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Phylogeny and classification of Rhagionidae, with implications for Tabanomorpha (Diptera: Brachycera)

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Abstract

This paper updates current knowledge of Rhagionidae and related taxa within the infraorder Tabanomorpha. An estimate of phylogeny for the group is presented, based on 127 morphological characters for 60 ingroup species and molecular characters consisting of 3200+ bp sequences of 28S rDNA for 38 ingroup species. The morphology and molecular datasets are analyzed separately and in a combined analysis, using parsimony, maximum likelihood, and Bayesian methods. Morphological and molecular data, when analyzed separately and in combination, yield similar hypotheses of the evolution within Tabanomorpha. Arthrocerinae (Rhagionidae), Chrysopilinae (Rhagionidae), Rhagioninae (Rhagionidae), Spaniinae (Rhagionidae), Tabanoidea (Pelecorhynchidae, Oreoleptidae, Athericidae, and Tabanidae), and Vermileonidae are recovered consistently. The relationships among the major tabanomorph clades, including *Austroleptis* Hardy and *Bolbomyia* Loew, remain weakly supported, however. Rhagionidae are recognized as a monophyletic group of four subfamilies and at least 15 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* Becker, *Ptiolina* Zetterstedt, *Spania* Meigen, *Spaniopsis* White, and *Symphoromyia* Frauenfeld. *Litoleptis* Chillcott is also placed in this group, however this could not be confirmed because females of this genus were not available. The concept of *Omphalophora* is clarified and the genus is resurrected from synonymy with *Ptiolina*. On this basis, several species are newly transferred to *Omphalophora;* they include *O. cinereofasciata* (Schummel 1837) **n. comb.**, *O. fasciata* (Loew 1869b) **n. comb.**, *O. majuscula* (Loew 1869b) **n. comb.**, and *O. nigripilosa* (Hardy & McGuire 1947) **n. comb**. Chrysopilinae is defined by having scale-like setae on the thorax and femur, as in *Chrysopilus* Macquart, *Schizella* Bezzi, and *Stylospania* Frey. *Solomomyia* Nagatomi is recognized as a new junior synonym of *Chrysopilus*. Seven new names within the genus *Chrysopilus* are created for binomials that are preoccupied. These include *C. amulus* Kerr **nom. nov.** for *C. latifrons* Williston 1901 (preoccupied by *C. latifrons* Bezzi 1898), *C. batak* Kerr **nom. nov.** for *C. tomentosus* Meijere 1924 (preoccupied by *C. tomentosus* Bigot 1887), *C. mawambus* Kerr **nom. nov.** for *C. obscuripes* Brunetti 1927 (preoccupied by *C. obscuripes* Speiser 1923), *C. meunieri* Kerr **nom. nov.** for *C. nagatomii* Evenhuis 1994 (preoccupied by *C. nagatomii* Yang & Yang 1991), *C. occidentalis* Kerr **nom. nov.** for *C. lucifer* Adams 1904 (preoccupied by *C. lucifer* Walker 1852), and *C. amorimi* Kerr **nom. nov.** for *C. fascipennis* Bromley in Curran 1931 (preoccupied by *C. fascipennis* (Brunetti 1920)). *Chrysopilus sinensis* (Yang *et al.* 1997) **n. comb.** is transferred from *Spatulina* Szilády, where this species was originally placed. Arthrocerinae contains a single genus, *Arthroceras* Williston. Phylogenetic analyses consistently show strong support for a clade consisting of Arthrocerinae, Chrysopilinae, and Spaniinae; most females of these subfamilies have spermathecal duct accessory glands. Spermathecal duct accessory glands are reported here for the first time and are unique in Tabanomorpha. Rhagioninae is the earliest branching subfamily of Rhagionidae. The saw sclerite in the larval mandible may be synapomorphic for this subfamily. Members of Rhagioninae include *Atherimorpha* White, *Desmomyia* Brunetti, *Rhagio* Fabricius, and *Sierramyia* Kerr **gen. nov.** *Atherimorpha setosus* (Philippi 1865) is recognized as a **new synonym** of *Atherimorpha praefica* (Philippi 1865) and *Neorhagio* Lindner 1924 is recognized as a **new synonym** of *Atherimorpha*. *Sierramyia* **gen. nov.** is erected for two species from Mexico that were originally placed in *Neorhagio* (type species: *Neorhagio caligatus* Santos 2006). *Rhagina* Malloch is recognized as a **new synonym** of *Rhagio*. As a result, *Rhagio yangi* Kerr **nom. nov.** is created for *R. sinensis* Yang & Yang 1993a (preoccupied by *R. sinensis* Yang & Nagatomi 1992, **n. comb.**). Two enigmatic genera, *Bolbomyia* Loew and *Austroleptis* Hardy are retained within their own families, Bolbomyiidae **status revised** and Austroleptidae, respectively. *Alloleptis tersus* Nagatomi & Saigusa is *incertae sedis* within Rhagionoidea. Comments on larval morphology of Tabanomorpha are given in light of this work. A key is given to all families of Tabanomorpha and genera of Rhagionidae. The genera of Austroleptidae, Bolbomyiidae, and Rhagionidae are diagnosed, re-described, and re-classified based on characters and relationships established by the phylogenetic analyses, with a list of included species for each genus. A history of the recent classification of Rhagionidae and related taxa is also provided.

Key words: Tabanoidea, Rhagionoidea, Austroleptidae, Bolbomyiidae, Arthrocerinae, Rhagioninae, Chrysopilinae, Spaniinae, *Sierramyia*, *Omphalophora*, systematics, new genus, phylogeny, taxonomy, combined analysis

Introduction

The order Diptera comprises over 150,000 species in approximately 188 families (Courtney *et al.* 2009; Evenhuis *et al.* 2010). As a group, flies represent one of the most prolific and important elements of our natural world (Skevington & Dang 2002). 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 classified in the suborder Brachycera and represent most of the dipteran diversity in the world today (Krzeminski 1992; Krzeminski 1998; Mostovski & Jarzembowski 2000; Rohdendorf 1991; Wiegmann *et al.* 2003; Woodley 1989; Yeates & Lambkin 1998; Yeates & Wiegmann 1999; Yeates 2002).

Very little of the origin of Brachycera is known. The sister taxon is uncertain and the arrangement of the basal branches of its phylogenetic tree is mostly speculative (Amorim & Silva 2002; Griffiths 1994; Hennig 1968; Hennig 1973; Oosterbroek & Courtney 1995; Rohdendorf 1974; Rohdendorf 1991; Sinclair 1992; Wood & Borkent 1989; Woodley 1989). Rhagionids (formerly known as the Leptidae) are medium sized flies, ranging from approximately 4–20 mm in length, that are typically collected by sweeping vegetation in sheltered, often moist, forest clearings or woodlands that are often of high elevation and/or mountainous. The family is 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., Friedrich & Tautz 1997; Griffiths 1994; Grimaldi & Cumming 1999; Hennig 1967; Hennig 1973; Kovalev 1982; Nagatomi 1977; Sinclair *et al.* 1994; Wiegmann *et al.* 2000; Woodley 1989; Yeates 2002). 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; Wiegmann *et al.* 2003). The family lacks any synapomorphies however, and the phylogenetic relationships of the genera have not been examined in a systematic phylogenetic framework. 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.

In addition to Rhagionidae, the brachycerous infraorder Tabanomorpha contains Vermileonidae, Pelecorhynchidae, Oreoleptidae, Athericidae, and Tabanidae (as family or subfamily lineages). *Bolbomyia* Loew may represent an additional family (Sinclair *et al.* 1994), although most recently has been proposed as a subfamily within Rhagionidae (Stuckenberg 2001). *Austroleptis* Hardy may also be included in Tabanomorpha, but there is speculation that it may belong in Xylophagomorpha (Sinclair *et al.* 1994) as a separate family-level lineage. Stuckenberg (2001) recognized *Austroleptis* as a family-level unit within Tabanomorpha. Stuckenberg (2001) also recognized Spaniidae, a lineage traditionally placed within Rhagionidae.

Characters that have been used to unite Tabanomorpha are the apomorphic presence of a brush on the larval mandible, retractile larval head, bulbous clypeus of adults, and ventrolaterally expanded first segment of the cercus in adult females (Sinclair 1992; Wiegmann *et al.* 2000; Woodley 1989; Zloty *et al.* 2005). It has been suggested that the Acroceridae and Nemestrinidae (Nemestrinoidea) may also belong within Tabanomorpha (Griffiths 1994; Nagatomi 1992; 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).

The taxonomy of Rhagionidae has been unstable because there are few extensively scored morphological characters that provide support hypotheses of relationship among its members. Therefore when new morphological synapomorphies are proposed (such as the presence of aedeagal tines (Sinclair *et al.* 1994)), few additional sources of evidence are on hand to corroborate or refute such ideas. *Pelecorhynchus* Macquart, for example, has been placed as sister to Rhagionidae on the basis of male and female genitalic characters

(Nagatomi 1977), within Rhagionidae based on female abdominal characters (Stuckenberg 2001), and, along with *Glutops* Burgess and *Pseudoerinna* Shiraki, sister to Athericidae and Tabanidae based on larval characters (Teskey 1970a; Sinclair 1992; Woodley 1989). Similarly, *Bolbomyia* may be located among Xylophagidae (James 1965b, presumably on account of its flattened clypeus), among Rhagionidae because 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.* 1994).

It is not known whether morphology is a sufficient 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., Felsenstein 2004; Hillis *et al.* 1994; Huelsenbeck 1995; Huelsenbeck & Bollback 2001; Huelsenbeck & Crandall 1997; Huelsenbeck *et al.* 2002; Huelsenbeck & Rannala 1997; Huelsenbeck *et al.* 2001; Rannala *et al.* 1998) have already shown promise in helping to resolve ancient divergences and will certainly gain more favor as morphological inquiries are exhausted (Baker & Gatesy 2002; Hillis & Wiens 2000). 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.

Wiegmann *et al.* (2000) showed that 28S nuclear ribosomal DNA may be used to track divergences among rhagionid and related genera. Their 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. No previous molecular study, however, has tested the monophyly of Rhagionidae in light of several recent, conflicting hypotheses for the group (Sinclair 1992; Stuckenberg 2001; Woodley 1989). At issue is the position of three key taxon groups: *Austroleptis*, *Bolbomyia*, and Spaniinae (recognized at the family level by Stuckenberg 2001).

In taxa such as *Austroleptis*, 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. Most have placed the genus in Tabanomorpha but its location within this group has been disputed (Hardy 1920a; Steyskal 1953; Hardy 1955; Nagatomi 1982a; 1984; Woodley 1989; Stuckenberg 2001). *Austroleptis* is traditionally considered a primitive member of Rhagionidae (Hardy 1920a; Nagatomi 1982a). Chillcott (1963) suggested that within Rhagionidae, *Austroleptis* had affinities to *Bolbomyia*, *Litoleptis*, *Archicera* Szilády (= *Spania* Meigen), and *Hilarimorpha* Schiner. 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 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.* 1994).

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 cercal segments (Nagatomi 1982a). 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 Rhagionidae have not been tested in a phylogenetic context. Its proper status, therefore, remains somewhat uncertain.

Recent classification of Tabanomorph taxa, excluding Tabanidae

In 1973, Hennig placed the genera of Rhagionidae into three subfamilies as follows: Arthrocerinae: (*Arthroceras*, *Arthroteles*, *Atherimorpha*, *Austroleptis*, *Bolbomyia*, *Glutops*, *Heterostomus* Bigot), Rhagioninae (*Atherix* group (*Atherix*), *Rhagio* group (*Chrysopilus*, *Dialysis* Walker, *Rhagio*, *Schizella*, *Symphoromyia*), and *Spania* group (*Litoleptis*, *Omphalophora* Becker, *Ptiolina*, and *Spania*)), and Vermileoninae (*Lampromyia* Macquart, *Vermileo* Macquart and *Vermitigris* Wheeler) (Hennig 1973).

Stuckenberg (1973) subsequently created Athericidae, showing that *Atherix* and its allies were more closely related to Tabanidae than to the remaining members of Rhagionidae. The sister group relationship between the genera of Athericidae and Tabanidae is now clear, based on strong morphological and molecular evidence (Sinclair 1992; Sinclair *et al.* 1994; Stuckenberg 1973; Stuckenberg 2001; Wiegmann *et al.* 2000; Wiegmann *et al.* 2003; Woodley 1989).

In 1977, Nagatomi erected Vermileonidae for *Lampromyia*, *Vermileo*, and *Vermitigris* on account of their highly autapomorphic morphology and life history (Hennig 1967; Hennig 1973; Nagatomi 1977; Wheeler 1918, 1931; Williston 1886). When this group was raised to family rank, Nagatomi speculated that the family was either sister to the tabanomorph families (Pelecorhynchidae, Rhagionidae, Athericidae, and Tabanidae) or sister to the entire lower Brachycera (Nagatomi 1977). 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 Rhagionidae, within the Tabanomorpha clade, although this result did not definitively preclude Vermileonidae being located outside of Tabanomorpha (Wiegmann *et al.* 2000; Stuckenberg 2001).

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 authority* 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 Xylophagidae. Similarly, the placement of *Austroleptis*, *Bolbomyia*, *Glutops*, *Hilarimorpha*, and *Pseudoerinna* continued to be debated among authors (Griffiths 1994; Grimaldi & Cumming 1999; Kovalev 1981; Krivosheina 1971; Nagatomi 1977; Stuckenberg 2001; Teskey 1981b). Nagatomi (1982a) presented an updated concept of the family, including an intuitive phylogenetic tree to represent his ideas of the rhagionid phylogeny as part of a landmark monograph of Rhagionidae. Nagatomi's work presented a significant advance in understanding the extant diversity of the group, but his hypotheses were not developed using a cladistic approach and the composition of Rhagionidae remained untested.

New developments in systematic phylogenetic methods created a new era of inquiry into the relationships among genera of the Tabanomorpha, and more specifically, of Rhagionidae. Naturally, as researchers applied more rigorous approaches to the study of 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 (Hennig 1973; Krivosheina 1967; Malloch 1917; Roberts 1969; Steyskal 1953; Teskey 1970a; Thomas 1974; Tsacas 1962; 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 Pelecorhynchidae *sensu lato* (*Glutops*, *Pelecorhynchus*, and *Pseudoerinna*) were recognized as a separate family, sister to Athericidae and Tabanidae, and not part of Rhagionidae in any sense.

The limits and location of Pelecorhynchidae have been labile for some time. 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 *Silvius* Meigen (Tabanidae). *Pelecorhynchus* species were placed in Tabanidae, within their own subfamily, the Pelecorhynchinae (Enderlein 1922). *Pelecorhynchus* remained in Tabanidae until Mackerras and Fuller (1942) created the family Pelecorhynchidae. Steyskal (1953) considered *Pelecorhynchus* closely related to *Coenomyia* Latreille and placed these genera together in Coenomyiidae (now included in Xylophagidae), along with *Arthroteles* (Rhagionidae) and *Stratioleptis* Pleske (including *Odontosabula* Matsumura, 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 Tabanidae (Steyskal 1953; Hardy 1955). Teskey (1970a) removed *Glutops* from Xylophagidae (Coenomyiidae *sensu* Steyskal) to Pelecorhynchidae (*sensu* Mackerras & Fuller 1942) on account of similarities of larval and pupal morphology between *Pelecorhynchus* and *Glutops*. This was controverted by Krivosheina (1971) who proposed that *Glutops* be placed in its own family, based on a comparative morphological study of all developmental stages. Kovalev (1981) synonymized Glutopidae with Rhagionidae, however, and Nagatomi (1982a) recognized the Glutopinae, placing *Pseudoerinna* with *Glutops*, as a subfamily of Rhagionidae. Pelecorhynchidae remained a family represented by the single genus, *Pelecorhynchus*, according to Nagatomi (1982a). Although Stuckenberg (2001) asserted that Pelecorhynchidae were "always ranked by Nagatomi as a subfamily of Rhagionidae," this was in fact not the case. Stuckenberg was the first to locate *Pelecorhynchus* within Rhagionidae, as a member of the Pelecorhynchinae, which also included *Glutops* and *Pseudoerinna* (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 Pelecorhynchidae are sister to Athericidae, Oreoleptidae, 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 *Pseudoerinna*. The larva of *Pseudoerinna* is unknown.

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), and 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 1982b; Nagatomi 1982c; Nagatomi 1982d; Nagatomi 1984; Nagatomi 1991; Nagatomi 1992; Nagatomi & Soroida 1985).

Consistent with the trend of decreasing the breadth of the rhagionid concept, which started with Stuckenberg (1973; removal of Athericidae) and Nagatomi (1977; removal of Vermileonidae), and continued through the work of Woodley (1989; removal of Pelecorhynchidae *sensu lato*), Sinclair *et al.* (1994) examined the male genitalia in lower Brachycera and determined that *Bolbomyia* also should be removed from Rhagionidae. *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. Stuckenberg (2001) has rejected this argument, however, and retained *Bolbomyia* within Rhagionidae, placing it within its own subfamily, the Bolbomyiinae.

Rhagionidae was further reduced by the formation of a newly recognized family, Spaniidae (Stuckenberg 2001). The origins of Spaniidae begin with Frey (1954), who established the subfamily Spaniinae for *Bolbomyia* (as *Cechenia* Frey), *Spania*, *Ptiolina*, and *Omphalophora* Becker on the basis of having a bare laterotergite and short stylate antennae. At the time, these were distinguished as the smallest rhagionids known. Nagatomi (1982a) removed *Bolbomyia* to 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 separation between female basal cercal segments, the lack of a ventral process on the basal cercal segment of the female, and tergite 10 short or absent were distinguishing characters for 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 (1982a). No unambiguous synapomorphies for the group have been recognized.

In a study principally devoted to new fossil brachyceran forms, Grimaldi & 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 & Cumming 1999).

Hardy originally described *Austroleptis* as a leptid (=Rhagionidae) (Hardy 1920a). However, in 1953, it was placed in Xylophagidae (Steyskal 1953) and more recently, others have speculated that it belongs within Xylophagomorpha on account of its larvae having been reared from wood, as is the case for most Xylophagidae (Colless & McAlpine 1991; Sinclair *et al.* 1994). Nagatomi (1982a, 1991) considered *Austroleptis* sister to the rest of 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 did not identify the sister group of this lineage or its relationship to other lower Brachyceran families (Stuckenberg 2001).

The development of molecular techniques allowed for a new approach to solving these issues in Diptera (e.g., Carreno & Barta 1998; Friedrich & Tautz 1997; Pawlowski *et al.* 1996; Pelandakis & Solignac 1993). 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, Pelecorhynchidae were recovered as sister to Athericidae and Tabanidae, a result consistent with Sinclair (1992) and Woodley (1989). Rhagionidae were recovered as a monophyletic group, sister to the Vermileonidae. The most contentious genera of Rhagionidae (*e.g.*, *Bolbomyia* and *Austroleptis*) were not sampled, however.

A common refrain from these papers is that a comprehensive monographic treatment of the rhagioniform genera is 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., Grimaldi & Cumming 1999; Krivosheina 1991; Sinclair 1992; Sinclair *et al.* 1994; Wiegmann *et al.* 2000; Wiegmann *et al.* 2003), systematic studies involving incomplete taxon sampling (e.g., Stuckenberg 2001; Wiegmann *et al.* 2000), or analyses derived from the published literature (e.g., Amorim & Silva 2002; Woodley 1989; Yeates 2002). 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.

A phylogenetic revision of Rhagionidae (and related families and genera) is presented herein based on a combined molecular and morphological analysis using parsimony and likelihood methods. A revised classification is presented and a key to world genera of the clade is included. Hennig (1973) and others (McAlpine 1981) have used the term Tabanoidea to refer to the entire infraorder Tabanomorpha (Woodley 1989). However, in this work, I refer to superfamily Tabanoidea as the clade containing Pelecorhynchidae, Oreoleptidae, Tabanidae, and Athericidae, exclusively.

Phylogenetic analysis of Rhagionidae and related taxa

Material and methods

Taxon sampling. The breadth of taxon sampling was determined on the basis of availability of specimens for study and their importance for testing specific hypotheses of relationship, as discussed above. Species were used as terminals, an approach that is best for reconstructing phylogenetic relationships (Wiens 1998; Yeates 1995). 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 1998; Rennala *et al.* 1998). Where possible, highly autapomorphic species exemplars were avoided.

TABLE 1. Taxon sampling for morphological analysis.

Taxon	Family	Region	Geographic Distribution of specimens examined
Alloleptis tersus	Rhagionidae	OR	Indonesia: Sulawesi
Arthroceras fulvicorne	Rhagionidae	NA	USA: UT
Arthroceras pollinosum	Rhagionidae	NA	USA: CA, CO, OR, NM, WA, WN
Arthroteles bombyliiformis	Rhagionidae	AT	South Africa: Cape Province
Arthroteles cinerea	Rhagionidae	AT	South Africa: Drakensberg
Atherimorpha atrifemur	Rhagionidae	NT	Chile: Chiloé, Llanquihue, Malleco, Osorno Provinces
Atherimorpha montana	Rhagionidae	AU	Australia: Tasmania
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 collessi	Austroleptidae	AU	Australia: NSW
Austroleptis multimaculata	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 rhagiodes	Rhagionidae	NA	Costa Rica: San José
Chrysopilus thoracicus	Rhagionidae	NA	USA: MD, TN
Chrysops vittatus	Tabanidae	NA	USA: MD
Dasyomma atratulum	Athericidae	NT	Chile: Chiloé
Dasyomma coeruleum	Athericidae	NT	Chile: Chiloé
Dasyomma vittatum	Athericidae	NT	Chile: Chiloé
Desmomyia thereviformis	Rhagionidae	OR	India: E. Punjab
Dichelacera marginata	Tabanidae	NT	Colombia: Antioqua
Glutops rossi	Pelecorhynchidae	NA	Canada: Alberta, British Columbia
Isalomyia irwini	Vermileonidae	AT	Madagascar
Lampromyia canariensis	Vermileonidae	AT	Spain: Canary Islands
Leptynoma hessei	Vermileonidae	AT	South Africa: Cape
Litoleptis alaskensis	Rhagionidae	NA	USA: AK
Omphalophora fasciata **n. comb.**	Rhagionidae	NA	Canada: Saskatchewan
Omphalophora lapponica	Rhagionidae	PA	Finland: Petsamo, Ponoj
Omphalophora majuscula **n. comb.**	Rhagionidae	NA	USA: AK
Oreoleptis torrenticola	Oreoleptidae	NA	Data from Zloty *et al.* 2005
Pelecorhynchus personatus	Pelecorhynchidae	AU	Australia: NSW, Queensland
Pseudoerinna jonesi	Pelecorhynchidae	NA	USA: WN
Ptiolina mallochi	Rhagionidae	NA	USA: AK
Ptiolina zonata	Rhagionidae	NA	Canada: Manitoba, NWT, Yukon; USA: AK, WA
Rhagio costatus	Rhagionidae	NA	USA: CA, WA
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 sp.	Rhagionidae	NT	Mexico: Chiapas
Solomomyia gressitti	Rhagionidae	OR	Solomon Islands
Spania nigra	Rhagionidae	PA	Austria: Tirol; Switzerland: Om; USA: WN

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TABLE 1. (continued)

Taxon	Family	Region	Geographic Distribution of specimens examined
Spaniopsis clelandi	Rhagionidae	AU	Australia: ACT, NSW
Spaniopsis longicornis	Rhagionidae	AU	Australia: NSW, Victoria
Stylospania lancifera	Rhagionidae	OR	Philippines: Samar
Suragina concinna	Athericidae	NA	USA: TX
Symphoromyia atripes	Rhagionidae	NA	USA: CA
Symphoromyia cruenta	Rhagionidae	NA	USA: CA
Symphoromyia hirta	Rhagionidae	NA	USA: CT, MD, PA, VA
Tabanus atratus	Tabanidae	NA	USA: GA
Tabanus rufofrater	Tabanidae	NA	USA: GA
Tabanus subsimilis	Tabanidae	NA	USA: TX
Vermileo opacus	Vermileonidae	NA	USA: CA
Vermileo vermileo	Vermileonidae	PA	Israel: Nahal Tut; Spain: Balearic Islands
Arthropeas americana	Xylophagidae	NA	USA: MI
Coenomyia ferruginea	Xylophagidae	NA	USA: MD, MN
Dialysis rufithorax	Xylophagidae	NA	USA: MD, VA
Exeretonevra angustifrons	Xylophagidae	AU	Australia: NSW
Heterostomus curvipalpis	Xylophagidae	NT	Chile
Xylophagus lugens	Xylophagidae	NA	USA: MD, VA
Pachygaster montana	Stratiomyidae	PA	USA: NM

The ingroup taxa sampled for morphological characters include representatives from all of the genera in Rhagionidae recognized by Nagatomi (1982a). Outgroup taxa included representatives from all families within Tabanomorpha, as well as several genera within Xylophagomorpha. Table 1 shows species used in the morphological analysis.

A summary of species, source, and GenBank accession numbers for taxa used in the molecular analysis is shown in Table 3. Twenty 28S rDNA sequences representing 20 species in 15 genera of Tabanomorpha have been published previously (Wiegmann *et al.* 2000). Of these, seven species in four genera are currently placed in Rhagionidae. The sequence identified as *Ptiolina 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* (= *Omphalophora fasciata* **n. comb.**) 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.

For the combined analyses, the intersection of taxa in morphological and molecular datasets was sampled for the combined analyses. In some cases, the genera in the combined analysis are a chimera of two different species (see Table 4). 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.

Specimen loans were provided via the following people and institutions: David A. Grimaldi, American Museum of Natural History, New York (AMNH); Dan J. Bickel, Max Moulds and David K. McAlpine, Australia Museum, Sydney (AMSA); David K. Yeates, Australian National Insect Collection, Canberra (ANIC); Bernhard Merz, Muséum d'Histoire Naturelle, Geneva; John E. Chainey, Natural History Museum, London (BMNH); Neal L. Evenhuis, B. P. Bishop Museum, Honolulu (BPBM); Keve Ribardo, California Academy of Sciences, San Francisco (CAS); Jeffrey Cumming, Canadian National Collection of Insects, Ottawa (CNC); James K. Liebherr, Cornell University, Ithaca (CU); Stephen A. Marshall and Matthias Buck, University of Guelph, Ontario (DEBU); Manuel Zumbado, Instituto Nacional de Biodiversidad, Heredia, Costa Rica (INBIO); Donald W. Webb, Illinois Natural History Survey, Champaign (INHS); Gregory W. Courtney, Iowa State Insect Collection, University of Iowa State, Ames (ISUC); Brian V. Brown, Natural History Museum of Los Angeles County, Los Angeles (LACM); Philip D. Perkins, Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Pekka Vilkamaa, Zoological Museum, University of Helsinki, Helsinki (MZHF); Thomas Pape, Naturhistoriska Riksmuseet, Stockholm (NHRS); David A. Barraclough and Brian R. Stuckenberg, Natal Museum, Pietermaritzburg, South Africa (NMSA); Hans-Peter Tschorsnig, Staatliches Museum für Naturkunde, Stuttgart (SMNS); and Joachim Zeigler, Museum für Naturkunde, Berlin (ZMHB). Fresh specimens suitable for molecular study were provided by Donald W. Webb (*Omphalophora fasciata* **n. comb.**), David Yeates (*Spaniopsis* spp.),; Richard Bashford (*Atherimorpha* spp., *Chrysopilus* sp.); Amnon Frieberg (*V. vermileo*); and Shelah Morita (*Arthroteles cinerea*).

TABLE 2. Species with incomplete morphological sampling.

Species	Gender unavailable for direct examination	Comment
Alloleptis tersus	Female	Female unknown.
Austroleptis collessi	Female	Female scored using Nagatomi & Iwata (1976).
Dasyomma vittatum	Male	Specimen unavailable; original description by Malloch (1932) utilized, but limited.
Isalomyia irwini	Male	Male undescribed and unknown.
Leptynoma hessei	Female	Specimen unavailable; original description by Stuckenberg (1965) utilized, but limited.
Litoleptis alaskensis	Female	Female undescribed. One female deposited in the Canadian National Collection, but subsequently loaned and apparently lost. Female examined by Nagatomi (1982).
Pseudoerinna jonesi	Male	Male scored using Nagatomi (1984).
Sierramyia sp.	Male	Male scored using Nagatomi (1984) and Santos (2006).
Stylospania lancifera	Female	Species known from a single male individual.
Symphoromyia atripes	Male	Male undescribed and unavailable.
Oreoleptis torrenticola	Male and Female	Both sexes of this species scored using Zloty *et al.* (2005).

Laboratory methods for morphological data. 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 was 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 let sit in a small dish of water, with two drops of 100% glacial acetic acid for 10–15 minutes. It was then rinsed in 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* spp. 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. 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. Additional SEM images of *Chrysopilus thoracicus* (Fabricius) (Figs. 65, 66) were generated with a JEOL JSM-6300 Scanning Electron Microscope and captured using Gatan DigitalMicrograph 3.10.0 software.

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* Bigot 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* Hardy & McGuire and *P. zonata* Hardy & McGuire.

TABLE 3. Taxon sampling for molecular analyses.

Species	Family	Locality	Source	GenBank Accession Numbers
Arthroceras fulvicorne	Rhagionidae	USA: UT	New sequence	DQ415517
Arthroteles cinerea	Rhagionidae	South Africa	New sequence	HM770491
Atherimorpha atrifemur	Tabanidae	Chile	New sequence	DQ415518
Atherimorpha montana	Rhagionidae	Tasmania	New sequence	DQ415522
Atherimorpha nemoralis	Rhagionidae	Chile	New sequence	DQ415519
Atherimorpha vernalis	Rhagionidae	Tasmania	New sequence	DQ415520
Atherix variegata	Athericidae	USA: WI	GenBank	AF238565, AF238541, AF238517
Austroleptis collessi	Austroleptidae	Tasmania	New sequence	DQ415523
Austroleptis multimaculata	Austroleptidae	Tasmania	New sequence	DQ415524
Austroleptis rhyphoides	Austroleptidae	Tasmania	New sequence	DQ415525
Bolbomyia nana	Bolbomyiidae	Quebec	New sequence	DQ415526
Chrysopilus quadratus	Rhagionidae	USA: MD	New sequence	DQ415527
Chrysopilus rhagiodes	Rhagionidae	Costa Rica	New sequence	DQ415528
Chrysopilus thoracicus	Rhagionidae	USA: MD	New sequence	DQ415529
Chrysopilus sp.	Rhagionidae	Tasmania	New sequence	DQ415531
Chrysops vittatus	Tabanidae	USA: MD	New sequence	DQ415542
Dasyomma coeruleum	Athericidae	Chile	New sequence	DQ415532
Dasyomma vittatum	Athericidae	Chile	New sequence	DQ415533
Glutops rossi	Pelecorhynchidae	USA: WA	GenBank	AF238570, AF238546, AF238521
Isalomyia irwini	Vermileonidae	Madagascar	Genbank	AF238552, AF238528, AF238506
Leptynoma hessei	Vermileonidae	South Africa	Genbank	AF238552, AF238528, AF238506
Omphalophora fasciata **n. comb.**	Rhagionidae	Saskatchewan	New sequence	DQ415534
Pelecorhynchus personatus	Pelecorhynchidae	Australia	GenBank	AF238569, AF238545, AF238520
Ptiolina sp.	Rhagionidae	USA: CO	New Sequence	HM770492
Rhagio mystaceus	Rhagionidae	USA: IL	GenBank	AF238510 , AF238531, AF238555
Rhagio vertebratus	Rhagionidae	USA: IL	GenBank	AF238509 ,AF238532, AF238556
Spaniopsis clelandi	Rhagionidae	Tasmania	New sequence	DQ415537
Spaniopsis longicornis	Rhagionidae	Australia	New sequence	DQ415538
Symphoromyia atripes	Rhagionidae	USA: IL	GenBank	AF238559, AF238535
Symphoromyia hirta	Rhagionidae	USA: IL	New sequence	DQ415539
Symphoromyia sp.	Rhagionidae	USA: AK	New sequence	DQ415540
Tabanus atratus	Tabanidae	USA: NC	GenBank	AF238568, AF238544, AF238519
Tabanus rufofrater	Tabanidae	USA: GA	GenBank	AF238561, AF238537, AF238513
Tabanus subsimilis	Tabanidae	USA: MD	New sequence	DQ415541
Vermileo opacus	Vermileonidae	USA: CA	New sequence	HM770493
Vermileo vermileo	Vermileonidae	Israel	New sequence	DQ415543
Arthropeas magna	Xylophagidae	Saskatchewan	GenBank	AF238549, AF238525, AF238503
Dialysis elongata	Xylophagidae	USA: NC	GenBank	AF238551, AF238527, AF238505
Coenomyia ferruginea	Xylophagidae	USA: TN	GenBank	AF238550, AF238526, AF238504
Exeretonevra angustifrons	Xylophagidae	Australia	New sequence	HM770494
Heterostomus curvipalpis	Xylophagidae	Chile	New sequence	HM770495
Xylophagus abdominalis	Xylophagidae	USA: NC	New sequence	HM770496
Pachygaster leachii	Stratiomyidae	England	GenBank	AF238548, AF238524, AF238502
Pantophthalmus sp.	Pantophthalmidae	Costa Rica	GenBank	AF238547, AF238523, AF238501

Laboratory methods for molecular data. 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. DNA specimen vouchers and their DNA are deposited in the frozen tissue collection of the California State Collection of Arthropods (CSCA), Sacramento, CA.

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. The PCR was done using a Biometra PCR machine with the following program: 95°C initial denature step of three 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 & 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 re-suspended 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 4. Taxon sampling for combined analysis.

Taxon for morphological characters	Taxon for molecular characters (if different)	Family
Arthroceras fulvicorne		Rhagionidae
Arthroteles cinerea		Rhagionidae
Atherimorpha atrifemur		Rhagionidae
Atherimorpha montana		Rhagionidae
Atherimorpha nemoralis		Rhagionidae
Atherimorpha vernalis		Rhagionidae
Atherix pachypus	*Atherix variegata*	Athericidae
Austroleptis collessi		Austroleptidae
Austroleptis multimaculata		Austroleptidae
Bolbomyia nana		Rhagionidae
Chrysopilus quadratus		Rhagionidae
Chrysopilus rhagiodes		Rhagionidae
Chrysopilus thoracicus		Rhagionidae
Chrysops vittatus		Tabanidae
Dasyomma coeruleum		Athericidae
Dasyomma vittatum		Athericidae
Glutops rossi		Pelecorhynchidae
Isalomyia irwini		Vermileonidae
Leptynoma hessei		Vermileonidae
Omphalophora fasciata **n. comb.**		Rhagionidae
Ptiolina zonata	*Ptiolina* sp.	Rhagionidae
Pelecorhynchus personatus		Pelecorhynchidae
Rhagio mystaceus		Rhagionidae
Rhagio vertebratus		Rhagionidae
Spaniopsis clelandi		Rhagionidae
Spaniopsis longicornis		Rhagionidae
Symphoromyia atripes		Rhagionidae
Symphoromyia hirta		Rhagionidae
Tabanus atratus		Tabanidae
Tabanus rufofrater		Tabanidae
Tabanus subsimilis		Tabanidae
Vermileo opacus		Vermileonidae
Vermileo vermileo		Vermileonidae
Arthropeas americana	*Arthropeas magna*	Xylophagidae
Coenomyia ferruginea		Xylophagidae
Dialysis rufithorax	*Dialysis elongata*	Xylophagidae
Exeretonevra angustifrons		Xylophagidae
Heterostomus sp.		Xylophagidae
Xylophagus lugens	*Xylophagus abdominalis*	Xylophagidae
Pachygaster montana	*Pachygaster leachii*	Stratiomyidae

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 M 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. Sequence 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.

The aligned molecular data set consisted of 3096 characters. Most of the sequence data were well conserved in the sampled taxa and the alignment was obvious for most of the dataset (2712 characters; 391 parsimony informative) and the sequences were aligned manually. Where sequence alignment was not obvious, stem and loop structures were identified using the 28S rRNA secondary structure model of *Drosophila melanogaster* as a reference (Hancock *et al.* 1988). Stems were confirmed by compensatory changes within these regions, aligned appropriately, and included in the analysis (52 characters; 39 parsimony informative). Unalignable regions were found in loops and hypervariable length stems within the expansion segments (539 characters) and excluded from all analyses. Location details of these character set regions, including nucleotide numbers that correspond to the secondary structure model of *Drosophila melanogaster* (Hancock *et al.* 1988), are contained within the data file. The data file showing alignment and character set designations is deposited at TreeBASE (*last accessed 20 May 2010*: http://www.treebase.org).

Phylogenetic analysis. The phylogenetic analysis of Tabanomorpha is presented in three sections. The first treats the morphology of the group, the second section is a molecular treatment, and the third is a combined, simultaneous analysis of both morphological and molecular data.

Morphological data was analyzed using parsimony; 1000 heuristic search replicates were performed using *PAUP* 4.0b10* (Swofford 2001), 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. Bremer support values (Bremer 1988) were calculating using *TreeRot* (Sorenson 1999). MacClade 4.03 (Maddison & Maddison 2000) was used to analyze character change and support in the phylogenetic tree.

The molecular data was analyzed using parsimony (MP), maximum likelihood (ML), and Bayes inference (BI). For MP analyses, characters were unordered and assigned equal weights at all sites (Fitch 1971). Heuristic search replicates (n = 1000) were performed in *PAUP* 4.0b10* (Swofford 2001) with random-taxon-addition, tree bisection reconnection (TBR) branch swapping, steepest descent and 'MulTrees' Parsimony bootstrap analyses were performed with 1000 repetitions, each with 30 random-taxon-addition TBR heuristic searches (Felsenstein 1985).

Modeltest 3.06 (Posada & Crandall 1996) was used to select among 56 nested models of sequence evolution for the ML analyses. 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). The parameters found by Modeltest were then re-estimated and optimized using the most likely tree found by a GTR+I+Γ search with nearest-neighbor interchange (NNI) branch swapping and three random taxon addition sequences. This was done for three iterations, at which time the parameters converged on identical values. The final ML heuristic search was conducted using the GTR+I+Γ model and optimized parameters with five random taxon addition sequences, tree-bisection reconnection (TBR) branch swapping, and steepest descent option active. ML bootstrap analyses were performed with 100 repetitions, each with three random-taxon-addition NNI heuristic searches.

Bayesian inference of the molecular data set was implemented using MrBayes 3.0b4 (Ronquist & Huelsenbeck 2003). Markov chain set for four million generations, with sampling every 200th generation for a total of 20,000 tree samples. Stems and loops were set as separate partitions. Each partition retained their own set of parameters and rates were allowed to vary across all partitions. The GTR+I+Γ doublet model was applied to the stem regions and a standard GTR+I+Γ model was set for the loop regions. 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 were considered burn-in and discarded. Burn-in was set to 250 (=50,000 generations). The posterior distribution of trees sampled from the Markov chain was summarized using the 'sumt' command.

The morphological and molecular data sets were combined and full, simultaneous MP and BI analyses were carried out following the procedures as above. Parsimony bootstrap analyses were performed with 1000 repetitions, each with 5 random-taxon-addition TBR heuristic searches. Partitioned Bremer Support (PBS) support values were calculating using *TreeRot* (Sorenson 1999).

Tests of alternative hypotheses. Hypotheses regarding the monophyly and placement of Pelecorhynchidae, Vermileonidae, *Bolbomyia*, *Austroleptis*, and Rhagionidae were tested in combined parsimony analyses of the molecular and morphological data. This was done by carrying out MP heuristic searches, with nodes constrained according to hypothesized arrangements (Table 6). The hypotheses were evaluated individually by comparing the difference in length between the most parsimonious constrained (predicted, given the hypothesis) and unconstrained (actual, given the data) trees. The Kishino-Hasegawa and Wilcoxon sign-rank tests were applied using *PAUP* 4.0b10* (Swofford 2001) to determine if the difference between predicted and actual trees was significant.

Results

Morphological characters and character state coding

A total of 126 morphological characters were compiled and their character state coding is detailed below. The complete scoring matrix is provided in Table 5.

Adult head

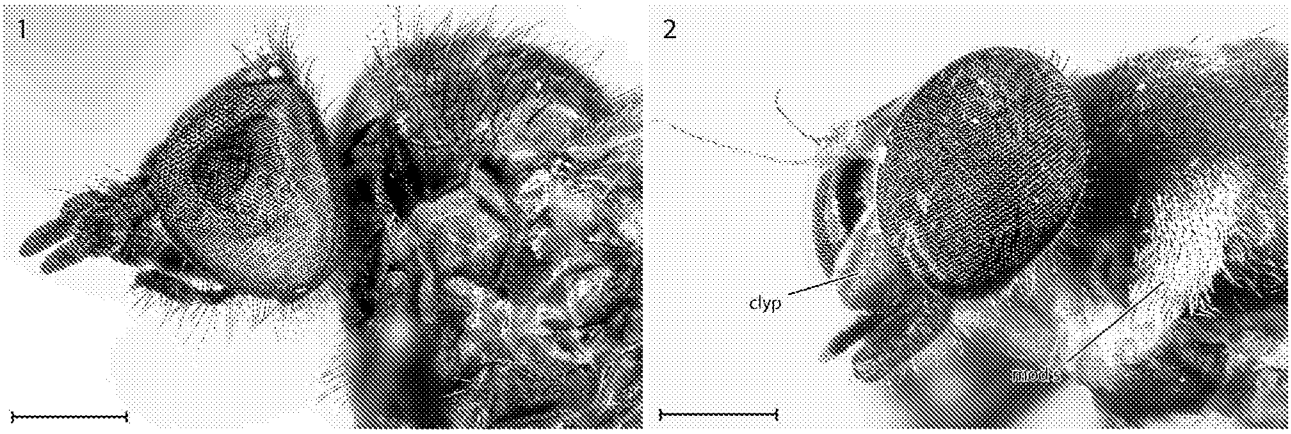
1. Head width. (1) Wider than thorax (2) approximately same width as thorax (3) narrower than thorax. Teskey used head width to characterize *Glutops* (Teskey 1970b: 1171). Most taxa surveyed here have a head that is approximately the same width as the thorax, although there is variation among species within genera (*Chrysopilus*, *Rhagio*, *Spaniopsis*) and even within species (*Chrysopilus quadratus* (Say), *Spaniopsis clelandi* Ferguson, *Symphoromyia cruenta* Coquillett). The differences between approximately the same width and wider may be subtle, as in the case of *Pseudoerinna jonesi* (Cresson) where the state is scored as head wider than thorax.

2. Clypeus. (1) Bulbous (2) not bulbous. The bulbous clypeus is a putative synapomorphy for Tabanomorpha (Woodley 1989). All Rhagionidae have this character. In *Austroleptis*, the clypeus is recessed, as in Xylophagidae (Fig. 1). The clypeus in *Litoleptis* is nearly flat, as it is in *Bolbomyia*. For both of these genera, the clypeus is scored as bulbous, although it is only slightly so. I examined 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 (and nearly beak-like, as in *Schizella furcicornis* (Fig. 2)). An attempt was made to score the relative sharpness of the break between the eye and clypeus, but this is variable within large genera such as *Chrysopilus* and *Symphoromyia*, exhibiting a gradual cline among exemplars, made it impossible to define potentially phylogenetically informative morphs suitable for scoring..

3. Eyes (setation). (1) Conspicuously setose (2) sparsely setose. Upon close inspection, ommatrichia (Colless & McAlpine 1991) are visible in most species of brachyceran flies. *Alloleptis tersus* Nagatomi & Saigusa, *Coenomyia ferruginea* (Scopoli) and *Pseudoerinna jonesi* (but not *P. fuscata* Shiraki) have eyes that are conspicuously setose.

4. Eyes in male (separation). (1) Holoptic (2) dichoptic. Males in these genera have eyes that either touch centrally (holoptic) or are separated (dichoptic). 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.

5. Eyes in male (dorsally flattened). (1) Flattened dorsally (2) not flattened dorsally. 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* (Fig. 1), *Glutops*, *Symphoromyia*, and many tabanids including *Dichelacera* Macquart and *Tabanus*.

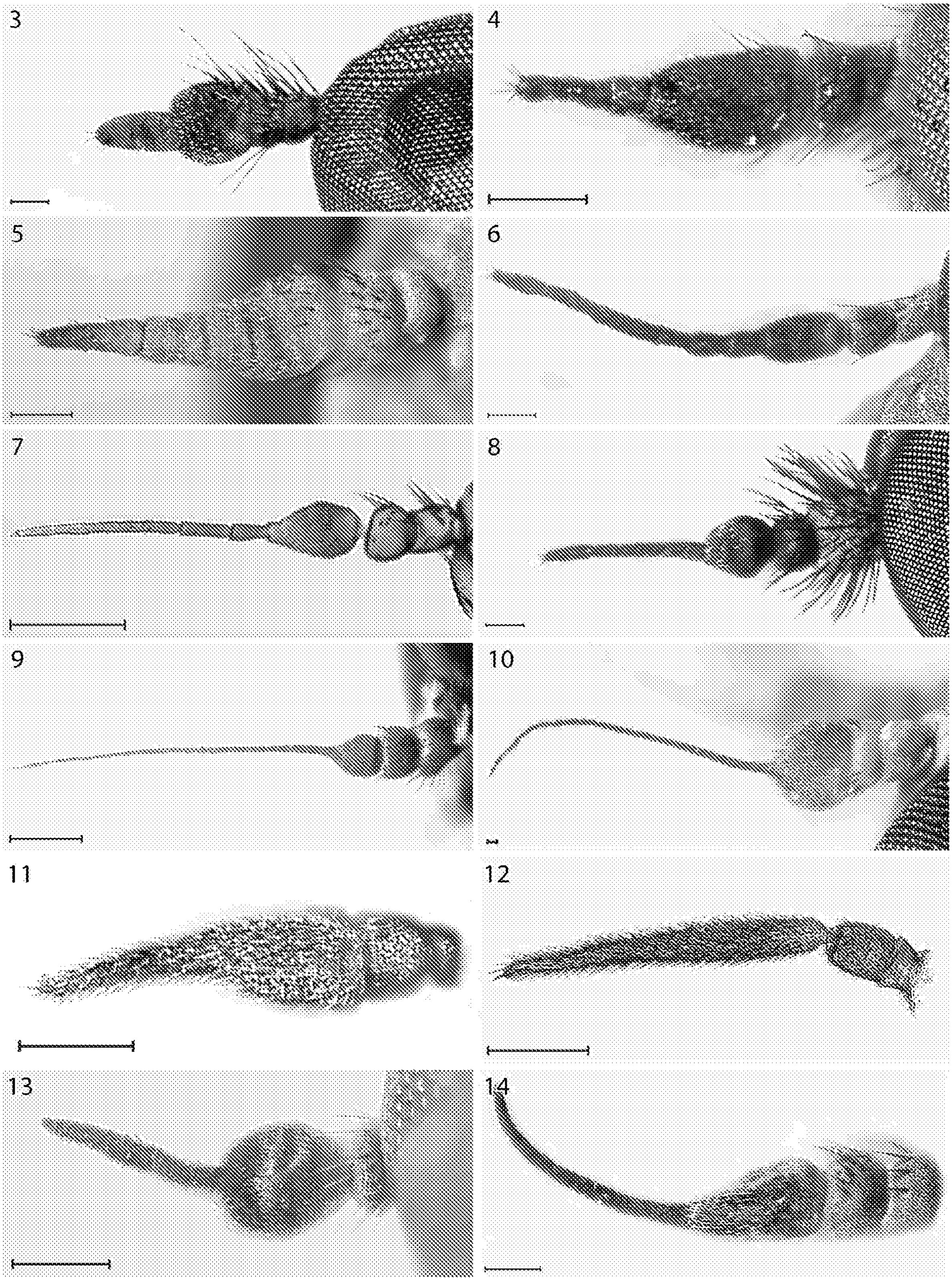


FIGURES 1–2. Austroleptidae and Rhagionidae, scale bar = 0.5 mm. 1, *Austroleptis multimaculata* [USNMENT00025739], lateral view ; 2, *Schizella furcicornis* [USNMENT00025863], oblique lateral view. *Abbreviations: clyp = clypeus; mod s = modified setae.*

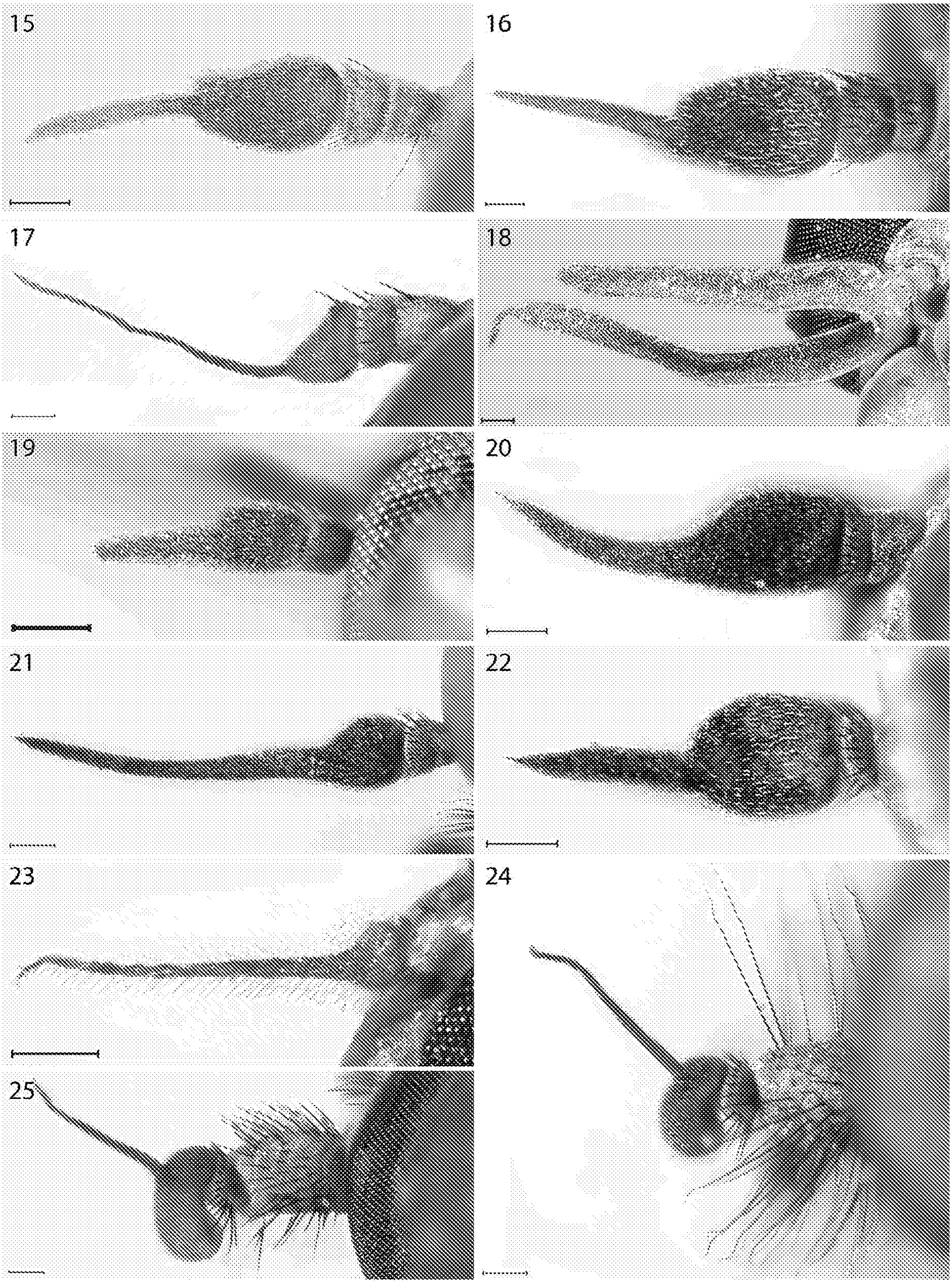
6. Eyes in male (facets). (1) Facets evenly distributed, of equal size (2) facets evenly distributed, gradually smaller toward ventral margin (3) facets split into upper and lower areas. Differential sizing of eye facets may also be associated with swarming behavior (e.g., McAlpine & Munroe 1968; Downes 1969). 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). William J. Turner (pers. comm.) has seen *Chrysopilus* and *Rhagio* species swarm in Washington state; D.M. Wood (pers. comm.) has witnessed *Glutops* and *Bolbomyia* hilltopping in Gatineau Park, Quebec. *Symphoromyia* is also a well-known swarmer (Shemanchuk & Weintraub 1961).

7. Scape. (1) Smaller than pedicel (2) approximately the same size as pedicel (3) clearly larger than pedicel. In some species of Tabanomorpha, the scape is much larger than pedicel (Figs. 24–25). This may be informative at the genus level for *Atherimorpha*, *Desmomyia*, *Dichelacera*, *Glutops*, *Lampromyia*, *Pelecorhynchus*, *Symphoromyia*, and *Vermileo*.

8. First flagellomere (lateral compression). (1) Laterally compressed (2) rounded in cross section. In most taxa, the amount of lateral compression of the first flagellomere is easily scored. Species of *Austroleptis*, *Chrysopilus*, *Rhagio*, and *Symphoromyia* have first flagellomere clearly laterally compressed (e.g., Figs. 3, 10, 17, 25), whereas in species of *Arthroceras*, *Arthroteles*, *Glutops*, *Pseudoerinna*, *Pelecorhynchus*, and Xylophagidae, the first flagellomere is rounded in cross section (e.g., Figs. 5–6). There are cases, however, where congenerics may differ in having laterally compressed or rounded first flagellomere. For example *Omphalophora fasciata* (Loew) **n. comb.** has a clearly flattened first flagellomere (Fig. 13), whereas *O. majuscula* (Loew) **n. comb.** has the first flagellomere rounded (Fig. 14). Variation of this kind 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, yet still at least oval in cross section. In these instances, the scoring may be subtle. *Stylospania lancifera* Frey is scored as having a laterally compressed first flagellomere.



FIGURES 3–14. Antennae, lateral view, scale bar = 0.1 mm (except where noted). 3, *Austroleptis multimaculata* [USNMENT00025739]; 4, *Bolbomyia nana* [USNMENT00022909]; 5, *Arthroceras fulvicorne* [USNMENT00022731]; 6, *Arthroteles cinerea* [USNMENT00023229]; 7, *Atherimorpha nemoralis* [USNMENT00028402]; 8, *Atherimorpha praefica* [USNMENT00024941]; 9, *Chrysopilus ornatus* [USNMENT00025947], scale bar = 1.0 mm; 10, *Chrysopilus quadratus* [USNMENT00025948]; 11, *Litoleptis alaskensis* PARATYPE [USNMENT00024417]; 12, *Litoleptis chilensis* HOLOTYPE; 13, *Omphalophora fasciata* [USNMENT00025460]; 14, *Omphalophora majuscula* [USNMENT00025471].



FIGURES 15–25. Antennae (cont.), lateral view, scale bar = 0.1 mm. 15, *Ptiolina edeta* [USNMENT00023016]; 16, *Ptiolina zonata* [USNMENT00022846]; 17, *Rhagio scolopaceus* [USNMENT00023194]; 18, *Schizella furcicornis* [USNM00025870]; 19, *Spania nigra* [USNMENT00025865]; 20, *Spaniopsis clelandi* [USNMENT00025409]; 21, *Spaniopsis mackerrasi* [USNMENT00025556]; 22, *Spaniopsis rieki* [USNMENT00022653]; 23, *Stylospania lancifera* HOLOTYPE; 24, *Symphoromyia hirta*, male [USNMENT00028585]; 25, *Symphoromyia hirta*, female [USNMENT00028622].

9. Antennal flagellum (presence of break). (1) Gradually tapered (2) with abrupt change between the first flagellomere and those distal to it. Hennig (1972) proposed that a break between the first flagellomere and those distal to it could be a synapomorphy for Rhagionidae. The break may be somewhat subtle, as in species of *Arthroteles* (Fig. 6). In *Arthroteles*, the first flagellomere is distinct in that it is not only enlarged, but the flagellomeres distal to it are smaller, cylindrical, and not tapering. Examples of gradually tapering antennae include species of *Arthroceras* (Fig. 5) and *Pelecorhynchus*.

10. Segment(s) distal to first flagellomere (where abrupt change evident). (1) Segmented flagellomeres (2) stylus (3) arista. 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* (Fig. 6), *Atherimorpha* (Figs. 7–8), *Austroleptis* (Fig. 3), and *Bolbomyia* (Fig. 4) 2) stylate, as in *Litoleptis* (Figs. 11–12), *Omphalophora* (Figs. 13–14), *Ptiolina* (Figs. 15–16), *Spania* (Fig. 19), and *Spaniopsis* (Figs. 21–22) or 3) aristate, as in *Atherix*, *Chrysopilus* (Figs. 9–10), *Dialysis*, *Lampromyia*, *Rhagio* (Figs. 17), *Suragina* Walker, *Symphoromyia* (Figs. 24–25), and *Vermileo*. Nagatomi (1982a) has also asserted that having an antenna with a tapering, stylate first flagellomere distinguishes subfamily Spaniinae.

11. Arista. (1) Microsetose (2) pruinose. 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.

12. Parafacials in male. (1) Not swollen (2) swollen. 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.

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: 304). The mouthparts show a high degree of plasticity and it appears that their morphology is generally more indicative of feeding behavior than common ancestry. An obvious example is the shared retention of mandibles among the blood feeders (Tabanidae, Athericidae, *Symphoromyia*, and *Spaniopsis*). Due to its destructive nature, sampling internal mouthpart features was not possible for many taxa.

13. Cardo. (1) Absent (2) not swollen (3) swollen. The cardo in *Pelecorhynchus personatus* (Walker) is conspicuously inflated (Fig. 33). The cardo is also enlarged in *Pseudoerinna jonesi* and *Symphoromyia cruenta*. This structure is apparently absent in *Dasyomma atratulum* Malloch, *Dialysis rufithorax* (Say), *Chrysopilus* species and *Suragina concinna* (Williston).

14. Palpal segment number. (1) One-segmented (2) two-segmented. The reduction in palpomere number from three to two is a synapomorphy for Brachycera (Hennig 1973; Woodley 1989). The number of palpal segments (either one or two) varies across Tabanomorpha, however.

15. Palpal segment relative length. (1) Proximal segment longer than distal segment (2) proximal and distal segments about the same length (3) distal segment longer than proximal segment. For genera with two palpomeres, the length of palpal 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* Loew. In this species, the proximal segment is longer than the distal segment in males whereas in the female, the reverse is true.

16. Mandibles. (1) Absent (2) present. Mandibles are required for blood feeding. Not surprisingly, mandibles are present in all the blood feeding flies (*Atherix*, *Dasyomma*, *Dichelacera*, *Spaniopsis* (Fig. 32), *Suragina*, *Symphoromyia*, and *Tabanus*) and are absent in all non-blood feeding flies (e.g., Fig. 33).

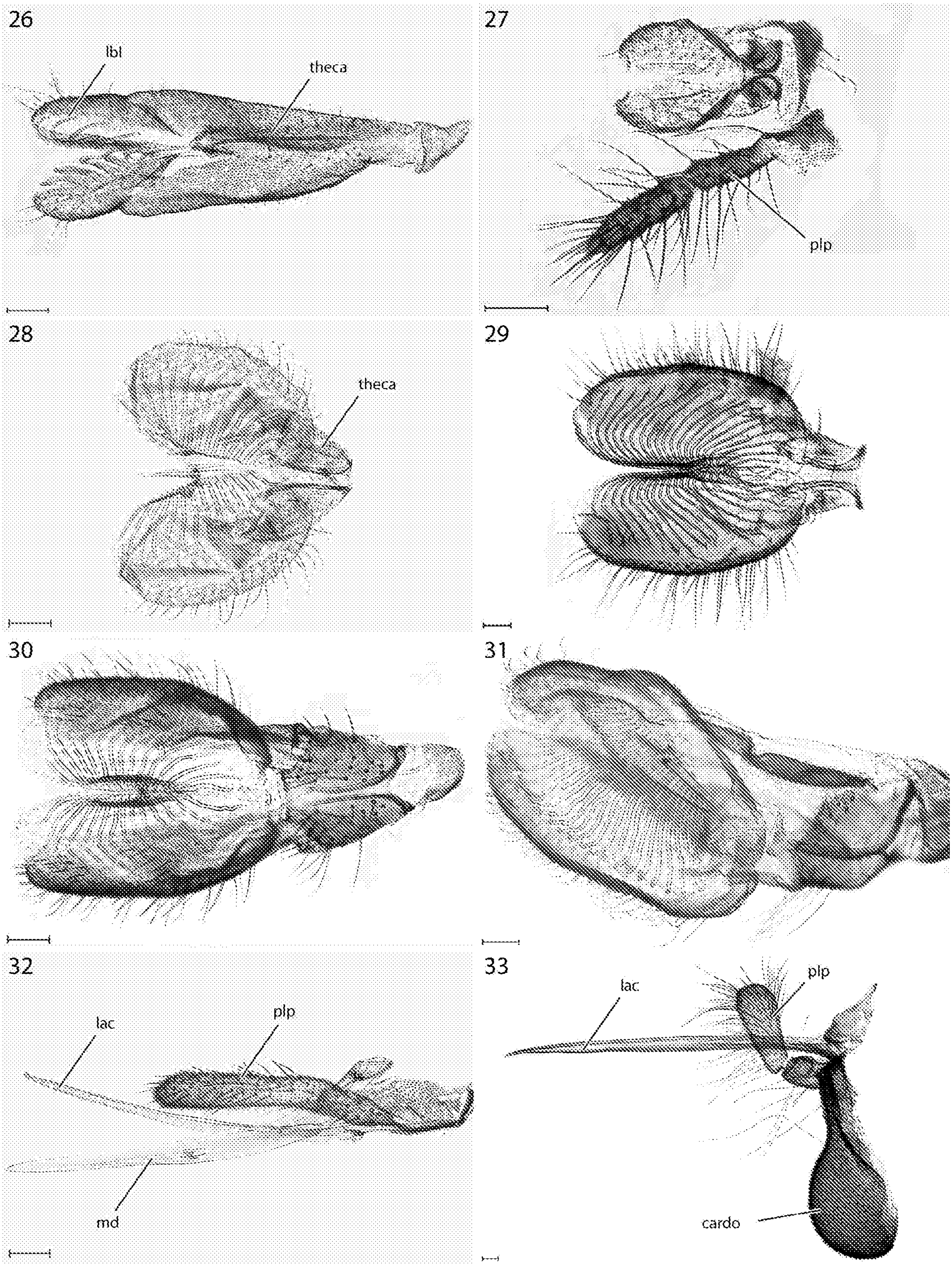
17. Lacinia length. (1) Shorter than palpus (2) longer than palpus. Lacinia were scored relative to the length of the palpus. This character was much easier to score when the head was dissected. In undissected specimens, the lacinia were sometimes visible, however, most often the lacinia were concealed and no scoring was possible. Since the heads of rare species were not dissected, there are a number of taxa unscored for this character. *Pseudoerinna*, *Tabanus*, *Vermileo*, *Lampromyia*, *Suragina*, and *Dialysis* were scored from illustrations (Nagatomi & Soroida 1985).

18. Theca (elongation). (1) Elongate (2) short. 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* (Fig. 26), *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 (e.g., Figs. 27–31). Most *Dasyomma* species are as *D. atratulum* (scored here) in having a short theca, however in at least one *Dasyomma* species (*D. coeruleum* Macquart), the theca is elongate. Similarly, *Symphoromyia* species may either have short or long thecae.

19. Theca (lateral sclerite composition). (1) Lateral sclerites separated (2) lateral sclerites adjacent and or separated by medial suture (3) fused into single sclerite, without medial suture. The theca is often divided by a medial suture. States of the theca seem naturally divided into three states; lateral sclerites separate (e.g., Fig. 29), lateral sclerites adjacent and/or separated by medial suture (e.g., Fig. 31), or fused into single sclerite, without medial suture (as in *Arthroteles* and most tabanids and athericids). This character is most easily viewed after the head is dissected. Therefore, there are a number of taxa not scored for this character since head dissections were not carried out on rare taxa.

20. Pseudotracheae. (1) Present (2) absent. *Bolbomyia* (Fig. 27), *Litoleptis*, and *Lampromyia* are the only taxa surveyed that did not have pseudotracheae. *Austroleptis* has distinctive pseudotracheae that have taenidia-like ribbing (Fig. 26). Other taxa, such as *Arthroceras* show some transverse ribbing of the pseudotracheal channels (Fig. 28), 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 is scored for phylogenetic analysis.

21. Occiput. (1) Rounded, with smooth transition from dorsal to posterior part of head (2) flattened, concave posteriorly. The concave occiput present in members of Tabanidae is characteristic for the family. *Pelecorhynchus* has a similar head shape.



FIGURES 26–33. Mouthparts, ventral view, scale bar = 0.1 mm. 26, *Austroleptis multimaculata* [USNMENT00025905]; 27, *Bolbomyia nana* [USNMENT00025904]; 28, *Arthroceras pollinosum* [USNMENT00022625]; 29, *Rhagio mystaceus* [USNMENT00025908]; 30, *Spaniopsis clelandi* [USNMENT25907]; 31, *Symphoromyia* sp. [USNMENT00025909]; 32, *Spaniopsis clelandi* [USNMENT25907]; 33, *Pelecorhynchus fusconiger* [USNMENT00025360]. *Abbreviations: lac = lacinia; lbl = labellum; md = mandible; plp = palp.*

Adult thorax

22. Dorsum setation. (1) All setae of equal length (2) acrostichal, dorsocentral, and intra-alar setae distinguished from other setae on dorsum. Species of South American *Atherimorpha* are distinguished from congeners in Australia by having rows of dorsal setae that are stronger and longer than other setae of the dorsum.

23. Scale-like colored setae. (1) Absent (2) present. Flattened, scale-like setae reflecting blue, red, or golden colors (e.g., Fig. 2) and are present in *Chrysopilus, Schizella,* and apparently in *Stylospania* (although it is difficult to determine, given the poor state of the holotype). *Pelecorhynchus* may have similarly colored setae, but they are not flattened and are of a different nature.

24. Proepimeron. (1) Absent (2) present, reduced (3) present, well developed. The proepimeron is variously developed among genera within Tabanomorpha, yet consistent within genera. The proepimeron is located posterior to the proepisternum and anterior to 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* Meigen, the proepimeron is apparently absent. In most taxa (*Arthroceras*, *Atherimorpha*, *Atherix*, *Austroleptis*, *Bolbomyia*, *Rhagio*, and others), the proepimeron is roughly rectangular, approximately twice as long (dorsoventrally) as wide (anterior-posteriorly) (Fig. 37). In *Chrysopilus*, *Schizella*, and *Stylospania*, however, the proepimeron is reduced and slender (Fig. 36).

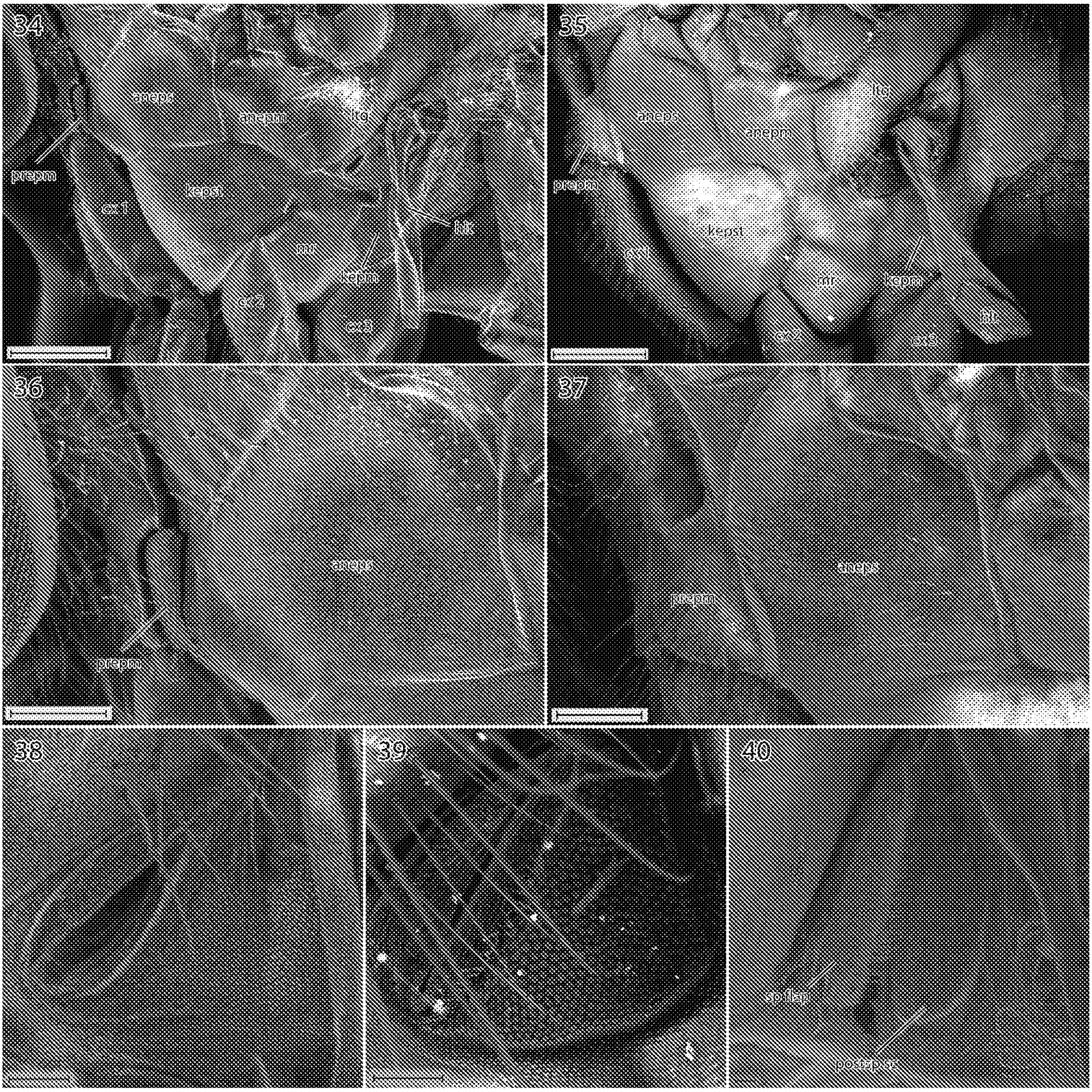
25. Proepimeron setation. (1) Setose (2) bare. The proepimeron may be with or without setae. *Rhagio* and *Desmomyia* are the only Rhagionidae *sensu lato* with setose proepimera (Fig. 37). Other genera with setae-bearing proepimera are *Arthropeas* Loew, *Atherix*, *Coenomyia*, *Dichelacera*, *Suragina*, and *Tabanus*.

26. Anepisternum setation. (1) Bare or with one or two setae (2) setose, bearing at least more than two setae. 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 simplified into two states: 1) anepisternum bare or with one or two setae or 2) setose, bearing at least more than two setae. All *Rhagio* species scored here have at least one anepisternal seta. *Ptiolina* have a bare anepisternum (e.g., *P. zonata*, *P. mallochi*) while *Omphalophora* species, approximately half the surface of the anepisternum is covered with setae (e.g., *O. lapponica* Frey, *O. majuscula*).

27. Laterotergite form. (1) Katatergite swollen, differentiated from anatergite (2) katatergite and anatergite indistinguishable. 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* and *Sierramyia* Kerr, gen. nov.). The katatergite is 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 many *Symphoromyia* species, the katatergite is swollen in the female, but indistinguishable from the anatergite in the male.

28. Laterotergite setation. (1) Bare (2) setose. The presence or absence of laterotergite setae is a commonly used character in taxonomic keys to distinguish genera of Tabanomorpha.

29. Laterotergite setal arrangement. (1) Present throughout laterotergite (2) present mostly on katatergite (3) present on katatergite only. 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, *Pseudoerinna jonesi*, *Schizella* species, *Arthropeas americana* Loew, *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.



FIGURES 34–40. Thoracic sclerites, lateral view, scanning electron micrographs. 34, *Chrysopilus quadratus*, sb = 0.5 mm; 35, *Rhagio mystaceus*, sb = 0.5 mm; 36, *Chrysopilus quadratus*, sb = 0.2 mm; 37, *Rhagio mystaceus*, sb = 0.2 mm; 38, *Chrysopilus quadratus*, posterior spiracle, sb = 0.05 mm; 39, *Rhagio mystaceus*, posterior spiracle, sb = 0.05 mm; 40, *Pelecorhynchus fusconiger*, posterior spiracle, sb = 0.05 mm. *Abbreviations: anepm = anepimeron; aneps = anepisternum; cx = coxa; hlt = halter; kepst = katepisternum; kepm = katepimeron; ltg = laterotergite; mr = meron; postsp sc = postspiracular scale; prepm = proepimeron; sp flap = spiracular flap.*

30. Posterior thoracic spiracle. (1) Without lappets (2) with lappets. The upper margin of the posterior thoracic spiracle may be produced in the form of a lappet that apparently may be used to close the spiracle airway (e.g., in *Pelecorhynchus*, Fig. 40). The presence of lappets 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* (Wiedemann) and *Chrysopilus thoracicus*) in these cases, the spiracle is scored as not having lappets (Fig. 38). Flaps were scored as present when it was clear the lappets themselves could close the spiracle airway, without constriction of the surrounding membrane.

31. Posterior thoracic spiracle lining. (1) Not lined with microsetae (2) lined with microsetae. 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.

32. Postspiracular scale. (1) Absent (2) present. The presence of a postspiracular scale is a putative synapomorphy for Tabanidae and Athericidae (Stuckenberg 1973). Species of *Pelecorhynchus* also have this character state (Fig. 40). In *Pseudoerinna 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 *Pseudoerinna jonesi*. The postspiracular sclerite is also broadly raised in species of *Rhagio* (Fig. 39), although with a different orientation than what is found in the tabanids, athericids, and pelecorhynchids.

33. Postspiracular sclerite setation. (1) Bare (2) setose. The postspiracular sclerite is setose only among xylophagid taxa. A possible exception is *Exeretonevra* Macquart and *Heterostomus* (not included in this matrix), where although the postspiracular sclerite is setose, setae are found only on its dorsal margin.

34. Setation posterior to postspiracular sclerite. (1) Bare (2) setose. 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, *Pseudoerinna jonesi*, *Symphoromyia* species, and *Xylophagus lugens*.

35. Proscutellum. (1) Present (2) absent. 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* Meigen, and *Vermileo vermileo* (Linnaeus). It is clearly present in *Rhagio costatus* (Loew), however, it is absent in other species of *Rhagio* species examined.

36. Subscutellum form. (1) Not bulbous (2) bulbous. Species of *Atherix*, *Dasyomma*, *Dichelacera*, *Pelecorhynchus*, *Pseudoerinna*, and *Tabanus* have a raised, swollen area of the subscutellum visible. In all other taxa surveyed, the subscutellum is smooth.

37. Subscutellum setation. (1) Bare (2) setose. In xylophagid taxa, the subscutellum is setose, at least within the lateral margins.

Wing

38. Lower calypter. (1) Reduced (2) present. An invagination indicates the separation between upper and lower calypters. In 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.

39. Alula development. (1) No curvature, reduced (2) narrow curvature (3) broad curvature. The lack of an alula is very evident in species of *Sierramyia* (Fig. 59) 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. 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.

40. Alula shape. (1) Curvature shifted distally (2) rounded evenly. 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. This state is also seen in species of *Glutops*, *Pelecorhynchus*, *Pseudoerinna*, *Spania*, and *Spaniopsis* (Figs. 60–62). The alula is scored as evenly rounded where the mean of the distribution of the alular area is at or near its center (e.g., Figs. 41, 43, 50, 53, 55, 63).

41. Sc-r crossvein location. (1) Positioned proximal of the humeral crossvein (h) (2) positioned distal to h by less than length of h (3) positioned distal to h by the approximate length of h (4) positioned distal to h by more than length of h (5) located approximately midway between h and the origin of the radial-sector. 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* is autapomorphic in having sc-r located on the proximal side of the humeral crossvein. Unfortunately, because of the pleated nature of the wing and the fact that the sc cell is usually oriented vertically, the position of the Sc-r crossvein is most easily viewed from an anterior perspective and is rarely captured in figures or illustrations.

42. R_1 setation, dorsal surface. (1) Setose (2) bare. The presence of setae on dorsal surface of R_1 is the common condition for most lower flies. *Litoleptis*, *Lampromyia*, and *Vermileo*, however, are exceptions to this.

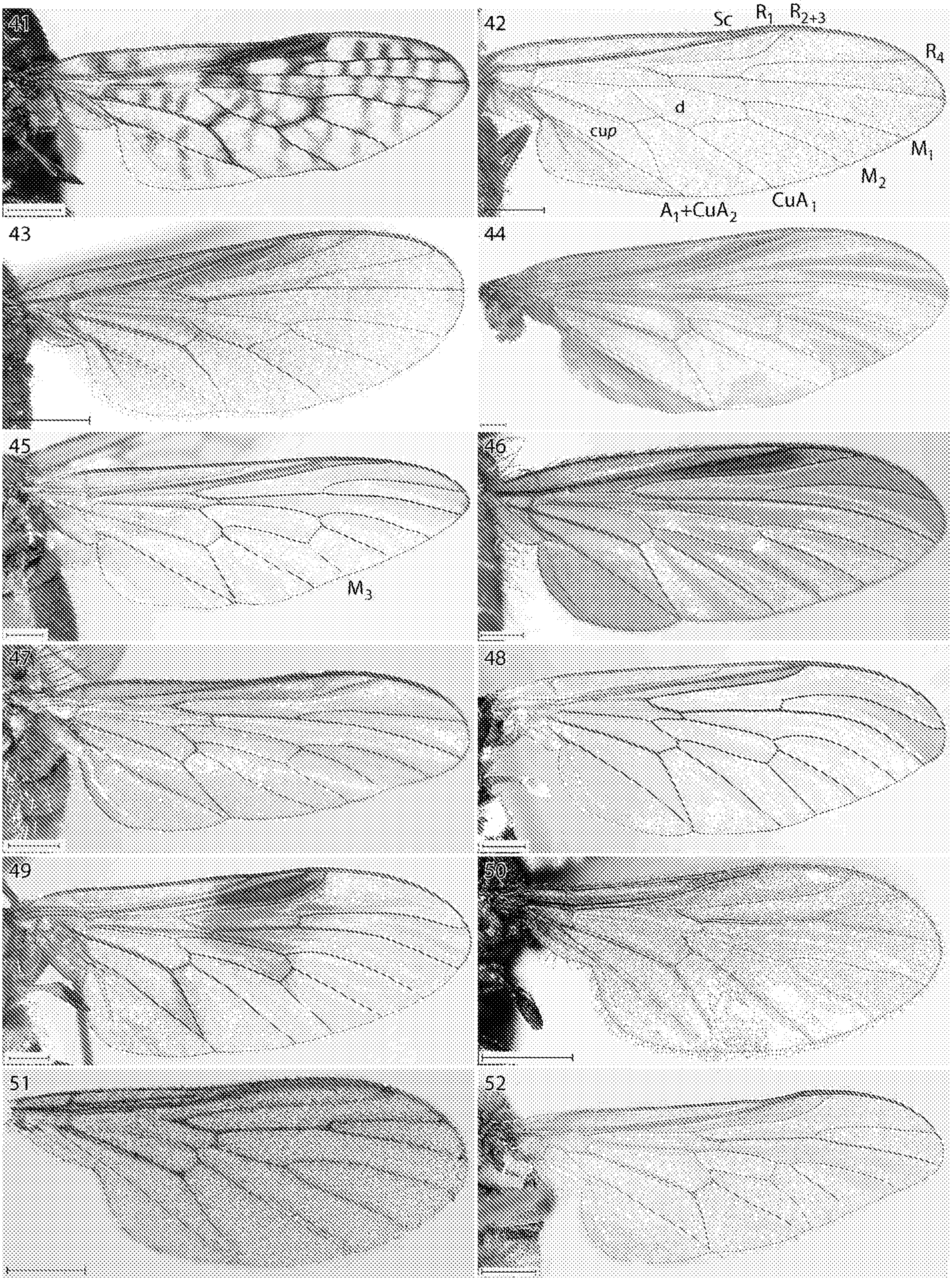
43. R_1 setation, ventral surface. (1) Bare (2) setose. The lack of setae on ventral surface of R_1 is the common condition for most lower flies. Ventral R_1 setae are found in some, but not all species of *Atherimorpha*, *Austroleptis*, and *Xylophagus* however. Due to the limited taxon sampling of *Austroleptis* and *Xylophagus*, the morphological diversity of these genera is not fully represented in the matrix.

44. Wing veins R_1 and R_{2+3} at wing margin (orientation). (1) Meet together at wing margin (2) close together at wing margin (3) separated at wing margin (4) widely separated 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 Athericidae is for wing veins R_1 and R_{2+3} to meet together at the wing margin (Stuckenberg 1973). Where R_{2+3} is not joined to R_1 but clearly closer to R_1 than to R_4, it is scored as 'close together at wing margin' (e.g., Figs. 41, 44, 48, 52, 57, 62, 63). Where R_{2+3} is closer to R_1 than to R_4 at the wing margin, but ending near the center of cell r_1, it is scored as 'separated at wing margin' (e.g., Figs. 43, 45, 60). When R_{2+3} was closer to R_4 than to R_1, it is scored as 'widely separated at wing margin' (e.g., Figs. 50–51). Tabanidae have R_{2+3} closer to R_4 than to R_1, as do species of *Glutops*, *Lampromyia*, *Pelecorhynchus*, *Pseudoerinna*, and *Vermileo*.

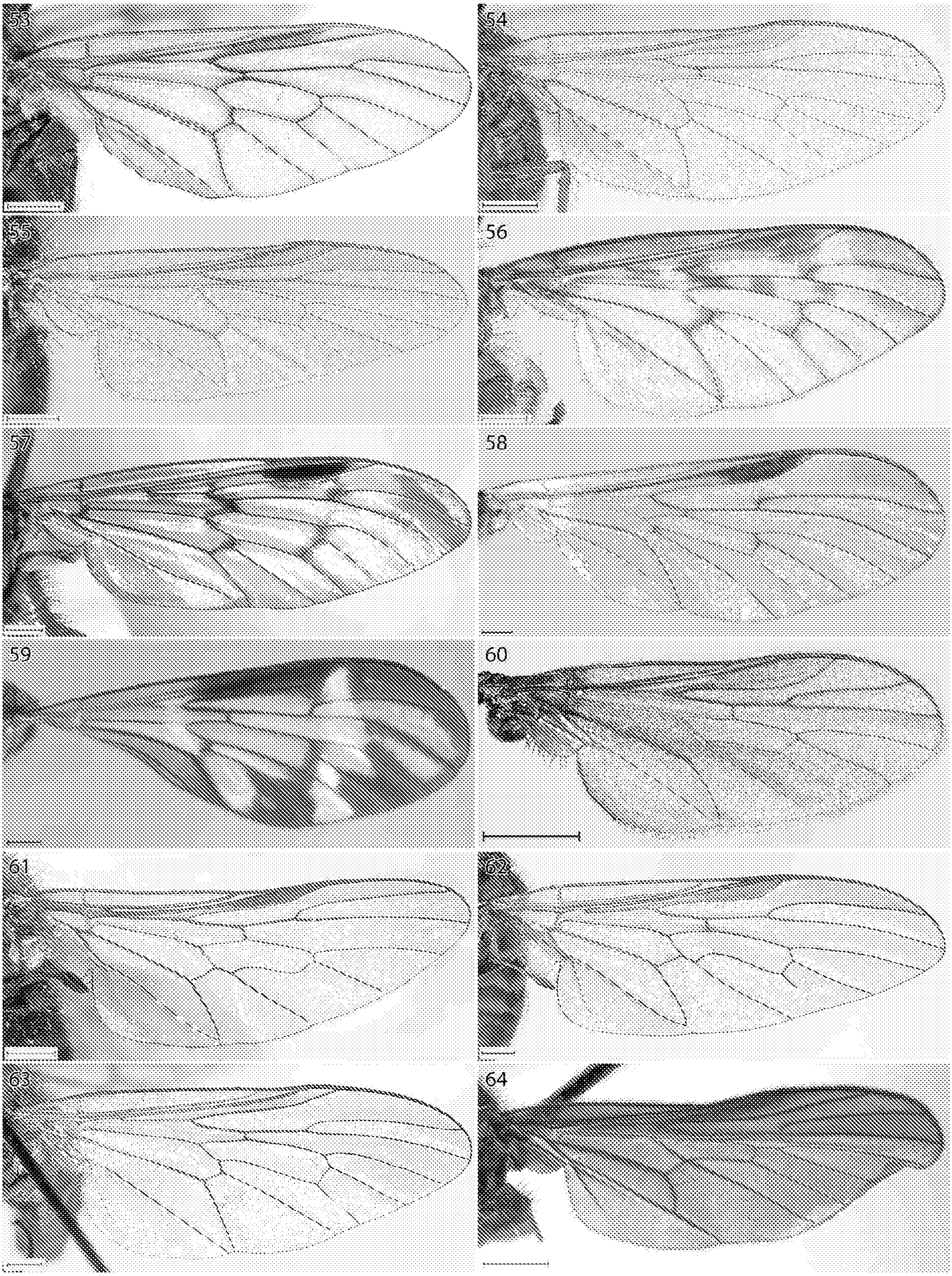
45. Position of R_4–R_5 fork. (1) Distal to distal end of cell dm (2) proximal or directly above distal end of cell dm. Grimaldi & Cumming (1999: 16) note that the base of fork R_4–R_5 is at the same level as the distal end of cell dm, and not distal to it in Rhagionidae. This, they propose, is a potential 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 leading margin of wing, wing base/tip, etc.). I've scored this character by orienting the wing so that its attachment point at the thorax is held horizontal to the wing tip. The R_4–R_5 fork could then be determined on the basis of its position above, relative to cell dm. For example, figures 43, 49, 52, 53, 57, and 64 show the R_4–R_5 fork distal to cell dm. Figures 41, 42, 44–49, 54–56, and 58–63 show the R_4–R_5 fork above cell dm. Species of *Rhagio* may have the base of the R_4–R_5 fork proximal of (as in *R. mystaceus* (Macquart)), directly above (as in *R. plumbeus* (Say), *R. vertebratus* (Say)), or distal to the distal end of cell dm (as in *R. costatus*). *Atherimorpha* and *Omphalophora* species showed similar intrageneric variation for this character.

46. R_4 at base. (1) Strongly curved or angled (2) relaxed, not strongly curved (3) nearly straight. The curvature of R_4 at its base has been proposed as a possible a synapomorphy for Rhagionidae (Grimaldi & Cumming 1999; Stuckenberg 2001: 16). 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 R_4 (e.g., Fig. 48). However, the flexure at the base of 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* (Say) males, the flexure is less severe than in the females and the character is scored as ambiguous. The basal curvature of R_4 in *Rhagio incurvatus* Malloch **n. comb.** is much less abrupt than in other species of *Rhagio*, however it is 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.

47. R_4 at apex. (1) Straight or nearly straight apically (2) curving towards the leading margin of the wing apically. Taxa also vary in the amount of curvature of the apical portion of R_4, as it meets the margin of the wing. In species of *Pelecorhynchus* for example, R_4 veers anteriorly to create a distinctive curvature. In most Tabanidae, R_4 also meets the margin of the wing anteriorly, however the curvature is less pronounced. If R_4 is apically curved so that it is directed anteriorly, it is scored as curving towards the leading margin of the wing (as in *Atherix*, *Pelecorhynchus*, *Tabanus*, and others). If the apical portion of R_4 is straight and directed toward the wing tip, it is scored as straight or nearly straight apically (as in rhagionid taxa; e.g., Figs. 41–64). In some cases, such as in *Omphalophora 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 is scored as nearly straight.



FIGURES 41–52. Wings, scale bar = 0.5 mm. 41, *Austroleptis multimaculata* [USNMENT00025745]; 42, *Austroleptis* sp. (South America) [USNMENT00022609]; 43, *Bolbomyia nana* [USNMENT00024060]; 44, *Arthroceras gadi* [USNMENT00022628]; 45, *Arthroteles cinerea* [USNMENT00023231]; 46, *Atherimorpha atrifemur* [USNMENT00024560]; 47, *Atherimorpha triangularis* [USNMENT00028519]; 48, *Chrysopilus ornatus* [USNMENT00025947]; 49, *Chrysopilus quadratus* [USNMENT00025948]; 50, *Litoleptis alaskensis* PARATYPE [USNMENT00024417]; 51, *Litoleptis chilensis* HOLOTYPE; 52, *Omphalophora fasciata* [USNMENT00025460].



FIGURES 53–64. Wings (cont.), scale bar = 0.5 mm. 53, *Omphalophora majuscula* [USNMENT00025471]; 54, *Ptiolina nitida* [USNMENT00022957]; 55, *Ptiolina zonata* [USNMENT00022842]; 56, *Rhagio punctipennis* [USNMENT00025946]; 57, *Rhagio scolopaceus* [USNMENT00023193]; 58, *Schizella furcicornis* [USNM00025870]; 59, *Sierramyia* sp. [CSCA08B129], 60, *Spania nigra* [USNMENT00025865]; 61, *Spaniopsis clelandi* [USNMENT00025397]; 62, *Spaniopsis longicornis* [USNMENT00025293]; 63, *Symphoromyia flavipalpis* [USNMENT00025944]; 64, *Alloleptis tersus* HOLOTYPE.

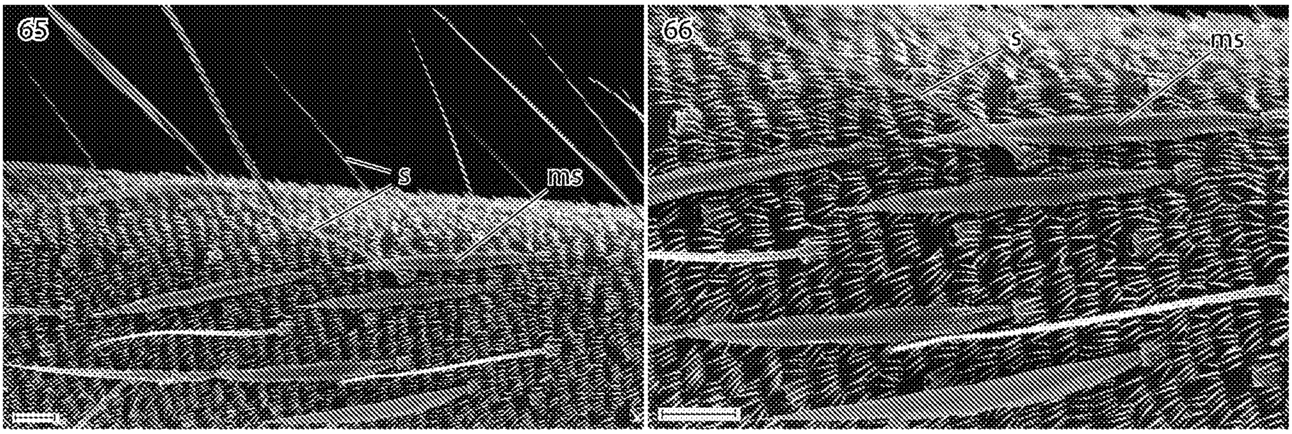
48. Position of R_4 and R_5 at margin. (1) R_5 anterior to or ending at wing tip (2) R_5 and R_4 encompass wing tip (3) R_4 ending at or posterior to wing tip. Intrageneric variation of this character is present in at least *Austroleptis*, *Chrysopilus*, *Rhagio* and *Symphoromyia*. It may be an important distinction, however, in distinguishing between species of *Omphalophora* and *Ptiolina*.

49. Alignment of R_5. (1) Aligned with R_{4+5} or changing direction only slightly at fork with R_{4+5} (2) clearly changing direction at fork with R_{4+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 47. There are inherent problems in scoring a character such as this, since the variation in the flexure of R_{4+5} at the point where R_4 and R_5 originate is continuous and it may be 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 is scored as straight (e.g., Fig. 44). In cases where the divergence appears at an angle greater than this (e.g., Fig. 53), the character is scored as changing direction.

50. M_3 wing vein. (1) Present, reaching wing margin (2) incompletely present, not reaching wing margin (3) absent. The absence of the third medial vein has been proposed as a synapomorphy for a natural group composed of *Austroleptis*, *Bolbomyia*, and *Litoleptis* (Grimaldi & Cumming 1999: Figs. 41–43, 50–51). This group may also include fossil taxa *Mesobolbomyia* Grimaldi & Cumming, *Pauromyia* Ren, *Probolbomyia* Ussatchev, and *Zarzia* Zaitzev (Grimaldi & Cumming 1999). The state of being incompletely present is defined by an M_3 wing vein not reaching the wing margin. *Spania nigra* specimens may have a complete or incomplete M_3 wing vein. *Spaniopsis clelandi* specimens also show variation in either having M_3 incompletely present (e.g., Fig. 62) or absent (Fig. 61).

Legs

51. Femoral scales. (1) Present (2) absent. At the base of the femora, particularly the fore femur, setae may be modified into scales that lie flat against the dorsal surface. These scales may be difficult to see because of their orientation, structure, and often have the same color as the femur. Scanning electron micrographs, however, show these special scales very clearly (Figs. 65–66). This character is present in the chrysopiline genera: *Chrysopilus*, *Schizella*, and *Stylospania*.



FIGURES 65–66. *Chrysopilus thoracicus* [CSCA08B325], fore femur, oblique lateral view. Scale bar = 0.02 mm. *Abbreviations: ms = modified seta; s = seta.*

52. Fore tibial spur. (1) Absent (2) one. 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*, *Pseudoerinna*, *Vermileo*, and *Xylophagus* have a fore tibial spur. All other taxa lack fore tibial spurs.

53. Mid tibial spur. (1) Absent (2) one (3) two. *Litoleptis* species lack a mid tibial spur and *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.

54. Hind tibial spur. (1) Absent (2) one (3) two. The presence or absence of the hind tibial spur is 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.

55. Hind coxal tubercle. (1) Absent (2) present. The hind coxal tubercle is a small, anterior-facing protuberance of the hind coxa, usually visible from the anterolateral 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 *Pseudoerinna jonesi* and the species of *Sierramyia* examined. Additional tabanid species, belonging to *Chrysops*, *Esenbeckia* Rondani, and *Haematopota* Meigen were examined. These also lack the hind coxal tubercle. However, while absent in all tabanids, it is present in all athericids examined, including *Atrichops* Verrall (not in the matrix).

Male Genitalia

56. Epandrium aspect ratio. (1) Wider than long (2) longer than wide. The epandrium is longer than wide in *Pelecorhynchus*, *Pseudoerinna*, *Suragina*, *Atherix*, and *Dasyomma*. In all other taxa, the epandrium is scored as wider than long (e.g., Figs. 67–69, 72, 79, etc.), however, this character is variable within Tabanidae. In *Tabanus atratus*, for instance, it is wider than long, however in other species, such as *Tabanus sulcifrons* Macquart, the epandrium is longer than wide. The epandrium is also longer than wide in *Esenbeckia incisuralis* (Say) and *Heptatoma pellucens* (Fabricius), however, in *Haematopota pechumani* Stone & Philip, *Chrysops lateralis* Wiedemann, and *Scaptia dorsoguttata* (Macquart), it is wider than long. In *Dichelacera marginata* Macquart and *Hybomitra atrobasis* (McDunnough) the sclerite is approximately as wide as long. *Dichelacera marginata* is scored as wider than long. *Spaniopsis longicornis* Ferguson was also scored as wider than long (as *Spaniopsis clelandi* and *Spaniopsis marginipennis* Ferguson), but nearly as wide as long.

57. Anterior margin of epandrium. (1) Strongly notched (2) modestly curved (3) not emarginate. If the anterior emargination reaches near the midline of the epandrium, it is scored as strongly notched (e.g., Figs. 69, 72). Otherwise, the anterior margin of the epandrium is scored as modestly curved as long as there is some emargination (e.g., Figs. 68, 79). In cases where the anterior margin is flat, or rounded anteriorly, it is scored as not emarginate (as in the case of *Glutops rossi*, *Pelecorhynchus personatus*, and *Vermileo opacus* (Coquillett)). 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 epandrium not emarginate anteriorly, however in *Glutops punctatus* Wirth, there is a modestly curved emargination.

58. Curvature of epandrium. (1) Simple, not containing the hypandrium ventrally (2) wrapped laterally, surrounding the cerci and hypoproct posteriorly and containing the hypandrium ventrally. The epandria in most Tabanomorpha and all of Rhagionidae *sensu* Woodley (1989) are nearly flat and are positioned directly above the hypandrium, so that they are separated by a horizontal gap. However, in species of *Pelecorhynchus* (but not *Glutops*), *Vermileo*, *Lampromyia*, *Suragina*, and *Atherix* (as in *Atrichops*), the epandrium is enlarged and rounded 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.

59. Cercus. (1) Attached to the subepandrial complex (subepandrial membrane or hypoproct) (2) attached directly to the epandrium via connective membrane. The cerci may be directly attached to the epandrium 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 *Glutops*, *Pelecorhynchus*, *Pseudoerinna*, Tabanidae, and Athericidae from all the other taxa is the origin of the cerci. The cerci may be separated from the epandrium by a membrane (as in species of *Glutops*) but their point of attachment is directly to the epandrium (e.g., Figs. 85–86). In other taxa, cerci are attached to the hypoproct, tergite 10, or subepandrial membrane. In *Coenomyia ferruginea*, the cerci are adjacent to the epandrium, but are firmly attached to the hypoproct. Some connective membrane exists between the epandrium and the cerci in *Coenomyia ferruginea*, but this appears to be a secondary attachment.

60. Tergite 10. (1) Absent, membrane only (2) present, sclerotized. Tergite 10 (subepandrial sclerite in Sinclair *et al.* 1994) may be present between the epandrium and the cerci. Tergite 10 is scored as present only when the subepandrial structure is sclerotized. Sclerotization and the presence of tergite 10 are most easily viewed from the posterior perspective. Tergite 10 is present in *Chrysopilus*, *Ptiolina* and *Symphoromyia*. For taxa where the cercus attaches directly to the epandrium, this character was not scored because in these cases, there is character non-independence. The lack of tergite 10 is a necessary condition to allow for the direct attachment of cerci to the epandrium.

61. Tergite 10 form. (1) Undivided (2) divided. Tergite 10 is 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 tergite 10 were not scored for this character.

62. Setation of tergite 10. (1) Tomentose (2) setose. The presence or absence of tergite 10 setae is scored. In *Ptiolina* and *Symphoromyia*, the sclerite bears setae, whereas in *Chrysopilus*, the structure is tomentose. Taxa that lack tergite 10 were not scored for this character.

63. Hypoproct setation. (1) Setose (2) tomentose. The presence or absence of hypoproct setae is 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.

64. Cercus 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 cercus (3) widely displaced from one another, separation distance greater than three quarters

width of cercus. The lateral distance between cerci of the male genitalia were measured at their base. Cerci directly adjacent to one another is observed in *Alloleptis tersus*, *Arthroceras pollinosum* Williston (but not *A. fulvicorne* Nagatomi), *Arthroteles*, *Atherimorpha*, *Austroleptis*, *Chrysopilus*, *Tabanus*, and in some *Omphalophora*, *Ptiolina*, *Rhagio*, and *Symphoromyia* species. Partially displaced cerci were commonly found in athericid taxa. Widely displaced cerci are exemplified by *Spania nigra* (Fig. 81).

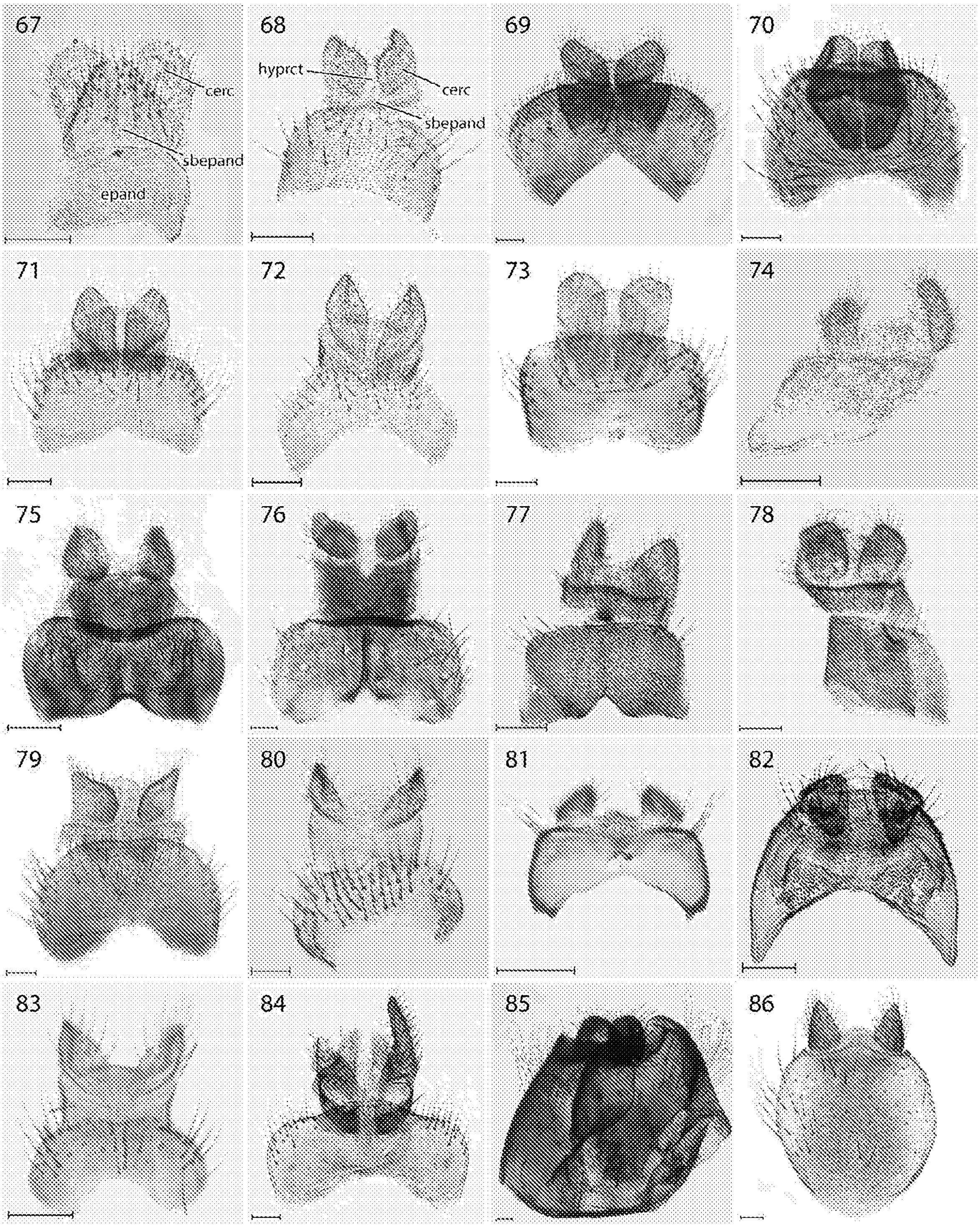
65. Hypandrium. (1) Fused entirely to gonocoxites (2) separated partially from the gonocoxites by an incomplete suture (3) separated from the gonocoxites by a complete suture. The hypandrium is scored as 'free' when it is separated from the gonocoxites by a complete suture (i.e., not fused to the gonocoxites; e.g., Figs. 89, 92, 102, 107). There is an intermediate condition where the hypandrium is fused anteriorly and partially free from the gonocoxites posteriorly. This condition is found in species of *Arthroceras* and *Symphoromyia* (Figs. 90, 106) 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 hypandrium and the gonocoxites are fused (e.g., Figs. 87, 93, 97, 99) .

Since the hypandrium is separated from the gonocoxites in Nematocera and in many basal brachycerans including Bombyliidae, Therevidae, and Asilidae (Sinclair *et al.* 1994), as well as in taxa scored here, the state is considered generally considered plesiomorphic. The fusion of the hypandrium with the gonocoxites is a putative synapomorphy for Tabanidae + Athericidae (Woodley 1989; Sinclair *et al.* 1994). Some members of the Xylophagomorpha have a fused hypandrial sclerite, however. Within Pelecorhynchidae, and even within *Pelecorhynchus*, there is variation of this character. *Glutops* and *Pseudoerinna* have a free hypandrial sclerite, while most *Pelecorhynchus* have gonocoxites fused to the hypandrium. In *P. personatus*, the hypandrium is free but is very narrow and different in form than the typically broad, smoothly triangular sclerite (as in *Glutops* and other taxa including *Pseudoerinna*).

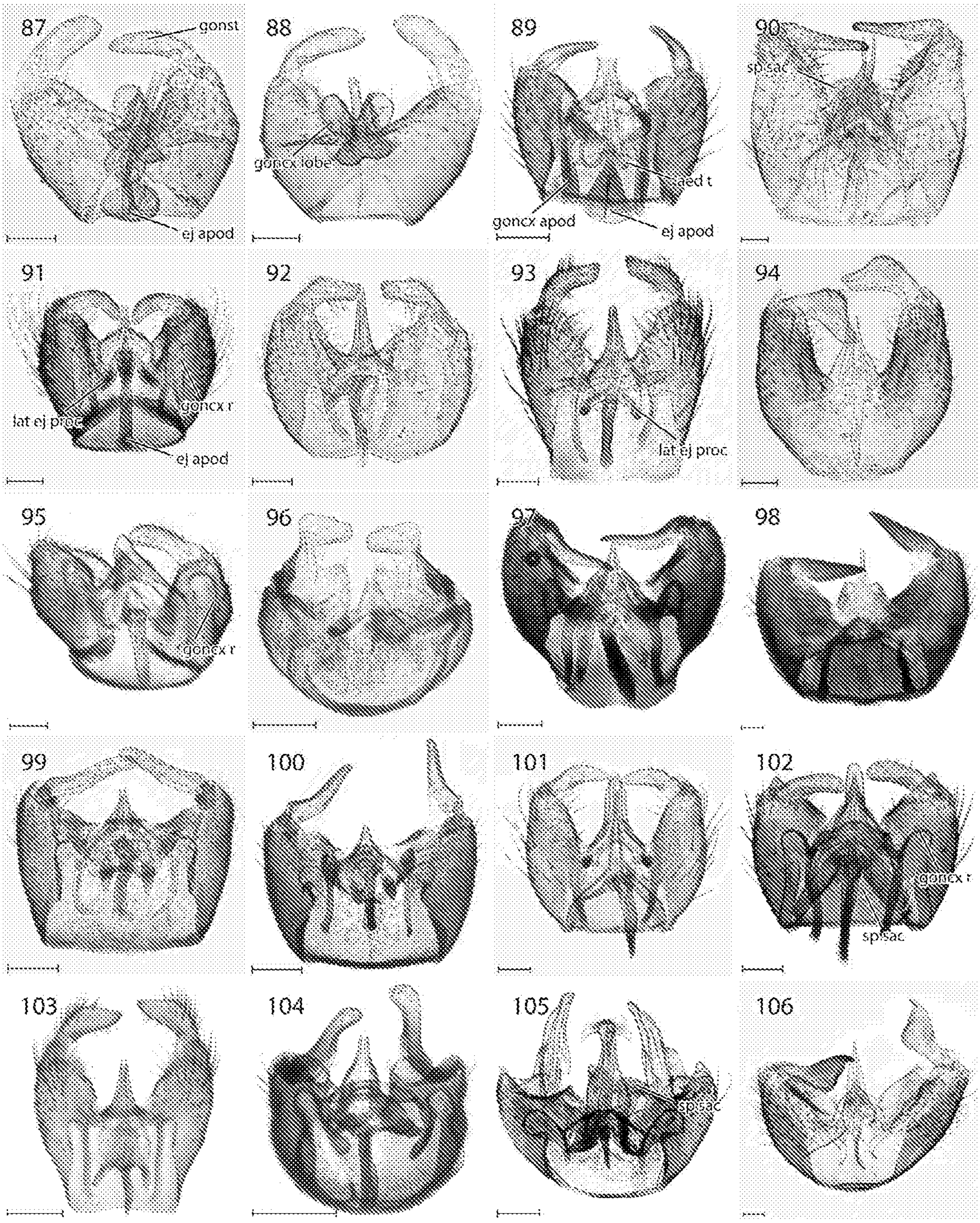
66. Gonocoxal ridge. (1) Dorsal sinuous ridge present, leading to gonocoxal apodeme (2) smooth dorsally, without sinuous ridge leading to gonocoxal apodeme. The dorsal side of the gonocoxite may have a sinuous ridge that leads to the gonocoxal apodeme (e.g., Figs. 91, 95, 102). This is lacking in Athericidae, Tabanidae, Vermileonidae, and many Xylophagidae, as well as *Alloleptis tersus*, *Austroleptis multimaculata* Hardy, *Chrysopilus quadratus* (unlike most *Chrysopilus* species), *Litoleptis alaskensis* Chillcott, and *Stylospania lancifera*.

67. Gonocoxal apodeme. (1) Present (2) absent. The presence or absence of gonocoxal apodemes is scored. *Austroleptis* and *Litoleptis* are the only taxa where the gonocoxal apodemes are absent.

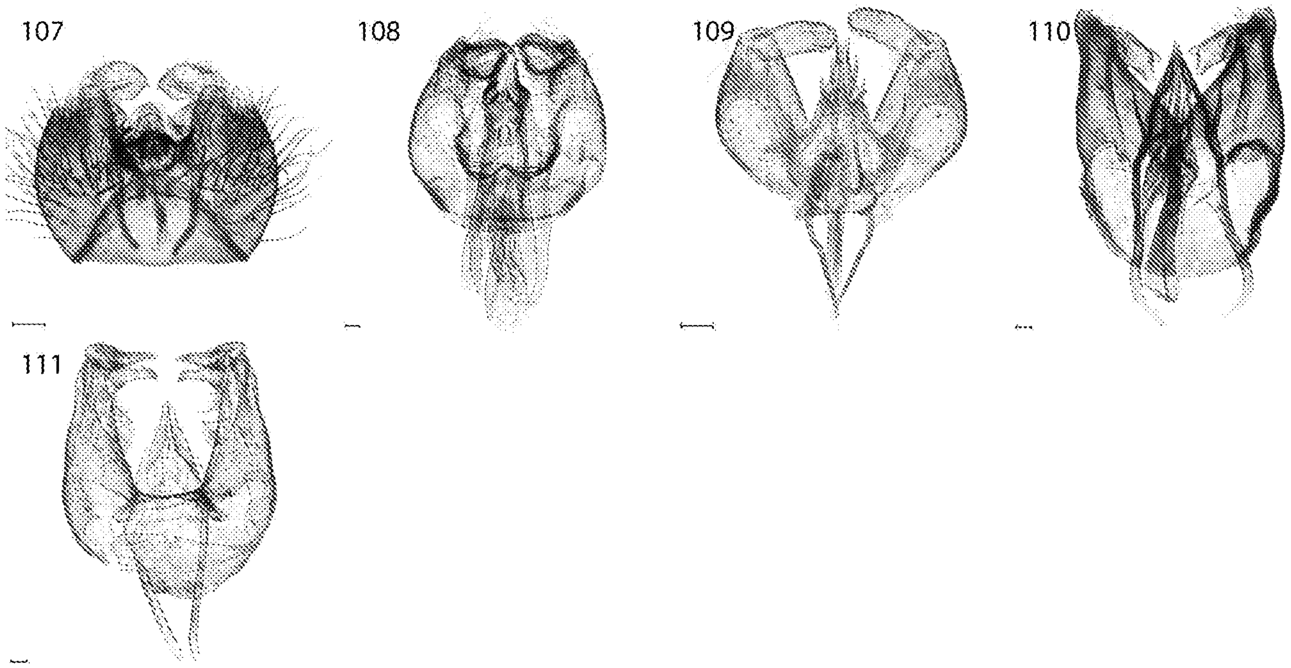
68. Gonocoxal apodeme length. (1) Short or long enough to reach anterior margin of hypandrium (2) extending well beyond anterior margin of hypandrium. The length of the gonocoxal apodeme is scored by noting the position at its apex, relative to the anterior margin of the hypandrium and scored as either 1) short, or long enough to reach the anterior margin of the hypandrium (e.g., Figs. 92, 95, 102, 107) or 2) extending well beyond the anterior margin of the hypandrium (e.g., Fig. 108). The long length of the gonocoxal apodemes has been given as evidence to support Athericidae + Tabanidae (Stuckenberg 1973; Sinclair *et al.* 1994), although the character is lacking in *Xeritha* Stuckenberg (as noted in Sinclair *et al.* 1994). *Austroleptis* spp. and *Litoleptis alaskensis* are not scored for this character since they lack gonocoxal apodemes.



FIGURES 67–86. Male terminalia, epandria, dorsal view, scale bar = 0.1 mm. 67, *Austroleptis multimaculata* [USNMENT00025739]; 68, *Bolbomyia nana* [USNMENT00024051]; 69, *Arthroceras leptis* [USNMENT00022613]; 70, *Arthroteles bombyliiformis* [USNMENT00024986]; 71, *Atherimorpha triangularis* [USNMENT00028418]; 72, *Chrysopilus quadratus* [USNMENT00025951]; 73, *Desmomyia thereviformis* [USNMENT00025267]; 74, *Litoleptis alaskensis* HOLOTYPE; 75, *Omphalophora fasciata* [USNMENT00025461]; 76, *Omphalophora majuscula* [USNMENT00025472]; 77, *Ptiolina edeta* [USNMENT00023011]; 78, *Ptiolina obscura* [USNMENT00025937]; 79, *Rhagio mystaceus* [USNMENT00025230]; 80, *Schizella woodleyi* [USNM00025871]; 81, *Spania nigra* [USNMENT00025868]; 82, *Spaniopsis clelandi* [USNMENT00025396]; 83, *Stylospania lancifera* [USNMENT00025234]; 84, *Symphoromyia hirta* [USNMENT00025791] (left cercus missing); 85, *Pelecorhynchus personatus* [USNMENT00025896]; 86, *Suragina concinna* [USNMENT00025958]. *Abbreviations: cerc = cercus; epand = epandrial sclerite; sbepand = subepandrial sclerite.*



FIGURES 87–106. Male terminalia (cont.), hypandria, dorsal view (except where noted), scale bar = 0.1 mm. 87, *Austroleptis multimaculata* [USNMENT00025739]; 88, *Austroleptis multimaculata* [USNMENT00025739] ventral view, aedeagus removed; 89, *Bolbomyia nana* [USNMENT00024051]; 90, *Arthroceras pollinosum* [USNMENT00022601]; 91, *Arthroteles bombyliiformis* [USNMENT00024986]; 92, *Atherimorpha triangularis* [USNMENT00028418]; 93, *Chrysopilus quadratus* [USNMENT00025951]; 94, *Chrysopilus* sp. [USNMENT00025952]; 95, *Desmomyia thereviformis* [USNMENT00025267]; 96, *Litoleptis alaskensis* [USNMENT00024416]; 97, *Omphalophora fasciata* [USNMENT00025461]; 98, *Omphalophora majuscula* [USNMENT00025472]; 99, *Ptiolina nitida* [USNMENT00025933]; 100, *Ptiolina zonata* [USNMENT00022846]; 101, *Rhagio plumbeus* [USNMENT00025949]; 102, *Rhagio punctipennis* [USNMENT00025950]; 103, *Stylospania lancifera* [USNMENT00025234]; 104, *Spania nigra* [USNMENT00025868]; 105, *Spaniopsis marginipennis* [USNMENT00025249]; 106, *Symphoromyia hirta* [USNMENT00025791]. *Abbreviations: aed t = aedeagal tine; ej apod = ejaculatory apodeme; enaed proc = endoaedeagal process; goncx apod = gonocoxal apodeme; goncx lobe = gonocoxal lobe; goncx r = gonocoxal ridge; gonst = gonostylus; lat ej proc = lateral ejaculatory process; sp sac = sperm sac.*



FIGURES 107–111. Male terminalia (cont.), hypandria (cont.), dorsal view, scale bar = 0.1 mm. 107, *Glutops rossi* [USNMENT00025231]; 108, *Pelecorhynchus fusconiger* [USNMENT00025897]; 109, *Atherix pachypus* [USNMENT00025209]; 110, *Tabanus atratus* [USNMENT00025959]; 111, *Esenbeckia incisuralis* [USNMENT00025968].

69. 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. The relative lengths of the medial and lateral margins leading to the gonocoxal apodemes were scored (Fig. 112). Athericidae and Tabanidae have relatively short medial margins, so that what may be called the parameral bridge (the transverse structure spanning the parameral sheath and sperm sac, joining the gonocoxites dorsomedially), is shifted anteriorly (Fig. 112A). In addition to Athericidae and Tabanidae, other taxa that have gonocoxal apodemes with relatively short inner margins are *Lampromyia canariensis* Macquart, *Vermileo vermileo*, *Pelecorhynchus personatus*, and *Xylophagus lugens*. *Austroleptis multimaculata* and *Litoleptis alaskensis* are not scored for this character since they lack gonocoxal apodemes. *Rhagio* and *Bolbomyia* spp. display the putatively primitive state where the medial margins of the gonocoxal apodemes are longer than their lateral margins (Figs. 112A, 112B).

112

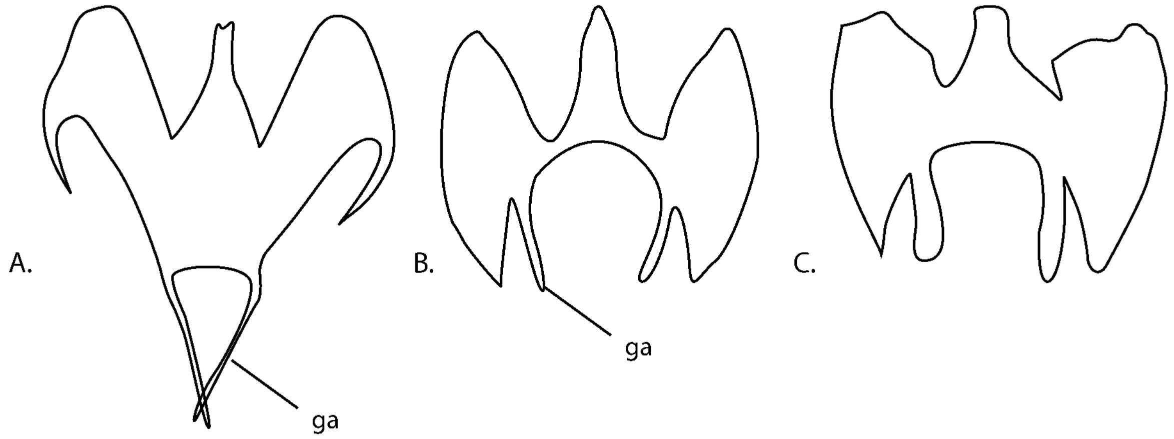


FIGURE 112. Dorsal outline of gonocoxites for illustration of Character 69, origin of gonocoxal apodeme. (A) *Atherix pachypus* is an example where the medial margins of the gonocoxal apodemes are shorter than the lateral margins. (B) In *Rhagio plumbeus* and (C) *Bolbomyia nana* the lateral margins of the gonocoxal apodemes are shorter than the medial margins. *Abbreviations: ga = gonocoxal apodeme.*

70. Sperm sac. (1) Not expanded ventrally (2) expanded and bulbous ventrally (with or without distinct lobes). The sperm sac surrounds the aedeagus posteriorly. The character is scored as bulbous when it is expanded and flush with the gonocoxites ventrally (e.g., Fig. 102). In cases where it is not expanded ventrally, it appears to envelope the aedeagus tightly (as in *Austroleptis*, *Bolbomyia*, *Spania*, and others).

71. Bulbous sperm sac. (1) Without distinct lobes (2) with distinct lobes. Where the sperm sac is bulbous, it may be produced into paired swellings (lobes). It is scored as having lobes only when membranous lobes were distinctly present. Such lobes were present in species of *Arthroceras*, *Ptiolina*, *Spaniopsis*, and *Symphoromyia* (e.g., Figs. 90, 105). 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 sperm sac) and are sclerotized (instead of membranous) (Fig. 88). The sperm sac itself is unmodified in *Austroleptis*. For taxa that do not have a bulbous sperm sac, this character was not scored.

72. Lateral ejaculatory process associated with M32 flexor muscle. (1) Absent (2) present, integrated into sperm sac membrane (3) present, free of sperm sac posteriorly. Lateral ejaculatory processes (*sensu* Sinclair *et al.* 1994) along the anterodorsal wall of the sperm sac that are associated with the M32 flexor muscle (Ovtshinnikova 1989) are present in two forms. In *Desmomyia thereviformis* Brunetti, all *Rhagio* species (including *R. incurvatus*), and *Sierramyia* spp., the lateral ejaculatory processes are thin, lightly sclerotized structures that are integrated into the sperm sac (e.g., Fig. 122). In all species of *Arthroceras*, *Arthroteles*, *Atherimorpha*, *Chrysopilus*, *Ptiolina*, *Spaniopsis*, *Symphoromyia*, and in *Glutops rossi*, *Pseudoerinna jonesi*, *Schizella furcicornis* Bezzi, and *Spania nigra*, the lateral ejaculatory 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*, these lateral aedeagal processes are not present. This has led to misunderstandings of these 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 ejaculatory processes. Zloty *et al.* (2005) pointed out additional lateral ejaculatory processes associated with aedeagal tines in the male genitalia of oreoleptids, tabanids, and athericids and defined them as homologous to the structures defined here. However, the muscle attachments of these processes are at different points and on different structures and are not homologized here.

73. Ejaculatory apodeme length. (1) Reduced, nearly absent (2) short, not reaching anterior margin of hypandrium (3) moderately long, reaching the anterior margin of hypandrium (4) long, reaching beyond the anterior margin of hypandrium. The length of the ejaculatory apodeme is scored by noting the position at its apex, relative to the anterior margin of the hypandrium. Although the ejaculatory apodeme is continuously varied to some degree, ejaculatory apodeme length was divided into four discrete categories: 1) reduced, nearly absent (as in *Litoleptis* spp., Fig. 96) 2) short, not reaching anterior margin of the hypandrium (e.g., Figs. 100, 105), 3) moderately long, reaching the anterior margin of the hypandrium (e.g., Figs. 90, 92, 95), or 4) long, reaching beyond the anterior margin of the hypandrium (e.g., Figs. 89, 101, 108).

74. Ejaculatory apodeme form. (1) Cylindrical (2) laterally compressed (3) compressed dorsoventrally (4) tripartite (5) umbruculate. The form of the ejaculatory apodeme is scored as either cylindrical, laterally compressed, compressed dorsoventrally, tripartite, or umbruculate (umbrella-shaped) anteriorly. Tripartite is a term used describe the structure when it is dorsally compressed laterally and ventrally compressed dorsoventrally, as in the case of *Bolbomyia nana* (Fig. 89). *Austroleptis* species are distinctive by having the ejaculatory apodeme umbrella-shaped at its apex (Fig. 113). Where the ejaculatory apodeme is very clearly laterally compressed, the character is easily scored (e.g., Fig. 104). However, the form of the ejaculatory apodeme is often difficult to characterize. The ejaculatory apodemes of *Chrysopilus ferruginosus* and *Ptiolina zonata*, for example, are mostly cylindrical, but also laterally compressed to a degree. For these species, the character is scored as an ambiguity, present as both a cylindrical 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 cylindrical when only viewed from above. Generally, ejaculatory apodeme forms were consistent within genera, however, difficulties inherent in its scoring seem to discount its resolving power.

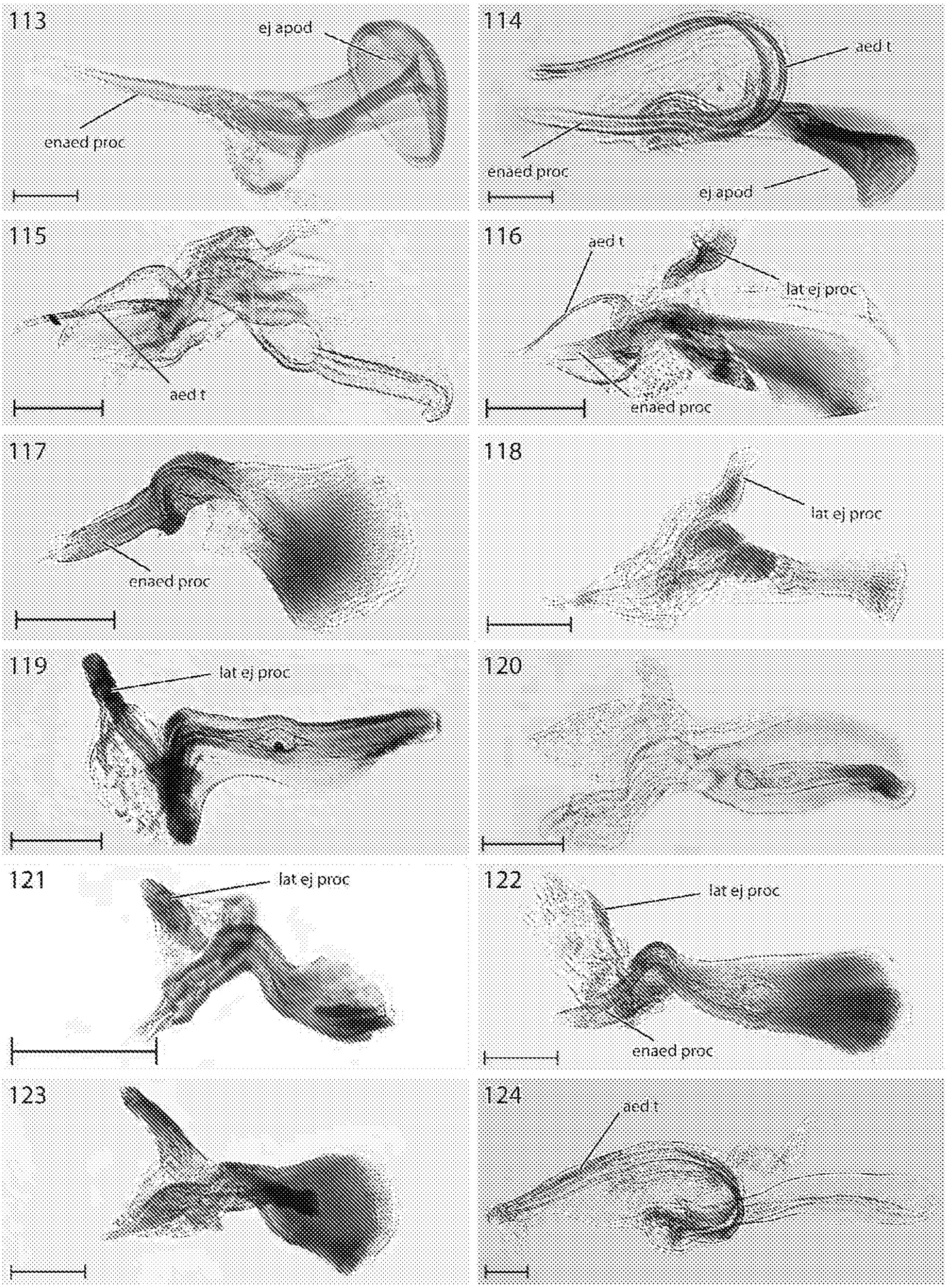
75. Aedeagal tines. (1) Absent (2) present. The presence or absence of aedeagal tines is scored. The tines are present in Athericidae (Fig. 124), Oreoleptidae, Tabanidae, *Bolbomyia* (Fig. 114), and *Arthroceras* (Figs. 115, 116). The presence of aedeagal tines has been proposed as a synapomorphy to unite Athericidae + Tabanidae + *Bolbomyia* (Sinclair *et al.* 1994).

76. Endoaedeagal process. (1) Present (2) absent. The endoaedeagal process (Sinclair *et al.* 1994) 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 Brachycera (Sinclair *et al.* 1994). Sinclair *et al.* (1994) 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 ejaculatory 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.

Particularly within *Ptiolina* and *Omphalophora*, the character is free to vary, in ways that may make scoring problematic. In *Omphalophora majuscula* and *O. lapponica*, for example, an endoaedeagal component is clearly present (anterior to the ‘precursor’ sclerites), but it is broad, blunt, and short. In *O. fasciata*, the landmark ‘precursor’ sclerites are present and clearly mark the posterior apex of the ejeculatory apodeme; the endoaedeagal component is absent in this species. In *P. nitida* Wahlberg, the posterior end of the ejaculatory 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. *Ptiolina edeta* (Walker), *P. mallochi*, *P. obscura* Fallén, and *P. zonata* are similar to *P. nitida* in form.

In many *Chrysopilus* species, the posterior end of the ejaculatory 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 ejeculatory 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 ejaculatory apodeme and does not penetrate the sperm sac. Therefore it is not scored as the endoaedeagal process.

77. Endoaedeagal process form. (1) Laterally compressed (2) rounded, narrowly conical (3) dorsoventrally flattened. 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* (including *R. incurvatus*), and also in *Desmomyia thereviformis*, the endoaedeagal process is very distinctly laterally compressed (like a butter knife). 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 dorsoventrally flattened endoaedeagal process, and a separate state was designated on account of this.



FIGURES 113–124. Male terminalia (cont.), aedeagi, lateral view, scale bar = 0.1 mm. 113, *Austroleptis multimaculata* [USNMENT00025739]; 114, *Bolbomyia nana* [USNMENT00024051]; 115, *Arthroceras fulvicorne* [USNMENT00022601]; 116, *Arthroceras pollinosum* [USNMENT00022737]; 117, *Arthroteles bombyliiformis* [USNMENT00024986]; 118, *Atherimorpha* sp. [USNMENT00028418]; 119, *Chrysopilus* sp. [USNMENT00025242]; 120, *Omphalophora lapponica* [USNMENT00025921]; 121, *Ptiolina edeta* [USNMENT00023011]; 122, *Rhagio mystaceus* [USNMENT00025230]; 123, *Symphoromyia trivittata* [USNMENT00028573]; 124, *Suragina concinna* [USNMENT00025980]. *Abbreviations: aed apod = aedeagal apodeme; aed t = aedeagal tine; lat ej proc = lateral ejaculatory process; enaed proc = endoaedeagal process.*

Female abdomen

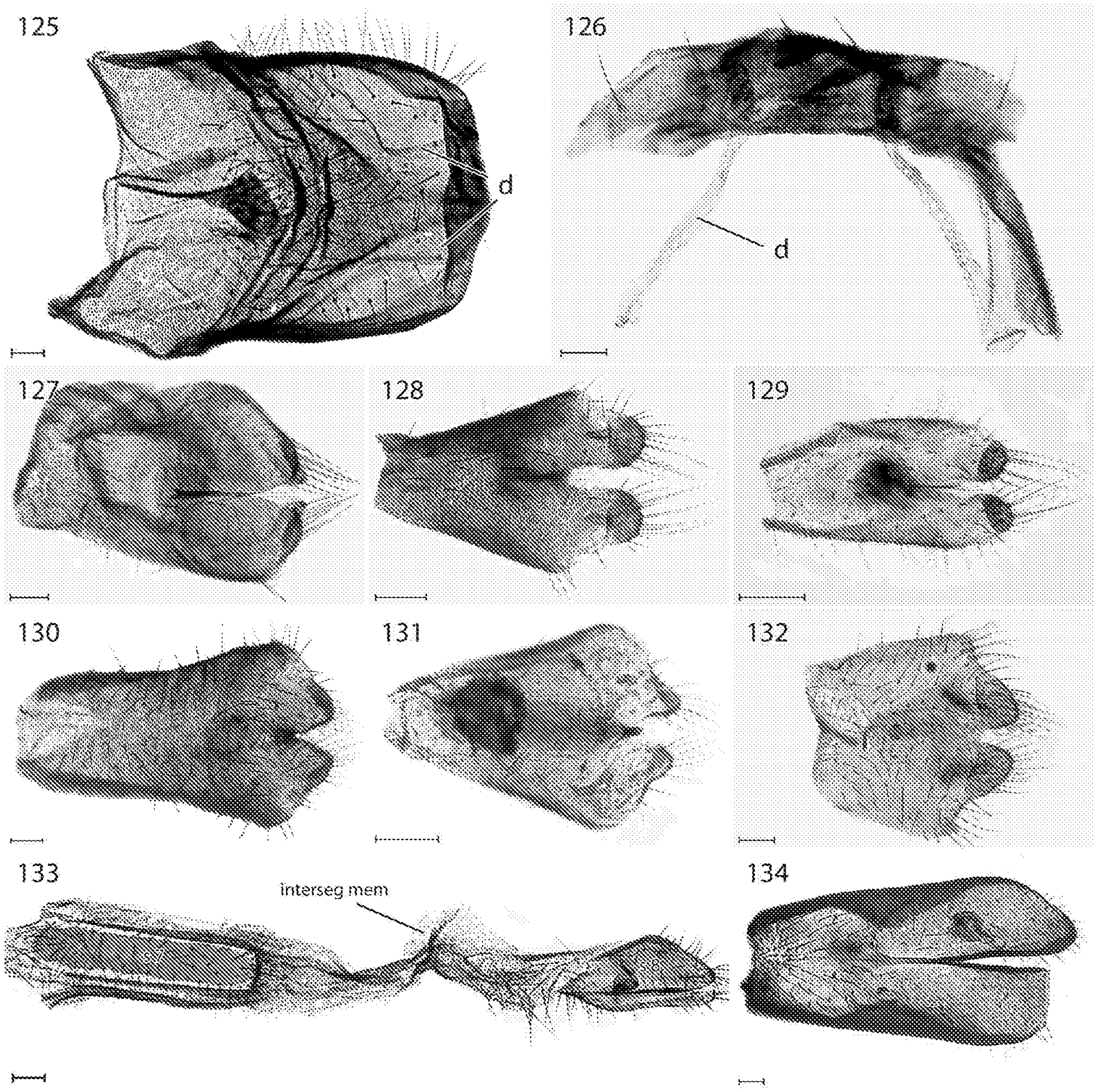
78. Tergite 1. (1) Entire (2) divided by medial seam. Tabanidae are distinctive in having a medial seam that divides tergite 1 into two parts. While Stuckenberg (1973) notes "there is a conspicuous trend towards a medial division of the first tergite" in Athericidae, a longitudinal seam similar to the one exhibited by tabanids is not present among the athericid species studied (contrary to scoring of Zloty *et al.* (2005)). Stuckenberg (1973) also stated that the first tergite of *Spaniopsis* females is divided, however I did not find this to be the case. While a fold or modest notch is often present in *Spaniopsis*, it is not divided as in Tabanidae.

79. Tergite 7. (1) Much longer than wide (2) about as long as wide (3) much wider than long. The shape of tergite 7 is 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* Burgess also has a square tergite 7. This character is consistent within genera, and may be used to distinguish between allied taxa *Ptiolina* and *Omphalophora*. In *Arthroceras pollinosum*, tergite 7 is clearly longer than wide. This is also the case for *Arthroceras fulvicorne* Nagatomi, however Nagatomi & Iwata (1976) illustrate tergite 7 in *Arthroceras japonicum* Nagatomi as apparently wider than long. In *Arthroceras leptis* (Osten Sacken), tergite 7 is about as long as wide. Tergite 7 in *Arthroteles cinerea* Stuckenberg 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* Bezzi. Stuckenberg (2001) noted that this may be an important character.

80. Intersegmental membrane between segments 7 and 8. (1) Especially long (2) short, as throughout abdomen. In some taxa, there is a distinctly long intersegmental length between the distal segments of the female abdomen (e.g., Fig. 133). Stuckenberg (1973, 2001) and Zloty *et al.* (2005) have used this as justification to support family-level 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 region 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 (= '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, where flies of this type 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.

81. Sternite 8. (1) Entire (2) divided. In *Austroleptis* species it appears that the sternite 8 is divided into anterior and posterior segments. Sternite 8 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 is present in *Austroleptis*, the interpretation of Nagatomi & Iwata invokes the duplication of sternite nine. Assuming that sternite 8 is divided into two parts, all segments are present and accounted for. In some species, such as in an undescribed *Austroleptis* 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.



FIGURES 125–134. Female sternite 8, ventral view, scale bar = 0.1 mm. 125, *Pelecorhynchus personatus* [USNMENT00025882]; 126, *Pelecorhynchus elegans* [USNMENT00025880]; 127, *Arthroceras fulvicorne* [USNMENT00022736]; 128, *Arthroteles bombyliiformis* [USNMENT00025017]; 129, *Atherimorpha nemoralis* [USNMENT00025109]; 130, *Rhagio incisus* [USNMENT00025873]; 131, *Sierramyia* sp. [USNMENT00022656]; 132, *Symphoromyia hirta* [USNMENT00028587]; 133, *Glutops singularis* [USNMENT00025338], showing intersegmental membrane between sternites 7 and 8; 134, *Pelecorhynchus personatus* [USNMENT00025882]. *Abbreviations: d = duct; interseg mem = intersegmental membrane; s = sternite.*

82. Sternite 8 length. (1) Wider than long (2) as wide as long (3) longer than wide (4) elongated, more than twice as long as wide. The length of sternite 8 is scored relative to its width: 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., as in members of Xylophagidae). This character was generally consistent within genera and helps to distinguish between *Omphalophora* (longer than wide) and *Ptiolina* (as wide as long). *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).

83. Sternite 8 cleavage. (1) Present (2) absent. 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 (e.g., Figs. 127–129, 131, 132). 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. The notch is absent in all members of Athericidae, Tabanidae, and Vermileonidae and in *Austroleptis*, *Spania nigra*, and *Spaniopsis*.

Female terminalia (external structures)

84. Tergite 9 length. (1) Not reduced (2) reduced. 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.

85. Tergite 9 anteriorly-directed ventrolateral processes. (1) Normal, without such projections (2) with narrow anteriorly-directed ventrolateral projections, enveloping sternite 9. Anteriorly-directed ventrolateral extensions enveloping sternite 9 represent a special modification of tergite 9 (Figs. 143–150). The ventrolateral processes of tergite 9 are actually firmly attached to sternite 9 laterally, via thick membranous tissue. Surprisingly, this has not been noted by previous authors. Where present, it is obvious only after careful dissection. The feature is found exclusively in all species of *Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*.

86. Tergite 10 form. (1) Entire (2) split into two separate lateral sclerites. Female tergite 10 is scored either as entire or split into two separate lateral sclerites. This character is not applicable for *Pseudoerinna jonesi*, where tergite 10 is absent. Nagatomi & Iwata (1976) show tergite 10 of *Atherix basilica* Nagatomi as entire, however in *Atherix pachypus*, it is split (as the illustration of *Atherix ibis* (Fabricius) in Nagatomi & Iwata (1976: 38, fig. 26)). Tergite 10 is entire in *Arthroceras pollinosum*, *A. leptis*, *A. fulvicorne*, and *A. subaquilum* Nagatomi, however it is illustrated as partially spit in *A. japonicum* by Nagatomi & Iwata (1976: 22, fig. 12).

87. Sternite 10 position. (1) Nearly completely anterior to first cercal segment (2) posterior half below first cercal segment (3) almost entirely underneath cercal segment(s). The position of sternite 10 is scored relative to the first cercal 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 cercal segment (~10% below basal cercal segment), 2) posterior half below first cercal segment (approximately 20–50% below first cercal segment, 80–50% below tergite 10), or 3) entirely or almost entirely underneath cercal 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. In *Lampromyia canariensis*, tergite 10 is missing yet sclerite 10 is nearly completely anterior to the first cercal segment. Therefore, it is coded differently than in *Atherix pachypus* where tergite 10 is also absent, but sternite 10 is produced directly below the first cercal segment (as other athericids, tabanids, and *Vermileo vermileo*).

88. Cercus segmentation. (1) Two-segmented (2) one-segmented. The cercus may be one- or two-segmented. The apparent loss of one cercal segment (or fusion of two cercal segments) is a putative synapomorphy for Athericidae + Tabanidae. Species of *Austroleptis* also have a single cercal segment.

89. Basal cercal segment elongation. (1) Not elongated (2) elongated (3x longer than wide or more). The basal cercal segment is scored as either elongated or not. Basal cercal segments that are at least three times as long as wide are considered elongate. This is the condition in *Arthropeas americana*, *Coenomyia ferruginea*, *Dialysis rufithorax*, and *Xylophagus lugens* (the xylophagids included in this study). Otherwise, the basal cercal segment is scored as not elongate.

90. Basal cercal segment separation. (1) Adjacent dorsally (2) cerci separated from one another dorsally by approximately the width of the cercal segment. The dorsal position of the basal cercal segments, in relation to one another, is 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.'

91. Basal cercal segment ventral lobe. (1) Ventral portion of basal cercal segment not expanded, second cercal segment placed centrally or ventrally (2) ventral portion of basal cercal segment expanded, extending mostly ventrally, rounded; second cercal segment placed dorsally (3) ventral portion of basal cercal segment expanded, extended mostly posteriorly and nearly parallel-sided; second cercal segment placed dorsally. The first cercal 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; length of the first cercal segment below second cercal segment attachment. The position of the attachment point of the second cercal segment helps evaluate the state of this character. The last state, where the ventral portion of the basal cercal segment is expanded and nearly parallel-sided accounts for the distinct lobe in species of *Glutops*, *Pelecorhynchus*, *Pseudoerinna*, and *Vermileo*.

92. Ventral lobes of basal cercal segment. (1) Curve ventrally towards one another to form a ring (2) do not form a ring. When looking at the female terminalia from the posterior view, the ventral apices of the basal cercal segment may curve inwardly to meet one another medially, forming a circle or ring. Stuckenberg (2001) has pointed out this character and has advocated its use in phylogenetic analysis. Although this character appears to depend in some degree on the presence or absence of ventral lobes of the basal cercal segments, I found that the 'basal cercal segment inwardly curved' state may be present in taxa without prominent first cercal segment lobing (e.g., *Chrysopilus* spp. and *Schizella furcicornis*). Conversely, some taxa with ventrally-directed lobes (*Symphoromyia hirta* Johnson and *Arthroteles bombyliiformis*) do not have inwardly curving basal cercal segments.

93. Second cercal segment. (1) Not elongated (2) narrow, elongated (3x longer than wide or more). The second cercal segment is scored as either elongated or not. Basal cercal segments 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 cercal segment is scored as not elongate.

94. Cercus apical sensory pits. (1) Present (2) absent. The terminal cercal segment may or may not have what is called an apical sensory pit (e.g., Fig. 150). 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 is scored as present in this taxon.

Female terminalia (internal structures)

95. Tergite 8 ducts. (1) Absent (2) present. There are a pair of thin ducts that arise from the posterior margin of tergite 8 in species of *Glutops*, *Pelecorhynchus*, and in *Pseudoerinna jonesi* (Figs. 125–126). The ducts are inconspicuous and are most easily seen after staining with 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.

96. Number of spermathecae. (1) One (2) two (3) three. 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 observed to differ from the standard condition.

97. Sclerotization of spermathecae. (1) Not sclerotized (2) lightly sclerotized (3) sclerotized. After dissection, the sclerotized portions maintained a light brown color to varying degrees. The degree of sclerotization of the spermathecae 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 (e.g., Figs. 169–170). Spermathecae with brown or dark brown coloration were scored as sclerotized (e.g., Figs. 147, 160, 162, 164, 147, 166). Although there may be phylogenetic signal in this character, congeneric and even conspecific differences (which may be associated with age) were observed (e.g., in *Rhagio* spp.).

98. Spermathecal duct 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. Spermathecal ducts varied in length and this aspect is 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 (e.g., Figs., 147–148). Moderate spermathecal ducts are more than three times but less than five times the length of sternite 9 (e.g., Fig. 161, 165). Long spermathecal ducts are longer than five times the length of sternite 9, but not so long as to be difficult to measure (as in *Arthroceras* spp.). Very long spermathecal ducts fold upon themselves many times (e.g., as in *Xylophagus*). *Pseudoerinna 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, *Pseudoerinna jonesi* is scored as an ambiguity, having both of these states.

99. Spermathecal duct accessory glands. (1) Absent (2) present. There is what appears to be an accessory gland that arises from the spermathecal duct in species of *Arthroceras*, *Omphalophora*, *Ptiolina*, *Schizella*, *Spania*, *Spaniopsis*, *Symphoromyia*, and in some species of *Chrysopilus* (e.g., Figs. 159–166). The spermathecal duct accessory glands may be inconspicuous but are most easily seen after staining with chlorozol black. Perhaps on account of their inconspicuous nature, these glands have not been noted by previous authors. Since female genitalia of most of these taxa had been examined and even illustrated by previous authors, this character was the most surprising of those developed for this dataset. Furthermore, since functional structures such as accessory glands are unlikely to arise *de novo* very frequently, such a character is likely to have phylogenetic utility. The shape of the accessory glands was approximately the same throughout and was always membranous, without sclerotization. Species of *Chrysopilus* may or may not have spermathecal duct accessory glands. One species that lacks spermathecal duct accessory glands is *C. alaskaensis* Hardy. This species 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 may be that *C. alaskaensis* is an atypical species, which has survived the ecological pressures associated with the harsh Alaskan climate and has lost the spermathecal duct accessory glands secondarily. Other species that lack spermathecal duct accessory glands are *C. panamensis* Curran (Costa Rica) and *C. quadratus* (USA). Species that have these glands include *C. thoracicus*, *C. ferruginosa*, *C. calopterus* (Schiner) (Brasil), *C. rhagoides* Bromley (Costa Rica) and *C. testaceipes* Bigot (USA).

100. Spermathecal duct accessory gland placement. (1) Ducts arise at approximately the proximal third of the spermathecal ducts (2) arise at approximately halfway along the length of the spermathecal ducts / arise at approximately the distal third of the spermathecal ducts (3) arise at the base of each spermatheca. 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 the distal third of the spermathecal ducts (e.g., Fig. 165). However this character may be useful for supporting some natural groups. For instance, the observed species of *Ptiolina* (e.g., *P. edeta*, *P. mallochi*, and *P. zonata*) have spermathecal duct accessory glands that arise directly from the base of the spermathecae (e.g., Fig. 147). This differed from the observed species of *Omphalophora* (*O. fasciata*, *O. lapponica*, and *O. majuscula*), where the spermathecal duct accessory glands arise at approximately the distal third of the spermathecal ducts (e.g., Fig. 162). In *Arthroceras pollinosum*, the spermathecal duct accessory glands arise approximately halfway along the length of the spermathecal ducts. In *Arthroceras fulvicorne*, however, the glands arise near 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.

101. Circular ridge of ejection apparatus. (1) Absent (2) present. In many Tabanidae and in most Athericidae, there is a circular ridge at the distal end of the sclerotized ejection apparatus (e.g., Figs. 155–157). *Bolbomyia nana* was also scored as having this character state, although the ridge is more distinctly rounded than in tabanid and athericid taxa (Fig. 136). 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*. *Oreoleptis torrenticola* Zloty, Sinclair & Pritchard was not available for scoring.

102. Sclerotized ring at base of spermathecal ducts. (1) Absent (2) present. In *Bolbomyia nana*, *Spania nigra*, and species of *Spaniopsis*, there is a narrow ring of sclerotized tissue present near the base of the spermathecal ducts (e.g., Fig. 149).

103. Spermathecal duct swelling. (1) Absent (2) present. In *Bolbomyia*, there is a distinct swelling approximately halfway along each spermathecal duct. Although this feature was not found in any other taxon, it is unusual enough to merit mention.

104. Spermathecal duct ejection apparatus. (1) Sclerotized (2) not sclerotized. The ejection apparatus of the spermathecal ducts may or may not be sclerotized. Upon staining with chlorozol black, membranous tissue of the spermathecal ducts turn blue, whereas areas of sclerotization remain light brown or brown. Spermathecal ducts were scored as sclerotized if any brown coloration was detected near their base.

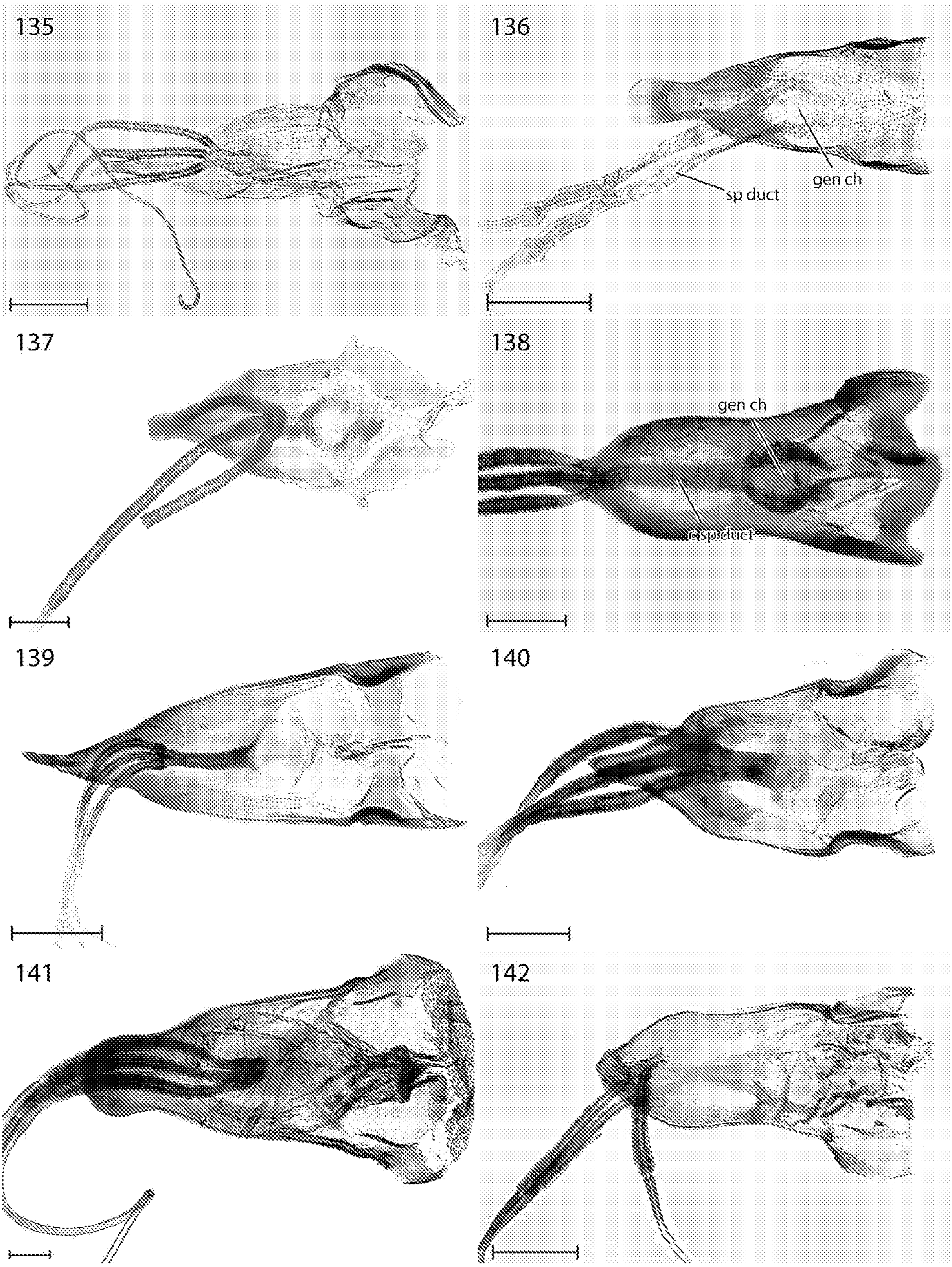
105. Common spermathecal duct. (1) Present (2) absent. The spermathecal ducts most often originate from a single duct that leads from the genital chamber, the common spermathecal duct. However, in some taxa, this common spermathecal duct is absent. In *Bolbomyia nana* and *Pseudoerinna jonesi*, the ducts lead directly to the genital chamber (Figs. 136 and 154, respectively). In some species, such as *Suragina concinna*, the common spermathecal duct appears to have been lost. Since *B. nana* has two spermathecal ducts whereas *P. jonesi* and *S. concinna* have three, the process of gaining/losing the common spermathecal duct is likely different between them. In many pelecorhynchids and athericids, the common spermathecal duct is so short as to be nearly absent (e.g., Figs. 153, 155–157). However it is scored as present in these taxa.

106. Common spermathecal duct. (1) Without any special modifications (2) enlarged pilose and tapering. In species of *Vermileo* and *Lampromyia*, the common spermathecal duct retains chlorozol black dye very strongly and the structure appears finely matted or micropilose, with an uneven surface (e.g., Fig. 158). In other genera, where the common spermathecal duct is thickened, the dye stains smoothly throughout and the common spermathecal ducts are cylindrical.

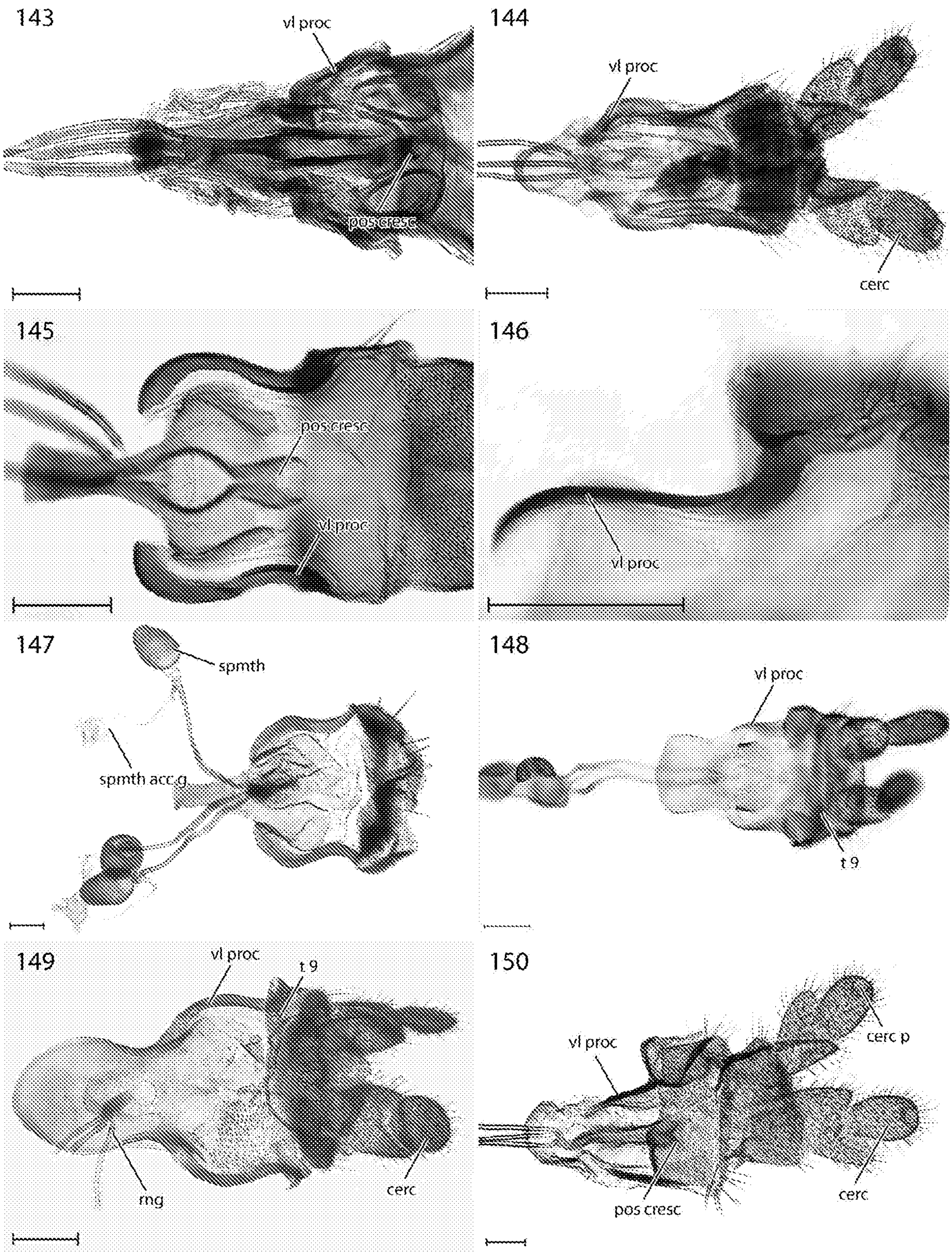
107. Common spermathecal duct diameter. (1) Narrower than individual ducts (2) not enlarged (approximate diameter of individual duct) (3) approximately equal to combined spermathecal duct diameter) (4) enlarged (larger than summation of duct diameters). It was found that the common spermathecal duct may vary in diameter. The most common condition is having the common duct diameter approximately equal to the combined diameter of the spermathecal ducts. Species of some genera (e.g., *Chrysopilus*, *Rhagio*, and *Vermileo*) may either exhibit this condition or an enlarged common spermathecal duct, greater than the summation of the spermathecal duct diameters. *Glutops rossi*, *Isalomyia irwini*, and *Pelecorhynchus personatus* also had enlarged common spermathecal ducts. This character is scored for taxa that have a duct-like common spermathecal duct only. *Lampromyia canariensis* and *Vermileo vermileo* have a modified common spermathecal duct and therefore, are not scored here.

109. Genital chamber, surrounding area. (1) Membranous, sclerotization of sternite 9 laterally contained (2) tightly defined by medial sclerotization of sternite 9. 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. However, in species of *Omphalophora*, *Ptiolina*, *Spania*, *Spaniopsis*, and *Symphoromyia*, the area of the genital chamber is tightly defined by medial sclerotization of sternite 9 (e.g., Figs. 143, 145, 147–150). 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.

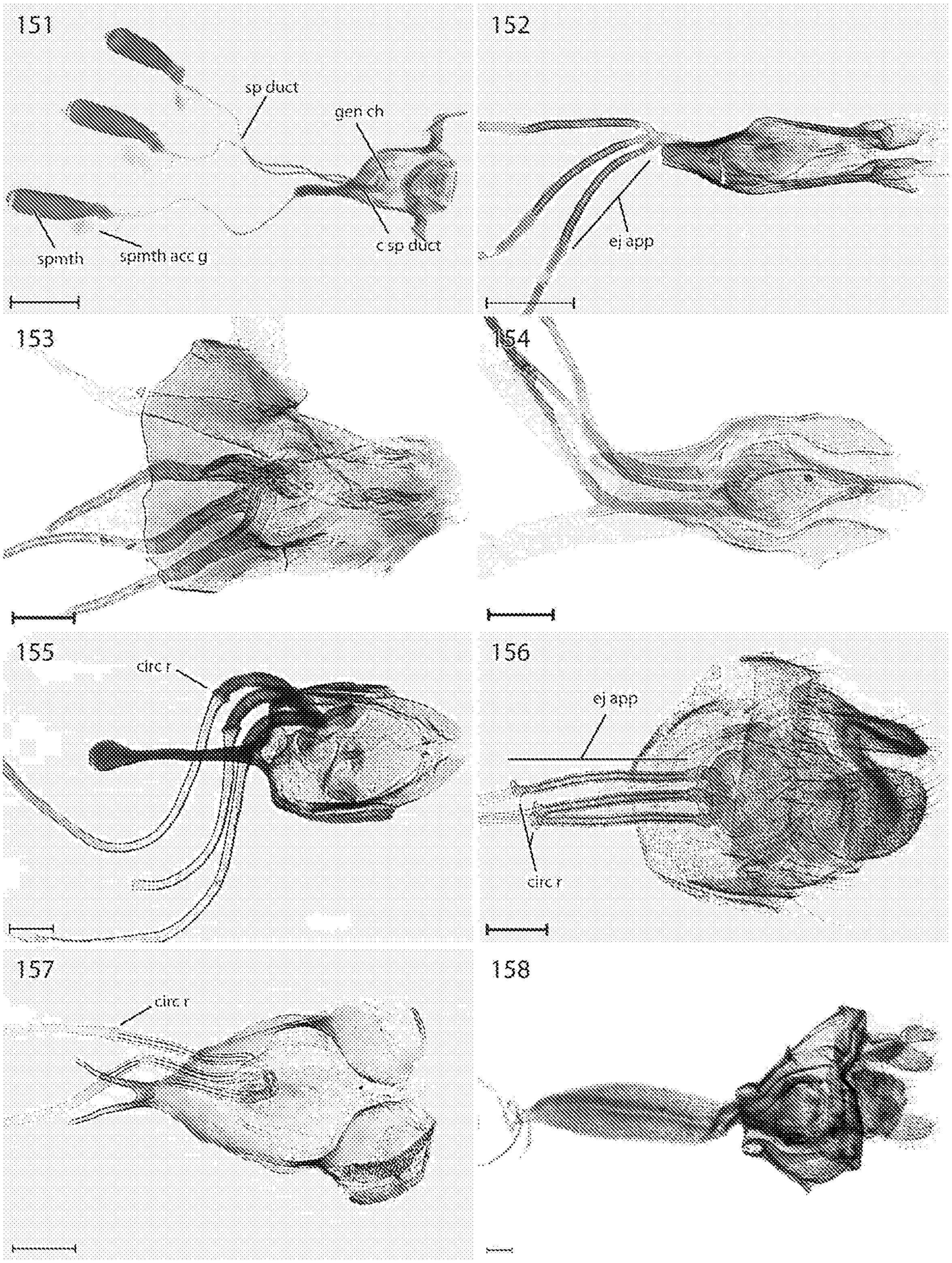
110. Genital chamber shape. (1) Circular (2) teardrop or almond-shaped (3) elongate, parallel-sided in part. When surrounded by membrane, the exact boundaries of the genital chamber, itself composed of membranous tissue, are often poorly defined. Therefore scoring membranous boundaries of the genital chamber is particularly susceptible to subjective interpretation, error, or inconsistency. Because of this, this character is scored only for taxa where the genital chamber area was defined by sternite 9 medial 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 is scored as either circular (e.g., Fig. 149), teardrop- or almond-shaped (e.g., Figs. 145, 148), or elongate, in part parallel-sided (e.g., Fig. 143, 150). Both species of *Symphoromyia* in this sample are scored as having an elongate, parallel-sided genital chamber, however in *S. plagens* Williston, the genital chamber is teardrop shaped.



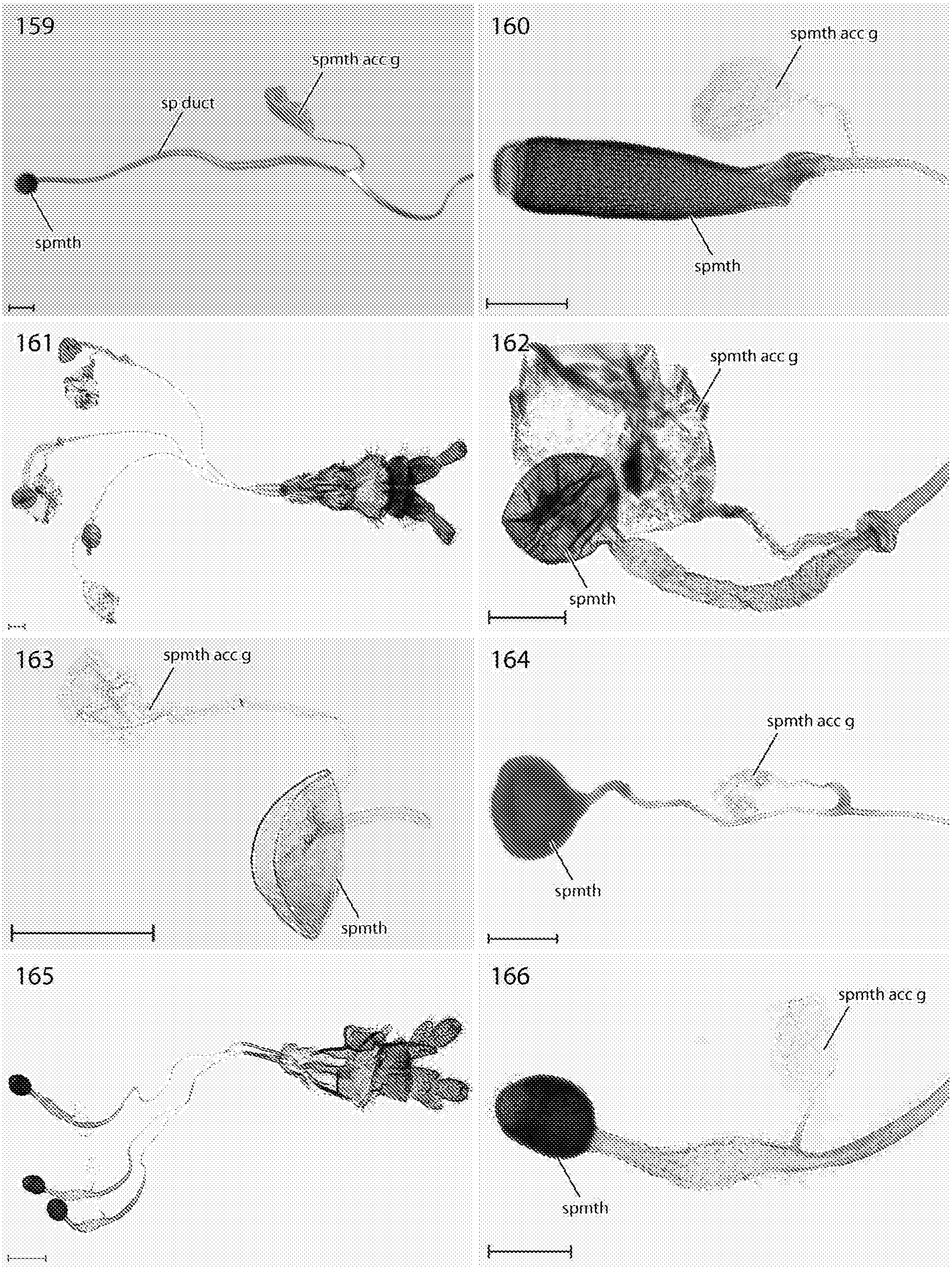
FIGURES 135–142. Female terminalia, sternite 9, dorsal view, scale bar = 0.1 mm. 135, *Austroleptis multimaculata* [USNMENT00024145]; 136, *Bolbomyia nana* [USNMENT00022946]; 137, *Arthroceras pollinosum* [USNMENT 00025219]; 138, *Arthroteles bombyliiformis* [USNM ENT00025017]; 139, *Atherimorpha nemoralis* [USNMENT00025109]; 140, *Desmomyia thereviformis* [USNMENT00025628]; 141, *Rhagio palpalis* [USNMENT00025879]; 142, *Sierramyia* sp. [USNMENT00022656]. *Abbreviations: sp = spermathecal duct; gen ch = genital chamber.*



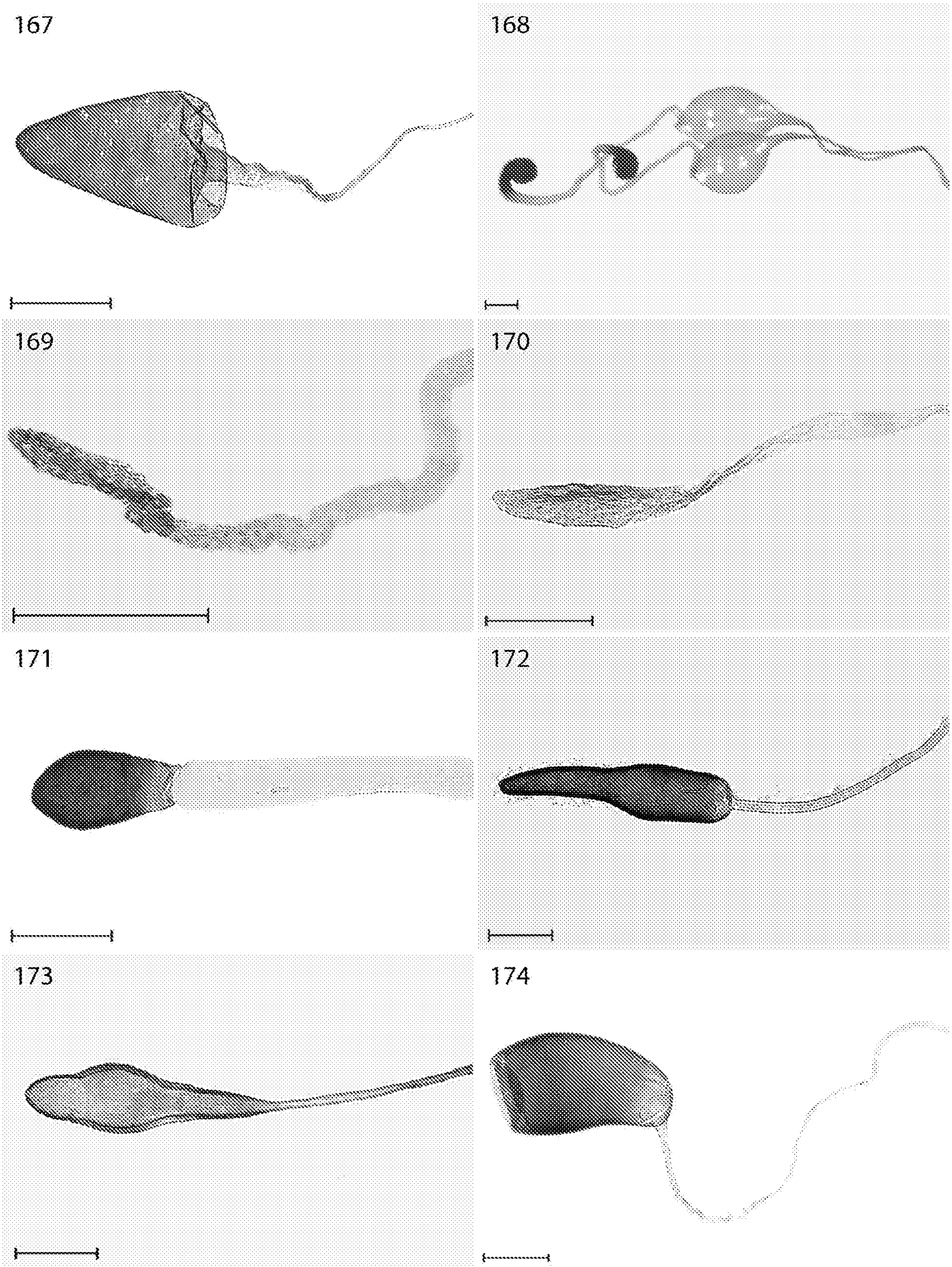
FIGURES 143–150. Female terminalia (cont.), dorsal view (except where noted), scale bar = 0.1 mm. 143, *Omphalophora majuscula* [USNMENT00025474]; 144, *Omphalophora fasciata* [USNMENT00025463]; 145, *Ptiolina mallochi* [USNMENT00022953]; 146, *Ptiolina zonata* [USNMENT00022841], lateral view; 147, *Ptiolina zonata* [USNMENT00022841]; 148, *Spania nigra* [USNMENT00024389]; 149, *Spaniopsis clelandi* [USNMENT00025398]; 150, *Symphoromyia hirta* [USNMENT00028587]. *Abbreviations: cerc = cercus; cerc p = cercus sensory pit; pos cresc = posterior crescent; rng = ring of sclerotization; spmth = spermatheca; spmth acc g = spermathecal accessory gland; t = tergite; vl proc = ventrolateral process.*



FIGURES 151–158. Female terminalia (cont.), dorsal view, scale bar = 0.1 mm. 151, *Chrysopilus testaceipes* [USNMENT00025876]; 152, *Chrysopilus* sp. [USNMENT00025877]; 153, *Pelecorhynchus elegans* [USNMENT00025880]; 154, *Pseudoerinna jonesi* [USNMENT00025319]; 155, *Atherix pachypus* [USNMENT00025886]; 156, *Atrichops* sp. [USNMENT00025248]; 157, *Dasyomma coeruleum* [USNMENT00025213]; 158, *Vermileo vermileo* [USNMENT00025793]. *Abbreviations: c sp duct = common spermathecal duct; circ r = circular ridge; ej app = ejaculatory apparatus; gen ch = genital chamber; sp duct = spermathecal duct; spmth = spermatheca; spmth acc g = spermathecal accessory gland; t = tergite; vl proc = ventrolateral process.*



FIGURES 159–166. Female terminalia (cont.), spermathecal structures, dorsal view, scale bar = 0.1 mm. 159, *Arthroceras fulvicorne* [CSCA08B320]; 160, *Chrysopilus thoracicus* [USNMENT00025875]; 161, *Omphalophora majuscula* [USNMENT00025474]; 162, *Omphalophora majuscula* [USNMENT00025474]; 163, *Spania nigra* [USNM ENT00024389]; 164, *Spaniopsis clelandi* [USNMENT 00025398]; 165, *Symphoromyia hirta* [USNMENT00028587]; 166, *Symphoromyia hirta* [USNMENT00028587]. *spmth = spermatheca; spmth acc g = spermathecal accessory gland; sp duct = spermathecal duct.*



FIGURES 167–174. Female terminalia (cont.), spermathecae, dorsal view, scale bar = 0.1 mm. 167, *Austroleptis* sp. [USNMENT00025761]; 168, *Bolbomyia* sp. [CSCA07Y111]; 169, *Desmomyia thereviformis* [USNMENT00025628]; 170, *Rhagio* sp. [USNM ENT 00025853]; 171, *Suragina concinna* [USNMENT00025797]; 172, *Pelecorhynchus fusconiger* [USNMENT00025883]; 173, *Pseudoerinna jonesi* [USNMENT00025319]; 174, *Vermileo vermileo* [USNMENT00025793].

111. Sternite 9, posterior end. (1) Fused posteriorly (2) free posteriorly, in single plane (3) free posteriorly, in two planes. The posterior end of sternite 9 (posterior of the genital chamber) has three typical forms. The posterior end of sternite 9 may be fused posterior of the genital chamber, in a single plane. The posterior end of sternite 9 may also be free and in this condition, with or without vertically-oriented apodemes. When the vertical apodemes are absent, the posterior end of sternite 9 is oriented in a single plane. When the apodemes are present, there are vertical and horizontal components that extend into two planes.

112. Sternite 9, posteromedial form. (1) Held horizontal (2) held vertical medially. 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 (Nagatomi 1982a, Stuckenberg 1956b).

113. Sternite 9, posterior margin. (1) Not crescent-shaped (2) crescent-shaped. *Omphalophora*, *Ptiolina*, and *Symphoromyia* 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 (e.g., Figs. 143, 147, 150). This character is inapplicable for taxa whose sternite 9 posterior margin is free.

Larval characters

Most larvae I examined were not determined to species. Therefore I use only characters known to be conserved at the genus level and above. Characters may have uncertainty at the species or genus level were precluded.

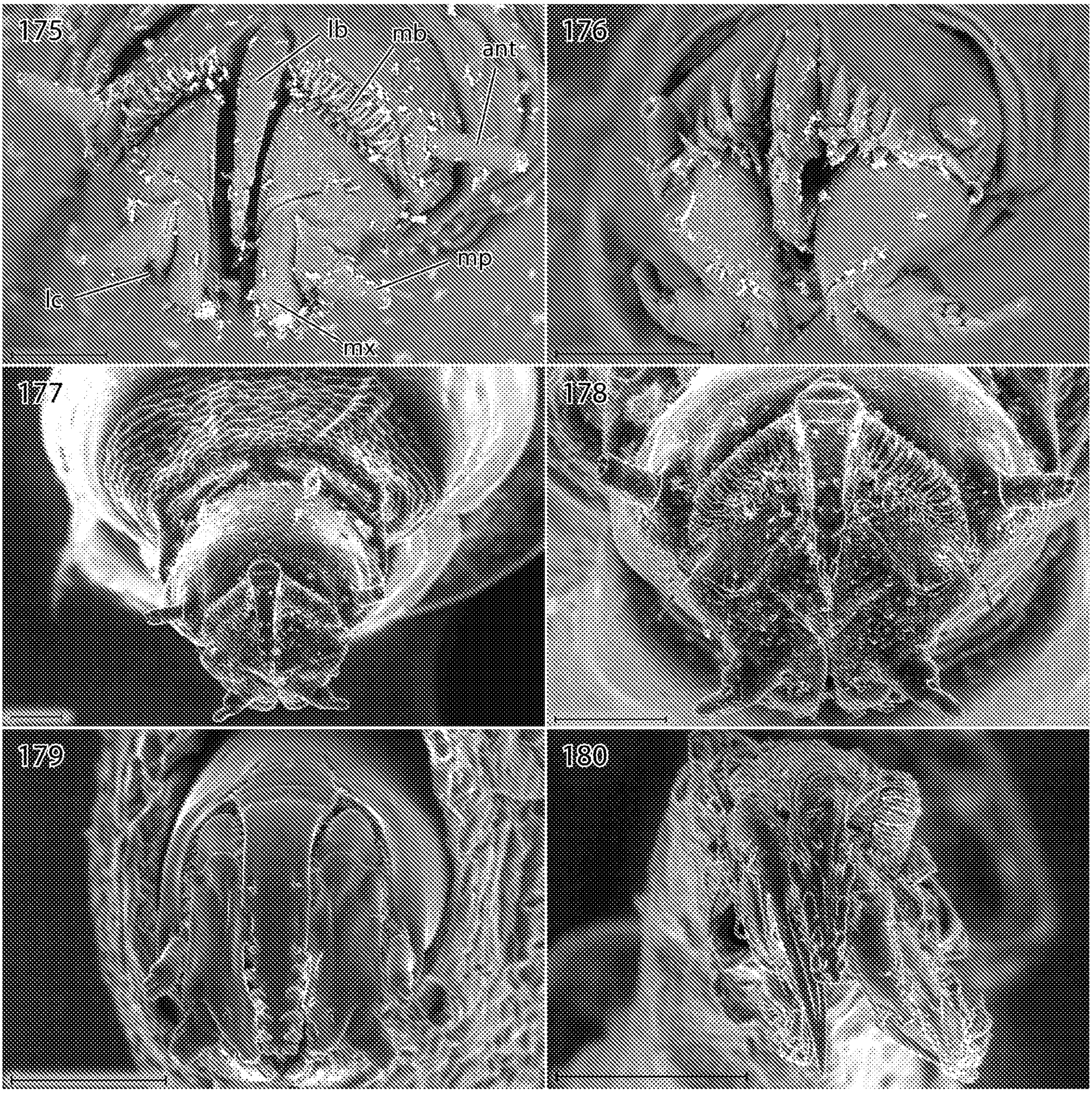
114. Head capsule. (1) Not retractile (2) retractile. Woodley (1989) asserted that all known larvae of Tabanomorpha have a retractile head. This is apparently an autapomorphic condition of the group.

115. Head capsule position. (1) Retractile within long folded membrane (2) retractile without such membrane. The oreoleptid, athericid, and tabanid larvae are distinctive in that the head is attached to a long extensible membrane that is typically folded back within the first thoracic segment.

116. Head capsule length. (1) Less than 4.5 times longer than greatest width (2) more than 4.5 times longer than greatest width. 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.

117. Head capsule shape. (1) Not cone-shaped (2) cone-shaped. The xylophagid taxa have a distinctive, strongly sclerotized cone-shaped head capsule that is a putative synapomorphy for this clade (James 1981, Woodley 1989, Palmer *et al.* 2000).

118. Saw sclerite of basal mandibular sclerite. (1) Absent (2) present. The saw sclerite is an autapomorphy for *Rhagio* (Tsacas 1962, Roberts 1969). It is located in a ventral position, adoral to the basal mandibular sclerite (Fig. 184).



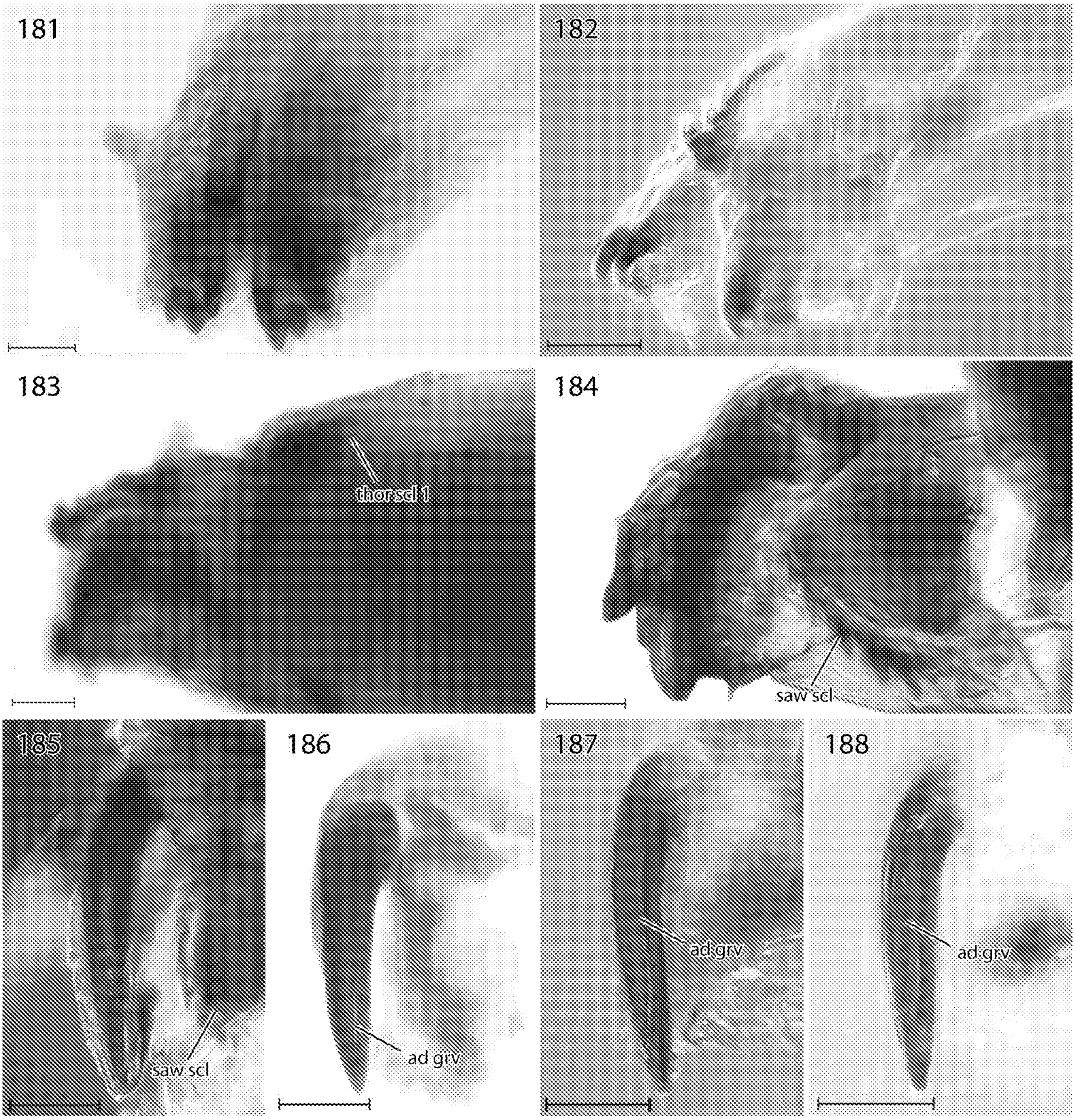
FIGURES 175–180. Larvae, heads, anterior view, scanning electron micrograph, scale bar = 0.1 mm. 175, *Chrysopilus* sp.; 176, *Rhagio* sp.; 177, *Symphoromyia* sp.; 178, *Symphoromyia* sp.; 179, *Pelecorhynchus* sp.; 180, *Glutops rossi*. *Abbreviations: ant = antenna; lb = labrum; lc = lacinia; mb = mandibular brush; mp = maxillary palp; mx = maxillary.*

119. Maxillary palpus form. (1) Segments sclerotized, cylindrical (2) soft, segments poorly differentiated. In species of Athericidae, the maxillary palpus has a distinctive form that is sclerotized, thin, somewhat elongate and cylindrical. In other taxa, the maxillary palpus is soft, not sclerotized, and its segments are poorly differentiated.

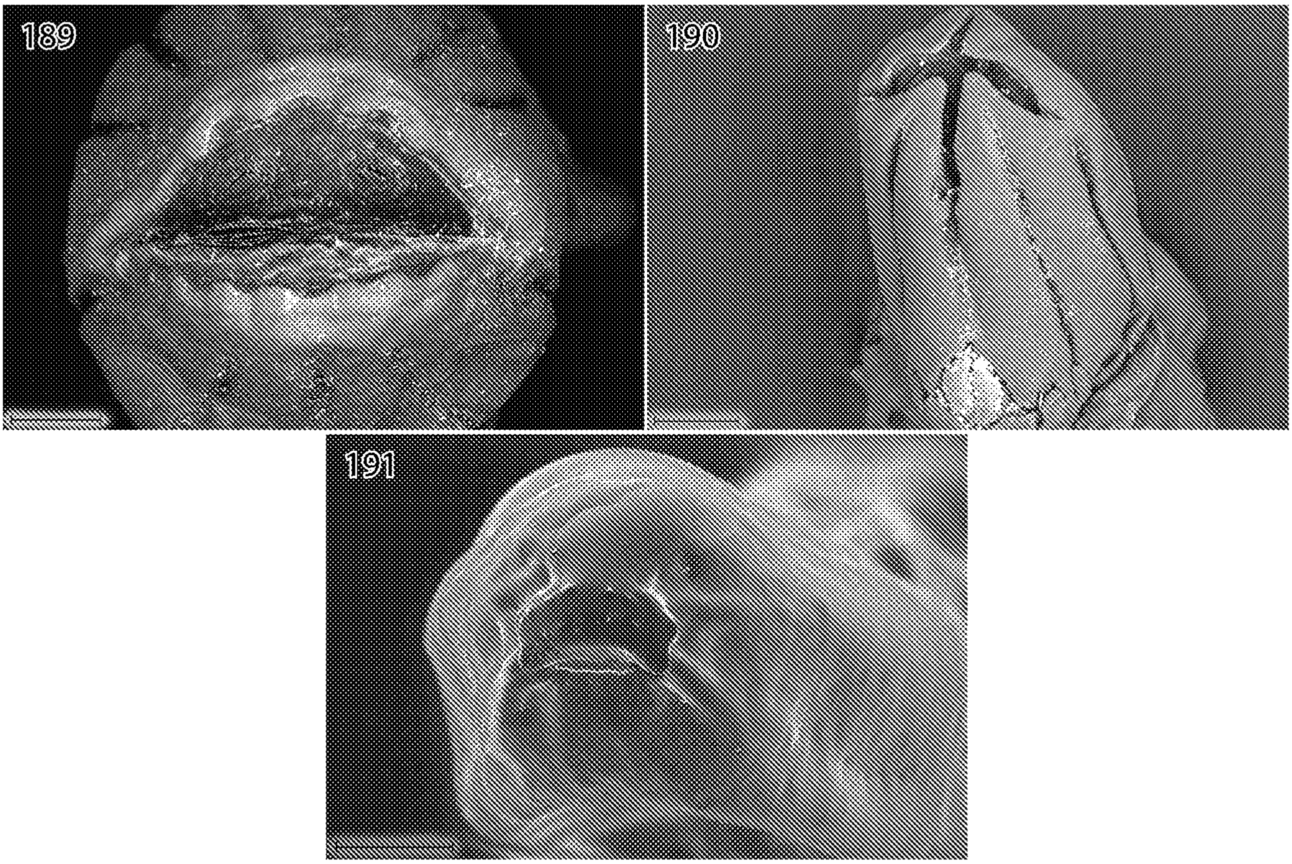
120. Enlarged salivary pump. (1) Absent (2) present. An enlarged, sac-like salivary pump is present in *Oreoleptis*, Athericidae, and Tabanidae (Teskey 1969; Zloty *et al.* 2005).

121. Anterior margin of thorax. (1) Ruffled (2) not ruffled. The anterior margin of the first thoracic sclerite of *Ptiolina* and *Symphoromyia* bears a distinctive ultrastructural pattern (Figs. 177, 183). 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.

122. Eversible proleg. (1) Absent (2) present. This is known to be present only in Vermileonidae (Teskey 1981c).



FIGURES 181–188. Larvae (cont.), dissected head and mouthparts, viewed through compound microscope with Nomarski projection, scale bar = 0.1 mm. 181. *Ptiolina* sp., anterior oblique view; 182. *Ptiolina* sp., lateral view; 183. *Ptiolina* sp., lateral view; 184. *Rhagio mystaceus*, lateral view; 185. *Rhagio mystaceus*, right mandibular hook, oblique inner view; 186. *Symphoromyia* sp., right mandibular hook, oblique inner view; 187. *Dasyomma* sp., right mandibular hook, oblique inner view; 188. *Atherix* sp., right mandibular hook, oblique inner view. *Abbreviations: ad grv = adoral groove; saw scl = saw sclerite; thor scl = thoracic sclerite.*



FIGURES 189–191. Larvae (cont.), terminal segment, scale bar = 0.2 mm. 189, *Symphoromyia* sp., posterior view; 190, *Rhagio* sp., oblique posterior view; 191, *Pelecorhynchus* sp., posterior view.

123. Crocheted locomotory prolegs. (1) Absent (2) present. *Oreoleptis* and Athericidae are distinguished by having a series of abdominal crocheted prolegs. In *Oreoleptis*, the prolegs are absent on the first abdominal segment, an autapomorphy (Zloty *et al.* 2005).

124. Unpaired abdominal proleg segment eight. (1) Absent (2) present. *Oreoleptis* and Athericidae are also distinguished by having an unpaired crocheted proleg on the last abdominal segment (Zloty *et al.* 2005).

125. Graber's organ. (1) Absent (2) present. This is an autapomorphy of Tabanidae, found in all known larvae (Teskey 1969).

126. Hind segment sclerotization. (1) Not sclerotized (2) strongly sclerotized. The xylophagid taxa are unique among taxa sampled here in having the hind segment partly sclerotized.

127. Thick, waxy integument. (1) Absent (2) present. The larvae of *Pelecorhynchus* and *Glutops* species have a tough, waxy covering that is unlike that found in other known tabanomorph larvae. Teskey (1970a) noted "the shapes and relative sizes of the segments [of *Glutops* and *Pelecorhynchus* larvae] and the characteristics of their integuments are essentially identical."

TABLE 5. The morphological character data. Characters are in sequential order in groups of ten; ambiguous character states are enclosed in parentheses.

	10	20	30	40	50	60	70	80	90	100	110	120	
Alloleptis tersus	2111211221	?21(12)3112?1	1113212 1?1	1111?11131	3124221111	2122112111	??21121111	??3111?1??	??????????	??????????	??????????	??????????	??????
Arthroceras fulvicorne	(12)1212(23)221?	?1?231?211	1113222211	1111111131	4112221211	2132211111	??12211112	233(12)212111	1311112111	1211123322	1111?1321?	2?????????	??????
Arthroceras pollinosum	112123211?	?122311211	1113222211	1112211131	4112221211	2132211111	??11211112	2332212111	1311111111	1211123322	111111321?	2?????????	??????
Arthroteles bombyliiformis	2121132221	?122312121	1113212221	1111111131	4113221211	2133212111	??21311112	1332111111	1311111111	221112111?	111111331?	32????????	??????
Arthroteles cinerea	2121132221	?122312131	1113212221	1111111131	4113221211	2133212111	??21311112	1342111111	1311111111	221112121?	111121331?	32????????	??????
Atherimorpha atrifemur	2121212121	?12231?221	1213211221	1111211121	4123221211	2133212111	??11311112	1342111111	1311111111	121112131?	1111?1331?	32????????	??????
Atherimorpha montana	(12)121212121	?122311221	1113212221	1111211121	4113121211	2133112111	??21311112	1322111111	1311111111	121112131?	111111331?	32????????	??????
Atherimorpha nemoralis	2121212121	?122311221	1213212221	2111211121	4123121211	2133212111	??11311112	1342111111	1311111111	121112131?	111221331?	32????????	??????
Atherimorpha vernalis	2122212121	?12231?221	1113212221	1111211121	5113221211	2133212111	??21311112	1331111111	1311112111	221112121?	1112?1321?	32????????	??????
Atherix pachypus	2122222123	2122321231	1113121231	1211211131	3111222211	213322222?	??12121221	?14222?132	12211232?1	??1212(23)31?	211121311?	2??2221112	112211
Austroleptis collessi	2221132121	?122212121	11132121?1	1111211131	3112221113	2133112111	??11112??1	?135112132	23211232?1	??1212????	??????????	??????????	??????
Austroleptis multimaculata	2221132121	?122212121	11132121?1	1111(12)21131	3112221113	2133112111	??11122??1	?135112131	2?211132?2	??1212221?	111111321?	31????????	??????
Bolbomyia nana	2121232121	?122(23)11222	11132121?1	1111211131	3113121113	2233212111	??22311111	?144212112	1311112111	221111(23)11?	22211???1?	31????????	??????
Chrysopilus ferruginosus	1121222123	1111?11221	1122222211	2111211131	4112221211	1132211112	2121111112	133(12)12?111	1311112111	1(12)12123323	111111221?	31?2111121	111111
Chrysopilus panamensis	1121222123	1111?11221	1122222211	1112211131	3112211211	1132212112	2121111112	132212?111	1311122111	1(12)1112331?	111121321?	31?2111121	111111
Chrysopilus quadratus	(12)121222123	1111?11221	1122222211	1111211131	3112211211	1132211112	2121121112	134212?111	1311112111	111212321?	111211331?	31?2111121	111111
Chrysopilus rhagiodes	1121222123	1111?1?2?1	1122222211	2111211131	(34)112211211	1132212112	2121121111	?33212?111	1311122111	1212122223	111121331?	31?2111121	111111
Chrysopilus thoracicus	2121222123	1111?11221	1122222211	11122111(23)1	3112211311	1132212112	2121111112	132212?111	1311122111	1111123124	111111421?	31?2111121	111111
Chrysops vittatus	122123321?	?222322131	2113121231	1211121232	3114122221	213312112?	??111212?2	1141212232	12111212?1	??1212321?	211121221?	1?12221122	111121
Dasyomma atratulum	2121222123	1112322231	1113221231	1211121131	4111121211	223322212?	??22121222	113122?132	12111232?1	??1212221?	111221311?	2??2221112	112211
Dasyomma coeruleum	21112?2123	1112321131	1113221231	1211111131	?11122(12)211	223322212?	??22121222	113122?132	12111232?1	??1212321?	211221311?	2??2221112	112211
Dasyomma vittatum	21112?2123	1112321131	1113221231	2211111131	?111(12)22211	223322212?	??22121222	113122?132	13111232?1	??1212331?	211221211?	2??2221112	112211
Desmomyia thereviformis	21212(13)3123	22?1?1?2?1	1113121231	1111211121	4112221211	2133212111	??22311112	1232111111	13?1112111	2?1?12231?	111221311?	31????????	??????
Dichelacera marginata	112112311?	?222322131	2113121232	2211121232	3114122221	213111112?	??11121222	1?42212232	12211232?1	??1213331?	211111311?	2??2221122	111121
Glutops rossi	112113321?	?222(12)12221	11132221?1	2(12)12121132	3114121211	?13221312?	??22311112	1331112121	1311113111	321122311?	111221411?	2??2121122	111111
Isalomyia irwini	212221311?	?1?1?12132	1113212231	?11121111?	6214122211	22331?????	??????????	???????132	112111?111	121212311?	111221431?	2??2111121	121111
Lampromyia canariensis	2122213123	21?1?12132	1113221231	211121111?	621412?221	2233112211	??21121121	?1?112?132	1221112111	1212?2311?	111222??1?	2??2111121	121111
Leptynoma hessei	2122213121	?121?12131	1113212231	211121111?	6114122221	2(12)33122111	??21122??1	?12112?1??	??????????	??????????	??????????	???2111121	121111
Litoleptis alaskensis	2122231122	?1?1?1?2?2	11132121?1	1111211121	1214121123	?11111112?	??23122??1	?11212????	??????????	??????????	??????????	??????????	??????
Omphalophora fasciata	2121232122	?1?231?2?1	11132221?1	1111111131	(45)112121221	2132212112	12?2111112	23321??121	1311211112	1221123223	1112113223	1?2???????	??????
Omphalophora lapponica	2121222122	?1?231?2?1	11132221?1	1111111131	4113221221	2132212112	1221111112	2322112111	1311211112	1221123223	111(12)113223	1?2???????	??????
Omphalophora majuscula	2121222222	?12231?2?1	11132221?1	1111111131	4113221221	2132212112	1222111112	2331112111	1311211112	1221123223	1112113223	1?2???????	??????
Oreoleptis torrenticola	312122221?	?1?231?2?1	1113?2?2?1	?111221131	?113121211	2133122112	1122121221	?343212132	1321123111	221212331?	??11?132??	???2221112	11221?
Pelecorhynchus personatus	212123321?	?232312121	21132221?2	2212121232	?114122221	213311322?	??22311221	?141112111	1311123111	321222311?	111221411?	2??2121121	111111
Pseudoerinna jonesi	111122221?	?1323122?1	1113222212	2212121132	3114122221	223312212?	??21311112	1333112111	13111?3112	3212222(12)1?	11121???1?	2?????????	??????
Ptiolina mallochi	2121232122	?12231?2?1	11132121?1	1111(12)11131	4112221111	2132212112	1211111112	232212?131	1211211112	1221123124	1111113122	1?22111121	211111
Ptiolina zonata	2121232122	?122311221	11132121?1	1111211131	4112221111	2132211112	1212111112	232(12)12?131	1211211112	1221123124	1111113122	1?22111121	211111
Rhagio costatus	2121212123	2111?112?1	1113121231	2111111131	5112111211	2133212111	??21311112	1232111111	1311112111	211212131?	111111211?	31?2111221	111111
Rhagio mystaceus	2121212123	2111?11211	1113121231	2111211121	5112211211	2133212111	??12311112	1242111111	1311112111	211212131?	111111311?	31?2111221	111111
Rhagio plumbeus	2121222123	2121?112?1	1113121231	1111211121	5112211211	2133212111	??11311112	1242111111	1311112111	211212131?	111111431?	31?2111221	111111
Rhagio scolopaceus	3121212123	2121?112?1	11131(12)1231	2111211121	5112211311	2133212111	??21311112	1242111111	1311112111	211212131?	1112?1411?	31?2111221	111111
Rhagio sinensis	2121212123	2121?1?2?1	1113121231	2111211131	5112211211	2133212111	??11311112	1242111111	1311112111	2?1?12131?	111211321?	31?2111221	111111
Rhagio vertebratus	2121212123	2121?1?221	11131(12)1231	2111211121	51122(12)1211	2133212111	??21311112	1242111111	1311112111	211212131?	111211211?	31?2111221	111111
Rhagina incurvatus	1121212123	21?1?112?1	1113111231	1111211121	5112121221	2133212111	??22311112	1242111111	1311112111	211112231?	111111311?	3?????????	??????
Schizella furcicornis	1122212123	1121?1?2?1	1122222211	1111211131	?112211211	?132212111	??23111112	134112?111	1311111111	1112123323	111121221?	31????????	??????
Sierramyia sp.	2122212(12)23	21?1?1?2?1	1113221231	111111111?	5112221211	2133112111	??22311112	124211?111	1311112111	211212?3??	111211311?	31????????	??????
Solomomyia gressitti	1122211123	1111?1???1	1112222211	1111211131	4112211211	1132211112	2121121112	123212?111	1311112111	1(12)12123223	1112?1331?	31????????	??????
Spania nigra	2121231122	?121?1?221	11132121?1	1111(12)11132	411322111(12)	213121112?	??23111111	?33212?132	1122211112	122212(12)124	1222213122	1?1???????	??????
Spaniopsis clelandi	(12)121232122	?121?22221	11132211?1	1111111132	411222111(23)	213121112?	??23111112	232212?132	1122211112	1212123223	1212113221	1?1???????	??????
Spaniopsis longicornis	1121232122	?121?2?221	11132221?1	1111111132	4112221112	213121112?	??12111112	233212?132	1122212112	1212123223	1212?13121	1?1???????	??????
Stylospania lancifera	1122212122	?1?1?1?2?1	11?2212211	1111211131	4112211211	?132212111	??22121112	133212????	??????????	??????????	??????????	??????????	??????
Suragina concinna	2121212123	2112322121	1113121231	2211111131	3111222211	213322222?	??23121222	114322?132	12211222?1	??1212331?	21211???1?	2??22211?2	112111
Symphoromyia atripes	2121133123	213232?121	1113121231	2112111131	4112221211	21321?????	??????????	???????131	1311211111	1211123223	1111213223	1?22111121	211111
Symphoromyia cruenta	(12)12(12)133123	223232?121	111322(12)231	2112111131	5112221211	2132212112	2221211112	2332112131	1311211111	1211123223	1111113323	1?22111121	211111
Symphoromyia hirta	2121123123	2122322221	1113222231	2112111131	5112221211	2132212112	2212211112	2322112131	1311211111	2211123223	1111113323	1?22111121	211111
Tabanus atratus	122113211?	?222222131	2113121232	2211121232	3114122221	213111112?	??11121222	1143212232	12211222?1	??1212(23)?1?	211121311?	2??2221122	111121
Tabanus rufofrater	122113311?	?222322131	2113121212	221?121232	3124122221	213111112?	??11121122	1131212232	11211222?1	??1212321?	211121311?	1?12221122	111121
Tabanus subsimilis	122113111?	?22232?131	2113121232	221?121232	3114122221	213111112?	??11121122	113(12)212232	11211222?1	??1212311?	211121?11?	1?12221122	111121
Vermileo opacus	2222213121	?221?11221	1113211231	111121111?	6214122222	223311312?	??21111121	?141112132	1121121112	321212321?	111221431?	2??2111121	121111
Vermileo vermileo	2222213123	21?2211221	1113211221	211?21111?	6214121221	2233112211	??21121121	?1411??132	1121113111	3212?2311?	111222??1?	2??2111121	121111
Arthropeas americana	222122221?	?121?11231	1113121211	2122212131	4112222211	2233212111	??12121112	1133112111	1411122121	122212331?	111221321?	2??1112121	111112
Coenomyia ferruginea	321121321?	?122111231	1113121211	2122212131	(45)112222211	2233112111	??12121112	1131112131	1411123121	122212221?	221221321?	2??1112121	111112
Dialysis rufithorax	2221212223	2111?12221	1113222211	2121212121	5112111211	2233212111	??11121112	1342113111	1411122121	122213331?	111111121?	2??1112121	111112
Exeretonevra angustifrons	222221321?	?1122112(12)1	1113122211	21?1111?31	5113212121	2233111111	??12221112	233212?132	1211112112	122212121?	111221?11?	2??1112121	111112
Xylophagus lugens	122221321?	?122(13)1?221	1111?22211	212221211?	4122121111	2233112211	??2112112?	?143112111	1411123121	121212141?	111111131?	2??1112121	111112

Analysis of morphological data

Parsimony heuristic searches found 2905 most parsimonious trees; length = 693, CI = 0.247, RI = 0.684, RC = 0.169, HI = 0.753 (Fig. 192). The strict consensus of these trees shows a monophyletic Tabanomorpha, with tabanoid taxa nearly completely resolved. The phylogenetic structure of the remaining tabanomorph taxa, however, remains largely ambiguous.

The monophyly of Tabanomorpha is supported by the retractile larval head (Woodley 1989; character 113). Tabanoidea contains four families (Pelecorhynchidae, Oreoleptidae, Athericidae, and Tabanidae) and is supported by having a postspiracular scale (character 32; although lacking in some taxa), a bulbous subscutellum (character 36; lacking in *Suragina concinna*), and an elongate larval head capsule (character 114). The monophyly of Pelecorhynchidae is supported by the presence of paired ducts arising from the posterior margin of tergite 8 (character 94). This is a new character, and the first adult synapomorphy developed for the family. The ventral process of the female first cercal segment in these taxa is distinctive and has been recognized as a possible synapomorphy for Pelecorhynchidae (character 90; Woodley 1989), however an explicit definition of this character is problematic as other tabanomorph taxa also have elongated first cercal segments (e.g., *Vermileo*). The thick, waxy outer layer of the larva also supports Pelecorhynchidae (character 126), although the larva of *Pseudoerinna* species is not known. The close relationship between Athericidae, Oreoleptidae, and Tabanidae is supported by having exceptionally long gonocoxal apodemes (character 68), aedeagal tines (character 75), larval head capsule withdrawn into folded membrane (character 114), and enlarged salivary pump (character 119). *Oreoleptis* is recovered as sister to Athericidae and Tabanidae, consistent with previous morphological analysis (Zloty *et al.*, 2005). Although *Oreoleptis* has wing veins R_1 and R_{2+3} separated at the wing margin and a two-segmented female cercus, it shares a number of special conditions of the larva known only within Athericidae including sclerotized and cylindrical maxillary palpus (character 119), crocheted locomotory prolegs (character 123), and unpaired abdominal proleg segment eight (character 124). Athericidae and Tabanidae are united on the basis of a single-segmented female cercus (character 88; independently derived in *Austroleptis*) and a narrow ridge marking the distal end of the ejection apparatus of the spermathecal duct in the female (character 101, although this was not scored for *Oreoleptis*). The monophyly of Athericidae is supported by the autapomorphic condition of wing veins R_1 and R_{2+3} which meet together at the wing margin (character 44) and Tabanidae is united by flattened, concave occiput (character 21), developed lower calypter (character 38), and presence of Graber's organ (character 125).

Early divergences among Vermileonidae and the rest of Tabanomorpha are unresolved. Vermileonidae is clearly monophyletic and highly autapomorphic to the degree that some character homology assessments, particularly in the male and female genitalia, are difficult. The common spermathecal duct in *Vermileo* sp., for example, is highly modified into an enlarged, pilose structure that tapers distally. Vermileonidae is recovered within a polytomy among the remainder of non-tabanoid Tabanomorpha. *Atherimorpha* and *Arthroteles* are united on the basis of female sternite 9 held in vertical position medially (character 112), although South American *Atherimorpha* species are united with *Arthroteles bombyliiformis* (South Africa) by the shared presence of two setal sizes of the thorax (character 22) to the exclusion of *Atherimorpha vernalis* White (Australia). Chrysopilinae are recovered as a monophyletic group composed of *Chrysopilus* (including *Solomomyia*), *Schizella*, and *Stylospania*. The chrysopilines are supported by three synapomorphies; the presence of metallic- or scale-like thoracic setae (character 30, Fig. 2), the presence of a reduced proepimeron sclerite (character 24, Figs. 34, 36), and flattened, appressed setae (or 'scales') on the legs, especially on the femur (character 51). These scales may be difficult to see because of their orientation, structure, and often have the same color as the femur. Scanning electron micrographs, however, show these modified setae very clearly (Figs. 65–66). Chrysopilinae also tend to have pilose aristae (character 11) and the gonostyli of the male genitalia tend to be heavily setose (not scored; Figs. 93, 103). *Rhagio* spp. and relatives (*Desmomyia thereviformis* and *Sierramyia* sp.) are united by homoplasious characters, including hypandrium separated partially from the gonocoxites by an incomplete suture (character 65) and lateral ejaculatory process associated with M32 flexor muscle integrated into sperm sac membrane (character 72). The remaining taxa are united at the genus level, but lack further phylogenetic structure above the species level.

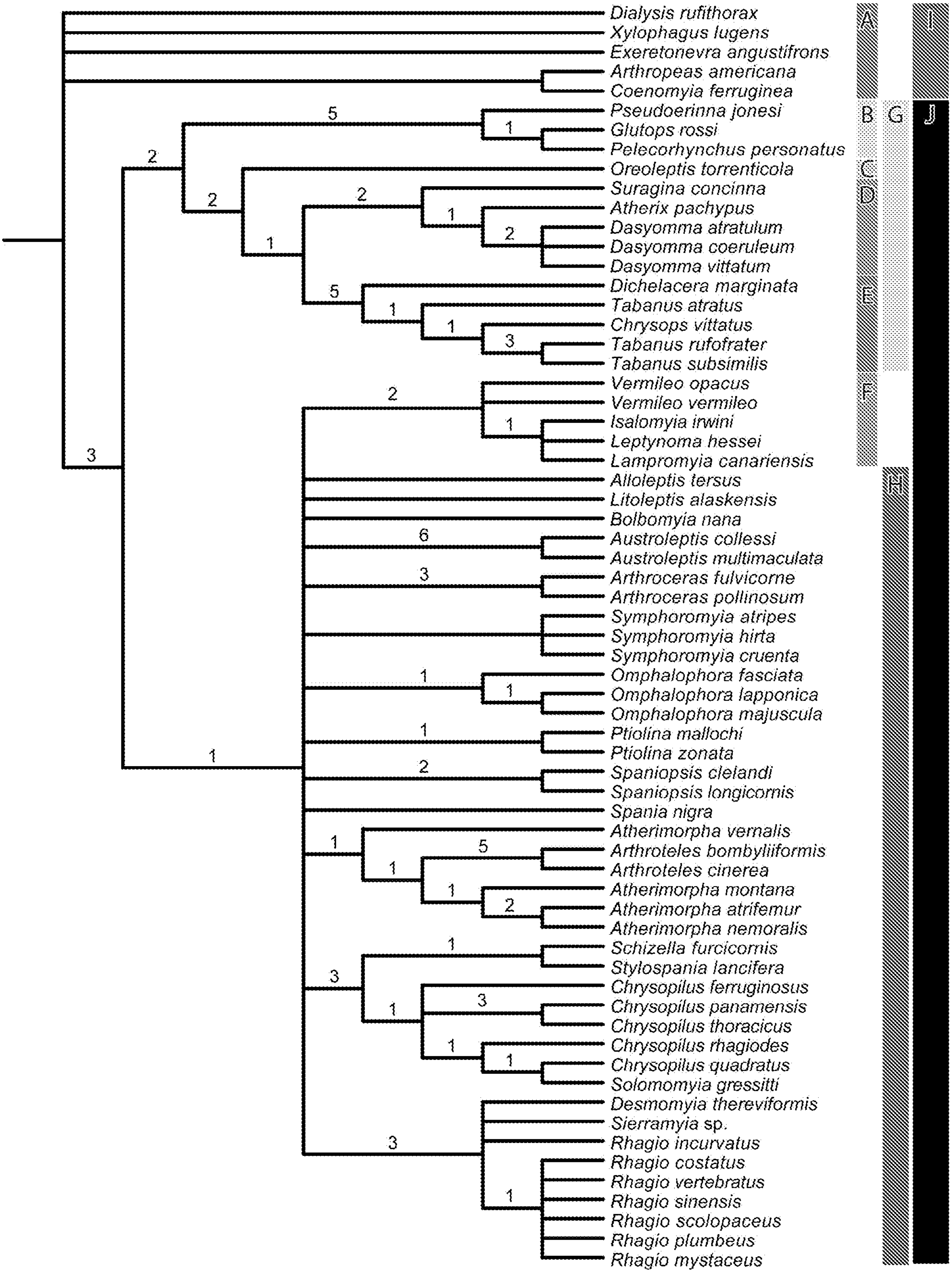
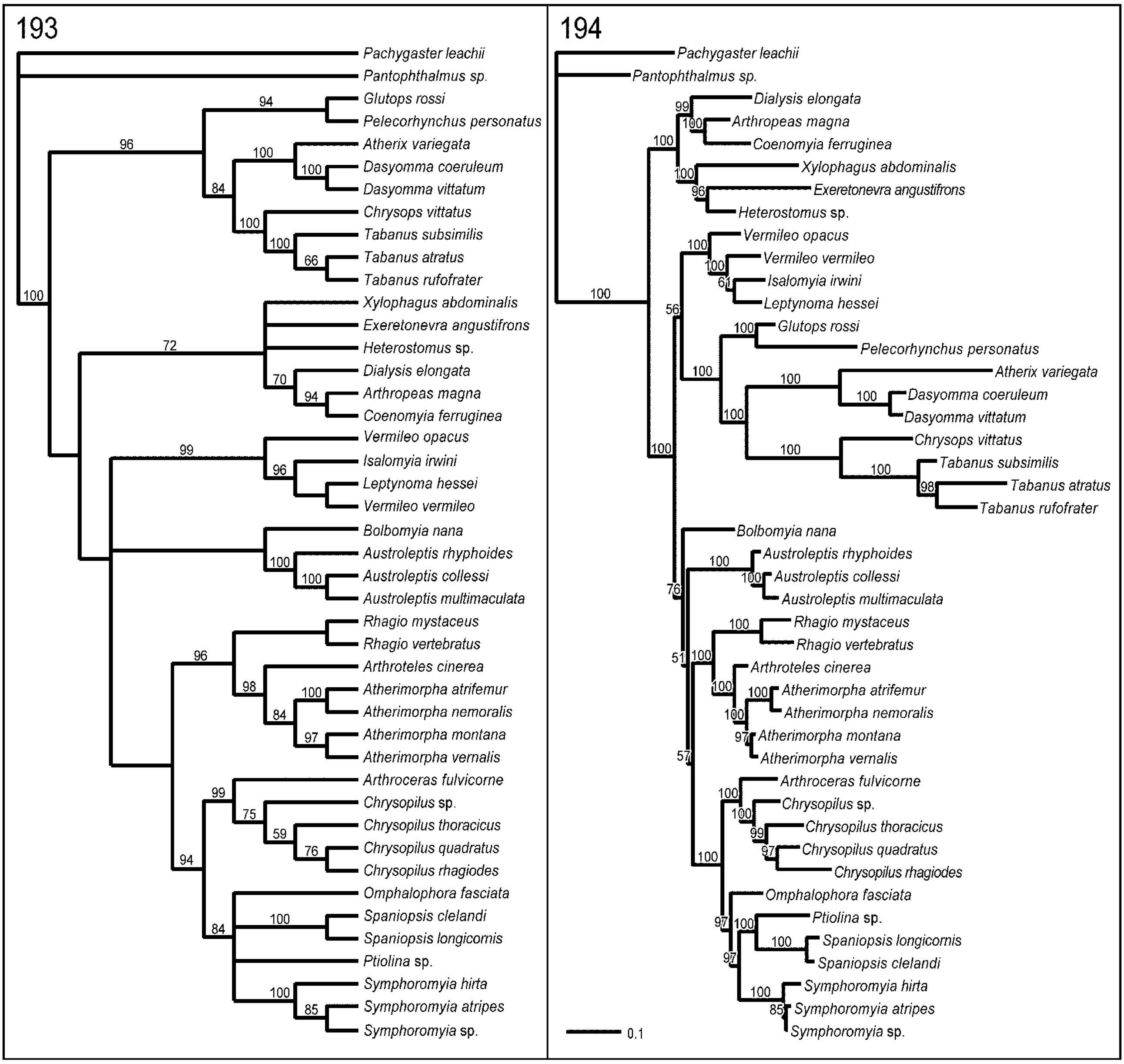


FIGURE 192. Figure 192. Strict consensus of 2905 MPTs generated from the morphological matrix. Bremer support values noted above supported branches. *Classification along right margin; A = Xylophagidae, B =Pelecorhynchidae , C =Oreoleptidae , D = Athericidae, E = Tabanidae, F =Vermileonidae, G = Tabanoidea, H = Rhagionoidea, I = Xylophagomorpha, J = Tabanomorpha.*

Analysis of molecular data

The mean base frequencies of the matrix were A= 0.30024, C=0.17850, G=0.23893, T=0.28233 (Chi-square test of homogeneity of base frequencies across taxa = 38.709256 (df=132), P = 1.00000000). The differences between optimal topologies generated by MP, ML, and BI analyses were not significant when subjected to Kishino-Hasegawa and Templeton (Wilcoxon signed-ranks) tests. However, sister group relationships between the major clades are not resolved consistently across methods (Figs. 193–195).

Parsimony analysis results in 20 most parsimonious trees (Fig. 193). In the strict consensus of these trees, Tabanomorpha is paraphyletic, with Tabanoidea recovered sister to Xylophagidae and remaining tabanomorph families. MP analyses are susceptible to long branch attraction problems (e.g., Huelsenbeck 1997) and the long branches found in Tabanoidea by other methods (Figs. 194, 195) suggest this result is misleading. Both Bayes and maximum likelihood methods recover a monophyletic Tabanomorpha (Figs. 194, 195, respectively). The relationship between Vermileonidae and the rest of Tabanomorpha, however, differs between model-based methods.



FIGURES 193–194. Analysis of 28S rDNA data. 193, Strict consensus of 20 MPTs from parsimony analysis. Bootstrap values above 50% are noted above supported branches (TBR, nreps = 1000 / addseq reps = 5). 194, Bayes tree. Posterior probabilities are noted above branches.

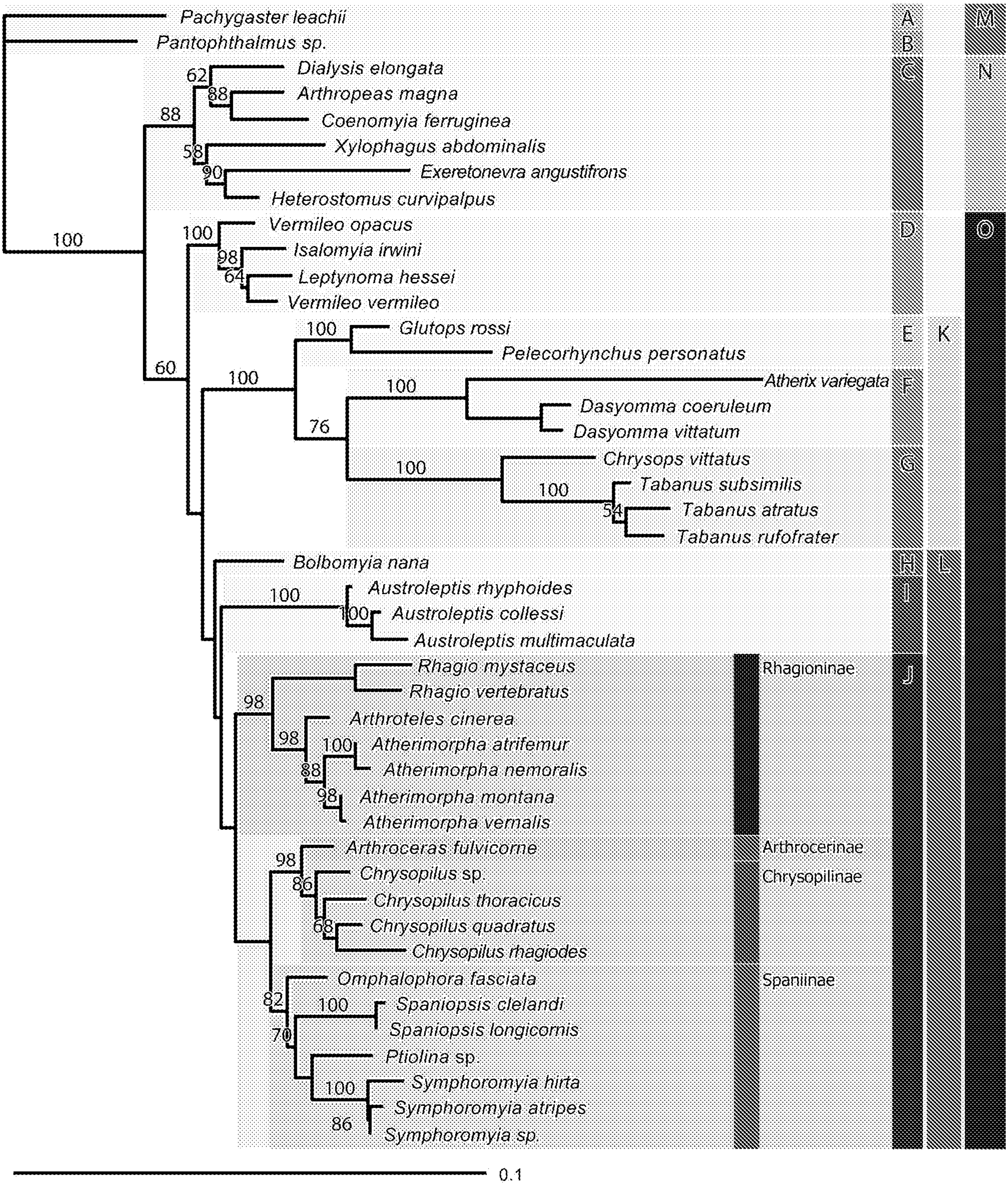


FIGURE 195. Analysis of 28S rDNA data, continued. Maximum Likelihood analysis. Bootstrap values greater than 50% are above supported branches (NNI, nreps = 100 / addseq reps = 3). *Classification along right margin; A = Stratiomyidae, B =Panthophthalmidae , C = Xylophagidae, D = Vermileonidae , E = Pelecorhynchidae, F =Athericidae, G = Tabanidae, H = Bolbomyiidae, I = Austroleptidae, J = Rhagionidae, K = Tabanoidea, L = Rhagionoidea, M = Stratiomyomorpha, N = Xylophagomorpha, O = Tabanomorpha.*

As a family, Vermileonidae is well supported, however the genus *Vermileo* is rendered strongly paraphyletic. Rhagionoidea is formed by *Bolbomyia, Austroleptis*, and the rhagionid taxa. The relationship among rhagionid subfamilies are consistent across methods, showing Rhagioninae (Spaniinae (Arthrocerinae + Chrysopilinae)).

Within Rhagioninae, *Atherimorpha* is monophyletic with respect to *Arthroteles* and together are sister to *Rhagio*. Spaniinae consists of *Omphalophora, Ptiolina*, *Spaniopsis*, and *Symphoromyia*; in the MP strict consensus, these taxa form a polytomy. In the model-based methods, *Ptiolina* is recovered either sister to *Spaniopsis* spp. (BI) or *Symphoromyia* spp. (ML). *Omphalophora* and *Ptiolina* are never recovered as sister taxa.

New World *Chrysopilus* are monophyletic in the molecular analysis, as are Australian *Chrysopilus*, Neotropical *Atherimorpha*, and Australian *Atherimorpha*.

Analysis of combined data

These results of the combined analysis are very similar to the results of the molecular treatment above, with a few exceptions. The most parsimonious tree (Fig. 196) shows Vermileonidae sister to Tabanoidea, which together, are sister to the clade formed by Rhagionoidea. *Austroleptis* and *Bolbomyia* form a clade sister to Rhagionidae. Within Spaniinae, *Symphoromyia* is sister to the rest of the group, which is recovered as *Omphalophora* (*Ptiolina* + *Spaniopsis*).

Given these results, further morphological evidence can be brought to bear. *Austroleptis* and *Bolbomyia* are united by the shared loss of wing vein M_3 although this condition is a relatively weak indicator of support; it is also present in *Litoleptis* and, to some degree, *Spania* and *Spaniopsis*. Both *Austroleptis* and *Bolbomyia* are distinguished more by their own, unusual suite of autapomorphic conditions than for their putative alliances with other rhagionid taxa. *Austroleptis* species are unusual in having a recessed clypeus (character 2), unusual pseudotrichia morphology (character 20), absence of gonocoxal apodeme (characters 67), gonocoxal lobes (character 71), unusual ejeculatory apodeme form (character 74), divided female sternite 8 (character 81), and one-segmented female cercus (character 88). *Bolbomyia* are also unique, distinguished by lacking pseudotracheae (character 20), and having a fore tibial spur (character 52), unusual ejeculatory apodeme form (character 74), aedeagal tines (character 75), two spermathecae instead of three (character 96), spermathecal ducts with distinct swollen area (character 103), and spermathecal ducts that lead directly to the genital chamber (character 105).

Rhagioninae consist of the genera *Arthroteles*, *Atherimorpha*, and *Rhagio*; the monophyly of which is supported by the butter-knife form of the endoaedeagal process, which is strongly laterally compressed (character 77, Fig. 117, 122). This character may be used to justify adding *Desmomyia* and *Sierramyia* to the subfamily. *Rhagio* and its nearest relatives are also united by having lateral ejaculatory processes that are integrated into the sperm sac membrane (character 72). Larval features that support the monophyly of the genus *Rhagio* include basal larval mandible with saw sclerite (character 118; Fig. 185) and mandibular brush with fewer than 25 setae (not scored; Fig. 176). These synapomorphies may be more inclusive once larvae of related taxa within Rhagioninae are found and described.

TABLE 6. Hypothetical taxonomic groupings were tested using the combined molecular and morphological data. The difference between unconstrained and constrained MPTs was measured using Kishino-Hasegawa and Templeton signed-rank tests. The p-values are shown below. When multiple most parsimonious constraint trees were found (indicated in parentheses below), the p-values were averaged. Significant p-values are shown in bold.

Concept	Constraint	Test statistic: Kishino-Hasegawa / Templeton signed-rank (number of equally MP constraint trees)	Increase in steps of MP constraint tree
Composition of Rhagioninae			
Rhagioninae *sensu* Nagatomi 1982	(*Atherimorpha* + *Arthroteles* + *Bolbomyia* + *Chrysopilus* + *Rhagio* + *Symphoromyia*)	**0.0008**/ **0.0008** (2)	31
Rhagioninae *sensu* Stuckenberg 2001	(*Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Rhagio* + *Symphoromyia*)	**<0.0001** / **<0.0001** (1)	23
Position and monophyly of Spaniinae			
Spaniidae (exclusive of *Symphoromyia*), Rhagionidae *sensu* Stuckenberg (Stuckenberg 2001)	(*Spaniopsis* + *Omphalophora* + *Ptiolina*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Bolbomyia* + *Chrysopilus* + *Glutops* + *Pelecorhynchus* + *Rhagio* + *Symphoromyia*)	**0.0001** / **<0.0002** (3)	43
Spaniidae (exclusive of *Symphoromyia*), Rhagionidae *sensu* Woodley, 1989	(*Spaniopsis* + *Omphalophora* + *Ptiolina*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Austroleptis* + *Bolbomyia* + *Chrysopilus* + *Rhagio* + *Symphoromyia*)	**<0.0001** / **<0.0001** (1)	25
Spaniidae (exclusive of *Symphoromyia*), Rhagionidae containing *Bolbomyia* but not *Austroleptis*, Pelecorhynchidae	(*Spaniopsis* + *Omphalophora* + *Ptiolina*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Bolbomyia* + *Chrysopilus* + *Rhagio* + *Symphoromyia*)	**0.0007** / **0.0007** (1)	25
Spaniidae (exclusive of *Symphoromyia*), Rhagionidae exclusive of *Austroleptis*, *Bolbomyia*, and Pelecorhynchidae	(*Spaniopsis* + *Omphalophora* + *Ptiolina*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Rhagio*)	**<0.0001** / **<0.0001** (1)	23
Spaniidae (inclusive of *Symphoromyia*), Rhagionidae *sensu* Woodley, 1989	(*Spaniopsis* + *Omphalophora* + *Ptiolina* + *Symphoromyia*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Austroleptis* + *Bolbomyia* + *Chrysopilus* + *Rhagio*)	**0.0011** / **.0011** (1)	16
Spaniidae (inclusive of *Symphoromyia*), Rhagionidae exclusive of *Austroleptis*, *Bolbomyia*, and Pelecorhynchidae	(*Spaniopsis* + *Omphalophora* + *Ptiolina* + *Symphoromyia*) + (*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Rhagio*)	**0.0013** / **0.0013** (1)	12
Spaniinae within Rhagionidae (Woodley 1989)	(*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*)	1.0000 / 1.0000 (1)	0
Omphalophora and *Ptiolina* monophyletic	(*Omphalophora* + *Ptiolina*)	0.2145 / 0.2144 (2)	5
Position of *Austroleptis* and *Bolbomyia*			
Austroleptis within or sister to Xylophagidae (Sinclair *et al.* 1994)	(*Austroleptis* + Xylophagidae)	0.7317 / 0.7316 (1)	2
Austroleptis within Rhagionidae *sensu* Woodley (modified to exclude *Bolbomyia*)	(*Austroleptis* + *Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*)	0.3459 / 0.3458 (1)	4
Austroleptis and *Bolbomyia* within Rhagionidae (Woodley 1989)	(*Austroleptis* + *Arthroceras* + *Atherimorpha* + *Arthroteles* + *Bolbomyia* + *Chrysopilus* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*)	1.0000 / 1.0000 (1)	0

continued next page

TABLE 6. (continued)

Concept	Constraint	Test statistic: Kishino-Hasegawa / Templeton signed-rank (number of equally MP constraint trees)	Increase in steps of MP constraint tree
Austroleptis and *Bolbomyia* exclusive of Rhagionidae *sensu* Woodley (modified to exclude these taxa)	(*Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*)	1.0000 / 1.0000 (1)	0
Austroleptis and *Bolbomyia* form natural group (Grimaldi & Cumming 1999)	(*Bolbomyia* + *Austroleptis*)	1.0000 / 1.0000 (1)	0
Bolbomyia sister to Athericidae, Oreoleptidae, and Tabanidae (Sinclair *et al.* 1994)	(*Bolbomyia* + (Athericidae + Oreoleptidae + Tabanidae))	**0.0214**/ **0.0180** (2)	24
Bolbomyia sister to or within Tabanoidea (James 1965)	(*Bolbomyia* + Pelecorhynchidae + Athericidae + Oreoleptidae + Tabanidae)	0.5847 / 0.5735 (3)	5
Bolbomyia within Rhagionidae sensu Woodley, exclusive of Austroleptidae (Stuckenberg 2001)	(*Bolbomyia* + *Arthroceras* + *Atherimorpha* + *Arthroteles* + *Chrysopilus* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Spaniopsis* + *Symphoromyia*)	0.6624 / 0.6623(2)	2
Bolbomyia sister to or within Xylophagomorpha (James 1965)	(*Bolbomyia* + Xylophagidae)	0.1057 / 0.1461 (3)	11
Monophyly and Position of Pelecorhynchidae			
Rhagionidae includes *Glutops* (Nagatomi 1982a)	(*Atherimorpha* + *Arthroteles* + *Austroleptis* + *Bolbomyia* + *Chrysopilus* + *Glutops* + *Omphalophora* + *Ptiolina* + *Rhagio* + *Symphoromyia* + *Spaniopsis*)	**<0.0001** / **<0.0001** (1)	42
Rhagionidae includes *Glutops* and *Pelecorhynchus* (Stuckenberg 2001)	(*Atherimorpha* + *Arthroteles* + *Bolbomyia* + *Chrysopilus* + *Glutops* + *Pelecorhynchus* + *Rhagio* + *Symphoromyia*)	0.0534 / 0.0611 (3)	18
Glutops and *Pelecorhynchus* (with *Pseudoerinna*) form monophyletic unit (Woodley 1989; Sinclair 1992; Stuckenberg 2001)	(*Glutops* + *Pelecorhynchus*)	1.0000 / 1.0000 (1)	0
Position of Vermileonidae			
Vermileonidae exclusive of Xylophagidae and other tabanomorph groups (=Vermileonomorpha) (Nagatomi 1977; Griffiths 1994)	Vermileonidae + (Xylophagidae + Rhagionidae + Pelecorhynchidae + Tabanidae + Athericidae)	1.0000 / 1.0000 (1)	0
Vermileonidae, basal clade of Tabanomorpha (Nagatomi 1977; Sinclair *et al.* 1994)	(Vermileonidae + (other tabanomorph taxa))	0.6438 / 0.6438 (2)	1

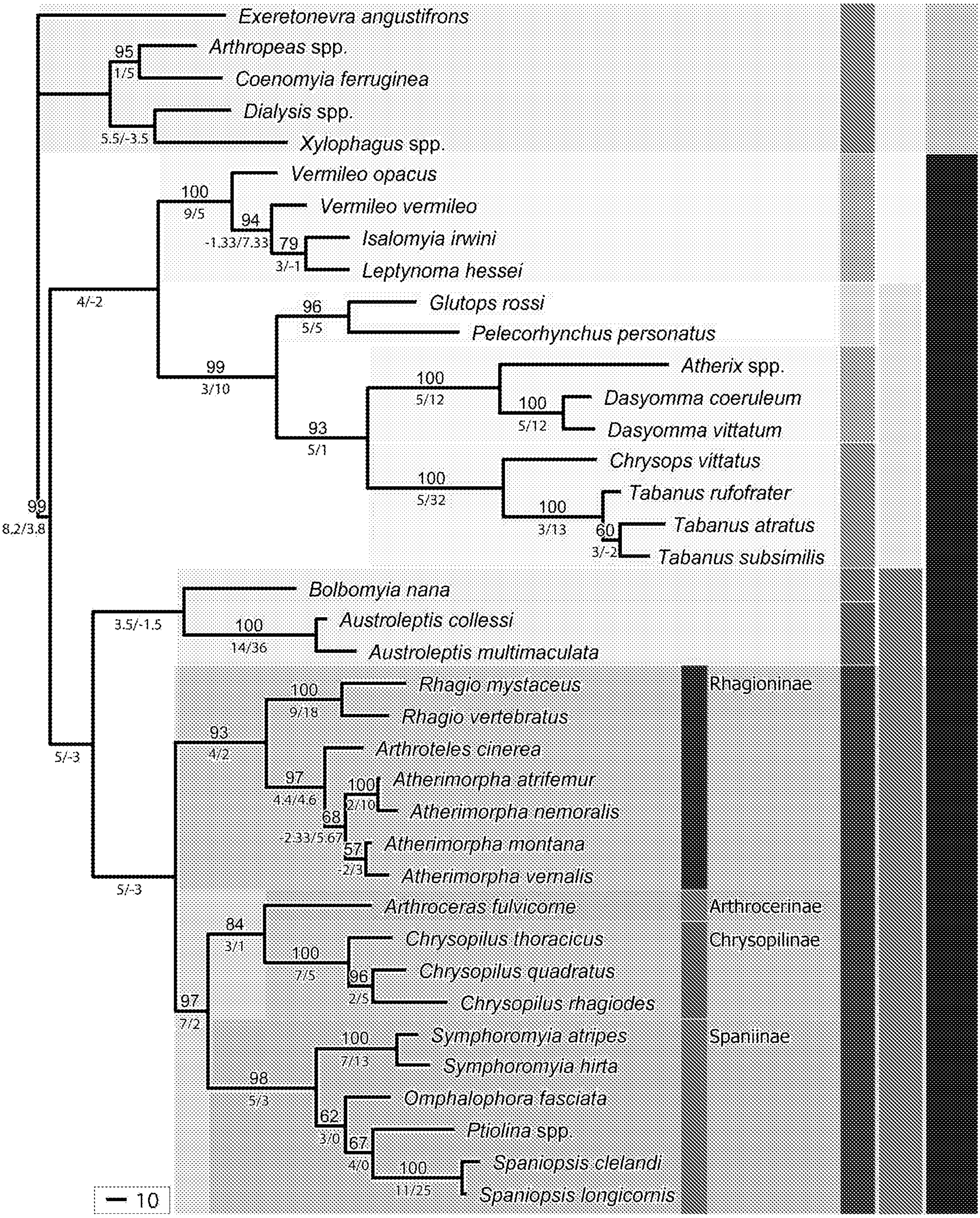


FIGURE 196. The most parsimonious tree of the combined data set, composed of morphological and molecular characters. Bootstrap values greater than 50% are above supported branches (TBR, nreps = 1000 / addseq reps = 5). Partitioned Bremer Support values are below supported branch (morphology partition/molecular partition); the sum of these values equals the overall decay (BS). The Bayesian analysis of the same data set yields the same topology and similar branch lengths for the ingroup, with posterior probabilities of 95% or higher for Tabanomorpha and the early divergences within this group. *Classification along right margin; A = Xylophagidae, B =Vermileonidae , C = Pelecorhynchidae, D = Athericidae, E = Tabanidae, F =Bolbomyiidae, G = Austroleptidae, H = Rhagionidae, I = Tabanoidea, J = Rhagionoidea, K = Xylophagomorpha, L = Tabanomorpha.*

The common ancestry of Chrysopilinae, Spaniinae, and Arthrocerinae is supported by the shared presence of spermathecal duct accessory glands (character 99; Figs. 159–166). These structures, which are delicate and faint even after staining, have been overlooked by previous workers (Nagatomi 1952, Nagatomi 1986, Nagatomi & Iwata 1976, Webb 1977b). Within this clade, Chrysopilinae is supported by a number of characters, presented in the morphological results above. On the basis of these characters, *Schizella*, *Stylospania*, and *Chrysopilus* (including *Solomomyia*) may be placed together in this group. Spaniinae is defined by the shared presence of an anterior-facing lateral process of tergite 9, enveloping sternite 9 in the female (character 85; Figs. 143–150) and the female genital chamber is tightly defined by medial sclerotization of sternite 9 (character 109; Figs. 143, 145, 147–150). Given these defining characters, *Spania nigra* may confidently be placed in this group (and the reduction of female tergite 9 (character 84) suggests *Spaniopsis* is its sister group). The larvae of *Symphoromyia* and *Ptiolina* have an unusually scalloped first thoracic segment that is potentially another synapomorphy for this clade (character 121; Figs. 177, 183). Within Spaniinae, a group that includes *Omphalophora*, *Ptiolina*, *Spania*, and *Spaniopsis* is supported by the wide separation of basal cerci in the female (character 90) and a bare laterotergite (character 28; unique among taxa with spermathecal duct accessory glands). These taxa are also distinctive in having a stylate antenna (character 10; although also present in *Stylospania lancifera*, a chrysopiline). On the basis of this antennal feature, *Litoleptis* may be added to this group, although a female is needed to confirm this placement. Additional characters to support this grouping *Litoleptis* here include the direct epandrial attachment of the cercus (character 59) and male cercus widely separated (character 64; as *Spaniopsis clelandi* and *Spania nigra*). A number of character states distinguish *Arthroceras* and support placement in its own subfamily. These include the round, gradually tapered, and multi-segmented antenna (characters 8, 9, 10) and aedeagal tines in the male (character 75). Furthermore, Arthrocerinae lack the character states (such as a modified female tergite 9 and modified leg and/or thoracic setae) that define its most closely related subfamilies.

The results of the constrained analysis are shown in Table 6. Arrangements that support Spaniidae (Stuckenberg 2001) are significantly different from the most parsimonious trees generated from the combined data set. Given this data set, previous concepts of Rhagioninae (Nagatomi 1982; Stuckenberg 2001) are also significant departures from the most parsimonious arrangements. Various placements of *Austroleptis* and *Bolbomyia* cannot be ruled out, however, the data rejects *Bolbomyia* as a member of Tabanoidea. Pelecorhynchidae *sensu* Nagatomi (1982) is significantly different from the MPTs. Forcing *Glutops* and *Pelecorhynchus* into Rhagionidae adds 18 steps to the most parsimonious tree, just short of significantly different test values however.

Discussion

Over the course of the long history of the concept of 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. The data 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. In support of this notion, the concept of Spaniidae is soundly rejected in the constrained analysis of the combined data. The single common ancestor of *Chrysopilus* and *Rhagio* and all of its descendents, however, do not form a group that includes *Austroleptis* and *Bolbomyia.* The divergence of *Austroleptis* from among the sampled set appears quite ancient, where the resolving power of the 28S rDNA is relatively weak. On account of this, alternate hypotheses of relationship for *Austroleptis* aren't easily rejected. Only two additional steps are required to place this genus as sister group to the Xylophagomorpha. Unlike any other tabanomorph known, *Austroleptis* has been reared from wood (Colless & McAlpine 1991) and recently Stuckenberg (2001) elevated the subfamily Austroleptinae to family level on account of autapomorphic features of the head, male genitalia, and female abdomen. Although *Austroleptis* may be more closely related to Rhagionidae than to Tabanoidea, this sister group relationship remains tenuous and it seems wise to conserve Austroleptidae. *Austroleptis* species are autapomorphic to such a degree in behavioral, morphological, and molecular traits that they can be recognized as their own separate entity within Tabanomorpha, at the level of other families in the group. A similar argument may be advanced for *Bolbomyia*, another highly autapomorphic taxon within Tabanomorpha (although larval morphology and habits among *Bolbomyia* species are unknown). Given the results here (Figs. 193–196), it follows that the status of Bolbomyiinae, *sensu* Stuckenberg (2001), should be revised. For convenience, the entity containing Rhagionidae, Austroleptidae, and Bolbomyiidae may be referred to as Rhagionoidea (= non-vermileonid, non-tabanoid tabanomorphs).

Features that unite Spaniinae (characters 85, 109) are readily apparent, however, *Symphoromyia* has not been grouped within the subfamily in the modern era. *Symphoromyia* differs from other spaniines in several aspects, most conspicuously in the form of the antenna. In addition to sharing diagnostic features of the female terminalia, spaniines share a special resemblance in their compact habitus. This 'gestalt' is difficult to describe but may have been responsible for confusion among early taxonomic workers. *Symphoromyia* was originally established by Frauenfeld (1867) to clarify the distinction of species that had been mistakenly placed in *Ptiolina*.

Ptiolina as previously recognized (Nagatomi 1982a; Nartshuk 1995) was recovered as a grade of two lineages in the morphological phylogenetic analysis (Figs. 193–196). I examined the type of *Omphalophora lapponica* and dissected the female terminalia. Examination of its morphology reveals that *Omphalophora* Becker is a valid concept, defined by a rich suite of characters. The female genitalia are especially important in demonstrating important differences between *O. lapponica* and its congeners from true *Ptiolina* species. These differences are consistent with other differences evident in the male genitalic, wing, thoracic, and to some degree, antennal morphologies. The thoracic and wing characters separating *Ptiolina* and *Omphalophora* were confirmed in the type of *O. oculata* by P. Vilkamaa (pers. comm.), corroborating the species synonymies proposed by Nartshuk (1995). For more a more detailed discussion of morphological differences between *Omphalophora* and *Ptiolina*, see notes provided for *Omphalophora* in the systematics section below.

The position of *Alloleptis tersus* remains unclear. It does not appear to be a member of Chrysopilinae, Arthrocerinae, Rhagioninae, or Spaniinae, nor does it bear any apparent synapomorphies that define the other tabanomorph groups. This may change as specimens become available for examination. However, presently, this genus must be considered *incertae sedis* within Rhagionoidea, either forming its own clade within the superfamily or as a member of Rhagionidae.

Additional comments on larval morphology

The presence of a larval mandibular brush [= 'cephalic brush' (Cameron 1934; Teskey 1970a; Webb 1977a), 'setaceous region' (Cook 1949), 'spinose area' (Mackerras & Fuller 1942), 'borstenfeld' (Schremmer 1951), 'champ de'épines' (Tsacas 1962), 'bristle area' (Roberts 1969)] is a synapomorphy for Tabanomorpha (not scored; Sinclair 1992). In Pelecorhynchidae, Athericidae, and Tabanidae, the mandibular brush is associated with the mandibles by way of an articulated rod. As the mandibles are adducted downward, the articulated rod is lifted (Pechuman & Teskey 1981: 464).

Sinclair (1992) proposed that the association of the mandibular brush with an articulated rod (= 'sclerotized stem' of Webb 1977a) is a synapomorphy uniting Tabanidae and Athericidae. The rod is articulated and can be moved up and down in both Athericidae and Tabanidae (and presumably, Oreoleptidae). Sinclair (1992) also proposed that the rod is held vertically in Athericidae, whereas in Tabanidae, the rod is held horizontally.

When the mandibular sclerites are dissected, however, I found that the articulated rod may be in the vertical, oblique, or horizontal position. This is true regardless of whether the taxon 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 & Teskey

(1981a: 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 consistent with the observation of articulated rod positions in dissected larvae of these groups. 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. Pechuman & Teskey (1981: 473) illustrate the articulated rod in *Tabanus reinwardtii* Wiedemann in the horizontal position. Teskey (1970a: 1132) illustrates the articulated rod in *Glutops* (Pelecorhynchidae) in the vertical position. Courtney *et al.* (2000: 108) have a line drawing of *Hybomitra epistates* Osten Sacken (Tabanidae) with the articulated rod clearly in the vertical position. The position of the articulated rod position is not visible in SEM photos of *Atherix* sp., *Glutops* sp., and *Tabanus* sp. (Courtney *et al.* 2000) and, making matters more difficult, is often reduced to a small sclerotized stem (Webb 1977a).

The mandibular brush appears to work similarly in Rhagionidae, as illustrated in *Chrysopilus auratus* (Fabricius) (Tsacas 1962: 176). However for this and other rhagionids, the brush is associated with cuticular tissue. In *Ptiolina*, there is no mandibular brush, although the cuticle is roughened at the point at which the mandibular brush arises in related taxa (e.g., *Symphoromyia* spp.) and appears homologous to the area containing the mandibular brush. 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.

During feeding, the mandibular hooks may be appressed together to form a food canal (Courtney *et al.* 2000; Schremmer 1951; Sinclair 1992; Tsacas 1962). This is known as the suctorial type (Stuckenberg 2001; 'promuscis-type' of Sinclair 1992; 'Saugmandible' of Schremmer 1951). The suctorial-type functioning of mandibular hooks as a feeding tube requires at least three integrated morphological features. Firstly, the adoral surface of the mandibular hooks must complement one another in shape, so that they meet flush, centrally. Second, the groove on the adoral surface of the mandibular hook must match so that when the hooks are appressed together, a channel is formed. Third, 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. Sinclair (1992) suggested that the suctorial type is the basal condition for Brachycera, associated with the transition to vertical mobility in the larval mandibles (Sinclair 1992: 237–238). The classic example of the suctorial-type mouthparts is Old World *Vermileo* spp. (Schremmer 1951; Tsacas 1962; Ludwig *et al.* 1996). In New World *Vermileo* spp., however, the mandibles are strikingly different; they are blunt, reduced in size, and do not meet medially (pers. obs.). Therefore, it is not surprising that *Vermileo* is shown as paraphyletic with respect to other vermileonids, with quite strong support in the analyses (Figs. 193–196). It turns out that most taxa within Tabanomorpha and Xylophagomorpha have mandibles that work in conjunction with the maxillae, as a unit, in a vertical manner, and may operate independent of the other pair (Teskey 1970a: 1131; Courtney *et al.* 2000: 105). Rather than having the mandibles affixed together medially to form a feeding tube, the more likely primitive condition for Brachycera is simply having a mandible with a medial groove. This groove allows a passageway for food to pass to the hypopharynx when the mandibles are pushed together during feeding. The groove may also serve as a poison canal (Woodley 1989; Sinclair 1992) although it seems reasonable to doubt this would be an efficient delivery mechanism for paralyzing prey (Stuckenberg 2001; Zloty *et al.* 2005).

Systematics

Key to adult genera of Rhagionoidea

The following key includes leads for Athericidae, Oreoleptidae, Pelecorhynchidae, Tabanidae, Vermileonidae, and Xylophagidae, members of which may be mistaken for Rhagionidae. Austroleptidae and Bolbomyiidae are also included.

1\. Clypeus flat or recessed 23

Clypeus bulbous or at least slightly swollen 2

2(1). Postspiracular sclerite with scale or slender ridge 18

Postspiracular sclerite smooth and flat 3

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

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

Hind tibial spur two; laterotergite setose; 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 R_1 bare; Alaska, Chile, Japan .... *Litoleptis* Chillcott (in part)

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

5(4). Body greater than 4 mm in length; length of 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 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; Holarctic .... *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 8

8(7). Anepisternum bare; R_5 anterior to or ending at wing tip; R_{2+3} about as long or shorter than R_5; 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; R_4 and R_5 encompass wing tip; R_{2+3} clearly longer than R_5; 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; palpus two-segmented; scale-like thoracic setae with structural color never present; ventral sperm sac of male genitalia with paired lobes 12

Macrochaetae of hind tibia present; palpus one-segmented; scale-like thoracic setae with structural color often present; ventral sperm sac 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 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 dorsoapical 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; Holarctic .... *Arthroceras* Williston

13(3). Palpus two-segmented; first antennal flagellomere enlarged bearing segmented stylus; setae of laterotergite arranged in row(s).. 17

Palpus one-segmented; first antennal flagellomere enlarged basally, fused with distinct arista-like apical extension; setae of laterotergite in arranged in tuft(s).. 14

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 (in part)

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(14). Alula completely reduced, without any curvature; R_{2+3} setulose; proepimeron bare; Mexico.. *Sierramyia* **gen. nov.**

Alula present, with narrow or broad curvature; R_{2+3} bare; proepimeron setose; Holarctic, including Mesoamerica. 16

16(15). First hind tarsomere of male swollen; scape clearly larger than pedicel; India and China....... *Desmomyia* Brunetti

First hind tarsomere of male not swollen; scape about the same size as pedicel ; Holarctic......... *Rhagio* Fabricius

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, first segment of female cercus with pronounced postero-ventral lobe.. PELECORHYNCHIDAE.. 21

Tuft of setae posterior to postspiracular sclerite absent; female cercus one- or two-segmented; if two-segmented, first segment of female cercus without elongate lobe 19

19(18). Lower calypter developed; first abdominal sclerite with median notch or suture.. TABANIDAE

Lower calypter undeveloped; first abdominal sclerite without median notch or suture.. 20

20(19). R_1 and R_{2+3} meet together or close together at wing margin; female cercus one-segmented........... ATHERICIDAE

R_1 and R_{2+3} separated at wing margin; female cercus two-segmented .... *Oreoleptis* Zloty, Sinclair & Pritchard OREOLEPTIDAE

21(18). Laterotergite setose; eyes conspicuously setose; short fore tibial spur present .... *Pseudoerinna* Shiraki

Laterotergite bare; eyes inconspicuously setose; fore tibial spur lacking.. 22

22(21). Hind tibial spur one; R_{2+3} and R_4 nearly straight; subscutellum enlarged, noticeably bulbous; Holarctic.. *Glutops* Burgess

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

23(1). Postspiracular sclerite setose.. XYLOPHAGIDAE

Postspiracular sclerite without setae 24

24(23). Laterotergite setose; M_3 present; anal lobe reduced; eyes in male evenly distributed, of equal size; Holarctic.. *Vermileo* Macquart VERMILEONIDAE (in part)

Laterotergite bare; 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; palpus one-segmented; first antennal flagellomere elongate, stylate; R_1 and R_{2+3} widely separated at wing margin; Alaska, Chile, Japan.. *Litoleptis* Chillcott (in part)

Mid and hind leg with two tibial spurs; palpus two-segmented; first antennal flagellomere bearing segmented stylus; R_1 and R_{2+3} close together at wing margin 26

26(25). Fore tibial spur absent; female cercus one-segmented; female tergite 7 much wider than long; three spermathecae; theca elongate; pseudotracheae 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; theca compact; pseudotracheae absent; eyes in male rounded dorsally; hypandrium separated from the gonocoxites by a complete suture; aedeagal tines present; Holarctic .... *Bolbomyia* Loew BOLBOMYIIDAE

Austroleptidae Nagatomi

Genus *Austroleptis* Hardy

Figs. 1, 3, 26, 41–42, 67, 87–88, 113, 135, 167.

Austroleptis Hardy 1920a: 126. Type species *Austroleptis rhyphoides* Hardy 1920a, 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, 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 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 are small to moderately sized flies (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 M_3 and from *Litoleptis* by the multisegmented flagellum, 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 flagellum and the presence of hind tibial spurs.

Description. *Head*. Clypeus not bulbous. Scape approximately 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 pseudotracheae, longer or shorter than palpus. Theca elongate, lateral sclerites tightly adjacent, apparently fused with suture. Palpus two-segmented; proximal and distal segments subequal in length. Stipes surrounded by membrane above theca, directed posteriorly (very reduced). Cardo not swollen. Lacinia longer than palpus, 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 variable (as in *A. collessi*). Anepisternum bare. Laterotergite bare. Postspiracular scale absent. Proscutellum present. Subscutellum enlarged. Wing hyaline or lightly infuscate, membrane with or without markings, with or without pterostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wing tip or past wing tip (to at least R_5). Humeral crossvein (h) well developed. Sc-r crossvein weakly developed, positioned distal to h by less than length of h. Dorsal side of

R_1 setulose, ventral side with or without setulae; R_4 and R_5 with or without setulae; all cells and other wing veins bare. R_{2+3} sinuous, apical third ultimately bends slightly anteriorly, toward leading edge of wing margin; 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, posterior to, or ending at wing tip; clearly longer than R_{4+5} (r-m to R_4 origin). M_3 wing vein absent. Origin of CuA_1 at discal cell. CuA_2 reaches wing margin, about 2/3 length of posterior vein of cell bm. Alula with broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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 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. Epandrium wider than long, modestly curved anteriorly. Tergite 10 absent. Hypoproct triangular (rounded posteriorly), flattened; anterior margin entire, evenly sclerotized; appearing posteriorly lobed, with paired region of increased sclerotization; setose. Cercus directly adjacent to epandrium; 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 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, subequal in length to 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 cercal segments. Cercus one-segmented; separated from one another dorsally by approximate width of second cercal segment; without apical sensory pits.

Larva. Unknown (however, see below).

Biology. *Austroleptis* is usually confined to mountainous regions and is reportedly a visitor of flowers (Colless & McAlpine 1991). At Cradle Mountain National Park, in central Tasmania, I collected *Austroleptis multimaculata* males and females on the leaves of flowering *Richea scoparia* Hooker, however I did not see the insects feed. Less is known about the South American members of this genus (Nagatomi & Nagatomi 1987), which are rarely collected. *Austroleptis* larvae are uncharacterized, but have been reared inadvertently from rotting wood (Colless & McAlpine 1991).

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.

Bolbomyiidae Stuckenberg *status revised*

Genus *Bolbomyia* Loew

Figs. 4, 27, 43, 68, 89, 114, 136, 168.

Bolbomyia Loew 1850: 39. Type species *Bolbomyia nana* Loew 1862: 188, by subsequent monotypy.
Misgomyia Coquillett 1908: 145. Type-species *Misgomyia obscura* Coquillett 1908, by original designation.

Cekendia Szilády 1934a: 264 (as subgenus of *Ptiolina* Zetterstedt 1842). Type species *Ptiolina* (*Cekendia*) *wuorentausi* Szilády 1934, 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. Each of the spermathecal ducts has a noticeable bulbous swelling along its length. 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; 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 tibiae, 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 M_3, by having only one hind tibial spur, and antenna with enlarged first flagellomere with a single-segmented style.

Description. *Head.* Clypeus not bulbous. Scape approximately 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 pseudotracheae, shorter than palpus. Theca short and stout; lateral sclerites adjacent and touching, but mostly separated. Palpus two-segmented; distal segment longer than or subequal in length as proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palpus, 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, pterostigma absent or lightly present. Lower calypter reduced. Upper calypter well developed with broad curvature, lobe-like, width twice length or less. Costa extends past wing tip, to approximately R_5. Humeral crossvein well developed. Sc-r crossvein absent or weakly developed, positioned distal to h by less than 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 slightly toward wing tip; 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 cell bm. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, modestly curved anteriorly. Tergite 10 absent. Hypoproct triangular (rounded posteriorly); rounded, virtually encircling cerci; not fused with cercus; anterior and posterior margins entire, evenly sclerotized; tomentose, without setae.

Cercus displaced away from epandrium; partially displaced from one another, separation distance approximately half width of single cercus; held horizontal in relation to rest of abdomen; in posterior view cupped, forming circular outline medially. Hypandrium separated from gonocoxites by complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Sperm sac 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 length of sternite 9. Spermathecal duct accessory glands absent, but ducts with large swelling at approximately mid-point along their length. 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 cercal 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 ring (sometimes slightly arched medially, but forming narrow elliptical opening only). Basal cercal segment adjacent dorsally. Second cercal segment not elongated, with apical sensory pits.

Larva. Unknown.

Biology. 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 (USA). Jeff Cumming, Richard Vockeroth, and others including myself, have had success sweeping *Bolbomyia nana* from low-lying vegetation in small forest clearings in and around the hill-top of King Mountain, Gatineau National Park, in Quebec (Canada). Details of its life history are not known. The flight period appears to be exceptionally short, lasting only a couple weeks or perhaps as little as a few days per year (depending on weather conditions).

Members of the genus inhabit the Russian Far East, Canada, and the USA. One species is known from Baltic amber.

Literature. Webb (1987a) provides a key for the extant species of the world.

Rhagionidae Latreille

Arthrocerinae Williston

Genus *Arthroceras* Williston

Figs. 5, 28, 44, 69, 90, 115–116, 127, 137, 159.

Arthroceras Williston 1886: 107. Type species *Arthroceras pollinosum* Williston 1886, by subsequent designation (Coquillett 1910: 510).

Ussuriella Paramonov 1929: 181. Type species *Ussuriella gadi* Paramonov 1929, by monotypy.

Pseudocoenomyia Ôuchi 1943: 493. Type species *Pseudocoenomyia sinensis* Ôuchi 1943, by original designation.

Diagnosis. No single, obvious autapomorphic feature is known to define *Arthroceras* conclusively. However, it retains the following unique combination of primitively- and more recently-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, 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 (Fig. 5). They may be distinguished from *Glutops* Burgess (Pelecorhynchidae) by their setose laterotergite and parafacials not swollen and from *Pseudoerinna* Shiraki (Pelecorhynchidae) by the absence of 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 pseudotracheae, longer or shorter than palpus. Theca short and stout, divided into two separate, lateral sclerites. Palpus two-segmented; distal segment longer than proximal segment. Stipes convergent toward one another medially. Lacinia present, shorter than palpus, 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 wing tip or just past wing tip, to R_5. Humeral crossvein well developed. Sc-r crossvein present, very weakly developed, positioned distal to h by approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends anteriorly slightly, toward wing tip. Length of R_{2+3} longer than R_5, but less than twice as long. R_{4+5} aligned with R_5. 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 contain 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 cell bm, less than 2/3 length of posterior vein of cell bm. M_3 present. Alula full, rounded, with broad curvature. Anal lobe well developed. Cell cu*p* 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.

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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 absent. Hypoproct triangular (rounded posteriorly), setose. Cercus base held underneath epandrium. 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 gonocoxites by incomplete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Sperm sac 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 length of sternite 9, but not so long as to be difficult to measure; not inflated at base of spermathecae. Spermathecal duct accessory glands arise at approximately halfway along the length of the spermathecal ducts. Ejection apparatus of spermathecal ducts thickened, sclerotized, with furrows. Common spermathecal duct thickened, subequal in length to 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 cercal 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 ring. Basal cercal segment adjacent dorsally. Second cercal segment not elongated with or without apical sensory pits.

Larva. Unknown.

Biology. Members of this genus are found in the Russian Far East, Canada, and the USA. *Arthroceras* and *Spania* exhibit similar distributions (Nagatomi 1966). Their biology is not known.

Literature. Key to *Arthroceras* of the world in Nagatomi (1966). Key to Nearctic species in Webb (1987b).

Notes. In the Palearctic catalogue (Majer 1988), *Arthroceras pollinosum* is given as the type species for the genus, by original designation. Webb (1987b) states that the type species is *Arthroceras pollinosum* by 'original description.' Both are incorrect. Williston (1886) created *Arthroceras* for two species, *Arthroceras pollinosum* and *Arthroceras leptis* (Osten Sacken) and did not explicitly designate the type species for the genus. James (1965) correctly gives credit to Coquillett (1910) for the type species designation.

The earliest family group name available for *Arthroceras* is Arthrocerinae, even though the correct stem for this genus is Arthrocerat- (Sabrosky, 1999).

Chrysopilinae Bezzi

Genus *Chrysopilus* Macquart

Figs. 9–10, 34, 36, 38, 48–49, 65–66, 72, 93–94, 119, 151–152, 160, 175.

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: lxviii. 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).
Poppiusiella Frey 1918: 30 (as subgenus). Type species *Chrysopilus arctica* Frey 1918, by original designation.
Achrysopilus Szilády 1934a: 255 (as subgenus; no type species given; name invalid by article 13.3 of the ICZN code).
Sapporomyia Szilády 1934a: 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**.
Solomyia Nagatomi 1982a: 68. Incorrect original spelling.
Poppinsiella Nartshuk 1995: 18. Misspelling.*Chrysopyla*
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 (scale-like), 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; 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. 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 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 pseudotracheae, longer or shorter than palpus. Theca short and stout, divided into lateral sclerites that are tightly adjacent, apparently fused with suture. Palpus one-segmented. Stipes surrounded by membrane above theca, directed posteriorly (very reduced). Lacinia present, shorter than palpus, 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 enlarged or not. Wing hyaline or infuscate, with or without markings; pterostigma present or absent. Lower calypter reduced. Upper calypter variously developed. Costa extends to wing tip or past wing tip. Humeral crossvein well developed. Sc-r crossvein absent or variously developed, positioned distal to h by less than length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. R_1 and R_{2+3} close together at wing margin. R_{2+3} sinuous, apical third ultimately bends slightly anteriorly, toward leading edge of wing margin, length of R_{2+3} about as long 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 cell bm. CuA_2 greater than 2/3 length of posterior vein of cell bm. M_3 present. Alula full, rounded, with broad curvature. Anal lobe well developed. Cell cu*p* 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 reaches internal 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 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. Sperm sac 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 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 as long as 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 cercal 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 ring, visible in the posterior perspective. Basal cercal segment adjacent dorsally. Second cercal 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 palpus soft, segments poorly differentiated; three maxillary palpomeres. Antenna last segment entire (as nub). Antenna three-segmented. Unpaired salivary pump absent. Posterior tentorial expansion free, with thin extension produced dorsally.

Biology. *Chrysopilus* is cosmopolitan, found on all continents except Antarctica, throughout the tropics, up to near 4000 masl 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 1997). *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. Larval *Chrysopilus* are predators of oligochaetes and soft-bodied insect larvae and may be aquatic, associated with streamside vegetation, or, like *Rhagio*, may be found in moist soils that are rich in organic matter (Roberts 1969; Thomas 1978a, 1978b, 1997; Tsacas 1962). In addition to this, Paramonov (1962) notes that *Chrysopilus* larvae eat the eggs of *Schistocerca* and *Dociostaurus* (Orthoptera).

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.

Literature. Keys to North America, eastern Europe, China, Japan and Africa are provided by Hardy (1949), Narchuk (1969), Yang *et al.* (1997), Nagatomi (1978)and Stuckenberg (1965, 1997), respectively.

Notes. Lindner (1923) designated the Palaearctic species *Chrysopilus obscuripennis* Loew as the type species for *Bicalcar* Lindner. 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 *Chrysopilus 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*.

I have seen the type of *Chrysopilus arctica* Frey and agree with Nagatomi (1982a: 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.

Nagatomi (1982a: 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 species of *Chrysopilus* by having wing vein CuA_1 arising from the discal cell and 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)." This is not an unusual character state for females of any genus within Tabanomorpha. While the features of the wing in *Solomomyia* appear unique, 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*, persistence of *Solomomyia* as a separate genus is unjustified.

The species concept of *Chrysopilus rufipes* Macquart is uncertain, but placement in *Chrysopilus* has been established (Hardy 1920a; Oldroyd *in* Paramonov 1962), despite its recognition as unplaced by Nagatomi & Evenhuis (1989). Hardy (1920a) 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.

Yang *et al.* (1997: 256) described *Spatulina sinensis* from a single male specimen from Shaanxi, China and remarked 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 gonostyles are thick, with 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*, as *Chrysopilus sinensis* (Yang, Yang & Nagatomi), **new combination**.

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 for *C. nagatomii* Evenhuis, named after the original worker.

Genus *Schizella* Bezzi

Figs. 2, 18, 58, 80.

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 (3.7–6.3 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; 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. The males of *Schizella* 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 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 pseudotracheae, longer than palpus. Theca short and stout. Palpus 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; pterostigma present or absent. Lower calypter reduced. Upper calypter well developed, but margin with curvature narrow, width more than twice length. Costa extends past wing tip (to at least R_5). Humeral crossvein well developed. Sc-r crossvein absent. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. R_1 and R_{2+3} close together at wing margin. R_{2+3} sinuous, apical third ultimately bends anteriorly slightly, toward leading edge of wing margin, length of R_{2+3} about as long 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 present. Origin of CuA_1 at cell bm. Cell m_3 parallel-sided at margin. CuA_2 greater than 2/3 length of posterior vein of cell bm. Alula full, rounded, with broad curvature. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 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. Sperm sac 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 length of sternite 9, but not so long as to be difficult to measure, not inflated at base of spermathecae. Spermathecal duct accessory glands 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 as long as 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 ring, visible in posterior perspective. Basal cercal segment adjacent dorsally. Second cercal segment not elongated, without apical sensory pits.

Larva. Unknown.

Biology. Unknown. Members of this genus are found exclusively in the Philippines.

Literature. Nagatomi (1982a) gives a cursory treatment of the genus. Kerr (2003) provides a key to all species.

Genus *Stylospania* Frey

Figure 23, 83, 103.

Stylospania Frey 1954: 23. Type species *Stylospania lancifera* Frey 1954, 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 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; 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. Also, the *Stylospania* males are dichoptic, which is a relatively rare condition for *Chrysopilus*.

Description. *Head.* Clypeus bulbous. Scape approximately 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 pseudotracheae, longer than palpus. Theca short. Palpus one-segmented. Mandibles absent.

Thorax. Mesonotum without vittae. Setae of dorsum all of equal length. Specimen lacks metallic- or scale-like thoracic setae, although these are likely present. Proepimeron reduced, bare. Anepisternum bare. Laterotergite setose throughout, katatergite and anatergite indistinguishable. Thoracic surface between base of halter and postspiracular sclerite without setulae. Thoracic spiracle without flaps, nor with setulae. Postspiracular scale absent. Postspiracular sclerite without setulae. Thoracic surface immediately posterior to postspiracular sclerite bare. Proscutellum absent. Subscutellum inconspicuous, not enlarged. 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 weakly developed, positioned distal to h by approximate length of h. Dorsal side of R_1 setulose, ventral side bare. R_1 and R_{2+3} close together at wing margin (R_{2+3} clearly closer to R_1 than to R_4). 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 contain wing tip. R_5 aligned with R_{4+5}. M_3 reaches 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. Epandrium wider than long, modestly curved anteriorly. Epandrium simple, not containing hypandrium ventrally. Tergite 10 absent. Hypoproct rectangular; wider than long; tomentose, without setae. Cerci partially displaced from one another, separation distance approximately half width of single cercus. Hypandrium fused entirely to gonocoxites. Gonocoxite smooth dorsally, without sinuous ridge leading to gonocoxal apodeme. Gonocoxal apodemes long enough to reach anterior margin of hypandrium. Sperm sac 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.

Biology. Unknown.

Literature. In addition to the original literature (Frey 1954), Nagatomi (1982a) provides a brief Diagnosis of this genus.

Rhagioninae Latreille

Genus *Arthroteles* Bezzi

Figs. 6, 45, 70, 91, 117, 128, 138.

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*); laterotergite setose; tibial spur formula 0:2:2; 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 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* 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 pseudotracheae. Hypopharynx, labium, and labrum very elongate; theca lateral sclerites adjacent, apparently fused with suture. Palpus 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 palpus; 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 ventral half (katatergite). Proscutellum present. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly infuscate, without markings. Pterostigma absent. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends past wing tip (to at least R_5). Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by 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 anteriorly toward wing tip (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 contain wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin). M_3 present. Cell m_3 convergent at margin. Origin of CuA_1 at cell bm. CuA_2 about 2/3 length of posterior vein of cell bm. Alula with broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 absent. Hypoproct triangular, tomentose, without setae. Cercus base held underneath epandrium, 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 gonocoxites by complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Sperm sac 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 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 cercal 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 ring. Basal cercal segment adjacent dorsally. Second cercal segment not elongated. Cercus with apical sensory pits.

Larva. Unknown.

Biology. *Arthroteles* 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 1956a). Stuckenberg (1956a) 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 species-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. *Arthroteles orophila* is active in November. The flight of *A. longipalpis* occurs in July, and may overlap to some degree with *A. bombyliiformis*.

Literature. Illustrations of mouthparts, antenna, wing, male and female genitalia, and dichotomous key to species is given by Stuckenberg (1956a). A new species is illustrated by Nagatomi & Nagatomi (1990a).

Genus *Atherimorpha* White

Figs. 7–8, 46–47, 71, 92, 118, 129, 139.

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*].
Therevirhagio Lindner 1925: 20. Type species *Therevirhagio setosiradiatus* Lindner 1925, by monotypy.
Philippoleptis Malloch 1931: 276 (as subgenus). Type species *Leptis praefica* Philippi 1865, by original designation.
Aritherimorpha Nagatomi 1982a: 44 (*lapsus*).
Neorhagio Lindner 1924: 75. Type species *Leptis setosa* Philippi 1865, by monotypy. **New Synonymy.**

Diagnosis. 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 M_3 present.

Atherimorpha are very *Rhagio*-like in form and behavior, but can be distinguished from this genus by the antenna, which has 3–7 flagellomeres, and by having two-segmented palpus. Species of *Atherimorpha* are most similar to *Arthroteles* in the form of the antenna, but differ in that the first flagellomere is larger in comparison to the other flagellomeres and the remaining flagellomeres are narrower. *Atherimorpha* species may be distinguished immediately from *Arthroteles* by their short, fleshy proboscis. *Atherimorpha* are distributed in South America, South Africa, and Australia. Among these faunas, South America is the richest in terms of species number and morphological form and color, although many remain undescribed.

Description. *Head*. Clypeus bulbous. Scape approximately 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 pseudotracheae, longer or shorter than palpus. Theca short and stout, lateral theca sclerites adjacent and touching, but mostly separated. Palpus two-segmented; distal segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palpus, 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 ventral half (katatergite). Postspiracular scale absent. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline or lightly to darkly infuscate; without markings. Pterostigma present or absent. Lower calypter reduced. Upper calypter well developed, with reduced curvature, width more than twice length. Costa extends to wing tip (between R_4 and R_5). Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by less than length of h, by approximate length of h, or by more than 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 anteriorly slightly, toward wing tip. 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 contain 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 cell bm. M_3 present. Cell m_3 parallel-sided at margin. CuA_2 greater than 2/3 length of posterior vein of cell bm. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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. Epandrium usually wider than long (longer than wide in *A. albohirta* and *A. praefica*), strongly notched anteriorly. Tergite 10 absent. Hypoproct margins entire, setose. Cercus base held underneath epandrium. 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 gonocoxites by complete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Sperm sac 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 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, subequal in length to 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 cercal 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 ring. Basal cercal segment adjacent dorsally. Second cercal segment not elongated. Cercus with apical sensory pits.

Larva. Unknown.

Biology. 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* does not occur (Malloch 1932b). 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.

Atherimorpha is distributed in a typical Gondwanan fashion, found in Australia, Patagonia, and South Africa.

Literature. A revision of the African fauna, including a key to species, is given by Nagatomi & Nagatomi (1990c). Malloch (1932b) gives a key to the Neotropical species. Paramonov (1962) treats the Australian species and provides a key.

Notes. 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 (1932b: 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*. A specimen in the AMNH collection 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. This species is a junior synonym of *Atherimorpha praefica* Philippi, **new synonymy**.

Genus *Desmomyia* Brunetti

Figs. 73, 95, 140, 169.

Desmomyia Brunetti 1912: 462. Type species *Desmomyia thereviformis* Brunetti 1912, 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 (5.0–6.7 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, 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 the absence of scale-like thoracic setae, 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 pseudotracheae, as long as palpus or longer. Theca short and stout. Palpus 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 with katatergite swollen, differentiated from anatergite. Laterotergite setose, on ventral half (katatergite) only. Postspiracular scale absent. Proscutellum absent. Subscutellum not enlarged nor lengthened; inconspicuous. Wing hyaline, without markings. Pterostigma present. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa extends to wing tip. Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by 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 anteriorly slightly, toward leading edge of wing margin. Length of R_{2+3} about as long 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 contain 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 cell bm. M_3 present. Cell m_3 convergent at margin. Length of CuA_2 v. posterior vein of cell bm less than 1/2 length of posterior vein of cell bm. Alula narrow curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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. 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. Epandrium wider than long, modestly curved anteriorly. Tergite 10 absent. Hypoproct tomentose, setae absent. Cercus base held underneath epandrium. Cerci partially displaced from one another, separation distance approximately half width of single cercus. Cerci, in posterior view flat, held in horizontal orientation. Hypandrium separated partially from gonocoxites by incomplete suture. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes short or long enough to reach anterior margin of hypandrium. Sperm sac 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 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 cercal 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 ring. Basal cercal segment adjacent dorsally. Second cercal segment not elongated, without apical sensory pits.

Larva. Unknown.

Biology. *Desmomyia* is known only from India (Brunetti 1912; Yang *et al.* 1997).

Literature. Yang *et al.* (1997) illustrate the species from China.

Genus *Rhagio* Fabricius

Figs. 17, 29, 35, 37, 39, 56–57, 79, 101–102, 122, 130, 141, 170, 176, 184–185, 190.

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 1932a: 117. Type species *Leptis incurvata* Meijere 1911. **New synonymy**. See notes below.

Rhagionella Szilády 1934a: 239 (as subgenus). Type species *Nemotelus maculatus* De Geer 1776, by original designation.

Rhagiella Szilády 1934a: 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; 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 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 pseudotracheae, length variable. Theca short and stout, lateral thecal sclerites separated. Palpus one-segmented, often with constriction, making it appear that there are two palpomeres. Stipes convergent toward one another medially or surrounded by membrane above theca, directed posteriorly. Cardo not swollen. Lacinia shorter than palpus; 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 ventral half (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 pterostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa ends before or approximately at wing tip Humeral crossvein well developed. Sc-r crossvein present, well developed, positioned distal to h by more than 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 slightly anteriorly or back toward wing tip. 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 present. Cell m_3 parallel-sided at margin. Origin of CuA_1 at cell bm. CuA_2 greater than 1/2 length of posterior vein of cell bm and greater or less than 2/3 length of posterior vein of cell bm. Alula with narrow or broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* 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 reaches internal base of metasternal furcum as incomplete, thin extension.

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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 absent. Hypoproct with or without setae. Cercus attached to hypoproct, displaced away from epandrium; partially displaced from one another, separation distance approximately half width of single cercus. Cerci, in posterior view flat. Hypandrium separated from gonocoxites by 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. Sperm sac 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 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 cercal 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 ring, visible in posterior perspective. Basal cercal segment adjacent dorsally. Second cercal 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 palpus soft, segments poorly differentiated; three maxillary palpomeres. Antenna last segment entire (nub). Antenna three-segmented. Unpaired salivary pump absent. Posterior tentorial expansion free, with thin extension produced dorsally.

Biology. Adult *Rhagio* have been reported as predaceous on other insects (Kellogg 1908; Leonard 1930; Narchuk 1969, 1988; Paramonov 1962) 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 (Ferguson 1915; Heim & Leprevost 1892; Lindner 1925) but these accounts are certainly false. It is remarkable, actually, how little is known regarding the adult stage of these common, widespread flies. *Rhagio* adults are generally active between April and September.

Rhagio Fabricius is distributed throughout the Holarctic reaching its southernmost extension in the Oriental Region where it is found in Java and Sumatra. Species formerly placed in *Rhagina* are restricted to China and Java.

Literature. Leonard (1930) gives a key to the species of North America. James (1964, 1965b) revised the species of western North America and Chillcott (1965) revised the species of eastern North America. Narchuk (1969) provides a key to the species of Russia. Yang *et al.* (1997) give a key to species of China.

Notes. The *Catalogue of Palaearctic Diptera* (Majer 1982) errs in listing *Leptis tristis* Schummel 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* (Schummel).

The phylogenetic analysis of morphological characters (Fig. 192) does not clarify the position of *Rhagina* with respect to the *Rhagio* lineage. However, I maintain that until a more targeted taxon sampling of this area is used to test and confirm the monophyly of *Rhagio sensu stricto*, the concept of *Rhagina* remains uncertain and should be treated as a junior synonym of *Rhagio* based on the observations noted below.

Yang *et al.* (1997: 187) state that *Rhagina* males lack tergite 10, whereas in *Rhagio*, it is present. However I find the male genitalia of these taxa indistinguishable; both lack T10. Although the wing in *Rhagio incurvatus* (Meijere) is distinctive, there is an apparent grade of states for this character within the group, especially as one examines the wing of *Rhagio sinensis* Yang & Nagatomi which has a sinuous R_{2+3} vein, but not distinctively so, and not far removed from venation found in some *R. hirtus* (Say) and *R. dichomaticus* Chillcott specimens. Another distinctive feature of *Rhagina* emphasized by Nagatomi (1982a) and Yang *et al.* (1997) is a prominent ventro-apical 'hump' on the hind femur. Despite this, Yang *et al.* (1997: 115) indicate that the presence or absence of such a hump does not necessarily determine the genus *Rhagina*. I have also noticed that this may be a variable character in both *Rhagio* and *Rhagina*. Although most commonly absent in *Rhagio*, I have observed the hind femoral process in an undescribed *Rhagio* species from Laos.

Genus *Sierramyia*, new genus

Figs. 59, 131, 142.

Sierramyia Type species *Neorhagio caligatus* Santos 2006: 51, by present designation.

Diagnosis. Characters that I regard as autapomorphic for the genus *Sierramyia* include the weakly developed or absent anal lobe of the wing, so that the alular incision is rounded and open broadly or absent; the upper calypter reduced; and the proepimeron bare. The swollen hypandrium, which is 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 seems likely.

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. 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* species may be distinguished from all *Rhagio* species and the related genus *Desmomyia* by having a bare proepimeron and by having setulae on at least the dorsal surface of R_5 and on the ventral surface of R_{2+3} and R_4. *Sierramyia* species differ from *Chrysopilus* and related chrysopiline genera such as *Schizella* and *Stylospania* by having two hind tibial spurs and by the absence of scale-like thoracic setae.

Description. *Head.* Clypeus bulbous. Scape approximately same size as or shorter than pedicel. First flagellomere oval in cross section, lightly compressed laterally; enlarged basally, bearing fused, bare arista-like extension. Eyes inconspicuously setulose, dichoptic. Palpus 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 ventral half (katatergite) only. Postspiracular scale absent. Proscutellum shallowly present. Subscutellum not enlarged nor lengthened; inconspicuous. Wing membrane darkly infuscate, with hyaline markings, or entirely hyaline; with or without pterostigma. Lower calypter reduced. Upper calypter underdeveloped, with narrow curvature, width more than twice length. Costa reaching approximately to wing tip. Humeral crossvein well developed, Sc-r crossvein weakly developed, positioned distal to h by a little more than 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 anteriorly slightly, toward wing tip; about same length as R_5; with setulae on 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 setulae. R_4 and R_5 contain wing tip. R_5 clearly longer than R_{4+5} (r-m to R_4 origin); dorsal side setulose, ventral side bare. M_3 present. Cell m_3 parallel-sided at margin. Origin of CuA_1 at cell bm. Length of CuA_2 v. posterior vein of cell bm about same as 1/2 length of posterior vein of cell bm. Alula reduced. Anal lobe reduced. Cell cu*p* 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.

Abdomen. Male terminalia with epandrium simple, not containing hypandrium ventrally. Epandrium subcircular, wider than long, modestly curved anteriorly. Tergite 10 absent. Hypoproct rounded posteriorly. Hypoproct flattened, distinct from sclerites above cerci; tomentose, without setae. Cerci partially displaced from one another, separation distance approximately half width of single cercus. Hypandrium separated from gonocoxites by complete suture, expanded anteriorly. Gonocoxite with sinuous dorsal ridge, leading to gonocoxal apodeme. Gonocoxal apodemes long enough to reach anterior margin of hypandrium. Sperm sac 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 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; sternite 8 longer than wide. Female terminalia with three spermathecae. Spermathecal ducts longer than five times 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 cercal 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 ring, visible in posterior perspective (curving slightly ventrally; not obvious). Basal cercal segment adjacent dorsally. Second cercal segment not elongated. Cercus with or without apical sensory pits.

Larva. Unknown.

Biology. All *Sierramyia* species are endemic to mountainous areas (at 1500 masl or greater) in Mexico.

Literature. Nagatomi (1982a, 1984) illustrates wing, antenna, and male genitalia of two undescribed species belonging to this genus. Santos (2006) described the only two species in the genus, providing illustrations of the head, antenna, wing, male genitalia, and female genitalia for each species; it is possible that one or both of these were previously studied by Nagatomi. It is keyed to the genus level as "Undescribed Genus A" by Kerr (2009).

Notes. Nagatomi (1982a) 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. As a matter of convenience, Santos (2006) elected to retain this designation for two new species, which he described. Judging from the photos, illustrations, and diagnosis given by Nagatomi (1982a) and Santos (2006), the undescribed species of '*Neorhagio*' *sensu* Nagatomi and the species described by Santos (2006) are clearly not members of *Atherimorpha*. The genus *Sierramyia* **gen. nov.** is erected for these species. I was able to examine a female of what appears to be the same species that was examined by Nagatomi (1982a) and referred to as '*Neorhagio*' sp. A.

Santos (2006) indicates the presence of aedeagal tines in both *S. caligatus* and *S. nagatomii*. I have not been able to inspect male *Sierramyia* specimens, but I believe Santos' interpretation of these structures is in error. These small, often lightly sclerotized structures are also easily observed in most species of *Rhagio*, but they are clearly associated with the sperm sac and are not homologous with aedeagal tines observed in *Arthroceras*, *Bolbomyia*, Athericidae, and Tabanidae.

Spaniinae Frey

Genus *Litoleptis* Chillcott

Figs. 11–12, 50–51, 74, 96.

Litoleptis Chillcott 1963: 1186. Type species *Litoleptis alaskensis* Chillcott 1963, by original designation.

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 ejeculatory 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 (1.8–2.7 mm); black in color; with hyaline wings; dichoptic eyes in the male; antenna bearing a single, elongated, tapering flagellomere; bare laterotergite; discal cell and 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, China, 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. *Litoleptis* differs from *Hilarimorpha* in having a pulvilliform empodium; antenna bearing a single, tapering flagellomere; and 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, dorsal surface of wing membrane bare, lack of tibial spurs, and males 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 pseudotracheae, about as long as palpus. Theca short and stout. Palpus one-segmented. Tentorium low on 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 pterostigma. Lower calypter reduced. Upper calypter triangular in form, underdeveloped. Upper calypter with broad curvature, lobe-like, width twice length or less. Costa stops before wing tip or extends past wing tip. Humeral crossvein weakly developed. Sc-r crossvein present, well developed, positioned at proximal side of 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 anteriorly slightly, toward leading edge of wing margin; 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 cell bm. 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. Epandrium wider than long; strongly notched anteriorly. Tergite 10 absent. Hypoproct triangular (rounded posteriorly); flattened, distinct from sclerites above cerci; with or without setae. Cercus displaced away from epandrium; 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. Sperm sac 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. Unknown.

Biology. *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).

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*.

Notes. The holotype and paratype of *Litoleptis alaskensis* were collected at Cape Thompson, Alaska, 26–29 July 1961, by B.S. Heming. There are two Cape Thompsons in Alaska. The one where *L. 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.

Genus *Omphalophora* Becker

Figs. 13–14, 52–53, 75–76, 97–98, 120, 143–144, 161–162.

Omphalophora Becker 1900: 12. Type species *Omphalophora oculata* Becker 1900, by monotypy.

Diagnosis. The monophyly of *Omphalophora* is supported by the unique form of 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.

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; anepisternum setose; M_3 present; tibial spur formula 0:2:1; hind tibia without macrochaetae; female tergite 7 longer than wide; female tergite 9 with ventrolateral arms, extending posteriorly, surrounding and fusing to sternite 9 laterally; 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 a setose anepisternum, veins R_{4+5} containing the wing tip, female tergite 7 clearly longer than wide (in *Ptiolina*, this tergite is clearly wider than long), and in the male, the tergite 10 is as wide as long or nearly oval and the gonostylus comes to a sharp point apically. For more details on the differences between *Omphalophora* and *Ptiolina*, see discussion below. *Omphalophora* may be confused with *Symphoromyia* but are immediately distinguished 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 the absence of fore tibial spurs, and by having 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 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 pseudotracheae, length variable. Theca short and stout, with medial suture. Palpus one- or two-segmented. When two-segmented, distal palpomere longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, shorter than palpus, 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 setose 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 wing tip. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by approximate length of h or more. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. R_1 and R_{2+3} separated by various degrees at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends anteriorly slightly, toward leading edge of wing margin. 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 contain 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 present. M-cu crossvein present. Origin of CuA_1 at cell bm. CuA_2 greater than 1/2 length, less than 2/3 length of posterior vein of cell bm. Anal lobe well developed. Alula full, rounded with broad curvature. Cell cu*p* open or 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. Epandrium wider than long, modestly curved anteriorly. Tergite 10 present, undivided, narrow (clearly wider than long), setose. Hypoproct present, setose. Cercus base held underneath epandrium, or directly adjacent to epandrium. 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. Sperm sac forming separate, distinct lobes ventrally. Lateral ejaculatory processes present, not part of sperm sac posteriorly. Ejaculatory apodeme short or moderately long, reaching anterior margin of hypandrium in some species. Ejaculatory apodeme rod-shaped or laterally compressed. Aedeagal tines absent. Endoaedeagal process present; short, blunt, rounded. Female sternite 8 longer than wide. Female terminalia with tergite 9 entire, with anteriorly-directed ventrolateral projections, attached to and enveloping sternite 9. Spermathecae three, clubbed, sclerotized. Spermathecal ducts more than three times but less than five times length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands arise at approximately distal third of the spermathecal ducts. Spermathecal ducts near junction with common duct not sclerotized. Common spermathecal duct thickened; of moderate length, about same length as 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 ring. Basal cercal segment separated from one another dorsally by approximate width of the second cercal segment. Second cercal segment narrow, elongated (~3x longer than wide or more), with apical sensory pits.

Larva. Unknown.

Biology. The biology of *Omphalophora* species is not known.

Literature. *Omphalophora* species descriptions and treatments are almost entirely contained within the body of work covering the genus *Ptiolina*. Hardy & McGuire (1947) provide a key to North American species. Narchuk (1969) gives a key to eastern European species.

Notes. In 1900, Becker established *Omphalophora oculata*, a new genus and species from West Siberia. Frey added *Omphalophora lapponica* (Frey 1911) and another species was added later, when Szilády transferred *Chrysopilus arctica* Frey to the genus (Szilády 1934a). Nagatomi (1982a) examined all three types of these species and determined that *Chrysopilus arctica* Frey was erroneously placed in *Omphalophora* by Szilády (1934a) and was a true *Chrysopilus* species, in agreement with Narchuk (1969). For the *Omphalophora* species, Nagatomi noted that R_{2+3} is straight in its apical portion, wing cell sc is wider at wing margin than r_1, R_5 at wing margin beyond wing tip and the posterior cubital cell (cu*p*) 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 (1934a), 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) synonymized *O. lapponica* and *P. uralensis* with *Omphalophora oculata* (Becker) and at the same time, re-assigned *Omphalophora* to junior synonym status (= *Ptiolina*). Nagatomi also treated *Omphalophora* as a synonym of *Ptiolina* (Nagatomi 1982a).

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 *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* and *Spaniopsis* (Fig. 14; compare with Figs. 11–12, 20–21). In many *Ptiolina* (e.g., *P. edeta*, *P. zonata*, and others), the first flagellomere is enlarged but flattened laterally, with a clear break between the stylus and the first flagellomere (Figs. 15–16). However, enough overlap of antennal morphologies exists between *Omphalophora* and *Ptiolina* to break down the reliability of this character system. In *Omphalophora* species (at that time, represented by *O. oculata* and *O. lapponica*), Nagatomi (1982a: 56) noted that R_{2+3} is straight in its apical portion, wing cell sc is wider at wing margin than cell r_1 ("wing vein R_5 at wing margin beyond wing tip"), and cell cu*p* is open. Now that more species are added to *Omphalophora* based on male and female genitalic characters (discussed below), a greater understanding of the evolution of wing venation in the two groups may be developed. Vein R_{2+3}, for example, is not always straight in its apical portion in *Omphalophora* and cu*p* is not always open at the margin. At least one wing character consistently separates *Omphalophora* and *Ptiolina*, however. In *Omphalophora*, wing veins R_4 and R_5 contain the wing tip (Figs. 52–53) whereas in *Ptiolina*, R_5 is anterior to the wing tip (Figs. 54–55). In many *Omphalophora*, R_{2+3} is longer than the length of R_5, however this character is less reliable (in *O. nigripilosa*, R_{2+3} 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. Relative length of wing cells sc and r_1 is not a discrete and reliable feature distinguishing *Omphalophora* and *Ptiolina*.

Thoracic morphology is similar between the two groups, with one noticeable difference. The anepisternum of *Omphalophora* species is setose near the posterior margin whereas in *Ptiolina*, this sclerite is completely bare. Tibial spurs have been identified as a character that may assist separating *Omphalophora* and *Ptiolina* (Narchuk 1969). I could not find any meaningful differences in size, number, or placement of tibial spurs, however.

Omphalophora exhibit several distinctive characters in the male genitalia that instantly distinguish it from *Ptiolina* (Figs. 75–78, 97–100). The most pronounced feature is that each gonostylus comes to a sharp point apically (Figs. 97–98), as opposed to in *Ptiolina*, where the gonostylus is rounded apically (Figs. 99–100). *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 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 tergite 10 is either as wide as long or squared and nearly oval (as in *O. fasciata*) (Figs. 75–76). Whereas in *Ptiolina*, tergite 10 is narrow rectangular, approximately three times as wide as long (Figs. 77–78). The hypoproct is tomentose in *Omphalophora*, setose in *Ptiolina*. The epandrium is also much more firmly secured to tergite 10 , and the cerci more firmly attached to the hypoproct, (in a single plane) in *Omphalophora*. In *Ptiolina*, the epandrial and subepandrial sclerites (tergites 9 and 10) tend to rest at a perpendicular angle, loosely attached, after being cleared and placed in glycerol. Separation between cerci seems to vary at the species level, independent of higher level patterns and the form of the epandrium (e.g., notching or curvature of the posterior and/or anterior margin) does not appear to resolve differences at the generic level. While a medial line of increased sclerotization of the epandrium (as evidenced by *O. lapponica* and especially *O. majuscula*) is more common in *Omphalophora* (e.g., Fig. 76), it is an unreliable character to differentiate *Omphalophora* and *Ptiolina*.

In *Omphalophora*, the female tergite 7 is clearly longer than wide, whereas in *Ptiolina* this tergite is clearly wider than long. Tergite 9 in *Omphalophora* is bulbous laterally and tapers posteriorly, with a length that is greater than half its width. In *Ptiolina*, tergite 9 is rectangular and narrow; its length is less than half its width. Also in *Ptiolina*, the ventrolateral arms of tergite 9 are easily distinguished, forming a modest s-curve when observed in the dorsal/ventral perspective (e.g., Fig. 145). The distal, anterior tip of these ventrolateral arms is fused to sternite 9 to varying degrees (e.g., lightly fused as in *P. zonata* or firmly attached as in *P. mallochi*), 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* (Figs. 143–148). 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 of *Ptiolina* species 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 (e.g., Fig. 147). 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. 161–162). 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*; 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 both groups. 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).

Body size was an important consideration for distinguishing *Omphalophora* and *Ptiolina* in the past (Hardy & McGuire 1947). This was probably attributable to the fact that the original species placed in *Omphalophora* are particularly large (e.g., *O. oculata*). Their size, however, is largely independent of ancestry at the genus level. *Omphalophora fasciata* and *Omphalophora nigripilosa*, for example, are comparable in size to some of the smallest species in the *Ptiolina*.

Genus *Ptiolina* Zetterstedt

Figs. 15–16, 54–55, 77–78, 99–100, 121, 145–147, 181–183.

Ptiolina Zetterstedt 1842: 226. Type species *Leptis obscura* Fallén 1814, by subsequent designation of Frauenfeld 1867: 497. See notes below.

Eurytion Jaennicke 1867: 99. Type species *Eurytion paradoxus* Jaennicke 1867, by monotypy.

Tyolina Walker 1848: 220. Misspelling.

Spatulina Szilády 1942: 625. Type species *Spatulina engeli* Szilády 1942, by monotypy.

Diagnosis. The monophyly of *Ptiolina* is supported by the unique form of female tergite 9 which is rectangular and narrow, with ventrolateral arms that are easily distinguished from sternite 9.

Ptiolina species are small to moderately sized, robust flies (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, usually laterally compressed in cross section; mandibles absent; laterotergite bare; anepisternum bare; M_3 present; tibial spur formula 0:2:1; hind tibia without macrochaetae; tergite 9 with ventrolateral arms, extending posteriorly, surrounding sternite 9 laterally but largely free; female spermathecal ducts with accessory glands. *Ptiolina* is restricted to the Holarctic Region. *Ptiolina* is most readily confused with *Omphalophora*. It may be distinguished from this genus by having a bare anepisternum, R_{4+5} anteriorly displaced from the wing tip, female tergite 7 clearly wider than long, and in the male, the gonostylus comes to a blunt point apically. For more details on the differences between *Ptiolina* and *Omphalophora*, see discussion above. *Ptiolina* may be immediately distinguished from *Symphoromyia* 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 the absence of fore tibial spurs, and by having 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 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 pseudotracheae, length variable. Theca short and stout, with medial suture. Palpus one- or two-segmented. When two-segmented, distal palpomere longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, shorter than palpus, 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 wing tip (in *P. nitida*, it extends past wing tip). Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins without setulae. R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends anteriorly slightly, toward leading edge of wing margin. Length of R_{2+3} shorter than or about 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 present. M-cu crossvein present. Origin of CuA_1 at cell bm. CuA_2 greater than 1/2 length, less than 2/3 length of posterior vein of cell bm. Anal lobe well developed. Alula full, rounded with broad curvature. Cell cu*p* 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. Epandrium wider than long, modestly curved or strongly notched anteriorly. Tergite 10 present, undivided, narrow (clearly wider than long), setose. Hypoproct present, tomentose or setose. Cercus base held underneath epandrium, or directly adjacent to epandrium. 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. Sperm sac 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 reduced. Female sternite 8 as wide as long. Female terminalia with tergite 9 entire, with narrow anteriorly-directed ventrolateral projections, mostly free, enveloping sternite 9. Spermathecae three, clubbed, sclerotized. Spermathecal ducts no more than three times length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands arise at base of each spermatheca. Spermathecal ducts near junction with common duct sclerotized and somewhat 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. 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 ring. Basal cercal segment separated from one another dorsally by approximate width of second cercal segment. Second cercal 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 (or very reduced). 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 palpus soft, segments poorly differentiated, three-segmented. Antenna apparently one-segmented, dome-shaped, short. Unpaired salivary pump absent. Posterior tentorial expansion fused to each other posteriorly, with thin extension produced anteriorly.

Biology. *Ptiolina* larvae 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 & Anderson 1982). *Ptiolina obscura* Fallén (= *P. nigrina* Wahlberg), however, apparently feeds on the liverwort species *Marchantia polymorpha* (Nartshuk 1995). *Ptiolina* larvae have weakened and reduced mouthparts, a condition that is appears wholly unsuitable for predation.

Literature. Hardy & McGuire (1947) provide a key to North American species. Narchuk (1969) gives a key to eastern European species.

Notes. 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.

Genus *Spania* Meigen

Figs. 19, 60, 81, 104, 148, 163.

Spania Meigen 1830: 335. Type species *Spania nigra* Meigen 1830, by monotypy.
Archicera Szilády 1934a: 264. Type species *Archicera avavorum* Szilády 1934a, by monotypy.

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 species are 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; 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 the absence of hind tibial spurs and its small size. *Spania* is approximately the same size as *Bolbomyia*, however, it has a stylate antenna and 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 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 pseudotracheae, longer than palpus. Theca short and stout, with medial suture. Palpus 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).

Thorax. Mesonotum lacking vittae, black or brown, without dorsocentral bristles. Anepisternum bare. Postspiracular sclerite smooth, bare. Proscutellum narrowly present or absent. Subscutellum slightly swollen or not. 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 well developed. Sc-r crossvein absent or weakly developed, positioned distal to h by approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third ultimately bends anteriorly slightly, toward leading edge of wing margin. Length of R_{2+3} about as long 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 cell bm greater than 1/2 length, less than 2/3 length of posterior vein of cell bm. Alula with broad curvature that is slightly shifted distally. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 absent. Hypoproct elliptical, flattened, tomentose, without setae. Cercus directly adjacent to epandrium; 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. Sperm sac 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 length of sternite 9, with swelling halfway between genital chamber and spermathecae. Spermathecal duct accessory glands arise at base of each spermatheca. Spermathecal ducts sclerotized and thickened into 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 cercal segment not elongated, without ventral process, separated from each other dorsally by approximate width of second cercal segment. Ventral lobes of first segment of cercusdo not curve ventrally towards one another to form ring. Second cercal segment narrow, elongated (~2.5x longer than wide or more), without apical sensory pits.

Larva. Undescribed, but see Biology below.

Biology. Although the larvae of *Spania nigra* Meigen have not been characterized, Mik (1896) reportedly found a *Spania nigra* larva mining in the thallus of *Pellia neesiana* (Bryophyta: Pelliaceae), a liverwort species (Nartshuk 1995).

Literature. Nagatomi & Saigusa (1982) give a key to the Japanese fauna that includes all species.

Notes. Szilády (1934: 264) distinguished *Archicera* from *Ptiolina* and *Spania* by the antennal flagellum, which he stated, had faintly visible divisions. This feature, as Nagatomi (1982a: 54) has noted, is within the morphological variation already 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 has been treated as a synonym of *Spania nigra* (Majer 1988). The holotype of *Archicera avarorum* has been destroyed [Hungary National History Museum, Budapest]. Therefore a neotype, preferrably a specimen from either Austria or Croatia, needs to be designated for *Archicera avarorum* so that its appropriate taxonomic status may be documented formally.

Genus *Spaniopsis* White

Figs. 20–22, 30, 32, 61–62, 82, 105, 149, 164.

Spaniopsis White 1915: 43. Type species *Spaniopsis tabaniformis* White 1915, 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 & 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 this study. In all other taxa 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; 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 the absence of 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 the absence of hind tibial spurs. The genus may be distinguished from *Atherimorpha* most easily by its robust body, the form of its antenna, M_3 absent or incomplete, laterotergite bare, and hind tibia without spurs.

Description. *Head.* Clypeus bulbous. Scape approximately 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 palpus, with pseudotracheae. Theca short and stout; formed by two sclerites, slightly separated medially. Palpus one-segmented. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia longer than palpus, 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 not. 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 wing tip. Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by approximate length of h. Dorsal side of R_1 setulose, ventral side bare. All other wing veins bare. R_1 and R_{2+3} separated at wing margin. R_{2+3} sinuous, apical third ultimately bends anteriorly slightly, toward leading edge of wing margin. 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 cell bm). Alula with broad curvature that is slightly shifted distally. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 absent. Hypoproct triangular (rounded posteriorly), flattened, tomentose, without setae. Cercus directly adjacent to epandrium; 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. Sperm sac 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 length of sternite 9, not inflated at base of spermathecae. Spermathecal duct accessory glands arise at approximately the distal third of the spermathecal ducts. Spermathecal ducts sclerotized and thickened into 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 as long as 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 cercal segment separated from one another dorsally by approximate width of second cercal segment. Ventral lobes of first segment of cercus not curving ventrally towards one another to form ring. Second cercal segment not elongated, without apical sensory pits.

Larva. Unknown.

Biology. Similar to *Symphoromyia*, *Spaniopsis* adult females take blood meals from vertebrate hosts (Colless & McAlpine 1991; Ferguson 1915). *Spaniopsis* reportedly prefers shady, humid habitats, often at high elevation sites (Paramonov 1962). *Spaniopsis* adults may be collected in Australia between November and May. Although species of this genus may be bothersome to humans, none are considered medically or economically important.

Literature. Paramonov (1962) gives a key to all *Spaniopsis* species (treated as *Spania*).

Notes. 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 mid tibial spurs and the hind tibia lack spurs entirely.

Genus *Symphoromyia* Frauenfeld

Figs. 24–25, 31, 63, 84, 106, 123, 132, 150, 165–166, 177–178, 186, 189.

Symphoromyia Frauenfeld 1867: 496. Type species *Atherix melaena* Meigen 1820, by original designation.
Sympheromyia Schiner 1868: 910 (lapsus).
Parapheromyia Becker 1921: 42. Type species *Atherix crassicornis* Panzer 1806, by original designation. See notes below.
Paraphoromyia Becker 1922 (incorrect subsequent spelling). See notes below.
Axinicera Turner 1974: 861. Type species *Symphoromyia johnsoni* Coquillett 1894, by original designation.
Pogonaria Turner 1974: 861. Type species *Symphoromyia pachyceras* Williston 1886, by original designation.
Ochleromyia Turner 1974: 862. Type species *Symphoromyia kinkaidi* Aldrich 1915, by original designation.

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 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; 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 the absence of a scale on the postspiracular sclerite and in addition to this, from Athericidae by an elongated scape and R_{2+3} meeting the margin at some distance away from R_1; and from Tabanidae by having an aristate antenna and 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 the absence of scale-like thoracic setae.

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 pseudotracheae, length variable. Theca short and stout, with medial suture. Palpus two-segmented, distal segment longer than proximal segment. Stipes surrounded by membrane above theca, directed posteriorly. Lacinia present, longer than palpus, 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. 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 wing tip (between R_4 and R_5). Humeral crossvein well developed. Sc-r crossvein weakly developed, positioned distal to h by approximate length of h. 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. R_{2+3} sinuous, apical third of R_{2+3} ultimately bends anteriorly slightly, toward leading edge of wing margin. 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 present. M-cu crossvein present. Origin of CuA_1 at cell bm near discal cell. M_3 cell at margin convergent. CuA_2 length between 1/2 and 2/3 the length of posterior vein of cell bm. Alula with broad, evenly rounded curvature. Anal lobe well developed. Cell cu*p* 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. Epandrium wider than long, strongly notched anteriorly. Tergite 10 present, divided medially, setose. Hypoproct present. Cercus base held underneath epandrium or directly adjacent to epandrium. Cerci partially displaced from one another, separation distance approximately half 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. Sperm sac 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 length of sternite 9, inflated at base of spermathecae. Spermathecal duct accessory glands 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 cercal segment adjacent dorsally. Ventral lobes of first segment of cercus sometimes curve ventrally towards one another to form ring, usually are flat and compressed medially. Second cercal segment not elongated, with apical sensory pits.

Larva. Body with 11 segments (not including head segment), smooth ventrally. Head capsule not folded within second thoracic segment, composed of a single, undivided plate (dorsal plate), less than 4.5 times longer than greatest width, 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 palpus soft, three-segmented, poorly differentiated. Antenna apparently one-segmented, bifurcated. Unpaired salivary pump absent. Posterior tentorial expansion fused to each other, with thin extension produced anteriorly.

Biology. Perhaps the most well known rhagionids are *Symphoromyia* 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 (Cockerell 1923; Frohne 1953a, 1953b, 1959; Knab & Cooley 1912; Shemanchuk & 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 (Chvála 1983; Knab & Cooley 1912; Turner 1979). Some *Symphoromyia* species, however, and even perhaps most of the species of this genus seem not to attack people (Sommerman 1962; Turner 1979; Turner & Chillcott 1973). *Symphoromyia* adults tend to be most active during the summer months, however, occasionally may be seen in flight during early spring. 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. In general, larval rhagionids are thought to be predators of other insect larvae (Foote 1991). However Sommerman (1962) noted that *Symphoromyia* larvae are slow moving and apparently are not predaceous; their association with moss indicates that they may be at least partially herbivorous (Sommerman 1962).

Literature. Aldrich (1915) gives a key to North American species, but there are numerous undescribed species in the region. Narchuk (1969) gives a key to eastern European species. Turner (1974) proposes species-groups within the genus. Sommerman (1962) provides natural history information for the larval stages.

Notes. Previous authors have referenced the genus name of *Parapheromyia* to Becker (1921: 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.

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). Therefore the name *Paraphoromyia* Becker may be validated by prevailing usage (ICZN 1999: article 33.3.1). This matter needs to be resolved by the ICZN.

Incertae sedis

Genus *Alloleptis* Nagatomi & Saigusa

Figure 64

Alloleptis Nagatomi & Saigusa 1982a: 40. Type species *Alloleptis tersus* Nagatomi & Saigusa 1982a, 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 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 (1982a, 1984). *Head.* Clypeus slightly bulbous. Scape slightly smaller than pedicel. First flagellomere enlarged bearing two-segmented stylus. Eyes conspicuously setulose; male holoptic. Palpus 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 palpus one-segmented). Mandibles absent.

Thorax. Mesonotum and scutellum dark, with long, erect setae. Wing membrane infuscate, without markings, without pterostigma. Lower calypter reduced. Upper calypter well developed, with broad curvature, lobe-like, width twice length or less. Costa apparently extends past wing tip 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 wing tip. M_3 present. Cell m_3 parallel-sided at margin. Origin of CuA_1 at crossvein separating discal and basal medial cells. Length of CuA_2 vs. posterior vein of cell bm less than 1/2 length of posterior vein of cell bm. Alula with broad curvature, rounded evenly. Anal lobe well developed. Cell cu*p* closed (CuA_2 + A_1 vein as long or longer than CuA_2). Laterotergite bare. Subscutellum inconspicuous. Tibial spur formula 0:1:1.

Abdomen is "comparatively long and narrow" (Nagatomi 1982a: 41). Male genitalia with epandrium simple, not containing hypandrium ventrally. Epandrium wider than long, modestly curved anteriorly. Tergite 10 absent. Hypoproct tomentose, without setae. Cercus base held underneath epandrium. 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. Sperm sac 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. Unknown.

Biology. Unknown.

Literature. Illustrations of wing and head in Nagatomi (1982a); male genitalia illustrated in Nagatomi (1984).

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Appendix. List of included species; synonyms are indented.

I. Austroleptidae

Austroleptis	**Author, reference**	**Type country**
Austroleptis atrata	Nagatomi & Nagatomi 1987: 141	Chile
Austroleptis atriceps	Malloch 1932b: 203	Chile
Austroleptis breviflagella	Nagatomi & Nagatomi 1987: 148	Chile
Austroleptis collessi	Paramonov 1962: 138	Australia
Austroleptis fulviceps	Malloch 1932b: 202	Chile
Austroleptis multimaculata	Hardy 1920a: 128	Australia
Austroleptis penai	Nagatomi & Nagatomi 1987: 153	Chile
Austroleptis rhyphoides	Hardy 1920a: 127	Australia

II. Bolbomyiidae

Bolbomyia	**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 1934a: 264)	Russia
Bolbomyia macgillisi	Chillcott 1961: 634	USA

III. Rhagionidae

A. Arthrocerinae

Arthroceras	**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*; Ôuchi 1943: 493)	China

B. Chrysopilinae

Chrysopilus	**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
Chrysopilus albicornis	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 americanus	(as *Chrysopila*; Schiner 1868: 197)	'South America'
Chrysopilus amulus	Kerr, **new name**	Mexico
Chrysopila latifrons	Williston 1901: 266. Preoccupied by *Chrysopilus latifrons* Bezzi 1898: 32.	Italy

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
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	Van der 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 in Curran 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 aymara	Lindner 1924: 72	Peru
Chrysopilus azurinus	Frey 1954: 19	Philippines
Chrysopilus balbii	Santos & Amorim 2007: 5	Brazil
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	Meijere 1924: 13. Preoccupied by *Chrysopilus tomentosus* Bigot 1887: 104.	Sumatra
Chrysopilus beameri	Hardy 1949: 152	USA
Chrysopilus beckeri	Krivosheina 2008: 211	Austria
Chrysopilus unicolor	Becker 1922: 71. Preoccupied by *Chrysopilus unicolor* Brunetti 1909: 432.	Austria
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

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
Chrysopilus terminalis	Macquart 1846: 234	"Columbia, Venezuela"
Chrysopilus calchaqui	Coscarón & Coscarón 1995: 267	Argentina
Chrysopilus caligatus	Santos & Amorim 2007: 27	Brazil
Chrysopilus calopterus	(as *Leptis*; Schiner 1868: 197)	Brazil
Chrysopilus camargoi	Santos & Amorim 2007: 19	Brazil
Chrysopilus capillosus	Santos & Amorim 2007: 9	Brazil
Chrysopilus choui	Yang & Yang 1989: 243	China
Chrysopilus chlorophthalmus	Loew 1840: 4	not given; Europe
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 amorimi	Kerr, **new name**	Brazil
Chrysopilus fascipennis	Bromley in Curran 1931: 8. Preoccupied by *Chrysopilus fascipennis* (Brunetti 1920: 123).	Brazil
Chrysopilus dauricus	Frey 1954: 22	Russia
Chrysopilus davisi	Johnson 1912: 4	USA
Chrysopilus decisus	(as *Leptis*; Walker 1857: 15)	Malaya
Chrysopilus decoratus	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 dubius	Krivosheina & Sidorenko 2006: 890	Russia
Chrysopilus duplicatus	Krivosheina & Sidorenko 2006: 890	Russia
Chrysopilus edgari	Paramonov 1962: 130	Australia
Chrysopilus egregius	Meijere 1919: 22	Sumatra
Chrysopilus elegans	Schiner 1868: 198	Colombia
Chrysopilus erythrophthalmus	Loew 1840: 3	Poland
Leptis hyalipennis	Roser 1840: 52	not given; Europe
Chrysopilus erythrophthalmus dudai	Krivosheina 2006: 58	'Ojovio'; 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

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
Macellopalpus flaveolus	Bigot 1886: xlviii [48]	Papua New Guinea
Macellopalpus fulvidus	Brunetti 1909: 424	India
Chrysopilus frater	Brunetti 1909: 431	Burma
Chrysopilus ferruginosus dimidiatus	Frey 1954: 18	Vietnam
Chrysopilus ferruginosus philippinus	Frey 1954: 18	Philippines
Chrysopilus ferruginosus burmanicus	Frey 1954: 19	Burma
Chrysopilus fijiensis	Webb 2006: 25	Fiji
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 flavicomus	Krivosheina & Sidorenko 2006: 887	Russia
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
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	Coscarón & Coscarón 1995: 263	Argentina
Chrysopilus grandis	Yang & Yang 1993a: 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	Meijere 1914: 31	Indonesia
Chrysopilus fenestratus	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 hyalinus	Santos & Amorim 2007: 23	Brazil
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

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
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
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 kurentzovi	Krivosheina & Sidorenko 2007: 589	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 leleji	Krivosheina & Sidorenko 2008: 413	Russia
Chrysopilus lemur	Stuckenberg 1965: 124	Madagascar
Chrysopilus leonardi	Curran 1931: 4	Puerto Rico
Chrysopilus leptiformis	Kertész 1902: 148	Peru
Chrysopilus lii	Yang *et al.* 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	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 macularis	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?)
Chrysopilus magnipennis	Brunetti 1909: 213	Sumatra
Chrysopilus malaisei	Frey 1954: 21	Burma
Chrysopilus marmoratus	Brunetti 1909: 429	India
Chrysopilus marumbiensis	Coscarón & Coscarón 2005: 2009	Brazil
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)

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
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 microphallus	Santos & Amorim 2007: 19	Brazil
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 nigriculus	Krivosheina & Sidorenko 2006: 892	Russia
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 1993b: 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	Germany ("Harz")
Chrysopilus nudus	Cresson 1919: 177	USA
Chrysopilus obscuralatus	Yang & Yang 1989: 245	China
Chrysopilus ningxianus	Yang & Yang 1991: 94	China
Chrysopilus obscuratus	Meijere 1914: 30	Java
Chrysopilus obscuribarbus	(as *Chrysopila*; Loew) 1869a: 53	'Central Asia'
Chrysopilus obscuripennis	Loew 1873: 99	'Hadschyabad' (Iran)
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	Meijere 1911: 288	Java
Chrysopilus opalescens	Brunetti 1920: 134	Ceylon
Chrysopilus opalizans	Meijere 1913: 49	Indonesia
Chrysopilus ornatipennis	(as *Chrysophilus*; Brunetti 1909: 212)	India
Chrysopilus ornatus	(as *Leptis*; Say 1823: 34)	USA
Chrysopilus orphnopterus	Santos & Amorim 2007: 7	Brazil
Chrysopilus pallipes	(as *Chrysopila*; Loew 1869a: 54)	Greece
Chrysopilus pallipilosus	Yang & Yang 1992: 354	China
Chrysopilus palparis	Loew 1869a: 50	Greece
Chrysopilus panamensis	Curran 1931: 2	Panama
Chrysopilus paradoxus	Krivosheina & Sidorenko 2008: 414	Russia
Chrysopilus parvus	Yang *et al.* 1997: 161	China
Chrysopilus peruanus	Kertész 1902: 149	Peru

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
Chrysopilus phaeopterus	Santos & Amorim 2007: 25	Brazil
Chrysopilus philippii	Lindner 1924: 70	Peru
Chrysopilus pilosus	Leonard 1930: 152	USA
Chrysopilus pingquanus	Yang *et al.* 1997: 163	China
Chrysopilus pingxianganus	Yang & Yang 1992: 353	China
Chrysopilus plaumanni	Santos & Amorim 2007: 11	Brazil
Chrysopilus plebeius	Williston 1901: 264	Mexico
Chrysopilus poecilopterus	(as *Chrysophilus*; Bezzi 1912: 450)	Taiwan
Chrysopilus amamiensis	Nagatomi 1968: 33	Japan
Chrysopilus praestigmaticus	Evenhuis 1994: 292	Germany
Chrysopilus stigmaticus	Statz 1940: 129	Germany
Chrysopilus pretiosus	Loew 1869a: 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 1869a: 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
Chrysopilus dispar	Van der 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 in Curran 1931: 8	Panama
Chrysopilus rotundipennis	Loew 1861: 317	USA
Chrysopilus rufipes	Macquart 1850: 103	Australia
Chrysopilus ruiliensis	Yang & Yang 1990: 280	China
Chrysopilus saffranus	(as *Leptipalpis*; Bigot 1887: 108)	Chile
Chrysopilus sauteri	Bezzi 1907: 564	Taiwan
Leptis basalis	Matsumura 1915: 39. Preoccupied by *Chrysopilus basalis* Walker 1860: 285.	Japan
Chrysopilus matsumurai	Nagatomi 1968: 42	Japan
Chrysopilus schlingeri	Webb 2006: 27	Fiji
Chrysopilus schnusei	Lindner 1924: 74	Peru
Chrysopilus segmentatus	Brunetti 1909: 430	Nepal
Chrysopilus semipictus	Santos & Amorim 2007: 14	Brazil
Chrysopilus sericeus	Bromley in Curran 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 1869a: 49	Italy
Chrysopilus sigillatus	Lindner 1930: 65	Costa Rica
Chrysopilus silvaticus	Nagatomi 1968: 53	Japan
Chrysopilus sinensis **n. comb.**	(as *Spatulina;* Yang *et al.* 1997: 256)	China
Chrysopilus silvicola	Nagatomi 1968: 54	Japan
Chrysopilus similis	Brunetti 1920: 138	Ceylon
Chrysopilus simillimus	Meijere 1914: 29	Java
Chrysopilus simonovi	Krivosheina & Sidorenko 2006: 887	Russia
Chrysopilus simplex	Meijere 1904: 97	Java
Chrysopilus smaragdinus	Kertész 1902: 145	Peru
Chrysopilus sobolevae	Makarkin & Sidorenko 2001: 8	Russia
Chrysopilus sogai	Stuckenberg 1965: 120	Madagascar
Chrysopilus sordidus	Brunetti 1920: 143	India

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APPENDIX (continued)

Chrysopilus	**Species reference**	**Species Type Country**
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*	Cockerell 1921: 471	England (Eocene/Oligocene)
Chrysopilus strigipennis	Meijere 1914: 26	Java
Chrysopilus stylatus	Walker 1864: 208	Indonesia
Chrysopilus subalpicolus	Krivosheina 2006: 586	Switzerland
Chrysopilus subamurensis	Krivosheina & Sidorenko 2006: 894	Russia
Chrysopilus subaquilis	Nagatomi 1968: 56	Japan
Chrysopilus subauratus	Krivosheina 2006: 713	Romania
Chrysopilus subluteolus	Krivosheina 2006: 209	Ukraine
Chrysopilus subpingquanus	Krivosheina & Sidorenko 2007: 593	Russia
Chrysopilus subsplendidus	Krivosheina 2006: 720	Romania
Chrysopilus subtrimaculatus	Krivosheina & Sidorenko 2007: 593	Russia
Chrysopilus subugensis	Krivosheina & Sidorenko 2007: 596	Russia
Chrysopilus sucini	Stuckenberg 1965: 138	Madagascar
Chrysopilus suomianus	(as *Achrysopilus*; Szilády 1934a: 256)	Finland
Chrysopilus superbus	Stuckenberg 1965: 140	Madagascar
Chrysopilus tanakai	Nagatomi 1978: 451	Japan
Chrysopilus tasmaniensis	White 1915: 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	van 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 1978b: 311	France
Chrysopilus trifasciatus	Walker 1860: 284	Mexico
Chrysopilus trimaculatus	Yang & Yang 1989: 245	China
Chrysopilus tsacasi	Thomas 1979: 136	Morocco
Chrysopilus tuckeri	Bezzi 1926: 320	South Africa
Chrysopilus turkestanus	Lindner 1931: 85	Turkestan
Chrysopilus ugensis	Nagatomi 1968: 59	Japan
Chrysopilus ungaranensis	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 variipilus	Krivosheina & Sidorenko 2006: 897	Russia
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 vitreus	Santos & Amorim 2007: 15	Brazil
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

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Chrysopilus	**Species reference**	**Species Type Country**
Chrysopilus yezonis	Nagatomi 1968: 61	Japan
Chrysopilus yunnanensis	Yang & Yang 1990: 279	China
Chrysopilus zanjensis	Stuckenberg 1965: 154	Madagascar

APPENDIX (continued)

***Chrysopilus* nomina dubia**	**Author, reference**
Musca asiliformis	Preyssler 1791: 99
Leptis cristatus	Fabricius 1775: 782

Schizella	**Author, reference**	**Type country**
Schizella furcicornis	Bezzi 1917: 119	Philippines
Schizella pulchrina	Frey 1954: 25	Philippines
Schizella woodleyi	Kerr 2003: 454	Philippines

Stylospania	**Author, reference**	**Type country**
Stylospania lancifera	Frey 1954: 23	Philippines

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Arthroteles	**Author, reference**	**Type country**
Arthroteles bombyliiformis	Bezzi 1926: 322	South Africa
Arthroteles cinerea	Stuckenberg 1956a: 329	South Africa
Arthroteles longipalpis	Nagatomi & Nagatomi 1990a: 312	South Africa
Arthroteles orophila	Stuckenberg 1956a: 327	South Africa

Atherimorpha	**Author, reference**	**Type country**
Atherimorpha agathae	Paramonov 1962: 167	Australia
Atherimorpha albipennis	Bezzi 1926: 318	South Africa
Atherimorpha albohirta	Malloch 1932b: 208	Argentina
Atherimorpha alisae	Paramonov 1962: 158	Australia
Atherimorpha angustifrons	Nagatomi & Nagatomi 1990c: 44	South Africa
Atherimorpha atrifemur	Malloch 1932b: 210	Chile
Atherimorpha bevisi	Stuckenberg 1956b: 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 1990c: 52	South Africa
Atherimorpha edgari	Paramonov 1962: 164	Australia
Atherimorpha edwardsi	Malloch 1932b: 212	Chile
†*Atherimorpha festuca*	Jell & Duncan 1986: 181	Australia
Atherimorpha flavicorpus	Nagatomi & Nagatomi 1990c: 57	South Africa
Atherimorpha flavofasciata	Paramonov 1962: 161	Australia
Atherimorpha flavolateralis	Malloch 1932b: 213	Argentina
Atherimorpha fulva	Hardy 1920a: 121	Australia
Atherimorpha fusca	Malloch 1932b: 213	Chile
Atherimorpha fuscicoxa	Malloch 1932b: 215	Chile
Atherimorpha gracilipennis	Nagatomi & Nagatomi 1990c: 59	South Africa
Atherimorpha grisea	(as *Leptis*; Philippi 1865: 774)	Chile
Atherimorpha hirtula	Bigot 1887: 116	Chile
Atherimorpha imitans	Malloch 1932b: 211	Chile
Atherimorpha infuscata	Paramonov 1962: 162	Australia

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Atherimorpha	**Author, reference**	**Type country**
Atherimorpha irwini	Nagatomi & Nagatomi 1990c: 59	South Africa
Atherimorpha lamasi	Santos 2005: 39	Brazil
Atherimorpha latipennis	Stuckenberg 1956b: 144	South Africa
Atherimorpha longicornu	Nagatomi & Nagatomi 1990c: 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 1990c: 74	South Africa
Atherimorpha praefica	(as *Leptis*; Philippi 1865: 772)	Chile
Leptis setosus	(Philippi 1865: 773), **new synonymy**	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
Atherimorpha scutellaris	Malloch 1932b: 214	Chile
Atherimorpha setosiradiata	(as *Therevirhagio*; Lindner 1925: 20)	Australia
Atherimorpha stuckenbergi	Nagatomi & Nagatomi 1990c: 79	South Africa
Atherimorpha subannulata	(as *Leptis*; Philippi 1865: 771)	Chile
Atherimorpha tonnoiri	Paramonov 1962: 159	Australia
Atherimorpha triangularis	Malloch 1932b: 234	Chile
Atherimorpha uptoni	Paramonov 1962: 163	Australia
Atherimorpha vernalis	White 1915: 42	Australia
Atherimorpha victoriana	Paramonov 1962: 160	Australia
Atherimorpha villosissima	Paramonov 1962: 158	Australia

Desmomyia	**Author, reference**	**Type country**
Desmomyia sinensis	Yang *et al.* 1997: 181	China
Desmomyia thereviformis	Brunetti 1912: 462	India

Rhagio	**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
Rhagio albus	Yang *et al.* 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)	not given, prob. Sweden
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*; 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 1993b: 48	China
Rhagio basimaculatus	Yang & Yang 1993b: 48	China
Rhagio beckeri	Lindner 1923: 7	France

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Rhagio	**Author, reference**	**Type country**
† *Rhagio bifurcatus*	(as *Palaeohilarimorpha*; Meunier 1902: 400)	Baltic Region (Eocene/Oligocene)
Rhagio biroi	Szilády 1934b: 8. No specimen has been designated the type of this species.	India
Rhagio bisectus	Yang *et al.* 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 cartereaui	(as *Leptis*; Gobert 1877: 67)	France
Rhagio cavannae	(as *Leptis*; Bezzi 1898: 28)	Italy
Rhagio centrimaculatus	Yang & Yang 1993b: 47	China
Rhagio chillcotti	James 1965a: 333	Canada
Rhagio choui	Yang *et al.* 1997: 205	China
Rhagio chrysopilaeformis	(as *Leptis*; Bezzi 1898: 31)	Italy
Rhagio chrysostigma	(as *Leptis*; Loew 1857: 33)	Yugoslavia
Rhagio cinerascens	(as *Leptis*; Röder 1884: 41)	Italy
Rhagio cinereus	(as *Leptis*; Bellardi 1861: 95)	Mexico
Rhagio cingulatus	(as *Leptis*; Loew 1856: 28)	Russia
Rhagio cingulatus canescens	Szilády 1934a: 243	France
Rhagio conspicuus	Meigen 1804: 299	Russia
Leptis janotae	Nowicki 1867: 349	Czechoslovakia
Leptis conspicuus alpinus	Loew 1869a: 35	Austria
Leptis conspicuus florentinus	Loew 1869a: 34	Italy
Leptis marchalii	Pierre 1889: 5	France
Rhagio corsicanus	Becker 1910: 640	France
Rhagio costalis	Matsumura 1911: 68	Russia
Rhagio costatus	(as *Leptis*; Loew 1862: 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 flavoniger	Coquillett *in* Baker 1904: 20	USA
Leptis pleuralis	Adams 1904: 441	USA
Rhagio discoidalis	(as *Leptis*; Brunetti 1912: 463)	India
Rhagio elenae	Soboleva 1987: 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 *et al.* 1997: 207	China

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Rhagio	**Author, reference**	**Type country**
Rhagio gracilis	(as *Leptis*; Johnson 1912: 3)	USA
Rhagio graeculus	(as *Leptis*; Loew 1869a: 32)	Greece
Rhagio grandis	Szilády 1934a: 248	France
Rhagio guadarramensis	Czerny & Strobl 1909: 166	Spain
Rhagio guangxiensis	Yang & Yang 1993b: 46	China
Rhagio guizhouensis	Yang & Yang 1992: 587	China
Rhagio hainanensis	Yang *et al.* 1997: 212	China
Rhagio hangzhouensis	Yang & Yang 1989: 291	China
Rhagio huashanensis	Yang *et al.* 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 incurvatus	(as *Leptis*; Meijere 1911: 291)	Java
Rhagio insularis	Becker 1921: 55	Greece
Rhagio iriomotensis	Nagatomi & Nagatomi 1990b: 38	Japan
Rhagio itoi	Nagatomi 1952: 11	Japan
Rhagio japonicus	Matsumura 1916: 346	Japan
Rhagio javanus	Lindner 1925: 21	Java
Rhagio jinxiuensis	Yang & Yang 1993b: 50	China
Rhagio karafutonis	Matsumura 1916: 343	Japan
Rhagio latifasciatus	Okada 1941: 256	Japan
Rhagio latipennis	(as *Leptis*; Loew 1856: 19)	Germany
Rhagio libanonicus	Szilády 1934a: 252	Lebanon
Rhagio lineola	Fabricius 1794: 275	Denmark
Rhagio albifrons	Meigen 1804: 300	Austria
Leptis albifrons monticola	Egger 1860: 668	Austria
Leptis lineola monticola	Egger 1860: 348	Austria
Leptis lineola andalusica	Strobl 1909: 166	Spain
Leptis lineola polonica	Szilády 1934a: 241	Poland
Rhagio longshengensis	Yang & Yang 1993b: 50	China
Rhagio longzhouensis	Yang & Yang 1993b: 49	China
Rhagio luteus	Soboleva 1984: 122	Russia
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 stigmatica	Zetterstedt 1842: 218	Sweden
Leptis bimaculatus	Gobert 1877: 77	France
Leptis maculatus obscurus	Strobl 1898: 420	Bosnia
Rhagio maculatus dalmaticus	Szilády 1934a: 240	Croatia
Rhagio maculatus macedonicus	Szilády 1934a: 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
Rhagio maolanus	Yang & Yang 1993c: 280	China
Rhagio matsumurae	Lindner 1923: 11	Japan
Rhagio medeae	Iacob 1971: 353	Romania
Rhagio meridionalis	Yang & Yang 1993a: 2	China
Rhagio miyonis	Nagatomi 1952: 7	Japan
Rhagio mongolicus	Lindner 1923: 6	Mongolia
Rhagio montanus	Becker 1921: 54	Italy
Rhagio montanus striatus	Szilády 1934a: 244	Poland
Rhagio montivagus	Edwards 1919: 29	Sumatra

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Rhagio	**Author, reference**	**Type country**
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 *et al.* 1997: 227	China
Rhagio niger	(as *Leptis*; Wiedemann in Meigen 1820: 98)	Portugal
Rhagio niger trajani	Szilády 1934a: 243	Romania
Rhagio notatus	(as *Leptis*; Meigen 1820: 95)	not given; Europe
Rhagio notatus nigricans	Szilády 1934a: 248	Czechoslovakia
Rhagio ochraceus	(as *Leptis*; Loew 1862: 187)	USA
Rhagio olgae	Soboleva 1987: 94	Russia
Rhagio olsufjevi	Soboleva 1989: 401	Russia
Rhagio orestes	Chillcott 1965: 792	USA
Rhagio pallidipennis	Becker 1921: 55	Greece
Rhagio pallidistigma	(as *Leptis*; Meijere 1924: 14)	Sumatra
Rhagio palpalis	(as *Leptis*; Adams 1904: 442)	USA
Rhagio costatus limbatus	Leonard 1930: 96	USA
Rhagio pandellei	(as *Leptis*; Gobert 1877: 66)	France
Rhagio perdicaceus	Frey 1954: 11	China
Rhagio perezii	(as *Leptis*; Gobert 1877: 65)	France
Rhagio perrisii	(as *Leptis*; Gobert 1877: 66)	France
Rhagio petrovae	Soboleva 1989: 403	Russia
Rhagio philippinensis	Frey 1954: 11	Philippines
Rhagio pilosus	Yang *et al.* 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 1990b: 41	Malaysia
† *Rhagio samlandicus*	(as *Leptis*; Meunier 1916: 277)	Baltic Region
Rhagio sardous	Szilády 1934a: 247	Italy
Rhagio scapulifer	(as *Leptis*; Bigot 1887: 113)	Japan
Rhagio schmidti	Lindner 1931: 205	Algeria
Rhagio scolopaceus	(as *Musca*; Linnaeus 1758: 590)	Sweden
Sylvicola solitarius	Harris 1780: 100	not given; Europe
Sylvicola monotropus	Harris 1780: 101	not given; Europe
Rhagio scolopaceus hahnlei	Lindner 1923: 9	Germany
Rhagio separatus	Yang *et al.* 1997: 233	China
Rhagio shaanxiensis	Yang *et al.* 1997: 235	China
Rhagio shennonganus	Yang & Yang 1991: 276	China
Rhagio shimai	Nagatomi & Nagatomi 1990b: 46	Malaysia
Rhagio shirakii	Szilády 1934b: 9	Taiwan
Rhagio sikisimanus	Nagatomi 1972: 79	Japan
Rhagio simushirus	Soboleva 1989: 403	Russia
Rhagio sinensis	Yang & Nagatomi 1992: 88	China
Rhagio singularis	Yang *et al.* 1997: 240	China
Leptis sordidus	(as *Leptis*; Loew 1862: 74)	Turkey
Rhagio pilosus	(as *Leptis*; Loew 1865: 235)	Turkey
Rhagio stigmosus	Yang *et al.* 1997: 242	China
Rhagio strigosus	(as *Leptis*; Meigen 1804: 299)	France

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APPENDIX (continued)

Rhagio	**Author, reference**	**Type country**
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 1859: 505)	Russia
Rhagio tipuliformis	Fabricius 1794: 273	Germany
Rhagio tonsa	(as *Leptis*; Loew 1869a: 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
Leptis cinereus	Zetterstedt 1842: 221	Sweden
Leptis ephippium	Zetterstedt 1842: 219	Sweden
Leptis nigriventris	Loew 1869a: 33	Germany
Leptis tringarius goebelii	Strobl 1893: 29	Austria
Rhagio tringarius tripustulatus	Szilády 1934a: 246	not given; Europe
Rhagio tristis	(as *Leptis*; Schummel 1837: 109)	Germany
Rhagio tuberculatus	Yang *et al.* 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
Leptis stigma	Schummel 1837: 108	Poland
Leptis striola	Meigen 1838: 61	Austria
† *Rhagio wheeleri*	Melander 1949: 29	USA (Miocene)
Rhagio yangi	Kerr, **new name**	China
Rhagio sinensis	Yang & Yang 1993a: 1. Preoccupied by *Rhagio sinensis* (Yang & Nagatomi 1992: 88).	China
Rhagio yasumatsui	Nagatomi 1972: 83	Japan
Rhagio zhejiangensis	Yang & Yang 1989: 290	China

APPENDIX (continued)

***Rhagio* nomina nuda**	**Author, reference**
Leptis acutangulus	Meunier 1899: 177
Leptis albicornis	Say 1823: 38
Leptis distans	Hennig 1967: 39
Leptis flexus	Meunier 1899: 177
Leptis recurvus	Meunier 1899: 177
Leptis validus	Meunier 1899: 177

Sierramyia	**Author, reference**	**Type country**
Sierramyia caligatus **n. comb.**	(as *Neorhagio*; Santos 2006: 51)	Mexico
Sierramyia nagatomii **n. comb.**	(as *Neorhagio*; Santos 2006: 54)	Mexico

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D. Spaniinae

Species tentatively placed in the genus *Ptiolina* are indicated by an asterisk (*). These species require inspection to verify their placement.

Litoleptis	**Author, reference**	**Type country**
Litoleptis alaskensis	Chillcott 1963: 1187	USA
Litoleptis chilensis	Hennig 1972: 6	Chile
† *Litoleptis fossilis*	Arillo *et al*. 2009	Spain (Lower Albian, Cretaceous)
Litoleptis orientalis	(as *Hilarimorpha*; Frey 1954: 25)	Philippines

Omphalophora	**Author, reference**	**Type country**
Omphalophora alapponica	(as *Ptiolina*; Makarkin & Sidorenko 2001: 5)	Russia
Omphalophora cinereofasciata	(as *Leptis*; Schummel 1837: 109) **n. comb.**	"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 1869b: 164) **n. comb.**	Canada
Omphalophora lapponica	Frey 1911: 16	Finland
Omphalophora leleji	(as *Ptiolina*; Makarkin & Sidorenko 2001: 2)	Russia
Omphalophora majuscula	(as *Ptiolina*; Loew 1869b: 165) **n. comb.**	Canada
Omphalophora nagatomii	(as *Ptiolina*; Makarkin & Sidorenko 2001: 3)	Russia
Omphalophora nigripilosa	(as *Ptiolina*; Hardy & McGuire 1947: 9) **n. comb.**	USA
Omphalophora oculata	Becker 1900: 106	Russia
Ptiolina uralensis	Becker 1921: 62	Russia

Ptiolina	**Author, reference**	**Type country**
*Ptiolina alberta**	Leonard in Curran 1931: 259	Canada
Ptiolina attenuata	Nagatomi 1986: 311	Japan
*Ptiolina augusta**	Curran 1931: 249	Canada
*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
Ptiolina grandis	Frey 1918: 31	Russia
Ptiolina arctica	Becker 1921: 62	Russia
*Ptiolina latifrons**	Nagatomi 1986: 312	Taiwan
*Ptiolina longipilosa**	Nagatomi 1986: 314	Japan
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
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
Tyolina tristis	Walker 1848: 220	Great Britain
Ptiolina nigrina	Wahlberg 1854: 215	Sweden
Ptiolina nigripes	Zetterstedt 1859: 4975	Sweden
Ptiolina obsoleta	Leonard in Curran 1931: 250	USA
*Ptiolina paradoxa**	(as *Eurytion*; Jaennicke 1867: 99)	Switzerland
Ptiolina wodzickii	Frauenfeld 1867: 497	not given; Europe
Ptiolina lapidaria	Nowicki 1868: 74	Poland
Spania grisea	Strobl 1892: 124	Austria

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APPENDIX (continued)

Ptiolina	**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

Spania	**Author, reference**	**Type country**
Spania kyushuensis	Nagatomi & Saigusa 1982: 226	Japan
Spania naitoi	Nagatomi & Saigusa 1982: 229	Japan
Spania nigra	Meigen 1830: 335	not given; Europe
Spania nigra americana	Johnson 1923: 70	USA
Archicera avavorum	Szilády 1934a: 268	Austria, Croatia

Spaniopsis	**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 1915: 44	Australia
Spaniopsis vexans	Ferguson 1915: 238	Australia

APPENDIX (continued)

Symphoromyia	**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
Symphoromyia crassicornis	(as *Atherix*; Panzer 1806: 10)	"Hartz;" Europe
Leptis griseola	Fallén 1814: 7	Sweden
Atherix grisea	Meigen 1820: 109	not given; Europe
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 *et al.* 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
Symphoromyia melaena	(as *Atherix*; Meigen 1820: 109)	"Neapal" (Italy)
Atherix maura	Meigen 1820: 109	not given: Europe
Atherix pilosa	Meigen 1820: 109	not given; Europe
Symphoromyia montana	Aldrich 1915: 133	USA
Symphoromyia nana	Turner & Chillcott 1973: 15	USA
Symphoromyia pachyceras	Williston 1886: 287	USA

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APPENDIX (continued)

Symphoromyia	**Author, reference**	**Type country**
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
Symphoromyia sackeni	Aldrich 1915: 139	USA
Symphoromyia securifera	Coquillett 1904: 171	USA
Symphoromyia sinensis	Yang *et al.* 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

APPENDIX (continued)

***Symphoromyia* nomina dubia**	**Author, reference**
Symphoromyia picea	Walker 1848: 219

IV. *Incertae Sedis*

Alloleptis	**Author, reference**	**Type country**
Alloleptis tersus	Nagatomi & Saigusa 1982a: 41	Celebes