

PHYLOGENY OF THE MICROCADDISFLIES WITH A REVISION OF THE GENUS
LEUCOTRICHIA MOSELY (TRICHOPTERA: HYDROPTILIDAE)

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DEDICATION

*This dissertation is dedicated to my friends and family, who made all of this possible. You know who you are and you know what you've done.
Thank you.*

DISCLAIMER

The species names provided in the following text are provisional and are not published within the meaning of the International Code of Zoological Nomenclature (ICZN1999; Article 9). The names and nomenclatural acts established in this dissertation are, therefore, not available within the meaning of the Code (ICZN, Article 10).

ABSTRACT

Hydroptilidae Stephens, 1836 is the most diverse family [6 subfamilies, 76 genera (including 3 fossil genera), and over 2,100 species] belonging to the order Trichoptera. The family is cosmopolitan, occurring in all faunal regions of the world. A summary of the general morphology, biology, and taxonomic history and an overview of historically recognized taxa of Hydroptilidae are provided.

Monophyly of Hydroptilidae and each of the 6 subfamilies was tested using 90 ingroup taxa, mitochondrial DNA (COI), and ribosomal RNA (D1-3). Maximum likelihood and Bayesian analysis methods were used to estimate phylogeny. Monophyly was recovered for Hydroptilidae, but not Ptilocolepidae. Monophyly was also recovered for the subfamilies Leucotrichiinae, Neotrichiinae, Ochrotrichiinae, and Stactobiinae. Monophyly for the subfamilies Hydroptilinae and Orthotrichiinae was not recovered. The genera *Alisotrichia* and *Cerasmatrichia* were recovered as a clade separate from all other subfamilies, as was the genus *Byrsopteryx*. The genus *Dibusa*, formerly *incertae sedis*, was recovered as sister to all other hydroptilids genera, excluding *Palaeagapetus* and *Ptilocolepus*. The genus *Orphninostrichia*, also formerly *incertae sedis*, was recovered within one clade of Hydroptilinae genera. Several taxonomic changes were necessary for classification to reflect phylogeny.

Accordingly, I propose that the ptilocolepid genera *Palaeagapetus* and *Ptilocolepus* be returned to Hydroptilidae as 2 genera separate from any subfamily. I also propose that the status of *Alisotrichia*, *Byrsopteryx*, and *Cerasmatrichia* be changed to *incertae sedis* within Hydroptilidae and that *Dibusa* and *Orphninostrichia* be removed from *incertae sedis*.

A species-level revision of *Leucotrichia* was also completed, including a generic diagnosis, illustrations, a key, and descriptions of males. A total of 43 species were treated, 13 described as new: *Leucotrichia angelinae*, **new species** (Venezuela), *L. denticulata*, **new species** (Mexico), *L. dianeae*, **new species** (Costa Rica), *L. fulminea*, **new species** (Ecuador), *L. hispida*, **new species** (Costa Rica), *L. kateae*, **new species** (Venezuela), *L. pectinata*, **new species** (Ecuador), *L. procera*, **new species** (Brazil), *L.*

repanda, **new species** (Venezuela), *L. rhomba*, **new species** (Costa Rica), *L. riostoumae*, **new species** (Ecuador), *L. sidneyi*, **new species** (Venezuela), and *L. tapantia*, **new species** (Costa Rica).

Descriptions and new records for hydroptilid species found in Brazil and Venezuela were also provided. Illustrations and descriptions of males were given for all new species. A total of 10 new species were described: *Acostatrichia digitata*, **new species** (Venezuela), *Betrichia alibrachia*, **new species** (Brazil), *Hydroptila cressae*, **new species** (Venezuela), *Leucotrichia bicornuta*, **new species** (Brazil), *Metrichia bostrychion*, **new species** (Venezuela), *Ochrotrichia spira*, **new species** (Venezuela), *Oxyethira bettyae*, **new species** (Venezuela), *Oxyethira quiramae*, **new species** (Venezuela), *Oxyethira redunca*, **new species** (Venezuela), and *Rhyacopsyche shorti*, **new species** (Venezuela). New records were provided for 2 species: *Neotrichia feolai* Santos and Nessimian, 2009 (Venezuela) and *Oxyethira picita* Harris and Davenport, 1999 (Venezuela).

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Chapter I. Taxonomic review and phylogeny of the family Hydroptilidae Stephens (Trichoptera) inferred from mitochondrial DNA and ribosomal RNA

INTRODUCTION

In terms of species diversity, Hydroptilidae are the largest family in the order Trichoptera, including 6 subfamilies, 76 genera (including 3 fossil genera), and over 2,100 species found in all faunal regions of the world (Holzenthall *et al.*, 2011). Other large families in the order include Leptoceridae with around 2,000 species, Hydropsychidae with just over 1,800 species, and Philopotamidae with almost 1,200 species (Holzenthall *et al.*, 2011). However, the family is also the smallest family in the order in terms of body size, with adults ranging from between 1.5 mm to usually no more than 5 mm in length (Holzenthall *et al.*, 2007). Of the subfamilies, 3 are largely endemic to the Neotropical faunal region (Leucotrichiinae, Neotrichiinae, and Ochrotrichiinae), though some of the included species are distributed well into North America.

Hydroptilinae occurs in the Old World, but does include 2 large cosmopolitan genera (*Hydroptila* and *Oxyethira*) and several genera that are endemic to the Australasian or Afrotropical faunal regions. The subfamily Orthotrichiinae is small, but includes the cosmopolitan genus *Orthotrichia*, while the subfamily Stactobiinae is a varied collection of genera that are either endemic to a particular region or occur in a wider distribution throughout multiple regions. The larval stage is undescribed for many genera. The closely related Ptilocolepidae are a small family, formerly considered to be a subfamily within Hydroptilidae, which currently contains 2 genera distributed throughout the Holarctic

faunal region.

The objectives of this study were to 1) test the monophyly of both Hydroptilidae and Ptilocolepidae, 2) evaluate the monophyly of the traditionally recognized subfamilies within Hydroptilidae, and 3) infer relationships within and between Hydroptilidae and Ptilocolepidae. This was the first study to use modern statistical methods and molecular data in a phylogenetic assessment of the family and was based on an analysis of both mitochondrial DNA and nuclear ribosomal RNA characters for 90 species representing both families, all hydroptilid subfamilies, and 31 genera.

Results of this study confer taxonomic stability to the family, refine the current classification system, and provide a new phylogenetic framework in which to place new species and genera.

General morphology and biology

The hydroptilids, like all Trichoptera, are holometabolous with a terrestrial adult stage and aquatic larval and pupal stages. Members of the family are typically minute, with few exceeding 5.0 mm in body length, which has led to their common name, the microcaddisflies. The adults are attracted to ultraviolet lights and may congregate in huge numbers at collecting sites, giving them the potential to be one of the most commonly collected of all Trichoptera. As this research focused on the use of molecular data, an in-depth account of hydroptilid morphology will not be given here; however, features that have traditionally been considered of importance for hydroptilid taxonomy are briefly described here.

Larva. Hydroptilids display various structural adaptations for the wide range of aquatic environments they occur in, making them one of the most diverse caddisfly families regarding the form of larvae and larval cases (Marshall, 1979). In Nielsen's (1948) classic work on hydroptilid larvae, he gave a very detailed account of larval morphology and biology; unfortunately, it is a fairly limited view of the family as a whole, since he expounded on only 5 of the more specialized genera within Hydroptilidae (*Agraylea*, *Hydroptila*, *Ithytrichia*, *Orthotrichia*, and *Oxyethira*). However, Nielsen's work laid an excellent foundation for future trichopterists and made Marshall's (1979) more general account of larval morphology possible.

One of the characteristic features of hydroptilid larvae is the simple form of hypermetamorphosis that they undergo. Marshall (1979) commented that it had not been confirmed if ptilocolepid larvae also underwent hypermetamorphosis, but it has since been confirmed that the ptilocolepids do experience the same changes, although not as pronounced as that of the hydroptilids (Wells, 2010). Early instars I-IV of both families are relatively smaller (0.5-2.7 mm in length), of short duration, and free-living and caseless, while final instar V is larger (2.0-7.0 mm in length) and constructs a portable or secondarily fixed case (Marshall, 1979). The final instar also functions as the growing stage of the hydroptilid life cycle, during which the abdomen becomes greatly enlarged (Marshall, 1979). The early instars I-IV can be characterized by features associated by their absence of a case, including narrowly tapering abdomens, freely projecting anal prolegs, and long, fine setae on the body that can offer resistance to sinking and helps the larva to swim and disperse (Marshall, 1979).

The case-building larvae of instar V are prognathous and campodeiform, similar to the “saddle-case” bearing glossosomatids, as opposed to the hypognathous and eruciform “tube-case” building families (Marshall, 1979). Instar V tends to be more easily identified and distinct among the genera and can be separated from all other Trichoptera larvae by a combination of features, including the enlarged abdomen, 3 pairs of well developed thoracic tergites, an absence of segmentally arranged tracheal gills, a fusion of the well developed abdominal prolegs to the sides of abdominal segment X, and, while the number of abdominal tergites may vary, there is always one present on abdominal segment IX (Marshall, 1979; Wiggins, 1996). Hydroptilid larvae have dorsal sclerotized rings on abdominal segments II/III to VII/VIII which have not been recorded in ptilocolepid larvae; these rings may be regions of specialized chloride epithelial cells adapted for ionic absorption and osmoregulation (Wichard, 1976; Wiggins, 1977). Features of the thoracic legs of instar V have proven useful at the generic level in hydroptilid taxonomy; for example, though basically ambulatory, they may be modified to be robust for clinging to substrate in swiftly moving waters, long and slender for vegetation dwellers, or may bear a specialized process that aids in the manipulation of algal filaments (Marshall, 1979). In instar V, the abdomen becomes hugely distended; the overall form and shape of the abdominal expansion is unique and typically characteristic for each genus (Marshall, 1979).

The larval case constructed during the final instar is often referred to as a “purse-case,” a term coined by Ross (1967) to separate hydroptilid cases from glossosomatid “saddle-cases” and limnephiloid “tube-cases.” The typical “purse-case” consists of 2

closely apposed silken halves into which various organic or inorganic particles may be incorporated; the 2 halves are joined along the lateral margins, leaving narrow openings at the anterior and posterior ends, and may be either laterally or dorso-ventrally compressed (Marshall, 1979). As the larval abdomen increases in size during the final instar, the case is subsequently expanded by splitting the margins, adding new layers of silk, and then resealing them (Nielsen, 1948; Wiggins, 1996).

Pupa. As in most Trichoptera, hydroptilid pupae are exarate, dectitious, and do not offer many features useful for identification past the family level (Marshall, 1979). Aside from the absence of any structural features used to positively characterize other caddis families, hydroptilid pupae might be recognized by the absence of abdominal gills or lateral lines, the presegmental dorsal abdominal plates on segments III-VII, the postsegmental plates on segments III-V, and their relatively small size (1.5-6.0 mm in length) (Marshall, 1979). Overall, the pupal case is similar to the larval case, but firmly attached to the substrate and with the anterior and posterior openings sealed; once the case is attached and sealed, the larva spins one final internal lining and adopts a characteristic resting posture in which the thorax becomes distended, the abdomen straightens, and the intersegmental grooves become less obvious (Barnard, 1971). Ptilocolepid and hydroptilid pupae can be separated based on the presence or absence of medial teeth on the mandibles: in Hydroptilidae medial teeth are absent, while in Ptilocolepidae either 1 (*Palaeagapetus*) or 2 (*Ptilocolepus*) teeth are present (Marshall, 1979).

Adult. Features that comprise the generally accepted typical hydroptilid form

include small size (1.2-6.0 mm forewing length); narrow, pointed wings with long setal fringes along the anal margin and reduced venation; and a dense layer of setae on the wings and body parts that creates a general appearance of pubescence (Marshall, 1979). While most genera bear setae that are white and either black or brown in hue, giving them a mottled appearance, some tropical genera are known to boast patches of distinct metallic hues. As the overall size of genera decreases, the wings also become reduced, leading to decreasingly distinct venation and increasingly longer setal fringes to compensate for the loss of wing membrane area (extreme examples of reduced wings and venation can be seen in the genera *Chrysotrichia* and *Neotrichia*) (Marshall, 1979). Because of this reduction in venation, venational features that are of taxonomic importance in other families of larger caddisflies are not constant in hydroptilid genera and are considered unreliable taxonomic characters.

On the head capsule, dorsal ocelli vary from 0 to 2 to 3 and, posteriorly, there is typically a pair of dorsal postoccipital lobes or warts which may be modified as eversible scent-dispersing organs (ex: *Hydroptila*). In some genera (ex: *Leucotrichia*), the head may bear modifications, such as patches of scales or setiferous protuberances. Antennal segments, typically the basal-most, in some genera may also be modified to appear elongated or enlarged. On the thorax, taxonomically important features at the subfamily and generic levels include the shape of the meso- and metathoracic nota and the presence or absence of transverse sutures. The posterior mesothoracic katepisternal suture is typically present in ptilocolepids and absent in hydroptilids, a feature first noted by Ross (1956) and later confirmed by Marshall (1979). Wings of some genera may also bear

modifications (ex: *Abtrichia*, *Costatrichia*), such as patches of scales or a costal “pouch” or “bulla.” The spur formula, which refers to the number of spines present on the tibiae, is another important diagnostic feature used in hydroptilid taxonomy. The formula indicates the number of spines on the fore-, mid-, and hind tibiae, respectively, with 4 being the maximum number of spines on any one leg (2 preapical and 2 apical) (Marshall, 1979); for example, the formula for the genus *Leucotrichia* is 1, 3, 4.

The hydroptilid abdomen consists of the typical eleven basic segments, with segments X and XI generally being regarded as one, and the sclerites of the posterior segments modified to form the genitalic structures, which provide features of taxonomic importance at both the generic and specific levels; most hydroptilid species are known from male specimens only. Segment IX forms a distinct genital capsule with a membranous posterior concavity, out of which originates segment X, the phallus, and any ventral appendages (Marshall, 1979). Segment X is present as a tergite only, is usually completely membranous but may be weakly sclerotized, varies considerably in size and shape, and may fuse ventrally with structures beneath the phallus to form a structure known as the “phallic tube” or “phallocrypt” (Marshall, 1979). Inferior appendages, often referred to as “claspers,” are single-segmented, in contrast to the 2-segmented condition generally found in many other caddis families, and vary greatly in size, shape, and whether or not they bear additional processes or setae; these appendages can provide taxonomically important features at both the generic and specific levels (Marshall, 1979). The phallus (also sometimes referred to as the aedeagus, penis, or copulatory organ) is essentially a long, slender, sclerotized tube that varies structurally between groups. In the

Hydroptilinae, Neotrichiinae, and Orthotrichiinae, the phallus bears a spiral “titillator” and is divided into a proximal half bearing an ejaculatory duct and a distal half bearing an intromittent organ. In Leucotrichiinae, the phallus bears a complicated median complex with “windows,” “loops,” and a membranous apex. In Ochrotrichiinae, the phallus may be very slender or heavily spined, whereas in Stactobiinae, the phallus is essentially a common median duct bearing a pair of lateral processes that may be fused (Marshall, 1979). Overall not much is really known about the comparative morphology of hydroptilid male genitalia and the terminology of different structures varies greatly between authors. For example, Marshall (1979) uses the term “subgenital” to refer to any structures occurring ventral to the phallus; when separate and paired, she calls them “appendages” (which have been referred to variously as “intermediate appendages,” “lateral penis-sheaths,” or “parameres”) and when they are fused refers to the structure as a “plate” (“lower penis cover” or “ventral plate of X”). Oláh and Johanson (2008) argued for the use of appendicular terminology (“gonopods,” “paraprocts,” “cercus,” etc.) over the directional terms (appendages referred to as “inferior,” “intermediate,” “superior,” etc.). Their work, however, addressed Trichoptera as a whole and did not address the complex genitalia of Hydroptilidae in specific, as Marshall’s (1979) monograph did. For this reason, I will follow Marshall’s (1979) terminology when referring to any genitalic structures. Further work regarding hydroptilid male genitalia is needed to infer the homology of these structures.

Female genitalia of hydroptilids are of the generalized trichopteran condition, a simple “telescopic ovipositor” or “oviscapt” which consists of modified abdominal

segments VIII-X and a gonopore occurring ventrally between segments IX and X (Marshall, 1979; Scudder, 1971). The posterior margin of the ringlike segment VIII provides features that can be of taxonomic importance, such as dorsal and ventral processes or rows or setae (Marshall, 1979).

Ptilocolepidae. While some of the above description can be extended to the ptilocolepids, there are some fundamental differences that can be used to differentiate between the 2 families. While ptilocolepid larvae closely resemble those of hydroptilids, the adults look more similar to small rhyacophilids or glossosomatids. They are relatively larger than hydroptilids (4.0-6.0 mm in length) and their wings are relatively broad with rounded apices and short marginal setal fringes (Marshall, 1979). The wings also boast a much more complete venation that resembles that of primitive rhyacophilids, differing in the subcosta of the forewing and the fusion of various veins in the hindwing (Ross, 1956). Ptilocolepid venation differs from hydroptilids by the presence of a distinct discoidal cell, separate M_3 and M_4 , and a forked Cu_1 in the forewing (Marshall, 1979). Additionally, ptilocolepids bear short, unmodified macrotrichia in a sparse, scattered distribution on their body, which gives them more of an overall granulose appearance, rather than pubescent.

Placement of Hydroptilidae within Trichoptera

In general, the placement of Hydroptilidae has typically been aligned with Rhyacophilidae, although its relationship has changed based on whether adult or larval features are emphasized. Pictet (1834) was the first to formally observe that in both sexes,

hydroptilids bear maxillary palpi with 5 segments. In the first formal review of the family, Eaton (1873) agreed with Pictet's original observations and also recognized the relationship between adult hydroptilids and members of the family Rhyacophilidae, leading him to place the family in the old trichopteran subdivision Aequipalpia, later known as Aequipalpia. McLachlan (1880) also regarded the family as a member of Aequipalpia, but placed the family between the "tube-case" building families Sericostomatidae and Leptoceridae, not aligned with Rhyacophilidae, based on the case building habits of the larval hydroptilids. Mosely (1939b) considered Hydroptilidae to be closely related to Rhyacophilidae due to morphological similarities shared between adults while Milne and Milne (1939) considered Hydroptilidae to be more closely related to Glossosomatidae (then a subfamily within Rhyacophilidae) than Glossosomatidae was to Rhyacophilidae due to the structure of the case and features and behaviors of the larvae.

In the first comprehensive attempt to establish a phylogenetic arrangement of Trichoptera, Ross (1956) proposed a new classification, based on comparative study of both adult and immature morphological features and case-making behaviors of the larvae, in which 2 major evolutionary lineages of caddisflies were proposed: the "fixed retreat division" and the "case-maker division." The latter group included the families that Ross (1956) considered to be the most primitive: the free-living Rhyacophilidae, which he concluded gave rise to the more primitive transportable-case building glossosomatids, which then gave rise to the more advanced "saddle-case" building Glossosomatidae, which in turn gave rise to the "purse-case" building Hydroptilidae.

The order Trichoptera has since traditionally been thought of as divided into 3

suborders which are based on the morphology and behavior of both the adult and immature stages (Morse, 1997; Wiggins, 2004). Annulipalpia have larvae that spin silken retreats and nets for filter feeding, Integripalpia have larvae that construct portable tube cases and create water currents within the cases by undulating their bodies, and Spicipalpia have larvae that make closed-cocoons and are generally predators or grazers (Wiggins, 2004). Spicipalpia, the suborder traditionally encompassing Hydroptilidae, Hydrobiosidae, Glossosomatidae, and Rhyacophilidae, is somewhat tenuous in its placement within Trichoptera and seldom recovered as monophyletic. Morse (1997) provided a review of the phylogenies that had been published for Trichoptera and outlined the different conclusions made regarding the placement of Spicipalpian families. Originally established by Weaver (1984), he concluded that Spicipalpia was monophyletic and sister to Annulipalpia. Weaver and Morse (1986) later agreed with Weaver. Wiggins and Wichard (1989) placed a monophyletic Spicipalpia as sister to Annulipalpia + Integripalpia. A series of workers contested the monophyly of the suborder, namely Ross (1967), Frania and Wiggins (1997), and Ivanov (1997).

In 2001 and subsequently, molecular data and additional phylogenetic methods were used to elucidate the higher relationships of Trichoptera. Molecular studies of relationships (Holzenthal *et al.*, 2007; Kjer *et al.*, 2001, 2002) have failed to recover a monophyletic “Spicipalpia”, but concluded that the included “Spicipalpian” families + Integripalpia were sister to Annulipalpia, agreeing with Ross (1967). In the most recent study using molecular data to explore these relationships, Malm *et al.* (2013) agreed that “Spicipalpia” was not monophyletic, but instead placed the included families all at the

base of Trichoptera. The placement of Spicipalpia, and by association Hydroptilidae, within Trichoptera remains controversial.

Important works and researchers of microcaddisflies

Noted trichopterists. As mentioned above, the first formal review of Hydroptilidae was completed by Eaton (1873), at which time he established 4 new genera (*Ithytrichia*, *Orthotrichia*, *Oxyethira*, and *Phrixocoma*) and described several new species. Since then, due to the work of many active trichopterists, the family has expanded considerably and will probably continue to do so.

Mosely was a prolific worker and may be one of the best known trichopterists; his work includes taxa described from Great Britain and across Europe, Australia and New Zealand, and South America (1924; 1933, 1934, 1937, 1939a, 1939b; 1939, 1948; Mosely and Kimmins, 1953). Kimmins, a successor of Mosely and known best for his revision of the British species of *Oxyethira* (1958), once commented that the hydroptilids were Mosely's favorite group (1951).

Ross, another prolific trichopterist, described many new taxa from the Nearctic faunal region (1938, 1939, 1941a, 1941b, 1944, 1948, 1956, 1967). He was also the first trichopterist to discontinue using wing venation in the descriptive taxonomy of hydroptilids, which, due to their small size and the resulting reduced venation, does not provide reliable characteristics in the way it does with members of larger taxa. Instead, Ross utilized more stable features of the head, thorax, and abdomen to separate genera and as indicators of possible phylogenetic relationships between taxa.

Flint is another American trichopterist with an incredibly productive history of descriptive taxonomy within Hydroptilidae. He is particularly well known for his work in Central and South America (1962; 1964, 1967a, 1967b, 1968a, 1968b, 1968c, 1970b, 1971, 1972a, 1972b, 1974, 1980, 1981, 1991, 1992; Flint and Bueno-Soria, 1998; Flint and Harris, 1991; Flint *et al.*, 1994; 1993; Harris *et al.*, 2002a, 2002b, 2002c).

Additional hydroptilid workers from the late 19th century, throughout the 20th century, and now currently have included Angrisano: Argentina (1984 [1985], 1989, 1995a, 1995b; Angrisano and Burgos, 2002; Angrisano and Sganga, 2005, 2009, 2010); Bowles: USA (Bowles *et al.*, 1999; Mathis and Bowles, 1989); Bueno-Soria: Mexico, Central America (1983, 1984 [1985], 1999; 2002, 2009; Bueno-Soria and Santiago-Fragoso, 1997; Harris and Bueno-Soria, 1993); Harris: USA, Central America (1985, 1986, 1989, 1990; Harris and Holzenthal, 1990, 1993, 1994, 1997, 1999; Harris and Huryn, 2000; Harris *et al.*, 2002b); Kjaerandsen: Africa (1997; 2004); Klapálek: Europe (1902); Malicky: Europe, Indonesia, Thailand (González and Malicky, 1980, 1988, 1998, 1999, 2010; Malicky and Chantaramongkol, 2007; Malicky *et al.*, 2011); Martynov: Europe, Russia (1910, 1913a, 1913b, 1924, 1934, 1935); McLachlan: Europe (1880); Morton: Europe, North America (1887, 1888, 1904, 1905, 1934); Oláh: Vietnam, Indonesia, South America (1989; 2012; Oláh and Flint, 2012); Johanson: East Africa, Australia, Southeast Asia (1992; Oláh and Johanson, 2010, 2011); Ris: Europe (1894); Schmid: Iran, Pakistan, Sri Lanka (1949, 1958a, 1958b, 1959a, 1959b, 1960). Wells: Australia, Indonesia, New Guinea, Malaysia (1978, 1979, 1980, 1982, 1985, 1990a, 1990b, 1990c, 1993, 1995, 1997, 2005, 2012; Wells and Huisman, 1992; Wells and

Malicky, 1997; Wells and Wichard, 1989).

Taxonomic history and previous phylogenetic treatments of Hydroptilidae

Hydroptilidae. The family Hydroptilidae was first erected in 1836 by Stephens for the genera *Hydroptila*, *Agraylea*, and *Narycia*. However, the only species of the genus *Narycia* that was figured, *Narycia elegans*, subsequently proved to be a moth from the family Psychidae. The remaining genera, *Hydroptila* and *Agraylea*, could be distinguished from other trichopteran families by the “cleft-like” openings of the larval cases and by the filiform antennae and unfolded posterior wings of the adults (Marshall, 1979). The cases and larvae of *Hydroptila pulchricornis* and *Oxyethira flavicornis* had actually been described previously by Pictet (1834) as a unique taxon under the general name “les Hydroptiles.” For this reason, McLachlan (1880) considered Pictet (1834), and not Stephens, to be the true founder of the family Hydroptilidae.

In 1948, Nielsen made the first attempt to divide Hydroptilidae, which was becoming a large and heterogeneous group, into subfamilies. Based on morphological similarities of the larvae, he proposed the subfamilies Orthotrichiinae for the genera *Ithytrichia* and *Orthotrichia* and Hydroptilinae for the genera *Agraylea*, *Hydroptila*, and *Oxyethira*. While other genera, such as *Ptilocolepus* and *Stactobia*, had been established by this time, Nielsen commented on their relative position within the family but declined to formally place them in either of his proposed subfamilies. At this time, Nielsen also placed Hydroptilidae between the “saddle-case” building Glossosomatinae and the “tube-case” building Integripalpia, based on features of the larvae and pupae. In this work,

Nielsen also described in great detail the morphology, life histories, and feeding and case building behaviors of 5 microcaddisfly genera, which provided a very accurate, but fairly restricted, overview of microcaddisflies in general.

Botosaneanu (1956) established the subfamily Stactobiinae for the previously unplaced genus *Stactobia* and what he referred to as “its immediate relatives,” which most likely included the genera *Plethotrichia*, *Plethus*, *Lamonganotrichia*, *Stactobiella*, and probably *Catoxyethira* (Marshall, 1979).

In Ross’s (1956) new classification, the “purse-case” making hydroptilids, included in the “case-maker division,” were divided into the subfamilies Ptilocolepinae, for the genera *Palaeagapetus* and *Ptilocolepus*, and Hydroptilinae for all of the remaining genera; Hydroptilinae was further divided into the tribes Hydroptilini and Neotrichiini. Flint (1970) later declined to follow Ross’s (1956) classification and proposed another new classification in which he proposed the subfamily Leucotrichinae (subsequently corrected to Leucotrichiinae) for the genus *Leucotrichia* and its related genera and retained Hydroptilinae, Orthotrichiinae, Ptilocolepinae, and Stactobiinae as separate and distinct subfamilies.

Marshall (1979) provided the first review of Hydroptilidae at the generic level, including all 42 genera described at the time. For each genus, she included information regarding nomenclature, distribution, morphology of adult and immature stages, biology, and possible species groupings. Marshall also wrote keys to the subfamilies, at the time considered tribes, for the adult stage and to the genera for both the adult and immature stages. The phylogeny of the family was discussed and a new classification offered.

Marshall's proposed classification was based on that of Ross (1956) by recognizing only 2 subfamilies, Hydroptilinae and Ptilocolepinae. However, it also reflected the classification proposed by Flint (1970) by dividing Hydroptilinae into 6 tribes that corresponded to the subfamilies he had proposed: Hydroptilini, Leucotrichiini, Neotrichiini, Ochrotrichiini, and Stactobiini, and with the addition of the newly proposed Ochrotrichiini. The morphological-based phylogeny proposed by Marshall, shown in Figure 1, was not based on any statistical analyses and therefore offers no support values for any of the proposed relationships. This phylogeny represents the last attempt to assess the relationships of the subfamilies and genera of Hydroptilidae as a whole.

In 2010, Wells wrote a review of hydroptilid studies published from the time of Marshall's (1979) review up through 2009; in this work, she reviewed hydroptilid taxonomy, included new discoveries regarding aspects of the biology of some species, and suggested that future work should place emphasis on life history studies.

The most recent attempt to provide an analysis of relationships within Hydroptilidae was that of Oláh and Johanson (2011), a work in which they described many new species from the Neotropical faunal region and referred to the subfamilies as tribes. In this paper, Oláh and Johanson provided several tables containing either features or character states of species groups, subgenera, generic clusters, or genera in tribes. However, the tables did not cover all of the taxa present in the paper: no information on generic features or character states were provided for *Hydroptila* or any of the included stactobiine genera (*Bredinia*, *Flintiella*, and *Orinocotrichia*). Nor was there any prose presented to discuss the information outlined in the tables. As interpreted from the tables,

several genera were transferred between subfamilies or from *incertae sedis* status, but, as no discussion or justification for the changes was provided, the classification listed in the section below (“Overview of traditionally recognized taxa of Hydroptilidae and Ptilocolepidae”) does not reflect these proposals. In summary, the current taxonomy of Hydroptilidae that is recognized for informing the design of the phylogenetic study is that of Marshall (1979) and Morse (2006). 6 hydroptilid subfamilies are treated: Hydroptilinae, Leucotrichiinae, Neotrichiinae, Ochrotrichiinae, Orthotrichiinae, and Stactobiinae.

Ptilocolepidae. The family Ptilocolepidae, which was once considered to be a group within Hydroptilidae and is considered in recent classifications as a distinct family of its own, includes the genera *Ptilocolepus* and *Palaeagapetus*. The type species was originally described in *Rhyacophila* and therefore placed in the family Rhyacophilidae (Pictet, 1834), but was subsequently shown to be a senior synonym of *Ptilocolepus turbidus*, making the type species *Ptilocolepus granulatus* (Hagen, 1855). Thienemann (1904) noted similarities between the larvae of *P. granulatus* and both members of Hydroptilidae and Glossosomatidae, which led Ulmer (1907) to transfer the genus to Hydroptilidae. Subsequently, Martynov (1913a) established the subfamily Ptilocolepinae for *Ptilocolepus*, but it was retained in Rhyacophilidae. Ross (1956) transferred Ptilocolepinae to Hydroptilidae and redefined it to include *Palaeagapetus* (incorrectly referring to it as Palaeagapetinae). Kristensen (1997) suggested that *Ptilocolepus* and *Palaeagapetus* together may represent the sister-group of all other Trichoptera.

In 2001, Ptilocolepidae was elevated to the family status at which it currently

resides, effectively also elevating each of the 6 tribes within Hydroptilinae to the rank of subfamily (Malicky, 2001). Malicky claimed that previous authors had placed differing levels of importance on morphological features of either the adults or the larvae, which led to the group being placed in different families at different times. He stated that, because all these characters should be considered equally, it was appropriate to raise the group to family rank of Ptilocolepidae. Subsequently, the deeper-level relationships within Trichoptera were explored using molecular data and both the monophyly of Ptilocolepidae and its status as a family were questioned (Holzenthal *et al.*, 2007). According to the work of Holzenthal *et al.* (2007), Ptilocolepidae consistently grouped with Hydroptilidae, indicating that the elevation to family status might be an unnecessary taxonomic change. Malicky (2008) countered by referring to the differences in geographical distribution of the 2 families, stating that the high level of endemism shown by Hydroptilidae and the relictary distribution of Ptilocolepidae were additional evidence that the families were distinct from one another. In summary, 6 hydroptilid subfamilies and 2 ptilocolepid genera are treated; a taxonomic review of all hydroptilids and ptilocolepid genera are provided.

Review of traditionally recognized subfamilies and genera of Hydroptilidae and Ptilocolepidae

The following account is a summary of the historically recognized taxa of Hydroptilidae and Ptilocolepidae. A more detailed morphological diagnosis of 42 of the genera can be found in Marshall's (1979) monograph. Since 1979, 37 additional genera

have been described. In almost all cases, genera have been established without reference to derived characters to support reciprocal monophyly. Only one study has included a phylogenetic assessment when establishing new genera (Kjaerandsen, 1997). 23 of the 79 genera (29%), including the 3 fossil genera, are monotypic. See Fischer (1961, 1971) for a complete bibliography of the literature published until 1960. Taxonomic classification presented in this overview mainly follows that of “Trichoptera World Checklist” (Morse, 2006). Numbers of species are from the “Trichoptera World Checklist” (Morse, 2006), with additions from Zoological Record on-line through 2013. The list of genera informed taxon selection for the phylogenetic study and the results of that study and taxonomic implications are provided in “An Updated Phylogenetic Framework For Hydroptilidae” (under Conclusions).

Family HYDROPTILIDAE Stephens, 1836

Hydroptilidae Stephens, 1836:151 [Type genus: *Hydroptila* Dalman, 1819]. —Marshall, 1979:135 [review of the genera]. —Wiggins, 1996:1-457 [larvae of the North American genera]. —Waringer and Graf, 1997:72 [atlas of species in Australia, central Europe, and Palearctic region; key to larvae]. —Kachalova in Medvedev, 1998:179 [diagnostic characters of adults]. —Flint, Holzenthal, and Harris, 1999:82 [catalog of Neotropical species].

The family Hydroptilidae exhibits a cosmopolitan distribution, with members occurring in all major faunal regions except for Antarctica. Currently recognized within

the family are 6 distinct subfamilies, containing over 2,100 species: Hydroptilinae, Leucotrichiinae, Neotrichiinae, Ochrotrichiinae, Orthotrichiinae, and Stactobiinae. Each subfamily can be characterized by fundamental morphological features of the adult, larval, and pupal stages (Marshall, 1979). Despite the heterogeneous nature of the family, these features unite the subfamilies and can be used to separate them from the genera of Ptilocolepidae. Great variation exists among the genera of Hydroptilidae; both cool- and warm-adapted genera occur in a variety of habits, including swiftly-flowing montane streams, splash zones of waterfalls, seeps, rivers of varying sizes, and even occasionally still pond waters. In general, larvae are detritus-feeders but some groups specialize on the intracellular contents of filamentous green algae.

Subfamily HYDROPTILINAE Stephens, 1836

Hydroptilidae Stephens, 1836:151 [Type genus: *Hydroptila* Dalman, 1819].

Hydroptilinae consists of 26 genera occurring in all biogeographic regions of the world, excluding the polar regions. As Marshall (1979) noted, the subfamily may seem to be very heterogenous and varied in morphological features of both the adults and larvae, but can be united by a number of basic similarities, including features of the adult thorax and male genitalia and the larval association with green filamentous algae. Marshall (1979) further divided the subfamily into 3 subgroups based on characteristics of the male and female genitalia and general larval appearances and habitats. The *Agraylea*-group, including the genera *Agraylea*, *Allotrichia*, *Dhatrichia*, *Microptila*, and

Ugandatrichia, is based on the larger and more generalized appearance of the adults in comparison to other hydroptilids and the distinctive male genitalia. The *Hydroptila*-group, essentially the genus *Hydroptila*, is also united by the distinct form of the male genitalia and can be separated from other groups and genera by the postoccipital scent caps of the males and the absence of ocelli. The *Oxyethira*-group, including *Oxyethira*, *Paroxyethira*, *Tricholeiochiton*, and *Xuthotrichia*, exhibits more variety than the others in features of the adults and the genitalic form, but is united by similarities in the larval form. The larval stage is unknown for the genera *Austratrichia*, *Cyclopsiella*, *Jabitrichia*, *Kholaptila*, *Maeyaptila*, *Missitrichia*, *Mulgravia*, *Paucicalcaria*, *Sutheptila*, *Tangatrichia*, *Vietrichia*, *Wlitrichia*, and *Xuthotrichia*.

Genus *Acanthotrichia* Wells, 1982

Acanthotrichia Wells, 1982:267 [Type species: *Acanthotrichia bilamina* Wells 1982, original designation]. —Wells, 1985:15 [larva].

Acanthotrichia is a monotypic genus occurring in Australia. Based on features of the male genitalia, it was placed in Hydroptilinae and may be most closely related to the genera *Tricholeiochiton* and *Paroxyethira* (Wells, 1982). The larval stage was described by Wells (1985).

Genus *Acritoptila* Wells, 1982

Acritoptila Wells, 1982:262 [Type species: *Acritoptila globosa* Wells 1982, original

designation]. Wells, 1985:15 [larva]. —Wells, 1997:1 [checklists, larvae, species].

Acritoptila consists of 14 species occurring in Australia. It can be distinguished from members of *Austratrichia* and *Mulgravia* by differences in the inferior appendages of the male genitalia (Wells, 1982). Wells (1985) described the larvae of *A. globosa* and *A. margaretae* and stated that the larvae of *Acritoptila* were indistinguishable from those of *Hellyethira*.

Genus *Agraylea* Curtis, 1834

Nanoagraylea Botosaneanu, 1995:2 [fossil subgenus of *Agraylea*].

Agraylea Curtis, 1834:217 [Type species: *Agraylea sexmaculata* Curtis 1834, subsequent designation by Wes2od, 1840]. —Kachalova in Medvedev, 1998:182 [diagnostic characters of adults].

Agraules Agassiz, 1846:32 [Unjustified emendation of *Agraylea* according to Fischer, 1961].

Hydrochestria Kolenati, 1848:103 [Type species: *Agraylea sexmaculata* Curtis 1834, subsequent designation by Kimmins, 1950]. —Kimmins, 1950:58 [to synonymy].

The genus *Agraylea* currently contains 2 subgenera. The subgenus *Agraylea* consists of 8 species, including 1 fossil species known from Baltic amber. The subgenus occurs in a Holarctic distribution. The subgenus *Nanoagraylea* consists of 3 fossil species (Botosaneanu, 1995). According to Marshall (1979), the extant members of the genus are

most similar morphologically to *Allotrichia*, from which they differ in hindwing venation, but features of the male genitalia are similar to those of the genera *Dhatrichia* and *Ugandatrichia*. Larval descriptions of *A. cognatella*, *A. multipunctata*, and *A. sexmaculata* were given by Solem (1972), Nielsen (1948), and Barnard (1971), respectively.

Genus *Allotrichia* McLachlan, 1880

Allotrichia McLachlan, 1880:508 [Type species: *Allotrichia pallicornis* Eaton 1873, monotypic]. —Botosaneanu, 1992: [treated as subgenus of *Agraylea*]. —Kachalova in Medvedev, 1998:182 [diagnostic characters of adults]. —Malicky, 2005:545 [treated as genus]. —Ivanov, 2011:183 [referred to as distinct genus].

Allotrichia consists of 10 species, including 2 fossil species known from Baltic amber. The genus occurs in a Palaearctic distribution. Marshall (1979) noted that the genus is morphologically very similar to *Agraylea* and that the 2 may be synonymous, that is *Agraylea* may be a junior subjective synonym of *Allotrichia*. The larvae of *A. pallicornis* were described by Giudicelli and Vaillant (1967).

Genus *Austratrichia* Wells, 1982

Austratrichia Wells, 1982:259 [Type species: *Austratrichia nevoissi* Wells 1982, original designation].

The monotypic genus *Austratrichia* is endemic to Australia. It is most similar to the genus *Hellyethira*. According to Wells (1982), the genus can be distinguished using characters of the male genitalia (Wells, 1982). The larval stage is unknown.

Genus *Cyclopsiella* Kjaerandsen, 1997

Cyclopsiella Kjaerandsen, 1997:234 [Type species: *Cyclopsiella anderseni* Kjaerandsen 1997, original designation].

The monotypic genus *Cyclopsiella*, recorded only from Ghana, can be distinguished from all other hydroptilid genera by having only a single medial ocellus and a lack of postoccipital lobes (Kjaerandsen, 1997). Kjaerandsen (1997) stated that the male genitalia of *Cyclopsiella* share some similarities with the genera *Hydroptila* and *Hellyethira*, yet, in the accompanying parsimony analysis, *Cyclopsiella* grouped with the genera *Jabitrachia*, *Oxyethira*, and *Tangatrichia*. The larval stage is unknown.

Genus *Dhatrichia* Mosely, 1948

Dhatrichia Mosely, 1948:78 [Type species: *Dhatrichia inasa* Mosely 1948, original designation]. —Kjaerandsen, 2004:131 [revision; keys to males, females, larvae, and pupae].

The genus *Dhatrichia* consists of 14 species recorded from Burkina Faso, Ghana, Madagascar, Tanzania, Yemen, and Zaire. While Marshall (1979) stated that *Dhatrichia*

shared similarities in the male genitalia with *Agraylea* and in the thorax with *Microptila*, Kjaerandsen (2004) postulated that the genus was actually sister to either *Kumanskiella* or *Microptila*. The larvae of *D. ankasaensis*, *D. hunukani*, *D. lerabae*, *D. minuta*, and *D. wliensis* were first described by Kjaerandsen (2004).

Genus *Hellyethira* Neboiss, 1977

Hellyethira Neboiss, 1977:42 [Type species *Hellyethira valleculea* Neboiss 1977, original designation]. —Wells, 1985:10 [larva]. —Wells, 1997:1 [checklist, key to larvae of Australian species].

The genus *Hellyethira* consists of 42 species occurring in Australia. It can be distinguished from the genera *Paroxyethira* and *Orthotrichia* by differences in wing venation (Neboiss, 1977). Wells (1985) stated that the larvae of the genus were indistinguishable from those of *Acritoptila*, but described the larval stage of *H. simplex* and of many others from the genus.

Genus *Hydroptila* Dalman, 1819

Hydroptila Dalman, 1819:125 [Type species *Hydroptila tineoides* Dalman 1819, monotypic]. —Bueno, 1984:83 [revision of Mexican and Central American species]. Wells, 1997:1 [checklist, key to species of larvae]. —Kachalova in Medvedev, 1998:185 [diagnostic characters of adults]. —Harris and Holzenthal, 1999:16 [key to Central American species].

Phrixocoma Eaton, 1873:132 [Type species: *Hydroptila sparsa* Curtis 1834, original designation]. —McLachlan, 1880:511 [to synonymy].

Hydropneuma Enderlein, 1929:232 [Type species: *Hydropneuma juba* Enderlein 1929, original designation]. —Nybom, 1948:5 [to synonymy].

Hydroptilina Martynov, 1934:117 [Type specimen *Hydroptilina angustipennis* Martynov 1934, monotypic]. —Fischer, 1971:289 [to synonymy, following Lepneva, 1953:406]. —Marshall, 1979:200 [considered as a synonym of *Hydroptila*].

Oxydroptila Martynov, 1935:114 [Type species *Oxydroptila furcata* Martynov 1935, original designation]. —Marshall, 1979:200 [to synonymy].

Oeceotrichia Ulmer, 1951:85 [Type species *Oeceotrichia elongata* Ulmer 1951, original designation]. —Marshall, 1979:200 [to synonymy].

Pasirotrichia Ulmer, 1951:90 [Type species *Pasirotrichia crenata* Ulmer 1951, original designation]. —Marshall, 1979:200 [to synonymy].

Sumatranotrichia Ulmer 1951:87 [Type species *Sumatranotrichia trullata* Ulmer 1951, original designation]. —Marshall, 1979:200 [to synonymy].

Hydroptila is a large, cosmopolitan genus occurring in all regions excluding polar regions. It is the most species-rich genus in the family, consisting of 422 species. Marshall (1979) divided *Hydroptila* into thirteen species groups (*capensis*, *consimilis*, *dikirilagoda*, *forcipata*, *losida*, *occulta*, *pulchricornis*, *sparsa*, *tigurina*, *tineoides*, *uncinata*, *vectis*, *waubesiana*) which she thought might one day be recognized as subgenera, based on distribution and form of the male and female genitalia. Despite the

large number of species and the proposed species groups, she also listed several characters that unite the genus, including basic structure of the genitalia, thorax, absence of ocelli, presence of dorsal postoccipital scent-organs in male adults, and the general appearance of the immature stage. The larvae of *H. delineata* were described by Sibley (1926a), with the larvae of many other species having been described since (Botosaneanu and Giudicelli, 1981; Botosaneanu and Sykora, 1963; Fahy, 1971; Flint, 1964; Hanna, 1961; Hicken, 1967; Ito and Kawamura, 1980; Jacquemart, 1965; Jacquemart and Coineau, 1962; Keiper and Foote, 1999; Lepneva, 1932, 1964; Nielsen, 1948; Ross, 1944; Wells, 1985; Wells, 1997).

Genus *Jabitrichia* Wells, 1990

Jabitrichia Wells, 1990:108 [Type species: *Jabitrichia dostinei* Wells 1990, original designation]. —Kjaerandsen and Andersen, 2002:134 [revision].

The genus *Jabitrichia* contains 4 species recorded from northern Australia, Malaysia, Thailand, Angola, and Ghana. *Jabitrichia* shares morphological similarities with both *Hydroptila* and *Oxyethira*, but differs enough that the definition of either genus would have required considerable modification to accommodate the addition (Wells, 1990c). *Jabitrichia* and *Hydroptila* share a spur formula (0, 2, 4), a lack of ocelli, similar pattern of wing color, and form of thoracic scutellae, while *Jabitrichia* and *Oxyethira* share a forewing without a jugal lobe, the general form of the female genitalia, and reductions of particular structures of the male genitalia (Wells, 1990c). In their

morphological analysis, Kjaerandsen and Andersen (2002) placed the genus as sister to *Oxyethira*. The larval stage is unknown.

Genus *Kholaptila* Malicky and Chantaramongkol, 2007

Kholaptila Malicky and Chantaramongkol, 2007:1024 [Type species *Kholaptila serrata* Malicky and Chantaramongkol 2007, original designation].

The monotypic genus *Kholaptila* has been recorded from Nepal. Malicky and Chantaramongkol (2007) placed the genus in Hydroptilinae based on the absence of the transverse suture of the mesoscutellum. There are some similarities between *Kholaptila* and *Microptila* in the male genitalia (Malicky and Chantaramongkol, 2007). The larval stage is unknown.

Genus *Maeyaptila* Malicky and Chantaramongkol, 2007

Maeyaptila Malicky and Chantaramongkol, 2007:1025 [Type species *Maeyaptila xuthos* Malicky and Chantaramongkol 2007, original designation].

The monotypic genus *Maeyaptila* occurs in Thailand. Malicky and Chantaramongkol (2007) placed the genus in Hydroptilinae due to the absence of the transverse suture of the mesoscutellum, the spur formula (0, 2, 4), the lack of ocelli, and the general structure of the male genitalia. They also noted, however, that some of the genitalic structures were also similar to those of *Scelotrichia*, a member of Stactobiinae,

making the placement somewhat tenuous (Malicky and Chantaramongkol, 2007). The larval stage is unknown.

Genus *Microptila* Ris, 1897

Microptila Ris, 1897:416 [Type species: *Microptila minutissima* Ris, monotypic]. —Graf 2004:31 [larva of type species].

The genus *Microptila* consists of 16 species occurring in the West Palearctic faunal region. Marshall (1979) commented that adult *Microptila* bear similarities with those of the genus *Dhatrichia*. The larvae of *M. minutissima* were described by Graf (2004).

Genus *Missitrichia* Wells, 1991

Missitrichia Wells, 1991:508 [Type species *Missitrichia nusam* Wells 1991, original designation].

Missitrichia currently contains 2 species occurring in Papua New Guinea and Indonesia. There are several similarities between *Missitrichia* and *Hydroptila*, but the 2 can be distinguished by differences in wing venation, features of the adult head, and features of the male genitalia (Wells, 1991). The larvae are unknown.

Genus *Mulgravia* Wells, 1982

Mulgravia Wells, 1982:262 [Type species *Mulgravia coronata* Wells 1982, original designation]. —Wells, 1997:1 [included in checklist of Australian hydroptilid species].

The genus *Mulgravia* consists of 2 species known from Australia. Adults of the genus share many similarities with *Hellyethira* but can be distinguished by several features of the male genitalia (Wells, 1982). The larval stage is unknown.

Genus *Oxyethira* Eaton, 1873

Oxyethira Eaton, 1873:143 [Type species *Hydroptila costalis* Curtis 1834, type species original designation, is a species of *Orthotrichia* according to Neboiss (1963).

Oxyethira costalis Curtis sensu Eaton 1873, is probably *Oxyethira flavicornis* (Pictet) 1834]. —Kelley, 1984:435 [revision, as subgenus]. —Kelley, 1985:230 [revision]. —Wells, 1997:1-28 [checklist, larvae of Australian species]. —Kachalova in Medvedev, 1998 [diagnostic characters of adults].

Lagenopsyche Müller, 1879:39 [Type species *Lagenopsyche spirogyrae* Müller, subsequent designation by Fischer 1961:112]. —Müller, 1887:338 [withdrawn in favor of *Oxyethira*]. —Kelley, 1984:436 [to synonymy].

Argyrobothrus Barnard, 1934:392 [Type species *Argyrobothrus velocipes* Barnard 1934, monotypic]. —Ross, 1948:202 [to synonymy]. —Kelley, 1984:438 [as subgenus].

Loxotrichia Mosely, 1937:165 [Type species *Loxotrichia azteca* Mosely 1937, original designation]. —Ross, 1944:133 [to synonymy]. —Kelley, 1984:442 [as subgenus].

Dampfitrichia Mosely, 1937:169 [Type species *Dampfitrichia ulmeri* Mosely 1937, monotypic]. —Ross, 1944:133 [to synonymy]. —Kelley, 1984:438 [as subgenus].

Oxytrichia Mosely, 1939:289 [Type species *Oxyethira mirabilis* Morton 1904, original designation]. —Kimmins, 1966:114 [Type species returned to *Oxyethira*, thus synonymizing genus]. —Kelley, 1984:438 [as subgenus].

Stenoxyethira Kimmins, 1951:194 [Type species *Stenoxyethira minima* Kimmins 1951, original designation]. —Kelley, 1984:438 [to synonymy with *Oxyethira*].

Gnathotrichia Ulmer, 1951 [Type species *Gnathotrichia isabellina* Ulmer 1951, original designation]. —Marshall, 1979:207 [to synonymy with *Stenoxyethira*].

Dactylotrichia Kelley, 1984:459 [Type species *Oxyethira santiagensis* Flint 1982, original designation, as subgenus].

Trichoglene Neboiss, 1977:43 [Type species *Trichoglene columba* Neboiss 1977, original designation]. —Wells, 1981:106 [considered a synonym of *Oxyethira*]. —Kelley, 1983:2442 [as subgenus].

Holarctotrichia Kelley, 1984:456 [Type species *Oxyethira distinctella* McLachlan 1880, original designation, as subgenus]. —Kelley, 1986:777 [revision].

Mesotrichia Kelley, 1984:458 [Type species *Oxyethira jamaicensis* Flint 1968, original designation, as subgenus]. —Özdikmen 2007:444 [preoccupied in Apidae by Wes2od, 1838:112, replaced with *Kellyella*].

Tanytrichia Kelley, 1984:459 [Type species *Oxyethira longissima* Flint 1974, original designation, as subgenus].

Pacificotrichia Kelley, 1989:196 [Type species *Pacificotrichia oropedion* Kelley 1989,

original designation, as subgenus].

Kelleyella Özdikmen, 2007:444 [Type species *Oxyethira jamaicensis* Flint 1968, original designation, replacement name for *Mesotrichia*]. Kelley, 1984:458 [treated as subgenus *Mesotrichia*].

The genus *Oxyethira* is a large genus of 203 species with a near world-wide distribution, excluded only from the polar regions, and particularly diverse in Africa, Australia, and southeast Asia. The larvae are distinct and known for feeding on green filamentous algae (Marshall, 1979). The genus was divided into eleven species groups (*azteca*, *bidentata*, *distinctella*, *falcata*, *flavicornis*, *mirabilis*, *pallida*, *rivicola*, *simplex*, *ulmeri*, and *zeronia*) based on features of the male genitalia (Marshall, 1979). The genus was later divided into 11 subgenera, as listed above, which do not correspond to Marshall's species groups (Kelley, 1984, 1989).

The larvae of *Oxyethira* were first described, under the name *Lagenopsyche spirogyrae*, by Müller (1879b), with many other species having been described since (Back, 1983; Barnard, 1934; Flint, 1964; Hickin, 1967; Hudson, 1886; Ito and Kawamura, 1984; Jacquemart, 1973; Jacquemart and Coineau, 1962; Keiper and Walton, 1999; Lepneva, 1964; Macdonald, 1950; Morton, 1887; Mosely and Kimmins, 1953; Nielsen, 1948; Ross, 1944; Ulmer, 1957; Wells, 1985).

Genus *Paroxyethira* Mosely, 1924

Paroxyethira Mosely, 1924:760 [Type species: *Paroxyethira hendersoni* Mosely,

subsequent designation by Mosely and Kimmins, 1953:515]. —Wells and Johanson, 2012:330 [review of New Caledonian species].

Paroxyethira consists of 17 species recorded from New Zealand, New Caledonia, Vanuatu, and Fiji. Marshall (1979) considered the genus to be closely related to *Xuthotrichia*, based on similarities of the adult head and thorax, the female genitalia, and larval morphology and habits. Generalized figures of *Paroxyethira* larvae were given by Leader (1968), with a more detailed description given later (Leader, 1972).

Genus *Paucicalcaria* Mathis and Bowles, 1989

Paucicalcaria Mathis and Bowles, 1989:187 [Type species *Paucicalcaria ozarkensis* Mathis and Bowles 1989, original designation].

The monotypic genus *Paucicalcaria* has been recorded only from Magazine Mountain in Arkansas, USA. Based on similarities of the genitalia and thoracic nota and the lack of ocelli, Mathis and Bowles (1989) placed it as most closely related to *Hydroptila*. The genus can be distinguished from all other hydroptilids by its unique tarsal formula (0, 1, 2) (Mathis and Bowles, 1989). The larval stage is unknown.

Genus *Sutheptila* Malicky and Chantaramongkol, 2007

Sutheptila Malicky and Chantaramongkol, 2007:1024 [Type species: *Sutheptila kjaerandseni* Malicky and Chantaramongkol 2007, original designation.]

The monotypic genus *Sutheptila* is recorded from Thailand. Malicky and Chantaramongkol (2007) placed the genus in Hydroptilinae based on the absence of the transverse suture of the mesoscutellum. They also commented that the general form of the male genitalia was similar to that of *Microptila*, but that the phallus differed noticeably (Malicky and Chantaramongkol, 2007). The larval stage is unknown.

Genus *Tangatrichia* Wells and Andersen, 1995

Tangatrichia Wells and Andersen, 1995:161 [Type species: *Tangatrichia gracilentata* Wells and Andersen 1995, original designation].

The monotypic genus *Tangatrichia*, occurring in Tanzania, shares similarities in the wings and form of the male genitalia with members of Stactobiinae (Wells and Andersen, 1995). However, it has been placed within Hydroptilinae based on the presence of ocelli and the basic structure of the male genitalia and shares similarities with both *Hydroptila* and *Jabirichia* (Wells and Andersen, 1995). The larval stage is unknown.

Genus *Tricholeiochiton* Kloet and Hincks, 1944

Leiochiton Guinard, 1879:139 [Type species: *Leiochiton fagesii* Guinard 1879, monotypic, preoccupied by *Leiochiton* Curtis, 1831 in Coleoptera].

Tricholeiochiton Kloet and Hincks, 1944:97 [Replacement name for *Leiochiton* Guinard 1879]. —Wells, 1982:252 [revision]. —Wells, 1997:1-28 [checklist of Australian

species, larvae]. —Wells, 1998:81 [distribution].

Synagotrichia Ulmer, 1951:81 [Type species: *Synagotrichia fortensis* Ulmer 1951, original designation and monotypic]. —Marshall, 1979:210 [to synonymy].

Tricholeiochiton includes 11 species occurring in Europe, southeast Asia, Australia, and South America. The genus is most likely closely related to *Oxyethira*, based on the general form of the larvae and features of the adult head and thorax (Marshall, 1979). The larvae of *T. fagesii* have been described by both Lepneva (1970) and Wells (1985).

Genus *Ugandatrichia* Mosely, 1939

Ugandatrichia Mosely, 1939:36 [Type species: *Ugandatrichia minor* Mosely 1939, original designation]. —Marshall, 1979:198 [revision].

Moselyella Kimmins, 1951:195 [Type species: *Ithytrichia violacea* Morton, original designation]. —Schmid, 1960 [to synonymy].

The genus *Ugandatrichia* consists of 30 relatively large species occurring in Africa and south and southeast Asia. The genus was synonymized with *Microptila* by Schmid (1960), but later reinstated by Marshall (1979). Marshall (1979) considered *Ugandatrichia* to be more closely related to *Agraylea* than *Microptila*, based on similarities of the form of the male genitalia and the thoracic nota. The larvae of *U. rhodesiensis* were described by Scott (1976), with several other species having since been provided (Hsu and Chen, 2002; Ito and Ohkawa, 2012; Laudee, 2008; Vaillant, 1984).

Genus *Vietrichia* Oláh, 1989

Vietrichia Oláh, 1989:272 [Type species: *Vietrichia linghia* Oláh 1989, original designation].

The monotypic genus *Vietrichia* is known only from Vietnam. Members of the genus can be separated from all other hydroptilids by the spur formula (0, 2, 4), the convex, pentagonal mesoscutellum, and the general structure of the male genitalia (Oláh, 1989). Using Marshall's (1979) key to hydroptilids, Oláh (1989) placed the genus in Hydroptilinae, based on the symmetrical male genitalia, a phallus that was not thread-like in appearance, and the absence of a transverse suture on the mesoscutellum. The larval stage is unknown.

Genus *Wlitrichia* Kjaerandsen, 1997

Wlitrichia Kjaerandsen, 1997:230 [Type species: *Wlitrichia introvertica* Kjaerandsen 1997, original designation].

The monotypic genus *Wlitrichia* has been recorded only from Ghana. Kjaerandsen (1997) stated that, in general, *Wlitrichia* is very similar morphologically to *Hydroptila*, but the male genitalia very closely resemble that of the subgenus *Loxotrichia* (*Oxyethira*) and differ distinctly in the structure of the inferior appendages. In the parsimony analysis done by Kjaerandsen (1997) using morphological characters, *Wlitrichia* grouped with the

genera *Hydroptila* and *Paucicalcaria*. The larval stage is unknown.

Genus *Xuthotrichia* Mosely, 1934

Xuthotrichia Mosely, 1934:139 [Type species *Xuthotrichia ochracea* Mosely 1934, original designation].

Xuthotrichia consists of 2 species endemic to Australia. The characteristic male genitalia are asymmetrical and very complex. The genus may be closely related to *Paroxyethira*, based on features of the adult head and thorax; the 2 genera together may be allied to *Oxyethira* (Marshall, 1979). The larval stage is unknown.

Subfamily LEUCOTRICHIIINAE Flint, 1970

Leucotrichiinae Flint, 1970:2 [Type genus: *Leucotrichia* Mosely, 1934].

Leucotrichiinae consists of 17 genera occurring predominantly in Central and northern South America, with a few species recorded from North America and a few as far south as Chile. Flint (1970) established the subfamily for the genus *Leucotrichia* and several closely related genera. In the original description, Flint stated that there was no single character that defined the group as separate from other hydroptilid adults. However, he did consider the following set of characters to be diagnostic when all present: modified head and antennae, ocelli reduced to 2 in males, and the presence of a basal costal “pouch” or “bulla” on the male forewing. The basic structure of the male

genitalia also proved to be difficult to clearly define and Flint merely noted that the form displayed “something characteristic”. Marshall (1979) gave a more detailed description, but also noted that, while it may seem to form a distinct unit, the subfamily was very difficult to define. Further, she also stated that the genera are difficult to distinguish. Features used to establish genera have been inconsistent, with some genera originally established and defined based on characteristics of the head, antennae, and wings, while others were based on characteristics of the genitalia (Marshall, 1979).

Leucotrichiinae shares many morphological similarities with members of Stactobiinae, but this observation may indicate convergent evolution and not a shared common ancestry (Marshall, 1979). Bowles *et al* (1999) assessed genera of Stactobiinae occurring in the New World. They transferred several to Leucotrichiinae based on four larval characters that they concluded were derived for Leucotrichiinae, including: 1) absence of a larval case, 2) separate pleural sclerites on the prothorax, 3) an undivided meso- and metanota, and 4) accessory denticles on the anal claw. Several genera have been transferred back and forth between Leucotrichiinae and Stactobiinae, indicating that the limits between the subfamilies are poorly defined and in need of further research. Larval descriptions have been made for most genera, excluding *Ascotrichia*, *Betrichia*, and *Costatrichia*.

Genus *Abtrichia* Mosely, 1939

Abtrichia Mosely, 1939:224 [Type species *Abtrichia antennata* Mosely 1939, original designation]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus

cluster].

The genus *Abtrichia* is represented by 3 species recorded from southern Brazil, Argentina, and French Guiana. The genus can be distinguished from others by the highly modified adult male head and basal antennal segment (Marshall, 1979). Flint described the larvae of *A. antennata* and considered them to be very similar to those of *Zumatrichia antilliensis*, differing only in the dorsal head surface (1972b).

Genus *Acostatrichia* Mosely, 1939

Acostatrichia Mosely, 1939:228 [Type species: *Acostatrichia plaumanni* Mosely 1939, original designation]. —Angrisano and Sganga, 2010:56 [larva]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

Acostatrichia consists of 6 species distributed through much of South America. While the larvae of *A. simulans* was described by Angrisano and Sganga (2010), the female is still unknown. Both Mosely (1939a) and Marshall (1979) noted that *Acostatrichia* is most similar to the genus *Costatrichia*, differing only in the wing venation and the unmodified antennae.

Genus *Alisotrichia* Flint, 1964

Alisotrichia Flint, 1964:46 [Type species: *Alisotrichia hirudopsis* Flint 1964, original designation]. —Flint, 1970:24 [revision]. —Harris and Holzenthal, 1993:155

[phylogeny]. —Bowles, Harris and Bueno-Soria, 1999:51 [larval description, taxonomic position]. —Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

Rioptila Blickle and Denning, 1977:299 [Type species: *Rioptila arizonica* Blickle and Denning 1977, original designation]. —Harris and Holzenthal, 1993:155 [to synonymy].

The genus *Alisotrichia* contains 56 species, including one fossil species known from Dominican amber. The distribution of the genus extends from the southwestern United States, through Mexico and Central America into Venezuela, and also the Antilles. The genus was first placed in Leucotrichiinae by both Flint (1964) and Marshall (1979), but has since been transferred to Stactobiinae (Harris and Holzenthal, 1993) and then returned to Leucotrichiinae (Bowles *et al.*, 1999). Flint (1970) divided *Alisotrichia* into several species groups based on adult features, which Marshall (1979) claimed were not well defined and declined to discuss them further. Harris and Holzenthal (1993) later divided the genus into 8 species groups based on tibial spur formula, antennal structure, and features of the male genitalia. The 3 basal species groups have since been transferred to genera of their own (*blantoni*, *dominicensis*, and *quemada* to *Mejicanotrichia*, *Cerasmatrichia*, and *Scelobotrichia*, respectively). The larvae of the type species, *A. hirudopsis*, was first described by Flint (1964) and several additional species have been described since (Botosaneanu, 1990, 1994; Flint, 1968b). Larvae of *Alisotrichia* are distinct from all other larvae of Leucotrichiinae in that, instead of building a case during

the fifth and final instar, they remain free-living until pupation (Marshall, 1979).

Genus *Anchitrichia* Flint, 1970

Anchitrichia Flint, 1970:14 [Type species *Anchitrichia spangleri* Flint 1970, original designation]. —Pes and Hamada, 2004:31 [new records]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

The 4 species currently contained within the genus *Anchitrichia* occur in a distribution throughout Central America extending south to Argentina. Marshall (1979) commented that, while *Anchitrichia* may prove to be synonymous with one or more of the other genera of Leucotrichiinae, the genus may be very closely related to *Zumatrichia* and can be distinguished by several adult morphological features, including the relatively larger body size, the unmodified antennae, and the general form of the male genitalia. The larvae of *A. spangleri* were described by Flint (1970) and those of *A. duplifurcata* by Guahyba (1991).

Genus *Ascotrichia* Flint, 1983

Ascotrichia Flint, 1983:35 [Type species: *Ascotrichia frontalis* Flint 1983, original designation]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

Ascotrichia is a small genus of 2 species occurring in eastern South America. When

establishing the genus, Flint (1983) stated that it clearly belonged in Leucotrichiinae and that it was most closely related to *Abtrichia*, but could be easily distinguished by differences in the head, antennae, and forewings. The larvae are unknown.

Genus *Betrichia* Mosely, 1939

Betrichia Mosely, 1939:230 [Type species: *Betrichia zilbra* Mosely 1939, original designation]. — Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

Betrichia is a genus consisting of 9 species distributed through eastern South America. The larval stage is unknown. As species have been added to *Betrichia*, the characters originally given to define the genus have proven instead to be specific; there are no precise diagnostic characters that can be used to clearly distinguish members of the genus from other genera of Leucotrichiinae (Marshall, 1979).

Genus *Byrsopteryx* Flint, 1981

Byrsopteryx Flint, 1981:27 [Type species: *Byrsopteryx mirifica* Flint 1981, original designation]. — Harris and Holzenthal, 1994:154 [revision, placement, transferred to Stactobiini]. — Bowles, Harris, and Bueno-Soria, 1999:45 [returned to Leucotrichiini]. — Botosaneanu, 2000:252 [larva, case]. — Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

Byrsopteryx consists of 16 species occurring in southern Central America, South America, and the Lesser Antilles. In the original description, Flint (1981) stated that the general appearance and behavior of living *Byrsopteryx* adults was very similar to adults of *Alisotrichia* and that the 2 genera were probably very closely related, despite the larval body form differing greatly between the 2. Flint (1981) assigned *Byrsopteryx* to Leucotrichiinae based on the basic larval and adult morphology, despite the portable larval case. He stated that the genus did not fit well in the subfamily. *Byrsopteryx* was later transferred to Stactobiinae (Harris and Holzenthal, 1994) and subsequently returned to Leucotrichiinae (Bowles *et al.*, 1999). A description of the larva of *B. mirifica* was provided by Holzenthal and Harris (1991).

Genus *Celaenotrichia* Mosely, 1934

Celaenotrichia Mosely, 1934:158 [Type species: *Celaenotrichia edwardsi* Mosely 1934, original designation]. —Harris and Flint, 1993:101 [redescription, larva, placement]. —Bowles, Harris, and Bueno-Soria, 1999:45 [taxonomic position]. —Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

Celaenotrichia is a monotypic genus recorded from Chile and Argentina. The genus was first placed in Leucotrichiinae by Marshall (1979), transferred to Stactobiinae by Harris and Flint (1993), and then returned to Leucotrichiinae by Bowles *et al.* (1999). Marshall (1979) asserted that characteristic features of the genus include the distinct

structure of the male genitalia and the unmodified antennae and forewings. Larvae were first described by Harris and Flint (1993).

Genus *Cerasmatrichia* Flint, Harris, and Botosaneanu, 1994

Cerasmatrichia Flint, Harris, and Botosaneanu, 1994:360 [Type species: *Cerasmatrichia trinitatis* Flint, Harris, and Botosaneanu 1994, original designation]. —Bowles, Harris, and Bueno-Soria, 1999:46 [taxonomic position]. —Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

Cerasmatrichia consists of 8 species distributed in the Neotropical faunal region from Costa Rica south to Peru, east to Trinidad, and throughout the Lesser Antilles. The genus, once included in *Alisotrichia* as the *dominicensis* species group, was originally placed in Stactobiinae but has since been transferred to Leucotrichiinae (Bowles *et al.*, 1999). Flint *et al.* (1994) mention in the original description that the tarsal formula of *Cerasmatrichia* (1, 3, 4) differs from the rest of *Alisotrichia* in that no members of the latter genus bear a fore-tibial spur. The larvae of *C. spinosa* have been described by Flint *et al.* (1994).

Genus *Ceratotrichia* Flint, 1992

Ceratotrichia Flint, 1992:527 [Type species: *Ceratotrichia fairchildi* Flint 1992, original designation]. —Pes and Hamada, 2004:31 [Larva, pupa]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

The genus *Ceratotrichia* currently contains 3 species recorded from Panama, northern South America, Bolivia, and Brazil. In the original description, Flint (1992) stated that *Ceratotrichia* was most closely related to *Zumatrichia*, in that the 2 genera shared the male reduction of ocelli, a basic wing venation, and the general structure of both male and female genitalia. He also stated that the male secondary sexual modifications were quite different between the 2 genera: the modifications to the antennae occur on different segments, *Ceratotrichia* lacks the deep indentation on the head present in *Zumatrichia*, and *Zumatrichia* lacks the specialized brushes and patches of hairs present on the forewings of *Ceratotrichia*. The larvae of an unidentified species of *Ceratotrichia* were described by Pes and Hamada (2004).

Genus *Costatrichia* Mosely, 1937

Costatrichia Mosely, 1937:166 [Type species: *Costatrichia lodora* Mosely 1937, original designation]. —Flint, 1970:11 [revision]. —Holzenthal and Harris, 1999:540 [revision, key to species]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

The genus *Costatrichia* consists of 12 species distributed from Mexico through Central America and south to southeast South America. Flint (1970) separated *Costatrichia* from *Zumatrichia* based on the presence of 3 ocelli in males and the generally unmodified antennal segments of the former. Marshall (1979) asserted that it

was not possible to satisfactorily define this genus and that some members would key out with other genera. The genus was divided by Holzenthal and Harris (1999) into 2 species groups (*simplex* and *lodora*) based on adult features present on the head, wings, and male genitalia. The larval stage is unknown.

Genus *Eutonella* Müller, 1921

Eutonella Müller, 1921:531 [Type species: *Eutonella peltopsychoides* Müller 1921, monotypic]. —Ulmer, 1957:316 [systematic placement]. —Flint, Holzenthal, and Harris 1999:76 [transferred from Psychomyiidae].

Eutonella is a monotypic genus of uncertain systematic position recorded from South America. Only the figure of a pupal mandible is known for the genus and it could be placed in either Hydroptilidae or Psychomyiidae (Flint *et al.*, 1999b). The mandible lacks teeth or serrations, a state that Müller (1921) concluded was only exhibited by the microcaddisflies, placing it in Hydroptilidae (Flint *et al.*, 1999b). Ulmer (1957) associated the mandible with a series of unnamed cases from Müller's earlier works; the descriptions of the cases led Flint *et al.* (1999b) to place *Eutonella* in Leucotrichiinae.

Genus *Leucotrichia* Mosely, 1934

Leucotrichia Mosely, 1934:157 [Type species: *Leucotrichia melleopicta* Mosely 1934, original designation]. —Flint, 1970:3 [key, revision]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

The genus *Leucotrichia* consists of 30 species, including one fossil species known from Dominican amber. Its distribution includes most of the United States, Central and northern South America, the Greater Antilles, and the southernmost Lesser Antilles. 2 main species groups were outlined by Flint (1970) based on adult features including ocelli number, the presence of head modifications, and the presence of a process or brush of setae on abdominal sternite VII. While the larva of *L. pictipes* was first described as that of *Ithytrichia confusa*, the larvae and cases for many other species have since been described (Lloyd, 1915; Wiggins, 1996).

Genus *Mejicanotrichia* Harris and Holzenthal, 1997

Mejicanotrichia Harris and Holzenthal, 1997:129 [Type species: *Alisotrichia blantoni* Flint 1970, original designation]. —Bueno-Soria and Barba-Alvarez, 1999:122 [key to males]. —Bowles, Harris, and Bueno-Soria, 1999:51 [taxonomic position]. —Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

Mejicanotrichia consists of 7 species occurring in the Neotropical faunal region. The genus was once included in *Alisotrichia* as the *blantoni* species group (Harris and Holzenthal, 1993). The modified male forewings and features of the male genitalia separate *Mejicanotrichia* from the rest of *Alisotrichia* (Harris and Holzenthal, 1997). Wiggins (1996) gave a description of the larvae under the genus *Alisotrichia* (Harris and Holzenthal, 1993).

Genus *Peltopsyche* Müller, 1879

Peltopsyche Müller, 1879:144 [Type species: *Peltopsyche sieboldi* Müller 1879, subsequence selection of Fischer, 1961]. —Ulmer, 1957:172 [bibliography, discussion].

The genus *Peltopsyche* is represented by 2 species recorded from Brazil. In the original descriptions only a few larval features and the basal antennal segments of males are figured. Marshall (1979) commented that, because the general larval morphology is very similar to that of *Zumatrichia* and the case is highly similar to that of *Leucotrichia*, *Peltopsyche* may one day prove to be a senior synonym of one or more of the other leucotrichiine genera.

Genus *Scelobotrichia* Harris and Bueno-Soria, 1993

Scelobotrichia Harris and Bueno-Soria, 1993:75 [Type species: *Scelobotrichia contrerasi* Harris and Bueno-Soria 1993, original designation]. —Bowles, Harris, and Bueno-Soria, 1999:47 [larva, taxonomic position]. —Oláh and Johanson, 2011:142 [placement in *Celaenotrichia* genus cluster].

The genus *Scelobotrichia* contains 3 species occurring in Mexico. The genus was once included in *Alisotrichia* as the *quemada* species group (Harris and Bueno-Soria, 1993). The enlarged basal antennal segment and the unique lobe on the fore-tibia separate

Scelobotrichia from the rest of *Alisotrichia* (Harris and Bueno-Soria, 1993). It was originally placed in Stactobiinae by Harris and Bueno (1993) and was then transferred to Leucotrichiinae by Bowles *et al.* (1999). Descriptions of the larvae of *S. contrerasi* and *S. profunda* were given by Bowles *et al.* (1999).

Genus *Zumatrichia* Mosely, 1937

Zumatrichia Mosely, 1937:187 [Type species: *Zumatrichia filosa* Mosely 1937, original designation]. —Flint, 1970:16 [revision]. —Pes and Hamada, 2004:31 [new records]. —Oláh and Johanson, 2011:152 [placement in *Leucotrichia* genus cluster].

Zumatrichia contains 24 species occurring in Central to northern South America, throughout the Lesser Antilles, and also in Mexico and the United States. Marshall (1979) outlined 4 main species groups (*filosa*, *galtena*, *multisetosa*, and *palmaria*) within the genus based on features of the male genitalia, a modification of the 5 originally outlined by Flint (1970). Larval descriptions have been written for *Z. antilliensis*, *Z. anomalopectera*, *Z. multisetosa*, and *Z. notosa* (Flint, 1968a; Wiggins, 1996).

Subfamily NEOTRICHIIINAE ROSS, 1956

Neotrichiini Ross, 1956:18 [Type genus: *Neotrichia* Morton, 1905].

The subfamily Neotrichiinae contains 4 genera occurring in the Nearctic and Neotropical faunal regions. The name Neotrichiinae, as the tribe Neotrichiini, was first

used by Ross (1956) in a phylogenetic diagram, although a diagnosis was not outlined until Marshall (1979). Notable features are their exceptionally small adult size (generally less than 2 mm), even for microcaddisflies, and larvae possess cylindrical cases and associated limnephiloid-like morphological features, as opposed to the more typical hydroptilid purse-case (Marshall, 1979). Larval descriptions have been provided for all genera.

Genus *Kumanskiella* Harris and Flint, 1992

Kumanskiella Harris and Flint, 1992:581 [Type species: *Kumanskiella karenae* Harris and Flint 1992, original designation].

The genus *Kumanskiella* includes 2 species recorded from Cuba and Puerto Rico. Both the larvae and adults possess features that are intermediate between the genera *Mayatrichia* and *Neotrichia*, but did not fit well within the limits of either previously established genus (Harris and Flint, 1992). Harris and Flint (1992) gave a larval description for the type species, *K. karenae*.

Genus *Mayatrichia* Mosely, 1937

Mayatrichia Mosely, 1937:182 [Type species: *Mayatrichia ayama* Mosely 1937, original designation]. —Ross, 1944:160, 728 [revision]. —Harris and Holzenthal, 1990:453 [revision].

Mayatrichia currently consists of 7 species occurring widely through North and Central America. Diagnostic characteristics of the adults include features of the thorax and male genitalia (Harris and Holzenthal, 1990). Descriptions of the larvae and cases have been given for *M. ayama* (Ross, 1944) and *M. ponta* (Wiggins, 1996).

Genus *Neotrichia* Morton, 1905

Cyllene Chambers, 1873:124 [Type species *Cyllene minutisimella* Chambers 1873, monotypic. Preoccupied several times, *vide* Fischer, 1961].

Neotrichia Morton, 1905: 72 [Type species: *Neotrichia collata* Morton 1905, monotypic]. —Harris and Rasmussen, 2010:25 [key, descriptions of *Neotrichia caxima* group]. —Oláh and Johanson, 2011:168 [species groups reviewed].

Microsiphon Müller, 1921:525 [Type species: no species ever included. Preoccupied by Del Guercio, 1970]. —Flint, Holzenthal, and Harris, 1999:77 [to synonymy].

Exitrichia Mosely, 1937:170 [Type species: *Exitrichia anahua* Mosely 1937, original designation]. —Ross, 1944:154 [to synonymy].

Dolotrichia Mosely, 1937:177 [*Dolotrichia canixa* Mosely 1937, original designation]. —Ross, 1944:154 [to synonymy].

Guerrotrichia Mosely, 1937:179 [Type species: *Guerrotrichia caxima* Mosely 1937, original designation]. —Ross, 1944:154 [to synonymy].

Lorotrichia Mosely, 1937:181 [Type species: *Lorotrichia hiaspa* Mosely 1937, original designation]. —Ross, 1944:154 [to synonymy].

Neotrichia consists of 141 species occurring in North, Central, and South America and the West Indies and is one of the most species-rich hydroptilid groups in the Neotropics (Flint *et al.*, 1999a). Marshall (1979) commented that *Neotrichia* could be divided into groups that correspond roughly to genera that were originally described by Mosely (1937) and subsequently synonymized by Ross (1944). However, the addition of many new species to the genus has since weakened Marshall's diagnosis of the species groups. *Neotrichia* can be separated from other genera in Neotrichiinae by the tibial spur formula (0, 2, 3) and features of the complicated male genitalia. Larvae of *N. minutissimella* were first described by Ross (1944) and many others have been described since (Botosaneanu, 1994; Flint, 1964; Wiggins, 1996).

Genus *Taraxitrichia* Flint and Harris, 1991

Taraxitrichia Flint and Harris, 1991: 441 [Type species: *Taraxitrichia amazonensis* Flint and Harris 1991, original designation]. —Pes and Hamada, 2003:1-7 [larva].

Taraxitrichia is a monotypic genus recorded from Brazil and the territory of Amazonas in Venezuela. When trying to identify the original specimens using Marshalls' (1979) hydroptilid key, Flint and Harris (1991) found that they ended at a couplet that resulted in either *Hydroptila* or *Orthotrichia*, but that the specimens did not fit into either option and instead warranted a new genus. Characters important in diagnosis of the genus include the absence of ocelli, the spur formula (0, 3, 4), and male genitalia sharing similarities with that of *Mayatrichia* (Flint and Harris, 1991). The larvae, described by

Pes and Hamada (2003), live in freshwater sponges.

Subfamily OCHROTRICHIINAE Marshall, 1979

Ochrotrichiini Marshall, 1979:184 [Type genus: *Ochrotrichia* Mosely, 1934].

Ochrotrichiinae is a New World subfamily containing 6 genera that are distributed through North and Central America. Marshall (1979) commented that the group may some day be considered a subgroup of Hydroptilinae, but outlined certain morphological and larval behavioral traits, such as the complex genitalia and the larval detritus-feeding habits, that she considered made it distinct. Larval descriptions have been provided for all genera except *Angrisanoia*.

Genus *Angrisanoia* Özdikmen, 2008

Paratrichia Angrisano, 1995:507 [Type species: *Ochrotrichia (Paratrichia) cebollati*

Angrisano, 1995, monotypic. Originally described as a subgenus of *Ochrotrichia*. — Angrisano, 2002:405 [elevation to genus]. — Angrisano and Sganga, 2009:62 [treated as genus]. — Özdikmen, 2008:615 [preoccupied in Scenopinidae by Kelsey, 1969, replaced with *Angrisanoia*].

Angrisanoia Özdikmen, 2008:615 [Type species: *Ochrotrichia cebollati* Angrisano 1995, original designation]. — Angrisano, 1995:507 [treated as *Paratrichia*, subgenus of *Ochrotrichia*]. — Oláh and Johanson, 2011:235 [redescription].

The genus *Agrisanoia* currently contains 4 species recorded from Argentina, French Guiana, Venezuela, and Uruguay. Angrisano (1995a) originally established it, under the name *Paratrichia*, as a monotypic subgenus of *Ochrotrichia*, but neglected to explicitly state which morphological features were used to define it. Angrisano (2002) later elevated it to generic status, due to the elevation of the other *Ochrotrichia* subgenera, *Metrichia* and *Ochrotrichia*, by Flint and Bueno (1998). The larvae are unknown.

Genus *Metrichia* Ross, 1938

Metrichia Ross, 1938:9 [Type species: *Orthotrichia nigritta* Banks 1907, original designation]. —Flint, 1968:48 [to status of subgenus in *Ochrotrichia*]. —Wiggins, 1996:92 [proposed generic status]. —Flint and Bueno, 1998:489 [elevation to genus, checklist, bibliography]. —Bueno-Soria, 2002:241 [key to males of Mexican species]. —Bueno-Soria and Holzenthal, 2003:174 [diagnosis, key to males of Central American species]. —Angrisano and Sganga, 2005:121 [key to males and larvae of Argentinian species]. —Oláh and Johanson, 2011:203 [redescription].
Argentitrichia Jacquemart, 1963:339 [Type species: *Argentitrichia bulbosa* Jacquemart 1963, monotypic]. —Marshall, 1979:186 [to synonymy].

The genus *Metrichia* consists of 103 species in a Neotropical distribution, recorded from the southwestern United States, throughout Central and South America, and both the Greater and Lesser Antilles. *Metrichia* is most closely related to the genus *Ochrotrichia*, for which it was once considered to be a subgenus (Marshall, 1979). Males

have characteristic dorsolateral setal brushes on abdominal segments V and VI and internal abdominal sacs (Marshall, 1979). Larvae have been associated and described for *M. nigritta* (Edwards and Arnold, 1961; Wiggins, 1996) and *M. juana* (Flint, 1964).

Genus *Nothotrichia* Flint, 1967

Nothotrichia Flint, 1967:56 [Type species: *Nothotrichia illiesi* Flint 1967, original designation]. —Harris and Armitage, 1997:123 [redescription, placement]. —Oláh and Johanson, 2011:203 [redescription]. —Parys and Harris, 2013:590 [larva].

Nothotrichia contains 5 species recorded from California, Chile, Costa Rica, and Brazil. Marshall (1979) was unable to place the genus in a subfamily. Harris and Armitage (1997) added it to Ochrotrichiinae, based upon a suggestion made by Kelley (1992), with the admission that they were still determining synapomorphies. Following the Trichoptera World Checklist (Morse, 2006) Holzenthal *et al.* (2007) listed *Nothotrichia* as a member of Orthotrichiinae. Oláh and Johanson (2011) reversed this placement, indicating that *Nothotrichia* belongs in Ochrotrichiinae and agreeing with Harris and Armitage's (1997) assessment. The first larval description for this genus was recently given for *N. shasta* (Parys and Harris, 2013).

Genus *Ochrotrichia* Mosely, 1934

Polytrichia Sibley, 1926:102 [Type species: *Ithytrichia confusa* Morton 1905, monotypic; preoccupied].

Ochrotrichia Mosely, 1934:162 [Type species: *Ochrotrichia insularis* Mosely, 1934, original designation; although synonymized with *Polytrichia* by Mosely (1937), Ross (1944) recognized *Polytrichia* as preoccupied and resurrected *Ochrotrichia*]. Denning and Blickle, 1972:141 [review]. —Oláh and Johanson, 2011:213 [redescription].

The genus *Ochrotrichia* currently contains 203 species, including 5 fossil species known from Dominican amber. Extant species occur throughout North, Central, and South America. Flint (1972a) attempted to divide the genus into species groups, but as species continued to be added, the group definitions proved too weak to be upheld. *Ochrotrichia* is probably closely related to *Metrichia*, but males of the former often have much more complicated genitalic structures (Marshall, 1979). Larvae have been associated and described for several species (Keiper and Harris, 2002; Roldán-Perez, 1988; Ross, 1944; Wiggins, 1996). The pupae of a species from Costa Rica was recorded as being parasitized by a ceraphronid wasp (Luhman *et al.*, 1999).

Genus *Ragatrichia* Oláh and Johanson, 2011

Ragatrichia Oláh and Johanson, 2011:239 [Type species: *Ragatrichia ragada* Oláh and Johanson 2011, original designation].

The genus *Ragatrichia* includes 5 species recorded from French Guiana and Argentina. The original description placed the genus near *Metrichia* (Oláh and Johanson, 2011). While differences in the form of the male genitalia are used to separate the 2

genera, the presence of a “harpago” on the inferior appendage of *Ragatrichia* male genitalia is unique within Hydroptilidae (Oláh and Johanson, 2011). Larvae have been described for *R. yatay* as *Rhyacopsyche* (Angrisano, 2002).

Genus *Rhyacopsyche* Müller, 1879

Rhyacopsyche Müller, 1879:40 [Type species: nomen nudum]; 1879:143 [Type species: *Rhyacopsyche hagenii* Müller 1879, monotypic]; 1880:121; 1880:72. —Flint, 1971:516 [definition, revision]. —Wasmund and Holzenthal, 2007:1 [revision, key]. —Oláh and Johanson 2011:203 [redescription].

Rhyacopsyche includes 25 species occurring primarily in Central and South America. The genus was originally established for a single Brazilian species described solely on the basis of larval cases and was subsequently named *hagenii* (Müller, 1879b). Description of the adults and larvae were first published by Thienemann (1905). According to Flint’s description of the genus (1971), the larvae of *Rhyacopsyche* are very similar to those of both *Ochrotrichia* and *Hydroptila*, the adults are similar to *Metrichia* and can only be separated using features of the male and female genitalia. Larvae have been described for *R. hagenii* (Thienemann, 1905), *R. mexicana* (Flint, 1971), and *R. mutisi* (Mey and Joost, 1990).

Subfamily ORTHOTRICHINIENAE Nielsen, 1948

Ochrotrichiini Nielsen, 1948:186 [Type genus: *Orthotrichia* Eaton, 1873].

While currently containing 3 genera, the subfamily Orthotrichiinae was originally established for *Orthotrichia* and *Ithytrichia* based on several morphological and behavioral affinities of the larvae (Nielsen, 1948). However, as noted by Marshall (1979), the adults and larvae of each of these 2 genera are very distinct from one another and they may later be found to form distinct groups of their own. Larval descriptions have been provided for all genera.

Genus *Ithytrichia* Eaton, 1873

Ithytrichia Eaton, 1873:139 [Type species: *Ithytrichia lamellaris* Eaton 1873, original designation]. —Ross, 1944:123 [revision of North American species]. —Kachalova in Medvedev, 1998:188 [diagnostic characters of adults]. —Moulton, Harris, and Slusark, 1999:233 [distribution, review of North American species].

The genus *Ithytrichia* consists of 7 species occurring in a primarily Holarctic distribution, but with a single species recorded from northcentral Mexico and another from northwestern Argentina. Similarities shared between the larvae, including features of the mandibles, thoracic sternites, and the fore-coxae, led Nielsen (1948) to conclude that the genera *Ithytrichia* and *Orthotrichia* were closely related. Detailed larval descriptions have been given for *I. lamellata* (Nielsen, 1948) and *I. ferni* (Rueda Martín, 2006), while the North American species were reviewed by Wiggins (1996).

Genus *Orthotrichia* Eaton, 1873

Orthotrichia Eaton, 1873:141 [Type species: *Hydroptila angustella* McLachlan 1865, original designation]. —Ross, 1944:139 [revision of North American species]. —Kingsolver and Ross, 1961:28 [revision of North American species].

Clymene Chambers, 1873:114 [Type species: *Clymene aegerfasciella* Chambers 1873, monotypic]. —Flint, 1966:135 [to synonymy].

Javanotrichia Ulmer, 1951:75 [Type species: *Javanotrichia maeandrica* Ulmer 1951, original designation]. —Marshall, 1979:213 [to synonymy].

Orthotrichiella Ulmer, 1951:79 [Type species: *Orthotrichiella ranauana* Ulmer 1951, original designation]. —Marshall, 1979:213 [to synonymy].

Baliotrichia Ulmer, 1951:88 [Type species: *Baliotrichia litoralis* Ulmer 1951, original designation]. —Marshall, 1979:213 [to synonymy].

The large, cosmopolitan genus *Orthotrichia* consists of 234 species and is particularly species-rich in southeast Asia, Australia, and Africa. Marshall (1979) commented on the characteristic asymmetrical genitalia of the males and divided the genus into 4 species groups (*angustella*, *litoralis*, *costalis*, and *aegerfasciella*), with the possibility of a fifth (*kokodana*). Wells (1992) has observed one species group of *Orthotrichia* occurring within the pupal cases of various hydroptychid species and concluded that the *Orthotrichia* larvae may be preying upon the hydroptychid pupae. Larval descriptions are given for *O. costalis* (1948), *O. angustella* (Jacquemart, 1962), and several others (Ulmer, 1957; Wells, 1985; Wiggins, 1996).

Genus *Saranganotrichia* Ulmer, 1951

Saranganotrichia Ulmer, 1951:58 [Type species: *Saranganotrichia decussata* Ulmer 1951, original designation]. —Marshall 1979:216 [synonymized with *Ithytrichia* Eaton, 1873]. —Malicky, 2009:16 [resurrected from synonymy].

Huayptila Malicky and Chantaramongkol, 2007:1025 [Type species: *Huayptila kaosoidao* Malicky and Chantaramongkol 2007, original designation]. —Malicky, 2009:16 [to synonymy].

Saranganotrichia consists of 4 species recorded from Thailand and Indonesia. The genus was established by Ulmer (1951) based largely on features of the wings, which are no longer considered reliable characters in Hydroptilidae. Based on similarities in the larvae and the cases, the genus was synonymized with *Ithytrichia* by Marshall (1979), who also expressed doubts about the quality of Ulmer's original preparations of larval *Saranganotrichia*. The genus was later resurrected by Malicky (2009), based on a re-examination of the larval material. The larval stage of *S. decussata* was described by Ulmer (1957).

Subfamily STACTOBIINAE Botosaneanu, 1956

Stactobiinae Botosaneanu, 1956:382 [Type genus: *Stactobia* McLachlan, 1880]. Wells, 1990:817 [systematics, new records]. —Bowles, Harris and Bueno-Soria, 1999:43 [larval morphology, systematics]. —Harris, Flint, and Holzenthal, 2002:58 [key to

Neotropical genera]. —Malicky and Chantaramongkol, 2007:1042 [discussion of taxonomic limits].

The subfamily Stactobiinae currently consists of 12 described genera with a Holarctic distribution, although generic diversity may be greatest in southeast Asia (Wells, 1990a). It was originally established for the genus *Stactobia* and other closely related genera, which at the time were not named (Botosaneanu, 1956). Most likely, Botosaneanu intended to include the genera *Stactobiella*, *Plethus*, *Plethotrichia*, and *Lamonganotrichia* (Marshall, 1979). Ulmer (1957) and Schmid (1959a) provided additional comments regarding the relationships between these and other genera (*Chrysotrichia*, *Macrostactobia*, *Madioxyethira*, *Parastactobia*, *Pseudoxyethira*). Flint (1970) subsequently placed *Plethus* and *Lamonganotrichia* in Stactobiinae, based on morphological features of the larvae and their cases.

Subsequent works have re-evaluated the status and composition of Stactobiinae. Marshall (1979) concluded that incorrect interpretations of the spur formula, presence of ocelli, and features of the wing venation had led to errors in original generic diagnoses. The grouping that she presented was instead based on features of the male and female genitalia, head and thoracic structures, and amended ocellar counts and spur formulas. Wells (1990a) also re-evaluated Stactobiinae and remarked on the difficulty of maintaining the group when she had to modify and expand Marshall's (1979) description of the subfamily in order to account for variations in the spur formula and wing venation. In this work, Wells provided a redescription of the subfamily, a modification based on

Marshall's work, that included features of the adult, pupa, and mature larva. Bowles *et al.* (1999) agreed that uniting Stactobiinae was problematic and stated that several of the New World genera in particular shared many similar features with members of Leucotrichiinae. Based on a suite of larval characters they considered to be derived for Leucotrichiinae, Bowles *et al.* transferred several genera to Leucotrichiinae. These authors stated that they could not find any uniquely derived larval characters to unite Stactobiinae. Malicky and Chantaramongkol (2007) briefly commented on the taxonomic limits of Stactobiinae, agreed that the subfamily is difficult and that generic limits were often ambiguous. They did not offer any characters that could be used to define or unite the subfamily. Larval descriptions are available for all genera except *Orinocotrichia* and *Tizatetrichia*.

Genus *Bredinia* Flint, 1968

Bredinia Flint, 1968:50 [Type species: *Bredinia dominicensis* Flint 1968, original designation]. —Harris, Holzenthal, and Flint, 2002:13 [redescription, revision]. —Angrisano, 2002:398 [female, larva].

16 species currently represent the genus *Bredinia*, which occurs in the Lesser Antilles and is restricted in distribution to the Neotropical faunal region. Flint (1968a) considered *Bredinia* to have affinities with several different genera placed outside of Stactobiinae (*Alisotrichia*, *Mayatrichia*, *Neotrichia*), but stated that similarities in the thoracic nota and the male genitalia made the genus most similar to *Stactobiella* (1968a).

Genus *Catoxyethira* Ulmer, 1912

Catoxyethira Ulmer, 1912:82 [Type species: *Catoxyethira fasciata* Ulmer 1912, monotypic].

Sperotrichia Marlier, 1978:294 [Type species: *Sperotrichia mali* Marlier 1978, original designation]. —Marshall, 1979:171 [to synonymy].

Parastactobia Schmid, 1958:48 [Type species: *Parastactobia talakalahena* Schmid 1958, original designation]. —Malicky and Chantaramongkol, 2007:1053 [redescription]. —Oláh and Johanson, 2010:62 [to synonymy].

The genus *Catoxyethira* consists of 66 species occurring mostly in Africa. A single species, *C. prima*, has been recorded from the Philippines and southeast Asia (Mey, 2003). The larva and case of an unidentified species, later placed in *Catoxyethira*, were described by Ulmer (1912b). Several structural similarities occurring in the spur formula and male genitalia are present in adults of *Catoxyethira* and *Stactobiella*, as noted by Morse (1974). Marshall (1979) also concluded that the genus belonged in the *Stactobiella*-group of Stactobiinae, based on features of the adult head and thorax.

Genus *Chrysotrichia* Schmid, 1958

Chrysotrichia Schmid, 1958:54 [Type species: *Chrysotrichia hatnagola* Schmid 1958, original designation]. —Wells, 1990:367 [larva].

Chrysotrichia currently consists of 61 species, occurring in south and southeast Asia. Schmid (1958b) concluded that the genus was most closely related to *Plethus*, due to similarities between the male genitalia, while Marshall (1979) stated that it was also very similar to the *ulmeri*-group of *Stactobiella*, based on features of the adult head and thorax and the male genitalia. The final instar larva of *C. berduri* has been described by Wells (1990b).

Genus *Flintiella* Angrisano, 1995

Flintiella Angrisano, 1995:502 [Type species: *Flintiella andreae* Angrisano 1995, original designation]. —Harris, Flint, and Holzenthal, 2002 [key to males].

The genus *Flintiella* is represented by 12 species occurring in the Neotropical faunal region. The female, larva, and case of *F. andreae* were described by Angrisano (1995a). Angrisano (1995a) established the genus based on the lack of ocelli and a tarsal formula (0, 2, 3) that was unique within the tribe to the Americas. Members of *Flintiella* are also similar in appearance to those of *Stactobiella*, differing mainly in genitalic features and the lack of ocelli (Flint *et al.*, 1999a).

Genus *Maetalaiptila* Malicky and Chantaramongkol, 2007

Maetalaiptila Malicky and Chantaramongkol, 2007:1055 [Type species: *Maetalaiptila pyramus* Malicky and Chantaramongkol 2007, original designation].

Maetalaiptila contains a single species occurring in Thailand. Malicky and Chantaramongkol (2007) established the genus based on features of the male genitalia and placed it in Stactobiinae because of the presence of the transverse suture on the mesoscutellum. The female and larva are unknown.

Genus *Niuginitrichia* Wells, 1990

Niuginitrichia Wells, 1990:820 [Type species: *Niuginitrichia bukamak* Wells 1990, original designation]. —Wells and Huisman, 2001:208 [new records].

The genus *Niuginitrichia* consists of 14 species occurring in Indonesia and New Guinea. Female, larva, pupa, and case were described by Wells (1990a). Wells (1990a) also noted that there were many similarities between *Niuginitrichia* and *Plethus*, but that the former could be clearly separated by the absence of ocelli and differences in the male genitalia.

Genus *Orientalitrichia* Koçak and Kemal, 2012

Scelotrichia Ulmer, 1951:73 [Type species: *Scelotrichia saranganica* Ulmer, 1951, original designation]. — Koçak and Kemal, 2012:4 [preoccupied in Hemiptera by Reuter, 1890:291, replaced with *Orientalitrichia*].

Madioxyethira Schmid, 1960:89 [Type species: *Madioxyethira milinda* Schmid 1960, original designation]. —Marshall, 1979:173 [diagnosis]. —Wells, 1990:373 [to synonymy with *Scelotrichia*].

Pseudoxyethira Schmid, 1958:44 [Type species: *Pseudoxyethira asgiriskanda* Schmid 1958, original designation]. —Wells, 1990:373 [to synonymy with *Scelotrichia*].
Orientalitrichia Koçak and Kemal, 2012:4 [Type species: *Scelotrichia saranganica* Ulmer, 1951, replacement name].

The genus *Orientalitrichia* is represented by 59 species occurring mainly in southeast Asia. A single species, *O. glandulosa*, has been recorded from Tanzania (Wells and Andersen, 1995). Marshall (1979) stated that the genus belonged in Stactobiinae due to the postoccipital lobes of the adult head, which were very similar to those of *Madioxyethira*, and the presence of the transverse suture on the adult thorax. Wells described the general form of the larval, pupa, and case of the genus (1990b).

Genus *Orinocotrichia* Harris, Flint, and Holzenthal, 2002

Orinocotrichia Harris, Flint, and Holzenthal, 2002:50 [Type species: *Orinocotrichia calcariga* Harris, Flint, and Holzenthal 2002, original designation].

Orinocotrichia is represented by 2 species, one occurring in Venezuela and the other in French Guiana. The larva is unknown. Based on similarities occurring in the adult head and the male and female genitalia, the genus is most closely related to *Flintiella* (Harris *et al.*, 2002b).

Genus *Plethus* Hagen, 1887

Plethus Hagen, 1887:643 [Type species: *Hydroptila cursitans* Hagen, monotypic].

Plethotrichia Ulmer, 1951:65 [Type species: *Plethotrichia baliana* Ulmer 1951, original designation]. —Marshall, 1979:168 [to synonymy].

27 species are currently included in the genus *Plethus*, occurring in south and southeast Asia. Ulmer (1957) provided larval descriptions of both *P. acutus* and *P. cruciatus*. Marshall (1979) considered *Plethus* to be most closely related to *Stactobia* and stated that it can be distinguished from *Stactobia* by its overall smaller size, less specialized genitalia, and larvae.

Genus *Stactobia* McLachlan, 1880

Stactobia McLachlan, 1880:505 [Type species: *Hydroptila fuscicornis* Schneider 1845, subsequent designation by Mosely 1933:162]. —Tobias, 1999:49 [distributional records, larval abundance]. —Malicky and Chantaramongkol, 2007:1042 [diagnostic characters of adults].

Afritrichia Mosely, 1939:35 [Type species: *Afritrichia aurea* Mosely 1939, original designation]. —Schmid, 1959:56 [to synonymy].

Aratrichia Mosely, 1948:76 [Type species: *Aratrichia fahjia* Mosely 1948, original designation]. —Schmid, 1959:51 [to synonymy].

Lamonganotrichia Ulmer, 1951:68 [Type species: *Lamonganotrichia crassa* Ulmer 1951, original designation]. —Marshall, 1979:165 [to synonymy].

The genus *Stactobia* presently consists of 145 species and occurs in southeast Asia, Africa, and in a general Palaearctic distribution. While *Stactobia* is one of the more successful hydroptilid genera in terms of species and abundance of individuals, it does not exhibit the success of broad geographical range present in other genera, such as *Hydroptila* or *Oxyethira* (Marshall, 1979). Vaillant (1956) provided the greatest contribution of knowledge of the biology of the genus, while Danecker (1961) gave a detailed life history. Marshall (1979) hypothesized that its complete absence from the Neotropical faunal region may be attributable to 2 potential factors: the typical slow rate of dispersal of montane-stream dwellers compared with the faster rate of dispersal of lowland vegetation dwellers and competition with the members of the highly successful subfamily Leucotrichiinae. The 6 species groups (*furcata*, *martynovi*, *nielsenii*, *vaillanti*, *bolzei*, and *japonica*) outlined by Marshall (1979) followed those of Schmid (1959a) and Jacquemart (1973). The macicolous larvae, unique within Hydroptilidae, live in thin sheets of water situated close to running-water habitats and can be found on rock surfaces near streams and (the sometimes nearly vertical) faces of waterfalls (Hynes, 1970; Marshall, 1979). Larval adaptations, required by the habitat, include dorso-ventral flattening, heavily sclerotized and fused tergites, and short, robust legs used for clinging (Marshall, 1979).

Genus *Stactobiella* Martynov, 1924

Stactobiella Martynov, 1924:57 [Type species: *Stactobia ulmeri* Siltala 1908, monotypic].

Tascobia Ross, 1944:124 [Type species *Stactobia palmata* Ross 1944, original designation]. —Ross, 1948:202 [to synonymy].

The genus *Stactobiella* is presently represented by 13 species, exhibiting a Holarctic distribution. Discussion of the larva of *S. palmata* has been provided by Ross (1944) and Wiggins (1996). Marshall (1979) concluded, based on the unspecialized larvae and basic hydroptilid form, that *Stactobiella* was a primitive member of Stactobiinae and, based on adult features, that it was most closely related to *Plethus* and *Stactobia*. The 3 species groups recognized by Marshall (*biramosa*, *brustia*, and *ulmeri*) followed those of Ross (1948) and were based on features of the male genitalia.

Genus *Tizatetrichia* Harris, Flint, and Holzenthal, 2002

Tizatetrichia Harris, Flint, and Holzenthal, 2002:55 [Type species: *Tizatetrichia costaricensis* Harris, Flint, and Holzenthal 2002, original designation].

Tizatetrichia contains a single species occurring in northwestern Costa Rica. The female and larva are unknown. Based on similarities occurring in the male genitalia, the genus is most closely related to *Bredinia* (Harris *et al.*, 2002b).

INCERTAE SEDIS

Genus *Burminoptila* Botosaneanu, 1981 †

Burminoptila Botosaneanu, 1981:75 [Type species: *Burminoptila bemeneha*

†Botosaneanu 1981, original designation].

The genus *Burminoptila* is represented by a single fossil species known from Burmese amber. No further information regarding diagnostic features or placement of the genus within Hydroptilidae was provided.

Genus *Caledonotrichia* Sykora, 1967

Caledonotrichia Sykora, 1967:585 [Type species: *Caledonotrichia illiesi* Sykora 1967, original designation]. Wells, 1995:229 [larva]. —Harris and Armitage, 1997:123 [placement]. —Holzenthall, Blahnik, Prather, and Kjer 2007:671 [placement]. —Oláh and Johanson, 2011:203 [diagnosis].

Caledonotrichia consists of 5 species occurring in New Caledonia. The male genitalia of this genus are noted as both very distinctive within Hydroptilidae and very difficult to homologize with those of other hydroptilid genera (Marshall, 1979; Sykora, 1967). Marshall (1979) stated that neither the adult nor the larval stage offered any clues regarding placement of the group within Hydroptilidae and left the genus *incertae sedis*. Harris and Armitage (1997) placed it in Ochrotrichiinae. The genus was subsequently returned to *incertae sedis* (Morse, 2006; Holzenthall *et al.* 2007). Oláh and Johanson (2011) indicated, without explanation, that *Caledonotrichia* may belong in the Ochrotrichiinae. Larval illustrations of *C. minor*, *C. illiesi*, and *C. sp.* are all found in Wells (1995).

Genus *Dibusa* Ross, 1939

Dibusa Ross, 1939:66 [Type species: *Dibusa angata* Ross 1939, original designation]. — Wiggins, 1977 [larva]. — Resh and Houp, 1986:30 [life history]. — Oláh and Johanson, 2011:203 [diagnosis].

The monotypic genus *Dibusa* occurs in the United States, recorded from Arkansas, Kentucky, North Carolina, Oklahoma, and Tennessee. Marshall (1979) did not place the genus in any of the established hydroptilid subfamilies, but she did comment on the unique form of the male genitalia and made note of similarities between *Dibusa* and the genera *Agraylea* and *Nothotrichia*. Oláh and Johanson (2011) indicated that *Dibusa* may belong in the Ochrotrichiinae. The larva was first described by Wiggins (1977) and a detailed life history and description of the larval association with the red alga *Lemanea australis* were given by Resh and Houp (1986).

Genus *Dicaminus* Müller, 1879

Dicaminus Müller, 1879:39 [Type species: *Diaulus ladislavii* Müller 1879, subsequently monotypic]. — Ulmer, 1957:172 [references].

Diaulus Müller 1879:142 [Type species: *Diaulus ladislavii* Müller 1879, monotypic]. — Ulmer, 1957:173 [to synonymy].

Dicaminus consists of a single species occurring in South America. Müller (1879a)

described several atypical larval cases with small dorsal chimneys under the generic name *Dicaminus*. The material was from Brazil, but neither a larval description nor a specific epithet was provided. He then subsequently made reference to these same cases under the name *Diaulus ladislavii* (Müller, 1879b). *Diaulus* was later synonymized with *Dicaminus* (Ulmer, 1957). A number of cases with dorsal chimneys have been found in material from Argentina, Bolivia, Ecuador, Panama, and Venezuela (Botosaneanu and Flint, 1982). Some of these contain male metamorphotypes of *Metrichia* spp., which suggests that *Dicaminus* may prove to be either synonymous with or closely related to *Metrichia* (Flint *et al.*, 1999a). Neither the adult or the larval stage has been described.

Genus *Electrotrichia* Ulmer, 1912 †

Electrotrichia Ulmer, 1912:42 [Type species: *Electrotrichia subtilis* † Ulmer 1912, monotypic].

The genus *Electrotrichia* is represented by a single fossil species known from Baltic amber. Marshall (1979) stated that the genus may share similarities with members of the Hydroptilinae in the wing shape and spur formula.

Genus *Macrostactobia* Schmid, 1958

Macrostactobia Schmid, 1958:46 [Type species: *Macrostactobia elawalikanda* Schmid 1958, original designation]. —Wells and Huisman, 1992:93 [larva].

Macrostactobia consists of 2 species recorded from Sri Lanka and West Malaysia. Schmid (1958b) stated that, due to its relatively larger size and complete wing venation, the genus was somewhat primitive. He placed it in a branch of Stactobiinae that also included the genera *Parastactobia*, *Plethus*, and *Chrysotrichia*. Marshall (1979) noted that the male genitalia were unique and that the antennae were typical of Stactobiinae, but declined to place the genus and left it *incertae sedis*. The larva for *M. runcing* was described by Wells and Huisman (1992).

Genus *Maydenoptila* Neboiss, 1977

Maydenoptila Neboiss, 1977:44 [Type species: *Maydenoptila cuneola* Neboiss 1977, original designation]. —Wells, 1985:22 [larva]. —Wells, 1997:9 [checklist of Australian species, key to larvae]. —Harris and Armitage, 1997:123 [placement]. —Holzenthall, Blahnik, Prather, and Kjer, 2007:671 [placement]. —Oláh and Johanson, 2011:203 [diagnosis].

The genus *Maydenoptila* consists of 8 species occurring in Australia and the island of Tasmania. Placed in the subfamily Ochrotrichiinae by Harris and Armitage (1997), it was placed as *incertae sedis* by Holzenthall *et al* (2007). Oláh and Johanson (2011) indicated, without explanation, that *Maydenoptila* may belong in Ochrotrichiinae but did not formally transfer it to the subfamily. Descriptions of the larval stage of *M. rupina*, *M. baynesi*, *M. cuneola*, and *M. pseudorupina* were given by Wells (1985).

Genus *Novajerseya* Botosaneanu, Johnson, and Dillon, 1998 †

Novajerseya Botosaneanu, Johnson, and Dillon, 1998:225 [Type species: *Novajerseya glesumica* Botosaneanu, Johnson, and Dillon 1998, original designation].

The genus *Novajerseya* is represented by a single fossil species known from Upper Cretaceous amber found in New Jersey. No further information regarding diagnostic features or placement of the genus within Hydroptilidae was provided.

Genus *Orphninostrichia* Mosely, 1934

Orphninostrichia Mosely, 1934:138 [Type species: *Orphninostrichia maculata* Mosely 1934, original designation]. —Wells, 1985:19 [larva]. —Wells, 1997:1-28 [checklist of Australian species, key to larvae]. —Wells, 1999:221 [new species, zoogeography, new records]. Wells, 2002:221 [key for males]. —Wells, 2010:48 [redescription].

The genus *Orphninostrichia* consists of 20 species occurring in Australia. The genus was established on the basis of unique wing venation and unique male genitalia (Mosely, 1934). Marshall (1979) left the genus as *incertae sedis*, but did comment on possible affinities with Hydroptilinae and noted ways in which *Orphninostrichia* differed from the genera *Hydroptila* and *Oxyethira*. Wells (1987) also considered the genus to belong to Hydroptilinae. Holzenthal *et al.* (2007) treated the genus as *incertae sedis*. The larvae of *O. maculata* was described by Wells (1985).

Family PTILOCOLEPIDAE Martynov, 1913

Palaeagapetinae Ross, 1956:18 [Type genus: *Palaeagapetus* Ulmer 1912, as

Paleagapetus].

Ptilocolepinae Martynov, 1913:22 [Type genus: *Ptilocolepus* Kolenati 1848]. —Ito, 1998:85 [world distribution, biology, recent and fossil taxa]. —Malicky, 2001:20 [elevated from subfamily of Hydroptilidae]. —Malicky, 2005:542 [confirmed as distinct]. —Malicky, 2008:43 [family status discussed with respect to work of Thienemann, 1904].

The family Ptilocolepidae contains 2 small genera known to occur in a Holarctic distribution. The adults bear a resemblance to some of the smaller members of the caddisfly family Glossosomatidae, while the larval stage indicates an affinity with Hydroptilidae. Males bear highly specialized male genitalia that are characteristic of the group (Marshall, 1979). The larvae of both genera can be found in small montane springs on vegetation, stones, or other submerged surfaces and are often found in association with bryophytes (Ito, 1998).

Genus *Palaeagapetus* Ulmer, 1912

Palaeagapetus Ulmer, 1912:35 [Type species: *Palaeagapetus rotundatus* Ulmer 1912, monotypic].

11 species of *Palaeagapetus*, including 2 fossil species, occur in a mostly East

Palaearctic distribution, with a few distributed across the Nearctic faunal region. Characters that unite the genus can be found in features of the wing venation, spur formula, and the male genitalia (Marshall, 1979) The larvae of *P. celsus* were described by Flint (1962).

Genus *Ptilocolepus* Kolenati, 1848

Ptilocolepus Kolenati, 1848:102 [Type species: *Ptilocolepus turbidus* Kolenati 1848, monotypic]. —Fischer, 1961:80 [*P. turbidus* synonymized with *Rhyacophila granulatus* Pictet, 1834]. —Malicky, 2001:20 [taxonomic notes].

This genus contains 7 species recorded in a Palaearctic distribution and, at different times, has been placed in the families Rhyacophilidae, Hydroptilidae, and Glossosomatidae (Malicky, 1983; Martynov, 1913a; Pictet, 1834; Ulmer, 1907). Features used to identify members of *Ptilocolepus* include wing venation and the general structure of the male genitalia (Marshall, 1979). The larvae of *P. granulatus* have been described by Thienemann (1904) and Jacquemart and Coineau (1962).

MATERIALS AND METHODS

Selection of Taxa

The taxa included in this study were chosen in to represent the overall taxonomic

diversity of the family Hydroptilidae by including examples of all subfamilies and as many extant genera as possible. A list of the specimens from which DNA was sequenced for this study is presented in Table 1.

Ingroup. The ingroup, Hydroptilidae and Ptilocolepidae, included 90 species representing a total of 31 genera. Representatives from both ptilocolepid genera and all 6 traditionally recognized hydroptilid subfamilies were included as ingroup taxa. As many genera from each subfamily were obtained as possible and all taxa from which DNA was successfully sequenced and amplified were included in the dataset. 9 of the 26 genera of Hydroptilinae, 11 of the 17 genera of Leucotrichiinae, 2 of the 4 genera of Neotrichiinae, 3 of the 6 genera of Ochrotrichiinae, 2 of the 3 genera of Orthotrichiinae, 2 of the 12 genera of Stactobiinae, 2 of the 9 *incertae sedis* genera of Hydroptilidae, and both of the genera of Ptilocolepidae were included. Large genera, such as *Hydroptila* and *Oxyethira*, were sampled more extensively to account for high species richness.

Outgroup. The outgroup consisted of 14 species including members from the families Glossosomatidae, Hydrobiosidae, and Rhyacophilidae. These families represent the families traditionally included in “Spicipalpia,” along with Hydroptilidae and Ptilocolepidae (Malm *et al.*, 2013).

Depositories

Specimens sequenced for this study were obtained from the National Museum of Natural History, Washington, DC, USA (NMNH); University of Minnesota Insect Collection, St. Paul, MN, USA (UMSP), Clemson University Arthropod Collection,

Clemson, SC, USA (CUAC); Entomology Collection, Museum Victoria, Melbourne, Victoria, Australia (MVMA); Zoological Museum, University of Bergen, Bergen, Norway (ZMUB); and Departamento de Zoología y Antropología Física, Universidad de Santiago de Compostela, Santiago de Compostela, Spain (USDC). Additionally, Dave Ruitter (Grants Pass, OR), Alice Wells, (Australian Biological Resources Study, Canberra, ACT, Australia), and Tomiko Ito, (Hokkaido Aquatic Biology, Hokkaido, Japan) generously donated several specimens from their private collections to UMSP. This specimen data set was supplemented with additional sequences obtained from Dr. Karl Kjer's on-going research in caddisfly systematics at Rutgers, the State University of New Jersey, New Brunswick, NJ, USA (RUIC). Voucher materials from specimens that were successfully sequenced are deposited at the National Museum of Natural History, Washington, DC, USA (NMNH); University of Minnesota Insect Collection, St. Paul, MN, USA (UMSP), Clemson University Arthropod Collection, Clemson, SC, USA (CUAC); Zoological Museum, University of Bergen, Bergen, Norway (ZMUB); and Departamento de Zoología y Antropología Física, Universidad de Santiago de Compostela, Santiago de Compostela, Spain (USDC). DNA aliquots from these species are currently being stored frozen at RUIC and UMSP. All specimens from which DNA was sequenced for this study were affixed with a barcode label (4 mil polyester, 8 x 14 mm, code 49) bearing a unique alphanumeric sequence beginning with the prefix UMSP. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection and to provide unique identification of specimens. Specimen-level taxonomic,

locality, and other information, are stored in the University of Minnesota Insect Collection Biota Trichoptera Database using the open-source software Biota v. 3.0 (Colwell, 2012).

DNA Sequences

Gene choice

The usefulness of a specific gene for any given level of relationships within a phylogeny is dependent in part on its rate of evolution. Genes that both minimize the frequency of multiple nucleotide substitutions and also maximize the occurrence of non-homoplasious shared character states are preferred (Simon *et al.*, 1994). Nucleotide positions are less likely to differ in more closely related species, making genes with higher proportions of unconstrained sites more appropriate when studying closely related taxa (Simon *et al.*, 1994).

For this study, I chose to use a fragment of the mitochondrial cytochrome oxidase I gene (COI), also known as the “barcode gene,” and the first, second, and third variable regions of the large subunit nuclear ribosomal RNA (D1-3 subregions of the 28SrRNA). I originally intended to also include a fragment of nuclear DNA (CAD), but was unable to successfully amplify the targeted gene sequence. Despite optimization attempts involving various magnesium concentrations, reagents added to the Accuzyme Mix (see “DNA extraction, amplifying, and sequencing” section below), different primers modified from Johanson and Malm (2010), and a variety of temperatures, times, and cycles during PCR,

successful amplification of CAD never occurred for any specimens, regardless of age or preservation method.

Mitochondrial DNA. Mitochondrial genes evolve relatively rapidly, making them a more appropriate gene choice for phylogenetic studies of taxa that are closely related (Simon *et al.*, 2006). COI has proven useful for a variety of studies involving closely related species; it has been used to reveal cryptic species diversity or to assign previously unidentified specimens to a species (Ball *et al.*, 2005; Hebert *et al.*, 2003; Hebert *et al.*, 2004), to assign species to genera (Hebert *et al.*, 2003), and to resolve phylogenetic relationships among genera (Nyman *et al.*, 2006). In a study analyzing the higher-level phylogeny of Trichoptera, COI was found to be useful for resolving relationships among the taxa at the “tips,” or external nodes representing descendent species, of the tree (Kjer *et al.*, 2001, 2002).

There are also several practical reasons for using COI in a phylogenetic analysis. COI, as a mitochondrial gene, is maternally inherited and, therefore, very infrequently affected by recombination and paralogy (Hebert *et al.*, 2003; Simon *et al.*, 2006). Mitochondrial genes are also easily amplified using traditional polymerase chain reaction (PCR) methods (Zhou *et al.*, 2007) and their sequences are easy to align because they are protein coding and are affected by few insertions or deletions (Hebert *et al.*, 2003). Additionally, primers for the COI fragment have been developed specifically for Trichoptera by Kjer *et al.* (2001). For these reasons, COI was an appropriate gene choice for aid in resolving the relationships at the tips of the hydroptilid phylogeny.

Ribosomal RNA. Ribosomal RNA (rRNA) sequences are fundamental parts of the

ribosome that are folded into defined structures responsible for essential biological functions, such as protein synthesis (Noller *et al.*, 1992). This secondary structure is more highly conserved than the sequence of nucleotides (Fox and Woese, 1975; Gutell *et al.*, 1994; Kjer, 1995) and sequence variations that contribute to differences between species may also play a role in maintaining the RNA secondary structure (Smit *et al.*, 2007). rRNA is of ancient origin, dating back to the earliest forms of life, and occurs in all known extant species; it is commonly used in phylogenetic studies and to establish evolutionary relationships between taxa (Pace, 1997; Smit *et al.*, 2007). rRNA sequences evolve more slowly than mitochondrial genes, making them an appropriate gene choice to help resolve deeper levels of the hydroptilid phylogeny. Additionally, primers for the D1-3 fragments have been developed specifically for Trichoptera by Kjer *et al.* (2001) and Zhou *et al.* (2007). For these reasons, the D1-3 fragments were an appropriate choice to aid in resolving the relationships at the deeper levels of the hydroptilid phylogeny.

DNA extraction, amplifying, and sequencing

DNA was extracted from pinned or 95% ethanol-preserved museum specimens. In cases of ethanol-preserved specimens, attempts were made to use the most recently collected specimens available. Due to the physically minute size of individual specimens, the head, thorax and legs were all taken for extraction purposes. In all cases, genitalia were retained as specimen voucher material and the specimen data were entered into the University of Minnesota Insect Collection (UMSP) Biota Trichoptera Database. Genitalia were prepared for preservation following the lactic acid method, procedures for which are

explained in detail by Blahnik *et al.* (2007). DNA was extracted and sequenced in either the laboratory of Dr. Karl Kjer, Rutgers University, or of Dr. Susan Weller, University of Minnesota. DNA was extracted using the DNEasy Blood and Tissue Kit (Qiagen, Inc.) with 20 µl of Proteinase K (Qiagen, Inc.). Targeted gene sequences were then amplified using polymerase chain reaction (PCR) with Accuzyme Mix (Bioline) and the primers listed in Table 2. An additional 0.25 µl of magnesium per specimen was utilized when amplifying the mitochondrial DNA (COI). The PCR mix underwent the time and temperature cycles listed, with the different annealing temperatures for each targeted gene sequence as stated in Table 3. PCR products were cleaned and purified with either the QIAquick PCR Purification Kit (Qiagen, Inc.) or ExoSAP-IT (Affymetrix, Inc.). DNA concentrations were estimated by UV visualization of SYBR Safe (Invitrogen, Life Technologies) stained 1% agarose gel with Tris-borate-EDTA (TBE) electrophoresis buffer using standard techniques. Sequences were visualized and recorded using the Applied Biosystems (ABI) 3730xl Sequencer at the University of Minnesota Genomics center. Each DNA fragment was sequenced from both directions.

Sequence alignment

Forward and reverse sequence fragments were edited and aligned in the program Geneious (Geneious Pro, ver. 5.6.3, created by Biomatters). Consensus sequences for mitochondrial DNA (COI) were aligned using translation alignment in Geneious, while consensus sequences for ribosomal RNA (D1-3) were aligned using the MUSCLE alignment. Gaps and ambiguous sequences were coded as missing (-). Nucleotides were

treated as unordered characters with 4 alternative states.

Phylogenetic analysis

Data partitions

The complete dataset included 101 taxa; it was a concatenation of the COI, D1, D2, and D3 fragments and consisted of 2380 characters in total. The concatenated dataset was analyzed with 6 data partitions: COI codons 1, 2, and 3 and rRNA fragments D1, D2, and D3.

As is typical, 100% of the gene fragments chosen for this study were not successfully sequenced for every species in the dataset. Although it was not possible to include data from every gene for every species, representation was adequate for all major clades. In a few situations, genera were represented by only a few species between which the recovered gene sequences did not overlap (ex: COI and D2 for *Species 1*, D1 and D3 for *Species 2*). In these instances, voucher material from the individual specimens was examined and identification was re-confirmed before combining the non-overlapping sequences as a single taxon.

Analyses

Maximum likelihood. Maximum likelihood analyses were implemented in the program RAxML. Analysis utilized a general time reversible (GTR) model with a gamma-distributed rate of heterogeneity and an ML estimated alpha-parameter (Gu et al.,

1995; Yang, 1993, 1994a, 1994b). All free model parameters were estimated by RAxML; nucleotide frequencies were estimated from the data. 100 rapid bootstrap inferences were run, followed by a thorough maximum likelihood search for the best-scoring tree.

Analyses using RAxML were carried out on the RAxML BlackBox interface (Stamatakis et al., 2008), which can be accessed at <http://embnet.vital-it.ch/raxml-bb/>.

Bayesian. Bayesian analyses were implemented in the program MrBayes 3.1.2 (Huelsenbeck, 2000; Huelsenbeck and Ronquist, 2001) using Metropolis Coupled Markov Chain Monte Carlo sampling (MCMCMC) to explore possible tree topologies and parameter space in proportion to posterior probabilities (Lewis, 2001; Ronquist et al., 2005). Analysis utilized a GTR model with a gamma-distributed rate of heterogeneity, an estimated proportion of invariable sites, and a Dirichlet prior probability density. Under the Metropolis algorithm, chains are used to explore probability peaks; a “cold”(Felsenstein, 2004) chain that becomes caught on an isolated low probability peak may be able to escape by swapping locations with a “heated” chain on a higher probability peak (Lewis, 2001; Ronquist et al., 2005). For each analysis, 2 runs of 4 chains each (3 “heated,” 1 “cold”) were implemented for 20,000,000 generations, with chains being sampled every 1000th generation. Analyses using MrBayes were carried out on the CIPRES Science Gateway web interface (Miller et al., 2010), which can be accessed at <http://www.phylo.org/portal2/login!input.action>.

RESULTS

Results of phylogenetic analyses

Figures 2-10 display the phylogeny resulting from the procedures described above; the topology presented indicates nodes where there is agreement between the analyses run on RAxML and MrBayes. In 2 instances in which nodes were not in complete agreement regarding topology, that particular node was collapsed (see *Oxyethira* and *Byrsopteryx* in Figures 3 and 7).

Maximum likelihood. Bootstrap (BS) values are indicated below nodes, BS values of 80% or higher are subjectively considered supported, following Kjer *et al* (2002). BS values < 50 are subjectively considered unsupported and represented in Figure 2 by a dash (—).

Bayesian. Chain swapping was determined to be successful upon examination of the log and mcmc files. Trees that had not yet reached the likelihood plateau (5,000) were discarded as burn-in and the remainder were used to calculate posterior probabilities. Posterior probability (PP) values are indicated above nodes. Clades with PP values ≥ 0.95 are considered supported, following Holzenthal *et al.* (2007).

Summary of analyses

Ptilocolepidae

A monophyletic Ptilocolepidae was not recovered; *Ptilocolepus* was recovered as paraphyletic with Hydroptilidae in both analyses, though neither had strong nodal support

(PP: 0.827, BS: <50) (Fig 2). *Palaeagapetus* was also recovered as paraphyletic with *Ptilocolepus* + Hydroptilidae in both analyses, though, again, neither had strong nodal support (PP: 0.871, BS: 62).

Hydroptilidae

A monophyletic Hydroptilidae was recovered in both analyses but did not have strong bootstrap support (PP: 0.938, BS: 70) (Fig. 2).

Hydroptilinae: the subfamily Hydroptilinae was not recovered as a single monophyletic clade, but both analyses recovered the same topology regarding Hydroptilinae genera (see Figure 2 for indication of placement of Hydroptilinae nodes 1 and 2). *Microptila orienthula* was recovered as sister to *Orthotrichia cristata* + Neotrichiinae, but with no support from either analysis (PP: 0.567, BS: <50) (Figs. 2, 9). *Ugandatrichia* was recovered as sister to *Ithytrichia lamellaris* + Hydroptilinae node 1, but was not supported (PP: 0.833, BS: <50) (Figs. 2, 3). Hydroptilinae node 1 included the traditionally recognized hydroptiline genera *Agraylea*, *Hellyethira*, *Oxyethira*, and *Paroxyethira* and was well supported by the Bayesian analyses (PP: 0.953, BS: <50). It also included the taxa *Orphninostrichia squamosa*, placed in close relation to *Paroxyethira*. The genera *Agraylea* (PP: 0.997, BS: 87) and *Oxyethira* (PP: 0.96, BS: 72) in this clade were each well supported by the Bayesian analyses. Hydroptilinae node 2 recovered *Allotrichia pallicornis* as sister to the genus *Hydroptila*, but is not well supported (PP: 0.81, BS: <50) (Figs. 2, 4). The monophyly of *Hydroptila* was recovered with good support from both analyses (PP: 1.0, BS: 98).

Leucotrichiinae: the genera *Alisotrichia* and *Cerasmatrichia* were recovered, not with the rest of the currently recognized leucotrichiine genera, but as a separate clade with no support (PP: 0.532, BS: <50) (Figs. 2, 6). Additionally, the genus *Byrsopteryx* was also recovered separated from the subfamily Leucotrichiinae. *Byrsopteryx* was recovered as a monophyletic unit of its own with strong support from both analyses (PP: 1.0, BS: 96) (Figs. 2, 7). The monophyly of the rest of the leucotrichiine genera represented in this study were recovered with good support from both analyses (PP: 1.0, BS: 92) (Figs. 2, 5). Generally, within the leucotrichiine clade, genera were either represented by a single taxon or their monophyly was not recovered.

Ochrotrichiinae: the monophyly of the subfamily Ochrotrichiinae was recovered by both analyses, though not with good support (PP: 0.867, BS: <50) (Figs. 2, 8).

Orthotrichiinae: the monophyly of the subfamily Orthotrichiinae was not recovered by either analysis in this study. *Ithytrichia lamellaris* was recovered as sister to the clade descending from Hydroptilinae node 1, though with no support (PP: 0.808, BS: <50) (Figs. 2, 3). *Orthotrichia cristata* was recovered as sister to the subfamily Neotrichiinae, also with no support (PP: 0.676, BS: <50) (Figs. 2, 9).

Neotrichiinae: the monophyly of the subfamily Neotrichiinae was recovered, but with no support (PP: 0.662, BS: 51). Monophyly was recovered for the genus *Mayatrichia* with good support (PP: 0.997, BS: 95) and for the genus *Neotrichia* with no support (PP: 0.561, BS: 83) (Figs. 2, 9).

Stactobiinae: the monophyly of the stactobiine genera (*Stactobia*, *Stactobiella*) was recovered with strong support (PP: 0.995, BS: 95) (Figs. 2, 10).

Incertae sedis: 2 taxa representing genera previously considered *incertae sedis* were included in this study. The monotypic genus *Dibusa* was recovered at the base of the hydroptilid clade as sister to all other hydroptilid genera included in this study with good support from the Bayesian analysis (PP: 0.938, BS: 70) (Fig. 2). The genus *Orphninostrichia*, represented by a single species, was recovered as a member of one of the hydroptiline clades. *Orphninostrichia squamosa* + *Paroxyethira* was recovered with strong support from the Bayesian analysis (PP: 1.0, BS: 79) (Fig. 3).

DISCUSSION

Ptilocolepidae

Neither the monophyly of Ptilocolepidae or the genus *Palaeagapetus* was recovered in this study; the monophyly of the genus *Ptilocolepus* was recovered. The 2 ptilocolepid genera were recovered as paraphyletic with respect to Hydroptilidae (Fig. 2). Ptilocolepidae was also not recovered in a previous study exploring the relationships among the families of Trichoptera (Holzenthal *et al.*, 2007). No members of Ptilocolepidae were represented in the recent Malm *et al.* (2013) study using molecular data to explore the relationships of the suborders within Trichoptera. Ptilocolepidae has thus far failed to be recovered as a monophyletic unit in any recent studies employing statistical analyses. Because of the lack of support for a monophyletic Ptilocolepidae, I propose that *Palaeagapetus* and *Ptilocolepus* be returned to Hydroptilidae not as the

subfamily Ptilecolepinae but as 2 distinct genera separate from all other currently recognized hydroptilid subfamilies.

Hydroptilidae

The monophyly of Hydroptilidae was recovered in this study (Fig. 2).

Hydroptilinae: a single monophyletic hydroptiline unit was not recovered in this study. 2 genera (*Microptila* and *Ugandatrichia*) and 2 larger clades (Hydroptilinae nodes 3 and 4) were instead recovered (Figs. 2-4). It is possible that this represents the appropriate placement of these genera, but, as Hydroptilinae is a very diverse and widely distributed group, obtaining still more taxa may help to further resolve the topology.

In her review, Marshall (1979) noted the group's success in diversity and distribution and the very heterogeneous appearance of the subfamily when viewed as a whole. She also commented that the group could consist of 3 subgroups distinguishable by affinities in the male and female genitalia and the general appearance and habits of the larvae: the *Agraylea* group, the *Hydroptila* group, and the *Oxyethira* group. In the currently presented phylogeny, the 2 larger clades (Hydroptilinae nodes 1 and 2) may represent these groups, while the remaining 2 genera (*Microptila*, *Ugandatrichia*) may be anomalies of the dataset or products of the alignment. The clade resulting from Hydroptilinae node 1 may represent Marshall's (1979) *Agraylea* + *Oxyethira* groups, while the clade resulting from Hydroptilinae node 2 may represent the *Hydroptila* group (Figs. 2-4).

Leucotrichiinae: the genera *Alisotrichia*, *Byrsopteryx*, and *Cerasmatrichia* were not

recovered with the rest of the currently recognized leucotrichiine genera (Figs. 2, 6, 7). Given their history of being transferred between Leucotrichiinae and Stactobiinae, it is not surprising that their most appropriate placement within Hydroptilidae is not with either subfamily. However, since the node recovered for *Alisotrichia* + *Cerasmatrichia* had very poor support, they cannot be considered a clade of their own with any confidence. And, although the node recovered for *Byrsopteryx* was strongly supported, there was no strong nodal support for its arrangement in the phylogeny regarding other taxa. I suggest that all 3 be removed from Leucotrichiinae and considered *incertae sedis* within Hydroptilidae. And while the monophyly for Leucotrichiinae, minus the 3 genera just mentioned, was recovered with strong support, there was very little support for any of the included genera or the relationships among them (Figs. 2, 5). This reinforces Marshall's (1979) comment that, although the leucotrichiine genera are far from distinct and clear-cut, the subfamily itself does appear to form a unique clade within Hydroptilidae. Further work and closer inspection is clearly needed to redefine the generic limits and relationships within this family.

Neotrichiinae: the subfamily Neotrichiinae was recovered, but with poor support (Figs. 2, 9).

Ochrotrichiinae: the subfamily Ochrotrichiinae was recovered, but with poor support (Figs. 2, 8). When first established by Marshall (1979), she stated that the features on which she based the group may one day prove to be secondarily derived from the general form of the Hydroptilinae and that Ochrotrichiinae may indeed prove to be a subgroup of Hydroptilinae. At least in this study, the evidence does not support

Marshall's conjecture.

Orthotrichiinae: the subfamily Orthotrichiinae was not recovered as a monophyletic unit (Figs. 2, 3, 9). Nielsen (1948) considered the 2 genera for which Orthotrichiinae was originally established (*Ithytrichia* and *Orthotrichia*) to be derived from a common ancestor because of a large number of shared larval features. However, in Marshall's (1979) opinion, while the larvae do share a number of morphological and behavioral similarities, both the larvae and adults are very distinct for each genus and *Ithytrichia* may one day be considered a distinct unit separate from Orthotrichiinae. I was only able to successfully sequence 2 taxa from this subfamily, *Ithytrichia lamellaris* and *Orthotrichia cristata*. More representatives from both genera and others within the subfamily may be necessary to understand the phylogenetic placement of Orthotrichiinae. Although a monophyletic Orthotrichiinae was not recovered, there was no nodal support for its arrangement in the given phylogeny and I do not suggest any changes to its currently recognized taxonomy.

Stactobiinae: the subfamily Stactobiinae was recovered with strong support (Figs. 2, 10). Given previous researchers' difficulty in finding morphological features that could be used to unite this group, further work and detailed observations are needed to more clearly define this subfamily.

Incertae sedis: As mentioned above, I suggest adding the genera *Alisotrichia*, *Byrsopteryx*, and *Cerasmatrichia* to the list of those currently considered *incertae sedis*. I also suggest removing 2 genera from this taxonomic consideration. The monotypic genus *Dibusa* was recovered near the base of the hydroptilid phylogeny; it received good

support from the Bayesian analysis as sister to all other hydroptilid genera, excluding the 2 previously considered as Ptilocolepidae (*Palaeagapetus*, *Ptilocolepus*) (Fig. 2). And the genus *Orphninostrichia*, though only represented in this study by a single species, was recovered nested within a clade of hydroptiline genera (Fig. 3). This placement is independently corroborated by Marshall's (1979) consideration that the genus shared similarities with other members of Hydroptilinae.

CONCLUSIONS

The objectives of this analysis were to 1) test the monophyly of both Hydroptilidae and Ptilocolepidae, 2) evaluate the monophyly of the traditionally recognized subfamilies within Hydroptilidae, and 3) infer relationships within and between Hydroptilidae and Ptilocolepidae. This was the first study to use modern statistical methods and molecular data in a phylogenetic assessment of the family and was based on an analysis of both mitochondrial DNA and nuclear ribosomal RNA characters and 90 species representing both families, all hydroptilid subfamilies, and 31 genera. Results of this study confers taxonomic stability to the family, refines the current classification system, and provides a new phylogenetic framework in which to place new species and genera.

While many of the traditionally recognized subfamilies were recovered, there was not strong nodal support for all of them. The addition of other genes, such as the nuclear

DNA fragment CAD which is considered more conservative and would be more phylogenetically informative at deeper levels of the phylogeny, would benefit this study. Additionally, given the level of diversity and global distribution of Hydroptilidae, the inclusion of more taxa may also produce a more strongly supported topology.

To accurately reflect the phylogeny presented in this study, several taxonomic changes are needed. Proposed changes are listed in the following section, “An updated phylogenetic framework for Hydroptilidae.”

An updated phylogenetic framework for Hydroptilidae

Table 4 represents my suggestion for an updated taxonomic framework for Hydroptilidae, based on the work presented here. It also includes a summary of the distribution and number of species included in each genus. Genera that could not be sequenced or were not represented in this study have been left unchanged and in their current placement, as listed above in the section “Overview of traditionally recognized taxa of Hydroptilidae and Ptilocolepidae.”

BIBLIOGRAPHY

- Agassiz, J. L. R. (1846) Nomenclatur zoologicus. *Index Universalis* 32.
- Angrisano, E. B. (1984 [1985]) Nuevas especies de Hydroptilidae Argentinos (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 43: 1-5.
- Angrisano, E. B. (1989) *Rhyacopsyche yatay*, una nueva especie de Hydroptilidae de la Argentina (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 46: 157-159.
- Angrisano, E. B. (1995a) Contribución al conocimiento de los Trichoptera del Uruguay. II. Familia Hydroptilidae. *Revista Brasileira de Entomologia* 39: 501-516.
- Angrisano, E. B. (1995b) Contribución para el conocimiento de las *Oxyethira* neotropicales (Trichoptera, Hydroptilidae). *Physis (Buenos Aires), Sección B* 50: 27-35.
- Angrisano, E. B. (2002) Contribution to the knowledge on Trichoptera of El Palmar National Park (Argentina). Description of the immature stages of *Bredinia* sp. and *Rhyacopsyche yatay* (Hydroptilidae). *Nova Supplementa Entomologica (Proceedings of the 10th International Symposium on Trichoptera)* 15:395-406.
- Angrisano, E. B. and Burgos, G. N. (2002) Contribución para el conocimiento do los Leucotrichiini (Trichoptera: Hydroptilidae). Tres especies nuevas de la Argentina. *Revista de la Sociedad Entomológica Argentina* 61:103-109.
- Angrisano, E. B. and Sganga, J. V. (2005) Contribution to the knowledge of the genus *Metrichia* Ross from Argentina (Trichoptera: Hydroptilidae: Ochrotrichiini). *Aquatic Insects* 27:113-123.
- Angrisano, E. B. and Sganga, J. V. (2009) New species of Hydroptilidae (Trichoptera) from Salto Encantado Provincial Park (Misiones province, Argentina). *Zootaxa* 2162: 57-68.
- Angrisano, E. B. and Sganga, J. V. (2010) Preimaginal stages of *Acostatrichia simulans* Mosely 1939, a Neotropical microcaddisfly (Trichoptera: Hydroptilidae: Leucotrichiinae). *Zootaxa* 2480: 54-60.
- Back, R. C. (1983) Larva and pupa of *Oxyethira leonensis* (Trichoptera: Hydroptilidae). *Florida Entomologist* 66: 389-392.
- Ball, S. L., Hebert, P. D. N., Burian, S. K. and Webb, J. M. (2005) Biological identifications of mayflies (Ephemeroptera) using DNA barcodes. *Journal of the North American Benthological Society* 24: 508-524.
- Banks, N. (1907) New Trichoptera and Psocidae. *Journal of the New York Entomological Society* 15: 162-166.
- Barnard, K. H. (1934) South African caddis-flies (Trichoptera). *Transactions of the Royal Society of South Africa* 21: 291-394.
- Barnard, P. C. (1971) The larva of *Agraylea sexmaculata* Curtis (Trichoptera, Hydroptilidae). *Entomologist's Gazette* 22: 253-257.
- Blahnik, R. J., Holzenthal, R. W. and Prather, A. L. (2007) The lactic acid method for clearing Trichoptera genitalia. In: J. Bueno-Soria, R. Barba-Álvarez and B. J. Armitage (Eds), *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, pp. 9-14.

- Blickle, R. L. and Denning, D. G. (1977) New species and a new genus of Hydroptilidae (Trichoptera). *Journal of the Kansas Entomological Society* 50: 287-300.
- Botosaneanu, L. (1956) Recherches sur les Trichoptères de Bulgarie recueillis par MM. le Prof. A. Balkanov et B. Rusev (Trichoptera). *Beiträge zur Entomologie* 6: 354-402.
- Botosaneanu, L. (1981) On a false and a genuine caddis-fly from Burmese Amber (Insecta: Trichoptera, Homoptera). *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 8: 73-78.
- Botosaneanu, L. (1990) Results of a trichopterological (Insecta: Trichoptera) travel to the Lesser Antilles in 1989. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 60: 39-48.
- Botosaneanu, L. (1992) *Fauna Palaestina. Insecta 6: Trichoptera of the Levant: imagines*. Jerusalem: The Israel Academy of Sciences and Humanities.
- Botosaneanu, L. (1994) A study of the larvae of caddisflies (Trichoptera) from Cuba. *Tropical Zoology* 7: 451-475.
- Botosaneanu, L. (1995) Caddis Flies (Trichoptera) from Turonian (Upper Cretaceous) amber of New Jersey. *American Museum Novitates* 3140: 1-7.
- Botosaneanu, L. (2000) Étude d'une faunule madicole de Guadeloupe: compléments à la connaissance des Trichoptères de l'Île. *Annales de Limnologie* 36: 249-259.
- Botosaneanu, L. and Flint, O. S., Jr. (1982) On some Trichoptera from northern Venezuela and Ecuador (Insecta). *Beaufortia* 32: 13-26.
- Botosaneanu, L. and Giudicelli, J. (1981) Observations morphologiques, éthologiques et écologiques sur *Hydroptila hirra* Mosely (Trichoptera: Hydroptilidae). In: G. P. Moretti (Ed), *Proceedings of the 3rd International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 21-29.
- Botosaneanu, L., Johnson, R. O. and Dillon, P. R. (1998) New caddisflies (Insecta: Trichoptera) from Upper Cretaceous amber of New Jersey, U.S.A. *Polskie Pismo Entomologiczne* 67: 219-231.
- Botosaneanu, L. and Sykora, J. (1963) Nouvelle contribution à la connaissance des Trichoptères de Bulgarie. *Acta Fauna Entomologica Musei Nationalis Pragae* 9: 121-142.
- Bowles, D. E., Harris, S. C. and Bueno-Soria, J. (1999) An assessment of New World Stactobiini (Trichoptera: Hydroptilidae: Hydroptilinae) larvae with new larval descriptions of *Alisotrichia*, *Mejicanotrichia*, and *Scelobotrichia*. In: H. Malicky and P. Chantaramongkol (Eds), *Proceedings of the 9th International Symposium on Trichoptera*. Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, pp. 43-52.
- Bueno-Soria, J. (1983) Three new species of *Ochrotrichia* (Metrichia) from Chiapas, Mexico (Trichoptera: Hydroptilidae). *Proceedings of the Biological Society of Washington* 96: 79-83.
- Bueno-Soria, J. (1984 [1985]) Estudios en insectos acuáticos II. revision para México y Centroamérica del género *Hydroptila* Dalman, 1819 (Trichoptera: Hydroptilidae). *Folia Entomológica Mexicana* 59: 79-138.
- Bueno-Soria, J. (1999) Studies in aquatic insects XV: new species of *Neotrichia* and first

- record of *Oxyethira hilosa* (Trichoptera: Hydroptilidae) from Mexico. *Entomological News* 110: 113-117.
- Bueno-Soria, J. (2002) The genus *Metrichia* Ross (Trichoptera: Hydroptilidae) from Mexico. *Transactions of the American Entomological Society* 128: 223-243.
- Bueno-Soria, J. (2009) A review of the genus *Ochrotrichia* Mosely (Trichoptera: Hydroptilidae) from Mexico and Central America. *Transactions of the American Entomological Society* 135: 59-160.
- Bueno-Soria, J. and Barba-Álvarez, R. (1999) Studies in aquatic insects XVI: two new species of the microcaddisfly genus *Mejicanotrichia* (Trichoptera: Hydroptilidae) from Mexico, with a key to the species in the genus. *Entomological News* 110: 118-122.
- Bueno-Soria, J. and Holzenthal, R. W. (2003) New species and records of the microcaddisfly genus *Metrichia* Ross from Costa Rica (Trichoptera: Hydroptilidae). *Studies on Neotropical Fauna and Environment* 38: 173-197.
- Bueno-Soria, J. and Santiago-Fragoso, S. (1997) Studies in aquatic insects XII: descriptions of nineteen new species of the genus *Ochrotrichia* Mosely (Trichoptera: Hydroptilidae) from Mexico and Central America. *Proceedings of the Entomological Society of Washington* 99: 359-373.
- Chambers, V. T. (1873) Micro-Lepidoptera. *Canadian Entomologist* 5:110-115, 124-128.
- Colwell, R. K. (2012) Biota 3: The Biodiversity Database Manager. Available from <http://viceroy.eeb.uconn.edu/Biota/biota>.
- Curtis, J. (1834) Description of some hitherto nondescript British species of mayflies of anglers. *The London and Edinburgh Philosophical Magazine and Journal of Science* 3: 120-125, 212-218.
- Dalman, J. W. (1819) Nogra nya insecta-genera beskriřna. *Vetenskaps-Akademiens Handlingar* 40: 117-127.
- Danecker, E. (1961) Studien zur hydropetrischen fauna. Biologie und Ökologie von *Stactobia* und *Tinodes* (Insecta, Trichoptera). *Internationale Revue der Gesamten Hydrobiologie* 46: 214-254.
- Denning, D. G. and Blickle, R. L. (1972) A review of the genus *Ochrotrichia* (Trichoptera: Hydroptilidae). *Annals of the Entomological Society of America* 65: 141-151.
- Eaton, A. E. (1873) On the Hydroptilidae, a family of the Trichoptera. *Transactions of the Entomological Society of London* 2: 125-149.
- Edwards, S. W. and Arnold, C. R. (1961) The caddis flies of the San Marcos river. *Texas Journal of Science* 13: 398-415.
- Enderlein, G. (1929) Entomologica Canaria 2. *Zoologischer Anzeiger* 84: 221-234.
- Fahy, E. (1971) The larva of *Hydroptila forcipata* (Eaton) (Trich., Hydroptilidae). *The Entomologist's Monthly Magazine* 107: 145-148.
- Felsenstein, J. (2004) *Inferring Phylogenies* (Second ed.). Sunderland, Massachusetts: Sinauer Associates.
- Fischer, F. C. J. (1961) *Philopotamidae, Hydroptilidae, Stenopsychidae. Trichopterorum Catalogus* 2. Amsterdam: Nederlandsche Entomologische Vereeniging.
- Fischer, F. C. J. (1971) *Supplement to Vol. I and II. Trichopterorum Catalogus* 12.

Amsterdam: Nederlandsche Entomologische Vereeniging.

- Flint, O. S., Jr. (1962) The immature stages of *Palaeagapetus celsus* Ross (Trichoptera: Hydroptilidae). *Bulletin of the Brooklyn Entomological Society* 42: 40-44.
- Flint, O. S., Jr. (1964) The caddisflies (Trichoptera) of Puerto Rico. *University of Puerto Rico, Agricultural Experiment Station, Technical Paper* 40: 1-80.
- Flint, O. S., Jr. (1966) On the identity of *Clymene aegerfasciella* Chambers. *Proceedings of the Entomological Society of Washington* 68: 135.
- Flint, O. S., Jr. (1967a) Studies of Neotropical Caddisflies II, Trichoptera collected by Prof. J. Illies in the Chilean subregion. *Beiträge zur Neotropischen Fauna* 5:45-68.
- Flint, O. S., Jr. (1967b) Studies of Neotropical caddis flies, IV: new species from Mexico and Central America. *Proceedings of the United States National Museum* 123: 1-24.
- Flint, O. S., Jr. (1968a) Bredin-Archbold-Smithsonian Biological Survey of Dominica, 9. The Trichoptera (Caddisflies) of the Lesser Antilles. *Proceedings of the United States National Museum* 125: 1-86.
- Flint, O. S., Jr. (1968b) The Caddisflies of Jamaica. *Bulletin of the Institute of Jamaica, Science Series* 19: 1-68.
- Flint, O. S., Jr. (1968c) New species of Trichoptera from the Antilles. *Florida Entomologist* 51: 151-153.
- Flint, O. S., Jr. (1969) Studies of Neotropical caddis flies, IX: new genera and species from the Chilean subregion. *Proceedings of the Entomological Society of Washington* 71: 497-514.
- Flint, O. S., Jr. (1970) Studies of Neotropical caddisflies, X: *Leucotrichia* and related genera from North and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 60: 1- 64.
- Flint, O. S., Jr. (1971) Studies of Neotropical caddis flies, XI: the genus *Rhyacopsyche* in Central America (Hydroptilidae). *Proceedings of the Biological Society of Washington* 83: 515-526.
- Flint, O. S., Jr. (1972a) Studies of Neotropical caddisflies, XIII: the genus *Ochrotrichia* for Mexico and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 118: 1-28.
- Flint, O. S., Jr. (1972b) Studies of Neotropical caddisflies, XIV: on a collection from northern Argentina. *Proceedings of the Biological Society of Washington* 85: 223-248.
- Flint, O. S., Jr. (1974) The Trichoptera of Surinam. Studies of Neotropical caddisflies, XV. *Studies on the Fauna of Suriname and other Guyanas* 14: 1-151, plates 151-154.
- Flint, O. S., Jr. (1980) Studies on Neotropical caddisflies, XXVI: new species from Argentina (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 39: 137-142.
- 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.

- Flint, O. S., Jr. (1982) Studies of Neotropical caddisflies, XXXI: five new species from Argentina (Trichoptera). *Entomological News* 93: 43-47.
- Flint, O. S., Jr. (1983) Studies of Neotropical caddisflies, XXXIII: new species from austral South America (Trichoptera). *Smithsonian Contributions to Zoology* 377: 1-100.
- 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.
- Flint, O. S., Jr. (1992) Studies of Neotropical caddisflies, XXXVIII: a review of the classification and biology of the Neotropical microcaddisflies, with the description of a new genus (Trichoptera: Hydroptilidae: Leucotrichiini). In: D. Quintero and A. Aiello (Eds), *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, Oxford, pp. 525-531.
- Flint, O. S., Jr. and Bueno-Soria, J. (1998) Studies of Neotropical caddisflies LVI: descriptions of five new species of the genus *Metrichia* Ross (Trichoptera: Hydroptilidae) from Pakitza, Peru, with a checklist and bibliography of the described species of the genus. *Proceedings of the Entomological Society of Washington* 100: 489-496.
- Flint, O. S., Jr. and Harris, S. C. (1991) Studies of Neotropical caddisflies, XLII: *Taraxatrichia amazonensis*, a new genus and species of microcaddisfly from Venezuela (Trichoptera: Hydroptilidae). In: C. Tomaszewski (Ed), *Proceedings of the 6th International Symposium on Trichoptera*. Adam Mickiewicz University Press, Poznan, Poland, pp. 411-414.
- Flint, O. S., Jr., Harris, S. C. and Botosaneanu, L. (1994) Studies of Neotropical caddisflies, L: the description of *Cerasmatrichia*, new genus, a relative of *Alisotrichia*, with the descriptions of new and old species and the larva (Trichoptera: Hydroptilidae). *Proceedings of the Biological Society of Washington* 107: 360-382.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999a) *Catalog of the Neotropical Caddisflies (Trichoptera)*. Columbus, Ohio: Special Publication, Ohio Biological Survey.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999b) Nomenclatural and systematic changes in the Neotropical caddisflies. *Insecta Mundi*, 13, 73-84.
- Fox, G. E. and Woese, C. R. (1975) The architecture of 5S rRNA and its relation to function. *J. Mol. Evol.* 6: 61-76.
- Frانيا, H. E. and 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.
- Giudicelli, J. and Vaillant, F. (1967) La larve et la nymphe d'*Allotrichia pallicornis* Eaton (Trichoptera). *Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Universite de Grenoble* 57-58: 29-36.
- González, M. A. and Malicky, H. (1980) Eine neue *Allotrichia* (Trichoptera: Hydroptilidae) von der Iberischen Halbinsel. *Entomologische Zeitschrift* 90: 214-216.

- Graf, W., Waringer, J. and Zika-Romer, J. (2004) The larva of *Microptila minutissima* Ris, 1897 (Trichoptera: Hydroptilidae). *Aquatic Insects* 26: 31-38.
- Gu, X., Fu, Y.-X. and Li, W.-H. (1995) Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Molecular Biology and Evolution* 12: 546-557.
- Guahyba, R. R. (1991) Estágios imaturos de *Anchitrichia duplifurcata* Flint, 1983 (Trichoptera, Hydroptilidae). *Revista Brasileira de Entomologia* 35: 121-125.
- Guinard, E. (1879) Métamorphose d'un genre nouveau de Phryganide (*Leiochton Fagesii*). *Académie des Sciences et Lettres de Montpellier, Mémoires de la Section des Sciences* 9: 139-144.
- Gutell, R. R., Larsen, N. and Woese, C. R. (1994) Lessons from an evolving rRNA: 16S and 23S rRNA structures from a comparative perspective. *Microbiol. Rev.* 58: 10-26.
- Hagen, H. A. (1855) Versuch, die Phryganiden Pictet's zu bestimmen. *Stettiner Entomologische Zeitung* 16: 204-210.
- Hagen, H. A. (1887) Ueber *Plethus cursitans*. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 37: 643-645.
- Hanna, H. M. (1961) The larvae of *Hydroptilasparsa* Curtis (Trichoptera: Hydroptilidae). *Entomologist's Gazette* 12: 69-75.
- Harris, S. C. (1985) New Hydroptilidae (Trichoptera) from Alabama. *Journal of the Kansas Entomological Society* 58: 248-253.
- Harris, S. C. (1986) Hydroptilidae (Trichoptera) of Alabama with descriptions of three new species. *Journal of the Kansas Entomological Society*, 59, 609-619.
- Harris, S. C. (1989) New Trichoptera from Alabama. *Journal of the New York Entomological Society* 97: 309-316.
- Harris, S. C. (1990) New species of *Neotrichia* (Trichoptera: Hydroptilidae) from Central and South America. *Journal of the New York Entomological Society* 98: 246-260.
- Harris, S. C. and Armitage, B. J. (1997) New member of the Chilean genus *Nothotrichia* from North America (Trichoptera: Hydroptilidae). In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 123-128.
- Harris, S. C. and Bueno-Soria, J. (1993) *Scelobotrichia*, a new genus of microcaddisflies from Mexico (Trichoptera: Hydroptilidae). *Folia Entomológica Mexicana* 87: 73-83.
- Harris, S. C. and Flint, O. S., Jr. (1992) Studies of Neotropical caddisflies, XLVII; *Kumanskiella*, a new genus from Cuba and Puerto Rico. *Journal of the New York Entomological Society* 100: 581-593.
- Harris, S. C. and Flint, O. S., Jr. (1993) Studies of Neotropical caddisflies, XLVIII; the larva of *Celaenotrichiaedwardsi* Mosely, with an assessment of the genus (Trichoptera: Hydroptilidae). In: C. Otto (Ed), *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 101-106.
- Harris, S. C., Flint, O. S., Jr. and Holzenthal, R. W. (2002a) Review of the Neotropical genus *Flintiella* (Trichoptera: Hydroptilidae: Stactobiini). *Journal of the New*

- York Entomological Society* 110: 65-90.
- Harris, S. C., Flint, O. S., Jr. and Holzenthal, R. W. (2002b) Two new genera of Hydroptilidae from the neotropics (Trichoptera: Hydroptilidae: Stactobiini). *Journal of the New York Entomological Society* 110: 49-64.
- Harris, S. C. and Holzenthal, R. W. (1990) Hydroptilidae (Trichoptera) from Costa Rica: the genus *Mayatrichia* Mosely. *Journal of the New York Entomological Society* 98: 453-460.
- Harris, S. C. and Holzenthal, R. W. (1993) Phylogeny of the species groups of *Alisotrichia*, *sensu lato*, with the description of a new species from Costa Rica (Trichoptera: Hydroptilidae). In: C. Otto (Ed), *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 155-160.
- Harris, S. C. and Holzenthal, R. W. (1994) Hydroptilidae (Trichoptera) of Costa Rica and the Neotropics: Systematics of the genus *Byrsopteryx* Flint (Stactobiini). *Journal of the New York Entomological Society* 102: 154-192.
- Harris, S. C. and Holzenthal, R. W. (1997) *Mejicanotrichia*, a new genus of microcaddisflies from Mexico and Guatemala (Trichoptera: Hydroptilidae). In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 123-128.
- Harris, S. C. and Holzenthal, R. W. (1999) Hydroptilidae (Trichoptera) of Costa Rica: the genus *Hydroptila* Dalman. *Studies on Neotropical Fauna and Environment* 34: 16-51.
- Harris, S. C., Holzenthal, R. W. and Flint, O. S., Jr. (2002) Review of the Neotropical genus *Bredinia* (Trichoptera: Hydroptilidae: Stactobiini). *Annals of Carnegie Museum* 71: 13-45.
- Harris, S. C. and Huryn, A. D. (2000) New and rare microcaddisflies (Trichoptera: Hydroptilidae) from the eastern United States. *Entomological News* 111: 77-83.
- Harris, S. C. and Rasmussen, A. K. (2010) The *Neotrichia caxima* Group (Trichoptera: Hydroptilidae) in the southeastern United States. *Zootaxa* 2608: 25-44.
- Hebert, P. D. N., Cywinska, A., Ball, S. L. and deWaard, J. R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, Series B* 270: 313-321.
- Hebert, P. D. N., Penton, E. H., Burns, J. M., Janzen, D. H. and 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.
- Hickin, N. E. (1967) *Caddis larvae: larvae of the British Trichoptera*. London: Hutchinson.
- Holzenthal, R. W., Blahnik, R. J., Kjer, K. M. and Prather, A. P. (2007) An update on the phylogeny of caddisflies (Trichoptera). In: J. Bueno-Soria, R. Barba-Alvarez and B. Armitage (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. and Kjer, K. M. (2007) Order

- Trichoptera Kirby, 1813 (Insecta), caddisflies. *Zootaxa* 1668: 639-698.
- Holzenthal, R. W. and Harris, S. C. (1991) The larva of *Byrsopteryx mirifica* Flint, with an assessment of the phylogenetic placement of the genus within the Leuchotrichiini (Trichoptera: Hydroptilidae). In: C. Tomaszewski (Ed), *Proceedings of the 6th International Symposium on Trichoptera*. Adam Mickiewicz University Press, Poznan, Poland, pp. 403-407.
- Holzenthal, R. W. and Harris, S. C. (1999) The genus *Costatrichia* Mosely in Costa Rica, with a review of the Neotropical species (Trichoptera: Hydroptilidae). *Proceedings of the Entomological Society of Washington* 101: 540-568.
- Holzenthal, R. W., Morse, J. C. and Kjer, K. M. (2011) Order Trichoptera Kirby, 1813. In: Zhang, Z.-Q. (Ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 209-211.
- Hsu, L.-P. and Chen, C.-S. (2002) A new species of *Ugandatrichia* (Trichoptera: Hydroptilidae) from Taiwan. *Pan-Pacific Entomologist* 78: 74-79.
- Hudson, G. V. (1886) On the metamorphosis of the caddis fly. *Trans. N. Z. Inst.* 18: 213-214.
- Huelsenbeck, J. P. (2000) *MRBAYES: Bayesian inference of phylogeny*: Distributed by the author. Department of Biology, University of Rochester, New York.
- Huelsenbeck, J. P. and Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- Hynes, H. B. N. (1970) *The ecology of running waters*. Liverpool.
- Ito, T. (1998) The biology of the primitive, distinctly crenophilic caddisflies, Ptilocolepinae (Trichoptera, Hydroptilidae). A review. In: L. Botosaneanu (Ed), *Studies in Crenobiology - The Biology of Springs and Springbrooks*. Backhuys Publishers, Leiden, The Netherlands, pp. 85-94.
- Ito, T. and Kawamura, H. (1980) Morphology and biology of the immature stages of *Hydroptila itoi* Kobayashi (Trichoptera, Hydroptilidae). *Aquatic Insects* 2: 113-122.
- Ito, T. and Kawamura, H. (1984) Morphology and ecology of immature stages of *Oxyethira actua* Kobayashi (Trichoptera, Hydroptilidae). *Japanese Journal of Limnology* 45: 313-317.
- Ito, T. and Ohkawa, A. (2012) The genus *Ugandatrichia* Mosely (Trichoptera, Hydroptilidae) in Japan. *Zootaxa* 3394: 48-58.
- Ivanov, V. D. (1997) Rhyacophiloidea: a paraphyletic taxon. In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 189-193.
- Ivanov, V. D. (2011) Caddisflies of Russia: Fauna and biodiversity. *Zoosymposia* 5: 171-209.
- Jacquemart, S. (1962) La larve d'*Orthotrichia angustella* MacLachlan (Trichoptere, Hydroptilidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 38: 1-10.
- Jacquemart, S. (1963) Deux Trichoptères nouveaux d'Argentine. In: C. Delamare and E. Rapaport (Eds), *Biologie de l'Amerique Australe, vol. 2*. Centre National de la Recherche Scientifique, Paris, pp. 339-342.

- Jacquemart, S. (1965) Resultats de l'expedition Belge an Moyen-Orient (Premiere note). Sept Trichoptères nouveaux de Turquie et d'Iran. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 41: 1-19.
- Jacquemart, S. (1973) Description de deux trichoptères hydroptilides nouveaux et de l'imago de *Stactobia monnioti* Jacquemart (Ile de Rhodes). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 49: 1-16.
- Jacquemart, S. and Coineau, Y. (1962) Missions S. Jacquemart dans les Pyrenees Orientales (2me note). Les Hydroptilides des Alberes. *Bulletin de l'Institut Royal des Sciences Naturalles de Belgique* 38: 1-81.
- Johanson, K. A. (1992) A catalog of the caddis flies of East Africa (Insecta, Trichoptera). *Steenstrupia* 18: 113-141.
- Johanson, K. A. and Malm, T. (2010) Testing the monophyly of Calocidae (Insecta: Trichoptera) based on multiple molecular data. *Molecular Phylogenetics and Evolution* 54: 535-541.
- Keiper, J. B. and Foote, B. A. (1999) Biology and immature stages of two species of Hydroptilidae Dalman (Trichoptera: Hydroptilidae) which consume *Cladophora* (Chlorophyta). *Proceedings of the Entomological Society of Washington* 101: 514-521.
- Keiper, J. B. and Harris, S. C. (2002) Biology and immature stages of *Ochrotrichia footei* (Trichoptera: Hydroptilidae), a new microcaddisfly from a torrential mountain stream. *Proceedings of the Entomological Society of Washington* 104: 291-299.
- Keiper, J. B. and Walton, W. E. (1999) Biology and morphology of *Oxyethira arizona* Ross (Trichoptera: Hydroptilidae). *Pan-Pacific Entomologist* 75: 212-200.
- Kelley, R. W. (1983) The micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae): morphology, biogeography, evolution and classification. In: *Department of Entomology*. Clemson University, Clemson, South Carolina, p. 431.
- Kelley, R. W. (1984) Phylogeny, morphology and classification of the micro-caddisfly genus *Oxyethira* Eaton (Trichoptera: Hydroptilidae). *Transactions of the American Entomological Society* 110: 435-463.
- Kelley, R. W. (1985) Revision of the micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae). Part II: subgenus *Oxyethira*. *Transactions of the American Entomological Society* 111: 223-253.
- Kelley, R. W. (1986) Revision of the micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae) Part III: subgenus *Holarctotrichia*. *Proceedings of the Entomological Society of Washington* 88: 777-785.
- Kelley, R. W. (1989) New species of micro-caddisflies (Trichoptera: Hydroptilidae) from New Caledonia, Vanuatu and Fiji. *Proceedings of the Entomological Society of Washington* 91: 190-202.
- Kelley, R. W. (1992) Phylogenetic relationships of micro-caddisfly genera (Hydroptilidae). *Bulletin of the North American Benthological Society* 9: 145 (Abstract).
- Kelsey, L. P. (1969) A revision of the Scenopinidae (Diptera) of the world. *Bulletin of the United States National Museum* 277: 1-336.
- Kimmins, D. E. (1950) The type-species of certain genera in the Trichoptera. *The*

- Entomologist* 83: 58-60.
- Kimmins, D. E. (1951) Indian caddisflies IV. New genera and species of the family Hydroptilidae. *Annals and Magazine of Natural History* 4: 193-213.
- Kimmins, D. E. (1958) The British species of the genus *Oxyethira* (Trichoptera: Hydroptilidae). *Entomologist's Gazette* 9: 7-17.
- Kimmins, D. E. (1966) A revised check-list of the British Trichoptera. *Entomologist's Gazette* 17: 111-120.
- Kingsolver, J. M. and Ross, H. H. (1961) New species of Nearctic *Orthotrichia* (Hydroptilidae, Trichoptera). *Illinois State Academy of Science Transactions* 54: 28-33.
- Kjaerandsen, J. (1997) *Wlitrichia introvertica* new genus, new species, and *Cyclopsiella anderseni* new genus, new species, two new monobasic genera of microcaddisflies from Ghana (Trichoptera: Hydroptilidae: Hydroptilini). In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 227-237.
- Kjaerandsen, J. (2004) A revision of the Afrotropical genus *Dhatrichia* (Trichoptera, Hydroptilidae). *Zoologica Scripta* 33: 131-185.
- Kjaerandsen, J. and Andersen, T. (2002) A review of *Jabitrichia* Wells, 1990 (Trichoptera: Hydroptilidae), with the description of a new Afrotropical species. *Nova Supplementa Entomologica (Proceedings of the 10th International Symposium on Trichoptera)* 15: 133-144.
- Kjer, K. (1995) Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Mol. Phylogenet. Evol.* 4: 314-330.
- Kjer, K. M., Blahnik, R. J. and Holzenthal, R. W. (2001) Phylogeny of Trichoptera (Caddisflies): Characterization of signal and noise within multiple datasets. *Systematic Biology* 50: 781-816.
- Kjer, K. M., Blahnik, R. J. and Holzenthal, R. W. (2002) Phylogeny of caddisflies (Insecta, Trichoptera). *Zoologica Scripta* 31: 83-91.
- Klapálek, F. (1902) O morfologii krowoku a privesku pohlavnich u Trichopter. I. Rhyacophilidae, Philipotamidae, et Hydroptilidae. *Rozpravy Ceske Akademie ved a umeni, Praze* 9: 39 p.
- Kloet, G. S. and Hincks, W. D. (1944) Nomenclatorial notes on two generic names in the Trichoptera. *Entomologist, London* 77: 97.
- Koçak, A. Ö. and Kemal, M. (2012) A generic nomenclatural correction among microcaddisflies in the Orientalic region (Hydroptilidae, Trichoptera). *Centre for Entomological Studies Ankara Miscellaneous Papers* 158: 4-5.
- Kolenati, F. A. (1848) *Genera et species Trichopterorum. Pars prior. Heteropalpoidea*. Prague.
- Kristensen, N. P. (1997) Early evolution of the Lepidoptera + Trichoptera lineage: phylogeny and the ecological scenario. In: P. Grandcolas (Ed), *The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios*. Mémoires du Muséum national d'histoire naturelle, Éditions du Muséum, Paris, pp. 253-271.

- Laudee, P. (2008) Larval morphology and diagnosis of the giant microcaddisfly species, *Ugandatrichia* spp. (Hydroptilidae: Trichoptera) in Thailand. *Zootaxa* 1825: 29-39.
- Leader, J. P. (1968) Hairs of the Hydroptilidae (Trichoptera). *Tane, Journal of the Auckland University Field Club* 16: 121-129.
- Leader, J. P. (1972) The New Zealand Hydroptilidae (Trichoptera). *Journal of Entomology (Series B)* 41: 191-200.
- Lepneva, S. G. (1932) Zum Studium der Trichopterenlarven in den Wasserbecken der Systeme des Dnipro und des Sud-Bugs. *Zh. bio-zool. Tsyklu Kyiv* 3: 71-115.
- Lepneva, S. G. (1953) *Trichoptera in Animal World of the USSR*.
- Lepneva, S. G. (1964) [Larvae and pupae of the suborder Annulipalpia. Trichoptera. II (1)]. *Zoologicheskogo Instituta Akademii Nauk SSSR (N.S.)* 88: 1-562.
- Lepneva, S. G. (1970) Fauna of the USSR, Trichoptera II (1). Larvae and pupae of the Annulipalpia. *Zoological Institute of the Academy of Science of the USSR, New Series* 88: 1-638.
- Lewis, P. O. (2001) Phylogenetic systematics turns over a new leaf. *TRENDS in Ecology and Evolution* 16: 30-37.
- Lloyd, J. T. (1915) Notes on *Ithytrichia confusa* Morton. *Canadian Entomologist* 47: 117-121.
- Luhman, J. C., Holzenthal, R. W. and Kjaerandsen, J. K. (1999) New host record of a ceraphronid (Hymenoptera) in Trichoptera pupae. *Journal of Hymenoptera Research* 8: 126.
- Macdonald, W. W. (1950) The larvae of *Mystacides azurea* L., *Cyrnus flavidus* McLachlan and *Oxyethira simplex* Ris (Trichoptera). *Proceedings of the Royal Entomological Society of London* 25: 19-28.
- Malicky, H. (1983) *Atlas of European Trichoptera. Series Entomologica* 24. Dordrecht: Dr W Junk.
- Malicky, H. (1988) Eine neue *Stactobia* (Trichoptera: Hydroptilidae) aus der Ost-Türkei. *Entomologische Zeitschrift* 98: 63-64.
- Malicky, H. (1998) Über einige *Hydroptila* - Arten aus der *occulta*-Gruppe (Trichoptera, Hydroptilidae). *Stapfia* 55: 395-397.
- Malicky, H. (1999) The net-spinning larvae of the Giant Microcaddisfly, *Ugandatrichia* spp. (Trichoptera, Hydroptilidae). In: H. Malicky and P. Chantaramongkol (Eds), *Proceedings of the 9th International Symposium on Trichoptera*. Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, pp. 199-204.
- Malicky, H. (2001) Construction behavior for new pupal cases by case-making caddis larvae: reply to Wiggins. (Trichoptera: Integripalpia). *Braueria* 28: 9.
- Malicky, H. (2001) Notes on the taxonomy of *Rhadicoleptus*, *Ptilocolepus* and *Pseudoneureclipsis*. *Braueria* 28: 19-20.
- Malicky, H. (2005) Ein kommentiertes Verzeichnis der Köcherfliegen (Trichoptera) Europas und des Mediterrangebietes. *Linzer Biologische Beiträge* 37: 533-596.
- Malicky, H. (2006) Caddisflies from Bardia National Park, Nepal, with a preliminary survey of Nepalese species (Insecta, Trichoptera). *Entomofauna* 27: 241-263.
- Malicky, H. (2008) On the migrations of *Ptilocolepus* through the Trichoptera system.

- Braueria* 35: 43-44.
- Malicky, H. (2009) Beiträge Kenntnis asiatischer Trichopteren [Contribution on the knowledge of Asian Trichoptera.]. *Braueria* 36: 11-58.
- Malicky, H. (2010) *Atlas of Southeast Asian Trichoptera*. Chiangmai: Chiangmai University.
- Malicky, H. and Chantaramongkol, P. (2007) Beiträge zur Kenntnis asiatischer Hydroptilidae (Trichoptera). *Linzer Biologische Beiträge* 39: 1009-1099.
- Malicky, H., Ivanov, V. and Melnitsky, S. (2011) Descriptions of 27 new caddisflies (Insect, Trichoptera) from Lombok, Bali and Java (Indonesia), with comments on known ones. *Linzer Biologische Beiträge* 43.
- Malm, T., Johanson, K. A. and Wahlberg, N. (2013) The evolutionary history of Trichoptera (Insecta): A case of successful adaptation to life in freshwater. *Systematic Entomology* 38: 459-473.
- Marlier, G. (1978) Sur une collection de Trichoptères de l'Afrique occidentale. *Revue de Zoologie Africaine* 92: 283-302.
- 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. V. (1910) Les Trichoptères de la Sibérie et des régions adjacentes. II. La sous f. des Brachycentrinae, les fam. des Molannidae, Leptoceridae, Hydropsychidae, Philopotamidae, Polycentropidae, Psychomyidae, Rhacophilidae et des Hydroptilidae. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint Pétersbourg* 15: 351-429.
- Martynov, A. V. (1913a) Contribution to the knowledge of the Trichopterous fauna of the Caucasus. (In Russian). *Travaux Laboratoire Zoologie Univ. Warsaw* 1913: 1-111.
- Martynov, A. V. (1913b) Contributions a la faune des Trichoptères du Caucase. II. Trichoptères de la province de batoum et des environs du Novyj Afon. *Horae Societatis Entomologicae Rossicae* 40: 30 p.
- Martynov, A. V. (1924) Rucheyniki (caddisflies [Trichoptera])[in Russian]. In: N. N. Bogdanova-Kat'kova (Ed), *Prakticheskaya entomologiya, Volume 5*, Leningrad, p. iv + 384.
- Martynov, A. V. (1934) Tableaux analytiques de la faune de l'U.R.S.S. Trichoptera Annulipalpia. I. *Opred. Faune SSSR* 13: 343.
- Martynov, A. V. (1935) On a collection of Trichoptera from the Indian Museum. Part I. Annulipalpia. *Records of the Indian Museum* 37: 93-209.
- Mathis, M. L. and Bowles, D. E. (1989) A new microcaddisfly genus (Trichoptera: Hydroptilidae) from the interior highlands of Arkansas, U.S.A. *Journal of the New York Entomological Society* 97: 187-191.
- McLachlan, R. (1865) Trichoptera Britanica. A monograph of British species of caddisflies. *Transactions of the Entomological Society of London, Series 3* 5: 1-184.
- McLachlan, R. (1880) *A monographic revision and synopsis of the Trichoptera of the European fauna. Part 9, pp. 501-523 (with supplement, pp. xiii-lxxxiv), plates 52-59*. London: John van Voorst.
- Medvedev, G. S. (1998) Keys to the insects of the European part of the USSR. Volume

- IV. Part VI: Megaloptera, Raphidioptera, Neuroptera, Mecoptera and Trichoptera. In. Science Publishers, Inc, Enfield, pp. i-xvii, 1-302.
- Mey, W. (2003) Contribution to the knowledge of the caddisfly fauna of the Philippines, V (Insecta, Trichoptera). *Insecta Koreana* 20: 425-452.
- Mey, W. and Joost, W. (1990) *Rhyacopsychemutisi* n.sp. - A new microcaddisfly with an unusual larva from Colombia (Trichoptera, Hydroptilidae). *Studies on Neotropical Fauna and Environment* 25: 133-138.
- Miller, M. A., Pfeiffer, W. and Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010*, New Orleans, LA, pp. 1-8.
- Milne, M. J. and Milne, L. J. (1939) Evolutionary trends in caddis worm case construction. *Annals of the Entomological Society of America* 32: 533-542.
- Morse, J. C. (1974) New caddisflies (Trichoptera) from southern Africa. *Journal of the Kansas Entomological Society* 47: 328-344.
- Morse, J. C. (1997) Phylogeny of Trichoptera. *Annual Review of Entomology* 42: 427-450.
- Morse, J. C. (2006) Trichoptera World Checklist. Available from <http://entweb.clemson.edu/database/trichopt/index.htm> (accessed 7 February 2014).
- Morton, K. J. (1887) On the cases of *Oxyethira costalis* Curt. *The Entomologist's Monthly Magazine* 23: 201-202.
- Morton, K. J. (1888) The larva and case of *Ithytrichia lamellaris*, Eaton, with references to other species of Hydroptilidae. *The Entomologist's Monthly Magazine* 24: 171-175.
- Morton, K. J. (1904) Further notes on the Hydroptilidae belonging to the European fauna, with descriptions of new species. *Transactions of the Entomological Society of London* 1904: 323-328.
- Morton, K. J. (1905) North American Hydroptilidae. *Bulletin of the New York State Museum* 86: 63-75, plates 13-15.
- Morton, K. J. (1934) Habits of the larvae of Hydroptilidae (Trichoptera). *Journal of the Society for British Entomology* 1: 44-45.
- Mosely, M. E. (1924) New Zealand Hydroptilidae (order Trichoptera). *Transactions of the New Zealand Institute* 55: 670-673.
- Mosely, M. E. (1933) The genus *Stactobia*, McLach. (Trichoptera). *Stylops* 2: 162-165.
- 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.
- Mosely, M. E. (1939a) The Brazilian Hydroptilidae (Trichoptera). *Novitates Zoologicae*, 41: 217-239.
- Mosely, M. E. (1939b) *The British caddis flies (Trichoptera). A collector's handbook. With an introduction by N.D.Riley*. London: Geo. Routledge and Sons, Ltd.
- Mosely, M. E. (1939) Trichoptera. Ruwenzori Expedition 1934-35. *British Museum*

- (*Natural History*) 3: 1-40.
- Mosely, M. E. (1948) Trichoptera. Expedition to South-West Arabia 1937-8. *British Museum (Natural History)* 1: 67-86.
- Mosely, M. E. and Kimmins, D. E. (1953) *The Trichoptera of Australia and New Zealand*. London: British Museum (Natural History).
- Moulton, S. R., II, Harris, S. C. and Slusark, J. P. (1999) The microcaddisfly genus *Ithytrichia* Eaton (Trichoptera: Hydroptilidae) in North America. *Proceedings of the Entomological Society of Washington* 101: 233-241.
- Müller, F. (1879a) Notes on the cases of some South Brazilian Trichoptera. *Transactions of the Royal Entomological Society of London* 4: 131-144.
- Müller, F. (1879b) Über Phryganiden (letters to his brother). *Zoologischer Anzeiger* 2: 38-40, 180-182, 283-284, 404-407.
- Müller, F. (1880 [1878]) Sobre as casas construidas pelas larvas de insectos Trichopteros da Provincia de Santa Catharina. *Archivos do Museu Nacional, Rio de Janeiro* 3: 99-134, 209-214, plates 138-111.
- Müller, F. (1881) Über die von den Trichopterenlarven der provinz Santa Catharina verfertigten Gehäuse. *Zeitschrift für Wissenschaftliche Zoologie* 35: 47-87, plates 44-45.
- Müller, F. (1887) Eine deutsche *Lagenopsyche*. *Entomologische Nachrichten* 13: 337-340.
- Müller, F. (1921) Briefe un noch nicht veröffentliche Abhandlungen aus dem nachlass 1854-1897. In: A. Möller (Ed), *Fritz Müller: Werke, Briefe und Leben*, 2. G. Fischer, Jena, pp. 383-642.
- Neboiss, A. (1963) The Trichoptera types of species described by J. Curtis. *Beiträge zur Entomologie* 13: 582-635.
- Neboiss, A. (1977) A taxonomic and zoogeographic study of Tasmanian caddis flies (Insecta: Trichoptera). *Memoirs of the National Museum of Victoria* 38: 1-208, plates 201-203.
- Nielsen, A. (1948) Postembryonic development and biology of the Hydroptilidae. A contribution to the phylogeny of the caddis flies and to the question of the origin of the case-building instinct. *Biologiske Skrifter* 5: 1-200.
- Noller, H. F., Hoffarth, V. and Zimniak, L. (1992) Unusual resistance of peptidyl transferase to protein extraction procedures. *Science* 256: 1416-1419.
- Nybom, O. (1948) Iter entomologicum et botanicum ad Insulas Madeiram et Azores anno 1938 a Richard Frey, Ragnar Stora et Carl Cedercreutz facturn. No 14. The Trichoptera of the Atlantic islands. *Commentationes Biologicae, Helsinki* 8: 1-19.
- Nyman, T., Zinovjev, A. G., Vikberg, V. and Farrell, B. D. (2006) Molecular phylogeny of the sawfly subfamily Nematinae (Hymenoptera: Tenthredinidae). *Systematic Entomology* 31: 569-583.
- Oláh, J. (1989) Thirty-five new hydroptilid species from Vietnam (Trichoptera, Hydroptilidae). *Acta Zoologica Hungarica* 35: 255-293.
- Oláh, J. (2012) New species and records of Trichoptera from Batanta and Waigeo Islands (Indonesia, Raja Empat Archipelago, Papua (Irian Jaya)). *Braueria* 39.
- Oláh, J. and Johanson, K. A. (2008) Reasoning an appendicular and functional caddisfly

- genital terminology. *Braueria* 35: 29-40.
- Oláh, J. and Johanson, K. A. (2010) Description of 46 new Old World Hydroptilidae (Trichoptera). *Folia Entomologica Hungarica* 71: 1-91.
- Oláh, J. and Johanson, K. A. (2011) New Neotropical Hydroptilidae (Trichoptera). *Annales Historico-Naturales Musei Nationalis Hungarici* 103: 117-255.
- Oláh, J. and O. S. Flint, J. (2012) Description of new species in the Leucotrichiini tribe (Trichoptera: Hydroptilidae). *Annales Historico-Naturales Musei Nationalis Hungarici* 104: 1-83.
- Özdikmen, H. (2007) A nomenclatural act: Replacement names for two homonymous caddisfly generic names (Trichoptera). *Munis Entomology and Zoology* 2: 443-444.
- Özdikmen, H. (2008) A nomenclatural act for caddis flies (Trichoptera). *Munis Entomology and Zoology* 3: 614-616.
- Pace, N. R. (1997) A molecular view of microbial diversity and the biosphere. *Science* 276: 734-740.
- Parys, K. A. and Harris, S. C. (2013) Larva of *Nothotrichia shasta* Harris and Armitage (Trichoptera: Hydroptilidae) from California, USA, with its phylogenetic and taxonomic implications. *Zootaxa* 3620: 589-595.
- Pes, A. M. O. and Hamada, N. (2003) The occurrence of *Taraxitrichia* Flint and Harris, 1992 (Trichoptera: Hydroptilidae) in Brazil, with description of the final larval stage. *Zootaxa* 328: 1-7.
- Pes, A. M. O. and Hamada, N. (2004) *Ceratotrichia* Flint, 1992 (Trichoptera: Hydroptilidae) larval and pupal description and new genus records for Brazil. *Entomotropica* 19: 31-37.
- Pictet, F. J. (1834) *Recherches pour servir à l'histoire et l'anatomie des Phryganides*. Geneva: A. Cherbuliez.
- Resh, V. H. and Houp, R. E. (1986) Life history of the caddisfly *Dibusa angata* and its association with the red alga *Lemanea australis*. *Journal of the North American Benthological Society* 5: 28-40.
- Reuter (1890) [Title unknown]. *Revue ent. Franç.* 9: 291.
- Ris, F. (1894) Vier Schweizerische Hydroptiliden. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 9: 131-134.
- Ris, F. (1897) Neuropterologischer sammelbericht 1894-96. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 9: 415-442.
- Roldán-Perez, G. (1988) *Guía para el Estudio de los Macroinvertebrados Acuáticos del Departamento de Antioquia*. Antioquia, Colombia: Universidad de Antioquia.
- Ronquist, F., Huelsenbeck, J. P. and Mark, P. v. d. (2005) *MrBayes 3.1, Manual*: Florida State University.
- Ross, H. H. (1938) Lectotypes of North American caddisflies in the Museum of Comparative Zoology. *Psyche* 45: 1-61.
- Ross, H. H. (1939) New species of Trichoptera from the Appalachian region. *Proceedings of the Entomological Society of Washington* 41: 63-72.
- Ross, H. H. (1941a) Descriptions and records of North American Trichoptera. *Transactions of the American Entomological Society* 67: 35-126.

- Ross, H. H. (1941b) New species of Trichoptera from Canada and northern United States. *Canadian Entomologist* 73: 15-19.
- Ross, H. H. (1944) The caddisflies or Trichoptera of Illinois. *Bulletin of the Illinois Natural History Survey* 23: 1-326.
- Ross, H. H. (1948) Notes and descriptions of Nearctic Hydroptilidae (Trichoptera). *Journal of the Washington Academy of Sciences* 38: 201-206.
- Ross, H. H. (1956) *Evolution and Classification of the Mountain Caddisflies*. Urbana: University of Illinois Press.
- Ross, H. H. (1967) The evolution and past dispersal of the Trichoptera. *Annual Review of Entomology* 12: 169-206.
- Rueda Martin, P. A. (2006) New record of the genus *Ithytrichia* (Trichoptera: Hydroptilidae) for South America, with descriptions of male, larva and pupa of a new species from northwestern Argentina. *Aquatic Insects* 28: 251-256.
- Schmid, F. (1949) Les Trichoptères de la collection Navás. *Eos-Revista Española Entomologia* 25: 305-426.
- Schmid, F. (1958a) Contribution à l'étude des Trichoptères néotropicaux III. *Mitteilungen aus dem Zoologischen Museum in Berlin* 34: 183-217.
- Schmid, F. (1958b) Trichoptères de Ceylan. *Archiv für Hydrobiologie* 54: 1-173.
- Schmid, F. (1959a) Le genre *Stactobia* Mch. *Miscelanea Zoologica, Barcelona* 1: 1-56.
- Schmid, F. (1959b) Trichoptères d'Iran (Trichoptera). *Beiträge zur Entomologie* 9: 199-219; 199 (193-194): 376-412; 199 (195-196): 682-698; 199 (197-198): 760-799.
- Schmid, F. (1960) Trichopteres du Pakistan. III (Hydroptilidae, Philopotamidae, Polycentropodidae). *Tijdschrift voor Entomologie* 103: 83-109.
- Schneider, W. G. (1845) Verzeichnis der von Herrn Oberlehrer Zeller in Jahre 1844 in Sicilien und Italien gesammelten Neuropteren mit beschreibung einiger neuen arten. *Stettiner Entomologische Zeitung* 6: 338-346.
- Scott, K. M. F. (1976) The larval and pupal stages of *Ugandatrichia* Mosely (Trichoptera: Hydroptilidae) from Rhodesia, with the description of a new species. *Annals of the Cape Provincial Museums (Natural History)* 11: 117-127.
- Scudder, G. G. E. (1971) Comparative morphology of insect genitalia. *A. Rev. Ent.* 16: 379-406.
- Sibley, C. K. (1926a) A preliminary biological survey of the Lloyd-Cornell Reservation: studies on Trichoptera. *Bull. Lloyd Libr.* 27: 102-108, 185-247.
- Sibley, C. K. (1926b) Studies on Trichoptera. *Bulletin of the Lloyd Library* 27: 186-221.
- Siltala (Silfvenius), A. J. (1908) Zur Trichopteren-Fauna der Nördlichen Fenno-Skandia. *Acta Societatis pro Fauna et Flora Fennica* 31: 19 p.
- Simon, C., Buckley, T. R., Frati, F., Stewart, J. B. and Beckenbach, A. (2006) Incorporating molecular evolution into phylogenetic 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.
- Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. and Flook, P. (1994) Evoluton, 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.
- Smit, S., Widmann, J. and Knight, R. (2007) Evolutionary rates vary among rRNA structural elements. *Nucleic Acids Research* 35: 3339-3354.
- Solem, J. O. (1972) The larvae of *Agraylea cognatella* McLachlan (Trichoptera, Hydroptilidae). *Norsk Entomologisk Tidsskrift* 19: 77-79.
- Stamatakis, A., Hoover, P. and Rougemont, J. (2008) A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology* 75: 758-771.
- Stephens, J. F. (1836) *Illustrations of British Entomology; or a Synopsis of Indigenous Insects: Containing their Generic and Specific Distinctions; with an Account of their Metamorphoses, Times of Appearance, Localities, Food, and Economy, as far as Practicable. Mandibulata. Vol. VI. [Trichoptera, pages 146-208]*. London: Baldwin and Cradock.
- Sykora, J. L. (1967) Trichoptera collected by prof. J. Illies in New Guinea and New Caledonia. *Pacific Insects* 9: 585-595.
- Thienemann, A. (1904) *Ptilocolepus granulatus* Pict., eine Uebergangsform von den Rhyacophiliden zu den Hydroptiliden. *Allgemeine Zeitschrift für Entomologie* 9: 418-424, 437-441.
- Thienemann, A. (1905) Trichopterenstudien I-III. *Zeitschrift für Wissenschaftliche Insektenbiologie* 1: 285-291.
- Tobias, W. (1999) Köcherfliegen-Neufunde vom unteren Main in Hessen (Trichoptera). *Entomologische Zeitschrift* 109: 49-55.
- Ulmer, G. (1907) Trichoptera, in Wytzman, P. (Ed.). *Genera Insectorum* 60: 1-259.
- Ulmer, G. (1912a) *Die Trichopteren des Baltischen Bernsteins. Beiträge zur Naturkunde Preussens, 10*. Leipzig: Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg.
- Ulmer, G. (1912b) Trichoptera aus Äquatorial-Afrika. *Wiss. Ergebn. Deutsche Zentralafrika Exped.* 4: 81-125.
- Ulmer, G. (1951) Köcherfliegen (Trichopteren) von den Sunda-Inseln. Teil I. *Archiv für Hydrobiologie, Supplement* 19: 1-528.
- Ulmer, G. (1957) Köcherfliegen (Trichopteren) von den Sunda-Inseln. Teil III. Larven und Puppen der Annulipalpia. *Archiv für Hydrobiologie, Supplement* 23: 109-470.
- Vaillant, F. (1956) Recherches sur la fauna madicole de France, de Corse et d'Afrique du Nord. *Mèm. Mus. natn. Hist. nat. Paris (A)* 11: 1-258.
- Vaillant, F. (1984) The hydroptilid larvae living on dripping rocks. In: J. C. Morse (Ed), *Proceedings of the 4th International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 407-412.
- Wallengren, H. D. J. (1891) Skandinavien Neuroptera. Andra afdelningen. *Svenska Akademien Handlingar* 24: 1-173.
- Waringer, J. and Graf, W. (1997) *Atlas der Österreichischen Köcherfliegenlarven, unter Einschluss der angrenzenden Gebiete [Atlas of Austrian caddisfly larvae, with inclusion of adjacent areas.]*. Vienna: Facultas Universitätsverlag.
- Wasmund, A. M. and Holzenthal, R. W. (2007) A revision of the Neotropical caddisfly genus *Rhyacopsyche*, with the description of 13 new species (Trichoptera: Hydroptilidae). *Zootaxa* 1634: 1-59.

- Weaver, J. S., III (1984) The evolution and classification of Trichoptera. Part I: the groundplan of Trichoptera. In: J. C. Morse (Ed), *Proceedings of the 4th International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 413-419.
- Weaver, J. S., III and Morse, J. C. (1986) Evolution of feeding and case-making behavior in Trichoptera. *Journal of the North American Benthological Society* 5: 150-158.
- Wells, A. (1978) A review of the Australian genera *Xuthotrichia* Mosely and *Hellyethira* Neboiss (Trichoptera: Hydroptilidae), with descriptions of new species. *Australian Journal of Zoology* 27: 311-329.
- Wells, A. (1979) The Australian species of *Orthotrichia* Eaton (Trichoptera: Hydroptilidae). *Australian Journal of Zoology* 27: 585-622.
- Wells, A. (1980) A review of the Australian genera *Orphnino-trichia* Mosely and *Maydenoptila* Neboiss (Trichoptera: Hydroptilidae), with descriptions of new species. *Australian Journal of Zoology* 28: 627-645.
- Wells, A. (1981) The genera *Oxyethira* Eaton, *Gnathotrichia* Ulmer and *Stenoxyethira* Kimmins (Trichoptera: Hydroptilidae) in Australia. *Australian Journal of Zoology* 29: 103-118.
- Wells, A. (1982) *Tricholeiochiton* Kloet and Hincks and new genera in the Australian Hydroptilidae (Trichoptera). *Australian Journal of Zoology* 30: 251-270.
- Wells, A. (1985) Larvae and pupae of Australian Hydroptilidae (Trichoptera), with observations on general biology and relationships. *Australian Journal of Zoology, Supplementary Series* 113: 1-69.
- Wells, A. (1987) On the biogeography of the *Oxyethira* group, tribe Hydroptilini (Hydroptilinae, Hydroptilidae, Trichoptera). In: M. Bournaud and H. Tachet (Eds), *Proceedings of the 5th International Symposium on Trichoptera*. Dr. W. Junk, Dordrecht, The Netherlands, pp. 133-138.
- Wells, A. (1990a) The hydroptilid tribe Stactobiini (Trichoptera: Hydroptilidae) in New Guinea. *Invertebrate Taxonomy* 3: 817-849.
- Wells, A. (1990b) The micro-caddisflies (Trichoptera: Hydroptilidae) of North Sulawesi. *Invertebrate Taxonomy* 3: 363-406.
- Wells, A. (1990c) New species and a new genus of micro-caddisfly from northern Australia, including the first Australian record of the tribe Stactobiini (Trichoptera: Hydroptilidae). *Transactions of the Royal Society of South Australia* 114: 107-128.
- Wells, A. (1991) The hydroptilid tribes Hydroptilini and Orthotrichini in New Guinea (Trichoptera: Hydroptilidae: Hydroptilinae). *Invertebrate Taxonomy* 5: 487-526.
- Wells, A. (1992) The first parasitic Trichoptera. *Ecological Entomology* 17: 299-302.
- Wells, A. (1993) Micro-caddisflies (Trichoptera: Hydroptilidae) from Bali, Indonesia. *Zoologische Mededelingen (Leiden)* 67: 351-359.
- Wells, A. (1995) New Caledonian Hydroptilidae (Trichoptera), with new records, descriptions of larvae and a new species. *Aquatic Insects* 17: 223-239.
- Wells, A. (1997) A preliminary guide to the identification of larval Hydroptilidae (Insecta: Trichoptera). *Co-operative Research Centre for Freshwater Ecology Identification Guide* 13: 1-28.
- Wells, A. (1998) Two new species of Hydroptilidae (Trichoptera) from Tasmania's

- World Heritage Area. *Australian Entomologist* 25: 81-84.
- Wells, A. (1999) The micro-caddisflies of Lord Howe Island (Hydroptilidae: Trichoptera: Insecta). *Aquatic Insects* 21: 221-230.
- Wells, A. (2002) Three new species of *Orphnino-trichia* Mosely (Trichoptera: Hydroptilidae) from Barrington Tops, New South Wales, a distribution extended, and remarks on generic placement. *Australian Journal of Entomology* 41: 221-225.
- Wells, A. (2005) Parasitism by hydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. *Australian Journal of Entomology* 44: 385-391.
- Wells, A. (2010) Five new species and new records of Hydroptilidae (Trichoptera) from the Wet Tropics of northeastern Queensland. *Zootaxa* 2641: 47-54.
- Wells, A. (2010) Thirty years of hydroptilid studies - 1979 to 2009. *Denisia* 29: 437-443.
- Wells, A. (2012) New synonyms in the Australian micro-caddisfly fauna (Trichoptera: Hydroptilidae). *Zootaxa* 3177.
- Wells, A. and Andersen, T. (1995) Tanzanian micro-caddisflies (Trichoptera: Hydroptilidae). *Tijdschrift voor Entomologie* 138: 143-167.
- Wells, A. and Huisman, J. (1992) Micro-caddisflies in the tribe Hydroptilini (Trichoptera: Hydroptilidae: Hydroptilinae) from Malaysia and Brunei. *Zoologische Mededelingen (Leiden)* 66: 91-126.
- Wells, A. and Huisman, J. (2001) New hydroptilid caddisfly species from southern Sulawesi (Insecta: Trichoptera: Hydroptilidae). *Zoologische Mededelingen (Leiden)* 75: 207-216.
- Wells, A. and Johanson, K. A. (2012) Review of the New Caledonian species of *Paroxyethira* Mosely, 1924 (Trichoptera: Hydroptilidae). *Zootaxa* 3478: 330-344.
- Wells, A. and Malicky, H. (1997) The micro-caddisflies of Sumatra and Java (Trichoptera: Hydroptilidae). *Linzer Biologische Beiträge* 29: 173-202.
- Wells, A. and Wichard, W. (1989) Caddisflies of Dominican amber VI. Hydroptilidae (Trichoptera). *Studies on Neotropical Fauna and Environment* 24: 41-51.
- Westwood, J. O. (1838) Description of a new genus of exotic bees. *Transaction of the Entomological Society of London* 2: 112-113.
- Westwood, J. O. (1840) *An Introduction to the Modern Classification of Insects Founded on Natural Habits and Corresponding Organisation of the Different Families*. London: Longman, Orme, Brown, Green, and Longmans.
- Wichard, W. (1976) Morphologische Komponenten bei der Osmoregulation von Trichopterenlarven. In: H. Malicky (Ed), *Proceedings of the 1st International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 171-177.
- Wiggins, G. B. (1977) *Larvae of the North American caddisfly genera (Trichoptera)*. Toronto: University of Toronto Press.
- Wiggins, G. B. (1996) *Larvae of the North American Caddisfly Genera (Trichoptera)* (2nd ed.). Toronto: University of Toronto Press.
- Wiggins, G. B. (2004) *Caddisflies: the underwater architects*. Toronto: University of Toronto Press.
- Wiggins, G. B. and Wichard, W. (1989) Phylogeny of pupation in Trichoptera, with

- proposals on the origin and higher classification of the order. *Journal of the North American Benthological Society* 8: 260-276.
- Yang, Z. (1993) Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates differ over sites. *Molecular Biology and Evolution* 10: 1396-1401.
- Yang, Z. (1994a) Estimating the pattern of nucleotide substitution. *Journal of Molecular Evolution* 39: 105-111.
- Yang, Z. (1994b) Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Systematic Biology* 44: 384-399.
- Zhou, X., Kjer, K. M. and 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.

Table 1. Determination and depository of specimens sequenced.

INGROUP			
Hydroptilidae			
		Depository	
Hydroptilinae			
<i>Agraylea</i>	<i>cognatella</i>	ZMUB	
	<i>multipunctata</i>	RUIC	
	<i>sexmaculata</i>	RUIC	
	<i>saltesea</i>	RUIC	
	<i>pallicornis</i>	USDC	
<i>Allotrichia</i>	<i>simplex</i>	UMSP	
<i>Helyethira</i>	<i>forcipata</i>	ZMUB	
<i>Hydroptila</i>	<i>gunda</i>	CUAC	
	<i>hamata</i>	CUAC	
	<i>losida</i>	UMSP	
	<i>oguranis</i>	UMSP	
	<i>scamandra</i>	UMSP	
	<i>tineoides</i>	ZMUB	
	<i>vectis</i>	RUIC	
	<i>Microptila</i>	<i>orienthula</i>	UMSP
	<i>Oxyethira</i>	<i>absona</i>	RUIC
		<i>bidentata</i>	RUIC
<i>falcata</i>		RUIC	
<i>frici</i>		ZMUB	
<i>grisea</i>		CUAC	
<i>janella</i>		CUAC	
<i>rivicola</i>		RUIC	
<i>rossi</i>		RUIC	
<i>Paroxyethira</i>		<i>hendersoni</i>	NMNH
		<i>tillyardi</i>	NMNH
<i>Ugandatrichia</i>	<i>maliwan</i>	RUIC	
	<i>sp.</i>	RUIC	
Leucotrichiinae			
<i>Abtrichia</i>	<i>antennata</i>	UMSP	
	<i>squamosa</i>	UMSP	
	<i>veva</i>	NMNH	
<i>Alisotrichia</i>	<i>fundorai</i>	NMNH	
	<i>hirudopsis aitija</i>	NMNH	
<i>Anchitrichia</i>	<i>duplifurcata</i>	UMSP	
	<i>spangleri</i>	RUIC	
<i>Ascotrichia</i>	<i>surinamensis</i>	NMNH	
	<i>sp.</i>	RUIC	
<i>Betrichia</i>	<i>sp.</i>	RUIC	
<i>Byrsopteryx</i>	<i>abrelata</i>	UMSP	
	<i>chaconi</i>	UMSP	
	<i>esparta</i>	UMSP	
	<i>gomezi</i>	UMSP	
	<i>solisi</i>	UMSP	

Table 1 (cont.)

		Depository
	<i>tapanti</i>	UMSP
	<i>tica</i>	UMSP
<i>Cerasmatrichia</i>	<i>trinitatis</i>	NMNH
	<i>wirthi</i>	NMNH
<i>Ceratotrichia</i>	<i>flavicomma</i>	NMNH
<i>Leucotrichia</i>	<i>fairchildi</i>	RUIC
	<i>pictipes</i>	RUIC
	<i>sarita</i>	NMNH
<i>Zumatrichia</i>	<i>anomalopectera</i>	NMNH
	<i>diamphidia</i>	RUIC
	<i>rhamphoides</i>	UMSP
Neotrichiinae		
<i>Mayatrichia</i>	<i>ayama</i>	NMNH
	<i>rualda</i>	UMSP
<i>Neotrichia</i>	<i>esmalda</i>	UMSP
	<i>minutisimella</i>	UMSP
	<i>vibrans</i>	UMSP
Ochrotrichiinae		
<i>Metrichia</i>	<i>fontismoreaui</i>	NMNH
	<i>neotropicalis</i>	UMSP
	<i>nigritta</i>	UMSP
	<i>patagonica</i>	UMSP
	<i>platigona</i>	NMNH
	<i>spica</i>	UMSP
	<i>yalla</i>	NMNH
<i>Ochrotrichia</i>	<i>alsea</i>	UMSP
	<i>eliaga</i>	RUIC
	<i>logana</i>	RUIC
	<i>limonensis</i>	UMSP
	<i>oregona</i>	UMSP
	<i>panamensis</i>	RUIC
	<i>tarsalis</i>	UMSP
	<i>tenanga</i>	UMSP
<i>Rhyacopsyche</i>	<i>andina</i>	UMSP
	<i>dikrosa</i>	UMSP
	<i>hagenii</i>	UMSP
	<i>mexicana</i>	UMSP
Orthotrichiinae		
<i>Ithytrichia</i>	<i>lamellaris</i>	USDC
<i>Orthotrichia</i>	<i>crystata</i>	UMSP
Stactobiinae		
<i>Stactobia</i>	<i>makartshenkoi</i>	NMNH
	<i>nybomi</i>	NMNH
<i>Stactobiella</i>	<i>delira</i>	UMSP
	<i>martynovi</i>	RUIC
	<i>tshistjakovi</i>	UMSP

Table 1 (cont.)

		Depository
<i>Incertae sedis</i>		
<i>Dibusa</i>	<i>angata</i>	NMNH
<i>Orphnino-trichia</i>	<i>squamosa</i>	UMSP
Ptilocolepidae		
<i>Palaeagapetus</i>	<i>celsus</i>	RUIC
	<i>ovatus</i>	NMNH
<i>Ptilocolepus</i>	<i>extensus</i>	USDC
	<i>granulatus</i>	RUIC
OUTGROUP		
Glossosomatidae		
<i>Agapetus</i>	<i>pinatus</i>	RUIC
<i>Anagapetus</i>	<i>debilis</i>	RUIC
<i>Culoptila</i>	<i>hamata</i>	RUIC
<i>Glossosoma</i>	<i>nigrior</i>	RUIC
<i>Matrioptila</i>	<i>jennae</i>	RUIC
<i>Protoptila</i>	<i>tenebrosa</i>	RUIC
Hydrobiosidae		
<i>Apsilochorema</i>	<i>gisbum</i>	RUIC
<i>Atopsyche</i>	<i>callosa</i>	RUIC
	<i>sp.</i>	RUIC
<i>Taschorema</i>	<i>evansi</i>	RUIC
<i>Ulmerochorema</i>	<i>onychion</i>	RUIC
Rhyacophilidae		
<i>Rhyacophila</i>	<i>brunnea</i>	RUIC
	<i>coloradensis</i>	RUIC
	<i>fuscula</i>	RUIC

Table 2. Primers used in polymerase chain reactions for this study.

Primer	Sequence (5' to 3')	Reference
COI F	TAATTGGAGGATTTGGWAAYTG	Kjer <i>et al.</i> , 2001
COI R	CCYGGTAAAATTTAAAATATAAACTTC	Kjer <i>et al.</i> , 2001
D1 up	GGAGGAAAAGAAACTAACAAGGATT	Kjer <i>et al.</i> , 2001
D1 dn	CAACTTTCCTTACGGTACT	Kjer <i>et al.</i> , 2001
D2up4	GAGTTCAAGAGTACGTGAAACCG	Zhou <i>et. al.</i> , 2007
D2dnB	CCTTGGTCCGTGTTTCAAGAC	Zhou <i>et. al.</i> , 2007
D3up	ACCCGTCTTGAAACACGGAC	Kjer <i>et al.</i> , 2001
D3DnTr2	CTATCCTGAGGGAAACTTCGGA	Kjer <i>et al.</i> , 2001

Table 3. PCR settings (cycles, temperature, time) for each targeted gene sequence.

Repetitions	Temperature (°C)	Time
1X	94	3 minutes
	94	30 seconds
40X	52 - COI	30 seconds
	56 - D1	
	57 - D2	
	61 - D3	
	72	30 seconds
	72	7 minutes
1X	4	hold

Table 4. An updated taxonomic framework for Hydroptilidae. Abbreviations for biogeographical regions: AT = Afrotropical, AU = Australasian, HO = Holarctic, NA = Nearctic, NT = Neotropical, OR = Oriental, PA = Palaeartic.

	# of Species	Distribution
Family Hydroptilidae Stephens, 1836		
Genus <i>Dibusa</i> Ross, 1939 *formerly <i>incertae sedis</i>	1	NA
Genus <i>Palaeagapetus</i> Ulmer, 1912 *formerly placed in Ptilocolepidae	11	PA, NA
Genus <i>Ptilocolepus</i> Kolenati, 1848 *formerly placed in Ptilocolepidae	7	PA, NA
Subfamily Hydroptilinae Stephens, 1836		
Genus <i>Acanthotrichia</i> Wells, 1982	1	AU
Genus <i>Acritoptila</i> Wells, 1982	14	AU
Genus <i>Agraylea</i> Curtis, 1834	11	HO
Genus <i>Allotrichia</i> McLachlan, 1880	10	PA
Genus <i>Austratrichia</i> Wells, 1982	1	AU
Genus <i>Cyclopsiella</i> Kjaerandsen, 1997	1	AT
Genus <i>Dhatrichia</i> Mosely, 1948	14	AT
Genus <i>Helyethira</i> Neboiss, 1977	42	AU
Genus <i>Hydroptila</i> Dalman, 1819	422	cosmopolitan
Genus <i>Jabitrachia</i> Wells, 1990	4	AT, AU, OR
Genus <i>Kholaptila</i> Malicky and Chantaramongkol, 2007	1	OR
Genus <i>Maeyptila</i> Malicky and Chantaramongkol, 2007	1	OR
Genus <i>Microptila</i> Ris, 1897	16	PA
Genus <i>Missitrichia</i> Wells, 1991	2	AU
Genus <i>Mulgravia</i> Wells, 1982	2	AU
Genus <i>Orphninostrichia</i> Mosely, 1934 *formerly <i>incertae sedis</i>	20	AU
Genus <i>Oxyethira</i> Eaton, 1873	203	cosmopolitan
Genus <i>Paroxyethira</i> Mosely, 1924	17	AU
Genus <i>Paucicalcaria</i> Mathis and Bowles, 1989	1	NA
Genus <i>Sutheptila</i> Malicky and Chantaramongkol, 2007	1	OR
Genus <i>Tangatrachia</i> Wells and Andersen, 1995	1	AT
		AT, AU, OR,
Genus <i>Tricholeiochiton</i> Kloet and Hincks, 1944	11	PA
Genus <i>Ugandatrichia</i> Mosely, 1939	30	AT, OR
Genus <i>Vietrichia</i> Oláh, 1989	1	OR
Genus <i>Wlitrichia</i> Kjaerandsen, 1997	1	AT
Genus <i>Xuthotrichia</i> Mosely, 1934	2	AU
Subfamily Leucotrichiinae Flint, 1970		
Genus <i>Abtrichia</i> Mosely, 1939	3	NT
Genus <i>Acostatrichia</i> Mosely, 1939	6	NT
Genus <i>Anchitrichia</i> Flint, 1970	4	NT
Genus <i>Ascotrichia</i> Flint, 1983	2	NT
Genus <i>Betrichia</i> Mosely, 1939	9	NT
Genus <i>Celaenotrichia</i> Mosely, 1934	1	NT
Genus <i>Ceratotrichia</i> Flint, 1992	3	NT
Genus <i>Costatrichia</i> Mosely, 1937	12	NT
Genus <i>Eutonella</i> Müller, 1921	1	NT
Genus <i>Leucotrichia</i> Mosely, 1934	30	NA, NT
Genus <i>Mejicanotrichia</i> Harris and Holzenthal, 1997	7	NT

Table 4 (cont.)

	# of Species	Distribution
Genus <i>Peltopsyche</i> Müller, 1879	2	NT
Genus <i>Scelobotrichia</i> Harris and Bueno-Soria, 1993	3	NT
Genus <i>Zumatrichia</i> Mosely, 1937	24	NT
Subfamily Neotrichiinae Ross, 1956		
Genus <i>Kumanskiella</i> Harris and Flint, 1992	2	NT
Genus <i>Mayatrichia</i> Mosely, 1937	7	NA, NT
Genus <i>Neotrichia</i> Morton, 1905	141	NA, NT
Genus <i>Taraxitrichia</i> Flint and Harris, 1991	1	NT
Subfamily Ochrotrichiinae Marshall, 1979		
Genus <i>Angrisanoia</i> Ozdikmen, 2008	4	NT
Genus <i>Metrichia</i> Ross, 1938	103	NA, NT
Genus <i>Nothotrichia</i> Flint, 1967	5	NA, NT
Genus <i>Ochrotrichia</i> Mosely, 1934	203	NA, NT
Genus <i>Ragatrichia</i> Oláh and Johanson, 2011	5	NT
Genus <i>Rhyacopsyche</i> Müller, 1879	25	NT
Subfamily Orthotrichiinae Nielsen, 1948		
Genus <i>Ithytrichia</i> Eaton, 1873	7	HO, NT
Genus <i>Orthotrichia</i> Eaton, 1873	234	cosmopolitan
Genus <i>Saranganotrichia</i> Ulmer, 1951	4	OR
Subfamily Stactobiinae Botosaneanu, 1956		
Genus <i>Bredinia</i> Flint, 1968	16	NT
Genus <i>Catoxyethira</i> Ulmer, 1912	66	AT, AU
Genus <i>Chrysotrichia</i> Schmid, 1958	61	OR
Genus <i>Flintiella</i> Angrisano, 1995	12	NT
Genus <i>Maetalaiptila</i> Malicky and Chantaramongkol, 2007	1	OR
Genus <i>Niuginitrichia</i> Wells, 1990	14	AU, OR
Genus <i>Orientalitrichia</i> Koçak and Kemal, 2012	59	OR
Genus <i>Orinocotrichia</i> Harris, Flint, and Holzenthal, 2002	2	NT
Genus <i>Plethus</i> Hagen, 1887	27	OR
Genus <i>Stactobia</i> McLachlan, 1880	145	AT, OR, PA
Genus <i>Stactobiella</i> Martynov, 1924	13	HO
Genus <i>Tizatetrichia</i> Harris, Flint, and Holzenthal, 2002	1	NT
<i>Incertae sedis</i>		
Genus <i>Alisotrichia</i> Flint, 1964 *formerly placed in Leucotrichiinae	56	NA, NT
Genus <i>Byrsopteryx</i> Flint, 1981 *formerly placed in Stactobiinae	16	NT
Genus <i>Burminoptila</i> Botosaneanu, 1981 †	1	†
Genus <i>Caledonotrichia</i> Sykora, 1967	5	AU
Genus <i>Cerasmatrixia</i> Flint, Harris, and Botosaneanu, 1994 *formerly placed in Leucotrichiinae	8	NT
Genus <i>Dicaminus</i> Müller, 1879	1	NT
Genus <i>Electrotichia</i> Ulmer, 1912 †	1	†
Genus <i>Macrostactobia</i> Schmid, 1958	2	OR
Genus <i>Maydenoptila</i> Neboiss, 1977	8	AU
Genus <i>Novajerseya</i> Botosaneanu, Johnson, and Dillon, 1998 †	1	†

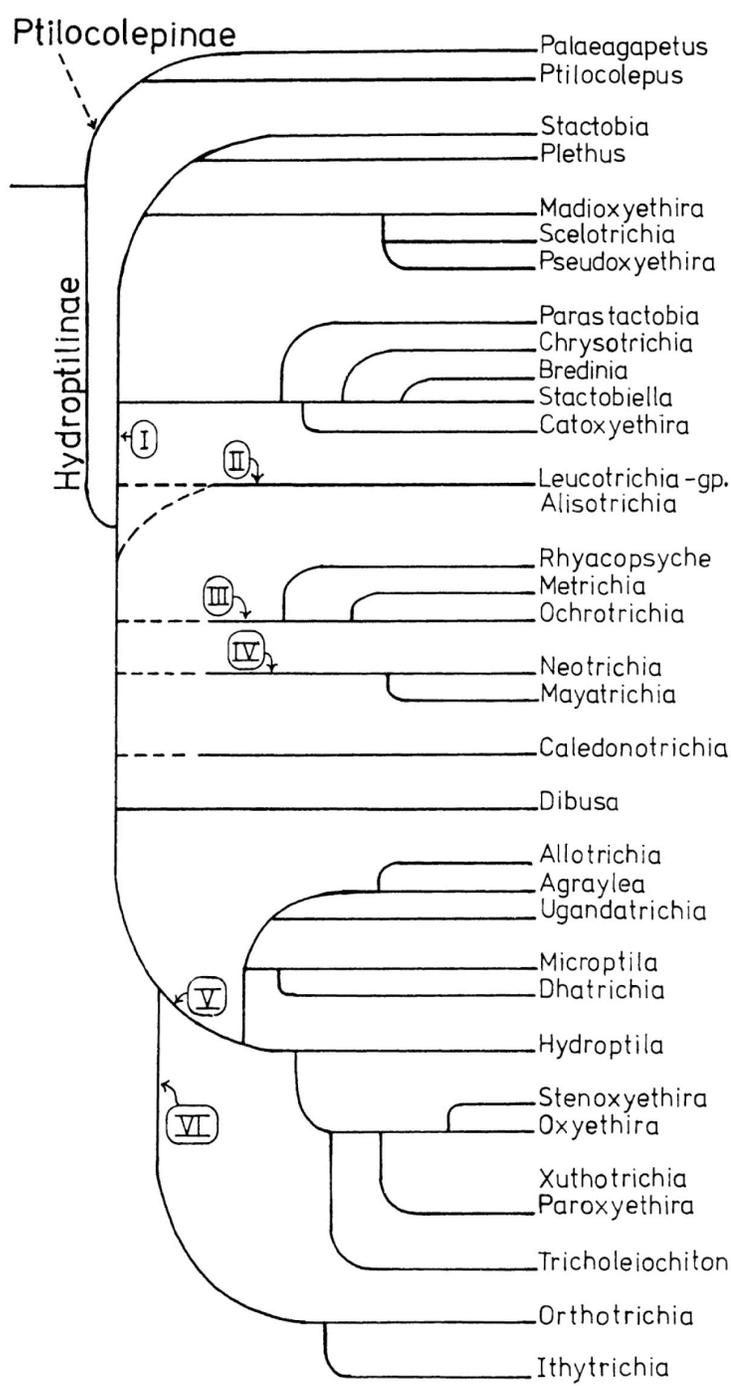


Figure 1. Phylogeny of Hydroptilidae, taken from Marshall (1979). Based on morphological data; generic relationships (I, Stactobiini; II, Leucotrichiini; III, Ochrotrichiini; IV, Neotrichiini; V, Hydroptilini; VI, Orthotrichiini).

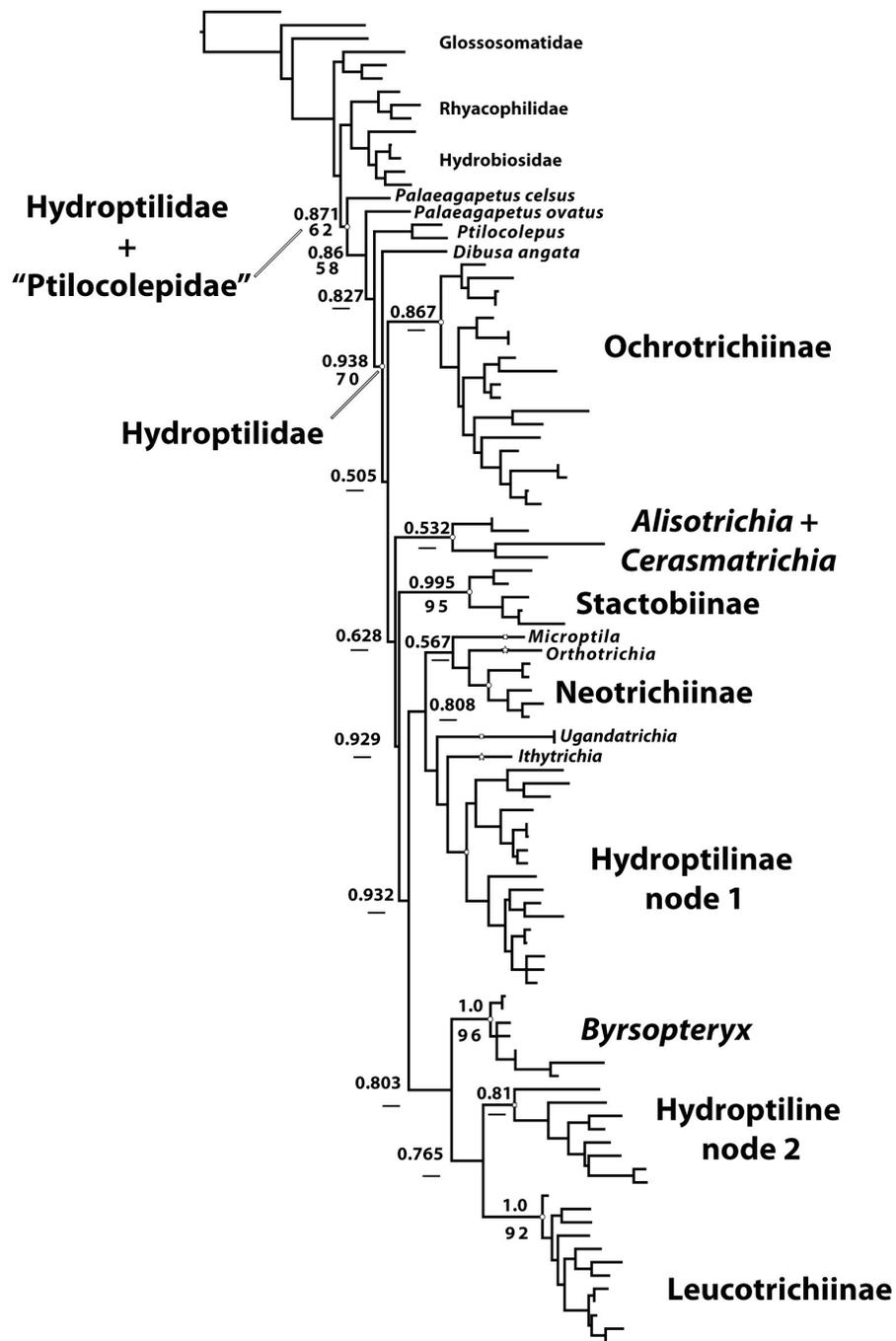


Figure 2. Phylogeny of Hydroptilidae, entire analysis. Outgroups included Hydrobiosidae, Glossosomatidae, and Rhyacophilidae. Posterior probability values are indicated above internodes, bootstrap values are indicated below internodes (values < 50 represented by —). The same tree is used as the source of Figures 3-10. ○ = monophyletic clade, □ = Hydroptilinae, ☆ = Orthotrichiinae.

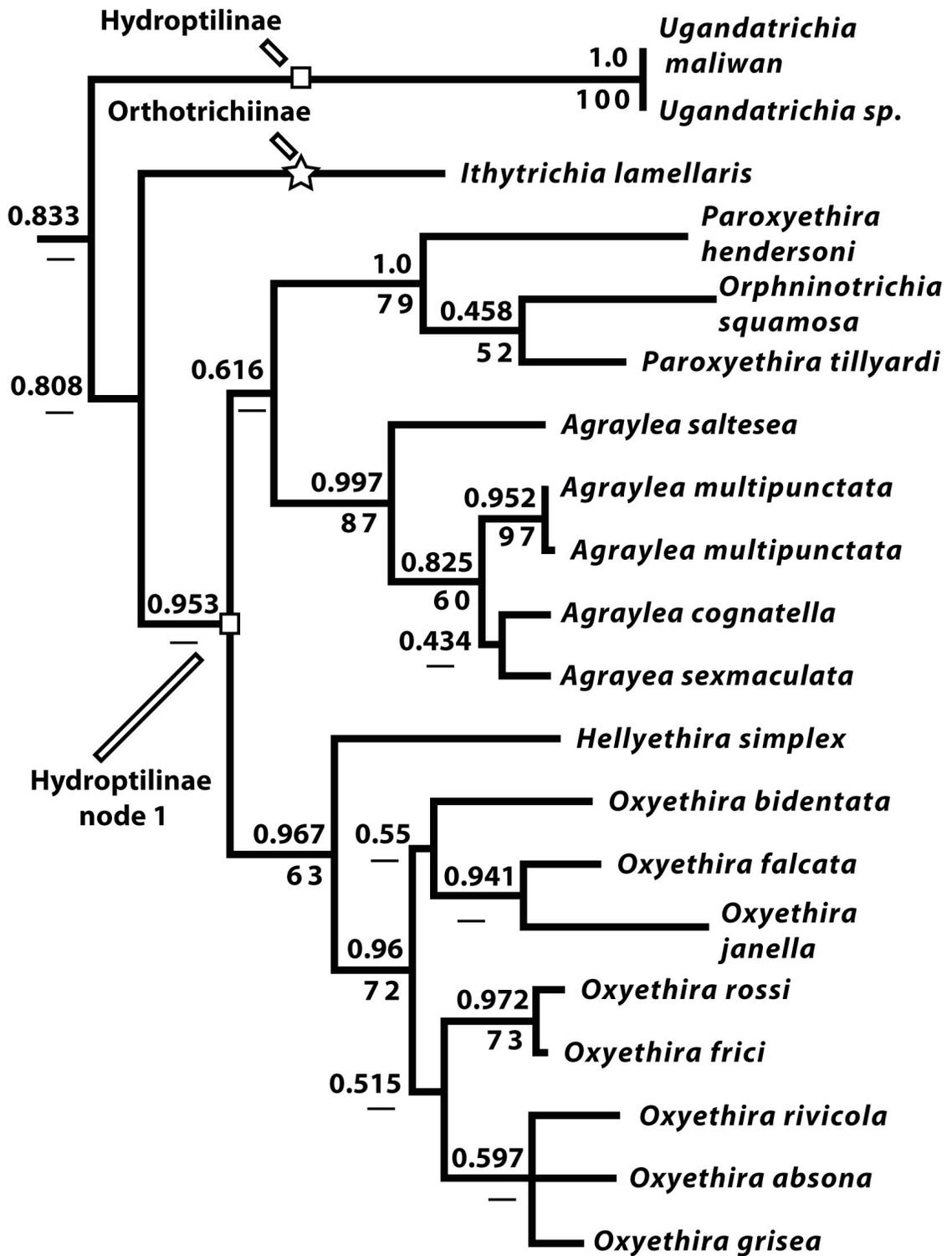


Figure 3. Phylogeny of Hydroptilidae, Hydroptilinae node 1 + *Ithytrichia lamellaris* + *Ugandatrichia*. Symbols as in Figure 1.

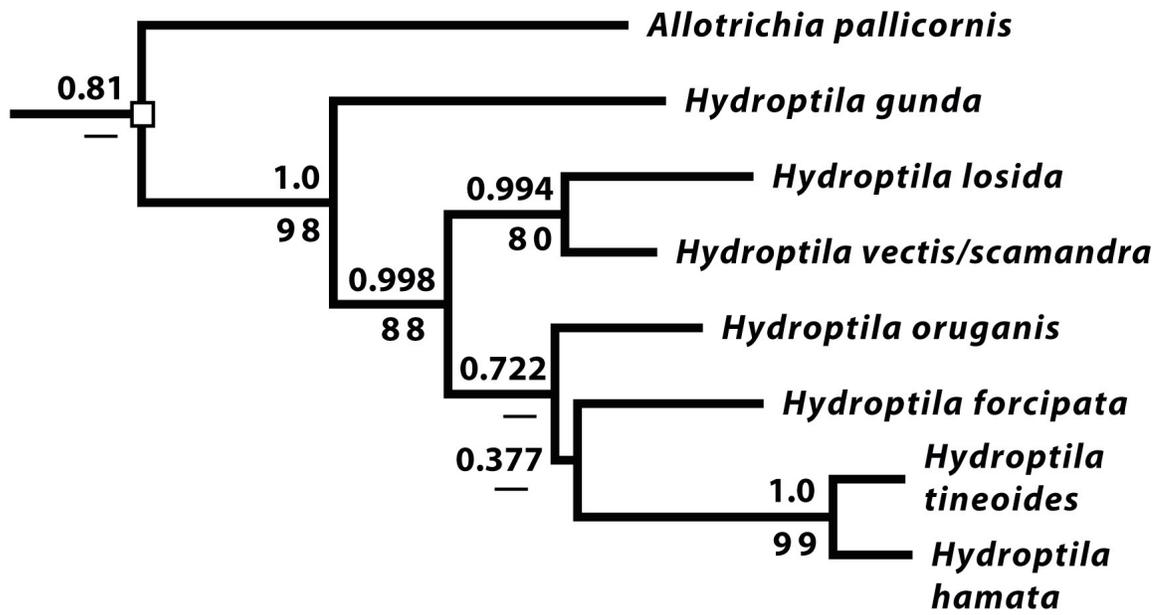


Figure 4. Phylogeny of Hydroptilidae, Hydroptilinae node 2. Symbols as in Figure 1.

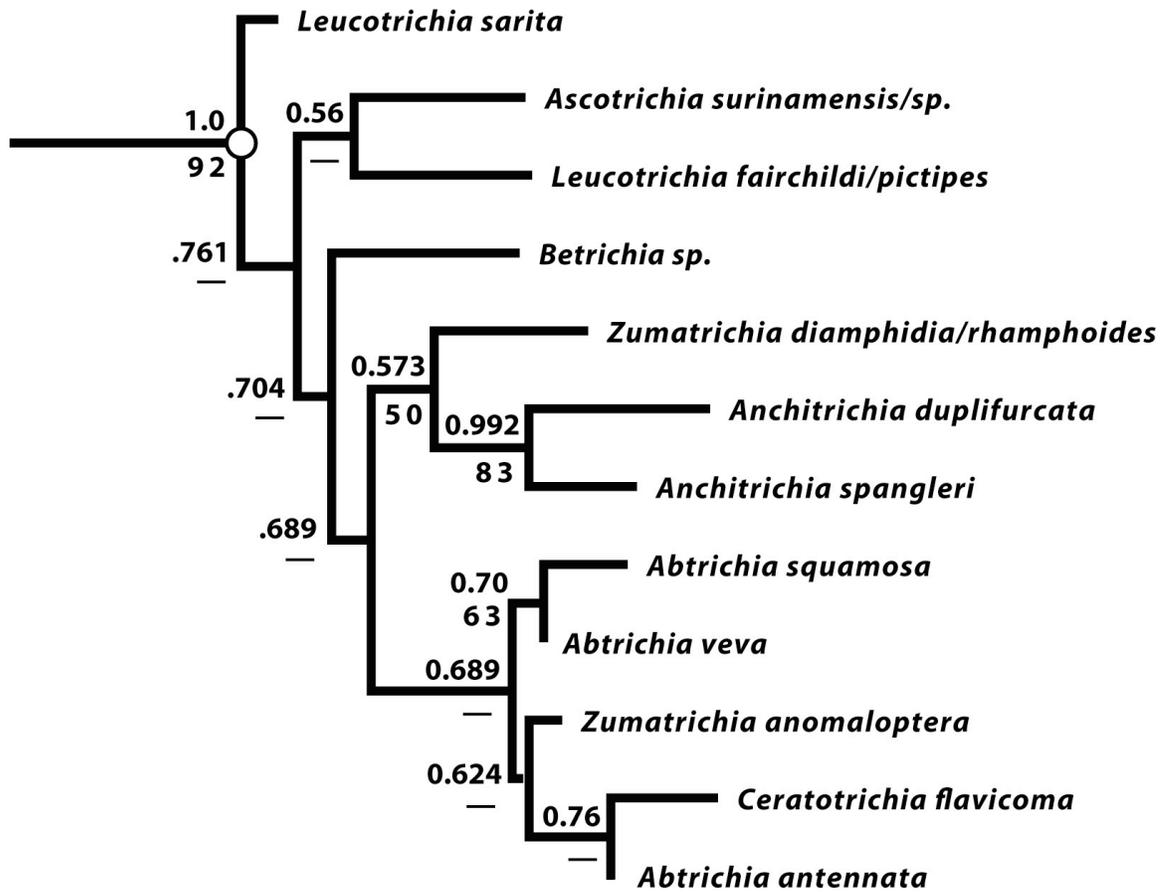


Figure 5. Phylogeny of Hydroptilidae, Leucotrichiinae. Symbols as in Figure 1.

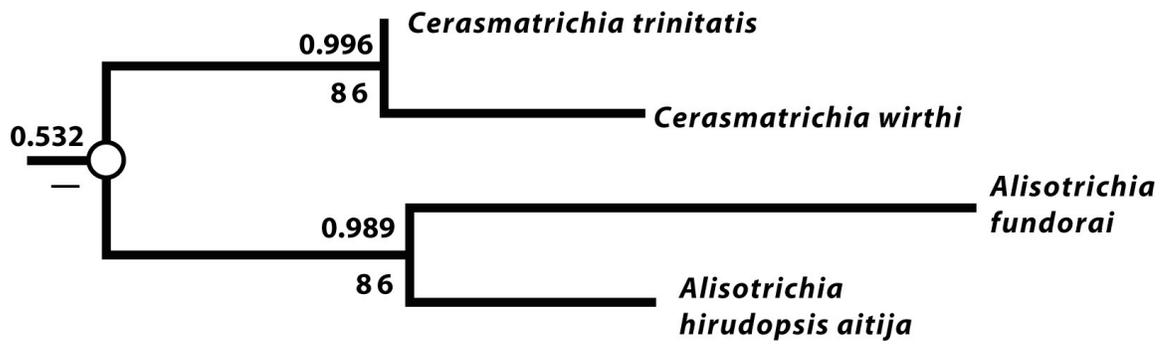


Figure 6. Phylogeny of Hydroptilidae, *Alisotrichia* + *Cerasmatrichia*. Symbols as in Figure 1.

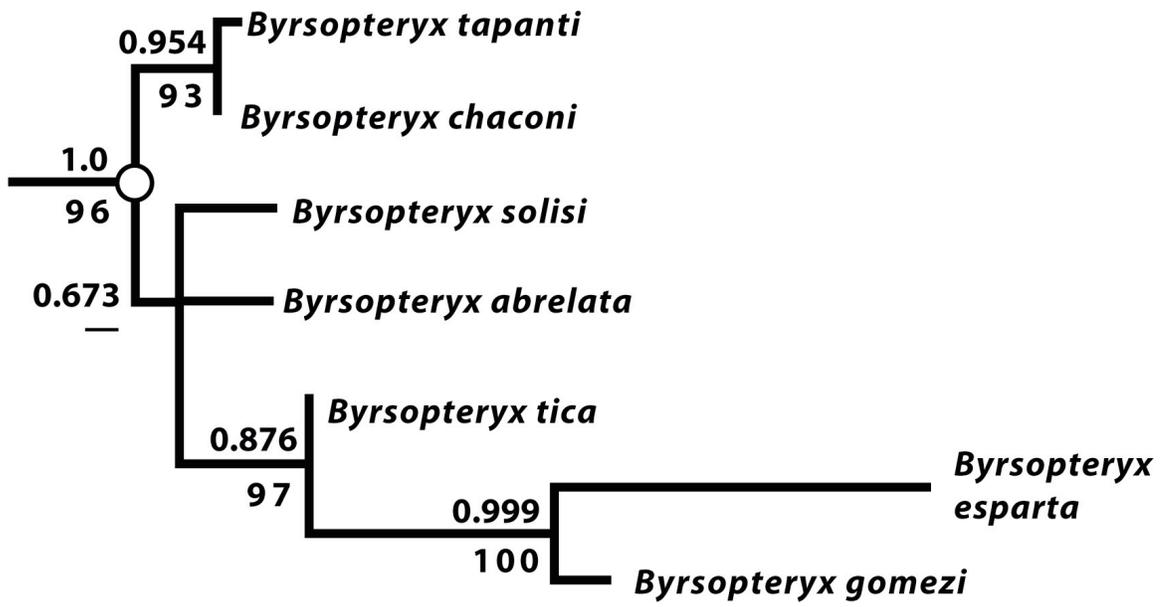


Figure 7. Phylogeny of Hydroptilidae, *Byrsopteryx*. Symbols as in Figure 1.

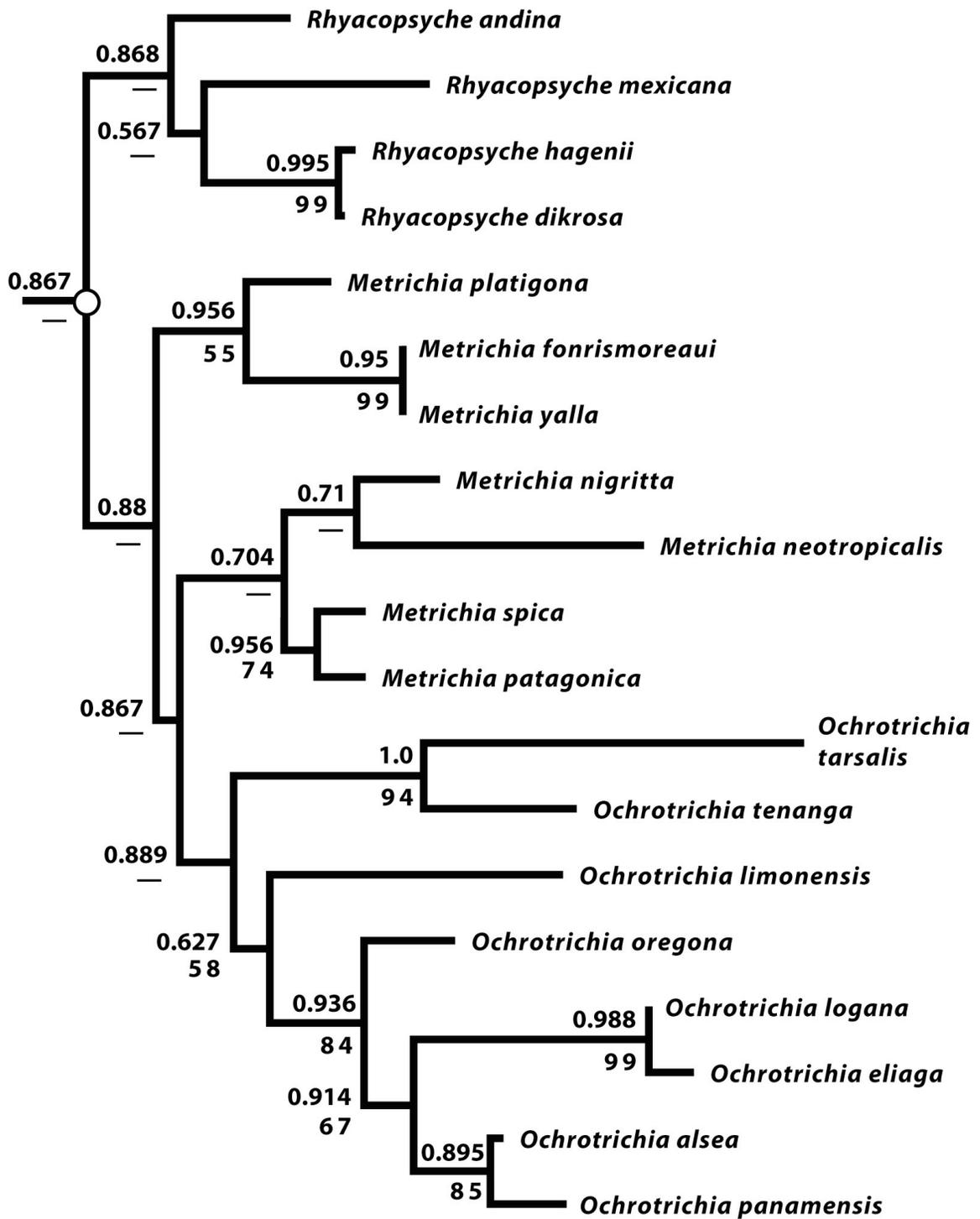


Figure 8. Phylogeny of Hydroptilidae, Ochrotrichiinae. Symbols as in Figure 1.

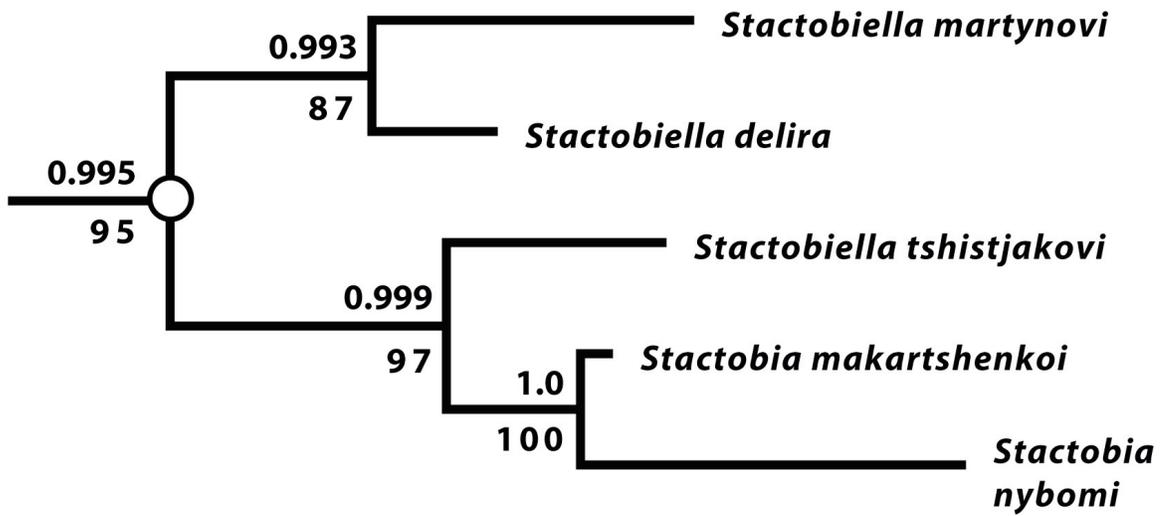


Figure 10. Phylogeny of Hydroptilidae, Stactobiinae. Symbols as in Figure 1.

Chapter II. A revision of the Neotropical caddisfly genus *Leucotrichia* Mosely, 1934 (Hydroptilidae: Leucotrichiinae)

INTRODUCTION

The genus *Leucotrichia* Mosely, 1934 belongs to the family Hydroptilidae, the micro- or purse-case making caddisflies, and is the type genus for the subfamily Leucotrichiinae. The genus was originally established for a single species, *Leucotrichia melleopicta*, from Mexico (Tabasco). Additional species descriptions and distributions have been provided by numerous authors and the genus now contains a total of 29 extant species (Table 1). A single fossil species, *Leucotrichia adela*, is known from Dominican amber. The genus is endemic to the New World and its distribution includes most of the continental USA, Central America, and northern South America (Table 1) (Flint *et al.*, 1999).

In the original description, Mosely (1934) referred to the presence of ocelli, antennal joints in series of white and brown, a well-developed frenulum arising from the subcosta on the hind wing, legs with very dense setae, and a 1, 3, 4 tibial spur formula in the generic diagnosis. Structures of the maxillary and labial palpi were not described by Mosely. Features of the male genitalia and a forewing measurement of 2 mm were given in the species description of *L. melleopicta*. Male genitalia features included the flattened terminal dorsal segment covering the genitalia, the deeply excised terminal ventral segment bearing setose margins, a spade-shaped “penis sheath,” and a slender process on

the penultimate abdominal segment. Illustrations of the wing venation and the male genitalia were included in the description of the type species (Mosely, 1934, figs. 46-47).

As additional new species were described and placed in *Leucotrichia*, Flint (1970), in his generic revision, noted that there were certain characters that could be used to unite 2 species groups within the genus. Additional details regarding these species groups are discussed under “Species Relationships.” In his revision, Flint also provided several additional characters for generic-level diagnosis that had not been included in the original generic description by Mosely. Included were the pentagonal metascutellum, the heavily sclerotized trianguloid plate of tergite X, the subgenital plate extending ventrally from the ventral angles of tergite X to the base of the inferior appendages, the subapical spine of the inferior appendages, and the midlength complex of the phallus. Details regarding the wings were not included in Flint’s revision. In her review of all hydroptilid genera known at the time, Marshall (1979) stated that the wings of *Leucotrichia* were unmodified and made no mention of the well-developed frenulum originally mentioned by Mosely (1934).

Larvae have been associated with some species of *Leucotrichia*, but many are still unassociated (Flint *et al.*, 1999). The known larvae are typical of the Leucotrichiinae in that large sclerites are present on 8 or 9 abdominal segments, only the pronotum is divided longitudinally, all legs are short and robust, and the submentum is divided (Flint, 1970). The genus can be recognized, however, by the rugose or papillate head, single tarsal claw, and femora bearing spiniform dorsal setae (Marshall, 1979). Wiggins (1996) noted the lack of lacunae on the dorsal abdominal sclerites and that the basal seta on each

tarsal claw is not enlarged. The first 4 instars are strongly depressed, generally no more than 5 mm in length, and are free-living and found in fast flowing water on the upper surface of rocks, grazing on periphyton (McAuliffe, 1982; Wiggins, 1996). During the fifth and final retreat dwelling instar, the larva constructs a fixed, silken shelter within which it lives and continues to feed by extending its forelegs from openings in either end of the retreat (Flint, 1991; Wiggins, 1996). During this time, the larva displays extreme lateral distention of abdominal segments V-VII (Wiggins, 1996). The retreats are generally flattened, oval cases no longer than 5.5 mm, slightly domed, and tightly attached to the surface of a rock or boulder. (Marshall, 1979; Wiggins, 1996).

Like other members of Hydroptilidae, *Leucotrichia* adults are minute, although by reaching a length of 5 mm they represent some of the larger species in the family. Many species bear patches of bright green setae on their forewings, which may fade to a lighter green or yellow color in older, pinned specimens. Adults occasionally come to light at night, but usually are collected from marginal foliage during the day with a net (Flint *et al.*, 1999). Females have been associated for some species, but many remain unassociated.

The most recent works to assess *Leucotrichia* include those done by Flint (1970), Marshall (1979), and Oláh and Johanson (2011). In Flint's (1970) revision, he proposed the subfamily Leucotrichiinae for *Leucotrichia* and its related genera: *Abtrichia*, *Acostatrichia*, *Alisotrichia*, *Anchitrichia*, *Betrichia*, *Costatrichia*, *Peltopsyche*, and *Zumatrichia*. He also stated that the subfamily could be divided into 2 definite units, 1 consisting of *Alisotrichia* and the other consisting of all the other genera. Aside from this

division, Flint made no mention of a more definite placement of *Leucotrichia* in regards to generic relationships within the subfamily. In Marshall's (1979) review, at which time there were still only 10 described species of *Leucotrichia*, she also refrained from stating to which other genera *Leucotrichia* might be most closely related. Since then, many new species have been described and added to the genus, including 2 described by Oláh and Johanson (2011). In this same work, Oláh and Johanson also divided Leucotrichiinae into 2 generic clusters: the *Leucotrichia* genus cluster, which included *Abtrichia*, *Acostatrichia*, *Anchitrichia*, *Ascotrichia*, *Betrichia*, *Ceratotrichia*, *Costatrichia*, *Leucotrichia*, and *Zumatrichia*, and the *Celaenotrichia* genus cluster, which included *Alisotrichia*, *Byrsopteryx*, *Celaenotrichia*, *Cerasmatrichia*, *Mejicanotrichia*, and *Scelobotrichia*. The *Leucotrichia* genus cluster can be distinguished from the *Celaenotrichia* genus cluster by members that share a modified spur formula and the typical leucotrichiine phallic median complex originally described in 1970 by Flint (Oláh and Johanson, 2011). Table 2 summarizes the features briefly outlined by Oláh and Johanson (2011) that can be used to distinguish the genus *Leucotrichia* from other members of the *Leucotrichia* genus cluster.

In addition to the characters listed in Table 2, I propose a few previously mentioned characters that can be used to distinguish members of the genus. The structure of the subgenital plate mentioned by Flint (1970), with the presence of the ventral arm, and occasionally the dorsal arm, is a synapomorphy of *Leucotrichia* (Figs. 2A, 10A). Additionally, I propose the very prominent row of elongate setae along the posterolateral margin of segment IX as unique to *Leucotrichia* (Fig. 2A). The genus *Leucotrichia* is

monophyletic based on these characters, which can be used to separate them from other leucotrichiine genera. The well-developed frenulum of the hind wing, first mentioned by Mosely (1934) in the original description, combined with the absence of any wing modifications, such as a pouch or bulla, although not a uniquely derived synapomorphy of the genus, is helpful when distinguishing *Leucotrichia* from other genera (Fig. 1E).

The subfamily Leucotrichiinae has been recovered as a clade using molecular evidence and modern statistical methods with strong nodal support for its monophyly, as discussed in Chapter 1 of this dissertation. However, the genera traditionally recognized as members of the subfamily have historically been difficult to separate (Flint, 1970; Marshall, 1979). Further work is needed to delimit the genera and properly assess their taxonomic and phylogenetic status. This review of *Leucotrichia* was undertaken as a first attempt to define the boundaries of the leucotrichiine genera. This review improves our knowledge of the genus by defining characters that separate *Leucotrichia* from other leucotrichiine genera (discussed above) and by establishing a standardized terminology of the male genitalic structures among species of the genus. Additionally, I re-describe and illustrate the 30 known *Leucotrichia* species and describe 13 new species, bringing the total number of species to 43. Finally, I provide a key to the males of *Leucotrichia*.

MATERIALS and METHODS

Specimen preparation and observation

To observe structural features of the male genitalia, soft tissues were cleared following procedures explained in detail by Blahnik *et al.* (2007). Abdomens, including genitalia, were removed from specimens using microscissors and placed individually in carefully labeled Pyrex® test tubes (10 x 75 mm), each containing 2-3 milliliters of 85% lactic acid. Test tubes were then heated in a Fischer Scientific dry bath incubator at approximately 120°C for 30-35 minutes. At the end of this time, abdomens were carefully removed from the test tubes and rinsed in ethanol to gently flush away any remaining lactic acid. For some specimens, the head was also removed and cleared to more easily observe modifications and eversible structures obscured by dense setae. For specimen examination, cleared genitalia were placed in a standard glass microscope depression slide (1.5 cm diameter x 3 mm deep well) with glycerin and glass microbeads (average diameter 0.5 mm). The glass microbeads held the genitalia in place and allowed structures to be viewed in precise lateral, dorsal, and ventral positions. Genitalia were examined with an Olympus BX41 compound microscope at 250-500 X magnification. Due to their small size and reduced venation, the wings of Hydroptilidae do not provide reliable taxonomic characters (Marshall, 1979; Schmid, 1998). For these reasons, forewing length only has been provided in species descriptions.

Illustrations and descriptions

Structures were traced in pencil with the use of an Olympus drawing attachment (model U-DA) mounted on the microscope. Pencil sketches were then scanned (Fujitsu ScanSnap S1500M scanner), edited in Adobe Photoshop (v. 9.0.2, Adobe Systems Inc.),

and used as a template in Adobe Illustrator (v. 13.0.2, Adobe Systems Inc.) to be digitally inked. Electronic “drawing” was completed with the aid of a graphics tablet (Bamboo Splash, Wacom Company, Limited). Species descriptions were constructed using the program DELTA (Dallwitz *et al.*, 1999 onwards), which uses a species x character state data matrix to produce natural-language descriptions and promote consistency in descriptive taxonomy.

Description of female specimens has been deferred for several reasons. Since female specimens were available for less than half of the species addressed in this study (18 of 43), comprehensive female descriptions for each species were not possible. Of the females examined, no noticeable or informative differences were observed. While some female specimens were collected from the same locality and date as males, there is still some uncertainty of association. For these reasons, species descriptions reflect observation of male specimens only. Females of some species were included in “Material Examined” for the purpose of establishing a record of occurrence and because presumptive association may prove useful for future studies.

Morphological terminology

Morphological terminology used for male genitalia was adapted from Marshall (1979) and Flint (1970). For simplicity, paired structures are discussed in the singular. Terminology for specific structures is indicated in Figures 1-2, 7, and 9. The wing venation terminology of Figure 1E follows the Comstock-Needham system as interpreted by Ross (1956) and Marshall (1979).

Depositories

Types and material examined for this study are deposited at the Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Mexico City, Mexico, (CNIN); Coleção Entomológica Professor José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (DZRJ); Instituto Miguel Lillo, Tucumán, Argentina, (IML); Illinois Natural History Survey, Champaign, Illinois, USA (INHS); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela (MIZA); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museo de Zoología, Universidad Tecnológica Indoamérica, Quito, Ecuador (MZUTI); Natural History Museum, London, United Kingdom (NHM); Swedish Museum of Natural History, Stockholm, Sweden (NHRS); National Museum of Natural History, Washington, D.C., USA (NMNH); Dr. Janós Oláh Private Collection, presently under national protection of the Hungarian Natural History Museum, Hungary (OPC); University of Minnesota Insect Collection, Saint Paul, Minnesota, USA (UMSP); and Zoologisch Museum Universiteit van Amsterdam, The Netherlands (ZMUA).

Specimen management followed the procedures outlined by Holzenthal and Anderson (2004). Each pinned specimen examined during the study was affixed with a barcode label (4 mil polyester, 8 x 14 mm, code 49) bearing a unique alphanumeric sequence beginning with the prefix UMSP. Specimens in alcohol were given a single

barcode label to represent all those in a single vial. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection and to provide unique identification of specimens. Specimens that had already been affixed with a label bearing a unique identification number from their home depository were not given an additional UMSP barcode. Specimen-level taxonomic, locality, collection, and other information are stored in the University of Minnesota Insect Collection Biota Trichoptera Database using the open-source software Biota v. 3.0 (Colwell, 2012).

SYSTEMATICS

Generic Description

Genus *Leucotrichia* Mosely, 1934

Leucotrichia Mosely, 1934:157 [Type species: *Leucotrichia melleopicta* Mosely 1934, original designation]. Flint, 1970:3 [key, revision]. —Marshall, 1979:178 [review of the genus]. —Oláh and Johanson, 2011:152 [discussion of *Leucotrichia* genus cluster].

Male. Length of forewing ca. 2.0–5.0 mm. Wings unmodified, in that they lack a pouch,

bullae, or patches of scales; forewing broad basally, acute apically; hind wing narrow, more acute than forewing, with row of hooked setae basal to cross vein r (Fig. 1E), edges with long setal fringe. Head with 2 or 3 ocelli; bearing setae and pair of setiferous posterolateral warts, dorsal region sometimes bearing modifications such as eversible posterolateral warts, patches of scales in place of setae, or setiferous protuberances (Figs. 1A, 3, 4); antennae generally simple and unmodified, in that all flagellomeres are of uniform size and shape, except in some species in which they may be elongate or have an inflated appearance (Figs. 1A, 3, 4). Maxillary palps with 5 segments, labial palps with 3 segments (Fig. 1B). Tibial spur count 1, 3, 4 (Fig. 1D). Mesoscutellum with transverse suture; metascutellum pentagonal (Fig. 1C). *Genitalia*. Abdominal sternum VII with single mesoventral process or tuft of prominent setae (Fig. 2B, 34B). Sternum VIII produced posteroventrally beneath segment IX (Fig. 2B), with a posteromesal division (Fig. 2D). Segment IX completely open ventrally (Fig. 2D), posterolateral margin with row of prominent setae (Fig. 2A). Tergum X with heavily sclerotized lateral plates, consisting of ventral and dorsal sclerites, and membranous apex (Fig. 2A). Subgenital plate connected dorsally to ventral angles of tergum X sclerites, produced ventrally as elongate mesal sclerite extending to base of inferior appendage, sometimes with dorsal arm (Fig. 10A), always with ventral arm (Fig. 2A, 10A). Inferior appendage simple, elongate, sometimes fused mesoventrally, generally with dorsal spine (Fig. 2A, 2D). Phallus tubular basally, constricted at midlength with median complex bearing basal loop and pair of spherical "windows" (Figs. 8E, F), basal loop sometimes extended on pair of basal supports (Fig. 10F); apex large, membranous, sac-like, generally bearing spines or

sclerites.

Species relationships

The species of *Leucotrichia* are divided into 2 main species groups based on adult features, as originally defined by Flint (1970). The *pictipes* species group is considerably smaller in species diversity than the *melleopicta* species group consisting of only *L. fairchildi*, *L. imitator*, *L. pictipes*, and *L. sarita* (Table 1).

Characters that distinguish members of the *L. melleopicta* species group include males bearing 3 ocelli, a mesoventral process on sternum VII, an unmodified head (except for *L. chiriquiensis*), and 1 or 2 large patches of colored setae on the forewings. These characters all seem to represent the primitive state and should not be used to establish monophyly of the *melleopicta* group, although they can perhaps be used as diagnostic features to help identify species within the genus.

Characters distinguishing the *L. pictipes* species group include males bearing 2 ocelli, either a brush of setae or a simple point on sternum VII, a modified head (except for *L. imitator*) as discussed above under the generic description, and colored spots or linear setal patterns on the forewings. These characters, particularly the reduced number of ocelli and the modifications to the head, may represent synapomorphies for this group of species within the genus.

While the specialized members of the *pictipes* group may form a monophyletic species group, the same cannot be said with certainty of the members of the *melleopicta* group, as they share no synapomorphies that could unite them. Despite being much larger

in terms of species numbers, no synapomorphic adult characters were found within the *melleopicta* group that could be used to support its monophyly or to divide it into monophyletic species groups. The 2 species groups, *melleopicta* and *pictipes*, are retained here for historical relevance. All species newly described here have 3 ocelli and are placed in the *melleopicta* species group, which is consistent with its definition.

Species Descriptions

Leucotrichia melleopicta Mosely, 1934, type species

Fig. 1, 2

melleopicta Mosely, 1934:157 [Type locality: Mexico, Tabasco, Teapa; NHM; male]. — Flint, 1970:5 [male], 1981:25 [distribution].

Diagnosis. This species is similar to *L. mutica*. Both of these species possess an inferior appendage that is broadest mesally in lateral view and digitate in ventral view and the dorsal sclerite of the phallus in each species has an apical emargination. *Leucotrichia melleopicta* can be recognized by the enlarged apex of the mesoventral process on sternum VII, the apical emargination of the ventral arm of the subgenital plate, and the basal fusion of the inferior appendages.

Description. *Male.* Length of forewing 1.9–2.5 mm (n=9). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia.* Abdominal

sternum VII with elongate mesoventral process with enlarged apex. Sternum VIII in ventral view with posterior margin concave with rounded mesal emargination. Segment IX anterolateral margin straight, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with tridentate posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm arched mesally, apex slightly flared (Fig. 2A), in ventral view with rounded apical emargination. Inferior appendage broadest mesally, apex rounded, bearing single dorsal spine; in ventral view fused basally, subspatulate. Phallus with "windows" of median complex not apparent, basal loop composed of 2 separate filaments, apex bearing dorsal sclerite with crenulate margins and pair of elongate internal sclerites.

Material examined. *Holotype male*: **MEXICO: Tabasco:** Teapa, collected in March, H. H. Smith, slide mounted (NHM). *Nontypes*: **MEXICO:Veracruz:** Laguna Escondido, 28.iii.1976, J. Bueno, 7 males, 2 females (in alcohol) (NMNH); **VENEZUELA: Aragua:** Río El Limón, fish hatchery, Maracay, 3-6.ii.1976, C.M. and O.S. Flint, Jr., 1 female (NMNH); Río El Limón, fish hatchery, Maracay, 19-20.v.1975, F.H. Weibezahn, 1 male (in alcohol) (NMNH).

***Leucotrichia adela* Wells and Wichard, 1989 †**

Fig. 5

□ *adela* Wells and Wichard, 1989:42 [Type locality: Dominican Republic NMNH; male; in amber].

Diagnosis. This species is known only from the male fossil holotype preserved in Dominican amber. While some characteristics of *L. adela* were originally described as difficult to examine and understand, Wells and Wichard (1989) did remark that the species shared similarities in the shape and form of abdominal segment IX and the genitalia with those of *L. chiriquiensis* and *L. tubifex*. It seems appropriate to place it in the *melleopicta* species group, due to the presence of 3 ocelli, an unmodified head, and a mesoventral process on sternum VII.

Description. Redescribed from Wells and Wichard (1989). *Male.* Length of forewing 1.4 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. *Genitalia.* Genitalia obscured and difficult to interpret. Abdominal sternum VII with slender, elongate mesoventral process. Sternum VIII in ventral view with posterior margin concave. Posterior margin of segment IX concave in dorsal view. Membranous apex of tergum X rounded. Inferior appendage bract-like.

Material examined. *Holotype male:* Fossil holotype deposited at NMNH, but unable to be located.

***Leucotrichia alisensis* Rueda Martín, 2011**

Fig. 6

alisensis Rueda Martín, 2011:4 [Type locality: Argentina, Tucumán, Parque Nacional Campo de Los Alisos, Río de las Pavas; IML; male metamorphotype; larva, pupa].

Diagnosis. *Leucotrichia alisensis* is similar to *L. yungarum*; in each, the ventral arm of the subgenital plate is acute in lateral view and the apex of the inferior appendage is digitate in ventral view. Additionally, the shape of the inferior appendage in lateral view is similar in both species, particularly the rounded basal area. *Leucotrichia alisensis* can be recognized by the V-shaped concave posterior margin of sternum VIII, which is U-shaped in *L. yungarum*, and by the curved anterolateral projection which is absent in *L. yungarum*.

Description. Redescribed from Rueda Martín (2011). *Male.* Head unmodified, with 3 ocelli; antennae unmodified. *Genitalia.* Abdominal sternum VII with mesoventral process not apparent. Sternum VIII in ventral view with posterior margin concave with small mesal emargination. Segment IX anterolateral margin with curved ventrolateral production, posterolateral margin irregular. Membranous apex of tergum X slender, extending posteriad, with mesodorsal projection. Subgenital plate with dorsal arm not apparent; ventral arm narrow, apex acute. Inferior appendage rounded basally, apex digitate; in ventral view basally subquadrate. Phallus apex with light dorsal sclerites.

Material examined. *Holotype male:* Holotype deposited at IML, but unable to be obtained.

Etymology. Named for the National Park Campo de Los Alisos, Tucumán,

Argentina, the location where the holotype was collected.

***Leucotrichia angelinae*, new species**

Fig. 7

Diagnosis. *Leucotrichia angelinae*, n. sp., is most similar to *L. fulminea*, n. sp. These species share several similarities in the mesoventral process of sternum VII, inferior appendage, subgenital plate, and phallus, as discussed under *L. fulminea*. In ventral view, the inferior appendage of *L. angelinae* has an oval shape, while the inner margin in *L. fulminea* is concave. *Leucotrichia angelae* can also be distinguished by the presence of a short dorsal arm on the subgenital plate, which is lacking in *L. angelinae*.

Description. *Male.* Length of forewing 3.6–4.4 (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light green and dark brown setae; thorax dark brown with dark brown setae and mint green setae at edges, brown ventrally; leg segments with brown setae. Forewings covered with fine mottled light gray-green setae with dark brown setae along edges. *Genitalia.* Abdominal sternum VII with digitate mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin shallowly concave, posterior margin irregular. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex with dorsal and ventral lobes. Subgenital plate with

dorsal arm short, curved dorsad, tapering apically; ventral arm elliptic with basal projection, in ventral view obovate with 2 small apical projections. Inferior appendage apex rounded, without dorsal spine; in ventral view oval, with subquadrate basal projection on outer margin. Phallus apex bearing pair of slender mesodorsal sclerites and pair of pointed apicodorsal sclerites extending outwards.

Holotype male: VENEZUELA: Mérida: Cacuta, 10 km E Tabay, 22.ii.1976, C.M. and O.S. Flint (UMSP000142591) (NMNH). *Paratypes*: Same data as holotype, 1 male, 1 female (NMNH); 19 km N Mérida, 5600 ft, 9.ii.1978, blacklight, Andean mountain forest, J.B. Heppner, 1 male (UMSP).

Etymology. Named in honor of Angel Fowler, friend and colleague, for all her help in the field.

***Leucotrichia ayura* Flint, 1991**

Fig. 8

ayura Flint, 1991:41 [Type locality: Colombia, Dpto. Antioquia, 12 km NW Medellín, road to San Pedro; NMNH; male].

Diagnosis. *Leucotrichia ayura* is most similar to *L. repanda*, n. sp. Both species bear a small mesoventral process on sternum VII, an elongate sternum VIII with a concave posterolateral margin, an anterolaterally produced margin on segment IX, an inferior

appendage curving slightly dorsad with a truncate apex, and a phallus apex with elongate dorsal sclerites. The elongate sclerites in *L. ayura* are U-shaped in lateral view, making this species distinct from *L. repanda*. The phallus apex of *L. ayura* also bears a pair of small subapicodorsal spines that are absent in *L. repanda*. Additionally, the inferior appendages of *L. ayura* are separate, while they are fused in *L. repanda*.

Description. *Male.* Length of forewing 2.3–2.9 mm (n=8). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with bright yellow setae; thorax dark brown with bright yellow setae dorsally, brown ventrally; leg segments with dark brown setae. Forewings covered with fine bright yellow setae, apical 1/2 with brown setae. *Genitalia.* Abdominal sternum VII with small, digitate mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin slightly produced mesally, posterolateral margin with shallow mesal depression; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite simple; ventral sclerite with rounded projection on posterior margin; membranous apex rounded. Subgenital plate with dorsal arm not apparent; ventral arm digitate with small apical projection, in ventral view with rounded apical emargination. Inferior appendage broadest basally, apex truncate, bearing single dorsal spine; in ventral view digitate, with basal projection on outer margin. Phallus apex bearing pair of elongate dorsal sclerites (U-shaped and with slightly enlarged dorsal apex in lateral view) and pair of small, dark, subapicodorsal spines.

Material examined. *Holotype male:* **COLOMBIA: Antioquia:** 12 km NW Medellín, rd. to San Pedro, 13.ii.1983, O.S. Flint, Jr. (USNM 104529) (NMNH).

Paratypes: Same data as holotype, 2 males, 1 female (NMNH); **COLOMBIA**:

Antioquia: Quebrada Agua Mala, 34 km NW Medellín, 14.ii.1983, O.S. Flint, Jr., 2 males (NMNH); 12 km NW Medellín, rd. to San Pedro, 20.ii.1984, C.M. and O.S. Flint, Jr., 1 male (NMNH); Quebrada La Ayurá above Envigado, 21.ii.1984, C.M. and O.S. Flint, Jr., 1 male (NMNH); Quebrada La Ayurá, Mun. Envigado, elev. 1750 m, 29.iii-28.iv.1983, trap B, U. Matthias, 3 males, 2 females (in alcohol) (NMNH). *Nontypes*:

COLOMBIA: Antioquia: 7 km E San Jerónimo, 23.ii.1984, C.M. and O.S. Flint, Jr., 1 female (NMNH).

Etymology. Assumedly named for Quebrada La Ayurá, the location where some of the paratypes were collected.

***Leucotrichia bicornuta* Thomson, 2012**

Fig. 9

bicornuta Thomson, 2012:4 [Type locality: Brazil, Rio de Janeiro, Panedo, Rio das Pedras, Três Bacias; DZRJ; male].

Diagnosis. This species is similar to *L. dianeae*, n. sp., *L. extraordinaria*, and *L. tapantia*, n. sp. In each of these species, the posterolateral margin of sternum VIII is produced, with the apex of the production bearing either prominent setae or a peg-like seta. The shape of the phallus apex is also similar in each of these species, with each bearing a pair

of membranous apical lobes and lacking any external spines or sclerites. *Leucotrichia bicornuta* differs from the other 3 species in having fused inferior appendages and a distinct, irregularly shaped dorsal arm of the subgenital plate.

Description. *Male.* Length of forewing 2.5–3.4 mm (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII with digitate mesoventral process with small basal ridge. Sternum VIII posteromesal production bearing long, prominent setae; in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin irregular; in dorsal view anterior margin convex, posterior margin concave. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with tridentate posterior margin; membranous apex suborbicular. Subgenital plate with dorsal arm irregular, bent sharply dorsad (Fig. 9A); ventral arm short, digitate, with basal projection, laterally obscured from view by inferior appendage (Fig. 9A), in ventral view with rounded apical emargination. Inferior appendage arched mesally, apex hooked dorsally, bearing single dorsal spine; in ventral view entirely fused, apex with emargination. Phallus apex bearing paired apicodorsal lobes, no spines or sclerites apparent.

Material examined. *Holotype male:* **BRAZIL: Rio de Janeiro:** Panedo, Rio das Pedras, Três Bacias, 22°24'32.2"S 44°33'06.6"W, elev. 735 m, 6.iii.2008, Nessimian, Dumas, de Souza, and Braga (in alcohol) (UMSP000014084) (DZRJ). *Paratypes:* **Brazil: Rio de Janeiro:** Itatiaia, Parque Nacional do Itatiaia, Rio Camp Belo, 22°27'17.32"S 44°36'37.47"W, elev. 705 m, 13.iv.2007, light, Santos, Dumas, Ferreira, Jr., and

Nessimian, 2 males, 1 female (in alcohol) (DZRJ).

Etymology. *Bi*, Latin for “double”; *cornutus*, Latin for “horned,” referring to the 2 apicodorsal lobes of the phallus.

***Leucotrichia botosaneanui* Flint, 1996**

Fig. 10

botosaneanui Flint, 1996:86 [Type locality: Tobago, big waterfall 4 km S Charlotteville, NMNH; male]. —Botosaneanu and Sakal, 1992:201 [biology, as *limpia*]. — Botosaneanu and Alkins-Koo, 1993:8 [larva, as *limpia*, according to Flint, 1996:86].

Diagnosis. *Leucotrichia botosaneanui* is most similar to *L. chiriquiensis*, *L. hispida*, n. sp., *L. limpia*, and *L. viridis*. In all these species, the phallus bears a similar combination of characteristics: elongate basal supports on the midlength complex; a pair of small, membranous, apical lobes; and a membranous “bulge” on the ventral surface. Additionally, the posterolateral margin of sternum VIII is produced in each of these species. *Leucotrichia botosaneanui* can be separated from the other 4 species by the small, double-pointed mesoventral process on sternum VII and the pair of lateral sinuate sclerites present ventrolaterally on the phallus apex.

Description. *Male*. Length of forewing 2.0–2.3 mm (n=6). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with yellow and dark brown

setae; thorax dark brown with dark brown and yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine yellow setae, apical 1/4 with dark brown setae. *Genitalia*. Abdominal sternum VII with small, double-pointed mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally; in dorsal view anterior margin shallowly concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex amorphous. Subgenital plate with dorsal arm slender, digitate; ventral arm tapering apically, in ventral view with small apical emargination and slightly subapically constricted. Inferior appendage short, with small basal emargination, broadest mesally, bearing single dorsal spine; in ventral view subspatulate, apex slightly produced. Phallus with median complex bearing elongate basal supports, apex bearing pair of apicodorsal lobes, pair of dark dorsal sclerites, and pair of lateral sinuate sclerites.

Material examined. *Holotype male*: **TOBAGO**: Charlotteville, 4 km S, big waterfall, elev. 125 m, 11°19'N 60°33'W, 10.vi.1993, by net, O.S. Flint, Jr. and W.N. Mathis (USNM 105436) (NMNH). *Paratypes*: Same data as holotype, 3 males, 2 females (NMNH); same data as holotype, 1 male (in alcohol) (NMNH); **TRINIDAD**: streamlet below Maracas Waterfall, elev. 250 m, 10°44'N 61°24'W, 18.vi.1993, UV light, N.E. Adams and W.N. Mathis, 1 female (NMNH); Lalaja Rd. streamlet, elev. 520 m, 10°43'N 61°17'W, 26.vi.1993, UV light, N.E. Adams and W.N. Mathis, 1 male, 1 female (NMNH).

Etymology. Named in honor of Dr. Lazare Botosaneanu, a naturalist and

entomologist formerly of the Zoological Museum of the University of Amsterdam.

***Leucotrichia brasiliانا* Sattler and Sykora, 1977**

Fig. 11

brasiliانا Sattler and Sykora, 1977:239 [Type locality: Brazil, Amazonas Staat, bereich des Rio Marauía, bei Tapuruquara, oberer Rio Negro; type depository unknown; male; larva, pupa, case].

Diagnosis. This species is most similar to *L. sidneyi*, n. sp. The phallus apex in both species bears a membranous “bulge” on the ventral surface (Fig. 11D), a pair of apical lobes, and no apical spines or sclerites. In *L. brasiliانا*, the phallus apex bears a pair of lateral sclerites that are U-shaped in lateral view and not present in *L. sidneyi*. The membranous portion of the phallus apex of *L. brasiliانا* is truncate in both lateral and dorsal view, while it is small and rounded in *L. sidneyi*.

Description. Holotype unknown, topotypes pharate adults. *Male*. Length of forewing 1.3–1.7 (n=2). Head unmodified, but with mandibles (pharate adult), with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia*. Abdominal sternum VII with mesoventral process broken (indicated in Fig. 11C). Sternum VIII torn in all specimens and difficult to examine in lateral view; in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin with

shallow mesal depression; in dorsal view anterior margin straight, posterior margin broadly concave. Tergum X with dorsal sclerite slender, elongate; ventral sclerite large, semielliptic, with tridentate posterior margin; membranous apex truncate. Subgenital plate with dorsal arm not apparent; in ventral view ovate. Inferior appendage broadest basally, apex rounded, bearing single dorsal spine; in ventral view broadly rounded on outer margin. Phallus apex bearing pair of elongate sclerites (U-shaped in lateral view) and pair of apicodorsal lobes.

Material examined. *Topotypes*: **BRAZIL: Amazonas:** from Sattler collection 23, Sattler, 2 larvae, 2 male metamorphotypes, 4 adult metamorphotypes of undetermined gender (NMNH).

Etymology. Assumedly named for the country of Brazil, where the species was collected.

***Leucotrichia brochophora* Flint, 1991**

Fig. 12

brochophora Flint, 1991:41 [Type locality: Colombia, Dpto. Antioquia, Quebrada Espadera, 7 km E Medellín, road to Sta. Elena; NMNH; male].

Diagnosis. This species is most similar to *L. lerma*, *L. padera*, and *L. rhomba*, n. sp. Each of these species possess a phallus with no spines and few, if any, elongate sclerites on the

membranous apex; a mild, broad production on the posterolateral margin of sternum VIII; and a produced anterolateral margin on segment IX. *Leucotrichia brochophora* can be recognized by the presence of basal supports on the basal loop of the phallus midlength complex, a small mesoventral process on sternum VI, and stout pegs on the posterolateral margin of segment IX, all of which are absent in the other 3 species.

Description. *Male.* Length of forewing 5.2 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head cleared in holotype, brown, denuded; thorax brown with dark brown and yellow setae dorsally, brown ventrally; leg segments with light brown setae. Forewings covered with fine yellow setae, apical 1/3 with dark brown setae. *Genitalia.* Abdominal sternum VI with small pointed mesoventral process (Fig. 12D), obscured by setae in lateral view. Abdominal sternum VII with mesoventral process broken (indicated in Fig. 12D). Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin convex with stout peg-like setae dorsolaterally; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite simple; ventral sclerite lower half bent anteriorly; membranous apex suborbicular. Subgenital plate with dorsal arm not apparent; ventral arm tapering apically, in ventral view apex broadly rounded. Inferior appendage with knoblike basal projection, apex truncate, bearing single dorsal spine; in ventral view with subbasal subtriangular emargination on inner margin, apex rounded. Phallus with median complex bearing basal supports; apex bearing 3 pairs of elongate sclerites: 1st pair dorsal and with shallow apical emargination, 2nd pair dorsal and with small apical projection, 3rd pair lateral and slender.

Material examined. *Holotype male*: **COLOMBIA: Antioquia:** Quebrada Espadera, 7 km E Medellín, road to Sta. Elena, 24.ii.1983, O.S. Flint, Jr. (USNM 104527) (NMNH).

***Leucotrichia chiriquiensis* Flint, 1970**

Fig. 4A, 13

chiriquiensis Flint, 1970: 6 [Type locality: Panama, Chiriqui, Alto Lino above Boquete; NMNH; male; larva, case].

Diagnosis. *Leucotrichia chiriquiensis* is most similar to *L. botosaneanui*, *L. hispida*, n. sp., *L. limpia*, and *L. viridis*. These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. botosaneanui*. This species differs from the other 4 in having a small set of dorsal hooks between the apical lobes of the phallus apex. It can most easily be separated from the others by the modifications present in the antennae and head.

Description. *Male*. Length of forewing 2.1–2.9 mm (n=31). Head with short, black, contiguous setae anteriorly (which leave irregular shapes when removed) and a pair of internal structures filled with similar setae, with 3 ocelli; antennae with scape elongate, anterior face indented and filled with dense patch of setae. Dorsum of head dark brown with light yellow setae; thorax dark brown with yellow setae dorsally, brown ventrally;

leg segments with brown setae. Forewings covered with fine yellow setae, apical 1/4 with patch of brown setae. *Genitalia*. Abdominal sternum VII with slender, elongate mesoventral process with apex enlarged, rugose in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin with shallow mesal depression; in dorsal view anterior margin concave, posterior margin broadly convex. Tergum X with dorsal sclerite slender, bent ventrad; ventral sclerite semielliptic with tridentate posterior margin; membranous apex suborbicular. Subgenital plate bent mesally; with dorsal arm not apparent; ventral arm tapering apically, curved ventrad, in ventral view base subtriangular and apex rounded. Inferior appendage dorsomesally "humped," bearing single dorsal spine; in ventral view with small subapical emargination on inner margin. Phallus with median complex bearing elongate basal supports, apex bearing pair of elongate lateral sclerites and pair of dorsal hooks between pair of apical lobes.

Material examined. *Holotype male (pharate): PANAMA: Chiriqui:* Alto Line above Boquete, 16-17.vii.1967, O.S. Flint, Jr. and Ortiz, (in alcohol) (USNM 70896) (NMNH). *Paratypes:* Same data as holotype, 2 males, 1 female (pharates) (in alcohol) (NMNH). *Nontypes: COSTA RICA:* Cartago, Reserva Tapantí, Río Grande de Orosi, elev. 1650 m, 9.686N 83.756W, 18-21.iii.1987, Holzenthal, Hamilton, and Heyn, 28 males; Cartago, Reserva Tapantí, Río Grande de Orosi, elev. 1650 m, 9.686°N 83.756°W, 18-21.iii.1987, Holzenthal, Hamilton, and Heyn, 5 females (UMSP).

Etymology. Assumedly named for Chiriquí Province in Panama, where the holotype was collected.

***Leucotrichia denticulata*, new species**

Fig. 14

Diagnosis. *Leucotrichia denticulata*, n. sp., can be separated from all other *Leucotrichia* species by a suite of characteristics found on the phallus. The presence of the pair of mesolateral lobes, pair of large apically-hooked sclerites, and pair of apical lobes bearing peg-like setae create a phallus distinct to *L. denticulata* (Figs. 14E, F).

Description. *Male.* Length of forewing 3.7–4.2 mm (n=2). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII with digitate mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin shallowly concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with crenulate posterior margin; membranous apex suborbicular. Subgenital plate with dorsal arm digitate; ventral arm rounded basally, tapering apically, in ventral view sublanceolate. Inferior appendage arched mesally, apex truncate, bearing single dorsal spine; in ventral view entirely fused, with basal projection on outer margin, apex with emargination. Phallus apex bearing pair of mesolateral lobes, pair of hooked mesodorsal sclerites, and pair of apical lobes with row of peg-like setae.

Holotype male: **MEXICO: Nuevo Leon:** Municipio de Santiago, Arroyo San Juan

on road to Laguna de Sanchez, 3.5 km W La Cienegra, 25°24'N 100°17'W, 1400m, 13.v.1989, Harris and Contreras (in alcohol) (UMSP000142916) (UMSP). *Paratype*: Same data as holotype, 1 male (in alcohol) (UMSP).

Etymology. *Denticulatus*, Latin for “with small teeth,” referring to the row of peg-like setae on the apical lobes of the phallus.

***Leucotrichia dianaeae*, new species**

Fig. 15

Diagnosis. This species is similar to *L. bicornuta*, *L. extraordinaria*, and *L. tapantia*, n. sp. These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. bicornuta*. Of these species, *L. dianaeae*, n. sp., is most similar to *L. tapantia*, as discussed under *L. tapantia*. The apical lobes of the phallus apex of *L. dianaeae* arise from the same apicomeral location on the apex, while those of *L. tapantia* are separated from each other in more apicolateral locations. Additionally, the mesal projection on the posterior margin of sternum VIII is pointed in *L. dianaeae* and rounded in *L. tapantia*. The rugose ventral surface of the apex of the mesoventral process on sternum VII separates *L. dianaeae* from all 3 of the other species.

Description. *Male*. Length of forewing 3.4–4.1 mm (n=10). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with yellow setae; thorax

dark brown with dark brown and yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine yellow setae with dark brown setae at edges and apex. *Genitalia*. Abdominal sternum VII with pointed, rugose mesoventral process with small basal ridge. Sternum VIII lateral production elongate, extending dorsad, apex bearing tuft of prominent setae (Fig. 15B), in ventral view with posterior margin concave with small, pointed mesal projection (Fig. 15D). Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with tridentate posterior margin; membranous apex subquadrate. Subgenital plate with dorsal arm digitate; ventral arm slender, arched mesally, apex acute, in ventral view oblong. Inferior appendage broadest basally, apex digitate, bearing single dorsal spine; in ventral view with basal projection on outer margin and emargination on inner margin. Phallus apex bearing pair of internal apodemes, pair of broad mesolateral membranous lobes, apex divided into pair of lateral lobes.

Holotype male: **COSTA RICA**: Cartago, Reserva Tapantí, waterfall, ca. 1km (road) NW tunnel, 9.69°N 83.76°W, 2-3.viii.1990, el. 1600 m, Holzenthal, Blahnik, and Muñoz (UMSP000201649) (UMSP). *Paratypes*: same data as holotype, 9 males (UMSP); Cartago, Reserva Tapantí, waterfall, ca. 1km (road) NW tunnel, 9.69°N 83.76°W, 2-3.viii.1990, el. 1600m, Holzenthal, Blahnik, and Muñoz, 1 male (in alcohol) (UMSP); Cartago, Reserva Tapantí, waterfall, ca. 1 km (road) NW tunnel, 9.69°N 83.76°W, 10.vi.1988, el. 1600m, C.M. and O.S. Flint and R.W. Holzenthal, 1 male (NMNH).

Etymology. Named in honor of R. E. Thomson's mother, Diane Thomson, who has

always been supportive of her daughter's entomological inclinations.

***Leucotrichia dinamica* Bueno-Soria, 2010**

Fig. 16

dinamica Bueno-Soria 2010:23 [Type locality: Mexico, Distrito Federal, Delgación Magdalena-Contreras, Parque “Los Dinamos”; CNIN; male].

Diagnosis. *Leucotrichia dinamica* is distinct from all other species in the genus due to the presence of the large scissor-like apical sclerites on the phallus apex (Fig. 16F). The semielliptic sclerite found on the basal loop of the phallus midlength complex is also unique to *L. dinamica*.

Description. *Male.* Length of forewing 5.1 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII with acute mesoventral process with apex enlarged in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin produced dorsolaterally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex truncate. Subgenital plate with dorsal arm slender, arched mesally, apex slightly hooked dorsad; in ventral view, ovate and produced apically with small emargination; ventral arm digitate, apex slightly

hooked dorsad, in ventral view oval. Inferior appendage dorsomesally "humped," apex acute, bearing single dorsal spine; in ventral view with elongate basal projection strongly bent inward, apex strongly curved outward. Phallus with basal loop with mesal semielliptic sclerite and removed from "windows," apex bearing pair of elongate internal sclerites and pair of scissor-like apical sclerites.

Material examined. *Holotype male*: **MEXICO: Distrito Federal:** Delegación Magdalena-Contreras, Parque "Los Dinamos," elev. 3091 m, 29.vi.2007, M. Razo and R. Juarez (in alcohol) (UMSP000140694) (CNIN).

Etymology. Named for Los Dinamos, the location where the holotype was collected.

***Leucotrichia extraordinaria* Bueno-Soria, Santiago-Fragoso, and Barba-Álvarez, 2001**

Fig. 17

extraordinaria Bueno-Soria, Santiago-Fragoso, and Barba Álvarez, 2001:145 [Type locality: Mexico, Tabasco, Municipio de Huimanguillo, Arroyo las Flores, Villa de Guadalupe 2ª sección Los Chimalapas, km 5 Ruta Malpasito-Carlos A. Madrazo, 17°22'05"N, 93°36'25"W; CNIN; male].

Diagnosis. This species is similar to *L. bicornuta*, *L. dianaeae*, and *L. tapantia*, n. sp.

These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. bicornuta*. *Leucotrichia extraordinaria* can be easily recognized by the single peg-like seta that occurs on the apex of the posterolateral production of sternum VIII; the other 3 species all bear long, prominent setae in this location. The posterolateral production is also much narrower and more acute in *L. extraordinaria* than in the other 3 species. Additionally, the concave posterior margin of sternum VIII, when viewed ventrally, is much more rounded in *L. extraordinaria* than in *L. bicornuta*. It also lacks the small mesal projection present in both *L. tapantia* and *L. dianaeae*.

Description. *Male*. Length of forewing 2.4 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia*. Abdominal sternum VII with digitate mesoventral process. Sternum VIII posteroventral production bearing single peg-like spine, in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite broadest mesally, dorsal and ventral apices knoblike; membranous apex with 2 digitate projections and 1 large subtriangular projection extending posteriad. Subgenital plate with dorsal arm tapering apically, extending dorsad; ventral arm tapering apically, apex slightly hooked dorsad, in ventral view with small apical emargination. Inferior appendage dorsomesally "humped," bearing single dorsal spine; in ventral view sinuate. Phallus apex bearing multiple pairs of elongate internal sclerites and pair of apical membranous lobes.

Material examined. *Holotype male*: **MEXICO: Tabasco:** Municipio de Huimanguillo, Arroyo las Flores, Villa de Guadalupe 2ª sección Los Chimalapas, km 5 Ruta Malpasito-Carlos A. Madrazo, 17°22'05"N 93°36'25"W, 26.vi.1999, J. Bueno and R. Barba (in alcohol) (UMSP000140695) (CNIN).

Etymology. *Extraordinaria*, Spanish indicating “uncommon,” referring to the shape of sternum VIII.

***Leucotrichia fairchildi* Flint, 1970**

Fig. 3A, 18

fairchildi Flint, 1970:10 [Type locality: Panama, Cocle, El Valle; MCZ; male]; 1968:38 [male, female, Grenada, but misidentified as *sarita*]. —Botosaneanui and Sakal, 1992:201 [biology]. —Flint and Sykora, 1993:54 [Grenada, but misidentified as *sarita*]. —Botosaneanui and Alkins-Koo, 1993:7 [larva, case]. —Leucotrichiini, case 2 Botosaneanui and Alkins-Koo, 1993:14 [female]. —Flint 1996:86 [to synonymy].

Diagnosis. *Leucotrichia fairchildi* is similar to *L. imitator*, *L. pictipes*, and *L. sarita*; the *pictipes* species group consists of these 4 species. In addition to the similarities discussed under “Species Relationships,” these species also possess similarities in the shape of the inferior appendage and sternum VII, when seen in lateral view, and in the presence of

hollow sections of the subgenital plate (Fig. 18A). While the head modifications of *L. fairchildi* may be most similar to those of *L. pictipes*, the broadened basal flagellum of the antennae and the setiferous protuberance on the dorsum of the head make *L. fairchildi* easily distinguishable from *L. pictipes* (Fig. 3A). And both the peglike setae present on the phallus apex (Figs. 18E, F) and the small mesoventral process on sternum VII in place of prominent setae (Fig. 18B) are characteristics that separate *L. fairchildi* from all 3 of the other species.

Description. *Male.* Length of forewing 2.1–3.1 mm (n=53). Head with posterolateral wart large, eversible, with membranous lobe beneath; anteromesally with asymmetrical, setiferous protuberance, with 2 ocelli; antennae with scape enlarged, basal flagellum very broad. Dorsum of head dark brown with light yellow setae; thorax dark brown with light yellow setae dorsally, brown ventrally; leg segments with brown and yellow setae. Forewings covered with fine brown setae with bands of yellow setae basally and scattered patches of yellow setae apically. *Genitalia.* Abdominal sternum VII with short, pointed mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin produced dorsolaterally, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite slender, elongate; ventral sclerite semielliptic with tridentate posterior margin; membranous apex amorphous. Subgenital plate bulbous, with hollow interior; with dorsal arm not apparent; ventral arm slender, acute, extending dorsad, in ventral view lanceolate. Inferior appendage straight, with small apicodorsal projection, bearing single dorsal spine; in ventral view apex hooked inward, broadly rounded on outer

margin. Phallus apex trilobed, 2 lateral lobes with darkened dorsal margin, all 3 lobes bearing peglike setae on dorsal surface.

Material examined. *Holotype male*: Holotype deposited at MCZ, but unable to be located. *Nontypes*: **COLOMBIA: Antioquia:** Quebrada La Jiménez, Municipio Sopetrán, elev. 780 m, trap C, 1983-1984, U. Matthias, 2 females (in alcohol) (NMNH); Quebrada La Jiménez, Municipio Sopetrán, elev. 780 m, trap C, 13.vii.1983, U. Matthias, 1 female (in alcohol) (NMNH); Quebrada La Jiménez, Municipio Sopetrán, elev. 780 m, trap C, 22.v.1983, U. Matthias, 3 males, 3 females (in alcohol) (NMNH); **Tolima:** Armero, near Guayabal, 2-10.ii.1977, #58 malaise trap, E.L. Peyton, 3 males (NMNH); Armero, near Guayabal, 2-10.ii.1977, malaise trap, E.L. Peyton, 1 male (in alcohol) (NMNH); **COSTA RICA: Guanacaste:** Parque Nacional Guanacaste, ca. 0.7 km N Est. Maritza, 10.96°N 85.50°W, 31.viii.1990, el. 550 m, Huisman and Quesada, 3 males (UMSP); Parque Nacional Guanacaste, ca. 0.7 km N Est. Maritza, 10.96°N 85.50°W, 31.viii.1990, el. 550 m, Huisman and Quesada, 6 females (UMSP); **ECUADOR:** Quevedo, 36 km NE, elev. 1100', 21.vii.1976, black light, Jeffrey Cohen, 7 males (in alcohol) (NMNH); **EL SALVADOR:** 2 mi. N of Candelaria, 7.viii.1967, O.S. Flint, Jr., 1 male (NMNH); **GRENADA:** 2 mi. E of L. Grand Etang, 4-8.viii.1963, O.S. Flint, Jr., 7 males and 4 females (NMNH); 2 mi. E of L. Grand Etang, 4-8.viii.1963, O.S. Flint, Jr., 7 males, 10 females (in alcohol) (NMNH); St. Andrew, Great R., LaForce Bridges, 12°07.6'N 61°39.8'W, 19.ix.1996, O.S. Flint, Jr., 2 females (in alcohol) (NMNH); St. John, Concord Valley, 12°07.0'N 61°44.0'W, 14.ix.1996, O.S. Flint, Jr., 2 females (in alcohol) (NMNH); **PANAMA:** Barro Colorado Island, Snyder-Molino trail, marker 3,

light trap III, 10-16.iii.1989, H. Wolda, 1 male (in alcohol) (NMNH); **TOBAGO:** Charlotteville, 5 km S, Hermitage R., 11°19'N 60°34'W, 10-11.vii.1993, UV light, O.S. Flint, Jr. and N.E. Adams, 1 male (NMNH); Speyside, 1 km NW, Doctor Riv., 11°18'N 60°32'W, 12.vi.1993, UV light, O.S. Flint, Jr. and N.E. Adams, 1 male (in alcohol) (NMNH); Speyside, 1 km NW, Doctor Riv., 11°18'N 60°32'W, 12.vi.1993, by net, O.S. Flint, Jr., 4 males (NMNH); St. John, Speyside, 1 km NW, Doctor Riv., 11°18'N 60°32'W, 12-13.vi.1993, W.N. Mathis, 1 male (NMNH); Parlatuvier West River, 11°18'N 60°39'W, 14.vi.1993, by net, O.S. Flint, Jr., 1 male, 1 female (NMNH); **TRINIDAD:** Marianne R., 9 km S, Blanchisseuse, 10°46'N 61°18'W, 25.vi.1993, by net, O.S. Flint, Jr., 4 males (NMNH); Marianne R., 9 km S, Blanchisseuse, 10°46'N 61°18'W, 28.vi.1993, UV light, O.S. Flint, Jr. and N.E. Adams, 1 male (in alcohol) (NMNH); Paria River, stream, iii.1985, light trap, V. Jones, 7 males (in alcohol) (NMNH); Maracas Falls, elev. 270 m, 10°44'N 61°24'W, 18.vi.1993, UV light, O.S. Flint, Jr., 1 female (in alcohol) (NMNH); **VENEZUELA: Sucre:** Península de Paria, Puerto Viejo, “Río el Pozo,” 11°43.073'N 62°28.569'W, elev. 20 m, 3.iv.1995, Holzenthal, Flint, and Cressa, 1 female (NMNH).

Etymology. Named in honor of G. Fairchild, the collector of the holotype specimen.

***Leucotrichia forrota* Oláh and Johanson, 2011**

Fig. 19

forrota Oláh and Johanson, 2011:160 [Type locality: Peru, San Martín Province, Río Huallaga tributary, small river passing Chazuta, NHRS; male].

Diagnosis. This species is similar to *L. inops* and *L. riostoumae*, n. sp. In all 3 species, the phallus apex is elongate, tubular, curving both ventrad and laterad, and bearing elongate sclerites or apodemes. *Leucotrichia forrota* can be easily recognized from the other 2 species in having a slender, elongate, fused inferior appendage and a subgenital plate that is fused and continuous with both the ventral and dorsal sclerites of tergum X.

Description. *Male.* Length of forewing 4.6–5.2 mm (n=62). Head with posterolateral warts pronounced, with 3 ocelli; antennae unmodified. Dorsum of head brown with yellow setae; thorax brown with yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine brown setae with stripe of yellow setae running the length of basal 1/2 and scattered patches of yellow setae on apical 1/2. *Genitalia.* Abdominal sternum VII with rugose mesoventral process with apex enlarged in ventral view. Sternum VIII in ventral view with posterior margin concave with pointed mesal emargination. Segment IX anterolateral margin produced mesally, posterolateral margin straight; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite with crenulate posterior margin; membranous apex truncate. Subgenital plate fused with ventral sclerite of tergum X; with dorsal arm not apparent; ventral arm slender, digitate, with truncate basal projection, in ventral view oblong with apex rounded. Inferior

appendage slender, elongate, apex hooked dorsally, bearing single dorsal spine; in ventral view entirely fused, with basal projection on inner margin, with 2 small apicomeral projections. Phallus apex elongate, coiled, bearing multiple elongate internal sclerites.

Material examined. *Holotype male*: **PERU: San Martín Province:** Río Huallaga tributary, small river passing Chazuta, 6°34.665'S 76°08.209'W, light, loc. 11, 10.i.2009, T. Malm and K.A. Johanson (in alcohol) (NHRS-KAJO 000000329) (NHRS). *Paratypes*: **ECUADOR: Napo:** Tena, 26.v.1977, blacklight, P.J. Spangler and D.R. Givens, 1 male (in alcohol) (NMNH); Tena, 25.v.1977, blacklight, P.J. Spangler and D.R. Givens, 1 male, 1 female (in alcohol) (NMNH); **Pastaza:** Puyo, 3 km N, blacklight, 30.v.1975, Cohen and Langley, 7 males (in alcohol) (NMNH); Puyo, 30.i.1976, blacklight, P.J. Spangler *et al.*, 1 male (in alcohol) (NMNH); Puyo, 3km W, 15.vii.1976, blacklight, J. Cohen, 1 male (in alcohol) (NMNH); Puyo, 5.v.1977, blacklight, P.J. Spangler and D.R. Givens, 4 males (in alcohol) (NMNH); Puyo, 7.v.1977, blacklight, #17, P.J. Spangler and D.R. Givens, 4 males (in alcohol) (NMNH); Puyo, 11.v.1977, blacklight, P.J. Spangler and D.R. Givens, 2 males (in alcohol) (NMNH); Puyo, 13.v.1977, blacklight, P.J. Spangler and D.R. Givens, 2 males (in alcohol) (NMNH); Puyo, 1.5 km S, 14.v.1977, #43, P.J. Spangler and D.R. Givens, 1 male (in alcohol) (NMNH); Puyo, 16.v.1977, blacklight, #51, P.J. Spangler and D.R. Givens, 2 males (in alcohol) (NMNH); Puyo, 2 km N, 30.v.1975, blacklight, Langley and Cohen, 6 males (in alcohol) (NMNH); Puyo, 8-11.ii.1976, blacklight, P.J. Spangler *et al.*, 1 male (in alcohol) (NMNH); Puyo, 15.v.1977, blacklight, #47, P.J. Spangler and D.R. Givens, 1 male, 1 female (in alcohol) (NMNH); Puyo, 30.i.1976, blacklight, P.J. Spangler *et al.*, 2 males (in alcohol) (NMNH); Puyo,

21.v.1977, blacklight, #67, P.J. Spangler and D.R. Givens, 2 males, 1 female (in alcohol) (NMNH). *Nontypes*: **ECUADOR: Napo:** Tena, 4 km S, 26.v.1977, #81, P.J. Spangler and D.R. Givens, 3 males, 11 females (NMNH); Tena, 17 km SW, 28.v.1977, #88, P.J. Spangler and D.R. Givens, 4 males, 6 females (NMNH); Tena, 17 km SW, 26.v.1977, #80, P.J. Spangler and D.R. Givens, 1 male (NMNH); **Pastaza:** Puyo, 1.5 km S, 14.v.1977, #43, P.J. Spangler and D.R. Givens, 5 females (NMNH); Puyo, 9.v.1975, blacklight, #29, P.J. Spangler and D.R. Givens, 1 male (NMNH); Puyo, 3 km N, 30.v.1975, Cohen and Langley, 9 males, 6 females (NMNH); Puyo, 6.v.1977, blacklight, P.J. Spangler and D.R. Givens, 4 males (in alcohol) (NMNH); **PERU:** Cuzco: Pilcopata, elev. 600 m, premontane moist forest, 11-14.xii.1979, J.B. Heppner, 1 male, 1 female (in alcohol) (NMNH).

Etymology. *Forrott*, Hungarian for “fused,” referring to the completely fused inferior appendage.

***Leucotrichia fulminea*, new species**

Fig. 20

Diagnosis. *Leucotrichia fulminea*, n. sp., is most similar to *L. angelinae*. Both species possess a long, slender mesoventral process on sternum VII; a broad, rounded inferior appendage; a subgenital plate with a small apical emargination in the ventral arm when viewed ventrally; and a phallus bearing a pair of subapicodorsal sclerites that each point

laterad. *Leucotrichia fulminea* can be distinguished by the rugose ventral surface of the mesoventral process and the 3 small setae on the inferior appendage, each of which are absent in *L. angelinae*. Near the base of the subapicodorsal sclerite on the phallus there is also a bend that can be seen in the lateral view that is not present in *L. fulminea*.

Description. *Male.* Length of forewing 4.7–4.9 mm (n=7). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light yellow and dark brown setae; thorax dark brown with dark brown and light yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine light yellow setae mesally with dark brown setae along the edges. *Genitalia.* Abdominal sternum VII with elongate, rugose mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin shallowly concave, posterior margin irregular. Tergum X with dorsal sclerite slender, bent ventrad; ventral sclerite large, semielliptic, with tridentate posterior margin; membranous apex with dorsal and ventral lobes, rhomboid in dorsal view. Subgenital plate with dorsal arm not apparent; ventral arm rounded basally, arched mesally, tapering apically, in ventral view with rounded apical emargination. Inferior appendage apex rounded, bearing 3 small dorsal setae; in ventral view inner margin crenulate. Phallus apex bearing multiple internal apodemes and pair of pointed subapicodorsal sclerites extending outward.

Holotype male: **ECUADOR:** Cañar, Río Chachas, 2910m, 3 km N Zhud, 17.ix.1990, O.S. Flint (UMSP000140611) (NMNH). *Paratypes:* same data as holotype, 5 males (NMNH); same data as holotype, 1 male (UMSP).

Etymology. *Fulmineus*, Latin for “of lightning,” referring to the shape of the pointed dorsal sclerites on the phallus, which resemble lightning bolts when viewed laterally.

***Leucotrichia gomezi* Flint, 1970**

Fig. 21

gomezi Flint, 1970:7 [Type locality: Dominican Republic, La Palma, 12 km E. El Río; NMNH; male; larva, case].

Diagnosis. This species is most similar to *L. tubifex*; in both species, sternum VIII is subquadrate in lateral view and the mesoventral process of segment VII is simple and pointed. The shape of the inferior appendage in each species is similar, with a small mesodorsal point on the dorsal margin when viewed laterally and a digitate apex when viewed ventrally. *Leucotrichia gomezi* differs from *L. tubifex* in a combination of traits present on the phallus: the presence of large apical lobes, the large dorsal sclerite, and the basal supports of the midlength complex basal loop, none of which are present in *L. tubifex*. Additional similarities and differences are discussed under *L. tubifex*.

Description. *Male.* Length of forewing 4.3–5.0 mm (n=15). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with light brown setae; thorax brown with bronze setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine bronze setae. *Genitalia.* Abdominal sternum VII with acute

mesoventral process. Sternum VIII in ventral view with posterior margin very shallowly concave. Segment IX anterolateral margin produced mesally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite slender, elongate; ventral sclerite small, reniform; membranous apex with small dorsal lobe and larger, subtriangular ventral lobe. Subgenital plate with dorsal arm triangular; ventral arm slender, apex slightly hooked dorsad, laterally obscured from view by inferior appendage, in ventral view oblong with small basal emargination and apex rounded. Inferior appendage broadest basally, with small dorsomesal point, apex truncate, bearing single dorsal spine; in ventral view basally subquadrate, apically digitate. Phallus with median complex bearing short basal supports; apex bearing large, flat dorsal sclerite with large, rounded, apical emargination; paired elongate internal sclerites; 2 large, membranous dorsal lobes with apices curving ventrad; 1 smaller, mesoventral lobe (Fig. 21E).

Material examined. *Holotype male*: **DOMINICAN REPUBLIC**: La Palma, 12 km E of El Río, 2-13.vi.1969, Flint and Gomez (USNM 70897) (NMNH). *Paratypes*: **DOMINICAN REPUBLIC**: same data as holotype, 14 males, 1 female (NMNH); Convento, 12 km S of Constanza, 6-13.vi.1969, Flint and Gomez, 2 females (NMNH).

Etymology. Named after Gomez, one of the collectors of the holotype specimen.

***Leucotrichia hispida*, new species**

Fig. 22

Diagnosis. *Leucotrichia hispida*, n. sp., is most similar to *L. botoaneanui*, *L. chiriquiensis*, *L. limpia*, and *L. viridis*. These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. botoaneanui*. *Leucotrichia hispida* is distinct from the other 4 species in having an extremely rugose apex on the mesoventral process of sternum VII, a prominent tuft of setae on the posteroventral production of sternum VIII, and no external spines or sclerites on the phallus apex.

Description. *Male.* Length of forewing 4.2–5.0 mm (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light yellow and dark brown setae; thorax dark brown with light yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with scattered patches of light yellow setae. *Genitalia.* Abdominal sternum VII with large, rugose mesoventral process and row of prominent setae (Fig. 22D). Sternum VIII posteroventral production bearing stout, prominent setae, in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex small, suborbicular. Subgenital plate with dorsal arm not apparent; ventral arm broadest basally, apex slightly hooked dorsad, in ventral view oblong with small apical emargination. Inferior appendage broadest basally, apex digitate, bearing single dorsal spine; in ventral view with pair of digitate basal projections, inner margin

crenulate. Phallus with median complex bearing elongate basal supports; apex bearing ventral "bulge" (Fig. 22E), pair of small apicodorsal lobes, and small sclerotized internal structure between apical lobes (Fig. 22F).

Holotype male: COSTA RICA: San José, Río Savegre, 9°33.9'N 83°48'W, 2270 m, 7-8.viii.2001, D. and W.N. Mathis (UMSP000140610) (NMNH). *Paratypes*: same data as holotype, 1 male (NMNH), 1 male (UMSP).

Etymology. *Hispidus*, Latin for "bristly," referring to the extremely rugose apex of the mesoventral process of sternum VII.

***Leucotrichia imitator* Flint, 1970**

Fig. 4B, 23

imitator Flint, 1970:8 [Type locality: Mexico, Vera Cruz, Plan del Río Ver, Rt. 140, km 368; NMNH ; male; larva, case].

Diagnosis. *Leucotrichia imitator* is similar to *L. fairchildi*, *L. pictipes*, and *L. sarita*. *Leucotrichia imitator* is most similar to *L. pictipes* in having a phallus with multiple membranous, asetiferous lobes arising from the apex (Figs. 23E, F). *Leucotrichia imitator* can be distinguished by having 3 lobes arising from the same apical location, while *L. pictipes* has 2 pairs of symmetrically arranged lobes. *Leucotrichia imitator* is unique in that it has the reduced number of ocelli in male specimens, but does not also

have some degree of head modifications (Fig 4B).

Description. *Male.* Length of forewing 3.1–3.9 mm (n=22). Head unmodified, with 2 ocelli; antennae unmodified. Dorsum of head brown with light brown setae; thorax dark brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine dark brown setae with scattered bands of light yellow setae. *Genitalia.* Abdominal sternum VII with mesoventral process replaced by tuft of dense, prominent setae. Sternum VIII in ventral view with posterior margin pointedly concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin broadly concave. Tergum X with dorsal sclerite slender, elongate; ventral sclerite semielliptic with tridentate posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm with small knoblike basal projection, tapering apically, curved dorsad, in ventral view lanceolate. Inferior appendage straight, with small pointed subdorsobasal projection, bearing single dorsal spine; in ventral view basally subquadrate, apex hooked inward. Phallus apex bearing pair of internal sclerites and 3 digitate apical lobes.

Material examined. *Holotype male:* **MEXICO: Veracruz:** Plan del Río Ver, Rt. 140 km 368, 23.vii.1965, Flint and Ortiz (USNM 70898) (NMNH). *Paratypes:* Same data as holotype, 2 males (NMNH); **COSTA RICA: Puntarenas:** Río Seco, NW of Esparta, 23.vii.1967, O.S. Flint, Jr., 2 males (in alcohol) (NMNH); **GUATEMALA: El Progreso:** San Agustín Acasaguastlán, 11-21.viii.1965, Flint and Ortiz, 2 males, 1 female (NMNH); **Suchitepéquez:** Puente Ixtacapa, near San Antonio, 18-19.vi.1966, Flint and

Ortiz, 1 male (NMNH). *Nontypes*: **COSTA RICA: Puntarenas:** Quebrada Portera nr Portera Grande, 5.vii.1992, T. Shepard, 13 males (in alcohol) (UMSP); **MEXICO: Sonora:** Yaqui River, Hwy 16, near Tonichi, 19.viii.1986, Baumann, Sargent, and Kondratieff, 1 male, 1 female (in alcohol) (NMNH).

***Leucotrichia inflaticornis* Botosaneanu, 1993**

Fig. 3B, 24

inflaticornis Botosaneanu, in Botosaneanu and Alkins-Koo, 1993:10 [Type locality:

Trinidad, 2nd. order stream at “La Laja,” catchment of Rio Guanapo; ZMUA; male; larva, case]. —Botosaneanu and Sakal, 1992:201 [biology].

Diagnosis. *Leucotrichia inflaticornis* can be separated from other *Leucotrichia* species by the inflated basal segments of the antennae (Fig. 3B), for which it was named, and the lack of mesoventral process on sternum VII. Additionally, the phallus apex bears 4 pairs of distinct dark spines.

Description. Holotype pharate adult, abdomen missing, genitalia redescribed from Botosaneanu and Alkins-Koo (1993). *Male*. Length of forewing 1.2 mm (n=1). Head unmodified, with 3 ocelli; antennae scape normal, next 5–6 basal flagellum broadened similar to that of *L. pictipes*. Color in alcohol brown, denuded. *Genitalia*. Abdominal sternum VII with mesoventral process not apparent. Sternum VIII in ventral view with

posterior margin pointedly concave. In dorsal view anterior margin of segment IX convex, posterior margin concave. Membranous apex of tergum X suborbicular. Subgenital plate apically bilobed, with small pointed projection at base of each lobe. Inferior appendage apex truncate; in ventral view entirely fused. Phallus with median complex present but only slightly developed, apex bearing 4 pairs of symmetrically arranged stout, dark spines.

Material examined. *Holotype male*: **TRINIDAD**: 2nd order stream at “La Laja,” catchment of Rio Guanapo (in alcohol) (UMSP000140327) (ZMUA).

Etymology. Specific epithet refers to the inflated appearance of basal antennal segments.

***Leucotrichia inops* Flint, 1991**

Fig. 25

inops Flint, 1991:43 [Type locality: Colombia, Dpto. Antioquia, 12 km E Medellín, road to Sta. Elena; NMNH; male].

Diagnosis. This species is similar to *L. forrota* and *L. riostoumae*, n. sp. These species share a similar combination of characteristics present in the phallus, as discussed under *L. forrota*. Of these species, *L. inops* is most similar to *L. riostoumae*. Each of these species possess a convex posterolateral margin on sternum VIII; an anterolateral production on

segment IX; an unfused inferior appendage that is basally subquadrate, apically hooked, and lacking a dorsal spine; and an apparent lack of midlength complex on the phallus.

Leucotrichia inops can be distinguished by the small tuft of apical setae on the phallus and the shape of the membranous apex of tergum X, which is larger and extends further posteriad than that of *L. riostoumae*. Also, in *L. inops* the concave posterior margin of sternum VIII is V-shaped, while it is shallowly rounded in *L. riostoumae*.

Description. *Male.* Length of forewing 3.5–4.0 mm (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light gray-green setae on anterior edge; thorax brown with dark brown and light gray-green setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine mottled light gray-green setae with dark brown setae on apical 1/3. *Genitalia.* Abdominal sternum VII with acute mesoventral process with small basal ridge, apex enlarged in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin with curved ventrolateral production, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite semielliptic with crenulate posterior margin; membranous apex subtriangular. Subgenital plate with dorsal arm digitate; ventral arm acute, extending dorsad, in ventral view oblong. Inferior appendage basally subquadrate, apex hooked dorsally, without dorsal spine; in ventral view subtriangular, outer margin crenulate. Phallus with median complex not apparent; apex elongate, curved strongly both ventrad and posteriad; with very slender, elongate sclerites; apex bearing tuft of small spines.

Material examined. *Holotype male:* **COLOMBIA: Antioquia:** 12 km E Medellín, rd. to Santa Elena, 6.ii.1983, O.S. Flint, Jr. (USNM 104530) (NMNH). *Paratypes:* **COLOMBIA: Antioquia:** Quebrada La Iguaná, 17 km NW Medellín, rd. to San Jerónimo, 14-15.ii.1983, O.S. Flint, Jr., 1 male (NMNH); Quebrada La Iguaná, 17km NW Medellín, rd. to San Jerónimo, 22.ii.1984, C.M. and O.S. Flint, Jr., 1 female (NMNH). *Nontypes:* **ECUADOR: Pichincha:** 2.3 km S Tandayapa, elev. 1800 m, 6.ix.1990, O.S. Flint, Jr., 1 male (NMNH).

***Leucotrichia interrupta* Flint, 1991**

Fig. 26

interrupta Flint, 1991:41 [Type locality: Colombia, Dpto. Antioquia, Quebrada Espadera, 7 km E Medellín, on road to Sta. Elena; NMNH; male].

Diagnosis. *Leucotrichia interrupta* can be separated from all other species in the genus by the unique form of the phallus apex, which is trilobed and with the 2 lateral lobes appearing more bulbous than lobe-like. A second characteristic unique to *L. interrupta* is the slender sclerite arising from the base of the “windows” of the midlength complex and following the anterior edge of each of the lateral lobes. The inferior appendage is also distinct in its large, subtriangular shape when viewed laterally.

Description. *Male.* Length of forewing 3.5 mm (n=1). Head unmodified, with 3

ocelli; antennae unmodified. Dorsum of head brown with yellow setae; thorax dark brown with bright yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine yellow setae, apical 1/4 with dark brown setae. *Genitalia*. Abdominal sternum VII with mesoventral process broken (indicated in Fig. 26D). Sternum VIII in ventral view with posterior margin very shallowly concave. Segment IX anterolateral margin produced mesally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite simple; ventral sclerite simple; membranous apex truncate. Subgenital plate with dorsal arm hollow, triangular (Fig. 26A); ventral arm slender, tapering apically, curved ventrad, in ventral view subovate. Inferior appendage subtriangular, without dorsal spine; in ventral view entirely fused, apically digitate. Phallus apex trilobed; lateral lobes bulbous and with slender, elongate, sinuate sclerite along outer edge; short spines present on dorsal surface of all 3 lobes.

Material examined. *Holotype male*: **COLOMBIA: Antioquia:** Quebrada Espadera, 7 km E Medellín, rd. to Santa Elena, 24.ii.1983, O.S. Flint, Jr. (USNM 104528) (NMNH). *Paratypes*: Same data as holotype, 1 female (NMNH).

***Leucotrichia kateae*, new species**

Fig. 27

Diagnosis. *Leucotrichia kateae*, n. sp., is known only from the male holotype. This

species is most similar to *L. tritoven*. Similarities between these species in the inferior appendage and the phallus are discussed under *L. tritoven*. *Leucotrichia kateae* can be easily recognized from *L. tritoven* by the mesoventral process of sternum VII, which is noticeably much larger and has a rugose ventral surface. The inferior appendage of *L. kateae* is longer than that of *L. tritoven* when viewed ventrally, and has a crenulate margin that is lacking in *L. tritoven*. *Leucotrichia kateae* also bears a pair of small, curved, pointed sclerites on the phallus that are lacking in *L. tritoven*.

Description. *Male.* Length of forewing 2.4 mm (n=1). Head missing. Thorax brown with light brown setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine light yellow setae, inner edge with longitudinal stripe of brown setae. *Genitalia.* Abdominal sternum VII with elongate, rugose mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin slightly produced ventrolaterally, posterolateral margin irregular; in dorsal view anterior margin shallowly concave, posterior margin concave. Tergum X with dorsal sclerite slender; ventral sclerite with rounded projection on posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm broadest basally, tapering apically; ventral arm slender, digitate, in ventral view sublanceolate. Inferior appendage dorsomesally "humped," apex truncate, bearing single dorsal spine; in ventral view inner and outer margins crenulate. Phallus apex bearing multiple obscured internal structures; small pair of pointed, curved, mesal sclerites; pair of mildly sinuate, subapicolateral sclerites; pair of apicodorsal membranous lobes.

Holotype male: **VENEZUELA: Aragua:** 1 km E Estación Biológica Rancho

Grande, 10.352°N67.680°W, el. 1100 m, 27.i.1994, Holzenthal, Cressa, and Rincón, 1 male (UMSP000201690) (UMSP).

Etymology. Named in honor of R. E. Thomson's sister, Kate Thomson, who had to put up with a sister who loves bugs.

***Leucotrichia laposka* Oláh and Johanson, 2011**

Fig. 28

laposka Oláh and Johanson, 2011: 162 [Type locality: Peru, San Martín Province, creek crossing road Juan Guerra-Chazuta, 14 km (rd.) E Colombia Bridge, NHRS; male].

Diagnosis. *Leucotrichia laposka* can be easily separated from all other *Leucotrichia* species by the apparent absence of the entire subgenital plate. The trilobed apex of the phallus is also proportionately much larger in this species than in any other in the genus. The rows of elongate spines along the mesal lobe are also unique to *L. laposka* and, when viewed laterally, suggest the appearance of the spur of a cowboy boot.

Description. *Male.* Length of forewing 2.4–2.8 mm (n=5). Head with posterolateral warts pronounced, originally described as "hinged" but everscibility was not apparent, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII with slender, acute mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex,

posterolateral margin irregular with small knob-like structure mesally; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite bent ventrad, continuous with ventral sclerite; ventral sclerite bent dorsad; membranous apex with large, membranous, apicoventrally hooked projection. Subgenital plate not apparent. Inferior appendage flat, elongate, dorsal margin crenulate, without dorsal spine but sparsely setose; in ventral view fused basally, subquadrate. Phallus apex large, trilobed; mesal lobe with rows of large, elongate spines.

Material examined. *Holotype male*: **PERU: San Martín Province**: creek crossing road Juan Guerra-Chazuta, 14 km (rd.) E Colombia Bridge, 6°35.594'S 76°13.172'W, light, loc. 09, 9.i.2009, T. Malm and K.A. Johanson (in alcohol) (NHRS-KAJO 000000328) (NHRS). *Paratypes*: **PERU: San Martín Province**: La Catarata de Ahuashiyascu, 6°27.544'S 76°18.192'W, light, loc. 07, 7.i.2009, T. Malm and K.A. Johanson, 2 males (in alcohol) (NHRS), 2 males (in alcohol) (OPC).

Etymology. *Laposka*, Hungarian for diminutive form of “flat,” referring to the broadened inferior appendage.

***Leucotrichia lerma* Angrisano and Burgos, 2002**

Fig. 29

lerma Angrisano and Burgos, 2002:106 [Type locality: Argentina, Salta, Río Lesser, 18 km NW Salta; IML; male].

Diagnosis. This species is most similar to *L. brochophora*, *L. padera*, and *L. rhomba*, n. sp. These species share a similar form in the apex of the phallus, sternum VIII, and segment IX, as discussed under *L. brochophora*. *Leucotrichia padera* differs from these species in the hooked appearance of the lateral sclerite of tergum X and the subtriangular appearance of the inferior appendage in ventral view.

Description. Redescribed from Angrisano and Burgos (2002). *Male*. Length of forewing 2.9 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. *Genitalia*. Abdominal sternum VII with slender, elongate mesoventral process. Sternum VIII in ventral view with posterior margin concave with row of prominent setae. Segment IX anterolateral margin produced mesally, posterolateral margin convex. Tergum X with lateral sclerite with apicoventral hook on posterior margin. Membranous apex of tergum X amorphous. Subgenital plate with dorsal arm not apparent; ventral arm tapering apically, apex slightly hooked dorsad. Inferior appendage digitate, apex hooked dorsally, bearing single dorsal spine; in ventral view subtriangular. Phallus apex bearing pair of ventral sclerites.

Material examined. *Holotype male*: Holotype deposited at IML, but unable to be obtained.

Etymology. Named for Valle de Lerma, the location where the holotype was collected.

***Leucotrichia limpia* Ross, 1944**

Fig. 30

limpia Ross, 1944:273 [Type locality: United States, Texas, Fort Davis, Limpia Creek; INHS; male.] —Flint, 1970:6 [male]; 1996:86 [correction of errors in 1970 paper].

Diagnosis. *Leucotrichia limpia* is most similar to *L. botosaneanui*, *L. chiriquiensis*, *L. hispida*, and *L. viridis*. These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. botosaneanui*. The mesodorsal spines and short spines on the apical lobes of the phallus apex (Figs. 30E, F) and the small single-pointed mesoventral process of sternum VII separate *L. limpia* from the other 4 species in this group.

Description. *Male.* Length of forewing 3.0–4.6 mm (n=13). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light yellow setae; thorax dark brown with light yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with scattered patches of light yellow setae. *Genitalia.* Abdominal sternum VII with short, acute mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin straight; in dorsal view anterior margin concave, posterior margin convex. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex small, suborbicular. Subgenital plate with dorsal arm digitate, with slight mesal constriction;

ventral arm broadest basally, tapering apically, in ventral view obovate. Inferior appendage basally subquadrate, apex truncate, bearing single dorsal spine; in ventral view entirely fused, subtriangular. Phallus with median complex bearing basal supports; apex bearing pair of stout spines dorsally, many short spines mesoventrally, and 2 membranous apical lobes bearing many short spines dorsally.

Material examined. *Holotype male*: **USA: Texas**: Fort Davis, along Limpia Creek, 19.iv.1939, H.H. and J.A. Ross (INHS Trichoptera #22335) (INHS). *Allotype female*: Same data as for holotype (INHS). *Nontypes*: **COSTA RICA: Puntarenas**: roadside seep, route 2 just W km 234, 8.976°N 83.299°W, el. 100m, 20.ii.1986, Holzenthal, Morse, and Fasth, 1 male, 1 female (UMSP); **MEXICO: Chiapas**: Chorreadero, Chiapa de Corzo, 11.viii.1967, O.S. Flint, Jr., 1 male, 2 females (NMNH); **Oaxaca**: Tamazulapan, 7-8.vi.1967, Flint and Ortiz, 1 male (NMNH); **San Luis Potosí**: Rancho Quemada, Rt. 85 km 353, 4-6.viii.1966, O.S. Flint, Jr., 1 male (NMNH); **USA: Arizona**: Yavapai Co., spring outfall at Bubbling Ponds Fish Hatchery, Page Springs, 23.iv.1993, S.R. Moulton and K.W. Stewart, 1 male, 1 female (in alcohol) (NMNH); Coconino Co., West Fork, 16 mi SW Flagstaff, elev. 6500', 5.viii.1961, R.W. Hodges, 1 female (NMNH); Tucson, 2033 E. Helen St., 12.x.2010, R.B. Nagle, 1 male (NMNH); Tucson, 2033 E. Helen St., 12.x.2010, R.B. Nagle, 1 female (NMNH); **Texas**: Val Verde Co., Devils River, Dolan Creek., 29° 53.4'N 100°59.6'W, 3.vi.1967, C.M. and O.S. Flint, Jr., 1 male (NMNH); Brewster Co., Big Bend National Park, Windows Creek, 5-10.iv.1993, J. Gelhaus, 1 female (NMNH); Val Verde Co., Devils River, Dolan Falls area, elev. 360 m, 17.v.1993, at light along Devils River, J. Gelhaus #589, Nelson, and

Koenig, 2 males, 3 females (in alcohol) (NMNH); Val Verde, Co., Devils River, Dolan Falls, 29°53.0'N 100°59.6'W, 2.vi.1997, C.M. and O.S. Flint, Jr., 1 male, 5 females (in alcohol) (NMNH); Brewster Co., Big Bend National Park, Chisos Mountains, spring fed creek in Oak Canyon (Window Trail), elev. 1425 m, 103°20'N 29°17'W, malaise trap, 5-11.iv.1993, J. Gelhaus #559 and D. Koenig, 2 males, 2 females (in alcohol) (NMNH); Val Verde Co., Devils River, Dolan Creek, 29°53.4'N 100°59.6'W, 3.vi.1997, C.M. and O.S. Flint, Jr., 2 females (NMNH); Brewster Co., Big Bend National Park, Windows Creek, 5-10.iv.1993, J. Gelhaus, 2 females (NMNH); Val Verde Co., San Felipe Springs, Del Rio, 29°22.1'N 100°53.1'W, 1.vi.1997, C.M. and O.S. Flint, Jr., 9 females (NMNH).

Etymology. Named for Limpia Creek, the location where the holotype was collected.

***Leucotrichia mutica* Flint, 1991**

Fig. 31

mutica Flint, 1991:39 [Type locality: Colombia, Dpto. Antioquia, Quebrada Honda, Marsella, 12km SW Fredonia; NMNH; male].

Diagnosis. This species is similar to *L. melleopicta*. These species share similarities in the phallus and the shape of the inferior appendage, as discussed under *L. melleopicta*. *Leucotrichia mutica* can be distinguished from *L. melleopicta* by the basal ridge on the

mesoventral process of sternum VII, the ovate shape of the ventral arm of the subgenital plate in ventral view, and the dorsal sclerite on the phallus, which is much smaller than that of *L. melleopicta*.

Description. *Male.* Length of forewing 3.0 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head cleared, brown, denuded; thorax brown with light yellow setae dorsally, brown ventrally; leg segments with golden brown setae. Forewings covered with fine yellow setae, apical 1/3 with dark brown setae. *Genitalia.* Abdominal sternum VII with acute mesoventral process with small basal ridge, apex rounded in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin straight; in dorsal view anterior margin sharply concave, posterior margin broadly concave. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex truncate in dorsal view. Subgenital plate with dorsal arm not apparent; ventral arm broadest mesally, apex acute, laterally obscured from view by inferior appendage, in ventral view ovate. Inferior appendage dorsomesally "humped," apex rounded, bearing single dorsal spine; in ventral view digitate. Phallus with basal half broken and missing; median complex not apparent; apex bearing single dorsal sclerite and pair of lateral sclerites; dorsal sclerite ovate, with apical emargination; lateral sclerites slender, sinuate.

Material examined. *Holotype male:* **COLOMBIA: Antioquia:** Quebrada Honda, Marsella, 12 km SW Fredonia, elev. 1450 m, 22.ii.1983, O.S. Flint, Jr. (USNM 04525) (NMNH).

***Leucotrichia padera* Flint, 1991**

Fig. 32

padera Flint, 1991:41 [Type locality: Colombia, Dpto. Antioquia, Quebrada Espadera, 7 km E Medellín, road to Sta. Elena; NMNH; male].

Diagnosis. This species is most similar to *L. brochophora*, *L. lerma*, and *L. rhomba*, n. sp. These species share a similar form in the apex of the phallus, sternum VIII, and segment IX, as discussed under *L. brochophora*. *Leucotrichia padera* differs from these species by the presence of the dorsal arm of the subgenital plate (Fig. 32A), which is absent in the other 3 species. It can also be recognized by the shape of the ventral arm of the subgenital plate in ventral view, which appears large and obovate with a rounded apical emargination (Fig. 32D).

Description. *Male.* Length of forewing 3.0 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head cleared, brown, denuded; thorax brown with light yellow setae dorsally, light brown ventrally; leg segments with brown setae. Forewings covered with fine brown setae with 2 broad patches of light yellow setae, apex with dark brown setae. *Genitalia.* Abdominal sternum VII with elongate mesoventral process curving dorsad. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin straight; in dorsal view

anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite small, reniform; ventral sclerite subdeltoid; membranous apex suborbicular. Subgenital plate elongate, mildly sinuate, extending dorsally along posterior edge of tergum X ventral sclerite; with dorsal arm digitate, apex enlarged; ventral arm with basal projection, broadest mesally, apex slightly hooked dorsad, in ventral view obovate with rounded apical emargination. Inferior appendage broadest basally, apex hooked dorsally, bearing single dorsal spine; in ventral view with basal projection on inner margin, apically digitate. Phallus apex bearing pair of elongate dorsolateral sclerites and internal ventral apodeme.

Material examined. *Holotype male*: **COLOMBIA: Antioquia:** Quebrada Espadera, 7 km E Medellín, road to Santa Elena, 6.iii.1984, C.M. and O.S. Flint, Jr. (USNM 104526) (NMNH).

Etymology. Assumedly named for Quebrada Espadera, the location where the holotype was collected.

***Leucotrichia pectinata*, new species**

Fig. 33

Diagnosis. *Leucotrichia pectinata*, n. sp., can be separated from all other species in the genus by several unique characteristics. The most striking characteristic is the apex of the phallus, which is broadened into a “fan-shape” and bears a row of peg-like setae on the

posterior margin (Fig. 33F). In lateral view, sternum VIII bears a large posterodorsal production (Fig. 33B) in contrast to the more common posteroventral production. Additionally, sternum VII bears a row of prominent setae in addition to the mesoventral process (Fig. 33D).

Description. *Male.* Length of forewing 4.5–4.7 (n=2). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with light yellow and dark brown setae; thorax dark brown with dark brown and light yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with 2 large patches of light yellow setae, 1st on apical 1/2 and 2nd on basal 1/2.

Genitalia. Abdominal sternum VII with slender mesoventral process with row of prominent setae basally. Sternum VIII with posterodorsal production, in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin convex; in dorsal view anterior margin straight, posterior margin concave. Tergum X with dorsal sclerite simple; ventral sclerite semielliptic with crenulate posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm with basal projection, tapering apically, in ventral view oblong with digitate basal projection. Inferior appendage with small basal emargination, apex hooked dorsally, bearing single dorsal spine; in ventral view outer margin crenulate. Phallus apex "fan-shaped," with posterior margin bearing row of peg-like setae.

Holotype male: **ECUADOR:** Tungurahua, 13 km E Baños, 1550 m, 15.ix.1990, O.S. Flint, (UMSP000140619) (NMNH). *Paratype:* Tungurahua, Baños (39 km E),

25.i.1976, 4200 ft, blacklight, Spangler *et al.*, 1 male (NMNH).

Etymology. *Pectinatus*, Latin for “comblike, toothed,” referring to the row of peg-like setae along the broad apical margin of the phallus.

***Leucotrichia pictipes* (Banks, 1911)**

Fig. 3C, 34

pictipes (Banks), 1911:359 [Type locality: United States, New York, Johnstown, Hales Creek; MCZ; male; in *Orthotrichia*]. —Ross, 1938:10 [as *Stactobia pictipes* (Banks)]. —Ross, 1944:120 [to *Leucotrichia*]. —Flint, 1970:10 [male, distribution]. —Nielsen, 1948:11 [misidentified as *Ithytrichia confusa* Morton].

Diagnosis. *Leucotrichia pictipes* is similar to *L. fairchildi*, *L. imitator*, and *L. sarita*.

Leucotrichia pictipes bears patches of scales, both on the dorsum of the head and the eversible membranous lobe beneath the posterolateral wart, which are absent in all 3 of the other species. The genitalia of *L. pictipes* are similar to that *L. imitator*, in having multiple membranous lobes arising from the apex of the phallus. While *L. imitator* has 3 lobes, *L. pictipes* can be distinguished by having 2 sets of symmetrically arranged lobes.

Description. *Male.* Length of forewing 2.5–4.0 (n=88). Head with patches of scales dorsally; posterolateral warts large, eversible, with scaled membranous lobes revealed when everted, with 2 ocelli; antennae with scape slightly enlarged, pedicel subtriangular,

next 3 flagellum narrow and compact. Dorsum of head brown with yellow setae; thorax brown with yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine brown setae with transverse stripe of yellow setae on basal 1/2 and small scattered patches of yellow setae on apical 1/3. *Genitalia*. Abdominal sternum VII with mesoventral process replaced by tuft of dense, prominent setae. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin broadly concave. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with tridentate posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm hollow, apex acute (Fig. 34A), in ventral view base with crenulate margin, apex rounded. Inferior appendage digitate, bearing single dorsal spine; in ventral view apex rounded. Phallus apex bearing U-shaped internal apodeme, broad ventral sclerite, and 2 pairs of membranous apicodorsal lobes.

Material examined. *Holotype male*: **USA: NEW YORK:** Johnstown, Hales Creek, collected in June, Alexander (MCZ11597) (MCZ). *Nontypes*: **MEXICO:** **Chihuahua:** Riito, Hwy 16, 10 mi E Yepachi, 28.vi.1987, Kondratieff and Baumann, 1 male, 1 female (in alcohol) (NMNH); **USA: California:** Tulare Co., 3 Rivers, 13.viii.1975, J.L. Cross, 19 males, 8 females (in alcohol) (NMNH); American River, Sacramento, 18.vi.1985, C.M. and O.S. Flint, Jr., 1 female (in alcohol) (NMNH); **Colorado:** Grand Co., Colorado River near Hot Sulphur Springs, 4.viii.1973, R.W. Baumann and W.P. Stark, 1 male, 2 females (in alcohol) (NMNH); Fremont Co., Cañon City, 27-29.v.1987, G.F. and J.F. Hevel, 2 males, 2 females (in alcohol) (NMNH);

Maryland: Frederick Co., Small Creek, Hwy 77, 30.vi.1972, Baumann and Cross, 1 male (in alcohol) (NMNH); **Montana:** Madison Co., Madison River at Norris, 21.vi.1978, Groemhild, 4 males, 3 females (in alcohol) (NMNH); **New Mexico:** Sandoval Co., Valles Caldera National Preserve, Lower San Antonio Creek, NW border of Preserve, 35°57.8'N106°36.9'W, 2.vii.2008, Parmenter *et al.*, 17 males, 11 females (in alcohol) (NMNH); Sandoval Co., Caldera National Preserve, along E Fork Jemez River, "Dagobah," 35°50.2'N 106°30.1'W, 30.vi.2008, Parmenter *et al.*, 1 male (in alcohol) (NMNH); **Oregon:** Douglas Co., S Umpqua River, 5 mi below junction of Myrtle Creek, Stn. M., 3.vi.1976, M.J. Stansburg, 2 males, 1 female (in alcohol) (NMNH); **Pennsylvania:** Warren Co., Spring Creek, 1.5 mi S Spring Creek village, 41°51.3'N 79°32.4'W, 28.viii.1998, O.S. Flint, Jr., 1 male (in alcohol) (NMNH); Warren Co., Lainard Bush, Spring Creek, 41°52'N 79°32'W, 4.vi.2000, L. Bush, 1 male (in alcohol) (NMNH); **Virginia:** Bath Co., Jackson River, Rt. 603, 2 mi S Rt. 687, 11.ix.1979, C.M. and O.S. Flint, Jr., 1 male, 1 female (in alcohol) (NMNH); Farquier Co., Broad Thoroughfare Gap, 27.v.1961, O.S. Flint, Jr., 2 males, 3 females (in alcohol) (NMNH); Bath Co., Jackson River at Rt. 603 bridge, 24.v.1974, B. Strickler, 1 male (in alcohol) (NMNH); Fauquier Co., Broad Run, Thoroughfare Gap, 15.vii.1974, O.S. Flint, Jr., 1 male, 2 females (in alcohol) (NMNH); Fauquier Co., Broad Run, Thoroughfare Gap, 10.v.1974, O.S. Flint, Jr., 25 males, 20 females (in alcohol) (NMNH); **West Virginia:** Pendleton Co., Smoke Hole Camp, 28-29.viii.1963, R. and O. Flint, 2 males, 2 females (in alcohol) (NMNH); **Wisconsin:** St. Croix County, Apple River at Somerset on Highway 64, 22.v.1993, R.J. Blahnik, 1 male (UMSP); St. Croix County, Apple River at

Somerset on Highway 64, 22.v.1993, R.J. Blahnik, 1 female (UMSP); Douglas Co., Upper St. Croix River near Gordon, 26.v.1994, R.J. Blahnik, 1 male (UMSP); Douglas Co., Upper St. Croix River near Gordon, 26.v.1994, R.J. Blahnik, 1 female (UMSP);

Wyoming: Teton Co., Crawfish Creek, tributary to Lewis River, 12.v.1992, G. Roemhild, 2 males, 1 female (in alcohol) (NMNH); Yellowstone National Park, Madison Junction, 19.viii.1962, P. and P. Spangler, 1 male (in alcohol) (NMNH).

***Leucotrichia procera*, new species**

Fig. 4C, 35

Diagnosis. This species is known only from the male holotype. *Leucotrichia procera* can be separated from all other species in the genus by the unique projection on the dorsal margin of the inferior appendage, which extends even with the dorsal surface of tergum X (Fig. 35A). The phallus is also very simple, lacking any of the spines or sclerites commonly found in other species in the genus. Additionally, the scape of the antennae is enlarged and there is a patch of scales, in place of setae, on the dorsum of the head (Fig. 4C).

Description. *Male.* Length of forewing 3.4 mm (n=1). Head with patches of scales dorsally, with 3 ocelli; antennae with enlarged scape, remaining flagellum missing. Dorsum of head brown with light yellow and dark brown setae; thorax dark brown with light yellow setae dorsally, dark brown ventrally; leg segments with dark brown setae.

Forewings covered with fine dark brown setae with scattered patches of light yellow setae. *Genitalia*. Abdominal sternum VII with acute mesoventral process with small basal ridge, apex enlarged, rugose in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin broadly concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite sinuate; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm with both basal projection and apex pointing ventrad, in ventral view with apical point very prominent. Inferior appendage with setose dorsal margin and prominent, elongate, curved dorsal projection; in ventral view with basal projection on outer margin, apex of dorsal projection curving inward. Phallus apex bearing pair of small subapicodorsal lobes, no sclerites or spines.

Holotype male: **BRAZIL**: Minas Gerais, Córrego da Serra de Ouro, Fino, Vale do Tropeiro, 20°12.371'S 43°38.581'W, el. 1000 m, 8.x.2000, Paprocki, Salgado, and Isaac (UMSP000047406) (MZUSP).

Etymology. *Procerus*, Latin for “tall, slender, long,” referring to the slender, elongate projection of the inferior appendage.

***Leucotrichia repanda*, new species**

Fig. 36

Diagnosis. This species is most similar to *L. ayura*. These species share similarities in the mesoventral process of sternum VII, the shape of sternum VIII, the shape of the inferior appendage, and sclerites observed on the phallus apex, as discussed under *L. ayura*.

Leucotrichia repanda, n. sp., can be easily distinguished from *L. ayura* by the presence of a pair of sharply bent dorsal sclerites, a pair of curved lateral sclerites, and an apical tuft of setae on the phallus apex, all of which are absent in *L. ayura*. The presence of 3 apicodorsal setae on the inferior appendage also separates *L. repanda* from *L. ayura*, which is lacking these setae.

Description. *Male.* Length of forewing 1.9–2.4 mm (n=13). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with yellow and brown setae; thorax dark brown with yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with large patch of bright yellow setae on basal 1/3. *Genitalia.* Abdominal sternum VII with short mesoventral process. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin produced mesally, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite elongate, with crenulate dorsal margin; ventral sclerite slender, simple; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm broadest basally, apex slightly hooked dorsad, in ventral view appearing "winged." Inferior appendage apex acute, bearing single mesodorsal seta and 3 apicodorsal setae; in ventral view entirely fused, apex with emargination. Phallus apex bearing apical setal tuft and 3 pairs of sclerites: 1st pair dorsal, sharply bent dorsad; 2nd pair dorsal, elongate; 3rd pair lateral,

broad, curved anteriorly.

Holotype male: **VENEZUELA: Sucre**: Península de Paria, Santa Isabel, Río Sta. Isabel, 10°44.294'N 62°38.954'W, el. 20 m, 4.iv.1995, Holzenthal, Flint, and Cressa (UMSP000201685) (UMSP). *Paratypes*: same data as holotype, 3 males, 2 females (UMSP); same data as holotype, 1 male, 1 female (MIZA); **Aragua**: Est. Exp. Cataurito, ca. 32 km E Villa de Cura, 1100 m, 1.ii.1983, O.S. Flint, Jr., 2 males, 1 female (in alcohol) (NMNH); Est. Exp. Cataurito, 28.i.1983, O.S. Flint, Jr., 1 male (NMNH); Est. Exp. Cataurito, 1.ii.1983, O.S. Flint, Jr., 7 males (NMNH).

Etymology. *Repandus*, Latin for “bent backward, turned up,” referring to the bent shape of the 1st pair of dorsal sclerites on the phallus.

***Leucotrichia rhomba*, new species**

Fig. 37

Diagnosis. *Leucotrichia rhomba*, n. sp., is known only from the male holotype. This species is most similar to *L. brochophora*, *L. lerma*, and *L. padera*. These species share a similar form in the apex of the phallus, sternum VIII, and segment IX, as discussed under *L. brochophora*. *Leucotrichia rhomba* can be separated from the other 3 species by the size and shape of the mesoventral process of sternum VII (Figs. 37B, D). The apex of the process is enlarged and, in ventral view, rhomboid and rugose. The posterior margin of sternum VIII is also much more deeply concave in *L. rhomba* than in any of the other 3

species.

Description. *Male.* Length of forewing 2.4 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with yellow and dark brown setae; thorax brown with light brown setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine brown setae with light yellow patch extending from basal 3/4 along the length of outer edge. *Genitalia.* Abdominal sternum VII with elongate mesoventral process with apex enlarged; in ventral view apex rhomboid, rugose. Sternum VIII in ventral view with posterior margin deeply concave. Segment IX anterolateral margin produced mesally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite with rounded projection on posterior margin; membranous apex subtriangular. Subgenital plate fused with ventral sclerite of tergum X; with dorsal arm not apparent; ventral arm digitate with basal projection, in ventral view oblong. Inferior appendage broadest mesally, apex hooked dorsally, bearing single dorsal spine; in ventral view entirely fused, oval, basally enlarged, apex with emargination. Phallus apex not well expanded, bearing pair of internal apodemes.

Holotype male: **COSTA RICA: Puntarenas:** Río Jaba at rock quarry, 1.4 km (air) W Las Cruces, 8.79°N 82.97°W, 9.viii.1990, el. 1150 m, Holzenthal, Blahnik, and Muñoz, 1 male (UMSP000201350) (UMSP).

Etymology. *Rhombus*, Latin for “rhomboid,” a quadrilateral of which only the opposite sides and angles are equal, referring to the shape of the enlarged apex of the mesoventral process of sternum VII.

***Leucotrichia riostoumae*, new species**

Fig. 38

Diagnosis. This species is similar to *L. forrota* and *L. inops*. These species share a similar combination of characteristics present in the phallus, as discussed under *L. forrota*. Of these species, *L. riostoumae*, n. sp., is most similar to *L. inops*, as discussed under *L. inops*. *Leucotrichia riostoumae* can be distinguished by the rugose ventral surface of the mesoventral process of sternum VII, which is lacking in *L. inops*. The membranous ridges along the apex of the phallus, which give it a star-like appearance when viewed dorsally, are also a feature unique to *L. riostoumae*.

Description. *Male*. Length of forewing 3.6–4.2 mm (n=11). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with yellow and dark brown setae; thorax dark brown with bright yellow setae dorsally, dark brown ventrally; leg segments with dark brown setae. Forewings covered with fine dark brown setae with large patch of yellow setae on basal 2/3. *Genitalia*. Abdominal sternum VII with digitate, rugose mesoventral process with small basal ridge. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin produced dorsolaterally, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin broadly convex. Tergum X with dorsal sclerite simple; ventral sclerite with rounded projection on posterior margin; membranous apex small. Subgenital plate with dorsal arm

digitate, broadest basally; ventral arm slender, digitate, in ventral view triangular. Inferior appendage basally subquadrate, apex rounded, without dorsal spine; in ventral view apically digitate. Phallus with basal loop not apparent; apex curving ventrad and laterad, with series of membranous points appearing stellate in dorsal view.

Holotype male: **ECUADOR**: Imbabura, Reserva los Cedros, Río de la Plata, 00.32495°N 78.78084°W, el. 1587 m, 18.x.2011, Holzenthal, Ríos, Encalada, and Acosta, (UMSP000140832) (UMSP). *Paratypes*: same data as holotype, 5 males (UMSP); same data as holotype, 3 males (MZUTI); same data as holotype, 2 males (NMNH).

Etymology. Named in honor of Dr. Blanca Ríos-Touma, an aquatic ecologist and colleague who helped collect the holotype specimen.

***Leucotrichia sarita* Ross, 1944**

Fig. 4D, 39

sarita Ross, 1944:274 [Type locality: United States, Texas, Balmorhea, along stone irrigation flume; INHS; male]. —Flint, 1970:9 [male, larva, case, distribution].

Diagnosis. *Leucotrichia sarita* is similar to *L. fairchildi*, *L. imitator*, and *L. pictipes*. *Leucotrichia sarita* is distinct from *L. imitator* and possesses a more modified head, due to the presence of eversible posterolateral warts (Fig. 4D). It does not have any of the further head modifications found on either *L. fairchildi* or *L. pictipes*. The presence of the

membranous lobes on the phallus terminating in sclerotized points also distinguishes *L. sarita* from the other 3 species of the *pictipes* species group.

Description. *Male.* Length of forewing 2.1–3.0 mm (n=306). Head with posterolateral wart large, eversible, with membranous lobe beneath, with 2 ocelli; antennae unmodified. Dorsum of head brown with yellow setae; thorax brown with dark brown and yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with stripe of yellow setae running the length of basal 1/3 and scattered patches of yellow setae near apex. *Genitalia.* Abdominal sternum VII with mesoventral process replaced by few dark, prominent setae. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with crenulate posterior margin; membranous apex with dorsal and ventral lobes. Subgenital plate with dorsal arm not apparent; ventral arm hollow, subtriangular, with basal projection, curved dorsad, in ventral view lanceolate. Inferior appendage straight, digitate, bearing single dorsal spine; in ventral view broadly fused, apex rounded, with small apical "lip" (Fig. 39D). Phallus apex bearing pair of mesolateral lobes ending in sclerotized point and numerous small apical spines on dorsal and lateral surface.

Material examined. *Holotype male:* USA: TEXAS: Balmorhea, along stone irrigation flume, 19.iv.1939, H.H. and J.A. Ross (in alcohol) (INHS Trichoptera #22339) (INHS). *Nontypes:* COSTA RICA: Alajuela: Río Agrio, ca. 3.5 km NE Bajos del Toro, 10.243°N 84.279°W, 20.viii.1990, el. 1290m, Holzenthal *et al.*, 5 males, 9 females

(UMSP); **Cartago:** Reserva Tapanti, Quebrada Palmitos and falls, 9.72°N 83.78°W, 23.viii.1990, el. 1400 m, Holzenthal and Huisman, 1 male (UMSP); **Guanacaste:** Parque Nacional Guanacaste, El Hacha, Queb. Alcornoque, 11.009N 85.577W, 26. vii.1987, el. 250m, Holzenthal, Morse, and Clausen, 1 male (in alcohol) (UMSP); **Las Canas:** 13.vii.1965, P.J. Spangler, 1 female (NMNH); Río Seco, NW of Esparta, 23.vii.1967, O.S. Flint, Jr., 1 male (in alcohol) (NMNH); 13.vii.1965, P.J. Spangler, 4 males, 20 females (in alcohol) (NMNH); **Puntarenas:** Río Jaba at rock quarry, 1.4km (air) W Las Cruces, 8.79°N 82.97°W, 9.viii.1990, el. 1150m, Holzenthal, Blahnik, and Muñoz, 1 male (UMSP); **GUATEMALA: Retalhuleu:** Puente El Niño, 16.vii.1966, Flint and Ortiz, 1 female (NMNH); **San Marcos:** Puente Ixben, 15.vii.1966, Flint and Ortiz, 3 males (NMNH); **Suchitepéquez:** Cuyotenango, 10-20.vi.1966, Flint and Ortiz, 1 female (NMNH); **MEXICO: Chiapas:** Rt. 35, 4 km N Arriaga, 9.xii.1975, C.M. and O.S. Flint, Jr., 1 male (in alcohol) (NMNH); near Pijijiapan, 5.vii.1965, P.J. Spangler, 1 male (in alcohol) (NMNH); **Guerrero:** Acahuizotla, 10.xu.1982, J. Bueno and E. Borrera, 1 male (in alcohol) (NMNH); **Michoacán:** San Lorenzo, Rt. 15 km 206, 14-15.vii.1966, Flint and Ortiz, 4 males, 2 females (NMNH); same, 3 males, 2 females (in alcohol) (NMNH); **Morelos:** Xochitepec, 12-14.vii.1965, Flint and Ortiz, 8 males, 3 females (NMNH); near Xochitepec, Rt. 95 km 91, 1.viii.1965, O.S. Flint, Jr., 7 males, 9 females (in alcohol) (NMNH); **Oaxaca:** Isthmus Tehuantepec, Jaltepec, 21.v.1964, F.S. Blanton, 1 male (in alcohol) (NMNH); Tehuantepec, 23.vii.1964, P.J. Spangler, 6 females (in alcohol) (NMNH); **Veracruz:** near El Lencero, Rt. 140 km 437, 22.vii.1965, Flint and Ortiz, 5 males (NMNH); Plan del Río Ver, Rt. 140 km 368, 23.vii.1965, Flint and Ortiz, 2 males,

7 females (NMNH); Fortín de las Flores, ?.vi.1964, light trap, F.S. Blantoni, 1 male (in alcohol) (NMNH); Río Tacolapan, Rt. 180 km 551, 25-26.vii.1966, Flint and Ortiz, 1 male (in alcohol) (NMNH); Cultlahuac, 10-12.viii.1964, P.J. Spangler, 2 males, 5 females (in alcohol) (NMNH); **USA: California:** Truckee, 8.viii.1915, H.G. Dyar, 1 female (NMNH); **Maryland:** Washington Co., C and O Canal, Harpers Ferry Vicinity, 7.v.1972, G.F. and S. Hevel, 1 female (NMNH); Montgomery Co., Potomac River, Cardero Creek recreation area, 5.ix.1976, J. Heppner, 1 male (NMNH); **Nevada:** Reno, 2.viii.1916, H.G. Dyar, 2 males, 5 females (NMNH); Reno, 3.viii.1916, H.G. Dyar, 54 males, 3 females (NMNH); **New Mexico:** Jemez Springs, 4.vii.1953, W.W. Wirth, 1 male (NMNH); **Oregon:** Klamath Lake, 27.vii.????, Dyar and Caudell, 3 males, 2 females (NMNH); **Texas:** Val Verde Co., Devils River, Dolan Falls area, elev. 360 m, 17-20.v.1993, malaise trap with UV light at spring along Dolan Creek, Gelhaus #589, Nelson, and Koenig, 8 males, 7 females (in alcohol) (NMNH); Val Verde Co., San Felipe Springs, Del Rio, 29°22.1'N 100°53.1'W, 1.vi.1997, C.M. and O.S. Flint, Jr., 169 males, 88 females (NMNH); **Virginia:** Highland Co., Locust Springs, beaver ponds, 12.ix.1979, C.M. and O.S. Flint, Jr., 1 female (NMNH); Fauquier Co., Broad Run, Thoroughfare Gap, 10.v.1974, O.S. Flint, Jr., 3 males, 6 females (NMNH); Madison, Criglersville, 1.6 km NW, 38°28.4'N 78°19.9'W, elev. 185 m, 19.v.2005, W.N. and D. Mathis, 1 male (NMNH).

***Leucotrichia sidneyi*, new species**

Fig. 40

Diagnosis. *Leucotrichia sidneyi*, n. sp., is most similar to *L. brasiliانا*. These species share similarities in a suite of characters observed on the phallus, as discussed under *L. brasiliانا*. *Leucotrichia sidneyi* can be separated by the absence of a dorsal spine on the inferior appendage, pairs of separate dorsal and ventral sclerites on the phallus apex, and a much shallower concave posterior margin on sternum VIII than *L. brasiliانا*.

Additionally, the inferior appendages are fused in *L. sidneyi* and separate in *L. brasiliانا*.

Description. *Male*. Length of forewing 2.9–3.0 mm (n=6). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with yellow setae; thorax dark brown with golden yellow setae dorsally, brown ventrally; leg segments with dark brown setae. Forewings covered with fine mottled green-yellow setae with dark brown setae on edges. *Genitalia*. Abdominal sternum VII with elongate mesoventral process with apex enlarged, rugose in ventral view. Sternum VIII in ventral view with posterior margin concave or concave with pointed mesal emargination. Segment IX anterolateral margin convex, posterolateral margin convex; in dorsal view anterior margin convex, posterior margin concave. Tergum X with dorsal sclerite slender; ventral sclerite with rounded projection on posterior margin; membranous apex suborbicular. Subgenital plate with dorsal arm not apparent; ventral arm rounded basally, apex truncate, in ventral view oblong with base slightly enlarged and apex broadly rounded. Inferior appendage broadest mesally, apex rounded, without dorsal spine; in ventral view entirely fused, basally enlarged, apex truncate. Phallus apex bearing pair of dorsal sclerites, ventral

sclerite, and membranous ventral "hump."

Holotype male: VENEZUELA: T. F. A.: Camp IV, 0°58'N 65°57'W, Cerro d. l. Neblina, 760m, 15-18.iii.1984, O.S. Flint, Jr. (UMSP000140465) (NMNH). *Paratypes*: same data as holotype, 3 males, 11 females (NMNH); same data as holotype, 2 males, 2 females (UMSP).

Etymology. Named in honor of R. E. Thomson's father, Sid Thomson, a fly fisherman and the only other member of the family who can recognize a caddisfly.

***Leucotrichia tapantia*, new species**

Fig. 41

Diagnosis. This species is similar to *L. bicornuta*, *L. dianaeae*, and *L. extraordinaria*.

These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. bicornuta*. Of these species, *L. tapantia*, n. sp., is most similar to *L. dianaeae*. Each have a large tuft of prominent setae at the apex of the posterolateral production of sternum VIII; a small, mesal projection on the posterior margin of sternum VIII, and larger, more prominent apical lobes on the phallus apex than either *L. bicornuta* or *L. extraordinaria*. Characters that can be used to distinguish *L. tapantia* from *L. dianaeae* include a much longer basal loop of the phallus midlength complex and the absence of a dorsal arm on the subgenital plate. The prominent apical point of the ventral arm on the subgenital plate, when viewed ventrally,

and the presence of 2 small dorsal setae, in addition to the single dorsal spine, on the inferior appendage separate *L. tapantia* from all 3 of the other species.

Description. *Male.* Length of forewing 3.4–3.9 mm (n=19). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head dark brown with yellow setae; thorax dark brown with yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with broad streak of yellow setae down outer edge. *Genitalia.* Abdominal sternum VII with short, pointed mesoventral process. Sternum VIII lateral production elongate, extending dorsad, apex bearing tuft of prominent setae (Fig. 41B), in ventral view with posterior margin concave with digitate mesal projection (Fig. 41D). Segment IX anterolateral margin convex, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite slender; ventral sclerite semielliptic with crenulate posterior margin; membranous apex small. Subgenital plate with dorsal arm not apparent; ventral arm slender, sinuate, broadest mesally, in ventral view with apical point very prominent. Inferior appendage straight, bearing 1 large dorsal spine and 2 small setae; in ventral view fused basally, digitate. Phallus apex bearing internal apodemes and pair of prominent apicodorsal lobes.

Holotype male: **COSTA RICA: Cartago:** Reserva Tapantí, waterfall, ca. 1km (road) NW tunnel, 9.69°N 83.76°W, 2-3.viii.1990, el. 1600m, Holzenthal, Blahnik, Muñoz (UMSP000201359) (UMSP). *Paratypes:* same data as holotype, 46 males (UMSP); same data as holotype, except 10.vi.1988, C.M. and O.S. Flint, R.W. Holzenthal, 13 males (NMNH).

Etymology. Named for Reserva Tapantí, the location where the holotype was collected, as suggested by Dr. Steve Harris, an aquatic biologist and Trichoptera taxonomist at Clarion University.

***Leucotrichia termitiformis* Botosaneanu, 1993**

Fig. 42

termitiformis Botosaneanu, in Botosaneanu and Alkins-Koo, 1993:13 [Type locality: Trinidad, stream below Maracas waterfall; ZMUA; male; larva]. —Botosaneanu and Sakal, 1992:201 [biology].

Diagnosis. *Leucotrichia termitiformis* can be recognized by the shape of the inferior appendage, which is somewhat similar to *L. tubifex*. In lateral view, the inferior appendage is large and truncate; in ventral view, it is large, fused, and slightly spatulate. The inferior appendage of *L. tubifex* differs in having a small mesodorsal point and in being separate and smaller in size. Additionally, sternum VIII lacks peg-like setae in *L. termitiformis* and is more laterally elongate than that of *L. tubifex*.

Description. Phallus of holotype missing, redescribed from Botosaneanu and Alkins-Koo (1993). *Male*. Length of forewing 3.9 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Color in alcohol brown, denuded. *Genitalia*. Abdominal sternum VII with digitate mesoventral process. Sternum VIII in ventral view with

posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin convex; in dorsal view anterior margin shallowly concave, posterior margin concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite sinuate; membranous apex not well developed. Subgenital plate fused with ventral sclerite of tergum X; with dorsal arm slender, tapering apically; ventral arm slender, with basal projection, apex slightly hooked dorsad, in ventral view oblong. Inferior appendage large, apex truncate, bearing single dorsal spine; in ventral view entirely fused, with basal projection on outer margin, apex with emargination. Phallus with median complex bearing 2 separate basal filaments; apex bearing dark, U-shaped, dorsomesal sclerite and pair of apicolateral sclerites.

Material examined. *Holotype male*: **TRINIDAD**: stream below Maracas waterfall (in alcohol) (UMSP000140326) (ZMUA).

Etymology. Specific epithet refers to the typical “termitiform” shape of the larval abdominal segments.

***Leucotrichia tritoven* Flint, 1996**

Fig. 43

tritoven Flint, 1996:89 [Type locality: Trinidad, streamlet, Lalaja Road, 10°43'N, 61°17'W; NMNH; male].

Diagnosis. *Leucotrichia tritoven* is most similar to *L. kateae*. In both of these species, the dorsal spine of the inferior appendage is located on a dorsomesal “hump” (Fig. 43A).

There is also a pair of membranous lobes arising from the apex of the phallus in each of these species, from the base of which a pair of large, pointed sclerites also arises. A pair of elongate, apically curling sclerites on the phallus makes *L. tritoven* distinct from *L. kateae*, which lacks these elongate sclerites. Additionally, the dorsal arm of the subgenital plate in *L. tritoven* is digitate, while in *L. kateae* it is apically acute.

Description. *Male.* Length of forewing 1.5–2.0 mm (n=24). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with light yellow setae; thorax brown with light yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine yellow setae with dark brown setae at edges and apex.

Genitalia. Abdominal sternum VII with digitate mesoventral process with small basal ridge. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin produced mesally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite slender, elongate; ventral sclerite semielliptic; membranous apex suborbicular. Subgenital plate with dorsal arm digitate, apex truncate; ventral arm digitate, laterally obscured from view by inferior appendage, in ventral view triangular. Inferior appendage dorsomesally “humped,” apex rounded, bearing single dorsal spine; in ventral view with mitten-like “thumb” on inner margin (Fig. 43D). Phallus apex bearing U-shaped internal apodeme, pair of apical membranous lobes, and 2 pairs of elongate sclerites: 1st pair lateral, elongate, apically curled, 2nd pair acute, apicodorsal sclerites extending anteriorly.

Material examined. *Holotype male:* **TRINIDAD:** Lalaja Road, streamlet, 10°43'N 61°17'W, elev. 520 m, 26.vi.1993, by net, O.S. Flint, Jr. and W.N. Mathis (USNM 105437) (NMNH). *Paratypes:* Same data as holotype, 3 males, 1 female (NMNH); Lalaja Road, Guanapo River, elev. 480 m, 10°43'N 61°17'W, 26.vi.1993, by net, O.S. Flint, Jr. and W.N. Mathis, 2 males, 1 female (in alcohol) (NMNH); **TOBAGO:** Charlotteville, 4 km S, big waterfall, 11°19'N 60°33'W, elev 125 m, 10.vi.1993, by net, O.S. Flint, Jr. and W.N. Mathis, 1 male (in alcohol) (NMNH); Roxborough, 6.5 km N, B1/5, elev. 390 m, 11°17'N 60°35'W, 14.vi.1993, by net, O.S. Flint, Jr. and W.N. Mathis, 6 males (NMNH); **VENEZUELA:** Sucre Parque Nacional, Península de Paria, Uquire, Río La Viuda, 10°42.830'N 61°57.661'W, elev. 15 m, 30.iii-1.iv.1995, Holzenthal, Flint, and Cressa, 10 males, 3 females (NMNH). *Nontypes:* **GUYANA:** Dubulay Ranch, Warniabo Creek, 5°39.8'N 57°53.4'W, 14-19.iv.1995, O.S. Flint, Jr., malaise trap night collection, 1 male (in alcohol) (NMNH).

***Leucotrichia tubifex* Flint, 1964**

Fig. 44

tubifex Flint, 1964:44 [Type locality: Puerto Rico, Maricao, at fish hatchery; NMNH; male; female, larva, pupa, case]; 1970:7 [male, larva, case, distribution]. — Botosaneanu, 1991:116 [distribution]. — Botosaneanu and Bolland, 1997:71 [parasitized by mite, genus *Leptus*].

Diagnosis. *Leucotrichia tubifex* can be recognized by the bulbous apex of the phallus.

This species is similar to *L. gomezi* in the subquadrate appearance of sternum VIII when viewed laterally and differs in bearing small peg-like setae on a small posteroventral production not present in *L. gomezi*. The posterior margin of sternum VIII is convex and U-shaped in *L. tubifex*, while it is straight and without emargination in *L. tubifex*.

Additional similarities and differences are discussed under *L. gomezi*.

Description. *Male.* Length of forewing 3.6-5.2 (n=24). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with yellow setae; thorax brown with yellow setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine golden yellow and tan setae. *Genitalia.* Abdominal sternum VII with short, pointed mesoventral process. Sternum VIII posteroventral production bearing small peg-like setae, in ventral view with posterior margin concave. Segment IX anterolateral margin convex, posterolateral margin straight; in dorsal view anterior margin shallowly concave, posterior margin concave. Tergum X with dorsal sclerite continuous with ventral sclerite; ventral sclerite small with rounded emargination on posterior margin; membranous apex extending down to base of subgenital plate. Subgenital plate fused with ventral sclerite of tergum X; with dorsal arm not apparent; ventral arm rounded basally, curved dorsad, apex acute, in ventral view subovate with rounded apical emargination. Inferior appendage with small dorsomesal point, apex truncate, bearing single dorsal spine; in ventral view with subquadrate basal projection on outer margin, with 2 small apicomesal projections. Phallus apex with 1 dorsal, 1 ventral,

and 1 pair of lateral elongate sclerites, apex bulbous.

Material examined. *Holotype male:* **PUERTO RICO:** Maricao Fish Hatchery, 23.xii.1962, P and P Spangler (in alcohol) (USNM 66885) (NMNH). *Nontypes:*

DOMINICAN REPUBLIC: La Estrelleta Province: 4 km SE Río Limpio, elev. ca. 760 m, 24-25.v.1973, D. and M. Davis, 1 male (NMNH); **La Vega:** Jarabacoa, 1-2 km S, 19°06.9'N 70°37.0'W, elev. 520 m, 8-21.v.1995, W.N. Mathis, 1 male, 2 females (NMNH); Jarabacoa, 3-4.vi.1969, Flint and Gomez, 1 male (in alcohol) (NMNH); Salto Guasara, 9.5 km W Jarabacoa, elev. 680 m, 10°04.4'N 70°42.1'W, 9.v.1995, O.S. Flint, Jr., 1 male (NMNH); Río Baiguate, 1-2 km S Jarabacoa, elev. 520 m, 19°06.9'N 70°37.0'W, 809.v.1995, O.S. Flint, Jr., 3 males, 5 females (NMNH); Jarabacoa, 13.xi.1984, P. and P. Spangler and R. Faitoute, 1 male (in alcohol) (NMNH);

Pedernales: Pedernales, 21 km N, elev. 270 m, 18°09.3'N 71°45.6'W, Río Mulito, 18.iii.1999, W.N. Mathis, 1 female (NMNH); **JAMAICA: St. Andrews Parish:** Chestervale, Yallahs River, 24-25.vii.1962, Farr, O., and R. Flint, 1 male, 2 females (NMNH); Chestervale, Yallahs River, 17.vii.1963, Flint and Farr, 5 males, 1 female (NMNH); St. Andrew Parish, Newcastle, M.P.16.5, 18.vii.1963, Flint and Farr, 1 male (NMNH); Yallahs River, Hill Gap, elev 920 m, 18°05.1'N 76°41.1'W, 26.iv.2000, O.S. Flint, Jr., 3 males (NMNH); Mavis Bank, Yallahs River, 4.3 km SE, 18°1.4'N 76°38.1'W, elev. 480 m, 22-23.iv.2000, W.N. Mathis, 1 female (NMNH); **PUERTO RICO: Jayuya:** 2 km E Río Saliente, 18°12.8'N 66°33.9'W, 22.ix.1995, D. and W.N. Mathis, 2 males (NMNH); **Ponce:** Real Anon, at Río Inabon, 18°7'N 66°34'W, 30.vi.2008, W.E. Steiner, J.M. Swearingen, O.H. Garrido, and A.R. Perez-Asso, at black light in gap of mixed

montane rain forest, 3 males (in alcohol) (NMNH).

***Leucotrichia viridis* Flint, 1967**

Fig. 45

viridis Flint, 1967:10 [Type locality: Guatemala, Izabal, Las Escobas near Matias de Galvez; NMNH; male]; 1970:5 [male, distribution].

Diagnosis. *Leucotrichia viridis* is most similar to *L. botosaneanui*, *L. chiriquiensis*, *L. hispida*, and *L. limpia*. These species share a similar combination of characteristics present in the phallus and the posterolateral margin of sternum VIII, as discussed under *L. botosaneanui*. *Leucotrichia viridis* is distinct from the others in having 2 dorsal spines on the inferior appendage (Fig. 45A), while the others bear only a single spine. In ventral view, the mesoventral process of sternum VII is much wider than that of the other species and the apex is much more enlarged (Fig. 45D). The pair of ventral, ovate sclerites on the phallus apex of *L. viridis* is distinct and not present in the other 4 species (Fig. 45E).

Description. *Male*. Length of forewing 2.3–3.1 mm, 1 individual 1.6 mm (n=68). Head unmodified, with 3 ocelli; antennae unmodified. Dorsum of head brown with light yellow setae; thorax brown with yellow setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine mottled yellow and brown setae, apex with brown setae. *Genitalia*. Abdominal sternum VII with large mesoventral process with

apex enlarged, rugose in ventral view. Sternum VIII in ventral view with posterior margin concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin irregular; in dorsal view anterior margin concave, posterior margin straight. Tergum X with dorsal sclerite small, simple; ventral sclerite semielliptic with tridentate posterior margin; membranous apex not well developed. Subgenital plate with dorsal arm not apparent; ventral arm arched mesally apex truncate, in ventral view obovate. Inferior appendage broadest basally, arched mesally, bearing 1 large and 1 small dorsal spine; in ventral view with broad mesal constriction. Phallus with median complex bearing elongate basal supports; apex bearing pair of small, membranous lobes and 2 pairs of sclerites: 1st pair dorsolateral and sinuate, 2nd pair ventral and ovate.

Material examined. *Holotype male:* **GUATEMALA: Izabal:** Las Escobas near Matias de Galvez, 14-16.viii.1965, Flint and Ortiz (USNM 69586) (NMNH). *Paratypes:* Same data as holotype, 14 males, 3 females (in alcohol); same data as holotype, 33 males (in alcohol) (NMNH). *Nontypes:* **EL SALVADOR:** Lake Ilopango, 5.viii.1967, O.S. Flint, Jr., 1 female (NMNH); **MEXICO: Puebla:** Patla, 16.iv.1975, J. Bueno-Soria, 1 male, 1 female (in alcohol) (NMNH); **Veracruz:** Fortín de las Flores, 17.v.1964, Blanton *et al.*, 11 males (in alcohol) (NMNH); Veracruz Río, 3 km N Chocaman, 2.v.1981, C.M. and O.S. Flint, Jr., 7 males, 1 female (NMNH); **PANAMA: Chiriqui:** David, Rovira, 13.vii.1964, elev. 2200', A. Broce, 1 male, 1 female (in alcohol) (NMNH).

***Leucotrichia yungarum* Angrisano and Burgos, 2002**

Fig. 4E, 46

yungarum Angrisano and Burgos, 2002:105 [Type locality: Argentina, Salta, Finca Jakúllica, IML; male].

Diagnosis. *Leucotrichia yungarum* is similar to *L. alisensis*; the 2 species share a similar shape in both the inferior appendage and the ventral arm of the subgenital plate when viewed laterally. In ventral view, the apex of the inferior appendage is digitate in both species. In *L. yungarum*, the concave posterior margin of sternum VIII is U-shaped and without any emargination (Fig. 46C), while the same margin in *L. alisensis* is V-shaped and with a small mesal emargination. *Leucotrichia yungarum* also differs from *L. alisensis* in its lack of anterolateral production in segment IX. Additionally, *L. yungarum* bears an additional pair of posterolateral warts on the head that is not present in *L. alisensis* (Fig. 4E).

Description. Redescribed from Angrisano and Burgos (2002). *Male*. Length of forewing 3.0 mm (n=1). Head with 2 pairs of posterolateral warts, with 3 ocelli (only 2 given in illustration); antennae unmodified. *Genitalia*. Abdominal sternum VII with short mesoventral process (not illustrated). Sternum VIII posteroventral production bearing small peg-like setae, in ventral view with posterior margin concave. Segment IX anterolateral margin produced mesally, posterolateral margin convex; in dorsal view anterior margin concave, posterior margin concave. Tergum X with dorsal sclerite slender, elongate; ventral sclerite simple; membranous apex not well developed.

Subgenital plate with dorsal arm not apparent; ventral arm extending dorsad, apex acute. Inferior appendage broadest basally, bearing single dorsal spine; in ventral view with lateral margins parallel. Phallus apex relatively short, without sclerites or spines.

Material examined. *Holotype male*: Holotype deposited at IML, but unable to be obtained.

Etymology. Named for the phytogeographical region “Yungas,” cloud forest, of northeast Argentina, where the holotype was collected.

Key to the males of *Leucotrichia*

All extant species are included. In most cases, it should be possible to identify species by simple visual comparisons to illustrations and by referring to the species diagnoses and descriptions. The following key is intended to help highlight features of the male head and genitalia that are most useful in identifying species and should be used in partnership with the illustrations and descriptions provided.

- 1. With 2 ocelli *pictipes* group 2
 - With 3 ocelli *melleopicta* group 5

- 2(1). Head modified, with eversible posterolateral warts (Figs. 3A, 3C, 4D) 3
 - Head unmodified *Leucotrichia imitator* Flint, 1970

3(2). Without further modifications to the antennae or head	
..... <i>Leucotrichia sarita</i> Ross, 1944	
With modified basal antennal segments and with either patches of scales on dorsum of head and on membranous lobes beneath posterolateral warts or with setiferous protuberance on dorsum of head (Figs. 3A, 3C)	4
4(3). Patches of scales present on dorsum of head and on membranous lobes beneath posterolateral warts; setiferous protuberance on dorsum of head absent (Fig. 3C)	
..... <i>Leucotrichia pictipes</i> (Banks, 1911)	
Patches of scales absent from dorsum of head and from membranous lobes beneath posterolateral warts; setiferous protuberance on dorsum of head present (Fig. 3A)	
..... <i>Leucotrichia fairchildi</i> Flint, 1970	
5(1). With 1 additional pair of posterolateral warts, 2 pairs in total (Fig. 4E)	
..... <i>Leucotrichia yungarum</i> Angrisano and Burgos, 2002	
With 1 pair of posterolateral warts	6
6(5). With modified basal antennal segments, either broadened or elongated (Figs. 3B, 4A, 4C)	7
Without modifications to the antennae	9
7(6). With scape not elongate, following 5-6 antennal segments broadened (Fig. 3B)	
..... <i>Leucotrichia inflaticornis</i> Botosaneanu, 1993	

With scape elongate, following 5-6 antennal segments not broadened (Figs. 4A, 4C)	8
8(7). Head with short, black setae anteriorly; without scales (Fig. 4A)
.....	<i>Leucotrichia chiriquiensis</i> Flint, 1970
Head without short, black setae; with patches of scales dorsally (Fig. 4C)
.....	<i>Leucotrichia procera</i> , new species
9(6). Phallus slender and tubular, curving strongly ventrad (Figs. 19E, 25E, 38E) 10
Phallus not slender and tubular or curving strongly ventrad 12
10(9). Phallus apex with a series of membranous ridges, appearing stellate in dorsal view (Fig. 38F) <i>Leucotrichia riostoumae</i> , new species
Phallus without series of membranous ridges, not appearing stellate 11
11(10). Inferior appendages fused in ventral view, digitate in lateral view (Figs. 25A, D)
.....	<i>Leucotrichia forrota</i> Oláh and Johanson, 2011
Inferior appendages separate in ventral view, basally subquadrate in lateral view (Figs. 19A, D) <i>Leucotrichia inops</i> Flint, 1991
12(9). Phallus median complex with basal supports (see Fig. 10F) 13
Phallus median complex without basal supports 18

13(12). With small, pointed mesoventral process on abdominal segment VI (Fig. 12D)	
.....	<i>Leucotrichia brochophora</i> Flint, 1991
Without mesoventral process on abdominal segment VI	14
14(13). Phallus apex with pair of sinuate sclerites ventrolaterally (Fig. 10E)	
.....	<i>Leucotrichia botosaneanui</i> Flint, 1996
Phallus apex without pair of sinuate sclerites ventrolaterally	15
15(14). Mesoventral process on abdominal segment VII short, acute, apex pointed in	
ventral view (Figs. 21D, 30D)	16
Mesoventral process on abdominal segment VII large, elongate, apex rounded in	
ventral view (Figs. 22D, 45D).....	17
16(15). Phallus apex with pair of stout dorsal spines, 2 membranous apical lobes (Fig.	
30E, F)	<i>Leucotrichia limpia</i> Ross, 1944
Phallus apex without pair of dorsal spines, 2 membranous dorsal lobes and 1	
mesoventral lobe (Fig. 21E, F)	<i>Leucotrichia gomezi</i> Flint, 1970
17(15). Posteroventral production bearing cluster of stout, prominent setae (Fig. 22B)	
.....	<i>Leucotrichia hispida</i> , new species
Posteroventral production not bearing cluster of stout, prominent setae	

.....	<i>Leucotrichia viridis</i> Flint, 1967	
18(12). Posterior margin projection of sternum VIII bearing prominent or peg-like seta(e) (see Figs. 9B, 17B)		19
Posterior margin projection of sternum VIII without prominent or peg-like setae		23
19(18). Posterior margin projection of sternum VIII bearing cluster of prominent setae (see Figs. 9B, 15B)		20
Posterior margin projection of sternum VIII bearing peg-like seta(e) (Figs. 17B, 44B)		22
20(19). Inferior appendages fused in ventral view		
.....	<i>Leucotrichia bicornuta</i> Thomson, 2012	
Inferior appendages separate in ventral view		21
21(20). Sternum VIII posterior margin with small, pointed mesal projection in ventral view; inferior appendage bearing single dorsal spine (Figs. 15A, D)		
.....	<i>Leucotrichia dianee</i> , new species	
Sternum VIII posterior margin with digitate mesal projection in ventral view; inferior appendage bearing 1 large dorsal spine and 2 small setae (Figs. 41A, D)		
.....	<i>Leucotrichia tapantia</i> , new species	

22(19). Phallus apex with pair of apical membranous lobes (Fig. 17F)	
..... <i>Leucotrichia extraordinaria</i> Bueno-Soria <i>et al.</i> , 2001	
Phallus apex bulbous, without apical lobes (Fig. 44F)	
..... <i>Leucotrichia tubifex</i> Flint, 1964	
23(18). Abdominal sternum VII with both mesoventral process and row of prominent setae; sternum VIII with posterodorsal projection (Figs. 33B, D)	
..... <i>Leucotrichia pectinata</i> , new species	
Abdominal sternum VII with only mesoventral process; sternum VIII without posterodorsal projection	24
24(23). Abdominal sternum VII with mesoventral process apex rhomboid in ventral view (Fig. 37D)	
..... <i>Leucotrichia rhomba</i> , new species	
Abdominal sternum VII with mesoventral process apex not rhomboid in ventral view	25
25(24). Segment IX with anterolateral margin with curved ventrolateral projection (Fig. 6A)	
..... <i>Leucotrichia alisensis</i> Rueda-Martín, 2011	
Segment IX with anterolateral margin not with curved ventrolateral projection ..	26
26(25). Phallus apex bearing a large pair of scissors-like apical sclerites (Fig. 16F)	
..... <i>Leucotrichia dinamica</i> Bueno-Soria, 2010	

Phallus apex not bearing large scissors-like apical sclerites	27
27(26). Inferior appendages partially or entirely fused in ventral view (see Figs. 26D, 28D, 42D)	28
Inferior appendages separate in ventral view	34
28(27). Inferior appendages fused basally in ventral view	29
Inferior appendages entirely fused in ventral view	30
29(28). Phallus trilobed, with rows of large spines; subgenital plate absent (Figs. 28A, F)	<i>Leucotrichia laposka</i> Oláh and Johanson, 2011
Phallus not trilobed, without large spines; subgenital plate present	<i>Leucotrichia melleopicta</i> Mosely, 1934
30(28). Inferior appendages with dorsal spines or setae	31
Inferior appendages without dorsal spine or setae	33
31(30). Inferior appendages bearing single mesodorsal seta and 3 apicodorsal setae (Fig. 36A)	<i>Leucotrichia repanda</i> , new species
Inferior appendages either bearing less than 3 apicodorsal setae or, if bearing 3 apicodorsal setae, without single mesodorsal seta	32

32(31). Phallus apex with peg-like setae (Fig. 14E, F)	
.....	<i>Leucotrichia denticulata</i> , new species
Phallus apex without peg-like setae	
.....	<i>Leucotrichia termitiformis</i> Botosaneanu, 1993
33(30). Phallus apex trilobed, short spines present on dorsal surface	
.....	<i>Leucotrichia interrupta</i> Flint, 1991
Phallus apex not trilobed, short spines not present	
.....	<i>Leucotrichia sidneyi</i> , new species
34(27). Phallus apex with pair of apical membranous lobes (see Fig. 11E)	35
Phallus apex without apical membranous lobes	37
35(34). Inferior appendages with dorsomesal “hump” in lateral view (Figs. 27A, 43A) 36	
Inferior appendages without dorsomesal “hump” in lateral view (Fig. 11A)	
.....	<i>Leucotrichia brasiliana</i> Sattler and Sykora, 1977
36(35). Inferior appendages with mitten-like “thumb” in ventral view (Fig. 43D)	
.....	<i>Leucotrichia tritoven</i> Flint, 1996
Inferior appendages without mitten-like “thumb”	
.....	<i>Leucotrichia kateae</i> , new species

37(34). Inferior appendages apically hooked (Figs. 29A, 32A)	38
Inferior appendages not apically hooked	39
38(37). Subgenital plate with dorsal arm present (Fig. 32A)	
..... <i>Leucotrichia padera</i> Flint, 1991	
Subgenital plate with dorsal arm not apparent (Fig. 29A)	
..... <i>Leucotrichia lerma</i> Angrisano and Burgos, 2002	
39(37). Inferior appendages with dorsal spines or setae	40
Inferior appendages without dorsal spine or setae	
..... <i>Leucotrichia angelinae</i> , new species	
40(39). Inferior appendages with single dorsal spine	41
Inferior appendages with 3 dorsal setae (Fig. 20A)	
..... <i>Leucotrichia fulminea</i> , new species	
41(40). Posterior margin of abdominal segment VIII with ventrolateral projection (Fig.	
31B)	<i>Leucotrichia mutica</i> Flint, 1991
Posterior margin of abdominal segment VIII without ventrolateral projection (Fig.	
8B)	<i>Leucotrichia ayura</i> Flint, 1991

BIBLIOGRAPHY

- Angrisano, E. B. and Burgos, G. N. (2002) Contribución para el conocimiento do los Leucotrichiini (Trichoptera: Hydroptilidae). Tres especies nuevas de la Argentina. *Revista de la Sociedad Entomológica Argentina* 61: 103-109.
- Banks, N. (1911) Description of new species of North American neuropteroid insects. *Transactions of the American Entomological Society* 37: 335-360, plates 311-313.
- Blahnik, R. J., Holzenthal, R. W. and Prather A. L. (2007) The lactic acid method for clearing Trichoptera genitalia. In: Bueno-Soria J., Barba-Álvarez R., Armitage BJ (Eds) *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, 9-14.
- Botosaneanu, L. (1991) Amsterdam expedition to the West Indian Islands, report 71. Trichoptères d'Haïti. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 61: 113-134.
- Botosaneanu, L. and Alkins-Koo, M. (1993) The caddis flies (Insecta: Trichoptera) of Trinidad and Tobago, West Indies. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 63: 5-45.
- Botosaneanu, L. and Bolland, H. R. (1997) A mite (Acari: Erythraeidae) as unusual parasite on an adult caddisfly (Trichoptera: Hydroptilidae) from the Dominican Republic (West Indies). *Studies on the Natural History of the Caribbean Region* 73: 71-76.
- Botosaneanu, L. and Sakal, D. (1992) Ecological observations on the caddisflies (Insecta: Trichoptera) from Trinidad and Tobago (W. Indies). *Revue d'Hydrobiologie Tropicale* 25: 197-207.
- Bueno-Soria, J. (2010) Some new Trichoptera (Glossosomatidae, Hydroptilidae, Hydropsychidae and Polycentropodidae) from Mexico. *Proceedings of the Entomological Society of Washington* 112: 22-31.
- Bueno-Soria, J., Santiago-Fragoso, S. and Barba-Alvarez, R. (2001) Studies in aquatic insects, XVIII: new species and new record of caddisflies (Trichoptera) from Mexico. *Entomological News* 112: 145-158.
- Colwell, R. K. (2012) Biota 3: The Biodiversity Database Manager. Available from <http://viceroy.eeb.uconn.edu/Biota/biota>.
- Dallwitz, M. J., Paine, T. A. and Zurcher, E. J. (1999 onwards) User's guide to the DELTA editor. Available from: <http://delta-intkey.com/>.
- Flint, O. S., Jr. (1968) Bredin-Archbold-Smithsonian Biological Survey of Dominica, 9. The Trichoptera (Caddisflies) of the Lesser Antilles. *Proceedings of the United States National Museum* 125: 1-86.
- Flint, O. S., Jr. (1970) Studies of Neotropical caddisflies, X: *Leucotrichia* and related genera from North and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 60: 1- 64.
- 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.
- 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.
- Flint, O. S., Jr. (1996) Studies of Neotropical caddisflies LV: Trichoptera of Trinidad and Tobago. *Transactions of the American Entomological Society* 122: 67-113.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999) Catalog of the Neotropical Caddisflies (Trichoptera). *Special Publication, Ohio Biological Survey*, Columbus, Ohio, 1-239 pp.
- Flint, O. S., Jr. and Sykora, J. L. (1993) New species and records of caddisflies (Insecta: Trichoptera) from the Lesser Antilles, with special reference to Grenada. *Annals of Carnegie Museum* 62: 47-62.
- Holzenthal, R. W. and Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa* 511: 1-80.
- Marshall, J. E. (1979) A review of the genera of the Hydroptilidae (Trichoptera). *Bulletin of the British Museum (Natural History) Entomology* 39: 135-239.
- McAuliffe, J. R. (1982) Behavior and life history of *Leucotrichia pictipes* (Banks) (Trichoptera: Hydroptilidae) with special emphasis on case reoccupancy. *Canadian Journal of Zoology* 60: 1557-1561.
- Mosely, M. E. (1934) New exotic Hydroptilidae. *Transactions of the Royal Entomological Society of London* 82: 137-163.
- Oláh, J. and Johanson, K. A. (2011) New Neotropical Hydroptilidae (Trichoptera). *Annales Historico-Naturales Musei Nationalis Hungarici* 103: 117-255.
- 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 Martín, P. A. (2011) New Hydroptilidae and new records from north-western Argentina and Bolivia (Trichoptera: Hydroptilidae). *Aquatic Insects* 33: 1-11.
- Sattler, W. and Sykora, J. L. (1977) Über eine, besonders durch ihr Bauinstinkt, merkwürdige neotropische Köcherfliege - *Leucotrichia brasiliiana* n. sp. *Amazonia* 6: 137-255.
- 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.
- Thomson, R. (2012) Descriptions of new species of Leucotrichiinae (Trichoptera: Hydroptilidae) from Brazil. *Psyche* 2012: 1-7.
- Wells, A. and Wichard, W. (1989) Caddisflies of Dominican amber VI. Hydroptilidae (Trichoptera). *Studies on Neotropical Fauna and Environment* 24: 41-51.
- Wiggins, G. B. (1996) *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press, Toronto, 457 pp.

Table 1. *Leucotrichia* species, distributions, and species groups (Trichoptera: Hydroptilidae: Leucotrichiinae) (☐=extinct).

<i>Leucotrichia</i> species	Distribution	Species group
<i>L. adela</i> Wells and Wichard, 1989 †	Dominican amber	<i>melleopicta</i>
<i>L. alisensis</i> Rueda-Martín, 2011	Argentina	<i>melleopicta</i>
<i>L. angelinae</i> , new species	Venezuela	<i>melleopicta</i>
<i>L. ayura</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. bicornuta</i> Thomson, 2012	Brazil	<i>melleopicta</i>
<i>L. botosaneanui</i> Flint, 1996	Tobago, Trinidad	<i>melleopicta</i>
<i>L. brasiliiana</i> Sattler and Sykora, 1977	Brazil	<i>melleopicta</i>
<i>L. brochophora</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. chiriquiensis</i> Flint, 1970	Panama	<i>melleopicta</i>
<i>L. denticulata</i> , new species	Mexico	<i>melleopicta</i>
<i>L. dianae</i> , new species	Costa Rica	<i>melleopicta</i>
<i>L. dinamica</i> Bueno-Soria, 2010	Mexico	<i>melleopicta</i>
<i>L. extraordinaria</i> Bueno-Soria, Santiago-Fragoso, and Barba-Alvarez, 2001	Mexico Colombia, Grenada, Panama, Tobago, Trinidad,	<i>melleopicta</i>
<i>L. fairchildi</i> Flint, 1970	Venezuela	<i>pictipes</i>
<i>L. forrota</i> Oláh and Johanson, 2011	Peru, Ecuador	<i>melleopicta</i>
<i>L. fulminea</i> , new species	Ecuador	<i>melleopicta</i>
<i>L. gomezi</i> Flint, 1970	Dominican Republic	<i>melleopicta</i>
<i>L. hispida</i> , new species	Costa Rica	<i>melleopicta</i>
<i>L. imitator</i> Flint, 1970	Costa Rica, Guatemala, Mexico	<i>pictipes</i>
<i>L. inflaticornis</i> Botosaneanu, 1993	Trinidad	<i>melleopicta</i>
<i>L. inops</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. interrupta</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. kateae</i> , new species	Venezuela	<i>melleopicta</i>
<i>L. laposka</i> Oláh and Johanson, 2011	Peru	<i>melleopicta</i>
<i>L. lerma</i> Angrisano and Burgos, 2002	Argentina	<i>melleopicta</i>
<i>L. limpia</i> Ross, 1944	Mexico, U.S.A.	<i>melleopicta</i>
<i>L. melleopicta</i> Mosely, 1934	Mexico, Venezuela	<i>melleopicta</i>
<i>L. mutica</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. padera</i> Flint, 1991	Colombia	<i>melleopicta</i>
<i>L. pectinata</i> , new species	Ecuador	<i>melleopicta</i>
<i>L. pictipes</i> (Banks, 1911)	U.S.A., Mexico	<i>pictipes</i>
<i>L. procera</i> , new species	Brazil	<i>melleopicta</i>
<i>L. repanda</i> , new species	Venezuela	<i>melleopicta</i>
<i>L. rhomba</i> , new species	Costa Rica	<i>melleopicta</i>
<i>L. riostoumae</i> , new species	Ecuador Costa Rica, El Salvador, Guatemala, Mexico,	<i>melleopicta</i>
<i>L. sarita</i> Ross, 1944	U.S.A.	<i>pictipes</i>
<i>L. sidneyi</i> , new species	Venezuela	<i>melleopicta</i>
<i>L. tapantia</i> , new species	Costa Rica	<i>melleopicta</i>
<i>L. termitiformis</i> Botosaneanu, 1993	Trinidad	<i>melleopicta</i>
<i>L. tritoven</i> Flint, 1996	Tobago, Trinidad, Venezuela	<i>melleopicta</i>
<i>L. tubifex</i> Flint, 1964	Dominican Republic, Haiti, Jamaica, Puerto Rico	<i>melleopicta</i>
<i>L. viridis</i> Flint, 1967	El Salvador, Guatemala, Mexico, Panama	<i>melleopicta</i>
<i>L. yungarum</i> Angrisano and Burgos, 2002	Argentina	<i>melleopicta</i>

Table 2. Character states of genera in the *Leucotrichia* genus cluster, modified from Oláh and Johanson (2011). “Modifications” of the head, antennae, and wings, compared to the “unmodified” conditions of these structures, are discussed below in the generic description.

<i>Genus</i>	Number of ocelli	Head	Antennae	Wing	Spine on sternum VIII	Process on segment IX	Inferior appendages
<i>Abtrichia</i>	2	m	m	m	-	+	s
<i>Acostatrichia</i>	3	u	u	m/u	-/+	-/+	s
<i>Anchitrichia</i>	2	u	u	u	+	-	s
<i>Ascotrichia</i>	2	m	u	u	+	+	f
<i>Betrichia</i>	2-3	m/u	m/u	u	-/+	-	f
<i>Ceratotrichia</i>	2	m	m	u	+	-	s
<i>Costatrichia</i>	3	u	m/u	m/u	-/+	-/+	s
<i>Leucotrichia</i>	2-3	m/u	m/u	u	-	-	s/f
<i>Zumatrichia</i>	2	m	m	u	-/+	+	s/f

m = modified, u = unmodified, - = absent, + = present, s = separate, f = fused

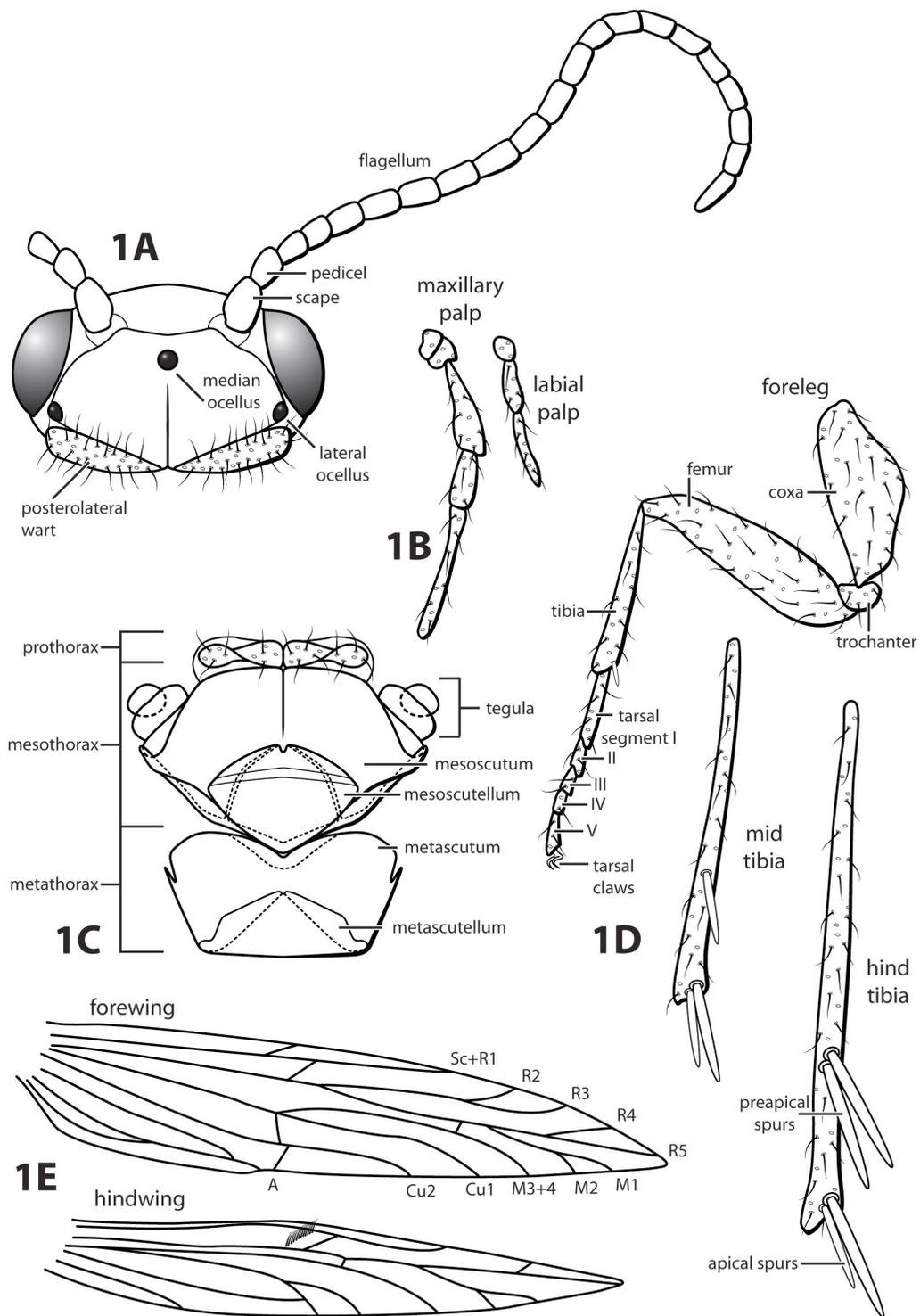


FIGURE 1. *Leucotrichia melleopicta* Mosely, 1934 (holotype, NHM). **A** head and antennae, dorsal **B** palps **C** thorax, dorsal **D** legs and spur formula (1.3.4) **E** wings.

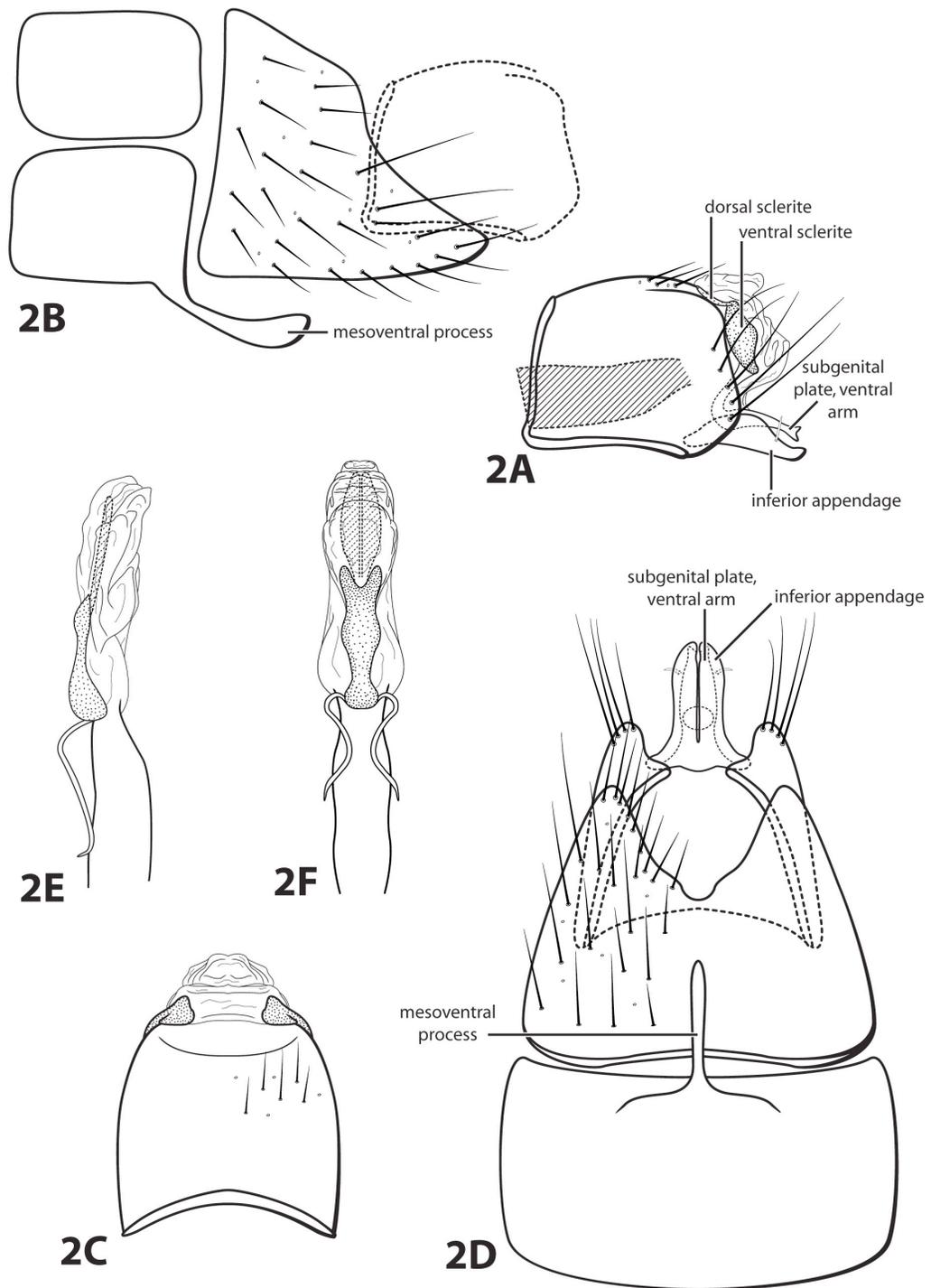


FIGURE 2. *Leucotrichia melleopicta* Mosely, 1934 (holotype, NHM). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

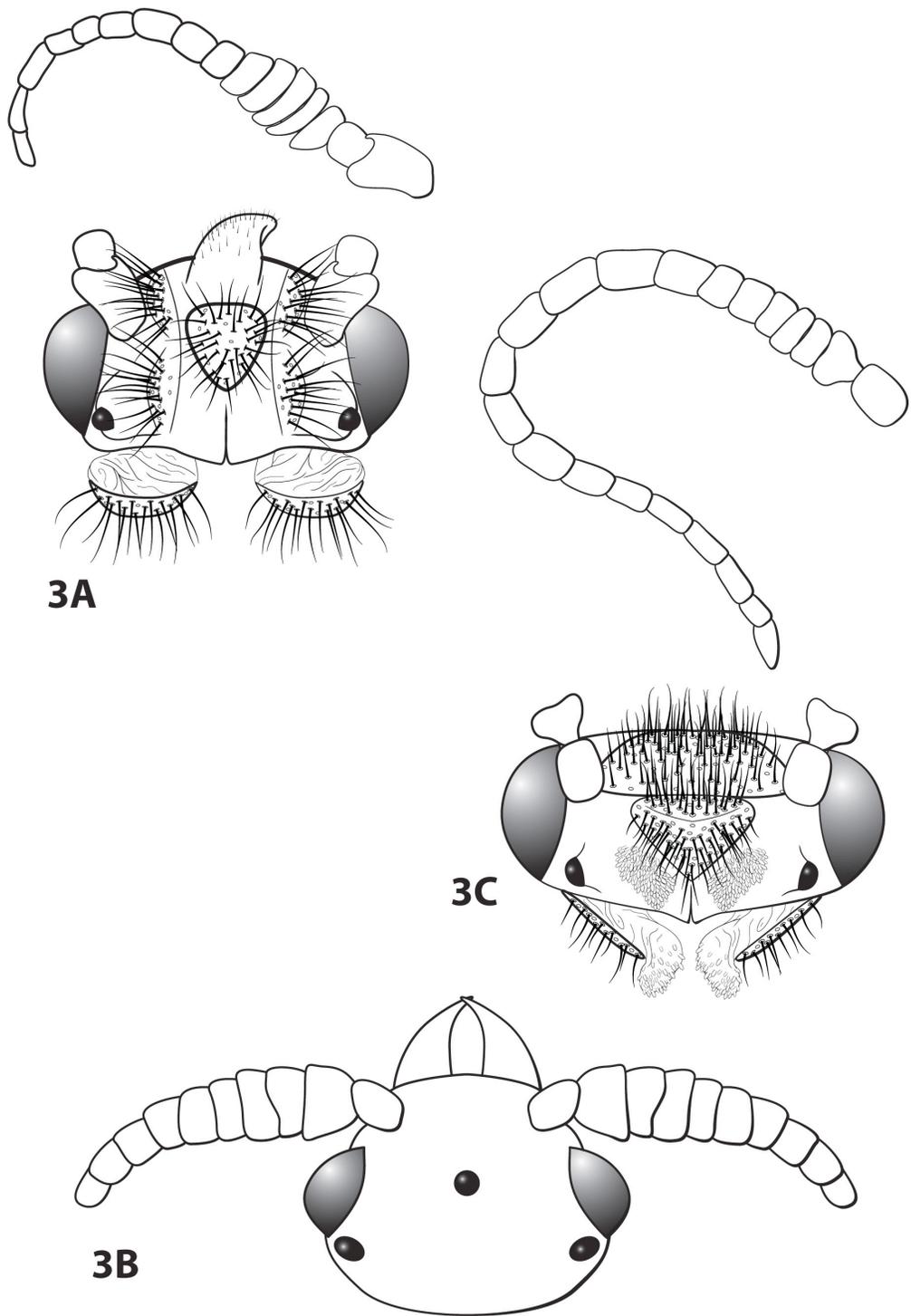


FIGURE 3. Head and antennae: **A** *Leucotrichia fairchildi* Flint, 1970 (UMSP000140357) **B** *Leucotrichia inflaticornis* Botosaneanu, 1993 (UMSP000140327) **C** *Leucotrichia pictipes* (Banks, 1911) (MCZ11597).

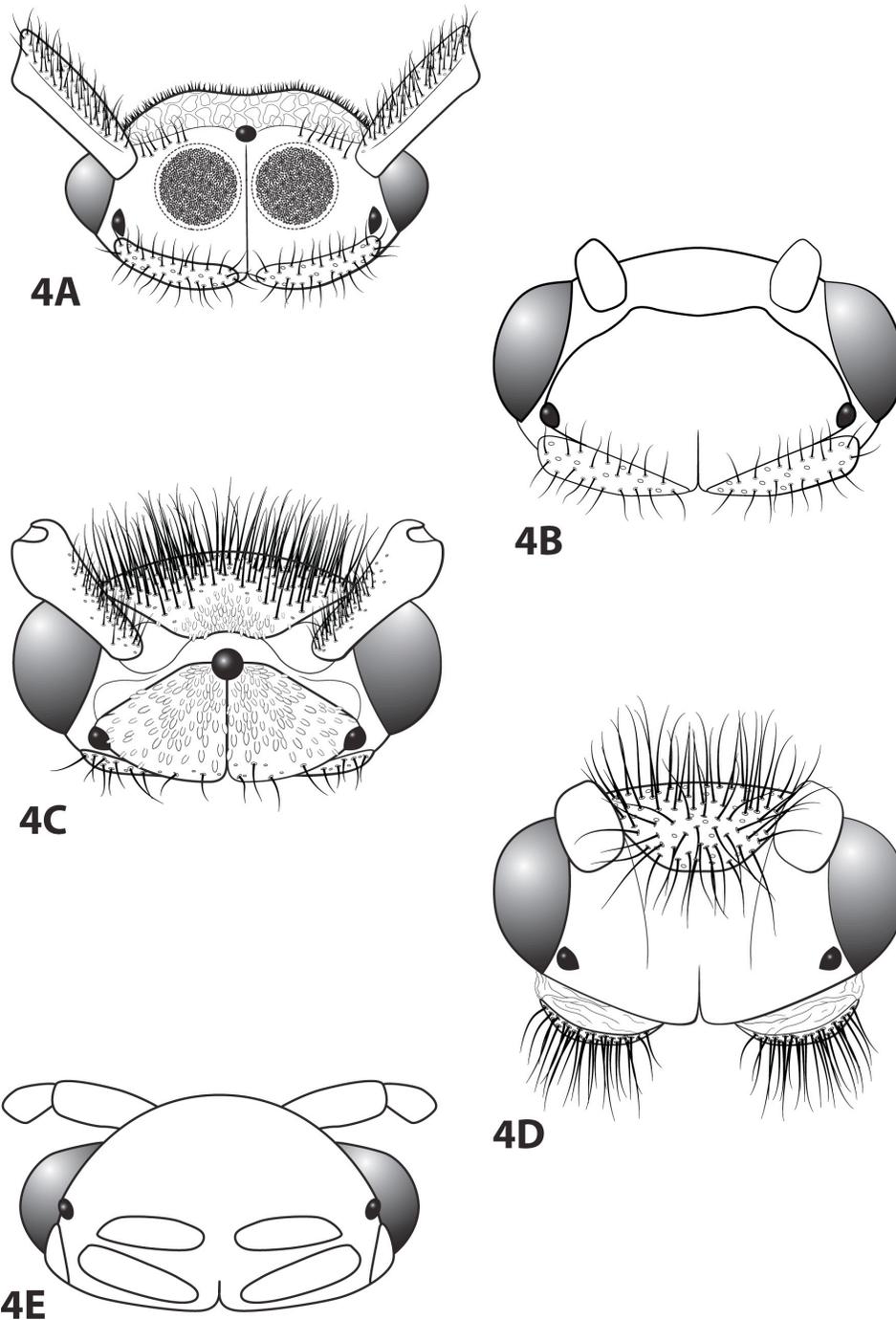
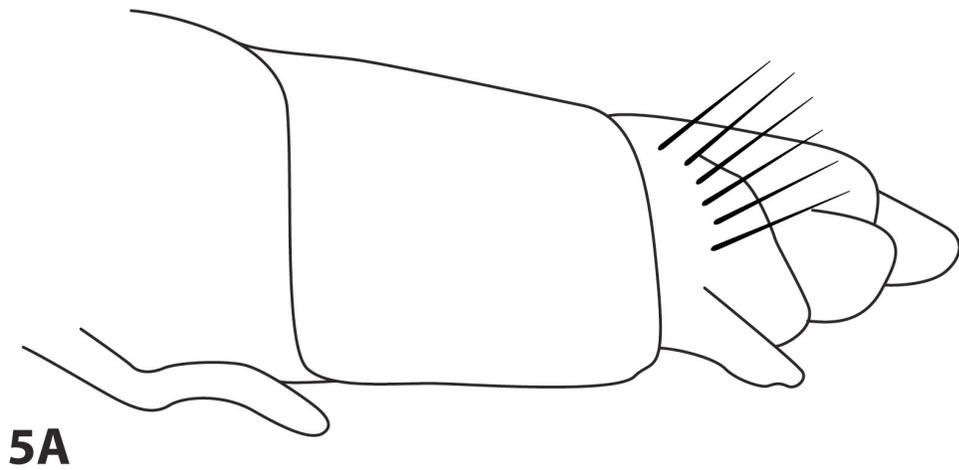
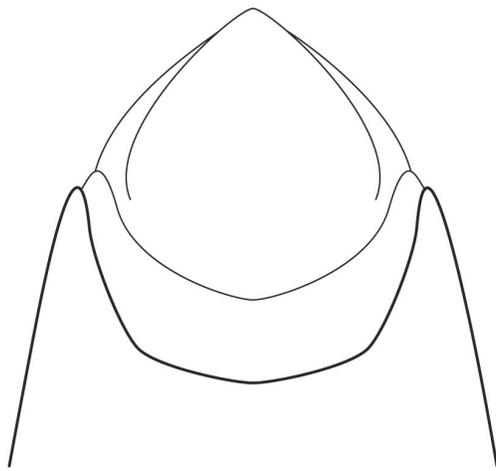


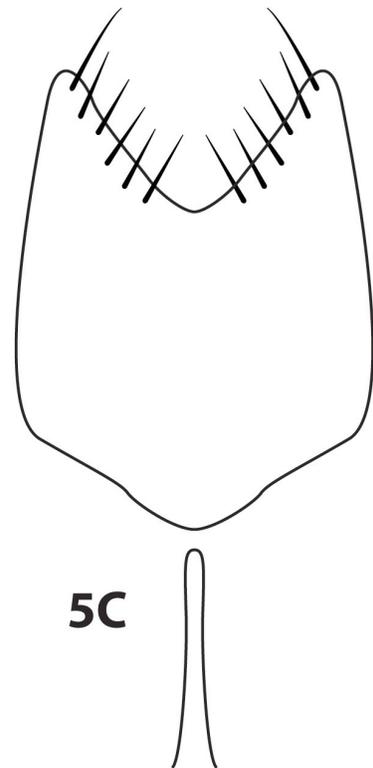
FIGURE 4. Head and scape: **A** *Leucotrichia chiriquiensis* Flint, 1970 (USNM70896) **B** *Leucotrichia imitator* Flint, 1970 (USNM70898) **C** *Leucotrichia procera*, **new species** (UMSP000XXXX) **D** *Leucotrichia sarita* Ross, 1944 (INHS22339) **E** *Leucotrichia yungarum* Angrisano and Burgos, 2002 (redrawn from Angrisano and Burgos, 2002).



5A



5B



5C

FIGURE 5. *Leucotrichia adela* Wells and Wichard, 1989 (redrawn from Wells and Wichard, 1989). Male genitalia: **A** segments VII-X, lateral **B** segments IX -X, dorsal **C** mesoventral process of segment VII and segment VIII, ventral.

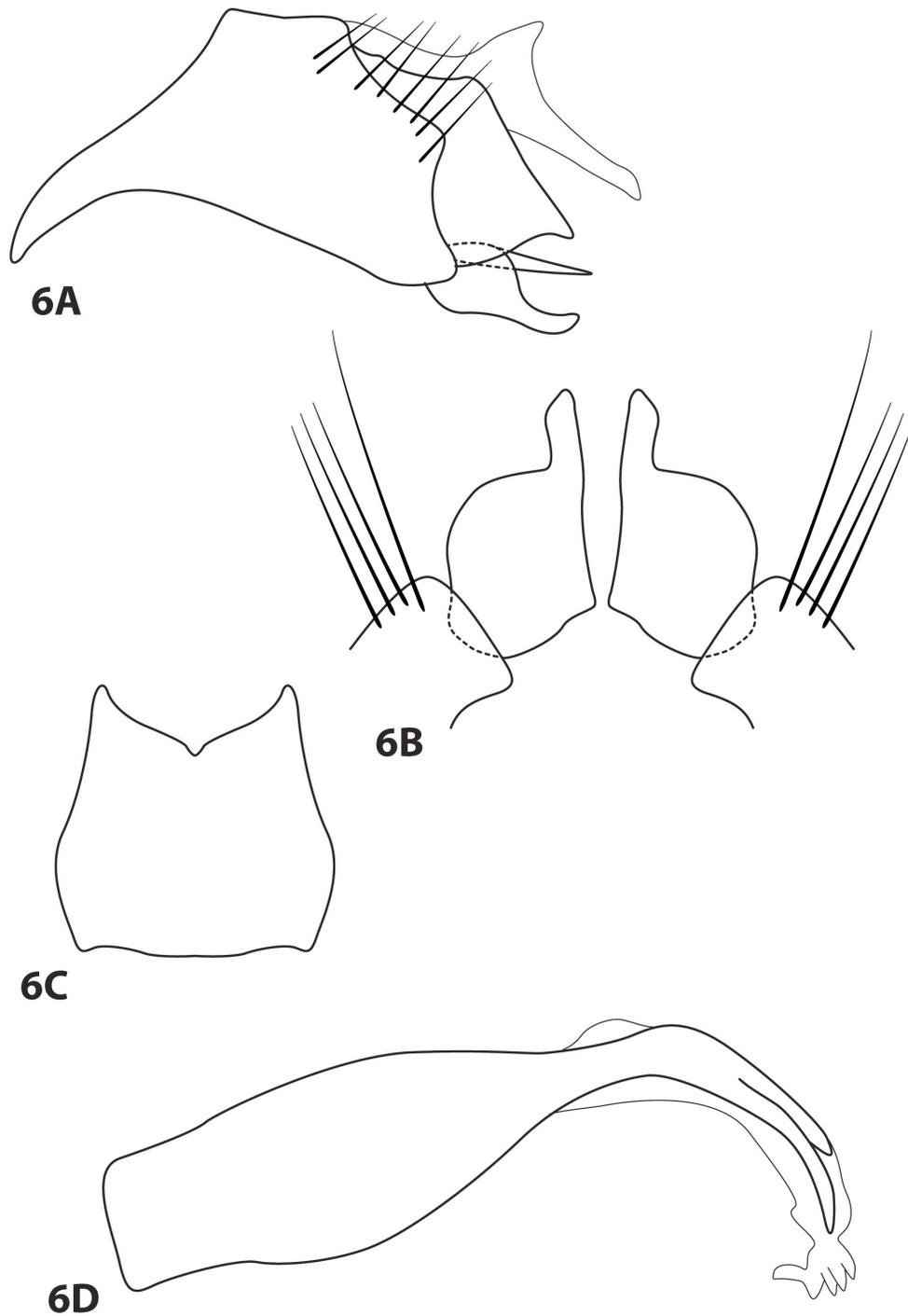


FIGURE 6. *Leucotrichia alisensis* Rueda Martín, 2011 (redrawn from Rueda Martín, 2011). Male genitalia: **A** segments IX-X, lateral **B** apex of segment IX and inferior appendage, ventral **C** segment VIII, ventral **D** phallus, lateral.

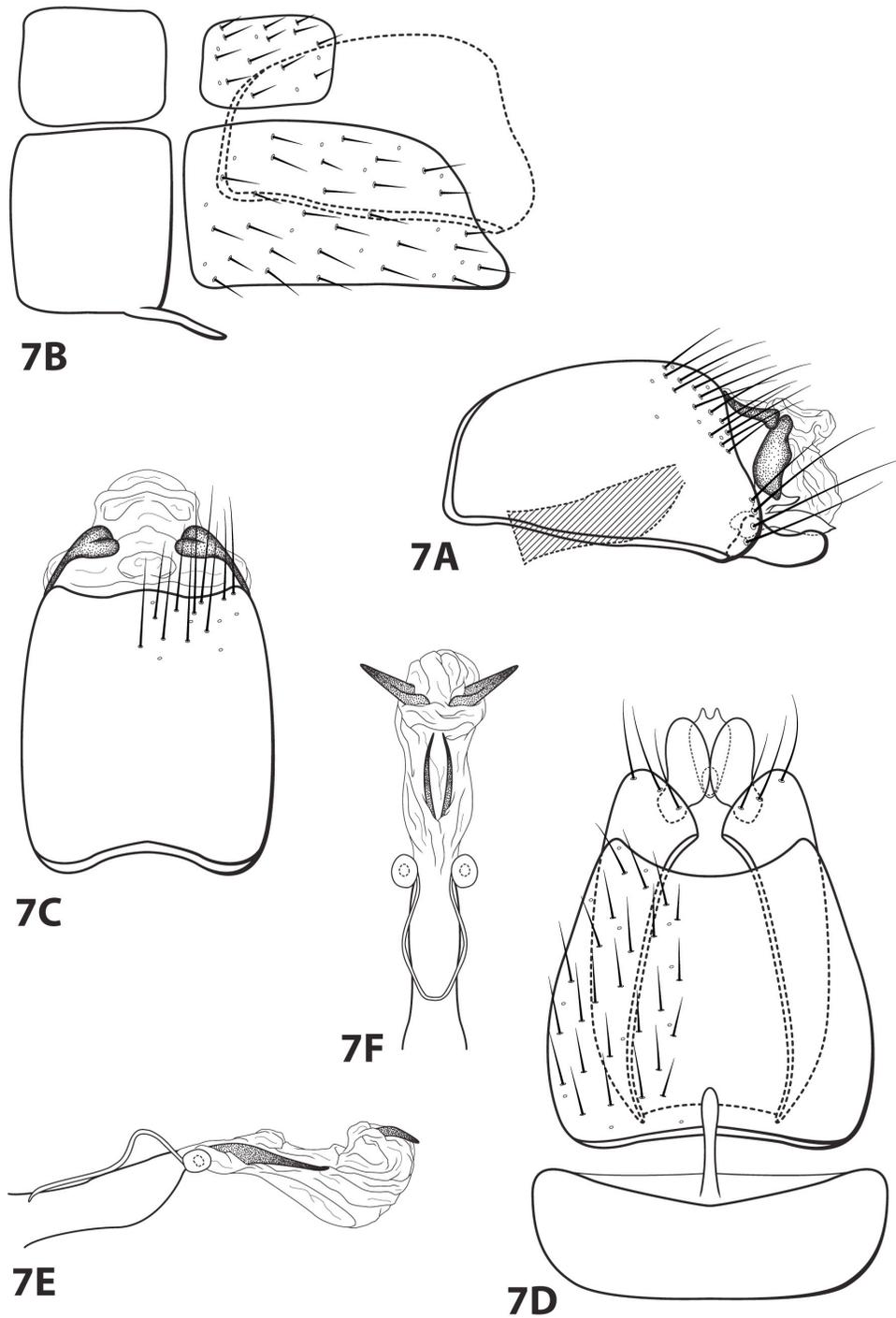


FIGURE 7. *Leucotrichia angelinae*, new species (UMSP000142591). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

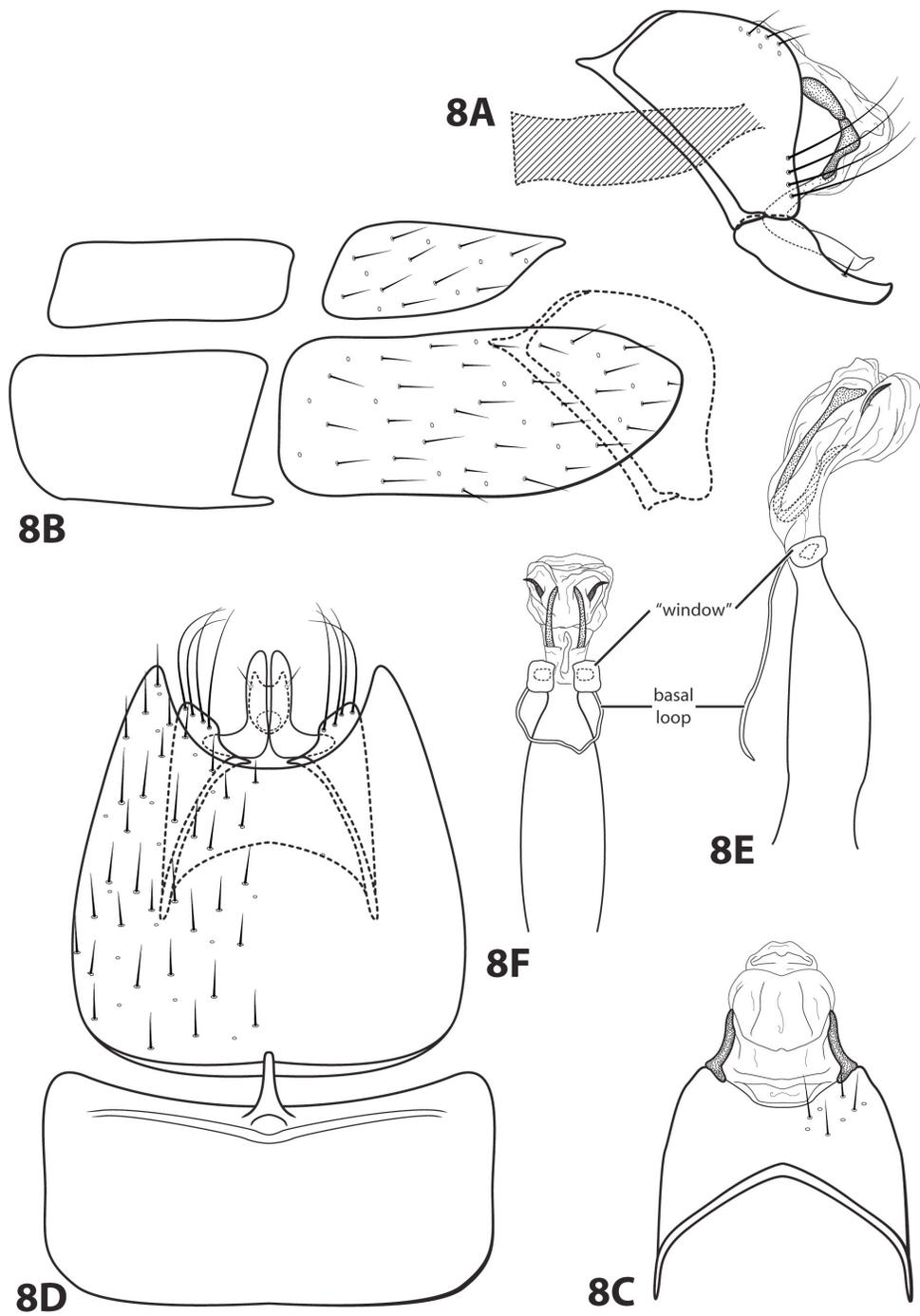


FIGURE 8. *Leucotrichia ayura* Flint, 1991 (USNM104529). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

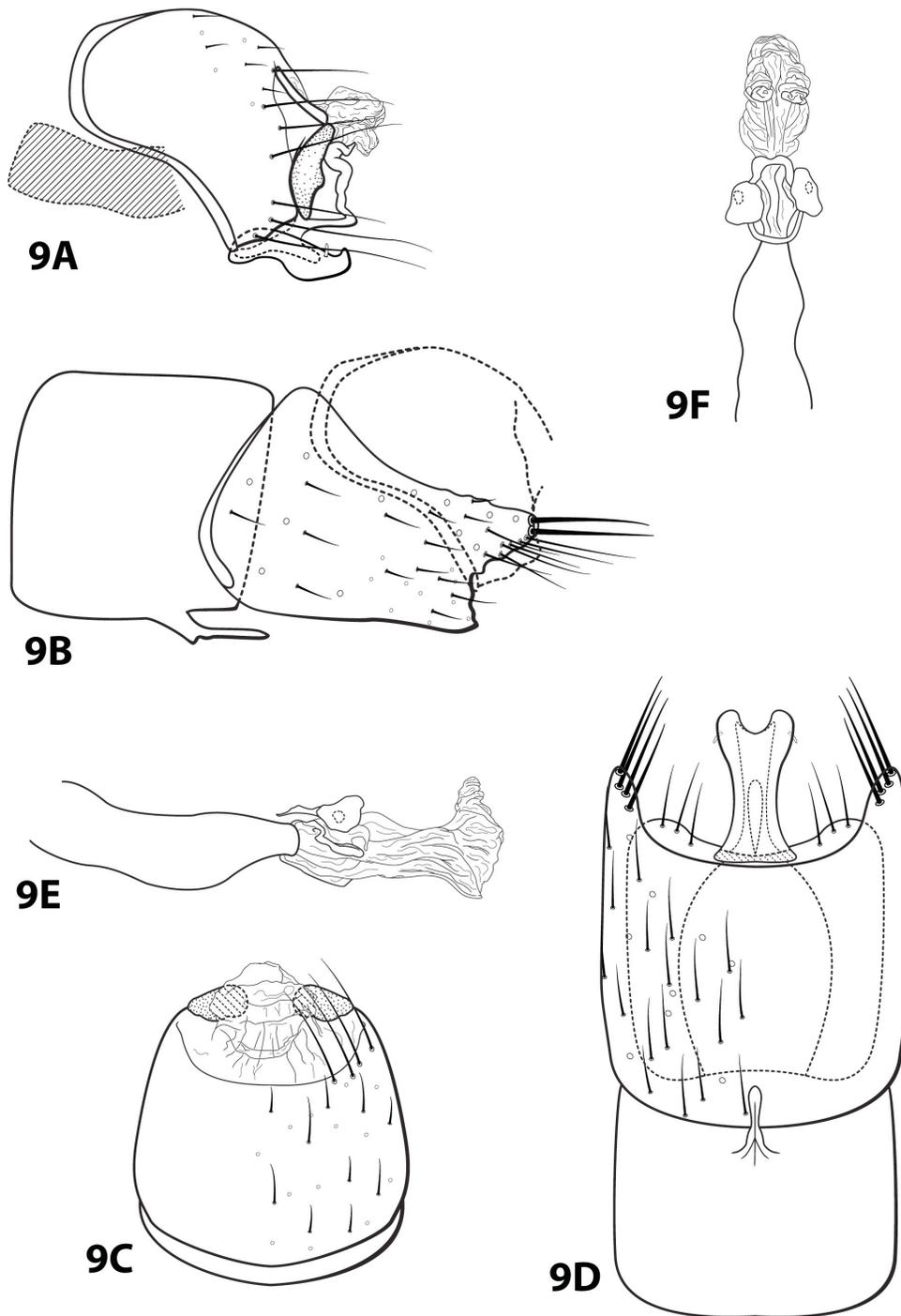


FIGURE 9. *Leucotrichia bicornuta* Thomson, 2012 (UMSP000014084). Male genitalia: **A** segment IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

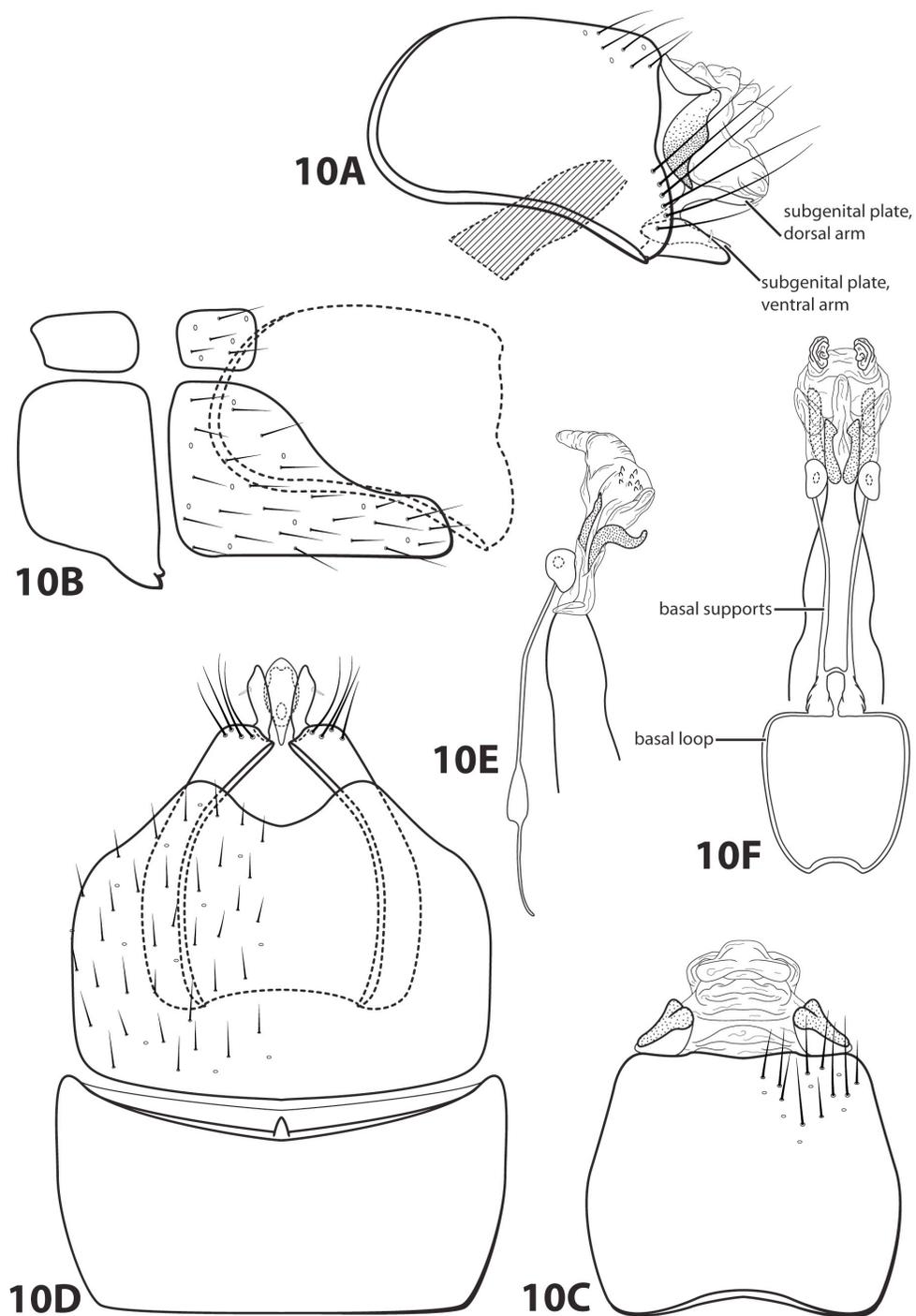


FIGURE 10. *Leucotrichia botosaneanui* Flint, 1996 (USNM105436). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

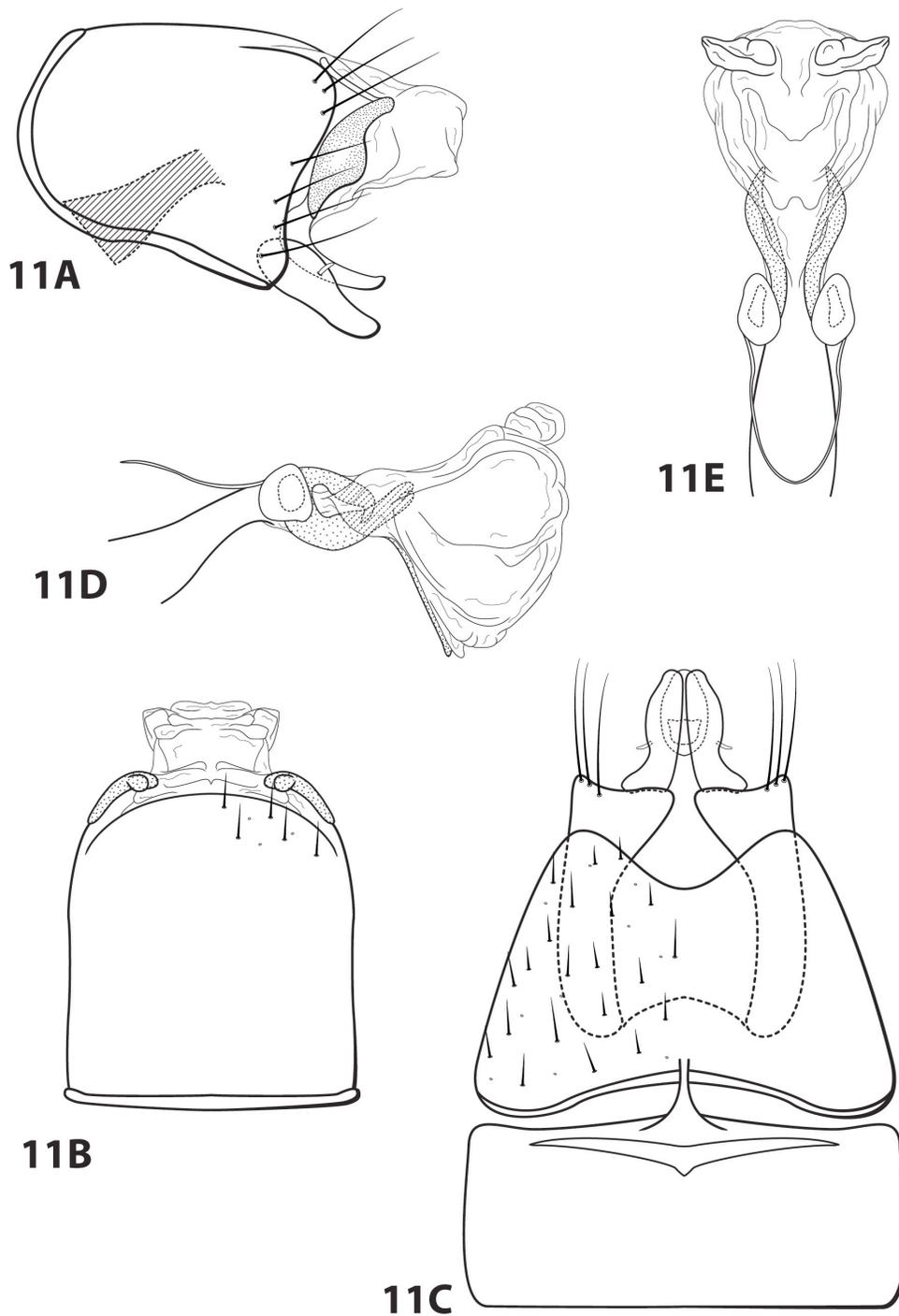


FIGURE 11. *Leucotrichia brasiliiana* Sattler and Sykora, 1977 (UMSP000140138). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments IX-X, dorsal **C** segments VII-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

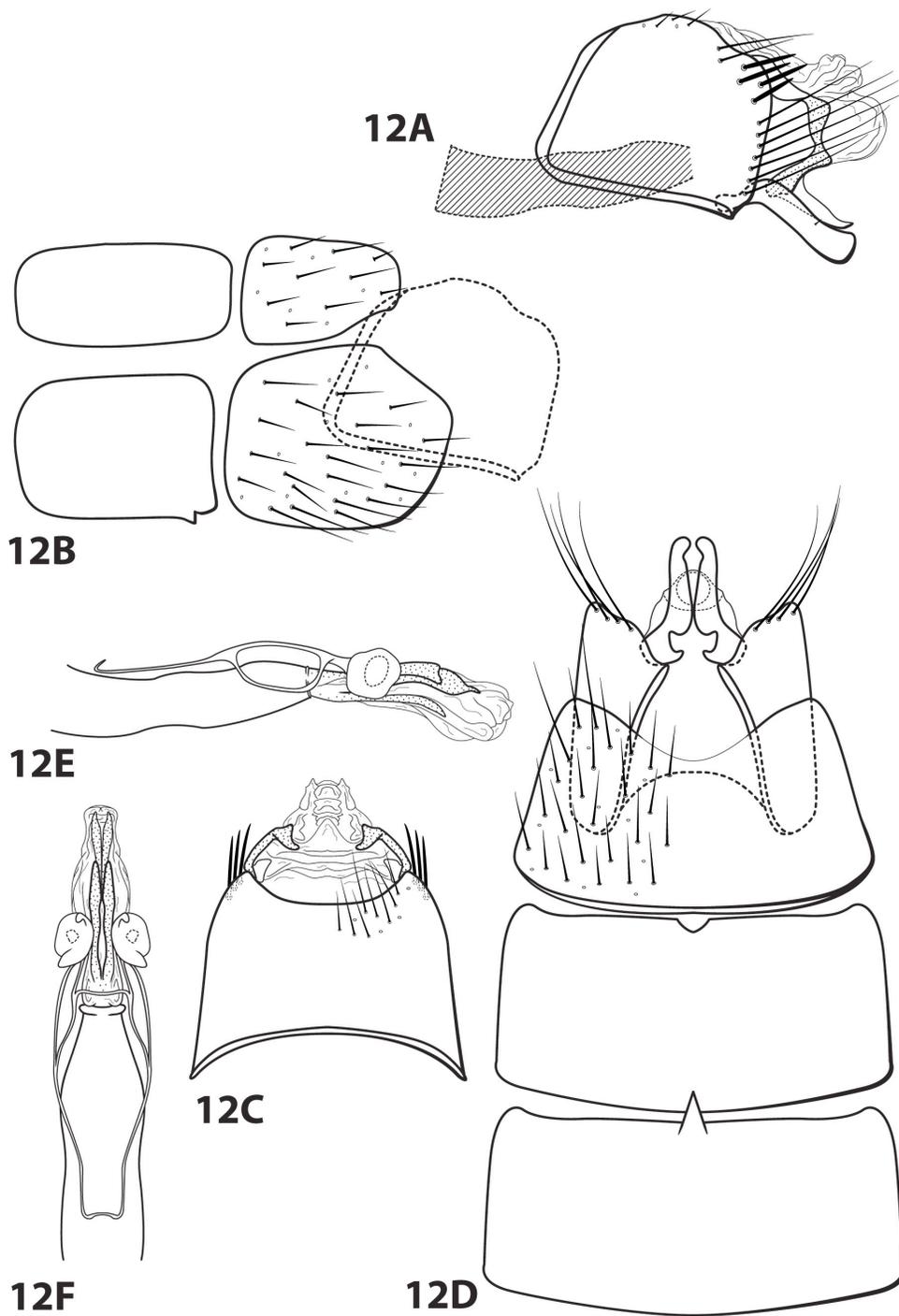


FIGURE 12. *Leucotrichia brochophora* Flint, 1991 (USNM104527). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VI-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

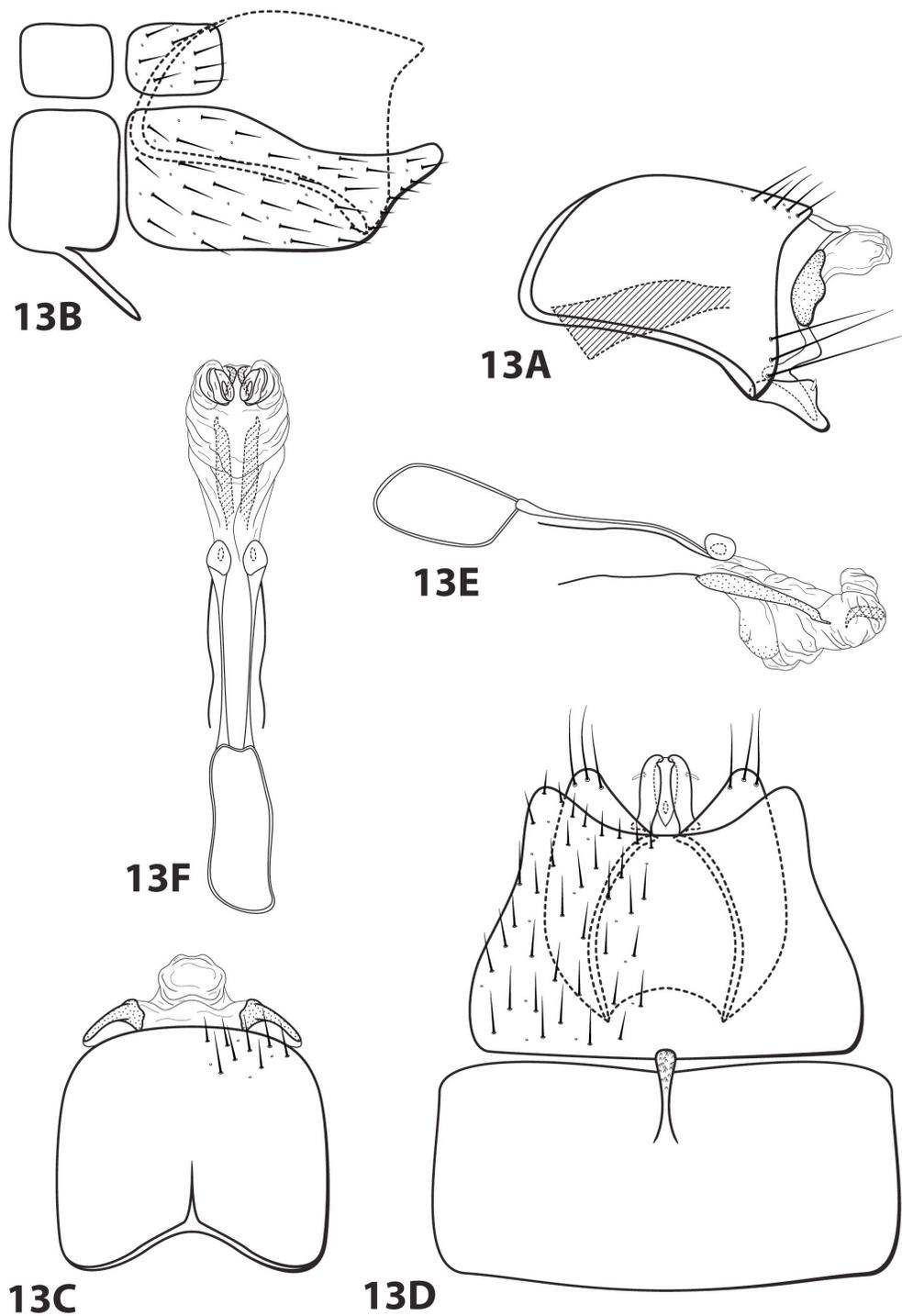


FIGURE 13. *Leucotrichia chiriquiensis* Flint, 1970 (USNM70896). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

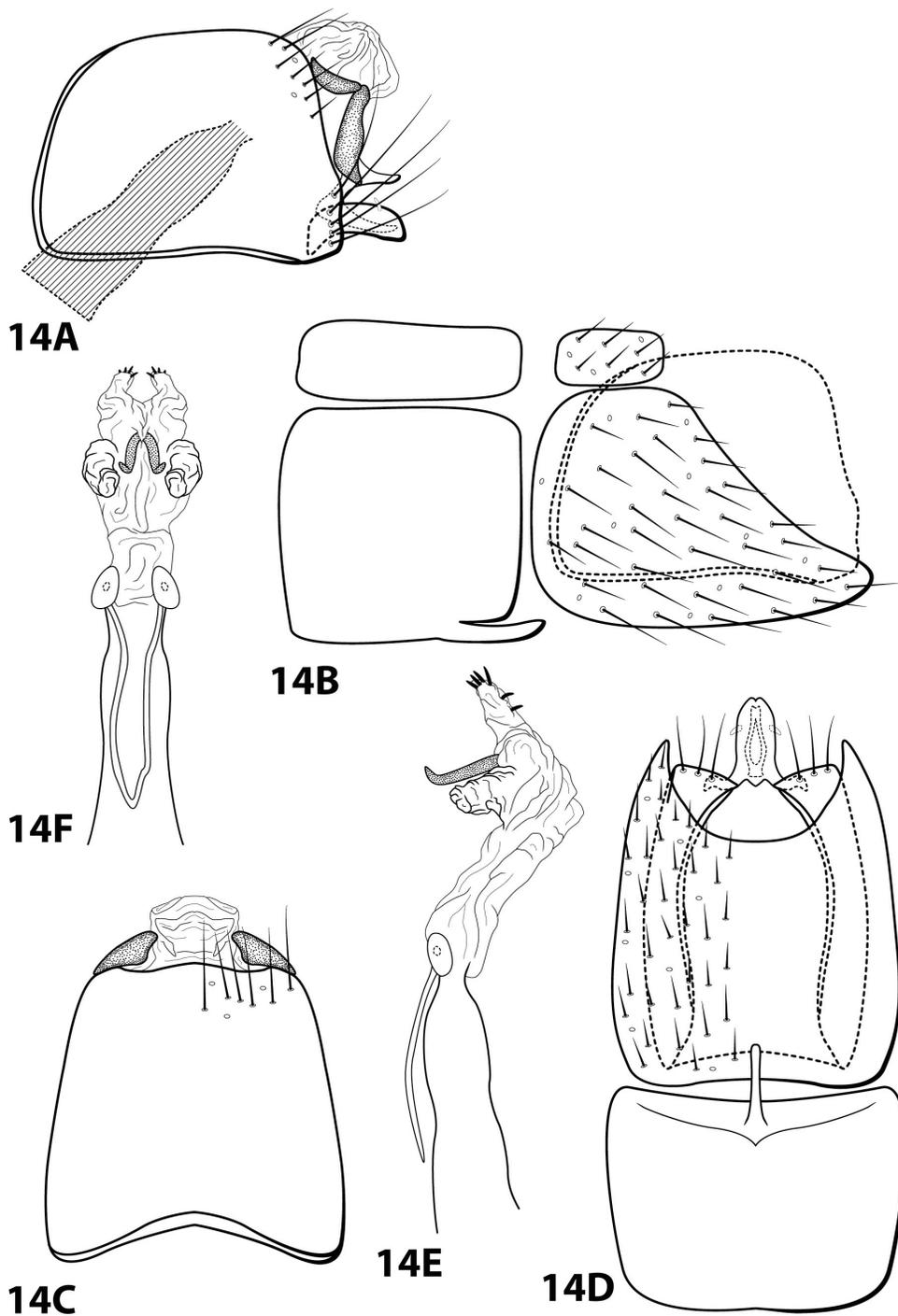


FIGURE 14. *Leucotrichia denticulata*, new species (UMSP000142916). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

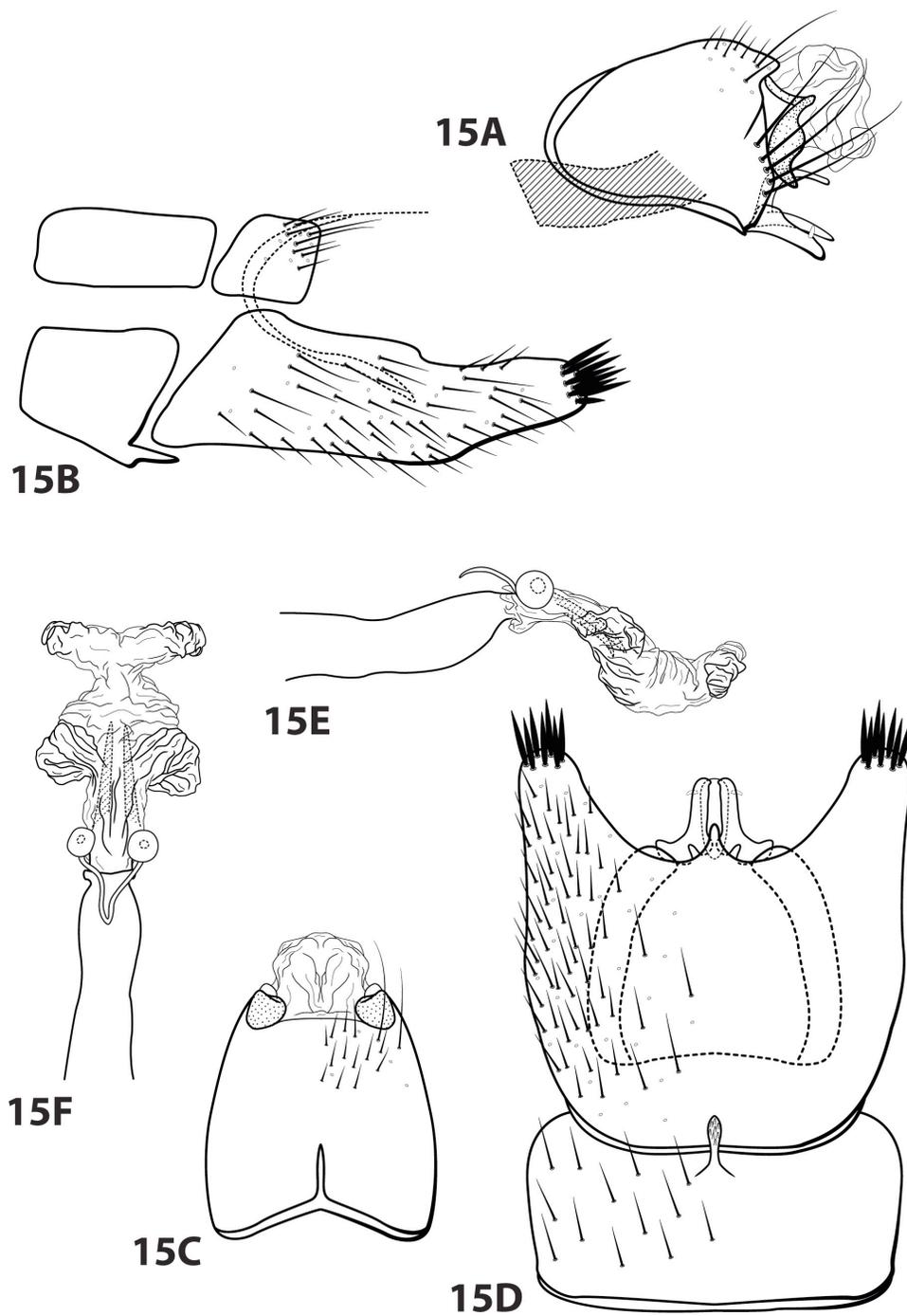


FIGURE 15. *Leucotrichia dianeae*, new species (UMSP000201649). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

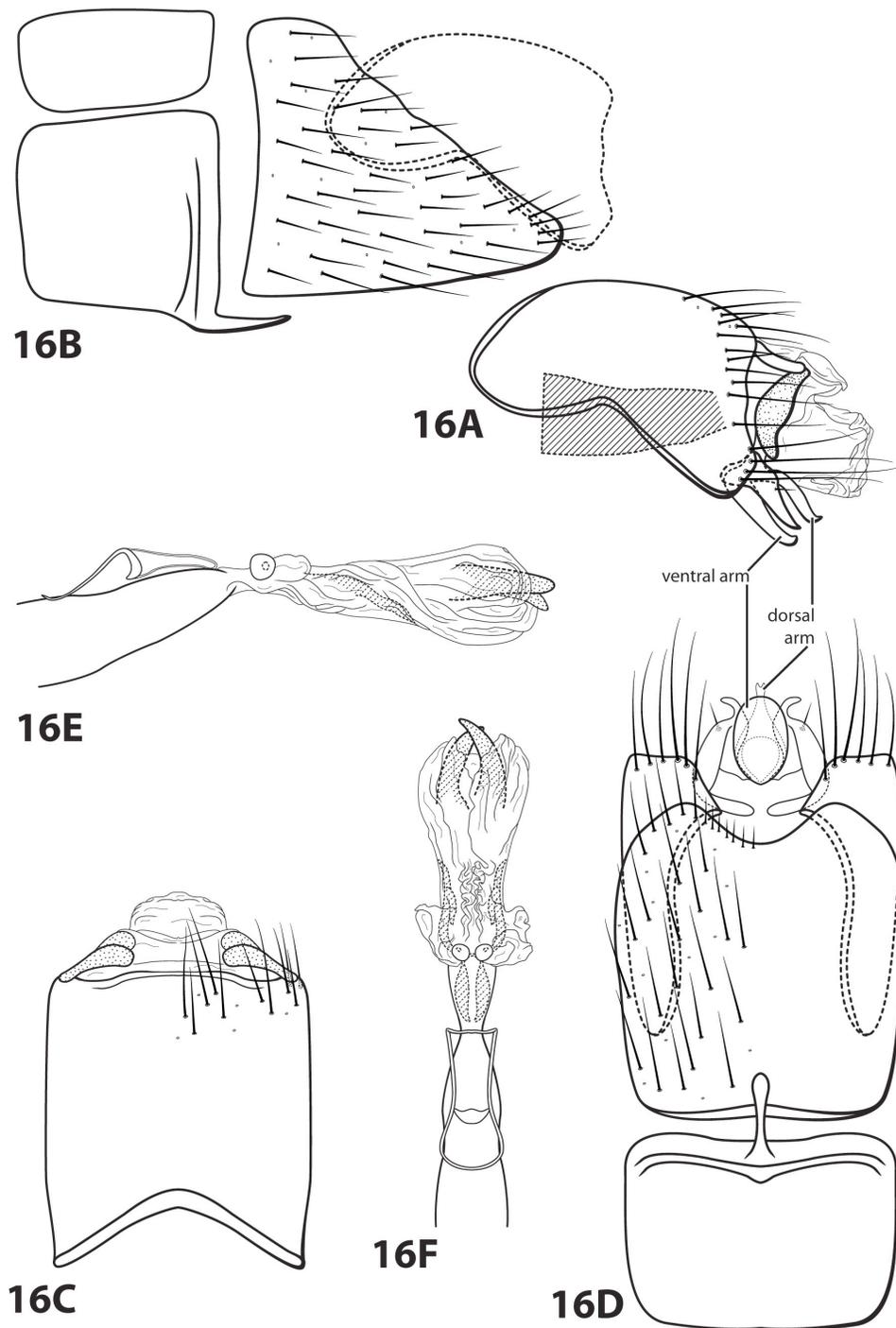


FIGURE 16. *Leucotrichia dinamica* Bueno-Soria, 2010 (UMSP000140694). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

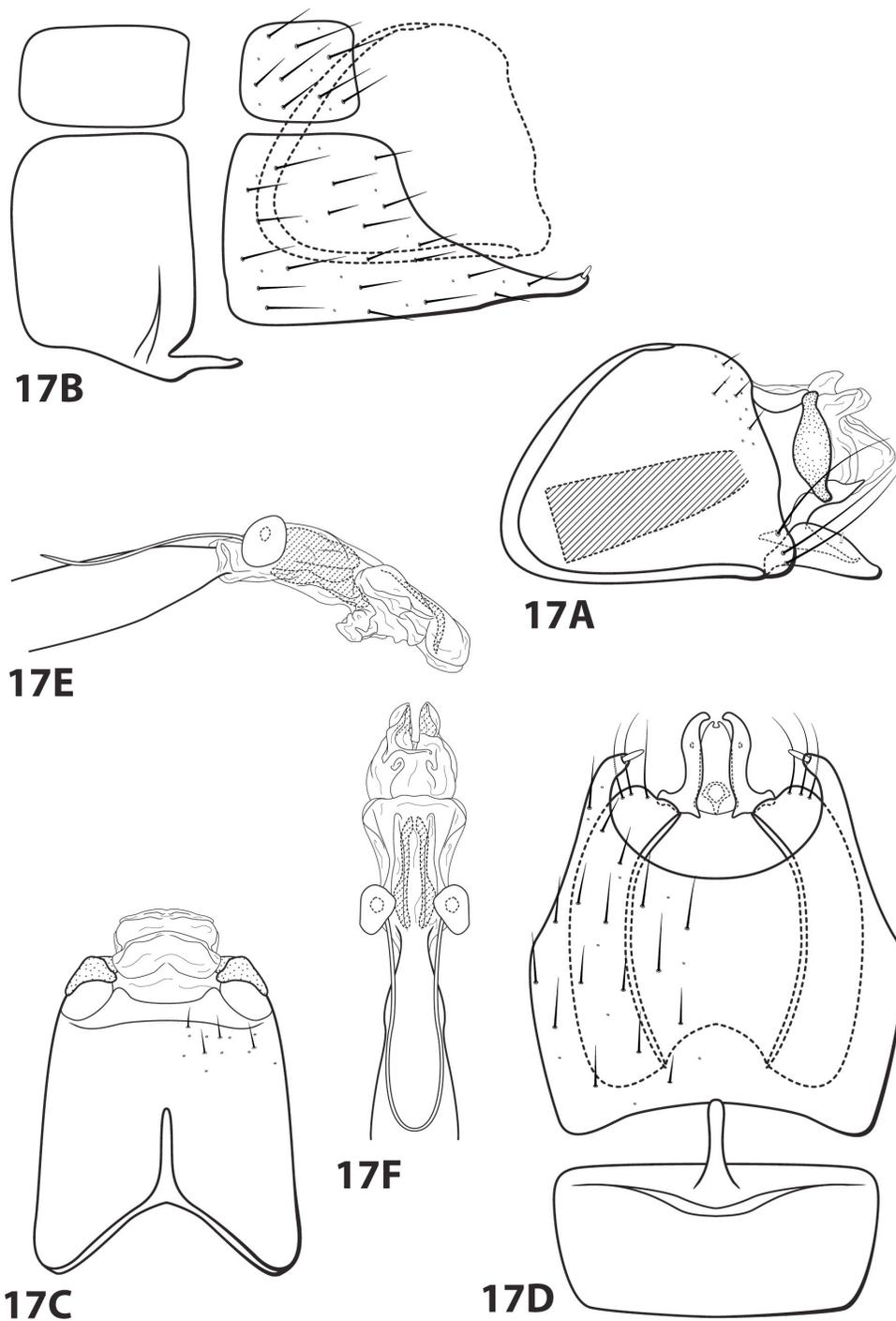


FIGURE 17. *Leucotrichia extraordinaria* Bueno-Soria, Santiago-Fragoso, and Barba-Álvarez, 2001 (UMSP000140695). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

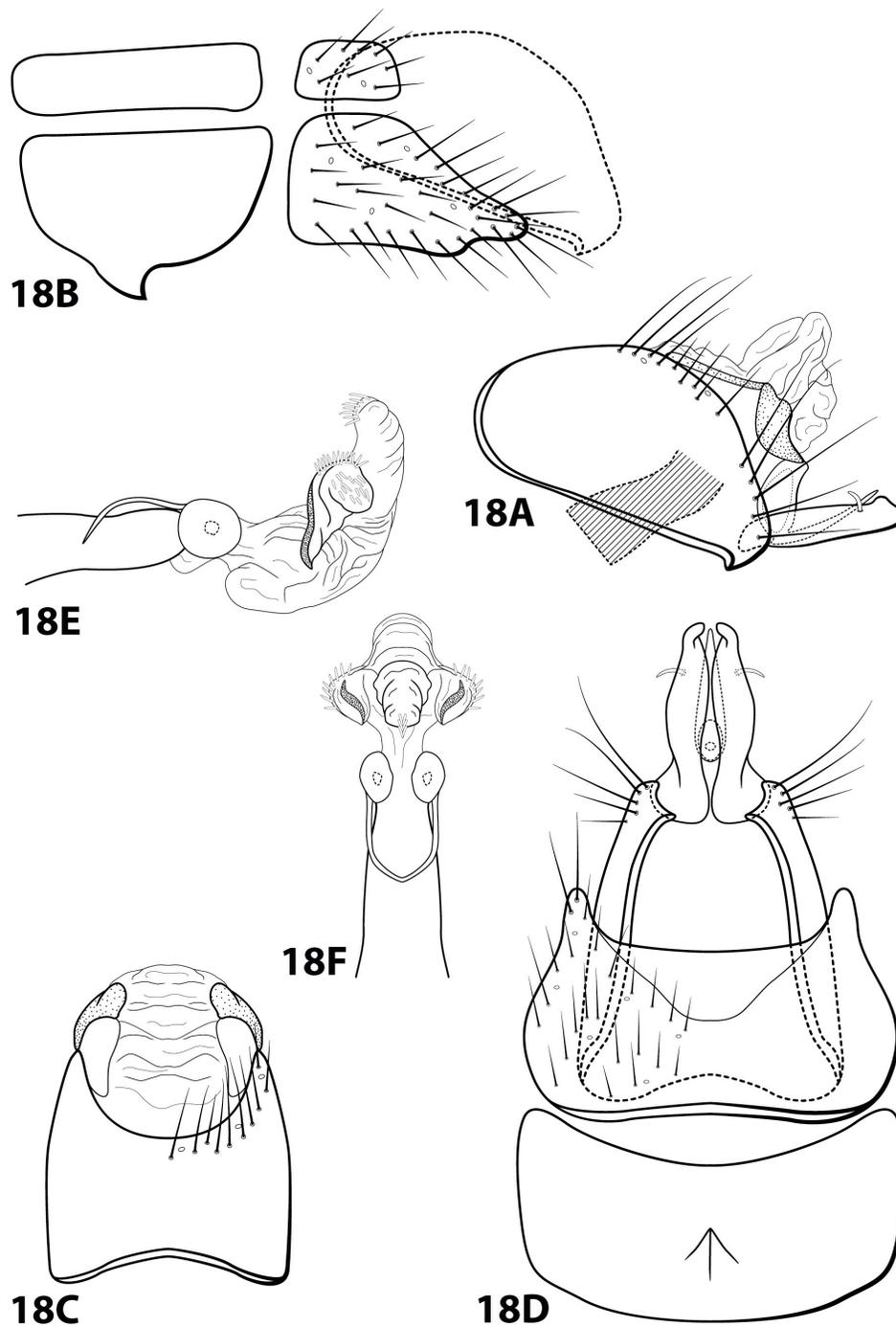


FIGURE 18. *Leucotrichia fairchildi* Flint, 1970 (UMSP000140357). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

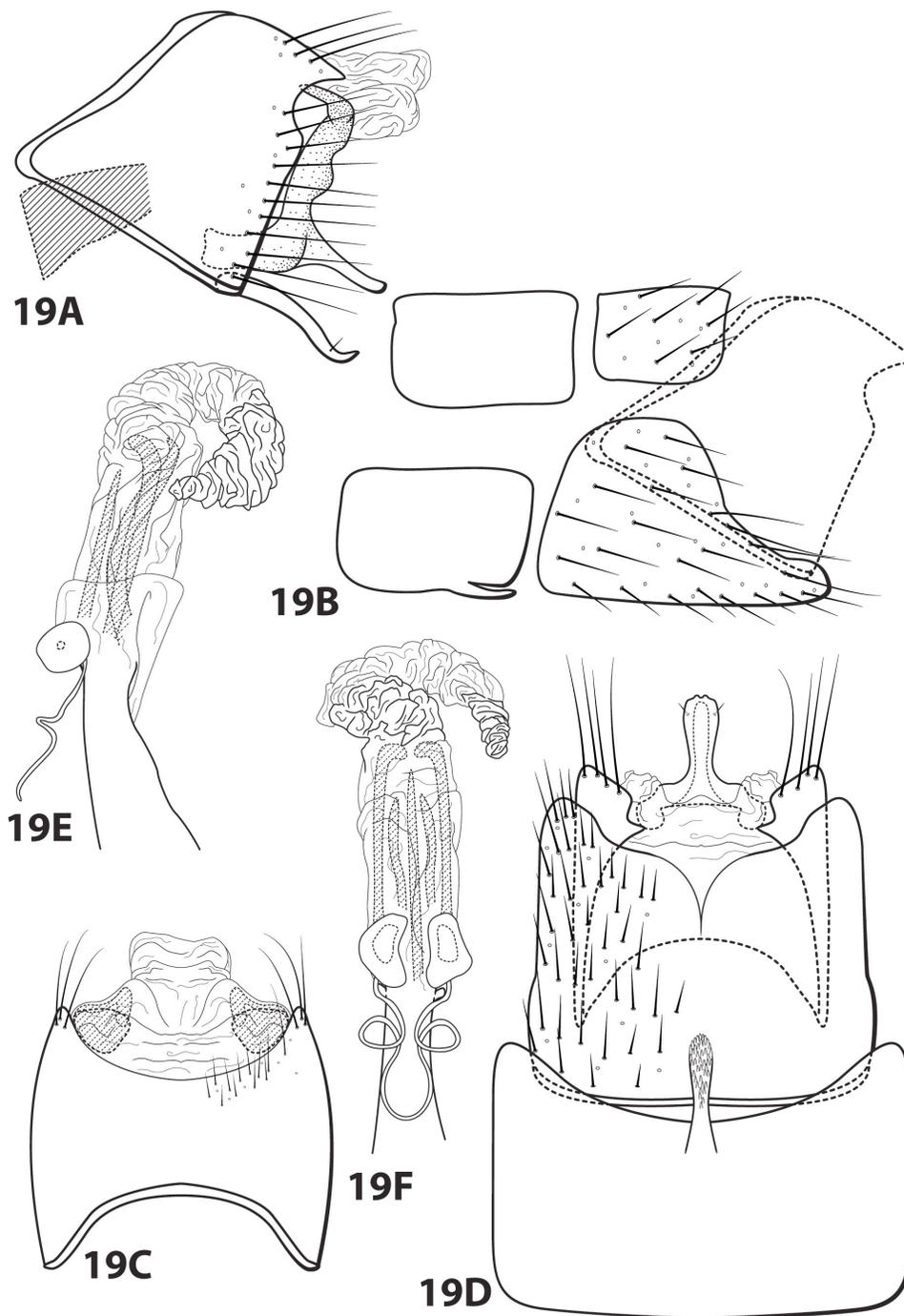


FIGURE 19. *Leucotrichia forrota* Oláh and Johanson, 2011 (NHRSKAJ000000329). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

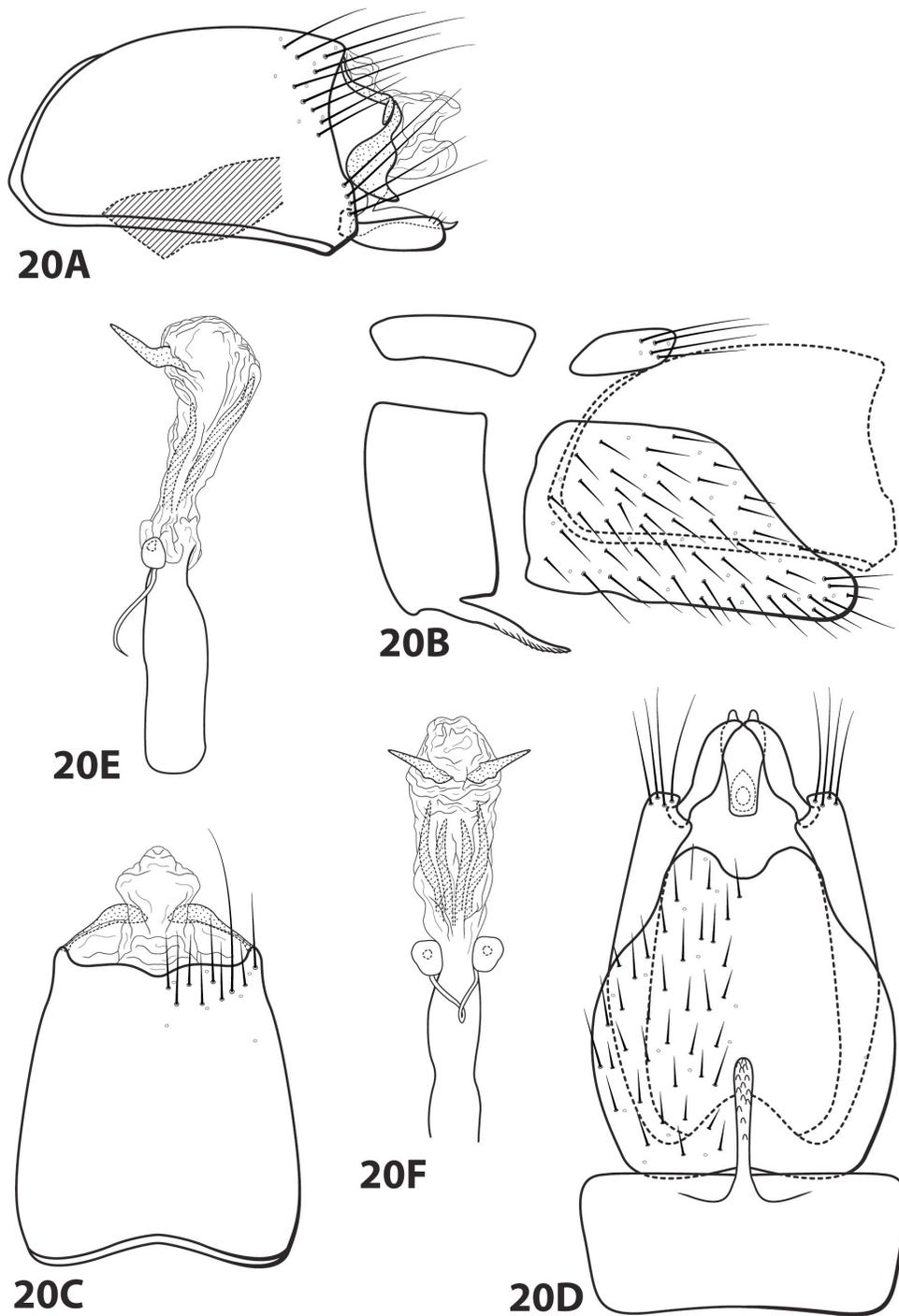


FIGURE 20. *Leucotrichia fulminea*, new species (UMSP000140611). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

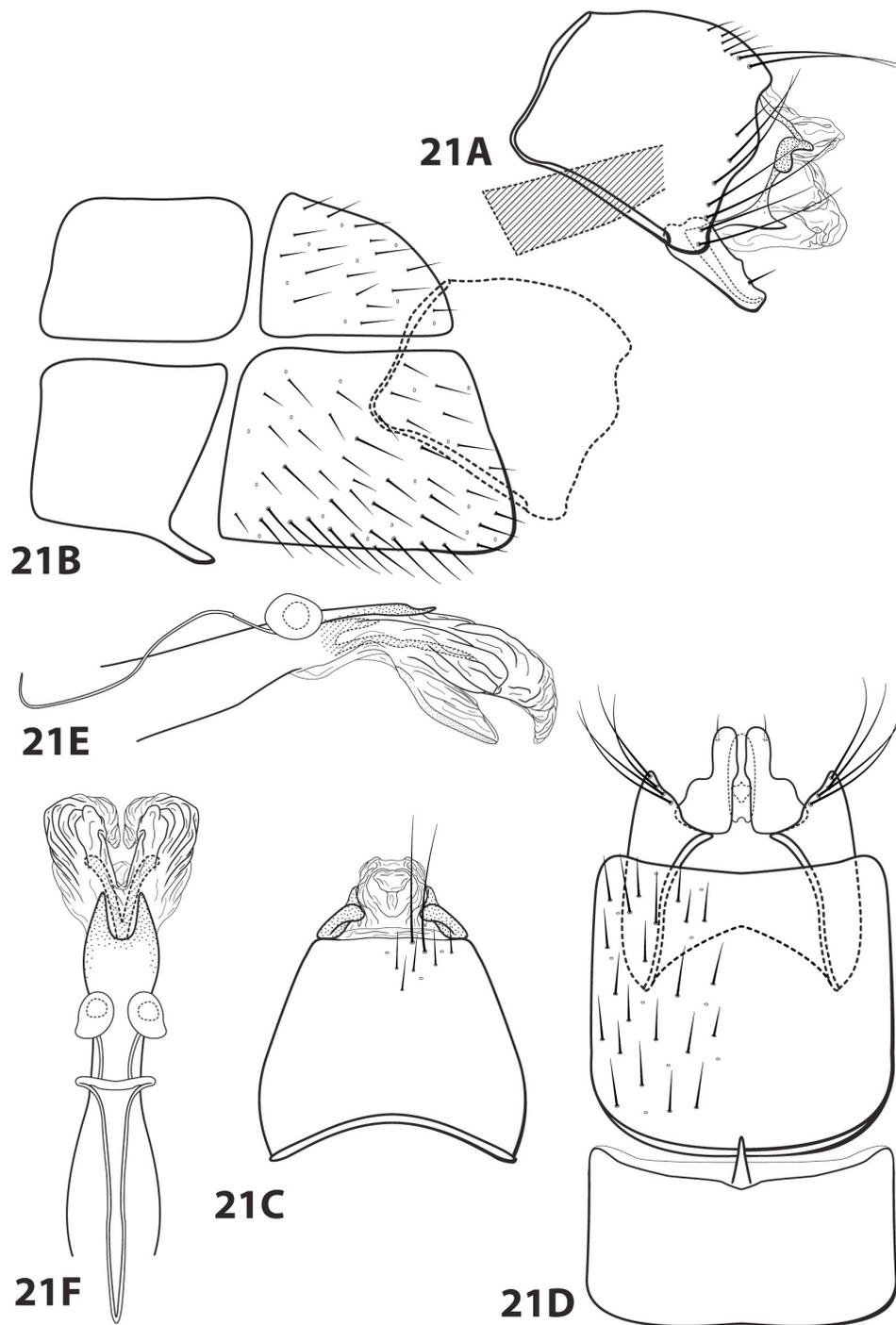


FIGURE 21. *Leucotrichia gomezi* Flint, 1970 (USNM70897). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

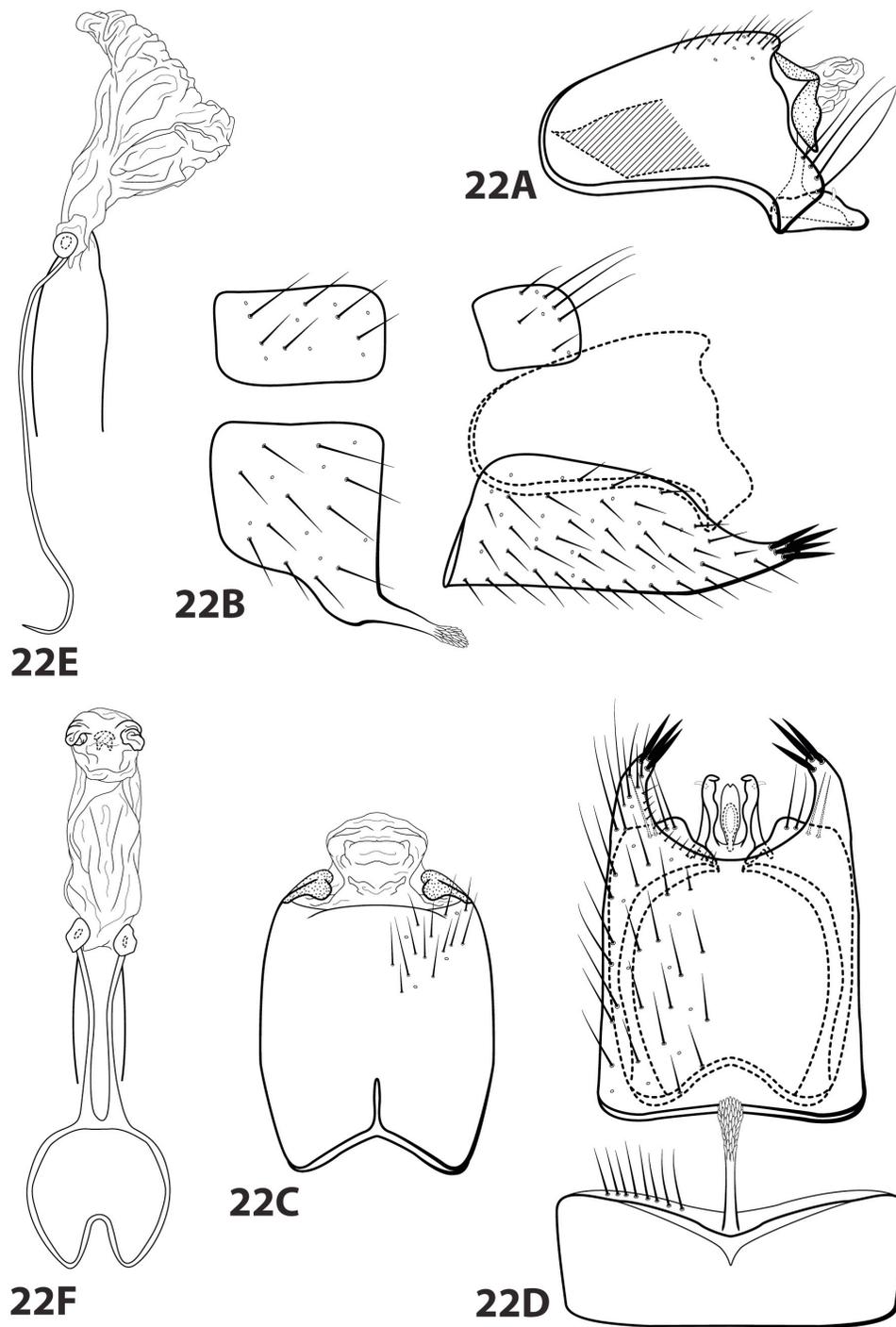


FIGURE 22. *Leucotrichia hispida*, new species (UMSP000140610). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

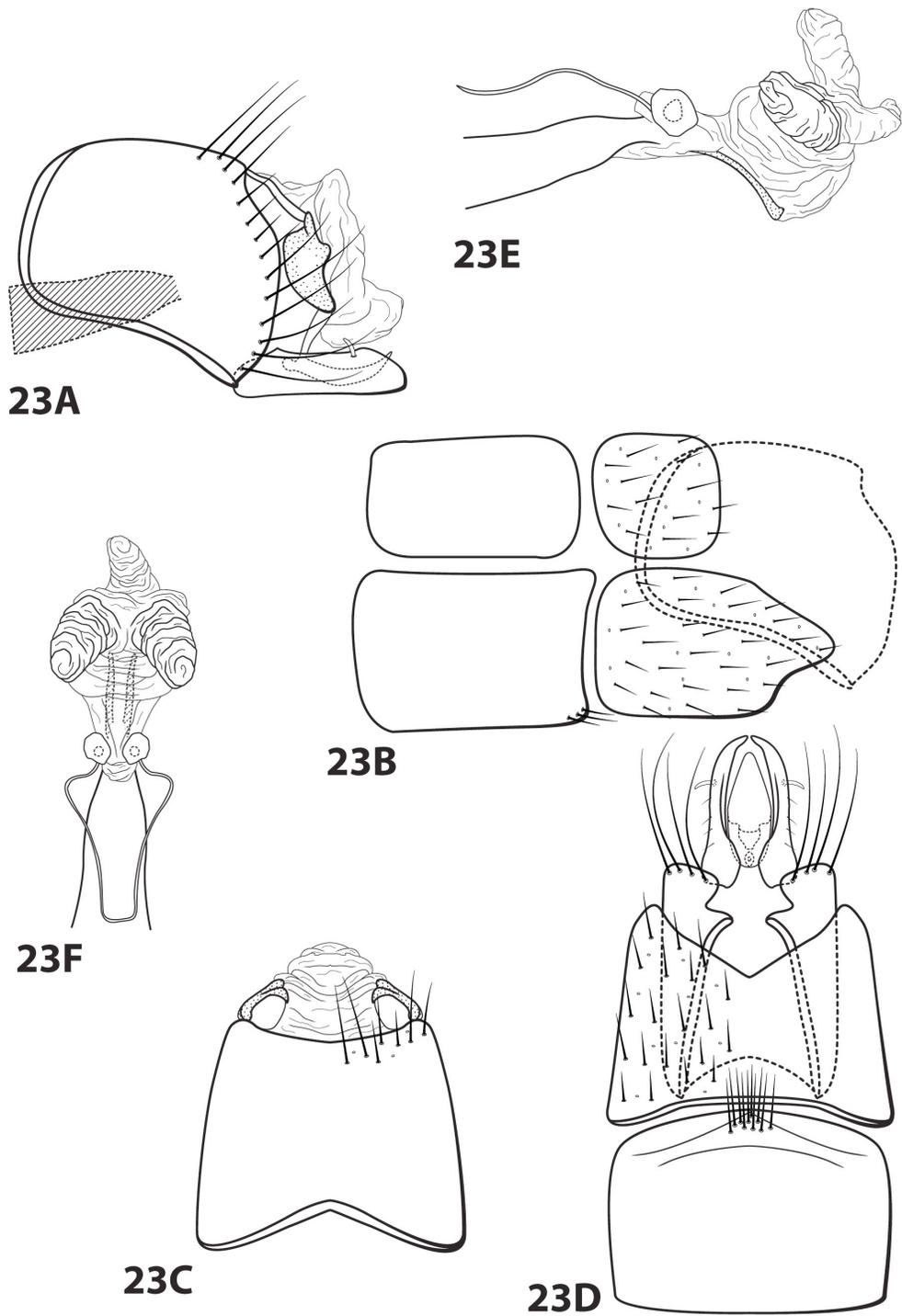


FIGURE 23. *Leucotrichia imitator* Flint, 1970 (USNM70898). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

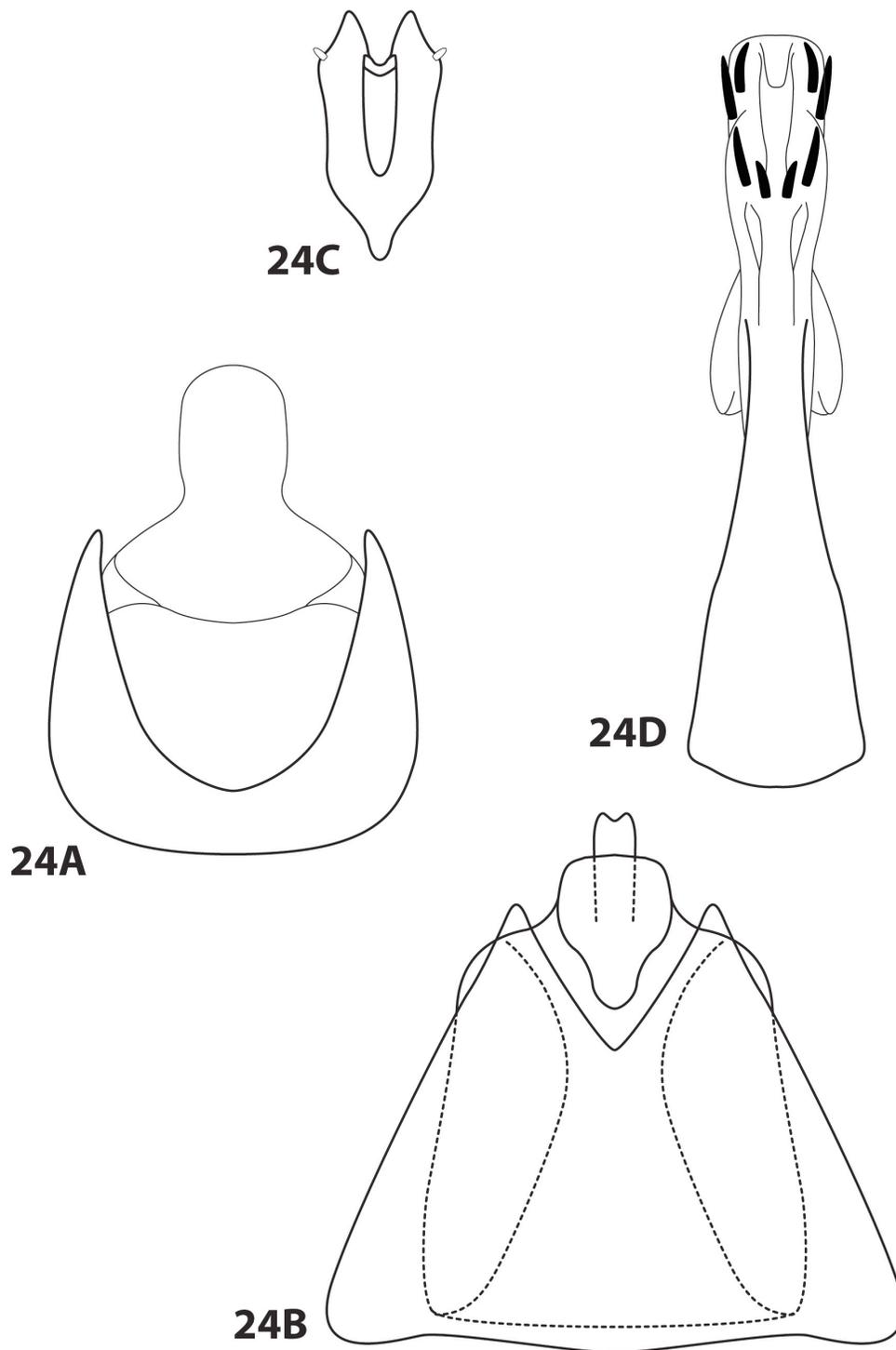


FIGURE 24. *Leucotrichia inflaticornis* Botosaneanu, 1993 (redrawn from Botosaneanu and Alkins-Koo 1993). Male genitalia: **A** segment IX, dorsal **B** segments VIII-IX, ventral **C** subgenital plate, not to scale, view not given **D** phallus, ventral.

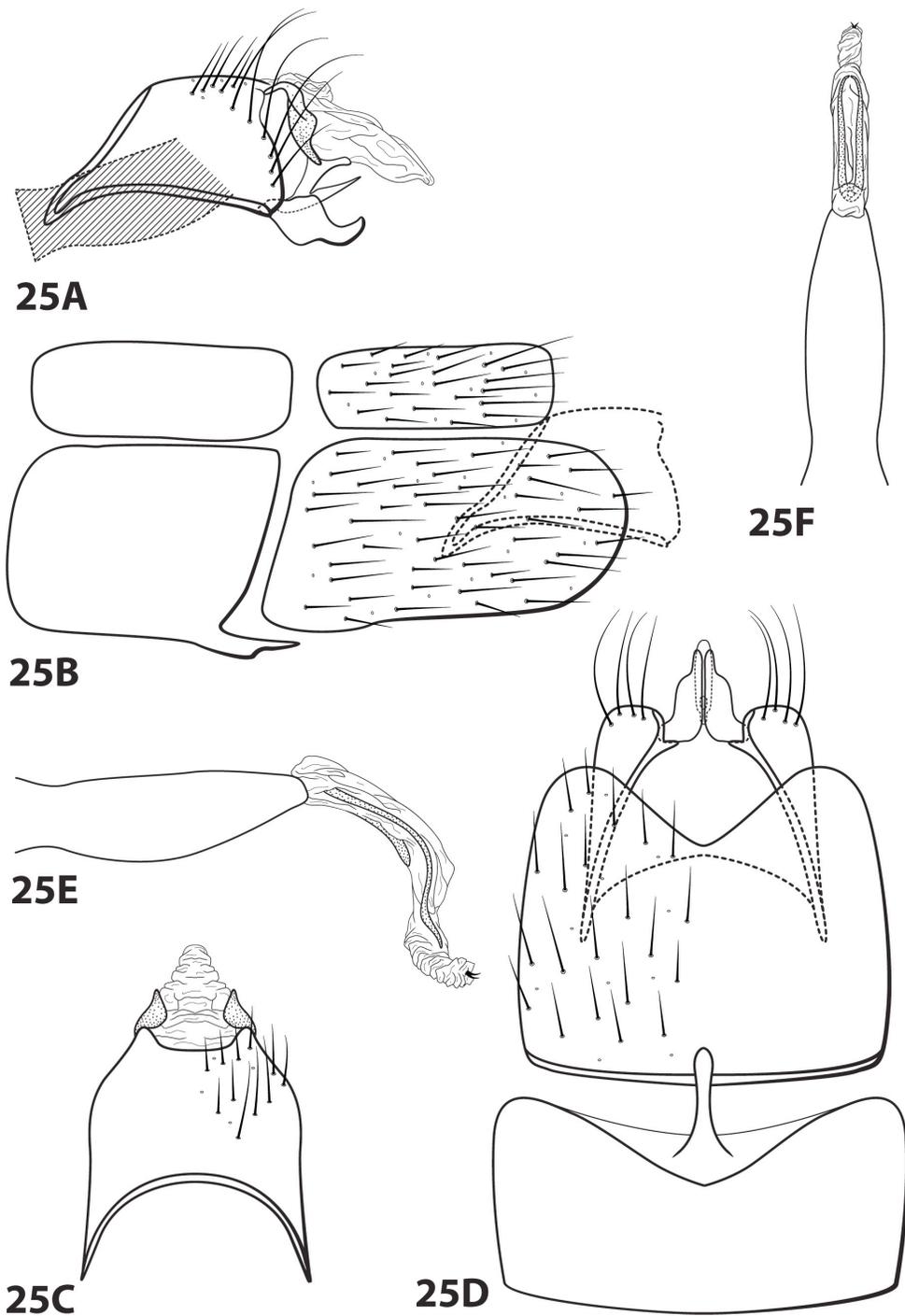


FIGURE 25. *Leucotrichia inops* Flint, 1991 (USNM104530). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

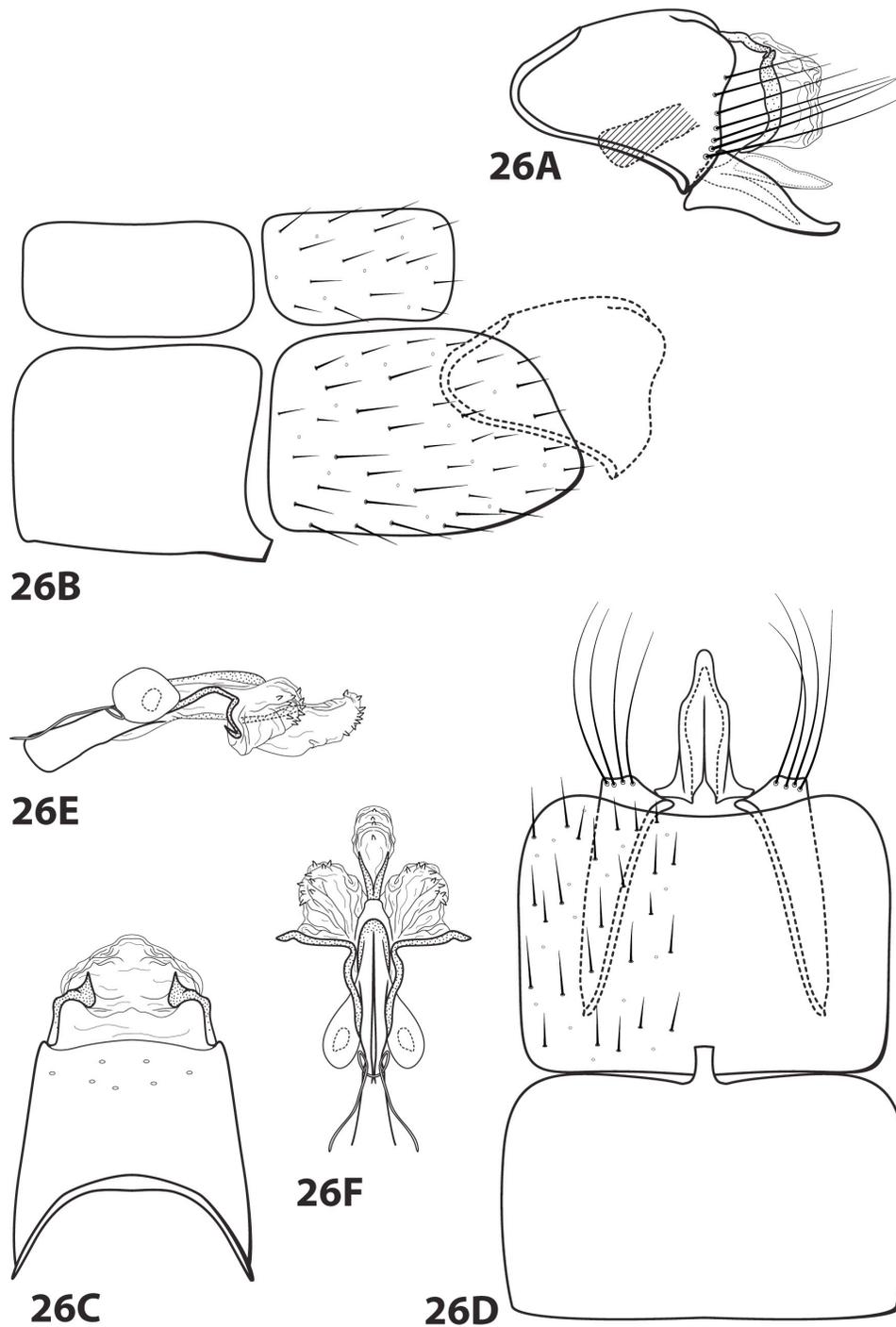


FIGURE 26. *Leucotrichia interrupta* Flint, 1991 (USNM104528). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

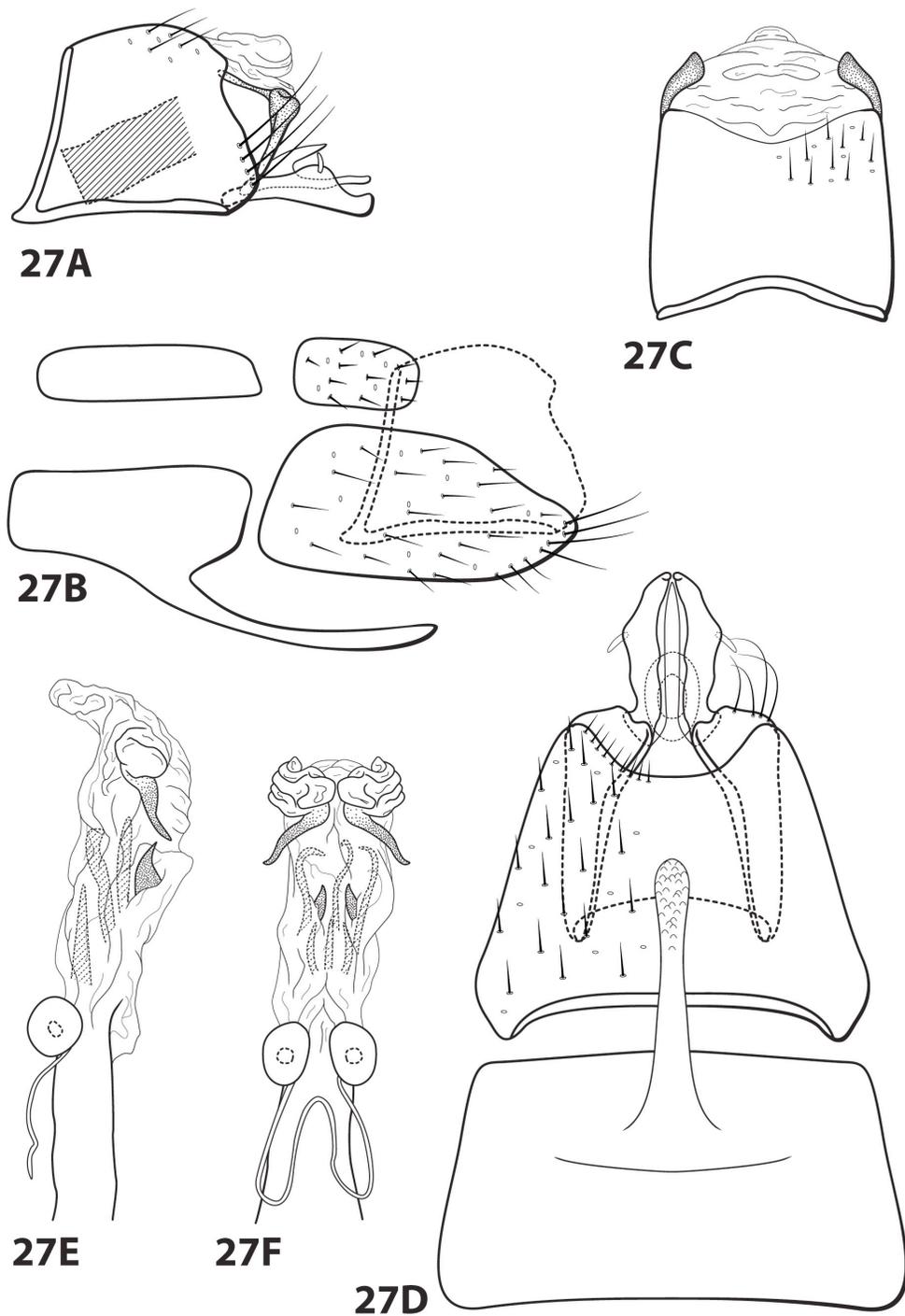


FIGURE 27. *Leucotrichia kateae*, new species (UMSP000201690). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

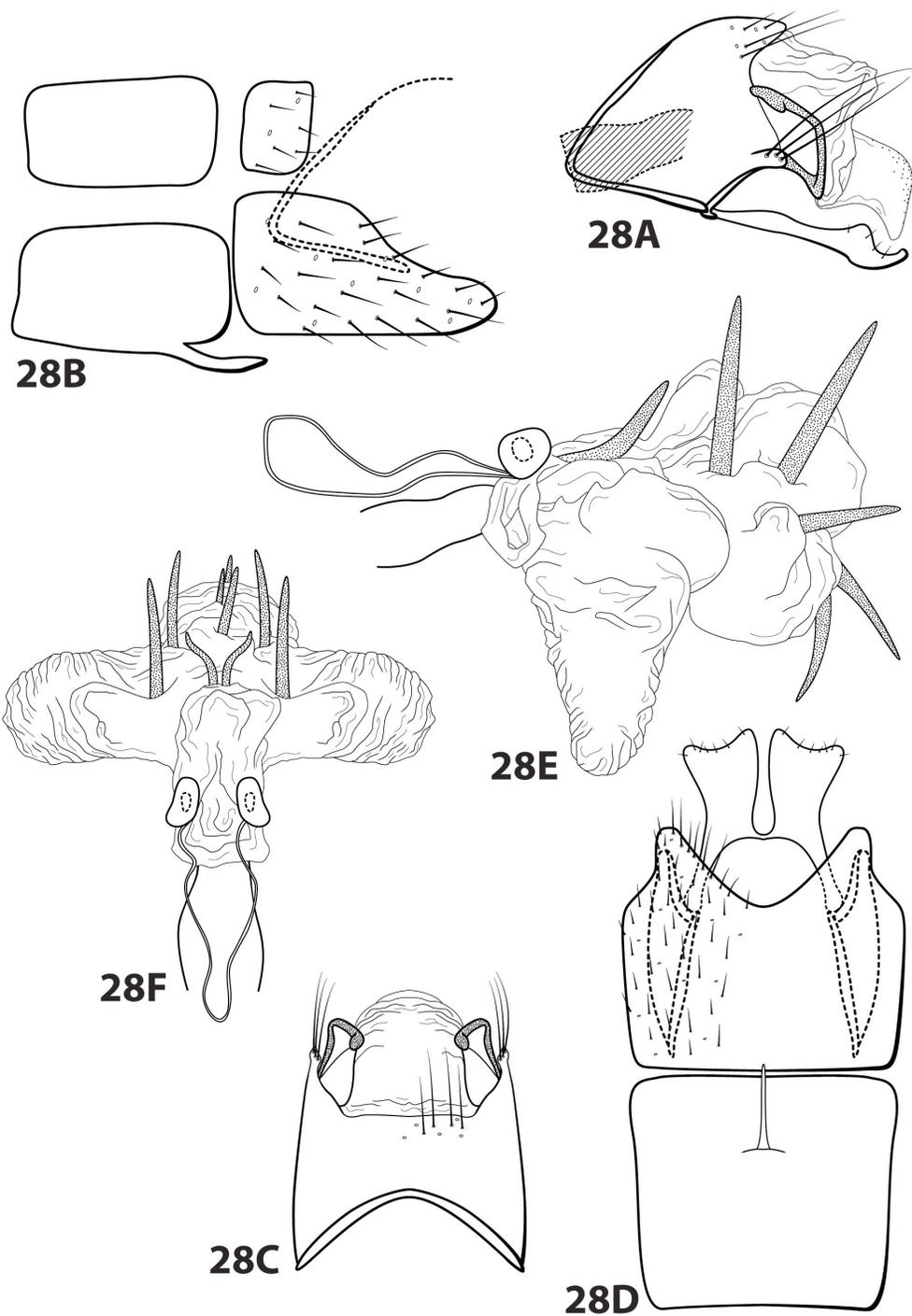


FIGURE 28. *Leucotrichia laposka* Oláh and Johanson, 2011 (NHRSKAJ0000000328). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

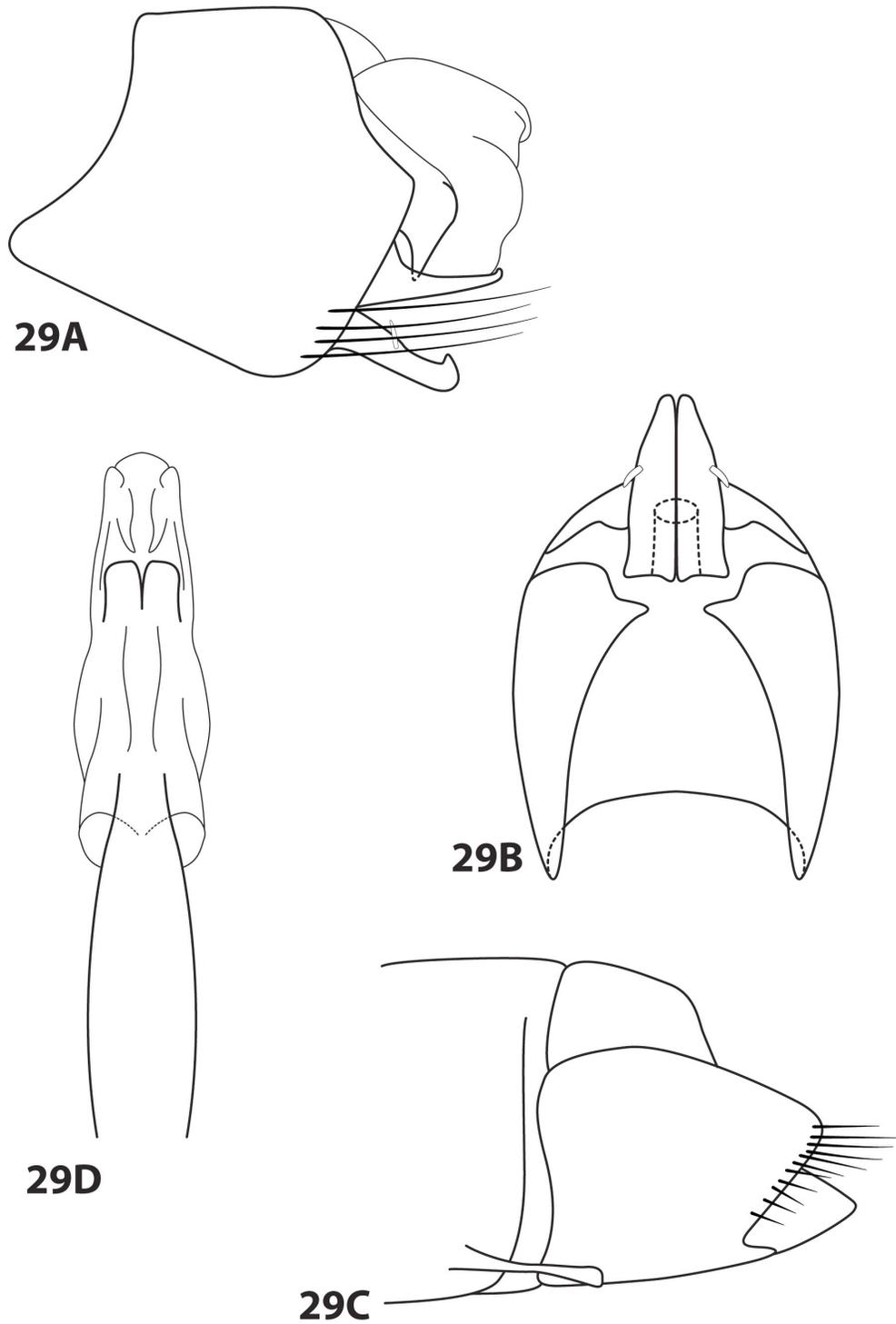


FIGURE 29. *Leucotrichia lerma* Angrisano and Burgos, 2002 (redrawn from Angrisano & Burgos 2002). Male genitalia: **A** segments IX-X, lateral **B** segment IX, ventral **C** segment VII-VIII, oblique **D** phallus, view not given.

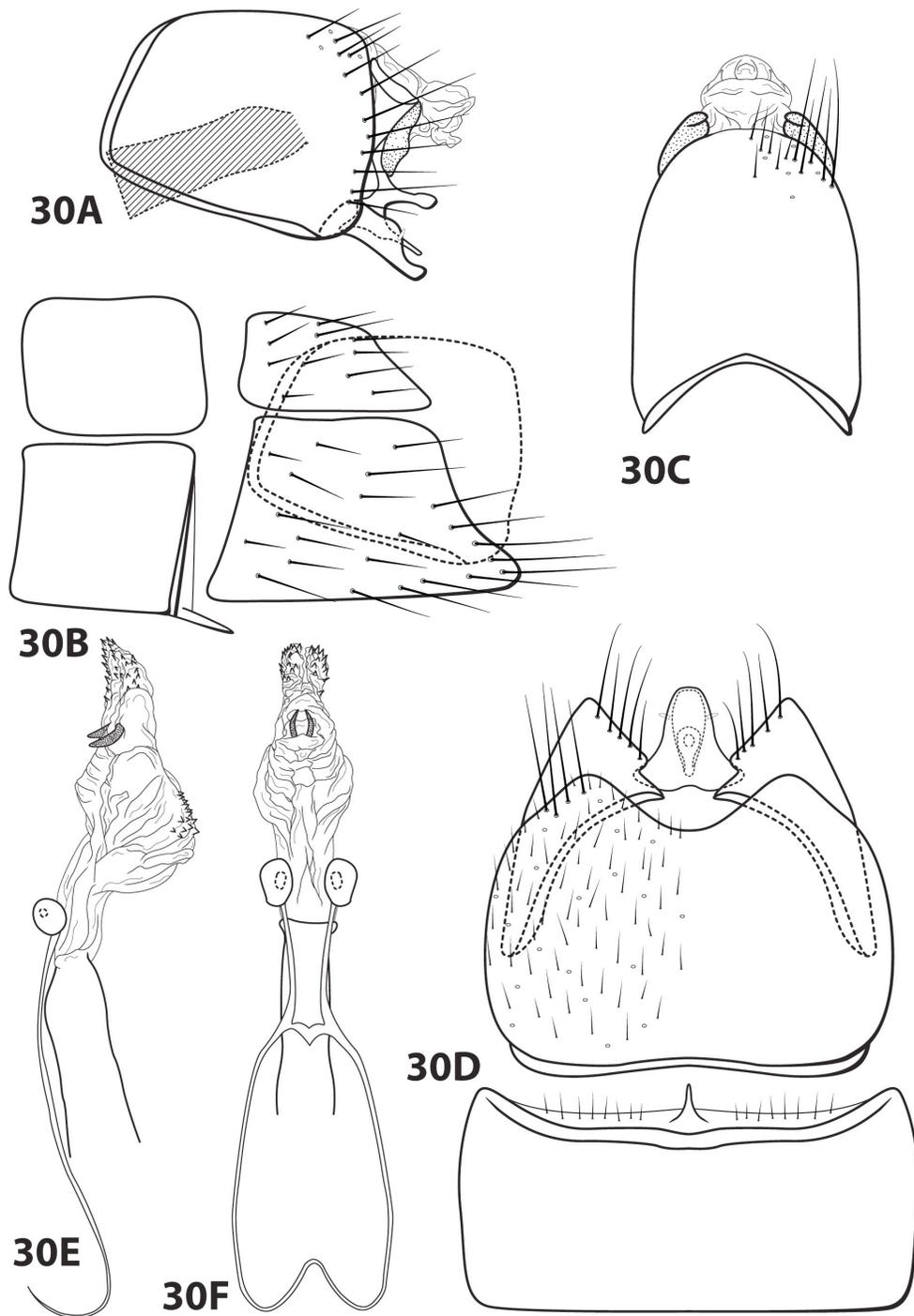


FIGURE 30. *Leucotrichia limpia* Ross, 1944 (INHS22335). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

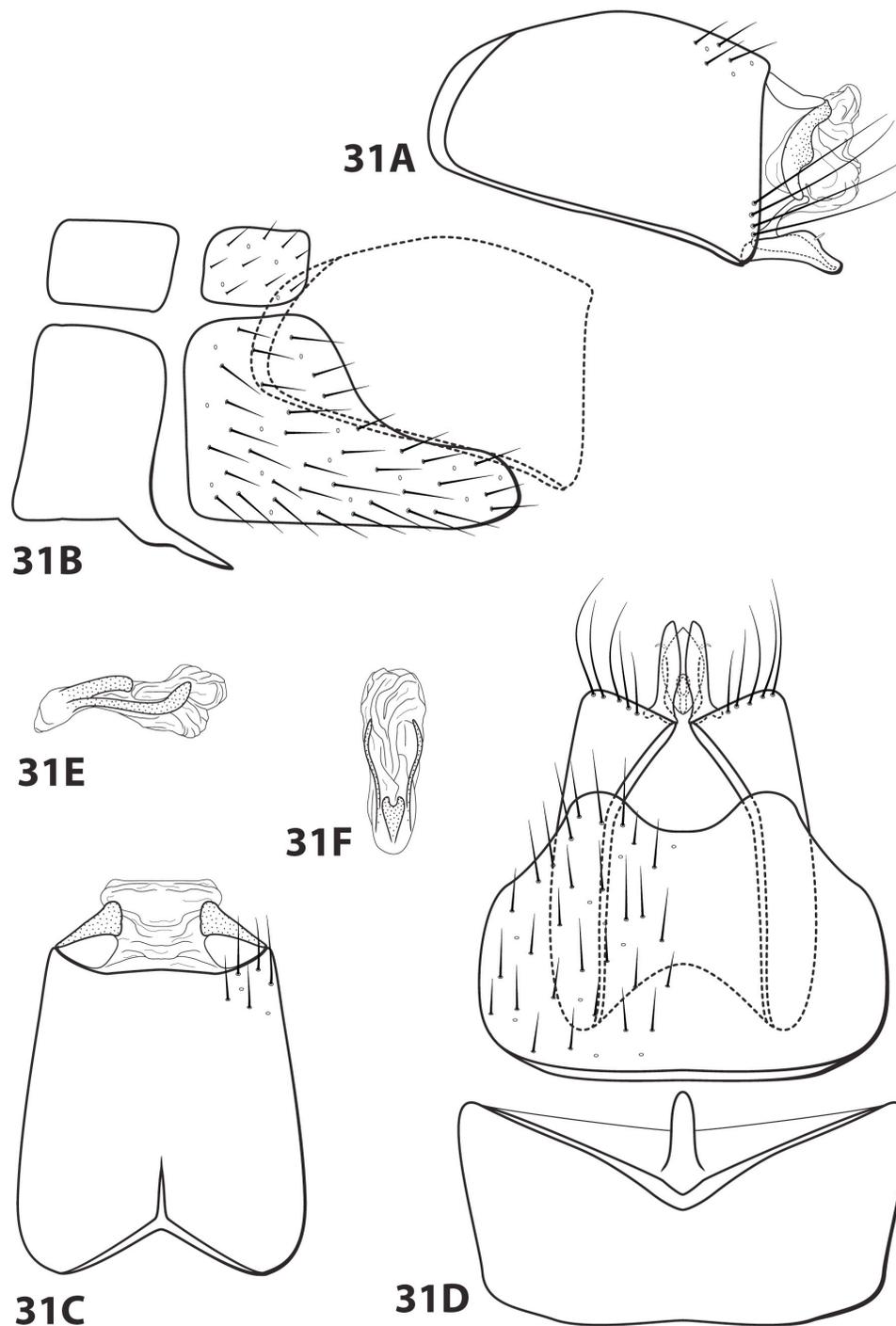


FIGURE 31. *Leucotrichia mutica* Flint, 1991 (USNM04525). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

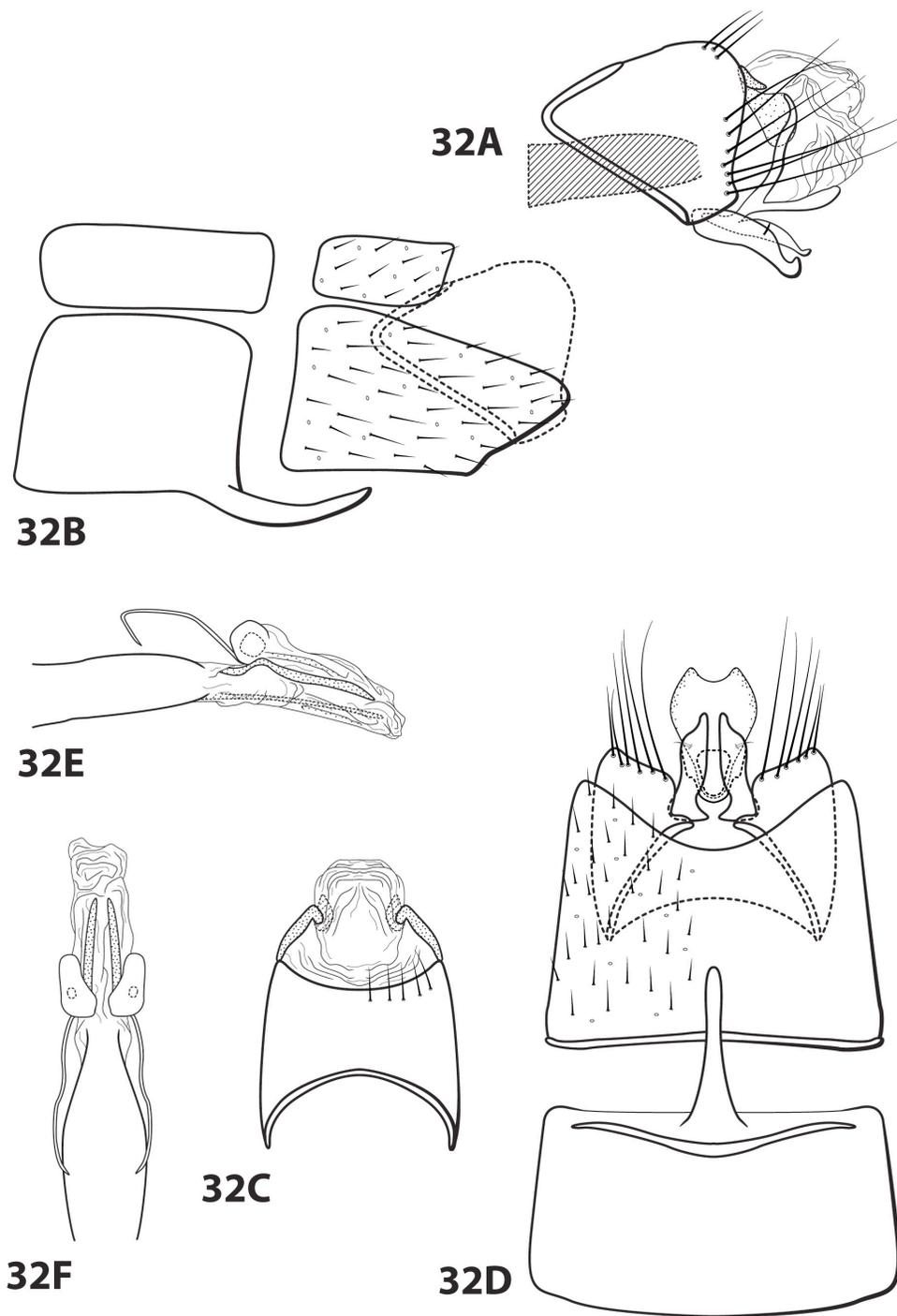


FIGURE 32. *Leucotrichia padera* Flint, 1991 (USNM104526). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

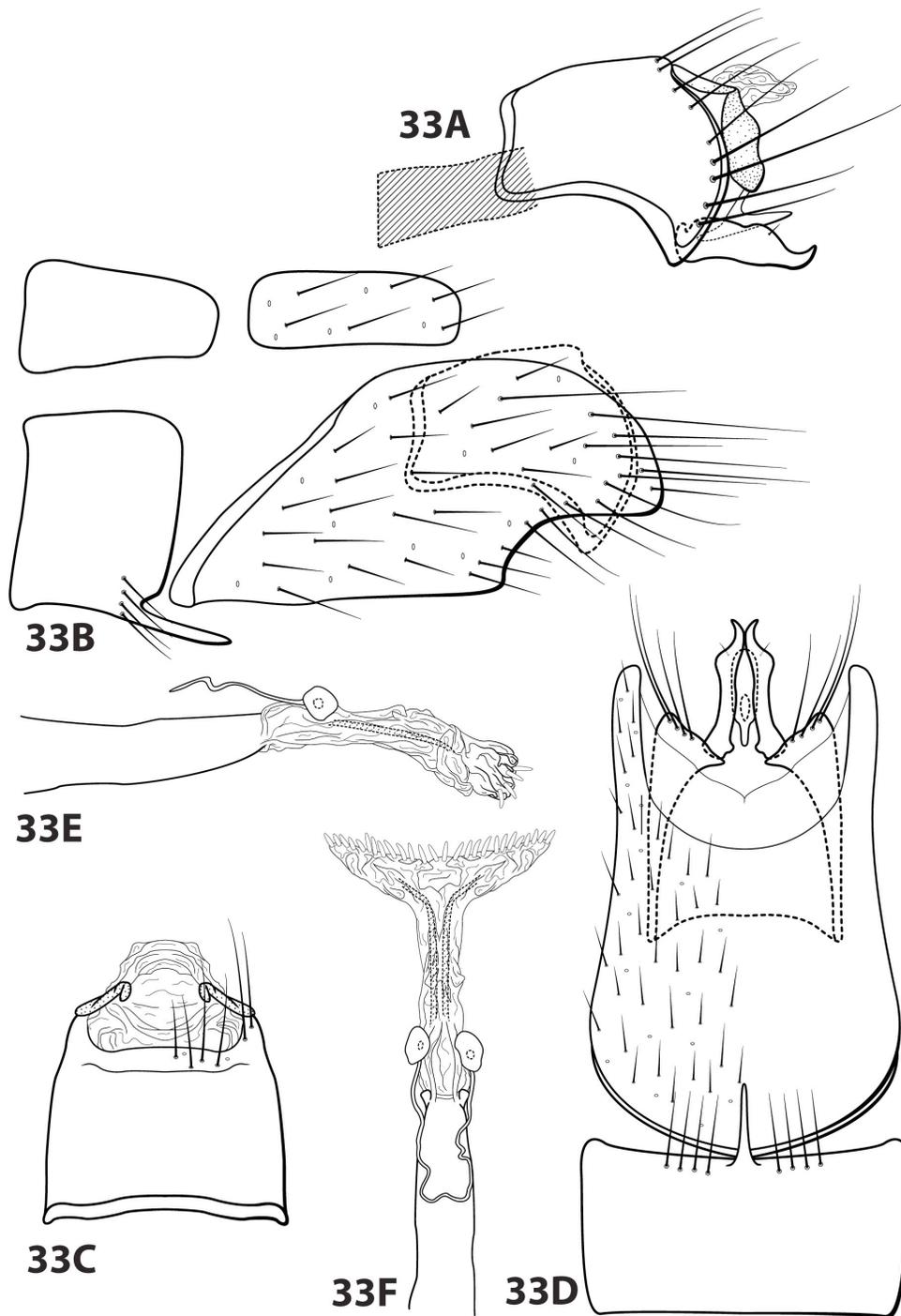


FIGURE 33. *Leucotrichia pectinata*, new species (UMSP000140619). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

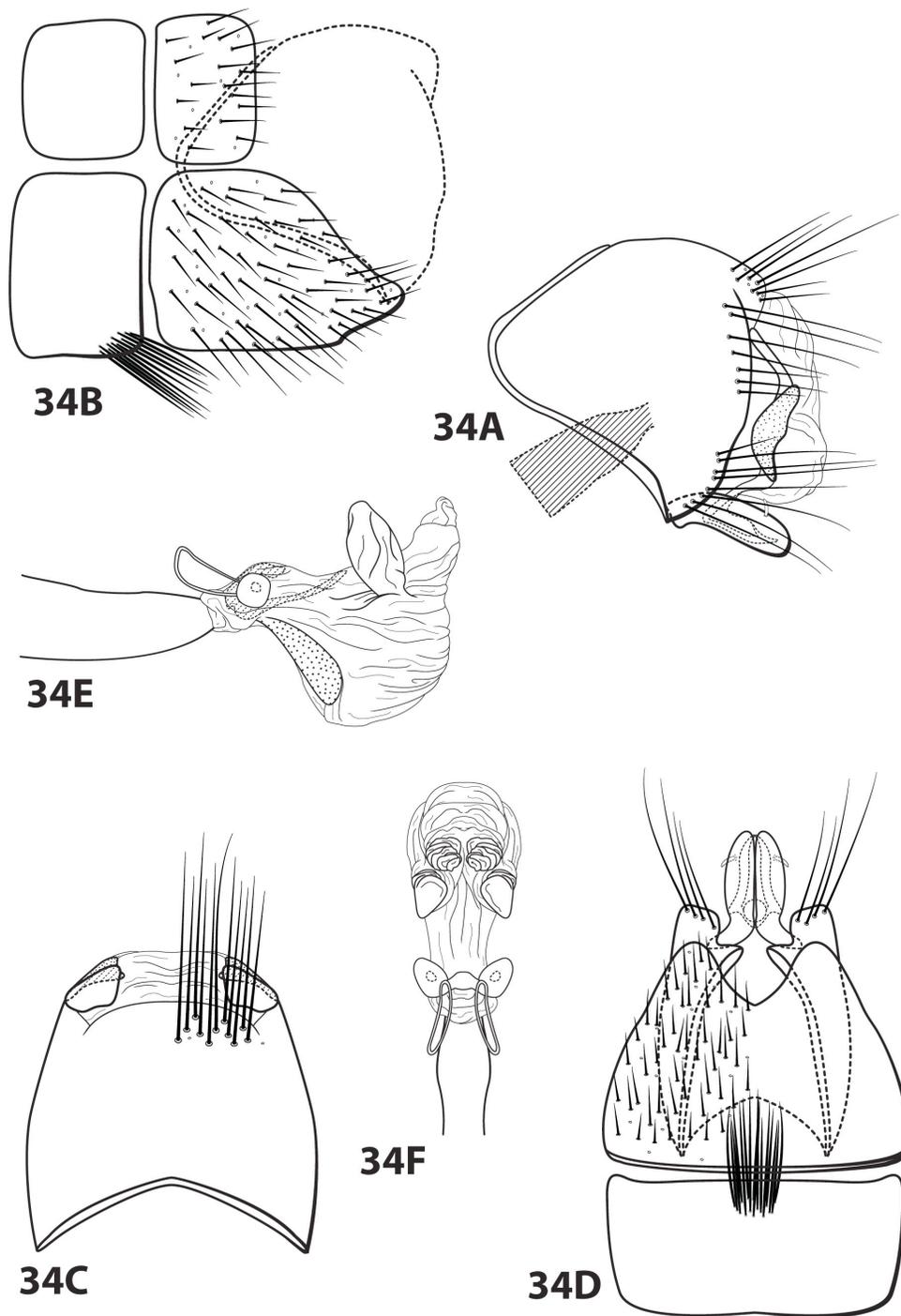


FIGURE 34. *Leucotrichia pictipes* (Banks, 1911) (MCZ11597). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

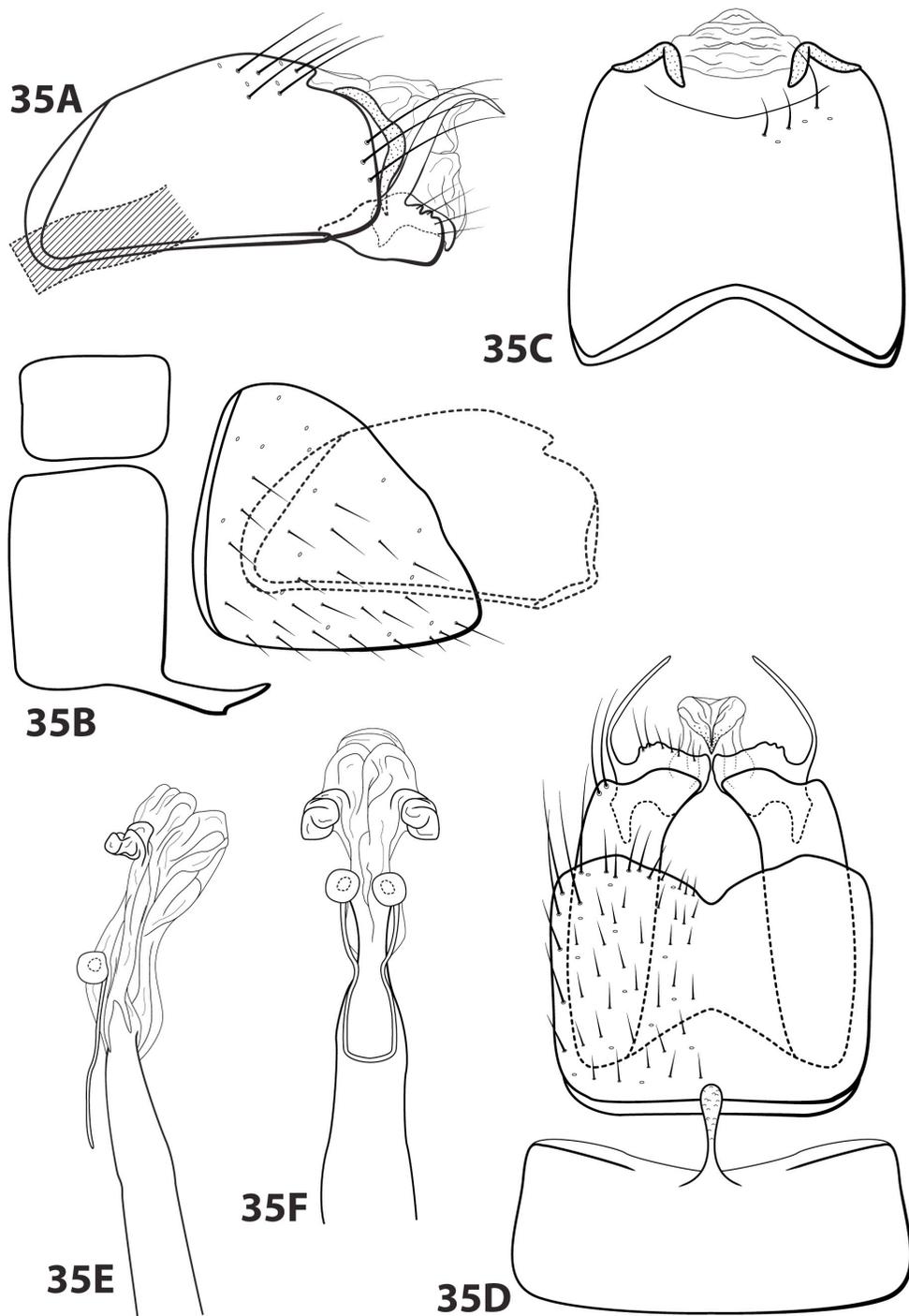


FIGURE 35. *Leucotrichia procera*, new species (UMSP000047406). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

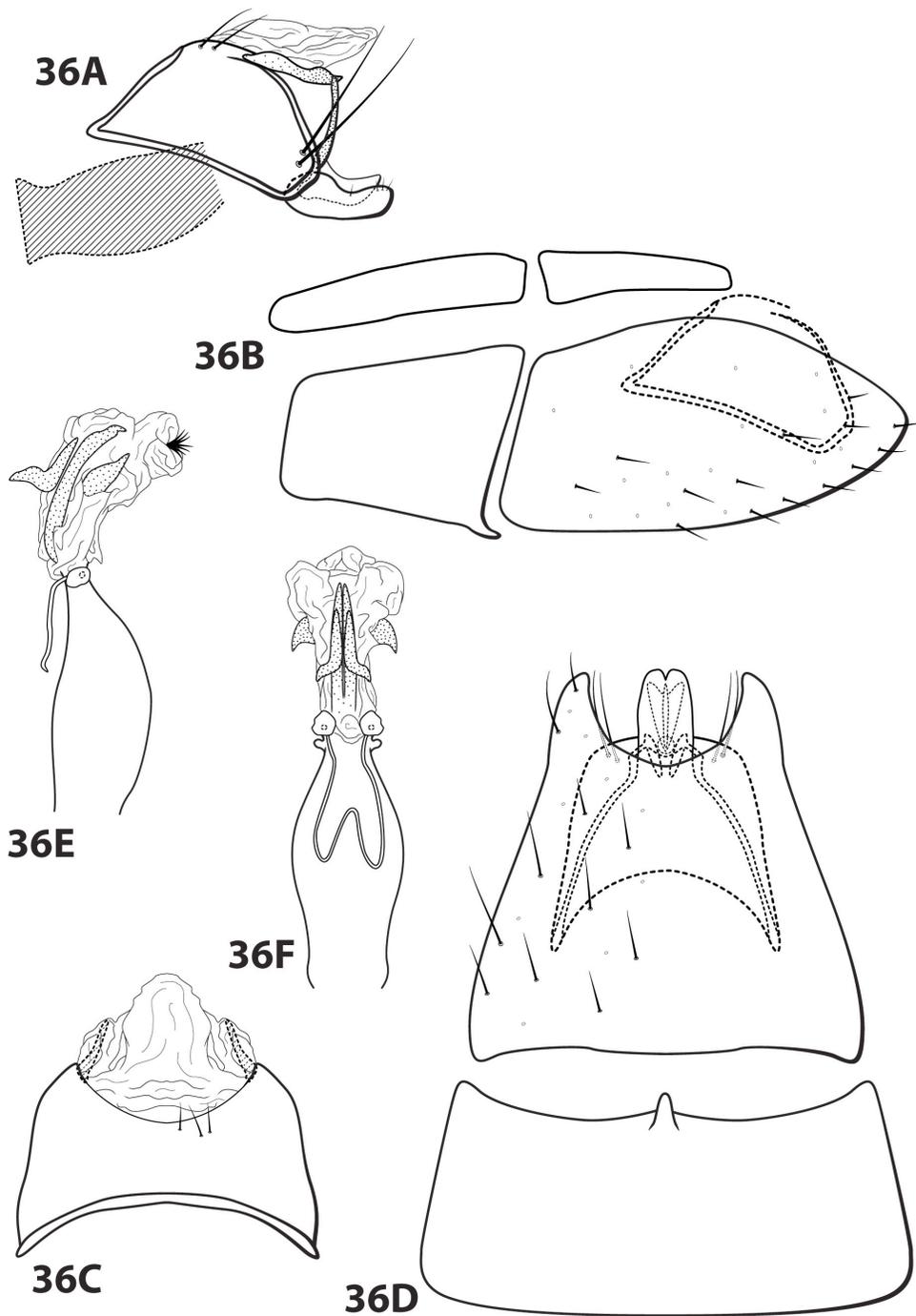


FIGURE 36. *Leucotrichia repanda*, new species (UMSP000201685). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

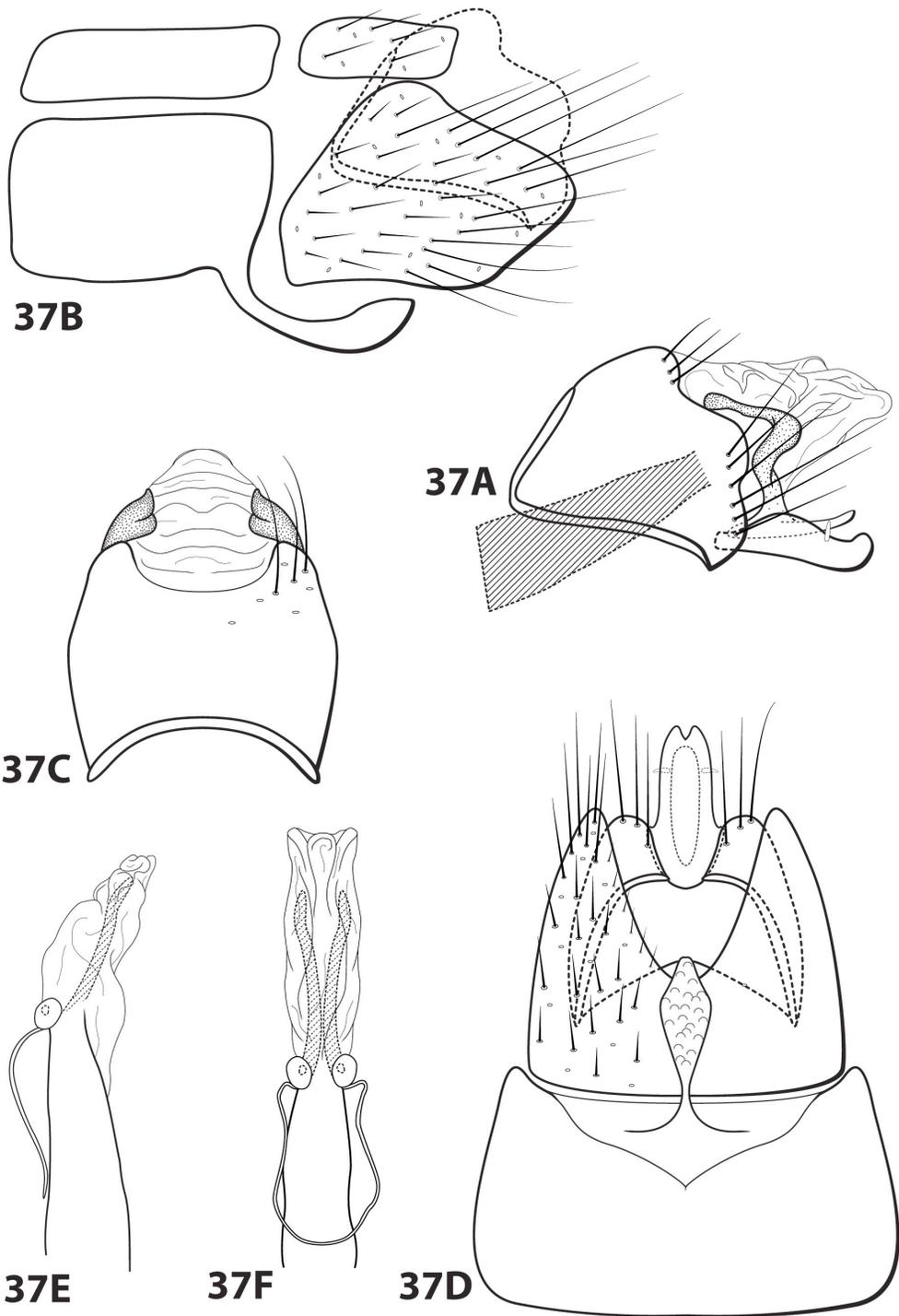


FIGURE 37. *Leucotrichia rhomba*, new species (UMSP000201350). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

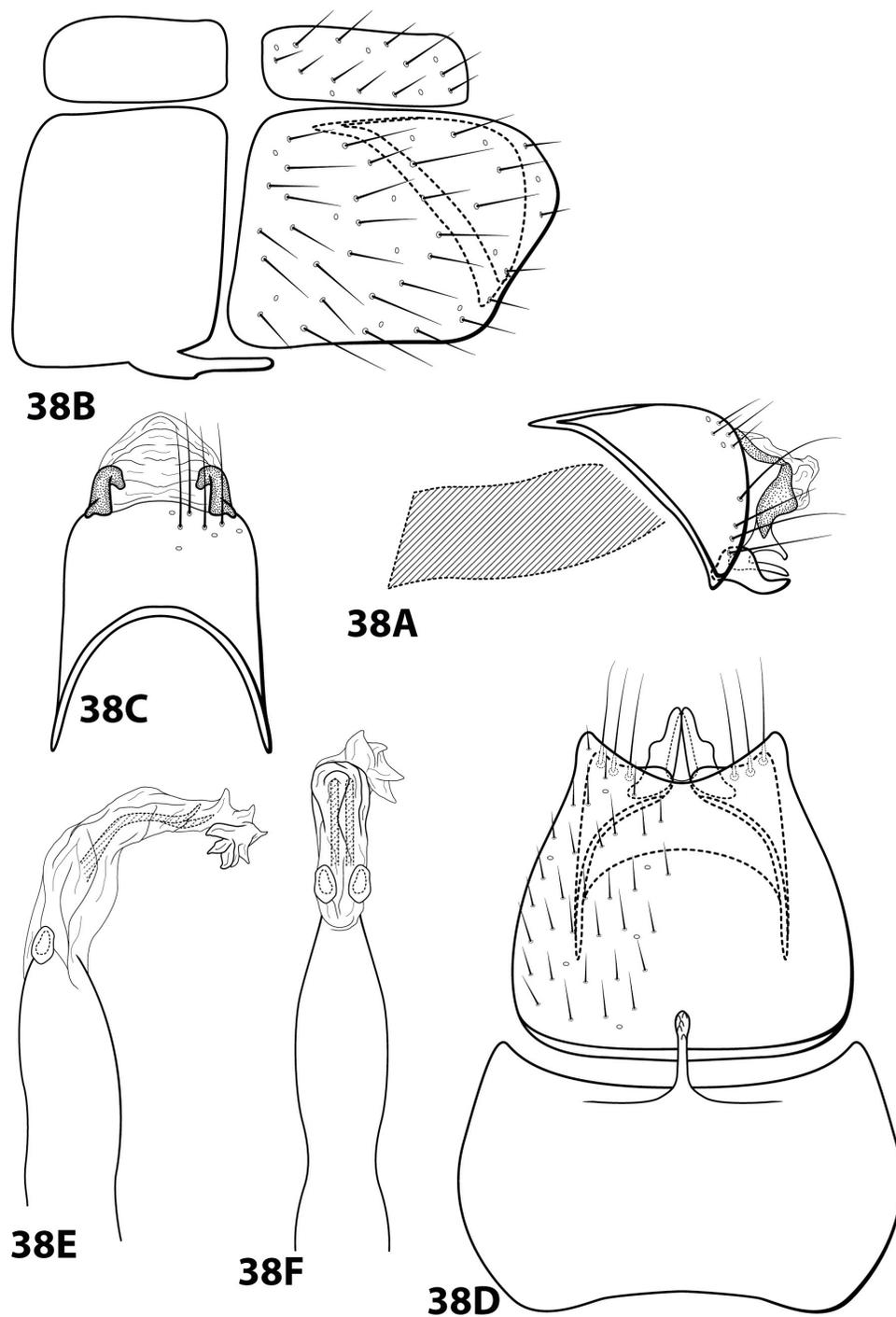


FIGURE 38. *Leucotrichia riostoumae*, new species (UMSP000140832). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

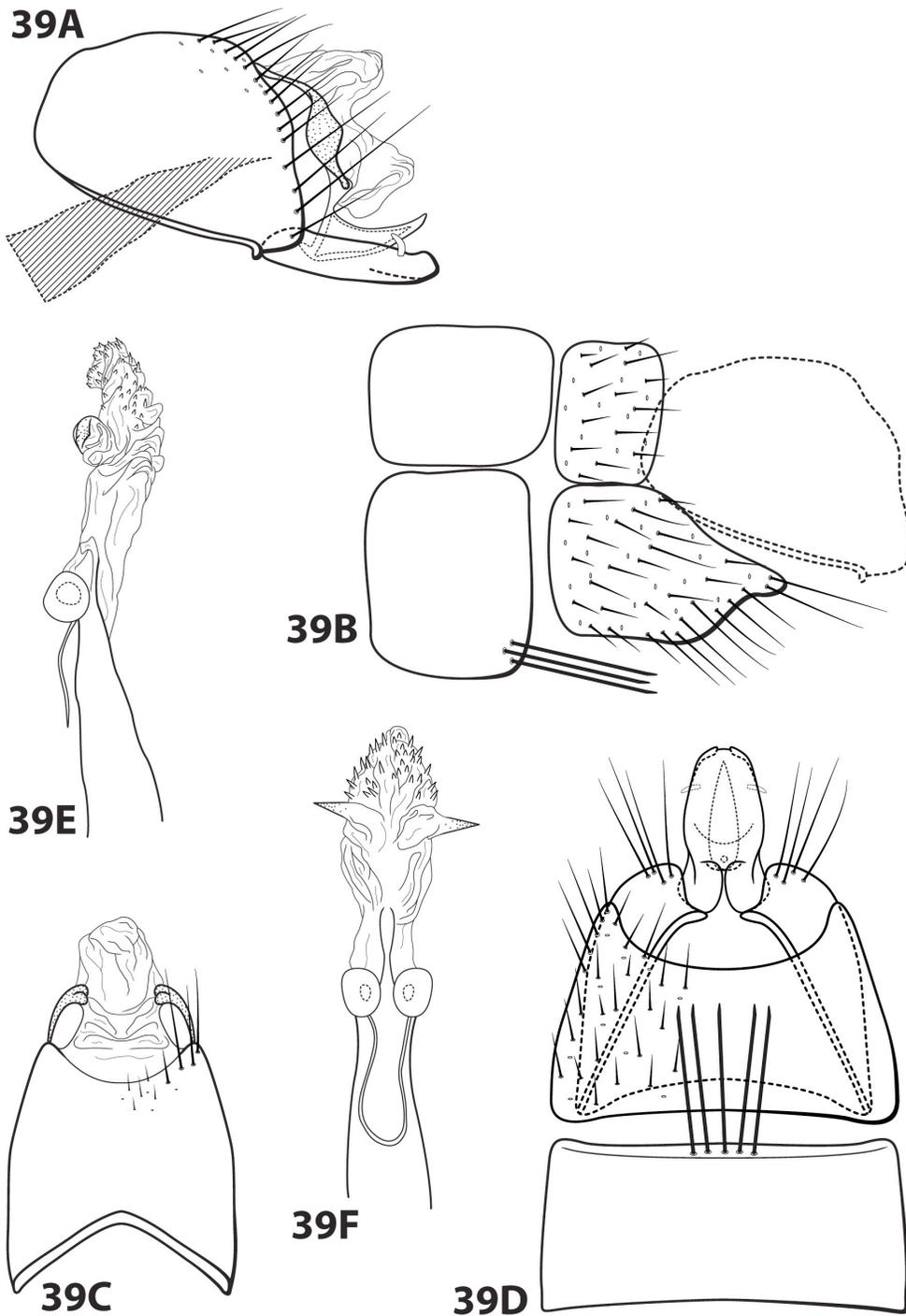


FIGURE 39. *Leucotrichia sarita* Ross, 1944 (INHS22339). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

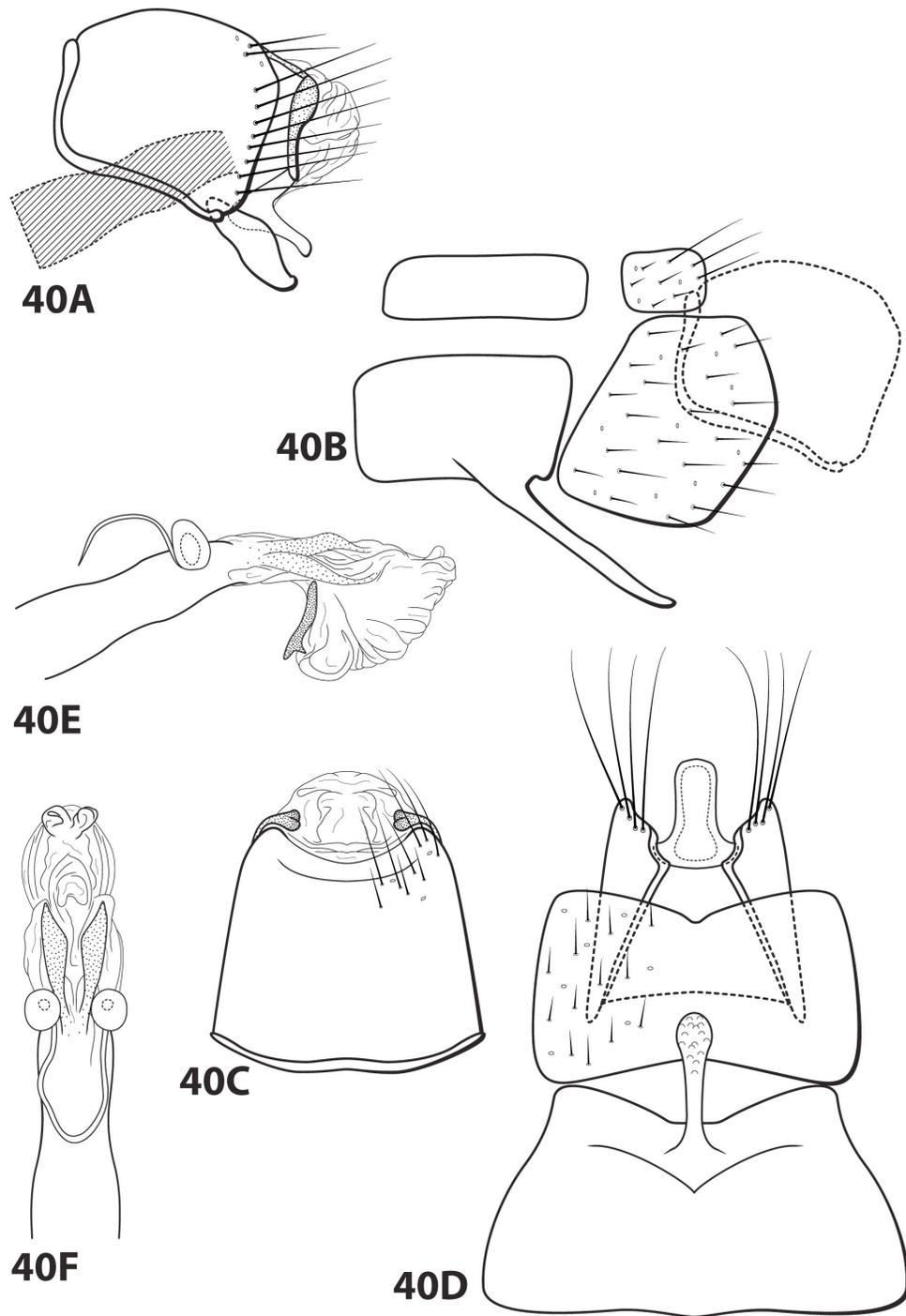


FIGURE 40. *Leucotrichia sidneyi*, new species (UMSP000140465). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

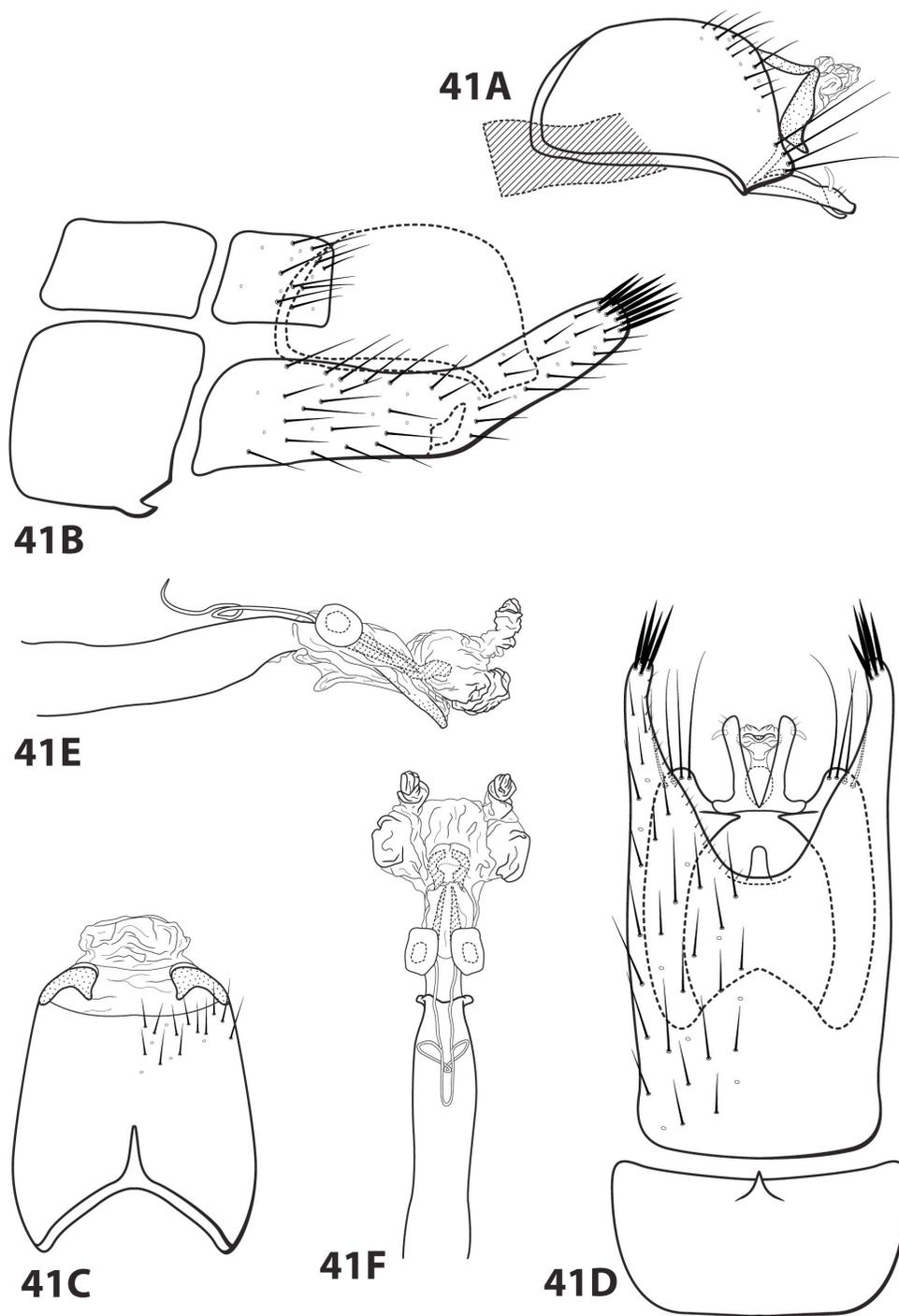


FIGURE 41. *Leucotrichia tapantia*, new species (UMSP000201359). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

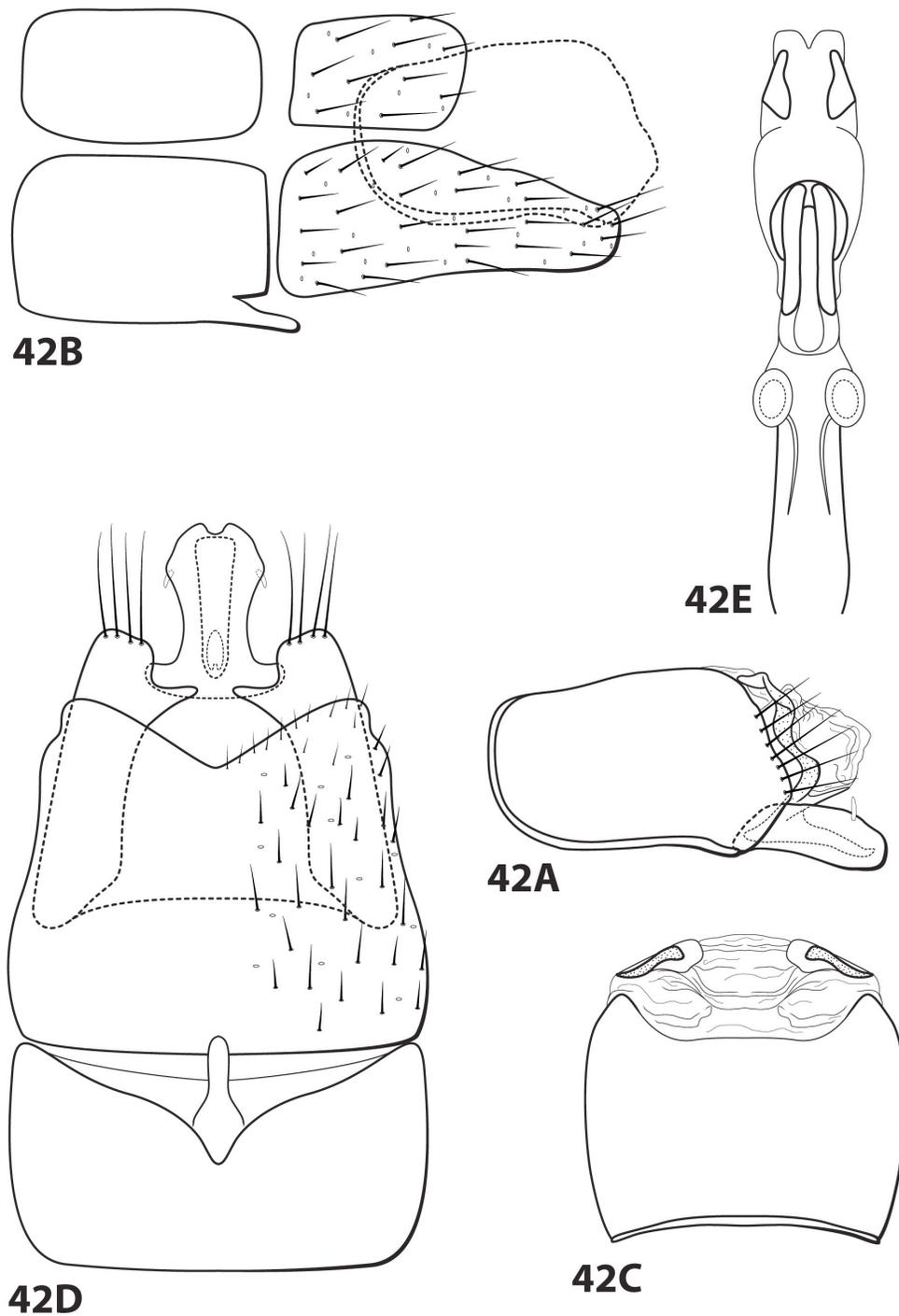


FIGURE 42. *Leucotrichia termitiformis* Botosaneanu, 1993 (UMSP000140326). Male genitalia: **A** segments IX-X, lateral **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, dorsal, redrawn from original illustration.

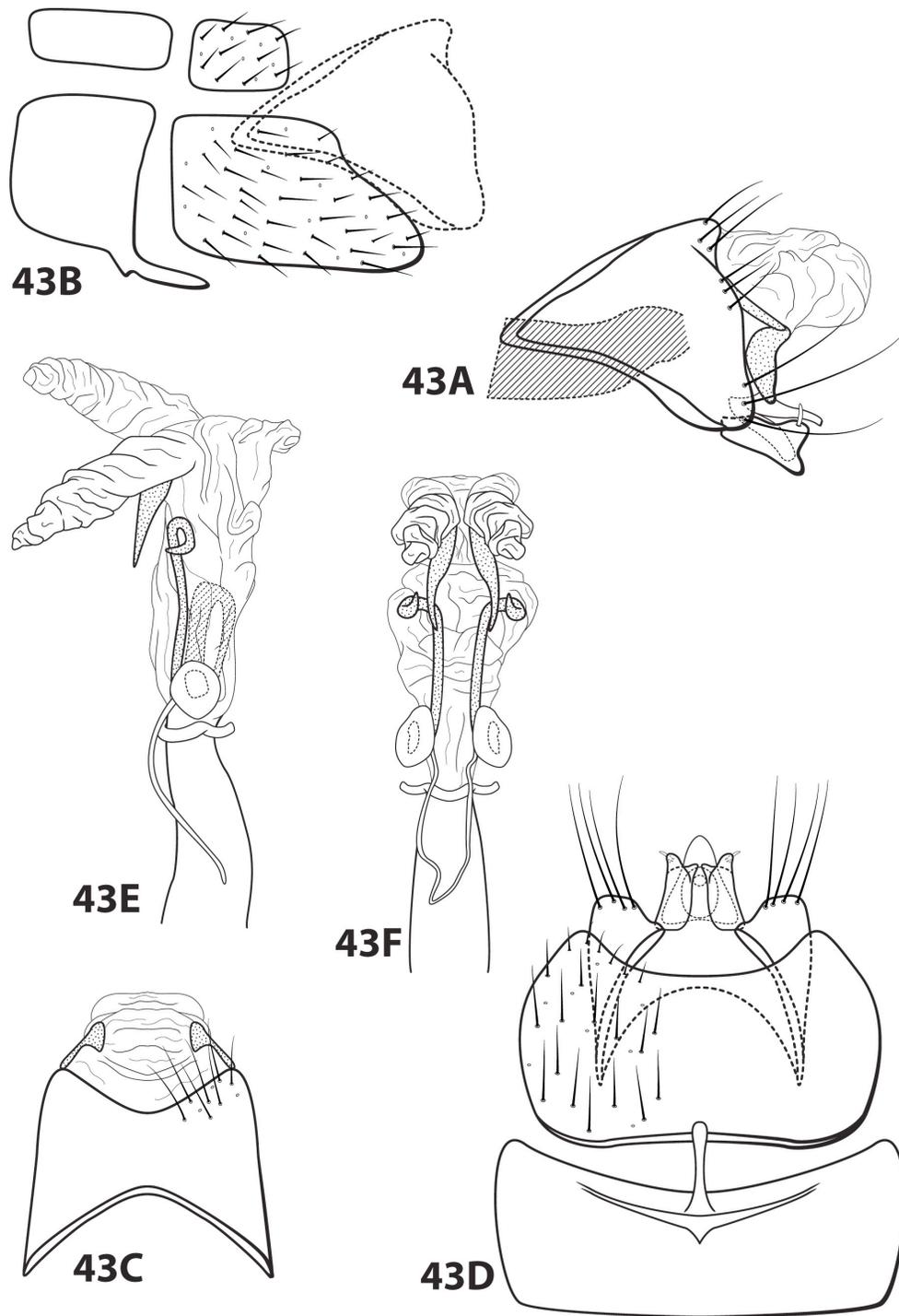


FIGURE 43. *Leucotrichia tritoven* Flint, 1996 (USNM105437). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

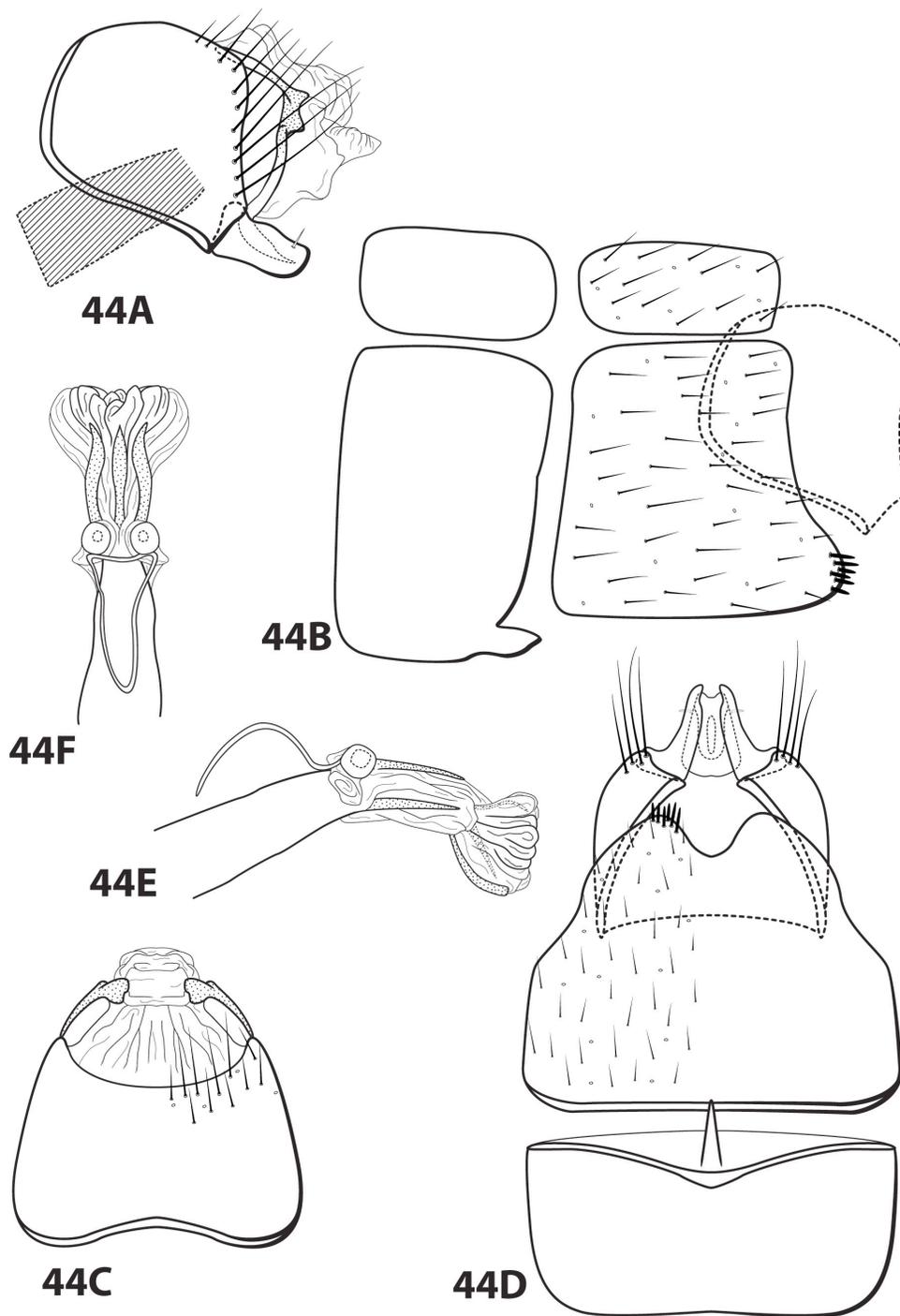


FIGURE 44. *Leucotrichia tubifex* Flint, 1964 (USNM66885). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

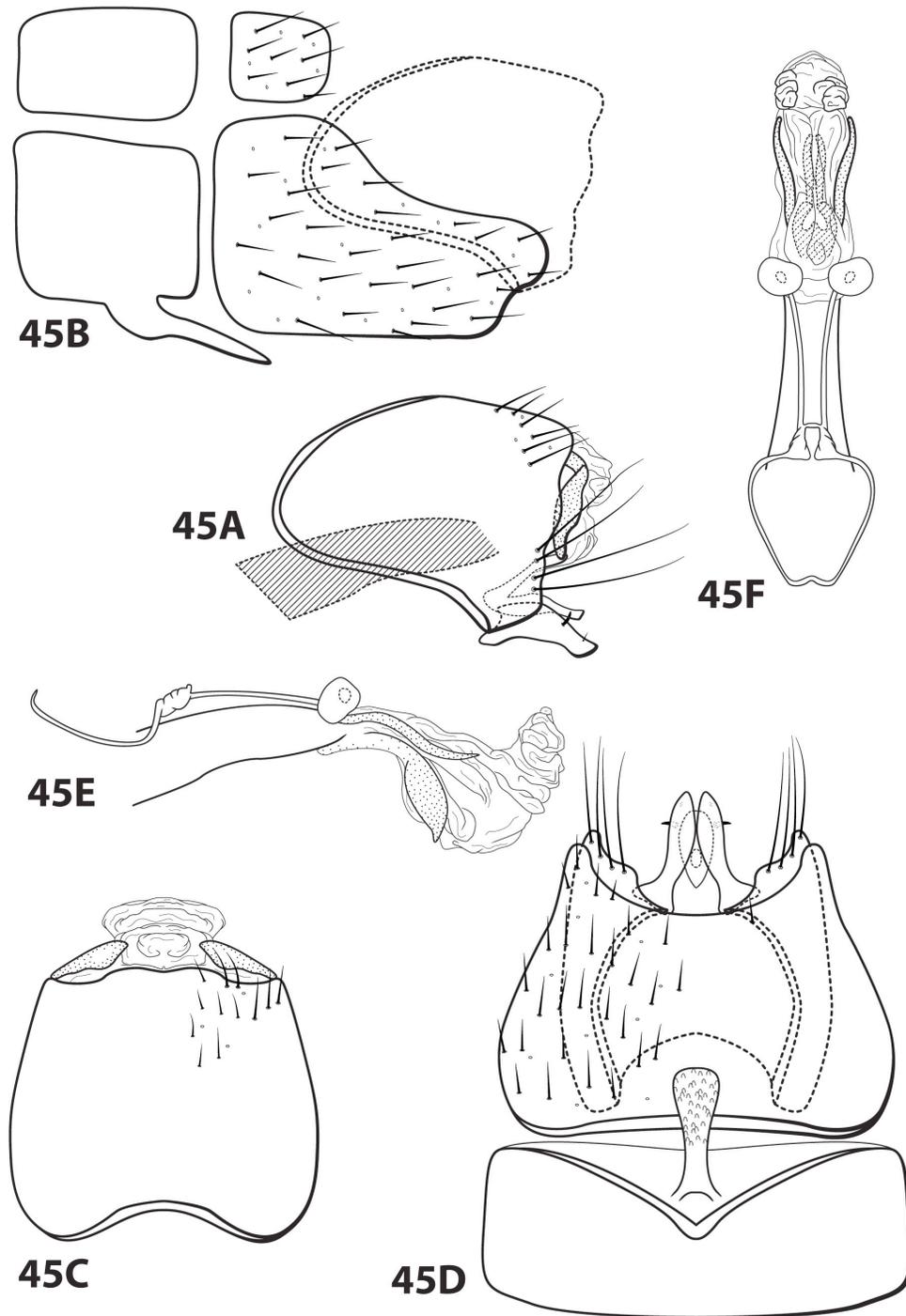


FIGURE 45. *Leucotrichia viridis* Flint, 1967 (USNM69586). Male genitalia: **A** segments IX-X, lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX margin, lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

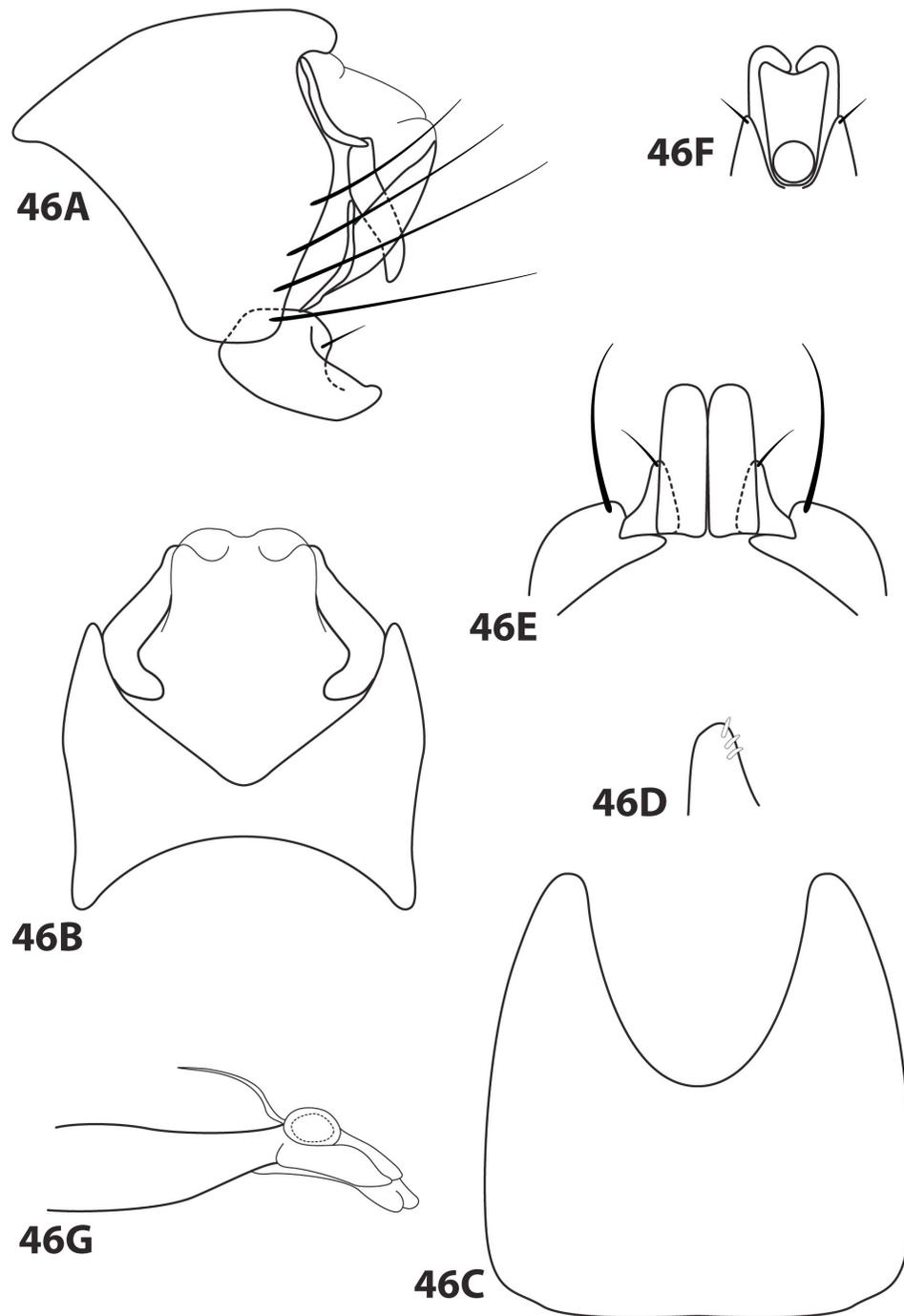


FIGURE 46. *Leucotrichia yungarum* Angrisano and Burgos, 2002 (redrawn from Angrisano and Burgos, 2002). Male genitalia: **A** segments IX-X, lateral **B** segment IX, dorsal **C** segment VIII, ventral **D** apex of segment VIII, dorsal **E** apex of segment IX and inferior appendage, ventral **F** inferior appendage and subgenital plate, dorsal **G** phallus, lateral.

Chapter III. New species and records of Hydroptilidae (Trichoptera) from Venezuela

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SUMMARY

Eight new species of Hydroptilidae (Trichoptera) from Venezuela are described: *Acostatrichia digitata* **sp. n.**, *Hydroptila cressae* **sp. n.**, *Metrichia botrychion* **sp. n.**, *Ochrotrichia spira* **sp. n.**, *Oxyethira bettyae* **sp. n.**, *Oxyethira quiramae* **sp. n.**, *Oxyethira redunca* **sp. n.**, and *Rhyacopsyche shorti* **sp. n.** New country records for Venezuela of 2 additional species, *Neotrichia feolai* Santos and Nessimian, 2009 and *Oxyethira picita* Harris and Davenport, 1999, are also provided. Illustrations of male genitalia are provided with each description.

INTRODUCTION

Caddisflies, or Trichoptera, are a diverse order of insects with ~15,000 described species and 100s of new species awaiting description (Holzenthal *et al.*, 2011). Trichoptera faunal diversity is particularly impressive in the Neotropical biogeographical region, where recent inventories have revealed up to 75% of collected species to be undescribed (Holzenthal *et al.*, 2007). Hydroptilidae is the largest family in the order,

including 75 genera, ~2,000 described species found all over the world, and a high number of undescribed species. As their common name, microcaddisflies, suggests, hydroptilids are minute with few larger than 5 mm. The aquatic larvae construct portable or fixed silken purse-like cases in the final instar (Wiggins, 2004). The larvae of many species feed on algae, while some feed on moss microphylls (Wiggins, 2004; Carins and Wells, 2008). Some have been known to be predatory, while others are parasitoids (Wells, 1985, 2005). In this paper, we describe 8 new hydroptilid species in 6 genera from Venezuela. We also provide new country records for Venezuela for 2 species, *Neotrichia feolai* Santos and Nessimian, 2009 and *Oxyethira picita* Harris and Davenport, 1999. The material was collected as part of a project under the direction of Dr. Andrew Short, University of Kansas, USA, to inventory the aquatic Coleoptera and other aquatic insect orders of Venezuela. In June, 2010, a team of 4 American and 4 Venezuelan entomologists collected aquatic insects in the southern half of Venezuela, including the *llanos* of Guarico state, the southern tributaries of the upper to middle Orinoco River basin, and the *Gran Sabana* of Bolivar state, and, in northern Venezuela, the Turimiquire Mountains of Monagas state. About 90 species of Trichoptera were collected, including about 25 new species of which the new Hydroptilidae are described here.

MATERIALS AND METHODS

Morphological terminology used for male genitalia of specimens in the genus

Oxyethira follows that of Kelley (1984), for the genus *Metrichia* that of Flint (1972), and for the genus *Rhyacopsyche* that of Wasmund and Holzenthal (2007). All others follow the terminology of Marshall (1979). For simplicity, paired structures are discussed in the singular. Procedures for specimen preparation followed those explained in detail by Blahnik *et al.* (2007). For specimen examination and illustration, cleared genitalia were placed in a watch glass with glycerin and small glass beads. The glass beads held the genitalia in place and allowed structures to be viewed in precise lateral, dorsal, and ventral positions. Genitalia were examined with an Olympus BX41 compound microscope at 250–500 x magnification. Structures were traced in pencil with the use of a *camera lucida* (drawing tube) mounted on the microscope. Pencil sketches were then scanned (Fujitsu ScanSnap S1500M scanner), edited in Adobe Photoshop (v. 9.0.2, Adobe Systems Inc.), and used as a template in Adobe Illustrator (v. 13.0.2, Adobe Systems Inc.) to be digitally inked. Electronic “drawing” was completed with the aid of a graphics tablet (Bamboo Fun, Wacom Company, Limited). Species descriptions were constructed using the program DELTA (Dallwitz *et al.*, 1999) and specimen management followed the procedures outlined by Holzenthal and Andersen (2004). Each pinned specimen examined during the study was affixed with a barcode label (4 mil polyester, 8 x 14 mm, code 49) bearing a unique alphanumeric sequence beginning with the prefix UMSP. Specimens in alcohol were given a single barcode label to represent all those in a single vial. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection. Types of species described and other material examined are deposited in the

University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), and the Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (MIZA).

TAXONOMY

Acostatrichia digitata Thomson and Holzenthal, sp. n.

urn:lsid:zoobank.org:act:85981ECC-3397-4968-ACBC-B6EE2098DA5B

http://species-id.net/wiki/Acostatrichia_digitata

Fig. 1

Diagnosis. This species is most similar to *Acostatrichia fimbriata* Flint, 1974 but can be distinguished by a mesoventral process on abdominal segment VII with an apex that is truncate and rugose, not pointed. The posterolateral process of abdominal segment VIII bears digitate projections apically, unlike the spines on *A. fimbriata*. Additionally, the subgenital appendage of *A. digitatus* is pointed apically instead of rounded.

Description. *Male.* Length of forewing 2.7 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head dark brown with pale yellow setae; thorax dark brown with pale yellow setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine yellow setae and small scattered patches of dark brown setae. *Genitalia.* Abdominal sternum VII with

long mesoventral process, apex truncate, rugose. Segment VIII anterolateral margin straight, posterolateral margin greatly elongate into narrow structure bearing digitate apical projections; ventrally posterior margin concave, mildly crenulated. Segment IX anterolateral margin acute, posterolateral margin broadly convex; with mesolateral quadrate structure bearing prominent setae (see Fig. 1A); dorsally with posterior margin straight. Subgenital appendage paired, broadly rounded with apicoventral point, dorsally with rounded emargination on inner edge. Inferior appendage setose, narrow, rod-like, fused latero-ventrally with subgenital appendage, in ventral view with semiquadrate apical emargination (see Fig. 1D). Tergum X membranous, triangular in dorsal view. Phallus tubular basally with median complex bearing basal loop and pair of circular “windows,” apex with pair of elliptic plates, strongly sclerotized mesolaterally.

Material examined. Holotype male: VENEZUELA: Bolívar: E Tumeremo, W Bochinche, Río Botonamo, 07°25.462'N, 61°14.318'W, 150 m, 13.vii.2010, UV light, Holzenthal, Thomson, Cressa (UMSP000095201) (UMSP).

Etymology. The Latin word *digitatus* meaning “having fingers,” referring to the digitate projections on the posterolateral process of the VIIIth segment.

***Hydroptila cressae* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:22765A69-4EE1-4DA6-BB78-E100D0C6EF33

http://species-id.net/wiki/Hydroptila_cressae

Fig. 2

Diagnosis. This species is most similar to *Hydroptila denza* Ross, 1948, but differs in the shape of the projection on the posterolateral margin of abdominal segment IX. This projection is more pointed and is curved downward, or decurved, in *H. cressae*, while it is straight and more blunt in *H. denza*. The triangular subgenital process seen in *H. denza* is not apparent in *H. cressae*. Additionally, tergum X of *H. cressae* contains an internal apodeme that is not apparent in *H. denza*.

Description. *Male.* Length of forewing 2.0 mm (n=1). Head unmodified, without ocelli; antennae unmodified. Tibial spur count 0, 2, 4. Dorsum of head brown with pale yellow setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine light brown setae with small dark brown patch of setae at apex. *Genitalia.* Abdominal sternum VII with simple, slender, pointed mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin convex, posterolateral margin with pointed projection, curving slightly ventrad; dorsally with posterior margin convex. Inferior appendage setose, with narrow base, apex truncate with pair of dark points on internal face. Tergum X membranous, extending past inferior appendage, containing internal sclerotized apodeme (see Fig. 2A). Phallus narrow, elongate; apex membranous, ovate, with elongate, slender spines extending past membranous region.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, “Río Curvita,” 04°31.237'N, 61°31.591'W, 869 m, 15–16.vii.2010, UV light, Holzenthal, Thomson, Cressa (UMSP000095196) (UMSP).

Etymology. Named in honor of Dr. Claudia Cressa, an aquatic ecologist at the Universidad Central de Venezuela and friend and colleague of the authors.

***Metrichia bostrychion* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:13F7C864-63DB-4360-92FA-D3CB3331DBA3

http://species-id.net/wiki/Metrichia_bostrychion

Fig. 3

Diagnosis. This species is most similar to *Metrichia anisoscola* (Flint, 1991), but differs in the shape of the inferior appendage, which is less elongate in *M. bostrychion* and more suborbicular. The dorsolateral hook in *M. bostrychion* is also stouter than that of *M. anisoscola*. *Metrichia bostrychion* can also be distinguished by the 3rd spine on the phallus which spirals dorsally.

Description. *Male.* Length of forewing 1.8 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head dark brown with white setae; thorax dark brown with white and dark brown setae dorsally, brown ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with small patch of light brown setae at apex. Abdomen with internal sacs between segments IV–V. Dorsolateral setal brushes on segments IV and V. *Genitalia.* Abdominal sternum VII with short, pointed mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VII– VIII,

posterolateral margin convex; dorsally with posterior margin membranous, flat. Preanal appendage (cercus) short, rounded. Dorsolateral hook stout, strongly decurved (see Fig. 3A). Inferior appendage suborbicular with shallow posterolateral emargination, extends as high as segment IX. Tergum X membranous, apex subdeltoid in dorsal view. Phallus widest at base, narrowing to median constriction, membranous apex with 3 spines, 1st and 3rd slender, elongate, 2nd spiraling dorsad.

Material examined. Holotype male: VENEZUELA: Monagas: Guachero Cave National Park at La Paila waterfall, 10°10.322'N, 63°33.315'W, 1110 m, 20–21. vii.2010, sweep net, Holzenthal, Thomson (UMSP000095197) (UMSP).

Paratype. Same data as holotype, 1 female (UMSP).

Etymology. The diminutive of the Greek word *bostrychos* meaning “curl,” referring to the small spiral in the second apical spine on the phallus.

***Neotrichia feolai* Santos and Nessimian, 2009, redescription and new country record**

http://species-id.net/wiki/Neotrichia_feolai

Fig. 4

Neotrichia feolai Santos and Nessimian, 2009: 766 [Type locality: Brazil, Amazonas, Rio Preto da Eva (tributary to Rio Preto da Eva); INPA; male].

Diagnosis. *Neotrichia feolai* was previously only known from the male holotype

collected from Brazil, Amazonas. Eight males were collected for the first time from Venezuela, representing a new record in this study for the country. Original illustrations did not include the distinctive subgenital appendage, but specimens from Venezuela match all other characteristics of the Brazilian species perfectly. Some of our specimens are dry, while the holotype was collected in alcohol, allowing us to describe coloration. We have also described and illustrated the subgenital plate not seen in the original illustration. According to the original authors, this species is most similar to *Neotrichia biuncifera* Flint, 1974. The shapes and lengths of the bracteole and inferior appendage are similar, but *N. feolai* can be distinguished by having only a single spine at the apex of the phallus.

Redescription. *Male.* Length of forewing 1.6–1.9 mm (n=8). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0, 2, 3. Dorsum of head brown with light brown setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine light brown setae with small patches of dark brown setae. *Genitalia.* Abdominal sternum VII without mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin strongly narrowing, withdrawn into segment VIII, posterolateral margin fused dorsally with tergum X (see Fig. 4B). Subgenital plate fused, diamond-shaped with pair of apico-ventral setae, posterior margin bearing paired row of sclerotized spines within membranous layer (see Figs. 4A, 4C). Bracteole spatulate, extended evenly with inferior appendage. Inferior appendage setose, laterally narrow and rod-like, fused lateroventrally with subgenital appendages, ventrally with semiquadrate apical emargination. Tergum X

membranous, bearing minute dorsal setae, with deep emargination both laterally and dorsally, dorsal lobe with sclerotized apex. Phallus with wide tubular base narrowing to median constriction, membranous apex with spiral process and slender apical spines.

Material examined. VENEZUELA: Guárico: Santa Rita, Morichal de los Becerros, 08°09.044'N, 62°35.149'W, 66 m, 6.vii.2010, UV light, Holzenthal, Thomson, 8 males (5 in alcohol) (UMSP, NMNH, MIZA).

***Ochrotrichia spira* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:83832CD2-268B-4AA3-A5EC-F6FAB463D9F6

http://species-id.net/wiki/Ochrotrichia_spira

Fig. 5

Diagnosis. This species is most similar to *Ochrotrichia raposa* Bueno-Soria and Santiago-Fragoso, 1992. Both have a simple, threadlike phallus and the large inferior appendage bears patches of black pegs on its internal face. The inferior appendage of *O. spiralis*, however, is parallel-sided with a truncate apex. Also, the sclerotized processes extending from tergum X of *O. spiralis* are easily distinguishable from those of *O. raposa*, in particular the large, spiral process.

Description. Male. Length of forewing 2.6–2.7 mm (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0, 3, 4. Dorsum of head dark brown with pale yellow setae; thorax light brown with light brown setae dorsally, light brown

ventrally; leg segments with light brown setae and patches of dark brown. Forewings covered with fine brown setae with small patches of dark brown setae near apex.

Genitalia. Abdominal sternum VII with short, rounded mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin concave, posterolateral margin fused dorsally with tergum X. Inferior appendage setose, 3 times longer than wide, parallel-sided, apex truncate, inner surface bearing many short, stout spines distributed as in Figs. 5A, 5C. Tergum X sclerotized, highly developed with 3 processes: 1st simple, slender pointed; 2nd with heavily sclerotized edge, large subapical point, small apical point; 3rd strongly spiraled, extended past other processes. Phallus tubular, elongate, threadlike.

Material examined. Holotype male: VENEZUELA: Monagas: Guachero Cave National Park, 10°10.322'N, 63°33.315'W, 1110 m, 20–21.vii.2010, UV light, Holzenthal, Thomson, Cressa (UMSP000095193) (UMSP).

Paratypes. Same data as holotype, 2 males (UMSP, NMNH).

Etymology. The Latin word *spiralis* meaning “spiral,” referring to the strongly spiraled process extending from tergum X.

***Oxyethira (Tanytrichia) bettyae* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:9B85F4D2-070A-4192-BD8D-E4DF432D19AA

http://species-id.net/wiki/Oxyethira_bettyae

Fig. 6

Diagnosis. This species is placed in the subgenus *Tanytrichia* according to the characters given by Kelley (1985): segment VIII venter excised to anterior margin, segment IX elongate and extending into segment VI, the absence of segment IX dorsum, and a phallus bearing two long lateral processes originating at the midlength. This species is most similar to *Oxyethira longissima* Flint, 1974. The phallus is very similar, bearing long paired processes sharply bent back anteriorly. However, the subgenital process of *O. longissima* is more strongly arched and much more slender in lateral view than that of *O. bettyae*. Also, when viewed ventrally, the bilobed process of *O. bettyae* is wider basally than *O. longissima*.

Description. *Male.* Length of forewing 2.0–2.2 mm (n=6). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0, 3, 4. Dorsum of head dark brown with pale yellow setae; thorax brown with light brown setae dorsally; leg segments with light brown setae. Forewings covered with fine light brown setae and small scattered patches of dark brown setae and golden brown setae. *Genitalia.* Abdominal sternum VII with simple, pointed mesoventral process with small patch of stout pegs basally. Segment VIII anterolateral margin straight, posterolateral margin pointed; dorsally posterior margin with rounded emargination; ventrally posterior margin with deeply divided. Segment IX anterolateral margin very narrow and very elongate, withdrawn into segments VI–VIII, posterolateral margin straight, not extended posteriorly past segment VIII. Subgenital process fused, apex with small rounded emargination (see Fig. 6C). Bilobed process slender, extending posteriad. Inferior appendage fused with deep apical emargination, sparsely setose, heavily sclerotized, apex acute, upturned in lateral view. Tergum X

membranous, quadrate dorsally, oblong ventrally. Phallus with tubular basal half, apical half membranous; 2 long, lateral processes beginning at midlength, very sharply curved backward, or recurved.

Material examined. Holotype male: VENEZUELA: Guárico: UCV San Nicolasito Field Station, 08°8.296'N, 66°24.459'W, 62 m, 5.vii.2010, UV light, Holzenthal, Thomson (UMSP000095178) (UMSP).

Paratypes. Same data as holotype, 1 male (UMSP); **Venezuela: Bolívar:** Los Pijiguaos at rock outcrop, 6°35.617'N, 66°49.238'W, 80 m, 7–8.vii.2010, UV light trap, Holzenthal, Thomson, 5 males (in alcohol) (UMSP, NMNH, MIZA).

Etymology. Named in honor of the first author's grandmother, Betty Welter, who passed away while this work was in progress.

***Oxyethira picita* Harris and Davenport, 1999, new country record**

Oxyethira picita Harris and Davenport, 1999: 35 [Type locality: Peru, Loreto, edge of Rio Sucusari backwater, adjoining Explorama lodge; NMNH; male]. -Santos *et al.*, 2009: 36, 43 [distribution].

Diagnosis. *Oxyethira picita* was previously known only from the male holotype collected from Peru, Loreto. A single male was collected at a later date from Brazil, Amazonas (Santos *et al.*, 2009). Five males were now collected for the first time from Venezuela,

representing a new record for the country. All five males were collected in alcohol. *Oxyethira picita* was placed in the subgenus *Tanytrichia* by Harris and Davenport (1999), although it was suggested that it also displayed some similarity to the subgenus *Loxotrichia*. The original description and illustration of *O. picita* are detailed and well done; further description or illustration was not thought necessary.

Material examined. VENEZUELA: Bolívar: Campamento R.o Aro, 07°37.443'N, 64°08.324'W, 90 m, 10–11.vii.2010, UV light, Holzenthal, Thomson, 4 males (in alcohol) (UMSP, MIZA). **VENEZUELA: Bolívar:** 30 km S Upata, roadside marsh, 07°22.239'N, 61°44.233'W, 163 m, 12.viii.2010, Short, Tellez, Camacho, 1 male (in alcohol) (NMNH).

***Oxyethira (Dactylotrichia) quiramae* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:6C447B87-EA39-4D06-A28A-0702345D2930

http://species-id.net/wiki/Oxyethira_quiramae

Fig. 7

Diagnosis. This species is placed in the subgenus *Dactylotrichia* according to the characters given by Kelley (1985): segment VIII venter excised nearly to the anterior margin and segment IX venter extending anteriorly through segments VIII–VI. This species is most similar to *Oxyethira hozosa* Harris and Davenport, 1999. Both species have short, blunt, ventrally triangular inferior appendages and a phallus with a distal

curved process and an ejaculatory duct enclosed within the membranous apex. *O. quiramae* can be distinguished by a subgenital plate that is not as strongly decurved and lacks an acute apex in lateral view. Also, in *O. quiramae*, segment IX extends anteriorly past the posterior margin of abdominal segment VI.

Description. *Male.* Length of forewing 1.8–1.9 mm (n=3). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0, 3, 4. Dorsum of head brown with light brown setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine brown setae with small scattered patches of light brown setae and small patches of dark brown setae near margins and apex. *Genitalia.* Abdominal sternum VII with simple, digitate mesoventral process with large patch of stout pegs basally. Segment VIII anterolateral margin straight, posterolateral margin convex with small mesal emargination; dorsally posterior margin with rounded emargination; ventrally deeply excised. Segment IX anterolateral margin narrow and elongate, withdrawn into segments VI–VIII, posterolateral margin straight, not extended posteriorly past segment VIII. Subgenital process fused distomesally, apex with shallow emargination, curving ventrad (see Fig. 7C). Bilobed process slender, curved, not extending posteriorly past segment VIII. Inferior appendage reduced, triangular, heavily sclerotized (see Fig. 7C). Tergum X not apparent. Phallus with tubular basal half, apical half membranous; apex elongate, slender, pointed, curving dorsad and sharply recurved.

Material examined. Holotype male: VENEZUELA: Guárico: UCV San Nicolasito Field Station, 08°8.296'N, 66°24.459'W, 62 m, 5.vii.2010, UV light,

Holzenthal, Thomson (UMSP000095179) (UMSP).

Paratypes. Same data as holotype, 2 males (NMNH, MIZA).

Etymology. Named in honor of Gina Quiram, a friend and colleague of the first author, for all her help in the field.

***Oxyethira redunca* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:C8A428D1-6558-479C-8AF8-8857D6E2A5FB

http://species-id.net/wiki/Oxyethira_redunca

Fig. 8

Diagnosis. We have been unable to assign this species to a subgenus. The deep ventral excision of abdominal segment VIII and the extension of segment IX anteriorly into segment VII make it somewhat similar to *Loxotrichia*. However, the absence of a subgenital process precludes it from being placed with certainty in any of the current subgenera and distinguishes it from all other species.

Description. *Male.* Length of forewing 2.4 mm (n=1). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0, 3, 4. Dorsum of head brown with pale yellow setae; thorax brown with pale yellow setae dorsally, pale yellow ventrally; leg segments with brown setae. Forewings covered with fine brown setae and elongate patches of light brown setae and small patches of dark brown setae near margins and apex. *Genitalia.* Abdominal sternum VII with spatulate mesoventral process. Segment

VIII anterolateral margin straight, posterolateral margin acutely convex; dorsally posterior margin with deep acute emargination; ventrally posterior margin with deep rounded emargination. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VII–VIII, posterolateral margin acute, not extending past segment VIII; dorsally bearing paired, elongate, slender processes, basal half extending posteriorly, apical half strongly bent anteriorly. Subgenital process not apparent. Bilobed process not apparent. Inferior appendage setose, laterally narrow and rod-like, fused latero-ventrally with subgenital appendages, ventrally with semiquadrate apical emargination. Tergum X membranous, large, bearing elliptic patch of minute setae dorsally (see Fig. 8B). Phallus with tubular basal half, apical half membranous, convex ventrally, apex curving dorsad.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, “Río Curvita,” 4°31.237'N, 61°31.591'W, 869 m, 15–16.vii.2010, UV light, Holzenthal, Thomson, Cressa (UMSP000095176) (UMSP).

Etymology. The Latin word *reduncus* meaning “bent backward,” referring to the sharply bent dorsal processes of segment IX.

***Rhyacopsyche shorti* Thomson and Holzenthal, sp. n.**

urn:lsid:zoobank.org:act:56EB1974-52AA-4EE1-9F95-357CD2AC3A4A

http://species-id.net/wiki/Rhyacopsyche_shorti

Fig. 9

Diagnosis. This species is most similar to *Rhyacopsyche otarosa* Wasmund and Holzenthal, 2007. Both species display an inferior appendage with a bifid apex bearing a large rounded dorsal lobe. However, the ventral lobe is broadly pointed in *R. shorti* and truncate in *R. otarosa*. Additionally, when seen dorsally, the dorsolateral lobes of segment IX are rounded in *R. shorti*, not acicular as in *R. otarosa*.

Description. *Male.* Length of forewing 2.6–2.7 mm (n=2). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head brown with dark brown setae and light brown patch between antennae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with dark brown setae. Forewings covered with golden brown setae with small patches of dark brown setae at margins and apex. *Genitalia.* Abdominal sternum VII without mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VII–VIII, posterolateral margin with rounded setae-bearing dorsolateral lobe and truncate mesolateral lobe. Inferior appendage with rounded mesodorsal projection bearing setae, setae directed anteriorly; apex heavily sclerotized, curving dorsad, acute. Tergum X membranous, round in dorsal view, contracted inside dorsolateral lobes of segment IX. Phallus basally tubular, elongate, narrow, apex membranous and with thickened spines.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, “Río Curvita,” 04°31.237'N, 61°31.591'W, 869 m, 15–16.vii.2010, UV light, Holzenthal, Thomson, Cressa (UMSP000095199) (UMSP).

Paratype. Same data as holotype, 1 male (UMSP).

Etymology. Named in honor of Dr. Andrew Short, an entomologist at the University of Kansas and friend and colleague of the authors.

BIBLIOGRAPHY

- Blahnik, R. J., Holzenthal, R. W. and Prather, A. (2007) The lactic acid method for Clearing Trichoptera genitalia. *In*: Bueno-Soria, J., Barba-Alvarez, R. and Armitage, B. (Eds) *Proceedings of the XIIIth International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, 9–14.
- Bueno-Soria, J. and Santiago-Fragoso, S. (1992) Studies in aquatic insects, XI: seven new species of the genus *Ochrotrichia* (*Ochrotrichia*) from South America (Trichoptera: Hydroptilidae). *Proceedings of the Entomological Society of Washington* 94: 439–446.
- Dallwitz, M. J., Paine, T. A. and Zurcher, E. J. (1999) User's guide to the DELTA Editor. <http://deltaintkey.com/> [accessed 6 February 2012]
- Carins, A. and Wells, A. (2008) Contrasting modes of handling moss for feeding and case-building by the caddisfly *Scelotrichia willcarinsi* (Insecta: Trichoptera). *Journal of Natural History* 42: 2609–2615. doi: 10.1080/00222930802354308
- Flint, O. S., Jr. (1972) Studies of Neotropical caddisflies, XIV: on a collection from northern Argentina. *Proceedings of the Biological Society of Washington* 85: 223–248.
- Flint, O. S., Jr. (1974) Studies of Neotropical caddisflies, XV: the Trichoptera of Surinam. *Studies on the Fauna of Suriname and other Guianas* 14: 1–151.
- 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. doi: 10.5479/si.00810282.520
- Harris, S. C. and Davenport, L. J. (1999) New species of Hydroptilidae (Trichoptera) from the Amazon region of northeastern Peru. *Proceedings of the Entomological Society of Washington* 101: 26–38.
- Holzenthal, R. W. and Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa* 511: 1–80.
- Holzenthal, R. W., Blahnik, R. J., Prather, A. L. and Kjer, K. M. (2007) Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. *Zootaxa* 1668: 639–698.
- Holzenthal, R. W., Morse, J. C. and Kjer, K. M. (2011) Order Trichoptera Kirby, 1813. *In*: Zhang, Z. Q. (Ed) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 209–211.
- Kelley, R. W. (1984) Phylogeny, morphology and classification of the micro-caddisfly genus *Oxyethira* Eaton (Trichoptera: Hydroptilidae). *Transactions of the American Entomological Society* 110: 435–463.
- Marshall, J. E. (1979) A review of the genera of the Hydroptilidae (Trichoptera). *Bulletin of the British Museum (Natural History) Entomology Series* 39: 135–239.
- Ross, H. H. (1948) Notes and descriptions of Nearctic Hydroptilidae (Trichoptera). *Journal of the Washington Academy of Sciences* 38: 201–206.
- Santos, A. P. M., Henriques-Oliveira, A. L. and Nessimian, J. L. (2009) New species and records of *Oxyethira* Eaton (Trichoptera: Hydroptilidae) from Amazonas State, Brazil. *Zootaxa* 2169: 35–44.
- Santos, A. P. M. and Nessimian, J. L. (2009) New species and records of *Neotrichia*

- (Trichoptera: Hydroptilidae) from Central Amazonia, Brazil. *Zoologia* 26: 758–768.
- Wasmund, A. M. and Holzenthal, R. W. (2007) A revision of the Neotropical caddisfly genus *Rhyacopsyche*, with the description of 13 new species (Trichoptera: Hydroptilidae). *Zootaxa* 1634: 1–59.
- Wells, A. (1985) Larvae and pupae of Australian Hydroptilidae (Trichoptera), with Observations on general biology and relationships. *Australian Journal of Zoology, Supplementary Series* 113: 1–69. doi: 10.1071/AJZS113
- Wells, A. (2005) Parasitism by hydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. *Australian Journal of Entomology* 44: 385–391. doi: 10.1111/j.1440-6055.2005.00492.x
- Wiggins, G. B. (2004) *Caddisflies: The Underwater Architects*. University of Toronto Press, Toronto, 292 pp.

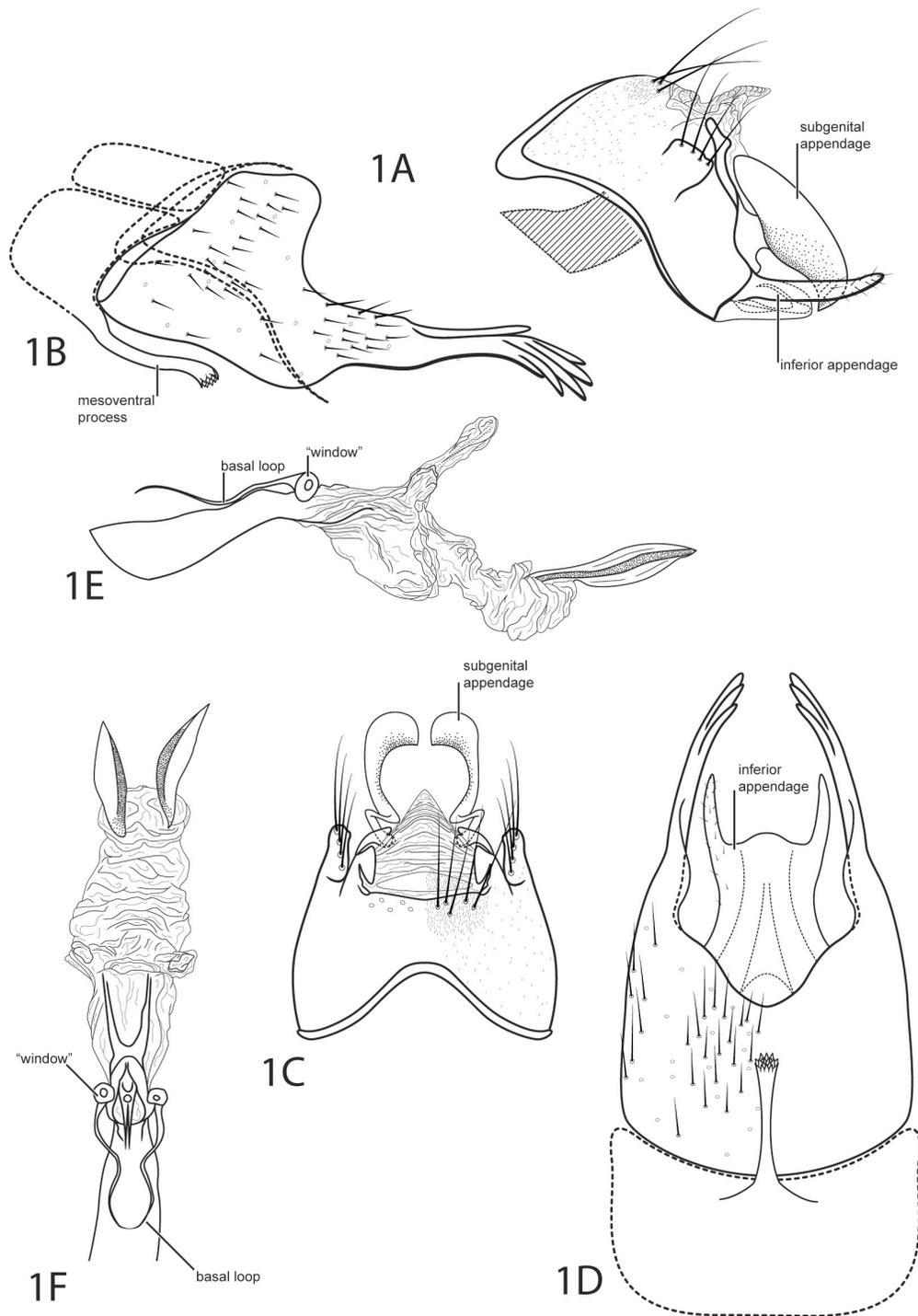


FIGURE 1. *Acostatrichia digitata*, new species (UMSP000095201). Male genitalia: **A** segments VII-X, lateral (base of phallus cross-hatched) **B** segments IX-X, dorsal **C** segments VII-IX, ventral **E** phallus, lateral **F** phallus, dorsal.

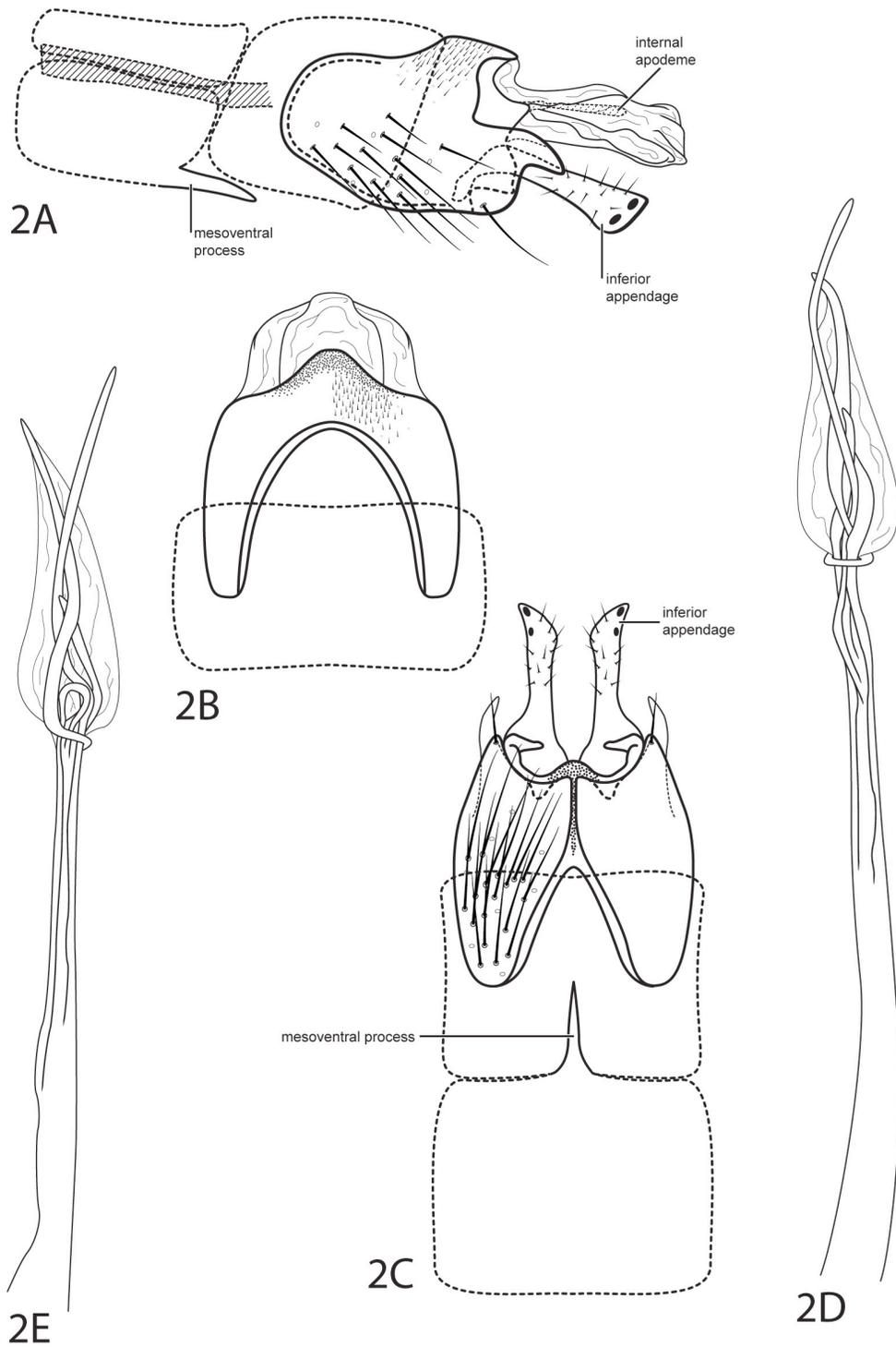


FIGURE 2. *Hydroptila cressae*, new species (UMSP000095196. Male genitalia: **A** segments VII-X, lateral (base of phallus cross-hatched) **B** segments IX-X, dorsal **C** segments VII-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

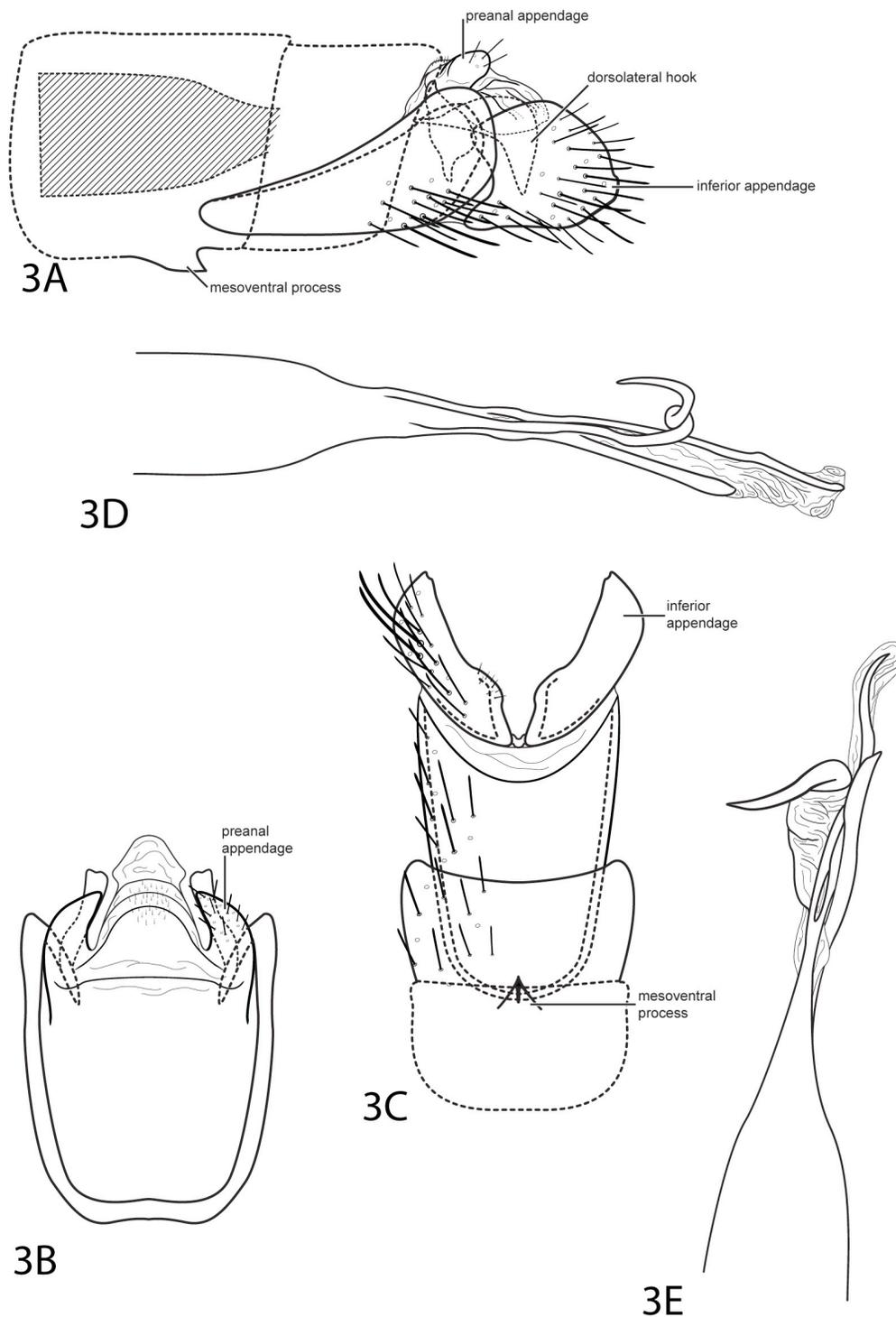


FIGURE 3. *Metrichia bostrychion*, new species (UMSP000095197). Male genitalia: **A** segments VII-X, lateral (base of phallus cross-hatched) **B** segments IX-X, dorsal **C** segments VII-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

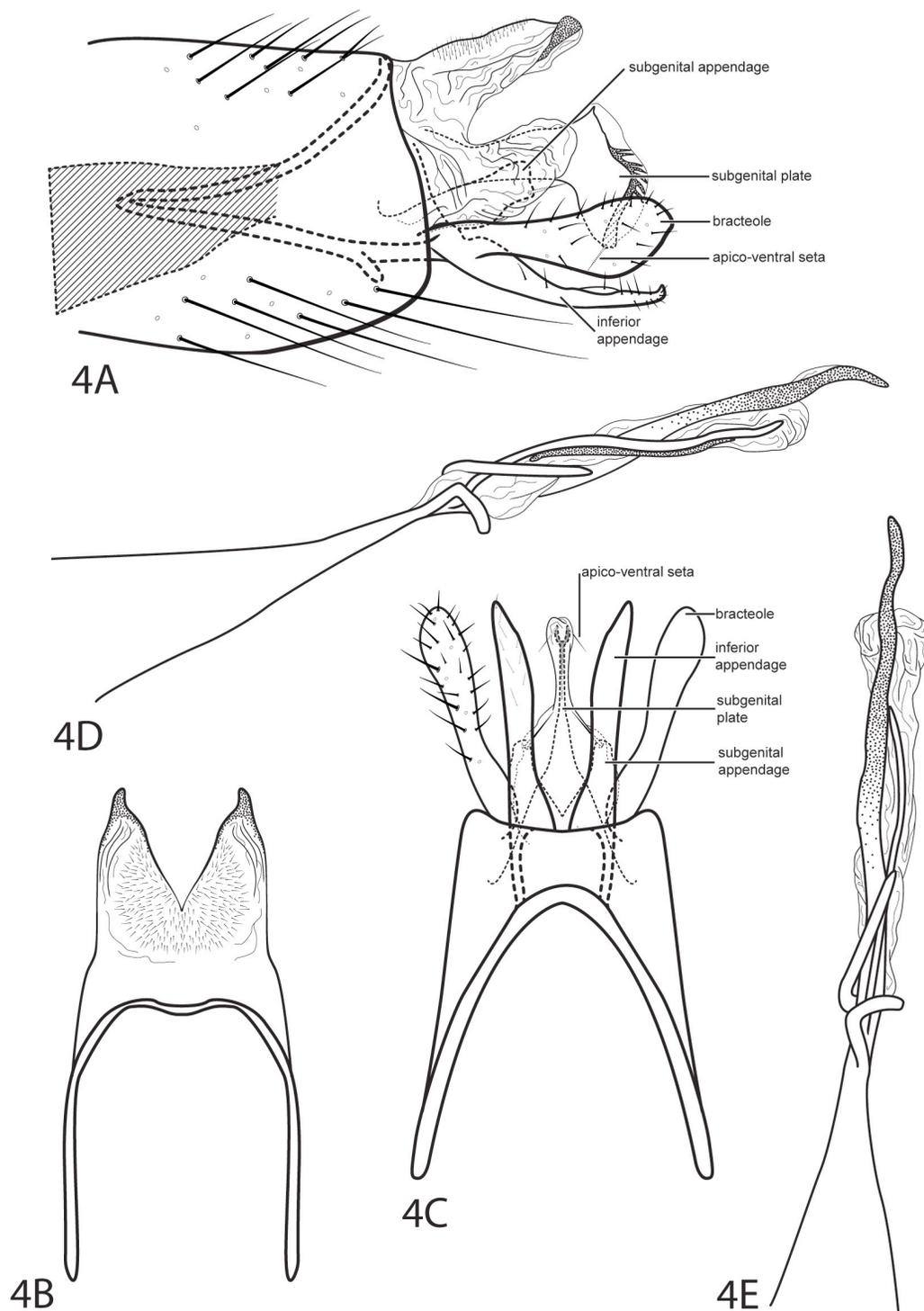


FIGURE 4. *Neotrichia feolai*, Santos and Nessimian, 2009. Male genitalia: **A** segments VIII-X, lateral (base of phallus cross-hatched) **B** segments IX-X, dorsal **C** segment IX, ventral **D** phallus, lateral **E** phallus, dorsal.

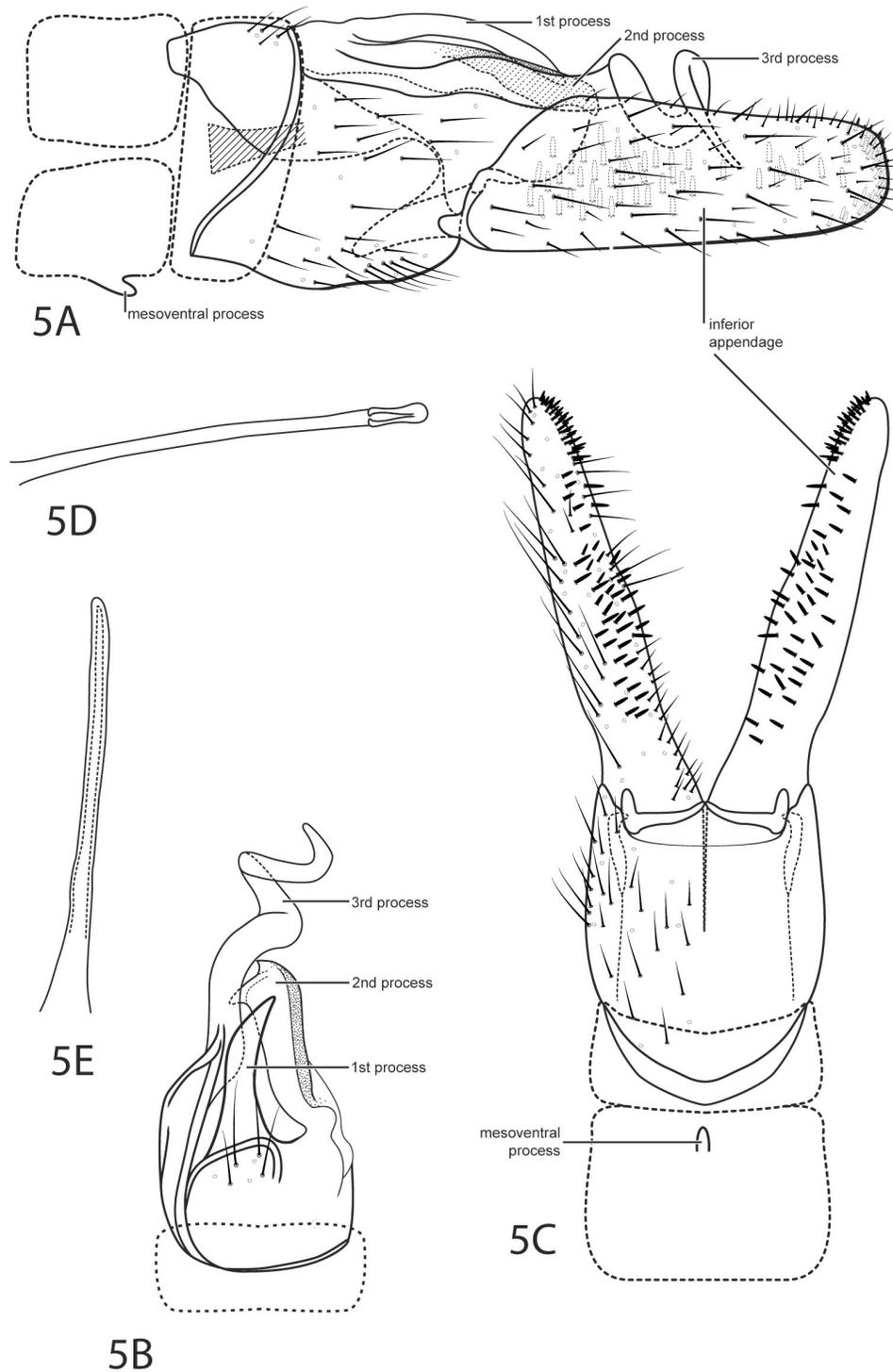


FIGURE 5. *Ochrotrichia spira*, **new species** (UMSP000095193). Male genitalia: **A** segments VII-X, lateral (base of phallus cross-hatched) **B** segments VIII-X, dorsal **C** segments VII-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

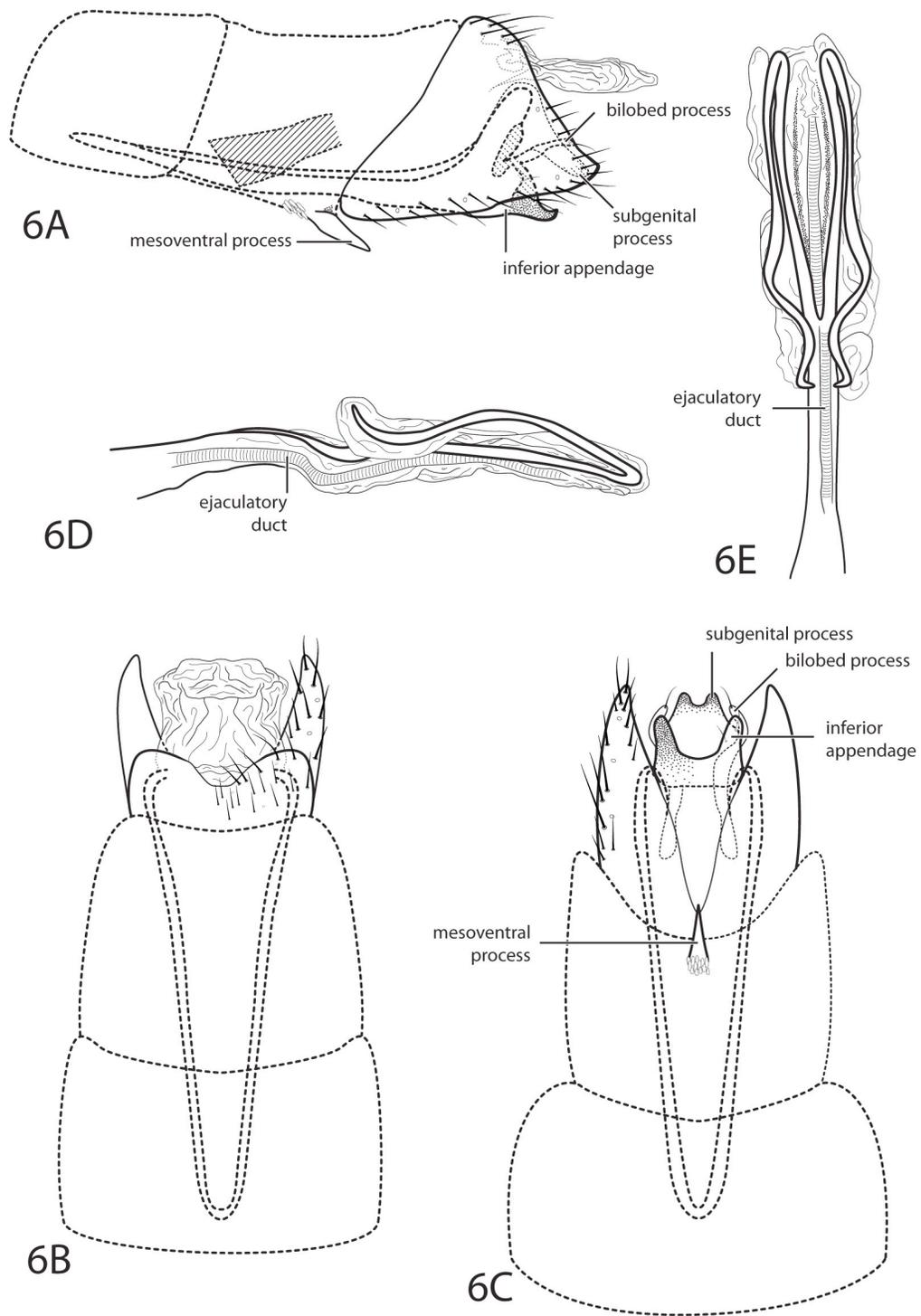


FIGURE 6. *Oxyethira bettyae*, new species (UMSP000095178). Male genitalia: **A** segments VI-IX, lateral (base of phallus cross-hatched) **B** segments VI-X, dorsal **C** segments VI-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

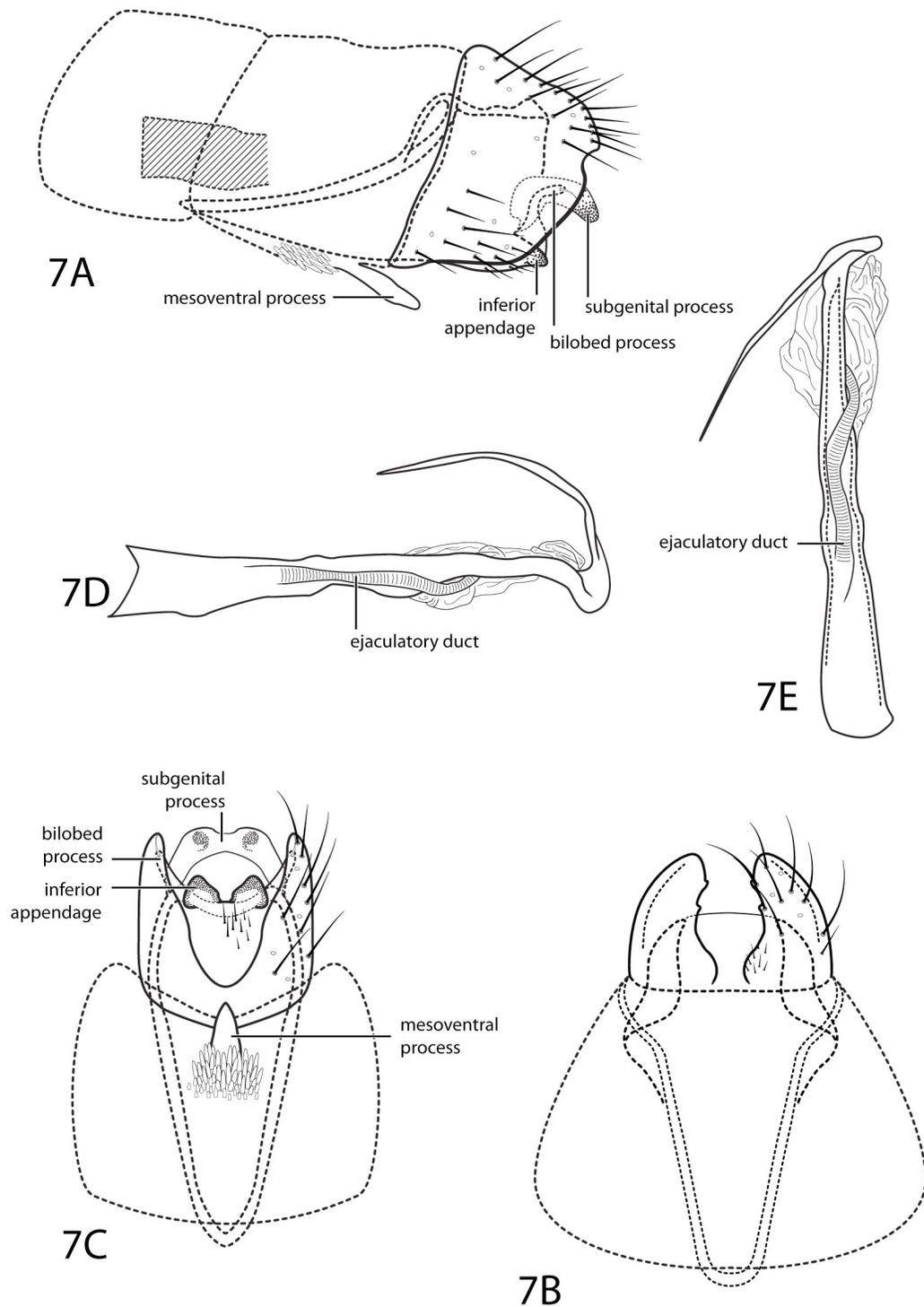


FIGURE 7. *Oxyethira quiramae*, new species (UMSP000095179). Male genitalia: **A** segments VI-IX, lateral (base of phallus cross-hatched) **B** segments VII-IX, dorsal **C** segments VII-IX, ventral **D** phallus, lateral **E** phallus, dorsal.

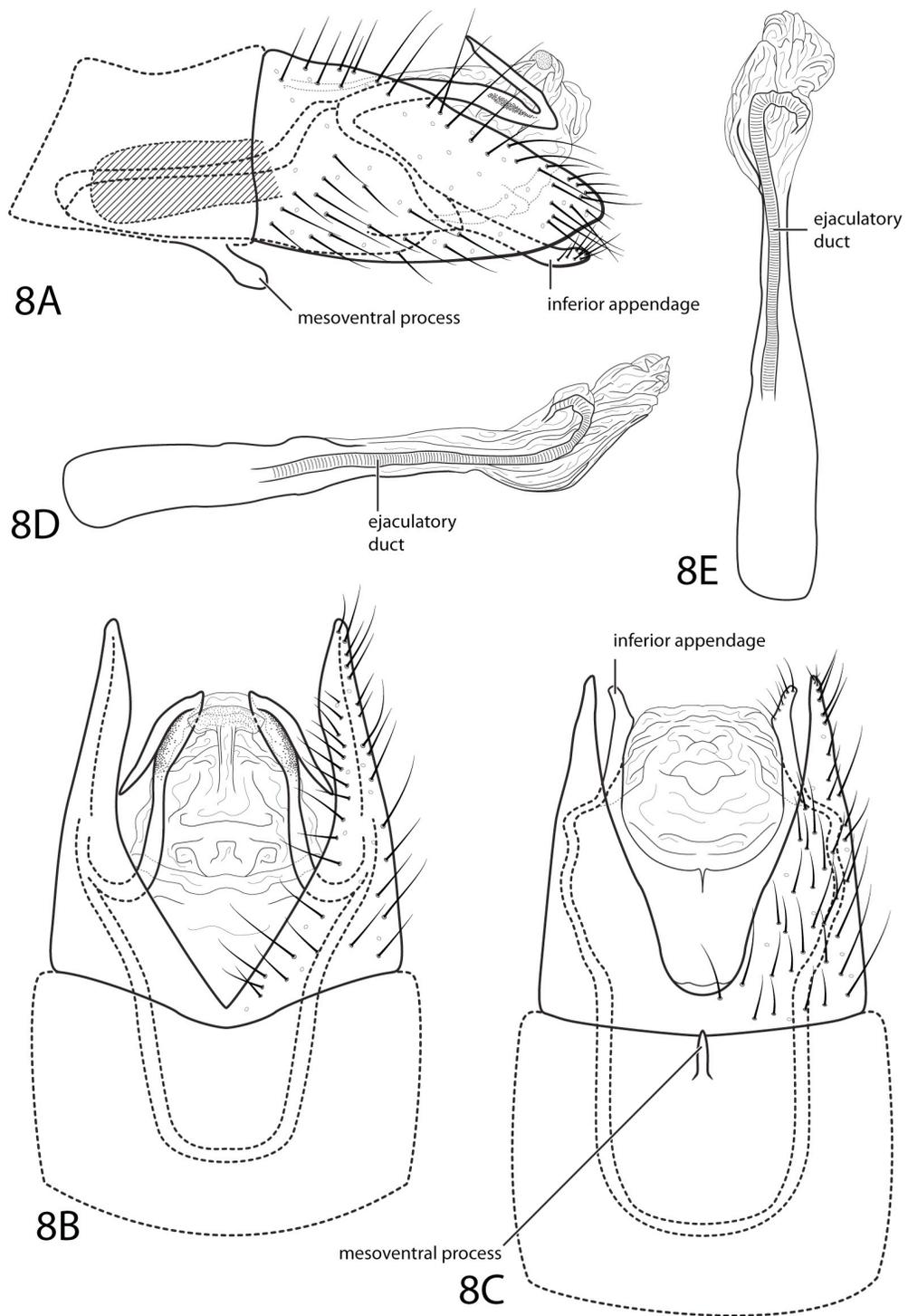


FIGURE 8. *Oxyethira redunca*, new species (UMSP000095176). Male genitalia: **A** segments VII-X, lateral (base of phallus cross-hatched) **B** segments VII-X, dorsal **C** segments VII-X, ventral **D** phallus, lateral **E** phallus, dorsal.

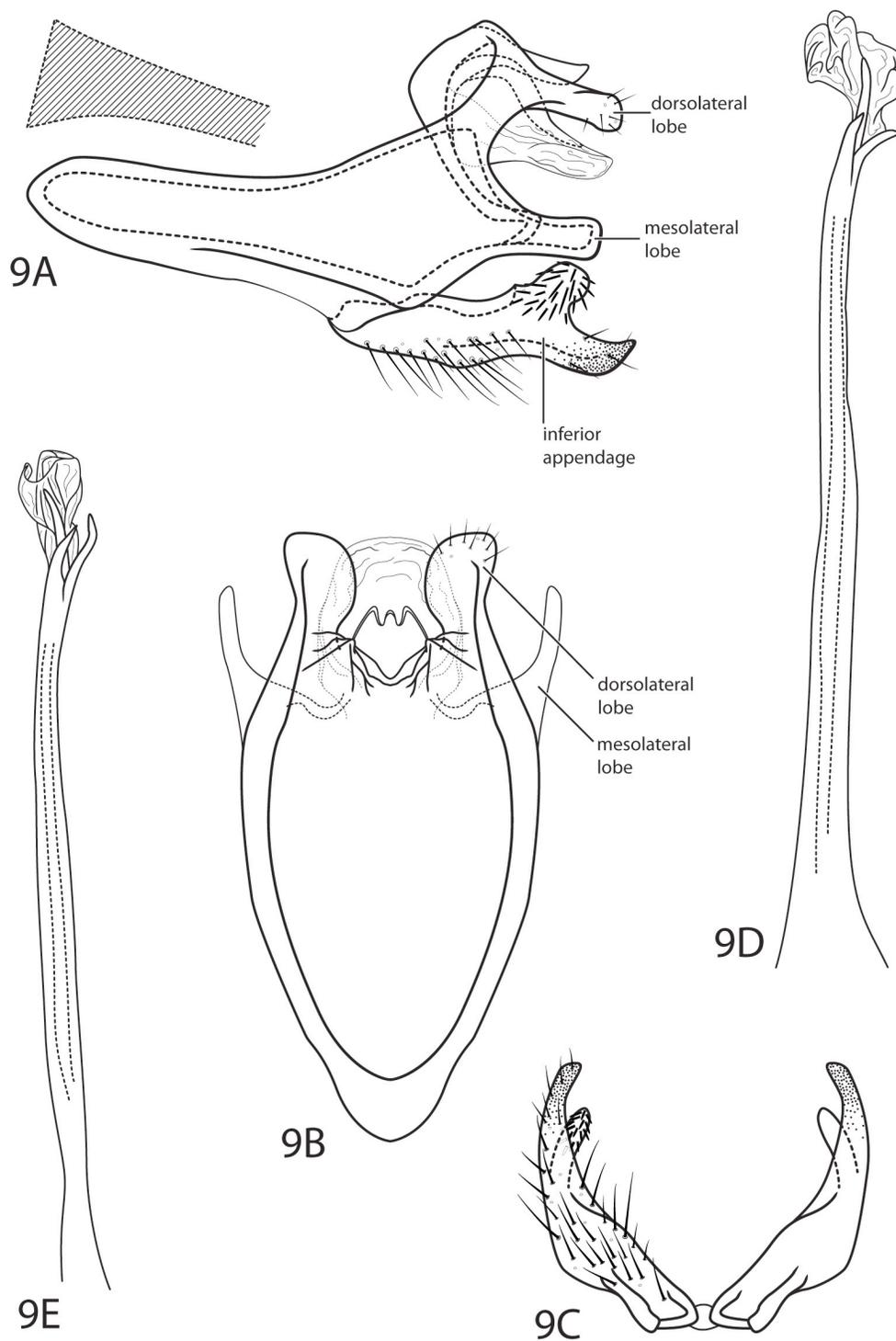


FIGURE 9. *Rhyacopsyche shorti*, new species (UMSP000095199). Male genitalia: **A** segments IX-X, lateral (base of phallus cross-hatched) **B** segments IX-X, dorsal **C** inferior appendages, ventral **D** phallus, lateral **E** phallus, dorsal.

Chapter IV. Descriptions of New Species of Leucotrichiinae (Trichoptera: Hydroptilidae) from Brazil

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SUMMARY

2 new species of Hydroptilidae (Trichoptera) from Brazil are described: *Betrichia alibrachia* sp. n. and *Leucotrichia bicornuta* sp.n. Both genera are members of the subfamily Leucotrichiinae. Illustrations of male genitalia are provided with each description. These additions bring the total world fauna of *Betrichia* to 9 species and *Leucotrichia* to 29 species.

INTRODUCTION

The subfamily Leucotrichiinae (type genus *Leucotrichia* Mosely, 1934) was established by Flint (1970) and currently contains 16 genera: *Abtrichia*, *Acostatrichia*, *Alisotrichia*, *Anchitrichia*, *Ascotrichia*, *Betrichia*, *Celaenotrichia*, *Cerasmatrichia*, *Ceratotrichia*, *Costatrichia*, *Eutonella*, *Leucotrichia*, *Mejicanotrichia*, *Peltopsyche*, *Scelobotrichia*, and *Zumatrichia* (Morse, 2012). The distribution of the subfamily is limited to the New World and found predominantly in Central America (Marshall, 1979; Flint *et al.*, 1999).

Mosely (1939) established the genus *Betrichia* for a single species, *Betrichia zilbra*, from Brazil (Santa Catarina). No exact reasons were stated, but presumably the genus was erected on account of venational, antennal, and general male genitalic features (Marshall, 1979). Additional species and distributions have been provided by Angrisano (1995), Flint (1972, 1974, 1983), and Oláh and Johanson (2011). Up to and including species described by Oláh and Johanson (2011), *Betrichia* contained a total of 8 extant species (Table 1) (Morse, 2006). As a genus, its distribution is limited to eastern South America (Table 1) (Flint *et al.*, 1999). Immature stages are unknown (Marshall, 1979). Adults are attracted to lights and can generally be found near lowland rivers (Flint *et al.*, 1999).

Mosely (1934) established the genus *Leucotrichia* for a single species, *Leucotrichia melleopicta*, from Mexico (Tabasco) (Mosely, 1934). Additional species descriptions and distributions have been provided by Angrisano and Burgos (2002), Banks (1911), Botosaneanu (Botosaneanu and Alkins-Koo, 1993), Bueno-Soria (2010), Bueno-Soria *et al.* (2001), Flint (1964, 1970, 1991, 1996), Oláh and Johanson (2011), Ross (1944), Rueda Martín (2011), Sattler and Sykora (1977), and Wells and Wichard (1989). Up to and including species described by Oláh and Johanson (2011) and Rueda Martín (2011), *Leucotrichia* contained a total of 28 extant species (Table 1) (Morse, 2006). The distribution of the genus includes most of the continental USA, the Greater and southern Lesser Antilles, Central America, and northern South America (Table 2) (Flint *et al.*, 1999). A single fossil species, *Leucotrichia adela*, is known from Dominican amber (Wells and Wichard, 1989). Adults occasionally come to light but are usually taken by

net during the day from marginal foliage (Flint *et al.*, 1999).

In this paper, I describe 2 new species, *Betrichia alibrachia* and *Leucotrichia bicornuta*, from Brazil. This brings the total world fauna of *Betrichia* to 9 and of *Leucotrichia* to 29.

TAXONOMY

Leucotrichiinae Flint, 1970

Past attempts at dividing Hydroptilidae into suprageneric units based primarily on larval morphology generally have produced groups of genera that were not or could not be placed into easily distinguishable groups (Flint, 1970). *Leucotrichia* and its closely related genera have often proven to be a somewhat aberrant unit in these attempts. Flint (1970) stated that, although there was no single characteristic that could be used to consistently separate adults from other subfamilies, a combination of characters were diagnostic for Leucotrichiinae when present. These characters included the reduction of ocelli to 2, the presence of modified setae, the presence of a basal costal pouch on the forewing, and something characteristic in the form of the male genitalia that was hard to define exactly, but likely includes the “window” and basal loop medially on the phallic apparatus. The character that was absolutely distinctive and primarily responsible for Flint’s (1970) establishment of Leucotrichiinae was the larval shelter; the shelter is no more than a dorsal covering nor is it moveable, characteristics not possessed by any other

genus.

In her revision of the genera of Hydroptilidae, Marshall (1979) recognized only 2 subfamilies: Ptilocolepinae and Hydroptilinae; Leucotrichiini was included within Hydroptilinae, due to the many features characteristic of Hydroptilinae in general. Marshall (1979) also stated that although Leucotrichiini does form a distinct group within Hydroptilinae, it was impossible to exactly define the genera, since species from 2 or more genera often key out with one another in generic-level keys.

Malicky (2001) elevated Ptilocolepinae to family rank Ptilocolepidae, leaving only 1 subfamily of 6 tribes in Hydroptilidae. This effectively raised each tribe back to the subfamily status originally designated by Flint (1970).

***Betrichia* Mosely, 1939**

In the original description, Mosely (1939) mentioned the presence of ocelli (the type-specimen bears 2), short antennae with a long basal joint, elongate wings with acute produced apices, and a 1, 3, 4 tibial spur formula as being part of the diagnosis of the genus. Maxillary palpi were missing from the holotype, the single specimen that was examined, and so was unavailable for description. Genitalic features and a forewing measurement of 3 mm were included in the species description of *B. zilbra* (Mosely, 1939). Among the genitalic features mentioned were the deeply excised apical margin of tergite VIII, the shallowly excised apical margin of tergite IX with apical angles produced into a pair of irregular rounded lobes, a phallus with a pair of stout sheaths, and a slender process on sternite VII. Wing venation and male genitalia were illustrated in the

description of the type-species (Mosely, 1939).

In her review of the genera of Hydroptilidae, Marshall (1979) concluded that the combination of features given in the original generic description was not unique to *Betrichia* and that there are no precise diagnostic features that distinguish it from other genera. Of the additional species added to the genus, most differ noticeably in some way from the type-species. For example, *Betrichia argentinica* shares similar genitalic features with the type-species, but also bears 3 ocelli and simple antennae. The male genitalic features of *Betrichia surinamensis* differ greatly from that of the type species and *Betrichia bispinosa* bears a basal costal pouch not found throughout the genus. Flint (1974) has stated that the establishment of additional genera to sort out such variation should wait until the South American Trichoptera fauna is better understood. According to Marshall (1979), all small leucotrichiine genera, such as *Betrichia*, should be placed in a group together, as characters originally diagnosed as generic features have proven to be specific as additional species have been described. Marshall's (1979) summary of male genitalic features reflects the variation now found within the genus, including features such as a variable subgenital plate, variable tergite X, and sternite VIII and segment IX each with or without posterolateral processes.

***Leucotrichia* Mosely, 1934**

In the original description, Mosely (1934) mentioned the presence of ocelli, antennal joints grouped in series of white and brown, a well-developed frenulum on the hindwing, arising from the subcosta, very densely setose legs, and a 1, 3, 4 tibial spur

formula as being part of the generic diagnosis. Maxillary palpi were mentioned as difficult to observe. Male genitalic features and a forewing measurement of 2 mm were included in the species description of *L. melleopicta* (Mosely, 1934). Among the genitalic features mentioned were the flattened terminal dorsal segment covering the genitalia, the deeply excised terminal ventral segment bearing setose margins, a spade-shaped “penis sheath,” and a slender process on the penultimate abdominal segment. Wing venation and male genitalia were illustrated in the description of the type-species (Mosely, 1934).

As additional new species were described and placed in *Leucotrichia*, Flint (1970) noted that, despite variation in antennae, number of ocelli, and dorsal structure of the head, there were certain other features that could be used to unite 2 species groups within the genus. Characters that Flint (1970) found distinguished the *L. melleopicta* species group include males bearing 3 ocelli, a mesoventral process on sternum VII, an unmodified head (except for *L. chiriquiensis*), and 1 or 2 large areas of greenish or whitish setae on the forewings. Characters that Flint (1970) found distinguished the *L. pictipes* species group include males bearing 2 ocelli, either a brush of setae or a point on sternum VII, a modified head (except for *L. imitator*), and spots or linear greenish or whitish marks on the forewings.

Flint (1970) also provided a generic-level diagnosis, including additional characters not in the original diagnosis. Mentioned, among other features, were the pentagonal metascutellum, the heavily sclerotized trianguloid plate of tergite X, the subgenital plate extending ventrally from the ventral angles of tergite X to the base of the inferior appendages, the subapical spine of the inferior appendages, and the midlength complex of

the phallus. Flint (1970) did not mention the wings in his generic diagnosis, while Marshall (1979) stated in her review of hydroptilid genera that the wings are unmodified, but made no mention of a well-developed frenulum on the hindwing.

Larvae have been associated with some species in the genus, but many are still unassociated (Flint *et al.*, 1999). The larvae are generally typical of the Leucotrichiinae but can be distinguished by their rugose or papillate head, single tarsal claw, and femora bearing spiniform dorsal setae (Marshall, 1979). The larvae, which are strongly depressed and may reach up to 5 mm in length, are free-living and found in running water on the upper surface of rocks, grazing on periphyton, until the final instar (McAuliffe, 1982; Wiggins, 1996). During this final retreatdwelling instar, they also display extreme lateral distention of abdominal segments V–VII (Wiggins, 1996). The silken retreats are generally flattened ovals up to 5.5 mm in length, slightly domed, with a circular opening at each end, attached tightly to rocks in fast flowing waters (Flint *et al.*, 1999; Marshall, 1979; Wiggins, 1996).

MATERIALS AND METHODS

Morphological terminology used for male genitalia of specimens follows that of Marshall (1979). For simplicity, paired structures are discussed in the singular. Procedures for specimen preparation followed those explained in detail by Blahník *et al.* (2007). For specimen examination and illustration, cleared genitalia were placed in a

watch glass with glycerin and small glass beads. The glass beads held the genitalia in place and allowed structures to be viewed in precise lateral, dorsal, and ventral positions. Genitalia were examined with an Olympus BX41 compound microscope at 250–500 x magnification. Structures were traced in pencil with the use of an Olympus model U-DA drawing attachment mounted on the microscope. Pencil sketches were then scanned (Fujitsu ScanSnap S1500M scanner), edited in Adobe Photoshop (v. 9.0.2, Adobe Systems Inc.), and used as a template in Adobe Illustrator (v. 13.0.2, Adobe Systems Inc.) to be digitally inked. Electronic “drawing” was completed with the aid of a graphics tablet (Bamboo Fun, Wacom Company, Limited). Illustrations shown in Figures 1 and 2 were produced from holotype specimens. Species descriptions were constructed using the program DELTA (Dallwitz *et al.*, 2012) and specimen management followed the procedures outlined by Holzenthal and Andersen (2004). Individual specimens examined during the study were associated with a barcode label (4 mil polyester, 8 x 14 mm, code 49) bearing a unique alphanumeric sequence beginning with the prefix UMSP. Vials of alcohol containing multiple specimens were given a single barcode label to represent all those in the vial. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection. Types of species described and other material examined are deposited in the Coleção Entomológica Professor José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (DZRJ), and the University of Minnesota Insect Collection, St Paul, Minnesota (UMSP).

NEW SPECIES DESCRIPTIONS

Betrichia alibrachia, new species

Figure 1

Material. Holotype male: Brazil: Rio de Janeiro: Resende, Ribeirás do Palmital, 22°25'26.2"S, 44°44'21.6"W, 969 m, 8.iii.2008, white light, collected by Nessimian, Dumas, de Souza, and Braga (in alcohol) (UMSP0000140290) (DZRJ). **Paratypes:** same data as holotype (9 males) (in alcohol) (DZRJ); Resende, Riacho no km 4 BR 354, 22°23'20"S, 44°45'16"W, 1411 m, 9.iii.2008, white light, collected by Nessimian, Dumas, de Souza, and Braga (1 male) (in alcohol) (DZRJ); Itatiaia, Parque Nacional do Itatiaia, ponte no Lago Azul, 22°27'02.8"S, 44°36'50.2"W, 29.viii.2009, UV light, collected by Cardoso-Costa and de Souza (1 male) (in alcohol) (DZRJ); Resende, Ribeirás do Palmital, 22°25'26.2"S, 44°44'21.6"W, 969 m, 8.iii.2008, UV light, collected by Nessimian, Dumas, de Souza, and Braga (2 males) (in alcohol) (UMSP); Nova Friburgo, Macaé de Cima, Rio Macaé, 22°24'46.0"S, 42°31'16.2"W, 13.ix.2009, collected by Santos (1 male, 1 female) (in alcohol) (DZRJ).

Description Male. Length of forewing 1.8–2.6 mm (n = 9). Head unmodified, with 3 ocelli; antennae unmodified. Wings unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII mesoventral process acute. Segment VIII anterolateral margin acute, posterolateral margin with 3 projections, 1st

and 3rd slender, elongate with single prominent seta, 2nd less pronounced, with single seta; in ventral view posterior margin acutely concave. Segment IX anterolateral margin with 2 pairs of elongate apodemes extended anteriorly, as in Figures 1(a) and 1(c), posterolateral margin setose, rounded; with elongate mesolateral rasp-like structure within membranous layer, extended anteriorly into segment VI, with triangular sclerotized structure at base of membranous layer, apex curving dorsad; dorsally segment IX with anterior margin concave. Subgenital plate not apparent. Inferior appendage apparently fused basally to segment IX, elongate, quadrate basodorsally, apex subacute, extended posteriorly further than tergum X. Tergum X membranous, rounded dorsally, apex emarginate in lateral view. Phallus tubular basally, with median complex bearing basal loop and pair of circular “windows,” apex with rounded ventral membranous projection.

Diagnosis. This species has several features that distinguish it from all other species in the genus. It lacks both an apparent subgenital plate and apical spines or sclerites on the phallus. It also bears an elongate rasp-like process extending anteriorly from segment IX. This process is not present elsewhere in the genus, or in any other genera of which I am aware.

Etymology. *Alius*, Latin for “another;” *brachium*, Latin for “arm,” referring to the very unusual rasp-like structure extending anteriorly from segment IX.

Leucotrichia bicornuta, new species

Figure 2

Material. Holotype male: Brazil, Rio de Janeiro, Panedo, Rio das Pedras, Três Bacias, 22°24'32.2"S, 44°33'06.5"W, 735 m, 6.iii.2008, collected by Nessimian, Dumas, de Souza, and Braga (in alcohol) (UMSP000014084) (DZRJ). **Paratypes:** Brazil, Rio de Janeiro, Itatiaia, Parque Nacional do Itatiaia, Rio Camp Belo, 22°27'17.32"S, 44°36'37.47"W, 705 m, 13.iv.2007, light, collected by Santos, Dumas, Ferreira, Jr., and Nessimian (2 males, 1 female) (in alcohol) (DZRJ).

Description Male. Length of forewing 2.5–3.4 mm (n = 3). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Color in alcohol brown, denuded. *Genitalia.* Abdominal sternum VII mesoventral process basally broad, rounded apically. Segment VIII anterolateral margin convex, posterolateral margin with single rounded projection bearing prominent setae; in ventral view posterior margin broadly concave. Segment IX anterolateral margin broadly produced dorsolaterally, posterolateral margin setose, broadly convex; dorsally with anterior margin broadly convex. Subgenital plate extending from ventral angle of tergum X, ventral arm extending to base of inferior appendage. Inferior appendage without setae, narrow basally, not extended posteriorly past tergum X, with small spine dorsally, apex curving dorsad, in ventral view apex with rounded emargination. Tergum X with semielliptic sclerite with tridentate posterior margin; with membranous suborbicular projection apically. Phallus tubular basally, with median complex bearing basal loop and pair of circular “windows,” membranous apex bearing paired dorsal lobes.

Diagnosis. This species is most similar to *Leucotrichia ayura* Flint, 1991, a member of the *Leucotrichia melleopicta* species group. *Leucotrichia bicornuta* is distinguished by the ventral arm of the subgenital plate, which does not project as far posteriad as that of *L. ayura* and then bends dorsad instead of remaining straight. *Leucotrichia bicornuta* is also distinguished by the lack of dorsal sclerites or apical spines on the phallus. Also, in *L. bicornuta*, the inferior appendages are broadly fused mesally; in *L. ayura* they are separate.

Etymology. *Bi*, Latin for “double;” *cornutus*, Latin for “horned,” referring to the 2 apicodorsal lobes of the phallus.

BIBLIOGRAPHY

- Angrisano, E. B. (1995) Contribución al conocimiento de los Trichoptera del Uruguay. II. Familia Hydroptilidae. *Revista Brasileira de Entomologia* 39: 501–516.
- Angrisano, E. B. and Burgos, G. N. (2002) Contribución para el conocimiento de los Leucotrichiini (Trichoptera: Hydroptilidae). Tres especies nuevas de la Argentina. *Revista de la Sociedad Entomológica Argentina* 61: 103–109.
- Banks, N. (1911) Description of new species of North American neotoperoid insects. *Transactions of the American Entomological Society* 37: 335–360.
- Blahnik, R. J., Holzenthal, R. W. and Prather, A. (2007) The lactic acid method for clearing Trichoptera genitalia. In: Bueno-Soria, J., Barba-Alvarez, R. and Armitage, B. (Eds) *Proceedings of the XIIth International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, 9–14.
- Botosaneanu, L. and Alkins-Koo, M. (1993) The caddis flies (Insecta: Trichoptera) of Trinidad and Tobago, West Indies. *Bulletin de l'Institut des Sciences Naturelles de Belgique, Entomologie* 63: 5–45.
- Bueno-Soria, J. (2010) Some new Trichoptera (Glossosomatidae, Hydroptilidae, Hydropsychidae and Polycentropodidae) from Mexico. *Proceedings of the Entomological Society of Washington* 112: 22–31.
- Bueno-Soria, J., Santiago-Fragoso, S. and Barba-Alvarez, R. (2001) Studies in aquatic insects, XVIII: New species and new record of caddisflies (Trichoptera) from Mexico. *Entomological News* 112: 145–158.
- Dallwitz, M. J., Paine, T. A. and Zurcher, E. J. (1999) User's guide to the DELTA Editor. <http://deltaintkey.com/> [accessed 6 February 2012]
- Flint, O. S., Jr. (1964) The caddisflies (Trichoptera) of Puerto Rico. *University of Puerto Rico, Agricultural Experiment Station, Technical Paper* 40: 1–80.
- Flint, O. S., Jr. (1970) Studies of Neotropical caddisflies, X: *Leucotrichia* and related genera from North and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 60: 1–64.
- Flint, O. S., Jr. (1972) Studies of Neotropical caddisflies, XIV: on a collection from northern Argentina. *Proceedings of the Biological Society of Washington* 85: 223–248.
- Flint, O. S., Jr. (1974) Studies of Neotropical caddisflies, XV: the Trichoptera of Surinam. *Studies on the Fauna of Suriname and other Guyanas* 14: 1–151.
- Flint, O. S., Jr. (1983) Studies of Neotropical caddisflies, XXXIII: new species from austral South America (Trichoptera). *Smithsonian Contributions to Zoology* 377: 1–100.
- 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.
- Flint, O. S., Jr. (1996) Studies of neotropical caddisflies LV: Trichoptera of Trinidad and Tobago. *Transactions of the American Entomological Society* 122: 67–113.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999) *Catalog of the Neotropical Caddisflies (Insecta: Trichoptera)*. Special Publication of the Ohio Biological

- Survey, Columbus, Ohio, USA.
- Holzenthal, R. W. and Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa* 511: 1–80.
- Malicky, H. (2001) Notes on the taxonomy of *Rhadicoleptus*, *Ptilocolepus* and *Pseudoneureclipsis*. *Braueria* 28: 19–20.
- Marshall, J. E. (1979) A review of the genera of the Hydroptilidae (Trichoptera). *Bulletin of the British Museum (Natural History) Entomology Series* 39: 135–239.
- McAuliffe, J. R. (1982) Behavior and life history of *Leucotrichia pictipes* (Banks) (Trichoptera: Hydroptilidae) with special emphasis on case reoccupancy. *Canadian Journal of Zoology* 60: 1557–1561.
- Morse, J. C. (2006) Trichoptera World Checklist. Available from <http://entweb.clemson.edu/database/trichopt/index.htm> (accessed 7 February 2014).
- Mosely, M. E. (1934) New exotic Hydroptilidae. *Transactions of the Royal Entomological Society of London* 82: 137–163.
- Mosely, M. E. (1939) The Brazilian Hydroptilidae (Trichoptera). *Novitates Zoologicae* 41: 217–239.
- Oláh, J. and Johanson, K. A. (2011) New Neotropical Hydroptilidae (Trichoptera). *Annales Historico-Naturales Musei Nationalis Hungarici* 103: 117–255.
- Ross, H. H. (1944) The caddisflies or Trichoptera of Illinois. *Bulletin of the Illinois Natural History Survey* 23: 1–326.
- Rueda Martín, P. A. (2011) New Hydroptilidae and new records from north-western Argentina and Bolivia (Trichoptera: Hydroptilidae). *Aquatic Insects* 33: 1–11.
- Sattler, W. and Sykora, J. L. (1977) Über eine, besonders durch ihr Bauinstinkt, merkwürdige neotropische Kocherfliege— *Leucotrichia brasiliana* n. sp. *Amazonia* 6: 137–255.
- Wells, A. and Wichard, W. (1989) Caddisflies of Dominican amber VI. Hydroptilidae (Trichoptera). *Studies on Neotropical Fauna & Environment* 24: 41–51.
- Wiggins, G. B. (1996) *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press, Toronto.

Table 1: Species and distributions of *Betrichia* and *Leucotrichia*.

<i>Species</i>	<i>Distribution</i>
<i>Betrichia</i>	
<i>argentinica</i> Flint, 1972	Argentina, Uruguay
<i>bispinosa</i> Flint, 1974	Surinam
<i>hamulifera</i> Flint, 1983	Argentina, Paraguay, Uruguay
<i>longistyla</i> Flint, 1983	Brazil
<i>occidentalis</i> Flint, 1974	Surinam
<i>rovatka</i> Oláh and Johanson, 2011	French Guiana
<i>uruguayensis</i> Angrisano, 1995	Uruguay
<i>zilbra</i> Mosely, 1939	Brazil, Uruguay
<i>Leucotrichia</i>	
<i>alisensis</i> Rueda-Martín, 2011	Argentina
<i>ayura</i> Flint, 1991	Colombia
<i>botosaneanui</i> Flint, 1996	Tobago, Trinidad
<i>brasiliansa</i> Sattler and Sykora, 1977	Brazil
<i>brochophora</i> Flint, 1991	Colombia
<i>chiriquiensis</i> Flint, 1970	Panama
<i>dinamica</i> Bueno-Soria, 2010	Mexico
<i>extraordinaria</i> Bueno-Soria <i>et al.</i> , 2001	Mexico
<i>fairchildi</i> Flint, 1970	Colombia, Grenada, Panama, Tobago, Trinidad, Venezuela
<i>forrota</i> Oláh and Johanson, 2011	Peru, Ecuador
<i>gomezi</i> Flint, 1970	Dominican Republic
<i>imitator</i> Flint, 1970	Costa Rica, Guatemala, Mexico
<i>inflaticornis</i> Botosaneanu, 1993	Trinidad
<i>inops</i> Flint, 1991	Colombia
<i>interrupta</i> Flint 1991	Colombia
<i>laposka</i> Oláh and Johanson, 2011	Peru
<i>lerma</i> Angrisano and Burgos, 2002	Argentina
<i>limpia</i> Ross, 1944	Mexico, U.S.A.
<i>melleopicta</i> Mosely, 1934	Mexico, Venezuela
<i>mutica</i> Flint, 1991	Colombia
<i>padera</i> Flint, 1991	Colombia
<i>pictipes</i> (Banks, 1911)	U.S.A., Mexico
<i>sarita</i> Ross, 1944	Costa Rica, El Salvador, Guatemala, Mexico, U.S.A.
<i>termitiformis</i> Botosaneanu, 1993	Trinidad
<i>tritoven</i> Flint, 1996	Tobago, Trinidad, Venezuela
<i>tubifex</i> Flint, 1964	Dominican Republic, Haiti, Jamaica, Puerto Rico
<i>viridis</i> Flint, 1967	El Salvador, Guatemala, Mexico, Panama
<i>yungarum</i> Angrisano and Burgos, 2002	Argentina

Table 2: Species groups of *Leucotrichia*.

<i>L. melleopicta</i> species group	<i>L. pictipes</i> species group	<i>Incertae sedis</i>
<i>L. ayura</i>	<i>L. fairchildi</i>	<i>L. alisensis</i>
<i>L. brochophora</i>	<i>L. imitator</i>	<i>L. botosaneanu</i>
<i>L. chiriquiensis</i>	<i>L. pictipes</i>	<i>L. brasiliana</i>
<i>L. dinamica</i>	<i>L. sarita</i>	<i>L. forrota</i>
<i>L. extraordinaria</i>		<i>L. laposka</i>
<i>L. gomezi</i>		<i>L. lerma</i>
<i>L. inflaticornis</i>		<i>L. mutica</i>
<i>L. inops</i>		<i>L. termitiformis</i>
<i>L. interrupta</i>		<i>L. tritoven</i>
<i>L. limpia</i>		<i>L. yungarum</i>
<i>L. melleopicta</i>		
<i>L. padera</i>		
<i>L. tubifex</i>		
<i>L. viridis</i>		

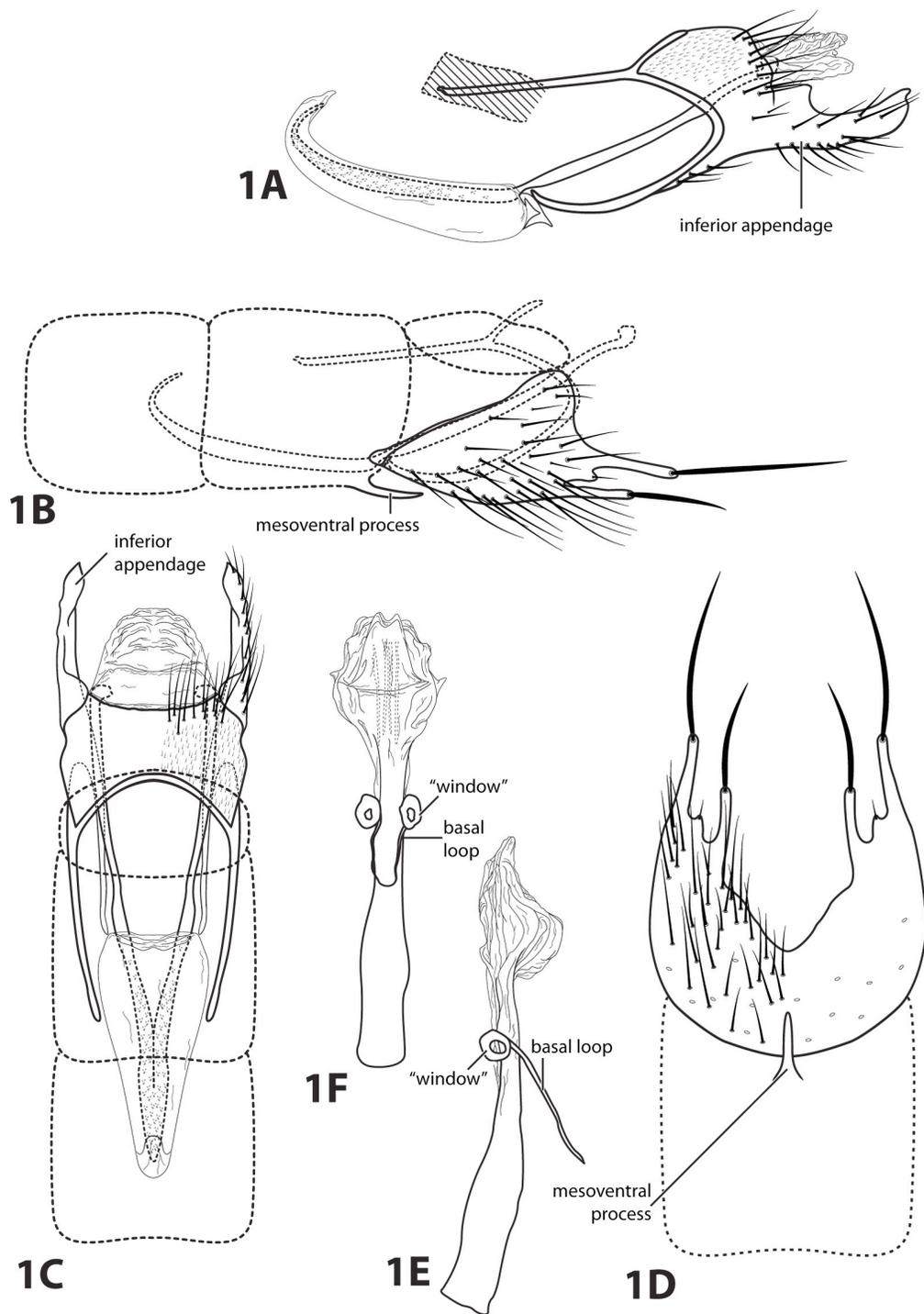


FIGURE 1. *Betrichia alibrachia*, new species (UMSP0000140290). Male genitalia: **A** segments IX-X, left lateral (base of phallus crosshatched) **B** segments VI-VIII and segment IX anterolateral margin, left lateral **C** segments VI-X, dorsal **D** segments VII-VII, ventral **E** phallus, left lateral **F** phallus, dorsal.

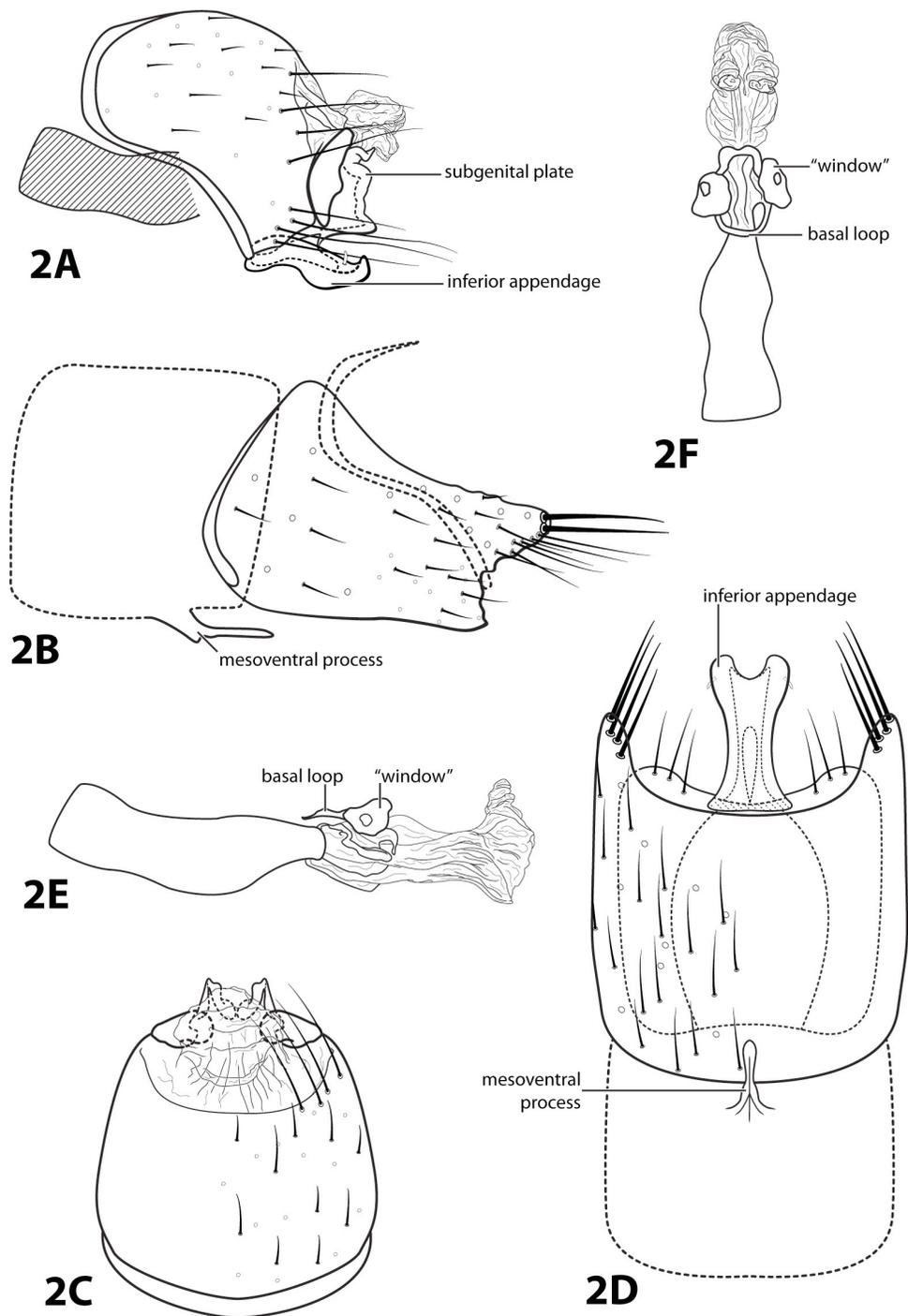


FIGURE 2. *Leucotrichia bicornuta*, new species (UMSP000014084). Male genitalia: **A** segments IX-X, left lateral (base of phallus crosshatched) **B** segments VII-VIII and segment IX anterolateral margin, left lateral **C** segments IX-X, dorsal **D** segments VII-IX, ventral **E** phallus, left lateral **F** phallus, dorsal.

COMPLETE BIBLIOGRAPHY, Chapters I-IV

- Agassiz, J. L. R. (1846) Nomenclatur zoologicus. *Index Universalis* 32.
- Angrisano, E. B. (1984 [1985]) Nuevas especies de Hydroptilidae Argentinos (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 43: 1-5.
- Angrisano, E. B. (1989) *Rhyacopsyche yatay*, una nueva especie de Hydroptilidae de la Argentina (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 46: 157-159.
- Angrisano, E. B. (1995a) Contribución al conocimiento de los Trichoptera del Uruguay. II. Familia Hydroptilidae. *Revista Brasileira de Entomologia* 39: 501-516.
- Angrisano, E. B. (1995b) Contribución para el conocimiento de las *Oxyethira* neotropicales (Trichoptera, Hydroptilidae). *Physis (Buenos Aires), Sección B* 50: 27-35.
- Angrisano, E. B. (2002) Contribution to the knowledge on Trichoptera of El Palmar National Park (Argentina). Description of the immature stages of *Bredinia* sp. and *Rhyacopsyche yatay* (Hydroptilidae). *Nova Supplementa Entomologica (Proceedings of the 10th International Symposium on Trichoptera)* 15:395-406.
- Angrisano, E. B. and Burgos, G. N. (2002) Contribución para el conocimiento do los Leucotrichiini (Trichoptera: Hydroptilidae). Tres especies nuevas de la Argentina. *Revista de la Sociedad Entomológica Argentina* 61:103-109.
- Angrisano, E. B. and Sganga, J. V. (2005) Contribution to the knowledge of the genus *Metrichia* Ross from Argentina (Trichoptera: Hydroptilidae: Ochrotrichiini). *Aquatic Insects* 27:113-123.
- Angrisano, E. B. and Sganga, J. V. (2009) New species of Hydroptilidae (Trichoptera) from Salto Encantado Provincial Park (Misiones province, Argentina). *Zootaxa* 2162: 57-68.
- Angrisano, E. B. and Sganga, J. V. (2010) Preimaginal stages of *Acostatrichia simulans* Mosely 1939, a Neotropical microcaddisfly (Trichoptera: Hydroptilidae: Leucotrichiinae). *Zootaxa* 2480: 54-60.
- Back, R. C. (1983) Larva and pupa of *Oxyethira leonensis* (Trichoptera: Hydroptilidae). *Florida Entomologist* 66: 389-392.
- Ball, S. L., Hebert, P. D. N., Burian, S. K. and Webb, J. M. (2005) Biological identifications of mayflies (Ephemeroptera) using DNA barcodes. *Journal of the North American Benthological Society* 24: 508-524.
- Banks, N. (1907) New Trichoptera and Psocidae. *Journal of the New York Entomological Society* 15: 162-166.
- Banks, N. (1911) Description of new species of North American neuropteroid insects. *Transactions of the American Entomological Society* 37: 335-360, plates 311-313.
- Barnard, K. H. (1934) South African caddis-flies (Trichoptera). *Transactions of the Royal Society of South Africa* 21: 291-394.
- Barnard, P. C. (1971) The larva of *Agraylea sexmaculata* Curtis (Trichoptera, Hydroptilidae). *Entomologist's Gazette* 22: 253-257.
- Blahnik, R. J., Holzenthal, R. W. and Prather, A. L. (2007) The lactic acid method for clearing Trichoptera genitalia. In: J. Bueno-Soria, R. Barba-Álvarez and B. J.

- Armitage (Eds), *Proceedings of the 12th International Symposium on Trichoptera*. The Caddis Press, Columbus, Ohio, pp. 9-14.
- Blickle, R. L. and Denning, D. G. (1977) New species and a new genus of Hydroptilidae (Trichoptera). *Journal of the Kansas Entomological Society* 50: 287-300.
- Botosaneanu, L. (1956) Recherches sur les Trichoptères de Bulgarie recueillis par MM. le Prof. A. Balkanov et B. Rusev (Trichoptera). *Beiträge zur Entomologie* 6: 354-402.
- Botosaneanu, L. (1981) On a false and a genuine caddis-fly from Burmese Amber (Insecta: Trichoptera, Homoptera). *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 8: 73-78.
- Botosaneanu, L. (1990) Results of a trichopterological (Insecta: Trichoptera) travel to the Lesser Antilles in 1989. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 60: 39-48.
- Botosaneanu, L. (1991) Amsterdam expedition to the West Indian Islands, report 71. Trichoptères d'Haïti. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 61: 113-134.
- Botosaneanu, L. (1992) *Fauna Palaestina. Insecta 6: Trichoptera of the Levant: imagines*. Jerusalem: The Israel Academy of Sciences and Humanities.
- Botosaneanu, L. (1994) A study of the larvae of caddisflies (Trichoptera) from Cuba. *Tropical Zoology* 7: 451-475.
- Botosaneanu, L. (1995) Caddis Flies (Trichoptera) from Turonian (Upper Cretaceous) amber of New Jersey. *American Museum Novitates* 3140: 1-7.
- Botosaneanu, L. (2000) Étude d'une faunule madicole de Guadeloupe: compléments à la connaissance des Trichoptères de l'Île. *Annales de Limnologie* 36: 249-259.
- Botosaneanu, L. and Alkins-Koo, M. (1993) The caddis flies (Insecta: Trichoptera) of Trinidad and Tobago, West Indies. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 63: 5-45.
- Botosaneanu, L. and Bolland, H. R. (1997) A mite (Acari: Erythraeidae) as unusual parasite on an adult caddisfly (Trichoptera: Hydroptilidae) from the Dominican Republic (West Indies). *Studies on the Natural History of the Caribbean Region* 73: 71-76.
- Botosaneanu, L. and Flint, O. S., Jr. (1982) On some Trichoptera from northern Venezuela and Ecuador (Insecta). *Beaufortia* 32: 13-26.
- Botosaneanu, L. and Giudicelli, J. (1981) Observations morphologiques, éthologiques et écologiques sur *Hydroptila hirra* Mosely (Trichoptera: Hydroptilidae). In: G. P. Morettii (Ed), *Proceedings of the 3rd International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 21-29.
- Botosaneanu, L., Johnson, R. O. and Dillon, P. R. (1998) New caddisflies (Insecta: Trichoptera) from Upper Cretaceous amber of New Jersey, U.S.A. *Polskie Pismo Entomologiczne* 67: 219-231.
- Botosaneanu, L. and Sakal, D. (1992) Ecological observations on the caddisflies (Insecta: Trichoptera) from Trinidad and Tobago (W. Indies). *Revue d'Hydrobiologie Tropicale* 25: 197-207.
- Botosaneanu, L. and Sykora, J. (1963) Nouvelle contribution à la connaissance des

- Trichoptères de Bulgarie. *Acta Fauna Entomologica Musei Nationalis Pragae* 9: 121-142.
- Bowles, D. E., Harris, S. C. and Bueno-Soria, J. (1999) An assessment of New World Stactobiini (Trichoptera: Hydroptilidae: Hydroptilinae) larvae with new larval descriptions of *Alisotrichia*, *Mejicanotrichia*, and *Scelobotrichia*. In: H. Malicky and P. Chantaramongkol (Eds), *Proceedings of the 9th International Symposium on Trichoptera*. Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, pp. 43-52.
- Bueno-Soria, J. (1983) Three new species of *Ochrotrichia* (Metrichia) from Chiapas, Mexico (Trichoptera: Hydroptilidae). *Proceedings of the Biological Society of Washington* 96: 79-83.
- Bueno-Soria, J. (1984 [1985]) Estudios en insectos acuaticos II. revision para México y Centroamerica del genero *Hydroptila* Dalman, 1819 (Trichoptera: Hydroptilidae). *Folia Entomologica Mexicana* 59: 79-138.
- Bueno-Soria, J. (1999) Studies in aquatic insects XV: new species of *Neotrichia* and first record of *Oxyethira hilosa* (Trichoptera: Hydroptilidae) from Mexico. *Entomological News* 110: 113-117.
- Bueno-Soria, J. (2002) The genus *Metrichia* Ross (Trichoptera: Hydroptilidae) from Mexico. *Transactions of the American Entomological Society* 128: 223-243.
- Bueno-Soria, J. (2009) A review of the genus *Ochrotrichia* Mosely (Trichoptera: Hydroptilidae) from Mexico and Central America. *Transactions of the American Entomological Society* 135: 59-160.
- Bueno-Soria, J. (2010) Some new Trichoptera (Glossosomatidae, Hydroptilidae, Hydropsychidae and Polycentropodidae) from Mexico. *Proceedings of the Entomological Society of Washington* 112: 22-31.
- Bueno-Soria, J. and Barba-Álvarez, R. (1999) Studies in aquatic insects XVI: two new species of the microcaddisfly genus *Mejicanotrichia* (Trichoptera: Hydroptilidae) from Mexico, with a key to the species in the genus. *Entomological News* 110: 118-122.
- Bueno-Soria, J. and Holzenthal, R. W. (2003) New species and records of the microcaddisfly genus *Metrichia* Ross from Costa Rica (Trichoptera: Hydroptilidae). *Studies on Neotropical Fauna and Environment* 38: 173-197.
- Bueno-Soria, J. and Santiago-Fragoso, S. (1992) Studies in aquatic insects, XI: seven new species of the genus *Ochrotrichia* (*Ochrotrichia*) from South America (Trichoptera: Hydroptilidae). *Proceedings of the Entomological Society of Washington* 94: 439-446.
- Bueno-Soria, J. and Santiago-Fragoso, S. (1997) Studies in aquatic insects XII: descriptions of nineteen new species of the genus *Ochrotrichia* Mosely (Trichoptera: Hydroptilidae) from Mexico and Central America. *Proceedings of the Entomological Society of Washington* 99: 359-373.
- Bueno-Soria, J., Santiago-Fragoso, S. and Barba-Alvarez, R. (2001) Studies in aquatic insects, XVIII: New species and new record of caddisflies (Trichoptera) from Mexico. *Entomological News* 112: 145-158.
- Carins, A. and Wells, A. (2008) Contrasting modes of handling moss for feeding and

- case-building by the caddisfly *Scelotrichia willcarinsi* (Insecta: Trichoptera). *Journal of Natural History* 42: 2609–2615. doi: 10.1080/00222930802354308
- Chambers, V. T. (1873) Micro-Lepidoptera. *Canadian Entomologist* 5:110-115, 124-128.
- Colwell, R. K. (2012) Biota 3: The Biodiversity Database Manager. Available from <http://viceroy.eeb.uconn.edu/Biota/biota>.
- Curtis, J. (1834) Description of some hitherto nondescript British species of mayflies of anglers. *The London and Edinburgh Philosophical Magazine and Journal of Science* 3: 120-125, 212-218.
- Dallwitz, M. J., Paine, T. A. and Zurcher, E. J. (1999 onwards) User's guide to the DELTA editor. Available from: <http://delta-intkey.com/>.
- Dalman, J. W. (1819) Nogra nya insecta-genera beskripta. *Vetenskaps-Akademiens Handlingar* 40: 117-127.
- Danecker, E. (1961) Studien zur hydropetrischen fauna. Biologie und Ökologie von *Stactobia* und *Tinodes* (Insecta, Trichoptera). *Internationale Revue der Gesamten Hydrobiologie* 46: 214-254.
- Denning, D. G. and Blicke, R. L. (1972) A review of the genus *Ochrotrichia* (Trichoptera: Hydroptilidae). *Annals of the Entomological Society of America* 65: 141-151.
- Eaton, A. E. (1873) On the Hydroptilidae, a family of the Trichoptera. *Transactions of the Entomological Society of London* 2: 125-149.
- Edwards, S. W. and Arnold, C. R. (1961) The caddis flies of the San Marcos river. *Texas Journal of Science* 13: 398-415.
- Enderlein, G. (1929) Entomologica Canaria 2. *Zoologischer Anzeiger* 84: 221-234.
- Fahy, E. (1971) The larva of *Hydroptila forcipata* (Eaton) (Trich., Hydroptilidae). *The Entomologist's Monthly Magazine* 107: 145-148.
- Felsenstein, J. (2004) *Inferring Phylogenies* (Second ed.). Sunderland, Massachusetts: Sinauer Associates.
- Fischer, F. C. J. (1961) *Philopotamidae, Hydroptilidae, Stenopsychidae. Trichopterorum Catalogus* 2. Amsterdam: Nederlandsche Entomologische Vereeniging.
- Fischer, F. C. J. (1971) *Supplement to Vol. I and II. Trichopterorum Catalogus* 12. Amsterdam: Nederlandsche Entomologische Vereeniging.
- Flint, O. S., Jr. (1962) The immature stages of *Palaeagapetus celsus* Ross (Trichoptera: Hydroptilidae). *Bulletin of the Brooklyn Entomological Society* 42: 40-44.
- Flint, O. S., Jr. (1964) The caddisflies (Trichoptera) of Puerto Rico. *University of Puerto Rico, Agricultural Experiment Station, Technical Paper* 40: 1-80.
- Flint, O. S., Jr. (1966) On the identity of *Clymene aegerfasciella* Chambers. *Proceedings of the Entomological Society of Washington* 68: 135.
- Flint, O. S., Jr. (1967a) Studies of Neotropical Caddisflies II, Trichoptera collected by Prof. J. Illies in the Chilean subregion. *Beiträge zur Neotropischen Fauna* 5:45-68.
- Flint, O. S., Jr. (1967b) Studies of Neotropical caddis flies, IV: new species from Mexico and Central America. *Proceedings of the United States National Museum* 123: 1-24.
- Flint, O. S., Jr. (1968a) Bredin-Archbold-Smithsonian Biological Survey of Dominica, 9.

- The Trichoptera (Caddisflies) of the Lesser Antilles. *Proceedings of the United States National Museum* 125: 1-86.
- Flint, O. S., Jr. (1968b) The Caddisflies of Jamaica. *Bulletin of the Institute of Jamaica, Science Series* 19: 1-68.
- Flint, O. S., Jr. (1968c) New species of Trichoptera from the Antilles. *Florida Entomologist* 51: 151-153.
- Flint, O. S., Jr. (1969) Studies of Neotropical caddis flies, IX: new genera and species from the Chilean subregion. *Proceedings of the Entomological Society of Washington* 71: 497-514.
- Flint, O. S., Jr. (1970) Studies of Neotropical caddisflies, X: *Leucotrichia* and related genera from North and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 60: 1- 64.
- Flint, O. S., Jr. (1971) Studies of Neotropical caddis flies, XI: the genus *Rhyacopsyche* in Central America (Hydroptilidae). *Proceedings of the Biological Society of Washington* 83: 515-526.
- Flint, O. S., Jr. (1972a) Studies of Neotropical caddisflies, XIII: the genus *Ochrotrichia* for Mexico and Central America (Trichoptera: Hydroptilidae). *Smithsonian Contributions to Zoology* 118: 1-28.
- Flint, O. S., Jr. (1972b) Studies of Neotropical caddisflies, XIV: on a collection from northern Argentina. *Proceedings of the Biological Society of Washington* 85: 223-248.
- Flint, O. S., Jr. (1974) The Trichoptera of Surinam. Studies of Neotropical caddisflies, XV. *Studies on the Fauna of Suriname and other Guyanas* 14: 1-151, plates 151-154.
- Flint, O. S., Jr. (1980) Studies on Neotropical caddisflies, XXVI: new species from Argentina (Trichoptera). *Revista de la Sociedad Entomológica Argentina* 39: 137-142.
- 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.
- Flint, O. S., Jr. (1982) Studies of Neotropical caddisflies, XXXI: five new species from Argentina (Trichoptera). *Entomological News* 93: 43-47.
- Flint, O. S., Jr. (1983) Studies of Neotropical caddisflies, XXXIII: new species from austral South America (Trichoptera). *Smithsonian Contributions to Zoology* 377: 1-100.
- 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.
- Flint, O. S., Jr. (1992) Studies of Neotropical caddisflies, XXXVIII: a review of the classification and biology of the Neotropical microcaddisflies, with the description of a new genus (Trichoptera: Hydroptilidae: Leucotrichiini). In: D. Quintero and A. Aiello (Eds), *Insects of Panama and Mesoamerica: Selected Studies*. Oxford University Press, Oxford, pp. 525-531.
- Flint, O. S., Jr. (1996) Studies of Neotropical caddisflies LV: Trichoptera of Trinidad

- and Tobago. *Transactions of the American Entomological Society* 122: 67-113.
- Flint, O. S., Jr. and Bueno-Soria, J. (1998) Studies of Neotropical caddisflies LVI: descriptions of five new species of the genus *Metrichia* Ross (Trichoptera: Hydroptilidae) from Pakitza, Peru, with a checklist and bibliography of the described species of the genus. *Proceedings of the Entomological Society of Washington* 100: 489-496.
- Flint, O. S., Jr. and Harris, S. C. (1991) Studies of Neotropical caddisflies, XLII: *Taraxatrichia amazonensis*, a new genus and species of microcaddisfly from Venezuela (Trichoptera: Hydroptilidae). In: C. Tomaszewski (Ed), *Proceedings of the 6th International Symposium on Trichoptera*. Adam Mickiewicz University Press, Poznan, Poland, pp. 411-414.
- Flint, O. S., Jr., Harris, S. C. and Botosaneanu, L. (1994) Studies of Neotropical caddisflies, L: the description of *Cerasmatrichia*, new genus, a relative of *Alisotrichia*, with the descriptions of new and old species and the larva (Trichoptera: Hydroptilidae). *Proceedings of the Biological Society of Washington* 107: 360-382.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999a) *Catalog of the Neotropical Caddisflies (Trichoptera)*. Columbus, Ohio: Special Publication, Ohio Biological Survey.
- Flint, O. S., Jr., Holzenthal, R. W. and Harris, S. C. (1999b) Nomenclatural and systematic changes in the Neotropical caddisflies. *Insecta Mundi*, 13, 73-84.
- Flint, O. S., Jr. and Sykora, J. L. (1993) New species and records of caddisflies (Insecta: Trichoptera) from the Lesser Antilles, with special reference to Grenada. *Annals of Carnegie Museum* 62: 47-62.
- Fox, G. E. and Woese, C. R. (1975) The architecture of 5S rRNA and its relation to function. *J. Mol. Evol.* 6: 61-76.
- Frania, H. E. and 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.
- Giudicelli, J. and Vaillant, F. (1967) La larve et la nymphe d'*Allotrichia pallicornis* Eaton (Trichoptera). *Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Université de Grenoble* 57-58: 29-36.
- González, M. A. and Malicky, H. (1980) Eine neue *Allotrichia* (Trichoptera: Hydroptilidae) von der Iberischen Halbinsel. *Entomologische Zeitschrift* 90: 214-216.
- Graf, W., Waringer, J. and Zika-Romer, J. (2004) The larva of *Microptila minutissima* Ris, 1897 (Trichoptera: Hydroptilidae). *Aquatic Insects* 26: 31-38.
- Gu, X., Fu, Y.-X. and Li, W.-H. (1995) Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Molecular Biology and Evolution* 12: 546-557.
- Guahyba, R. R. (1991) Estágios imaturos de *Anchitrichia duplifurcata* Flint, 1983 (Trichoptera, Hydroptilidae). *Revista Brasileira de Entomologia* 35: 121-125.
- Guinard, E. (1879) Metamorphose d'un genre nouveau de Phryganide (*Leiochton* Fagesii). *Académie des Sciences et Lettres de Montpellier, Mémoires de la*

- Section des Sciences* 9: 139-144.
- Gutell, R. R., Larsen, N. and Woese, C. R. (1994) Lessons from an evolving rRNA: 16S and 23S rRNA structures from a comparative perspective. *Microbiol. Rev.* 58: 10-26.
- Hagen, H. A. (1855) Versuch, die Phryganiden Pictet's zu bestimmen. *Stettiner Entomologische Zeitung* 16: 204-210.
- Hagen, H. A. (1887) Ueber *Plethus cursitans*. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 37: 643-645.
- Hanna, H. M. (1961) The larvae of *Hydroptilasparsa* Curtis (Trichoptera: Hydroptilidae). *Entomologist's Gazette* 12: 69-75.
- Harris, S. C. (1985) New Hydroptilidae (Trichoptera) from Alabama. *Journal of the Kansas Entomological Society* 58: 248-253.
- Harris, S. C. (1986) Hydroptilidae (Trichoptera) of Alabama with descriptions of three new species. *Journal of the Kansas Entomological Society*, 59, 609-619.
- Harris, S. C. (1989) New Trichoptera from Alabama. *Journal of the New York Entomological Society* 97: 309-316.
- Harris, S. C. (1990) New species of *Neotrichia* (Trichoptera: Hydroptilidae) from Central and South America. *Journal of the New York Entomological Society* 98: 246-260.
- Harris, S. C. and Armitage, B. J. (1997) New member of the Chilean genus *Nothotrichia* from North America (Trichoptera: Hydroptilidae). In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 123-128.
- Harris, S. C. and Bueno-Soria, J. (1993) *Scelobotrichia*, a new genus of microcaddisflies from Mexico (Trichoptera: Hydroptilidae). *Folia Entomológica Mexicana* 87: 73-83.
- Harris, S. C. and Davenport, L. J. (1999) New species of Hydroptilidae (Trichoptera) from the Amazon region of northeastern Peru. *Proceedings of the Entomological Society of Washington* 101: 26-38.
- Harris, S. C. and Flint, O. S., Jr. (1992) Studies of Neotropical caddisflies, XLVII; *Kumanskiella*, a new genus from Cuba and Puerto Rico. *Journal of the New York Entomological Society* 100: 581-593.
- Harris, S. C. and Flint, O. S., Jr. (1993) Studies of Neotropical caddisflies, XLVIII; the larva of *Celaenotrichiaedwardsi* Mosely, with an assessment of the genus (Trichoptera: Hydroptilidae). In: C. Otto (Ed), *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 101-106.
- Harris, S. C., Flint, O. S., Jr. and Holzenthal, R. W. (2002a) Review of the Neotropical genus *Flintiella* (Trichoptera: Hydroptilidae: Stactobiini). *Journal of the New York Entomological Society* 110: 65-90.
- Harris, S. C., Flint, O. S., Jr. and Holzenthal, R. W. (2002b) Two new genera of Hydroptilidae from the neotropics (Trichoptera: Hydroptilidae: Stactobiini). *Journal of the New York Entomological Society* 110: 49-64.
- Harris, S. C. and Holzenthal, R. W. (1990) Hydroptilidae (Trichoptera) from Costa Rica: the genus *Mayatrichia* Mosely. *Journal of the New York Entomological Society*

98: 453-460.

- Harris, S. C. and Holzenthal, R. W. (1993) Phylogeny of the species groups of *Alisotrichia*, *sensu lato*, with the description of a new species from Costa Rica (Trichoptera: Hydroptilidae). *In*: C. Otto (Ed), *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 155-160.
- Harris, S. C. and Holzenthal, R. W. (1994) Hydroptilidae (Trichoptera) of Costa Rica and the Neotropics: Systematics of the genus *Byrsopteryx* Flint (Stactobiini). *Journal of the New York Entomological Society* 102: 154-192.
- Harris, S. C. and Holzenthal, R. W. (1997) *Mejicanotrichia*, a new genus of microcaddisflies from Mexico and Guatemala (Trichoptera: Hydroptilidae). *In*: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 123-128.
- Harris, S. C. and Holzenthal, R. W. (1999) Hydroptilidae (Trichoptera) of Costa Rica: the genus *Hydroptila* Dalman. *Studies on Neotropical Fauna and Environment* 34: 16-51.
- Harris, S. C., Holzenthal, R. W. and Flint, O. S., Jr. (2002) Review of the Neotropical genus *Bredinia* (Trichoptera: Hydroptilidae: Stactobiini). *Annals of Carnegie Museum* 71: 13-45.
- Harris, S. C. and Huryn, A. D. (2000) New and rare microcaddisflies (Trichoptera: Hydroptilidae) from the eastern United States. *Entomological News* 111: 77-83.
- Harris, S. C. and Rasmussen, A. K. (2010) The *Neotrichia caxima* Group (Trichoptera: Hydroptilidae) in the southeastern United States. *Zootaxa* 2608: 25-44.
- Hebert, P. D. N., Cywinska, A., Ball, S. L. and deWaard, J. R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, Series B* 270: 313-321.
- Hebert, P. D. N., Penton, E. H., Burns, J. M., Janzen, D. H. and 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.
- Hickin, N. E. (1967) *Caddis larvae: larvae of the British Trichoptera*. London: Hutchinson.
- Holzenthal, R. W. and Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa* 511: 1-80.
- Holzenthal, R. W., Blahnik, R. J., Kjer, K. M. and Prather, A. P. (2007) An update on the phylogeny of caddisflies (Trichoptera). *In*: J. Bueno-Soria, R. Barba-Alvarez and B. Armitage (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. and Kjer, K. M. (2007) Order Trichoptera Kirby, 1813 (Insecta), caddisflies. *Zootaxa* 1668: 639-698.
- Holzenthal, R. W. and Harris, S. C. (1991) The larva of *Byrsopteryx mirifica* Flint, with an assessment of the phylogenetic placement of the genus within the Leuchotrichiini (Trichoptera: Hydroptilidae). *In*: C. Tomaszewski (Ed),

- Proceedings of the 6th International Symposium on Trichoptera*. Adam Mickiewicz University Press, Poznan, Poland, pp. 403-407.
- Holzenthall, R. W. and Harris, S. C. (1999) The genus *Costatrichia* Mosely in Costa Rica, with a review of the Neotropical species (Trichoptera: Hydroptilidae). *Proceedings of the Entomological Society of Washington* 101: 540-568.
- Holzenthall, R. W., Morse, J. C. and Kjer, K. M. (2011) Order Trichoptera Kirby, 1813. *In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa* 3148: 209-211.
- Hsu, L.-P. and Chen, C.-S. (2002) A new species of *Ugandatrichia* (Trichoptera: Hydroptilidae) from Taiwan. *Pan-Pacific Entomologist* 78: 74-79.
- Hudson, G. V. (1886) On the metamorphosis of the caddis fly. *Trans. N. Z. Inst.* 18: 213-214.
- Huelsenbeck, J. P. (2000) *MRBAYES: Bayesian inference of phylogeny*: Distributed by the author. Department of Biology, University of Rochester, New York.
- Huelsenbeck, J. P. and Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- Hynes, H. B. N. (1970) *The ecology of running waters*. Liverpool.
- Ito, T. (1998) The biology of the primitive, distinctly crenophilic caddisflies, Ptilocolepinae (Trichoptera, Hydroptilidae). A review. *In: L. Botosaneanu (Ed), Studies in Crenobiology - The Biology of Springs and Springbrooks*. Backhuys Publishers, Leiden, The Netherlands, pp. 85-94.
- Ito, T. and Kawamura, H. (1980) Morphology and biology of the immature stages of *Hydroptila itoi* Kobayashi (Trichoptera, Hydroptilidae). *Aquatic Insects* 2: 113-122.
- Ito, T. and Kawamura, H. (1984) Morphology and ecology of immature stages of *Oxyethira actua* Kobayashi (Trichoptera, Hydroptilidae). *Japanese Journal of Limnology* 45: 313-317.
- Ito, T. and Ohkawa, A. (2012) The genus *Ugandatrichia* Mosely (Trichoptera, Hydroptilidae) in Japan. *Zootaxa* 3394: 48-58.
- Ivanov, V. D. (1997) Rhyacophiloidea: a paraphyletic taxon. *In: R. W. Holzenthall and O. S. Flint, Jr. (Eds), Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 189-193.
- Ivanov, V. D. (2011) Caddisflies of Russia: Fauna and biodiversity. *Zoosymposia* 5: 171-209.
- Jacquemart, S. (1962) La larve d'*Orthotrichiaangustella* MacLachlan (Trichoptere, Hydroptilidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 38: 1-10.
- Jacquemart, S. (1963) Deux Trichoptères nouveaux d'Argentine. *In: C. Delamare and E. Rapaport (Eds), Biologie de l'Amerique Australe, vol. 2*. Centre National de la Recherche Scientifique, Paris, pp. 339-342.
- Jacquemart, S. (1965) Resultats de l'expedition Belge an Moyen-Orient (Premiere note). Sept Trichoptères nouveaux de Turquie et d'Iran. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 41: 1-19.
- Jacquemart, S. (1973) Description de deux trichoptères hydroptilides nouveaux et de

- l'imago de *Stactobia monnioti* Jacquemart (Ile de Rhodes). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 49: 1-16.
- Jacquemart, S. and Coineau, Y. (1962) Missions S. Jacquemart dans les Pyrenees Orientales (2me note). Les Hydropilides des Alberes. *Bulletin de l'Institut Royal des Sciences Naturalles de Belgique* 38: 1-81.
- Johanson, K. A. (1992) A catalog of the caddis flies of East Africa (Insecta, Trichoptera). *Steenstrupia* 18: 113-141.
- Johanson, K. A. and Malm, T. (2010) Testing the monophyly of Calocidae (Insecta: Trichoptera) based on multiple molecular data. *Molecular Phylogenetics and Evolution* 54: 535-541.
- Keiper, J. B. and Foote, B. A. (1999) Biology and immature stages of two species of Hydroptilidae Dalman (Trichoptera: Hydroptilidae) which consume *Cladophora* (Chlorophyta). *Proceedings of the Entomological Society of Washington* 101: 514-521.
- Keiper, J. B. and Harris, S. C. (2002) Biology and immature stages of *Ochrotrichia footei* (Trichoptera: Hydroptilidae), a new microcaddisfly from a torrential mountain stream. *Proceedings of the Entomological Society of Washington* 104: 291-299.
- Keiper, J. B. and Walton, W. E. (1999) Biology and morphology of *Oxyethira arizona* Ross (Trichoptera: Hydroptilidae). *Pan-Pacific Entomologist* 75: 212-200.
- Kelley, R. W. (1983) The micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae): morphology, biogeography, evolution and classification. In: *Department of Entomology*. Clemson University, Clemson, South Carolina, p. 431.
- Kelley, R. W. (1984) Phylogeny, morphology and classification of the micro-caddisfly genus *Oxyethira* Eaton (Trichoptera: Hydroptilidae). *Transactions of the American Entomological Society* 110: 435-463.
- Kelley, R. W. (1985) Revision of the micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae). Part II: subgenus *Oxyethira*. *Transactions of the American Entomological Society* 111: 223-253.
- Kelley, R. W. (1986) Revision of the micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae) Part III: subgenus *Holarctotrichia*. *Proceedings of the Entomological Society of Washington* 88: 777-785.
- Kelley, R. W. (1989) New species of micro-caddisflies (Trichoptera: Hydroptilidae) from New Caledonia, Vanuatu and Fiji. *Proceedings of the Entomological Society of Washington* 91: 190-202.
- Kelley, R. W. (1992) Phylogenetic relationships of micro-caddisfly genera (Hydroptilidae). *Bulletin of the North American Benthological Society* 9: 145 (Abstract).
- Kelsey, L. P. (1969) A revision of the Scenopinidae (Diptera) of the world. *Bulletin of the United States National Museum* 277: 1-336.
- Kimmins, D. E. (1950) The type-species of certain genera in the Trichoptera. *The Entomologist* 83: 58-60.
- Kimmins, D. E. (1951) Indian caddisflies IV. New genera and species of the family Hydroptilidae. *Annals and Magazine of Natural History* 4: 193-213.
- Kimmins, D. E. (1958) The British species of the genus *Oxyethira* (Trichoptera:

- Hydroptilidae). *Entomologist's Gazette* 9: 7-17.
- Kimmins, D. E. (1966) A revised check-list of the British Trichoptera. *Entomologist's Gazette* 17: 111-120.
- Kingsolver, J. M. and Ross, H. H. (1961) New species of Nearctic *Orthotrichia* (Hydroptilidae, Trichoptera). *Illinois State Academy of Science Transactions* 54: 28-33.
- Kjaerandsen, J. (1997) *Wlitrichia introvertica* new genus, new species, and *Cyclopsiella anderseni* new genus, new species, two new monobasic genera of microcaddisflies from Ghana (Trichoptera: Hydroptilidae: Hydroptilini). In: R. W. Holzenthal and O. S. Flint, Jr. (Eds), *Proceedings of the 8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, Ohio, pp. 227-237.
- Kjaerandsen, J. (2004) A revision of the Afrotropical genus *Dhatrichia* (Trichoptera, Hydroptilidae). *Zoologica Scripta* 33: 131-185.
- Kjaerandsen, J. and Andersen, T. (2002) A review of *Jabitrichia* Wells, 1990 (Trichoptera: Hydroptilidae), with the description of a new Afrotropical species. *Nova Supplementa Entomologica (Proceedings of the 10th International Symposium on Trichoptera)* 15: 133-144.
- Kjer, K. (1995) Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Mol. Phylogenet. Evol.* 4: 314-330.
- Kjer, K. M., Blahnik, R. J. and Holzenthal, R. W. (2001) Phylogeny of Trichoptera (Caddisflies): Characterization of signal and noise within multiple datasets. *Systematic Biology* 50: 781-816.
- Kjer, K. M., Blahnik, R. J. and Holzenthal, R. W. (2002) Phylogeny of caddisflies (Insecta, Trichoptera). *Zoologica Scripta* 31: 83-91.
- Klapálek, F. (1902) O morfologii krowoku a privesku pohlavnich u Trichopter. I. Rhyacophilidae, Philipotamidae, et Hydroptilidae. *Rozprawy Ceske Akademie ved a umeni, Praze* 9: 39 p.
- Kloet, G. S. and Hincks, W. D. (1944) Nomenclatorial notes on two generic names in the Trichoptera. *Entomologist, London* 77: 97.
- Koçak, A. Ö. and Kemal, M. (2012) A generic nomenclatural correction among microcaddisflies in the Orientalic region (Hydroptilidae, Trichoptera). *Centre for Entomological Studies Ankara Miscellaneous Papers* 158: 4-5.
- Kolenati, F. A. (1848) *Genera et species Trichopterorum. Pars prior. Heteropalpoidea*. Prague.
- Kristensen, N. P. (1997) Early evolution of the Lepidoptera + Trichoptera lineage: phylogeny and the ecological scenario. In: P. Grandcolas (Ed), *The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios*. Mémoires du Muséum national d'histoire naturelle, Éditions du Muséum, Paris, pp. 253-271.
- Laudee, P. (2008) Larval morphology and diagnosis of the giant microcaddisfly species, *Ugandatrichia* spp. (Hydroptilidae: Trichoptera) in Thailand. *Zootaxa* 1825: 29-39.
- Leader, J. P. (1968) Hairs of the Hydroptilidae (Trichoptera). *Tane, Journal of the*

- Auckland University Field Club* 16: 121-129.
- Leader, J. P. (1972) The New Zealand Hydroptilidae (Trichoptera). *Journal of Entomology (Series B)* 41: 191-200.
- Lepneva, S. G. (1932) Zum Studium der Trichopterenlarven in den Wasserbecken der Systeme des Dnipro und des Sud-Bugs. *Zh. bio-zool. Tsyklu Kyiv* 3: 71-115.
- Lepneva, S. G. (1953) *Trichoptera in Animal World of the USSR*.
- Lepneva, S. G. (1964) [Larvae and pupae of the suborder Annulipalpia. Trichoptera. II (1)]. *Zoologicheskogo Instituta Akademii Nauk SSSR (N.S.)* 88: 1-562.
- Lepneva, S. G. (1970) Fauna of the USSR, Trichoptera II (1). Larvae and pupae of the Annulipalpia. *Zoological Institute of the Academy of Science of the USSR, New Series* 88: 1-638.
- Lewis, P. O. (2001) Phylogenetic systematics turns over a new leaf. *TRENDS in Ecology and Evolution* 16: 30-37.
- Lloyd, J. T. (1915) Notes on *Ithytrichia confusa* Morton. *Canadian Entomologist* 47: 117-121.
- Luhman, J. C., Holzenthal, R. W. and Kjaerandsen, J. K. (1999) New host record of a ceraphronid (Hymenoptera) in Trichoptera pupae. *Journal of Hymenoptera Research* 8: 126.
- Macdonald, W. W. (1950) The larvae of *Mystacides azurea* L., *Cyrnus flavidus* McLachlan and *Oxyethira simplex* Ris (Trichoptera). *Proceedings of the Royal Entomological Society of London* 25: 19-28.
- Malicky, H. (1983) *Atlas of European Trichoptera. Series Entomologica 24*. Dordrecht: Dr W Junk.
- Malicky, H. (1988) Eine neue *Stactobia* (Trichoptera: Hydroptilidae) aus der Ost-Türkei. *Entomologische Zeitschrift* 98: 63-64.
- Malicky, H. (1998) Über einige *Hydroptila* - Arten aus der *occulta*-Gruppe (Trichoptera, Hydroptilidae). *Stapfia* 55: 395-397.
- Malicky, H. (1999) The net-spinning larvae of the Giant Microcaddisfly, *Ugandatrichia* spp. (Trichoptera, Hydroptilidae). In: H. Malicky and P. Chantaramongkol (Eds), *Proceedings of the 9th International Symposium on Trichoptera*. Faculty of Science, Chiang Mai University, Chiang Mai, Thailand, pp. 199-204.
- Malicky, H. (2001) Construction behavior for new pupal cases by case-making caddis larvae: reply to Wiggins. (Trichoptera: Integripalpia). *Braueria* 28: 9.
- Malicky, H. (2001) Notes on the taxonomy of *Rhadicoleptus*, *Ptilocolepus* and *Pseudoneureclipsis*. *Braueria* 28: 19-20.
- Malicky, H. (2005) Ein kommentiertes Verzeichnis der Köcherfliegen (Trichoptera) Europas und des Mediterrangebietes. *Linzer Biologische Beiträge* 37: 533-596.
- Malicky, H. (2006) Caddisflies from Bardia National Park, Nepal, with a preliminary survey of Nepalese species (Insecta, Trichoptera). *Entomofauna* 27: 241-263.
- Malicky, H. (2008) On the migrations of *Ptilocolepus* through the Trichoptera system. *Braueria* 35: 43-44.
- Malicky, H. (2009) Beiträge Kenntnis asiatischer Trichopteren [Contribution on the knowledge of Asian Trichoptera.]. *Braueria* 36: 11-58.
- Malicky, H. (2010) *Atlas of Southeast Asian Trichoptera*. Chiangmai: Chiangmai

University.

- Malicky, H. and Chantaramongkol, P. (2007) Beiträge zur Kenntnis asiatischer Hydroptilidae (Trichoptera). *Linzer Biologische Beiträge* 39: 1009-1099.
- Malicky, H., Ivanov, V. and Melnitsky, S. (2011) Descriptions of 27 new caddisflies (Insect, Trichoptera) from Lombok, Bali and Java (Indonesia), with comments on known ones. *Linzer Biologische Beiträge* 43.
- Malm, T., Johanson, K. A. and Wahlberg, N. (2013) The evolutionary history of Trichoptera (Insecta): A case of successful adaptation to life in freshwater. *Systematic Entomology* 38: 459-473.
- Marlier, G. (1978) Sur une collection de Trichoptères de l'Afrique occidentale. *Revue de Zoologie Africaine* 92: 283-302.
- 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. V. (1910) Les Trichoptères de la Sibérie et des régions adjacentes. II. La sous f. des Brachycentrinae, les fam. des Molannidae, Leptoceridae, Hydropsychidae, Philopotamidae, Polycentropidae, Psychomyidae, Rhacophilidae et des Hydroptilidae. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de Saint Pétersbourg* 15: 351-429.
- Martynov, A. V. (1913a) Contribution to the knowledge of the Trichopterous fauna of the Caucasus. (In Russian). *Travaux Laboratoire Zoologie Univ. Warsaw* 1913: 1-111.
- Martynov, A. V. (1913b) Contributions a la faune des Trichoptères du Caucase. II. Trichoptères de la province de batoum et des environs du Novyj Afon. *Horae Societatis Entomologicae Rossicae* 40: 30 p.
- Martynov, A. V. (1924) Rucheiniki (caddisflies [Trichoptera])[in Russian]. In: N. N. Bogdanova-Kat'kova (Ed), *Prakticheskaya entomologiya, Volume 5*, Leningrad, p. iv + 384.
- Martynov, A. V. (1934) Tableaux analytiques de la faune de l'U.R.S.S. Trichoptera Annulipalpia. I. *Opred. Faune SSSR* 13: 343.
- Martynov, A. V. (1935) On a collection of Trichoptera from the Indian Museum. Part I. Annulipalpia. *Records of the Indian Museum* 37: 93-209.
- Mathis, M. L. and Bowles, D. E. (1989) A new microcaddisfly genus (Trichoptera: Hydroptilidae) from the interior highlands of Arkansas, U.S.A. *Journal of the New York Entomological Society* 97: 187-191.
- McAuliffe, J. R. (1982) Behavior and life history of *Leucotrichia pictipes* (Banks) (Trichoptera: Hydroptilidae) with special emphasis on case reoccupancy. *Canadian Journal of Zoology* 60: 1557-1561.
- McLachlan, R. (1865) Trichoptera Britanica. A monograph of British species of caddisflies. *Transactions of the Entomological Society of London, Series 3* 5: 1-184.
- McLachlan, R. (1880) *A monographic revision and synopsis of the Trichoptera of the European fauna. Part 9, pp. 501-523 (with supplement, pp. xiii-lxxxiv), plates 52-59*. London: John van Voorst.
- Medvedev, G. S. (1998) Keys to the insects of the European part of the USSR. Volume IV. Part VI: Megaloptera, Raphidioptera, Neuroptera, Mecoptera and Trichoptera.

- In. Science Publishers, Inc, Enfield, pp. i-xvii, 1-302.
- Mey, W. (2003) Contribution to the knowledge of the caddisfly fauna of the Philippines, V (Insecta, Trichoptera). *Insecta Koreana* 20: 425-452.
- Mey, W. and Joost, W. (1990) *Rhyacopsychemutisi* n.sp. - A new microcaddisfly with an unusual larva from Colombia (Trichoptera, Hydroptilidae). *Studies on Neotropical Fauna and Environment* 25: 133-138.
- Miller, M. A., Pfeiffer, W. and Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010*, New Orleans, LA, pp. 1-8.
- Milne, M. J. and Milne, L. J. (1939) Evolutionary trends in caddis worm case construction. *Annals of the Entomological Society of America* 32: 533-542.
- Morse, J. C. (1974) New caddisflies (Trichoptera) from southern Africa. *Journal of the Kansas Entomological Society* 47: 328-344.
- Morse, J. C. (1997) Phylogeny of Trichoptera. *Annual Review of Entomology* 42: 427-450.
- Morse, J. C. (2006) Trichoptera World Checklist. Available from <http://entweb.clemson.edu/database/trichopt/index.htm> (accessed 7 February 2014).
- Morton, K. J. (1887) On the cases of *Oxyethira costalis* Curt. *The Entomologist's Monthly Magazine* 23: 201-202.
- Morton, K. J. (1888) The larva and case of *Ithytrichia lamellaris*, Eaton, with references to other species of Hydroptilidae. *The Entomologist's Monthly Magazine* 24: 171-175.
- Morton, K. J. (1904) Further notes on the Hydroptilidae belonging to the European fauna, with descriptions of new species. *Transactions of the Entomological Society of London* 1904: 323-328.
- Morton, K. J. (1905) North American Hydroptilidae. *Bulletin of the New York State Museum* 86: 63-75, plates 13-15.
- Morton, K. J. (1934) Habits of the larvae of Hydroptilidae (Trichoptera). *Journal of the Society for British Entomology* 1: 44-45.
- Mosely, M. E. (1924) New Zealand Hydroptilidae (order Trichoptera). *Transactions of the New Zealand Institute* 55: 670-673.
- Mosely, M. E. (1933) The genus *Stactobia*, McLach. (Trichoptera). *Stylops* 2: 162-165.
- 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.
- Mosely, M. E. (1939a) The Brazilian Hydroptilidae (Trichoptera). *Novitates Zoologicae*, 41: 217-239.
- Mosely, M. E. (1939b) *The British caddis flies (Trichoptera). A collector's handbook. With an introduction by N.D.Riley*. London: Geo. Routledge and Sons, Ltd.
- Mosely, M. E. (1939) Trichoptera. Ruwenzori Expedition 1934-35. *British Museum (Natural History)* 3: 1-40.

- Mosely, M. E. (1948) Trichoptera. Expedition to South-West Arabia 1937-8. *British Museum (Natural History)* 1: 67-86.
- Mosely, M. E. and Kimmins, D. E. (1953) *The Trichoptera of Australia and New Zealand*. London: British Museum (Natural History).
- Moulton, S. R., II, Harris, S. C. and Slusark, J. P. (1999) The microcaddisfly genus *Ithytrichia* Eaton (Trichoptera: Hydroptilidae) in North America. *Proceedings of the Entomological Society of Washington* 101: 233-241.
- Müller, F. (1879a) Notes on the cases of some South Brazilian Trichoptera. *Transactions of the Royal Entomological Society of London* 4: 131-144.
- Müller, F. (1879b) Über Phryganiden (letters to his brother). *Zoologischer Anzeiger* 2: 38-40, 180-182, 283-284, 404-407.
- Müller, F. (1880 [1878]) Sobre as casas construidas pelas larvas de insectos Trichopteros da Provincia de Santa Catharina. *Archivos do Museu Nacional, Rio de Janeiro* 3: 99-134, 209-214, plates 138-111.
- Müller, F. (1881) Über die von den Trichopterenlarven der provinz Santa Catharina verfertigten Gehäuse. *Zeitschrift für Wissenschaftliche Zoologie* 35: 47-87, plates 44-45.
- Müller, F. (1887) Eine deutsche *Lagenopsyche*. *Entomologische Nachrichten* 13: 337-340.
- Müller, F. (1921) Briefe un noch nicht veröffentlichte Abhandlungen aus dem nachlass 1854-1897. In: A. Möller (Ed), *Fritz Müller: Werke, Briefe und Leben*, 2. G. Fischer, Jena, pp. 383-642.
- Neboiss, A. (1963) The Trichoptera types of species described by J. Curtis. *Beiträge zur Entomologie* 13: 582-635.
- Neboiss, A. (1977) A taxonomic and zoogeographic study of Tasmanian caddis flies (Insecta: Trichoptera). *Memoirs of the National Museum of Victoria* 38: 1-208, plates 201-203.
- Nielsen, A. (1948) Postembryonic development and biology of the Hydroptilidae. A contribution to the phylogeny of the caddis flies and to the question of the origin of the case-building instinct. *Biologiske Skrifter* 5: 1-200.
- Noller, H. F., Hoffarth, V. and Zimniak, L. (1992) Unusual resistance of peptidyl transferase to protein extraction procedures. *Science* 256: 1416-1419.
- Nybom, O. (1948) Iter entomologicum et botanicum ad Insulas Madeiram et Azores anno 1938 a Richard Frey, Ragnar Stora et Carl Cedercreutz factum. No 14. The Trichoptera of the Atlantic islands. *Commentationes Biologicae, Helsinki* 8: 1-19.
- Nyman, T., Zinovjev, A. G., Vikberg, V. and Farrell, B. D. (2006) Molecular phylogeny of the sawfly subfamily Nematinae (Hymenoptera: Tenthredinidae). *Systematic Entomology* 31: 569-583.
- Oláh, J. (1989) Thirty-five new hydroptilid species from Vietnam (Trichoptera, Hydroptilidae). *Acta Zoologica Hungarica* 35: 255-293.
- Oláh, J. (2012) New species and records of Trichoptera from Batanta and Waigeo Islands (Indonesia, Raja Empat Archipelago, Papua (Irian Jaya)). *Braueria* 39.
- Oláh, J. and Johanson, K. A. (2008) Reasoning an appendicular and functional caddisfly genital terminology. *Braueria* 35: 29-40.

- Oláh, J. and Johanson, K. A. (2010) Description of 46 new Old World Hydroptilidae (Trichoptera). *Folia Entomologica Hungarica* 71: 1-91.
- Oláh, J. and Johanson, K. A. (2011) New Neotropical Hydroptilidae (Trichoptera). *Annales Historico-Naturales Musei Nationalis Hungarici* 103: 117-255.
- Oláh, J. and O. S. Flint, J. (2012) Description of new species in the Leucotrichiini tribe (Trichoptera: Hydroptilidae). *Annales Historico-Naturales Musei Nationalis Hungarici* 104: 1-83.
- Özdikmen, H. (2007) A nomenclatural act: Replacement names for two homonymous caddisfly generic names (Trichoptera). *Munis Entomology and Zoology* 2: 443-444.
- Özdikmen, H. (2008) A nomenclatural act for caddis flies (Trichoptera). *Munis Entomology and Zoology* 3: 614-616.
- Pace, N. R. (1997) A molecular view of microbial diversity and the biosphere. *Science* 276: 734-740.
- Parys, K. A. and Harris, S. C. (2013) Larva of *Nothotrichia shasta* Harris and Armitage (Trichoptera: Hydroptilidae) from California, USA, with its phylogenetic and taxonomic implications. *Zootaxa* 3620: 589-595.
- Pes, A. M. O. and Hamada, N. (2003) The occurrence of *Taraxitrichia* Flint and Harris, 1992 (Trichoptera: Hydroptilidae) in Brazil, with description of the final larval stage. *Zootaxa* 328: 1-7.
- Pes, A. M. O. and Hamada, N. (2004) *Ceratotrichia* Flint, 1992 (Trichoptera: Hydroptilidae) larval and pupal description and new genus records for Brazil. *Entomotropica* 19: 31-37.
- Pictet, F. J. (1834) *Recherches pour servir à l'histoire et l'anatomie des Phryganides*. Geneva: A. Cherbuliez.
- Resh, V. H. and Houp, R. E. (1986) Life history of the caddisfly *Dibusa angata* and its association with the red alga *Lemanea australis*. *Journal of the North American Benthological Society* 5: 28-40.
- Reuter (1890) [Title unknown]. *Revue ent. Franç.* 9: 291.
- Ris, F. (1894) Vier Schweizerische Hydroptiliden. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 9: 131-134.
- Ris, F. (1897) Neuropterologischer sammelbericht 1894-96. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 9: 415-442.
- Roldán-Perez, G. (1988) *Guia para el Estudio de los Macroinvertebrados Acuaticos del Departamento de Antioquia*. Antioquia, Colombia: Universidad de Antioquia.
- Ronquist, F., Huelsenbeck, J. P. and Mark, P. v. d. (2005) *MrBayes 3.1, Manual*: Florida State University.
- Ross, H. H. (1938) Lectotypes of North American caddisflies in the Museum of Comparative Zoology. *Psyche* 45: 1-61.
- Ross, H. H. (1939) New species of Trichoptera from the Appalachian region. *Proceedings of the Entomological Society of Washington* 41: 63-72.
- Ross, H. H. (1941a) Descriptions and records of North American Trichoptera. *Transactions of the American Entomological Society* 67: 35-126.
- Ross, H. H. (1941b) New species of Trichoptera from Canada and northern United States.

- Canadian Entomologist* 73: 15-19.
- Ross, H. H. (1944) The caddisflies or Trichoptera of Illinois. *Bulletin of the Illinois Natural History Survey* 23: 1-326.
- Ross, H. H. (1948) Notes and descriptions of Nearctic Hydroptilidae (Trichoptera). *Journal of the Washington Academy of Sciences* 38: 201-206.
- Ross, H. H. (1956) *Evolution and Classification of the Mountain Caddisflies*. Urbana: University of Illinois Press.
- Ross, H. H. (1967) The evolution and past dispersal of the Trichoptera. *Annual Review of Entomology* 12: 169-206.
- Rueda Martín, P. A. (2006) New record of the genus *Ithytrichia* (Trichoptera: Hydroptilidae) for South America, with descriptions of male, larva and pupa of a new species from northwestern Argentina. *Aquatic Insects* 28: 251-256.
- Rueda Martín, P. A. (2011) New Hydroptilidae and new records from north-western Argentina and Bolivia (Trichoptera: Hydroptilidae). *Aquatic Insects* 33: 1-11.
- Santos, A. P. M., Henriques-Oliveira, A. L. and Nessimian, J. L. (2009) New species and records of *Oxyethira* Eaton (Trichoptera: Hydroptilidae) from Amazonas State, Brazil. *Zootaxa* 2169: 35-44.
- Santos, A. P. M. and Nessimian, J. L. (2009) New species and records of *Neotrichia* (Trichoptera: Hydroptilidae) from Central Amazonia, Brazil. *Zoologia* 26: 758-768.
- Sattler, W. and Sykora, J. L. (1977) Über eine, besonders durch ihr Bauinstinkt, merkwürdige neotropische Köcherfliege - *Leucotrichia brasiliana* n. sp. *Amazonia* 6: 137-255.
- Schmid, F. (1949) Les Trichoptères de la collection Navás. *Eos-Revista Española Entomología* 25: 305-426.
- Schmid, F. (1958a) Contribution à l'étude des Trichoptères néotropicaux III. *Mitteilungen aus dem Zoologischen Museum in Berlin* 34: 183-217.
- Schmid, F. (1958b) Trichoptères de Ceylan. *Archiv für Hydrobiologie* 54: 1-173.
- Schmid, F. (1959a) Le genre *Stactobia* Mch. *Miscelanea Zoologica, Barcelona* 1: 1-56.
- Schmid, F. (1959b) Trichoptères d'Iran (Trichoptera). *Beiträge zur Entomologie* 9: 199-219; 199 (193-194): 376-412; 199 (195-196): 682-698; 199 (197-198): 760-799.
- Schmid, F. (1960) Trichopteres du Pakistan. III (Hydroptilidae, Philopotamidae, Polycentropodidae). *Tijdschrift voor Entomologie* 103: 83-109.
- 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.
- Schneider, W. G. (1845) Verzeichnis der von Herrn Oberlehrer Zeller in Jahre 1844 in Sicilien und Italien gesammelten Neuropteren mit beschreibung einiger neuen arten. *Stettiner Entomologische Zeitung* 6: 338-346.
- Scott, K. M. F. (1976) The larval and pupal stages of *Ugandatrichia* Mosely (Trichoptera: Hydroptilidae) from Rhodesia, with the description of a new species. *Annals of the Cape Provincial Museums (Natural History)* 11: 117-127.
- Scudder, G. G. E. (1971) Comparative morphology of insect genitalia. *A. Rev. Ent.* 16: 379-406.

- Sibley, C. K. (1926a) A preliminary biological survey of the Lloyd-Cornell Reservation: studies on Trichoptera. *Bull. Lloyd Libr.* 27: 102-108, 185-247.
- Sibley, C. K. (1926b) Studies on Trichoptera. *Bulletin of the Lloyd Library* 27: 186-221.
- Siltala (Silfvenius), A. J. (1908) Zur Trichopteren-Fauna der Nördlichen Fenno-Skandia. *Acta Societatis pro Fauna et Flora Fennica* 31: 19 p.
- Simon, C., Buckley, T. R., Frati, F., Stewart, J. B. and Beckenbach, A. (2006) Incorporating molecular evolution into phylogenetic 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.
- Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. and 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.
- Smit, S., Widmann, J. and Knight, R. (2007) Evolutionary rates vary among rRNA structural elements. *Nucleic Acids Research* 35: 3339-3354.
- Solem, J. O. (1972) The larvae of *Agraylea cognatella* McLachlan (Trichoptera, Hydroptilidae). *Norsk Entomologisk Tidsskrift* 19: 77-79.
- Stamatakis, A., Hoover, P. and Rougemont, J. (2008) A Rapid Bootstrap Algorithm for the RAxML Web Servers. *Systematic Biology* 75: 758-771.
- Stephens, J. F. (1836) *Illustrations of British Entomology; or a Synopsis of Indigenous Insects: Containing their Generic and Specific Distinctions; with an Account of their Metamorphoses, Times of Appearance, Localities, Food, and Economy, as far as Practicable. Mandibulata. Vol. VI. [Trichoptera, pages 146-208]*. London: Baldwin and Cradock.
- Syhora, J. L. (1967) Trichoptera collected by prof. J. Illies in New Guinea and New Caledonia. *Pacific Insects* 9: 585-595.
- Thienemann, A. (1904) *Ptilocolepus granulatus* Pict., eine Uebergangsform von den Rhyacophiliden zu den Hydroptiliden. *Allgemeine Zeitschrift für Entomologie* 9: 418-424, 437-441.
- Thienemann, A. (1905) Trichopterenstudien I-III. *Zeitschrift für Wissenschaftliche Insektenbiologie* 1: 285-291.
- Thomson, R. (2012) Descriptions of new species of Leucotrichiinae (Trichoptera: Hydroptilidae) from Brazil. *Psyche* 2012: 1-7.
- Thomson, R. and Holzenthal, R. W. (2012) New species and records of Hydroptilidae (Trichoptera) from Venezuela. *ZooKeys* 185: 19-39.
- Tobias, W. (1999) Köcherfliegen-Neufunde vom unteren Main in Hessen (Trichoptera). *Entomologische Zeitschrift* 109: 49-55.
- Ulmer, G. (1907) Trichoptera, in Wytzman, P. (Ed.). *Genera Insectorum* 60: 1-259.
- Ulmer, G. (1912a) *Die Trichopteren des Baltischen Bernsteins. Beiträge zur Naturkunde Preussens, 10*. Leipzig: Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg.
- Ulmer, G. (1912b) Trichoptera aus Äquatorial-Afrika. *Wiss. Ergebn. Deutsche Zentralafrika Exped.* 4: 81-125.

- Ulmer, G. (1951) Köcherfliegen (Trichopteren) von den Sunda-Inseln. Teil I. *Archiv für Hydrobiologie, Supplement* 19: 1-528.
- Ulmer, G. (1957) Köcherfliegen (Trichopteren) von den Sunda-Inseln. Teil III. Larven und Puppen der Annulipalpia. *Archiv für Hydrobiologie, Supplement* 23: 109-470.
- Vaillant, F. (1956) Recherches sur la fauna madicole de France, de Corse et d'Afrique du Nord. *Mèm. Mus. natn. Hist. nat. Paris (A)* 11: 1-258.
- Vaillant, F. (1984) The hydroptilid larvae living on dripping rocks. In: J. C. Morse (Ed), *Proceedings of the 4th International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 407-412.
- Wallengren, H. D. J. (1891) Skandinavians Neuroptera. Andra afdelningen. *Svenska Akademien Handlingar* 24: 1-173.
- Waringer, J. and Graf, W. (1997) *Atlas der Österreichischen Köcherfliegenlarven, unter Einschluss der angrenzenden Gebiete [Atlas of Austrian caddisfly larvae, with inclusion of adjacent areas.]*. Vienna: Facultas Universitätsverlag.
- Wasmund, A. M. and Holzenthal, R. W. (2007) A revision of the Neotropical caddisfly genus *Rhyacopsyche*, with the description of 13 new species (Trichoptera: Hydroptilidae). *Zootaxa* 1634: 1-59.
- Weaver, J. S., III (1984) The evolution and classification of Trichoptera. Part I: the groundplan of Trichoptera. In: J. C. Morse (Ed), *Proceedings of the 4th International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 413-419.
- Weaver, J. S., III and Morse, J. C. (1986) Evolution of feeding and case-making behavior in Trichoptera. *Journal of the North American Benthological Society* 5: 150-158.
- Wells, A. (1978) A review of the Australian genera *Xuthotrichia* Mosely and *Hellyethira* Neboiss (Trichoptera: Hydroptilidae), with descriptions of new species. *Australian Journal of Zoology* 27: 311-329.
- Wells, A. (1979) The Australian species of *Orthotrichia* Eaton (Trichoptera: Hydroptilidae). *Australian Journal of Zoology* 27: 585-622.
- Wells, A. (1980) A review of the Australian genera *Orphnino-trichia* Mosely and *Maydenoptila* Neboiss (Trichoptera: Hydroptilidae), with descriptions of new species. *Australian Journal of Zoology* 28: 627-645.
- Wells, A. (1981) The genera *Oxyethira* Eaton, *Gnathotrichia* Ulmer and *Stenoxyethira* Kimmins (Trichoptera: Hydroptilidae) in Australia. *Australian Journal of Zoology* 29: 103-118.
- Wells, A. (1982) *Tricholeiochiton* Kloet and Hincks and new genera in the Australian Hydroptilidae (Trichoptera). *Australian Journal of Zoology* 30: 251-270.
- Wells, A. (1985) Larvae and pupae of Australian Hydroptilidae (Trichoptera), with observations on general biology and relationships. *Australian Journal of Zoology, Supplementary Series* 113: 1-69.
- Wells, A. (1987) On the biogeography of the *Oxyethira* group, tribe Hydroptilini (Hydroptilinae, Hydroptilidae, Trichoptera). In: M. Bournaud and H. Tachet (Eds), *Proceedings of the 5th International Symposium on Trichoptera*. Dr. W. Junk, Dordrecht, The Netherlands, pp. 133-138.
- Wells, A. (1990a) The hydroptilid tribe Stactobiini (Trichoptera: Hydroptilidae) in New Guinea. *Invertebrate Taxonomy* 3: 817-849.

- Wells, A. (1990b) The micro-caddisflies (Trichoptera: Hydroptilidae) of North Sulawesi. *Invertebrate Taxonomy* 3: 363-406.
- Wells, A. (1990c) New species and a new genus of micro-caddisfly from northern Australia, including the first Australian record of the tribe Stactobiini (Trichoptera: Hydroptilidae). *Transactions of the Royal Society of South Australia* 114: 107-128.
- Wells, A. (1991) The hydroptilid tribes Hydroptilini and Orthotrichini in New Guinea (Trichoptera: Hydroptilidae: Hydroptilinae). *Invertebrate Taxonomy* 5: 487-526.
- Wells, A. (1992) The first parasitic Trichoptera. *Ecological Entomology* 17: 299-302.
- Wells, A. (1993) Micro-caddisflies (Trichoptera: Hydroptilidae) from Bali, Indonesia. *Zoologische Mededelingen (Leiden)* 67: 351-359.
- Wells, A. (1995) New Caledonian Hydroptilidae (Trichoptera), with new records, descriptions of larvae and a new species. *Aquatic Insects* 17: 223-239.
- Wells, A. (1997) A preliminary guide to the identification of larval Hydroptilidae (Insecta: Trichoptera). *Co-operative Research Centre for Freshwater Ecology Identification Guide* 13: 1-28.
- Wells, A. (1998) Two new species of Hydroptilidae (Trichoptera) from Tasmania's World Heritage Area. *Australian Entomologist* 25: 81-84.
- Wells, A. (1999) The micro-caddisflies of Lord Howe Island (Hydroptilidae: Trichoptera: Insecta). *Aquatic Insects* 21: 221-230.
- Wells, A. (2002) Three new species of *Orphnino-trichia* Mosely (Trichoptera: Hydroptilidae) from Barrington Tops, New South Wales, a distribution extended, and remarks on generic placement. *Australian Journal of Entomology* 41: 221-225.
- Wells, A. (2005) Parasitism by hydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. *Australian Journal of Entomology* 44: 385-391.
- Wells, A. (2010) Five new species and new records of Hydroptilidae (Trichoptera) from the Wet Tropics of northeastern Queensland. *Zootaxa* 2641: 47-54.
- Wells, A. (2010) Thirty years of hydroptilid studies - 1979 to 2009. *Denisia* 29: 437-443.
- Wells, A. (2012) New synonyms in the Australian micro-caddisfly fauna (Trichoptera: Hydroptilidae). *Zootaxa* 3177.
- Wells, A. and Andersen, T. (1995) Tanzanian micro-caddisflies (Trichoptera: Hydroptilidae). *Tijdschrift voor Entomologie* 138: 143-167.
- Wells, A. and Huisman, J. (1992) Micro-caddisflies in the tribe Hydroptilini (Trichoptera: Hydroptilidae: Hydroptilinae) from Malaysia and Brunei. *Zoologische Mededelingen (Leiden)* 66: 91-126.
- Wells, A. and Huisman, J. (2001) New hydroptilid caddisfly species from southern Sulawesi (Insecta: Trichoptera: Hydroptilidae). *Zoologische Mededelingen (Leiden)* 75: 207-216.
- Wells, A. and Johanson, K. A. (2012) Review of the New Caledonian species of *Paroxyethira* Mosely, 1924 (Trichoptera: Hydroptilidae). *Zootaxa* 3478: 330-344.
- Wells, A. and Malicky, H. (1997) The micro-caddisflies of Sumatra and Java (Trichoptera: Hydroptilidae). *Linzer Biologische Beiträge* 29: 173-202.

- Wells, A. and Wichard, W. (1989) Caddisflies of Dominican amber VI. Hydroptilidae (Trichoptera). *Studies on Neotropical Fauna and Environment* 24: 41-51.
- Westwood, J. O. (1838) Description of a new genus of exotic bees. *Transaction of the Entomological Society of London* 2: 112-113.
- Westwood, J. O. (1840) *An Introduction to the Modern Classification of Insects Founded on Natural Habits and Corresponding Organisation of the Different Families*. London: Longman, Orme, Brown, Green, and Longmans.
- Wichard, W. (1976) Morphologische Komponenten bei der Osmoregulation von Trichopterenlarven. In: H. Malicky (Ed), *Proceedings of the 1st International Symposium on Trichoptera*. Dr. W. Junk, The Hague, pp. 171-177.
- Wiggins, G. B. (1977) *Larvae of the North American caddisfly genera (Trichoptera)*. Toronto: University of Toronto Press.
- Wiggins, G. B. (1996) *Larvae of the North American Caddisfly Genera (Trichoptera)* (2nd ed.). Toronto: University of Toronto Press.
- Wiggins, G. B. (2004) *Caddisflies: the underwater architects*. Toronto: University of Toronto Press.
- Wiggins, G. B. and Wichard, W. (1989) Phylogeny of pupation in Trichoptera, with proposals on the origin and higher classification of the order. *Journal of the North American Benthological Society* 8: 260-276.
- Yang, Z. (1993) Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates differ over sites. *Molecular Biology and Evolution* 10: 1396-1401.
- Yang, Z. (1994a) Estimating the pattern of nucleotide substitution. *Journal of Molecular Evolution* 39: 105-111.
- Yang, Z. (1994b) Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Systematic Biology* 44: 384-399.
- Zhou, X., Kjer, K. M. and 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.