ABSTRACT

Title of Dissertation: REVISION OF THE GENERA OF THE RHAGIONIDAE OF THE WORLD (DIPTERA: BRACHYCERA)

Peter H. Kerr, Doctor of Philosophy, 2004

Dissertation Directed by: Charles Mitter

Norman E. Woodley

As a group, flies represent one of the most prolific and important elements of our natural world. The order Diptera comprises approximately 150,000 species in approximately 142 families. My research focuses on the Rhagionidae (formerly known as the Leptidae), a family of flies considered to contain some of the most primitive living members of the dipteran suborder Brachycera and believed to have diversified as early as 170 million years ago. The taxonomic classification of the Rhagionidae has been unstable for decades because there are few morphological characters that can be used to support hypotheses of relationship among its members. Much of the morphology in this group, however, has not been examined systematically.

An independent estimate of phylogeny for the group is carried out and presented here, based on 208 morphological characters for 43 ingroup species and molecular characters consisting of 3200+ bp sequences of 28S rDNA of 34 ingroup species. The goal of this work is to better understand how the genera of the Rhagionidae relate to one another and to their kin within the infraorder Tabanomorpha. Ultimately, this knowledge is fundamental for developing a stable classification system for the group.

The Rhagionidae are recognized as a monophyletic group containing four subfamilies containing a total of 17 extant genera. The subfamily Spaniinae is defined by a special modification of tergite 9 of the female genitalia, which is shared by members of *Omphalophora*, *Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*. *Omphalophora* Becker is resurrected from synonymy with *Ptiolina*. Spaniinae is defined by having scale-like thoracic hairs, as in *Chrysopilus*, *Schizella* and *Stylospania*. Arthroceratinae contains a single enigmatic genus, *Arthroceras*. Most females belonging to these three subfamilies have spermathecal duct accessory glands. These structures are reported here for the first time and are unique in Tabanomorpha. The Rhagioninae is the most primitive subfamily of the Rhagionidae. The saw sclerite in the larval mandible may be synapomorphic for this subfamily. Members of Rhagioninae include *Atherimorpha*, *Desmomyia*, *Rhagio*, and *Sierramyia* **gen nov**. *Rhagina* Malloch is recognized as a junior synonym of *Rhagio*. The Bolbomyiidae are recognized at the family level for the first time. *Alloleptis tersus* is *incertae sedis* within Tabanomorpha.

Two new species are described: *Schizella woodleyi* (from Luzón, Philippines) and *Sierramyia chiapasensis* (from Chiapas, Mexico). A key is given to the genera of the Rhagionidae with dichotomies leading to all families of Tabanomorpha. Genera of Austroleptidae, Bolbomyiidae, and Rhagionidae are diagnosed and described, with a list of included species for each genus.

REVISION OF THE GENERA OF THE RHAGIONIDAE OF THE WORLD (DIPTERA: BRACHYCERA)

by

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Dissertation submitted to the Faculty of the Graduate School of the University of Maryland, College Park in partial fulfillment of the requirements for the degree of Doctor of Philosophy 2004

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This dissertation should not be considered a scientific publication for the purposes of zoological nomenclature.

In honor of Cynthia Virginia Kerr Gould,

my loving grandmother,

who taught me to appreciate a fascinating world.

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Chapter 1. General Introduction to the Genera of the Rhagionidae and Related Taxa.

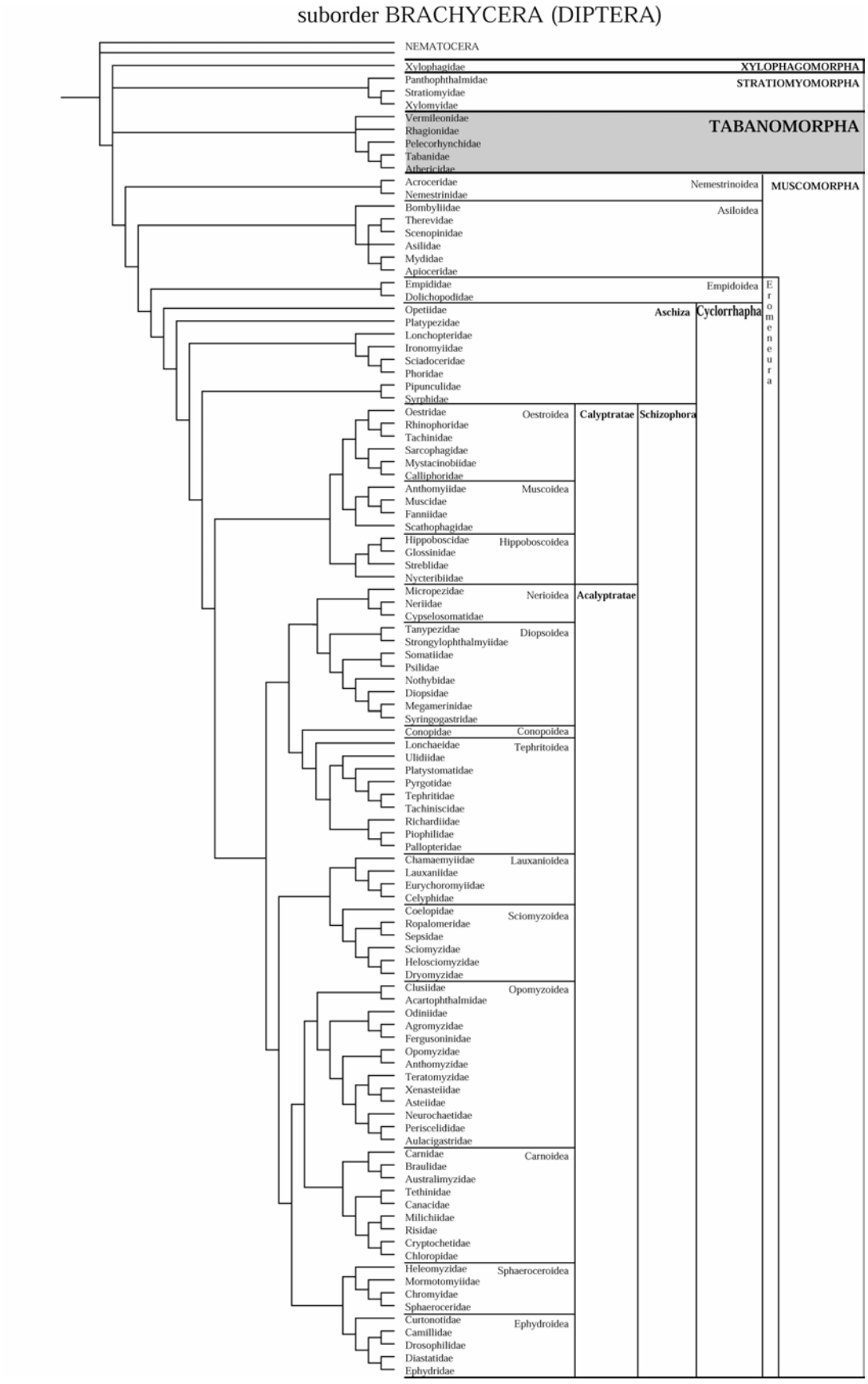
Overview

The order Diptera comprises approximately 128,000 species in approximately 142 families (Brown, 2001). As a group, flies represent one of the most prolific and important elements of our natural world (Skevington and Dange, 2002). Through their history, they have evolved a fantastic array of divergent forms that have allowed them to fill diverse ecological roles. As pollinators, scavengers, parasites, disease vectors, insect predators and a source of food to many other organisms, flies are an integral, essential part of virtually every ecosystem in the world (Vockeroth, 2002). Secondary to the origin of the halter and the structural flight mechanisms that define the Diptera as a monophyletic order, the innovations of larval mandible and adult antennal morphologies arose in the Late Triassic and spurred the biological radiation of flies that are now classed in the suborder Brachycera and represent most of the dipteran diversity in the world today (Rohdendorf, 1991; Krzeminski, 1992; Krzeminski, 1998; Yeates and Lambkin, 1998; Yeates and Wiegmann, 1999; Mostovski and Jarzembowski, 2000; Wiegmann et al., 2003).

Very little of the origin of the Brachycera is known. The sister taxon is uncertain and the arrangement of the basal branches of its phylogenetic tree is mostly speculative (Hennig, 1968; Hennig, 1973; Rohdendorf, 1974; Wood and Borkent, 1989; Rohdendorf, 1991; Oosterbroek and Courtney, 1995; Amorim and Silva, 2002). My research focuses on the Rhagionidae (formerly known as the Leptidae), an extant

family of flies considered to contain some of the most primitive living members of the Brachycera and for this reason, receives much attention by those interested in higher level Dipteran systematics (e.g., Hennig, 1967; Hennig, 1973; Nagatomi, 1977; Kovalev, 1982; Woodley, 1989; Griffiths, 1994; Friedrich and Tautz, 1997; Grimaldi and Cumming, 1999; Wiegmann et al., 2000; Yeates, 2002). The family lacks any synapomorphies to join its members, however, and the phylogenetic relationships of the genera have not been examined in a systematic phylogenetic framework (Felsenstein, 2004). Understanding the phylogeny of the genera of Rhagionidae will provide stability to the classification of this family and may provide insights into the early evolution of Brachycera.

Figure 1. Brachycerous Diptera tree of life (adapted from Yeates and Wiegmann, 1999). Rhagionidae are located within Tabanomorpha, at the base of the tree.


suborder BRACHYCERA (DIPTERA)
NEMATOCERA
Xylophagidae
XYLOPHAGOMORPHA
Panthophthalmidae
Stratiomyidae
Xylomyidae
STRATIOMYOMORPHA
Vermileonidae
Rhagionidae
Pelecorhynchidae
Tabanidae
Athericidae
TABANOMORPHA
Acroceridae
Nemestrinidae
Nemestrinoidea
MUSCOMORPHA
Bombyliidae
Therevidae
Scenopinidae
Asilidae
Mydidae
Apioceridae
Asiloidea
Empididae
Dolichopodidae
Empidoidea
Eremoneura
Opetiidae
Platypezidae
Lonchopteridae
Ironomyiidae
Sciadoceridae
Phoridae
Pipunculidae
Syrphidae
Aschiza
Cyclorrhapha
Oestridae
Rhinophoridae
Tachinidae
Sarcophagidae
Mystacinobiidae
Calliphoridae
Oestroidea
Calyptratae
Schizophora
Anthomyiidae
Muscidae
Fanniidae
Scathophagidae
Muscoidea
Hippoboscidae
Glossinidae
Streblidae
Nycteribiidae
Hippoboscoidea
Micropezidae
Neriidae
Cypselosomatidae
Nerioidea
Acalyptratae
Tanypezidae
Strongylophthalmyiidae
Somatiidae
Psilidae
Nothybidae
Diopsidae
Megamerinidae
Syringogastridae
Diopsoidea
Conopidae
Conopoidea
Lonchaeidae
Ulidiidae
Platystomatidae
Pyrgotidae
Tephritidae
Tachiniscidae
Richardiidae
Piophilidae
Pallopteridae
Tephritoidea
Chamaemyiidae
Lauxaniidae
Eurychoromyiidae
Celyphidae
Lauxanioidea
Coelopidae
Ropalomeridae
Sepsidae
Sciomyzidae
Helosciomyzidae
Dryomyzidae
Sciomyzoidea
Clusiidae
Acartophthalmidae
Odiniidae
Agromyzidae
Fergusoninidae
Opomyzidae
Anthomyzidae
Teratomyzidae
Xenasteiidae
Asteiidae
Neurochaetidae
Periscelididae
Aulacigastridae
Opomyzoidea
Carnidae
Braulidae
Australimyzidae
Tethinidae
Canacidae
Milichiidae
Risidae
Cryptochetidae
Chloropidae
Carnoidea
Heleomyzidae
Mormotomyiidae
Chromyidae
Sphaeroceridae
Sphaeroceroidea
Curtonotidae
Camillidae
Drosophilidae
Diastatidae
Ephydridae
Ephydroidea

Recent Classification

Rhagionidae belong to the infraorder Tabanomorpha that currently includes from three to seven other families. The limits of Tabanomorpha are not entirely resolved, but all agree that in addition to Rhagionidae, the Tabanomorpha contain the following taxa (as family or subfamily lineages): Athericidae, Pelecorhynchidae, Spaniidae, and Tabanidae. *Bolbomyia* Loew may represent an additional family (Sinclair et al., 1993), although this has not been formally proposed. These taxa are what I will call the 'core tabanomorph taxa.' *Austroleptis* may also be included here, but for now will not, since there is speculation that it may belong in the Xylophagomorpha (Sinclair et al., 1993). Most of the genera that make up the core tabanomorphs, aside from Tabanidae, were originally placed in the Rhagionidae. Characters that have been used to unite the Tabanomorpha are the apomorphic presence of a brush on the larval mandible, larval head retractile, adult with convex bulbous clypeus, and ventrolaterally expanded first segment of the cercus in adult females (Woodley, 1989; Sinclair, 1992; Wiegmann et al., 2000). It has been suggested that the Acroceridae and Nemestrinidae (Nemestrinoidea) may also belong within the Tabanomorpha (Nagatomi, 1992; Griffiths, 1994; Stuckenberg, 2001), however no systematic study has supported this notion. Molecular evidence supports Tabanomorpha exclusive of the Nemestrinoidea (Wiegmann et al., 2000; Wiegmann et al., 2003), as does a recent synthetic morphological study by Yeates (2002). The Xylophagomorpha (Xylophagidae) have been shown to be sister to the Tabanomorpha, with weak support (Wiegmann et al., 2000), and some authors prefer to combine these taxa at a higher level, maintaining the name Tabanomorpha in a more inclusive sense

(Griffiths, 1994; Stuckenberg, 2001). Since so many of the non-tabanid tabanomorph taxa were once placed in the Rhagionidae, and in many cases, their taxonomy continues to affect the placement of rhagionid genera, a brief note on the taxonomy of each of these groups is presented.

In 1973, Stuckenberg created Athericidae, showing that *Atherix* and its allies were more closely related to Tabanidae than to the remaining members of Rhagionidae, where these genera were originally placed. The sister group relationship between the genera of Athericidae and Tabanidae is now clear, based on strong morphological and molecular evidence (Stuckenberg, 1973; Woodley, 1989; Sinclair, 1992; Sinclair et al., 1993; Wiegmann et al., 2000; Stuckenberg, 2001; Wiegmann et al., 2003).

Hardy originally described *Austroleptis* as a leptid (=Rhagionidae) (Hardy, 1920a). However, in 1953, it was placed in the Xylophagidae (Steyskal, 1953) and more recently, others have speculated that it belongs within the Xylophagomorpha on account of its larvae having been reared from wood, as is the case for most Xylophagidae (Colless and McAlpine, 1991; Sinclair et al., 1993). Nagatomi (1982a; 1991) considered *Austroleptis* a basal taxon of the Rhagionidae and erected the subfamily Austroleptinae to account for it, although he did not rule out the idea that it may represent a lineage outside of Rhagionidae. In 2001, Stuckenberg elevated Austroleptinae to family level, however could not provide evidence to support, nor did he provide speculation, as to the sister group of this lineage or its relationship to other lower Brachyceran families.

Bolbomyia Loew was originally described as a xylophagid, from specimens preserved in amber (Loew, 1850). Chillcott (1961) located this genus within the Rhagionidae, but James (1965) preferred its original placement in the Xylophagidae. In 1982, *Bolbomyia* was treated by Nagatomi (1982a) as a rhagionid however its placement has since been questioned. Sinclair et al. (1993) concluded that *Bolbomyia* may be more closely related to Athericidae and Tabanidae than to the rest of the rhagionid genera, based on the shared presence of the aedeagal tine in the male genitalia. Stuckenberg (2001) rejected this argument, however, and retained *Bolbomyia* within the Rhagionidae, placing it within its own subfamily, the Bolbomyiinae.

Macquart established the genus *Pelecorhynchus* in 1850, for an Australian species, *P. maculipennis* Macquart. This species is a synonym of *P. personatus* (Walker) that was originally described as a member of the genus *Silvius* Meigen (Tabanidae). *Pelecorhynchus* species were placed in Tabanidae, within their own subfamily created by Enderlein in 1922, the Pelecorhynchinae. *Pelecorhynchus* remained in the Tabanidae until 1942 when Mackerras and Fuller created the family Pelecorhynchidae. Steyskal (1953) considered *Pelecorhynchus* closely related to *Coenomyia* and placed these genera together in the Coenomyiidae (now Xylophagidae), along with *Arthroteles* (Rhagionidae) and *Stratioleptis* (=*Odontosabula*, Xylophagidae). Although this may appear as a major departure from previous classification, the coenomyiid lineage at that time was still considered a close relative of the Tabanidae (Steyskal, 1953; Hardy, 1955). In 1970, Teskey

removed *Glutops* from the Xylophagidae (Coenomyiidae *sensu* Steyskal) to the Pelecorhynchidae (*sensu* Mackerras & Fuller, 1942) on account of similarities of larval morphology between *Pelecorhynchus* and *Glutops*. Krivosheina (1971), however, erected the family Glutopidae to accommodate *Glutops*. Kovalev (1981) synonymized Glutopidae with Rhagionidae, however, and Nagatomi (1982) recognized the Glutopinae, placing *Pseudoerrina* with *Glutops*, as a subfamily of the Rhagionidae. Pelecorhynchidae remained a family represented by the single genus, *Pelecorhynchus*, according to Nagatomi (1982). Stuckenberg, however, recognized all three genera as members of the Pelecorhynchinae, a subfamily of the Rhagionidae (2001). Molecular evidence supports Teskey's assertion that *Glutops* and *Pelecorhynchus* form a monophyletic group (Wiegmann et al., 2000; Wiegmann et al., 2003). Furthermore, the molecular evidence suggests that the Pelecorhynchidae are sister to the Athericidae and Tabanidae lineage (Wiegmann et al., 2000; Wiegmann et al., 2003). Larval morphology also putatively supports this placement (Woodley, 1989; Sinclair, 1992; although see Stuckenberg, 2001). There have not been any adult morphological synapomorphies proposed to support the monophyly of *Glutops*, *Pelecorhynchus*, and *Pseudoerrina*. The larva for *Pseudoerrina* is not known.

The origins of the Spaniidae begin with Frey, who in 1954 established the subfamily Spaniinae for *Bolbomyia* Loew (as *Cechenia* Frey), *Spania* Meigen, *Ptiolina* Zetterstedt and *Omphalophora* Becker on the basis of having a bare laterotergite and short stylate antennae (Frey, 1954). At the time, these were distinguished as the

smallest rhagionids known. Nagatomi (1982) removed *Bolbomyia* to the Rhagioninae and considered the structure of the female terminalia as the most important source of characters to define the subfamily Spaniinae. Nagatomi asserted that a wide amount of separation between female first cerci, the lack of a ventral process on the basal cercus of the female, and tergite 10 short or absent were distinguishing characters for the Spaniinae. On the basis of these features and an antenna with a tapering, stylate first flagellomere, Nagatomi added *Spaniopsis* to the subfamily. He also added *Litoleptis*, but since he did not have a *Litoleptis* female available for examination, this placement was presumably based on a single antennal character. There is some degree of homoplasy among all of these characters, however, and Stuckenberg (2001) specifically questioned the usefulness of the female postabdomen for phylogenetic inquiry. Nonetheless, Stuckenberg (2001) raised Spaniinae to family rank without any changes from the arrangement proposed by Nagatomi (1982). No unambiguous synapomorphies for the group have been recognized.

The taxa that comprise the family Vermileonidae were also originally placed in the Rhagionidae, and later recognized as a separate subfamily (Williston, 1886; Hennig, 1967; Hennig, 1973). In 1977, Nagatomi (1977) raised this group to family rank and speculated that the family was either basal to the tabanomorph families (Pelecorhynchidae, Rhagionidae, Athericidae, and Tabanidae) or basal to the entire lower Brachycera. Nagatomi preferred the latter arrangement, judging the vermileonid lineage to be very old, however he did not use explicit methods to make this determination and conceded that the phylogenetic placement of this family

grouping remained unclear (Nagatomi, 1977). Teskey (1981c) regarded the family as being related to the Asiloidea, based on characters of the male terminalia and larval mouthparts. This placement was rejected by Woodley (1989), however, who tentatively placed the family within Tabanomorpha, *incertae sedis* based on the retractile head of the vermileonid larva. Griffiths (1994) proposed a new infraorder, Vermileonomorpha, to account for the family. Molecular evidence presented by Wiegmann et al. (2000) locates the Vermileonidae as sister to the genera of the Rhagionidae, within the Tabanomorpha clade, although this result did not definitively preclude Vermileonidae being located outside of the Tabanomorpha (Wiegmann et al., 2000; Stuckenberg, 2001).

For simplicity, I recognize the Tabanomorpha classification, including the genera of families contained therein, of Woodley (1989) as current. Woodley's conservative assessment of the Rhagionidae includes *Austroleptis*, *Bolbomyia*, and the Spaniidae, exclusive of the Pelecorhynchidae. Tabanomorpha is defined as containing the Athericidae, Pelecorhynchidae, Rhagionidae, Tabanidae, and Vermileonidae. Xylophagidae is removed to the Xylophagomorpha. I add here, however, a few exceptions to Woodley's classification scheme (1989). *Sierramyia* gen. nov. is used as a replacement name for *Neorhagio* Lindner. Also, *Archicera* Szilády is treated as a junior synonym of *Spania* Meigen. A more detailed history of the development of the family concept of Rhagionidae follows.

History of the Concept of Rhagionidae

The taxonomic history of Rhagionidae involves nearly all of the great workers in Diptera, including Linnaeus, Fabricius, Latreille, Macquart, Westwood, Becker, and Hennig, among others (Linnaeus, 1758; Fabricius, 1775; Latreille, 1802; Latreille, 1804; Fabricius, 1805; Latreille, 1809; Macquart, 1834; Macquart, 1840; Westwood, 1840a; Westwood, 1840b; Macquart, 1850; Macquart, 1855; Westwood, 1876; Becker, 1900b; Becker, 1900c; Becker, 1900a; Becker, 1921; Hennig, 1952; Hennig, 1955; Hennig, 1967; Hennig, 1968; Hennig, 1972; Hennig, 1973). In the following account, I report the development of the Rhagionidae family concept, beginning with the original species placed in the group. In parentheses, I indicate the currently valid binomial combination for each species mentioned, if different from its original form. Once the basis for the family is established, I track family boundaries at the genus level. Junior synonyms are followed by their currently valid senior synonyms, in parentheses.

The genus *Rhagio* was established by Fabricius in 1775 for four species originally placed in *Musca* by Linnaeus in 1758: *M. scolopaceus* Linnaeus (=*Rhagio scolopaceus* (Linnaeus)), *R. vermileo* Fabricius (=*R. tringarius* (Linnaeus)), *R. tringarius* Fabricius (=*nomina dubia*), and *Rhagio diadema* Fabricius (=*nomina dubia*). Although Linnaeus originally used these same species epithets in combination with *Musca*, *Rhagio tringarius* and *R. diadema* of Fabricius' work were based on misidentifications of the original material and did not pertain to the original Linnaean

concepts. *Rhagio tringarius* and *R. diadema*, therefore, were retained as original Fabricius names.

At this time, antenna and mouthparts were the primary characters relied upon for the classification of flies. Fabricius' diagnosis of *Rhagio* was an example of this. It read simply, "the mouthparts of the group are without a sheath [= mandibles]. Two palpi, setose, extend near the base of the proboscis. The antennae are cylindrical, setose." Although these features are common to species of *Rhagio*, they scarcely preclude other, non-related groups and the vague premise on which this genus was established became immediately problematic for classification above the genus level. In 1802, Latreille erected the family 'Rhagionides', containing the original *Rhagio* species and *R. atratus* Fabricius (= *nomina dubia*), plus *Dolichopus ungulatus* Linnaeus (Dolichopodidae), and *Dolichopus virens* Scopoli (=*Liancalus virens* (Scopoli), Dolichopodidae) (Latreille, 1802). [*R. diadema* Fabricius was not mentioned in this work however it is presumed that the species remained in *Rhagio* at this time.] In 1803, Meigen created *Atherix* for what he believed was *Rhagio diadema* Fabricius (but was actually originally described as *Sylvicola melancholia* Harris, according to Coquillett (1910)). *Atherix* remained within the family. In subsequent work, Latreille placed 'Rhagionides' within a higher context, in the Proboscidea, the largest of four Dipteran higher-level groups, which contain 13 other families including muscids, syrphids, and tipulids. Latreille's definition of the 'Rhagionides' at this time included *Rhagio* Fabricius, *Atherix* Meigen (Athericidae), *Pachystomus* Latreille (= *Xylophagus* Meigen), and *Ortochile* Latreille (Dolichopodidae) (Latreille, 1809).

Latreille placed *Dolichopus* in its own family, yet retained another dolichopodid, *Ortochile* Latreille, within the 'Rhagionides'.

Samouelle was the first to use the family group name correctly, as Rhagionidae, in 1819. However, since Fabricius emended the genus name of *Rhagio* to *Leptis* in 1805, most authors used *Leptis* for the genus name, and consequently, Leptidae as the family group name. Fabricius changed the name *Rhagio* because he argued that it was too similar to *Rhagium*, a cerambycid beetle. Although Latreille was aware of Fabricius' change of *Rhagio* to *Leptis*, he was one of the few authors to continue to use the name *Rhagio* (Latreille, 1809: 287).

In 1820, Meigen documented the expansion of the family 'Leptides', which had grown to 35 species (Meigen, 1820) in three genera: *Leptis*, *Atherix*, and *Clinocera* (Empididae). The following year, Wiedemann maintained *Clinocera* in the family, however not without some reservation (Wiedemann, 1821). As a footnote next to *Clinocera*, Wiedemann wrote, "in the meantime I maintain this genus at this position, perhaps it will prevail after productive investigations."

In 1826, Macquart monographed the family and moved *Clinocera* Meigen to Empididae (Macquart, 1826). This improved the cohesiveness of the rhagionid concept. He also added a new genus, *Chrysopilus*, to distinguish several species formerly in *Rhagio*. The family concept now included *Rhagio*, *Atherix*, and *Chrysopilus*. Macquart's follow-up work in the group came in 1834, where he gave a

brief introduction and description of each genus, for which he attempted to establish a classificatory framework. Leptidae were placed as a tribe in the family Brachystomes (subdivision Tetrachoeta), which contained 10 other tribes: 'Mydasiens', 'Asiliques', 'Hybotides' (=Empididae) Empides', 'Vesiculeux' (=Acroceridae), 'Nemestrinides', 'Xylotomes' (=Therevidae), 'Bombyliers', 'Syrphies', and 'Dolichopodes'. He placed leptids between the therevids and acrocerids. In addition to *Leptis, Chrysopilus,* and *Atherix*, he added the genus *Spania* Meigen (originally described in 1830 without a family designation), *Clinocera*, and *Vermileo* Macquart (Vermileonidae). He created the genus *Vermileo* for *Musca vermileo* Linnaeus (not to be confused with *Rhagio vermileo* Fabricius). In 1840, Macquart expanded the concept of the group further by adding genera from outside of Europe. *Lampromyia* Meigen (Vermileonidae), originally placed in Bombyliidae, but on account of its similarity to *Vermileo*, was moved to Leptidae. *Dasyomma* (Athericidae), a new genus from Chile, was also added (Macquart, 1840).

That same year, Westwood placed Leptidae in Division 'Brachocera' (defined by having antennae short, not having more than three distinct joints and palpi 1- or 2-jointed) in the stirps Tanystoma (defined by having antenna ends with arista and pupa incomplete) which contains families Tabanidae, Bombyliidae, Anthracidae (=Bombyliidae), Acroceridae, Empididae, Tachydromiidae (=Empididae), Hybotidae (=Empididae), Asilidae, Mydasidae, Therevidae, Leptidae, Dolichopidae, and Scenopinidae (Westwood, 1840a). The Stratiomyidae, Beridae (=Stratiomyidae), and Coenomyiidae, were placed in another stirps, Notocantha, on account of having

articulated flagellum. *Clinocera* was retained in Leptidae as a "bridge" to Dolichopodidae, due to its wing venation (Westwood, 1840a). The genus *Ptiolina* was named for a new species and was added to the family in 1842 by Zetterstedt, who worked on the Diptera of Scandinavia (Zetterstedt, 1842).

Throughout the 1850's Francis Walker consistently changed the generic limits of the Leptidae. In 1851, working on the Diptera of Great Britain, he placed the Leptids in Brachycera with all other families except Hypocera (=Phoridae), and Eproboscidea (=Hippoboscidae, Nycteribiidae), and the nematocerans (Walker, 1851). The regional leptid fauna included five genera: *Leptis*, *Chrysopila* (=*Chrysopilus* Macquart), *Atherix*, *Ptiolina*, and *Spania*. In 1856, Walker added *Syneches* Walker (currently Empididae) (Walker, 1856). However, in this publication, he confused *Leptis* with *Chrysopilus* so that new *Chrysopilus* species were described as members of *Leptis*. *Leptis* and *Rhagio*, consequently, were treated as separate genera and *Chrysopilus* was not mentioned. Three years later, he added another new genus, *Suragina* Walker (Athericidae) (Walker, 1859).

In 1856, J.M.F. Bigot introduced a vastly broader concept of the Leptidae than what previous workers had determined. According to Bigot, the family comprised 12 genera, nine of which were newly located. In addition to *Rhagio*, *Ptiolina*, and *Psammorycter* (=*Vermileo*), he added *Anthalia* Zetterstedt (Empididae), *Baryphora* Loew (Therevidae), *Chauna* Loew (Stratiomyidae), *Exeretonevra* Macquart (Xylophagidae), *Lampromyia* Meigen (Vermileonidae), *Leptipalpus* Rondani

(=*Chrysopilus*), *Microcera* Zetterstedt (=*Heleodromia*, Empididae), *Pelechoidecera* Bigot (=*Atherix*), and *Wiedemannia* Zetterstedt (Empididae) (Bigot, 1856). *Spania* was actually also included, as a junior synonym of *Ptiolina*.

The first attempt at cataloging the Diptera of North America was published during this era (Osten Sacken, 1858). In his treatment, Osten Sacken did not recognize the work of Bigot. According to his interpretation, the Leptidae remained a relatively small family in the Nearctic Region, confined to 26 species in three genera: *Leptis*, *Syneches*, and *Atherix*. The difference between the number of genera placed in the family by Osten Sacken and the number of genera placed in the family by Bigot (1856) indicated more than simply a difference of faunal diversity in the two regions. The family concept was interpreted in different ways in different parts of the world. A transatlantic rift in the recognition of family delimitations marked this era, exacerbated by limited-scope regional treatments.

In 1862, Loew (Loew, 1862) published monographs of Diptera of North America where he outlined a different concept of the Rhagionidae. His interpretation was similar to that of Schiner (1862), including *Leptis*, *Atherix*, *Vermileo*, *Chrysopilus*, and *Spania* (*sensu* Walker, including *Ptiolina*). In addition to these genera, he added *Dasyomma*, *Nodutis* Meigen (=*Atherix* Meigen, Athericidae), and *Triptotricha* Loew (= *Dialysis* Walker, Xylophagidae). As Bigot (1856), Loew made a point to exclude the genus *Syneches* from Leptidae, citing this placement as 'one of the many errors which we meet with in the writings of Mr. Walker.'

In 1867, Frauenfeld recognized that the interpretation of the genus name *Ptiolina* Zetterstedt had been inconsistent among researchers (Frauenfeld, 1867). The interpretation of the genus by Schiner (1862), Walker (1851), and Haliday (1833), was significantly different from that originally set forth by Zetterstedt in his *Insecta Lapponica* (Frauenfeld, 1867). Frauenfeld corrected the confusion by giving the name *Symphoromyia* to the natural group of species that mistakenly were placed together under the name *Ptiolina* by Schiner and others.

In a list of North American species of Diptera, Osten Sacken added *Pheneus* Walker (=*Vermileo* Macquart, Vermileonidae) to Leptidae, which was reduced from eight (*sensu* Loew, 1862) to six genera in North America (Osten Sacken, 1858; Osten Sacken, 1874a; Osten Sacken, 1874b). The misinterpretation of the genus *Ptiolina* Zetterstedt continued, however, as the name was listed as a senior synonym of *Spania* Meigen (Osten Sacken, 1874b).

In 1878, Burgess described a new genus, *Glutops*. In discussing the systematic position of this genus, he argued that if *Arthropeas* was admitted into the Leptidae, then *Glutops* would naturally follow (Burgess, 1878). *Arthropeas* was placed provisionally among the Xylophagidae based on its antennae. Burgess noted however, that Osten Sacken was inclined to subordinate the structure of the antennae in *Arthropeas* to its general habitus, which was undoubtedly that of a leptid. Indeed, many genera would follow under this interpretation because it left the family without

any defining character. This marked the beginning of treating Rhagionidae as the explicit, universal catchall for *incertae sedis* genera of the lower Brachycera (Fig. 2).

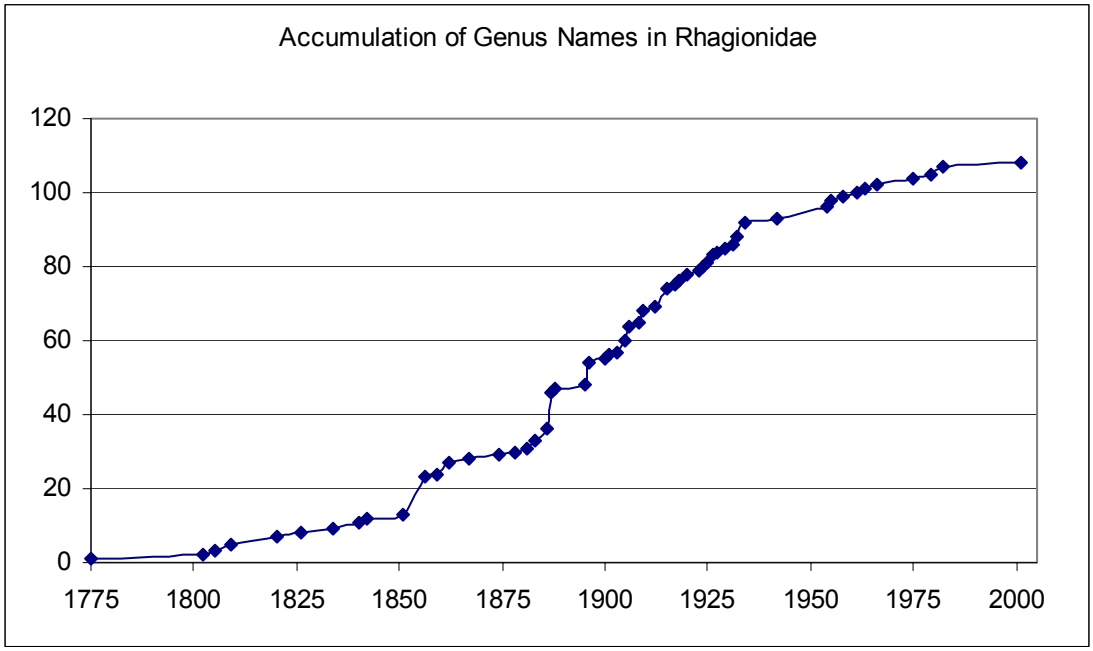


Figure 2. Accumulation of Genus Names in Rhagionidae. The period between 1878 to 1934 marked an expansive period for the concept of Rhagionidae, as the boundaries of this family were exceptionally porous. The x-axis indicates year and the y-axis indicates the accumulation of genus names placed within Rhagionidae.

Twenty years after publishing his catalogue of North American Diptera, Osten Sacken came out with a second edition, revised and updated (Osten Sacken, 1878). Although Osten Sacken attempted to check specimens and recognize synonymies, his taxonomic judgment was rather skewed by personal biases. For instance, he rejected priority of names given by Walker of the British Museum because of a lack of trust in

this researcher's work. He preferred to give priority of such names to colleague and co-author Loew. He took the opportunity to explain his aversion to Walker in a lengthy criticism: "Mr. Walker's identifications of the species of former authors are often, I may say in most cases, incorrect... These facts are given as a warning for entomologists not to trouble themselves too much about the interpretation of Mr. Walker's descriptions, because in most cases, they will find themselves misled by the very data furnished by him." Furthermore, Osten Sacken did not utilize the emerging implications of evolutionary theory on taxonomy and classification. Echoing perceptions of pre-Darwinian authorities, he expressed the desire to place families in "a satisfactory linear arrangement."

Osten Sacken divided the family into sections Psammorycterina Loew and Leptina Osten Sacken (Osten Sacken, 1878). Section Psammorycterina included two genera, *Triptotricha* (=*Dialysis*, Xylophagidae) and *Pheneus* (=*Vermileo*, Vermileonidae). Section Leptina included six genera, *Chrysopilus*, *Leptis*, *Ptiolina*, *Spania*, *Atherix*, and *Glutops*. He did not follow Burgess' suggestion to place *Arthropeas* in Leptidae, instead locating this genus within Coenomyiidae. In subsequent work, Osten Sacken made *Leptynoma* Westwood a junior synonym of *Lampromyia* Macquart, and in agreement with Macquart and Schiner, placed the genus in Leptidae (Osten Sacken, 1883).

During this period, Williston noted that the addition of *Triptotricha* (=*Dialysis*, Xylophagidae) and *Glutops* to Leptidae provided "exceptions to the distinctive

characters of the family, and will make the limits very hard to define." (Williston, 1886). The work of Bigot in 1887 immediately shows this to be true (Bigot, 1887). Similar to his 1856 treatise, Bigot chose to redefine the family in the broadest terms. The limits of Rhagionidae were unclear enough to allow the inclusion of an ever greater diversity of taxa from other families in Lower Brachycera. In Bigot's interpretation, the family comprised 23 genera, at least 12 of which were newly placed into the family (Bigot, 1887). Most of these taxa were placed in the Empididae. These new additions included *Apolysis* Loew (Bombyliidae), *Bergenstammyia* Mik (=*Clinocera* Meigen, Empididae), *Chamadaepsia* Mik (=*Wiedemannia* Zetterstedt, Empididae), *Dialysis* Walker, *Eucelidia* Mik (=*Wiedemannia* Zetterstedt, Empididae), *Eurytion* Jaennicke (=*Ptiolina* Zetterstedt), *Heleodromyia* Haliday (Empididae), *Kowarzia* Mik (=*Clinocera* Meigen, Empididae), *Macellopalpus* Bigot (=*Chrysopilus* Macquart), *Roederia* Mik (=*Wiedemannia* Zetterstedt, Empididae), *Ruppiella* Wiedemann (Therevidae), and *Philolutra* Mik (=*Wiedemannia* Zetterstedt, Empididae). He does not include generic names indiscriminately, however. He excluded *Spania* Meigen and *Ptiolina* Zetterstedt, considering them *incertae sedis* because of the poor description of these genera. He also excluded *Pheneus* Walker, *Nodutis* Meigen, *Exeretonevra* Macquart, and *Pelechoidocera* Bigot.

At this point discussion arose as to whether include *Hilarimorpha* Schiner in the Leptidae, a genus that very much resembles a genus now placed in the family, *Litoleptis* Chillcott. Schiner originally described *Hilarimorpha* as an empidid, but

later changed his opinion and claimed it was a leptid (Schiner, 1860). Primarily basing their opinions on larval characters, Mik and Brauer came out against this revised opinion of Schiner (Brauer, 1880; Mik, 1881). Williston also argued that *Hilarimorpha* did not belong in Leptidae (Williston, 1885; Williston, 1888). This led to a telling insight into the family concept, provided by Osten Sacken (1890) in arguing the Hilarimorpha was a leptid, "Prof. Mik says that *Hilarimorpha* has only four posterior cells, and therefore cannot be a Leptid, which ought to have five. [*Agnotomyia* is] a Leptid with the exceptional number of four posterior cells. Prof. Mik further says that *Hilarimorpha* has no pulvilliform empodium. The genus *Lampromyia* affords an instance that a pulvilliform empodium may not be developed in a Leptid. Again he says that the posterior branch of the fork of the third vein in the Leptidae is always behind the apex of the wing and not before it, as in *Hilarimorpha*. But *Spania* is a Leptid, and yet that vein ends before the apex of its wing." The family had grown to the point where there were no longer any defining characters which held the group together.

This led Williston, in 1896, to subordinate Xylophagidae and Coenomyiidae to subfamilies of the Leptidae on account that the "sole character which can be used to distinguish the families-the structure of the third antennal joint- divides the group unnaturally, throwing with the Xylophagidae forms whose affinities are greatest with the Leptidae, notwithstanding the antennal character" (Williston, 1896). Thus, the leptid fauna was listed in his Manual of North American Diptera as having 15 genera (increased from six genera in the previous treatment) divided into three subfamilies:

subfamily Xylophaginae, containing *Arthropeas* Loew, *Coenomyia* Latreille, *Rachicerus* Walker, and *Xylophagus* Meigen; subfamily Arthroceratinae, containing *Subulomyia* Williston (for *Subula* Meigen, occupied name (=*Xylomyia* Bezzi)), *Glutops* Burgess, and *Arthroceras* Williston; and subfamily Leptinae, containing *Dialysis* Walker, *Triptotricha* Loew (= *Dialysis* Walker), *Leptis*, *Chrysopila*, *Spania*, *Ptiolina*., *Atherix*, and *Symphoromyia*. He placed *Hilarimorpha* Schiner in the Empididae (Williston, 1896).

Becker, along with other European dipterists, rejected the notion that Xylophagidae and Coenomyiidae were subfamilies in the Leptidae (Becker, 1900a). In his 1900 treatment, however, he included *Hilarimorpha* Schiner and also *Arthropeas* Loew, with some reservation (Becker, 1900a).

Bezzi treated the Palearctic Brachycera in 1903, making significant modifications of the 'Leptididae' (Bezzi, 1903). In a complicated new interpretation of the group, he retained the synonymous names *Rhagio* Fabricius and *Leptis* Fabricius by making *Vermileo* Macquart a junior synonym of *Rhagio*. The newly defined *Rhagio* concept was then placed with *Lampromyia* Macquart in subfamily Rhagioninae. *Leptis* Fabricius, meanwhile was placed with *Atherix* Meigen in another subfamily, Leptidinae. Another subfamily was erected, the Chrysopilinae, to contain *Omphalophora* Becker (=*Ptiolina*), *Chrysopilus*, *Symphoromyia*, *Ptiolina*, *Spania*, and *Hilarimorpha*. Subsequent authors largely ignored these changes.

By 1905, the leptid fauna in the Catalog of North American Diptera contained 19 genera (Aldrich, 1905). *Bolbomyia* Loew, *Chiromyza* Wiedemann (Stratiomyidae), *Coenomyia* Latreille (Coenomyiidae), *Mythicomyia* Coquillett (Bombyliidae), *Rachicerus* Walker (Xylophagidae), and *Xylomyia* Rondani (Xylomyiidae) were new additions to the North American list. *Pheneus* Walker (=*Vermileo*) was reinstated and *Ptiolina* Zetterstedt was treated as a junior synonym of *Spania* Meigen. Above the family level, Aldrich classified leptids, inclusive of Xylophagidae and Coenomyiidae, with Stratiomyidae, Tabanidae, and Acanthomeridae (= Pantophthalmidae) in the Orthorrhaphous Brachycera. Having no defining features, the Leptidae became the well established home to basal brachycerans that were not obviously stratiomyids, tabanids, or pantophthalmids.

A year later, Lameere (1906) recommended that Nemestrinidae be subordinated to subfamily rank in Leptidae. This added the following nemestrinids to the Leptidae: *Hirmoneura* Meigen, *Rhynchocephalus* Fischer (= *Nemestrinus* Latreille), *Fallenia* Meigen, and *Nemestrinus* Latreille. Verrall, in reference to this work, would later say "throughout the paper [Lameere] exhibits such an absolute want of personal study of the Diptera and of their literature as to render his writings worse than useless for students" (Verrall, 1909). No subsequent publications followed the proposal of subordinating Nemestrinidae.

In an updated version of Manual of North American Diptera, Williston reviewed the higher-level classification schemes for Diptera up to that point "in order that the tyro

in their study may not reach the erroneous conclusion that any system is authoritative" (Williston, 1908). He argued that a modification of the classification system must reflect a modern evolutionary framework. This was not easy, however, and he conceded that "nearly all these lines of evolution are polyphyletic, resulting in numerous cases of parallel resemblances which must be taken into account in any attempt at *true* classification. In other words, the evolution of characters in the different lines of descent does not proceed *pari passu*, and opinions will always differ as to the different values to be assigned to the specialized characters." At this time, Williston continued to support a broad definition of the family. His definition of the family remained virtually unaltered from the 1896 treatment (Williston, 1908).

The catalog of world Diptera was also published in 1908, authored by Calman Kertész (Kertész, 1908). He treated the family as Rhagionidae, rather Leptidae, diligently noting that *Leptis* was a junior synonym of *Rhagio* because the emendation of Fabricius was unjustified. His treatment contained 20 genera in 274 species, exclusive of the xylophagids and coenomyiids. The following genera were included; *Arthroceras*, *Atherix*, *Chrysopilus*, *Dasyomma* (Athericidae), *Dialysis*, *Glutops* (Pelecorhynchidae), *Hilarimorpha* (Hilarimorphidae), *Lampromyia* (Vermileonidae), *Mythicomyia* (Bombyliidae), *Pheneus* (=*Vermileo*, Vermileonidae), *Ptiolina*, *Rhagio*, *Spania*, *Suragina* (Athericidae), *Symphoromyia*, *Triptotricha* (=*Dialysis*, Xylophagidae), and *Vermileo*.

Verrall adopted an intermediate view in regards to the status of Leptidae, accepting the opinions of Kertész, yet broadening the concept to include the xylophagids and coenomyiids and a new genus, *Atrichops*, for *Atherix crassicornis* Meigen (Athericidae) (Verrall, 1909). Above the family level, Verrall proposed a classification scheme that placed the Stratiomyidae, Acanthomeridae, Leptidae, Tabanidae, Nemestrinidae, and Cyrtidae together in the Eremochaeta. "My reasons for this are the evident gradations through *Beris* and *Xylomyia* to *Xylophagus* and *Coenomyia*... The Acanthomeridae also are obviously intermediate between the Stratiomyidae and Leptidae and may lead on to the Tabanidae. There may be stepping-stones, though I write with little confidence, from the Tabanidae through the long proboscis of the Pangoninae to the Nemestrinidae, and then the superfamily would end with the Cyrtidae, from which 'Natura non facit saltum' to such tromopterous Bombyliidae as the bare humpbacked *Glabellula*, *Platypygus*, etc." His classification suffered by adhering to the notions that evolution proceeds in a linear fashion, discounting the tree-like division of relatedness between natural groups.

During the first part of the twentieth century, most of the contributions to the development of Rhagionidae (for the most part, still called Leptidae) came from collections made outside of Europe and North America. Brunetti, working in India, created the new genus *Desmomyia* and placed it in the subfamily Arthroceratinae on account of its similarity to *Arthroceras* (Brunetti, 1912), although this was probably based on a misconception of *Arthroceras*, since *Desmomyia* is quite different from *Arthroceras*, most notably in antennal form. *Desmomyia* may easily be confused with

Rhagio, which it highly resembles. While working on the Philippine Diptera, Bezzi described the new genus *Schizella* (Bezzi, 1917). Based on his collections in Tasmania, White created three new genera, *Atherimorpha*, *Spaniopsis*, and *Clesthenia* (Therevidae) (White, 1914) and Hardy described another genus, *Austroleptis,* from Australia (Hardy, 1920a). In his revision of Neotropical Rhagionidae, Lindner described the genus, *Neorhagio* (=*Atherimorpha*), from Chile (Lindner, 1924) and the following year, described the genus *Therevirhagio* (=*Atherimorpha*), from Australia (Lindner, 1925). During this time, Lindner also described the genus, *Bicalcar* (=*Chrysopilus*), from a specimen collected in South America by Loew for which he established the subfamily Bicalcarinae (Lindner, 1923).

In 1926, Bezzi treated the South African Rhagionidae, excluding what were considered the subfamilies Hilarimorphinae, Xylophaginae, and the Coenomyinae (Bezzi, 1926). According to his interpretation, the family consisted of seven genera, divided into four subfamilies (Vermileoninae, Rhagioninae, Chrysopilinae, and Arthrotelinae). Along with *Lampromyia*, *Atrichops*, *Atherix*, *Atherimorpha*, and *Chrysopilus*, two newly described genera were added to the family; *Pachybates* (Athericidae) and *Arthroteles*, for which he created the new subfamily Arthrotelinae.

The debate of whether or not to include the Hilarimorphidae, Xylophagidae, and the Coenomyidae as subfamilies of the Rhagionidae or as distinct families continued during this period. Unable to resolve the debate by examining adults, researchers turned to the larvae and pupal stages of these organisms. In 1926, based on

examination of rhagionid larvae and pupae, Greene concluded that the groups were indivisible (Greene, 1926). His conclusion was based mainly on the form of the spiracle in the pupa, which is constant for each family. “Should this group be divisible into three families one would expect to find three distinct forms of spiracles, but in the material available only one type occurs, which very strongly confirms my impression that these insects do not belong to more than one family.” This result conflicted with Malloch who decided that the Xylophagids and Leptids were not only separate but also belonged in different superfamilies, based on larval and pupal characters (Malloch, 1917). Greene’s work marked one of the last times Xylophagidae and Coenomyidae were subordinated to subfamily rank within Rhagionidae.

In his revision of the North American Rhagionidae, Leonard deferred judgement of whether or not to include Xylophagidae and Coenomyidae in the Rhagionidae (Leonard, 1930). He stated: “With the present evidence at hand and without making a more critical study of the family as a whole and its relation to the more closely allied families I do not feel qualified” in delimiting the family concept. Therefore, he relied on the Rhagionidae concept, *sensu latu*, of Williston (1908) and included the groups as subfamilies. In a follow up paper he conceded, “I have not felt myself sufficiently well acquainted with the delimiting characters of several families nearly related to the Rhagionidae (*sensu latu*) to attempt to say very definately to which families several genera should really belong” (Leonard, 1931).

In 1931, Malloch gave a history of the *Rhagio* name and testified that "Rhagionidae" was the correct term for the family concept (Malloch, 1931). However, his paper was not recognized by English-speaking authors outside of the United States, many of whom continued to use the name Leptidae for the remainder of their careers (that last into the 1960s). In Malloch's 1932 treatment, Rhagioninae include *Atherimorpha* White, *Dasyomma* Macquart, *Dasyommina* (=*Dasyomma*), *Rhagina*, *Chrysopilus*. Arthroceratinae includes A*ustroleptis* Hardy, *Heterostomus* Bigot, *Arthroceras* Williston, and *Arthropeas* Loew (Malloch, 1932b).

Szilády published a catalogue of the Palearctic rhagionids in 1934 (Szilády, 1934). He divided the family into three subfamilies, Bicalcarinae (including *Bicalcar* (=*Chrysopilus*)), Vermileoninae (including *Vermileo* and *Lampromyia*), and Rhagioninae (including *Rhagio* (and new subgenera *Rhagionella* and *Rhagiella*), *Atrichops* (Athericidae), *Atherix* (Athericidae), *Hilarimorpha* (Hilarimorphidae), *Symphoromyia*, *Chrysopilus*, *Omphalophora* (=*Ptiolina*), and *Ptiolina* (including *Spania* and new subgenera *Cekendia* and *Archicera*). He also added two new genera to this subfamily, *Sapporomyia* (=*Chrysopilus*) and *Atherigia* (Athericidae).

Hennig reviewed dipteran systematics, placing a special emphasis on the phylogenetic value of larval characters (Hennig, 1952). He transferred *Xylophagus* to a separate family, the Erinnidae (=Xylophagidae). Soon after, Steyskal performed a similar review of larval characters and reached conclusions consistent with those of Hennig (Steyskal, 1953). Groups such as the Xylophaginae were distinct enough to

merit recognition as separate families. He placed 17 genera in the Rhagionidae; *Atherix* (Athericidae), *Atrichops* (Athericidae), *Bicalcar* (=*Chrysopilus*), *Chrysopilus*, *Dasyomma* (Athericidae), *Dialysis*, *Lampromyia*, *Omphalophora* (=*Ptiolina*), *Paraphoromyia* (=*Symphoromyia*), *Ptiolina*, *Rhagina* (=*Rhagio*), *Rhagio*, *Spania*, *Spaniopsis*, *Suragina* (Athericidae), *Symphoromyia*, and *Vermileo* (Vermileonidae) (Steyskal, 1953). He transferred *Atherimorpha* and *Austroleptis* to the Xylophagidae and put *Arthroceras*, *Arthropeas*, *Arthroteles*, *Bolbomyia*, and *Glutops* in the Coenomyiidae.

In 1961, Chillcott revised the genus *Bolbomyia* and placed the genus in the Rhagionidae, although he noted: "The correct assignment of this rather primitive genus is difficult. The combination of the two-jointed sytle, tibial spurs on all three legs, primitive wing venation and genitalia, and pulvilliform tarsal empodium does not fit any of the present subfamilies of Rhagionidae" (Chillcott, 1961).

Several years later, Chilcott described a new rhagionid genus from Alaska, *Litoleptis* (Chillcott, 1963). In this work, he also redescribed the genus *Cekendia* and synonymyzed the genus with *Bolbomyia*. His study of these genera led him to believe that a natural group within the Rhagionidae comprised the following genera: *Litoleptis*, *Bolbomyia*, *Hilarimopha*, *Archicera* and *Austroleptis*.

In the Catalogue of North American Diptera (James, 1965), *Hilarimorpha* was placed in its own family, Hilarimorphidae while *Arthroceras*, *Arthropeas*, *Bolbomyia,*

Coenomyia, *Glutops*, *Rachicerus*, and *Xylophagus* were placed in the Xylophagidae. Shortly afterwards, Nagatomi argued that *Arthroceras* was more closely related to *Rhagio* and its allies than to *Coenomyia* or *Xylophagus* and transferred the genus to the Rhagionidae (Nagatomi, 1966).

In 1966, Stuckenberg reported that the family Rhagionidae included five genera of the Neotropical region (*Atherimorpha* White, *Austroleptis* Hardy, *Chrysopilus* Macquart, *Dasyomma* Macquart, and *Neorhagio* Lindner) (Stuckenberg, 1966). In this work he added another genus from Brazil, *Xeritha*, a close relative of *Atherix*. James later increased this number to seven, although his interpretation of the family was quite different from that of Stuckenberg (James, 1968). James excluded *Atherimorpha*, *Austroleptis*, and *Xeritha* from the Rhagionidae, and included *Vermileo*, *Atherix*, *Chrysopilus*, *Dasyomma*, *Neorhagio*, *Rhagio*, and *Suragina*.

In 1970, Teskey proposed that *Glutops* Burgess be placed in the Pelecorhynchidae (Teskey, 1970a). His observations were based on newly discovered larval and pupal characters of the genus, which were remarkably similar to the same stages of *Pelecorhynchus*. The following year, however, Krivosheina proposed that *Glutops* be placed in its own family, based on a comparative-morphological study of all developmental stages (Krivosheina, 1971).

In 1973, Hennig established a new Diptera classification, which included a treatment of the Rhagionidae (Hennig, 1973). Hennig placed the genera of the Rhagionidae into

three subfamilies as follows: Arthroceratinae: *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Austroleptis*, *Bolbomyia*, *Glutops*, *Heterostomus*; Rhagioninae, Atherix group: *Atherix*; Rhagio group: *Chrysopilus*, *Dialysis*, *Rhagio*, *Schizella*, *Symphoromyia*; Spania group: *Litoleptis*, *Omphalophora*, *Ptiolina*, and *Spania*; Vermileoninae: *Lampromyia*, *Vermileo* and *Vermitigris*. Perhaps inspired by his work, both the *Atherix* group and its allies and the Vermileoninae were later recognized as families. Stuckenberg (1973) established Athericidae to include the genera *Atherix* Meigen, *Atrichops* Verrall, *Suragina* Walker, *Pachybates* Bezzi, *Trichacantha* Stuckenberg, *Dasyomma* Macquart, and *Xeritha* Stuckenberg. In 1977, Nagatomi erected Vermileonidae for *Lampromyia* Macquart, *Vermileo* Macquart, and *Vermitigris* Wheeler on account of their highly autapomorphic morphology and life history (Nagatomi, 1977).

Although the limits of the rhagionid concept decreased significantly with the establishment of Athericidae and Vermileonidae, the make-up of what was left of Rhagionidae remained taxonomically unstable and the family lacked a coherent definition. In 1978, for example, Webb transferred *Dialysis* back to Rhagionidae in his revision of the genus (Webb, 1978). Three years later, in the Manual of Nearctic Diptera, James (1981) returned *Dialysis* to the Xylophagidae. Similarly, the placement of *Austroleptis*, *Bolbomyia*, *Glutops*, *Hilarimorpha*, and *Pseudoerinna* continued to be debated among authors (Krivosheina, 1971; Nagatomi, 1977; Kovalev, 1981; Teskey, 1981b; Griffiths, 1994; Grimaldi and Cumming, 1999; Stuckenberg, 2001).

Nagatomi (1982) presented an updated concept of the family, including an intuitive tree to represent his ideas of the rhagionid phylogeny as part of a landmark monograph of the Rhagionidae (Fig. 1). *Pelecorhynchus* was shown as the sister group to the rest of the Rhagionidae, which under his concept, included genera that had typically been placed in the Pelecorhynchidae; *Glutops* and *Pseudoerinna*. These genera were considered the most primitive in Nagatomi's scheme. *Austroleptis* was also recognized as an early offshoot of the rhagionid lineage, which includes *Alloleptis*, *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Bolbomyia*, *Chrysopilus*, *Desmomyia*, *Litoleptis*, *Neorhagio*, *Ptiolina*, *Rhagina*, *Rhagio*, *Schizella*, *Solomomyia*, *Spania*, *Spaniopsis*, *Stylospania*, and *Symphoromyia*. Although this arrangement was not arrived at using a cladistic approach, and therefore the monophyly of Rhagionidae remained untested, Nagatomi's work was a significant advance in understanding the extant diversity of the group.

At this time, cladistic phylogenetic methods were being developed and applied for the first time, creating a new era of inquiry into the relationships among genera of the Tabanomorpha, and more specifically, of the Rhagionidae. Naturally, as researchers applied more rigorous approaches to the systematic study of the Rhagionidae, new phylogenetic hypotheses emerged. Woodley (1989) was the first to approach the group on modern cladistic grounds, providing a summary of the family, its generic composition, and the placement of the family into a larger context, within Tabanomorpha and Brachycera. His support for phylogenetic relationships relied

principally on larval characters developed by other workers (Malloch, 1917; Steyskal, 1953; Tsacas, 1962; Krivosheina, 1967; Roberts, 1969; Teskey, 1970a; Hennig, 1973; Thomas, 1974; Webb, 1983). Larvae for many rhagionid genera are not known or poorly described, but Woodley's work provided a stabilizing force for rhagionid classification. For the most part, Woodley's concept of Rhagionidae overlapped with Nagatomi's 1982 concept, although the genera of the Pelecorhynchidae *sensu lato* (*Glutops*, *Pelecorhynchus*, and *Pseudoerinna*) were recognized as a separate family, sister to the Athericidae and Tabanidae, and not part of the Rhagionidae in any sense.

Sinclair (1992) presented a treatise of the larval mandible and associated mouthpart structures in Diptera in order to evaluate, among other ideas, Woodley's hypothesis of the orthorrhaphous brachyceran phylogeny (Woodley, 1989). In this work, Sinclair confirmed the larval characters that Schremmer (1951), Teskey (1969; 1970a; 1981a), Hennig (1973) had originally studied and that Woodley had used to construct his cladogram. Sinclair considered the larval mandible of Rhagionidae as a "groundplan condition" of Brachycera and did not find any evidence to support rhagionid monophyly (Sinclair, 1992). However, based on the association of an articulated rod with the larval mandibular brush, Sinclair supported the sister group relationship between Pelecorhynchidae and Athericidae + Tabanidae that Woodley had recognized. This contradicted Nagatomi (1982a), who continued to publish an expanded definition of Rhagionidae that included *Glutops* and *Pseudoerinna* (Nagatomi, 1982c; Nagatomi, 1982b; Nagatomi, 1982e; Nagatomi, 1982d; Nagatomi, 1984; Nagatomi and Soroida, 1985; Nagatomi, 1991; Nagatomi, 1992).

Consistent with the trend of decreasing the breadth of the rhagionid concept, which started with Stuckenberg (1973; removal of the Athericidae) and Nagatomi (1977; removal of the Vermileonidae), and continued through the work of Woodley (1989; removal of Pelecorhynchidae *sensu lato*), Sinclair, Cumming, and Wood (1993) examined the male genitalia in lower Brachycera and determined that *Bolbomyia* was more closely related to Athericidae and Tabanidae than to the rest of the rhagionid genera. *Bolbomyia* is a very small fly that has a flattened clypeus, a tibial spur on its fore leg, and aberrant wing venation and its placement has always been somewhat controversial. At first glance, it certainly does not recall the typical rhagioniform habitus. At various times, it has been considered a xylophagid (Loew, 1850; James, 1968), but evidence for this placement has been considered weak and its eventual placement within Rhagionidae apparently occurred for no better reason than its lack of defining (synapomorphic) characters. Sinclair et al. (1993) argued that the presence of aedeagal tines was an important but overlooked character that in fact provided strong evidence for the proper placement of *Bolbomyia*. Rather than sharing common ancestry with the rhagionid or xylophagid genera, they asserted that the genus has a close relationship with Athericidae and Tabanidae (Sinclair et al., 1993).

In a study principally devoted to new fossil brachyceran forms, Grimaldi and Cumming (1999) noted that wing venation may be an important source of phylogenetically informative characters. They proposed that the relative position of fork R_4-R_5 with respect to cell dm and the curvatures of R_5 (straight) and R_4 (with a

sharp bend at its base) may serve as synapomorphies for most Rhagionidae. They noted that some of the most controversial members of the family, namely *Austroleptis*, *Bolbomyia*, and *Litoleptis*, do not exhibit this wing morphology and there was reason to believe, based on the shared loss of wing vein CuA_1, that these genera form a distinct monophyletic entity that includes some extinct forms (Grimaldi and Cumming, 1999).

The development of molecular techniques allowed for a new approach to solving these issues in Diptera (e.g., Pelandakis and Solignac, 1993; Pawlowski et al., 1996; Friedrich and Tautz, 1997; Carreno and Barta, 1998). Wiegmann et al. (2000) were the first to use this type of data in an effort to answer specific questions regarding the higher-level relationships in Tabanomorpha. In their analysis using 28S rDNA, the Pelecorhynchidae were recovered as sister to Athericidae and Tabanidae, a result consistent with Sinclair (1992) and Woodley (1989). The Rhagionidae were recovered as a monophyletic group, sister to the Vermileonidae. The most contentious genera of the Rhagionidae (*e.g.*, *Bolbomyia* and *Austroleptis*) were not sampled, however. Within the Rhagionidae, *Rhagio* was recovered basal to *Symphoromyia*, which was sister to *Ptiolina* and *Chrysopilus*.

Stuckenberg flatly rejected most of these notions in a bold reassessment of the family (2001). He argued that *Bolbomyia* and the entire Pelecorhynchidae form a part of Rhagionidae, but in a new sense that excluded taxa that he believed belong in the separate, newly recognized families Austroleptidae and Spaniidae. Although it was a

notable departure from contemporary treatments of the group, Stuckenberg's hypothesis closely parallels the ideas of Nagatomi (1982). Austroleptinae Nagatomi and Spaniinae Nagatomi were simply elevated to the family level. Although Stuckenberg asserted that the Pelecorhynchidae were "always ranked by Nagatomi as a subfamily of Rhagionidae, a conclusion he defended categorically," Pelecorhynchinae *sensu* Stuckenberg was, in fact, a novel arrangement. Nagatomi considered Pelecorhynchidae to contain a single genus, *Pelecorhynchus*, sister to the Rhagionidae. The other genera often considered to be pelecorhynchids, *Glutops* and *Pseudoerinna* (Teskey, 1970a; Teskey, 1970b; Woodley, 1989; Sinclair et al., 1993; Wiegmann et al., 2000; Wiegmann et al., 2003), were placed by Nagatomi within the rhagionid subfamily Glutopinae (Nagatomi, 1982a). Stuckenberg was therefore the first to locate *Pelecorhynchus* within Rhagionidae. Also, Stuckenberg was the first to recognize the subfamily Bolbomyiinae, to account for the unusual genus *Bolbomyia* (Stuckenberg, 2001).

A common refrain from these most recent papers is that a comprehensive monographic treatment of the rhagioniform genera is sorely needed. Current, conflicting classifications are either based on intuition developed from years of taxonomic experience in the group (e.g., Nagatomi, 1982a; Stuckenberg, 2001), primarily or exclusively single character systems (e.g., Krivosheina, 1991; Sinclair, 1992; Sinclair et al., 1993; Grimaldi and Cumming, 1999; Wiegmann et al., 2000; Wiegmann et al., 2003), systematic studies involving incomplete taxon sampling (e.g., Wiegmann et al., 2000; Stuckenberg, 2001), analysis derived from the published

literature (e.g., Woodley, 1989; Amorim and Silva, 2002; Yeates, 2002), or incomplete combinations of these components. Therefore, although great strides have been made in the development of the concept of the family Rhagionidae and related genera, a definitive, well-supported classification has not been realized.

Biology

Adults.

Rhagionids are medium sized flies, ranging from approximately 4- 20mm in length, that are typically collected by sweeping vegetation in sheltered, rather moist, forest clearings or woodlands which are often of high elevation and/or mountainous.

Perhaps the most well known rhagionids are *Symphoromyia* and *Spaniopsis* whose adult females take blood meals from vertebrate hosts. In various areas throughout its range, *Symphoromyia* has been regarded as a bothersome pest, particularly in mountainous or high latitude regions (Knab and Cooley, 1912; Cockerell, 1923; Frohne, 1953b; Frohne, 1953a; Frohne, 1959; Shemanchuk and Wintraub, 1961; among many others, see Turner, 1979), and in some cases, the bite of *Symphoromyia* species has caused inflammation, swelling, and even severe allergic reaction (Knab and Cooley, 1912; Turner, 1979; Chvala, 1983). It is interesting to note, however, that biting is largely restricted to North America, even though the distribution of *Symphoromyia* extends through Asia and Europe (Chvala, 1983). Even within the Nearctic region, some species of *Symphoromyia* seem not to attack people (Sommerman, 1962; Turner and Chillcott, 1973; Turner, 1979). *Symphoromyia* adults tend to be most active during the summer months, however, occasionally may be seen

in flight during early spring. Species of *Spaniopsis* may also be pests and all are known to bite (Ferguson, 1915; Colless and McAlpine, 1991). *Spaniopsis* reportedly prefers shady, humid habitats, often at high elevation sites (Paramonov, 1962). *Spaniopsis* adults may be collected in Australia between November and May. Despite the fact that species of *Symphoromyia* and *Spaniopsis* may be pestiferous, they are not considered medically or economically important. None serve as vectors of disease.

Arthroteles Bezzi is noteworthy for its specialized flower-feeding behavior, restricted to the mountain ranges of the Western Cape Province and the escarpment in eastern South Africa (Stuckenberg, 1956). Stuckenberg (1956) reports that *Arthroteles cinerea* resembles bombyliids in flight and is most often collected on the flower heads of *Helichrysum* spp. (Asteraceae). Interestingly, *Arthroteles* apparently has specific-specific, or nearly species-specific periods of activity. Historically, *A. cinerea* adults are collected in March, whereas *A. bombyliiformis* are collected in August or September. *A. orophila* is active in November. The flight of *A. longipalpis* occurs in July, and may overlap to some degree with *A. bombyliiformis*.

In South America, *Atherimorpha* is principally associated with *Nothofagus*-dominated woodlands, although a few species of *Atherimorpha* are found in arid and scrubby habitats to the north of Santiago and in Brazil where *Nothofagus* is not found (Malloch, 1932a). In Australia, *Atherimorpha* species may inhabit dense scrub and or wet montane forests (sometimes in association with an Australian species of *Nothofagus*). Few notes are available on the biology of South African *Atherimorpha*,

but records show that they are also mostly collected in mountainous regions. In all habitats, it appears that *Atherimorpha* species gravitate towards small, slow moving streams, which presumably, provide moist soil substrate for their larval development.

Austroleptis Hardy is another genus usually confined to mountainous regions and is reportedly a visitor of flowers (Colless and McAlpine, 1991). At Cradle Mountain National Park, in central Tasmania, I collected *Austroleptis multimaculata* males and females on the leaves of flowering *Richea scoparia*, however I did not see the insects feed. Less is known about the South American members of this genus (Nagatomi and Nagatomi, 1987), which are rarely collected.

Chillcott (1963) reports that females of *Bolbomyia* are frequently collected from flowers, whereas the males are usually at rest on nearby vegetation. D. Webb (pers. comm.) collected *Bolbomyia nana* in a small forest clearing with a fern understory in North Carolina. Jeff Cumming, Richard Vockeroth, and others including myself, have had success sweeping *Bolbomyia nana* from low-lying vegetation in small forest clearings at King Mountain, Gatineau National Park, in Quebec. Details of its life history are not known. The flight period appears to be exceptionally short, lasting only a couple weeks or it appears, perhaps as little as a few days per year (depending on weather conditions).

Adult *Rhagio* Fabricius and *Chrysopilus* Macquart have been reported as predaceous on other insects (Kellogg, 1908; Leonard, 1930; Paramonov, 1962; Narchuk, 1969;

Narchuk, 1988) but this has never been confirmed and is unlikely given their gawky movements and the generalized morphology of their mouthparts. *Rhagio scolopacea* has even been reported as a bloodfeeder (Heim and Leprevost, 1892; Ferguson, 1915; Lindner, 1925) but these accounts are certainly false. It is remarkable, actually, how little is known regarding the adult stage of these common, widespread genera. *Rhagio* adults are generally active between April and September. *Chrysopilus* adults may be found throughout the year in tropical habitats, and become more seasonal, relative to their latitudinal displacement from the equator. In temperate climates, they are most common throughout the summer in both the northern and southern hemispheres.

There is nothing written specifically regarding the adult biology of *Arthroceras*, *Litoleptis, Ptiolina*, or *Spania* as far as I know. The flight period for these genera may be exceptionally short, perhaps on the scale of a few weeks. Most often the flight period of these flies coincides with the spring or early summer, although *Arthroceras* appear to have a longer window of activity, in some years between April and August.

Larvae.

Among the rhagionid genera, only *Chrysopilus*, *Rhagio*, *Symphoromyia*, and *Ptiolina* have described larvae.

Rhagionid larvae are most commonly cited as predators on a variety of insects (James and Turner, 1981; Foote, 1991). Foote, for instance, specifically identifies *Symphoromyia* as an insect predator (Foote, 1991). However, in a very careful study

of the immatures of *Symphoromyia* species in Alaska, Sommerman (1962) noted that *Symphoromyia* larvae are slow moving and apparently are not predaceous. Similarly, *Ptiolina* are slow moving, "shining green in life," and feed on mosses, according to Brindle (1959). Others have also noted an association of *Ptiolina* and moss (Brauer, 1883; Lane and Anderson, 1982). *Ptiolina nigrina* Wahlberg, however, apparently feeds on the liverwort species *Marchantia polymorpha* (Nartshuk, 1995). *Ptiolina* species have weakened and reduced mouthparts, a condition that is obviously unsuitable for predation (pers. obs.). Although the larvae of *Spania nigra* Meigen have not been characterized, Mik (1896) reportedly found a *Spania nigra* larva in the thallus of *Pellia neesiana*, another liverwort species (Mik, 1896). It is interesting to note that although the food source for *Symphoromyia* is not known, species of this genus are associated with moss and I suspect that it may similarly provide at least some, if not all of their food intake (Sommerman, 1962).

Larval *Chrysopilus* Macquart may be aquatic, associated with streamside vegetation, or, like *Rhagio* Fabricius, may be found in moist soils that are rich in organic matter. Both are predators of oligochaetes and soft-bodied insect larvae (Tsacas, 1962; Roberts, 1969; Thomas, 1978a; Thomas, 1978b; Thomas, 1997). In addition to this, Paramonov (1962) notes that *Chrysopilus* larvae eat the eggs of *Schistocerca* and *Dociostaurus* (Orthoptera). The lifespan of *Chrysopilus auratus* larvae is long, lasting well over a year (Alexandre, 1970 in Thomas, 1997), although the pupal period may last less than two weeks (Tsacas, 1962). This is type of cycle is presumed to be the

case for most rhagionid genera, as it is for most Athericidae and Tabanidae (Thomas, 1997).

Austroleptis larvae are uncharacterized, but have been reared inadvertently from rotting wood (Colless & McAlpine, 1991).

Paramonov (1962) asserts that the larvae of Rhagionidae "penetrate into and devour beetles… some larvae are saprophagous or, very rarely, coprophagous." No references, either to authors or specific genera, are made however. His claims regarding the Rhagionidae, as here composed, are not confirmed and in my opinion, should be disregarded.

Diversity

The Rhagionidae, according to the definition of Woodley (1989), currently contain approximately 604 extant species in 19 genera. The largest genera are *Atherimorpha*, *Chrysopilus*, *Ptiolina*, *Rhagio*, and *Symphoromyia*, which comprise 88% of the total species. *Chrysopilus* is by far the largest genus with 302 species. In order of decreasing species diversity (species number in parenthesis), the currently-recognized rhagionid genera follow: *Rhagio* (161), *Atherimorpha* (50), *Symphoromyia* (35), *Ptiolina* (23), *Austroleptis* (8), *Arthroceras* (7), *Arthroteles* (4), *Bolbomyia* (4), *Rhagina* (4), *Litoleptis* (3), *Schizella* (3), *Desmomyia* (2), *Alloleptis* (1), *Sierramyia* (1), *Solomomyia* (1), *Spania* (1), *Spatulina* (1), and *Stylospania* (1). There are dozens of undescribed species of *Atherimorpha* from South America and *Chrysopilus* and

Symphoromyia also are likely to have many more species than is currently recognized. There are at least several undescribed *Austroleptis* species from South America, as well. A list of all extant rhagionid species is given at the end of the generic treatments in chapter three.

Since Rhagionidae lack diagnostic features to define its members, it is difficult to assess the diversity of fossils that may pertain to the group. Even for extant species, the family is largely known as a grouping of convenience for unusual lower brachycerans that may or may not belong to the same lineage. This provides fertile dumping grounds for fossil genera in particular, many of which are established from poorly preserved specimen remnants. Currently, there are 44 extinct species in 23 fossil genera that are classified as rhagionids (Evenhuis, 1994). Even if some of these genera are misplaced, it appears likely that living representatives display only a fraction of the diversity of form once present in the Rhagionidae (and certainly in the Tabanomorpha).

Fossil Record

The order of appearance of fossils that are now classified as rhagionids (Evenhuis, 1994) is summarized in Table 1. Evidence suggests that the Rhagionidae (or rhagionid-like forms) were very abundant in ancient times. In Baltic amber, for instance, the Rhagionidae are reported to be 'by far' the most common of the lower brachycerous families (Larsson, 1978). Compression fossil assemblages in Siberia

also suggest faunal dominance for much of the history of Brachycerous dipteran life on earth (M. Mostovski, pers. comm.).

The rhagionid lineage is an old assemblage of genera, which appears to have reached a significant level of diversity by at least the Middle Jurassic (Kovalev, 1981; Evenhuis, 1994). The oldest fossil currently placed in the Rhagionidae is *Palaeobolbomyia sibirica*, which is compressed in sediments dated at 187 MYA (Kovalev, 1982; Stuckenberg, 2001). Molecular dating using 28S ribosomal DNA estimates that basal divergences of the Tabanomorpha lineage began approximately 170 MYA (Wiegmann et al., 2003).

A study of rhagionid fossil taxonomy in light of new phylogenetic information is a topic for future work. Can characters derived from fossil and extant flies be compared? If so, are they consistent with patterns found in extant groups? Fossil wing vein patterns are usually preserved, and therefore, are often the most highly relied upon feature of a compression fossil. Do wing characters serve as a faithful predictor of phylogenetic relationship in this group?

Table 1. Presence of Rhagionidae in the fossil record.

Era	Period	Epoch	Extant Genera	Extinct Genera
Cenozoic	Tertiary	Pliocene		
		Miocene		*Dipterites*
		Oligocene	*Rhagio*	
		Eocene	*Bolbomyia*, *Chrysopilus*, *Symphoromyia*	
		Paleocene		
Mesozoic	Cretaceous	Upper		*Zarzia*
		Middle		
		Lower	*Atherimorpha*, *Ptiolina*	*Jersambromyia*, *Mesobolbomyia*, *Mongolomyia*, *Palaeochrysopilus*
	Jurassic	Upper		*Mesorhagiophryne*, *Mesostratiomyia,* *Palaeoarthroteles*, *Palaeostratiomyia,* *Protorhagio*, *Rhagiophryne*, *Scelerhagio,* *Stratiomyiopsis*
		Middle		*Ija*, *Jurabrachyceron*, *Kubekovia*, *Paleobolbomyia*, *Palaeobrachyceron*

Biogeography

The largest genus of the Rhagionidae, *Chrysopilus* Macquart, is found throughout the globe, including one species that extends into the tundra (Nartshuk, 1995), and another as high as 4000masl in the Neotropics (pers. obs.). The Palaearctic and Oriental regions are the most species-rich areas for *Chrysopilus*, although there are certainly many more species in the Neotropical region than are currently recognized.

Rhagio Fabricius is distributed throughout the Holarctic reaching its southernmost extension in the Oriental region where it is found in Java and Sumatra. Putative close relatives of *Rhagio* such as *Rhagina* Malloch and *Desmomyia* Brunetti have localized distributions within the range of *Rhagio*. *Rhagina* is restricted to China and Java, and *Desmomyia* is known only from India (Brunetti, 1912; Yang et al., 1997). *Sierramyia* may also be related to these genera. It has been collected only from mountainous regions of Mexico.

Atherimorpha White is distributed in a typical Gondwanan fashion, found in Australia, Patagonia, and South Africa. Its putative sister taxon, *Arthroteles* Bezzi (Stuckenberg in Nagatomi and Nagatomi, 1990) is endemic to South Africa. Fossil evidence suggests that the biogeographical history of this lineage may actually be more complicated than simple Gondwanan vicariance. A fossil specimen reported to have strong affinities to *Arthroteles*, *Palaeoarthroteles mesozoicus*, was found and described from Transbaikalia (Russia), in sediments aged between the Upper Jurassic and Lower Cretaceous (Kovalev and Mostovski, 1997).

Bolbomyia Loew was originally described from the Baltic region as a fossil in amber, and living members of the genus inhabit the Russian Far East, Canada, and the USA. *Arthroceras* Williston and *Spania* Meigen exhibit similar distributions, and into Asia (Nagatomi, 1966).

Litoleptis is unusual in having a pan-Pacific distribution, with species endemic to Alaska, the Philippines, China, and Chile (Chillcott, 1963; Hennig, 1972; Yang et al., 1997).

Studies of current distributional patterns of living genera in light of new phylogenetic evidence may provide insights into the biogeographic history of lineages within the Tabanomorpha. Fossils are an important element, however, in providing evidence to refute hypotheses of vicariance and illuminate other aspects of biogeographic patterns that are germane to the study of Rhagionidae as a whole (Rosen, 1990). The group appears old and anciently abundant enough to have been distributed throughout Laurasia and Gondwanaland before the breakup of these continents. Therefore, at least some current biogeographic patterns may be explained as the survival of relict populations of formerly cosmopolitan species.

Phylogenetic Hypotheses

Although most authorities have incorporated their ideas of phylogeny into a classification scheme, others have proposed groupings without formalizing their

recommendations for changes in taxonomic rank or placement. In this section, I will briefly review the most recent and pertinent phylogenetic ideas, sometimes represented by classifications alone, and how they differ from one another regarding Rhagionidae and other genera within the Tabanomorpha. These are the phylogenetic hypotheses I intend to test in this study.

1. Monophyly and Position of Pelecorhynchidae.

    a. *Glutops*, *Pelecorhynchus*, and *Pseudoerrina* a paraphyletic unit (Krivosheina, 1971; Nagatomi, 1982a).
    b. *Glutops*, *Pelecorhynchus*, and *Pseudoerrina* a monophyletic unit (Woodley, 1989; Sinclair, 1992; Stuckenberg, 2001).
    c. All three genera a clade, within Rhagionidae (Stuckenberg, 2001).
    d. All three genera a clade, sister to Athericidae + Tabanidae (Woodley, 1989; Sinclair, 1992; Wiegmann et al., 2000; Wiegmann et al., 2003).
    e. *Glutops* and *Pseudoerrina* sister clade to the rest of Rhagionidae (Nagatomi, 1982a).
    f. *Glutops* a clade outside of Rhagionidae (Krivosheina, 1971).

2. Position of Vermileonidae.

    a. Vermileonidae outside of Tabanomorpha, suitable for separate infraordinal rank recognition (Nagatomi, 1977; Nagatomi, 1991; Griffiths, 1994; Stuckenberg, 2001).
    b. At the base of Tabanomorpha (Nagatomi, 1977; Sinclair et al., 1993).

c. Sister of Rhagionidae within Tabanomorpha (Wiegmann et al., 2000; Yeates, 2002; Wiegmann et al., 2003).

3. Position of *Bolbomyia*.

a. A xylophagid (Loew, 1850; James, 1965).

b. A member of Rhagioninae (Nagatomi, 1982a).

c. A member of a separate subfamily, Bolbomyiinae, within Rhagionidae (Stuckenberg, 2001).

d. Together with *Austroleptis* and *Litoleptis*, within or outside of Rhagionidae (Grimaldi and Cumming, 1999).

e. Sister taxon to Athericidae + Tabanidae (Sinclair et al., 1993).

4. Position of *Austroleptis*

a. A separate subfamily, Austroleptinae, within Rhagionidae (Nagatomi, 1982a).

b. A monotypic family, within Tabanomorpha (Stuckenberg, 2001).

c. A xylophagomorph (James, 1965; Colless and McAlpine, 1991; Sinclair et al., 1993).

d. Together with *Bolbomyia* and *Litoleptis*, within or outside of Rhagionidae (Grimaldi and Cumming, 1999).

5. Monophyly and Position of Spaniidae.

a. Spaniinae (-idae) form a monophyletic unit within Rhagionidae (Nagatomi, 1982a).

b. Spaniidae a clade outside of Rhagionidae (Stuckenberg, 2001).

6. Monophyly of *Chrysopilus*.

a. *Chrysopilus* monophyletic with respect to *Schizella* and *Solomomyia* (Nagatomi, 1982a).

7. Monophyly of *Rhagio*.

a. *Rhagio* monophyletic with respect to *Rhagina* and *Desmomyia* (Nagatomi, 1982a).

8. Monophyly of *Atherimorpha*.

a. *Atherimorpha* monophyletic with respect to *Arthroteles* (Stuckenberg in Nagatomi and Nagatomi, 1990).

Chapter 2. Phylogenetic Analysis of the Genera of the Rhagionidae and Related Taxa.

Introduction

Shared inheritance of both genotypic and phenotypic characters through common ancestry is our evidence of evolution and the relatedness of living organisms. The following research attempts to gather these characters together, systematically, to understand the relationships among rhagionid genera and their place in lower Brachycera.

Traditional morphological techniques have generated many robust hypotheses on the phylogeny of many organisms, attesting to the rigor of morphological study. However previous work on the rhagioniform Diptera has been limited to particularly accessible character systems, such as antennal, wing, and thoracic morphologies, and may have produced a somewhat distorted view of underlying phylogenetic patterns. A comprehensive, systematic approach is taken here to develop and evaluate characters of the head including the internal mouthparts, thorax, abdomen, male genitalia, and female genitalia. One of the major aims of this effort is to develop new, phylogenetically informative characters, as well as adopt and evaluate character systems used in the past.

The value of morphology for phylogenetic analysis has recently been in some dispute, with the popularity and acknowledged utility of molecular systematic methods for addressing phylogenetic problems (Baker and Gatesy, 2002; Scotland et al., 2003;

Jenner, 2004). Phylogenetic analyses based on morphology alone may lack statistical power to assess branch support adequately simply due to the few number characters that available for morphological analysis. The decision of whether to study morphology or molecular characters is, for the most part however, a false dichotomy. It is readily apparent that the two data types are complimentary, as each serves as an independent source of evidence regarding the phylogeny of the group. The hypotheses generated from each source may be compared against one another and the data from each may also be combined as part of a total evidence approach, to yield a combined hypothesis. Wiegmann et al. (2000) showed that 28S nuclear ribosomal DNA that may be used to track divergences among rhagionid and related genera. His work provides the foundation for further work that I develop here, to complement and compare against independent estimates of phylogeny for the group generated from morphological data.

The three sections of this chapter are thus laid out as followed. The opening section treats the morphology of the group, in which over two hundred characters were generated and scored for 34 species of Rhagionidae *sensu* Woodley (1989) in 18 genera (*Alloleptis*, *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Austroleptis*, *Bolbomyia*, *Chrysopilus*, *Desmomyia*, *Litoleptis*, *Ptiolina*, *Rhagio*, *Schizella*, *Sierramyia* (='*Neorhagio*' in Nagatomi, 1982a), *Spania*, *Spaniopsis*, *Stylospania*, *Symphoromyia*), 3 species of Pelecorhynchidae *sensu* Woodley (1989) in 3 genera (*Glutops rossi*, *Pseudoerrina jonesi*, *Pelecorhynchus personatus*), 2 species of Vermileonidae in 2 genera (*Lampromyia canariensis*, *Vermileo vermileo*), 2 species

of Athericidae in 2 genera (*Atherix pachypus* and *Dasyomma atratulum*), and 2 species of Tabanidae in 2 genera (*Dichelacera marginata* and *Tabanus atratus*). Four species of xylophagid taxa (*Arthropeas americana*, *Coenomyia ferruginea*, *Dialysis rufithorax*, *Xylophagus lugens*) were used as outgroup taxa. This data is analyzed using maximum parsimony.

The second section of this chapter is a molecular treatment of the group. An approximately 3000bp stretch of 28S rDNA is amplified for molecular phylogenetic analysis for 22 species of Rhagionidae *sensu* Woodley (1989) in 8 genera (*Atherimorpha*, *Austroleptis*, *Bolbomyia*, *Chrysopilus*, *Ptiolina*, *Rhagio*, *Spaniopsis*, *Symphoromyia*), 2 species of Pelecorhynchidae *sensu* Woodley (1989) in 2 genera (*Glutops rossi* and *Pelecorhynchus personatus*), 3 species of Vermileonidae in 2 genera (*Leptynoma* and *Vermileo*), 3 species of Athericidae in 2 genera (*Atherix* and *Dasyomma*), and 4 species of Tabanidae in 2 genera (*Chrysops* and *Tabanus*). Sequences of *Pachygaster leachii* (Stratiomyiidae), *Pantophthalmus* sp. (Pantophthalmidae), and xylophagid taxa (*Arthropeas magnum*, *Coenomyia ferruginea*, *Dialysis elongate*, *Exeretonevra angustifrons*, *Heterostomus* sp., and *Xylophagus abdominalis*) were taken from GenBank and used as outgroup taxa. This data is analyzed using maximum parsimony and maximum likelihood optimality criteria.

The third section of this chapter combines the morphological and molecular data of the previous sections using two techniques to arrive at a best-estimate phylogeny of

the group. The first technique uses a concatenated morphological and molecular data set for simultaneous analysis using maximum parsimony and Bayesian inference. The second approach is a type of supertree analysis, in which a parsimony analysis is conducted on a matrix representation of the trees generated from the morphological and molecular data. This analysis gives an overall picture of the hypotheses generated from both morphological and molecular analyses in a single tree diagram, in which all taxa are included.

A re-classification of the group based on the phylogenetic analyses of this chapter is addressed in Chapter 3.

Morphological Treatment

Introduction

A thorough understanding of the morphological diversity present in the Rhagionidae and related groups is a necessary step in satisfying three primary aims of this study. The first aim is to find new, phylogenetically informative characters particularly in character systems that have been overlooked in the past, such as the internal structures of the female terminalia and characters revealed by using SEM technology. The second aim is to evaluate characters and/or character systems that have been used in the past, and develop these character systems further by using a greater taxon sampling. A large matrix consisting of new and well-developed characters and a full complement of taxa is essential in accomplishing the third aim, which is the application of modern cladistic methods to develop a rigorous hypothesis of phylogenetic relationship for the group based on morphology (Hillis et al., 1994; Rannala et al., 1998).

Thus far, groupings based on morphological characters have led to discordant classification schemes. *Pelecorhynchus* Macquart, for example, has been placed as sister to the Rhagionidae on the basis of male and female genitalic characters (Nagatomi, 1977), within the Rhagionidae based on female abdominal characters (Stuckenberg, 2001), and, along with *Glutops* and *Pseudoerrina*, sister to the Athericidae and Tabanidae based on larval characters (Teskey, 1970; Sinclair, 1992; Woodley, 1989). Similarly, *Bolbomyia* Loew may be located among the Xylophagidae because of its flattened clypeus (James, 1965), among the Rhagionidae

on account of an elongated intersegmental region in the female abdomen (Nagatomi, 1982a; Stuckenberg, 2001), together with *Austroleptis* and *Litoleptis* (inside or outside of Rhagionidae) because it lacks wing vein M_3 (Grimaldi & Cumming, 1999), or as sister to Athericidae and Tabanidae on account of having aedeagal tines in the male genitalia (Sinclair et al., 1993).

In taxa such as *Austroleptis* Hardy, highly autapomorphic morphology has caused higher level taxonomic instability (Nagatomi, 1982a; Nagatomi, 1984). *Austroleptis* has evolved in such a way that it shares few character states with possible relatives, obscuring its relation to the rest of Lower Brachycera. Thus, ecological information, such as larval feeding habits, has been used as a surrogate to direct morphological evidence as a basis for proposed classification (Colless & McAlpine, 1991; Sinclair et al., 1993). Stuckenberg preferred to use the derived state of *Austroleptis* as evidence for supporting its own, family-level recognition (Stuckenberg in Nagatomi, 1982a; Stuckenberg, 2001). Similarly, the autapomorphic morphology of *Litoleptis* Chillcott has led to speculation regarding its classification (Chillcott, 1963; Hennig, 1972; Grimaldi & Cumming, 1999).

Morphology may be an insufficient source of information for tracking tabanomorph lineage divergences that may be as much as 170 million years old (Wiegmann et al., 2003). Advances in molecular systematics and statistics-based methods of phylogenetic inference (e.g., Hillis et al., 1994; Huelsenbeck, 1995; Huelsenbeck and Crandall, 1997; Huelsenbeck and Rannala, 1997; Rannala et al., 1998; Huelsenbeck

and Bollback, 2001; Huelsenbeck et al., 2001; Huelsenbeck et al., 2002; Felsenstein, 2004) have already shown promise in helping to resolve ancient divergences and will certainly gain more favor as morphological inquiries are exhausted (Hillis and Wiens, 2000; Baker and Gatesy, 2002). Study of tabanomorph morphology however is far from exhausted. Most of the disagreement in the classification of taxa such as *Pelecorhynchus*, *Bolbomyia*, and *Austroleptis* is the result of studying a limited set of characters and/or taxa. A better understanding of tabanomorph morphology clearly is needed to refine classifications based on morphology and to provide a larger context for molecular studies.

Materials and Methods

Laboratory Methods

The abdomens of pinned, dried specimens were dabbed with a small amount of approximately 5% KOH to soften the tissue and allow for the entire abdomen (females) or terminal segments (males) to be gently torn off. For mouthpart dissections, the entire head is taken. The abdomen or head was then placed in 10% KOH solution in a vial warmed in a hot water bath (~95°C) for approximately 10 minutes. The material was removed and rinsed thoroughly with water. For males, the terminalia were dissected by separating the epandrium from the gonocoxites. This was done either in water or glycerin. For females, the lateral membrane separating the dorsal (tergites) and ventral (sternites) sclerites of the abdomen was split to expose the internal tissues. The specimens were then placed in a saturated solution of chlorozol black in water for approximately 5-7 minutes for staining. Excess dye was removed in water and further dissections of the female terminalia were carried out in

water, 80% ethanol, or glycerin. Preparations were placed on a microscope slide, in a small pool of glycerin, covered with a cover slip, and photographed digitally. Digital images were captured using a JVC KY-F70 top mounted digital camera, and enhanced using AutoMontage photo imaging software. For long-term preservation, terminalia are stored in glycerin in a genitalia vial and are mounted on the pin underneath the specimen and label(s).

Scanning electron microscopy (SEM) was carried out for larval specimens to illustrate surface structure in *Pelecorhynchus* sp., *Glutops rossi* Pechuman, *Vermileo* sp., *Rhagio* sp., *Symphoromyia* sp., and *Chrysopilus* sp. A cross section cut was made with micro scissors to excise both the anterior segments (containing the head) and the posterior segments containing the terminal segment. These sections were rinsed in hydrogen peroxide solution (H_2O_2), transferred to 100% EtOH, then soaked twice for several minutes in pure hexamethyldisilazane (HMDS) under a fume hood and allowed to dry. The specimens were then affixed to SEM flat-disc mounts with water-soluble Elmer's glue. Adults were mounted directly onto SEM mounts. SEM imaging was done at the Smithsonian Institution Scanning Electron Microscopy Core, in the National Museum of Natural History, with the assistance of Scott Whittaker, Smithsonian SEM Lab Manager. All images were taken using the Philips XL-30 ESEM with LaB6 filament and the SIS AnalySIS Image analysis package, in the low vacuum mode using water vapor.

The larval characters are used to help resolve taxa at the genus level. Species-level differences of tabanomorph larvae are very poorly documented and as a result, larvae included in this study were identifiable to genus level only. Larval characters scored for *Atherix pachypus* were taken from several undetermined *Atherix* species and ambiguities represent apparently interspecific differences between specimens. Similarly, all *Chrysopilus*, all *Rhagio*, and all *Symphoromyia* species were scored from the same set of congeneric larval specimens. Character coding, therefore, is identical for species within these genera and do not help to resolve infrageneric relationships. A single larval specimen identified as *Ptiolina* sp. was used to score *P. mallochi* and *P. zonata*.

Taxon Sampling

The ingroup taxa sampled here include representatives from all of the genera in Rhagionidae recognized by Nagatomi (1982), with the exception of the monotypic genus *Solomomyia*, which is characterized as a close relative of *Chrysopilus* (Nagatomi, 1982a) and *Alloleptis*, a genus only known from a male specimen (Nagatomi, 1982a). Outgroup taxa included representatives from all families within Tabanomorpha, as well as several genera within the Xylophagomorpha. Table 11 shows the species used in the morphological phylogenetic analysis, along with their recent family designations, and the geographic distribution of the specimens examined for each species. The scoring of several species was restricted to limited availability of specimens. These species are listed in Table 12, with explanations.

The breadth of taxon sampling was determined on the basis of availability of specimens for study and the importance of taxa for testing specific hypotheses of relationship. These hypotheses include the monophyly and position of Pelecorhynchidae (Krivosheina, 1971; Nagatomi, 1982a; Stuckenberg, 2001; Woodley, 1989; Sinclair, 1992; Wiegmann et al., 2000); the monophyly and position of Spaniinae (Nagatomi, 1982a; Stuckenberg, 2001); the monophyly of *Chrysopilus* (Bezzi, 1917; Nagatomi, 1982a), *Rhagio* (Malloch, 1932a; Nagatomi, 1982a; Yang and Nagatomi, 1992; Yang et al., 1997), and *Atherimorpha* (Nagatomi, 1982a, 1990); the position of Vermileonidae (Nagatomi, 1977, 1991; Griffiths, 1994; Stuckenberg, 2001; Sinclair et al., 1993; Wiegmann et al., 2000; Yeates, 2002); the position of *Bolbomyia* (James, 1965; Nagatomi, 1982a; Sinclair et al., 1993; Grimaldi & Cumming, 1999; Stuckenberg, 2001); and the position of *Austroleptis* (Nagatomi, 1982a; Colless & McAlpine, 1991; Stuckenberg, 2001; Sinclair et al., 1993; McAlpine). Species were used as terminals, an approach that is best for reconstructing phylogenetic relationships (Yeates, 1995; Wiens, 1998). In most cases, multiple exemplars were used to sample species diversity, especially for large genera within Rhagionidae, and to increase the accuracy of phylogenetic inference (Hillis, 1996; Rennala et al., 1998). Where possible, highly autapomorphic exemplars were avoided.

A USNM ENT barcode label was attached to the pin of all specimens examined, except most non-dissected specimens belonging to the genera *Rhagio* and *Chrysopilus*. The barcodes provide a unique identifier to each specimen, and are

tracked using a FilemakerPro database. The database of rhagionid specimens is published on the National Museum of Natural History, Entomology Department web server and may be viewed at http://entomology.si.edu/Entomology/Rhagionidae/Search.lasso.

Table 2. Taxon sampling, morphological analysis.

Taxa	Recent Family Placement	Region	Geographic Distribution of specimens examined
Alloleptis tersus	Rhagionidae	OR	Indonesia: Sulawesi
Arthroceras pollinosum	Rhagionidae	NA	USA: CA, CO, OR, NM, WA, WN
Arthroteles bombyliiformis	Rhagionidae	AT	South Africa: Cape Province
Atherimorpha atrifemur	Rhagionidae	NT	Chile: Chiloé, Llanquihue, Malleco, Osorno Provinces
Atherimorpha nemoralis	Rhagionidae	NT	Chile: Arauco, Cautín, Chiloé, Llanquihue, Malleco, Osorno, Valdivia Provinces
Atherimorpha vernalis	Rhagionidae	AU	Australia: Tasmania
Atherix pachypus	Athericidae	NA	USA: CO, MT
Austroleptis multimaculata	Rhagionidae/ Austroleptidae	AU	Australia: Tasmania
Bolbomyia nana	Rhagionidae	NA	Canada: Ontario, Quebec USA: MD, MI, NY, PA, VA
Chrysopilus ferruginosus	Rhagionidae	OR	Philippines: Luzon
Chrysopilus panamensis	Rhagionidae	NT	Costa Rica: Limón
Chrysopilus quadratus	Rhagionidae	NA	USA: MD, NH, PA
Chrysopilus thoracicus	Rhagionidae	NA	USA: MD, TN
Dasyomma atratulum	Athericidae	NT	Chile: Chiloé
Desmomyia thereviformis	Rhagionidae	OR	India: E. Punjab.
Dichelacera marginata	Tabanidae	NT	Colombia: Antioqua
Glutops rossi	Rhagionidae/ Pelecorhynchidae/ Glutopidae	NA	Canada: Alberta, British Columbia
Lampromyia canariensis	Vermileonidae	AT	Spain: Canary Islands
Litoleptis alaskensis	Rhagionidae/ Spaniidae	NA	USA: AK
Pelecorhynchus personatus	Rhagionidae/ Pelecorhynchidae	AU	Australia: NSW, Queensland
Pseudoerrina jonesi	Rhagionidae/ Pelecorhynchidae	NA	USA: WN
Ptiolina lapponica	Rhagionidae/ Spaniidae	PA	Finland: Petsamo, Ponoj
Ptiolina majuscula	Rhagionidae/ Spaniidae	NA	USA: AK
Ptiolina mallochi	Rhagionidae/ Spaniidae	NA	USA: AK

Taxa	Recent Family Placement	Region	Geographic Distribution of specimens examined
Ptiolina zonata	Rhagionidae/ Spaniidae	NA	Canada: Manitoba, NWT, Yukon USA: AK, WA
Rhagio costatus	Rhagionidae	NA	USA: CA, WA
Rhagio hirtus	Rhagionidae	NA	USA: IN, MD, NH, PA, VA
Rhagio mystaceus	Rhagionidae	NA	USA: MI, MD, NH, NJ, VA, VT
Rhagio plumbeus	Rhagionidae	NA	USA: PA, MN
Rhagio scolopaceus	Rhagionidae	PA	Switzerland: Grisons, Zurich
Rhagio sinensis	Rhagionidae	OR	China: Fukien
Rhagio vertebratus	Rhagionidae	NA	USA: PA, ME
Rhagina incurvatus	Rhagionidae	OR	Indonesia: Java
Schizella furcicornis	Rhagionidae	OR	Philippines: Luzon, Mindanao
Sierramyia chiapasensis	Rhagionidae	NT	Mexico: Chiapas
Spania nigra	Rhagionidae/ Spaniidae	PA	Austria: Tirol Switzerland: Om USA: WN
Spaniopsis longicornis	Rhagionidae/ Spaniidae	AU	Australia: NSW
Spaniopsis clelandi	Rhagionidae/ Spaniidae	AU	Australia: ACT, NSW
Stylospania lancifera	Rhagionidae	OR	Philippines: Samar
Suragina concinna	Athericidae	NA	USA: TX
Symphoromyia hirta	Rhagionidae	NA	USA: CT, MD, PA, VA
Symphoromyia cruenta	Rhagionidae	NA	USA: CA
Tabanus atratus	Tabanidae	NA	USA: GA
Vermileo vermileo	Vermileonidae	PA	Isreal: Nahal Tut Spain: Balearic Islands
Arthropeas americana	Xylophagidae	NA	USA: MI
Coenomyia ferruginea	Xylophagidae/ Coenomyiidae	NA	USA: MD, MN
Dialysis rufithorax	Xylophagidae	NA	USA: MD, VA
Xylophagus lugens	Xylophagidae	NA	USA: MD, VA

Table 3. Species with incomplete sampling.

Species	Gender unavailable for direct examination	Comment
Alloleptis tersus	Male and Female	The male of this species was scored using the literature (Nagatomi, 1984). The female of *Alloleptis tersus* is unknown.
Litoleptis alaskensis	Female	A female of *Litoleptis alaskensis* was deposited in the Canadian National Collection, but subsequently loaned to the B. P. Bishop Museum. The Bishop Museum does not have a record of this and the specimen is not currently in Hawaii. The female of this species has been examined by Nagatomi (1982), however it is undescribed in the literature.
Pseudoerrina jonesi	Male	The male of this species was scored using Nagatomi

Species	Gender unavailable for direct examination	Comment
		(1984).
Stylospania lancifera	Female	This species is known from a single individual, which is male. The holotype was used for scoring.

Phylogenetic Analysis

Phylogenetic analyses were performed using two computer programs, on both PC and Macintosh operating systems. PAUP* 4.0b10 (Swofford, 2001) was used for maximum parsimony (MP) phylogenetic analyses. MrBayes 3.0b4 (Ronquist and Huelsenbeck, 2003) was used for Bayesian inference (BI).

For parsimony analyses, 1000 heuristic search replicates were performed with random-taxon-addition, tree bisection reconnection (TBR) branch swapping, steepest decent and 'MulTrees' options in effect. All characters were treated unordered and assigned equal weights. Scores of all MP trees were verified to avoid artifactually inflated sets of MP trees. In order to gauge the internal consistency of the data, bootstrap analyses (Felsenstein, 1985) were carried out. MP bootstrap analyses were performed with 1000 repetitions, each with 30 random-taxon-addition TBR heuristic searches. MacClade 4.03 (Maddison and Maddison, 2000) was used to analyze character change and support inherent in the phylogenetic tree.

Results

Morphological Characters and Character State Coding

The morphology, its scoring, and the particular character states present among the sampled taxa are detailed below. I begin with the head of the adult and work

posteriorly, covering aspects of the thorax, wing, legs, abdomen, male genitalia, and external and internal female genitalia. I follow this with a discussion of the larval characters. General notes and a summary of each major character system precede a more detailed discussion of each of the characters that were inspected over the course of the study. Not all characters were used for the phylogenetic analysis.

Alternative scorings of the same character are possible, given differing perspectives on perceived character evolution, especially for complex characters. In order to explore this realm of possible character state codings, some of the same characters were scored in several different ways. This was done as an explicit demonstration of how characters may be scored (or how they've been scored in the past), based on differing interpretations of character evolution.

Novel character codings may work for a limited taxon set, but can break down once a greater sampling is included. Even though these character codings ultimately fail, the effort in developing them is not necessarily for naught. The way in which they fail may be informative and for this reason, are preserved and discussed below.

In total, over two hundred characters were generated and scored for the included taxon set (Table 13). Ultimately, each character was evaluated on its consistency, clarity, and independence from other characters. Inferior, non-independent character state codings were eliminated for the phylogenetic analysis, which used approximately 150 characters.

Adult head.

[#2; note 1]. **Clypeus.** The bulbous clypeus is a putative synapomorphy for Tabanomorpha. All Rhagionidae *sensu lato* have this character, except *Austroleptis*. In *Austroleptis*, the clypeus is recessed, as in Xylophagidae. The clypeus in *Litoleptis* is nearly flat, as it is in *Bolbomyia*. For both of these genera, the clypeus was scored as bulbous, although it is only slightly so. I looked at many *Chrysopilus* species and there are differences within this genus in the form of the clypeus; some are produced anteriorly much more than in other *Chrysopilus* species. An attempt was made to score relative to the sharpness of the break between the eye and clypeus, but this is variable within large genera such as *Chrysopilus* and *Symphoromyia* and the lack of distinct differences between the variation of states among genera discouraged me from developing this aspect of the clypeus further.

[#3]. **Scape.** In some species of Tabanomorpha, the scape is much larger than pedicel. This occurs across a broad range of species, including members of *Atherimorpha*, *Desmomyia*, *Dichelacera*, *Glutops*, *Lampromyia*, *Pelecorhynchus*, *Symphoromyia*, and *Vermileo*. The scape is larger than the pedicel in two South American *Atherimorpha* species (*A. albohirta* and *A. praefica* (subgenus *Philippoleptis* Malloch)), however these species are apparently autapomorphic for this condition and are not included in this taxon sample.

[#4]. **First flagellomere (lateral compression).** In most taxa, the amount of lateral compression of the first flagellomere is easily scored. Species of *Symphoromyia*, *Chrysopilus*, and *Rhagio* have first flagellomere clearly laterally compressed, whereas in species of *Arthroteles, Arthroceras*, *Glutops*, *Pseudoerrina*, *Pelecorhynchus*, and Xylophagidae, the first flagellomere is rounded in cross section. There are cases, however, where congenerics may differ in having laterally compressed or rounded first flagellomere. For example *Ptiolina* (*Omphalophora*) *majuscula* has the first flagellomere rounded, whereas most *Ptiolina* species have a clearly flattened first flagellomere. Variation of this sort is also present in *Atherimorpha*. Some difficulties may exist in scoring this character, such as in *Stylospania*, where the cross section of the first flagellomere is laterally compressed somewhat, and oval in cross section. In these instances, the scoring may be subtle. *Stylospania lancifera* is scored as having a laterally compressed first flagellomere.

[#5]. **Antennal composition (not used in phylogenetic analysis).** Stuckenberg (1999) has hypothesized that the brachycerous antenna has evolved in a progressive fusion of segments, resulting in a transformation series that steadily concentrates 8 flagellomeres into a single, stylate flagellomere. As an example, he used character transformations apparent within the Vermileonidae. The fundamental flaw in his argument is that character homology is defined by the common ancestry of character states, arising from a single character. The reduction of the flagellomere in Brachycera may be the result of similar evolutionary pressures, but the transformations, for example, in Therevidae, Xylophagidae, and Empididae are

independent events and therefore, are analogous, and not homologous, to the transformation series apparent in Vermileonidae. Due to the complex nature of the evolution of the antenna, it is difficult to assess homology confidently, but I prefer to score the antenna as part of two characters rather than one. The character as scored here, I believe, may be susceptible for mistaking analogy for homology and is not used in the phylogenetic analysis. The modified characters are below.

[#6]. **Antennal flagellum (presence of break).** Hennig (1972) proposed that a break between the first flagellomere and those distal to it could be a synapomorphy for the Rhagionidae. There may be some confusion in this character, however. For example, *Arthroteles* is scored as having a distinct break whereas *Arthroceras* is scored as gradually tapering, even though the antennae are similar to one another. In *Arthroteles*, however, the first flagellomere is distinct in that it is not only enlarged, but the flagellomeres distal to it are smaller, cylindrical, and not tapering. In *Arthroceras*, each flagellomere tapers distally, starting with the first flagellomere. This is also the case in *Glutops*.

[#7]. **Segment(s) distal of first flagellomere.** Where there is an abrupt change in shape of the antenna after the first flagellomere, distal segments may be of three types: 1) as segmented flagellomeres (as in *Alloleptis*, *Arthroteles*, *Atherimorpha*, *Austroleptis*, and *Bolbomyia*) 2) stylate (as in *Litoleptis*, *Ptiolina*, *Spania*, and *Spaniopsis*) or 3) aristate (as in *Atherix*, *Chrysopilus*, *Dialysis*, *Lampromyia*, *Rhagio*, *Suragina*, *Symphoromyia*, and *Vermileo*). Nagatomi (1982) has also asserted that

having an antenna with a tapering, stylate first flagellomere distinguishes subfamily Spaniinae.

[#8]. **Arista.** The arista is scored as bare or microsetose is applicable for a subset of taxa (those with aristate antenna). There may be a continuum of character states, although most *Chrysopilus* species have an arista that is clearly more microsetose than most *Rhagio* species. Bare as used here indicates that the microsetae of the antenna are not prominent; that is, when they are shorter than the width of the arista. Under high magnification, such "bare" arista will reveal microsetae. [*R. gracilis* (Johnson) is as microsetose as *S. limata* Coquillett, but bare for most of the basal half and certainly less microsetose than in many *Chrysopilus* species.]

[#9]. **Eyes (microsetae).** At first, it appeared that many lower brachyceran flies had bare eyes, but upon very close inspection, short, sparsely distributed microsetae are visible in most species. *Alloleptis tersus*, *Coenomyia ferruginea* and *Pseudoerrina jonesi* have eyes that are conspicuously setose. It is worth mentioning however, that within the genus *Pseudoerrina*, this character state is not invariable. In *Pseudoerrina fuscata* (Nagatomi, 1982a: 39), the eyes are practically bare, as in most lower brachycerans.

[#10]. **Eyes in male (separation).** Males in these genera have eyes that either touch centrally (holoptic) or are separated (dichoptic). It is worth mention that although males of most *Arthroteles* species are holoptic, there is one species, *Arthroteles*

longipalpus Nagatomi & Nagatomi, where the male is dichoptic. Similarly, male dichoptism is known to occur in *Chrysopilus*, *Pelecorhynchus*, and *Rhagio*, although all species sampled for this study have holoptic males. Male holoptism is the most common condition for these genera and is most likely the plesiomorphic state.

[#11]. **Eyes in male (dorsally flattened).** Dorsally flattened head in males may be a morphological adaptation associated with swarming behavior. More dorsally-oriented eye surface area allows for greater vision in the vertical plane. The condition is found in *Arthroteles*, *Austroleptis*, *Glutops*, *Symphoromyia*, and many tabanids including *Dichelacera* and *Tabanus*.

[#12]. **Eyes in male (facets).** Differential sizing of eye facets may also be associated with swarming behavior. All species with dorsally flattened heads have facets either gradually tapering in size ventrally or divided into upper and lower areas. However, species with dorsally rounded heads may exhibit any of the eye facet arrangements (scored here). Turner (pers. com.) has seen *Chrysopilus* and *Rhagio* species swarm in Washington state; Wood (pers. com.) has witnessed *Glutops* hilltopping. *Symphoromyia* is also a well known swarmer (refs).

[#13]. **Parafacials in male.** In *Dichelacera* and *Tabanus*, parafacials are lightly protruding. It is also a distinctive feature of *Desmomyia*, *Pelecorhynchus* and *Glutops*. Some, but not all *Symphoromyia* species also have swollen parafacials.

[#14]. **Occiput.** The concave occiput present in members of Tabanidae is distinctive. *Pelecorhynchus* has a similar head shape.

[#15]. **Head width.** Teskey used the width of the head in relation to the thorax to characterize *Glutops* (1970: 1171). Most taxa surveyed here have a head that is approximately the same width as the thorax, although there is variation among species within genera (*Chrysopilus*, *Rhagio*, *Spaniopsis*) and even within species (*Chrysopilus quadratus*, *Spaniopsis clelandi*, *Symphoromyia cruenta*). The differences between approximately the same width and wider may be subtle, as in the case of *Pseudoerrina jonesi* (where the state is scored as head wider than thorax).

Adult mouthparts.

Nagatomi & Soroida (1985) carried out an exhaustive survey of the mouthparts of orthorrhaphous Brachycera and concluded that the adult mouthparts are of little value to help solve phylogenetic problems (1985, p. 304). The mouthparts show a high degree of plasticity; there are some trends, but no unambiguous changes were found to confirm known phylogenetic placements. It appears that mouthpart morphologies are generally more indicative of feeding behavior than common ancestry. Blood feeders *Symphoromyia* and *Spaniopsis*, for instance, share more characters with the Tabanidae and Athericidae than with the rest of the putative close relatives within the Rhagionidae or Spaniidae.

[#16]. **Labellum (not used in phylogenetic analysis).** Some rhagionids, such as *Sierramyia chiapasensis*, have a distinctively large labellum in relation to the size of

their palps. *Arthroteles* species exhibits the other extreme case, in having a much reduced labellum (despite its long proboscis). This character was scored for both sexes, when both were available, unless otherwise noted. A high amount of variation of this character within several species and genera suggests that labellum size is a fairly labile character, subject to shifting evolutionary pressures associated with feeding habit and/or habitat. The measure of labellum size itself is problematic since palp size, and other reference measures of the head, may vary independently. This may result in a large labellum being scored as short, for instance, in cases where the palps are especially long. For this reason, and for the apparent high rate of change of this character, it was removed from the phylogenetic analysis.

[#17]. **Pseudotrachae.** *Bolbomyia*, *Litoleptis*, and *Lampromyia* are the only taxa surveyed that did not have pseudotracheae. *Austroleptis* has distinctive pseudotracheae that have taenidia-like ribbing. Other taxa, such as *Arthroceras* show some transverse ribbing of the pseudotracheal channels, but none to such a strong degree as in *Austroleptis*. Variation of this kind in the pseudotracheae, however are difficult to score discretely. Therefore, only the presence or absence of pseudotracheae was scored for phylogenetic analysis.

[#18]. **Theca (elongation).** The theca is the sclerite at the ventrobasal area of the labellum. The length of the theca varies considerably among taxa, however two states were most readily apparent and easily scored. Where the theca is clearly longer than wide (such as in *Arthroteles*, *Austroleptis*, *Dichelacera*, and *Lampromyia*, among

other taxa), the character is scored as elongate. The theca is scored as short, where as wide as long or just slightly longer than wide. Most *Dasyomma* species are as *D. atratulum* (scored here) in having a short theca, however in at least one *Dasyomma* species (*D. coeruleum*), the theca is elongate. Similarly, *Symphoromyia* species may either have short or long thecae. It is divided medially into two sclerites in most basal brachycerans, however it is entirely fused as a single sclerite in *Atherix*, *Dasyomma*, *Dichelacera*, and presumably in other Tabanidae. *Atrichops* has a divided theca, and therefore, having a fused theca is not an unambiguous synapomorphy for the Athericidae + Tabanidae.

[#19]. **Theca (lateral sclerite composition; alternate scoring not used for phylogenetic analysis).** Variation is present in the way in which the theca is composed. The theca is often divided medially by a central suture. In this case, the lateral thecal surfaces are touching along the entire length medially, or are curved ")(" and showing some separation. At first, these states were scored independently (as currently scored). However both states are present within *Atherimorpha* and *Spaniopsis*, suggesting that the character was divided too finely and consequently, the two states were then lumped together (and scored in following character). This character is most easily viewed after the head is dissected. Therefore, there are a number of taxa, particularly the rare ones on loan, that are not scored for this character, since the dissection of the head was not carried out. This character is not included in the phylogenetic analysis.

[#20]. **Theca (lateral sclerite composition).** Characters of the theca were rescored so that the character states were more discrete, and therefore, more easily assessed. After looking at the full complement of specimens available, states of the theca seemed more naturally divided into three states; lateral sclerites separate, lateral sclerites adjacent and/or separated by medial suture, or fused into single sclerite, without medial suture.

[#21]. **Palp segment number.** The reduction in palp number from three to two is a synapomorphy for Brachycera. The number of palp segments varies across the Tabanomorpha, however, and it does not appear to be an especially conserved feature.

[#22]. **Palps (relative length of each segment).** For genera with two palps, the length of palp segments relative to one another is fairly consistent among congenerics. Most genera have distal segment longer than proximal segment, however, the proximal segment is longer than the distal segment in *Tabanus*, *Bolbomyia*, *Vermileo* and *Austroleptis*. There is also some variation within species. *Bolbomyia nana* may either have distal segment longer than proximal segment, or each segment approximately the same length. In *Glutops* species, the segments are approximately the same length in the females, whereas in the males, the proximal segment is longer than the distal segment. There is also sexual dimorphism of this character in *Xylophagus lugens*. In this species, the proximal segment is longer than the distal segment in males whereas in the female, the reverse is true.

[#23]. **Lateral ridge of clypeus.** The presence of a ridge along the lateral margin of the clypeus is evident in *Coenomyia ferruginea*, *Arthropeas americana*, and *Dialysis rufithorax*.

[#24]. **Location of oral margin.** The location of the mouthparts, relative to the rest of the head, may be variously placed. For example, the oral margin clearly confines the mouthparts to the anterior part of the head in *Coenomyia ferruginea*. Nagatomi (1990) mentioned this as a defining character for the Coenomyiidae. Ultimately, however, discrete differences of states between species across the entire data matrix could not be discerned and therefore, this character was not used in the phylogenetic analysis.

[#25]. **Position of stipes.** Where present, the position of the stipe was scored as converging toward one another, directed medially; attached to or in contact with tentorium at the back side of the head; or directed posteriorly. The difference between medially and posteriorly directed was sometimes subtle and several genera exhibit both of these states (*Rhagio* and *Atherimorpha*). *Dichelacera marginata*, *Glutops rossi*, *Lampromyia canariensis*, *Tabanus atratus*, and *Vermileo vermileo* were scored as having the stipe attached to or in contact with the tentorium. Stipe shape was also scored, but after scoring five genera (*Atherimorpha*, *Dichelacera Ptiolina*, *Spaniopsis*, and *Symphoromyia*), five different states were generated. It was clear the

shape was not only variable, it was difficult to describe accurately. For this reason, scoring of stipe shape was halted and not used in the phylogenetic analysis.

[#26]. **Cardo.** The cardo in *Pelecorhynchus personatus* is conspicuously inflated. The cardo is also enlarged in *Pseudoerrina jonesi* and *Symphoromyia cruenta*. This structure is apparently absent in *Dasyomma atratulum*, *Dialysis rufithorax*, *Chrysopilus* species and *Suragina concinna*.

[#27]. **Lacinia length.** Lacinia were scored relative to the length of the palps. This character was much easier to score when the head was dissected. In undissected specimens, the lacinia were sometimes visible, however, most often the lacinia were concealed and no scoring was possible. Since the heads of rare species were not dissected, there are a number of taxa unscored for this character. *Pseudoerrina*, *Tabanus*, *Vermileo*, *Lampromyia*, *Suragina*, and *Dialysis* were scored from illustrations (Nagatomi and Soroida, 1985).

[#28]. **Lacinia serration.** This character was scored for undissected specimens where the lacinia were visible, however, most often the lacinia were concealed. A number of species representing rare genera are not scored. Serrated lacinia may be associated with blood feeding. It is present in known blood feeders *Symphoromyia*, *Spaniopsis*, and *Dasyomma*, however it is also present in *Sylvicola* and the limited taxon sampling of this character makes it difficult to assert this correlation with confidence. It is not a

required feature for blood feeders, in any case, as *Tabanus* and *Dichelacera* apparently do not have serrated lacinia.

[#29]. **Mandibles.** Mandibles are required for blood feeding. Not surprisingly, mandibles are present in all the blood feeding flies (*Atherix*, *Dasyomma*, *Dichelacera*, *Spaniopsis, Suragina*, *Symphoromyia*, and *Tabanus*) and are absent in all non-blood feeding flies.

[not scored] **Epipharynx and hypopharynx.** Epipharynx is a straw-like appendage that varies in length somewhat, but not within discrete units of measurement. Therefore, no attempt was made to score this feature for phylogenetic analysis. Generally, the epipharynx form is canal-shaped, with a blunt apical opening. The hypopharynx subtends the epipharynx and is complementary in form. The epipharynx of *Bolbomyia nana* is unusual in that it comes to a sharp point.

[not scored] **Cibarial pump (general form).** The cibarial pump is an internal structure, located ventrad of the frons, connected to the base of the epipharynx ("basipharynx" of Peterson, 1916). Variation in form varies from nearly spherical as in *Bolbomyia nana* and *Austroleptis multimaculata*, to nearly parallel sided and elongate as in species of *Chrysopilus* and *Atherimorpha*. Scoring of cibarium shape is difficult because the variations differ subtly, along a spectrum of possibilities. Generally, outgroups have more compact, rounded cibarial pumps. In both *Spaniopsis* and *Symphoromyia*, near the posterior margin of the cibarial pump on its ventral

surface, there is a ‘c’ shaped carina, opened anteriorly. Illustrations of *Austroleptis collessi* and tabanids *Nagatomyia*, *Silvius*, and *Chrysops* in Nagatomi and Soroida (1985: p335; fig.202) show a carina in the same location, but upon inspection, they are of a different form. Although the presence of this carina is noted here, it was not scored for phylogenetic analysis because it is a subtle character likely subject to scoring error.

[#30]. **Cibarial pump length.** The cibarial pump is located internal to the clypeus and may either be relatively short or long. Since the width of the cibarial pump is held relatively constant, the length is defined by its proportion to the width. Cibarial pump length is scored as short when the width is the same as or greater than the length. When clearly longer than wide, the cibarial pump length is scored as long. Interestingly, the smallest taxa scored for this feature (*Austroleptis*, *Bolbomyia*, *Litoleptis*, *Ptiolina*, and *Spania*) all have short cibarial pumps. It is possible that the physical forces associated with scaling have an effect on this character. However, sampling for this character was limited. *Spaniopsis clelandi*, a small to moderately sized fly (appx. 4–5.5 mm) also has a short cibarium.

[#31]. **Cornu length.** The cornu are the dorsolateral extensions of the cibarial pump. Cornu are generally wispy and elongate, about as long as the cibarial pump. The length of the cornu was scored relative to the length of the cibarial pump. Since the length of the cibarial pump is free to vary independently, there is the possibility that a long cornu may be scored as short due to the presence of an especially long cibarial

pump (and vice-versa). However, since there are probably some allometric constraints of the cornu with respect to the cibarial pump, a particularly long cornu should be revealed by such scoring. Indeed, taxa with short cibarial pumps did not, as a consequence, automatically have a long cornu. *Bolbomyia nana* is the only taxon with a short cibarial pump and long cornu. Taxon sampling, however, was limited.

[#32]. **Cornu attachment.** Typically, the cornu extends freely, aside the pharyngeal pump. In *Spaniopsis* species, however, the cornu is fused to the pharyngeal pump. Nagatomi and Soroida (1985) illustrate *Atherix ibis* and *Suragina caerulescens* as having a fused cornu also, however I did not see this in any of the athericids over the course of my study. All other taxa examined have cornu that extend beyond the pharyngeal pump, in line with the cibarium. *Austroleptis* is autapomorphic in having apically microsetose cornu, however this was not scored for the phylogenetic analysis.

[#33]. **Pharyngeal pump width.** The pharyngeal pump is located internally, its anterior arm bound by the dorsal cornu of the cibarial pump. The pharyngeal pump takes two basic forms. One is displayed in *Chrysopilus*, *Rhagio*, *Ptiolina*, *Bolbomyia*, and other genera, including outgroups, where the pharyngeal pump is stretches between the dorsal cornu at its anterior-most extent, but for most of its length, is narrow. Alternatively, the pharyngeal pump may be anteriorly broad then narrowed posteriorly (as a bicycle saddle, turned backwards). The pharyngeal pump of

Arthroceras pollinosum is nearly the intermediate of these two forms. It is scored as anteriorly broad.

[#34]. **Pharyngeal cup (presence of concavity).** Where anteriorly broad, the pharyngeal pump is either mostly flat or with margins upturned to form a cupped structure. All blood feeders and a few other taxa cupped have a pharyngeal pump that for most or all of their length, is upturned at its margins. Interestingly, the pelecorhynchids show a broad, cupped pharyngeal pump form. Is this due to shared ancestry with the Tabanidae and Athericidae? There are some inconsistencies in the character distribution, however, as *Spania*, a putatively close relative to *Symphoromyia* and *Spaniopsis*, does not have a similarly shaped broad, cupped pharyngeal pump. *Arthroceras*, a non-blood feeder, also has a broad, cupped pharyngeal pump.

[#35]. **Pharyngeal pump length.** The length of the pharyngeal pump was scored relative to the length of the cibarial pump. The cibarial pump is free to vary and thus the relative metric may not be constant across taxa. There may also be problems with non-independence between the length of the pharyngeal pump and the length of the cibarial pump. A long cibarial pump (for sucking) may require a long pharyngeal (for swallowing). States are 1) longer than length of cibarial pump 2) approximately same length as cibarial pump 3) approximately half length of cibarial pump 4) very short, reduced.

Adult thorax.

[#36]. **Dorsum vittae.** Vittae are broad longitudinal stripes on the dorsal surface of the thorax. There is considerable variation of this character within Tabanidae, as well as within many genera (*Arthroceras*, *Coenomyia*, *Glutops*, *Ptiolina*, *Rhagio*, *Spaniopsis* and *Suragina*). There is also variation within species. In *Arthroteles bombyliiformis*, for example, vittae are more visible in females than in males. In *Austroleptis multimaculata* (and other *Austroleptis* species), vittae are only present in females. In *Coenomyia ferruginea*, specimens may be either vittate or not, regardless of gender.

[#37]. **Dorsum setation.** Some species of *Atherimorpha* are distinguished by having rows of dorsal setae that are stronger and longer than other setae of the dorsum. In *Austroleptis collessi*, dorsocentral bristles are lightly present. All other taxa surveyed, however, have dorsal setae of approximately the same length.

[#38]. **Presence of scale-like colored setae.** Flattened, scale-like setae reflecting blue, red, or golden colors and are present in *Chrysopilus, Schizella,* and apparently in *Stylospania* (although it is difficult to determine). *Pelecorhynchus* may have similarly colored setae, but they are not flattened and are of a different nature.

[#39]. **Proepimeron presence.** The proepimeron is variously developed among genera within Tabanomorpha, yet consistent within genera. The proepimeron is located posterior of the proepisternum and anterior of the anepisternum, ventral to the

area containing the anterior spiracle. Sometimes the proepimeron is difficult to locate, on account that it may be separated from the proepisternum and the anepisternum by a discrete, superficial suture. In *Xylophagus*, the proepimeron is apparently absent. In most taxa (*Arthroceras*, *Atherimorpha*, *Atherix*, *Austroleptis*, *Bolbomyia*, and others), the proepimeron is roughly rectangular, approximately twice as long (dorsoventrally) as wide (anterior-posteriorly). In *Chrysopilus*, *Schizella*, and *Stylospania*, however, the proepimeron is reduced and slender (as in Fig. 175).

[#40]. **Proepimeron setation.** The proepimeron may be with or without setae. *Rhagio* and *Desmomyia* are the only Rhagionidae *sensu lato* with setose proepimera. Other genera with setae-bearing proepimera are *Arthropeas*, *Atherix*, *Coenomyia*, *Dichelacera*, *Suragina*, and *Tabanus*.

[#41]. **Anepisternum setation (alternative coding not included in phylogenetic analysis).** As indicated by the large number of character states for this feature, there is a considerable amount of variation as to the degree in which the anepisternum is setose. This character may be better scored in two characters, presence of setae and the nature of these setae. This is a preliminary scoring that is modified below (not included in phylogenetic analysis).

[#42]. **Anepisternum setation (alternative coding not included in phylogenetic analysis).** Originally, I coded several more character states, detailing various setal patterns on the anepisternum (setose on upper margin only; setose on dorsal and

posterior margins; setose throughout posterior half; setose throughout upper half including entire anterior and posterior margins). However, there is a great amount of variability within genera and I think lumping these characters together is more informative than a fine-tuned approach, especially considering that the objective is to understand very old divergence patterns among these taxa. Not to mention, a more generalized approach is easier to score. This character may be ordered. If so, since there are four character states, some downweighting is appropriate. This is a preliminary scoring that is modified below (not included in phylogenetic analysis).

[#43]. **Anepisternum setation.** There is a considerable amount of variation as to the patterns and degree in which the anepisternum is setose among the taxa surveyed. This diversity was categorized by three basic states: 1) anepisternum bare or with one or two setae 2) less than one-half of sclerite area with setae 3) one half or more of sclerite area with setae. Although all *Rhagio* species scored here have at least a few anepisternal setae, the anepisternum is bare in *Rhagio maculatus*. This may be important, as a bare anepisternum is one of the putative autapomorphies of *Rhagina*, setting it apart from *Rhagio*. *Ptiolina* may either have a bare anepisternum (*P. zonata*, *P. mallochi*) or an anepisternum with approximately half its surface covered with setae (*P. lappomica*, *P. majuscula*). Specimens of *Spaniopsis longicornis* may have the anepisternum either bare or setose.

[#44]. **Laterotergite form.** The laterotergite is the thoracic area ventrolateral to the subscutellum. The laterotergite may be subdivided into dorsal (anatergite) and ventral

(katatergite) areas. The laterotergite may either be smooth and evenly surfaced or the katatergite may be swollen, and thereby differentiated from the anatergite. The anatergite and katatergite may also be defined by a faint, superficial medial suture (as in some *Rhagio* species and *Sierramyia chiapasensis*). The katatergite was scored as swollen and differentiated from the anatergite only in cases where the katatergite was clearly swollen (when viewed from the lateral perspective), otherwise the laterotergite subdivisions were scored as indistinguishable. In many taxa (*Chrysopilus*, *Glutops*, *Spaniopsis*, *Symphoromyia*), a slight depression of the laterotergite is present medially (apparently to allow freedom of movement for the halter). In these cases, the condition is scored as ana- and katatergites indistinguishable. In *Symphoromyia cruenta*, the katatergite is swollen in the female, but indistinguishable from the anatergite in the male.

[#45]. **Laterotergite setation.** The presence or absence of laterotergite setae is a major character for taxonomic keys used to distinguish genera of the Tabanomorpha.

[#46]. **Laterotergite setal arrangement.** Laterotergite setae are generally distributed in three different ways. Setae may be confined exclusively to the katatergite, found mostly on the katatergite and extending partially onto the anatergite, or found throughout all parts of the laterotergite. *Arthroceras* species, *Chrysopilus* species, *Pseudoerrina jonesi*, *Schizella* species, *Arthropeas americana*, *Coenomyia ferruginea*, and *Dialysis rufithorax* have setae distributed through the laterotergite.

Species of Athericidae, Tabanidae, as well as those belonging to *Desmomyia*, *Rhagio*, *Sierramyia*, and *Symphoromyia* have laterotergite setae restricted to the katatergite.

[#47]. **Microsetation between base of halter and postspiracular scale.** The thoracic surface between the base of the halter and the postspiracular sclerite is very small, and the microsetae that may be present in this area are often inconspicuous. Especially in very small specimens, it is easy to miscode this character as microsetae absent. For this reason, the character is not used in phylogenetic analysis.

[#48]. **Flaps of posterior thoracic spiracle.** The upper margin of the posterior thoracic spiracle may be produced in the form of a flap that apparently may be used to close the spiracle airway. The presence of flaps on the thoracic spiracle may be an adaptation to prevent desiccation, particularly for large flies. It is worth noting, however, that the large fly *Coenomyia ferruginea* does not have spiracular flaps. The margins of the thoracic spiracle are sometimes raised (as in *Chrysopilus ferruginosus* and *Chrysopilus thoracicus*) in these cases, the spiracle is scored as not having flaps. The presence of flaps was scored as such only when it was clear the length of the flap spanned the spiracle length (and could thus close the airway).

[#49]. **Posterior thoracic spiracle lining.** The presence or absence of microsetae lining the margin of the thoracic spiracles is likely a morphological response to particular environmental conditions. Genera with large ranges such as *Chrysopilus* and *Rhagio* exhibited infrageneric variation in this character. *Atherimorpha* is also

polymorphic for this character. However, all examined species of *Arthroceras*, *Arthroteles*, *Ptiolina*, and *Spaniopsis* (which comprise a greater sampling than included here) have bare thoracic spiracle margins.

[#50]. **Postspiracular scale.** The presence of a postspiracular scale is a putative synapomorphy for Tabanidae and Athericidae (Stuckenberg, 1973). Species of *Pelecorhynchus* also have this character state. In *Pseudoerrina jonesi*, the postspiracular scale is present, but reduced to a linear ridge. It may be present or absent species of *Glutops* (it is usually present). When present in *Glutops*, it is a linear ridge, similar in form to the scale in *Pseudoerrina jonesi*. The postspiracular sclerite is also broadly raised in species of *Rhagio*, although with a different orientation than what is found in the Tabanids, Athericids, and Pelecorhynchids (Figs. 175-177).

[#51]. **Postspiracular sclerite setation.** The postspiracular sclerite is setose only among xylophagid taxa. A possible exception is *Exeretonevra* and *Heterostomus* (not included in this matrix), where although the postspiracular sclerite is setose, setae are found only on the dorsal margin of the postspiracular sclerite.

[#52]. **Setation posterior to postspiracular sclerite.** In some taxa, there is a small, isolated tuft of setae conspicuously present posterior to the postspiracular sclerite, on what may be called the metanepisternum, between the halter and hind coxa. This feature is conspicuously present in species of *Pelecorhynchus*. It is also present in

species of *Arthroceras*, *Arthropeas americana*, some (but not all) *Chrysopilus*, *Coenomyia ferruginea*, *Glutops* species, *Pseudoerrina jonesi*, *Symphoromyia* species, and *Xylophagus lugens*.

[#53]. **Proscutellum.** Stuckenberg (2001) has asserted that the presence or absence of the proscutellum has phylogenetic significance at the generic level. As he describes it, the proscutellum is an arcing suture that creates a lenticular-shaped swelling at the posterior edge of the mesoscutum. In *Tabanus atratus*, for example, it is easily seen. It appears to be polymorphic in *Ptiolina mallochi*, *Spania nigra*, and *Vermileo vermileo*. It is clearly present in *Rhagio costatus*, however, absent in other *Rhagio* species.

[#54]. **Subscutellum form.** In species of *Atherix*, *Dasyomma*, *Dichelacera*, *Pelecorhynchus*, *Pseudoerrina*, and *Tabanus* have a raised, swollen area of the subscutellum is visible. In all other taxa surveyed, the subscutellum is smooth.

[#55]. **Subscutellum setation.** In the xylophagid taxa, the subscutellum is setose, at least within the lateral margins.

[#56]. **Postmetacoxal bridge (not used in phylogenetic analysis).** In order to see this character, the entire specimen must be cleared and the hind coxa removed. Stuckenberg (2001: 26) points out that "in Tabanidae, the epimera are extended ventromedially to form either a strengthened area in the median ventral membrane or

are joined to form a postmetacoxal bridge. In Athericidae, the modification is present but less visible, as a thin extension of the epimeron." This character is difficult to score and requires destructive dissection. Rare taxa were not scored. This character is not used for the phylogenetic analysis.

#57. **Postmetacoxal bridge type (not used in phylogenetic analysis).** There are four forms of the postmetacoxal bridge; a complete broad extension, an incomplete broad extension, a. complete thin extension, or an incomplete thin extension. How these postmetacoxal bridge forms are related to one another is unclear. Since this character is difficult to score reliably, it is not used for the phylogenetic analysis.

Wing.

[#58]. **Wing color (not used in phylogenetic analysis).** Although most species are constant with respect to the color of the wing surface, this is a highly variable character among species within the same genus. It is also problematic to score in that degrees of lightness/darkness are vague and subjective. Furthermore, such a character is unlikely to retain phylogenetic information for resolving deep lineage divergences among the lineages. For these reasons, this character was not included in the phylogenetic analysis.

[#59]. **Wing markings (not used in phylogenetic analysis).** The drawbacks of the previous character are, for the most part, similar to the previous character. Most species are constant with respect to the color of the wing markings, however the

character is variable among species within the same genus. And just as in wing surface color, color patterns are unlikely to retain phylogenetic information for resolving deep lineage divergences among the lineages. For these reasons, this character was not included in the phylogenetic analysis.

[#60]. **Pterostigma (not used in phylogenetic analysis).** Stuckenberg (2001:16) notes that the curvature of R_{2+3} is associated with the presence of a pterostigma within the Rhagionidae *sensu* Stuckenberg (2001). According to Stuckenberg, the prominence of the curvature was related to the size of the pterostigma. In some species of *Chrysopilus*, for instance, the curvature was strong when the pterostigma was large. The curvature of R_{2+3} that Stuckenberg points out, however, is very subtle (2001:17, fig. 11). I scored the presence or absence of the pterostigma as one part of Stuckenberg's assessment. The presence or absence of a pterostigma was judged on the amount of coloration between the apical area of R_1 and R_{2+3}. If there is any coloration at all, the pterostigma is scored as present. As with all characters scored by color, it seems unlikely that information regarding ancient evolutionary divergences may be retained. This is character is not used for the phylogenetic analysis.

[#61]. **Lower calypter.** An invagination indicates the separation between upper and lower calypter. In the Tabanidae, the lower calypter is well developed. In *Pelecorhynchus personatus*, the lower calypter is present, but not as large as in *Tabanus*, *Dichelacera* and other tabanids. In all other taxa, the lower calypter is fully reduced.

[#62]. **Upper calypter development.** The upper calypter is the membrane subtending the base of the wing. In Tabanidae, the upper calypter is smaller than the lower calypter and in *Tabanus atratus*, it appears absent. In *Coenomyia ferruginea*, *Dialysis rufithorax*, *Lampromyia canariensis*, *Sierramyia chiapasensis*, *Vermileo vermileo*, and *Xylophagus lugens*, the upper calypter is underdeveloped to some degree, in comparison to the other taxa which a have a fully rounded upper calypter. In these cases, where the upper calypter has a mostly straight margin, the character is scored as underdeveloped.

[#63]. **Upper calypter form (not used in phylogenetic analysis).** This is a reformulated version of the previous character. It is not discrete, however, and not used for the phylogenetic analysis.

[#64]. **Alula development.** The lack of alula is very evident in species of *Sierramyia* and among vermileonid taxa. However there is a gradation between having a fully reduced alula and having one that is fully developed. For the most part, however, most congenerics are consistently one type or another. The exception to this is *Rhagio*, where species may either have a narrow or broad alula area. Specimens with absolutely no convex curvature were obviously scored as reduced, with no curvature. Narrow curvature indicates curvature in the alula that is three times as wide as deep, or greater. Broad curvature indicates curvature of the alula which is less than three times as wide as deep, or less. These differences were scored by eye.

[#65]. **Alula shape.** The alula assumed one of two forms. The tabanids, for example, show a marked posterior shift of alula area distally, so that the alula area is nearly triangular. If the alular area is viewed as a distribution curve, the mean is located near the distal margin. This state is also seen in species of *Glutops*, *Pelecorhynchus*, *Pseudoerrina*, *Spania*, and *Spaniopsis*. The alula is scored as rounded evenly where the alular area is rounded, so that the mean of its distribution is at or near the center.

[#66]. **Anal lobe (not used in phylogenetic analysis).** The development of the anal lobe may be correlated with the reduction of the alula. In all cases where the anal lobe is scored as reduced (*Lampromyia canariensis*, *Sierramyia chiapasensis*, and *Vermileo vermileo*), the alula is also reduced. However, while the anal lobe is well developed in species of *Xylophagus*, these species also have a reduced alula. Although the scoring of this character doesn't overlap perfectly with the scoring of the alula, I suspect the two characters are constrained by non-independence with respect to one another. For this reason, the scoring of the development of the anal lobe was not included in the phylogenetic analysis.

[#67]. **Humeral crossvein strength (not used in phylogenetic analysis).** The humeral crossvein (h) was scored for relative strength. The humeral crossvein may be very faint, or present as a thick vein. However, over the course of scoring this character, it became apparent that it is variable even at the finest taxonomic scale (among specimens of the same species) and therefore it became obvious that such a

character is incapable of elucidating the branching pattern of ancient divergences. For this reason, it was removed for the phylogenetic analysis.

[#68]. **Humeral crossvein shape (not used in phylogenetic analysis).** The humeral crossvein (h) may be variously oriented or shaped across taxa. It may be arced (or 'bow-shaped') or straight and oriented acutely, obtusely, or perpendicularly with respect to the leading margin of the wing. However, as was the case for scoring the humeral crossvein for relative strength, it became apparent that the high variability of this character among conspecifics and congenerics suggests that it is not appropriate for use in reconstructing the phylogeny of the ingroup. There is also a large amount of subtlety to this character that may induce scoring error. For this reason, it was removed for the phylogenetic analysis.

[#69]. **Sc-r crossvein presence (not used in phylogenetic analysis).** The Sc-r crossvein was sometimes present as only a concentration of setae. In this case, it was scored as weakly developed, even though its position was clear. There is a lot of variation in this character. *Schizella* is the only taxon where the Sc-r crossvein is always absent, however this may be an artifact of a small sampling of this genus (6 specimens, 3 species). Given the variation of this character, it appears unlikely to be informative at the level necessary for revealing ancient evolutionary events. For this reason, it was removed for phylogenetic analysis.

[#70]. **Sc-r crossvein location.** The Sc-r crossvein was identified as a potentially useful character for phylogenetic analysis by Stuckenberg (2001). There is slight variation of this character within genera that results in a difference of scoring among congenerics (as in *Atherimorpha* and *Chrysopilus*); some of which is related to sexual dimorphism (*Coenomyia ferruginea*). The most notable divergence is present in species of *Lampromyia* and *Vermileo*, where the crossvein is placed approximately midway between h and the origin of the radial-sector. *Litoleptis* and *Sylvicola* are also autapomorphic in having sc-r located on the proximal side of the humeral crossvein.

[#71]. **Setation of R_1, dorsal surface.** The presence of setae on dorsal surface of wing vein R_1 is the common condition for most lower flies. *Litoleptis*, *Lampromyia*, and *Vermileo*, however, are exceptions to this.

[#72]. **Setation of R_1, ventral surface (not used in phylogenetic analysis).** The lack of setae on ventral surface of wing vein R_1 is the common condition for most lower flies. Ventral R_1 setae are found in some, but not all species of *Atherimorpha*, *Austroleptis*, and *Xylophagus* however. Due to the limited taxon sampling of *Austroleptis* and *Xylophagus*, the morphological diversity of these genera is not fully represented in the matrix. It is a logical to assume that the plesiomorphic condition is for the ventral R_1 wing vein to lack setae, in each of these genera (*Atherimorpha*, *Austroleptis*, and *Xylophagus*). In order to avoid misinterpretation of the data due to limited taxon sampling, this character was not used in phylogenetic analysis.

[#73]. **Orientation of wing veins R_1 and R_{2+3} at wing margin.** The position of R_{2+3} at the wing margin is scored, relative to the position of wing veins R_1 and R_4. A putative synapomorphy for members of the Athericidae is for wing veins R_1 and R_{2+3} to meet together at the wing margin (Stuckenberg, 1973). Yet the members belonging to the putative sister taxon of Athericidae, the Tabanidae, have R_{2+3} closer to R_4 than to R_1. Species of *Glutops*, *Lampromyia*, *Pelecorhynchus*, *Pseudoerrina*, and *Vermileo* also have a distally positioned R_{2+3} wing vein. Between these two extremes, the R_{2+3} wing vein may be positioned near R_1 (as in *Arthroceras*, *Chrysopilus*, *Desmomyia*, some *Ptiolina*, *Schizella*, *Sierramyia*, *Spania*, *Spaniopsis*, *Symphoromyia*, and the Xylophagidae) or displaced away from R_1, nearly between R_1 and R_4 (but closer to R_1 than to R_4) as in species of *Arthroteles*, *Atherimorpha*, *Bolbomyia*, and some species of *Ptiolina*.

[#74]. **Curvature of R_{2+3} (not used in phylogenetic analysis).** Stuckenberg (2001:16) notes that the curvature of R_{2+3} is associated with the presence of a pterostigma within the Rhagionidae *sensu* Stuckenberg 2001. According to Stuckenberg, the prominence of the curvature was related to the size of the pterostigma. In some species of *Chrysopilus*, for instance, the curvature was strong when the pterostigma was large. The curvature of R_{2+3} that Stuckenberg points out, however, is exceptionally subtle (2001:17, fig. 11). I scored this feature to the best of my abilities. However in many cases, such as in *Symphoromyia* species, many *Chrysopilus* species and even within some *Rhagio* species such as *R. plumbeus*, it could have been scored faithfully either as present or absent. How much of a curve

needs to be present in order for it to be scored as such? As a landmark, I used figure 11 showing *Rhagio scolopaceus* (Stuckenberg, 2001) as the exemplary condition where the curve is present. If the curve was not adjacent to the position of the pterostigma, as in *Rhagio scolopaceus* and as explained by Stuckenberg, the character was scored as absent. I also used *Spania nigra* (type species of Spaniidae sensu Stuckenberg) as the exemplar condition where the curve is not present. Stuckenberg notes that the portion of R_{2+3} apical to the pterostigma does not include the sinuous curve that he refers to as the character. However, it appears to me that the most substantial difference between the R_{2+3} in *Spania nigra* and that in *Rhagio scolopaceus* is the portion of the wing vein distal to the pterostigma. In *Spania nigra* (as in *Suragina concinna*, *Austroleptis* species, *Chrysopilus quadratus* (and other species including *Chrysopilus thoracicus* and *Chrysopilus panamensis*) and *Dasyomma atratulum*), R_{2+3} is virtually identical to *Rhagio scolopaceus* in its basal curvature. Only when the apical portion of the wing vein veers slightly back towards the wingtip (and not directly towards the leading margin of the wing) does the curvature mentioned by Stuckenberg become readily apparent. In one specimen of *Desmomyia thereviformis* [USNMENT00025269], the wings differ in such a way that the left wing should be scored as R_{2+3} curvature present, while in the right wing it is clearly absent.

[#75]. **R_{2+3} at wing margin (not used in phylogenetic analysis).** The curvature of the R_{2+3} wing vein apical of the pterostigma is highly correlated with the presence or absence of the special curvature of R_{2+3} pointed out by Stuckenberg (2001). In

Ptiolina lapponica and *Ptiolina majuscula*, the curve is scored as absent even though the R_{2+3} wing vein meets the wing margin at a close angle because of the placement of the pterostigma (it is not positioned inside the point of curvature, a necessary component of Stuckenberg's scoring). This character is not used for phylogenetic analysis for reasons given in the discussion of the previous character.

[#76]. **Setation of dorsal surface of R_{2+3} (not used in phylogenetic analysis).** The presence or absence of microsetae on the dorsal surface of wing vein R_{2+3} was scored. The apomorphic condition is the presence of microsetae, although this is present in only some species of *Atherimorpha*, and in *Sierramyia chiapasensis*. *Sierramyia* is the only genus-level taxon that is unambiguously scored as having microsetae on R_{2+3}. The genus is represented in this study by a single specimen, however. *Bolbomyia nana* has a bare dorsal R_{2+3}, however in its congener, *B. wuorentausi*, it is microsetose. The variable nature of this character suggests that it is not useful in deep-level phylogenetic analysis, and for this reason, it was removed.

[#77]. **Setation of ventral surface of R_{2+3} (not used in phylogenetic analysis).** The presence or absence of microsetae on the ventral surface of wing vein R_{2+3} was scored. The apomorphic condition is the presence of microsetae. The apomorphic condition is found in only some species of *Atherimorpha*, *Bolbomyia nana* and in *Sierramyia chiapasensis*. *Sierramyia* is the only genus-level taxon that is unambiguously scored as having microsetae on the ventral R_{2+3} wing vein. The genus is represented in this study by a single specimen, however. The variable nature of this

character suggests that it is unlikely to be informative for deep-level phylogenetic analysis, and for this reason, it was removed.

[#78]. **R_4-R_5 fork.** *Sylvicola* is distinct in lacking the R_4-R_5 fork. Since *Sylvicola* is not used in the phylogenetic analysis, this character is non-informative. All taxa share the same state.

[#79]. **Position of R_4-R_5 fork.** Grimaldi & Cumming (1999: 16) note that the base of fork R_4-R_5 is at the same level as the distal end of cell dm, and not distal to it in the Rhagionidae. This, they propose, is a potential synapomorphy for the family. The scoring is formulated so that it is consistent with their reasoning. Grimaldi & Cumming were not explicit in how this character should be scored, however, and the line separating proximal and distal positions can be positioned a number of ways (relative to wing leading margin, wing base/tip, etc.). I score this character by orienting the wing so that the base (the part that attaches to the thorax) is held horizontal to the wing tip. A vertical line could be drawn visually so that the position of the R_4-R_5 fork could be determined, relative to the distal end of cell dm. As scored, species of *Rhagio* may have the base of the R_4-R_5 fork proximal of (as in *R. mystaceus*), directly above (as in *R. plumbeus*, *R. hirtus*), or distal of the distal end of cell dm (as in *R. costatus*). Differences in scoring between *Atherimorpha* species are also present.

[#80]. **R_4 at base.** The curvature of wing vein R_4 at its base has been proposed as a possible a synapomorphy for the Rhagionidae (Grimaldi & Cumming, 1999; Stuckenberg, 2001: 16, fig. 11). The scoring of this character is very subtle. Undoubtedly, many species of *Chrysopilus* and *Rhagio* exhibit an obvious and abrupt change of direction at the base of wing vein R_4 (as illustrated in Stuckenberg, 2001: fig 11). However, the flexure at the base of wing vein R_4 is continuously variable across a range of curvatures and the point at which it ceases to become 'strong' is unclear. For this reason, I took scored wings as strongly curved or angled, when as illustrated (Stuckenberg, 2001: fig. 11). An abrupt change of direction was not a necessary condition for this scoring, although the bend had to be severe. In *Rhagio vertebratus* and *Rhagio hirtus* males, the flexure was less severe than in the females. The character was scored as ambiguous for these species. The basal curvature of R_4 in *Rhagina incurvatus* is much less abrupt than in species of *Rhagio*, however it was scored as strongly angled because the direction of the wing vein changes 90°. All other wings, with the basal curvature of R_4 smoothly changing direction (as in species of *Arthroteles*, *Atherimorpha*, *Atherix*, *Austroleptis*, *Bolbomyia*, *Dasyomma*, and *Ptiolina*, among others) were scored as relaxed, not strongly curved.

[#81]. **R_4 at apex.** Taxa also vary in the amount of curvature of the apical portion of wing vein R_4, as it meets the margin of the wing. In species of *Pelecorhynchus* for example, the R_4 vein veers anteriorly to create a distinctive curvature. In most Tabanidae, the R_4 vein also meets the margin of the wing anteriorly, however the curvature is less pronounced. The differences among most of the taxa, however, were

subtle for this character. The most obvious difference, to allowing for discrete coding, was the orientation of R_4 at the margin. If R_4 is apically curved so that it is directed anteriorly, it is scored as curving towards the leading margin of the wing. If the apical portion of R_4 was straight and directed toward the wingtip, it was scored as straight or nearly straight apically. In some cases, such as in *Ptiolina lapponica* and *Rhagio plumbeus*, R_4 was slightly curved anteriorly at the wing margin, but not enough to be directed toward the leading edge of the wing. Therefore, R_4 wing vein in these taxa was scored as nearly straight. In addition to *Dichelacera*, *Pelecorhynchus*, and *Tabanus* having an anteriorly-directed R_4 wing vein, *Arthropeas americana*, *Atherix pachypus*, *Coenomyia ferruginea*, *Pseudoerrina jonesi* and *Suragina concinna* also exhibit this condition. *Glutops rossi* and *Dasyomma atratulum* were scored as having R_4 straight (although their putative sister taxa were scored otherwise).

[#82]. **Position of R_4 and R_5 at margin.** This character scores the position of R_4 and R_5 relative to the wingtip. The wing veins may be anterior to the wingtip (i.e., R_5 is at or anterior to the wingtip), straddle the wingtip (i.e., R_4 and R_5 contain the wingtip between them), or be posterior to the wingtip (i.e., R_4 is at or posterior to the wingtip). Intrageneric variation of this character is present in at least *Austroleptis*, *Chrysopilus*, *Ptiolina*, *Rhagio* and *Symphoromyia*. In the case of *Austroleptis* and *Symphoromyia*, the ambiguity at the genus level is not recorded in the matrix, due to limited sampling. The apparent lability of this character below the genus level suggests that information regarding ancient evolutionary events is likely to be lost. The character is retained for phylogenetic analysis, however.

[#83]. **Alignment of R_5.** Grimaldi & Cumming (1999: 16) note that in Rhagionidae "vein R_5 is almost always straight and R_4 arises from it with a sharp bend at its base, often at 90°." The first part of this statement is scored here. The latter half of this statement, referring to the sharp bend at its base, is scored by character number #80. There are inherent problems in scoring a character such as this, as in other cases where the amount of curvature is characterized. Variation in the flexure of R_{4+5} at the point where R_4 and R_5 originate is continuous. It is unclear at what point, exactly, R_{4+5} ceases to be straight, in line with R_5. R_5 often arises from R_{4+5} with a clear, but small change of direction. If the change of direction was 10° or less, the character was scored as straight. Sometimes, however, R_{4+5} is arced apically towards the anterior wing margin, as in *Arthropeas americana* and *Coenomyia ferruginea*. In this case, the direction of R_{4+5} may be calculated as the average vector across its length or as the ultimate orientation of R_{4+5} where R_4 and R_5 arise. Differences in how this is calculated will affect the scoring. Arbitrarily, I chose to measure the direction of R_{4+5} by its approximate average vector.

[#84]. **M_3 wing vein.** The presence or absence of the third medial vein was scored. This has been proposed as a synapomorphy for a natural group composed of *Austroleptis*, *Bolbomyia*, and *Litoleptis*. This group may also include fossil taxa *Mesobolbomyia*, *Pauromyia*, *Probolbomyia*, and *Zarzia* (Grimaldi & Cumming, 1999). Since it is logical to assume that an incompletely present M_3 wing vein represents an intermediate step between the complete presence or absence of M_3, the

character may be ordered (it is not, however, in the phylogenetic analysis). The state of being incompletely present is defined by an M_3 which is present, but not reaching the wing margin. *Spania nigra* specimens may have a completely or incompletely present M_3 wing vein. *Spaniopsis clelandi* specimens also show variation in either having M_3 incompletely present or absent.

[#85]. **Halter knob size (not used in phylogenetic analysis).** The length of the halter knob was measured in comparison to the halter stem. Differences were arbitrarily limited to five separate states. States varied quite readily within genera and the variation of the knob/stem ratio was continuous. Since the difference between some states was minor and rather ambiguous (approximately 1/2 length of stem/ between 1/3–1/2 length of stem/ between 1/2–2/3 length of stem), scoring may have been particularly subject to experimental error. For this reason, the character was removed for phylogenetic analysis.

[#86]. **Halter stem (not used in phylogenetic analysis).** There are different microstructural patterns evident upon very high magnification of the base of the halter. SEM photos of this region in *Arthroceras*, *Arthroteles*, *Bolbomyia*, *Desmomyia*, and *Ptiolina* show these differences in detail. However there is a continuous gradation of states which make scoring particularly difficult. Although this character system was explored, it is not included in the phylogenetic analysis.

[#87]. **Anterodorsal setation of halter (not used in phylogenetic analysis).** This is the first of a two-part character, examining microsetae of the halter. There are different microsetal patterns evident upon very high magnification of the anterodorsal side of the halter stem and knob. However there is a multitude of patterns and devising a consistent and cohesive scoring for this character is particularly challenging. After examination of a wide range of taxa, it appears possible such character data may be informative at the species level. However, it is certainly too variable to provide information for deeper level divergences. It is not used for the phylogenetic analysis.

[#88]. **Ventroposterior setation of halter (not used in phylogenetic analysis).** This is the second of a two-part character, examining microsetae of the halter. There are different microsetal patterns evident upon very high magnification of the ventroposterior side of the halter stem and knob. However, just as previously noted, there is a multitude of patterns and devising a consistent and cohesive scoring for this character is particularly challenging. It is not used for the phylogenetic analysis.

Legs.

[#89]. **Fore tibial spur.** The presence or absence of the fore tibial spur was scored. The tibial spurs did not show any intrageneric variation; all species belonging to the same genus had the same tibial spur formula. Members of *Arthropeas*, *Bolbomyia*, *Coenomyia, Dialysis, Lampromyia*, *Pseudoerrina*, *Vermileo*, and *Xylophagus* have a fore tibial spur. All other taxa lack fore tibial spurs.

[#90]. **Mid tibial spur.** The presence or absence of the mid tibial spur was scored. The tibial spurs do not show any intrageneric variation, all species belonging to the same genus have the same tibial spur formula. *Litoleptis alaskensis* (and its congeners) lack(s) a mid tibial spur. *Alloleptis tersus* is the only taxon that bears a single mid tibial spur. All other species have two mid tibial spurs. In species of *Austroleptis*, these spurs are generally shortened more than in other genera.

[#91]. **Hind tibial spur.** The presence or absence of the hind tibial spur was scored. The tibial spurs do not show any intrageneric variation, all species belonging to the same genus have the same tibial spur formula. Species of *Dichelacera*, *Litoleptis*, *Spania*, *Spaniopsis* and *Tabanus* lack hind tibial spurs. *Alloleptis tersus*, and species of *Arthroceras*, *Chrysopilus, Ptiolina, Schizella, Stylospania,* and *Symphoromyia* have a single hind tibial spur. Species of *Rhagio, Sierramyia, Desmomyia, Arthroteles, and Atherimorpha* have two tibial spurs, as do species of *Austroleptis*, *Vermileo,* and members of Athericidae and Xylophagidae.

[#92]. **Hind coxal tubercle.** The hind coxal tubercle is a small, anterior-facing protuberance of the hind coxa, usually visible from the antero-lateral view. It is present in most taxa. It is absent in species of *Austroleptis*, *Coenomyia*, *Dichelacera*, *Litoleptis*, *Pelecorhynchus*, *Tabanus*, *Vermileo*, *Xylophagus*, as well as in *Pseudoerrina jonesi* and *Sierramyia chiapasensis*. Additional tabanid species, belonging to *Chrysops*, *Esenbeckia*, and *Haematopota* were examined; these also lack

the hind coxal tubercle. However, while absent in all tabanids, it is present in all athericids, including *Atrichops* (not in the matrix).

[#93]. **Hind tibial macrochaetae presence.** The presence or absence of hind tibial macrochaetae was scored. Macrochaetae are setae that are distinguishable by their greater girth and length. Some macrochaetae, however, may be easily overlooked. For this character, macrochaetae were scored as present for all species that clearly exhibited hind tibial setae of two sizes on the anterior and/or posterior faces of the leg (the dorsal ridge of the tibia usually has thicker setae; this area was not considered for scoring). The macrochaetae may be short, inconspicuous, and nearly flush with the tibial surface, as in species of *Chrysopilus*, *Rhagio* and *Arthroceras*. Alternatively, macrochaetae may be lengthened, conspicuous, and projecting out from the tibial surface. Rather than divide this feature into two characters (present/absent and small, inconspicuous/large, conspicuous), macrochaetae were scored as a single character with three states. I did not wish to overemphasize the importance of having or not having macrochaetae since in some genera, such as *Arthroteles*, these setae are very few in number and are nearly absent altogether. The fact that some but not all *Rhagio* species have small macrochaetae also suggests that the evolutionary distance between the presence and absence of these setae is not particularly large.

[#94]. **Hind tibial macrochaetae length (not used in phylogenetic analysis).** After thorough review of the macrochaetae, I decided to abandon this character. Information collected regarding this character was integrated into the previous

character. *Atherimorpha* may have particularly distinctive macrochaetae; they are usually longer than what is found in other taxa where macrochaetae are present although even within *Atherimorpha*, this character can be quite variable. It is not used for the phylogenetic analysis.

[#95]. **Hind tibial swelling.** It is reported that species of *Rhagina* often have a ventro-apical swelling on the hind tibia (Yang et al., 1997: 184). The presence or absence of this hind tibial condition was scored. Surprisingly, neither *Rhagina incurvatus* nor another *Rhagina* species (indet. from Borneo) had a noticeable ventro-apical swelling on the hind tibia. Ultimately, no taxa were scored as having such a swelling. This condition appears to be a species level distinction for *Rhagina sinensis* Yang & Nagatomi.

[#96]. **Hind metatarsus swelling.** *Desmomyia* is unique in having the first hind metatarsus of the male enlarged.

Male Genitalia.

[#97]. **Epandrial sclerite aspect ration.** The epandrial sclerite is longer than wide in *Pelecorhynchus*, *Pseudoerrina*, *Suragina*, *Atherix*, and *Dasyomma*. In all other taxa, the epandrial sclerite was scored as wider than long, however, this character is variable within the Tabanidae. In *Tabanus atratus*, for instance, it is wider than long, however in other species, such as *Tabanus sulcifrons*, the epandrial sclerite is longer than wide. The epandrial sclerite is also longer than wide in *Esenbeckia incisuralis* and *Heptatoma pullecens*, however, in *Haematopota pechumani*, *Chrysops lateralis*,

and *Scaptia australis*, it is wider than long. In *Dichelacera marginata* and *Hybomitra atrobasis* the sclerite is approximately as wide as long. *Dichelacera marginata* was scored as wider than long. *Spaniopsis longicornis* was also scored as wider than long (as *Spaniopsis clelandi* and *Spaniopsis marginipennis*), but nearly as wide as long.

[#98]. **Anterior margin of epandrial sclerite.** If the anterior emargination reaches near the midline of the epandrial sclerite, it is scored as strongly notched. Otherwise, the anterior margin of the epandrial sclerite is scored as modestly curved as long as there is some emargination. In cases where the anterior margin is flat, or convex anteriorly, it is scored as not emarginate. Within the genus *Atherimorpha*, species may be either modestly or strongly emarginate, however it is most common to have modest anterior emargination and all *Atherimorpha* species scored for the matrix share this state. Variation within *Chrysopilus* and *Ptiolina* is reflected in the matrix. The midline cut off point to define the separation between states was an arbitrary designation. The variation of this character is clearly continuous within and among genera. *Pelecorhynchus personatus* and *Glutops rossi* were the only taxa scored as having the epandrial sclerite not emarginate anteriorly, however in *Glutops punctatus*, there is a modestly curved emargination.

[#99]. **Curvature of epandrium.** The epandria in most of the Tabanomorpha and all of the Rhagionidae sensu Woodley (1989) are nearly flat and are positioned directly above the hypandrium, so that they are separated by a horizontal gap. In species of *Pelecorhynchus* (but not *Glutops*), *Vermileo*, *Lampromyia*, *Suragina*, and *Atherix* (as

in *Atrichops*), however, the epandrium is enlarged and convex dorsally, so that its lateral margins surrounds the cerci and hypoproct and contains the hypandrium ventrally. This is most easily viewed from the posterior perspective.

[#100]. **Cercus.** The cerci may be directly attached to the epandrial sclerite or attached to a detached structure complex. The detached structure may be simply the hypoproct (without any dorsal element) or it may be a subepandrial element in the form of a membrane or sclerite. A difference that separates *Austroleptis*, *Glutops*, *Pelecorhynchus*, *Pseudoerrina*, Tabanidae, and Athericidae from all the other taxa is the origin of the cerci. The cerci may be separated from the epandrial sclerite by a membrane (as in species of *Glutops*) but their point of attachment is directly to the epandrial sclerite. In other taxa, cerci are attached to the hypoproct or subepandrial sclerite or membrane. In *Coenomyia ferruginea*, the cerci are adjacent to the epandrial sclerite, but are firmly attached to the hypoproct. Some connective membrane exists between the epandrial sclerite and the cerci in *Coenomyia ferruginea*, but this appears to be a secondary attachment.

[#101]. **Subepandrial sclerite.** A structure- called the subepandrial sclerite (Sinclair, 1992) or tergite 10 (Nagatomi, 1984)- may be present between the epandrial sclerite and the cerci. The subepandrial sclerite is scored as present only when the subepandrial structure is sclerotized. Sclerotization and the presence of the subepandrial sclerite are most easily viewed from the posterior perspective. The subepandrial sclerite is present in *Chrysopilus*, *Ptiolina* and *Symphoromyia*. For taxa

where the cercus attaches directly to the epandrial sclerite, this character was not scored because in these cases, there is character non-independence. The lack of the subepandrial sclerite is a necessary condition to allow for the direct attachment of cerci to the epandrial sclerite.

[#102]. **Subepandrial sclerite form.** The subepandrial sclerite was scored as entire or divided medially. In *Chrysopilus* and *Symphoromyia*, the sclerite is separated into two parts, whereas in *Ptiolina*, the structure is undivided. Taxa that lack a subepandrial sclerite were not scored for this character.

[#103]. **Setation of subepandrial sclerite.** The presence or absence of subepandrial sclerite setae was scored. In *Ptiolina* and *Symphoromyia*, the sclerite bears setae, whereas in *Chrysopilus*, the structure is bare. Taxa that lack a subepandrial sclerite were not scored for this character.

[#104]. **Hypoproct form (not used in phylogenetic analysis).** An attempt was made to score the form of the hypoproct. The hypoproct takes on a number of shapes, including sagittate, pentagonal, oval, and rectangular. The variation of this character was continuous, however, and apparently varied freely among species of the same genus (as in *Rhagio*). Identifying distinct states from a continuous variation of form was, in the end, a very challenging and perhaps a foolhardy endeavor. I am not confident enough in the scoring of this character to include it for phylogenetic

analysis. The same can be said for the following character, which scores the presence or absence of hypoproct lobes. Neither character is used for the phylogenetic analysis.

[#105]. **Hypoproct, form in outline (not used in phylogenetic analysis).** The hypoproct may appear developed into faint lobes, distinguished by an increase of lateral sclerotization. Most genera with multiple species sampling exhibited both the presence and absence of lateral sclerotization and I suspect that this character varies at the species level, or perhaps even among individuals of the same species. For this reason, it is not included in the phylogenetic analysis.

[#106]. **Hypoproct setae.** The presence or absence of hypoproct setae was scored. This character varies at the species level within at least *Atherimorpha*, *Ptiolina*, and *Rhagio* and it may be unlikely that it is an important character for defining clades above the subgenus or species level. However, it is retained for phylogenetic analysis because it is an easily scored, discrete character.

[#107]. **Cercus shape (not used in phylogenetic analysis).** In some *Rhagio* species (*R. plumbeus*, for example) the cercus is nearly square or rectangular, whereas in most species of *Chrysopilus*, the form of the cercus is more eye-shaped, or leaf-shaped. I surveyed the rest of the taxa and ceased to score this character. Although clear differences in the form of the cercus may exist when comparing a limited number of taxa, it is not feasible to assess such irregular shapes, designate them into discrete categories, and score them over a large matrix of relatively distantly related

taxa. Thus, although differences in cercus shape were noted, they are not included in the phylogenetic analysis.

[#108]. **Cercus separation.** The lateral distance between cerci were measured and scored in three states. Measurements were made by eye. Cerci were scored as 1) directly adjacent to one another, separation distance one quarter width of cercus or less, 2) partially displaced from one another, separation distance approximately half the width of single cercus, or 3) widely displaced from one another, separation distance greater than three quarters width of cercus.

[#109]. **Cercus orientation (not used in phylogenetic analysis).** The angle at which the cerci are held was scored, relative to the epandrial sclerite. In some taxa, such as in species of *Pelecorhynchus*, the cerci are clearly oriented in a vertical fashion. Arbitrary cut off points were established for the designation of three separate states, although in reality, the character varied continuously. Cerci held at 0–20° relative to the epandrial sclerite were scored as 'horizontal,' cerci held at 21–70° relative the epandrial sclerite were scored as 'at angle,' and cerci held 71–90° relative the epandrial sclerite were scored as 'vertical.' The degree angles were approximated by eye. One fairly common problem was that in some species, such as *Atherix pachypus*, the cercus was flush with the epandrial sclerite dorsally yet rounded so that the ventral portion of the cercus was vertically oriented. How this condition related to the other states was unclear. Orientation of cerci was also affected by their treatment in the dissection process. Some may have been expanded or flattened inadvertently. For

these reasons, ultimately, there was little confidence in the scoring for this character and it was removed for phylogenetic analysis.

[#110]. **Cercus form, from posterior view (not used in phylogenetic analysis).** The cerci were scored as either curved or flattened, when viewed from the posterior perspective. The variation of this character was continuous and states were designated by approximate form. No distinct cut off point was devised, aside from 'mostly flat' versus 'mostly cupped, or curved,' which were approximated by eye. Curvature of the cerci may have been affected by the dissection process. Some may have been flattened inadvertently. For these reasons, ultimately, there was little confidence in the scoring for this character and it was removed for phylogenetic analysis.

[#111]. **Hypandrial sclerite.** The presence of a free hypandrial sclerite or one that is partially or completely fused with the gonocoxites was scored. Hypandrium is a term that refers to the entire ventral portion of the male genitalia (containing the gonocoxites, gonostylus, aedeagus and associated structures). The term 'hypandrium' is also used in specific reference to the ventral sclerite attached to the gonocoxites. When referring to this ventral sclerite of the hypandrium here, I prefer to use the term hypandrial sclerite in order to avoid confusion. The hypandrial sclerite is scored as 'free' when it is separated from the gonocoxites by a complete suture (i.e., it is not fused to the gonocoxites). There is an intermediate condition where the hypandrial sclerite is fused anteriorly and partially free from the gonocoxites posteriorly. This condition is found in species of *Arthroceras* and *Symphoromyia* and is scored as

'incompletely fused.' The third state is found in Athericidae, Tabanidae, Xylophagidae, and species of *Alloleptis*, *Austroleptis*, *Chrysopilus*, *Lampromyia*, *Litoleptis*, *Ptiolina*, *Schizella*, *Spania*, *Spaniopsis*, and *Vermileo*. In these taxa, the hypandrial sclerite and the gonocoxites are fused so that the ventral portion of the hypandrium is a single unit.

Since the hypandrial sclerite is separated from the gonocoxites in Nematocera and in many basal brachycerans including Bombyliidae, Therevidae, and Asilidae (Sinclair et al., 1993), as well as in taxa scored here, the state is considered generally considered plesiomorphic. The fusion of the hypandrial sclerite with the gonocoxites is a putative synapomorphy for Tabanidae + Athericidae (Woodley, 1989; Sinclair et al., 1993). The fact members of the outgroup Xylophagomorpha have a fused hypandrial sclerite, however, somewhat complicates the story of the evolution of this character within Tabanomorpha. Within the Pelecorhynchidae, and even within *Pelecorhynchus*, there is variation of this character. *Glutops* and *Pseudoerrina* have a free hypandrial sclerite, while most *Pelecorhynchus* have gonocoxites fused to hypandrium. In *P. personatus*, the hypandrial sclerite is free and is scored as such in the matrix. Yet the hypandrial sclerite in this species is very narrow and different in form than the typically broad, smoothly triangular sclerite (as in *Glutops* and other taxa including *Pseudoerrina*). The free hypandrial sclerite in *P. personatus* may represent a secondary transition.

[#112]. **Gonocoxal sinuous ridge.** The dorsal side of the gonocoxite may have a sinuous ridge that leads to the gonocoxal apodeme. This is lacking in Athericidae, Tabanidae, Vermileonidae, and many Xylophagidae, as well as *Alloleptis tersus*, *Austroleptis multimaculata*, *Chrysopilus quadratus* (unlike most *Chrysopilus* species), *Litoleptis alaskensis*, and *Stylospania lancifera*.

[#113]. **Gonocoxal apodeme presence.** The presence or absence of gonocoxal apodemes was scored. *Austroleptis* and *Litoleptis* are the only taxa where the gonocoxal apodemes are absent. I do not consider this a compelling synapomorphy for supporting common ancestry of these genera, although it is a rarely occurring feature. The reduction of such a structure may occur on account of a variety of independent evolutionary constraints.

[#114]. **Gonocoxal apodeme length.** The length of the gonocoxal apodeme was scored by noting the position at its apex, relative to the anterior margin of the hypandrium. Although the gonocoxal apodeme is continuously varied to some degree, two mutually exclusive states emerged. The gonocoxal apodemes were scored as either 1) short or long enough to reach the anterior margin of the hypandrium or 2) extending well beyond the anterior margin of the hypandrium. The long length of the gonocoxal apodemes has been given as evidence to support Athericidae + Tabanidae (Stuckenberg, 1973; Sinclair et al., 1993), although the character is lacking in *Xeritha* Stuckenberg (as noted in Sinclair et al., 1993). *Austroleptis multimaculata* and

Litoleptis alaskensis are not scored for this character since they lack gonocoxal apodemes.

[#115]. **Gonocoxal apodeme origin.** The relative lengths of the medial and lateral margins of the gonocoxal apodeme were scored. Relative length of the gonocoxal margins may be strikingly different among taxa. Athericidae and Tabanidae, for example, have very short medial gonocoxal margins in comparison to the lateral margins, so that what may be called the parameral bridge (the transverse structure spanning the parameral sheath, joining the gonocoxites dorsomedially), is shifted anteriorly. Instead of referring to the relative placement of the parameral bridge, I believe that scoring the relative lengths of the inner and outer margins of the gonocoxal apodeme is more discrete, objective, and consistent. In addition to the Athericidae and Tabanidae, other taxa that have gonocoxal apodemes with shorter inner margins are *Lampromyia canariensis*, *Vermileo vermileo*, *Pelecorhynchus personatus*, and *Xylophagus lugens*. *Austroleptis multimaculata* and *Litoleptis alaskensis* are not scored for this character since they lack gonocoxal apodemes.

[#116]. **Parameral sheath.** The parameral sheath surrounds the aedeagus posteriorly. Ventrally, the sheath is sometimes bulbous and/or produced into paired swellings ventrally. The character was scored as developed into bulbous sac ventrally when the parameral sheath was expanded so that it was flush with the gonocoxites ventrally. The sac was scored as having lobes only when membranous lobes were distinctly present. Such lobes were present in species of *Arthroceras*, *Ptiolina*, *Spaniopsis*, and

Symphoromyia. Interestingly, in species of *Austroleptis*, there are two centrally located, ventral hypandrial lobes. However in *Austroleptis*, the lobes arise from the gonocoxites (instead of from the parameral sheath) and are sclerotized (instead of membranous). I don't believe at the sclerotized gonocoxal lobes of *Austroleptis* are homologous with the membranous lobes of the parameral sheath found in other taxa. The parameral sheath itself is unmodified in *Austroleptis*. Therefore, *Austroleptis* was scored as not having the parameral sheath developed into a sac ventrally.

[#117]. **Lateral ejaculatory process.** Lateral aedeagal processes (*sensu* Sinclair, et al. 1993) are present in two forms. In *Desmomyia thereviformis*, all *Rhagio* species, *Rhagina incurvatus*, and *Sierramyia chiapasensis*, the lateral aedeagal processes are thin, lightly sclerotized structures that are integrated into the sperm sac. In all species of *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Chrysopilus*, *Glutops rossi*, *Pseudoerrina jonesi*, all *Ptiolina*, *Schizella furcicornis*, *Spania nigra*, all *Spaniopsis*, and all *Symphoromyia*, the lateral aedeagal processes are thickened, well sclerotized structures that are integrated into the sperm sac basally, but extend freely apically. In most taxa that have aedeagal tines, such as Athericidae, Tabanidae, and *Bolbomyia nana*, no lateral aedeagal processes are present. This has led to misunderstandings of the lateral aedeagal structures as possibly being homologous to the aedeagal tines. It is instructive to note here, however, that all *Arthroceras* species have both aedeagal tines and lateral aedeagal processes.

[#118]. **Ejaculatory apodeme length.** The length of the ejaculatory apodeme was scored by noting the position at its apex, relative to the anterior margin of the hypandrium. Although the gonocoxal apodeme is continuously varied to some degree, ejaculatory apodeme length was divided into four discrete categories. The gonocoxal apodemes were scored as 1) reduced, nearly absent, 2) short, not reaching anterior margin of the hypandrium, 3) moderately long, reaching the anterior margin of the hypandrium, or 4) long, reaching beyond the anterior margin of the hypandrium. Perhaps there should have been an additional state for especially long ejaculatory apodemes, such what is found in species of *Atherix* and *Dasyomma*. However since there is continuous variation in this character, it is difficult to score 'extra long' when there are few objective reference points. Perhaps on account of this type of variation, and the lack of intuitive and discrete length categories, states are generally not conserved at the genus level. The ejaculatory apodeme, for example, in species of *Chrysopilus*, may be short, moderately long, or long. Similarly, the length of the ejaculatory apodeme is not fixed in *Ptiolina*, *Rhagio*, *and Symphoromyia*. It is not used in the phylogenetic analysis.

[#119]. **Ejaculatory apodeme form.** The form of the ejaculatory apodeme was scored as either tubular, laterally compressed, compressed dorso-ventrally, tripartite, or umbruculate (umbrella-shaped) anteriorly. Tripartite is a term used describe the structure when it is dorsally compressed laterally and ventrally compressed dorso-ventrally, as in the case of *Bolbomyia nana*. *Austroleptis* species are distinctive by having the ejaculatory apodeme umbrella-shaped at its apex. In these and other cases,

such as in *Ptiolina fasciata* where the ejaculatory apodeme is very clearly laterally compressed, the character is easily scored. However, for other taxa, the form of the ejaculatory apodeme does not fall so neatly in a single category. The ejaculatory apodemes of *Chrysopilus ferruginosus* and *Ptiolina zonata*, for example, are mostly tubular, but also laterally compressed somewhat. For these species, the character is scored as an ambiguity, present as both a tubular and laterally compressed apodeme. Furthermore, it is important that the apodeme be examined from more than a single perspective since a laterally-compressed apodeme will look tubular when only viewed from above. Generally, ejaculatory apodeme forms were consistent within genera, however, I don't have a great deal of confidence in this character on account of the difficulties inherent in its scoring.

[#120]. **Aedeagal tines.** The presence or absence of aedeagal tines was scored. The tines are present in Athericidae, Tabanidae, *Bolbomyia*, and *Arthroceras*. The presence of aedeagal tines has been proposed as a synapomorphy to unite Athericidae+Tabanidae+*Bolbomyia* (Sinclair, et al., 1993).

[#121]. **Endoaedeagal process presence.** The endoaedeagal process (termed by Sinclair et al, 1993) is a slender, sharply pointed projection that extends posteriorly into the sperm sac. This structure has been proposed as one of three synapomorphies of the male genitalia which support the monophyly of the Brachycera (Sinclair et al, 1993). Sinclair et al. (1993) defined the origin of the endoaedeagal process at "the base of the aedeagal tines or the 'precursor' sclerites." Sometimes, as in some *Ptiolina*

species, however, the tines or 'precursor' sclerites are missing and the point at which the endoaedeagal process begins is not immediately obvious. Sometimes a break (in the form of a partial or complete suture, or as a small gap) is present between the aedeagal apodeme and endoaedeagal process, and this can be used to indicate where the endoaedeagal process begins. However, this suture or break is not always present. And across the lower Brachycera, the length of a posterior extension of the ejaculatory apodeme varies, so that scoring can be difficult in "almost completely reduced" situations.

In particular, within the genus *Ptiolina* the character is free to vary, in ways that may make scoring problematic. In *Ptiolina majuscula* and *P. lapponica*, for example, an endoaedeagal component is clearly present (anterior of the ‘precursor’ sclerites), but it is broad, blunt, and short. In *P. nitida*, the posterior end of the aedeagal apodeme is turned downward sharply, at the anterior boundary of the sperm sac and the landmark 'precursor' sclerites are missing in this species, so the precise point at which the endoaedeagal component begins is unclear. In *P. fasciata*, the landmark ‘precursor’ sclerites are present and clearly mark the posterior apex of the aedeagal apodeme; the endoaedeagal component is absent in this species. *P. edeta*, *P. mallochi*, *P. nigra*, *P. obscura*, and *P. zonata* are similar to *P. nitida* in form.

In many *Chrysopilus* species, the posterior end of the aedeagal apodeme is turned downward sharply, at the anterior boundary of the sperm sac just as it is in many *Ptiolina* species. In *Chrysopilus ferruginosa* and *C. quadratus*, there is an additional

structure posterior to the aedeagal apodeme, where the ‘precursor’ sclerites usually are located. This may be interpreted as a fusion of the two 'precursor' sclerites or an unrelated structure. In any case, it is not fused with the aedeagal apodeme and does not penetrate the sperm sac. Therefore it is not scored as the endoaedeagal process.

[#122]. **Endoaedeagal process form.** For taxa where the endoaedeagal process is present, the form of the endoaedeagal process is scored for three states. Species of *Arthroteles*, *Atherimorpha*, and *Rhagio*, and also in *Desmomyia thereviformis* and *Rhagina incurvatus*, the endoaedeagal process is very distinctly laterally compressed, taking the form of a butterknife. In other taxa, the endoaedeagal process is either narrowly conical, smoothly cylindrical, or dorsolaterally flattened. These states were rather continuous and blended with one another. *Dialysis rufithorax* was the only taxon with an unmistakable dorsoventrally flattened endoaedeagal process, and a separate state was designated on account of this.

[#123]. **Gonostylus setation (not used in phylogenetic analysis).** The relative amount of setation on the gonostylus is scored as either heavily or lightly present. This is a continuous character that lacks discrete boundaries between states, although the relative amount of gonostylar setation is generally conserved within each genus. *Chrysopilus* species, for instance, generally have densely arranged, robust gonostylar setae, as do putative allies *Schizella* and *Stylospania lancifera*. The continuous nature of this character, however, precluded it from being scored confidently and it was not used for phylogenetic analysis.

The gonostylus may take a number of shapes, some of which may provide useful information for use in phylogenetic analyses. In *Glutops rossi* and *G. punctatus*, for instance, gonostylus is full and rounded, with a distinctive inner margin that is s-shaped and bearing an internally directed hook apically. *Pelecorhynchus fusconiger* has a gonostylus with very similar characteristics. The inner margin is roughly s-shaped and at its terminus, bears an internally directed hook. However, the diversity of gonostylus form among *Pelecorhynchus* species suggests that scoring this is not necessarily so simple. In *P. elegans*, for instance, the gonostylus has an inner margin whose curvature is exaggerated into a thick medial swelling. In *P. personatus*, this swelling is narrow so that it nearly takes the form of a ridge. The distal area elongated and conical in *P. personatus*, however the inward facing hook is still present. In *P.* (*Archeomyia*) *mirabilis*, the inward facing ridge is produced into a long slender extension, making the gonostylus appear two-pronged and distally, the inward facing hook is missing. The transformation series of this feature, and the homology of the inward-facing swelling and distal hook may be intuitive within the Pelecorhynchidae, however, assessing the homology of shape across a broad array of taxa is far more daunting. I prefer to simply make note of similarities of gonostylar form that may be appreciated in light of a phylogenetic hypothesis rather than code these rather complicated forms *a priori*, for phylogenetic analysis. Therefore, it is not used for the phylogenetic analysis.

Female abdomen.

[#124]. **Terminal abdominal segments (not used in phylogenetic analysis).** Rhagionidae are known as Snipe flies, a name that refers to their evenly tapered abdomen. The character may vary strikingly among Tabanomorpha, where the female abdomen either may be evenly tapered or with a clear difference between wider basal segments and narrowed distal segments. If a straight line could be visualized along the lateral margins of the abdominal sclerites, the abdomen was scored as evenly tapered. In the cases where there is an abrupt size difference between basal and distal segments, the line is jagged in keeping with the margins of the sclerites. Species of *Pelecorhynchus* provide an example for this case. The amount of 'jag' required to invoke its recognition for being scored is not always self-evident. For example, in *Glutops punctatus*, the female abdomen there is an obviously abrupt size difference, yet in *Glutops rossi*, the break is much less clear. Without reference to *G. singularis*, *G. rossi* may appear evenly tapered. Upon closer inspection, however, there is a subtle but clear break between the fourth and fifth abdominal sclerites, just as in *G. singularis* (but less so). As the breaks revealing abrupt size differences between basal and distal segments become more subtle, the character begins to break down, as nearly all genera have species where abdominal sclerite width differences may be interpreted as either evenly or abruptly tapered. *Chrysopilus*, *Rhagio*, and *Spaniopsis* have species with smoothly tapering abdomen, although there is usually a difference between the basal segments of the abdomen and those distally, which have the ability to telescope within these segments. It is interesting to note that while in most species, as in *Pelecorhynchus*, *Glutops*, and *Schizella furcicornis*, the change in width occurs

between the fourth and fifth segments. In *Symphoromyia cruenta*, the constriction occurs between the fifth and sixth segments. Although the current character is not used for phylogenetic analysis, the nature of this character may be integrated into the analysis by taking into account related measures, such as the shape of tergite 7 and the intersegmental membrane distance between segments 7 and 8. These measures are associated with the form and ability for telescoping segments. This character was removed for phylogenetic analysis.

[#125]. **Tergite 7.** The shape of tergite 7 was scored as either clearly longer than wide, about as long as wide, or clearly wider than long. This determination was made after the sclerite was laid flat. *Glutops rossi* was the only taxon that is scored as about as long as wide. *Glutops singularis* also has a square tergite 7. This character is consistent within genera, except in *Ptiolina*, where tergite 7 may be wider than long or longer than wide. In *Arthroceras pollinosum*, tergite 7 is clearly longer than wide. This is also the case for *Arthroceras fulvicorne*, however Nagatomi & Iwata (1976) illustrate tergite 7 in *Arthroceras japonicum* as apparently wider than long. In *Arthroceras leptis*, tergite 7 is about as long as wide. Tergite 7 in *Arthroteles cinerea* is also illustrated by Nagatomi & Iwata (1976) as wider than long, however, I have examined this species and it is longer than wide, as it is in *Arthroteles bombyliiformis*. Stuckenberg (2001) noted that this may be an important character.

[#126]. **Intersegmental membrane between segments 7 and 8.** In some taxa, there is a distinctly long intersegmental length between the distal segments of the female

abdomen. Stuckenberg (2001) has pointed this out and has used it as a justification to support family relationships. Intersegmental length between the 7th and 8th segments is scored as 1) short, as throughout abdomen or 2) especially long. Where scored as especially long, the intersegmental region between tergites 7 and 8 is clearly longer than the intersegmental region between tergites 4 and 5. It is tempting to compare the 7/8 intersegmental region to the length of sternite 8. That was not done here, as sternite 8 may vary independently. Thus, the 7/8 intersegmental may be longer or shorter than the length of sternite 8. The 7/8 intersegmental of *Austroleptis multimaculata* is clearly longer than the intersegmental membranes anterior to this and is in apparent conflict with how Stuckenberg (2001) has scored the present character for the genus.

A long intersegmental length of the distal abdominal sclerites provides the ability to retract the terminal segments in a telescoping manner. Therefore, taxa with long distal intersegmentals may also be referred to as having an 'extensible abdomen.' This form seems to be a basic adaptation for oviposition in a terrestrial habitat, adapted for soft earth in saturated conditions and in leaf litter and mold, and this is where flies with extensible abdomen are most commonly found. The extensible abdomen occurs across a fairly broad spectrum of taxa within lower Brachycera, suggesting that it may be a very old character. In any case, I think these factors suggest that it may not be a reliable character for phylogenetic inference. If it is not plesiomorphic, then it at least appears vulnerable to change due to convergence (restraints of common habitat)

rather than (or at least as much as) change due to common ancestry. It is, however, included for phylogenetic analysis.

Female terminalia (external structures)

[#127]. **Tergite 9 length.** In *Spania nigra* and species of *Spaniopsis*, tergite 9 is reduced to a very narrow sclerite. This character state is not found in any of the other taxa.

[#128]. **Tergite 9 anterolateral arms.** There is a special modification of tergite 9, in which narrow, anteriorly-directed ventrolateral extensions (arms) are produced, enveloping sternite 9. The ventrolateral arms of tergite 9 are actually firmly attached to sternite 9 laterally, via thick membranous tissue. Surprisingly, this has not been noted by previous authors and appears phylogenetically informative. Where present, it is obvious only after careful dissection. The feature is found exclusively, in all species of *Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*. Since this character not only scores the presence of these arms, but also the fact that they are firmly attached to sternite 9 (an additional unique aspect of this modification), extra weighting of this character may be appropriate.

[#129]. **Tergite 10 length (not used in phylogenetic analysis).** Relative length of tergite 10 was first pointed out in Nagatomi & Iwata (1976: 36). The length of tergite 10 was compared against the width and scored in three ways: 1) absent, 2) present, reduced, 3) present, not reduced (length approximately equal to measured half width)

or 4) present, not reduced. Where the length of tergite 10 is measured to be less than half the width of the sclerite, it is scored as reduced. Tergite 10 is scored as not reduced where the length is approximately equal to, or greater than, half the width. Differences between the states of this character are subtle, however, and vulnerable to inconsistent scoring. This became clear as scoring progressed and scoring was stopped once this determination was made. For the taxa scored, variation within genera and families suggest that this character ought to be removed for phylogenetic analyses.

[#130]. **Tergite 10 form.** Female tergite 10 is scored either as entire or split into two separate lateral sclerites. This character is not applicable for *Pseudoerrina jonesi*, where tergite 10 is absent. Nagatomi & Iwata (1976) show tergite 10 of *Atherix basilica* as entire, however in *Atherix pachypus*, it is split (as the illustration of *Atherix ibis* in Nagatomi & Iwata (1976:38, fig 26)). Tergite 10 is entire in *Arthroceras pollinosum*, *A. leptis*, *A. fulvicorne*, and *A. subaquilum*, however it is illustrated as partially spit in *A. japonicum* by Nagatomi & Iwata (1976:22, fig 12).

[#131]. **Sternite 8 form.** In *Austroleptis multimaculata* (and congeners), it appears that the sternite 8 is divided into anterior and posterior segments. Sternite 8 in species of *Austroleptis* is shifted posteriorly so that the division of this sternite is positioned to allow for flexibility of the cerci and associated structures with respect to the rest of the abdomen. Nagatomi & Iwata (1976) have a different interpretation of this sternite in *Austroleptis*. Instead of considering it two parts of the same sclerite, they interpret

the anterior part as sternite 8 and the posterior part as sternite 9. Since the genital fork is homologous to sternite 9, however, and this present in *Austroleptis*, the interpretation of Nagatomi & Iwata invokes the duplication of sternite nine and subsequent reduction of the anterior copy, to a simple sclerite. I reject this interpretation as highly unlikely. Assuming that sternite 8 is simply divided into two parts, all segments are present and accounted for. In some species, such as in an undescribed species I've examined from South America, the division between the anterior and posterior areas of sternite 8 is inconspicuous. One could very easily miss seeing this division, and mistake the compound structure as a single, elongate sclerite. *Austroleptis* is autapomorphic for this feature.

[#132]. **Sternite 8 cleavage.** Sternite 8 is the sclerite underneath the genital furca, and the notch (or 'cleavage') along its posterior margin apparently allows for the male reproductive organ to reach the genital chamber. Originally, I tried to account for the diversity of form represented by the notch itself, which may be deep/shallow, narrow/broad, v-shaped/u-shaped, etc. But, ultimately, these differences proved to be exceedingly subtle and were subject to varying interpretation. There may be some pattern as to the form of the cleavage of the posterior margin of sternite 8, but I could not devise an unambiguous scoring metric that teased out this information for phylogenetic analysis. However, there is one major, easy-to-score feature of the posterior margin of sternite 8. This is simply the presence or absence of the notch. In *Dasyomma atratulum*, there is a medial suture that is very inconspicuous, yet the notch is scored as absent because the posterior margin itself is entire. All members of

Athericidae, Tabanidae, and Vermileonidae of this taxon set, are scored as lacking the posterior margin notch. The notch is also absent in *Austroleptis multimaculata*, *Spania nigra*, and species of *Spaniopsis*.

[#133]. **Sternite 8 length.** The length of sternite 8 was scored relative to its width, and placed into one of four separate categories; 1) wider than long, 2) as long as wide, 3) longer than wide, or 4) elongated. Elongated, in this sense, means that the sclerite is at least twice as long as wide or longer (e.g., sternite 8 in members of Xylophagidae). This character was generally consistent within genera, however, the sternite 8 of *Ptiolina* species may either be as long as wide or longer than wide. This difference within *Ptiolina* is actually a consistent character that, in corroboration with several other characters, helps to distinguish between *Omphalophora* and *Ptiolina*. *Spania nana* and species of *Spaniopsis* are the only taxa that have sternite 8 wider than long. The two divisions of sternite 8 in *Austroleptis multimaculata*, when added together, are elongate, but I prefer to leave this character unscored as the homology of the state may be disputed. Some of these differences in sternite 8 morphology may be viewed in the illustrations by Nagatomi & Iwata (1976).

[#134]. **Sternite 10 form (not used in phylogenetic analysis).** Sternite 10 may be sclerotized evenly or sclerotization may be weakened medially. Where the sclerotization is weakened, it appears as if the sclerite is divided into two lateral components, as in *Bolbomyia macgillisi*. The latter state is a relatively common feature, however, it is not always easy to detect. The lack of medial sclerotization

may be incomplete, or the sclerotization of sternite 10 may be weak across its entire length. This led to poor confidence in the accuracy of the scoring. My impression, after examining a broad sampling of taxa, is that this character is of minor importance (at best) for confirming or refuting hypotheses of relationship. For these reasons, the character was not included in phylogenetic analysis.

[#135]. **Sternite 10 shape (not used in phylogenetic analysis).** The form of sternite 10 took on a variety of shapes, which were scored as one of five states; 1) pentagonal, pointed posteriorly, 2) rectangular, 3) sagittate, 4) semi-circular, or 5) ovoid. Where sternite 10 is clearly five-sided, it is scored as roughly pentagonal. Typically, the pentagon shape is nearly regular. However, in *Ptiolina*, it is broad and clearly wider than long. A four-sided sternite 10, with minimal side curvature is scored as rectangular. Where sternite 10 is generally pentagonal in shape, pointing posteriorly, but bears lateral anterior lobes, it is scored as sagittate. Semi-circular sclerites are defined by having a straight anterior margin and a fully rounded posterior margin. If sternite 10 is rounded throughout, it is scored as ovoid. Where the anterior margin is flat and the posterior and lateral sides rounded, sternite 10 is scored as semi-circular. Sternite 10 may be rounded throughout and in this case, it is scored as ovoid. Although differences in shape among taxa are evident, these differences are exceedingly subtle and difficult to score consistently. Boundaries between semicircular, ovoid and rectangular, or between pentagonal, semi-circular, and sagittate, are often determined by slight differences of curvature that are rarely unambiguous. For this reason, the character is not used for phylogenetic analysis.

[#136]. **Sternite 10 position.** The position of sternite 10 was scored relative to the first cercus segment. Significant differences exist between species, and these differences are not altered by handling because connective tissue is short and structures are virtually immobile, even after manipulation in glycerol. The characters scored are 1) nearly completely anterior to first cercus segment (~10% below basal cercus), 2) posterior half below first cercus segment (approximately 20–50% below first cercal segment, 80–50% below tergite 10), or 3) entirely or almost entirely underneath cercus segments. Since the cercus attaches to tergite 10, this is another way to score the relative development of tergite 10 versus sternite 10. Where tergite 10 is reduced, the cercus is shifted anteriorly and the sternite 10 subtends a greater portion of the cercus. The relative length of tergite 10 was difficult to score confidently and for this reason, abandoned for use in phylogenetic analysis. While the present character is essentially a derivation of character #133 (tergite 10 absent, present/reduced, or present/not reduced), it is more discrete, easier to score, and thus in my opinion, more trustworthy. The overlap between the present character and character #133 isn't complete, however. In *Lampromyia canariensis*, for example, tergite 10 is missing, yet sclerite 10 is nearly completely anterior to the first cercus segment and is therefore coded differently than in *Atherix pachypus*, for example, where tergite 10 is also absent, but sternite 10 is produced directly below the first cercus segment as other athericids, tabanids, and in *Vermileo vermileo*.

[#137]. **Cercus segmentation.** The cercus may be one- or two-segmented. The loss of the basal cercus segment is a putative synapomorphy for Athericidae + Tabanidae. Species of *Austroleptis* also have a single cercus segment.

[#138]. **Basal cercus elongation.** The basal cercus is scored as either elongated or not. Basal cerci that are at least three times as long as wide are considered elongate. This is the condition in *Arthroceras americana*, *Coenomyia ferruginea*, *Dialysis rufithorax*, and *Xylophagus lugens* (the xylophagids included in this study). Otherwise, the basal cercus is scored as not elongate.

[#139]. **Basal cercus lobe (alternate character coding based on gestalt; not used in phylogenetic analysis).** The basal cercus was scored for the presence of a ventral process. The degree to which the ventral process must be present in order to be scored as such has not been established by previous authors who have examined this feature (Nagatomi and Iwata, 1976), and variation in the degree to which the lobe is present makes consistent scoring of this character difficult. The lobe was scored as present or absent according to 'gestalt.' For consistency and repeatability, a more precise scoring method is also devised, scored, and discussed in a subsequent scoring system. The present system uses 'expert' judgement, however, I place little confidence that the boundary between presence and absence of the first cercus lobe remains fixed across the entire sampling taxa here, and even less confidence in the prospect that the scoring here would be generated independently by another worker looking at the same material. The presence or absence of the first cercus segment, due to the

continuous nature of its variation, is largely subjective. For this reason, the scoring of this character is inappropriate for phylogenetic analysis.

[#140]. **Basal cercus lobe (alternate character coding based on extreme cases; not used in phylogenetic analysis).** Among most species of Tabanomorpha (with two cercus segments), there is a range of continuous states with respect to the degree of lobing of the first cercus segment. There appears to be an obvious, discrete gap between this range of morphological variation, however, and an extreme morphology evident in a few species. The basal cercus lobes in species of *Glutops*, *Pseudoerrina*, and *Pelecorhynchus*, and in *Vermileo vermileo*, appear well out of the range of variation present among other Tabanomorpha. They are distinct in extending posteriorly past the point of attachment of the second cercus, are nearly parallel-sided, and nearly as long or longer than the second cercus.

[#141]. **Basal cercus lobe (alternate character coding based on area ventral of first cercus, relative to width of second cercus; not used in phylogenetic analysis).** In species of *Pelecorhynchus*, *Pseudoerrina*, and *Glutops*, the ventral process is very conspicuous. However, aside from these extremes, there is continuous variation of this character when examined across a broad sampling of Tabanomorpha. Even among species in the genus *Chrysopilus*, many degrees of a ventral process are present, including the lack of such a structure. This variation clouds the point at which a ventral extension must be considered present. As an arbitrary but discrete metric, the width of the second cercus segment at point of attachment was compared

against the length of the first cercus segment ventral to this. The ventral process was scored as present where the length of the first cercus ventral to the ventral margin of the second cercus segment was equal to or greater than the width of the entire second cercus segment. Others may argue the appropriateness of this demarcation, especially as the width of the second cercus segment is free to vary and thus, may complicate the scoring of the ventral process of the first cercus segment. While this criticism identifies an obvious flaw inherent in the measurement, I have found that the width of the second cercus segment is mostly constant across tabanomorph taxa. The choice of determining a threshold for scoring the presence of a ventral process of the first cercus segment (equal to the width of the second cercus segment, at point of attachment) is much more problematic because 'borderline' cases abound. If a lobe is, by definition, at least as wide as the width of the second cercus segment, some cases, such as in *Arthroteles bombyliiformis*, an apparent lobe must be scored as absent. Conversely, if the threshold is loosened so that the lobe must be at least half the width of the second segment, obvious cases where the lobe is not present, such as in *Ptiolina*, a lobe will be scored as present. Ultimately, the many ways in which the basal cercus may vary confounds objective scoring schemes devised for scoring the lobe. The basal cercus may vary in the position of attachment of the second cercus, the posterior extension of the basal lobe (relative to the second cercus), and the ventral extension of the lobe (relative to the base of the first cercus segment). The latter two components, in particular, appear to vary continuously. The presence of a ventral process in the basal cercus segment is probably associated with egg-laying

behavior. This is a preliminary scoring of this character, modified below, and is not used for the phylogenetic analysis.

[#142]. **Second cercus position (not used in phylogenetic analysis).** In the process of understanding the morphological diversity of the female cercus, and taking into account the extent of its variation, I noticed that the placement of the second cercus segment on the basal segment was consistent within genera and discretely different among genera. Often, the placement of the second cercus segment was associated with the presence or absence of a ventral lobe (i.e., second segment dorsally placed in taxa with ventral lobes present), however, not always. Since this scoring of this character is much more easily and objectively determined, it may provide surrogate phylogenetic information not accessible when focusing on the presence or absence of the ventral lobe itself. Not scored for taxa with elongate first cercus segment, because apical margin of this segment is reduced (only one point of attachment possible). This is a preliminary scoring of this character, modified below, and is not used for the phylogenetic analysis.

[#143]. **Basal cercus lobe.** The first cercus segment postero-ventral lobe is a sometimes subtle feature that may distinguish itself in a number of ways. I've tried to break these confounding morphologies down into what I consider the major elements of what makes a lobe; gestalt, length of first cercus below second cercus attachment, and position of the attachment point of the second cercus. I've put the discrete, objectively scoreable states of the latter two components together into a single

character as a way to score the presence or absence of the lobe. An additional state is also added to account for the distinct lobe in species of *Glutops*, *Pelecorhynchus*, *Pseudoerrina*, and *Vermileo*.

Where the ventral length of the first cercus segment is equal to or longer than the width of the attachment point of the second cercus and the second cercus is attached dorsally (measured by the comparison of widths of the first cercus above and below the second cercus), then the lobe is considered present. In all of these cases, the taxon was also scored as having a lobe when measured by gestalt. Where the ventral length of the first cercus segment is shorter than the width of the attachment point of the second cercus and the second cercus is attached centrally or ventrally (measured by the comparison of widths of the first cercus above and below the second cercus), then the lobe is considered absent. In all of these cases, the taxon was also scored as lacking a lobe when measured by gestalt. In *Arthroceras pollinosum*, the basal cercus is expanded so that although the ventral length is greater than the width of the second cercus, but the second cercus segment is attached centrally. In *A. fulvicorne*, *A. leptis*, and *A. subaquilum*, this is also the case. The cases may be made for *Arthroceras* species in favor or against having a ventral lobe, depending on your predisposition. This state I've scored separately, as unclear. It appears more like a third condition in *Arthroceras* rather than ambiguous between two states. In *Atherimorpha atrifemur*, the second cercus is positioned dorsally, but the ventral portion of the basal cercus is not expanded. This taxon was scored as ambiguous; the lobe may be present (as in *Atherimorpha vernalis*) or absent (as in *Atherimorpha nemoralis*).

[#144]. **Ventral lobes of basal cercus.** When looked at the female terminalia from the posterior view, the ventral apices of the basal cerci may curve inwardly to meet one another medially, forming a circle or ring. Stuckenberg has pointed out this character and has advocated its use in phylogenetic analysis (2001). Although this character appears to depend in some degree on the presence or absence of ventral lobes of the basal cercus segments, I found that the 'basal cercus inwardly curved' state may be present in taxa without prominent first cercus lobing (*Chrysopilus* spp. and *Schizella furcicornis*). Conversely, some taxa with ventrally-directed lobes (*Symphoromyia hirta* and *Arthroteles bombyliiformis*) do not have inwardly curving basal cerci. In a great majority of cases, however, if the lobe is present, it curves inwardly and where the lobe is absent or posteriorly produced, there is no ventromedial curvature. There is logically some non-independence with the present character and the presence/absence of lobes. Therefore, this character may be downweighted for phylogenetic analysis.

[#145]. **Basal cercus separation.** The dorsal position of the basal cerci, in relation to one another, was scored for two states. Where the cerci are separated from one another dorsally by approximately the width of the second cercal segment at point of attachment, the state is scored as 'separated.' In other cases, the cerci are closer to one another dorsally and are scored as 'adjacent.'

[#146]. **Second cercus segment.** The second cercus is scored as either elongated or not. Basal cerci that are at least three times as long as wide are considered elongate. This is the condition in species of *Ptiolina*, *Spania nigra*, *Arthroceras americana*, *Coenomyia ferruginea*, and *Dialysis rufithorax*. Otherwise, the basal cercus is scored as not elongate.

[#147]. **Cercus apical sensory pits.** The terminal cercus segment may or may not have what is called an apical sensory pit. The sensory pit is a circular depression, located apically, on the lateral or posterior surface of the cercus. In many genera (*Chrysopilus*, *Pelecorhynchus*, *Rhagio*) the sensory pit may be present or absent. Among the species of *Rhagio* sampled for this dataset, all lack apical sensory pits however there are species with such pits, such as *Rhagio incisus*. In *Arthroceras pollinosum*, the apical sensory pit is very shallow and, arguably, may be scored as absent. However, the apical sensory pit is clearly present in all other *Arthroceras* species examined for this character (*A. fulvicorne*, *A. leptis*, *A. subaquilum*), in precisely the same location as where the shallow depression lies in *A. pollinosum*. Therefore, the apical sensory pit was scored as present in this taxon.

Female terminalia (internal structures)

[#148]. **Tergite 8 ducts.** There are a pair of thin ducts that arise from the posterior margin of tergite 8 in species of *Glutops*, *Pelecorhynchus*, and in *Pseudoerrina jonesi*. The ducts are very inconspicuous and are most easily seen after staining in chlorozol black. The ducts have not been recognized by previous authors and their

function is unknown. The ducts terminate anteriorly in a membranous sac or a clump of lightly sclerotized tissue.

[#149]. **Number of spermathecae.** The most common condition for Diptera is to have three spermathecae. However, *Dialysis* (Xylophagidae) has four and *Bolbomyia* (Rhagionidae) has two. These are the only genera I observed to differ from the standard condition. The nematoceran, *Sylvicola*, has a single spermatheca.

[#150]. **Shape of spermathecae (not used in phylogenetic analysis).** The shape of the spermatheca were scored into seven states. Clubbed spermathecae were defined by having increased girth leading up to a knob-like end. Spherical spermathecae are the most easily recognizable shape; a spherical form. Swollen spermathecae are widest at the apex and exhibit a smooth tapering down to its base. Oval spermathecae have a clear point of expansion (unlike the swollen form) and are oval in shape, with rounded ends. Elongate oval spermathecae also have a clear point of expansion but have an elongate form, with parallel sides, similar in shape to a fruiting cattail (*Typha* sp.). Eye-shaped spermathecae are similar in girth and shape to oval spermathecae, but are sharply pointed at both tips. Pear-shaped in form is enlarged and rounded at the base and narrowed distally. Sometimes taxa have misshapen spermathecae that are unscoreable. This is probably an artifact of age or other factors that occurs at the level of individual specimens. For a large part, spermathecal form varies in confounding ways that makes it difficult to assert homology between character states and within many genera, the diversity of form indicates that information regarding

deeper level phylogenetic events is probably not retained. For this reason, while the form of the spermathecae are noted in this character, it is not suitable for use in phylogenetic analyses.

[#151]. **Sclerotization of spermathecae.** After staining, the sclerotized portions maintained a light brown color to varying degrees. The amount of sclerotization varied continuously across the taxa of this dataset, however, degree of sclerotization was divided into three states. Spermathecae without any trace of brown coloration were scored as unsclerotized. Spermathecae with faint, light brown coloration were scored as lightly sclerotized. Spermathecae with brown or dark brown coloration were scored as sclerotized or well sclerotized. The difference between sclerotized and well sclerotized was most often ambiguous and for this reason, the two conditions were lumped into a single state. Although there may be weak phylogenetic signal in this character, it appears susceptible to relatively short term change. In *Rhagio*, for instance, there are differences across species and even within species. Some of these differences among specimens of the same species may be associated with differences in age.

[#152]. **Glandular hairs of spermathecae (not used in phylogenetic analysis).** At high magnification, small glandular hairs may be visible at the distal tip of the spermathecae. This character is most obvious in *Symphoromyia* species. However, it is a difficult character to score for many taxa and the scoring may be positively correlated with spermathecal size and ease of observation rather than actual

presence/absence. Although such hairs are obvious in extreme cases, this character may be inconsistent and unreliable. For this reason, it is determined unsuitable for phylogenetic analysis.

[#153]. **Spermathecal duct length.** Spermathecal ducts varied in length and this aspect was scored. Duct length is measured from the point of insertion of the common spermathecal duct into the genital chamber to the distal tip of the spermathecae. Short spermathecal ducts are no more than three times the length of sternite 9. Moderate spermathecal ducts are more than three times but less than five times the length of sternite 9. Long spermathecal ducts are longer than five times the length of sternite 9, but not so long as to be difficult to measure. Very long spermathecal ducts fold upon themselves many times, as a pile of spaghetti. *Pseudoerrina jonesi* is the only taxon that could not be scored confidently as having one of these four states. The ducts in this species are approximately three times the length of sternite 9, the boundary at which two states are divided. Because of this, *Pseudoerrina jonesi* was scored as an ambiguity, having both of these states.

[#154]. **Spermathecal duct accessory glands (presence).** There is what appears to be an accessory gland that arises from the spermathecal duct in species of *Arthroceras*, *Ptiolina*, *Spania*, *Spaniopsis*, *Symphoromyia*, and in some species of *Chrysopilus*. The spermathecal duct accessory glands may be very inconspicuous and are most easily seen after staining in chlorozol black. Perhaps on account of their inconspicuous nature, the spermathecal duct accessory glands have not been

recognized by previous authors. Since the female genitalia of most of these taxa have been examined and illustrated by previous authors, this character was probably the most surprising of those developed for this dataset. Furthermore, such a character is likely to have phylogenetic utility, since functional structures such as accessory glands are unlikely to arise *de novo* very frequently. The shape of the accessory glands was approximately the same throughout. In *Chrysopilus*, species may or may not have spermathecal duct accessory glands. In addition to *C. panamensis* (Costa Rica) and *C. quadratus* (USA), *C. alaskaensis* Hardy also lacks spermathecal duct accessory glands. *C. alaskaensis* is unusual in that it has robust legs, unlike any other *Chrysopilus* species I've seen. It also shows a reduction of the flattened, metallic thoracic setae that are typical for *Chrysopilus* species and their allies, such as *Schizella*. It appears to me that *C. alaskaensis* is an atypical species, which survives the ecological pressures associated with the harsh Alaskan climate and has lost the spermathecal duct accessory glands secondarily. In addition to *C. thoracicus* and *C. ferruginosa*, spermathecal duct accessory glands are also present in *C. calopterus* (Brasil), *C. rhagoides* (Costa Rica) and *C. testaceipes* (USA). It is important that this structure is referred to as the 'spermathecal duct accessory gland' and not simply the 'accessory gland' so as not to confuse it with the accessory gland posterior to the genital chamber, which is common to all flies.

[#155]. **Spermathecal duct accessory glands (origin).** The spermathecal duct accessory gland, where present, varied in its placement along the spermathecal duct. The spermathecal duct accessory glands of *Spaniopsis* and *Symphoromyia* arise at

approximately along the distal third of the spermathecal ducts. For many taxa, however, this character was variable within genera. However this character may be useful for supporting intrageneric phylogenetic relationships. Species of *Ptiolina* have either one of two states. *Ptiolina edeta*, *P. mallochi*, and *P. zonata* have spermathecal duct accessory glands that arise directly from the base of the spermathecae. In *Ptiolina fasciata*, *P. lapponica*, and *P. majuscula*, however, the spermathecal duct accessory glands arise at approximately the distal third of the spermathecal ducts. In *Arthroceras pollinosum*, the spermathecal duct accessory glands arise approximately halfway along the length of the spermathecal ducts however in *Arthroceras fulvicorne*, the glands arise at approximately the proximal third of the ducts. The position of the spermathecal duct accessory gland was also variable in *Chrysopilus*, where it may arise at the base of the spermathecae or at approximately the distal third of the spermathecal duct. This character is ordered. Due to the number of characters, it is also slightly downweighted so that the ordering does not exert undue influence on the structure of the tree.

[#156]. **Circular ridge of ejection apparatus.** In many Tabanidae, there is a circular ridge at the distal end of the sclerotized ejection apparatus. This circular ridge is also present in most Athericidae. *Bolbomyia nana* was also scored as having this character state, although the ridge is more distinctly rounded than in tabanid and athericid taxa and may not be homologous. Similarly, the rounded ridge in *Coenomyia ferruginea* compelled me to score this state as present in the species. The ridge is not present in *Dasyomma atratulum*, however it is plainly visible in congener, *D. coeruleum*.

[#157]. **Sclerotized ring at base of spermathecal ducts.** In *Spania nana* and species of *Spaniopsis*, a narrow ring of sclerotized tissue is present. Sometimes this is difficult to see, but presence/absence can be scored confidently after close examination.

[#158]. **Spermathecal duct swelling.** In *Bolbomyia*, there is a distinct swelling approximately halfway along each spermathecal duct. Although this feature was not found in any other taxon, it was unusual enough to merit mention.

[#159]. **Ejection apparatus furrows (presence; not used in phylogenetic analysis).** The ejection apparatus of the female (Evenhuis, 1989) may be recognized as a thickened area of the spermathecal ducts, near their base. Furrows of the ejection apparatus may be arranged perpendicular to the length of the duct so that they appear as rings, or the furrows may be arranged at an angle, as indicated in the next character. The furrows are exceptionally minute and require very high magnification for viewing. On account of this, I was unable to confidently determine in all cases. For this reason, it was removed for phylogenetic analysis.

[#160]. **Ejection apparatus furrows (form; not used in phylogenetic analysis).** Where the furrows of the ejection apparatus are present, the angle of the furrows were scored. The furrows may either run transversely, so that the spermathecal ducts appear ringed, or they may run at an angle from the center. On account of the high

magnification required to detect the ultrastructural patterns of the spermathecal duct, scoring was not always made with the highest confidence. For this reason, it was removed for phylogenetic analysis.

[#161]. **Insertion of spermathecal ducts.** In *Arthroceras pollinosum*, the spermathecal duct is partially folded internally, into the duct junction. In all other species in other genera, the ducts join smoothly.

[#162]. **Sclerotization of ejection apparatus.** The ejection apparatus of the spermathecal ducts may or may not be sclerotized. Upon staining with chlorozol black, the spermathecal ducts dye blue, except in areas of sclerotization, which light brown or brown. Spermathecal ducts were scored as sclerotized if any brown coloration was detected near their base.

[#163]. **Base of spermathecal ducts.** The spermathecal ducts may or may not be thickened near the junction with the common spermathecal duct. Where thickened, the ducts stain to a rich blue and have noticeably thicker walls. When not thickened, the ducts are a pale light blue. The spermathecal duct junction may or may not be thickened, in the same way. These two features are scored together because there seems to be some dependence between the states. In cases where the spermathecal ducts are enlarged, the thickness of the junction appears free to vary. However, in all cases where the spermathecal duct is not enlarged, the spermathecal duct junction is also not enlarged. *Pelecorhynchus personatus* is scored as not having a thickened

spermathecal duct junction, however, in *P. elegans*, the junction is thickened. Judging by the amount of variation of this character within genera, it appears rather homoplasious.

[#164]. **Common spermathecal duct (presence).** The spermathecal ducts most often originate from a single duct that leads from the genital chamber, which I call the common spermathecal duct. However, in some taxa, the common spermathecal duct is absent. Spermathecal ducts of *Bolbomyia nana*, *Pseudoerrina jonesi*, and *Suragina concinna*, for instance, lead directly to the genital chamber. In *P. jonesi* and *B. nana*, the ducts lead directly to the genital chamber. In *S. concinna*, the ducts converge at their base and meet the genital chamber very close to one another. Since *B. nana* has two spermathecal ducts whereas *P. jonesi* and *S. concinna* have three, the processes involved in the gain/loss of the common spermathecal duct may be different between them. In *Pelecorhynchus personatus* and *Glutops rossi*, the common spermathecal duct is so short as to be nearly absent. However it was scored as present in these taxa.

[#165]. **Common spermathecal duct (vermileonid modification).** The common spermathecal duct sometimes retains dye very strongly, yet the blue color of the dye is still mottled and uneven, as if the structure is finely matted, micropilose, or with an uneven surface. This condition is present in species of *Vermileo* and *Lampromyia*. In other genera, where the common spermathecal duct is thickened, the dye stains smooth throughout and the common spermathecal ducts are tubular. It may appear that several things are being scored here; thin or thickened and ability to retain dye or

not. However, I strongly doubt that the thickness of common spermathecal duct present in the vermileonids is homologous to the thickness seen in other taxa. In the vermileonids, the common spermathecal duct is much enlarged and is another condition, apart from being simply thickened. Retaining dye easily is an artifact of this condition that makes it easier to identify.

[#166]. **Common spermathecal duct enlargement.** The thickness of the common spermathecal duct was scored, relative to the thickness of the spermathecal ducts, and scored for four states: 1) thinner than individual ducts, 2) not thickened, approximately as thick as an individual duct, 3) thickened to approximate girth of individual duct volumes combined, and 4) thickened to larger girth than individual duct volumes combined. The continuous nature of this character made it difficult to define boundaries between states. The character states were devised on account of the facility of scoring common spermathecal duct girth compared to the girth of individual spermathecal ducts, rather than in recognition of patterns of variation among taxa. Difference in character state scoring for summation of duct volume ("equal to duct sum", or "slightly larger than this") is very similar. This difference, particularly in *Pelecorhynchus personatus* and *Tabanus atratus* is nearly negligible and may indicate that the character is divided too finely. This is also suggested by the high intrageneric variation, for example, as in *Chrysopilus* and *Rhagio*. This character was scored only for taxa with a duct-like common spermathecal duct. *Lampromyia canariensis* and *Vermileo vermileo* have a modified common spermathecal duct and therefore, are not scored here.

[#167]. **Common spermathecal duct, anterior end.** *Arthroteles bombyliiformis* has a ridge at the apical end of the common spermathecal duct, where the individual ducts arise. This is present in no other taxa.

[#168]. **Common spermathecal duct length.** The length of the spermathecal duct is also scored, relative to the largest diameter of the genital chamber. There are inherent problems of measurements of this sort, where the frame of reference (as the genital chamber) are free to vary. However, I have found this metric sufficient for scoring as they appear, from a general, 'gestalt' perspective. On account of the specially modified common spermathecal duct present in *Lampromyia canariensis* and *Vermileo vermileo*, these taxa are not scored for this character. This character was ordered for phylogenetic analysis.

[#169]. **Genital chamber, surrounding area.** The genital chamber is a membranous pouch from which the spermathecal ducts arise. Generally, the area of this pouch is surrounded by membrane that is attached to the surrounding sternite 9 sclerite. However, in species of *Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*, the area of the genital chamber is tightly defined by medial sclerotization of sternite 9. In *Arthropeas americana* and *Xylophagus lugens*, the genital chamber is hemmed in laterally by sternite 9 sclerotization, but a narrow membrane between the chamber and the sclerite precludes it from being scored as *Ptiolina* and its allies.

[#170]. **Genital chamber shape.** When surrounded by membrane, the exact boundaries of the genital chamber, itself composed of membranous tissue, are often poorly defined. I found that scoring membranous boundaries of the genital chamber was particularly susceptible to subjective interpretation and experimental error or inconsistency. Therefore, this character was scored only for taxa where the genital chamber area was defined by sternite 9 sclerotization. In these cases, the shape of the genital chamber is clear because the sclerotization immediately around it takes an obvious shape. The shape of the genital chamber was scored as 1) circular, 2) teardrop- or eye- shaped, or 3) elongate, in part parallel-sided. Tear-dropped shape is oval, rounded posteriorly and coming to a point anteriorly. Eye-shaped is oval, coming to a point at posterior and anterior ends. Both species of *Symphoromyia* in this sample are scored as having an elongate, parallel-sided genital chamber, however in *S. plagens*, the genital chamber is teardrop shaped.

[#171]. **Genital chamber size (not used in phylogenetic analysis).** The size of the genital chamber was scored relative to the size of sternite nine. Ultimately, however, the size of the genital chamber did not differ in any striking ways and I place little value in a character such as this. The size of the genital chamber varied continuously and differences in scoring were somewhat subjective. Therefore, it was removed for the phylogenetic analysis.

[#172]. **Accessory gland posterior to genital chamber (prominence; not used in phylogenetic analysis).** The accessory gland posterior to the genital chamber is

present in most flies. For this reason, the accessory gland attached to the spermathecal ducts must be called the "spermathecal duct accessory gland." If only "accessory gland" of the female genitalia is used, it would undoubtedly be confused with this structure, with which most people are familiar. In most cases, such as among species of *Rhagio*, the accessory gland posterior to the genital chamber is inconspicuous and visible only after extensive staining. However in some cases, particularly in the Xylophagidae, the accessory gland retains dye easily and is prominent. The scoring of the accessory glands as 'prominent' or 'not prominent' was determined subjectively, by eye. Unfortunately, however, there were gray areas of 'prominence' between the two extreme states exemplified by *Rhagio* and the Xylophagidae. In intermediate conditions, the state could be scored either as prominent or not prominent, with only subtle differences between them. Typically, as the morphology of the female genitalia, and particularly of the accessory gland, become more familiar, it was natural that even more lightly stained structures were perceived as more 'prominent.' The character, therefore, was prone to experimental error in scoring and is not adequate for phylogenetic analysis.

[#173]. **Common duct of accessory gland posterior to genital chamber (presence).** Typically, the accessory gland posterior to the genital chamber has a common duct that is divided distally, to form two ducts. The common duct of the posterior accessory gland is absent in *Tabanus* and *Pelecorhynchus*, however. The paired accessory gland ducts arise from membrane of sternite 9 separately in these taxa.

[#174]. **Common duct of accessory gland posterior to genital chamber (form; not used in phylogenetic analysis).** The accessory gland posterior to the genital chamber may be difficult to see since it often does not stain. It is also easy damaged during dissection. Therefore, I had little confidence in scoring this and other characters of the posterior accessory gland for a fair number of taxa. It appears that there are generally two forms of the accessory gland common duct. It may either lead smoothly to distally paired ducts or may forms an irregular, inflated shape at the point at which the slender distal ducts arise. However, since I am unsure as to the extent of experimental error for this character (and it may be significant), I prefer not to use this character for phylogenetic analysis.

[#175]. **Common duct of accessory gland posterior to genital chamber (length; not used in phylogenetic analysis).** The accessory gland posterior to the genital chamber may be difficult to see since it often does not stain. It is also easy damaged during dissection. Therefore, I had little confidence in scoring this and other characters of the posterior accessory gland for a fair number of taxa. It appears that the accessory gland common duct consistently varies in length. It may either be quite long (clearly longer than sternite 9) or short (as long as or shorter than sternite 9). However, since I am unsure as to the extent of experimental error for this character (and it may be significant), I prefer not to use this character for phylogenetic analysis.

[#176]. **Paired extensions of accessory gland posterior to genital chamber (presence; not used in phylogenetic analysis).** The accessory gland posterior to the genital chamber may be difficult to see since it often does not stain. It is also easy damaged during dissection. Therefore, I had little confidence in scoring this and other characters of the posterior accessory gland for a fair number of taxa. It appears that the distal form of the accessory gland common duct varies. There may or may not be paired ducts distally. However, since I am unsure as to the extent of experimental error for this character (and it may be significant), I prefer not to use this character for phylogenetic analysis.

[#177]. **Paired extensions of accessory gland posterior to genital chamber (length; not used in phylogenetic analysis).** The accessory gland posterior to the genital chamber may be difficult to see since it often does not stain. It is also easy damaged during dissection. Therefore, I had little confidence in scoring this and other characters of the posterior accessory gland for a fair number of taxa. Where present, the paired extensions of the accessory glands may vary in length. However, since I am unsure as to the extent of experimental error for this character (and it may be significant), I prefer not to use this character for phylogenetic analysis.

[#178]. **Ventral chamber duct.** In *Xylophagus lugens*, there is a long a ventral duct, very similar in form to the dorsal accessory gland posterior of the genital chamber. This structure was not seen in any other of the sampled taxa.

[#179]. **Sternite 9, anterior end.** The shape of the proximal end of sternite 9 was quite variable among the taxa sampled, with several autapomorphic conditions. Taxa exhibiting sternite 9 with tapered, pointed tip were designated as (1) pointed. *Rhagio* species and their allies exemplify this state. *Austroleptis multimaculata* is also scored as pointed, although the anterior end of sternite 9 is tapered, then has a narrow parallel-sided projection that is somewhat different than what is found in other taxa scored as having this state. When the anterior end of sternite 9 was short, smooth and rounded it was characterized as (2) rounded. Species of *Symphoromyia*, *Spaniopsis*, and several *Ptiolina* species were scored as having a rounded sternite 9. *Spania nigra* also has a short, broad sternite 9 anterior margin and was scored as rounded, however it is slightly more angular than in the other taxa scored as having the same state for this character. *Atherix pachypus* exhibits a peculiar form of sternite 9 in which the tip is elongated into a narrow stem then is capped with a swollen, knob-like protuberance. This was scored as (3) stem and knob. *Bolbomyia nana* is also scored as having a stem and knob shape although the stem is broader than that in *Atherix pachypus*. Species of Da*syomma* exhibit a peculiar form of sternite 9 in which the proximal end is forked as a swallowtail. This was scored as (4) forked. *Dichelacera marginata* and *Pseudoerrina jonesi* is also scored as forked, although the fork tines are very short in both of these species. In many species of *Chrysopilus*, the anterior end of sternite 9 is narrowed severely so that the extension is thin, and parallel sided. The stem is considered narrow because its width is less that one-quarter the width of sternite 9 at its middle. The tip is rounded. This condition is scored as (5) narrow, thin, with rounded point. A similar state is found in *Arthropeas americana*,

Coenomyia ferruginea, and *Dialysis rufithorax*. In these taxa, the tapering is equally abrupt but much less extensive, so that the distally end remains broad. This condition is scored as (6) narrowed and broadly rounded. In *Glutops rossi*, the anterior end of sternite 9 is parallel-sided, without any taper, with a fully rounded tip. This state is unique among the taxa scored here and is referred to as (7) longer than wide, parallel-sided, tip rounded. *Xylophagus lugens*, *Ptiolina mallochi*, and *P. zonata* have a similar morphology, scored as (8) expanded distally, and then truncated abruptly. In this state, the anterior end of sternite 9 smoothly broadens and is capped by a straight transverse margin. *Pelecorhynchus personatus*, *Vermileo vermileo*, and *Lampromyia canariensis* each have autapomorphic conditions that are scored as separate states. In *P. personatus*, the anterior end of sternite 9 is long, evenly tapered to narrow, rounded point, with wide, dark blue-staining membrane margins. In *V. vermileo*, sternite 9 is a very simple, nearly absent rounded sclerite. The sternite 9 of *L. canariensis*, is irregularly formed into a bulbous sclerotized sac. On account of this character having more than 9 states, it cannot be included in Bayesian analyses.

[#180]. **Sternite 9, posterior end.** The posterior end of sternite 9 (posterior of the genital chamber) has three typical forms. "free posteriorly, with two components (one medially positioned, other laterally positioned)" indicates that there is a vertical and horizontal component to sternite 9, posterior to the genital chamber. These components may be entirely fused or apparently branching. "Free posteriorly, in single projection" indicates that sternite 9 is does not join posterior to the genital chamber and has only a horizontal (or near horizontal) component.

[#181]. **Sternite 9, posteromedial form.** Species of *Arthroteles* and *Atherimorpha* are distinct in that the medial components of sternite 9 posterior to the genital chamber meet centrally. There, the components are held against one another, in the vertical plane. In many *Rhagio* species, the medial components of sternite 9 posterior to the genital chamber are angled and perhaps even vertical at times, as they abut the opening of the accessory gland duct. The medial components in *Rhagio* species do not meet centrally as in *Arthroteles* and *Atherimorpha*, but they are very similar in form. The grouping of *Atherimorpha* and *Arthroteles* has been suspected, but never supported by an explicit synapomorphy (Stuckenberg, 1956; Nagatomi, 1982a).

[#182]. **Sternite 9, posterior margin.** *Symphoromyia* and *Ptiolina* share a similar morphology at the posterior margin of the sternite 9. In these taxa, there is a narrow, crescent shaped emargination, directly posterior to the genital chamber. This character is inapplicable for taxa whose sternite 9 posterior margin is free.

Larval characters

I examined multiple species of *Chrysopilus*, *Rhagio*, and *Symphoromyia*, however, most of these were not determined to species. I was able to get a fair understanding of the diversity within each genus, however, and therefore attempted to develop genus-level (or higher) characters for all larvae. All species within each of these genera, then, were scored identically for larval characters. This includes *Ptiolina*, although only a single larval specimen was examined for this genus.

[#184]. **Retractile head.** The retractile head is a putative synapomorphy for the Tabanomorpha (Woodley, 1989)

[#185]. **Head capsule withdrawn into second segment.** The tabanid and athericid larvae are distinction in that the head is telescoped within the second thoracic segment. Note 2.

[#186]. **Dorsal plate.** The larval head capsule may be composed of a single, undivided plate or divided, forming a pair of metacephalic rods.

[#187]. **Head capsule length.** The head capsule is noticeably lengthened in *Atherix*, *Dasyomma*, *Glutops*, *Pelecorhynchus*, and *Tabanus*. In these taxa, the head capsule (or 'dorsal shield') is more than 4.5 times longer than greatest its width.

[#188]. **Head capsule shape.** The xylophagid taxa have a distinctive, strongly sclerotized cone-shaped head capsule that is a putative synapomorphy for this clade (James, 1981; Palmer and Yeates, 2000).

[#189]. **Mandibular brush.** Sinclair (1992) notes that the presence of a larval mandibular brush is a synapomorphy for the Tabanomorpha. Note 3.

In *Ptiolina*, there is no mandibular brush, although the cuticle is rough and distinctive at the point at which the mandibular brush arises in related taxa. Hence, I presume that the distinctive cuticle is homologous to the area containing the mandibular brush in related taxa such as *Symphoromyia*. The lack of a mandibular brush may be evidence of a different feeding behavior, as the mandibular brush is thought to play an important role in the predatory feeding habit, by anchoring the larvae within its prey as it feeds. However, *Vermileo*, which is a predator, also lacks a mandibular brush.

[#190]. **Mandibular brush association.** Sinclair (1992) proposed that the association of the mandibular brush with an articulated rod (=Sclerotized stem (Webb, 1977a) was a synapomorphy uniting Tabanidae and Athericidae. He also proposed that the rod was held vertical in Athericidae, whereas in Tabanidae, the rod was held horizontal, however I found the latter character to be an exceptionally variable condition. Taxa that do not have a mandibular brush are not scored here. The rod is articulated and can be moved up and down in both Athericidae and Tabanidae. I found that the position of this rod was held in any number of angles, and was largely independent of family grouping. This is corroborated by illustrations of this character in the literature, where the rod is shown in a variety of positions for both Athericidae and Tabanidae. Teskey (1981a: 69) illustrates *Tabanus marginalis* Fabricius with articulated rod in the vertical position; however, Pechuman & Teskey (1981: 473) illustrate the articulated rod in *Tabanus reinwardtii* in the horizontal position. Teskey (1970a: 1132) illustrates the articulated rod in *Glutops* (Pelecorhynchidae) in the

vertical position. Courtney et al. (1997: 108) have a line drawing of *Hybomitra epistates* Osten Sacken (Tabanidae) with the articulated rod clearly in the vertical position. The articulated rod, and its position, however, is not visible in SEM photos of *Atherix* sp., *Glutops* sp., and *Tabanus* sp. (Courtney et al., 1997). My observations of the articulated rod associated with mandibular brush in various taxa are consistent with what is shown in these SEM photographs. The articulated rod is not always easily observed. It is often reduced to a small sclerotized stem, as Webb notes (1977a).

When the mandibular sclerites are dissected, the articulated rod may be in the vertical, oblique, or horizontal position. This is true regardless of the taxon observed, whether it is Pelecorhynchidae, Athericidae, or Tabanidae. To some extent, this is expected, given what is known about the articulation, musculature, and putative function of this structure. On the nature of the articulated rod, Webb notes (1977a: 479): "I follow the speculation of Teskey (1969) that these spines are utilized like those of tabanid larvae in anchoring the head of the larva while it feeds within its prey." This is stated again in Pechuman and Teskey (1981: 464): "Mandibles… linked with subdorsal brushes of spines that are erected to anchor head within host when mandibles strike downward." Mackerras & Fuller (1942) note that the mandibular brush, "when the mouthparts are contracted and when protruded, they are free to project up and backwards." This is also explained in Courtney et al. (1997: 107). Thus, when the mandibular brush is erect and used to anchor the head, the articulated rod is in the vertical position. Otherwise, the articulated rod is in the

horizontal position. The capacity for mandibular brush movement is similar among pelecorhynchids, athericids, and tabanids and this is consistent with the observation of the position of the articulated rod in dissected larvae. For this reason, I chose not to attempt to score it the angle of the articulated rod.

The sister clade relationship of Athericidae and Tabanidae is well established on the basis of adult characters (Stuckenberg, 1973). Some of the character states most often used to indicate their common ancestry are thorax with postspiracular scale, female cercus single segmented, and male genitalia with aedeagal tines. In larval form, the position of articulated rod may be an invalid morphological character for corroborating current hypotheses of shared ancestry. However, I observed at least one unique condition shared between larval athericids and tabanids. In all of the specimens I examined, the first cephalic segment is entirely telescoped within the second cephalic segment. When the head is pulled anteriorly, the first segment, containing the head, is drawn out and is noticeably different from the other larval body segments. The first segment is elongate cylindrical and more slender than any of the posterior segments. In all other taxa when the head is pulled anteriorly, it becomes detached from the first cephalic segment.

[#191]. **Mandibular brush orientation (not used in phylogenetic analysis).** In larvae of *Chrysopilus*, *Rhagio*, and *Symphoromyia*, the mandibular brush clearly run transversely, between the antenna and labrum. In the larvae of *Atherix*, *Dasyomma*, and *Tabanus*, the mandibular brush is oriented along the sagittal plane. This character

may be non-independent with respect to the mandibular brush being associated with an articulated rod or fold of cuticle. For this reason, it is not included in the phylogenetic analysis.

[#192]. **Mandibular brush density.** Where the mandibular brush runs transversely (where it is associated with a cuticular fold), the brush may consist of few, thick setae, as in *Rhagio*. Or the mandibular brush may consist of many thin setae, as in *Chrysopilus* and *Symphoromyia*.

[#193]. **Mandibular hook.** The adoral surface of the mandibular hook may be scored for three separate states. The adoral surface may be smooth, as in species of *Rhagio* and *Ptiolina*. Alternatively, the adoral surface may either have an external groove open along its length (as in species of *Atherix*, *Chrysopilus*, and *Symphoromyia*) or an internal channel at its base, opening apically (as in species of *Atherix*, *Glutops*, and *Pelecorhynchus*).

Pelecorhynchidae, Athericidae, and Tabanidae putatively share the apomorphic character of having the mandibular hook with an internal canal, opening subapically. However, there is significant variation in the distribution of this character state among these taxa. In the *Tabanus* sp. that I have examined, the mandibular hook has a deep canal, similar to those in all athericids, but is only closed the very base. For the most part, it is an open canal, forming a deep groove. The canal starts nearly dorsally (subdorsally), runs along the adoral side, and ends subapically, along the dorsal

surface. From an anterior perspective, the groove ends dorsally. *Dasyomma* species (Athericidae) shows the mandibular hook with a deep grove along its entire length, including at its base. Also, *Halucitherix* (primitive Athericidae) has an external groove, open along its entire length along the mandibular hook.

In Courtney et al. (1997: 120), SEM photographs show *Glutops* as having a deep open groove subdorsally which is a closed channel along approximately the basal third of the mandibular hook. *Atherix* sp. and *Tabanus* sp. are shown to have a long internal channel with a relatively small, deeply channeled opening subapically.

The mandibular hooks when medially grooved, are reportedly appressed together to form a food canal (Schremmer, 1951; Tsacas, 1962; Sinclair, 1992; Courtney et al., 1997). This is known as the suctorial type (Stuckenberg, 2001; 'promuscis-type' of Sinclair, 1992; 'Saugmandible' of Schremmer, 1951). Sinclair (1992) has suggested that this is the basal condition for Brachycera, associated with the transition to vertical mobility in the larval mandibles (Sinclair, 1992: 237-238).

The evolution of mandibular hooks functioning as a feeding tube seems to require at least three integrated morphological features. One, the adoral surface of the mandibular hooks must complement on another in shape, so that they meet flush, centrally. Two, the groove on the adoral surface of the mandibular hook must match so that when the hooks are appressed together, a channel is formed. Three, there must

be some development of musculature to support lateral movement of the hooks, allowing them to come together and stay together against counteracting forces.

Tsacas (1962) reports having observed a feeding tube formed by the mandibular hooks being appressed medially in *Vermileo*. Initially, this seems difficult to believe, as the mouthparts of this larva are approximately 0.1 mm in length and are submerged, along with most of its head, within the prey as it feeds. However, the SEM images in Ludwig et al. (1996) are consistent with the feeding tube as illustrated and explained by Schremmer (1951). This is vastly different than what is seen in *Vermileo comstocki*, however. In *V. comstocki*, the mandibles are blunt, reduced in size, and do not meet medially. The canal or groove is difficult to see, if present in this species. In my observations, I have seen what may be a closed channel in one of two specimens of *V. comstocki*.

In my opinion, the highly specialized feeding behavior of *Vermileo* and the inconsistency of this character within the genus (or at least among close relatives if *Vermileo* proves to be paraphyletic) discounts the likelihood that the mandibular hook feeding tube is necessarily associated with the vertical movement of the mandibles that defines brachyceran larvae. In most taxa within the Tabanomorpha, it appears that a groove in the mandibular hook is not a specialized condition for feeding. The hooks may have a medial groove simply to allow a passageway for food to pass to the hypopharanx when the mandibles are incidentally pushed together during feeding. It doesn't make sense that the mandibles are affixed together medially to form a feeding

tube when, as Teskey (1970: 1131) writes, in most taxa the mandibles work in conjunction with the maxillae, as a unit, in a vertical manner, and may operate independent of the other pair (this is also mentioned in Courtney et al., 1997: 105).

Regarding Vermileonidae, Nagatomi et al. (1998: 142) stated "it seems that the poison canal in Vermileonidae occurs independently from that in the Pelecorhynchidae, Athericidae, and Tabanidae,' an apparent misinterpretation of Ludwig's description of the mandibular hook of *Vermileo vermileo*. Tsacas (1962: 214) and Ludwig (1996) observe that *Vermileo vermileo* and *Vermileo* sp., respectively, have an open groove (not a partially enclosed canal) along the adoral side of the mandibular hook. Sinclair (1992) doesn't describe the mandibular hook in *Vermileo* specifically, aside from saying that the genus displays the groundplan larval condition. Since distantly related taxa such *Xylophagus*, *Symphoromyia*, and *Thereva* share having an adoral groove on the mandibular hook, one presumes that this is the case also for the *Vermileo* species that he examined.

In at least some *Chrysopilus* species, for example, the groove on the adoral surface begins subdorsally, runs centrally, along the adoral surface, and ends subapically at a subdorsal position. The channel on each side, therefore, may meet at least along part of its length. However, along most of its length, the channel does not match its complement and cannot form a food canal (contrary to Tsacas, 1962). The plausibility of a mandibular hook food canal particularly suffers when considering aquatic

environments. Would a food canal work in water for such aquatic species such as *Chrysopilus tsacasi* (Thomas, 1978b)?

The mandibular hooks in *Ptiolina* are small, blunt, and without an external groove along its adoral surface. It appears unlikely that the hooks would be used in the same way as the sharp, serrated hooks in *Rhagio*, *Atherix*, *Tabanus*, and others. The mandibular hook of *Rhagio* has neither an external groove nor a partially closed channel. It is hollow, however.

Stuckenberg (2001: 11) opined "the ‘poison canal’ was stated to be hypothetical so has no operational significance for cladistic analysis." I must respond by saying that while the function of the grooves/canal of the mandibular hook are not certain the corresponding structures (regardless of function) must not be rejected *a priori* as unfit for cladistic analysis. Shared presence of physical features with apparent positional, structural, and ontological homologies, regardless of the function of these features, may provide useful evidence for evaluating phylogenetic hypotheses. If the grooves/canal of the mandibular hook do not serve as a poison canal in the Pelecorhynchidae and related taxa, as Stuckenberg suggests, this may lend even more weight as a useful character to score for phylogenetic analyses since the character is less prone to functional and environmental restraints which may change and force change, independently of ancestral lineages.

In *Rhagio*, the maxilla is closely associated with the mandibular hook. Ventrally, the lacinia envelops the hook so that an apparent channel is formed on the adoral side. This feature is most easily seen in dissected specimens that have not been cleared. This may assist in food uptake and compensate for not having a groove in the mandibular hook. Such a feature is not apparently present in *Symphoromyia*, however, in both this genus and *Ptiolina*, the maxilla are also closely associated with the mandibular hook. In *Atherix*, *Dasyomma*, and *Tabanus*, the mandibular hook is pronounced, exserted from the rest of the mouthparts, including the maxillae.

[#194]. **Sclerotization of maxilla (not used for phylogenetic analysis).** The sclerotization of the maxilla was more prominent in some taxa (e.g., *Symphoromyia*) than in others (e.g., *Vermileo*). However, this feature is difficult to score consistently, as the amount of the sclerotization is apt to vary and the point at which it is scored or not scored as sclerotized is not clear. SEM images cannot help in determining the state of this character. For these reasons, it was not used in phylogenetic analyses.

[#195]. **Saw sclerite of basal mandibular sclerite.** The saw sclerite is an autapomorphy for species of *Rhagio.* It is located in a ventral position, adoral to the basal mandibular sclerite.

[#196]. **Maxillary palp form.** In species of Athericidae, maxillary palp has a distinctive form. The maxillary palp is sclerotized, thin and tubular, with the

appearance of a cigarette. In other taxa, the maxillary palp is soft, not sclerotized, and its segments are poorly differentiated.

[#197]. **Maxillary palp segment number (not used in phylogenetic analysis).** The maxillary palp is usually not sclerotized and it is difficult to identify segment breaks, if present. For this reason, it was not used in phylogenetic analysis.

[#198]. **Last segment of antenna.** The terminal segment of the larval antenna may be split into two or more extensions. This character is most easily scored from SEM images.

[#199]. **Number of antennal segments (not used in phylogenetic analysis).** The number of antennal segments may vary, the antenna is often unsclerotized and it is difficult to judge how many segments are present. For this reason, it was not included in phylogenetic analysis.

[#200]. **Unpaired salivary pump.** In some larvae, there is a sac that is connected to the mouthparts via a long, central duct. It is difficult to follow to track the origin of this duct and verify to which mouthpart structure it is attached. The sac stains easily and is readily apparent in athericids and tabanids. I suspect that this is the 'huge, unpaired salivary pump" mentioned by Mainx (in Stuckenberg, 2001: 7). At the anterior margin of this pump is a pair of giant cells that Schremmer (1951) suspected were poison glands. The glands are not apparently present in *Glutops*, however, and

this potentially conflicts with the scoring of Sinclair (1992) and Woodley (1989). Since pelecorhynchids have poison canals (interpreted from partially enclosed mandible hooks), it logically follows that this sac structure should be present in *Glutops*.

Stuckenberg (2001) has refuted the contention that these are poison glands, arguing that in the original text, Schremmer (1951) only suspected that a pair of giant cells of salivary-gland nature represented poison glands. Furthermore, Stuckenberg (2001) pointed out, the gland ducts of these giant cells have not been followed to their anterior endpoint and therefore, an association with the mandibles has not been verified. This remains true, as I was unable to track the gland ducts directly to the mandibles and I could not see glandular cells with complete confidence, upon inspection with high magnification. These observations do not preclude the possibility that the sac and its associated elements form the apparatus for delivering poison into larval prey, however.

[#201]. **Posterior tentorial expansion.** The posterior tentorial expansion has two lateral arms that run for approximately the length of the dorsal plate. Posteriorly, the expansions may be free, fused to one another, or fused to the dorsal plate.

[#202]. **Anterior margin of thorax.** The anterior margin of the first thoracic sclerite of *Ptiolina* and *Symphoromyia* bears a distinctive ultrastructural pattern. In these taxa,

the surface area immediately posterior to the head is scalloped or scaled. This is not found in any of the other sampled taxa.

[#203]. **Thoracic segments, ventrally.** Athericidae, in particular, are distinct in having crocheted prolegs which are used to facilitate movement in rushing streams. *Glutops*, *Pelecorhynchus*, *Symphoromyia*, and the xylophagid taxa are smooth ventrally, whereas *Chrysopilus*, *Ptiolina*, and *Rhagio* have what are called 'creeping welts' on the ventral surface of the thoracic region. These welts are used to facilitate traction during movement.

[#204]. **Thick, waxy integument.** The larvae of *Pelecorhynchus* and *Glutops* species have a tough, waxy covering that is unlike that found in other known tabanomorph larvae. Teskey (1970) noted "the shapes and relative sizes of the segments [of *Glutops* and *Pelecorhynchus* larvae] and the characteristics of their integuments are essentially identical."

[#205]. **Spiracular system (not used in phylogenetic analysis).** The spiracular system may be apneustic (no spiracles present), propneustic (paired spiracles at front only), metapneustic (paired spiracles at back only), or amphipneustic (paired spiracles at front and back). However, this character was surprisingly hard to score because the spiracles are small and inconspicuous, and therefore are often difficult to find. I do not have a lot of confidence in the scoring this character and therefore do not use it in the phylogenetic analysis.

[#206]. **Hind segment sclerotization.** The xylophagid taxa are unique among taxa sampled here in having the hind segment sclerotized.

[#207]. **Spiracular disc.** The spiracular disc is the posterior face of the terminal segment which bears the terminal spiracles. Where present, it has a broad, open surface, as in Chrysopilus, Ptiolina, Rhagio, and Symphoromyia.

[#208]. **Hind segment form.** The hind segment may be produced into elongate respiratory siphon; be smooth, elongate oval (from the dorsal/ventral perspective) or longitudinally striated, with an inflated appearance.

Table 4**.** A list of the morphological characters and their state coding. Characters not used in the phylogenetic analyses are in italics.

Character	Character States
#1. <Gender known>	*1. male and female known* *2. only female known available* *3. only male known available*
#2. Clypeus	1. bulbous 2. not bulbous
#3. Scape	1. smaller than pedicel 2. approximately the same size as pedicel 3. clearly larger than pedicel
#4. First flagellomere <laterally compressed?>	1. laterally compressed 2. rounded in cross section
#5. <Antenna composition>	*1. antenna with many flagellomeres of similar shape and size, tapering distally* *2. first flagellomere of antenna enlarged bearing segmented stylus* *3. first flagellomere of antenna enlarged bearing stylus of single segment* *4. first flagellomere of antenna enlarged basally, bearing fused or distinct arista-like extension*
#6. Antennal flagellum <break after first flagellomere?>	1. gradually tapered 2. with abrupt change between the first flagellomere and those distal to it
#7. Segment(s) distal of first flagellomere <in cases where abrupt change evident>	1. segmented flagellomeres 2. fused or distinct stylus of single segment 3. fused or distinct arista
#8. Arista <microsetose?>	1. microsetose 2. bare
#9. Eyes	1. conspicuously microsetose

Character	Character States
<microsetose>	2. inconspicuously microsetose
#10. Eyes in male <separation>	1. holoptic 2. dichoptic
#11. Eyes in male <flattened dorsally>	1. flattened dorsally 2. not flattened dorsally
#12. Eyes in male <facets>	1. facets evenly distributed, of equal size 2. facets evenly distributed, gradually smaller toward ventral margin 3. facets split into upper and lower areas and smaller (more fine) ventrally
#13. Parafacials in male <swollen?>	1. not swollen 2. swollen
#14. Occiput <form>	1. rounded, with smooth transition from dorsal to posterior part of head 2. flattened, concave posteriorly
#15. Head <width>	1. wider than thorax 2. approximately same width as thorax 3. narrower than thorax
External Mouthparts	
#16. Labellum <size>	*1. longer than palps* *2. about the same size as palps* *3. shorter than palps*
#17. Pseudotracheae <presence>	1. present 2. absent
#18. Theca <elongate?>	1. elongate 2. short
#19. Theca lateral sclerites <fused, adjacent with suture, touching or separated?>	*1. separate* *2. adjacent and touching, but mostly separated* *3. tightly adjacent, apparently fused with suture* *4. fused into single sclerite*
#20. Theca <sclerite composition>	1. lateral sclerites separate 2. lateral sclerites adjacent and or separated by medial suture 3. fused into single sclerite, without medial suture

Character	Character States
#21. Palps <segment number>	1. one-segmented 2. two-segmented 3. three-segmented
#22. Palps <relative length of each segment, if two>	1. proximal segment longer than distal segment 2. proximal and distal segments about the same length 3. distal segment longer than proximal segment
#23. Lateral ridge of clypeus <presence>	1. absent 2. present, subtending mouthparts basally
#24. Oral margin <location>	*1. restricted to anterior part of head* *2. wraps around base to posterior portion of head*
#25. Stipes <position>	*1. apparently absent* *2. converging toward one another, directed medially* *3. attached to on in contact with tentorium at back side of head* *4. surrounded by membrane above theca, directed posteriorly*
#26. Cardo <presence>	1. apparently absent 2. not swollen 3. swollen
#27. Lacinia <length>	1. shorter than palps 2. longer than palps
#28. Lacinia <serrated?>	1. tip serrated 2. tip not serrated
#29. Mandibles <presence>	1. absent 2. present
Internal mouthparts	
#30. Cibarial pump <length>	1. short, as wide as long or wider 2. long, clearly not as wide as long
#31. Cornu <length>	1. shorter than cibarial pump 2. nearly as long as or longer than cibarial pump
#32. Cornu <attachment>	1. extending beyond pharyngeal pump 2. apically fused to pharyngeal pump
#33. Pharyngeal pump <width>	1. narrow along most of length 2. anteriorly broad

Character	Character States
#34. Pharyngeal pump <presence of cup>	1. forms cup-like structure 2. mostly flat along its length
#35. Pharyngeal pump <length>	1. longer than length of cibarial pump 2. approximately same length as cibarial pump 3. approximately half length of cibarial pump 4. short, reduced
Thorax	
#36. Dorsum <vittate?>	1. with vittae 2. without vittae
#37. Setae of dorsum <present>	1. all of equal length 2. acrostichal, dorsocentral, and intra-alar setae longer, distinguished from other setae of dorsum
#38. Metallic- or scale-like thoracic setae, often with structural color <present absent>	1. absent 2. present
#39. Proepimeron <reduced or absent?>	1. absent 2. reduced 3. present
#40. Proepimeron <setation>	1. setose 2. bare
#41. Anepisternum <setation>	*1. bare* *2. with one or two setae* *3. setose on upper margin only* *4. setose on dorsal and anterior margins* *5. setose on dorsal and posterior margins* *6. setose throughout posterior half* *7. setose throughout upper half, including entire anterior and posterior margins* *8. setose throughout entire sclerite*
#42. Anepisternum <setation2>	*1. bare* *2. with one or two setae* *3. variously setose along margins or throughout dorsal or posterior half of sclerite* *4. setose throughout entire sclerite*

Character	Character States
#43. Anepisternum <setation3>	1. bare or with one or two setae 2. less than one-half of sclerite area with setae 3. one-half or more of sclerite area with setae
#44. Laterotergite <form>	1. katatergite swollen, differentiated from anatergite 2. katatergite and anatergite indistinguishable
#45. Laterotergite <setation>	1. bare 2. setose
#46. Laterotergite <arrangement of setae>	1. present throughout laterotergite 2. present mostly on katatergite 3. present on katatergite only
#47. Microsetation between base of halter and postspiracular sclerite	*1. absent* *2. present*
#48. Thoracic spiracle <flaps below laterotergite?>	1. without flaps 2. with flaps
#49. Thoracic spiracle <lined with microsetae>	1. not lined with microsetae 2. lined with microsetae
#50. Postspiracular scale <presence>	1. absent 2. present
#51. Postspiracular sclerite <setae>	1. without setae 2. setose
#52. Thoracic surface immediately posterior to postspiracular sclerite <presence of setae>	1. bare 2. setose
#53. Proscutellum <lenticular swelling between the	1. present 2. absent

Character	Character States
scutellum and mesoscutum>	
#54. Subscutellum <form>	1. not bulbous 2. bulbous
#55. Subscutellum <setose?>	1. bare 2. setose on margins
#56. Postmetacoxal bridge <presence>	*1. absent* *2. present*
#57. Postmetacoxal bridge <type>	*1. complete broad extension* *2. incomplete broad extension* *3. complete thin extension* *4. incomplete thin extension*
Wing	
#58. Wing <surface membrane>	*1. hyaline* *2. membrane lightly infuscated* *3. membrane darkly infuscated*
#59. Wing <presence of markings>	*1. with markings* *2. without markings*
#60. Wing <presence of pterostigma>	*1. with pterostigma* *2. without pterostigma*
#61. Lower calypter	1. reduced 2. present
#62. Upper calypter <development>	1. absent 2. well developed, full and rounded 3. underdeveloped, with a straight edge, appearing triangular in form
#63. Upper calypter <shape in outline>	*1. with broad curvature, lobe-like, width twice length or less* *2. with reduced curvature, width more than twice length* *3. with narrow curvature, appearing stretched, width more than twice length*
#64. Alula <development>	1. no curvature, reduced 2. narrow curvature 3. broad curvature

Character	Character States
#65. Alula <shape in outline>	1. curvature shifted distally so that lobe appears more triangular than round 2. rounded evenly
#66. Anal lobe <development>	*1. well developed* *2. reduced*
#67. Humeral crossvein (h) <strength>	*1. well developed* *2. weakly developed*
#68. Humeral crossvein <shape>	*1. bow-shaped* *2. straight, acute angle apically at wing margin* *3. straight, obtuse angle apically at wing margin* *4. straight, perpendicular to wing margin*
#69. Sc-r crossvein <presence>	*1. present, well developed* *2. present, weakly developed* *3. absent*
#70. Sc-r crossvein <location>	1. proximal side of humeral crossvein (h), by less than length of h 2. positioned distal to the humeral crossvein (h), by less than the length of h 3. positioned distal to the humeral crossvein (h), by the approximate length of h 4. positioned distal to the humeral crossvein (h), by more than the length of h 5. located approximately midway between h and the origin of the radial-sector
#71. Dorsal surface of R_1 <setation>	1. microsetose 2. without microsetae
#72. Ventral surface of R_1 <setation>	*1. without microsetae* *2.microsetose*
#73. Wing veins R_1 and R_{2+3} <at wing margin>	1. meet together at wing margin 2. close together at wing margin (R_{2+3} clearly closer to R_1 than to R4) 3. separated at wing margin (R_{2+3} closer to R_1 than to R_4, but placed nearly between R_1 and R_4) 4. widely separated at wing margin (R_{2+3} closer to R_4 than to R_1)
#74. R_{2+3} curve <present>	1. present, beneath pterostigma, as illustrated by Stuckenberg (2001:fig 11)

Character	Character States
	2. absent
#75. Wing vein R_{2+3} <direction at margin>	*1. directed posteriorly, meeting wing at close angle* *2. directed toward wing margin, meeting margin abruptly* *3. directed posteriorly, but turned into the wing margin at terminus*
#76. Dorsal surface of R_{2+3} <setation>	*1. microsetose* *2. without microsetae*
#77. Ventral surface of R_{2+3} <setation>	*1. microsetose* *2. without microsetae*
#78. R_4-R_5 fork <presence>	1. present 2. absent
#79. Base of R_4-R_5 fork <location>	1. distal of distal end of cell dm 2. proximal or directly above distal end of cell dm
#80. R_4 at base <strongly curved?>	1. strongly curved or angled 2. relaxed, not strongly curved 3. nearly straight
#81. R_4 <apical portion>	1. straight or nearly straight apically 2. curving towards the leading margin of the wing apically
#82. <R_4 and R_5 position at margin>	1. R_5 anterior to or ending at wing tip 2. R_4 and R_5 encompass wing tip 3. R_4 ending at or posterior to wing tip
#83. R_5 <aligned with R_{4+5}?>	1. aligned with R_{4+5} 2. changing direction only slightly at fork with R_{4+5} 3. clearly changing direction at fork with R_{4+5}
#84. M_3 wing vein <presence>	1. present, reaching wing margin 2. incompletely present, not reaching wing margin 3. absent
#85. Halter knob <size; begins at base of depression or oval form>	*1. 1/3 or shorter than length of stem* *2. between 1/3–1/2 length of stem* *3. approximately 1/2 length of stem* *4. between 1/2–2/3 length of stem* *5. 2/3 or longer than length of stem*

Character	Character States
#86. Halter stem <cell arrangement>	*1. with clear parallel rows of fine microsetae* *2. with rows or ripples, but not clearly parallel entire length at base of stem* *3. without any parallel rows of microsetae*
#87. Anterodorsal side of halter <setation>	*1. bare* *2. with thick row of setae running along trailing edge of stem* *3. with thick row of setae running along leading edge of stem and setae present in row along trailing edge of knob* *4. mostly bare with few setae at base* *5. mostly bare with few, fine setae running along trailing edge* *6. longish setae at base of halteres, otherwise bare*
#88. Ventroposterior side of halter <setation>	*1. bare* *2. microsetae running along trailing edge in row* *3. microsetae loosely arranged at base and near trailing edge* *4. microsetae loosely arranged on mostly basal half and running along trailing edge of knob in row* *5. microsetae mostly present in apical half of knob* *6. microsetae running along both edges*
Legs	
#89. Fore tibial spur	1. absent 2. one
#90. Mid tibial spur	1. absent 2. one 3. two
#91. Hind tibial spur	1. absent 2. one 3. two
#92. Hind coxal tubercle <presence>	1. absent 2. present
#93. Hind tibial macrochaetae <presence>	1. absent 2. present; small, easily overlooked, nearly flush with sclerite surface 3. present; conspicuously present, obviously enlarged compared with other tibial setae
#94. Hind tibial macrochaetae <form>	*1. short* *2. lengthened*

Character	Character States
#95. Hind tibia <presence of ventro-apical swelling>	1. without ventro-apical swelling 2. with ventro-apical swelling
#96. First hind metatarsus of male <swollen or not?>	1. not swollen 2. swollen
Male Genitalia	
#97. Epandrial sclerite <form>	1. wider than long 2. longer than wide 3. absent
#98. Epandrial sclerite <anterior margin> (not scored where epandrial sclerite absent)	1. strongly notched anteriorly 2. modestly curved anteriorly 3. not emarginate anteriorly
#99. Epandrium <form, from posterior view> (not scored where epandrial sclerite absent)	1. simple, not containing hypandrium ventrally 2. wrapped laterally, surrounding cerci and hypoproct posteriorly and containing hypandrium ventrally
#100. Cercus <attachment point>	1. attached to subepandrial complex (subepandrial membrane or hypoproct) 2. attached directly to epandrium via membrane
#101. Subepandrial sclerite <presence>	1. absent 2. present as membrane 3. present as sclerite
#102. Subepandrial sclerite <form>	1. undivided 2. divided
#103. Subepandrial sclerite <setation>	1. bare 2. setose
#104. Hypoproct <form; outline>	*1. triangular (rounded posteriorly)* *2. sagittate* *3. two-pronged posteriorly* *4. rectangular; wider than long* *5. elongated; approximately twice as long as wide* *6. oval* *7. pentagonal*

Character	Character States
#105. Hypoproct <form, presence of lateral sclerotization?>	*1. lobes absent* *2. anterior and or posterior lobes present*
#106. Hypoproct <setae>	*1. setose* *2. tomentose, without setae*
#107. Cercus <leaf shaped or nearly square>	*1. squarish* *2. nearly leaf-shaped*
#108. Cerci <separation>	1. directly adjacent to one another, separation distance one quarter width of cercus or less 2. partially displaced from one another, separation distance approximately half the width of single cercus 3. widely displaced from one another, separation distance greater than three quarters width of cercus
#109. Cerci held <orientation>	*1. horizontal in relation to rest of abdomen* *2. at angle in relation to rest of abdomen* *3. vertical in relation to rest of abdomen*
#110. Cerci, in posterior view <form; curved or straight in posterior view>	*1. cupped, forming circular outline medially* *2. flat*
#111. Hypandrial sclerite	1. fused entirely to gonocoxites 2. separated partially from the gonocoxites by an incomplete suture 3. separated from the gonocoxites by a complete suture
#112. Gonocoxite <dorsal sinuous ridge presence>	1. dorsal sinuous ridge present, leading to gonocoxal apodeme 2. smooth dorsally, without sinuous ridge leading to gonocoxal apodeme
#113. Gonocoxal apodemes <presence>	1. present 2. absent
#114. Gonocoxal apodemes <length>	1. short or long enough to reach anterior margin of hypandrium 2. extending well beyond anterior margin of hypandrium

Character	Character States
#115. Gonocoxal apodeme <origin>	1. basal medial margin posterior to or at approximately the same transverse plane as basal lateral margin 2. basal medial margin anterior to basal lateral margin
#116. Parameral sheath <form>	1. not developed into bulbous sac ventrally 2. developed into bulbous sac ventrally, without distinct lobes 3. developed into bulbous sac ventrally, with distinct lobes
#117. Lateral ejaculatory processes <presence>	1. absent 2. present, integrated into sperm sac membrane 3. present, not part of sperm sac posteriorly (homology uncertain)
#118. Ejaculatory apodeme <length>	1. reduced, nearly absent 2. short, not reaching anterior margin of hypandrium 3. moderately long, reaching anterior margin of hypandrium 4. long, reaching beyond anterior margin of hypandrium
#119. Ejaculatory apodeme <form>	1. tubular 2. laterally compressed 3. compressed dorso-ventrally 4. tripartite; dorsally compressed laterally and ventrally compressed dorso-ventrally 5. umbrella-shaped anteriorly
#120. Aedeagal tines <presence>	1. absent 2. present
#121. Endoaedeagal process <presence>	1. present 2. absent
#122. Endoaedeagal process <form, compressed?>	1. strongly lateral compressed, as a butterknife 2. rounded, narrowly conical 3. dorso-ventrally flattened
#123. Gonostylus <setation>	*1. heavily setose* *2. lightly setose or nearly bare*
Female abdomen and terminalia	
#124. Terminal abdominal segments	*1. evenly tapered* *2. narrowed and telescoped within wider basal abdominal segments*
#125. Tergite 7	1. much longer than wide

Character	Character States
<shape>	2. about as long as wide 3. much wider than long
#126. Intersegmental membrane between segments 7 and 8 <presence>	1. especially long 2. short, as throughout abdomen
#127. Tergite 9 <length>	1. not reduced 2. reduced
#128. Tergite 9 <projections enveloping sternite 9>	1. normal, without such projections 2. with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9
#129. Tergite 10 <length>	*1. absent* *2. present, reduced (length less than half width)* *3. present, not reduced (length approximately equal to measured half width)* *4. present, not reduced (length more than half width)*
#130. Tergite 10 <split?>	1. entire 2. split into two separate lateral sclerites
#131. Sternite 8 <divided?>	1. sclerite entire, not divided into two segments 2. sclerite divided into two segments, anterior segment long and wide, posterior segment rounded, cupped
#132. Sternite 8 cleavage <presence>	1. present 2. absent
#133. Sternite 8 length <aspect ratio>	1. wider than long 2. as wide as long 3. longer than wide 4. elongated; more than twice as long as wide 5. wider than long or as wide as long (triangular, ovoid, or nearly square)
#134. Sternite 10 <form>	*1. entire* *2. sclerotization weakened centrally, making it appear as if sclerite divided into two lateral components* *3. split into two sclerites*
#135. Sternite 10	*1. triangular; nearly split into two sclerites*

Character	Character States
<shape>	*2. roughly pentagonal, pointed posteriorly* *3. roughly rectangular* *4. sagittate* *5. semi-circular* *6. ovoid*
#136. Sternite 10 <position>	1. nearly completely anterior to first cercus segment (~10% below basal cercus) 2. posterior half below first cercus segment 3. almost entirely underneath cercus segments
#137. Cercus <segmentation>	1. two-segmented 2. one-segmented
#138. Basal cercus <elongated or not>	1. not elongated 2. elongated (~3x longer than wide or more)
#139. Basal cercus lobe <presence absence; gestalt>	*1. present* *2. absent*
#140. Basal cercus lobe <presence, extreme case>	*1. within range of continuous states between present and absent, not parallel-sided, not nearly as long as second cercus* *2. conspicuously present, extending posterior to point of attachment of second cercus, nearly parallel sided, approximately as long as second cercus*
#141. Basal cercus lobe <presence absence; strict scoring>	*1. present, area ventral to first cercus equal to or longer than width of second cercus at point of attachment* *2. absent, area ventral to first cercus shorter than width of second cercus at point of attachment*
#142. Second cercus segment <position on first cercus segment (where first segment not elongate)>	*1. dorsal (width clearly shorter above second cercus than width below)* *2. central (width approximately equal below and above second cercus)* *3. ventral (width clearly longer above second cercus than width below)*
#143. Basal lobe <presence absence; compound>	1. absent; second cercus placed centrally or ventrally, ventral portion of basal cercus not expanded 2. unclear; second cercus placed centrally or ventrally, ventral portion of basal cercus expanded 3. present; second cercus placed dorsally, ventral portion of basal cercus expanded, extending mostly ventrally, rounded

Character	Character States
	4. present; second cercus placed dorsally, ventral portion of basal cercus expanded, extended mostly posteriorly and nearly parallel-sided
#144. Ventral lobes of basal cercus <forming circle from posterior view?>	1. curve ventrally towards one another to form a ring, visible in the posterior perspective 2. do not curve ventrally towards one another to form a ring
#145. Basal cerci <separation>	1. adjacent dorsally 2. separated from one another dorsally by approximately the width of the second cercal segment
#146. Second cercus segment <elongated?>	1. not elongated 2. narrow, elongated (~3x longer than wide or more)
#147. Cercus <apical sensory pits>	1. with apical sensory pits 2. without apical sensory pits
#148. Tergite 8 <with ducts?>	1. without any ducts 2. with pair of ducts arising from posterior margin of sclerite, terminating in clump of sclerotized tissue
#149. Spermathecae <number>	1. one 2. two 3. three 4. four
#150. Spermathecae <shape>	*1. clubbed* *2. spherical* *3. swollen* *4. oval* *5. elongate oval* *6. eye-shaped* *7. pear-shaped* *8. elongated and misshapen, with what appear to be trachea attached distally*
#151. Spermathecae <sclerotization>	1. not sclerotized 2. lightly sclerotized 3. sclerotized
#152. Glandular hairs	*1. absent*

Character	Character States
at distal tip of spermathecae <presence>	*2. present*
#153. Spermathecal ducts <length>	1. no more than three times the length of sternite 9 2. more than three times but less than five times the length of sternite 9 3. longer than five times the length of sternite 9, but not so long as to be difficult to measure 4. very long, folding upon themselves many times
#154. Spermathecal duct accessory glands <presence>	1. absent 2. present
#155. Spermathecal duct accessory glands <origin>	1. arise at approximately the proximal third of the spermathecal ducts 2. arise at approximately halfway along the length of the spermathecal ducts 3. arise at approximately the distal third of the spermathecal ducts 4. arise at the base of each spermatheca
#156. Circular ridge marking the distal terminus of the ejection apparatus	1. absent 2. present
#157. Ring of more heavy sclerotization near base of spermathecal ducts	1. absent 2. present
#158. Spermathecal ducts <swelling presence>	1. without swelling halfway between genital chamber and spermathecae 2. with swelling halfway between genital chamber and spermathecae
#159. Ejection apparatus <presence of furrows>	*1. furrows present* *2. furrows absent*
#160. Ejection apparatus <furrows at base, form>	*1. ultrastructural surface ringed* *2. ultrastructural surface furrowed at an angle*

Character	Character States
#161. Spermathecal ducts <insertion>	1. extended smoothly into junction duct tubing 2. visibly inserted within junction duct tubing
#162. Ejection apparatus <sclerotized?>	1. sclerotized 2. not sclerotized
#163. Junction and base of spermathecae <thickened?>	1. junction and base of spermathecal ducts not thickened 2. junction not thickened, base of spermathecal ducts thickened 3. junction and base of spermathecal ducts thickened
#164. Common spermathecal duct <presence>	1. present 2. absent
#165. Common spermathecal duct <type; specially modified?>	1. duct, without any special modifications 2. enlarged pilose tapering
#166. Common spermathecal duct <enlarged?>	1. thinner than individual ducts (distally) 2. not thickened (approximate thickness of individual duct) 3. thickened (approximate summation of duct volumes) 4. thickened (larger than summation of duct volumes)
#167. Common spermathecal duct <anterior end, at junction with spermathecal ducts>	1. without apical transverse ridge and suture at junction of spermathecal ducts 2. with apical transverse ridge and suture at junction of spermathecal ducts
#168. Common spermathecal duct <length, distance from duct junction to spermathecal opening>	1. short, shorter than longest diameter of genital chamber 2. moderate, about the same length as the longest diameter of genital chamber 3. long, clearly longer than longest diameter of genital chamber
#169. Genital chamber boundary <defined by membrane or sclerotization?>	1. membranous; sclerotization of sternite 9 laterally contained 2. tightly defined by medial sclerotization of sternite 9

Character	Character States
#170. Genital chamber <shape>	1. circular 2. teardrop- or eye- shaped 3. elongate, parallel-sided in part
#171. Genital chamber <size>	*1. reduced* *2. small, occupying fraction of sternite 9 area* *3. moderately sized* *4. elongate, occupying most of sternite 9 area*
#172. Accessory gland posterior to genital chamber <prominent?>	*1. inconspicuous, easily overlooked even after staining* *2. prominent, retains dye easily*
#173. Accessory gland posterior to genital chamber <common duct present?>	1. common duct present 2. common duct absent
#174. Accessory gland posterior to genital chamber <common duct form>	*1. distal end of common duct bulbous, knob-like* *2. distal end of common duct evenly tapered*
#175. Accessory gland posterior to genital chamber <length of common duct>	*1. long; common duct clearly longer than sternite 9* *2. short; common duct as long or shorter than sternite 9*
#176. Accessory gland posterior to genital chamber <presence of paired extensions?>	*1. with paired extensions posteriorly* *2. without paired extensions posteriorly*
#177. Accessory gland posterior to genital chamber <length of paired ducts>	*1. paired ducts long, clearly longer than common duct* *2. paired ducts short, as short or shorter than common duct*
#178. Ventral chamber duct	1. absent 2. present
#179. Sternite 9 anterior end	1. tapered to a point 2. as wide or wider than long, broadly rounded at tip

Character	Character States
<anterior end, shape>	3. stem and knob 4. forked 5. narrow, parallel-sided, round at tip 6. narrowed, but broadly rounded tip 7. longer than wide, parallel-sided, rounded tip 8. expanding distally, then truncated abruptly 9. autapomorphic state represented by *Pelecorhynchus personatus* 10. autapomorphic state represented by *Vermileo vermileo* 11. autapomorphic state represented by *Lampromyia canariensis*
#180. Sternite 9 <posterior end, split into two components?>	1. fused posteriorly 2. free posteriorly, in single projection 3. free posteriorly, with two components (one medially positioned, other laterally positioned)
#181. Posteromedial component of sternite 9 <medial projection>	1. held horizontal 2. held vertical medially
#182. Sternite 9 posterior margin <crescent shaped medially?>	1. not crescent-shaped 2. crescent-shaped
Larva	
#183. Larva <known or not>	*1. known* *2. unknown not available*
#184. Head <retractile>	1. retractile 2. not retractile
#185. Head capsule <withdrawn into second segment?>	1. not folded within second segment 2. withdrawn into second segment
#186. Head capsule (dorsal plate) <internal portion>	1. composed of a single, undivided plate 2. divided, forming a pair of metacephalic rods
#187. Head capsule <length>	1. less than 4.5 times longer than greatest width 2. more than 4.5 times longer than greatest width
#188. Head capsule <shape>	1. not cone-shaped 2. cone shaped

Character	Character States
#189. Mandibular brush <presence>	1. absent 2. present
#190. Mandibular brush <association>	1. associated with simple fold of cuticle 2. associated with articulated rod
#191. Mandibular brush <orientation>	*1. oriented along sagittal plane* *2. oriented along transverse plane*
#192. Mandibular brush <brush density>	1. consists of less than 25 setae (per brush) 2. consists of more than 25 setae (per brush)
#193. Mandibular hook <external surface>	1. without groove or canal 2. with external groove on adoral surface 3. canal with apical opening
#194. Maxilla <sclerotized?>	*1. not sclerotized* *2. sclerotized*
#195. Saw sclerite of basal mandibular sclerite <presence>	1. absent 2. present
#196. Maxillary palp	1. segments sclerotized, cylindrical 2. soft, segments poorly differentiated
#197. Maxillary palp segment number	*1. two* *2. three*
#198. Antenna <bifurcating?>	1. last segment multifurcated 2. last segment bifurcated 3. last segment entire
#199. Antenna <no. of segments>	*1. one-segmented* *2. two-segmented* *3. three-segmented*
#200. Central duct leading to unpaired salivary pump	1. present 2. absent
#201. Posterior tentorial expansion	1. fused to DP (dorsal plate) 2. free

Character	Character States
	3. fused to each other
#202. Anterior segment <with scalloping>	1. ruffled 2. not ruffled
#203. Thoracic segments <welts, prolegs?>	1. with creeping welts ventrally 2. with crocheted prolegs ventrally 3. smooth ventrally
#204. Thick waxy covering <presence>	1. absent 2. present
#205. Spiracular system	*1. apneustic <no spiracles present>* *2. propneustic <paired spiracles at front only>* *3. metapneustic <paired spiracles at back only>* *4. amphipneustic <paired spiracles at front and back>*
#206. Hind segment <sclerotized?>	1. not sclerotized posteriorly 2. sclerotized posteriorly
#207. Spiracular disc <presence>	1. absent 2. present
#208. Hind segment <form>	1. produced into elongate respiratory siphon 2. smooth, elongate oval (from dorsal ventral perspective) 3. longitudinally striated, with inflated appearance 4. soft, wrinkly, with a pair of setose projections

Maximum Parsimony Analysis of Morphological Data

MP heuristic searches found 24 most parsimonious trees. Fig. 4 shows the strict consensus of these trees (tree length = 657), with bootstrap support values above the branches, where the support is greater than 50% [statistics of one tree: consistency index (CI) = 0.3202, homoplasy index (HI) = 0.6798, CI excluding uninformative

characters = 0.3121, HI excluding uninformative characters = 0.6879, retention index (RI) = 0.6341, rescaled consistency index (RC) = 0.2030].

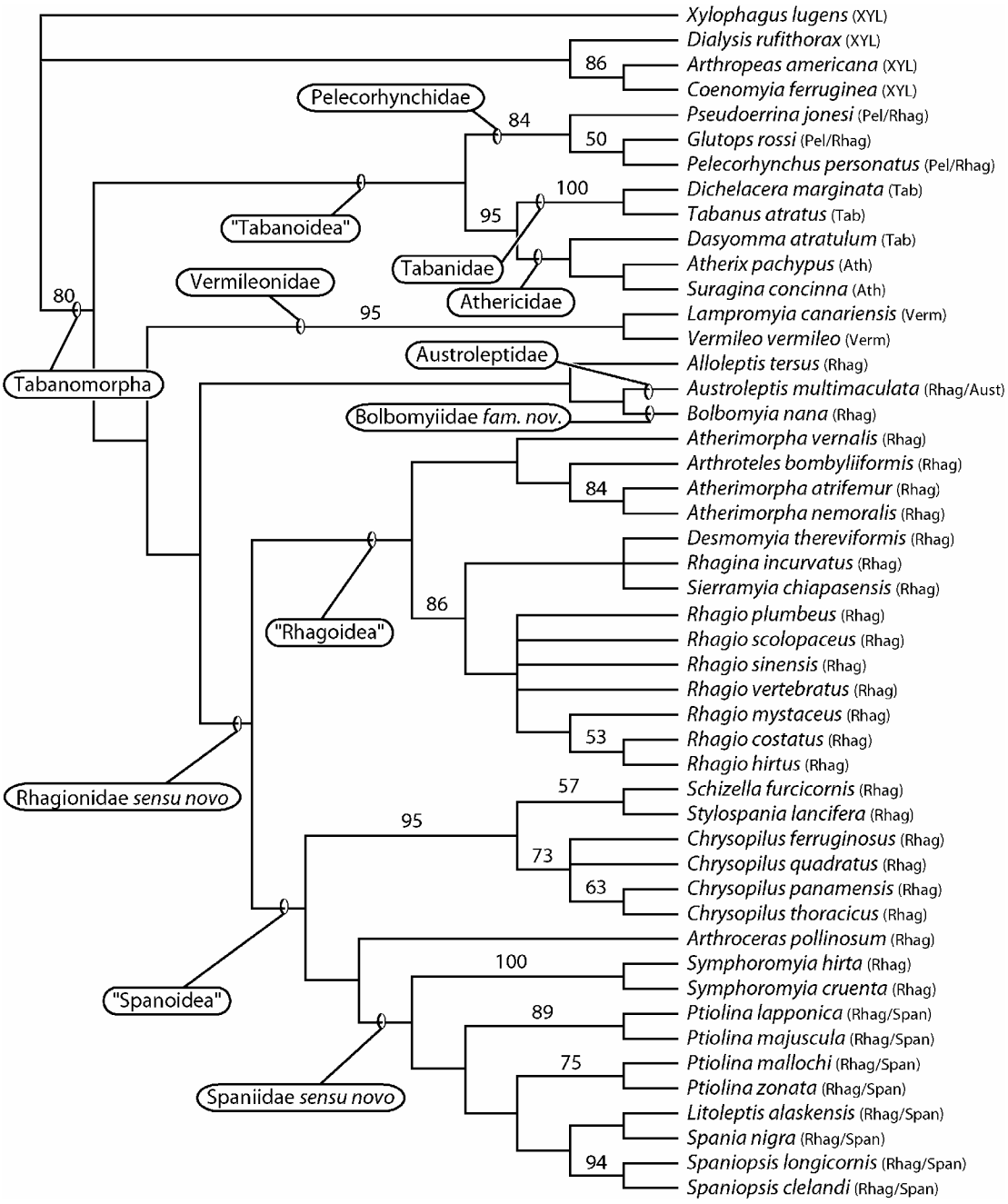


Figure 3. Strict consensus of 24 most parsimonious trees generated from the morphological matrix. Bootstrap values ≥ 50% are noted above supported branches (TBR, nreps = 1000 / addseq reps = 10).

The most parsimonious trees recover the same major groups as in the molecular analyses. The Tabanomorpha are shown as monophyletic, as is the Tabanoidea, Vermileonidae, Rhagioninae, Chrysopilinae, and Spaniinae. There is apparently more resolution in how they are related to one another, however. The Tabanoidea is recovered as the basal clade of Tabanomorpha, with Vermileonidae sister to the Rhagionidae in its broadest sense, including *Austroleptis*, *Bolbomyia*, Rhagioninae, Chrysopilinae, and Spaniinae). *Austroleptis multimaculata* and *Bolbomyia* are sister taxa and along with *Alloleptis tersus*, form the sister group to Rhagioninae, Chrysopilinae, and Spaniinae. Rhagioninae is sister to the clade formed by Chrysopilinae and Spaniinae.

The monophyly of the outgroup Xylophagomorpha, is supported by the elongated basal segment of the female cercus and several thoracic setal characters (postspiracular sclerite with setae, subscutellum setose on margins) in addition to the well known synapomorphy of having a highly sclerotized, cone-shaped larval head.

The monophyly of Tabanomorpha is supported by the retractile larval head. The Tabanoidea is recovered, including *Pseudoerrina jonesi* as the basal taxon of the pelecorhynchid lineage, which is sister to the Athericidae and Tabanidae of the dataset. Tabanoidea is supported by the presence of a postspiracular scale (Fig. 177; lacking in some specimens of *Glutops rossi*), a bulbous subscutellum (lacking in *Suragina concinna*), and exceptionally long gonocoxal apodemes (Fig. 164; however

absent in *Glutops* spp. and *Pseudoerrina jonesi*). Larval characters that may be used to define the Tabanoidea include an elongate head capsule (character 187; Fig. 197), and the mandibular brush associated with an articulated rod (character 190; Fig. 196). The monophyly of the Pelecorhynchidae is supported by the presence of paired ducts arising from the posterior margin of tergite 8 (Fig. 168). This is a new character, and the first adult synapomorphy developed for the family. The ventral process of the female first cercus segment in these taxa is distinctive and has been recognized as a possible synapomorphy for the group (Woodley, 1989; Figs. 158A, 166, 171A), however an explicit definition of this character is problematic as other tabanomorph taxa also have elongated first cercal segments (see discussion in Appendix A, regarding characters 140-143). The thick, waxy outer layer of the larva also supports this grouping, although the larva of *Pseudoerrina* species is not known. Additional characters that may support a close relationship between *Glutops* and *Pelecorhynchus* are the bare laterotergite, non-emarginate anterior margin of the epandrial sclerite. The sister group relationship between Tabanidae and Athericidae is supported principally by larval characters such as the presence of a salivary pump and the first thoracic segment withdrawn into the second thoracic segment. This sister group relationship is also supported by the shared presence of aedeagal tines in the male (independently derived in *Bolbomyia* and *Arthroceras*; Fig. 16), a single-segmented cercus (also present, but unrelated in *Austroleptis*), and a narrow ridge marking the distal end of the ejection apparatus of the spermathecal duct in the female (character 56). The monophyly of the Athericidae is supported by wing veins R_1 and R_{2+3} which autapomorphically meet together at the wing margin. Athericidae are also unique in

having the larval maxillary palp fully sclerotized and cylindrical (Fig. 195) and having crocheted larval prolegs.

The Vermileonidae are highly autapomorphic in many ways, particularly in regards to the male and female genitalia, to the degree that homology assessments for many characters were difficult for this taxon. The common spermathecal duct in vermileonids, for example, is highly modified into an enlarged, pilose structure that tapers distally. The wing is distinct in lacking an alula and anal lobe.

Increased sampling within Rhagionidae, in comparison with the molecular analysis, allows for a better understanding of the relationships present in this group. I have some reservation in the placement of all taxa, however, that are based on a single gender (*Litoleptis alaskensis*, *Sierramyia chiapasensis*, *Stylospania lancifera*) or entirely scored from the literature (*Alloleptis tersus*).

The sister group relationship between *Bolbomyia nana* and *Austroleptis multimaculata* is supported by the shared loss of wing vein M_3. Both of these taxa also lack setae on the laterotergite, a condition shared by *Alloleptis* which is recovered as sister to *Bolbomyia* and *Austroleptis.* The lack of laterotergite setae, however, is present in other species of Pelecorhynchidae and Spaniinae. The lack of setae on the laterotergite appears particularly associated with small size.

Taxa representing the chrysopilines (*Chrysopilus*), rhagionines (*Rhagio*), and spaniines (*Ptiolina* and *Symphoromyia*) have several larval features in common that provide evidence for their recency of common ancestry and support the monophyly of the Rhagionidae. The larval mandibular brush is associated with a simple fold of cuticle (hypothesized by Sinclair, 1992 as plesiomorphic; Fig. 186), a broad spiracular disc that is folded laterally, and a longitudinally striated, inflated larval hind segment (Fig. 187). Larvae of most taxa within this group (and possible sister taxa such as *Alloleptis*, *Austroleptis* and *Bolbomyia*) are not known, however. Based on the morphological analysis, Arthrocerinae belongs in the Rhagionidae although the larva of *Arthroceras* is also not known.

The monophyly of the Rhagioninae is supported by the (butter-knife) form of the endoaedeagal process, which is strongly laterally compressed (Fig. 107). *Rhagio* and its relatives are united by having lateral ejaculatory processes that are integrated into the sperm sac membrane. *Arthroteles* and *Atherimorpha* are united by having conspicuously present hind tibial macrochaetae and in the female genitalia, the posteromedial component of sternite nine is held in a horizontal plane. The South American *Atherimorpha* species are shown as more closely related to *Arthroteles bombyliiformis* (South Africa) than to *Atherimorpha vernalis* (Australia). This is supported by the shared presence of two setal sizes of the thorax. Stuckenberg has speculated that the South African *Atherimorpha* may be more closely related to *Arthroteles* than the other members of the group, however the fact that South American members of *Atherimorpha* may show this affinity is a new revelation

(Stuckenberg in Nagatomi & Nagatomi, 1990). Several larval features support the monophyly of the genus *Rhagio*. These include basal larval mandible with saw sclerite (Fig. 193) and mandibular brush with fewer than 25 setae (Fig. 186B). These synapomorphies may be more inclusive once the larvae of other putatively related taxa within the Rhagioninae are found and described.

Evidence supporting the common ancestry of the following clades is the shared presence of spermathecal duct accessory glands. This character is present within species of *Arthroceras*, *Chrysopilus*, *Ptiolina*, *Schizella*, *Spania*, *Spaniopsis*, and *Symphoromyia* (Figs. 40B, 62A, 64, 93A, 94-96, 126, 138, 149A, 150, 152-153). Female *Litoleptis* were not available, but this genus is placed in the Spaniinae tentatively on the basis of other characters. Within the Chrysopilinae, *Stylospania furcicornis* and *Stylospania lancifera* are recovered as sister taxa and form a monophyletic group along with *Chrysopilus*. These taxa form the basal lineage of the clade that composes Chrysopilinae, Arthrocerinae, and Spaniinae. The chrysopilines are supported by two synapomorphies; the presence of a reduced proepimeron sclerite (Fig. 175) and the presence of metallic- or scale-like thoracic setae (Fig. 112). All of these genera also tend to have pilose aristae and the gonostyli of the male genitalia tend to be heavily setose (Figs. 61, 117). The shared presence of a parameral sheath developed into ventral lobes in the male hypandrium supports the placement of *Arthroceras pollinosum* (Arthrocerinae) sister to the Spaniinae. The subfamily Spaniinae is defined by the shared presence of an anterior-facing lateral process of tergite 9, enveloping sternite 9 in the female (Figs. 94, 125A, 149-151; the state of

Litoleptis is unknown). The larvae of *Symphoromyia* and *Ptiolina* have an unusually scalloped first thoracic segment that is probably an additional synapomorphy for this clade (Figs. 186C, 190). Several features of the female terminalia *Ptiolina*, *Spania*, and *Spaniopsis* support their close relationship. These characters include a laterally displaced first cercus segment (Figs. 92, 93A, 125A, 139; *Symphoromyia* may also have this character, see Fig. 149); the genital chamber tightly defined by medial sclerotization; a wide, broadly rounded anterior sternite 9 area; and a posteriorly fused sternite 9 (Figs. 93-94, 125, 139A). These taxa also have stylate antennae (Figs. 73-76, 122, 127-130; see also *Litoleptis* spp., Fig. 70) and lack laterotergite setae. *Ptiolina* is recovered as a paraphyletic group, formed in a grade of two separate lineages. The *P. zonata* and *P. mallochi* clade are recovered as more closely related to *Spaniopsis* spp., *Spania nigra*, and *Litoleptis alaskensis*. Characters that support this relationship are the shared presence of a bare anepisternum (as *S. nigra* and *L. alaskensis*, but not *Spaniopsis* spp.), the R_{2+3} vein directed toward wing margin anteriorly (a character that was not used in phylogenetic analysis), the R_5 anterior to wing tip (Figs. 71, 81-82, 123, 132-135), the absence of an endoaedeagal process, a shortened spermathecal common duct (Figs. 94, 125, 139) and a tear-dropped shape of the genital chamber (Figs. 94, 125; as *S. nigra*, but not *Spaniopsis* spp.; *Litoleptis alaskensis* unscored for all female characters). Eliminating characters of the wing for phylogenetic analysis does not change this relationship (*Ptiolina* remains paraphyletic). The sister group relationship of *Spania* and *Spaniopsis* is supported by the reduction of female tergite 9 as a very narrow sclerite (Figs. 125A, 139).

Discussion

Monophyly of the Rhagionidae

Rhagionidae were recently redefined (Stuckenberg 2001). The most important putative synapomorphies proposed for Rhagionidae *sensu* Stuckenberg include tergite 7 of the female either as long as wide or much longer than wide (character 125); a wide intersegmental membrane between segments 7 and 8 of the female (character 126); basal segments of the female cerci closely adjacent dorsally (character 145); and basal segment of the female cerci with posteroventral lobes which curve ventrally towards one another to form a ring, as seen in posterior view (character 144). Stuckenberg lists other putative synapomorphies, but I have found these to be subjective and variable. Unfortunately the most consistent characters used to define the Rhagionidae *sensu* Stuckenberg are not unambiguous with respect to related taxa in lower Brachycera (see below). The autapomorphies listed for the family in Stuckenberg (2001: 16) are more appropriately considered suites of diagnostic characters that are currently used to define Rhagionidae.

Both putative synapomorphies relating to the female abdomen (tergite 7 square or elongate (character 125); presence of wide intersegmental membrane between segments 7 and 8 (character 126)) fail to distinguish Xylophagidae (*sensu* Woodley, 1989) from Rhagionidae *sensu* Stuckenberg. There is also some internal disagreement of the characters within Rhagionidae. A wide intersegmental membrane between segments 7 and 8 of the female is not present in *Bolbomyia* Loew, for instance.

Similarly, while most Rhagionidae *sensu* Stuckenberg have a square or elongate tergite 7 of the female abdomen, this is not exhibited in *Symphoromyia* Frauenfeld.

The proximity of the female cerci to one another dorsally is not a discrete character and therefore its scoring may be subject to interpretation (see Nagatomi & Iwata 1976). Nonetheless, when present, the basal female cerci are adjacent dorsally in many lower brachyceran taxa (e.g. xylophagids, coenomyiids) and the Rhagionidae *sensu* Stuckenberg are not exclusively defined by this character.

The monophyly of Rhagionidae in its broad sense, including *Austroleptis* and *Bolbomyia* is supported by the morphological phylogenetic analysis, although no single character defines the group. This concept conforms to Woodley (1989) and differs from Stuckenberg (2001) and Nagatomi (1982) in the exclusion of the pelecorhynchid genera from the family. It can be argued that family-level recognition of *Austroleptis* species (Stuckenberg, 2001) may be justified. Another new family concept, Spaniidae *sensu* Stuckenberg (2001), however is unwarranted. This group is neither monophyletic nor located outside of the clade containing other rhagionid groups. Evidence in favor of retaining the Rhagionidae as a single taxonomic unit is revealed in the special similarity of larval terminal segments shared among rhagionid genera *Chrysopilus*, *Ptiolina*, *Rhagio*, and *Symphoromyia*. The larvae of *Alloleptis*, *Austroleptis* and *Bolbomyia* are not known, however.

Pelecorhynchidae

The monophyly and position of the Pelecorhynchidae as recognized by Sinclair (1992), Sinclair et al. (1993), and Woodley (1989) are confirmed by the phylogenetic analysis of morphological characters. This may be somewhat surprising given the divergent morphology of *Pelecorhynchus*, particularly in regards to the male genitalia, when compared with *Glutops* (Figs 156-157, 164-165). *Pelecorhynchus* was originally placed in the Tabanidae (Hardy, 1920b) while *Glutops* has been variously placed in the Rhagionidae (Nagatomi, 1977; Kovalev, 1981; Nagatomi, 1982a; Nagatomi, 1984; Stuckenberg, 2001) or in its own group (Krivosheina, 1971). The male genitalia of *Pelecorhynchus* resemble species of Tabanidae in several ways (e.g., elongated gonocoxal apodemes (character 114), fused hypandrial sclerite (character 111), sinuate R_4 wing vein that diverges from R_5 and toward the leading margin of the wing in a conspicuous manner (character 81)), seeming to suggest that this genus has strong affinities to Tabanidae and may actually be more closely related to this family than to *Glutops.* The male genitalia of *Glutops* is bulbous laterally in a way that is similar to *Pelecorhynchus* and *Pseudoerinna*, but is otherwise primitive (Figs. 157, 164). The male genitalia of *Glutops* recalls *Rhagio* in that it apparently lacks noticeably derived features.

Several morphological features that suggest the pelecorhynchids are a monophyletic group are distinctive, but ultimately unscorable ‘gestalt’ characteristics. This includes the look of the eyes and swollen gena, and the roundedness of the male genitalia. Fortunately, there are other consistent features that may be scored as discrete

characters suitable for phylogenetic analysis and used as evidence of monophyly for the family. The monophyly of the Pelecorhynchidae is supported by the presence of paired ducts arising from the posterior margin of tergite 8 (character 148; Fig. 168). This is a new character, and the first adult synapomorphy developed for the family. The ventral process of the female first cercus segment in these taxa is distinctive and has been recognized as a possible synapomorphy for the group (Woodley, 1989; character 140; Figs. 158A, 166, 171A), however an explicit definition of this character is problematic as other tabanomorph taxa also have elongated first cercal segments (see discussion regarding characters 140-143). The thick, waxy outer layer of the larva (character 204) also supports this grouping, although the larva of *Pseudoerrina* species is not known. Additional characters that may support a close relationship between *Glutops* and *Pelecorhynchus* are the bare laterotergite (character 45) and non-emarginate anterior margin of the epandrial sclerite (character 98).

Definition of Chrysopilinae, Arthrocerinae, and Spaniinae

Three subfamilies of Rhagionidae are united by the presence of an accessory gland stemming from each of the spermathecal ducts (character 154). These structures, which are delicate and faint even after staining, have been overlooked by previous workers (Nagatomi, 1952; Nagatomi and Iwata, 1976; Webb, 1977b; Nagatomi, 1986). The Spaniinae, within this clade, are defined by the shared presence of ventrolateral arms, extending posteriorly from tergite 9, surrounding and fusing to sternite 9 laterally (character 128). Both of these features are consistent in resolving the groups, just as recovered in the phylogenetic analysis. However, in the morphological analysis, *Ptiolina* is paraphyletic as currently recognized (Fig. 5).

Particularly in most *Chrysopilus* specimens, the basal cercal lobes of the female clearly arc towards one another ventrally to form a circle, in line with the anus (character 144). Stuckenberg (2001) used this character as a synapomorphy of Rhagionidae. *Rhagio* species also exhibit this feature. I have found that when females die, however, the basal lobes of the cerci may dry and be fixed in a number of positions. Specimens may have the basal lobes appressed together medially or the basal lobes may be directed parallel or slightly laterally, creating space between the lobes. This variation, along with the imprecise nature of judging when the "ring" formed by the cerci is circular, creates difficulties in scoring this character. In my opinion, however, the basal cercal lobes of *Arthroteles* Bezzi*, Atherimorpha* White and *Symphoromyia* (Rhagionidae *sensu* Stuckenberg) females should not be scored differently from the *Spaniopsis* and *Ptiolina* Zetterstedt species (Spaniidae *sensu* Stuckenberg) that I have seen.

The close association of *Schizella* and *Chrysopilus* is self-evident. Species of both genera have derived, slightly flattened, often metallic-colored setae on the mesonotum (character 38) and the females of these genera are virtually indistinguishable. The possibility certainly exists that *Schizella* species represent an autapomorphic species group within the *Chrysopilus* lineage, distinguished only by the unusual antenna exhibited in the male (Fig. 113). Although there is some reason to believe *Schizella* species are derived forms of *Chrysopilus*, it is premature to synonymize the genera without more information. This is certainly the case in light of

this result, which shows a monophyletic *Chrysopilus*. Examination of the larva of *Schizella* would be particularly instructive to help answer the question of *Chrysopilus* monophyly.

Ptiolina and *Omphalophora*

The genus *Ptiolina* Zetterstedt as currently recognized (Nagatomi, 1982a; Nartshuk, 1995) was found to be a grade of two lineages in the morphological phylogenetic analysis (Fig. 5). This was somewhat of a surprising result given the close morphological similarity of *Ptiolina* and *Omphalophora*. Below I discuss the history of the *Ptiolina* and *Omphalophora* and morphological observations made during this study. Although some species remain undetermined regarding their generic designation (see list of included species for *Ptiolina*), the recognition of *Omphalophora* appears warranted.

In 1900, Becker established *Omphalophora oculata*, a new genus and species from West Siberia. Frey added *Omphalophora lapponica* Frey to the genus in 1911 and another species was added in 1918, when Szilády transferred *Chrysopilus arctica* Frey to the genus. In 1982, Nagatomi examined all three types of these species and determined that *Chrysopilus arctica* Frey was erroneously placed in *Omphalophora* by Szilády (1934) and was a true *Chrysopilus* species, in agreement with Narchuk (1969). For the *Omphalophora* species, Nagatomi noted that wing vein R_{2+3} is straight in its apical portion, wing cell sc is wider at wing margin than r1, wing vein R_5 at wing margin beyond wing tip and the anal cell is open. These features were believed to vary within *Ptiolina*, however, and he synonymized *Omphalophora* with

Ptiolina. Majer (1988) did not recognize Nagatomi's contribution and followed Szilády (1934), keeping all three species in *Omphalophora*. Narchuk (1969) indicated that *Omphalophora* differed from *Ptiolina* by its larger size and having a reduced or absent hind tibial spur. In addition to *O. lapponica* and *O. oculata*, *Ptiolina grandis* Frey and *P. uralensis* Becker shared these qualities and were consequently placed in *Omphalophora*. Later, however, Nartshuk (1995) adhered to a strict interpretation of *Omphalophora*, recognizing only a single species in the genus *O. lapponica* (Frey), which she then synonymized with *Ptiolina oculata* (Becker). In so doing, she assigned *Omphalophora* as a junior synonym of *Ptiolina*. Nagatomi also treated *Omphalophora* as a synonym of *Ptiolina* (Nagatomi, 1982a).

I examined the type of *Omphalophora lapponica* (Frey) and dissected the female terminalia. Examination of its morphology reveals that *Omphalophora* Becker is a valid concept, defined by a suite of characters that have not been fully analyzed previously. The female genitalia are especially important in demonstrating important differences between *O. lapponica* (Frey) and its allies, from the remaining *Ptiolina* species. These differences are consistent with other differences evident in the male genitalic, wing, thoracic, and to some degree, antennal morphologies. It seemed as if, everywhere I looked, there were consistent differences between *Omphalophora* and *Ptiolina* and the morphological evidence supporting the monophyly of each of these groups is quite strong.

Omphalophora and *Ptiolina* have also have divergent, but consistent morphologies in the length and form of tergites 7 and 9, the degree of fusion between tergite 9 and sternite 9, sternite form, size and shape of the genital chamber, spermathecal duct length, and spermathecal duct accessory gland position.

In *Omphalophora*, the 7th tergite is clearly longer than wide, whereas in *Ptiolina*, this tergite is clearly wider than long. Comparisons of the female terminalia of *Omphalophora* and *Ptiolina* are made with reference to Figs 81 and 95, which show the genitalia of these taxa, respectively. Tergite 9 in *Omphalophora* is bulbous laterally and tapers posteriorly, with a length that is greater than half its width (Fig. 81). In *Ptiolina*, tergite 9 is rectangular and narrow; its length is less than half its width (Fig. 95). Also in *Ptiolina*, the ventrolateral arms of tergite 9 are easily distinguished, forming a modest s-curve (as observed in the dorsal/ventral perspective). The distal (anterior) tip of these ventrolateral arms is fused to sternite 9 to varying degrees (e.g., lightly fused as in *P. zonata* Hardy & McGuire or firmly attached as in *P. mallochi* Hardy & McGuire), but for the most part, the arms of tergite 9 are free from sternite 9 posteriorly. There is no such separation in *Omphalophora*, where the ventrolateral arms are bound to sternite 9 by a thick membrane along their entire length. The form of sternite 9 itself differs significantly between *Omphalophora* and *Ptiolina*. In *Omphalophora*, sternite 9 is narrow posteriorly and then broadens as it extends anteriorly beyond the ventrolateral arms of tergite 9 and is broadly rounded apically (anteriorly). The genital chamber, formed at the base of the common spermathecal duct, is narrow, with lateral margins that are

nearly parallel, in line with a lengthened common spermathecal duct. In *Ptiolina*, sternite 9 is widest posteriorly, within the ventrolateral arms of tergite 9, and extends anteriorly as a narrow, nearly parallel-sided process which is flat truncated at its anterior apex. Female genitalia of *Omphalophora* also have partially sclerotized lobes located in the membrane between the ninth tergite and ninth sternite. The origin and homology of these structures are unclear. They are absent in species of *Ptiolina*.

The genital chamber occupies a larger area and the margins of which are clearly oval (not nearly parallel sided as in *Omphalophora*). The common spermathecal duct is reduced to a short length (less than the length of the genital chamber) in *Ptiolina* and the spermathecal ducts, themselves, are less than three times the length of sternite 9. Spermathecal duct accessory glands arise at or near the base of the sclerotized spermathecae (Fig. 96). In *Omphalophora*, the common spermathecal duct is lengthened to at least the same length as the genital chamber, or longer, and the spermathecal ducts are at least three times the length of sternite 9 or greater. The spermathecal duct accessory glands arise at approximately two-thirds to four-fifths the distal length (from sternite 9) leading to the spermathecae (Figs. 81, 95). The duct is wider and thicker between the accessory gland and the sclerotized spermatheca, suggesting that it may be an unsclerotized proximal expansion of the spermatheca. This is true for all taxa (in *Ptiolina*, see in particular, *P. mallochi* Hardy & McGuire; it is readily apparent in all *Omphalophora*). Spermathecal form appears to vary on a species level and does not distinguish between *Omphalophora* and *Ptiolina*; spermathecae may be oval, egg-shaped, or spherical, regardless of grouping.

Spermathecal sclerotization is generally well developed in *Ptiolina sensu lato*; any variation appears to be on a individual-level basis. The degree of lateral displacement between the basal cercal segments is also variable at the species level and is inadequate for distinguishing between *Omphalophora* and *Ptiolina* (not to mention difficult to score objectively on account of its continuous nature).

Omphalophora also exhibit several distinctive characters in the male genitalia that instantly distinguish it from *Ptiolina* (Figs 77-80, 89-94). The most pronounced feature is that each gonostylus comes to a sharp point apically (Figs 79-80), as opposed to in *Ptiolina*, where the gonostylus is rounded apically (Figs 92-94). *Omphalophora* also have an elongate aedeagal sheath, posterior of the gonocoxites medially, where it narrows. In *Ptiolina*, the aedeagal sheath tends to be shorter. Similarly, the gonocoxal apodemes tend to be longer in *Omphalophora* than in *Ptiolina*. This feature is less striking and therefore, perhaps more difficult to distinguish without directly comparing samples. However, in all of the samples I have examined, the gonocoxal apodemes of *Omphalophora* reach the anterior margin of the hypandrium when examined in a direct dorsal view; in *Ptiolina*, the gonocoxal apodemes end well short of this.

The epandrium is clearly different in *Omphalophora*, where the subepandrial sclerite is either as wide as long or squared and nearly oval (as in *P. fasciata*) (Figs. 77-78). Whereas in *Ptiolina*, the subepandrial sclerite is narrow rectangular, approximately three times as wide as long (Figs. 89-91). The hypoproct is tomentose in

Omphalophora; setose in *Ptiolina.* The epandrial sclerite is also much more firmly secured to the subepandrial sclerite, and the cerci more firmly attached to the hypoproct, (in a single plane) in *Omphalophora*. In *Ptiolina*, the epandrial and subepandrial sclerites tend to rest at a perpendicular angle, loosely attached, after being cleared and placed in glycerol (Fig. 89B). Separation between cerci seems to vary at the species level, independent of higher level patterns and the form of the epandrial sclerite (e.g., notching or curvature of the posterior and/or anterior margin) does not appear to resolve differences at the subgeneric level. While a medial line of increased sclerotization of the epandrial sclerite (as evidenced by *P. lapponica* and especially *P. majuscula*) is more common in *Omphalophora* (Figs. 77B, 78), it is an unreliable character to differentiate *Omphalophora* and *Ptiolina*.

In *Omphalophora* species (at that time, represented by *O. oculata* Becker and *O. lapponica* (Frey)), Nagatomi (1982: 56) noted that wing vein R_{2+3} is straight in its apical portion, wing cell sc is wider at wing margin than r1, "wing vein R_5 at wing margin beyond wing tip" and the anal cell is open. Now that more species are added to *Omphalophora* based on male and female genitalic characters, the distribution of wing character states has shifted. Wing vein R_{2+3}, for example, is not always straight in its apical portion in *Omphalophora* (see *P. fasciata* Loew and *P. nigripilosa* Hardy & McGuire; Figs. 75A, 76A) and the anal cell is not always open at the margin (see *P. fasciata* Loew, Fig. 75A; however all *Ptiolina* available for examination have closed anal cells). However, at least one wing character consistently separates *Omphalophora* and *Ptiolina*. In *Omphalophora*, wing veins R_4 and R_5 contain the

wingtip (Figs. 80, 81A) whereas in *Ptiolina*, R_5 is anterior to the wingtip (Figs. 76B, 88). In many *Omphalophora*, R_{2+3} is longer than the length of R_5, however this is character is less reliable (*P. nigripilosa* is not obviously longer). In *Ptiolina*, wing veins R_{2+3} and R_5 are either approximately equal in length, or R_5 is longer. I have found that the relative length of wing cells sc and r_1 is not a discrete and reliable feature distinguishing *Omphalophora* and *Ptiolina*.

Perhaps because of their accessibility, the antennae often receive special attention in taxonomic treatments, and this is certainly the case for *Omphalophora* and *Ptiolina*. Species within these groups have obvious differences in antennal morphology. The first flagellomere in *P.* (*Omphalophora*) *majuscula*, for example, is rounded, enlarged and conical at its base then smoothly tapered into an extended stylus, somewhat reminiscent of the antenna of species in *Litoleptis* Chillcott and *Spaniopsis* White (Fig 73B; compare with *Litoleptis*, Fig. 70, and *Spaniopsis*, particularly Figs. 127B and 128B). In many *Ptiolina* (e.g., *P. edeta*, *P. zonata*, others), the first flagellomere is enlarged but flattened laterally, with a clear break between the stylus and the first flagellomere (Figs. 74, 84B). However, enough overlap of antennal morphologies exists between *Omphalophora* and *Ptiolina* to break down the reliability of this character system. Generally, the first flagellomere of *Omphalophora* tends to be sub-globular oval or conical (three-dimensional) while in *Ptiolina*, it is laterally compressed (flattened). Differences in the way the specimen is collected and preserved may mask these differences however, and it is risky to base determinations on this alone (especially based on photos or illustrations from the lateral

perspective!). The first flagellomere may be smoothly integrated into the style, or there may be a break between style and first flagellomere, without regard to subgeneric affiliation. Similarly, first flagellomere profile form (from a lateral perspective) and antennal style length may vary independently, on the species level. I could not detect differences between male and female specimens, in particular, above differences that exist naturally between individuals within the same species.

Finally, I considered thoracic characters, body size, tibial spurs, and other features that may add to the evidence supporting two phylogenetic lineages within the genus *Ptiolina*. In the anepisternum of *Omphalophora* species is setose near the posterior margin whereas in *Ptiolina*, this sclerite is completely bare; lending further evidence of phylogenetic distance between the two groups.

Ptiolina male eyes are clearly split into upper and lower regions, where facets are larger above and smaller ventrally. *Omphalophora* males also have facets that are larger above and smaller below, however, there is a smooth transition and an abrupt demarcation where facet size changes is lacking.

Body size was an important consideration for distinguishing *Omphalophora* and *Ptiolina* in the past (Hardy and McGuire, 1947). This was probably attributable to the fact that the original species placed in *Omphalophora* are particularly large (*P. oculata* probably remains the largest in genus *Ptiolina*), which called attention to them. Their size, however, was largely independent of ancestry, as it would seem now

in light of further examination. *P*. (*Omphalophora*) *fasciata* and *P*. (*Omphalophora*) *nigripilosa*, for example, are comparable in size to some of the smallest species in the *Ptiolina*. Tibial spurs have also been identified as a character that may assist separating *Omphalophora* and *Ptiolina* (Narchuk, 1969). I could not find any meaningful differences of size, number, or placement of tibial spurs, however.

Table 5. Determination of *Ptiolina* species into *Ptiolina* and *Omphalophora* subgroups.

Current Genus	Original species	Original Author	Year	Species name status	Valid species	Biotic Region	Subgenus determination	Basis of determination
Ptiolina	*alberta*	Leonard	1931	valid	*alberta*	NA	indet.	not clear from description; although likely *Ptiolina*
Ptiolina	*arctica*	Becker	1900	junior synonym	*grandis*	PA	*Ptiolina*	synonymy
Ptiolina	*arctica*	Malloch	1923	junior synonym	*mallochi*	NA	*Ptiolina*	examination of holotype
Ptiolina	*attenuata*	Nagatomi	1986	valid	*attenuata*	OR	*Ptiolina*	(Nagatomi, 1986)
Ptiolina	*augusta*	Curran	1931	valid	*augusta*	NA	indet.	not clear from description; although likely *Ptiolina*
Ptiolina	*calamodytes*	Schiner	1868	junior synonym	*cinereofasciata*	PA	*Omphalophora*	synonymy
Ptiolina	*cinereofasciata*	(Schummel)	1837	valid	*cinereofasciata*	PA	*Omphalophora*	synonymy
Ptiolina	*dudai*	Lindner	1942	valid	*dudai*	PA	indet.	specimen not available
Ptiolina	*edeta*	(Walker)	1849	valid	*edeta*	NA	*Ptiolina*	examination of determined material
Ptiolina	*fasciata*	Loew	1869	valid	*fasciata*	NA	*Omphalophora*	examination of determined material
Ptiolina	*fulva*	Becker	1900	junior synonym	*cinereofasciata*	PA	*Omphalophora*	examination of determined material
Ptiolina	*grandis*	Frey	1918	valid	*grandis*	PA	*Ptiolina*	examination of determined material
Ptiolina	*grisea*	(Stroble)	1892	junior synonym	*paradoxa*	PA	indet.	specimen not available
Ptiolina	*grisea*	Curran	1931	junior synonym	*edeta*	NA	*Ptiolina*	examination of determined material
Ptiolina	*lapidaria*	Nowiczki	1868	junior synonym	*paradoxa*	PA	indet.	specimen not available
Ptiolina	*lapponica*	(Frey)	1911	junior synonym	*oculata*	PA	*Omphalophora*	examination of holotype
Ptiolina	*latifrons*	Nagatomi	1986	valid	*latifrons*	OR	indet.	specimen unavailable; description inadequate
Ptiolina	*longipilosa*	Nagatomi	1986	valid	*longipilosa*	OR	indet.	specimen unavailable; description inadequate
Ptiolina	*majuscula*	Loew	1869	valid	*majuscula*	NA	*Omphalophora*	examination of determined material
Ptiolina	*mallochi*	Hardy & McGuire	1947	valid	*mallochi*	NA	*Ptiolina*	examination of determined material

Current Genus	Original species	Original Author	Year	Species name status	Valid species	Biotic Region	Subgenus determination	Basis of determination
Ptiolina	*nervosa*	Nagatomi	1986	valid	*nervosa*	OR	indet.	specimen unavailable; description inadequate
Ptiolina	*nigra*	Zetterstedt	1842	junior synonym	*obscura*	PA	*Ptiolina*	examination of determined material
Ptiolina	*nigrina*	Wahlberg	1854	junior synonym	*obscura*	PA	*Ptiolina*	synonymy
Ptiolina	*nigripes*	Zetterstedt	1859	Junior synonym	*obscura*	PA	*Ptiolina*	synonymy
Ptiolina	*nigripilosa*	Hardy & McGuire	1947	valid	*nigripilosa*	NA	*Omphalophora*	examination of holotype
Ptiolina	*nitida*	Wahlberg	1854	valid	*nitida*	PA	*Ptiolina*	examination of determined material
Ptiolina	*nitidifrons*	Hardy & McGuire	1947	valid	*nitidifrons*	NA	*Ptiolina*	examination of holotype
Ptiolina	*obscura*	(Fallen)	1814	valid	*obscura*	PA	*Ptiolina*	examination of determined material
Ptiolina	*obsoleta*	Leonard in Curran	1931	valid	*obsoleta*	NA	*Ptiolina*	examination of determined material
Ptiolina	*oculata*	(Becker)	1900	valid	*oculata*	PA	*Omphalophora*	synonymy
Ptiolina	*paradoxa*	(Jaennicke)	1866	valid	*paradoxa*	PA	indet.	specimen not available
Ptiolina	*pelliticornis*	Becker	1900	valid	*pelliticornis*	PA	indet.	specimen not available
Ptiolina	*phragmitophila*	Schiner	1868	junior synonym	*cinereofasciata*	PA	*Omphalophora*	synonymy
Ptiolina	*shimai*	Nagatomi	1985	valid	*shimai*	OR	*Ptiolina*	(Nagatomi, 1985)
Ptiolina	*sphaeralis*	Nagatomi	1986	valid	*sphaeralis*	OR	indet.	specimen unavailable; description inadequate
Ptiolina	*tristis*	(Schummel)	1837	junior synonym	*obscura*	PA	*Ptiolina*	synonymy
Ptiolina	*tristis*	(Walker)	1949	junior synonym	*obscura*	PA	*Ptiolina*	synonymy
Ptiolina	*uralensis*	Becker	1921	junior synonym	*oculata*	PA	*Omphalophora*	synonymy
Ptiolina	*vicina*	Hardy & McGuire	1947	valid	*vicina*	NA	*Ptiolina*	examination of determined material
Ptiolina	*wodzickii*	Frauenfeld	1867	junior synonym	*paradoxa*	PA	indet.	specimen not available
Ptiolina	*zonata*	Hardy & McGuire	1947	valid	*zonata*	NA	*Ptiolina*	examination of determined material

Rhagioninae

Rhagio and *Rhagina*

All characters of *Rhagina* are also seen in *Rhagio* species, except for the exceptional wing characters seen in some species of *Rhagina*. Yang et al. note that *Rhagina* male lacks the subepandrial sclerite (tergite 10), whereas in *Rhagio*, it is present (Yang et al., 1997: 187), however, I find the male genitalia indistinguishable; both lack the subepandrial sclerite. The wing in *Rhagina incurvatus* de Meijere is distinctive, however, there appears to be a morphological grade in the genus, especially as one examines the wing of *Rhagina sinensis* Yang and Nagatomi (1997: 186) which has a sinuous R_{2+3} wing vein, but not distinctively so, and not far removed from venation found in some *R. hirtus* (Say) specimens and *R. dichomaticus* Chillcott. Another distinctive feature of *Rhagina* emphasized by Nagatomi (1982) and Yang et al. (1997) is a prominent ventro-apical 'hump' on the hind femur. This is a variable character in both *Rhagio* and *Rhagina,* however. Although most commonly absent in Rhagio, I have seen the 'hump' in an undescribed *Rhagio* species from Laos. Similarly, I have a *Rhagina* specimen which lacks such a hind tibial hump. Yang et al. indicate that the presence or absence of such a hump does not necessarily determine the genus (Yang et al., 1997: 115).

Atherimorpha

Stuckenberg suggested that South African members of the genus *Atherimorpha* may be more closely related to *Arthroteles* than to its nominal congeners. The results of this study may at first, seem to confirm this idea, since *Atherimorpha* is recovered

paraphyletic with respect to *Arthroteles*. However, South African *Atherimorpha* species were not included in the phylogenetic analysis. In the current analysis *Arthroteles bombyliiformis* is recovered as sister to two South American *Atherimorpha* species. While it is possible that the South American and South African *Atherimorpha* species form a clade that is sister to *Arthroteles*, I strongly doubt it. I have examined extensive collections of *Atherimorpha* from South America and Australia, as well as a synoptic collection of South African *Atherimorpha* species. The South American members are very diverse and in some cases, highly divergent (e.g., *A. albohirta*) however I believe that *Atherimorpha* is monophyletic on the basis of consistent similarity among species throughout their distribution. I expect that as more Australian and South African *Atherimorpha* species are scored and included in the analysis, a more accurate resolution of the relationships will be recovered and the monophyly of *Atherimorpha* will be supported. The odd result here is most likely an effect of poor taxon sampling of the genus.

Bolbomyia* and *Austroleptis

Austroleptis and *Bolbomyia* are grouped in the most parsimonious arrangement, consistent with Grimaldi and Cumming (1999). Nonetheless, the shared loss of the third medial vein does not seem like a particularly compelling synapomorphy. *Alloleptis tersus* is located as the sister of these genera, but there are no clear synapomorphies supporting this placement.

Molecular Treatment

Introduction

The taxonomic classification of the Rhagionidae has been unstable for decades because there are few morphological characters that can be used to support hypotheses of relationship among its members. When new morphological synapomorphies are proposed (such as the presence of aedeagal tines (Sinclair et al., 1993)), few additional sources of evidence are available to corroborate or refute such ideas (Stuckenberg, 2001). One potentially very powerful and independent source of evidence comes from molecular data.

The Tabanomorpha has already been studied in a molecular context to some degree (Wiegmann et al., 2000). No previous molecular study, however, has tested the monophyly of the Rhagionidae in light of several recent, conflicting hypotheses for the group (Sinclair, 1992; Stuckenberg, 2001; Woodley, 1989; Table 11). At issue is the position of three key taxon groups; *Austroleptis*, *Bolbomyia*, and Spaniinae (recognized at the family level by Stuckenberg, 2001).

Austroleptis Hardy is a highly autapomorphic genus that shares few character states with its relatives in Lower Brachycera and has puzzled morphological taxonomists for decades. Most have placed the genus in Tabanomorpha but its location within this group has been disputed (Hardy, 1920; Steyskal, 1953; Hardy, 1955; Nagatomi, 1982a, 1984; Woodley, 1989; Stuckenberg, 2001). *Austroleptis* is traditionally considered a primitive member of the Rhagionidae (Hardy, 1920; Nagatomi, 1982a).

Chillcott (1963) suggested that within Rhagionidae, *Austroleptis* had affinities to *Bolbomyia*, *Litoleptis*, *Archicera* (= *Spania*), and *Hilarimorpha*. Grimaldi & Cumming (1999) used similarities in wing morphology to argue that *Austroleptis* is most closely related only to *Bolbomyia* and *Litoleptis* (either within or outside of Rhagionidae). Stuckenberg preferred to use the derived condition of the genus as evidence for supporting its own, family-level recognition (Stuckenberg in Nagatomi, 1982a; Stuckenberg, 2001). It is not certain, however, that *Austroleptis* belongs in the Tabanomorpha. Ecological information, such as larval feeding habits, has been used as a surrogate to direct morphological evidence as a basis for its proposed placement in the Xylophagomorpha (Colless & McAlpine, 1991; Sinclair et al., 1993).

Similarly, *Bolbomyia* Loew has been variously been placed within Tabanomorpha or outside of it (Xylophagidae) due to the ambiguity of the morphological evidence. *Bolbomyia* has been placed in the Rhagionidae on account of an elongated intersegmental region in the female abdomen (Nagatomi, 1982a; Stuckenberg, 2001); together with *Austroleptis* and *Litoleptis* (inside or outside of Rhagionidae) because it lacks wing vein M_3 (Grimaldi & Cumming, 1999); or as sister to Athericidae and Tabanidae on account of having aedeagal tines in the male genitalia (Sinclair et al., 1993). James (1965) located *Bolbomyia* among the Xylophagidae because of its flattened clypeus (James, 1965).

The spaniine group of Rhagionidae (Hennig, 1973; Nagatomi, 1982a) includes *Ptiolina*, *Spania*, *Spaniopsis*, and *Litoleptis*. These taxa have been placed together on

the basis of their antennal form (short, stylate), short female abdominal intersegmental length, and the wide separation of the female cercus segments (Nagatomi, 1982). Recently, this group was raised to family level status (Stuckenberg, 2001). Stuckenberg (2001) did not suggest a sister taxon to the group, however, and the monophyly of the group and its placement with respect to the Rhagionidae have not been tested in a phylogenetic context. Its proper status, therefore, remains somewhat uncertain.

Materials and Methods

Taxon Sampling

Complete taxon sampling for molecular analysis of the Rhagionidae is difficult because so many of the genera of this family are rare. Nonetheless, ingroup taxa include representatives from all subfamilies of the genera in Rhagionidae recognized by Nagatomi (1982) and Stuckenberg (2001). Outgroup taxa included representatives from all families within Tabanomorpha, as well as a diversity of genera within the Xylophagomorpha and two genera from the Stratiomyiomorpha.

The breadth of taxon sampling was determined on the basis of availability of specimens for study and the importance of taxa for testing specific hypotheses of relationship including the monophyly and position of Pelecorhynchidae and Spaniidae, the monophyly of *Chrysopilus*, *Rhagio*, and *Atherimorpha*, as well as the position of Vermileonidae, *Bolbomyia*, and *Austroleptis*. Table 3 shows the species used in the molecular analysis, their source, locality, and recent family designations. Higher level classification follows Woodley (1989).

Newly determined sequences were combined with sequences from the literature, available from GenBank. Twenty 28S rDNA sequences representing twenty species in fifteen genera of Tabanomorpha have been published previously (Wiegmann et al., 2000). Of these, seven species in four genera are currently placed in Rhagionidae. Brian Wiegmann (North Carolina State University, Raleigh, NC, USA) supplied additional, unpublished sequences of *Exeretonevra angustifrons* Hardy, *Xylophagus abdominalis* Loew, and *Heterostomus* sp. The sequence identified as *P. fasciata* Loew (Wiegmann et al., 2000; GenBank accession numbers AF238554, AF238530, AF238508) showed very strong affinity with *Chrysopilus* species and not with the *P. fasciata* identified and used in this study (results not shown). Because a voucher for this specimen was not available to confirm identification, GenBank accessions AF238554, AF238530, and AF238508 were not included in this study. Sequences from Wiegmann et al. (2000) were shorter than those presented here, therefore identical sequences determined from the same species for this study were included in favor of the shorter sequences. A summary of species, source, and GenBank accession numbers is shown in Table 3.

Table 6**.** Taxon sampling for molecular analyses. Classification consistent with Woodley (1989) / Stuckenberg (2001).

Classification	Species	Locality	Source	GenBank Accession Numbers
STRATIOMYOMORPHA				
Stratiomyiidae	*Pachygaster leachii*	England	GenBank	AF238548, AF238524, AF238502
Pantophthalmidae	*Pantophthalmus sp.*	Costa Rica	GenBank	AF238547, AF238523, AF238501
XYLOPHAGOMORPHA				
Xylophagidae	*Arthropeas magnum*	Saskatchewan	GenBank	AF238549, AF238525, AF238503
	Dialysis elongata	North Carolina	GenBank	AF238551, AF238527, AF238505
	Exeretonevra angustifrons	Australia	B. Wiegmann, unpubl.	
	Heterostomus sp.	Costa Rica	B. Wiegmann, unpubl.	
	Coenomyia ferruginea	Tennessee	GenBank	AF238550, AF238526, AF238504
	Xylophagus abdominalis	North Carolina	B. Wiegmann, unpubl.	
TABANOMORPHA				
Athericidae	*Atherix variegata*	Wisconsin	GenBank	AF238565, AF238541, AF238517
	Dasyomma sp. 1	Chile	New sequence	
	Dasyomma sp. 2	Chile	New sequence	
Tabanidae	*Chrysops sp.*	Maryland	New sequence	
	Tabanus atratus	North Carolina	GenBank	AF238568, AF238544, AF238519
	Tabanus rufofrater	Georgia	GenBank	AF238561, AF238537, AF238513
	Tabanus sp.	Maryland	New sequence	
Rhagionidae	*Atherimorpha atrifemur*	Chile	New sequence	
	Atherimorpha sp. 1	Chile	New sequence	
	Atherimorpha sp. 2	Tasmania	New sequence	
	Atherimorpha sp. 3	Tasmania	New sequence	
	Atherimorpha vernalis	Tasmania	New sequence	
	Bolbomyia nana	Quebec	New sequence	
	Chrysopilus quadratus	Maryland	New sequence	
	Chrysopilus thoracicus	Maryland	New sequence	
	Chrysopilus sp. 1	Ecuador	New sequence	
	Chrysopilus sp. 2	Queensland, Australia	New sequence	
	Chrysopilus sp. 3	Tasmania	New sequence	
	Chrysopilus sp. 3	Tasmania	New sequence	
	Rhagio hirtus	Illinois	GenBank	AF238509 ,AF238532, AF238556
	Rhagio mystaceus	Illinois	GenBank	AF238510 , AF238531, AF238555
Pelecorhynchidae/ Rhagionidae	*Glutops rossi*	Washington	GenBank	AF238570, AF238546, AF238521
	Pelecorhynchus personatus	Australia	GenBank	AF238569, AF238545, AF238520
Rhagionidae/ Austroleptidae	*Austroleptis collessi*	Tasmania	New sequence	
	Austroleptis multimaculata	Tasmania	New sequence	
	Austroleptis rhyphoides	Tasmania	New sequence	
Rhagionidae/ Spaniidae	*Ptiolina fasciata*	Saskatchewan	New sequence	
	Spaniopsis clelandi	Tasmania	New sequence	
	Spaniopsis longicornis	Victoria, Australia	New sequence	
	Symphoromyia atripes	Illinois	GenBank	AF238559, AF238535
	Symphoromyia hirta	Illinois	GenBank	AF238558, AF238534, AF238512
	Symphoromyia sp.	Alaska	New sequence	
TABANOMORPHA/ VERMILEOMORPHA				
Vermileonidae	*Leptynoma hessei*	South Africa	Genbank	AF238552, AF238528, AF238506
	Vermileo opacus	California	GenBank	AF238553, AF238529, AF238507
	Vermileo sp.	Israel	New sequence	

Extraction

DNA was extracted from specimens stored in 85-100% ethyl alcohol with the Nucleon Phytopure resin-based extraction kit, using the protocol provided for small samples (Amersham Pharmacia, Uppsala, Sweden) or with the DNEasy Plant mini kit (Qiagen, Valencia, CA, USA). Quality of the extracted DNA was assessed via agarose gel electrophoresis and ethidium bromide staining.

Amplification

Amplification of 28S rRNA was performed using three primer pairs (rc28C-28E, rc28D-28K, and rc28Q-28Z) for the polymerase chain reaction (PCR). In cases where amplification of these regions failed, internal primers (28P, rc28P, 28H, rc28H, 28X, and/or rc28X) were used to amplify smaller fragments (Table 2; Fig. 1). The PCR was done using a Biometra PCR machine with the following program: 95°C initial denature step of 3 minutes followed by the amplification cycle of 95°C for 20 seconds, 54°C for 20 seconds, and 75° for 1 minute and 10 seconds. The cycle was repeated 30 times. After 10 minutes at 75°C, the products were cooled to 4°C. The resulting PCR products were purified using a modified polyethylene glycol (PEG) precipitation (Morgan and Soltis 1993). An equal volume of 20% weight:volume PEG 8000, 2.5 M NaCl was added to each PCR product, vortexed briefly and spun at 16,000g for 15 minutes. The solution was removed and the resulting DNA pellet was washed once with 80% cold ethanol. The solution was spun at 16,000g for 10 minutes and the ethanol was removed. The pellet was then air-dried and resuspended in 25 μl de-ionized water. The PEG-purified PCR product was quantified via agarose gel electrophoresis and ethidium bromide staining for subsequent sequencing reactions.

Table 7. 28S rDNA primers (from Wiegmann et al., 2000).

Primer	Sequence 3′- 5′
rc28C	CCG AAG TTT CCC TCA GGA TAG C
28P	GGC TTA CGC CAA ACA CTT CTA GGC
rc28P	TGG TAT GCG TAG AAG TGT TTG GC
28E	CCT TAT CCC GAA GTT ACG
rc28D	CCG CAG CTG GTC TCC AAG
28H	GGT TTC GCT GGA TAG TAG
rc28H	CTA CTA TCC AGC GAA ACC
28K	GAA GAG CCG ACA TCG AAG
rc28Q	GGA CAT TGC CAG GTA GGG AGT T
28X	CGG ATA CGA CCT TAG AGG CG
rc28X	CGC CTC TAA GGT CGT ATC CG
28Z	GCA AAG GAT AAG CTT CAG TGG

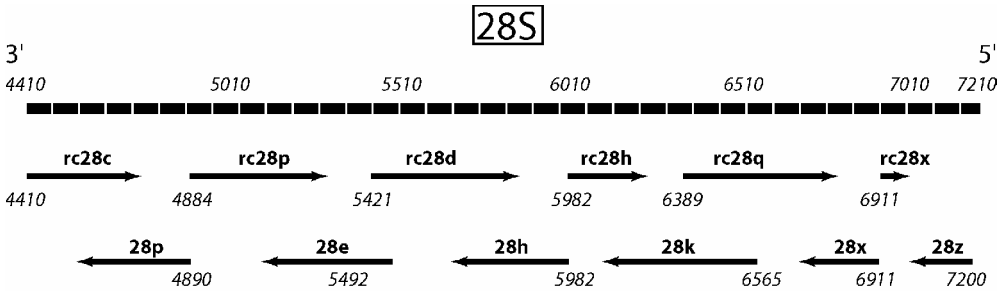


Figure 4. Primers used for sequencing of 28S rDNA gene.

Sequencing

Sequencing reactions were performed in 7 µl final volume (0.5 µl PEG-purified PCR product, 3.5 µl de-ionized water, 1.0 µl 2.5 µM primer, 1.5 µl 5X buffer [400 mM Tris pH 9.0, 10 mM $MgCl_2$], 0.5 µl BigDye Terminator Ready Reaction Mix v2 [Perkin Elmer Biosystems, Foster City, CA]), cycled and purified according to the manufacturer's protocols and resolved either using an ABI 377 slab gel sequencer performed by the University of Maryland Center for Agricultural Biotechnology or an ABI 3100 capillary sequencer. The resulting sequences were blasted against Genbank to confirm their identity. Sequenc fragments were edited and compiled using the computer program Sequencher 3.1.1 (Gene Codes Corporation, Ann Arbor, MI). Opposite strands were confirmed for all templates.

Sequence Alignment

The aligned 28S data matrix was 3201 base pairs in length. The average base frequencies of the entire matrix were A= 30.22%, C=17.33%, G=23.20%, T=29.26% and base composition did not significantly differ from these proportions among taxa (χ^2 = 52.542 (df=126), P = 1.0).

Many new sequences generated for this study were approximately 55bp longer at their 3' ends than the sequences acquired from GenBank, after primer ends had been discarded and the sequences aligned. Taxa that were shorter by comparison include *Arthropeas magnum* (55bp), *Atherix variegata* (46bp), *Chrysopilus quadratus* (46bp), *Coenomyia ferruginea* (55bp), *Dialysis elongata* (55bp), *Exeretonevra angustifrons* (55bp), *G. rossi* (55bp), *Heterostomus* sp. (55bp), *Leptynoma hessei* (55bp), *Pelecorhynchus personatus* (55bp), *Rhagio hirtus* (46bp), *Rhagio mystaceus* (46bp), *Symphoromyia hirta* (46bp), *Tabanus atratus* (55bp), *Tabanus rufofrater* (55bp), *Vermileo opacus* (55bp), *Xylophagus abdominalis* (55bp), *Pachygaster leachii* (55bp), and *Pantophthalmus* sp. (60bp). The region of 28S between primer pairs rc28C and 28E could not be amplified for *Atherimorpha* sp. 2 [Cradle Mountain Lodge, Tasmania, Australia], so the first 1134 bp of the aligned sequence are missing. The sequences acquired from GenBank were also partially incomplete in other areas. *Chrysopilus thoracicus* and *Symphoromyia atripes* were missing the first 503bp and 537bp of aligned sequence, respectively. The primer region between base pairs 442-557 of the missing set (116 bases, containing the starting ends of primers rc28P and 28P) was missing for many of the GenBank sequences including *Glutops rossi*, *Leptynoma hessei*, *Pelecorhynchus personatus*, *Tabanus atratus*, *Vermileo opacus*, *Pachygaster leachii*, and *Pantophthalmus* sp. Parts of this region was also missing for *Chrysopilus quadratus* (base pairs 480-537; a total of 58bp), *Coenomyia ferruginea* (504-524; 21bp), and *Dialysis elongata* (base pairs 464-551; 88 bp). The region about site 1770 of the aligned sequence is another area of relatively small regions of missing sequence for *Chrysops* sp. (new sequence; 1735-1789; 55bp), *G. rossi* (1735-

1805; 71bp), *Heterostomus* sp. (new sequence from B. Wiegmann; 1766-1798; 33 bp), *L. hessei* (1735-1849; 115bp), *P. personatus* (1734-1806; 73bp), *Tabanus rufofrater* (1735-1805; 71bp), *V. opacus* (1735-1811; 77bp), *P. leachii* (1721-1805; 85bp), and *Pantophthalmus* sp. (1735-1805; 71bp). The *Tabanus atratus* sequence also lacks a large part of sequence containing this area (1735-2293; 259bp). The *Atherix variegata* sequence ends at site 2744. *E. angustifrons*, *G. rossi*, and *V. opacus* ends are slightly shorter (ending at base pair 3078, 3071, and 3055), respectively than all of the other sequences which are cut at the 5' end at base pair 3102 of the aligned sequence.

The alignment is a process of determining homology between sequence sites and can have a large influence on the ultimate phylogeny produced. The structure of the 28S sequences is well known to have areas that are highly conserved and areas that are more free to vary due to the secondary structure of the molecule, consisting of stems and loops, respectively. Most of the 28S rDNA molecule is highly conserved and therefore, easily aligned. Within regions of the alignment that are subject to higher rates of evolution, phylogenetic signal is retained to varying degrees or lost entirely. Regions where phylogenetic signal is retained may be important to include so that tips of the branches may be more accurately resolved among closely related taxa, even though across other parts of the taxon sample the molecule may be saturated. At what point does saturation undermine homology assessment for phylogenetic analysis?

Generally, researchers invoke their own authority for deciding such matters. In some cases, any perceived uncertainties in the alignment process are excised from the phylogenetic analysis. Presumably, there is enough phylogenetic information within the more conserved regions to yield a biologically relevant phylogenetic tree. But are the results of these analyses compromised by the loss of phylogenetically useful information? May the baby thrown out with the bathwater using this approach?

On the other hand, allowing saturated positions in the analysis are certain to introduce additional noise, or even worse, may incorporate investigator bias that overrides true phylogenetic signal.

Where is the balance between maximizing phylogenetic information and minimizing noise and bias? An explicit approach was taken here to investigate this further, in a two step process. The first is to classify regions of the sequence according to the degree of saturation and difficulty of alignment. The second step is to evaluate the utility of these regions for phylogenetic analysis.

Ideally, the first step of this process would employ a model to quantify the amount of saturation of a given site, across the data set. Such a model would take several factors into account. First, it would detect accelerated rates of evolution within the molecule, presumably correlated with secondary structure loops. This may be inferred from secondary structure modeling or by other means, such as estimating evolutionary rates of specific sites given a tree, or manually designated as a region of alignment

ambiguity by the user. Once loop regions are identified, these are excluded and a maximum likelihood search is carried out to generate a phylogeny that may be used as the underlying topology for the homoplasy calculation. This would be an important component of the model since there is a correlation between character homoplasy and difficulty of homology assessment (i.e., alignment). The alignment of a constant site, for example, is trivial yet as steps are added to the site, the alignment becomes increasingly difficult. Therefore, some measure of homoplasy would be factored into the model as an indication of homology assessment uncertainty due to homoplasy.

Another aspect affecting alignment is the frequency of gaps. Alignment uncertainty is often associated with highly gapped characters and this uncertainty is not reflected in the homoplasy index. For example, characters of a saturated insertion present in two species will have a consistency index value of 1. Therefore, a correction must be incorporated into the model that accounts for the uncertainty of homology assessment due to the insertion of gaps.

The reliability of homology assessment may also be affected by neighboring sites. Sites that involve gaps or other uncertainties may invoke alternative alignments that affect the stability of homology assessment of neighboring sites. A character that has few gaps and a moderate level of homoplasy, for example, may intuitively have differing levels of certainty of homology depending on whether or not its neighbors

on each side are constant across the taxon set or are contained within a secondary structure loop.

The interaction and relative weights of model components for determining relative alignment uncertainty in an objective manner is a difficult proposition and a work in progress. Incorporating the secondary structure of ribosomal DNA into the alignment may be alternative to devising such a model. Mapping secondary structure is an arduous process however, that does not guarantee an improved alignment.

With a model approach in mind, characters were classified according to the degree of saturation and difficulty of alignment. This was done using the following methodology and criteria. First, sequences were arranged in congeneric clusters of no particular order and the base pairs were aligned by eye. Regions exhibiting increased rates of evolution were identified by eye and removed for a preliminary phylogenetic analysis using maximum likelihood. This preliminary analysis produced a biologically reasonable topology that was used as a guide to place close related taxa adjacent to one another in the alignment. The alignment was further refined by eye. The taxa were then arranged in alphabetical order and another pass of alignment refinements were made by eye. A second preliminary phylogenetic analysis was undertaken and the taxa were placed near closest relatives in the alignment, as indicated by the resulting topology.

Characters within regions of the molecule that exhibited accelerated rates of evolution were then classified as 'lowambig,' 'modambig,' 'highambig,'or 'unalign' based on the degree of uncertainty associated with their alignment, as determined by the ease of alignment between increasingly distantly related taxa. Areas exhibiting variation that was easy to align within closely related groups and across most of the taxon set designated as 'lowambig.' Areas of the sequence that were easily aligned between related groups, but more challenging to align between more distantly related groups were categorized as 'modambig.' Areas alignable only among close relatives were designated as 'highambig' sites. Characters that were unalignable even among closely related taxa were classified as 'unalign' and discarded for all analyses. All of these classifications of alignment ambiguity were done by eye, as an objective model has not been developed for such a process. Classifications were compared against one another for consistency across the alignment, and necessary modifications were made, as appropriate, to maintain adherence to the classification criteria listed above. The full alignment including all regions is archived in TreeBase (www.treebase.org).

The next step was to evaluate the utility of these regions for phylogenetic analysis. First, the effects of differing alignment decisions were explored by creating eight separate, successively more conservative matrices from the complete data set. Unambiguously aligned regions were included for all analyses. The data matrices created were as follows:

1) Only 'unalign' regions excluded; all other regions included (Alignment Set 1 (AS#1)).

2) ‘Ends’ and ‘unalign’ regions excluded; all other regions included (AS#2).

3) ‘Highambig’ and ‘unalign’ regions excluded; all other regions included (AS#3).

4) ‘Ends,’ ‘Highambig,’ and ‘unalign’ regions excluded; all other regions included (AS#4).

5) ‘Modambig,’ ‘Highambig’ and ‘unalign’ regions excluded; all other regions included (AS#5).

6) ‘Ends,’ ‘Modambig,’ ‘Highambig’ and ‘unalign’ regions excluded; all other regions included (AS#6).

7) ‘LowAmbig’ ‘Modambig,’ ‘Highambig’ and ‘unalign’ regions excluded; all other regions included (AS#7).

8) ‘LowAmbig’ ‘Ends,’ ‘Modambig,’ ‘Highambig’ and ‘unalign’ regions excluded; all other regions included (AS#8).

For each alignment set, a maximum parsimony heuristic search (tbr, nreps=1000) was conducted to generate one or more equally most parsimonious trees (MPTs). A strict and majority rule consensus tree was then calculated from this collection of trees for each alignment set (if there was only one MPT, this step was unnecessary).

A clear manner to decide upon the best alignment set is not immediately obvious. Since the number of characters varies between alignment sets, parsimony scores cannot be compared directly. Bootstrap values for these datasets, however, may be informative. A bootstrap analysis was conducted for each alignment set and a

bootstrap (majority rule) consensus tree was created. Bootstrap consensus trees and most parsimonious consensus trees were then compared for each alignment set. The fidelity in recovering bootstrap-supported most parsimonious trees may be an indication of the degree of internal consistency within the data. To quantify this consistency in a way that could be compared between alignment sets, the number of nodes present in both the bootstrap support consensus tree and the most parsimonious strict consensus tree was counted for each alignment set. Nodes present in both the bootstrap support consensus and most parsimonious majority rule (MR) tree were also counted for each alignment set as a secondary measure. The alignment set with the highest overlap between bootstrap and most parsimonious consensus trees, as counted by the number of shared nodes, was determined as the most internally consistent data set and chosen as the data set for all subsequent phylogenetic analyses.

Phylogenetic Analysis

Phylogenetic analyses were performed using two computer programs, on both PC and Macintosh operating systems. PAUP* 4.0b10 (Swofford 2002) was used for both maximum parsimony (MP) and maximum likelihood (ML) phylogenetic analyses.

For parsimony analyses, characters were unordered and assigned equal weights at all sites (Fitch, 1971). Heuristic search replicates (n = 1000) were performed with random-taxon-addition, tree bisection reconnection (TBR) branch swapping, steepest descent and 'MulTrees' options in effect. Scores of all MP trees were verified to avoid artifactually inflated sets of MP trees.

Modeltest 3.06 (Posada and Crandall, 1996) was used to select among 56 nested models of sequence evolution. Under the Akaike information criterion (AIC), the best fitting model was found to be the general-time-reversible model with invariant sites and gamma distributed rates for variable sites (GTR+I+Γ). An iterative series of searches were then performed to re-estimate the parameters until the parameters stabilized. A maximum likelihood heuristic search was conducted, using this model and the parameters estimated by Modeltest, with five random taxon addition sequences, tree-bisection reconnection (TBR) branch swapping, and steepest descent option active. The resulting tree provided the basis for re-estimating the parameters. The ML search and re-estimation of parameters based on the most likely tree was carried out again, as the parameters converged on identical values. These parameter values were used for ML analyses.

In order to gauge the internal consistency of the data, bootstrap analyses (Felsenstein 1985) were carried out. Parsimony bootstrap analyses were performed with 1000 repetitions, each with 30 random-taxon-addition TBR heuristic searches. ML bootstrap analyses were performed with 100 repetitions, each with three random-taxon-addition NNI heuristic searches.

Tests of alternative hypotheses using Maximum Parsimony

Hypotheses regarding the monophyly and placement of the Pelecorhynchidae, Vermileonidae, *Bolbomyia*, *Austroleptis*, and Rhagionidae were tested in light of the molecular evidence. This was done by constraining nodes to conform to hypothesized arrangements. Heuristic searches were then carried out, enforcing the constrained

nodes. The length of resulting most parsimonious trees constrained to fit each hypothesis was then compared with the most parsimonious unconstrained trees. Hypotheses were evaluated by the number of additional steps they incur on the data; greater additional steps indicate less concordance with the molecular data. The Kishino-Hasegawa and Wilcoxon sign-rank tests were also applied using PAUP* to compare constrained and unconstrained trees to determine if the hypotheses predicted signficantly different arrangements than what was found given the molecular data.

Results

Alignment region classification

Most of the 28S rDNA molecule is highly conserved and unambiguously aligned. The sizes of the regions subject to higher rates of evolution are listed in Table XX, by alignment classification type.

Table 3. Alignment region classifications.

Alignment classification	Total bp
Unambiguously aligned	2779
'Lowambig'	39
'Modambig'	123
'Highambig'	47
'Ends'	56
'Unalign'	190

Effects of alignment

The results of most parsimonious tree searches for each of the eight alignment sets are summarized in Table 4. The average pairwise genetic distances between each species and the rest of the sampled taxa, for the entire character matrix excluding the unalignable regions are shown in Table 6. The tabanids and stratiomyiomorph outgroups *Pachygaster leachii* and *Pantophthalmus* sp. are the most divergent (Table 7). The deviation from the mean of the average pairwise differences did not appear to change as the number of characters varied (no statistics applied however). From the bootstrap analyses, AS#4 was determined as the most internally consistent data set (Table 8).

Table 8. Relationships among the major taxa, evident in the Maximum Parsimony majority rule consensus trees of different alignment sets (AS).

excluded character sets of AS	**No. of MPTs**	**Tabanomorpha monophyly/ paraphyly**	**Sister group of Vermileonidae**	**Sister group of *Austroleptis***	**Sister group of *Bolbomyia***	**No. of resolved strict consensus nodes**
1. unalign	6	paraphyletic	Rhagionidae, *sensu lato*	Rhagioninae	*Austroleptis* + Rhagioninae	37
2. Ends, unalign	6	paraphyletic	Rhagionidae, *sensu lato*	Rhagioninae	*Austroleptis* + Rhagioninae	37
3. Highambig unalign	30	monophyletic	*Austroleptis* + Rhagioninae	Rhagioninae	Vermileonidae + (*Austroleptis* + Rhagioninae)	31
4. Ends, highambig unalign	6	monophyletic	*Bolbomyia*	Rhagioninae	Vermileonidae	36
5. Modambig, highambig, unalign	54	paraphyletic	Rhagioninae	(Spaniinae + Chrysopilinae) + (*Bolbomyia*+ (Rhagioninae + Vermileonidae))	Rhagioninae + Vermileonidae	30
6. Ends, modambig, highambig, unalign	21	paraphyletic	*Bolbomyia*	(Rhagioninae + (Spaniinae + Chrysopilinae)) + (*Bolbomyia*+ Vermileonidae)	Vermileonidae	32

excluded character sets of AS	No. of MPTs	Tabanomorpha monophyly/ paraphyly	Sister group of Vermileonidae	Sister group of *Austroleptis*	Sister group of *Bolbomyia*	No. of resolved strict consensus nodes
7. Lowambig, modambig, highambig, unalign	36	monophyletic	Rhagioninae + (Spaniinae + Chrysopilinae)	rest of Tabanomorpha	Tabanoidea	36
8. Ends, lowambig, modambig, highambig, unalign	27	monophyletic	Rhagioninae + (Spaniinae + Chrysopilinae)	rest of Tabanomorpha	Tabanoidea	27

Table 9. Relationships among the major taxa, evident in the Maximum Likelihood trees of different alignment sets (AS).

Alignment sets	Sequence length (bp)	Tabanomorpha monophyly/ paraphyly	Sister group of Vermileonidae	Sister group of *Austroleptis*	Sister group of *Bolbomyia*
1. Only unalign regions excluded	2944	monophyletic	Rhagionidae, *sensu lato*	Rhagioninae + (Chrysopilinae + Spaniinae)	*Austroleptis* (Rhagioninae + (Chrysopilinae + Spaniinae))
2. Ends and only unalign excluded	2888	monophyletic	Rhagionidae, *sensu lato*	Rhagioninae + (Chrysopilinae + Spaniinae)	*Austroleptis* (Rhagioninae + (Chrysopilinae + Spaniinae))
3. Highambig and unalign regions	2873	monophyletic	rest of	Rhagioninae +	Tabanoidea

Alignment sets	**Sequence length (bp)**	**Tabanomorpha monophyly/ paraphyly**	**Sister group of Vermileonidae**	**Sister group of *Austroleptis***	**Sister group of *Bolbomyia***
excluded			Tabanomorpha	(Chrysopilinae + Spaniinae)	
4. Ends, highambig and unalign regions excluded	2817	monophyletic	rest of Tabanomorpha	Rhagioninae + (Chrysopilinae + Spaniinae)	Tabanoidea
5. Modambig, highambig, and unalign regions excluded	2774	paraphyletic	*Bolbomyia* (together, they	Xylophagidae	Vermileonidae
6. Ends, modambig, highambig, and unalign regions excluded	2718	paraphyletic	*Bolbomyia* (together, they	Xylophagidae	Vermileonidae
7. Lowambig, modambig, highambig, and unalign regions excluded	2735	monophyletic	*Bolbomyia* + Tabanoidea	rest of Tabanomorpha	Tabanoidea
8. Ends, lowambig, modambig, highambig, and unalign regions excluded	2679	monophyletic	*Bolbomyia* + Tabanoidea	rest of Tabanomorpha	Tabanoidea

Table 10. Average pairwise genetic distance between each species and the rest of the sampled set. All characters included except the 'unalign' character set (AS #1). The mean of all pairwise distances is 0. 06139372.

Species	Avg vs. all other taxa	Deviation from mean
Arthropeas magnum	0.05553619	(0.0058575)
Atherimorpha atrifemur	0.054439048	(0.0069547)
Atherimorpha sp. 1 (South America)	0.055517143	(0.0058766)
Atherimorpha sp. 2 (Australia)	0.052862619	(0.0085311)
Atherimorpha sp. 3 (Australia)	0.050461429	(0.0109323)
Atherimorpha vernalis	0.052245714	(0.0091480)
Atherix variegata	0.078396905	0.0170032
Austroleptis multimaculata	0.060189048	(0.0012047)
Austroleptis rhyphoides	0.053920952	(0.0074728)
Austroleptis collessi	0.056150000	(0.0052437)
Bolbomyia nana	0.052441190	(0.0089525)
Chrysopilus quadratus	0.051426667	(0.0099671)
Chrysopilus thoracicus	0.058680000	(0.0027137)
Chrysopilus sp. 1 (Ecuador)	0.059182857	(0.0022109)
Chrysopilus sp. 2 (Australia)	0.050049048	(0.0113447)
Chrysopilus sp. 3 (Tasmania)	0.050351429	(0.0110423)
Chrysopilus sp. 3 (Tasmania)	0.050632857	(0.0107609)
Chrysops sp.	0.075362619	0.0139689
Coenomyia ferruginea	0.061550952	0.0001572
Dasyomma sp. 1 (Chile)	0.077999524	0.0166058
Dasyomma sp. 2 (Chile)	0.077398810	0.0160051
Dialysis elongata	0.059441905	(0.0019518)
Exeretonevra angustifrons	0.073409762	0.0120160
Glutops rossi	0.060331429	(0.0010623)
Heterostomus sp.	0.056274048	(0.0051197)
Leptynoma hessei	0.064375000	0.0029813
Pelecorhynchus personatus	0.071864762	0.0104710
Ptiolina fasciata	0.050122857	(0.0112709)
Rhagio hirtus	0.057822381	(0.0035713)
Rhagio mystaceus	0.059472619	(0.0019211)
Spaniopsis clelandi	0.054455476	(0.0069382)
Spaniopsis longicornis	0.053835238	(0.0075585)
Symphoromyia atripes	0.056689762	(0.0047040)
Symphoromyia hirta	0.055975238	(0.0054185)

Species	Avg vs. all other taxa	Deviation from mean
Symphoromyia sp. (Alaska)	0.051126429	(0.0102673)
Tabanus atratus	0.077501905	0.0161082
Tabanus rufofrater	0.089475238	0.0280815
Tabanus sp.	0.082094762	0.0207010
Vermileo opacus	0.053200238	(0.0081935)
Vermileo sp.	0.056690476	(0.0047032)
Xylophagus abdominalis	0.067588333	0.0061946
Pachygaster leachii	0.080747619	0.0193539
Pantophthalmus sp.	0.072639524	0.0112458

Table 11. Average pairwise genetic distance between each clade and the rest of the sampled set. All characters included except the 'unalign' character set (AS #1).

Clades	Avg pairwise distance vs. all other taxa	Avg. deviation from the mean
Outgroup	0.076693571	0.01529985
Xylophagidae	0.062300198	0.00090648
Tabanoidea	0.073573615	0.01217989
Vermileonidae	0.058088571	(0.00330515)
Rhagioninae	0.054688707	(0.00670501)
(Chrysopilinae + Spaniinae)	0.053543988	(0.00784973)
Bolbomyia	0.052441190	(0.00895253)
Austroleptis	0.056753333	(0.00464039)

Table 12. Overlap between most parsimonious consensus trees and bootstrap consensus trees. The highest overlap between all compatible majority rules consensus trees and bootstrap consensus trees occurs in alignment sets 3, 4, and 6. The highest overlap between strict consensus and bootstrap consensus trees occurs in alignment set #4.

Alignment sets (ASs)	**Sequence length**	**No. of MPTs**	**No. of Strict / MR consensus nodes consistent with bootstrap (all compatible) consensus tree**	**Clades with > 50% bootstrap values in strict consensus (bootstrap value)**
1. Only unalign regions excluded	2944	26	33 / 36	-
2. Ends and only unalign excluded	2888	6	33 / 36	-
3. Highambig and unalign regions excluded	2873	30	31 / 38	Monophyly of Tabanomorpha (68)
4. Ends, highambig and unalign regions excluded	2817	6	36 / 38	Monophyly of Tabanomorpha (65)
5. Modambig, highambig, and unalign regions excluded	2774	54	30 / 36	-
6. Ends, modambig, highambig, and unalign regions excluded	2718	21	32 / 38	-
7. Lowambig, modambig, highambig, and unalign regions excluded	2735	36	32 / 36	Monophyly of Tabanomorpha (69)
8. Ends, lowambig, modambig, highambig, and unalign regions excluded	2679	27	35 / 37	Monophyly of Tabanomorpha (71)

Maximum Parsimony Analysis of Molecular Dataset

Within Tabanoidea, the Pelecorhynchidae (*G. rossi* and *P. personatus*), Athericidae (*A. variegata* and *Dasyomma* spp.), and Tabanidae (*Tabanus* spp. and *Chrysops* sp.) are shown to be monophyletic, with Athericidae and Tabanidae sister taxa (Fig. 2). *Vermileo* is shown to be paraphyletic with respect to *Leptynoma hessei* in all analyses. In the Rhagioninae, both *Rhagio* and *Atherimorpha* are monophyletic, and within *Atherimorpha*, there are two monophyletic clades, consisting of South American and Australian species, respectively. Within Chrysopilinae, species of *Chrysopilus* are formed by monophyletic New World and Australian clades. Chrysopilinae is sister to the Spaniinae. Within Spaniinae, *Ptiolina* is recovered basal to sister genera *Spaniopsis* and *Symphoromyia*. *Bolbomyia* is recovered as sister to the vermileonids in the strict consensus. However, this relationship is only supported by a 20% bootstrap value. The internal relationships of each of these eight clades, where resolved, is consistent throughout all analyses, except for the Xylophagomorpha where there are varying internal relationships across the trees and the entire group is sometimes shown as paraphyletic (in alignment sets 7 and 8).

For all figures, the current taxonomic placement of each species is indicated in parenthesis next to the taxon name. A summary of the taxonomic abbreviations is presented in Table 10. The most parsimonious tree found for AS #4 is presented in Fig. 2.

Eight clades of the ingroup (exclusive of the stratiomyiomorphs *Pachygaster leachii* and *Pantophthalmus* sp.) were consistently recovered in all analyses (regardless of alignment), although the particular relationships between these clades were not. To facilitate reporting of the results and subsequent discussion, I will refer to these eight clades that are of interest. These are the Tabanoidea, Xylophagomorpha, Vermileonidae, Rhagioninae, Spaniinae, *Bolbomyia*, and *Austroleptis* (Table 9).

Table 13. Clades of interest.

Clade of interest	Taxonomic rank of clade	Taxa included in clade
Xylophagomorpha	Infraorder	Xylophagidae
Tabanoidea	Superfamily	Athericidae, Tabanidae, Pelecorhynchidae
Vermileonidae	Family	Vermileonidae (e.g., *Vermileo* and *Leptynoma*)
Rhagioninae	Subfamily	*Rhagio*, *Atherimorpha* (and related genera not represented in the molecular data set)
Spaniinae	Subfamily	*Ptiolina*, *Spania*, *Spaniopsis*, *Symphoromyia*
Chrysopilinae	Subfamily	*Chrysopilus* (and related genera not represented in the molecular data set)
Austroleptis	Genus (family?)	*Austroleptis*
Bolbomyia	Genus (family?)	*Bolbomyia*

Since Xylophagomorpha consists of a single family, the Xylophagidae, I may use these two terms interchangeably in reference to the same clade. The Xylophagomorpha in this sample includes *Arthropeas magnum*, *Coenomyia ferruginea*, *Dialysis elongata*, *Exeretonevra angustifrons*, *Heterostomus* sp., and *Xylophagus abdominalis*.

Hennig (1973) and others (McAlpine, 1981) have called the Tabanoidea the group that I consider the infraorder Tabanomorpha (Woodley, 1989). I consider the Tabanoidea in a new sense, as a superfamily that includes the families Pelecorhynchidae, Tabanidae, and Athericidae. In this sample, the tabanoid species are *Atherix variegata*, *Chrysops* sp., all species of *Dasyomma, Glutops rossi*, *Pelecorhynchus personatus*, and all species of *Tabanus*.

The subfamily Rhagioninae is recognized in a new sense here and includes only close relatives of *Rhagio*, and their relatives. For this sample, the rhagionines are represented by *Rhagio* and *Atherimorpha*.

The subfamily Spaniinae is also recognized in a new sense here. Spaniinae is defined by a synapomorphy present in the female terminalia which I will discuss below. In this sample, the Spaniinae includes *Ptiolina*, *Symphoromyia*, *Spania* and *Spaniopsis*.

The final two clades of interest are each represented by single genus, *Bolbomyia* and *Austroleptis*.

The average pairwise genetic distance between each of these clades and the rest of the sampled taxa is shown in Table 7.

Table 14. Taxonomic abbreviations.

Abbreviation	Family	Infraorder
Ath	Athericidae	Tabanomorpha
Pel/Rhag	Pelecorhynchidae *sensu* Woodley, 1989 or Rhagionidae *sensu* Stuckenberg 2001	Tabanomorpha
Rhag	Rhagionidae	Tabanomorpha
Tab	Tabanidae	Tabanomorpha
Rhag/Aust	Rhagionidae *sensu* Woodley, 1989 or Austroleptidae *sensu* Stuckenberg 2001	Tabanomorpha
Rhag/Span	Rhagionidae *sensu* Woodley, 1989 or Spaniidae *sensu* Stuckenberg 2001	Tabanomorpha
STR-Pant	Pantophthalmidae	Stratiomyomorpha
STR-Strat	Stratiomyiidae	Stratiomyomorpha
Verm	Vermileonidae	Tabanomorpha or Vermileonomorpha
XYL	Xylophagidae	Xylophagomorpha

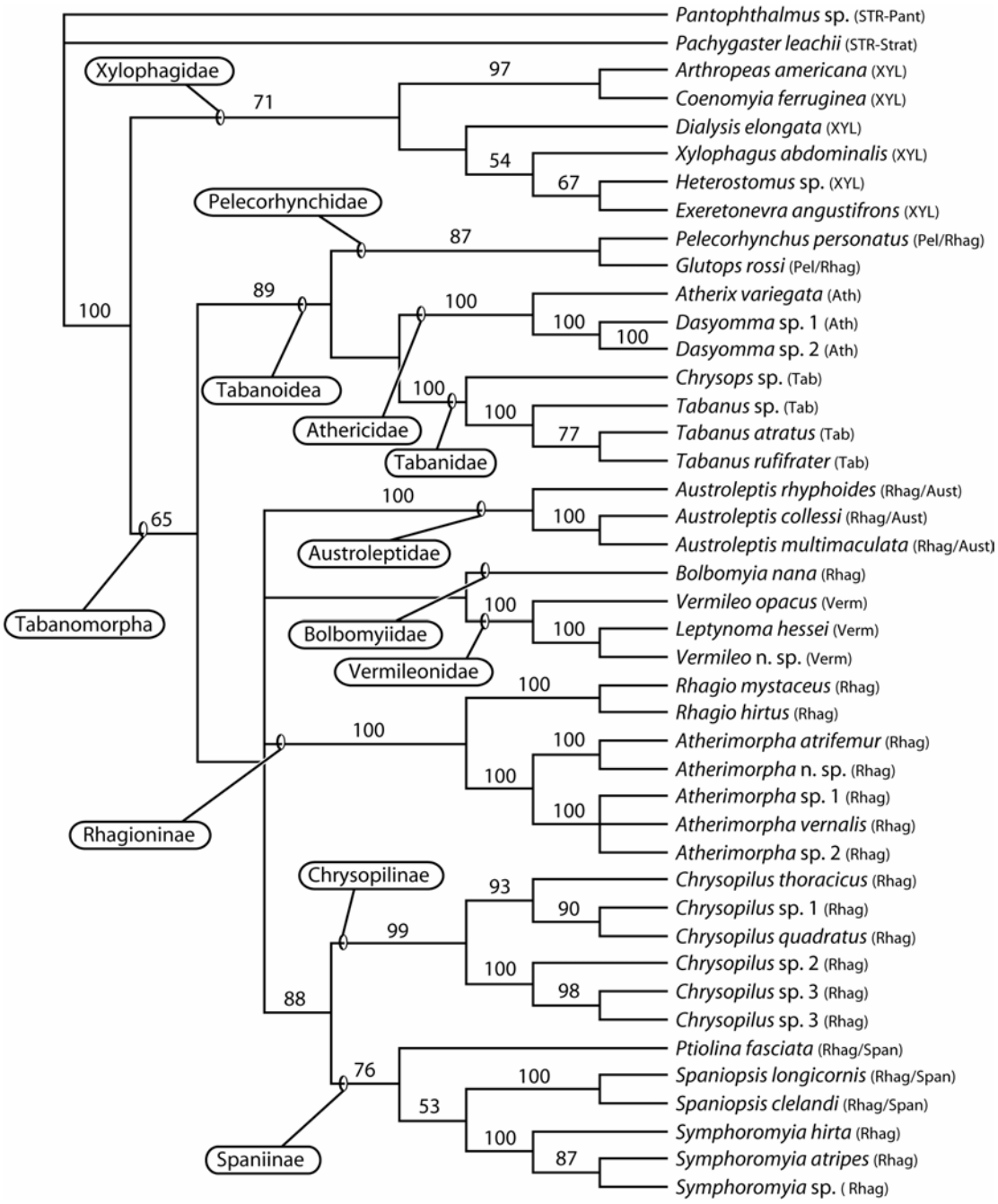


Figure 5. Maximum Parsimony analysis of 28S rDNA data (AS #4). Strict consensus of 6 most parsimonious trees. Bootstrap values ≥ 50% are noted above supported branches (TBR, nreps = 1000 / addseq reps = 10).

Maximum Likelihood Analysis of Molecular Dataset

In all of the trees, the eight major groups of interest (Table 9) were recovered as in MP analysis. The ML tree for AS # 4 is given in Fig. 3. The relationships within these groups are the same for all analyses. Within Xylophagidae, there are two clades. *D. elongata* is the sister to *A. magnum* + *C. ferruginea* in one clade and *X. abdominalis* is sister to *E. angustifrons* + *Heterostomus* sp. in the other. Each of the three tabanoid families is recovered as monophyletic, as are all genera. The Pelecorhynchidae are basal to Athericidae + Tabanidae. Within the Vermileonidae, *Vermileo* is recovered as paraphyletic with respect to *L. hessei* in all analyses. Rhagioninae retain a monophyletic *Rhagio* and *Atherimorpha* in the ML analyses, with *Atherimorpha* composed of a monophyletic South American and Australian clade, respectively. In Chrysopilinae, *Chrysopilus* spp. are divided into two clades, composed of Australian and New World species, respectively. The Chrysopilinae is sister to the Spaniinae, which show *P. fasciata* sister to *Spaniopsis* spp. + *Symphoromyia* spp.

The way in which each of these eight lineages are related to one another is unclear, except in regards to the relationship of Rhagioninae + (Chrysopilinae + Spaniinae) which is recovered in all analyses (regardless of alignment). This provides evidence in support of a monophyletic Rhagionidae, exclusive of *Bolbomyia* and *Austroleptis*. In the alignment chosen, Vermileonidae are sister to the rest of the Tabanomorpha, which is divided into two lineages. One is composed of *Bolbomyia* + Tabanoidea.

The other recovers *Austroleptis* sister to Rhagionidae (Rhagioninae, Chrysopilinae, and Spaniinae).

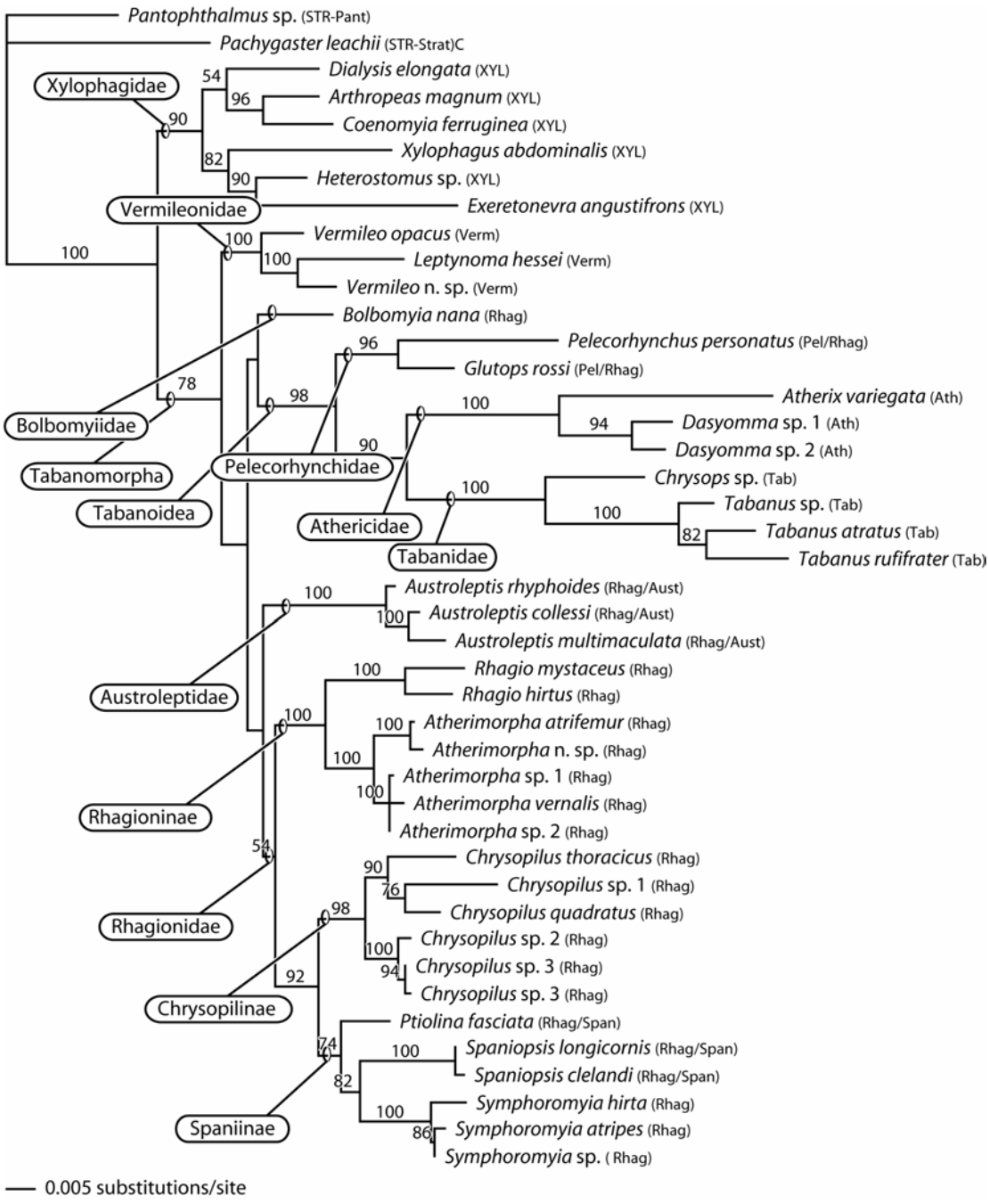


Figure 6. Maximum Likelihood analysis of 28S rDNA data (AS #4). Bootstrap values ≥ 50% are noted above supported branches (NNI, nreps = 50 / addseq reps = 3).

Discussion

Exploring the effects of alignment

Ultimately, the most desired sequence alignment is maximally phylogenetically informative yet minimally affected by noise and bias from non-phylogenetic sources. While this is self-evident in a theoretical framework, realizing such an ideal requires difficult practical decisions when working with a large, complex molecular dataset.

Perhaps the only justifiable alignment for use in phylogenetic analysis is one that excludes all sites where the homology is not certain. However, although rates may vary within a gene, such as is apparent for 28S rDNA, areas experiencing faster rates have not necessarily reached saturation for all taxa. Saturation in parts of the alignment may not preclude information for determining relationships among closer groups, where saturation has not yet been reached. Deciding at what point portions of the dataset ought to be removed on the basis of alignment is not clear in all cases. This may be important particularly for ribosomal DNA genes, where inherent evolutionary constraints associated with the secondary structure of the molecule produce regions of highly conserved sequence side-by-side with regions that are more free to vary. The molecule in its entirety may carry phylogenetic information, but the signal present in conserved regions alone may not be strong enough to be recognized amid natural phylogenetic noise. Furthermore, different methods of phylogenetic inference may have differing abilities to tolerate noise within a sample, so that the point at which a site should be excluded on the basis of uncertain homology

assessment may also differ, for example, depending on whether Maximum Parsimony or Maximum Likelihood methods are used.

Evaluating the Alignment Sets.

It is hard to evaluate the various alignment sets objectively, as the phylogenetic signal of the data set is heterogeneous in unpredictable ways, leading to uneven contributions of signal. Even though the datasets have been divided into increasingly smaller sets (from AS#1-8), the amount of signal does not necessarily taper at the smallest part of this range, in a corresponding manner. The 'noise' of the data may also similarly vary among the alignment sets, according to which sites are included, rather than the overall size of the data set. It can be argued, however, when the internal consistency of the data is higher, noise in the data will be minimized. Bootstrapping is a measure of the internal consistency of the data and may therefore provide a way in which two data matrices (developed from the same data set, but different due to different alignment decisions) may be evaluated for phylogenetic utility. The true alignment, like the true tree, is not known so gauging phylogenetic accuracy of one alignment over the other is a tricky proposition. The effects of various alignment decisions cannot be simply ignored, however, particularly with a variable-rate molecule such as large subunit rDNA. Homology assessment in molecular data is a very important step in developing robust phylogenetic hypotheses. A modest new method for choosing one alignment over the other has been presented here as a first attempt to both acknowledge the problem and treat it in an objective manner. Certainly this is an aspect of molecular systematics that needs much more attention.

Assessment of the Most Parsimonious Trees

Although it may not be immediately clear which of the 8 alignment sets most accurately reflects the common evolutionary history of the taxon set, several common themes become apparent in the parsimony analysis.

First, the composition of most nodes of the tree is maintained throughout all alignments. The formation and resolution of the Rhagioninae, Chrysopilinae, Spaniinae, Tabanoidea, and Vermileonidae is consistent throughout all 143 most parsimonious trees, totaled among all of the alignments. There is also consistency of alignment sets in regards to the basal nodes of the Tabanomorpha lineage. Alignment schemes did not affect support levels for these nodes; in all analyses, there is weak support at the base of the Tabanomorpha lineage. The relationships among the major tabanomorph clades, including *Austroleptis* and *Bolbomyia* at best, remain weakly supported. The sister group of each of the major groups remains uncertain.

Pairwise distances are susceptible to the same flaw that allows for long branch attraction; that is, the actual amount of sequence evolution may be underestimated because changes may be overwritten and unrecognized (e.g., a change from A to C, back to A). It is instructive to note, however, that Tabanoidea is comparatively quite distant from the rest of the taxa (Table 7). Comparatively long branches of Tabanoidea and the stratiomyiomorph outgroup taxa may induce maximum parsimony to misinterpret random overlap of sequence between these groups as synapomorphic change. As a result, in a few analyses (not shown), Tabanoidea is

pulled from the rest of the tabanomorph taxa, to a position sister to the Xylophagomorpha, rendering Tabanomorpha paraphyletic. This reconstruction is not recovered in any of the bootstrap consensus trees.

Assessment of the Most Likely Trees

Although there is no overlap between the four most likely trees and any of the most parsimonious trees, produced by all of the alignment data sets, similar patterns emerge in each of the analyses.

As in the MP analysis, the formation and resolution of Rhagioninae, Chrysopilinae, Spaniinae, Tabanoidea, and Vermileonidae remain consistent throughout. Similarly, support levels for nodes at the base of the Tabanomorpha lineage were exceptionally low; this area of the tree is particularly unstable. Unlike in the MP analyses, however, Rhagioninae is consistently recovered as sister taxa to the clade formed by Chrysopilinae and Spaniinae. Although recovered in all ML analyses, this relationship (Rhagioninae + (Chrysopilinae + Spaniinae) has low bootstrap support (55%).

Monophyly of Rhagionidae

Recent concepts of the Rhagionidae are rejected by the molecular evidence. A monophyletic Rhagionidae *sensu* Nagatomi (1982) invokes an additional 31 steps to the most parsimonious tree (Table 10). Similarly, the monophyly of Rhagionidae *sensu* Stuckenberg (2001) requires that 30 steps be added to the most parsimonious arrangement, given the data. Other concepts of the subfamily Rhagioninae (Nagatomi, 1982a; Stuckenberg, 2001) are also inconsistent with the molecular

results. As these are compound hypotheses, it is somewhat easier to discuss why such little support is afforded to them by examining their components. This is done in the following sections.

Table 15. Hypotheses tested in light of molecular evidence.

Concept	Authors	Constraint	Requisite increase in steps (MP)	Wilcoxon Signed-Rank Test (p value)	Kishino-Hasegawa Test (p value)
Monophyly and Position of Pelecorhynchidae					
Rhagionidae includes *Glutops*	Nagatomi, 1982a	*Atherimorpha*+ *Austroleptis* + *Bolbomyia* + *Chrysopilus* + *Glutops* + *Ptiolina* + *Rhagio* + *Symphoromyia* + *Spaniopsis*	31	0.0016*	0.0016*
Rhagionidae includes *Glutops* and *Pelecorhynchus*	Stuckenberg, 2001	*Atherimorpha*+ *Bolbomyia* + *Chrysopilus* + *Glutops* + *Pelecorhynchus* + *Rhagio* + *Symphoromyia*	30	0.0031*	0.0049*
Glutops and *Pelecorhynchus* (with *Pseudoerinna*) form monophyletic unit	Woodley, 1989; Sinclair, 1992; Stuckenberg, 2001	*Glutops* + *Pelecorhynchus*	0	-	-
Position of Vermileonidae					
Vermileonomorpha	Nagatomi, 1977; et al.	Vermileonidae + (Xylophagidae + Tabanomorpha)	13	0.0906	0.0906
Vermileonidae, basal clade of Tabanomorpha	Nagatomi, 1977; Sinclair et al., 1993	(Vermileonidae + (other tabanomorph taxa)	0	-	-

Concept	Authors	Constraint	Requisite increase in steps (MP)	Wilcoxon Signed-Rank Test (p value)	Kishino-Hasegawa Test (p value)
Position of *Bolbomyia*					
Bolbomyia within Tabanoidea	Sinclair et al., 1993	Pelecorynchidae (*Bolbomyia* + (Athericidae + Tabanidae))	20	0.0230*	0.0235*
Bolbomyia sister to Athericidae and Tabanidae	Sinclair et al., 1993	*Bolbomyia* + (Athericidae + Tabanidae)	20	0.0604	0.0610
Bolbomyia in Xylophagomorpha	James, 1965	*Bolbomyia* + Xylophagidae	8	0.1167	0.1167
Unnamed concept defined by lacking M_3 vein	Grimaldi and Cumming, 1999	*Bolbomyia* + *Austroleptis*	3	0.6744	0.7745
Position of *Austroleptis*					
Austroleptinae	Nagatomi, 1982a	(*Austroleptis* + (*Atherimorpha* + *Bolbomyia* + *Chrysopilus* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*))	5	0.4658	0.4659
Austroleptis placement in or sister to Xylophagidae	Sinclair et al., 1994	*Austroleptis* + Xylophagidae	5	0.3980	0.3981
Position and monophyly of Spaniidae					
Spaniinae / Spaniidae (exclusive of *Symphoromyia*)	Nagatomi, 1982a; Stuckenberg, 2001	*Spaniopsis* + *Ptiolina*	3	0.7142	0.7099

Concept	Authors	Constraint	Requisite increase in steps (MP)	Wilcoxon Signed-Rank Test (p value)	Kishino-Hasegawa Test (p value)
Composition of Rhagioninae					
Rhagioninae	Nagatomi, 1982a	*Atherimorpha* + *Bolbomyia* + *Chrysopilus* + *Rhagio* + *Symphoromyia*	22	0.0470*	0.0428*
Rhagioninae	Stuckenberg, 2001; et al.	*Atherimorpha* + *Chrysopilus* + *Rhagio* + *Symphoromyia*	17	0.1113	0.1066
Chrysopilus within Rhagioninae	Nagatomi, 1982a; et al.	*Chrysopilus* + (*Rhagio* and *Atherimorpha*)	10	0.2102	0.2114
Chrysopilus sister to *Rhagio*	-	*Chrysopilus* + *Rhagio*	19	0.0502	0.0512

Monophyly and composition of Pelecorhynchidae

Various hypotheses have been presented for the composition and placement of *Glutops* and *Pelecorhynchus* (Mackerras and Fuller, 1942; Teskey, 1970; Krivosheina, 1971; Nagatomi, 1982a; Woodley, 1989; Sinclair, 1992; Wiegmann et al., 2000; Stuckenberg, 2001; among others). Perhaps it should not be too surprising that the pelecorhynchid genera are recovered here as a monophyletic unit, sister to the Athericidae and Tabanidae, confirming the results of Wiegmann et al. (2000). The Wiegmann et al. study (2000) however used a smaller fragment of the molecule and examined the question only in terms of a single MP analysis. Here, the relationship is confirmed by both ML and MP analyses, in a way that may refute contentions that a biased alignment may have affected the results. Support values for this relationship are similar across alignment sets and similar to those found by Wiegmann et al. (2000).

These results appear to contradict the hypotheses that *Glutops* belongs in its own genus (Krivosheina, 1971); that *Glutops* is a part of Rhagionidae, exclusive of *Pelecorhynchus* (Nagatomi, 1982a); and that *Glutops* and *Pelecorhynchus* form a monophyletic group within the rhagionid lineage (Stuckenberg, 2001).

Monophyly and composition of Chrysopilinae and Spaniinae

In all analyses, *Chrysopilus* was placed as sister to *Ptiolina*, *Spaniopsis*, and *Symphoromyia*. The bootstrap values for this placement ranged from 62-100% in ML and 56-99% in MP. The lowest of these bootstrap values were recovered in alignments that generally had weak tree support throughout (AS #5 in ML, and AS #5

and AS#6 in MP). *Ptiolina* and *Spaniopsis* have been recognized as members of the Spaniinae (Nagatomi, 1982a; others) or as Spaniidae (Stuckenberg, 2001). However, the molecular data makes this pairing paraphyletic with respect to *Symphoromyia* in all analyses. Although only three additional steps are required to force *Ptiolina* and *Spaniopsis* together in the MP analysis (using AS # 4), bootstraps supporting a *Symphoromyia* and *Spaniopsis* sister group relationship are typically above 50% (appx. 73-78% in ML, 53% - 81% in MP). *Symphoromyia* has not been grouped with *Ptiolina* and *Spaniopsis* in the modern era although the genus was originally established by Frauenfeld to clarify the distinction of species that had been mistakenly placed in *Ptiolina*. *Symphoromyia* differs from *Spaniopsis* and *Ptiolina* in several aspects, most conspicuously in the form of the antenna, but these genera share a special resemblance in their compact habitus, which is difficult to describe. The same cannot be said about *Chrysopilus*, which has never been mistaken for any of the typical spaniine genera. Yet forcing *Chrysopilus* into the Rhagioninae, its traditional affiliation, adds 10 additional steps to the tree. Given this result, it is expected that morphological evidence may be found to support the relationship between *Chrysopilus* and the spaniine genera (including *Symphoromyia*). The morphological analysis that follows will discuss this further and provide new evidence that may independently support sister group relationship between Chrysopilinae and Spaniinae.

Bolbomyia

The position of *Bolbomyia* is unstable among the basal branches of Tabanomorpha. It may be recovered as sister to any of the major tabanomorph groups and none of these

relationships are strongly supported. Several hypotheses regarding its placement, however, apparently may be rejected.

The first is that *Bolbomyia* is sister to the Athericidae and Tabanidae (Sinclair et al., 1993). When the data are constrained to this relationship, an additional 20 steps are forced upon the most parsimonious arrangement. This suggests that aedeagal tines of the male genitalia may be homoplasious and the tines in *Bolbomyia* are not homologous to those in Athericidae and Tabanidae, as Sinclair et al. have asserted (1993).

Loew (1850) originally placed *Bolbomyia* in the Xylophagidae, a position that James (1965) retained in the Catalog of the Diptera of America North of America. Although the Xylophagidae concept of Loew and James were from different each other, and different from the Xylophagidae of today, *Bolbomyia* does not have a bulbous clypeus, a typical tabanomorph character and speculation may remain whether or not this genus belongs within the Tabanomorpha. When *Bolbomyia* is constrained as a xylophagomorph, eight steps are added to the most parsimonious tree. This is a clearly a less parsimonious arrangement for *Bolbomyia* than any of the possible positions in Tabanomorpha (outside of established groups), even though a specific sister group for *Bolbomyia* has not been recognized. Forcing *Bolbomyia* as sister to *Austroleptis* 3 steps are added.

Austroleptis

The phylogenetic signal of *Austroleptis* is similar to that found in *Bolbomyia*. The divergence of this genus from other taxa in the sampled set appears quite ancient, where the resolving power of the 28S rDNA is weak. It is recovered within Tabanomorpha in all analyses, and this is most likely its correct location, however on account of its poorly resolved status with respect to specific sister groups, alternate hypotheses aren't as easily rejected. Five additional steps are required to place this genus within the Xylophagomorpha; the same may be said for Nagatomi's concept of Austroleptinae, a subfamily sister to the rest of the Rhagionidae *sensu lato* (Nagatomi, 1982a). The suggestion that *Austroleptis* and *Bolbomyia* form a monophyletic entity (with other taxa, not included here), on the basis of the shared loss of the third medial vein (Grimaldi and Cumming, 1999) is not recovered in the most parsimonious arrangement, yet forcing such a sister group relationship adds only 3 steps to the tree. This seems like a reflection of the relatively poor resolving power of 28S rDNA for both of these taxa rather than the plausibility of this hypothesis, however.

Vermileonidae

The monophyly of Vermileonidae has never been disputed, on account of many morphological and behavioral synapomorphies. The placement of this family, however, is unclear and a number of authorities have called for its removal from Tabanomorpha (Nagatomi, 1977, 1991; Griffiths, 1994; Stuckenberg, 2001). Although its placement with respect to other tabanomorph taxa remains uncertain, the Vermileonidae do not appear to represent a separate infraorder. By forcing this

arrangement, 13 steps are added to the most parsimonious arrangement. Placing it anywhere within the Tabanomorpha, outside of the Tabanoidea, Rhagioninae, Chrysopilinae, and Spaniinae, adds one or no steps to the tree. Within Vermileonidae, *Vermileo* is shown as paraphyletic with respect to *L. hessei*, with strong support. Bootstrap values for the sister group relationship between *Vermileo sp.* (Israel) and *L. hessei* are 100% in all analyses, for all alignments. Although this may be a surprising result, *Vermileo* is an old, well established genus, the morphology of the larval mouthparts confirms that *Vermileo* of the New World (as *V. opacus*) exhibit striking differences from their congeners in the Old World (noted in Appendix A).

Combined Analysis

Introduction

The strength of an hypothesis may be determined by the quality of its support, from all sources of information that are available. There are many potential pitfalls for both morphological and molecular methods that in each case, may lead to positively misleading conclusions. Therefore, while considering independent lines of evidence separately is essential, the integration of this knowledge into a single synoptic hypothesis is the ultimate aim of phylogenetic systematics.

There has been some controversy regarding the combined approach. One may argue that by combining data sets, the 'total evidence' available is used and the analysis will consequently render a most conservative tree with the greatest descriptive and explanatory power. However, combining data sets of heterogeneous phylogenetic signal may give misleading results (de Queiroz et al., 1995). At the heart of this debate is whether or not there are separate classes of evidence. That is, can evidence be inherently different and therefore incapable of being compared simultaneously? Or are multiple lines of phylogenetic evidence simply the documentation of a single series of events from different perspectives? De Quieros et al. (1995) give an overview of this discussion.

If data sets are shown to be congruent (i.e., homogeneous) and to have the same underlying assumptions, the data may be combined (Bull et al., 1993). In such cases, combining data sets, theoretically, will enhance the detection of phylogenetic signal

and generate a more robust phylogenetic hypothesis. Even so, it is always good to keep a keen watch for imbalances. Regier and Shultz (1997) note that morphological characters may have undue influence when combining data sets given that typological approaches may lower the rate of homoplasy and thereby artificially increase phylogenetic signal.

This section evaluates the morphological and molecular contributions developed in previous sections in a combined analysis using three techniques. The first two use a concatenated morphological and molecular data set for simultaneous analysis using MP and BI. The final combined approach is a type of meta-analysis, which uses the trees generated independently by the morphological and molecular data, to give an overall "supertree" representation of the combined phylogenetic hypothesis.

Materials and Methods

Taxon Sampling

For the combined analyses, the intersection of taxa in morphological and molecular datasets was sampled for the combined analyses. The molecular data set excluded 'ends', 'highambig', and 'unalign' character sets (AS #4). In some cases, the genera in the combined analysis are a chimera of two different species (see Table 15). This was allowed only in cases where the genus was sampled once in the dataset and the monophyly of the species contained within the genus was irrefutable. In the supertree analysis, the dataset is the matrix representation of trees found in separate morphological (MP) and molecular (ML) analyses, so that all taxa are included.

Table 16**.** Combined analysis dataset; morphological and molecular taxon overlap.

Morphological characters	**Molecular characters**	**Recent Family Placement**
Atherimorpha atrifemur	*Atherimorpha atrifemur*	Rhagionidae
Atherimorpha vernalis	*Atherimorpha vernalis*	Rhagionidae
Atherix pachypus	*Atherix variegata*	Athericidae
Austroleptis multimaculata	*Austroleptis multimaculata*	Rhagionidae/ Austroleptidae
Bolbomyia nana	*Bolbomyia nana*	Rhagionidae
Chrysopilus quadratus	*Chrysopilus quadratus*	Rhagionidae
Chrysopilus thoracicus	*Chrysopilus thoracicus*	Rhagionidae
Dasyomma atratulum	*Dasyomma* sp.	Athericidae
Glutops rossi	*Glutops rossi*	Rhagionidae/ Pelecorhynchidae/ Glutopidae
Pelecorhynchus personatus	*Pelecorhynchus personatus*	Rhagionidae/ Pelecorhynchidae
Ptiolina majuscula	*Ptiolina fasciata*	Rhagionidae/ Spaniidae
Rhagio hirtus	*Rhagio hirtus*	Rhagionidae
Rhagio mystaceus	*Rhagio mystaceus*	Rhagionidae
Spaniopsis longicornis	*Spaniopsis longicornis*	Rhagionidae/ Spaniidae
Spaniopsis clelandi	*Spaniopsis clelandi*	Rhagionidae/ Spaniidae
Symphoromyia hirta	*Symphoromyia hirta*	Rhagionidae
Tabanus atratus	*Tabanus atratus*	Tabanidae
Vermileo vermileo	*Vermileo sp.*	Vermileonidae
Arthropeas americana	*Arthropeas magnum*	Xylophagidae
Coenomyia ferruginea	*Coenomyia ferruginea*	Xylophagidae/ Coenomyiidae
Dialysis rufithorax	*Dialysis elongata*	Xylophagidae
Xylophagus lugens	*Xylophagus abdominalis*	Xylophagidae

Combined Phylogenetic Analysis

The combined analyses were carried out in two parts. First, to gauge the contribution of signal from each of the two types of character data, separate analyses were performed, using only the morphological or molecular characters. The "pruned morphological" data set refers to the matrix that contains the combined analysis taxon set but includes only morphological characters. The "pruned molecular" data set refers to the matrix that contains the combined analysis taxon set but includes only molecular characters. The data was then combined and a full analysis of the data was carried out using MP and BI. A test was also performed to determine if the molecular and morphological data sets are deemed combinable by the partition homogeneity test.

MP analyses were carried out using PAUP* (Swofford, 2001). All characters were treated unordered, 1000 heuristic search replicates were performed with random-taxon-addition, tree bisection reconnection (TBR) branch swapping, steepest descent and 'MulTrees' options in effect. Scores of all MP trees were verified to avoid artifactually inflated sets of MP trees. In order to gauge the internal consistency of the data, bootstrap analyses were carried out for each of these analyses. MP bootstrap analyses were performed with 500 repetitions, each with 5 random-taxon-addition TBR heuristic searches.

For the BI analysis, each run was set for four million generations, with sampling every 200th generation for a total of 20,000 tree samples. Tree scores were plotted

against generation number to assess at what point stationarity was reached. All of the generations previous to the highest point stationarity are considered burn-in and discarded. The posterior distribution of trees sampled from the Markov chain was summarized using the 'sumt' command.

Weighting was done in both the MP and BI phylogenetic analyses so that the high number of molecular characters did not override the signal of the morphological data. Due to the acquisition bias (Lewis, 2001) of the morphological dataset, however, the number of constant characters of the sequence data was large and therefore, the average per character signal of the molecular dataset was much less than in the morphology matrix. Simply weighting each set by the inverse of the total character number would de-emphasize the signal in the molecular dataset. Therefore, characters of each dataset were weighted by the inverse of the number of phylogenetically informative characters.

Supertree analysis

The software program RadCon (Thorley and Page, 2000) was used to convert the set of trees generated by the separate and complete MP (morphology) and ML (sequence data) analyses into its matrix representation. The matrix was then analyzed using MP in PAUP*, consistent with the Matrix Representation using Parsimony (MRP) consensus method (Baum, 1992; Ragan, 1992; Sanderson et al., 1998). Two MRP analyses were carried out. The first analysis used two trees; the strict consensus of the trees from the molecular and morphological analyses, respectively. The second MRP

analysis used the most likely tree(s) from the molecular data and all of the most parsimonious trees found for the morphological data.

Results

Maximum Parsimony Analysis of Combined Data

Subset Taxon Sampling of Morphological Data

MP heuristic search of the pruned morphological dataset used for the combined analysis gave a single most parsimonious tree (Fig. 5). The reduced sampling produced a somewhat different topology than that from the full morphological dataset. A monophyletic Tabanomorpha is recovered, consisting of two clades. *Vermileo* sp. is recovered as sister to *Austroleptis* + Tabanoidea. In the other clade, *Bolbomyia nana* is sister to the remaining rhagionid taxa. In this analysis, *Chrysopilus* is sister to *Rhagio* spp., with 51% bootstrap support, to the exclusion of *Atherimorpha*. The Spaniinae are recovered sister to the group formed by *Atherimorpha*, *Chrysopilus*, and *Rhagio*.

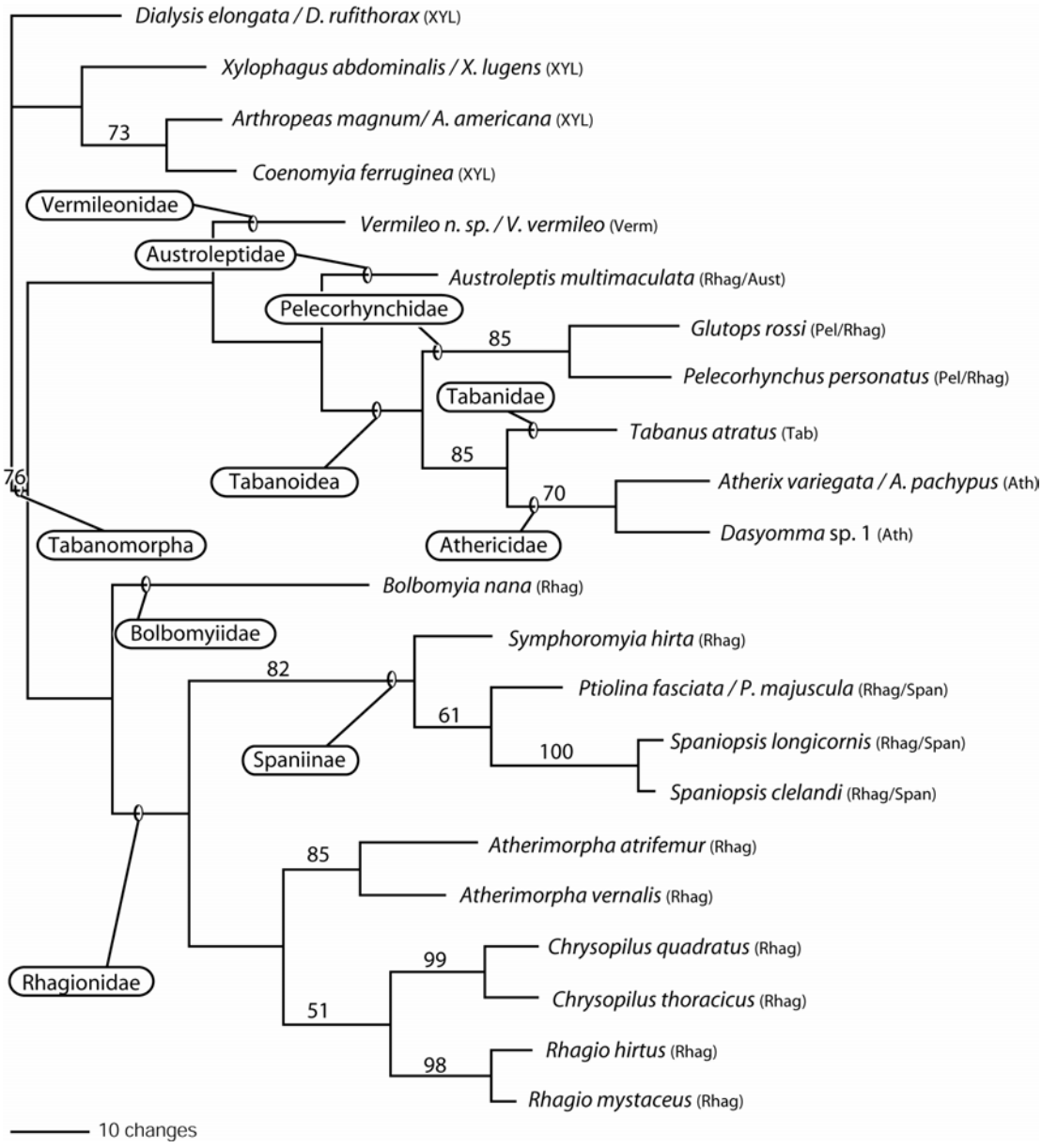


Figure 7. Maximum Parsimony analysis of pruned morphological matrix. Bootstrap values ≥ 50% are noted above supported branches (TBR, nreps = 500 / addseq reps = 5). The terminal named "*Dialysis elongata* / *A. rufithorax*" includes molecular information generated from the sequence of *D. elongata* and morphological information generated from specimens of *D. rufithorax*. The same is true for other terminals that have a combination of two names (e.g. "*Ptiolina fasciata* / *P. majuscula*"); these taxa are composed of molecular and morphological components generated from these species, respectively.

Subset Taxon Sampling of Molecular Data

MP heuristic search of the pruned morphological dataset used for the combined analysis also gave a single most parsimonious tree (Fig. 6). As in the morphological analysis, reduced sampling had a noticeable effect on the topology of the reduced molecular dataset. Again, a monophyletic Tabanomorpha is recovered, however, *Austroleptis* is the basal clade of the group. A comb-like topology of the major groups is recovered in the order from most basal to the most derived as: *Austroleptis*, *Vermileo*, Rhagioninae, Tabanoidea, and *Bolbomyia nana* + (Chrysopilinae + Spaniinae). Bootstrap support of greater than 50% is found for all of the major subgroups (Rhagioninae (84%), Tabanoidea (99%), Chrysopilinae + Spaniinae (78%)), Chrysopilinae (100%), and Spaniinae (90%), although *Pelecorhynchus personatus* is placed sister to the Tabanidae + Athericidae, to the exclusion of *Glutops rossi*. The paraphyly of Pelecorhynchidae is supported by a bootstrap value of 67% for *P. personatus* (*Tabanus* sp. (*Dasyomma* sp. + *Atherix* sp.)).

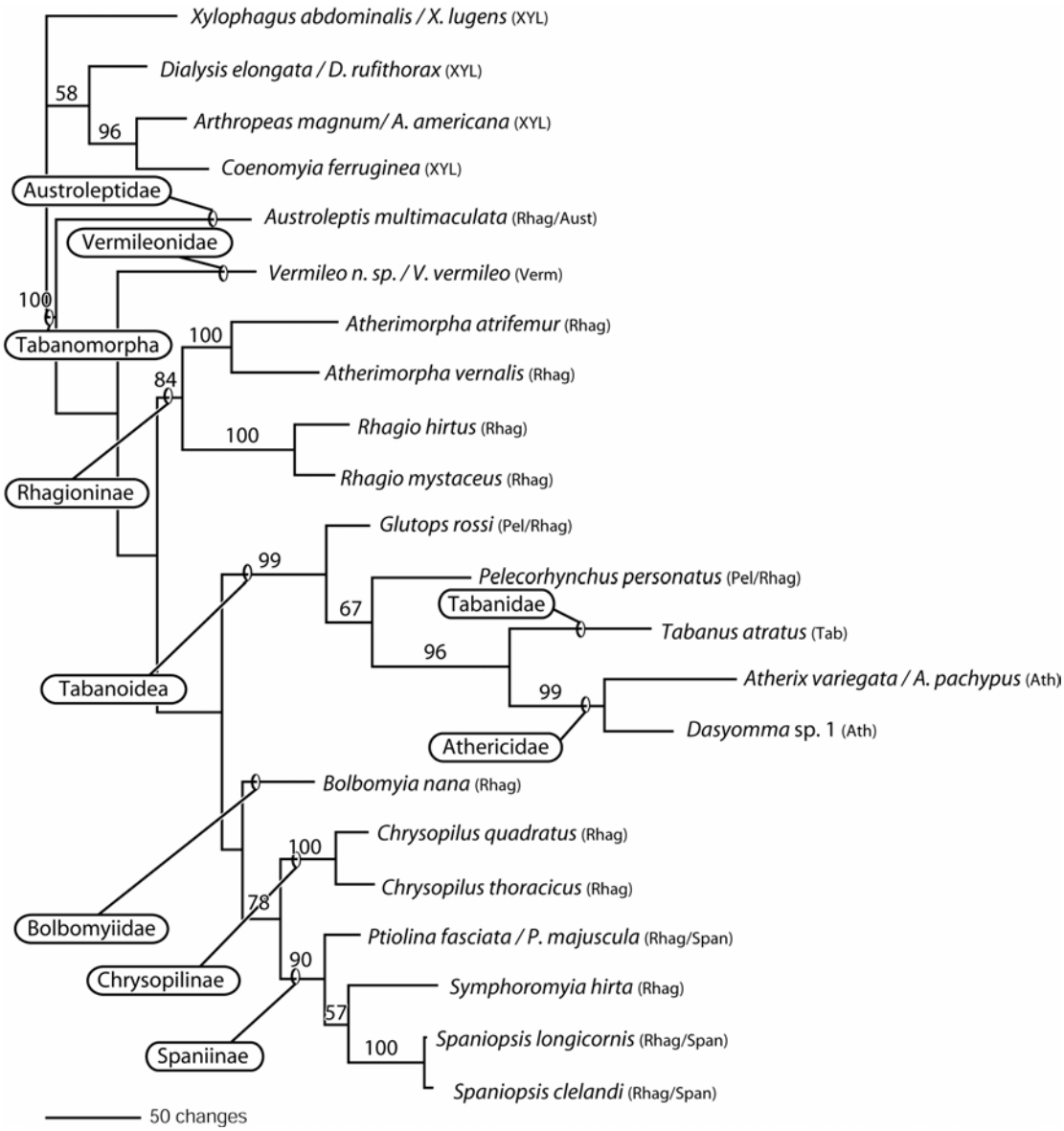


Figure 8. Maximum Parsimony analysis of pruned molecular matrix. Bootstrap values ≥ 50% are noted above supported branches (TBR, nreps = 500 / addseq reps = 5). The terminal named "*Dialysis elongata* / *A. rufithorax*" includes molecular information generated from the sequence of *D. elongata* and morphological information generated from specimens of *D. rufithorax*. The same is true for other terminals that have a combination of two names (e.g. "*Ptiolina fasciata* / *P. majuscula*"); these taxa are composed of molecular and morphological components generated from these species, respectively.

Partition Homogeneity Test

A partition homogeneity test showed that the data are combinable (P value = 0.057778).

Combined Sample of Morphology and Molecular Data

The MP heuristic search found a single most parsimonious tree (Fig. 7). Character sets are downweighted by number of parsimony informative characters (1/351 molecular, 1/127 morphological). Tree length is 3.49639.

The most parsimonious tree of the combined morphology and molecular sample has the same topology as the most parsimonious tree from the morphology maximum parsimony analysis. The Tabanoidea is recovered as the basal clade of Tabanomorpha, with Vermileonidae sister to the Rhagionidae in its broadest sense, including Rhagioninae, Chrysopilinae, Spaniinae, and *Austroleptis* and *Bolbomyia*. *Austroleptis multimaculata* and *Bolbomyia nana* are sister taxa and form the sister group to the clade formed by Rhagioninae, Chrysopilinae and Spaniinae. Rhagioninae is recovered as the sister taxon of Chrysopilinae plus Spaniinae. The relationships within Spaniinae are also preserved as in the morphological analysis. The difference between the results of the complete morphology and the combined analysis (aside from the difference in taxon sampling and character number) is the bootstrap support values for the various clades. In the combined analysis, bootstrap values are higher across the board. The Tabanomorpha are shown as monophyletic with a 99%

bootstrap, as is the Tabanoidea (94% bootstrap), Rhagioninae (86% bootstrap), Chrysopilinae and Spaniinae (78% bootstrap), and Spaniinae (78% bootstrap). Bootstrap values within these groups are also higher in the combined analysis. In regards to the morphological/molecular conflict as to the sister group of the *Spaniopsis* group (incl. *Spania* and perhaps *Litoleptis*), the combined analysis supports the morphological placement of *Ptiolina* + *Spaniopsis*. Although bootstrap values for the *Ptiolina* + *Spaniopsis* clade are less than 50% (48%), they are greater than the bootstrap values for a *Symphoromyia* + *Spaniopsis* clade (42%), and this is the relationship recovered in the most parsimonious reconstruction.

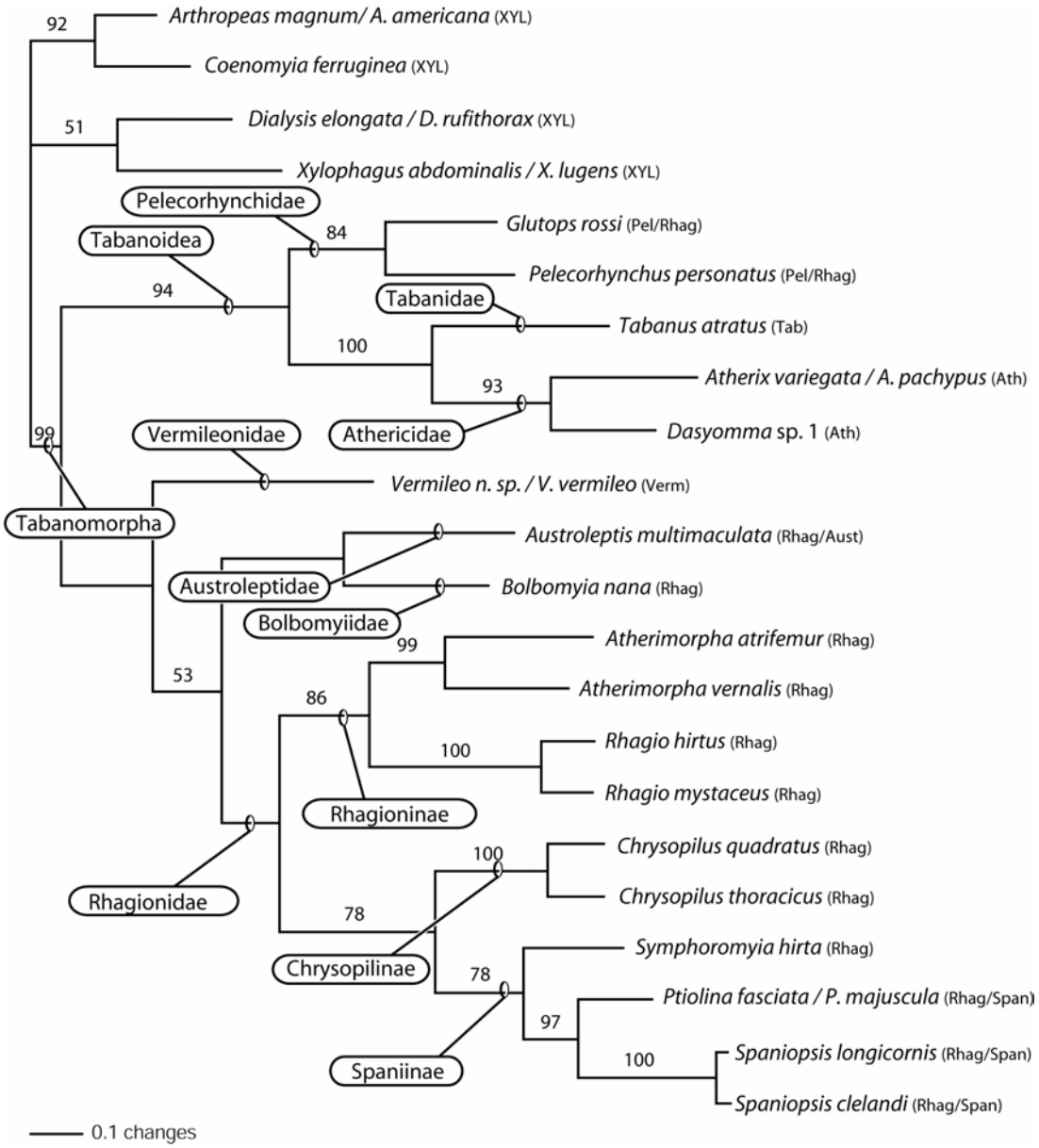


Figure 9. Maximum Parsimony analysis of combined matrix. Character sets downweighted by the number of parsimony informative characters within each set (1/351 molecular, 1/127 morphological). Bootstrap values ≥ 50% are noted above supported branches (TBR, nreps = 500 / addseq reps = 5).

Bayes Analysis of Combined Dataset

Subset Taxon Sampling of Morphological Data

Mr. Bayes uses the Mkv model (Lewis, 2001) to model morphological data, which is essentially a Jukes-Cantor model modified to allow for a greater number of character states (ref). The Bayes tree of the morphological data "pruned" subset gives a novel topology with weak posterior probabilities (Fig. 8). A monophyletic Tabanomorpha is recovered. At the base of the Tabanomorpha, *Vermileo* sp. is recovered as sister to Tabanoidea. The Spaniinae is maintained as a monophyletic group that is sister to a diverse clade that includes *Bolbomyia*, *Austroleptis*, Chrysopilinae, and a polyphyletic Rhagioninae. Sister to the *Atherimorpha* is *Bolbomyia* + *Austroleptis*. Sister to this, within the other subgroup, is a clade formed by *Chrysopilus* and *Rhagio.* The posterior probabilities of this diverse clade (and within it) are weak, however.

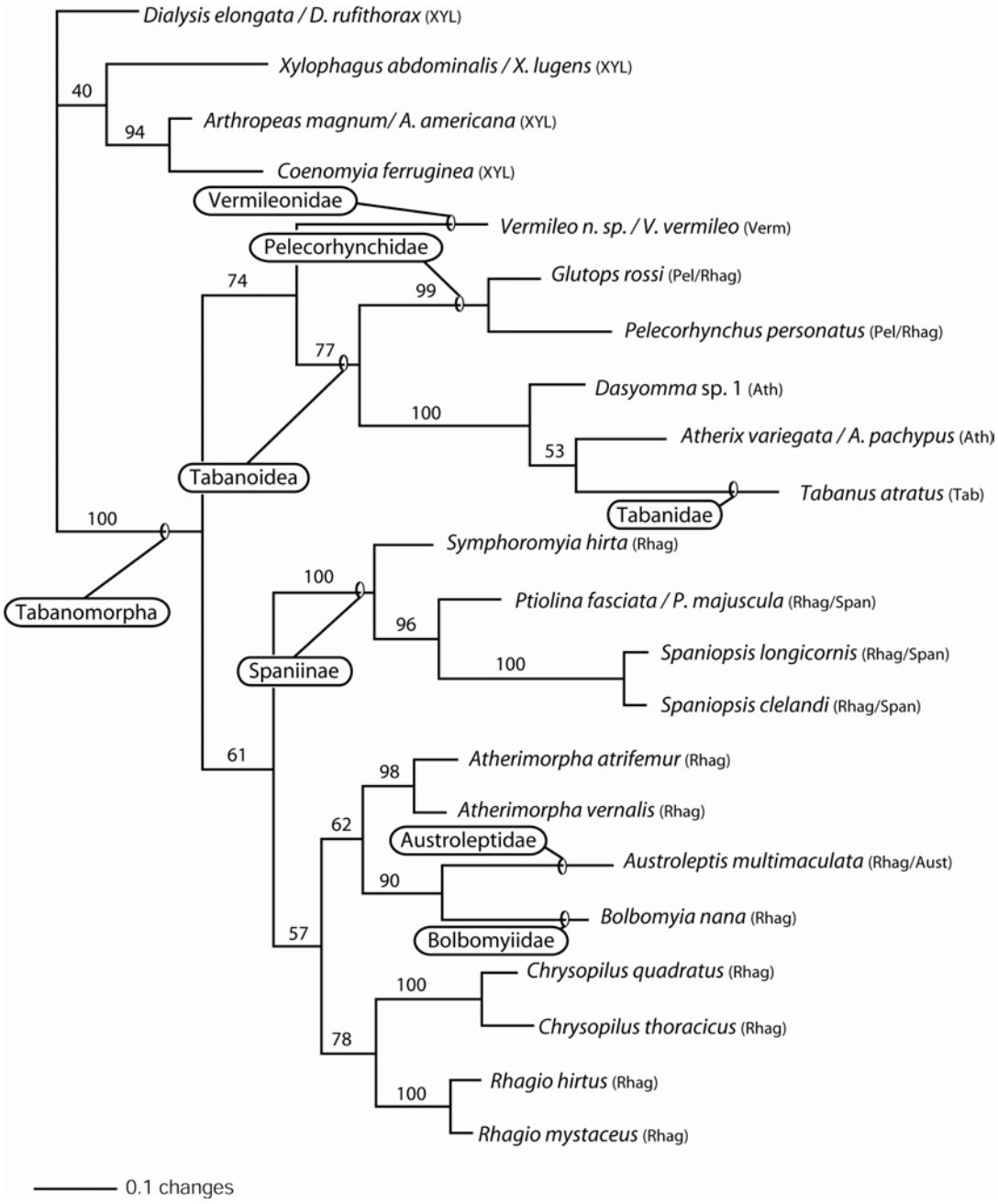


Figure 10. Bayesian tree for pruned morphology matrix. Posterior probabilities are noted above branches.

Subset Taxon Sampling of Molecular Data

Bayes analysis of the molecular data "pruned" subset yields yet another topology within the Tabanomorpha (Fig. 9). Within a monophyletic Tabanomorpha, *Vermileo* is the basal taxon. The tabanoid clade is located sister to the Rhagionidae in its broadest sense. In this construction, *Bolbomyia* is sister to *Austroleptis* + Rhagioninae, which in turn, is sister to the clade formed by monophyletic subfamilies Spaniinae and Chrysopilinae. Within the Spaniinae, *Ptiolina* is recovered as the basal taxon and there is a 93% posterior probability for the sister group relationship between *Symphoromyia* and *Spaniopsis*.

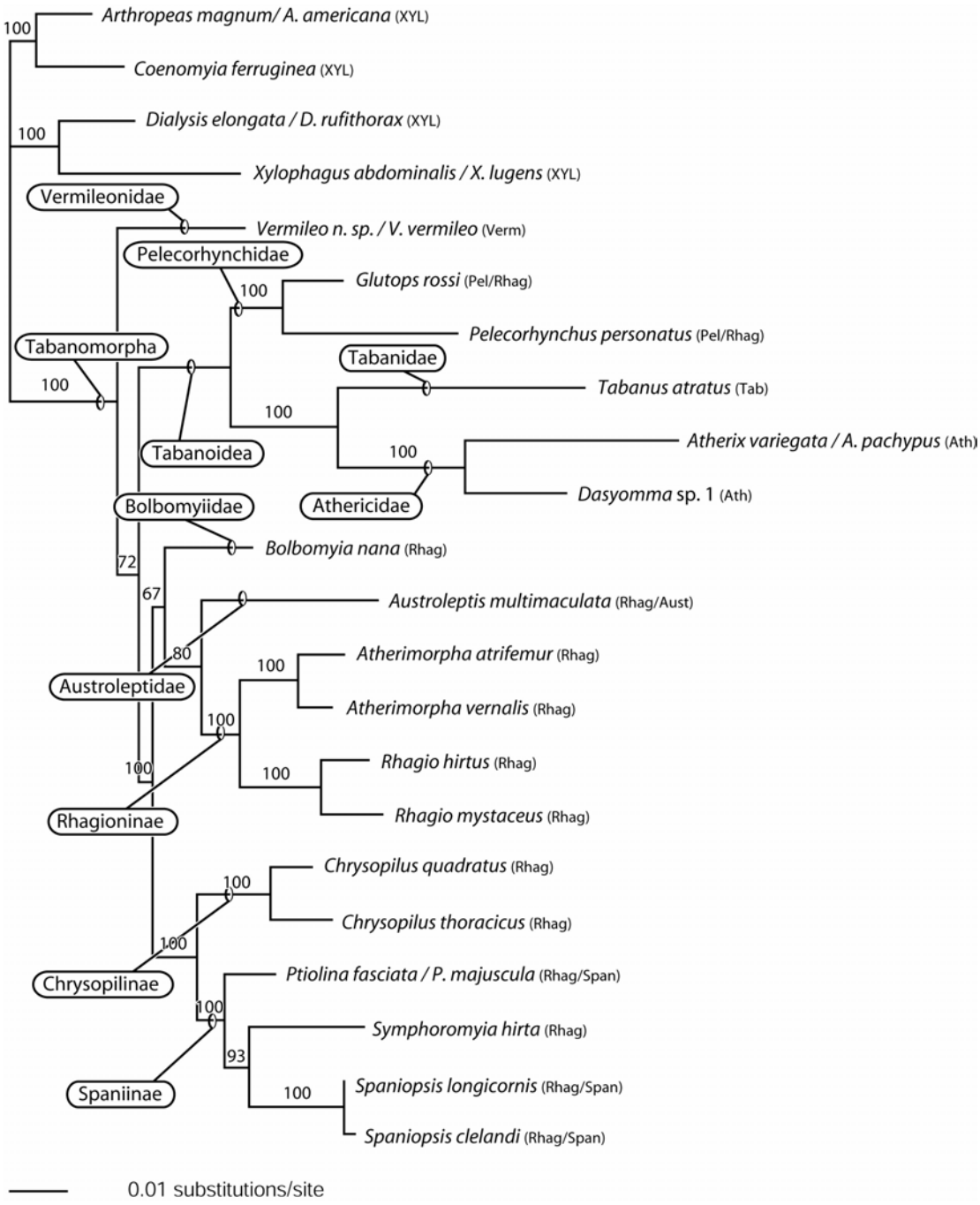


Figure 11. Bayesian tree generated from molecular characters of data matrix composed of taxa appropriate for a combined molecular and morphological analysis. Posterior probabilities are noted above branches.

Combined Analysis of Morphology and Molecular Data

Bayes analysis of the molecular data "pruned" subset yields yet another topology within the Tabanomorpha (Fig. 10). Within a monophyletic Tabanomorpha, *Vermileo* is the basal taxon, the tabanoid clade is then located sister to the Rhagionidae in the broadest sense. In this construction, *Bolbomyia* is sister to *Austroleptis* + Rhagioninae and together, these taxa are sister to the clade formed by Spaniinae and Chrysopilinae. Within the Spaniinae, *Ptiolina* is recovered as the basal group and there is a 93% posterior probability for the sister group relationship between *Symphoromyia* and *Spaniopsis*. Since posterior probabilities are known to often be overestimates of the actual support of the data (Douady et al., 2003), another representation of this result may be given in the form of a consensus tree restricted to posterior probability values of greater than 80%. This tree shows a monophyletic Rhagionidae *sensu lato*, without resolution of its basal lineages.

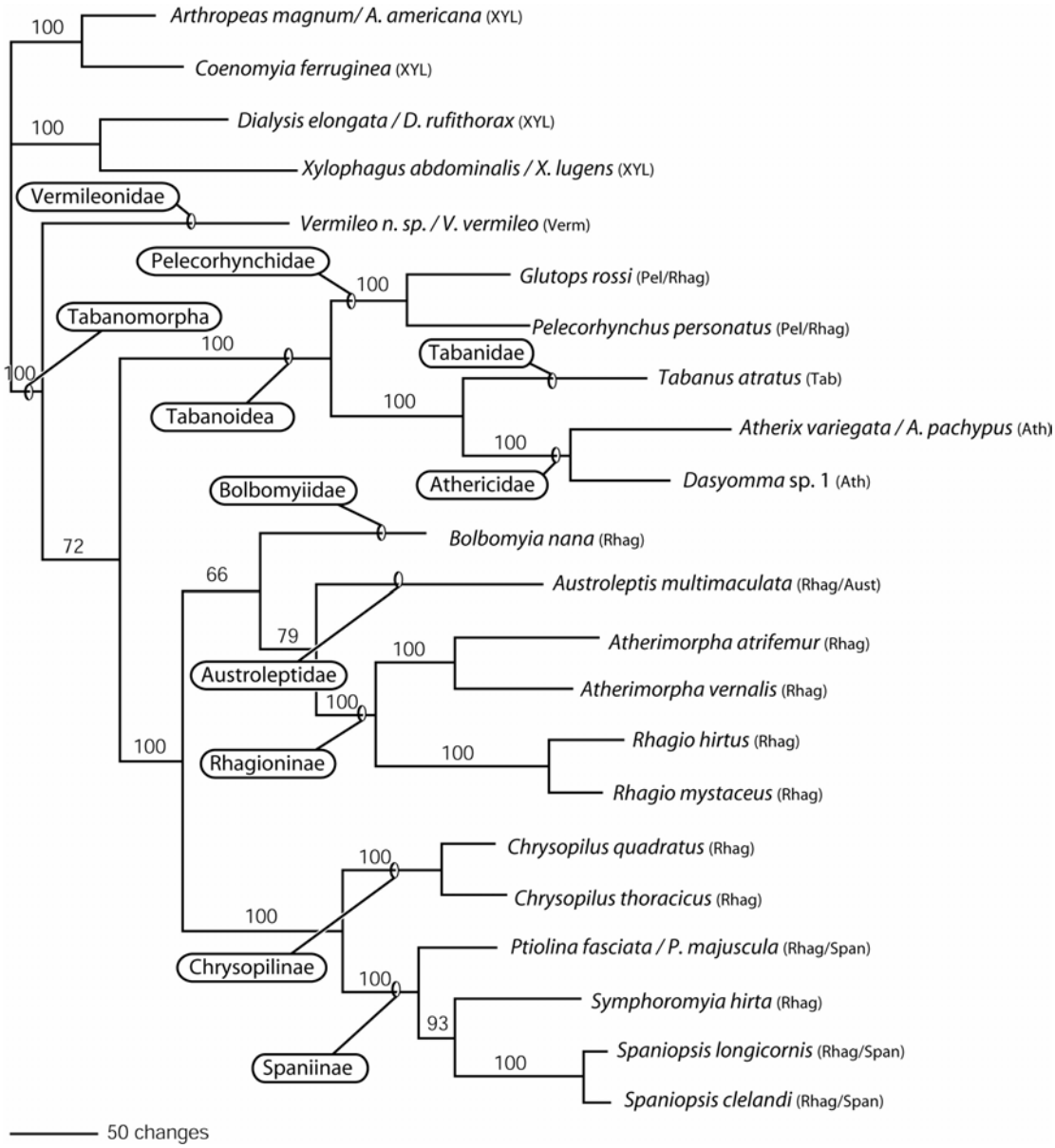


Figure 12. Bayesian tree for combined morphology and molecular data. Posterior probabilities are noted above branches.

Supertrees Analysis

Matrix Representation using Parsimony (MRP)

The supertree analysis is different from the two previous combined analyses by including all taxa, of both molecular and morphological datasets. This yields a tree

with 71 terminal taxa. The first MRP analysis combines two trees, each the strict consensus from the MP analysis of morphological data and the ML analysis of molecular data, respectively. This may be considered the most conservative interpretation of the combined results. The second MRP analysis allows all of the most likely (3) and most parsimonious (24) trees from the molecular and morphological analyses, respectively.

The MRP analysis of the strict consensus trees generated from molecular and morphological datasets yields 55733 trees. The strict consensus of these trees (Fig. 11) shows Xylophagomorpha fully resolved, sister to Tabanomorpha. Vermileonidae are sister to the Rhagionidae, *sensu lato*, whose basal clade is composed of *Alloleptis tersus*, *Bolbomyia nana*, and *Austroleptis* spp. The remainder of the tree shows Rhagioninae sister to Chrysopilinae plus Spaniinae, which are sister to one another. Within the Rhagioninae, *Atherimorpha* comprises two unresolved clades, one of which contains *Arthroteles bombyliiformis*. *Rhagio* is recovered as a monophyletic group, sister to a clade formed of *Desmomyia thereviformis*, and *Rhagina incurvatus* plus *Sierramyia chiapasensis*. Chrysopilinae is composed of *Chrysopilus*, *Schizella furcicornis*, and *Stylospania lancifera*, which are mostly unresolved. *Chrysopilus* may be paraphyletic with respect to *S. furcicornis*, *S. lancifera*, or both. *Arthroceras pollinosum* is sister to the Spaniinae and forms its own group, the Arthrocerinae. Within the Spaniinae, *Ptiolina* is again recovered as paraphyletic and sister to *Spaniopsis* (*L. alaskensis* + *S. nigra*), as in the morphological analysis.

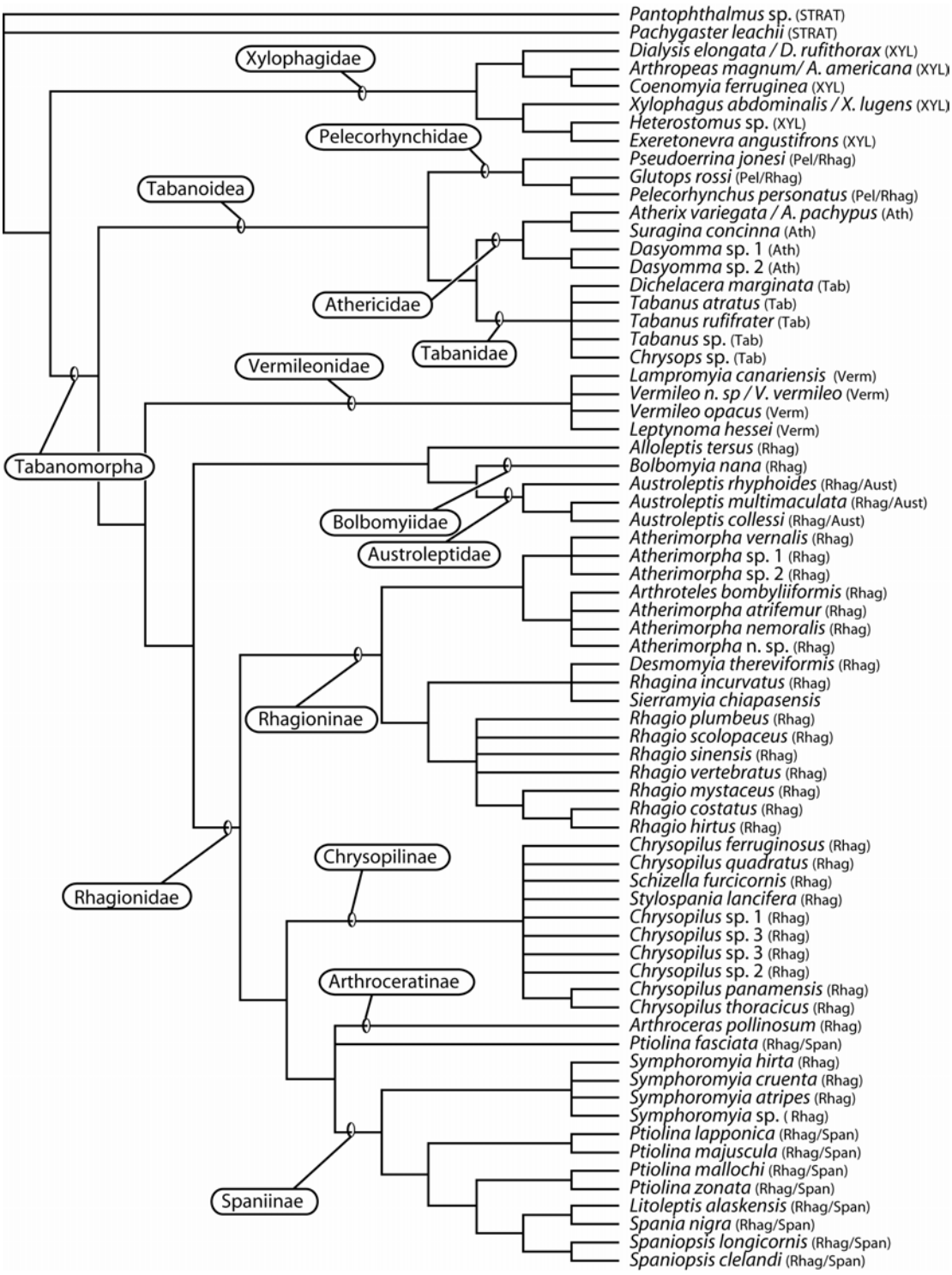


Figure 13. Strict consensus of 958299 trees from MRP analysis.

Discussion.

Combined analysis

The combined maximum parsimony analysis produced essentially the same topology as recovered using morphological data and the basal tabanomorph topology is consistent with the molecular tree recovered by Wiegmann et al. (2000).

More taxa or more characters? Both!

A coincidental result of this study involves the effects of taxon sampling (LeCointre et al., 1993; Hillis, 1998; Poe, 1998; Rosenberg and Kumar, 2001; Zwickl and Hillis, 2002; Hillis et al., 2003). Data sets with the full complement of taxa in the morphological and molecular analysis converge on similar topologies, and these resemble the topology of the combined analysis where, although the taxon sampling is reduced, there are an increased number of characters. When the taxon sampling is reduced for strictly morphological or molecular data sets, however, phylogenetic error becomes apparent. The trees produced by these sets are unusual. This result is consistent with those who have argued that both the number of characters and the number of taxa sampled are important for phylogenetic accuracy (Swofford et al., 1996). The results may also suggest that, at least in this case, the problems associated with a limited taxon sample may be overcome somewhat by adding more characters. Similarly, it appears that phylogenetic accuracy is improved with greater taxon sampling.

Bayes analysis

The Bayes analysis of the combined, full data set gives a result that is similar to the most likely tree when only the molecular data are considered. Vermileonidae are placed at the base of the Tabanomorpha, although the posterior probability of this placement is relatively low. The bayesian combined tree differs from the trees generated in other analyses in the placement of *Austroleptis* and *Bolbomyia* however these relationships also have low support. Since posterior probabilities are known to inflate support values (Douady et al., 2003), I prefer to collapse nodes with posterior probability values of less than 80%. When this is done, areas of the tree that have weak throughout the tree collapse. The monophyly of Rhagionidae, including *Austroleptis* and *Bolbomyia* is retained. Although the Bayes tree is a reasonable estimate of the relationships, I tend to give this tree less weight because the model on which the morphological data is based is very simple and may not accurately represent the evolution in this part of the data set. When nodes of low probability are collapsed, the tree is consistent with all other analyses.

Supertree analysis

Supertree analysis is an alternative method of deriving comprehensive topologies from various sources of character data. The input of supertree analysis, however, is in the form of trees and not the character data itself. This makes supertrees analysis vulnerable to confounding effects that may result in phylogenetic error, for a variety of reasons (Gatesy et al., 2002). The two biggest problems are that one, the input trees may be derived from different studies, employing different levels of phylogenetic rigor. A related issue is that the levels of support in each of the branches of the trees

are not incorporated into the supertree matrix. The second problem is that in many supertrees analyses, there is a redundancy of character data, resulting in nodes that are supported by multiple synapomorphies from different data sets, but ultimately are simply repetitions of the same character state.

The supertree analysis here avoids both of those problems. Each of the two input trees was generated by systematic phylogenetic analysis of equal rigor. Furthermore, the input trees were derived from completely independent data sets.

Gatesy et al. (2002) recommended that large trees be constructed using a supermatrix of all characters rather than employing supertree analysis from all available trees. The combined analysis in this study confirms that a 'supermatrix' may have improved resolving power over smaller matrices, analyzed alone. But what if taxon sampling is an issue? Many of the taxa included in the morphological data set were unavailable for molecular study. Therefore, the combined analysis was limited in scope.

There may be some justification for forming a supertree by simply grafting richly sampled morphological branches onto the molecular tree, where common ancestry may be assumed. However, I prefer to use the explicit methods of MRP.

The results of the supertree analysis were remarkable in that the recovered topology is consistent with the one found by the combined analysis.

Conclusions of the Phylogenetic Analysis.

Morphological and molecular data, when analyzed separately and in combination, yield similar hypotheses of the evolution within the Tabanomorpha. Tabanoidea (Pelecorhynchidae, Athericidae, and Tabanidae), Vermileonidae, Rhagioninae (*Atherimorpha*, *Desmomyia*, *Rhagina*, and *Rhagio*), Chrysopilinae (*Chrysopilus*, *Schizella*, and *Stylospania*), Arthrocerinae (*Arthroceras*), and Spaniinae (*Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*) are recovered consistently with high bootstrap support. *Sierramyia* and *Litoleptis* probably belong to Rhagioninae and Spaniinae, respectively, however limited taxon sampling prevents confirmation of this (*Sierramyia* male needed for examination of aedeagal form; *Litoleptis* female needed for confirmation of tergite 10 and spermathecal duct morphologies).

These data conflict with the most recent treatment of Tabanomorpha (Stuckenberg, 2001), particularly in regards to the composition of Rhagionidae. It has been shown here that *Glutops*, *Pelecorhynchus*, and *Pseudoerinna* do not belong in the Rhagionidae.

The morphology of *Bolbomyia* (consistent with 28S rDNA sequence data) suggests that it is distantly related to the rest of the rhagionid taxa and it may be placed in its own family, Bolbomyiidae.

Over the course of the long history of the concept of the Rhagionidae, the family was always considered (whether explicitly or not) to include the single common ancestor

of *Chrysopilus* and *Rhagio*, and all of its descendants. Evidence is presented here to show that *Chrysopilus* is more closely related to the spaniine group than it is to *Rhagio*. Thus, if Rhagionidae are defined on such terms today, descendents of the single common ancestor of *Chrysopilus* and *Rhagio* most certainly include the spaniine taxa. On this basis, Spaniinae should remain a subfamily within the Rhagionidae.

The evolution of blood feeding within Rhagionidae remains unclear. The molecular data suggest that blood feeding arose once within the Rhagionidae, in the ancestor of sister taxa *Symphoromyia* and *Spaniopsis*. The morphological data suggest, however, that with the consideration of additional genera, *Symphoromyia* and *Spaniopsis* are more distantly related; *Spaniopsis* forms a clade with *Litoleptis alaskensis* and *Spania nigra* that is sister to two separate lineages of *Ptiolina*. In interpreting the evolution of this behavior from a morphological perspective, one must conclude that blood feeding arose separately, once in each of the *Symphoromyia* and *Spaniopsis* lineages, respectively. The combined maximum parsimony analysis shows that the two hypotheses are equally parsimonious, while the bayesian inference of the combined data set is consistent with the single origin hypothesis. However, it is important to keep in mind that the combined sets do not include *L. alaskensis* and *S. nigra*, the putative sister taxa to *Spaniopsis*. Until greater sampling is carried out in this area of the tree, our understanding of blood feeding in Rhagionidae will remain clouded.

The position of *Alloleptis tersus* remains unclear. It does not appear to be a member of either Rhagioninae or Spaniinae, nor does it bear any apparent synapomorphies with any other known groups. This may change as specimens of this species become available for examination. However, presently, this genus must be considered *incertae sedis* within Tabanomorpha.

Consistent with other analyses that have examined the effect of taxon sampling, it appears that as more taxa are added to the matrix, phylogenetic accuracy is increased. Although the phylogeny of the major groups within Tabanomorpha is a difficult problem and remains unsettled to some degree, the results here indicate that efforts to amplify new sequences may be well rewarded. *Arthroceras* is of particular interest in this regard. More *Ptiolina* material will also be helpful to resolve the question of monophyly for the genus, as well as indicate with greater certainty its sister group.

Similarly, the addition of characters will certainly help resolve lesser known groups such as *Alloleptis*, *Litoleptis*, and *Sierramyia*. A determined effort must be made to collect more of this material. The importance of larval characters especially must be emphasized. Although larvae are rarely found, even for common genera, a successful systematic program to collect larval *Austroleptis*, *Arthroceras*, *Bolbomyia*, and *Atherimorpha*, in particular, seems possible. Fairly reliable localities are known for each of these genera, yet a thorough, painstaking search for these larvae has not been carried out. These efforts may at least generate information regarding the first instar

larva, since egg-laying may be induced from freshly collected, live females (J. Cumming, pers. comm.).

Based on the results of this phylogenetic analysis, I will propose a re-classification of the group. This reclassification is presented as part of Chapter 3.

Chapter 2 Notes.

Note 1. The first character [#1] is used to score the availability of male and female specimens in order to help avoid data-entry mistakes. In DELTA, certain character states may be programmed to control other characters. The character scored as having state 'male only', for example, renders all female characters inapplicable. DELTA blocks data-entry for inapplicable characters, as programmed by the user so that, as in this example, female character states cannot be scored for species that are without females available for examination. It is a bookkeeping character only and is removed from all analyses.

Note 2. The family of *Oreoleptis*, a new undescribed genus, is not clear to the authors who have collected larvae and reared adults (Szloty, Pritchard, and Sinclair, pers. comm.). I have not seen the adult, but I have read a brief description of its peculiarities. It has aedeagal tines as Athericidae + Tabanidae, but lacks a postspiracular scale and the female first cercus is two segmented. I have examined the larva and it is athericid in nearly all respects. All Athericidae that I have examined have elongate cylindrical palps that look like cigarettes, unlike those in any other larvae. They also uniquely have elongate prolegs armed with crochets apically, used

to adhere to its substrate. However, I have examined one *Halucitherix* that was already partially dissected so I cannot be sure that it does not have a telescoped first cephalic segment, as currently known Athericidae and Tabanidae. It appears to have a first segment similar to rhagionids.

Note 3. I use the term 'mandibular brush' as Woodley (1989) and Sinclair (1992), however, other terms have been used for this structure ('cephalic brush' (Cameron, 1934; Teskey, 1970; Webb; 1977), 'setaceous region' (Cook, 1949), 'spinose area' (Mackerras and Fuller, 1942), 'borstenfeld' (Schremmer, 1951), 'champ de'épines (Tsacas, 1962), 'bristle area' (Roberts, 1969)). In the tabanoids (Pelecorhynchidae, Athericidae, Tabanidae) the brush is associated with the mandibles by way of an articulated rod. As the mandibles are adducted downward, the articulated rod is lifted (Pechuman and Teskey (1981: 464). It appears to work similarly in the rhagionids, as illustrated in *Chrysopilus auratus* (Tsacas, 1962: 176). In the Rhagionidae, however, the brush is associated with cuticular tissue. Inherent in the term 'mandibular brush' may be an implicit assumption of functional association between the brush and mandibles. While the homology between the brush in tabanoids and the brush in rhagionids is not necessarily certain, the brush does seem functionally associated with the mandibles in all cases. Since this functional association is not immediately obvious, and the brush is a very conspicuous element of the larval head, the term 'cephalic brush' may be an appealing term, particularly in reference to Rhagionidae. However, the brush may be completely concealed by the cephalic sclerite, when the mandibles are abducted (as in SEM of *Pelecorhynchus*, Fig. <will be in next draft>).

In this case, the scoring may be affected solely by the position of the mandibles (cephalic brush apparently absent). Therefore, in my opinion, the term ‘mandibular brush’ is most appropriate.

Chapter 3. Definition of Rhagionid Genera and Related Taxa, and their Family Groups.

Introduction

This chapter is dedicated to updating current knowledge of the Rhagionidae and related taxa. The genera of Austroleptidae, Bolbomyiidae, and Rhagionidae are defined and re-classified based on characters and relationships established in the previous chapter.

Key to Adult Genera of Rhagionidae.

The following key includes leads for Athericidae, Tabanidae, Vermileonidae, and Xylophagidae; members of which may be mistaken for Rhagionidae. The key also includes Pelecorhynchidae (*Glutops* Burgess, *Pelecorhynchus* Macquart, and *Pseudoerrina* Shiraki) and Austroleptidae (*Austroleptis* Hardy), and Bolbomyiidae (*Bolbomyia* Loew) which have been placed in Rhagionidae by recent authors (Nagatomi, 1982a; Woodley, 1989; Stuckenberg, 2001, etc.). *Neorhagio* Lindner is an unavailable name and is replaced by *Sierramyia* Kerr (new genus). *Solomomyia* Nagatomi is considered a junior synonym of *Chrysopilus* Macquart, *Archicera* Szilády a junior synonym of *Spania* Meigen, and *Spatulina* Szilády a junior synonym of *Ptiolina* Zetterstedt. *Omphalophora* Becker *sensu* Kerr is treated herein.

1. Clypeus flat or recessed 23

   Clypeus bulbous or at least slightly swollen 2

2(1). Postspiracular sclerite with scale or slender ridge 19

   Postspiracular sclerite smooth and flat 3

3(2). Hind tibial spur absent; laterotergite bare; wing vein M_3 usually absent or reduced 4

Hind tibial spur one; laterotergite setose or bare; wing vein M_3 present, reaching wing margin 6

Hind tibial spur two; laterotergite setose; wing vein M_3 present, reaching wing margin 13

4(3). Lacking mid tibial spurs; discal cell absent; scape clearly smaller than pedicel; eyes in male dichoptic; dorsal surface of wing vein R_1 bare; Alaska, Chile, Japan ..... ***Litoleptis*** Chillcott

Mid leg with two tibial spurs; discal cell present; scape and pedicel approximately the same size; eyes in male holoptic; dorsal surface of wing vein R_1 microsetose; Australian, Holarctic..... 5

5(4). Body greater than 4 mm in length; length of wing vein R_{2+3} shorter than length of R_5; CuA_1 arises from discal cell; Australian ..... ***Spaniopsis*** White

Body less than 4 mm in length; length of wing vein R_{2+3} about the same length as R_5; CuA_1 arises from basal medial cell or at juncture between basal medial and discal cells; Palaearctic ..... ***Spania*** Meigen

6(3). Laterotergite setose..... 9

Laterotergite bare.....7

7(6). Eyes pilose; one mid tibial spur; body length less than 4 mm; Celebes (female unknown) .....***Alloleptis*** Nagatomi & Saigusa

Eyes without conspicuous microsetae; two mid tibial spurs; body length greater than 4 mm; Holarctic 7

8(7). Anepisternum bare; wing vein R_5 anterior to or ending at wing tip; wing vein R2+3 about as long or shorter than R5; spermathecal duct no more than three times the length of sternite 9; female tergite 9 short, length approximately one half width or less; spermathecal duct accessory glands arise from the base of the spermathecae; Holarctic .... ***Ptiolina*** Zetterstedt

Anepisternum setose; wing veins R_4 and R_5 encompass wing tip; wing vein R2+3 clearly longer than R5; spermathecal duct more than three times but less than five times the length of sternite 9; female tergite 9 longer, length greater than one half width; spermathecal duct accessory glands arise at approximately the distal third of the spermathecal ducts; Holarctic ..... ***Omphalophora*** Becker

9(6). Macrochaetae of hind tibia absent; palp two-segmented; scale-like thoracic setae with structural color never present; ventral parameral sheath of male genitalia with paired lobes 12

Macrochaetae of hind tibia present; palp one-segmented; scale-like thoracic setae with structural color often present; ventral parameral sheath of male genitalia without paired lobes 10

10(9). First antennal flagellomere elongate, stylate; anepisternum bare, hind coxal tubercle present; Philippines ..... ***Stylospania*** Frey

First antennal flagellomere ovoid, bearing long arista-like extension apically (in female; in male, various forms, but not stylate); anepisternum setose; hind coxal tubercle absent; Cosmopolitan 11

11(10) First antennal flagellomere of male highly modified, bifurcate; male dichoptic; Philippines ..... ***Schizella*** Bezzi

First antennal flagellomere of male as in female; males almost always holoptic; Cosmopolitan ..... ***Chrysopilus*** Macquart

12(9). First antennal flagellomere kidney-shaped, with dorso-apical arista; mandibles present; proscutellum usually present; hypandrium fused entirely to gonocoxites; Holarctic ..... ***Symphoromyia*** Frauenfeld

Antenna with many similarly sized antennal flagellomeres, tapering distally; mandibles absent; proscutellum absent; hypandrium separated partially from the gonocoxites by an incomplete suture; Nearctic ..... ***Arthroceras*** Williston

13(3). Palp two-segmented; first antennal flagellomere enlarged bearing segmented stylus; setae of laterotergite arranged in row(s)..... 18

Palp one-segmented; first antennal flagellomere enlarged basally, fused with distinct arista-like apical extension; setae of laterotergite in arranged in tuft14

14(13). Fore tibial spur one; dorsal surface of R_1 without microsetae; spermathecal duct no more than three times the length of sternite 9; female tergite 7 much wider than long ..... **VERMILEONIDAE**

Fore tibial spur absent; dorsal surface of R_1 microsetose; spermathecal duct longer than five times the length of sternite 9, but not so long as to be difficult to measure; female tergite 7 much longer than wide 15

15(2). Alula completely reduced, without any curvature; wing vein R2+3 setulose; proepimeron bare; Mexico ..... ***Sierramyia*** Kerr

Alula present, with narrow or broad curvature; wing vein R2+3 bare; proepimeron setose; Holarctic, including Mesoamerica 16

16(3). First hind metatarsus of male swollen; scape clearly larger than pedicel; India and China ..... ***Desmomyia*** Brunetti

First hind metatarsus of male not swollen; scape about the same size as pedicel ..... ***Rhagio*** Fabricius (including ***Rhagina*** Malloch)

17(13). Proboscis short, fleshy; alula with narrow curvature; female tergite 7 about as long as wide; cardo not swollen; South Africa, Australia, and South America..... ***Atherimorpha*** White

Proboscis elongate, sclerotized, specialized for nectarivory; alula with broad curvature; female tergite 7 much longer than wide; cardo swollen (as protuberance arising from base of palp); South Africa ..... ***Arthroteles*** Bezzi

18(2). Tuft of setae posterior to postspiracular sclerite present; female cercus two-segmented ..... **PELECORHYNCHIDAE** 20

Tuft of setae posterior to postspiracular sclerite absent; female cercus usually one-segmented 19

19(18). Wing veins R_1 and R_{2+3} meet together or close together at wing margin; lower calypter undeveloped; first abdominal sclerite without median notch or suture; Cosmopolitan..... **ATHERICIDAE**

Wing veins R_1 and R_{2+3} close together at wing margin; lower calypter developed; first abdominal sclerite with median notch or suture; Cosmopolitan..... **TABANIDAE**

20(18). Laterotergite setose; eyes conspicuously microsetose; short fore tibial spur present; Holarctic..... ***Pseudoerrina*** Shiraki

Laterotergite bare; eyes inconspicuously microsetose; fore tibial spur lacking; Cosmopolitan.....21

21(20). Hind tibial spur one; wing veins R_{2+3} and R_4 nearly straight; subscutellum enlarged, noticeably bulbous; Holarctic, including Mesoamerica ..... ***Glutops*** Burgess

Hind tibial spur two; wing veins R_{2+3} and R_4 sinuous, arcing toward anterior wing margin; subscutellum not enlarged; Australia and South America .....***Pelecorhynchus*** Macquart

22(1). Postspiracular scale present; lower calypter developed; first abdominal sclerite with median notch or suture; mandibles present; occiput flattened, concave posteriorly .....**TABANIDAE**

Postspiracular scale absent; lower calypter undeveloped; first abdominal sclerite without median notch or suture; mandibles absent; occiput rounded to various degrees 23

23(22). Postspiracular sclerite setose ..... **XYLOPHAGIDAE**

Postspiracular sclerite without setae 24

24(23). Laterotergite setose; wing vein M_3 present; anal lobe reduced; eyes in male evenly distributed, of equal size; Holarctic

.....***Vermileo*** Linnaeus **VERMILEONIDAE**

Laterotergite bare; wing vein M_3 absent; anal lobe well developed; eyes in male split into upper and lower areas and smaller in lower area.....25

25(24). Lacking mid and hind tibial spurs; palp one-segmented; first antennal flagellomere elongate, stylate; wing veins R_1 and R_{2+3} widely separated at wing margin; Alaska, Chile, Japan ..... ***Litoleptis*** Chillcott

Mid and hind leg with two tibial spurs; palp two-segmented; first antennal flagellomere bearing segmented stylus; wing veins R_1 and R_{2+3} close together at wing margin; Australian, Neotropical, Holarctic..... 26

26(25). Fore tibial spur absent; female cercus one-segmented; female tergite 7 much wider than long; three spermathecae; subscutellum bulbous; theca elongate; pseudotrachae present; eyes in male flattened dorsally; male hypandrium fused entirely to gonocoxites; aedeagal tines absent; Australia and South America..... ***Austroleptis*** Hardy **AUSTROLEPTIDAE**

Fore tibial spur present; female cercus two-segmented; female tergite 7 much longer than wide; two spermathecae; subscutellum inconspicuous; theca compact; pseudotrachae absent; eyes in male rounded dorsally; hypandrium

separated from the gonocoxites by a complete suture; aedeagal tines present; North America and Kamchatka ..... ***Bolbomyia*** Loew **BOLBOMYIIDAE**

Austroleptidae

Genus AUSTROLEPTIS Hardy

Figures 17-24, 178.

AUSTROLEPTIS Hardy, 1920: 126. Type species *Austroleptis rhyphoides* Hardy, 1920, by original designation.

DIAGNOSIS.

Austroleptis is unique among lower brachyceran taxa in having the cornu apically setulose and by having sternite 8 of the female terminalia laterally divided into two segments. In the male genitalia, the presence of paired sclerotized lobes arising ventrally, near the center of the gonocoxites, is another autapomorphic development. *Austroleptis* is also characterized by the combination of having a recessed clypeus, female cercus one-segmented, wing vein M_3 missing, and male genitalia without gonocoxal apodemes. Although *Austroleptis* is not unique among lower brachycerans in having each these four features, the phylogenetic placement of the genus suggests that most, if not all, of these character states are each independently derived and represent additional autapomorphies for the genus. Within Tabanomorpha, *Austroleptis* is unique in having a recessed clypeus and is the only taxon outside of Athericidae and Tabanidae that has one-segmented female cercus. Nagatomi & Iwata (1976: 43) and Nagatomi & Nagatomi (1987:140) state that *Austroleptis* is peculiar among the Tabanomorpha in having sternite 9; they were mistakenly referring to the posterior sclerite of sternite 8. All lower brachyceran flies retain sternite 9 (also

known as the genital fork, vaginal apodeme, or furca), in some form. *Austroleptis* is restricted to the southern hemisphere, in South America and Australia.

Austroleptis is a small to moderately sized fly (3.1 to 7.7 mm) of black, brown, brown and black, orangish or yellowish coloration. There is sexual dimorphism in the coloration; males are usually black or darker, whereas females often have at least some light brown or orange, if not entirely yellowish. All Australian *Austroleptis* have spotted wings, whereas South American *Austroleptis* wings are hyaline (although I have seen one undescribed *Austroleptis* species from Chile, Malleco Province, with infuscate wing veins). Antenna with basal flagellomere enlarged, oval, laterally compressed, bearing 2 to 4 distal flagellomeres; eyes in male holoptic; laterotergite bare; tibial spur formula 0:2:2 (spurs very short); and tibia without macrochaetae. Due to its unusual combination of character states (listed above) and its restricted distribution, *Austroleptis* is unlikely to be confused with related Diptera. In South America, it is most readily distinguished from *Atherimorpha* by its recessed clypeus, bare laterotergite and the absence of wing vein M_3 and from *Litoleptis* by the multisegmented flagellomere, spurs on mid and hind tibia, and the presence of the discal cell. In Australia, it is most readily distinguished from *Spaniopsis* by its multisegmented flagellomere and the presence of hind tibial spurs.

DESCRIPTION.

Head. Clypeus not bulbous. Scape approximately the same size as pedicel. Flagellomeres 3-5; first flagellomere enlarged, oval, laterally compressed, bearing setae; distal flagellomeres robust, cylindrical, short (except terminal flagellomere

which is more elongated). Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic, flattened dorsally, ommatidia split into dorsal and ventral areas and smaller ventrally. Labella with pseudotrachae, longer or shorter than palps. Theca elongate, lateral sclerites tightly adjacent, apparently fused with suture. Palps two-segmented; proximal and distal segments about the same length. Stipes surrounded by membrane above theca, directed posteriorly (very reduced). Cardo not swollen. Lacinia longer than palps, lacinia apex not serrated. Mandibles absent. Cibarial pump short, as wide as long or wider. Cornu shorter than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat; longer than length of cibarial pump. *Thorax*. Mesonotum with vittae. Dorsocentral bristles absent, all dorsal setae of equal length or present (as in *A. collessi*). Anepisternum bare. Laterotergite bare. Postspiracular scale absent. Proscutellum present. Subscutellum enlarged, noticeably bulbous. Wing hyaline or lightly infuscate, membrane with or without markings, with or without pseudostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wingtip or past wingtip (to at least R_5). Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by less than the length of h. Dorsal side of R_1 setulose, ventral side with or without setulae; wing veins R_4 and R_5 with or without setulae; all cells and other wing veins bare. R_{2+3} sinuous, apical third ultimately bends toward leading edge of wing margin (creating concave flex anteriorly); shorter than R_5. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 at base relaxed, not strongly curved, nearly straight apically. R_5 anterior to or ending at wing tip, or R_4 and R_5 encompass wing tip. R_5

anterior to, posterior to, or ending at wing tip; clearly longer than R_{4+5} (r-m to R_4 origin). Origin of CuA_1 at discal cell. M_3 wingvein absent. CuA_2 reaches wing margin, about 2/3 length of posterior vein of bm cell. M_3 wing vein absent. Alula with broad curvature, rounded evenly. Anal lobe well developed. Anal cell closed. Halter knob between 1/3–1/2 length of stem. Tibial spur formula 0:2:2. Mid and hind tibial spurs short. Hind coxal tubercle absent. Hind tibial macrochaetae absent. Postmetacoxal bridge present, as an incomplete, thin extension. *Abdomen*. Terminal abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 much wider than long. Intersegmental membrane between segments 7 and 8 short, as throughout abdomen. Sternite 8 sclerite elongated; more than twice as long as wide; divided into two segments, anterior segment long and wide, posterior segment rounded, cupped. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly), flattened; anterior margin entire, with an even amount of sclerotization; appearing posteriorly lobed, with paired region of increased sclerotization; setose. Cercus directly adjacent to epandrial sclerite; directly adjacent to one another, separation distance one quarter width of cercus or less; held horizontal in relation to rest of abdomen; in posterior view flat. Hypandrium fused entirely to gonocoxites. Gonocoxite smooth dorsally, without sinuous ridge leading to gonocoxal apodeme; ventrally, with paired, sclerotized, lobe-like processes. Gonocoxal apodemes absent. Lateral ejaculatory processes absent. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium. Ejaculatory apodeme laterally compressed, umbraculate (umbrella-

shaped) anteriorly. Aedeagal tines absent. Endoaedeagal process absent. Female terminalia with three spermathecae, clubbed, lightly to well sclerotized. Spermathecal ducts more than three times but less than five times the length of sternite 9, inflated at base of spermathecae. Spermathecal duct accessory glands absent. Ejection apparatus of spermathecal ducts sclerotized, with surface ringed furrows. Common spermathecal duct thickened, about the same length as the longest diameter of genital chamber. Genital chamber circular, small, occupying fraction of sternite 9 area. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end tapered to a point; posterior end with broad lateral extensions, free, held in vertical plane. Tergite 10 present. Tergite 10 narrow, split into two separate lateral sclerites; short (length less than half width). Sternite 10 roughly pentagonal, pointed posteriorly; almost entirely underneath cercus segments. Cercus one-segmented; separated from one another dorsally by approximately the width of the second cercal segment; without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. Paramonov (1962) provides a key to species for the Australian fauna. Nagatomi and Nagatomi (1987) provide a key to species for the Neotropical fauna.

List of included species

Species	Author, reference	Type country
Austroleptis atrata	Nagatomi & Nagatomi, 1987: 141	Chile
Austroleptis atriceps	Malloch, 1932: 203	Chile
Austroleptis breviflagella	Nagatomi & Nagatomi, 1987: 148	Chile
Austroleptis collessi	Paramonov, 1962: 138	Australia
Austroleptis fulviceps	Malloch, 1932: 202	Chile
Austroleptis multimaculata	Hardy, 1920: 128	Australia

Species	Author, reference	Type country
Austroleptis penai	Nagatomi & Nagatomi, 1987: 153	Chile
Austroleptis rhyphoides	Hardy, 1920: 127	Australia

Bolbomyiidae *status revised*

Genus BOLBOMYIA Loew

Figures 16c, 25-31, 179.

BOLBOMYIA Loew, 1850: 304. Type species *Bolbomyia nana* Loew, by subsequent monotypy (Loew, 1862: 188).

MISGOMYIA Coquillett, 1908: 145. Type-species *obscura* Coquillett, by original designation.

CEKENDIA Szilády, 1934: 264 (as subgenus of *Ptiolina* Zetterstedt, 1842). Type species *Ptiolina* (*Cekendia*) *wuorentausi* Szilády, by monotypy.

CECHENIA Frey, 1954: 9. Unjustified emendation.

DIAGNOSIS.

The best autapomorphy defining *Bolbomyia* species is the female terminalia, which have only two spermathecae and whose ducts lead directly to the genital chamber and attach to this structure independently, without joining into a common duct. Aedeagal tines are present in the male genitalia of *Bolbomyia*. Although aedeagal tines are also found in *Arthroceras* and in members of Athericidae and Tabanidae, the tines in *Bolbomyia* are likely independently derived and may represent another autapomorphic character state.

Species of *Bolbomyia* are small (2.3 to 3.5 mm), brown or black in color, with lightly infuscate wings, restricted to the north temperate region of North America and eastern Asia (Kamchatka). Males holoptic; antenna with basal flagellomere enlarged, elongate oval or subconical, laterally compressed, bearing 2 to 3 distal flagellomeres; laterotergite bare; wing vein M_3 absent; tibial spur formula 1:2:2; and tibia without macrochaetae. The fore tibial spur will separate *Bolbomyia* from nearly all other small brachycerans. *Litoleptis* is similar in size and appearance, but lacks tibial spurs on all tibia, bears a single elongate antennal flagellomere, and lacks the discal medial cell of the wing. *Ptiolina* is larger and more robust, and may be distinguished from *Bolbomyia* by the presence of wing vein M_3, by having only one hind tibial spur, and antenna with enlarged first flagellomere with a single-segmented style.

DESCRIPTION.

Clypeus not bulbous. Scape approximately the same size as pedicel. Flagellomeres 3 to 4; first flagellomere enlarged, elongate oval or subconical, laterally compressed, bearing weak setae; distal flagellomeres cylindrical, short (except terminal flagellomere which is more elongated). Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic, not flattened dorsally, ommatidia split into dorsal and ventral areas and smaller ventrally. Labella lacking pseudotrachae, shorter than palps. Theca short and stout; lateral sclerites adjacent and touching, but mostly separated. Palps two-segmented; distal segment longer than or about the same length as proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palps, tip not serrated. Mandibles absent. Cibarial pump short, as wide as long or wider. Cornu nearly as long as or longer than

cibarial pump. Pharyngeal pump narrow along most of length, mostly flat, longer than length of cibarial pump (cibarial pump very short). *Thorax*. Mesonotum without vittae. Dorsocentral setae not longer than other mesonotal setae. Anepisternum bare or bearing 1-2 setulae. Laterotergite bare. Postspiracular scale absent. Proscutellum present or absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing membrane lightly infuscate, without markings, pseudostigma absent or lightly present. Lower calypter reduced. Upper calypter well developed. Upper calypter with broad curvature, lobe-like, width twice length or less. Costa extends past wingtip, to approximately R_5. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed or absent; positioned distal to the humeral crossvein (h), by less than the length of h. Dorsal side of R_1 setulose, ventral side bare. Dorsal side of R_{2+3} with or without setulae, as ventral side. All other wing cells and veins bare. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward wingtip (creating convex flex anteriorly); longer than R_5, but less than twice as long. Base of R_4-R_5 fork distal of distal end of cell dm. R_4 at base relaxed, not strongly curved; nearly straight apically. R_5 anterior to, posterior to, or ending at wing tip; clearly longer than R_{4+5} (r-m to R_4 origin). M_3 wing vein absent. M-cu crossvein absent. Origin of CuA_1 at discal cell. CuA_2 greater than 2/3 length of posterior vein of bm cell. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Anal cell open. Halter knob 2/3 or longer than length of stem. Tibial spur formula 1:2:2. Hind coxal tubercle present. Hind tibial macrochaetae absent. Postmetacoxal bridge present as incomplete thin extension. *Abdomen*. Terminal abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 much longer than wide. Intersegmental membrane

between segments 7 and 8 short, as throughout abdomen. Sternite 8 cleavage superficial, open broadly; longer than wide or as long as wide. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly); rounded, virtually encircling cerci; not fused with cercus; anterior margin entire, with an even amount of sclerotization; posterior margin entire, with an even amount of sclerotization; tomentose, without setae. Cercus displaced away from epandrial sclerite; partially displaced from one another, separation distance approximately half the width of single cercus; held horizontal in relation to rest of abdomen; in posterior view cupped, forming circular outline medially. Hypandrium separated from the gonocoxites by a complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath not developed into bulbous sac or separate lobes. Lateral ejaculatory processes absent. Ejaculatory apodeme moderately long to long, reaching anterior margin of hypandrium, or somewhat beyond this. Ejaculatory apodeme tripartite; dorsally compressed laterally and ventrally, compressed dorso-ventrally. Aedeagal tines present. Endoaedeagal process present. Female terminalia with two spermathecae; spherical or elongate oval; sclerotization light to none. Spermathecal ducts less than three times the length of sternite 9. Spermathecal duct accessory glands absent. Circular ridge present at distal end of reinforced base of spermathecal ducts. Ejection apparatus of spermathecal ducts thickened, sclerotized, with ringed surface furrows; swelling present halfway between genital chamber and spermathecae. Common spermathecal duct absent.

Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end narrow with rounded tip; posterior end with narrow lateral extensions, free, held in vertical plane. Tergite 10 short (length less than half width). Sternite 10 roughly pentagonal, pointed posteriorly; posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, with ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring (sometimes slightly arched medially, but forming narrow elliptical opening only). Basal cerci adjacent dorsally. Second cercus segment not elongated, with apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. Webb (1987a) provides a key for the extant species of the world.

List of included species

Species (synonyms indented)	Author, reference	Type country
†*Bolbomyia loewi*	Meunier, 1902: 96	Baltic Region (Eocene/ Oligocene)
Bolbomyia melanderi	Chillcott, 1963: 1189	USA
Bolbomyia nana	Loew, 1862: 188	USA
Misgomyia obscura	Coquillett, 1908: 146	USA
Ptiolina mitis	Curran, 1931: 249	USA
Bolbomyia andiscalcella	Webb, 1969: 286	USA
Bolbomyia wuorentausi	(as *Cekendia*; Szilády, 1934: 264)	Russia
Bolbomyia macgillisi	Chillcott 1961: 634	USA

Rhagionidae

Genus ALLOLEPTIS Nagatomi and Saigusa

ALLOLEPTIS Nagatomi and Saigusa, 1982: 40. Type species *Alloleptis tersus* Nagatomi and Saigusa, by monotypy.

DIAGNOSIS.

Alloleptis is the only rhagionid genus with a tibial spur formula of 0:1:1. It is a small fly (body and wing length 3.8 mm), with antenna similar to those found in *Bolbomyia* (first flagellomere enlarged, bearing a short, two-segmented stylus). The antennal flagellomeres were lost prior to measurement and no illustration exists, however. *Alloleptis* may be distinguished immediately from *Bolbomyia* by having conspicuously setulose eyes and wing vein M_3 present. Other distinctive features include bare laterotergite, wing veins CuA_2 and A_1 join well before the wing margin (CuA_2+A_1 long), and the wings are darkly infuscate.

DESCRIPTION.

No specimens available for examination; character state scoring based on Nagatomi (1982, 1984). *Head*. Clypeus slightly bulbous. Scape slightly smaller than pedicel. First flagellomere enlarged bearing two-segmented stylus. Eyes conspicuously setulose; in male, holoptic. Palps one-segmented or two-segmented (the original description reads "probably two-segmented (if so, basal segment short)." The illustrations of the head (Nagatomi, 1982a: 56), however, show palp one-segmented). Mandibles absent. *Thorax*. Mesonotum and scutellum dark, with long, erect setae.

Wing membrane infuscate, without markings, without pseudostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa apparently extends past wingtip or at least to R_5. R_{2+3} nearly straight; longer than R_5, but less than twice as long. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 at base relaxed, not strongly curved, nearly straight apically. R_5 clearly longer than R_{4+5} (r-m to R_4 origin); ending at wingtip. M_3 wing vein present. Wing cell m3 parallel-sided at margin. Origin of CuA_1 at crossvein separating discal and basal medial cells. Length of CuA_2 v. posterior vein of bm cell less than 1/2 length of posterior vein of bm cell. Alula with broad curvature, rounded evenly. Anal lobe well developed. Anal cell closed (CuA_2 + A_1 vein as long or longer than CuA_2). Laterotergite bare. Subscutellum absent. Tibial spur formula 0:1:1. *Abdomen* is "comparatively long and narrow" (Nagatomi, 1982a: 41). Male genitalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite absent. Hypoproct tomentose, without setae. Cercus base held underneath epandrial sclerite. Cerci directly adjacent to one another, separation distance one quarter width of cercus or less. Hypandrium fused entirely to gonocoxites. Gonocoxite smooth dorsally, without sinuous ridge leading to gonocoxal apodeme. Gonocoxal apodemes very short. Parameral sheath narrow. Lateral ejaculatory processes present, integrated into sperm sac membrane. Ejaculatory apodeme moderately long, reaching slightly beyond margin, anteriorly; rod-shaped. Aedeagal tines absent. Endoaedeagal process present. Female are not known. *Larva*. The larvae are unknown.

LITERATURE. Illustrations of wing and head in Nagatomi (1982); male genitalia illustrated in Nagatomi (1984).

List of included species

Species (synonyms indented)	Author, reference	Type country
Alloleptis tersus	Nagatomi & Saigusa, 1982: 41	Celebes

Genus ARTHROCERAS Williston

Figures 16D, 32-41, 180.

ARTHROCERAS Williston, 1886: 107. Type species *Arthroceras pollinosum* Williston, by subsequent designation (Coquillett, 1910: 510). NOTE 1.

USSURIELLA Paramonov, 1929: 181. Type species *Ussuriella gadi* Paramonov, by monotypy.

PSEUDOCOENOMYIA Ôuchi, 1943: 493. Type species *Pseudocoenomyia sinensis* Ôuchi, by original designation.

DIAGNOSIS.

No obvious autapomorphic feature is known that defines *Arthroceras* conclusively. However, it retains the following unique combination of primitive and derived states: males are unique among orthorrhaphous flies in that their genitalia have both well-developed lateral ejaculatory processes and aedeagal tines. The spermathecal ducts of females are unique in that they are visibly inserted within the tubing that forms their

common junction, near the genital chamber. The female terminalia also have spermathecal duct accessory glands.

Arthroceras species are mid-sized to large (4.5 to 13 mm), black, gray, or often yellowish-colored flies that have a fairly long, tapering antenna consisting of 5-8 flagellomeres, mandibles absent, laterotergite setose, tibial spur formula 0:2:1, wing vein M_3 present; hind tibial macrochaetae absent; female tergite 9 without ventrolateral arms; female spermathecal ducts with accessory glands. *Arthroceras* are restricted to the Holarctic Region. They are distinguished from all other Rhagionidae by the form of their antenna, which is composed of 5-8 similarly sized flagellomeres, tapering distally (Figs. 12- 13). They may be distinguished from *Glutops* Burgess (Pelecorhynchidae) by their setose laterotergite and parafacials not swollen and from *Pseudoerrina* Shiraki (Pelecorhynchidae) by lacking conspicuously setulose eyes and fore tibial spurs.

DESCRIPTION.

Head. Clypeus bulbous. Scape smaller than or subequal to pedicel. First flagellomere slightly enlarged, round in cross section. Antenna with 5-8 flagellomeres of similar shape, tapering distally; terminal flagellomere usually more elongate. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic, ommatidia split into dorsal and ventral areas and smaller ventrally, not strongly flattened dorsally. Labella with pseudotrachae, longer or shorter than palps. Theca short and stout, divided into two separate, lateral sclerites. Palps two-segmented; distal segment longer than proximal segment. Stipes convergent toward one another medially. Lacinia present,

shorter than palps, tip not serrated. Mandibles absent. Cibarial pump long, clearly not as wide as long. Cornu nearly as long as or longer than cibarial pump. Pharyngeal pump moderately broad anteriorly, mostly flat along its length, approximately same length as cibarial pump (excluding cornu). *Thorax*. Mesonotum with or without vittae. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum setulose on dorsal and posterior margins. Laterotergite setose. Proscutellum absent. Subscutellum mostly flat or slightly bulbous. Wing hyaline, without markings, or membrane lightly infuscate. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wingtip or just past wingtip, to R_5. Humeral crossvein (h) well developed. Sc-r crossvein present, very weakly developed, positioned distal to the humeral crossvein (h), by the approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. Wing veins R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward wingtip (creating convex flex anteriorly). Length of R_{2+3} longer than R_5, but less than twice as long. R_{4+5} aligned with R_5. R_4 and R_5 contain wing tip. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 nearly straight apically. R_4 and R_5 encompass wing tip. R_5 aligned with R_{4+5}. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal side of central one-third of discal cell (or more centrally). CuA_1 origin at bm. CuA_2 greater than 1/2 length of posterior vein of bm cell, less than 2/3 length of posterior vein of bm cell. M_3 wing vein present. Alula full, rounded, with broad curvature. Anal lobe well developed. Anal cell open. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:2:1. Hind coxal tubercle absent. Hind tibial

macrochaetae absent. Postmetacoxal bridge absent. Epandrial sclerite wider than long. *Abdomen*. Abdominal segments evenly tapered. In female, last 3 abdominal segments telescoping; tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 especially long; sternite 8 as wide as long or wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly), setose. Cercus base held underneath epandrial sclerite. Cerci directly adjacent, separation distance one quarter width of cercus or less. Cerci, in posterior view cupped, forming circular outline medially. Hypandrium separated partially from the gonocoxites by an incomplete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath forming separate, distinct lobes ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium, rod-shaped or laterally compressed. Aedeagal tines present. Endoaedeagal process present. Female terminalia with three spermathecae, spherical, moderately to well sclerotized. Spermathecal ducts longer than five times the length of sternite 9, but not so long as to be difficult to measure; not inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at approximately halfway along the length of the spermathecal ducts. Ejection apparatus of spermathecal ducts thickened, sclerotized, with furrows. Common spermathecal duct thickened, about the same length as the longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to

genital chamber prominent, retains dye easily; with paired extensions posteriorly. Sternite 9 anterior end pointed, posterior end with broad extensions posteriorly that are held in horizontal plane. Tergite 10 partially split, short (length less than half width). Sternite 10 roughly pentagonal, pointed posteriorly, posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, with or without ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Basal cerci adjacent dorsally. Second cercus segment not elongated with or without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. Key to *Arthroceras* of the world in Nagatomi (1966). Key to Nearctic species in Webb (1987).

List of included species

Species (synonyms indented)	Author, reference	Type country
Arthroceras fulvicorne	Nagatomi, 1966: 46	Canada
Arthroceras fulvicorne nigricapite	Nagatomi, 1966: 49	USA
Arthroceras fulvicorne subsolanum	Nagatomi, 1966: 49	USA
Arthroceras subaquilum	Nagatomi, 1966: 59	USA
Arthroceras gadi	(as *Ussuriella*; Paramonov, 1929: 181)	Russia
Arthroceras japonicum	Nagatomi, 1954: 13	Japan
Arthroceras leptis	(as *Arthropeas*; Osten-Sacken, 1878: 223)	USA
Arthroceras pollinosum	Williston, 1886: 108	USA
Leptis pruinosus	Bigot, 1887: 115	USA
Arthroceras rubrifrons	Nagatomi, 1966: 56	Japan
Arthroceras sinense	(as *Pseudocoenomyia*; Ouchi, 1943: 493)	China

Genus ARTHROTELES Bezzi

Figures 42-48, 181.

ARTHROTELES Bezzi, 1926: 321. Type-species *Arthroteles bombyliiformis* Bezzi, 1926, by original designation.

DIAGNOSIS.

The most striking autapomorphy for this genus is the elongate, sclerotized proboscis, which is adapted for nectar feeding. At the base of the mouthparts, the cardo is swollen distinctively.

Species of *Arthroteles* are moderately sized (5 to 7.5 mm) flies of gray to dark gray coloration, having an antenna that bears seven to eight tapering flagellomeres (first flagellomere much larger than all others); eyes in male holoptic (with the exception of *A. longipalpus* Nagatomi & Nagatomi); laterotergite setose; tibial spur formula 0:2:2; wing vein M_3 present; short macrochaetae on all tibiae; female tergite 9 without ventrolateral arms; and female spermathecal ducts without accessory glands. *Arthroteles* is most similar to *Atherimorpha* in general form, but may be distinguished from this and all other related flies by the form of its mouthparts. It also differs from *Atherimorpha* in having hind coxal tubercles and short macrochaetae on all tibia.

DESCRIPTION.

Head. Clypeus bulbous, produced anteriorly. Scape approximately the same size as or slightly larger than pedicel. Flagellomeres 7-8, cylindrical; first flagellomere larger than other flagellomeres; terminal flagellomere more elongate than flagellomeres of

equal girth. Eyes inconspicuously setulose; in male, eyes holoptic or dichoptic (in *A. longipalpus* Nagatomi and Nagatomi only), flattened dorsally, ommatidia evenly distributed, of equal size (in *A. longipalpus* only) or ommatidia split into dorsal and ventral areas and smaller ventrally. Labella reduced, very short, with few pseudotrachae. Hypopharynx, labium, and labrum very elongate; theca lateral sclerites adjacent, apparently fused with suture. Palps two-segmented; distal segment longer than proximal segment. Lateral ridge of oral margin absent. Stipes surrounded by membrane above theca, directed posteriorly. Cardo swollen. Lacinia longer than palps; tip not serrated. Mandibles absent. Cibarial pump long, clearly not as wide as long. Cornu shorter than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat along its length, longer than length of cibarial pump. *Thorax.* Mesonotum with vittae. Dorsocentral bristles absent, all dorsal setae of equal length. Anepisternum bare. Laterotergite, katatergite, and anatergite indistinguishable. Laterotergite setose, in rows, mostly on katatergite. Proscutellum present. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly infuscate, without markings. Pseudostigma absent. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends past wingtip (to at least R_5). Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by the approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. R_{2+3} nearly straight, apical third of R_{2+3} ultimately bends slightly toward wingtip (creating concave flex posteriorly) (although very nearly straight). Length of R_{2+3} longer than R_5, but less than twice as long. Base of R_4-R_5

fork proximal or directly above distal end of cell dm. R_4 at base strongly curved or angled; nearly straight apically. R_4 and R_5 encompass wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). M_3 wing vein present. Wing cell m3 convergent at margin. Origin of CuA_1 at bm cell. CuA_2 about 2/3 length of posterior vein of bm cell. Alula with broad curvature, rounded evenly. Anal lobe well developed. Anal cell open. Halter knob between 1/3–1/2 length of stem. Tibial spur formula 0:2:2. Hind coxal tubercle present. Hind tibial macrochaetae present, short. *Abdomen*. Terminal abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 much longer than wide, intersegmental membrane between segments 7 and 8 especially long. Sternite 8 length wider than long or as wide as long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct triangular, tomentose, without setae. Cercus base held underneath epandrial sclerite, directly adjacent to one another, separation distance one quarter width of cercus or less. Cerci, in posterior view cupped, forming circular outline medially. Hypandrium separated from the gonocoxites by a complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, with shallowly paired swellings ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium, or long, reaching beyond anterior margin of hypandrium. Ejaculatory apodeme laterally compressed. Aedeagal tines absent. Endoaedeagal process present. Female terminalia with three spermathecae, swollen in shape, lightly sclerotized or

not sclerotized. Spermathecal ducts no more than three times the length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands absent. Spermathecal ducts near junction sclerotized, thickened, with surface furrows in rings. Spermathecal duct junction not thickened. Common spermathecal duct thickened, with apical transverse ridge and suture at junction of spermathecal ducts; long, clearly longer than longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end pointed; posterior end with broad lateral extensions, joined medially with seam, in vertical plane. Tergite 10 entire, short (length less than half width) (however, elongate in Nagatomi & Iwata, 1976). Sternite 10 entire, roughly pentagonal, pointed posteriorly; posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, with ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Basal cerci adjacent dorsally. Second cercus segment not elongated. Cercus with apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. Illustrations of mouthparts, antenna, wing, male and female genitalia, and dichotomous key to species is given by Stuckenberg (1956b). A new species is illustrated by Nagatomi and Nagatomi (1990a).

List of included species

Species (synonyms indented)	Author, reference	Type country
Arthroteles bombyliiformis	Bezzi, 1926: 322	South Africa
Arthroteles cinerea	Stuckenberg, 1956: 329	South Africa
Arthroteles longipalpis	Nagatomi & Nagatomi, 1990: 312	South Africa
Arthroteles orophila	Stuckenberg, 1956: 327	South Africa

Genus ATHERIMORPHA White

Figures 49-57.

ATHERIMORPHA White, 1915: 41. Type species *Atherimorpha vernalis* White, 1915, by monotypy.

BICALCAR Lindner, 1923: 4. Type species *Chrysopila obscuripennis* (Loew), 1873, by monotypy [misidentification = *Atherimorpha*]. NOTE 2.

THEREVIRHAGIO Lindner, 1925: 20. Type species *Therevirhagio setosiradiatus* Lindner, 1925, by monotypy.

PHILIPPOLEPTIS Malloch, 1931: 276 (as subgenus). Type species *Leptis praefica* Philippi, by original designation.

ARTHERIMORPHA Nagatomi, 1982a: 44 (lapsus).

NEORHAGIO Lindner, 1924: 75. Type species *Leptis setosa* Philippi, 1865, by monotypy. **NEW SYNONYMY.** NOTE 3.

DIAGNOSIS.

The phylogenetic analysis in the previous chapter indicated that South American *Atherimorpha* may be more closely related to the African genus *Arthroteles* than to other *Atherimorpha*. African species of *Atherimorpha* need to be studied further to verify this result.

The distinctive form of the antenna may provide evidence for the monophyly of the species of *Atherimorpha*. While the first flagellomere may vary in shape (from subglobose to onion-shaped to conical) and the total number of flagellomeres may also vary (3 to 7), the first flagellomere is always enlarged compared to the other flagellomeres, which are narrow and rod-like in form. Species of the genus *Atherimorpha* are small to moderately sized (4.4 to 11.4 mm) flies of coloration that varies from entirely gray or black and gray (as all Australian members of this genus) to brown, brown and yellow, entirely yellow, or orangish. Eyes in male holoptic or dichoptic, laterotergite setose, tibial spur formula 0:2:2, macrochaetae present on hind tibiae, and wing vein M_3 present.

Atherimorpha is very *Rhagio*-like in form and behavior, but can be distinguished from this genus by its antenna and by having two-segmented palps. *Atherimorpha* is most similar to *Arthroteles* in the form of its antenna, but it differs in that the first flagellomere is larger in comparison to the other flagellomeres and the other flagellomeres are narrower. *Atherimorpha* may be distinguished immediately from *Arthroteles* by its fleshy proboscis. *Atherimorpha* is distributed in South America, South Africa, and Australia and among these faunas, South America is the richest in terms of species number and morphological form and color, although many of these remain undescribed.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel or clearly larger than pedicel (as in *A. albohirta* and *A. praefica*). Flagellomeres 3 to 7; first flagellomere clearly larger than other flagellomeres, round in cross section or laterally compressed; round, conical, subglobose to globose, or fusiform; terminal flagellomere more elongate than other cylindrical flagellomeres. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic or dichoptic, not flattened dorsally, ommatidia evenly distributed, of equal size. Labella with pseudotrachae, longer or shorter than palps. Theca short and stout, lateral theca sclerites adjacent and touching, but mostly separated. Palps two-segmented; distal segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palps, tip not serrated. Mandibles absent. Cibarial pump long, clearly not as wide as long. Cornu shorter than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat along its length, approximately same length as cibarial pump. *Thorax*. Mesonotum with vittae. Dorsocentral bristles present or absent. Anepisternum bare. Laterotergite setose, in row(s), mostly on katatergite. Postspiracular scale absent. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly or darkly infuscate; without markings. Pseudostigma present or absent. Lower calypter reduced. Upper calypter well developed, with reduced curvature, width more than twice length. Costa extends to wingtip (between R_4 and R_5). Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed; positioned distal to the humeral crossvein (h), by less than the length of h, by the approximate length of h, or by more than the length of h. Dorsal side of R_1 setulose, ventral side with or without

setulae. Other wing veins and cells variously setulose or bare. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward wingtip (creating convex flex anteriorly). Length of R_{2+3} longer than R_5, but less than twice as long. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 at base strongly curved or angled, nearly straight apically. R_4 and R_5 encompass wing tip. R_5 aligned with R_{4+5}. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). Origin of CuA_1 at bm cell. M_3 wing vein present. Wing cell m3 parallel-sided at margin. CuA_2 greater than 2/3 length of posterior vein of bm cell. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Anal cell open or closed. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:2:2. Hind coxal tubercle absent. Hind tibial macrochaetae enlarged. First hind metatarsus of male not swollen. Postmetacoxal bridge absent. *Abdomen*. Terminal abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 about as long as wide, intersegmental membrane between segments 7 and 8 especially long, sternite 8 length wider than long or as wide as long (triangular, ovoid, or nearly square). Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite usually wider than long (longer than wide in *A. albohirta* and *A. praefica*), strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct margins entire, setose. Cercus base held underneath epandrial sclerite. Cerci directly adjacent to one another, separation distance one quarter width of cercus or less, held horizontal or at angle in relation to rest of abdomen; in posterior view, flat. Hypandrium separated from the gonocoxites by a complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of

hypandrium. Parameral sheath bulbous, with shallowly paired swellings ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium, laterally compressed. Aedeagal tines absent. Endoaedeagal process present. Female terminalia with three spermathecae, swollen, not sclerotized. Spermathecal ducts no more than three times the length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands absent. Spermathecal ducts near junction thickened, but not sclerotized, without surface furrows. Spermathecal duct junction thickened. Common spermathecal duct thickened, about the same length as the longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end pointed, posterior end with broad lateral extensions that meet medially, in vertical plane. Tergite 10 entire. Sternite 10 roughly rectangular, posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, with ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Basal cerci adjacent dorsally. Second cercus segment not elongated. Cercus with apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. A revision of the African fauna, including a key to species, is given by Nagatomi and Nagatomi (1990b). Malloch (1932a) gives a key to the Neotropical species. Paramonov (1962) treats the Australian species, and provides a key.

List of included species

Species (synonyms indented)	Author, reference	Type country
Atherimorpha agathae	Paramonov, 1962: 167	Australia
Atherimorpha albipennis	Bezzi, 1926: 318	South Africa
Atherimorpha albohirta	Malloch, 1932: 208	Argentina
Atherimorpha alisae	Paramonov, 1962: 158	Australia
Atherimorpha angustifrons	Nagatomi & Nagatomi, 1990: 44	South Africa
Atherimorpha atrifemur	Malloch, 1932: 210	Chile
Atherimorpha bevisi	Stuckenberg, 1956: 143	South Africa
Atherimorpha claripennis	(as *Leptis*; Philippi, 1865: 772)	Chile
Atherimorpha commoni	Paramonov, 1962: 164	Australia
Atherimorpha corpulenta	Paramonov, 1962: 166	Australia
Atherimorpha crassitibia	Nagatomi & Nagatomi, 1990: 52	South Africa
Atherimorpha edgari	Paramonov, 1962: 164	Australia
Atherimorpha edwardsi	Malloch, 1932: 212	Chile
†*Atherimorpha festuca*	Jell & Duncan, 1986: 181	Australia
Atherimorpha flavicorpus	Nagatomi & Nagatomi, 1990: 57	South Africa
Atherimorpha flavofasciata	Paramonov, 1962: 161	Australia
Atherimorpha flavolateralis	Malloch, 1932: 213	Argentina
Atherimorpha fulva	Hardy, 1920: 121	Australia
Atherimorpha fusca	Malloch, 1932: 213	Chile
Atherimorpha fuscicoxa	Malloch, 1932: 215	Chile
Atherimorpha gracilipennis	Nagatomi & Nagatomi, 1990: 59	South Africa
Atherimorpha grisea	(as *Leptis*; Philippi, 1865: 774)	Chile
Atherimorpha hirtula	Bigot, 1887: 116	Chile
Atherimorpha imitans	Malloch, 1932: 211	Chile
Atherimorpha infuscata	Paramonov, 1962: 162	Australia
Atherimorpha irwini	Nagatomi & Nagatomi, 1990: 59	South Africa
Atherimorpha latipennis	Stuckenberg, 1956: 144	South Africa
Atherimorpha longicornu	Nagatomi & Nagatomi, 1990: 59	South Africa
Atherimorpha lugens	(as *Leptis*; Philippi, 1865: 773)	Chile
Atherimorpha mcalpinei	Paramonov, 1962: 167	Australia
Atherimorpha mensaemontis	Stuckenberg, 1961: 116	South Africa
Atherimorpha montana	Hardy, 1927: 125	Australia
Atherimorpha nemoralis	(as *Leptis*; Philippi, 1865: 772)	Chile
Atherimorpha nigrata	(as *Leptis*; Philippi, 1865: 772)	Chile
Atherimorpha norrisi	Paramonov, 1962: 162	Australia
Atherimorpha occidens	Hardy, 1927: 126	Australia
Atherimorpha ornata	Nagatomi & Nagatomi, 1990: 74	South Africa
Atherimorpha praefica	(as *Leptis*; Philippi, 1865: 772)	Chile
Leptis setosus	(Philippi, 1865: 773) **Syn. Nov.**	Chile
Psilocephala macrochaeta	(Bigot, 1889: 325)	Chile
Psilocephala pilosa	(Bigot, 1889: 326)	Chile
Atherimorpha pusilla	Paramonov, 1962: 165	Australia
Atherimorpha rieki	Paramonov, 1962: 157	Australia

Species (synonyms indented)	Author, reference	Type country
Atherimorpha scutellaris	Malloch, 1932: 214	Chile
Atherimorpha setosiradiata	(as *Therevirhagio*; Lindner, 1925: 20)	Australia
Atherimorpha stuckenbergi	Nagatomi & Nagatomi, 1990: 79	South Africa
Atherimorpha subannulata	(as *Leptis*; Philippi, 1865: 771)	Chile
Atherimorpha tonnoiri	Paramonov, 1962: 159	Australia
Atherimorpha triangularis	Malloch, 1932: 234	Chile
Atherimorpha uptoni	Paramonov, 1962: 163	Australia
Atherimorpha vernalis	White, 1914: 42	Australia
Atherimorpha victoriana	Paramonov, 1962: 160	Australia
Atherimorpha villosissima	Paramonov, 1962: 158	Australia

Genus CHRYSOPILUS Macquart

Figures 58-65, 175, 186A.

CHRYSOPILUS Macquart, 1826: 403. Type species *Musca diadema* Linnaeus 1767, by designation of Westwood, 1840: 134 (misidentification) = *Rhagio aureus* Meigen, 1804.

LEPTIPALPUS Rondani, 1850: 183. Type species *Tabanus brasiliensis* Rondani 1850, by monotypy.

HELIOMYIA Doleschall, 1857: 402. Type species *Heliomyia ferruginea* Doleschall, 1857 [=*Leptis ferruginosus* Wiedemann, 1819], by monotypy.

MACELLOPALPUS Bigot, 1886: xlviii. Type species *Macellopalpus flaveolus* Bigot, 1886 [=*Leptis ferruginosus* Wiedemann, 1819], by monotypy.

†*PALEOCHRYSOPILA* Meunier, 1892: lxxxiii. Type species *Chrysopilus nagatomii* Evenhuis, 1994: 292 (= *Chrysopilus meunieri* Kerr, present work). NOTE 4.

POPPIUSIELLA Frey, 1918: 30 (as subgenus). Type species *Chrysopilus arctica*, by original designation. NOTE 5.

ACHRYSOPILUS Szilády, 1934: 255 (as subgenus; no type species given; name invalid by article 13.3 of the code).

SAPPOROMYIA Szilády, 1934: 233. Type species *Leptis basalis* Matsumura, 1915, by monotypy.

CHRYSOPILODES Frey, 1954: 15 (as subgenus). Type species *Chrysopilus boettcheri* Frey, 1954, by monotypy.

VARIOPILUS Frey, 1954: 22 (as subgenus). Type species *Chrysopilus aequicellulatus* Frey, 1954, by original designation.

SOLOMOMYIA Nagatomi, 1982a: 50. Type species *Solomomyia gressitti* Nagatomi, 1982a, by original designation. Correct original spelling by present revision. **New synonymy**. NOTE 6.

SOLOMYIA Nagatomi, 1982a: 68. Incorrect original spelling.

CHRYSOPILA, *CHRYSOPYLA*, errors for *Chrysopilus* Macquart.

DIAGNOSIS.

The monophyly of the species of *Chrysopilus* is uncertain, due to the recognition of *Schizella*, which shares all of the potential autapomorphies of the genus. These synapomorphies include thoracic setae that are slightly flattened, with a metallic sheen, often with structural color present and a reduced, bare proepimeron. *Chrysopilus* may also be paraphyletic with respect to *Stylospania*.

Chrysopilus species are delicate to fairly robust flies, variably sized (3.7 to 19 mm), usually with long, thin legs; black, gray, brown, or orange-brown; often with colored setae on thorax and/or abdomen that adds to color pattern. Wings are hyaline or infuscate, with or without markings; male holoptic (males dichoptic in a few African species; eyes separated in female); first flagellomere subcircular, laterally compressed, with terminal arista; mandibles absent; laterotergite setose; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia with short macrochaetae; tergite 9 without ventrolateral arms; female spermathecal ducts with accessory glands. *Chrysopilus* is cosmopolitan, found on all continents except Antarctica, throughout the tropics, up to near 4000m in Bolivia (pers. obs.); as far north as the Arctic circle, and as far south as Chiloé Island, Chile; in Africa, most *Chrysopilus* species are confined to humid montane forest (Stuckenberg, 1996). In the northern hemisphere, *Chrysopilus* species are most commonly confused with species of *Rhagio*, but may be distinguished by having a single hind tibial spur; arista with microsetae longer than width of arista; and a reduced, bare proepimeron. In the Philippines and possibly its surrounding area, *Chrysopilus* may be distinguished from *Schizella* and *Stylospania* solely by its antenna, which has the arista arising from the first flagellomere centrally (not ventrally), and is the same in both sexes (the female of *Stylospania* is unknown). In the southern hemisphere, *Chrysopilus* is distinguished from *Atherimorpha* by having a single hind tibial spur and aristate antenna.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere laterally compressed, rounded and slightly enlarged, bearing fused arista-like extension. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic or dichoptic, ommatidia evenly distributed, of equal size, or ommatidia split into dorsal and ventral areas and smaller ventrally, not flattened dorsally. Labella with pseudotrachae, longer or shorter than palps. Theca short and stout, divided into lateral sclerites that are tightly adjacent, apparently fused with suture. Palps one-segmented. Stipes surrounded by membrane above theca, directed posteriorly (very reduced). Lacinia present, shorter than palps, tip not serrated. Mandibles absent. Cibarial pump long, clearly not as wide as long. Cornu shorter than cibarial pump. Pharyngeal pump narrow and flat along most of length, approximately half the length of cibarial pump. *Thorax.* Mesonotum with or without vittae. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum setulose on dorsal margin only or setulose on dorsal and posterior margins. Laterotergite setose, throughout laterotergite. Metallic- or scale-like thoracic setae, often with structural color, present. Proscutellum absent. Subscutellum bulbous or not bulbous. Wing hyaline or infuscate, with or without markings; pseudostigma present or absent. Lower calypter reduced. Upper calypter variously developed. Costa extends to wingtip or past wingtip. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, or absent; positioned distal to the humeral crossvein (h), by less than the length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. Wing veins R_1 and R_{2+3} close together at wing margin. R_{2+3} sinuous, apical third ultimately bends toward leading edge of wing margin (creating concave flex anteriorly), length of R_{2+3} about the same length as R_5,

or longer. Base of R_4-R_5 proximal of, directly above, or distal of distal end of cell dm. R_4 at base usually strongly curved, leading directly to wing margin or with short proximal offshoot at point of curvature near R_5; along most of its length, nearly straight or lightly sinuous. R_4 and R_5 contain wing tip or R_4 ending at wing tip. R_5 longer or shorter than R_{4+5} (r-m to R_4 origin). R-m crossvein proximal to one-third of discal cell. Origin of CuA_1 at bm cell. CuA_2 greater than 2/3 length of posterior vein of bm cell. M_3 wing vein present. Alula full, rounded, with broad curvature. Anal lobe well developed. Anal cell closed. Halter knob between 1/3–1/2 length of stem. Tibial spur formula 0:2:1. Hind coxal tubercle absent. Hind tibial macrochaetae present, short. Postmetacoxal bridge present, reaching internally to base of metasternal furcum as incomplete thin extension. *Abdomen.* Abdominal segments evenly tapered. In female, last 3 abdominal segments telescoping; tergite 7 much longer than wide; intersegmental membrane between segments 7 and 8 especially long; sternite 8 as wide as long or wider than long. Male genitalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite present, divided medially, without setae. Hypoproct tomentose, without setae. Cerci directly adjacent to one another, separation distance one quarter width of cercus or less. Cerci, in posterior view flattened or lightly rounded. Hypandrium fused entirely to gonocoxites. Gonocoxite with or without dorsal sinuous ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, without paired swellings ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long to

long, reaching at least anterior margin of hypandrium. Ejaculatory apodeme rod-shaped or laterally compressed (often upside-down v-shaped in profile). Aedeagal tines absent. Endoaedeagal process absent. Female terminalia with three spermathecae, clubbed or swollen, lightly to moderately sclerotized. Spermathecal ducts no more than three times the length of sternite 9, not inflated at base of spermathecae, without swelling halfway between genital chamber and spermathecae. Spermathecal duct accessory glands present or absent; where present, arise at approximately the distal third of the spermathecal ducts or at the base of each spermatheca. Ejection apparatus of spermathecal ducts lightly sclerotized, not thickened, with surface furrows. Common spermathecal duct thickened, moderately long, about the same length as the longest diameter of genital chamber. Genital chamber elongate, occupying most of sternite 9 area. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end broadly paddle-shaped; posterior end with broad extensions posteriorly, held in vertical plane. Tergite 10 partially split or split into two separate lateral sclerites, short (length less than half width). Sternite 10 split into two sclerites, almost entirely underneath cercus segments. Cercus two-segmented. First segment of cercus not elongate, with or without ventral process. Ventral lobes of first segment of cercus curve ventrally towards one another to form a ring, visible in the posterior perspective. Basal cerci adjacent dorsally. Second cercus segment not elongated, with or without apical sensory pits. *Larva.* Body with 11 segments (not counting head). Thoracic segments with creeping welts ventrally. Head capsule not folded within second segment. Head capsule composed of a single, undivided plate (dorsal plate).

Head capsule less than 4.5 times longer than greatest width (1.5 width/ 4.5 length). Mandibular brush present, associated with simple fold of cuticle. Mandibular hook with external groove on adoral surface, smooth, without microsetae. Labral teeth developed, sclerotized, in two rows, converging anteriorly (teeth separated by central depression). Maxilla not sclerotized. Saw sclerite of mandibular base absent. Maxillary palp soft, segments poorly differentiated. Maxillary palp segment number three. Antenna last segment entire (as nub). Antenna three-segmented. Unpaired salivary pump absent. Posterior tentorial expansion free, with thin extension produced dorsally.

LITERATURE. Hardy (1949) gives to key to species of North America. Narchuk (1969) gives key to eastern European species. Yang et al. (1997) give key to species of China. Nagatomi (1978) gives key to species of Japan. For keys of *Chrysopilus* of Africa, see Stuckenberg (1965, 1996).

List of included species

Species (synonyms indented)	**Species reference**	**Species Type Country**
Chrysopilus aequalis	(as *Leptis*; Walker, 1848: 216)	Australia
Chrysopilus aequicellulatus	(as *Variopilus*; Frey, 1954: 22)	Argentina
Chrysopilus alaskaensis	Hardy, 1949: 147	USA
Chrysopi lus albicornis	de Meijere, 1914: 28	Java
Chrysopilus albobasalis	Brunetti, 1920: 140	India
Chrysopilus albopictus	Brunetti, 1909: 428	India
Chrysopilus alpicola	(as *Chrysopila*; Pokorny, 1886: 194)	Switzerland
Chrysopilus alternatus	Brunetti, 1920: 144	India
Chrysopilus amamiensis	Nagatomi, 1968: 33	Japan
Chrysopilus americanus	(as *Chrysopila*; Schiner, 1868: 197)	'South America'
Chrysopilus amulus	Kerr, **new name**.	Mexico
Chrysopila latifrons	Williston, 1901: 266. Preoccupied by *Chrysopilus*	Italy

Species (synonyms indented)	Species reference	Species Type Country
	latifrons Bezzi, 1898: 32.	
Chrysopilus amurensis	Soboleva, 1986: 112	Russia
Chrysopilus andersoni	Leonard, 1930: 131	USA
Chrysopilus andicola	Lindner, 1924: 71	Bolivia
Chrysopilus andringitrensis	Stuckenberg, 1965: 116	Madagascar
Chrysopilus androgynus	Paramonov, 1962: 123	Australia
†*Chrysopilus anglicus*	Cockerell, 1921: 471	England (Eocene/Oligocene)
Chrysopilus angustifacies	Hardy, 1949: 148	USA
Chrysopilus angustifrons	Frey, 1954: 18	Burma
Chrysopilus ankaratrae	Stuckenberg, 1965: 126	Madagascar
Chrysopilus anthracinus	Bigot, 1887: 105	USA
Chrysopilus antipoda	Bigot, 1887: 105	Australia
Chrysopilus antipodes	Nagatomi & Evenhuis, 1989: 298. *error*	Australia
Chrysopilus antongilensis	Stuckenberg, 1965: 150	Madagascar
Chrysopilus apicalis	Wulp, 1882: 119	Guadeloupe
Chrysopilus apicimaculatus	Yang & Yang, 1991: 274	China
Chrysopilus arctica	(as *Chrysopila*; Frey, 1918: 29)	Russia
Chrysopilus arctiventris	James, 1936: 343	USA
Chrysopilus argenteofasciatus	(as *Chrysopila*; Bromley, 1931: 9)	Guyana
Chrysopilus argenteus	Paramonov, 1962: 123	Australia
Chrysopilus argyrophorus	(as *Chrysopila*; Schiner, 1868: 199)	not given; South America
Chrysopilus ater	(as *Chrysopila*; Williston, 1896: 304	St. Vincent
Chrysopilus aterrimus	(as *Chrysopila*; Williston, 1901: 264)	Mexico
Chrysopilus atricornis	Stuckenberg, 1965: 149	Madagascar
Chrysopilus asiaticus	Lindner, 1923: 9	Central Asia
Chrysopilus auratus	(as *Atherix*; Fabricius, 1805: 73)	Denmark
Chrysopilus aureus	(as *Rhagio*; Meigen, 1804: 309)	not given; Europe
Rhagio diadema	Fabricius, 1775: 762. *misidentification*	"Lipsiae hortis"
Leptis vitripennis	Meigen, 1820: 101	not given; Europe
Rhagio aurulans	Meigen, 1820: 101	not given; Europe
Rhagio luridus	Meigen, 1820: 101	not given; Europe
Chrysopilus aureus meridionalis	Bezzi, 1898: 32	Italy
Chrysopilus austriacus	Kerr, **new name**	Austria
Chrysopilus unicolor	Becker, 1922: 71. Preoccupied by *Chrysopilus unicolor* Brunetti, 1909: 432.	Austria

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus aymara	Lindner, 1924: 72	Peru
Chrysopilus azurinus	Frey, 1954: 19	Philippines
Chrysopilus basalis	Walker, 1860: 285	Mexico
Chrysopilus basifasciatus	Paramonov, 1962: 124	Australia
Chrysopilus basiflavus	Yang & Yang, 1992: 355	China
Chrysopilus basilaris	(as *Leptis*; Say, 1823: 36)	USA
Chrysopilus batak	Kerr, **new name**	Sumatra
Chrysopilus tomentosus	de Meijere, 1924: 13. Preoccupied by *Chrysopilus tomentosus* Bigot, 1887: 104.	Sumatra
Chrysopilus beameri	Hardy 1949: 152	USA
Chrysopilus bequaerti	Curran,, 1931: 3	Cuba
Chrysopilus betsileorum	Stuckenberg, 1965: 118	Madagascar
Chrysopilus binoculatus	Edwards, 1915: 397	Indonesia
Chrysopilus binotatus	Loew, 1871: 62	Greece
Chrysopilus birmanensis	Brunetti, 1920: 137	Burma
Chrysopilus bisectus	Oldroyd, 1939: 17	Uganda
Chrysopilus bistriatipennis	Brunetti, 1927: 300	Malaya
Chrysopilus boettcheri	Frey, 1954: 15	Philippines
Chrysopilus brunneifrons	Kertész, 1902: 147	Peru
Chrysopilus caducus	(as *Leptis*; Wiedemann, 1828: 579)	Brazil
Chrysopilus terminalis	Macquart, 1846: 234	"Columbia, Venezuela"
Chrysopilus calchaqui	Coscaron & Coscaron, 1995: 267	Argentina
Chrysopilus calopterus	(as *Leptis*; Schiner, 1868: 579)	Brazil
Chrysopilus choui	Yang & Yang, 1989: 243	China
Chrysopilus chrysopiliformis	(as *Atherix*; Lindner, 1924: 69)	Bolivia
Chrysopilus clarapex	Frey, 1954: 18	Burma
Chrysopilus claricinctus	Lindner, 1923: 10	Central Asia
Chrysopilus clarus	(as *Leptis*; Walker, 1852: 164)	Brazil
Chrysopilus clemendoti	Stuckenberg, 1965: 131	Madagascar
Chrysopilus cochinensis	Brunetti, 1920: 136	India
Chrysopilus coeruleothorax	Lindner, 1925: 22	Fiji
Chrysopilus cognatus	Stuckenberg, 1965: 163	Madagascar
Chrysopilus collesi	Paramonov, 1962: 127	Australia
Chrysopilus commoni	Paramonov, 1962: 128	Australia
Chrysopilus connexus	Johnson, 1912: 108	USA
Chrysopilus consanguineus	Schiner, 1868: 197	Brazil
Chrysopilus correctus	Osten Sacken, 1882: 101	Philippines
Chrysopilus cricosphaerota	Speiser, 1914: 4	Cameroun
Chrysopilus cubensis	Curran, 1931: 5	Cuba
Chrysopilus dauricus	Frey, 1954: 22	Russia
Chrysopilus davisi	Johnson, 1912: 4	USA

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus decisus	(as *Leptis*; Walker, 1857: 15)	Malaya
Chrysopilus decoratus	de Meijere, 1911: 290	Java
Chrysopilus depressiconus	Frey, 1954: 20	Burma
Chrysopilus dilatus	Cresson, 1919: 177	USA
Chrysopilus diplostigma	Bezzi, 1917: 120	Philippines
Chrysopilus ditissimis	Bezzi, 1912: 451	Japan
Chrysopilus apyros	Séguy, 1948: 154	Japan
Chrysopilus dives	Loew, 1871: 62	Russia
Chrysopilus divisus	Hardy, 1949: 152	USA
Chrysopilus donato	Curran, 1931: 6	Panama
Chrysopilus edgari	Paramonov 1962: 130	Australia
Chrysopilus egregius	de Meijere,, 1919: 22	Sumatra
Chrysopilus elegans	Schiner, 1868: 198	Colombia
Chrysopilus erythrophthalmus	Loew, 1840: 3	Poland
Leptis hyalipennis	von Roser, 1840: 52	not given; Europe
Chrysopilus facetticus	Paramonov, 1962: 125	Australia
Chrysopilus fasciatus	(as *Leptis*; Say, 1823: 37)	USA
Leptis par	Walker, 1848: 215	USA
Chrysopilus fascipennis	(as *Macellopalpus*; Brunetti) 1920: 123	India
Chrysopilus fasciventris	Curran, 1931: 7	Panama
Chrysopilus fenestratus	(as *Chrysophilus*; Bezzi, 1912: 448)	Taiwan
Chrysopilus sanjodokeana	Matsumura, 1916: 348	Japan
Chrysopilus ferruginosus	(as *Leptis*; Wiedemann) 1819: 4	Indonesia
Heliomyia ferruginea	Doleschall, 1857: 402	Indonesia
Macellopalpus flaveolus	Bigot, 1886	Papua New Guinea
Chrysopilus frater	Brunetti, 1909: 431	Burma
Macellopalpus fulvidus	Brunetti, 1909: 424	India
Chrysopilus ferruginosus dimidiatus	Frey, 1954: 18	Vietnam
Chrysopilus ferruginosus philippinus	Frey, 1954: 18	Philippines
Chrysopilus ferruginosus burmanicus	Frey, 1954: 19	Burma
Chrysopilus fimbriatus	Stuckenberg, 1997: 238	South Africa
Chrysopilus flaveolus	(as *Leptis*; Meigen, 1820: 100)	"Alpen"
Chrysopilus flavibarbus	Adams, 1904: 438	USA
Chrysopilus cameroni	Curran, 1926: 170	USA
Chrysopilus aldrichi	James, 1936: 343	USA
Chrysopilus flaviscutellus	Yang & Yang, 1989: 290	China
Chrysopilus flavopilosus	Brunetti, 1920: 138	India
Chrysopilus flavopunctatus	Brunetti, 1909: 213	India
Chrysopilus foedus	Loew, 1861: 317	USA

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus fulvidus	Bigot, 1891: 370	Ivory Coast
Chrysopilus fuscicinctus	Brunetti, 1927: 299	Malaya
Chrysopilus fuscipes	Bigot, 1887: 103	France
Chrysopilus gansuensis	Yang & Yang, 1991: 95	China
Chrysopilus gemmiferus	Frey, 1954: 17	Laos
Chrysopilus georgianus	Hardy, 1949: 154	USA
Chrysopilus gilvipennis	Edwards, 1919: 30	Sumatra
Chrysopilus golbachi	Coscaron & Coscaron, 1995: 263	Argentina
Chrysopilus grandis	Yang & Yang, 1993: 3	China
Chrysopilus gratiosus	Paramonov, 1962: 131	Australia
Chrysopilus gravelyi	Brunetti, 1920: 137	India
Chrysopilus griffithi	Johnson, 1897: 119	USA
Chrysopilus griseipennis	Bezzi, 1912: 451	Formosa
Chrysopilus griveaudi	Stuckenberg, 1965: 113	Madagascar
Chrysopilus guangxiensis	Yang & Yang, 1992: 354	China
Chrysopilus guianicus	Curran, 1931: 5	Guyana
Chrysopilus guttipennis	Walker, 1861: 282	Indonesia
Chrysopilus guttulatus	de Meijere, 1914: 31	Indonesia
Chrysopilus fenestratus	de Meijere, 1913: 321. Preoccupied by *Chrysopilus fenestratus* Bezzi, 1912: 448.	Indonesia
Chrysopilus hakusanus	Nagatomi, 1978: 446	Japan
Chrysopilus hardyi	Nagatomi & Evenhuis, 1989: 297	Australia
Chrysopilus fascipennis	Hardy, 1933: 408. Preoccupied by *Chrysopilus fascipennis* (Brunetti, 1920: 123).	Australia
Chrysopilus helvolus	(as *Leptis*; Meigen, 1820: 100)	Switzerland
Chrysopilus heroicus	Paramonov, 1962: 126	Australia
Chrysopilus howei	Paramonov, 1962: 119	Lord Howe Island
Chrysopilus huashanus	Yang & Yang, 1989: 244	China
Chrysopilus hubeiensis	Yang & Yang, 1991: 274	China
Chrysopilus humeralis	Brunetti, 1912: 466	India
Chrysopilus humilis	Loew, 1874: 379	USA
Chrysopilus hybridus	Lindner, 1924: 73	Peru
Chrysopilus iani	Paramonov, 1962: 128	Australia
Chrysopilus illustris	Frey, 1954: 17	Burma
Chrysopilus imitator	Paramonov, 1962: 129	Australia
Chrysopilus impar	Walker, 1861: 282	Indonesia
Chrysopilus incidens	Curran, 1927: 95	Zaire
Chrysopilus indris	Stuckenberg, 1965: 151	Madagascar
Chrysopilus inka	Lindner, 1924: 73	Peru
Chrysopilus insularis	Schiner, 1868: 199	Nicobar Islands
Chrysopilus intermedius	Paramonov, 1962: 131	Australia
Chrysopilus intermedius	Bezzi, 1895: 42	Italy

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus invalidus	Williston, 1901: 265	Mexico
Chrysopilus irroratus	Schiner, 1868: 198	'South America'
Chrysopilus itoi	Nagatomi, 1958: 36	Japan
Chrysopilus ivontakae	Stuckenberg, 1965: 161	Madagascar
Chrysopilus jamaicensis	(as *Chrysopila*; Johnson, 1894: 273)	Jamaica
Chrysopilus keiseri	Stuckenberg, 1965: 158	Madagascar
Chrysopilus kimoroensis	Stuckenberg, 1965: 129	Madagascar
Chrysopilus kincaidi	Hardy, 1949: 156	USA
Chrysopilus komurae	Matsumura, 1911: 68	Russia
Chrysopilus kyotoensis	Frey, 1954: 23	Japan
Chrysopilus laetus	Zetterstedt, 1842: 224	Sweden
Chrysopilus lateralis	Oldroyd, 1939: 18	Uganda
Chrysopilus latifrons	Bezzi, 1898: 32	Italy
Chrysopilus latipennis	Stuckenberg, 1965: 156	Madagascar
Chrysopilus latistigma	Curran, 1931: 7	Panama
Chrysopilus latus	Brunetti, 1920: 143	India
Chrysopilus lemur	Stuckenberg, 1965: 124	Madagascar
Chrysopilus leonardi	Curran, 1931: 4	Puerto Rico
Chrysopilus leptiformis	Kertész, 1902: 148	Peru
Chrysopilus lii	Yang, Yang, and Nagatomi, 1997: 140	China
Chrysopilus lilianae	Soboleva, 1986: 114	Russia
Chrysopilus lineatus	Lindner, 1929: 267	Brazil
Chrysopilus lokobiensis	Stuckenberg, 1965: 144	Madagascar
Chrysopilus longipalpis	Hardy, 1949: 157	USA
Chrysopilus lucifer	Walker, 1852: 164	Colombia
Chrysopilus lucimaculatus	Yang & Yang, 1992: 355	China
Chrysopilus luctuosus	(as *Chrysophilus*; Brunetti, 1909: 430)	India
Chrysopilus luculentus	Nagatomi, 1968: 41	Japan
Chrysopilus ludens	Loew, 1861: 34	Cuba
Chrysopilus lugubrinus	de Meijere, 1924: 12	Sumatra
Chrysopilus lupinus	Osten Sacken, 1881: 420	Sumatra
Chrysopilus luteolus	(as *Leptis*; Fallén, 1814: 10)	Sweden
Chrysopilus mackerrasi	Paramonov, 1962: 120	Australia
Chrysopilus macu laris	Curran, 1931: 6	Puerto Rico
Chrysopilus maculipennis	(as *Chrysophilus*; Walker, 1857: 118)	Borneo
Chrysopilus madecassus	Stuckenberg, 1965: 134	Madagascar
Chrysopilus madecassus merinanus	Stuckenberg, 1965: 137	Madagascar
Chrysopilus maerens	Loew, 1873: 36	Not specified (Korfu or Herkulesbad?)

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus magnipennis	Brunetti, 1909: 213	Sumatra
Chrysopilus malaisei	Frey, 1954: 21	Burma
Chrysopilus marmoratus	Brunetti, 1909: 429	India
Chrysopilus mawambus	Kerr, **new name**	Africa ('Mawambi-Ukaika')
Chrysopilus obscuripes	Brunetti, 1927: 298. Preoccupied by *Chrysopilus obscuripes* Speiser, 1923: 98.	Africa ('Mawambi-Ukaika')
Chrysopilus mcalpinei	Paramonov, 1962: 121	Australia
†*Chrysopilus meunieri*	Kerr, **new name**	Baltic Region (Eocene/ Oligocene)
Chrysopilus nagatomii	Evenhuis 1994: 292. Preoccupied by *Chrysopilus nagatomii* Yang & Yang, 1991: 273.	Baltic Region (Eocene/ Oligocene)
Chrysopilus megacephalus	Stuckenberg, 1965: 142	Madagascar
Chrysopilus mexicanus	Bellardi, 1861: 196	Mexico
Chrysopilus modestus	Loew, 1872: 58	USA
Chrysopilus mojiangensis	Yang & Yang, 1989: 281	China
Chrysopilus montanorum	Paramonov, 1962: 132	Australia
Chrysopilus moramangensis	Stuckenberg, 1965: 160	Madagascar
Chrysopilus morimotoi	Nagatomi, 1968: 44	Japan
Chrysopilus mundus	Stuckenberg, 1965: 130	Madagascar
Chrysopilus mutabilis	Stuckenberg, 1965: 147	Madagascar
Chrysopilus nagatomii	Yang & Yang, 1991: 273	China
Chrysopilus nanus	Williston, 1901: 265	Mexico
Chrysopilus neimongolicus	Yang & Yang, 1990: 289	China
Chrysopilus nemoris	Stuckenberg, 1965: 153	Madagascar
Chrysopilus niger	Bellardi, 1862: 27	Mexico
Chrysopilus nigricauda	Beling, 1873: 547	Austria
Chrysopilus nigrifacies	Nagatomi, 1968: 44	Japan
Chrysopilus nigrimaculatus	Yang & Yang, 1991: 92	China
Chrysopilus nigrimarginatus	Yang & Yang, 1990: 281	China
Chrysopilus nigripalpis	Bezzi, 1912: 448	Formosa
Chrysopilus nigrocinctus	Brunetti, 1927: 297	Malaya
Chrysopilus ningminganus	Yang & Yang, 1993: 51	China
Chrysopilus nitidiventris	Tonnoir, 1927: 105	New Zealand
Chrysopilus niveofarinosus	Frey, 1954: 19	Philippines
Chrysopilus nobilipennis	Frey, 1954: 16	Philippines
Chrysopilus norrisi	Paramonov, 1962: 124	Australia
Chrysopilus nubecula	(as *Leptis*; Fallén, 1814: 9)	Sweden
Leptis auricollis	Meigen, 1820: 103	Europe ("Harz")
Chrysopilus nudus	Cresson, 1919: 177	USA
Chrysopilus obscuralatus	Yang & Yang, 1989: 245	China
Chrysopilus ningxianus	Yang & Yang, 1991: 94	China

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus obscuratus	de Meijere, 1914: 1630	Java
Chrysopilus obscuribarbus	(as *Chrysopila*; Loew) 1869: 99	'Central Asia'
Chrysopilus obscuripes	Speiser, 1923: 98	Malaya
Chrysopilus occidentalis	Kerr, **new name**	USA
Chrysopilus lucifer	Adams, 1904: 437. Preoccupied by *Chrysopilus lucifer* Walker, 1852: 164.	USA
Chrysopilus okutanii	Nagatomi, 1968: 49	Japan
Chrysopilus opacifrons	de Meijere, 1911: 288	Java
Chrysopilus opalescens	Brunetti, 1920: 134	Ceylon
Chrysopilus opalizans	de Meijere, 1913: 49	Indonesia
Chrysopilus ornatipennis	(as *Chrysophilus*; Brunetti, 1909: 212)	India
Chrysopilus ornatus	(as *Leptis*; Say, 1823: 34)	USA
Chrysopilus pallipes	(as *Chrysopila*; Loew, 1869: 54)	Greece
Chrysopilus pallipilosus	Yang & Yang, 1992: 354	China
Chrysopilus palparis	Loew, 1869: 50	Greece
Chrysopilus panamensis	Curran, 1931: 2	Panama
Chrysopilus parvus	Yang, Yang, and Nagatomi, 1997: 161	China
Chrysopilus pele	Kerr, **new name**	Brazil
Chrysopilus fascipennis	Bromley, 1931: 8. Preoccupied by *Chrysopilus fascipennis* (Brunetti, 1920: 123).	Brazil
Chrysopilus peruanus	Kertész, 1902: 149	Peru
Chrysopilus philippii	Lindner, 1924: 70	Peru
Chrysopilus pilosus	Leonard, 1930: 152	USA
Chrysopilus pingquanus	Yang, Yang, and Nagatomi, 1997: 163	China
Chrysopilus pingxianganus	Yang & Yang, 1992: 353	China
Chrysopilus plebeius	Williston, 1901: 264	Mexico
Chrysopilus poecilapterus	(as *Chrysophilus*; Bezzi, 1912: 450)	Taiwan
Chrysopilus stigmaticus	Statz, 1940: 129	Germany
Chrysopilus praetiosus	Loew, 1869: 55	Greece
Chrysopilus propinquus	Kertész, 1902: 146	Mexico
Chrysopilus proximus	(as *Leptis*; Walker, 1848: 214)	USA
Leptis propinquus	Walker, 1848: 215	USA
Chrysopilus puella	Williston, 1901: 265	Mexico
Chrysopilus pullus	Loew, 1869: 43	Germany
Chrysopilus pusilla	(as *Atherix*; Macquart 1855: 88)	Australia
Chrysopilus quadratus	(as *Leptis*; Say, 1823: 35)	USA
Leptis fumipennis	Say, 1823: 37	USA
Leptis reflexus	Walker, 1848: 216	USA

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus dispar	Wulp, 1867: 143	USA
Chrysopilus flavidus	Bigot, 1887: 104	USA
Leptipalpis limbipennis	Bigot, 1887: 107	USA
Leptipalpis obscuripennis	Bigot, 1887: 107	USA
Chrysopilus rhagiodes	Bromley, 1931: 8	Panama
Chrysopilus rotundipennis	Loew, 1861: 317	USA
Chrysopilus rufipes	Macquart, 1850: 103. NOTE 7	Australia
Chrysopilus ruiliensis	Yang & Yang, 1990: 280	China
Chrysopilus saffranus	(as *Leptipalpis*; Bigot, 1887: 108)	Chile
Chrysopilus sauteri	Bezzi 1907: 564	Taiwan
Chrysopilus matsumurai	Nagatomi, 1968: 42	Japan
Leptis basalis	Matsumura, 1915: 39	Japan
Chrysopilus schnusei	Lindner, 1924: 74	Peru
Chrysopilus segmentatus	Brunetti, 1909: 430	Nepal
Chrysopilus sericeus	Bromley, 1931: 9	Guyana
Chrysopilus shaanxiensis	Yang & Yang, 1989: 244	China
Chrysopilus shananus	(as *Chrysophilus*; Frey, 1954: 21)	Burma
Chrysopilus shibuyai	Nagatomi, 1968: 51	Japan
Chrysopilus siculus	Loew, 1869: 49	Italy
Chrysopilus sigillatus	Lindner, 1930: 65	Costa Rica
Chrysopilus silvaticus	Nagatomi, 1968: 53	Japan
Chrysopilus silvicola	Nagatomi, 1968: 54	Japan
Chrysopilus similis	Brunetti, 1920: 138	Ceylon
Chrysopilus simillimus	de Meijere, 1914: 29	Java
Chrysopilus simplex	de Meijere, 1904: 97	Java
Chrysopilus smaragdinus	Kertész, 1902: 145	Peru
Chrysopilus sogai	Stuckenberg, 1965: 120	Madagascar
Chrysopilus sordidus	Brunetti, 1920: 143	India
Chrysopilus chlorophthalmus	Loew, 1840: 4	not given; Europe
Chrysopilus splendidus	Meigen, 1820: 102	Germany
Chrysopilus squamithorax	Brunetti, 1927: 297	Malaya
Chrysopilus stigma	Brunetti, 1909: 432	Burma
Chrysopilus stigmatias	(as *Leptipalpus*; Bigot, 1887: 106)	USA
†*Chrysopilus stigmaticus*	Cockerel, 1921: 471	England (Eocene/Oligocene)
Chrysopilus strigipennis	de Meijere, 1914: 26	Java
Chrysopilus stylatus	Walker, 1864: 208	Indonesia
Chrysopilus subaquilis	Nagatomi, 1968: 56	Japan
Chrysopilus sucini	Stuckenberg, 1965: 138	Madagascar
Chrysopilus suomianus	(as *Achrysopilus*; Szilády, 1934: 256)	Finland
Chrysopilus superbus	Stuckenberg, 1965: 140	Madagascar
Chrysopilus tanakai	Nagatomi, 1978: 451	Japan

Species (synonyms indented)	Species reference	Species Type Country
Chrysopilus tasmaniensis	White, 1914: 40	Australia
Chrysopilus tenggeranus	Frey, 1934: 308	Java
Chrysopilus testaceipes	Bigot, 1887: 105	USA
Chrysopilus bellus	Adams, 1904: 438	USA
Chrysopilus testaceus	Loew, 1858: 367	South Africa
Chrysopilus rhodesiensis	Bruggen, 1960: 297	Zimbabwe
Chrysopilus thoracicus	(as *Leptis*; Fabricius, 1805: 70)	USA
Chrysopilus tomentosus	Bigot, 1887: 104	USA
Chrysopilus tonnoiri	Paramonov, 1962: 126	Australia
Chrysopilus torrentium	Thomas, 1978: 311	France
Chrysopilus trifasciatus	Walker, 1860: 284	Mexico
Chrysopilus trimaculatus	Yang & Yang, 1989: 245	China
Chrysopilus tsacasi	Thomas, 1979: 136	Morocco
Chrysopilus tuckerei	Bezzi, 1929: 320	South Africa
Chrysopilus turkestanus	Lindner, 1931: 85	Turkestan
Chrysopilus ugensis	Nagatomi, 1968: 59	Japan
Chrysopilus ungaranensis	de Meijere, 1911: 291	Java
Chrysopilus unicolor	Brunetti, 1909: 432	India
Chrysopilus unicus	Curran, 1931: 3	Panama
Chrysopilus vacillans	Walker, 1858: 89	Indonesia
Chrysopilus vadoni	Stuckenberg, 1965: 165	Madagascar
Chrysopilus valdivianus	Philippi, 1865: 774	Chile
Chrysopilus varius	Kertész, 1902: 150	Peru
Chrysopilus velutinus	Loew, 1861: 316	USA
Chrysopilus vespertinus	Stuckenberg, 1965: 145	Madagascar
Chrysopilus villosissimus	Paramonov, 1962: 129	Australia
Chrysopilus virtuosus	Nagatomi, 1958: 33	Japan
Chrysopilus waigiensis	(as *Leptipalpus*; Bigot, 1887: 108)	Indonesia
Chrysopilus wirthi	Stuckenberg, 1997: 241	South Africa
Chrysopilus xanthocromus	Yang & Yang, 1990: 280	China
Chrysopilus xanthopus	Hardy, 1949: 163	USA
Chrysopilus xizangensis	Yang & Yang, 1991: 93	China
Chrysopilus yerburyi	Brunetti, 1920: 139	Ceylon
Chrysopilus yezonis	Nagatomi, 1968: 61	Japan
Chrysopilus yunnanensis	Yang & Yang, 1990: 279	China
Chrysopilus zanjensis	Stuckenberg, 1965: 154	Madagascar

nomina dubia	Author, reference
Musca asiliformis	Preyssler, 1791: 99
Leptis cristatus	Fabricius, 1775: 782

Genus DESMOMYIA Brunetti

Figures 66-68, 182.

DESMOMYIA Brunetti, 1912: 462. Type species *Desmomyia thereviformis* Brunetti, by original designation.

DIAGNOSIS.

Desmomyia is characterized by having the antennal scape elongated, clearly longer than the pedicel; and the male hind first tarsomere enlarged. Both of these character states are autapomorphies for the genus.

Species of *Desmomyia* are mid-sized flies (5.0 to 6.7 mm) of gray, black, or brownish coloration; legs with some yellow or concolorous dark brown to black; wings lightly infuscate, with light markings; male holoptic (eyes widely separated in female); laterotergite setose, wing vein M_3 present, tibial spur formula 0:2:2, and hind tibia with or without short macrochaetae. *Desmomyia* is restricted to India and China. It is most likely to be confused with *Rhagio*, which is very similar in general appearance, and overlaps *Desmomyia* in its geographic distribution. The males of *Desmomyia* are distinguished by the autapomorphic characters of the antenna and hindleg mentioned above and may also be separated from nearly all *Rhagio* males by having pronounced, swollen parafacials. Females may be separated reliably from *Rhagio* by having the scape longer than pedicel. *Desmomyia* is distinguished from *Chrysopilus* by having two hind tibial spurs and by lacking thoracic setae that have a metallic sheen, in addition to the autapomorphic character states mentioned above.

DESCRIPTION.

Head. Clypeus bulbous. Scape clearly larger than pedicel. First flagellomere laterally compressed, enlarged basally, bearing fused or distinct arista-like extension. Eyes inconspicuously setulose; in male, ommatidia evenly distributed, of equal size, or ommatidia split into dorsal and ventral areas and smaller ventrally, holoptic, not flattened dorsally. Parafacials in male swollen. Labella with pseudotrachae, longer or about the same size as palps. Theca short and stout. Palps one-segmented. *Thorax.* Mesonotum with or without vittae. Dorsocentral bristles absent, all dorsal setae of equal length. Anepisternum setulose on dorsal and posterior margins. Laterotergite katatergite swollen, differentiated from anatergite. Laterotergite setose, on katatergite only. Postspiracular scale absent. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline, without markings. Pseudostigma present. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wingtip. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed; positioned distal to the humeral crossvein (h), by the approximate length of h. Dorsal side of R_1 setulose, ventral side of R_1 bare. All other wing veins without setulae. Apical third of R_{2+3} ultimately bends toward leading edge of wing margin (creating concave flex anteriorly). Length of R_{2+3} about the same length as R_5. Base of R_4-R_5 fork proximal to or directly above distal end of cell dm. R_4 at base relaxed, not strongly curved; nearly straight apically. R_4 and R_5 encompass wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein proximal to one-third of discal cell. Origin of CuA_1 at bm cell. M_3 wing vein present. Wing cell m3 convergent at margin. Length of CuA_2 v. posterior vein of

bm cell less than 1/2 length of posterior vein of bm cell. Alula narrow curvature, rounded evenly. Anal lobe well developed. Anal cell closed. Halter knob approximately 1/2 length of stem. Tibial spur formula 0:2:1. Hind coxal tubercle absent. Hind tibial macrochaetae present, short. First hind metatarsus of male swollen. Abdomen. Terminal *Abdomen.* Abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 much longer than wide; intersegmental membrane between segments 7 and 8 especially long. Sternite 8 sclerite entire, not divided into two segments, length wider than long or as wide as long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite absent. Hypoproct tomentose, setae absent. Cercus base held underneath epandrial sclerite. Cerci partially displaced from one another, separation distance approximately half the width of single cercus. Cerci, in posterior view flat, held in horizontal orientation. Hypandrium separated partially from the gonocoxites by an incomplete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, without paired swellings ventrally. Lateral ejaculatory processes present, integrated into sperm sac membrane. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium or long, reaching beyond anterior margin of hypandrium; laterally compressed. Aedeagal tines absent. Endoaedeagal process present. Female terminalia with three spermathecae, elliptical, lightly sclerotized. Spermathecal ducts longer than five times the length of sternite 9, but not so long as to be difficult to measure; not inflated at base of spermathecae. Spermathecal duct

accessory glands absent. Ejection apparatus of spermathecal ducts not sclerotized, without surface furrows. Spermathecal duct junction thickened. Common spermathecal duct thickened; short, shorter than longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end pointed; posterior end with broad lateral extensions which are joined medially with seam, in the vertical plane. Tergite 10 not greatly reduced. Sternite 10 entire, roughly pentagonal, pointed posteriorly; posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, without ventral process. Ventral portions of first segment of cercus do not curve ventrally, towards one another, to form a ring. Basal cerci adjacent dorsally. Second cercus segment not elongated, without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE. Yang et al. (1997) illustrate the species from China.

List of included species

Species (synonyms indented)	Author, reference	Type country
Desmomyia sinensis	Yang & Yang, 1997: 181	China
Desmomyia thereviformis	Brunetti, 1912: 462	India

Genus LITOLEPTIS Chillcott

Figures 69-72.

LITOLEPTIS Chillcott, 1963: 1186. Type species *Litoleptis alaskensis* Chillcott, by original designation. NOTE 8.

DIAGNOSIS.

Several autapomorphic features support the monophyly of *Litoleptis*. The wing lacks the medial crossvein (so that the discal cell is absent); all tibiae are without spurs; the male aedeagus is very weakly developed, lacking an aedeagal apodeme; and the gonocoxal apodemes are also absent. Unfortunately, the female terminalia have not been described in the literature and I have been unable to examine any females personally, so these characters remain unknown and its phylogenetic placement remains uncertain.

Litoleptis is composed of species that are small (1.8 to 2.7 mm); black in color; with hyaline wings; dichoptic eyes in the male; antenna bearing a single, elongated, tapering flagellomere; bare laterotergite; discal cell and wing vein M_3 absent; and tibial spur formula of 0:0:0. This genus also shows an unusual disjunct distribution; *Litoleptis* species are found in Alaska, Chile, and the Philippines. This is among the most distinctive of rhagioniform Diptera, however it is most likely to be confused with *Hilarimorpha*, an asiloid either placed in its own family, Hilarimorphidae, or within Bombyliidae. *Litoleptis* differs from *Hilarimorpha* in having a pulvilliform empodium; antenna bearing a single, tapering flagellomere; and wing veins R_5 and R_{4+5} subequal in length. *Litoleptis* may also be confused with *Spania* on account of its similar size and the shape of its antenna. *Litoleptis* may be distinguished from other small flies within Tabanomorpha, such as *Bolbomyia* and *Spania*, by the absence of the discal cell of the wing, dorsal surface of wing membrane bare, lack of tibial spurs, and eyes in male dichoptic.

DESCRIPTION.

Head. Clypeus slightly bulbous. Pedicel clearly larger than scape. First flagellomere laterally compressed or rounded in cross section. First flagellomere of antenna elongate as long tapering segment or oval and enlarged near base, with straight, tapering stylus. Eyes inconspicuously setulose; in male, dichoptic (but not widely separated), not flattened dorsally, ommatidia split into dorsal and ventral areas and smaller ventrally. Labella without pseudotrachae, about the same size as palps. Theca short and stout. Palps one-segmented. Tentorium low on the face. Mandibles absent. Cibarial pump long, narrow (clearly not as wide as long). *Thorax*. Mesonotum without vittae. Anepisternum bare. Laterotergite bare. Postspiracular scale absent. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline, without markings, without pseudostigma. Lower calypter reduced. Upper calypter triangular in form, underdeveloped. Upper calypter with broad curvature, lobe-like, width twice length or less. Costa stops before wingtip or extends past wingtip. Humeral crossvein (h) weakly developed. Sc-r crossvein present, well developed, positioned at proximal side of humeral crossvein (h), by less than length of h. All wing veins and cells bare. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward leading edge of wing margin (creating concave flex anteriorly); longer than R_5, but less than twice as long.Base of R_4-R_5 fork distal of distal end of cell dm. R_4 at base nearly straight entire length. R_5 anterior to, posterior to, or ending at wing tip; about as long as R_{4+5} (r-m to R_4 origin). M_3 wing vein absent. M-cu crossvein absent. Discal cell absent. CuA_2 greater than 2/3 length of posterior vein of bm cell. CuA_2 does not reach wing margin. Alula reduced, without curvature or with narrow

curvature. Alula full, rounded evenly. Anal lobe well developed. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:0:0. Hind coxal tubercle absent. Hind tibial macrochaetae absent. Postmetacoxal bridge absent. *Abdomen*. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long; strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly); flattened, distinct from sclerites above cerci; with or without setae. Cercus displaced away from epandrial sclerite; widely displaced from one another, separation distance greater than three quarters width of cercus; held vertical in relation to rest of abdomen; in posterior view flat. Hypandrium fused entirely to gonocoxites; in *L. alaskensis*, with broad ventral processes separated by a central notch. Gonocoxite smooth dorsally, without sinuous ridge leading to gonocoxal apodeme. Gonocoxal apodemes absent. Parameral sheath not developed into bulbous sac or separate lobes. Lateral ejaculatory processes absent. Ejaculatory apodeme reduced, nearly absent. Ejaculatory apodeme laterally compressed. Aedeagal tines absent. Endoaedeagal process absent. Female unavailable and remains undescribed. *Larva*. The larvae are unknown.

LITERATURE. Chillcott (1963) illustrated the head, wing, and male genitalia of *L. alaskensis*. Hennig (1972) compared the three species currently described in the genus, and illustrated the head, wing and male genitalia of *L. chilensis*.

List of included species

Species (synonyms indented)	Author, reference	Type country
Litoleptis alaskensis	Chillcott, 1963: 1187	USA
Litoleptis chilensis	Hennig, 1972: 6	Chile
Litoleptis orientalis	(as *Hilarimorpha*; Frey, 1954: 25)	Philippines

Genus OMPHALOPHORA Becker

Figures 73, 74A, 75, 76A, 77-83.

OMPHALOPHORA Becker 1900: 12. Type species *Omphalophora oculata* Becker, 1900: 13, by monotypy.

DIAGNOSIS.

The monophyly of *Omphalophora* is supported by the unique form of the female tergite 9, which is distinctively bulbous and tapers posteriorly. Partially sclerotized lobes located in the membrane between the ninth tergite and ninth sternite may also be a synapomorphy for the group. *Omphalophora* and *Ptiolina* are very similar in their antennal form and general habitus, but phylogenetic analysis reveals that they form a paraphyletic grade when grouped together. Therefore, the recognition of *Omphalophora* Becker is merited.

Omphalophora species are delicate to fairly robust flies, small to moderately sized (3.0 to 10.0 mm) that are entirely black or brown in color. Wings are hyaline or infuscate near wing veins; male holoptic, eyes separated in female; antenna with unsegmented terminal stylus, round or lightly laterally compressed in cross section; mandibles absent; laterotergite bare; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding and fusing to sternite 9 laterally; female spermathecal ducts with accessory glands. *Omphalophora* is restricted to the Holarctic Region. *Omphalophora* is easily confused with *Ptiolina*. It may be distinguished from this

genus by having setose anepisternum, wing veins R_{4+5} containing the wing tip, the female 7th tergite clearly longer than wide (in *Ptiolina*, this tergite is clearly wider than long), and in the male, the subepandrial sclerite is as wide as long or nearly oval and the gonostylus comes to a sharp point apically. Species of *Omphalophora* may be confused with *Symphoromyia* but is immediately distinguished from this genus by having the scape approximately the same size as the pedicel, first flagellomere longer than wide (elongated anteriorly, not reniform), and bare laterotergite. *Omphalophora* may be distinguished from *Bolbomyia* by the unsegmented style, by lacking fore tibial spurs, and by having wing vein M_3 present. *Omphalophora* is usually significantly larger than *Spania* and also differs by having a hind tibial spur.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere lightly compressed laterally or rounded in cross section (may vary from specimen to specimen), bearing stylus of single segment. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic, not strongly flattened dorsally, ommatidia evenly distributed, gradually smaller toward ventral margin. Labella with pseudotrachae, length variable. Theca short and stout, with medial suture. Palps one- or two-segmented. When two-segmented, distal palp segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, shorter than palps, not serrated at tip. Mandibles absent. Cibarial pump short, as long as wide or slightly longer than wide. Cornu shorter than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat, approximately same

length as cibarial pump. *Thorax.* Mesonotum usually with vittae, but may be without. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum haired throughout posterior half. Laterotergite bare. Proscutellum usually present. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly infuscate, without markings. Costa extends to R_5, at wingtip. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by approximate length of h or less. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. Wing veins R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward leading edge of wing margin, creating concave flex anteriorly. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 nearly straight apically or curving slightly towards anterior margin. R_4 and R_5 encompass wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal one-fifth to near halfway of discal cell. M_3 wing vein present. M-cu crossvein present. Origin of CuA_1 at bm cell. CuA_2 greater than 1/2 length, less than 2/3 length of posterior vein of bm cell. Anal lobe well developed. Alula full, rounded with broad curvature. Anal cell closed. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:2:1. Hind tibial spur short. Hind coxal tubercle absent. Hind tibial macrochaetae absent (long delicate setae sometimes present). Postmetacoxal bridge absent. *Abdomen.* Abdominal segments evenly tapered. In female, last 3 abdominal segments telescoped; tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 especially long; sternite 8 as wide as long or

wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite present, undivided, narrow (clearly wider than long), setose. Hypoproct present, setose. Cercus base held underneath epandrial sclerite, or directly adjacent to epandrial sclerite. Cerci displaced from one another, separation distance greater than three quarters width of cercus. Cerci, in posterior view flat or cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath forming separate, distinct lobes ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium. Ejaculatory apodeme tubular. Aedeagal tines absent. Endoaedeagal process present; short, blunt, rounded. Female terminalia with tergite 9 entire, with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Spermathecae three, clubbed, sclerotized. Spermathecal ducts more than three times but less than five times the length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at approximately the distal third of the spermathecal ducts. Spermathecal ducts near junction with common duct not sclerotized. Common spermathecal duct thickened; of moderate length, about the same length as the longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Accessory gland posterior to genital chamber common duct present with short paired extensions

posteriorly. Sternite 9 anterior end narrowly paddle-shaped, posterior end with broad extensions posteriorly, joined together in horizontal plane centrally, held in vertical plane laterally. Tergite 10 entire; short, length less than half width. Sternite 10 sclerotization weakened centrally, making it appear as if sclerite divided into two lateral components. Sternite 10 roughly rectangular or ovoid, pointed posteriorly. Cercus two-segmented. First segment of cercus not elongate, without ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Basal cerci separated from one another dorsally by approximately the width of the second cercal segment. Second cercus segment narrow, elongated (~3x longer than wide or more), with apical sensory pits. *Larva.* Unknown, probably very similar to *Ptiolina*.

LITERATURE.

Omphalophora species descriptions and treatments are almost entirely contained within the body of work covering the genus *Ptiolina*. Hardy and McGuire (1947) provide a key to North American species. Narchuk (1969) gives key to eastern European species.

List of included species

Species (synonyms indented)	Author, reference	Type country
Omphalophora cinereofasciata	(as *Leptis*; Schummel, 1837: 109)	"Sanderberg" Europe
Ptiolina phragmitophila	Schiner, 1868: 910	Austria
Ptiolina calamodytes	Schiner, 1868: 911	Slovakia
Ptiolina fulva	Becker, 1900: 110	Siberia
Omphalophora fasciata	(as *Ptiolina*; Loew, 1869: 164)	Canada
Omphalophora majuscula	(as *Ptiolina*; Loew, 1869: 165)	Canada
Omphalophora nigripilosa	(as *Ptiolina*; Hardy & McGuire,	USA

Species (synonyms indented)	Author, reference	Type country
	1947: 9)	
Omphalophora oculata	Becker, 1900: 106	Russia
Omphalophora lapponica	Frey, 1911: 16	Finland

Genus PTIOLINA Zetterstedt

Figures 74B, 76B, 84-96, 183-184, 188-192.

PTIOLINA Zetterstedt, 1842: 226. Type species *Leptis obscura* Fallén, by subsequent designation of Frauenfeld, 1867: 497. NOTE 9.

EURYTION Jaennicke, 1867: 99. Type species *Eurytion paradoxus* Jaennicke, 1867: 99, by monotypy.

TYOLINA Walker, 1848: 220. Misspelling.

SPATULINA Szilády, 1942: 625. Type species *Spatulina engeli* Szilády, by monotypy. NOTE 10.

DIAGNOSIS.

The monophyly of *Ptiolina* is supported by the unique form of the female tergite 9 which is rectangular and narrow, with ventrolateral arms that are easily distinguished from sternite 9.

Ptiolina species are delicate to fairly robust flies, small to moderately sized (3.0 to 10.0 mm), that are entirely black or brown in color. Wings are hyaline or infuscate near wing veins; male holoptic, eyes separated in female; antenna with unsegmented terminal stylus, round or laterally compressed in cross section; mandibles absent; laterotergite bare; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding

and fusing to sternite 9 laterally; female spermathecal ducts with accessory glands. *Ptiolina* is restricted to the Holarctic Region and although it is fairly distinctive for this region, it may be confused with *Symphoromyia. Ptiolina* may be immediately distinguished from this genus by having the scape approximately the same size as the pedicel, first flagellomere longer than wide (elongated anteriorly, not reniform), and bare laterotergite. *Ptiolina* may be distinguished from *Bolbomyia* by the unsegmented style, by lacking fore tibial spurs, and by having wing vein M_3 present. *Ptiolina* is usually significantly larger than *Spania* and also differs by having a hind tibial spur.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere enlarged, laterally compressed, bearing stylus of single segment. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic, not strongly flattened dorsally, ommatidia split into dorsal and ventral areas and smaller ventrally. Labella with pseudotrachae, length variable. Theca short and stout, with medial suture. Palps one- or two-segmented. When two-segmented, distal palp segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, shorter than palps, not serrated at tip. Mandibles absent. Cibarial pump short, as long as wide or slightly longer than wide. Cornu shorter than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat, approximately same length as cibarial pump. *Thorax.* Mesonotum with or without vittae. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum bare. Laterotergite bare. Proscutellum present or absent. Subscutellum not enlarged

nor lengthened; inconspicuous. Wing hyaline or lightly infuscate, without markings. Costa extends to R_5, at wingtip (in *P. nitida*, it extends past wingtip). Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by approximate length of h or less. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. Wing veins R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward leading edge of wing margin, creating concave flex anteriorly. Length of R_{2+3} shorter than or about the same length as R_5. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 nearly straight apically or curving slightly towards anterior margin. R_5 ending anterior to or at wing tip, clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal one-fifth to near halfway of discal cell. M_3 wing vein present. M-cu crossvein present. Origin of CuA_1 at bm cell. CuA_2 greater than 1/2 length, less than 2/3 length of posterior vein of bm cell. Anal lobe well developed. Alula full, rounded with broad curvature. Anal cell closed. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:2:1. Hind tibial spur short. Hind coxal tubercle absent. Hind tibial macrochaetae absent (long delicate setae sometimes present). Postmetacoxal bridge absent. *Abdomen.* Abdominal segments evenly tapered. In female, last 3 abdominal segments telescoped; tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 especially long; sternite 8 as wide as long or wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite present,

undivided, narrow (clearly wider than long), setose. Hypoproct present, setose. Cercus base held underneath epandrial sclerite, or directly adjacent to epandrial sclerite. Cerci displaced from one another, separation distance greater than three quarters width of cercus. Cerci, in posterior view cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath forming separate, distinct lobes ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme short or moderately long, not reaching anterior margin of hypandrium. Ejaculatory apodeme rod-shaped or laterally compressed. Aedeagal tines absent. Endoaedeagal process absent or present (when present, reduced). Female terminalia with tergite 9 entire, with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Spermathecae three, clubbed, sclerotized. Spermathecal ducts no more than three times the length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at the base of each spermatheca. Spermathecal ducts near junction with common duct sclerotized, thickened, with furrows. Common spermathecal duct thickened; short, shorter than longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Accessory gland posterior to genital chamber common duct present with short paired extensions posteriorly. Sternite 9 anterior end narrowly paddle-shaped, posterior end with broad extensions posteriorly, joined together in horizontal plane centrally, held in vertical plane laterally. Tergite 10 entire; short,

length less than half width. Sternite 10 sclerotization weakened centrally, making it appear as if sclerite divided into two lateral components. Sternite 10 roughly pentagonal, pointed posteriorly (very broad, wider than long; nearly rectangular). Cercus two-segmented. First segment of cercus not elongate, without ventral process. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Basal cerci separated from one another dorsally by approximately the width of the second cercal segment. Second cercus segment narrow, elongated (~3x longer than wide or more), with apical sensory pits. *Larva.* Body with 11 segments. Thoracic segments with creeping welts ventrally. Head capsule not folded within second segment. Head capsule composed of a single, undivided plate (dorsal plate). Head capsule less than 4.5 times longer than greatest width (1.5 width/5.0 length). Mandibular brush absent. Mandibular hook without groove or canal, smooth, without microsetae. Labral teeth very well developed, heavily sclerotized, in two rows, converging anteriorly. Maxilla sclerotized (strongly toothed, with three teeth). Saw sclerite of mandibular base absent. Maxillary palp soft, segments poorly differentiated, three-segmented. Antenna one-segmented. Antenna last segment entire, dome-shaped, short. Unpaired salivary pump absent. Posterior tentorial expansion fused to each other posteriorly, with thin extension produced anteriorly.

LITERATURE.

Hardy and McGuire (1947) provide a key to North American species. Narchuk (1969) gives key to eastern European species.

List of included species

Species tentatively placed in the genus are indicated by an asterisk (*). These species require inspection to verify their placement.

Species (synonyms indented)	Author, reference	Type country
*Ptiolina alberta**	Leonard in Curran, 1931: 259	Canada
Ptiolina attenuata	Nagatomi, 1986: 311	Japan
*Ptiolina augusta**	Curran, 1931: 249	Canada
Omphalophora cinereofasciata	(as *Leptis*; Schummel, 1837: 109)	"Sanderberg" Europe
Ptiolina phragmitophila	Schiner, 1868: 910	Austria
Ptiolina calamodytes	Schiner, 1868: 911	Slovakia
Ptiolina fulva	Becker, 1900: 110	Siberia
*Ptiolina dudai**	Lindner, 1942: 240	Austria
Ptiolina edeta	(as *Spania*; Walker, 1849: 489)	Canada
Atherix vidua	Walker, 1849: 1153	Canada
Ptiolina grisea	Curran, 1931: 251	USA
Omphalophora fasciata	(as *Ptiolina*; Loew, 1869: 164)	Canada
Ptiolina grandis	Frey, 1918: 31	Russia
Ptiolina arctica	Becker, 1921: 62	Russia
*Ptiolina latifrons**	Nagatomi, 1986: 312	Taiwan
*Ptiolina longipilosa**	Nagatomi, 1986: 314	Japan
Omphalophora majuscula	(as *Ptiolina*; Loew, 1869: 165)	Canada
Ptiolina mallochi	Hardy & McGuire, 1947: 8	USA
Ptiolina arctica	Malloch, 1923: 181. Preoccupied by *Ptiolina arctica* Becker, 1921: 62.	USA
*Ptiolina nervosa**	Nagatomi, 1986: 317	Japan
Omphalophora nigripilosa	(as *Ptiolina*; Hardy & McGuire, 1947: 9)	USA
Ptiolina nitida	Wahlberg, 1854: 215	Norway
Ptiolina nitidifrons	Hardy & McGuire, 1947: 10	USA
Ptiolina obscura	(as *Leptis*; Fallén, 1814: 11)	Sweden
Ptiolina nigra	Zetterstedt, 1842: 227	Sweden
Ptiolina nigrina	Wahlberg, 1854: 215	Sweden
Ptiolina nigripes	Zetterstedt, 1859: 4975	Sweden
Tyolina tristis	Walker, 1949: 220	Great Britain
Ptiolina obsoleta	(as *Ptiolina*; Leonard in Curran, 1931: 250)	USA
Omphalophora oculata	Becker, 1900: 106	Russia
Omphalophora lapponica	Frey, 1911: 16	Finland
Ptiolina uralensis	Becker 1921: 62	Russia
*Ptiolina paradoxa**	(as *Eurytion*; Jaennicke, 1866: 99)	Switzerland
Ptiolina lapidaria	Nowiczki, 1868: 74	Poland
Ptiolina wodzickii	Frauenfeld, 1867: 497	not given; Europe
Spania grisea	Strobl, 1892: 124	Austria

Species (synonyms indented)	Author, reference	Type country
*Ptiolina pelliticornis**	Becker, 1900: 113	Italy
Ptiolina shimai	Nagatomi, 1985: 211	Nepal
*Ptiolina sphaeralis**	Nagatomi, 1986: 320	Japan
Ptiolina vicina	Hardy & McGuire, 1947: 12	USA
Ptiolina zonata	Hardy & McGuire, 1947: 13	USA

Genus RHAGIO Fabricius

Figures 97-111, 176, 193.

RHAGIO Fabricius, 1775: 761. Type species *Musca scolopacea* Linnaeus, 1758, by subsequent designation of Latreille, 1810: 443.

LEPTIS Fabricius, 1805: 69 (unjustified emendation for *Rhagio* Fabricius, 1775). Type-species *Musca scolopacea* Linnaeus, 1758, automatic.

†*PALAEOHILARIMORPHA* Meunier, 1902: 400. Type species *Palaeohilarimorpha bifurcata* Meunier, 1902, by monotypy.

RHAGINA Malloch, 1932: 117. Type species *Leptis incurvata* de Meijere, 1911. ***New synonymy***. NOTE 11.

RHAGIONELLA Szilády, 1934: 239 (as subgenus). Type species *Nemotelus maculatus* De Geer, 1776, by original designation.

RHAGIELLA Szilády, 1934: 240 (as subgenus). Type species *Rhagio lineola* Fabricius, 1794, by original designation.

DIAGNOSIS.

The monophyly of the species of *Rhagio* is supported by a unique feature found in the larva. All *Rhagio* larvae have a saw sclerite attached ventrally to the basal mandibular sclerite. The autapomorphic nature of this character state is evident among

tabanomorph larvae. However, the larva of many *Rhagio* species remain undescribed and the larva of putatively closely related genera such as *Desmomyia* and *Atherimorpha*, among many other rhagionid taxa, are also not known.

Rhagio species are delicate to fairly robust flies, variably sized (4.2 to 18 mm); black, gray, brown, orange-brown, yellow or yellow and black. Wings are hyaline or infuscate, with or without markings; male holoptic or dichoptic, eyes separated in female; first flagellomere subcircular, laterally compressed, with terminal arista arising ventrally or from central position; mandibles absent; laterotergite setose; wing vein M_3 present; tibial spur formula 0:2:2; hind tibia with short macrochaetae when present; tergite 9 without ventrolateral arms; female spermathecal ducts without accessory glands. *Rhagio* is distributed throughout the Holarctic Region. *Rhagio* species are most commonly confused with species of *Chrysopilus*, but may be distinguished by having two hind tibial spurs; an arista that is nearly bare; and a prominently setose proepimeron. In India, and perhaps in surrounding areas, *Rhagio* may be distinguished from local *Desmomyia* by having the scape approximately the same size as pedicel and in the male, first tarsomere not enlarged. *Rhagio* is very similar in form to *Atherimorpha*, although their distributions are not sympatric. *Rhagio* may be distinguished immediately from *Atherimorpha* by having an aristate antenna.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere. First flagellomere of antenna enlarged; basally rounded in cross section or laterally compressed, bearing fused or arista-like extension. Eyes inconspicuously setulose; in male, holoptic or dichoptic (dichoptic in female), not flattened dorsally; ommatidia evenly distributed of equal size or ommatidia larger dorsally with smooth transition to slightly smaller ommatidia ventrally. Labella with pseudotrachae, length variable. Theca short and stout, lateral thecal sclerites separated. Palps one-segmented, often with constriction, making it appear that there are two palp segments. Stipes convergent toward one another medially or surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palps; tip not serrated. Mandibles absent. Cibarial pump long, clearly not as wide as long. Cornu nearly as long as or longer than cibarial pump. Pharyngeal pump narrow along most of length, mostly flat along its length, approximately same length as cibarial pump. *Thorax.* Mesonotum with or without vittae. Dorsocentral bristles absent, all dorsal setae of equal length. Anepisternum bare (*R. maculatus* De Geer, *R. dichomaticus* Chillcott), setulose on dorsal margin only, or throughout posterior half of sclerite. Laterotergite setose, on katatergite only. Postspiracular scale absent. Proscutellum present or absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly infuscate; with or without markings. Wing with or without pseudostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa ends before or approximately at wingtip Humeral crossvein (h) well developed. Sc-r crossvein present, well developed, positioned distal to the humeral crossvein (h), by more than the length of

h. Dorsal side of R_1 setulose, ventral side bare. All other wing cells and veins bare. R_{2+3} nearly straight or sinuous; longer than but less than twice as long as R_5; apical third ultimately bends either toward leading edge of wing margin (creating concave flex anteriorly) or toward wingtip (creating convex flex anteriorly). Base of R_4-R_5 fork proximal of, directly above, or distal of distal end of cell dm. R_4 at base strongly curved or angled; leads directly to wing margin or with short proximal offshoot at point of curvature near base; nearly straight or sinuous apically (as in *R. tuberculatus* (Yang et al., 1997: 245)); anterior to, ending at, or posterior to wing tip. R_5 clearly longer than R_{4+5} or about as long as R_{4+5} (r-m to R_4 origin). M_3 wing vein present. Wing cell m3 parallel-sided at margin. Origin of CuA_1 at bm cell. CuA_2 greater than 1/2 length of posterior vein of bm cell and greater or less than 2/3 length of posterior vein of bm cell. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Anal cell open or closed. Halter knob approximately 1/2 length of stem. Tibial spur formula 0:2:2. Hind coxal tubercle absent or present. Hind femora with or without ventro-apical swelling. Hind tibial macrochaetae absent or present; when present, short. First hind metatarsus of male not swollen. Postmetacoxal bridge present. Postmetacoxal bridge reaching to internal base of metasternal furcum as incomplete thin extension. Abdomen. Terminal *Abdomen.* Abdominal segments 5–10 evenly tapered from segments 1–4. In female, tergite 7 much longer than wide; intersegmental membrane between segments 7 and 8 especially long; sternite 8 length variable, wider than long to much longer than wide. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct with or without

setae. Cercus attached to hypoproct, displaced away from epandrial sclerite; partially displaced from one another, separation distance approximately half the width of single cercus. Cerci, in posterior view flat. Hypandrium separated from the gonocoxites by a complete or incomplete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, without paired swellings ventrally. Lateral ejaculatory processes present, integrated into sperm sac membrane. Ejaculatory apodeme long, reaching beyond anterior margin of hypandrium; laterally compressed. Aedeagal tines absent. Endoaedeagal process present, very reduced (as in *R. plumbeus*), or apparently absent (as in *R. punctipennis*). Female terminalia with three spermathecae, spherical or elliptical, lightly sclerotized or without sclerotization. Spermathecal ducts longer than five times the length of sternite 9, but not so long as to be difficult to measure. Spermathecal duct accessory glands absent. Ejection apparatus of spermathecal ducts thickened, lightly sclerotized, surface furrows that run at an angle. Spermathecal duct junction thickened. Common spermathecal duct thickened; short, shorter than longest diameter of genital chamber. Genital chamber oval, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end pointed; posterior end with broad lateral extensions, free, held in horizontal plane. Tergite 10 length aproximately equal to half measured width, or longer. Sternite 10 entire, roughly pentagonal, pointed posteriorly; posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, with or without ventral process. Ventral lobes of first segment of cercus

curve ventrally towards one another to form a ring, visible in the posterior perspective. Basal cerci adjacent dorsally. Second cercus segment not elongated, with or without apical sensory pits. *Larva.* Body with 11 segments, amphipneustic. Thoracic segments with creeping welts ventrally. Head capsule not folded within second segment, composed of a single, undivided plate (dorsal plate); less than 4.5 times longer than greatest width (2 width/ 5.5 length); not cone-shaped. Mandibular brush present, associated with simple fold of cuticle. Mandibular hook canal with apical opening. Hook serrate, transversely smooth. Stiff microsetae pointing anteriorly on dorsal ridge of mandibular hook absent. Labral teeth developed, sclerotized; in single row. Maxilla sclerotized (and thrice toothed, as in *Ptiolina*). Saw sclerite of mandibular base present. Maxillary palp soft, segments poorly differentiated. Maxillary palp segment number three. Antenna last segment entire (nub). Antenna three-segmented. Unpaired salivary pump absent. Posterior tentorial expansion free, with thin extension produced dorsally.

LITERATURE.

Chillcott (1965) gives a key to the species of Eastern North America. Narchuk (1969) provides a key to the species of Russia. Yang et al. (1997) give key to species of China.

List of included species

Species (synonyms indented)	Author, reference	Type country
Rhagio albicornis	(as *Leptis*; Say, 1823: 38)	USA
Xylophagus fasciatus	Say, 1829: 155	Canada
Leptis boscii	Macquart, 1840: 30	USA
Rhagio albipilosus	Becker, 1921: 47	Turkey

Species (synonyms indented)	Author, reference	Type country
Rhagio albus	Yang, Yang, and Nagatomi, 1997: 191	China
Rhagio algericus	(as *Leptis*; Becker, 1906: 282)	Algeria
Rhagio alumnus	Walker, 1852: 163	"South America"
Rhagio amurensis	Makarkin, 1992: 255	Russia
Rhagio annulatus	(as *Nemotelus*; De Geer, 1776: 164)	
Leptis conjugens	(as *Leptis*; Ruthe, 1831: 1214)	not given, prob. Sweden
Rhagio apiciflavus	Yang & Yang, 1991: 275	China
Rhagio apicipennis	(as *Leptis*; Brunetti, 1909: 423)	India
Rhagio arcuatus	(as *Leptis*; de Meijere, 1911: 292)	India
Rhagio ardea	Fabricius, 1794: 275	'Europe'
Rhagio asticta	Yang & Yang, 1994: 32	China
Rhagio balcanicus	(as *Leptis*; Strobl, 1902: 475)	Yugoslavia
Rhagio basiflavus	Yang & Yang, 1993: 48	China
Rhagio basimaculatus	Yang & Yang, 1993: 48	China
Rhagio beckeri	Lindner, 1923: 7	France
† *Rhagio bifurcatus*	(as *Palaeohilarimorpha*; Meunier, 1902: 400)	Baltic Region (Eocene/Oligocene)
Rhagio biroi	Szilády, 1934: 8. NOTE 12	India
Rhagio bisectus	Yang, Yang, and Nagatomi, 1997: 200	China
Rhagio bitaeniatus	(as *Leptis*; Bellardi, 1862: 26)	Mexico
Rhagio brunneipennis	Leonard, 1930: 92	USA
Rhagio calcaratus	Statz, 1940: 128	Germany
Rhagio californicus	Leonard, 1930: 93	USA
Rhagio cavannae	(as *Leptis*; Bezzi, 1898: 28)	Italy
Rhagio centrimaculatus	Yang & Yang, 1993: 47	China
Rhagio chillcotti	James, 1965: 333	Canada
Rhagio choui	Yang & Yang, 1997: 205	China
Rhagio chrysopilaeformis	(as *Leptis*; Bezzi, 1898: 31)	Italy
Rhagio chrysostigma	(as *Leptis*; Loew, 1857: 33)	Yugoslavia
Rhagio cinerascens	(as *Leptis*; von Röder, 1884: 2)	Italy
Rhagio cinereus	(as *Leptis*; Bellardi 1861: 95)	Mexico
Rhagio cingulatus	(as *Leptis*; Loew, 1856: 28)	Russia
Rhagio cingulatus canescens	Szilády, 1934: 243	France
Rhagio conspicuus	Meigen, 1804: 299	Russia
Leptis janotae	Nowicki, 1867: 349	Czechoslovakia
Leptis conspicuus alpinus	Loew, 1869: 35	Austria
Leptis conspicuus florentinus	Loew, 1869: 34	Italy
Leptis marchalii	Pierre, 1889: 5	France

Species (synonyms indented)	Author, reference	Type country
Rhagio corsicanus	Becker, 1910: 640	France
Rhagio costalis	Matsumura, 1911: 68	Russia
Rhagio costatus	(as *Leptis*; Loew, 1826: 187)	USA
Rhagio costimaculata	Matsumura, 1916: 330	Japan
Rhagio dichromaticus	Chillcott, 1965: 788	USA
Rhagio difficilis	Becker, 1921: 54	Greece
Rhagio dimidiatus	(as *Leptis*; Loew, 1863: 10)	USA
Leptis albibarbis	Bigot, 1887: 114	USA
Leptis pleuralis	Adams, 1904: 441	USA
Leptis flavoniger	Coquillett, 1904: 20	USA
Rhagio discoidalis	(as *Leptis*; Brunetti, 1912: 463)	India
Rhagio elenae	Soboleva, 1991: 96	Russia
Rhagio ephippium	(as *Leptis*; Zetterstedt, 1842: 219)	Sweden
Rhagio expansus	James, 1964: 564	USA
Rhagio franciscanus	James, 1964: 565	USA
† *Rhagio expassus*	(as *Leptis*; Meunier, 1910: 69)	Baltic Region (Eocene/ Oligocene)
† *Rhagio exporrectus*	(as *Leptis*; Meunier, 1910: 70)	Baltic Region (Eocene/ Oligocene)
† *Rhagio expositus*	(as *Leptis*; Meunier, 1910: 71)	Baltic Region (Eocene/ Oligocene)
† *Rhagio exsanguis*	(as *Leptis*; Meunier, 1910: 70)	Baltic Region (Eocene/ Oligocene)
† *Rhagio fascinatoris*	(as *Leptis*; Meunier, 1910: 71)	Baltic Region (Eocene/ Oligocene)
† *Rhagio ferus*	(as *Leptis*; Meunier, 1910: 72)	Baltic Region (Eocene/ Oligocene)
Rhagio filius	(as *Atherix*; Walker, 1848: 219)	USA
Rhagio flavicornis	(as *Leptis*; Macquart, 1826: 402)	Japan
Rhagio flavimedia	(as *Leptis*; Coquillett, 1898: 307)	Japan
Rhagio floridensis	Chillcott, 1965: 789	USA
Rhagio formosus	Bezzi, 1912: 445	Taiwan
†*Rhagio fossitius*	Melander, 1949: 29	USA (Miocene)
Rhagio freyae	Lindner, 1923: 8	Germany
Rhagio funebris	Meigen, 1820: 98	not given; Europe
Rhagio fuscipennis	(as *Leptis*; Meigen, 1820: 93)	Austria
Rhagio gansuensis	Yang & Yang, 1997: 207	China
Rhagio gracilis	(as *Leptis*; Johnson, 1912: 3)	USA
Rhagio graeculus	(as *Leptis*; Loew, 1869: 32)	Greece
Rhagio grandis	Szilády, 1934: 248	France
Rhagio guadarramensis	Czerny & Strobl, 1909: 166	Spain
Rhagio guangxiensis	Yang & Yang, 1993: 46	China
Rhagio guizhouensis	Yang & Yang, 1992: 587	China
Rhagio hainanensis	Yang, Yang, and Nagatomi, 1997: 212	China

Species (synonyms indented)	Author, reference	Type country
Rhagio hangzhouensis	Yang & Yang, 1989: 291	China
Rhagio huashanensis	Yang & Yang, 1997: 215	China
Rhagio idaeus	Bezzi, 1908: 390	Greece
Rhagio immaculatus	(as *Leptis*; Meigen, 1804: 301)	not given; Europe
Rhagio immaculatus hahnleae	Lindner, 1923: 9	Germany
Rhagio incisus	(as *Leptis*; Loew, 1872: 59)	USA
Rhagio insularis	Becker, 1921: 55	Greece
Rhagio iriomotensis	Nagatomi & Nagatomi, 1990: 38	Japan
Rhagio itoi	Nagatomi, 1952: 11	Japan
Rhagio japonicus	Matsumura, 1916: 346	Japan
Rhagio javanus	Lindner, 1925: 21	Java
Rhagio jinxiuensis	Yang & Yang, 1993: 50	China
Rhagio karafutonis	Matsumura, 1916: 343	Japan
Rhagio latipennis	(as *Leptis*; Loew, 1856: 19)	Germany
Rhagio libanonicus	Szilády, 1934: 252	Lebanon
Rhagio lineola	Fabricius, 1794: 275	Denmark
Rhagio albifrons	Meigen, 1804: 300	Austria
Leptis lineola monticola	Egger, 1860: 348	Austria
Leptis albifrons monticola	Egger, 1860: 668	Austria
Leptis lineola andalusica	Strobl, 1909: 166	Spain
Leptis lineola polonica	Szilády, 1934: 241	Poland
Rhagio longshengensis	Yang & Yang, 1993: 50	China
Rhagio longzhouensis	Yang & Yang, 1993: 49	China
Rhagio luteus	Soboleva, 1984: 122	Russia
Rhagio lutifaciatus	Okada, 1941: 256	Japan
Rhagio maculatus	(as *Nemotelus*; De Geer, 1776: 165)	not given; Europe
Rhagio annulatus	Meigen, 1804: 299	not given; Europe
Rhagio nigrofasciatus	Meigen, 1804: 301	not given; Europe
Leptis distigma	Meigen, 1820: 93	Germany
Leptis stigmaticus	Zetterstedt, 1849: 218	Sweden
Leptis bimaculatus	Gobert, 1877: 1	not given; Europe
Leptis maculatus obscurus	Strobl, 1898: 20	Bosnia
Rhagio maculatus dalmaticus	Szilády, 1934: 240	Croatia
Rhagio maculatus macedonicus	Szilády, 1934: 240	Macedonia
Rhagio maculifer	(as *Leptis*; Bigot, 1887: 113)	USA
Leptis hoodiana	Bigot, 1887: 115	USA
Rhagio maculifer concavus	Leonard, 1930: 94	USA
Rhagio maculipennis	(as *Leptis*; Loew, 1854: 1)	Turkey

Species (synonyms indented)	Author, reference	Type country
Rhagio maolanus	Yang & Yang, 1993: 280	China
Rhagio matsumurae	Lindner, 1923: 11	Japan
Rhagio medeae	Iacob, 1971: 353	Romania
Rhagio meridionalis	Yang & Yang, 1993: 2	China
Rhagio miyonis	Nagatomi, 1952: 7	Japan
Rhagio mongolicus	Lindner, 1923: 6	Mongolia
Rhagio montanus	Becker, 1921: 54	Italy
Rhagio montanus striatus	Lindner, 1934: 244	Poland
Rhagio montivagus	Edwards, 1919: 29	Sumatra
Rhagio morulus	Nagatomi, 1971: 39	Japan
Rhagio mystaceus	(as *Leptis*; Macquart, 1840: 30)	not given; North America
Rhagio naganensis	Nagatomi, 1952: 9	Japan
Rhagio nagatomii	Yang & Yang, 1997: 227	China
Rhagio niger	(as *Leptis*; Wiedemann in Meigen, 1820: 98)	Portugal
Rhagio niger trajani	Szilády, 1934: 243	Romania
Rhagio notatus	(as *Leptis*; Meigen, 1820: 95)	not given; Europe
Rhagio notatus nigricans	Lindner, 1934: 248	Czechoslovakia
Rhagio ochraceus	(as *Leptis*; Loew, 1862: 187)	USA
Rhagio olgae	Soboleva, 1991: 94	Russia
Rhagio olsufjevi	Soboleva, 1989: 401	Russia
Rhagio orestes	Chillcott, 1965: 792	USA
Rhagio pallidipennis	Becker, 1921: 55	Greece
Rhagio pallidistigma	(as *Leptis*; de Meijere, 1924: 14)	Sumatra
Rhagio palpalis	(as *Leptis*; Adams, 1904: 442)	USA
Rhagio costatus limbatus	Leonard, 1930: 96	USA
Rhagio perdicaceus	Frey, 1954: 11	China
Rhagio petrovae	Soboleva, 1989: 403	Russia
Rhagio philippinensis	Frey, 1954: 11	Philippines
Rhagio pilosus	Yang, Yang, and Nagatomi, 1997: 229	China
Rhagio plumbeus	(as *Leptis*; Say, 1823: 39)	USA
Rhagio poecilopterus	Bezzi, 1908: 389	Japan
Rhagio politaeniatus	(as *Leptis*; Bellardi, 1862: 27)	Mexico
Rhagio pollinosus	Leonard, 1930: 116	USA
Rhagio pseudasticta	Yang & Yang, 1994: 32	China
Rhagio puellaris	Nagatomi, 1971: 276	Japan
Rhagio pullata	(as *Chrysopila*; Coquillett, 1898: 307)	Japan
Rhagio punctipennis	(as *Leptis*; Say, 1823: 34)	USA
Rhagio rolandi	Becker, 1921: 48	France
Rhagio rondanii	Bezzi, 1908: 389	Italy
Rhagio sabahensis	Nagatomi & Nagatomi, 1990: 41	Malaysia

Species (synonyms indented)	Author, reference	Type country
† *Rhagio samlandicus*	(as *Leptis*; Meunier, 1916: 277)	Baltic Region
Rhagio sardous	Szilády, 1934: 247	Italy
Rhagio scapulifer	(as *Leptis*; Bigot, 1887: 113)	Japan
Rhagio schmidti	Lindner, 1931: 205	Algeria
Rhagio scolopaceus	(as *Musca*; Linnaeus, 1758: 590)	Sweden
Rhagio scolopaceus hahnlei	Lindner, 1923: 9	Germany
Sylvicola solitarius	Harris, 1780: 100	not given; Europe
Sylvicola monotropus	Harris, 1780: 101	not given; Europe
Rhagio separatus	Yang, Yang, and Nagatomi, 1997: 233	China
Rhagio shaanxiensis	Yang & Yang, 1997: 235	China
Rhagio shennonganus	Yang & Yang, 1991: 276	China
Rhagio shimai	Nagatomi & Nagatomi, 1990: 46	Malaysia
Rhagio shirakii	Szilády, 1934: 9	Taiwan
Rhagio sikisimanus	Nagatomi, 1972: 79	Japan
Rhagio simushirus	Soboleva, 1989: 403	Russia
Rhagio sinensis	Yang & Yang, 1993: 1	China
Rhagio singularis	Yang, Yang, and Nagatomi, 1997: 240	China
Leptis sordidus	(as *Leptis*; Loew, 1862: 74)	Turkey
Rhagio pilosus	(as *Leptis*; Loew, 1865: 235)	Turkey
Rhagio stigmosus	Yang, Yang, and Nagatomi, 1997: 242	China
Rhagio strigosus	(as *Leptis*; Meigen, 1804: 299)	France
Rhagio mellinus	Becker, 1921: 48	Spain
Rhagio subpilosus	(as *Leptis*; Becker, 1892: 23)	Switzerland
Rhagio taorminae	Becker 1921: 55	Italy
Rhagio terminalis	(as *Leptis*; Loew, 1861: 317)	USA
Rhagio tessella	(as *Leptis*; Motschulsky, 1889: 505)	Russia
Rhagio tipuliformis	Fabricius, 1794: 273	Germany
Rhagio tonsa	(as *Leptis*; Loew, 1869: 29)	Spain
Rhagio triangulata	(as *Leptis*; Brunetti, 1920: 127)	India
Rhagio tringarius	(as *Musca;* Linnaeus, 1758: 590)	Sweden
Erax rufus	Scopoli, 1763: 363 & 986	not given; Europe
Rhagio vermileo	Fabricius, 1775: 762	France
Nemotelus scolopaceus	De Geer, 1776: 162	not given; Europe
Sylvicola solivagus	Harris, 1780: 101	not given; Europe
Musca vermileo	Schrank, 1781: 441	Austria
Rhagio tringarius vanellus	Fabricius, 1794: 272	Denmark
Leptis tringarius simplex	Meigen, 1838: 61	not given; Europe
Leptis tringarius punctatus	Loew, 1840: 4	Poland

Species (synonyms indented)	Author, reference	Type country
Leptis cinereus	Zetterstedt, 1842: 221	Sweden
Leptis ephippium	Zetterstedt, 1842: 219	Sweden
Leptis tringarius goebelii	Strobl, 1893: 29	Austria
Leptis tringarius nigriventris	Loew, 1869: 33	Germany
Rhagio tringarius tripustulatus	Szilády, 1934: 246	not given; Europe
Rhagio tristis	(as *Leptis*; Schummel, 1837: 109). NOTE 13.	Germany
Rhagio tuberculatus	Yang, Yang, and Nagatomi, 1997: 244	China
Rhagio turcicus	Lindner, 1930: 87	Turkey
Rhagio venetianus	Becker, 1921: 54	Italy
Rhagio vermileonoides	Frey, 1954: 12	Burma
Rhagio vertebratus	(as *Leptis*; Say, 1823: 38)	USA
Rhagio intermedius	Walker, 1848: 212	Canada
Leptis hirtus	Loew, 1861: 318	USA
Leptis scapularis	Loew, 1861: 318	USA
Rhagio vitripennis	(as *Leptis*; Meigen, 1820: 91)	not given; Europe
Rhagio tringarius	Panzer, 1794: 20	Germany
Leptis stigma	Schummel, 1837: 108	Poland
Leptis striola	Meigen, 1838: 61	Austria
† *Rhagio wheeleri*	Melander, 1949: 29	USA (Miocene)
Rhagio yasumatsui	Nagatomi, 1972: 83	Japan
Rhagio zhejiangensis	Yang & Yang, 1989: 290	China

Nomina nuda	Author, reference
Leptis albicornis	Say, 1823: 38
Leptis acutangulus	Meunier, 1899: 177
Leptis distans	Hennig, 1967: 39
Leptis flexus	Meunier, 1899: 177
Leptis recurvus	Meunier, 1899: 177
Leptis validus	Meunier, 1899: 177

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Genus SCHIZELLA Bezzi

Figures 112-117.

SCHIZELLA Bezzi, 1917: 118. Type species *Schizella furcicornis* Bezzi 1917, by original designation.

DIAGNOSIS.

The monophyly of the species of *Schizella* is supported by the autapomorphic form of the male first flagellomere, which is expanded conspicuously into a bifurcate process.

Schizella species are delicate, small to mid-sized (3.7 to 6.3 mm) flies, with long, thin legs; thorax brown to orange-brown with blue-, purplish-, or golden-colored setae. Wings are hyaline, without markings; male holoptic, eyes separated in female; in female, arista produced ventrally; first flagellomere subcircular, laterally compressed; in male, first flagellomere enlarged and forked; arista short; mandibles absent; laterotergite setose; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia with short macrochaetae; tergite 9 without ventrolateral arms; female spermathecal ducts with accessory glands. *Schizella* is restricted to the Philippines and the males of this genus are unlikely to be confused with any other brachyceran genus, on account of their highly modified antenna. Females of *Schizella* are separated from most *Chrysopilus* species by having the arista produced ventrally from the first flagellomere.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere of female antenna enlarged basally, bearing long stylus, which originates anteroventrally. In male, first flagellomere enlarged and forked; arista short. Eyes

dichoptic in both sexes, inconspicuously setulose; ocelli evenly spaced, of equal size. Labella with pseudotrachae, longer than palps. Theca short and stout. Palps one-segmented. Mandibles absent. *Thorax.* Mesonotum without vittae. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum setulose on dorsal margin only. Laterotergite setose. Postspiracular scale absent. Metallic- or scale-like thoracic setae, often with structural color present. Postspiracular sclerite bare. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline, without markings; pseudostigma present or absent. Lower calypter reduced. Upper calypter well developed, but margin with curvature narrow, width more than twice length. Costa extends past wingtip (to at least R_5). Humeral crossvein (h) well developed. Sc-r crossvein absent. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. Wing veins R_1 and R_{2+3} close together at wing margin. R_{2+3} sinuous, apical third ultimately bends toward leading edge of wing margin (creating concave flex anteriorly), length of R_{2+3} about the same length as R_5, or longer. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 at base strongly curved or angled, often with short proximal offshoot at point of curvature near R_5, nearly straight apically. R_4 and R_5 encompass wing tip, or R_5 anterior to wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal side of central one-third of discal cell (or more centrally). M_3 wing vein present. Origin of CuA_1 at bm cell. Wing cell m3 parallel-sided at margin. CuA_2 greater than 2/3 length of posterior vein of bm cell. Alula full, rounded, with broad curvature. Anal lobe well developed. Anal cell open. Halter knob approximately 1/2 length of stem. Tibial spur formula 0:2:1. Hind coxal tubercle absent. Hind tibial

macrochaetae present, short. Postmetacoxal bridge absent. *Abdomen.* Abdominal segments evenly tapered. In female, last 3 abdominal segments telescoping; tergite 7 much longer than wide; intersegmental membrane between segments 7 and 8 especially long; sternite 8 length elongated; more than twice as long as wide. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct tomentose, without setae. Cerci widely displaced from one another, separation distance greater than three quarters width of cercus; held at angle in relation to rest of abdomen; in posterior view cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, without paired swellings ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme moderately long, reaching to at least anterior margin of hypandrium. Ejaculatory apodeme rod-shaped (upside-down v-shaped in profile). Aedeagal tines absent. Endoaedeagal process absent. Female terminalia with three spermathecae, clubbed, moderately to well sclerotized. Spermathecal ducts longer than five times the length of sternite 9, but not so long as to be difficult to measure, not inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at approximately the distal third of the spermathecal ducts. Ejection apparatus of spermathecal ducts lightly sclerotized, not thickened, without surface furrows. Common spermathecal duct thinner than individual ducts, about the same length as the longest diameter of genital chamber. Genital chamber elliptical,

elongate, occupying most of sternite 9 area. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end pointed, with broad extensions posteriorly that are held in horizontal plane. Tergite 10 present. Sternite 10 split into two sclerites. Cercus two-segmented. First segment of cercus not elongate, without ventral process. Ventral lobes of first segment of cercus curve ventrally towards one another to form a ring, visible in the posterior perspective. Basal cerci adjacent dorsally. Second cercus segment not elongated, without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE.

Nagatomi (1982) gives a cursory treatment of the genus. Below is a key to all species.

Key to Schizella species.

1. Notopleural setae white, reflecting bluish light; clypeus gray, clearly longer than broad 2

   Notopleural setae black, reflecting golden light; clypeus brown, nearly spherical ..... ***woodleyi*** **new species**

2(1). Notopleural setae purplish blue; abdomen brown throughout, body length greater than 4mm…….. ..... ***pulchrina*** **Frey**

   Notopleural setae light blue; abdomen brown anteriorly, dark brown posteriorly, body length less than 4mm ..... ***furcicornis*** **Bezzi**

Schizella woodleyi *new species*

Figs 46 - 50.

Type material: The male holotype is labeled “Mt. Apo, Mindanao Phil. Islds. C.F Clagg/Kidapayan Trail, 7-8,000ft, 20 Sep/HOLOTYPE ♂ Schizella woodleyi P.H. Kerr/[USNM ENT 00025872].” The paratype is labeled “Mt. Apo, Mindanao Phil. Islds., C.S. Clagg/Sibulan Riv. 7-8,000ft. 16 Sept/PARATYPE ♂ Schizella woodleyi P.H. Kerr/[USNM ENT 00025871]”. The holotype is in good condition. The specimen is missing its entire left midleg, right hindleg, and the right wing is torn slightly at the anal lobe. Many of the scutal setae are missing, however distinctive setae remain on and around the notopleuron and posteriorly, adjacent to the scutoscutellar suture. The paratype is missing almost all thoracic setae, both mid and hind legs and the distal/posterior portion of the right wing. The abdomen beyond the sixth segment is macerated and preserved in glycerol, in a microvial attached to the specimen pin. The holotype and paratype are deposited in the MCZ.

Species Diagnosis.

Schizella woodleyi differs from *S. pulchrina* Frey and *S. furcicornis* Bezzi in having black setae that reflect gold color when illuminated, especially on the notopleuron and anterior to the scutoscutellar suture. It also differs in having a brown clypeus that is nearly spherical in shape. Additionally, it is larger than the two other species in the genus.

Species Description.

Male: Total body length 5.5-6.3mm. General color light orange-brown, becoming dark brown posteriorly, legs light orange-brown becoming brown distally. Head (Fig. 46) generally dark brown under gray tomentum; inner eye margins converging slightly toward apex; frons 0.20 width of head at anterior ocellus, with central crease that deepens ventrally between antennal sockets; fronto-facial region at antennal sockets slightly prominent; ocellar tubercle dark brown, bare; face with light brown tomentum; gena bare; vertex and occiput dark brown under gray tomentum; antennae prominent, extending beyond width of head laterally, first flagellomere bifurcate, ventral extension of first flagellomere bearing stylus, ratio of segments (scape: pedicel: [dorsal extension of first flagellomere: ventral extension of first flagellomere]: stylus) 7:3:[41:49]:5, scape with length/width ratio 1.55, scape bare, pedicel with single longitudinal row of small dark brown setulae at middle of segment, flagellomere with dense vestiture of short silvery brown setulae, stylus vestiture similar but not as dense; clypeus light brown, nearly spherical, lightly covered with silver tomentum, otherwise bare; palp one-segmented, light orange-brown becoming brown distally, covered with silver tomentum, and with silver setae on proximal areas and brown setae distally; proboscis light orange-brown becoming brown distally, labella with silver setae. Thorax color orange brown dorsally and light orange brown laterally, very lightly tomentose throughout; scutum with short black setae except posteriorly, near scutoscutellar suture, where setae are black, flattened in a scale-like manner, and become gold when reflecting light; these scale-like black/gold setae are also present on and just dorsal to the notopleuron; anepisternum

with black and yellow setae along its anterior and dorsal margins; katepisternum and meron bare; anatergite with yellow setae, densely arranged, primarily along anterior and dorsal margins; katatergite with longer, black and yellow setae; postalar wall bare; coxae and femora same color as pleura; coxae bearing weak, black and yellow setae, somewhat sparsely arranged; femora bearing short, weak yellow setae throughout, except along dorsal and especially the distal end where setae are almost exclusively brown and nearly entirely appressed against the sclerite surface; tibiae yellowish but covered in dark brown, densely arranged setulae which make them appear darker in color, tibial setae sparse; tarsi darkening to brown distally, with dark brown, densely arranged setulae, setae present ventrally; wing (Fig. 50) primarily clear with brownish hue, pterostigma dark brown; anal cell open; vein R_4 arising nearly perpendicular to vein R_5, sharply curved toward wing margin, usually bearing short proximal stem at R_4 curvature; halter stem orange brown, knob orange dark brown. Abdomen slender, with tergites 1 and 2 light orange-brown or dirty yellow, tergites 3 and 4 completely dirty yellow or dark brown on anterior half and orange brown on posterior half; tergite 5 dark brown or dark brown on anterior half and orange brown or dirty yellow on posterior half; tergites 6-8 dark brown or orange brown or dirty yellow with brown along anterior and lateral margins; all sternites light orange-brown, darkening slightly towards terminalia; setae of tergites mostly black with a few yellow setae interspersed; setae of sternites brown and yellow, in about equal parts. Male terminalia (Figs. 47 - 49) brown, orange brown, or yellowish. Epandrial sclerite wider than long, with deep, rounded notch anteriorly; posterior margin weakly emarginate centrally; subepandrial sclerite absent; hypoproct present,

lacking setae (only tomentum present); cercus attached to hypoproct, displaced anteriorly from epandrial sclerite and laterally, from one another, by approximately the width of a single cercus; aedeagal guide forms bulbous sac, without paired swellings.

Female: Unknown.

Etymology: The specific epithet is given in honor of Norman E. Woodley who originally identified these specimens to genus at the Museum of Comparative Zoology in 1979 and recently called them to my attention. Without his assistance, these specimens and the new species they represent would remain unknown.

List of included species

Species (synonyms indented)	Author, reference	Type country
Schizella furcicornis	Bezzi 1917: 119	Philippines
Schizella pulchrina	Frey 1954: 25	Philippines
Schizella woodleyi	Kerr, present work.	Philippines

Genus SIERRAMYIA, NEW GENUS

Figures 118-121.

SIERRAMYIA Type species *Sierramyia chiapasensis* Kerr, new species, by present designation. NOTE 14.

DIAGNOSIS.

Characters that I regard as autapomorphic for the genus *Sierramyia* include the weakly developed or absent anal lobe, so that the alular incision is rounded and open broadly or absent; the upper calypter reduced; and the epimeron bare. The large size

of the labellum (which is longer than the width of the eye from a lateral perspective) and the swollen hypandrium, expanded anteriorly, may also be autapomorphic. The scarcity of examplars for this genus makes it difficult to assert more autapomorphies at the species group level. However, the *Sierramyia* species are very distinctive and their monophyly appears certain.

Species of *Sierramyia* are small to mid-sized flies (approximately 5.6 mm) that are slight of build and are similar to *Rhagio* in several aspects; laterotergite setose, tibial spur formula 0:2:2, antenna with round first flagellomere bearing terminal arista; arista bare; wings often infuscate or with markings; M_3 present. Both sexes are dichoptic. All *Sierramyia* species are endemic to mountainous areas (at 5000 feet or greater) in Mexico. They may be distinguished immediately from *Rhagio* and all other genera by the unusually modified wing that is weakly developed along its posterior margin, including a very reduced upper calypter. Additionally, *Sierramyia chiapasensis* may be distinguished from all *Rhagio* species and the related genus *Desmomyia* by having a bare epimeron and by having setulae on the dorsal surface of wing vein R_5 and on the ventral surface of wing veins R_{2+3} and R_4. *Sierramyia* species differ from *Chrysopilus* and related chrysopiline genera such as *Schizella* and *Stylospania* by having a bare arista, two hind tibial spurs, and by lacking thoracic setae with metallic sheen.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere first flagellomere oval in cross section, lightly compressed laterally;

enlarged basally, bearing fused, bare arista-like extension. Eyes inconspicuously setulose, dichoptic. Labella enlarged, longer than palps. Palps one-segmented. Mandibles absent. *Thorax.* Mesonotum without vittae. Dorsocentral bristles absent, all dorsal setae of equal length. Anepisternum setulose on dorsal margin only. Laterotergite setose, on katatergite only. Postspiracular scale absent. Proscutellum shallowly present. Subscutellum not enlarged nor lengthened; inconspicuous. Wing membrane darkly infuscate, with hyaline markings; without pseudostigma. Lower calypter reduced. Upper calypter underdeveloped, with narrow curvature, width more than twice length. Costa approximately to wingtip. Humeral crossvein (h) well developed, Sc-r crossvein weakly developed, positioned distal to the humeral crossvein (h), by a little more than the length of h. Dorsal side of R_1 setulose, ventral side of R_1 bare. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward wingtip (creating convex flex anteriorly); about the same length as R_5; with setulaeon both sides of membrane. Base of R_4-R_5 fork proximal of distal end of cell dm. R_4 at base relaxed, not strongly curved, nearly straight apically; dorsal side bare, ventral side with hair. R_4 and R_5 encompass wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin); dorsal side setulose, ventral side bare. M_3 wing vein present. Wing cell m3 parallel-sided at margin. Origin of CuA_1 at bm cell. Length of CuA_2 v. posterior vein of bm cell about the same as 1/2 length of posterior vein of bm cell. Alula reduced. Anal lobe reduced. Anal cell open. Halter knob between 1/3–1/2 length of stem. Tibial spur formula 0:2:2. Hind coxal tubercle absent. Hind tibia without ventro-apical swelling. In female, Abdomen. Terminal *Abdomen.* Abdominal segments 5–10 evenly tapered from segments 1–4. Tergite 7 much longer than wide. Intersegmental

membrane between segments 7 and 8 especially long. Tergite 8 with pair of ducts arising from posterior margin of sclerite, terminating in clump of sclerotized tissue. Sternite 8 longer than wide. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, modestly curved anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly), or pentagonal. Hypoproct flattened, distinct from sclerites above cerci; tomentose, without setae. Cerci partially displaced from one another, separation distance approximately half the width of single cercus. Hypandrium separated from the gonocoxites by a complete suture, expanded anteriorly. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes long enough to reach anterior margin of hypandrium. Parameral sheath bulbous, without paired swellings ventrally. Lateral ejaculatory processes present, integrated into sperm sac membrane. Ejaculatory apodeme long, reaching beyond anterior margin of hypandrium; laterally compressed. Aedeagal tines absent. Endoaedeagal process present, short. Female terminalia with three spermathecae. Spermathecal ducts longer than five times the length of sternite 9, but not so long as to be difficult to measure. Spermathecal duct accessory glands not present. Ejection apparatus of spermathecal ducts lightly sclerotized, thickened, with ringed surface furrows. Spermathecal duct junction thickened. Common spermathecal duct thickened; short, shorter than longest diameter of genital chamber. Genital chamber teardrop shaped, moderately sized. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end broadly pointed; posterior end with broad lateral extensions, free, held in horizontal plane. Tergite 10 length approximately as long as

half measured width, or longer. Sternite 10 entire, pentagonal, pointed posteriorly; posterior half below first cercus segment. Cercus two-segmented. First segment of cercus not elongate, without ventral process. Ventral lobes of first segment of cercus curve ventrally towards one another to form a ring, visible in the posterior perspective (curving slightly ventrally; not obvious). Basal cerci adjacent dorsally. Second cercus segment not elongated. Cercus without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE.

Nagatomi (1982, 1984) illustrates wing, antenna, and male genitalia of two undescribed species belonging to this new genus.

***Sierramyia chiapasensis* Kerr, new species**

Type material: The female holotype is labeled "Mexico: Chiapas/ Lago Montebello/ 16 07'N, 91 40'W/ 5000ft 14 July1969/ W.R.M. Mason /HOLOTYPE ♀ *Sierramyia chiapasensis* P.H. Kerr/[USNM ENT 00022656]." The specimen is in good condition. The head, wing, and legs are all in perfect condition. Most thoracic setae are missing, however. The abdomen beyond the first segment is macerated and preserved in glycerol, along with the dissected genitalia, in a microvial attached to the specimen pin. The spermatheca, however, is missing and undescribed. The holotype is deposited in the CNC.

Species Diagnosis.

Sierramyia chiapensis is distinguished from other species in the genus primarily by the coloration pattern on the wing, which is darkly infuscate brown, with two hyaline bands. The first band starts near the origin of the radial vein, passes through the distal portion of the basal cells, continues posteriorly and veers distally to occupy most of cell cua_1. The second hyaline band spans the wing transversely, starting in cell r3 near the apex of vein R_{2+3}, continuing posteriorly through cell r5 (slightly distal of R_{4+5} fork), and in each of the wing cells posterior of this to cell m3 where the band terminates at the wing margin at the apex of CuA_1. This is the only described species of *Sierramyia*. However, another species of the genus apparently has been illustrated in Nagatomi (1982: Fig. 42), and this species appears to have uniformly infuscate wings throughout, without hyaline bands.

Species Description

Female: Total body length 5.6mm. General color yellow with abdomen darkening to light brown distally, legs yellow, except for fore tarsus, which is light brown. Head (Fig. 45) brown dorsally and along most of frons where it is microtomentose, yellow ventrally; inner eye margins converging toward apex; frons 0.07 width of head at anterior ocellus; ocellar tubercle brown, bare; parafacials very narrow, practically absent; gena bare; postocular setae short, dark brown; occiput pollinose yellow, with short, brown or yellow setae; antenna yellow, except for arista which is brown; scape and pedicel of equal size; scape with short yellow setae; pedical with short black setae; first flagellomere round, slightly laterally flattened, slightly smaller than scape and pedicel, bearing terminal arista; arista bare, approximately the same length as the

width of one eye, viewed from the dorsal perspective; clypeus yellow, nearly spherical, lightly microtomentose, without setae; palp one-segmented, yellow, with black setae; proboscis yellow, labella long (longer than palp and longer than the width of the eye from a lateral perspective) with short yellow setae ventrally. Thorax yellow throughout; scutum with short brown setae; proepimeron bare; anepisternum with a few brown seta near dorsal and posterior margins; katepisternum and meron bare; anatergite bare; katatergite with brown and yellow setae, few in number (approximately 10 to 12); postalar wall bare; coxae and femora same color as pleura; coxae bearing yellow setae of moderate length; femora bearing short, brown setae, mostly appressed near the sclerite surface; tibia yellow, bearing short setae; fore tibia with yellow and brown setae, mid- and hindtibia with brown setae only; all tarsi with short brown setae; fore tarsus light brown, mid- and hindtarsus yellow; wing darkly infuscate brown, with two hyaline bands; the first band starts near the origin of the radial vein, passes through the distal portion of the basal cells, continues posteriorly and veers distally to occupy most of cell cua_1; the second hyaline band spans the wing transversely, starting in cell r3 near the apex of vein R_{2+3}, continuing posteriorly through cell r5 (slightly distal of R_{4+5} fork), and in each of the wing cells posterior of this to cell m3 where the band terminates at the wing margin at the apex of CuA_1; halter stem and knob yellow; stem long, with fine row of short black setae along trailing (dorsal) margin; short black setae also present, scattered on knob ventrally. Abdomen slender; tapering distally; yellowish brown, darkening to light brown distally; with brown and yellow setae. Sternite 8 longer than wide, at its widest point near posterior margin; sternite 9 broadly pointed posteriorly, lateral extensions free

anteriorly; genital chamber moderately sized, approximately the same length as the length of the common spermathecal duct; base of spermathecal ducts lightly sclerotized with conpicous transverse surface rings; spermathecal duct accessory glands absent; tergite 10 yellow, wider than long; sternite 10 yellow, pentagonal, pointed posteriorly; cercus yellow, two-segmented; first cercal segment with ventral process, which curves medially to form a ring when view from posterior perspective; second cercal segment without apical pits.

Male: Unknown.

Etymology. The specific epithet is in reference to the region in which the type specimen was collected.

Genus SPANIA Meigen

Figures 122-126.

SPANIA Meigen, 1830: 335. Type species *nigra* Meigen, by monotypy.

ARCHICERA Szilády, 1934: 264. Type species *Archicera avavorum* Szilády, 1934: 268, by monotypy. NOTE 15.

DIAGNOSIS.

I consider the reduced form of the female first segment of the cercus (approximately half the length or less of the fairly elongate second segment) and the form of female sternite 8, which lacks a medial invagination along its posterior margin, as

autapomorphic character states that define *Spania*. Since the closest relatives of *Spania* are mandibulate (*Spaniopsis* and *Symphoromyia*), the loss of mandibles may represent an additional autapomorphy.

Spania is small (2.1 to 3.0 mm), dark brown to black in color, and slight in build. Wings are lightly infuscate, especially along costal vein; male holoptic, eyes separated in female; antenna with stylus arising ventrally or terminally from enlarged flagellomere base, laterally compressed; mandibles absent; laterotergite bare; wing vein M_3 completely or incompletely present; tibial spur formula 0:2:0; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding and fusing to sternite 9 laterally; female spermathecal ducts with accessory glands arising near base of spermathecae. *Spania* is most likely to be confused with *Ptiolina* or *Bolbomyia*. It may be distinguished most easily from *Ptiolina* species by lacking hind tibial spurs and its small size. *Spania* is approximately the same size as *Bolbomyia*, however, it has a stylate antenna and wing vein M_3 at least incompletely present, and lacks fore and hind tibial spurs. *Spania* was once synonymized with *Spaniopsis* (Paramonov, 1962), however *Spania* may be distinguished from this genus by its small size, its delicate build, scape clearly smaller than the pedicel, and mandibles absent. *Spania* is restricted to the Holarctic Region, with a distribution that includes North America, Europe, and Japan.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere of antenna enlarged, laterally compressed, bearing ventro-apical stylus. Eyes in male ommatidia split into dorsal and ventral areas and smaller ventrally. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic. Parafacials in male not swollen. Labella with pseudotrachae, longer than palps. Theca short and stout, with medial suture. Palps one-segmented. Lacinia present, but very reduced. Lacinia apex not serrated. Mandibles absent. Cibarial pump short, as wide as long or wider. Cornu shorter than cibarial pump. Pharyngeal pump approximately same length as cibarial pump (including cornu). Mesonotum lacking vittae, black or brown, without dorsocentral bristles. Anepisternum bare. Postspiracular sclerite smooth, bare. Proscutellum narrowly present or absent. Subscutellum slightly swollen or absent. Laterotergite bare. Wing hyaline, without markings. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends past wing tip. Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, or absent; positioned distal to h, by the approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. Wing veins R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third ultimately bends toward leading edge of wing margin, creating concave flex anteriorly. Length of R_{2+3} about the same length as R_5. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 mostly straight apically. R_5 ending at wing tip or anterior to wing tip, clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal one-third to near halfway of discal cell. M_3 wing vein incompletely present (not reaching margin) or complete, reaching wing margin. Origin of CuA_1 at

discal cell or at crossvein separating discal and basal medial cells; m-cu crossvein absent. Length of CuA_2 v. posterior vein of bm cell greater than 1/2 length, less than 2/3 length of posterior vein of bm cell. Alula with broad curvature that is slightly shifted distally. Anal lobe well developed. Anal cell open or closed. Halter knob approximately 1/2 length of stem. Tibial spur formula 0:2:0. Hind coxal tubercle absent. Hind tibial macrochaetae absent. Postmetacoxal bridge absent. *Abdomen.* Abdominal segments evenly tapered. In female, tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 short, as throughout abdomen; sternite 8 sclerite entire, wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct elliptical, flattened, tomentose, without setae. Cercus directly adjacent to epandrial sclerite; widely displaced from one another, separation distance greater than three quarters width of cercus; held vertical in relation to rest of abdomen; in posterior view cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodemes. Gonocoxal apodemes short, not reaching anterior margin of hypandrium. Parameral sheath slightly bulbous ventrally, produced into slightly developed paired lobes or smooth. Ejaculatory apodeme laterally compressed; long, reaching anterior margin of hypandrium. Lateral ejaculatory processes present, integrated into sperm sac membrane. Aedeagal tines absent. Endoaedeagal process absent. Female terminalia with tergite 9 entire, with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Spermathecae three, spherical, lightly to moderately sclerotized. Spermathecal ducts

no more than three times the length of sternite 9, with swelling halfway between genital chamber and spermathecae. Spermathecal duct accessory glands present, arise at the base of each spermatheca. Spermathecal ducts sclerotized and thickened in a narrow ring near junction with common spermathecal duct, otherwise smooth, not enlarged, and unsclerotized. Common spermathecal duct thickened, short, shorter than longest diameter of genital chamber. Genital chamber teardrop shaped, small, occupying fraction of sternite 9 area. Accessory gland posterior to genital chamber present, inconspicuous, easily overlooked even after staining. Sternite 9 anterior end broadly paddle-shaped. Sternite 9 with broad posterolateral projections that are held at an angle. Tergite 10 present, entire, short (length less than half width). Sternite 10 present, entire, roughly rectangular. Cercus two-segmented. Basal cerci not elongated, without ventral process, separated from each other dorsally by approximately the width of second cercal segment. Ventral lobes of first segment of cercusdo not curve ventrally towards one another to form a ring. Second cercus segment narrow, elongated (~2.5x longer than wide or more), without apical sensory pits. *Larva*. The larva is undescribed, however immature *Spania nigra* Meigen were found mining the thallus of *Pellia neesiana* (Bryophyta: Pelliaceae) (Séguy, 1927; Mik, 1896 in Nartshuk, 1995).

LITERATURE.

Nagatomi & Saigusa (1982) give a key to the Japanese fauna that includes all species.

List of included species

Species (synonyms indented)	Author, reference	Type country
Spania kyushuensis	Nagatomi & Saigusa, 1982: 226	Japan
Spania naitoi	Nagatomi & Saigusa, 1982: 229	Japan

Species (synonyms indented)	Author, reference	Type country
Spania nigra	Meigen, 1830: 335	not given; Europe
Spania nigra americana	Johnson, 1923: 70	USA

Genus SPANIOPSIS White

Figures 127-139.

SPANIOPSIS White, 1914: 43. Type species *Spaniopsis tabaniformis* White, 1914, by monotypy.

DIAGNOSIS.

Although *Spaniopsis* is a distinctive genus, I could only find a single feature of the internal mouthparts that I consider unambiguously autapomorphic. In *Spaniopsis* species, the cornu is fused apically to the pharyngeal pump. I have not seen this in any other tabanomorph. Nagatomi and Soroida (1985) illustrate *Atherix ibis* and *Suragina caerulescens* as having a fused cornu also, however I did not see this in any of the athericids I examined over the course of my study. In all other taxa that I have examined, the cornu extends beyond the pharyngeal pump, in line with the cibarium.

Spaniopsis species are very stout bodied flies, small to moderately sized (3 to 6 mm), with generally gray or dark gray thorax, with the posterior margin of each abdominal tergite often lightened to light brown or faded yellow in color so that the abdomen appears banded. Wings are mostly hyaline and either only lightly infuscate in the costal vein area (more darkly in *S. marginipennis*), or infuscate near wing veins (as in *S. mackerrasi*); male holoptic, eyes separated in female; antenna with terminal stylus,

laterally compressed; mandibles present; laterotergite bare; wing vein M_3 incompletely present or absent; tibial spur formula 0:2:0; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding and fusing to sternite 9 laterally; female spermathecal ducts with accessory glands. *Spaniopsis* is restricted to Australia and is more likely to be confused with local Tabanidae and Athericidae than with Rhagionidae, especially given the annoying bloodfeeding behavior of the females. *Spaniopsis* may be distinguished from both Athericidae and Tabanidae by lacking a scale on the postspiracular sclerite and by the unsegmented, lanceolate form of the flagellum. *Spaniopsis* differs from *Austroleptis* by having a bulbous clypeus; a two-segmented palp; mandibles present; an unsegmented, lanceolate flagellum; and by lacking hind tibial spurs. The genus may be distinguished from *Atherimorpha* most easily by its robust body, the form of its antenna, wing vein M_3 absent or incomplete, laterotergite bare, and hind tibia without spurs. NOTE 16.

DESCRIPTION.

Head. Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere of antenna enlarged bearing stylus of single segment. Eyes in male ommatidia split into dorsal and ventral areas; smaller ventrally. Eyes inconspicuously setulose; in female, dichoptic; in male, holoptic. Parafacials in male not swollen. Labella longer than palps, with pseudotrachae. Theca short and stout; formed by two sclerites, slightly separated medially. Palps one-segmented. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia longer than palps, with serrated

tip. Mandibles present. Cibarial pump short, as wide as long or wider. Cornu shorter than cibarial pump, apically fused to pharyngeal pump. Pharyngeal pump anteriorly broad, forming cup-like structure, longer in total length than length of cibarial pump. *Thorax.* Mesonotum vittate. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum setulose throughout posterior half, except in *S. mackerrasi* Paramonov where anepisternum bare. Laterotergite bare. Postspiracular scale absent. Proscutellum present. Subscutellum slightly swollen or absent. Wing hyaline, with or without markings. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wingtip. Humeral crossvein (h) well developed. Sc-r crossvein weakly developed, positioned distal to h, by the approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. Wing veins R_1 and R_{2+3} separated at wing margin. Wing vein R_{2+3} sinuous, apical third ultimately bends toward leading edge of wing margin, creating concave flex anteriorly. Length of R_{2+3} clearly shorter than R_5. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 nearly straight apically. R_5 ending at or near wing tip, clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal one-third to near halfway of discal cell. M_3 wing vein incompletely present (not reaching wing margin) or absent. Origin of CuA_1 at discal cell; m-cu crossvein absent CuA_2 approximately 2/3 length of posterior vein of bm cell). Alula with broad curvature that is slightly shifted distally. Anal lobe well developed. Anal cell closed. Halter knob between 1/2–2/3 length of stem. Tibial spur formula 0:2:0. Hind coxal tubercle absent. Hind tibial macrochaetae absent. *Abdomen.* Abdominal segments evenly tapered. In female, last 3 abdominal segments

telescoped; tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 short, as throughout abdomen; sternite 8 as wide as long or wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite absent. Hypoproct triangular (rounded posteriorly), flattened, tomentose, without setae. Cercus directly adjacent to epandrial sclerite; widely displaced from one another, separation distance greater than three quarters width of cercus; held vertical in relation to rest of abdomen; in posterior view cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short, usually not long enough to reach anterior margin of hypandrium. Parameral sheath forming separate, distinct lobes ventrally. Ejaculatory apodeme short or long enough to reach anterior margin of hypandrium. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Aedeagal tines absent. Endoaedeagal process absent. Female terminalia with tergite 9 with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Spermathecae three, spherical, lightly to moderately sclerotized. Spermathecal ducts more than three times but less than five times the length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at approximately the distal third of the spermathecal ducts. Spermathecal ducts sclerotized and thickened in a narrow ring near junction with common spermathecal duct, otherwise slightly enlarged, lightly sclerotized, with small furrows on surface of ducts near base. Common spermathecal duct slightly thickened, about the same length as the longest diameter of genital chamber. Genital

chamber circular, small, occupying fraction of sternite 9 area. Accessory gland posterior to genital chamber inconspicuous, easily overlooked even after staining. Sternite 9 anterior end rounded; posterior end with narrow posterolateral extensions. Tergite 10 present, entire, short (length less than half width). Sternite 10 present, split into two sclerites. Cercus two-segmented. First segment of cercusnot elongated, without ventral process. Basal cerci separated from one another dorsally by approximately the width of the second cercal segment. Ventral lobes of first segment of cercus not curving ventrally towards one another to form a ring. Second cercus segment not elongated, without apical sensory pits. *Larva*. The larvae are unknown.

LITERATURE.

Paramonov (1962) gives a key to all *Spaniopsis* species (treated as *Spania*).

List of included species

Species (synonyms indented)	Author, reference	Type country
Spaniopsis clelandi	Ferguson, 1915: 240	Australia
Spaniopsis longicornis	Ferguson, 1915: 242	Australia
Spaniopsis mackerrasi	(as *Spania*; Paramonov, 1962: 140)	Australia
Spaniopsis marginipennis	Ferguson, 1915: 239	Australia
Spaniopsis rieki	(as *Spania*; Paramonov, 1962: 145)	Australia
Spaniopsis tabaniformis	White, 1914: 44	Australia
Spaniopsis vexans	Ferguson, 1915: 238	Australia

Genus STYLOSPANIA Frey

Figure 140.

STYLOSPANIA Frey, 1954: 23. Type species *Stylospania lancifera* Frey, by monotypy.

DIAGNOSIS.

This genus is based on a single male specimen collected from Samar, Catbalogan, Philippines. *Stylospania lancifera* bears most features found in *Chrysopilus*, but may be distinguished from this genus by its stylate flagellum. It too has a reduced, bare proepimeron and its genitalia are indistinguishable from those of males of many *Chrysopilus* species. The only known specimen of *Stylospania lancifera* is devoid of thoracic setae. The female is unknown.

Stylospania lancifera is a delicate fly, fairly small in size (appx. 4.5 mm), with long, thin legs; orange-brown. Wings are hyaline, without markings; male dichoptic; flagellum subcircular with long, tapering stylus; mandibles absent; laterotergite setose; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia with short macrochaetae; tergite 9 without ventrolateral arms. *Stylospania lancifera* is known to occur only in the Philippines. *Stylospania* may be distinguished from all *Chrysopilus* by its antenna, which has a stylate flagellum.

DESCRIPTION.

Clypeus bulbous. Scape approximately the same size as pedicel. First flagellomere laterally compressed. First flagellomere of antenna enlarged bearing stylus of single segment, stylus narrow, nearly arista-like. Eyes inconspicuously setulose; male dichoptic; ommatidia evenly distributed, of equal size; not flattened dorsally. Head wider than thorax. Labella with pseudotrachae, longer than palps. Theca short. Palps one-segmented. Mandibles absent. *Thorax.* Mesonotum without vittae. Setae of

dorsum all of equal length. Specimen lacks metallic- or scale-like thoracic hairs, although these are likely present. Proepimeron reduced, bare. Anepisternum bare. Laterotergite setose, katatergite and anatergite indistinguishable, setae present throughout laterotergite. Thoracic surface between base of halter and postspiracular sclerite without setulae. Thoracic spiracle without flaps, not lined with setulae. Postspiracular scale absent. Postspiracular sclerite without setulae. Thoracic surface immediately posterior to postspiracular sclerite bare. Proscutellum absent. Subscutellum not bulbous, bare. Wing hyaline, without markings. Wing with pterostigma. Lower calypter reduced. Upper calypter well developed, full and rounded, with broad curvature, lobe-like, width twice length or less. Alula broad, rounded evenly. Anal lobe well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by the approximate length of h. Dorsal side of R_1 setulose, ventral side bare. Wing veins R_1 and R_{2+3} close together at wing margin (R_{2+3} clearly closer to R_1 than to R4). Wing vein R_{2+3} directed toward wing margin, meeting margin abruptly. R_{2+3} bare on both dorsal and ventral surfaces of wing membrane. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 at base strongly curved or angled, straight or nearly straight apically. R_4 and R_5 encompass wing tip. R_5 aligned with R_{4+5}. Wing vein M_3 present, reaching wing margin. Tibial spur formula 0:2:1. Hind coxal tubercle present. Hind tibial macrochaetae present; small, easily overlooked, nearly flush with sclerite surface. Hind tibia without ventro-apical swelling. First hind metatarsus of male not swollen. *Abdomen.* Abdominal segments evenly tapered. Epandrial sclerite wider than long, modestly curved anteriorly. Epandrium simple, not containing hypandrium ventrally.

Subepandrial sclerite absent. Hypoproct rectangular; wider than long; tomentose, without setae. Cerci partially displaced from one another, separation distance approximately half the width of single cercus. Hypandrial sclerite fused entirely to gonocoxites. Gonocoxite smooth dorsally, without sinuous ridge leading to gonocoxal apodeme. Gonocoxal apodemes long enough to reach anterior margin of hypandrium. Parameral sheath developed into bulbous sac ventrally, without distinct lobes. Lateral ejaculatory processes present, part of sperm sac posteriorly, arising free of sperm sac membrane dorsally. Ejaculatory apodeme moderately long, reaching anterior margin of hypandrium, laterally compressed. Aedeagal tines absent. Endoaedeagal process absent. Gonostylus heavily setose. Larva unknown.

LITERATURE.

In addition to the original literature (Frey, 1954), Nagatomi (1982) provides a brief diagnosis of this genus.

List of included species

Species (synonyms indented)	Author, reference	Type country
Stylospania lancifera	Frey, 1954: 23	Philippines

Genus SYMPHOROMYIA Frauenfeld

Figures 141-154, 185, 186C-D, 187A, 194.

SYMPHOROMYIA Frauenfeld, 1867: 496. Type species *Atherix melaena* Meigen, by original designation.

SYMPHEROMYIA Schiner, 1868: 910 (lapsus).

PARAPHEROMYIA Becker, 1921: 42. Type species *Atherix crassicornis* Panzer, by original designation. NOTE 17.

PARAPHOROMYIA Becker, 1922 (incorrect subsequent spelling, validated under Article 33.3.1). NOTE 18.

DIAGNOSIS.

The autapomorphic development of the enlarged scape of *Symphoromyia* provides support for the monophyly of the genus. *Desmomyia* also has an enlarged scape, however, the distant phylogenetic placements of this genera indicate that this character state has evolved independently. Another autapomorphy for the genus is the shape of the aristate flagellomere, which is produced ventrally and is often kidney-shaped in profile.

Symphoromyia species are stout bodied flies, moderately sized (4.7 to 9 mm), with black, gray or gold-gray thorax, and abdomen colored gray, black, mixed black and yellow, black terminating with yellow, or entirely yellow. Wings are hyaline or lightly infuscate; male holoptic, eyes separated in female; antenna aristate; first flagellomere kidney-shaped or subcircular, expanded ventrally; laterally compressed; mandibles present; laterotergite bare; wing vein M_3 present; tibial spur formula 0:2:1; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding and fusing to sternite 9 laterally; female spermathecal ducts with accessory glands. *Symphoromyia* is restricted to the Holarctic Region and reaches its greatest diversity in North America. *Symphoromyia* may be confused with

local Tabanidae and Athericidae since females of some species are known to be bloodfeeders and can be a nuisance. *Symphoromyia* may be distinguished most easily from both Athericidae and Tabanidae by lacking a scale on the postspiracular sclerite and in addition to this, from the Athericidae by an elongated scape and wing vein R_{2+3} meeting the margin at some distance away from R_1; and from Tabanidae by having an aristate antenna and wing vein R_4 not sinuate, and nearly parallel to R_5. *Symphoromyia* is similar in form and color to several species of *Ptiolina*, but may be distinguished by the elongate scape (that is clearly larger than pedicel), the ventrally expanded first flagellomere, and setose laterotergite. *Symphoromyia* may be distinguished from *Chrysopilus* and *Rhagio* by the large size of the scape, the two-segmented palp, and presence of mandibles. Additionally *Symphoromyia* may be separated from *Rhagio* by having a bare proepimeron and a single hind tibial spur; and from *Chrysopilus* by lacking thoracic setae that have a metallic sheen.

DESCRIPTION.

Head. Clypeus bulbous. Scape clearly larger than pedicel. First flagellomere of antenna laterally compressed, enlarged bearing terminal or anterodorsal arista. Eyes inconspicuously setulose; in male, often flattened dorsally, holoptic or dichoptic, ommatidia split into dorsal and ventral areas and smaller ventrally. Parafacials in male swollen slightly or not swollen. Labella with pseudotrachae, length variable. Theca short and stout, with medial suture. Palps two-segmented, distal segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, longer than palps, with serrated tip. Mandibles present.

Cibarial pump long, clearly not as wide as long. Cornu nearly as long as or longer than cibarial pump, extending beyond pharyngeal pump. Pharyngeal pump anteriorly broad, forming cup-like structure, approximately same length as cibarial pump. Thorax. *Thorax.* Mesonotum with vittae. Dorsocentral bristles absent; all dorsal setae of equal length. Anepisternum setulose throughout posterior half. Laterotergite setose. Proscutellum present. Subscutellum inconspicuous. Wing hyaline, without markings or membrane lightly to moderately infuscate, brownish. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wingtip (between R_4 and R_5). Humeral crossvein (h) well developed. Sc-r crossvein present, weakly developed, positioned distal to the humeral crossvein (h), by the approximate length of h. Wing veins R_1 and R_{2+3} separated at wing margin. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. Wing vein R_{2+3} sinuous, apical third of R_{2+3} ultimately bends toward leading edge of wing margin creating concave flex anteriorly. Length of R_{2+3} shorter than R_5. Base of R_4-R_5 fork proximal or directly above distal end of cell dm. R_4 nearly straight apically. R_5 posterior or anterior to wing tip, clearly longer than R_{4+5} (r-m to R_4 origin). R-m crossvein at proximal one-third to near halfway of discal cell. M_3 wing vein present. M-cu crossvein present. Origin of CuA_1 at bm cell near discal cell. M_3 cell at margin convergent. CuA_2 length between ½ and 2/3 the length of the posterior vein of bm cell. Alula with broad, evenly rounded curvature. Anal lobe well developed. Anal cell open. Halter knob approximately 1/2 length of stem. Tibial spur formula 0:2:1. Hind coxal tubercle absent. Hind tibial macrochaetae absent. Postmetacoxal bridge absent. *Abdomen.* Abdominal segments evenly tapered. In

female, last 3 abdominal segments telescoped; tergite 7 much wider than long; intersegmental membrane between segments 7 and 8 especially long; sternite 8 as wide as long or wider than long. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrial sclerite wider than long, strongly notched anteriorly. Subepandrial sclerite present, divided medially, setose. Hypoproct present. Cercus base held underneath epandrial sclerite or directly adjacent to epandrial sclerite. Cerci partially displaced from one another, separation distance approximately half the width of single cercus. Cerci, in posterior view cupped, forming circular outline medially. Hypandrium fused entirely to gonocoxites. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short, usually not long enough to reach anterior margin of hypandrium. Parameral sheath forming separate, distinct lobes ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme short or long. Ejaculatory apodeme laterally compressed. Aedeagal tines absent. Endoaedeagal process present. Female terminalia with tergite 9 entire, with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Spermathecae three, spherical, moderately to well sclerotized. Spermathecal ducts more than three times but less than five times the length of sternite 9, inflated at base of spermathecae. Spermathecal duct accessory glands present, arise at approximately the distal third of the spermathecal ducts, thickened and lightly sclerotized, with furrows, near junction with common spermathecal duct. Spermathecal ducts furrows at base present. Common spermathecal duct thickened, long, clearly longer than longest diameter of genital chamber. Genital chamber teardrop shaped, moderately sized. Accessory gland

posterior to genital chamber inconspicuous, easily overlooked even after staining, common duct as long or shorter than sternite 9, with short paired extensions posteriorly. Sternite 9 anterior end rounded, posterior end with broad extensions posteriorly. Posterior end of sternite 9 joined together in horizontal plane centrally, held in vertical plane laterally. Tergite 10 entire, short, length less than half width. Sternite 10 split into two sclerites. Cercus two-segmented. First segment of cercus not elongate, without ventral process. Basal cerci adjacent dorsally. Ventral lobes of first segment of cercus sometimes curve ventrally towards one another to form a ring, usually are flat and compressed medially. Second cercus segment not elongated, with apical sensory pits. *Larva.* Body with 11 segments (not including head segment), smooth ventrally. Head capsule not folded within second segment, composed of a single, undivided plate (dorsal plate), less than 4.5 times longer than greatest width (2 width/7 length), not cone-shaped, with hole in dorsal shield around each antenna. Mandibular brush present, associated with simple fold of cuticle. Mandibular hook with external groove on adoral surface, serrate, otherwise smooth. Dorsal ridge of mandibular hook without anteriorly-directed microsetae. Labral teeth developed, sclerotized, in two rows, converging anteriorly. Maxilla sclerotized. Saw sclerite of mandibular base absent. Maxillary palp soft, segments three, poorly differentiated. Antenna last segment bifurcated, as nubs. Antenna apparently one-segmented. Unpaired salivary pump absent. Posterior tentorial expansion fused to each other, with thin extension produced anteriorly.

LITERATURE.

Aldrich (1915) gives key to North American species. Narchuk (1969) gives key to eastern European species. Turner (1974) proposes species-groups within the genus. Sommerman (1962) provides natural history information for the larval stages.

List of included species

Species (synonyms indented)	Author, reference	Type country
Symphoromyia algens	Leonard, 1931: 1	USA
Symphoromyia atripes	Bigot, 1887: 111	USA
Symphoromyia barbata	Aldrich, 1915: 120	USA
Symphoromyia cervivora	Turner & Chillcott, 1973: 6	USA
Symphoromyia cinerea	Johnson, 1903: 25	USA
Symphoromyia comata	Bigot, 1887: 111	USA
Atherix crassicornis	(as *Atherix*; Panzer, 1806: 10)	"Hartz;" Europe
Atherix grisea	Meigen, 1820: 109	not given; Europe
Leptis griseola	Fallén, 1814: 7	Sweden
Symphoromyia cruenta	Coquillett, 1894: 55	USA
Symphoromyia currani	Leonard, 1931: 2	USA
Symphoromyia fulvipes	Bigot, 1887: 110	USA
Symphoromyia hirta	Johnson, 1897: 120	USA
Symphoromyia flavipalpis	Adams, 1904: 439	USA
Symphoromyia immaculata	(as *Atherix*; Meigen, 1804: 294)	"Wiesen; " Europe
Symphoromyia inconspicua	Turner & Chillcott, 1973: 6	USA
Symphoromyia incorrupta	Yang, Yang, and Nagatomi, 1997: 251	China
Symphoromyia inquisitor	Aldrich, 1915: 127	USA
Symphoromyia inurbana	Aldrich, 1915: 127	USA
Symphoromyia johnsoni	Coquillett, 1894: 54	USA
Symphoromyia kincaidi	Aldrich, 1915: 129	USA
Symphoromyia limata	Coquillett, 1894: 54	USA
Atherix melaena	(as *Atherix*; Meigen, 1820: 109)	Nepal
Atherix maura	Meigen, 1820: 109	not given
Atherix pilosa	Meigen, 1820: 109	not given
Symphoromyia montana	Aldrich, 1915: 133	USA
Symphoromyia nana	Turner & Chillcott, 1973: 15	USA
Symphoromyia pachyceras	Williston, 1886: 287	USA
Symphoromyia pilosa	Aldrich, 1915: 135	USA
Symphoromyia plagens	Williston, 1886: 287	USA
Symphoromyia latipalpis	Bigot, 1887: 108	USA
Symphoromyia picticornis	Bigot, 1887: 109	USA
Symphoromyia pleuralis	Curran, 1930: 40	USA
Symphoromyia plumbea	Aldrich, 1915: 138	USA
Symphoromyia pullata	Coquillett, 1894: 56	USA

Species (synonyms indented)	Author, reference	Type country
Symphoromyia sackeni	Aldrich, 1915: 139	USA
Symphoromyia securifera	Coquillett, 1904: 171	USA
Symphoromyia sinensis	Yang & Yang, 1997: 253	China
Symphoromyia spitzeri	Chvála, 1983: 425	Uzbekistan
Symphoromyia trivittata	Bigot, 1887: 109	USA
Symphoromyia fera	Coquillett, 1894: 56	USA
Symphoromyia trucis	Coquillett, 1894: 55	USA
Symphoromyia truncata	Turner & Chillcott, 1973: 17	USA
Symphoromyia varicornis	(as *Atherix*; Loew, 1872: 58)	USA
Symphoromyia modesta	Coquillett, 1894: 54	USA

nomina dubia	Author, reference
Symphoromyia picea	Walker 1848: 219

Notes.

1. In the Palearctic Catalogue (Majer, 1988), *Arthroceras pollinosum* Williston is given as the type species for the genus *Arthroceras* Williston, by original designation. Webb (1987) states that the type species is *Arthroceras pollinosum* Williston by 'original description.' Both are incorrect. Williston (1886) created *Arthroceras* for two species, *Arthroceras leptis* (Osten Sacken) and *Arthroceras pollinosum* Williston and did not explicitly designate the type species for the genus. James (1965) correctly gives credit to Coquillett (1910) for the type species designation.

2. Lindner (1923) designated the Palaearctic species *Chrysopilus obscuripennis* Loew as the type species for *Bicalcar*. However, Hennig (1955) located the type material of *C. obscuripennis* and found that there were actually two specimens. One was a typical *Chrysopilus*, labeled as the type, which evidently Lindner never saw, and the other was a specimen of *Atherimorpha*, from an unknown source. The latter specimen was

the basis of Lindner's description. Thus, Lindner cited *Chrysopilus obscuripennis* Loew as the type species of *Bicalcar*, but had described the genus on the basis of a misidentification. Sabrosky (1999) states that the type of *Bicalcar* is *Chrysopila obscuripennis* Loew = "*Atherimorpha obscuripennis* (Loew)". This new combination is in error, however, since the specimen that Lindner used for the type species of *Bicalcar* was not *Chrysopilus*; rather, it was an unidentified *Atherimorpha* species, misidentified as *Chrysopilus obscuripennis*.

3. The original concept of *Neorhagio* Lindner has remained unresolved because the specimen that Lindner identified as *Leptis setosa* Philippi, the type species he designated for the genus, is lost. However, I concur with J. R. Malloch (1932: 206) who determined on the basis of his own knowledge of the Chilean fauna and on the basis of Philippi's original descriptions, that all of Philippi's species described in the genus *Leptis* belong to *Atherimorpha* White. I have a specimen on loan from the AMNH collection that bears on old determination label reading *Atherimorpha setosa* Philippi. "Angol – Chile, 12 Ocbre 1933, J Salazar / *Atherimorpha setosa* Phil. / USNMENT00025130." I designate this specimen as the neotype of *Leptis setosa* Philippi, in the interests of a stable taxonomy.

4. *Chrysopilus nagatomii* Evenhuis 1994 and *Chrysopilus nagatomii* Yang &Yang 1991 are primary homonyms. By the principle of priority, *C. nagatomii* Yang &Yang remains valid and *C.nagatomii* Evenhuis is a junior homonym. The replacement name *Chrysopilus meunieri* Kerr, new name, is given here, named after the original worker.

5. I have seen the type of *Chrysopilus arctica* Frey and agree with Nagatomi (1982: 56) and Nartshuk (1995: 18) that this species clearly belongs within *Chrysopilus*. Stuckenberg (1965) first discusses the confusion regarding *C. arctica* Frey, but did not have access to relevant material for making a determination at the time. Nartshuk (1995) eloquently describes the confusion regarding this species and justifies the correct placement, although she refers to *Poppiusiella* as *Poppinsiella*, in lapsus.

6. Nagatomi (1982: 50) comments, in the same passage containing the description of *Solomomyia*, that "this genus is certainly derived from *Chrysopilus*." The recognition of this genus, therefore, by Nagatomi's own admission, renders *Chrysopilus* a paraphyletic group. *Solomomyia gressitti* is distinguished from *Chrysopilus* species by having wing vein CuA_1 arising from the discal cell. Vein R_4 is also unusually long. Nagatomi mentions another character: "the large area behind ocelli does not make an acute angle with front and is visible in a direct frontal aspect (i.e., when line from antenna to median ocellus is kept horizontal)." I interpret him to mean vertical when he says horizontal. If this is the case and my interpretation is correct, this is not an unusual character state for females of any genus within Tabanomorpha. While the features of the wing in *Solomomyia* appear unique, relatively minor differences in wing venation such as this hardly merit the recognition of species group, in my opinion. Intrageneric differences of wing venation (and aberrant wing venation) are not uncommon in this area of Diptera. The male genitalia illustrated by Nagatomi (1984: Figs. 118-120) are identical to many *Chrysopilus* species. Since this and all

other character states, aside from the aberrant CuA_1 origin (and perhaps the long R_4 vein), are wholly consistent with the genus *Chrysopilus*, I do not believe that persistence of *Solomomyia* as a separate genus is justified. Paratypes of *Solomomyia gressitti* are not in the Bernice P. Bishop Museum, Honolulu, Hawaii; the Natural History Museum, London; nor at the National Museum of Natural History, Washington, D.C. as indicated in Nagatomi's publication (1982).

7. The species concept of *Chrysopilus rufipes* Macquart is uncertain, but placement in *Chrysopilus* is established (Hardy, 1920; Oldroyd in Paramonov, 1962) despite unplaced recognition for this species in Nagatomi & Evenhuis (1989). Hardy (1920) wrote that this species was as a junior synonym of *C. aequalis* (Walker) but Paramonov (1962:135) preferred to treat these taxa as separate species, citing difficulty in interpreting original types.

8. The holotype and paratype were collected in Cape Thompson, Alaska, 26-29 July 1961, by B.S. Henning. There are two Cape Thompsons in Alaska. The one where *Litoleptis alaskensis* was collected is (most likely) near the Project Chariot bioenvironmental study (which was active in the late 1950s to early 1960s). It is located on the Chukchi Sea coast, 26 mi SE of Point Hope, Arctic Slope; 68.14°N, 165.98°W.

9. In the Palearctic Catalogue (Majer, 1988), *Ptiolina obscura* Fallén is given as the type species for the genus *Ptiolina*, by original designation. However, Zetterstedt

(1842) placed two species in the new genus *Ptiolina*, without designating the type species. Frauenfeld (1867) designated the type species as *Ptiolina obscura* (Fallén) (1867: 467, in key), which was originally described as *Leptis obscura* Fallén.

10. Yang, Yang & Nagatomi (1997: 256) described *Spatulina sinensis* from a single male specimen from Shaanxi, China and remark that if the new species is not a true *Spatulina*, it would belong to a new genus. The authors note that *S. sinensis* differs from *Ptiolina* in having mid-upper face deeply sunken and occiput above the neck strongly concave. The head and abdomen are illustrated from the lateral view and the male genitalia are also illustrated, however, none of the putatively special features that they mention are visible. The specimen lacks antennal segments beyond the pedicel and no other potential autapomorphies are given in the text. The male genitalia are quite unlike those found in *Ptiolina* and it is unclear why the species is placed in *Spatulina*. Tergite 10 is split medially into two thin, lateral sclerites and the gonostyly are thick, with an obvious inward bend, exactly as it is in some species of *Chrysopilus*. The mid tarsus, hind femur, and all thoracic setae are also missing from the type specimen. All features illustrated and described are fully consistent with those found in species of *Chrysopilus*, including the deeply sunken face and concave occiput. For this reason, it is more appropriate to place this species in the genus *Chrysopilus*. *Chrysopilus sinensis* (Yang, Yang & Nagatomi), **new combination**.

11. All characters of *Rhagina* are also seen in *Rhagio* species, except for the exceptional wing characters seen in some species. Yang *et al*. note that *Rhagina* male

lacks the subepandrial sclerite (tergite 10), whereas in *Rhagio*, it is present (1997:187), however, I find the male genitalia indistinguishable; both lack the subepandrial sclerite. The wing in *Rhagina incurvatus* de Meijere is distinctive, however, there appears to be a morphological grade in the group, especially as one examines the wing of *Rhagina sinensis* Yang and Nagatomi (1997:186) which has a sinuous R_{2+3} wing vein, but not distinctively so, and not far removed from venation found in some *R. hirtus* (Say) specimens and *R. dichomaticus* Chillcott. Another distinctive feature of *Rhagina* emphasized by Nagatomi (1982) and Yang et al. (1997) is a prominent ventro-apical 'hump' on the hind femur. This is a variable character in both *Rhagio* and *Rhagina,* however. Although most commonly absent in Rhagio, I have seen the 'hump' in an undescribed *Rhagio* species from Laos. Similarly, I have a *Rhagina* specimen which lacks such a hind tibial hump. Yang et al. indicate that the presence or absence of such a hump does not necessarily determine the genus (1997:115).

12. No specimen was designated as the type of *Rhagio biroi* Szilády (1934).

13. The Catalogue of Palaearctic Diptera (Majer, 1982) errs in listing *Leptis tristis* Shummel, 1837:109 twice; as a junior synonym of *Ptiolina obscura* and as a valid species within the genus *Rhagio*. The species is recognized here as *Rhagio tristis* (Shummel), consistent with the Biosystematic Database of World Diptera (http://www.sel.barc.usda.gov/diptera/BIOSYS.HTM).

14. Nagatomi (1982) recognized that *Neorhagio* Lindner was likely a junior synonym of *Atherimorpha* White, but placed several undescribed specimens from Mexico in what he referred to as '*Neorhagio*'. He gave no explanation why these specimens belong to *Neorhagio* Lindner. Judging from the photos, illustrations, and diagnosis given by Nagatomi, the undescribed species of '*Neorhagio*' *sensu* Nagatomi actually belong to the new genus *Sierramyia*. The male genitalia are illustrated by Nagatomi (1984: 138).

15. Szilády (1934: 264) distinguished *Archicera* from *Ptiolina* and *Spania* by the antennal flagellum, which he stated, had faintly visible divisions. This feature, as Nagatomi (1982: 54) has noted, is within the morphological variation present within *Spania* (see Nagatomi & Saigusa, 1982). On account of the small size of *Archicera avarorum* and the description of the flagellomere as being lanceolate, this species is certainly placed among the *Spania* and is likely to be a synonym of *Spania nigra*. The holotype of *Archicera avarorum* has been destroyed [Hungary National History Museum, Budapest]. Therefore a neotype, preferrably a specimen from either Austria or Croatia, should be designated for *Archicera avarorum* so that its appropriate taxonomic status may be documented formally.

16. Paramonov (1962: 139) states in his diagnosis that *Spaniopsis* "only has one spur on the hind tibia (often very weak)." All *Spaniopsis* species, however, have two midtibial spurs and the hind tibia lack spurs entirely.

17. Previous authors have referenced the genus name to Becker, 1921, page 59. However, the original article spans three issues with separate dates, hence the disjunct pagination (pp. 41-48, 15 August 1921; pp. 54-64, 15 November 1921; pp. 69-72, 15 January 1922). Since the new genus name is published in the first installment of the article, even though the type species designation and full description is given on page 59 in November, 1921, the name *Parapheromyia* was initially validly established in the key on page 42 in August, 1921 and this is the date and pagination which should be referenced. Becker (1921: 59) states that the type species for *Parapheromyia* is *Symphoromyia crassicornix* Panzer. This was a lapsus for *Atherix crassicornis* Panzer.

18. Turner (1974: 859) explains that Becker used the name *Paraphoromyia* in subsequent publications in place of *Parapheromyia* and the subsequent spelling was followed by other workers. Furthermore, *Symphoromyia* is what he calls the "coordinate taxon" of *Parapheromyia* and therefore, should be similar in spelling (besides, he notes, *Paraphoromyia* is euphonious). Therefore, he concludes, the name *Parapheromyia* was introduced by Becker as a lapsus or perhaps by a copier's or printer's error. However, *Parapheromyia* is used consistently throughout the paper (in the key (p. 42), the generic description (p. 59), and twice in the discussion (p. 72)) and the name *Paraphoromyia* is never proposed. Therefore, there is no clear indication that *Parapheromyia* Becker was used in error in the original publication and the proposed emendation of Turner (1974: 859) does not satisfy article 32.5.1 of the code (ICZN, 1999). Furthermore, Becker makes no note of a spelling change in

the original paper, nor in corrigenda published by the author or the publisher and therefore, the proposed emendation also fails to satisfy article 33.2.1 of the code (ICZN, 1999). Since Becker's original publication, most authors have used *Paraphoromyia* as an incorrect subsequent spelling (article 33.3 of ICZN, 1999). As perhaps a surprising new twist to the latest edition of the code, the name *Paraphoromyia* Becker is ultimately validated, therefore, by prevailing usage (ICZN, 1999: article 33.3.1).

Appendix A. Figures.

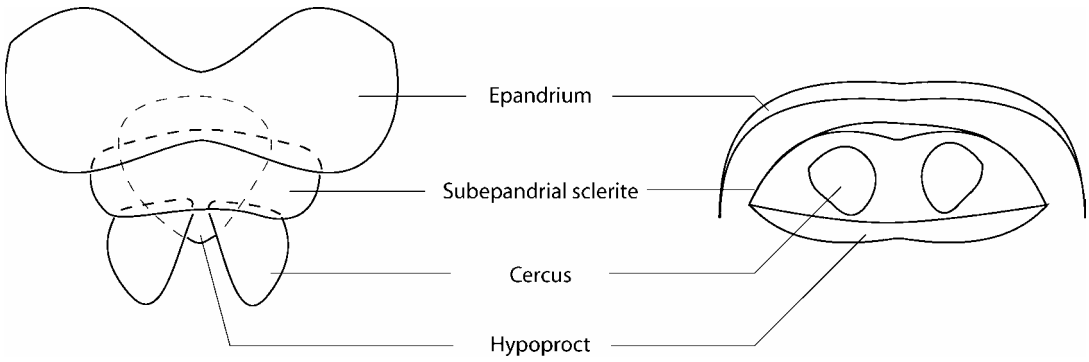


Figure 14. Schematic of the male genitalia, showing primary structures.

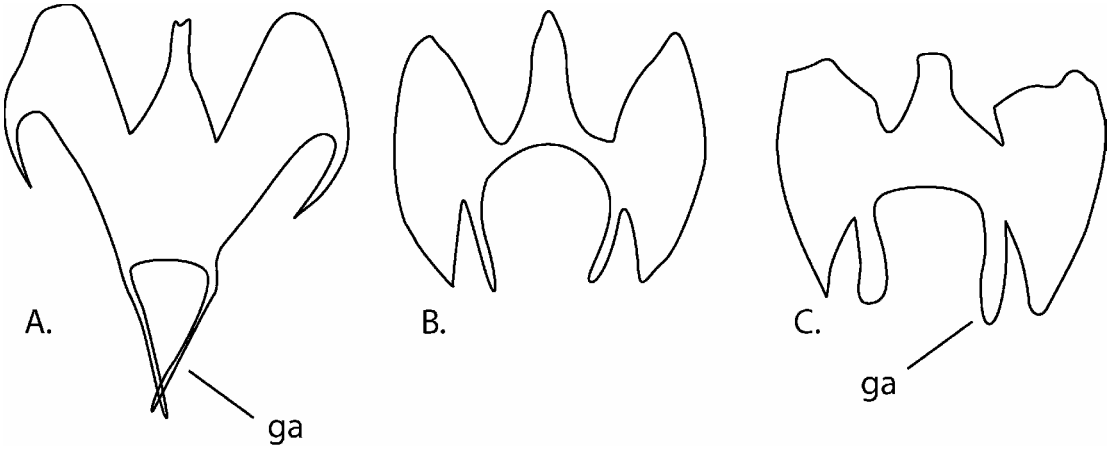


Figure 15. Dorsal outline of hypandrium for illustration of Character 118, origin of gonocoxal apodeme. (A) *Atherix pachypus* is an example where the medial margins of the gonocoxal apodems are shorter than the lateral margins. (B) In *Rhagio plumbeus* and (C) *Bolbomyia nana* the lateral margins of the gonocoxal apodemes are shorter than the medial margins. *ga = gonocoxal apodeme*.

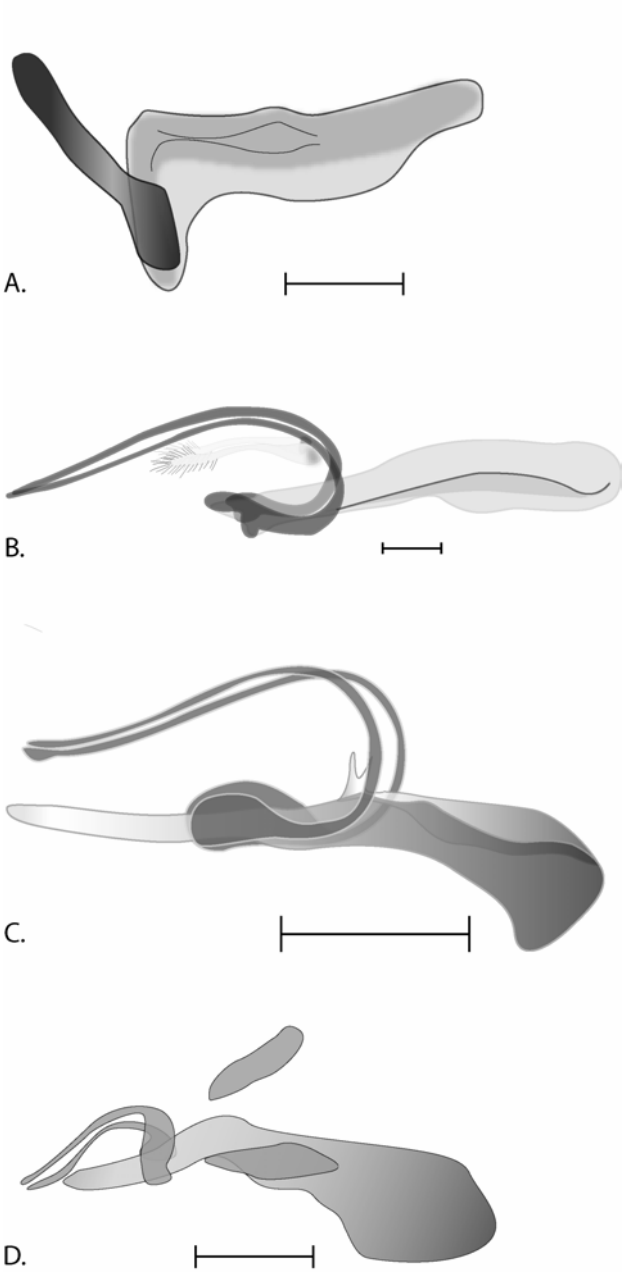


Figure 16. Aedeagus, lateral view. (A) *Chrysopilus* sp., with lateral ejaculatory apodemes [USNMENT00025242] (B) *Suragina concinna*, with aedeagal tines [USNMENT00025980] (C) *Bolbomyia nana*, with aedeagal tines. [USNMENT00024051] (D) *Arthroceras pollinosum*, with lateral ejaculatory apodemes and aedeagal tines [USNMENT00022737]. Scale bar = 0.1 mm.

Figure 17. Lateral view of *Austroleptis multimaculata* [USNMENT00025739]. Scale bar = 0.5 mm.

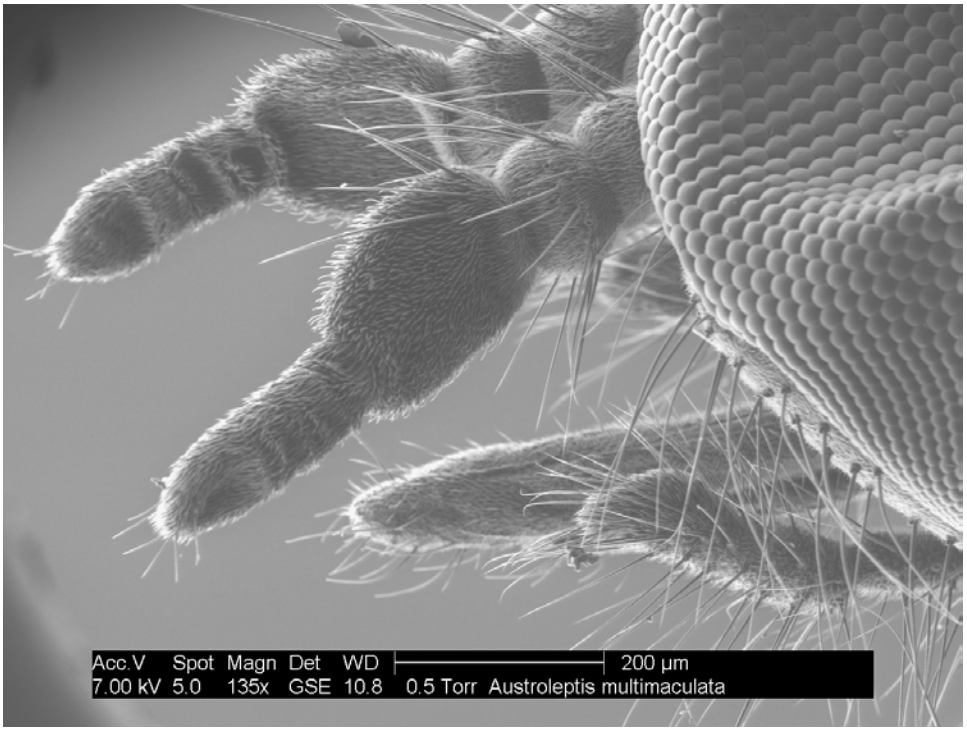


Figure 18. SEM image of antenna of *Austroleptis multimaculata*.

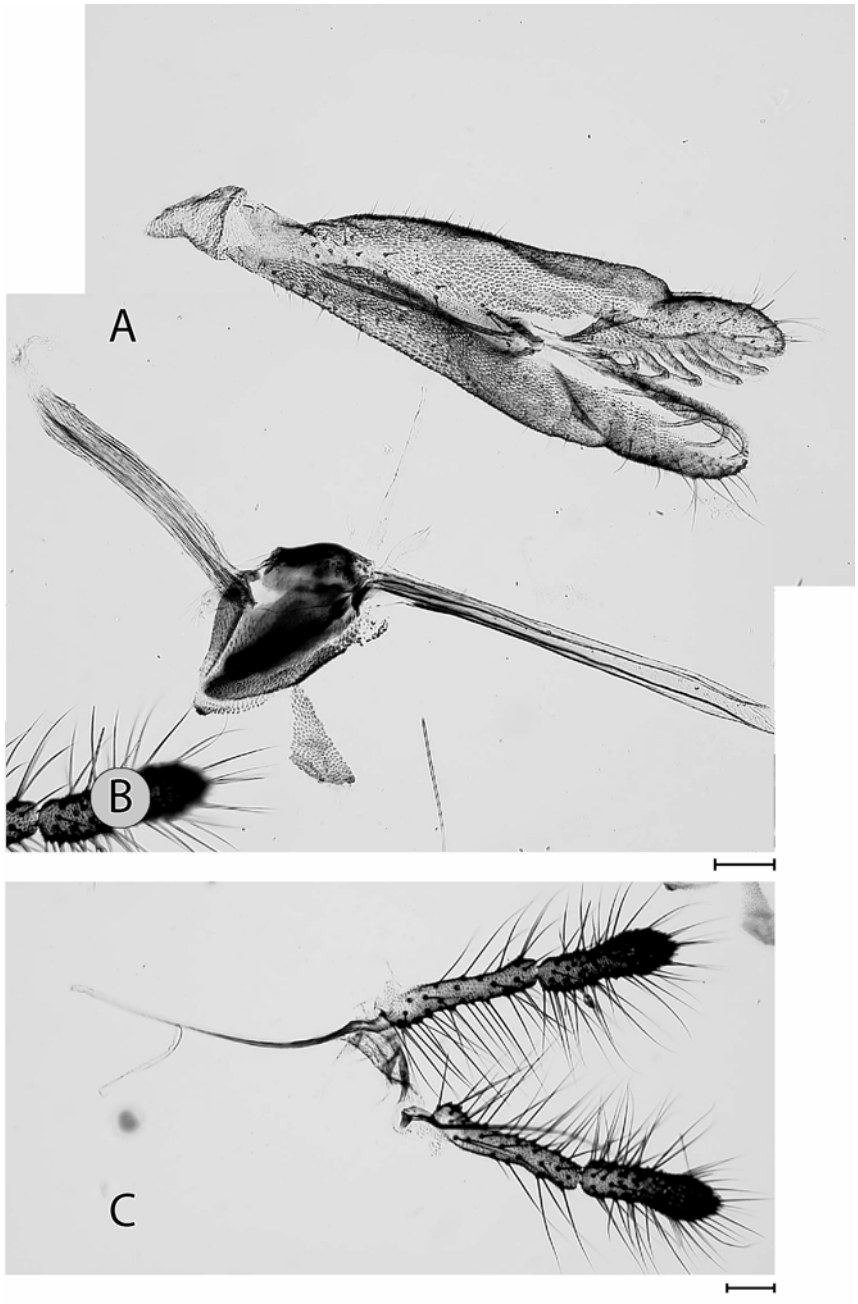


Figure 19. Mouthparts of *Austroleptis multimaculata* [USNMENT00025905]. (A) Labellum, ventral view (B) Hypopharynx and associated structures, lateral view (C) Palps and associated structures. Scale bar = 0.1 mm.

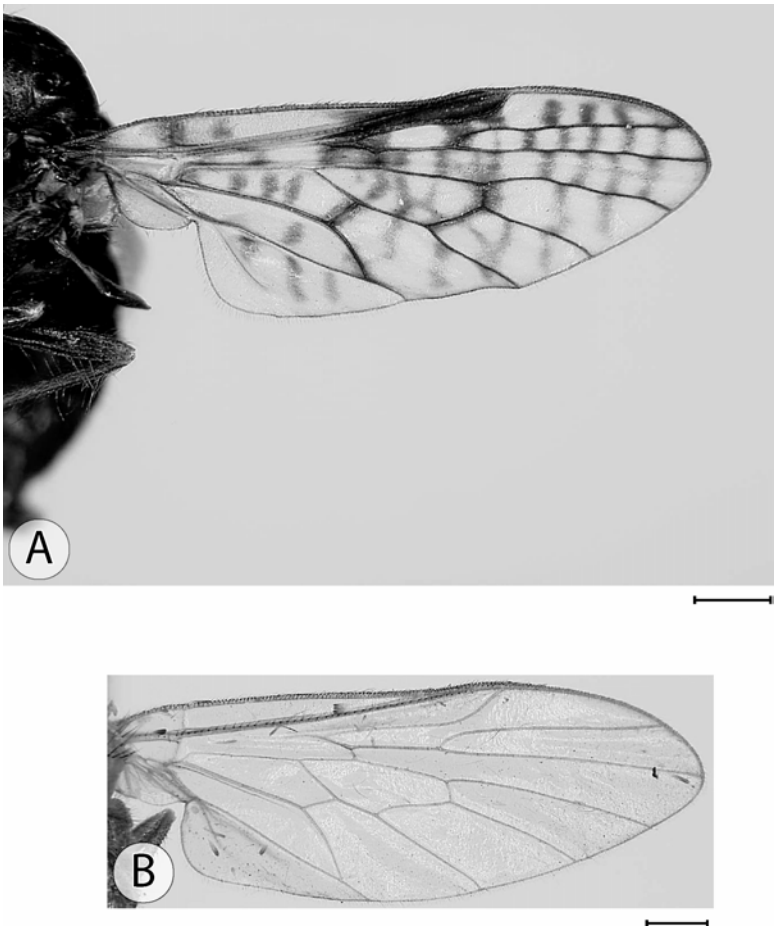


Figure 20. Wing in species of *Austroleptis*. (A) *A. multimaculata* [USNMENT00025745] (B) *Austroleptis sp.* (South America) [USNMENT00022609]. Scale bar = 0.5 mm.

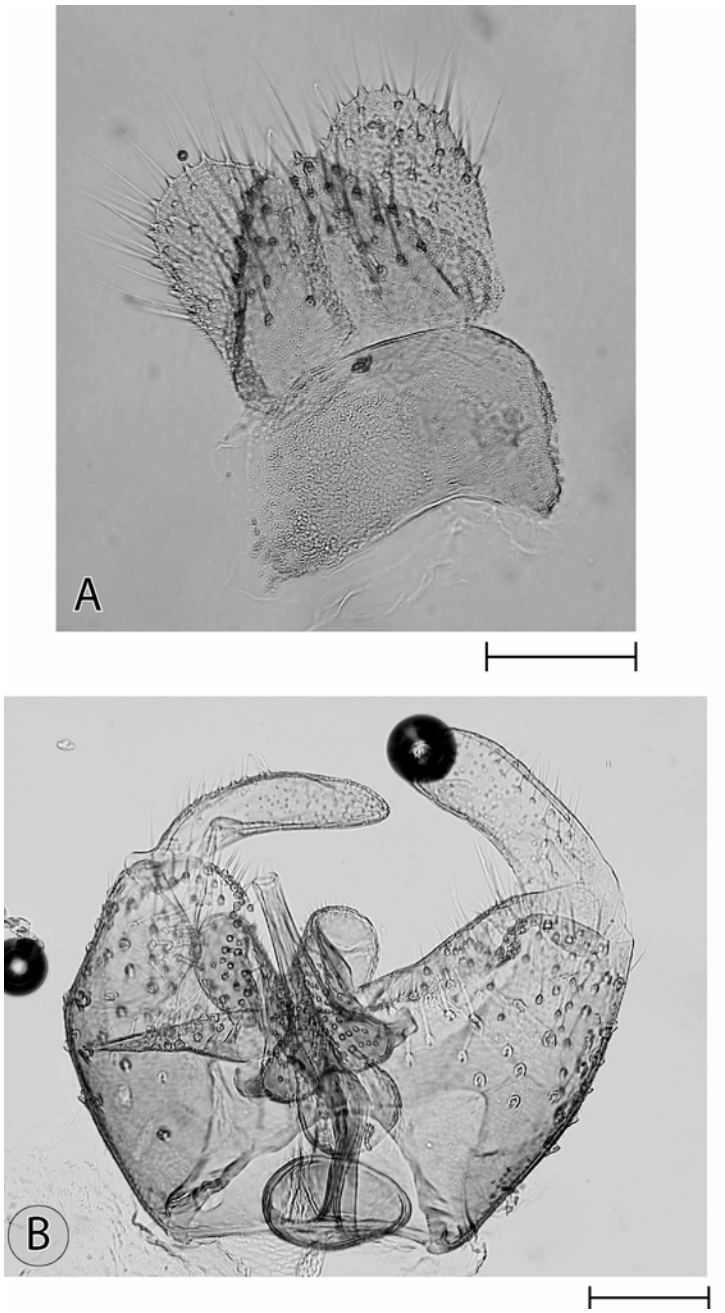


Figure 21. Male genitalia of *Austroleptis multimaculata* [USNMENT00025739]. (A) epandrium, dorsal view (B) hypandrium, dorsal view. Scale bar = 0.1 mm.

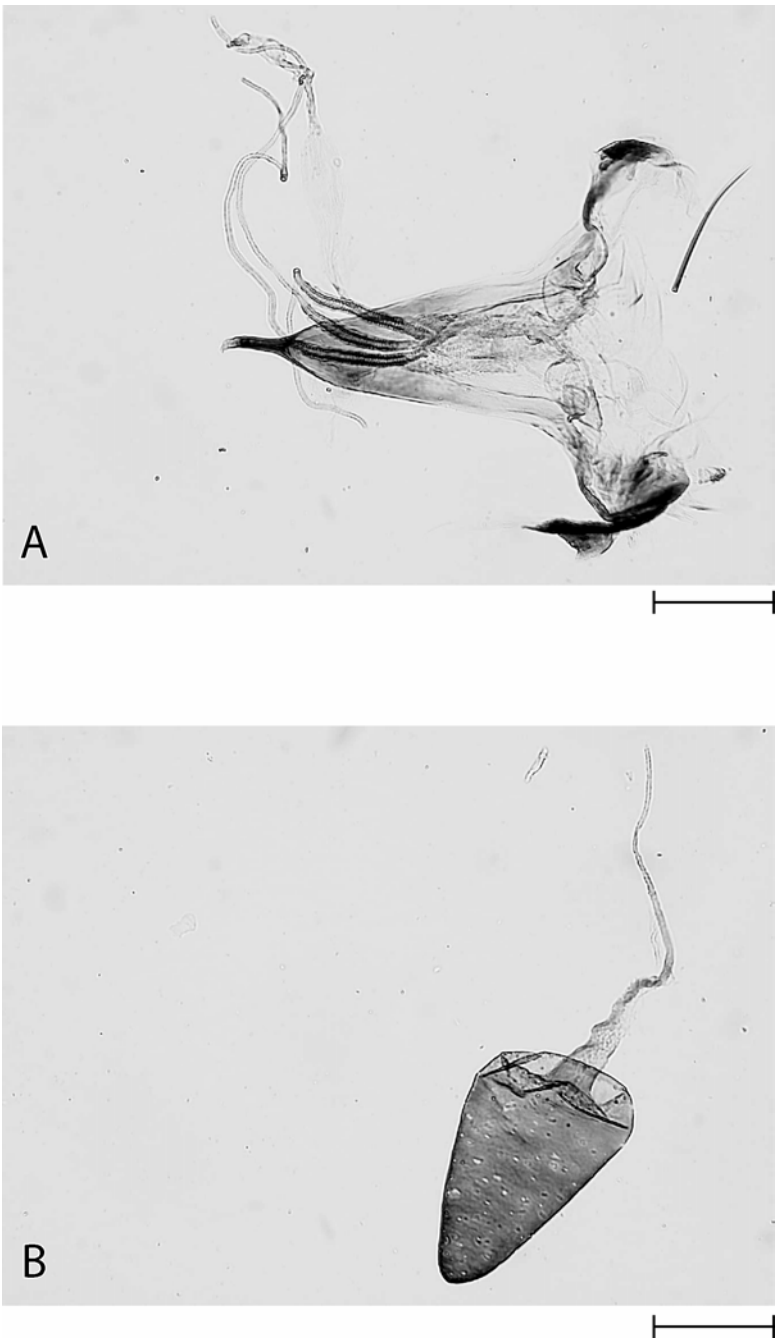


Figure 22. Internal structures of female genitalia of *Austroleptis* sp. [USNMENT00025761] (A) Sternite 9 and associated structures, dorsal view (B) Spermatheca. Scale bar = 0.1 mm.

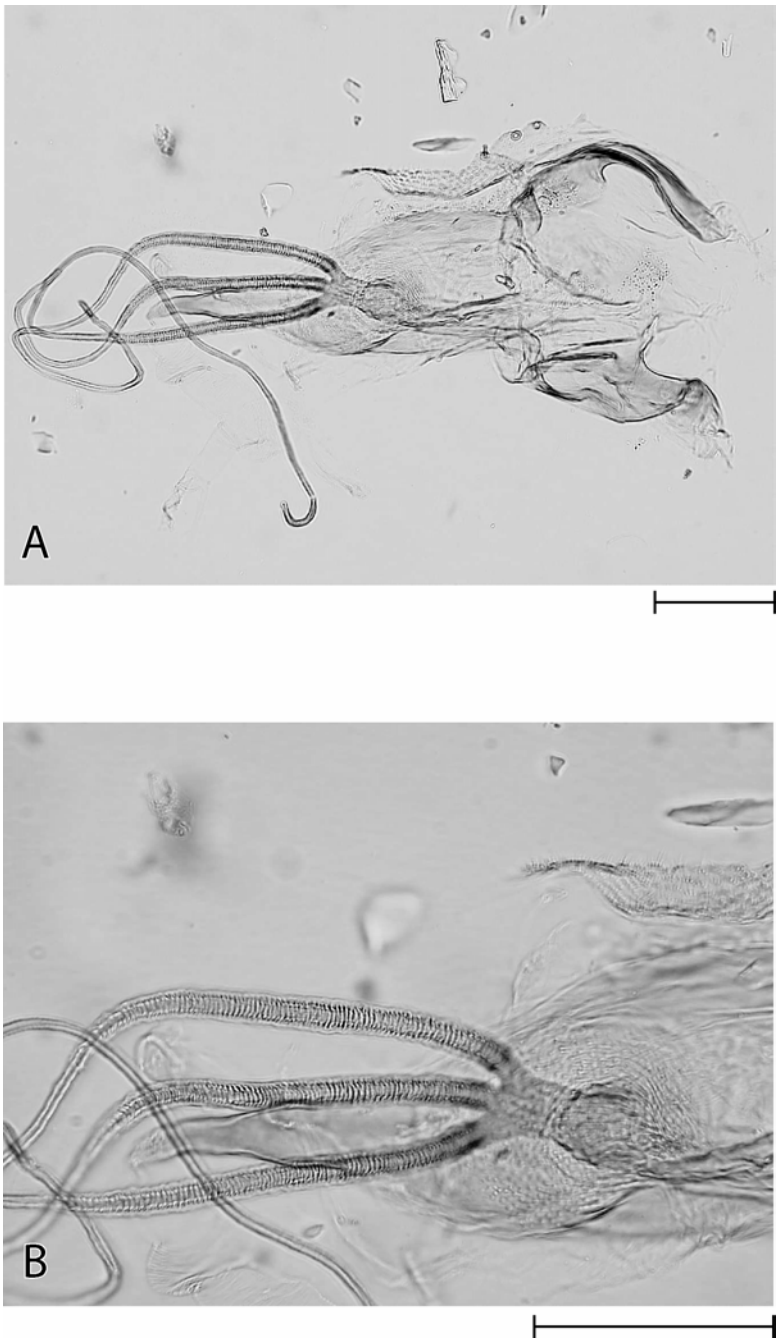


Figure 23. Internal structures of female genitalia of *Austroleptis multimaculata* [USNMENT00024145] (A) Sternite 9 and associated structures, dorsal view (B) Detail of genital chamber and ejaculatory process of spermathecal ducts. Scale bar = 0.1 mm.

Figure 24. Female tergite 10 and cercus of *Austroleptis* sp. [USNMENT00025761]. Scale bar = 0.1 mm.

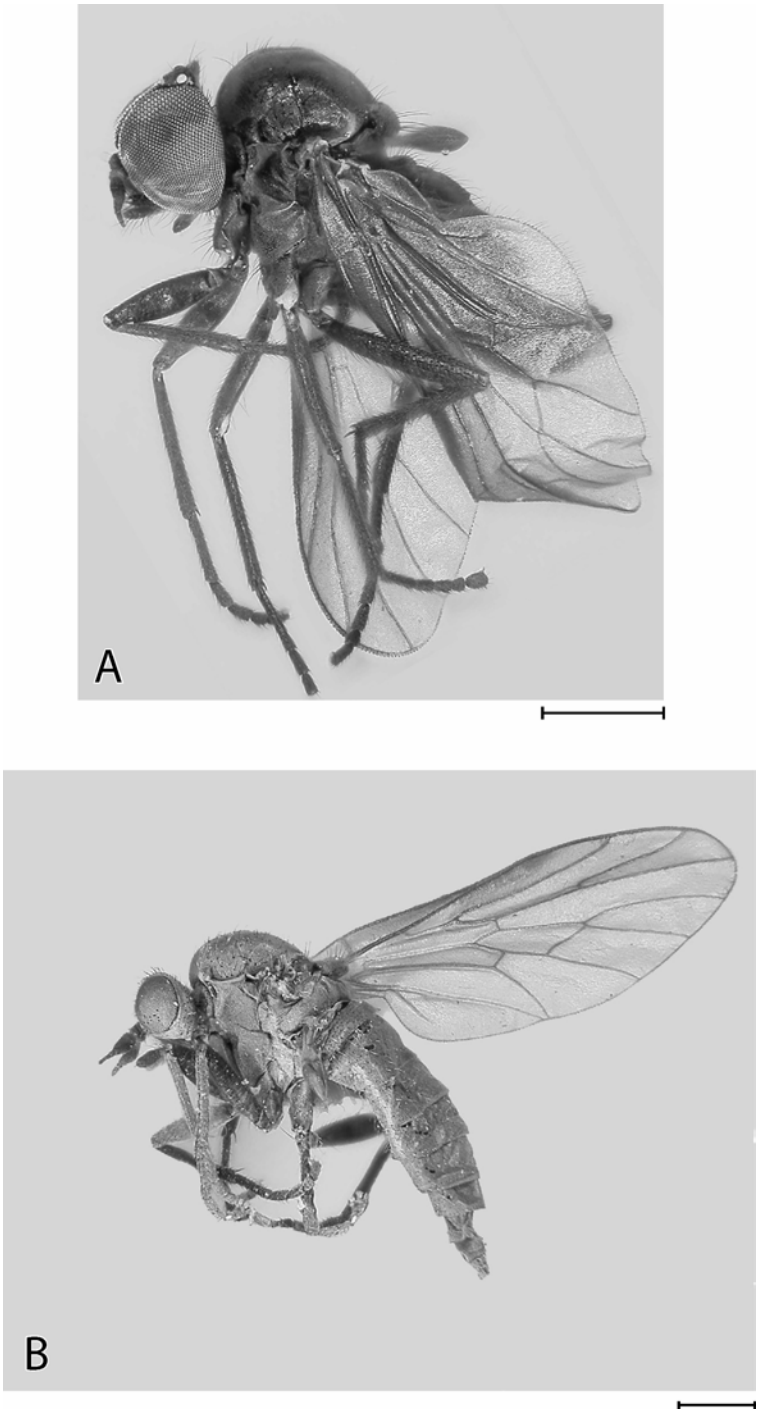


Figure 25. Habitus of *Bolbomyia nana*. (A) male, [USNMENT00025987] (B) female, [USNMENT00022909]. Scale bar = 0.5 mm.

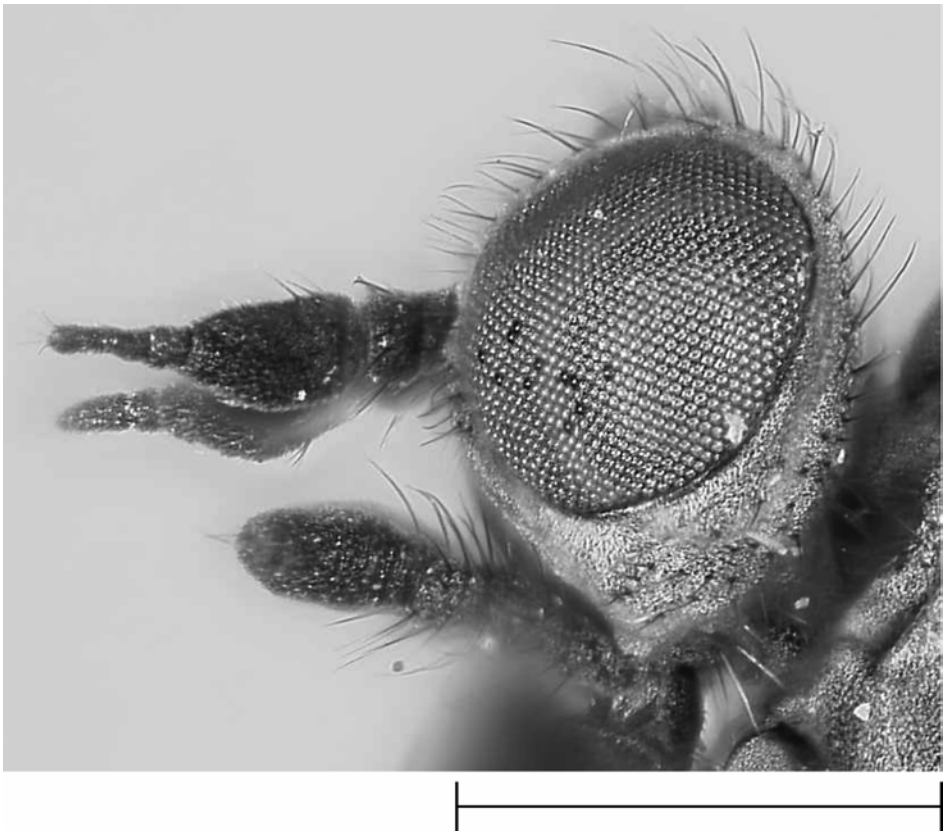


Figure 26. Head and antennal form of *Bolbomyia nana*, male [USNMENT00022909]. Scale bar = 0.5 mm.

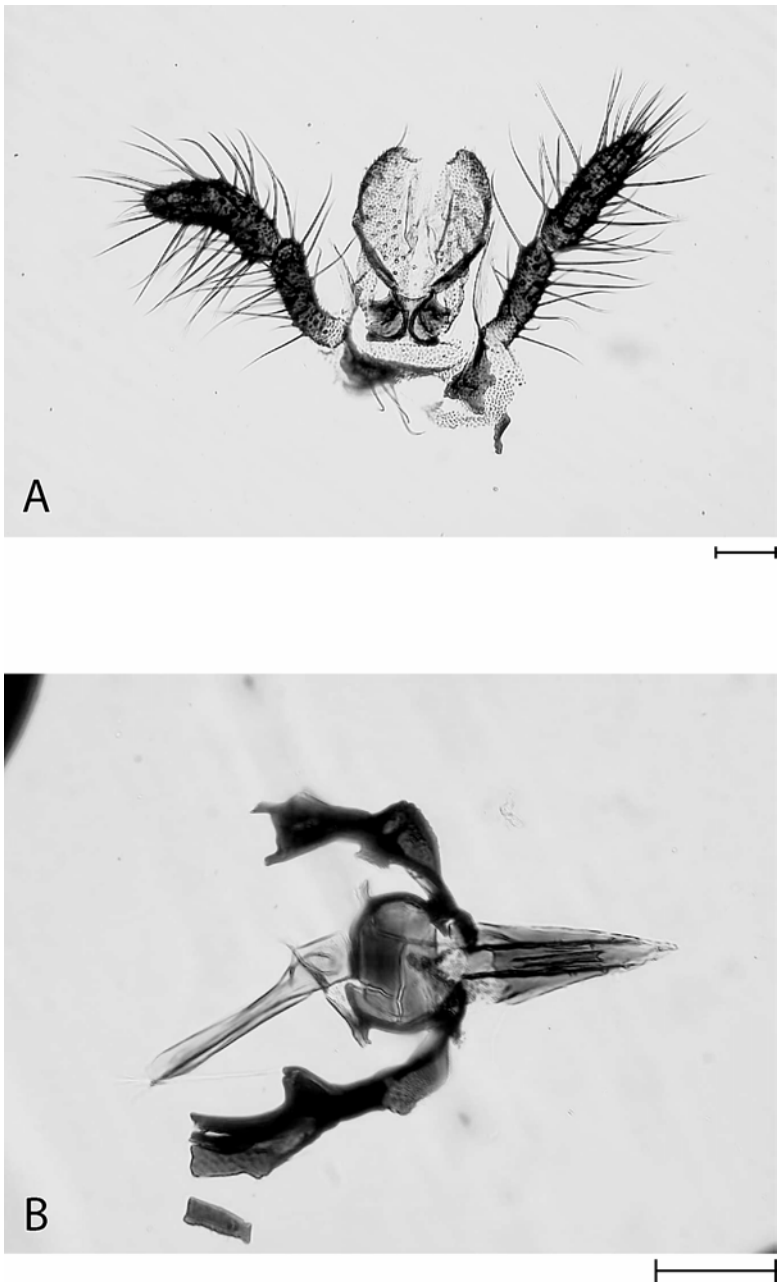


Figure 27. Mouthparts of *Bolbomyia nana* [USNMENT00025904]. (A) Labellum and palps (B) Hypopharynx and associated structures. Scale bar = 0.1 mm.

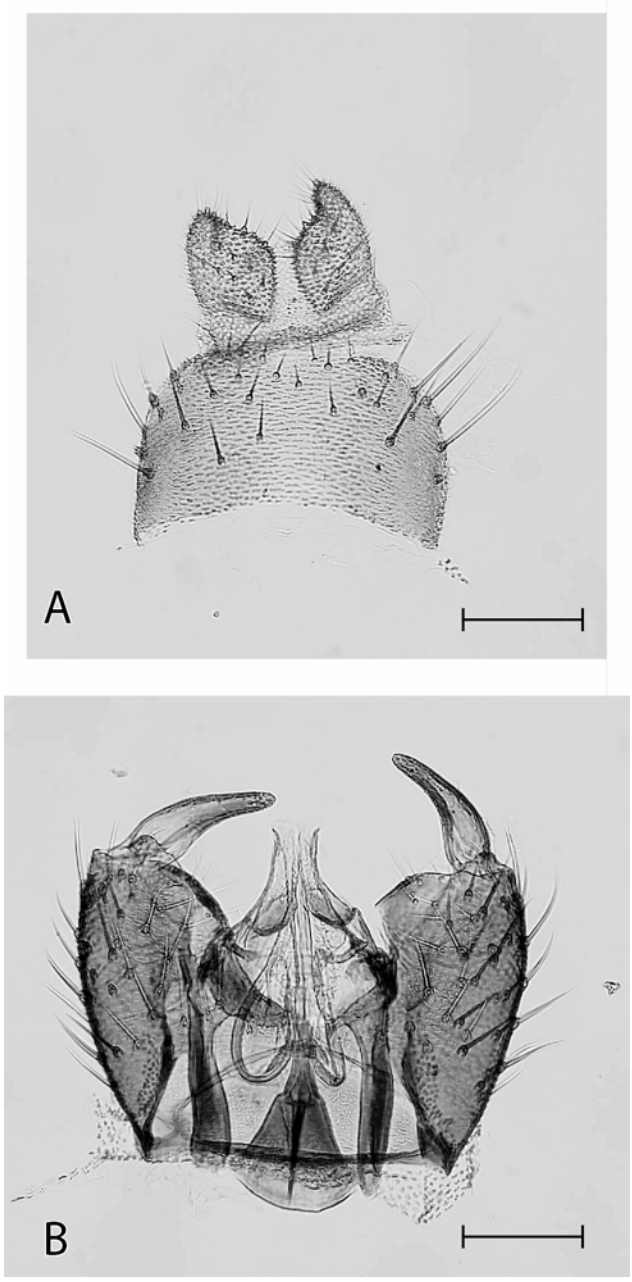


Figure 28. Male genitalia of *Bolbomyia nana* [USNMENT00024051]. (A) epandrium, dorsal view (B) hypandrium, dorsal view. Scale bar = 0.1 mm.

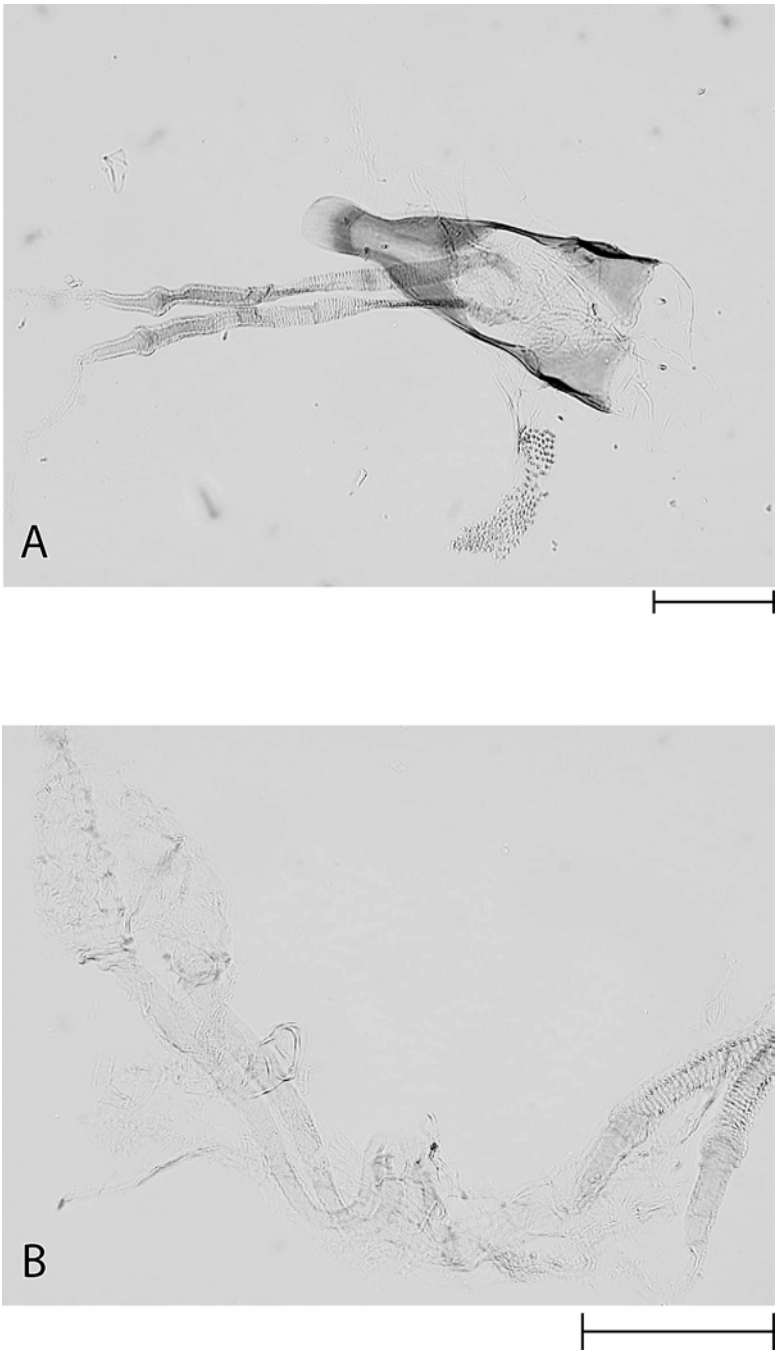


Figure 29. Internal structures of the female genitalia of *Bolbomyia nana*. (A) Sternite 9 [USNMENT00022946] (B) Spermathecae [USNMENT00022920]. Scale bar = 0.1 mm.

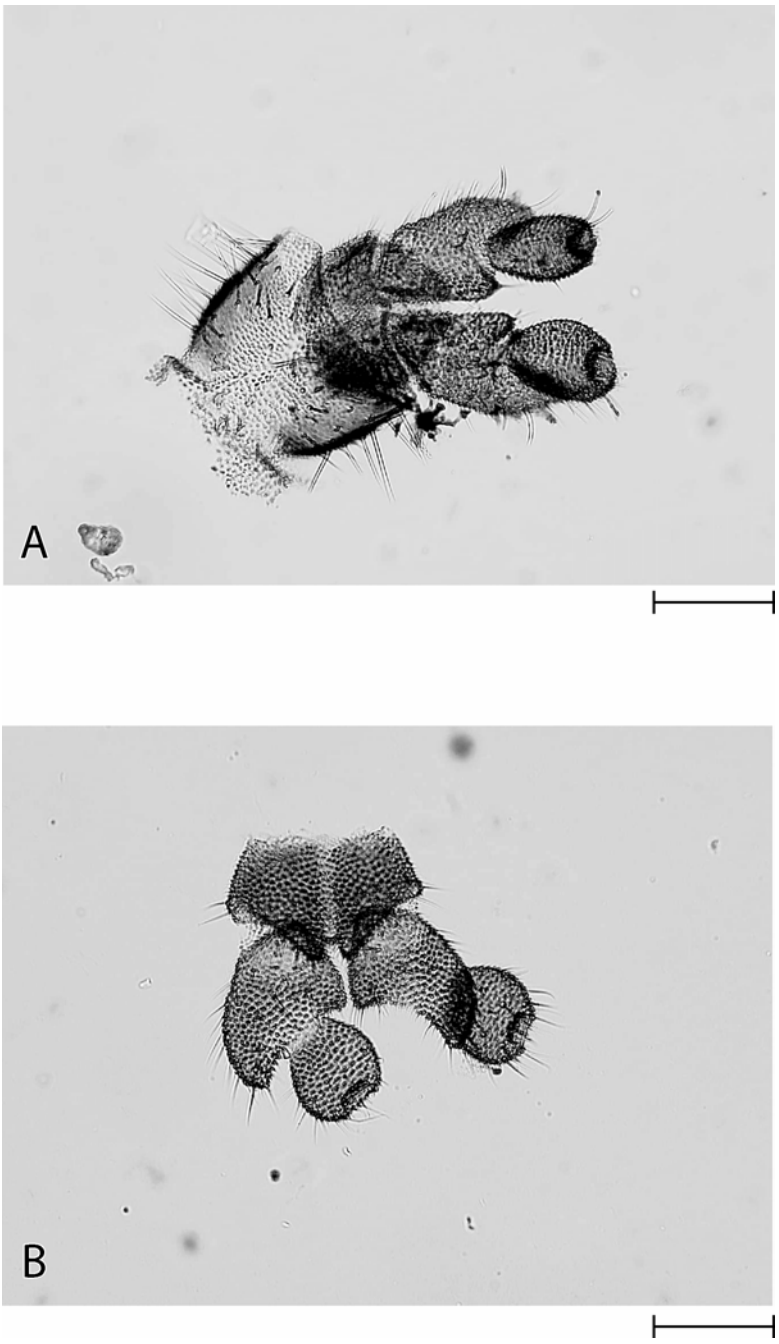


Figure 30. Female terminalia of *Bolbomyia nana*. (A) Dorsal view [USNMENT00022920] (B) Dorsal view of tergite 10, lateral view of left cercus [USNMENT00022946]. Scale bar = 0.1 mm.

Figure 31. Female sternite 8 of *Bolbomyia nana* [USNMENT00022920]. Scale bar = 0.1 mm.

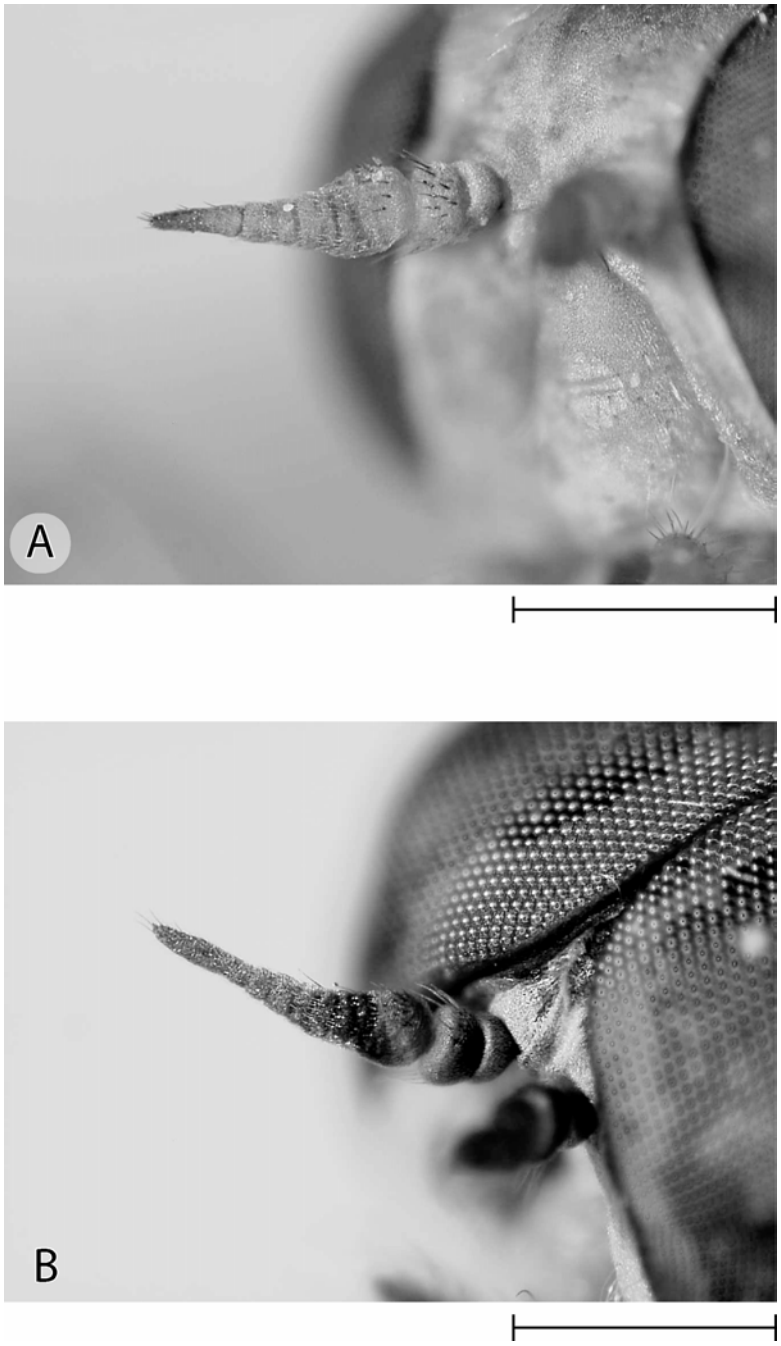


Figure 32. Antenna in species of *Arthroceras*. (A) *A. fulvicorne*, female, lateral view [USNMENT00022731] (B) *A. gadi*, male, oblique lateral view [USNMENT00022629]. Scale bar = 0.5 mm.

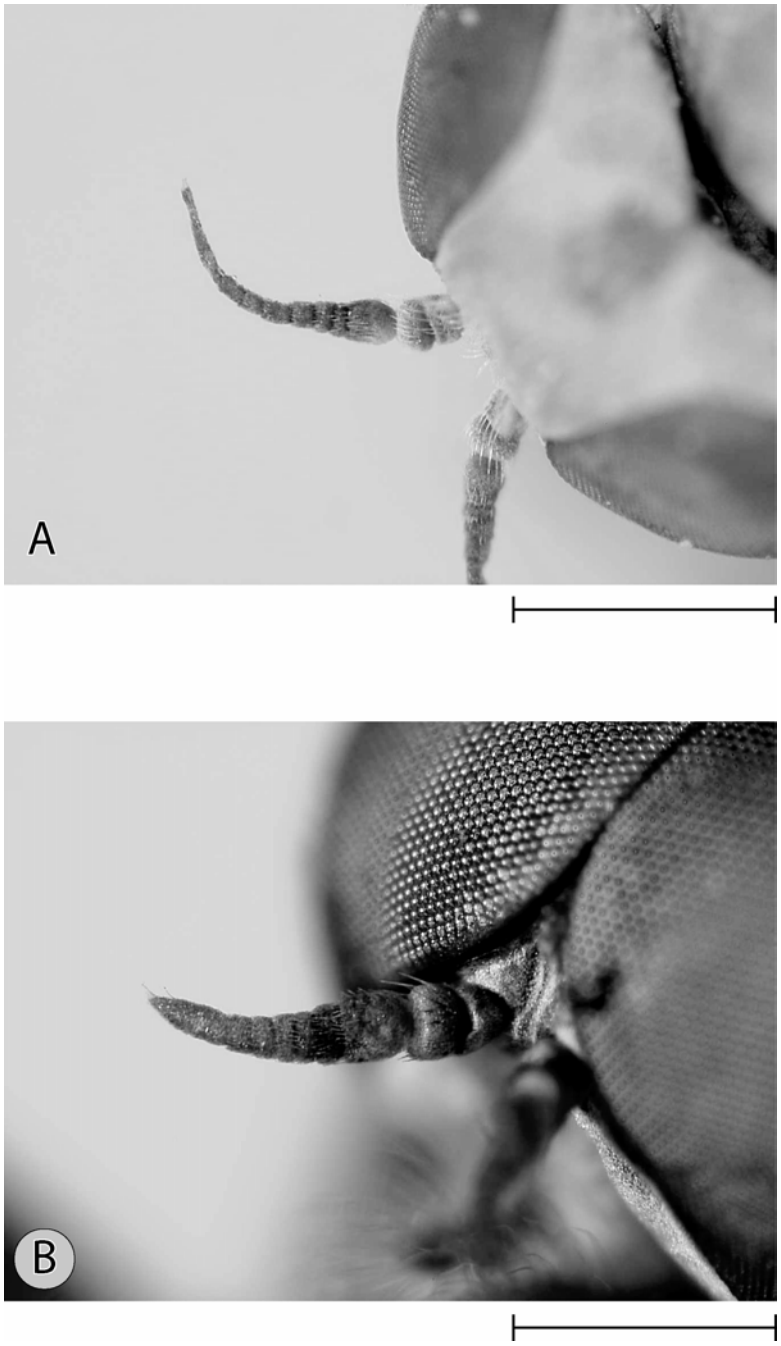


Figure 33. Antenna in species of *Arthroceras*. (A) *A. pollinosum*, female, dorsal view [USNMENT00025222] (B) *A. leptis*, male, oblique lateral view [USNMENT00022614]. Scale bar = 0.5 mm.

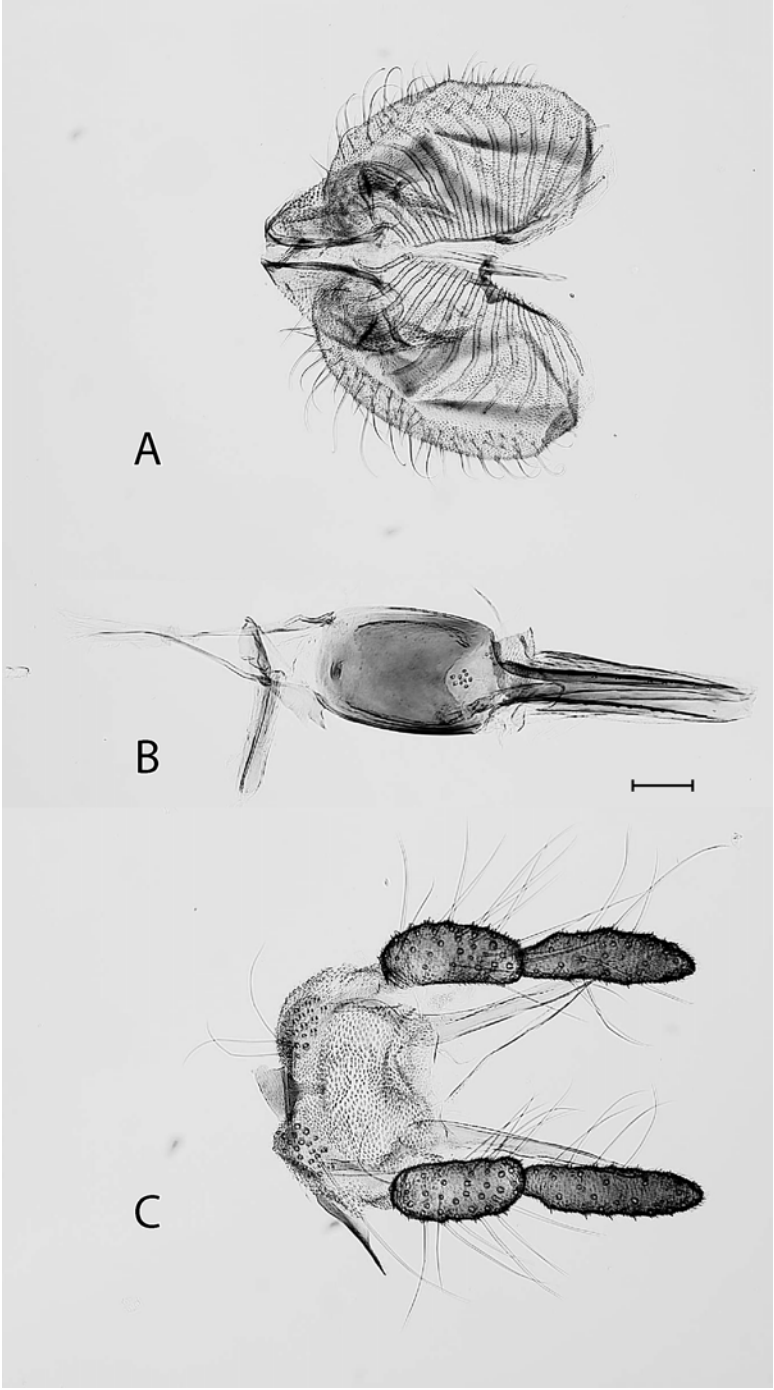


Figure 34. Mouthparts of *Arthroceras pollinosum* [USNMENT00022625]. (A) Labellum, ventral view (B) Hypopharynx, cibarial pump, and associated structures (C) Palps and lacinia, ventral view. Scale bar = 0.1 mm.

Figure 35. Wing in species of *Arthroceras*. (A) *A. fulvicorne*, female, dorsal view [USNMENT00022731] (B) *A. gadi*, female, ventral view [USNMENT00022628]. Scale bar = 0.5 mm.

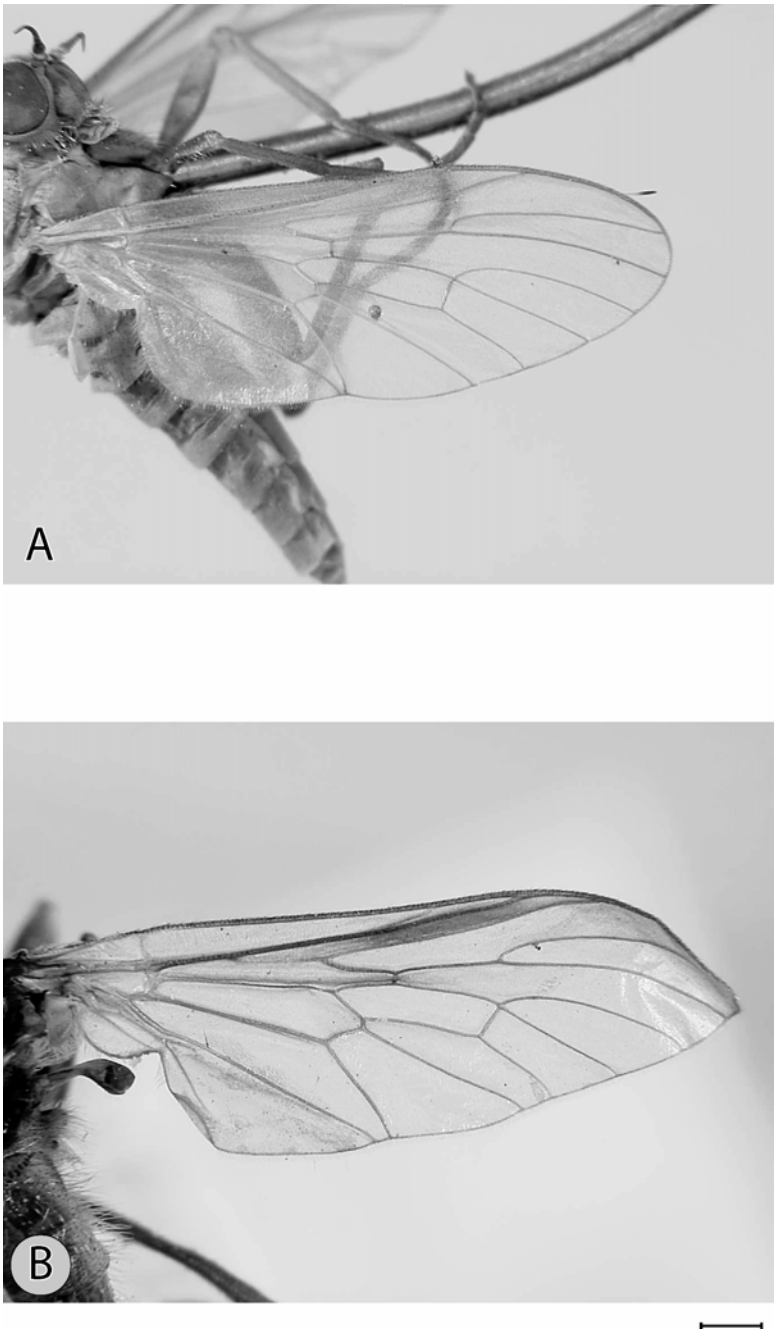


Figure 36. Wings in species of *Arthroceras*, dorsal view. (A) *A. pollinosum*, female [USNMENT00025222]. (B) *A. leptis*, male [USNMENT00022614]. Scale bar = 0.5 mm.

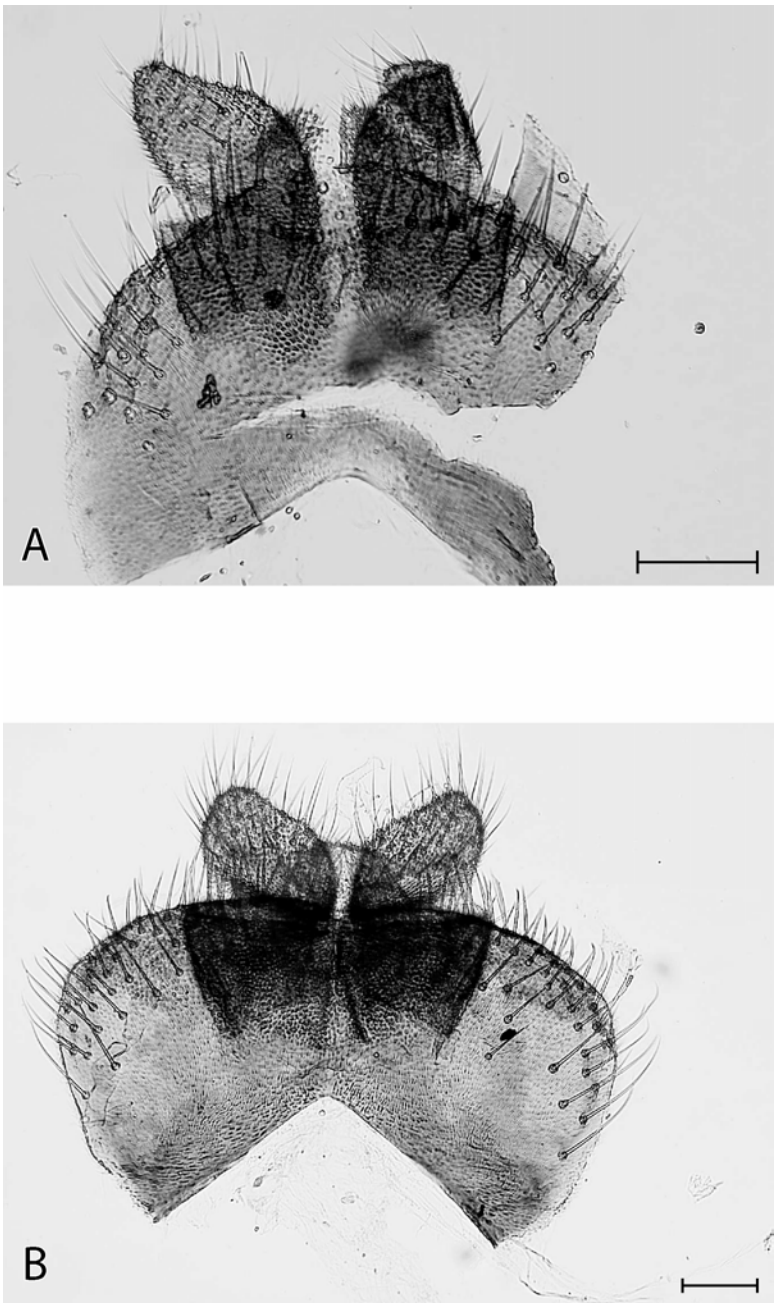


Figure 37. Epandria (male genitalia) in species of *Arthroceras*, dorsal view. (A) *A. fulvicorne* [USNMENT00022737] (B) *A. leptis* [USNMENT00022613]. Scale bar = 0.1 mm.

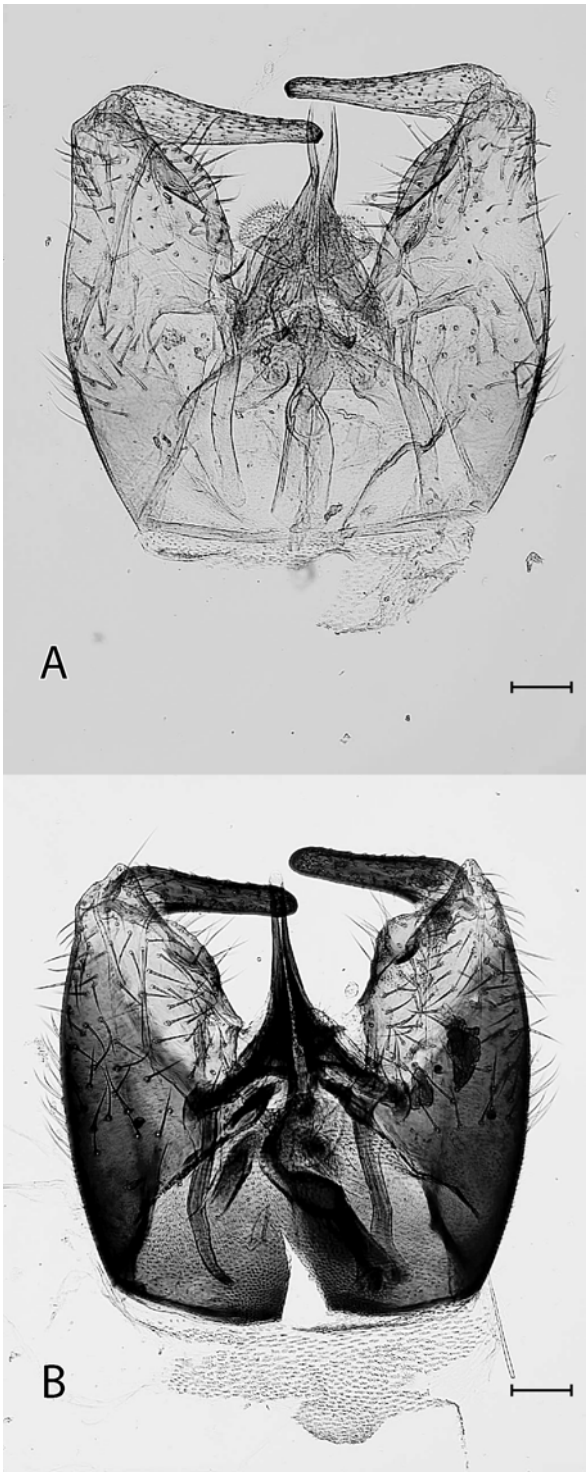


Figure 38. Dorsal view of hypandrium (male genitalia) in species of *Arthroceras*. (A) *A. fulvicorne* [USNMENT00022737] (B) *A. leptis* [USNMENT00022613]. Scale bar = 0.1 mm.

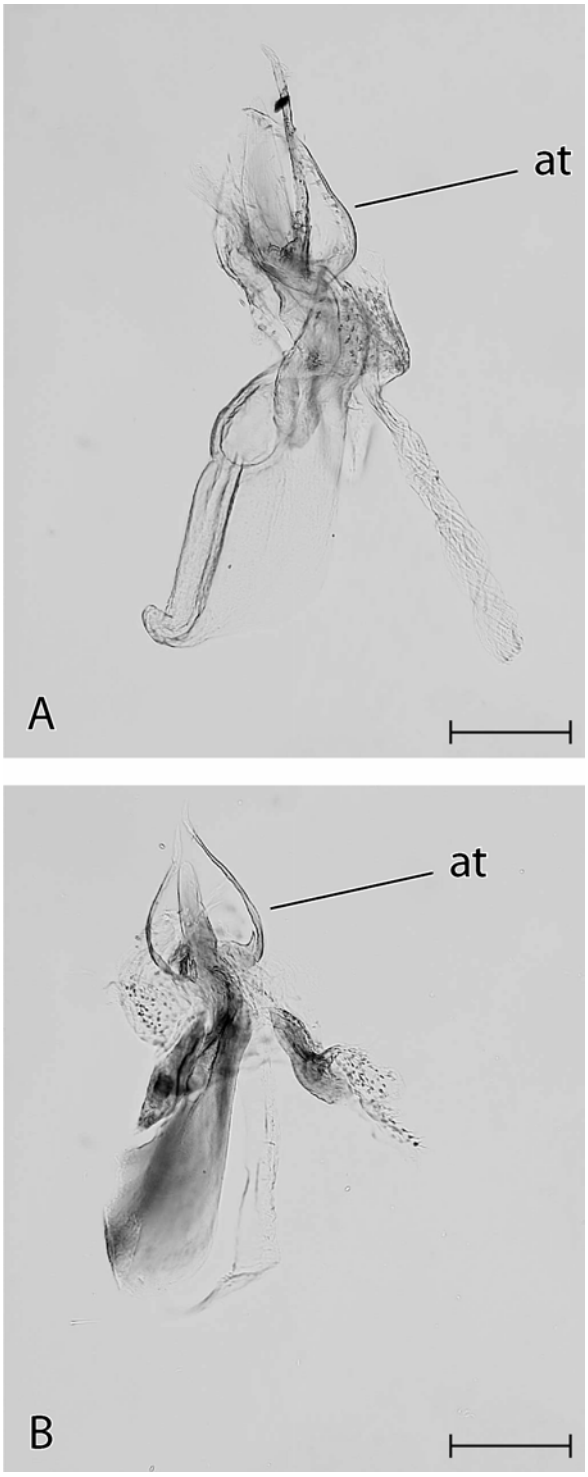


Figure 39. Aedeagus (male genitalia) in species of *Arthroceras*. Aedeagal tines (= *at*) are indicated. (A) *A. fulvicorne*, lateral view [USNMENT00022601] (B) *A. pollinosum*, dorsolateral view [USNMENT00022737]. Scale bar = 0.1 mm.

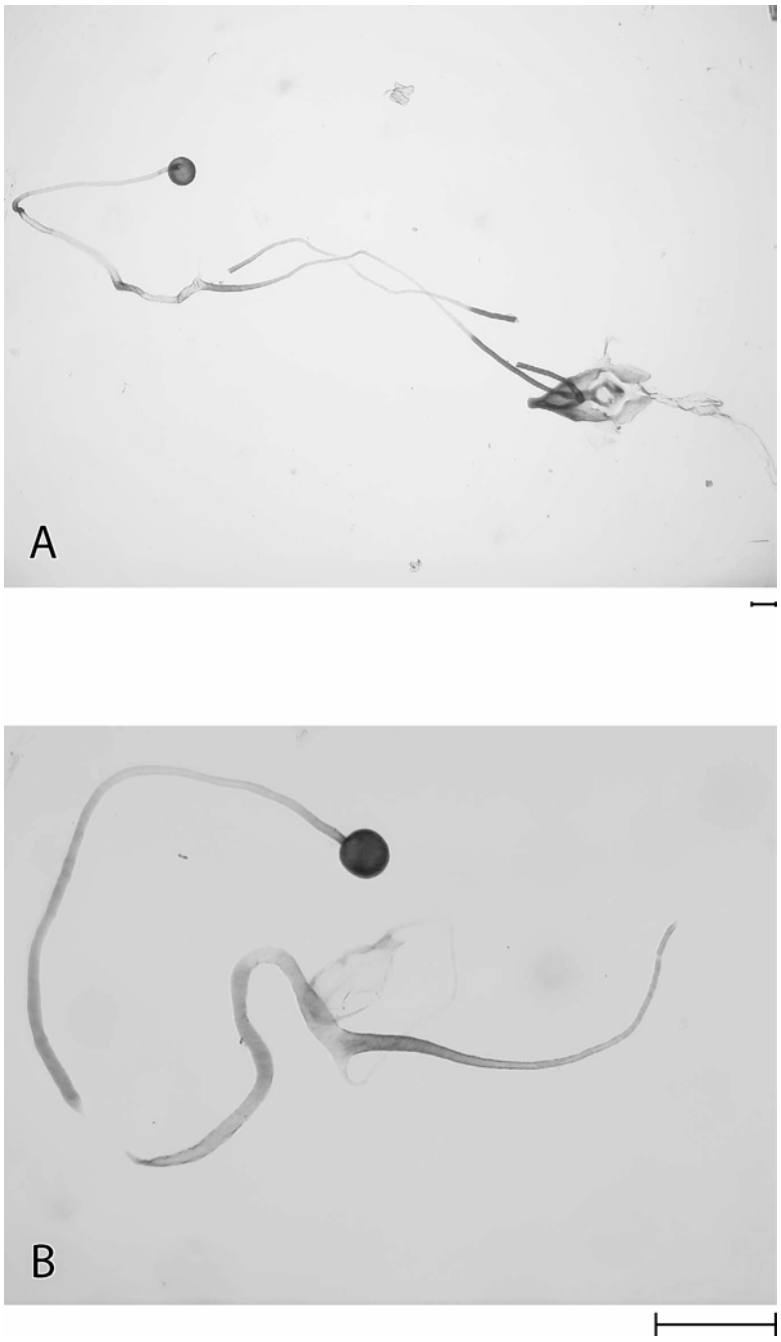


Figure 40. Female genitalia in *Arthroceras fulvicorne* USNM ENT 00025219. (A) Sternite 9, with associated spermathecal structures from the dorsal perspective. (B) Detail of spermathecal duct, with accessory gland. Scale bar = 0.1 mm.

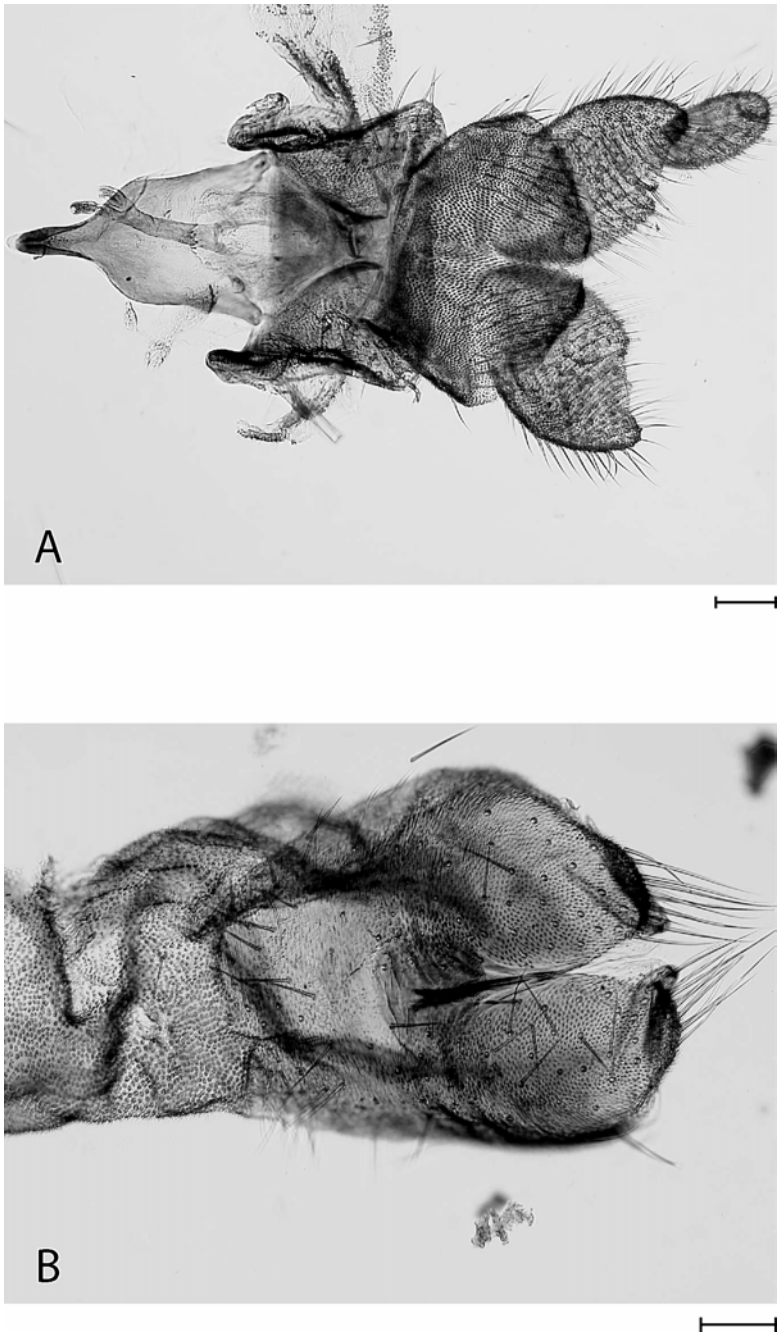


Figure 41. Female terminalia structures in *Arthroceras fulvicorne* [USNMENT00022736]. (A) Cerci and associated structures, partially dissected showing sternite 9 from dorsal perpective (B) Sternite 8, ventral view. Scale bar = 0.1 mm.

Figure 42. *Arthroteles cinerea*, female [USNMENT00023229]. Scale bar = 0.5 mm.

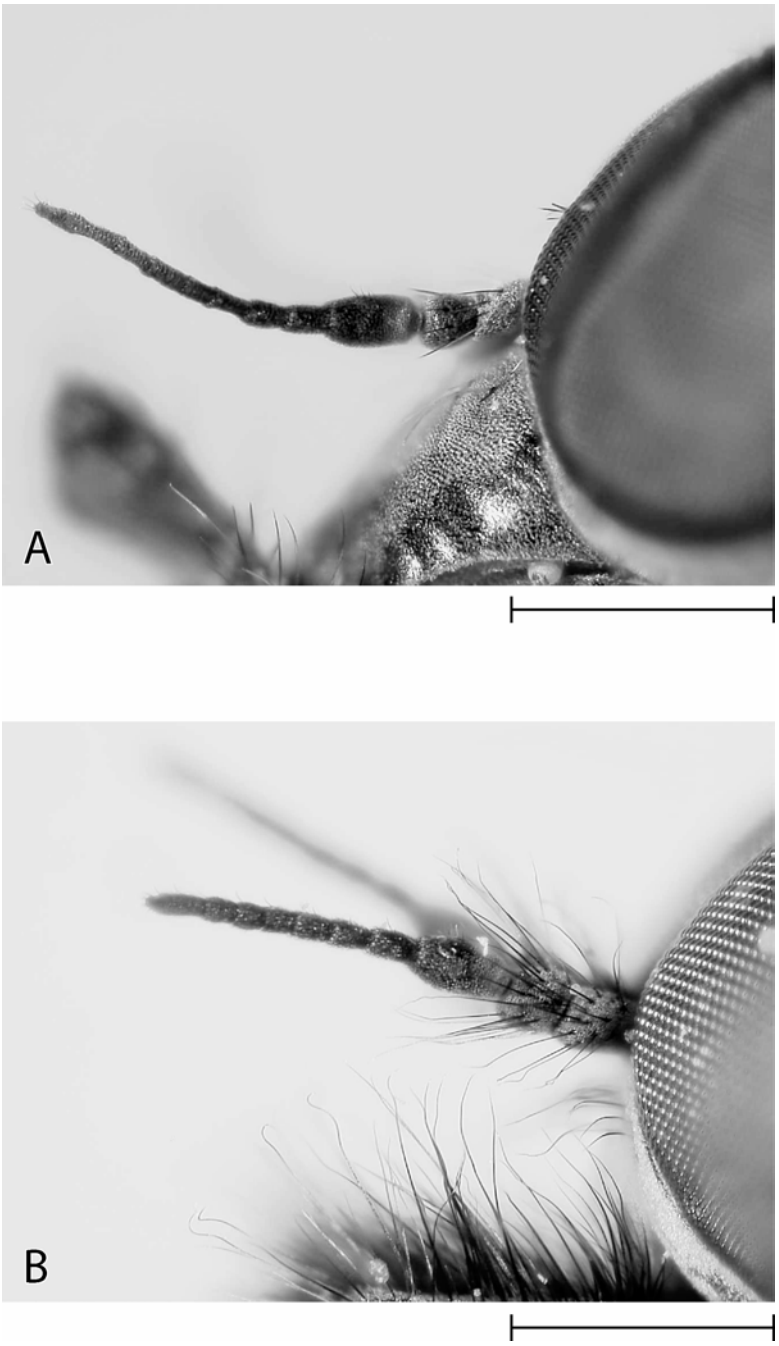


Figure 43. Antenna in species of *Arthroteles*, lateral view. (A) *A. cinerea*, female [USNMENT00023229] (B) *A. bombyliiformis*, male [USNMENT00025009]. Scale bar = 0.5 mm.

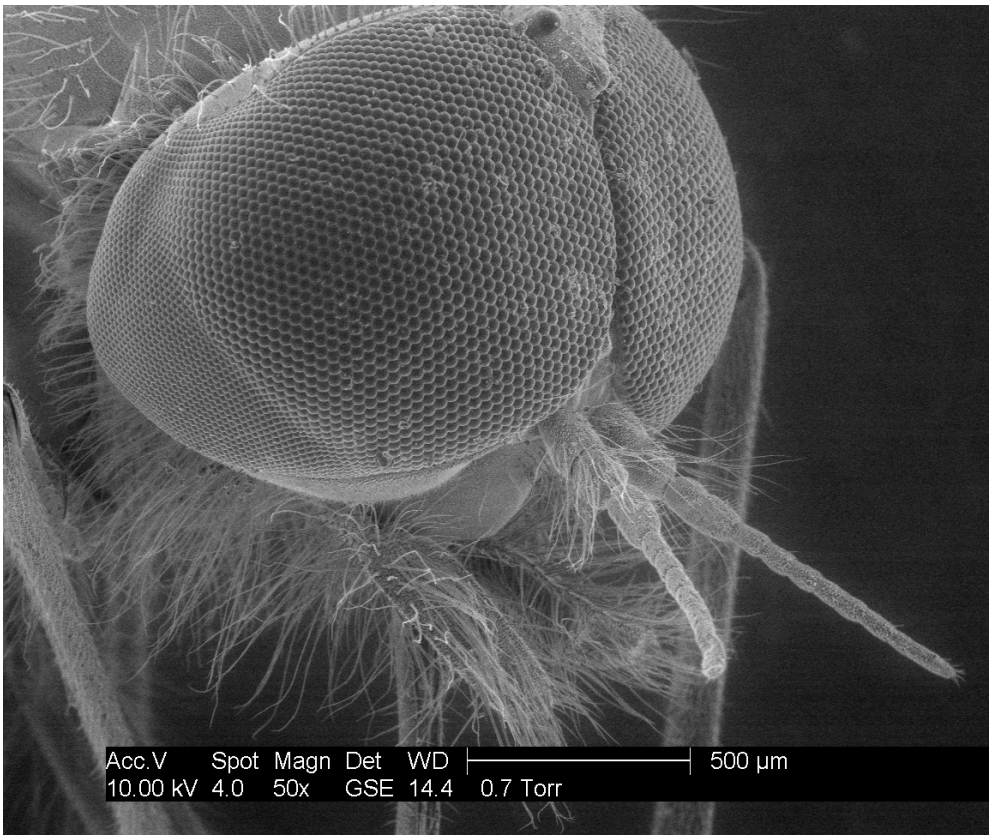


Figure 44. SEM image of head of *Arthroteles bombyliiformis*.

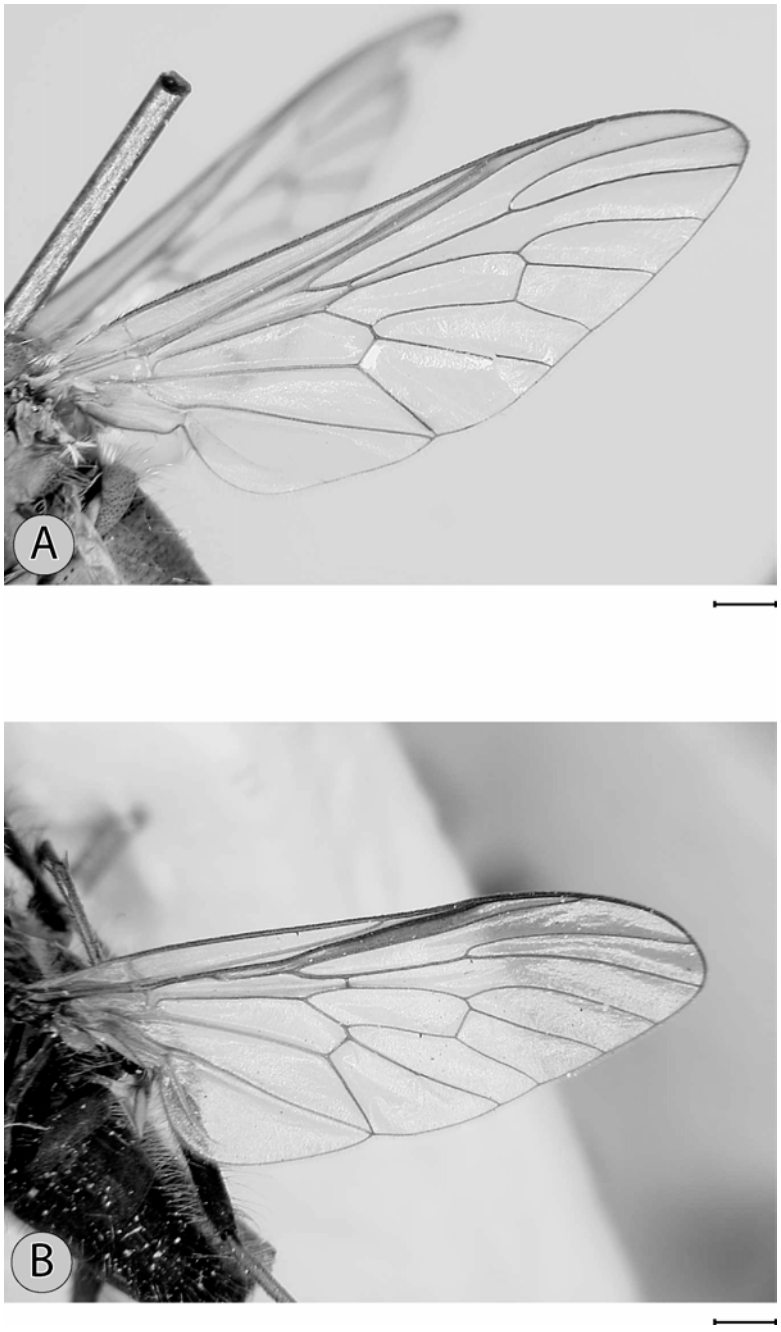


Figure 45. Wing in species of *Arthroteles*. (A) *A. cinerea*, male, ventral view [USNMENT00023231] (B) *A. bombyliiformis*, male, dorsal view [USNMENT000233230]. Scale bar = 0.5 mm.

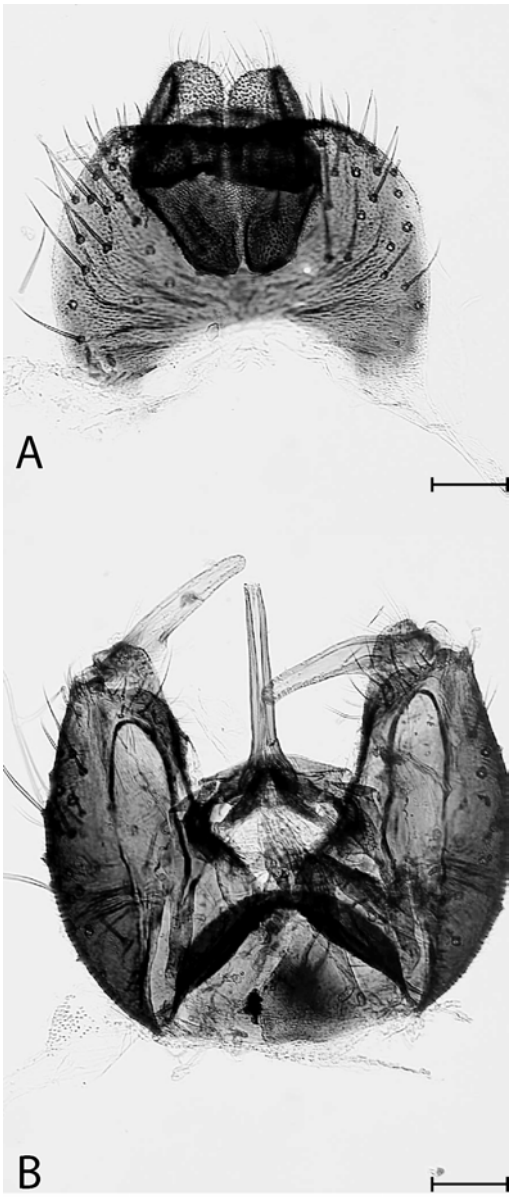


Figure 46. Male genitalia of *Arthroteles bombyliiformis* [USNMENT00024986]. (A) Epandrium, ventral view (B) Hypandrium, dorsal view. Scale bar = 0.1 mm.

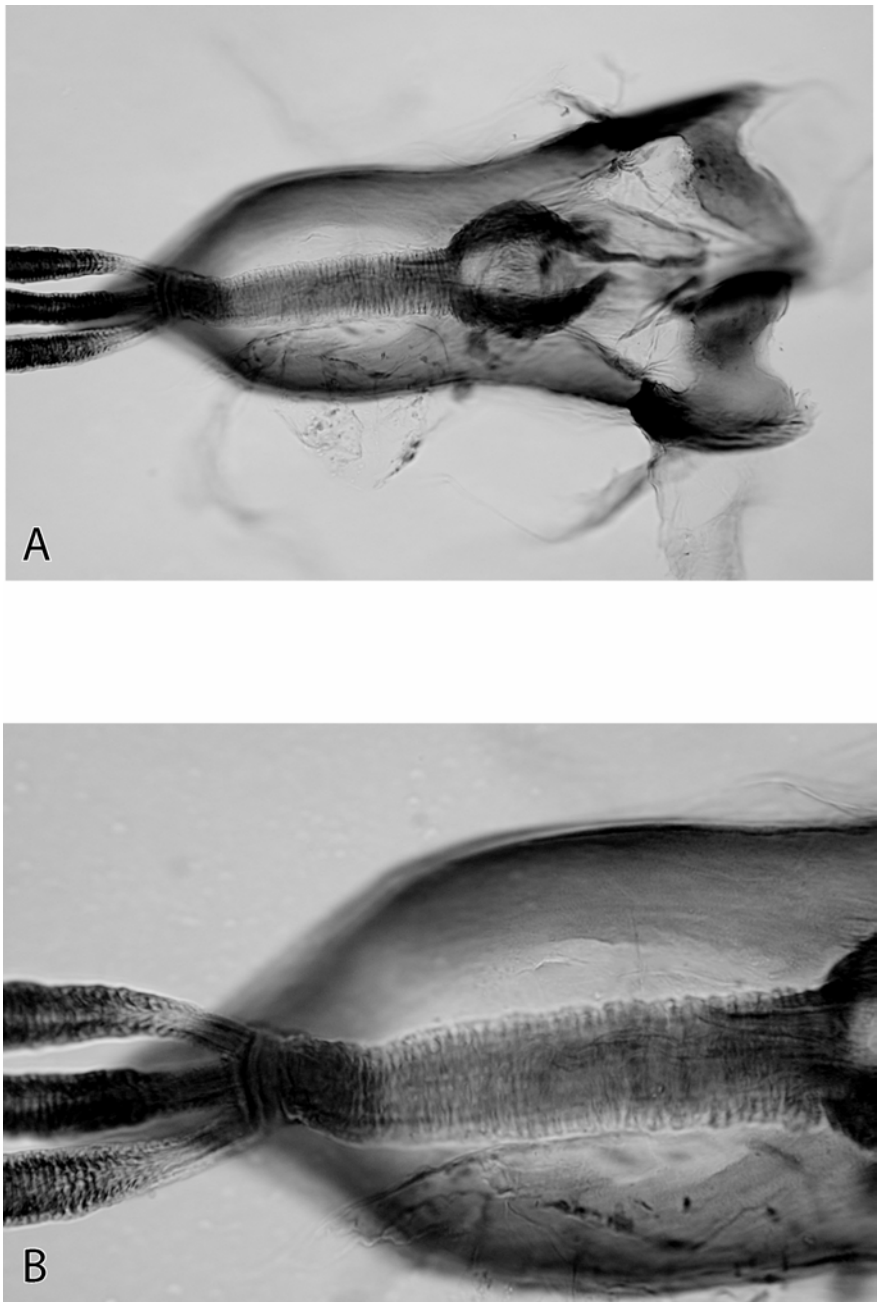


Figure 47. Sternite 9 (female genitalia) and associated structures of *Arthroteles bombyliiformis*.

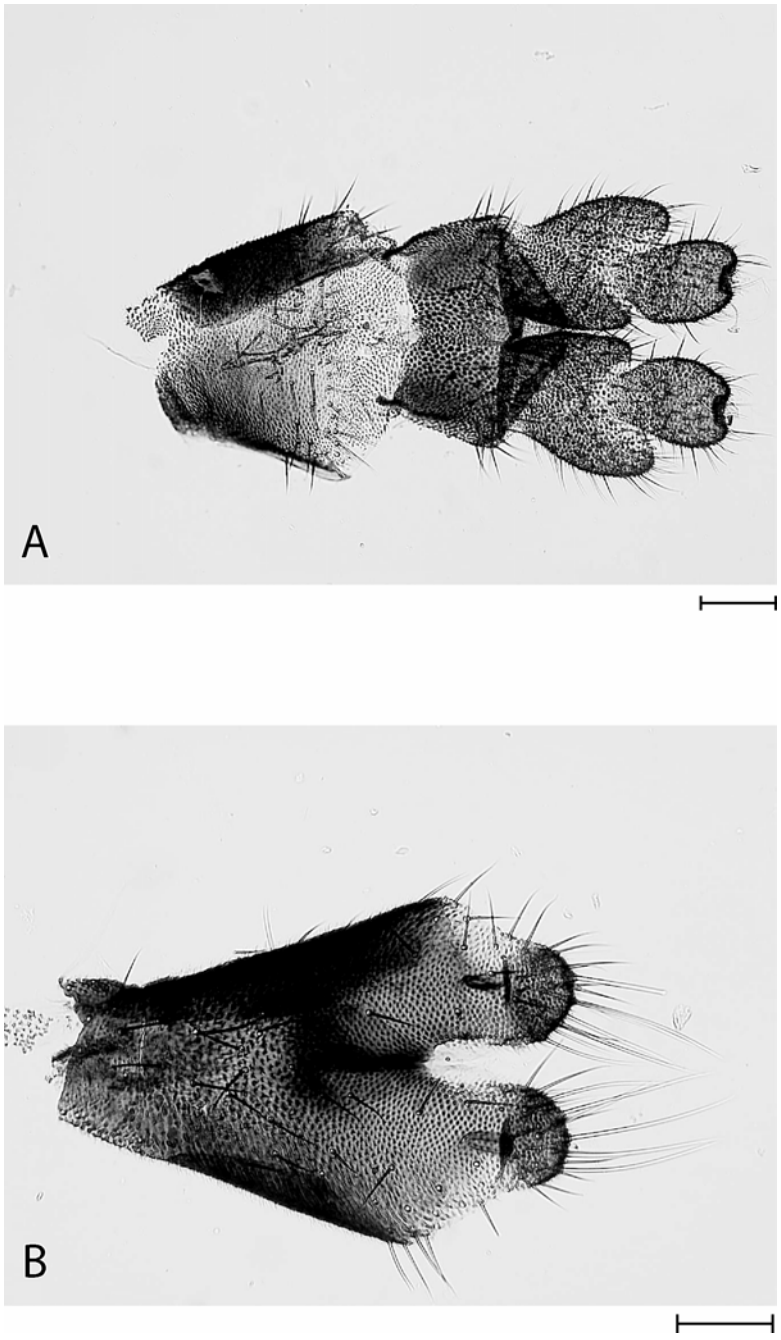


Figure 48. External structures of the female terminalia of *Arthroteles bombyliiformis* [USNMENT00025017]. (A) Tergite 10, dorsal view; and cerci, splayed flat, lateral view (B) Sternite 8, dorsal view. Scale bar = 0.1 mm.

Figure 49. Habitus of *Atherimorpha* sp. (South America), female [USNMENT00023370].

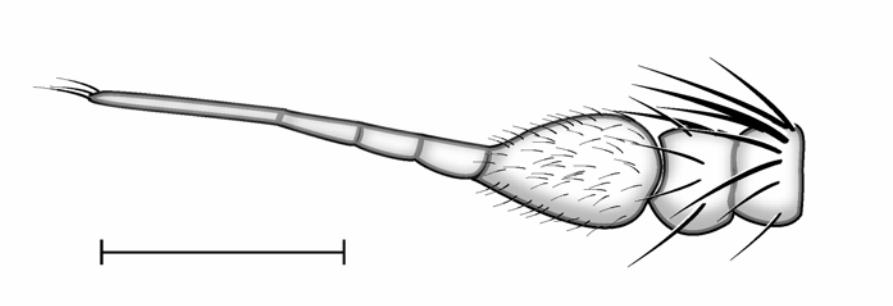


Figure 50. Antenna of *Atherimorpha atrifemur*. Scale bar = 0.5 mm.

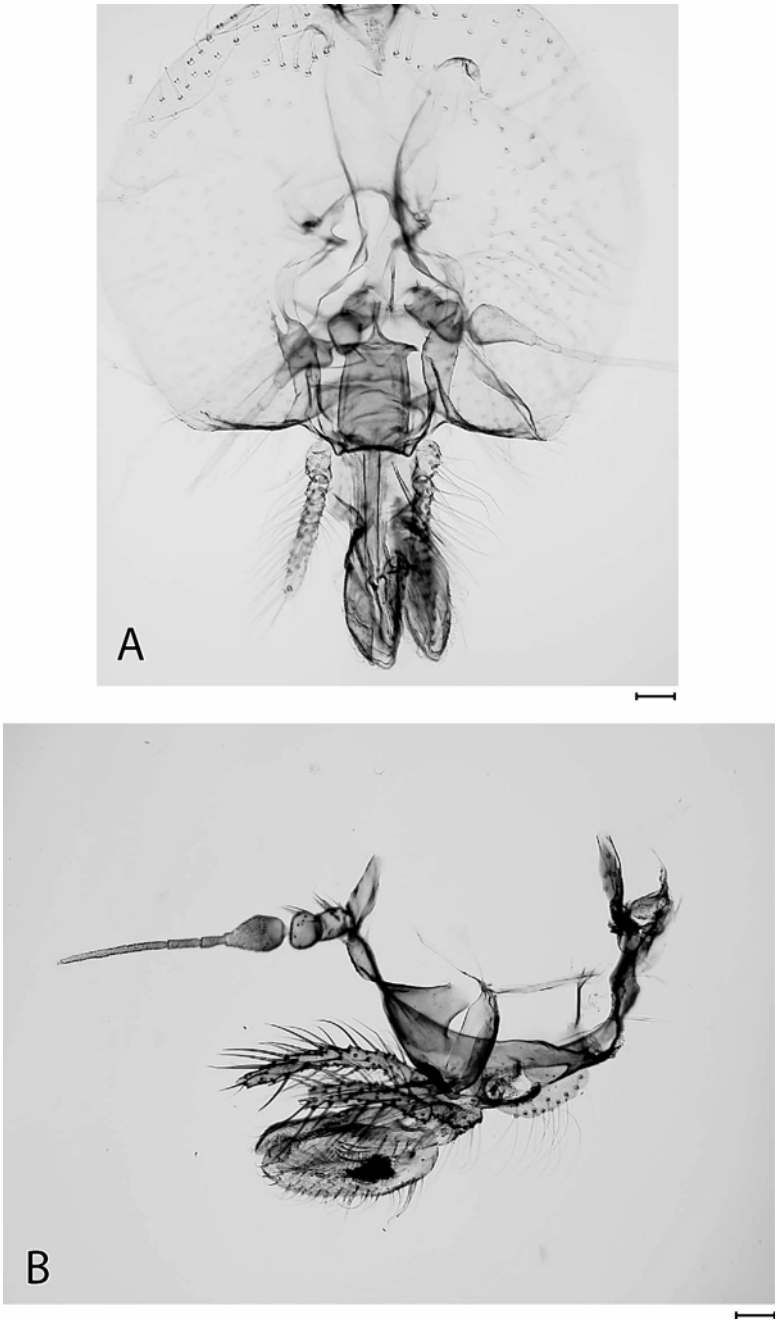


Figure 51. Macerated heads showing mouthparts of *Atherimorpha nemoralis*. (A) Posterior view [USNMENT28402] (B) Lateral view [USNMENT00025903]. Scale bar = 0.1 mm.

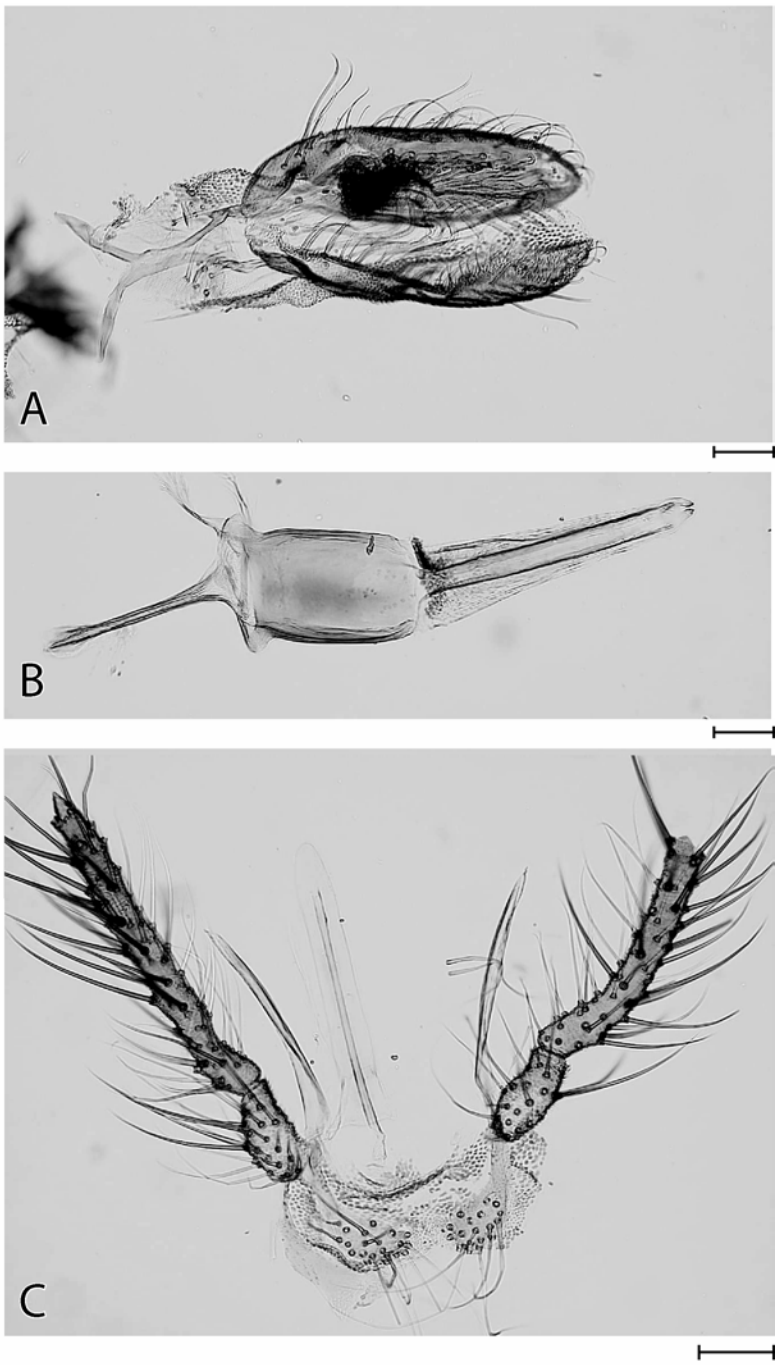


Figure 52. Mouthparts of *Atherimorpha nemoralis* [USNMENT00025903]. (A) Labellum (B) Hypopharynx and associated structures (C) Palps and associated structures. Scale bar = 0.1 mm.

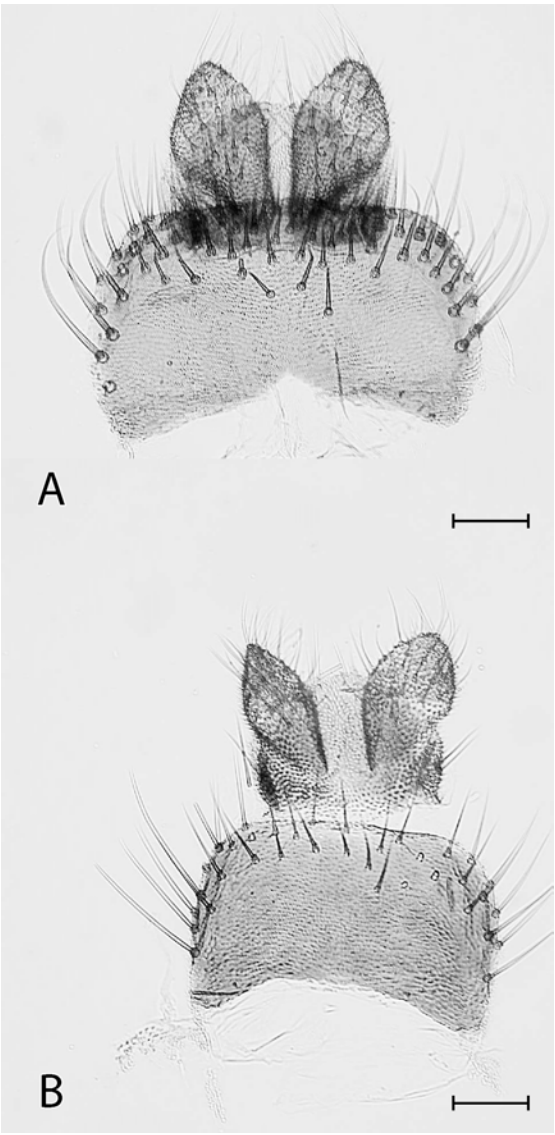


Figure 53. Epandrium in species of *Atherimorpha*. Dorsal view. (A) *A. triangularis* [USNMENT00028418] (B) *Atherimorpha* sp. (South America) [USNMENT00028520]. Scale bar = 0.1 mm.

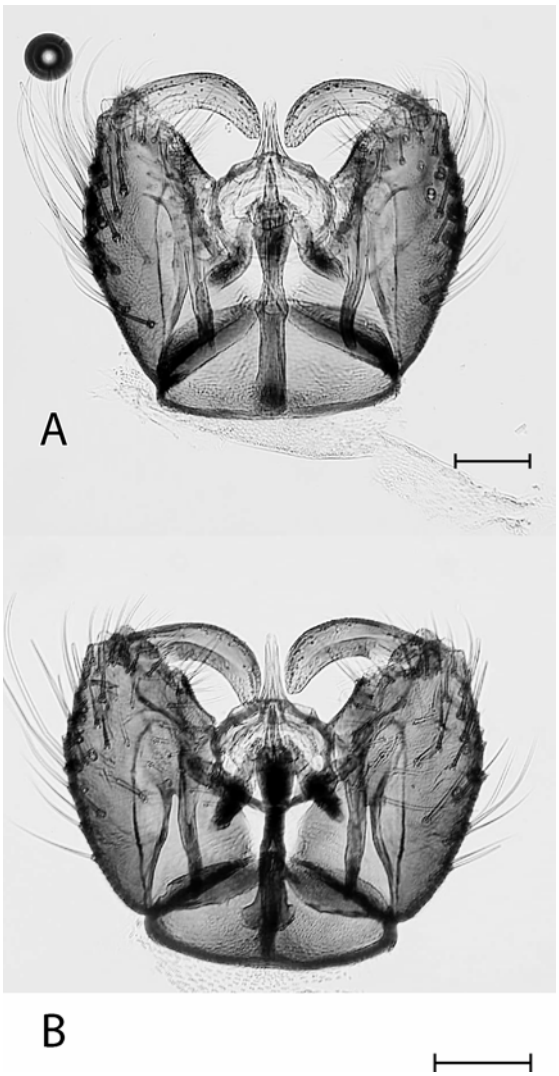


Figure 54. Hypandrium in species of *Atherimorpha*. Dorsal view. (A) *A. triangularis* [USNMENT00028418] (B) *Atherimorpha* sp. (South America) [USNMENT00028520]. Scale bar = 0.1 mm.

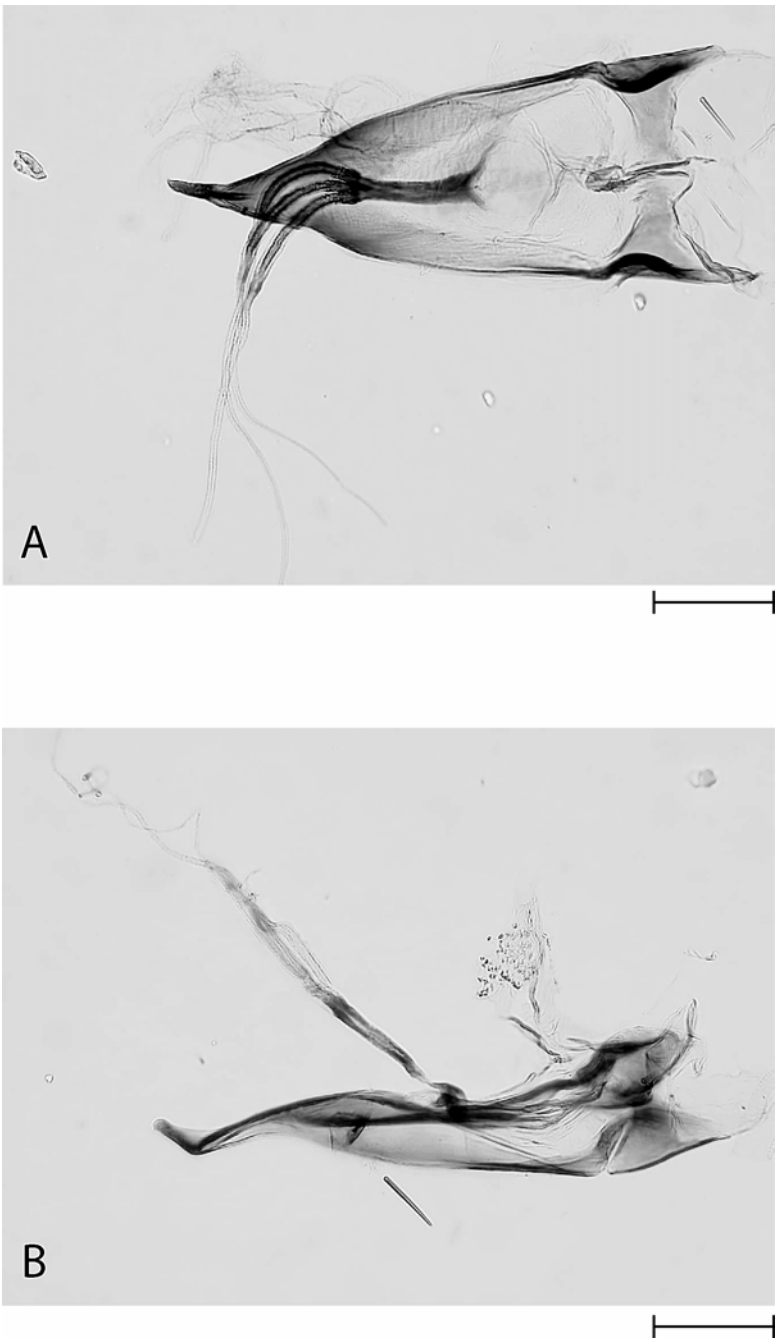


Figure 55. Internal structure of the female genitalia in *Atherimorpha nemoralis*. (A) Dorsal view [USNMENT00025317] (B) Oblique lateral view [USNMENT00025109]. Scale bar = 0.1 mm.

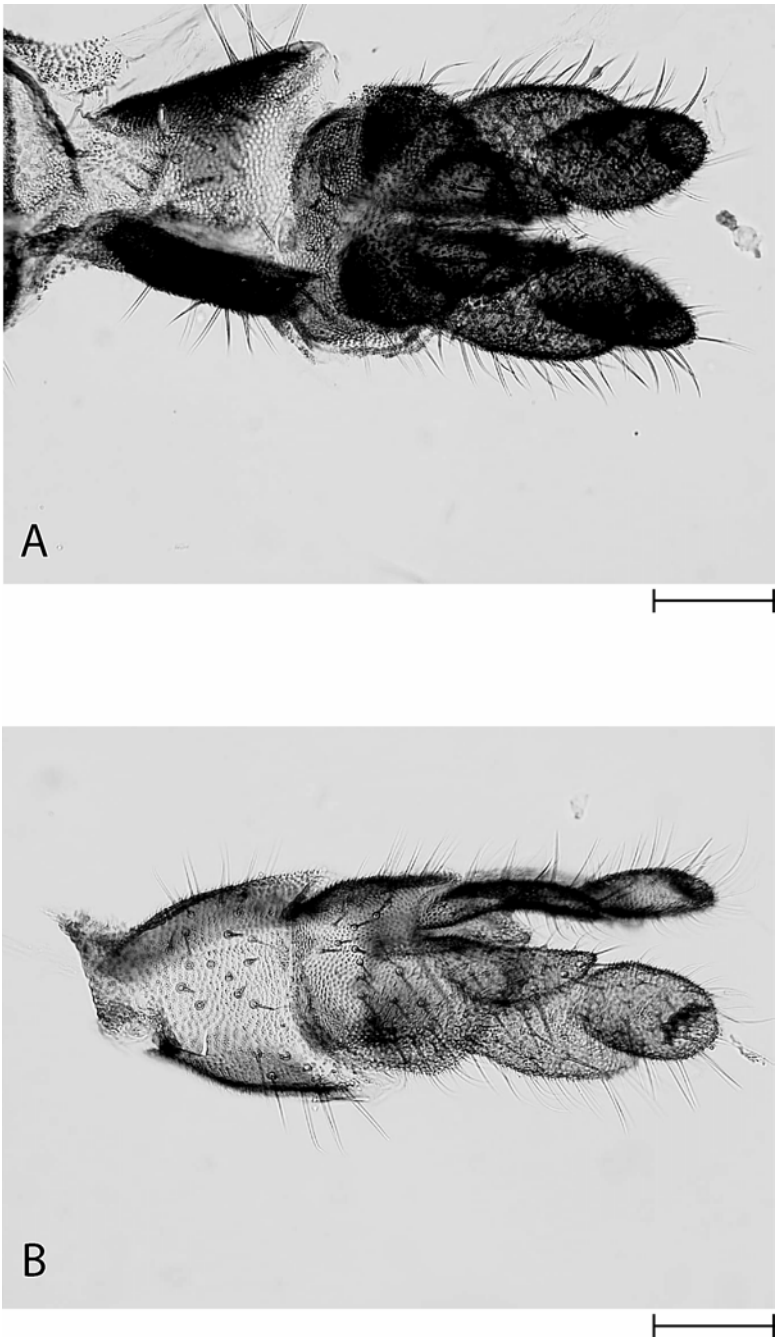


Figure 56. External structures of the female terminalia of *Atherimorpha nemoralis*. (A) Dorsal view [USNMENT00025317] (B) Oblique lateral view [USNMENT00025109]. Scale bar = 0.1 mm.

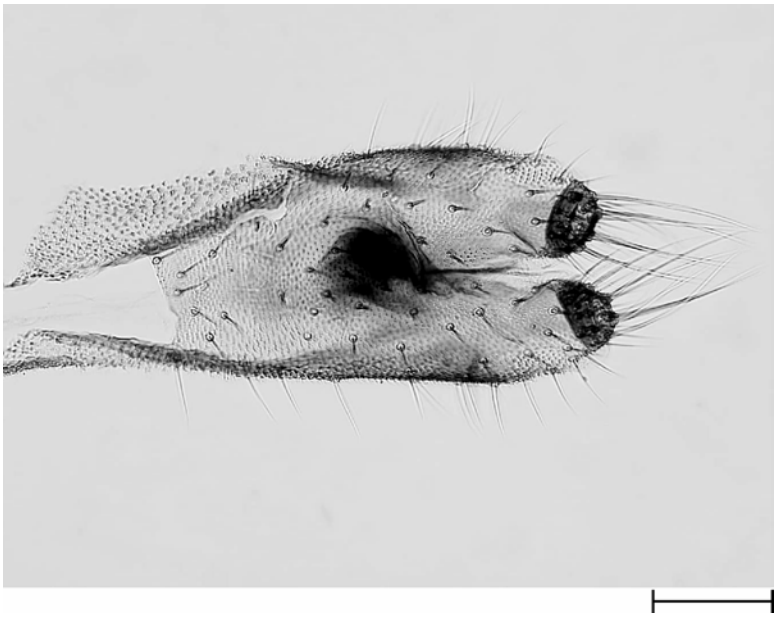


Figure 57. Female sternite 8 of *Atherimorpha nemoralis* [USNMENT00025109]. Dorsal view. Scale bar = 0.1 mm.

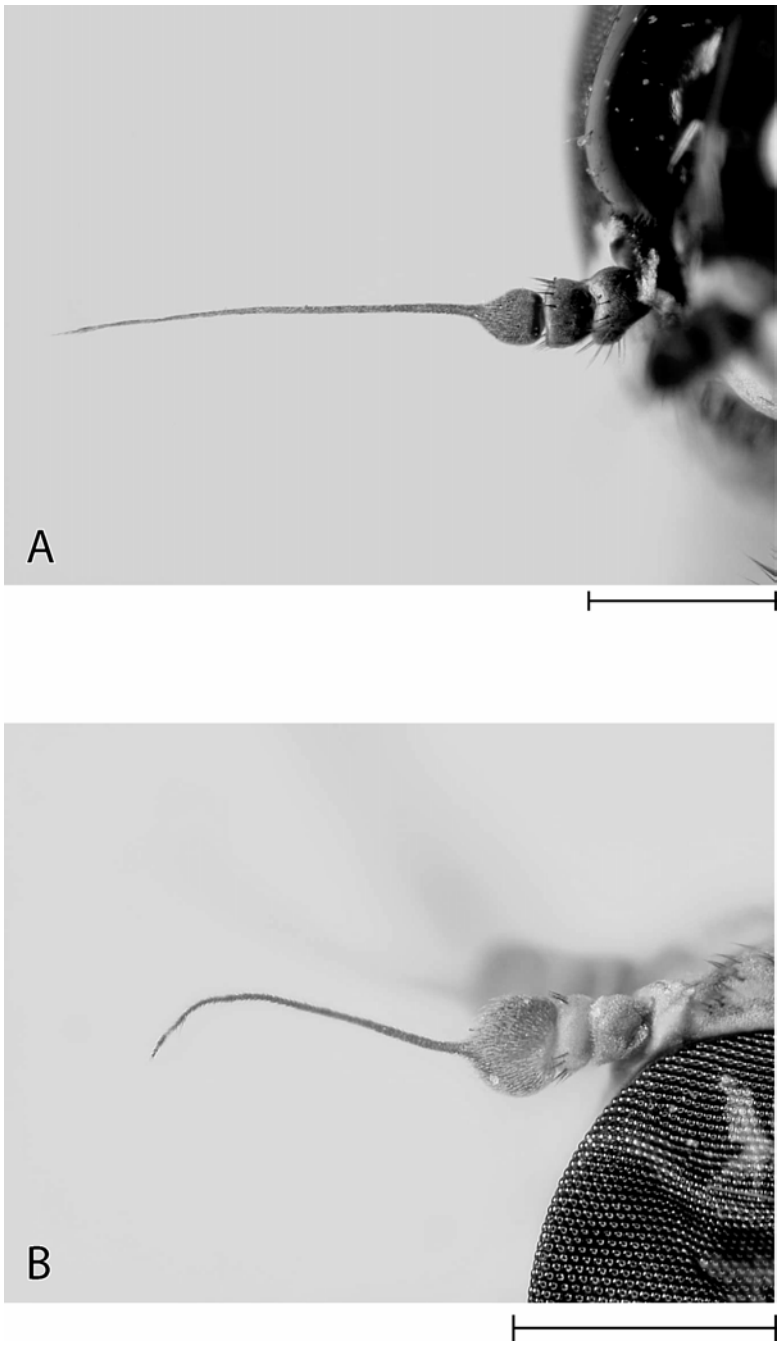


Figure 58. Antennal form in species of *Chrysopilus*, lateral view. (A) *C. ornatus*, female [USNMENT00025947] (B) *C. quadratus*, female [USNMENT00025948]. Scale bar = 0.5 mm.

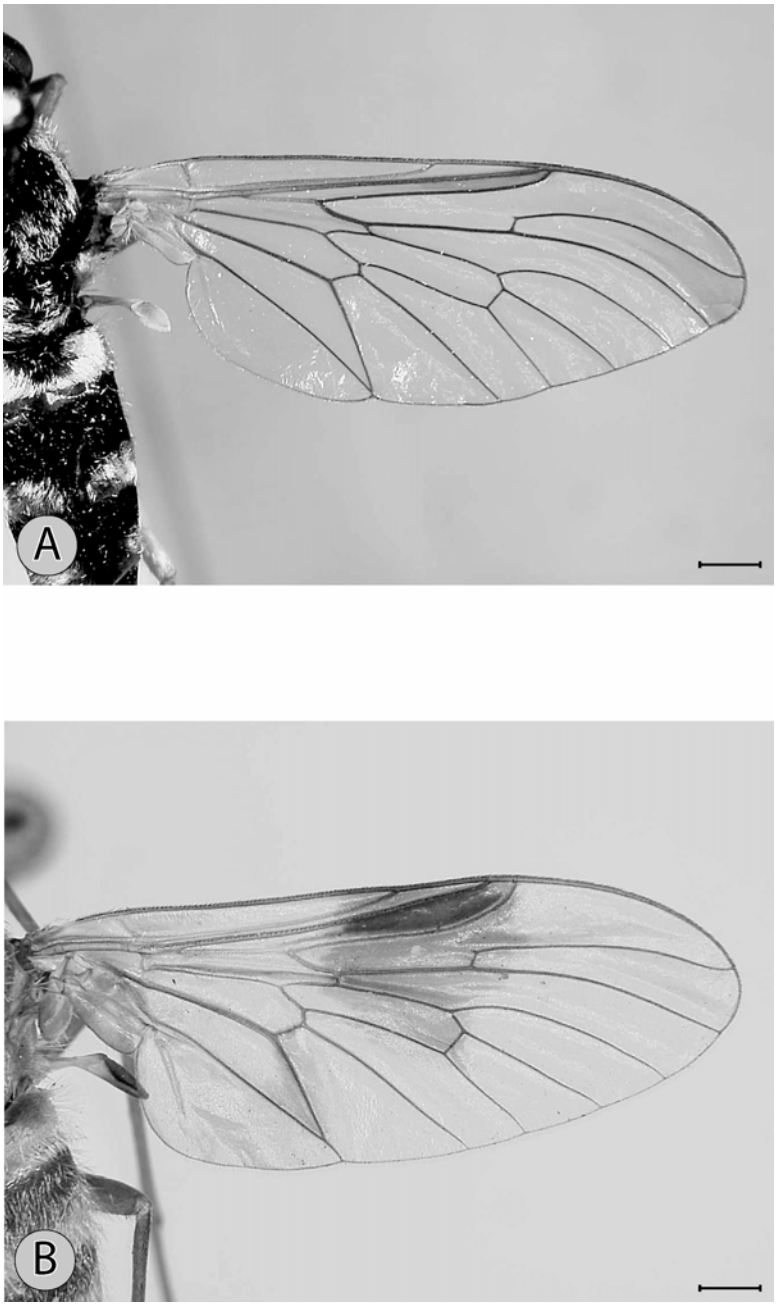


Figure 59. Wing of *Chrysopilus* species, dorsal view. (A) *C. ornatus* [USNMENT00025947] (B) *C. quadratus* [USNMENT00025948]. Scale bar = 0.5 mm.

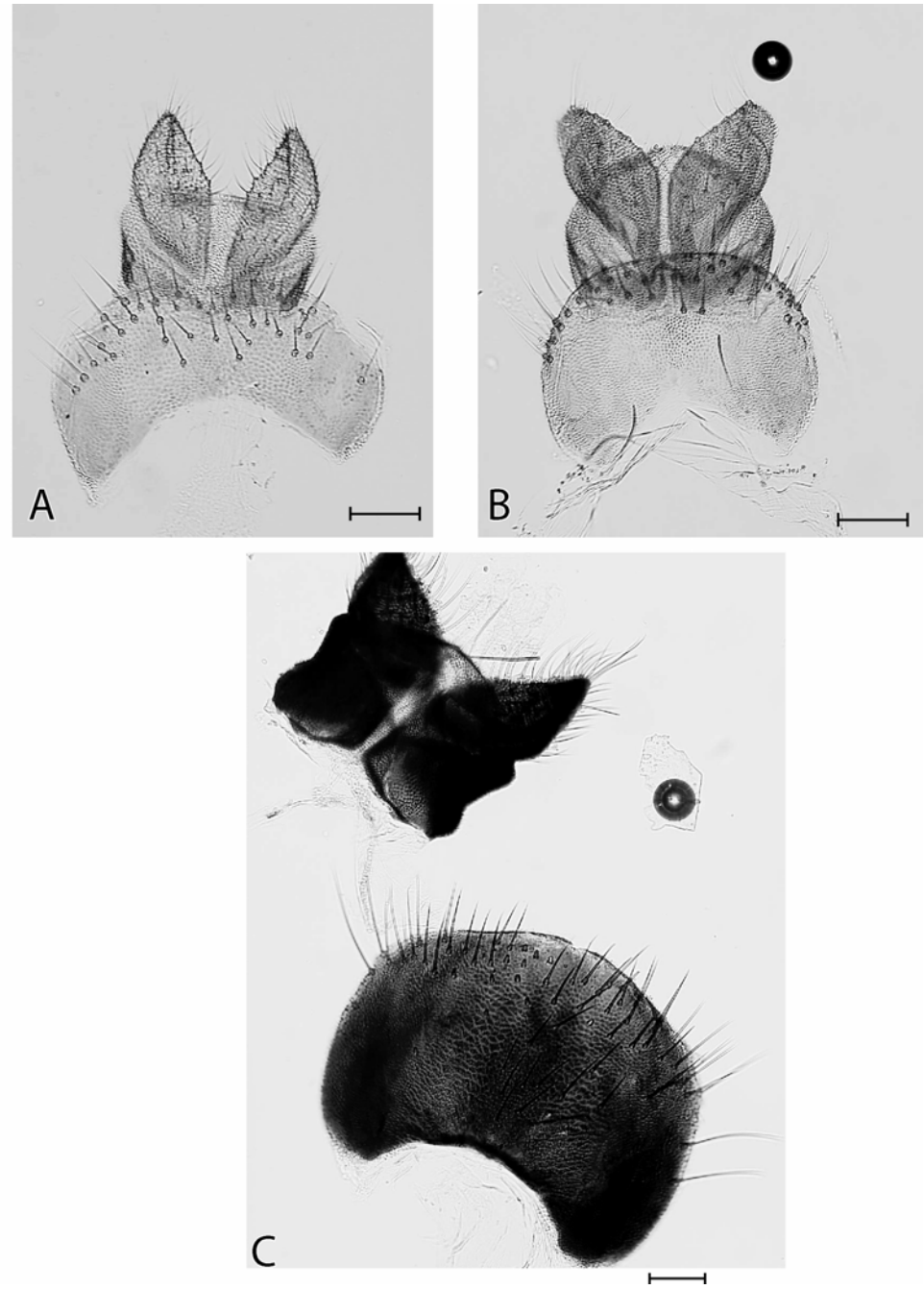


Figure 60. Epandrium in species of *Chrysopilus*, dorsal view. (A) *C. quadratus* [USNMENT00025951] (B) *Chrysopilus* sp. (New Caledonia) [USNMENT00025952] (C) *Chrysopilus thoracicus* [USNMENT00025242]. Scale bar = 0.1 mm.

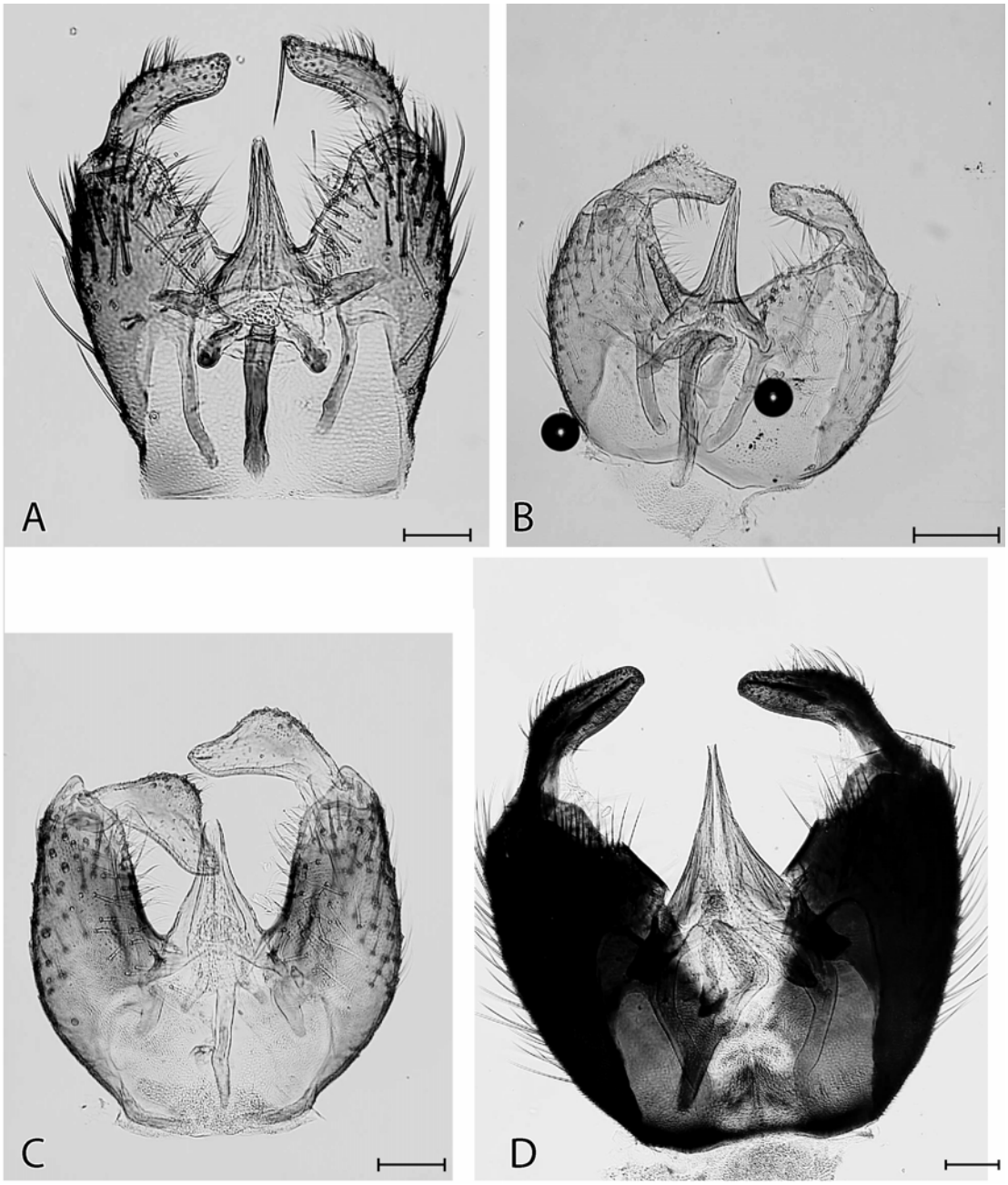


Figure 61. Hypandrium in species of *Chrysopilus*, dorsal view. (A) *C. quadratus* [USNMENT00025951] (B) *Chrysopilus rotundipennis* [USNMENT00025980] (C) *Chrysopilus* sp. (New Caledonia) [USNMENT00025952] (D) *Chrysopilus thoracicus* [USNMENT00025242]. Scale bar = 0.1 mm.

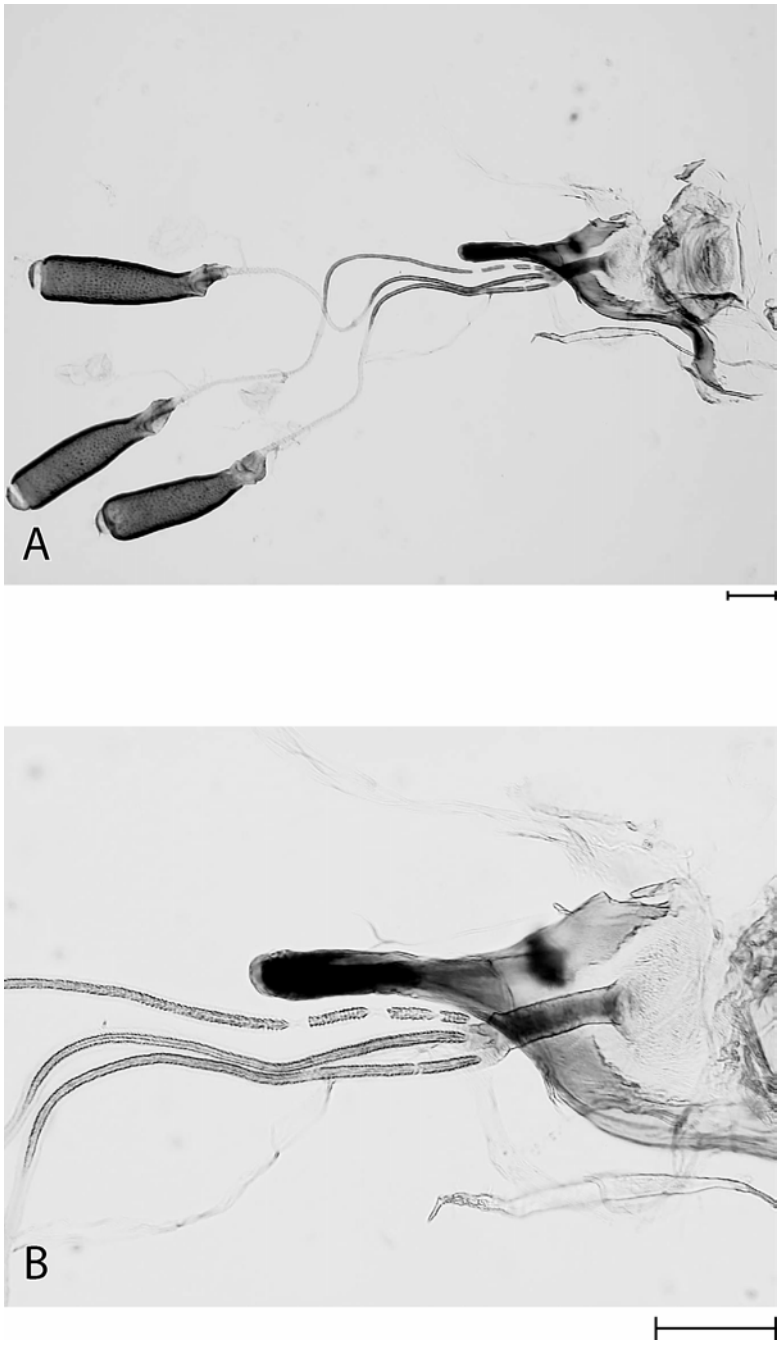


Figure 62. Internal structures of the female genitalia in *Chrysopilus thoracicus* [USNMENT00025875], dorsal view. Scale bar = 0.1 mm.

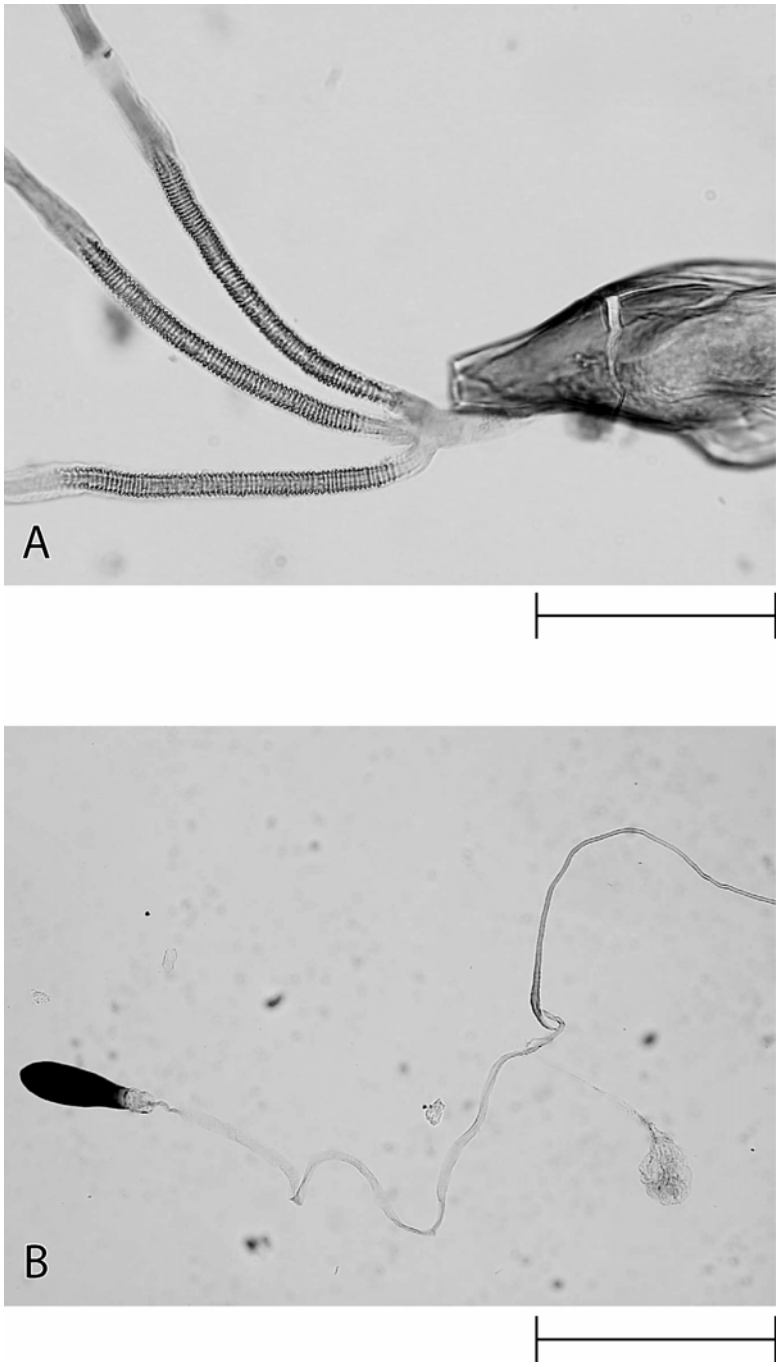


Figure 63. Internal structures of the female genitalia in Chrysopilus sp. [USNMENT00025877], ventral view. (A) Detail of furrowed and sclerotized ejaculatory process of the spermathecal ducts (B) Spermatheca. Scale bar = 0.1 mm.

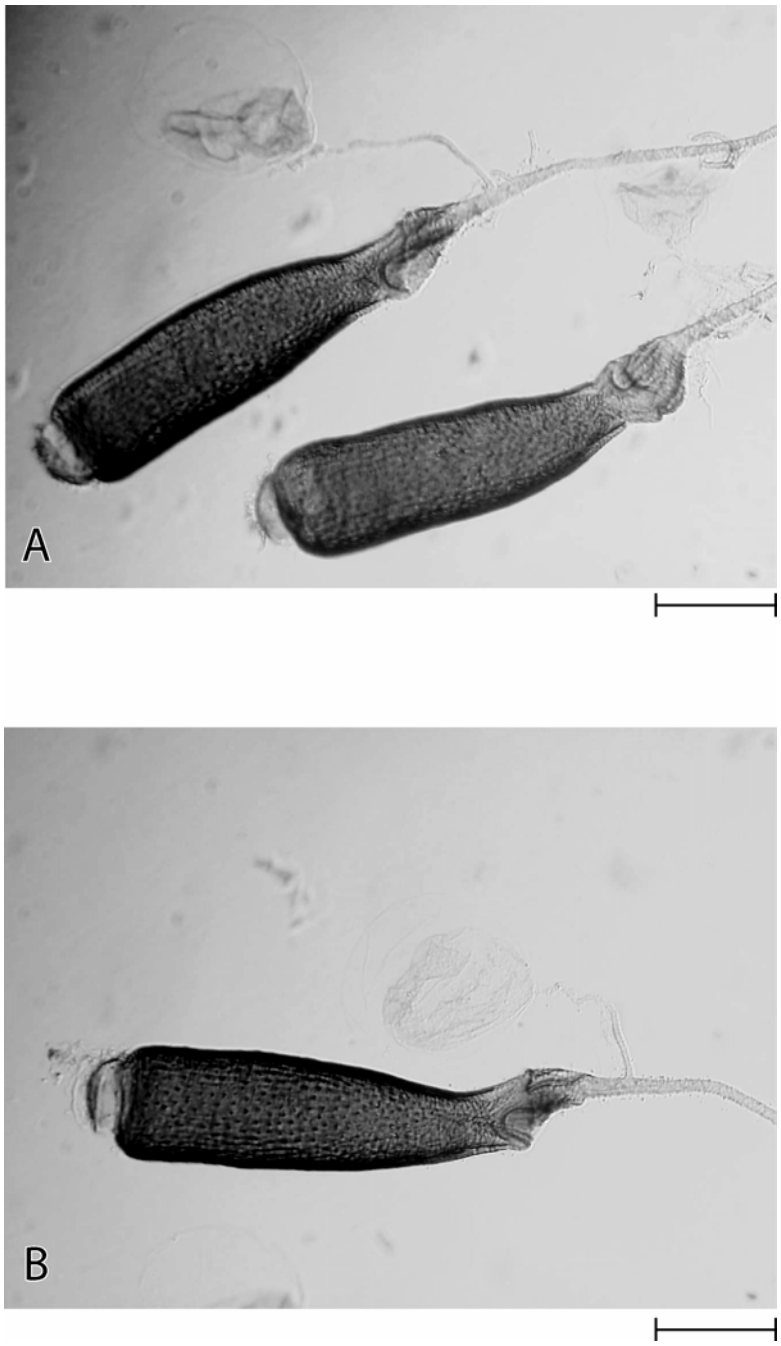


Figure 64. Spermathecae and spermathecal duct accessory gland in *Chrysopilus thoracicus* [USNMENT00025875]. Scale bar = 0.1 mm.

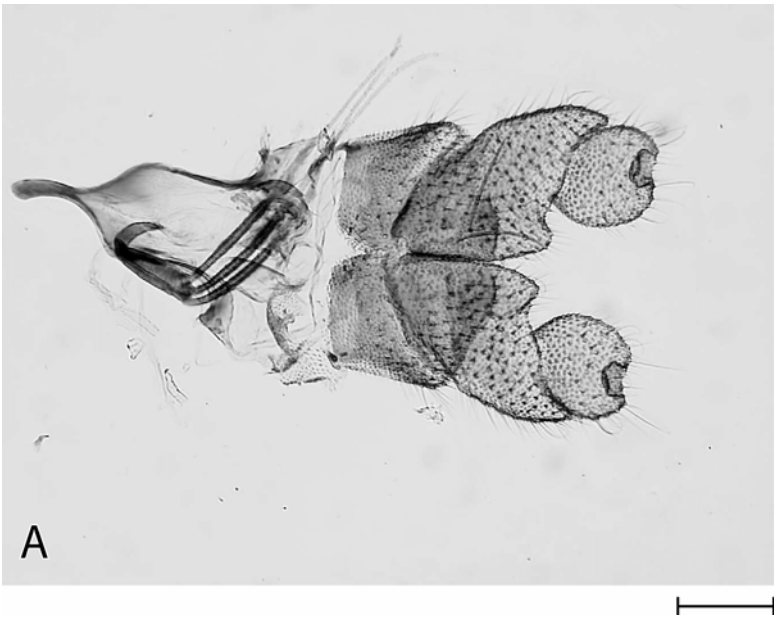


Figure 65. Partially dissected female terminalia of *Chrysopilus testaceipes* [USNMENT00025876], dorsal view. Scale bar = 0.1 mm.

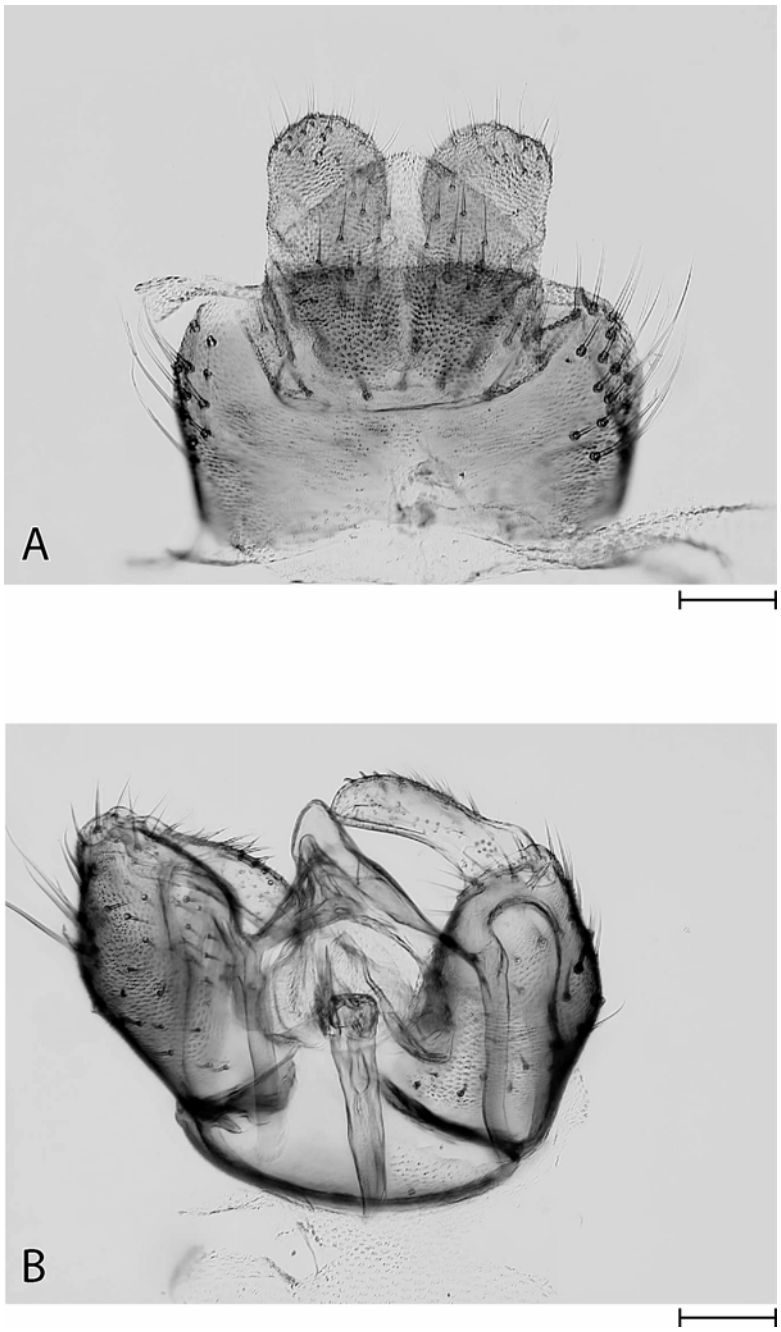


Figure 66. Male genitalia of *Desmomyia thereviformis* [USNMENT00025267]. (A) Epandrium, ventral view (B) Hypandrium, dorsal view. Scale bar = 0.1 mm.

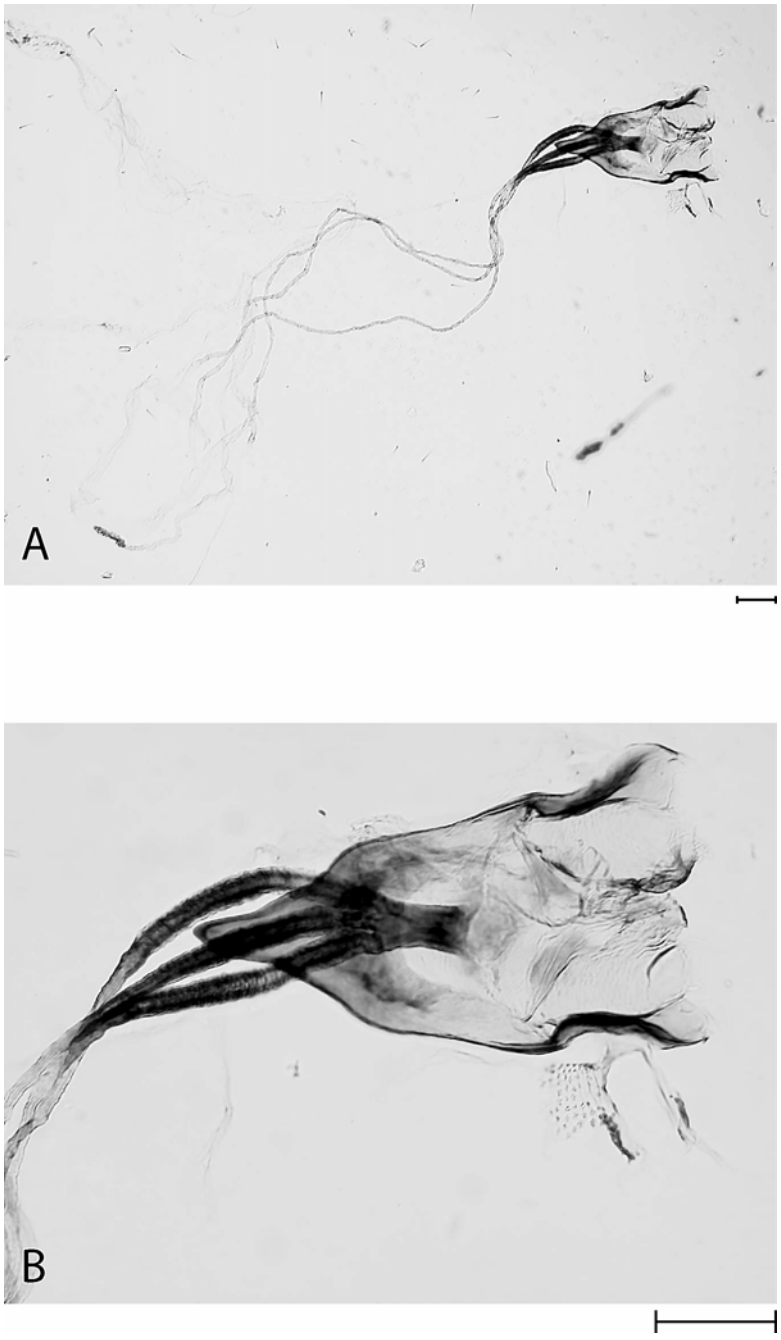


Figure 67. Sternite 9 (female genitalia) and associated structures of *Desmomyia thereviformis* [USNMENT00025628]. Scale bar = 0.1 mm.

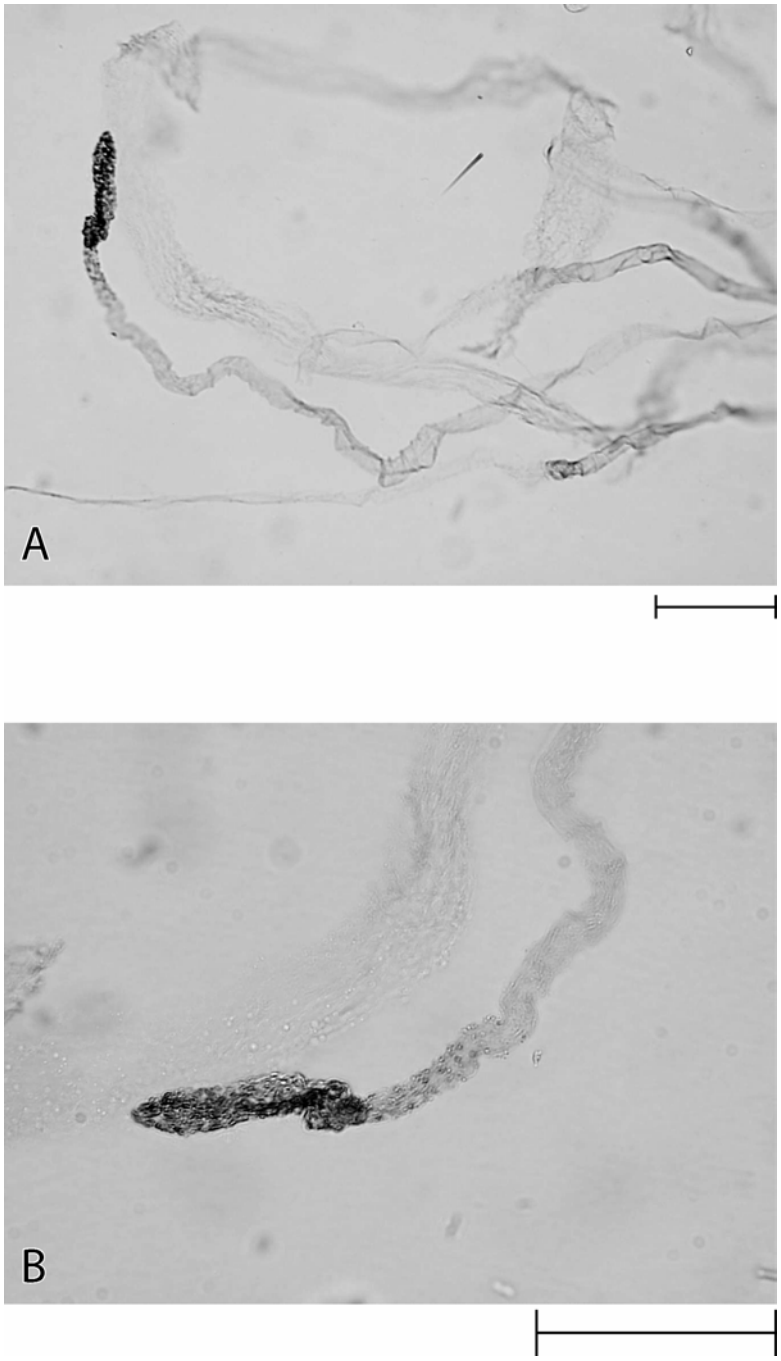


Figure 68. Spermathecae of *Desmomyia thereviformis* [USNMENT00025628]. Scale bar = 0.1 mm.

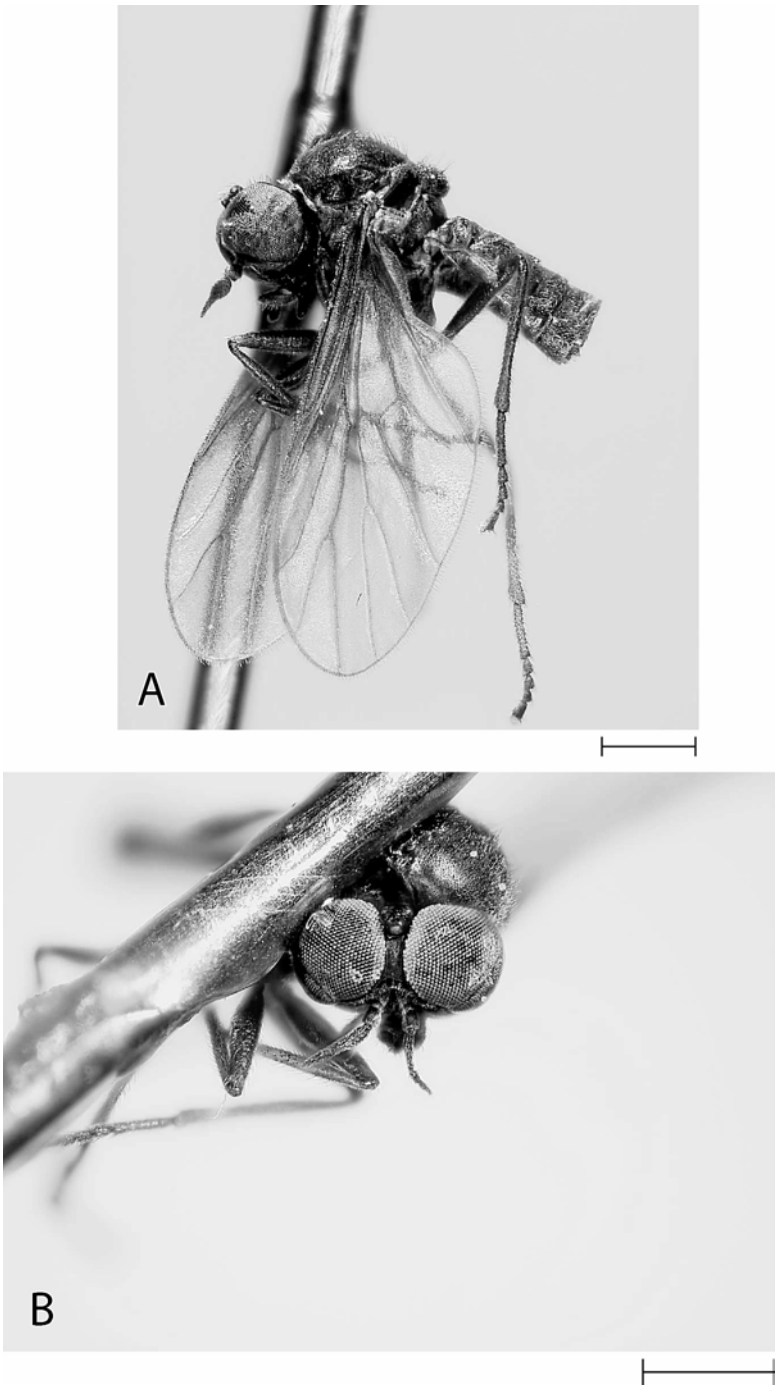


Figure 69. *Litoleptis alaskensis*, male. (A) Habitus, lateral view [USNMENT00024416, holotype] (B) head, anterior view [USNMENT00024417, paratype]. Scale bar = 0.5 mm.

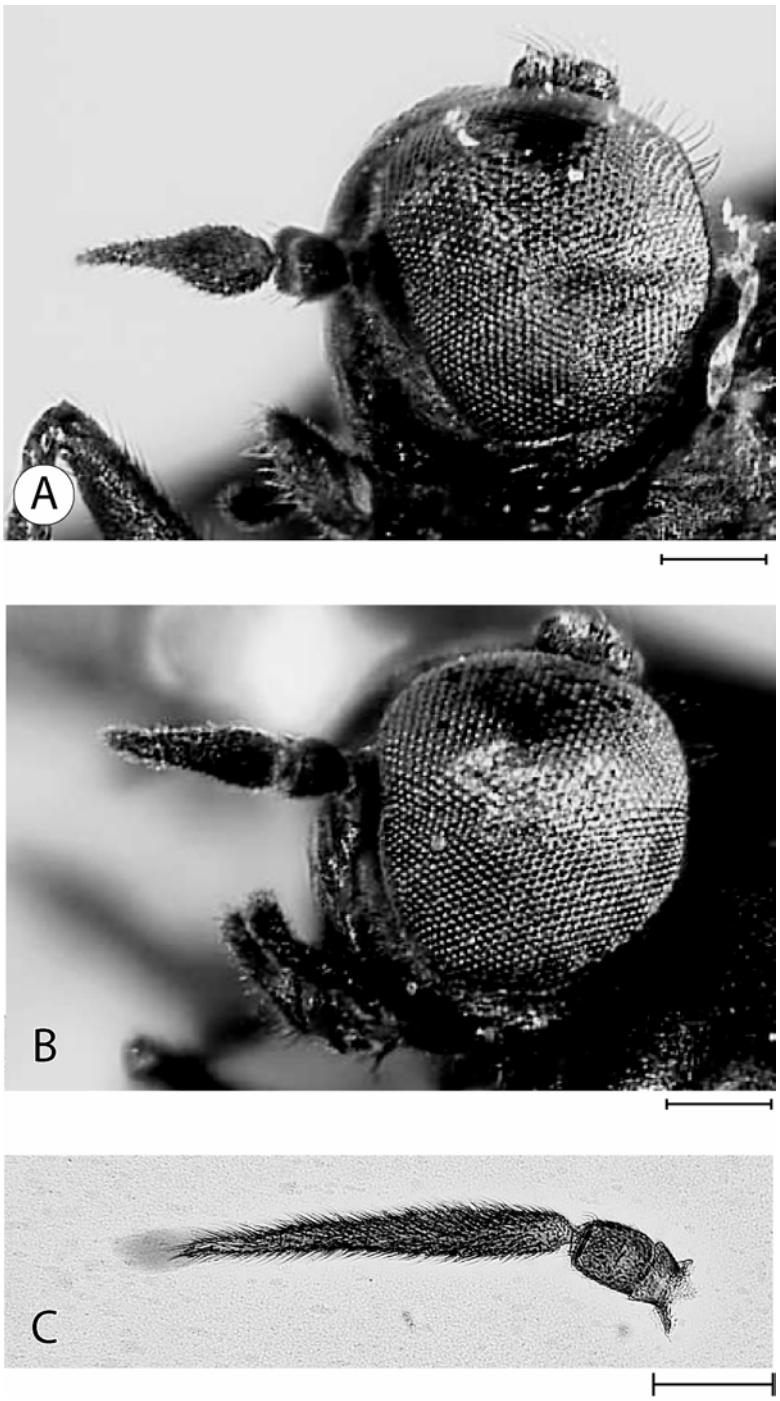


Figure 70. Antennal form in species of *Litoleptis*. (A) *L. alaskensis*, male [USNMENT00024416, holotype] (B) *L. alaskensis*, male [USNMENT00024417, paratype] (C) *L. chilensis* [no USNM barcode, slide mounted holotype]. Scale bar = 0.1 mm.

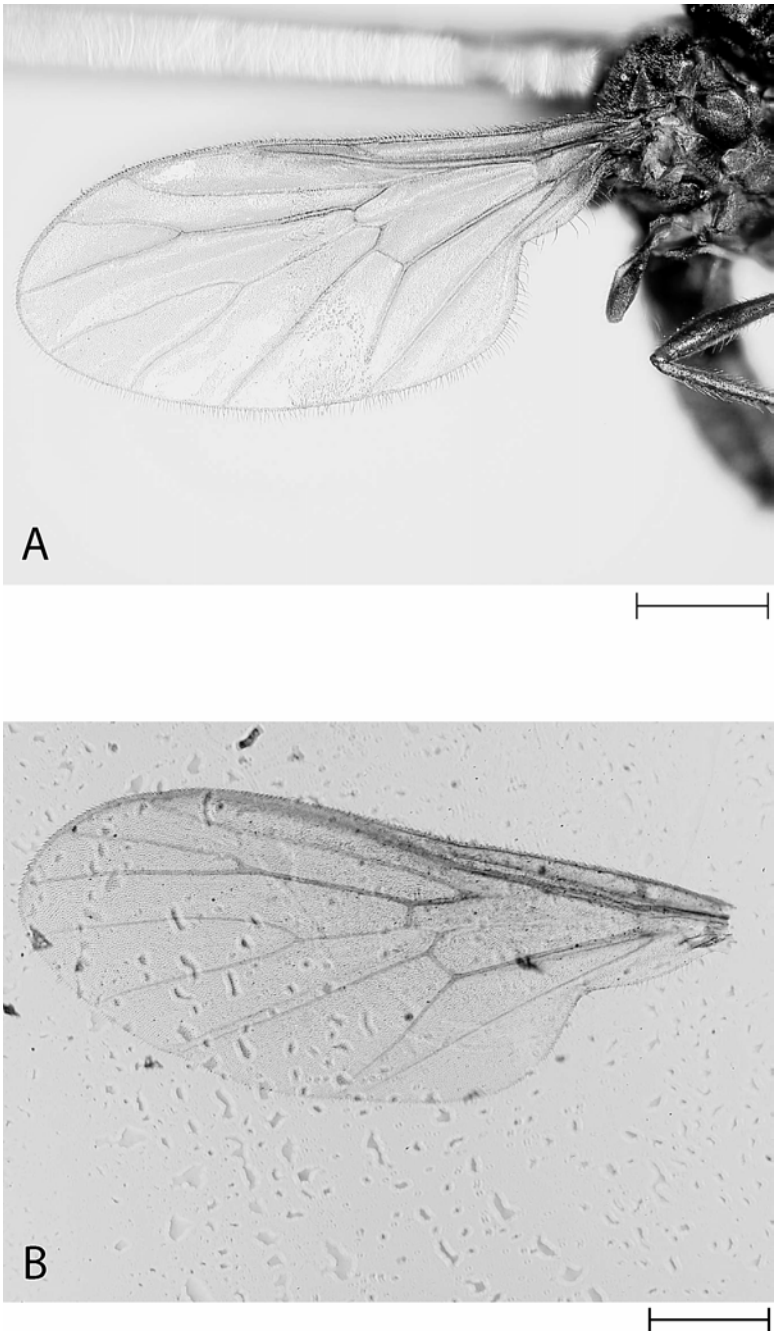


Figure 71. Wing in species of *Litoleptis*. (A) *L. alaskensis*, male [USNMENT00024417, paratype] (B) *L. chilensis*, male [no USNM barcode, slide mounted holotype]. Scale bar = 0.5 mm.

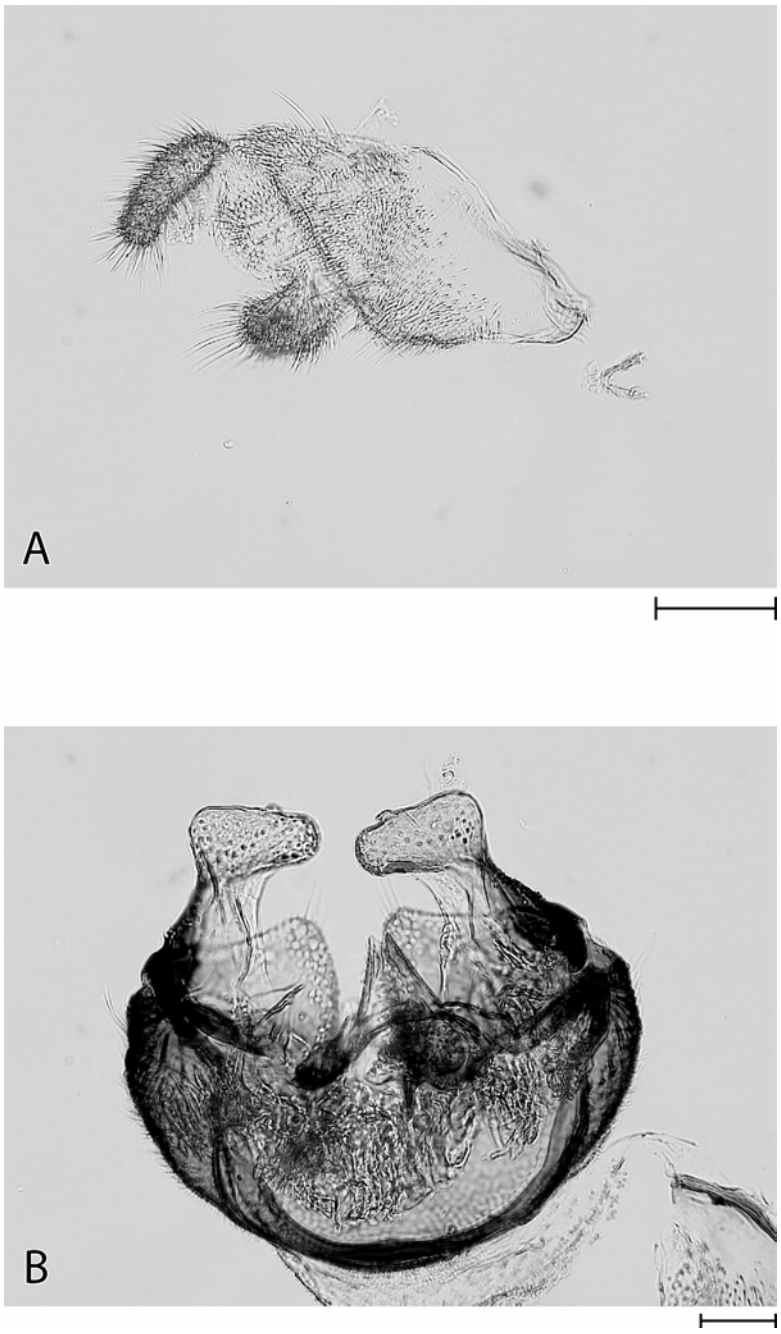


Figure 72. Male genitalia of *Litoleptis alaskensis*, holotype [USNMENT00024416]. (A) Epandrium, oblique dorsal view (B) Hypandrium, dorsal view. Scale bar = 0.1 mm.

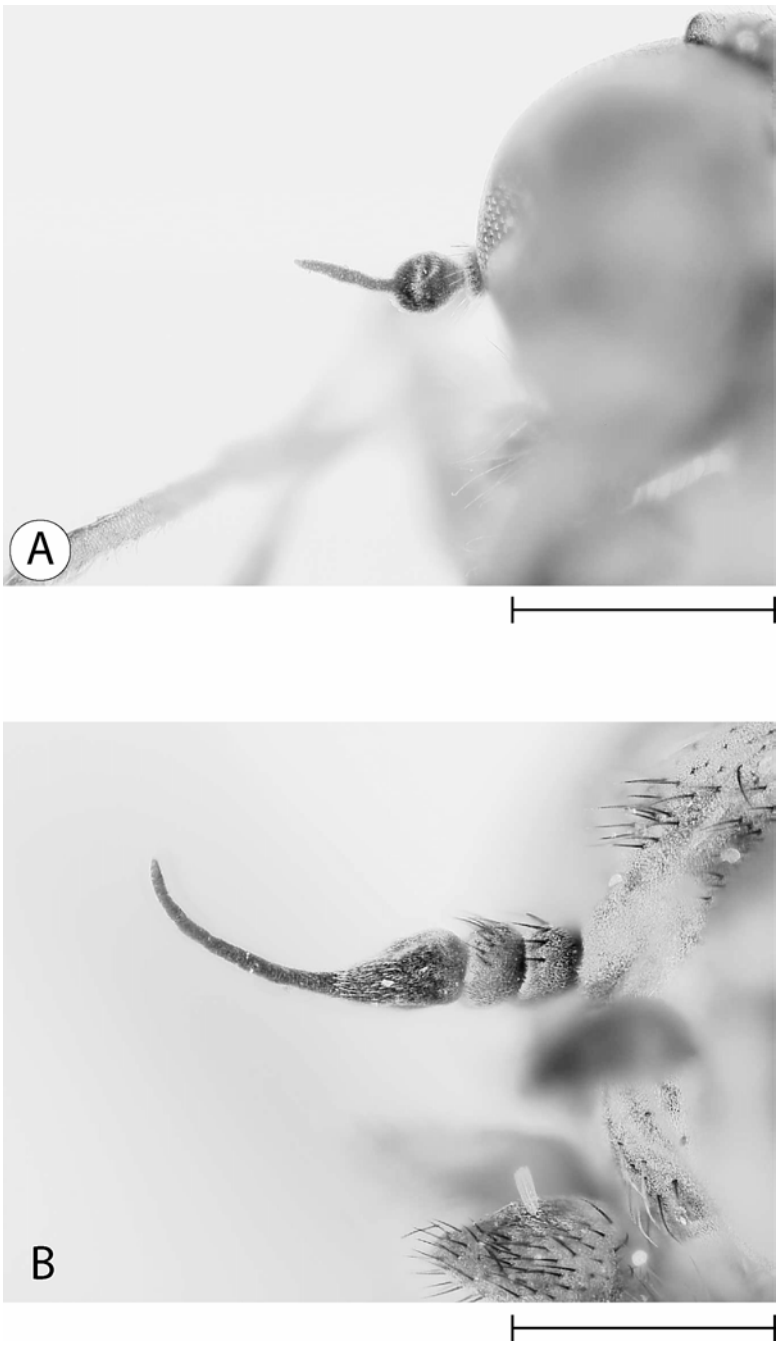


Figure 73. Antennal form in species of *Omphalophora*. (A) *O. fasciata*, male [USNMENT00025460] (B) *O. majuscula*, female [USNMENT00025471]. Scale bar = 0.5 mm.

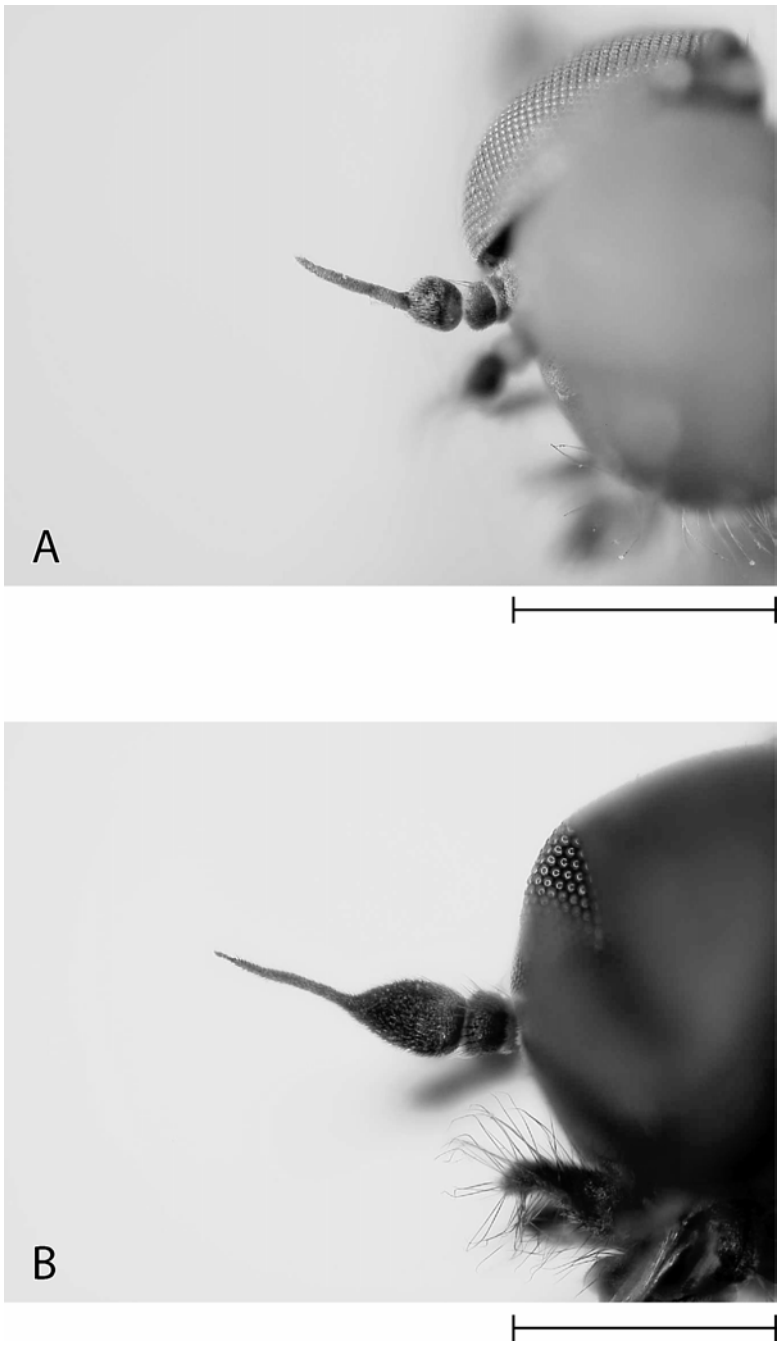


Figure 74. Antennal form in species of *Omphalophora* and *Ptiolina*. (A) *O. nigripilosa*, male [USNMENT00025204 HOLOTYPE] (B) *P. nitida*, male [USNMENT00022957]. Scale bar = 0.5 mm.

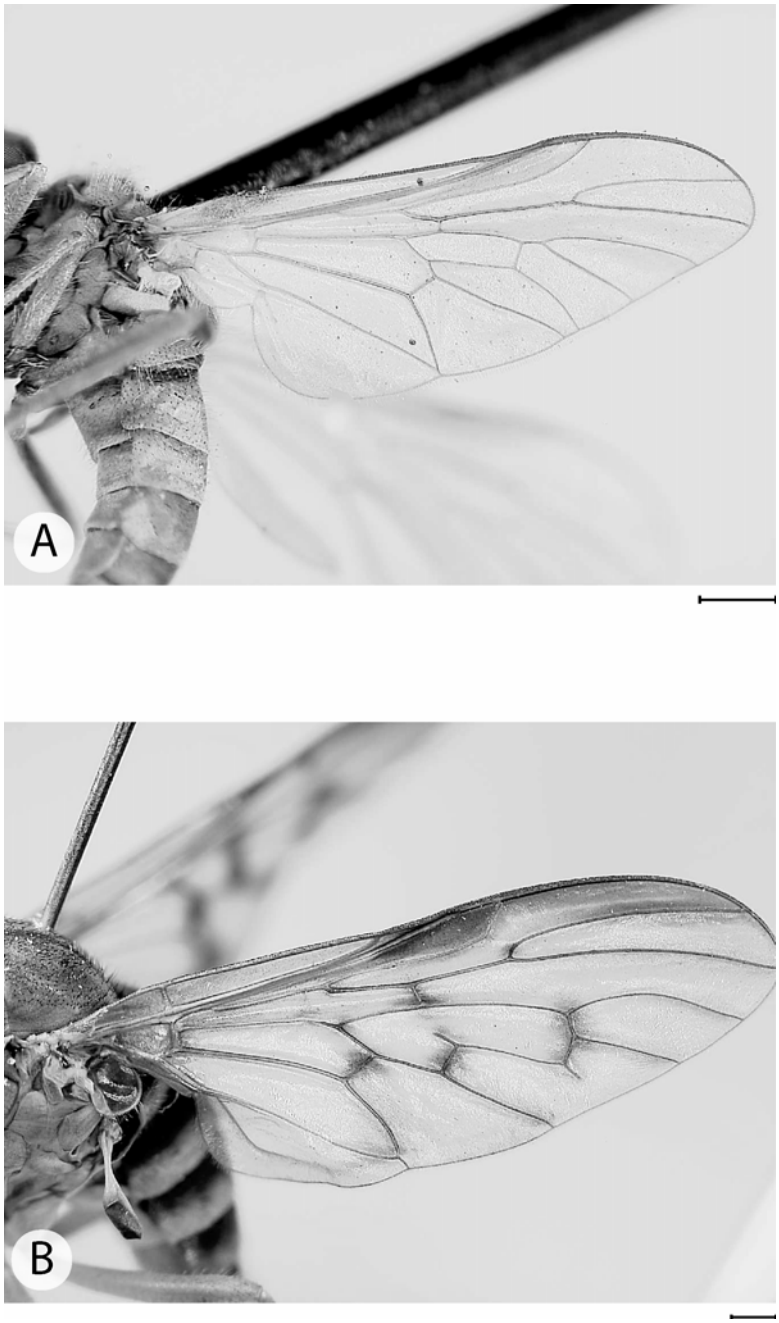


Figure 75. Wing in species of *Omphalophora*, ventral view. (A) *O. fasciata* [USNMENT00025460] (B) *O. majuscula* [USNMENT00025471]. Scale bar = 0.5 mm.

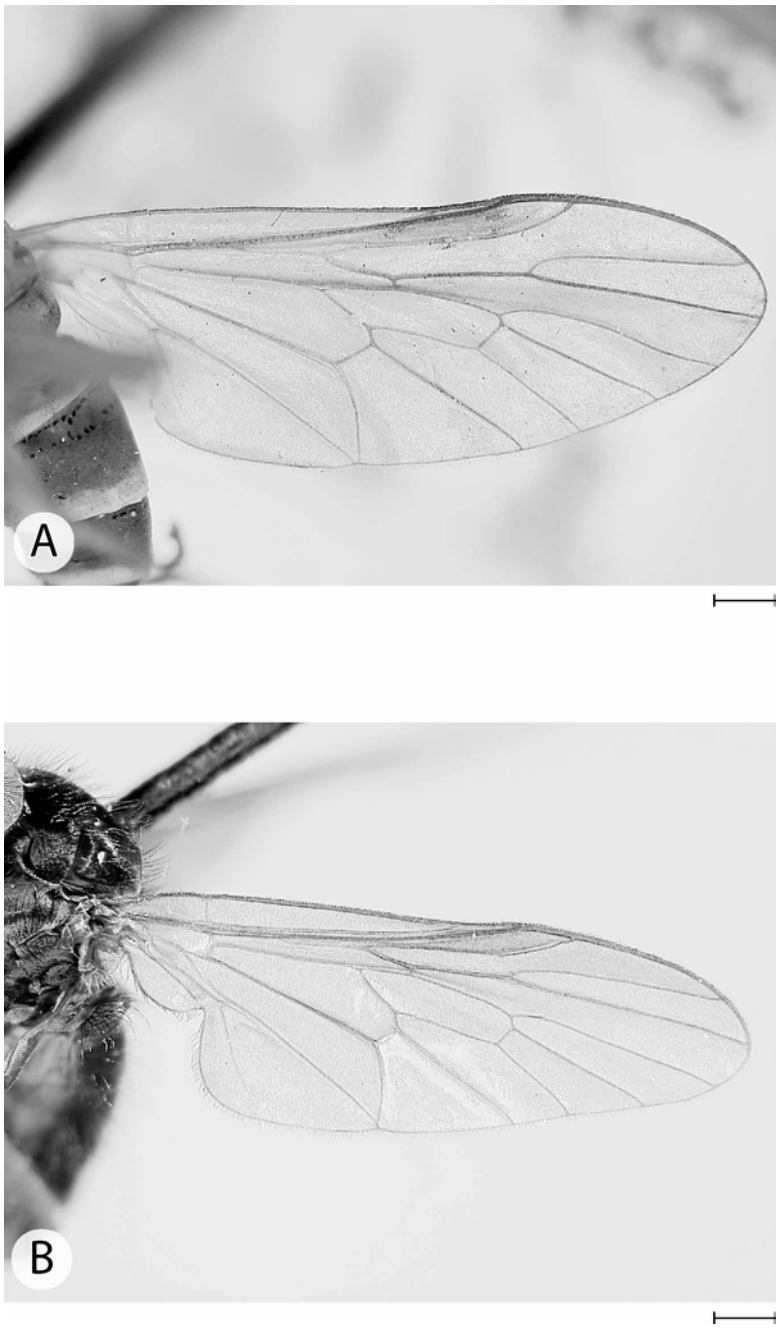


Figure 76. Wing in species of *Omphalophora* and *Ptiolina*, ventral view. (A) *O. nigripilosa* [USNMENT00025205, allotype] (B) *P. nitida* [USNMENT00022957]. Scale bar = 0.5 mm.

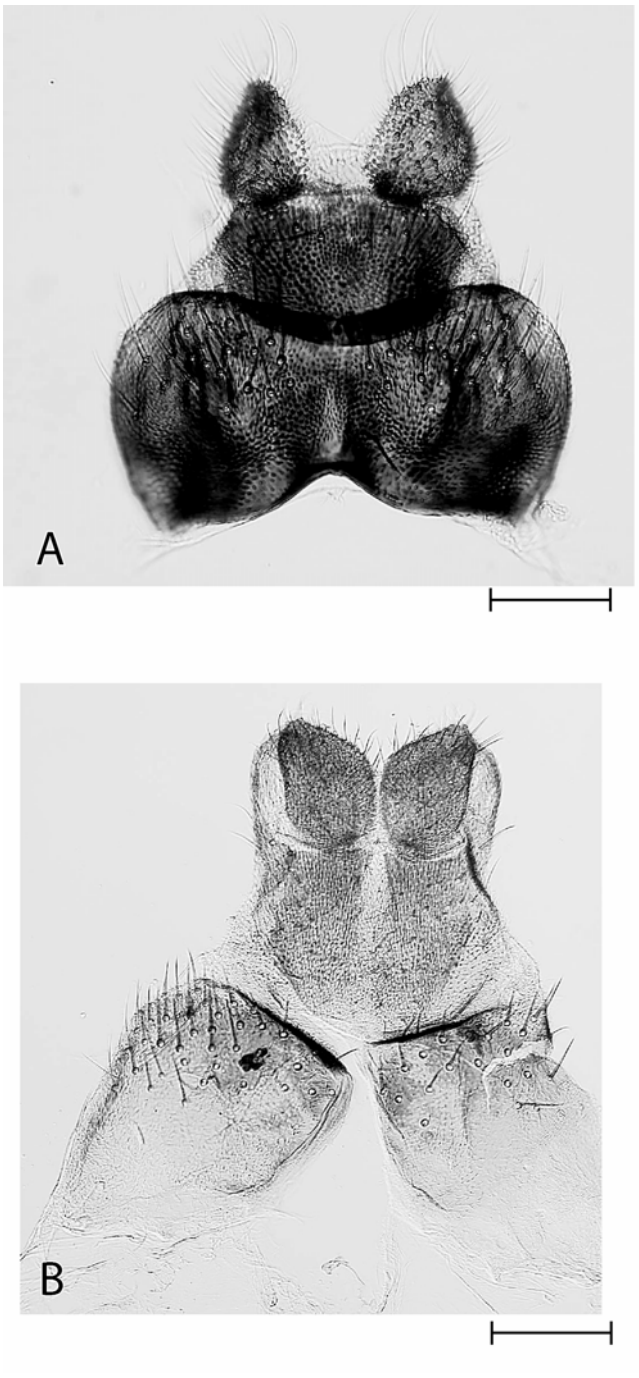


Figure 77. Epandrium (male genitalia) in species of *Omphalophora*, dorsal view. (A) *O. fasciata* [USNMENT00025461] (B) *O. lapponica* [USNMENT00025921]. Scale bar = 0.1 mm.

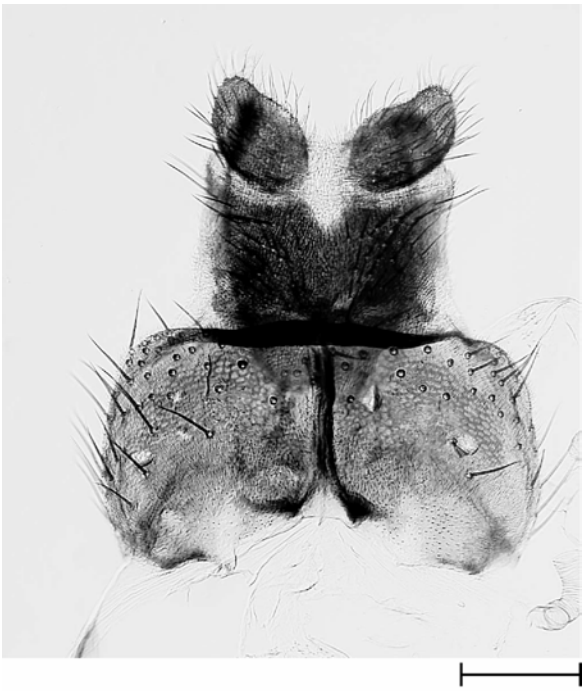


Figure 78. Epandrium (male genitalia) of *Omphalophora majuscula* [USNMENT00025472]. Scale bar = 0.1 mm.

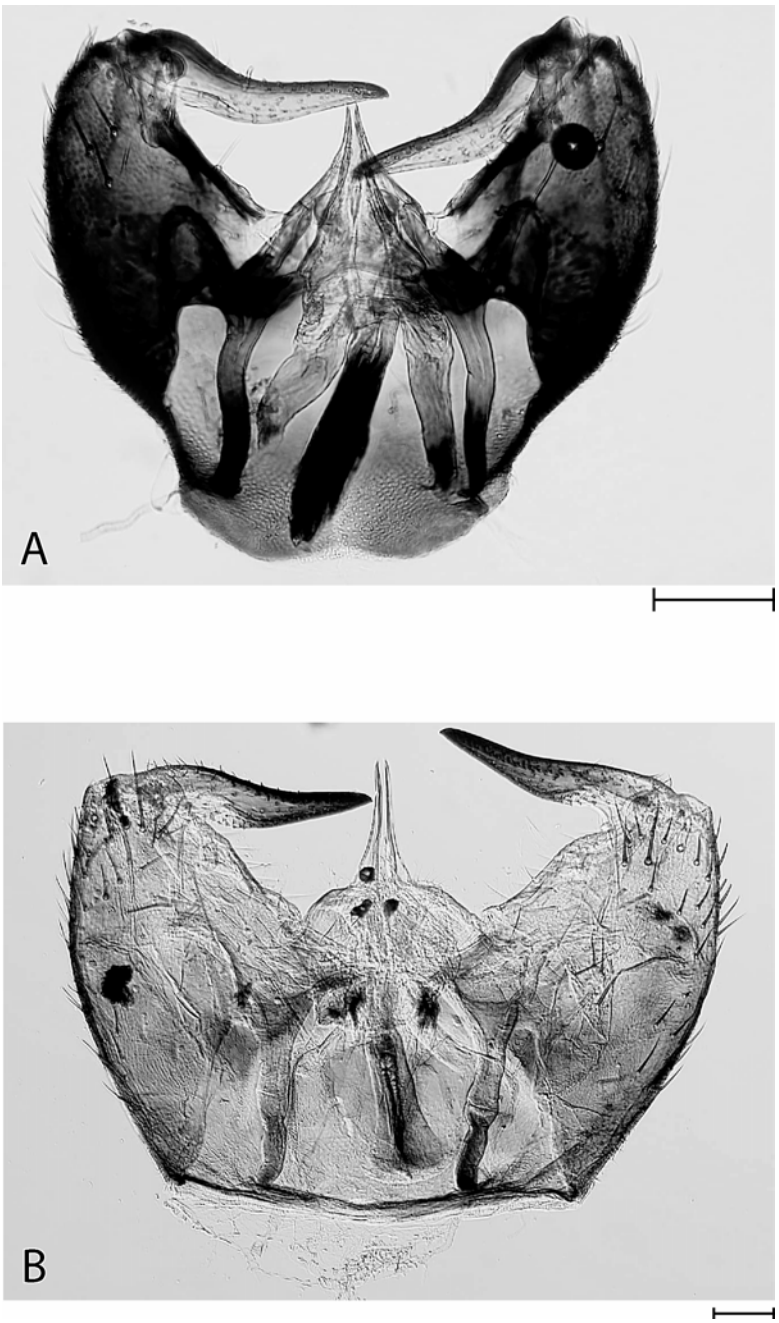


Figure 79. Hypandrium (male genitalia) in species of *Omphalophora*, dorsal view. (A) *O. fasciata* [USNMENT00025461] (B) *O. lapponica* [USNMENT00025921]. Scale bar = 0.1 mm.

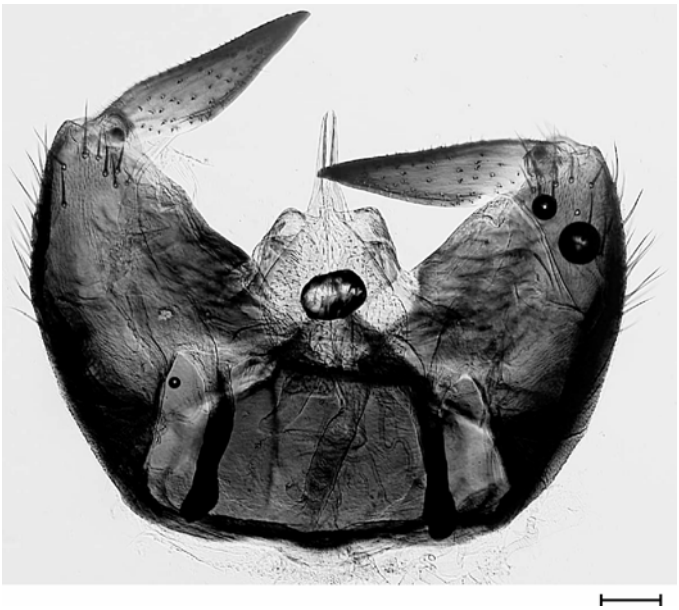


Figure 80. Hypandrium (male genitalia) of *Omphalophora majuscula* [USNMENT00025472]. Scale bar = 0.1 mm.

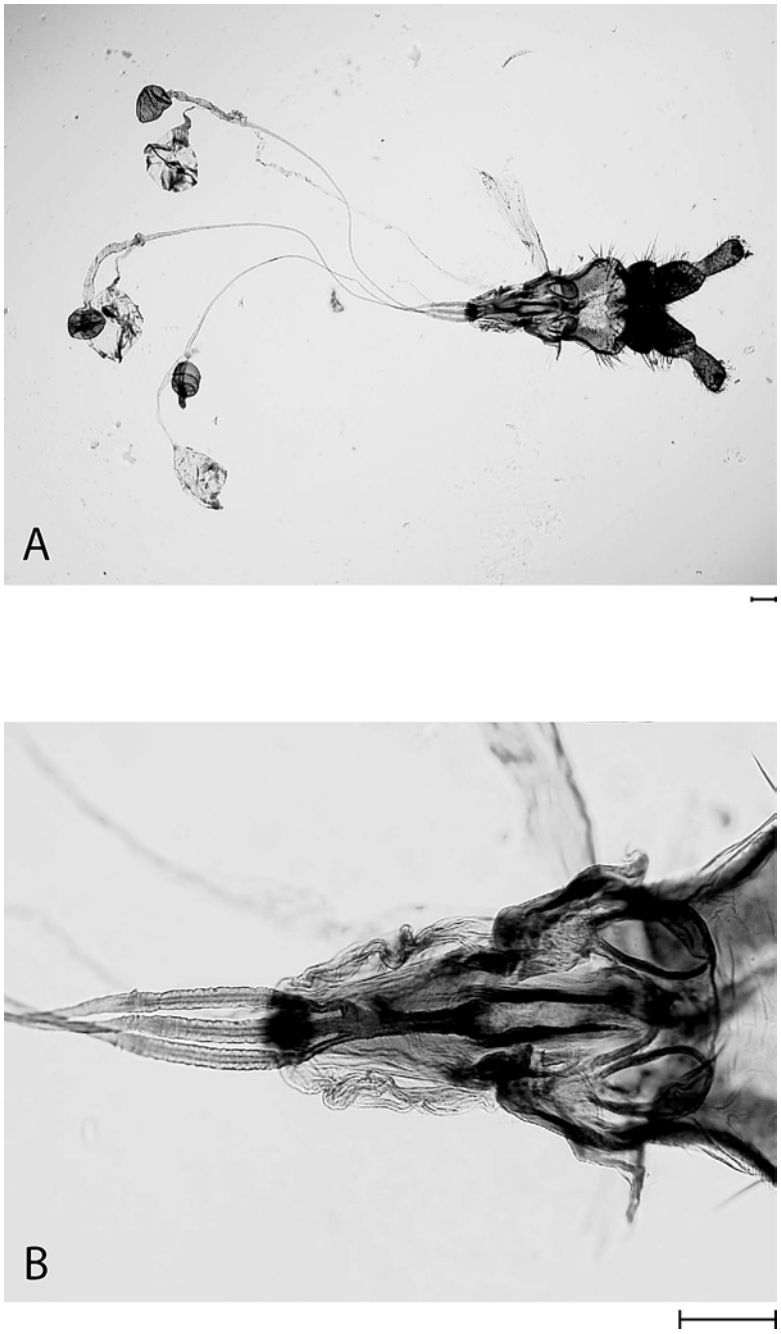


Figure 81. Dissected female terminalia of *Omphalophora majuscula*, dorsal view [USNMENT00025474]. Scale bar = 0.1 mm.

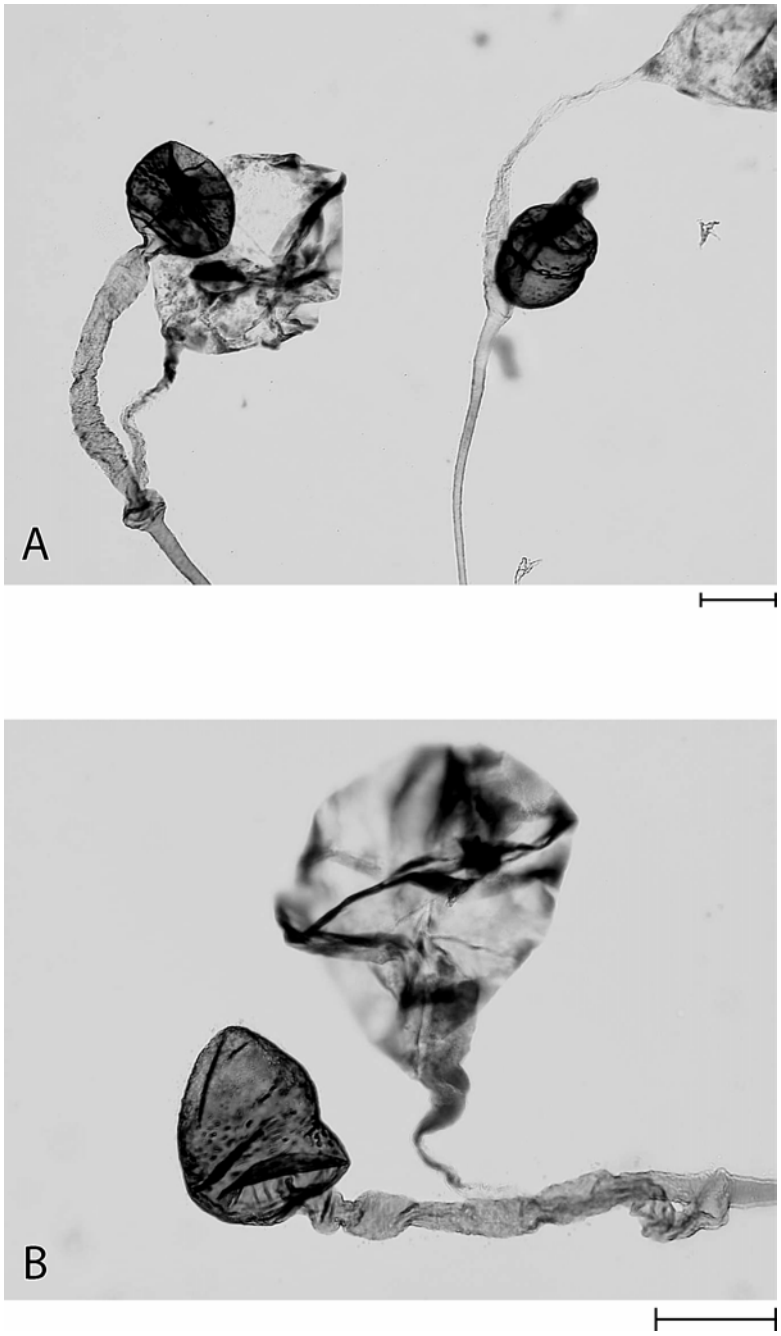


Figure 82. Spermatheca and spermathecal duct accessory glands of *Omphalophora majuscule* [USNMENT00025474]. Scale bar = 0.1 mm.

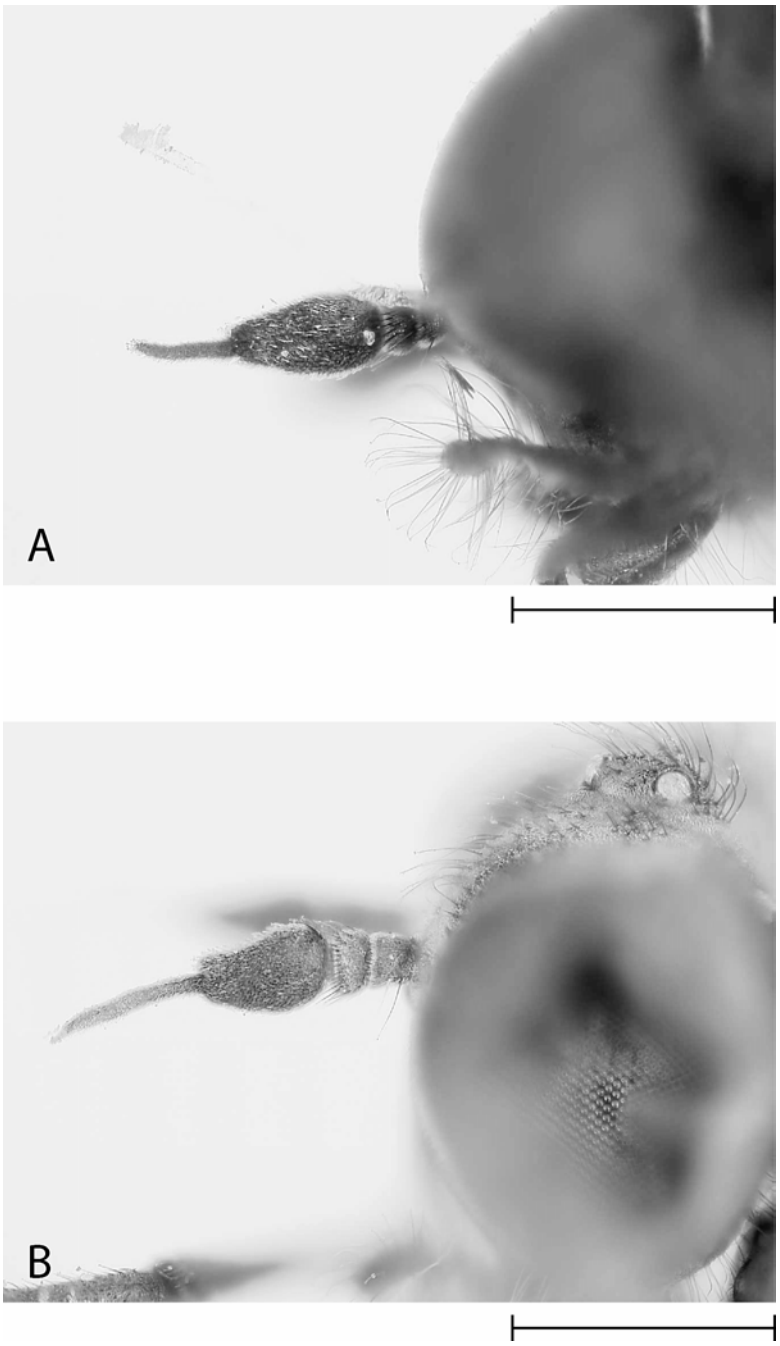


Figure 83. Antennal form in species of *Ptiolina*. (A) *P. edeta*, male [USNMENT00022657] (B) *P. edeta*, female [USNMENT00023016]. Scale bar = 0.5 mm.

Figure 84. Antennal form in species of *Ptiolina*. (A) *P. obscura*, male [USNMENT00023018] (B) *P. zonata*, female [USNMENT00022842]. Scale bar = 0.5 mm.

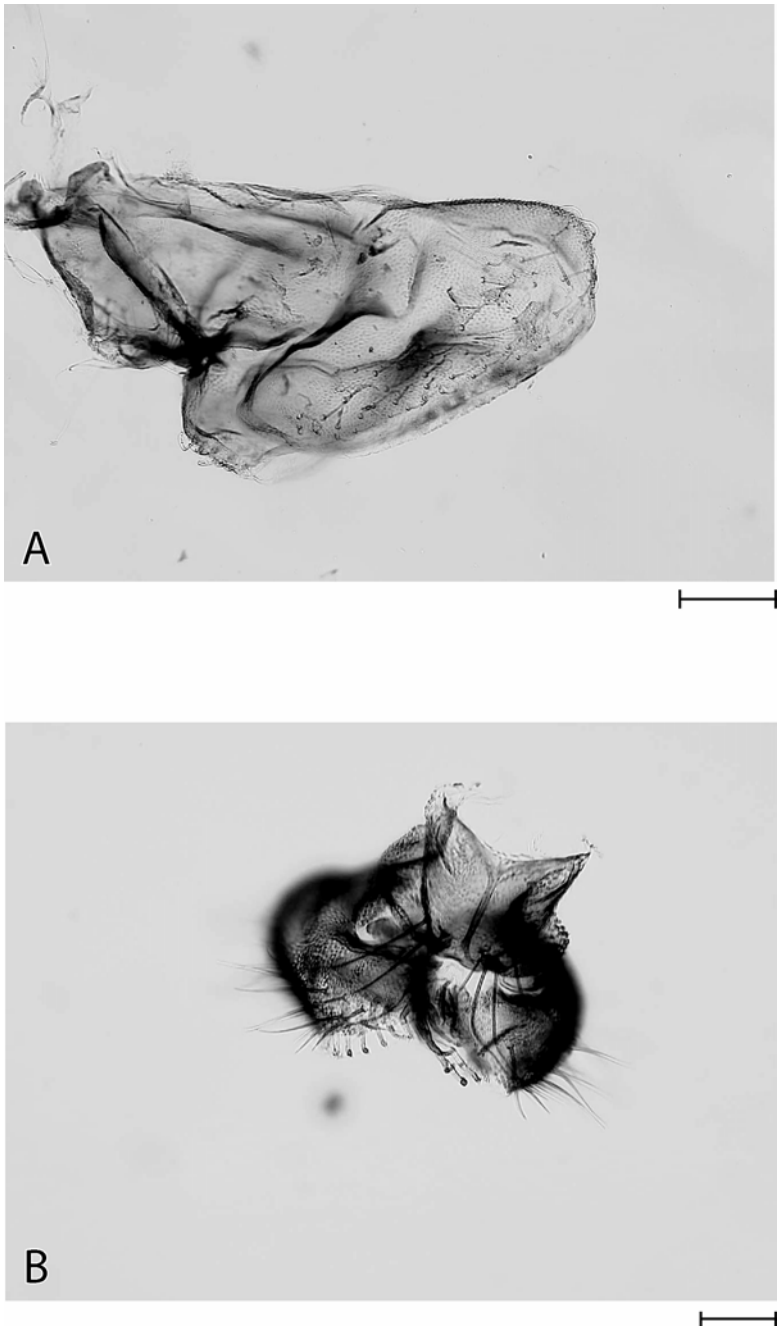


Figure 85. Labellum and theca in species of *Ptiolina*. (A) *Ptiolina* sp., male, posterior view [USNMENT00022845] (B) *P. zonata*, male, lateral view [USNMENT00023001]. Scale bar = 0.1 mm.

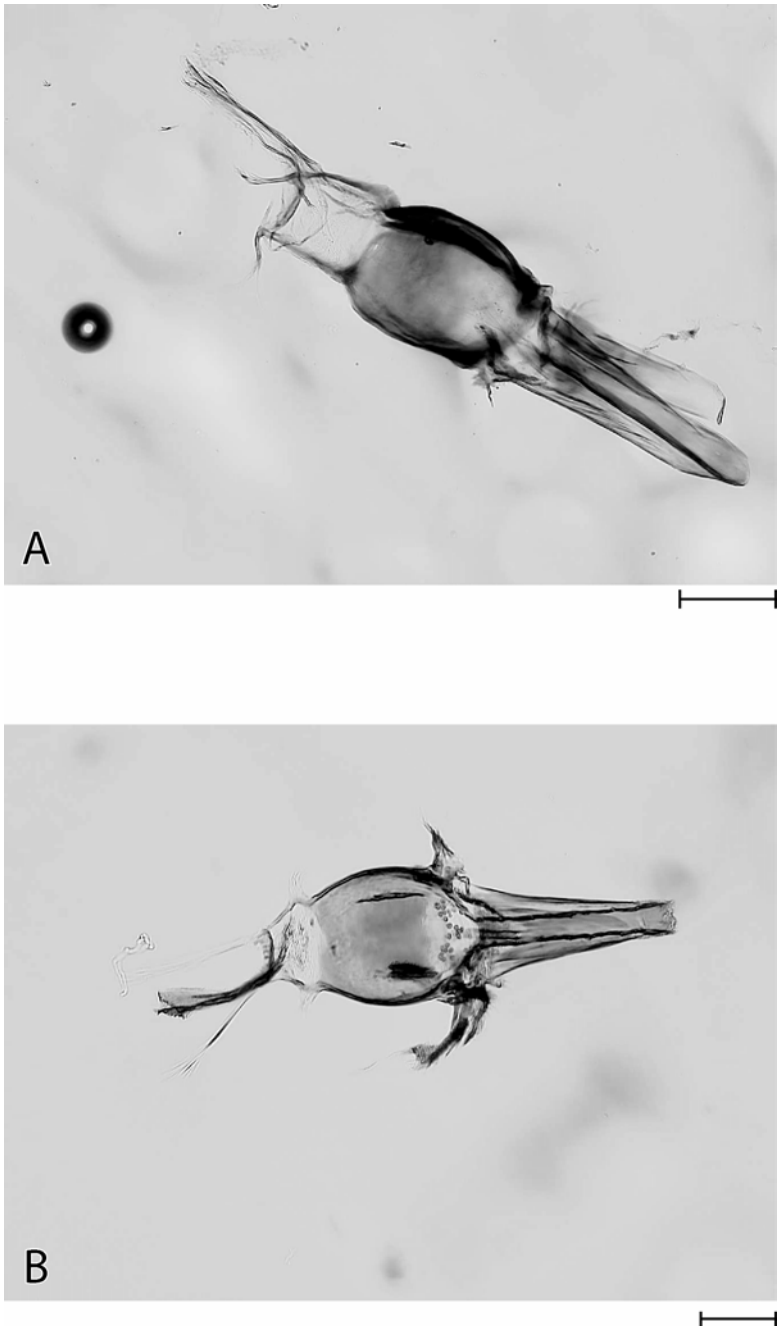


Figure 86. Hypopharynx, cibarial pump, and associated structures in species of *Ptiolina*, posterior view. (A) *Ptiolina* sp., male [USNMENT00022845] (B) *P. zonata*, male [USNMENT00023001]. Scale bar = 0.1 mm.

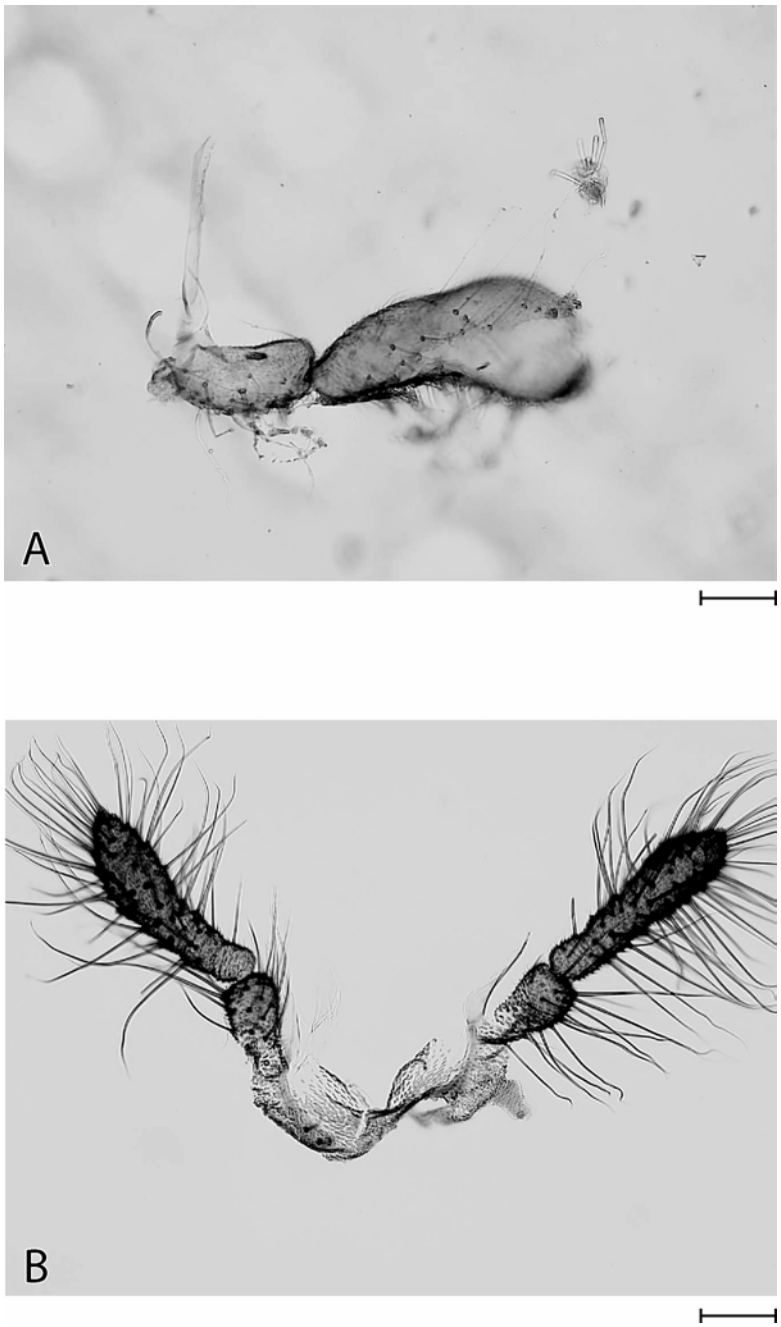


Figure 87. Palp and associated structures in *Ptiolina*. (A) *Ptiolina* sp., male [USNMENT00022845] (B) *P. zonata*, male [USNMENT00023001]. Scale bar = 0.1 mm.

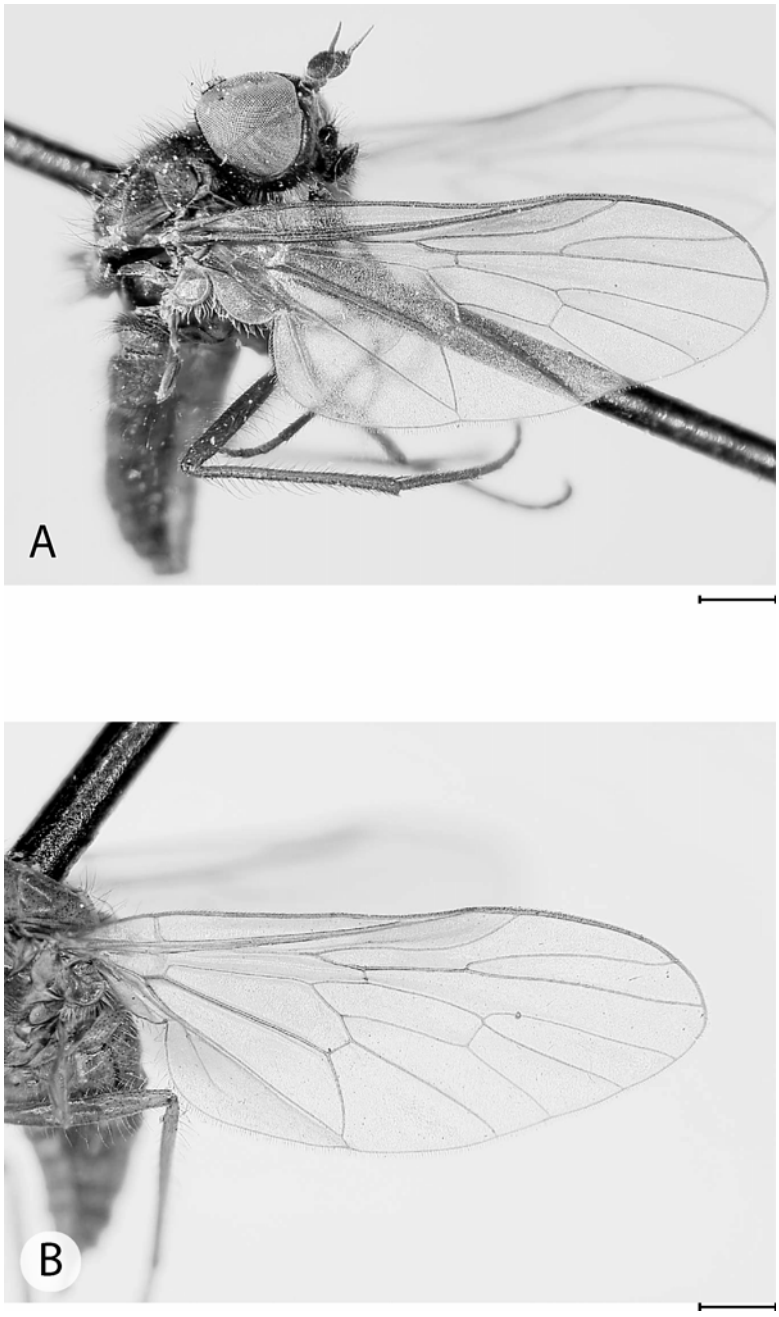


Figure 88. Wing in species of *Ptiolina*, ventral view. (A) *P. obscura* [USNMENT00023020] (B) *P. zonata* [USNMENT00022842]. Scale bar = 0.5 mm.

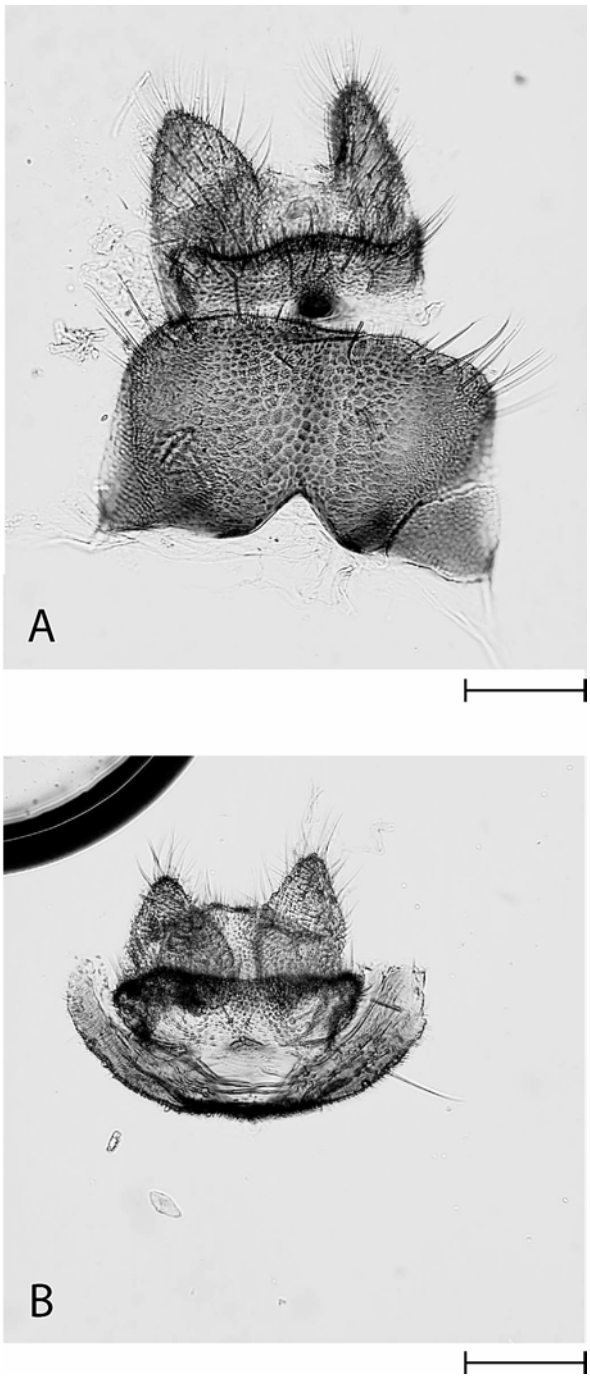


Figure 89. Epandrium (male genitalia) in species of *Ptiolina*, dorsal view. (A) *P. edeta* [USNMENT00023011] (B) *P. nigra* [USNMENT00025932]. Scale bar = 0.1 mm.

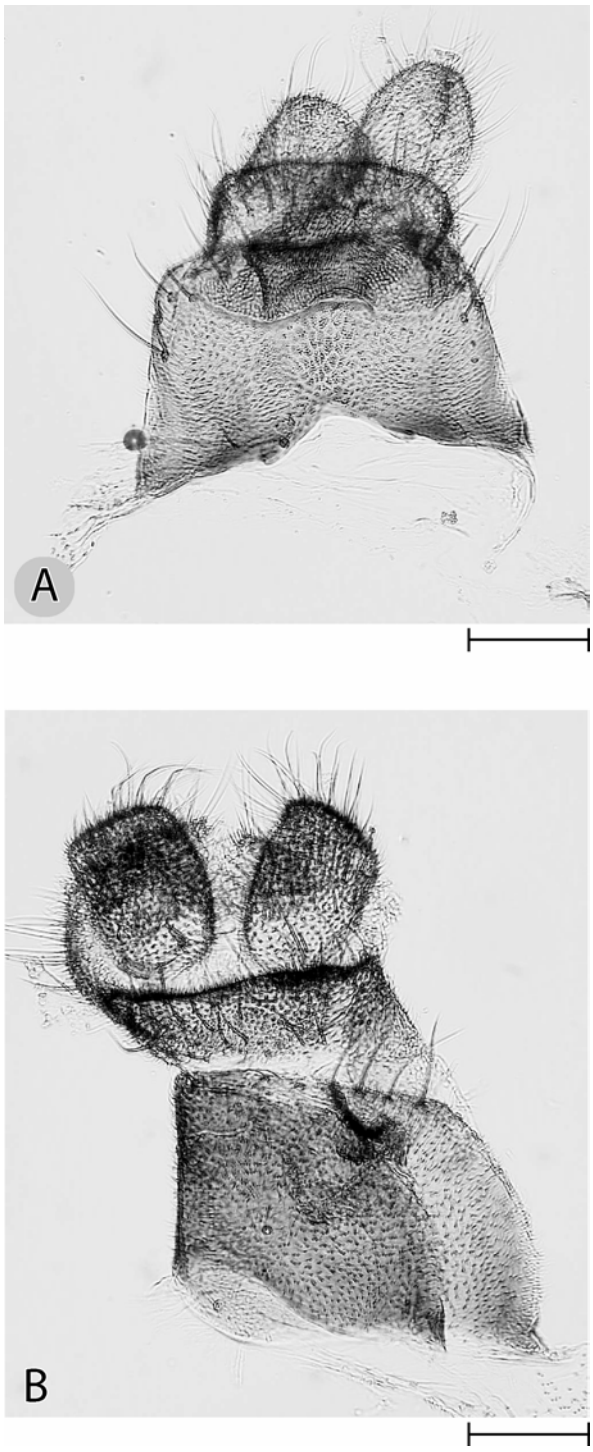


Figure 90. Epandrium (male genitalia) in species of *Ptiolina*, dorsal view. (A) *P. nitida* [USNMENT00025933] (B) *P. obscura* [USNMENT00025937]. Scale bar = 0.1 mm.

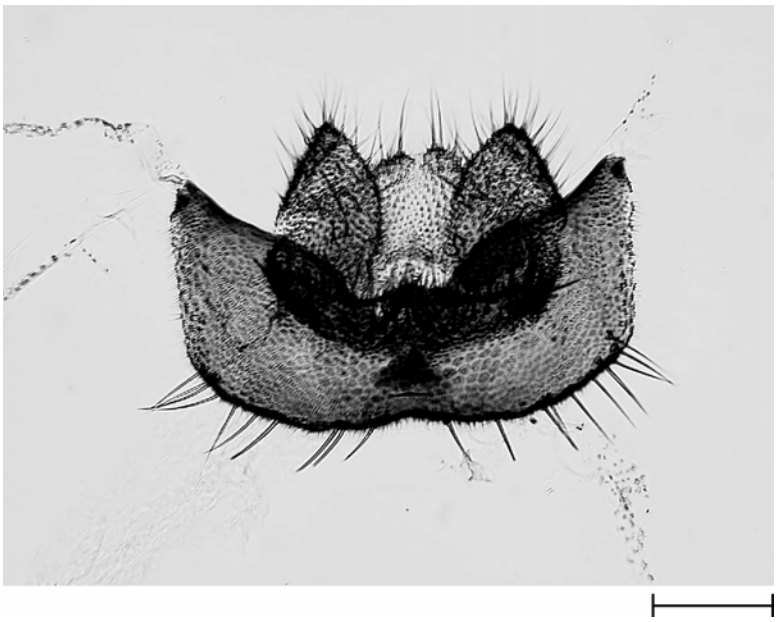


Figure 91. Epandrium (male genitalia) of *Ptiolina zonata* [USNMENT00022846]. Dorsal view. Note: subepandrial sclerite flipped upside-down, facing wrong direction. Scale bar = 0.1 mm.

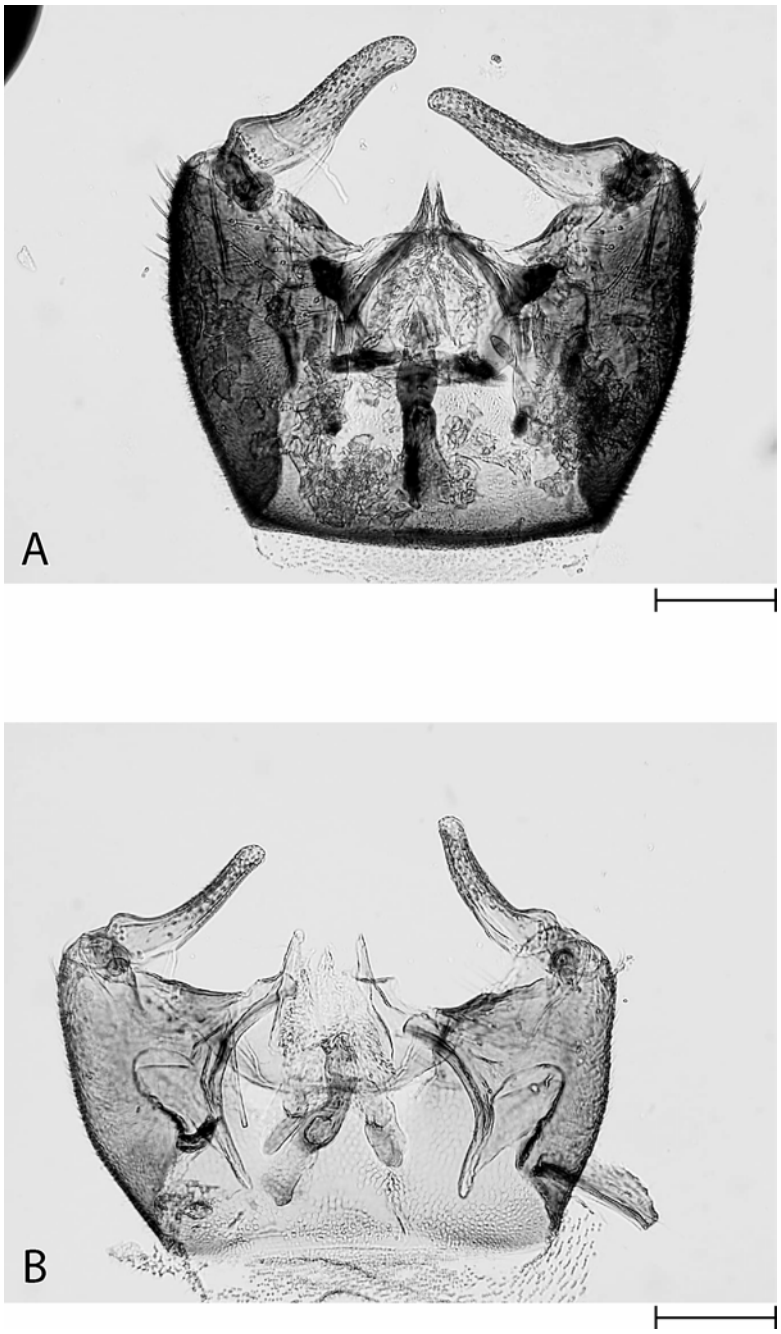


Figure 92. Hypandrium (male genitalia) in species of *Ptiolina*, dorsal view. (A) *P. edeta* [USNMENT00023011] (B) *P. nigra* [USNMENT00025932]. Scale bar = 0.1 mm.

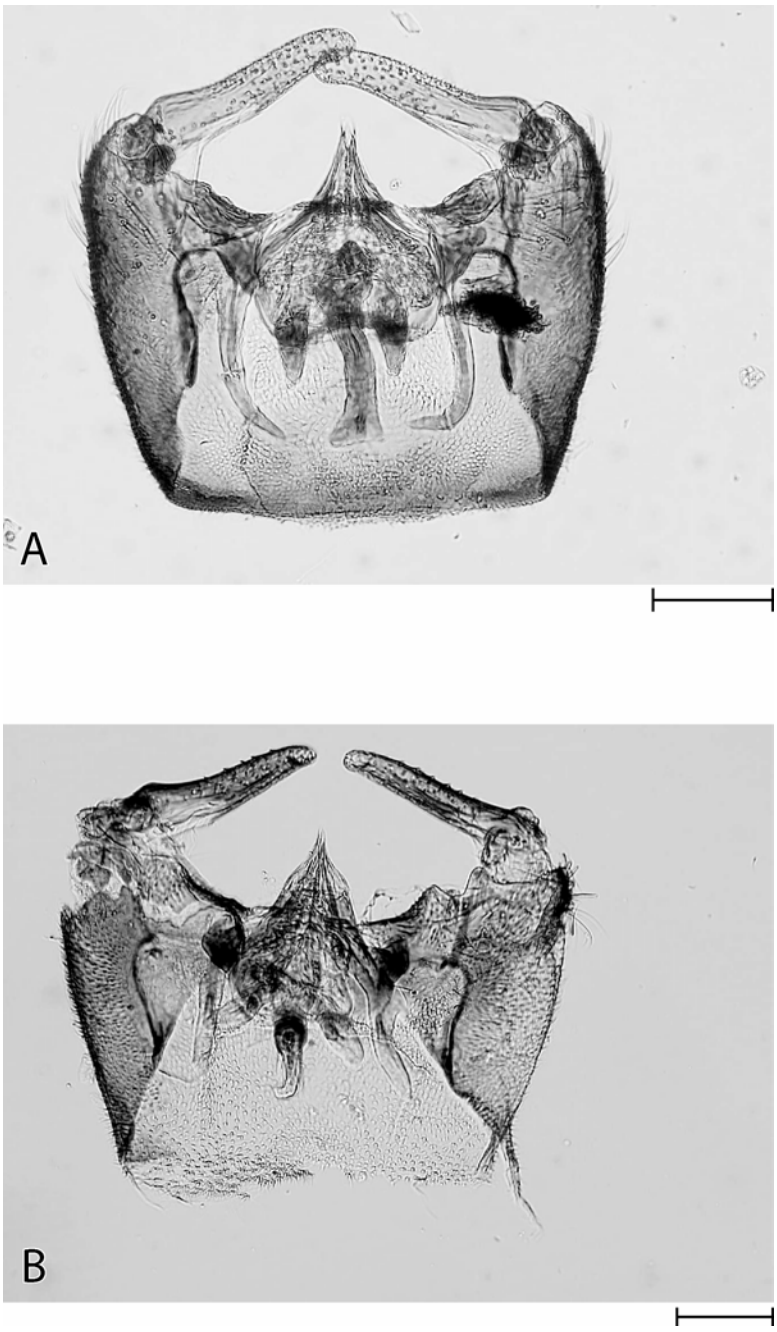


Figure 93. Hypandrium (male genitalia) in species of *Ptiolina*, dorsal view. (A) *P. nitida* [USNMENT00025933] (B) *P. obscura* [USNMENT00025937]. Scale bar = 0.1 mm.

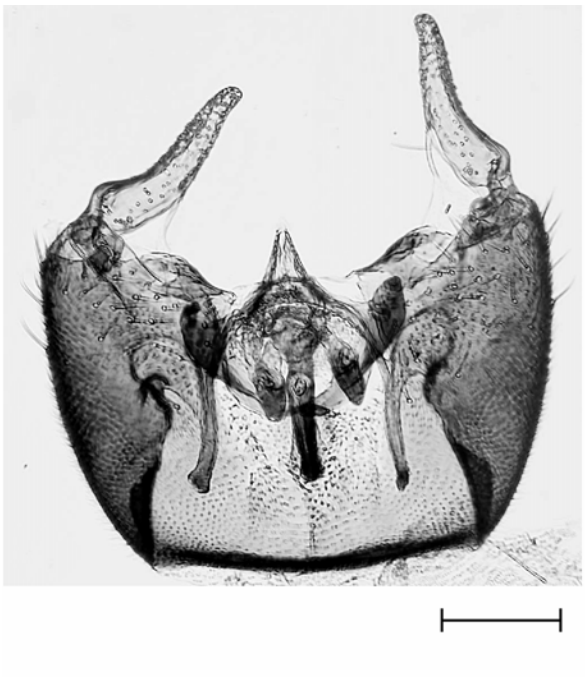


Figure 94. Hypandrium (male genitalia) of *Ptiolina zonata* [USNMENT00022846]. Scale bar = 0.1 mm.

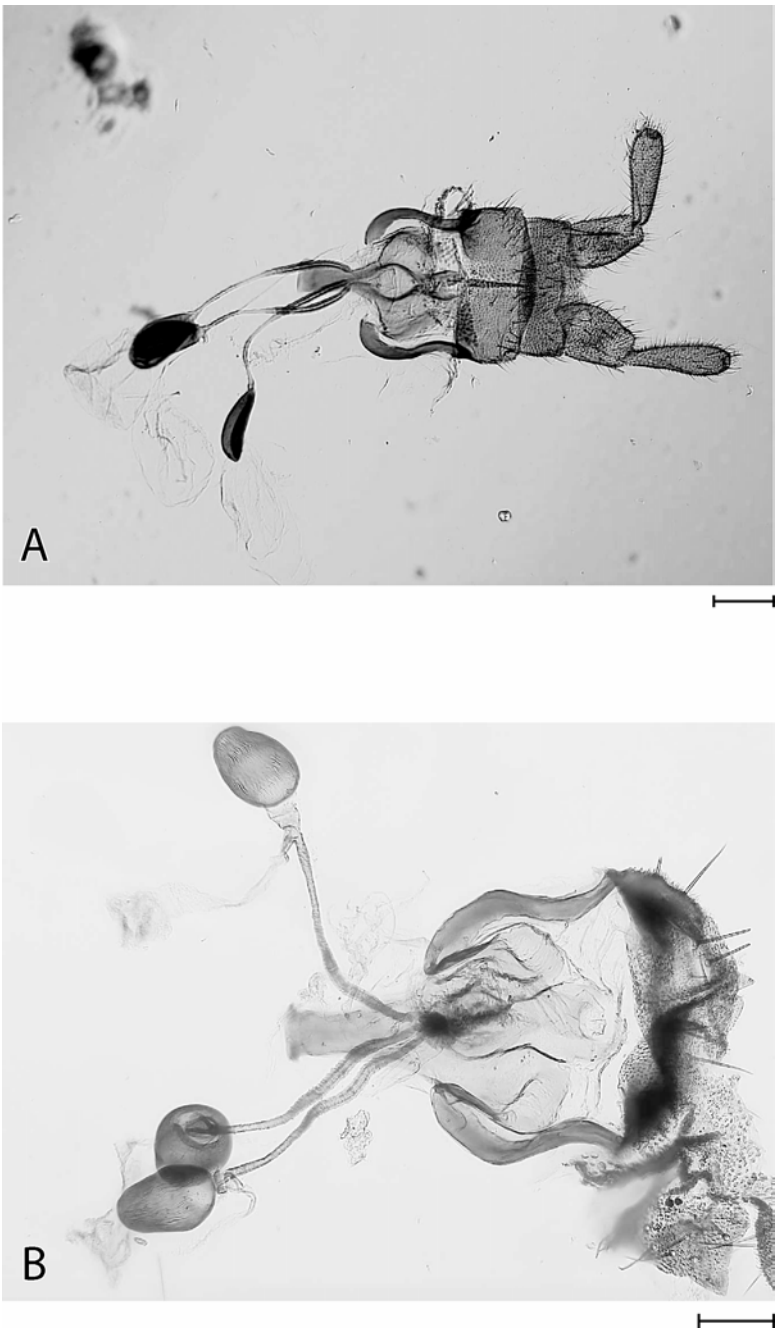


Figure 95. Dissected female terminalia in species of *Ptiolina*, dorsal view. (A) *P. zonata* [USNMENT00022841] (B) *P. mallochi* [USNMENT00022953]. Scale bar = 0.1 mm.

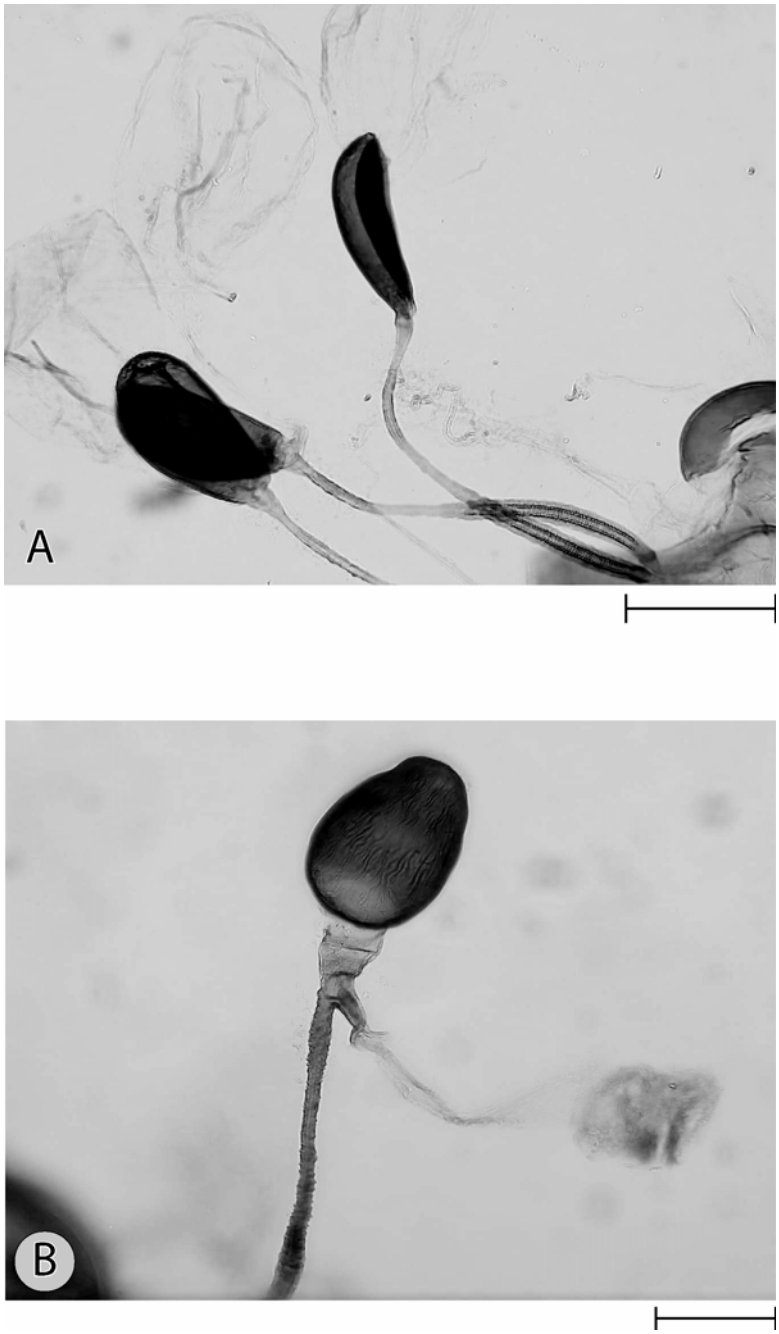


Figure 96. Spermatheca and spermathecal duct accessory glands in species of *Ptiolina*. (A) *P. zonata* [USNMENT00022841] (B) *P. mallochi* [USNMENT00022953]. Scale bar = 0.1 mm.

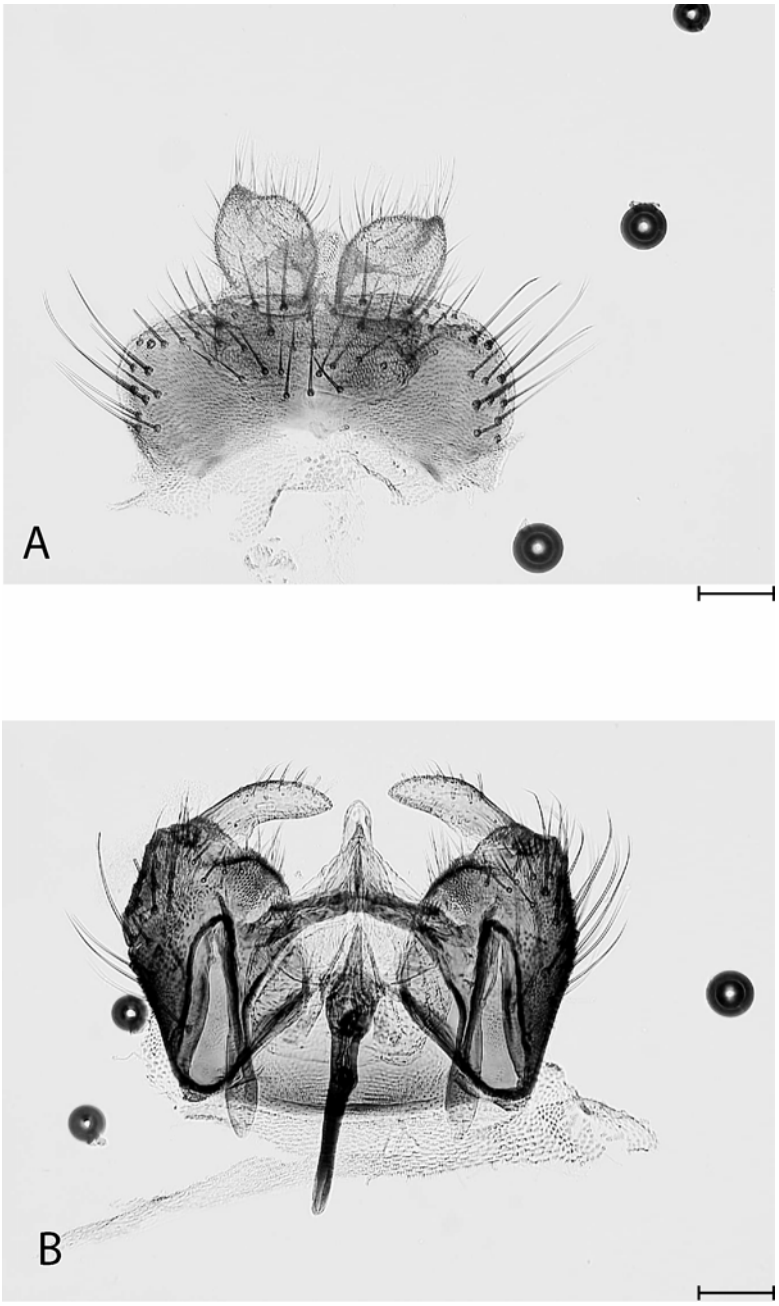


Figure 97. Male genitalia of *Rhagina incurvatus* [USNMENT00022728]. (A) Epandrium (B) Hypandrium. Scale bar = 1.0 mm.

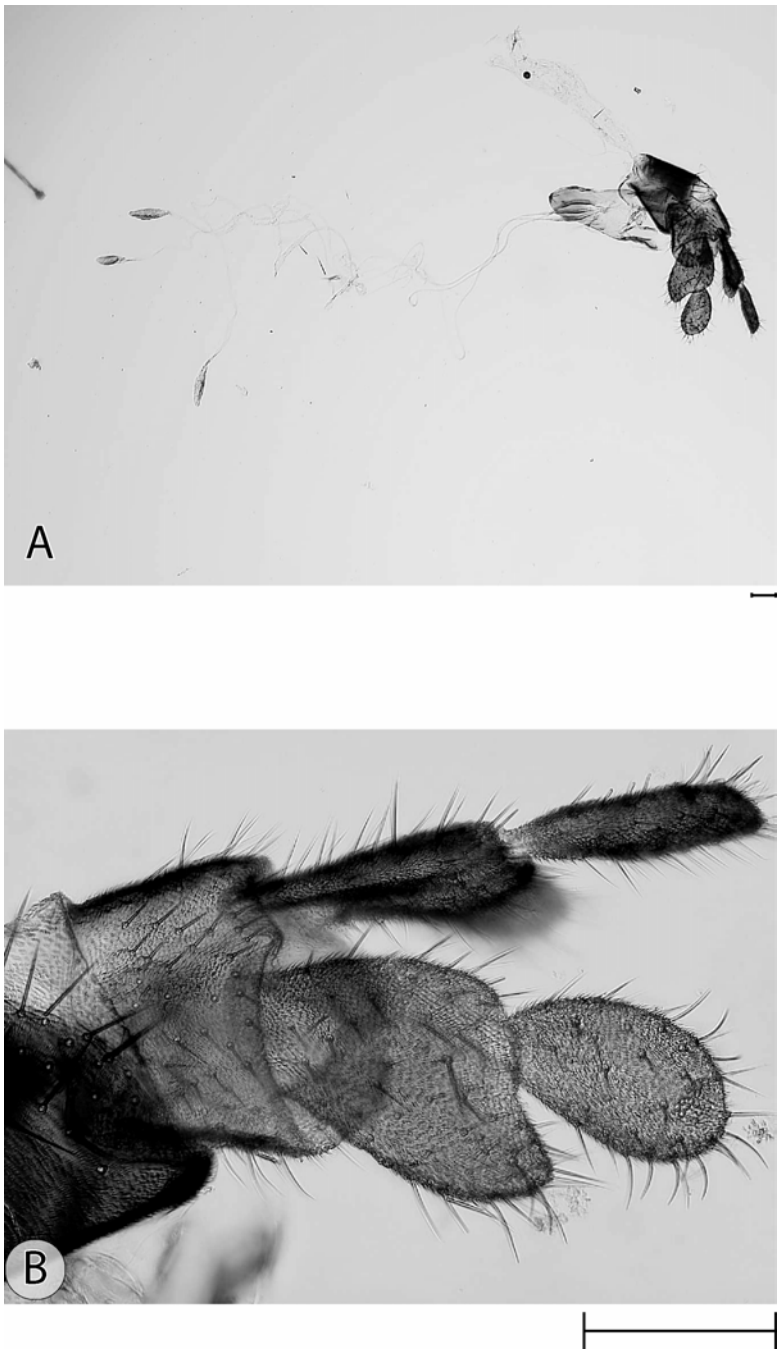


Figure 98. Female terminalia of *Rhagina incurvatus* [USNM ENT 00025853]. (A) Dissected, showing spermathecae (B) Detail of cerci. Scale bar = 0.1 mm.

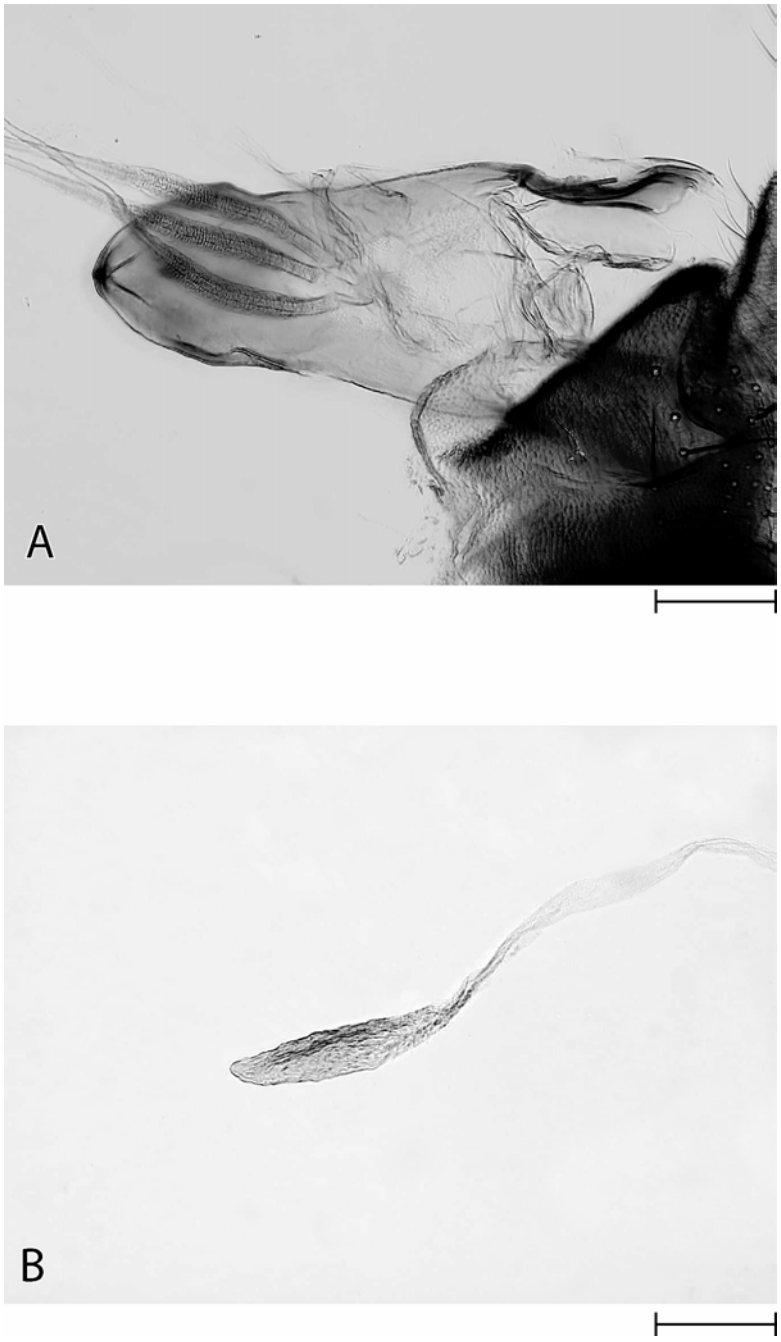


Figure 99. Internal structures of the female genitalia of *Rhagina incurvatus* [USNM ENT00025853]. (A) Dorsal view of sternite 9 (B) Spermatheca. Scale bar = 0.1 mm.

Figure 100. Habitus of *Rhagio mystaceus*, a common species in the Maryland/ DC area.

Figure 101. Antennal form in species of *Rhagio*, lateral view. (A) *R. punctipennis*, male [USNMENT00025946] (B) *R. scolopaceus*, male [USNMENT00023193]. Scale bar = 0.5 mm.

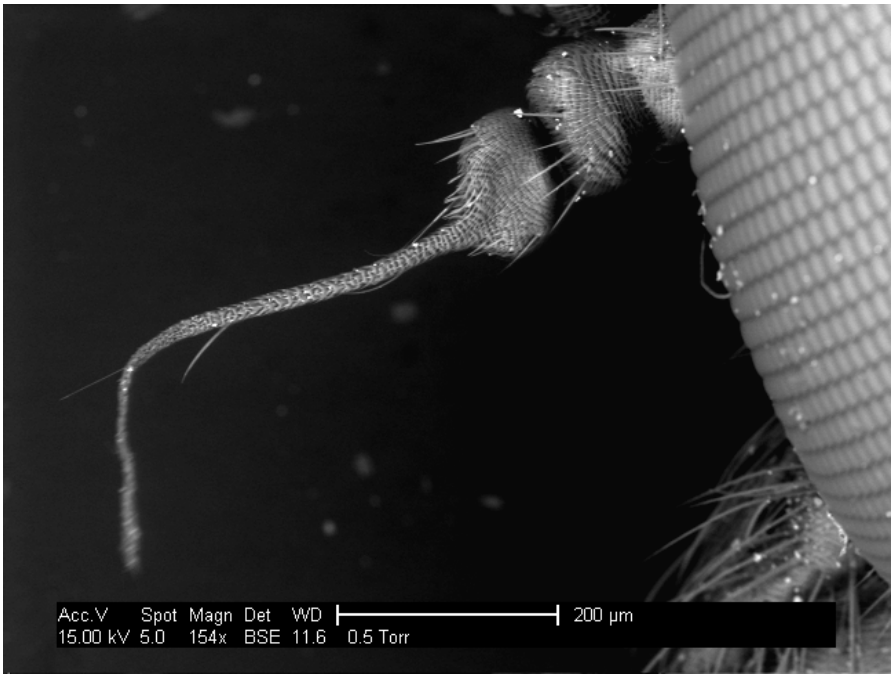


Figure 102. SEM image of antenna of *Rhagio mystaceus*.

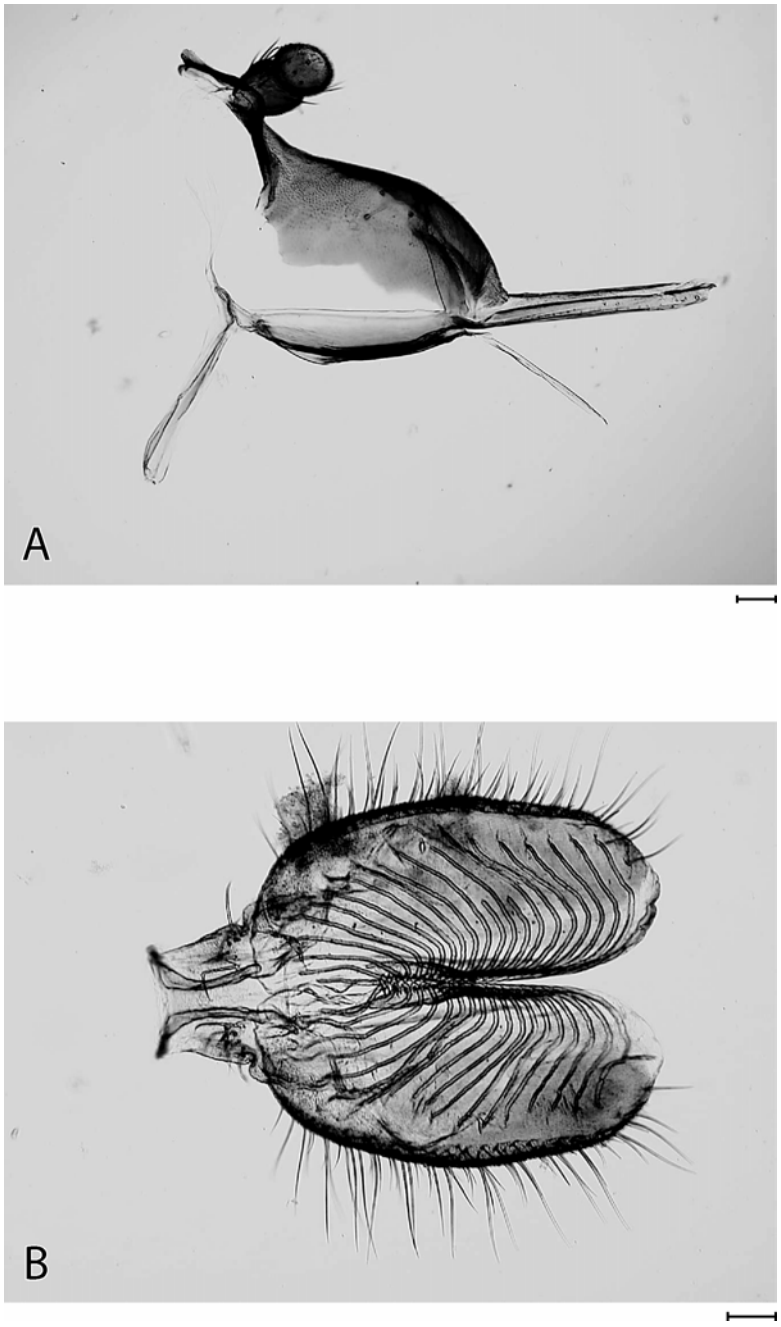


Figure 103. Mouthparts in *Rhagio mystaceus*. (A) Hypopharynx and associated structures, showing clypeus and scape and pedicel of antenna [USNMENT00025900] (B) Labellum [USNMENT00025908]. Scale = 0.1 mm.

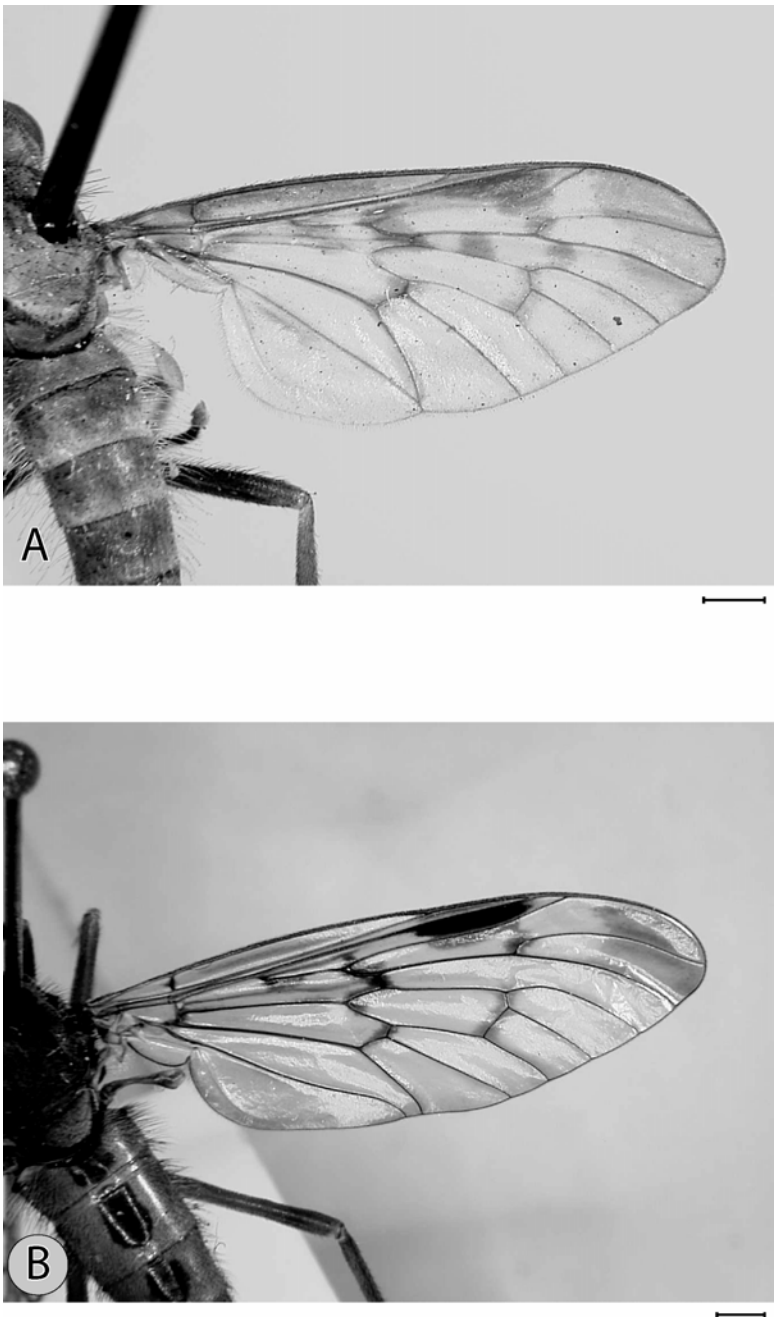


Figure 104. Wing of species of *Rhagio*, dorsal view. (A) *R. punctipennis*, male [USNMENT00025946] (B) *R. scolopaceus*, male [USNMENT00023193]. Scale bar = 0.5 mm.

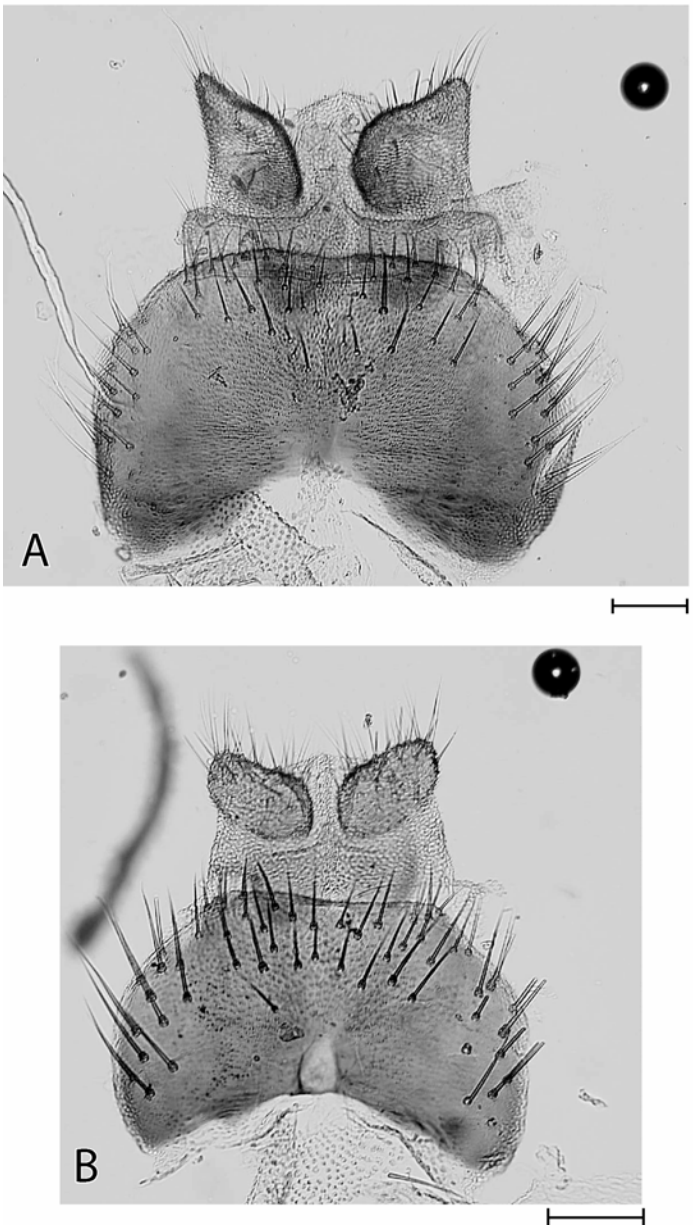


Figure 105. Epandrium in species of *Rhagio*, dorsal view. (A) *R. mystaceus* [USNMENT00025230] (B) *R. punctipennis* [USNMENT00025950]. Scale bar = 0.1 mm.

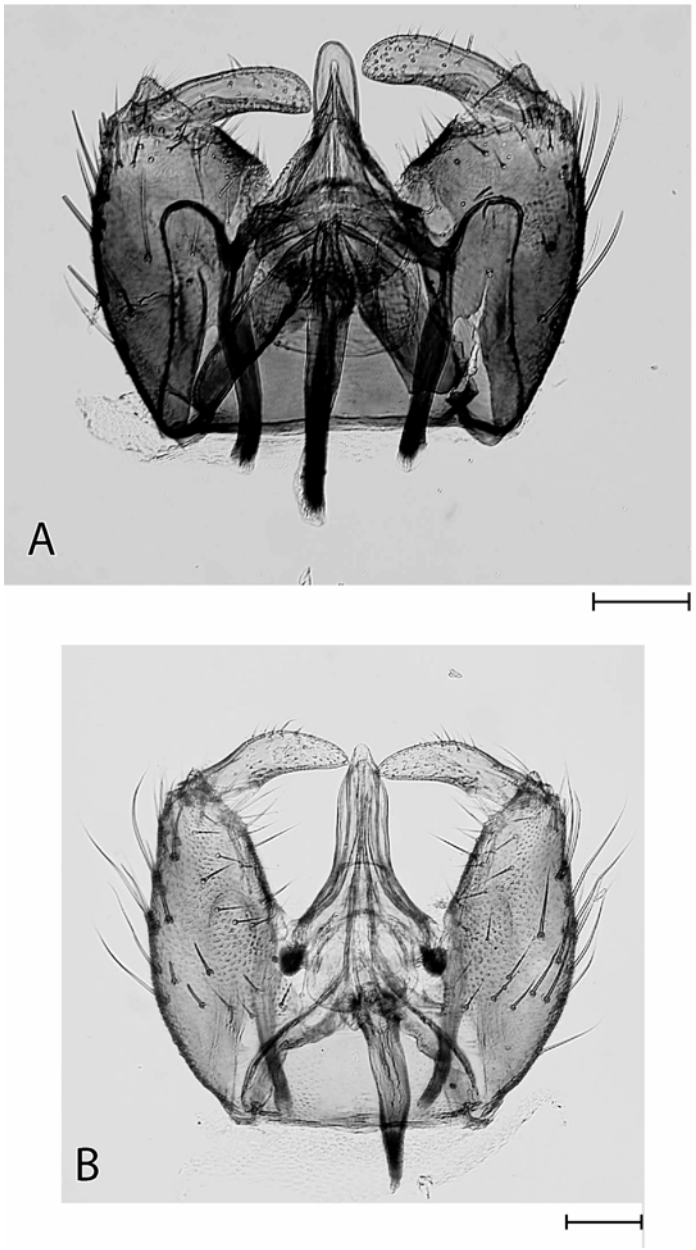


Figure 106. Hypandrium in species of *Rhagio*, dorsal view. (A) *R. plumbeus* [USNMENT00025949] (B) *R. punctipennis* [USNMENT00025950]. Scale bar = 0.1 mm.

Figure 107. Aedeagus (male genitalia) of *Rhagio mystaceus* [USNMENT00025230]. Scale bar = 0.1 mm.

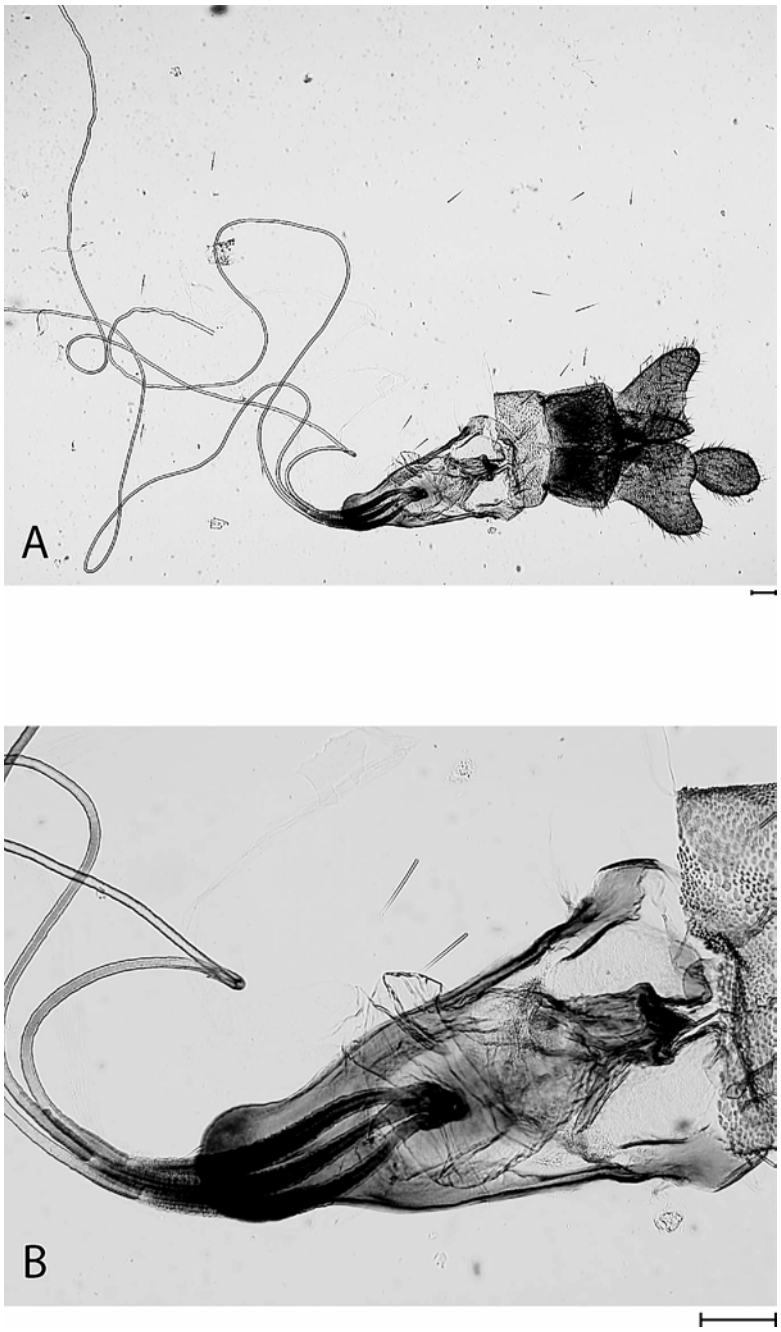


Figure 108. Female genitalia of *Rhagio palpalis* [USNMENT00025879]. Dorsal view. (A) Partially dissected terminalia (B) Sternite 9. Scale bar = 0.1 mm.

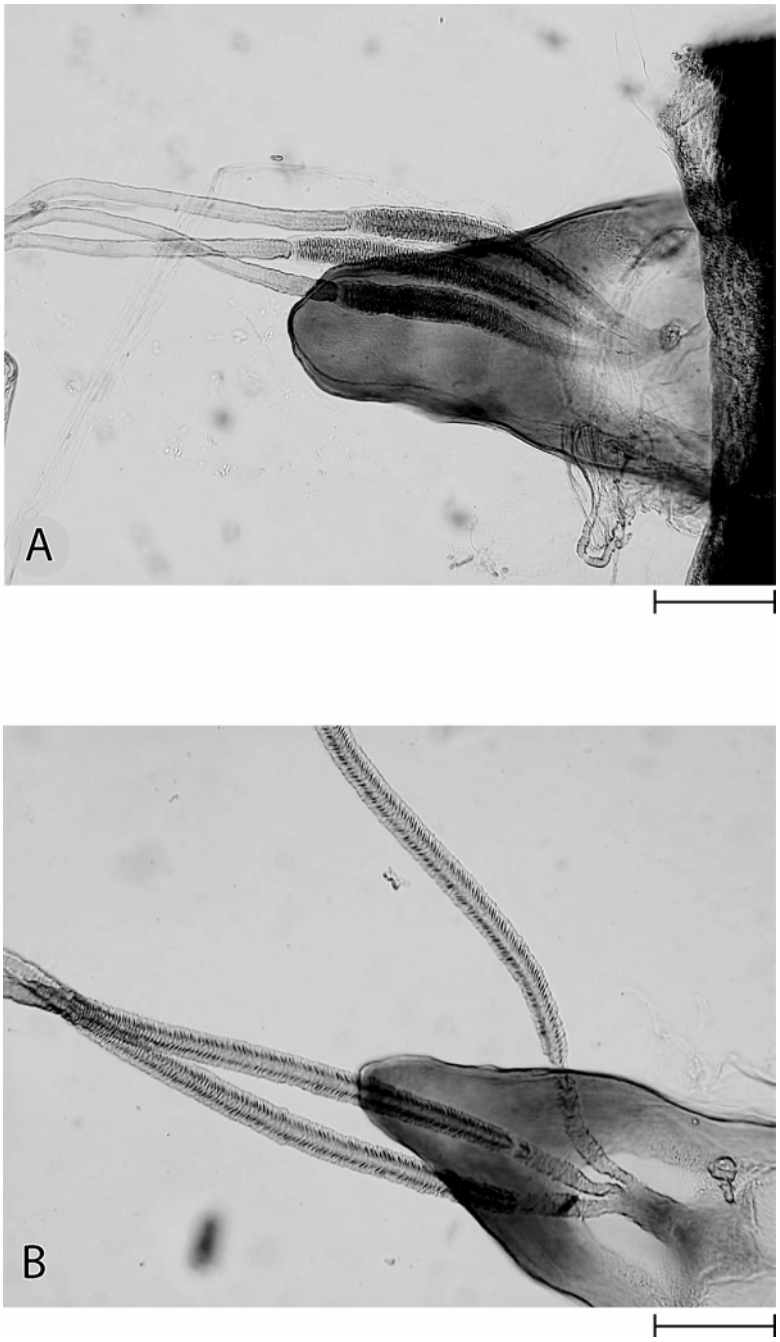


Figure 109. Anterior end of sternite 9 and base of spermathecal ducts at genital chamber in species of *Rhagio*. (A) *R. incisus* [USNMENT00025873] (B) *R. mystaceus* [USNMENT00025244]. Scale bar = 0.1 mm.

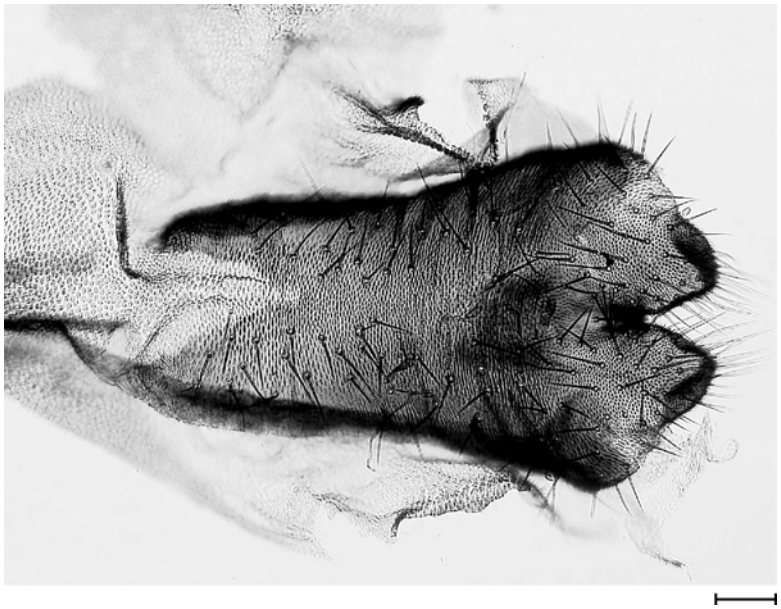


Figure 110. Sternite 8 of *Rhagio incisus* [USNMENT00025873]. Scale bar = 0.1 mm.

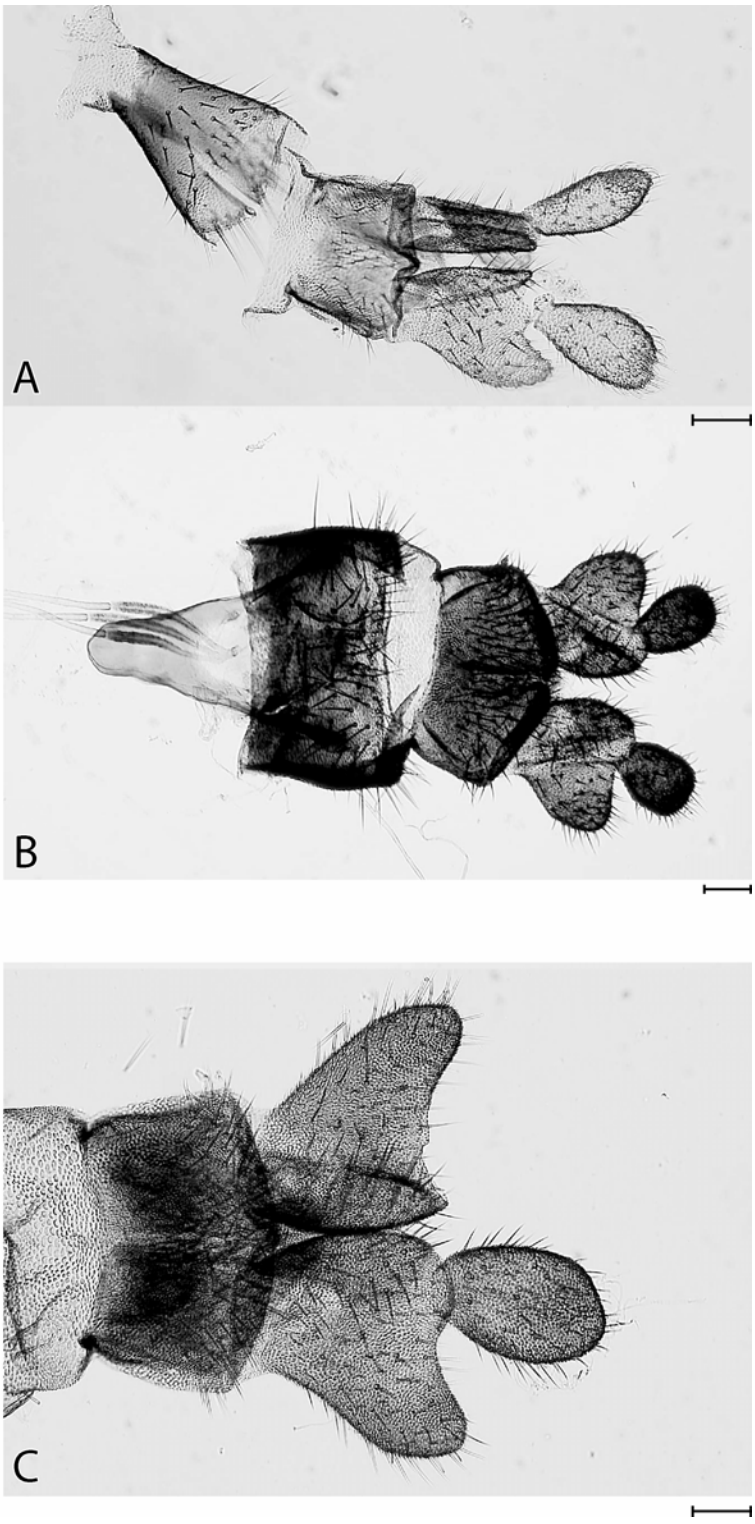


Figure 111. Cercus in species of *Rhagio*. (A) *R. hirtus* [USNMENT00023150] (B) *R. incisus* [USNMENT00025873] (C) *R. palpalis* [USNMENT00025879], missing left second cercus segment. Scale bar = 0.1 mm.

Figure 112. Lateral view of *Schizella furcicornis* [USNMENT00025863]. Scale bar = 0.5 mm.

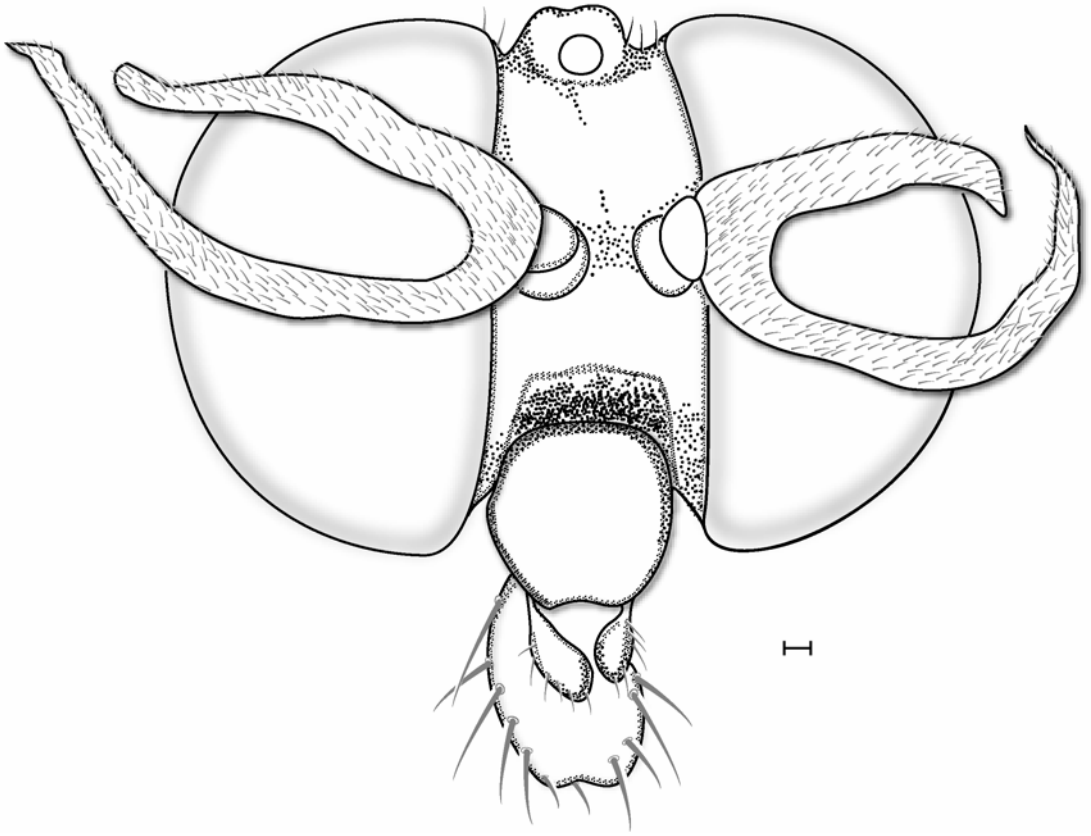


Figure 113. *Schizella woodleyi* Kerr, new species. Head, anterior view. Scale bar = 0.1 mm.

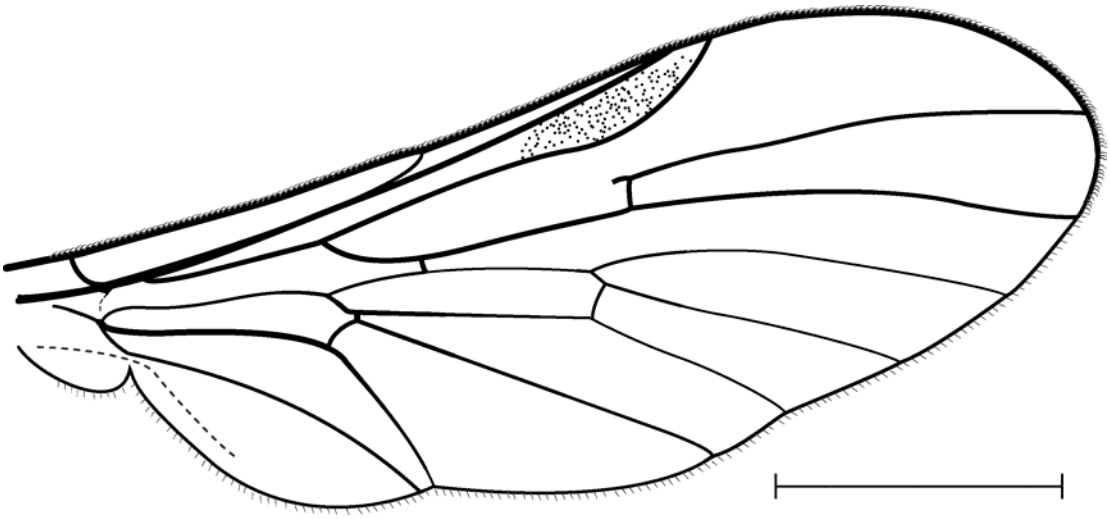


Figure 114. *Schizella woodleyi* Kerr, new species. Wing. Scale bar = 1.0 mm.

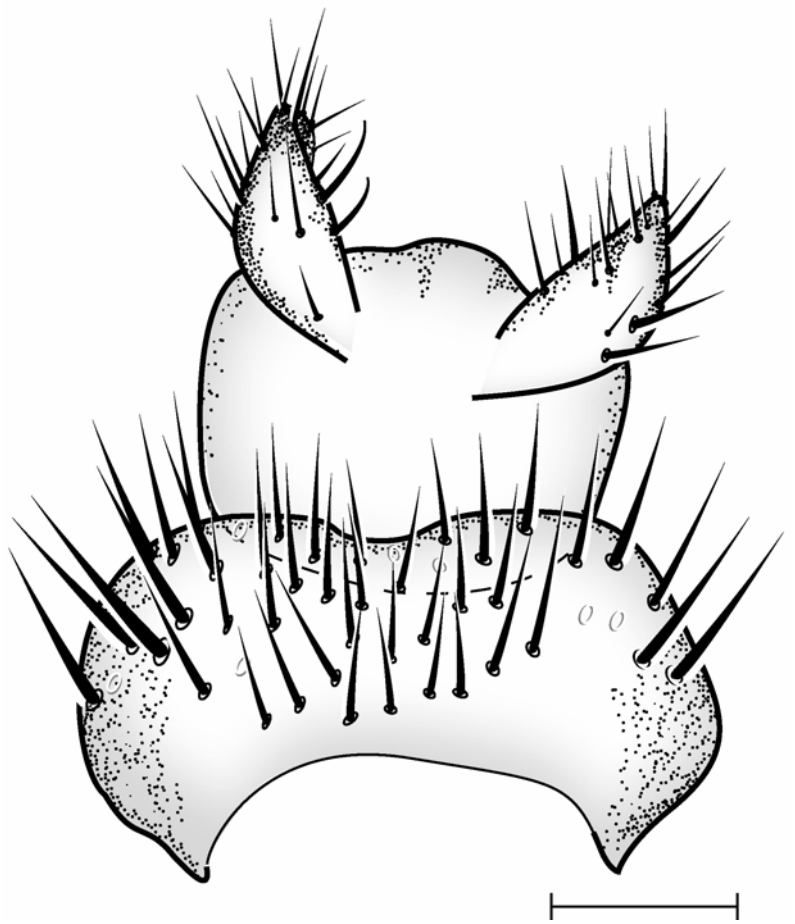


Figure 115. *Schizella woodleyi* Kerr, new species. Epandrium, dorsal view. Scale bar = 0.1 mm.

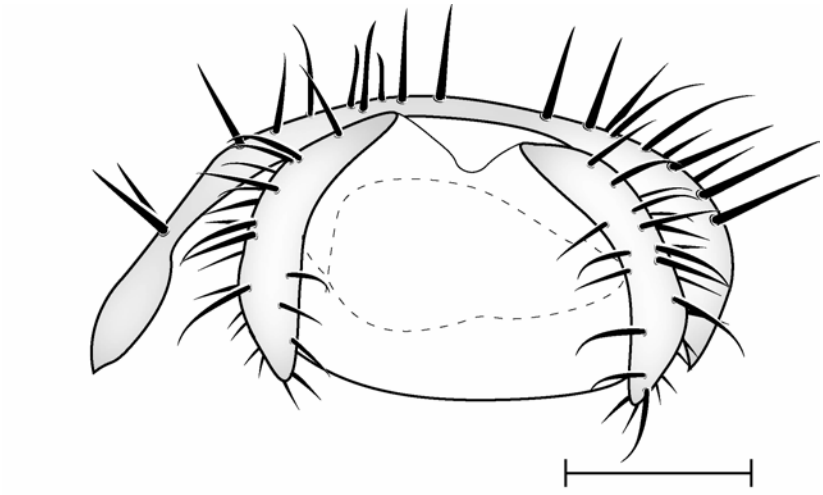


Figure 116. *Schizella woodleyi* Kerr, new species. Epandrium, posterior view. Scale bar = 0.1 mm.

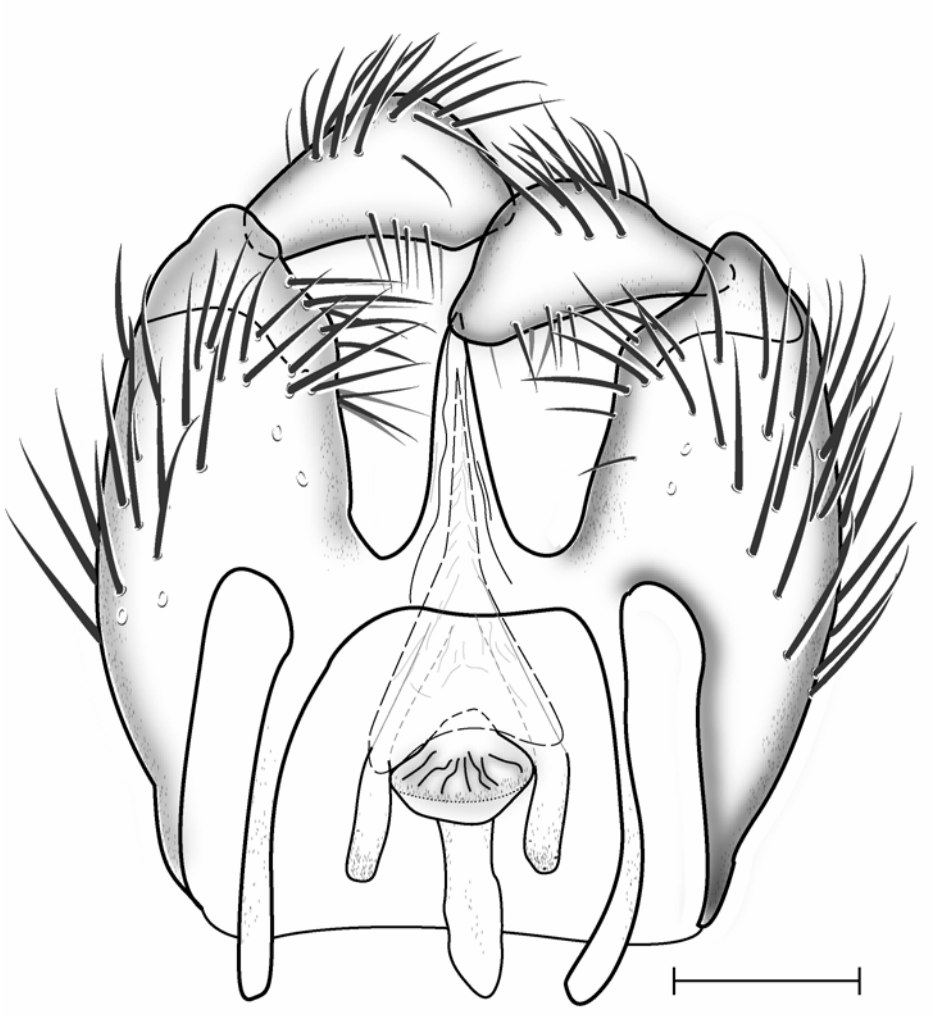


Figure 117. *Schizella woodleyi* Kerr, new species. Hypandrium, dorsal view. Scale bar = 0.1 mm.

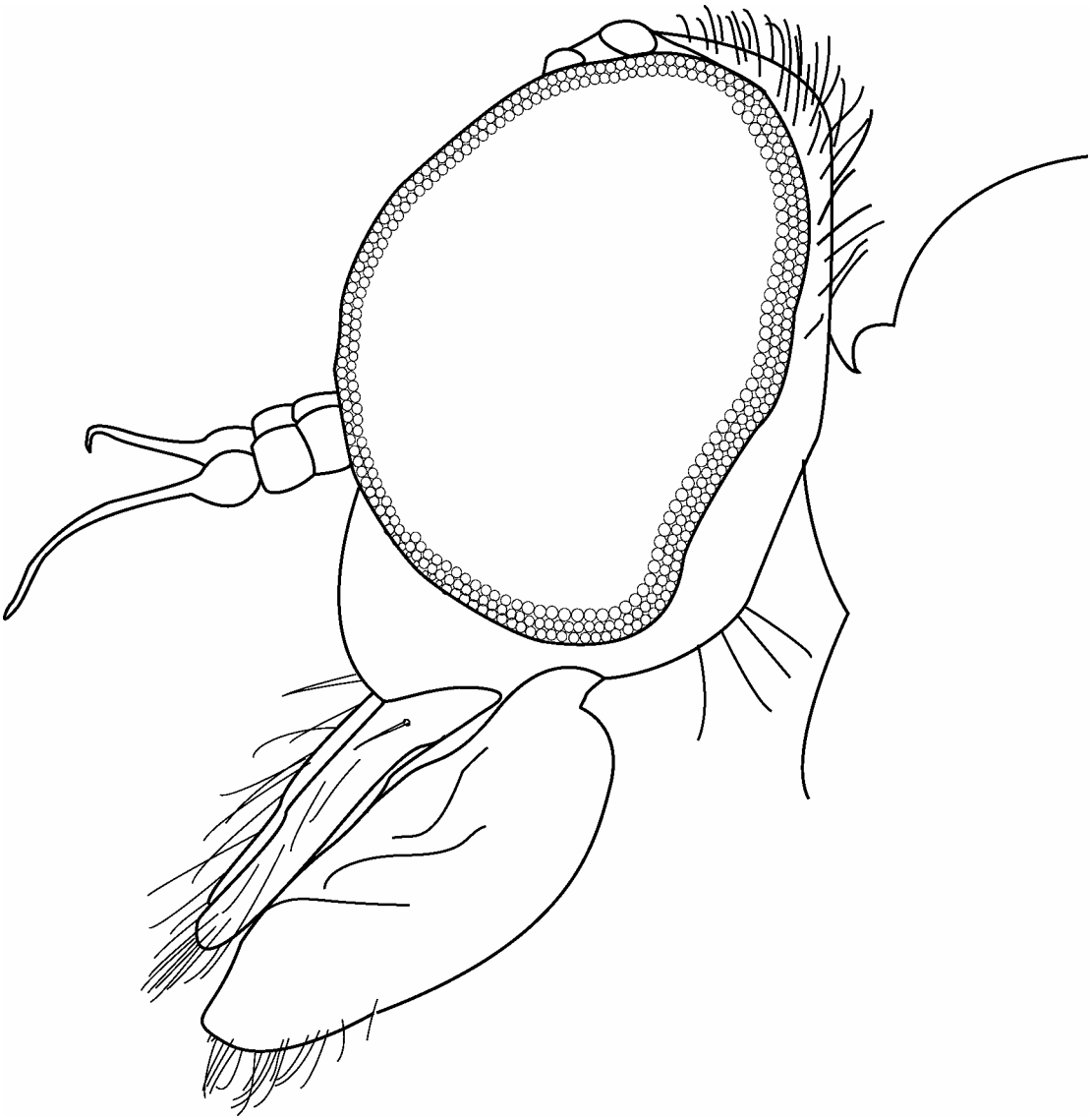


Figure 118. Lateral view of head, *Sierramyia chiapasensis*.

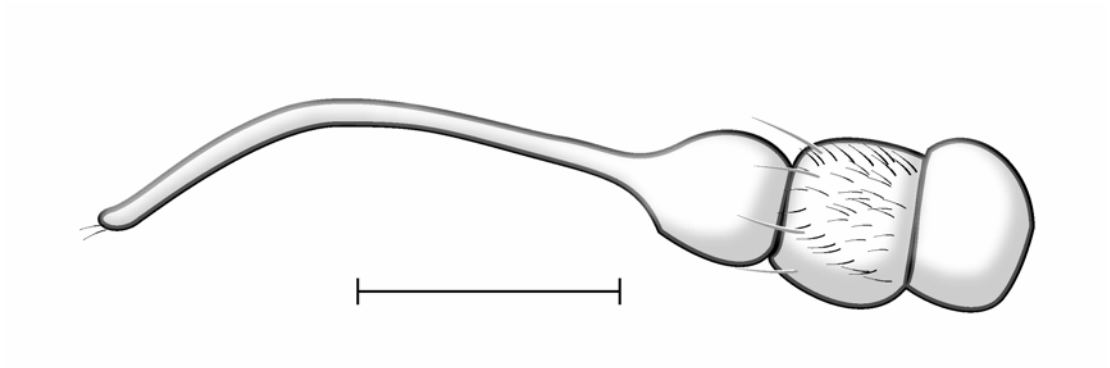


Figure 119. Antenna of *Sierramyia chiapasensis*. Scale bar = 0.5 mm.

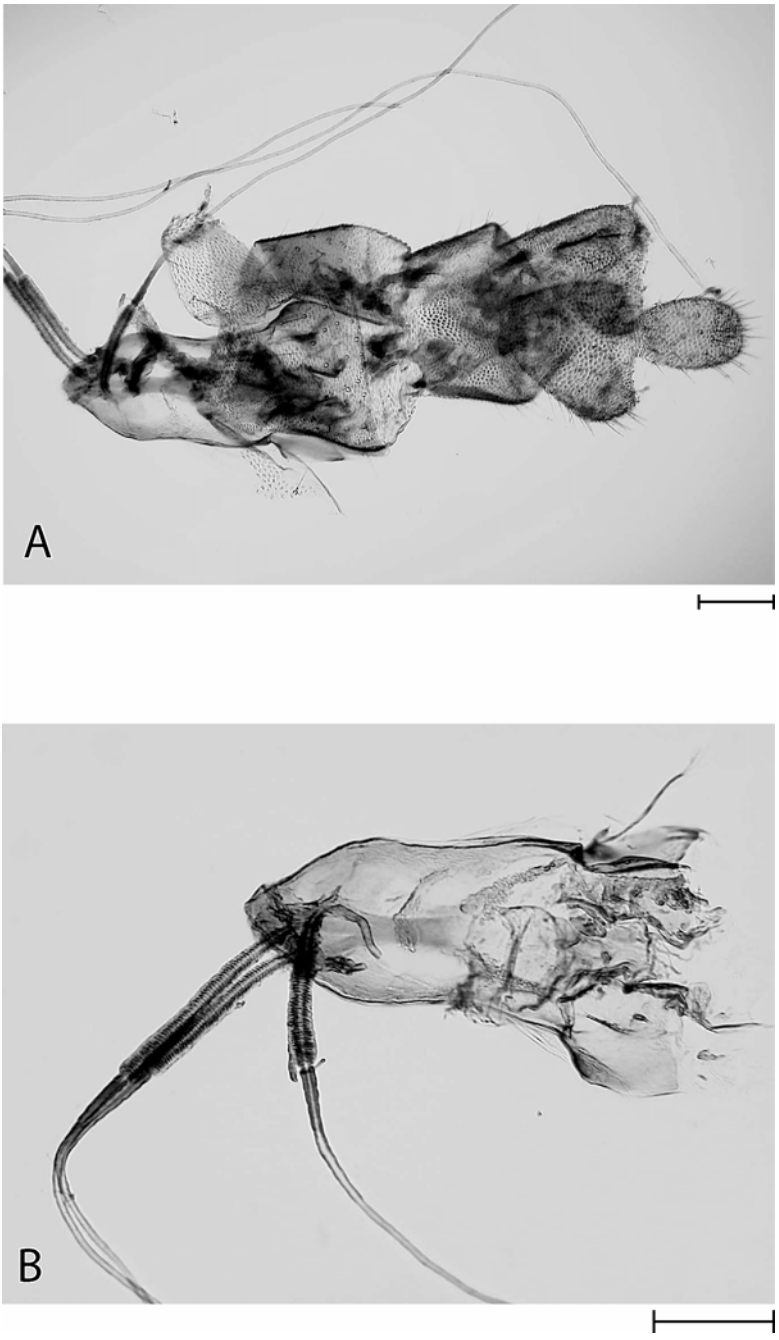


Figure 120. Female genitalia of *Sierramyia chiapensis* [USNMENT00022656]. (A) Terminal segments, lateral view (B) Sternite 9. Scale bar = 0.1 mm.

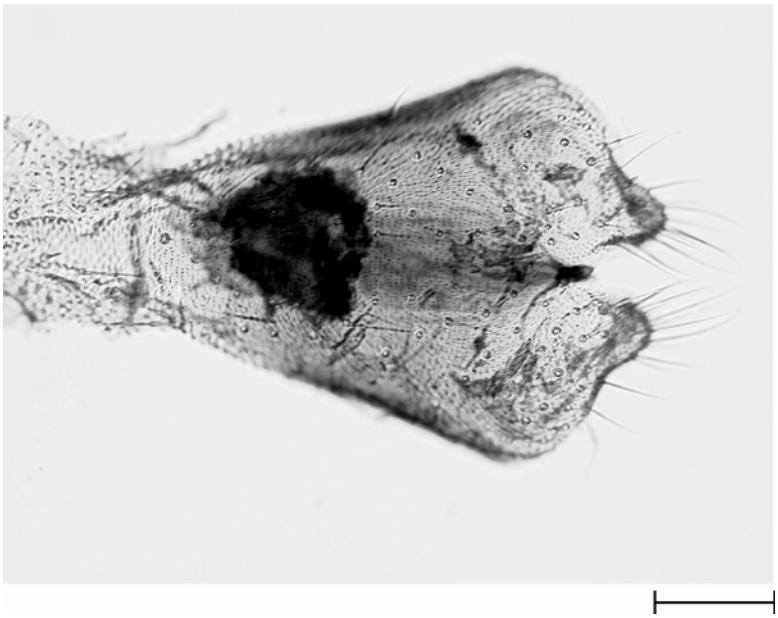


Figure 121. Female sternite 8 of *Sierramyia chiapensis* [USNMENT00022656], dorsal view. Scale bar = 0.1 mm.

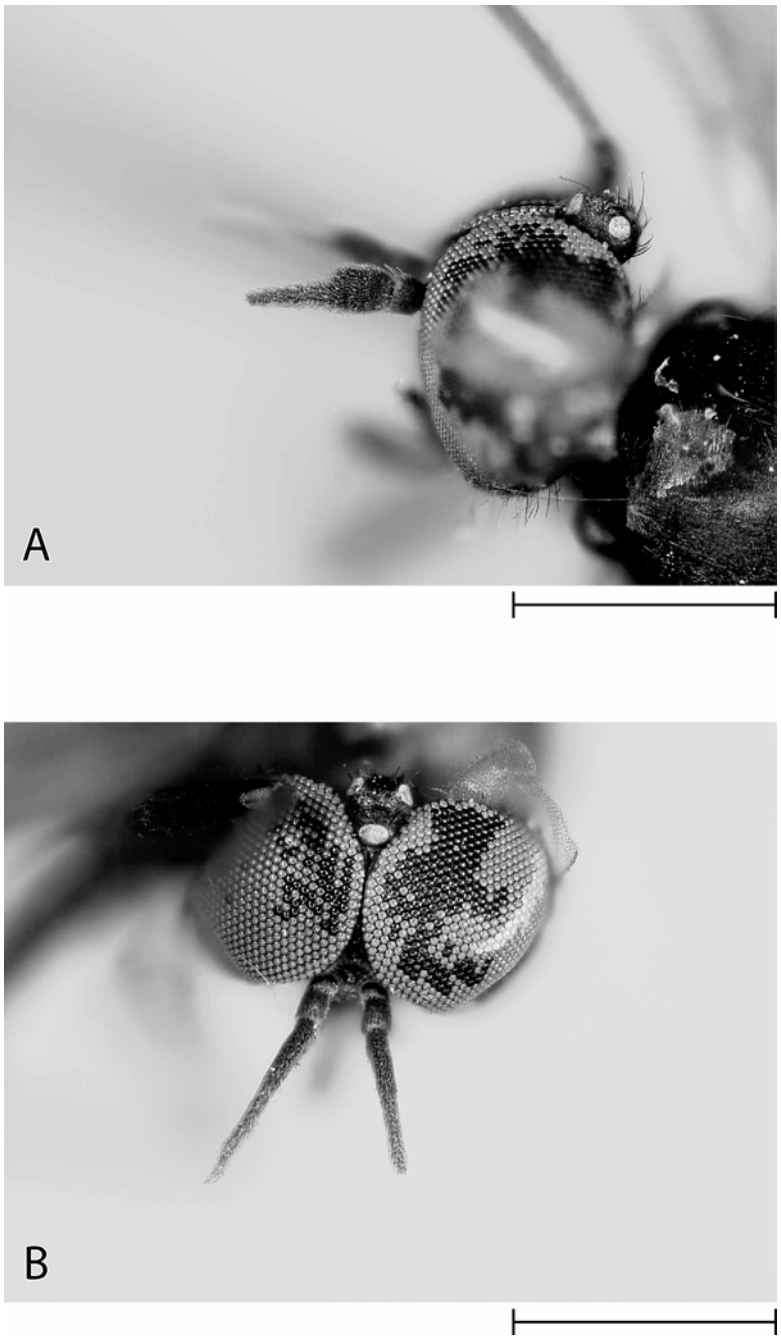


Figure 122. Antenna of *Spania nigra*, male [USNMENT00025865]. (A) lateral view (B) anterodorsal view. Scale bar = 0.5 mm.

Figure 123. Wing in *Spania nigra*, male, dorsal view [USNMENT00025865]. Scale bar = 0.5 mm.

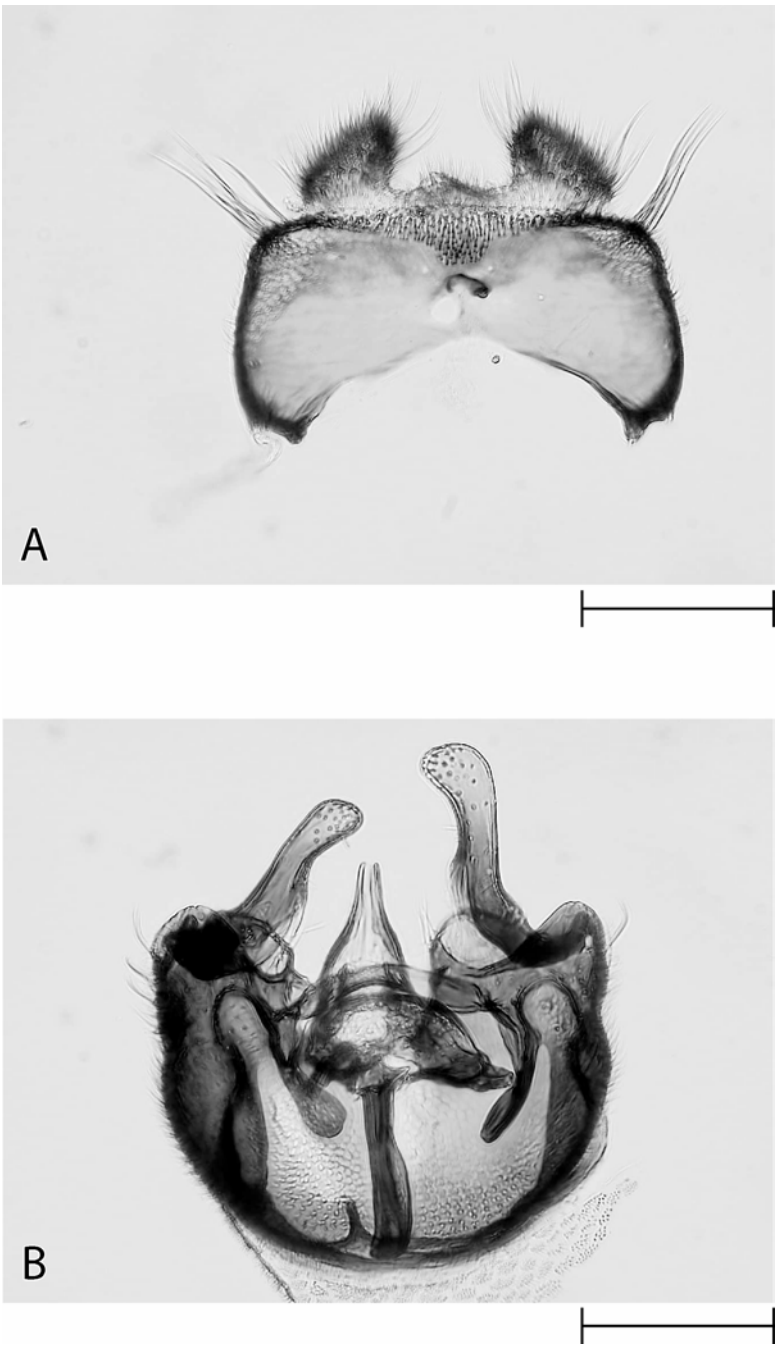


Figure 124. Male genitalia of *Spania nigra* [USNMENT00025868]. Dorsal view. (A) Epandrium (B) Hypandrium. Scale bar = 0.1 mm.

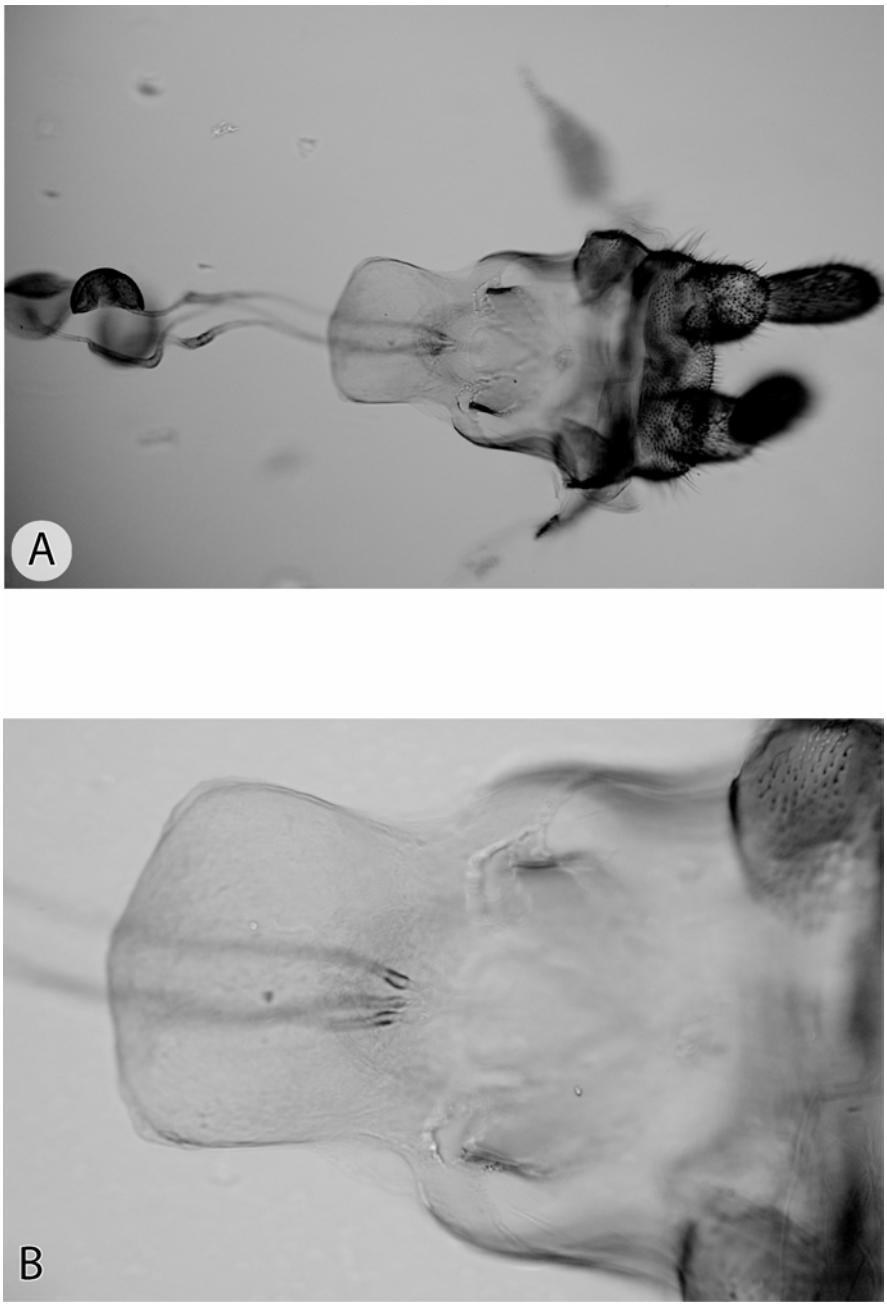


Figure 125. Female terminalia of *Spania nigra* [USNMENT00024389].

Figure 126. Spermatheca (imploded) and spermathecal duct accessory gland of *Spania nigra* [USNMENT00024389].

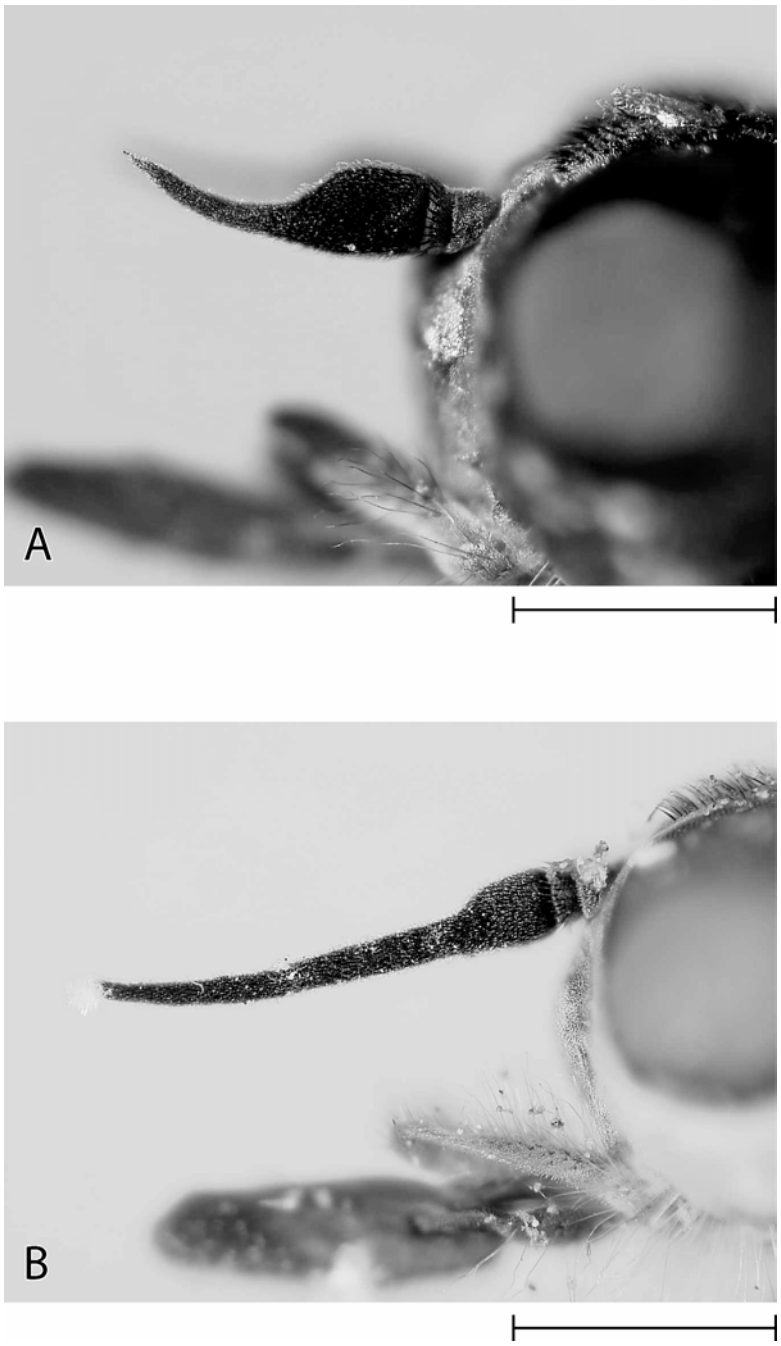


Figure 127. Antennal form in species of *Spaniopsis*. Lateral view. (A) *S. clelandi*, female [USNMENT00025409] (B) *S. longicornis*, female [USNMENT00022643]. Scale bar = 0.5 mm.

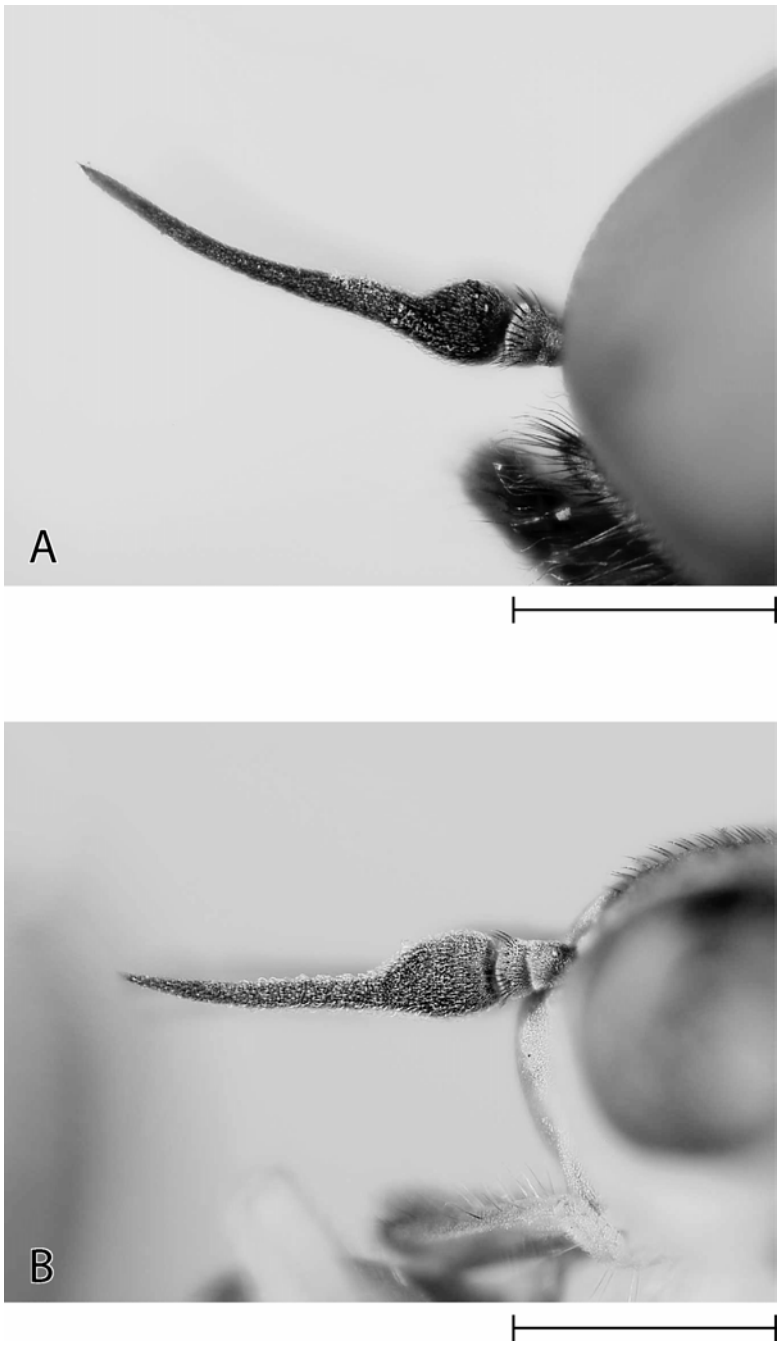


Figure 128. Antennal form in species of *Spaniopsis*. Lateral view. (A) *S. mackerrasi*, male [USNMENT00025556] (B) *S. marginipennis*, female [USNMENT00025412 – top specimen on pin]. Scale bar = 0.5 mm.

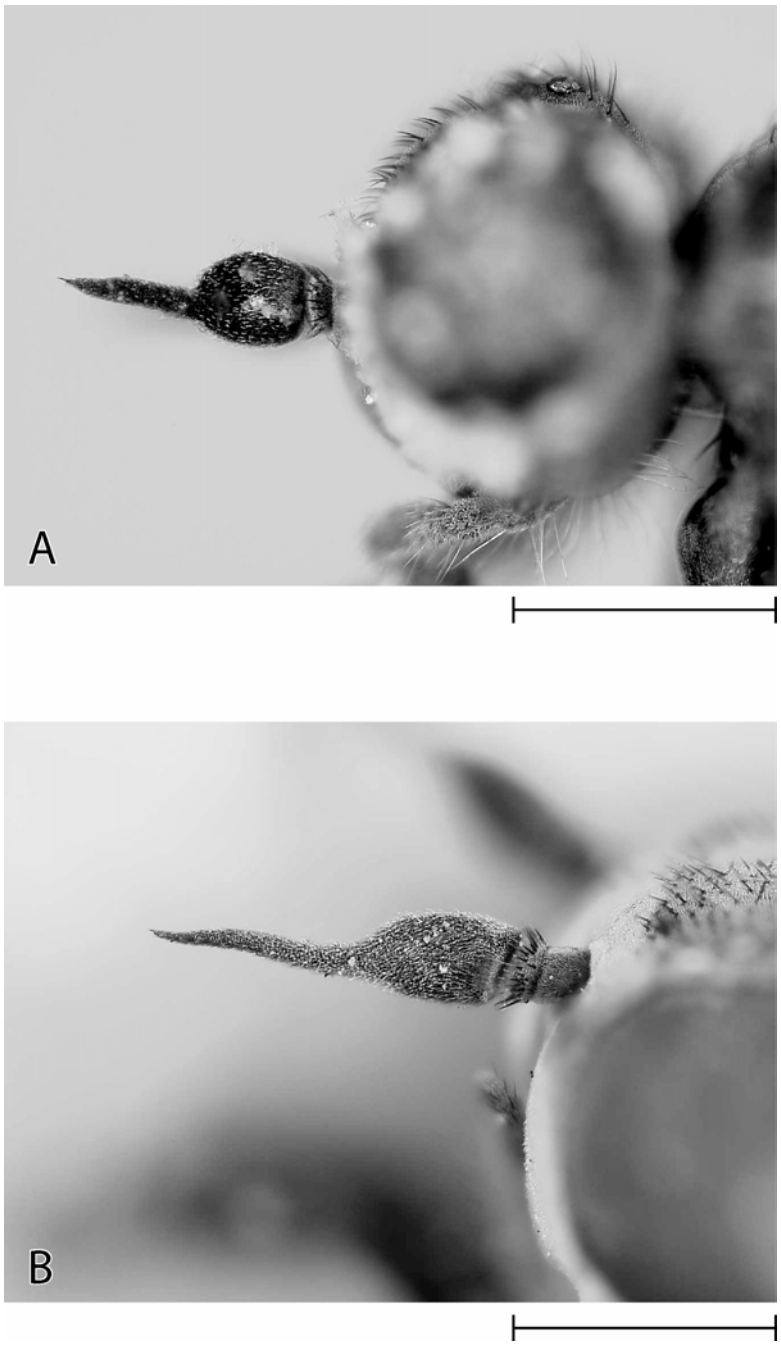


Figure 129. Antennal form in species of *Spaniopsis*. Lateral view. (A) *S. rieki*, female [USNMENT00022653] (B) *S. tabaniformis*, female [USNMENT00025568]. Scale bar = 0.5 mm.

Figure 130. Antenna of *Spaniopsis vexans*. Female, lateral view [USNMENT00025408]. Scale bar = 0.5 mm.

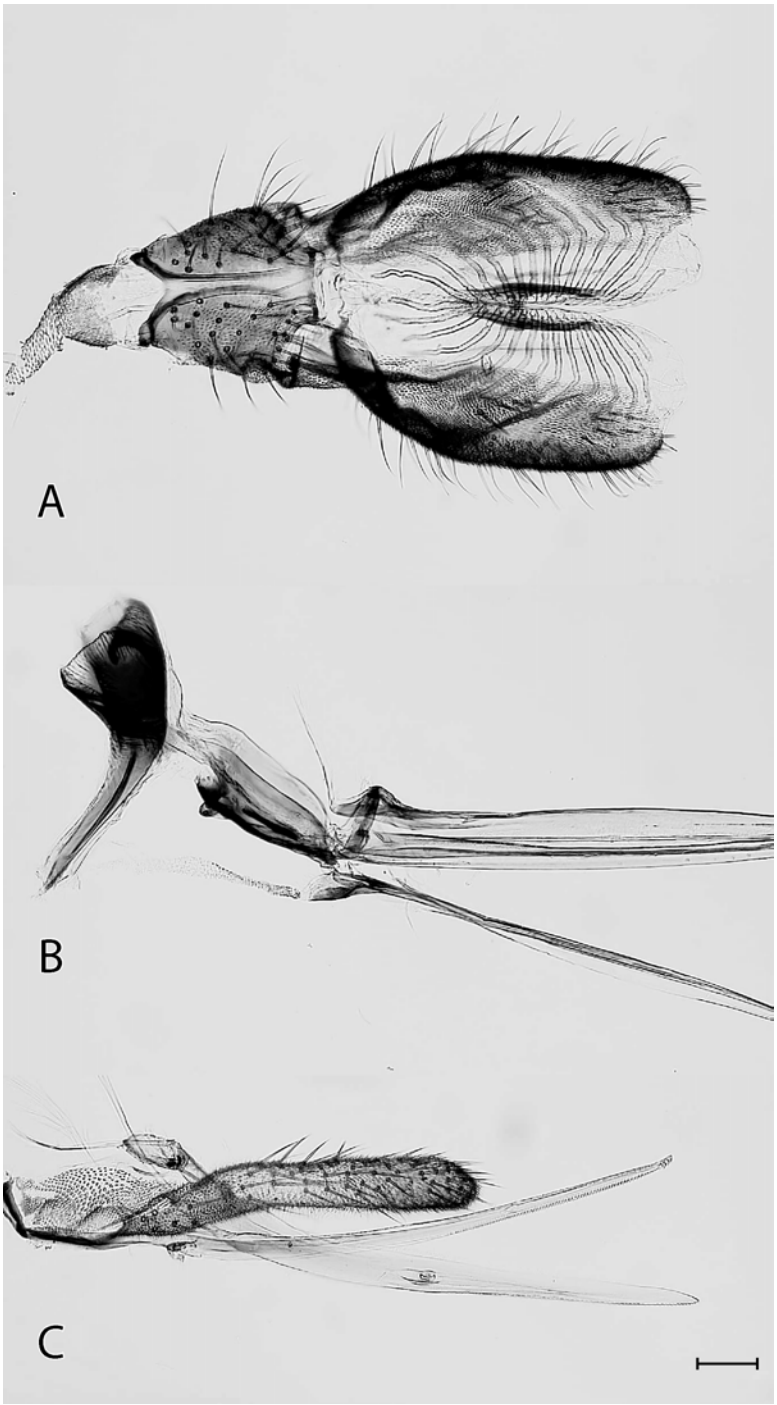


Figure 131. Mouthparts of *Spaniopsis clelandi* [USNMENT25907]. (A) Labellum, ventral view (B) Hypopharynx, cibarial pump, and associated structures, lateral view (C) Palp, mandible, and lacinia; lateral view. Scale bar = 0.1 mm.

Figure 132. Wing in species of *Spaniopsis*, ventral view. (A) *S. clelandi* [USNMENT00022649] (B) *S. mackerrasi* [USNMENT00025589]. Scale bar = 0.5 mm.

Figure 133. Wing in species of *Spaniopsis*. (A) *S. longicornis*, ventral view [USNMENT00025293] (B) *S. marginipennis*, dorsal view [USNMENT00025252]. Scale bar = 0.5 mm.

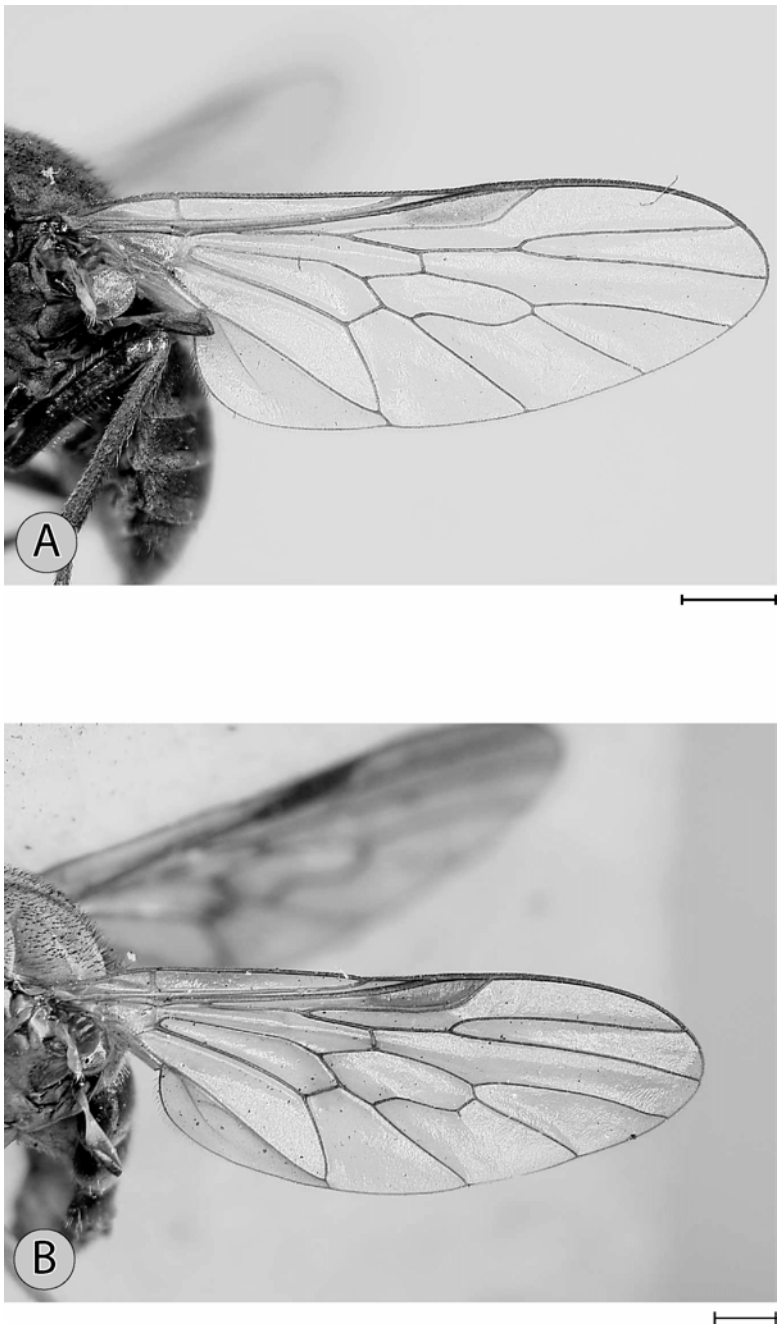


Figure 134. Wing in species of *Spaniopsis*, ventral view. (A) *S. rieki* [USNMENT00022655] (B) *S. tabaniformis* [USNMENT00025568]. Scale bar = 0.5 mm.

Figure 135. Wing in *Spaniopsis vexans*, dorsal view [USNMENT00025407]. Scale bar = 0.5 mm.

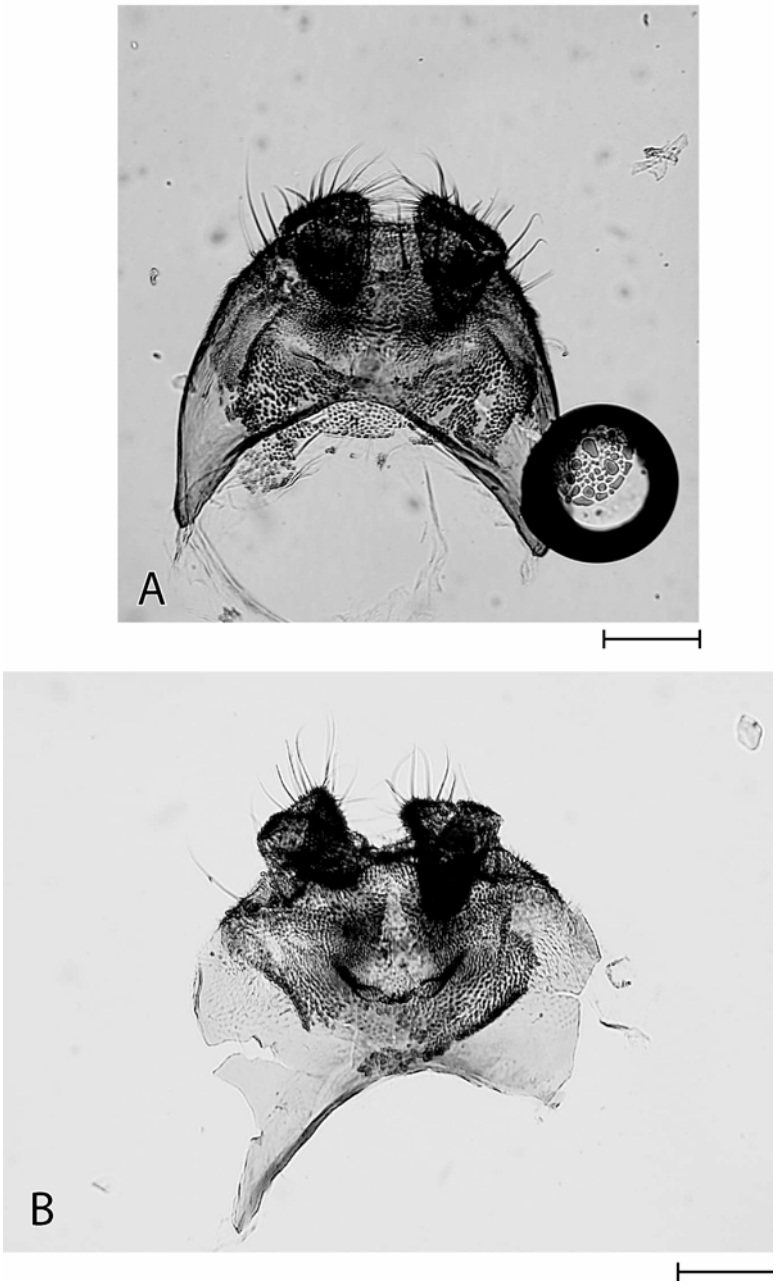


Figure 136. Epandrium in species of *Spaniopsis*, ventral view. (A) *S. clelandi* [USNMENT00025396] (B) *S. marginipennis* [USNMENT00025249]. Scale bar = 0.1 mm.

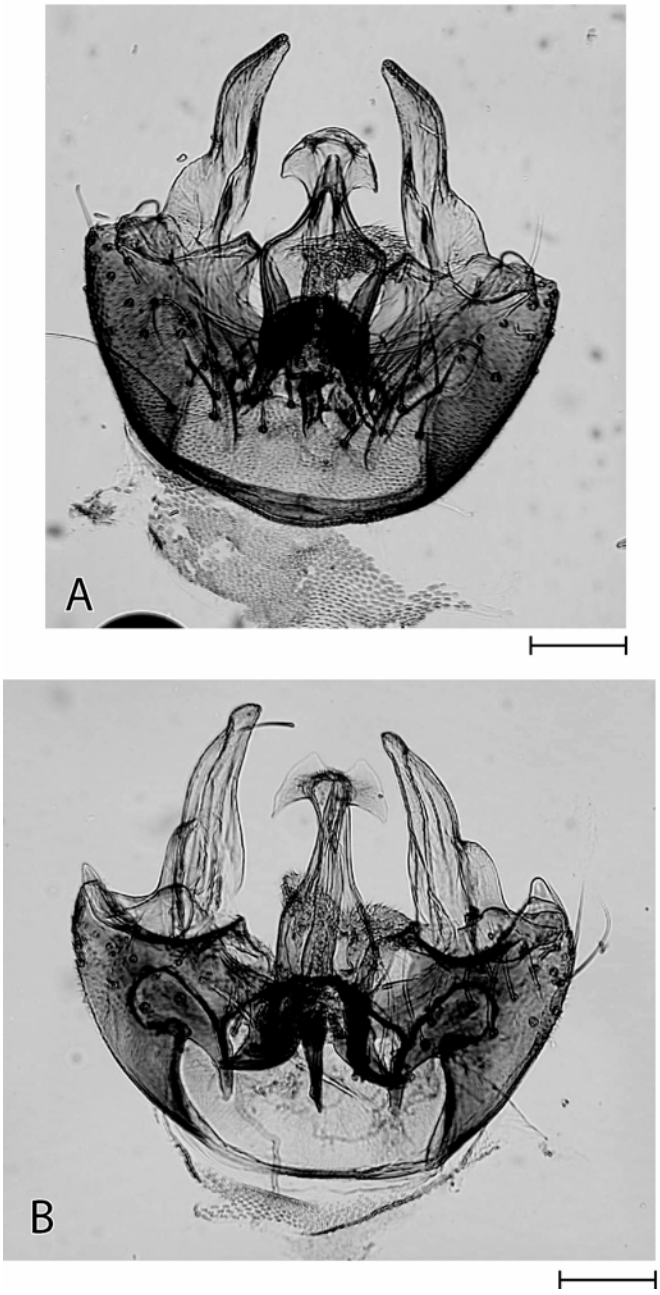


Figure 137. Hypandrium in species of *Spaniopsis*, dorsal view. (A) *S. clelandi* [USNMENT00025396] (B) *S. marginipennis* [USNMENT00025249]. Scale bar = 0.1 mm.

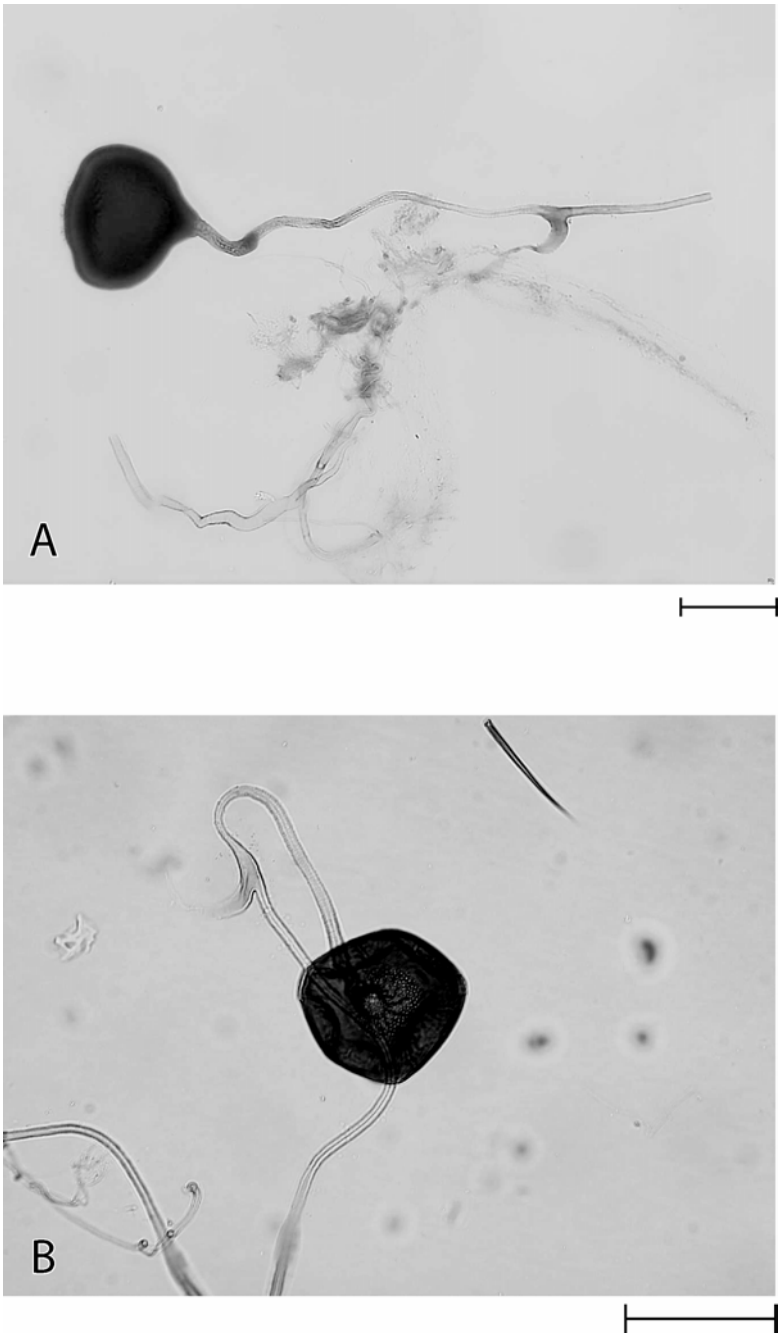


Figure 138. Spermathecae in species of *Spaniopsis*. (A) *S. clelandi* [USNMENT00025398] (B) *S. marginipennis* [USNMENT00025251]. Scale bar = 0.1 mm.

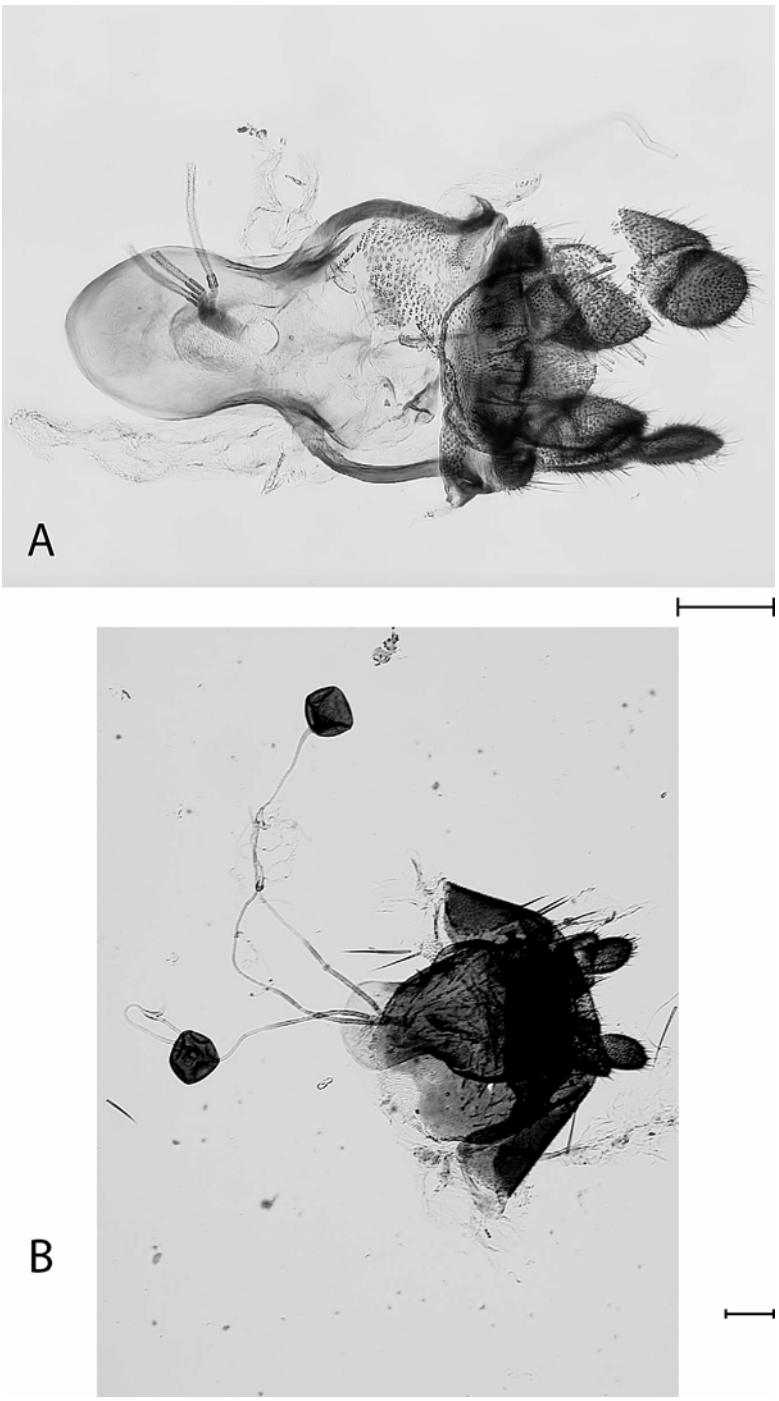
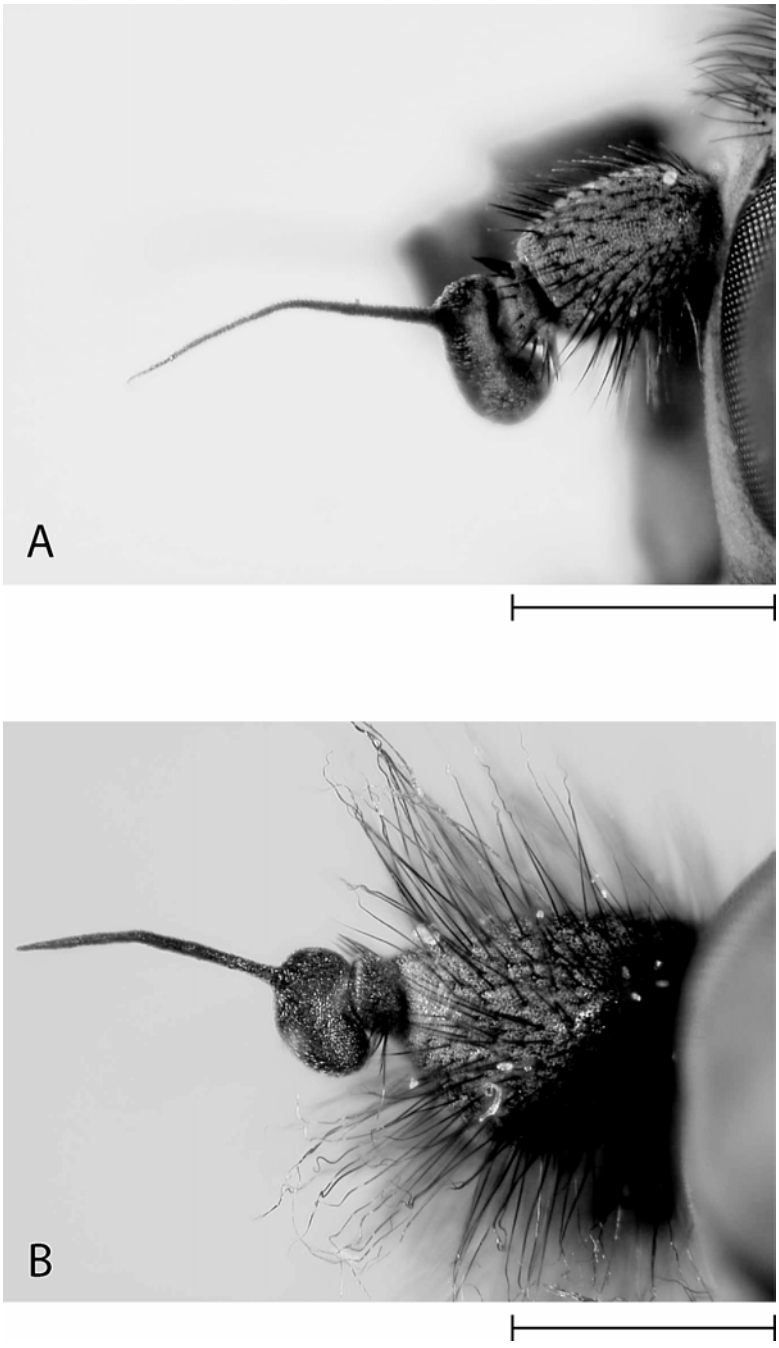


Figure 139. Female terminalia in species of *Spaniopsis*, dorsal view. (A) *S. clelandi* [USNMENT00025398] (B) *S. marginipennis* [USNMENT00025251]. Scale bar = 0.1 mm.

Figure 140. *Stylospania lancifera* [USNMENT00025234, holotype].



mm.

Figure 141. Antennal form in *Symphoromyia crassicornis*. (A) *S. crassicornis*, female [USNMENT00023210] (B) *S. crassicornis*, male [USNMENT00023208]. Scale bar = 0.5 mm.

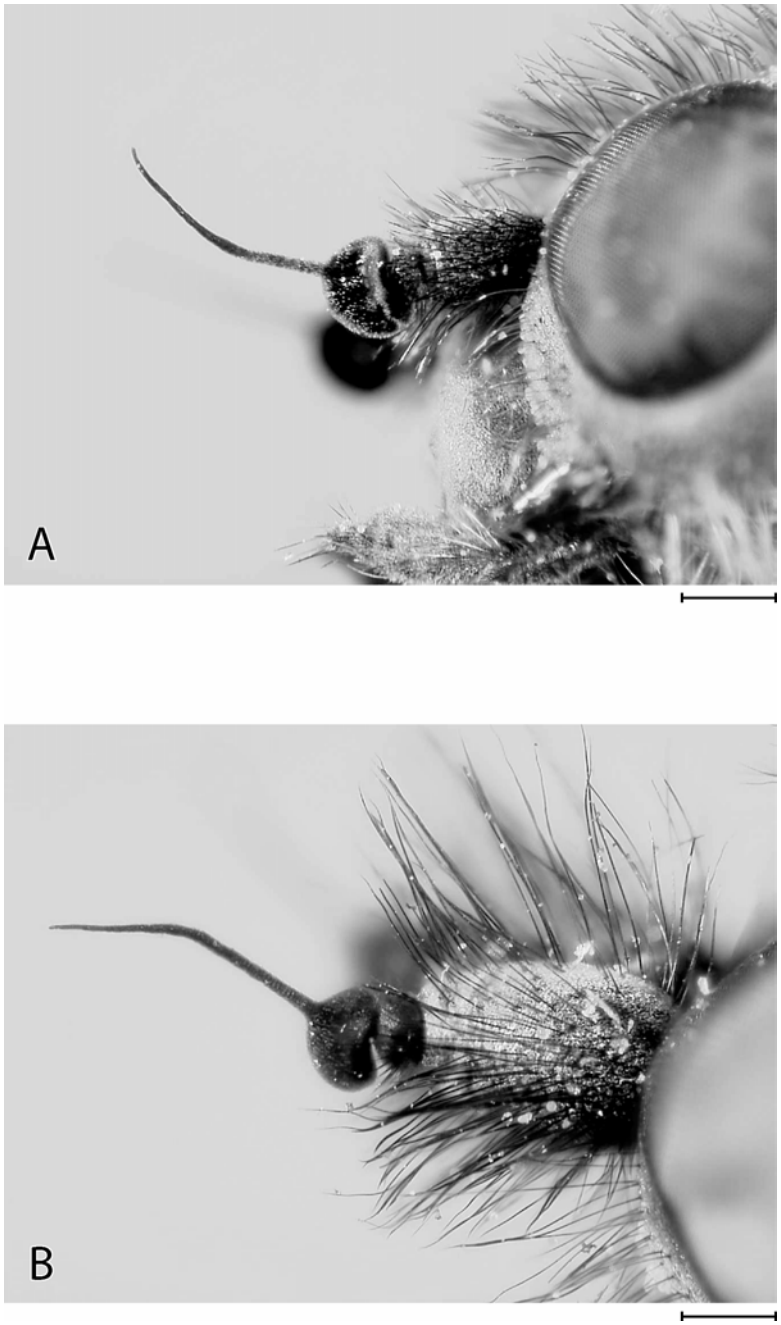


Figure 142. Antennal form in *Symphoromyia cruenta* (A) female [USNMENT00025941] (B) male [USNMENT00025942]. Scale bar = 1.0 mm.

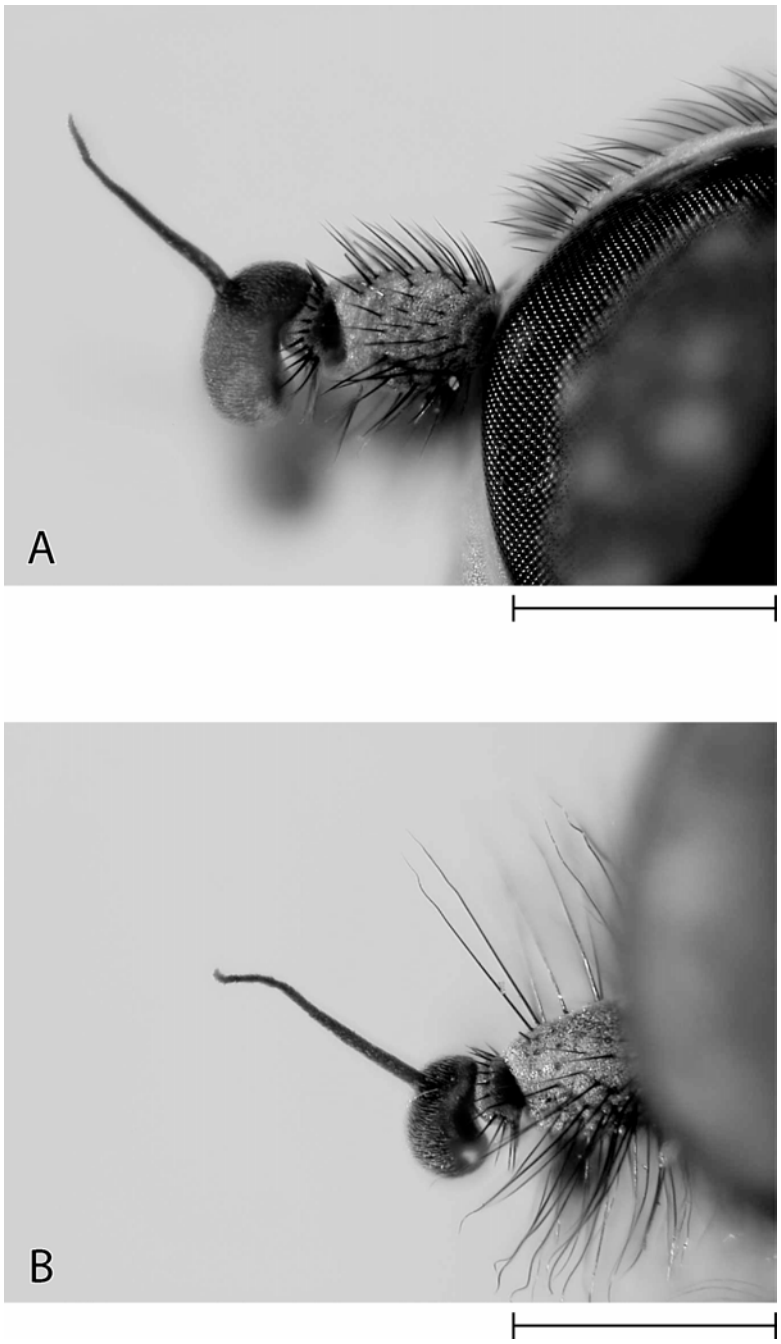


Figure 143. Antennal form in *Symphoromyia hirta*, lateral view (A) male [USNMENT00028585] (B) female [USNMENT00028622]. Scale bar = 0.5 mm.

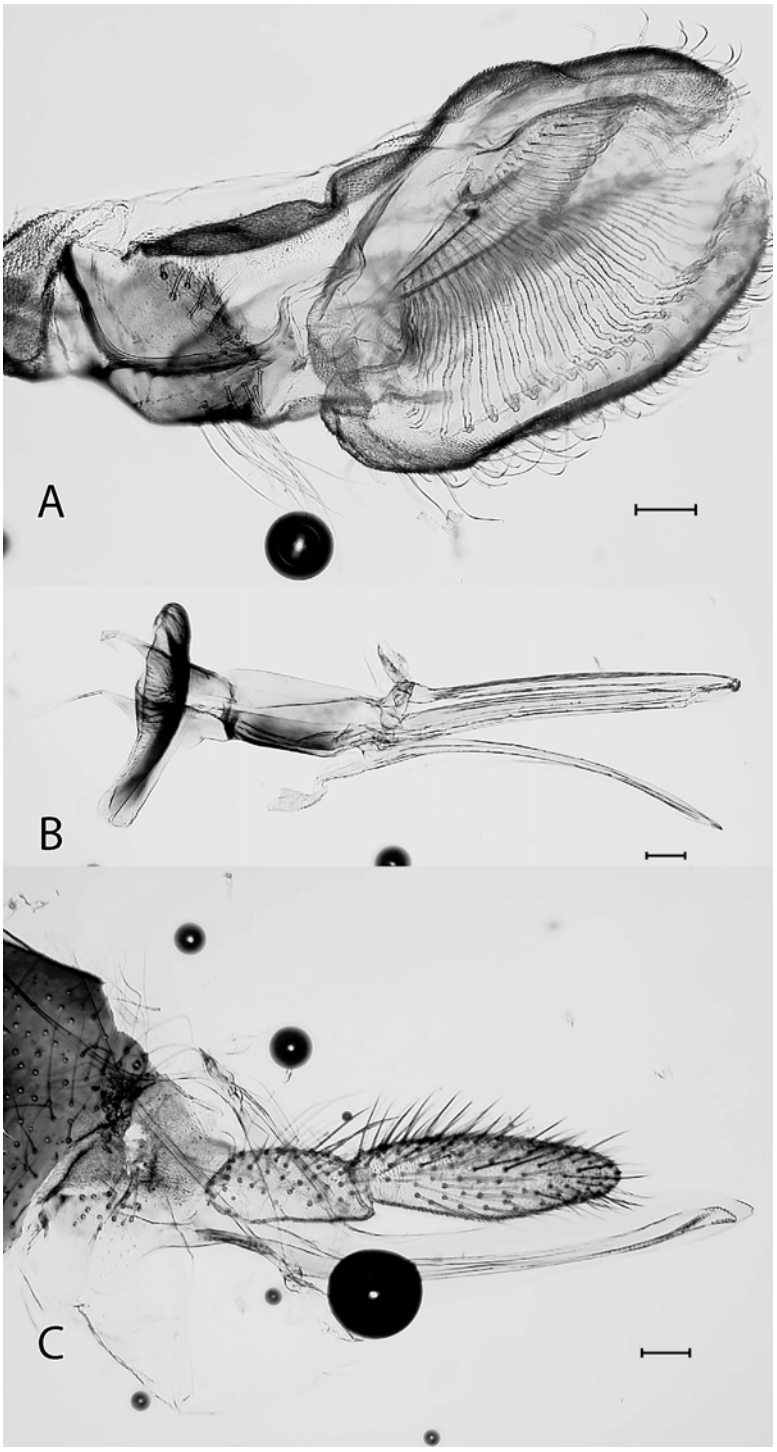


Figure 144. Mouthparts of *Symphoromyia* sp. [USNMENT00025909]. (A) Labellum, oblique ventral view (B) Hypopharynx, cibarial pump, and associated structures, lateral view (C) Palp and lacinia, lateral view. Scale bar = 0.1 mm.

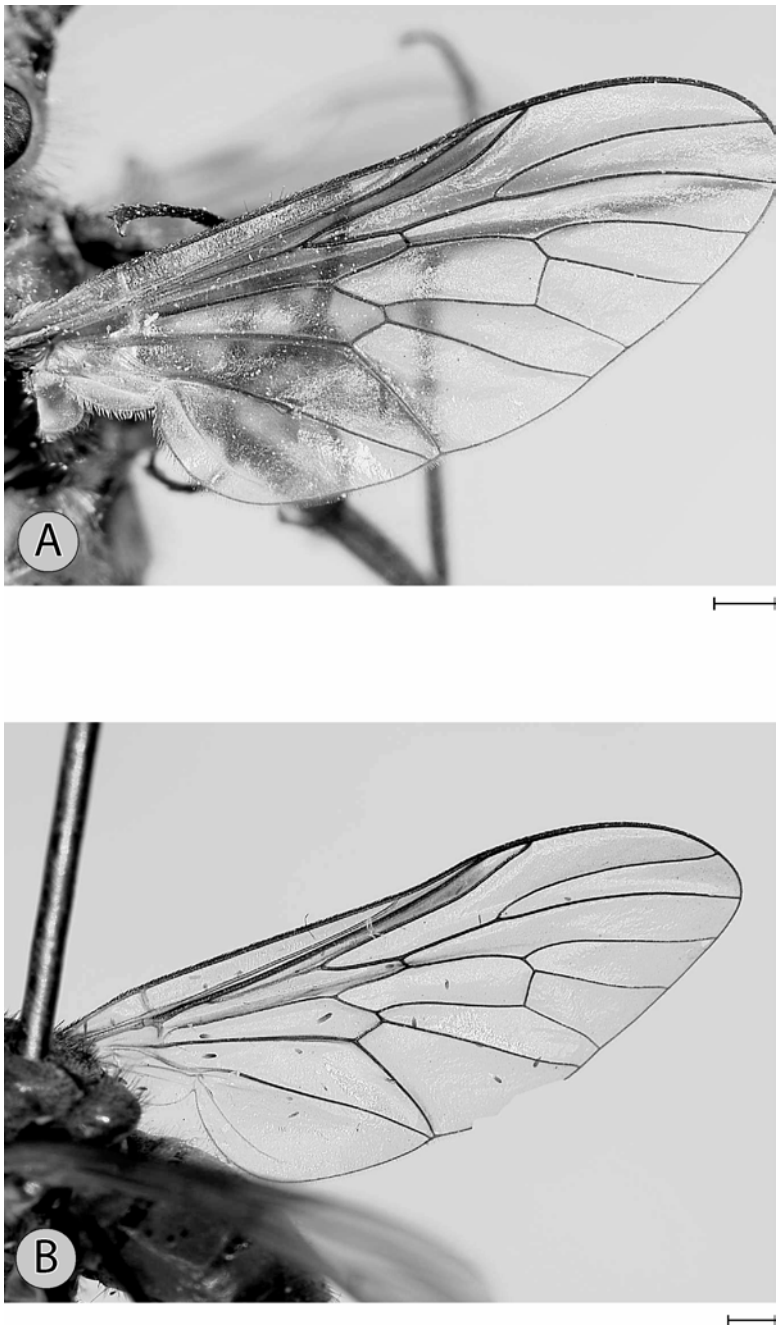


Figure 145. Wing in species of *Symphoromyia*. (A) *S. cruenta*, female [USNMENT00025941] (B) *S. crassicornis*, female [USNMENT00023211]. Scale bar = 0.5 mm.

Figure 146. Wing in species of *Symphoromyia*. (A) *S. hirta*, female [USNMENT00028605] (B) *S. flavipalpis*, female [USNMENT00025944]. Scale bar = 0.5 mm.

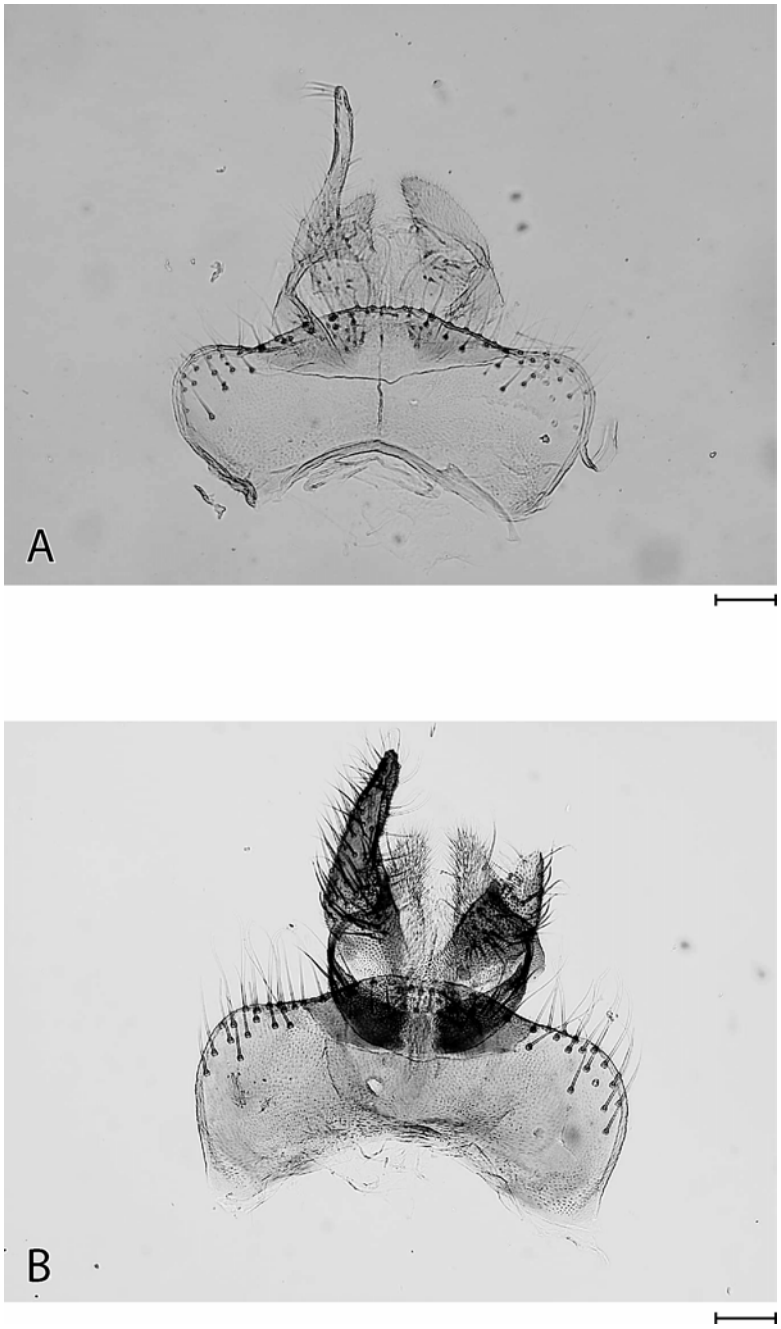


Figure 147. Epandrium (male genitalia) in species of *Symphoromyia*. (A) *S. crassicornis*, dorsal view [USNMENT00028629] (B) *S. hirta*, ventral view [USNMENT00025791]. Scale bar = 0.1 mm.

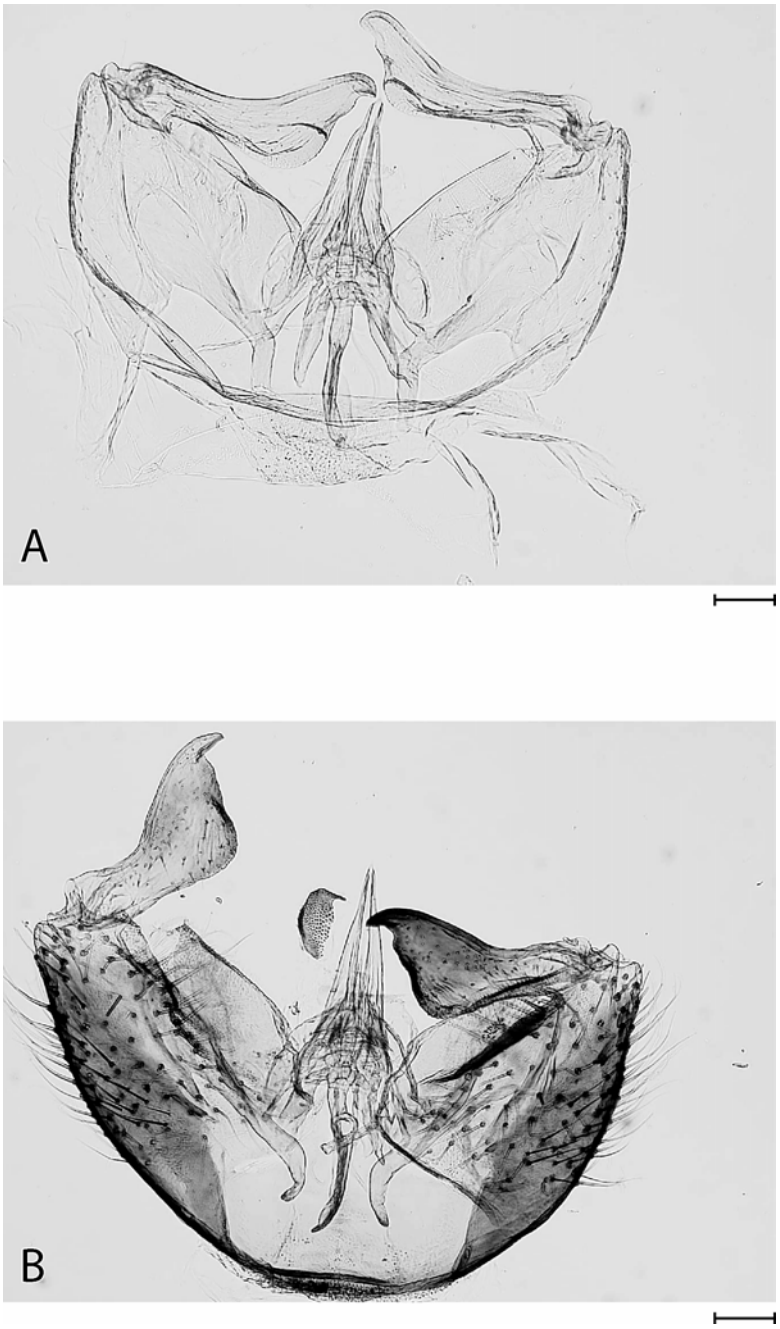


Figure 148. Hypandrium (male genitalia) in species of *Symphoromyia*, dorsal view. (A) *S. crassicornis* [USNMENT00028629] (B) *S. hirta* [USNMENT00025791]. Scale bar = 0.1 mm.

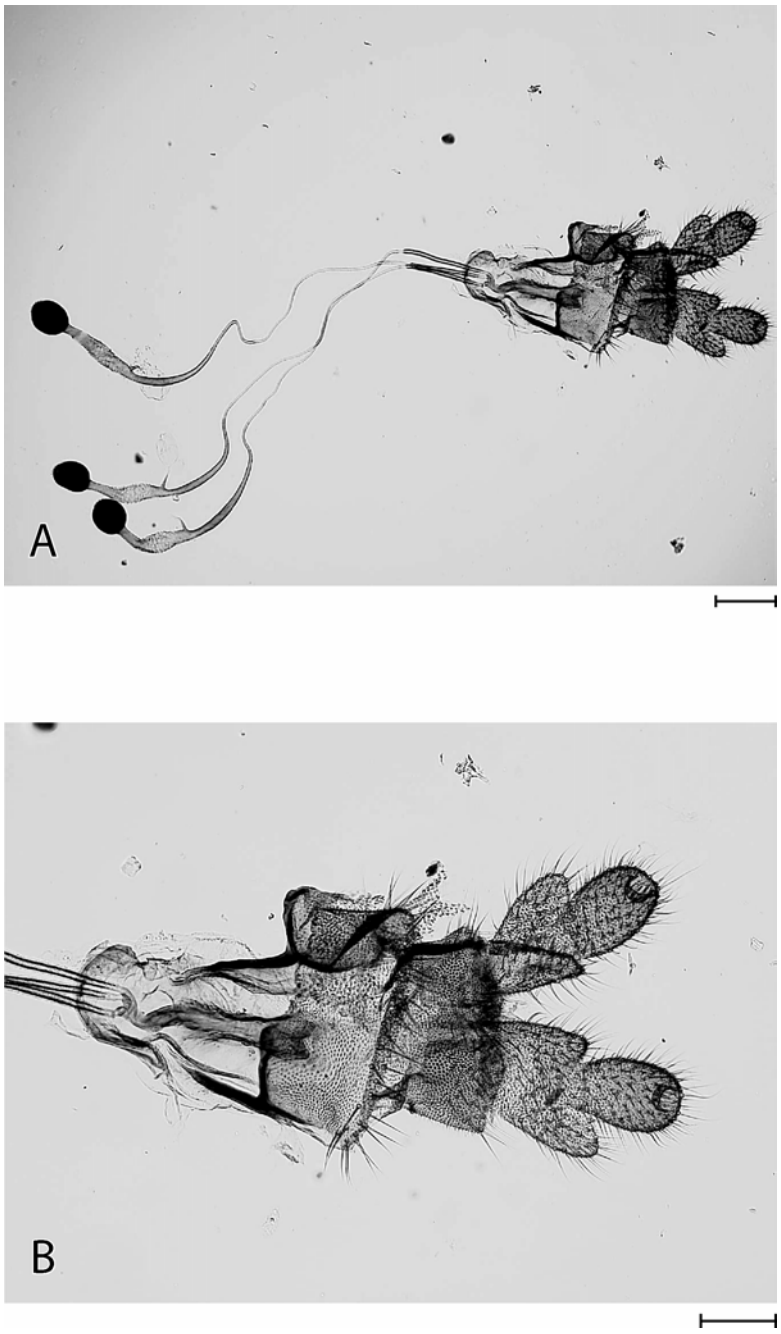


Figure 149. Female genitalia in *Symphoromyia hirta* [USNMENT00028587]. Scale bar = 0.1 mm.

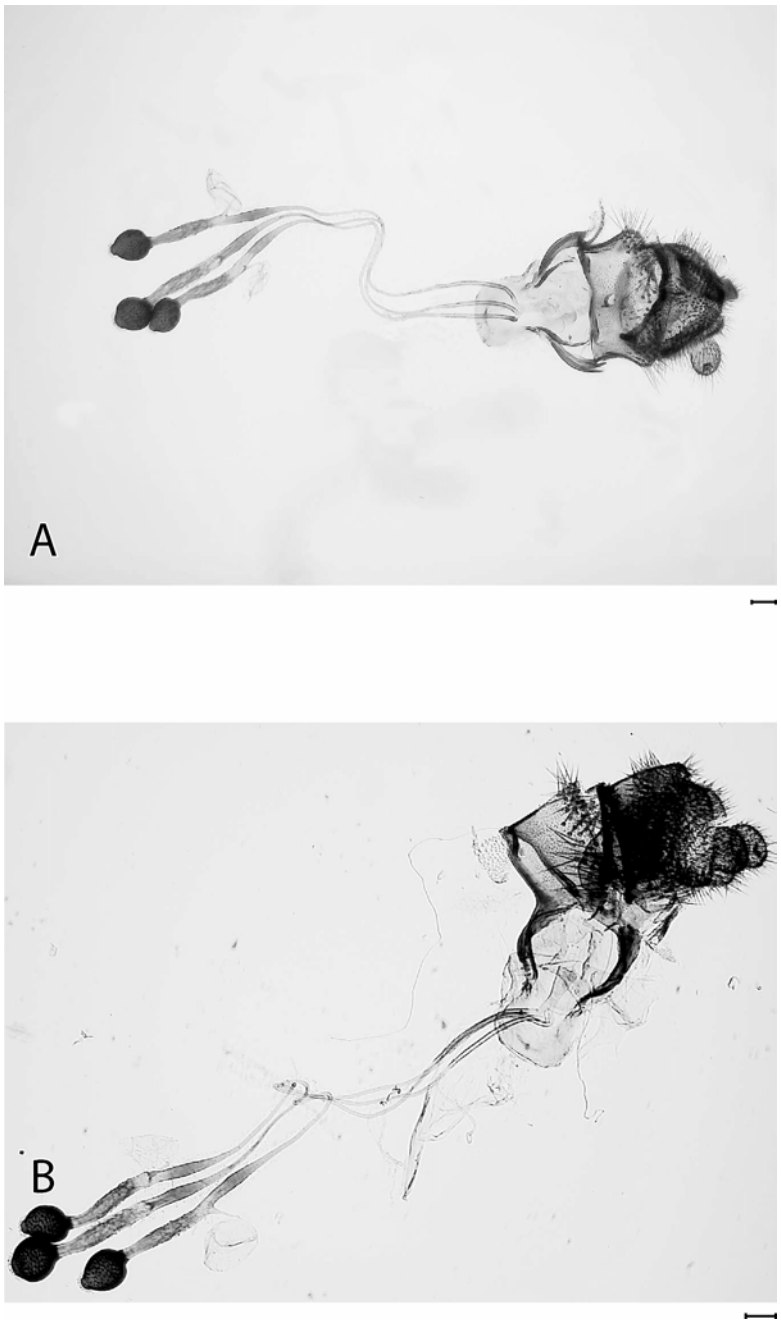


Figure 150. Female genitalia in *Symphoromyia plagens* [USNMENT00025792]. Scale bar = 0.1 mm.

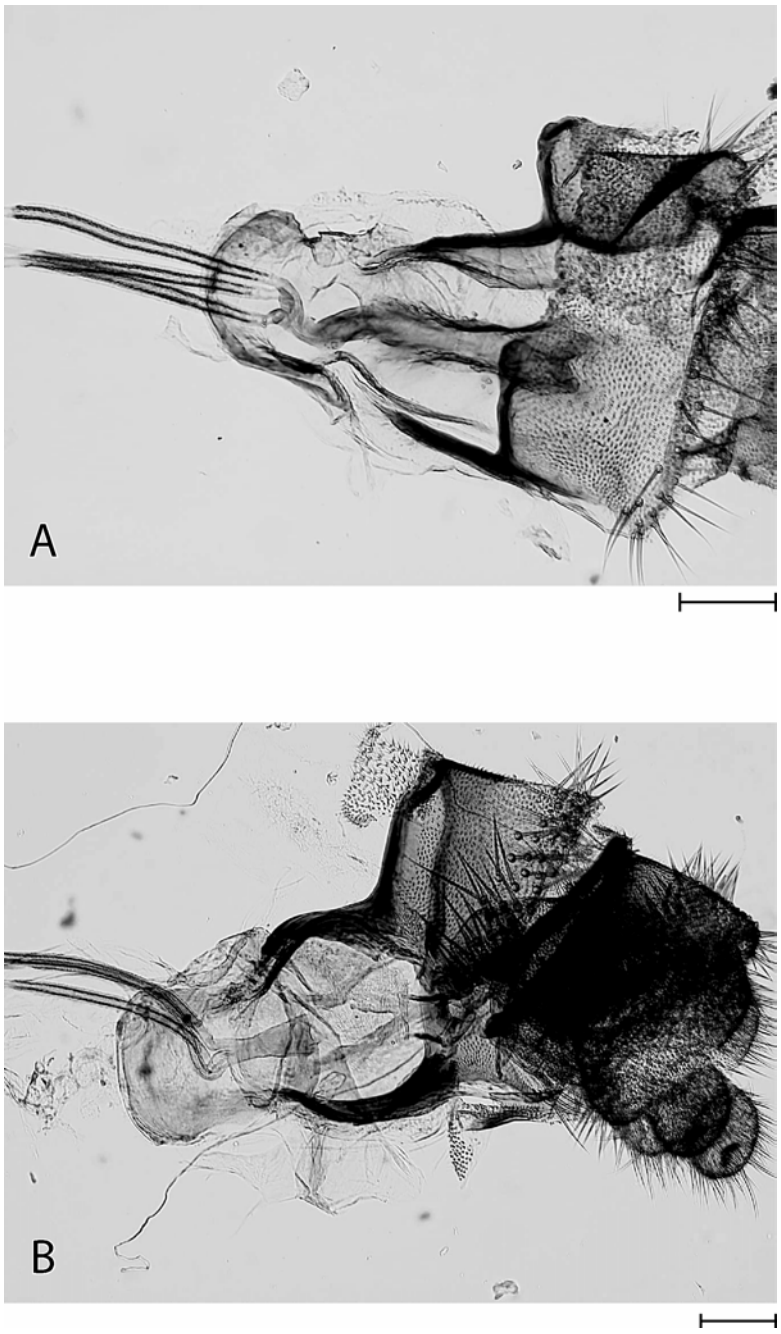


Figure 151. Dissected terminalia in *Symphoromyia* species. (A) *S. hirta* [USNMENT00028587] (B) *S. plagens* [USNMENT00025792]. Scale bar = 0.1 mm.

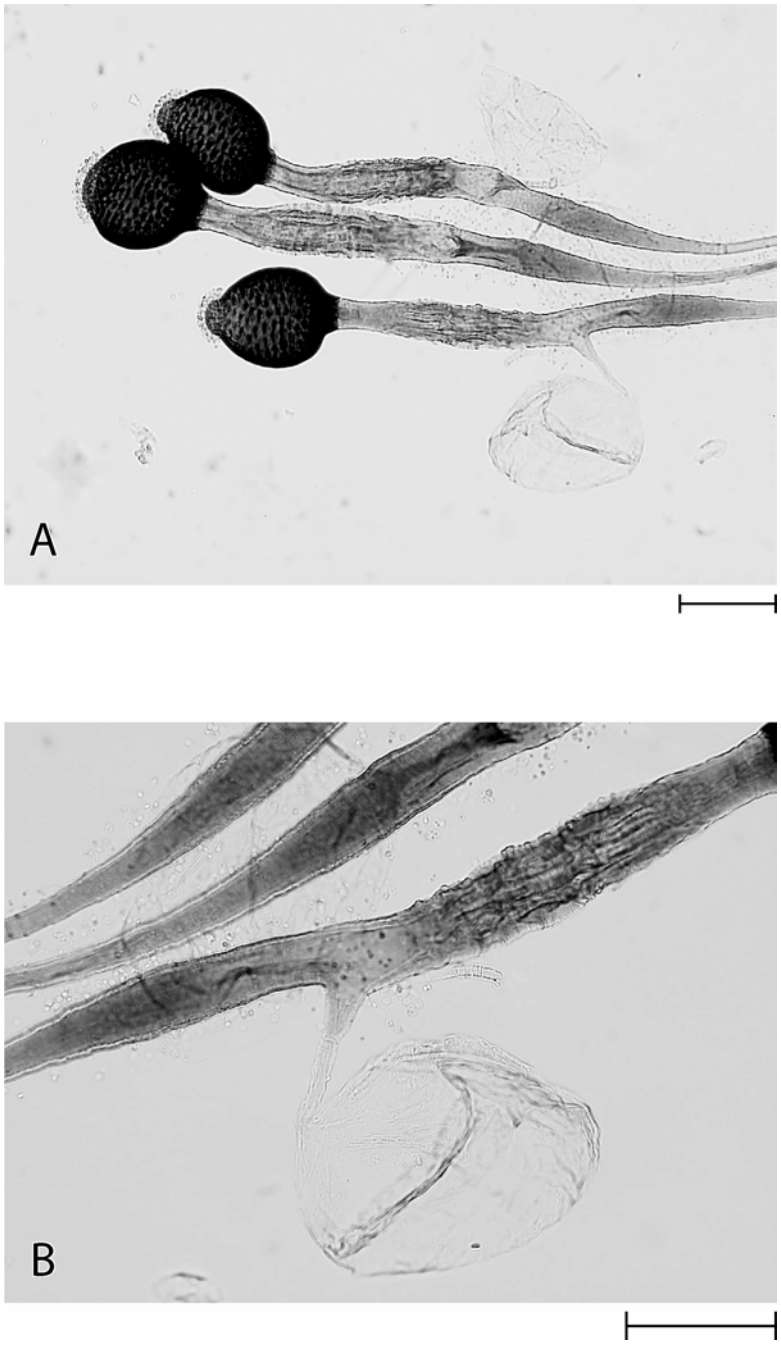


Figure 152. Spermathecae and spermathecal duct accessory glands of *Symphoromyia plagens* [USNMENT00025792]. Scale bar = 0.1 mm.

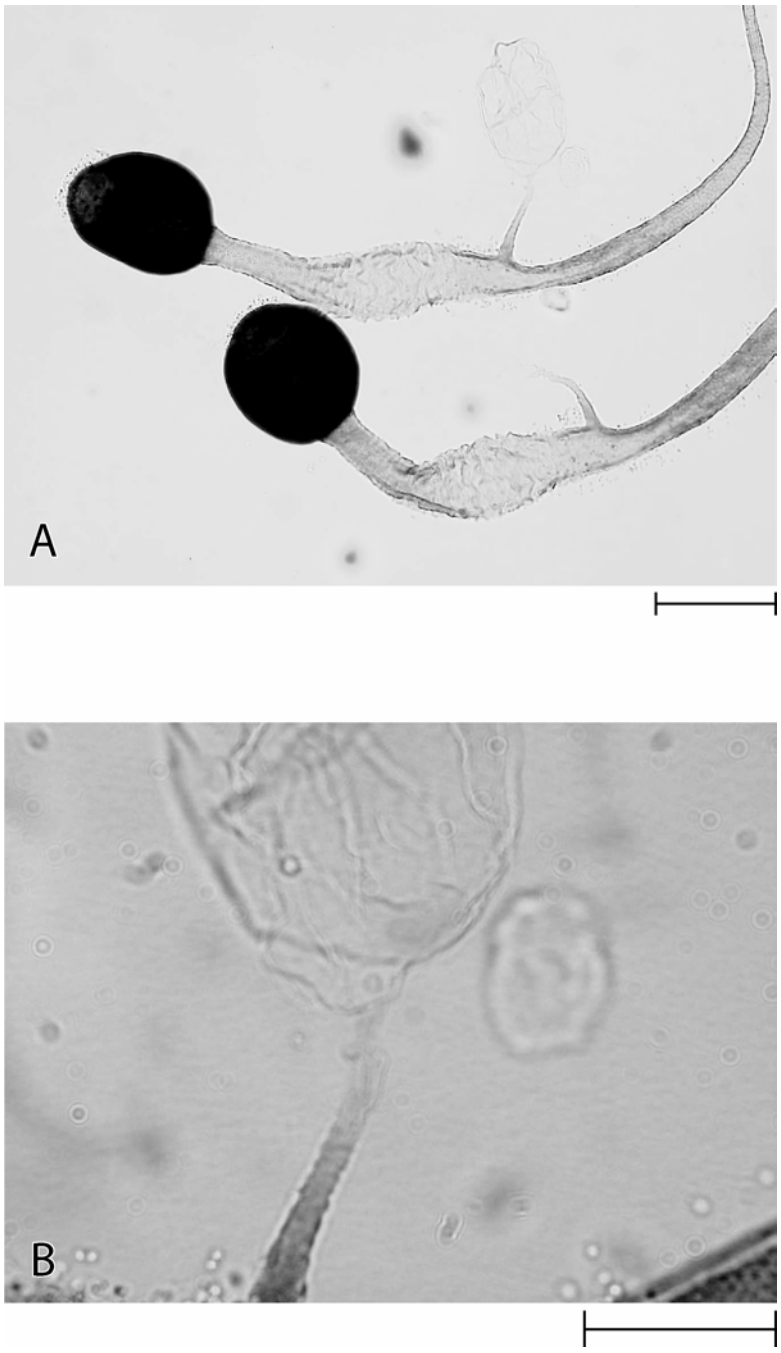


Figure 153. Spermathecae and spermathecal duct accessory glands of *Symphoromyia hirta* [USNMENT00028587]. Scale bar = 0.1 mm.

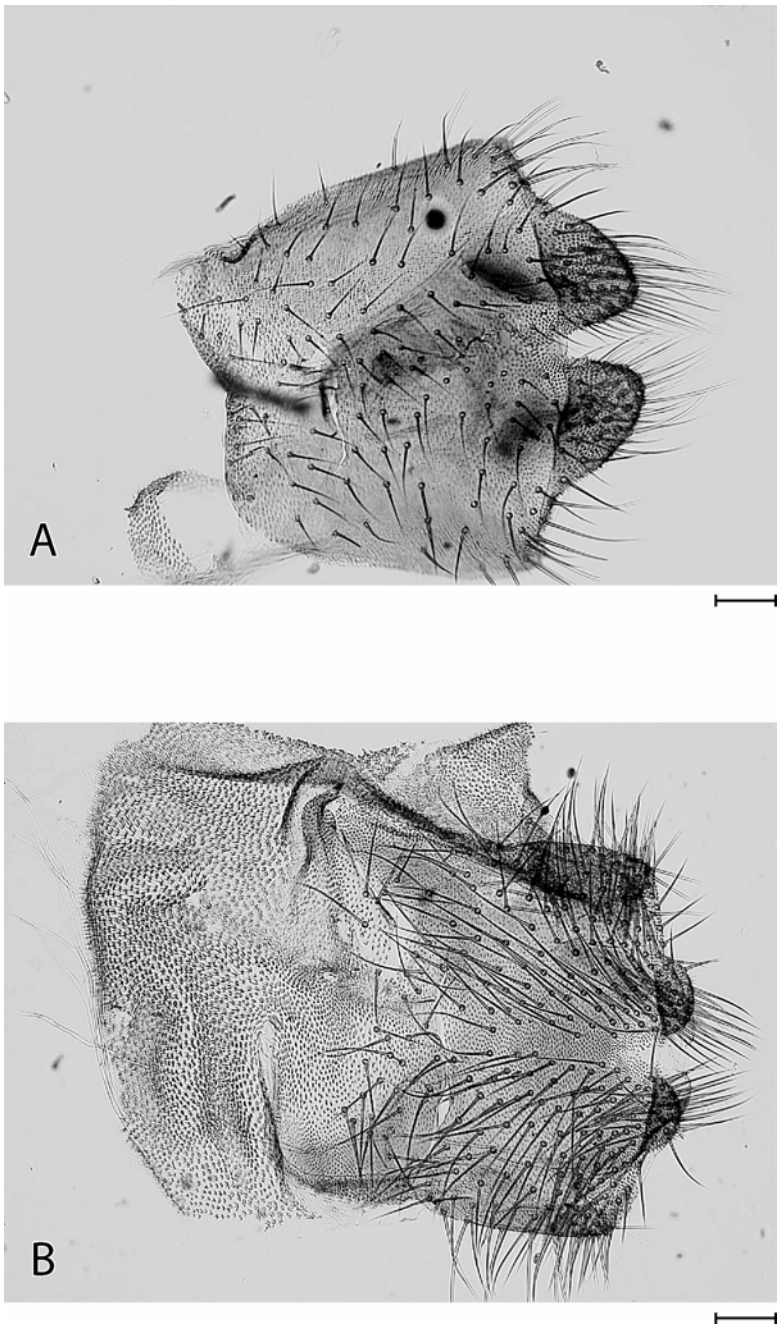


Figure 154. Sternite 8 in species of *Symphoromyia*, dorsal view. (A) *S. hirta* [USNMENT00028587] (B) *S. plagens* [USNMENT00025792]. Scale bar = 0.1 mm.

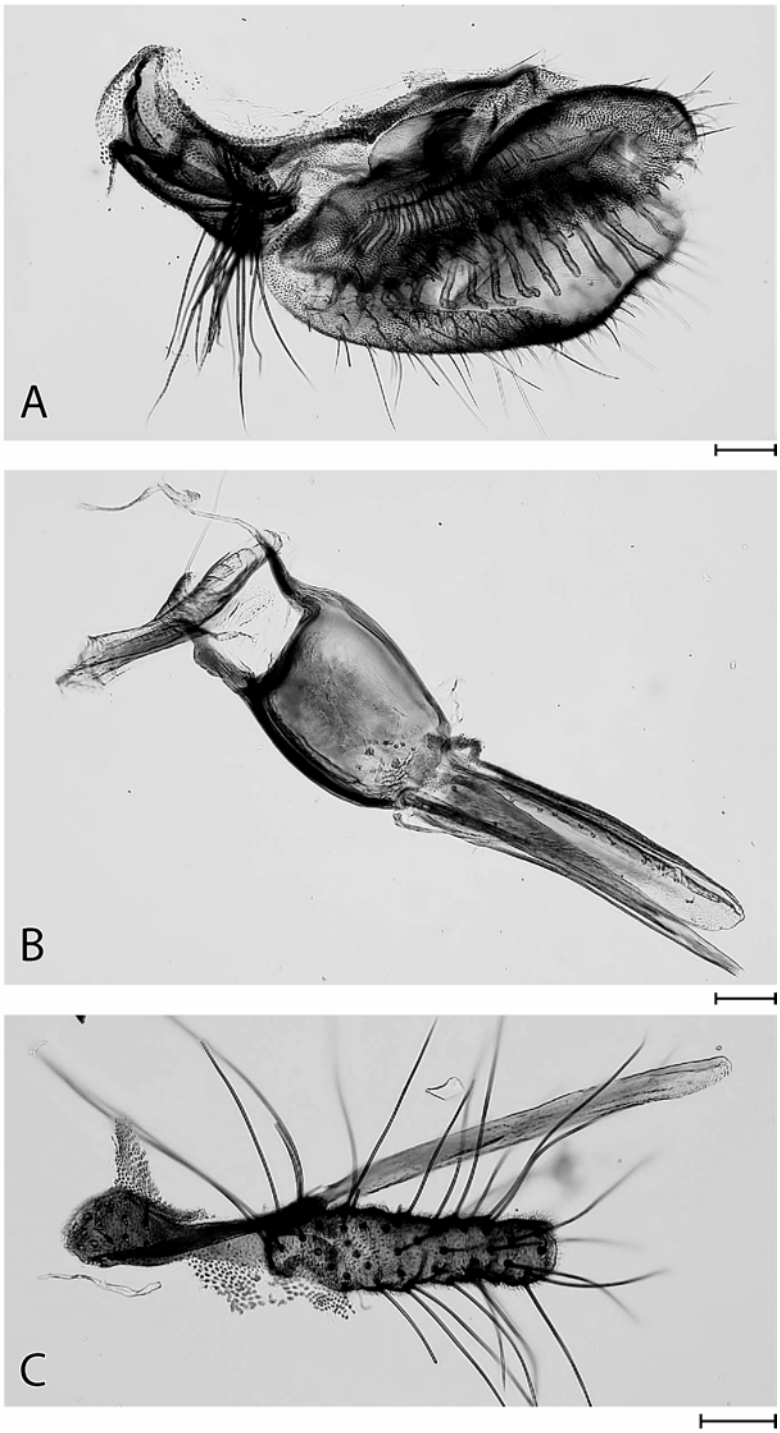


Figure 155. Mouthparts of *Glutops rossi* [USNMENT00025333]. (A) Labellum, lateral view (B) Hypopharynx, posterior view (C) Palps. Scale bar = 0.1 mm.

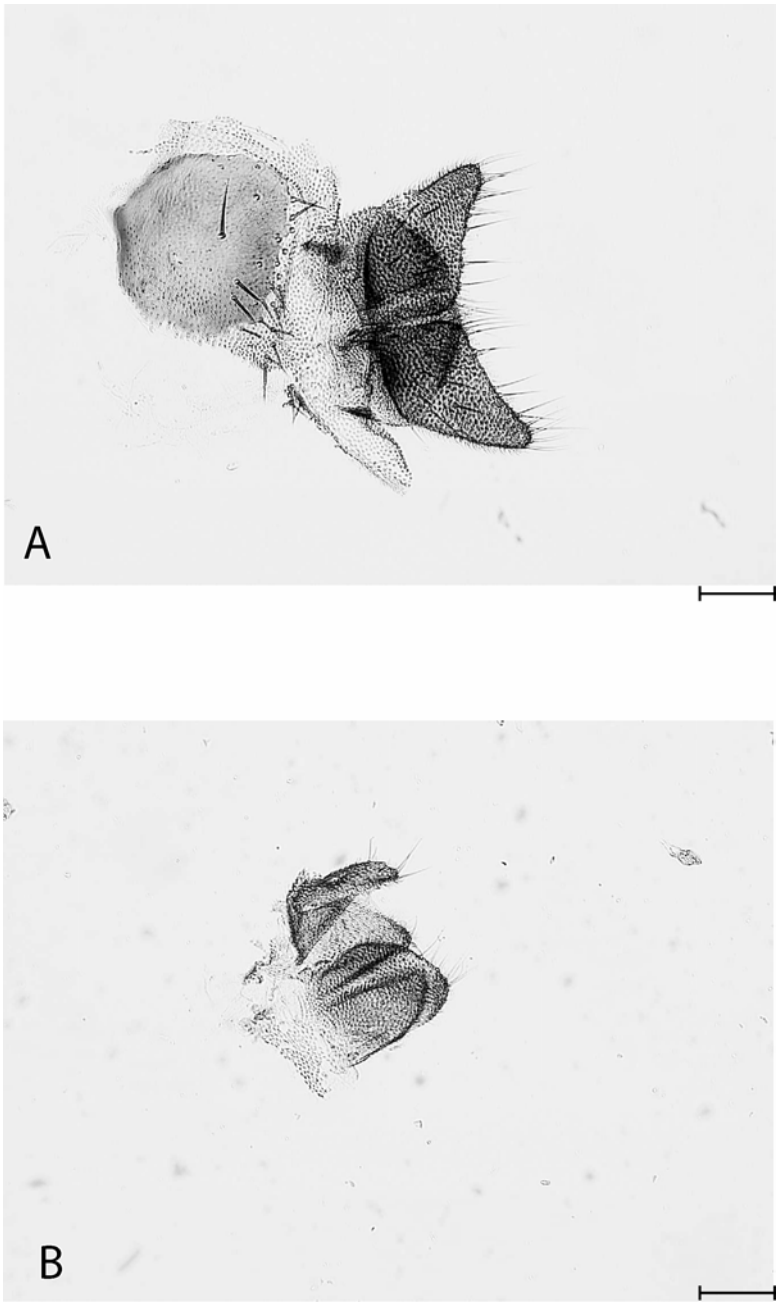


Figure 156. Epandrium in species of *Glutops*. Dorsal view. (A) *G. punctatus* [USNMENT00025327] (B) *G. rossi* [USNMENT00025231] (missing tergite 10). Scale bar = 0.1 mm.

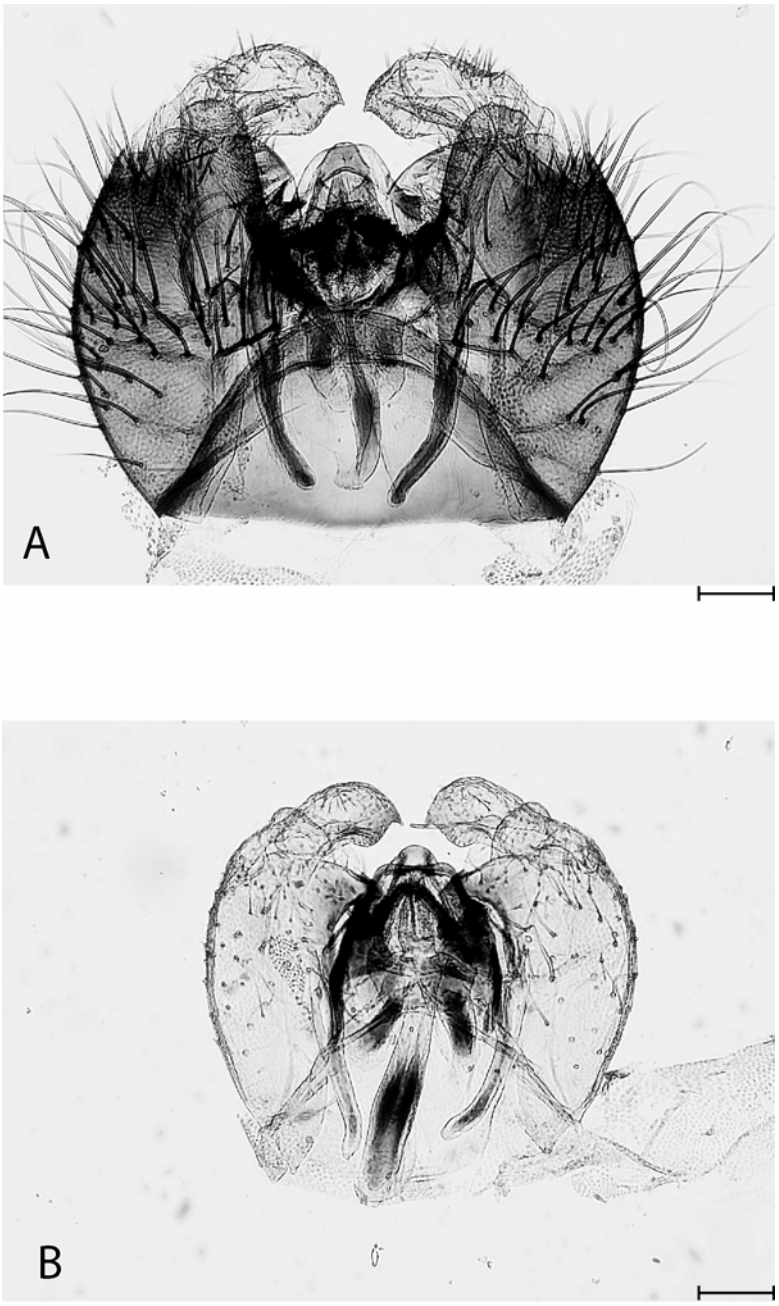


Figure 157. Hypandrium in species of *Glutops*. Dorsal view. (A) *G. punctatus* [USNMENT00025327] (B) *G. rossi* [USNMENT00025231]. Scale bar = 0.1 mm.

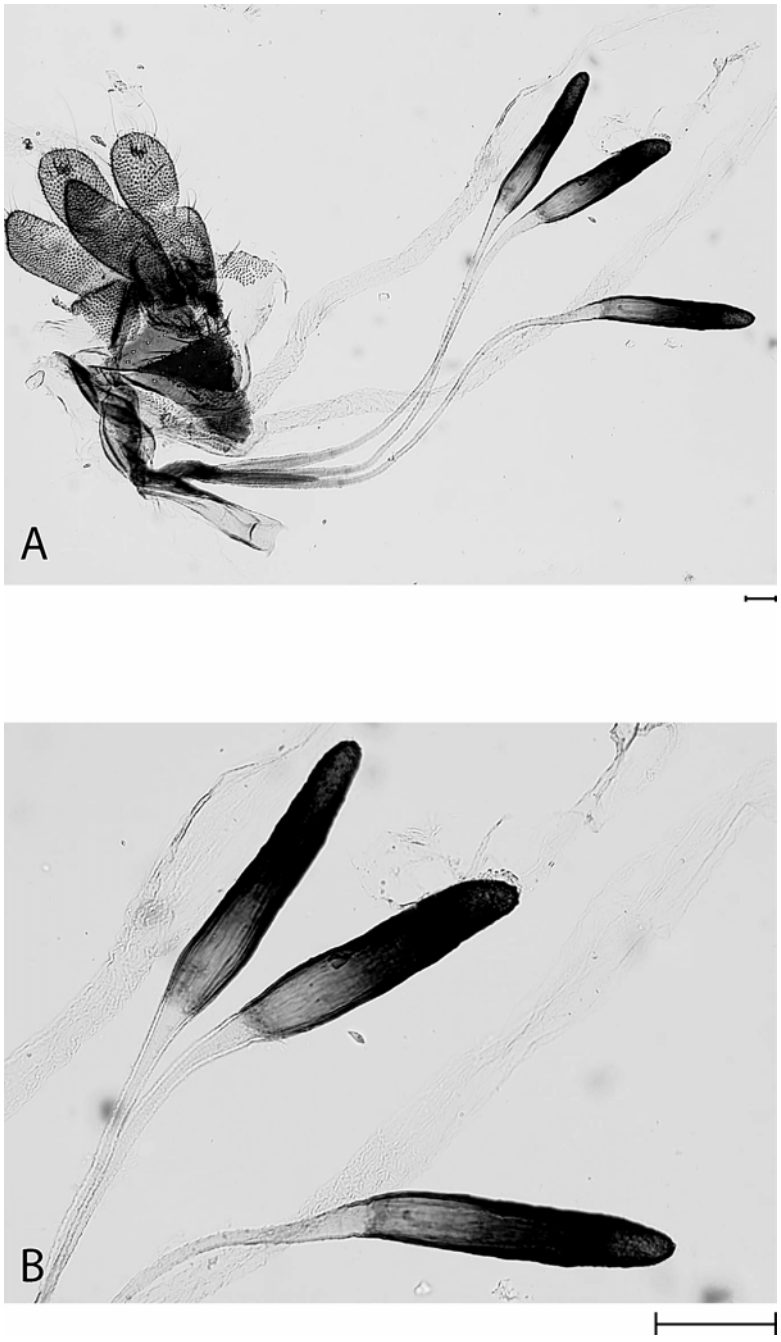


Figure 158. Female genitalia of *Glutops singularis* [USNMENT00025338]. (A) Dissected terminalia (B) Spermathecae. Scale bar = 0.1 mm.

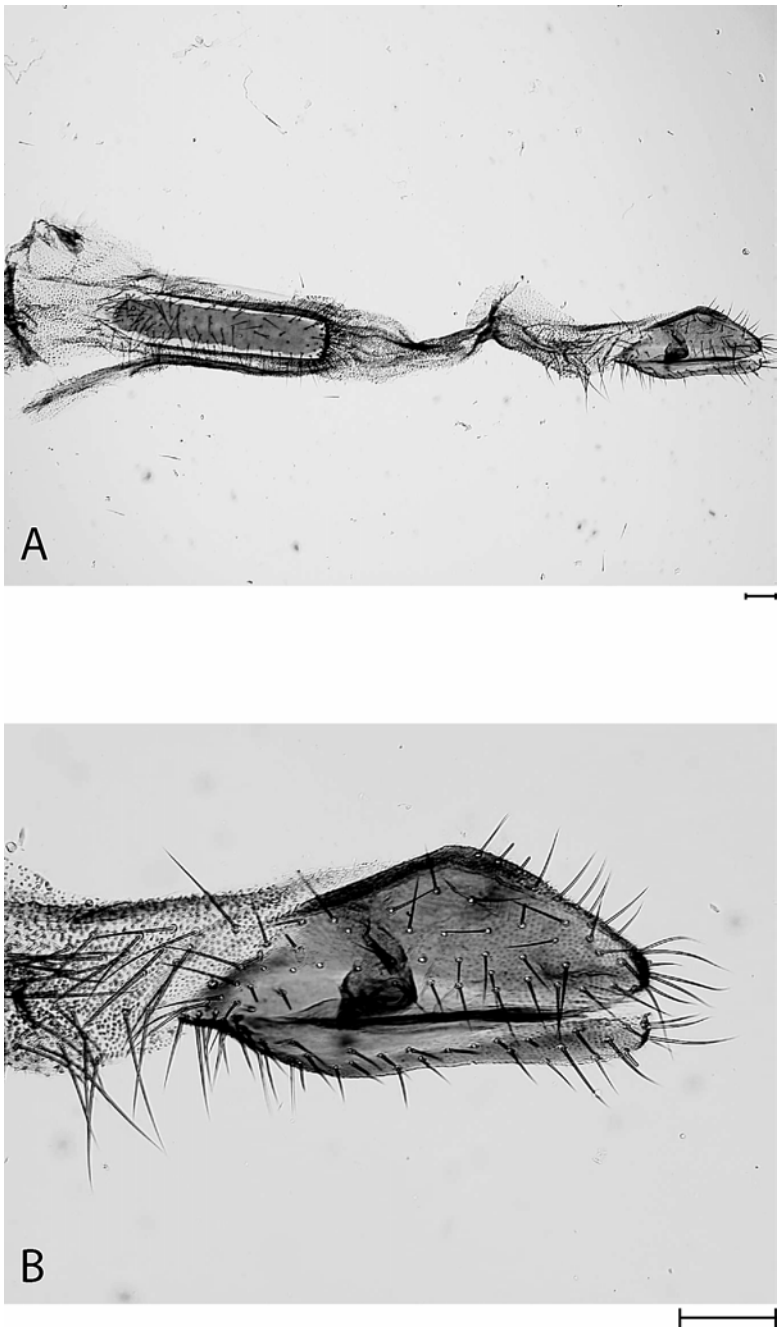


Figure 159. (A) Female sternites 7 and 8, showing long intersegmental region of *Glutops singularis* [USNMENT00025338] (B) Detail of sternite 8, lateral view (same specimen). Scale bar = 0.1 mm.

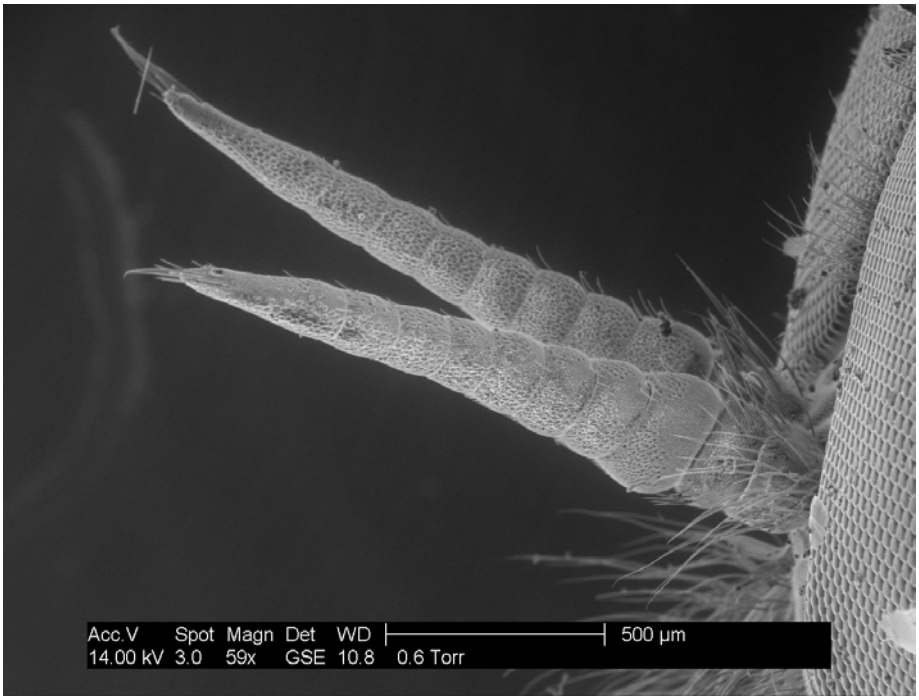


Figure 160. SEM image of antenna of *Pelecorhynchus fusconiger*.

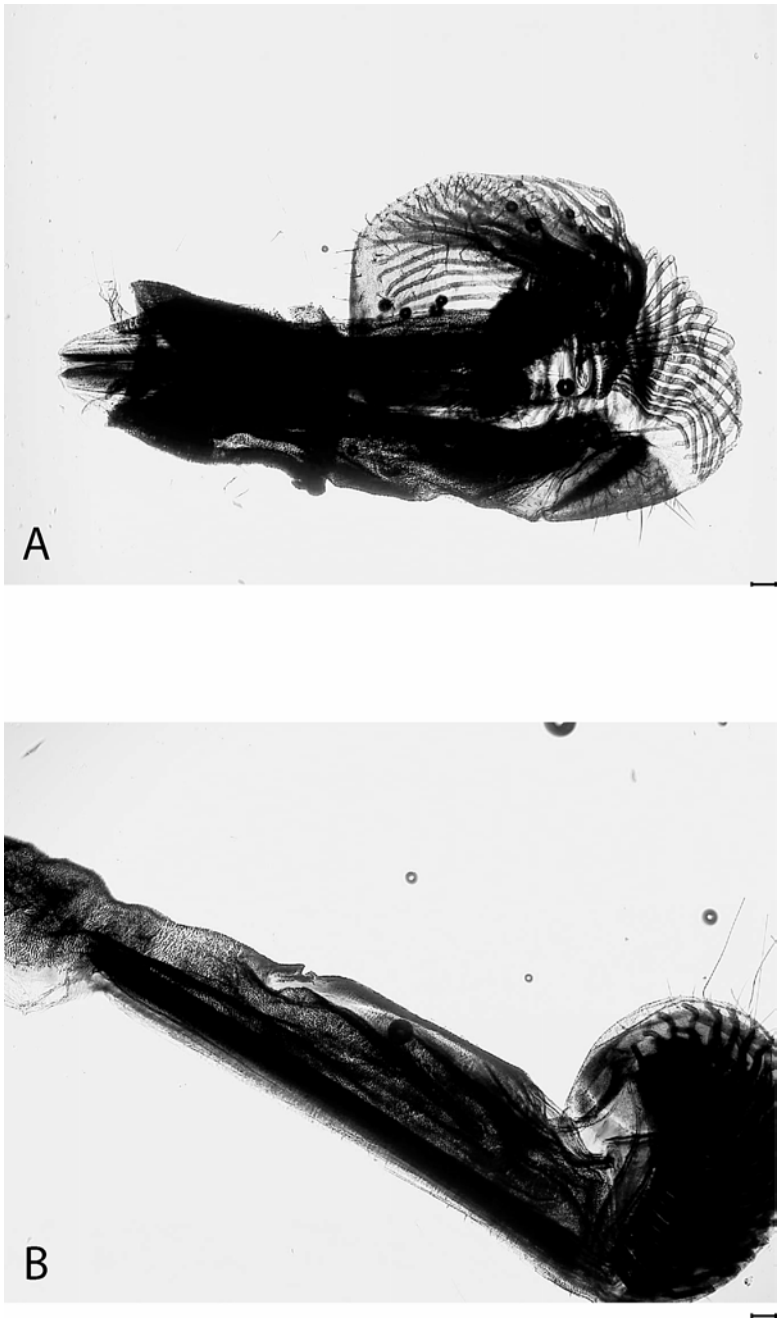


Figure 161. Labellum in species of *Pelecorhynchus*. (A) *P. fusconiger* [USNMENT00025360] (B) *P. personatus* [USNMENT00025385]. Scale bar = 0.1 mm.

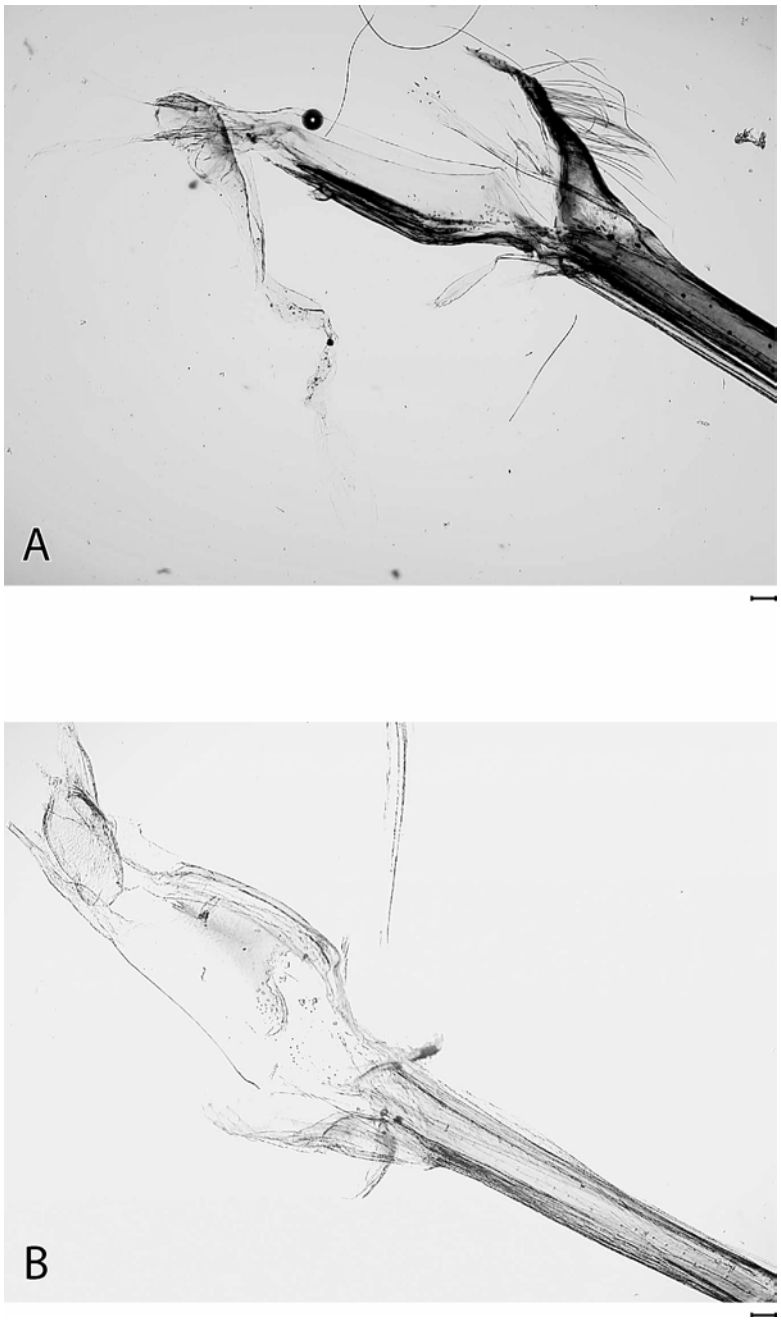


Figure 162. Internal mouthparts in species of *Pelecorhynchus*, lateral view. (A) *P. fusconiger* [USNMENT00025360] (B) *P. personatus* [USNMENT00025385]. Scale bar = 0.1 mm.

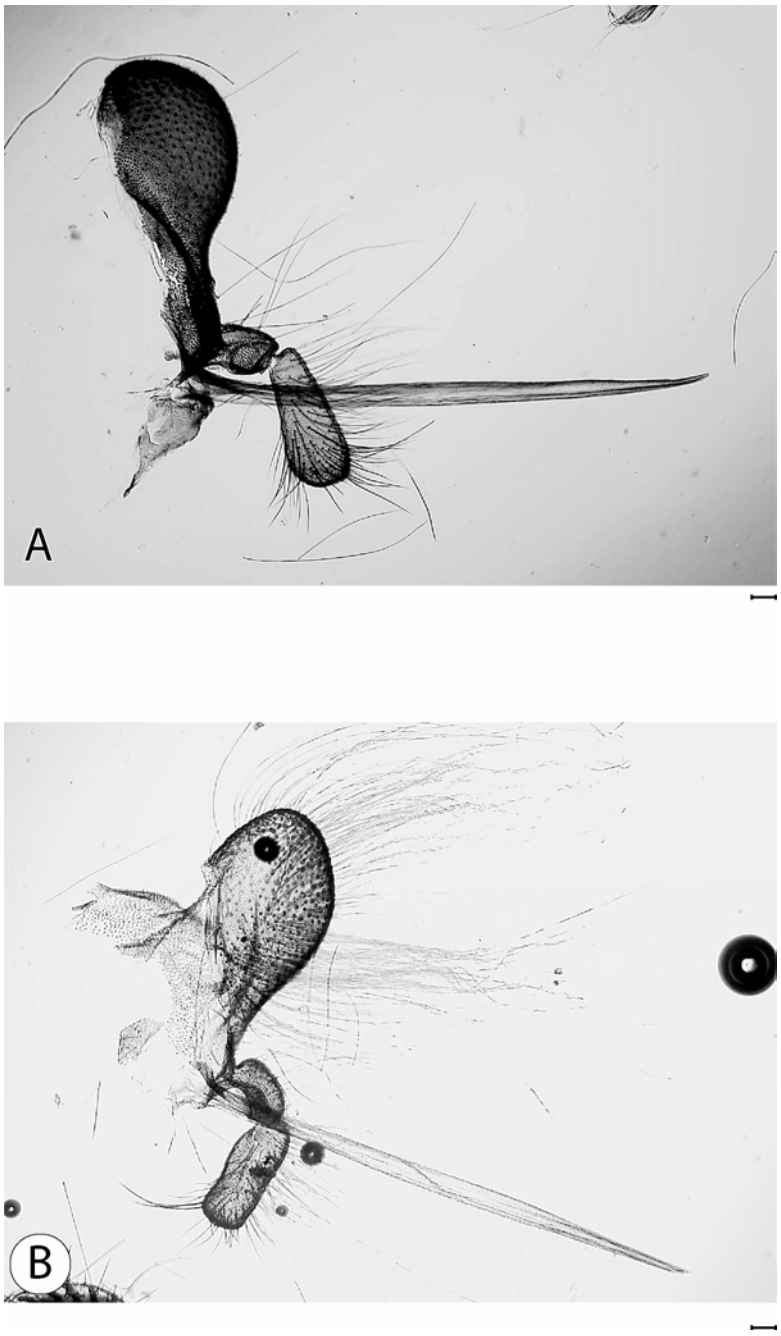


Figure 163. Palps and associated structures in species of *Pelecorhynchus*. (A) *P. fusconiger* [USNMENT00025360] (B) *P. personatus* [USNMENT00025385]. Scale bar = 0.1 mm.

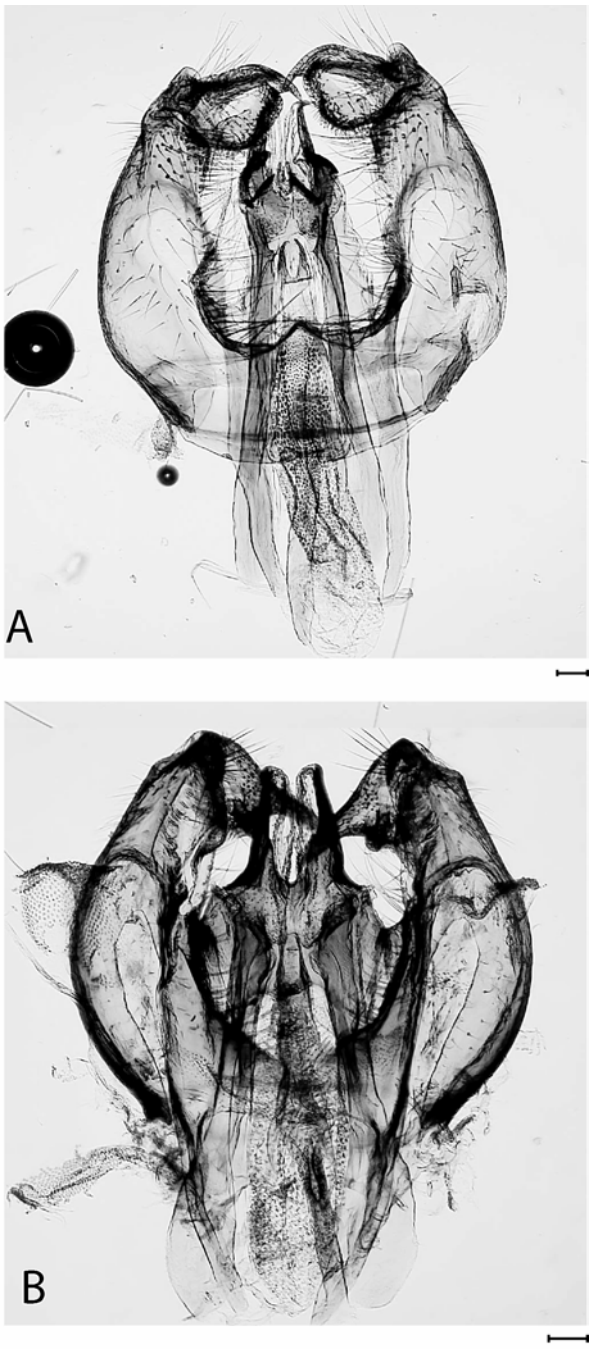


Figure 164. Hypandrium in species of *Pelecorhynchus*. (A) *P. fusconiger*, ventral view [USNMENT00025897] (B) *P. personatus*, dorsal view [USNMENT00025896]. Scale bar = 0.1 mm.

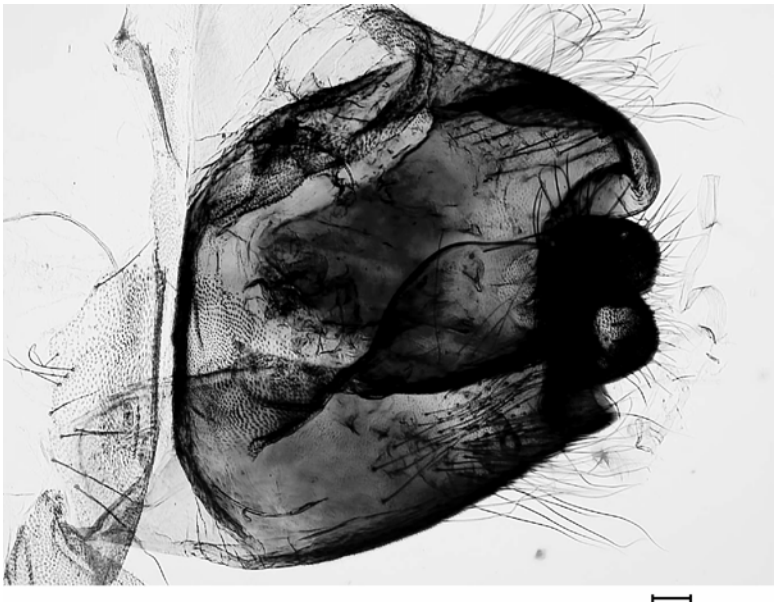


Figure 165. Epandrium in *Pelecorhynchus personatus* [USNMENT00025896]. Dorsal view. Scale bar = 0.1 mm.

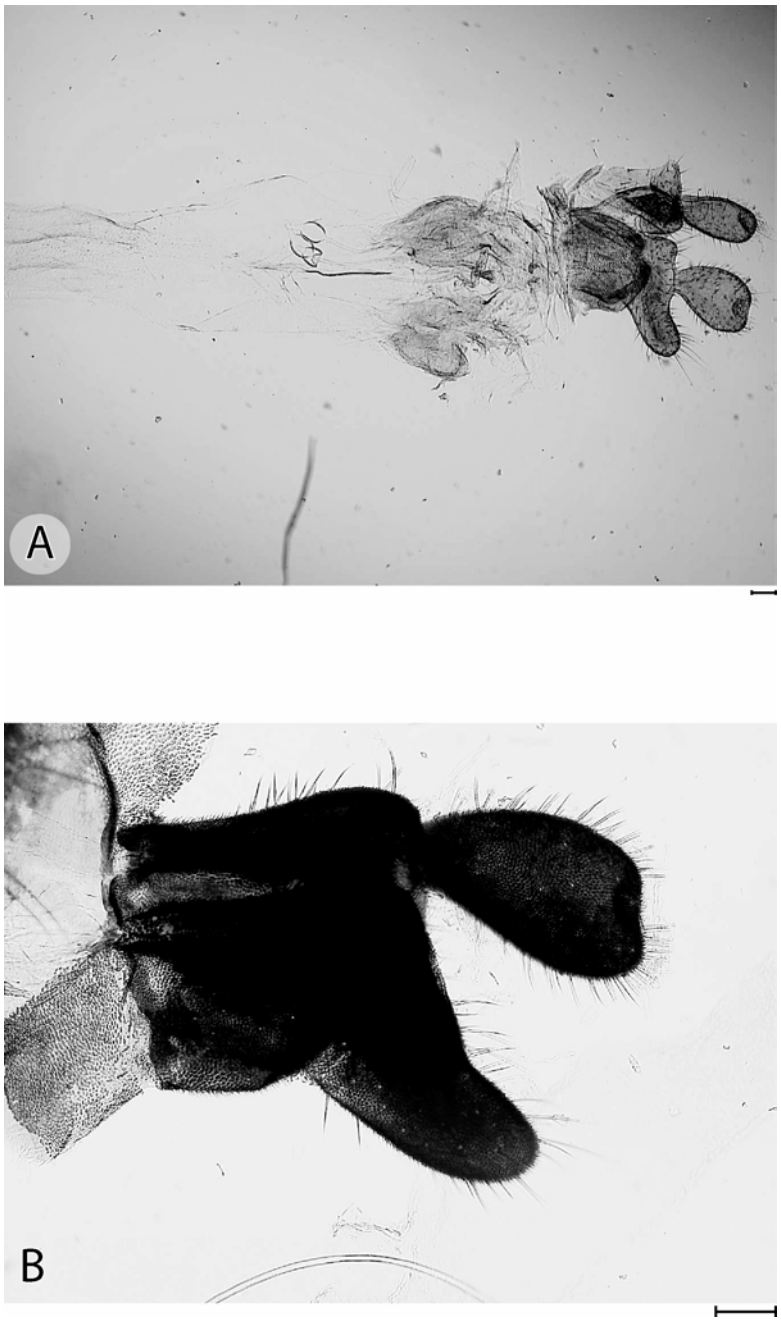


Figure 166. Female terminalia in species of *Pelecorhynchus elegans* [USNMENT00025881], lateral view. (A) Partially dissected (B) Detail of cercus. Scale bar = 0.1 mm.

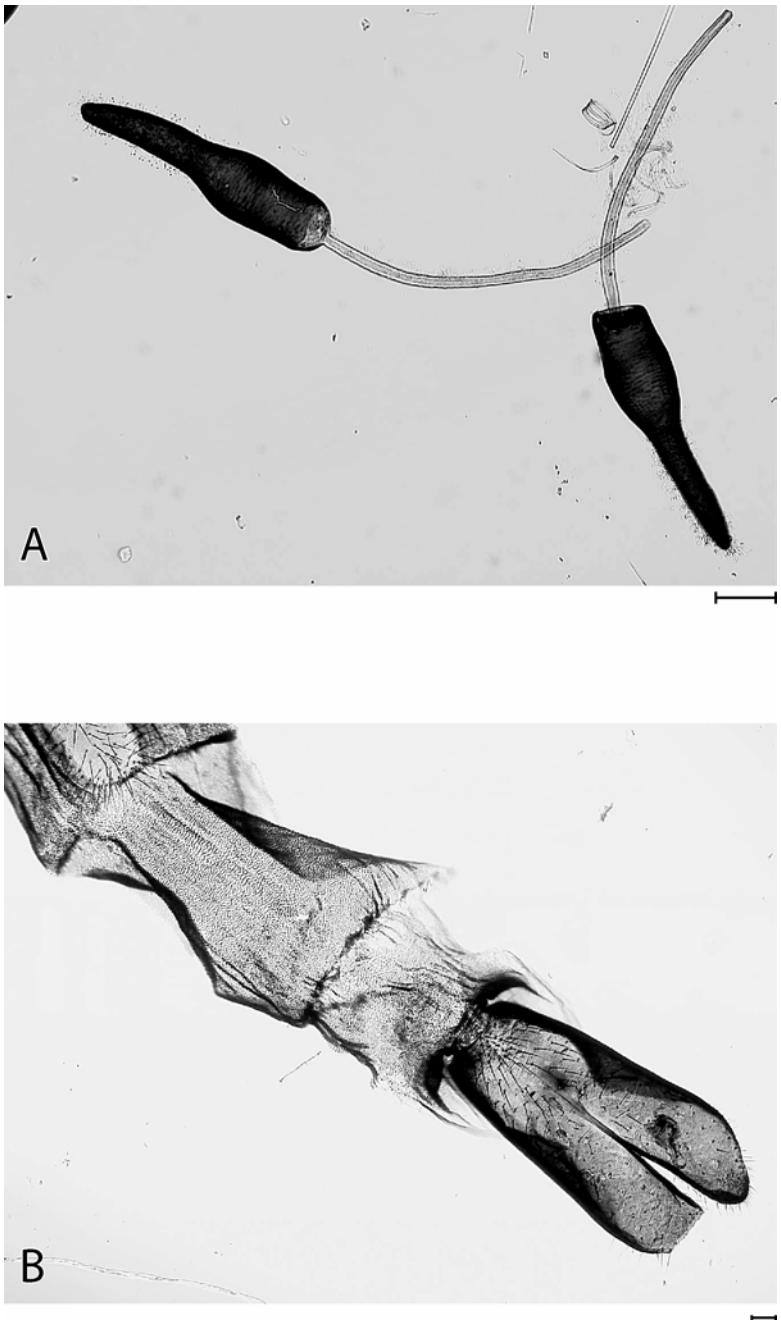


Figure 167. (A) Spermatheca of *Pelecorhynchus fusconiger* [USNMENT00025883] (B) Sternite 8, showing intersegmental membrane between sternites 7 and 8 in *Pelecorhynchus personatus* [USNMENT00025882]. Scale bar = 0.1 mm.

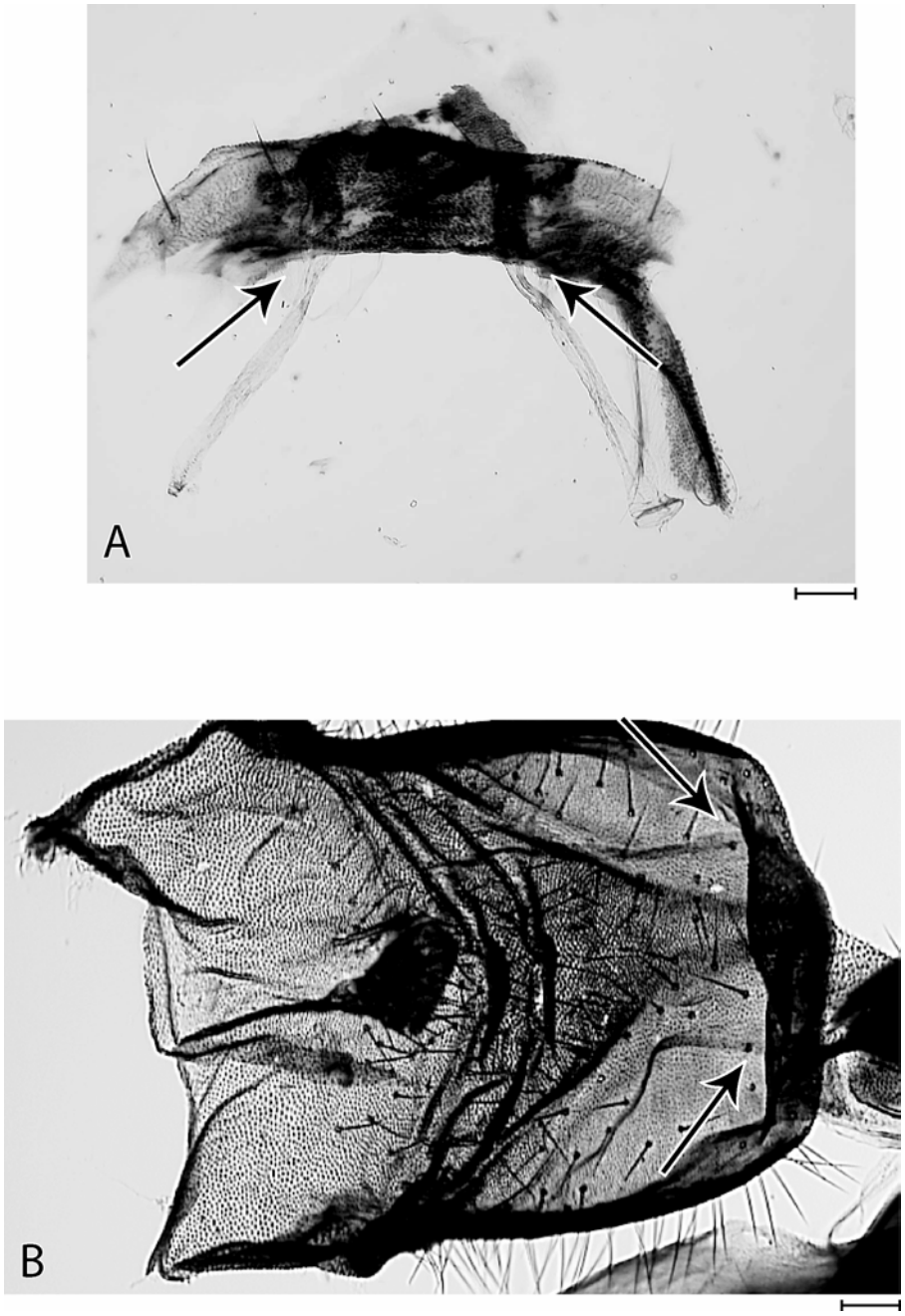


Figure 168. Tergite 8 of female *Pelecorhynchus*, showing ducts. (A) *P. elegans* [USNMENT00025880], anterior view (B) *P. personatus* [USNMENT00025882], ventral view. Scale bar = 0.1 mm.

Figure 169. Left lateral view of *Pseudoerinna jonesi* [USNMENT00025319]. Scale bar = 0.5 mm.

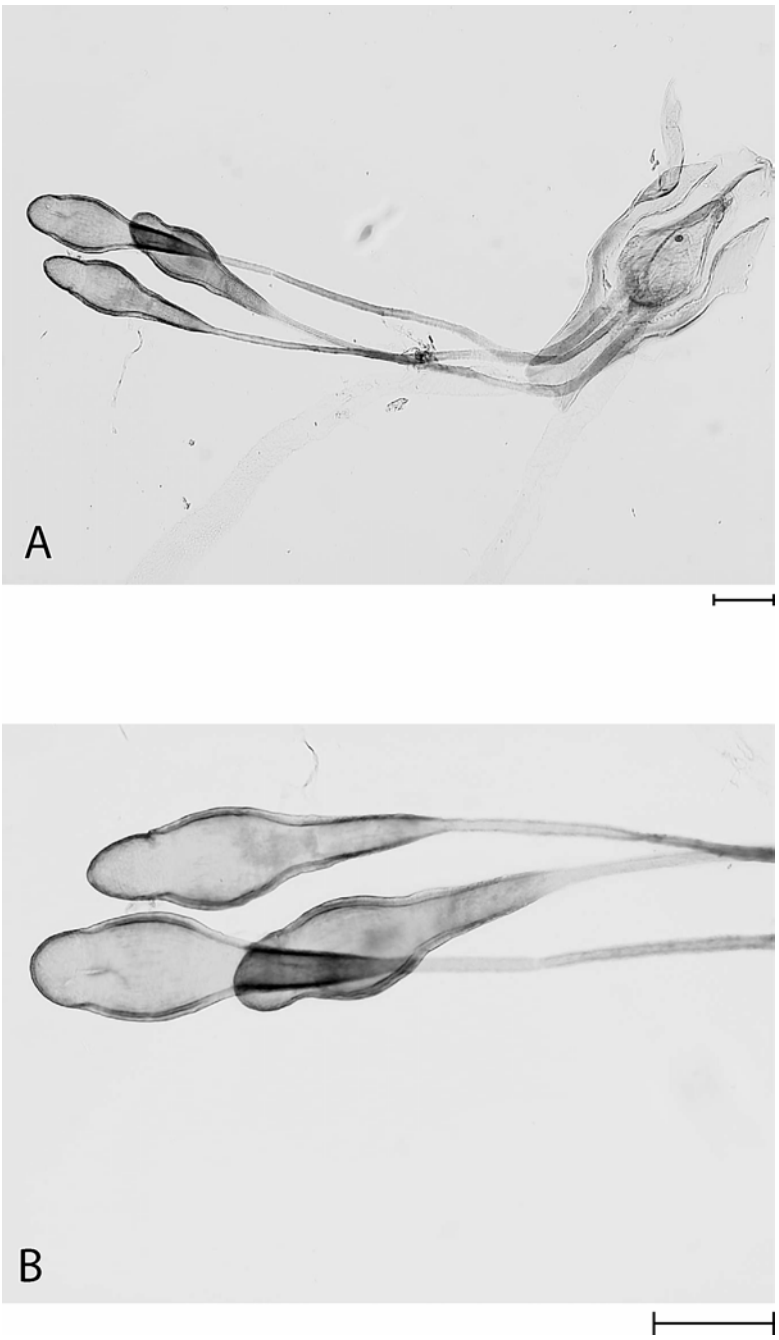


Figure 170. Internal structures of female genitalia of *Pseudoerinna jonesi* [USNMENT00025319]. (A) Sternite 9 and associated structures (B) Spermatheca. Scale bar = 0.1 mm.

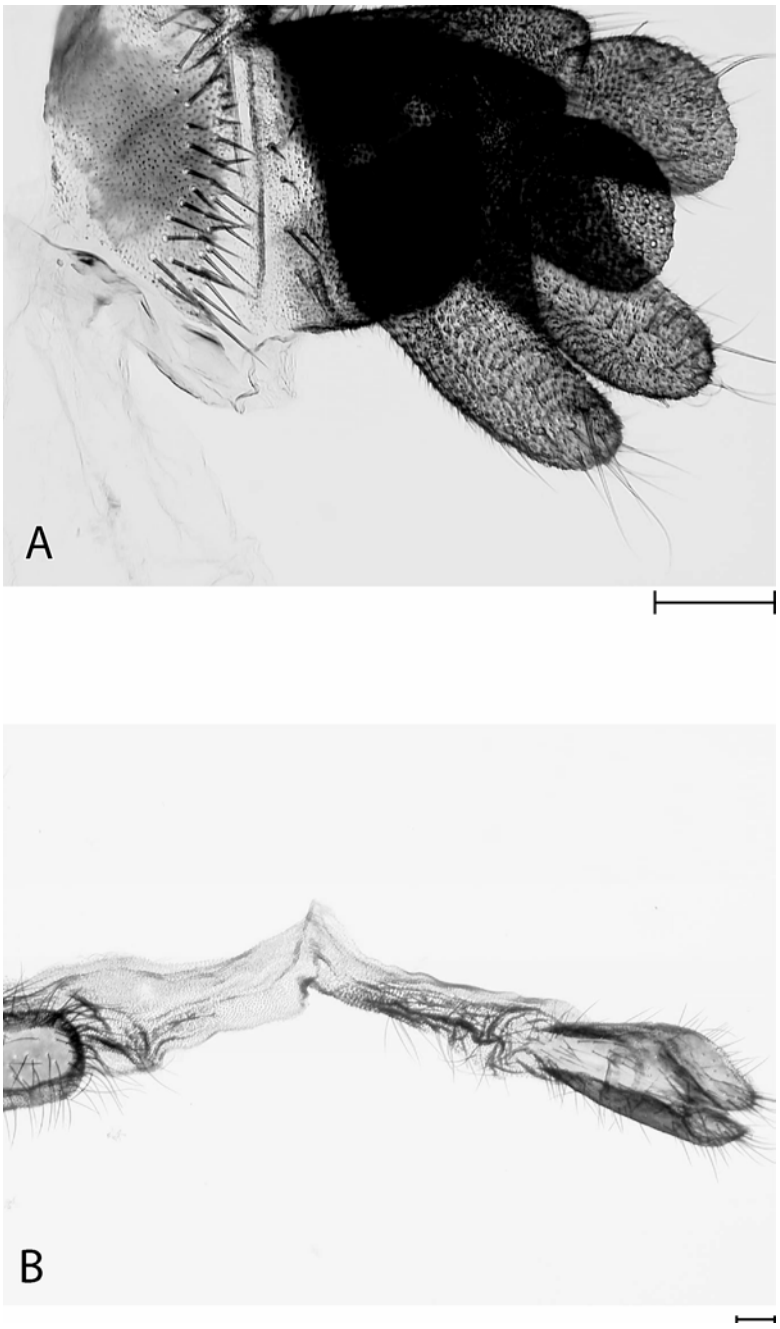


Figure 171. External structures of female genitalia of *Pseudoerinna jonesi* [USNMENT00025319]. (A) Cerci (B) Sternite 8, with proceeding intersegmental membrane. Scale bar = 0.1 mm.

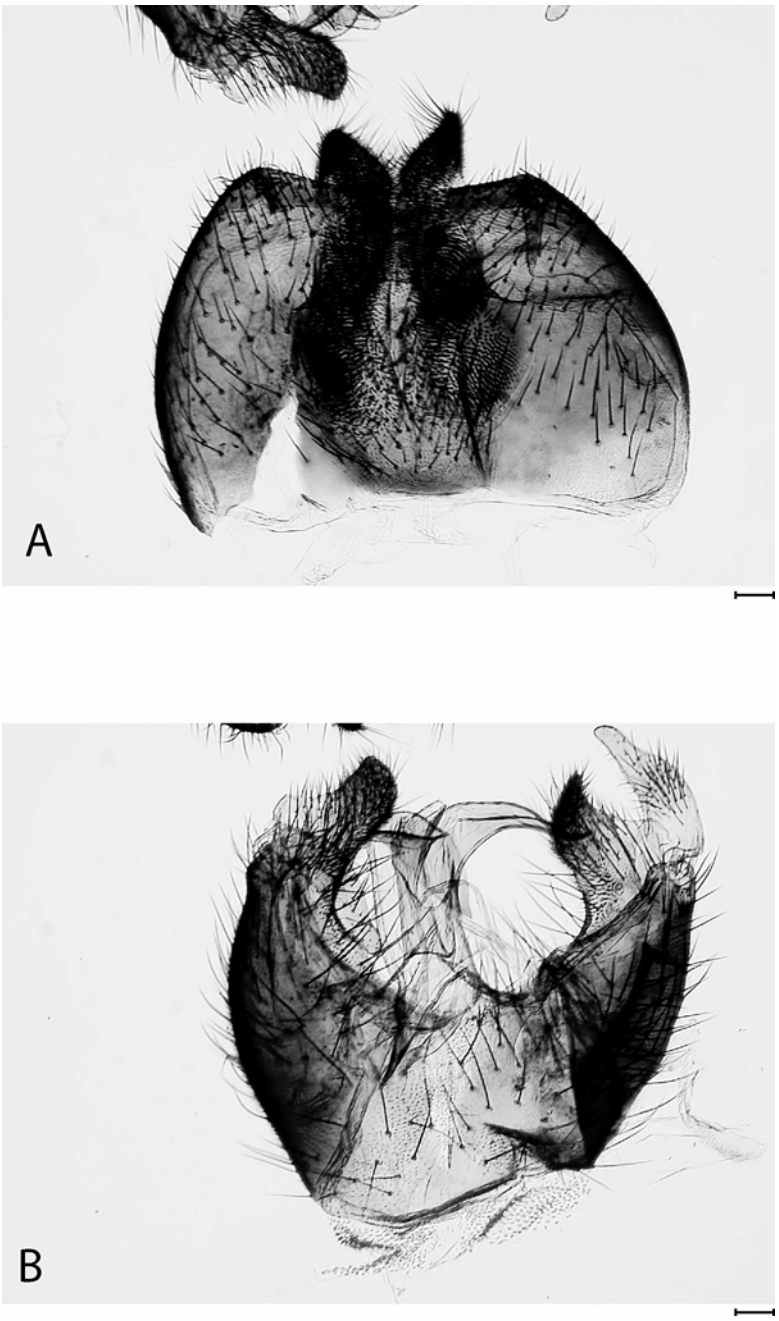


Figure 172. *Lampromyia* sp. [USNMENT00025955]. (A) Epandrium, ventral view (B) Hypandrium, dorsal view. Scale bar = 0.1 mm.

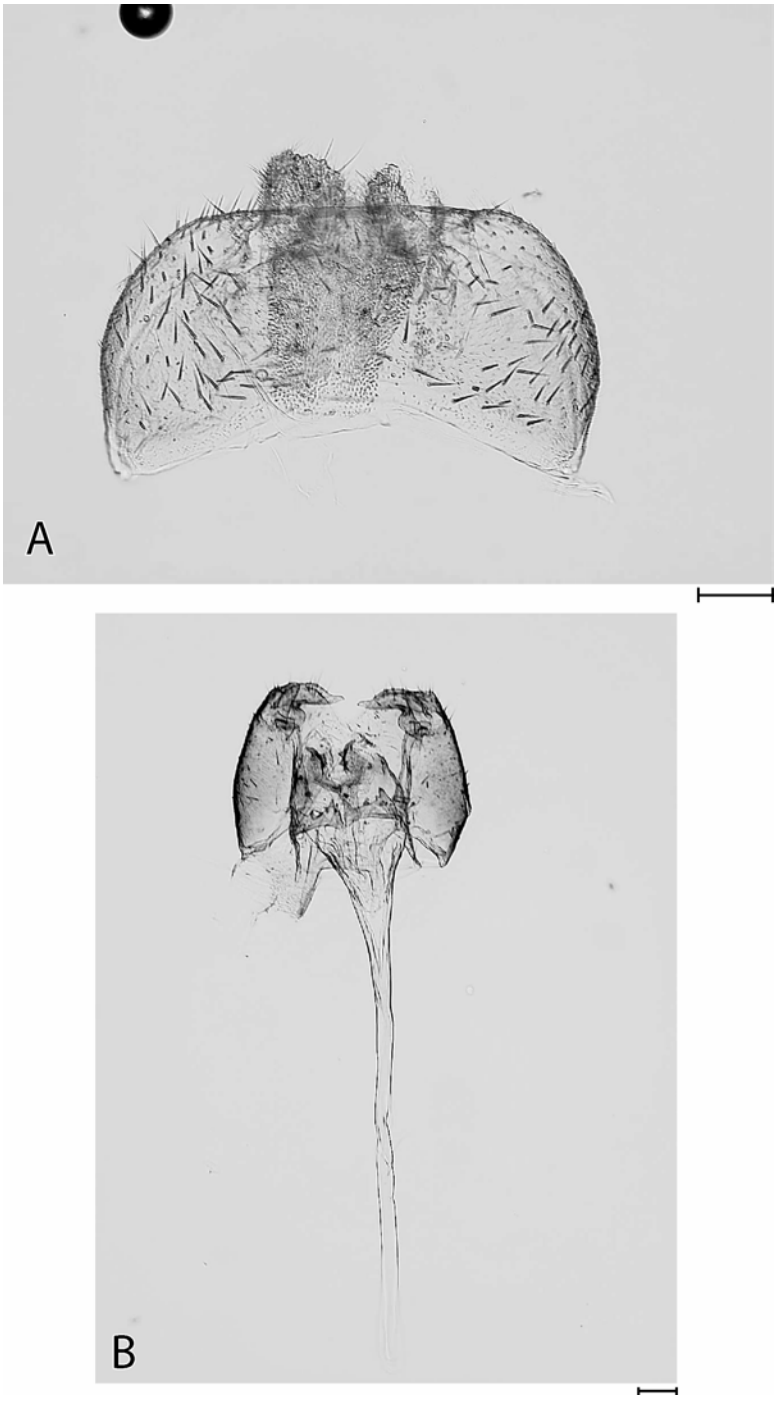


Figure 173. Male genitalia of *Vermileo vermileo* [USNMENT00025956]. (A) Epandrium, ventral view (B) Hypandrium, dorsal view. Scale bar = 0.1 mm.

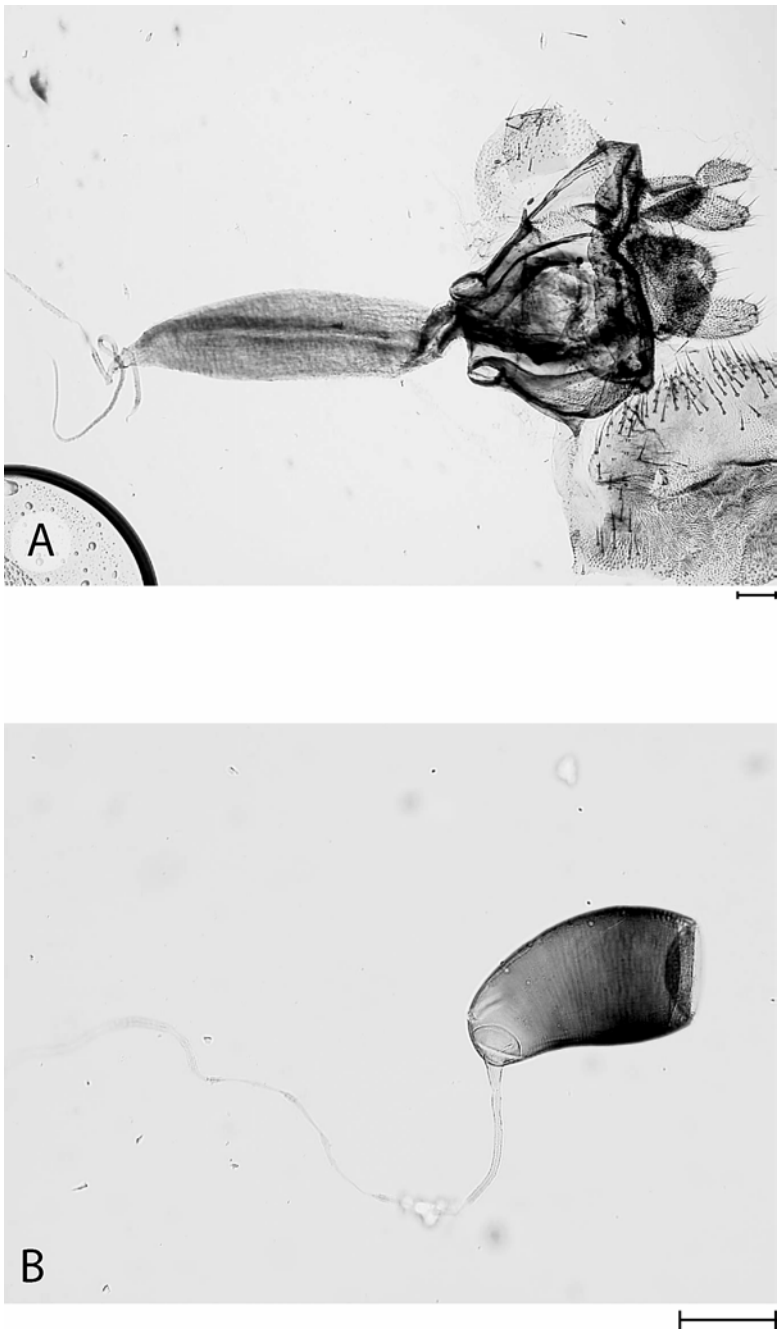


Figure 174. Structures of the female terminalia of *Vermileo vermileo* [USNMENT00025793]. (A) Partially dissected terminalia, showing highly autapomorphic common spermathecal duct (B) Spermatheca. Scale bar = 0.1 mm.

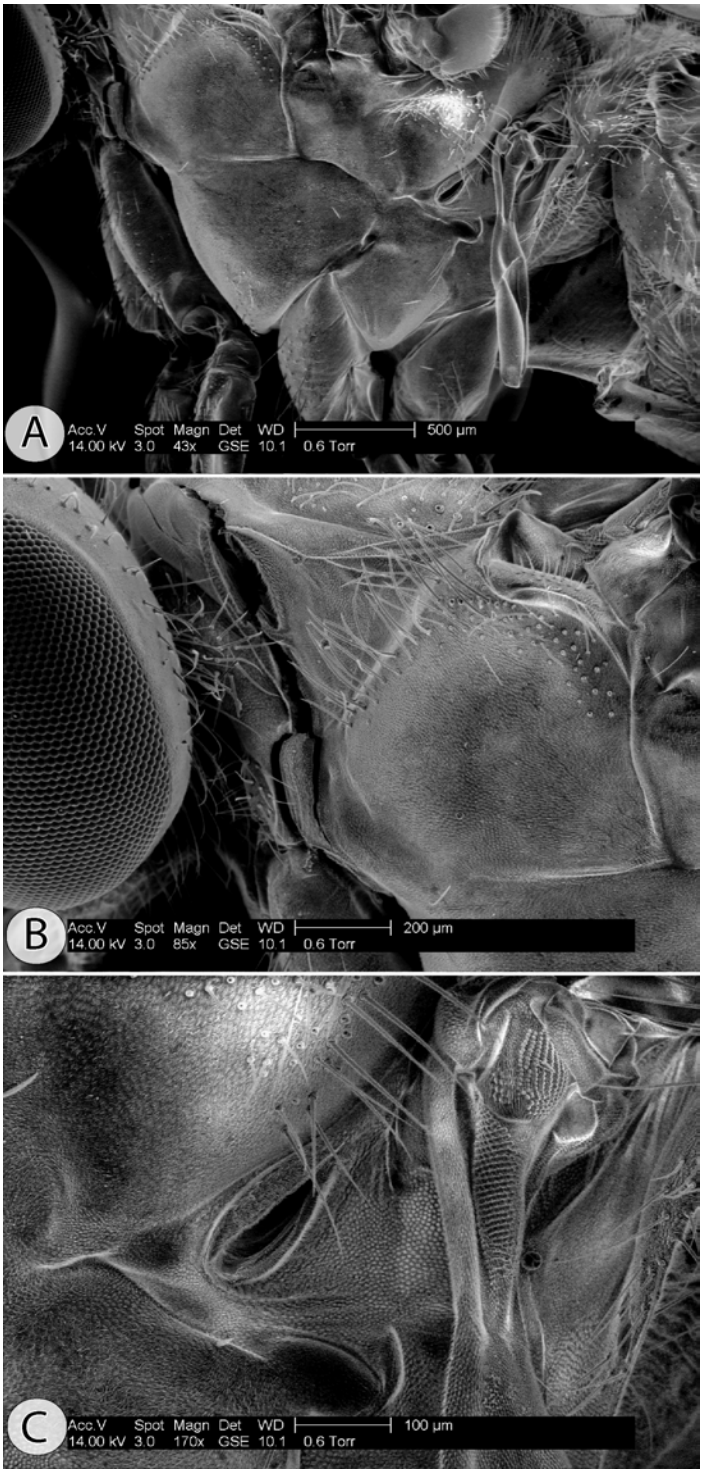


Figure 175. Thoracic structure of *Chrysopilus quadratus*, lateral view. (A) Entire thorax (B) Detail showing reduced proepimeron (D) Detail of postspiracle and halter.

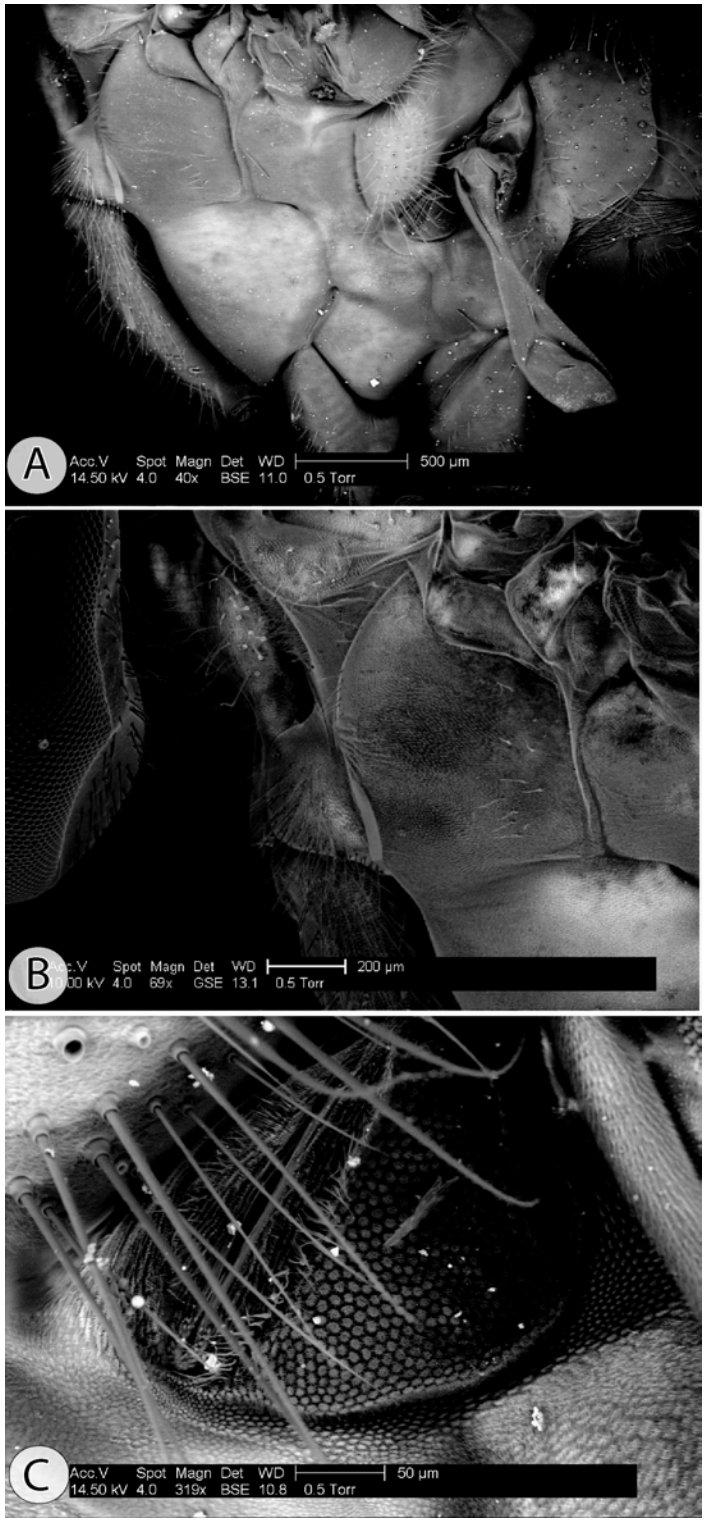


Figure 176. Thoracic structure of *Rhagio mystaceus*, lateral view. (A) Entire thorax (B) Detail showing anepisternum and setose proepimeron (D) Detail of postspiracle and halter.

Figure 177. Postspiracular scale of *Pelecorhynchus fusconiger*.

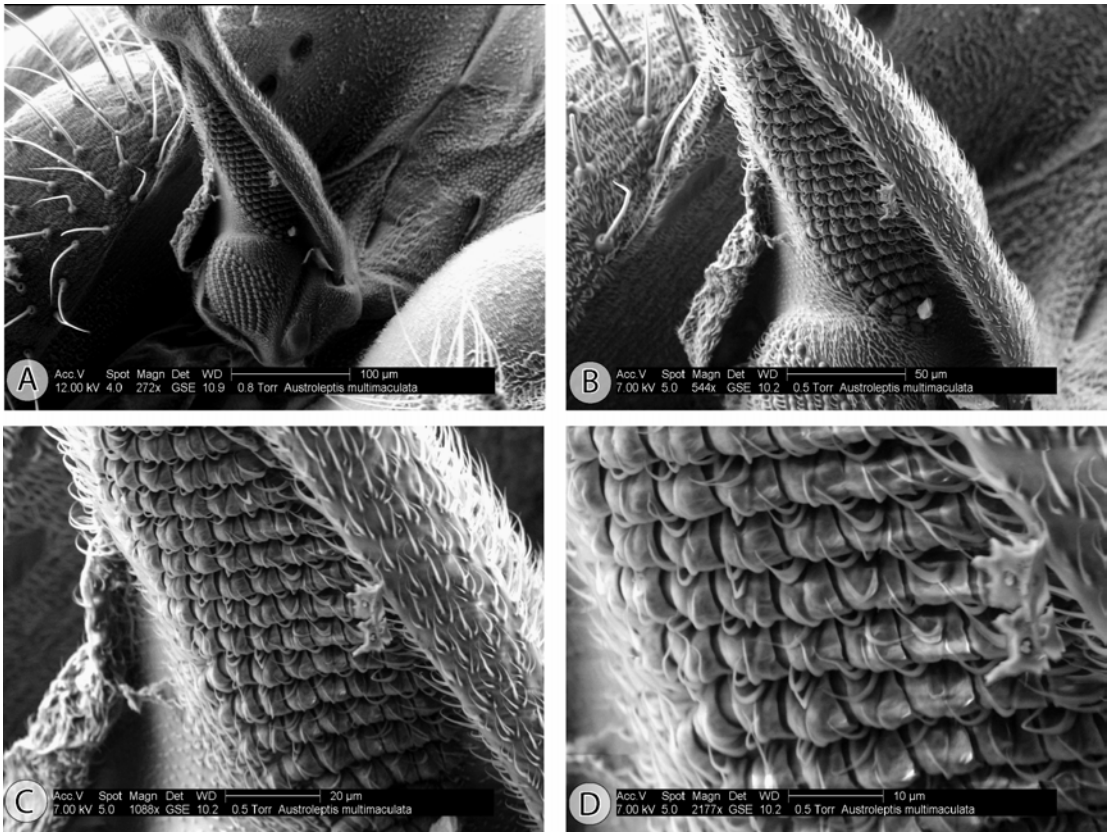


Figure 178. SEM of haltere of *Austroleptis multimaculata*.

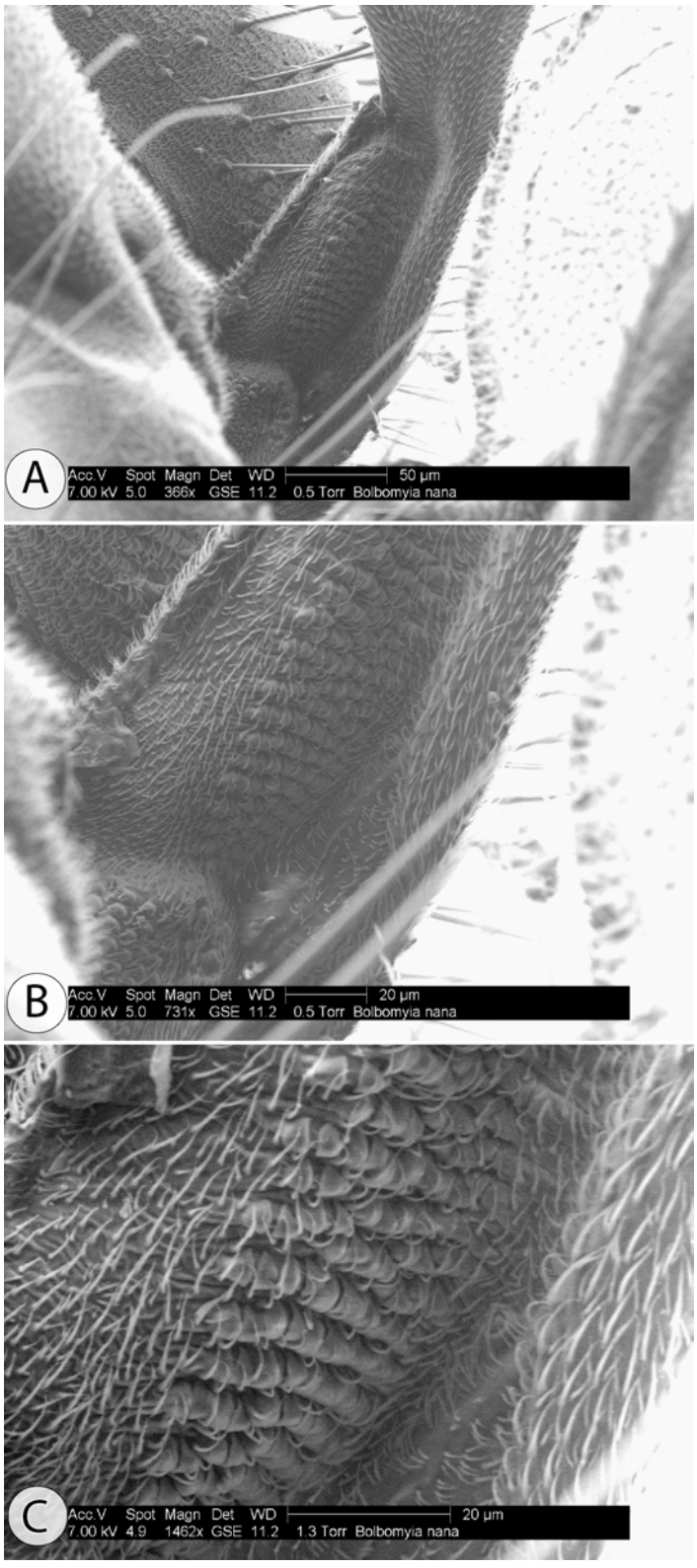


Figure 179. SEM of halter of *Bolbomyia nana.*

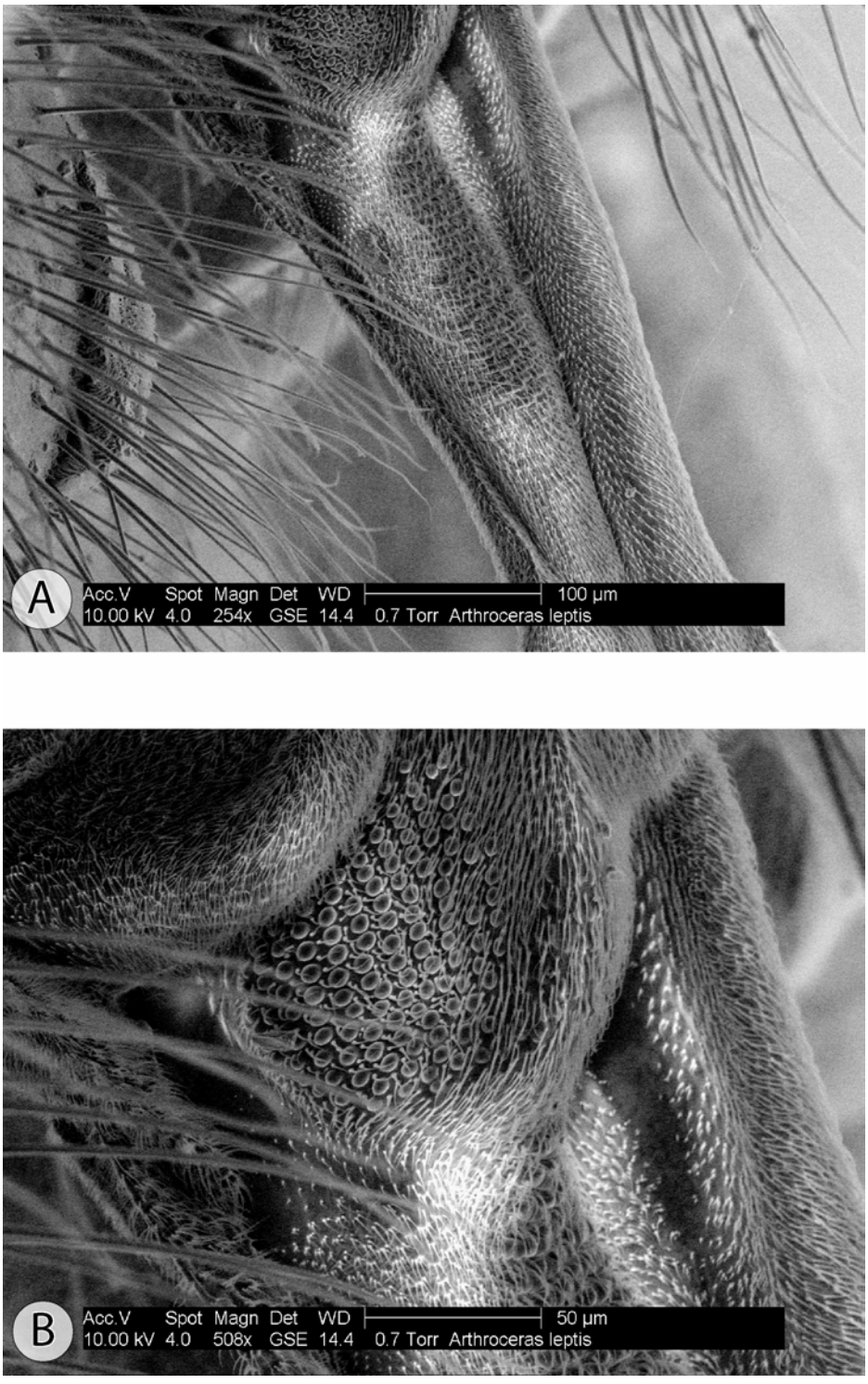


Figure 180. SEM of haltere in *Arthroceras leptis*.

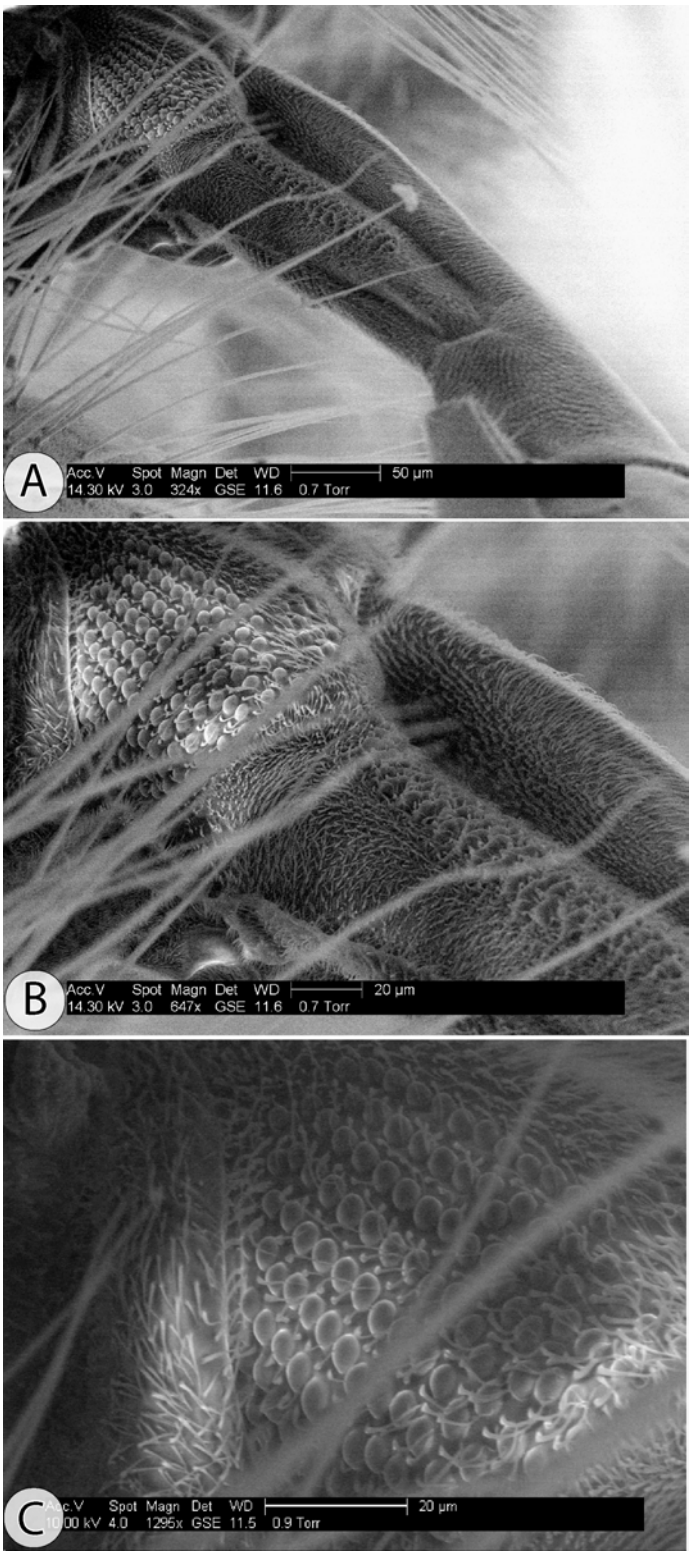


Figure 181. SEM of halter of *Arthroteles bombyliiformis*.

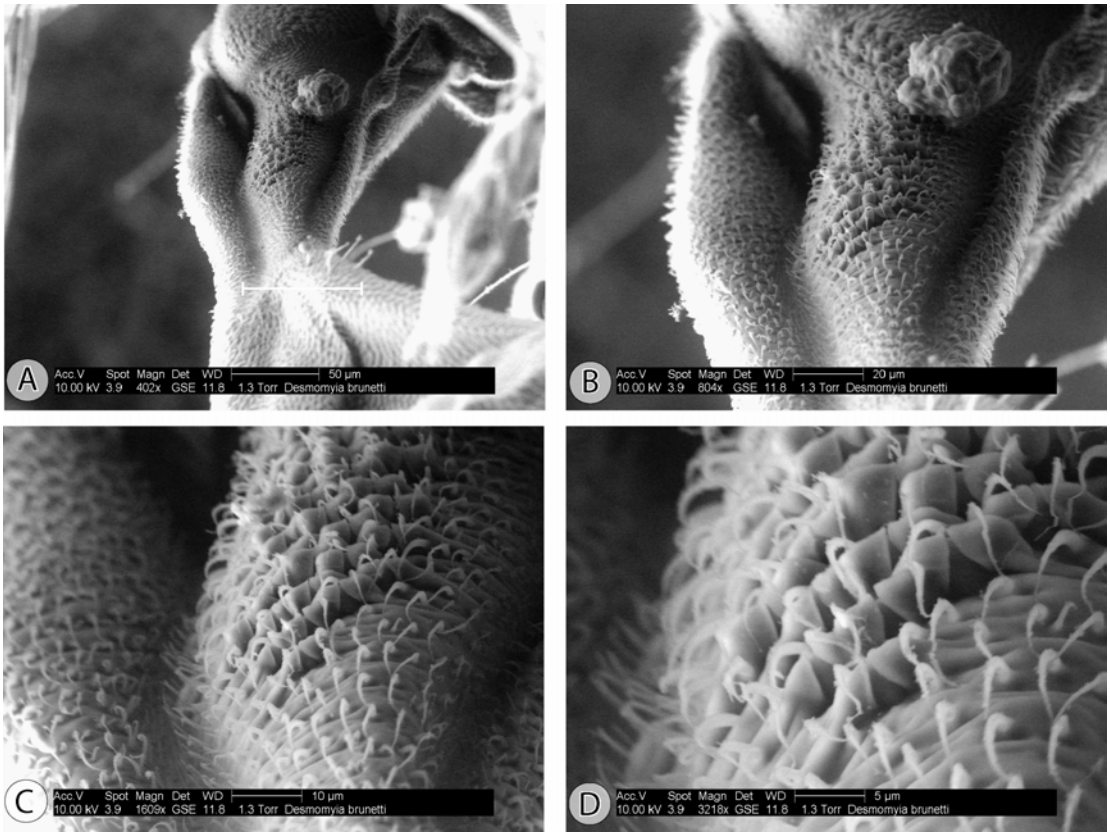


Figure 182. SEM images of haltere in *Desmomyia thereviformis*.

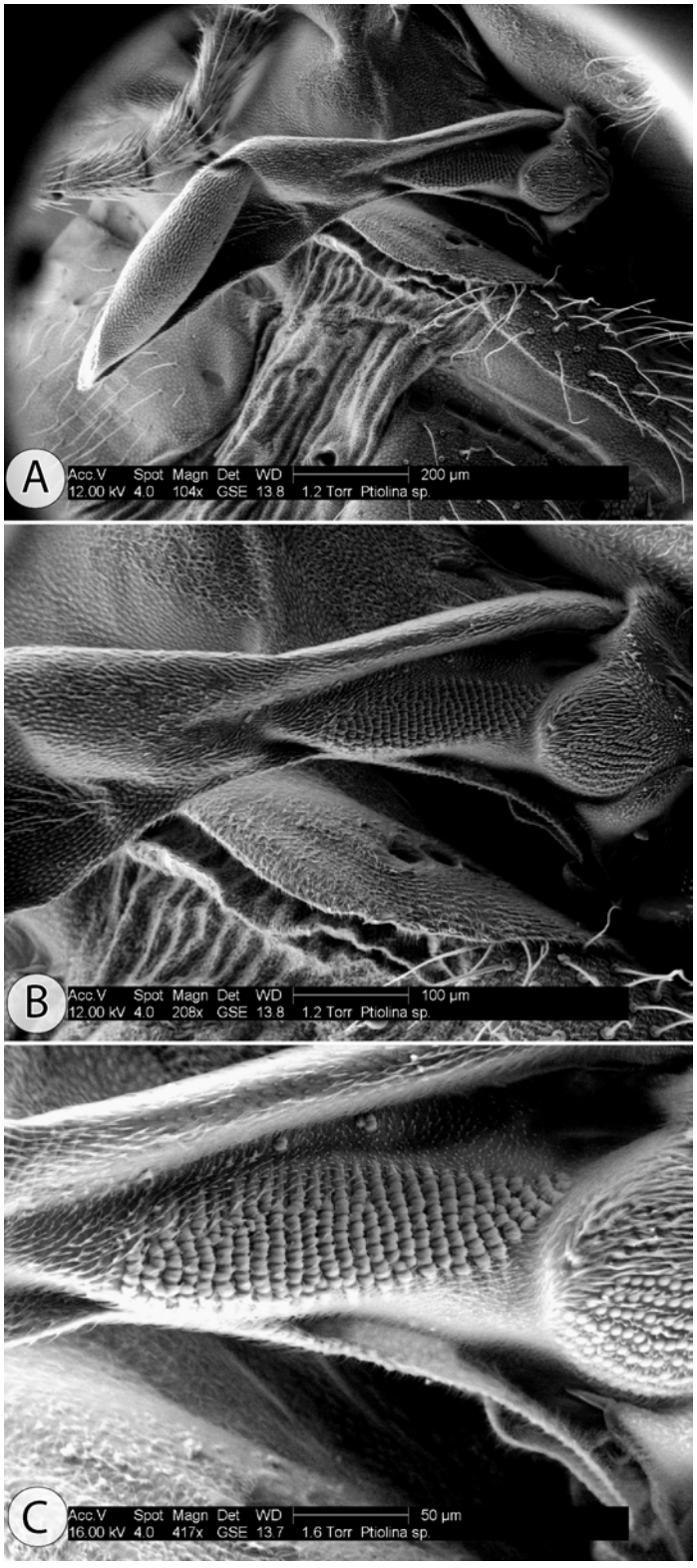


Figure 183. SEM images of halter in *Ptiolina* species.

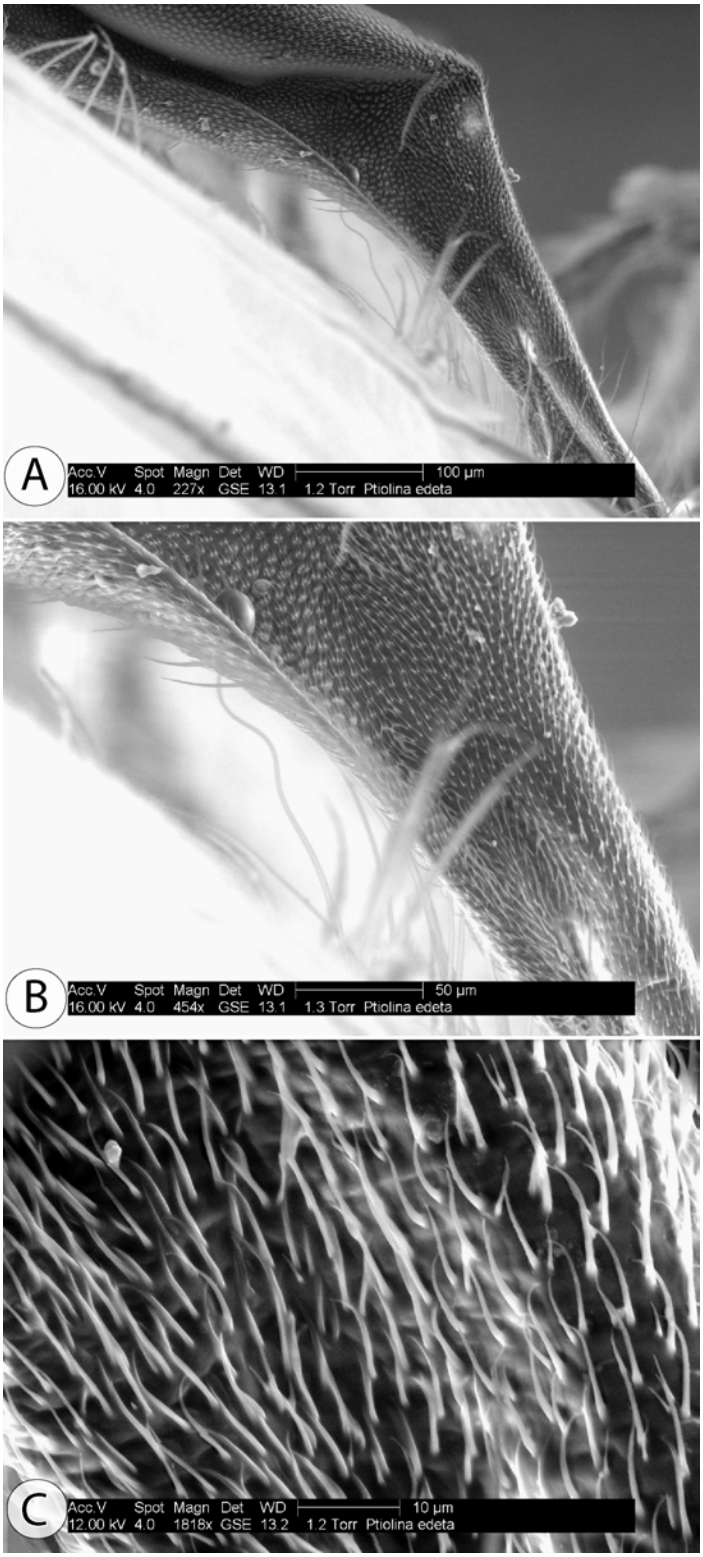


Figure 184. SEM images of halter of *Ptiolina edeta*.

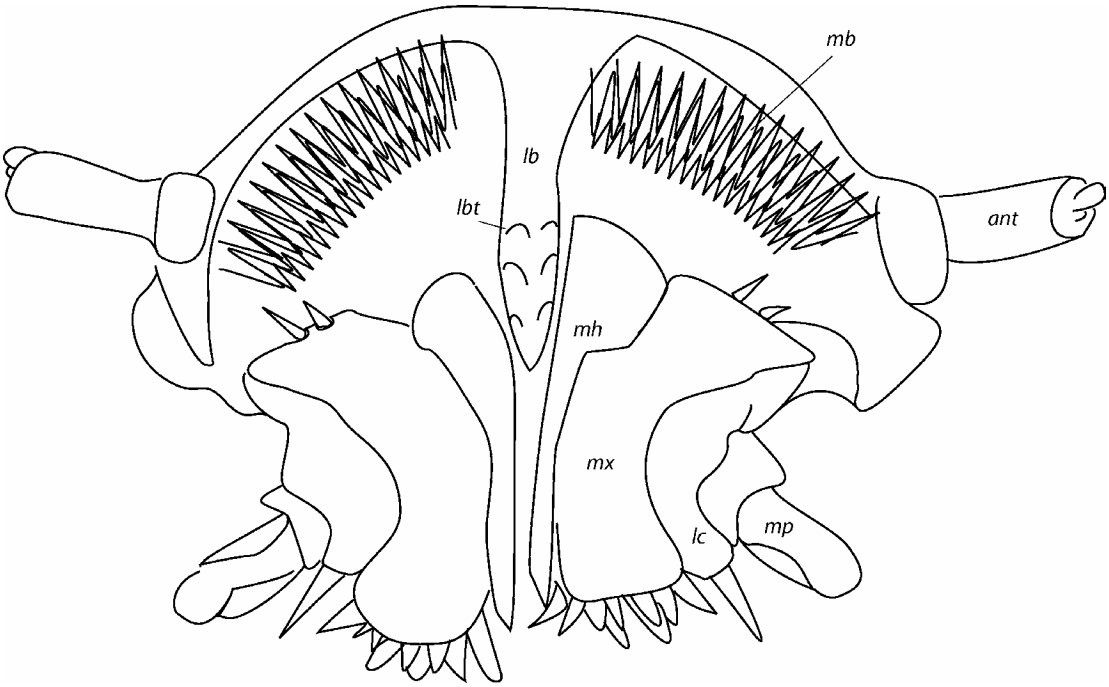


Figure 185. Anterior view of larval head *Symphoromyia* sp. Abbreviations: ant = antenna; lb = labrum; lbt = labral teeth; lc = lacinia; mb = mandibular brush; mh = mandibular hook; mx = maxilla; mp = maxillary palpus.

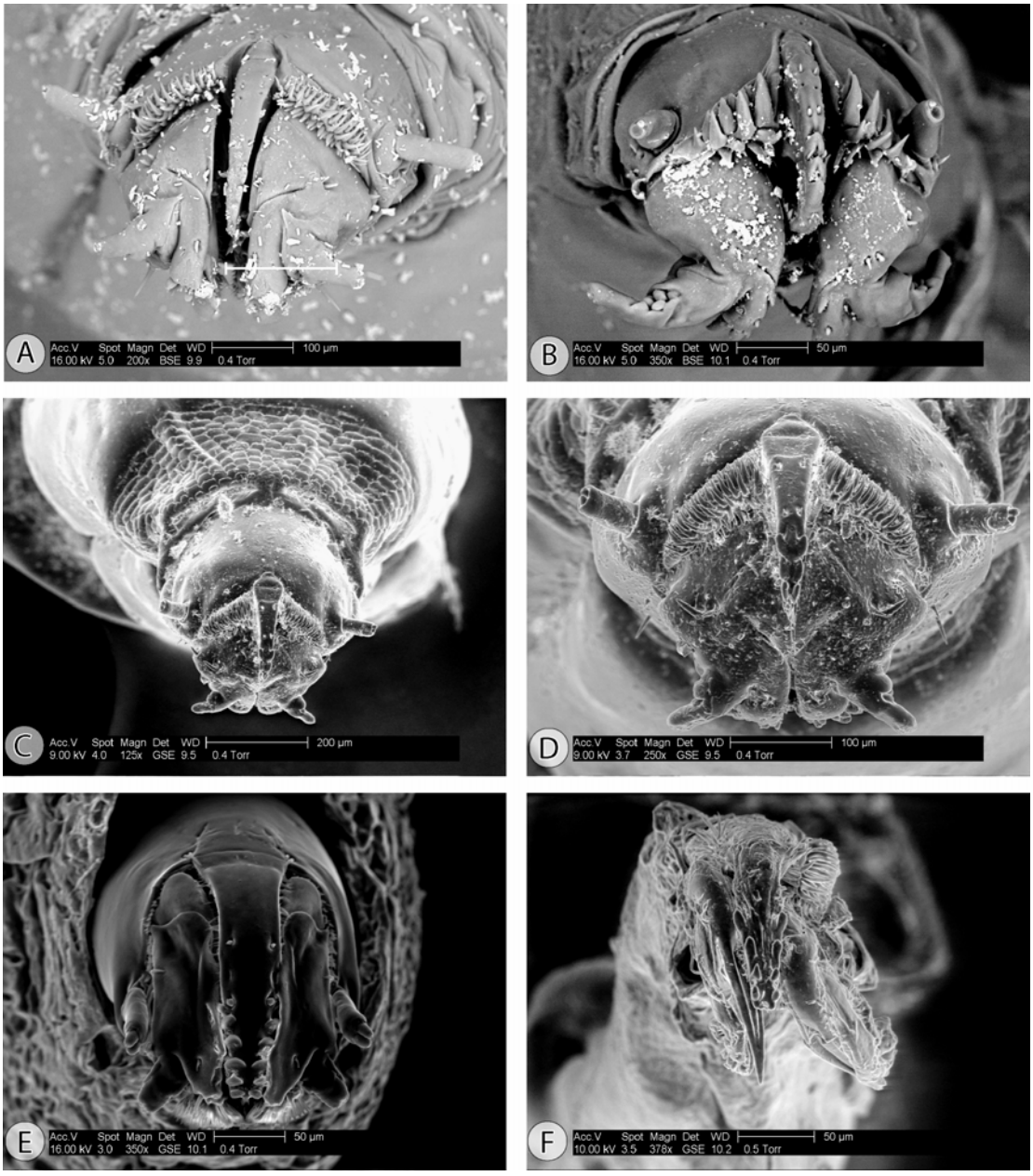


Figure 186. SEM images of the larval head. (A) *Chrysopilus* sp. (B) *Rhagio* sp. (C, D) *Symphoromyia* sp. (E) *Pelecorhynchus* sp. (F) *Glutops rossi*.

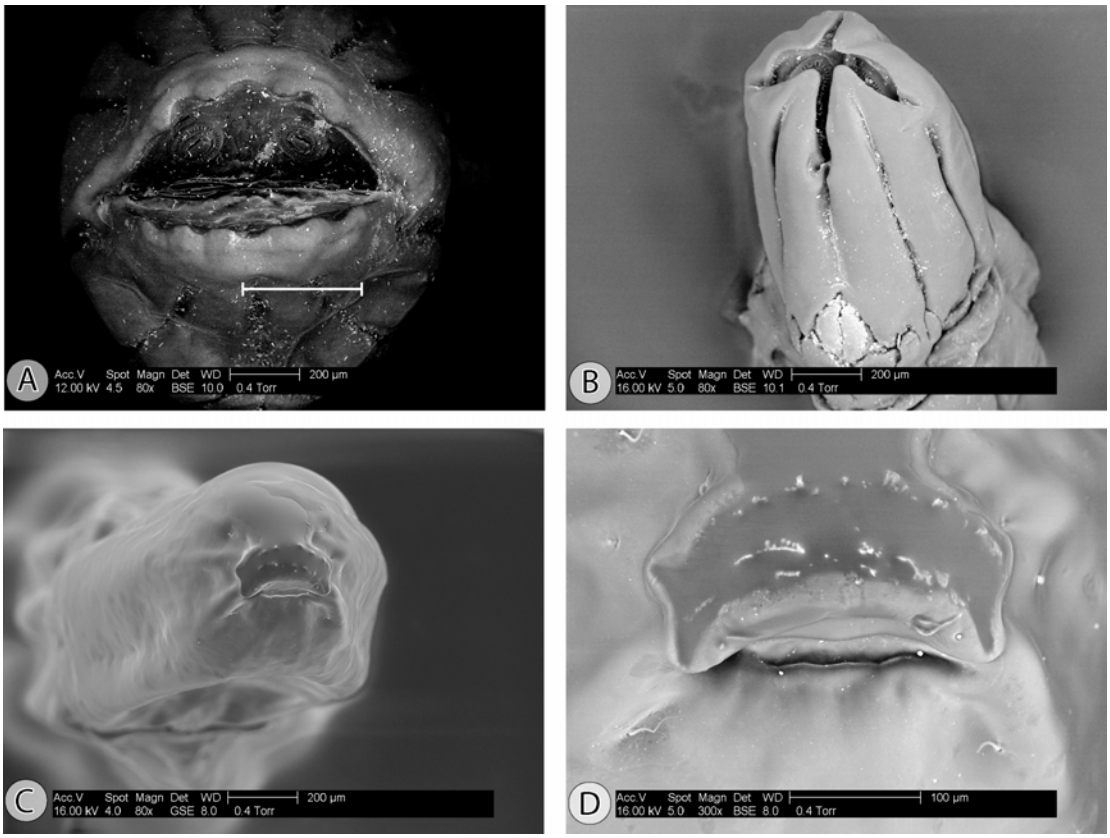


Figure 187. SEM images of the larval hind segment, posterior view (except in B, where oblique ventral view). (A) *Symphoromyia* sp. (B) *Rhagio* sp. (C, D) *Pelecorhynchus* sp.

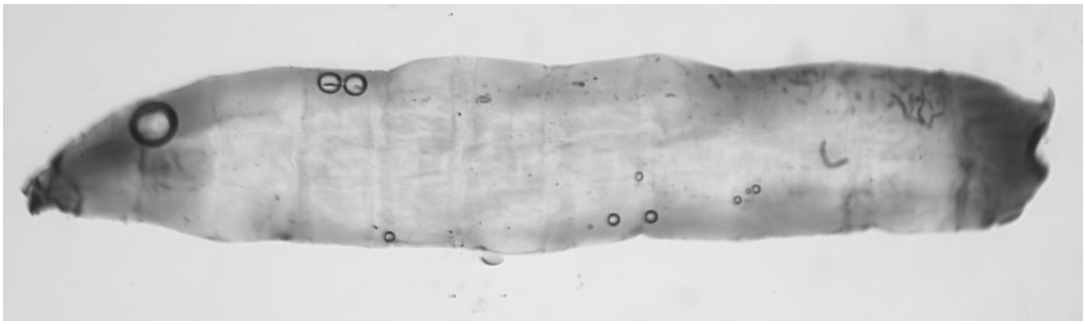


Figure 188. Habitus of *Ptiolina* sp. larva, lateral view.

Figure 189. Larva of *Ptiolina* sp. Anterior view, bright field illumination.

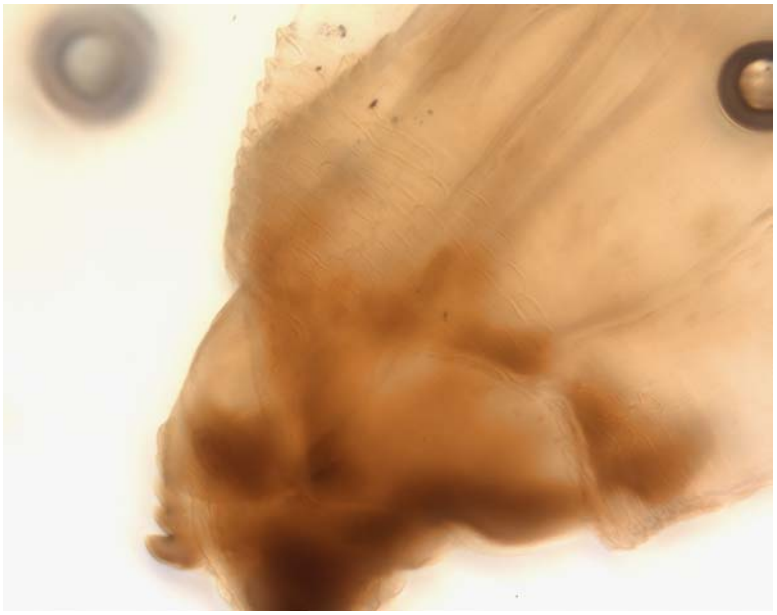


Figure 190. Lateral view of undissected *Ptiolina* sp. larva. Notice scalloping of first thoracic segment.

Figure 191. Lateral view of *Ptiolina* sp. larval head. Notice surface texture in absence of mandibular brush. Bright field illumination.

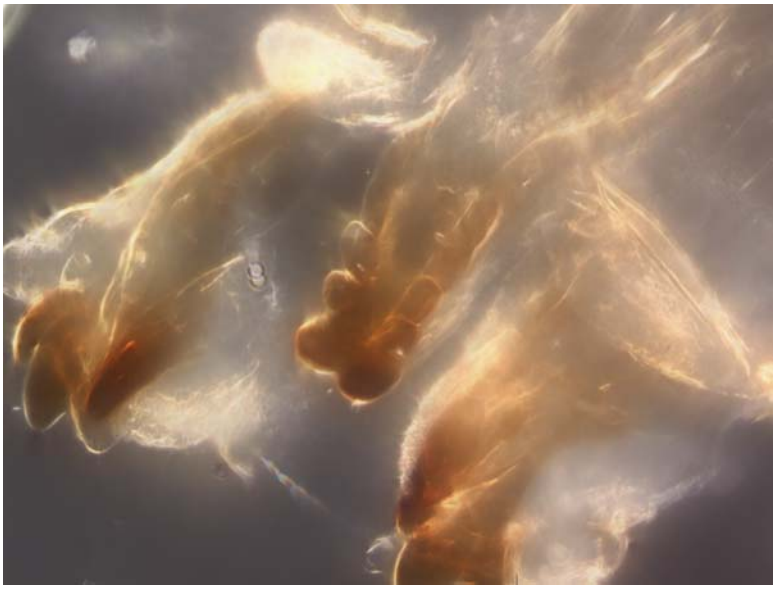


Figure 192. Oblique dorsal view of dissected *Ptiolina* sp. larval head. Bright field illumination.

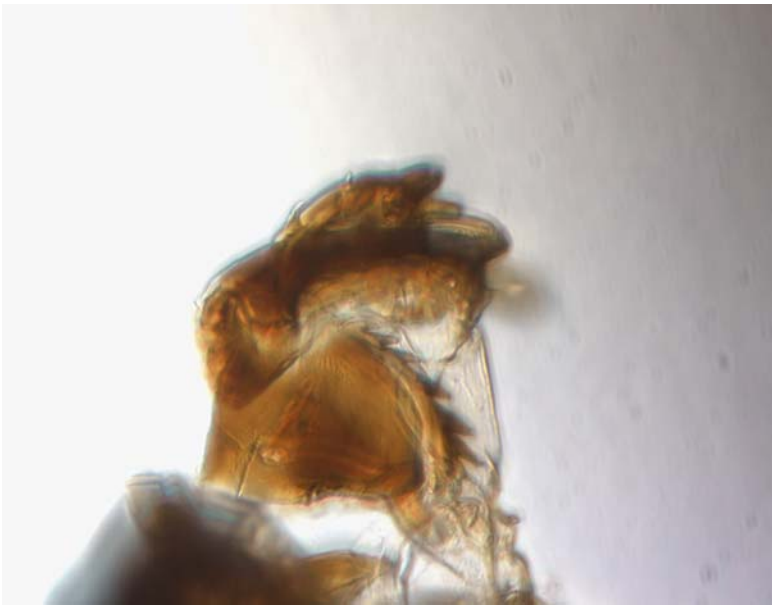


Figure 193. Adoral view of basal mandibular sclerite and mandibular hook of *Rhagio* sp., showing saw sclerite. Nomarski illumination.

Figure 194. Mandibular hook of *Symphoromyia* sp., showing adoral groove. Nomarski illumination.

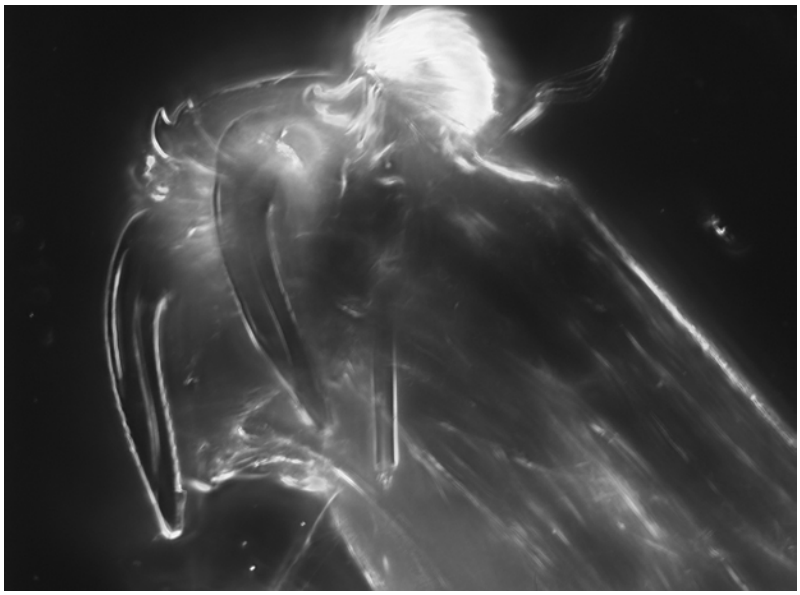


Figure 195. Larva of *Dasyomma* sp., lateral view, bright field illumination. Narrow, sclerotized palp evident.

Figure 196. Larva of *Dasyomma* sp., lateral view, bright field illumination. Rod associated with mandibular brush and inner groove of mandibular hook evident.

Figure 197. Larva of *Tabanus* sp., with head capsule extended from (pulled out of) first thoracic segment. Lateral view.

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