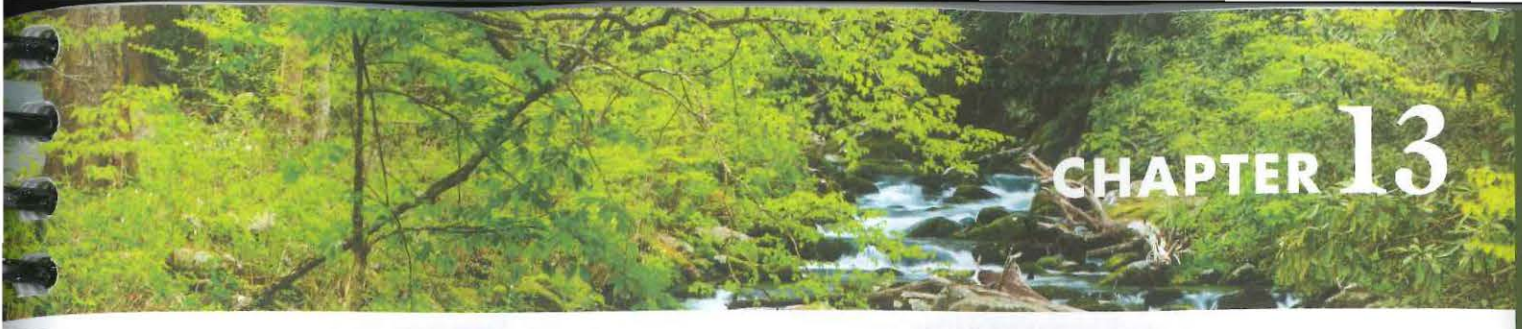

CHAPTER 13

EPHEMEROPTERA

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INTRODUCTION

Throughout North America mayflies occur in many types of freshwater habitats. The greatest diversity of species occurs in perennially cold (i.e., mean annual temperature $\leq$ 20°C) 2nd–3rd order streams of forested watersheds with good water quality and hydrologically complex channels dominated by loose rocky substrates, but with some areas of finer sediment and at least some submerged or emergent aquatic plants (often along channel margins or in deeper pools). In North America, mayfly diversity at all taxonomic levels peaks in the mid-latitude drainages of the unglaciated highlands of the east and southeastern United States. However, recent work on aquatic insect diversity of the northernmost parts of Canada using DNA barcodes has revealed an unexpectedly high level of mayfly diversity at high latitudes (Cordero *et al.* 2016). Mayfly diversity also depends on the occurrence of suitable habitat and its distribution over the longitudinal profile of the drainage system, which is strongly influenced by local climate and geomorphology. For most Nearctic mayflies the interspecific effects of predation and competition, which are important at the microhabitat scale, seem to have little influence on diversity patterns at the spatial scale of drainage basins. In addition, large scale mayfly distribution and diversity patterns show little agreement with broadly defined aquatic or terrestrial ecoregions (Abell *et al.* 2000; Griffith *et al.* 2009), which are based on landscape or drainage network variables that are seemingly not restrictive for many mayfly species. For many mayflies local patterns of commonness and/or rarity are more reflective of variables that determine the composition of the regional species pool, which in North America has been reshuffled several times over the history of the last 2 million years. The glaciers of the Pleistocene and subsequent changes to major drainage systems represent the most important geological events of the recent past affecting mayfly populations. However, the effects of much older geological events may still be evident in the genetic structure of populations and species—especially in the eastern and southeastern parts of the continent. The application of species distribution modeling to the complex mayfly species occurrences of the ancient drainages of eastern North America could be helpful in trying to understand the diversity and distribution of mayflies of this region. More recent anthropogenic activities, such as land clearing for agriculture and dams for industry, which began with European colonization, have continued to the present day. Recent perturbations include the discharge of chemical pollutants, dredging of channels, and removal of floodplain wetlands, as well as modern forms of land clearing for mining, forest products extraction, and urban development. All of these activities and others too numerous to name have produced widespread changes in the diversity and abundance of mayfly species. In drainages where 2nd and higher order streams have been extensively disturbed, minimally disturbed 1st order streams often have the highest local and regional diversity. Large river channels, ponds, lakes, reservoirs, and wetlands, usually have naturally lower overall mayfly diversity compared to small stream systems, but can have unique assemblages of species that do not occur in lotic habitats. Unfortunately, in many parts of North America, most large rivers, ponds, lakes, and wetlands have experienced some of the highest levels of disturbance. Currently, minimally disturbed large rivers, lakes, ponds, and wetlands only occur in the northernmost parts of North America (i.e., Alaska and far northern Canada).

Historically, most of the species-level work on mayflies was based on the male adult stage (imago), but many recent studies on the taxonomy and biology of mayflies have focused on the nymph.

The emphasis on the nymph is in part because of what has been viewed as the limited range of useful adult characters. Adults however, do have complex morphologies and show much variation within and between populations, which is poorly understood for most species. Adults also have a wide range of complex behaviors especially concerning mating, dispersal, and oviposition that are still poorly understood. Some of these behaviors may be taxonomically important. Perhaps the greatest problem in working with the adult stages of mayflies is that they are elusive. Unless adults of a particular species can be efficiently reared in the laboratory or come to lights or form conspicuous swarms during daylight hours they are infrequently encountered. The adults of some genera are so difficult to collect they are rarely seen, except by specialists, and even then in numbers that are too small for extensive comparative study. The adults of some genera and species are still unknown to science.

The eggs of many mayflies are usually deposited at the water surface, a few at a time or all at once in one or two clusters, but several other oviposition behaviors are known. The biological costs of different mayfly oviposition behaviors were comparatively studied by Encalada *et al.* (2007, 2012). They concluded that overall fitness costs concerning the chance of survival of females to complete oviposition were substantial and that these costs were associated with specific behaviors before the event of oviposition. Although most mayflies oviposit at the surface of the water, in some species of *Baetis,* the female crawls beneath the water and lays rows of eggs on rocks that are oriented in just the right way. One recently described species, *Eurylophella oviruptis*, can release eggs in a violent rupturing of the abdomen (Funk *et al.* 2008). Eggs of most mayflies have sticky coverings, frequently with specialized anchoring devices (Koss and Edmunds 1974; Kopelke and Müller-Liebenaue 1981; Provonsha 1990). Egg structures are useful in taxonomic and phylogenetic analyses for some groups of mayflies. Embryonic development usually takes a few weeks. True egg diapause has been confirmed experimentally in only a few mayfly species (Brittain 1982, 1990), but quiescence seems a likely event for many temperate zone mayflies. In many species, egg hatching may be delayed 3–9 months and eggs of at least one species of *Parameletus* may remain dormant for over 11 months (Edmunds *et al.* 1976). In other species, development proceeds directly. A number of mayfly species are known to depend on specific hatching temperatures (Brittain 1982, 1990; Knispel *et al.* 2006; Ward 1992).

Mayfly nymphs undergo numerous molts; examples of reported numbers of molts are 12 for *Baetisca rogersi* Berner, 27 for *Baetis tricaudatus* Dodds, and 40–45 for *Stenacron interpunctatum* (Walker). Because higher mortality tends to occur during rather than between molts, reduced numbers of instars should be adaptive. Exact counts of the number of molts are difficult to obtain and some totals reported may be overestimates. Length of nymphal life varies with temperature and is usually 3–6 months months. The period can be as short as 10–14 days in some Baetidae, Leptohyphidae, and Caenidae or as long as 2 years in *Hexagenia limbata* Serville in some cold habitats. Development of *Hexagenia limbata* Serville varies from 1 to 2 years in Lake Winnipeg in northern Canada, but the same species may develop in less than 17 weeks in warm canals in Utah and can be laboratory reared in 13 weeks. Some mayfly species may produce several broods a year. Such multivoltine species develop much faster in summer than do their overwintering broods. Currently, true diapause has not been reported for mayfly nymphs, but periods of extremely slow growth can occur when thermal conditions are less than optimal (Brittain 1990).

Mayfly nymphs are mostly collectors or scrapers (Chapter 6) and feed on a variety of detritus, algae, and some macrophyte and animal tissue. A few species are true carnivores and some are facultative shredders (Table 13A). Frequently, food habits vary during the growth period. Newly hatched nymphs tend to feed largely on fine particle detritus. Many instars later shift to ingestion of algae, and some eventually increase the amount of animal material eaten as they increase in size. *Siphlonisca aerodromia* Needham shifts from omnivorous to full carnivorous feeding in later stages of its development.

Mayflies have two winged-instars, the subadult (subimago) and the adult (imago). The winged, but usually nonreproductive subimago stage in the mayfly life cycle is unique among the living orders of insects. However, we know from fossils that several extinct orders of insects had two or more winged instars (Kukalova-Peck 1978). Subimagos of many species often perch on shoreline vegetation after emergence, but subimagos of extremely short-lived species alight for only 1–2 min or shed the subimaginal cuticle from all but the wings without alighting.

The length of the subimago stage tends to be correlated with the length of the adult life. It may be as short as a few minutes in species whose winged life is about 4 hours or less (e.g., *Ephoron*, *Tortopsis*, and *Caenis*) or as long as 24–48 hours in species with

longer lived imagos and depends on temperature. In warm climates the subimago often emerges at dusk and transforms into an adult before dawn. This tendency is greatest in some *Tricorythodes*. The males of *Tricorythodes* emerge after dusk and the females emerge a few hours before dawn; both sexes transform to adults by dawn. Mating swarms of *Tricorythodes* usually occur from early full sunlight until near noon.

Subimagos have a cuticle that is almost completely covered with a dense layer of microtrichia (Edmunds and McCafferty 1988). These microtrichia produce the subdued grayish and nonreflective appearance of the subimaginal cuticle compared to the glossy appearance of the adult cuticle. More importantly, they make the subimago relatively waterproof or at least highly resistant to wetting. Edmunds and McCafferty (1998) noted that nearly identical microtrichia occur on the wings of adult caddisflies, true flies, and other adult aquatic insects. The persistence of the subimago in extant mayflies may be largely explained by the reduced chance of being trapped in the surface film as the subimago escapes from its nymphal exuviae at the water–air interface or perhaps underwater. Important developmental changes in the relative proportion of the legs and male genitalia occur at the subimago to adult imago molt. The males of all mayfly species make this transformation from the subimago stage to the imago. Most females also make this transformation, but females of a few North American species mate and/or lay eggs as subimagos (e.g., *Tortopsis*, *Campsurus*, *Ephoron*, and some *Callibaetis*).

Adults of some species of *Baetis* emerge throughout the year even in strongly seasonal climates. Long emergence periods for mayflies characteristically occur where winters are relatively mild, such as the Pacific Coast and in the Southeast. Adults of most species live 2 hours to 3 days, but some live less than 90 min. The females of some genera may live for weeks. This is especially true for those ovoviviparous genera that hold eggs until they are ready to hatch, e.g., *Callibaetis* and *Cloeon* (Oehme 1972). A YouTube video from the Stroud Water Research Center (Avondale, PA) of *Cloeon dipterum* eggs hatching about 1 min after being released by the female imago is an amazing site and partially explains why this species is so successful.

EXTERNAL MORPHOLOGY

The following account of the external morphology of mayflies is a general overview and will facilitate use of the keys. Standard insect morphological terms used are according to Snodgrass (1935). Mayfly specific anatomical and morphological terms and conventions used are according to Edmunds *et al.* (1976), Hubbard (1995), and Kluge (1994, 2004).

Nymphs

Head (Fig. 13.1): The shape of the head capsule is variable and it may have a variety of processes, projections, and armature. Compound eyes are usually large, relative to the size of the head capsule, and are situated laterally or dorsally near the posterolateral margin of the head. The antennae usually arise anterior or ventral to the compound eyes. The antennae may vary in length from less than the width of the head to as much as half the length of the body. Typical mouthparts are illustrated in Figure 13.2. Mouthparts of specialist fine particle collectors (e.g., *Arthoplea*) and predators (e.g., *Acanthametropus*) vary extensively from this base plan with different types of mandibular and maxillary surfaces and modified maxillary and labial palps. Even the labrum can be extensively modified.

Thorax (Fig. 13.1): Developing wing pads occur on the meso- and metathorax, although metathoracic wing pads may be absent in some species. Each thoracic segment has a pair of well-developed legs. Basic segmental structure of legs is consistent throughout North American species, but tarsal claws are absent in *Dolania americana*. The legs of some genera are modified for special functions such as burrowing, filtering food, and grooming. Nymphs of the sand burrowing species *Dolania americana* seem to protect its ventrally oriented gills with its trailing hind legs while beneath the sand.

Abdomen (Fig. 13.1): All mayflies have a 10-segmented abdomen; however, some of the anterior segments may be concealed beneath the mesonotum or by developing wing pads. The terga may have spines and/or tubercles. The shape, presence, or absence of the posterolateral corners of abdominal terga can be used as taxonomic characters. To locate a particular abdominal segment number always count forward from segment X. Abdominal gills are the most variable nymphal structure. The simplest form is that of single lamellae, as occurs in *Baetis*, but the greatest variety of complex gill forms occurs in the Leptophlebiidae. Despite this obvious and diagnostic feature of the mayfly abdomen, some mayflies also have gill filaments at the bases of the thoracic coxae (e.g., *Isonychia*, *Camelobaetidius*, and *Heterocloeon*), or at the bases of the maxillae (*Isonychia*). Gill position on the abdomen is variable; gills may be ventral, lateral, or dorsal. Abdominal gills occur on segments I–VII or they may be absent from

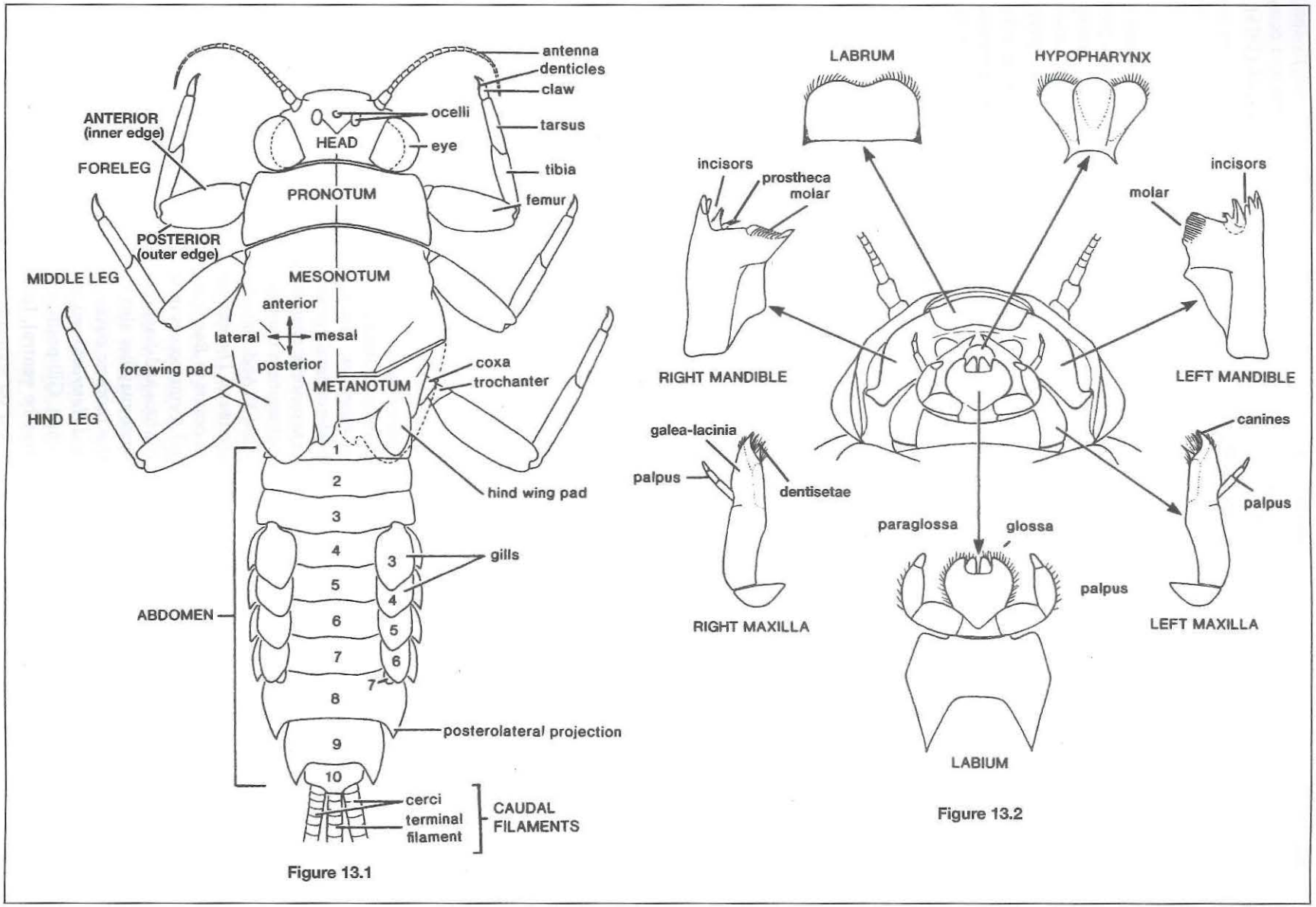


Figure 13.1 Dorsal view of *Ephemerella* sp. nymph (Ephemerellidae).

Figure 13.2 Ventral view of mouthparts of *Ephemerella* sp. nymph (Ephemerellidae).

one or more segments in various combinations. In referring to gill position, gill 4, for example, refers to the gills on abdominal segment IV whether or not there are gills on the first three segments.

Nymphs of most mayfly species have three well-developed caudal filaments, composed of a terminal filament and two cerci (Fig. 13.1). However in a few species, only the cerci are well-developed, the terminal filament is often represented by only a short rudiment or may appear to be entirely absent. When present, the terminal filament may vary in length and thickness relative to the cerci. Length of the caudal filaments varies from shorter than the body to two or three times its length.

Adults

Head (Fig. 13.157): The eyes are usually sexually dimorphic, those of the male being larger than those of the female. In males, the eye facets may be uniform in size or the upper facets may be larger than lower facets. In the Baetidae the upper facets of male compound eyes are turbinate, i.e., elevated on a stalk-like portion (Fig. 13.195). All adult mouthparts are vestigial and nonfunctional.

Thorax (Figs. 13.157 and 13.162): The prothoracic segment is frequently small and bears the forelegs. In males the dorsal pronotum is frequently obscured by the large compound eyes. The mesothoracic segment is the largest because it has the forewings and middle pair of legs and all of the musculature associated with these appendages. The large mesonotum is clearly visible between the bases of the forewings. The metathoracic segment, which is much smaller than the mesothoracic segment, has the hind legs and hind wings (which may be absent in some species). The thoracic segments are variously pigmented and variation in the structure of the pronotum and mesonotum are taxonomically useful. Kluge (1994) gives a detailed discussion of the many features of the thorax that are of systematic value. The forelegs of most mayflies show sexual dimorphism, with those of the male having very long tibiae and tarsi. The male forelegs are also much longer than the middle and hind legs. Often the male forelegs are as long as or longer than the body. In the Polymitarcyidae, the middle and hind legs of the male and all legs of the female are much reduced and presumably nonfunctional. In *Dolania* (Behningiidae) all the legs of both sexes are much reduced, but apparently are somewhat functional. Most mayflies have two pairs of wings; the somewhat triangular forewings and the much smaller and more variable hind wings. In the Caenidae, Leptohyphidae, and Baetidae the hind wings have become greatly reduced or completely lost in one or both sexes. The three wing margins are known as the costal, outer, and hind margin (Figs. 13.157 and 13.162). The mayfly wing is not flat, but has a regular series of corrugations or fluting with the longitudinal veins lying either on a ridge (indicated in the figures by +) or a furrow (indicated by –). The complex primitive venation of giant Carboniferous fossil mayflies (wingspread up to 45 cm) is presented by Kukalova-Peck (1985). The system of venational nomenclature proposed by Tillyard (1932) as discussed by Edmunds and Traver (1954) has been followed here. Abbreviations designating the major longitudinal veins and their convexity (+) or concavity (–) relative to wing fluting as viewed dorsally are as follows:

C (+)	=	costa
Sc (–)	=	subcosta
R_1 (+), R_2(–), R_3(–), R_{4+5}(–)	=	$radius_1$, $radius_2$, $radius_3$, $radius_{4+5}$
MA_1(+), MA_2(+)	=	medius $anterior_1$, medius $anterior_2$
MP_1(–), MP_2(–)	=	medius $posterior_1$, medius $posterior_2$
CuA (+)	=	cubitus anterior
CuP (–)	=	cubitus posterior
A_1 (+)	=	$anal_1$

R_2 through R_5 are often referred to as the radial sector (Rs) and arise from the stem vein R_1. Likewise vein groups MA_1, MA_2 and MP_1, MP_2 arise from respective stem veins MA and MP (although there are instances where MP_2 is only indirectly connected to MP via a crossvein). Intercalary veins lie between the principal veins. When intercalaries are long, they lie opposite the principal veins on either side; for example, IMA (intercalary medius anterior) is a furrow (–) vein lying between the two ridge (+) branches of MA (MA_1 and MA_2). Conversely, IMP is a ridge vein (+) in between the furrow veins of MP. The longer primary veins alternate as ridges and furrows at the wing margin. Two ridge veins of the forewing, MA and CuA, are important landmarks in locating and identifying the entire venation. Learning which veins are ridge veins (+) and which are furrow veins (–) is important for efficient use of the keys.

Abdomen (Figs. 13.157–13.159): the abdomen is composed of ten segments. Each segment is circular in cross section and consists of a dorsal tergum and a ventral sternum. The posterior portion of sternum 9 of the female is referred to as the subanal plate and in males (Fig. 13.158) as the subgenital plate (or styliger plate). The posterior margin of the male subgenital plate, which is variable in shape, gives rise to a pair of

slender and usually segmented appendages called the forceps (or claspers). Dorsal to the subgenital plate are the paired penes (Fig. 13.158). In most mayflies the penes are well-developed and at least partly sclerotized, but in the Baetidae they are membranous and extrudable. The male imago of *Parameletus croesus* was observed to have both sclerotized penes with spines and an extrudable copulatory structure (Burian 2017). Arising from the posterior portion of abdominal segment X in both sexes are the caudal filaments (Figs. 13.157 and 13.159). Most species have two caudal filaments, composed of the lateral cerci and a vestige terminal filament; others have three, the cerci and a well-developed terminal filament.

CURRENT STATUS AND RECENT CHANGES IN EPHEMEROPTERA SYSTEMATICS

The keys presented here are to the families and genera of North American taxa only; subfamilies and subgenera are not keyed. The basic arrangement of major taxonomic groups (suborders and families) used here is that of McCafferty (1997) because it still provides an efficient and familiar platform for organizing and presenting data on currently well-supported mayfly families, but this arrangement is not fixed. Several molecular studies have shown that there is much uncertainty in the current arrangement and the composition of some major taxonomic groups (Ogden and Whiting 2005; Ogden *et al.* 2008; Monaghan and Sartori 2009). More recent work by Webb *et al.* (2012) has indicated that there is much cryptic diversity among the lineages of North American mayflies that needs to be further explored. Some of these discoveries could likely result in changes to the current classification. Moreover, the attempt to create a cladistically congruent classification has proved difficult for some families and has resulted in several genera being placed into monobasic families. For example, *Ameletus* (previously placed in the Siphlonuridae) now occurs as the only genus in the family Ameletidae. The genus *Isonychia*, formerly in the subfamily of Oligoneuriidae, is the only genus in the family Isonychiidae. Landa and Soldán (1985) provided evidence that *Pseudiron* is a distinct lineage and is now recognized in its own family, Pseudironidae. However, Ogden and Whiting (2005) have shown that both *Pseudiron* and *Arthroplea* nest within the family Heptageniidae and perhaps should be returned to that family. Further studies of the Ephemeroidea have resulted in the reassignment of *Pentagenia* to the Palingeniidae (McCafferty 1991a). The lack of well-supported molecular phylogenies for large families such as Baetidae, Ephemerellidae, Leptophlebiidae, and Heptageniidae continues to be a problem affecting classification of genera.

Rare or geographically restricted genera, as well as all common genera, are included in keys to nymphs and adults. Although the inclusion of rare or restricted genera does increase the length of keys and their complexity, comprehensive keys are essential to the discovery and documentation of mayfly biodiversity. Many rare or geographically restricted genera, such as *Anepeorus*, *Waynokiops*, or *Kirmaushenkreena* occur in large rivers, large or remote lake systems, or at high latitudes where much effort and sometimes specialized collecting techniques are required. Other genera (e.g., *Caurinella* or *Siphlonisca*) are restricted to small streams or flooded stream margins and simply require being in the right place at the right time. Under the right circumstances rare taxa can seem locally abundant and relatively easy to observe, but most of the time substantial effort (and ingenuity) is required to find any evidence of their presence. Despite the difficulty in collecting and identifying rare taxa, their importance to biomonitoring or biosurvey efforts is clear. Data from rare or restricted taxa provide insights into diversity patterns and subtle changes in habitats that cannot be obtained from the study of common taxa alone. Only by documenting these taxa can a comprehensive understanding of mayfly biodiversity be achieved and applied.

The adult of the genus *Acanthametropus* (Acanthametropodidae) has been associated with its nymph by workers in Russia and this may provide some clues as to what the unknown adult of the North American species *A. pecatonica* is like. McCafferty and Wang (1994a) reunited *Analetris* and *Acanthametropus* in the family Acanthametropodidae based on a revised cladistic analysis.

The generic taxonomy of the Baetidae has substantially changed in recent years. The studies affecting the genera in this edition are those of Waltz and McCafferty (1987a,b,c,d; 1989); Waltz *et al.* (1985, 1994); McCafferty and Waltz (1990, 1995); Waltz (1994); Lugo-Ortiz and McCafferty (1998), Lugo-Ortiz *et al.* (1999); Waltz (2002); Hill *et al.* (2010); McCafferty *et al.* (2008, 2010); McCafferty (2011); Kluge (2011); and Jacobus and Wiersema (2014). Noteworthy recent changes include: the reestablishment of the genus *Labiobaetis* for what previously was known in North America as *Pseudocloeon*; the discovery of the new Nearctic genus *Waynokiops* (type species *W. dentatogriphus*) from impoundments in the central and southeastern United States; and the discovery of the new genus *Kirmaushenkreena* (type species *K. zarankoae*) from the Tehek Lake system north of Baker Lake, Nunavut, Canada. In addition,

further study of baetids has yielded some additional insight into the problem of separating nymphs of *Plauditus* and *Acentrella* that lack hind wing pads. Key characters concerning the shape and form of segment 3 of the labial palps have always been difficult to apply for separating these genera. From the description provided by Lugo-Ortiz and McCafferty (1998) the apex of labial palps varies from slightly truncate to slightly concave with the inner medial margin straight to slightly convex for the genus *Plauditus*. Unfortunately, these shape characters fail to separate two species of *Acentrella* (*A. lapponica* and *A. fergopagus*) from *Plauditus* in many instances. For species of these genera that lack hind wings a more consistent character seems to be the shape and form of spinules along the posterior margins of abdominal terga. For *Plauditus* these marginal spinules are distinctive conical shaped projections that may have a sharp point or may be broadly rounded—they never appear ragged or with multiple points. For *Acentrella* these spinules are poorly developed often with ragged sharp multiple points and never form a distinctive row along the posterior margin. In *Acentrella*, most of the time, these spinules seem to be similar to the surface sculpturing of the tergite. These characters of the posterior margins of abdominal terga were first described in detail by Waltz and McCafferty (1987). The reevaluation of generic characters for known North American adults of the genus *Fallceon* (McCafferty *et al.* 2008) has shown that what were believed to be consistent diagnostic characters of the coastal projection and male styliger plate were variable in at least one species. Recent studies by Kluge (2011) on the taxonomy of a group of non-African baetids showed that some species previously placed in the genus *Centroptilum* represent members of a new genus *Anafroptilum*. The primary diagnostic character specified by Kluge (2011) for nymphs of *Anafroptilum* is the absence of the patello-tibial suture on the forelegs (suture is present on mid and hind legs). In contrast, nymphs of *Centroptilum* have the patello-tibial suture present on all legs. Jacobus and Wiersema (2014) reviewed the status of the North American species placed in the genus *Centroptilum* and determined that most needed to be reassigned to *Anafroptilum*, but they also found that some species did not fit the criteria for either *Centroptilum* or *Anafroptilum* and needed to be placed in a new taxon. Subsequently, they reestablished the genus *Neocloeon* for these species. Although knowledge of characters useful for identifying genera and species of the nymph of the Baetidae has increased, substantially less is known about adult characters. For this reason, couplets separating adult Baetidae presented herein should be regarded as somewhat provisional. In fact, for some species of *Anafroptilum* and *Procloeon*, female imagos cannot be reliably identified below family. Finally, molecular studies using DNA barcodes has so far provided evidence to resurrect at least one species, *Baetis phoebus* McDunnough, that was considered a synonym of *B. flavistriga* McDunnough (Zhou *et al.* 2010). Currently, this species cannot be reliably diagnosed using standard morphological characters.

New analyses of the brachycercine mayflies of the family Caenidae by Sun and McCafferty (2008) have led to the discovery of several new genera and species. The study of North American species of what had been a single genus revealed that there were actual three genera present: *Brachycercus*, *Sparbaus*, and *Susperatus*. In addition, the new genus *Latineous* was separated from the exiting genus *Cercobrachys*. Sun and McCafferty (2008) also determined new tribe-level groups for this assemblage of species.

In Heptageniidae, the previous confusion concerning *Anepeorus* and *Spinadis* was clarified by Wang and McCafferty (2004). Also in agreement with their work, the subgenera *Iron* and *Ironopsis* of *Epeorus* are not recognized in the keys of this chapter. The subgenus *Maccaffertium* Bednarik was raised to the genus level reducing *Stenonema* to monotypic status containing only *S. femoratum* (Say). McCafferty (2010a, b) identified two new species of *Maccaffertium* from the central and southeastern United States. Currently, these two species are only known as nymphs*. Since 2004, attempts to elucidate the phylogenetic relationships of the supraspecific taxa of the Heptageniidae have made it clear that there are still many systematic problems at the genus-level to be resolved. Currently, it must be taken as an axiom that in the absence of a broad molecular phylogeny for the Heptageniidae, it is not possible to resolve the conflicting interpretations of relationships and the composition of some genera represented in the phylogenies by Kluge (2004) and Wang and McCafferty (2004), which where based entirely on morphological characters. Among problematic taxa, the relationships and classification of *Afghanurus* Demoulin, *Ecdyonurus* (Eaton), *Leucrocuta* Flowers, *Nixe* Flowers, and *Paracinygmula* Bajkova are of particular concern for North American mayfly workers. These genera have been discussed and variously synonymized in numerous studies (Jacob *et al.* 1995;

*Recent molecular phylogenetic work by Zembrzuski and Anderson (2018) determined *Maccaffertium* to be a paraphyletic group returning it to a subgenus of *Stenonema* along with all species listed therein (Zembrzuski, D. C., and F. E. Anderson. 2018. Clarifying the phylogenetic relationships and taxonomy of *Stenonema*, *Stenacron* and *Maccaffertium*, three common eastern North American mayfly genera. Molec. Phyl. and Evol. 128: 212–220.

Kluge 1980, 1988, 1997, 2004; McCafferty 2004; Tshernova 1978; Tshernova *et al.* 1986). McCafferty (2004) summarized most of the studies where synonymies were proposed and offered new diagnoses for *Ecdyonurus* (including the *simplicioides* species group), *Leucrocuta*, and *Nixe*. McCafftery's interpretation of the status of the *simplicioides* species group with regards to *Ecdyonurus* was largely based on the occurrence of a sclerous structure on the penes of male imagos of this group. He believed this feature was an apomorphic character and subsequently reassigned species previously placed in *Nixe* (*Akkarion* = *simplicioides* species group) into *Ecdyonurus*, which greatly broadened the definition of that genus and extended its range from Europe to North America. Although McCafferty (2004) recognized the important differences between the European species of *Ecdyonurus* that have nymphs with posteriorly directed pronotal flanges (i.e., *Ecdyonurus* s.s.) and members of the North American *simplicioides* species group that he placed in *Ecdyonurus* as both being worthy of individual group status, he justified not recognizing the *simplicioides* species group in the taxon *Afghanurus* as necessary to avoid possibly creating a paraphyletic taxon and to fulfill the goal of having a strictly phylogenetic classification. However, after careful reexamination of all published accounts of the taxonomic status of the genera noted above, as well as all figures and images of characters described by McCafferty (2004) as the basis for his decision to reassign species of *N.* (*Akkarion* = *simplicioides* species group) to *Ecdyonurus*, and taxonomic comments made by J.M. Webb concerning his previous and ongoing studies of the classification of genera of the Heptageniidae (Webb and McCafferty 2008) and his recent taxonomic notes concerning the status of *Afghanurus* (Jacobus *et al.* 2014, per. comm. 2017), and taking into account the global uncertainty about the phylogeny of the Heptageniidae it is clear that the rationale given by McCafferty (2004) in support of the decision not to recognize *Afghanurus* is no longer tenable. Although there is broad international consensus for the monophyletic group of European species of *Ecdyonurus* that have nymphs with posteriorly directed pronotal flanges (Bauernfeind and Soldan 2012; Kluge 2004; Webb and McCafferty 2008), there are different views as to the composition of *Afghanurus* and whether it should be a genus or subgenus. Based on all the available evidence, I believe Kluge (2004) offers the most explicit support for the recognition of the genus *Afghanurus* (which he lists as containing the junior synonyms *Nixe* Flowers and *Paracinygmula* Bajkova). Therefore, the genus *Afghanurus* Demoulin is herein recognized for North American species previously placed in *N.* (*Nixe*) s.s. and *N.* (*Akkarion* = *simplicioides* species group). The genus *Leucrocuta* is maintained according to apomorphic character support presented by Kluge (2004) and diagnoses given by McCafferty (2004) and Webb and McCafferty (2008).

Within Leptophlebiidae there have been only a few changes affecting genera in North American. Previously *Neochoroterpes* was elevated to the rank of genus (Henry 1993; McCafferty *et al.* 1993). The genus *Farrodes* is included in keys to both nymphs and adults. Flowers and Domingues (1992) established the genus *Hydrosmilodon* for the species previously known as *Traverella primanus* (Eaton). Most recently Tiunova and Kluge (2016) recognized both *Paraleptophlebia* and *Neoleptophlebia* as separate genera. The genus *Paraleptophlebia* is now restricted to those species with nymphs that have deeply forked abdominal gills lacking distinct tracheal branches and labial palps with segment 3 widest at its midpoint. Male imagos of *Paraleptophlebia* are characterized as having paired ventral appendages that arise from each penis lobe and are directed back toward the base of the penes (often curving laterally). The genus *Neoleptophlebia* is now restricted to those species that have gills that are not deeply forked and numerous distinct tracheal branches and labial palps with segment 3 widest near its base. The male imagos of *Neoleptophlebia* have a wide range of genital structures, but all lack the paired ventral appendages that are oriented as described above. Tiunova and Kluge (2016) list all North American species newly combined into *Neoleptophlebia*.

The family Leptohyphidae replaced Tricorythidae for all new world taxa previously listed in the subfamily Leptohyphinae (McCafferty and Wang 2000). Studies of the New World Leptohyphidae by Baumgardner (2008) have shown that *Ableptemetes*, *Homoleptohyphes*, and *Tricoryhyphes* are synonyms of *Tricorythodes*. In addition, Baumgardner determined that the genus *Asioplax* is a subgenus of *Tricorythodes*. Although these changes in nomenclature were first proposed by Baumgardner in his Ph.D. dissertation, which did not meet the criteria for publication according to the requirements of the International Code of Zoological Nomenclature (ICZN), he later included all of these changes in a conference abstract that was openly distributed online and was permanently archived in a record of the conferences contents (Baumgardner 2014). I believe because the abstract did not have a disclaimer according to recommendations of the ICZN, the distribution was not restricted to the participants of the conference, and the contents of the abstract (as well as all abstracts of that conference) are in a permanent open access archive, the abstract contents qualify as being unintentionally published, but published nonetheless according to most recent updates to the ICZN.

Therefore, *Ableptemetes*, *Homoleptohyphes*, and *Tricoryhyphes* will be recognized as junior synonyms of *Tricorythodes* and *Asioplax* is recognized as a subgenus of *Tricorythodes* pursuant to Baumgardner (2014).

In the Polymitarcyidae, Molineri (2010) revised the taxonomy of the genus *Tortopus* restricting it to the type species *T. igaranus* Needham and Murphy, as well as five sister species mostly restricted to Central and South America. Only the species *Tortopus circumfluus* Ulmer has been confirmed from Texas. In addition, Molineri created the new genus *Tortopsis* for all the remaining North American species previously placed in *Tortopus* as well as seven other species known from Central and South America.

In Potamanthidae, Bae and McCafferty (1991) showed that the North American species formerly assigned to *Potamanthus* were not congeneric with the Palearctic-Oriental *Potamanthus* and created the genus *Anthopotamus* for them (McCafferty and Bae 1990).

In Ephemerellidae, revisional studies by Jacobus and McCafferty (2008) have reviewed the status of all valid genera and have identified several new taxonomic entities and proposed several new synonymies. For North America, new monotypic genera include *Matriella*, *Penelomax*, *Tsalia*, and *Teloganopsis* (this only applies to *Teloganopsis* in North America, elsewhere in the world the genus contains more species). They also proposed new characters for separating nymphs of *Ephemerella* and *Serratella* and recognized three new subgenera within *Ephemerella* (i.e., *E.* [*Draeconia*] [for *E. needhami*], *E.* [*Scholitza*] [for *E. verruca*], and *E.* [*Vittapallia*] [for *E. tibialis*]). The adult of *Caurinella idahoensis* was described by Jacobus and McCafferty (2004) completing our knowledge of its life stages. The previously recognized genus *Dannella* that had been synonymized with *Timpanoga* was returned to full genus status (McCafferty 2000). Burian (2002) associated the nymphal and adult stages of *Eurylophella coxalis*, which was later reassigned to *Dentatella* by McCafferty and Jacobus (2003). Analyses of DNA barcode sequences published by Webb *et al.* 2012 (as supplemental data) showed *Dentatella* to be clearly a paraphyletic genus deeply embedded within *Eurylophella*, thus *D. coxalis* is returned to *Eurylophella* and *Dentatella* is herein considered a junior subjective synonym of *Eurylophella*. Finally, Alexander *et al.* (2009) studied the genetic lineages of nine taxonomically problematic species of *Ephemerella* using the cytochrome oxidase I (COI) barcode. Although evidence was found supporting some of the current taxonomy (which was entirely based on morphology), some problems were still unresolved using this method. In addition, they found that western *E. aurivillii* had such a high sequence divergence from eastern *E. aurivillii* that it might be appropriate to place the western population in a new genus. Lastly, Alexander *et al.* (2009) pointed out problems concerning incomplete mtDNA lineage sorting in this group of *Ephemerella* species and discussed the effectiveness of the cytochrome oxidase I (COI) barcode as a stand-alone method to resolve taxonomic problems.

All reported distributions should be regarded as incomplete. Such terms as abundant, common, uncommon, or rare are all relative to place, time, and collector. Although such terms as "rare or uncommon" have been somewhat quantified by international biodiversity organizations, such as Nature Serve®, they are still highly subjective when used in the absence of exhaustive surveys and life history studies. Rare can be interpreted as difficult to collect, active at the wrong time of day, or perhaps, indicative of a truly small and widely dispersed population. In any case, a collector using the optimum technique, at the right place and at right time may collect large numbers of what generally is considered a "rare" genus or species.

A final note to users of the keys presented here. The morphology of nymphs does change as individuals grow. Characteristics useful in determining a specimen to genus may not be evident or reliable until the middle stages of development. The key to nymphs presented here should be effective when applied to specimens at or beyond the mid-point of development. Although the key may work for early developmental stages of some taxa, it will likely fail for others.

KEYS TO THE FAMILIES AND GENERA OF EPHEMEROPTERA

Mature Nymphs

1 Thoracic mesonotum enlarged to form a shield extended to abdominal segment VI, abdominal gills enclosed beneath shield (Fig. 13.3) . . . . . ***BAETISCIDAE-Baetisca***

1' Thoracic mesonotum not enlarged as above; at least anterior abdominal gills exposed 2

2(1') Gills on abdominal segments II–VII forked and elongate-lanceolate, with margins fringed (Fig. 13.5); mandibular tusks projected forward and visible from above head (Figs. 13.7, 13.8); if tusks absent, head and thorax with pads of long spines (Fig. 13.9) 3

2' Gills on abdominal segments II–VII variable; if gills forked and elongate-lanceolate, margins not fringed (Fig. 13.6); mandibular tusks rarely present 7

3(2) Head and prothorax with dorsal pads of long spines (Fig. 13.9); mandibular tusks absent; abdominal gills ventral . . . . . ***BEHNINGIIDAE-Dolania americana***

3' Head and prothorax without pads of spines; mandibular tusks present (Figs. 13.7, 13.8); abdominal gills lateral or dorsal 4

4(3') Foretibiae more or less modified for burrowing, either broad or with tubercles (Fig. 13.7); abdominal gills held dorsally 6

4' Foretibiae unmodified, not adapted for burrowing (Fig. 13.8); abdominal gills held laterally 5

5(4') Mandibular tusks with many long setae (Fig.13.4). . . . . ***EUTHYPLOCIIDAE..Euthyplocia hecuba***

5' Mandibular tusks without many long setae (Fig. 13.8). . . . . ***POTAMANTHIDAE..Anthopotamus***

6(4) Tips of mandibular tusks curved upward, when viewed laterally (Fig. 13.10); ventral apex of hind tibiae developed as a distinct acute point (Fig. 13.12) 105

6' Tips of mandibular tusks not curved upward, when viewed laterally (Fig. 13.11); ventral apex of hind tibiae rounded (Fig. 13.13) . . . . . ***POLYMITARCYIDAE***....108

7(2') Two rows of long hair-like setae present on inner margins of femora and tibiae of forelegs (Fig. 13.14). 52

7' Long hair-like setae absent from forelegs, or not arranged as above 8

8(7') Gills on abdominal segment II operculate or semioperculate (i.e., partly covering succeeding pairs) (Fig. 13.15) 9

8' Gills on abdominal segment II neither operculate nor semioperculate, either similar to those on succeeding segments or absent 11

9(8) Gills on abdominal segment II triangular, subtriangular, or oval and not meeting medially (Fig. 13.15); gill lamellae on segments III–VI simple or bilobed, without fringed margins . . . . . ***LEPTOHYPHIDAE***...96

9' Gills on abdominal segment II quadrate, meeting or almost meeting medially (Fig. 13.16a); gill lamellae on segments III–VI with fringed margins (Fig. 13.16b) 10

10(9') Mesonotum with distinct rounded lobe on anterolateral corners (Fig. 13.17); gills on abdominal segment II operculate, fused medially; hind wing pads present . . . . . .***NEOEPHEMERIDAE***....***Neoephemera***

10' Mesonotum without anterolateral lobes (Fig. 13.18); gills on abdominal segment II operculate, but not fused medially; hind wing pads absent . . . . . .***CAENIDAE***....99

11(8') Gills absent on abdominal segment II, gills rudimentary or absent on segment I, and present or absent on segment III (Figs. 13.19, 13.44); abdominal gills when present on segments III–VII or IV–VII consist of oval anterior (i.e., dorsal) lamellae and posterior (i.e., ventral) lamellae with numerous lobes (Fig. 13.20); paired tubercles or spines often present on abdominal terga. . . . . ***EPHEMERELLIDAE***.....81

11' Gills present on abdominal segments I–V, I–VII, or II–VII; paired tubercles rarely present on abdominal terga 12

12(11') Body, including head, distinctly flattened; eyes and antennae dorsal; mandibles not visible in dorsally (Fig. 13.21) 54

12' Body not flattened (Figs. 13.22, 13.24) or if flattened, mandibles visible dorsally and form an integral part of the flattened head surface (Fig. 13.25) 13

13(12') Tarsal claws of forelegs differ in structure from those on middle and hind legs (Figs. 13.26, 13.27), tarsal claws of middle and hind legs long and slender, about as long as tibiae (Figs. 13.26, 13.27). 14

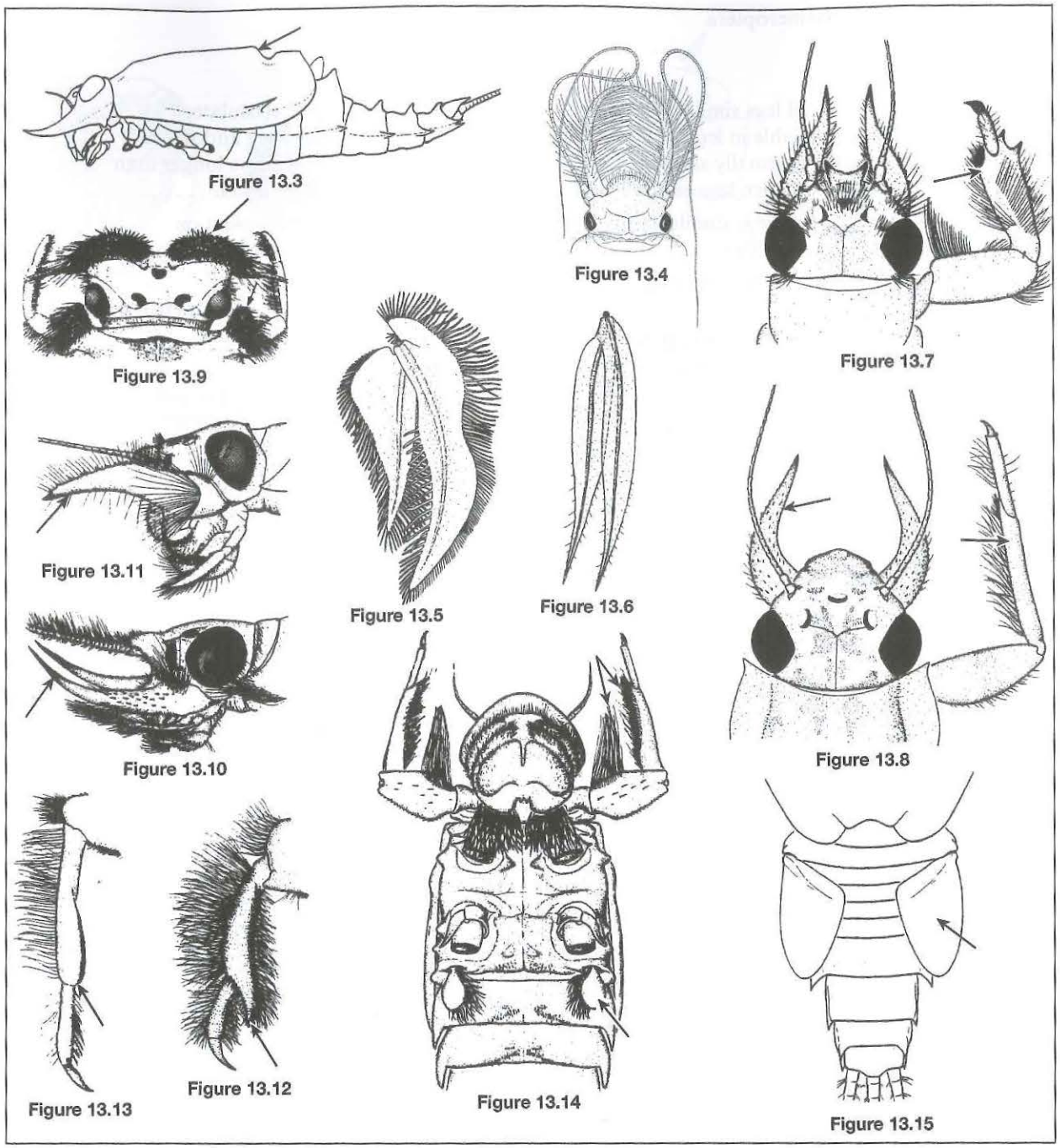


Figure 13.3 Lateral view of *Baetisca* sp. nymph (Baetiscidae), arrow indicates large mesonotum.
Figure 13.4 Dorsal view of head of *Euthyplocia* nymph (Euthyplociidae).
Figure 13.5 Abdominal gill 4 of *Ephoron* sp. nymph (Polymitarcyidae).
Figure 13.6 Abdominal gill 4 of *Paraleptophlebia* sp. nymph (Leptophlebiidae).
Figure 13.7 Dorsal view of head and foreleg of *Pentagenia vittigera* nymph (Palingeniidae).
Figure 13.8 Dorsal view of head and foreleg of *Anthopotamus* sp. nymph (Potamanthidae), arrows indicate surface of mandibular tusk and shape of foretibia.
Figure 13.9 Dorsal view of head and prothorax of *Dolania americana* nymph (Behningiidae), arrow indicates pads of spines.
Figure 13.10 Lateral view of head of *Ephemera* sp. nymph (Ephemeridae), arrow indicates curved mandibular tusks.
Figure 13.11 Lateral view of head of *Ephoron* sp. nymph (Polymitarcyidae).
Figure 13.12 Hind leg of *Hexagenia* sp. nymph (Ephemeridae).
Figure 13.13 Hind leg of *Ephoron* sp. nymph (Polymitarcyidae), arrow indicates apex of tibia.
Figure 13.14 Ventral view of anterior portion of *Lachlania* sp. nymph (Oligoneuriidae), arrows indicate tufts of long setae and abdominal gill 1.
Figure 13.15 Dorsal view of abdomen of *Tricorythodes* sp. nymph (Leptohyphidae), arrow indicates abdominal gill 2.

13' Tarsal claws of all legs similar, usually sharply pointed, but can also be spatulate; tarsal claws variable in length, if tarsal claws of middle and hind legs long and slender, then tarsal claws usually shorter than tibiae; if middle and hind tarsal claws longer than respective tibiae, then legs either bowed or labrum with deep V-shaped notch 15

14(13) Tarsal claws of forelegs simple, with long slender denticles; spinous pad present on forecoxae (Fig. 13.26a) . . . . . ***AMETROPODIDAE—Ametropus***

14' Tarsal claws of forelegs bifid (Fig. 13.27a); without spinous pad on forecoxae . . . . . ***METRETOPODIDAE***.....70

15(13') Gills on abdominal segments II–VII either forked (Fig. 13.6), in tufts (Fig. 13.28), have all margins fringed (Fig. 13.29), or have double lamellae that terminate in a single filament or multiple points (Figs. 13.30–13.32); apicolateral margin of maxillae with dense brush of long setae (Fig. 13.33) . . . . . ***LEPTOPHLEBIIDAE***.....71

15' Abdominal gills not as above; gills either more or less oval or heart-shaped; gill lamellae either single-, double-, or triple- folded (Figs. 13.35–13.38); gill lamellae with posterior surface membrane just covering individual tracheal branches in one rare genus (Fig. 13.39); abdominal gills never terminate as a sharp filament or with multiple points; apical margin of maxillae variable, but never with dense brush of long setae (Figs. 13.34, 13.43) 16

16(15') Labrum with median notch on anterior margin (notch absent only in *Apobaetis,* which lacks well-developed posterolateral projections on abdominal segments VI–IX); maxillae without pectinate spines; terminal filament variable, may be shorter than tergite X or subequal to cerci; antennae long, greater than two to three times width of the head (Fig. 13.42) or, antennae shorter than twice width of head . . . . . ***BAETIDAE***..23

16' Labrum without median notch on anterior margin; terminal filament subequal to cerci; antennae shorter than twice width of head (Fig. 13.41), or labrum with notched anterior margin and maxillae with pectinate spines (Fig. 13.43). 17

17(16') Tibiae and tarsi bowed; tarsal claws very long and slender, tarsal claws of hind legs about as long as hind tarsi (as in Fig. 13.26); rare; large rivers..***ACANTHAMETROPODIDAE*** 18

17' Tibiae and tarsi not bowed; tarsal claws usually not long and slender 19

18(17) Dorsum of abdomen with median hook-like tubercles; hook-like tubercle also present on thoracic sterna (Fig. 13.23) . . . . . ***Acanthametropus pecatonica***

18' Dorsum of abdomen without median hook-like tubercles; hook-like tubercle absent on thoracic sterna . . . . . ***Analetris eximia***

19(17') Maxillae with crown of pectinate spines (Fig. 13.43); abdominal gills roughly oval single lamellae, with a distinct sclerotized band along lateral margin and usually with a similar sclerotized band on (Fig. 13.35) or near the mesal margin (Fig. 13.36) . . . . . ***AMELETIDAE—Ameletus***

19' Maxillae without pectinate spines; abdominal gills variable; sclerotized bands or edges on abdominal gills not as above, usually much more restricted and often weakly sclerotized appearing nearly transparent . . . . . ***SIPHLONURIDAE***....20

20(19') Gills on abdominal segments I–II with double lamellae (in some species, lamellae also double on segments III–VII) (Fig. 13.37) 21

20' Gills on all abdominal segments with roughly oval single lamellae or heart-shaped (Fig. 13.40) 22

21(20) Gills on abdominal segments I–II subtriangular, broadest near apex (Fig. 13.37); tarsal claws of middle and hind legs slightly longer than those of forelegs . . . . . ***Siphlonurus***

21' Gills on abdominal segments I–II oval; tarsal claws of middle and hind legs distinctly longer than those of forelegs; rare, California . . . . . ***Edmundsius agilis***

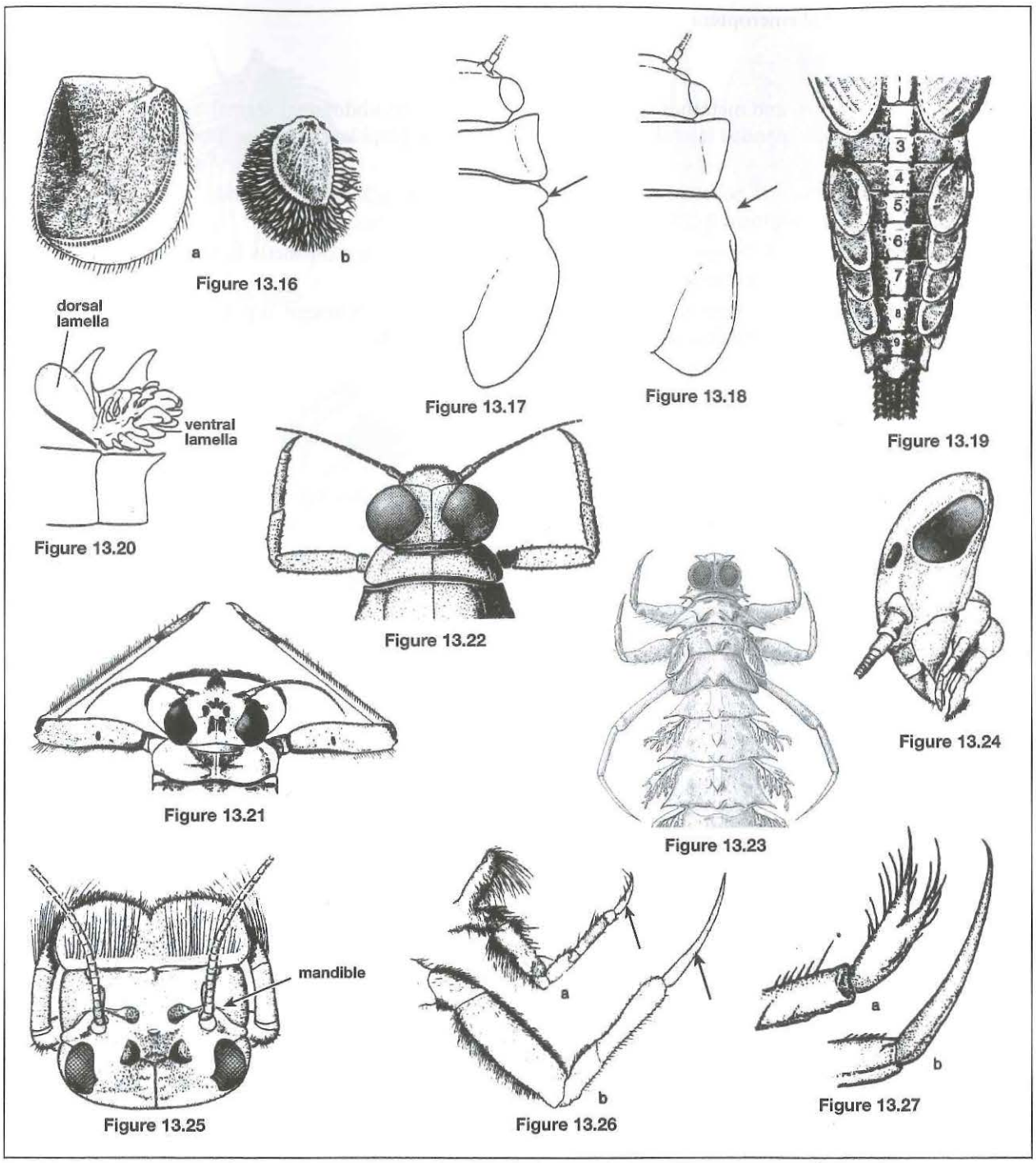


Figure 13.16 Gills 2 (a) and 4 (b) of *Caenis* sp. nymph (Caenidae).
Figure 13.17 Dorsal view of head and thorax of *Neoephemera* sp. nymph (Neoephemeridae).
Figure 13.18 Dorsal view of head and thorax of *Caenis* sp. (Caenidae).
Figure 13.19 Dorsal view of abdomen of *Ephemerella tibialis* nymph (Ephemerellidae).
Figure 13.20 Gill of segment III (dorsal lamella raised revealing ventral lamella) of *Drunella* sp. nymph (Ephemerellidae).
Figure 13.21 Dorsal view of head and prothorax of *Epeorus* sp. nymph (Heptageniidae).
Figure 13.22 Dorsal view of head and prothorax of *Parameletus* sp. nymph (Siphlonuridae).
Figure 13.23 Dorsal view of head and thorax of *Acanthametropus pecatonica* nymph (Acanthametropodidae).
Figure 13.24 Lateral view of head of *Baetis* sp. nymph (Baetidae).
Figure 13.25 Dorsal view of *Traverella* sp. nymph (Leptophlebiidae).
Figure 13.26 Foreleg (a) and hind leg (b) of *Ametropus* sp. nymph (Ametropodidae).
Figure 13.27 Tarsal claws of foreleg (a) and hind leg (b) of *Siphloplecton* sp. nymph (Metretopodidae).

22(20') Sterna of meso- and metathorax each with median tubercle; abdominal segments V–IX with greatly expanded lateral edges; segment 2 of labial palpi lacks digitate lobe; rare. . . . . ***Siphlonisca aerodromia***

22' Thoracic sterna lack tubercles; abdominal segments V–IX lack greatly expanded lateral edges; segment 2 of labial palpi with digitate lobe; uncommon . . . . . ***Parameletus***

23(16) Tarsal claws distinctly spatulate, with large apical denticles; tarsi distinctly bowed (Fig. 13.50); medium to large rivers . . . . . ***Camelobaetidius***

23' Tarsal claws sharply pointed, not spatulate; denticles present or absent, if present, smaller than above and oriented ventral (Figs. 13.52–13.54) 24

24(23') Median tubercles present on anterior of abdominal terga 25

24' Median tubercles absent from anterior of abdominal terga 26

25(24') Abdominal gills (or gills indicated by gill sockets) present on abdominal segments I–V only; gills extend ventrally from gill sockets . . . . . ***Baetodes***

25' Abdominal gills (or gills indicated by gill sockets) present on abdominal segments I–VII; gills oriented dorsally from gill sockets . . . . . ***Waynokiops dentatogriphus***

26(24') Apex of labial palpi simple and distinctly truncate (Figs. 13.55, 13.139–13.142); trachea of abdominal gills palmate (Fig. 13.56) or asymmetrical with most branches on one side (Fig. 13.57); abdominal gills simple or with dorsal flaps on one or more segments; caudal filaments with distinct dark band every third to fifth segment (Fig. 13.58 a,b) 27

26' Apex of labial palpi variable, not truncate as above or at most obliquely truncate (Figs. 13.51, 13.138); trachea of abdominal gills variable; abdominal gills simple or\large and compound (Fig. 13.59); caudal filaments rarely banded as above 31

27(26) Labrum with deep triangular median notch in distal margin (Fig. 13.106); paraglossae broad, longer than glossae; tarsal claws as long or longer than respective tarsi; abdominal gills simple . . . . . ***Pseudocentroptiloides***

27' Labrum not as above, with small median notch in anterior margin (Fig. 13.107); paraglossae subequal to glossae; tarsal claws usually shorter than respective tarsi; abdominal gills simple or with dorsal flaps 28

28(27') Mandibular incisors deeply cleft to base or united for less than half the height of incisors (Fig. 13.45): segment 3 of maxillary palpi subequal in length to segment 2 (Fig. 13.46); lateral setae present on proximal three-fourths of caudal filaments, apices of caudal filaments lack lateral setae; abdominal gills simple 29

28' Mandibular incisors united above base or fused to apex (Fig. 13.47); segment 3 of maxillary palpi, when present, shorter than segment 2 (Fig. 13.48); lateral setae of caudal filaments present to apices of filaments; abdominal gills simple, or with a dorsal flap at least on abdominal segment I. . . . . ***Procloeon***

29(28) Hind wing pads present. . . . . ***Anafroptilum*** (in part)

29' Hind wing pads absent 30

30(29') Tibiae of forelegs lack patello-tibial suture (Fig. 13.136); lateral margins of abdominal segments VIII and IX with few lateral spinules (Fig. 13.143); caudal filaments with distinct dark band near apices of filaments. . . . . ***Anafroptilum*** (in part *A. minor*)

30' Tibiae of forelegs with patella-tibial suture (Fig. 13.137); lateral margins of abdominal segments VIII and IX with many lateral spines (Fig. 13.144); caudal filaments lack dark band near apices of filaments, but may have multiple dark rings evenly spaced over the length of the filaments . . . . . ***Neocloeon***

31(26') All abdominal gills simple (Fig. 13.60). 33

31' Abdominal gills on one or more segments compound, with large basal flaps (Figs. 13.56, 13.59) 32

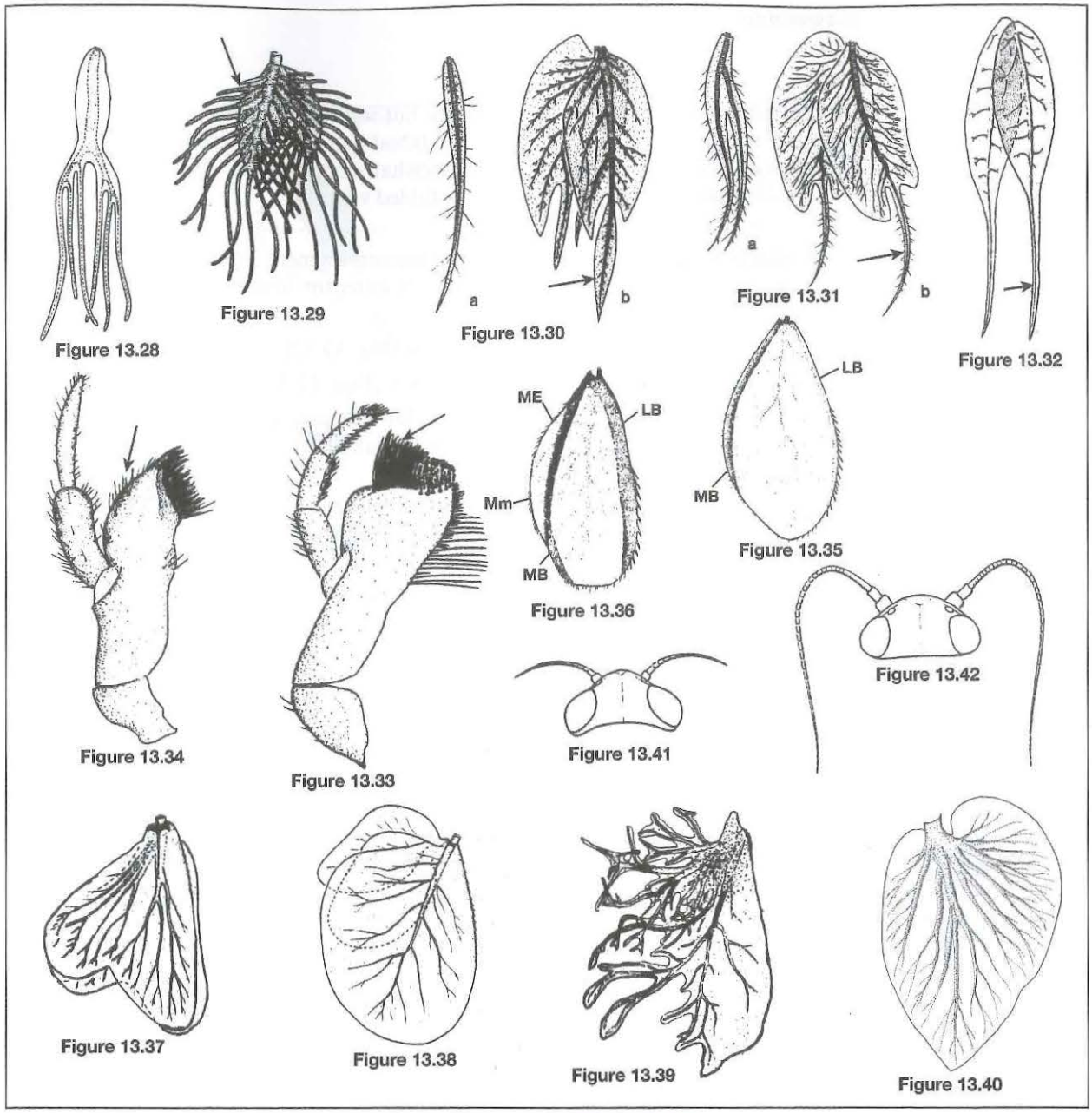


Figure 13.28 Abdominal gill 5 of *Habrophlebia* sp. nymph (Leptophlebiidae).

Figure 13.29 Abdominal gill 4 of *Traverella* sp. nymph (Leptophlebiidae), arrow indicates marginal fringe.

Figure 13.30 Abdominal gills 1 (a) and 4 (b) of *Choroterpes* sp. nymph (Leptophlebiidae), arrow indicates terminal filament.

Figure 13.31 Abdominal gills 1 (a) and 4 (b) of *Leptophlebia* sp. nymph (Leptophlebiidae), arrow indicates terminal filament.

Figure 13.32 Abdominal gill 4 of *Leptophlebia bradleyi* nymph (Leptophlebiidae), arrow indicates terminal filament.

Figure 13.33 Right maxilla of *Leptophlebia* sp. nymph (Leptophlebiidae).

Figure 13.34 Right maxilla of *Callibaetis* sp. nymph (Baetidae).

Figure 13.35 Abdominal gill 4 of *Ameletus* sp. nymph (Ameletidae); MB = mesal band; LB = lateral band (after Zloty and Pritchard 1997).

Figure 13.36 Abdominal gill 4 of *Ameletus* sp. nymph (Ameletidae); LB = lateral band; MB = mesal band; ME = mesal extension; Mm = mesal margin (after Zloty and Pritchard 1997).

Figure 13.37 Abdominal gill 4 of *Siphlonurus* sp. nymph (Siphlonuridae).

Figure 13.38 Abdominal gill 4 of *Analetris eximia* nymph (Acanthametropodidae).

Figure 13.39 Abdominal gill 4 of *Acanthametropus pecatonica* nymph (Acanthametropodidae).

Figure 13.40 Abdominal gill 3 of *Siphlonisca aerodromia* nymph (Siphlonuridae).

Figure 13.41 Dorsal view of head of *Siphlonurus* sp. nymph (Siphlonuridae).

Figure 13.42 Dorsal view of head of *Baetis* sp. nymph (Baetidae).

32(31') Hind wing pads present; labial palpi with three segments, but segment 2 inconspicuous making palpi appear two segmented; apical segment of labial palpi tapers to rounded tip and inner surface of apical segment can appear somewhat scoop-shaped (Fig. 13.51); abdominal gills with basal recurved flaps folded ventrally (Fig. 13. 59) ..... ***Callibaetis***

32' Hind wing pads absent; labial palpi with three distinct segments, segment 3 obliquely truncate (Fig. 13.138) and usually with a distinctly pointed outer tip; abdominal gills with basal recurved flaps folded dorsally (Fig. 13.56) ..... ***Cloeon dipterum***

33(31) Tarsal claws clearly less than half as long as respective tarsi (Fig. 13.52) 36

33' Tarsal claws half or more than half as long as respective tarsi (Figs. 13.53, 13.54) 34

34(33') Head with distinct genal projections extending laterally below compound eyes; labial palpi two segmented, segment 2 bulbous and covered with many long setae (Fig. 13.49) ..... ***Baetopus trishae***

34' Head without genal projections as above; labial palpi two or three segmented, but not as above; terminal segment of labial palpi either with apex truncated or somewhat triangular, but not as above 35

35(34') Tarsal claws almost as long as respective tarsi (Fig. 13.54); labrum without a notch on anterior margin ..... ***Apobaetis***

35' Tarsal claws about half as along as respective tarsi (Fig. 13.53); labrum with notch on anterior margin ..... ***Paracloeodes***

36(33) Villopore* present on all or some legs (Figs. 13.109, 13.113), if weakly developed, consisting of only two to three setae, then scape of antennae with a distal lobe; terminal filament subequal to cerci or reduced; mandibles without setae between prostheca and molars 37

36' Villopore absent on all legs; terminal filament subequal to cerci; scape of antennae lacks distal lobe; mandibles with setae on surface between prostheca and molars or if mandibles lack setae in this area the prostheca of the right mandible reduced to a single simple seta 45

37(36) Scape of antennae with distal lobe (Fig. 13.110); maxillary palpi with subapical excavation (Fig. 13.111); segment 2 of labial palpi with greatly expanded medial lobe (except in *L. longipalpus*, which has a much smaller lobe); villopore often reduced or apparently absent on forefemora ..... ***Labiobaetis***

37' Scape of antennae without distal lobe; maxillary palpi without subapical excavation; segment 2 of labial palpi variable, but not greatly expanded as above; villopore usually well-developed consisting of more than three setae 38

38(37') Segment 2 of maxillary palpi apically enlarged with a small apical projection; outer edge of femora, tibiae, and tarsi with row of clavate setae; terminal filament subequal to cerci; abdominal terga II, VII, and VIII distinctly darker than others (Fig. 13.108); hind wing pads present; rare ..... ***Barbaetis benfieldi***

38' Segment 2 of maxillary palpi not apically enlarged and without apical projection; outer edge of leg segments lack row of clavate setae; terminal filament length variable; abdominal terga variably patterned, but not as above; hind wing pads present or absent 39

39(38') Terminal filament well-developed, longer than tergite X; hind wing pads present ..... ***Baetis*** (in part)

39' Terminal filament reduced, ranging from minute stub to slightly longer than tergite X; hind wing pads absent or present 40

*– Slide mounting of leg and 400x magnification usually necessary to view this character effectively. Setae of the villopore reside in a small depression at edge of femora and are often pressed flat to the cuticle surface.

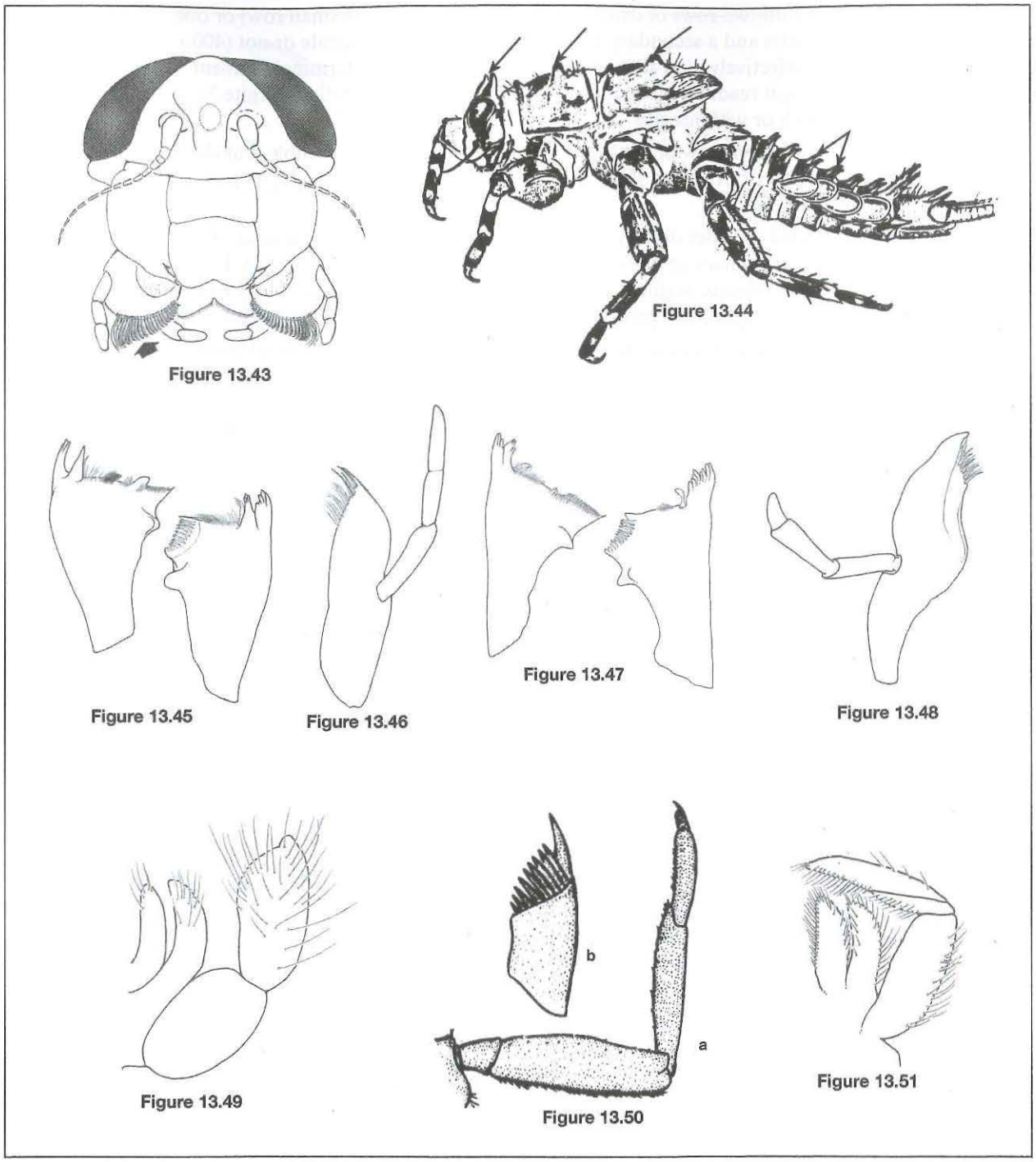


Figure 13.43 Anterior view of head of *Ameletus* sp. nymph (Ameletidae), arrow indicates pectinate setae on apex of maxilla.

Figure 13.44 Lateral view of *Drunella grandis* nymph (Ephemerellidae).

Figure 13.45 Right and left mandibles of *Anafroptilum* sp. nymph (Baetidae).

Figure 13.46 Maxilla of *Anafroptilum* sp. nymph (Baetidae).

Figure 13.47 Right and left mandibles of *Procloeon* sp. nymph (Baetidae).

Figure 13.48 Maxilla of *Procloeon* sp. nymph (Baetidae).

Figure 13.49 Ventral view of labium of *Baetopus trishae* nymph (Baetidae).

Figure 13.50 Leg (a) and claw (b) of *Camelobaetidius* sp. nymph (Baetidae).

Figure 13.51 Ventral view of labium of *Callibaetis* sp. nymph (Baetidae).

40(39') Tarsal claws with two rows of denticles (one large row and one small row) or one row of denticles and a secondary ridge that may be slightly serrate or not (400× required to effectively view these characters of tarsal claws); terminal filament minute (i.e., not readily visible dorsally) or visible stub shorter than tergite X; procoxae with or without gills 41

40' Tarsal claws with one row of denticles; terminal filament always visible, but short usually ranging from half to slightly greater than the length of tergite X; procoxae without gills 42

41(40) Tibiae expanded or wider distally (Fig. 13.128); tarsal claws with two rows of denticles, large primary row of denticles roughly subequal in length (Fig. 13.129); hind wing pads absent; segment 2 of labial palpi with narrow base (Fig. 13.127) and distinctly wider apical end; procoxae lack gills; cerci with dark median band . . . . . ***Iswaeon***

41' Tibiae more or less cylindrical, not expanded distally (Fig. 13.131); tarsal claws with two rows of denticles, large primary row of denticles with size increasing from base to apex of claw (Fig. 13.132); hind wing pads present as small to minute lobes or absent [**H. grande* lack hind wing pads]; segment 2 of labial palpi not as above, sides of segment 2 about parallel (Fig. 13.130); procoxal gills present or absent; cerci are usually unbanded [**H. grande* have banded cerci] . . . . . ***Heterocloeon***

42(40') Hind wing pads present (but sometimes reduced to a small thread-like flap) 44

42' Hind wing pads absent 43

43(42') Spinules on posterior margins of abdominal terga well-developed and single with conical or broadly rounded points (Fig. 13.133b); outer margins of femora, tibiae, and tarsi lack row of long setae; segment 3 of labial palpi with inner apical edge more or less straight, not forming a smooth curve to apex of segment (Fig. 13.118) . . . . . ***Plauditus***

43' Spinules on posterior margins of abdominal terga poorly developed and may have single or multiple sharp points that may appear somewhat saw-toothed, but not as above (Fig. 13.133a); outer margins of femora, tibiae, and tarsi with a row of long setae or femora and tibiae with few long setae and none on tarsi; segment 3 of labial palpi with inner apical edge smoothly curved to apex of segment (Fig. 13.115) . . . . . ***Acentrella*** (in part)

44(42) Segment 2 of labial palpi with well-developed medially projecting corner (Fig. 13.117); scale-like setae present abdominal terga . . . . . ***Baetis*** (in part)

44' Segment 2 of labial palpi without well-developed medially projecting corner (Fig. 13.115); scale-like setae absent from abdominal terga . . . . . ***Acentrella***

45(36') Abdominal gills on segments II–VII 46

45' Abdominal gills on segments I–VII 47

46(45) Segment 2 of labial palpi with well-developed digitate-lobe (Fig. 13.116); paraglossae rectangular and larger than glossae (Fig. 13.116); prostheca of right mandible robust and digitate apically . . . . . ***Americabaetis***

46' Segment 2 of labial palpi without well-developed digitate-lobe; paraglossae not rectangular, but more broadly rounded apically; prostheca of right mandible slender, bifid, and minutely pectinate (Fig. 13.121) . . . . . ***Diphetor hageni***

47(45') Tarsal claws without denticles; long, fine hair-like setae present on tibiae and tarsi; tufts of setae present on abdominal sterna II–VI; maxillary palpi reduced; prostheca of right mandible bifid . . . . . ***Cloeodes***

**Heterocloeon grande* is currently verified only from Tennessee and Kansas

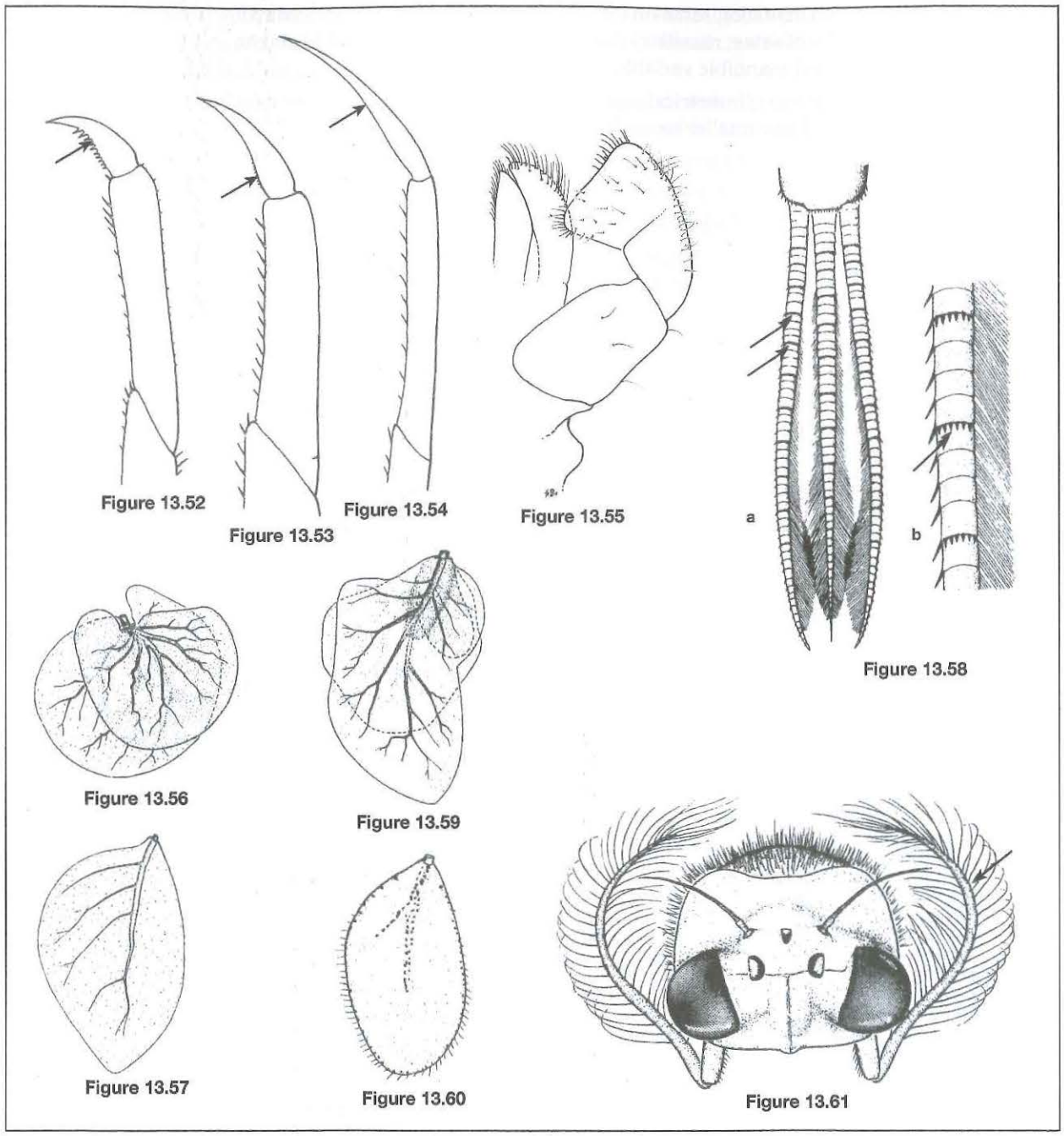


Figure 13.52 Tarsus and claw of *Baetis* sp. nymph (Baetidae).
Figure 13.53 Tarsus and claw of *Paracloeodes* sp. nymph (Baetidae).
Figure 13.54 Tarsus and claw of *Apobaetis* sp. nymph (Baetidae).
Figure 13.55 Ventral view of labium of *Anafroptilum conturbatum* (Baetidae).
Figure 13.56 Abdominal gill 1 of *Cloeon* sp. nymph (Baetidae).
Figure 13.57 Abdominal gill 4 of *Anafroptilum* sp. nymph (Baetidae).
Figure 13.58 Caudal filaments (a) and detail of cercus (b) of *Procloeon* sp. nymph (Baetidae).
Figure 13.59 Abdominal gill 2 of *Callibaetis* sp. nymph (Baetidae).
Figure 13.60 Abdominal gill 4 of *Baetis* sp. nymph (Baetidae).
Figure 13.61 Dorsal view of head of *Arthroplea bipunctata* nymph (Arthropleidae).

47' Tarsal claws with denticles; setae on legs short, usually blade-like; abdominal sterna lack tufts of setae; maxillary palpi variable, but not reduced as above; prostheca of right mandible variable 48

48(47') Tarsal claws with two symmetrical rows of denticles (Fig. 13.123) or one large primary row and one smaller secondary row 49

48' Tarsal claws with only one row of large primary denticles 50

49(48) Tarsal claws with two symmetrical rows of denticles, claws lack paired subapical setae; dorsal and ventral edges of forefemora with many long setae. . . . . ***Varipes***

49' Tarsal claws with one large primary row and one smaller secondary row of denticles, claws with paired subapical setae (Fig. 13.122); forefemora with only a dorsal row of short spine-like setae present; subarctic lakes, Nunavut . . . . . ***Kirmaushenkreena zarankoae***

50(48') Tarsal claws with one to three unpaired subapical setae (Fig. 13.124): labrum distinctly narrowed posteriorly with a variety of plumose setae along anterior margin (Fig. 13.125) . . . . . ***Moribaetis***

50' Tarsal claws without unpaired subapical setae; labrum not as above 51

51(50') Segment 2 of labial palpi with well-developed anteriorly projecting digitate-lobe (Fig. 13.114); abdominal gill 7 slender and apically pointed; antennal scape and pedicle with only a few scattered, hair-like setae . . . . . ***Acerpenna***

51' Segment 2 of labial palpi without well-developed anteriorly projecting digitate-lobe (if a lobe is present it is at most weakly developed and not thumb-like); abdominal gill 7 not noticeably slender or apically pointed; antennal scape and pedicle with robust and hair-like setae . . . . . ***Fallceon***

52(7) Gills on abdominal segment I dorsolateral, similar in position and structure to gills on segments II–VII; gill fibrils shorter than gill lamellae..***ISONYCHIIDAE***. . . . . ***Isonychia***

52' Gills on abdominal segment I ventral, gills on segments II–VII dorsal (Fig. 13.14); gill fibrils longer than gill lamellae or gill lamellae absent. . . . . ***OLIGONEURIIDAE***...53

53(52') Gill lamellae on segments II–VII oval, similar to lamellae of abdominal gill 1 (Fig. 13.14); tarsal claws present on forelegs . . . . . ***Lachlania***

53' Gill lamellae on segments II–VII slender and elongate, different from the ventrally oriented and multi-branched gill 1 that lacks lamellae; tarsal claws absent on forelegs . . . . . ***Homoeoneuria***

54(12) Tarsal claws as long as or longer than tarsi; tibiae and tarsi bowed; rare, large sandy rivers . . . . . ***PSEUDIRONIDAE***....***Pseudiron centralis***

54' Tarsal claws much shorter than tarsi; tibiae and tarsi straight 55

55(54') Segment 2 of maxillary palpi longer than width of head and usually held conspicuously at or behind the side of the head (Fig. 13.61); uncommon, edges of stream pools, pond margins, swamps, and bog swales. . . . . ***ARTHROPLEIDAE***...***Arthroplea bipunctata***

55' Segment 2 of maxillary palpi not greatly elongated, inconspicuous at side of head . . . . . ***HEPTAGENIIDAE***.....56

56(55') All abdominal gills ventral; gill lamellae slender and lanceolate-type with numerous thin filaments radiating from an area adjacent to lamellae base; 3 well-developed caudal filaments; rare; large rivers . . . . . ***Raptoheptagenia cruentata***

56' Abdominal gills lateral in position, at least on segments IV–VI; gill lamellae usually broad; gill filaments at base of lamellae variable, but not as above; two or three caudal filaments 57

57(56') With only two well-developed caudal filaments; terminal filament vestigial or absent; dense row of setae along anterior margin of head capsule 58

57' With three well-developed caudal filaments; anterior margin of head capsule without dense row of setae 61

58(57) Abdominal gills 1 and 2 inserted ventrally; gill 3 inserted ventrally or ventrolaterally; mouthparts adapted for predation; maxillary palpi thin; tarsal claws with a single basal tooth and lack denticles (Fig. 13.70) 59

58' Gills inserted laterally on segments II–VI; gill 1 may extend ventrally on segments I and VII (Fig. 13.62); maxillary palpi robust; tarsal claws without a basal tooth, but with three or more subapical denticles 60

59(58) Head and thorax without paired dorsal tubercles; posterior margins of abdominal terga with very small single dorsal median tubercles; femora broad and flat, 2.0–2.5 times width of respective tibiae; rare; large rivers of Northwest . . . . . ***Anepeorus rusticus***

59' Head and thorax with paired dorsal tubercles; posterior margins of abdominal terga with large, single dorsal tubercles medially; femora relatively narrow, 1.0–1.5 times width of respective tibiae; rare; large rivers . . . . . ***Spinadis simplex***

60(58') Well-developed paired tubercles present on hind margins of abdominal terga I–IX; maxillary incisors not enlarged . . . . . ***Ironodes***

60' Abdominal terga without paired tubercles; maxillary incisors distinctly enlarged . . . . . ***Epeorus***

61(57') Gills on abdominal segments I and VII enlarged and meet, or almost meet, beneath the abdomen forming ventral disk with other gills (Fig. 13.62); abdominal sternite I with anterolateral flanges that accept the base of gill 1 on each side of sternite I . . . . . ***Rhithrogena***

61' Gills on abdominal segments I and VII do not meet beneath the abdomen and usually are smaller than intermediate pairs of gills; abdominal sternite I lacks anterolateral flanges 62

62(61') Edges of maxillary palpi protrude at sides of head (Fig. 13.63); anterior edge of head capsule with distinct median notch; fibrilliform portion of abdominal gills 2–6 absent or composed of only a few fibrils (Fig. 13.64) . . . . . ***Cinygmula***

62' Edges of maxillary palpi do not protrude at sides of head or rarely so; anterior edge of head capsule lacks median notch or has only a slight indentation; fibrilliform portion of gills 2–6 with many fibrils 63

63(62') Gills on abdominal segment VII minute, not longer than posterolateral projections of segment VII (Fig. 13.65); rare . . . . . ***Macdunnoa***

63' Gills on abdominal segment VII much larger than above 64

64(63') Gills on abdominal segment VII reduced to slender filaments, different from gills on segments I–VI; central trachea of gill 7 absent or with few or no lateral branches (Figs. 13.66b, 13.67b, 13.68b) 65

64' Gills on abdominal segment VII similar to gills on segments I–VI, but smaller; trachea of gill 7 with lateral branches 67

65(64) Gills on abdominal segments I–VI with apices pointed (Fig. 13.66a); pronotum with paired median black marks that are often medial to pair of pale spots; head capsule lacks freckling of pale spots . . . . . ***Stenacron***

65' Gills on abdominal segments I–VI with apices rounded (Fig. 13.67a) or truncated (Fig. 13.68a); pronotum lacks paired black marks as above, head capsule freckled with pale spots over most of vertex and frons 66

66(65') Gills on abdominal segments I–VI with apices rounded or at least gills of middle segments with apices rounded (Fig. 13.67a) . . . . . ***Stenonema femoratum***

66' Gills on abdominal segments I–VI with apex truncated (Fig. 13.68a) . . . . . ***Stenonema*** (all other species)*

67(64') Gill lamellae of abdominal segment I less than half as long as those on segment II; fibrilliform portion of gill 1 much longer than its lamella (Fig. 13.69); labrum small, narrower at apex than at base (i.e., triangular in shape); Northwest . . . . . ***Cinygma***

*Recent molecular studies have reduced *Maccaffertium* to a subgenus of *Stenonema* and reassigned all its species to *Stenonema*. See citation in footnote on Page 269.

67' Gill lamellae of abdominal segment I two-thirds as long as those on segment II; fibrilliform portion of gill 1 usually subequal to or shorter than its lamella; labrum never narrower at apex than at base (i.e., not triangular) 68

68(67') Gills on abdominal segment VII with fibrilliform portion present and with numerous fibrils; lamellae of gill 1 similar in shape and position compared to lamellae of gills 2–7; tarsal claws usually lack denticles , but have one basal tooth (Fig. 13.70); glossae of labium pointed and closely spaced . . . . . ***Heptagenia****

68' Gills on abdominal segment VII without fibrilliform portion; lamella of gill 1 different in shape compared to lamellae of gills 2–7, lamellae of gill 1 often appearing banana-shaped and curved dorsally; tarsal claws with large distinct denticles (Fig. 13.71); glossae of labium quadrate and widely spaced. 69

69(68') Caudal filaments with well-developed fine interfacing setae (Fig. 13.78) or just cerci with fine setae along inner margins and terminal filament with only sparse scattered setae; head capsule usually less than or equal to width of the pronotum; head capsule occasionally with few scattered black spots near anterior margin . . . . . ***Afghanurus***

69' Caudal filaments without well-developed interfacing setae; head often wider than prontoum; head capsule often with several dark spots along anterior margin . . . . . ***Leucrocuta***

70(14') Margins of foreclaws densely covered with spines (>30 spines) that are only slightly shorter than the short terminal spines (Fig. 13.73); outer margin of abdominal gills 3–7 with two to seven large stout spines in addition to small setae; boreal distribution . . . . . ***Metretopus***

70' Margins of foreclaws sparsely covered with spines (<20 spines) that are thinner and slightly shorter than the long terminal spines (Fig. 13.27); outer margins of abdominal gills 3–7 with only small stout setae, no large stout spines as above . . . . . ***Siphloplecton***

71(15) Labrum as wide or wider than head capsule (Fig. 13.25). 72

71' Labrum much narrower than head capsule (Fig. 13.76) 73

72(71) Abdominal gill lamellae oval with fringed margins (Fig. 13.29); galea-lacinia of maxillae without large distinctive apical spine. . . . . ***Traverella***

72' Abdominal gill lamellae elliptical without fringed margins, but with short apical filament; galea-lacinia of maxillae with large distinctive apical spine (Fig. 13.77) . . . . . ***Hydrosmilodon***

73(71') Abdominal gills 2–7 consist of a cluster of slender filaments (Fig. 13.28) . . . . . ***Habrophlebia***

73' Abdominal gills 2–7 forked or bilamellate, but not as above (Figs. 13.30–13.32). 74

74(73') Abdominal gill 1 either with symmetrical slender single lamellae (Fig. 13.30a) or asymmetrically forked lamellae (Fig. 13.79a,b); abdominal gills 2–7 broadly bilamellate with tri-lobed apices. 75

74' Abdominal gill 1 with either symmetrically forked single lamellae (Fig. 13.31a) or bilamellate and either similar to or different from gills on succeeding segments (Figs. 13.31b, 13.32) 76

75(74) Abdominal gills 2–7 with dorsal lamellae larger than ventral lamellae and terminate in three apical lobes, median lobe longer and often wider than lateral lobes (Fig. 13.30b); dorsal setae of labrum arranged in two transverse rows; lateral margins of mandibles with setae restricted to middle of margins . . . . . ***Choroterpes***

* – Two species, *Heptagenia culacantha* and *H. solitaria,* have one or two minute apical denticles on the foreclaws. The taxonomic relevance of these features has not yet been determined, but all other generic characters place these taxa in *Heptagenia*

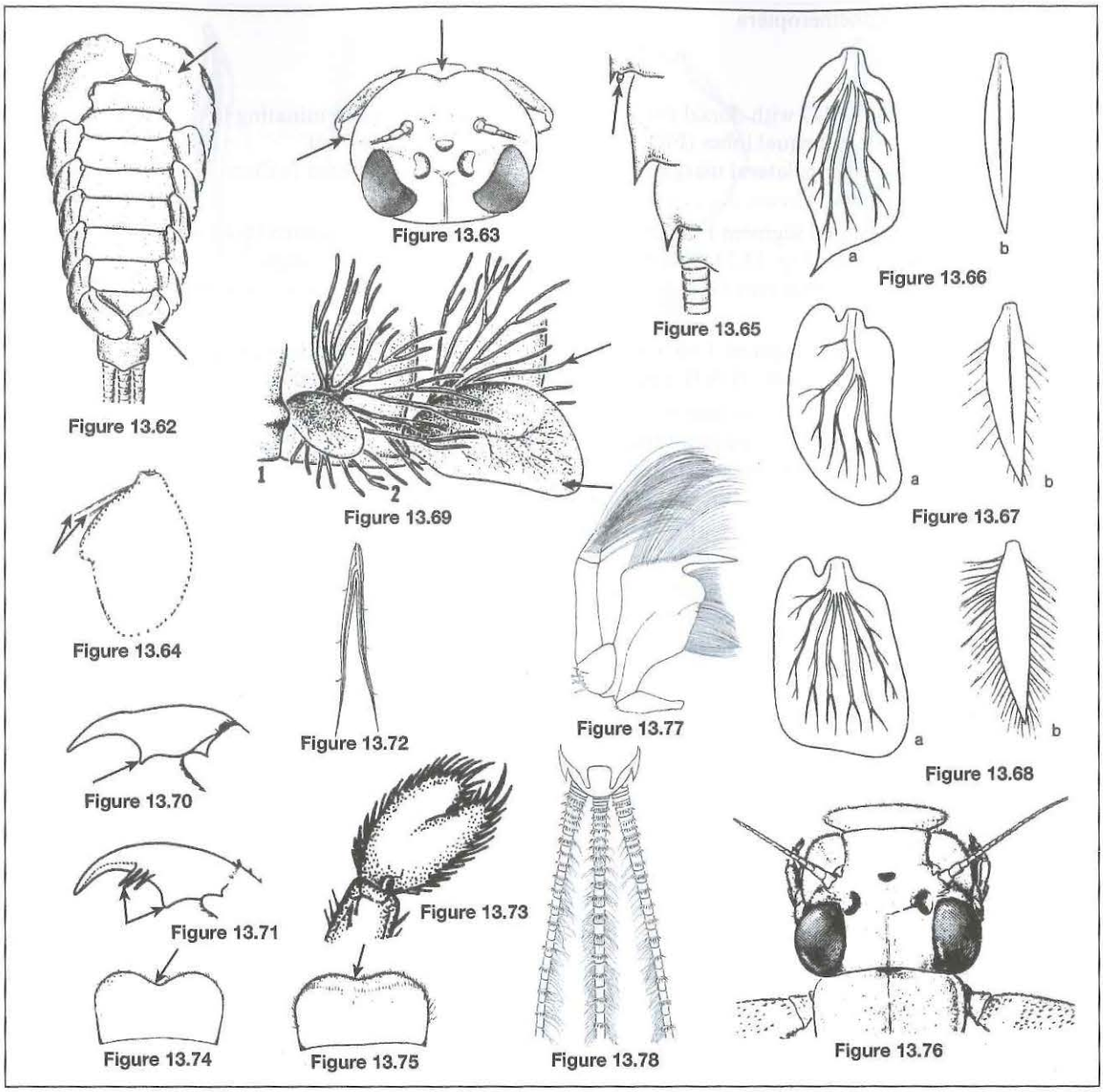


Figure 13.62 Ventral view of abdomen of *Rhithrogena* sp. nymph (Heptageniidae), arrows indicate edges of abdominal gills 1 and 7.

Figure 13.63 Dorsal view of head of *Cinygmula* sp. nymph (Heptageniidae), arrows indicate medial notch on head capsule and exposed edge of maxillary palp.

Figure 13.64 Abdominal gill 4 of *Cinygmula* sp. nymph (Heptageniidae), arrow indicates basal filaments.

Figure 13.65 Abdominal segments 7-10 of *Macdunnoa* sp. nymph (Heptageniidae), arrow indicates abdominal gill 7.

Figure 13.66 Abdominal gills 4 (a) and 7 (b) of *Stenacron* sp. nymph (Heptageniidae).

Figure 13.67 Abdominal gills 4 (a) and 7 (b) of *Stenonema* femoratum sp. nymph (Heptageniidae).

Figure 13.68 Abdominal gills 4 (a) and 7 (b) of *Stenonema* spp. nymph (Heptageniidae).

Figure 13.69 Abdominal gills 1 and 2 of *Cinygma* sp. nymph (Heptageniidae), arrows indicates basal filaments and gill lamella.

Figure 13.70 Tarsal claw of *Heptagenia* sp. nymph (Heptageniidae), arrow indicates basal tooth.

Figure 13.71 Tarsal claw of *Afghanurus* sp. nymph (Heptageniidae), arrows indicate denticles and basal tooth.

Figure 13.72 Abdominal gill 2 of *Paraleptophlebia guttata* (Leptophlebiidae).

Figure 13.73 Tarsal claw of foreleg of *Metretopus alter* nymph (Metretopodidae).

Figure 13.74 Labrum of *Habrophlebiodes americana* nymph (Leptophlebiidae), arrow indicates V-shaped median notch.

Figure 13.75 Labrum of *Paraleptophlebia debilis* nymph (Leptophlebiidae), arrow indicates shallow median indentation.

Figure 13.76 Dorsal view of head of *Thraulodes* sp. nymph (Leptophlebiidae).

Figure 13.77 Maxilla of *Hydrosmilodon* sp. nymph (Leptophlebiidae).

Figure 13.78 Caudal filaments of *Afghanurus* sp. nymph (Heptageniidae).

75' Abdominal gills 2–7 with dorsal and ventral lamellae similar and terminating in three slender, subequal lobes (Fig. 13.81); dorsal setae of labrum not arranged as above; lateral margins of mandibles with setae restricted to distal half of margins ..... ***Neochoroterpes***

76(74') Gills on abdominal segment I much narrower and shaped differently than those on segments II–VII (Fig. 13.31a); abdominal gills 2–7 terminate with a single slender filament that may (Fig. 13.31b) or may not be flanked by one or two blunt lobes (Fig. 13.32) ..... ***Leptophlebia***

76' Gills on abdominal segment I not conspicuously narrower or shaped differently than those on segments II–VII; abdominal gills 2–7 forked or bilamellate 77

77(76') Anterior margin of labrum with moderately deep V-shaped median notch (Fig. 13.74), base of notch lacks denticles; row of distinctive spinules present on posterior margins of abdominal terga VI or VII–X (Fig. 13.82); abdominal gills 2–7 with conspicuous lateral tracheal branches (Fig. 13.80) ..... ***Habrophlebiodes***

77' Anterior margin of labrum with either a shallow median indentation that is not distinctly V-shaped and lacks denticles or with a deeper notch that has 3–5 denticles or lacks an indentation, appearing nearly straight; posterior margins of abdominal terga I–X with or without row of minute spinules; abdominal gills 2–7 with or without conspicuous lateral tracheal branches 78

78(77') Labrum less than half the width of the head anterior to compound eyes and about as wide as anterior edge of the clypeus 79

78' Labrum more than half the width of the head anterior to compound eyes (Fig. 13.119) and wider than anterior edge of the clypeus 80

79(78) Abdominal gills forked almost to base and lack conspicuous lateral tracheal branches (Fig 13.72); segment 3 of labial palpi widest near base ..... ***Paraleptophlebia***

79' Abdominal gills with shallow fork (Fig. 13.80) and with many conspicuous lateral tracheal branches; segment 3 of labial palpi widest near middle ..... ***Neoleptophlebia***

80(78') Lateral margins of labrum rounded (Fig. 13.120) ..... ***Farrodes***

80' Lateral margins of labrum angular (Fig. 13.97) ..... ***Thraulodes***

81(11) Abdominal gills present on segments III–VII (Figs. 13.19, 13.44) 82

81' Abdominal gills present on segments IV–VII (Fig. 13.84) 93

82(81) Terminal filament at least 1.3 times as long as cerci ..... ***Caudatella***

82' Terminal filament subequal in length to cerci 83

83(82') Anterior margins of forefemora usually with conspicuous tubercles (Fig. 13.83); if tubercles absent (as in some western species), then head, thorax, and abdomen with long paired dorsal tubercles (Fig. 13.44) or abdominal sterna with attachment disk of long hair-like setae ..... ***Drunella***

83' Anterior margins or forefemora without conspicuous tubercles; dorsum of head, thorax and abdomen without large tubercles; abdominal sterna without disk of long hair-like setae 84

84(83') Tarsal claws with subapical denticle distinctly larger than preceding denticles, subapical denticle sometimes most distinctive on hind claw (Fig. 13.95); maxillary palpi absent ..... ***Teloganopsis deficiens***

84' Tarsal claws not as above with denticles gradually becoming larger from base to tip or all denticles roughly subequal in length; maxillary palpi present (but sometimes minute) 85

85(84') Body elongate and narrow with long and thin legs; abdominal terga each with a single rounded median protuberance ..... ***Penelomax septentrionalis***

85' Body and legs not as above; abdominal terga either with variable paired sharp or blunt median tubercles or paired median tubercles absent 86

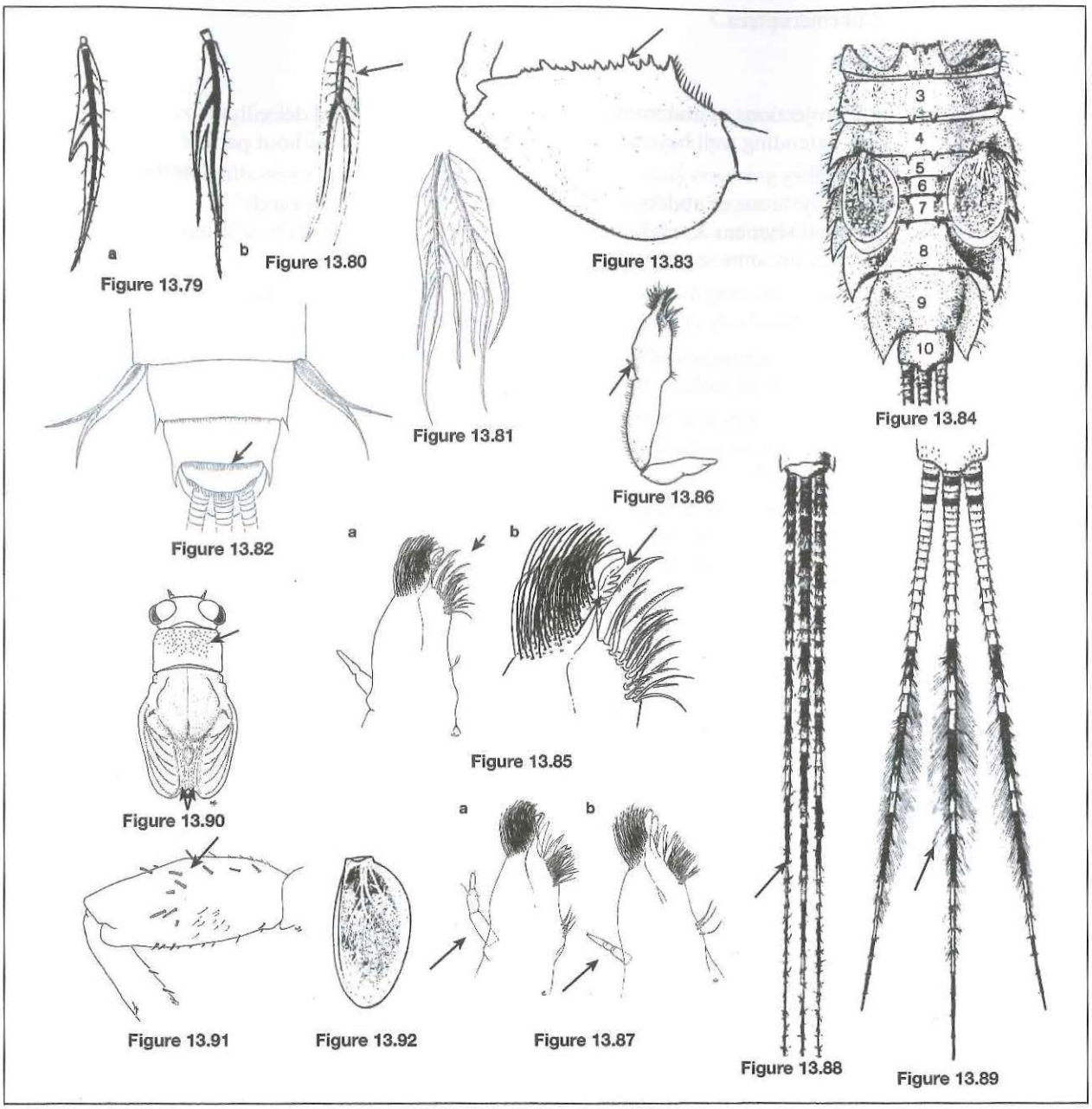


Figure 13.79 Abdominal gill 1 (a and b common variants) of *Neochoroterpes* sp. nymph (Leptophlebiidae).
Figure 13.80 Abdominal gill 4 of *Habrophlebiodes americana* nymph (Leptophlebiidae), arrow indicates lateral tracheal branches.
Figure 13.81 Abdominal gill 3 of *Neochoroterpes* sp. nymph (Leptophlebiidae).
Figure 13.82 Dorsal view of abdominal segments VII–X of *Habrophlebiodes americana* nymph (Leptophlebiidae), arrow indicates spinules on posterior margin of tergite IX.
Figure 13.83 Forefemur of *Drunella* sp. nymph (Ephemerellidae), arrow indicates large tubercles along anterior edge.
Figure 13.84 Abdominal terga of *Eurylophella* sp. (Ephemerellidae).
Figure 13.85 Maxilla of *Ephemerella tibialis* nymph (Ephemerellidae), arrow indicates serrations on maxillary canine (a) and enlarged view of apex (b)
Figure 13.86 Maxilla of *Matriella teresa* nymph (Ephemerellidae), arrow indicates minute maxillary palp.
Figure 13.87 Maxilla of *Ephemerella needhami* nymph (Ephemerellidae) (a) and maxilla of *Serratella serratoides* (Ephemerellidae) (b), arrows indicate large maxillary palp with distinct segments.
Figure 13.88 Caudal filaments of *Ephemerella tibialis* nymph (Ephemerellidae), arrow indicates whorls of spines at edges of segments.
Figure 13.89 Caudal filaments of *Ephemerella* sp. nymph (Ephemerellidae), arrow indicates numerous intersegmental hair-like setae.
Figure 13.90 Dorsal surface of head and thorax of *Ephemerella tibialis* (Ephemerellidae), arrows indicate excrescences on cuticle.
Figure 13.91 Forefemur of *Ephemerella needhami* (Ephemerellidae), arrow indicates position blunt setae on surface of segment.
Figure 13.92 Abdominal gill 2 of *Allenhyphes* sp. nymph (Leptohyphidae).

86(85') Posterolateral projections of abdominal segment IX large and curved dorsally (Fig. 13.126), extending well beyond segment X; abdominal terga without paired median tubercles . . . . . ***Caurinella idahoensis***

86' Posterolateral projections of abdominal segment IX not as above, tips rarely extending beyond segment X; abdominal terga usually with paired sharp or blunt median tubercles on some segments 87

87(86') Maxillary palpi minute composed of a single, extremely short subannulated segment with an apical seta (Fig. 13.86) or palpi absent 88

87' Maxillary palpi small composed of at least 2 complete segments (Figs. 13.85, 13.87) or one elongate segment with an apical seta 89

88(87) Middle of caudal filaments with spine-like setae at junctions of alternating segments; pro-and mesonotum lack minute cuticular excrescences*, but some small scattered bumps may be present. . . . . .***Matriella teresa***

88' Middle of caudal filaments not as above; pro- and mesonotum have numerous minute cuticular excrescences*, often most visible between developing forewing pads (Fig. 13.90); boreal and subarctic distribution . . . . . .***Ephemerella*** (in part *E. nuda* Nearctic populations only)

89(87') Abdominal terga with large, long, paired, sharp median spines (Fig. 13.96); forefemora without distal row of long setae . . . . . ***Tsalia berneri***

89' Abdominal terga with small (or short) paired sharp or blunt submedian tubercles or without paired submedian tubercles; forefemora with distal row of large setae (Fig. 13.91) 90

90(89') Large maxillary canine of galea-lacinia with several deep serrations (Fig. 13.85a,b); medial surfaces of pro- and mesonotum with several dark brown cuticular excrescences (Fig. 13.90), on pale specimens cuticular excrescences may also be pale . . . . . ***Ephemerella*** (in part *E. tibialis*)

90' Large maxillary canine of galea-lacinia lack serrations (Figs. 13.87a,b); medial surfaces of pro- and mesonotum with few dark brown excrescences 91

91(90') Median dorsal lobe of ventral lamella of abdominal gill 6 not deeply divided, with only a shallow medial division or slight apical indentation (Fig. 13.100); maxillary palpi usually long, extending two-thirds or more the length of galea-lacinia; caudal filaments with or without whorls of spine-like setae at edges of segments (Fig.13.88), apical half of caudal filaments usually with numerous intersegmental setae (Fig. 13.89) . . . . . ***Ephemerella*** (in part)

91' Median dorsal lobe of ventral lamella of abdominal gill 6 deeply divided (Fig. 13.99); maxillary palpi short, usually no more than half the length of the galea-lacinia; caudal filaments with whorls of spines and intersegmental setae variable 92

92(91') Posterior margins of abdominal terga with small sharp, paired submedian tubercles; posterior margins of abdominal terga not sinuate; caudal filaments with whorls of spine-like setae at edges of segments; apical half of caudal filaments usually with numerous intersegmental setae . . . . . ***Ephemerella*** (in part *E. alleni, E. verruca*)

92' Posterior margins of abdominal terga either lack small, sharp, paired submedian tubercles or have broad blunt paired submedian tubercles that appear as part of a distinctly sinuate posterior margin; caudal filaments with whorls of spine-like setae at edges of segments and lack intersegmental setae or with only sparse intersegmental setae . . . . . ***Serratella***

93(81') Abdominal gills on tergite IV operculate, largely covering those on segments V–VII with only about one-third of any succeeding gill visible (Fig. 13.84);

* – excrescences are minute irregular knob-like features of the cuticle and often difficult to observe on dark specimens—low angle illumination adds contrast and facilitates viewing this character

apical edges of gills 5 and 6 reach to or beyond the posterior margin of tergite VII 94

93' Abdominal gills on tergite IV semi-operculate, only partially covering gills on segments V–VI (gills on segment VII only covered by gills on segment VI); apical half of abdominal gills 5 and 6 visible, but only the apex of gill 6 reaches beyond the posterior margin of abdominal tergite VII . . . . . ***Attenella***

94(93) Tarsal claws without denticles; maxillae with palpi 95

94' Tarsal claws with denticles; maxillae without palpi . . . . . ***Eurylophella***

95(94) Filamentous gills of abdominal segment I originate at lateral margins of tergite; posterolateral projections of abdominal segments II–IX present, but not excessively long; abdominal terga without paired median tubercles . . . . . ***Dannella***

95' Filamentous gills of abdominal segment I originate on posterior edge of tergite before the lateral margin; posterolateral projections of abdominal segments II–IX present and extremely well-developed; abdominal terga usually with paired median tubercles on or near posterior margins, rarely paired tubercles absent . . . . . ***Timpanoga***

96(9) Posterior margins of abdominal terga I–VI without spinules; hind wing pads absent . . . . . ***Tricorythodes***

96' Posterior margins of abdominal terga I–VI with spinules (Figs. 13.93–13.94); hind wing pads present in males, sometimes absent in females 97

97(96') Elevated longitudinal ridge present on middle and hind tibiae (Fig 13.102); ventral lamellae of gill 2 distally constricted with outer and inner lobes subequal in length; outer lobe of ventral lamellae with a basal beak-like process . . . . . ***Leptohyphes***

97' Elevated longitudinal ridge absent on all tibiae, plumose setae may be present in this position (Fig. 13.103); ventral lamellae of gill 2 not distally constricted and outer lobe longer than inner lobe; outer lobe of ventral lamellae lacks beak-like process 98

98(97') Dorsal longitudinal row of plumose setae present on middle and hind tibiae (Fig. 13.103); forefemora with dorsal row of spatulate setae (Fig. 13.104) . . . . . ***Allenhyphes***

98' Dorsal longitudinal row of plumose setae absent on middle and hind tibiae; forefemora with dorsal row of spatulate setae (Fig. 13.105) . . . . . ***Vacupernius***

99(10') Head with three prominent ocellar tubercles; maxillary and labial palpi two-segmented; forelegs distinctly shorter than middle and hind legs 100

99' Head without ocellar tubercles; maxillary and labial palpi three-segmented; forelegs subequal in length to middle and hind legs. 104

100(99) Abdominal gill 2 operculate with posterior margin not parallel to anterior margin (Fig. 13.145), posterior margin usually a straight edge that is angled outward from midline of body . . . . . ***Brachycercus***

100' Abdominal gill 2 operculate with posterior margin roughly parallel, to anterior margin, posterior margin may be a straight or broadly rounded edge, but not angled as described above (Figs. 13.146–13.147) 101

101(100') Meso- and metathoracic sterna with medial tubercles (Fig. 13.148); median ocellar tubercle curved forward (i.e., anteriorly and/or ventrally) (Fig. 13.149) . . . . . ***Susperatus***

101' Meso- and metathoracic sterna without medial tubercles (Fig. 13.150): median ocellar tubercle straight or curved upward (i.e., dorsally) (Fig. 13.151) 102

102(101') Posterolateral projections of abdominal segment VI not curved toward midline of body (Fig. 13.152); segments of hind legs with few scattered long hair-like setae (Fig. 13.153); lateral ocellar tubercles usually with distinctly pointed apices . . . . . ***Sparbarus***

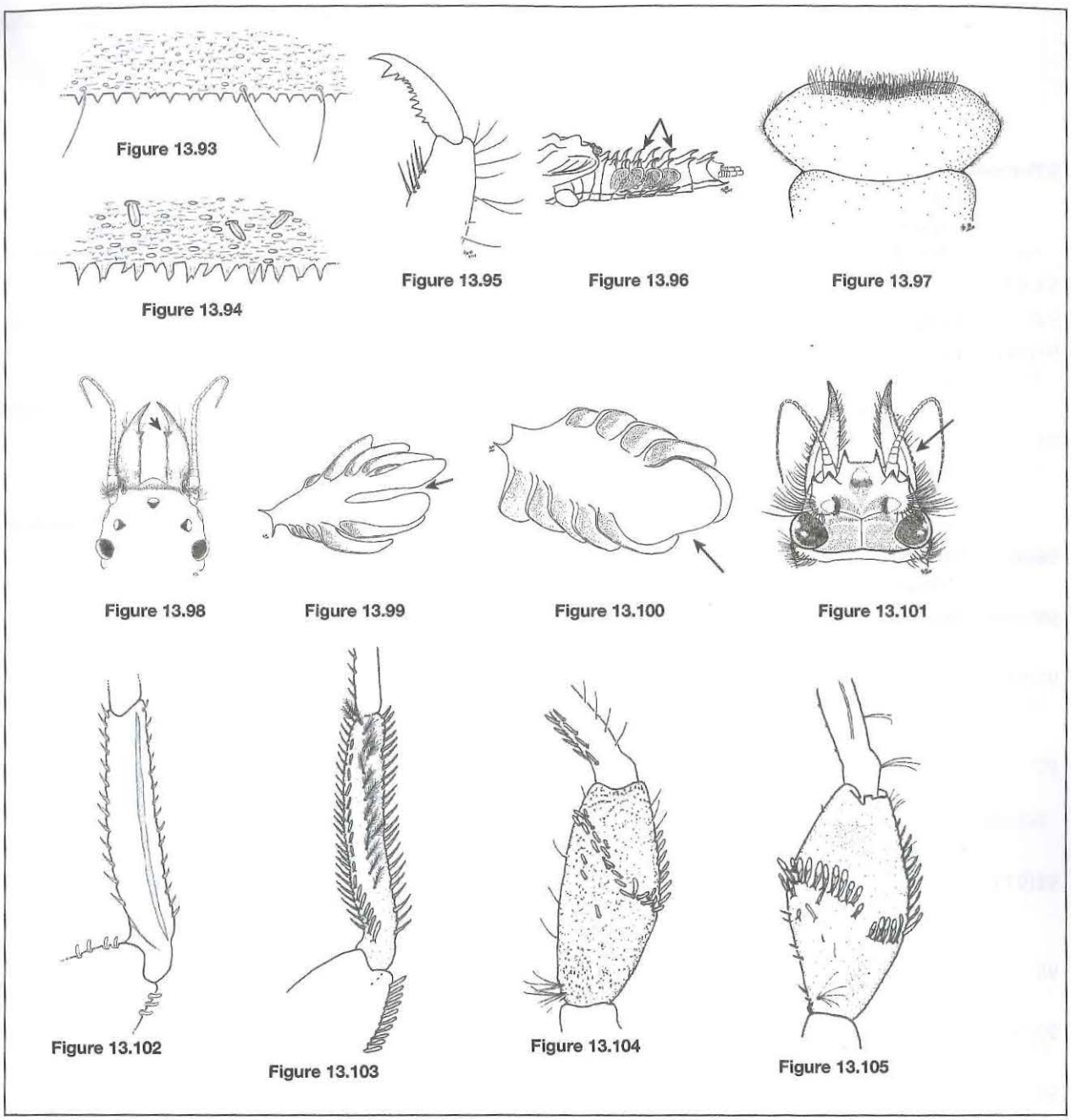


Figure 13.93 Posterior margin of abdominal tergite V of *Vacupernius packeri* nymph (Leptohyphidae).
Figure 13.94 Posterior margin of abdominal tergite V of *Leptohyphes* sp. nymph (Leptohyphidae).
Figure 13.95 Foreclaw and denticles of *Teloganopsis deficiens* (Ephemerellidae).
Figure 13.96 Lateral view of abdomen of *Tsalia berneri* (Ephemerellidae), with arrows indicating long, sharp, paired abdominal projections.
Figure 13.97 Dorsal view of labrum of *Thraulodes brunneus* (Leptophlebiidae).
Figure 13.98 Dorsal view of head and mandibular tusks of *Tortopsis* primus (Polymitarcyidae), arrow indicates single tubercle on inner margin.
Figure 13.99 Ventral lamella of abdominal gill 6 of *Serratella serratoides* (Ephemerellidae), arrow indicated deeply forked apical lobe.
Figure 13.100 Ventral lamella of abdominal gill 6 of *Ephemerella needhami* (Ephemerellidae), arrow indicated blunt apical lobe.
Figure 13.101 Dorsal view of head of *Pentagenia vittigera* (Palingeniidae), arrow indicates toothed keel on mandibular tusk.
Figure 13.102 Dorsal view of mid-tibia of *Leptohyphes* sp. nymph (Leptohyphidae).
Figure 13.103 Dorsal view of mid-tibia of *Allenhyphes* sp. nymph (Leptohyphidae).
Figure 13.104 Dorsal view of forefemur of *Allenhyphes* sp. nymph (Leptohyphidae).
Figure 13.105 Dorsal view of forefemur of *Vacupernius packeri* nymph (Leptohyphidae).

102' Posterolateral projections of abdominal segment VI distinctly curved toward midline of body (Fig. 13.154); segments of hind legs with many closely spaced long hair-like setae along outer and inner margins (Fig. 13.155); lateral ocellar tubercles usually short and broadly rounded (Fig. 13.156) 103

103(102') Lateral margins of labrum nearly straight such that labrum appears trapezoidal in shape; ventral surface of segment 1 of labial palpi without patch of long hair-like setae ..... *Latineosus*

103' Lateral margins of labrum distinctly rounded (i.e., convex) such that labrum appears oval in shape; ventral surface of segment 1 of labial palpi with patch of long hair-like setae ..... *Cercobrachys*

104(99') Inner margins of foretibiae and tarsi with row of stout spines; segment 3 of labial palpi subequal to or shorter than segment 2, with few long setae and spines; outer margins of operculate gills fringed with long hair-like setae; widespread ..... *Caenis*

104' Inner margins of foretibiae and tarsi densely covered with long setae; segment 3 of labial palpi twice as long as segment 2, densely covered with long setae; outer margins of operculate gills fringed with short bifurcate setae ..... *Amercaenis*

105(6) Mandibular tusks with a distinct lateral keel that is more or less toothed and with some multi-point spurs (Fig. 13.101) ..... *PALINGENIIDAE...Pentagenia*

105' Mandibular tusks without a toothed lateral keel (Fig.13.10) ..... *EPHEMERIDAE*...106

106(105') Antennae with whorls of long hair-like setae on most segments (Fig. 13.10); abdominal gills on segment I small, forked and lack fringe of filaments 107

106' Antennae with only short setae; abdominal gills on segment I small, single filaments ..... *Litobrancha recurvata*

107(106) Frontal process of head forked (as in Fig. 13.7) ..... *Ephemera*

107' Frontal process of head not forked, often rounded or conical ..... *Hexagenia*

108(6') Mandibular tusks with numerous tubercles on upper surface (Fig. 13.11); foretarsi rounded and clearly demarcated from foretibiae ..... *Ephoron*

108' Mandibular tusks with one to three tubercles on inner margin, foretarsi flattened and broadly fused with tibiae 109

109(108') Tubercles present near apex of inner margin of mandibular tusks 110

109' Tubercles only present on basal half of mandibular tusks ..... *Campsurus*

110(108') Mandibular tusks with one tubercle present on the inner subapical margin (Fig. 13.98) ..... *Tortopsis*

110' Mandibular tusks with two tubercles present on the inner subapical margin ..... *Tortopus*

Adults

1 Forewing venation greatly reduced, with only three or four longitudinal veins behind R_1, (Fig. 13.160); body dark ..... *OLIGONEURIIDAE*.....47

1' Forewing venation complete or only moderately reduced, numerous longitudinal veins present behind vein R_1 (Figs. 13.164–13.165, 13.190); body variable in color 2

2(1') Penes of male genitalia longer than forceps (Fig. 13.170); antennae of female inserted on prominent anterolateral projections (Fig. 13.171); first intercalary vein behind vein CuA of forewings subparallel to and almost as long as CuA; first intercalary vein attached to CuA by seven or more unbranched crossveins (Fig. 13.164) ..... *BEHNINGIIDAE—Dolania americana*

2' Penes of male genitalia shorter than forceps (Fig. 13.172); antennae of female not inserted as above; intercalary veins behind vein CuA variable; first intercalary vein behind CuA of forewings much shorter than CuA; few or no crossveins attaching first intercalary vein to CuA (Figs. 13.165, 13.167–13.169,13.175–13.176, 13.181 13.183–13.190) or crossveins anastomosed, especially near wing margin (Fig. 13.166) 3

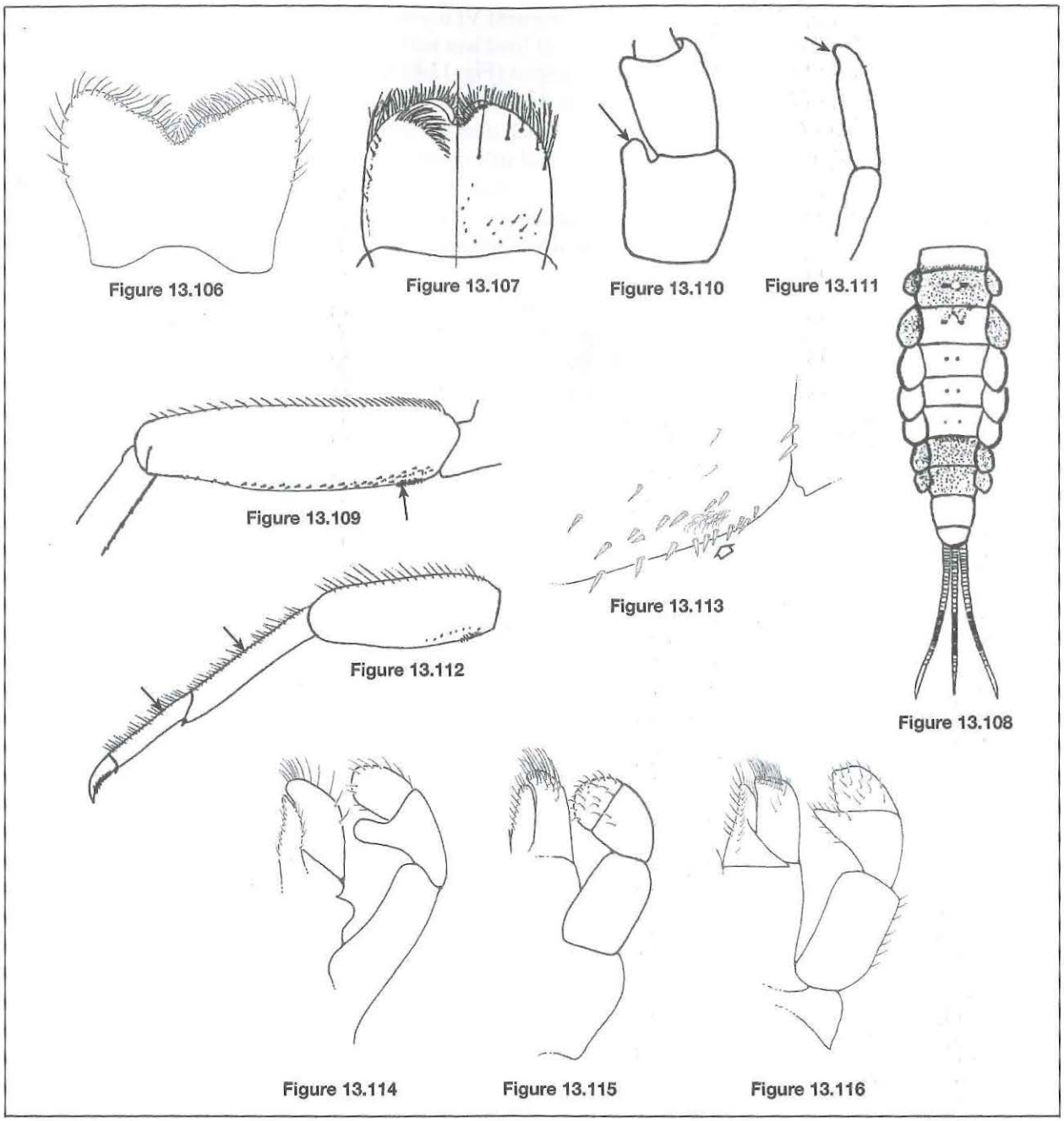


Figure 13.106 Dorsal view of labrum of *Pseudocentroptiloides* sp. nymph (Baetidae).
Figure 13.107 Labrum of *Procloeon* sp. nymph (Baetidae) (left, ventral view; right, dorsal view).
Figure 13.108 Abdomen (dorsal) of *Barbaetis benfieldi* nymph (Baetidae).
Figure 13.109 Villopore of *Baetis* sp. nymph (Baetidae), arrow indicates position of villopore at base of anterior edge of femur.
Figure 13.110 Antennal scape of *Labiobaetis* sp. nymph (Baetidae), arrow indicates lobe on scape.
Figure 13.111 Maxillary palp of *Labiobaetis* sp. nymph (Baetidae), arrow indicates slight excavation below tip of palp.
Figure 13.112 Foreleg of *Acentrella* sp. nymph (Baetidae).
Figure 13.113 Base of forefemur of *Baetis* sp. nymph (Baetidae), arrow indicating villopore (i.e., small patch of setae).
Figure 13.114 Ventral view of labium of *Acerpenna* sp. nymph (Baetidae).
Figure 13.115 Ventral view of labium of *Acentrella* sp. nymph (Baetidae).
Figure 13.116 Ventral view of labium of *Americabaetis* sp. nymph (Baetidae).

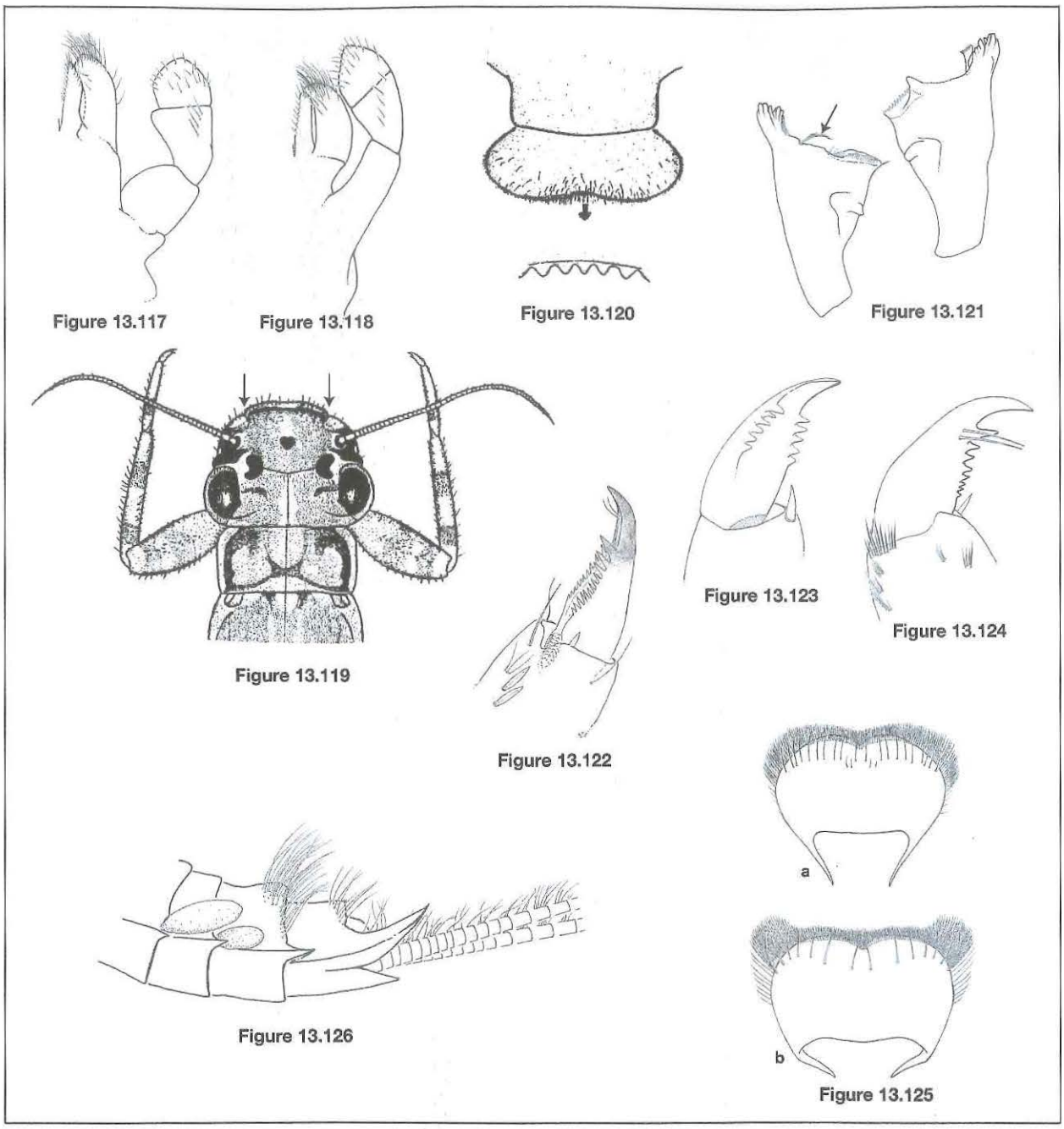


Figure 13.117 Ventral view of labium of *Baetis* sp. nymph (Baetidae).
Figure 13.118 Ventral view of labium of *Plauditus* sp. nymph (Baetidae).
Figure 13.119 Head capsule of *Farrodes texanus* nymph (Leptophlebiidae).
Figure 13.120 Labrum of *Farrodes* sp. nymph (Leptophlebiidae), with enlarged view of denticles in median notch.
Figure 13.121 Right and left mandibles of *Diphetor hageni* nymph (Baetidae).
Figure 13.122 Foretarsal claw of *Kirmaushenkreena zarankoae*(Baetidae).
Figure 13.123 Ventral view of the foreclaw of *Varipes* sp. nymph (Baetidae).
Figure 13.124 Lateral view of the foreclaw of *Moribaetis* sp. nymph (Baetidae).
Figure 13.125 Dorsal view of variations (a and b) of the labrum of *Moribaetis* sp. nymphs (Baetidae).
Figure 13.126 Lateral view of posterolateral projections of abdominal segments VIII and IX of *Caurinella* sp. nymph (Ephemerellidae).

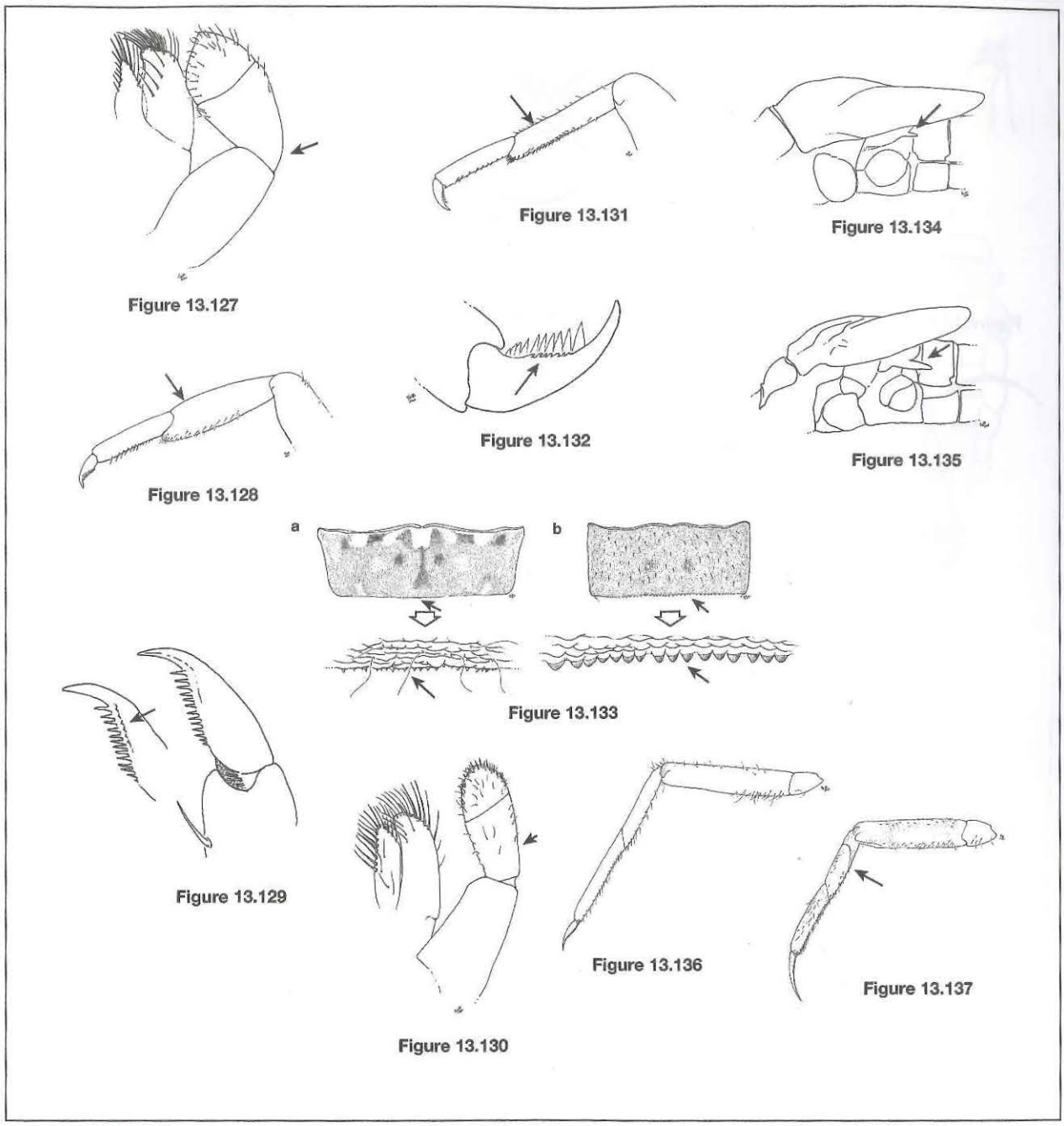


Figure 13.127 Ventral view of labium of *Iswaeon anoka* (Baetidae), with arrow indicating base of segment 2.
Figure 13.128 Foreleg of *Iswaeon anoka* (Baetidae), arrow indicates broad apical portion of leg segment.
Figure 13.129 Foreclaw of *Iswaeon anoka* (Baetidae), arrow indicating large and small rows of denticles.
Figure 13.130 Ventral view of labium of *Heterocloeon curiosum* (Baetidae), with arrow indicating base of segment 2.
Figure 13.131 Foreleg of *Heterocloeon curiosum* (Baetidae), arrow indicates uniform width of leg segment.
Figure 13.132 Foreclaw of *Heterocloeon curiosum* (Baetidae), arrow indicating large and small rows of denticles.
Figure 13.133 Tergite VII of *Acentrella parvula* (Baetidae) (a) and tergite IX of *Plauditus dubius* (Baetidae) (b), showing spines on posterior margins.
Figure 13.134 Lateral view of thorax of *Heterocloeon curiosum* (Baetidae), arrow indicates hind wing pad.
Figure 13.135 Lateral view of thorax of *Heterocloeon amplum* (Baetidae), arrow indicates hind wing pad.
Figure 13.136 Foreleg *Anafroptilum minor* (Baetidae), tibia lacks patello-tibial suture.
Figure 13.137 Foreleg *Neocloeon triangulifer* (Baetidae), tibia with patello-tibial suture indicated by arrow.

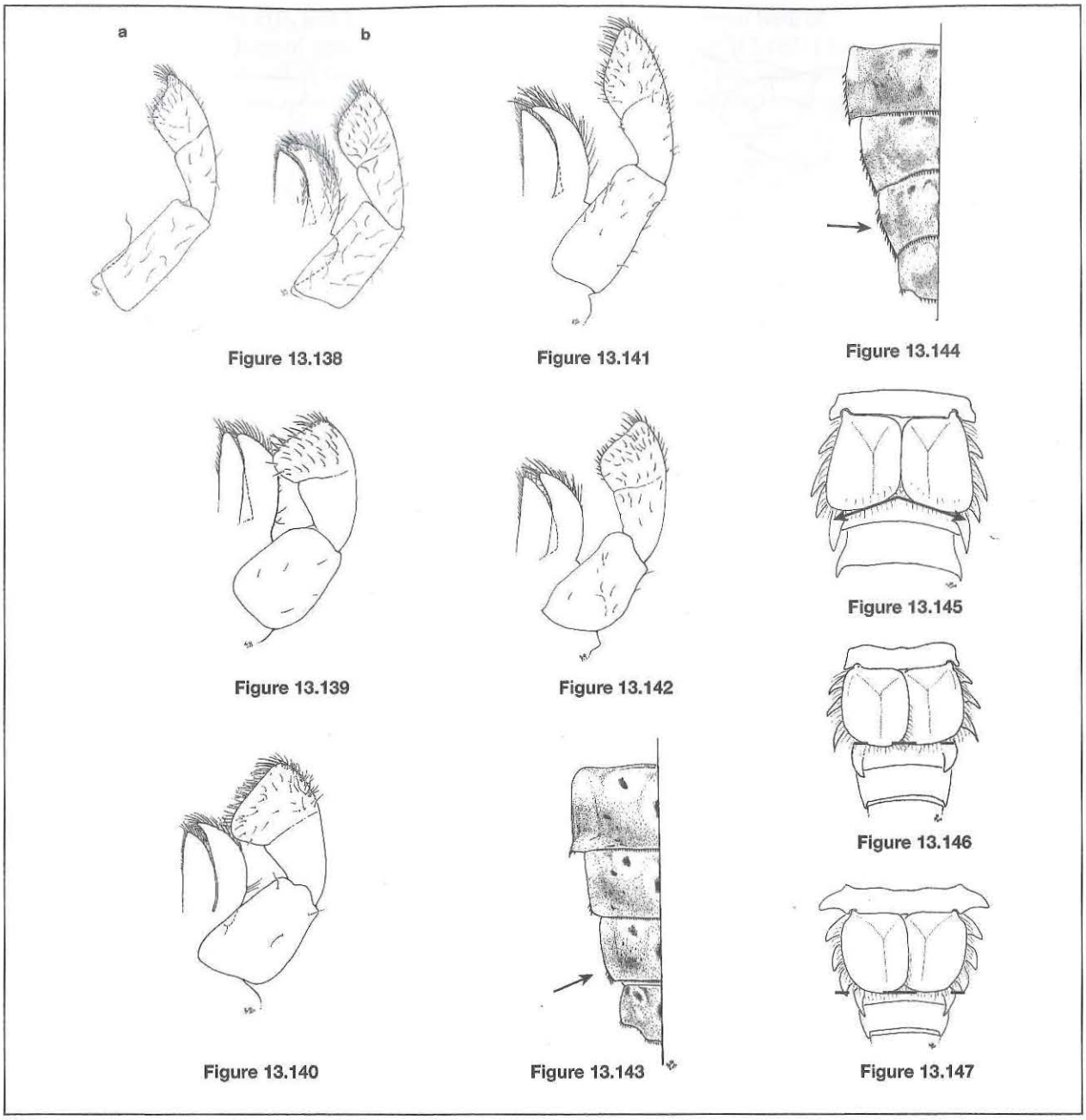


Figure 13.138 Ventral view of labium of *Cloeon dipterum* (Baetidae), two variants from same population: (a) variant with distinctly sinuous apical margin of palp and with distinct tip; (b) variant with only slightly sinuous apical margin of palp and with much reduced tip.

Figure 13.139 Ventral view of labium of *Procloeon rivulare* (Baetidae).

Figure 13.140 Ventral view of labium of *Procloeon viridoculare* (Baetidae).

Figure 13.141 Ventral view of labium of *Procloeon ingens* (Baetidae).

Figure 13.142 Ventral view of labium of *Procloeon simplex* (Baetidae).

Figure 13.143 Dorsal view of abdominal terga VII–X of *Anafroptilum minor* (Baetidae), arrow indicates spines along lateral margins.

Figure 13.144 Dorsal view of abdominal terga VII–X of *Neocloeon triangulifer* (Baetidae), arrow indicates spines along lateral margins.

Figure 13.145 Operculate abdominal gills of segment II of *Brachycercus nitidus* (Caenidae), dotted lines indicate outward sloping edges of operculate gills.

Figure 13.146 Operculate abdominal gills of segment II of *Sparbarus maculatus* (Caenidae), dotted lines indicate edges of operculate gills not sloping outward.

Figure 13.147 Operculate abdominal gills of segment II of *Sparbarus nasutus* (Caenidae), dotted lines indicate edges of operculate gills not sloping outward.

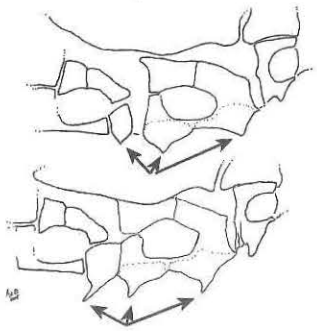


Figure 13.148

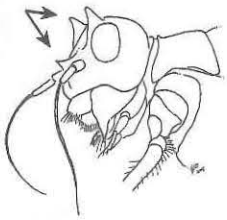


Figure 13.151

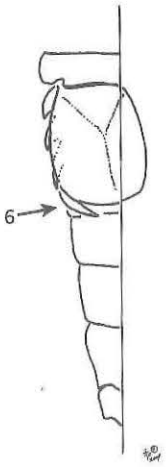


Figure 13.154

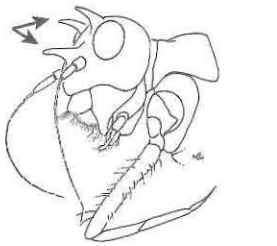


Figure 13.149

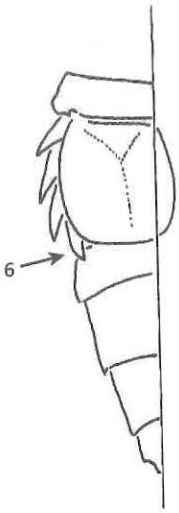
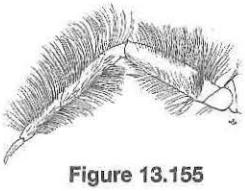


Figure 13.152



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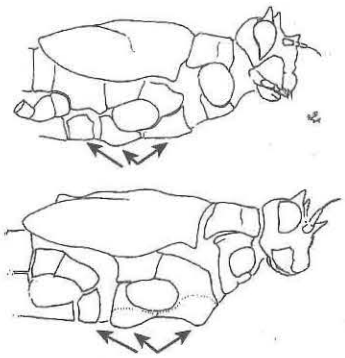

Figure 13.150

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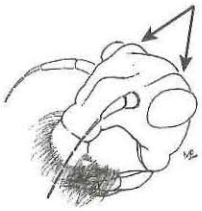


Figure 13.156

Figure 13.148 [Upper] Lateral view of thorax of *Susperatus prudens* (Caenidae), with arrows indicating sternal projections; [Lower] Lateral view of thorax of *Susperatus tuberculatus* (Caenidae) with arrows indicating sternal projections.

Figure 13.149 Lateral view of head of *Susperatus tuberculatus* (Caenidae), arrows indicate ocellar tubercles typical of *Susperatus* spp. (Caenidae).

Figure 13.150 [Upper] Lateral view of thorax of *Sparbarus maculatus* (Caenidae), with arrows indicating absence of sternal projections; [Lower] Lateral view of thorax of *S. choctaw* (Caenidae), with arrows indicating absence of sternal projections.

Figure 13.151 Lateral view of head of *Sparbarus* sp. (Caenidae) with arrows indicating ocellar tubercles that are of typical of both *Sparbarus* spp. and *Brachycercus* spp. (Caenidae).

Figure 13.152 Dorsal view of abdominal segments II–X of *Sparbarus maculatus* (Caenidae), with arrow indicating the position of the posterolateral projection of segment VI.

Figure 13.153 Hind leg of *Sparbarus maculatus* (Caenidae).

Figure 13.154 Dorsal view of abdominal segments II–X of *Cercobrachys etowah* (Caenidae), with arrow indicating the position of the posterolateral projection of segment VI.

Figure 13.155 Hind leg *Cercobrachys etowah* (Caenidae).

Figure 13.156 Lateral view of head of *Cercobrachys* spp. (Caenidae), arrows indicate blunt ocellar tubercles typical of genus.

3(2') Base of veins MP_2 and CuA in forewings strongly divergent from base of vein MP_1; base of vein MP_2 strongly bent towards CuA (Figs. 13.165–13.168) and sometimes fused at base with CuA; fork of vein MP usually less symmetrical; hind wings with numerous veins and crossveins; vein MA of hind wings unforked (Figs. 13.165–13.168) 4

3' Base of veins MP_2 and CuA in forewings not as above, base of vein MP_2 may only diverge from MP_1; fork of vein MP usually more symmetrical (Figs. 13.169, 13.175–13.176, 13.181, 13.183–13.190); hind wings variable, may be reduced or absent; if hind wings present, vein MA variable. 8

4(3) Costal angle of hind wings acute or at a right angle (Fig. 13.165b); vein A_1 of forewings unforked; costal crossveins of forewings basal of bullae weak or atrophied (Fig. 13.165a) . . . . . ***NEOEPHEMERIDAE—Neoephemera***

4' Costal angle of hind wings usually rounded (Figs. 13.166–13.168); if nearly acute or at right angles (Fig. 13.167) then vein A_1 of forewings forked near margin (Fig. 13.167); costal crossveins of forewings basal of bullae well-developed (Fig. 13.167) 5

5(4') Middle and hind legs of male and all legs of female feeble and nonfunctional; body color usually pale; wings often somewhat translucent and colorless or with gray or purplish gray shading . . . . . ***POLYMITARCYIDAE***.....96

5' All legs of both sexes well-developed and functional; color variable. 6

6 Vein MA_2 of forewings 1.33 to 3.00 times longer than base of vein MA (i.e., distance from base of MA to MA fork) (Fig. 13.163); male forceps with one long basal segment and one short terminal segment (Fig. 13.161) . . . . . ***EUTHYPLOCIIDAE...Euthyplocia hecuba***

6' Vein MA_2 of forewings range from shorter than to slightly longer than base of vein MA; male forceps either with two long basal segments and one or two short terminal segments or one long basal segment and two short terminal segments. 7

7(6') Vein A_1 of forewings, forked near margin (Fig. 13.167); abdomen usually yellowish with reddish or pinkish lateral stripes or spots on terga . . . . . ***POTAMANTHIDAE..,Anthopotamus***

7' Vein A_1 of forewings not forked near margin, attached to hind margin by three or more small veins (Fig. 13.168); abdomen of most species with distinctive dark contrasting patterns on terga and sterna. 93

8(3') Cubital intercalary veins of forewings consist of a series of small veins, often forking or sinuate that attach vein CuA to hind margin of wing (Figs. 13.169, 13.175). 9

8' Cubital intercalary veins of forewings variable, but not as above (Figs. 13.176, 13.181, 13.183, 13.186–13.187); sometimes absent (Fig. 13.184) 10

9(8) Remnants of gill tufts (often purplish colored) present at sides of vestigial maxillae and bases of forecoxae; forelegs largely or entirely dark, but middle and hind legs pale; vein MP of hind wings forked near margin (Fig. 13.175); terminal filament vestigial . . . . . ***ISONYCHIIDAE...Isonychia***

9' Remnants of gill tufts not present on vestigial maxillae and forecoxae; legs not colored as above; vein MP of hind wings forked near base or near middle, but not near wing margin (Figs. 13.169, 13.177); terminal filament variable 19

10(8') All three caudal filaments well-developed 11

10' Only two caudal filaments (cerci) well-developed and apparently present, terminal filament rudimentary or absent 14

11(10) Hind wings relatively large with one or more veins forked; costal projection shorter than wing width (Figs. 13.176, 13.181, 13.183) 12

11' Hind wings small with only two or three simple veins or hind wings absent (Figs. 13.189, 13.190); if hind wings present, costal projection long (1.5 to 3.0 times width of wing); costal projection straight or recurved (Fig. 13.188) 18

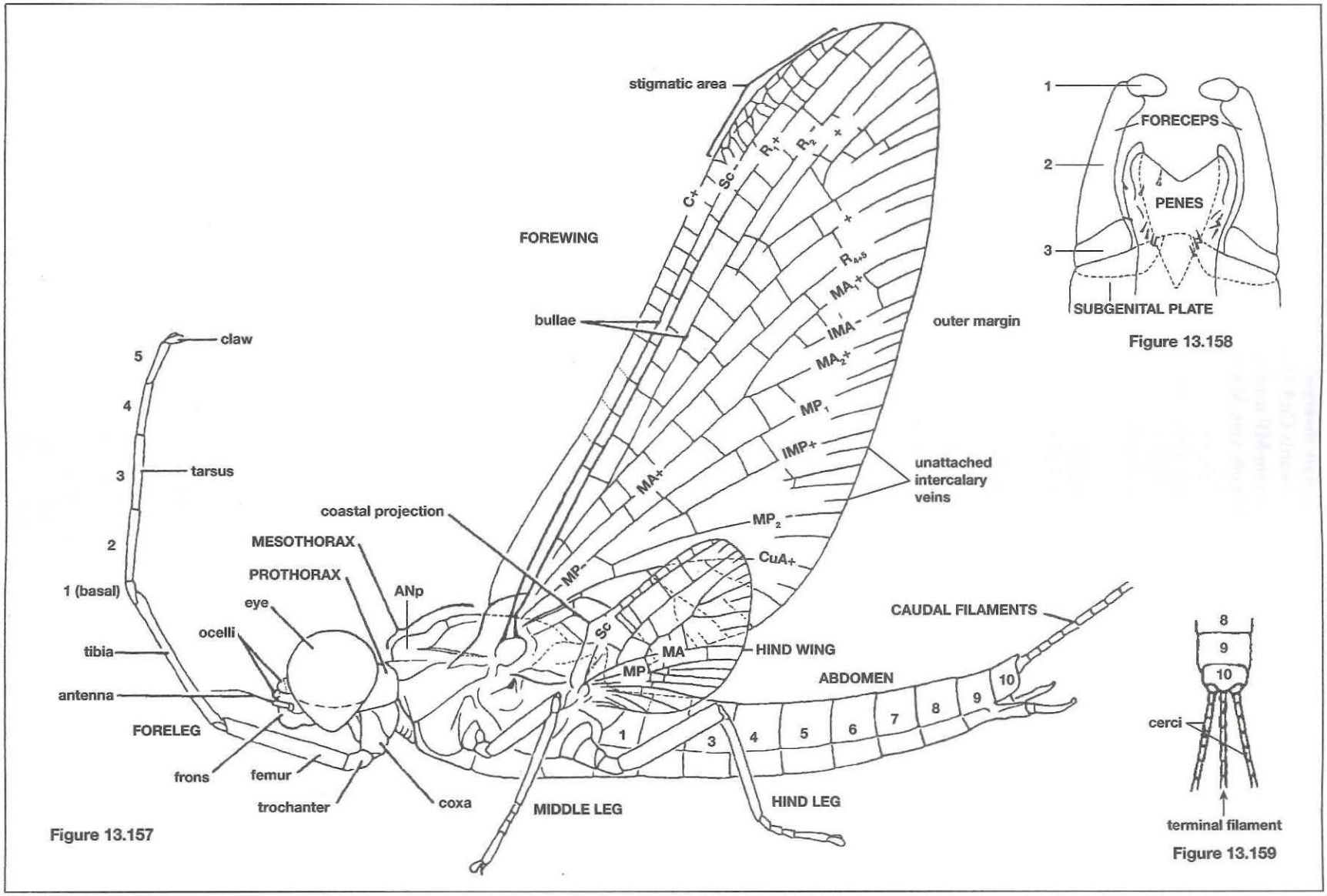


Figure 13.157 Lateral view of *Ephemerella* sp. male imago (Ephemerellidae), ANp = anteronotal protuberance.

Figure 13.158 Dorsal view of genitalia of *Ephemerella* sp. male imago (Ephemerellidae).

Figure 13.159 Dorsal view of apex of abdomen and caudal filaments of *Ephemerella* sp. female imago (Ephemerellidae).

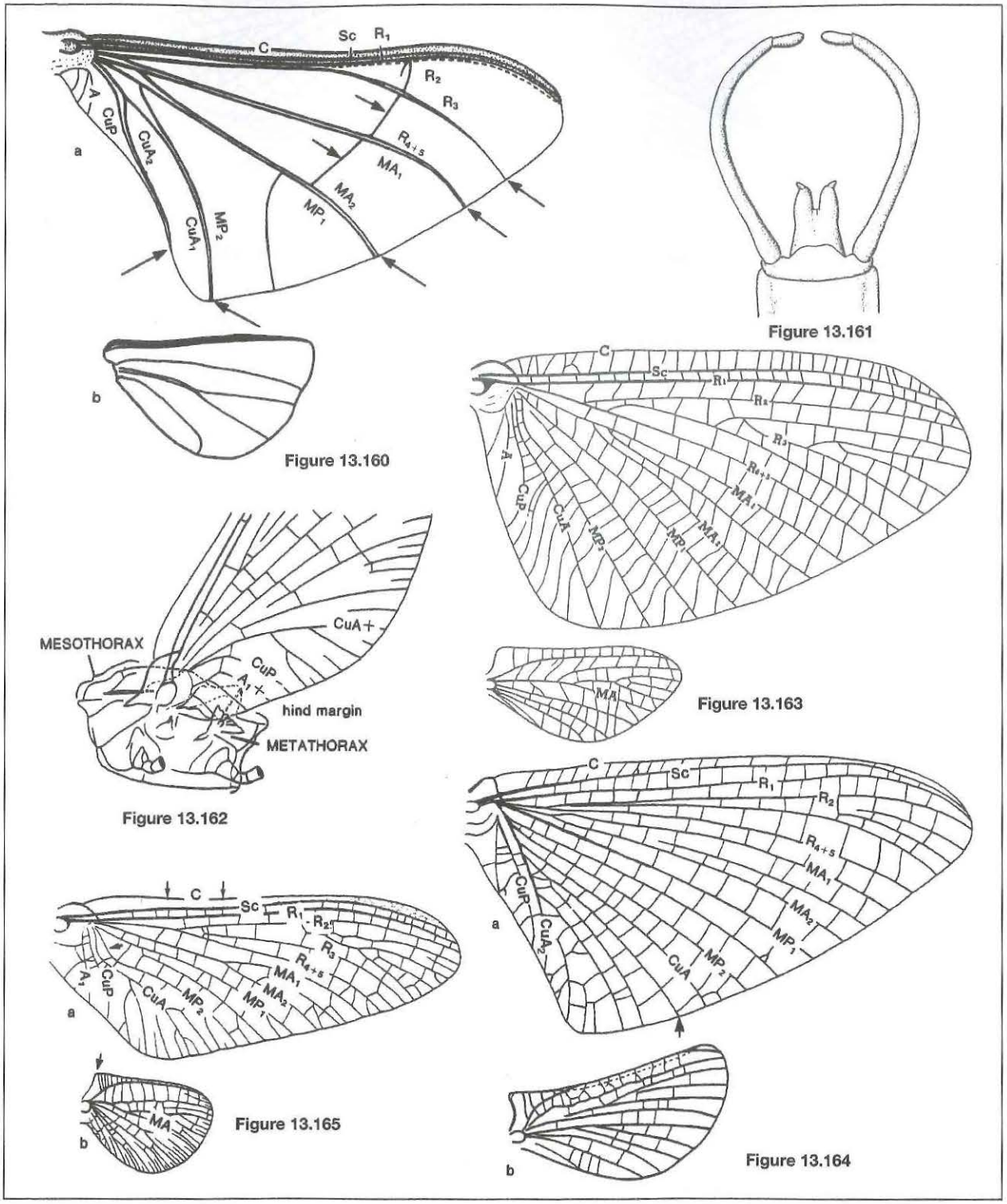


Figure 13.160 Forewing (a) and hind wing (b) of *Lachlania* sp. (Oligoneuriidae), arrows indicate primary veins and reduced crossveins.

Figure 13.161 Ventral view of male genitalia of *Euthyplocia* sp. (Euthyplociidae).

Figure 13.162 Lateral view of thorax and wing of *Ephemerella* sp. (Ephemerellidae).

Figure 13.163 Forewing (a) and hind wing (b) of *Euthyplocia* sp. (Euthyplociidae).

Figure 13.164 Forewing (a) and hind wing (b) of *Dolania americana* (Behningiidae), arrow indicates first intercalary vein behind vein CuA.

Figure 13.165 Forewing (a), arrows indicate curved base of veins MP_2 and CuA and weak costal crossveins and hind wing (b), arrow indicates acute costal angle in *Neoephemera* sp. (Neophemeridae).

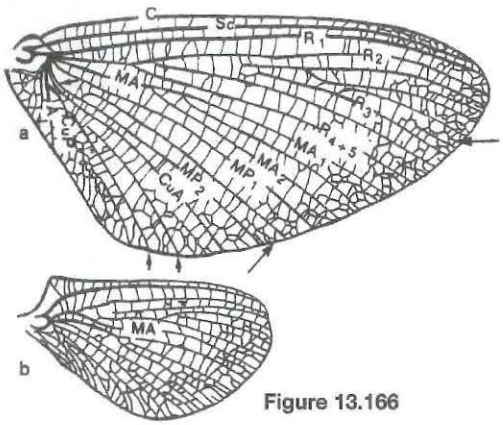
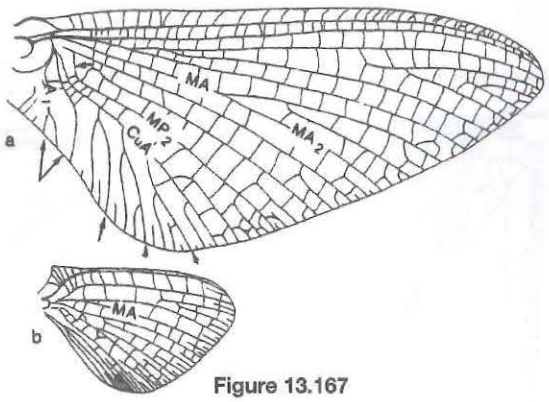


Figure 13.166



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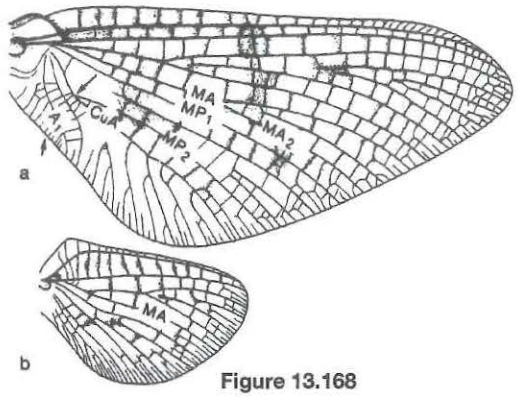


Figure 13.168

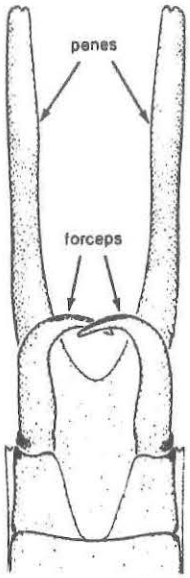


Figure 13.170

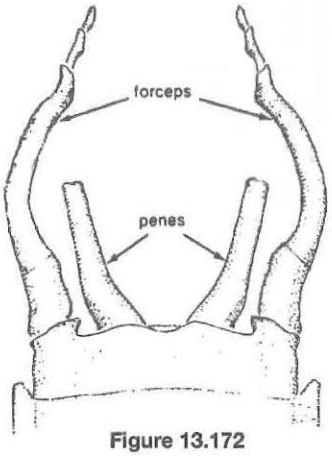


Figure 13.172

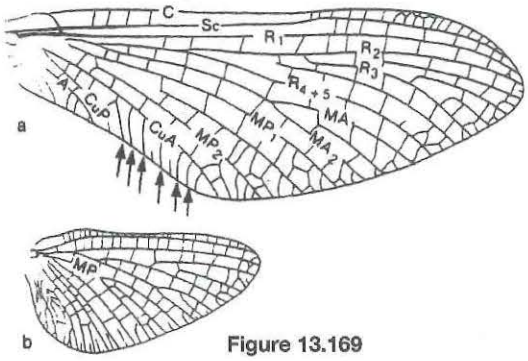


Figure 13.169

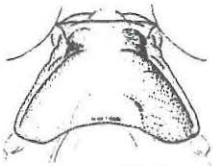


Figure 13.173

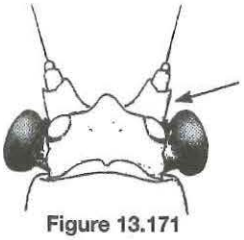


Figure 13.171

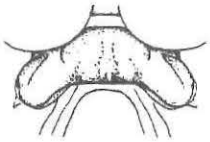


Figure 13.174

Figure 13.166 Forewing (a) and hind wing (b) of *Ephoron* sp. (Polymitarcyidae), arrows indicate curved bases of veins MP_2 and CuA and anastomosed crossveins near wing margin.

Figure 13.167 Forewing (a) and hind wing (b) of *Anthopotamus* sp. (Potamanthidae), arrows indicate curved bases of veins MP_2 and CuA and forked vein A_1.

Figure 13.168 Forewing (a) and hind wing (b) of *Ephemera* sp. (Ephemeridae).

Figure 13.169 Forewing (a) and hind wing (b) of *Siphlonurus* sp. (Siphlonuridae), arrows indicate cubital intercalary veins.

Figure 13.170 Ventral view of male genitalia of *Dolania americana* (Behningiidae).

Figure 13.171 Dorsal view of head of *Dolania americana* female imago (Behningiidae), arrow indicates prominent anterolateral projections.

Figure 13.172 Ventral view of male genitalia of *Pentagenia vittigera* (Palingeniidae).

Figure 13.173 Dorsal view of pronotum of *Ephemera* sp. male imago (Ephemeridae).

Figure 13.174 Dorsal view of pronotum of *Pentagenia vittigera* male imago (Ephemeridae).

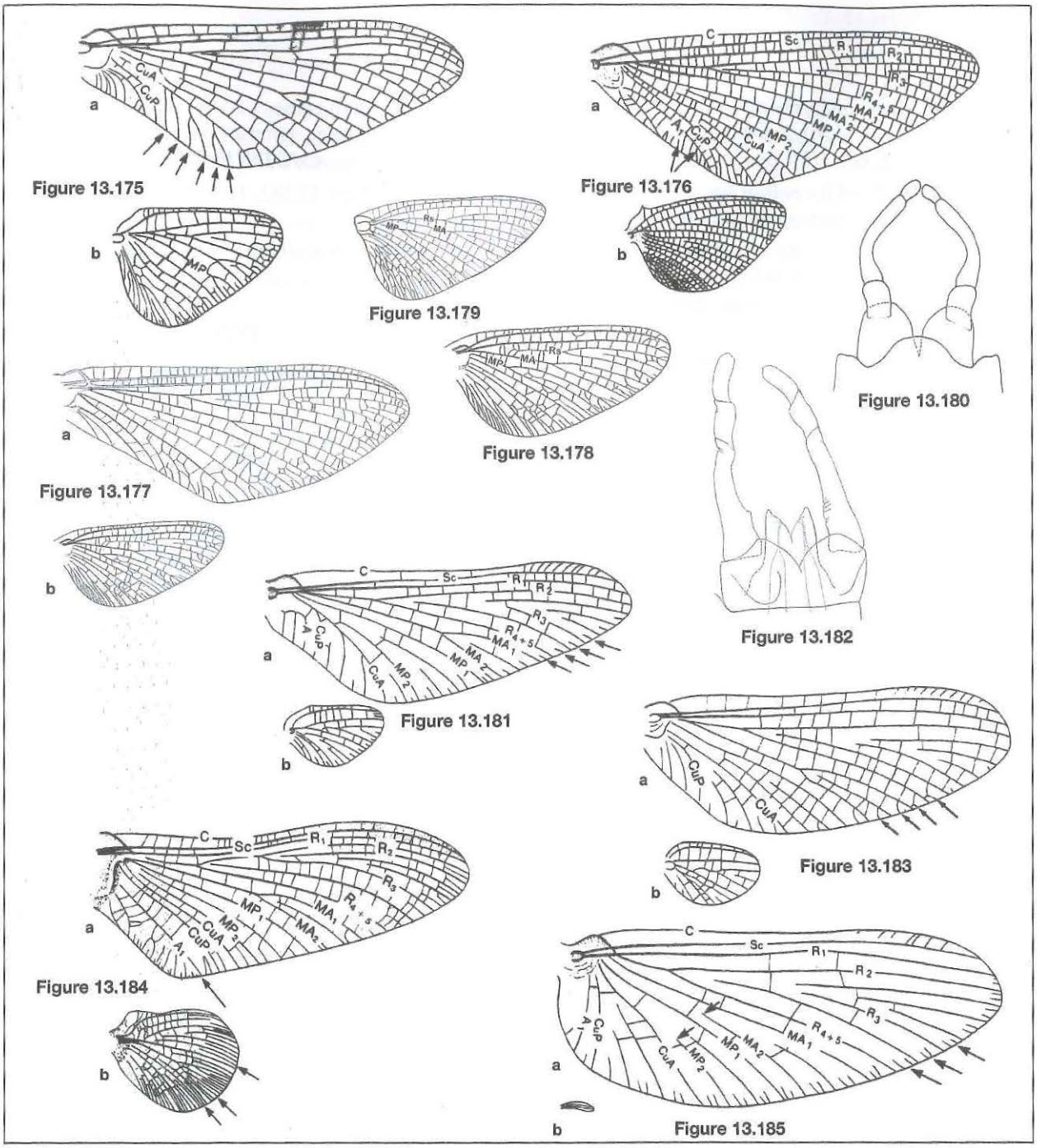


Figure 13.175 Forewing (a) and hind wing (b) of *Isonychia* sp. (Isonychiidae), arrows indicate cubital intercalary veins.

Figure 13.176 Forewing (a) and hind wing (b) of *Ametropus* sp. (Ametropodidae), arrows indicate cubital intercalary veins.

Figure 13.177 Forewing (a) and hind wing (b) of *Acanthametropus* sp. (from Russia) (Acanthametropodidae).

Figure 13.178 Hind wing of *Acanthametropus* sp. (from Russia) (Acanthametropodidae).

Figure 13.179 Hind wing of *Analetris eximia* (Acanthametropodidae).

Fig.13.180 Ventral view of male genitalia of *Analetris eximia* (Acanthametropodidae).

Figure 13.181 Forewing (a) and hind wing (b) of *Ephemerella* sp. (Ephemerellidae), arrows indicate detached marginal intercalary veins.

Figure 13.182 Ventral view of male genitalia of *Acanthametropus* sp. (Acanthametropodidae) [from Russia].

Figure 13.183 Forewing (a) and hind wing (b) of *Paraleptophlebia debilis* (Leptophlebiidae), arrows indicate attached marginal intercalary veins.

Figure 13.184 Forewing (a), arrow indicates vein A_1 and hind wing (b), arrow indicates marginal intercalary veins of *Baetisca rogersi* (Baetiscidae).

Figure 13.185 Forewing (a) and hind wing (b) of *Acentrella* sp. (Baetidae), arrow indicates paired detached marginal intercalary veins.

12(11) Vein A_1 of forewings attached to hind margin by series of small veins (Fig. 13.176); forewings with two pairs of cubital intercalary veins, anterior pair long, posterior pair very short ..... ***AMETROPODIDAE....Ametropus***

12' Vein A_1 of forewings not attached to hind margin as above (Figs. 13.181, 13.183); cubital intercalary veins not as above 13

13(12') Short, basally detached marginal intercalary veins present between primary wing veins along entire outer margins of fore- and hind wings (Fig. 13.181); male forceps with one short terminal segment (Figs. 13.240–13.246) ..... ***EPHEMERELLIDAE....74***

13' Short basally detached marginal intercalary veins usually absent along outer margins of wings (occasionally a small single unattached marginal vein may occur irregularly along wing margins); most marginal intercalary veins attached (Fig. 13.183); male forceps with two or three short terminal segments (Figs. 13.229–13.230, 13.281–13.283) ..... ***LEPTOPHLEBIIDAE.....64***

14(10') Hind wings with numerous, long, free marginal intercalary veins (Fig. 13.184); cubital intercalary veins absent in forewings with vein A_1 terminating in outer margin of wings (Fig. 13.184) ..... ***BAETISCIDAE...Baetisca***

14' Hind wings not as above or absent; if hind wings present then cubital intercalary veins present in forewings with vein A_1 terminating in hind margin of wings (Figs. 13.185–13.187 15

15(14') Short, basally detached, single or double marginal intercalary veins present in each interspace of forewings and veins MA_2 and MP_2 detached basally from their respective stem veins (Fig. 13.185); hind wings small or absent; penes of male membranous; upper portion of compound eyes of male turbinate (i.e., raised on a stalk-like lower portion; Fig. 13.195. ..... ***BAETIDAE*.....25***

15' Marginal intercalary veins attached basally to other veins; veins MA_2 and MP_2 attached basally (Figs. 13.187–13.188); hind wings relatively large; penes of male well-developed; compound eyes of male not turbinate 16

16(15') Hind tarsi apparently four segmented with basal segment fused or partially fused to tibiae (Figs. 13.192–13.193); hind tarsi longer than hind tibiae; one or two dissimilar pairs of cubital intercalary veins present (Figs. 13.186–13.187) 17

16' Hind tarsi distinctly five segmented (as in Fig. 13.194); hind tarsi shorter than hind tibiae; two pairs of cubital intercalary veins present similar to those in Fig. 13.186. ..... ***HEPTAGENIIDAE***.(in part)/ ***ARTHROPLEIDAE....48***

17(16) Compound eyes of male contiguous (i.e., touching) or nearly contiguous dorsally (similar to Fig. 13.219); foretarsi three times the length of foretibiae; abdomen of female not noticeably long and slender, posterior margin of sternite IX evenly convex without median notch ..... ***METRETOPODIDAE.....63***

17' Compound eyes of male separated dorsally by twice the width of median ocellus; foretarsi two times the length of foretibiae; abdomen of female distinctly long and slender, posterior margin of sternite IX with median notch (Fig. 13.191); rare, sand dominated rivers ..... ***PSEUDIRONIDAE...Pseudiron centralis***

18(11') Vein MA of forewings forming a more or less symmetrical fork; veins MP_2 and IMP extend less than three-fourths of distance to base of vein MP (Figs. 13.188, 13.189); male forceps two or three segmented; thorax usually black or gray ..... ***LEPTOHYPHIDAE.... 86***

*The genera *Baetopus, Barbaetis, Kirmaushenkreena, Varipes,* and *Waynokiops* are not included in this key because adults are either globally unknown or unknown for North American species.

18' Vein MA of forewings not as above, vein MA_2 attached basally by a crossvein; veins MP_2 and IMP almost as long as vein MP, and extend nearly to wing base (Fig. 13.190); male forceps one segmented; thorax usually brown ..... ***CAENIDAE***.... 89

19(9') Three caudal filaments, terminal filament distinctly longer than abdominal tergite X; hind wings one-half or more than one-half the length of forewings (Fig. 13.177); rare ..... ***ACANTHAMETROPODIDAE***.,...20

19' Two caudal filaments apparent, terminal filament vestigial; hind wings less than one-half as long as forewings 21

20(19) Rs fork of hind wings longer than MA fork (Fig. 13.179); male genitalia as in Fig. 13.180..... ***Analetris eximia***

20' Rs fork of hind wings shorter than MA fork (Fig. 13.178); male genitalia similar to Fig. 13.182..... ***Acanthametropus pecatonica****

21(19') Tarsal claws dissimilar, with each pair of claws having one sharp and one blunt claw (Fig. 13.208); costal projections of hind wings acute (Fig. 13.196) ..... ***AMELETIDAE***...***Ameletus***

21' Tarsal claws similar, with each pair of claws having two sharp claws (Fig. 13.209); costal projections of hind wings obtuse or weakly developed (Fig. 13.169b) ..... ***SIPHLONURIDAE***....22

22(21') Lateral margins of abdominal segments V–IX of male greatly expanded; tubercles present on sterna of meso- and metathorax; rare..... ***Siphlonisca aerodromia***

22' Lateral margins of abdominal segments V–IX not greatly expanded; without tubercles on thoracic sterna 23

23(22') Vein MP of hind wings simple, unforked; uncommon..... ***Parameletus***

23' Vein MP of hind wings forked (Fig. 13.169b) 24

24(23') Abdominal sterna III–VI pale with a brown transverse bar; rare; California ..... ***Edmundsius agilis***

24' Abdominal sterna not marked as above, usually with dark spots, longitudinal stripes, oblique stripes, U-shaped marks, or mostly dark ..... ***Siphlonurus***

25(15) Hind wings present with blunt costal projections; hind wings with ten or more crossveins; forewings of most species patterned; abdomen with distinct dark speckles ..... ***Callibaetis***

25' Hind wings present or absent, if present, then costal projections of hind wings never blunt, either pointed (Fig. 13.210), hooked (Fig. 13.211), or absent (Fig. 13.212); hind wings usually with less than six crossveins; forewings of most species without patterns; abdomen variable, rarely with speckles 26

26(25') Marginal intercalary veins of forewings occur singly; hind wings present or absent, if present, hind wings with costal projections hooked or recurved (similar to Fig. 13.211) 27

26' Marginal intercalary veins of forewings occur in pairs as in Fig. 13.185a; hind wings present or absent, if present, costal projections of hind wings variable, rarely hooked 31

27(26) Length of segment 3 of male forceps greater than two times its width; spine-like process (Fig. 13.254) usually present between forceps bases; hind wings present (except for *A. minor*, which lacks hind wings, but has small forewings (~3.0 mm) and black dashes on abdominal sterna) ..... ***Anafroptilum***

*-Adult of *A. pecatonica* unknown, wing and genitalia characters tentative based on only known adult from Siberia

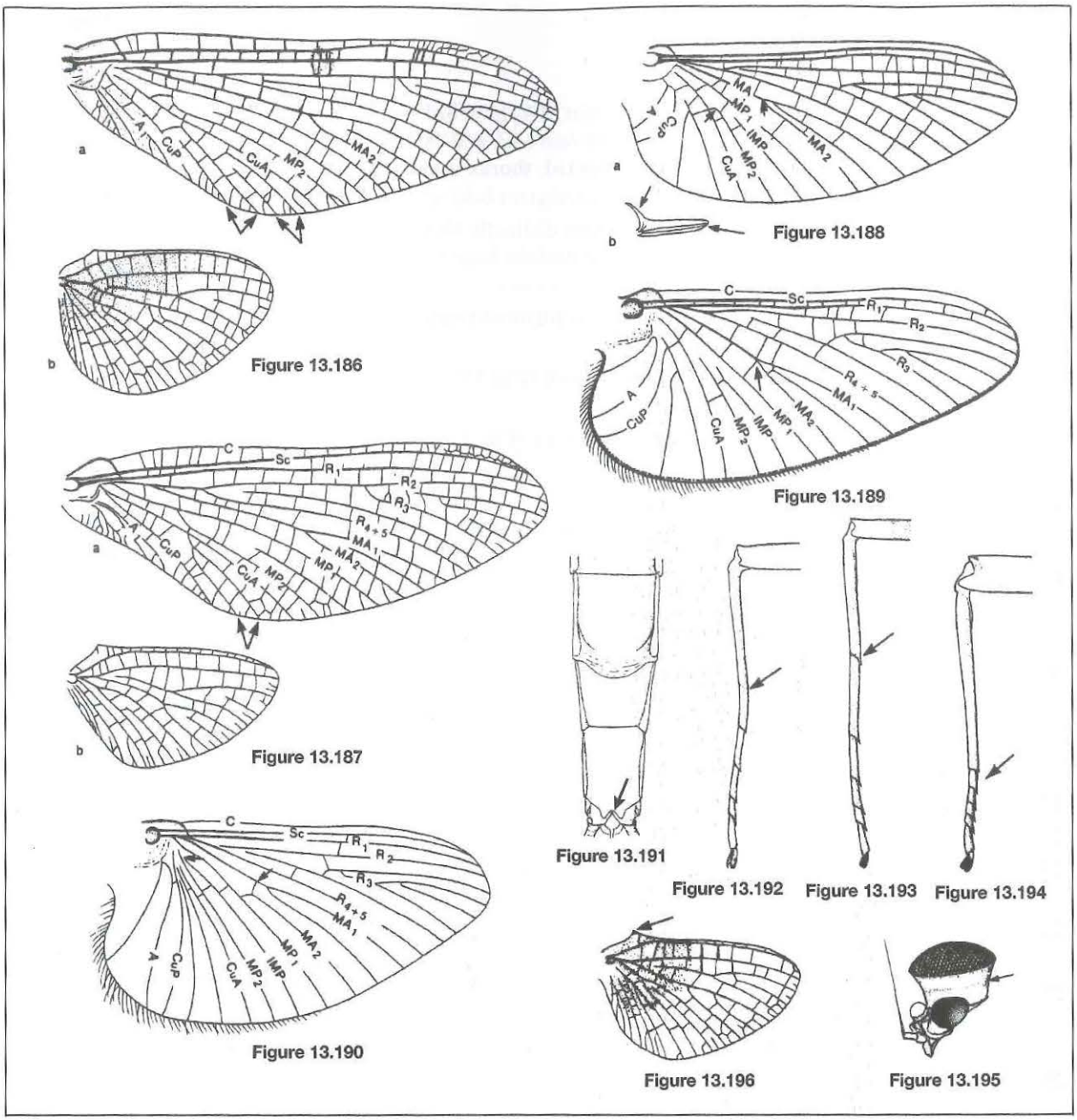


Figure 13.186 Forewing (a), arrows indicate cubital intercalary veins and hind wing (b) of *Siphloplecton* sp. (Metretopodidae).

Figure 13.187 Forewing (a), arrows indicate cubital intercalary veins and hind wing (b) of *Metretopus* sp. (Metretopodidae).

Figure 13.188 Forewing (a), arrows indicate vein MA fork and attached base of MP_2 and hind wing (b), arrows indicate costal projection and narrow shape of wing of *Leptohyphes* sp. (Leptohyphidae).

Figure 13.189 Forewing of *Tricorythodes* sp. male imago (Leptohyphidae), arrow indicates vein MA fork.

Figure 13.190 Forewing of *Caenis* sp. (Caenidae), arrow indicates connection of vein MA_2 with base of veins MP_2 and IMP.

Figure 13.191 Ventral view of apex of abdominal sternite IX of *Pseudiron centralis* female imago (Pseudironidae), arrow indicates median notch.

Figure 13.192 Hind tibia and tarsus of *Pseudiron centralis* imago (Pseudironidae), arrow indicates line of fusion of tarsal segment 1 with tibia.

Figure 13.193 Hind tibia and tarsus of *Siphloplecton* sp. imago (Metretopodidae), arrow indicates joint between tarsal segment 1 and tibia.

Figure 13.194 Hind tibia and tarsus of *Heptagenia* sp. imago (Heptageniidae), arrow indicates tarsus with 5 segments.

Figure 13.195 Lateral view of head of *Baetis* sp. male imago (Baetidae), arrow indicates extended base of upper part of compound eye.

Figure 13.196 Hind wing of *Ameletus* sp. imago (Ameletidae), arrow indicates acute costal projection.

Figure 13.197

Figure 13.198

Figure 13.199

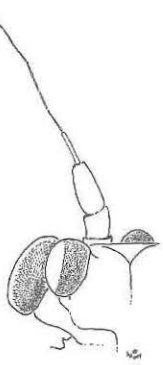
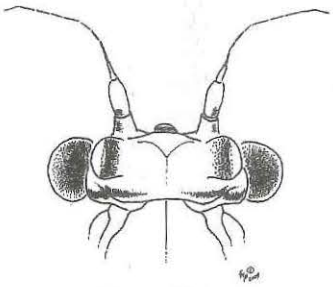


Figure 13.200



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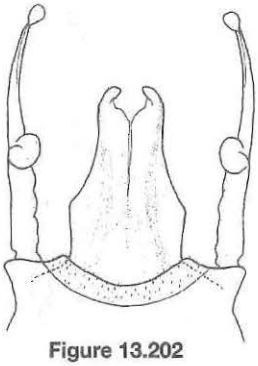
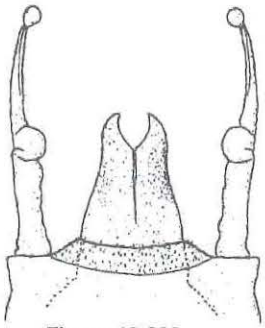


Figure 13.202



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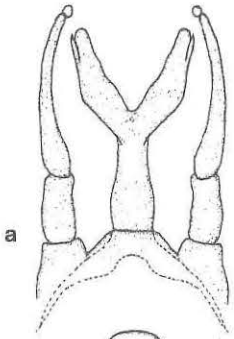

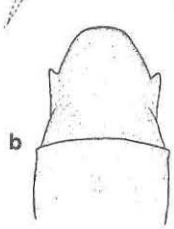

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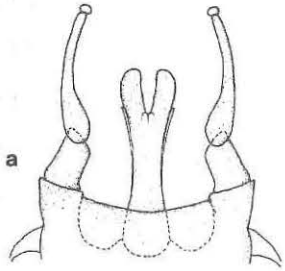

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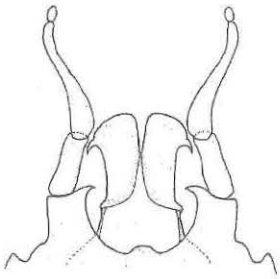

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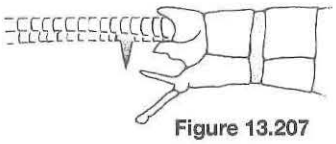


Figure 13.207

Figure 13.197 Lateral view of hind tarsus and apex of hind tibia of *Tricorythodes* (*Asioplax*) sp. (Leptohyphidae).

Figure 13.198 Lateral view of hind tarsus and apex of hind tibia of *Allenhyphes* sp. (Leptohyphidae).

Figure 13.199 Antenna of male imago of *Susperatus prudens* (Caenidae).

Figure 13.200 Head and antenna of male imago of *Cercobrachys etowah* (Caenidae).

Figure 13.201 Dorsal surface of head of male imago of *Sparbarus maculatus* (Caenidae).

Figure 13.202 Ventral view of male genitalia of *Tricorythodes* sp. (Leptohyphidae).

Figure 13.203 Ventral view of male genitalia of *Tricorythodes* sp. (Leptohyphidae).

Figure 13.204 Ventral view (a) of male genitalia and (b) female subanal plate of *Leptohyphes* sp. (Leptohyphidae).

Figure 13.205 Ventral view (a) of male genitalia and (b) female subanal plate of *Allenhyphes* sp. (Leptohyphidae).

Figure 13.206 Ventral view of male genitalia of *Vacupernius* sp. (Leptohyphidae).

Figure 13.207 Lateral view of apex of the abdomen and caudal filaments of *Allenhyphes* sp. male imago (Leptohyphidae).

27' Length of segment 3 of male forceps usually less than two times it's width; spine-like process never present between forceps bases, but variably shaped penes covers may be present; hind wings present or absent 28

28(27') Basal segments of male forceps with distinct quadrate projections on inner margins; abdominal sterna of females with either dark lateral triangular marks or dark blotches . . . . . ***Neocloeon***

28' Basal segments of male forceps variable, but without quadrate projections; abdominal sterna of females largely pale or variably marked, but not as above 29

29(28') Hind wings absent; male genitalia with distinct coniform penes cover between forceps bases; segment 3 of male forceps small and rounded; in females, pterostigma of forewings tinted brown and abdominal sterna with lateral longitudinal marks . . . . . ***Cloeon***

29' Hind wings present or absent; male genitalia with rounded or rectangular penes cover between forceps bases; segment 3 of male forceps usually elongate (at most two times as long as wide); in females pterostigma of forewings without brown pigment and abdominal sterna lack lateral longitudinal marks 30

30(29') Segment 2 of male forceps (Fig. 13.255) with distinct swelling or bulge on inner margin . . . . . ***Pseudocentroptiloides***

30' Segment 2 of male forceps without distinct swelling or bulge on inner margin . . . . . ***Procloeon***

31(26') Hind wings present; costal projections of hind wings present with broad bases (Fig. 13.213a,b) and acute apices; anterior margins of hind wings from wing articulations to apices of costal projections straight, producing characteristic shape of hind wings (Fig. 13.213a,b); medium to large rivers . . . . . ***Camelobaetidius***

31' Hind wings present or absent; if hind wings present costal projections present or absent, if present, shape variable, but if similar to above with acute apices then costal projections lack broad bases such that hind wings are not shaped as above (Fig. 13.214a,b) (*Fallceon thermophilos* seems to be the one critical exception having hind wings with small acute costal projections and broad bases producing a slightly modified, or elevated, wing margin. However, the terminal segment of male forceps of *F. thermophilos* is at least half as long as preceding segment) 32

32(31') Anteronotal protuberance (ANp) of mesothorax conical with distinctly pointed apex (Fig.13.256) or subconical with slightly rounded apex; hind wings present or absent, if present, hind wings without costal projection. 33

32' Anteronotal protuberance (ANp) of mesothorax not distinctly conical or subconical; ANp often rounded and not projecting dorsally; hind wings, when present, with or without a costal projection 35

33(32) Hind wings absent; abdominal terga II, and often VI, with median dark spot on anterior margin (dark spots occasionally occur on terga II–VI, spots on terga can sometimes be quite faint); abdominal sterna II–VII or II–VI or III–VI usually with distinct single median spot . . . . . ***Iswaeon***

33' Hind wings present or absent; abdominal terga II and VI not marked as above; abdominal sterna with or without distinct single median spots as above indicated above 34

34(33') Male genitalia as in Fig. 13.272, basal segments of male forceps with slight indentations along inner apical margins (inner margins of slide mounted material can appear to be almost straight because of chemical distortion produced by mounting media); terminal segments of forceps inserted off center in the end of segment 2 (Fig. 13.272); inner surface of segment 3 of forceps distinctly concave; hind wing present, but small to minute and usually lacking longitudinal veins (rarely with 2 longitudinal veins in *H. frivolum*) . . . . . ***Heterocloeon***

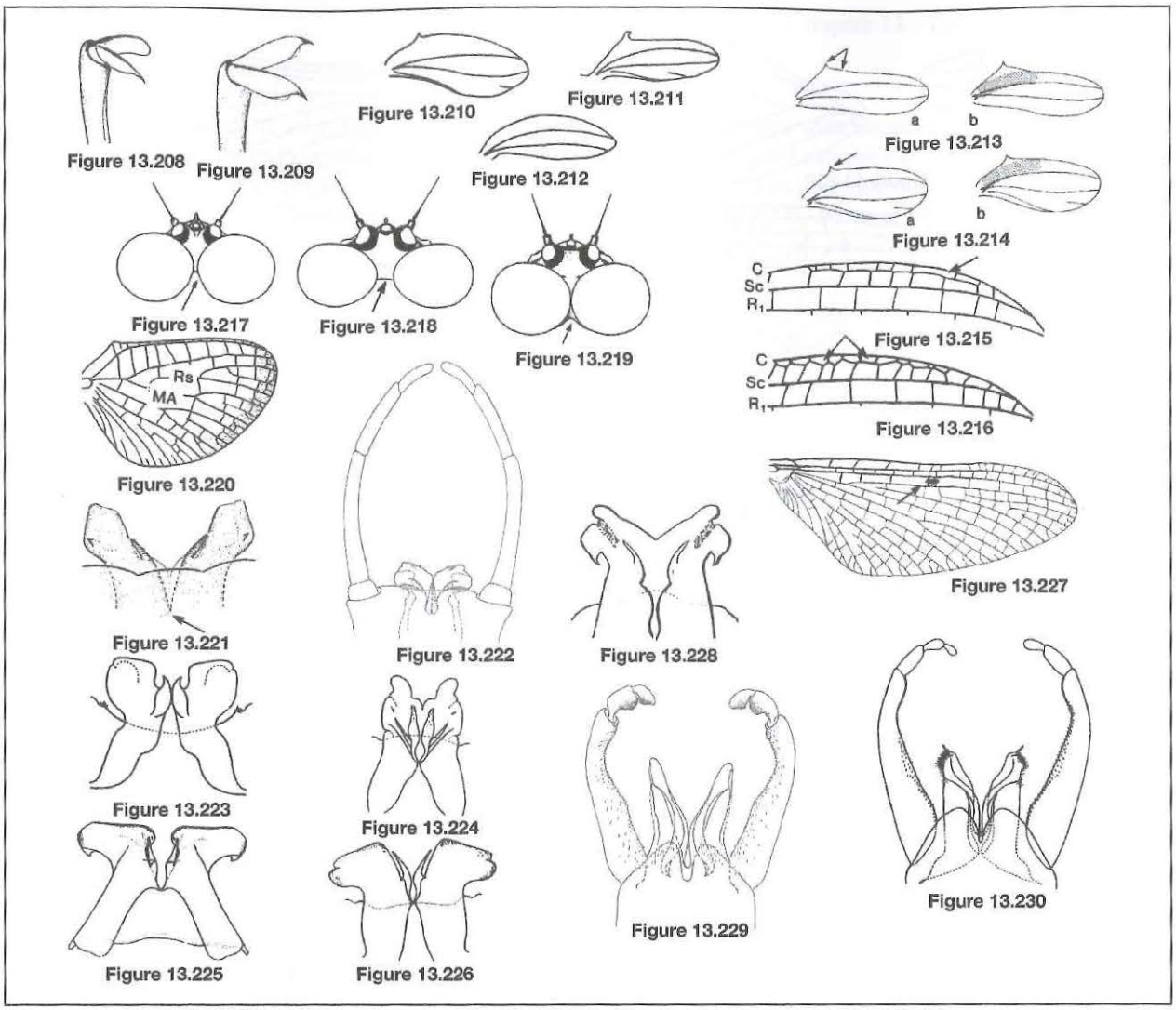


Figure 13.208 Tarsal claws of *Ameletus* sp. (Ameletidae) imago.
Figure 13.209 Tarsal claws of *Siphlonurus* sp. (Siphlonuridae) imago.
Figure 13.210 Hind wing of *Baetis* sp. (Baetidae) imago.
Figure 13.211 Hind wing of *Fallceon quilleri* (Baetidae) imago.
Figure 13.212 Hind wing of *Labiobaetis* sp. (Baetidae), imago.
Figure 13.213 Hind wing (a, b) of *Camelobaetidius* sp. (Baetidae) imago. Shaded arc on 13.213b shows shape of base of costal projection and adjacent wing margin.
Figure 13.214 Hind wing (a, b) of *Baetis* sp. (Baetidae) imago. Shaded arc on 13.214b shows shape of base of costal projection and adjacent wing margin.
Figure 13.215 Forewing stigmatic area of *Cinygma* sp. (Heptageniidae) imago.
Figure 13.216 Forewing stigmatic area of *Rhithrogena* sp. (Heptageniidae) imago.
Figure 13.217 Dorsal view of head of *Epeorus* (*Ironopsis*) sp. male imago (Heptageniidae), arrow indicates narrow space between compound eyes.
Figure 13.218 Dorsal view of head of *Ironodes* sp. male imago (Heptageniidae), arrow indicates wide space between compound eyes.
Figure 13.219 Dorsal view of head of *Epeorus* (*Iron*) sp. male imago (Heptageniidae), arrow indicates contiguous position of compound eyes.
Figure 13.220 Hind wing of *Stenonema* sp. (Heptageniidae) imago.
Figure 13.221 Penes of *Cinygmula* sp. male imago (Heptageniidae), arrow indicates split between penes almost to base.
Figure 13.222 Ventral view of male genitalia of *Afghanurus* sp. (Heptageniidae).
Figure 13.223 Penes of *Macdunnoa* sp. (Heptageniidae) male imago.
Figure 13.224 Penes of *Afghanurus* sp. (Heptageniidae) male imago.
Figure 13.225 Penes of *Stenonema femoratum* (Heptageniidae) male imago.
Figure 13.226 Penes of *Stenonema* sp. (Heptageniidae) male imago.
Figure 13.227 Forewing of *Stenacron* sp. (Heptageniidae) male imago. Arrow indicates dark spot in wing membrane spanning crossveins below bullae.
Figure 13.228 Penes of *Epeorus* (*Iron*) sp. (Heptageniidae) male imago.
Figure 13.229 Penes of *Leptophlebia* sp. (Leptophlebiidae) male imago.
Figure 13.230 Penes of *Leptophlebia* sp. (Leptophlebiidae) male imago.

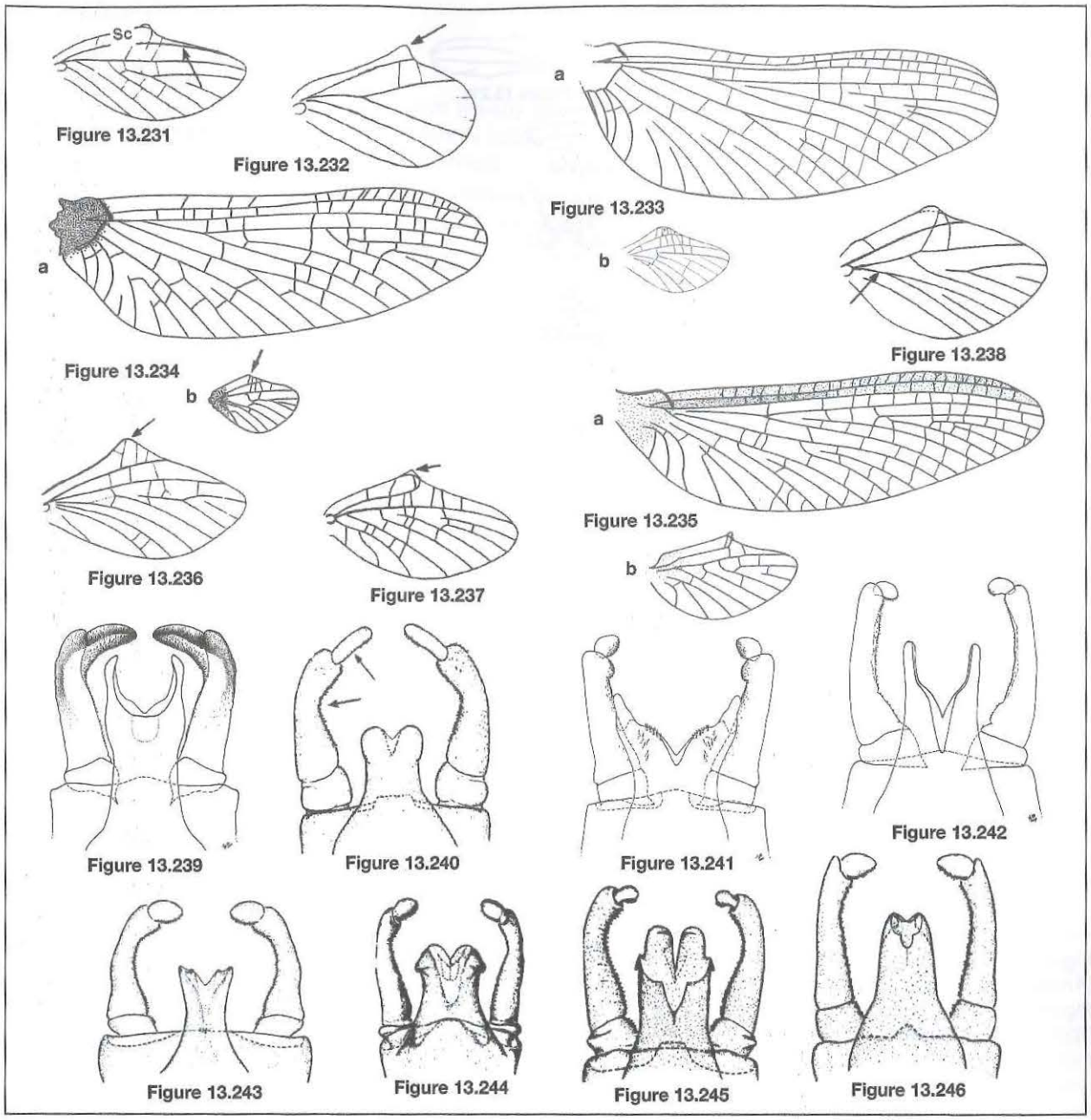


Figure 13.231 Hind wing of *Habrophlebia vibrans* (Leptophlebiidae) imago, arrow indicates terminus of vein Sc.

Figure 13.232 Hind wing of *Habrophlebiodes americana* (Leptophlebiidae) imago, arrow indicates distal position of costal projection.

Figure 13.233 Forewing (a) and hind wing (b) of *Neochoroterpes* sp. (Leptophlebiidae).

Figure 13.234 Forewing (a) and hind wing (b) of *Choroterpes* sp. (Leptophlebiidae), arrow indicates terminus of vein Sc.

Figure 13.235 Forewing (a) and hind wing (b) of *Hydrosmilodon* sp. (Leptophlebiidae).

Figure 13.236 Hind wing of *Choroterpes* sp. (Leptophlebiidae) imago, arrow indicates position of costal projection.

Figure 13.237 Hind wing of *Traverella* sp. (Leptophlebiidae) imago, arrow indicates acute costal projection.

Figure 13.238 Hind wing of *Thraulodes* sp. (Leptophlebiidae) imago, arrow indicates vein MP fork.

Figure 13.239 Dorsal view of male genitalia of *Tsalia berneri* (Ephemerellidae).

Figure 13.240 Male genitalia of *Drunella cornutella* (Ephemerellidae).

Figure 13.241 Male genitalia of *Ephemerella aurivillii* (Ephemerellidae).

Figure 13.242 Male genitalia of *Ephemerella needhami* (Ephemerellidae).

Figure 13.243 Male genitalia of *Ephemerella maculata* (Ephemerellidae).

Figure 13.244 Male genitalia of *Serratella levis* (Ephemerellidae).

Figure 13.245 Male genitalia of *Serratella serratoides* (Ephemerellidae).

Figure 13.246 Male genitalia of *Eurylophella lutulenta* (Ephemerellidae).

34' Male genitalia as in Fig. 13.273, basal segments of male forceps with broad distinct indentation on the inner margins (inner margins of slide mounted material can appear to have only a slight indentation because of chemical distortion produced by mounting media); terminal segments of forceps inserted in the center of the end of segment 2 (Fig. 13.273); inner surface of segment 3 of forceps not concave; hind wings present or absent, when present usually with only 2 longitudinal veins; . . . . . ***Acentrella***

35(32') Hind wings present in all known North American species; hind wings without costal projection (Fig. 13.212) or with greatly reduced costal projection; terminal segment of male forceps small and rounded . . . . . ***Labiobaetis***

35' Hind wings present or absent; if present, hind wings with distinct costal projection; terminal segment of male forceps variable 36

36(35') Hind wings present with costal projections (Fig. 13.211) hooked or straight; margins of hind wings distal of costal projections not modified (i.e., not elevated); terminal segment of male forceps elongate in North American species, at least half as long as preceding segment; bi-lobed process present between bases of male forceps (*Fallceon thermophilos* seems to be the one critical exception with hind wings having broad based costal projections producing modified, or slightly elevated, wing margins distal of costal projections and lacks the bi-lobed process between bases of forceps). . . . . ***Fallceon***

36' Hind wings present or absent, if present, costal projections acute and not hooked (only rarely appearing slightly curved); terminal segment of male forceps variable; bi-lobed process absent 37

37(36') Prominent coniform penes cover present between forceps bases, extending nearly two-thirds length of forceps bases; male compound eyes nearly contiguous posteriorly and widely divergent anteriorly (when viewed dorsally); hind wings absent in all known North American species; rare . . . . . ***Apobaetis***

37' Penes cover reduced to a low rectangular mass or absent; male compound eyes variable; hind wings present or absent 38

38(37') Hind wings with second longitudinal vein forked (Fig. 13.257), vertex of fork proximad and toward wing base; terminal segment of male forceps elongate . . . . . ***Diphetor hageni***

38' Hind wings present or absent, if present, hind wings with second vein simple, or if forked, vertex of fork occurs distally beyond middle of hind wing (some individuals of *Baetis magnus* and *B. diablis* may key here, with small round terminal segments of the forceps) 39

39(38') Hind wings present; costal projections acute and prominent (similar to Fig. 13.213a,b, but with curved anterior margin preceding costal projections); margins of hind wings distal of costal projection modified, or slightly elevated (sometimes described as "undulate"); terminal segment of male forceps about four times as long as wide. . . . . ***Acerpenna***

39' Hind wings present or absent, if present costal projections variable, not as acute or prominent as above; terminal segment of male forceps variable. 40

40(39') Male forceps with distinct mesal projections on segment 1 (Figs. 13.258 and 13.259) 41

40' Male forceps without distinct mesal projections as above or with a slight bulge at the position where mesal projections would occur (Fig. 13.264). 42

41(40) Hind wings present with two or three veins and costal projections (Fig. 13.260); forewings with brown shading around discal crossveins (Fig. 13.260); male genitalia as in Fig. 13.259. . . . . ***Moribaetis***

41' Hind wings absent or vestigial; forewings with brown shading restricted to costal and subcostal areas; male genitalia as in Fig. 13.258 . . . . . ***Baetodes***

42(40') Hind wings present . . . . . ***Baetis*** (in part)

42' Hind wings absent or if present small, slender with only two longitudinal veins 43

43(42') Small species, forewing length 2.5–4.5 mm; length of terminal segment of male forceps greater than or equal to two times its width; male genitalia without small rectangular plate between forceps bases. 44

43' Larger species, forewing length usually greater than 4.0 mm; terminal segment of male genitalia not elongate, only about as wide as long; male genitalia usually with small rectangular plate between forceps bases 45

44(43) Basal segment of male forceps large and cylindrical (Fig. 13.262), length of terminal segment of male forceps 2.5 to 3.0 times it's width; hind wings absent in known North American species, but adventive Neotropical species may occur in Mexico and U.S. Southwest that may have small slender hind wings with 2 longitudinal veins . . . . . ***Paracloeodes***

44' Basal segment of male forceps large with sides tapering toward base of segment 2 (Fig. 13.261); length of terminal segment of male forceps only about 2.5 times its width; hind wings absent . . . . . ***Americabaetis***

45(43') Segment 2 of male forceps with distinct inner bulge (Fig. 13.263). . . . . ***Cloeodes***

45' Segment 2 of male forceps without distinct inner bulge. 46

46(45') Male forceps strongly curved (Fig. 13.264); male genitalia with small rectangular or trapezoidal plate between forceps bases (after preservation rectangular plate may be withdraw and not visible); abdominal terga III and IV strongly pigmented with red medially, terga V and VI lightly washed in red (intensity of red pigment fades rapidly after preservation) . . . . . ***Plauditus***

46' Male forceps not strongly curved as above; rectangular plate between forceps bases usually absent (plate present in members of *fuscatus* species group, but shape variable); abdominal terga not pigmented as above . . . . . ***Baetis*** (in part)

47(1) Three caudal filaments present . . . . . ***Homoeoneuria***

47' Two caudal filaments (cerci) present . . . . . ***Lachlania***

48(16') Stigmatic area of forewings divided by a thin, more or less straight vein into two series of small cells (Fig. 13.215). . . . . ***HEPTAGENIIDAE*** (in part).... ***Cinygma***

48' Stigmatic area with simple or anastomosed crossveins or divided by an irregular vein into two series of small cells, but not as above (Fig. 13.216) 49

49(48') Vein MA of hind wings simple, unforked; uncommon. . . . . ***ARTHROPLEIDAE*** . . . . . ***Arthroplea bipunctata***

49' Vein MA of hind wings forked (Fig. 13.220) (females not keyed beyond this couplet) . . . . . ***HEPTAGENIIDAE*** (in part).....50

50(49') Male foretarsi one-half to three-fourths the length of foretibiae; male genitalia as in Figs. 13.265–13.266 51

50' Male foretarsi longer than foretibiae; male genitalia not as above 52

51(50) Male compound eyes widely separated (Fig. 13.268); margin of frontal shelf straight, with middle not produced ventrally; male genitalia with lateral margins of penes expanded apically (Fig. 13.266); rare . . . . . ***Spinadis simplex***

51' Male compound eyes almost meeting dorsally (Fig. 13.270); middle of frontal shelf distinctly produced ventrally; male genitalia with lateral margins of penes not apically expanded (Fig. 13.265); rare . . . . . ***Anepeorus rusticus***

52(50') Penes of male genitalia as in Fig. 13.267; forewing longitudinal veins brownish, crossveins dark; rare. . . . . ***Raptoheptagenia cruentata***

52' Penes of male genitalia not as above; venation variable 53

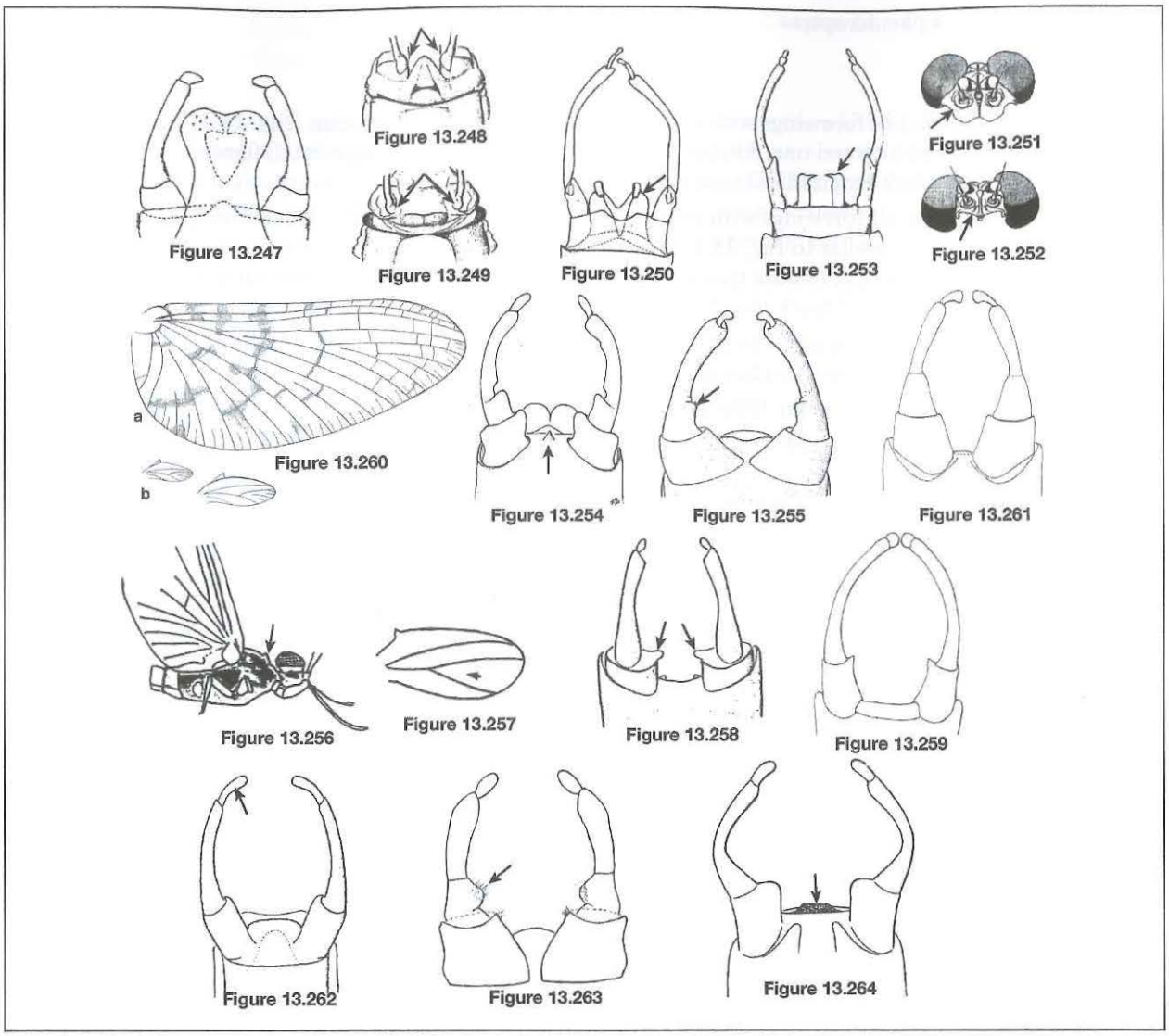


Figure 13.247 Dorsal view of male genitalia of *Dannella simplex* (Ephemerellidae).
Figure 13.248 Ventral view of pronotum of *Caenis* sp. (Caenidae) imago, arrows indicate position of forecoxae.
Figure 13.249 Ventral view of pronotum of *Brachycercus* sp. (Caenidae) imago, arrows indicate position of forecoxae.
Figure 13.250 Male genitalia of *Litobrancha recurvata* (Ephemeridae), arrow indicates ventrally curved tips of penes.
Figure 13.251 Anterior view of head of *Litobrancha recurvata* (Ephemeridae) male imago, arrow indicates edge of frons.
Figure 13.252 Anterior view of head of *Hexagenia limbata* (Ephemeridae) male imago, arrow indicates edge of frons.
Figure 13.253 Male genitalia of *Hexagenia* sp. (Ephemeridae), arrows indicate medially curved tips of penes.
Figure 13.254 Ventral view of male genitalia, *Anafroptilum ozarkense* (Baetidae), arrow indicates medial spine-like process between forceps bases.
Figure 13.255 Ventral view of male genitalia, *Pseudocentroptiloides* sp. (Baetidae), arrow indicates bulge on inner margin of forcep.
Figure 13.256 Right lateral view of head and thorax of *Acentrella* sp. (Baetidae) male imago. Arrow indicates conical ANp.
Figure 13.257 Hind wing of *Diphetor* sp. (Baetidae) imago, arrow indicates forked second vein.
Figure 13.258 Ventral view of male genitalia of *Baetodes* sp. (Baetidae), arrows indicates medial projections on basal segment of forceps.
Figure 13.259 Ventral view of male genitalia of *Moribaetis* sp. (Baetidae).
Figure 13.260 Forewing (a) and hind wing (b) of *Moribaetis* sp. (Baetidae) with enlarged view of hind wing.
Figure 13.261 Ventral view of male genitalia of *Americabaetis* sp. (Baetidae).
Figure 13.262 Ventral view of male genitalia of *Paracloeodes minutus* (Baetidae), arrow indicates elongate apical segment of forceps.
Figure 13.263 Ventral view of male genitalia of *Cloeodes* sp. (Baetidae), arrow indicates bulge on base of segment 2 of forcep.
Figure 13.264 Ventral view of male genitalia of *Plauditus cestus* (Baetidae), arrow indicates sclerotized plate between forceps bases.

53(52') Stigmatic areas of forewings with two to many anastomosing crossveins (Fig. 13.216); segment 1 of foretarsi one-third or less than one-third length of segment 2; femora often with dark longitudinal streak or median spot. . . . . ***Rhithrogena***

53' Stigmatic areas of forewings with or without anastomosing crossveins; if crossveins anastomosed (similar to Fig. 13.216) then segment 1 of foretarsi half or more than half length of segment 2; femora usually without dark longitudinal streak (but variably shaped dark medial mark may be present). 54

54(53) Segment 1 of foretarsi equal to or slightly longer than segment 2 (*Epeorus frisoni* has segment 1 slightly shorter than segment 2). 55

54' Segment 1 of foretarsi four-fifths to less than four-fifths the length of segment 2 56

55(54) Male compound eyes separated dorsally by more than width of median ocellus (Fig. 13.218); basal costal crossveins of forewings strongly developed, attached anteriorly to costa; uncommon. . . . . ***Ironodes***

55' Male compound eyes contiguous dorsally (Fig. 13.219) or separated by no more than width of median ocellus (Fig. 13.217); basal costal crossveins of forewings weakly developed, apparently detached anteriorly from costa . . . . . ***Epeorus***

56(54') Penis lobes of male genitalia separated or appearing separated medially almost to base (Fig. 13.221); segment 1 of male foretarsi usually two-thirds or more than two-thirds length of segment 2 . . . . . ***Cinygmula***

56' Penis lobes of male genitalia fused medially, at least in basal half (Figs. 13.223–13.226); segment 1 of foretarsi two-thirds or less than two-thirds length of segment 2, usually less than half length of segment 2 57

57(56') Forewings with two to three crossveins below bullae (between veins R_1 and R_2) connected or nearly connected by dark spot (Fig. 13.227), rarely only a dark spot present in membrane; basal crossveins between veins R_1 and R_2 with dark margins . . . . . ***Stenacron***

57' Forewings may have crossveins below bullae darkened or slightly clouded, but never as above; crossveins between R_1 and R_2 rarely with dark margins 58

58(57') Penes of male genitalia distinctly L-shaped (Figs. 13.225, 13.226); segment 1 of foretarsi usually one-third to two-thirds the length of segment 2 59

58' Penes of male genitalia not distinctly L-shaped (Figs. 13.223, 13.224); segment 1 of foretarsi usually one-fifth to one-half the length of segment 2 60

59(58) Posterior margins of abdominal terga III–VIII with dark median dot and lateral transverse submedian dashes; male penes as in Fig. 13.225. . . . . ***Stenonema femoratum***

59' Posterior margins of abdominal terga III–VIII variable, but not marked as above; male penes as in Fig. 13.226 . . . . . ***Stenonema*** (all other species)*

60(58') Compound eyes of male contiguous on vertex (similar to Fig. 13.219) or separated by less than the width of the median ocellus; male genitalia as in Figs. 13.222, 13.224; basal costal crossveins of forewings weakly developed. . . . . ***Afghanurus***

60' Compound eyes of male separated dorsally by at least the width of one lateral ocellus; male genitalia not as above; basal costal crossveins of forewings well-developed 61

61(60') Compound eyes of male separated by little more than diameter of one lateral ocellus (similar to Fig. 13.218); penes of male genitalia with large dorsolateral spines, discal spines absent . . . . . ***Heptagenia***

61' Compound eyes of male separated by three to five times the width of median ocellus; male genitalia not as above. 62

62(61') Compound eyes of male separated on vertex by about the width of one compound eye; median titillators of male genitalia slender; penes of male genitalia with large dorsolateral spines and discal spines; crossveins between veins C and Sc usually margined with brown . . . . . ***Leucrocuta***

*Recent molecular studies have reduced *Maccaffertium* to a subgenus of *Stenonema* and reassigned all its species to *Stenonema*. See citation in footnote on Page 269.

62' Compound eyes of male separated by width of four to five times the width of median ocellus; median titillators of male genitalia thick and abruptly narrowed apically; penes of male genitalia without discal spines or ridges (Fig. 13.223); crossveins of anterior half of male forewings tan to black, in female forewings crossveins pale brown or not colored, but none margined with color in either sex; rare. . . . . ***Macdunnoa***

63(17) Forewings with one pair of cubital intercalary veins present (Fig. 13.187); boreal distribution. . . . . ***Metretopus***

63' Forewings with two pairs of cubital intercalary veins present (Fig. 13.186); widespread. . . . . ***Siphloplecton***

64(13') Hind wings without costal projections (Fig. 13.183b) 65

64' Hind wings with distinct costal projections (Figs. 13.231–13.232, 13.236–13.238). 67

65(64) Penes of male genitalia with long, decurrent appendages (Figs. 13.229, 13.230); caudal filaments with terminal filament often shorter and thinner than cerci . . . . . ***Leptophlebia***

65' Penes of male genitalia variable (Figs. 13.281–13.283), not as above; all caudal filaments subequal. 66

66(65') Male genitalia with at least one pair of appendages that arise from ventral apices of penes and are more or less directed toward their fused base (Fig.13.281) . . . . . ***Paraleptophlebia***

66' Male genitalia with a wide range of apical appendages or processes that may stick out from apices of penes (Figs.13.282–13.283), but none that are distinctly directed toward their fused base as above . . . . . ***Neoleptophlebia***

67(64') Coastal projections of hind wings in distal half of wing margin (Fig. 13.232); uncommon . . . . . ***Habrophlebiodes***

67' Costal projections of hind wings near midpoint of wing margin (Figs. 13.231, 13.236–13. 238) 68

68(67') Vein Sc of hind wings extends well beyond costal projection (Fig. 13.231); uncommon . . . . . ***Habrophlebia***

68' Vein Sc of hind wings ends at or slightly beyond costal projection (Figs. 13.236–13.238) 69

69(68') Vein MP of hind wings forked (Fig. 13.238); uncommon . . . . . ***Thraulodes***

69' Vein MP of hind wings simple, unforked (Figs. 13.236, 13.237) 70

70(69') Costal projections of hind wings rounded (Fig. 13.236) 71

70' Costal projections of hind wings acute (Figs. 13.237, 13.269) 73

71(70) Vein MP_2 of forewings directly connected to vein MP_1 (Figs. 13.234, 13.235); posterior margin of female subanal plate with shallow median indentation. 72

71' Vein MP_2 of forewings not directly connected to vein MP_1 (Fig. 13.233); posterior margin of female subanal plate with distinctive deep median indentation . . . . . ***Neochoroterpes***

72(70) Vein Sc of hind wings straight where it meets wing margin beyond base of costal projections (Fig. 13.234); costal projections without small rounded apical lobe . . . . . ***Choroterpes***

72' Vein Sc of hind wings curved where it meets wing margin at base of costal projections (Fig. 13.235); costal projections with small rounded apical lobe (Fig. 13.235) . . . . . ***Hydrosmilodon***

73(70') Hind wings with eight or more longitudinal veins and twelve or more crossveins (Fig. 13.237); penes of male genitalia with a thin process arising near apex of each lobe and with tips directed inward and down toward fused base of penes . . . . . ***Traverella***

73' Hind wings with seven or fewer longitudinal veins and about three crossveins (Fig. 13.269); penes of male genitalia with short lateral process near apex of each lobe (Fig. 13.271) . . . . . ***Farrodes***

74(13) Imago and subimago with vestiges of gill sockets on abdominal segment III; eggs with one polar cap and usually somewhat smooth chorion (eggs of *Caurinella* have hexagonal pattern on surface) 75

74' Imago and subimago lack vestiges of gill sockets on abdominal segment III; eggs either lack polar caps or have two polar caps or if eggs have one polar cap then egg chorion is reticulate 83

75(74) Cerci one-fourth to three-fourths as long as terminal filament . . . . . ***Caudatella***

75' Cerci and terminal filament subequal in length (females not keyed beyond this couplet) 76

76(75') Terminal segment of male forceps more than two times as long as wide; inner margin of segment 2 of male forceps distinctly curved (Fig. 13.240) or strongly bowed . . . . . ***Drunella***

76' Terminal segment of male forceps not as above, shorter than twice its width (Fig. 13.246); inner margin of segment 2 of male forceps variable, but not strongly curved or bowed 77

77(76') Apical segment of male forceps articulated with second segment as in Fig. 13.239; penes of male genitalia with broad U-shaped median cleft; uncommon. . . . . ***Tsalia berneri***

77' Apical segment male forceps not as above (Figs. 13.241–13.242, 13.274–13.278). 78

78(77') Penes of male genitalia with long apical projections and stout spine-like setae along edge of median cleft (Fig. 13.274) . . . . . ***Penelomax septentrionalis***

78' Penes of male genitalia not as above. 79

79(78') Penes of male genitalia usually with acute lateral subapical projections (Figs. 13.244, 13.245), *Teloganopsis deficiens* and *Serratella frisoni* are exceptions with rounded or blunt subapical projections as in Fig. 13.275; segment 2 of male forceps can appear twisted or creased; segment 2 of male forceps without notch or cut-out for base of apical segment (Figs. 13.244, 13.245, 13.275) 80

79' Penes of male genitalia without subapical projections as above; segment 2 of male forceps may appear dorsoventrally compressed, but not twisted or creased; segment 2 of male forceps may have apical notch or cut-out to accommodate the base of apical segment. 81

80(79) Penes of male genitalia usually with acute subapical projections (Figs. 13.244, 13.245); segment 2 of male forceps appears twisted or creased . . . . . ***Serratella***

80' Penes of male genitalia with rounded subapical projections (Fig. 13.275); segment 2 of male forceps not as above with a round or subcylindrical cross section, but not twisted or creased . . . . . ***Teloganopsis deficiens***

81(79') Penes of male with dorsal and/or ventral spines and shaped as in Figs. 13.241, 13.243, 13.276–13.278 with apical portion distinctly expanded or lack dorsal and ventral spines with divergent tips as in Fig. 13.279 or lack dorsal and ventral spines with narrow elongate processes as in Fig. 13.242 . . . . . ***Ephemerella***

81' Penes of male genitalia not as above, more compact and without dorsal and/or ventral spines 82

82(81') Penes of male genitalia as in Fig. 13.280 with slightly flared apex, dorsal median excavation, and paired rough medial surfaces; apex of penes with ventral lateral indentions; apex of penes flexed dorsally (most obvious when viewed laterally); apices of segment 2 of male forceps distinctly indented or notched at joint with apical segment; apical segment of forceps more than two times as long as wide. . . . . ***Matriella teresa***

82' Penes of male genitalia not as above, apical portion slightly enlarged with a small median notch (details of dorsal surface of penes unknown); apices of segment 2 of

male forceps not indented or notched at joint with apical segment; apical segment of forceps only about two times as wide as long . . . . . ***Caurinella idahoensis***

83(74') Abdominal segments VI and VII of imago and subimago with poorly developed finger-like remnants of posterolateral projections; remnant gill socket on abdominal segment IV visible, but poorly developed; apical segment of male forceps distinctly elongate, about six times as long as wide; eggs without polar caps and with somewhat smooth chorion . . . . . ***Attenella***

83' Abdominal segment VII and often preceding segments of imago and subimago with well-developed finger-like remnants of posterolateral projections; remnant gill socket on abdominal segment IV relatively well-developed; apical segment of male forceps relatively short, length always less than three times the width; eggs with reticulate chorion and either have one or two polar caps or lack polar caps 84

84(83') Penes of male genitalia broadest at base, narrowing apically (Fig. 13.246); eggs without polar caps. . . . . ***Eurylophella***

84' Penes of male genitalia with apex laterally expanded with middle and base somewhat narrower than apex (Fig. 13.247); eggs with polar caps 85

85(84') Penes of male genitalia with long lateral apical lobes . . . . . ***Timpanoga***

85' Penes of male genitalia with short, rounded apical lobes (Fig. 13.247) . . . . . ***Dannella***

86(18) Hind wings absent; tarsi five segmented (Fig. 13.197); middle and hind tibiae of male and all tibiae of female with apex extended beyond tibial-tarsal joint (Fig. 13.197); male genitalia as in Figs 13.202 and 13.203 . . . . . ***Tricorythodes***

86' Hind wings present in males and absent or present in females; tarsi four segmented (Fig. 13.198); middle and hind tibiae of males and all tibiae of females with apex not extended beyond tibial-tarsal joint (Fig. 13.198); male genitalia not as above 87

87(86') Penes of male genitalia Y-shaped with long well-separated apical lobes with small incisions (Fig. 13.204a); foretibiae of known males heavily armored with sharp, stout setae ventrally; posterior margin of female subanal plate broadly rounded (Fig. 13.204b) . . . . . ***Leptohyphes***

87' Penes of male genitalia with apically separated lobes, but not distinctly Y-shaped (Figs. 13.205, 13.206); foretibiae of males without sharp, stout ventral setae; posterior margin of female subanal plate slightly concave (Fig. 13.205b) 88

88(87') Male terminal filament with large ventrally directed spine (Fig. 13.207); male genitalia as in Fig. 13.205a . . . . . ***Allenhyphes***

88' Male terminal filament without large ventral spine as above; male genitalia as in Fig. 13.206. . . . . ***Vacupernius packeri***

89(18') Prosternum half as long as wide and rectangular in shape; forecoxae widely separated, when viewed across venter of prothorax (Fig. 13.249); uncommon 90

89' Prosternum two to three times as long as wide and triangular in shape; forecoxae close together, when viewed across venter of prothorax (Fig. 13.248); (for positive genus determination must use species key in Provonsha, 1990) . . . . . ***Americaenis, Caenis***

90(89) Prosternum with a distinct tubercle 91

90' Prosternum without a distinct tubercle. 92

91(90) Pedicels of antennae more than 1.5 times longer than scapes (Fig. 13.199) . . . . . ***Susperatus***

91' Pedicels of antennae either only slightly longer than scapes (Fig. 13.200) or not more than 1.5 times the length of the scapes . . . . . ***Cercobrachys****

*—Adult of genus *Latineosus* is unknown and may key to this point in this key

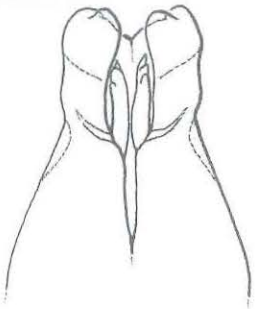


Figure 13.265

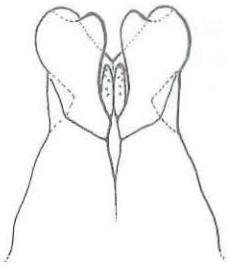


Figure 13.266

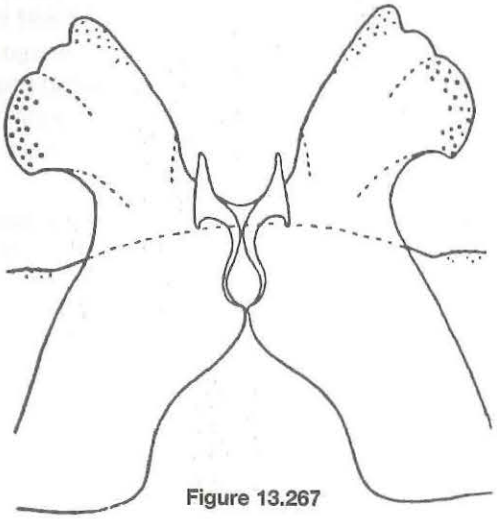


Figure 13.267

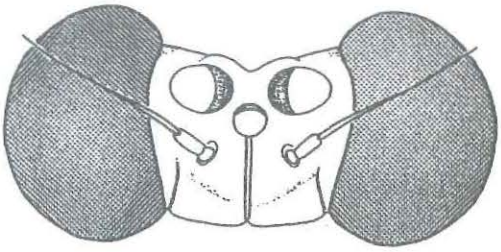


Figure 13.268

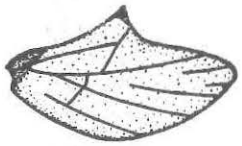


Figure 13.269

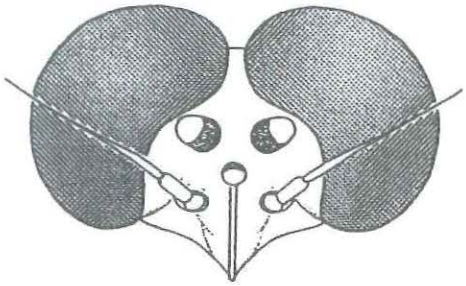


Figure 13.270

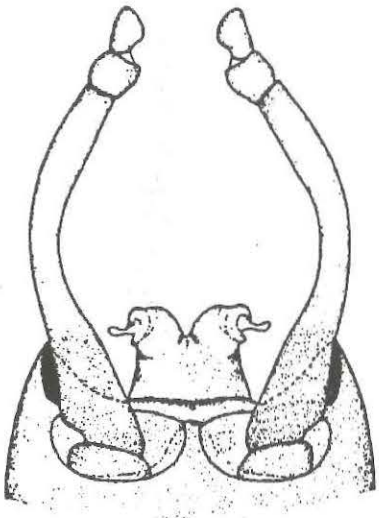


Figure 13.271

Figure 13.265 Ventral view of male genitalia of *Anepeorus rusticus* (Heptageniidae).
Figure 13.266 Ventral view of male genitalia of *Spinadis simplex* (Heptageniidae).
Figure 13.267 Dorsal view of male penes of *Raptoheptagenia cruentata* (Heptageniidae).
Figure 13.268 Frontal view of head of *Spinadis simplex* (Heptageniidae) male imago.
Figure 13.269 Hind wing of *Farrodes texanus* (Leptophlebiidae) imago.
Figure 13.270 Frontal view of head of *Anepeorus rusticus* (Heptageniidae) male imago.
Figure 13.271 Ventral view of male genitalia of *Farrodes texanus* (Leptophlebiidae).

92(90') Occipital of head with one or two dark transverse bands posterior to lateral occelli (Fig. 13.201) ..... ***Sparbarus***

92' Occipital of head lacks dark transverse bands as above ..... ***Brachycercus***

93(7') Pronotum of males and females large, but not more than twice as wide as long (Fig. 13.173); shape of pronotum varies from trapezoidal to rectangular; penes of male genitalia variable, ranging from hooked or beak-like processes to straight and tapering (Figs. 13.250, 13.253), but not long and tubular; caudal filaments of female longer than body ..... ***EPHEMERIDAE***.....94

93' Pronotum of males and females short, about three times as wide as long (Fig. 13.174); penes of male genitalia long and tubular (Fig. 13.172); caudal filaments of female shorter than body; large rivers ..... ***PALINGENIIDAE***...***Pentagenia***

94(93) Crossveins of forewings near bullae crowded together (Fig. 13.168a); forewings, and sometimes hind wings, with distinct pattern of dark markings (Fig. 13.168a); length of terminal filament subequal to cerci ..... ***Ephemera***

94' Crossveins of forewings near bullae not crowded together; fore- and hind wings without pattern of dark markings as above, but crossveins may be darkened or membranes of wings may be tinted amber or purplish-brown; terminal filament vestigial or distinctly shorter than cerci 95

95(94') Head with frons greatly expanded below compound eyes (Fig. 13.251); penes of male genitalia recurved ventrally (Fig. 13.250); membranes of wings tinted amber or purplish brown; uncommon ..... ***Litobrancha recurvata***

95' Head with frons not extending below compound eyes (Fig. 13.252); penes of male genitalia not recurved as above, but may be hooked or curved medially (e.g., Fig. 13.253); membranes of fore- and hind wings transparent or occasionally slightly tinted yellow ..... ***Hexagenia***

96(5) Outer margin of forewings with dense network of small reticulate veins (Fig. 13.166) ..... ***Ephoron***

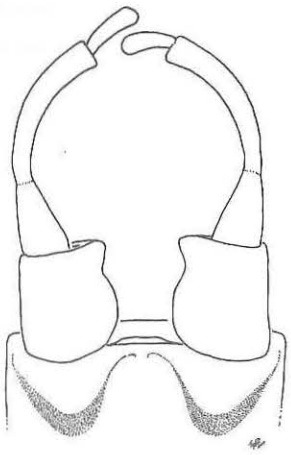
96' Outer margin of forewings without dense network of small reticulate veins, wing margins with few or no small veins 97

97(96') Middle and hind legs present in both sexes, but reduced and shriveled 98

97' Middle and hind legs of males greatly reduced to stubs, legs terminate with blade-like femora; females lack legs; uncommon ..... ***Campsurus***

98(97) Male abdominal sternite IX divided longitudinally by median groove or furrow separating sternite IX into two sclerous plates ..... ***Tortopus***

98' Male abdominal sternite IX solid, not divided by median groove as above ..... ***Tortopsis***



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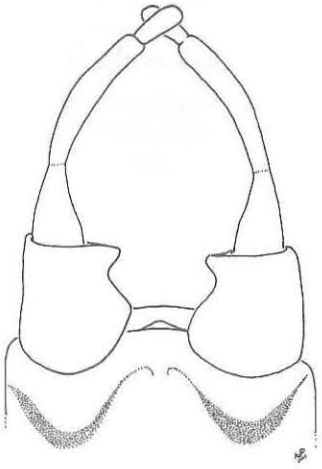


Figure 13.273

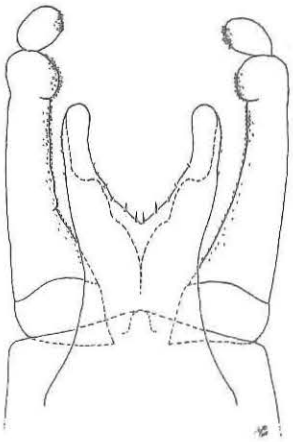


Figure 13.274

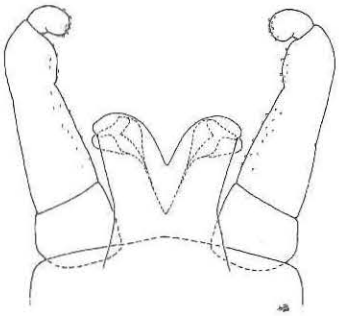


Figure 13.275

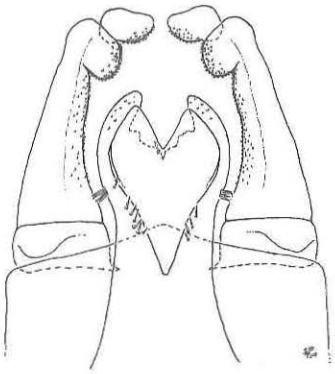


Figure 13.276

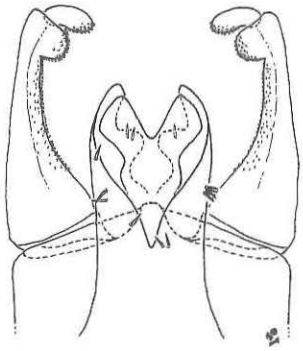


Figure 13.277

Figure 13.272 Ventral view of intact male genitalia of *Heterocloeon curiosum* (Baetidae).
Figure 13.273 Ventral view of intact male genitalia of *Acentrella turbida* (Baetidae).
Figure 13.274 Dorsal view of male genitalia of *Penelomax septentrionalis* (Ephemerellidae).
Figure 13.275 Dorsal view of male genitalia of *Teloganopsis deficiens* (Ephemerellidae).
Figure 13.276 Dorsal view of male genitalia of *Ephemerella subvaria* (Ephemerellidae).
Figure 13.277 Dorsal view of male genitalia of *Ephemerella invaria* (Ephemerellidae).

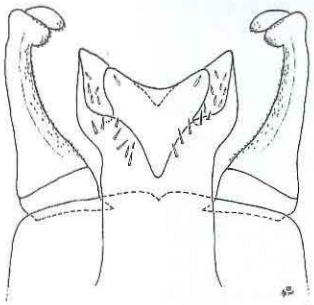
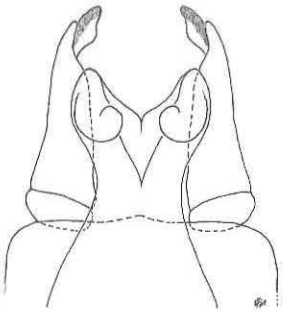


Figure 13.278



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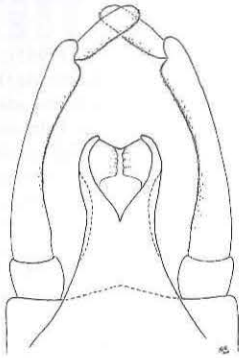

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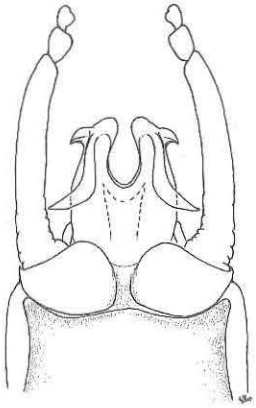

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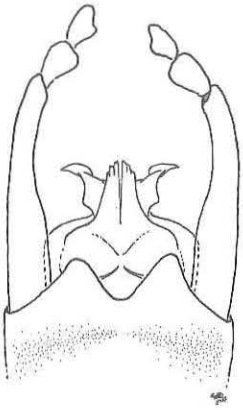

Figure 13.282

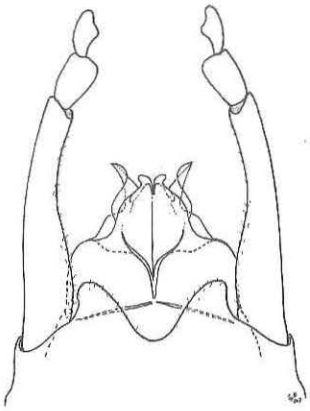

Figure 13.283

Figure 13.278 Dorsal view of male genitalia of *Ephemerella dorothea* (Ephemerellidae).
Figure 13.279 Dorsal view of male genitalia of *Ephemerella tibialis* (Ephemerellidae).
Figure 13.280 Dorsal view of male genitalia of *Matriella teresa* (Ephemerellidae).
Figure 13.281 Ventral view of male genitalia of *Paraleptophlebia strigula* (Leptophlebiidae).
Figure 13.282 Ventral view of male genitalia of *Neoleptophlebia mollis* (Leptophlebiidae).
Figure 13.283 Ventral view of male genitalia of *Neoleptophlebia adoptive* (Leptophlebiidae).

ADDITIONAL TAXONOMIC REFERENCES

General

Tillyard (1932); Needham *et al.* (1935); Edmunds and Traver (1954); Day (1956); Edmunds (1959); Koss (1968); Koss and Edmunds (1974); Edmunds *et al.* (1976); Pennak (1978); McCafferty and Edmunds (1979); McCafferty (1981, 1990, 1991a,b); Edmunds and McCafferty (1988); McCafferty *et al.* (1990); Hilsenhoff (1995); McCafferty (1997); Wang *et al.* (1997); McCafferty and Wang (2000); McCafferty and Davis (2001); Thorp and Covich (2001); Ward *et al.* (2002); Kluge (2004); McCafferty (2004); Pescador and Richards (2004); Ogden and Whiting (2005); Domínguez *et al.* (2006); Jacobus and McCafferty (2006, 2008); Sun *et al.* (2006); Taylor and Kennedy (2006); Jacobus *et al.* (2014); and Morse *et al.* (2017).

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Alabama: Kondratieff and Harris (1986).
Alaska: Randolph and McCafferty (2005); Rinella *et al.* (2012).
Arkansas: McCafferty and Provonsha (1978).
Canada: All Provinces and Territories: McCafferty and Randolph (1998).
Connecticut: Burian and Bednarik (1994).
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Illinois: Burks (1953).
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Intermountain West [Detailed records for Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, Wyoming, with supplemental checklists for—Alberta (Canada), British Columbia (Canada), Chihuahua (Mexico), Sonora (Mexico)]: McCafferty *et al.* (2012).
Maine: Burian and Gibbs (1991).
Michigan: Leonard and Leonard (1962).
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Minnesota: Lager *et al.* (1982).
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Nebraska: McCafferty *et al.* (2001).
Nevada: Baumann and Kondratieff (2000).
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New York: Jacobus and McCafferty (2001); Meyers *et al.* (2011).
North Carolina: Beaty *et al.* (2013).
North Dakota: Guenther and McCafferty (2005).
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Tennessee: Long and Kondratieff (1996).
Texas: Baumgardner (1995); Baumgardner *et al.* (1997); Lugo-Ortiz and McCafferty (1995).
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*Klubertanz, T. H. 2016. Mayfly larva of Wisconsin. Coop. Ext. Publ. (G4074), University of Wisconsin, Madison, Madison, WI, viii + 291pp.

Yukon: Harper and Harper (1997).
Yukon and Northwest Territory: Giberson and Burian (2017).

Taxonomic treatments at the family and generic levels

Acanthametropodidae: McCafferty (1991c); McCafferty and Wang (1994a).
Ameletidae: Zloty (1996); Zloty and Pritchard (1997).
Ametropodidae: Allen and Edmunds (1976); McCafferty (2001); Jacobus (2013).
Baetidae: Cohen and Allen (1978); Morihara and McCafferty (1979a, b, c); Waltz and McCafferty (1985, 1987a,b,c,d, 1989, 1996); Waltz *et al.* (1985, 1994); Lowen and Flannagan (1990a,b; 1991); McCafferty and Waltz (1990, 1995); McCafferty *et al.* (1994); Waltz (1994); Lugo-Ortiz and McCafferty (1995); Lugo-Ortiz and McCafferty (1996a); Lugo-Ortiz and McCafferty (1996b); Waltz *et al.* (1996); Wang and McCafferty (1996); McCafferty (1997); Waltz and McCafferty (1997); Lugo-Ortiz and McCafferty (1998a); Lugo-Ortiz and McCafferty (1998b); Lugo-Ortiz and McCafferty (1998c); McCafferty and Lugo-Ortiz (1998); Lugo-Ortiz *et al.* (1999); Waltz and McCafferty (1999); McCafferty and Randolph (2000); McCafferty and Jacobus (2001); Waltz (2002); McCafferty *et al.* (2005); Jacobus and McCafferty (2006); McCafferty *et al.* (2008); Hill *et al.* (2010); Burian and Meyers (2011); McCafferty (2011); Jacobus and Wiersema (2014); Gorski *et al.* (2015).
Baetiscidae: Berner (1955); Berner and Pescador (1980); Pescador and Berner (1981).
Behningiidae: Edmunds and Traver (1959); McCafferty (1975); Hubbard (1994).
Caenidae: Provonsha and McCafferty (1985); Soldan (1986); Provonsha (1990); Burian *et al.* (1997); Sun and McCafferty (2008).
Ephemerellidae: Allen and Edmunds (1959, 1961a, 1961b, 1962a, 1962b, 1963a, 1963b,1965); Allen (1980, 1984); McCafferty (1977, 1985, 1992a); Funk and Sweeney (1995); Funk *et al.* (1988); McCafferty and Wang (1994b); Funk and Sweeney (1994); Jacobus *et al.* (2006); Jacobus and McCafferty (2003); Jacobus and McCafferty (2004a, 2004b); Jacobus and McCafferty (2008); Jacobus (2010).
Ephemeridae: Spieth (1941); McCafferty (1975, 1994).
Heptageniidae: Edmunds and Allen (1964); Lewis (1974); Flowers and Hilsenhoff (1975); Bednarik and McCafferty (1979); Lehmkuhl (1979b); Bednarik and Edmunds (1980); Flowers (1980, 1982); McCafferty and Provonsha (1984, 1985, 1988); Whiting and Lehmkuhl (1987a,b); McCafferty (1990, 1991a,b); McCafferty (2004); Wang and McCafferty (2004); Webb and McCafferty (2008, 2011).
Isonychiidae: Kondratieff and Voshell (1983, 1984); McCafferty (1989).
Leptohyphidae: Allen (1967); Wiersema and McCafferty (2000); Wiersema and McCafferty (2004); Baumgardner (2014).
Leptophlebiidae: Traver and Edmunds (1967); Berner (1975); Peters (1980); McCafferty (1992b); Henry (1993); McCafferty *et al.* (1993); Burian (1995); Burian (2001); Flowers and Dominguez (1992); Tiunova and Kluge (2016).
Metretopodidae: Berner (1978); Klemesten *et al.* (2015).
Neoephemeridae: Berner (1956); Schmude *et al.* (2012); Holland *et al.* (2016).
Oligoneuriidae: Edmunds *et al.* (1958); Edmunds (1961); Pescador and Peters (1980).
Polymitarcyidae: McCafferty (1975); Molineri (2010).
Potamanthidae: McCafferty (1975); McCafferty and Bae (1990, 1992); Bae and McCafferty (1991).
Pseudironidae: Pescador (1985).
Siphlonuridae: Burian (2017).

Table 13A Summary of ecological and distributional data for Ephemeroptera (mayflies). (For definition of terms see Tables 6A–6C; tolerance values are taken from Barbour et al. (1999) and represent either the mean (when the range of values within a region was <= 3) or median (when the range of values within a region was > 3); table prepared by K. W. Cummins, R. W. Merritt, S. K. Burian, R. D. Waltz, and M. B. Berg.)

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
Ephemeroptera - Mayflies													
	Acanthametropodidae (2)												
		Acanthametropus	*pecatonica*	Lotic—depositional (large rivers)	Swimmers; clingers	Predators (engulfers)	Illinois (Rock River), South Carolina, Georgia, Wisconsin						795, 1595
		Analetris	*eximia*	Lotic—depositional (large rivers)	Swimmers; clingers	Predators (engulfers)	Wyoming, Utah, Saskatchewan						1598, 1595, 3476
	Ameletidae (35) - Combmouthed Minnow Mayflies												
		Ameletus (35)		Lotic—erosional and depositional	Swimmers; clingers	Scrapers; collectors—gatherers (detritus, diatoms)	Widespread	2.1	0.0		0.0		201, 202, 1376, 1396, 2124, 2593, 3823, 4240, 4286, 4348, 4602, 5845, 6328, 6336
	Siphlonuridae (25) - Primitive Minnow Mayflies			Generally lentic	Swimmers; climbers	Collectors—gatherers					7.0		1376, 1589, 1590, 1585, 1598, 3179, 3496, 4286, 4599

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Edmundsius	*agilis*	Lotic—erosional (fishless streams)			California mountains						1598
		Parameletus (4)		Lentic—vascular hydrophytes	Swimmers; climbers		West, Ontario, Quebec, Wisconsin, Maine						1598, 5559
		Siphlonisca	*aerodromia*	Lentic—littoral		Predators (engulfers)	Quebec, Newfoundland and Labrador, Maine, New York						2099, 2101, 2100, 2797, 2890
		Siphlonurus (19) (1 recently presumed extinct)		Lentic—littoral (vascular hydrophytes or sediments); lotic—depositional	Swimmers; climbers	Collectors—gatherers; scrapers; predators (engulfers; especially Tanytarsus in pools); shredders—herbivores?	Widespread	2.6	7.0		7.0		691, 1591, 1598, 2124, 3023, 4126, 4286, 4482, 5404, 6208, 3272
	Metretopodidae (9) - Cleft-Footed Minnow Mayflies			Generally lotic—erosional	Generally swimmers; clingers	Generally predators (engulfers); collectors—gatherers							1376, 1590, 1585, 1598, 3496, 4286, 4599
		Metretopus (2)		Lotic—erosional	Swimmers; clingers		Canada, Alaska, upper Midwest, Maine						1598, 2292

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Siphloplecton (7)		Lotic—erosional and depositional; lentic—margins	Swimmers; clingers	Collectors—gatherers	Canada, upper Midwest, Southeast, Northeast	3.1	2.0			2.0	475, 1061
	Baetidae (161) - Small Minnow Mayflies			Generally lotic—erosional and depositional	Generally swimmers; clingers	Generally collectors—gatherers; scrapers					4.0	4.0	201, 861, 1376, 1590, 1585, 1598, 1991, 3179, 3496, 4286, 4393, 4599, 4809, 6370, 1204, 6205
		Acentrella (9)		Lotic—erosional	Swimmers; clingers	Collectors—gatherers	Widespread	3.6			4.0	4.0	
		Acerpenna (3)		Lotic—erosional	Swimmers; clingers	Collectors—gatherers	Widespread	3.7	4.0	1.7		4.0	475, 2890
		Americabaetis (3)		Lotic—erosional	Swimmers; clingers	Collectors—gatherers	Southwestern US						6506
		Anafroptilum (8)		Lotic—depositional	Swimmers; clingers	Collectors—gatherers (detritus, diatoms); facultative scrapers	Widespread	6.3	2.0	2.7	2.0	2.0	1077, 1585, 2124, 4077, 1991, 3373, 4501, †
		Apobaetis (3)		Lotic—depositional (sand)	Swimmers; clingers		California, Colorado, Georgia, Kansas, Texas						1598, 3679

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Baetis (21)		Lotic—erosional and depositional; lentic—littoral, vascular hydrophytes	Swimmers; clingers and climbers at rest	Collectors—gatherers (detritus, diatoms); facultative scrapers	Widespread	1.8-8	5.5	2.8	1-5	6.0	252, 691, 979, 1061, 1140, 1538, 2124, 2770, 3023, 3271, 3670, 4071, 4077, 4119, 4126, 4240, 5348, 5438, 6361, 251, 2019, 3484, 6327, 1174, 3226, 5544, 274, 2165, 3437, 3717, 2292, 4992, 4993, 5379, 1175, 208, 1455, 2566, 201, 202, 4602, 6594, 1396, 2801, 3223, 4500, 4695, 4857, 5377, 6328, 2027, 2768, 6413, 6530, 6774, 6492, 3384, 4070
		Baetodes (16)		Lotic—erosional	Clingers	Scrapers	Texas, Arizona, Oklahoma, Utah						1598
		Baetopus	*trishae*	Lotic—depositional	Swimmers; clingers	Collectors—gatherers?	North Carolina						
		Barbaetis	*benfieldi*	Lotic—erosional	Swimmers; clingers	Collectors—gatherers	Southeast						
		Callibaetis (11)		Lentic—vascular hydrophytes	Swimmers; clingers	Collectors—gatherers (filamentous algae)	Widespread	9.3	9.0	5.6	9.0	9.0	475, 1026, 1290, 1598, 4286, 2987

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Camelobaetidius (9)		Lotic—erosional and depositional	Swimmers; clingers		Northwest, Southwest, Central						1598
		Cloeon	*dipterum*	Lentic—vascular hydrophytes	Swimmers; clingers	Collectors—gatherers	Midwest, Northeast	7.4	4.0	3.5			728, 729, 1033, 1034, 2293, 4500, 5849, 4334, 4419, 1242, 3951
		Cloeodes (4)		Lentic and lotic—depositional	Swimmers; clingers	Collectors—gatherers	Northwest, Southwest						1242
		Diphetor	*hageni*	Lotic—erosional and depositional	Swimmers; clingers		Widespread			2.3	5.0		1396
		Fallceon (6)		Lotic—erosional and depositional	Swimmers; clingers		Widespread						2220, 3353
		Heterocloeon (9)		Lotic—erosional	Swimmers; clingers	Scrapers	Midwest, Southeast, Ontario, Colorado	3.6					1598, 3242, 4188
		Iswaeon (3)		Lotic—erosional and depositional	Swimmers; clingers	Collectors—gatherers	Widespread					4.0	3181, 3913
		Kirmaushenkreena	*zarankoae*	Lentic—sublittoral, sand and silt at 10m depth		Collectors—gatherers? (indicated by mouthpart structure)	Nunavut						3885

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Labiobaetis (7)		Lotic—depositional	Swimmers; clingers		Widespread	4.4	4.0	1.7	5.0		2900, 3353
		Moribaetis (3)		Lotic—edges of channel	Swimmers; clingers	Collectors—gatherers?	Extreme southern US						
		Neocloeon (2)		Lotic—edges of channel	Swimmers; clingers	Collectors—gatherers (detritus, diatoms); scrapers	Widespread	3.8					
		Paracloeodes (4)		Lotic—depositional (sand)	Swimmers	Scrapers	West, Midwest, Southwest, South	8.7					1598
		Plauditus (10)		Lotic—erosional and depositional	Swimmers; clingers	Collectors—gatherers	Widespread					4.0	
		Procloeon (21)		Lotic—depositional; lentic—littoral	Swimmers; clingers	Collectors—gatherers (detritus, diatoms); scrapers	Widespread						475
		Pseudocentroptiloides (2)		Lotic—erosional and depositional	Swimmers; clingers	Collectors—gatherers	Midwest, Southwest, Northeast						
		Varipes	*lasiobrachius*	Lotic—depositional sandy substrates	Swimmers; clingers?	Collectors—gatherers?	Mexico						
		Waynokiops	*dentatogriphus*	Lentic—Impoundments, sandy substrates in littoral zone	Swimmers; clingers?	Collectors—gatherers? (indicated by mouthpart structure)	Midwest, Southeast						

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
	Ametropodidae (2) - Sand Minnows												
		Ametropus (2)		Lotic—erosional (gravel-sand) and depositional (sand) (large rivers)	Burrowers (shallow, with eyes and gills exposed)	Collectors—filterers (using vortices),—gatherers (diatoms)	West, Northwest, Michigan						1064, 1376, 1590, 1585, 1598, 4286, 4599, 5572
	Oligoneuriidae (9) - Brushleg Mayflies			Generally lotic	Clingers and burrowers	Generally collectors—filterers							1064, 6492, 61, 91
		Homoeoneuria (5) (=*Oligoneuria* of Spieth and Burks)		Lotic—depositional (large rivers)	Burrowers	Collectors—filterers	Southwest (north to Utah), lower Midwest (north to Indiana, Nebraska), Southeast						475, 1598, 4633
		Lachlania (4)		Lotic—erosional and depositional	Clingers	Collectors—filterers (filamentous algae from current)	West						1376, 1590, 1585, 1598, 2831, 4286, 4599
	Isonychiidae (16) - Brush-Legged Mayflies												
		Isonychia (16) (1 recently presumed extinct)		Lotic—erosional	Swimmers; clingers	Collectors—filterers (very fine particles); predators (engulfers)	Widespread	3.8	2.0	1.9		2.0	475, 795, 1052, 1077, 2218, 2900, 3698, 4695, 5404, 5843, 6263, †

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
	Pseudironidae (1) - Crabwalker Mayflies												
		Pseudiron	*centralis*	Lotic—depositional (large rivers on sand)	Sprawlers	Predators (engulfers, uses vortices to search for prey)	West, Midwest, Southeast						475, 795, 1052, 1077, 2218, 2900, 3698, 4695, 5404, 5843, 6263, †
	Heptageniidae (126) - Flathead Mayflies			Generally lotic and lentic—erosional	Generally clingers	Generally scrapers; facultative collectors—gatherers					4.0		471, 861, 1376, 1452, 1590, 1585, 1598, 1991, 2801, 3179, 3496, 3679, 4599, 5339, 6370, 6413, 2958, 6296
		Afghanurus (13)		Lotic—erosional and depositional	Clingers; swimmers?	Scrapers; facultative collectors—gatherers	Widespread			5.1	2.0		1880, 2124, 4240, 3881
		Anepeorus	*rusticus (=Acanthamola)*	Lotic—erosional and depositional (including large rivers)	Sprawlers?; clingers?	Predators (engulfers, primarily midges)	Northwest Canada and US						1367, 1588, 1598, 3353
		Cinygma (3)		Lotic—erosional	Clingers	Scrapers; facultative collectors—gatherers	West				4.0		168, 1598, 6492

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Cinygmula (10)		Lotic—erosional	Clingers	Scrapers (diatoms); facultative collectors—gatherers (detritus, diatoms)	West, Northeast, Southeast	0.0			4.0		979, 1396, 1598, 2124, 4119, 6328, 4255, 4804, 4593
		Epeorus (19) (=*Iron* + *Ironopsis*)		Lotic—erosional	Clingers	Scrapers; facultative collectors—gatherers	Widespread	1.3	0.0		1.5		168, 201, 202, 979, 2124, 2693, 4081, 4082, 4096, 3484, 5404, 6328, 6789, 3066, 2335, 6414, 6492, 2270
		Heptagenia (11)		Lotic—erosional	Clingers (swimmers)	Scrapers; facultative collectors—gatherers	Widespread	2.4	3.0	1.9	4.0		475, 1090, 2510, 2900, 3023, 4127, 4239, 4240, 6328, 6338, 2312, 2768
		Ironodes (5)		Lotic—erosional	Clingers	Scrapers; facultative collectors—gatherers	West				4.0		1598, 3484, 4286, 4612
		Leucrocuta (10)		Lotic—erosional and depositional (slowflowing warm waters)	Clingers	Scrapers; collectors—gatherers	Widespread	1.2	1.0	2.4	1.0		1880, 4126

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Macdunnoa (3)		Lotic—erosional and depositional	Clingers	Scrapers; facultative collectors—gatherers	Midwest, Southeast						475, 3478
		Raptoheptagenia	*cruentata*	Lotic—erosional	Swimmers; clingers	Predators (engulfers)	Arkansas, Illinois, Indiana, Montana, Nebraska, Ohio, Tennessee, Manitoba, Saskatchewan						3353
		Rhithrogena (23)		Lotic—erosional	Clingers	Scrapers; facultative collectors—gatherers (detritus, diatoms)	Widespread	0.0	0.0		0.0		201, 202, 1598, 2124, 2165, 3023, 3973, 5404, 6328, 3976, 2027, 5196, 6492
		Spinadis	*simplex*	Lotic—erosional and depositional	Sprawlers?	Predators (engulfers of midge larvae)	Northeastern Canada, northeastern and southeastern US						
		Stenacron (7)		Lotic and lentic—erosional	Clingers	Scrapers; facultative collectors—gatherers	East and Central (to Arkansas, Minnesota)	1.7-7.1	7.0	3.1		4.0	475, 1077, 1598, 3377, 3973, 3974, 6696, †

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Stenonema (19)		Lotic and lentic—erosional (depositional)	Clingers (under loose cobbles and boulders)	Scrapers; facultative collectors—gatherers	Widespread	0.3-7.5	1-5	2.3	2.0	4.0	513, 1077, 1598, 1603, 1880, 2124, 2334, 2335, 2900, 3010, 3225, 3241, 3377, 3437, 3881, 4071, 4126, 4127, 4142, 4240, 4695, 5007, 5404, 5544, 5611, 6036, 6272, 6392, †
	Arthropleidae (1) - Flatheaded Mayflies												
		Arthroplea	*bipunctata*	Lentic—littoral; lotic depositional	Swimmers; clingers	Collectors—filterers (using vortices)	Northeast (to Wisconsin and Ohio)						694, 1598
	Ephemerellidae (68) - Spiny Crawler Mayflies			Lotic—erosional; some depositional and in macrophytes, a few lentic vascular hydrophytes	Generally clingers; some sprawlers and swimmers	Generally collectors—gatherers (detritus, algae); some scrapers; few shredders (detritivores and herbivores); 1 predator (engulfer)	Widespread				1.0		167, 471, 979, 1077, 1590, 1585, 1598, 1991, 3496, 4071, 4286, 4599, 5404, 6719
		Attenella (4)		Lotic—erosional and depositional	Clingers (detritus, algae)	Collectors—gatherers	West, East	2.6	3.0		3.0		475, 1598, 2472, 6328

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Caudatella (5)		Lotic—erosional and depositional	Clingers	Collectors—gatherers (detritus, algae); scrapers?	West				1.0		1061, 1598, 2472, 3484
		Caurinella	*idahoensis*	Lotic—erosional	Clingers	Collectors—gatherers?	Idaho				0.0		2918
		Dannella (3)		Lotic—depositional	Clingers; sprawlers	Collectors—gatherers	East, Widespread	1.9	3.0	1.2			
		Drunella (12)			Clingers; sprawlers	Scrapers; facultative predators (engulfers, e.g. D. grandis, doddsi, spinifera, and coloradensis); some facultative collectors—gatherers	Widespread	0.1			0.0		2472, 3484, 4623, 4857, 6328, 6644, 1595, 2124, 3709, 3710, 6530
		Ephemerella (17)		Lotic—erosional and depositional	Clingers; some swimmers	Collectors—gatherers; scrapers (E. infrequens, a shredder)	Widespread	0-4	1.0	2.9	1.0		475, 511, 513, 1598, 2471, 2472, 2900, 3344, 3437, 3973, 3977, 3978, 4192, 4240, 4611, 4857, 5572, 5128, 5845, 5848, 6327, 5127, 5379, 6617, 4986, 6642, 3384

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Eurylophella (16)		Lotic—erosional and depositional; lentic—vascular hydrophytes	Clingers; sprawlers	Collectors—gatherers, (E. funeralis, a shredder)	West, East	0.3-5.1	1-5	2.1		4.0	475, 1598, 2345, 2900, 2024, 4695, 5845, 786
		Matriella	*teresa*	Lotic—erosional	Clingers	Collectors—gatherers	West						
		Penelomax	*septentrionalis*	Lotic—erosional and depositional	Clingers, crawlers	Scrapers; facultative collectors	East	2.1					3913
		Serratella (5)		Lotic—erosional and depositional	Clingers	Collectors—gatherers (detritus)	Widespread	2.1	2.0	1.3	1.0	2.0	475, 1598, 2472, 4126, 1598, 4623, 6328, 6492
		Teloganopsis	*deficiens*	Lotic—erosional	Clingers; sprawlers	Collectors—gatherers (detritus)	East						3922
		Timpanoga	*hecuba*	Lotic—erosional and depositional	Clingers; sprawlers	Collectors—gatherers	Western US, Canada				7.0		
		Tsalia	*berneri*	Lotic—erosional and depositional	Clingers; sprawlers	Collectors—gatherers; facultative scrapers?	Southeast	0.0					
	Leptohyphidae (36) (=Tricorythidae) - Little Stout Crawler Mayflies			Generally lotic—depositional; lentic—littoral	Generally clingers; sprawlers	Generally collectors—gatherers; a few collectors—filterers					4.0		1376, 1590, 1585, 1598, 1991, 3496, 4286, 4599, 4498
		Ableptemetes	*distinctus*	Lotic	Sprawlers?		Extreme southern US						
		Allenhypes	*vescus*	Lotic	Sprawlers?	Collectors—gatherers?	Extreme southern US						

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Leptohyphes (11)		Lotic—depositional	Clingers	Collectors—gatherers; facultative scrapers and shredders—detritivores	Utah, Texas, Maryland	2.0					1598, 2220, 2890
		Tricorythodes (22)		Lotic—depositional; lentic—littoral (sediments)	Sprawlers; clingers	Collectors—gatherers; facultative scrapers	Widespread	5.4	4.0	2.7	4.5	4.0	1598, 2124, 2330, 3271, 3670, 3934, 4332, 475, 1396, 1455, 5404, 1138, 2220, 2900, 4695, 6644, 6646, 6509, †
		Vacupernius	*packeri*	Lotic—depositional	Sprawlers; clingers	Collectors—gatherers?	Extreme southern US						
Ephemeroptera	Neoephemeridae (5)					Collectors—gatherers?							1376, 1590, 1585, 1598, 4286, 4599
		Neoephemera (5)		Lotic—depositional	Sprawlers; clingers	Collectors—gatherers?	East	2.1					475, 1598
	Caenidae (36) - Small Square-Gill Mayflies										7.0		1376, 1590, 1585, 1598, 4501
		Amercaenis (2)		Lotic—depositional	Sprawlers	Collectors—filterers	Midwest, Southeast						3179, 3496, 4286, 4599
		Brachycercus (4)		Lotic—depositional	Sprawlers	Collectors—gatherers	East, Central, Southwest, Idaho and Wyoming	3.5	3.0		3.0		475, 1598
		Caenis (13)		Lotic—depositional; lentic—littoral (sediments)	Sprawlers; climbers	Collectors—gatherers; scrapers	Widespread	7.6	7.0	3.1	7.0	7.0	1026, 1077, 3670, 4112, 5348, 1138, 3040, 4826, 2900, 4695, 3010, †

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Cercobrachys (7)		Lotic—depositional	Sprawlers	Collectors—gatherers	West, Southeast						475
		Latineosus	*cibola*	Lotic (Rio Grande R.)	Sprawlers	Collectors—gatherers?	Texas, Mexico						
		Sparbarus (6)		Lotic—depositional	Sprawlers	Collectors—gatherers	Widespread	3.5	3.0		3.0		
		Susperatus (3)		Lotic—depositional	Sprawlers	Collectors—gatherers	West, East	3.5	3.0		3.0		
	Baetiscidae (12) - Armored Mayflies												1376, 1590, 1585, 1598, 3179, 4594, 3496, 4599, 4678
		Baetisca (12)		Lotic—depositional (sand, with detritus)	Sprawlers; clingers	Collectors—gatherers; scrapers	Widespread	1.4	5.0			4.0	469, 956, 1598, 3474, 4631, 4632, 5404, 6492
	Leptophlebiidae (87) - Prong-Gilled Mayflies			Generally lotic—erosional							2.0		471, 475, 1376, 1590, 1585, 1598, 2842, 3179, 3496, 4286, 4499, 4599, 1991, 5196, 6370, 6296, 2270
		Choroterpes (5)		Lotic—erosional and depositional; lentic—littoral (sediments)	Clingers; sprawlers	Collectors—gatherers, scrapers	Widespread			4.0			1077, 3679, 3926, 4286, 4501, 4500, 6328
		Farrodes (7)		Lotic	Clingers; sprawlers		Southwestern US						1367, 1598, 405, 4742, 4743
		Habrophlebia	*vibrans*	Lotic—depositional and erosional			East						475, 1566, 3436, 3437, †

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**Emphasis on trophic relationships

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Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Habrophlebiodes (4)		Lotic—erosional and depositional	Swimmers; clingers; sprawlers	Scrapers; collectors—gatherers	East, Midwest	0.0					475
		Hydrosmilodon	*primanus*	Lotic—erosional	Clingers; sprawlers	Collectors—gatherers?	Extreme southern US						4743
		Leptophlebia (7)		Lotic—erosional (sediments and detritus)	Swimmers; clingers; sprawlers	Collectors—gatherers (fine particles); facultative shredders—detritivores	Widespread	6.4	4.0		2.0		472, 690, 691, 1065, 1069, 1137, 2480, 2843, 4112, 4119, 4260, 419, 475, 3437, 5289, 5404, 4695, 4857, 5845, 5853, 785, 3010, †
		Neochoroterpes (4)		Lotic—erosional and depositional; lentic—littoral (sediments)	Clingers; sprawlers	Collectors—gatherers; scrapers (fine particles)	West, Southwest						
		Neoleptophlebia (7)		Lotic—erosional (sediments and detritus)	Swimmers; clingers; sprawlers	Collectors—gatherers (coarse detritus, diatoms); facultative shredders—detritivores	Widespread	1.2	1.0	2.8	1-4	1.0	
		Paraleptophlebia (32)		Lotic—erosional (sediments and detritus)	Swimmers; clingers; sprawlers	Collectors—gatherers (coarse detritus, diatoms); facultative shredders—detritivores	Widespread	1.2	1.0	2.8	1-4	1.0	475, 979, 1137, 1598, 2124, 2165, 2840, 5404, 1033, 3827, 5379, 2698, 3484, 4602, 278, 1441, 6492, 6530, 3235

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**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Thraulodes (15)		Lotic—erosional	Clingers; sprawlers	Collectors—gatherers; facultative scrapers	Southwest US						1598, 6038, 405, 4743, 2890
		Traverella (6)		Lotic—erosional and depositional	Clingers	Collectors—filterers or collectors—gatherers	Northwest Canada, western US to Indiana						1598, 6338, 4743, 2312
	Behningiidae (1)												1376, 1590, 1585, 1598, 1593, 1991, 4286, 4599, 4642
		Dolania	*americana*	Lotic—depositional (sand)	Burrowers	Predators (engulfers, Chironomidae)	Southeast US, Wisconsin						1814, 1815, 5845, 2447, 1598, 6060, 475, 6492, †
	Potamanthidae (4) - Hackgill Mayflies												3179, 4286, 4599, 4498
		Anthopotamus (4)		Lotic—depositional	Burrowers	Collectors—filterers	East, Midwest	1.6	4.0	3.2			1598, 2843, 3990, 1660, 3909, 5404, 317, 3910, 4200
	Ephemeridae (14) - Common Burrowing Mayflies										4.0		471, 1376, 1590, 1585, 1598, 3179, 3496, 3539, 1991, 4286, 4599
		Ephemera (6) (1 recently presumed extinct)		Lotic and lentic—depositional (sand-gravel)	Burrowers	Collectors—gatherers; predators (engulfers); filterers	Widespread	1.1	1.0	3.1	4.0		238, 687, 1077, 4040, 4222, 2510, 4482, 5404, 3344, 3347, 4695, 5845, †

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**Emphasis on trophic relationships

(continued)

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
		Hexagenia (7)		Lentic and lotic—depositional (sand-silt)	Burrowers	Collectors—gatherers (fine particles, possibly also filter at mouth of burrow)	Widespread	4.7	6.0	3.1	6.0	6.0	2358, 2715, 2716, 2791, 2379, 4126, 4286, 5404, 2510, 6865, 6866, 6867, 475, 1112, 3103, 4879, 2103, 4512, 5544, 6481, 693, 1975, 1977, 1978
		Litobrancha	*recurvata*	Lotic—depositional (small streams and rivers)	Burrowers		East	0.0	6.0				946, 1598
Ephemeroptera	Euthyplociidae (1)												
		Euthyplocia	*hecuba*	Lotic—erosional	Sprawlers	Collectors—gatherers	Extreme southern Mexico						
	Palingeniidae (1) - Riverbed Burrower Mayflies												
		Pentagenia (2) (1 recently presumed extinct)		Lotic—depositional (hard clay banks, large rivers)	Burrowers	Collectors—gatherers; passive filterers	Central, Southeast						1064, 1598, 3103

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships

Table 13A Continued

Taxa (number of species in parentheses)								Tolerance Values					
Order	Family	*Genus*	*Species*	Habitat	Habit	Trophic Relationships	North American Distribution	SE	UM	M	NW	MA*	Ecological References**
Ephemeroptera	Polymitarcyidae (7) - Pale Burrowing Mayflies										2.0		1590, 1585, 1594, 4040, 4286, 4599
		Campsurus (2)			Burrowers		Texas						1598
		Ephoron (2)		Lotic—erosional and depositional; lentic—littoral (sediments)	Burrowers	Collectors—gatherers; filterers	Widespread	1.5	2.0				687, 1598, 2843, 5404, 2106, 4695
		Tortopus (1)		Lotic—depositional (hard clay banks, large rivers)	Burrowers	Collectors—gatherers (coarse detritus)	Southwest						475, 1064, 3202, 5375
		Tortopsis (2)		Lotic—depositional (hard clay banks, large rivers)	Burrowers	Collectors—gatherers (coarse detritus)	Midwest (north to Manitoba), Southeast; Mexico						

*SE = Southeast, UM = Upper Midwest, M = Midwest, NW = Northwest, MA = Mid-Atlantic
**Emphasis on trophic relationships