within Bibionini unresolved. Generic relationships within tribe Bibionini are unresolved probably due to the unknown immature stages of three of the four genera (*Bibionellus*, *Enicoscolus*, *Bibiodes*), the unknown males of *Enicoscolus*, and the lack of characters supporting *Bibio* as a monophyletic group. Locating these additional life stages or accumulating fresh material of these rare genera for molecular analysis may be necessary to resolve relationships in this clade.

Despite the lack of characters supporting *Bibio* as a monophyletic group, it is retained as a distinct genus here until further study can resolve relationships within Bibionini. Therefore, eleven genera of Bibionidae are recognized in the generic revision; eight extant genera and three fossil genera. The three fossil genera, *Fushunoplecia* Hong, *Clothonopsis* Hong & Wang, and *Megeana* Meunier were not available for study and thus the status of these taxa and their placement within Bibionidae is unresolved. The extant genera are: *Hesperinus* Walker, *Penthetria* Meigen, *Plecia* Wiedemann, *Bibio* Geoffroy, *Bibiodes* Coquillett, *Bibionellus* Edwards, *Enicoscolus* Hardy, and *Dilophus* Meigen. Several new generic synonyms are proposed. The fossil genus *Bibiopsis* Heer is a junior synonym of *Penthetria*. The fossil genus *Epiplecia* Giard and the extant subgenera *Heteroplecia* Hardy and

Pleciodes Hardy are treated as junior synonyms of *Plecia*. The fossil genus *Lithosomyia* Carpenter is a junior synonym of *Bibio*, and the fossil genus *Bibiodites* Cockerell is a junior synonym of *Bibiodes*. Two genera previously included in the family Bibionidae are removed from the family. The fossil genus *Mesopleciella* Rohdendorf belongs in the extinct family Protopleciidae and the family placement of the fossil genus *Longicornia* could not be determined.

Results of the phylogenetic analysis also reveal several interesting aspects of the higher classification of Diptera. The restricted concept of Bibionomorpha (node 3: Sciaroidea + (Bibionidae + Pachyneuridae)) and a clade consistent with Wood & Borkent's (1989) Psychodomorpha (node 39) were both unambiguously supported. Consequently, the results did not support Neodiptera, as proposed by Michelsen (1996), because of the placement of Trichoceridae within the neodipteran clade. Furthermore, Axymyiidae was not supported as the most basal member of Bibionomorpha (Oosterbroek & Courtney 1995) or associated with the genus *Pachyneura* (Hennig 1973, Amorim 1992); rather, it is at the base of the tree with Tipulidae. Lastly, Sciaroidea is not supported as a monophyletic group; Ditomyiidae is in an unresolved polytomy with a clade including the remainder of Sciaroidea. This result may be due to inadequate sampling from this very diverse assemblage of flies and additional examination of the monophyly of this taxon is clearly needed.

This study is the most comprehensive and rigorous study of the family Bibionidae to date. It provides significant advances in our understanding of relationships within Bibionidae, and the phylogenetic relationship of bibionids to other nematoceran flies. Yet, history clearly indicates that no study is the final study; the addition of new information, characters, and exemplars continues to change the face of the topology we stare at. Considering this, the author humbly offers this study as a building block in our search for the one tree and our ultimate understanding of the phylogenetic relationships of flies.

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APPENDICES

APPENDIX I – ABBREVIATIONS USED IN FIGURES

a1	antennal article 1
a2	antennal article 2
Ab1	abdominal segment one (Ab2, Ab3, etc.)
acs	apical circlet of spines of fore tibia
ada	anteriorly directed apodemes of aedeagal plate
adat	apical, dorsal antennal tubercle
adm	adminiculum
ag	accessory gland
agd	accessory gland duct
al	anal lobe
amo	anteromedial ocellus
an	anterior notum
anepst	anepisternum
ap	aedeagal plate
apgl	apical point of galeolacinia
ar	adminicular rods
as	antennal sensillae
asf	anterolateral spine of frontoclypeus
asp	anterior spiracle
ata	anterior tentorial arm
avs	anteroventral stemmata
bp	basiphallus
bs	basisternum
bsl	basisternal lobe
cb	cibarial bar
cd	cardo
cd1-4	setae 1-4 of the cardo
cer	cercus
cs	coeloconical sensillae
cx	coxa
db	dorsal bridge
dc	dorsocervical(s)
dp	distiphallus
dps	dorsoposterior stemmata
dr	dorsal region of compound eye
ds	dorsal sclerite
e	endophallus (basiphallus + distiphallus)
ea	ejaculatory apodeme
ea(ad)	apical differentiation of ejaculatory apodeme
ea(s)	shaft of ejaculatory apodeme

eb	eye bridge
ec	epandrial cleft
ecs	ecdysial scar(s) of posterior spiracle
ed	ejaculatory duct
el	ecdysial lines
ep	epandrium
epip	epipharynx
epsl	episternal lobe
es	endoaedeagal spine
fem	femur
fr	furrow
ft	frontal tubercle
ga	gonocoxal apodemes
gf	genital fork
gl	galeolacinia
glos	glossa
gp	gonophyses
gs	gonostylus
gx	gonocoxite
gxs	gonocoxal socket
hb	hind basitarsus
hp	hypandrium
hs	hypopharyngeal sclerites
hyp	hypopharynx
if	intersegmental fissures
kepst	katepisternum
lbs	laterobasal sclerite of palpifer
lc	laterocervical
lea	lateral ejaculatory apodemes
le ea	lateral extensions of ejaculatory apodeme
lgl	laterobasal lobe of galeolacinia
llg	lateral lobe of gonocoxite
lp	labial palps
ls	labial synsclerite
ltg	laterotergite
M31	muscle 31 (*sensu* Ovtshinnikova 1994a)
M32	muscle 32 (*sensu* Ovtshinnikova 1994a)
ma	median apodeme of paramere
ma ea	median apodeme of ejaculatory apodeme
mand	mandible
mel	median epandrial lobe(s)
mes	mesothorax
met	metathorax

metsp	metathoracic spiracle
mla	membranous labial area
mls	median lobe of synsternogonocoxite
mp	maxillary palp
mpf	maxillary palpifer
ms	medial spines of fore tibia
mr	meron
mtkepst	metakatepisternum
nps	noto-pleural suture
oc	ocelli
pc	precervical
pcb	precoxal bridge
pel	primary epandrial lobes
pgb	post genal bridge
pl	paired lobes of synsternogonocoxite
plrs	pleural suture
pls	posterior labial sclerite
pm	posterior mentum
pn	posterior notum
post sp	posterior spiracle
pp	posterior processes of paramere
prepm	proepimeron
prepst	proepisternum
prm	prementum (labium)
pro	prothorax
ps	penis sac
pss	parapsidal sutures
pt	phallotrema
rs	radial suture
S10	sternite 10
sc	sensory cone
sd	salivary duct
sgp	subgenital plate
sgx	synsternogonocoxite
sp7	spiracle seven
sp8	spiracle eight
spm	spermatheca
sr1	sensory region 1
sr2	sensory region 2
T9	tergite 9
T10	tergite 10
ta	triangular area of compound eye
tar	tarsus

tib	tibia
tns	transnotal suture
to	tibial organ
tsp	tibial spine
tsr	tibial spur
tts	transverse thoracic spines
vla	ventrolateral apodeme of paramere
vps	ventral prothoracic sclerites
vr	ventral region of compound eye

APPENDIX II – REARING NOTES

Because numerous bibionid and outgroup larvae and pupae used in this study were previously unknown or are uncommon these notes detail the larval habitat, natural history, and specific rearing conditoins of individual taxa to aid future investigators. Rearing methods follow those described in the "METHODS" section unless otherwise discussed below.

Trichoceridae: *Trichocera tetonensis* Alexander: This species was reared from fruiting bodies of the fungus *Suillus* (prob. *caerulescens* (Boletaceae)). Larvae pupated in the soil and did not spin a cocoon. Pupal exuvia were typically found at the soil surface after adult emergence suggesting that pupae migrate to the surface before eclosion.

Axymyiidae: new species (Oregon, USA): Several unsuccessful attempts at rearing this species from the larval stage were made. However, all stages were collected from large, waterlogged, partially rotten (no bark), logs of Western Red Cedar (*Thuja plicata* Donn.). Logs were always partially submerged in small streams and thus far have only been found in "old growth" forest. Larvae were not in submerged parts of the log, but often occurred in the "splash zone." Adults were very difficult to locate in the field and were most easily attained by collecting pupa and keeping them in moist, cool, wood debris until adult emergence. Placing a malaise trap directly over logs and tying the lateral baffles of the trap low to the ground (much like an emergence trap) also yielded a few adults.

Pachyneuridae and Ditomyiidae: *Cramptonomyia spenceri* Alexander (Pachyneuridae) and *Symmerus coqulus* Garrett (Ditomyiidae): Larvae of both these taxa are found in the fallen, rotten sticks (ca. 4-11 inches in diameter) of Alder (*Alnus rubra* Bong.)(Vockeroth 1974 and D.M. Wood pers. comm.). Sticks were left intact, placed in a large aquarium with a screen lid, and partially covered with wet fallen leaves. The pupal exuvia of both species conspicuously project from the rotten wood after adult emergence. Larvae of *S. coqulus* were also found in rotten sticks of Water Birch (*Betula occidentalis* Hook).

Australosymmerus fuscinervis (Edwards) and *A.* (*Crionisca*) *aculeata* (Edwards) (Ditomyiidae): Although these species were not included in the analysis, the genus *Australosymmerus* is considered the most primitive Ditomyiidae (Blaschke-Berthold 1994), which in turn is considered by some to be the most primitive subgroup of Mycetophilidae *sensu lato* (e.g. Matile 1990, 1997). Therefore, larvae of this group were sought after and reared to broaden the context of the comparative morphological analysis when investigating larval structures of Sciaroidea. The immature stages of these taxa were previously unknown but were located by visiting the adult localities recorded by Colless (1970) and Monroe (1974). Larvae and pupae were found in fallen, slightly rotten branches (ca. 8-11 cm in diameter) of *Eucalyptus* sp. Larval skins are attached or adjacent to the posterior end of the pupa which makes larva/pupal association possible. Pupae were kept in wood debris in, 40 dram, snap-cap, plastic containers, until adult emergence. Larvae of both species were sometimes found together in a single log.

Bolitophilidae: *Bolitophila bucera* Shaw: This species was reared from an unidentified mushroom in dense Douglas fir forest. Larvae pupated in the soil and did not spin a cocoon. Pupae apparently migrate to the soil surface prior to eclosion (as observed in *Trichocera*) since exuvia were found protruding from the soil after adult eclosion.

Keroplatidae: *Keroplatus terminalis* Coq.: Larvae of this species were found spinning mucous webs on the ventral surface of the woody fruiting bodies of Polyporaceae (*Fomitopsis pinicola*) that were growing on fallen Douglas fir logs (*Pseudotsuga menziesii* (Mirbel)). Fruiting bodies were collected and placed in a ten gallon aquarium until adults emerged. Larvae were observed to spin cocoons on the ventral surface of the fruiting body or in cracks between fruiting bodies. Pupation and adult eclosion occurred within the cocoon.

Mycetophilidae: *Mycetophila favonica* Chandler: Larvae were reared from the fruiting bodies of *Suillus* (prob. *caerulescens* (Boletaceae)). Larvae pupated in the soil. After burrowing into the soil the larvae were observed to first create an oval "cell" in the soil which was then lined with silken threads drawn from the larval mouthparts. This silken lining eventually became the loosely woven cocoon in which the larvae pupated. The adult eclosed within the cocoon and remained there for some time before breaking through the cocoon wall and digging to the surface of the soil. The pupal exuvia and larval skin were then found within the silken subterranean cocoon. Some individuals of this species were reared individually by tearing off a small piece of the fruiting body which included only a single larva and placing it in a small snap-cap 40 dram plastic vial on a small amount of potting soil.

Anisopodidae: *Mycetobia divergens* Walker: Larvae of this species are associated with the oozing wounds of numerous kinds of trees (Teskey 1976). This species was easily reared on several occasions by transferring oozing sludge from wounds on the trunks of Elm (*Ulmus* sp.) into a jar. Pupation occurred directly in the media or on the sides of the rearing container.

Bibionidae: *Hesperinus brevifrons* Walker: Larvae of this species have been collected from rotten balsam poplar (*Populus balsamifera* L.) (D.M. Wood pers. comm. 1998). Larvae were also collected from a rotten stump which was probably *Populus angustifolia* James or *P. acuminata* Rydb. (David Leatherman, Colorado State Forest Service, pers. comm.). However, an attempt at rearing the larvae using the methods listed above for *Symmerus* and *Cramptonomyia* was unsuccsseful.

Bibiodes aestivus Melander: Although extensively hunted, the immature stages of *Bibiodes* remain unknown. However, on one occasion a single pupa of *B. aestivus* was found in the soil along the edge of a rock in very open dry country (sagebrush/grass). It was initially unknown whether or not the pupa represented *Bibiodes*. Therefore, it was placed in a 40 dram plastic vial to allow the adult to eclose, along with a small bit of soil and dead grass stems that it was among. Surprisingly, three adults of *Bibiodes aestivus* emerged (2 males and 1 female).

Because it seemed very unlikely that two pupae could have been overlooked in the very small amount of soil collected, the inside of the dead grass stems were examined and proved to be hollowed-out and containing frass. Therefore, it is possible that the larvae of this genus are boring into dead stems to avoid desiccation in the dry and sometimes sandy soils that are characteristic of the high-desert habitat with which they are associated. Unfortunately, the larval and pupal skins could not be found after adult emergence, possibly due to the large number of soil nematodes. Further observations of the adults confirmed that, like other Bibioninae, female *Bibiodes* dig a chamber in the soil with the fore tibial spine and lay a cluster of white, rod-shaped eggs. Although it is unknown whether or not the eggs that were laid in captivity were fertilized, they did not hatch and were mostly destroyed by soil nematodes.

APPENDIX III – CHARACTER STATE CHANGES BY NODE

The following list of character state changes is based on ACCTRAN optimization and lists changes by each node of the tree. Nodes are identified by number in figures 3 and 4, but the character changes listed below are based on the topology of the tree presented in figure 3. The following list of changes does not include character states for terminals since this information can be obtained in the data matrix provided in Appendix IV. The format for listing character state changes used here is: character number followed by a colon, followed by the first character state, followed by one or two arrows, followed by the second characters state. A single arrow (>) represents an ambiguous character state change and two arrows (>>) indicates an unambiguous change.

node 1) 24:0>>2, 31:0>2, 53:0>>1, 57:1>0, 79:1>>0, 93:0>2, 100:2>>1, 102:1>>0, 104:0>>1, 107:0>>1, 114:2>>0, 118:0>1, 132:0>1, 133:0>1, 135:1>0, 163:0>1, 167:0>1, 175:0>1, 195:0>1.

node 2) 15:1>>0, 16:0>1, 27:0>1, 48:0>1, 67:1>>0, 72:0>1, 103:0>2, 105:0>>1, 119:1>>0, 133:1>2.

node 3) 25:0>>1, 51:1>0, 82:1>>0, 98:0>1, 116:2>0, 131:1>>2, 157:0>>1, 180:0>1, 182:0>>1, 183:0>3, 184:0>1, 206:0>1, 211:0>1, 212:0>1.

node 4) 24:2>>1, 28:0>>1, 29:0>1, 56:1>>3, 73:1>>0, 108:0>>1, 110:0>1, 132:1>0, 140:0>>1, 142:0>>1, 148:0>>1, 151:0>1, 152:0>>1, 156:0>1, 165:1>>0, 166:0>>1, 172:0>>1, 177:0>>1, 179:0>1, 181:0>>1, 186:0>1, 194:0>1, 195:1>0, 205:0>>1.

node 5) 10:2>>5, 15:0>>1, 26:1>>0, 31:2>>1, 57:0>1, 67:0>>1, 68:0>>1, 79:0>>1, 98:1>0, 114:0>1, 115:1>2, 135:0>>1, 149:0>>1, 169:0>1, 170:0>>1, 171:0>>1, 175:1>>0, 211:1>0.

node 6) 1:0>>1, 3:0>>1, 11:0>>1, 14:0>>1, 29:1>0, 41:0>>1, 42:0>>1, 46:0>>1, 61:0>1, 80:0>1, 125:0>1, 132:0>1, 141:0>>1, 145:0>1, 150:0>>1, 153:0>>1, 158:0>>1, 169:1>2, 209:1>>0, 210:0>1.

node 7) 10:5>>7, 99:0>1, 110:1>0, 112:0>1, 114:1>0, 137:0>>1, 151:1>2, 160:1>>0, 164:0>>1, 167:1>>0, 168:0>>1.

node 8) 93:2>>1, 94:0>>1, 95:3>>0, 99:1>4, 113:0>>1, 116:0>>1, 122:0>2, 126:2>>0, 140:1>>0, 163:1>>0.

node 9) 21:0>>1, 72:1>0, 80:1>0, 82:0>>1, 87:0>>1, 99:4>5.

node 10) 41:1>>0, 42:1>>0, 72:0>1, 85:0>1, 207:0>1.

node 11) 46:1>>0, 90:0>>2, 91:0>>1, 122:2>>0.

node 12) 80:0>>1, 96:0>>2.

node 13) 19:1>2, 76:1>>0, 77:0>>1, 99:5>>3, 117:1>>0, 126:1>>0.

node 14) 83:0>>1, 84:0>>2, 85:1>0, 95:0>>2, 102:0>1.

node 15) 10:8>>7, 56:3>1, 85:1>0, 95:0>1, 109:0>>1.

node 16) 42:0>>1, 80:1>>0, 95:1>2.

node 17) 17:0>>2, 46:0>>2, 77:1>>0, 83:0>>1, 84:0>>2.

node 18) 19:2>>0, 87:1>>0, 91:1>>2, 92:0>>1, 96:2>>0, 97:0>>1, 99:3>6.

node 19) 71:1>>0.

node 20) 99:5>B, 109:0>>1.

node 21) 41:1>>0, 42:1>>0, 79:1>0.

node 22) 46:1>>2, 71:1>0, 80:1>B, 81:0>B, 82:0>B.

node 23) 4:0>>1, 16:1>>0, 27:1>>0, 28:1>>0, 30:1>>0, 31:1>0, 33:0>>1, 44:0>>1, 50:0>1, 53:1>>0, 56:3>>1, 58:0>>1, 60:0>>2, 61:1>0, 62:1>>0, 67:1>>0, 69:0>>1, 96:0>>1, 103:2>0, 104:1>>0, 105:1>0, 108:1>>0, 125:1>0, 145:1>0, 161:0>1, 165:0>1, 183:3>>0, 207:0>>1, 210:1>0.

node 24) 14:1>>0, 31:0>2, 36:0>>1, 103:0>1, 113:0>>2, 115:2>>1, 158:1>0.

node 25) 10:7>9, 18:1>0, 34:0>>1, 35:0>>1, 90:0>>2, 91:0>>1, 92:0>>2, 93:2>>1, 125:0>1, 126:2>1, 139:3>2.

node 26) 49:0>>1, 57:1>>0.

node 27) 5:0>>1, 10:7>>4, 22:0>>1, 24:1>>0, 37:0>>1, 40:0>>1, 46:1>>0, 79:1>>0, 80:1>J, 81:0>3, 82:0>J, 112:1>0, 151:2>1, 161:1>2.

node 28) 18:1>0, 81:3>J, 110:0>>1, 114:0>>1, 117:0>C.

node 29) 72:1>>0, 80:J>Q, 82:J>Q, 104:0>>2, 105:0>D, 124:0>>1.

node 30) 89:1>>0, 126:2>>1, 152:1>>2, 205:1>>0.

node 31) 29:0>1, 46:1>>2, 71:1>>0, 99:0>P, 207:0>1.

node 32) 12:0>>1, 13:1>0, 55:0>>1, 76:1>>0, 99:0>7, 122:0>2.

node 33) 102:0>>1, 104:1>>0, 105:1>>0, 108:1>>2, 119:0>>1, 131:2>>1.

node 34) 27: 1>0, 30:1>>0, 43:0>>1, 51:0>1, 52:0>1, 70:0>1, 80:0>F, 81:0>F, 82:0>F, 103:2>0, 136:0>>1, 143:0>>1, 164:0>>1, 173:1>>2, 187:0>>1.

node 35) 31:2>>0, 52:1>2, 54:0>>1, 55:0>>1, 59:0>>1, 64:0>>1, 88:1>>0, 89:1>>0, 96:0>>1, 105:1>0, 110:1>0, 112:0>>1, 113:0>>2, 121:0>>1, 122:0>>2, 144:0>1, 156:1>0, 194:1>0.

node 36) 45:0>>1, 57:0>1, 158:0>1, 159:0>>1, 160:1>B, 161:0>A, 162:0>A, 170:0>1, 183:3>2, 188:0>>1, 189:0>>1, 191:0>>1, 192:0>>1, 193:0>>1, 196:0>>1, 199:0>1, 207:1>2.

node 37) 24:2>>0, 27:1>0, 39:1>0, 53:1>0, 60:0>>2, 62:1>0, 68:0>>1, 74:0>>1, 86:0>1, 96:0>1, 103:2>0, 104:1>>2, 105:1>F, 169:0>>2, 179:0>1, 208:0>>1, 209:1>>0.

node 38) 17:1>0, 25:1>>0, 26:1>>0, 70:0>>1, 71:1>>0, 72:1>>0, 75:0>>1, 87:0>>1, 93:2>0, 105:F>G, 160:B>C, 161:A>B, 162:A>B.

node 39) 47:1>0, 71:1>>0, 81:0>5, 88:1>0, 96:0>2, 103:2>3, 104:1>>2, 117:0>G, 118:1>0, 120:1>>0, 127:1>>0, 137:0>>1, 147:0>>1, 160:1>2, 174:0>1, 179:0>2, 188:0>>1, 189:0>>1, 190:0>1, 197:0>>1, 198:0>>1, 200:0>>1, 201:0>>1, 203:0>>1, 204:0>1, 207:0>>3.

node 40) 1:0>2, 2:0>1, 11:0>1, 27:1>0, 45:0>>1, 53:1>>0, 57:0>1, 68:0>>1, 72:1>0, 74:0>1, 75:0>>1, 80:0>3, 93:2>>0, 96:2>3, 108:0>1, 128:1>>2, 129:1>>0, 131:1>0, 134:1>>0, 136:0>2, 139:3>>1, 167:1>0, 168:0>>1, 177:0>>1, 183:0>2.

node 41) 24:2>>1, 28:0>>1, 52:0>2, 67:0>>1, 88:0>1, 153:0>>2, 162:0>>1, 169:0>>3, 202:1>>0.

node 42) 1:2>0, 2:1>0, 11:1>0, 14:0>1, 39:0>>1, 47:0>1, 55:0>>1, 56:1>>3, 59:0>1, 64:0>1, 65:0>>1, 66:0>>1, 73:1>>0, 74:1>0, 82:1>5, 103:3>2, 128:2>>3, 130:1>>0, 131:0>2, 179:2>0, 185:0>1.

node 43) 10:2>7, 16:1>0, 26:1>>0, 38:1>>0, 46:0>>1, 49:0>>1, 50:0>>1, 51:1>>0, 55:0>>2, 58:0>>1, 60:0>>2, 62:1>>0, 76:1>0, 80:3>N, 81:5>P, 82:1>N, 101:0>>1, 103:3>0, 105:1>A, 106:1>0, 107:1>A, 108:1>D, 109:0>D, 110:0>D, 111:0>D, 114:0>2, 115:1>E, 117:G>K, 119:0>>1, 132:1>0, 133:2>1, 142:0>1, 149:0>1, 157:0>1, 158:0>1, 160:2>1, 165:1>0, 166:0>3, 173:1>0, 174:1>0, 175:1>0, 180:0>D, 209:1>0.

node 44) 1:0>1, 3:0>>1, 4:0>>1, 5:0>>1, 9:0>>1, 11:0>1, 16:0>1, 20:0>>1, 31:0>1, 38:1>>0, 48:0>1, 56:1>>2, 62:1>>0, 75:0>>2, 78:0>>1, 87:0>1, 92:0>>2, 94:0>>1, 95:3>>1, 96:0>2, 108:0>B, 109:0>B, 110:0>B, 111:0>B, 112:0>>1, 113:0>>5, 115:1>A, 116:2>>0, 123:1>>0, 138:0>>1, 139:3>>2, 146:1>>0, 154:1>>0, 160:1>>3, 164:0>>2, 169:0>>3, 170:0>>2, 178:0>>1, 179:0>2, 180:0>A, 183:0>2, 190:0>1, 199:0>>2, 204:0>1.

APPENDIX IV – DATA MATRIX

Polymorphic characters scored as "0&1" are indicated below by an astrix (*) and those scored as "1&2" are indicated by a number sign (#). Characters states begin at the top left with character 1 and end at the bottom right with character 212; characters are organized into blocks of 10 to facilitate locating specific characters.

Ctenophora angustipennis
000000AA04 000110*120 0000000001 0000000100 ?000000000 1100011013
0101001003 0100010011 1100000110 00103010?2 0100000AAA A002C2A011
1210020001 0000101030 0000010000 0031000001 0000120000 0000000000
0001010000 0000000000 0100100010 10

Plecia lusca
100000BB08 1011110010 10??101101 1000000100 0000001100 0010011000
1110001100 ??0001000A AA12001111 10112000A1 0121111110 0110211101
0010111111 21210010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia nearctica
1010010008 1011100020 1011101101 1000000100 1100011100 0010031000
0110001100 1100010010 0111021111 10103000B1 0121111110 1110211101
0010111111 2121101030 1100110111 2111111100 0001010121 1110011011
1131010000 0001000000 0100110001 01

Plecia americana
1010010008 1011110010 10??101101 1000000100 1100011100 0010031000
1110001100 1000010010 0000001110 00110000C1 0021111110 0110211101
0210101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia plagiata
1010010007 1011111120 1011101101 1000000100 1100011100 0010031000
1110001100 1000010010 0100021110 00112000D1 0021111100 0110210101
0210101111 21211010?? 1100010111 2111111100 0001010121 1100011011
1131010000 0001000000 0100010001 01

Plecia bicolor
1010010008 1011100020 10??101101 1000000100 1100011100 0010031000
1110001100 1000010010 0111100111 10103000E1 0021111110 1110211101
0210111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia ephippium
1010010007 1011110010 10??101101 1000000100 0000011100 0010031000
2110001100 1100010010 0100101110 00103000F1 0021111100 0110211101
0210111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia zernyi
1010010008 1011111120 10??101101 1000000100 0000001100 0010031000
0110001100 1100001011 0100101112 1011020031 0021111100 0120210101
0010101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia freemani
1?10?10007 101?112?20 10??101101 1000000100 0100021100 0010011000
1110001100 1100000010 0112001112 1011220031 0021111110 0110210101
0010101111 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia sinensis
1010010008 1011110010 10??101101 1000000100 0000001100 0010031000
1110001100 0100010011 0100?11112 1011020051 0021111100 0110211101
0010111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia zamboanga
1010010008 1011110000 10??101101 1000000100 0000001100 0010011000
0110001100 0100010011 0100101111 11110200G1 0121111100 0110211101
0010111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia amplipennis
1010010007 1011110000 10??101101 1000000100 0000001100 0010031000
#110001100 0100001011 0110100112 21103010H1 0121111110 0110210111
0010101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia dimidiata
1010010009 1011102?20 10??101101 1000000100 1100021100 0010031000
0110001000 1000010010 0100020111 11103000J1 0021111110 0110211101
0210111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia aruensis
1010010008 1011110000 10??101101 1000000100 0000001100 0010031000
1110001100 0100010011 010010011? ?0103200K1 0121111120 0110210101
0210111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia erebea
1010010008 1011101120 00??101101 1000000100 0000021100 0010031000
0110001100 ??0001000B BB00000111 10110000L1 0021111110 0140210101
0210101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia robusta
1?00?10008 101?111?20 10??101101 1000000100 1100001100 0010011000
1110001100 1100010011 01??001110 00110000M1 0021111110 0110210111
0210101111 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia paenerubescens
1?10?10007 101?112?20 10??101101 1000000100 0100021100 0010011000
1110001100 1100000010 0112000112 1011220031 0021111100 0110210101
0210101111 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia yabaensis
1?10?10007 101?110?20 10??101101 1000000100 1100001100 0010011000
1110001100 *1000001010* 1100001112 1011220031 0021111110 0110210101
0010101111 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia hadrosoma
1010010007 1011111120 00??101101 1000000100 0000011100 0010031000
1110001100 110001000C CC13000110 0011000041 0021111100 0120210101
0010101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia nagatomii
1010010008 1011111?20 10??101101 1000000100 0000001100 0010011000
1110001000 0000000010 0111001110 00110000N1 0021111100 0110211111
0210101111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia imposter
1010010008 1011112220 10??101101 1000000100 0000001100 0010031000
1110001100 1100010010 0112001112 1111200051 0221111100 0110211101
0010111111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Plecia mallochi
1000010007 1011110000 1011101101 1000000100 0000001100 0010011000
1110001110 1100011011 0100000112 2101101061 0021111110 0110110101
0110101111 2121101030 1100110111 2111111100 0001010121 1110011011
1131010000 0??10?0000 0100111??? ??

Plecia thulinigra
1010010007 1011111120 00??1?1111 1000000100 ??0?0?1100 0010031000
1110001110 ?100010011 0013001110 0011000041 0021011100 0120210100
0010101111 2121101030 1100110111 2111111100 0001010121 1110011011
1131010000 0??10?0000 0100110??? ??

Plecia nr. *quatei*
1010010007 1011111?20 00??101101 1000000100 0000021100 0010031000
1110001100 010001000D DD?2020110 0011000041 0021111100 0110210101
0?10101111 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Penthetria japonica
1010010005 1011112220 00??101111 1000000100 1100021100 0010021000
1110001100 000001000E EE00000100 00203000P1 0011111101 0001?00101
0010111111 21211000?? 1100110111 1211111101 0010011021 1110011011
1131010000 0001000000 0100011001 01

Penthetria nigrita
1010010005 1011111120 00??101111 1000000100 1100021100 0010031000
1110001100 0100010011 0000000100 00203000Q1 0021111201 0001?00101
0010111111 21211000?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Penthetria funebris
1010110006 1011111120 0011101101 1000000100 1100011100 0010031000
1110001010 1100000011 1100000100 0020300001 0021111101 0001?0J101
0010111111 2121100031 1100110111 1211111101 0010011021 1110011011
1131010000 0001000000 0100010001 01

Bibio albipennis
101*010008 1010101120 0011100000 2010010100 1101011101 0000011102
?010000110 1100010010 0100000110 0020310011 0110111000 0120100100
0010021111 2121101031 1100010111 2111111000 1011110121 1110011011
1101010000 0001000000 0100111000 01

Bibio niggerrimus
1011110008 1011101120 00??100000 0010010100 1101021101 0000011102
?010000110 1100010011 0100000110 0020310011 0010111000 0120100100
0010021111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Bibiodes aestivus
1011010007 1010101120 00??100000 2010010100 1101011101 0000000102
?010000100 1100010010 0000000110 0020310091 0010011000 0120100101
0110021111 2121101031 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Bibionellus barettoi
1011010009 1010100020 00??100000 2011110100 1101011101 0000011102
0010000110 1100010011 0000000112 1210310021 0010011000 0120100101
0110111111 2121101021 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Bibionellus sp.
1?11?1000A 10??101?20 00??100000 0011110100 1101011101 0000011102
?010000110 1100010011 0100000112 1210310021 0000011000 0120100???
???????1?? 212110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Enicoscollus dolichocephalus
?0??11000? ???010?0?0 00??100000 2010010100 ??0?0?1111 0000010102
?0100001?? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ??????1031 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Enicoscollus brachycephalus
?0??11000? ???010?1?0 001?100000 2010010100 ??0?0?1111 0000010102
?0100001?? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ??????103? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Dilophus serotinus
1011110006 1011101020 0110100000 0010001101 1101001101 0000011102
?010000110 110001000J JJ00000110 00203100?1 0120011001 000120C101
0010021111 2121101031 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Dilophus nigrostigma
1011110004 1011101220 01??100000 0010001101 1101021100 0000011102
?010000110 110001000K KK00000100 00203100?1 0000011001 0001?2E101
0110021111 21211010?? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Dilophus sayi
1011110005 1011101120 0110100000 0010001101 1001001100 0000011102
?010000110 100000000Q RQ00000110 00203100?1 0002D11000 0000200110
0111021111 2121101031 1100010111 1111111100 2011010121 1110011011
1101010000 0001000000 0100111000 01

Dilophus febrilis
1011110004 1010101120 0110100000 0010001101 1100001101 0000011102
?010000110 100001000R 3R00000110 00203100?1 0002E11000 0000120101
0011021111 2121101031 1100010111 1111111100 2011110121 1110011011
1101010000 0001000000 0100111000 01

Hesperinus brevifrons
0000010005 0100111120 0011101111 1000000100 0000001100 0010131000
0110001100 1100000010 0011020110 00203000R1 0120011201 0001200111
0210021111 1021100031 0100010110 1101111001 0010011011 1110011011
1131010000 0001000000 0100110010 01

Hesperinus nigratus
0000010005 0100111120 00??1?1111 1000000100 0000001100 0010131000
0110001100 1100000011 0100100110 0010300071 0120011201 0001200110
0010021111 1021100003? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Hesperinus cuspidistilus
0?00?10005 01??111?20 0011101111 1000000100 0000001100 0010131000
0110001100 1100000010 0000000110 0020300081 0021111101 0001200101
0210021111 202110???? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Cramptonomyia spenceri
0000010002 0000011120 0011110110 0000000100 0010001100 1211130010
0111010001 110001000F FF00021000 0020310101 0001?11100 0120100101
1210021111 2021010031 0111010100 1101101001 0011011000 0120111011
11310?1000 0000000000 0100110010 11

Haruka elegans
0000010003 1010011120 00??110110 0000000100 0110001100 1211130010
01110001?0 110001000H HH00000000 0020310101 0101011100 0122G2B101
1210021111 2021010?1 ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ????????10 1?

Pachyneura fasciata
0000011001 0010011120 0011110110 2000000100 0010001100 1100030000
0110000001 110001000G GG00000110 0020300101 0001111101 0000100011
0000?11111 2021010031 0110010100 0101111001 0011011000 *120111011
11110?1000 0001000000 0100110?10 11

Symmerus coqulus
2100011101 0011000130 0012101001 0100000110 0010000101 0010010000
0110010002 0110100010 0000000110 00003201?1 0321111000 000012F100
0010021111 2121020020 0000010000 0001101001 0002101000 1010110000
0131000000 0000101000 0100001010 10

Rhynchosciara americana
2100011102 00110?1120 0010110100 0100000100 0000101101 0000031002
?010000100 1111000002 4400010110 0020310101 0002F11000 0000100101
0010021111 2121020020 0000010000 000110101B AA12101021 0010110011
0121000110 1110110000 0100012100 11

Keroplatus terminalis
0000011102 1011000030 001000000? 2100000100 0000101100 001000000?
0110000101 0011100010 0000111?0 00103101?1 0032G11000 0000100111
0010021111 212102102? 0000010000 0041000B1C BB02101021 0010110011
0121000110 1110110010 0100012100 11

Bolitophila bucera
0000011002 0001011120 0012111001 2100000110 0000101100 0010111000
1110000000 1100000004 6600000110 00203001?1 0021111101 0120200101
0010001211 0111000020 0000010001 000110111D CC10101102 0000010001
01210?0110 1110110010 00?1012010 11

Mycetophila favonica
000001?202 001000?120 0010001221 2100000110 0010100101 0000011002
0010000101 001110000? 2300001??0 00003211?1 0002K11111 011??2Q101
0110021111 212100002? 0000010000 000110111E DD11141021 000011001?
01210?0110 1110110010 01?0012100 11

Axymyiidae n. sp.
1011110012 1010111131 001001000? 1000000000 0000001100 1100021000
?010001100 101021011? 0100001110 0201120002 0100010BBB B152A00011
0000021111 1001100120 0000000000 0000100003 0002120032 001001012A
0020000001 0000000020 0001000010 00

Axymyia furcata
1011110012 1010111121 001001000? 1000000000 0000011100 1100021000
?010001001 101020011? 0100001110 0201120002 0100010CCC C152B00000
0000021111 1001100121 0000000000 0000100003 0002100032 001001012B
00200?0?01 0000000020 0101000010 00

Sylvicola cinctus
0000010012 0011011140 0011010101 2000000110 0000101100 1200131010
0111111100 000011000L LL00000110 00003300?1 0021111100 000012G000
0010020300 2120021010 ????????? ????????? ????????? ?????????
????????? ????????? ????????? ??

Sylvicola fenestralis
0000010002 001?011120 00??010101 2000000110 0000101100 1200131010
0111111100 00001AAAB3 55CAAAA110 00003300?1 0022H11100 000012N000
0010020300 2120021010 0000011000 0021100002 0110100130 0011111000
00201?0111 0000101101 1011003010 00

Mycetobia divergens
2100010002 1010011120 0011111111 1000000100 0000100100 1200011003
0110001100 00111?011? N100011110 00103300?1 0432C11100 000?D2L100
001?021201 0??0021020 0000011000 0021100002 0110100130 001111102C
00200?0111 0000101101 1011003010 00

Scatopse notata
2100010007 1010001120 0012000001 2000000000 0000110111 0000211102
?010000100 002220002N PN000#?010 0000330001 1002A0ADDD D002E2K010
0110020201 0010021010 0100011010 0001101101 0010030100 000001102D
00200?0111 0000101101 1111003000 00

Arthria analis
210001100A 1010001120 0010000000 ?011010000 0000111111 0000201102
?010000110 10111?000P QP00000??0 0001130001 1002B2BEEE EAAAF2M010
001?020401 101?00101? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??

Trichocera tetonensis
0000011000 0010011120 0002011001 2000000100 0000000000 1110010010
1101000000 0110010000 7700000000 00203200?0 A032J11000 012022P000
0010020111 1?01001030 0000011100 1211100002 0011101000 101111002E
0000100111 0000101101 1111003010 00

Dialysis dispar
100001000B 1010101120 0012010001 2000000200 1100001000 1210030010
2111101001 101010000M MM00001110 0020310001 0001011000 000022H111
0211021111 1111*0003? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??