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Revision and phylogeny of the caddisfly subfamily Protoptilinae (Trichoptera: Glossosomatidae) inferred from adult morphology and mitochondrial DNA

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ABSTRACT

Protoptilinae Ross, 1956, is the most diverse subfamily belonging to the saddle- or tortoise-case-making caddisfly family Glossosomatidae Wallengren, 1891. The subfamily has a disjunct distribution: 5 genera are known from the East Palaearctic and Oriental regions; the remaining 13 are restricted to the Nearctic and Neotropical regions. Monophyly of Protoptilinae and each of 17 genera was tested using 80 taxa, 99 morphological characters, and mitochondrial DNA (COI). Additionally, homologies of morphological characters were assessed across genera and a standardized terminology for those structures was established. Mitochondrial DNA data were unavailable for 55 of the 80 taxa included in this study. To test the effects of the missing molecular data, 5 different datasets were analyzed using both parsimony and Bayesian methods. There was incongruence between the COI and morphological data, but results suggest the inclusion of COI data in a combined analysis, although incomplete, improved the overall phylogenetic signal. Bayesian and parsimony analyses of all 5 datasets strongly supported the monophyly of Protoptilinae. Monophyly of the following genera was also supported: *Canoptila* Mosely, 1939; *Culoptila* Mosely, 1954; *Itauara* Müller, 1888; *Mastigoptila* Flint, 1967; *Mortoniella* Ulmer, 1906; *Protoptila* Banks, 1904; and *Tolhuaca* Schmid, 1964. Several taxonomic changes were necessary for classification to reflect phylogeny accurately. Accordingly, *Matrioptila* Ross, 1938; *Poeciloptila* Schmid, 1991; *Temburongpsyche* Mal-

icky, 1992; and *Nepaloptila* Kimmins, 1964, are designated new junior synonyms of *Padunia* Martynov, 1910. Additionally, the endemic Caribbean genera *Campsiophora* Flint, 1964, and *Cubanoptila* Sykora, 1973, are designated new junior synonyms of *Cariboptila* Flint, 1964. Diagnoses and a key to the subfamilies of Glossosomatidae and world genera of Protoptilinae incorporating these taxonomic changes are provided.

Key words: taxonomy, identification key, male genitalia, female genitalia, morphology, COI, missing data, combined analyses

INTRODUCTION

Protoptilinae Ross, 1956, is 1 of 3 subfamilies belonging to the saddle-, or tortoise-case-making caddisfly family Glossosomatidae Wallengren, 1891. The other 2 subfamilies are Agapetinae Martynov, 1913 [1912] (~200 species), containing *Agapetus* Curtis, 1834; *Catagapetus* McLachlan, 1884; and *Electragapetus* Ulmer, 1912 (6 spp.), and known from the Nearctic, East and West Palaearctic, Australasian, Oriental, and Afrotropical biogeographic regions; and Glossosomatinae Wallengren, 1891 (~100 spp.), consisting of *Anagapetus* Ross, 1938, and *Glossosoma* Curtis, 1834, and known from the Nearctic, East and West Palaearctic, and Oriental regions (Morse 2013). Protoptilinae is the most diverse subfamily with 310 species (including 5 fossil spp.) and 17 genera (Holzenthal *et al*. 2007b, Morse 2013). The subfamily has a disjunct distribution (Fig. 1): 4 genera are known from the East Palaearctic and Oriental regions; the remaining 13 are restricted to the Nearctic and Neotropical regions (Morse 2013). Protoptilinae is the only glossosomatid subfamily to occur in the Neotropics, and it is there where the subfamily reaches its greatest diversity (280 species) and also exhibits a high degree of endemism at both the species and genus levels.

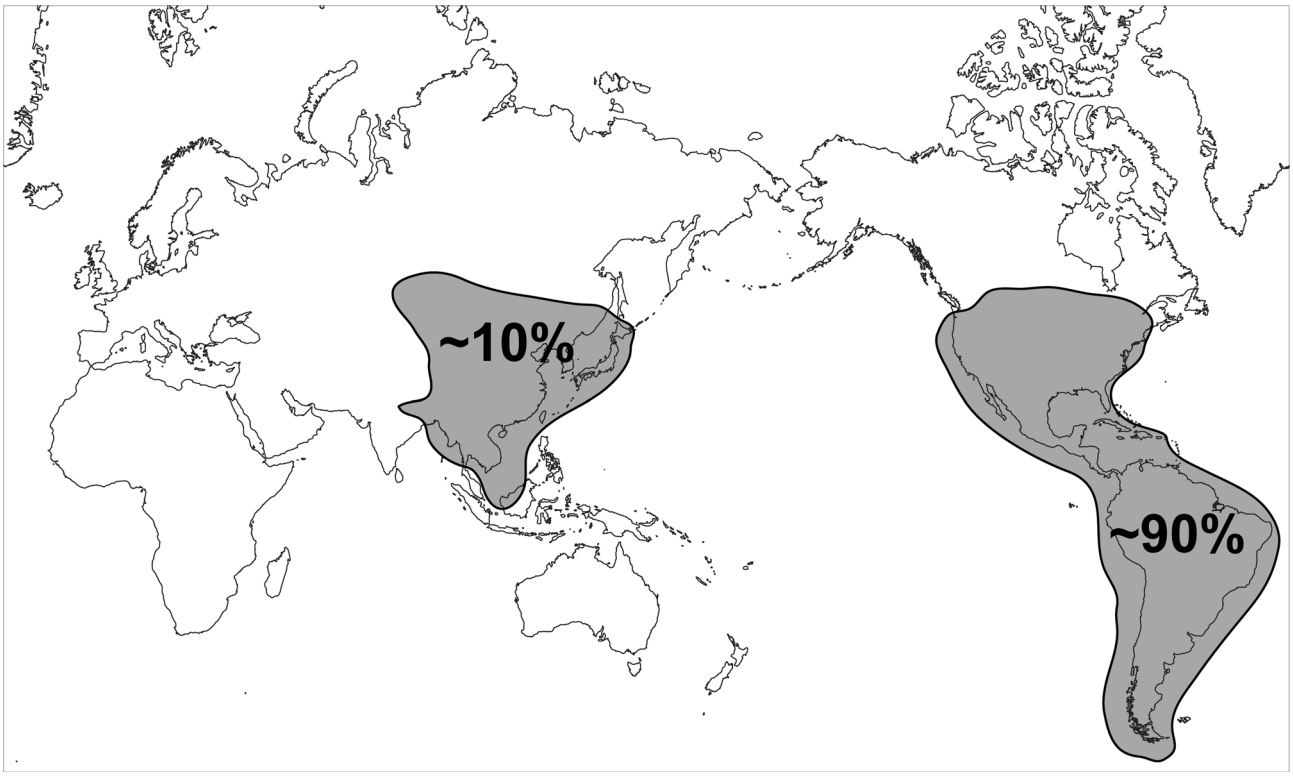

FIGURE 1. Approximate known distribution of Protoptilinae. The Neotropical region is the most diverse for this subfamily, with 280 out of 310 described species.

The objectives of this study were to 1) test the monophyly of Protoptilinae, 2) evaluate the monophyly of individual genera traditionally placed in Protoptilinae, and 3) infer relationships among genera. Additionally, homologies of morphological characters were assessed across genera and a standardized terminology for those structures was established. Generic boundaries were also delimited, resulting in new diagnoses and a key to the adults of world Protoptilinae. This was the first study to use modern cladistic and Bayesian methods in a

phylogenetic assessment of the subfamily, and was based on an analysis of 99 morphological characters and 80 taxa, representing all 17 known genera. Furthermore, it was the first comprehensive study of Protoptilinae to incorporate molecular data. Results of this study imparts taxonomic stability and clarifies classification, provides a new phylogenetic framework to place new species, and provides insight into current distribution patterns, historical biogeography, and the evolution of certain adaptations and life history traits.

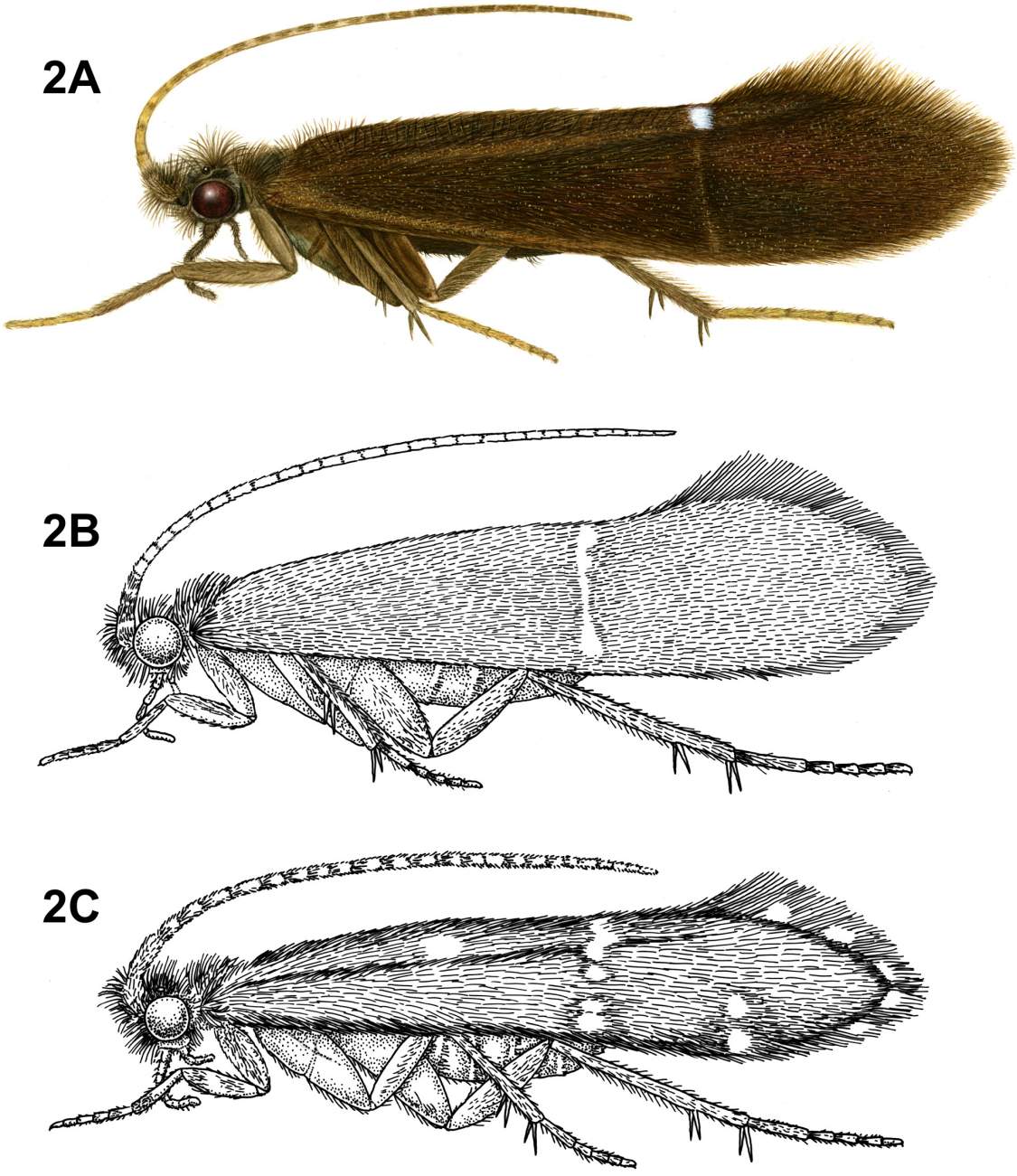

FIGURE 2. Adult. (A) *Itauara* species. (B) *Mortoniella* species. (C) *Protoptila* species.

General morphology and biology

Members of Protoptilinae are so minute (1.5–6.0 mm) that they were once thought to belong to Hydroptilidae, the microcaddisflies (Walker 1852). In general, adults have rather narrow wings, which are held "tent-like" at rest. Forewings have a long fringe of setae apically, and tend to be various shades of black or brown (Fig. 2A), although many species have conspicuous white transverse bars (Fig. 2B) or spots (Fig. 2C). Protoptilines have 3 ocelli (Fig. 5), 5-segmented maxillary palps (Fig. 6E), and setal warts on the head and thorax (Fig. 5). Wing venation varies

widely among and sometimes even within genera, although all protoptilines have a row of stout setae along the Cu2 vein in the forewing (Figs. 7–14) which perhaps acts as a wing coupling device in concert with a fringe of setae along the costal margin of the hind wing (Stocks 2010). There has been an extreme diversification of male genitalia, possibly the result of sexual selection (Ward & Pollard 2002). Structures of the female genitalia also vary throughout the subfamily, although differences are much more conserved and tend to be internal.

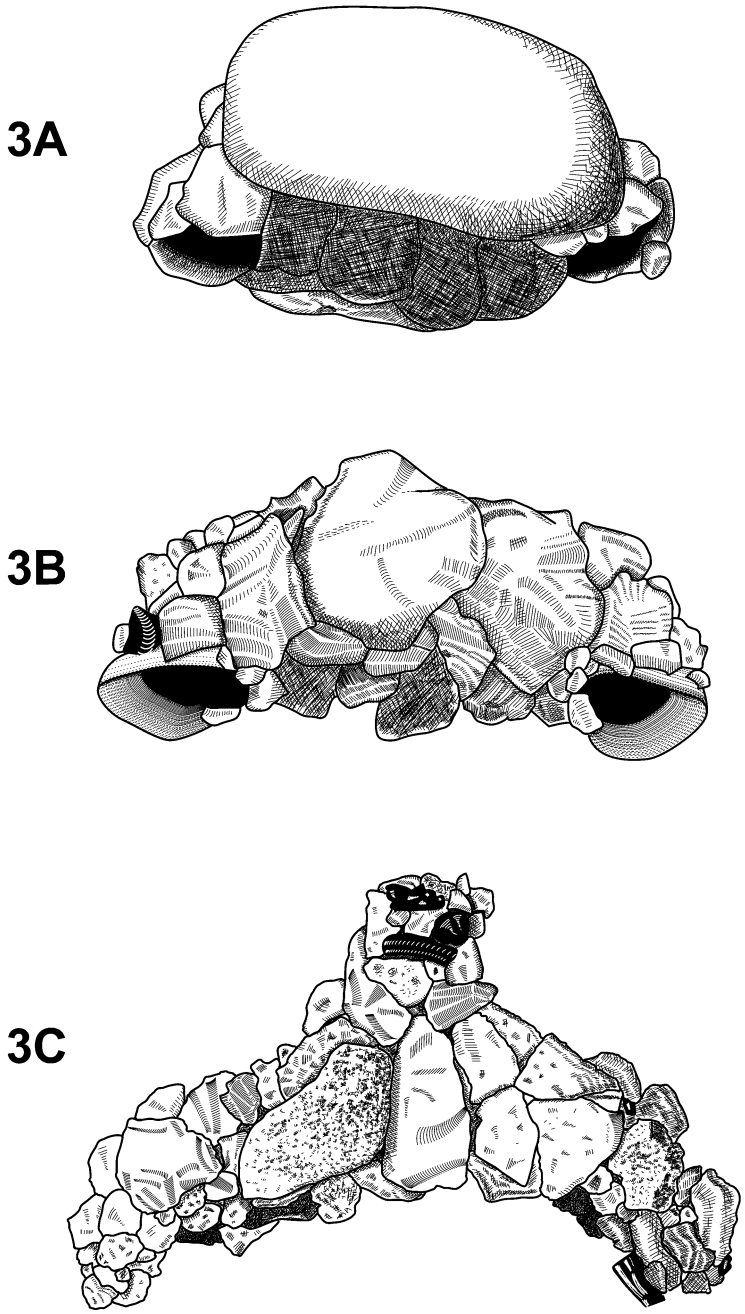

FIGURE 3. Larval cases. (A) *Protoptila* species. (B) *Culoptila moselyi* Denning. (C) *Culoptila unispina* Blahnik & Holzenthal. (Modified from Blahnik & Holzenthal 2006.)

Like other glossosomatid larvae, protoptilines graze on diatoms, periphyton, and fine organic particulates from the exposed surfaces of submerged rocks and other substrates (Wiggins 1996, 2004). Larvae are generally found in lotic habitats, with some species preferring large, warm rivers and others preferring small, cooler streams. Protoptiline larvae construct portable "tortoise" or "saddle" cases of small sand grains or pebbles, typical of other glossosomatids (Fig. 3) (Wiggins 1996, 2004). Within Protoptilinae, some slight variations occur to this basic case architecture. For example, *Culoptila unispina* Blahnik & Holzenthal, 2006, builds a more elongate case with a central open turret (Blahnik & Holzenthal 2006) (Fig. 3C). Other *Culoptila* species are known to construct partial

"collars" of silk fastened around the periphery of the anterior and posterior openings (Wiggins 1996). Cases of *Matrioptila jeanae* (Ross, 1938) and *Padunia alpina* Kagaya & Nozaki, 1998, tend to be slightly flattened dorsoventrally (Kagaya & Nozaki 1998, Wiggins 1996). Many species use rather uniformly sized pieces of fragments throughout the case, although species of *Protoptila* affix a larger stone on each side (Fig. 3A) (Wiggins 1996). Variation in the position of respiratory openings can be observed with some occurring on the dorsum near the posterior and anterior ends (Wiggins 1996), while in other species openings are irregularly spaced throughout the case (Flint 1964).

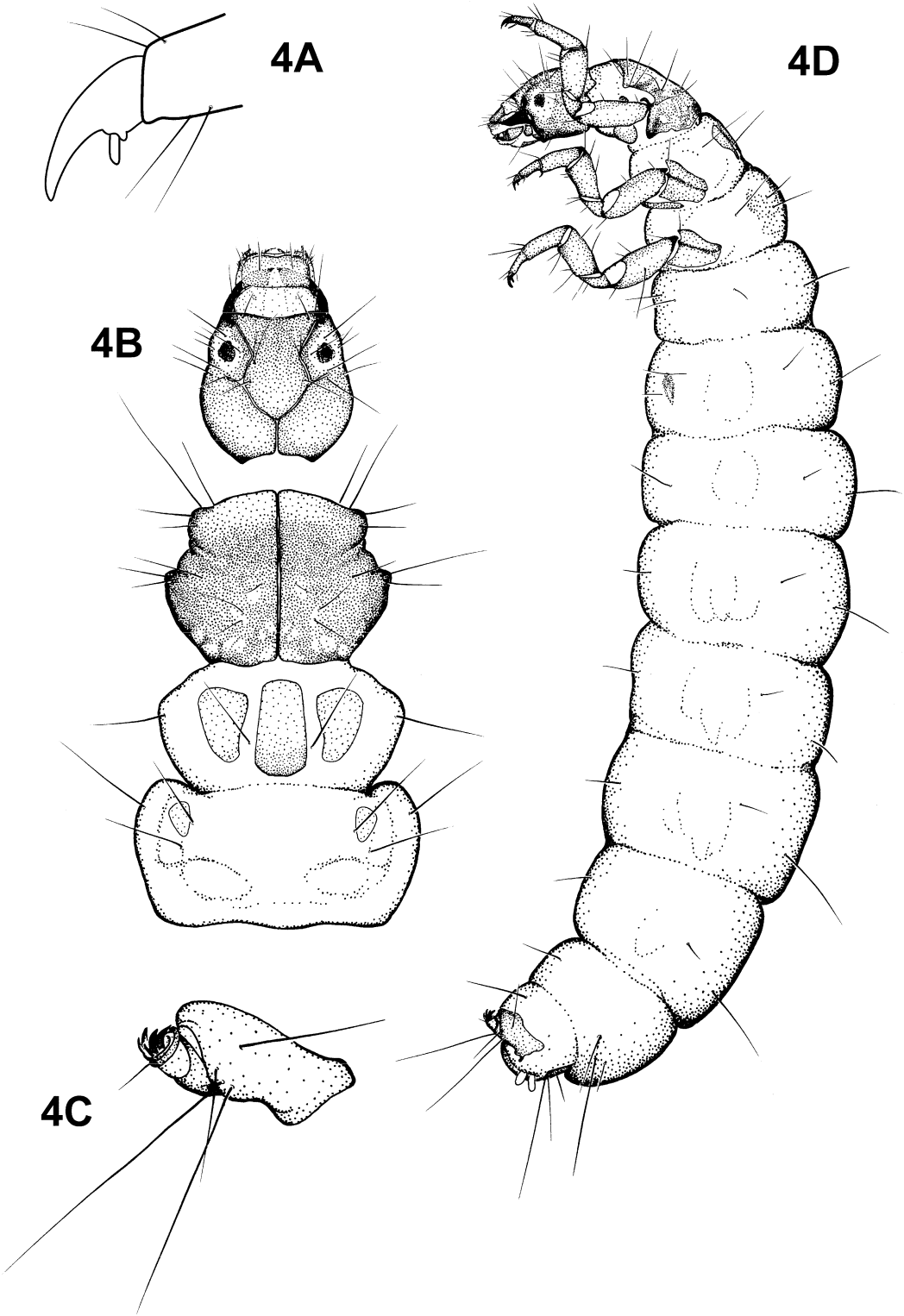

FIGURE 4. *Culoptila* species. (A) Metatarsal claw. (B) Head and thorax, dorsal. (C) Anal claw. (D) Larva, left lateral. (Figure modified from Holzenthal & Blahnik 2006.)

Glossosomatid larvae have hypognathous mouthparts adapted to grazing. The mandibles have a uniform scraping edge lacking separate teeth, and the labrum has a membranous fringe (Wiggins 1996, 2004). Other typical glossosomatid larval characteristics include a heavily sclerotized pronotum with prominent prosternal sclerites, a lack of abdominal gills, segment IX bearing a dorsal sclerite, and the basal half of the anal prolegs fused with the abdomen (Wiggins 2004). Protoptilinae larvae (Fig. 4) differ from other glossosomatids by having 1) a mesonotum with 3 sclerites, 2) a metanotum with 2 small sclerites, 3) a V-shaped ventral apotome on the head, and 4) anal proleg claws with 4 or more accessory hooks (Morse & Holzenthal 2008, Wiggins 1996). However, immature stages have been described for only just over half of the protoptiline genera, and within those genera, very few species are known. Therefore, it is impossible to know if these characteristics are typical for the subfamily, certain genera, or are species specific. Among protoptilines whose larvae are known, variation occurs in the shape of the tarsal claws, shape of the mesonotal sclerites, and the number of accessory hooks on the anal claws.

Taxonomic history and previous phylogenetic treatments of Protoptilinae

The first protoptiline species to be described, *Protoptila tenebrosa* (Walker, 1852), was described in *Hydroptila* (Hydroptilidae). Banks (1904) later described the genus *Protoptila* in Hydroptilidae, but he noted that it differed from most other hydroptilids by lacking erect hairs on the wings and having 4 tibial spurs on the mesothoracic legs. Mosely (1937) suggested that *Protoptila* might be better placed in Rhyacophilidae than Hydroptilidae. Consequently, Ross (1938) transferred *Protoptila* to Glossosomatinae, then a subfamily of Rhyacophilidae, based on similarities of the immature stages, a lack of setation on the abdomen, and the general structure of the male and female genitalia. Later, in a posthumous work, Mosely (1954) transferred from Hydroptilidae to Glossosomatinae *Antoptila* Mosely, 1939 (junior synonym of *Itauara* Müller, 1888); *Canoptila* Mosely, 1939; *Culoptila* Mosely, 1954; *Mexitrichia* Mosely, 1937 (junior synonym of *Mortoniella* Ulmer, 1906); and *Mortoniella* Ulmer, 1906. Mosely (1954) expressed his inclination to create a new subfamily within Rhyacophilidae to contain these "kindred" genera, but ultimately accepted the views of Ross (1938) and Ulmer (in a letter to Mosely partly quoted by Mosely 1954), that the immature stages of the *Protoptila* group showed a close relationship to Glossosomatinae. Subsequently, Ross (1956) elevated Glossosomatinae to family status and established Protoptilinae as a subfamily. Eventually, 2 other genera originally described in Hydroptilidae, *Padunia* Martynov, 1910, and *Scotiotrichia* Mosely, 1934, and another originally placed in Sericostomatidae, *Tolhuaca* Schmid, 1964, were transferred to Protoptilinae (Flint 1967b, Marshall 1979, Schmid 1958).

Historically, descriptions of new protoptiline species have tended to be rather regional in scope, and as a result, the taxonomic literature is somewhat scattered. Late 19th to early- through mid-20th century protoptiline workers included Müller: SE Brazil (1888, 1921); Ulmer: Ecuador (1906); Banks: United States (1904); Mosely: Argentina, Chile, SE Brazil, Mexico (1934, 1937, 1939, 1954); Martynov: Siberia (1910, 1929, 1934); Ross: United States: (1938, 1941, 1944, 1956); and Tsuda: Korea (1942). Contemporary workers have included Angrisano: Argentina, Uruguay (1993, 1997); Botosaneanu: Venezuela, Caribbean (1977, 1994, 1996, 1998); Bueno: Mexico (1983, 1984); Bueno & Santiago: Mexico (1979, 1996); Flint: Caribbean, North, Central & South America (1963, 1964, 1967a, 1968, 1971, 1974, 1981, 1983, 1991, 1992); Kagaya & Nozaki: Japan (1998); Kimmins: Nepal (1964); Kumanski: Cuba (1987); Malicky: Brunei (1995); Malicky & Chantaramongkol: Thailand (1992); Morse: United States (1988); Schmid: Argentina, Bolivia, Chile, India (Schmid 1958, 1959, 1964, 1990); Sykora: Bolivia, Cuba, Ecuador, Venezuela (Botosaneanu & Sykora 1973, Sykora 1999); Tian & Li: China (1986); and Wichard: Dominican amber fossils (Wichard 1989, 1995). Most recently, regional descriptions of protoptiline species have included works by Blahnik & Holzenthal: Central and South America (2006, 2008, 2011); Santos & Nessimian: Brazil (2009) Flint & Sykora: Dominican Republic (2004); Holzenthal: Chile (2004); Holzenthal & Blahnik: Costa Rica (2006); Rueda-Martín & Gibon: Argentina, Bolivia (2008); Malicky: Vietnam (2009); Malicky & Chantaramongkol: Thailand (2009, Malicky *et al*. 2006); Malicky & Silamon: Thailand (2012); Nishimoto & Nozaki: Japan (2007); Robertson & Holzenthal: Bolivia, Brazil, Guyana, Peru, Venezuela (2005, 2008, 2011); and Wichard: Dominican and Mexican amber fossils (2007, Wichard *et al*. 2006).

Very few published works exist regarding phylogenetic relationships among Protoptilinae genera. Ross (1956) provided 1 of the earliest reviews of the subfamily in which he proposed 2 major protoptiline lineages. Noting the ancestral features of *Matrioptila* (a monotypic genus from North America), Ross (1956) believed the genus represented the "first discovered step in protoptiline evolution" and eventually gave rise to the more widespread

Antoptila lineage in the Neotropics, culminating in *Protoptila*. Schmid (1990) discussed possible relationships between the Asian and American genera, concluding that it was impossible to determine from which continent the subfamily originated. Morse & Yang (1993) provided a useful table summarizing the wing venation of 15 protoptiline genera. They also listed the following putative synapomorphies of Protoptilinae: 1) larval tarsal claw seta beside tarsal claw process, 2) larvae with 4 accessory hooks on anal claw, 3) adult foretibial spur absent, 4) forewing fork V absent, and 5) forewing crossveins aligned (Morse & Yang 1993). Five comprehensive revisions of individual protoptiline genera have been published, treating a total of 82 species. These revisions included discussions of possible phylogenetic relationships among genera. Blahnik & Holzenthal revised *Culoptila* (2006) and the Mexican and Central American species of *Mortoniella* (2008). Robertson & Holzenthal revised the genera *Tolhuaca* (2005), *Canoptila* (2006), and *Itauara* (2011). In a higher-level phylogenetic analysis of Trichoptera, Kjer *et al.* (2001) recovered a monophyletic Protoptilinae, although only 2 genera were represented. In another study, with 3 Protoptilinae genera represented, Kjer *et al.* (2007) again found a monophyletic Protoptilinae with the 2 Neotropical representatives, *Culoptila* and *Protoptila* forming a clade. Holzenthal *et al.* (2007a) recovered *Matrioptila* as sister to a monophyletic Neotropical clade. Apart from these works, neither a further phylogenetic assessment of the subfamily nor a phylogeny have ever been published.

Overview of traditionally recognized genera of Protoptilinae

The following account is an overview of the historically recognized genera of Protoptilinae. The reader is directed to the section, "A phylogenetic framework for classification and diagnoses" (under Conclusions) for information regarding a revised taxonomic classification of the genera of Protoptiline based on the results of this research. Unless mentioned, immature stages and biology are unknown.

Campsiophora Flint, 1964

Four species for this genus are known, 1 each from Puerto Rico, Jamaica, Cuba, and quite curiously, Thailand. Flint (1964) remarked that *Campsiophora* was probably related to *Culoptila* and *Cariboptila* because of similarities in the male genitalia but established it as a new genus based on differences in wing venation, lack of enlarged tegulae, and the presence of a hair pencil in the forewing. Malicky & Silalom (2012) recently described a new monotypic genus, reportedly from Thailand, *Muanpaipsyche areopagita*. However, after comparing figures given by Malicky & Silamon (2012) with those of Flint (1964), we communicated to Dr. Malicky that this new genus was almost certainly *Campsiophora pedophila* because of nearly identical male genitalia and wing venation. Malicky later synonomized the genus, but retained the species (Malicky 2013). Larvae and pupae of *Campsiophora* are known to occur in large numbers on rocks in riffles of large lowland rivers and perhaps in smaller numbers in small mountain streams (Flint 1964, 1968). Larvae construct typical tortoise-shaped cases (Flint 1964, 1968). Females have been described for the 3 Caribbean species (Flint 1964, 1968).

Canoptila Mosely, 1939

Two species are described for this genus from the Atlantic Forest of southeastern Brazil. Mosely (1939) established *Canoptila* from a single species in Hydroptilidae, based on wing venation and male genitalic features, but later (Mosely 1954) transferred it to the *Protoptila* group of Glossosomatinae, then a subfamily within Rhyacophilidae. Putative synapomorphies supporting the monophyly of the genus include: 1) the presence of long, spine-like, posterolateral processes on tergum X, 2) the highly membranous digitate parameres on the endotheca, and 3) the unique combination of both forewing and hind wing venational features (Robertson & Holzenthal 2006). Robertson & Holzenthal (2006) suggested that *Canoptila* was most closely related to the more derived protoptiline genera based on structures of the mesothorax and wing venation. The immature stages and biology are unknown. The female was described for *Canoptila williami* Robertson & Holzenthal, 2006.

Cariboptila Flint 1964

Eleven species of *Cariboptila* are known from Cuba, Dominican Republic, Jamaica, and Puerto Rico. Flint (1964) noted similarities to *Culoptila* and *Campsiophora*, but established *Cariboptila* as a new genus based on differences in wing venation, lack of enlarged tegulae, and lack of a hair pencil on the forewing. Larvae construct typical tortoise-shaped cases (Flint 1964, 1968). Larvae and pupae are found on stones in small, clear, cool streams

at higher elevations (Flint 1964, 1968). Females have been described for several species (Botosaneanu 1996, Flint & Sykora 2004).

Cubanoptila Sykora, 1973, in Botosaneanu & Sykora 1973

Five extant species have been described from Cuba, and a single species was described from Jamaica. Sykora (in Botosaneanu & Sykora 1973) distinguished *Cubanoptila* from other genera based on features of the male antennae, the structure of tergum VIII, and wing venation. Sykora (in Botosaneanu & Sykora 1973) also noted similarities in forewing venation to *Culoptila* and hind wing venation to some species of *Protoptila*. Immature stages and females have been described for several species (Botosaneanu & Sykora 1973, Botosaneanu 1977, 1998). Four fossil species are known from Miocene amber from the Dominican Republic: *C. grimaldii* Wichard, 1995; *C. longiscapa* Wichard, 2007; *C. mederi* Wichard, 1989; and *C. poinari* Wichard, 1989.

Culoptila Mosely, 1954

This genus contains 26 extant species, and is mostly endemic to Mexico and Central America, although several species occur in the southwestern United States and 1 in the eastern United States. Mosely (1954) first established *Culoptila* within the *Protoptila* group of Glossosomatinae, then a subfamily of Rhyacophilidae. He distinguished the genus based on the unusually enlarged male tegulae and associated concertina-shaped glandular structures, and differences in wing venation and male genitalic features (Mosely 1954). Blahnik & Holzenthal (2006) remarked in their recent revision that the genus probably is most closely related to the endemic Caribbean genera *Campsiophora*, *Cariboptila*, and *Cubanoptila*. Immature stages and females are known for several species (Blahnik & Holzenthal 2006). *Culoptila* spp. construct typical tortoise-shaped cases of small grains of sand or with larger lateral stones and are known to occur in large rivers, as well as small springs and seepages (Blahnik & Holzenthal 2006; Houghton & Stewart 1998a, 1998b; Wiggins 1996). Houghton & Stewart (1998a, 1998b) provided details of life history and case building behavior. A single fossil species, *C. aguilerai* Wichard, 2006, was described from Miocene amber from Chiapas, Mexico.

Itauara Müller, 1888

Itauara contains 22 species and is known from Argentina, Brazil, Guyana, Peru, and Venezuela (Robertson & Holzenthal 2011). Müller (1888) first used the name *Itauara* without any included species or illustrations but in a later work (Müller 1921) provided sketches of the female forewing venation and some larval parts. Based on similarities in wing venation and of cases and larval parts, Flint *et al*. (1999) made *Antoptila* a synonym of *Itauara*, designated *A. brasiliana* (Mosely, 1939) as the type species, and transferred the 3 other known species of *Antoptila* to *Itauara*. Ross (1956) suggested that *Itauara* (then *Antoptila*) represented a point at the base of a lineage culminating in *Protoptila*. In our recent revision of the genus, we determined the homologies and established standardized terminology of the male genitalic structures among species (Robertson & Holzenthal 2011). Angrisano (1993) described the immature stages and female of the type species and females of *I. guarani* (Angrisanno, 1993) and *I. plaumanni* (Flint, 1974). Larvae construct typical tortoise-shaped cases of large and small grains of sand and are known to occur in sandy bottom streams with scarce vegetation where they attach their cases to Characeae algae (Angrisano 1993).

Mastigoptila Flint, 1967

Mastigoptila contains 9 species, all of which are endemic to Chile. Flint (1967b) established *Mastigoptila* as a new genus based on differences in wing venation and the asymmetrical form of the male genitalia. Valverde & Miserendino (1998) provided details of the immature stages and biology of *M. longicornuta* (Schmid, 1958). Although female allotypes have been designated for 3 species, none have been described.

Matrioptila Ross, 1956

This monotypic genus is restricted to the Appalachian Mountains of the southeastern United States. Its sole species, *Matrioptila jeanae* (Ross, 1938) was originally placed in *Protoptila*. Ross (1956) established *Matrioptila* as a new genus based on wing venational features and the presence of distinct claspers in the male genitalia. He suggested that it represented an archaic genus at the base of protoptiline evolution. Ross (1938) described the female, and Flint (1962) and Wiggins (1996) described the immature stages and discussed biology. *Matrioptila* is known to occur in cold, clear, rapid mountain streams.

Merionoptila Schmid, 1959

This genus contains a single species, *Merionoptila wygodzinskyi* Schmid, 1959, known from northern Argentina. Schmid (1959) established the genus based on its rather unusual morphology. *Merionoptila* has a large head, bulky thorax, hairy eyes, very long and hairy legs, and a relatively reduced abdomen (Schmid 1959). Additionally, the wings and venation of the male are extremely reduced while the female is completely brachypterous (Schmid 1959). As discussed by Schmid (1959), *Merionoptila* has been observed "skating" on the surface of small streams and he noted similarity of morphological features with those of other surface skaters, most notably *Anomalopteryx* Stein, 1874 (=*Anomalopterygella* Fischer, 1966), and *Limnoecetis tanganicae* Marlier, 1955. Although Schmid (1959) recognized that *Merionoptila* belonged in Protoptilinae, he admitted that its placement within the subfamily was difficult to determine since the subfamily was poorly known at the time. Nonetheless, he suggested that *Merionoptila* was more closely related to *Antoptila* (=*Itauara*) than the other known protoptiline genera (Schmid 1959).

Mortoniella Ulmer, 1906

Mortoniella is the largest genus in the subfamily with 97 described species from Mexico, Central, and South America. Ulmer (1906) first established *Mortoniella* in Hydroptilidae for a single species, *M. bilineata* Ulmer, 1906, from Ecuador. Mosely (1937) later described an additional genus, *Mexitrichia*, for a species from Mexico. Although he noted similarity between the 2 genera, Mosely (1937) differentiated *Mexitrichia* from *Mortoniella* based on its absence of apical fork V in the hind wing and what he considered to be important male genitalic differences. Historically, *Mortoniella* consisted of species from South America, and was more narrowly defined than *Mexitrichia*, whose members were known from Mexico and Central America. In subsequent works, other authors (Flint 1963, Sykora 1999) continued to recognize the 2 as distinct genera based on their apparent differences in hind wing venation, male genitalia, and immature stages. However, Blahnik & Holzenthal (2008) determined that *Mortoniella*, as historically defined, was based on a plesiomorphic wing character, and therefore did not adequately meet the principal of reciprocal monophyly by modern cladistic standards. Additionally, they attested that the male genitalia of *Mexitrichia* and *Mortoniella* were very similar (Blahnik & Holzenthal 2008). Consequently, the 2 genera were synonomized and species originally placed in *Mexitrichia* were transferred to *Mortoniella* (Blahnik & Holzenthal 2008). Immature stages and females have been described for a few species (*e.g.*, Blahnik & Holzenthal 2008, Botosaneanu & Alkins-Koo 1993, Flint 1963). Larvae are known to occur in fast flowing rivers and streams (Flint 1963).

Nepaloptila Kimmins, 1964

This genus consists of 4 species and is known from Nepal and Thailand. Kimmins (1964) remarked that the type species resembled a small *Agapetus* but placed it in Protoptilinae based on its absence of mesoscutellar warts, presence of rounded warts on the mesoscutum, and presence of stout setae on Cu2 in the forewing. Kimmins (1964) noted similarities in wing venation and male genitalia to *Matrioptila* but suggested *Nepaloptila* had more primitive features because of its retention of apical fork V in the forewing. Female paratypes were designated for *N. ruangjod* Malicky & Chantaramongkol, 1992, but were neither illustrated nor described.

Padunia Martynov, 1910

Padunia contains 16 species and is known from eastern and central Siberia, Mongolia, Japan, Korea, Thailand, and Vietnam. Martynov (1910) originally described the genus in Hydroptilidae based on the wing venation of the females of *P. adelungi* Martynov, 1910, and remarked that the genus was probably related (although not closely) to *Agraylea* Curtis, 1834, and *Mortoniella*. Martynov (1929) later provided an illustration of the male genitalia from the type species and the genitalia and head of *P. lepnevae* Martynov, 1929. Subsequently, Tsuda (1942) described a new genus, *Uenotrichia* in Hydroptilidae, which Fischer (1971) later mistakenly elevated as a senior synonym to *Padunia*. Interestingly, Ulmer (in a letter to Mosely partly quoted by Mosely 1954) and Mosely (1954) suggested that *Padunia* might in fact belong to the "*Protoptila* group," but did not transfer it at the time. However, in her revision of the family Hydroptilidae, Marshall (1979) determined that the genus belongs to the Protoptilinae within Glossosomatidae based on similarities of the thorax, male genitalia, and wing venation to *Matrioptila* and *Nepaloptila*. Additionally, she correctly identified *Padunia* as the senior synonym to *Uenotrichia* based on date priority (Marshall 1979). Kagaya & Nozaki (1998) described the female and provided details of immature stages

and biology of Japanese *Padunia*. Larvae construct tortoise-shaped cases that are somewhat flattened dorsoventrally, and live in cold mountain streams (Kagaya & Nozaki 1998).

Poeciloptila Schmid, 1991 [1990]

Poeciloptila is comprised of 7 species and is known from China, India, and Thailand. Schmid (1990) first established the genus based on features of the male genitalia, including: 1) membranous lateral faces of the Xth segment, and 2) a large ventral branch of the phallic apparatus. As for its position within Protoptilinae, Schmid stated simply, "Il n'est pas spécialement apparenté à *Nepaloptila*." ["It is not especially related to *Nepaloptia.*" Translation from Schmid 1990]. Although Schmid (1990) designated female allotypes and paratypes for 2 species, he did not describe or illustrate the specimens.

Protoptila Banks, 1904

Protoptila currently contains 95 described species and has a distribution ranging from Canada through South America. Banks (1904) originally described the genus in Hydroptilidae; however, he noted that it differed from most hydroptilids by lacking erect hairs on the wings and having 4 tibial spurs on the mesothoracic legs. Mosely (1937) suggested that species of *Protoptila* might be more closely related to those of Glossosomatinae than Hydroptilidae. Subsequently, Ross (1938) transferred *Protoptila* to Glossosomatinae, then a subfamily of Rhyacophilidae. Morse (1988) and Blahnik & Holzenthal (2006) interpreted and homologized structures of the male genitalia. Distinctive features of the genus include: 1) an enlarged, flattened, phallic apodeme, and 2) a posteriorly projecting sternum VIII (Holzenthal & Blahnik 2006). Blahnik & Holzenthal (2008) suggested *Protoptila* was the likely sister taxon to *Mortoniella* because both have short, articulated, rod-like appendages arising from the posteroventral margin of the phallobase that fit into modified pockets. Immature stages and females have been described for several species (Ross 1944, Wiggins 1996). Larvae build typical tortoise-shaped cases, often with a large stone positioned on each side (Wiggins 1996). They are known to occur in clear, forested streams, but are particularly abundant in warm, lowland rivers (Holzenthal & Blahnik 2006, Flint 1968).

Scotiotrichia Mosely, 1934

This genus contains a single species, *Scotiotrichia ocreata* Mosely, 1934, and is known from Bariloche, Argentina, and adjoining areas in Chile. Mosely (1934) originally established the genus in Hydroptilidae, but noted that its wing venation was much more complete than typically found in the family. Schmid (1958) later transferred the genus to Protoptilinae. The female has not been described.

Temburongpsyche Malicky, 1995

The genus is known from a single species, *Temburongpsyche anakan* Malicky, 1995, from Brunei. Malicky (1995) commented that the wing venation of *Temburongpsyche* matches that of *Padunia* and agrees with *Poeciloptila*. He also noted that the dorsal warts on the head and thorax correspond to those of *Nepaloptila* (Malicky 1995). Nonetheless, Malicky (1995) established *Temburongpsyche* as a new genus based on several derived features of the male. These include 1) a broad, ring-like segment IX, 2) reduction of "various appendices" along the posterior margin of segment IX, 3) an "enormously large and thick phallus," and 4) a tibial spur formula of 0,3,3. Malicky (1995) illustrated the female genitalia.

Tolhuaca Schmid, 1964

Tolhuaca contains 2 species, 1 known from Chile, the other from southeastern Brazil. Schmid (1964) originally placed the genus in Sericostomatidae, commenting on the similarity of the male genitalia to those of Brachycentrinae, at that time a subfamily within Sericostomatidae. Later, Flint (1967) transferred *Tolhuaca* to Protoptilinae, noting that the wing figures in the original description were transposed with those of *Austrocentrus griseus* Schmid, 1964 (Helicophidae). Schmid (1964) remarked that although *Tolhuaca* has complete wing venation, a primitive feature of Trichoptera, the male genitalia are very simple and derived, thus "…it is impossible to assign a phyletic position to the genus." However, Robertson & Holzenthal (2005) determined that *Tolhuaca* deserves a basal placement in Protoptilinae based on its retention of the foretibial spur, presence of mesoscutellar setal warts, and the oviscapt structure of the female genitalia.

MATERIAL AND METHODS

Selection of Taxa

The taxa included in this study were chosen in an attempt to represent the overall morphological and taxonomic diversity of each genus within the subfamily Protoptilinae. Additionally, the taxa selected represented all biogeographical regions where Protoptilinae is known to occur. Head, thoracic, wing venation, and male genitalic characters are based on observations of individual species rather than groups of species or higher taxa (Prendini 2001). When possible, multiple specimens of the same species were examined to account for possible intraspecific variation. Therefore, the material examined, listed in Table 1, includes for each species the name of the species, country localities, and number of specimens examined. Composite coding (Maddison 1993) was used for a single, family-level larval character and 3 female genitalic characters (discussed further under the section *Characters and states for cladistic analysis*). Larval descriptions are unavailable for most protoptiline species; however, based on the absence of exceptions among known species, all Glossosomatidae species probably build portable "tortoise" or "saddle"-shaped cases (Wiggins 1996, 2004). Descriptions of female genitalic morphology also are limited among Protoptilinae species. Morphology of the female genitalia is highly conserved at the generic level and above, with species differentiated by the shape of internal structures of the vaginal apparatus. The female genitalic characters chosen for this analysis are especially conserved and therefore composite taxon coding was used when females of certain species were unknown. In such cases, the data used to code a particular species may be based on a closely related species from the same biogeographic region where the female has been positively associated with the male (Table 2). A list of specimens used for DNA sequencing, including individual museum accession numbers and BOLD Barcode index numbers (BIN), is presented in Table 3.

TABLE 1. Material examined for phylogenetic analyses. For each species, the country locality, number of specimens examined, and type status. Numbers after species of *Itauara* and *Mortoniella* refer to accessions in database.

Species	Country	# Specimens	Type
Ptilocolepus granulatus	Austria, Switzerland	2	–
Anagapetus debilis	United States	2	–
Glossosoma alascense	United States	2	–
Glossosoma intermedium	United States	2	–
Agapetus rossi	United States	2	–
Agapetus species (Australia)	Australia	1	–
Tolhuaca cupulifera	Chile	8	Holotype
Tolhuaca brasiliensis	Brazil	3	Holotype
Nepaloptila coei	Nepal	1	Holotype
Nepaloptila kanikar	Thailand	3	Paratype
Nepaloptila jisunted	Thailand	1	Paratype
Nepaloptila ruangjod	Thailand	1	Paratype
Matrioptila jeanae	United States	4	–
Padunia adelungi	Mongolia	8	–
Padunia alpina	Japan	2	Paratype
Padunia forcipata	Japan	4	–
Padunia burebista	Thailand	2	Paratype
Padunia lepnevae	Russia	1	–
Padunia karaked	Thailand	4	Paratype
Poeciloptila atyalpa	India	2	Holotype
Poeciloptila falcata	India	2	Holotype
Poeciloptila briatec	Thailand	3	Paratype

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TABLE 1. (Continued)

Species	Country	# Specimens	Type
Poeciloptila maculata	China	1	–
Temburongpsyche anaken	Brunei	1	Paratype
Scotiotrichia ocreata	Argentina	4	Holotype
Merionoptila wygodzinskyi	Argentina	2	Holotype
Campsiophora pedophila	Puerto Rico	4	Paratype
Campsiophora arawak	Jamaica	4	Paratype
Campsiophora mulata	Cuba	3	Paratype
Cariboptila aurulenta	Dominican Republic	3	Paratype
Cariboptila caab	Dominican Republic	7	Paratype
Cariboptila hispanolica	Dominican Republic	8	Paratype
Cariboptila jamaicensis	Jamaica	3	Paratype
Cariboptila orophila	Puerto Rico	4	Paratype
Cubanoptila botosaneanui	Cuba	3	Paratype
Cubanoptila cubana	Cuba	9	Paratype
Cubanoptila muybonita	Cuba	4	Paratype
Cubanoptila purpurea	Cuba	5	Paratype
Culoptila cascada	Costa Rica	3	Holotype
Culoptila hamata	Costa Rica	3	Holotype
Culoptila thoracica	United States	3	–
Canoptila bifida	Brazil	3	Holotype
Canoptila williami	Brazil	9	Holotype
Itauara brasiliana	Brazil	10+	Holotype
Itauara guarani	Argentina	4	Holotype
Itauara plaumanni	Brazil	4	Holotype
Itauara amazonica	Brazil	6	Holotype
Itauara blahniki	Brazil	3	–
Itauara emilia	Brazil	1	–
Itauara rodmani	Brazil	4	–
Itauara julia	Brazil	10+	–
Itauara simplex	Brazil	2	–
Itauara tusci	Brazil	10+	–
Itauara flinti	Brazil	1	–
Itauara jamesii	Brazil	1	–
Itauara charlotta	Brazil	1	–
Itauara alexanderi	Brazil	1	–
Itauara stella	Brazil	3	–
Itauara lucinda	Brazil	2	–
Itauara unidentata	Guyana	3	–
Itauara bidentata	Guyana	2	–
Itauara guyanensis	Guyana	4	–
Itauara ovis	Guyana, Venezuela	6	–
Itauara peruensis	Peru	6	–

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TABLE 1. (Continued)

Species	Country	# Specimens	Type
Mastigoptila bicornuta	Chile	2	Holotype
Mastigoptila longicornuta	Chile	4	Holotype
Mastigoptila ruizi	Chile	4	Holotype
Mortoniella elongata	Colombia	3	–
Mortoniella limona	Venezuela	3	–
Mortoniella meralda	Costa Rica, Mexico	4	–
Mortoniella teutona	Brazil	4	–
Mortoniella bilineata	Ecuador	4	–
Mortoniella denticulata	Venezuela	4	–
Mortoniella roldani	Colombia	4	–
Mortoniella marini	Bolivia	10+	–
Mortoniella eduardoi	Bolivia	2	–
Mortoniella froehlichi	Brazil	4	–
Protoptila maculata	United States	4	–
Protoptila bribri	Costa Rica	4	Holotype
Protoptila diablita	Bolivia	10+	Holotype

TABLE 2. List of taxa for which female data were unavailable. For each species, the composite taxon used is listed.

Species	Composite taxon
Poeciloptila briatec	*Poeciloptila atyalpa*
Poeciloptila maculata	*Poeciloptila atyalpa*
Canoptila bifida	*Canoptila williami*
Itauara emilia	*Itauara stella*
Itauara flinti	*Itauara simplex*
Itauara jamesii	*Itauara stella*
Itauara charlotta	*Itauara simplex*
Itauara alexanderi	*Itauara stella*
Itauara ovis	*Itauara guyanensis*

Ingroup. The ingroup, Protoptilinae, included 74 species representing all 17 traditionally recognized genera in the subfamily. At least 3 species were chosen from each genus to represent morphological diversity. For monotypic genera or those with only 2 included species, all species were studied. These included *Matrioptila jeanae* (SE USA); *Scotiotrichia ocreata* (Argentina); *Temburongpsyche anakan* Malicky, 1995 (Brunei); *Merionoptila wygodzinskyi* (Argentina); *Canoptila bifida* Mosely, 1939, and *C. williami* (SE Brazil); and *Tolhuaca cupulifera* Schmid, 1964 (Chile) and *T. brasiliensis* Robertson & Holzenthal, 2005 (SE Brazil). *Mortoniella* was sampled more rigorously than other genera (10 species) to account for its high species richness, morphological diversity, and wide distribution across the Neotropics. Additionally, a total of 21 *Itauara* species (including 17 recently described species) were sampled to test the monophyly of the genus.

Outgroup. The outgroup consisted of 6 species, including representatives of Hydroptilidae and the 2 other subfamilies in Glossosomatidae, Glossosomatinae and Agapetinae. Taxa were chosen to represent the major lineages of each subfamily. Additionally, we examined several species of Rhyacophilidae but omitted them from the analysis because many male genitalic and wing venational features were too divergent to polarize states within Protoptilinae.

TABLE 3. List of specimens sequenced for DNA and associated University of Minnesota Insect Collection (UMSP) accession numbers and University of Guelph BOLD Barcode Index Numbers (BIN), when applicable.

Species	UMSP accession number	BOLD BIN
Agapetus species (Australia)	UMSP000116850	AAJ7155
Anagapetus debilis	UMSP000084345	AAE5949
Cariboptila caab	UMSP000210889	AAK2843
Cariboptila hispanolica	UMSP000210890	AAR6920
Cubanoptila botosaneanui	UMSP000124342	AAR4874
Cariboptila aurulenta	UMSP000210891	AAW4343
Culoptila hamata	UMSP000000468	AAR5515
Glossosoma alascense	UMSP000210874	–
Glossosoma intermedium	UMSP000208799	AAA9475
Itauara rodmani	UMSP000081856	AAW9092
Itauara julia	UMSP000082824	AAW9094
Itauara tusci	UMSP000070956	AAW9093
Mastigoptila bicornuta	UMSP000210870	AAK7595
Mastigoptila longicornuta	UMSP000084060	AAJ1575
Mastigoptila ruizi	UMSP000210822	AAF1190
Matrioptila jeanae	UMSP000039624	–
Mortoniella marini	UMSP000210892	AAX4548
Mortoniella eduardoi	UMSP000210893	AAX4546
Mortoniella limona	UMSP000073459	AAE4529
Mortoniella teutona	UMSP000085401	AAG1493
Mortoniella froehlichi	UMSP000086603	AAX4547
Mortoniella roldani	UMSP000041301	AAE4524
Padunia lepnevae	UMSP000107053	AAX1887
Protoptila diablita	UMSP000210895	AAX8582
Tolhuaca cupulifera	UMSP000115152	AAK2072

Depositories

Material examined for this study is deposited at The Natural History Museum, London, UK (BMNH); National Museum of Natural History, Washington, DC, USA (NMNH), Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada (CNC); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenas Aires, Argentina (MACN), University of Minnesota Insect Collection, Saint Paul, USA (UMSP), and Universiteit van Amsterdam, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam, The Netherlands (ZMUA). Additionally, Dr. Hans Malicky, Lunz am See, Austria, generously donated several specimens from his private collection to UMSP. All specimens or lots of alcohol specimens examined in this study were affixed with a barcode label with a unique 9 digit alphanumeric code starting with the prefix UMSP. This prefix indicates that the specimen has been databased at UMSP, but it is not meant to imply possession by UMSP. Specimen-level taxonomic, locality, and other information, are stored in the University of Minnesota Insect Collection Biota Trichoptera Database using the software program Biota (Colwell 2003).

Morphology

Specimen preparation and observation

To observe certain structural features of the male and female genitalia, soft tissues were cleared using a lactic acid method outlined in detail by Holzenthal & Anderson (2004) and Blahnik *et al*. (2007). For some specimens,

the entire individual was cleared (after removing the wings) to more easily observe external structures obscured by setae, such as thoracic warts. Specimens that were over-cleared or lightly sclerotized were stained. Such specimens were immersed in a small watch-glass containing Chlorazole Black E (Sigma Chemical Co.) dissolved in glycerin for 15 minutes to several hours, depending on the size and condition of the specimen. Stained specimens were then rinsed in distilled water to remove any excess stain. Specimens were examined in a small watch-glass containing glycerin using an Olympus SZX12 dissecting microscope or Olympus BX41 compound microscope. To observe wing venation, wing mounts of each species were prepared following the protocols of Blahnik & Holzenthal (2004). Wing preparations were then digitally photographed using a Leica EC3 digital camera mounted on an Olympus SZX12 dissecting microscope. Digital images will be made available through Morphbank (www.morphbank.net).

Morphological terminology

Morphological terminology for male and female genitalia was adapted from Blahnik & Holzenthal (2006, 2008), Holzenthal (2004), Holzenthal & Blahnik (2006), Morse (1988), Nielson (1957, 1980), Nishimoto & Nozaki (2007), and Schmid (1990). Terminology for head, thoracic, and leg morphology follows that of Wiggins (1996). Wing venation terminology follows the Comstock-Needham system as interpreted by Ross (1956) and Schmid (1998).

Character sources and assessment

Most of the 99 morphological characters in this analysis are novel. However, some characters have been previously discussed in a phylogenetic context or analysis of other Trichoptera taxa in the literature. Sources where certain characters were previously coded and used in a phylogenetic analysis are listed after each character under the section "*Characters and states for cladistic analysis."* Characters previously discussed in the literature in a phylogenetic analysis or assessment, but modified, reinterpreted, and coded to fulfill the purposes of this analysis, are noted by stating "in part" after the source.

Each character was evaluated in terms of ability to be interpreted and scored consistently and in terms of whether it is shared uniquely by 2 or more taxa. Characters were included in the analysis if their states could be discretely delimited and clearly determined based on a point of reference (*e.g.*, characters 3, 8). Characters demonstrating continuous variation (*e.g.*, wing length) or inconsistent scoring among taxa (*e.g.*, wing color) were not used. Although not necessarily parsimony-informative, autapomorphic or constant characters were included in the character matrix because they are potentially informative at higher taxonomic levels.

Character coding

Character coding and homology assessment have strong implications for reconstructing phylogeny (Hawkins *et al*. 1997, Lee & Bryant 1999). Ideally, coding should reflect one's observations and determinations of homologies of structures. In this study, characters were determined based on primary homology and confirmed through character congruence (Patterson 1982). The criteria for the determination of primary homology include similarity in position (topological connections), similarity in composition, and linkage by intermediate forms (transformation series) (Remane 1952). However, sometimes structures hypothesized to be homologous have diverged so greatly that they are absent in some taxa. Characters related to the details of a structure would be inapplicable for taxa in which the structure is missing. This creates a challenge for coding those characters since coding depends on assumptions of primary homology assessments, character independence, and hierarchical relationships between characters (Hawkins *et al*. 1997, Lee & Bryant 1999, Strong & Lipscomb 1999). Many different coding approaches have been proposed to deal with inapplicable characters including reductive, composite (multistate), non-additive binary, and presence-absence coding, among others (Hawkins *et al*. 1997, Lee & Bryant 1999, Maddison 1993, Pleijel 1995, Strong & Lipscomb 1999).

To address inapplicable data in this study, reductive coding was used. A character was first coded to account for the presence or absence of a particular feature and additional character(s) were coded to address variations of the feature. Taxa coded as absent for the first character were assigned a dash ("–") for subsequent inapplicable characters. Although the program PAUP* does not distinguish a dash from a question mark (? = missing data), but treats both as one of the other existing states (Strong & Lipscomb 1999), a dash has been assigned to indicate that the character is inapplicable rather than missing. However, the program MrBayes treats dashes as a separate

character state, and therefore dashes were changed to question marks in the character matrix used in Bayesian analyses.

One critique of the reductive coding approach is that when a "?" is optimized into one of the other existing states, it may affect the optimization of the character at higher taxonomic levels to the detriment of local optimization of clades at lower levels (Maddison 1993, Strong & Lipscomb 1999). Nonetheless, reductive coding was preferred over other coding strategies for several reasons. First, 2 (or more) distinctly separate homologous conditions (transformation events) exist for many characters in this study, 1 relating to the presence or absence of a feature, and another (or more) relating to the details of the feature. The presence of a particular structure may be a synapomorphy for some taxa, while the details of that structure may be informative at more-refined taxonomic levels. By coding the conditions as separate characters, this phylogenetic information is retained. If the conditions were coded as a single multistate character (*i.e*., "composite coding," Maddison 1993) taxa could be potentially grouped together based on conditions that are not applicable to them, rendering them informative in determining phylogenetic relationships when they should not (Strong & Lipscomb 1999). Additionally, absence coding and non-additive binary coding may assume incorrectly that absences are homologous, thereby resulting in artificial inflation (*i.e*., over-weighting) of the absence state (Strong & Lipscomb 1999).

Composite, or multistate coding (Maddison 1993) was used in a few instances: 1) when the absence state was an autapomorphy for a single taxon (*e.g*., character 76), 2) if the absence of a character was assumed to be homologous among taxa (*e.g*., character 70), and 3) when the character transformational series are clear and absence is 1 condition of that series (*e.g*., character 61).

To minimize *a priori* assumptions regarding evolution, rooting by outgroup comparison was used to determine the polarities of characters (Schuh & Brower 2009, Cassis & Schuh 2010). Therefore, no assumptions should be made as to the individual coding of a particular state. State 0 (or 1, 2, 3, etc.) may either be the plesiomorphic state or a derived state.

Mitochondrial DNA

Gene choice

The phylogenetic usefulness of a particular gene for a particular level of relationships depends in part on its rate of evolution. Preferred genes are those that minimize the incidence of multiple nucleotide substitutions while maximizing the number of non-homoplasious, shared character states (Simon *et al*. 1994). In closely related species, nucleotide positions are less likely to vary, thus genes containing higher proportions of unconstrained sites are more appropriate (Simon *et al*. 1994). For more distantly related species, nucleotide positions can be expected to vary more, so genes with lower proportions of unconstrained sites are preferred (Simon *et al*. 1994).

For this study we chose to use the "Folmer region" (Folmer *et al*. 1994) at the 5' end of the cytochrome *c* oxidase subunit I mitochondrial gene region (COI), which has also been selected as the "barcode gene" for animals. Mitochondrial genes are considered to be more rapidly evolving than nuclear genes, and thus more appropriate for phylogenetic studies of closely related taxa (Simon *et al*. 2006). COI has most frequently been used to identify and assign unknown specimens to a species or reveal cryptic species diversity (Ball *et al*. 2005, Hebert *et al*. 2003, Hebert *et al*. 2004, Pauls *et al*. 2010). However, COI has also been shown to be useful in assigning species to genera (Hebert *et al*. 2003) and it has been used in resolving phylogenetic relationships among genera in insects (Nyman *et al*. 2006). In a higher-level phylogenetic analysis of Trichoptera, COI became saturated rapidly, although it might potentially be useful for resolving relationships among genera at the tips of the tree (Kjer *et al*. 2001). That useful phylogenetic information is retained at the level of this study is confirmed by the fact that a monophyletic Protoptilinae (although only represented by 2 genera) was recovered by Kjer *et al*. (2001).

COI was also chosen for practical reasons such as the fact that the COI fragment is easily amplified with primers developed specifically for caddisflies by Kjer *et al*. (2001). Some of the COI data were freely obtained from the Trichoptera Barcode of Life initiative in Guelph, to which we are major contributors. In addition, because it is protein coding with few insertions and deletions, it is relatively easy to align COI sequences (Hebert *et al*. 2003).

DNA extraction, amplification, and sequencing

DNA was extracted from pinned or 70–80%-ethanol-preserved museum specimens. In a few cases, DNA was extracted from specimens less than 1 year old and preserved in 95% ethanol. For most specimens, the head, thorax, and legs were taken; however, in instances where specimens were limited or only available from type material, a single leg was taken. In all cases, the wings and genitalia were retained as vouchers and the specimen data were entered into the University of Minnesota Insect Collection (UMSP) Biota Trichoptera Database. For most specimens, DNA was extracted and sequenced while visiting the laboratory of Dr. Karl Kjer, Rutgers University. However, in an effort to obtain more complete sequence data, some specimens, along with aliquots taken from stock samples at Rutgers were sent to the University of Guelph, Ontario, Canada (Guelph) for sequencing. Standard barcoding protocols for DNA extraction, amplification, and sequencing at Guelph followed those detailed by deWaard *et al*. (2008), Hajibabaei *et al*. (2005), and Ivanova *et al*. (2006). At Rutgers, DNA was extracted using the DNeasy Tissue Kit (QIAGEN Inc.) with 20 µl of Proteinase K (10 ml) (QIAGEN Inc.). The "Folmer region" (Folmer *et al*. 1994) at the 5' end of the cytochrome *c* oxidase subunit I mitochondrial region (COI) was then amplified using polymerase chain reaction (PCR) with Taq Master Mix Kit (QIAGEN, Inc.) and the primers listed in Table 4. The PCR mix was preheated to 94ºC followed by 35 or 40 cycles (95ºC, 3 min.; 94ºC, 30 sec.; 50ºC, 30 sec.; 72ºC, 30 sec.; 72C, 7 min.; 4ºC, 4 min). The QIAquick PCR purification kit (QIAGEN, Inc.) was used to clean PCR products. DNA concentrations were estimated by UV visualization of ethidium bromide stained 1% agarose gel with Tris-acetate-EDTA (TAE) electrophoresis buffer using standard techniques. Sequences were visualized and recorded using the Applied Biosystems 3100 Automated DNA Sequencer at the School for Environmental and Biological Sciences Sequencing Facility at Rutgers University. Each DNA fragment was sequenced from both directions.

Sequence alignment

Both forward and reverse sequence fragments were aligned using the program ABI Prism Sequence Navigator (ver. 1.0.1, Mac OS; Applied Biosystems). Consensus sequences were then aligned using ClustalX, ver. 2.0.11, Mac OS (Larkin *et al*. 2007) and MacClade, ver. 4.06, Mac OS (Maddison & Maddison 2000). Ambiguous nucleotides were coded as missing (?). There were no gaps.

TABLE 4. Primers used in polymerase chain reactions for this study.

Primer	Sequence (5' to 3')	Reference
COI 1709Fs	TAATTGGAGGATTTGGAAATTG	Zhou *et al*. 2007
COI 1709Fg	TAATTGGAGGATTTGGWAAYTG	Zhou *et. al*. 2007
COI 1751F	GGATCACCTGATATAGCATTCCC	Zhou *et. al*. 2007
COI 2191R	CCYGGTAAAATTAAAATATAAACTTC	Zhou *et. al*. 2007
COI 2355R	GCTCGTGTATCWACGTCTAT	K. Kjer, *personal communication*
LepF1	ATTCAACCAATCATAAAGATATTGG	Hebert *et al*. 2004
LepR1	TAAACTTCTGGATGTCCAAAAAATCA	Hebert *et al*. 2004
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*. 1994
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*. 1994
MLepF1	GCTTTCCCACGAATAAATAATA	Hajibabaei *et al*. 2006
MLepR1	CCTGTTCCAGCTCCATTTTC	Hajibabaei *et al*. 2006

Phylogenetic analysis

Treatment of morphological characters

Ninety-nine morphological characters were included in the analysis, including 62 binary characters and 37 multi-state characters, with a total of 288 character states (Appendix 1). Seven characters were parsimony uninformative (autapomorphic or constant) but were included in the character matrix because they are potentially

informative at higher taxonomic levels. However, uninformative characters were excluded in parsimony analyses for the purpose of calculating tree statistics since their inclusion may artificially inflate values (Bryant 1995, Yeates 1992). Since the likelihood model specified morphological characters as variable, for Bayesian analyses constant morphological characters were excluded from the data matrix (Lewis 2001a). Autapomorphic characters were included in the Bayesian analysis. All characters were treated as unordered (non-additive) (Fitch 1971) and equally weighted (Wilkinson 1992) to minimize the number of *a priori* assumptions regarding evolution.

Data partitions.
The complete data matrix included 80 taxa (Appendix 2). All taxa were scored for nearly all morphological characters; however, COI sequences were successfully obtained for only 25 taxa (including 10 of 18 protoptiline genera). Although it was not possible to include COI data for all genera, the major clades were adequately represented by these taxa. Nonetheless, the remaining 55 taxa (69%) were missing a significant portion of the data (87% of characters or 658 COI base pairs). It has been suggested that the inclusion of taxa lacking a proportion of characters may obscure relationships among taxa with complete data, decrease the probability of finding the correct tree, or lead to an increase in number of equally parsimonious trees and decrease in resolution (Huelsenbeck 1991, Wiens & Reeder 1995, Wilkinson 1995). However, other studies have suggested that including large amounts of missing data may actually improve phylogenetic accuracy, resolution, and placement of taxa (Egge & Simons 2009, Kearney 2002, Wiens 1998, 2003a, 2003b, 2005, 2006, 2009).

To test the effects of including a large set of taxa with missing molecular data, 5 different datasets were analyzed, using parsimony and Bayesian methods. "TOTAL" datasets included all 80 taxa; "SUBSET" datasets excluded incomplete taxa:

TOTAL COMBO: 80 taxa; morphology and COI
TOTAL MORPH: 80 taxa; morphology
SUBSET COMBO: 25 taxa; morphology and COI
SUBSET MORPH: 25 taxa; morphology
SUBSET COI: 25 taxa; COI

Analyses

Character matrices were constructed and character state transformations were mapped using MacClade 4.08 (Maddison & Maddison 2000). Four datasets were analyzed using the principal of parsimony and also Bayesian inference to explore the data under different evolutionary assumptions and models. However, the SUBSET COI dataset was only analyzed using Bayesian inference because of the known failure of parsimony to correct for multiple changes at the same nucleotide site or to accommodate parallel changes on two long branches (*i.e.,* long branch attraction) (Yang & Rannala 2012). Under the principal of parsimony, the preferred tree (hypothesis) is the one that requires the fewest number of evolutionary changes (=steps) or homoplasy (Kitching *et al*. 1998, Schuh 2000, Swofford *et al*. 1996, Wiley 1981). Bayesian phylogenetic inference is a model-based likelihood approach that determines the probabilities of a group (clade) existing on a tree given the observed data, a probabilistic model of evolution, and an explicit probabilistic description of prior beliefs (Kolaczkowski & Thornton 2009, Lewis 2001b).

Parsimony. Parsimony analyses were implemented in PAUP* v. 4.0 beta (Swofford 2003). Heuristic searches were conducted using stepwise taxon addition with 1000 random addition sequences (RAS) and Tree-Bisection-Reconnection (TBR) branch swapping, MULTREES option off. Heuristic searches were initially implemented with the MULTREES option in effect (the default command in PAUP* to save all minimal trees); however, this resulted in large numbers of trees and searches were not completed. Although the goal in parsimony analysis has long been to find each and every possible most parsimonious tree (MPT), it has been suggested that this is unnecessary in many cases. Since a strict consensus tree is created from all trees found, it may be more efficient to obtain the minimum number of trees needed to produce the same consensus tree that would be produced by all possible MPTs (Goloboff 1999, 2002). Saving multiple trees per TBR replication produces trees that are in the same local optimum, while trees from new, independent substitutions may be more likely to lead to different optima (Goloboff 1999, 2002). Hence, it is more beneficial and computationally efficient to save fewer trees to allow for the completion of more RAS (Goloboff 1999, 2002). Castlebury *et al*. (2002) demonstrated that consensus trees

generated with MULTREES option implemented (MAXTREES set to 5000) were identical to the strict consensus of those generated with the MAXTREES option off. Non-parametric bootstrap analysis (Felsenstein 1985) for each dataset was conducted using 1000 pseudoreplicates, each with 100 RAS. Bremer support values (Bremer 1988), also known as the decay index (DI), were not calculated for these studies. As pointed out by a number of authors, the DI is not a statistical measure (Zander 2004) and can be misleading, since low values do not necessarily mean there is little support for a clade. The DI does not take into account the relative amounts of contradictory or favorable evidence for a particular group (Goloboff & Farris 2001) and is not comparable between trees or even between nodes on the same tree (DeBry 2001).

Bayesian. Bayesian analyses were implemented in the program MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) using Metropolis-coupled Markov Chain Monte Carlo sampling (MCMCMC), which explores possible tree topologies and parameter space in proportion to their posterior probabilities (Lewis 2001b, Ronquist *et al*. 2005). Using the Metropolis algorithm (Felsenstein 2004), a designated "cold" Markov chain can escape from an isolated low probability peak by swapping with a "heated" chain that may be on a higher probability peak (Lewis 2001b, Ronquist *et al*. 2005). Analyses using MrBayes were carried out on the BioHPC web interface of the Computational Biology Service Unit computer cluster, located at Cornell University (http://cbsuapps.tc.cornell.edu/index.aspx).

Parameters. Morphological datasets (TOTAL MORPH and SUBSET MORPH) were assigned the Markov k (Mk) model, which specifies equal rates of character state change and deemed appropriate for discrete morphological data (Lewis 2001a). The Mk model is similar to a Jukes-Cantor (JC) model used with molecular data, except that it has a variable number of states (2–10) (Ronquist *et al*. 2005). Because rates of evolution are assumed to vary among individual morphological characters (*e.g*., male genitalic characters may evolve faster than larval characters), coding parameters were set to "variable" (*lset* coding = variable) to allow for possible rate heterogeneity (Lewis 2001). As recommended by Lewis (2001a), a discrete gamma-shape (Γ) distribution parameter was invoked (*lset* rates = gamma). Recent studies have favored the inclusion of the gamma parameter for discrete morphological data based on Bayes Factor analysis (Bond & Hedin 2006, Müller & Reisz 2006, Nylander *et al*. 2004, among others).

For the COI dataset (SUBSET COI), a General Time Reversal model with a gamma distribution and invariants model of rate heterogeneity (GTR + Γ + I) (*lset* nst = 6 rates = invgamma) was set as determined most appropriate by the program Modeltest v. 3.4 (Posada & Crandall 1998). Combined datasets (TOTAL COMBO and SUBSET COMBO) were analyzed using separate evolutionary models for each data partition (COI, GTR + Γ + I; morphology, Mk + Γ).

For all datasets, with the exception of the TOTAL COMBO dataset, 2 parallel analyses, each with 12 chains (11 hot, 1 cold) were run for 1 x 10^7 generations, sampling trees every 1000^{th} generation. The analysis for the TOTAL COMBO dataset used 4 chains (3 hot, 1 cold) because the analysis did not appear to be proceeding sufficiently upon examination of the progress file. Analyses were examined using the program Tracer v. 1.4.1 (Rambaut & Drummond 2007) to ensure stationarity (convergence) was achieved between 2 tree samples and to determine appropriate burn-in (number of trees discarded). The program FigTree v. 1.2.3 (Rambaut 2007) was used to examine trees and posterior probability values.

Hypothesis testing

When different datasets support different tree topologies, it is possible that 1 of the topologies simply represents a suboptimal version of the other (Larson 1994). To explore topological incongruence and conflicting topologies among the different data partitions, hypothesis testing was conducted under a Bayesian framework. A 95% credible set of unique topologies for each dataset was compiled using the *sumt* command in MrBayes (Brandley *et al*. 2005, Buckley 2002, Buckley *et al*. 2002). These tree sets were then searched for congruent topological hypotheses using the *CONSTRAINTS* and *FILTER* option in PAUP*. The occurrence of any number of trees congruent with the constraint tree from the 95% credible interval indicates that the hypothesis of monophyly cannot be rejected (Buckley *et al*. 2002).

RESULTS

Results of phylogenetic analyses

Parsimony. The parsimony analysis of the TOTAL COMBO dataset (80 taxa, 757 characters) resulted in 20 equally parsimonious trees (Length: 1880) with the strict consensus shown on Fig. 33. The TOTAL MORPH dataset (80 taxa, 90 characters) resulted in 2 equally parsimonious trees (Length: 463) (Fig. 35). A total of 2 equally parsimonious trees resulted from the SUBSET COMBO dataset (25 taxa, 757 characters) (Length: 1576) (Fig. 36). The SUBSET MORPH dataset (25 taxa, 99 characters) resulted in 12 equally parsimonious trees (Length: 218) (Fig. 38). Bootstrap (BS) support values ≥ 50% are indicated above internodes.

Bayesian. Chain swapping was determined to be successful in analyses of all 5 datasets (tree universe was thoroughly sampled) upon examination of the log and the MCMCMC files. A total of 50% of the total samples (5000 trees) were discarded as burn-in as determined by inspecting the Tracer file (Rambaut & Drummond 2007). The remaining 50% (5000 trees) were used to calculate posterior probabilities. Majority-rule cladograms are presented for TOTAL COMBO (Fig. 32), TOTAL MORPH (Fig. 34), SUBSET MORPH (Fig. 39), and SUBSET COMBO (Fig. 37) datasets. A phylogram is presented for the SUBSET COI dataset (Fig. 40). Posterior probability (PP) values are indicated above internodes.

Summary of analyses (Tables 5, 6)

Apart from some contradictory results obtained from the analysis of the SUBSET COI dataset (discussed below), topologies among different datasets analyzed under Bayesian and parsimony methods are fairly similar. Monophyly for the subfamily Protoptilinae was recovered for all datasets under both Bayesian and parsimony approaches. In all analyses and all datasets, except the SUBSET COI dataset, *Tolhuaca* is sister to all Protoptilinae, and is most strongly supported in analyses for the TOTAL MORPH and SUBSET MORPH datasets. In all datasets, under both Bayesian and parsimony analyses, the Asian taxa *Nepaloptila, Padunia, Poeciloptila,* and *Temburongpsyche* form a well-supported clade with the Nearctic monotypic genus *Matrioptila* nested within it, hereafter referred to as the **Asian Clade**. A monophyletic group consisting of all Neotropical taxa minus *Tolhuaca* (= **Neotropical Clade**) was recovered with strongest support under Bayesian and parsimony analyses of the TOTAL COMBO and TOTAL MORPH datasets. The Neotropical Clade was recovered with weaker support under parsimony and Bayesian methods for the SUBSET COMBO dataset and Bayesian methods for the SUBSET MORPH dataset. Within the Neotropical Clade, the genera *Campsiophora*, *Cariboptila*, and *Cubanoptila* (= **Caribbean Clade**) was strongly supported in analyses of the TOTAL COMBO, TOTAL MORPH, SUBSET COMBO, and SUBSET MORPH datasets, and the Bayesian analysis of the SUBSET COI dataset.

Results from analyses of the 3 SUBSET datasets (MORPH, COMBO, COI), can neither refute nor support the monophyly of individual genera, due to limited sampling. Therefore, monophyly for individual genera must be assessed based on the 2 TOTAL datasets (MORPH, COMBO). Monophyly for the following genera was strongly supported under both analyses for both TOTAL datasets: 1) *Tolhuaca*, 2) *Protoptila*, 3) *Mastigoptila*, 4) *Canoptila*, and 5) *Culoptila*. A monophyletic *Itauara* was recovered in all analyses but most strongly supported in the Bayesian analyses. *Mortoniella* was recovered as a monophyletic group in both analyses of the TOTAL COMBO dataset, but in the TOTAL MORPH dataset, *Mortoniella* was paraphyletic. Monophyly for the monotypic genera *Scotiotrichia* and *Merionoptila* is neither refuted nor supported and their placement among the Neotropical protoptiline genera remains ambiguous.

While some groups may have found strong support under only 1 method of analysis or in a single dataset, monophyly for most of the aforementioned clades was not contradicted, except in the analysis of the SUBSET COI dataset. The SUBSET COI dataset did not place *Tolhuaca* as sister to all Protoptilinae, but instead placed it within the Neotropical clade, nested within *Mortoniella*.

Finally, since none of the datasets analyzed under parsimony or Bayesian methods were able to recover monophyletic groups for the following taxa, their current taxonomy is challenged. These are: 1) *Nepaloptila*, 2) *Padunia*, 3) *Campsiophora*, 4) *Cariboptila*, and 5) *Cubanoptila*.

TABLE 5. Summary of results for evaluating the monophyly of various clades for morphology, COI, and combined datasets under Bayesian and parsimony phylogenetic analyses. Posterior probability (PP) and bootstrap (BS) support values are reported for various clades. Asterisks indicate strong support, dashes indicate analyses that did not recover a particular clade.

	Protoptilinae		(*Tolhuaca* (other Protoptilinae))		(Asian (other Protoptilinae))		Neotropical		Caribbean	
Dataset	**PP**	**BS**	**PP**	**BS**	**PP**	**BS**	**PP**	**BS**	**PP**	**BS**
TOTAL COMBO	1.00*	85*	0.88	60	1.00*	83*	1.00*	75*	1.00*	90*
TOTAL MORPH	1.00*	92*	1.00*	95*	0.87	70*	1.00*	90*	1.00*	94*
SUBSET COMBO	1.00*	98*	0.89	68	1.00*	100*	0.64	52	1.00*	94*
SUBSET MORPH	1.00*	98*	0.99*	98*	1.00*	99*	0.72	–	1.00*	98*
SUBSET COI	1.00*	N/A	–	N/A	1.00*	N/A	–	N/A	1.00*	N/A

TABLE 6. Summary of results for evaluating the monophyly of different genera for morphology, COI, and combined datasets under Bayesian and parsimony phylogenetic analyses. Posterior probability (PP) and bootstrap (BS) support values are reported for each genus. Asterisks indicate strong support, dashes indicate analyses that did not recover a particular clade.

	TOTAL COMBO		TOTAL MORPH	
Taxon	**PP**	**BS**	**PP**	**BS**
Campsiophora	–	–	–	–
Canoptila	1.00*	100*	1.00*	99*
Cariboptila	–	–	–	–
Cubanoptila	–	–	–	–
Culoptila	1.00*	97*	1.00*	98*
Itauara	0.98*	56	0.99*	55
Mastigoptila	1.00*	100*	0.99*	95*
Matrioptila	–	–	–	–
Merionoptila	N/A	N/A	N/A	N/A
Mortoniella	0.91	< 50	–	–
Nepaloptila	–	–	–	–
Padunia	–	–	–	–
Poeciloptila	–	–	–	< 50
Scotiotrichia	N/A	N/A	N/A	N/A
Temburongsyche	–	–	–	–
Tolhuaca	1.00*	94*	0.99*	96*

Hypothesis testing

There was considerable topological incongruence between the COI and morphological datasets, mostly concerning the placement of *Tolhuaca*. Although *Tolhuaca* was recovered as sister to all other Protoptilinae in all datasets except the SUBSET COI, the inclusion of COI data in the COMBO datasets lowered both posterior probability and bootstrap values. Additionally, in the COI dataset, *Tolhuaca* was nested within the Neotropical clade with the Asian clade (*Matrioptila* and *Padunia*) as sister to all other protoptilines. To explore this apparent conflict in evidence, trees with differing topologies were constructed to represent each of the 2 hypotheses: 1) The Asian taxa constrained within Protoptilinae and *Tolhuaca* constrained to the outgroup [= (*Tolhuaca* (other Protoptilinae)), (Figs. 41A, 42A)], and 2) *Tolhuaca* constrained within Protoptilinae and the Asian taxa constrained to the outgroup

[= (Asian (other Protoptilinae)), (Figs. 41B, 42B)]. In the Bayesian tests, the constraint topology occurred at least once in each of the 95% confidence intervals, therefore failing to reject either hypothesis for all datasets (Table 7).

TABLE 7. Bayesian topological incongruence test results for alternative Protoptilinae hypotheses evaluated against morphology, COI, and combined datasets. The number and percentage of trees containing the constrained topology of interest from the 95% credible interval (CI) of trees from the posterior distribution from Bayesian analyses is reported. If a particular topology occurs in the 95% CI, that hypothesis cannot be rejected.

		(*Tolhuaca* (other Protoptilinae))		(Asian (other Protoptilinae))	
Dataset	**Total # trees within CI**	**# trees retained**	**% trees retained**	**# trees retained**	**% trees retained**
TOTAL COMBO	9502	8408	0.8848	1084	0.1140
TOTAL MORPH	9502	9474	0.9970	15	0.0015
SUBSET COMBO	4150	3718	0.8959	428	0.1031
SUBSET MORPH	8816	8741	0.9914	46	0.0052
SUBSET COI	3097	1	0.0003	3095	0.9993

DISCUSSION

Effects of missing data in combined analysis

Approximately 70% of taxa from the TOTAL COMBO dataset are missing a significant portion of the data (87% of total characters or 658 COI base pairs). Including taxa with missing molecular data may obscure relationships among more complete taxa, decrease the probability of finding the correct tree, lead to an increase in number of equally parsimonious trees and decrease in resolution, or positively mislead model-based methods (Huelsenbeck 1991, Lemmon *et al*. 2009, Wiens & Reeder 1995, Wilkinson 1995). Conversely, some studies suggest that including more taxa even though they are lacking large amounts of data may actually improve phylogenetic accuracy, resolution, and placement of taxa (Egge & Simons 2009; Kearney 2002; Wiens 1998, 2003a, 2003b, 2005, 2006; Wiens 2009; Wiens & Reeder 1995).

Did the inclusion of COI characters with missing data obscure or improve the phylogenetic estimate for Protoptilinae? In the present study, including large amounts of missing COI data in the parsimony analysis increased the number of MPTs from 2 to 20, and resulted in a slight decrease in resolution when compared to the morphology-only tree (Figs. 33, 35). However, in the Bayesian analysis (Fig. 32), the resolution slightly increased when compared to the morphology-only tree (Fig. 34). Such differences in resolution may simply be an artifact of how the different analytical programs treat missing data. In MrBayes, missing characters are treated as missing data, and therefore do not contribute any phylogenetic information to the analysis (Ronquist *et al*. 2005). However in PAUP*, missing data are coded with a "?" and optimized as one of the other existing states (Strong & Lipscomb 1994, Wiens 1998). Thus, in a parsimony analysis, taxa with missing entries may "bounce" to different positions on a tree, decreasing resolution and consequently lowering support measures (Dos Santos & Falaschi 2007, Kearney & Clark 2003, Wilkinson 2003). Nonetheless, the differences in resolution between the 2 analyses are minor, and none of the collapsing clades exhibited strong nodal support in the morphology tree. Therefore, the topologies resulting from analyses of the TOTAL MORPH and TOTAL COMBO are largely congruent.

It appears that the combined approach was better able to recover the monophyly of *Mortoniella*, despite the presence of a large portion of missing COI data for many taxa. Missing entries may not be as much of an issue when the overall number of characters is large (Wiens 2006), as was the case with this study. The independent datasets (COI or morphology alone) may have been too "noisy" as a result of possible convergence of morphological characters or multiple nucleotide substitutions in the COI data. The combination of these data may have provided just enough phylogenetic signal to allow an otherwise suboptimal tree (which included a monophyletic *Mortoniella*) to emerge as optimal. Although support measures were lower for some higher-level groups in the combined analyses, this may be more a result of character conflict (discussed below) rather than effects of missing data (Kearney & Clark 2003). The fact that trees resulting from analyses of the SUBSET

COMBO dataset (which did not contain missing data) were congruent with the TOTAL COMBO dataset is further evidence that the inclusion of missing data did not have detrimental effects in this study.

Conflicting evidence between morphological and COI datasets

The consensus tree resulting from the analysis of the SUBSET COI data is not congruent with analyses of the other datasets (combined and morphology). Differences mostly involve the placement of *Tolhuaca* and the Asian Clade. Analyses of morphological data strongly place *Tolhuaca* as sister to all remaining protoptiline taxa (Figs. 38, 39), as do combined analyses, albeit with weaker support (Figs. 36, 37). Indeed, the morphology of *Tolhuaca* is considered to be very plesiomorphic (complete wing venation, presence of mesoscutellar warts, female oviscapt). However, when the COI data are analyzed separately, the Asian Clade (represented by *Matrioptila jeanae* and *Padunia lepnevae*), was found to be sister to all remaining Protoptilinae and *Tolhuaca* was placed within a paraphyletic *Mortoniella* (Fig. 40). Bayesian hypothesis testing failed to reject the possibility of both hypotheses in all datasets (Tab. 7).

The mitochondrial COI gene, also known as the "DNA barcode," is considered to be rapidly evolving and thus more appropriate for phylogenetic analyses of closely related taxa (Simon *et al*. 2006). In Trichoptera, COI has been found to be unreliable for resolving relationships deep in the tree and is potentially informative only at the tips of the Trichoptera tree, which were not tested (Kjer *et al*. 2001). In Protoptilinae, COI may be inappropriate for resolving relationships at among-genera or higher taxonomic levels. Divergence values among protoptiline genera may be too large, possibly resulting in numerous homoplasious substitutions at deeper levels of the tree. Although the COI data performed better at the species-level, grouping species of *Mastigoptila* and *Itauara*, it still failed to recover a monophyletic *Mortoniella* despite its supposed appropriateness for discerning relationships among closely related taxa.

The poor phylogenetic performance of COI in discerning relationships among and within genera of Protoptilinae, may be the result of a combination of factors. The presence of long or uneven terminal branches separated by short internodes suggests that long-branch attraction (LBA) may be playing a role (Felsenstein 1978). Bayesian methods are not thought to be as susceptible to LBA because, unlike parsimony, model-based parametric methods can take into account branch lengths and unobserved substitutions, given an appropriate model of evolution (Heath *et al*. 2008, Swofford *et al*. 1996). However, a recent study demonstrated that Bayesian methods are not always immune to the effects of LBA, especially when nucleotide sites evolve heterogeneously (Kolaczkowski & Thornton 2009).

Finally, although the SUBSET datasets were complete (no missing data), the analyses may have suffered from poor taxon sampling. Of the 25 taxa sampled in these datasets, only 9 of 17 protoptiline genera were represented, and for all but 4 of these genera, only a single species was represented. Insufficient taxon sampling can result in decreased phylogenetic accuracy, resolution, and clade support (Heath *et al*. 2008, Hedtke *et al*. 2006). Additionally, *Mortoniella* was sampled more densely, with 6 species included in the analyses. In sparsely sampled regions of the tree, less phylogenetic information is available, so more densely sampled sections of the tree (*Mortoniella*) will have longer branch lengths (Fitch & Bruschi 1987, Heath *et al*. 2008, Simon *et al*. 2006). The addition of more taxa can increase accuracy by dispersing homoplasy across the tree, thereby reducing the effects of LBA (Heath *et al*. 2008).

Differing support measures between analyses for same datasets

In this study, sometimes the same node was recovered in both the parsimony and Bayesian analyses for a particular dataset, but with differing support values. In general, posterior probability values were higher than corresponding bootstrap values when recovering several clades. For example, with *Itauara*, Bayesian analyses yielded stronger support than parsimony in both the TOTAL COMBO (PP: 0.98; BS: 56) and TOTAL MORPH (PP: 0.99; BS: 55) datasets. This is consistent to what other studies using both empirical and simulation data found (Alfaro *et al*. 2003, Erixon *et al*. 2003, Leach & Reeder 2002, Wilcox *et al*. 2002). Posterior probability values have been interpreted as being comparable to bootstrap values given the appropriate priors (Durbin *et al*. 1998, Efron *et al*. 1996, Huelsenbeck *et al*. 2001), and approximate equivalent values for comparing the 2 support measures have been proposed (Simmons *et al*. 2004, Zander 2004). However, just as Bayesian and parsimony methods of phylogenetic

inference have different underlying assumptions, so do their respective confidence measures. Posterior probability and bootstrap frequencies are not equivalent measures of confidence (Alfaro *et al*. 2003, Erixon *et al*. 2003), and as such, each value must be interpreted differently. Posterior probabilities measure confidence that the hypothesis is correct given the data and specified model (Alfaro *et al*. 2003, Lewis 2001a). Bootstrap values measure the sensitivity of the results to sampling error associated with collecting characters from hypothesized character distribution (Alfaro *et al*. 2003). Consequently, discrepancies between the 2 values can provide additional insight into the dataset being analyzed (Alfaro *et al*. 2003).

Posterior probability values may be more sensitive to phylogenetic signal than bootstrapping. In Bayesian analysis, higher confidence can be assigned to short internodes with small amounts of character change, and so may have lower incidences of type II error (rejecting the correct hypothesis) (Alfaro *et al*. 2003, Erixon *et al*. 2003). Bootstrapping, on the other hand, may require more data to obtain high confidence on short internodes, even if those nodes are correct (Alfaro *et al*. 2003, Erixon *et al*. 2003). However, PP may also be more susceptible to assigning high support values to very short incorrect internodes (type I errors) (Alfaro *et al*. 2003, Erixon *et al*. 2003). Of course, bootstrapping with parsimony is not immune to type I error since it may be more sensitive to LBA, and in those situations more likely to assign high support values to incorrect internodes (Alfaro *et al*. 2003). In this study, clades with high PP and moderate BS values may indicate that the node in question 1) has a high probability of being correct (given the present data and a correct model of evolution), and 2) is highly sensitive to the underlying character matrix and may not be recovered when additional characters are added (Alfaro *et al*. 2003, Holder & Lewis 2003).

CONCLUSIONS

Concluding remarks for the phylogenetic analysis

This study was the first to test the monophyly of Protoptilinae and its included genera and the first to hypothesize generic relationships by incorporating a large morphological dataset (nearly 100 characters) and a thorough sampling of taxa including representatives of all traditionally recognized genera and from all biogeographic regions. Additionally, this study was the first to infer phylogenetic relationships within the family Glossosomatidae using molecular data. The inclusion of missing data in combined analyses did not pose much of a problem in this study. Analyses of the independent COI dataset may have suffered from a number of problems including long-branch attraction, or incomplete taxon sampling. Although relying solely on COI data may have yielded spurious results, including these data in a combined analysis appears to have improved the overall phylogenetic signal. Had the COI been strongly contractictory to the morphological data, it would likely have influenced the topology of the combined data.

As COI seemed to be inappropriate for reconstructing protoptiline phylogeny at the genus and higher levels, this study would benefit from the addition of other genes, especially those that are considered more conservative. For example, nuclear genes may prove to be more phylogenetically informative at deeper regions of the tree. Additionally, combining nuclear and mitochondrial data is useful because incongruence (or congruence) can reveal important aspects of species histories (*e.g*., whether or not shared ancestral polymorphisms are indeed a problem in Protoptilinae) (Simon *et al*. 1994, Simon *et al*. 2006). Additionally, increased taxon and character sampling may improve the overall accuracy and resolution of the analyses.

Given the previous discussion, the Bayesian analysis of the TOTAL COMBO dataset (Fig. 32), represents the best approximation of protoptiline phylogeny. It contains the most data (both morphology and COI) and includes the most taxa. Additionally, the Bayesian analysis of the TOTAL COMBO dataset is more resolved and has higher support values for several clades than the parsimony analysis. Several taxonomic changes are needed to reflect this phylogeny accurately. As demonstrated by this study, several taxa do not meet the criterion of reciprocal monophyly. However, classification changes should reflect only clades that were strongly supported, not contradicted in other analyses, and had supporting morphological evidence. Such proposed changes are discussed in the following section.

A phylogenetic framework for classification and diagnoses of genera

Subfamily Protoptilinae Ross, 1956: 149

The monophyly of Protoptilinae has been corroborated by this study. Monophyly was recovered in all analyses of all datasets, and strongly supported in all except the parsimony analysis of the SUBSET COI dataset. This study corroborated 2 of the 5 putative synapomorphies of Protoptilinae identified by Morse & Yang (1993) including: 1) foretibial spur hair-like or absent (Fig. 6B) (character 17), 2) forewing crossveins forming a relatively straight line along anastomosis (Fig. 7A) (character 47). Morse & Yang (1993) also listed an absence of apical fork V in the forewing as a possible synapomorphy of Protoptilinae, but this analysis did not support that character. Additionally, since larval characters were not included in this study, we were unable to evaluate the putative larval characters (tarsal claw seta beside process; anal claw with 4 accessory hooks) suggested by Morse & Yang (1993). Another unique synapomorphy of Protoptilinae identified in this study is the presence of a row of erect setae along the Cu2 in the forewing (Fig. 7A) (character 41).

Diagnosis of Protoptilinae. Protoptilines are very minute caddisflies. As such, they may be confused with members of the family Hydroptilidae; however, protoptilines can easily be separated based on their presence of mesocutal setal warts. Perhaps the most identifiable feature of Protoptilinae is the absence of a foretibial spur, or a hair-like condition of this spur. Other distinctive features include the row of erect setae along Cu2 in the forewing, and the linear aspect of the forewing crossveins.

Adult. Length of forewing: 1.5–6 mm. Body, wings, and appendages pale brown, tawny brown, or fuscous, often intermingled with rufous or golden hairs. Wings often with few pale cream-colored or white hairs, specks or spots, and transverse line along anastomosis. Forewing with long fringe of setae along apical margin; hind wing with long fringe of setae along posterior margin. Head broader than long, vertex rounded. 3 ocelli. Mesal setal warts of pronotum widely spaced, not touching mesally. Mesoscutum with 2 pairs of setal warts; mesoscutellar setal warts usually absent, or if present, small and round. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Tibial spur formula variable; foretibial preapical spur absent, foretibial apical spur either absent or hair-like. Fore- and hind wing venation variable, ranging from complete to extremely reduced. Forewing R1 unforked; crossveins, when visible, forming relatively straight line along anastomosis; row of stout, erect setae present along Cu2. Male genitalia extremely variable among genera and species. Preanal appendages absent.

Genus *Canoptila* Mosely, 1939

Canoptila Mosely, 1939: 218 [Type species: *Canoptila bifida* Mosely, 1939, by original designation].

All of the analyses recovered a strongly supported monophyletic *Canoptila*. A weak sister relationship between *Scotiotrichia* and *Canoptila* was recovered in the parsimony analysis of the TOTAL MORPH dataset. The analysis confirmed a putative unique synapomorphy identified by Robertson & Holzenthal (2006): the presence of membranous and digitate parameres (character 86) (Figs. 15B, D). However, the presence of long spine-like posterolateral process on tergum X and wing venational features were not found to be unambiguous synapomorphies of *Canoptila.*

Diagnosis of *Canoptila* (Figs. 5B, 9A, 9B, 15, 31B). As noted by Robertson and Holzenthal (2006), the genus *Canoptila* is easily identified by the presence of certain structures of the male genitalia (Fig. 15): 1) a pair of long spine-like processes on the posterolateral margins of tergum X, and 2) paired, highly membranous digitate parameres arising basoventrally on the endotheca. *Canoptila* is most similar in forewing venation (Fig. 9A) to *Cariboptila*, *Itauara*, and *Mastigoptia* based on the presence of forks I, II, and III, the intersection of Cu1 and Cu2 near anastomosis, and absence of A3. However, *Canoptila* can be distinguished from these species by the length of the stem of fork II: in *Canoptila* the stem is longer than the fork whereas in the other genera, the stem is shorter or no longer than the fork. Hind wing (Fig. 9B) venation of *Canoptila* is nearly identical to that of *Scotiotrichia*, and is very similar to those of *Cariboptila* and *Protoptila* having only apical fork II present and only 1 anal vein. Although indistinguishable from *Scotiotrichia*, the hind wings of *Cariboptila* and *Protoptila* are narrow and scalloped past the anastomosis, whereas in *Canoptila*, the margins are nearly parallel. *Canoptila* has telescopic

glandular structures (Fig. 5B) arising from the tegulae, as in many species of *Culoptila*. However, in *Culoptila*, these structures are "concertina-shaped" (Mosely 1954) and positioned posterolaterally, whereas in *Canoptila*, they are tubular in shape and arise more anteriorly.

Adult. Body, wings, and appendages nearly uniformly fuscous or tawny brown, tibia and tarsi yellowish brown. Head (Fig. 5B) broader than long, vertex rounded, with large anteromesal setal wart, 2 distinct pairs of suboval anterior setal warts, small suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short with elongate setae apically; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts. Mesothorax (Fig. 5B) wider than long, with paired telescopic tegular glands; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 9A) relatively narrow, with margins nearly parallel, apex oblique. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile; fork II petiolate, stem longer than fork; fork III petiolate, stem longer than fork; Cu1 complete, reaching wing margin; Cu1 and Cu2 intersecting near anastomosis; row of erect setae present below Cu2; A3 absent; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 9B) margins nearly parallel, tapering only slightly past anastomosis; apical fork II present; Sc and R1 fused basally; A2 absent. Tibial spurs 1,4,4, foretibial spur extremely reduced and hair-like. Sternum VI process (Fig. 15A) elongate and digitate, apex subacute, associated with weak oblique apodeme posteriorly.

Male genitalia (Fig. 15). Preanal and inferior appendages absent. Segment IX anterior margin fairly straight; tergum IX well developed, relatively broad, simple, without processes; sternum IX uniformly narrow, mesally, without modification. Tergum X completely fused to tergum IX forming ridge at line of fusion; dorsomesal margin bifid or subquadrate; dorsolateral margin with highly setose, rounded or subquadrate lobes; ventrolateral margin with paired very elongate, spine-like process directed inwardly. Parameres present, arising laterally from endotheca, membranous, bulbous, with sclerotized or asperous apices. Phallobase reduced, lightly sclerotized, with paired row or patches of setae ventrolaterally. Endophallus highly membranous, enlarged and convoluted when evaginated, bearing 1 to several pairs of large, pointed, sclerotized processes, lightly sclerotized apically or with terminal sclerite.

Female genitalia (Fig. 31B). (Female known only for *C. williami*.) Truncate posteriorly, not extensible. Abdominal segment VIII short, synscleritous, posterolateral margin slightly incised. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Cariboptila* Flint, 1964

Cariboptila Flint, 1964: 17 [Type species: *Cariboptila orophila* Flint, 1964, by original designation]
Campsiophora Flint, 1964: 14 [Type species: *Campsiophora pedophila* Flint, 1964, by original designation] **new synonym**
Cubanoptila Sykora, 1973, in Botosaneanu & Sykora 1973: 383 [Type species: *Cubanoptila cubana* Sykora, 1973, by **new, subsequent designation**] **new synonym**
Muangpaipsyche Malicky & Silalom, 2012: 22 [Type species: *Muangpaipsyche areopagita* Malicky & Silalom, 2012, by monotypy; Malicky 2013, as synonym of *Campsiophora*] **new synonym**

None of the analyses of any dataset in this study were able to recover a monophyletic *Cariboptila* as historically constituted. Flint (1964) established *Cariboptila* and *Campsiophora* in the same paper, and distinguished the 2 genera based on 1) the level of branching of the apical forks 1 and 2 relative to each other in the forewing, and 2) the presence of a hair pencil on the inner surface of the forewing in *Campsiophora*. However, differences in the relative position of the apical forks are quite variable and homoplastic throughout the subfamily and 1 of the 2 states must be plesiomorphic and thus not appropriate for defining taxa by cladistic standards. Additionally, the hair pencil in the forewing is not consistently found in all *Campsiophora*. Sykora (in, Botosaneanu & Sykora 1973), distinguished *Cubanoptila* from other protoptiline genera based on features of the antennae, wing venation, and a plate-like tergum VIII. While the presence of small spines on the 3rd antennal article does appear to be unique to *Cubanoptila*, the other characters proposed for the establishment of *Cubanoptila* are not and, in these analyses, the *Cubanoptila* species are nested within *Cariboptila*, and thus the groups are not reciprocally monophyletic at the generic level. Furthermore, larval morphology of the 3 genera is not significantly different,

with all 3 possessing tarsal claws with a short and broad seta. Therefore, to reflect phylogeny accurately, the following species are hereby transferred to *Cariboptila* (**all new combinations**): from *Campsiophora*: *C. arawak* (Flint), *C. mulata* (Botosaneanu), *C. pedophila* (Flint); and from *Cubanoptila*: *C. botosaneanui* (Kumanski), *C. cubana* (Sykora), *C. madremia* (Botosaneanu), *C. muybonita* (Sykora), *C. purpurea* (Sykora), *C. tridens* (Botosaneanu). Although simultaneously published, as first revisers we prefer the name *Cariboptila* as the senior synonm over *Campsiophora*, despite "page priority." The use of *Cariboptila* will impart more nomenclatural stability since fewer species need to be transferred. Furthermore, the name alludes to their occurrence in the Caribbean.

Malicky & Silalom (2012) described a new monotypic genus, reportedly from Thailand, *Muanpaipsyche areopagita*. However, after we informed Dr. Malicky that this new genus is almost certainly *Cariboptila pedophila* (Flint, 1964) because of nearly identical male genitalia and wing venation (compare figures given by Malicky & Silamon 2012, page 23 with our Figs. 8 & 18), Malicky synonomized the genus, but not the species (Malicky 2013). We hereby designate the species *C. arepagita*, as a **new junior synonom** of *C. pedophila*. It is extremely doubtful that this single species would be found both in the Caribbean and Thailand, but is rather the likely result of a mislabeled specimen or other curatorial lapse.

No type species was designated explicitly in the original description of *Cubanoptila*. Flint *et al*. (1999) erred in stating that *Cubanoptila cubana* is the type species by "original designation." *Cubanoptila cubana* is here designated as the type species of *Cubanoptila* by "virtual tautonomy" in compliance with Recommendation 69A.2 of the International Code of Zoological Nomenclature (1999).

Monophyly of the redefined *Cariboptila* was strongly supported in all analyses with the following 3 unique synapomorphies: 1) antennal scape greater than or equal to 3 times the length of the pedicel (Fig. 6A) (character 3), 2) tergum IX dorsal lateral process bearing 1 or more elongate apical setae (Figs. 16A, C) (character 73), 3) inferior appendages present as broad, highly setose, prominent plate-like projections fused basoventrally to phallobase (Figs. 16A, B) (character 82).

Diagnosis of *Cariboptila* (Figs. 6A, 7C, 7D, 8, 16–18)**.** Perhaps the most distinctive feature of the genus *Cariboptila* is its extremely long antennal scape (Fig. 6A), which is often associated with androconia. Many species also have stout setae along the 3rd antennal segment, although this is not completely diagnostic for the genus. Another diagnostic feature is the short discoidal cell in the forewing. The males of 2 species of *Padunia* [*P. falcata* (Schmid, 1991) and *P. phyllis* (Malicky & Chantaramongkol, 2007)] also have a short discoidal cell, but in these species the wings are highly modified. *Cariboptila* is most similar in forewing venation to *Canoptila*, *Itauara*, and *Mastigoptia* based on the presence of forks I, II, and III, the intersection of Cu1 and Cu2 near the anastomosis, and the absence of A3. However, *Cariboptila* can be distinguished from these genera based on its presence of a short discoidal cell in the forewing. The hind wing venation of *Cariboptila* is nearly identical to that of *Canoptila*, *Scotiotrichia*, and *Protoptila*, having only apical fork II and only a single anal vein, yet can be differentiated from these genera based on differences of the forewing. In the forewing of *Protoptila,* A3 is present; in *Scotiotichia*, fork III is absent; and *Canoptila*'s forewing has a short discoidal cell.

Diagnostic characters of the male genitalia include the broad, highly setose plate-like inferior appendages, the digitate process of tergum IX, which usually bears 1 or more elongate apical setae, and the lateral branches of tergum X whose dorsolateral margins have sclerotized short, flattened, inwardly curved processes or irregular setose processes and ventrolateral margins bearing 1 or several large, highly sclerotized spines or spine-like setae. The male genitalia of *Cariboptila* are most similar to those of *Culoptila* in that both are completely lacking, or have a strap-shaped, sternum IX, and an enlarged phallobase. The 2 genera are easily differentiated by differences in the shapes of terga IX and X, the inferior appendages, and wing venation. The genera *Tolhuaca* and *Scotiotrichia* also have a reduced sternum IX and enlarged phallobase, but can be easily separated from *Cariboptila* by other genitalic features or differences in wing venation. *Tolhuaca* has complete forewing venation and the phallic apparatus lacks elongate spines or processes. In the forewing of *Scotiotrichia*, fork III is absent.

Adult. Body, wings, and appendages pale or tawny brown, often intermingled with rufous or golden hairs. Wings often with few pale cream-colored or white hairs, spots, or transverse line along anastomosis and small white specks or spots along apical margin. Head broader than long, vertex rounded, either with 1 distinct pair, 1 divided pair, or 2 distinct pairs of suboval anterior setal warts, small or large suboval posterior warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape more than 3 times as long as pedicel, often with androconia; 3rd antennal segment occasionally with stout spine-like setae (Fig. 6A). Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as

1st and 2nd segments combined. Prothorax with 2 large, subtriangular or suboval pronotal setal warts. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval, or occasionally elongate anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Figs. 7C, 8A, 8C) relatively narrow, with margins nearly parallel, apex oblique. Males occasionally with hair pencil along anal margin (Fig. 8C) or callosity in anal or apical costal region of forewing. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile or only slightly petiolate with extremely short stem; fork II petiolate or sessile, but when petiolate, stem shorter or about as long as fork; fork III petiolate, stem usually longer than fork, occasionally same length; Cu1 complete, reaching wing margin; Cu1 and Cu2 intersecting near anastomosis, or completely fused; row of erect setae present along Cu2; A3 absent; crossveins forming relatively linear transverse cord; discoidal cell shorter than Rs vein. Hind wing (Figs. 7D, 8B, 8D) narrow and scalloped past anastomosis; apical fork II present; Sc and R1 fused basally; A2 absent. Tibial spurs either 0,4,4 or 1,4,4, foretibial spur extremely reduced and hair-like. Sternum VI process present, shape variable, ranging from flattened dorsoventrally, short and digitate, to thumb-like and prominent, apex also variable, either pointed, rounded, or subquadrate, often associated with weak oblique apodeme posteriorly.

Male genitalia (Figs. 16–18). Preanal appendages absent. Tergum VIII occasionally forming dorsal plate subtending tergum IX and X (Fig. 17A, 17B). Sternum VIII without modification. Segment IX anterior margin rounded or fairly straight, posterolateral margin without lateral process or lobes; tergum IX well developed, relatively broad, with paired, dorsolateral, often digitate process usually bearing 1 or more elongate apical setae; sternum IX usually completely absent, or if present, consisting only of small ventral membranous strap. Tergum X subtended by tergum IX; dorsomesal margin bifid or subquadrate, or with single broad, plate-like process, or irregular with several small processes; dorsolateral margin with sclerotized short, flattened, inwardly curved process, or with irregular setose processes; ventrolateral margin bearing 1 or several large, highly sclerotized spines or spine-like setae, directed mesad. Inferior appendages present, ventrally as broad, highly setose, prominent plate-like projection fused ventrobasally to phallobase, often invaginated apicomesally, with setose, elongate, broad and plate-like, or multilobed lateral appendages. Parameres absent. Phallobase extremely enlarged, sclerotized, and occupying nearly all of genital capsule, forming ventral portion of genitalia. Phallic apparatus with 1 to several pairs of elongate phallic spines and/or highly curving processes. Endophallus membranous, enlarged and convoluted when invaginated.

Female genitalia. (Females unknown for many species.) Truncate posteriorly, not extensible. Abdominal segment VIII broad or short, sometimes incomplete midventrally with elongate sclerite. Sternum IX often forming triangular lobes. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Culoptila* Mosely, 1954

Culoptila Mosely, 1954: 336 [Type species: *Culoptila aluca* Mosely, 1954, by original designation].

Monophyly for *Culoptila* was strongly supported in all analyses with the following unique synapomorphies: 1) an incomplete Cu1 on the forewing (character 38), and 2) inferior appendages comprised of simple, paired, long or short process, fused to one another basally and to ventral surface of phallobase (character 82). Blahnik and Holzenthal (2006) hypothesized that *Culoptila* was most closely related to the Caribbean genera *Campsiophora*, *Cariboptila*, and *Cubanoptila.* In this study, a sister relationship between *Culoptila* and the Caribbean taxa was recovered with weak nodal support in the parsimony analysis of the TOTAL MORPH dataset, and in both analyses of the SUBSET MORPH dataset.

Diagnosis of *Culoptila* (Figs. 3B, 3C, 4, 7A 7B, 19). The genus *Culoptila* can be identified by both forewing and hind wing venation. In the forewing, only apical forks I–IV are present, fork V is absent. Additionally, Cu1 is incomplete, not reaching the wing margin. In the hind wing, only apical forks II and III are present. Another distinctive feature, although not completely diagnostic for the genus as already noted by Blahnik and Holzenthal (2006), is the presence of enlarged tegulae on the mesothorax of males, which accommodate an extensible concertina-like glandular structure. The genus *Canoptila* also possesses extensible glandular structures associated with the tegulae, but these differ in shape from those of *Culoptila.*

Other diagnostic features of the genus occur in the male genitalia, most notably the absence or extreme small

size of sternum IX, and a greatly enlarged phallobase. As noted above, and in the works by Robertson & Holzenthal (2005) and Blahnik & Holzenthal (2006), the genera *Cariboptila* and *Tolhuaca* have similar reductions of the sterna and inflated phallobases; however, these genera can be easily separated from *Culoptila* based on differences in wing venation and other characters of the male genitalia. Terga IX and X are differently shaped in *Cariboptila*, and unlike *Culoptila, Cariboptila* lacks apical fork III in the hind wing. *Tolhuaca* has complete forewing venation and lacks elongate phallic spines. Another diagnostic feature of *Culoptila* is the presence of an apical phallotremal sclerite, although this structure is sometimes difficult to see and may not be easily identified (Blahnik & Holzenthal 2006).

Adult. Body, wings, and appendages pale brown to fuscous. Wings often with white transverse line along anastomosis or conspicuous spot at the arculus. Head broader than long, vertex rounded, with pair of small anteromesal setal warts, pair of distinct, suboval anterior setal warts, small suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts. Mesothorax shape variable, usually wider than long, but occasionally longer than wide to accommodate enlarged tegulae of males bearing paired concertina-shaped glandular processes; mesoscutum with pair of elongate anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 7A) relatively narrow, with margins nearly parallel, apex oblique. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, III, and IV present; Sc and R1 distinct along their entire lengths; fork I petiolate, but with extremely short stem; fork II petiolate or sessile, stem shorter than fork; fork III petiolate, stem longer than fork; fork IV petiolate, stem about as long as fork; Cu1 incomplete, not reaching wing margin; Cu1 and Cu2 intersecting near anastomosis; row of erect setae present along Cu2; A3 absent; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 7B) narrow and scalloped past anastomosis; apical forks II and III present; Sc and R1 fused basally; A2 present, not looped. Tibial spurs 1,4,4, foretibial spur extremely reduced and hair-like. Sternum VI process present, short, often somewhat circular in lateral view, apex subquadrate or rounded, associated with weak oblique apodeme posteriorly. Male genitalia (Fig. 19). Preanal appendages absent. Segment IX anterior margin rounded; tergum IX well developed, relatively broad, simple, without processes; sternum IX absent. Tergum X incompletely fused to tergum IX with membrane or lightly sclerotized region ventrolaterally; dorsomesal margin subquadrate; dorsolateral margin without processes; ventrolateral margin with paired elongate processes attached ventrolaterally to tergum IX and directed ventrad and sometimes anterad. Inferior appendages present (except in *C. cantha* Ross, 1938, and *C. plummerensis* Blahnik & Holzenthal, 2006), as simple, paired long or short appendages, fused to one another basally and to ventral surface of phallobase. Parameres absent. Phallobase extremely enlarged, lightly sclerotized, and occupying nearly all of genital capsule, with sclerotized, projecting apex posterodorsally. Phallic apparatus with 1 or 2 phallic spines of varying length and shape.

Female genitalia. (Females unknown for many species.) Truncate posteriorly, not extensible. Abdominal segment VIII short, usually synscleritous, but sometimes incomplete midventrally and laterally. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Itauara* Müller, 1888

Itauara Müller, 1888: 275 [Type species: *Antoptila brasiliana* Mosely, 1939, subsequent selection by Flint *et al*. 1999].
Antoptila Mosely, 1939: 219 [Type species: *Antoptila brasiliana* Mosely, 1939, by original designation] Flint *et al*. 1999, to synonymy.

A monophyletic group consisting of 21 *Itauara* species was recovered in all analyses of this study. The unique synapomorphy of *Itauara* is the presence of a dorsal sheath covering a ventral membranous portion of the phallus (character 95).

Diagnosis of *Itauara* (Figs. 9C, 9D, 20)**.** The genus *Itauara* can be identified by features of the male genitalia. The phallic apparatus consists of a sclerotized dorsal sheath covering a very membranous ventral portion, an apparent posterior extension of the phallobase or phallicata. In some species, this sclerotized dorsal sheath seems to detach from the ventral membrane apically to reveal a single dorsomesal process or spine (*e.g*., *I. amazonica* Flint,

1971). *Mortoniella* has a similar dorsomesal process or spine, but in *Mortoniella* it arises internally from the phallobase, whereas in *Itauara* it appears to arise dorsobasally from this sclerotized sheath. In some species (*I. guarani* and *I. plaumanni*), the sheath produces a dorsolateral flange, although this character is not diagnostic for the genus. Another genitalic feature characteristic of *Itauara* is an extremely reduced phallobase. In most species, the phallobase is barely visible, consisting of a small, very lightly sclerotized, or entirely membranous structure. The genera *Mastigoptila* and *Canoptila* display similar reductions or absences of the phallobase, but can easily be separated from *Itauara* by other genitalic characters: *Mastigoptila* has an elongate, whip-like process arising from the membranes of the phallocrypt; *Canoptila* has highly membranous digitate parameres. When present (they are absent in many species), the inferior appendages are rather distinct for *Itauara*, consisting of a single or apically bifid process produced mesally and fused to the phallobase basoventrally.

The forewing venation of *Itauara* is most similar to that of *Cariboptila* and *Canoptila*, with apical forks I–III and a lack of 3A. *Canoptila* can be differentiated from *Itauara* by having stout setae occurring below Cu2 whereas in *Itauara* the setae occur along the vein. *Cariboptila* can be differentiated from *Itauara* by the presence of a short discoidal cell, that of *Itauara* being long. The hind wing venation of *Itauara* is variable, with either apical forks II, III, and V or II and V or III only (*I. amazonica*) or II only.

Adult. Body, wings, and appendages pale or tawny brown, often intermingled with rufous or golden hairs, tibia and tarsi yellowish brown (Fig. 2A). Wings usually with partial white transverse line along anastomosis not reaching costal margin, or with conspicuous white spot at arculus (Fig. 2A). Head broader than long, vertex rounded, with pair of small anteromesal setal warts or with large anteromesal setal wart, either 1 distinct pair or 1 divided pair of suboval anterior setal warts, small or large suboval posterior warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 9C) usually relatively narrow, with margins nearly parallel, occasionally narrowed past anastomosis or much reduced, apex oblique or rounded. Male occasionally with callosity present in apical costal region of forewing. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile or only slightly petiolate with extremely short stem; fork II petiolate or sessile, but when petiolate, stem length variable; fork III petiolate, stem variable in length; Cu1 complete, reaching wing margin; Cu1 and Cu2 intersecting near anastomosis; row of erect setae present along Cu2; A3 absent; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 9D) margins nearly parallel, tapering only slightly past anastomosis, or narrow and scalloped past anastomosis; venation variable, with either apical forks II, III, and V present or II and V present or III present (*I. amazonica*) or II present; Sc and R1 fused basally or converging near wing margin; A2 absent. Tibial spurs 1,4,4, rarely 1,3,4, foretibial spur extremely reduced and hair-like. Sternum VI process present, short and digitate or thumb-like and prominent, apex rounded or attenuate and pointed, usually associated with oblique apodeme posteriorly.

Male genitalia (Fig. 20). Segment IX anterior margin rounded, posterolateral margin without lateral processes or lobes; tergum IX usually not well developed, simple, and without processes; sternum IX without modification, except in *I. brasiliana* (Mosely, 1939), which bears 2 pairs of elongate, seta-like processes. Tergum X incompletely fused to tergum IX ventrolaterally or rarely (*I. amazonica*) completely fused and indistinguishable from tergum IX, shape extremely variable; dorsomesal margin may be simple without processes, bifid apicomesally with single broad plate-like process, or irregular with several small processes; dorsolateral margin either simple structure without processes, or more commonly with small paired lobes, elongate and down-turned and finger-like processes, or irregular setose processes; ventrolateral margin with paired elongate or broad flange-like processes directed ventrad and sometimes anterad, or with 1 or more irregular, paired, setose, digitate lobes directed posterad. Inferior appendages either present or absent; when present, consisting of single or apically bifid process produced mesally, broadest at base and fused to phallobase ventrobasally. Parameres present except in *I. brasiliana,* arising either ventrobasally from phallobase or laterally from endotheca, sclerotized, shape variable. Phallobase extremely small and difficult to discern. Phallic apparatus with sclerotized dorsal sheath covering membranous ventral portion, sometimes receding to a single dorsomesal process arising dorsobasally from phallobase, phallicata occasionally with dorsolateral flange, or occasionally with dorsomesal spine arising posterior of phallobase.

Endophallus highly membranous, enlarged and convoluted when evaginated, occasionally bearing small apical spine-like sclerites and processes.

Female genitalia. (Females unknown for many species.) Truncate posteriorly, not extensible. Abdominal segment VIII short, synscleritous, posterolateral margin slightly incised. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Mastigoptila* Flint, 1967

Mastigoptila Flint, 1967: 49 [Type species: *Mastigoptila curvicornuta* Flint, 1967, by original designation].

Monophyly of *Mastigoptila* was supported in all analyses in this study. A synapomorphy of *Mastigoptila* is markedly asymmetrical inferior appendages, fused to the phallocrypt ventrobasally (character 82) (Fig. 20A).

Diagnosis of *Mastigoptila* (Figs. 12C, 12D, 21)**.** The most distinctive feature of *Mastigoptila* is the profoundly asymmetrical aspect of the male genitalia. The phallic apparatus is tubular, asymmetrical, and often arcuate. The inferior appendages form an asymmetrical complex consisting of differently shaped and sized right and left setose appendages, which are fused together basally and ventrobasally with a lightly sclerotized phallocrypt. In some species, 1 of the inferior appendages also bears an elongate spinelike process. Another identifying feature is the presence of an elongate whiplike process arising from membranes of the phallocrypt on 1 side of the genitalia. The phallobase is also apparently absent.

The forewing venation of *Mastigoptila* is similar to that of *Canoptila* and identical to that of some species of *Itauara*. The forewing of *Mastigoptila* can be differentiated from that of *Canoptila* by having a sessile apical fork II. Unlike *Mastigoptila, Itauara* has symmetrical genitalia.

Adult. Body, wings, and appendages nearly uniformly fuscous. Wings sometimes with light spot at arculus and faint transverse line along anastomosis. Head broader than long, vertex rounded, pair of distinct, suboval anterior setal warts, small suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short with elongate setae apically; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts. Mesothorax wider than long, of some species with tegular glands; mesoscutum usually with pair of elongate anteromesal setal warts, although occasionally entire anteromesal region setose with no distinct patch, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing relatively narrow, with margins nearly parallel, apex oblique. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile; fork II sessile; fork III petiolate, stem about as long as fork, occasionally slightly longer; Cu1 complete, reaching wing margin; Cu1 and Cu2 intersecting near anastomosis; row of erect setae present below Cu2; A3 absent; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing margins nearly parallel, tapering only slightly past anastomosis; apical forks II, III, and V present; Sc and R1 converging near wing margin; A2 absent. Tibial spurs either 0,4,4 or 1,4,4; foretibial spur extremely reduced and hair-like. Sternum VI process present, flattened laterally, apex attenuate and pointed, often associated with weak oblique apodeme posteriorly. Sternum VII occasionally with small mesal point.

Male genitalia. Preanal appendages absent. Segment IX anterior margin rounded, posterolateral margin without lateral process or lobes; tergum IX strap-like, simple, without processes; sternum IX uniformly narrow, mesally without modification. Tergum X incompletely fused to tergum IX, with membrane or lightly sclerotized region ventrolaterally; dorsomesal margin subquadrate or excavate; dorsolateral margin either hood-like, without processes or with 1 or more large, horn-like processes; ventrolateral margin usually simple, but occasionally bearing small lobes or processes. Inferior appendages present, markedly asymmetrical, consisting of elongate spine-like processes and setose lobes, sometimes bifid, fused to phallocrypt ventrobasally. Parameres absent. Phallobase apparently absent. Phallic apparatus asymmetrical, tubular and often arcuate with posteriorly projecting apex, sclerotized or rugose, with small membranous protuberances, highly convoluted internal membranes with occasional small spines.

Female genitalia. (Females unknown for most species.) Truncate posteriorly, not extensible. Abdominal segments VIII and IX not fused.

Genus *Merionoptila* Schmid, 1959

Merionoptila Schmid, 1959: 482 [Type species: *Merionoptila wygodzinskyi* Schmid, 1959, by original designation].

Schmid (1959) suggested that the monotypic genus *Merionoptila* was more closely related to *Antoptila* (=*Itauara*) than to the other known protoptiline genera. This study can neither refute nor support that possibility since the placement of *Merionoptila* remains unresolved. The following are apomorphies of *Merionoptila*: 1) stem of forewing fork I longer than fork (character 26) (Fig. 10A), 2) forewing crossvein r-m absent (character 45) (Fig. 10A), 3) sternum VI mesal process absent, and 4) inferior appendage bulbous, fused ventromedially to the endotheca and projecting ventrad (character 82) (Fig. 22A, C).

Diagnosis of *Merionoptila* (Figs. 10A, 10B, 22). This monotypic genus has quite distinctive morphology among protoptilines. Its thorax is quite broad, it has highly setose legs and eyes, and extremely reduced wings—all apparently adaptations for skating across the water surface, a behavior first reported by Wygodzinski in a letter to Schmid (1959). The forewing is reduced in size, but has rather typical venation, with apical forks I–III present, although fork I may be difficult to see. The hind wing is even more reduced, and it is nearly impossible to discern the venation. The male genitalia of *Merionoptila* are rather simple, with a sclerotized, tubular phallic apparatus, directed dorsally at the apex. Inferior appendages are quite distinct, consisting of a highly setose, bulblike process, projecting ventrad and fused basally to the ventral portion of the phallobase.

Adult. Body, wings, and appendages nearly uniformly fuscous. Head broader than long, vertex rounded, with pair of small anteromesal setal warts, pair of distinct, suboval anterior setal warts, small suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Eyes setose. Maxillary palps 5-segmented, 1st membranous and bulbous, 2nd segment very short; last 3 segments each nearly same length as 1st and 2nd segments combined. Thorax broad and robust. Prothorax with 2 large, subtriangular or suboval pronotal setal warts. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 10A) much reduced, apex rounded. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, and III present, fork I very difficult to discern; Sc and R1 distinct along their entire lengths; fork I petiolate; fork II petiolate, stem longer than fork; fork III petiolate, stem longer than fork; Cu1 complete, reaching wing margin; Cu1 and Cu2 completely fused; row of erect setae present along Cu2; A3 absent; crossveins difficult to discern, but apparently forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 10B) extremely reduced; apical forks not clearly identifiable; Sc and R1 fused basally; A2 absent. Mesothoracic legs extremely setose. Tibial spurs 0,2,4. Sternum VI process absent.

Male genitalia (Fig. 22). Preanal appendages absent. Segment IX anterior margin rounded; tergum IX uniformly narrow, simple, without processes; sternum IX uniformly narrow, mesally without modification. Tergum X fused to tergum IX dorsomesally, or "hinged"; dorsomesal margin divided or bifid apicomesally; dorsolateral margin with small paired lobes; ventrolateral margin with irregular, paired setose lobes. Inferior appendages present, bulbous, highly setose, fused ventromedially to endotheca and projecting ventrad. Parameres absent. Phallobase simple, subtriangular in lateral view. Phallic apparatus simple, tubular, projecting posterad, without spines or processes. Endophallus membranous, enlarged and convoluted when invaginated.

Female genitalia. (A female specimen for this monotypic genus has not been positively associated with the male. In the original description, Schmid reported that a single female was captured, but at a different locality from the type specimens captured. Thus, only basic female genitalic characters are briefly described.) Truncate posteriorly, not extensible.

Genus *Mortoniella* Ulmer, 1906

Mortoniella Ulmer, 1906: 95 [Type species: *Motoniella bilineata*, by monotypy].

Mexitrichia Mosely, 1937: 158 [Type species: *Mexitrichia leroda*, by original designation] Blahnik & Holzenthal 2008, to synonymy.

Paraprotoptila Jacquemart, 1963: 342 [Type species: *Paraprotoptila armata*, by monotypy] Flint *et al*. 1999, to synonymy with *Mexitrichia*.

A monophyletic *Mortoniella* including a single undescribed species from Brazil was recovered with weak support in analyses of the TOTAL COMBO and SUBSET COMBO datasets. However, in analyses of the TOTAL MORPH and SUBSET MORPH datasets, *Mortoniella* was found to be paraphyletic, and in the SUBSET COI dataset, polyphyletic. Blahnik and Holzenthal (2008) synonomized *Mexitrichia* with *Mortoniella* based on similarities of the male genitalia and the fact that *Mexitrichia* was historically defined based on the presence of apical fork V in the hind wing, a plesiomorphic character for Trichoptera. It is perhaps the retention of this and other primitive characters (*e.g.*, an unmodified tergum X and sternum VIII), that accounts for the difficulty in recovering its monophyly in some datasets. We sampled species from both *Mortoniella* and *Mexitrichia*, as previously defined. Based on morphological evidence, and the fact that a monophyletic *Mortoniella* that included the *Mexitrichia* species was recovered in combined analyses, the decision by Blahnik and Holzenthal (2008) to synonymize *Mexitrichia* with *Mortoniella* is justified by this study. A synapomorphy of *Mortoniella* is that the inferior appendages form a composite structure consisting of paired processes fused together basally and to the ventral margin of the phallic apparatus and ventrolaterally to the endotheca, with associated articulated appendages fitting into pockets (character 82) (Figs. 23A, D).

Diagnosis of *Mortoniella* (Figs. 2B, 11A, 11B, 23). The genus *Mortoniella* is diagnosed based on several unique structures of the male genitalia, termed the "phallic ensemble" by Blahnik and Holzenthal (2008). The male genitalia are characterized by the presence of a dorsomesal spine or process arising internally from the phallobase, which varies in shape among species. The dorsomesal spine or process articulates with the phallicata, which sometimes bears a dorsolateral process that may function as a guide for the spine (Blahnik & Holzenthal 2008). Tergum X is usually excavated dorsomesally to accommodate the spine. Some species of *Itauara* have a similar dorsomesal spine, but in this genus, the spine arises posteriorly as an apparent extension of the phallobase. The inferior appendages of *Mortoniella* are also distinct among protoptilines. They are fused to one another basally and to the ventral part of endotheca, and enclose a pair of sclerotized pockets on the mesal surface. These pockets are associated with pair of small, digitate, articulated appendages arising from the posteroventral part of the phallobase. Members of the genus *Protoptila* also bear the small articulated appendages that fit into associated pockets. However, in *Protoptila*, the inferior appendages are apparently absent. The 2 genera can also be separated based on differences in the shape of tergum X, the lack of a dorsomesal spine in *Protoptila*, and an unmodified sternum VIII, which is posteriorly projecting in *Protoptila*.

The forewing venation of *Mortoniella* is most similar to that of *Protoptila*, with apical forks I, II, and III present, a completely fused Cu1 and Cu2, and the presence of 3A (although in some species of both genera, 3A is absent). However, *Mortoniella* can sometimes be distinguished by the row of erect setae, which is positioned only slightly below the Cu2 vein in *Mortoniella*, but far below the Cu2 vein in *Protoptila*. The hind wing venation of *Mortoniella* is quite variable, with either apical forks II, III, and V or II and III only or II only present.

Adult. Body, wings, and appendages nearly uniformly fuscous or tawny brown. Wings often with white transverse line along entire length of anastomosis (Fig. 2B). Head broader than long, vertex rounded, either 1 distinct pair or 1 divided pair of suboval anterior setal warts, large suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 11A) shape variable, relatively broad past anastomosis in most species, more narrow in others, apex rounded, occasionally with scale-like setae. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile; fork II sessile; fork III petiolate, stem variable in length; Cu1 complete, reaching wing margin; Cu1 and Cu2 completely fused; row of erect setae present slightly below Cu2; A3 when present, looped; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 11B) shape variable, relatively broad past anastomosis in most species, more narrow with margins nearly parallel in other species; venation variable, either with apical forks II only, or II and III only, or II, III, and V present; Sc and R1 fused basally; A2 when present, looped. Tibial spurs either 0,4,4 or 1,4,4; foretibial spur extremely reduced and hair-like. Sternum VI process present, shape variable, subtriangular, elongate and digitate, short and digitate, or laterally flattened, apex rounded or attenuate and pointed, usually associated with oblique apodeme posteriorly.

Male genitalia (Fig. 23). Preanal appendages absent. Segment IX anterior margin rounded, posterolateral margin without lateral process or lobes; tergum IX uniformly narrow, simple, without processes; sternum IX uniformly narrow, mesally without modification. Tergum X fused to tergum IX dorsomesally, or "hinged"; dorsomesal margin excavated, divided or bifid apicomesally, but sometimes with single, prominent, elongate process; dorsolateral margin without processes, as small paired lobes, or with irregular setose processes; ventrolateral margin without processes, with irregular, paired setose lobes, or with 1 or more irregular, paired, setose, digitate lobes directed posterad. Inferior appendages present, forming composite structure consisting of paired processes fused together basally, ventrolaterally to endotheca, and to ventral margin of phallobase associated with articulated appendages. Phallobase with small pair of articulated digitate, rod-like appendages with membranous apices, associated with modified pockets ventrobasally. Parameres present, arising dorsolaterally from endotheca, sclerotized, sinuous or mostly straight. Phallic ensemble with single dorsomesal spine or process emerging internally from phallobase. Endophallus membranous, enlarged and convoluted when invaginated, sometimes with sclerotized regions and spines.

Female genitalia. (Females unknown for many species.) Truncate posteriorly, not extensible. Abdominal segment VIII short, synscleritous, posterolateral margin slightly incised, dorsal and ventral margins sometimes invaginated posteromesally. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Padunia* Martynov, 1910

Padunia Martynov, 1910: 425 [Type species: *Padunia adelungi* Martynov, 1910, by monotypy]
Matrioptila Ross, 1956: 164 [Type species: *Protoptila jeanae* Ross, 1938, by original designation] **new synonym**
Nepaloptila Kimmins, 1964: 37 [Type species: *Nepaloptila coei* Kimmins, 1954, by original designation] **new synonym**
Poeciloptila Schmid, 1991: 243 [Type species: *Poeciloptila falcata* Schmid, 1991, by original designation] **new synonym**
Temburongpsyche Malicky, 1995: 15 [Type species: *Temburongpsyche anakan* Malicky, 1995, by original designation] **new synonym**
Uenotrichia Tsuda, 1942: 228 [Type species: *Uenotrichia fasciata* Tsuda, 1942, by monotypy]; Fischer, 1971, as senior synonym of *Padunia*; Marshall, 1979, as junior synonym of *Padunia*.

The Asian Clade is comprised of genera from the East Palaearctic and Oriental regions (*Padunia*, *Nepaloptila*, *Poeciloptila*, *Temburongpsyche*) and the Nearctic region (*Matrioptila*). In all the TOTAL datasets, a paraphyletic *Nepaloptila* is basal to a subclade containing these remaining genera. Within this subclade, *Padunia* as traditionally constituted, was recovered as a paraphyletic taxon in all analyses of the TOTAL datasets. Additionally, a sister relationship was consistently found between the type species, *Padunia adelungi*, and *Matrioptila jeanae*. Relationships of the remaining 5 *Padunia* species included in the analyses were either unresolved or paraphyletic, interspersed with species of *Poeciloptila* and *Temburongpsyche*.

Kimmins (1964) remarked that the male genitalia of *Nepaloptila* resembled those of *Matrioptila* but differentiated the 2 genera based on *Nepaloptila*'s retention of fork V in the forewing. However, complete wing venation is plesiomorphic for Trichoptera and thus this character is not appropriate for defining *Nepaloptila* by current cladistic standards.

Likewise, Ross (1956) defined *Matrioptila* based on several plesiomorphic characters (retention of fork V in the hind wing, separate course of Cu2 in forewing, and distinct claspers in male genitalia). Although *Matrioptila* can be distinguished from the other Asian genera by the absence of fork V in the forewing, this fork apparently has been lost independently several times in the evolution of Protoptilinae lineages and, at this taxonomic level, may simply be autapomorphic for the species.

Poeciloptila was primarily defined by 2 male genitalic features: 1) membranous lateral faces of segment X, which enables segment X to "rock downwards," and 2) a large ventral branch of phallus (Schmid 1991). However, examination of *Poeciloptila* revealed the lateral faces of tergum X to be lightly sclerotized and immobile, rather than membranous, a characteristic that is not uncommon in other protoptiline genera. Furthermore, the ventral branch of the phallus is not unique to *Poeciloptila*, being present in some species of *Padunia*, *Nepaloptila*, and *Matrioptila*.

Malicky (1995) established *Temburonpsyche* as a new genus based on its broad, ring-like segment IX, reduction of various "appendices" in the form of "finger"-like processes along the margin of segment IX, a large phallus, and tibial spur formula 0,3,3. Yet, a broad ring-like segment IX is plesiomorphic in Trichoptera.

Additionally, many of these genera have a somewhat enlarged phallus and the various finger-like processes along the margin of segment IX are most likely homologous to similar processes in some species of the other genera, which have also apparently undergone a reduction. Finally, *Matrioptila* shares the 0,3,3 spur formula, so this character is not unique to *Temburongpsyche*. Furthermore, Malicky (1995) also remarked that the wing venation of *Temburongpsyche* corresponds closely to that of *Padunia* and *Poeciloptila,* and the head and thoracic warts are similar to those of *Nepaloptila*.

To sum, many of these genera were defined solely on plesiomorphic characters or features that are not unique to the particular taxon. Although the larvae of *Nepaloptila*, *Poeciloptila* and *Temburongsyche* are unknown, the larvae of *Matrioptila* and *Padunia* are very similar—both construct dorsoventrally flattened cases, have "trifid" tarsal claws with 3 equally sized processes, and similarly shaped mesonotal sclerites. Furthermore, the female genitalia of these 5 genera are very similar in shape. Therefore, to reflect phylogeny accurately, the following species are hereby transferred to *Padunia* (all **new combinations**): from *Matrioptila*: *P. jeanae* (Ross), from *Nepaloptila*: *P. coei* (Kimmins), *P. jisunted* (Malicky & Chantaramongkol), *P. kanikar* (Malicky & Chantaramongkol), *P. ruangjod* (Malicky & Chantaramongkol); from *Poeciloptila*: *P. almodad* (Malicky & Chantaramongkol), *P. atyalpa* (Schmid), *P. eringena* (Malicky & Silalom), *P. falcata* (Schmid), *P. maculata* (Tian & Li), and *P. phyllis* (Malicky & Chantaramongkol); and from *Temburongpsyche*: *P. anakan* (Malicky). Additionally, *Padunia briatec* (Malicky & Chantaramongkol), which was transferred to *Poeciloptila* by Schmid (1991), is hereby returned to *Padunia* (**restored combination**).

Monophyly of this newly defined *Padunia* was recovered in all analyses based on the following synapomorphies: 1) the phallobase has its dorsal margin forming a sclerotized sheath that is produced anteriorly, with its ventral margin membranous or absent (character 90) (Figs. 24A, B); 2) segments VIII and IX of the female genitalia are fused (character 99) (Fig. 31C).

Diagnosis of *Padunia* (Figs. 6D, 13, 14, 24–27, 31C). The male genitalia of *Padunia* are quite variable among species. Nonetheless, the genus can be diagnosed principally by the structure of the phallobase. The phallobase is very elongate and tubular with a dorsal margin consisting of a sclerotized sheath produced anteriorly. Ventrally, the phallobase is not sclerotized, but highly membranous, or even apparently absent. Another distinctive feature of *Padunia* is the subtriangular aspect of the anterior margin of segment IX. However, this character is not completely diagnostic for the genus since the segment IX anterior margin of 1 species is slightly rounded (*P. coei*) and another is straight (*P. anakan*). The female genitalia of *Padunia* are also distinct among protoptilines, with segments VIII, IX, and X fused together dorsally. Another diagnostic feature of *Padunia* is the presence of a pair of distinct setal patches on the mesoscutellum. These patches differ from the round conspicuous setal warts present in *Tolhuaca*, but because they may be difficult to see for most species, they may be easily overlooked and have not been rendered or discussed in any any previous species diagnoses or descriptions.

The forewing venation of *Padunia* is either complete [*P. coei*, *P. kanikar* (Malicky & Chantaramongkol, 1992), *P. jisunted* (Malicky & Chantaramongkol, 1992), *P. ruangjod*] or incomplete, with apical forks I, II, and V present. While *Tolhuaca* also has complete forewing venation (plesiomorphic for Trichoptera), the latter condition (presence of apical forks I, II, and V only), is unique among Protoptilinae. The hind wing of *Padunia* is most similar to certain species of *Itauara*, having apical forks II and V present, however the 2 genera can be easily separated based on differences in the male genitalia.

Adult. Body, wings, and appendages nearly uniformly fuscous. Wings often with conspicuous white, broad, transverse marks in anal region and along anastomosis. Head broader than long, vertex rounded, pair of distinct, suboval anterior setal warts, large suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large subtriangular or suboval pronotal setal warts, occasionally covered with dense scale-like setae. Mesothorax usually wider than long, but longer than wide in *P. jeanae*, without apparent tegular glands; mesoscutum with pair of elongate anteromesal setal warts, suboval posterolateral warts; mesoscutellum with pair of small, round, distinct setal patches. Forewing (Figs. 13A, 13C, 14A, 14C) relatively broad past anastomosis or with margins nearly parallel, apex rounded or subacute, occasionally with scale-like setae. Male occasionally with callosity present in anal and apical costal region of forewing. Forewing venation either complete or incomplete; when incomplete, with apical forks I, II, and V present; Sc and R1 usually distinct along their entire lengths, occasionally intersecting near costal margin; fork I sessile or only slightly petiolate with extremely short stem; fork II sessile or only slightly petiolate with extremely short stem; fork III petiolate, stem

about as long as fork; fork IV petiolate, stem about as long as fork; fork V petiolate, or sessile; Cu1 complete, reaching wing margin; Cu1 and Cu2 distinct along their entire lengths; row of erect setae present along Cu2; A3 looped, if present; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein, except in *P. falcata* and *P. phyllis* in which the males have highly modified wings with broad half-ellipse-shaped flap along costal margin folding to cover about half wing. Hind wing margins nearly parallel, tapering only slightly past anastomosis; venation variable, either with apical forks II only, or II and III only, or II, III, and V (*P. bilineata* species group); Sc and R1 separate or converging near wing margin; A2 absent. Tibial spurs variable, either 0,4,4; 0,4,3; 0,3,3; or 1,4,3; foretibial spur extremely reduced and hair-like. Males occasionally with pair of finger-like lateral processes on sternum V associated with glandular structures (Fig. 6D). Sternum VI process present, short and digitate, elongate and digitate, or tooth-like point; apex rounded or attenuate and pointed, usually associated with oblique apodeme posteriorly.

Male genitalia (Figs. 25–27). Terga VII and VIII interstitial region occasionally with glandular structure dorsomesally and dorsolaterally. Segment IX anterior margin usually subtriangular, or rarely, slightly rounded (*P. coei*) or straight (*P. anakan*), posterolateral margin occasionally with lateral processes or lobes; tergum IX well developed, relatively broad; sternum IX usually narrow, occasionally broad (*P. anakan*). Tergum X completely fused to and indistinguishable from segment IX, except in *P. anakan* in which tergum X appears to be membranous. Inferior appendages present, although often vestigial, or 2 distinct appendages fused to one another basally, attached ventrally to phallus and articulating with segment IX (*P. jeanae*) or fused completely and integrated with segment IX, forming either elongate or short paired ventrolateral processes or single ventromesal process, sometimes bifid. Parameres absent. Phallobase simple, elongate tubular structure, dorsal margin with sclerotized sheath produced anteriorly, with membranous or apparently absent ventral margin. Phallic apparatus occasionally with apicoventral branch and bearing 1 or more apical spines.

Female genitalia (Fig. 31C). Truncate posteriorly, not extensible. Abdominal segment VIII syncleritous, anterolateral margin slightly subtriangular or projecting, posterolateral margin often deeply incised. With segments VIII, IX, and X fused, bearing pair of short digitate cerci apically.

Genus *Protoptila* Banks, 1904

Protoptila Banks, 1904: 215 [Type species: *Beraea* ? *maculata* Hagen, 1861, by original designation].

A monophyletic *Protoptila* was strongly supported in all analyses and based on the following synapomorphies suggested by Blahnik and Holzenthal (2006): 1) phallobase with an axe-shaped dorsal apodeme (character 93) (Fig. 28C); 2) sternum VIII projecting medially and subtending segment IX to which it is partially fused (character 63) (Figs. 28A, B). A 3rd synapomorphy of *Protoptila* includes a ventromesal process on sternum IX projecting posterad (character 72) (Figs. 28A, B).

Diagnosis of *Protoptila* (Figs. 2C, 3A, 6E, 11C, 11D, 28). The genus *Protoptila* can be recognized by several distinct features of the male genitalia. The dorsum of the phallobase has an enlarged, flattened, often axe-shaped phallic apodeme. *Protoptila* can also be characterized by the shape of sternum VIII, which projects posterad and subtends sternum IX, to which it is often fused. Additionally, tergum VIII usually has elongate setae along its posterior margin. Tergum X is also distinct among protoptilines, composed of lateral branches, with basal and apical portions. Like *Mortoniella*, *Protoptila* also has small, sclerotized, digitate, articulated appendages attached to the phallobase ventrally that fit into modified pockets on the posteroventral portion on the phallobase. However, unlike *Mortoniella*, *Protoptila* apparently lacks the associated inferior appendages. The 2 genera can also be separated by differences in the shapes of tergum X and sternum VIII.

The forewing venation is most similar to *Mortoniella*, with apical forks I, II, and III present, a completely fused Cu1 and Cu2, and 3 anal veins present (although some species of both genera have no 3A). However, the 2 can usually be separated by the row of erect setae, which is positioned far below the Cu2 vein in *Protoptila*.

Adult. Body, wings, and appendages pale or tawny brown, often intermingled with rufous or golden hairs, tibia and tarsi yellowish brown. Wings often with few pale cream-colored or white hairs, spots, or transverse line along anastomosis and small white specks or spots along apical margin (Fig. 2C). Head broader than long, vertex rounded, either 1 distinct pair or 1 divided pair of suboval anterior setal warts, small suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2

times length of pedicel. Maxillary palps (Fig. 6E) 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax with 2 large, subtriangular or suboval pronotal setal warts, occasionally covered with dense scale-like setae. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval anteromesal setal warts, although occasionally entire region setose with no distinct patch, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 11C) relatively narrow, with margins nearly parallel, apex oblique. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I, II, and III present; Sc and R1 distinct along their entire lengths; fork I sessile; fork II sessile; fork III petiolate, stem longer than fork; Cu1 complete, reaching wing margin; Cu1 and Cu2 completely fused; row of erect setae present below Cu2; A3 looped, if present; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 11D) narrow and scalloped past anastomosis; apical fork II present; Sc and R1 fused basally; A2 absent. Tibial spurs 1,4,4; foretibial spur extremely reduced and hair-like. Sternum VI process present, laterally flattened or subtriangular, apex attenuate and pointed, usually associated with oblique apodeme posteriorly.

Male genitalia (Fig. 28). Preanal appendages absent. Tergum VIII posterior margin with elongate setae. Sternum VIII projecting medially and subtending segment IX. Segment IX anterior margin rounded, posterolateral margin occasionally with lateral processes or lobes; tergum IX usually strap-like or narrow, simple, without processes; mesally, with ventromesal projection directed posterad. Tergum X partially fused to tergum IX, consisting of lateral branches with basal and distal segments, often articulated; dorsomesal margin divided or bifid apicomesally. Inferior appendages absent. Parameres either present or absent; when present, arising laterally from endotheca, often membranous basally, with apical sclerotization and spine, variable in shape. Phallobase not apparently reduced, with enlarged, flattened, often axe-head shaped apodeme dorsally; small pair of articulated digitate, rod-like appendages with membranous apices, associated with modified pockets ventrally; and often with paired, posteriorly projecting processes. Phallic apparatus with varying shape of phallicata, and associated spines and processes. Endophallus membranous, enlarged and convoluted when invaginated, sometimes with sclerotized regions and spines.

Female genitalia. Truncate posteriorly, not extensible. Abdominal segment VIII short, synscleritous, posterolateral margin slightly incised. Sternum VIII often with rounded ventrolateral lobes. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Scotiotrichia* Mosely, 1934

Scotiotrichia Mosely, 1934: 160 [Type species: *Scotiotrichia ocreata* Mosely, 1934, by original designation].

Placement of the monotypic genus *Scotiotrichia* remains unresolved. A sister relationship between *Scotiotrichia* and *Canoptila* was weakly supported in the parsimony analysis of the TOTAL MORPH dataset.

Diagnosis of *Scotiotrichia* (Figs. 10C, 10D, 29)**.** *Scotiotrichia* can be recognized by distinct features of the male genitalia and forewing venation. Among protoptilines, the forewing venation of *Scotiotrichia* is unique, having only apical forks I and II. The male genitalia are simple, with a greatly enlarged and hood-like tergum X. Segment IX is narrow dorsally and straplike ventrally. The phallobase is greatly enlarged, and has a pair of small lateral processes medially, and another pair posterolaterally. The endophallus of *Scotiotrichia* is large and highly membranous and contains a pair of large, tooth-like processes ventrally. The male genitalia are quite reminiscent of those of *Tolhuaca* in that both have large phallobases, strap-like sterna IX, and large endophallic membranes. However, the shape of the phallobase differs between the 2 genera: That of *Tolhuaca* is rounded and much more produced apicomesally whereas in *Scotiotrichia*, the dorsal and ventral margins are straight. *Culoptila* and *Cariboptila* also have enlarged phallobases and strap-like or absent sterna IX, but can easily be differentiated from *Scotiotrichia* based on their retention of inferior appendages and differences in forewing venation.

Adult. Head broader than long, vertex rounded, pair of distinct, suboval anterior setal warts, large suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short; 2nd segment bulbous; last 3 segments each nearly as long as 1st and 2nd segments combined. Prothorax with 2 large, subtriangular or suboval pronotal setal warts. Mesothorax wider than long, without apparent tegular glands; mesoscutum with pair of suboval anteromesal setal warts, suboval posterolateral warts; mesoscutellum sparsely setose, without distinct setal warts. Forewing (Fig. 10C) relatively narrow, with margins nearly parallel, apex oblique. Male without apparent forewing callosity. Forewing venation incomplete, with apical forks I and II

present; Sc and R1 distinct along their entire lengths; fork I sessile; fork II petiolate; Cu1 complete, reaching wing margin; Cu1 and Cu2 intersecting near anastomosis; row of erect setae present below Cu2; A3 absent; crossveins difficult to discern, but apparently forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 10D) margins nearly parallel, tapering only slightly past anastomosis; apical fork II present; Sc and R1 fused basally; A2 absent. Tibial spurs 1,2,3; foretibial spur extremely reduced and hair-like. Sternum VI process present, short and digitate, apex rounded, associated with strong oblique apodeme posteriorly.

Male genitalia (Fig. 29). Preanal and inferior appendages absent. Segment IX anterior margin rounded, posterolateral margin without lateral process or lobes; tergum IX strap-like, simple, without processes; sternum IX strap-like, mesally, without modification. Tergum X extremely large and hood-like, without processes or lobes, incompletely fused to tergum IX with membrane or lightly sclerotized region ventrolaterally; dorsomesal margin subquadrate. Inferior appendages absent. Parameres absent. Phallobase extremely enlarged, lightly sclerotized with small, stout setae ventrally, medially with small, paired lateral processes, apicomedially with smaller paired processes. Phallic apparatus simple, without spines or processes. Endophallus membranous, enlarged and convoluted when invaginated, bearing single pair of tooth-like downturned spines ventrally.

Female genitalia. Rather elongate posteriorly, but not apparently extensible. Abdominal segment VIII syncleritous, relatively short. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

Genus *Tolhuaca* Schmid, 1964

Tolhuaca Schmid, 1964: 336 [Type species: *Tolhuaca cupulifera* Schmid, 1964, by original designation].

Monophyly of *Tolhuaca* was strongly supported in all analyses. Furthermore, a sister relationship to the remaining Protoptilinae was found in all analyses, except in the SUBSET COI dataset. Synapomorphies of *Tolhuaca* include a highly inflated, barrel-shaped phallobase and an absence of inferior appendages, although these apomorphies are not unique to the genus.

Diagnosis of *Tolhuaca* (Figs. 5A, 6B, 6C, 12A, 12B, 30, 31A). The genus *Tolhuaca* can be recognized by features of the thorax, and male and female genitalia. Among protoptilines, *Tolhuaca* is distinct in having a pair of conspicuous round setal warts on the mesoscutellum, the plesiomorphic condition in Trichoptera. *Padunia* also has setal warts on the mesoscutellum, but they differ from those of *Tolhuaca* in being more patch-like and less conspicuous. The phallobase of *Tolhuaca* is extremely enlarged and barrel-shaped, with a sclerotized projection apicomesally. An additional distinct feature includes the large, tubular endophallus, which is highly membranous and contains several sclerotized spines and other internal structures. The male genitalia are similar to those of *Scotiotrichia*, *Cariboptila*, and *Culoptila*—each have enlarged phallobases and reduced or absent sterna IX. However, these genera can be separated based on differences in the shape of the phallobase and wing venation. The female genitalia are also unique among Protoptilinae. They are elongate and oviscapt, and have 2 pairs of rod-like internal apodemes. The female genitalia of *Scotiotrichia* are also rather elongate, but do not appear to be oviscapt, and lack the rod-like apodemes. The forewing venation of *Tolhuaca* is complete, like that of some species of *Padunia*, yet these genera are easily separated by differences in the shape of sternum IX in the male genitalia.

Adult. Tibia and tarsi yellowish brown. Head (Fig. 5A) broader than long, vertex rounded, with pair of small anteromesal setal warts, pair of distinct, elongate anterior setal warts, large suboval posterior setal warts, suboval or triangular and bulging posterolateral setal warts. Ocelli present. Antennal scape less than or equal to 2 times length of pedicel. Maxillary palps 5-segmented, 1st and 2nd segments short with elongate setae apically; 2nd segment bulbous; last 3 segments each nearly as long as 1st and 2nd segments combined. Prothorax (Fig. 5A) with 2 large subtriangular or suboval pronotal setal warts. Mesothorax (Fig. 5A) longer than wide, without apparent tegular glands; mesoscutum with pair of elongate anteromesal setal warts, suboval posterolateral warts; mesoscutellum with pair of small, round, distinct setal warts. Forewing (Fig. 12A) relatively broad past anastomosis, apex rounded, with erect or retrorse setae along some veins, most noticeably along Cu2. Male without apparent forewing callosity. Forewing venation complete; Sc and R1 distinct along their entire lengths; fork I petiolate, but with extremely short stem, or sessile; fork II sessile; fork III petiolate, stem shorter than fork; fork IV petiolate, stem shorter than fork; fork V sessile; Cu1 complete, reaching wing margin; Cu1 and Cu2 distinct along their entire lengths; row of erect setae present along Cu2; A3 looped; crossveins forming relatively linear transverse cord; discoidal cell longer than Rs vein. Hind wing (Fig. 12B) broad past anastamosis; apical forks II, III, and V present; Sc and R1 fused basally or converging near wing margin; A2 present, looped. Tibial spurs 1,4,4; foretibial spur extremely reduced and hair-like (Fig. 6B, 6C). Sternum VI process present, thumb-like and prominent or elongate and digitate, apex rounded, associated with strong oblique apodeme posteriorly.

Male genitalia (Fig. 30). Preanal and inferior appendages absent. Segment IX anterior margin rounded; tergum IX well developed, relatively broad, simple, without processes; sternum IX strap-like. Tergum X completely fused to tergum IX but with membranous connection visible; dorsomesal margin divided or bifid apicomesally; dorsolateral margin without processes; ventrolateral margin with small, irregular, paired setose lobes. Parameres absent. Phallobase extremely enlarged, barrel-shaped, lightly sclerotized with small, stout setae, without processes, produced and sclerotized apicomesally. Phallic apparatus simple, without spines or processes. Endophallus membranous, greatly enlarged, and rather tubular when evaginated, with sclerous spines or rod-like structures internally.

Female genitalia (Fig. 31A). Extensible oviscapt. Abdominal segment VIII syncleritous, about as wide as long. Internally, with 2 pairs of long, slender, sclerotized, rod-like apodemes arising from lateral margins of segments VIII and IX and extending cephalad to segments VI and VII, respectively. Segments IX and X closely associated, with pair of small digitate cerci dorsolaterally.

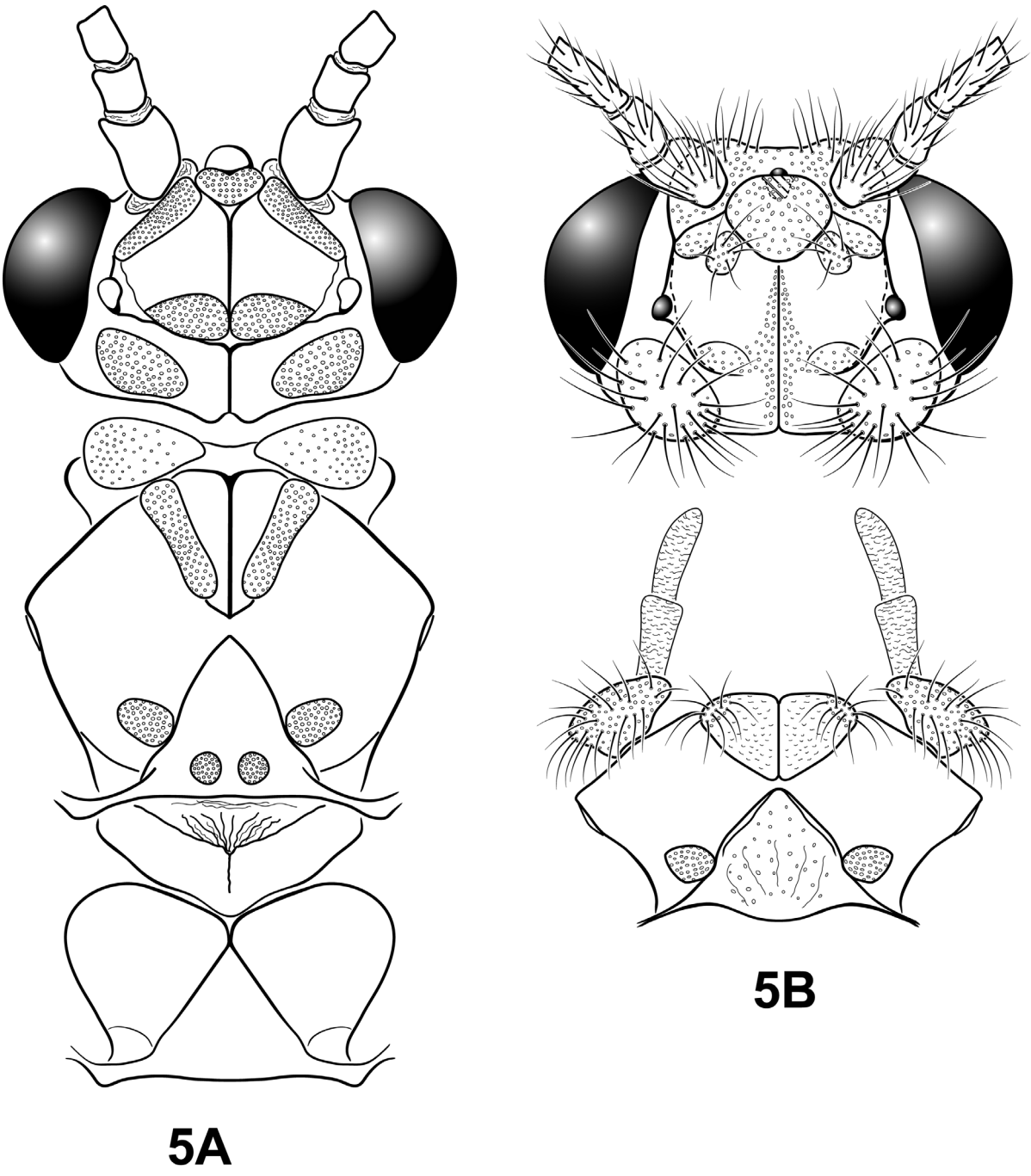

FIGURE 5. (A) *Tolhuaca cupulifera* Schmid, adult head and thorax, dorsal. (B) *Canoptila bifida* Schmid, adult head and mesothorax, dorsal.

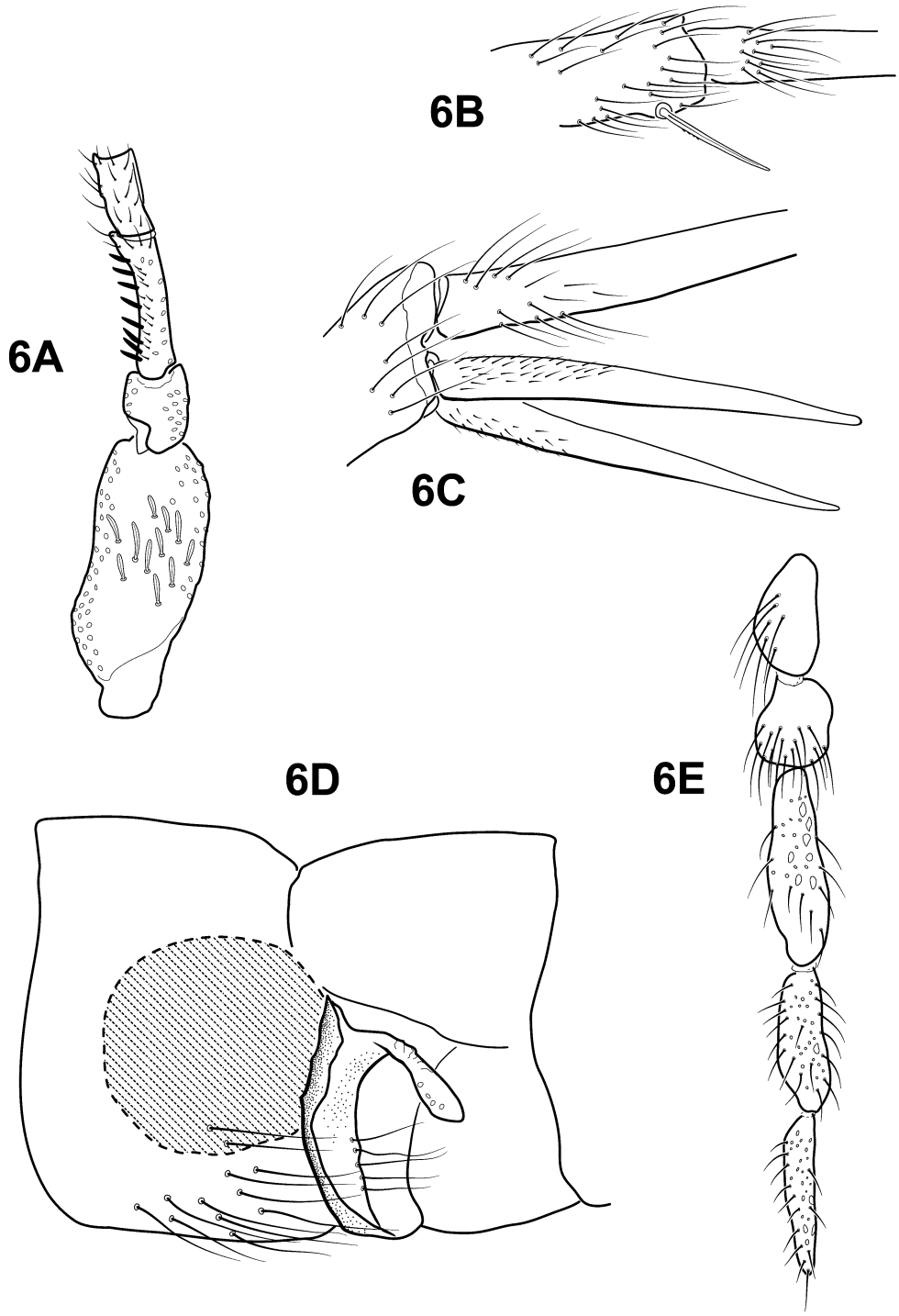

FIGURE 6. Adult. (A) *Cariboptila cubana* (Sykora), antennal segments 1–4, left lateral. (B, C) *Tolhuaca cupulifera* Schmid, foretibial (B) and mesotibial spurs, left lateral (C), at same scale for comparison. (D) *Padunia adelungi* Martynov, left lateral view of left lateral process of sternum V and associated internal glandular structure. (E) *Protoptila* species, maxillary palp, left lateral.

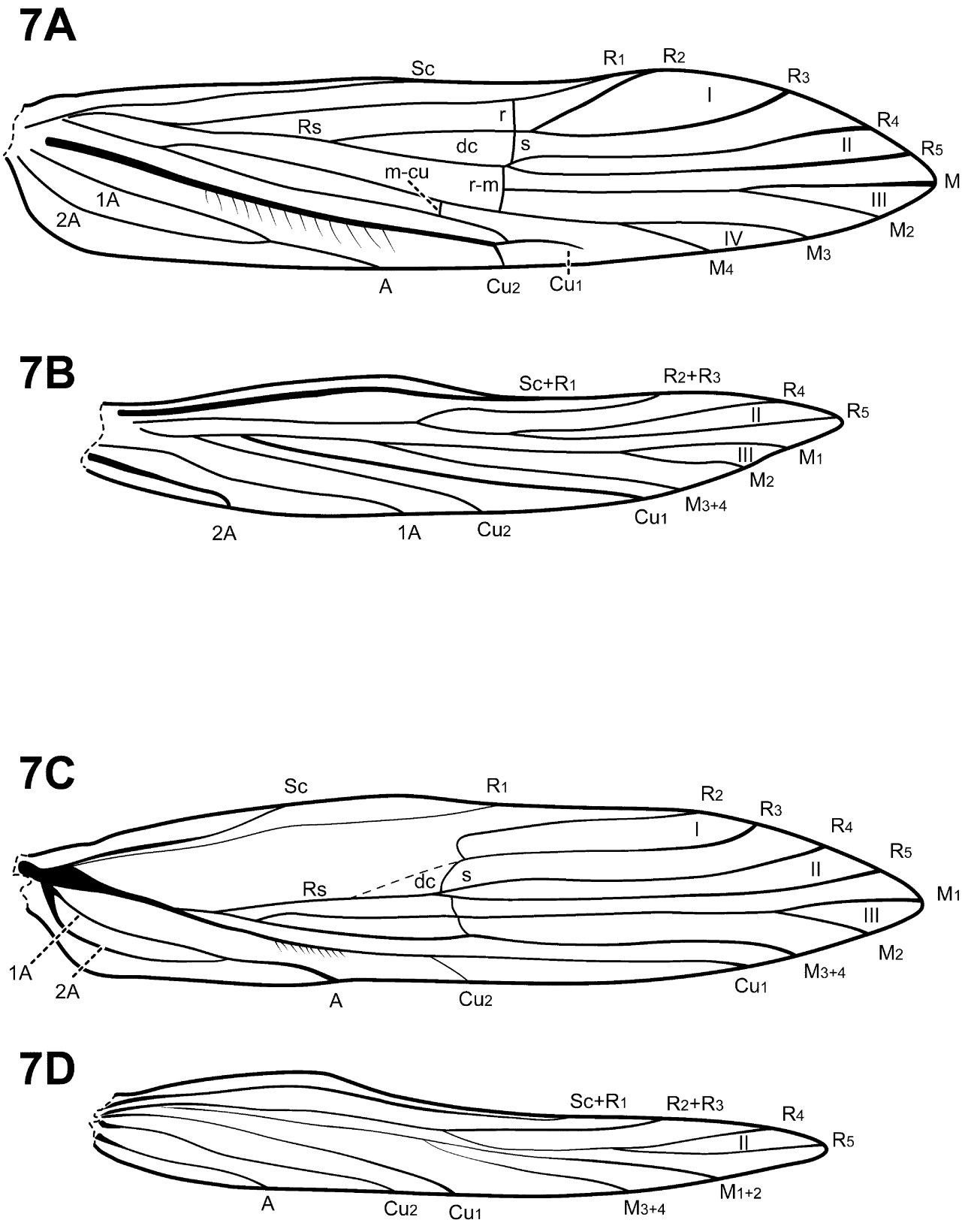

FIGURE 7. Fore- and hind wings. (A, B) *Culoptila hamata* Blahnik & Holzenthal. (C, D) *Cariboptila cubana* (Sykora). Wings between taxa not to scale.

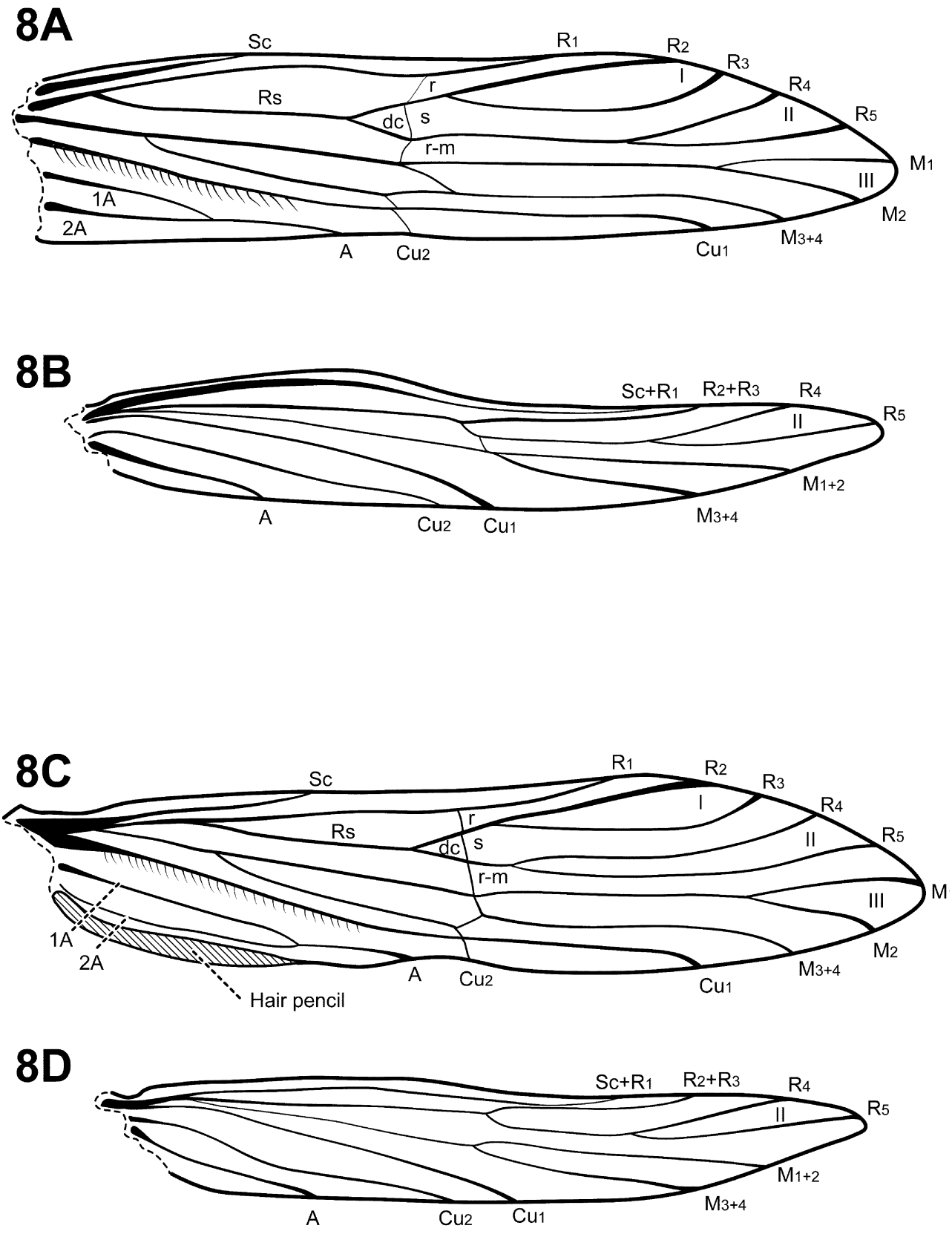

FIGURE 8. Fore- and hind wings. (A, B) *Cariboptila orophila* Flint. (C, D) *Cariboptila pedophila* (Flint). Wings between taxa not to scale.

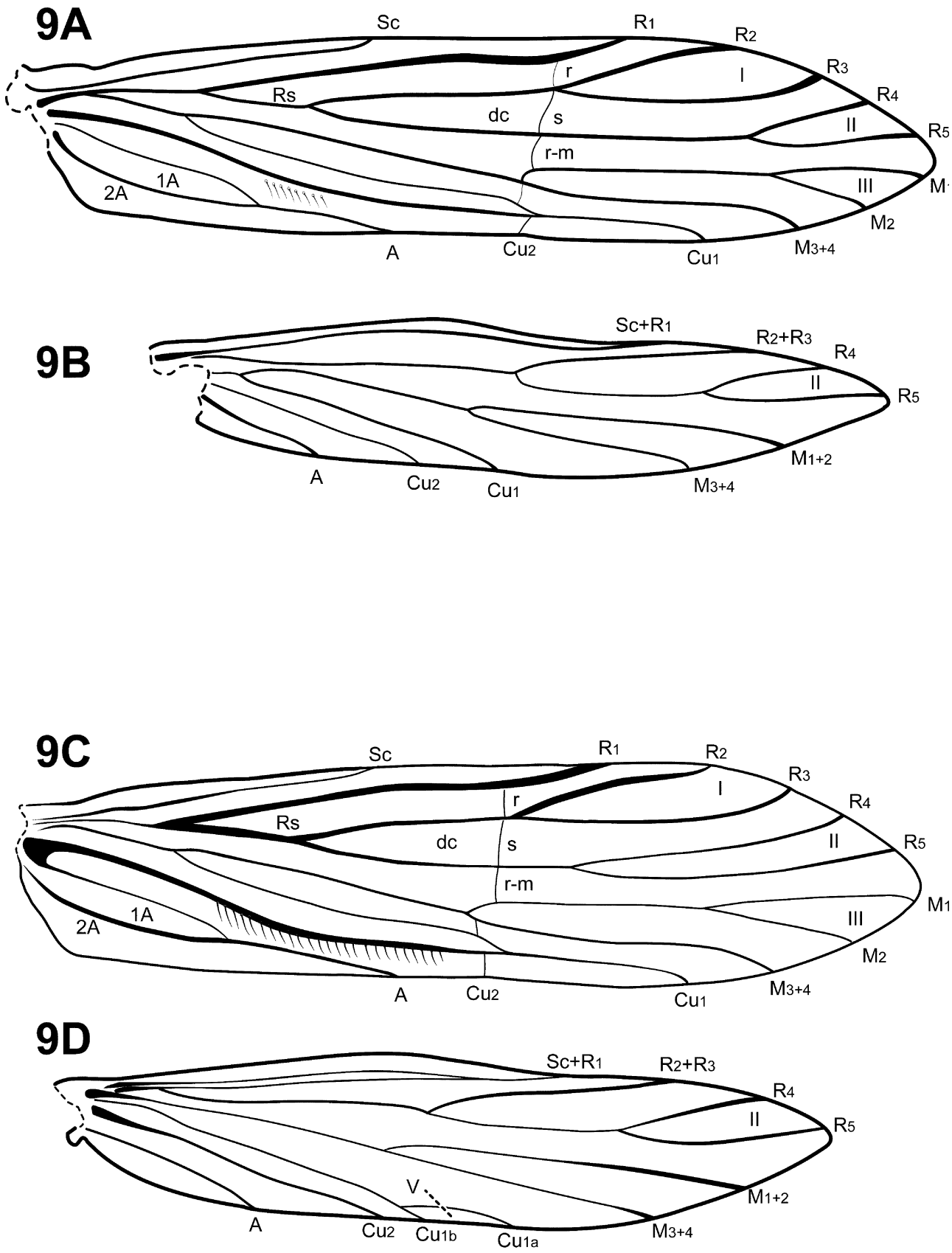

FIGURE 9. Fore- and hind wings. (A, B) *Canoptila bifida* Schmid. (C, D) *Itauara brasiliana* (Mosely). Wings between taxa not to scale.

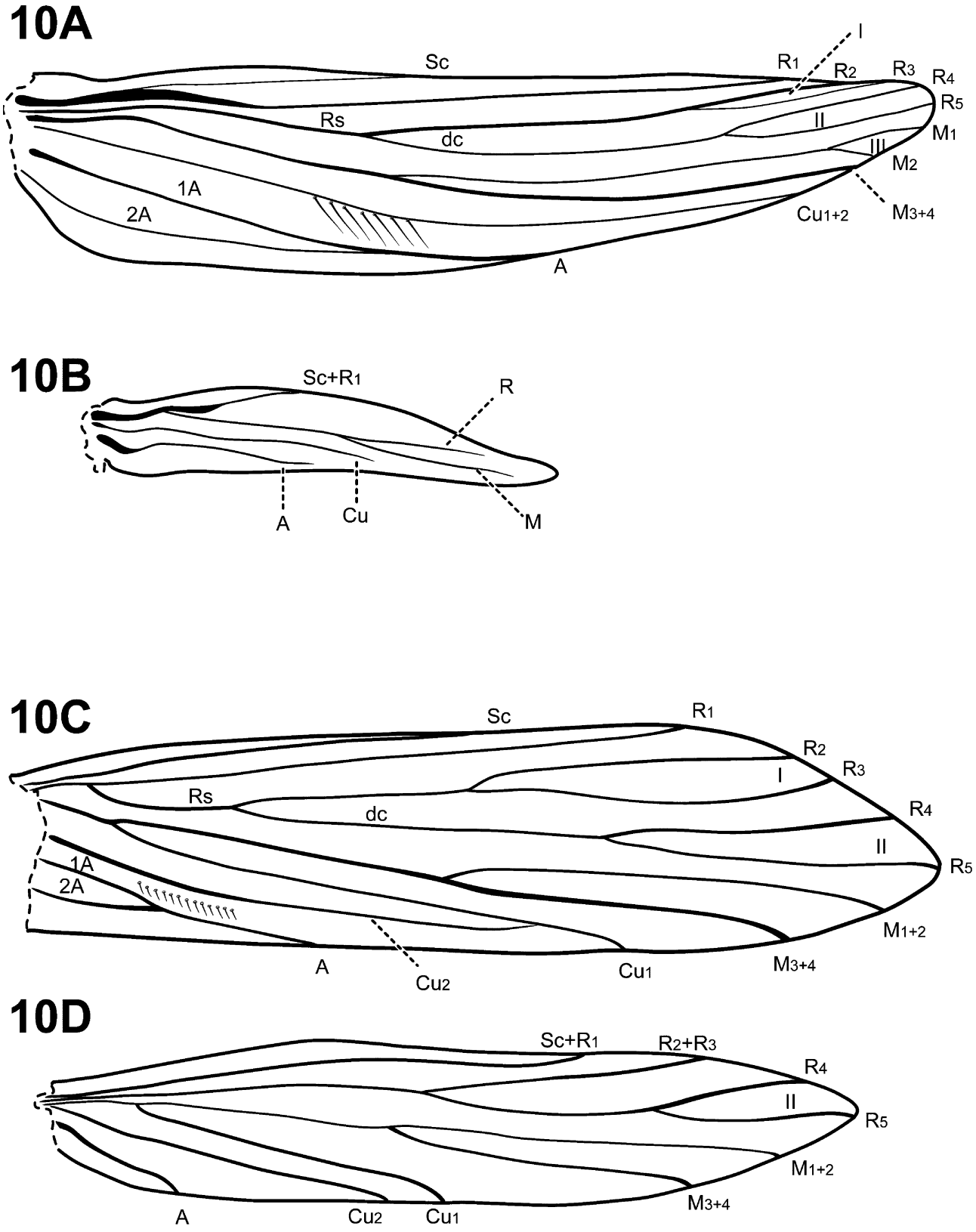

FIGURE 10. Fore- and hind wings. (A, B) *Merionoptila wygodzinskyi* Schmid. (C, D) *Scotiotrichia ocreata* Mosely. Wings between taxa not to scale.

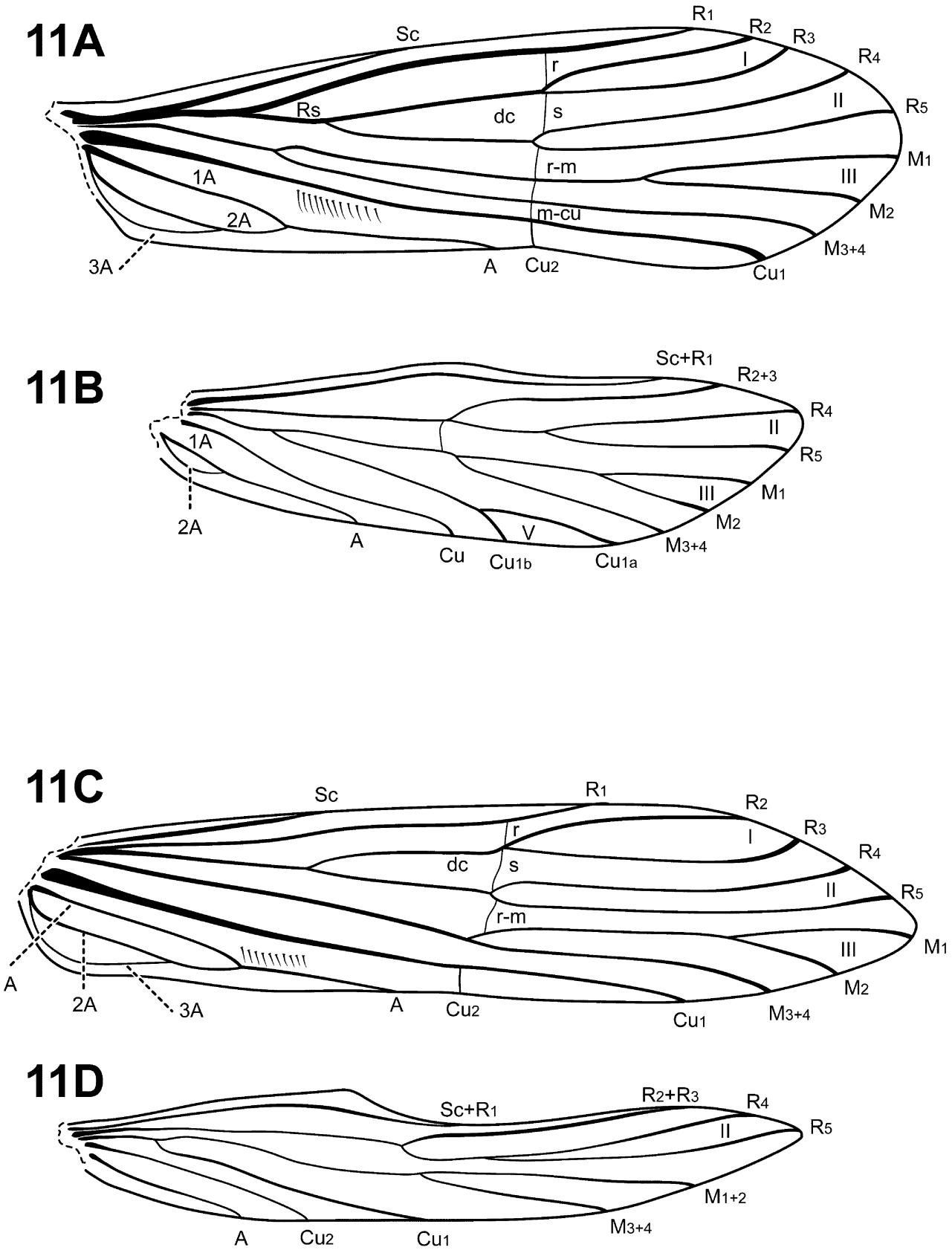

FIGURE 11. Fore- and hind wings. (A, B) *Mortoniella roldani* Flint. (C, D) *Protoptila maculata* Banks. Wings between taxa not to scale.

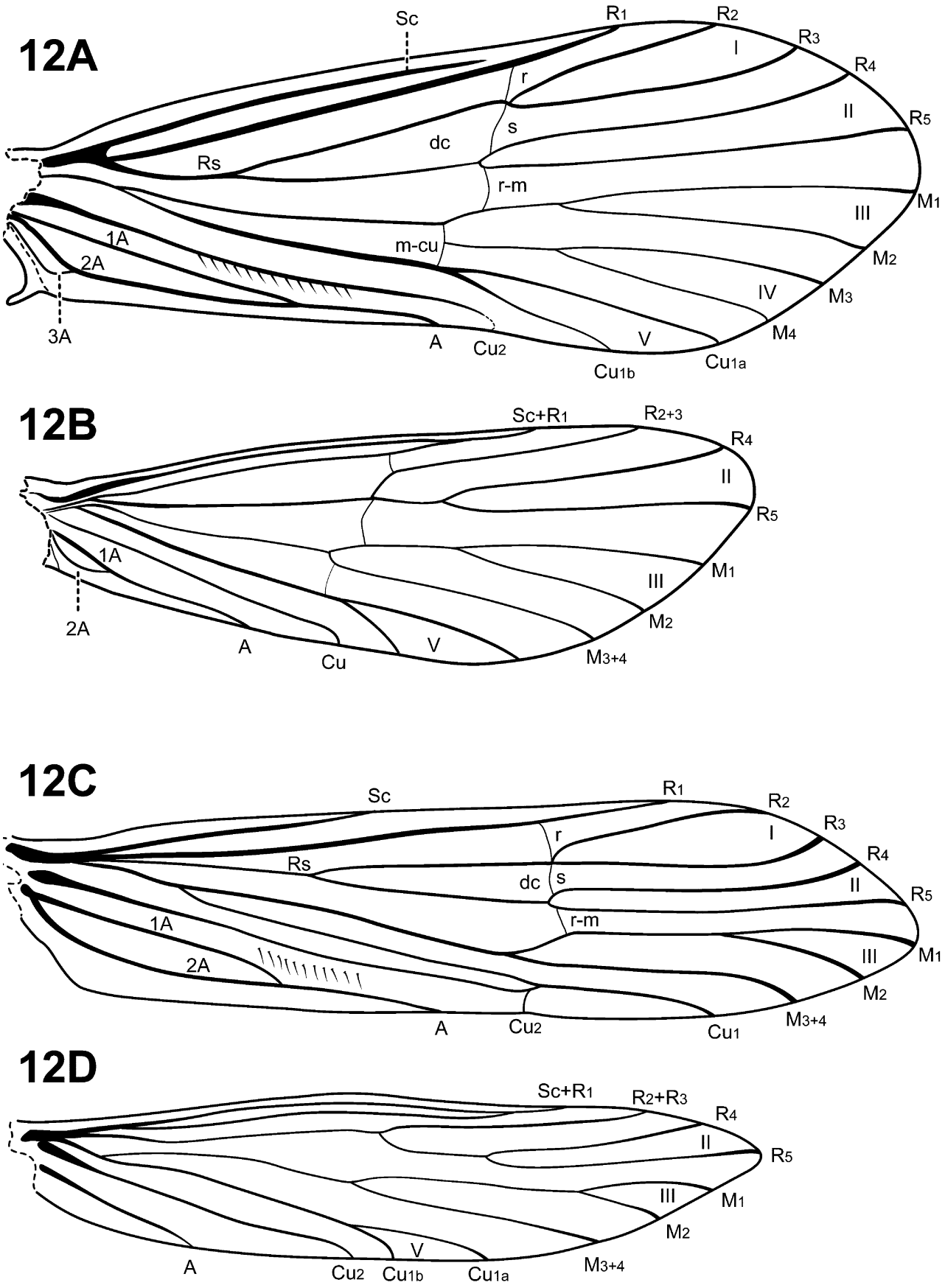

FIGURE 12. Fore- and hind wings. (A, B) *Tolhuaca cupulifera* Schmid. (C, D) *Mastigoptila longicornuta* Flint. Wings between taxa not to scale.

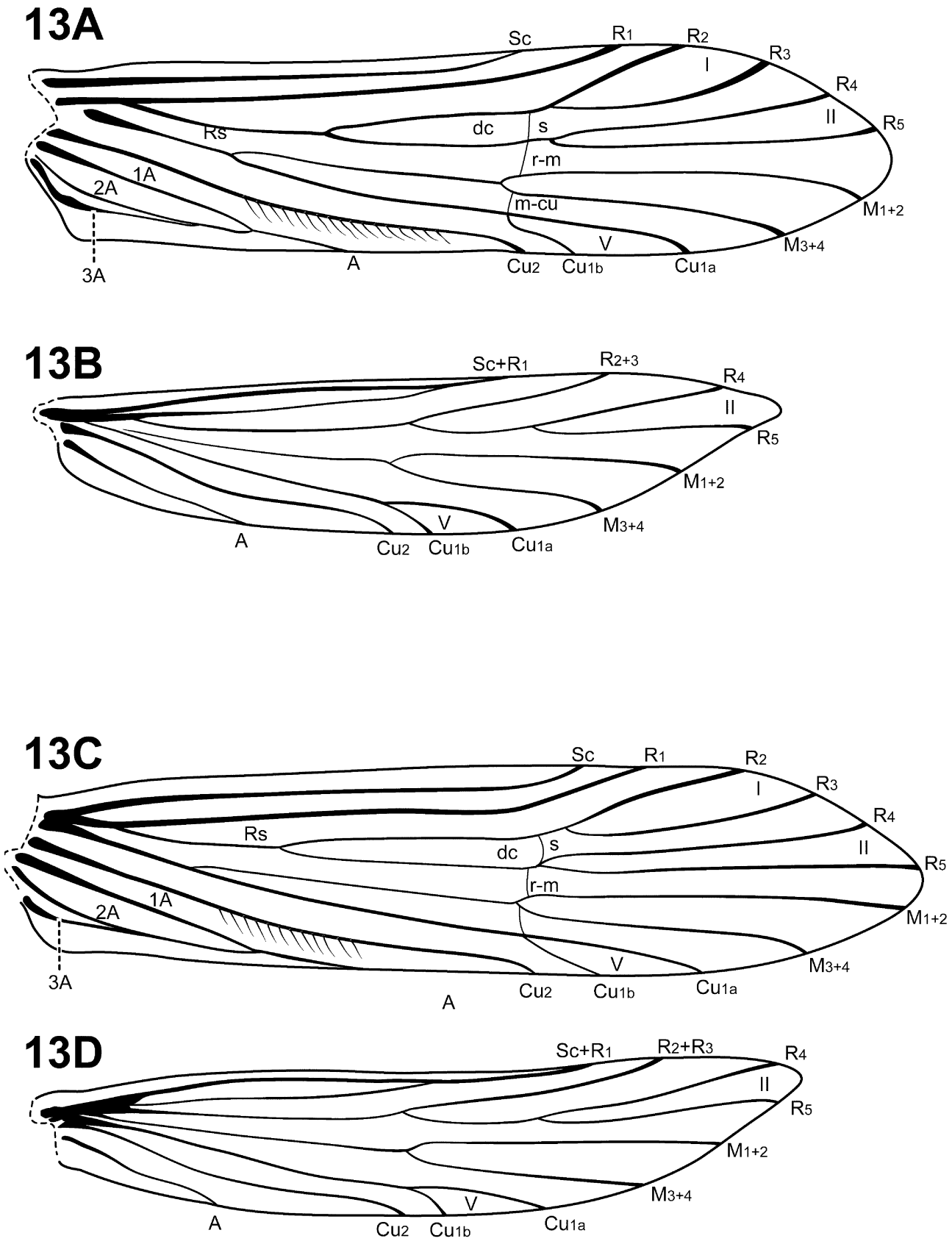

FIGURE 13. Fore- and hind wings. (A, B) *Padunia adelungi* Martynov. (C, D) *Padunia jeanae* (Ross). Wings between taxa not to scale.

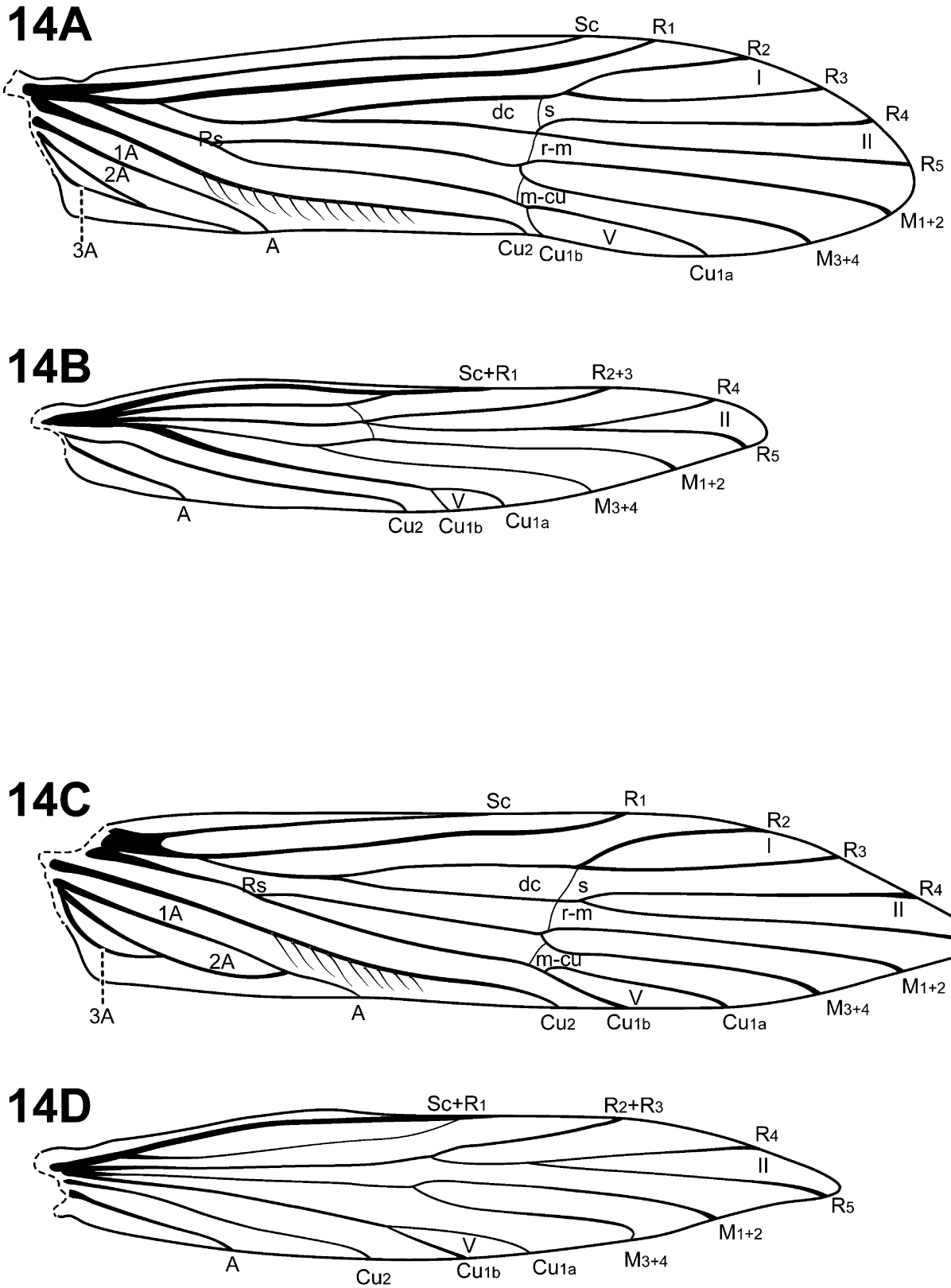

FIGURE 14. Fore- and hind wings. (A, B) *Padunia briatec* Malicky & Chantaramongkol. (C, D) *Padunia anaken* (Malicky). Wings between taxa not to scale.

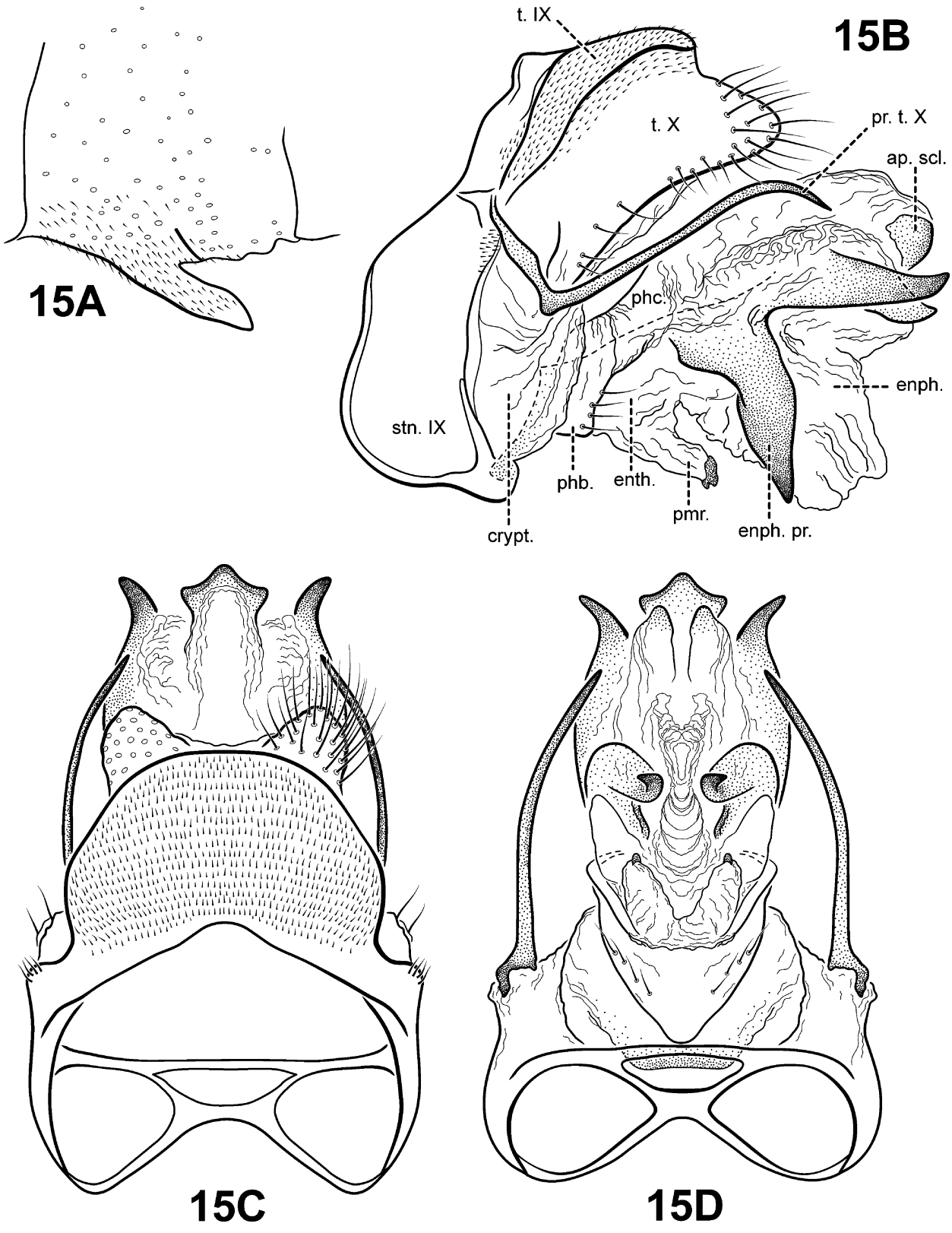

FIGURE 15. *Canoptila bifida* Schmid. (A) Process of sternum VI, left lateral. (B) Genitalia, left lateral. (C) Genitalia, dorsal. (D) Genitalia, ventral. Abbreviations: ap. scl. = apical sclerite; crypt = phallocrypt; enph. = endophallus; enph. pr. = endophallic process; enth. = endotheca; phb = phallobase; phc. = phallicata; pmr. = paramere; pr. t. X = process of tergum X; stn. IX = sternum IX; t. IX = tergum IX; t. X. = tergum X.

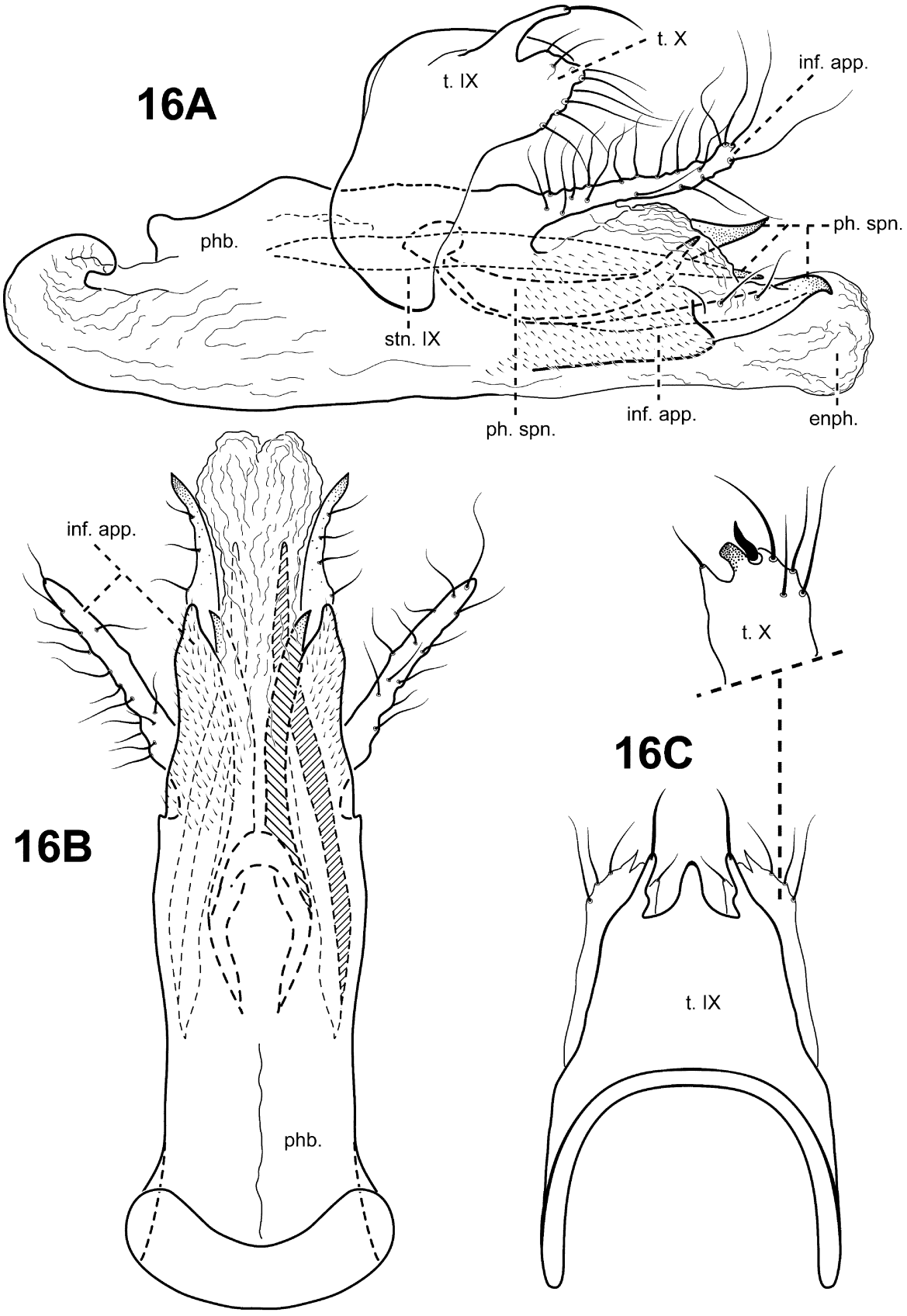

FIGURE 16. *Cariboptila orophila* Flint, male genitalia. (A) Left lateral view. (B) Ventral view of phallic apparatus. (C) Dorsal view of terga IX and X. Inset is enlarged dorsal view of tergum X. Abbreviations: inf. app. = inferior appendage; enph. = endophallus; ph. spn. = phallic spine; phb. = phallobase; stn. IX = sternum IX; t. VIII = tergum VIII; t. IX = tergum IX; t. X = tergum X.

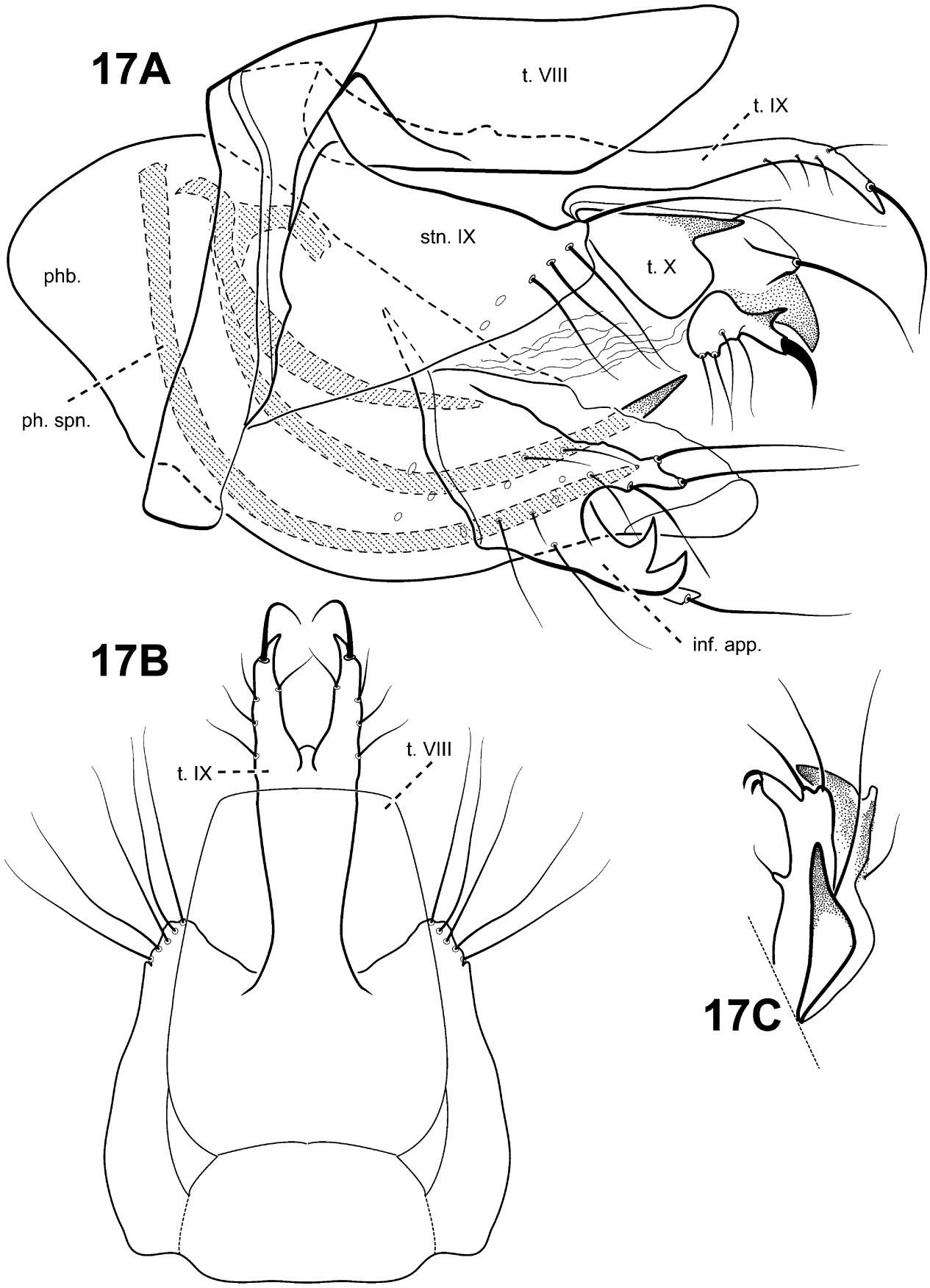

FIGURE 17. *Cariboptila cubana* (Sykora), male genitalia. (A) Left lateral view of genital capsule and phallic apparatus. (B) Dorsal view of terga VIII and IX. (C) Dorsal view of processes of tergum X. Abbreviations: inf. app. = inferior appendage; phb. = phallobase; ph. spn. = phallic spine; stn. IX = sternum IX; t. VIII = tergum VIII; t. IX = tergum IX; t. X = tergum X.

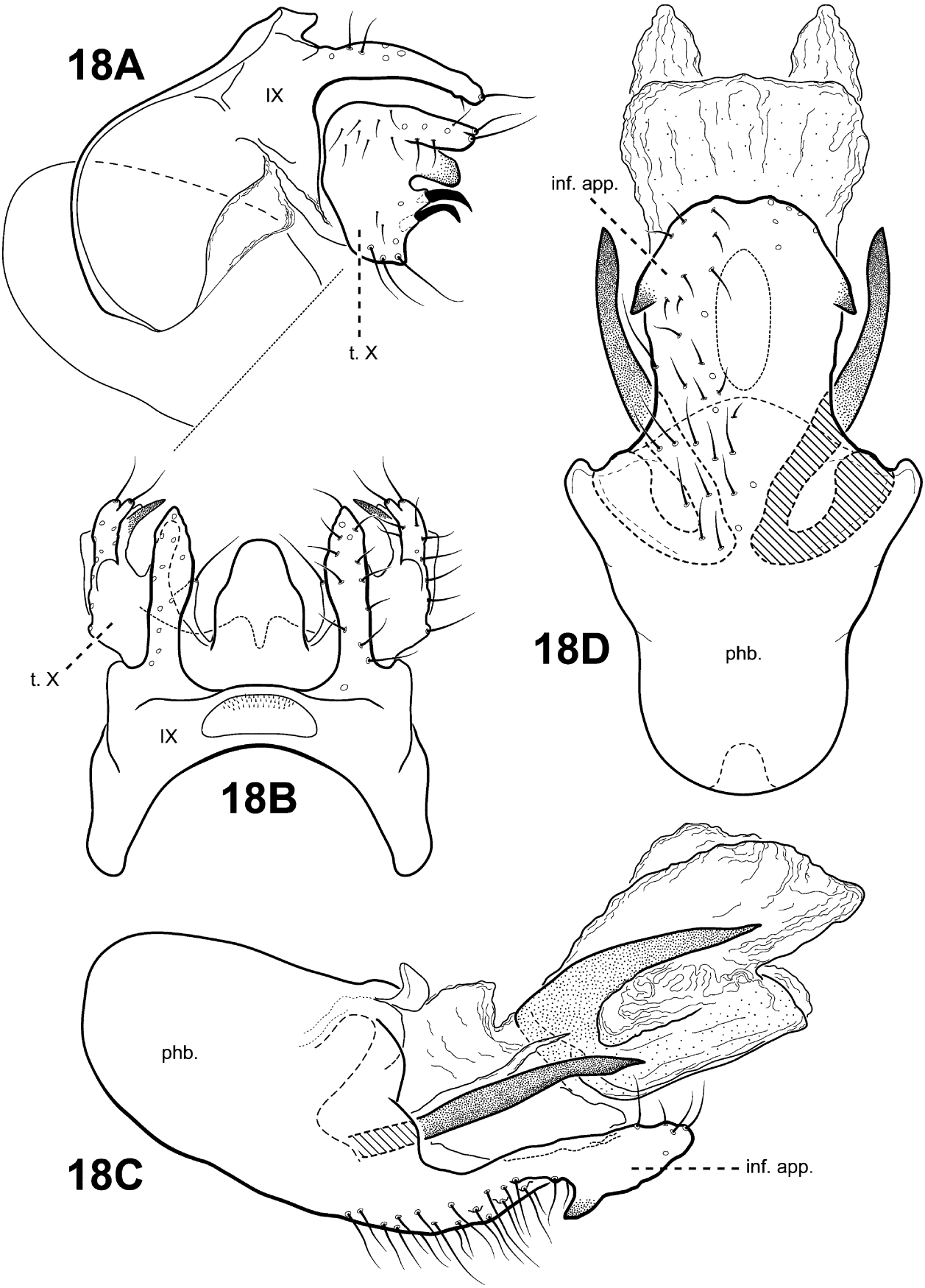

FIGURE 18. *Cariboptila pedophila* (Flint), male genitalia. (A) Left lateral view of genital capsule (terga IX and X), showing insertion of phallobase. (B) Dorsal view of terga IX and X. (C) Left lateral view of phallic apparatus. (D) Ventral view of genital capsule. Abbreviations: inf. app. = inferior appendage; phb. = phallobase; IX = segment IX; t. X = tergum X.

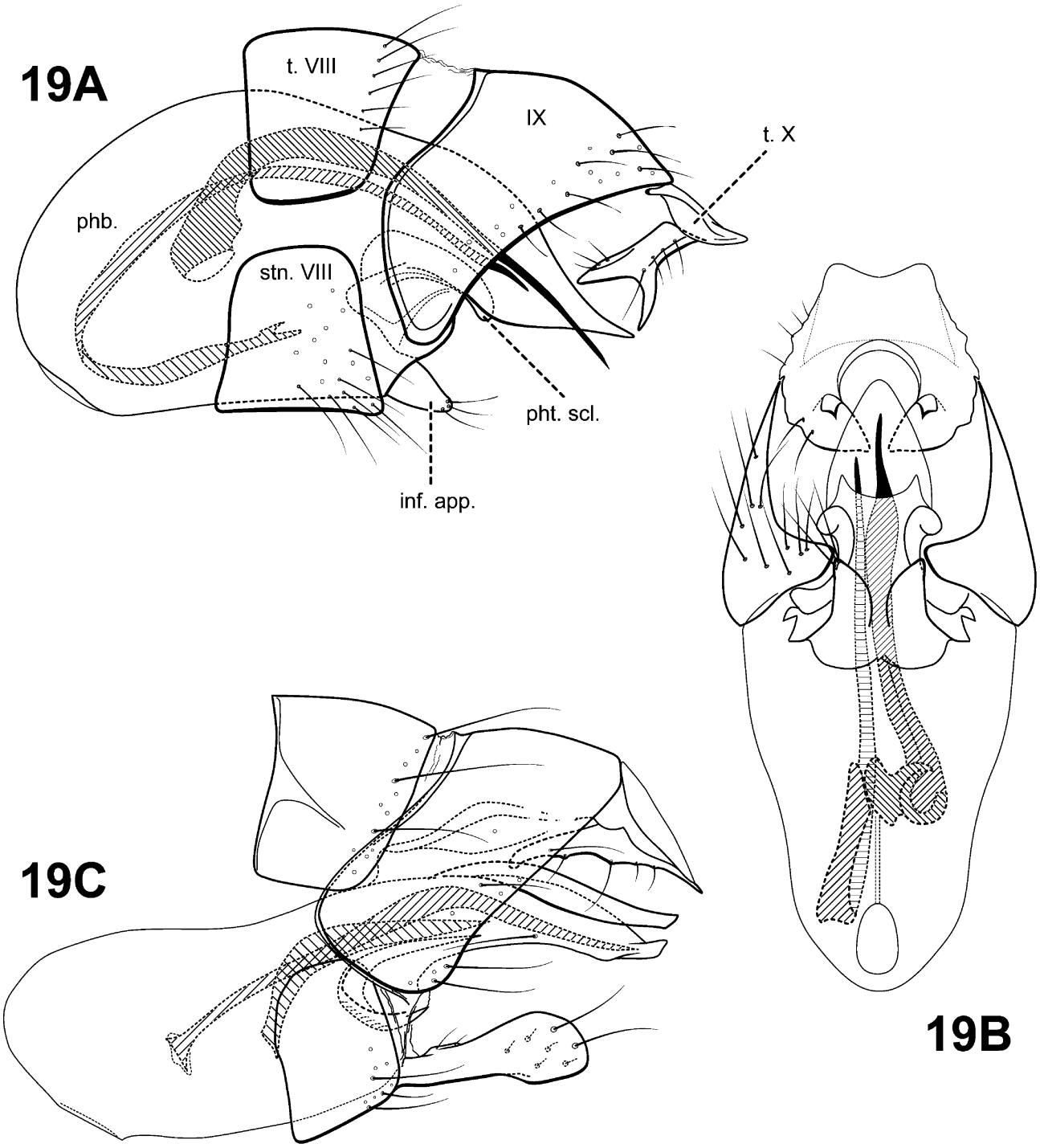

FIGURE 19. Male genitalia. (A, B) *Culoptila aluca* Mosely. (A) Left lateral. (B) Ventral. (C) *Culoptila amberia* Mosely, left lateral. Abbreviations: inf. app. = inferior appendage; phb = phallobase; pht. scl. = phallotremal sclerite; stn. VIII = sternum VIII; IX = segment IX; t. VIII = tergum VIII; t. IX = tergum IX; t. X. = tergum X. (Modified from Blahnik & Holzenthal 2006.)

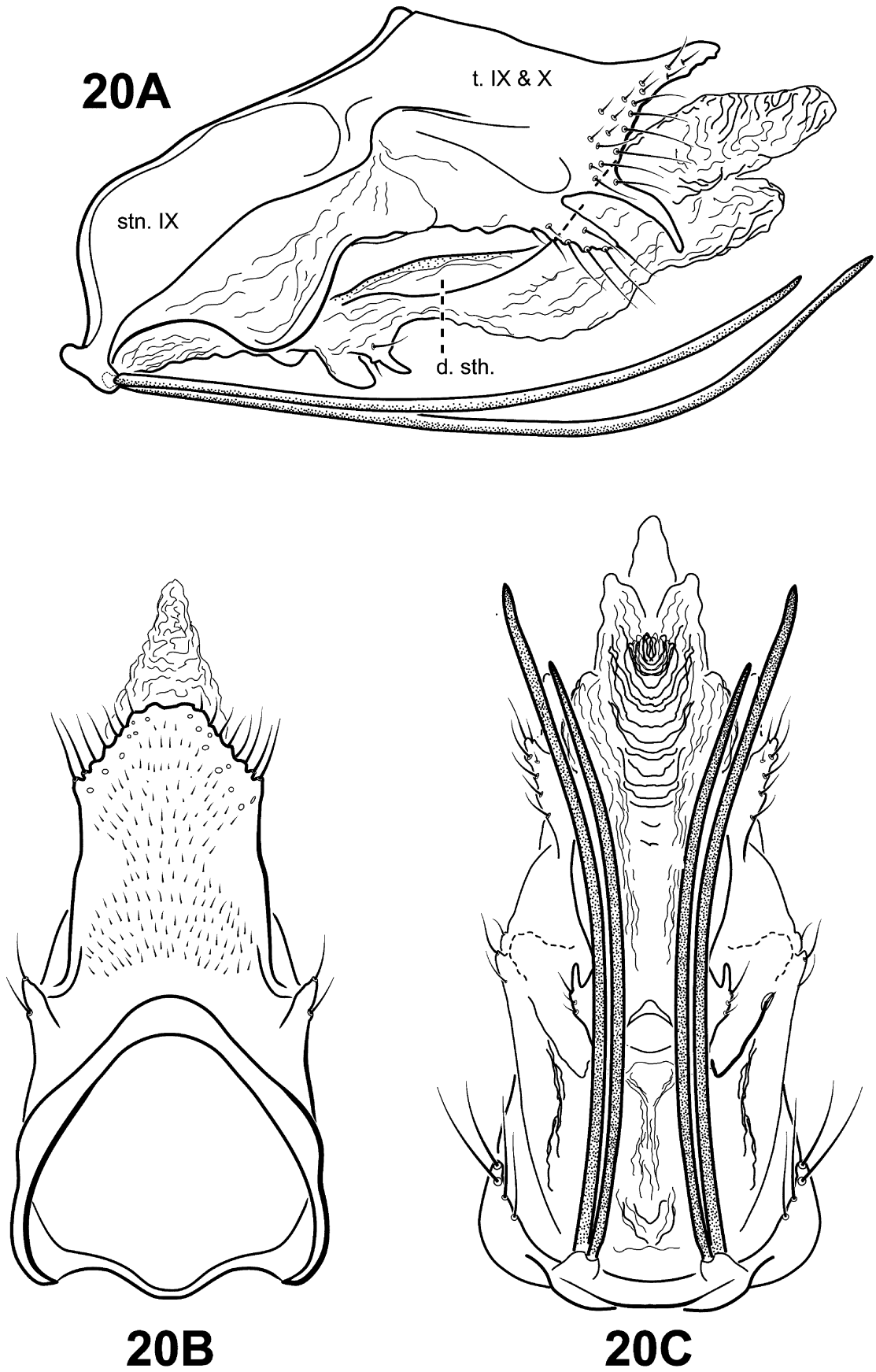

FIGURE 20. *Itauara brasiliana* (Mosely), male genitalia. (A) Left lateral view of genital capsule (terga IX and X) and phallic apparatus. (B) Dorsal view of terga IX and X. (C) Ventral view of phallic apparatus and genital capsule. Abbreviations: d. sth. = dorsal sheath; stn. IX = sternum IX; t. IX = tergum IX; t. X = tergum X.

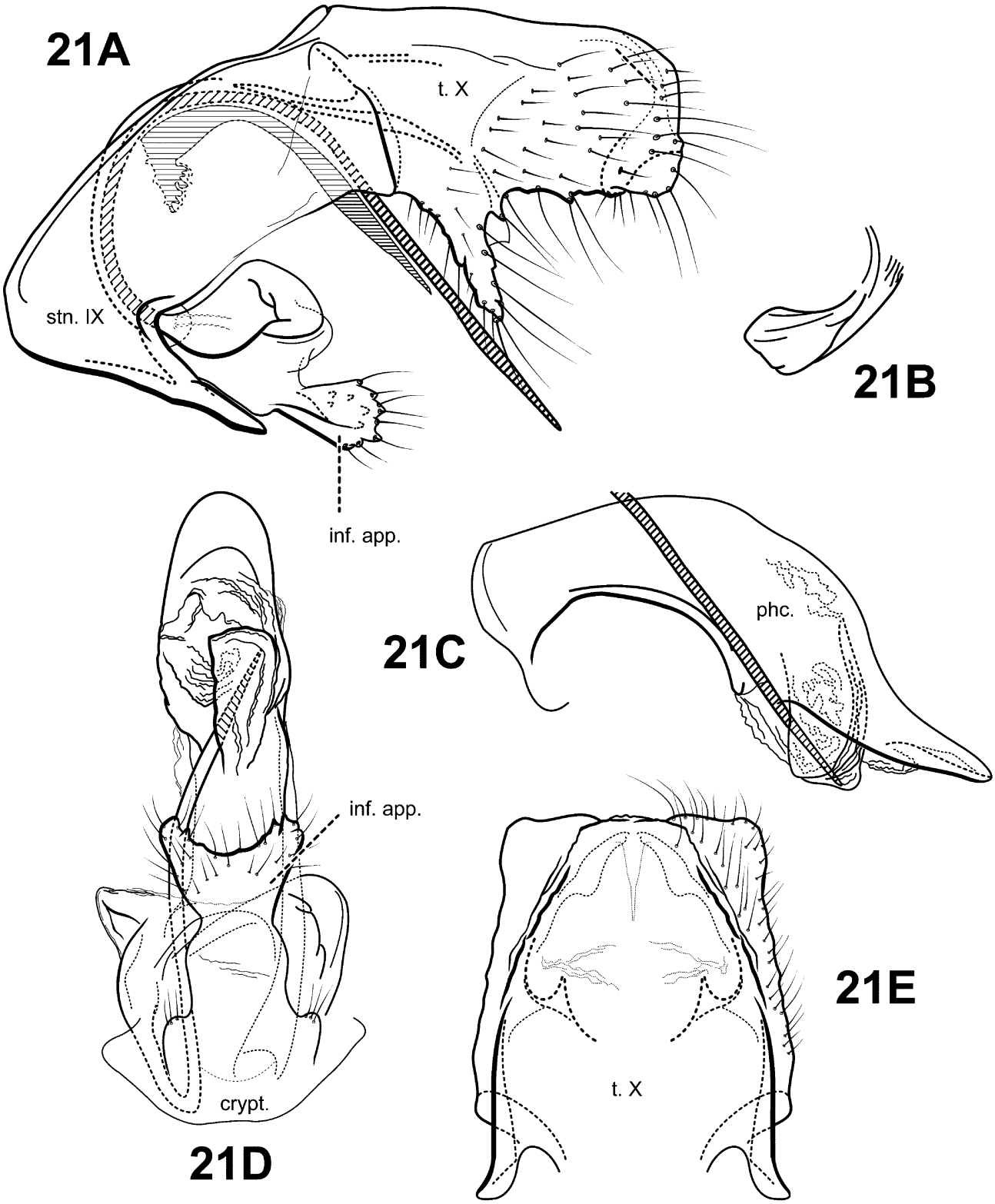

FIGURE 21. *Mastigoptila elae* Holzenthal, male genitalia. (A) Left lateral view of genital capsule and base of phallic apparatus. (B) Right lateral view of right inferior appendage. (C) Left lateral view of phallic apparatus (showing insertion of apex of recurved basodorsal process of left inferior appendage. (D) Ventral view phallic apparatus. (E) Dorsal view of tergum X. Genitalia, dorsal. Abbreviations: crypt = phallocrypt; inf. app. = inferior appendage; phc. = phallicata; stn. IX = sternum IX; t. X. = tergum X. (Modified from Holzenthal 2004.)

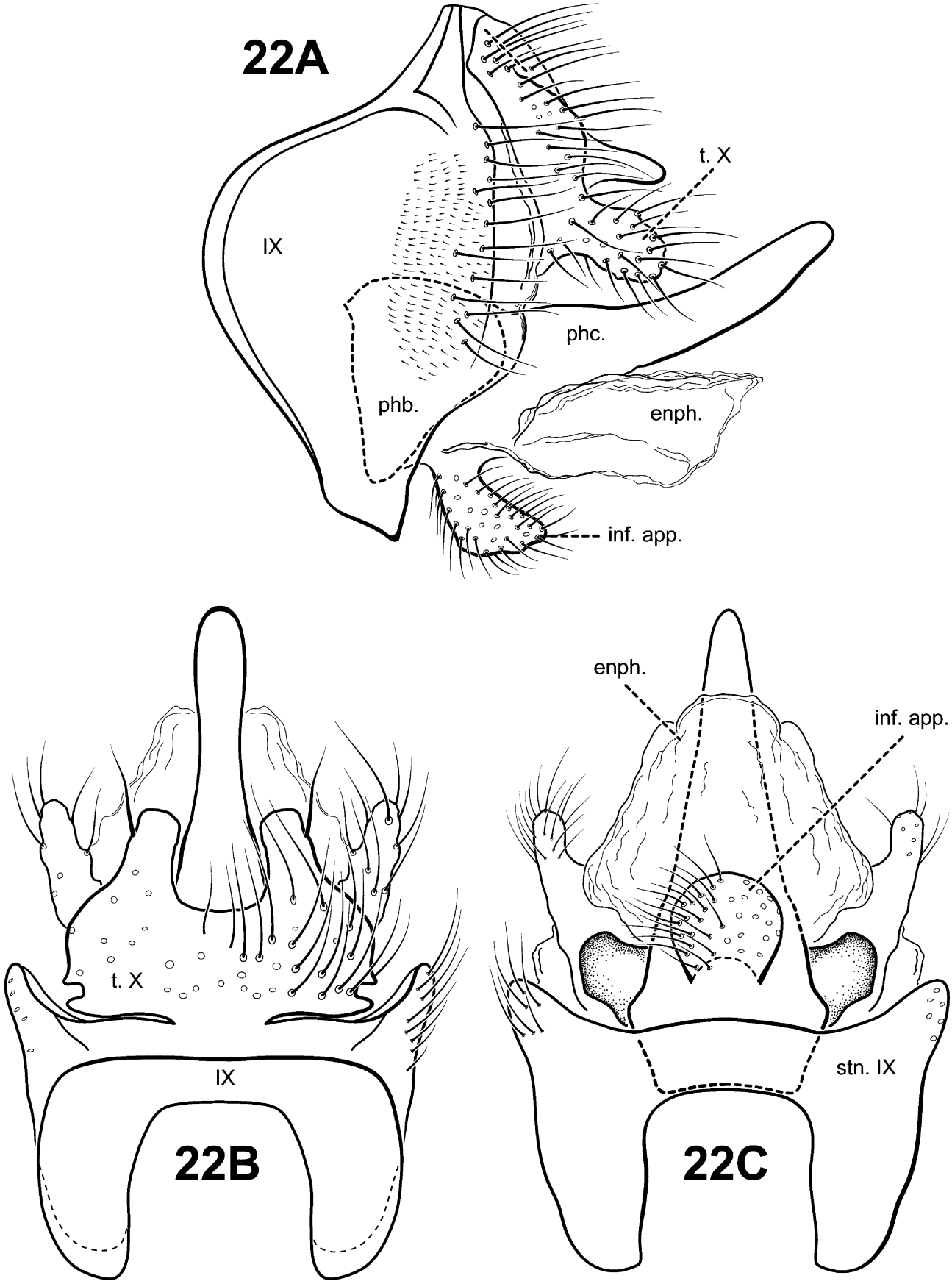

FIGURE 22. *Merionoptila wygodzinskyi* Schmid, male genitalia. (A) Left lateral view. (B) Dorsal view. (C) Ventral view. Abbreviations: enph. = endophallus; phb = phallobase; inf. app. = inferior appendage; phc. = phallicata; stn. IX = sternum IX; t. X. = tergum X.

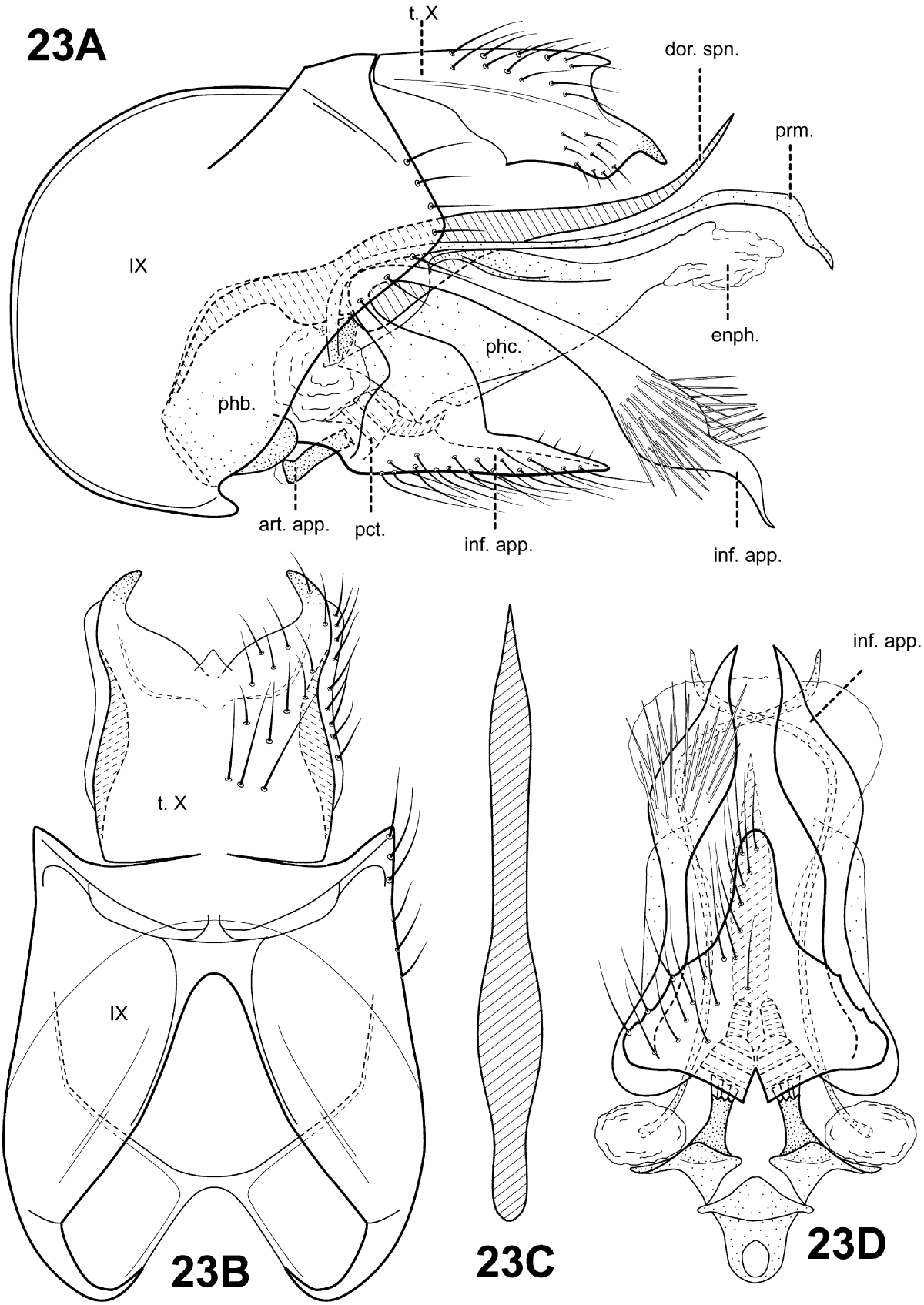

FIGURE 23. *Mortoniella akantha* Blahnik & Holzenthal, male genitalia. (A) Left lateral view. (B) Dorsal view. (C) Phallic spine, dorsal view. (D) Phallic apparatus, ventral view. Abbreviations: art. app. = articulated appendage; dor. spn. = dorsal phallic spine; enph. = endophallus; phb = phallobase; inf. app. = inferior appendage; pct. = pocket; phc. = phallicata; prm. = paramere; IX = segment IX; t. X. = tergum X. (Modified from Blahnik & Holzenthal 2008.)

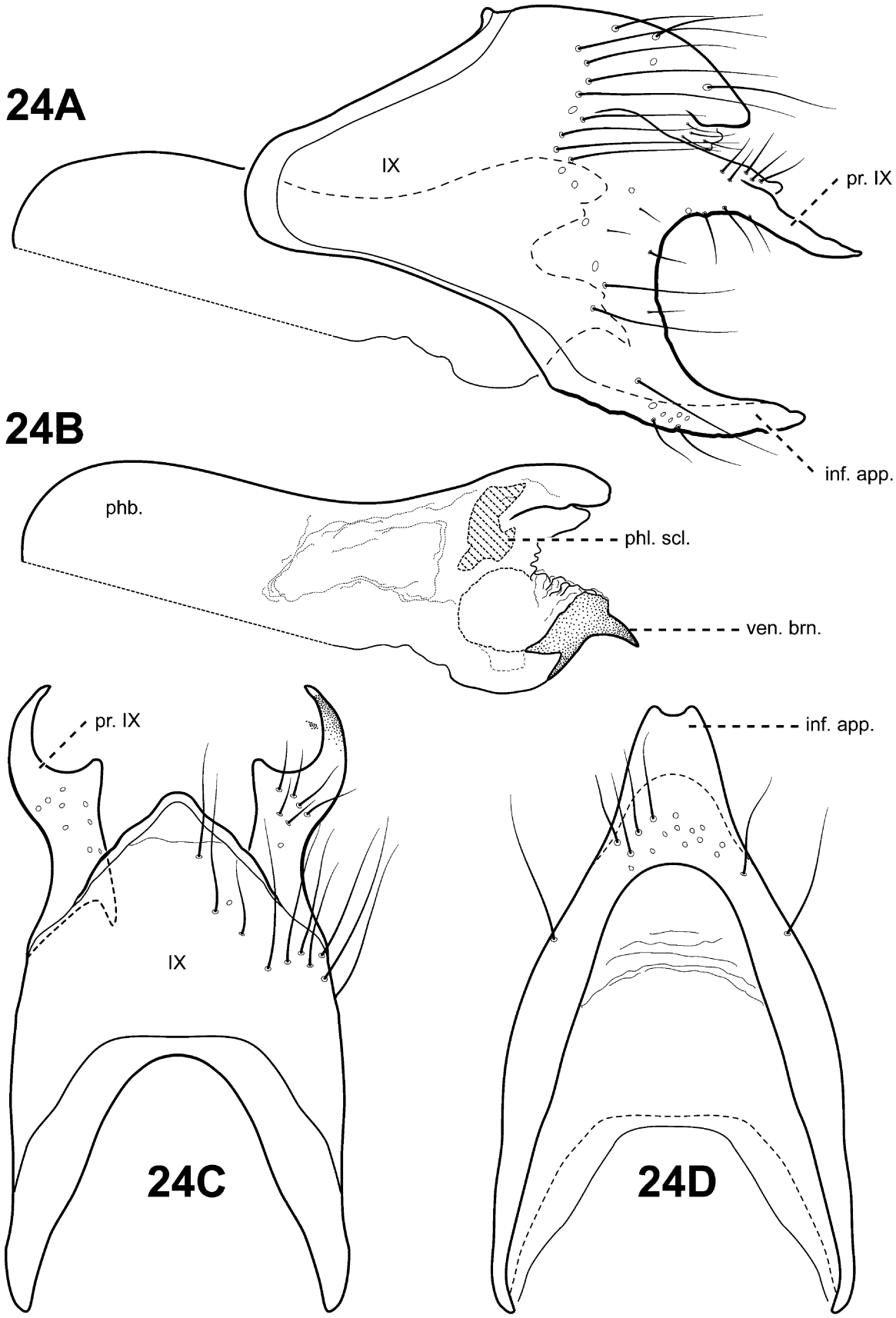

FIGURE 24. *Padunia adelungi* Martynov, male genitalia. (A) Left lateral view of genital capsule (terga IX and X). (B) Left lateral view of phallic apparatus. (C) Dorsal view of terga IX and X. (D) Ventral view of genital capsule. Abbreviations: inf. app. = inferior appendage; phb. = phallobase; IX = segment IX; phl. scl. = phallotremal sclerite; pr. IX = process of segment IX; ven. brn. = ventral branch.

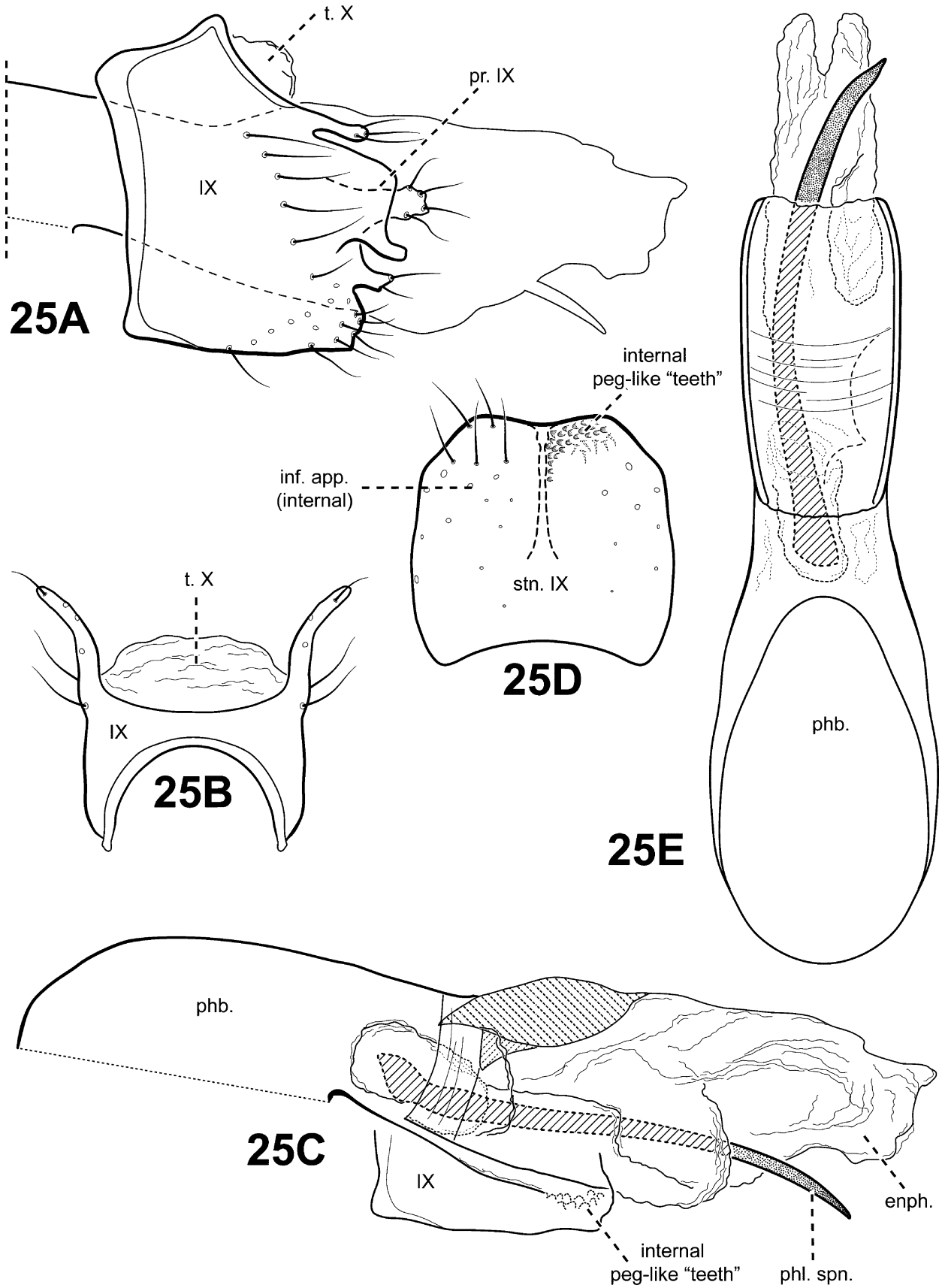

FIGURE 25. *Padunia anakan* (Malicky), male genitalia. (A) Left lateral view of genital capsule showing insertion of phallic apparatus. (B) Dorsal view of terga IX and X. (C) Left lateral view of phallic apparatus. (D) Dorsal view of sternum IX. (E) Ventral view of phallic apparatus capsule. Abbreviations: enph. = endophallus; inf. app. = inferior appendage; phb. = phallobase; phl. spn. = phallic spine; pr. IX= process of segment IX; stn. IX = sternum IX; t. IX = tergum IX; t. X = tergum X.

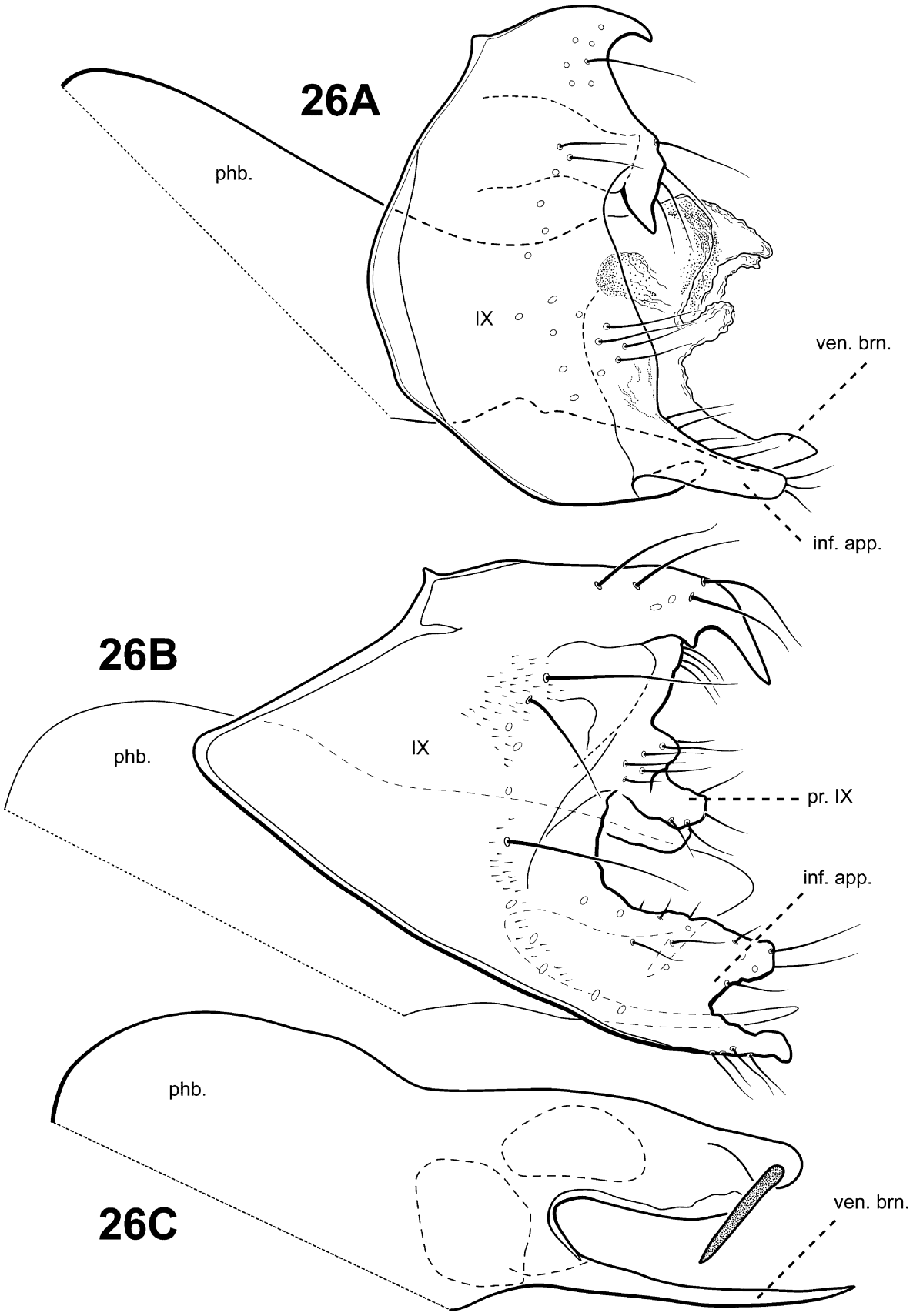

FIGURE 26. Male genitalia. (A) *Padunia coei* (Kimmins), holotype, left lateral view of genital capsule and phallic apparatus. (B) *Padunia falcata* (Schmid), holotype, left lateral view of genital capsule. (C) Same, left lateral view of phallic apparatus. Abbreviations: inf. app. = inferior appendage; phb. = phallobase; IX = segment IX; t. IX = tergum IX; pr. IX = process of segment IX; ven. brn. = ventral branch.

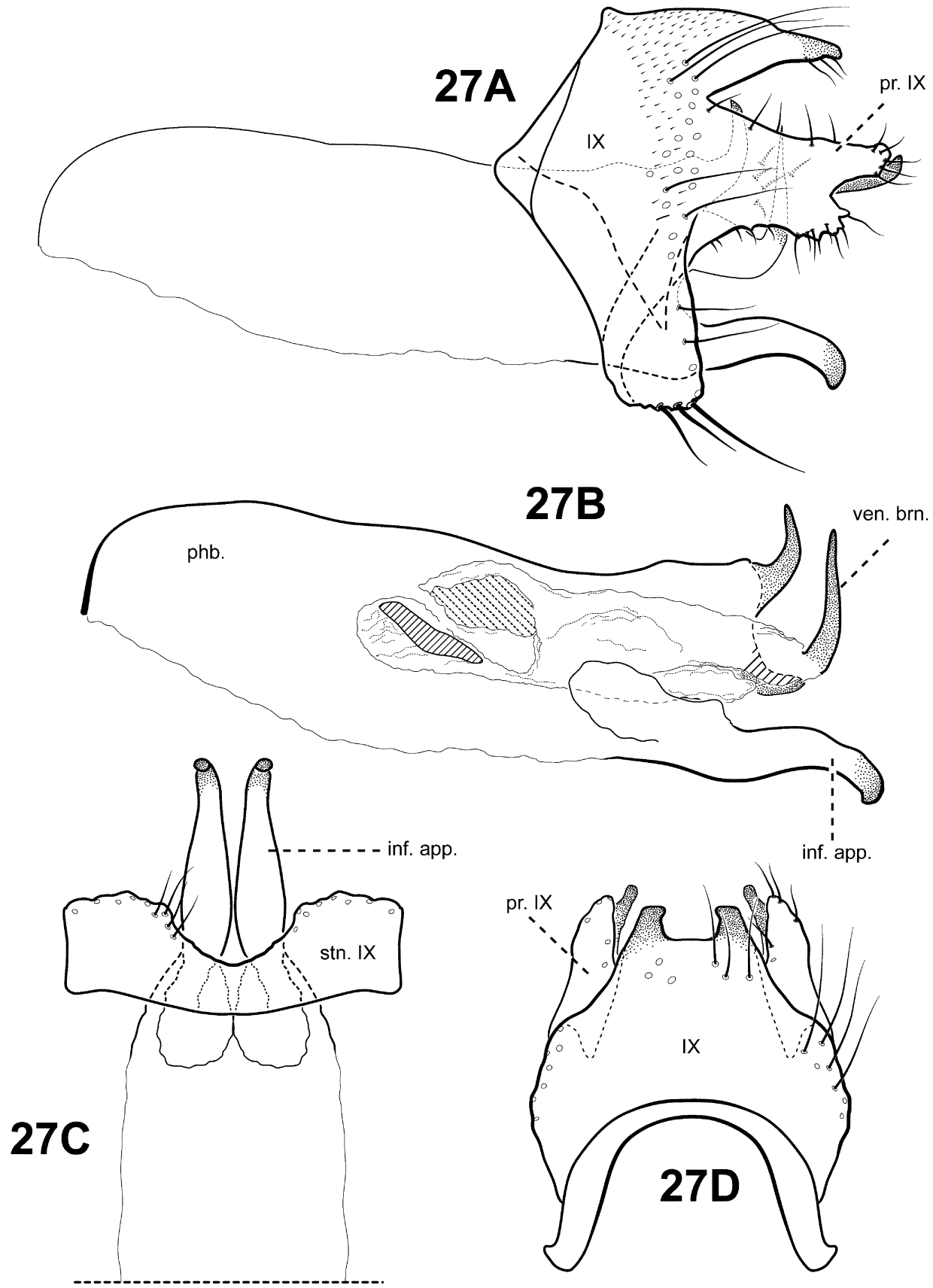

FIGURE 27. *Padunia jeanae* (Ross), male genitalia. (A) Left lateral view of genital capsule and phallic apparatus. (B) Left lateral view of phallic apparatus. (C) Ventral view of sternum IX and apex of phallic apparatus detailing insertion of inferior appendages. (D) Dorsal view of genital capsule (terga IX and X). Abbreviations: inf. app. = inferior appendage; phb. = phallobase; stn. IX = sternum IX; t. IX = tergum IX; pr. IX = process of segment IX; ven. brn. = ventral branch.

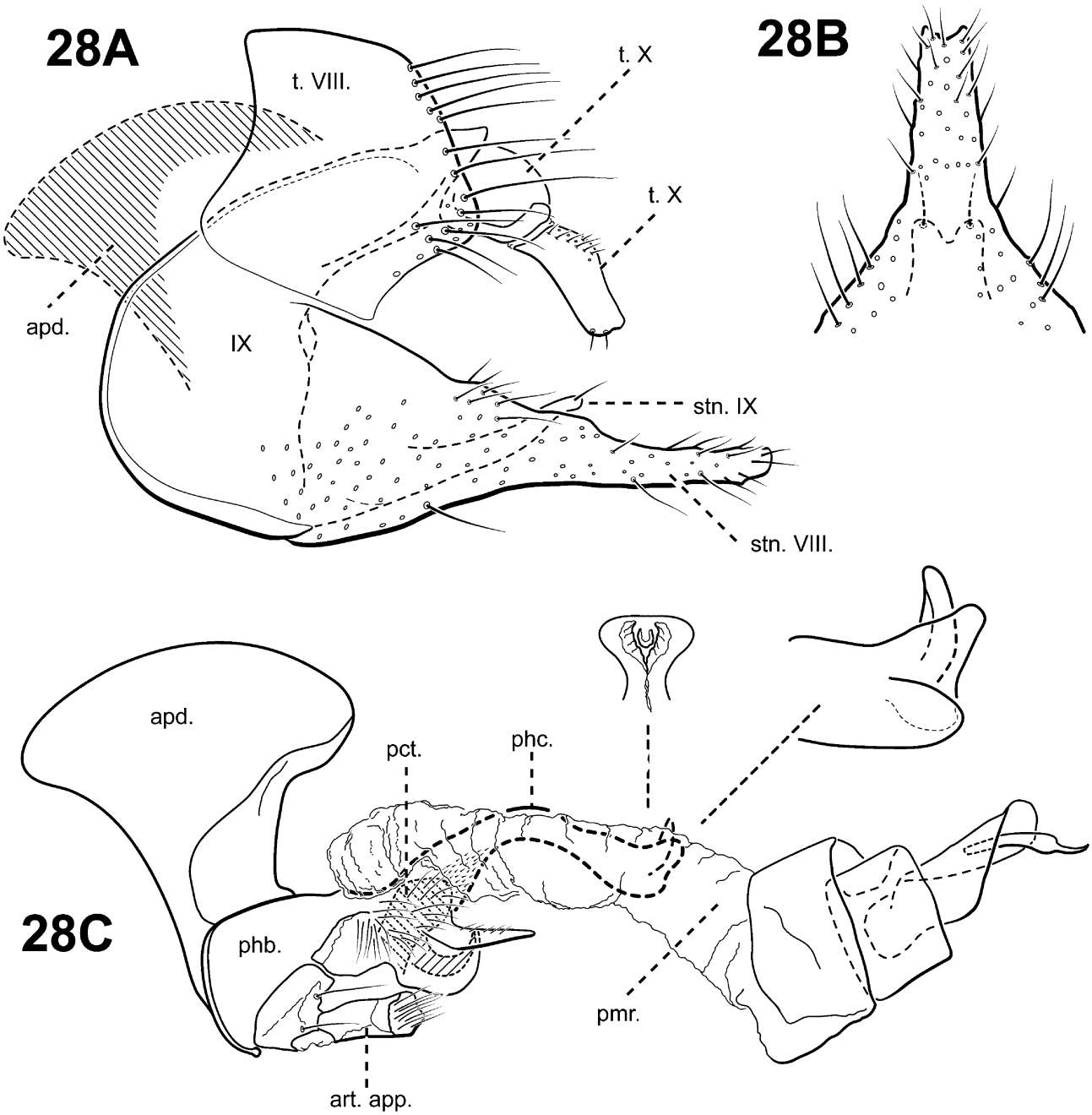

FIGURE 28. *Protoptila diablita* Robertson & Holzenthal, male genitalia. (A) Left lateral view of genital capsule, phallic apparatus removed. (B) Ventral view of sterna VIII and IX. (C) Left lateral view of phallic apparatus. Left inset is ventral view of apex of phallus; right inset is enlarged lateral view of apex of phallus. Abbreviations: apd. = apodeme; art. app. = articluated appendage; inf. app. = inferior appendage; pct. = pocket; phb. = phallobase; phc. = phallicata; pmr. = paramere; IX = segment IX; stn. VIII = sternum VIII; stn. IX = sternum IX; t. VIII = tergum VIII; t. IX = tergum IX; t. X = tergum X.

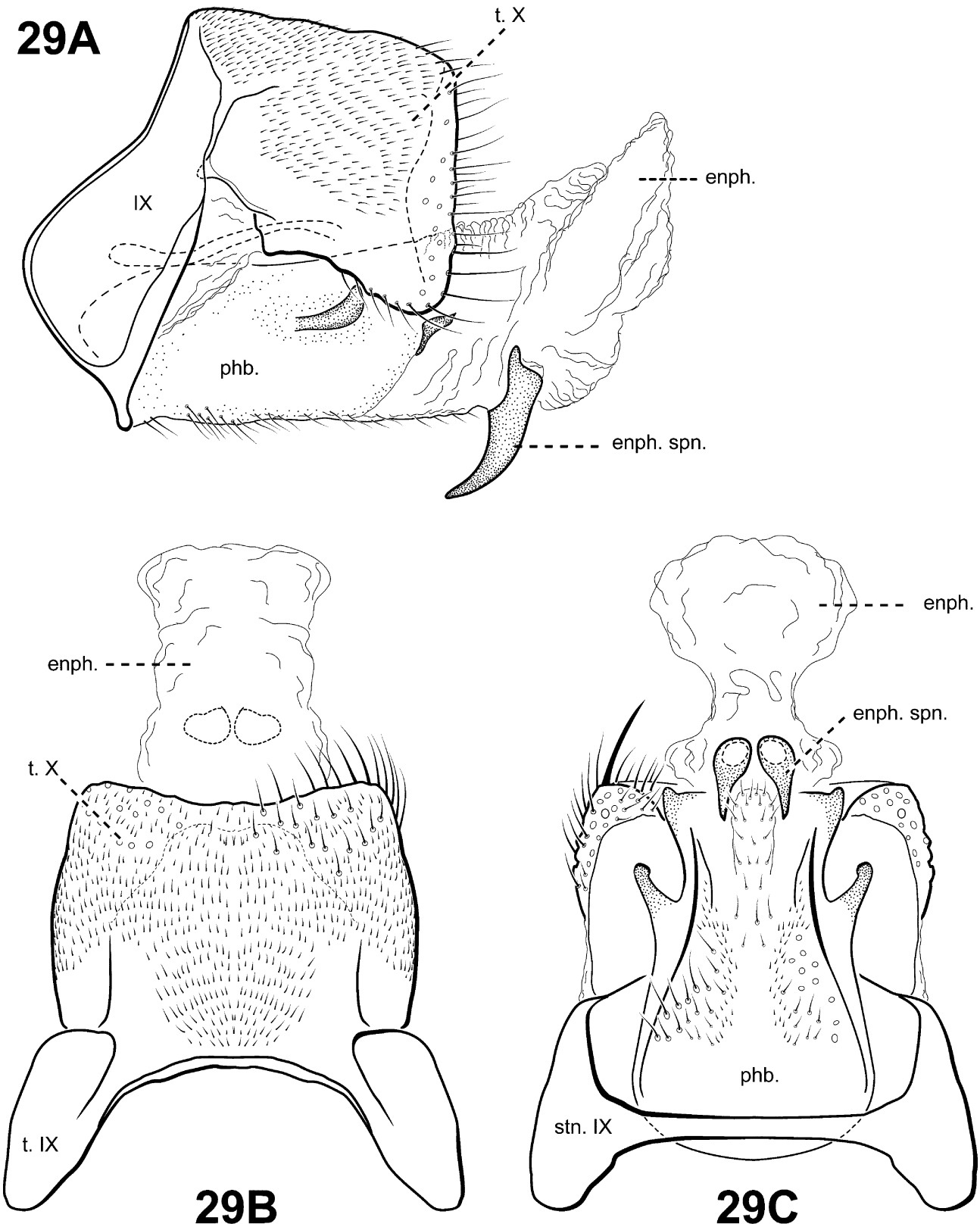

FIGURE 29. *Scotiotrichia ocreata* Mosely, male genitalia. (A) Left lateral view. (B) Dorsal view. (C) Ventral view. Abbreviations: enph. = endophallus; enph. spn. = endophallic spine; phb = phallobase; t. X = tergum X; stn. IX = sternum IX; t. IX = tergum IX; t. X. = tergum X.

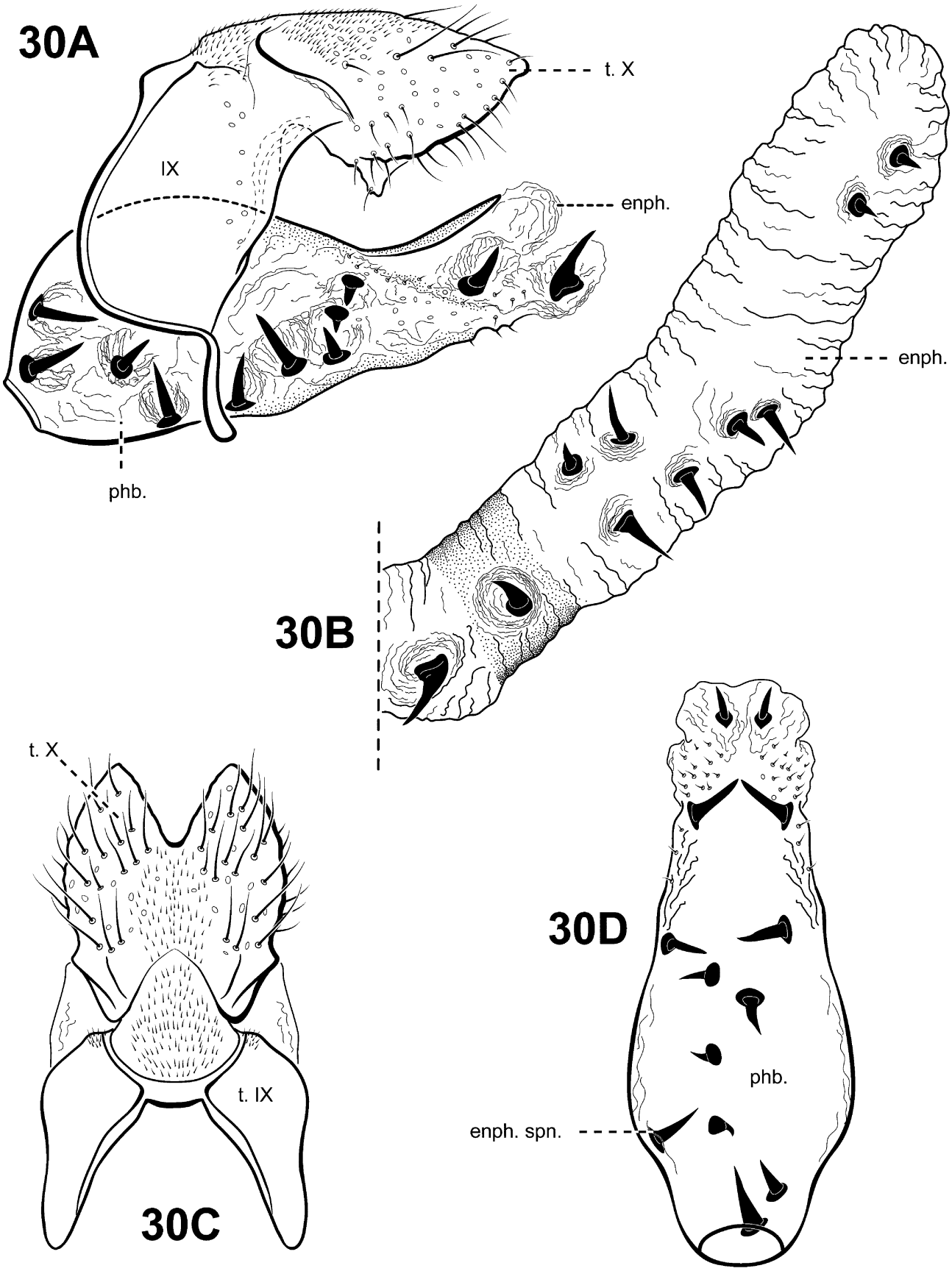

FIGURE 30. *Tolhuaca cupulifera* Schmid, male genitalia. (A) Left lateral view. (B) Left lateral view of fully everted endophallus. (C) Dorsal view. (D) Ventral view of phallobase with retracted endophallus. Abbreviations: enph. = endophallus; enph. spn. = endophallic spine; phb = phallobase; t. IX = tergum IX; t. X = tergum X.

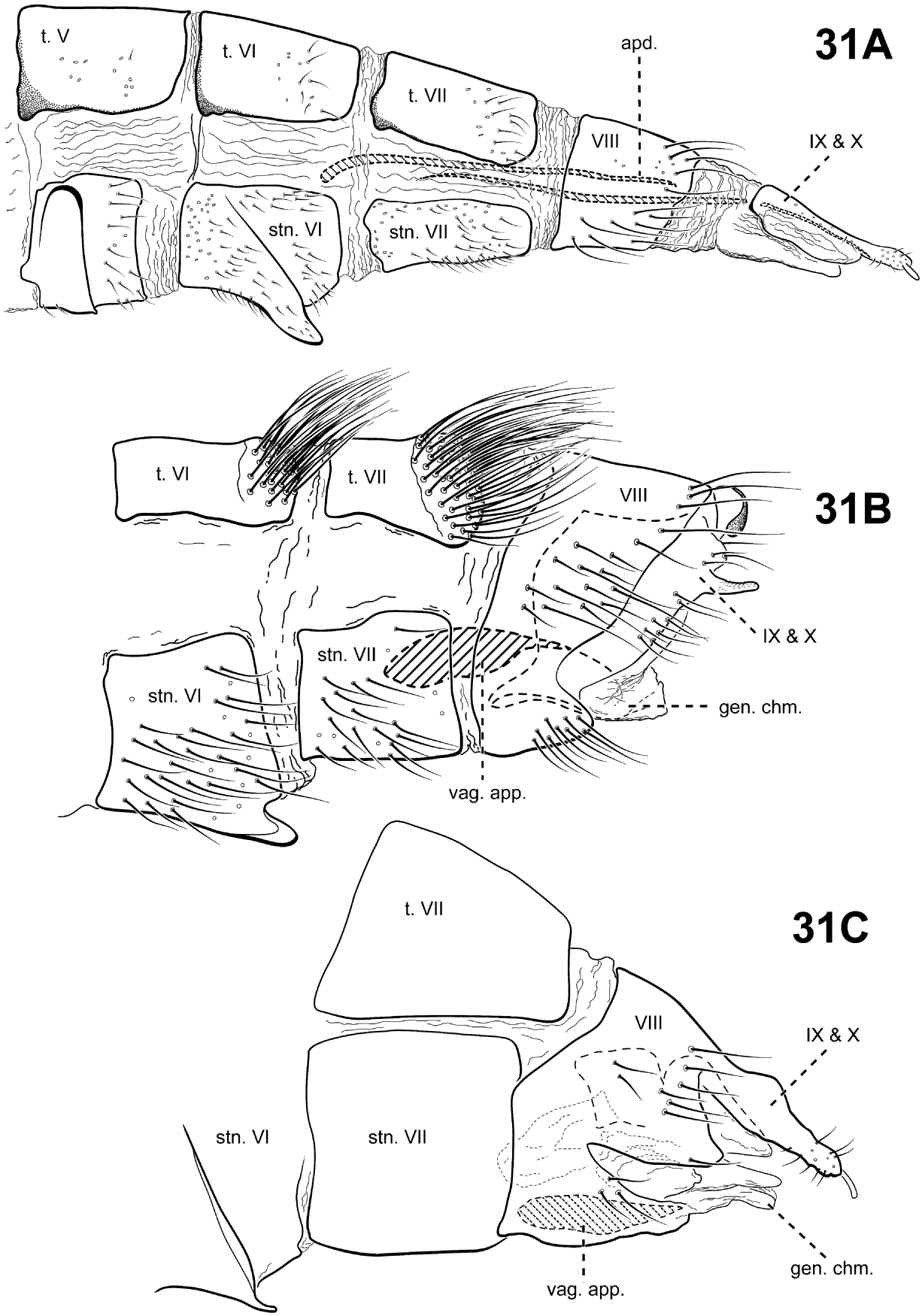

FIGURE 31. Female genitalia, left lateral view. (A) *Tolhuaca cupulifera* Schmid. (B) *Canoptila williami* Robertson & Holzenthal. (C) *Padunia jeanae* (Ross). Abbreviations: apd. = apodeme; gen. chm. = genital chamber; stn. = sternum; t. = tergum; vag. app. = vaginal apparatus.

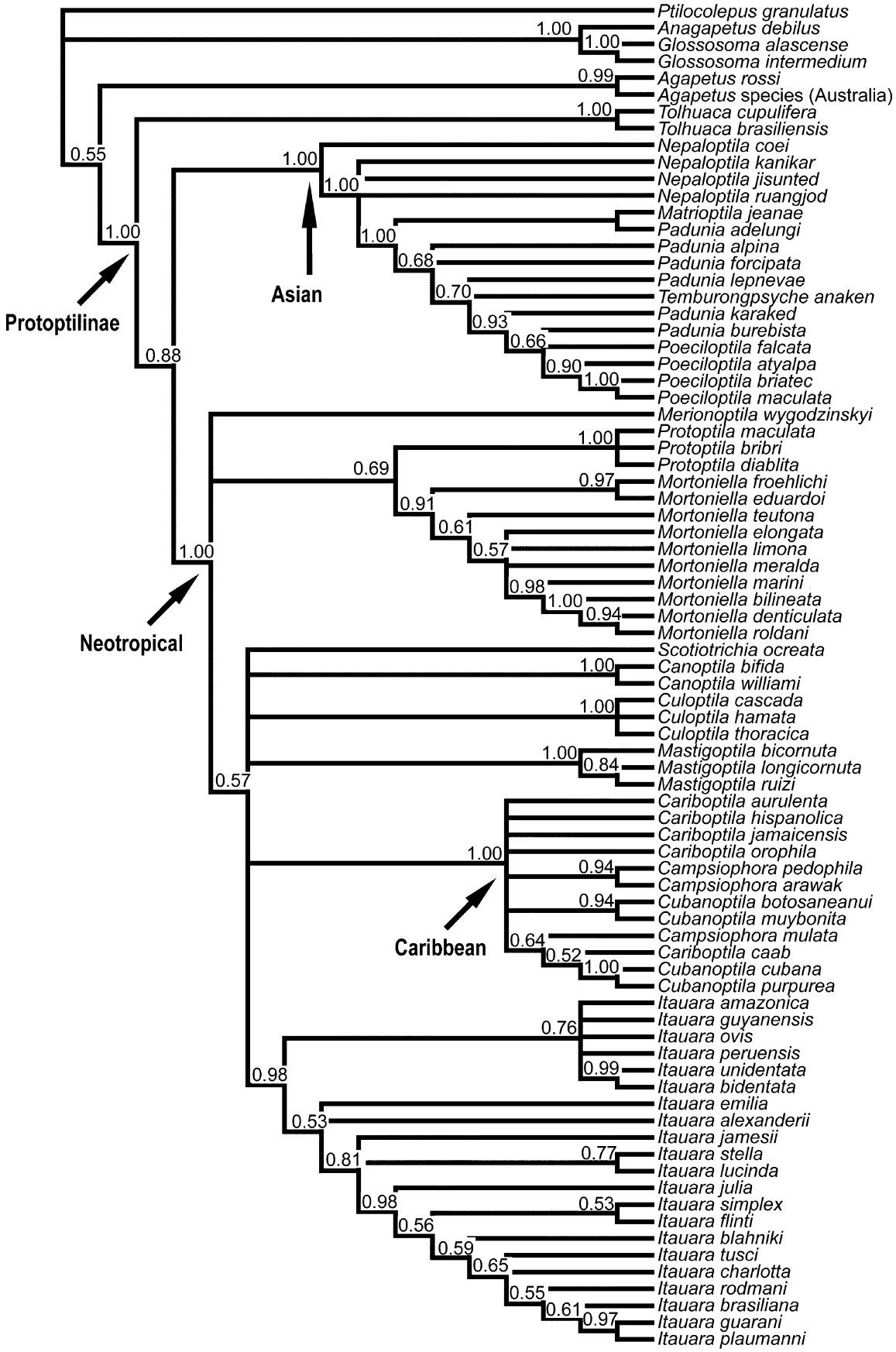

FIGURE 32. Phylogeny of protoptiline caddisflies based on Bayesian analysis of TOTAL COMBO dataset (80 taxa, 757 characters) under the models Mk + Γ (morphological data partition) and GTR + I + Γ (COI data partition). Posterior probability values are indicated above internodes.

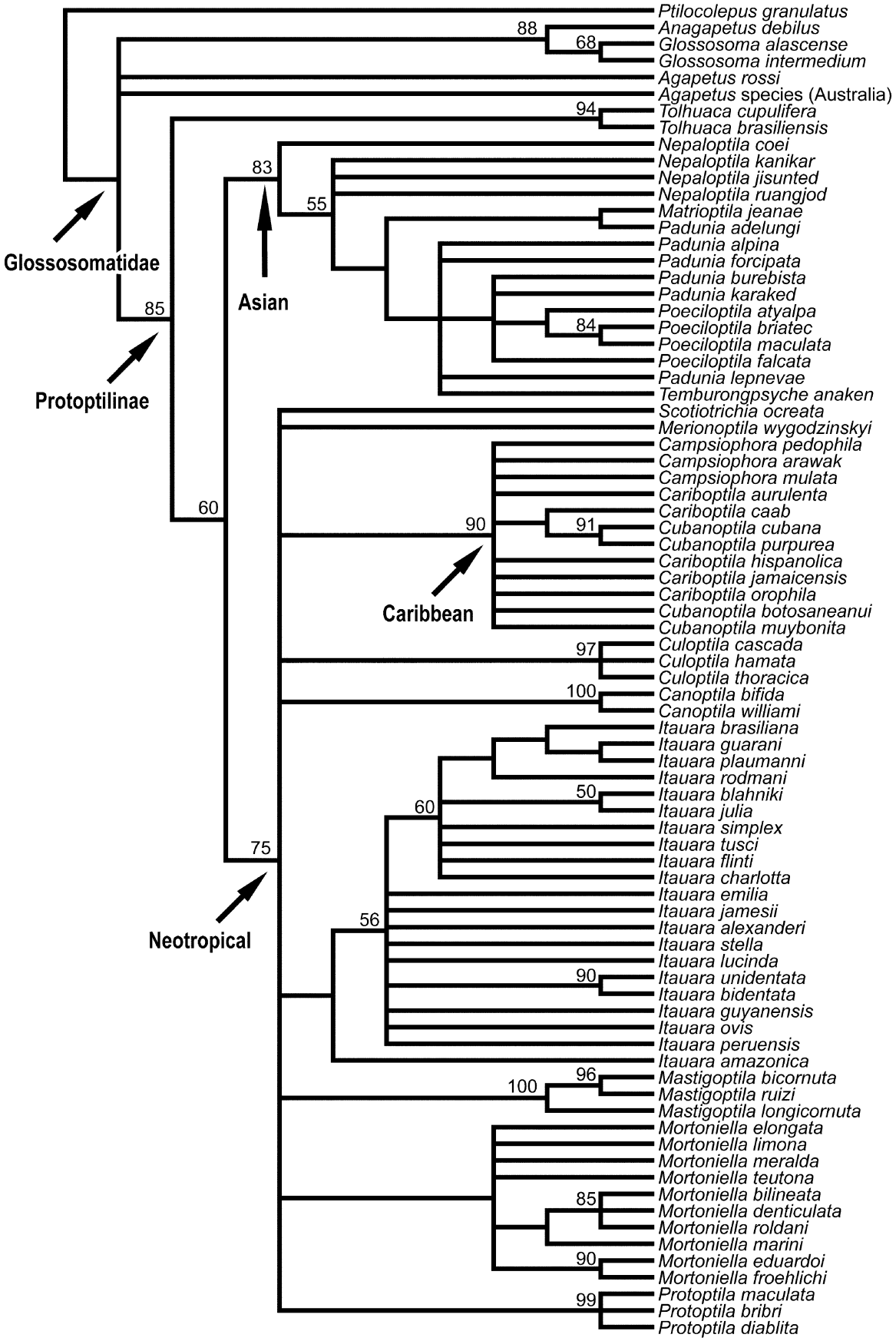

FIGURE 33. Phylogeny of protoptiline caddisflies based on parsimony analysis of TOTAL COMBO dataset (80 taxa, 757 characters). Strict consensus of 20 equally parsimonious trees (Length: 1880; CI: 0.356; RI: 0.575; RC: 0.205). Bootstrap values ≥50% are indicated above internodes.

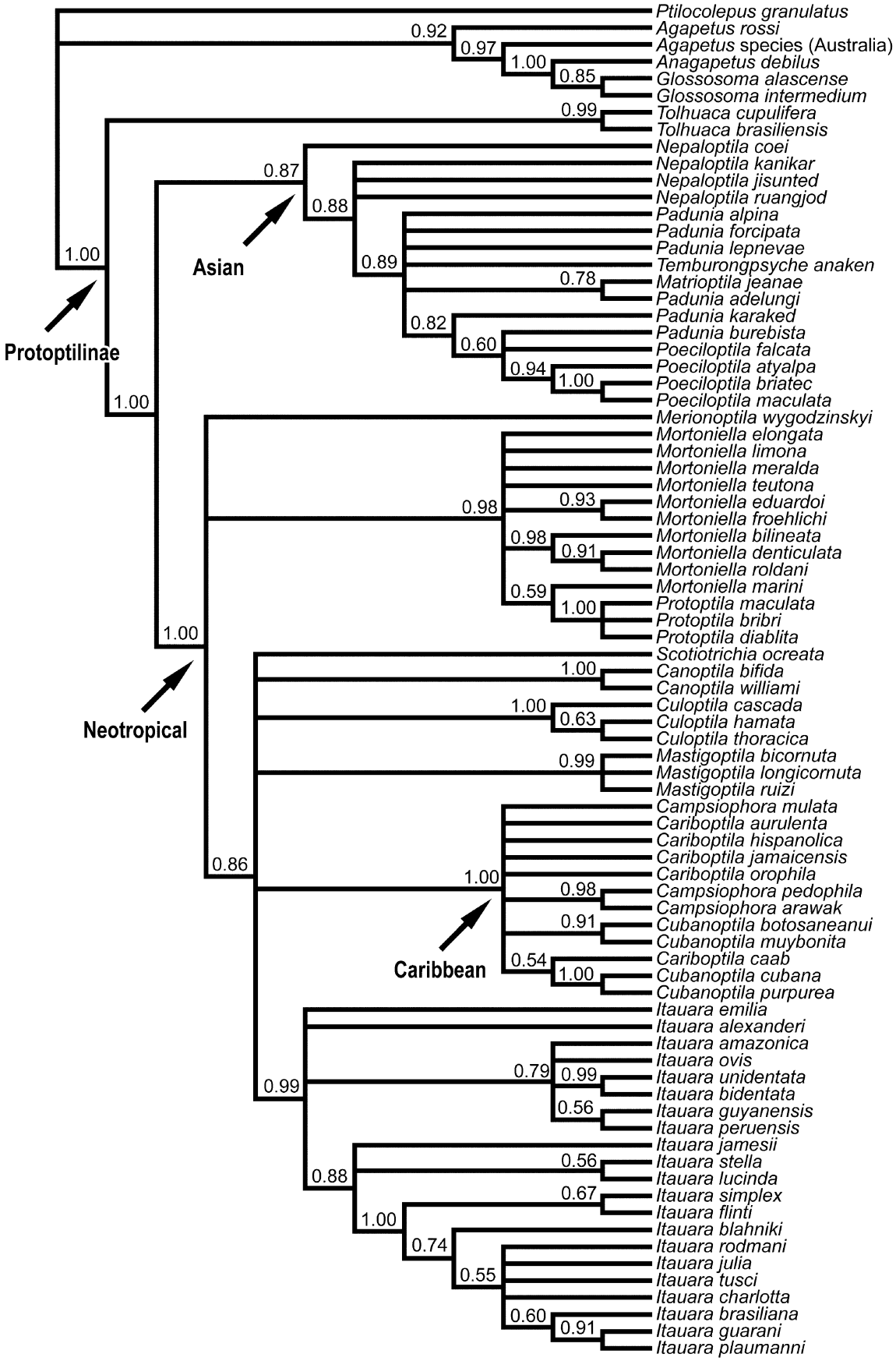

FIGURE 34. Phylogeny of protoptiline caddisflies based on Bayesian analysis of TOTAL MORPH dataset (80 taxa, 99 characters) under an Mk + Γ model. Posterior probability values are indicated above internodes.

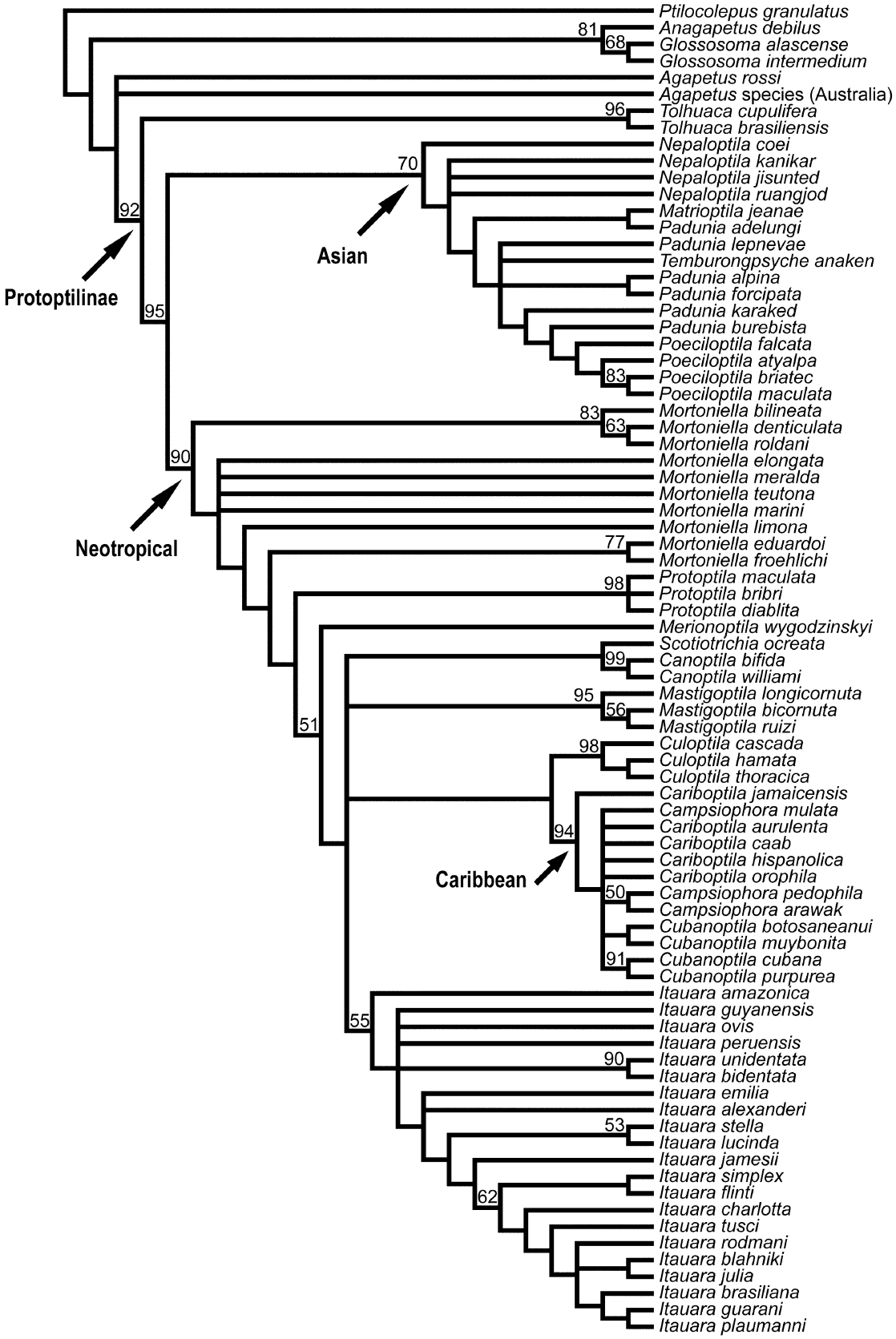

FIGURE 35. Phylogeny of protoptiline caddisflies based on parsimony analysis of TOTAL MORPH dataset (80 taxa, 99 characters). Strict consensus of 2 equally parsimonious trees (Length: 463; CI: 0.339; RI: 0.789; RC: 0.267). Bootstrap values ≥50% are indicated above internodes.

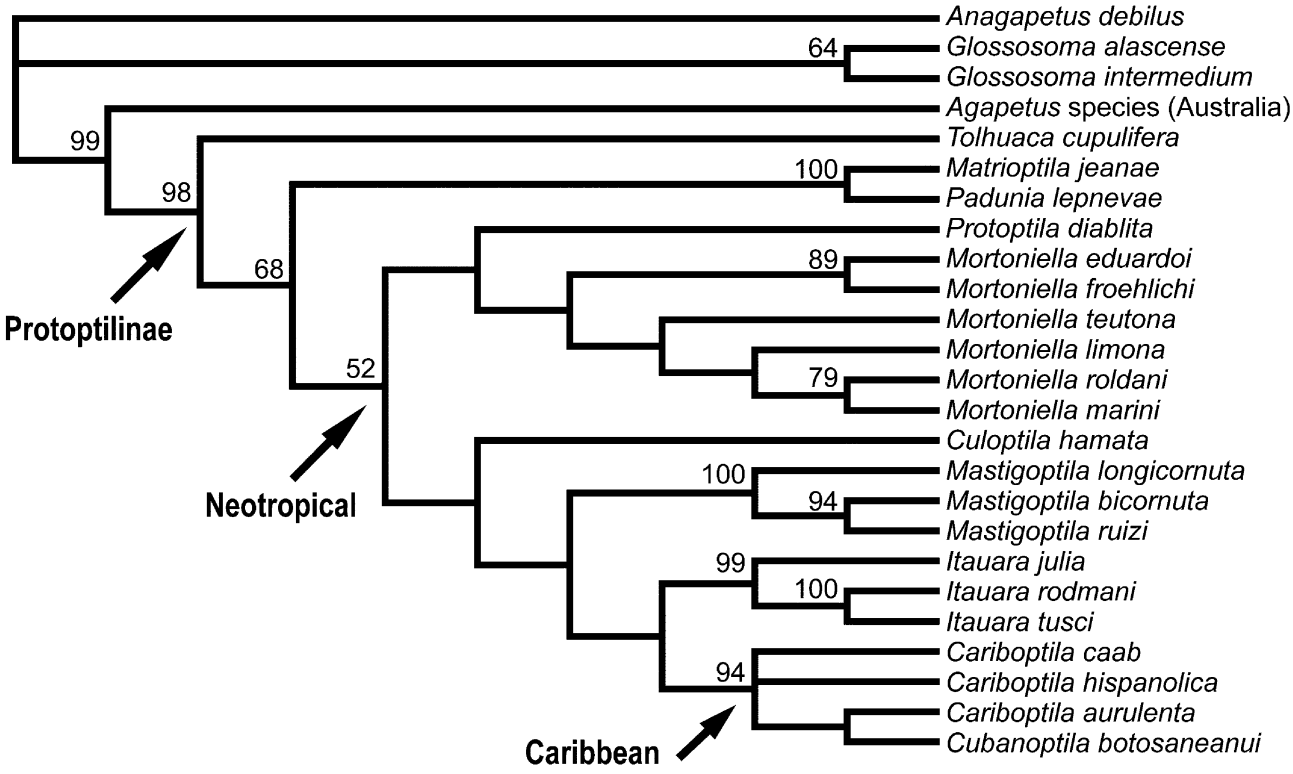

FIGURE 36. Phylogeny of protoptiline caddisflies based on parsimony analysis of SUBSET COMBO dataset (25 taxa, 757 characters). Strict consensus of 2 equally parsimonious trees (Length: 1576; CI: 0.365; RI: 0.435; RC: 0.159). Bootstrap values ≥50% are indicated above internodes.

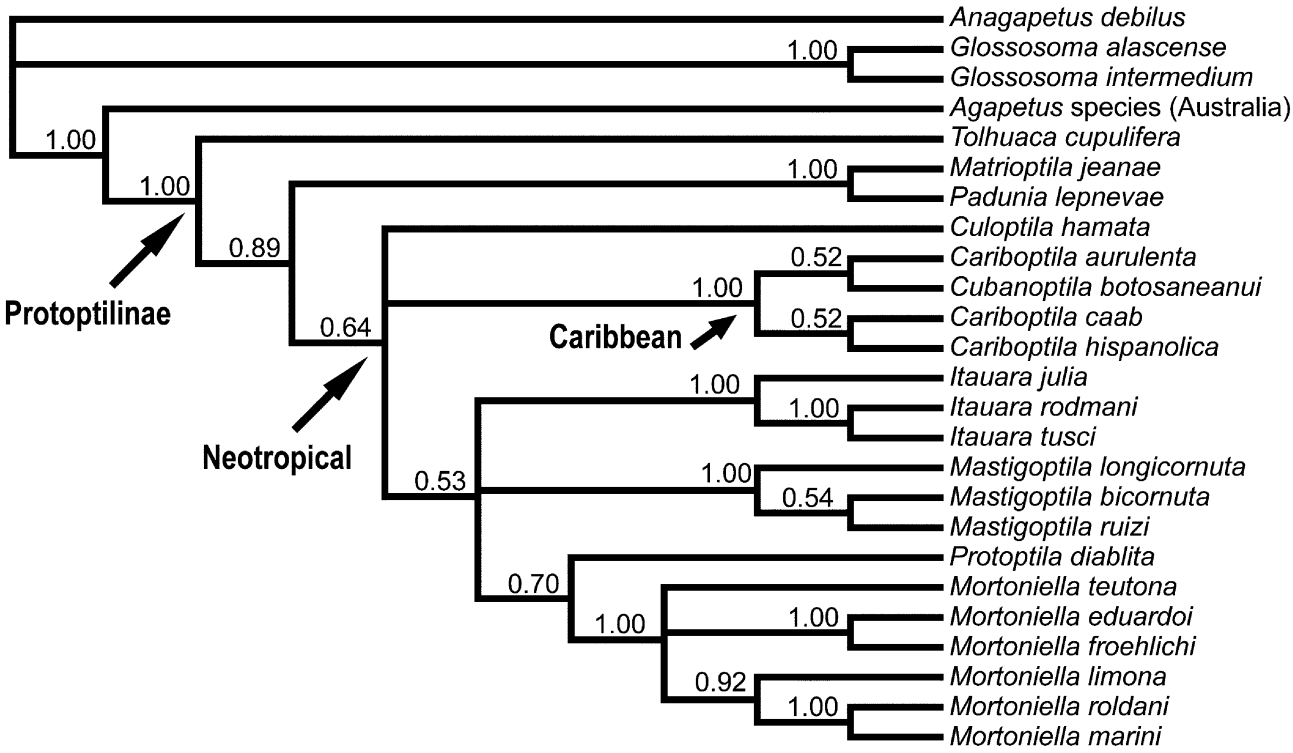

FIGURE 37. Phylogeny of protoptiline caddisflies based on Bayesian analysis of SUBSET COMBO dataset (25 taxa, 757 characters) under the models Mk + Γ (morphological data partition) and GTR + I + Γ (COI data partition). Posterior probability values are indicated above internodes.

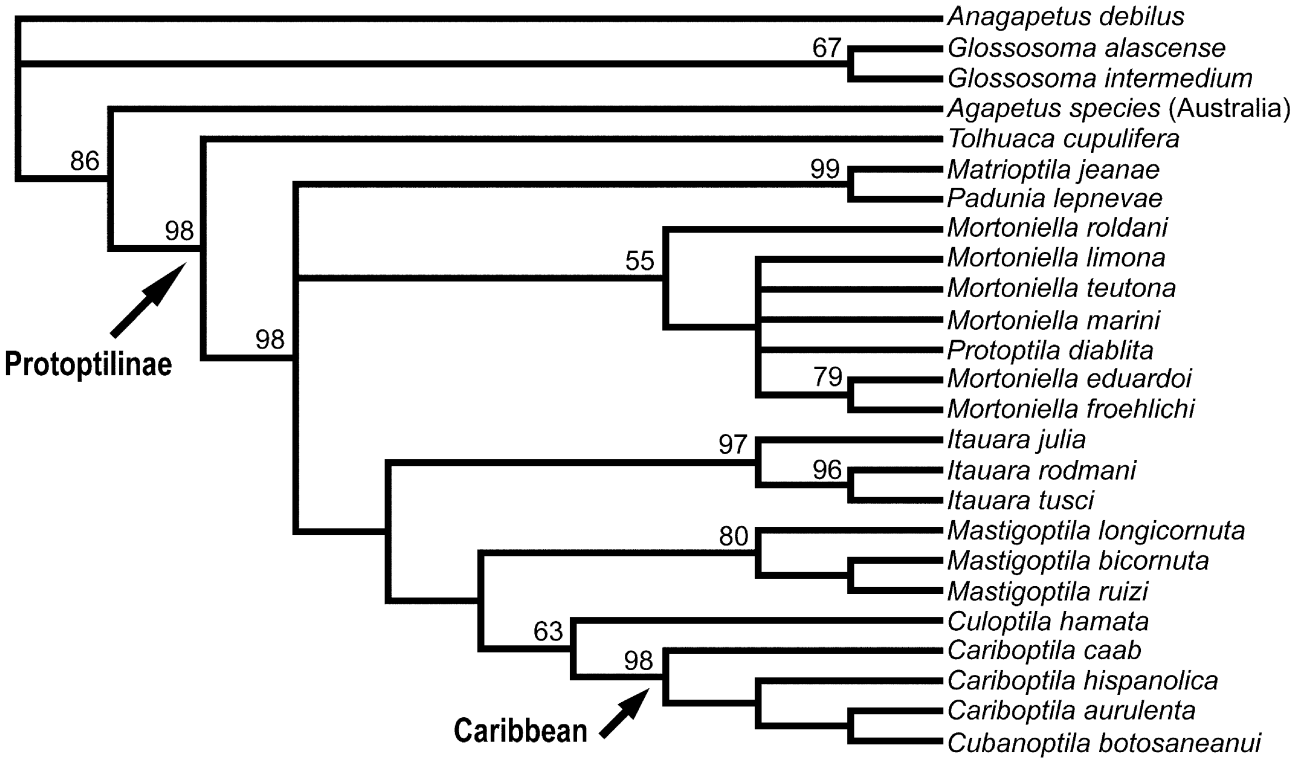

FIGURE 38. Phylogeny of protoptiline caddisflies based on parsimony analysis of SUBSET MORPH dataset (25 taxa, 99 characters). Strict consensus of 12 equally parsimonious trees (Length: 218; CI: 0.569; RI: 0.752; RC: 0.428). Bootstrap values ≥50% are indicated above internodes.

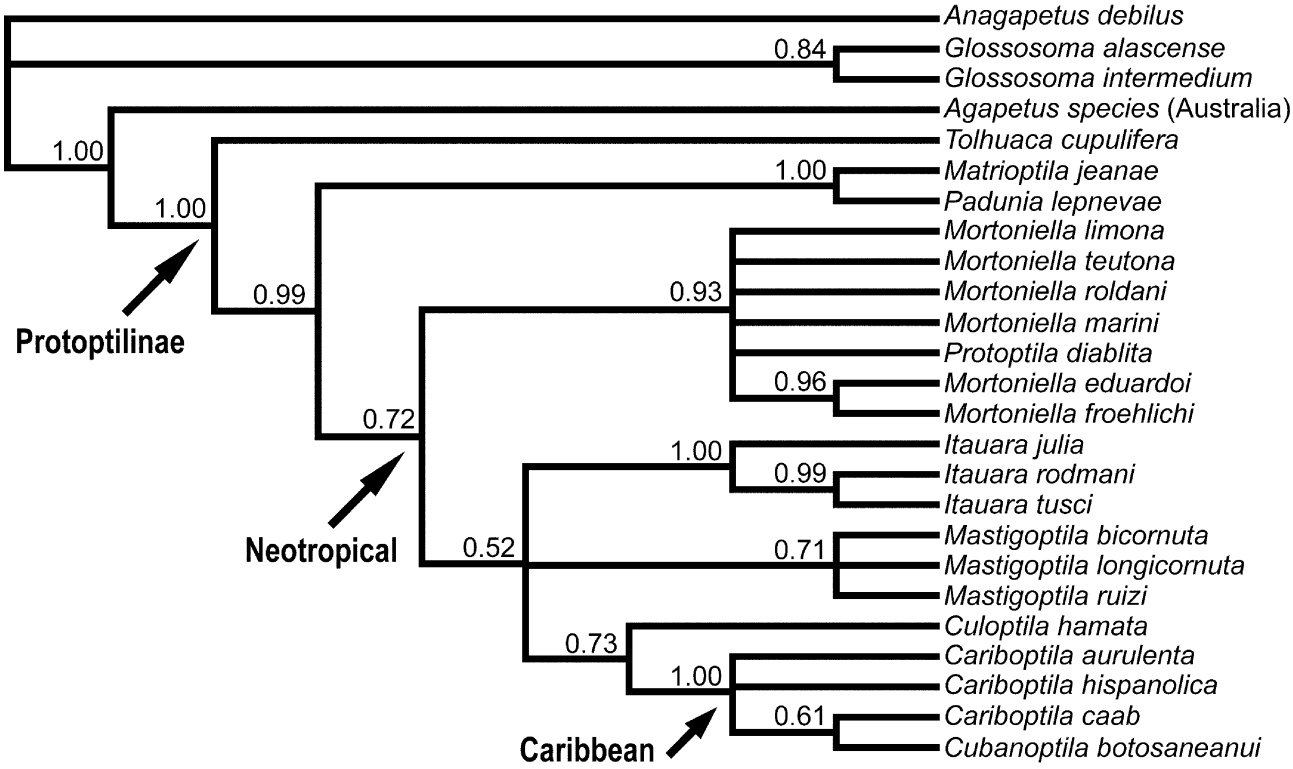

FIGURE 39. Phylogeny of protoptiline caddisflies based on Bayesian analysis of SUBSET MORPH dataset (25 taxa, 99 characters) under an Mk + Γ model. Posterior probability values are indicated above internodes.

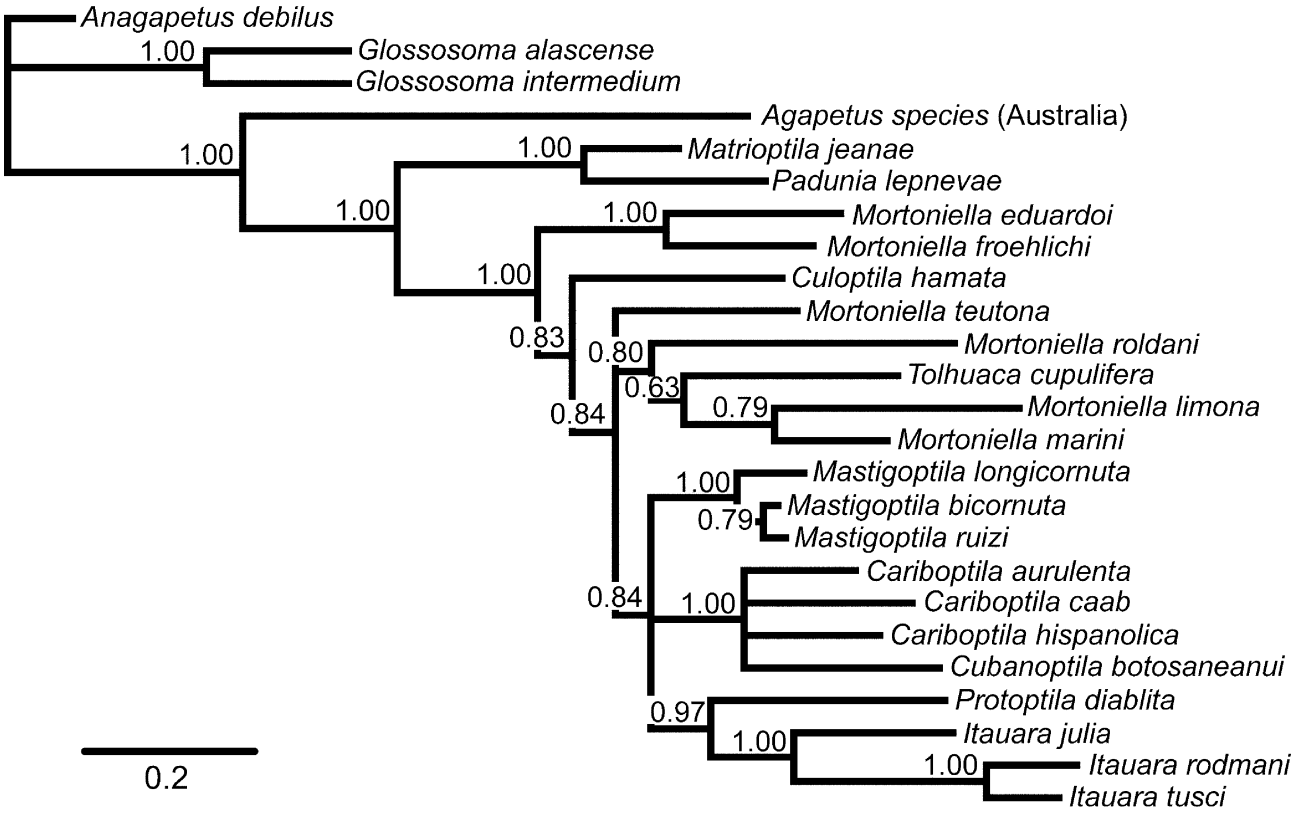

FIGURE 40. Phylogeny of protoptiline caddisflies based on Bayesian analysis of SUBSET COI dataset (25 taxa, 658 characters) under a GTR + I + Γ model. Posterior probability values are indicated above internodes.

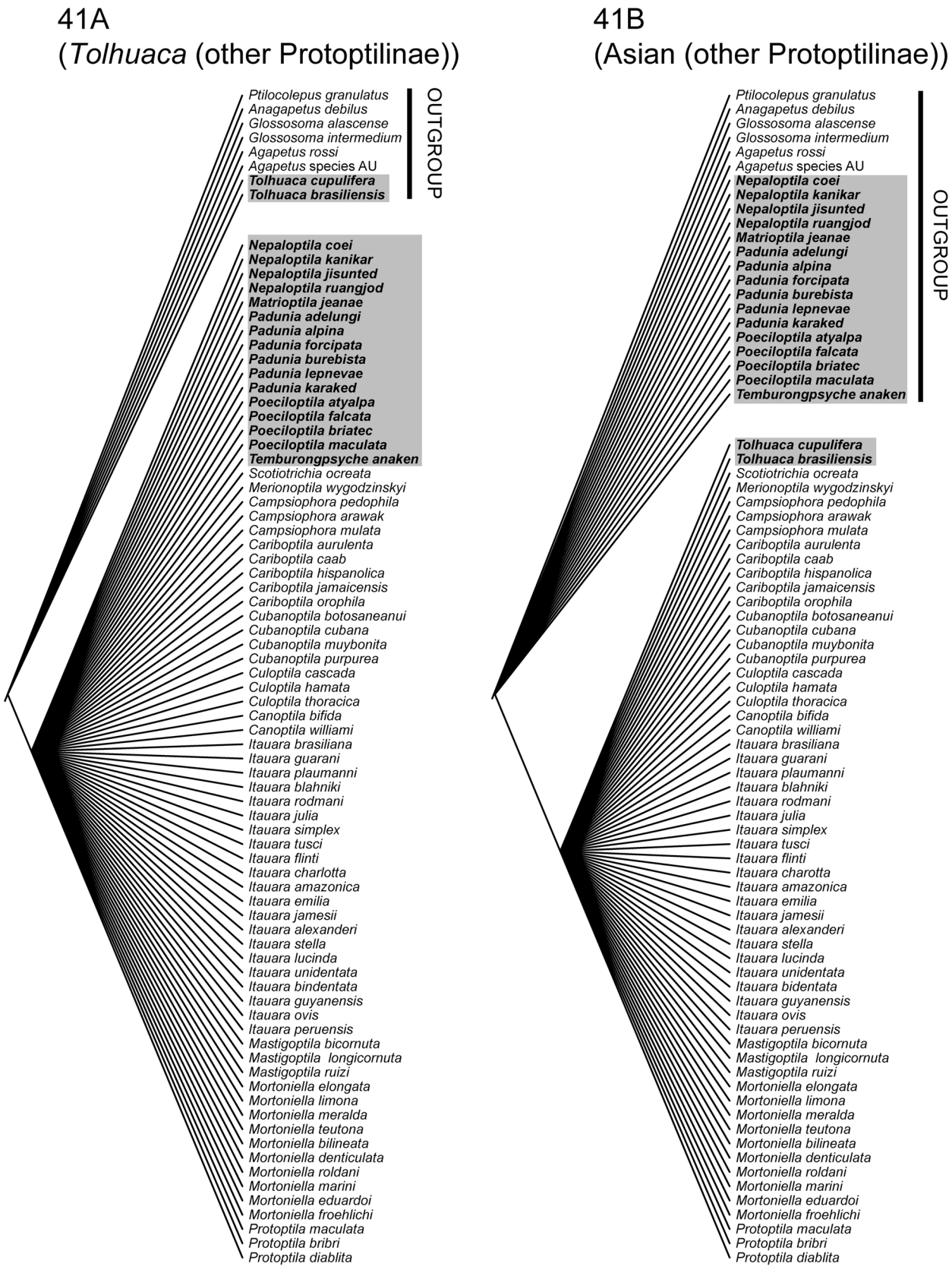

FIGURE 41. Constraint trees of alternative hypotheses for Protoptilinae phylogeny used for Bayesian topological incongruence tests of TOTAL COMBO and TOTAL MORPH datasets. A—(*Tolhuaca* (other Protoptilinae)): *Tolhuaca* is constrained to the outgroup and a monophyletic Protoptilinae includes the Asian clade. B—(Asian (other Protoptilinae)): The Asian clade is constrained to the outgroup and a monophyletic Protoptilinae includes *Tolhuaca*.

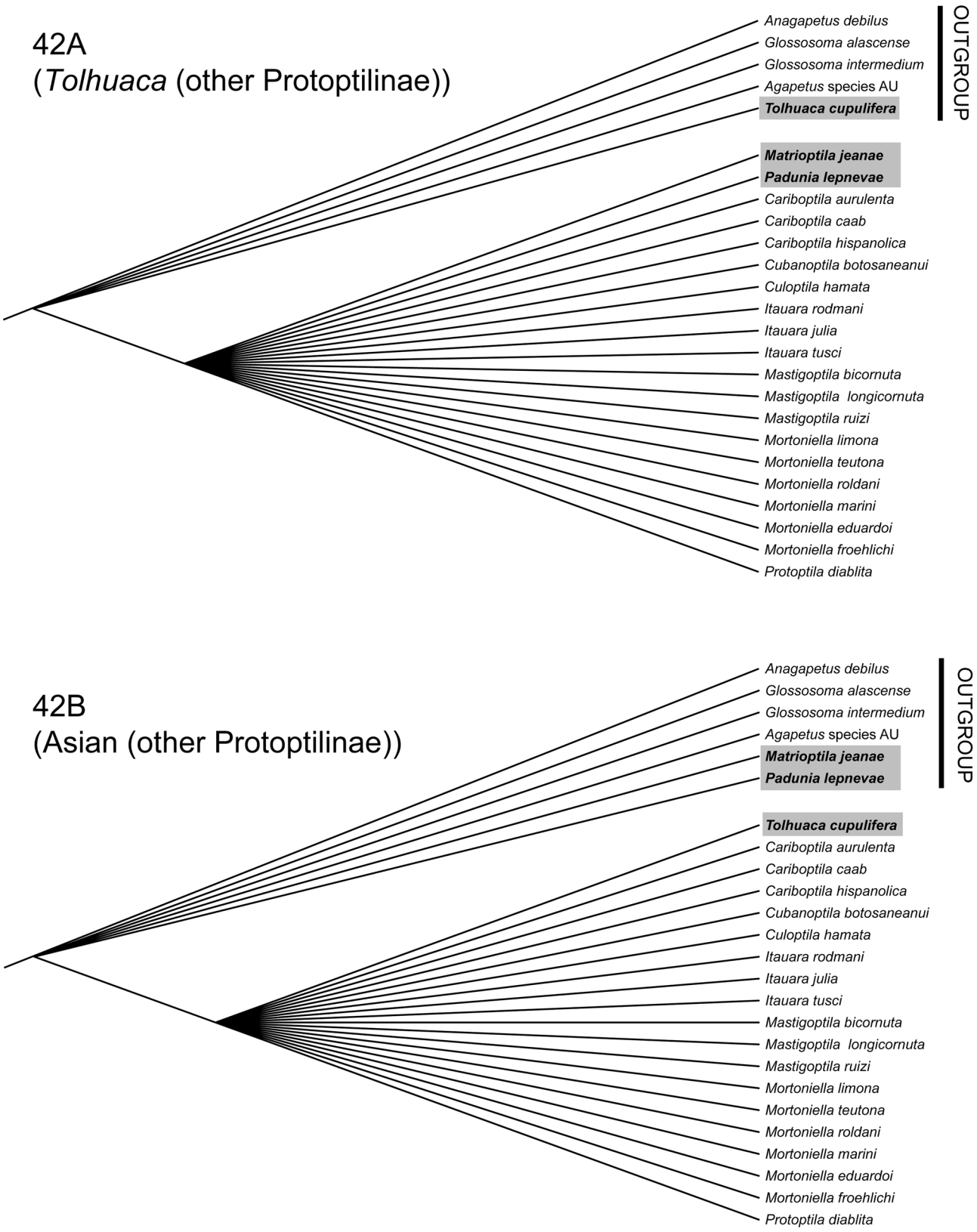

FIGURE 42. Constraint trees of alternative hypotheses for Protoptilinae phylogeny used for Bayesian topological incongruence tests of SUBSET COMBO, SUBSET MORPH, and SUBSET COI datasets. A—(*Tolhuaca* (other Protoptilinae)): *Tolhuaca* is constrained to the outgroup and a monophyletic Protoptilinae includes the Asian clade. B—(Asian (other Protoptilinae)): The Asian clade is constrained to the outgroup and a monophyletic Protoptilinae includes *Tolhuaca*.

Key to the Subfamilies of Glossosomatidae

1. Forewing R1 forked (Morse & Yang 2004, Fig. 8) . . . . . Glossosomatinae
   Forewing R1 unforked (Fig. 7A) 2
2(1). Forewing with row of erect setae along or below Cu2 (Fig. 7A), foretibial spur absent or hair-like (Fig. 6B) . . .. Protoptilinae
   Forewing without row of erect setae (Morse & Yang 2004, Fig. 8), foretibial spur well developed (Ross 1944, Fig. 104) . . . . . Agapetinae

Key to the Word Genera of Protoptilinae

1. Phallobase absent or extremely reduced (Figs. 15B, 20A, 21A) 3
   Phallobase present, not reduced (Figs. 15B, 22A, 23A, 28C) 2
2. Phallobase extremely enlarged (Figs. 16A, 17A, 18C, 19, 24B, 25C, 26, 27B, 29A, 30A) 9
   Phallobase not extremely enlarged, moderately sized (Figs. 22A, 23A, 28A) 5
3(1). Male genitalia markedly asymmetrical (Fig. 21D); forewing row of stout setae below Cu2, approximately halfway between Cu2 and 1A (Fig. 12C) . . . . . *Mastigoptila*
   Male genitalia not markedly asymmetrical; forewing row of stout setae along (Fig. 7A) or just slightly below Cu2 (Fig. 11A) 4
4(3). Tergum X with pair of long, spine-like processes arising from posterolateral margins (Figs. 15B–D); parameres membranous, with sclerotized apices (Figs. 15B, D) . . . . . *Canoptila*
   Tergum X without pair of long, spine-like processes arising from posterolateral margin (Figs. 20A–C); parameres absent, or when present, sclerotized (Figs. 20A, C) . . . . . *Itauara*
5(1). Phallobase with small, digitate rod-like articulated appendages associated with sclerotized pocket on venter (Figs. 23A, D; 28C) 6
   Phallobase without small, digitate rod-like articulated appendages associated with sclerotized pocket (Figs. 22A, C) 7
6(5). Sternum VIII projecting posteriorly (Fig. 28A, 28B), subtending segment IX; row of stout setae below Cu2, approximately halfway between Cu2 and 1A (Fig. 11C) . . . . . *Protoptila*
   Sternum VIII unmodified (Fig. 23A); forewing row of stout setae along or just slightly below Cu2 (Fig. 11A) . . . *Mortoniella*
7(5). Fore- and hind wings extremely reduced in size (Figs. 10A, 10B) . . . . . *Merionoptila*
   Fore- and hind wings not extremely reduced (Figs. 13A–D) 8
8(7). Forewing with apical forks I, II, and V (Figs. 13A, 13C, 14A, 14C); tergum X without pair of long, spine-like processes arising from posterolateral margin; parameres absent, or when present, sclerotized; phallobase elongate and tubular, with sclerotized dorsal margin projecting anteriorly, ventral margin open or membranous (Figs. 24A, 24B, 25A, 25C, 25E, 26, 27A, 27B, 29A, 29C) . . . . . *Padunia*
   Forewing with apical forks I–III present (Fig. 9A); tergum X with pair of long, spine-like processes arising from posterolateral margin; parameres membranous, with sclerotized apices; phallobase not elongate and tubular, lightly sclerotizated with paired row or patches of setae ventrolaterally (Figs. 15B, 15C, 15D) . . . . . *Canoptila*
9(2). Tergum X greatly enlarged and hoodlike (Fig. 29A); forewing row of stout setae below Cu2; forewing with apical forks I and II (Fig. 10C) . . . . . *Scotiotrichia*
   Tergum X not greatly enlarged or hoodlike (Fig. 19A); forewing row of stout setae along Cu2 (Fig. 7A) 10
10(9). Forewing Cu1 incomplete, not reaching wing margin; with apical forks I–IV (Fig. 7A). . . . . *Culoptila*
   Cu1 complete, reaching wing margin (Fig. 12A); with apical forks I, II, III (Fig. C) or I, II, V (Figs. 12A) 11
11(10). Mesoscutellum with pair of distinct, round setal warts (Fig. 5A); endophallus very membranous, greatly enlarged and elongate when evaginated, twice or more the length of segments IX and X (Fig. 30B). . . . . *Tolhuaca*
   Mesoscutellum sparsely setose or with pair of indistinct setal patches (Fig. 5B); endophallus not apparent or not greatly enlarged or elongate when evaginated (Figs. 18C, 24B, 25C) 12
12(11). Forewing with apical forks I, II, and V (Figs. 13A, 13C, 14A, 14C); sternum IX not absent or reduced (Fig. 24A); antennal scape length less than or about equal to 2 times length of pedicel (Fig. 5) . . . . . *Padunia*
   Forewing with apical forks I–III present (Figs. 7C, 8A, 8C); sternum IX absent or extremely reduced (Figs. 16A, 17A, 18A); antennal scape length greater than or equal to 3 times length of pedicel (Fig. 6A) . . . . . *Cariboptila*

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REFERENCES

Alfaro, M.E., Zoller, S. & Lutzoni, F. (2003) Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markov Chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. *Molecular Biology and Evolution*, 20, 255–266.
http://dx.doi.org/10.1093/molbev/msg028

Angrisano, E.B. (1993) Contribution al conocimiento del genero *Antoptila* Mosely (Trichoptera: Glossosomatidae). *Revista de la Sociedad Entomológica Argentina*, 52, 57–62.

Angrisano, E.B. (1997) Los Trichoptera del Uruguay. III. Familias Philopotamidae, Hydrobiosidae y Glossosomatidae. *Revista de la Sociedad Entomológica Argentina*, 56, 55–58.

Ball, S.L., Hebert, P.D.N., Burian, S.K. & Webb, J.M. (2005) Biological identifications of mayflies (Ephemeroptera) using DNA barcodes. *Journal of the North American Benthological Society*, 24, 508–524.
http://dx.doi.org/10.1899/04-142.1

Banks, N. (1904) Two new species of Hydroptilidae. *Entomological News*, 15, 116.

Blahnik, R.J. & Holzenthal, R.W. (2004) Collection and curation of Trichoptera, with an emphasis on pinned material. *Nectopsyche, Neotropical Trichoptera Newsletter*, 1, 8–20.

Blahnik, R.J. & Holzenthal, R.W. (2006) Revision of the genus *Culoptila* (Trichoptera: Glossosomatidae). *Zootaxa*, 1233, 1–52.

Blahnik, R.J. & Holzenthal, R.W. (2008) Revision of the Mexican and Central American species of *Mortoniella* (Trichoptera: Glossosomatidae: Protoptilinae). *Zootaxa*, 1711, 1–72.

Blahnik, R.J. & Holzenthal, R.W. (2011) Revision of the austral South American species of *Mortoniella* (Trichoptera: Glossosomatidae: Protoptilinae). *Zootaxa,* 2851, 1–75.

Blahnik, R.J., Holzenthal, R.W. & Prather, A.L. (2007) The lactic acid method for clearing Trichoptera genitalia. *In*: Bueno-Soria, J., Barba-Alvarez, R. & Armitage, B.J. (Eds.) *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, pp. 9–14.

Bond, J.E. & Hedin, M. (2006) A total evidence assessment of the phylogeny of North American euctenizine trapdoor spiders (Araneae, Mygalomorphae, Cyrtaucheniidae) using Bayesian inference. *Molecular Phylogenetics and Evolution*, 41, 70–85.
http://dx.doi.org/10.1016/j.ympev.2006.04.026

Botosaneanu, L. (1977) Trichoptères (imagos) de Cuba, capturés par moi-meme en 1973 (Insecta, Trichoptera). *Fragmenta Entomologica*, 13, 231–284.

Botosaneanu, L. (1994) A study of the larvae of caddisflies (Trichoptera) from Cuba. *Tropical Zoology*, 7, 451–475.
http://dx.doi.org/10.1080/03946975.1994.10539267

Botosaneanu, L. (1996) Caddis flies (Trichoptera) from the Dominican Republic (West Indies). II. All families except Hydroptilidae; with general observations for Hispaniola. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie*, 66, 5–26.

Botosaneanu, L. (1998) On several *Hydropsyche* from Iran - with description of a new species (Trichoptera: Hydropsychidae). *Entomologische Zeitschrift*, 108, 496–500.

Botosaneanu, L. & Alkins-Koo, M. The caddis flies (Insecta: Trichoptera) of Trinidad and Tobago, West Indies. *Bulletin de l'Insitut Royal des Sciences Naturelles de Belgique, Entomologie*, 63, 5–45.

Botosaneanu, L. & Sykora, J. (1973) Sur quelques Trichoptéres (Insecta: Trichoptera) de Cuba. *In*: *Résultats des Expéditions Biospéologiques cubano-roumaines Cuba*. Editura Academiei Republicii Socialiste România., Bucharest, pp. 379–407.
Brandley, M.C., Schmitz, A. & Reeder, T.W. (2005) Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology*, 54, 373–390. http://dx.doi.org/10.1080/10635150590946808
Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42, 795–803. http://dx.doi.org/10.2307/2408870
Bryant, H.N. (1995) Why autapomorphies should be removed: A Reply to Yeates. *Cladistics*, 11, 381–384. http://dx.doi.org/10.1111/j.1096-0031.1995.tb00097.x
Buckley, T.R. (2002) Model misspecification and probalistic tests of topology: Evidence from empirical data sets. *Systematic Biology*, 51, 509–523. http://dx.doi.org/10.1080/10635150290069922
Buckley, T.R., Arensburger, P., Simon, C. & Chambers, G.K. (2002) Combined data, Bayesian phylogenetics, and the origins of the New Zealand cicada genera. *Systematic Biology*, 51, 4–18. http://dx.doi.org/10.1080/106351502753475844
Bueno-Soria, J. (1983) Five new species of caddisflies (Trichoptera) from Mexico. *Proceedings of the Entomological Society of Washington*, 85, 450–455.
Bueno-Soria, J. (1984) Three new species of the genus *Protoptila* from Mexico and Costa Rica (Trichoptera: Glossosomatidae). *Proceedings of the Biological Society of Washington*, 97, 392–394.
Bueno-Soria, J. & Santiago-Fragoso, S. (1979) Una nueva especie del género *Protoptila* Banks (Trichoptera: Glossosomatidae) de Veracruz, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología*, 50, 477–480.
Bueno-Soria, J. & Santiago-Fragoso, S. (1996) Studies in aquatic insects X: Descriptions of five new species of genus *Culoptila* Mosely (Trichoptera: Glossosomatidae) from México. *Proceedings of the Biological Society of Washington*, 109, 446–452.
Cassis, G. & Schuh, R.T. (2009) Systematic methods, fossils, and relationships within Heteroptera (Insecta). *Cladistics*, 26, 262–280. http://dx.doi.org/10.1111/j.1096-0031.2009.00283.x
Castlebury, L.A., Rossman, A.Y., Jaklitsch, W.J. & Vasilyeva, L.N. (2002) A preliminary overview of the Diaporthales based on large subunit nuclear ribosomal DNA sequences. *Mycologia*, 94, 1017–1031. http://dx.doi.org/10.2307/3761867
Colwell, R.K. (2003) *Biota 2*: *The Biodiversity Database Manager*. Sunderland, Massachusetts.
DeBry, R.W. (2001) Improving interpretation of the decay index for DNA sequence data. *Systematic Biology*, 50, 742–752. http://dx.doi.org/10.1080/106351501753328866
deWaard, J.R., Ivanova, N.V., Haijbabaei, M. & Hebert, P.D.N. (2008) Assembling DNA barcodes: Analytical protocols. *In*: Martin, C.C. (Ed.) *Environmental Genomics, Methods in Molecular Biology*. Humana Press, pp. 275–283. http://dx.doi.org/10.1007/978-1-59745-548-0_15
Dos Santos, C.M. & Falaschi, R.L. (2007) Missing data in phylogenetic analysis: Comments on support measures. *Darwiniana*, 45, 25–26.
Durbin, R., Eddy, S., Krogh, A. & Mitchison, G. (1998) *Biological Sequence Analysis*: *Probalistic Models of Proteins and Nucleic Acids*. Cambridge University Press, Cambridge, U.K., 368 pp.
Efron, B., Halloran, E. & Holmes, S. (1996) Bootstrap confidence levels for phylogenetic trees. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 7085–7090. http://dx.doi.org/10.1073/pnas.93.14.7085
Egge, J.D. & Simons, A.M. (2009) Molecules, morphology, missing data and the phylogenetic position of a recently extinct madom catfish (Actinopterygii: Ictaluridae). *Zoological Journal of the Linnean Society*, 155, 60–75. http://dx.doi.org/10.1111/j.1096-3642.2008.00432.x
Erixon, P., Svennblad, B., Britton, T. & Oxelman, B. (2003) Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology*, 52, 665–673. http://dx.doi.org/10.1080/10635150390235485
Felsenstein, J. (1978) Cases in which parsimony and compatibility methods will be positively misleading. *Systematic Zoology*, 27, 401–410. http://dx.doi.org/10.2307/2412923
Felsenstein, J. (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, 39, 783–791. http://dx.doi.org/10.2307/2408678
Felsenstein, J. (2004) *Inferring Phylogenies. Second Edition*. Sinauer Associates, Sunderland, Massachusetts, 664 pp.
Fischer, F.C.J. (1966) *Leptoceridae Pars 2*. *Trichopterorum Catalogus VII*. Nederlandsche Entomologische Vereeniging, Amsterdam, iii + 163 pp.
Fischer, F.C.J. (1971) *Supplement to Vols. I and II*, *Trichopterorum Catalogus XII*. Nederlandsche Entomologische Vereeniging, Amsterdam, vii + 311 pp.

Fitch, W.M. (1971) Toward defining the course of evolution: Minimum change for a specific tree topology. *Systematic Zoology*, 20, 406–416.
http://dx.doi.org/10.2307/2412116
Fitch, W.M. & Bruschi, M. (1987) The evolution of prokaryotic ferredoxins – with a general method correcting for unobserved substitutions in less branched lineages. *Molecular Biology and Evolution*, 4, 381–394.
Flint, O.S. Jr. (1962) The immature stages of *Matrioptila jeanae* (Ross) (Trichoptera: Glossosomatidae). *Journal of the New York Entomological Society*, 70, 64–67.
Flint, O.S. Jr. (1963) Studies of Neotropical caddis flies, I: Rhyacophilidae and Glossosomatidae (Trichoptera). *Proceedings of the United States National Museum*, 114, 453–478.
http://dx.doi.org/10.5479/si.00963801.114-3473.453
Flint, O.S. Jr. (1964) The caddisflies (Trichoptera) of Puerto Rico. *University of Puerto Rica, Agricultural Experiment Station, Technical Paper*, 40, 1–80.
Flint, O.S. Jr. (1967a) Studies of Neotropical caddis flies, IV: New species from Mexico and Central America. *Proceedings of the United States National Museum*, 123, 1–24.
http://dx.doi.org/10.5479/si.00963801.123-3608.1
Flint, O.S. Jr. (1967b) Trichoptera collected by Prof. J. Illies in the Chilean subregion. *Beiträge zur Neotropischen Fauna*, 5, 45–68.
http://dx.doi.org/10.1080/01650526709360395
Flint, O.S. Jr. (1968) The caddisflies of Jamaica. *Bulletin of the Institute of Jamaica, Science Series*, 19, 1–68.
Flint, O.S. Jr. (1971) Studies of Neotropical caddisflies, XII: Rhyacophilidae, Glossosomatidae, Philopotamidae, and Psychomyiidae from the Amazon Basin (Trichoptera). *Amazoniana*, 3, 1–67.
Flint, O.S. Jr. (1974) Studies of Neotropical caddisflies, XVIII: New species of Rhyacophilidae and Glossosomatidae (Trichoptera). *Smithsonian Contributions to Zoology*, 169, 1–30.
http://dx.doi.org/10.5479/si.00810282.169
Flint, O.S. Jr. (1981) Studies of Neotropical caddisflies, XXVIII: The Trichoptera of the Río Limón Basin, Venezuela. *Smithsonian Contributions to Zoology*, 330, 1–61.
http://dx.doi.org/10.5479/si.00810282.330
Flint, O.S. Jr. (1983) Studies of Neotropical caddisflies, XXXIII: New species from austral South America (Trichoptera). *Smithsonian Contributions to Zoology*, 377, 1–100.
http://dx.doi.org/10.5479/si.00810282.377
Flint, O.S. Jr. (1991) Studies of Neotropical caddisflies, XLV: The taxonomy, phenology, and faunistics of the Trichoptera of Antioquia, Colombia. *Smithsonian Contributions to Zoology*, 520, 1–113.
http://dx.doi.org/10.5479/si.00810282.520
Flint, O.S. Jr. (1992) New species of caddisflies from Puerto Rico (Trichoptera). *Proceedings of the Entomological Society of Washington*, 94, 379–389.
Flint, O.S. Jr., Holzenthal, R.W. & Harris, S.C. (1999) Nomenclatural and systematic changes in the Neotropical caddisflies. *Insecta Mundi*, 13, 73–84.
Flint, O.S. Jr. & Sykora, J.L. (2004) Caddisflies of Hispaniola, with special reference to the Dominican Republic (Insecta: Trichoptera). *Annals of Carnegie Museum*, 73, 1–60.
Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxydase subunit from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
Frania, H.E. & Wiggins, G.B. (1997) Analysis of morphological and behavioural evidence for the phylogeny and higher classification of Trichoptera (Insecta). *Life Sciences Contributions, Royal Ontario Museum*, 160, 1–67.
http://dx.doi.org/10.5962/bhl.title.53487
Goloboff, P.A. (1999) Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics*, 15, 415–428.
http://dx.doi.org/10.1111/j.1096-0031.1999.tb00278.x
Goloboff, P.A. (2002) Chapter 4. Techniques for analyzing large data sets. *In*: DeSalle, R. (Ed.) *Methods and Tools in Biosciences and Medicine*: *Techniques in Molecular Systematics and evolution*. Birkhauser Verlag Basel, Switzerland.
Goloboff, P.A. & Farris, J.S. (2001) Methods for quick consensus estimation. *Cladistics*, 17, 526–534.
http://dx.doi.org/10.1006/clad.2000.0156
Haijbabaei, M., deWaard, J.R., Ivanova, N.V., Ratnasingham, S., Dooh, R.T., Kirk, S.L., Mackie, P.M. & Hebert, P.D.N. (2005) Critical factors for assembling a high volume of DNA barcodes. *Philisophical Transactions of the Royal Society B - Biological Sciences*, 360, 1959–1967.
http://dx.doi.org/10.1098/rstb.2005.1727
Hawkins, J.A., Hughes, C.E. & Scotland, R.W. (1997) Primary homology assessment, characters and character states. *Cladistics*, 13, 275–283.
http://dx.doi.org/10.1111/j.1096-0031.1997.tb00320.x
Heath, T.A., Hedtke, S.M. & Hillis, D.M. (2008) Taxon sampling and the accuracy of phylogenetic analyses. *Journal of Systematics and Evolution*, 46, 239–257.

Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, Series B*, 270, 313–321.
http://dx.doi.org/10.1098/rspb.2002.2218

Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 14812–14817.
http://dx.doi.org/10.1073/pnas.0406166101

Hedtke, S.M., Townsend, T.M. & Hillis, D.M. (2006) Resolution of phylogenetic conflict in large data sets by increased taxon sampling. *Systematic Biology*, 55, 522–529.
http://dx.doi.org/10.1080/10635150600697358

Holder, M. & Lewis, P.O. (2003) Phylogeny estimation: Traditional and Bayesian approaches. *Nature Reviews*, 4, 275–284.
http://dx.doi.org/10.1038/nrg1044

Holzenthal, R.W. (2004) Three new species of Chilean caddisflies (Insecta: Trichoptera). *Proceedings of the Entomological Society of Washington*, 106, 110–117.

Holzenthal, R.W. & Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa*, 511, 1–80.

Holzenthal, R.W. & Blahnik, R.J. (2006) The caddisfly genus *Protoptila* in Costa Rica (Trichoptera: Glossosomatidae). *Zootaxa*, 1197, 1–37.

Holzenthal, R.W., Blahnik, R.J., Kjer, K.M., Prather, A. (2007) An update on the phylogeny of caddisflies (Trichoptera). *In*: Bueno-Soria, J., Barba-Alvarez, R., Armitage, B. (Eds.), *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, pp. 143–153.

Holzenthal, R.W., Blahnik, R.J., Prather, A.L. & Kjer, K.M. (2007) Order Trichoptera Kirby, 1813 (Insecta), caddisflies. *Zootaxa*, 1668, 639–698.

Houghton, D.C. & Stewart, K.W. (1998a) Immature life history descriptions and distribution of *Culoptila cantha* (Ross) (Trichoptera: Glossosomatidae). *Proceedings of the Entomological Society of Washington*, 100, 511–520.

Houghton, D.C. & Stewart, K.W. (1998b) Life history and case-building behavior of *Culoptila cantha* (Trichoptera: Glossosomatidae) in the Brazos River, Texas. *Annals of the Entomological Society of America*, 91, 59–70.

Huelsenbeck, J.P. (1991) When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology*, 40, 458–469.
http://dx.doi.org/10.2307/2992240

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
http://dx.doi.org/10.1093/bioinformatics/17.8.754

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, 294, 2310–2314.
http://dx.doi.org/10.1126/science.1065889

Ivanova, N.V., deWaard, J.R. & Hebert, P.D.N. (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, 6, 998–1002.
http://dx.doi.org/10.1111/j.1471-8286.2006.01428.x

Kagaya, T. & Nozaki, T. (1998) Notes on Japanese *Padunia* Martynov (Trichoptera: Glossosomatidae), with the description of a new species. *Aquatic Insects*, 20, 97–107.
http://dx.doi.org/10.1076/aqin.20.2.97.4499

Kearney, M. (2002) Fragmentary taxa, missing data, and ambiguity: Mistaken assumptions and conclusions. *Systematic Biology*, 51, 369–381.
http://dx.doi.org/10.1080/10635150252899824

Kearney, M. & Clark, J.M. (2003) Problems due to missing data in phylogenetic analyses including fossils: A critical review. *Journal of Vertebrate Paleontology*, 23, 263–274.
http://dx.doi.org/10.1671/0272-4634(2003)023[0263:pdtmdi]2.0.co;2

Kimmins, D.E. (1964) On the Trichoptera of Nepal. *Bulletin of the British Museum* (*Natural History*) *Entomology*, 15, 33–55.

Kitching, I.J., Forey, P.L., Humphries, C.J. & Williams, D.J. (1998) *Cladistics, 2nd edition. The Theory and Practice or Parsimony Analysis*. Oxford University Press, Oxford, 228 pp.

Kjer, K.M., Blahnik, R.J. & Holzenthal, R.W. (2001) Phylogeny of Trichoptera (Caddisflies): Characterization of signal and noise within multiple datasets. *Systematic Biology*, 50, 781–816.
http://dx.doi.org/10.1080/106351501753462812

Kolaczkowski, B. & Thornton, J.W. (2009) Long-branch attraction bias and inconsistency in Bayesian phylogenetics. *PLoS ONE*, 4:e7891.
http://dx.doi.org/10.1371/journal.pone.0007891

Kumanski, K.P. (1987) On caddisflies (Trichoptera) of Cuba. *Acta Zoologica Bulgarica*, 34, 3–35.

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P.A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, 23, 2947–2948.
http://dx.doi.org/10.1093/bioinformatics/btm404

Larson, A. (1994) The comparison of morphological and molecular data in phylogenetic systematics. *In*: Schierwater, B., Streit, B., Wagner, G.P. & DeSalle, R. (Eds.) *Molecular Ecology and Evolution*: *Approaches and Applications*. Birkhauser, Basel,

Switzerland.
Leach, A.D. & Reeder, T.W. (2002) Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): A comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology*, 51, 44–68.
http://dx.doi.org/10.1080/106351502753475871
Lee, D.C. & Bryant, H.N. (1999) A reconsideration of the coding of inapplicable characters: Assumptions and problems. *Cladistics*, 15, 373–378.
http://dx.doi.org/10.1111/j.1096-0031.1999.tb00273.x
Lemmon, A.R., Brown, J.M., Stanger-Hall, K. & Lemmon, E.M. (2009) The effect of ambiguous data on phylogenetic estimates obtained by Maximum Likelihood and Bayesian inference. *Systematic Biology*, 58, 130–145.
http://dx.doi.org/10.1093/sysbio/syp017
Lewis, P.O. (2001a) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50, 913–925.
http://dx.doi.org/10.1080/106351501753462876
Lewis, P.O. (2001b) Phylogenetic systematics turns over a new leaf. *TRENDS in Ecology & Evolution*, 16, 30–37.
Maddison, D.R. & Maddison, W.P. (2000) *MacClade 4*: *Analysis of phylogeny and character evolution, Version 4.0*. Sinauer Associates, Sunderland, Massachusetts.
Maddison, W.P. (1993) Missing data versus missing characters in phylogenetic analysis. *Systematic Biology*, 42, 576–581.
http://dx.doi.org/10.1093/sysbio/42.4.576
Malicky, H. (1995) Weitere neue Kocherfliegen (Trichoptera) aus Asien. *Braueria*, 22, 11–26.
Malicky, H. (2013) Synonyms and possible synonyms of Asiatic Trichoptera. *Braueria*, 40, 41–54.
Malicky, H. & Chantaramongkol, P. (1992) Neue Köcherfliegen (Trichoptera) aus Thailand und angrenzenden Ländern. (Arbeiten über thailändische Köcherfliegen Nr. 11.) *Braueria*, 19, 13–23.
Malicky, H. & Chantaramongkol, P. (2009) Beiträge Kenntnis asiatischer Trichopteren. *Braueria*, 36, 11–58.
Malicky, H., Chantaramongkol, P., Changthong, N., Nuntakwang, A. & Thamsenanupap, P. (2006) Beschreibungen einiger Köcherfliegen aus Nord-Thailand (Trichoptera) (Arbeit Nr. 41 über thailändische Köcherfliegen.) *Braueria*, 33, 39–42.
Malicky, H. & Silamon, S. (2012) Eine neue Gattung und vier neue Arten von Trichopteren aus Thailand. *Braueria*, 39, 22–24.
Marlier, G. (1955) Un trichoptère pélagique nouveau du lac Tanganika. *Revue de Zoologie et de Botanique Africaines*, 52, 150–155.
Marshall, J.E. (1979) A review of the genera of the Hydroptilidae (Trichoptera). *Bulletin of the British Museum* (*Natural History*) *Entomology*, 39, 135–239.
Martynov, A.B. (1910) Les Trichoptères de la Sibèrie et des régions adjacentes. II. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint Pétersbourg*, 15, 351–429.
Martynov, A.B. (1913) Къ познанію фауны Trichoptera Кавказа I. (Къ отчету о командировкъ). [Contribution to the knowledge of the Trichopterous fauna of the Caucasus.] (In Russian). *Raboti iz zoologicheskago Kabineta Varshavskago de Varsovie* [*Travaux du Cabinet zoologique de l'Universit de Varsovie*], 1912, 1–111, pls. I–IX.
Martynov, A.B. (1929) On a collection of Trichoptera from the River Bija and from the vicinities of the Lake Teletzkoje. *Konowia, Vienna*, 8, 293–311, 216 figs.
Martynov, A.V. (1934) *Tableaux analytiques de la faune de l'URSS, publiés par l'institut zoologisque de l'Académie des sciences. Trichoptera Annulipalpia. I.* Travaux de I'nstitute Zoologique de l'Académie des Science de l'URSS, 343 pp.
Morse, J.C. (1988) A new species of *Ceraclea* (*Athripsodina*) (Trichoptera: Leptoceridae) from Lake Tanganyika. *Revue de Zoologie Africaine*, 102, 43–45.
Morse, J.C. (2013) Trichoptera World Checklist. Available from http://entweb.clemson.edu/database/trichopt/index.htm (accessed 18 February 2013).
Morse, J.C. & Holzenthal, R.W. (2008) Chapter 18, Caddisfly genera. *In*: Merritt, R.W., Cummins, K.W. & Berg, M.A. (Eds.) *An Introduction to the Aquatic Insects of North America, 4th edition*. Kendall/Hunt, Dubuque, pp. 481–552.
Morse, J.C. & Yang, L. (1993) Higher classification of the Chinese Glossosomatidae (Trichoptera). *In*: Otto, C. (Ed.) *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 139–148.
Morse, J.C. & Yang, L. (2004) The world subgenera of *Glossosoma* Curtis (Trichoptera: Glossosomatidae), with a revision of the Chinese species of *Glossosoma* subgenera *Synafophora* Martynov and *Protoglossa* Ross. *Proceedings of the Entomological Society of Washington*, 106, 52–73.
Mosely, M.E. (1934) New exotic Hydroptilidae. *Transactions of the Royal Entomological Society of London*, 82, 137–163.
Mosely, M.E. (1937) Mexican Hydroptilidae (Trichoptera). *Transactions of the Royal Entomological Society of London*, 86, 151–189.
http://dx.doi.org/10.1111/j.1365-2311.1937.tb00242.x
Mosely, M.E. (1939) The Brazilian Hydroptilidae (Trichoptera). *Novitates Zoologicae*, 41, 217–239.
Mosely, M.E. (1954) The *Protoptila* group of the Glossosomatinae (Trichoptera: Rhyacophilidae). *Bulletin of the British Museum (Natural History) Entomology*, 3, 317–346.
Müller, F. (1888) Larven von Mücken und Haarflüglern mit zweierlei abwechselnd thätigen Athemwerkzeugen. *Entomologische Nachrichten*, 14, 273–277.
Müller, F. (1921) Briefe un noch nicht veröffentliche Abhandlungen aus dem nachlass 1854–1897. *In*: Möller, A. (Ed.) *Fritz*

Müller: *Werke, Briefe und Leben, 2*. G. Fischer, Jena, pp. 383–642.
Müller, J. & Reisz, R.R. (2006) The phylogeny of early eureptiles: Comparing parsimony and Bayesian approaches in the investigation of a basal fossil clade. *Systematic Biology*, 55, 503–511.
http://dx.doi.org/10.1080/10635150600755396
Nichols, S.W. (1989) *The Torre-Bueno Glossary of Entomology by J.R. de la Torre-Bueno*, *Revised Edition*. New York Entomological Society, New York, 840 pp.
Nielsen, A. (1957) A comparative study of the genital segments and their appendages in male Trichoptera. *Biologiske Skrifter*, 8, 1–159.
Nielsen, A. (1980) A comparative study of the genital segments and the genital chamber in female Trichoptera. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter*, 23, 1–200.
Nishimoto, H. & Nozaki, T. (2007) New species of *Padunia* Martynov (Trichoptera: Glossosomatidae) from Japan. *In*: Bueno-Soria, J., Barba-Álvarez, R. & Armitage, B.J. (Eds.) *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, pp. 229–242.
Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P. & Joséluis, N.-A. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology*, 53, 47–67.
http://dx.doi.org/10.1080/10635150490264699
Nyman, T., Zinovjev, A.G., Vikberg, V. & Farrell, B.D. (2006) Molecular phylogeny of the sawfly subfamily Nematinae (Hymenoptera: Tenthredinidae). *Systematic Entomology*, 31, 569–583.
http://dx.doi.org/10.1111/j.1365-3113.2006.00336.x
Patterson, C. (1982) Morphological characters and homology. *In*: Friday, J.J.A. & Friday, A.E. (Eds.) *Problems in phylogenetic reconstruction*. Academic Press, London, pp. 21–74.
Pauls, S., Blahnik, R.J., Zhou, X., Wardwell, C.T., & Holzenthal, R.W. (2010) DNA barcode data confirm new species and reveal cryptic diversity in Chilean *Smicridea* (*Smicridea*) (Trichoptera: Hydropsychidae). *Journal of the North American Benthological Society*, 29, 1058–1074.
http://dx.doi.org/10.1899/09-108.1
Pleijel, F. (1995) On character coding for phylogeny reconstruction. *Cladistics*, 11, 309–315.
Posada, D. & Crandall, K.A. (1998) MODELTEST: Testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
http://dx.doi.org/10.1093/bioinformatics/14.9.817
Prendini, L. (2001) Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology*, 50, 290–300.
http://dx.doi.org/10.1080/10635150118650
Rambaut, A. (2007) FigTree v1.3. Available from http://tree.bio.ed.ac.uk/software/figtree/ (Accessed 15 August 2009)
Rambaut, A. & Drummond, A.J. (2007) Tracer v1.4, Available from http://beast.bio.ed.ac.uk/Tracer (accessed 5 August 2009).
Remane, A. (1952) *Die Grundlagen des Naturlichen Systems der Vergleichenden Anatomie und der Phylogenetik*. Akademische Verlagsgesellschaft, Leipzig, Germany
Robertson, D.R. & Holzenthal, R.W. (2005) The Neotropical caddisfly genus *Tolhuaca* (Trichoptera: Glossosomatidae). *Zootaxa*, 1063, 53–68.
Robertson, D.R. & Holzenthal, R.W. (2006) The Neotropical caddisfly genus *Canoptila* (Trichoptera: Glossosomatidae). *Zootaxa*, 1272, 45–59.
Robertson, D.R. & Holzenthal, R.W. (2008) Two new species and a new record of *Protoptila* from Bolivia (Trichoptera: Glossosomatidae: Protoptilinae). *Annals of the Entomological Society of America*, 101, 465–473.
http://dx.doi.org/10.1603/0013-8746(2008)101[465:tnsaan]2.0.co;2
Robertson, D.R. & Holzenthal, R.W. (2011) Revision of the Neotropical caddisfly genus *Itauara* Müller, 1888 (Trichoptera, Glossosomatidae). *ZooKeys*, 114, 41–100.
http://dx.doi.org/10.3897/zookeys.114.1405
Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
http://dx.doi.org/10.1093/bioinformatics/btg180
Ronquist, F., Huelsenbeck, J.P. & van der Mark, P. (2005) MrBayes 3.1 Manual. Florida State University. Available from http://mrbayes.csit.fsu.edu/mb3.1_manual.pdf (Accessed 5 October 2009)
Ross, H.H. (1938) Descriptions of Nearctic caddis flies (Trichoptera) with special reference to the Illinois species. *Bulletin of the Illinois Natural History Survey*, 21, 101–183.
Ross, H.H. (1941) Descriptions and records of North American Trichoptera. *Transactions of the American Entomological Society*, 67, 35–126.
Ross, H.H. (1944) The caddisflies or Trichoptera of Illinois. *Bulletin of the Illinois Natural History Survey*, 23, 1–326.
Ross, H.H. (1956) *Evolution and Classification of the Mountain Caddisflies*. University of Illinois Press, Urbana, 213 pp.
Rueda Martin, P.A. & Gibon, F.M. (2008) New species of Glossosomatidae from Bolivia with new records from Bolivia and northwestern Argentina (Trichoptera: Glossosomatidae). *Annales de Limnologie*, 44, 215–225.
http://dx.doi.org/10.1051/limn:2008006

Santos, A.P.M. & Nessimian, J.L. (2009) A new species of *Protoptila* Banks (Trichoptera: Glossosomatidae: Protoptilinae) from Brazil. *Acta Amazonica*, 39, 723–726.
http://dx.doi.org/10.1590/s0044-59672009000300030
Schmid, F. (1958) Contribution a l'etude des Trichoptères Neotropicaux III. *Mitteilungen aus dem Zoologischen Museum in Berlin*, 34, 183–217.
http://dx.doi.org/10.1002/mmnz.19580340110
Schmid, F. (1959) Contribution a l'etude des trichoptères Neotropicaux IV. *Acta Zoologica Lilloana*, 17, 477–483.
Schmid, F. (1964) Contribution a l'etude des trichopteres neotropicaux V. *Tijdschrift voor Entomologie*, 107, 307–339.
Schmid, F. (1989) Les hydrobiosides (Trichoptera, Annulipalpia). *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Entomologie*, 59, 1–154.
Schmid, F. (1990 [1991]) Quelques nouveaux trichoptères indiens (Trichoptera). *Naturaliste Canadien*, 117, 239–251.
Schmid, F. (1998) *The insects and arachnids of Canada, Part 7. Genera of the Trichoptera of Canada and adjoining or adjacent United States.* NRC Research Press, Ottawa, 319 pp.
Schuh, R.T. & Brower, A.V.Z. (2009) *Biological Systematics*: *Principles and Applications, 2nd edition*. Cornell University Press, Ithaca, 311 pp.
Simmons, M.P., Pickett, K.M. & Miya, M. (2004) How meaningful are Bayesian support values? *Molecular Biology and Evolution*, 21, 188–199.
http://dx.doi.org/10.1093/molbev/msh014
Simon, C., Buckley, T.R., Frati, F., Stewart, J.B. & Beckenbach, A. (2006) Incorporating molecular evolution into phylogeneitc analysis, and a new compilation of conserved polymerase chain reaction primers for animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics*, 37, 545–579.
http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110018
Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 652–682.
Stein, J.P.E.F. (1874) Beitrag zur Kenntniss der Phryganeiden des Altvaters und einiger anderer. *Stettiner Entomologische Zeitung*, 35, 244–253.
Stocks, I.C. (2010) Comparative and functional morphology of wing coupling structures in Trichoptera: Annulipalpia. *Journal of Morphology*, 271, 152–168.
http://dx.doi.org/10.1002/jmor.10788
Strong, E.E. & Lipscomb, D. (1999) Character coding and inapplicable data. *Cladistics*, 15, 363–371.
http://dx.doi.org/10.1111/j.1096-0031.1999.tb00272.x
Swofford, D.L. (2003) PAUP* Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4. Sinauer Associates, Sunderland, Massachusetts.
Swofford, D.L., Olsen, G., J., Waddell, P.J. & Hillis, D.M. (1996) Phylogenetic Inference. *In*: Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.) *Molecular Systematics, 2nd edition*. Sinauer Associates, Sunderland, Massachusetts, pp. 407–514.
Sykora, J.L. (1999) Genus *Mortoniella* and its distribution in South America (Trichoptera, Glossosomatidae, Protoptilinae). *In*: Malicky, H. & Chantaramongkol, P. (Eds.) *Proceedings of the 9th International Symposium on Trichoptera*. Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, pp. 377–387.
Tian, L. & Li, Y. (1986) Four new species of the caddisflies on Hengduan Mountain, China. *Journal of Nanjing Agricultural University*, 2, 50–54.
Tsuda, M. (1942) Zur Kenntnis den Koreanischen Trichopteren. *Memoirs of the College of Science, Kyoto Imperial University, Series B*, 17, 227–237.
Ulmer, G. (1906) Neuer beitrag zur kenntnis aussereuropäischer Trichopteren. *Notes from the Leyden Museum*, 28, 1–116.
Valverde, A.d.C. & Miserendino, M.L. (1998) Aportos al conocimiento do los estados preimaginales de *Mastigoptila longicornuta* (Trichoptera: Glossosomatidae). *Revista de la Sociedad Entomológica Argentina*, 57, 49–55.
Walker, F. (1852) *Cataloque of the Specimens of Neuropterous Insects in the Collection of the British Museum, Part I*: *Phryganides-Perlides*. British Museum, London, 192 pp.
Wallengren, H.D.J. (1891) Skandinaviens Neuroptera. Andra afdelningen. *Svenska Akademien Handlingar*, 24, 1–173.
Ward, J.B. & Pollard, S.D. (2002) Mating plugs and exaggerated genitalia: Possible consequences of sexual selection on two species of Trichoptera from New Caledonia. *In*: Mey, W. (Ed.), *Nova Supplementa Entomologica* (*Proceedings of the 10th International Symposium on Trichoptera*), 15, 249–252.
Wichard, W. (1989) Köcherfliegen des Dominikanischen Bernsteins. VII. Fossile Arten der Gattung *Cubanoptila* Sykora, 1973. *Mitteilungen Münchener Entomologischen Gesellschaft*, 79, 91–100.
Wichard, W. (1995) Köcherfliegen des Dominikanischen Bernsteins VIII. *Cubanoptila grimaldii* n. sp., eine weitere fossile Art der Glossosomatidae (Insecta, Trichoptera). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 78, 159–165.
Wichard, W. (2007) Overview and descriptions of caddisflies (Insecta, Trichoptera) in Dominican amber (Miocene). *Stuttgarter Beiträge zur Naturkunde Serie B* (*Geologie und Paläontologie*), 366, 1–51.
Wichard, W., Kraemer, M.M.S. & Luer, C. (2006) First caddisfly species from Mexican amber (Insecta: Trichoptera). *Zootaxa*, 1378, 37–48.

Wiens, J.J. (1998) Does adding characters with missing data increase or decrease phylogenetic accuracy? *Systematic Biology*, 47, 625–640.
http://dx.doi.org/10.1080/106351598260635
Wiens, J.J. (2003a) Incomplete taxa, incomplete characters, and phylogenetic accuracy: Is there a missing data problem? *Journal of Vertebrate Paleontology*, 23, 297–310.
Wiens, J.J. (2003b) Missing data, incomplete data, and phylogenetic accuracy. *Systematic Biology*, 52, 528–538.
http://dx.doi.org/10.1080/10635150390218330
Wiens, J.J. (2005) Can incomplete taxa rescue phylogenetic analyses from long-branch attraction? *Systematic Biology*, 54, 731–742.
http://dx.doi.org/10.1080/10635150500234583
Wiens, J.J. (2006) Missing data and the design of phylogenetic analyses. *Journal of Biomedical Informatics*, 39, 34–42.
http://dx.doi.org/10.1016/j.jbi.2005.04.001
Wiens, J.J. (2009) Paleontology, genomics, and combined-data phylogenetics: Can molecular data improve phylogeny estimation for fossil taxa? *Systematic Biology*, 58, 87–99.
http://dx.doi.org/10.1093/sysbio/syp012
Wiens, J.J. & Reeder, T.W. (1995) Combining data sets with different numbers of taxa for phylogenetic analysis. *Systematic Biology*, 44, 548–558.
http://dx.doi.org/10.1093/sysbio/44.4.548
Wiggins, G.B. (1996) *Larvae of the North American Caddisfly Genera* (*Trichoptera*), *2nd Edition*. University of Toronto Press, Toronto, 457 pp.
Wiggins, G.B. (2004) *Caddisflies*: *The Underwater Architects*. University of Toronto Press, Toronto, 292 pp.
Wilcox, T.P., Zwickl, T.A., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25, 361–371.
Wiley, E.O. (1981) *Phylogenetics*: *The Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons, Inc., New York, 439 pp.
Wilkinson, M. (1992) Ordered versus unordered characters. *Cladistics*, 8, 375–385.
http://dx.doi.org/10.1111/j.1096-0031.1992.tb00079.x
Wilkinson, M. (1995) Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology*, 44, 501–514.
http://dx.doi.org/10.2307/2413657
Wilkinson, M. (2003) Missing entries and multiple trees: Instability, relationships, and support in parsimony analysis. *Journal of Vertebrate Paleontology*, 23, 311–323.
http://dx.doi.org/10.1671/0272-4634(2003)023[0311:meamti]2.0.co;2
Yang, Z. & Rannala, B. (2012) Molecular phylogenetics: principals and practice. *Nature Reviews Genetics*, 13, 303–314.
http://dx.doi.org/10.1038/nrg3186
Yeates, D. (1992) Why remove autapomorphies? *Cladistics*, 8, 387–389.
http://dx.doi.org/10.1111/j.1096-0031.1992.tb00080.x
Zander, R.H. (2004) Minimal values for reliability of bootstrap and jackknife proportions, decay index, and Bayesian posterior probability. *PhyloInformatics*, 2, 1–13.
Zhou, X., Kjer, K.M. & Morse, J.C. (2007) Associating larvae and adults of Chinese Hydropsychidae caddisflies (Insecta: Trichoptera) using DNA sequences. *Journal of the North American Benthological Society*, 26, 719–742.
http://dx.doi.org/10.1899/06-089.1

APPENDIX 1.

Morphological characters and states for cladistic analysis.

1. *Type of larval case*. 0: free-living; 1: purse-like; 2: tortoise- or saddle-like.
   Adult-larval associations have been determined for only a few taxa in this study. Although it is possible that larval characters may be highly conserved at the genus level, this is an untested assumption, casting doubt on an analysis of most larval characters. Furthermore, since a primary goal of the study was to test the monophyly of individual genera, it was not deemed appropriate to use composite taxon sampling for genus-level larval characters. On the other hand, because no exceptions are known, it is widely accepted that all Glossosomatidae larvae construct tortoise-like cases (Wiggins 2004). Consequently, only this single larval character was coded and scored for the analysis.

Head & thorax

2. *Shape of head.* 0: wider than long (Fig. 5); 1: longer than wide; 2: length = width.
   State 0 is observed in all taxa.
3. *Length of antennal scape*. 0: ≤2x length of pedicel; 1: ≥3x length of pedicel (Fig. 6A).
   State 1 is present in the Caribbean genera (*Campsiophora*, *Cariboptila*, *Cubanoptila*).
4. *3rd antennal segment*. 0: without stout spine-like setae; 1: with stout spine-like setae (Fig. 6A).
   State 1 is present in *Cubanoptila*.
5. *Length of maxillary palpi 1st & 2nd segments* (Frania & Wiggins 1997) in part. 0: 1st segment shorter than 2nd segment; 1: 1st segment = 2nd segment (Fig. 6E); 2: 1st segment longer than 2nd segment.
6. *Number of anterior setal warts*. 0: 1 distinct pair (Fig. 5A); 1: 1 pair, each wart constricted medially; 2: 2 distinct pairs (Fig. 5B); 3: patchy, sparsely setose.
7. *Shape of anterior setal warts*. 0: elongate (Fig. 5A); 1: suboval (Fig. 5B); 2: irregular, patchy.
8. *Posterior setal wart size*. 0: large, extending from lateral ocellus and meeting or almost meeting at medial suture (Fig. 5A); 1: small, not extending from lateral ocellus or meeting at medial suture (Fig. 5B).
9. *Posterolateral setal wart shape*. 0: suboval or triangular and bulging (Fig. 5); 1: elongate.
   State 0 is observed in all protoptilines and some of the outgroups.
10. *Mesothorax shape*. 0: longer than wide (Fig. 5A); 1: wider than long (Fig. 5B); 2: length = width.
11. *Mesothorax tegular glands presence*. 0: present (Fig. 5B); 1: absent.
12. *Anteromesal mesoscutal wart shape*. 0: elongate (Fig. 5A); 1: suboval (Fig. 5B); 2: entire region setose, no distinct wart.
13. *Anteromesal mesoscutal wart position*. 0: anterior (Fig. 5B); 1: mesal; 2: lateral (Fig. 5A).
   State 2 is characteristic of taxa having elongate anteromesal mesoscutal warts.
14. *Mesoscutellar wart presence* (Kimmins 1964, in part; Ross 1956, in part). 0: present (Fig. 5A); 1: absent (Fig. 5B).
   The presence of mesoscutellar warts is considered a primitive characteristic of Trichoptera. Among the Protoptilinae, mesoscutellar warts are absent in all Neotropical taxa except *Tolhuaca*.
15. *Mesoscutellar wart shape and position*. 0: 2 distinct small circular warts posterior; 1: 2 distinct small circular patches posterior; 2: 2 distinct large suboval warts or patches lateral.
16. *Number of foretibial spurs* (Ross 1956, in part) 0: two; 1: one; 2: zero; 3: three.
   Either state 1 or 2 is observed among Protoptilinae.
17. *Foretibial spur development* (Morse & Yang 1993, Ross 1956, in part). 0: hair-like (Fig. 6B); 1: well-developed.
   When a single foretibial spur is present in protoptiline taxa, it is always hair-like.
18. *Number of mesotibial spurs* (Frania & Wiggins 1997, in part). 0: four; 1: three; 2: two.
19. *Number of metatibial spurs*. 0: four; 1: three.

Wings

20. *Shape of forewing* (Ross 1967, in part). 0: broad past anastamosis (Fig. 12A); 1: margins nearly parallel (Fig. 7A); 2: narrow past anastomosis, much reduced (Fig. 10A).
21. *Male anal region forewing callosity* (Morse & Yang 1993; Morse & Yang 2004, in part). 0: present; 1: absent.
   Wing callosity is defined as a visible thickening of the wing cuticle. Morse & Yang (2004) described 3 general patterns of callosity observed in the anal region of the male forewing in *Glossosoma*. However, for the purposes of this study, we coded this character as absent or present.
22. *Male apical costal region forewing callosity.* 0: present; 1: absent.
23. *Male forewing hair pencil*. 0: absent; 1: present on inner surface of anal angle (Fig. 8C).
   A hair pencil is defined as a modified fringe of elongate setae associated with androconial glands (Nichols 1989). State 1 is observed in *Campsiophora pedophila* and *Campsiophora arawak* Flint, 1968.
24. *Forewing R1* (Morse and Yang 1993). 0: forked; 1: unforked.
   State 0 is observed in the outgroup genera *Anagapetus* and *Glossosoma*.
25. *Forewing apical fork I in relation to crossvein* s. 0: sessile (Fig. 11A); 1: petiolate (Fig. 7A).
26. *Stem of forewing fork I length.* 0: about the same length as the fork; 1: longer than fork; 2: shorter than fork (Fig. 10A).

State 2 is observed in almost all taxa with a petiolate apical fork I. State 0 is observed in the outgroup taxon *Ptilocolepus granulatus* (Pictet, 1834). State 1 is an autapomorphy for *Merionoptila wygodzinskyi*.

27. *Forewing apical fork II in relation to crossvein* r-m. 0: sessile (Fig. 7C); 1: petiolate (Fig. 8A).
28. *Stem of forewing fork II length*. 0: about the same length as fork (Fig. 8A); 1: longer than fork (Fig. 9A); 2: shorter than fork (Fig. 9C).
29. *Forewing apical forks I and II.* 0: branching at same level (Fig. 8C) 1: fork I branching before fork II (Fig. 8A) 2: fork II branching before fork I (Fig. 7A).
30. *Forewing apical fork III presence* (Morse & Yang 1993, in part; Ross 1956, in part). 0: present; 1: absent (Fig. 10C).
State 1 is observed in *Matrioptila, Padunia, Poeciloptila, Temburongpsyche,* and *Scotiotrichia*.
31. *Forewing apical fork III in relation to crossvein* m-cu. 0: sessile; 1: petiolate.
State 1 is observed in all taxa with fork III present, with the exception of the outgroup taxon *Glossosoma*.
32. *Stem of forewing fork III length.* 0: about the same length as fork; 1: longer than fork; 2: shorter than fork.
33. *Forewing apical fork IV presence* (Morse & Yang 1993, in part; Ross 1956, in part). 0: present; 1: absent.
34. *Forewing apical fork IV in relation to crossvein* m-cu. 0: sessile; 1: petiolate.
35. *Stem of forewing fork IV length.* 0: about the same length as fork; 1: longer than fork; 2: shorter than fork.
36. *Forewing apical fork V* (Kimmins 1964, in part; Morse & Yang 1993; Ross 1956, in part; Schmid 1990, in part). 0: present; 1: absent.
37. *Forewing apical fork V in relation to crossvein* m-cu. 0: sessile; 1: petiolate.
38. *Forewing Cu1.* 0: complete, reaching wing margin; 1: incomplete, not reaching wing margin (Fig. 7A).
State 1 is observed in *Culoptila*.
39. *Forewing Cu1 and Cu2 intersection* (Ross 1956, in part). 0: intersecting near anastomosis (Fig. 7A); 1: separate, not intersecting (12A); 2: completely fused (Fig. 11A).
40. *Forewing A3 looping*. 0: looped (Fig. 11C); 1: absent.
41. *Forewing Cu2 row of erect setae presence* (Kimmins 1964, in part; Mosely 1954, in part; Ross 1956, in part). 0: absent; 1: present (Figs. 7–14).
State 1 is observed in all Protoptilinae.
42. *Forewing Cu2 row of erect setae position* (Ross 1956, in part). 0: along Cu2 (Fig. 7A); 1: below Cu2 (Fig. 9A, 10C).
43. *Forewing crossvein* r *presence*. 0: present (Fig. 7A); 1: absent (Fig. 7C).
44. *Forewing crossvein* s *presence* (Morse & Yang 1993). 0: present; 1: absent.
45. *Forewing crossvein* r-m *presence.* 0: present; 1: absent.
46. *Forewing discoidal cell length*. 0: as long as or longer than Rs vein (Fig. 7A); 1: shorter than Rs vein (Fig. 7C, 8A).
47. *Forewing crossveins* r, s, *and* r-m alignment (Mosely 1954, in part; Ross 1956, in part; Morse & Yang 1993, in part). 0: forming relatively straight line; 1: not forming straight line.
48. *Forewing crossvein* m-cu *presence*. 0: present; 1: absent.
49. *Hind wing shape*. 0: broad past anastomosis (Fig. 12B); 1: margins nearly parallel (Fig. 9B); 2: narrow past anastomosis or scalloped along costal margin (Fig. 7D); 3: much reduced (Fig. 10B).
50. *Hind wing apical fork I presence* (Morse & Yang 1993, in part; Ross 1956, in part). 0: present; 1: absent.
51. *Hind wing apical fork II presence* (Morse & Yang 1993, in part). 0: present; 1: absent.
52. *Hind wing apical fork III presence* (Morse & Yang 1993, in part). 0: present; 1: absent.
53. *Hind wing apical fork V presence* (Morse & Yang 1993, in part; Ross 1956, in part). 0: present; 1: absent.
54. *Hind wing A2 presence*. 0: present; 1: absent.
55. *Hind wing A2 looping*. 0: not looped; 1: looped.
56. *Hind wing A3 presence*. 0: present; 1: absent.

Male pregenitalic abdominal structures

57. *Sternum V lateral process presence*. 0: absent; 1: present (Fig. 6D).
The lateral process is associated with glandular structures on segment V in males. State 1 is observed in *Matrioptila* and some species of *Padunia* and *Nepaloptila*. The process is also present in the outgroup taxon *Ptilocolepus granulatus*.
58. *Sternum VI mesal process presence*. 0: absent; 1: present (Fig. 15A).
State 0 is an autapomorphy of *Merionoptila wygodzinskyi*. The presence of small points or processes on sterna VI and VII is plesiomorphic in Trichoptera (Schmid 1989).
59. *Shape of sternum VI mesal process apex*. 0: pointed or attenuate; 1: rounded; 2: bilobate; 3: subquadrate.
60. *General shape of sternum VI mesal process*. 0: tooth-like point; 1: elongate and digitate; 2: subtriangular; 3: circular; 4: flattened dorsoventrally; 5: thumb-like and prominent; 6: short and digitate.
61. *Sternum VI mesal process apodeme*. 0: absent; 1: strong; 2: weak.
62. *Sternum VII mesal process presence*. 0: without mesal process; 1: with prominent mesal process; 2: with small mesal point.
State 2 appears in the outgroup taxa *Anagapetus* and *Glossosoma* and the protoptiline species *Campsiophora mulata*.

Male genitalia

63. *Sternum VIII modification*. 0: projecting medially and subtending segment IX to which it is partially fused (Figs. 27A,B);

1: not projecting medially.
State 0 is a synapomorphy of *Protoptila*.

64. *Terga VII and VIII dorsomesal, intersegmental region modifications.* 0: with no modification; 1: with glandular structure.
65. *Terga VII and VIII dorsolateral, intersegmental region modification*. 0: with paired glandular structure; 1: without modification.
66. *Tergum VIII dorsal plate presence*. 0: absent; 1: present [subtending terga IX and X (Figs. 17A, B)].
67. *Anterior margin of segment IX shape*. 0: fairly straight (Fig. 27A); 1: rounded (Fig. 18A); 2: subtriangular (Fig. 24A).
68. *Posterior margin of segment IX processes or lobes presence*. 0: absent; 1: present (Fig. 24A,C).
State 1 is present in *Matrioptila*, *Padunia*, *Poeciloptila*, and *Temburongpsyche*.
69. *Tergum IX shape dorsally*. 0: strap-like, very narrow; 1: uniformly narrow; 2: uniformly broad.
70. *Sternum IX shape ventrally*. 0: strap-like, very narrow (Fig. 30A); 1: uniformly narrow (Fig. 20); 2: uniformly broad (Fig. 25A,D); 3: absent (Fig. 16A).
71. *Sternum IX lateral margins*. 0: constricted; 1: not constricted.
72. *Sternum IX mesal modifications*. 0: without modification; 1: with ventromesal projection posteriorly (Fig. 28A,B); 2: with 2 pairs of elongate seta-like spines ventrolaterally (Fig. 20A,C).
State 1 is observed in *Protoptila*. The 2 pairs of elongate seta-like spines (State 2) is an autapomorphy of *Itauara brasiliana*. These spines are superficially similar in appearance to the elongate parameres of certain other *Itauara* species, but are not homologous structures.
73. *Tergum IX paired dorsolateral process presence*. 0: present [each usually bearing 1 or more elongate apical setae (Fig. 16A,C)]; 1: absent.
State 0 is observed in the Caribbean taxa *Campsiophora*, *Cariboptila*, and *Cubanoptila*.
74. *Tergum X attachment*. 0: completely fused to and indistinguishable from segment IX (Fig. 24); 1: incompletely fused to segment IX with membrane or lightly sclerotized region connecting segment X ventolaterally (Fig. 28A,C); 2: mostly separate segment from segment IX; 3: fused dorsomesally, or "hinged" (Fig. 22); 4: partially fused to segment IX, consisting of basal and distal segments (Fig. 28).
State 2 is considered the primitive condition and is present in the outgroup taxa *Ptilocolepus*, *Anagapetus*, and *Glossosoma*. State 3 is observed in *Merionoptila* and *Mortoniella*. State 4 is observed in *Protoptila*.
75. *Tergum X position*. 0: subtended by segment IX (Fig. 16–18); 1: not subtended by segment IX.
State 0 is observed in the Caribbean taxa *Campsiophora*, *Cariboptila*, and *Cubanoptila*.
76. *Tergum X dorsomesal region* (Morse & Yang 1993, in part). 0: absent or vestigial 1: present, mostly membranous (Fig. 25A,C); 2: present, mostly sclerotized.
77. *Tergum X dorsomesal margin*. 0: with single, elongate, prominent process; 1: irregular with several small processes; 2: divided or bifid apicomesally; 3: subquadrate; 4: subtriangular; 5: with a single broad, plate-like process.
There is a great diversity among the shapes and number of processes/lobes of Tergum X. No doubt, many of these states are homoplastic at higher taxonomic levels. However, they may be informative at the species level.
78. *Tergum X dorsolateral margin*. 0: with paired elongate, down-turned, finger-like processes; 1: with irregular setose processes; 2: with small paired lobes; 3: without processes; 4: with upturned sclerotized points; 5: membranous; 6: with forked paired process; 7: with teeth-like spines; 8: with 1 or more large, horn-like processes; 9: with short, flattened, inwardly curved process (Fig. 16C, 17A,C, 18A,B).
(See Character 77 comment). State 4 is an autapomorphy for the outgroup taxon, *Agapetus rossi* Denning 1941.
79. *Tergum X ventrolateral margin*. 0: with paired, broad, flange-like processes; 1: with 1 or more irregular, paired, setose, digitate lobes directed posteriorly; 2: with paired very elongate, spine-like process directed inwardly; 3: with small irregular, paired, setose lobes; 4: with paired elongate processes attached ventrolaterally to segment IX and directed ventrally and sometimes anteriorly (Fig. 19A,C); 5: without processes or lobes; 6: bearing 1 or several large, highly sclerotized spines or spine-like setae, directed mesad (Fig. 16C, 17A,C, 18A,B).
(See Character 77 comment). State 4 is observed in *Culoptila*. State 6 is observed in the Caribbean taxa *Campsiophora*, *Cariboptila*, and *Cubanoptila*.
80. *Preanal appendages presence*. 0: absent; 1: present.
Preanal appendages are absent in Protoptilinae and the outgroup taxa *Anagapetus debilis* (Ross, 1938) and *Glossosoma intermedium* (Klapálek, 1892).
81. *Inferior appendages presence* (Ross 1956, in part). 0: present; 1: absent.
In Trichoptera, inferior appendages are defined as 1- or 2-segmented gonopods, arising ventrally from segment IX and often connected to each other at their bases (Holzenthal *et al*. 2007b). Functionally, these structures serve as claspers, grasping the female during copulation. Among the Protoptilinae, the inferior appendages have undergone such extensive evolution that many structures are often no longer identifiable as “claspers.” For example, in some species the inferior appendages appear to have migrated from segment IX to be attached to the phallobase (Ross 1956). In other species, the inferior appendages have been completely lost.
82. *Inferior appendage shape*. 0: 2 distinct appendages attached to segment IX and articulating with phallus basally; 1: fused completely (non-articulating) and integrated with segment IX, forming either elongate or shortened paired ventrolateral processes, or single ventromesal process, sometimes bifid (Fig. 24A,D); 2: 2 distinct appendages attached ventrally to phallus and articulating with IX (Fig. 27A,B,C); 3: markedly asymmetrical, fused to phallocrypt ventrobasally (Fig. 21A,D); 4: composite structure consisting of paired processes fused together basally and to ventral margin of phallic

apparatus and ventrolaterally to endotheca, associated with articulated appendages fitting into pockets (Fig. 23A,C); 5: bulbous, fused ventromedially to endotheca and projecting ventrad (Fig. 22A,C); 6: broad, highly setose, prominent plate-like projection fused ventrobasally to phallobase, sometimes invaginated apicomesally or with broad lateral processes (Fig. 16A,B); 7: simple, paired long or short processes, fused to one another basally to ventral surface of phallobase (Fig. 19); 8: single or apically bifid process produced mesally, broadest at base, fused to phallobase ventrobasally.

Inferior appendages were identified and homologized based on their general position and structure. An evident transformational series is present from the simple condition of paired articulating appendages attached to segment IX, to the various conditions observed in Protoptilinae. In some species, the inferior appendages may function to evert or guide the phallus, in others, they are so reduced that they have apparently lost all functionality. In several subgenera of *Glossosoma*, Morse and Yang (2004) considered Ross's (1956) "fixed spiny lobes of the aedeagus" to be the inferior appendages. However, we believe these processes, based on their position and structure, are actually parameres and therefore we agree with Ross's original homology assessment in which the inferior appendages appear as ventral projections of sternum IX. State 0 is observed in all outgroup taxa and is considered the plesiomorphic condition in Trichoptera (Schmid 1989). State 1 is observed in *Nepaloptila*, *Padunia*, *Poeciloptila*, and *Temburongpsyche*. This character was especially phylogenetically informative at the generic level.

83. *Inferior appendage segments* (Frania & Wiggins 1997, in part; Morse & Yang 1993, in part). 0: with 2 articles; 1: with 1 article.

    State 0 is plesiomorphic in Trichoptera. The 1-article condition is observed in all Glossosomatidae and results from the loss of the harpago, or its fusion to the coxopodite (Holzenthal *et al*. 2007b)
84. *Parameres* (Frania & Wiggins 1997, in part; Morse & Yang 1993, in part). 0: absent; 1: present.

    Parameres are paired processes arising from the endotheca (Holzenthal *et al*. 2007b). No doubt, parameres have been lost several times independently. Additionally, many taxa have structures resembling parameres, but it is unclear if they are truly homologous to parameres or are novel structures. For example, several taxa in the Caribbean genera have spine-like features; however, as they do not appear to arise from the endotheca, we do not consider them to be true parameres.
85. *Paramere position*. 0: arising ventrobasally from fused endotheca and phallobase; 1: laterally from endotheca; 2: dorsolaterally from endotheca.

    State 1 is the plesiomorphic condition in Trichoptera.
86. *Paramere sclerotization*. 0: sclerotized and rod-like (Fig. 23A); 1: membranous and digitate (Fig. 15B, D).
87. *Paramere shape*. 0: mostly straight; 1: ram's horn-like; 2: tusk-like and curving upward dorsally; 3: elongate and mostly curving downward; 4: serrate with 1 or 2 processes; 5: spatulate and straight; 6: digitate lobe with bulbous apex bearing short spine-like, stout setae; 7: elongate sinuous; 8: bulbous.
88. *Phallic apparatus*. 0: with single dorsomesal process arising internally from phallobase (Fig. 23A,C); 1: with single dorsomesal process arising dorsobasally from phallobase; 2: without single dorsomesal process.
89. *Phallobase*. 0: extremely reduced, often membranous (Fig. 15B,D); 1: not apparently reduced; 2: extremely enlarged (Fig. 16A,B); 3: absent (Fig. 21).
90. *Phallobase dorsal margin.* 0: with sclerotized sheath produced anteriorly, with ventral margin membranous or absent (Fig. 24A,B); 1: without sclerotized sheath, ventral margin sclerotized.
91. *Phallobase appendages* (Blahnik & Holzenthal 2008, in part). 0: without paired articulated, rod-like appendages with membraneous apices; 1: with paired articulated, small, digitate, rod-like appendages with membranous apices (Fig. 23A,C).
92. *Phallobase ventrobasally* (Blahnik & Holzenthal 2008, in part). 0: without modified pockets; 1: with modified pockets (Fig. 23A,C).
93. *Phallobase apodeme*. 0: with axe-shaped dorsal apodeme (Fig. 28C); 1: without dorsal apodeme.
94. *Phallicata*. 0: with sclerotized dorsolateral flange; 1: without flange.
95. *Phallicata dorsum*. 0: without dorsal sheath; 1: with dorsal sheath covering membranous ventral portion (Fig. 20A).
96. *Phallicata apically*. 0: without ventral branch; 1: with ventral branch bearing 1 or more apical spines (Fig. 24B).

Female genitalia

97. *Shape of the female genitalia apex* (Frania & Wiggins 1997, in part; Ross 1967, in part). 0: extensible oviscapt (Fig. 31A); 1: not extensible, but rather with modified appendicular parts of abdominal segments VIII and IX (Fig. 31B,C).

    State 0, an extensible oviscapt is the primitive condition in Trichoptera (Schmid 1989) and consists of a prolongation or modification of the posterior abdominal segments which functions as an ovipositor (Nichols 1989).
98. *Elongate internal apodemes* (Frania & Wiggins 1997, in part; Ross 1967, in part). 0: vestigial or absent; 1: present as 2 pairs of long, slender sclerotized rods arising from the lateral margins of segments VIII and IX and extending cephalad to segments VI and VII, respectively (Fig. 31A).

    State 1, the presence of elongate apodemes is a pleisiomorph for Amphiesmenoptera (Schmid 1989).
99. *Segments VIII and IX*. 0: fused (Fig. 31C); 1: not fused.

    State 0 is observed in *Matrioptila*, *Nepaloptila*, *Padunia*, *Poeciloptila*, and *Temburongpsyche*. State 1 is the plesiomorphic condition.

APPENDIX 2. Data Matrix. Dash (-) indicates inapplicable data; question mark (?) indicates missing data.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
Ptilocolepus granulatus	1	0	0	0	1	0	0	1	0	1	1	0	2	0	2	1	1	1	0	0	1	0	0	1	1
Anagapetus debilus	2	0	0	0	1	0	1	1	1	1	1	0	2	0	0	0	1	0	0	0	1	1	0	0	0
Glossosoma alascense	2	0	0	0	1	3	2	1	1	2	1	0	2	1	-	0	1	0	0	0	0	0	0	0	0
Glossosoma intermedium	2	0	0	0	1	0	0	1	1	1	1	0	2	0	2	0	1	0	0	0	0	0	0	0	0
Agapetus rossi	2	0	0	0	1	0	0	1	0	2	1	0	2	0	0	0	1	0	0	0	1	1	0	1	0
Agapetus species (Australia)	2	0	0	0	1	0	0	1	1	1	1	0	2	0	0	0	1	0	0	0	1	0	0	1	0
Tolhuaca cupulifera	2	0	0	0	1	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	1	1	0	1	0
Tolhuaca brasiliensis	2	0	0	0	1	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	1	1	0	1	1
Nepaloptila coei	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	0	0	1	1	0	1	1
Nepaloptila kanikar	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	1	0	1	0	0	1	1
Nepaloptila jisunted	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	1	0	1	0	0	1	1
Nepaloptila ruangjod	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	1	0	1	0	0	1	1
Matrioptila jeanae	2	0	0	0	2	0	1	0	0	0	1	0	2	0	1	2	-	1	1	1	1	1	0	1	1
Padunia adelungi	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	1	0	0	1	1	1	0	0	1	1
Padunia alpina	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	1	0	0	1	1	1	0	0	1	1
Padunia forcipata	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	1	0	0	1	1	1	0	0	1	1
Padunia burebista	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	0	0	0	1	0
Padunia lepnevae	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	1	1	1	1	0	1	1
Padunia karaked	2	0	0	0	?	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	1	0	0	1	1
Poeciloptila atyalpa	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	1	1	0	1	0
Poeciloptila falcata	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	1	1	0	1	0
Poeciloptila briatec	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	1	1	0	1	0
Poeciloptila maculata	2	0	0	?	?	0	1	0	0	1	1	0	2	0	1	2	-	0	0	1	1	1	0	1	0
Temburongpsyche anaken	2	0	0	0	1	0	1	0	0	1	1	0	2	0	1	2	-	1	1	1	1	0	0	1	0
Scotiotrichia ocreata	2	0	0	0	2	0	1	1	0	1	1	1	2	1	-	1	0	2	1	1	1	1	0	1	0
Merionoptila wygodzinskyi	2	0	0	0	0	0	1	1	0	1	1	1	2	1	-	2	-	2	0	2	1	1	0	1	1
Campsiophora pedophila	2	0	1	0	1	0	1	0	0	1	1	1	2	1	-	1	0	0	0	1	1	0	1	1	0
Campsiophora arawak	2	0	1	0	1	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	0	1	1	0
Campsiophora mulata	2	0	1	0	1	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	0
Cariboptila aurulenta	2	0	1	0	1	2	1	0	0	1	1	0	2	1	-	2	-	0	0	1	1	0	0	1	0
Cariboptila caab	2	0	1	0	2	0	1	1	0	1	1	1	0	1	-	2	-	0	0	1	1	0	0	1	0
Cariboptila hispanolica	2	0	1	0	2	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	0	0	1	0

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APPENDIX 2. (Continued)

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Ptilocolepus granulatus	0	0	-	2	0	1	1	0	1	2	0	0	0	1	0	0	-	0	0	0	1	1	0	0	1
Anagapetus debilus	-	0	-	2	0	1	2	0	1	0	0	1	0	1	0	0	-	0	0	0	1	1	0	0	0
Glossosoma alascense	-	0	-	2	0	0	-	0	1	2	0	1	0	1	0	0	-	0	0	0	1	1	0	0	0
Glossosoma intermedium	-	0	-	2	0	0	-	0	1	2	0	1	0	1	0	0	-	0	0	0	1	1	0	0	0
Agapetus rossi	-	0	-	2	0	1	2	0	1	1	0	0	0	1	0	0	-	0	0	0	1	1	0	0	1
Agapetus species (Australia)	-	0	-	2	0	1	2	0	1	1	0	0	0	1	0	0	-	0	0	0	1	1	0	0	0
Tolhuaca cupulifera	-	0	-	2	0	1	2	0	1	2	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Tolhuaca brasiliensis	2	0	-	2	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Nepaloptila coei	2	0	-	2	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Nepaloptila kanikar	2	0	-	2	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Nepaloptila jisunted	2	0	-	2	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Nepaloptila ruangjod	2	0	-	2	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Matrioptila jeanae	2	0	-	0	1	-	-	1	-	-	1	-	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia adelungi	2	0	-	2	1	-	-	1	-	-	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia alpina	2	1	2	2	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia forcipata	2	1	2	0	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia burebista	-	0	-	0	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia lepnevae	2	1	2	1	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Padunia karaked	2	1	2	0	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Poeciloptila atyalpa	-	0	-	0	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Poeciloptila falcata	2	0	-	2	1	-	-	1	-	-	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1
Poeciloptila briatec	2	0	-	2	1	-	-	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1
Poeciloptila maculata	-	0	-	2	1	-	-	1	-	-	0	1	0	1	1	1	0	1	1	0	0	0	0	1	1
Temburongpsyche anaken	-	1	2	1	1	-	-	1	-	-	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1
Scotiotrichia ocreata	-	1	2	1	1	-	-	1	-	-	1	-	0	0	1	1	1	0	0	0	0	0	1	1	1
Merionoptila wygodzinskyi	1	1	1	0	0	1	1	1	-	-	1	-	0	2	1	1	0	1	1	1	0	-	1	3	1
Campsiophora pedophila	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Campsiophora arawak	-	1	2	0	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Campsiophora mulata	-	0	-	0	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Cariboptila aurulenta	-	1	1	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Cariboptila caab	-	0	-	0	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Cariboptila hispanolica	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1

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APPENDIX 2. (Continued)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Ptilocolepus granulatus	1	1	0	0	0	1	1	1	0	0	2	0	1	0	1	0	0	0	1	1	1	0	1
Anagapetus debilus	0	0	0	0	0	0	0	1	0	0	1	2	1	0	1	0	0	0	2	2	1	0	1
Glossosoma alascense	0	0	0	0	0	0	0	1	1	4	1	2	1	0	1	0	2	0	2	2	1	0	1
Glossosoma intermedium	0	0	0	0	0	0	0	1	1	4	1	2	1	0	1	0	0	0	2	1	1	0	1
Agapetus rossi	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	1	0	1	2	1	0	1
Agapetus species (Australia)	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1	0	2	0	1	2	1	0	1
Tolhuaca cupulifera	0	0	0	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1
Tolhuaca brasiliensis	0	0	0	0	1	1	0	1	1	5	1	0	1	0	1	0	1	0	1	0	1	0	1
Nepaloptila coei	0	0	0	1	-	1	0	1	1	1	1	0	1	0	1	0	1	0	1	2	1	0	1
Nepaloptila kanikar	0	0	0	1	-	1	1	1	1	6	1	0	1	0	1	0	2	0	1	2	1	0	1
Nepaloptila jisunted	0	0	0	1	-	1	?	1	?	?	1	0	1	0	1	0	2	0	1	2	1	0	1
Nepaloptila ruangjod	0	0	0	1	-	1	?	1	?	?	1	0	1	0	1	0	2	0	1	2	1	0	1
Matrioptila jeanae	0	1	0	1	-	1	1	1	1	0	2	0	1	0	1	0	2	1	2	1	1	0	1
Padunia adelungi	0	1	0	1	-	1	1	1	1	0	1	0	1	0	1	0	2	1	1	1	1	0	1
Padunia alpina	0	1	0	1	-	1	1	1	1	6	1	0	1	0	1	0	2	1	1	2	1	0	1
Padunia forcipata	0	1	0	1	-	1	1	1	1	6	1	0	1	0	1	0	2	1	1	2	1	0	1
Padunia burebista	0	1	0	1	-	1	0	1	0	6	1	0	1	0	1	0	2	1	1	1	1	0	1
Padunia lepnevae	0	1	0	1	-	1	1	1	0	6	1	0	1	0	1	0	2	1	1	2	1	0	1
Padunia karaked	0	1	0	1	-	1	0	1	0	6	1	0	1	0	1	0	2	1	1	1	1	0	1
Poeciloptila atyalpa	0	1	0	1	-	1	0	1	0	1	1	0	1	1	1	0	2	1	1	1	0	0	1
Poeciloptila falcata	0	1	0	1	-	1	0	1	0	1	1	0	1	0	1	0	2	1	1	2	1	0	1
Poeciloptila briatec	0	1	0	1	-	1	0	1	1	6	1	0	1	1	0	0	2	1	1	1	0	0	1
Poeciloptila maculata	0	1	1	1	-	1	0	1	1	6	1	0	1	1	0	0	2	1	1	1	0	0	1
Temburongpsyche anaken	0	1	0	1	-	1	?	1	?	?	1	0	1	1	1	0	0	1	1	2	1	0	1
Scotiotrichia ocreata	0	1	1	1	-	1	0	1	1	6	1	0	1	0	1	0	1	0	0	0	1	0	1
Merionoptila wygodzinskyi	1	1	1	1	-	1	0	0	-	-	0	0	1	0	1	0	1	0	1	1	1	0	1
Campsiophora pedophila	0	1	1	1	-	1	0	1	3	4	2	0	1	0	1	0	1	0	1	3	1	0	0
Campsiophora arawak	0	1	1	1	-	1	0	1	0	6	2	0	1	0	1	0	1	0	1	3	1	0	0
Campsiophora mulata	0	1	1	1	-	1	0	1	3	4	2	2	1	0	1	0	0	0	2	0	1	0	0
Cariboptila aurulenta	0	1	1	0	0	1	0	1	3	4	2	0	1	0	1	0	1	0	2	3	1	0	0
Cariboptila caab	0	1	1	0	0	1	0	1	1	6	2	0	1	0	1	0	1	0	2	3	1	0	0
Cariboptila hispanolica	0	1	1	1	-	1	0	1	1	4	2	0	1	0	1	0	1	0	2	3	1	0	0

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APPENDIX 2. (Continued)

	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Ptilocolepus granulatus	2	1	2	3	3	5	1	0	0	0	0	-	-	-	2	3	-	-	-	-	-	0	0	0	1	1
Anagapetus debilus	2	1	2	2	3	5	0	0	0	1	0	-	-	-	2	1	1	0	0	1	1	0	0	0	1	1
Glossosoma alascense	2	0	1	2	3	5	1	0	0	1	0	-	-	-	2	1	1	0	0	1	1	0	0	0	1	1
Glossosoma intermedium	2	1	0	2	3	5	0	0	0	1	1	2	0	6	2	1	1	0	0	1	1	0	0	0	1	1
Agapetus rossi	0	1	1	2	4	5	1	0	0	1	0	-	-	-	2	1	1	0	0	1	1	0	0	0	1	1
Agapetus species (Australia)	0	1	1	2	3	5	1	0	0	1	0	-	-	-	2	1	1	0	0	1	1	0	0	0	1	1
Tolhuaca cupulifera	0	1	2	2	3	3	0	1	-	-	0	-	-	-	2	2	1	0	0	1	1	0	0	0	1	1
Tolhuaca brasiliensis	0	1	2	2	3	3	0	1	-	-	0	-	-	-	2	2	1	0	0	1	1	?	0	0	1	1
Nepaloptila coei	0	1	2	4	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	?	?	?
Nepaloptila kanikar	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Nepaloptila jisunted	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	?	?	?
Nepaloptila ruangjod	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	?	?	?
Matrioptila jeanae	0	1	2	2	3	5	0	0	2	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Padunia adelungi	0	1	2	4	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Padunia alpina	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Padunia forcipata	0	1	2	0	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Padunia burebista	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	0	1	0	0
Padunia lepnevae	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Padunia karaked	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Poeciloptila atyalpa	0	1	2	4	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Poeciloptila falcata	0	1	2	0	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	1	1	0	0
Poeciloptila briatec	0	1	2	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	0	1	0	0
Poeciloptila maculata	0	1	2	1	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	0	1	0	0
Temburongpsyche anaken	?	1	1	3	3	5	0	0	1	1	0	-	-	-	2	1	0	0	0	1	1	0	0	1	0	0
Scotiotrichia ocreata	1	1	2	3	3	5	0	1	-	-	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Merionoptila wygodzinskyi	3	1	2	2	1	3	0	0	5	1	0	-	-	-	2	1	1	0	0	1	1	0	0	1	0	1
Campsiophora pedophila	1	0	2	5	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Campsiophora arawak	1	0	2	5	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Campsiophora mulata	1	0	2	1	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cariboptila aurulenta	1	0	2	0	1	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cariboptila caab	1	0	2	1	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cariboptila hispanolica	1	0	2	0	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1

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APPENDIX 2. (Continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cariboptila orophila	2	0	1	0	1	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	0	0	0	1	1
Cubanoptila botosaneanui	2	0	1	1	1	0	1	1	0	1	1	1	0	1	-	2	-	0	0	1	0	1	0	1	0
Cubanoptila cubana	2	0	1	1	2	1	1	0	0	1	1	1	2	1	-	1	0	0	0	1	1	0	0	1	0
Cubanoptila muybonita	2	0	1	1	2	0	1	1	0	1	1	1	2	1	-	2	-	0	0	1	0	0	0	1	0
Cubanoptila purpurea	2	0	1	1	2	0	1	1	0	1	1	1	0	1	-	2	-	0	0	1	1	0	0	1	0
Culoptila cascada	2	0	0	0	2	0	1	1	0	1	0	0	2	1	-	1	0	0	0	1	1	1	0	1	1
Culoptila hamata	2	0	0	0	2	0	1	1	0	1	0	0	2	1	-	1	0	0	0	1	1	1	0	1	1
Culoptila thoracica	2	0	0	0	2	0	1	1	0	0	0	0	2	1	-	1	0	0	0	1	1	1	0	1	1
Canoptila bifida	2	0	0	0	2	2	1	1	0	1	0	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Canoptila williami	2	0	0	0	2	2	1	1	0	1	0	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Itauara brasiliana	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	0
Itauara guarani	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	1
Itauara plaumanni	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	0
Itauara amazonica	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara blahniki	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara emilia	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara rodmani	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara julia	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara simplex	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	1
Itauara tusci	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara flinti	2	0	0	0	2	1	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	1
Itauara charlotta	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	0	0	1	0
Itauara jamesii	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara alexanderii	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara stella	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara lucinda	2	0	0	0	2	0	1	1	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara unidentata	2	0	0	0	2	0	1	0	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara bidentata	2	0	0	0	2	0	1	0	0	1	1	1	0	1	-	1	0	0	0	2	1	1	0	1	0
Itauara guyanensis	2	0	0	0	2	0	1	0	0	1	1	1	0	1	-	1	0	1	0	2	1	1	0	1	0
Itauara ovis	2	0	0	0	2	0	1	0	0	1	1	1	0	1	-	1	0	0	0	1	1	1	0	1	0
Itauara peruensis	2	0	0	0	2	0	1	0	0	1	1	1	0	1	-	1	0	0	0	2	1	1	0	1	0
Mastigoptila bicornuta	2	0	0	0	2	0	1	1	0	1	0	0	2	1	-	1	0	0	0	1	1	1	0	1	0
Mastigoptila longicornuta	2	0	0	0	2	0	1	1	0	1	0	0	2	1	-	2	-	0	0	1	1	1	0	1	0

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APPENDIX 2. (Continued)

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Cariboptila orophila	2	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Cubanoptila botosaneanui	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	1	0	0	1	0	0	2	1
Cubanoptila cubana	-	0	-	0	0	1	1	1	-	-	1	-	0	2	1	1	0	1	0	0	1	0	0	2	1
Cubanoptila muybonita	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	1	0	0	2	1
Cubanoptila purpurea	-	0	-	0	0	1	1	1	-	-	1	-	0	2	1	1	0	1	0	0	1	0	0	2	1
Culoptila cascada	2	1	2	1	0	1	1	0	1	0	1	-	1	0	1	1	0	0	0	0	0	0	0	2	1
Culoptila hamata	2	0	-	2	0	1	1	0	1	0	1	-	1	0	1	1	0	0	0	0	0	0	0	2	1
Culoptila thoracica	2	0	-	0	0	1	1	0	1	0	1	-	1	0	1	1	0	0	0	0	0	0	0	2	1
Canoptila bifida	-	1	1	1	0	1	1	1	-	-	1	-	0	0	1	1	1	0	0	0	0	0	0	1	1
Canoptila williami	-	1	1	1	0	1	1	1	-	-	1	-	0	0	1	1	1	0	0	0	0	0	0	1	1
Itauara brasiliana	-	1	2	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara guarani	2	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara plaumanni	-	1	2	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara amazonica	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara blahniki	-	0	-	0	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara emilia	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara rodmani	-	1	2	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara julia	-	0	-	0	0	1	2	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara simplex	2	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara tusci	-	1	2	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara flinti	2	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara charlotta	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara jamesii	-	1	2	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara alexanderii	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara stella	-	1	0	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara lucinda	-	1	0	1	0	1	0	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	1	1
Itauara unidentata	-	1	1	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara bidentata	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara guyanensis	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara ovis	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Itauara peruensis	-	1	0	1	0	1	1	1	-	-	1	-	0	0	1	1	0	0	0	0	0	0	0	2	1
Mastigoptila bicornuta	-	0	-	0	0	1	0	1	-	-	1	-	0	0	1	1	1	0	0	0	0	0	0	1	1
Mastigoptila longicornuta	-	0	-	0	0	1	1	1	-	-	1	-	0	0	1	1	1	0	0	0	0	0	0	1	1

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APPENDIX 2. (Continued)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Cariboptila orophila	0	1	1	1	-	1	0	1	3	6	2	0	1	0	1	0	1	0	2	3	1	0	0
Cubanoptila botosaneanui	0	1	1	0	0	1	0	1	0	6	0	0	1	0	1	0	1	0	2	3	1	0	0
Cubanoptila cubana	0	1	1	0	0	1	0	1	0	6	2	0	1	0	1	1	0	0	2	3	1	0	0
Cubanoptila muybonita	0	1	1	1	-	1	0	1	0	6	0	0	1	0	1	0	1	0	2	3	1	0	0
Cubanoptila purpurea	0	1	1	0	0	1	0	1	0	6	2	0	1	0	1	1	0	0	2	3	1	0	0
Culoptila cascada	0	0	1	0	0	1	0	1	3	8	1	0	1	0	1	0	1	0	2	3	1	0	1
Culoptila hamata	0	0	1	0	0	1	0	1	3	8	1	0	1	0	1	0	1	0	2	3	1	0	1
Culoptila thoracica	0	0	1	0	0	1	0	1	3	8	1	0	1	0	1	0	1	0	2	3	1	0	1
Canoptila bifida	0	1	1	1	-	1	0	1	1	6	2	0	1	0	1	0	0	0	1	1	1	0	1
Canoptila williami	0	1	1	1	-	1	0	1	1	6	2	0	1	0	1	0	0	0	1	1	1	0	1
Itauara brasiliana	0	1	0	1	-	1	0	1	1	5	2	0	1	0	1	0	1	0	0	1	1	2	1
Itauara guarani	0	0	1	1	-	1	0	1	1	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara plaumanni	0	0	1	1	-	1	0	1	0	6	0	0	1	0	1	0	1	0	0	1	1	0	1
Itauara amazonica	1	0	1	1	-	1	0	1	0	6	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara blahniki	0	0	0	1	-	1	0	1	1	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara emilia	0	1	1	1	-	1	0	1	1	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara rodmani	0	0	0	1	-	1	0	1	1	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara julia	0	0	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara simplex	0	1	1	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara tusci	0	0	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara flinti	0	1	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara charlotta	0	0	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara jamesii	0	1	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara alexanderii	0	1	0	1	-	1	0	1	1	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara stella	0	1	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara lucinda	0	1	0	1	-	1	0	1	0	5	2	0	1	0	1	0	1	0	0	1	1	0	1
Itauara unidentata	0	1	1	1	-	1	0	1	0	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara bidentata	0	1	1	1	-	1	0	1	0	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara guyanensis	0	1	1	1	-	1	0	1	0	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara ovis	0	1	0	1	-	1	0	1	0	6	1	0	1	0	1	0	1	0	0	1	1	0	1
Itauara peruensis	0	1	1	1	-	1	0	1	0	6	1	0	1	0	1	0	1	0	1	1	1	0	1
Mastigoptila bicornuta	0	0	0	1	-	1	0	1	0	7	1	0	1	0	1	0	1	0	0	1	1	0	1
Mastigoptila longicornuta	0	0	0	1	-	1	0	1	0	7	1	0	1	0	1	0	1	0	0	1	1	0	1

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APPENDIX 2. (Continued)

	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Cariboptila orophila	1	0	2	0	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cubanoptila botosaneanui	1	0	2	2	1	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cubanoptila cubana	1	0	2	0	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cubanoptila muybonita	1	0	2	5	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Cubanoptila purpurea	1	0	2	0	9	6	0	0	6	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Culoptila cascada	1	1	2	3	3	4	0	0	7	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Culoptila hamata	1	1	2	3	3	4	0	0	7	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Culoptila thoracic	1	1	2	3	3	4	0	0	7	1	0	-	-	-	2	2	1	0	0	1	1	0	0	1	0	1
Canoptila bifida	0	1	2	2	3	2	0	1	-	1	1	1	1	8	2	0	1	0	0	1	1	0	0	1	0	1
Canoptila williami	0	1	2	3	3	2	0	1	-	1	1	1	1	8	2	0	1	0	0	1	1	0	0	1	0	1
Itauara brasiliana	1	1	2	4	1	3	0	1	-	-	0	-	-	-	2	0	1	0	0	1	1	1	0	1	0	1
Itauara guarani	1	1	2	0	3	3	0	1	-	-	1	0	0	7	2	0	1	0	0	1	0	1	0	1	0	1
Itauara plaumanni	1	1	2	4	1	3	0	1	-	-	1	0	0	7	2	0	1	0	0	1	0	1	0	1	0	1
Itauara amazonica	0	1	2	2	3	5	0	0	8	1	1	1	0	0	1	0	1	0	0	1	1	1	0	1	0	1
Itauara blahniki	1	1	2	0	3	1	0	1	-	-	1	0	0	2	2	0	1	0	0	1	1	1	0	1	0	1
Itauara emilia	1	1	2	0	3	0	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara rodmani	1	1	2	4	1	1	0	1	-	-	1	0	0	2	2	0	1	0	0	1	0	1	0	1	0	1
Itauara julia	1	1	2	3	2	0	0	1	-	-	1	0	0	0	2	0	1	0	0	1	0	1	0	1	0	1
Itauara simplex	1	1	2	4	3	1	0	1	-	-	1	0	0	3	2	0	1	0	0	1	1	1	0	1	0	1
Itauara tusci	1	1	2	1	1	1	0	1	-	-	1	0	0	2	2	0	1	0	0	1	0	1	0	1	0	1
Itauara flinti	1	1	2	0	3	1	0	1	-	-	1	0	0	3	2	0	1	0	0	1	0	1	0	1	0	1
Itauara charlotta	1	1	2	1	1	5	0	1	-	-	1	0	0	3	2	0	1	0	0	1	0	1	0	1	0	1
Itauara jamesii	1	1	2	2	3	0	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara alexanderii	1	1	2	0	3	0	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara stella	1	1	2	0	3	0	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara lucinda	1	1	2	0	3	0	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara unidentata	1	1	2	3	0	0	0	0	8	1	1	1	0	4	1	0	1	0	0	1	1	1	0	1	0	1
Itauara bidentata	1	1	2	3	0	0	0	0	8	1	1	1	0	4	1	0	1	0	0	1	1	1	0	1	0	1
Itauara guyanensis	1	1	2	0	1	3	0	0	8	1	1	1	0	7	2	0	1	0	0	1	1	1	0	1	0	1
Itauara ovis	1	1	2	2	3	3	0	0	8	1	1	1	0	1	2	0	1	0	0	1	1	1	0	1	0	1
Itauara peruensis	1	1	2	2	3	3	0	0	8	1	1	1	0	0	2	0	1	0	0	1	1	1	0	1	0	1
Mastigoptila bicornuta	1	1	2	3	8	5	0	0	3	1	0	-	-	-	2	3	1	0	0	1	1	0	0	1	0	1
Mastigoptila longicornuta	1	1	2	3	8	5	0	0	3	1	0	-	-	-	2	3	1	0	0	1	1	0	0	1	0	1

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APPENDIX 2. (Continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Mortoniella elongata	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	2	-	0	0	1	1	1	0	1	0
Mortoniella limona	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Mortoniella meralda	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	2	-	0	0	1	1	1	0	1	0
Mortoniella teutona	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Mortoniella bilineata	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	2	-	0	0	1	1	1	0	1	0
Mortoniella denticulata	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	2	-	0	0	1	1	1	0	1	0
Mortoniella roldani	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Mortoniella marini	2	0	0	0	1	1	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Mortoniella eduardoi	2	0	0	0	1	0	1	1	0	1	1	1	2	1	-	2	-	1	0	1	1	1	0	1	0
Mortoniella froehlichi	2	0	0	0	1	1	1	1	0	1	1	1	2	1	-	2	-	1	0	1	1	1	0	1	0
Protoptila maculata	2	0	0	0	1	1	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Protoptila bribri	2	0	0	0	2	0	1	1	0	1	1	1	2	1	-	1	0	0	0	1	1	1	0	1	0
Protoptila diablita	2	0	0	0	2	1	1	1	0	1	1	2	2	1	-	1	0	0	0	1	1	1	0	1	0

APPENDIX 2. (Continued)

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Mortoniella elongata	-	0	-	0	0	1	1	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	1	1
Mortoniella limona	-	0	-	0	0	1	0	1	-	-	1	-	0	2	1	1	0	0	0	0	0	0	0	1	1
Mortoniella meralda	-	0	-	0	0	1	0	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	1	1
Mortoniella teutona	-	0	-	0	0	1	0	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	1	1
Mortoniella bilineata	-	0	-	0	0	1	2	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	0	1
Mortoniella denticulata	-	0	-	0	0	1	2	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	0	1
Mortoniella roldani	-	0	-	0	0	1	2	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	0	1
Mortoniella marini	-	0	-	0	0	1	2	1	-	-	1	-	0	2	0	1	0	0	0	0	0	0	0	2	1
Mortoniella eduardoi	-	0	-	0	0	1	0	1	-	-	1	-	0	2	1	1	0	0	0	0	0	0	0	1	1
Mortoniella froehlichi	-	0	-	0	0	1	0	1	-	-	1	-	0	2	1	1	0	0	0	0	0	0	0	1	1
Protoptila maculata	-	0	-	0	0	1	1	1	-	-	1	-	0	2	0	1	1	0	0	0	0	0	0	2	1
Protoptila bribri	-	0	-	0	0	1	1	1	-	-	1	-	0	2	0	1	1	0	0	0	0	0	0	2	1
Protoptila diablita	-	0	-	0	0	1	1	1	-	-	1	-	0	2	1	1	1	0	0	0	0	0	0	2	1

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APPENDIX 2. (Continued)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Mortoniella elongata	0	0	1	1	-	1	0	1	1	2	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella limona	0	0	1	1	-	1	0	1	1	2	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella meralda	0	0	1	1	-	1	0	1	1	2	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella teutona	0	1	1	1	-	1	0	1	1	2	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella bilineata	0	0	0	0	1	1	0	1	0	1	2	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella denticulata	0	0	0	0	1	1	0	1	0	6	2	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella roldani	0	0	0	0	1	1	0	1	0	6	2	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella marini	0	0	1	1	-	1	0	1	0	2	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella eduardoi	0	1	1	1	-	1	0	1	0	7	1	0	1	0	1	0	1	0	1	1	1	0	1
Mortoniella froehlichi	0	1	1	1	-	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	1
Protoptila maculata	0	1	1	1	-	1	1	1	0	7	1	0	0	0	1	0	1	0	0	2	1	1	1
Protoptila bribri	0	1	1	1	-	1	0	1	0	7	2	0	0	0	1	0	1	0	1	2	1	1	1
Protoptila diablita	0	1	1	1	-	1	0	1	0	2	1	0	0	0	1	0	1	0	1	2	1	1	1

APPENDIX 2. (Continued)

	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Mortoniella elongata	3	1	2	0	2	5	0	0	4	1	1	2	0	7	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella limona	3	1	2	2	2	3	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella meralda	3	1	2	3	2	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella teutona	3	1	2	2	2	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella bilineata	3	1	2	2	3	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella denticulata	3	1	2	2	3	1	0	0	4	1	0	-	-	-	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella roldani	3	1	2	2	3	1	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella marini	3	1	2	2	1	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella eduardoi	3	1	2	2	2	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Mortoniella froehlichi	3	1	2	2	2	5	0	0	4	1	1	2	0	0	0	1	1	1	1	1	1	0	0	1	0	1
Protoptila maculata	4	1	2	2	2	5	0	1	-	-	1	1	0	0	2	1	1	1	1	0	1	0	0	1	0	1
Protoptila bribri	4	1	2	2	2	5	0	1	-	-	1	1	0	0	2	1	1	1	1	0	1	0	0	1	0	1
Protoptila diablita	4	1	2	2	2	5	0	1	-	-	1	1	0	0	2	1	1	1	1	0	1	0	0	1	0	1