Order Trichoptera Kirby, 1813 (Insecta), Caddisflies*

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Abstract

The taxonomy, diversity, and distribution of the aquatic insect order Trichoptera, caddisflies, are reviewed. The order is among the most important and diverse of all aquatic taxa. Larvae are vital participants in aquatic food webs and their presence and relative abundance are used in the biological assessment and monitoring of water quality. The species described by Linnaeus are listed. The morphology of all life history stages (adults, larvae, and pupae) is diagnosed and major features of the anatomy are illustrated. Major components of life history and biology are summarized. A discussion of phylogenetic studies within the order is presented, including higher classification of the suborders and superfamilies, based on recent literature. Synopses of each of 45 families are presented, including the taxonomic history of the family, a list of all known genera in each family, their general distribution and relative species diversity, and a short overview of family-level biological features. The order contains 600 genera, and approximately 13,000 species.

Key words: Trichoptera, caddisflies, morphology, taxonomy, phylogeny, distribution, diversity, Linnaeus

Introduction

Phryganea. *Os edentulum: Palpis IV. Antennae thorace longiores. Alae incumbentes: inferioribus plicatis.* [Phryganea. Mouth without teeth: Palps IV. Antennae longer than thorax. Wings reclined: inferior wings folded.]
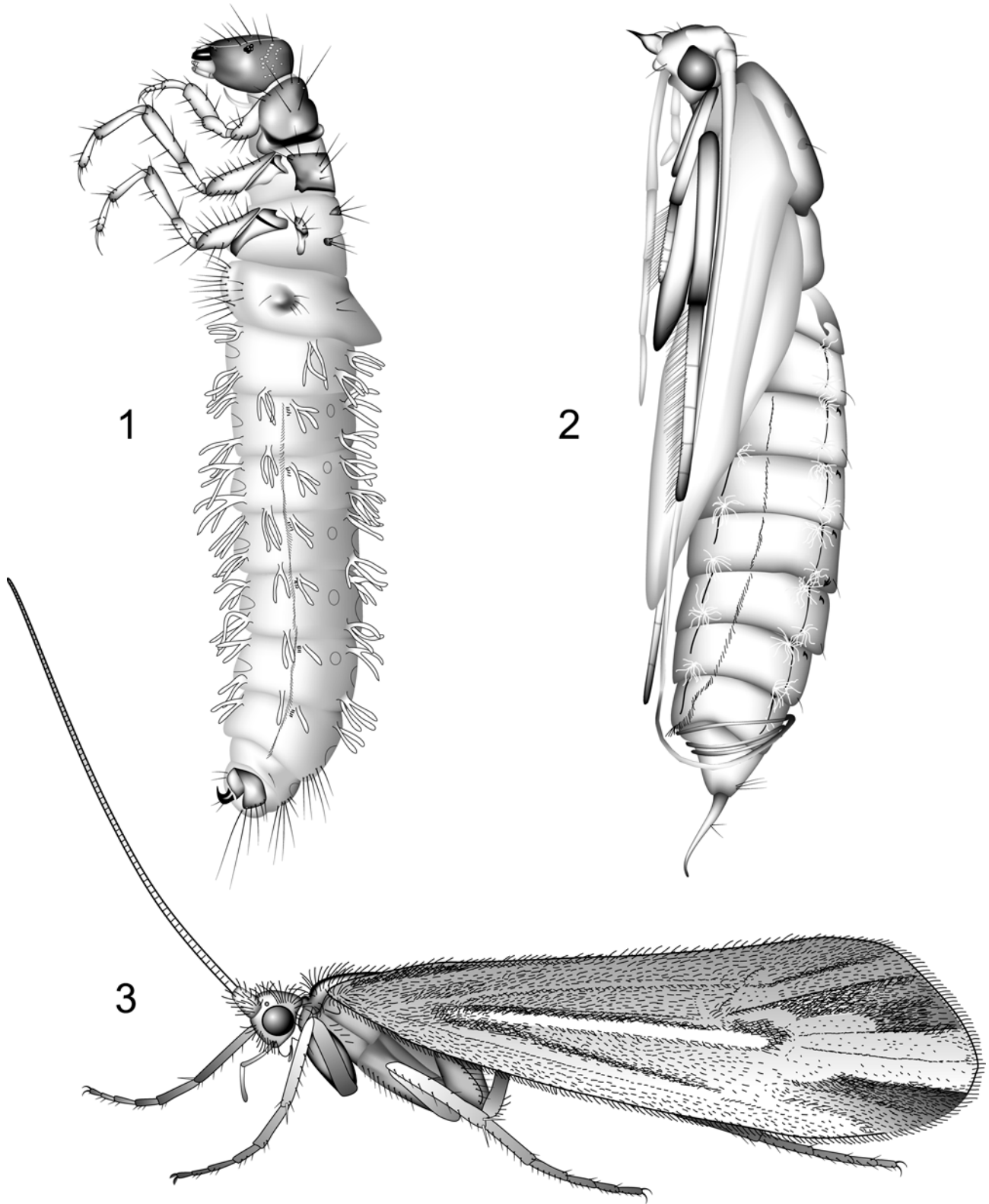
FIGURES 1–3. Trichoptera life history stages. 1–larva, *Halesochila taylori* (Limnephilidae); 2–pupa, *Ceraclea* sp. (Leptoceridae); 3–adult, *Hesperophylax designatus* (Limnephilidae).

In the 10th edition of *Systema Naturae*, Linnaeus (1758) described 18 "Insecta Neuroptera" within the genus *Phryganea*. All but 4 of these, along with 7 species subsequently described by him (Linnaeus 1761, 1767), are now included in the insect order Trichoptera (Figs. 1–3) (Table 1). The name of the order was first established by Kirby (1813) in a footnote of a paper describing the insect order Strepsiptera. Kirby noted, "If these

remarks appear to entomologists well founded, and it be thought right to consider *Phryganea* as constituting a new order, I think it might be distinguished, since the wings of all the known species are hairy, by the name of *Trichoptera*." Other names used for the order during the early 19th century included Lophiacera Billberg, Plicipennes Latreille, and variations of Phryganea, such as Phryganides Latreille and Phryganina Newman (see Fischer 1960 for other early names). Since Linnaeus's original description, the order has grown to include about 13,000 extant species described from all faunal regions, making it the 7th largest insect order. The order is divided into 45 families containing about 600 genera (Table 2). It currently follows Orthoptera, the grasshoppers, crickets, and their relatives, in known species diversity, but the caddisfly fauna generally is much less well known. Recent inventories in Brazil, China, Thailand, Ghana, and New Caledonia, for example, have documented faunas where up to 75% of the collected species are undescribed. Much of this newly discovered diversity occurs in the world's biodiversity "hotspots" (Myers et al. 2000), making continued collection and description of the fauna a priority.

TABLE 1. Current status of the "Trichoptera" described by Linnaeus.

Systema Naturae, 10th ed., 1758

Phryganea phalaenoides	=	*Semblis phalaenoides* (L.) (Phryganeidae)
Phryganea striata	=	*Oligotrichia striata* (L.) (Phryganeidae)
Phryganea grisea	=	*Limnephilus griseus* (L.) (Limnephilidae)
Phryganea grandis	=	*Phryganea grandis* L. (Phryganeidae)
Phryganea rhombica	=	*Limnephilus rhombicus* (L.) (Limnephilidae)
Phryganea bimaculata	=	*Neureclipsis bimaculata* (L.) (Polycentropodidae)
Phryganea flavilatera	=	*Sialis flavilatera* (L.) (Megaloptera: Sialidae) *
Phryganea bicaudata	=	*Diura bicaudata* (L.) (Plecoptera: Perlodidae) *
Phryganea nigra	=	*Mystacides nigra* (L.) (Leptoceridae)
Phryganea longicornis	=	*Mystacides longicornis* (L.) (Leptoceridae)
Phryganea filosa	=	according to Fischer (1966) a synonym of *Oecetis ochracea* (Curtis, 1825) (Leptoceridae)
Phryganea waeneri	=	*Tinodes waeneri* (L.) (Psychomyiidae)
Phryganea albifrons	=	*Athripsodes albifrons* (L.) (Leptoceridae)
Phryganea bilineata	=	*Athripsodes bilineatus* (L.) (Leptoceridae)
Phryganea nebulosa	=	*Taeniopteryx nebulosa* (L.) (Plecoptera: Taeniopterygidae) *
Phryganea fusca	=	*Leuctra fusca* (L.) (Plecoptera: Leuctridae) *
Phryganea flava	=	according to Fischer (1968) a synonym of *Limnephilus centralis* Curtis, 1834 (Limnephilidae)

Fauna Suecica, 2nd ed., 1761

Tinea robertella	=	*Ceraclea robertella* (L.) (Leptoceridae)
Phryganea reticulata	=	*Oligostomis reticulata* (L.) (Phryganeidae)
Phryganea azurea	=	*Mystacides azureus* (L.) (Leptoceridae)
Phryganea ciliaris	=	*Notidobia ciliaris* (L.) (Sericostomatidae)
Phryganea umbrosa	=	according to Fischer (1962) a synonym of *Polycentropus flavomaculatus* (Pictet, 1834) (Polycentropodidae)
Phryganea minuta	=	*Beraeodes minutus* (L.) (Beraeidae)
Phryganea saltatrix	=	*Meromyza saltatrix* (L.) (Diptera: Chloropidae) *

Systema Naturae, 12th ed., 1767

Phryganea marginata	=	*Chimarra marginata* (L.) (Philopotamidae)

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* = not Trichoptera

TABLE 2. Classification of Trichoptera. Adapted from Holzenthal et al. (2007) and Kjer et al. (2001, 2002). See Morse (2006) and Wiggins (2004) for slightly different interpretations. (Afr=Afrotropical, Au=Australasian, Hol=Holarctic, Na=Nearctic, Neo=Neotropical, Or=Oriental, Pa=Palearctic). Species numbers from Morse (2006) and *Zoological Record*.

	Approximate number of species	Distribution
ANNULIPALPIA		
Dipseudopsidae	170	Afr, Au, Hol, Or
Ecnomidae	360	Cosmopolitan
Hydropsychidae	1500	Cosmopolitan
Philopotamidae	1000	Cosmopolitan
Polycentropodidae	650	Cosmopolitan
Psychomyiidae	420	Afr, Au, Hol, Or
Stenopsychidae	90	Afr, Au, Pa (east Asia), Neo, Or
Xiphocentronidae	140	Afr, Hol, Neo, Or
"SPICIPALPIA"		
Glossosomatidae	650	Cosmopolitan
Hydrobiosidae	400	Au, Na (sw USA), Neo, Or, Pa (east Asia)
Hydroptilidae	2000	Cosmopolitan
Rhyacophilidae	700	Hol, Or
INTEGRIPALPIA		
PLENITENTORIA		
Apataniidae	200	Hol, Or
Brachycentridae	110	Hol, Or
Goeridae	170	Afr, Au, Hol, Or
Kokiriidae	10	Au, Neo
Lepidostomatidae	410	Cosmopolitan
Limnephilidae	900	Au, Hol, Neo, Or
Oeconesidae	20	Au
Phryganeidae	80	Hol, Or
Phryganopsychidae	< 10	Pa (east Asia), Or
Pisuliidae	< 20	Afr
Plectrotarsidae	5	Au
Rossianidae	2	Na
Uenoidae	80	Hol, Or
BREVITENTORIA		
"Leptoceroidea"		
Atriplectididae	4	Afr (Seychelles), Au, Neo
Calamoceratidae	175	Cosmopolitan
Leptoceridae	1800	Cosmopolitan
Limnocentropodidae	15	Pa (east Asia), Or
Molannidae	40	Hol, Or
Odontoceridae	115	Au, Hol, Neo, Or
Philorheithridae	25	Au, Neo
Tasimiidae	10	Au, Neo
Sericostomatoidea		
Anomalopsychidae	25	Neo
Antipodoeciidae	1	Au
Barbarochthonidae	1	Afr (s Africa)
Beraeidae	50	Afr, Hol
Calocidae	20	Au
Chathamiidae	5	Au
Conoesucidae	40	Au
Helicophidae	35	Au, Neo
Helicopsychidae	250	Cosmopolitan
Hydrosalpingidae	1	Afr (s Africa)
Petrothrincidae	15	Afr (s Africa, Madagascar)
Sericostomatidae	100	Afr, Hol, Neo, Or

Among the orders of primary aquatic insects (dragonflies, mayflies, stoneflies, dobsonflies), Trichoptera is the largest and ranks in diversity with aquatic nematoceran Diptera, many of which are actually found in saturated soil and peripheral aquatic habitats. There are about 1000 more caddisfly species than the other primary aquatic orders combined. When comparing caddisfly diversity to other orders with aquatic representatives, there are less than half as many aquatic beetles (about 5000 species), only 2000 aquatic bugs, and few aquatic moths, wasps, lacewings, or scorpionflies (Grimaldi & Engel 2005). Recent reviews of Trichoptera, including biology and phylogeny, have been provided by Kjer et al. (2001, 2002), Morse (1997, 2003), and Wiggins (2004).

Trichoptera larvae are important and beneficial components of the trophic dynamics and energy flow in the lakes, rivers, and streams they inhabit (Resh & Rosenberg 1984). These freshwater aquatic habitats and their inhabitants are among the most severely impacted and environmentally threatened in the world because these surface waters receive and amplify abuses to the landscape, including such effects as sedimentation; pollution from industry, mining, and agriculture; sewage contamination; acid rain; and water diversion for agricultural and metropolitan uses. The impact of climate change on Trichoptera communities is just now being investigated and studies indicate that local extinctions of species are likely, especially in alpine, headwater streams (Brown et al. 2007). Trichoptera are considered among the most useful and important aquatic organisms for monitoring these effects, and are widely used in biomonitoring surveys, many of which are now mandated by federal and municipal statutes in developed countries (Dohet 2002, Lenat 1993, Resh 1993, Resh & Unzicker 1975).

Trichoptera are also important as the sister taxon to one of the megadiverse insect orders, Lepidoptera, the butterflies and moths, the two constituting the superorder Amphiesmenoptera (from the Greek, *amphiesma*, meaning "garment" or "dress" and referring to the dense clothing of hairs or scales in these insects) (Kristensen 1991). Like Lepidoptera, Trichoptera adults are terrestrial and have their wings covered with setae (secondarily modified into scales in Lepidoptera). Also, like Lepidoptera, larvae of Trichoptera spin silk, and it is the numerous uses of silk in constructing retreats and larval cases that are keystone adaptations accounting for the ecological diversity and success of the order as a whole (Mackay & Wiggins 1979, Wiggins 2004). Basal diversification of Amphiesmenoptera dates back at least to the Triassic, and basal diversification of existing lineages of Trichoptera dates back at least to the middle Jurassic (Grimaldi & Engel 2005, Ivanov 2002, Ivanov & Sukatcheva 2002, Kristensen 1997); the earliest prototrichopteran dates to the mid-Early Permian (Ivanov & Sukatcheva 2002). Thus, Trichoptera represent a significant and important branch on the Tree of Life, whose present distribution and biogeography is reflective of those past events that have affected the distribution and diversification of Earth's entire freshwater biota.

In addition to their ecological and evolutionary importance, Trichoptera have always held the fascination of both amateur and professional biologists because of their striking and varied larval retreat, net, and case-making behaviors. The case-making behavior of some species may account for the English common name, caddisfly. Although the origin of the word is obscure, it has been suggested to derive from cadaz or cadace (caddys), a word of variable spelling used in Elizabethan times to refer to a ribbon made from a certain kind of yarn sold by traveling vendors, who because of this were sometimes called "cadice men." Cadice men would pin samples of their wares to their clothing, a habit which may have suggested the name caddisfly or caddisworm for the aquatic larvae, who exhibit the analogous behavior of attaching bits of leaves and twigs to the outside of their cases (Hickin 1967).
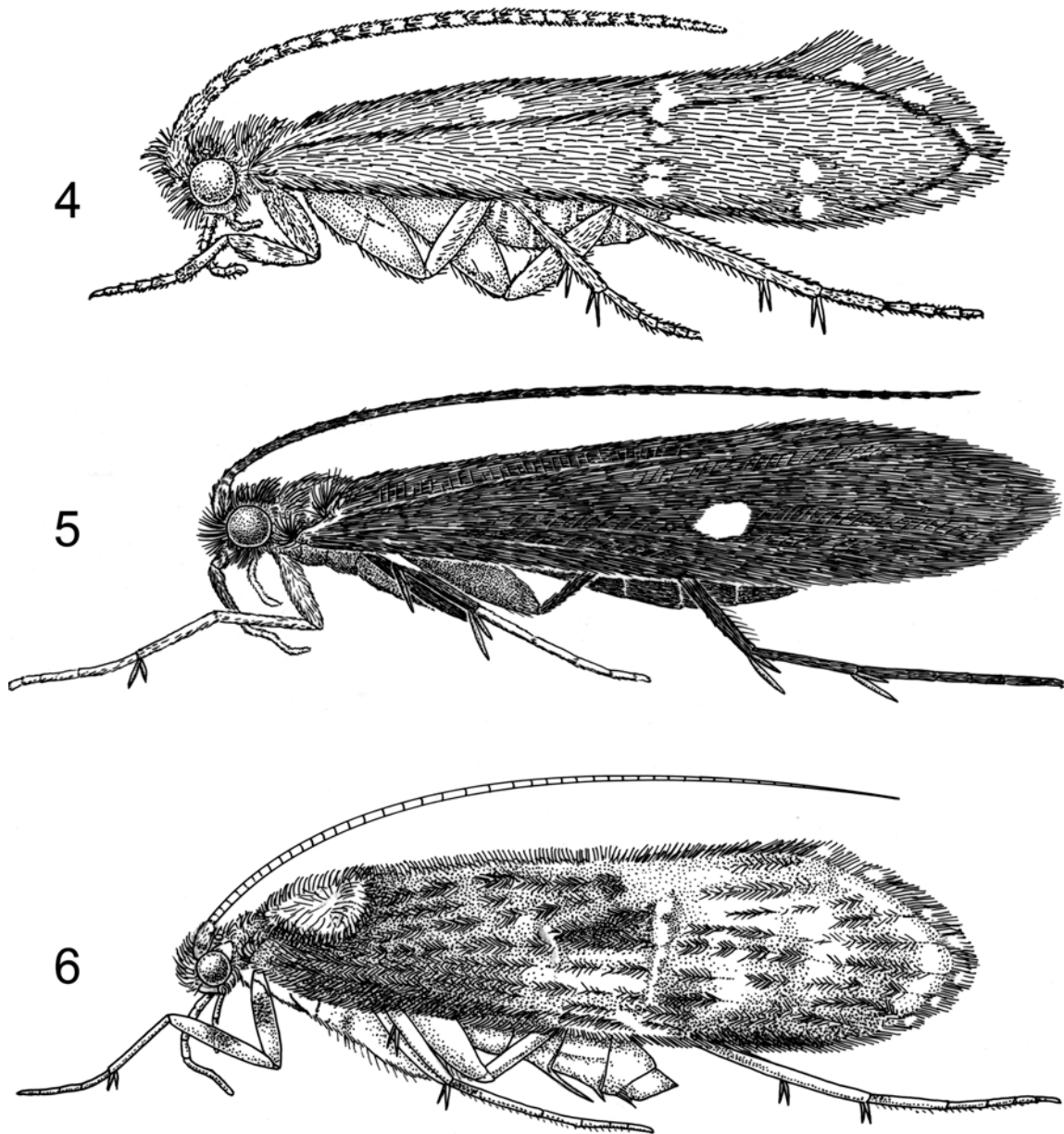
FIGURES 4–6. Trichoptera adults. 4–*Protoptila ixtala* (Glossosomatidae); 5–*Xiphocentron* sp. (Xiphocentronidae); 6–*Atopsyche callosa* (Hydrobiosidae).

Morphology

Adults

Adult Trichoptera are terrestrial and resemble small moths as they flit about in riparian and shoreline vegetation. Although seldom encountered by the general collector, they often occur in large numbers in lakeside or streamside habitats. A black light placed by a northern lake or tropical lowland river on a moonless, warm, humid night can attract 1000s of individuals and scores of species. Both pairs of wings and the body are covered with setae or hairs, reflected in the etymology of Kirby's name for the order, from the Greek words *trichos*, hair, and *ptera*, wings. Occasionally patches of scales also occur on the wings and other parts of the body. Caddisfly adults are usually brown, gray, yellow, beige, or other somber shades or combinations of color, probably an adaptation allowing them to hide during the day in vegetation (Figs. 4-6). A number of species, however, are brightly colored with yellow, red, orange, green, silver, blue, or sometimes

iridescent colored hairs and scales on the wings and thorax (Figs. 7-10). In either case, the distinct patterns of differently colored hairs on the wings frequently allow recognition of the species, much as in their often more colorful lepidopteran cousins. Body length of adults ranges from 1.5-3 mm in the smallest Hydroptilidae and some Glossosomatidae to about 4.5 cm in the largest Phryganeidae.
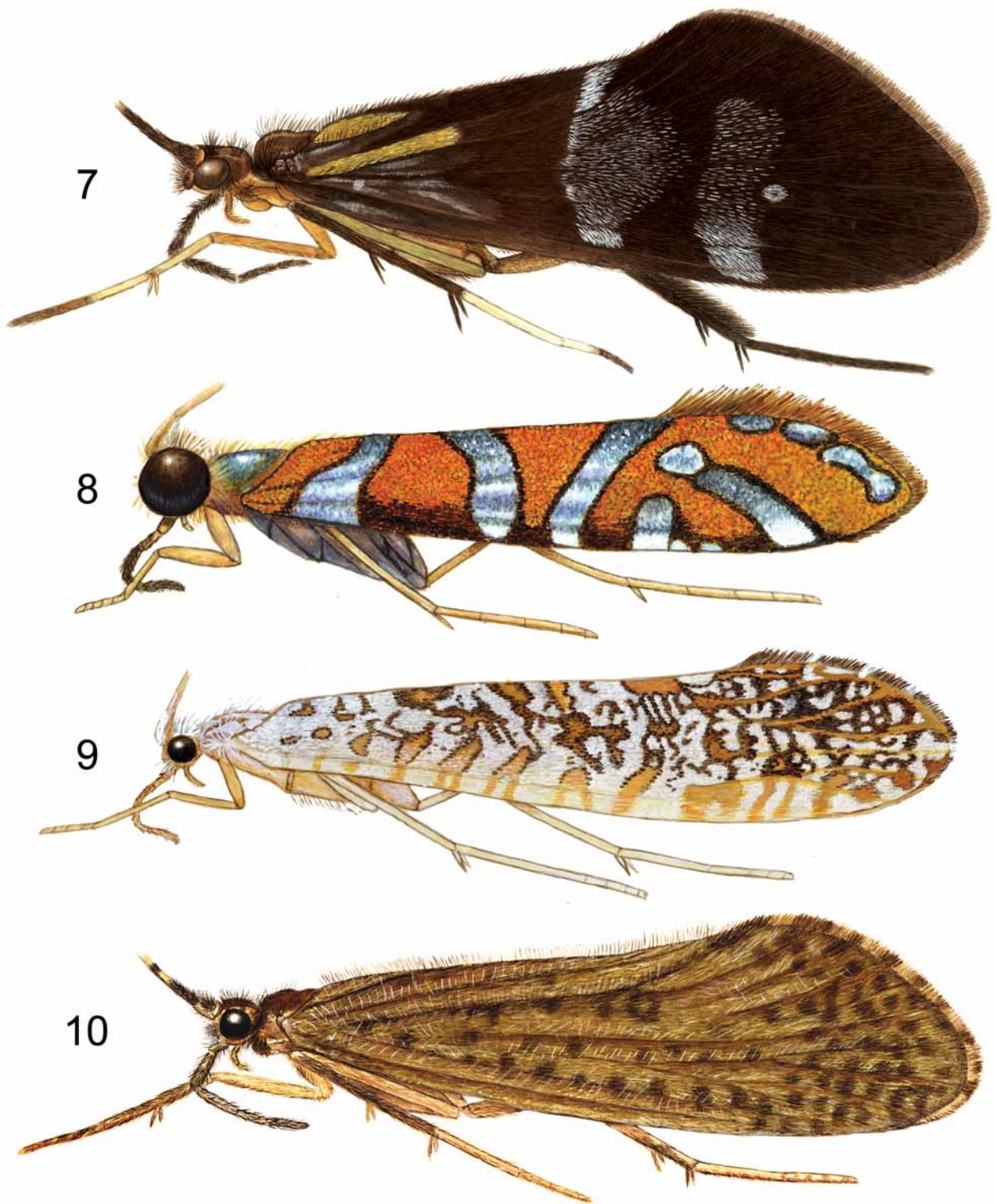
FIGURES 7–10. Trichoptera adults. 7–*Phylloicus abdominalis* (Calamoceratidae); 8–*Nectopsyche* sp. (Leptoceridae); 9–*Nectopsyche punctata* (Leptoceridae); 10–*Banyallarga vicaria* (Calamoceratidae).

Wiggins and Currie (2008) provided a well illustrated overview of adult, pupal, and larval morphology and Schmid (1989) discussed the major features of Trichoptera adult morphology. In addition, Betten (1934) included detailed information on the diversity of morphological structures found in the order, including special features of the head and mouthparts, the thorax and its appendages, especially the wings, and the abdomen and its structures.
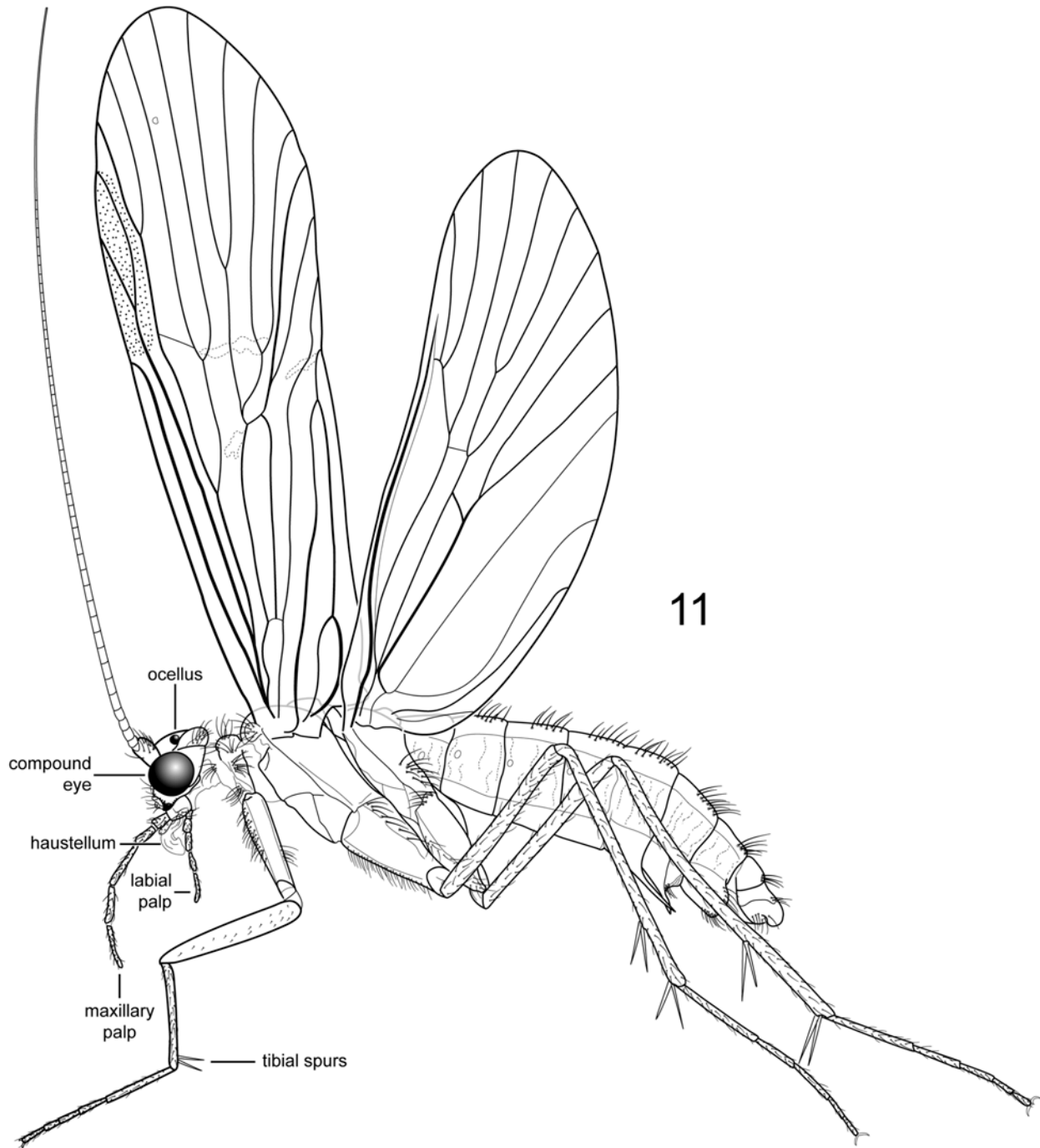

FIGURE 11. Trichoptera adult, *Atopsyche* sp., female (Hydrobiosidae).
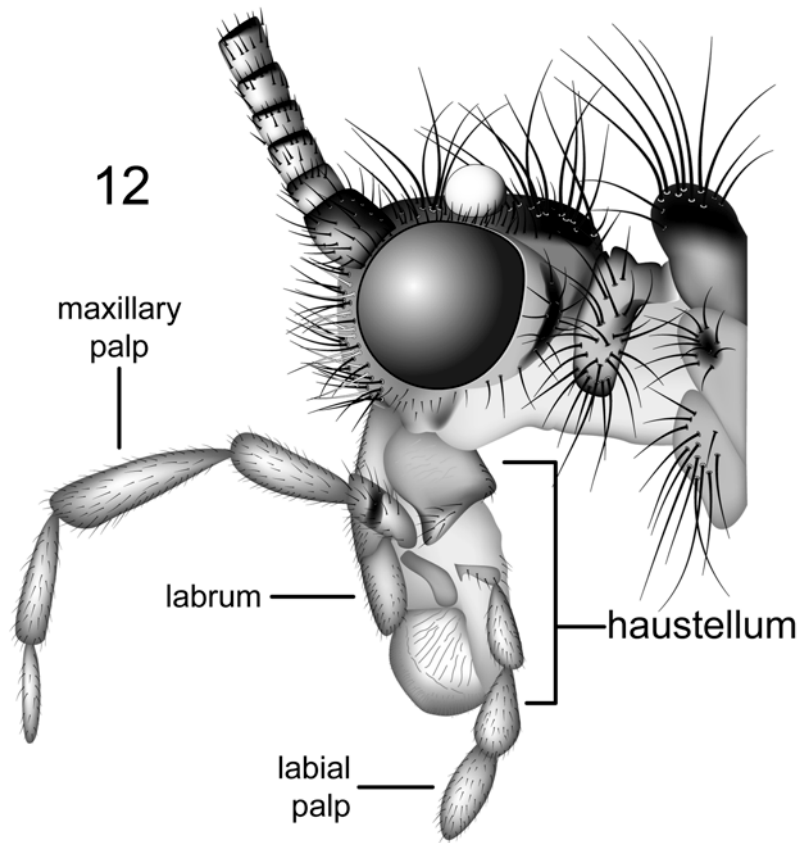
FIGURE 12. Trichoptera adult, *Ptilostomis ocellifera*, head and mouthparts, lateral (Phryganeidae).

In addition to wing vestiture, a number of additional adult morphological features help diagnose the order (Fig. 11), of which the mouthparts are probably the most important. Adult mouthparts are reduced. The mandibles are absent or highly vestigial and non-functional, at least as biting organs, but the maxillary and labial palps are prominent and composed of 5 and 3 segments, respectively. In males of some species, the maxillary palps may have reduced segmentation and bear secondary sexual modifications or both; in only a few species are the palps absent. The major feature of the caddisfly mouthparts is the haustellum (Fig. 12), a unique structure for the order (Crichton 1957, 1991, 1993). The haustellum is formed from a fusion of the apex of the labium (the prelabium) and the hypopharynx to form a short proboscis. The haustellum is membranous at its apex and has channels formed from rows of fine hairs that aid in soaking up water or sugary liquids. The compound eyes are well developed, but in several groups those of the male are significantly larger than those of the female. Three simple eyes, or ocelli, are present in several families. In most species the antennae are filamentous and about as long as the body, but in some families they can be several times longer than the body; in males of some Philorheithridae the antennae are pectinate. The scape is the largest segment of the antenna and in males of many species it is further enlarged and bears modified setae, scales, or glandular structures. The head, especially in males may have additional structures, such as eversible glands, pilifers, of patches of modified scales or hairs. Internally, the head contains the tentorium, which varies in shape and complexity among the various families (Neboiss 1991b).

LINNAEUS TERCENTENARY: PROGRESS IN INVERTEBRATE TAXONOMY
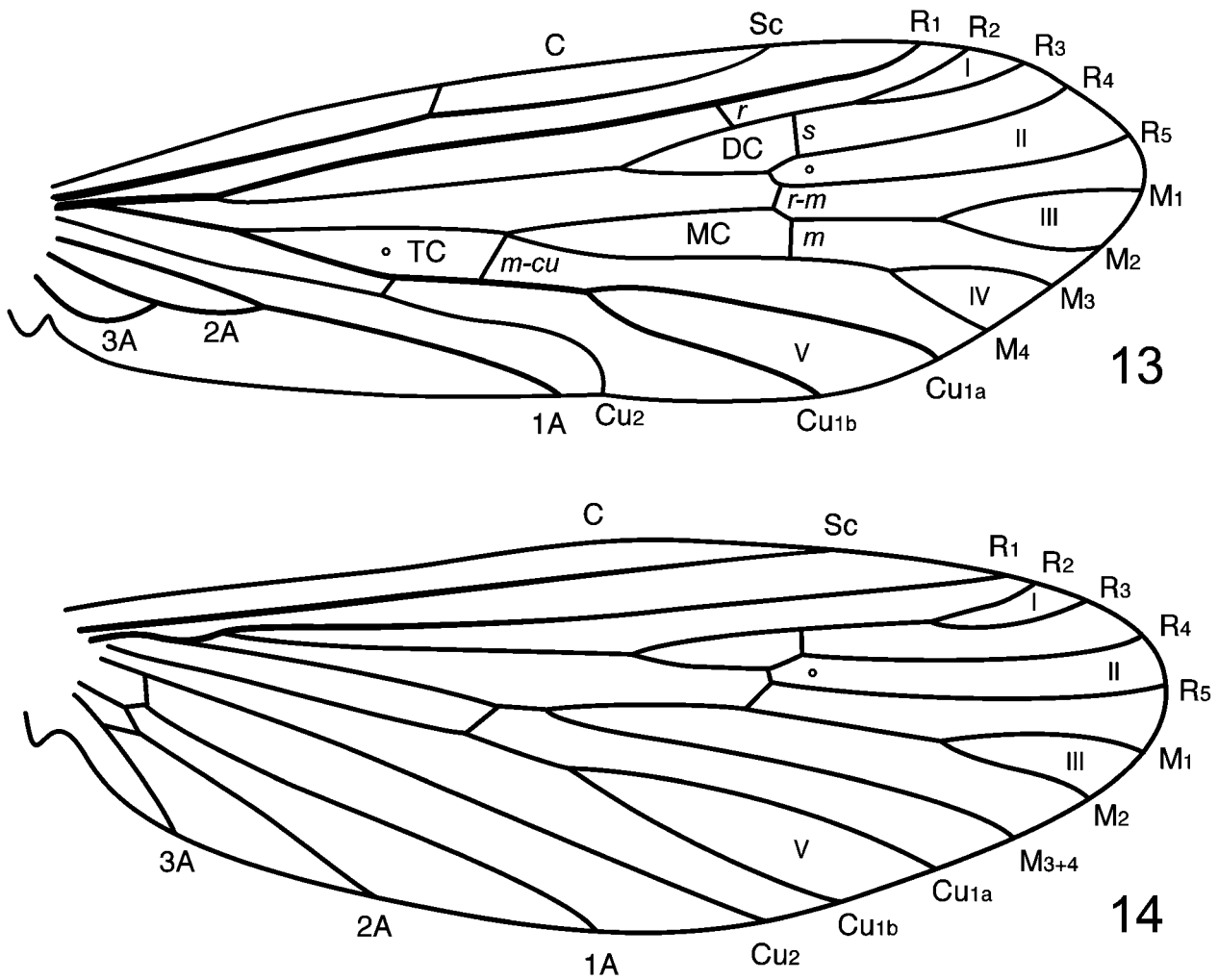
FIGURES 13–14. Trichoptera wing venation, generalized. 13–forewing; 14–hind wing.

Wing shape is variable, but the forewings are somewhat longer than the hind wings, although the hind wings may be broader. In the Hydroptilidae, the wings are usually narrow and very attenuate. Reduced wings, microptery and brachyptery, are known in a few species. Males very often have secondary sexual modifications on the wings, such as heavily scaled regions, secondary folds, swellings in the membrane, long tufts of hairs, etc. Wing venation is complete in the most primitive lineages. Following the convention of Schmid (1998) and beginning on the anterior edge of the forewing, the major veins include the costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal veins (A) (Figs. 13-14). The radius branches into the 1st radius (R_1) and the radial sector (R_S), which further subdivides into veins R_{2+3} and R_{4+5} and then into 4 branches, R_2, R_3, R_4, and R_5. The media (M) is divided into anterior (MA) and posterior (MP) branches; each of which is subdivided again into veins M_1 and M_2, and into veins M_3 and M_4, respectively. The cubitus (Cu) is also divided into 2 branches, an anterior or 1st cubitus (Cu_1), always attached basally to the base of M and subdivided apically into 2 branches (Cu_{1a} and Cu_{1b}), and an undivided posterior or 2nd cubitus (Cu_2). The posterior edge of the forewing bears 3 anal veins (1A, 2A, and 3A), which in Trichoptera are looped or coalesce to form a very characteristic double-Y configuration. Forewing branches of the Rs, M, and Cu_1 are numbered as wing forks 1-5 (I-V) from the anterior margin of the wing. Important forewing cells include the discoidal cell (DC) formed by the branching of Rs into R_{2+3} and R_{4+5} and closed apically by the sectorial crossvein, the medial cell (MC) formed by the branching of M into MA and MP and closed apically by the

medial crossvein, and the thyridial cell (TC) formed by the branching of M and Cu$_1$ and closed apically by crossvein m-cu. Lying at the base of fork 2 (R$_4$ + R$_5$) in almost all Trichoptera is the nygma, a small corneous sensory spot; a similar spot, the thyridium, occurs in the thyridial cell of some species. The region along the anterior edge of the forewing, between the apices of the Sc and R$_1$, is sometimes thickened and forms the pterostigma. The region at the posterior edge, where the apex of Cu$_2$ and 1A often fuse, is slightly inflexed and referred to as the arculus. In some species, the apical forewing forks and crossveins more or less align to form a slightly diagonal line referred to as the chord. Hind wing venation is essentially similar to that of the forewing, but is often more reduced; in particular MP does not branch into M$_3$ and M$_4$ (thus fork 4 is always absent) and the anal veins each reach the wing margin and vary in number from 1 to 5. A complete complement of wing veins is found in the more primitive families and genera, with loss and fusion of veins occurring commonly throughout the order. Wings are generally held rooflike or tentlike when folded over the body, but in some groups they are held flat like those of most Lepidoptera.
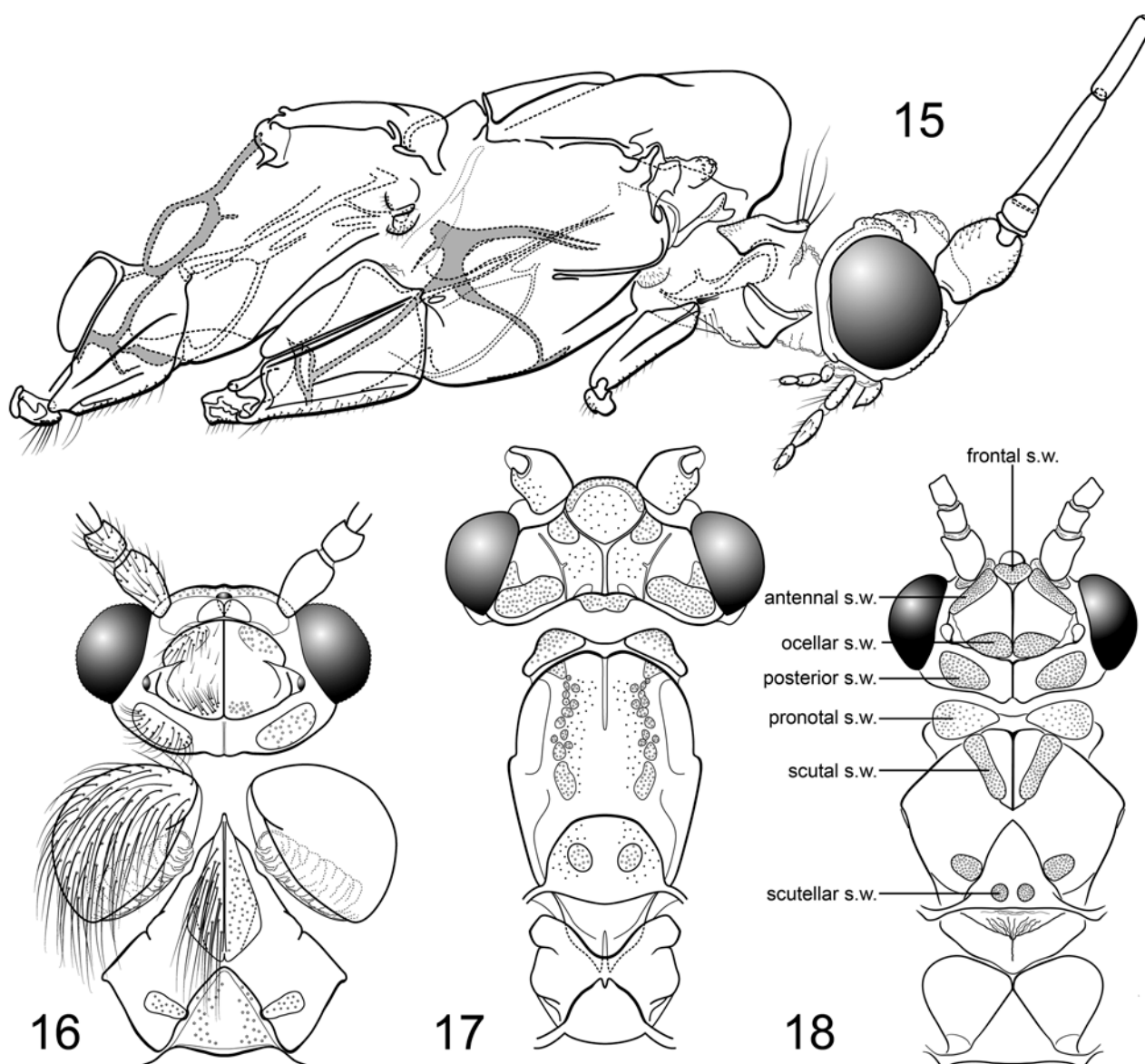
FIGURES 15–18. Trichoptera adults. 15.–*Amazonatolica hamadae*, head and thorax, lateral (Leptoceridae); 16–*Culoptila thoracica*, head and thorax, with modified tegulae, dorsal (Glossosomatidae); *Tagalopsyche kjaerandseni*, head and thorax, dorsal (Leptoceridae); 18–*Tolhuaca cupulifera*, head and thorax, dorsal (Glossosomatidae). Setose wart (= s.w.) terminology after Ivanov (1990).
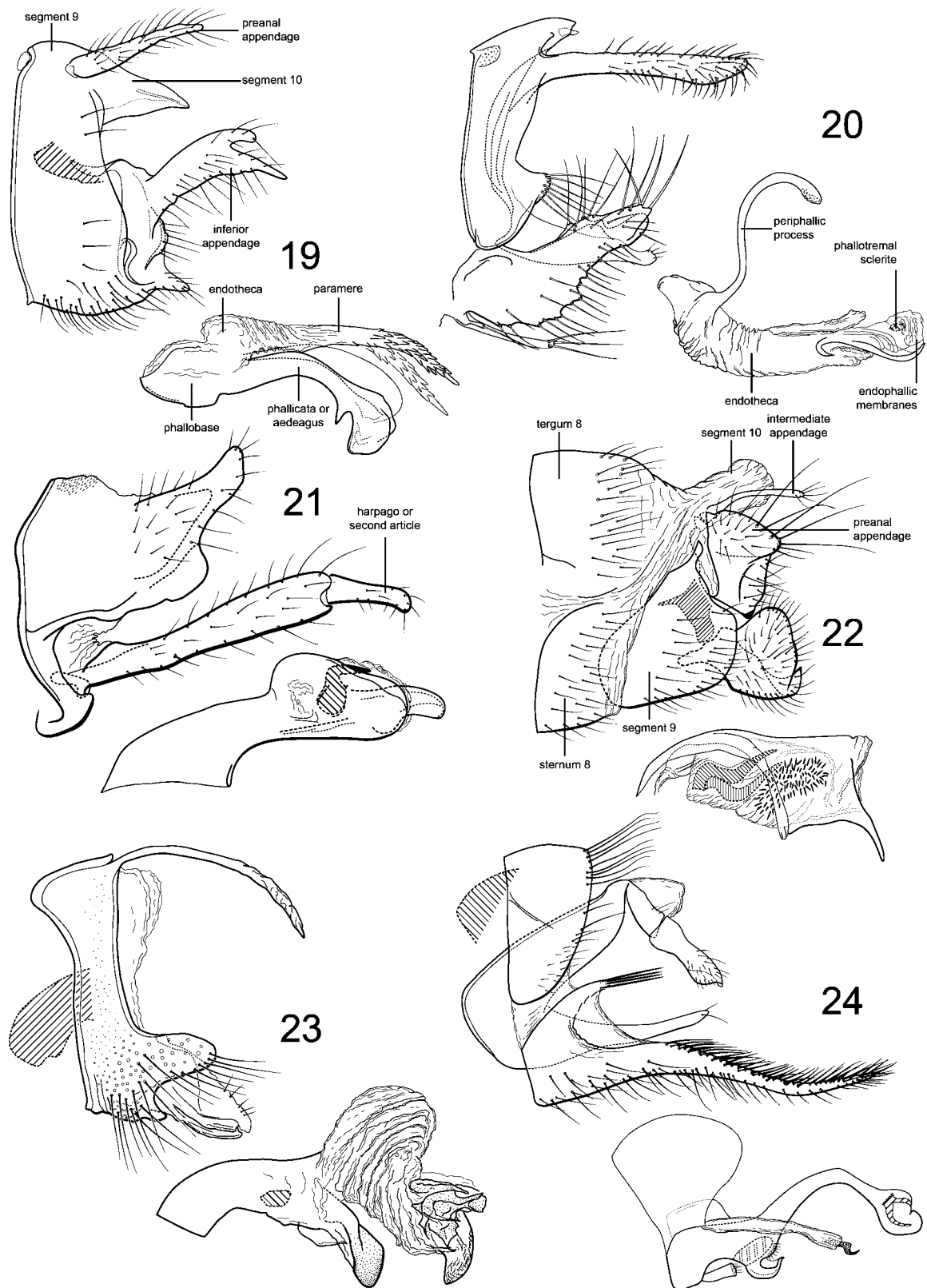
FIGURES 19–24. Trichoptera male genitalia; genital capsule and phallus (separate), lateral. 19–*Fernandoschmidia amudita* (Leptoceridae); 20–*Nectopsyche dorsalis* (Leptoceridae); 21–*Smicridea figueroai* (Hydropsychidae); 22–*Polycentropus neblinensis* (Polycentropodidae); 23–*Contulma fluminensis* (Anomalopsychidae); 24–*Protoptila trichoglossa* (Glossosomatidae).

The prothorax is small and underdeveloped compared to the wing-bearing pterothorax (composed of the meso- and metathoraces). The mesothorax and metathorax each bear taxonomically important coxal and pleural sclerites, wart-bearing notal sclerites, and internal apodemes (Fig. 15) (Tindall 1965). Legs are long and slender, with the forelegs being the shortest; however, the middle legs of some females have expanded tibiae and tarsi for swimming below the water's surface for oviposition. Tibial spurs on the legs are conspicuous and number 3 on the foreleg (1 preapical, 2 apical) and 4 each on the other legs (2 preapical, 2 apical) in the most primitive condition; however, reductions and modifications in spur number and morphology occur throughout the order such that the "spur formula," given variously as 3-4-4, 1-2-2, etc., is an important taxonomic character (Baszio & Richter 2002). The head and thorax bear characteristic setose warts comprised of clearly delineated, slightly convex, setose regions of the cuticle (Figs. 16-18) (Ivanov 1990, Olah & Johanson 2007).

In most cases, the abdomen is without modifications, except the 5th abdominal sternum bears a pair of glandular structures in almost all families (Ivanov & Melnitsky 2002); these play an important role in pheromonal communication (Bergmann et al. 2002, Ivanov & Löfstedt 1999, Löfstedt et al. 1994) or chemical defense (Duffield et al. 1977). One or more of abdominal sterna 6-8 (9 in *Chimarra*) may bear a median sclerotized process or projection ("hammer") that functions in substrate vibrational communication (Ivanov 1997b).

All of these components of the morphology, but especially characteristics of the antennae and palps, presence or absence of ocelli, spur formula, setose warts, and wing venation are used to identify the various families and genera. The male genitalia, associated with abdominal segments 9 and 10, are conspicuous, complex, and contain the primary characters for delineating genera and identifying the species (Figs. 19-24) Numerous workers have discussed the morphology of Trichoptera male genitalia and there is considerable controversy regarding the origin and homology of structures (Ivanov 2005, Morse 1975, Nielsen 1957, Ross & Unzicker 1977, Schmid 1970, 1979, 1989). In the male, abdominal segment 9 has the tergum and sternum fused into a sclerotized ring; there are no pleural sclerites, *per se* (segment 8 is the last typical abdominal segment bearing a distinct tergum and sternum and membranous pleural regions). Segment 10 is much shorter and narrower than segment 9 and its shape is very variable. It can be entirely membranous, but typically it is sclerotized dorsally and laterally, and concave, reduced, and membranous ventrally. Segment 10 can bear several pairs of appendages, including the dorsal superior or preanal appendages and the ventrolateral medial or intermediate appendages (the intermediate appendages may not be homologous across Trichoptera). While typically assigned to segment 10, the preanal appendages often lie between segments 9 and 10 or are fused to segment 9; it is probably best not to assign the preanal appendages categorically to segment 10 (J.C. Morse, personal communication). In any case, the preanal appendages are typically large, digitiform, and setose, but they can be small or very commonly absent. True cerci are lacking in male Trichoptera. The anus is situated at or near the apex of segment 10 and is surrounded by 3 very small sclerites, the dorsal epiproct and a pair of lateral paraprocts (these pertaining to segment 11 according to Nielsen and most prominent in *Rhyacophila*; they are inconspicuous in almost all other Trichoptera). Ventrally, segment 9 bears a pair of 1- or 2-segmented gonopods, the inferior appendages or claspers; in their 2-segmented condition they consist of a basal coxopodite or gonocoxite and apical harpago or gonostyle (or simply the 1st and 2nd articles of some authors). The 1-segmented condition results from the loss of the harpago or its fusion to the coxopodite; sometimes the coxopodite itself is fused to segment 9. The inferior appendages are usually united to each other at their bases. The phallus is a complex, tubular structure displaying much variation across the order. It lies below segment 10 and above the base of the inferior appendages within the phallocrypt, a membranous cavity formed in the intersegmental membranes between the venters of segments 9 and 10. The phallic apodeme is formed by the fusion of the base of the phallus with the anterior wall of the phallocrypt; it is typically at least partially sclerotized and the ejaculatory duct leads into it. A sclerotized rim, the phallic shield, may form in the phallocrypt membranes at their junction with the phallobase and these may bear

periphallic processes (Morse 1975). Distally, beyond the phallic apodeme, the phallus consists of the sclerotized phallobase, a connecting membranous endotheca, and an apical, protractile, sclerotized aedeagus or phallicata; some authors (e.g., Morse 1975) prefer the latter term, because the term aedeagus has been applied to the entire phallus. The endotheca bears a pair of parameres in some families and often spines in various numbers and configurations in others. In the majority of Trichoptera, the phallus is a single tube resulting from fusion of the phallobase and aedeagus or loss of one or the other. The apex of the aedeagus bears the opening of the ejaculatory duct. In some taxa there is a tube or membranous sac, the endophallus, invaginated at the end of the aedeagus, into which the ejaculatory duct enters; its distal end at the gonopore opening bears a small, U-shaped sclerite, the phallotremal sclerite. Upon this groundplan morphology, tremendous variation and complexity has evolved in the male genitalia, perhaps driven by sexual selection (Ward & Pollard 2002).

Females lack a true ovipositor, but instead have the terminal abdominal segments (segments 8-10 or 11) either elongated into a protrusible oviscapt for placing eggs on the substrate or modified into a shorter apparatus for forming and holding the egg mass (Figs. 25-27). Female genitalia (Nielsen 1980) are much simplified compared to those of the male, but internal structures that engage the apex of the phallus during copulation and accept the male ejaculate are often complex and species specific.
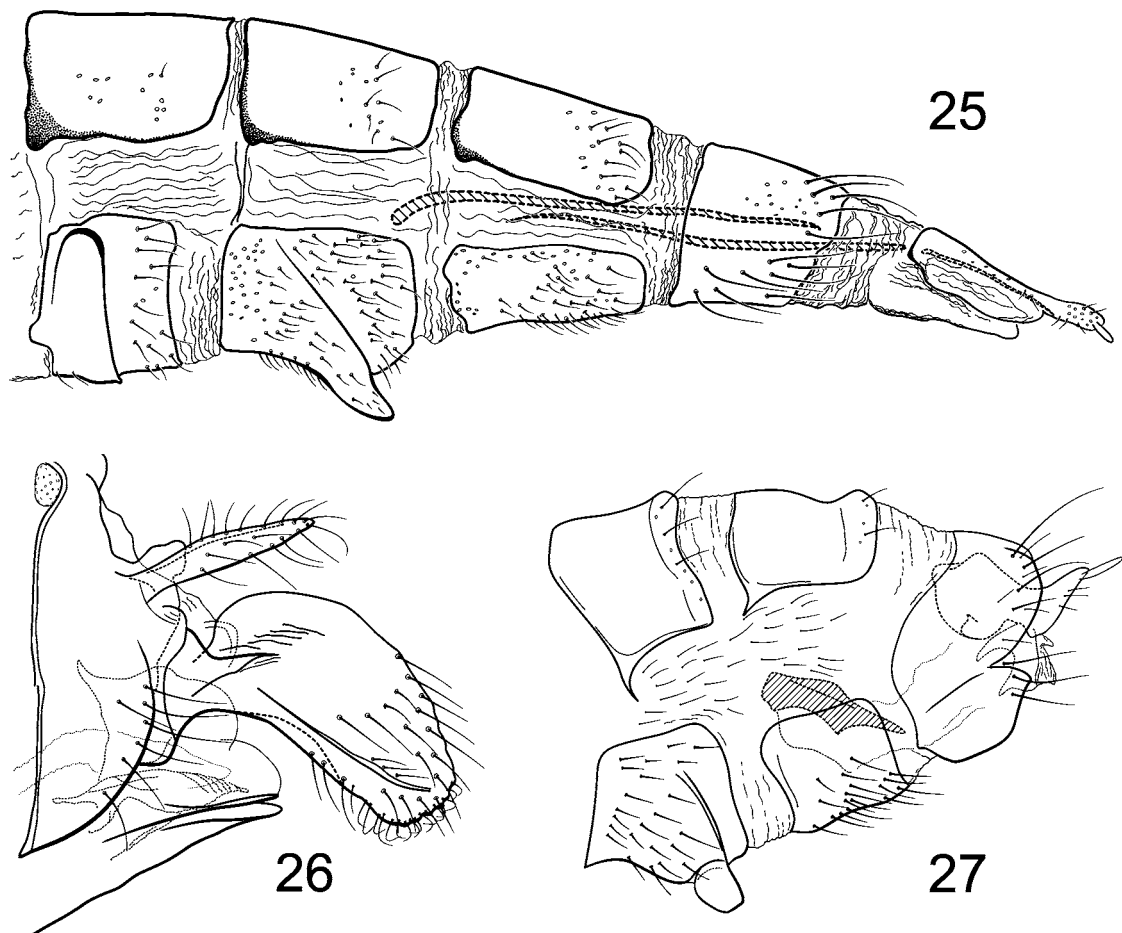

FIGURES 25–27. Trichoptera female genitalia, lateral. 25–*Tolhuaca cupulifera* (Glossosomatidae); 26–*Tagalopsyche aethiopica* (Leptoceridae); 27–*Culoptila bidentata* (Glossosomatidae).
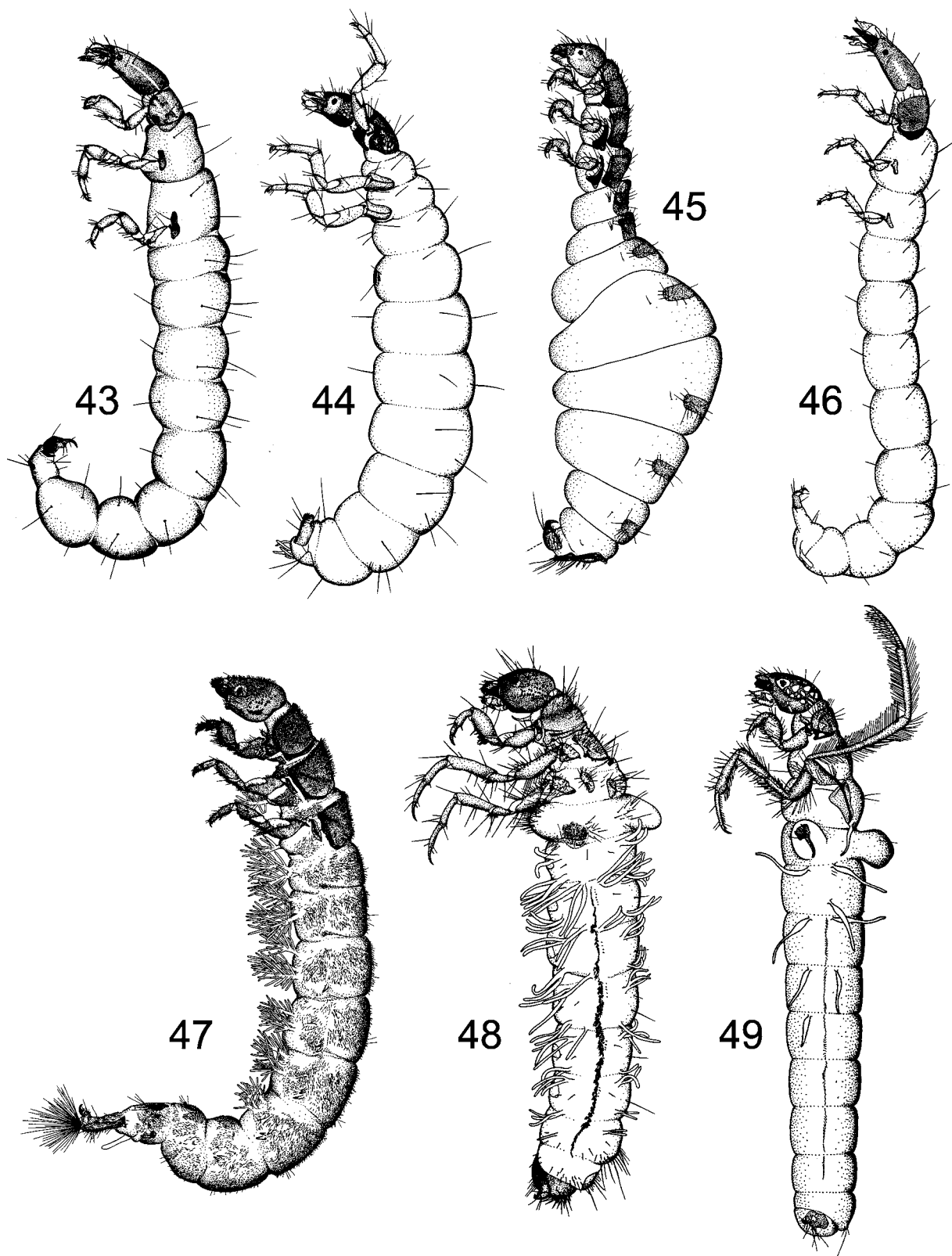
Larvae

The aquatic larvae of Trichoptera construct a portable case (Integripalpia, and 2 of 4 families of "Spicipalpia") or fixed retreat (Annulipalpia), except for those of a couple of "free-living" spicipalpian families. The net, retreat, case, and pupal structures of caddisfly larvae are among the most intricate and complex structures built by insects, at least among the non-social orders (Figs. 28-42).

Larvae possess a distinct head, thorax, and abdomen (Figs. 43-49). The larval head capsule is fully developed and sclerotized. Larval eyes are always present and consist of a few stemmata. The antennae are very short and single-segmented, although in the long-horned caddisflies (Leptoceridae) and in some microcaddisflies (Hydroptilidae) the antennae are much longer and conspicuous. Unlike adults, larval mouthparts are well developed and consist of a small labrum, a pair of well-developed mandibles, a pair of short, compact maxillae, and a labium. The labrum is a simple, flap-like lobe, but in Philopotamidae it is highly modified as a membranous T-shaped structure. The maxillae and labium form a composite structure. Short maxillary and labial palps are usually present. The opening of the silk gland is at the apex of the labium, which in some groups is drawn out as a slender, protruding structure. Mandibles of shredders and herbivores are broad, with apical cutting teeth, while those of scrapers are more elongate with entire edges. In predaceous larvae, such as in the genus *Oecetis*, the apical teeth are more pointed. Each thoracic segment is distinct and bears a pair of segmented legs. These are either more or less the same length or the forelegs are the shortest and the hind legs the longest. Legs are unmodified in most species, but in some groups the forelegs are raptorial and in others the hind legs are long and slender and bear rows of long swimming hairs. Larvae of some Brachycentridae have rows of hairs on the middle and hind legs used for filtering food particles from currents and those of Limnocentropodidae and a species of *Drusus* (Limnephilidae) have strong spines for snagging prey from the current (Bohle 1983). Tarsi are 1-segmented and tarsal claws are single. In all families the prothorax bears a pair of heavily sclerotized pronotal plates, very narrowly separated along the midline by a suture. In some families, notably the Hydropsychidae and Hydroptilidae, the mesothorax and metathorax are also heavily sclerotized, but in other families these segments are entirely membranous or with lesser degrees of sclerotization. The prothorax of a few families in the Plenitentoria bears a ventral prothoracic horn. The abdomen consists of 10 segments and is almost entirely membranous. The abdomen is usually bare except for a few scattered setae, but in the Hydropsychidae it is densely covered with short modified hairs and scale-hairs. The abdomen lacks abdominal prolegs except for a pair of anal prolegs on the last abdominal segment, with each proleg bearing a strong anal claw; there are small sclerites at the bases of the anal claws and on the anal prolegs. In the case-making Integripalpia the 1st abdominal segment usually bears eversible dorsal and lateral spacing humps. Abdominal gills may or may not be present. When present they are filamentous and may occur singly on one to several abdominal segments, in tufts of many filaments, or as highly branched stalks. They can occur in subdorsal, dorsolateral, ventrolateral, and/or subventral rows. In some Rhyacophilidae, tufted gills occur on the thorax. An abdominal lateral fringe of minute filaments is present in several families, as well as forked lamellae (Kerr & Wiggins 1995). Regions of specialized osmoregulatory cells, the chloride epithelia, are present in some families. Abdominal segment 9 usually bears a dorsal sclerite, especially in the case-making families. The position of the antenna in relation to the eye, thoracic sclerotization, gill morphology, mandibular structure, leg morphology, and case or retreat structure, among other features, are important in identifying the different families and genera. Characters for separating species often involve differences in setal pattern and morphology (Mathis 1997, Williams & Wiggins 1981), and color patterns on the head and thorax, but most species are unknown or unassociated in the larval stage, except in North America, Europe, and Japan where the larval stages are much better known. The application of "DNA barcoding" using a region of the mitochondrial COI gene as well as other gene sequences offers a reliable and speedy method of associating larvae and adults of Trichoptera (Graf et al. 2005, Shan et al. 2004, Waringer et al. 2007, Zhou et al. 2007).
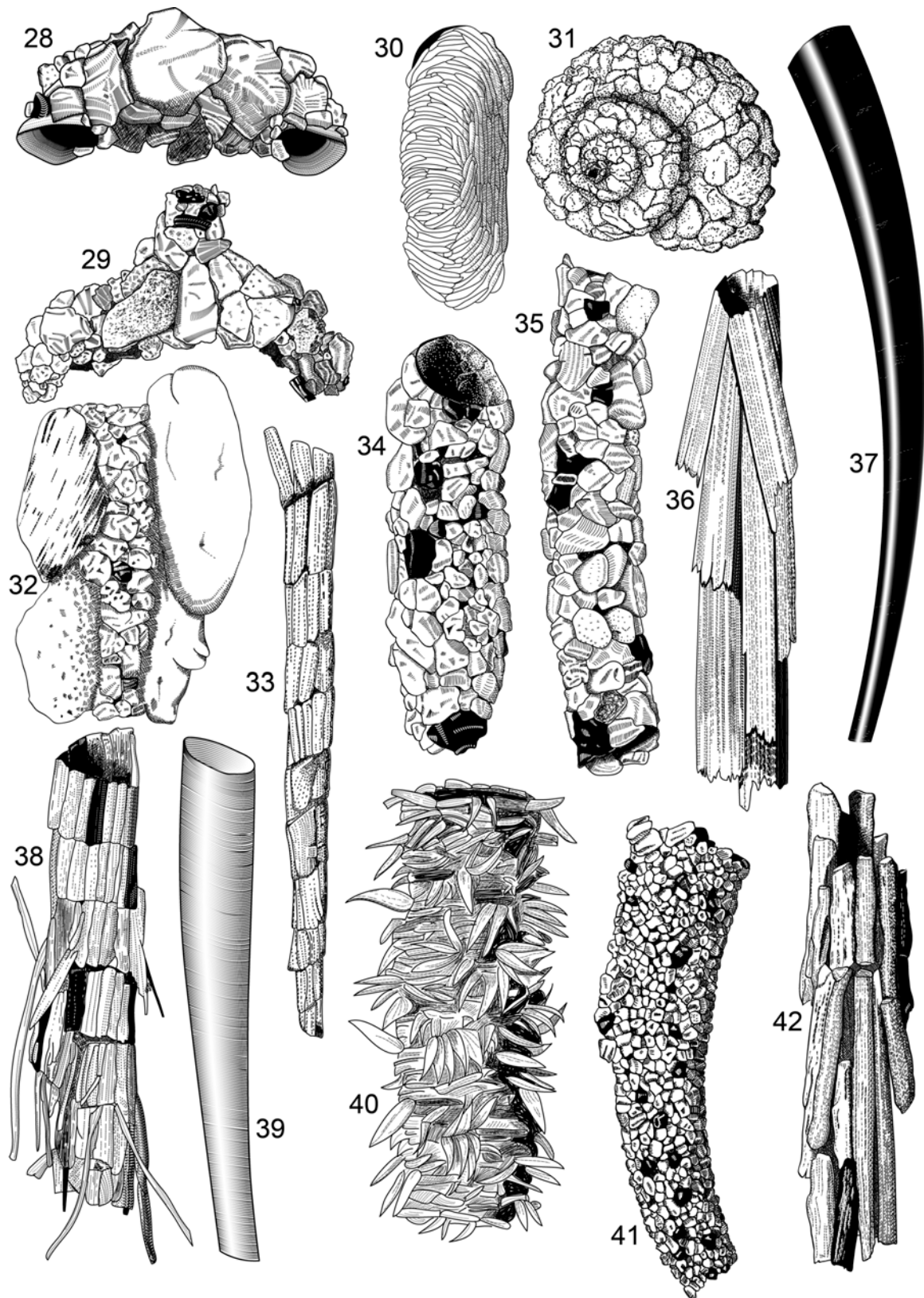
FIGURES 28–42. Trichoptera larval cases. 28–*Culoptila moselyi* (Glossosomatidae); 29–*Culoptila unispina* (Glossosomatidae); 30–*Dibusa angata* (Hydroptilidae); 31–*Helicopsyche borealis* (Helicopsychidae); 32–*Goera fuscula* (Goeridae); 33–*Triaenodes tardus* (Leptoceridae); 34–*Discosmoecus* sp. (Limnephilidae); 35–*Setodes incertus* (Leptoceridae); 36–*Sphagnophylax meiops* (Limnephilidae); 37–*Grumicha grumicha* (Sericostomatidae); 38–*Banksiola dossauria* (Phryganeidae); 39–*Leptocerus americanus* (Leptoceridae); 40–*Phanocelia canadensis* (Limnephilidae); 41–*Lepania cascada* (Goeridae); 42–*Anabolia bimaculata* (Limnephilidae).

FIGURES 43–49. Trichoptera larvae. 43–*Atopsyche* sp. (Hydrobiosidae); 44–*Protoptila* sp. (Glossosomatidae); 45–*Byrsopteryx mirifica* (Hydroptilidae); 46–*Chimarra* sp. (Philopotamidae); 47–*Calosopsyche* sp. (Hydropsychidae); 48–*Limnephilus* sp. (Limnephilidae); 49–*Nectopsyche gemmoides* (Leptoceridae).

Pupae

Trichoptera pupae are of the exarate type, with the antennae, legs, and developing wings free from the body (Fig. 2). Mandibles are dectitious in most families, usually cross each other apically, and point forward (Fig. 50). Antennae lie ventrolaterally along the thorax and abdomen. In species with long antennae, they are coiled around the end of the abdomen. The thorax is unmodified, but the thoracic legs often have swimming hairs. The abdomen bears remnants of the larval gills and has characteristic paired hook plates dorsally that aid the pupa in exiting the pupal shelter (Fig. 51 and insets). A lateral fringe is also present. The abdomen ends in a pair of anal processes (Fig. 52), which, together with the number, arrangement, and morphology of hookplates and mandible morphology, help diagnose the different families.
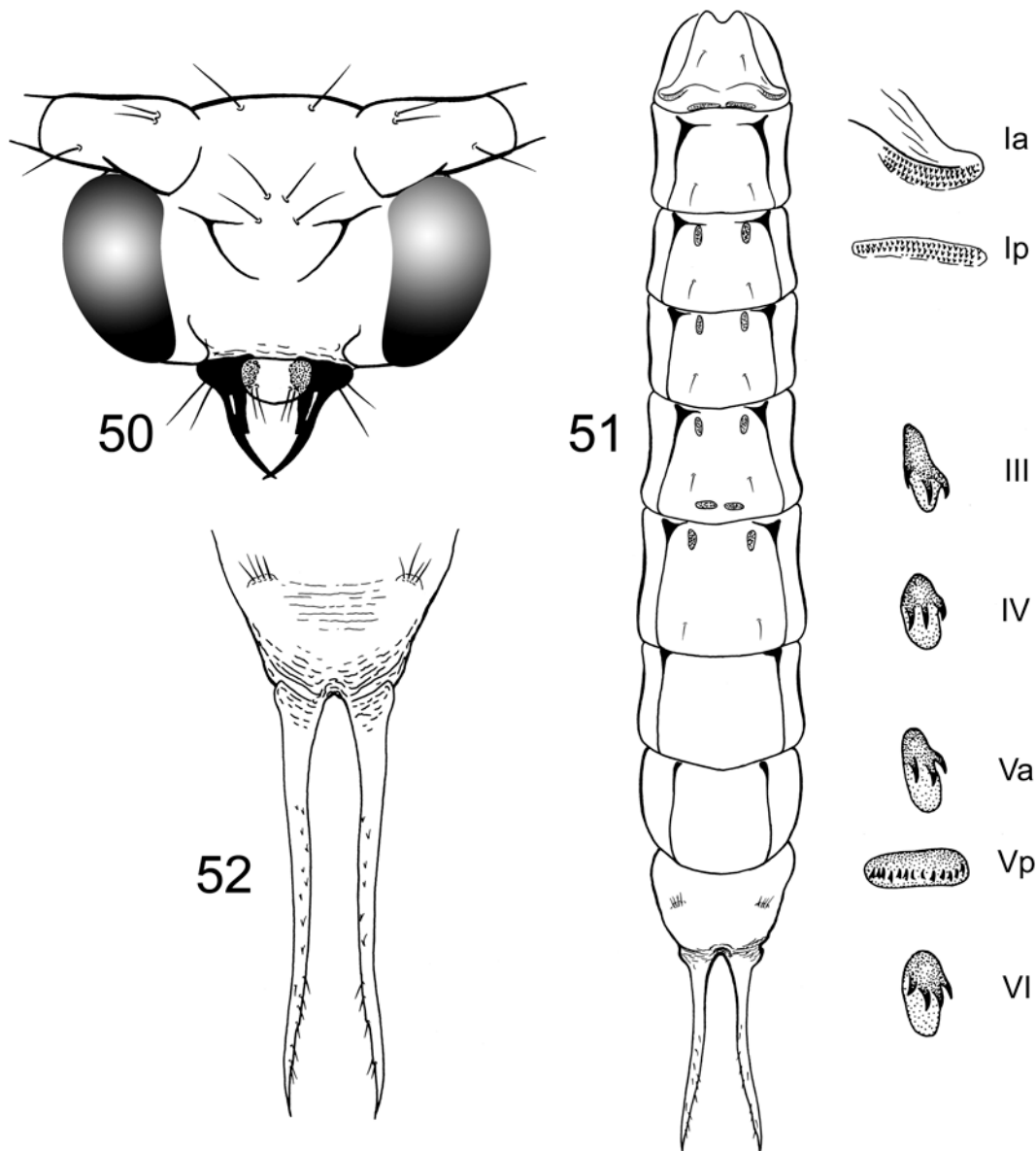
FIGURES 50–52. Trichoptera pupa, *Triaenodes tica* (Leptoceridae). 50–head, frontal; 51, abdomen, dorsal, hookplates enlarged; 52–anal processes, enlarged, dorsal.

Classification and phylogeny

Two currently recognized suborders, Annulipalpia and Integripalpia, are largely characterized by differences in the way silk is used, whether to produce nets or tubes, or as glue to make various types of portable cases,

incorporating sand and small pebbles, or bits of leaves and twigs, each genus or even species building its own particular style of case. Larvae of 4 other families, often called "Spicipalpia" and regarded as a 3rd suborder by some authors, are free-living, or make dome or purse cases.

The monophyly of the order Trichoptera is very well established, as is that of Amphiesmenoptera (Kjer 2004, Kristensen 1975, Wheeler et al. 2002, Whiting 2002). Following is a list of some characters that have been proposed as synapomorphic for the order (Ivanov 2002, Ivanov & Sukatcheva 2002, Kristensen 1975, 1991, 1997, Morse 1997, Weaver 1984): larvae aquatic, apneustic (no open spiracles), respiration epidermal, often by filamentous abdominal gills; larval tentorium reduced, delicate; larval antennae greatly reduced; larval abdominal segments 1-9 without ventral prolegs; larval abdominal segment 9 with dorsal tergite; adult mandibles reduced, with loss of mandibular articulation; adult prelabium joined with hypopharynx to form a unique "haustellum" which serves as a lapping/sponging organ.

There has been considerable disagreement about the relationships among the suborders of Trichoptera and their included families. This has resulted not only in different hypotheses about the evolutionary history of the group, but also in a confusion in the use of taxonomic categories, since different authors use different terminology, or have been inconsistent in how certain taxonomic categories have been used. In general, 3 major groups have been recognized, more or less corresponding to the different ecological adaptations of the larvae. We refer to these by their currently accepted subordinal names, Annulipalpia, "Spicipalpia," and Integripalpia, each in its most restricted sense and as used by Wiggins (2004). However, the respective superordinal names of Hydropsychoidea, Rhyacophiloidea, and Limnephiloidea, respectively (Neboiss 1991a, Ross 1956), have sometimes been used to refer to groups of equivalent taxonomic coverage.

Because case or retreat-making behavior has been used in constructing theories of caddisfly phylogenetic relationships, it is useful to review these behaviors for the major groups. The suborder Annulipalpia includes 8 families whose larvae make retreats and spin silken capture nets. They are usually confined to running water, from torrents to meandering channels, but a few occur in standing water. They construct a capture net immediately adjacent to a fixed retreat, situated in the current to filter fine organic matter or larger particles, depending on the mesh size. Mesh diameters vary from a few to several 100 microns, depending on the species, allowing species to specialize on different sizes of food particles. Larvae glean the mesh with their mouthparts for food and repair broken sections or spin new nets with silk from their labial glands. In some, the labium is modified to produce multiple strands simultaneously. Some species construct a fixed, serpentine, silk-lined detritus tube on stationary substrate and feed on fine surface deposits or periphyton. Others live within a modified portion of the net itself and capture living invertebrate prey that come in contact with a peripheral silken webbing. A few build filtering tubes buried in sandy substrates. Some Neotropical species build portable silk and detritus tubes (Muñoz-Quesada & Holzenthal 1997). Annulipalpian pupation behavior is varied. Most build a small chamber of mineral or plant fragments, internally lined with silk, adjacent to the retreat or modified from it; it may have a loose silken cocoon spun inside, attached or free from the shelter.

The "Spicipalpia" includes species with several different larval habits and a total of 4 families. The free-living and predaceous families Rhyacophilidae and Hydrobiosidae build no larval structures, except for a terminal shelter in which to pupate. They are usually carnivorous and crawl on the bottom substrate to actively search out aquatic invertebrate prey. They occasionally secrete silken safety lines; in the event they are swept off the substrate by the current, they can work their way back to a safe purchase. Larvae of Hydrobiosidae have modified raptorial forelegs to help facilitate their carnivorous habits, and in both families the mandibles and tarsal claws are sharply pointed. While they build no larval structures, last instar larvae in these 2 families construct a dome-like pupal enclosure of mineral fragments within which they spin a pupal cocoon. Members of the spicipalpian family Hydroptilidae (including the Ptilocolepinae) are among the smallest of caddisflies, as reflected in the commonly used name "micro-caddisflies." Fully-grown larvae and adults are usually no more than 5 mm or so, and some much smaller. They are free-living until the last larval instar (the 5th), and then they construct a portable case or one cemented to the substrate in which the larvae eventually pupate.

These tiny caddisfly larvae display "hypermetamorphosis" in which the 1st 4 larval instars are very small, free-living, and are passed through rather quickly, while the 5th instar larva builds a case and resembles a more typical caddisfly larva, expect that the abdomen is commonly very distended. The 5th instar larva is the primary feeding stage, holding the major food reserves for pupal and adult development. Hydroptilid larvae build a variety of cases that converge on 3 main types. These include the more common "purse cases," consisting of 2 compressed silken valves often incorporating or covered with fine detritus, sand grains, filamentous algal strands, or pieces of foliose algae. The valves are joined dorsally and ventrally, but open at the ends, forming a residence for the larva. Other hydroptilids build an oval, depressed, fixed, retreat-like case. In the final group, tubular cases similar to those of Integripalpia are constructed, but these are thought to be a modification of the purse-case. Hydroptilids feed by collecting fine organic matter or by scraping diatoms and other periphyton from rock surfaces. More specialized ones pierce algal cells and suck out the cell contents or feed directly on liverworts. The remaining spicipalpian family, the Glossosomatidae, the tortoise-case or saddle-case makers, fashion a case very similar to that of a turtle, consisting of a dorsal dome of small sand grains and pebbles and, to complete the analogy to a turtle, a transverse strap beneath the dome, with the anterior and posterior ends of the larva protruding from the 2 ventral openings simultaneously. The tortoise-case makers construct a new and larger case with each larval instar and then pupate within a cocoon within the last larval case, after removing the ventral strap and attaching the case to the substrate. Glossosomatids are universally scrapers of diatoms, other algae, and fine organic ooze that settles on the surfaces of submerged rocks and other substrate.

Larvae in the suborder Integripalpia, containing 33 families, construct a tubular case. The case, however, can be made from very different materials or formed in peculiar ways in various species (see family summaries below). The larva extends its head and legs out the anterior end of the case as it feeds and crawls on the substrate. To increase the size of the case, they simply extend or add to the anterior end with each larval instar, eventually pupating inside the slightly modified larval case. Case-making larvae are primarily detritivores. They feed by shredding and ingesting dead leaves and other plant parts largely of riparian origin. Predation is also common among the case-makers, but herbivory on living plants is less common. Other case-makers feed by scraping the diatoms, other algae, and fine detritus that makes up the periphyton or biofilm. A very few are filterers or snag drifting prey.

There is broad agreement about the monophyly of 2 of these major taxonomic groups, the Annulipalpia and Integripalpia, and considerable disagreement about the monophyly of "Spicipalpia" and the relative placement of taxa within this group.

Morse (1997) provided a thorough summary of the hypotheses of relationships proposed for the major groups of Trichoptera and also of the status of phylogenetic work at the family and genus level undertaken up to about 1996. Ross (1956, 1967) was the first to identify explicitly any derived characters for caddisfly taxa. He recognized 2 monophyletic suborders, Annulipalpia (equivalent to his superfamily Hydropsychoidea) and Integripalpia (Fig. 53). These subordinal names were first established by Martynov (1924). Ross's Integripalpia contained 2 superfamilies, Rhyacophiloidea and Limnephiloidea. These superfamilies are equivalent to "Spicipalpia" and Integripalpia, as used here. However, Ross's Rhyacophiloidea ("Spicipalpia") was paraphyletic as originally defined. Further, his hypothesis of the relationships among the 3 rhyacophiloid families (Rhyacophilidae [including Hydrobiosidae], Glossosomatidae, and Hydroptilidae) and the Limnephiloidea was based mainly on a presumed evolutionary transformation in larval case/pupal cocoon making behavior. Ross lacked morphological synapomorphies at his Glossosomatidae + Hydroptilidae + Limnephiloidea node and had only 1 at his Hydroptilidae + Limnephiloidea node. Thus his behavioral transformation series is supported by only 1 non-behavioral character.

ANNULIPALPIA (Hydropsychoidea)

Rhyacophilidae (incl. Hydrobiosidae)

Glossosomatidae

Hydroptilidae

SPICIPALPIA (Rhyacophiloidea)

INTEGRIPALPIA (Limnephiloidea)

53

(Ross 1956, 1967)

ANNULIPALPIA

SPICIPALPIA

INTEGRIPALPIA

54

(Weaver 1984)

SPICIPALPIA

ANNULIPALPIA

INTEGRIPALPIA

55

(Wiggins & Wichard 1989)

ANNULIPALPIA

Rhyacophilidae

Hydrobiosidae

Glossosomatidae

Hydroptilidae

INTEGRIPALPIA

56

(Ivanov 2002)

FIGURES 53–56. Phylogenetic relationships of Trichoptera suborders, alternative hypotheses. 53–hypothesis of Ross; 54–hypothesis of Weaver; 55–hypothesis of Wiggins and Wichard; 56–hypothesis of Ivanov. See text for explanation.

Weaver (1984, 1992a, 1992b, also Weaver & Morse 1986) was the first to apply cladistic principles to caddisfly higher-level classification and examined about twice as many morphological characters as Ross (Fig. 54). Weaver (1984) concluded that Spicipalpia (which he treated as an infraorder within a more broadly defined suborder Annulipalpia) was monophyletic and had a sister-taxon relationship to the infraorder Curvipalpia (= Annulipalpia of Ross and as used here). Weaver restricted his concept of Integripalpia to include only the Limnephiloidea of Ross, and this is the sense in which it is used here. Following Ross's (1967) division of Integripalpia into subordinate taxa, Weaver (1984) established the infraorders Plenitentoria, to include Ross's "limnephilid branch," and Brevitentoria, to include Ross's "leptocerid branch." Within the latter he recognized 2 superfamilies, Leptoceroidea and Sericostomatoidea.

Later, in a series of papers, Wiggins and Wichard advocated an evolutionary relationship between Annulipalpia and Integripalpia, based on an interpretation of pupal cocoon evolution in Trichoptera (Wichard 1991, Wichard et al. 1997, Wichard et al. 1993, Wiggins 1992, Wiggins & Wichard 1989) (Fig. 55). Their phylogeny is based on the hypothesis that the closed, semipermeable cocoons of parchmentlike silk found in the spicipalpian families represent the groundplan condition of the order, and the cocoons of permeable silk with ventilation openings found in the Annulipalpia and Integripalpia are derived. A more detailed account of behavioral evolution in Trichoptera is found in the works of Frania and Wiggins (1997) and Wiggins (2004), who hypothesized that the ancestral habitat for the order Trichoptera was in cool, flowing, well-oxygenated

water. This can be contrasted with the theory of Weaver and Morse (1986), who proposed that the ancestral trichopteran habitat was in subterranean silk-lined tubes in saturated soil. However, Kristensen (1997) pointed out that silk-lined tubes in Lepidoptera do not appear until the 8th branch from the base of the tree, in Neolepidoptera (Exoporia), and thus this adaptation cannot be assumed to be ancestral within Trichoptera. Based on their hypothesis of evolution in the group, Wiggins, Wichard, and Frania elevated Weaver's infraorder Spicipalpia to a 3rd suborder, coordinate with Annulipalpia and Integripalpia. According to Wiggins (1992), the pupation hypothesis was not intended as a statement of higher-level trichopteran relationships; the recognition of Spicipalpia was one of convenience, since it serves to focus discussion on the unresolved problem of subordinal relationships in Trichoptera. In terms of phylogeny, these workers preferred to consider the relationships of the 3 suborders as unresolved.

In the study by Frania and Wiggins (1997), the relative relationships among the 3 suborders of Trichoptera were tested using a computer assisted parsimony analysis of 70 morphological larval and adult characters, which included the majority of families in the order. Characters were polarized using a hypothetical caddisfly ancestor, whose character states were inferred through consideration of character states in Mecoptera and Lepidoptera. The results could be considered equivocal, since they do not support either monophyly of "Spicipalpia" or its position as the sister-taxon to Annulipalpia + Integripalpia. The strict consensus phylogeny most closely resembles the hypothesis of Ivanov (1997a, 2002).

Ivanov (2002, see also Ivanov & Sukatcheva 2002) proposed that Hydroptilidae and Glossosomatidae of the "Spicipalpia" are allied to the Integripalpia, and that Rhyacophilidae and Hydrobiosidae are sister taxa allied to the Annulipalpia (Fig. 56). Earlier, Ivanov (1997a) specifically challenged Weaver's hypothesis of spicipalpian monophyly, providing evidence that each of Weaver's 4 spicipalpian apomorphies are plesiomorphic. Ivanov and Sukatcheva (2002) recognized 2 large superordinal-level clades within "advanced Trichoptera" (to distinguish these from extinct Protomeropina): Hydropsychina (Annulipalpia plus Rhyacophilidae and Hydrobiosidae) and Phryganeina (Integripalpia plus Hydroptilidae and Glossosomatidae). Frania and Wiggins similarly found Hydroptilidae to be closely related to Integripalpia, but the relationship of Glossosomatidae was less certain, depending on the analysis performed. Using selected characters, they suggested that Glossosomatidae might be allied to Hydrobiosidae and Rhyacophilidae sister to Annulipalpia, but were uncertain about the relationship of Hydroptilidae. In the cladograms presented, it was sister taxon to the Integripalpia, suggesting that "Spicipalpia" may not be monophyletic.

The first combined molecular and morphological analysis of subordinal relationships in Trichoptera was that of Kjer et al. (2001, 2002), who used a molecular dataset of several gene fragments, including mitochondrial, and nuclear DNA, and also included the morphological characters of Frania and Wiggins. Forty-three of 45 families were included, and both parsimony and likelihood analyses were performed. In Kjer et al.'s analysis, Annulipalpia and Integripalpia were monophyletic and "Spicipalpia" was paraphyletically arranged at the base of the Integripalpia, as in Ross's hypothesis. The relationship of spicipalpians to Integripalpia was strongly supported, and Kjer et al. (2001, 2002) rejected the separation of some families of spicipalpians with Annulipalpia, as in the Ivanov (1997a, 2002) and Frania and Wiggins (1997) morphology-based hypotheses. In fact, a differentially weighted analysis performed by Kjer et al. (2001) of the Frania and Wiggins (1997) morphological data recovered a phylogenetic hypothesis that was identical to that of Ross (1967) (Fig. 53). However, paraphyly of "Spicipalpia" was only weakly supported and the possibility that "Spicipalpia" is monophyletic could not be eliminated. Some partitions of the data supported a monophyletic "Spicipalpia," and by most analytical criteria, a monophyletic "Spicipalpia" was only slightly suboptimal.

An updated phylogeny of Trichoptera was presented by Holzenthal et al. (2007) based on the same 4 independent datasets (nuclear rRNA, EF-1α, COI, and morphology) as in the Kjer et al. phylogeny, but included more complete sequence data for many taxa as well as more taxa (up to 210 taxa representing all families of Trichoptera except Antipodoeciidae). This analysis also included Prather's morphological dataset from her work within the Integripalpia and her re-analysis of some of Frania and Wiggins's character

interpretation and coding (Prather 2002). The most recent analyses were performed using differentially weighted parsimony and Bayesian methods. Results were congruent with previous analyses, with additional resolution at more recent nodes. The following monophyletic clades were strongly supported (Fig. 57): Annulipalpia, Integripalpia, Plenitentoria, Brevitentoria, and Sericostomatoidea. Monophyly of Leptoceroidea was not supported. "Spicipalpia" (Glossosomatidae, Hydrobiosidae, Rhyacophilidae, Hydroptilidae), while not itself monophyletic, grouped with Integripalpia in a strongly supported monophyletic clade. Additional clades supported by the most recent analyses (Holzenthal et al. 2007) (Fig. 57) included, within Annulipalpia, Philopotamoidea (Stenopsychidae + Philopotamidae) sister to Hydropsychidae + Psychomyioidea, with Xiphocentronidae and Psychomyiidae sister families within Psychomyioidea. Within Plenitentoria, Plectrotarsidae emerged as the sister to the remaining taxa in the infraorder, Phryganopsychidae + (Kokiriidae + Pisuliidae) formed a clade sister to the remaining families, and Limnephilidae *sensu lato* was monophyletic (Goeridae, Rossianidae, Uenoidae, Apataniidae + Limnephilidae, *sensu stricto*). Within Brevitentoria, the only suprafamilial groupings that were supported with any confidence were Calamoceratidae + Molannidae and Hydrosalpingidae + Petrothrincidae. The position of Hydroptilidae as sister to Integripalpia was influenced strongly by the morphological data; this relationship was not recovered by any molecular data. The clade "Spicipalpia" + Integripalpia was consistently recovered from a wide variety of analytical methods, and has been robust to the addition of taxa and data. Its recovery relied most heavily on the nuclear rRNA data, and rRNA is evolving at a rate that is appropriate for the resolution of subordinal groupings, at least in Trichoptera.
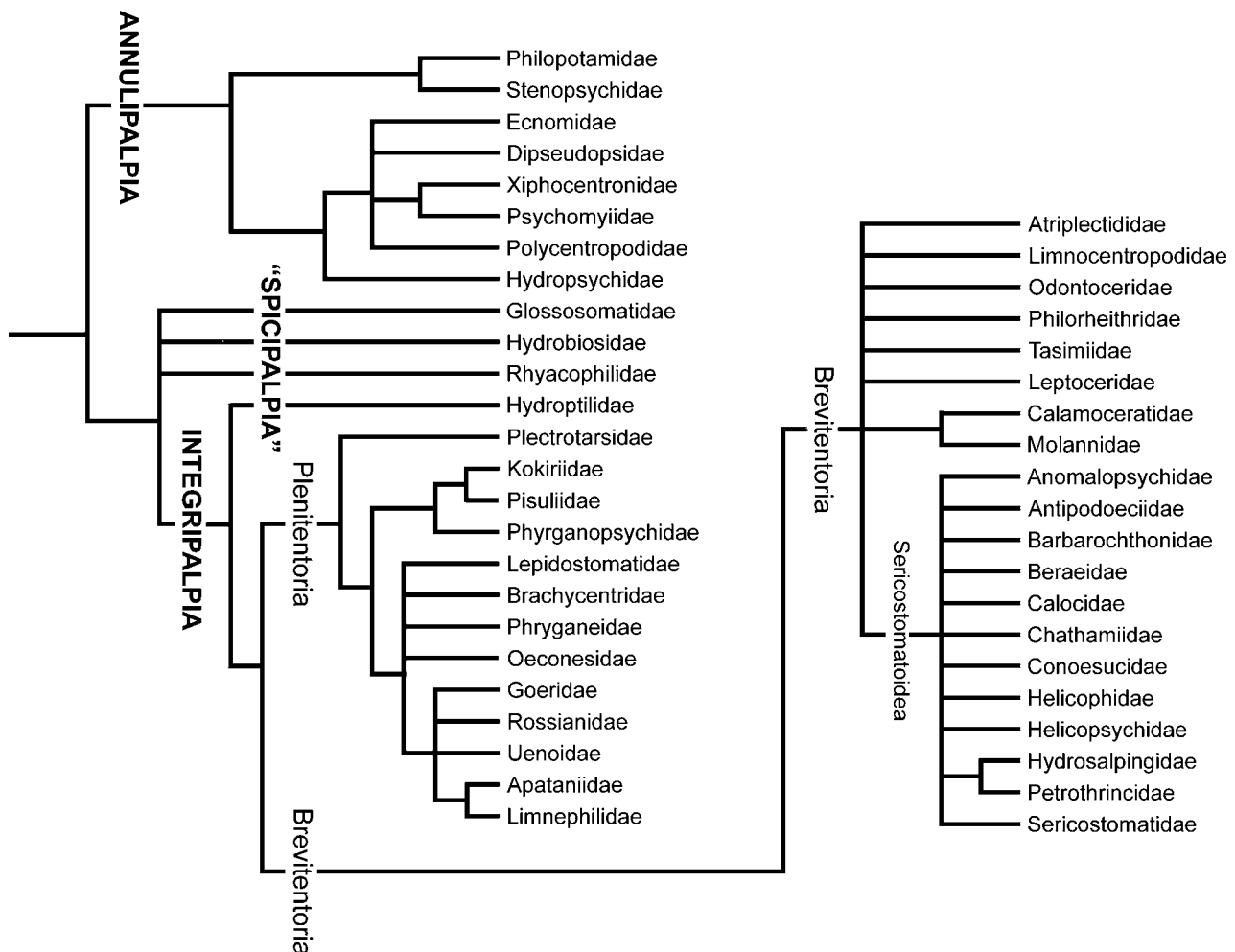
FIGURE 57. Phylogeny of Trichoptera based on Kjer et al. (2001, 2002) and Holzenthal et al. (2007) showing those nodes that were supported by both Bayesian and differentially weighted parsimony analyses. Support was defined as posterior probabilities above 90% in the Bayesian analysis. We also include nodes that were supported by at least 2 independent datasets (see Kjer et al. 2001, fig. 11, for explanation). The placement of Antipodoeciidae within Sericostomatoidea is based on the study by de Moor (in Scott 1993).

In the most recent molecular analysis, compared to earlier ones, relationships among some families within Annulipalpia and Limnephiloidea approached stability. On the other hand, relationships among families of "Spicipalpia," "Leptoceroidea," and Sericostomatoidea are still unresolved. Of particular interest is the question of relationships among families of "Spicipalpia," which remains the major unresolved issue in trichopteran systematics. Additional effort to answer this question is probably warranted, due to its inherent interest and the implications that different patterns of relationships have for the interpretation of the evolution of case and retreat-making behaviors, pupal structures and pupation behavior, and other biological attributes. For a discussion of taxonomic definitions of superfamilies and other subordinal groupings, including morphological characters shared by these groups, see the works of Frania and Wiggins (1997), Ivanov (2002), and Weaver (1984), and references cited therein.

Synopsis of the families

This synopsis includes only extant taxa. About 650 fossil species are known, including case, wing, and body impressions from the late Paleozoic and early Mesozoic as well as Baltic, Dominican, and other amber inclusions from the Cenozoic. Ivanov and Sukatcheva (2002), Wichard (2007), and Ulmer (1912) provided extensive reviews of this fauna. In preparing this synopsis, extensive use was made of the *Trichopterorum Catalogus* (Fischer 1960-1973), Trichoptera World Checklist (Morse 2006), and the print and online versions of *Zoological Record* available through the University of Minnesota Libraries. Figures for numbers of taxa should be considered approximate in most cases and quickly subject to change; new taxa are being described frequently, especially from the Neotropical and Oriental regions. References to works on phylogenetic relationships include only those published since Morse's (1997) review. Literature cited in this section and throughout this review is that abstracted by *Zoological Record* through the end of October, 2007. While we have done our best to include all pertinent taxonomic literature, some references may have been inadvertently omitted; we have not tried to review the numerous ecological papers published on Trichoptera. Families are listed in alphabetical order by suborder for Annulipalpia and "Spicipalpia," and alphabetically by infraorder and superfamily for Integripalpia (see Fig. 57 and Table 2).

ANNULIPALPIA

Dipseudopsidae: Dipseudopsidae is a relatively small family of about 170 species originally recognized by Ulmer (1904) as a subfamily of Polycentropodidae. Similarities in the larvae in the 2 major subfamilies provided convincing evidence that *Hyalopsyche*, at one time assigned to a separate family, Hyalopsychidae Lestage (e.g., Neboiss 1989), should be included with *Dipseudopsis* in the Dipseudopsidae (Wells & Cartwright 1993). Currently, 8 genera are recognized in 3 subfamilies: Dipseudopsinae with *Dipseudopsis* Walker (ca. 80 species widespread in Africa and Asia), *Limnoecetis* Marlier (2 African species), and *Protodipseudopis* Ulmer (5 African species); Hyalopsychinae with *Hyalopsyche* Ulmer (10 Asian species), *Hyalopsychella* Ulmer (2 species from Borneo and Sulawesi), and *Phylocentropus* Banks (ca. 10 species from eastern North America, Southeast Asia, and Japan); and Pseudoneureclipsinae with *Pseudoneureclipsis* (more than 60 species from the western Palearctic, Oriental, and Afrotropical regions) and *Antillopsyche* Banks (4 species from the Greater Antilles). The latter subfamily was only relatively recently transferred to Dipseudopsidae from Polycentropodidae (Li et al. 2001, Tachet et al. 2001), based on cladistic considerations. Only *Pseudoneureclpsis* Ulmer was officially transferred to Dipseudopsidae, but *Antillopsyche* would have to be transferred also by inference, since it was placed in the same subfamily by Flint (1964). Larvae construct and live in elaborate nets, formed into elongate silken tubes covered with sand. These tubes are buried in the sediment in *Phylocentropus*, functioning like a siphon with the larva occupying a lateral branch. The larvae of

Pseudoneureclipsinae have a very different morphology and ecology from typical Dipseudopsidae (Flint 1964, Tachet et al. 2001) and their placement in this family should be considered provisional.

Ecnomidae: This is a small to moderately sized family established by Ulmer (1903) first as a subfamily of Hydropsychidae, later as a subfamily within Psychomyiidae, and then as a family (Lepneva 1970), with the majority of the known diversity found in a single genus, *Ecnomus* McLachlan. However, this has changed in recent years as many new species and even genera have been recognized, primarily from the Australasian region. Eight genera are recognized, of which *Ecnomus* is the largest, with more than 260 species widespread in the Palearctic, Oriental, Afrotropical, and Australasian regions. *Austrotinodes* Schmid is largely endemic to the Neotropics with about 40 species, a few extending into the extreme southwestern USA. A 2nd New World genus, *Chilocentropus* Navás from Chile, is a *nomen dubium*; its type, of unknown sex, is presumed lost. The Australasian fauna has several endemic genera, each with about 10-20 species: *Agmina* Ward and Schefter (New Caledonia), *Daternomina* Neboiss (Australia, mostly Tasmania), and *Ecnomina* Kimmins (Australia, New Zealand, and New Caledonia). Two genera, with about 15 species total, are endemic to Africa: *Parecnomina* Kimmins and *Psychomyiellodes* Mosely. Li and Morse (1997c) provided a phylogenetic analysis of the 5 genera then known in the family and of the Chinese species of *Ecnomus*. The larvae of *Ecnomus* are well known (Lepneva 1970, Scott 1968, Ulmer 1957) as are those of *Austrotinodes* (Bowles 1995, Wiggins 1996). They construct tubes of silk and fine sand grains that are attached to rocks, wood, or submerged vegetation, and occur in both running and standing water.

Hydropsychidae: Hydropsychidae, with about 1,500 described species, is the 3rd largest family in Trichoptera and the most diverse of the net-spinning annulipalpians. It was established by Curtis (1835) and, like most of the families described early in the history of the order, its composition has changed substantially over the years, achieving its modern definition with the work of Ulmer (1907b). Five subfamilies are currently recognized: Arctopsychinae, Macronematinae, Hydropsychinae, Diplectroninae, and Smicrideinae. The monophyly and phylogenetic relationships among these subfamilies has been the subject of recent studies (Geraci et al. 2005, Schefter 1996, 2005), but a stable generic classification has yet to be achieved. Arctopsychinae, often recognized as a separate family (e.g., Fischer 1963, Schmid 1968), is widespread in the Holarctic and Oriental regions. Three genera are recognized, with *Arctopsyche* McLachlan and *Parapyche* Betten the largest, each with about 2 dozen species, and *Maesaipsyche* Malicky and Chantaramongkol the smallest, with 2 Southeast Asian species. Macronematinae, with 17 genera, is found in all biogeographical regions. The largest genera include *Leptonema* Guerin-Meneville with more than 125 species, largely in the Neotropics, but with a significant fauna in Africa and Madagascar and some extending into the southwestern USA, and the cosmopolitan *Macrostemum* Kolenati, with about 100 species. Other genera, with about 20-30 species each, include *Macronema* Pictet (Neotropical), *Amphipsyche* McLachlan (Afrotropical, Oriental, Palearctic), and *Polymorphanisus* Walker (Afrotropical, Oriental). The other genera each contain 10 or fewer species and include: *Aethaloptera* Brauer (India, Africa, Russian far east), *Baliomorpha* Neboiss (Australasian), *Blepharopus* Kolenati (Neotropical), *Centromacronema* Ulmer (Neotropical), *Leptopsyche* McLachlan (Australasian), *Oestropsyche* Brauer (Sri Lanka), *Plectromacronema* Ulmer (Neotropical), *Protomacronema* Ulmer (Afrotropical), *Pseudoleptonema* Mosely (Oriental), *Pseudomacronema* Ulmer (Neotropical), *Synoestropsis* Ulmer (Neotropical), and *Trichomacronema* Schmid (Oriental). Hydropsychinae currently contains 19 genera from all biogeographic regions, although it barely reaches the northern Neotropical region, and is absent from South America, where it is replaced by species of Smicrideinae and Macronematinae. The largest genera include *Hydropsyche* Pictet (ca. 275 species), *Ceratopsche* Ross and Unzicker, often considered a subgenus of *Hydropsyche* (ca. 100 species), and *Cheumatopsyche* Wallengren (ca. 260 species). Other, medium-sized genera (10-50 species) include *Potamyia* Banks (mostly eastern Palearctic and Oriental, but with 1 Nearctic species), *Hydromanicus* Brauer (Afrotopical, Oriental), and

Calosopsyche Ross and Unzicker (Central America, Greater Antilles). The other genera contain less than 10 species each and include: *Abacaria* Mosely, *Aoteapsyche* McFarlane, *Austropsyche* Banks, *Caledopsyche* Kimmins, and *Orthospsyche* McFarlane (Australasian), *Herbertorossia* Ulmer (Australasian, Oriental), *Hydatomanicus* Ulmer (Oriental), *Hydatopsyche* Ulmer and *Hydronema* Martynov (Oriental, Palearctic), *Symphitopsyche* Ulmer (Afrotopical), *Mexipsyche* Ross and Unzicker and *Plectropsyche* Ross (Neotropical), and *Streptopsyche* Ross and Unzicker (Greater Antilles). The subfamily Smicrideinae was relatively recently established by Schefter (1996). The species had been previously placed in Hydropsychinae. Smicrideinae contains only 3 genera: *Smicridea* McLachlan, with 2 large subgenera, *Smicridea* and *Rhyacophylax* Müller (175 species total, mostly Neotropical in distribution, but extending into the southwestern United States), *Smicrophylax* Neboiss (5 Australasian species), and *Asmicridea* Mosely (2 Australasian species). Diplectroninae is a small subfamily with most of its diversity in a single genus, *Diplectrona* (ca. 120 species from all biogeographic regions, but concentrated in the Oriental and Australasian regions and absent from South America). Schefter (1996) provided evidence that neither the genus nor the subfamily may be monophyletic. Other genera included in Diplectroninae, none with more than a dozen species, include *Homoplectra* Ross (North America), *Oropsyche* Ross (eastern North America), *Sciadorus* Barnard (South Africa), and *Diemeniluma* Neboiss (Tasmania). In addition to the generic phylogenetic studies listed above, Mey (1996, 1999c, 2003) has provided important phylogenetic and biogeographic analyses of southeast Asian *Hydropsyche*. The nets of hydropsychids are typically attached to rocks in flowing waters and are used to capture detritus or microorganisms from the stream, but some species, particularly those in the subfamily Arctopsychinae capture and consume live prey. Net structure and function varies considerably. In the genus *Macrostemum*, a subdivided subterranean structure is constructed of rocks to function like a siphon, drawing the current over a specially constructed net, which is tended by the larva. Larvae of hydropsychids are often very abundant and are important in the nutrient dynamics of the rivers and streams they inhabit.

Philopotamidae: Philopotamidae was established by Stephens (1829) as 1 of only 3 families then recognized for Trichoptera. Although the family, as originally conceived, included both *Chimarra* Stephens and *Philopotamus* Stephens, representing the 2 major lineages now recognized for Philopotamidae, it also included taxa in such widely diverse families as Psychomyiidae, Polycentropodidae, Hydroptilidae, Goeridae, and Lepidostomatidae. The genus *Chimarra* was subsequently transferred to other families (Psychomyiidae, Rhyacophilidae, Hydropsychidae) and did not return to Philopotamidae until Ulmer (1907b) defined the family in its modern concept. Ross (1956) produced the only general hypothesis for evolutionary trends in the family, although he left relationships among the major lineages largely unresolved. More recently Blahnik (1997, 1998, 2002, 2005) and Flint (1998) provided comprehensive reviews of all Neotropical species in the family except those in *Wormaldia*, including analyses of phylogenetic relationships. Three subfamilies are currently recognized for the family. Paulianodinae contains the monotypic genus *Paulianodes* Ross from Madagascar. However, the genus contains about a dozen undescribed species (Gibon et al. 1999). Ross (1956) considered *Paulianodes* the most primitive genus in the family, based on wing venational characters. Chimarrinae contains 3 genera: *Chimarra* Stephens, with about 570 described species and many additional undescribed ones, found in all biogeographical regions, is one of the largest genera in the order Trichoptera; *Chimarrhodella* Lestage (11 species) is Neotropical in distribution; and *Edidiehlia* Malicky is a monotypic genus from Sumatra. The subfamily Philopotaminae contains 16 genera, most of relatively restricted distribution: the largest is *Wormaldia* McLachlan (130 species), from all biogeographical regions (although barely reaching the Australasian); *Dolophilodes* Ulmer (ca. 50 species), widespread in the Nearctic, Palearctic, and Oriental regions; *Gunungiella* Ulmer (60+ species) and *Kisaura* Ross (30+ species), from the Oriental region; *Hydrobiosella* Tillyard (25 species), from the Australasian region; *Sortosa* Navás (20 species), from the Chilean subregion of the Neotropics; *Alterosa* Blahnik (22 species), from southern and southeastern Brazil; and *Philopotamus* Stephens (10 species), from Europe. Small genera, each with less than

5 species, include: *Cryptobiosella* Henderson, *Neobiosella* Wise, and *Xenobiosella* Henderson, all from New Zealand; *Dolomyia* Schmid and *Dolopsyche* Schmid, from India; *Thylakion* Barnard, from Africa; and *Fumonta* Ross and *Sisko* Ross, from North America. Despite the quite divergent genitalia of adult males in Chimarrinae and Philopotaminae, larvae throughout the family have a very uniform appearance and construct similar nets, elongate sock-like tubes of very fine mesh size, generally attached to the underside of rocks. Larvae graze microorganisms and detritus from the net by means of a membranous, T-shaped labrum, a unique and diagnostic character for the family.

Polycentropodidae: The family was established by Ulmer (1903), originally as a subfamily, and subsequently raised to family level (Ulmer 1906). As originally formulated, it also included taxa now placed in Dipseudopsidae. Some workers considered the family a subfamily of Psychomyiidae for many years after its establishment. As currently recognized, the family includes 2 subfamilies. Kambaitipsychinae contains only 1 genus, *Kambaitipsyche* Malicky, with 2 species from Thailand and Burma. It was only speculatively placed in the family Polycentropodidae when the genus was established and differs significantly from other polycentropodids (Malicky 1991). It is quite possible that its phylogenetic position will be changed as a result of future research. Polycentropodinae contains a number of genera whose definition remains problematic, confounded in part by the lumping of the genera *Plectrocnemia* Stephens, *Holocentropus* McLachlan, and *Polycentropus* Curtis into the genus *Polycentropus* by New World workers and by over reliance on venational characters in the definition of genera. Accordingly, the following lists of generic abundance should be considered provisional estimates, based on the current taxonomy. It should be expected that the number of genera and their composition will change over time. Large genera include: *Polycentropus* Curtis (> 170 species) from all biogeographical regions, *Polyplectropus* Ulmer (>150 species) from all biogeographical regions except the western Palearctic, *Plectrocnemia* Stephens (ca. 100 species) from all regions except the Afrotropical and Neotropical, *Holocentropus* McLachlan (17 species) from the Holarctic and Oriental regions, *Cernotina* Ross (ca. 60 species) predominantly Neotropical, but also North America, *Nyctiophylax* Brauer (including subgenus *Paranyctiophylax* Neboiss) (90 species) from all biogeographical regions except the western Palearctic, and *Cyrnus* Stephens (ca. 15 species) from the Palearctic. Smaller genera, with 10 or fewer species each, include: *Cyrnellus* Banks from the Nearctic and Neotropical regions, *Adectophylax* Neboiss and *Tasmanoplegas* Neboiss from the Australasian region, *Cyrnodes* Ulmer and *Eodipseudopsis* Marlier from the Afrotropical region, *Pahunamaya* Schmid from the Afrotropical and Oriental regions, *Cyrnopsis* Martynov from the Oriental region, *Neucentropis* Martynov from the Palearctic region, *Neureclipsis* McLachlan from the Holarctic and Australasian regions, and *Neurocentropus* Navás, 1 *nomen dubium* species from Spain. A large number of genera and species are also known from amber and other fossil deposits; the family is especially diverse in Baltic amber deposits. Since Morse's review of phylogenetic studies within the Trichoptera, Li and Morse (1997b) and Li et al. (2001) published papers investigating taxonomic and phylogenetic issues within the family. Larvae of polycentropodids construct a variety of different nets, either as a larval retreat or as a capture net; many or most of the species are predaceous, often recognizable by having mottled heads and accessory teeth on their anal claws. Adults are generally grey, tawny, or brown caddisflies, often with golden or white spots and patterns on the wings; a few are black.

Psychomyiidae: The family name Psychomyiidae was established by Walker (1852) and has been variably defined throughout the history of caddisfly taxonomy. At one time it included most of the taxa of Annulipalpia other than Philopotamidae and Hydropsychidae. As other families in Annulipalpia were recognized, the name has been more restrictively used. As currently defined, Psychomyiidae is a moderately sized family of net making caddisflies, widespread, but largely centered in the Oriental region and absent in the Neotropical region. Only 1 endemic genus, *Zelandoptila* Tillyard, with 2 species, is known from New Zealand and Australia. An additional 8 genera are known, of which *Tinodes* Curtis with 200+ species in the

Palearctic, Oriental, Afrotropical and western Nearctic regions, and *Psychomyia* Latreille with almost 140 species predominantly from India, and eastern and southeastern Asia, but with several species also from the Holarctic region, are by far the largest. In a gesture of immeasurable kindness, Schmid (1997) established over 40 patronyms for contemporary caddisfly workers when describing new species of Indian *Psychomyia*. *Paduniella* Ulmer, with about 50 species, is predominantly Oriental, extending to Indonesia and the Philippines, but also to Africa, the Palearctic, and (1 species) North America. Other, much smaller genera, include *Eoneureclipsis* Kimmins (India and Southeast Asia), *Lype* McLachlan (Holarctic, Oriental, and Afrotropical regions), *Metalype* Klapalek (Palearctic and Oriental regions), *Padangpsyche* Malicky (1 species from Sumatra), and *Psychomyiella* Ulmer (Oriental and eastern Palearctic regions). Li and Morse (1997a, 1997d) provided cladistic analyses of the genera in the family and of the species in *Paduniella*, respectively. Most larvae of psychomyiids construct nets formed into elongate, irregularly shaped silken tubes covered with sand and debris and attached to the surface of rocks, tree limbs, or other substrates, in or somewhat above the water level. The larvae apparently graze on diatoms and other algae growing in or near the tubes; they are known to even cultivate algae in the tube's silken mesh, eating the old portions of the tube while building new portions to serve as silken gardens. The tubes are extended as the larva grows or are moved as the larva interacts with other larvae (Hasselrot 1993).

Stenopsychidae: This is a small family of large and rather remarkable caddisflies, some very brightly colored, whose larvae are found in elongate tubular nets attached to rocks in the strong currents of relatively pristine rivers. The family name was established by Martynov (1926), who included the 3 genera now recognized: *Stenopsyche* McLachlan (ca. 80 species, widespread in the eastern Palearctic and Oriental regions, but with 1 Afrotropical species), *Stenopspychodes* Ulmer (9 species from Australia), and *Pseudostenopsyche* Döhler (3 species from southern Chile). The family was subsequently revised by Schmid (1969). *Stenopsychodes* was originally placed in Polycentropodidae, mostly because adults lack ocelli. It is now placed in its own subfamily, Stenopsychodinae. However, relationships among the 3 genera have not been resolved and *Pseudostenopsyche* is placed in Stenopsychodinae largely because of its plesiomorphic retention of ocelli. Larvae of several species of *Stenopsyche* have been described and their biology is well known (Tanida 2002, provided a detailed account). The larva has a very elongate head and sclerotized labrum with membranous margins bearing dense fringes of short setae. The labrum, with its setal brush, is apparently used to groom the tubular nets, much as is the membranous labrum of philopotamids. The diet is said to be microphagous (Lepneva 1970), but larvae of other species feed on insects as well as organic material (Tanida 2002). Larvae of *Pseudostenopsyche* and *Stenopsychodes* have not been described. The adults have prominent wing patterns, often with black and golden hairs, and in some species the mouthparts are extended and the mandibles are prominent (Schmid 1969).

Xiphocentronidae: The family Xiphocentronidae was established by Ross (1949) for what he considered a very unusual small black caddisfly from Mexico. The family initially included only 3 species, the type species, *Xiphocentron bilimeki* Brauer, and 2 new species described by Ross, 1 from Mexico and the other from China, the latter now placed in *Melanotrichia*. When the larva of *Xiphocentron* was described by Edwards (1961), he recognized its close similarity to larvae of Psychomyiidae (as currently defined) and proposed that Xiphocentronidae should probably be synonymized with it. Larvae of both families have a similar overall appearance, with stout body and short legs, and a modified prothoracic trochantin, although that of Xihocentronidae is less hatchet-shaped and partly membranous basally. Schmid (1982) revealed the considerable diversity and widespread distribution of the family in a monograph devoted to it. The family status of Xiphocentronidae has generally been recognized since then. Schmid transferred several genera to the family and established the current taxonomic infrastructure, including the establishment of 4 new genera. His work included some 93 species, 73 newly described, or over half the total of about 140 now known for the

family. As currently defined, Xiphocentronidae is a small family of 7 genera, including *Abaria* Mosely (ca. 20 species from the Oriental and Afrotropical regions), *Cnodocentron* Schmid (12 species from the southwestern USA to northern South America, as well as India and Southeast Asia), *Drepanocentron* Schmid (ca. 30 species from India, Malaysia, and the Philippines), *Machairocentron* Schmid (5 species from Central America and northern South America), *Melanotrichia* Ulmer (ca. 30 species from the eastern Palearctic and Oriental regions), *Proxiphocentron* Schmid (3 species from India and Southeast Asia), and *Xiphocentron* Brauer (ca. 45 species widespread in the Neotropical region, extending into Mexico, the southwestern USA, and the Greater Antilles). Larvae apparently graze diatoms and algae from rocks and typically inhabit elongate silken tubes covered with fine sand grains, either below the water line or extending onto the splash zone above the water surface, much like those of psychomyiids. However, Muñoz-Quesada and Holzenthal (1997) described the larva of a species of *Xiphocentron* from Costa Rica with the unusual habit of constructing a portable tube, short and arched, with openings at the anterior and posterior ends, giving the structure a shape something like that of a classic telephone handle.

"SPICIPALPIA"

Glossosomatidae: This taxon was established by Wallengren (1891), originally as a subfamily of Rhyacophilidae. Glossosomatidae was officially raised to family level by Ross (1956). Three subfamilies are recognized. Agapetinae has 3 genera, *Agapetus* Curtis (more than 200 species from all biogeographical regions, except the Neotropical), *Catagapetus* McLachlan (2 western Palearctic species), and *Electragapetus* Ulmer, originally described from Baltic amber, but now with 3 extant species from the eastern Palearctic. Glossosomatinae has 2 genera, *Glossosoma* Curtis (120+ species from the Holarctic and Oriental regions) and *Anagapetus* Ross (6 species from western North America). Protoptilinae, whose tiny species were at one time included in Hydroptilidae (e.g., Mosely 1937), has 17 genera from the Neotropical, Nearctic, Palearctic, and Oriental regions. It is most diverse in the Neotropical region, where it is the only subfamily recognized. Genera include: *Campsiophora* Flint, *Cariboptila* Flint, and *Cubanoptila* Sykora, all from the Greater Antilles, *Canoptila* Mosely (southeast Brazil), *Culoptila* Mosely (North and Central America), *Itauara* Müller (Neotropical), *Mastigoptila* Flint (southern Chile and adjacent Argentina), *Matrioptila* Ross (eastern USA), *Merionoptila* Schmid (Argentina), *Mexitrichia* Mosely (Neotropical), *Mortoniella* Ulmer (Neotropical), *Nepaloptila* Kimmins (Oriental), *Padunia* Martynov (Oriental and eastern Palearctic), *Poeciloptila* Schmid (Oriental), *Protoptila* Banks (Nearctic and Neotropical), *Scotiotrichia* Mosely (Argentina), *Temburongpsyche* Malicky (Brunei), and *Tolhuaca* Schmid (Chile, southeast Brazil). Most of these genera have only a few to several species, but *Protoptila* has about 90 species, and *Mexitrichia* and *Mortoniella* have about 25-30 species each. The Neotropical diversity is very incompletely described; many additional new species are known and new collections regularly produce an abundance of others. Robertson and Holzenthal (2006) and Yang and Morse (2002) discussed phylogenetic considerations within and among certain genera.

Hydrobiosidae: Hydrobiosidae is a moderately sized family, originally established by Ulmer (1905) as a subfamily of Rhyacophilidae. The entire family was the subject of an extensive global revision by Schmid (1989). In many respects, Hydrobiosidae represents the Southern Hemisphere or Gondwanan equivalent of Rhyacophilidae. In contrast to the lack of generic diversity in Rhyacophilidae, some 50 genera are recognized for Hydrobiosidae. Most of the generic diversity is found in either the Chilean subregion of the Neotropics or in the Australasian region. However, in each region there is a diverse genus with species that extend well beyond the ancestral Gondwanan range of the family. In the Neotropics, the genus *Atopsyche* Banks (ca. 120 species) is widespread and extends northward to Central America, Mexico, and the southwestern United States. Within the Australasian fauna, the genus *Apsilochorema* (50+ species) extends into the Oriental and western Palearctic regions. A review of the species groups of *Apsilochorema* and their relationships was provided by Mey (1999a) and Ward et al. (2004) presented a phylogeny of the genera in the family. Blahnik

and Gottschalk (1997) discussed the phylogenetic position of some Costa Rican species of *Atopsyche*. The remaining genera include: *Amphichorema* Schmid, *Androchorema* Flint, *Apatanodes* Navás, *Australobiosis* Schmid, *Cailloma* Ross and King, *Clavichorema* Schmid, *Heterochorema* Schmid, *Iguazu* Ross and King, *Isochorema* Schmid, *Metachorema* Schmid, *Microchorema* Schmid, *Neoatopsyche* Schmid, *Neochorema* Schmid, *Neopsilochorema* Schmid, *Nolganema* Navás, *Parachorema* Schmid, *Pomphochorema* Flint, *Pseudoradema* Schmid, *Rheochorema* Schmid, *Schajavskoya* Flint, and *Stenochorema* Schmid from the Chilean subregion of the Neotropics, with a few extending northward along the Andes; and *Allobiosis* Mosely, *Allochorema* Mosely, *Atrachorema* McFarlane, *Austrochorema* Mosely, *Costachorema* McFarlane, *Edpercivalia* McFarlane, *Erichorema* Ward, *Ethochorema* Neboiss, *Hydrobiosis* McLachlan, *Hydrochorema* Tillyard, *Ipsebiosis* Neboiss, *Koetonga* Neboiss, *Megogata* Neboiss, *Moruya* Neboiss, *Neurochorema* Tillyard, *Poecilochorema* Schmid, *Psyllobetina* Banks, *Psilochorema* McLachlan, *Ptychobiosis* Neboiss, *Synchorema* Tillyard, *Tanjilana* Neboiss, *Tanorus* Neboiss, *Taschorema* Mosely, *Tiphobiosis* Tillyard, *Traillochorema* McFarlane, *Ulmerochorema* Kimmins, and *Xanthochorema* Kimmins from the Australasian region (Australia, New Zealand, New Guinea, and New Caledonia). Most of these genera have only a few species, but some contain 10-20 or so. Larvae are free-living and actively predaceous; no structure is constructed by the larva until pupation, when a dome-shaped pupal chamber is built of rocks and cemented to the substrate. In larvae of many genera of Hydrobiosidae, the shortened foretibia and tarsus close against a concave extension of the femur, producing a chelate foreleg useful for grasping and holding prey. Adult males are remarkable for the complexity and variability of their genitalia.

Hydroptilidae: This family of caddisflies is the smallest in the order in terms of body size (adults range from about 1.5 mm to about 5 mm or so), but it is the largest in species diversity, with about 2,000 described species found on every habitable continent. The family was established by Stephens (1836) and was recognized as a subfamily of Phryganeidae by very early workers (e.g., Westwood 1840), but the distinctive nature of the family was long recognized (Pictet 1834). The family is divided into 2 subfamilies, Hydroptilinae Stephens 1836, and Ptilocolepinae Martynov 1913, although Martynov (1913) considered the later a subfamily of Rhyacophilidae. Recently, Malicky (2001, 2005) elevated Martynov's subfamily to full family status, Ptilocolepidae Martynov 1913. For the purposes of this review, however, we retain its position as a subfamily within Hydroptilidae. It should be noted that in recent molecular studies (Holzenthal et al. 2007, Kjer et al. 2001, 2002), *Ptilocolepus* and *Palaeagapetus* consistently grouped with other Hydroptilidae, making their elevation to family a redundant taxonomic change that adds no new information to our current understanding of family relationships and loses information about the phylogenetic relationships of these genera with other hydroptilids. Wiggins (2004) suggested that taxonomy progresses best when based on rigorous analysis of phylogenetic relationships; such an analysis of the Hydroptilidae has not been done since Marshall's (1979) review of the family. Examples of such studies on subsets of hydroptilid genera are those of Kjaerandsen (1997, 2004, Kjaerandsen & Andersen 2002). *Ptilocolepus* Kolenati (Europe, India, Southeast Asia) and *Palaeagapetus* Ulmer (North America, far east of Russia, Japan) are small genera of about 10 species each, noted for their primitive wing venation. The nominotypical subfamily contains about 70 genera, divided into 6 tribes; 6 genera are *incertae sedis* in the subfamily (Marshall 1979, Morse 2006) (Table 3). Three tribes are largely endemic to the Neotropics, Leucotrichiini Flint, Neotrichiini Ross, and Ochrotrichiini Marshall, although some genera, e.g., *Leucotrichia* Mosely, *Neotrichia* Morton, and *Ochrotrichia* Mosely, the later 2 with well over 100 species each, have significant diversity well into North America. The Hydroptilini Stephens is primarily Old World in distribution, with 7 and 4 of its 23 genera endemic to Australasia and the Afrotropics, respectively; none of these genera have more than about 1 dozen species, and most have only 1 or a few. Additional monotypic genera include *Hydroptilina* Martynov (Russian Far East), *Paucicalcaria*

TABLE 3. The genera of Hydroptilinae and their distribution. Adapted from Marshall (1979) and Morse (2006). (Afr=Afrotropical, Au=Australasian, Hol=Holarctic, Na=Nearctic, Neo=Neotropical, Or=Oriental, Pa=Palearctic).

Tribe Hydroptilini Stephens

Acanthotrichia Wells, 1982 . . . . Au
Acritoptila Wells, 1982. . . . . Au
Agraylea Curtis, 1834. . . . . Hol
Allotrichia McLachlan, 1880 . . . . Pa
Austratrichia Wells, 1982. . . . . Au
Cyclopsiella Kjaerandsen, 1997 . . . . Afr
Dhatrichia Mosely, 1948 . . . . Afr
Hellyethira Neboiss, 1977 . . . . Au, Pa, Or
Hydroptila Dalman, 1819 . . . . Cosmopolitan
Hydroptilina Martynov, 1934. . . . . Pa
Jabitrichia Wells, 1990 . . . . Afr, Au, Or
Microptila Ris, 1897. . . . . Afr, Or, Pa
Missitrichia Wells, 1991. . . . . Au
Mulgravia Wells, 1982. . . . . Au
Oxyethira Eaton, 1873 . . . . Cosmopolitan
Paroxyethira Mosely, 1924 . . . . Au
Paucicalcaria Mathis and Bowles, 1989 . . . . .Na (Arkansas)
Tangatrichia Wells and Andersen, 1995 . . . . Afr
Tricholeiochiton Kloet and Hincks, 1944. . . . . Au, Neo, Or, Pa
Ugandatrichia Mosely, 1939 . . . . .Afr, Au, Neo
Vietrichia Olah, 1989 . . . . Or (Vietnam)
Wlitrichia Kjaerandsen, 1997. . . . . Afr
Xuthotrichia Mosely, 1934. . . . . Au

Tribe Leucotrichiini Flint, 1970

Abtrichia Mosely, 1939 . . . . Neo
Acostatrichia Mosely, 1939 . . . . Neo
Alisotrichia Flint, 1964. . . . . Neo (+sw USA)
Anchitrichia Flint, 1970 . . . . Neo
Ascotrichia Flint, 1983 . . . . Neo
Betrichia Mosely, 1939 . . . . Neo
Celaenotrichia Mosely, 1934 . . . . Neo
Cerasmatrichia Flint, Harris, and Botosaneanu, 1994 . . . . Neo
Ceratotrichia Flint, 1992 . . . . Neo
Costatrichia Mosely, 1937. . . . . Neo
Eutonella Müller, 1921. . . . . Neo
Leucotrichia Mosely, 1934. . . . . .Neo, Na
Mejicanotrichia Harris and Holzenthal, 1997 . . . . Neo (Mexico)
Peltopsyche Müller, 1879. . . . . Neo
Scelobotrichia Harris and Bueno-Soria, 1993 . . . . Neo
Zumatrichia Mosely, 1937 . . . . Neo (+sw USA)

Tribe Neotrichiini Ross, 1956

Kumanskiella Harris and OS Flint, 1992 . . . . Neo
Mayatrichia Mosely, 1937 . . . . .Neo, Na
Neotrichia Morton, 1905 . . . . .Neo, Na
Taraxitrichia Flint and Harris, 1991. . . . . .Neo

Tribe Ochrotrichiini Marshall, 1979

Metrichia Ross, 1938 . . . . Neo (+sw USA)
Ochrotrichia Mosely, 1934 . . . . .Neo, Na
Rhyacopsyche Mueller, 1879 . . . . Neo

......continued

TABLE 3 (continued)

Tribe Orthotrichiini Nielsen, 1948

Ithytrichia Eaton, 1873 . . . . Hol, Or

Nothotrichia Flint, 1967 . . . . Neo, Na

Orthotrichia Eaton, 1873 . . . . Cosmopolitan

Tribe Stactobiini Botosaneanu, 1956

Bredinia Flint, 1968 . . . . Neo

Byrsopteryx Flint, 1981 . . . . Neo

Catoxyethira Ulmer, 1912 . . . . Au, Or

Chrysotrichia Schmid, 1958 . . . . Au, Or

Flintiella Angrisano, 1995 . . . . Neo

Niuginitrichia Wells, 1990 . . . . Au

Orinocotrichia Harris, Flint, and Holzenthal, 2002 . . . . Neo

Parastactobia Schmid, 1958 . . . . Or

Plethus Hagen, 1887 . . . . Or

Scelotrichia Ulmer, 1951 . . . . Old World

Stactobia McLachlan, 1880 . . . . Old World

Stactobiella Martynov, 1924 . . . . Hol, Or

Tizatetrichia Harris, Flint, and Holzenthal, 2002 . . . . Neo

incertae sedis

Caledonotrichia Sykora 1967 . . . . Au (New Caledonia)

Dibusa Ross, 1939 . . . . Na

Dicaminus Mueller, 1879 . . . . Neo

Macrostactobia Schmid, 1958 . . . . Or

Maydenoptila Neboiss, 1977 . . . . Au

Orphninotrichia Mosely, 1934 . . . . Au

Mathis and Bowles (Arkansas, USA), and *Vietrichia* Olah (Vietnam). *Agraylea* Curtis occurs across the Holarctic and has about 20 species. The other Hydroptilini genera are more widespread across several biogeographical regions and include 2 large cosmopolitan genera, *Hydroptila* Dalman with about 400 described species and *Oxyethira* with about 200. Orthotrichiini is a small tribe of 3 genera, of which *Orthotrichia* is cosmopolitan and contains over 150 species. Stactobiini is a heterogeneous assemblage of genera endemic to a single region or more broadly distributed across several regions; *Stactobia* is the most species rich with about 150 species found only in the Old World. Nielsen (1948) studied the biology of Hydroptilidae. Hydroptilid larvae are highly diverse in form, habitat, and feeding behavior. Although most construct cases of silk or sand, some construct flat, fixed shelters, while others remain free-living until pupation. Many genera remain unknown in the larval stage. The family is the *terra incognita* of Trichoptera (Flint 1992b).

Rhyacophilidae: Rhyacophilidae is a relatively large family, originally established by Stephens (1836). At one time the family included also Glossosomatidae and Hydrobiosidae and other taxa, but its definition has progressively become more restricted. Evolutionary relationships of the family were discussed by Ross (1956) and the family was the subject of a large revision by Schmid (1970). The family is predominantly north temperate and is found in North America, Europe, and Asia, but also extends into India and the tropical areas of southeastern Asia. Currently most of the diversity is included in a single genus, *Rhyacophila* Pictet, the largest genus in Trichoptera, with over 700 species and additional ones regularly being described. In addition to the landmark works of Ross and Schmid on *Rhyacophila*, Prather and Morse (2001) studied the phylogeny of the *R. invaria* group from eastern North America and Mey (1999b) investigated the biogeography of Southeast Asian members of the genus. Other genera include *Himalopsyche* Banks (ca. 50 species, predominantly in the eastern Palearctic and Oriental regions, but with 1 species from western North America),

Philocrena Lepneva (1 species from Georgia, western Palearctic), and *Fansipangana* Mey (a single species recently described from Vietnam). The family is 1 of 2 (the other being Hydrobiosidae) that includes species that are free-living and predaceous as larvae, constructing a domed pupal chamber of rocks at maturity. As the etymology of the family name indicates, the larvae frequent cool, fast flowing rivers and streams. Larvae in the genus *Himalopsyche*, and some in the genus *Rhyacophila*, possess abdominal and thoracic gills, quite different from those in Integripalpia or Hydropsychidae.

INTEGRIPALPIA

Plenitentoria

Apataniidae: This is a northern and montane group found in North America, Europe, and Asia. The family names dates to Wallengren (1886), but for most of its history it was included as a subfamily of Limnephilidae. Wiggins (1996) treated the group as a distinct family and subsequent workers have accepted this designation. There are nearly 200 species in 18 genera, divided into 2 subfamilies. The Apataniinae contains the largest genus, *Apatania* Kolenati (nearly 100 species, Holarctic), as well as *Apataniana* Mosely (Palearctic, Oriental), *Apatidelia* Mosely (China), 4 monotypic genera: *Talgara* Mey (Kazakhstan), *Radema* Martynov (Russia), *Thamastes* Hagen (Siberia), *Proradema* Mey (Siberia), and 5 small genera endemic to Lake Baikal: *Baicalina* Martynov (5 species), *Protobaicalina* Ivanov (4 species), *Protoradema* Ivanov (2 species), *Baicalinella* Martynov (monotypic), and *Baicaloides* Martynov (monotypic). The subfamily Moropsychinae contains the genera *Moropsyche* Banks (30 species, East Palearctic and Oriental), and *Notania* Mosely (5 species, Oriental). Four genera, *Allomyia* Banks (Nearctic and eastern Palearctic, 23 species), *Manophylax* Wiggins (Nearctic and eastern Palearctic, 6 species), *Moselyana* Denning (Oregon, monotypic), and *Pedomoecus* Ross (Pacific northwest of North America, monotypic), form a monophyletic group (Gall 1994) separate from either subfamily. Apataniid larvae construct cases of small rock pieces, although *Manophylax* larvae also add plant pieces to the upper surface (Wiggins 2004). Corbet (1966) documented parthenogenesis in some species of *Apatania*. Larvae occur in cool running waters, but at high elevations and extreme northern latitudes, some species of *Apatania* are found in lakes. Most larvae graze periphyton from rocks with scraper mandibles. Some species also occur in hygropetric habitats, some of which are dry for much of the year. The larvae of *Moselyana* are found in spring seepages, and are detritivores with toothed mandibles.

Brachycentridae: This is a Northern Hemisphere family found in both the Old and New Worlds. Ulmer (1903) originally established this group as a subfamily of Sericostomatidae. It now contains 6 genera and a little over 100 species. Three of these genera are monotypic: *Adicrophleps* Flint (Nearctic), *Amiocentrus* Ross (Nearctic), and *Dolichocentrus* Martynov (southeastern Siberia). *Eobrachycentrus* Wiggins (Japan and western North America) contains only half a dozen species. *Brachycentrus* Curtis (ca. 30 species) and *Micrasema* McLachlan (ca. 75 species) are both widespread across the Holarctic and Oriental regions. Larvae construct cases from plant or rock materials, and some species use silk alone for part of the case. Several genera build 4-sided cases. The family is ecologically diverse. They inhabit running waters, but may be found in slow-flowing marshy channels. Some genera feed on aquatic moss; others are filter-feeders. Some North American species of *Brachycentrus* can be found in thermal streams with temperatures as high as 34°C that smell strongly of hydrogen sulfide (Wiggins 2004).

Goeridae: This is a widely distributed family, found on all continents except South America and Australia. Ulmer (1903) originally described this group as a subfamily of Sericostomatidae. Flint (1960) and other North American workers considered it a subfamily of Limnephilidae, but other authors either always considered it a separate family (Schmid 1980) or elevated the group to its place as a separate family (Wiggins 1996). The Goeridae are divided into 3 subfamilies. Goerinae Ulmer contains most of the genera, each with 1 or only a few species: *Archithremma* Martynov (central eastern Siberia), *Gastrocentrella* Ulmer (Sumatra), *Silonella*

Fischer (France, Spain), *Gastrocentrides* Ulmer (Burma, Indonesia), *Goeracea* Denning and *Goerita* Ross (North America), and *Lithax* McLachlan (widespread across the western Palearctic). *Silo* Curtis is the second largest genus with over a dozen western Palearctic species. The largest genus *Goera* Stephens (ca. 130 species) is found in all biogeographic regions except the Neotropical, but with scant representation in the Afrotropics (1 species in southern Africa) and Australasia (2 species from the southwest Pacific). Larcasinae Navás contains 1 genus, *Larcasia* Navás (6 species, Palearctic and Oriental); and Lepaniinae Wiggins contains only 1 species endemic to northwestern North America, *Lepania cascada* Ross. Parker (1998) reviewed the genus *Goerita*, established its monophyly, and discussed the phylogenetic relationships among its 3 species. Larvae of Goeridae construct cases entirely of rock fragments; some genera incorporate larger rock fragments laterally. Most larvae live in cool running waters and are grazers on periphyton. *Lepania* larvae are detritivores in spring seepages (Wiggins 1973b). *Archithremma ulachensis* Martynov is unusual in having a terrestrial pupa (Levanidova & Vshivkova 1984).

Kokiriidae: McFarlane (1964) erected the plectrotarsid subfamily Kokiriinae when he described *Kokiria miharo* from New Zealand. Subsequently, Ross (1967) raised it to family status and included the Chilean species *Rhynchopsyche fusca* Schmid (originally described in Brachycentridae) in the new family. Neboiss (1974) described *Tanjistomella verna,* the first record of the family in Australia; in that work he also referred the New Caledonian genus *Mecynostomella* Kimmins (originally placed in Sericostomatidae) to Kokiriidae. Neboiss later described 2 more Australasian genera, *Taskiria* and *Taskiropsyche*. Flint et al. (1999) considered *Rhynchopsyche fusca* a junior synonym of *Pangullia faziana* Navás (originally described in Limnephilidae). Johanson (2003b) recently revised *Mecynostomella* and nearly doubled the described species diversity of Kokiriidae, so that it now consists of 15 species described from New Zealand, New Caledonia, Chile, and Australia. The larvae are predatory, and live in sandy deposits of small streams and lakes. Larval cases are constructed from sand, and are dorsoventrally depressed and flanged around the edge. This family has been considered by various authors to be closely allied with either limnephiloid or leptoceroid families, in the latter case possibly because of the similarity of the larval cases to those of molannids and some *Ceraclea* (Leptoceridae). However, the characters proposed by Frania and Wiggins (1997) to support a close relationship with Molannidae have not held up to re-examination (Prather 2002), nor are they corroborated in recent molecular studies (Holzenthal et al. 2007, Kjer et al. 2001, 2002).

Lepidostomatidae: This family is widely distributed throughout the Northern Hemisphere, and extends southward to Panama, New Guinea, and the Afrotropical region. It was originally described by Ulmer (1903) as a subfamily of Sericostomatidae. It is divided into 2 subfamilies. The nominotypical subfamily contains 3 genera and most of the species: *Hummeliella* Forsslund is a monotypic genus from China; *Lepidostoma* Rambur contains most of the diversity in the family (ca. 380 species; Afrotropical, Australasian, Palearctic, and Nearctic); and *Paraphlegopteryx* Ulmer (ca. 20 species) is widespread in the East Palearctic and Oriental regions. The subfamily Theliopsychinae Weaver, 1993 contains 4 genera: *Crunoecia* McLachlan and *Martynomyia* Fischer are West Palearctic genera with only a handful of species each; *Theliopsyche* Banks is a Nearctic genus with half a dozen species; and *Zephyropsyche* Weaver is a small genus (4 species) from South and Southeast Asia. Larval cases are generally square in cross section and constructed of quadrate leaf or bark pieces. Some species build cylindrical cases of sand grains as early instars and switch to 4-sided cases as they mature; a few retain the sand grain cases throughout larval development. Larvae are generally inhabitants of cool streams and springs, but they may also occur along the shorelines of lakes. They are primarily detritivores. Weaver (1988) provided a synopsis of the North American species and a review of the world species (Weaver 2002), where he synonymized several genera, formerly separated by secondary sexual characters of the male, with *Lepidostoma*. Myers and Sperling (2002) looked at the relationships of the subgenera of *Lepidostoma*, based on mitochondrial DNA sequence data.

Limnephilidae: This is the largest family in the Plenitentoria, with approximately 900 described species. At higher latitudes and elevations, it is the dominant group in much of the Northern Hemisphere. The family was first established by Kolenati (1848) and includes species described by Linnaeus in *Systema Naturae*, 10th ed. (Table 1). Schmid (1955) resolved the family into its current classification (Table 4), with refinements by Wiggins and colleagues (Vineyard & Wiggins 1988, Wiggins 1973a, Wiggins et al. 1985). The family is divided into 4 subfamilies, Dicosmoecinae Schmid, Drusinae Banks, Limnephilinae Kolenati, and Pseudostenophylacinae Schmid. The Dicosmoecinae, with fewer than 100 described species, are considered the most primitive of the limnephilid subfamilies, and include the only Southern Hemisphere taxa in the family; of its 19 genera, 7 are endemic to South America and 1, *Archaeophylax* Kimmins, is endemic to Australia (Wiggins 2002). The Drusinae are restricted to the Palearctic region. Of the 8 genera in this subfamily, only *Drusus* Stephens contains more than half a dozen species; many of these are micro-endemics. Recent molecular studies have questioned the generic classification of Drusinae (Pauls et al. 2007). The nominotypical subfamily contains over 60 genera, divided into 4 tribes. Chaetopterygini Hagen, with 10 genera, are a Palearctic group with about 60 species. Chilostigmini Schmid are a group of 11 small genera, with approximately 40 Old and New World species. The tribe Limnephilini Kolenati (21 genera, ca. 300 species) includes most of the lentic genera of the Limnephilidae; it also includes *Limnephilus* Leach, the most species-diverse genus, with nearly 200 described species widely distributed across the Holarctic region and as far south as Central America; 2 anomalous genera, *Sphagnophylax* Wiggins and Winchester, and *Thermophylax* Nimmo have been tentatively assigned to the Limnephilini, but this remains in some dispute (Morse 2006). The Stenophylacini Schmid (ca. 200 species) is primarily Old World in distribution, although 4 of its 23 genera are endemic to North America; 1 genus *Mesophylax* McLachlan, is found in Ethiopia and Arabia (Malicky 1998, 1999). Pseudostenophylacinae is a small subfamily of 5 genera and about 100 species (Schmid 1990), with predominantly Oriental and Asian Palearctic distribution; the largest genus *Pseudostenophylax* Martynov (80 species, primarily Oriental) is represented in North America by 3 species.

This is arguably the most ecologically diverse caddisfly family, as larvae occupy the full range of habitats. Limnephilid larvae are found in lakes, streams, and marshes. Some species of *Ironoquia* live in temporary pools and streams. *Desmona* larvae have been observed leaving the water at night to feed on shoreline plants (Erman 1981, Wiggins & Wisseman 1990), and a North American species of *Philocasca* Ross has an entirely terrestrial larva. Limnephilid larvae use both plant and mineral materials in their cases; the general trend in the family is that larvae in cool running waters use rock material, while those in warmer lentic habitats use plant material (Wiggins 1996).

Oeconesidae: This is a small family of 6 genera and fewer than 20 described species. Tillyard (1921) described the family originally as a tribe of Sericostomatinae. The monotypic genus *Tascuna* Neboiss is found in Tasmania. The other genera, *Oeconesus* McLachlan (5 species), *Pseudoeconesus* McLachlan (9 species), *Zelandopsyche* Tillyard (2 species) and the monotypic genera *Zepsyche* McFarlane and *Tarapsyche* McFarlane, are endemic to New Zealand. Larval cases are of plant and rock materials (Cowley 1978). Larvae feed on plant debris in small forested streams (Cowley 1978, Winterbourn & Davis 1976).

TABLE 4. The genera of Limnephilidae and their distribution. Adapted from Morse (2006). (Afr=Afrotropical, Au=Australasian, Hol=Holarctic, Na=Nearctic, Neo=Neotropical, Or=Oriental, Pa=Palearctic).

Subfamily Dicosmoecinae Schmid, 1955

Allocosmoecus Banks, 1943 . . . . .Na

Amphicosmoecus Schmid, 1955 . . . . .Na

Anomalocosmoecus Schmid, 1957 . . . . .Neo

Antarctoecia Ulmer, 1907 . . . . .Neo

Archaeophylax Kimmins, 1953 . . . . .Au

Austrocosmoecus Schmid, 1955 . . . . .Neo

Cryptochia Ross, 1950 . . . . .Na

Dicosmoecus McLachlan, 1875 . . . . Hol

Ecclisocosmoecus Schmid, 1964 . . . . Hol

Ecclisomyia Banks, 1907 . . . . Hol

Eocosmoecus Wiggins and Richardson, 1989 . . . . .Na

Evanophanes Banks, 1940 . . . . Or

Ironoquia Banks, 1916 . . . . Hol

Metacosmoecus Schmid, 1955 . . . . .Neo

Monocosmoecus Ulmer, 1906 . . . . .Neo

Nothopsyche Banks, 1906 . . . . Pa, Or

Onocosmoecus Banks, 1943 . . . . Hol

Platycosmoecus Schmid, 1964 . . . . .Neo

Verger Navas, 1918 . . . . .Neo

Subfamily Drusinae Banks, 1916

Anomalopterygella Fischer, 1966 . . . . Pa

Cryptothrix McLachlan, 1867 . . . . Pa

Drusus Stephens, 1833 . . . . Pa

Ecclisopteryx Kolenati, 1848 . . . . Pa

Hadimina Sipahiler, 2002 . . . . Pa

Leptodrusus Schmid, 1955 . . . . Pa

Metanoea McLachlan, 1880 . . . . Pa

Monocentra Rambur, 1842 . . . . Pa

Subfamily Limnephilinae Kolenati, 1848

Tribe Chaetopterygini Hagen, 1858

Annitella Klapalek, 1907 . . . . Pa

Badukiella Mey, 1979 . . . . Pa

Chaetopterna Martynov, 1913 . . . . Pa

Chaetopteroides Kumanski, 1987 . . . . Pa

Chaetopterygopsis Stein, 1874 . . . . Pa

Chaetopteryx Stephens, 1829 . . . . Pa

Kelgena Mey, 1979 . . . . Pa

Pseudopsilopteryx Schmid, 1952 . . . . Pa

Psilopteryx Stein, 1874 . . . . Pa

Rizeiella Sipahiler, 1986 . . . . Pa

Tribe Chilostigmini Schmid, 1955

Brachypsyche Schmid, 1952 . . . . Pa

Chilostigma McLachlan, 1876 . . . . Hol

Chilostigmodes Martynov, 1914 . . . . Hol

Desmona Denning, 1954 . . . . .Na

Frenesia Betten and Mosely, 1940 . . . . .Na

Glyphopsyche Banks, 1904 . . . . .Na

Grensia Ross, 1944 . . . . Hol

TABLE 4 (continued)

Tribe Chilostigmini Schmid, 1955

Homophylax Banks, 1900 . . . . Na

Phanocelia Banks, 1943 . . . . Na

Pielus Navás, 1935 . . . . Or

Psychoglypha Ross, 1944 . . . . Na

Tribe Limnephilini Kolenati, 1848

Anabolia Stephens, 1837 . . . . Hol, Or

Arctopora Thomson, 1891 . . . . Hol

Asynarchus McLachlan, 1880 . . . . Hol, Or

Clistoronia Banks, 1916 . . . . Na, Neo (Mexico)

Crenophylax Ruiter and Nishimoto 2007 . . . . Na

Glyphotaelius Stephens, 1833 . . . . Pa

Grammotaulius Kolenati, 1848 . . . . Hol, Or

Halesochila Banks, 1907 . . . . Na

Hesperophylax Banks, 1916 . . . . Na

Lenarchus Martynov, 1914 . . . . Hol

Lepnevaina Wiggins, 1987 . . . . Pa

Leptophylax Banks, 1900 . . . . Na

Limnephilus Leach, 1815 . . . . Hol, Neo, Or

Nemotaulius Banks, 1906 . . . . Hol, Or

Philarctus McLachlan, 1880 . . . . Hol, Or

Platycentropus Ulmer, 1905 . . . . Na

Psychoronia Banks, 1916 . . . . Na

Rhadicoleptus Wallengren, 1891 . . . . Pa

Rivulophilus Nishimoto, Nozaki, and Ruiter, 2001 . . . . Pa

Sphagnophylax Wiggins and Winchester, 1984 . . . . Na

Thermophylax Nimmo, 1995 . . . . Pa

Tribe Stenophylacini Schmid, 1955

Acrophylax Brauer, 1867 . . . . Pa

Allogamus Schmid, 1955 . . . . Pa

Anisogamodes Martynov, 1924 . . . . Pa

Anisogamus R McLachlan, 1874 . . . . Pa

Chionophylax Schmid, 1951 . . . . Pa

Chyranda Ross, 1944 . . . . Na

Clostoeca Banks, 1943 . . . . Na

Consorophylax Schmid, 1955 . . . . Pa

Enoicyla Rambur, 1842 . . . . Pa

Enoicylopsis Navás, 1917 . . . . Pa

Halesus Stephens, 1836 . . . . Hol

Hydatophylax Wallengren, 1891 . . . . Hol

Isogamus Schmid, 1955 . . . . Pa

Leptotaulius Schmid, 1955 . . . . Pa

Melampophylax Schmid, 1955 . . . . Pa

Mesophylax McLachlan, 1882 . . . . Pa, Or

Parachiona Thomson, 1891 . . . . Pa

Philocasca Ross, 1941 . . . . Na

Platyphylax McLachlan, 1871 . . . . Pa

Potamophylax Wallengren, 1891 . . . . Pa

Psilopterna Martynov, 1915 . . . . Pa, Or

Pycnopsyche Banks, 1905 . . . . Na

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TABLE 4 (continued)

Tribe Stenophylacini Schmid, 1955	
Stenophylax Kolenati, 1848	Pa, Or
Subfamily Pseudostenophylacinae Schmid, 1955	
Aplatyphylax Kimmins, 1950	Or
Astenophylina Mosely, 1936	Or
Astratodina Mosely, 1936	Pa, Or
Phylostenax Mosely, 1935	Pa, Or
Pseudostenophylax Martynov, 1909	Hol, Or

Phryganeidae: Linnaeus's original taxon is now a relatively small family confined to the more northern latitudes. Leach (1815) circumscribed the Linnaean genus *Phryganea* to the species *P. grandis*, and placed the genus *Phryganea* in the tribe Phryganides with *Limnephilus*. Burmeister (1839) was the first to use the name Phryganeidae, as a subfamily of Phryganeodea; Burmeister's Phryganeidae included species currently placed in Sericostomatidae and Limnephilidae. By the late 19ᵗʰ century, most workers recognized a unit similar to the modern concept of Phryganeidae. Wiggins (1998) published a landmark treatise on the Phryganeidae, the only full-length book devoted to an entire family of caddisflies, which serves as the definitive reference. The family currently contains some 80 extant species in 15 genera. One genus, the monotypic *Yphria* Milne, from the Sierra Nevada of California and southern Oregon, is assigned to its own subfamily, Yphriinae. All other genera are in Phryganeinae. The nominotypical genus *Phryganea*, as currently recognized, contains only a handful of species from Asia, Europe, and North America. The largest genera (neither with more than 20 described species) are *Agrypnia* Curtis, found across the northern latitudes of Europe, Asia, and North America, and *Eubasilissa* Martynov, which is entirely Asian. Species in the latter genus include the largest extant caddisflies. Most genera contain only a handful of species: *Banksiola* Martynov (Nearctic), *Hagenella* Martynov (Holarctic), *Neurocyta* Navás (mountains of northern India and bordering countries), *Semblis* Fabricius (Palearctic), *Oligotricha* Rambur (Palearctic, with 1 species extending into Alaska and the Yukon). Four genera are monotypic: *Agrypnetes* McLachlan (Palearctic), *Beothukus* Wiggins (Nearctic); *Fabria* Milne (Nearctic); and *Trichostegia* Kolenati (northern and central Europe). Except in *Yphria*, which incorporates rock fragments into its case, phryganeid larvae construct cases of plant material, cut to size and fastened together in rings or a continuous spiral. Maybe because of their conspicuous size, adults of many phryganeid species have developed chemical and/or mechanical defense systems; many species produce an odiferous fluid from the anal opening when handled, and - uniquely within the Trichoptera - at least some species of *Eubasilissa* have urticating setae on the thorax and wings. Larvae are generally found among aquatic plants in ponds and marshes; some occur in slow flowing waters, a few are found in temporary pools and deep lake waters. Predation and herbivory are common larval feeding strategies in this family.

Phryganopsychidae: This family contains a single genus, *Phryganopsyche* Wiggins, with only a few Asian species found from the Himalayas to Japan and the Russian Far East. These species were originally placed in Phryganeidae (as *Phryganopsis*, a name preoccupied in the Lepidoptera). The larvae, previously unknown, turned out to be very different from phryganeid larvae, and Wiggins (1959) erected a new family to accommodate these anomalous species. Wiggins and Gall (1993) concluded that the family was a "phylogenetic relict," which could not be allied with certainty to any of the families of Plenitentoria. Wiggins (2004) placed it in its own superfamily. In the most recent molecular analysis (Holzenthal et al. 2007), Phryganopsychidae formed a clade with Kokiriidae and Pisuliidae. The larval case, constructed of plant debris, is very different from that of other case-makers: it is much longer than the larva and is not rigid, and in some ways bears more resemblance to an annulipalpian tube than an integripalpian case. Before pupation, the

larva constructs a rigid case of woody materials (Wiggins 2004). Larvae are detritivores, and live in marginal pools of streams and springs.

Pisuliidae: This small family is found in tropical Africa and Madagascar. Ross (1967) was the first to consider this group a family. It contains 2 genera, *Pisulia* Marlier (6 species) and *Silvatares* Navás (10 species); the latter was originally described in Calamoceratidae. Stoltze (1989) revised the family in its entirety. Larvae construct cases of leaf and wood pieces. *Pisulia* larvae occupy hygropetric habitats; *Silvatares* larvae are found in small streams. Larvae are detritivorous shredders.

Plectrotarsidae: This is a very small Australasian family of 3 genera and 5 species. The family was erected by Mosely (1953). At one time it included *Kokiria*, now in its own family. The family now consists of 2 monotypic genera, *Liapota* Neboiss and *Nanoplectrus* Neboiss, and *Plectrotarsus* Kolenati (3 species). The phylogenetic position of the family is equivocal (Gall & Wiggins 1999). In the most recent molecular hypothesis (Holzenthal et al. 2007), it emerged as sister to all other Plenitentoria, but not allied with the Phryganeidae or Phryganopsychidae as indicated in other studies (Frania & Wiggins 1997, Ivanov & Sukatcheva 2002, Wiggins 2004). Larval cases are constructed of plant pieces; the larvae are shredding detritivores, found in shallow flowing waters with abundant vegetation.

Rossianidae: This family contains only 2 species *Goereilla baumanni* Denning and *Rossiana montana* Denning, described originally in Goeridae and Limnephilidae, respectively. Gall (1997) erected the family to accommodate these 2 species after his phylogenetic analysis recovered them as a sister clade to Limnephilidae + Apataniidae, Uenoidae, and Goeridae (Gall 1994). Both species are known only from western North America; neither is commonly collected. *Goereilla baumanni* larvae are found in the organic muck of spring seeps. *Rossiana montana* larvae occur in stream gravel deposits under moss or in hygropetric habitats. Larvae of both species use rock fragments to construct stout, slightly curved cases.

Uenoidae: This family is found in North America, eastern Asia, and southern Europe. It was originally described by Iwata (1927) as a subfamily of Sericostomatidae. The family was revised by Wiggins et al. (1985); several taxonomic and phylogenetic works were published subsequently (Vineyard & Wiggins 1987, 1988, Vineyard et al. 2005, Wiggins & Erman 1987, Wiggins & Wisseman 1992). The 7 genera are divided into 2 subfamilies. Thremmatinae Martynov contains the genera *Neophylax* McLachlan (ca. 40 species, Holarctic), *Oligophlebodes* Ulmer (7 species, western North America), and *Thremma* McLachlan (7 species, Mediterranean region). The nominotypical subfamily includes *Uenoa* Iwata (11 species) and 3 genera endemic to western North America: *Farula* Milne (11 species), *Neothremma* Dodds and Hisaw (7 species), and *Sericostriata* Wiggins, Weaver, and Unzicker (monotypic). Larvae of Thremmatinae construct stout cases of coarse rock particles (e.g., *Neophylax*) or fine-grained, flattened, cases resembling the freshwater limpet *Ancylus* (e.g., *Thremma*). Larvae of Uenoinae are more slender and construct cases of fine sand or silk (Wiggins et al. 1985). The larval diet in Uenoidae is diatoms and fine organic particles scraped from rock surfaces. Generally, larvae are found in cool, fast-flowing headwaters; however, in the genus *Neophylax*, some species occur in downstream warmer waters.

INTEGRIPALPIA
    BREVITENTORIA
        "Leptoceroidea"

Atriplectididae: The family shows a disjunct Gondwanan distribution with species in Australia, including Tasmania, the Neotropics (northern Andes, southeast Brazil), and the Seychelles. It was erected by Neboiss

(1978) to accommodate the Australasian species *Atriplectides dubius* Mosely, originally described in the Leptoceridae subfamily Triplectidinae and later transferred to the Odontoceridae (Mosely & Kimmins 1953). Upon discovery of the very unusual larval stage, Neboiss established the family and also transferred the monotypic Seychelles genus *Hughscottiella auricalla* Ulmer, originally described in Odontoceridae, to Atriplectididae. Neboiss (1999) described a 2nd Australasian species *Atriplectides ikmaleus* and Holzenthal (1997) described a new genus and species from Peru, *Neoatriplectides froehlichi*, such that the family now contains 4 species. The larval stages of all 3 genera are known (Holzenthal 1997, Marlier 1978, Neboiss 1978) and are unique within the Trichoptera in that the head, pro- and mesonota are narrow, elongate, and retractile. Larvae feed as scavengers by cutting a small opening in the body of dead arthropods, thus allowing them to insert their head and anterior thorax to feed on the internal tissues (Malicky 1997). They are found in sandy bottom sediments of small streams and lakes.

Calamoceratidae: The family has long been recognized within the Trichoptera, being first established by Ulmer (1906). The nominotypical genus was included in a "section" of Leptoceridae by McLachlan and a few other early workers. The 8 genera are well defined and together comprise about 175 species from around the world. *Anisocentropus* McLachlan and *Phylloicus* Müller are the largest genera in the family with over 60 species each. The former is widespread in the Paleotropics of Africa, Asia, and Australia, with 1 outlying species in eastern North America. *Phylloicus* is endemic to the Neotropics, with several species extending their range into the southwestern USA. *Banyallarga* Navás is another Neotropical endemic of less than 20 species. The Neotropical fauna was recently revised in its entirety by Prather (2003, 2004). The other species-rich genus in the family is *Ganonema* McLachlan, with about 20 species in the Oriental and eastern Palearctic regions. Smaller genera, with no more than 2 or 3 species each, include: *Ascalaphomerus* Walker (China), *Calamoceras* Brauer (Europe), *Georgium* Fischer (Japan, Thailand), and *Heteroplectron* McLachlan (eastern and western North America, Japan). Larvae of the family are well known for their flattened cases made of large pieces of excised leaves that completely camouflage the larva from above. Others build tubular cases of sand grains or hollow a twig to use as a case. The larvae inhabit the slower, depositional areas of small streams and rivers where they feed as shredders of leaf litter and other plant detritus. Larvae of a Brazilian species inhabit the "tanks" of water trapped by the leaf axils of bromeliads. Adults of many species have very brightly colored and patterned wings imparted by thickened hairs or scales. Many are more active during the day than most Trichoptera, as they engage in diurnal mating behavior.

Leptoceridae: The long-horned caddisflies comprise 1 of the 3 largest families in the order with about 1,800 described species. The family is about equal in diversity to the Hydropsychidae and only surpassed by the microcaddisflies, Hydroptilidae, in total known species richness. In all of these families, many more new species assuredly await discovery and description, especially from tropical regions around the world. The family was first established by Leach (1815) and includes several species described by Linnaeus in *Systema Naturae*, 10th ed. (Table 1). Nineteenth century workers also included species now in Odontoceridae, Molannidae, Calamoceratidae, and Beraeidae in Leptoceridae, but by the early 20th century modern family concepts were for the most part established. Forty-seven genera are known at present in the family, but new genera are still being described, for example *Fernandoschmidia* Holzenthal and Andersen (2007), and recent generic synonymies have also occurred, for example *Ylodes* is a junior synonym of *Triaenodes* (Holzenthal & Andersen 2004). The family is divided into 2 subfamilies, the nominotypical subfamily Leptocerinae Leach of cosmopolitan distribution and Triplectidinae Ulmer, having a primarily Southern Hemisphere distribution in the Neotropics and Australasia, with a putative triplectidine larva in southern Africa (de Moor 1997). Two genera in particular are widespread and diverse on all continents, *Oecetis* McLachlan with about 400 described species and *Triaenodes* McLachlan with about 230 known species. *Setodes* Rambur, with about 220 species in very diverse in the Old World, especially India and Southeast Asia, but in the New World it is

represented by only a handful of eastern North American species and 1 on Cuba. Other large genera, with about 100-150 species each, include *Adicella* McLachlan (Palearctic, Afrotropical, Oriental), *Athripsodes* Billberg (Afrotropical, Palearctic), *Ceraclea* Stephens (Nearctic, Afrotropical, Palearctic), and *Leptocerus* Leach (Palearctic, Afrotropical, Oriental, with a single species in the New World). *Nectopsyche* Müller, with about 60 species, is a characteristic component of the Neotropical fauna; species in the genus also occur well into North America. The Neotropics is home to a number of endemic genera, including *Achoropsyche* Holzenthal, *Amazonatolica* Holzenthal & Oliveira Pes, *Amphoropsyche* Holzenthal, *Atanatolica* Mosely, *Brachysetodes* Schmid, *Grumichella* Müller, and *Neoathripsodes* Holzenthal. The Australasian region holds the largest diversity of endemic genera, including *Condocerus* Neboiss, *Gracilipsodes* Sykora, *Lectrides* Mosely, *Leptorussa* Mosely, *Notoperata* Neboiss, *Russobex* St. Clair, *Symphitoneuria* Ulmer, *Symphitoneurina* Schmid, *Triplectidina* Mosely, *Triplexa* Mosely, *Triplexina* Mosely, and *Westriplectides* Neboiss; all but *Leptorussa* are members of the Triplectidinae. Three additional triplectidine genera show a trans-Antarctic pattern between Australasia and the Neotropics, *Hudsonema* Mosely, *Notalina* Mosely, and *Triplectides* Kolenati, the latter the largest genus in the subfamily with about 65 species, some of which occur in India, Southeast Asia, and Japan. The Afrotropics has a rich fauna of Leptocerinae, especially within *Athripsodes*, *Ceraclea*, *Leptocerus*, *Oecetis*, and *Triaenodes*, but it also has several endemic genera, including *Axiocerina* Ross, *Leptocho* Barnard, *Leptocerina* Mosely, *Blyzophilus* Andersen & Kjaerandsen, *Ptochoectis* Ulmer, *Hemileptocerus* Ulmer, and *Sericodes* Schmid. The Oriental region has a staggering diversity of *Setodes* and *Oecetis* species, especially in India, and also harbors a few endemic genera as well, including *Fernandoschmidia* Holzenthal & Andersen, *Leptoceriella* Schmid, and *Poecilopsyche* Schmid. *Erotesis* McLachlan with 2 European and 1 Japanese species is the only genus endemic to the Palearctic region. Remaining genera within the family, all members of Leptocerinae, occur across 2 or 3 biogeographical regions and include *Homilia* McLachlan (Europe, Afrotropical), *Mystacides* Berthold (Holarctic, Oriental), *Parasetodes* McLachlan (Palearctic, Afrotropical, Oriental), *Tagalopsyche* Banks (Afrotropical, Oriental), and *Trichosetodes* Ulmer (Palearctic, Afrotropical, Oriental). The placement of *Nietnerella* Kimmins, with a single species from Sri Lanka, within the family is equivocal. Phylogenetic studies within the family, in addition to those reviewed by Morse (1997), include Calor et al. (2006), Manuel et al. (2005), Morse and Yang (2002), Stuart and Currie (2002), and Yang and Morse (2000). Larvae of the family construct a wide diversity of cases, perhaps the most diverse in the order. Cases are fundamentally tubular, but can be made entirely of silk secretions, of plant pieces arranged spirally or laid transversely, or of large leaf fragments to form a flattened case. Others make simple tubular cases of sand grains, strongly or only slightly tapered towards the posterior ends; sometimes there are larger stones placed laterally. *Mystacides* larvae incorporate long conifer needles or leaf stems that trail off the end of the case. Some genera make irregular cases of plant fragments, while others hollow a twig or use the abandoned cases of other caddisflies as their own. Some *Ceraclea* build flat, limpet-like cases of sand grains, while those that feed on freshwater sponge incorporate sponge pieces and spicules in their cases. The larvae of *Leptecho helicotheca* Scott from South Africa build snail-shaped cases remarkably similar to those of *Helicopsyche*. Larvae are found everywhere, from high mountain torrents, through all orders of streams, to large lowland rivers. In northern latitudes, they are common in lakes and in the tropics they occur in oxbow lakes and other standing waters, even temporary ones; some are semi-terrestrial and inhabit the sides of waterfalls where they are wet by the splash. Larvae feed as leaf detritus shredders, periphyton scrapers, and predators, even on freshwater sponge. Adults are often very abundant and come to lights by the 1000s. Their long, slender antennae and generally narrow forewings are distinguishing features. There are quite a few genera that have brightly colored and iridescent hairs and scales on the wings, making them among the most beautiful of caddisflies.

Limnocentropodidae: The family contains a single genus, *Limnocentropus* Ulmer, and 15 species occurring in India and Nepal, China, Southeast Asia (including Borneo), and Japan. The genus was created for the

Japanese species *L. insolitus* Ulmer, and originally included in the Phryganeidae (Ulmer 1907a). The genus *Kitagamia* Iwata, and its coordinate family Kitagamiidae Tsuda, is a synonym of *Limnocentropus*. The family Limnocentropidae was established by Tsuda (1942) as a replacement name for Kitagamiidae, later emended to Limnocentropodidae by Kimmins (1950). Larvae live in torrential waters and attach their cases to rocks by a strong, silken peduncle, about as long as or longer than the case. The case itself is made of small rocks with silken denticles incorporated in some species. Larvae are large, robust, and predaceous. The case is positioned to extend in the current so that the larva can collect drifting insects with its strong, stout, outstretched spiny legs (Wiggins 1969). Unlike the vast majority of Trichoptera, adults have well developed, sclerotized mandibles.

Molannidae: The family contains only 2 genera, *Molanna* Curtis with about 2 dozen species and *Molannodes* McLachlan with about 1 dozen species. *Indomolannodes* Wiggins is a junior synonym of *Molannodes* according to Malicky (2000). Members of the family were at one time included as a "section" or tribe of Leptoceridae by McLachlan and others, but were established as a family by Wallengren (1891). The family occurs across the Holarctic region as well as India, Sri Lanka, and Southeast Asia, including parts of the Indonesian archipelago. Larvae construct heavy, depressed cases of sand grains with large lateral and anterior expansions that serve to hide the larva from above and facilitate protection from predators as well as from overturning by waves (Otto 2000) or sinking in soft sediments. They live on the sandy bottoms of lakes, often at considerable depths, and the sandy depositional areas of streams and springs. The larval food consists of algae, including diatoms, leaf litter detritus, and aquatic invertebrates. Adults of some species tend to roll the wings around the body and hold themselves at an angle while at rest, thus resembling a small twig or tiny branch.

Odontoceridae: In earlier days, the family was considered a "section" of Leptoceridae (e.g., Walker) or as a subfamily of Leptoceridae (e.g., Ulmer), but later workers considered Odontocerinae Wallengren (1891) to be a distinct family. The family contains about 115 extant species in 14 genera, scattered about the Old and New Worlds. Four genera are endemic to North America, 3 in the West (*Namamyia* Banks, *Nerophilus* Banks, and *Parthina* Denning) and 1 in the East (*Pseudogoera* Carpenter). Of the 2 additional genera found in North America, *Marilia* Müller reaches its greatest diversity in the Neotropics (ca. 45 species), with additional species in China, Southeast Asia, and Australia, and *Psilotreta* Banks occurs in eastern North America, India, Nepal, Southeast Asia, China, Korea, and Japan. In addition to many species of *Marilia*, the Neotropics harbors 2 endemic monotypic genera, both from southeastern Brazil, *Barypenthus* Burmeister and *Anastomoneura* Huamantinco and Nessimian. The Australasian fauna is poorly represented by only a couple of species of *Marilia* and 2 species of the endemic genus *Barynema* Banks. Southeast Asia is home to 2 endemic genera, *Inthanopsyche* Malicky and *Lannapsyche* Malicky, in addition to those mentioned above. Only the nominotypical genus, *Odontocerum* Leach, occurs in Europe. The family is not known from Africa, but a single monotypic genus with equivocal placement in the family (Neboiss 1978) was described from the Seychelles, *Leptodermatopteryx* Ulmer. Larvae live in springs and small to medium-sized streams and rivers, some are associated with waterfalls. They seem to prefer slow flowing areas or depositional zones, where they may burrow in the sandy substrate. Cases are made of sand grains or larger mineral fragments and are very resistant to crushing due to reinforcing silken mortar applied by the larva between sand grains. Larvae are omnivorous, feeding on organic detritus, vascular plants, moss, and algae as well as aquatic arthropods.

Philorheithridae: This is another small family of about 25 species that shows a trans-Antarctic distribution, with genera endemic to Australia, Tasmania, New Zealand, or southern Chile and adjacent Argentina. There are 8 genera, with about 2-6 species each, distributed as follows: southern Chile, Argentina (*Mystacopsyche* Schmid, *Psilopsyche* Ulmer), southeast Australia, Tasmania (*Austrheithrus* Mosely, *Aphilorheithrus* Mosely,

Kosrheithrus Mosely, *Ramirheithrus* Neboiss, *Tasmanthrus* Mosely), and New Zealand (*Philorheithrus* Hare). The 2 earliest named genera, *Psilopsyche* Ulmer and *Philorheithrus* Hare, were originally described in the Odontoceridae and Sericostomatidae, respectively. Mosely (1936) established the family, with *Philorheithrus* as its type genus. The semi-raptorial morphology of the fore- and midlegs of the larvae reveal their predatory behavior. Larvae construct stout, tubular cases of sand grains and live on or in sandy bottom sediments in small to medium-sized rivers. In the males of most species, there is a pair of "pilifers:" digitate, semimembranous structures, emerging dorsad of the maxillary palps and held in front of the face. Some males have pectinate antennae. In general, these are rather large caddisflies, with wing lengths of about 1-1.5 cm.

Tasimiidae: This small family contains only 4 genera, 2 in southern Chile and 2 in southeast Australia and Tasmania, for a total of 9 species. The Chilean fauna is composed of 2 species, each in a monotypic genus, *Charadropsyche penicillata* Flint and *Trichovespula macrocera* Schmid. *Tasimia* Mosely contains 5 species from southeastern Australia and Tasmania, while *Tasiagma* Neboiss has 1 species in Australia and Tasmania and 1 on Lord Howe Island, lying between Australia and New Zealand. The family was established by Riek (1968) for the genus *Tasimia*, originally described in the Sericostomatidae; *Trichovespula* was first included in Lepidostomatidae, and later transferred to Tasimiidae by Flint (1969). Larvae all seem to build narrow to broad, flattened, tubular cases of sand grains with anterior and lateral flanges of larger mineral fragments (Flint 1967, 1999). They live in small, shallow streams where they cling to the faces of rocks. They probably feed on periphyton and organic sediments growing or adhering to the rock surfaces.

INTEGRIPALPIA

 Brevitentoria

  Sericostomatoidea

Anomalopsychidae: The family was established by Flint (1981) for 2 Chilean species formerly included in the Sericostomatidae: *Contulma cranifer* Flint and *Anomalopsyche minuta* Schmid. It is the only caddisfly family fully endemic to the Neotropics and now contains 26 species (Holzenthal & Flint 1995, Holzenthal & Robertson 2006), distributed in the mountainous regions from Costa Rica south to Chile and in the highlands of southeastern Brazil. The larvae of both genera have been described (Flint 1981, Holzenthal & Flint 1995) and inhabit seeps, spring-runs, and small to medium-sized streams in forested areas as well as those above the tree line in the northern Andes. Many species frequent the splash zone of waterfalls and cascades, where they are often found in aquatic moss. The larvae have scraping mandibles and more than likely feed on periphyton. They build cylindrical, slightly curved cases of sand grains. As a whole, members of the family are rare and infrequently collected; adults fly to lights, but are as easily collected with an aerial net during the day.

Antipodoeciidae: The family is endemic to eastern Australia and still contains a single species, *Antipodoecia turneri* Mosely. The species was originally described in the Sericostomatidae, but Ross (1967) established a new family, Antipodoeciidae, to accommodate it in his attempt to rectify the then polyphyletic composition of the Sericostomatidae, *sensu lato*. It is a small insect with a forewing length of only 3.5 mm; nothing of substance has been published on its biology. The larvae build slightly curved and tapered, cylindrical cases of sand grains. It is the only caddisfly family not yet included in a molecular phylogenetic analysis of family relationships within the order.

Barbarochthonidae: This endemic South African family was established by Scott (1985, 1993) to accommodate a single species, *Barbarochthon brunneum* Barnard, first described in the Sericostomatidae (Barnard 1934). The small dark brown adults have a conspicuous cream colored pronotum and are common in the western and southern Cape region at mid- to high elevations. Larvae occur in both fast-flowing torrents as well as pools, and are typically associated with marginal vegetation, including clumps of submerged *Scirpus*;

they feed as leaf detritivores. The long, slender, curved, tapered case is made entirely of darkened silk except for some transverse rows of small sand grains towards the posterior end.

Beraeidae: This small family, established by Wallengren (1891), is comprised of 7 genera and about 50 species. It reaches its greatest diversity in the western Palearctic region, where 5 genera occur (*Beraea* Stephens, *Beraeamyia* Mosely, *Ernodes* Wallengren, *Beraeodes* Eaton, and *Beraeodina* Mosely, the latter 2 monotypic). The genus *Beraea* also occurs in eastern North America, where 3 species are known. A single genus, *Notoernodes*, with 2 species, occurs in Tanzania. Elsewhere the family is found only in Japan, where it is represented by the genus, *Nippoberaea* Botosaneanu, Nozaki, & Kagaya, containing a single species, *N. gracilis* (Nozaki & Kagaya). Most beraeid larvae build slightly to strongly tapered cases of small sand grains and live in springs, seeps, and small streams, usually among aquatic mosses, leaf litter deposits, roots of emergent plants, and other dense, marginal vegetation or in the marginal organic sediments (Hamilton 1985). Gut contents of *Beraea gorteba* Ross in southeastern North America included small pieces of vascular plants, fungal mycelia, and other organic material, but no animal parts (Hamilton 1985), foodstuffs probably typical of most species in the family.

Calocidae: This is another family, endemic to Australia and New Zealand, established by Ross (1967) to accommodate genera originally placed in Sericostomatidae, Beraeidae, or Odontoceridae. As with other new families established in this paper, Ross gave no family diagnosis or indication of included genera. In the same paper, he placed *Pycnocentrella eruensis* Mosely, originally described in Beraeidae, in his newly created family Pycnocentrellidae, later synonymized with Calocidae by Neboiss (1977). The New Zealand genus *Alloecentrella* Wise, first described in Beraeidae and at times included in the Helicophidae was formally transferred from Calocidae to Helicophidae by Henderson and Ward (2007); their phylogenetic analysis revealed its close affinity to other helicophid genera. In its present composition, the family now contains 6 genera endemic to Australia (*Caenota* Mosely, *Caloca* Mosely, *Calocoides* Neboiss, *Pliocaloca* Neboiss, *Tamasia* Mosely) and 1 endemic to New Zealand (*Pycnocentrella*), with a total of 19 species. One Tasmanian species is terrestrial and lives under moss and leaf litter in wet sclerophyll forest, but others occur in small, woodland streams among plant roots and accumulations of detritus (Jackson 1998, Neboiss 1979). They construct slightly curved and tapered cylindrical cases of small rock fragments or somewhat flattened cases of 2 dorsal and 2 ventral rows of leaf material (Jackson 1998). Adults are small to rather large (forewing lengths 5-14 mm) and have dark forewings patterned with irregular white spots. In males of some genera, the antennal scape has expandable lobes and the head bears long, expandable filaments (Neboiss 1986).

Chathamiidae: The family was first described as a subfamily within Rhyacophilidae by Tillyard (1925) to accommodate the species *Chathamia brevipennis* Tillyard, a species endemic to the Chatham Islands, a group of 10 small islands 800 km east of New Zealand. It was later moved to the Philanisidae by Wise (1965), a family erected by Mosely (in Mosely & Kimmins 1953) to accommodate *Philanisus plebeius* Walker, first described in Hydropsychidae and later included in Sericostomatidae by Ulmer (1907b). Riek (1976) synonymized Philanisidae with Chathamiidae and provided a comprehensive review of the family, including a discussion of phylogeny and the description of 2 new species. Ward (1995) described a 3rd species of *Philanisus*, such that the family contains 5 species, distributed as follows: *Chathamia brevipennis* Tillyard (Chatham Islands), *C. integripennis* Riek (New Zealand), *Philanisus plebeius* Walker (New Zealand, southeast Australia), *P. fasciatus* Riek (Kermadec Islands, ca. 1000 km NNE of New Zealand), and *P. mataua* Ward (New Zealand). Ulmer (in Mosely & Kimmins 1953) described the larva of *P. plebeius*, long known to inhabit marine intertidal rock pools (Hudson 1904), but it was not until the late 1970s when the remarkable biology and life-history of the species was fully revealed (Anderson & Lawson-Kerr 1977, Winterbourn & Anderson 1980). The larvae and pupae of the species, and assumed all members of the family, are among the

very few fully marine insects. The females oviposit through the papular pores of intertidal starfish where the eggs undergo embryonic development. After hatching, the 1st instar larvae leave the starfish through the same pores and construct cases of calcareous algae. Larvae feed on non-calcareous Rhodophyceae. Adult females have long oviscapts, probably facilitating the insertion of eggs in the starfish. Adults of the Chatham Island species are brachypterous, but those of other species are fully winged.

Conoesucidae: Ross (1967) established the subfamily Conoesucinae within the Sericostomatidae for Australasian genera with "atrophied" scutal warts, but he did not name the included genera or offer any other diagnosis. Later, Neboiss (1977) elevated the subfamily to family status, provided a detailed diagnosis, and included 6 Australasian genera in the family, all formerly included in the Sericostomatidae. Additional sericostomatid genera have been transferred to Conoesucidae such that the family now contains a dozen genera and ca. 40 species, endemic to either southeastern Australia and Tasmania (*Coenoria* Mosely, *Conoesucus* Mosely, *Costora* Mosely, *Hampa* Mosely, *Lingora* Mosely, *Matasia* Mosely) or New Zealand (*Beraeoptera* Mosely, *Confluens* Wise, *Olinga* McLachlan, *Periwinkla* McFarlane, *Pycnocentria* McLachlan, *Pycnocentrodes* Tillyard). The larvae live in small, cool, fast-flowing streams where they feed on leaf litter detritus, algae, and moss. Their cases are made of sand, small rocks, plant parts, or silk; cases are tubular and only slightly curved. Adult males have shortened, membranous maxillary palps that are held out in front of the face. Ward (1995) reported that adults of a New Zealand species of *Pycnocentria* were common and active during hot summer days on streamside sedges, herbs, and grasses.

Helicophidae: The helicophids are a small family of caddisflies found in Australia, New Zealand, and now New Caledonia as well as austral South America (southern Chile and adjacent Argentina), one of several caddisfly families showing this trans-Antarctic biogeographical distribution pattern. The family was created by Mosely (in Mosely and Kimmins 1953) to accommodate a new genus and 2 new species, *Helicopha astia* Mosely and *H. hortena* Mosely, both from New South Wales. Additional genera have been transferred to the family from Beraeidae, Calocidae, and Sericostomatidae and described within the family itself, the most recent of these being *Briama* Johanson and Ward from New Caledonia and *Heloccabus* Neboiss from eastern Australia, the later placed provisionally in the family (Johanson & Ward 2001, Neboiss 2002). In addition, the endemic New Zealand genus *Alloecentrella* was just transferred to the family from Calocidae by Henderson & Ward (2007). Thus, the current accounting of the 11 genera in the family, for a total of about 35 species, is as follows: *Alloecella* Banks (Australia), *Alloecentrella* Wise (New Zealand), *Alloecentrellodes* Flint (Chile), *Austrocentrus* Schmid (Argentina, Chile), *Briama* Johanson and Ward (New Caledonia), *Eoseriocostoma* Schmid (Argentina, Chile), *Helicopha* Mosely (Australia, New Caledonia), *Heloccabus* Neboiss (Australia), *Microthremma* Schmid (Chile), *Pseudosericostoma* Schmid (Chile), and *Zelolessica* McFarlane (New Zealand). Henderson (2007), Johanson (2003a), and Neboiss (2002) studied phylogenetic relationships among some members of the family; interestingly Henderson & Ward's (2007) cladogram did not group *Heloccabus* with other helicophids included in their data matrix. The current placement of many genera in the family is equivocal and a revision of the entire family and others in the Sericostomatoidea is needed (Flint 1992a). Helicophid larvae build tubular cases of sand grains, plant material, including almost entirely of pieces of moss, or entirely of silk; some Chilean species construct broad, flat cases of small mineral fragments. They live in clear, fast flowing, forested streams and spring runs, often associated with aquatic moss. Adults of many species are small, rare, and infrequently collected, although those of the Chilean genus *Eoseriocostoma* are common and widespread (Flint 1992).

Helicopsychidae: The snail-case caddisflies of the family Helicopsychidae were first recognized as the subfamily Helicopsychinae of Sericostomatidae by Ulmer (1906) and were retained there by a number of European workers well into the 1950s, most notably Ulmer himself (Ulmer 1955). Ross (1944) and other

American workers considered the group a distinct family, reflecting its current status. As presently constituted, the family contains only 2 genera, the cosmopolitan *Helicopsyche* von Siebold with about 250 species, and the New Zealand endemic genus *Rakiura* McFarlane, with a single species, *R. vernale* McFarlane. Several previously recognized genera, including *Cochliopsyche* Müller (Neotropical), *Petrotrichia* Ulmer (Afrotropical, including Madagascar and the Seychelles, but absent from southern Africa), and *Saetotrichia* Brauer (Australia, New Zealand, New Caledonia), were relegated as subgenera of *Helicopsyche* by Johanson (1998). In the same paper, Johanson described 2 additional subgenera of *Helicopsyche*: *Feropsyche* (Nearctic, Neotropical) and *Galeopsyche* (Korea, Vietnam). The nominotypical subgenus occurs in the Palearctic and Oriental regions. As a whole the family is poorly represented in the Northern Hemisphere, but reaches its greatest diversity in the tropics of the Old and New Worlds (Johanson 1997); the Neotropics alone hosts about 100 species. Larvae of the genus are the familiar and remarkable snail-case builders. These helical, sand grain cases are so similar to snails that early workers described these insects as molluscs. Lea (1834) went so far as to say of *Valvata arenifera* (=*Helicopsyche borealis*), "It has the singular property of strengthening its whirls by the agglutination of particles of sand, and by which it is entirely covered." While all helical, there is great diversity in the height of cases, the number and openness of the whorls, the size of mineral material, and the amount of silk incorporated. All helicopsychid larvae appear to feed as scrapers on periphyton and other organic matter on the exposed surfaces of rocks. They are found in slow flowing lowland streams as well as springs, small fast-flowing streams, and the wave-washed shores of lakes in temperate regions; they also occur in the hyporheic zone (Williams et al. 1983) and in thermal springs (Resh et al. 1984). The biology of the North American species, *H. borealis* (Hagen) is well known (Vaughn 1985a, b, 1987). Since Morse's (1997) review of phylogenetic studies within the Trichoptera, Johanson has undertaken significant analyses of evolutionary relationships within *Helicopsyche* (Johanson 1998, 2001, 2002, Johanson & Willassen 1997).

Hydrosalpingidae: The family contains only a single species *Hydrosalpinx sericea* described by Barnard (1934). He placed the species only within the "Aequipalpia" in the "neighbourhood of Molannidae-Beraeidae," but not within a specific family. Fischer (1970) had the genus listed under Helicopsychidae, but noted Scott's (1967) opinion that it may belong to the Beraeidae. It was not until 1985 that a new family, Hydrosalpingidae, was established for the genus (Scott 1985), which was more fully diagnosed and described some years later (Scott 1993). The species is endemic to the western and southwestern Cape Province of South Africa. Once common in cool acidic mountain streams, the species is now considered rare, possibly due to predation by introduced trout. Larvae feed on algae and detritus. Their tubular cases characteristically have a slightly flared anterior end and are made entirely of golden-brown silk. The discarded cases are often occupied by species of *Athripsodes* (Leptoceridae). Adults are medium-sized, densely hairy, golden brown caddisflies. Males have unusually long and slender maxillary and labial palps.

Petrothrincidae: The family was established by Scott (1985) for 2 species from South Africa, *Petrothrincus circularis* Barnard and *P. triangularis* (Hagen) (originally described from the case only and included in *Molanna*); Scott (1993) later described a 3rd South African species, *P. demoori* and expanded the diagnosis and description of the family. All of the South African species are endemic to the Cape Province. In his original description of the genus, Barnard (1934) could not place *Petrothrincus* within any known family and referred it only to "Aequipalpia." Fischer (1964, 1972) and others continued to catalog the genus within the Molannidae. Weaver (1997) recorded the family from Madagascar for the first time and described 3 additional species in a new genus, *Gyrocarisa* Weaver, to which 2 other species were added later by Malm and Johanson (2005). Recently, *Gyrocarisa* was synonymized with *Petrothrincus* by Johanson and Olah (2006), who described 5 additional Malagasy species. As of now, the family contains a single genus, *Petrothrincus*, containing 14 species from South Africa and Madagascar. The larvae live in small, cool streams in the

mountains and foothills in fast flowing riffles as well as pools. They construct broad, depressed, limpet-like cases similar to those seen in European *Thremma*, some North American *Ceraclea*, and in Chilean *Eosericostoma*; at least among the South African species the case can be circular or triangular. Larvae feed as scrapers on periphyton and the organic sediment that collects on the surfaces of rocks. Weaver (1997) noted several modifications of the female abdomen and wings, including long hairs on the hind wings, for holding the large eggmass above the abdomen and between the folded wings, possibly in a protective posture.

Sericostomatidae: The family was established by Stephens (1836) as Sericostomidae (later emended by McLachlan 1874 to Sericostomatidae). Over the years, the family has been used as a "dumping ground" for genera unable to be placed with confidence in other families. Fischer (1970) listed 26 genera in Sericostomatidae and stated, "Several of these genera may belong to the Lepidostomatidae, a few others probably to the Beraeidae. For some of the genera from the Australian region one or more subfamilies will have to be created." In fact, all of the Australian genera once included in Sericostomatidae have been moved to other families, most newly created for them (e.g., Antipodoeciidae, Conoesucidae, Tasimiidae), such that the family no longer occurs in the Australasian region. In other regions, other families were established for genera originally described in Sericostomatidae (e.g., Anomalopsychidae from the Neotropics, Barbarochthonidae from South Africa). As presently constituted the family contains 19 genera and only 100 or so species. The distribution of these genera is cosmopolitan, except for Australia, New Zealand, and their biogeographically associated islands, but the genera are for the most part restricted within their regions. In Africa, the family occurs only in South Africa where 5 endemic genera occur (*Aclosma* Morse, *Aselas* Barnard, *Cheimacheramus* Barnard, *Petroplax* Barnard, and *Rhoizema* Barnard, the later also recently described from Madagascar). In the Neotropics, the genera are endemic to southern Chile and adjacent Argentina (*Chiloecia* Navás, *Myotrichia* Schmid, *Notidobiella* Schmid, and *Parasericostoma* Schmid) and to southern and southeastern Brazil and adjacent Argentina (*Grumicha* Müller). In North America, 2 genera are endemic to the eastern half of the continent (*Agarodes* Banks and *Fattigia* Ross) and 1 genus, *Gumaga* Tsuda occurs in the western portion of the region. *Gumaga* is also found in the Oriental region where a genus endemic to India also occurs (*Asahaya* Schmid). Five genera occur in the western Palearctic region from northern and southern Europe, northern Africa, east to the Caucasus, Iran, and the Arabian peninsula (*Cerasma* McLachlan, *Notidobia* Stephens, *Oecismus* McLachlan, *Schizopelex* McLachlan, and *Sericostoma* Latreille). In addition to the 19 genera formally assigned to the family, several additional anomalous genera are known within the superfamily Sericostomatoidea that have not been assigned to a family. For completeness of coverage, these genera are: *Ceylanopsyche* Fischer from Sri Lanka, *Karomana* Schmid from India, *Mpuga* Schmid from India, *Ngoya* Schmid from India, and *Seselpsyche* Malicky from the Seychelles. Schmid (1993) and Malicky (1993) discuss the status of these enigmatic genera. The larvae of Sericostomatidae build tubular, strongly to slightly curved and tapered cases of sand grains or of silk alone. In Brazil, the long, slender silken cases of *Grumicha* were used as adornments by the Tupí-Guarani Indians. Sericostomatid larvae inhabit streams and lakes, the latter especially in temperate regions; they often burrow in sandy deposits. The primary food source is leaf litter detritus. Males of many species have modified antennal scapes with scent scales or scent glands, eversible glands on the face, or mask-like maxillary palps, or a combination of these.

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