TRANSACTIONS OF THE AMERICAN ENTOMOLOGICAL SOCIETY VOLUME 134, NUMBERS 1+2: 185-274, 2008

Revision of Ephemerellidae Genera (Ephemeroptera)

LUKE M. JACOBUS AND W. P. MCCAFFERTY

[LMJ] Current address: Dept. Biology, Indiana University, Bloomington, Indiana 47405, USA

[WPM] Dept. Entomology, Purdue University, West Lafayette, Indiana 47907, USA

ABSTRACT

The generic classification of Ephemerellidae Klapálek (Ephemeroptera) is reviewed and revised. Taxonomic status quo is maintained for the subfamily Timpanoginae Allen, except that *Melanameleus* Tiensuu (Ameletidae McCafferty) is not synonymous with *Eurylophella* Tiensuu. Data from the external morphology of eggs, larvae and adults of Ephemerellinae, s.s., species are coded into a data matrix and analyzed via the parsimony criterion of PAUP* to construct phylogenetic trees. A higher classification of Ephemerellinae is proposed based on the naming of groups from these trees. Two tribes are recognized and redefined: Ephemerellini, s.s., and Hyrtanellini Allen. Ephemerellini contains eleven genera: *Drunella* Needham [= *Eatonella* Needham, new synonym; = *Myllonella* Allen, new synonym; = *Tribrochella* Allen, new synonym; = *Unirhachella* Allen, new synonym], *Caurinella* Allen, *Ephemerella* Walsh, *Matriella*, new genus, *Tsalia*, new genus, *Caudatella* Edmunds, *Notacanthella*, new genus, *Spinorea*, new genus, *Adoranexa*, new genus, *Ephacerella* Paclt and *Cincticostella* Allen [= *Rhionella* Allen, new synonym]. The genus *Notacanthella* contains two subgenera: *Notacanthella*, s.s., and *Samiocca*, new subgenus. The genus *Ephemerella* contains six subgenera: *Zonadia*, new subgenus, *Hosoba*, new subgenus, *Draeconia*, new subgenus, *Scholitza*, new subgenus, *Vittapallia*, new subgenus, and *Ephemerella*, s.s. [= *Chitonophora* Bengtsson]. Hyrtanellini contains six genera: *Penelomax*, new genus, *Teloganopsis* Ulmer [= *Amurella* Kluge, new synonym; = *Kangella* Sartori, new synonym; = *Uracanthella* Belov, new synonym], *Serratella* Edmunds, *Quatica*, new genus, *Hyrtanella* Allen and Edmunds and *Torleya* Lestage [= *Crinitella* Allen and Edmunds, new synonym]. Four replacement names are established for species: *Drunella fuso*, new name [=*Ephemerella fusongensis* Su and Gui nec *Ephemerella fusongensis* Su and You], *Serratella occiprens*, new name [= *Ephemerella imanishii* Gose nec *Ephemerella imanishii* Allen], *Serratella tsuno*, new name [= *Ephemerella cornuta* Gose nec *Ephemerella cornuta* Morgan] and *Cincticostella braaschi*, new name [= *Ephemerella serrata* Braasch nec *Ephemerella serrata* Morgan]. New generic combinations are given for 41 species. Generic identification keys are provided for egg, larva and male adult stages of Ephemerellidae.

INTRODUCTION

The family Ephemerellidae Klapálek (Ephemeroptera: Furcatergalia) contains some of the most striking larvae among extant mayflies. Its species have been called by a number of charismatic common names, including pricklebacks (Needham and Christenson 1927), tip-tails (Needham and Christenson 1927), midboreal mayflies (Milne and Milne 1980) and spiny crawlers (McCafferty 1981, 1985).

Ephemerellidae is an abundant and widespread group of aquatic organisms. Its species are distributed throughout the Oriental, Nearctic and Palearctic zoogeographic regions including Palearctic northern Africa (Dakki and El Agbani 1983, Gagneur and Thomas 1988), in climates ranging from the tropics (e.g., Edmunds and Polhemus 1990) to the arctic (e.g., Harper and Harper 1981). Larvae are found in the benthos of aquatic habitats ranging from torrential streams (e.g., Allen and Edmunds 1963c) to the edgewaters of lakes (e.g., Smith et al. 1981). Ephemerellids are especially plentiful in high gradient streams (Hilsenhoff 1972, Yoon et al. 1985). For example, a sampling density of 13,746 ephemerellid larvae per square meter was reported by Leonard and Leonard (1962) for the North Branch of the AuSable River near Lovells, Michigan, U.S.A. The family Ephemerellidae accounts for an estimated 11% of Ephemeroptera diversity in the Nearctic region, 8% in the Palearctic Region and 5% in the Oriental Region (Barber-James et al. 2008), representing one of the most diverse groups of mayflies in the Northern Hemisphere (McCafferty and Wang 2000).

The ephemerellids are an important dietary component of several insectivores, including certain birds (McDunnough 1931b, Jenkins and Ormerod 1996, Feck and Hall 2004) and salmonid and other fishes (Needham 1927, Tshernova 1952, Bajkova 1967, Bell et al. 1994, Kreivi et al. 1999, Laine 2001, Fochetti et al. 2003). "These are the trout stream mayflies *par excellence*. Probably no other mayflies [are] so important to both fish and fisherman" (Leonard and Leonard 1962).

Most species are environmentally sensitive and can be used for monitoring a variety of disturbances and pollutants (e.g., Hilsenhoff 1982, 1988; Cain et al. 2003; Maret et al. 2003; Prusha and Clements 2004; Licht et al. 2004; Buchwalter et al. 2007). The environmental sensitivity of Ephemerellidae is demonstrated by their extirpation from many of their historic habitat locales. For example, Burks (1947, 1953) discussed the disappearance of ephemerellids from the Mississippi and Rock Rivers in Illinois, U.S.A. Landa and Soldán (1985) and Vidinova and Russev (1997) discussed the displacement of *Serratella mesoleuca* (Brauer) from streams in Europe and considered it possibly threatened by extinction. Even more common species, such as the widespread Palearctic species, *Torleya major* (Klapálek), also are being displaced (Landa and Soldán 1985). Ephemerellids stand to be impacted greatly by global climate shifts (Poff et al. 2001, Sala et al. 2001) and continued degradation of freshwater habitats (Revenga et al. 2000).

As illustrated above, ephemerellid mayflies are an important and sensitive part of freshwater and riparian communities and, as such, they have been critical components of freshwater ecological research. Historically, few other mayfly groups have been reported more often in the scientific literature (Clifford 1980). Environmental monitoring professionals and community ecologists (Gotelli 2004) often rely on genus level identifications of ephemerellids for their work (e.g., King and Richardson 2002, Bennett et al. 2004, Kitchin 2005). Unfortunately, the generic dispositions of many species have been inconsistent and largely unclear (Edmunds 1959, Thomas et al. 1999, Tong and Dudgeon 2000, Ogden et al. 2008), resulting in binomial combinations that vary by geographic region or taxonomic specialist. The taxonomic histories of some widespread species are illustrative of this phenomenon (Ogden et al. 2008).

Uracanthella punctisetae (Matsumura), for example, occurs throughout Asia (Tong and Dudgeon 2000, Ishiwata 2001, Beketov and Kluge 2003), and it has been included in the genera *Drunella* Needham, *Ephemerella* Walsh, *Serratella* Edmunds and *Uracanthella* Belov (see Ishiwata 2001). Zaika (2000) listed the species as belonging to *Torleya* Lestage, but as a subgenus of *Ephemerella*.

TAXONOMIC HISTORY OF EPHEMERELLIDAE

Poda (1761) described *Ephemera ignita* Poda from Europe, and the species has been placed variously in the genera *Ephemerella*, *Serratella* or *Torleya*, depending on the specialist consulted. This was the first ephemerellid species recognized, and it is among the first of mayflies named under the system of Linnaeus (1758). Walsh (1862) described the first genus relegated to this group for the North American species *Ephemerella excrucians* Walsh. Although Klapálek (1909) was the first to recognize Ephemerellidae as a formal family and has authorship of the taxon, the concept dates back to Eaton's (1883–1888) *Ephemerella* section VI. Traver (1935) recognized this group as a subfamily of Baetidae Leach. The group was recognized again as a family by Edmunds and Traver (1954). Edmunds et al. (1963) and Allen (1965, 1980, 1984) subsequently revised concepts of the family.

During the last two decades, Ephemerellidae has been refined further as part of an effort to have taxonomic classifications of Ephemeroptera that reflect phylogenetic hypotheses (McCafferty 1991). For example, certain genera of the family Teloganodidae Allen, including *Ephemerellina* Lestage, *Lithogloea* Barnard, *Manohyphella* Allen and *Teloganodes* Eaton, originally were included in Ephemerellidae before being moved to their own family, based on shared apomorphic characterstics of the maxillae and abdominal gills (McCafferty and Wang 1997, 2000). An additional morphological characteristic, the larval coxal projections having stout and spatulate setae, has been found to define this family (Jacobus and McCafferty 2006b). Other genera that have been part of historic concepts of Ephemerellidae include *Austremerella* Riek (Austremerellidae McCafferty and Wang), *Melanemerella* Ulmer (Melanemerellidae Demoulin: Melanemerellinae, s.s.), *Teloganella* Ulmer (Melanemerellidae: Teloganellinae McCafferty and Wang), *Philolimnias* Hong (Philolimniidae Jacobus and McCafferty) and *Vietnamella* Tshernova (Vietnamellidae Allen) (Jacobus and McCafferty 2006b).

Each of the aforementioned taxa and five other families together comprise the monophyletic superfamily Ephemerelloidea Demoulin (Ogden and Whiting 2005, Jacobus and McCafferty 2006b), which is defined by alate stages that share an apomorphic venation of the forewing and by larvae that have labial palp segment 3 and glossae reduced in size, a loss of musculature associated with the maxillary palp, and paraglossae that are fused with the mentum (McCafferty and Wang 2000, Kluge 2004, Jacobus and McCafferty 2006b). The other five families include: Ephemerythidae Gillies; Machadorythidae Edmunds, Allen and Peters; Tricorythidae Lestage (including subfamilies Ranorythinae Oliarinony and Elouard, Madecassorythinae Elouard and Oliarinony, and Tricorythinae s.s.); Dicercomyzidae Edmunds and Traver; and Leptohyphidae Edmunds and Traver (including subfamilies Coryphorinae Molineri, Peters and ZuÒiga; Tricorythodinae Wiersema and McCafferty; and Leptohyphinae, s.s.). Ephemerelloidea and Caenoidea Spieth, which includes the families Caenidae Klapálek and Neoephemeridae Needham, Traver and Hsu, together form the infraorder Pannota McCafferty and Edmunds. This infraorder is characterized generally by larvae that have the forewingpads fused for over one-half of their length (McCafferty and Edmunds 1979). Kluge et al. (1995), McCafferty (1997), Wang et al. (1997), McCafferty and Wang (2000), Molineri and DomÌnguez (2003), Kluge (2004) and Jacobus and McCafferty (2006b) have made subsequent contribtions to the concept of Pannota.

Ephemerellidae is a monophyletic group (Ogden and Whiting 2003, Jacobus and McCafferty 2006b) that is defined by the apomorphic loss of gills 2 from the larval abdomen (McCafferty and Wang 2000) and a male genital forceps segment 1 that has its length much less than its width (Jacobus and McCafferty 2006b). Prior to the work of Edmunds (1959), species fitting the current concept of Ephemerellidae were placed variously in the genera *Ephemerella*, *Chitonophora* Bengtsson, *Drunella*, *Eurylophella* Tiensuu, *Timpanoga* Needham, *Teloganopsis* Ulmer, or *Torleya*. Edmunds (1959) included all species, except *Teloganopsis media* Ulmer, in the genus *Ephemerella*, but he recognized several subgenera, including some he described at that time; one of these subgenera was subsequently renamed (Edmunds 1971). Allen (1965) later reduced *Teloganopsis* to subgeneric ranking, and Allen (1971) described two additional subgenera from Asia. Allen and Edmunds (1976) described the genus *Hyrtanella* Allen and Edmunds from Borneo. Tshernova (1972) recognized the subgeneric groups of *Ephemerella* as genera, and later, Allen (1980) did the same. Allen (1980) also named three new subgenera under *Drunella* (in addition to *Eatonella* Needham and *Drunella* s.s.), one new subgenus under *Cincticostella* Allen, and he established the tribe Hyrtanellini Allen for the genus *Hyrtanella*, which was monospecific at the time. In addition to those genus groups treated by Allen (1980), three additional genera have been described (Belov 1979, Allen 1984, Kang and Yang 1995), and two additional subgenera have been named (Kluge 1997, 2004). Two of these more recently described genera have been renamed (Paclt 1994, Sartori 2004).

In the most recent classifications of Ephemerelloidea by McCafferty and Wang (2000) and Jacobus and McCafferty (2006b), the family Ephemerellidae included the following extant genera: *Attenella* Edmunds, *Caudatella* Edmunds, *Caurinella* Allen, *Cincticostella* [= *Asiatella* Tshernova], *Crinitella* Allen and Edmunds, *Dannella* Edmunds, *Dentatella* Allen, *Drunella*, *Ephacerella* Paclt, *Ephemerella* [=*Chitonophora*], *Eurylophella*, *Hyrtanella*, *Kangella* Sartori, *Serratella*, *Teloganopsis*, *Timpanoga*, *Torleya*, and *Uracanthella*. Five subgenera have been recognized under the genus *Drunella*: *Drunella* s.s., *Eatonella*, *Myllonella* Allen, *Tribrochella* Allen, and *Unirhachella* Allen. *Cincticostella* contained two subgenera (*Cincticostella* s.s. and *Rhionella* Allen), and the genus *Ephemerella* contained two valid subgenera (*Ephemerella*, s.s., and *Amurella* Kluge). Kluge (2004) named an additional subgenus of *Ephemerella*, but this was a *nomen nudum*, as indicated by Soldán (2007).

In addition to *Philolimnias* (now in Philolimniidae), several fossil genera have been included in Ephemerellidae. Brauer et al. (1889) described *Mesoneta* Brauer, Redtenbacher and Ganglbauer, and Tshernova (1962) placed it in Ephemerellidae. Tshernova (1969) later moved this genus to its own family group, Mesonetidae Tshernova. Zhang and Kluge (2007) recently discussed its relationships. Demoulin (1954) placed one species of fossilized Jurassic Ephemeroptera from China (Ping 1935) in the genus *Turfanerella* Demoulin, and Lin (1986) described *Clephemera* Lin, an additional ephemerellid genus representing a fossilized larva. The classification and relationships of these latter two fossil genera are uncertain (McCafferty1990, Zhang and Kluge 2007).

The extant ephemerellid genera listed above are grouped into two subfamilies: Timpanoginae Allen and Ephemerellinae, s.s. (McCafferty and Wang 2000, Jacobus and McCafferty 2006b). Ephemerellinae is defined by the absence of gills 1 on the larval abdomen, and Timpanoginae is defined by the absence of gills 3 on the larval abdomen and the absence of associated gill-socket vestiges on the alate stages (McCafferty and Wang 1994).

THE STATE OF TIMPANOGINAE SYSTEMATICS

The taxonomy and classification of extant species and genus groups within the subfamily Timpanoginae, which includes genera *Attenella*, *Dannella*, *Dentatella*, *Eurylophella* and *Timpanoga*, have been investigated and debated relatively extensively over the past few decades (Allen 1977a; McCafferty 1977, 1978, 2000; Funk et al. 1988; Funk and Sweeney 1994; McCafferty and Wang 1994, 2000; Burian 2002; McCafferty et al. 2003; Kluge 2004; Jacobus and McCafferty 2006b; Funk et al. 2008). Although the results of Ogden et al. (2008) indicate that the phylogenetic relationships of Timpanoginae genera require further study, the genera are well-defined, and classification of species into those genera is generally consistent.

The five genera of Timpanoginae currently are classified into three tribes within the subfamily: Attenellini McCafferty, Eurylophellini McCafferty and Timpanogini, s.s. One fossil, *Timpanoga viscata* (Demoulin, 1968), is placed to this subfamily, but its generic and tribal affinities are uncertain (McCafferty and Wang 2000).

Attenellini contains only the Nearctic genus *Attenella*, which is comprised of four species. These four species share a presumably apomorphic elongation of the male genital forceps segment 3 (McCafferty 1977, McCafferty and Wang 1994). McCafferty and Wang (1994: Fig. 18) provided a cladogram for the genus, based on eight morophological characters associated with dorsal spines on the head, thorax and abdomen; the shape of gills; the relative development of abdominal posterolateral projections; and the coloration of caudal filaments.

Timpanogini is comprised of the genera *Timpanoga* and *Dannella*, and it is defined by larval characteristics, including the absence of denticles on the claws and somewhat enlarged abdominal gills 4 (McCafferty 1977, McCafferty and Wang 1994). *Timpanoga* contains one extant species, *T. hecuba* (Eaton), which is known from the western Nearctic region. *Timpanoga hecuba* has two nominal subspecies: *T. h. hecuba* and *T. hecuba pacifica* (Allen and Edmunds) (Allen and Edmunds 1959). *Dannella* contains three nominal, Nearctic species, and McCafferty (1977: Figs. 17–19) formulated an hypothesis about their phylogeny based on four morphological characters associated with the development of larval mouthparts and lateral abdominal processes.

Eurylophellini is a monophyletic group that contains the genera *Dentatella* and *Eurylophella* (Burian 2002, McCafferty et al. 2003, Jacobus and McCafferty 2006b, Ogden et al. 2008). These genera share several larval apomorphies, including gills 4 that are nearly fully operculate, a loss of the maxillary palp (McCafferty 1977, McCafferty and Wang 1994), and an increased number of medial setae on the maxilla (interpretation modified from that of McCafferty 1977 and McCafferty and Wang 1994). Also, the eggs share a synapomorphic loss of the polar cap (Jacobus and McCafferty 2006b), and McCafferty (1977) noted a shared apical narrowing of the penes. The eastern Nearctic genus *Dentatella* is monospecific (Burian 2002, McCafferty et al. 2003). Extant *Eurylophella* are known from the Nearctic and western Palearctic regions. McCafferty and Wang (2000) considered a report of *Eurylophella* from Madagascar (Allen and Edmunds 1963c) to be dubious and based either on a labeling error or on a misidentification. Funk et al. (1988) and Funk and Sweeney (1994) reviewed and revised eastern Nearctic species and species groups, and they provided detailed, comparative descriptions of those species. Funk et al. (2008) very recently described a new, eastern Nearctic species with novel reproductive strategies, bringing the total number of Nearctic species to fifteen. The far western Nearctic species, *Eurylophella lodi* (Mayo) is discussed by Allen and Edmunds (1963b). Allen and Edmunds (1963b) and Studemann and Tomka (1987) discussed the Palearctic fauna.

Edmunds and Traver (1954) tentatively listed the monospecific Palearctic genus *Melanameletus* Tiensuu, 1935:15, as a junior synonym of *Eurylophella* Tiensuu, 1935:20, based on a remark by J. A. Lestage (Tiensuu 1939) regarding the familial placement of *Melanameletus*, even though types never were examined (Allen and Edmunds 1963b). However, Hubbard (1990) and McCafferty and Wang (2000) listed *Melanameletus* as a *bona fide* synonym of *Eurylophella*. We do not consider the two genera to be synonymous. The holotype of *Melanameletus brunnescens* Tiensuu is a female adult (Sortavala, Ristoja, 18-VI-1931) from the Karelian Republic of Russia, formerly of Finland, that is housed in the Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland (Silfverberg 1989). Considering the original description (Tiensuu 1935: Figs. 6–7) and electronic images of the holotype kindly provided to us by Jyrki Muona (Helsinki, Finland), we were able to recognize that *Melanameletus brunnescens* belongs to the family Ameletidae McCafferty, rather than Ephemerellidae, based on its wing venation, dissimilar claws, and vestigial median caudal filament (Studemann et al. 1988). Additional adjustments to Ameletidae taxonomy and classification may be required based on these findings, but revisions to that family are beyond the scope of this study.

THE STATE OF EPHEMERELLINAE SYSTEMATICS

The systematics of Ephemerellinae have not been explored to the same extent as Timpanoginae. Eaton (1883–1888) and Lestage (1925) provided reviews of the global fauna, and Studemann and Landolt (1997) studied eggs based on exemplars from around the world. In contrast to these, other notable systematic studies prior to the 21st Century were mostly regional in focus. These included, for example, taxonomic reviews of North America (Walley 1930; McDunnough 1931b; Traver 1935; Edmunds 1959; Allen and Edmunds 1961, 1962, 1963a, 1965; Allen 1968), Asia (Allen and Edmunds 1963c, Allen 1971, Bae et al. 1998), Japan (Gose 1980, 1985), Korea (Yoon and Kim 1981, Yoon and Bae 1988), Taiwan (Kang and Yang 1995), China (You and Gui 1995; Zhou and Su 1997; Zhou et al. 1997a,b, 2000), Vietnam (Allen 1986), the Russian Far East (Tshernova et al. 1986), Europe (Gonzales del Tanago and Garcia de Jalon 1983, Studemann and Tomka 1987, 1989, Studemann et al. 1989, Jacob 1993, Studeman et al. 1995) and Turkey (Kazanci 1987, 1990, 1991).

The dawn of the 21st Century marked a resurgence of interest in biological systematics, in general (Mitter 1999, Wheeler 2004), and in the systematics of Ephemeroptera (DomÌnguez 2001), in particular. With regards to Ephemerellinae, this time period has seen an increase in discovery of undocumented variation and the first global comparisons of many species, resulting in modified species concepts and numerous new synonyms (Bae et al. 2000, Jacobus and McCafferty 2000, Ishiwata 2001, McCafferty 2001, Jacobus and McCafferty 2002a,b, Ishiwata 2003, Jacobus and McCafferty 2003a,b,c, 2004b, Jacobus et al. 2003, 2004, Kluge 2004, Jacobus et al. 2005a, Zhou et al. 2006). A few new species have been described (Tong and Dudgeon 2000, Zhou et al. 2000, Alba-Tercedor and Derka 2003, Jacobus and Sartori 2004, Jacobus et al. 2004, 2007, Kluge et al. 2004, Jacobus and McCafferty 2006a), and several taxa have had metamorphic stages described for the first time (Ishiwata 2000, Jacobus and McCafferty 2001, Jacobus et al. 2002, 2003, Jacobus and McCafferty 2004a, Jacobus and Sartori 2004, Jacobus et al. 2004, 2006, 2007). Geographic range extensions (e.g., Ishiwata 2001, Quan et al. 2002, Beketov and Kluge 2003, Jacobus and McCafferty 2003c, Webb et al. 2004, Jacobus et al. 2005b, Randolph and McCafferty 2005) and historical misidentifications (Bae et al. 2000, Jacobus and McCafferty 2003bc, McCafferty et al. 2006, Jacobus et al. 2007) also have been discovered. Examination of specimens collected recently from Thailand revealed that the presumably monospecific genus *Kangella* is not endemic to Taiwan, resulting in the recognition that Taiwan has no endemic mayfly genera (Jacobus et al. 2005b).

Kluge (2004) recently provided a comprehensive review of Ephemerellinae, including a listing of all nominal species and the formulation of some phylogenetic hypotheses. However, many species were regarded as *incertae sedis*. Ogden et al. (2008) conducted preliminary phylogenetic analyses of historic Ephemerellidae genera and some species groups based on selected species. However, their sampling of species was very limited and they did not address issues of taxonomy and classification.

Almost one-half of all nominal Ephemerellinae species have fallen to synonomy (Brittain and Sartori 2003, Barber-James et al. 2008). This is attributed primarily to the geographically restricted nature of many previous taxonomic studies, as elaborated above (e.g., Allen 1974), and to early taxonomists' typological concepts that did not account for natural variability. However, some species now presumed to be polytypic might be complexes of cryptic species, given that these tendencies are seen in ephemerellid groups (Funk et al. 1988, 2008; Williams et al. 2006) and that very recent field and molecular studies have revealed biological differences, at least at a local scale (e.g., Chandler et al. 2006; Alexander et al., unpublished; Funk et al., unpublished; Xin Zhou et al., unpublished). Resolving such issues via morphological data is complicated by interspecific differences that are sometimes subtle and by the high degree of intraspecific variation that is common among ephemerellids (Funk et al. 2008). Landa (1973) suggested that the group has experienced considerable speciation since the last ice age, and it still may be in the midst of this process.

Lestage (1917) noted the great diversity of Ephemerellidae larvae, but the relative similarity of the shortlived adults. As a result, most studies have focused on characters associated with the larval stage (e.g., Walley 1930, Allen 1975). Edmunds (1959) emphasized that the disparity between larval and adult differences was due to separate rates of evolution for the two life stages, which would confound efforts to create genera easily distinguishable as both of these commonly identifiable stages, if that were an important criterion for recognizing genera (Edmunds 1962).

Also remarkable regarding generic classification are some egregious taxonomic mistakes that have been made in this group, including those noted by McDunnough (1938), Allen (1973), Edmunds and Murvosh (1995), and Jacobus and McCafferty (2003b, 2004b). For example, the concept of the western Nearctic species *Ephemerella altana* Allen was found to include adults and larvae from different genera that had been incorrectly associated with one another (Jacobus and McCafferty 2003b). In another example, the same author established two species names, each combined with a different genus, based on a single specimen from Thailand (Edmunds and Murvosh 1995).

Revisionary studies of Ephemerellinae classification to date (with the limited exception of Kluge 2004) have been based in phenetic taxonomy, and, as indicated by McCafferty (1991), incorporated arbitrary limits in defining generic boundaries. Due to the inherent weaknesses of these approaches and the geographically restricted nature of most studies, many character states are distributed apparently randomly through current genera (Landa et al. 1982, Studemann et al. 1995, Studemann and Landolt 1997, DomÌmguez and Cuezzo 2002, Ogden et al. 2008), with generic attributions of many species being inconsistent and largely unclear (Edmunds 1959, Thomas et al. 1999, Tong and Dudgeon 2000, Ogden et al. 2008).

Edmunds (1973), Tomka and Elpers (1991) and Ogden et al. (2008) emphasized that the systematics of Ephemerellidae would be soluble only if the entire fauna were studied in a comparative manner. Undertaking such a study at the present time is imperative considering some of the imminent threats facing ephemerelline mayflies on a global scale, such as climate change, the effects of human population growth, destruction of habitats and competition from invasive species. Not only do these factors potentially impact the mayflies, but they also may have a disastrous effect on any future ability of scientists to study the systematics of this group of very sensitive organisms in an adequate manner (Beutel and Pohl 2006).

MATERIALS AND METHODS

The objective of this study is the revision of Ephemerellidae genera based on a comparative study of the world fauna. Except as noted above for the genus *Eurylophella*, we maintain the taxonomic status quo for the well-studied subfamily Timpanoginae and otherwise focus on the lesser-studied subfamily, Ephemerellinae. Species from this latter group are treated as Operational Taxonomic Units (OTUs), in order to obtain trees that can provide phylogenetic bases for classification. External morphological characters associated with the known life history stages of these OTUs are coded into a data matrix, and the matrix is subjected to computational phylogenetic analyses. External morphological data were chosen for this first comprehensive study of Ephemerellinae, in order to allow for the most inclusive, timely, and cost-effective sampling, considering the number of species, the wide geographic distribution of the subfamily and the restricted distributions of some specific taxa, which are limited to remote locales or regions currently embroiled in dangerous political turmoil.

All valid Ephemerellinae species are used as OTUs, except as noted below, and their respective specific epithets are utilized as labels on the data matrix and trees. Subspecies are excluded. Current synonyms for species are listed in the Taxonomy section.

The species *Attenella attenuata* (McDunnough) is utilized as an outgroup for rooting all trees, because it is the type species of the genus *Attenella*, the most morphologically pleisiotypic genus of Ephemerellinae's sister group, Timpanoginae (Edmunds 1971; McCafferty 2000; McCafferty and Wang 1994, 2000; McCafferty et al. 2003; Jacobus and McCafferty 2006b). Although Ogden et al. (2008) indicated an alternate phylogenetic relationship of *Attenella* to other ephemerellid genera based on molecular data, the morphological characteristics hypothetically remain as the most pleisiotypic of the family (McCafferty 1977) and therefore retain their utiliy for comparative analyses of morphological data. Certain species were excluded from this study. Edmunds and Allen (1957) established *nomen dubium* status for *Ephemerella consimilis* Walsh, 1862, and *Ephemerella unicornis* Needham, 1905, and Ishiwata (2001) did the same for *Ephemerella gose* Okazaki, 1984. *Ephemerella molita* McDunnough, 1930, recently was designated to be a *nomen dubium* by Jacobus and McCafferty (2007). The following species names should be considered *nomen nuda* because they have no descriptive data associated with them, nor do they have any designated type specimens: *Ephemerella plumosa* Morgan, 1911; *Ephemerella spinosa* Morgan, 1911; *Drunella paradinai* Alba-Tercedor, 1982; *Ephemerella chantauense* Kluge, 2004; and *Ephemerella kogistana* Kluge, 2004.

Jacobus and McCafferty (2004b) recognized four nominal species as junior synonyms of *Drunella cryptomeria* (Imanishi), based on stage associations by Ishiwata (2001). Subsequently, Nikita Kluge (pers. comm.) kindly noted some discrepancies between the type concept of *D. cryptomeria* and the collective concept of the other four putatively synonymous species, based on his examination of types and series of reared specimens not seen by Ishiwata (2001) and Jacobus and McCafferty (2004b). Thus, for the purposes of this study, the oldest of the four junior names, *D. lepnevae* (Tshernova), is considered valid. *Drunella cryptomeria* is not coded as an OTU, and thereby excluded from all analyses, but it is included in the Taxonomy section. It may prove to be a junior synonym of *D. ishiyamana* (Matsumura) (Kluge, pers. comm.). Kluge (unpubl.) also noted that *D. lepnevae* larvae often cohabit with those of *D. ishiyamana* (sensu Jacobus and McCafferty 2004b), providing a plausible explanation of the historical confusion surrounding these species.

The remaining material examined is listed below and deposited with the following individuals or institutions: The Natural History Museum, London, England [BMNH]; Brigham Young University, Provo, Utah [BYU]; California Academy of Sciences, San Francisco, California [CAS]; the Canadian National Collection of Insects, Ottawa, Ontario [CNC]; C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Ft. Collins, Colorado [CSUC]; Hokkaido University, Sapporo, Japan [EIHU]; Florida A&M University, Tallahassee, Florida [FAMU]; Illinois Natural History Survey, Champaign, Illinois [INHS]; Iowa State University, Ames, Iowa [ISUI]; Jeff M. Webb (specimens temporarily in the care of LMJ, Nashville, Indiana) [JMW]; Musée de Zoologie, Lausanne, Switzerland [MZL]; Purdue University Entomological Research Collection, West Lafayette, Indiana [PERC]; Royal Ontario Museum, Toronto, Ontario [ROM]; Seoul Women's University, Seoul, Korea [SWU]; University of Michigan Museum of Zoology, Ann Arbor, Michigan [UMMZ]; Wilbur R. Enns Entomology Museum, University of Missouri, Columbia, Missouri [UMRM]; and Virginia Polytechnic Institute and State University, Blacksburg, Virginia [VPIC]. Some material was collected as part of the All Taxa Biodiversity Inventory of Great Smoky Mountains National Park (Sharkey 2001, Parker et al. 2007).

Some figures were modified or redrawn from the following sources: Alba-Tercedor and Sánchez-Ortega 1982; Allen 1971; Allen and Edmunds 1961, 1962, 1963ac, 1976; Bajkova 1967; Belov 1979; Burks 1953; Edmunds and Murvosh 1995; Engblom 1996; Harper and Hawkins 1984; Imanishi 1937b; Jacobus and McCafferty 2004a; Kang and Yang 1995; Kluge et al. 2004; Kondratieff et al. 1981; Landa 1969; Marie et al. 1999; Mayo 1951; Smith 1935; Spieth 1940; Studemann and Landolt 1997; Studemann and Tomka 1987; Studemann et al. 1989, 1992; Su and You 1988; Tong and Dudgeon 2000; Traver 1934, 1935; Tshernova 1952; Ueno 1931; Ulmer 1939; Xu et al. 1980; Yoon and Bae 1988; Zhou et al. 2000.

Some literature sources were obtained or verified by using Hubbard's (2008) virtual library and working bibliography of literature on the mayflies of the world. OTU labels utilized in this study are listed below and correspond to the specific epithets included in the Taxonomy section. OTUs were evaluated for this study based on the following specimens. In some cases, literature was used in lieu of actual specimens because certain life history stages were not available for us to study or certain structures were missing from those specimens available to us. Unknown eggs, larvae and male adults are indicated below. In the Taxonomy section, synonymous species names are listed based only on their original combinations, because only the original and current combinations have any applicability to the present taxonomy based on the terms of the most recent edition of the International Code of Zoological Nomenclature (1999).

OPERATIONAL TAXONOMIC UNITS

aculea—Material examined: Korea, Gyeonggi-do, Kapyong Kapyongcheon (St), 12-V-1999, one male adult and associated exuviae (reared; maxilla in vial) [SWU-EPH-3190]; Kwang Nung, 3-IV-1960, G Field, one larva (holotype)[PERC]. Egg unknown.

albai—Material examined: Rio Agueda/El Payo (E, Salamanca), alt 700 m, 18–20-VIII-1988, Leg Landolt, Studemann, 10093, four larvae, two male adults, two female adults [PERC]. Literature consulted: Studemann et al. (1995: Figs. 22–24); Studemann and Landolt (1997: Figs. 28–29).

allegheniensis—Material examined: USA, Virginia, Montgomery Co, Little R at Rt 787, 8-IX-1980, BC Kondratieff, one male adult, associated larval exuviae [VPIC]. Egg unknown.

alleni—Material examined: USA, Washington, Pierce Co, springfed stream, Westside Rd 1.2 mi N Hwy 706, Mt Rainier NP, 16-VI-2004 (emerged 23-VI-2004), Kondratieff, Schmidt, five male adults, two female adults, associated exuviae [PERC]. Literature consulted: Jacobus et al. (2003).

apopsis—Material examined: USA, Colorado, Chase Lake, 11000', 24-VII-1947, CP Alexander, one male adult (holotype; forelegs missing) [PERC]. These collection data are questionable, based on entries from Alexander's field notebooks, which were made during a visit to the state of Washington in July 1947. The field notebooks are housed in the Smithsonian Institution Archives, Washington, D.C., U.S.A. (Record Unit 7298: Div 6-Box 65-Folder 8; D4-B72-F2,4&8). The collection data listed here should be considered valid, however, until further investigation is completed. Egg and larva unknown.

atagosana—Material examined: Japan, Honshu, Nara, Higashi-yoshino, Omata, Omata Stream, Kuramae Bridge, 5-V-2001, T Fujitani, one larva [PERC]; Tokyo, Ange R, Hachiouji-shi, 30-IV-1985, S Ishiwata, one male adult [PERC]. Korea, Jeollabuk-do, Muju, Deokyusan (Mt), 2-V-1983, YJ Bae, one female adult (reared; eggs dissected) [SWU-EPH-1606]; Donggureung, Namyangju, 10-V-1994, YJ Bae, one male adult, associated exuviae [SWU-EPH-1614].

attenuata—Material examined: Canada, Ontario, Ottawa, Ottawa Golf Club, 30-VII-1924, JH McDunnough, one male adult (holotype 1277) [CNC]; USA, Massachussets, Montague, Cranberry Stream, 30-VI-1961, JR Traver, one male adult (pinned; exuviae in vial, spec. cr 30) [PERC]. USA, Tennessee, Scott Co, Big South Fork NRRA, Clear Fork at Burnt Mill Bridge Access, 36°23'17"N, 84°37'47"W (NAD27), 11-VI-2003, JM Webb, LM Jacobus, three larvae (dissected maxilla and leg in microvial) [PERC]; USA, Virginia, Montgomery Co, Little R along Little Camp Rd, 37°00'07"N, 80°24'59"W, 15-VI-2003, JM Webb, LM Jacobus, two larvae (dissected tarsus in vial) [PERC]. Literature consulted: Studemann and Landolt (1997: Fig. 13–14).

aurivillii—Material examined: Canada, Nova Scotia, Wallace R, Hwy 102, 24-VI-1980, R Demaray, one male adult, one female adult, associated exuviae (reared) [VPIC]; Quebec, Bradore Bay, 26-VII-1929, WJ Brown, one male adult [PERC]. USA, Oregon, Marion Co, Silver Falls SP, 22-IV-1967, E Evans, two larvae [PERC]. Literature consulted: Studemann et al. (1995: Figs. 4–6); Studemann and Landolt (1997: Fig. 39); Ishiwata et al. (2000: Figs. 3J–3K).

basalis—Material examined: Japan, Osaka Pref, nr Kisiwade City, Tohara, small stream in mountains, 22-V-1988, GB, EC Wiggins et al, one larva [ROM-882013]. Literature consulted: Imanishi (1937a; 1937b: Fig. 1); Okazaki (1984: Fig. 25).

bauernfeindi—Literature consulted: Marie et al. (1999). Egg and male adult unknown.

berneri—Material examined: USA, Virginia, Henry Co, Smith R at Rt674, 26-IV-1980, emerged 7-V-1980, Kondratieff, one male adult, two female adults, associated exuviae (eggs dissected) [VPIC].

braaschi—Literature consulted: Braasch (1981: Figs. 1–5). Egg and male adult unknown.

brocha—Material examined: Taiwan, Hsinchu Hsien, Wufeng, 1991-10-24(I), SC Kang, HC Chang, one larva (paratype). Literature consulted: Kang and Yang (1995: Figs. 18–19). Male adult unknown.

catawba—Material examined: USA, Tennessee, Sevier Co, Great Smoky Mountains NP, Bunches Cr, 14-VII-1999 (emerged 17–25-VII-1999), B Nichols, L Curry, (reared by J Cooper), two male adults and associated exuviae [PERC]. Egg unknown.

changbaishanensis—Literature consulted: Su and You (1988: Figs. 1–9); You and Gui (1995: Figs. 144a–c). Larva unknown.

chinoi—Material examined: Japan, Kyoto, Oe-cho, Hobi, Yura stream, 10-IX-1997, T Fujitani, one larva [PERC]. Egg and male adult unknown.

christineae—Material examined: Malaysia (east), Sabah, Liwagu R, Liwagu Cave, southeast of headquarters, 1525m, (S7e), 14–15-VIII-1972, GF&CH Edmunds, one larva (paratype) [PERC]. Egg and male adult unknown.

coheri—Material examined: Nepal, Palung, 5850', 17-IV-1957, EI Coher, two larvae (holotype; paratype, mouthparts on slide) [PERC]; Thailand, Mae Hong Son, River Nam Lang, Soppong, 3–27/IV/2003, Braasch, four larvae, three male adults, one female subimago [PERC]; Mae Hong Son Prov, Namtok Mae Surin NP, Nam Mae Surin, above falls, 18°56'N, 98°04'E, 1220 m, 15-X-2002, GW Courtney, one larva [ISUI]. Literature consulted: Jacobus and Sartori (2004: Fig. 20); Jacobus et al. (2007).

coloradensis—Material examined: USA, Utah, Salt Lake Co, Mill Cr., Mill Creek Canyon, WL Peters, K Terry, three male adults [PERC]; Montana, Glacier NP, Avalanche Cr at Avalanche Campground, 10-IX-1958, RW Baumann, two male subimagos, four larvae [PERC]. Literature consulted: Studemann and Landolt (1997: Figs. 52–53).

colossa—Literature consulted: Kang and Yang (1995: Figs. 4, 11–13). Male adult unknown.

commodema—Material examined: Thailand, Chiengmai Prov, small stream and waterfalls, Doi Sutep, west of Chiengmai (elev 1450'), 8-IX-1964, WL & JG Peters, eight larvae (paratopotypes) [PERC]. Egg and male adult unknown.

corpulenta—Material examined: Nepal, Trisuli, Khola before Dhunche, 1950 m NN, 30-IV-1978, Sivec, two larvae (paratypes) [PERC]. Egg and male adult unknown.

deficiens—Material examined: USA, North Carolina, Haywood Co, Plott Cr at end of Rt 1173, 7-VII-1981, Kondratieff, two larvae [VPIC]; Virginia, Carroll Co, New R at Rt 606, 11-VII-1980 (emerged 18-VI) [sic?], Kondratieff, one male adult (reared), associated larval exuviae [VPIC]; Hanover Co, South Anna Falls at Rt 657, 1-IX-1977, Kondratieff, three male adults, four female adults, one larva [VPIC]. Literature consulted: Koss (1968: Figs. 40, 42); Studemann and Landolt (1997: Figs. 26–27).

doddsii—Material examined: USA, Montana, Missoula Co, Lolo Cr, 0.6 mi NE Lolo Pass, 46°38'37"N, 114°34'44"W (WGS84), 28-VII-2002, WP McCafferty, LM Jacobus, two larvae [PERC]; Utah, Utah Co, Aspen Grove Cr, VI-1965, GF Edmunds, one male adult [PERC]. Literature consulted: Studemann and Landolt (1997: Fig. 54), Allen and Edmunds (1962: Figs 28–33).

dorothea—Material examined: USA, California, Santa Clara Co, Smith Cr, Mt Hamilton, 7-IV-1951, WC Day, seven male adults (reared), two female adults (reared), two sets larval exuviae, one larva [CAS]; Virginia, Nelson Co, Hargove Cr at Rt 651 off Rt 718, 3-V-1980, Kondratieff, 33 male adults, 32 female adults, three male subimagos, four sets subimago exuviae, ten sets larval exuviae, eight larvae [VPIC]. Literature consulted: Koss (1968).

edmundsi—Material examined: USA, Montana, Sanders Co, Vermilion R, 6-VI-2005 (emerged 19-VI-2005), RL Newell, two male adults (reared), associated exuviae [PERC]. Literature consulted: Jacobus et al. (2006: Fig. 3).

elongatula—Material examined: Japan, Ibaraki, Tomobe, Taira-cho, 9-II-2002, T Fujitani, seven larvae [PERC]; Osaka, Kaizuka, Sobura, 15-IV-2001, T Fujitani, one male adult [PERC]. Japan (no other data), Pryer, one male adult, two female adults [BMNH]. Literature consulted: Ishiwata (2003: Figs. 3–4).

euphratica—Literature consulted: Kazanci (1987: Figs. 1–12); Kazanci (1990: Figs. 6–8, 17–18). Egg unknown.

excrucians—Material examined: USA, Montana, McCone Co, Missouri R at Lewis & Clark RA, 8 mi SE of Wolf Point at SR13, 48°4’2”N, 105°32’18”W (WGS84), 27-VII-2002, WP McCafferty, LM Jacobus, one male adult (reared), two female adults, one male subimago, one female subimago, three sets subimago exuviae, four sets larval exuviae, four larvae [PERC]; Utah, Utah Co, South Fork Provo R at Hwy 35 above Woodland, 27-V-2000, DNA holotype E08, one larva [BYU]. Literature consulted: Koss (1968); Jacobus and McCafferty (2003b).

femorata—Material examined: Thailand, Mae Hong Son Prov, Namtok Maw Pang, 19°22’N, 98°22’E, 850 m, 19-III-2002, “L-305,” Sites, Vitheeprada, Kirawanich, one larva [UMRM]. Literature consulted: Jacobus et al. (2005a). Egg and male adult unknown.

flavilinea—Material examined: USA, Montana, Madison R below Pallisades, 2-VII-1981, AR Ryther, seven larvae [PERC]; Madison 2 miles below Pallisade, 20-VII-1981, three male adults [PERC]. Literature consulted: Allen and Edmunds (1962). Egg unknown.

frisoni—Material examined: USA, Indiana, Montgomery Co, Little Sugar Cr at bridge N SR32, 4 mi E of Crawfordsville, 1-VI-1973, WP McCafferty, AV Provonsha, K Black, “MP110,” 32 larvae (mouthparts on slide) [PERC]; Missouri, Mammoth Springs, 6-VI-1937, HH Ross, two male adults [PERC]. Egg unknown.

fusca—Material examined: Taiwan, Taichung, Hoping, Wuling Farm, 1500 m, 18-V-1986, PS Yang, KJ Huang, one larva (paratype) [MZL]. Literature consulted: Kang and Yang (1995: Figs. 14–17). Male adult unknown.

fusongensis—Literature consulted: Su and You (1988: Figs. 10–14). Egg and larva unknown.

gilliesi—Material examined: Nepal, Katmandu, Choban Gorge, 20-XII-1960, MT Gillies (holotype) [PERC]. Egg and male adult unknown.

glebosa—Material examined: Taiwan, Taitung Hsien, 500 m, 15-XII-1990, SC Kang, one larva (paratype) [MZL]. Literature consulted: Kang and Yang (1995: Fig. 8). Male adult unknown.

gosei—Material examined: China, He Nan Prov, Song Xian Co, Bai Yun Shan, 19-VII-2002, Jianxi Cui et al, one larva [PERC]. Egg and male adult unknown.

gracilis—Material examined: three larvae [PERC] Note: No collection data are associated with these specimens, but they were identified and donated by Nikita Kluge (St. Petersburg, Russia), who has examined the types of the species (Kluge 1995). Egg and male adult unknown.

grandipennis—Material examined: Thailand, R Nam Lang, Soppong, LF, 3.02-05.03.04, Braasch, two male adults [PERC]; Mae Hong Son Prov, Namtok Mae Surin NP, Mae Nam Pai, 19-III-2002, 19°21’N, 97°59’E, 310 m, GW Courtney, four larvae [ISUI]. Vietnam, Loa Cai, Sapa Muong Hoa Ho R, 5–

12-V-1995, D Currie, B Hubley, ROM956005, one larva [ROME]. Literature consulted: Jacobus et al. (2004).

grandis—Material examined: Canada, Saskatchewan, stream at km 150 of Hwy 905, 57°25.21'N, 103°55.77'W, 13-VI-2000, emerged 22-VI, JM Webb, one male adult (genitalia and foreleg on slide), associated exuviae [JMW]; Low Cr at Hwy 904, 54°49'26"N, 108°28'40"W, 10-VI-2001, emerged 13-VI, JM Webb, M Pollock, one male adult, associated exuviae [JMW]. USA, Utah, Washington Co, Santa Clara R at Pine Valley, 26-V-1971, WP McCafferty, larval mouthparts on slide [PERC]. Egg unknown.

heterocaudata—Material examined: USA, Idaho, Custer Co, at lights, Big Lost R, 3 mi north of Mackay on alt. US93, 6000', 25-VII-1964, SL Jensen, PS Lombardi, FD Isenberg, one male adult [PERC]. Wyoming, Yellowstone NP, Firehole R., Biscuit Basin, 21-VI-1946, GF Edmunds, Jr., three larvae [PERC]; YNP, Nez Perce Cr. at hwy. jct. betw. Madison Junction and Old Faithful, 7200', 25-VI-1964, SL Jensen, JW Richardson, three larvae (parts on slide) [PERC]. Egg unknown.

hispanica—Material examined: Spain, Valdesqui, Los Cotos, Rio Lozoya, 1800 m alt., 16-VII-1986, four larvae, one female adult [PERC]. Literature consulted: Studemann and Tomka (1987: Figs. 15–16, 27); Studemann et al. (1995: Figs. 25–27); Studemann and Landolt (1997: Fig. 22).

hispida—Material examined: USA, North Carolina, Swain Co, Great Smoky Mountains NP, Twentymile Cr at Twentymile Trailhead, near Twentymile Ranger Station, 35°28'07"N, 83°52'34"W (NAD27), 18-V-2001, CD & RP Randolph, LM Jacobus, two larvae [PERC]; same stream, but 3-IV-1934, JG Needham, one larva (holotype) [PERC]. USA, Tennessee, Blount Co, Great Smoky Mountains NP, trib Forge Cr, Gregory Ridge Trail, near camp 12, 35.5539°N, 83.8381°W, 25-V-2001, B Heinold, one male adult [INHS]. Egg unknown.

hystrix—Material examined: USA, Idaho, Lemhi Co, Spring Cr 1.5 mi NE Shoup, Salmon NF, 2/10-VII-1964, CR Whitt, IR Thornton, subimago [PERC]. Montana, Ravalli Co, E Fk Bitterroot R, 10 mi above jct with W Fk Bitterroot R, 24-VI-1965, JR Grierson, one larva [PERC]. Washington, Pierce Co, Mount Rainier NP, springfed stream, Westside Rd, 1.2 mi N of Hwy 706, 16-VI-2004, emerged 21-VI, Kondratieff, Schmidt, three male adults, one female adult, associated larval exuviae [PERC].

idahoensis—Material examined: USA, Idaho, Idaho Co, Bridge Cr at Hoodoo Lake Rd (FR360), 46°21'53"N, 114°38'11"W (WGS84), 1708m elev, 29-VII-2002, WP McCafferty, LM Jacobus, three male adults, two female adults, one male subimago, two female subimagos, associated exuviae (alates emerged 9-VIII through 17-VIII), four larvae [PERC]; same data, one male adult, one set larval exuviae [CSUC]. Literature consulted: Jacobus and McCafferty (2004a: Fig.1).

ignita—Material examined: United Kingdom, England, North Yorkshire, R Skirfare, 1 mi north of Kilnsey, 17-VIII-1996, F Lloyd, one larva [PERC]. Switzerland, Limmat R at Zurich, 5-VII-1964, GF Edmunds, Jr, six male adults [PERC]. Literature consulted: Studemann et al. (1995: Figs. 7–9, 40–43); Studemann and Landolt (1997: Figs. 42–44).

ikonomovi—Material examined: Greece, Ipiros, Voidomatis R at Klidonia, alt 500 m, 9-VII-1988, Landolt, Studemann, three larvae, one male adult [PERC].

Spain, Sierra Nevada, Rio Tzevelez, Tzevelez, 21-VI-1953, J Aubert, H Bertrand, three larvae [MZL]. Literature consulted: Studemann et al. (1989: Figs. 3–6); Studemann et al. (1995: Figs. 10–12); Studemann and Landolt (1997: Fig. 19).

indica—Literature consulted: Kapur and Kripalani (1961: Figs. 1a–b). Egg, larva and male adult unknown.

insolta—Material examined: Thailand, Mae Hong Son Prov, Namtok Maw Pang, 19°22'N, 98°22'E, 850m, 14-X-2002, CMU team, one larva [ISUI]. Egg and male adult unknown.

invaria—Material examined: USA, Virginia, Bedford Co, Big Otter R at US460, 24-IV-1982, Kondratieff, two male adults, one male subimago, four female adults, associated exuviae [VPIC]; Giles Co, Little Stony Cr at Rt 460, Pembroke, 19-IV-1980, emerged 29-IV, Kondratieff, two male adults, one set larval exuviae [VPIC]. Tennessee, Anderson Co, Clinch R mile 78.5, 24-V-2001, 4:30pm, alates [PERC]. Literature consulted: Smith (1935); Koss (1968); Jacobus and McCafferty (2003b).

ishiwatai—Material examined: Japan, Nara, Kawakami, Unokawa, Nakai Stream, 1-VI-2002, T Fujitani, two male adults [PERC]; Tochigi Pref, Kunu R at Kinu Bridge, Utsunomiya-shi, 14-V-1991, S Ishiwata, one larva [PERC]. Egg unknown.

ishiyamana—Material examined: Japan, Ishiyama, 7-VIII-1903, one male adult (*D. ishiyamana* type) [EIHU]; Japan, Nara, Kawakami, Unokawa, Nakai Stream, 8-VI-2002, T Fujitani, seven larvae [PERC]; Japan, Tochigi Pref., Yudaki Falls, 7km north of Lake Chuzenji, 12-VII-2002, Terry & Jarvis, DNA holotype EP204, larvae [BYU]. Literature consulted: Okazaki (1984: Fig. 26; identified as *D. cryptomeria*).

jacobi—Material examined: USA, Washington, Whatcom Co, Swamp Cr, 9-VIII-1966, RE Vandermay, seven larvae [CAS]; same locale and collector, 14-VIII-1966, one male adult (genitalia on slide) [CAS]. Egg unknown.

japonica—Material examined: Japan, Kyoto Pref, Yura Stream at Habi, Oe Town, 31-III-1998, T Fujitani, two larvae (maxilla on slide) [PERC]. Literature consulted: Ishiwata (1987: Fig. 1). Egg unknown.

jinghongensis—Material examined: Thailand, Mae Hong Son Prov, R Nam Lang, Soppong, light trap from benthos, 3–27-IV-2003, Braasch, four male adults, one female adult, three larvae [PERC]. Egg unknown.

karia—Material examined: Turkey, Mula, Fethiye-Antalya Rd, Kemer Town, 200 m, 20-VII-1987, three larvae [BMNH—1989-83]. Egg and male adult unknown.

kohnoi—Material examined: Japan, Nagano Pref, Hase, Sugishima, Mibu Stream, 23-V-2001, T Fujitani, one larva [PERC]; Takeshi, Takeshi Stream, 20-V-2001, T Fujitani, one larva [PERC]; Tochigi Pref, Yu R at Oku-Nikko, 27-V-1946, M Kohno, one larva (paratype) [PERC]. Literature consulted: Okazaki (1984: Fig. 49). Male adult unknown.

kozhovi—Material examined: Korea, Myohyang Mts, Hyansan str, I Hyangson, 28-V-1986, ten larvae [PERC]. Literature consulted: Bajkova (1972: Figs. 33–34); Studemann and Landolt (1997: Figs. 37–38).

lacuna—Material examined: Thailand, Mae Hong Son, River Nam Lang, Soppong, 4-II–5-III-2004, Braasch, two larvae, two male subimagos, two female subimagos [PERC]. Egg unknown.

lata—Material examined: Canada, Quebec, Wakefield, 28-VII-1926, GS Walley, one male adult (*inflata* paratype) [PERC]. USA, Virginia, Giles Co, Sinking Cr at Rt 42, Newport, 26-V-1981, emerged 2-VI, Kondratieff, five male adults, three female adults, associated exuviae [VPIC]. Literature consulted: Koss (1968: Figs. 43–44); Koss and Edmunds (1974: Fig. 129). Studemann and Landolt (1997: Figs. 45–46, 48–49).

lepnevae—Material examined: Mongolia, Egiyn-gol, 40km S of Khubsugul, 23/24-VIII-1997, N Kluge, two male adults, one set subimago exuviae, one male subimago emerging from larval exuviae, one larva [PERC]. Literature consulted: Studemann and Landolt (1997: Fig. 47).

levanidovae—Material examined: Korea, Gangwon-do Jeongseon-gun Imgye-myeon (St), V-1984, ten larvae [SWU—EPH-1406]; Gyeonggi-do Namyangji-si Cheonmasan (Mt), 6-V-1995, one male adult (reared) [SWU—EPH-1410]. Literature consulted: Ishiwata (2003: Figs. 7–8).

levis—Material examined: USA, California, Napa Co, Capell Cr, 14-VI-1952, WC Day, one male adult, two sets larval exuviae, three larvae (paratypes) [PERC]. Egg unknown.

longforceps—Literature consulted: Gui et al. (1999: 342) [Changfa Zhou (Nanjing, China) kindly shared illustrations of this OTU and photos of specimens that had been compared to the holotype]. Egg and larva unknown.

longicaudata—Material examined: Korea, Gyeonggi-do Namyangju-si Kwangrung (St), 16-I-1983, larvae [SWU—EPH-3193]; same locale, but 15-IV-1984, one male adult [SWU—EPH-3192]. Literature consulted: Okazaki (1984: Figs. 34–35) [data omitted: images poor].

longipennis—Literature consulted: Zhou et al. (1997a: Figs. 6–9). Egg and larva unknown.

lutosa—Material examined: Taiwan, Nantou Hsien, Shuili, 290m elev, 1991-11-18(A), SC Kang, one larva (paratype) [MZL]. Literature consulted: Kang and Yang (1995: Figs. 22–25). Male adult unknown.

maculata—Material examined: USA, California, Napa Co, Hopper Cr, 2-V-2000, larvae (eggs dissected) [PERC]; San Luis Obispo Co, blacklight at Tassajara Cr, 7 mi. north of San Luis Obispo, 6-VI-1971, JD Pinto, one male adult [PERC].

major—Material examined: Germany, Stream Fulda, D-36110 Schlitz/Pfordt, 16-IV-2002, R Lieske, ten larvae (some gills removed) [PERC]; Simmerbach (a confluence of the Nahe River, a left hand tributary of the River Rhine), 3-V-2003 (reared to 18-V-2003), A Haybach, three male adults, two female adults (all reared), five subimago exuviae [PERC]. Literature consulted: Studemann et al. (1995: Figs. 30–32); Studemann and Landolt (1997: Figs. 20–21).

media—Material examined: Malaysia (east), Sabah, Liwagu R at Liwagu Cave, southeast of Kinabalu NP Headquarters, 1525 m, S7, 14–15-VIII-1972, WL & JG Peters, one larva [FAMU]; Liwagu R at bridge, Ranau, 335 m, S4e, 11–16-VIII-1972, GF & CG Edmunds, four male adults, two male subimagos, associated subimago exuviae [PERC]; Sungai Moyog, 3 mi E of Penampung, 27-IX-1978, GF & CH Edmunds, three male subimagos, three female subimagos (eggs dissected) [PERC]. Note: Just prior to submitting this paper for publication, Michel Sartori (Lausanne, Switzerland) informed us that at least some of these specimens might represent an undescribed species. To the best of our knowledge, data listed in character matrices for OTU media remain accurate and the results of phylogenetic analyses are not affected. Taxonomic issues will be dealt with elsewhere (Sartori et al., in progress).

mesoleuca—Material examined: Poland, R Warta at Ostrowsko, 1-VI-1966, Keffermüller, three male adults [PERC]. Spain, Sierra de Catorla, Rio Guadelquivir, Puente de la Reina, 28-V-1959, J Aubert, four larvae [MZL]. Literature consulted: Studemann et al. (1995: Figs. 13–15, 44–45); Studemann and Landolt (1997: Figs. 23–25).

micheneri—Material examined: USA, Arizona, Yavapai Co, Verde R above Clarksdale, off Hwy 89, 12-V-1969, RW Koss, AV Provonsha, one male adult, one male subimago, two female subimagos, one set subimago exuviae, seven sets larval exuviae, two larvae [PERC]; New Mexico, Catron Co, Gila R at jct. W Little Cr, 42 mi north of Silver City, 15-VII-1967, R&D Koss, one male adult (genitalia on slide) [PERC]. Egg unknown.

mikhaili—Literature consulted: Tiunova (1995: Figs. 1–9). Egg unknown.

montana—Material examined: Taiwan, Taichung, Hoping, Wuling Farm, 1620m elev, 20-I-1987, PS Yang, KJ Huang, one larva (paratype) [MZL]. Literature consulted: Kang and Yang (1995: Figs. 9–10). Male adult unknown.

mucronata—Material examined: Germany, stream Breitenbach nr D-361 Schlitz/Pfordt, 16-IV-2002, Reimo Lieske, 12 larvae [PERC]; Taunus mountains, R. Wisper, 7°55'E, 50°09'N,•H100 m elev, 12-V-2004, A Haybach, two male adults, one female adult, one female subimago, all associated exuviae (reared) [PERC]. Literature consulted: Studemann and Landolt (1995: Figs. 16–18); Studemann and Landolt (1997: Fig. 12).

naga—Material examined: Malaysia, Selangor, Gombak R, 9 mi N of Kuala Lumpur on Bentong Rd, 9-I-1969, JE Bishop 24-VIII-1969, one male adult [FAMU]; same locale, but 27-VIII-1969, one larva (paratype) [FAMU]. Thailand, Mae Hong Son, Namtok Mae Surin National Park, Nam Mae Surin, above falls, gravel substrate, 18°56'N, 98°04'E, 1220m elev, 15-X-2002, CMU team, one larva [ISUI]. Literature consulted: Jacobus et al. (2004: Fig. 5).

needhami—Material examined: USA, Indiana, Elkhart Co, Elkhart R, 1 mi southeast of Millersburg at bridge on gravel road, 21-V-1972, WP McCafferty, AV Provonsha, one male adult, associated exuviae [PERC]; Bartholomew Co, White Cr, private farm crossing south of Co Rd 930 South, 39°03'02"N, 85°58'01"W, 19-IV-2005, LM Jacobus, JM Webb, JM Hwang, MW Jacobus, one larva [PERC]; Michigan, Arenac Co, Omer, Rifle R at public access site, 44°02'41"N, 83°51'20"W, 24-VI-2002, LM Jacobus, BL Hass, subimago (eggs dissected), associated exuviae [PERC].

nepalica—Material examined: China, Henan Prov, Song-xian Co, Tian-chi Mtn, alt 1061 m, CF Zhou, LI Peng, three larvae, one male adult [PERC]. Nepal, Lalitpur, creek above Godawari, on rd to Phulchowki, 8-VII-1994, GW Courtney, two larvae [ISUI]. Literature consulted: Kang and Yang (1995: Figs. 20–21); Jacobus et al. (2004).

nigra—Material examined: Japan, Nagano, Takeshi, Takeshi stream, 20-V-2001, T Fujitani, one larva [PERC]; Kanagawa, Fujino-machi, Sawai R, 17-V-1985, S Ishiwata, one male adult, one male subimago [PERC]. Literature consulted: Ishiwata (2003: Figs. 11–12).

nigromaculata—Literature consulted: Xu et al. (1980: 60); You and Gui (1995: Figs. 140a–f). Egg and larva unknown.

notata—Material examined: Germany, Baden-Württ., Donau / Riedlingen, 540 m alt, 28-V-1988, three larvae, three sets of larval exuviae [PERC]. Literature consulted: Studemann et al. (1992: Figs. 334, 338); Studemann et al. (1995: Figs. 19–21); Studemann and Landolt (1997: Fig. 11).

nuda—Material examined: Altai, Kosh-Agach, Riv Chuya, 4-VIII-1987, N Kluge, one male adult (reared), associated exuviae [PERC]. Alaska, S Slope, Monument Cr, 1 mi above confluence with Sheenjak R, Yukon R System, 29-VII-1972, 67/57/45N, 143/13/00W, one larva [PERC]. Literature consulted: Studemann and Landolt (1997: Fig. 16).

occiprens—Material examined: Korea, Gyeonggi-do Pocheon, Sanjeong Lake, 27-VII-1995, three larvae [SWU–EPH1630]. Literature consulted: Ishiwata (2000: Fig. 13). Egg probably unknown; illustration by Okazaki (1984: Fig. 33) possibly egg of OTU orientalis.

oriens—Material examined: Thailand, Namtok Maw Pang, leaf pack, 19°22'N, 98°22'E, 850 m elev, 19-III-2002, GW Courtney, one larva (paratype) [FAMU]. Egg and male adult unknown.

orientalis—Material examined: Korea, Gangwon-do Jeongseon-gun Imgye-myeon, V-1984, two larvae [SWU—EPH-1440]. No locale data, but 28–29-VI-1982, one male adult and associated subimago exuviae [PERC; No collection data are associated with the male adult, but it was identified and donated by Nikita Kluge (St. Petersburg, Russia)]. Literature consulted: Okazaki (1984: Figs. 19–20); Ishiwata (2003: Figs. 15–16).

padunica—Material examined: Russia, Primorskiy Kray, River Narva (= Sidime), 12-VII-1980, V Belov, one larva (one maxilla on slide) [PERC]. Literature consulted: Kazlauskas (1963); Tiunova (1995: Fig. 10). Egg unknown.

paradinasi—Material examined: Spain, Lugo, Rio Asma in Chantada, 480 m alt, 20-VII-1986, Landolt, Studemann, Tomka, two larvae, one male adult (reared) and associated exuviae [PERC]. Literature consulted: Studemann et al. (1995: Figs. 1–3); Studemann and Landolt (1997: Figs. 17–18).

pascalae—Material examined: Island of Borneo, Indonesia, East Kalimantan, Riv Seturan, Loc Seturan, Aff cours principal, 3°00'05"N, 116°30'48"E, 28/III/2001, P Derleth, B Feldmeyer, three larvae (paratypes) [PERC]. Literature consulted: Jacobus and Sartori (2004).

pelosa—Material examined: USA, Idaho, Lemhi Co, Salmon R below jct Panther Cr, ca 8.5 mi W of Shoup, Salmon NF, 6–16-VII-1964, one male adult [PERC]; California, Los Angeles Co, Elizabeth Lake, 16-V-1951, one larva (mouthparts on slide) [PERC]. Egg unknown.

*percult*a—Material examined: Vietnam, stream 6 km south of Dalat, 1400 m elev, 20-VI-1961, NR Spencer, four larvae (paratopotypes) [PERC]. Egg and male adult unknown.

punctisetae—Material examined: Japan, Shizuoka, Shimizu, Kakita Stream, Kakitagawa Bridge, 23-IV-2001, one larva [PERC]. North Korea, Myohyang Mts, Str Hyangson, 28-V-1986, five male adults, one female adult [PERC]. Literature consulted: Okazaki (1984: Fig. 36).

quadrata—Literature consulted: Kluge et al. (2004: Figs. 1–9). Egg and male adult unknown.

sachalinensis—Material examined: Japan, Fukushima Pref, Tatenouchi-mura, Kita-aizu-gun, 14-V-1950, M. Kohno, one larva (*bifurcata* paratopotype) [PERC]; Nagano, Hase, Sugishima, Mibu Stream, 23-V-2001, T Fujitani, one larva [PERC]. Literature consulted: Ueno (1931: Figs. 32–33); Ishiwata (2001). Egg unknown.

septentrionalis—Material examined: USA, Massachusetts, Amherst, 3-VI-1939, JR Traver, eight male adults, eight female adults [PERC]; Tennessee, Blount Co, Abrams Cr at Cades Cove Loop Rd, Great Smoky Mountains NP, stream bank (flowing water), 35°35'36"N, 83°50'42"W (NAD27), 16-V-2003, LM&BLH Jacobus, one larva [PERC]. Literature consulted: Smith (1935).

serrata—Material examined: USA, North Carolina, Macon Co, Cullasaja R at Rt 1672, 7-VII-1989, Kondratieff, 21 male adults, six female adults (eggs extracted from one), three male subimagos, subimago exuviae [VPIC]; Virginia, Mongomery Co, Little R along Little Camp Rd, 37°00'07"N, 80°24'59"W, 15-VI-2003, JM Webb, LM Jacobus, three larvae [PERC].

serratoides—Material examined: USA, Virginia, Montgomery Co, Little R at Rt 787, 12-VII-1981, Kondratieff, two male adults, five female adults, associated exuviae (reared) [VPIC]. Egg unknown.

setigera—Material examined: Korea, Chungcheongbuk-do Jecheon Bongyang Nomogyegok, 22-VIII-1995, 17 larvae [SWU—EPH-1652]. Mongolia, "SRP03072202" sweep, Sanaa (collector), one male adult, one male subimago, three female adults [PERC]. Literature consulted: Okazaki (1984: Fig. 31); Studemann and Landolt (1997: Figs. 35–36).

soldani—Material examined: Vietnam, Ha Son Binh Prov, small unnamed stream, about 5 km NW of Ba Vi, 15-XI-1984, T Soldán, one larva [PERC]. Egg and male adult unknown.

solida—Material examined: Korea, Jeollabuk-do, Muju, Deogyusan, 20-V-1983, four larvae [SWU]. Literature consulted: Tiunova (1988). Egg unknown.

spinifera—Material examined: USA, Montana, Missoula Co, Lolo Cr, 0.6 mi NE of Lolo Pass, 46°38'37"N, 114°34'44"W (WGS84), 28-VII-2002, WP McCafferty, LM Jacobus, 13 larvae [PERC]; Washington, Pierce Co, Hillside stream, 1.5 mi N Hwy 706 Westside Rd, Mt Rainier NP, 14-VII-2003, Kondratieff & Schmidt, one male adult (reared), associated larval exuviae [CSUC]. Egg unknown.

submontana—Material examined: Tajikistan, Kolai-Humb. Distr, Pamirs, nr nulvand, 20-IX-1987, N Kluge, one male adult, one set subimago exuviae, one male subimago, two larval exuviae [PERC]. Literature consulted: Studemann and Landolt (1997: Figs. 50–51).

subsolana—Material examined: Afghanistan, Kabul Prov, Kabul R, Kotasungi, 31-V-1967, M Nazim, one larva (holotype; mouthparts dissected and missing from vial) [PERC]. Literature consulted: Allen (1973: Figs. 1, 9, 10). Egg unknown.

subvaria—Material examined: Canada, Quebec, Cascades Point, 3-VI-1930, GS Walley, one male adult (genitalia missing), one female adult (paratypes) [PERC]. USA, Massachusetts, Hampshire Co, South Hadley, 4-V-1939, JR Traver, two male adults, one male subimago, one female subimago, associated exuviae (reared) [PERC]. Literature consulted: Burks (1953); Koss (1968); Koss and Edmunds (1974: Fig. 130).

teresa—Material examined: USA, California, Napa Co, Garnett Cr, 1-V-2000, larvae (dissected for eggs) [PERC]; San Mateo Co, San Gregorio Cr, 17-VI-1950, WC Day, three male adults, two female adults, one larva [CAS].

tianmushanensis—Literature consulted: You and Gui (1995: Figs. 141a–e). Egg and larva unknown.

tibialis—Material examined: USA, Idaho, Custer Co, Ω mi north of Mackay on US alt 93, 5891' elev, 25-VII-1964, SL Jensen, PS Lombardi, FD Isenberg, male adults [PERC]; Montana, Lewis and Clark Co, Little Prickly Pear Cr at Prickly Pear Fishing Access, 1 mi north of Interstate 15 Exit 219, on Rec Rd, 46°55'48"N, 112°07'22"W (WGS84), 28-VII-2002, WP McCafferty, LM Jacobus, one larva [PERC]. Literature consulted: Studemann et al. (1995: Figs. 28–29).

triacantha—Literature consulted: Tshernova (1949: Figs. 41–47); Yoon and Bae (1988: Figs. 7–9); Ishiwata et al. (2000: Figs. 3b–e).

trispina—Material examined: Japan, Nara, Higashi-Yoshino, Omata, Omata Stream, Kuramae Bridge, 5-V-2002, T Fujitani, three larvae [PERC]. Literature consulted: Okazaki (1984: Fig. 50). Male adult unknown [adult described as *trispina* by Ueno (1931) is actually that of *sachalinensis* (Ishiwata 2001)].

tsuno—Material examined: Japan, Nara, Kawakami, Unokawa, Nakai-keikoku, 5-V-2002, T Fujitani, one larva [PERC]; Nara, Kawakami, Unokawa, Nakai Stream, 8-VI-2002, T Fujitani, four male adults [PERC]. Egg unknown.

tuberculata—Material examined: USA, North Carolina, Swain Co, Great Smoky Mountains NP, Kanati Fork, 0.3 km upstream from Newfound Gap Rd (US441), Kenati Fork Trailhead at 35°35'14"N, 83°21'48"W (NAD27), 26-IX-2002, LM&PD Jacobus, one larva [PERC]; South Carolina, Oconee Co, E Fk Chattooga R, Rt 107, 1 km S of North Carolina state line, 35°N, 83°04'W, 3-X-1997, S Spichiger, one male adult (genitalia on slide), associated exuviae (reared) [PERC]. Literature consulted: Jacobus and McCafferty (2004b).

uenoi—Material examined: Nepal, Nawakot & Sindhu Dists., Ω mi N Gulbhanjyang (on lower trail), elev ca 7100', 18-IX-1968, C Weins, one larva (eggs removed from abdomen) [PERC]. Literature consulted: Ueno (1953: Figs. 1–19). Male adult unknown.

velmae—Material examined: USA, California, Fresno Co, Huntington Lake, Sample Meadow, 2200m, 10-VII-1984, J MacDonald, two larvae [PERC]. Egg and male adult unknown.

verruca—Material examined: USA, Oregon, Benton Co, Parker Cr, Mary's Peak, 28-VI-1980, one male adult (penes on slide), one female adult (eggs extracted), associated exuviae (reared) [PERC].

walkeri—Material examined: USA, Michigan, Crawford Co, AuSable R, T26N, R2W, Sec13 (some labels read "at Rieth Haven"), 26/VI-18/VII/1948, JW&FA Leonard, two male adults, five female adults, one female subimago, four sets subimago exuviae, five sets larval exuviae [UMMZ]; Tennessee, Blount Co, Middle Prong at Tremont Rd, 50m upstream from gate, Tremont, GRSM, 35°38'25"N, 83°41'23"W, 11-VI-2003, JM Webb, LM Jacobus, 10 larvae [PERC]. Literature consulted: Koss (1968).

zapekinae—Material examined: Korea, Gyeonggi-do Kapyong Sudongcheon, 9-VII-1993, four larvae [SWU—EPH-1661]. Literature consulted: Bajkova (1972: Figs. 35–36); Studemann and Landolt (1997: Figs. 30–32).

CHARACTERS

Life stages from each OTU were screened for characters, with some eggs being examined via Scanning Electron Microscopy at the Life Science Microscopy Facility, Purdue University. Based on the examination of the specimens and published descriptions indicated above, MacClade (Maddison and Maddison 2005) was used to build a data matrix that includes characters taken from the egg, larva and adult stages. OTUs were scored for characters in alphabetical order to reduce potential bias in coding character states.

Certain characters were excluded from consideration for analysis, including autapomorphies of individual species, coloration and internal anatomy (following e.g., McCafferty 2004). Some characters historically associated with ephemerellid generic identification (see, e.g., Day 1956; Edmunds 1959; Allen and Edmunds 1963a, 1965; Edmunds and Waltz 1996; Waltz and Burian 2008), such as the degree of reduction of the maxillary palp, were excluded from analysis. For example, the comparison of lengths of maxillary palps on all known larvae revealed that no delineation could be made between those palps formerly considered "reduced" and those not so considered. Another such character excluded from analysis was the presence or absence of hairlike setae on the caudal filaments. Although some species have many of these setae, and others have none, a great number of species have these setae distributed sparsely across only certain regions of the caudal filaments or have these setae variably present or absent, depending on the individual examined (e.g., Jacobus et al. 2003).

The following characters are used for phylogenetic analysis, with their states indicated by arbitrary (except for Character 8) numerals in parentheses. The terms "strands" and "mesh" are from Koss (1968), referring to the polygonal reticulations on the egg chorion and the spaces enclosed by these reticulations, respectively. The term tubercle historically has been used in reference to various structures associated with the body armature of larvae, but it is used here only for the small, central processes found on the mesh of the egg chorion of certain species. In general, protrusions from the integument are called spines. Such protrusions on the forefemur that have a terminal seta are called chalazae. "Frontoclypeal projections" (e.g., Allen and Edmunds 1962) actually are part of neither the frons nor the clypeus; they are referred to here as subantennal spines. The term "starlike" (Studemann and Tomka 1987) is used to describe the thoracic setae illustrated in Figure 36.

For the purposes of the phylogenetic analyses, character 8 is designated to have "ordered" states, and all others have "unordered" states (Swofford 2002, Maddison and Maddison 2005). No other weighting is used.

Egg

1. Chorion with: ridged strands (Figs. 1, 3–5, 12, 13) = 0; furrowed strands (Figs. 6, 7) =1; no reticulation (Figs. 2, 8–11, 14, 15) =3; dimples (Fig. 17) = 4.
2. Mesh, if present: with multiple tubercles (Figs. 1, 3) = 0; with a single, central process (Fig. 4, 5) = 2; smooth (Fig. 12) = 3.

Larva

3. Suboccipital spines: present (e.g., Fig. 19) = 1; absent = 0.
4. Paired, sharp frontal spines: absent = 0; present (Fig. 18) = 1.
5. Frontal shelf: not projected = 0; projected anteriorly (Fig. 19) = 1.

6. Medial ocellar spine: absent or very short = 0; greatly elongate (Fig. 18) = 1.
7. Subantennal spines: absent = 0; present (Fig. 20) = 1.
8. Mandibular canines: not greatly enlarged (Fig. 21) = 0; offset from plane of mola at a distance greater than their length, but not tusklike (Fig. 22) = 1; tusklike (Fig. 23) = 2.
9. Maxillary palp: present = 0; absent = 1.
10. Maxillary palp segment 2: bare = 0; with whorl of long setae distally (Fig. 30) = 1; densely covered with setae (Fig. 29) = 2.
11. Distal field of setae on maxilla: not numerically increased (Figs. 24, 30) = 0; numerically increased (Figs. 25, 28, 29) = 1.
12. Maxillary crown: attenuate (Figs. 24, 30) = 0; expanded (Fig. 29) = 1; flattened (Fig. 28) = 2.
13. Maxillary canines: sharp or spoonlike (Fig. 24) =0; fused and reduced to a wide blade (Figs. 26, 27) = 1; vestigial (Fig. 28) = 2.
14. Maxillary canine blade length: subequal to width (Fig. 26) = 0; much less than width (Fig. 27) = 1.
15. Maxillary canines: laterally smooth, rarely serrate at extreme base (Fig. 24) = 0; laterally serrate for most of their length (Fig. 25) = 1.
16. Distribution of lacinial setae on maxilla: clumped distally (Figs. 24, 29) = 0; distributed more or less evenly along inner margin between medial setae and apex (Figs. 28, 29) = 1.
17. Prothoracic anterolateral projections: very subtle or absent = 0; prominent (Fig. 32) = 1.
18. Prothoracic sternum: concave anteriorly (Fig. 40) = 0; with anterior projection (Fig. 39) = 1.
19. Mesal plate: unadorned = 0; with paired ridges or spines on posterior margin (Fig. 35) = 1.
20. Mesothoracic anterolateral projection: absent = 0; broad and blunt (Fig. 32) = 1; notched, sometimes with posterior portion sharp and elongate (Figs. 33, 34) = 2.
21. Mesothoracic, brown excrescences (not spicules): absent = 0; present (Figs. 37, 38) = 1.
22. Forefemur: not enlarged (Fig. 45) = 0; enlarged (Figs. 46, 47) = 1.
23. Leading margin of forefemur: smooth (Fig. 45) = 0; with stout chalazae (Figs. 46, 47) = 1.
24. Forefemur upper surface: smooth (Figs. 45) = 0; ridged or sculpted (Fig. 47) = 1.
25. Chalazae on upper face of forefemur: absent (Figs. 45, 46) = 0; present (Fig. 47) = 1.
26. Foretibial apical projection: absent = 0; present (Fig. 46) = 1.
27. Second row of denticles on claw: absent = 0; present (Fig. 43) = 1.
28. Distal palisade of denticles on claw: absent = 0; present (Fig. 42) = 1.
29. Distalmost denticle on claw: not greatly enlarged = 0; greatly enlarged (Fig. 44) = 1.
30. Abdominal tergal spines: paired = 0; reduced to tufts of setae (Fig. 54) = 1; absent = 2; single (Fig. 49) = 3.
31. Anterior ridges of paired abdominal spines: subparallel or absent = 0; obliquely oriented in anteriormost half (Fig. 52) = 1.
32. Posterior margins of abdominal terga: without bristlelike setae = 0; with bristelike setae, usually long (Fig. 51) = 1.
33. Posterior abdominal terga with dorsally projecting setae: absent = 0; present (Fig. 55) = 1.
34. Lateral margins of abdominal tergal posterolateral projections: with setae (Figs. 52, 53) = 0; without setae = 1.
35. Setae on lateral margins of abdominal tergal posterolateral projections: numerous and generally spatulate (Fig. 52) = 0; numerically reduced, stout and spinelike (Fig. 53) = 1.
36. Gills 1: present = 0; absent = 1.

37. Gills 3: present = 0; absent = 1.
38. Strong, transverse band of weakened membrane on gills 3: absent = 0; present (Fig. 50) = 1.
39. Ventral lamella of gill 6: deeply cleft (Fig. 56) = 0; with lateral lobes apparently fused (Fig. 57) = 1.
40. Gill 7 inserted: near posterolateral corner = 0; on middle of tergum = 1.
41. Dorsally projecting row of setae on caudal filaments: absent = 0; present (Fig. 55) = 1.
42. Length of medial filament relative to abdomen: nearly subequal = 1; much longer, usually equal to, or greater than, body length = 2; less than half = 0.
43. Development of cerci relative to medial filament [states also present in subimago and adult]: subequal = 0; reduced = 1.

Male adult

44. Proximal hook on foretarsus: absent = 0; present (Fig. 60) = 1.
45. Genital forceps segment 3: spherical or ovoid = 0; length more than 2x width (Figs. 68, 81) = 1.
46. Genital forceps segment 2: without any of the following modifications = 0; somewhat twisted and flattened (Fig. 76, 77) = 1; with medial crease (Figs. 79, 84–86) = 2; with triangular apical expansion (Fig. 66) = 3; with quadrate apical expansion (Fig. 74, 75) = 4; swollen and bowed (Fig. 81) = 5.
47. Dorsolateral projection of gonopore: absent = 0; present and usually very sharp (e.g., Figs. 61, 62, 66, 67, 68, 69, 77) = 1.
48. Sublateral spinulelike setae on outer margin of penes lobes: absent = 0; present (Fig. 76) = 1.
49. Apicoventral spinelike setae on penes: absent = 0; present (Figs. 65, 75) = 1.
50. Dorsomedial spinelike setae on penes lobes: absent = 0; present (Figs. 74, 75) = 1.

ANALYSIS

Prior to this study a few species groups had been hypothesized to be monophyletic, primarily by Kluge (2004), based on the examination of morphological characters. We use these morphology-based hypotheses, in general, as bases for establishing a revised classifcation. Kluge (2004) recognized a large clade, hereafter referred to as the fused-gill clade, defined by the apomorphic loss of the medial cleft of the ventral lamella of gill 6 of larvae. Two of the OTUs in this study, nuda and tibialis, were not considered by Kluge (2004) to be part of the fused-gill clade. Microscopic examination of late larval instars revealed that the ventral lamellae of gills 6 of these OTUs are not deeply cleft as indicated, for example, by Tshernova (1949: Fig. 92); rather, the deep cleft is absent, and the lateral lobules are enlarged (Fig. 59). OTUs nuda and tibialis are included in the fused-gill clade in the following analyses, because the deep cleft is absent in later instars.

Within the fused-gill clade, Kluge (2004) recognized as monophyletic: the heterocaudata clade, defined here as having the medial filament more robust and much longer than the cerci in the larva, subimago and adult stages; the grandis clade, defined here as having the length of segment 3 of the male genital forceps at least twice its width *and* the forefemur of larvae almost always enlarged or with marginal chalazae; and the nigra clade, defined here as having larvae with denticulate canines on the maxilla that sometimes are reduced to a broad blade *and* larvae with distinctive anterolateral projections on the mesothorax.

Outside the fused-gill clade, Studemann and Tomka (1989), Vidinova and Russev (1997) and Marie et al. (1999) have discussed the mesoleuca group, which contains at least three very similar species, included in this study as OTUs mesoleuca, bauernfeindi and subsolana. This group was not subjected to phylogenetic analysis, and it is considered here to be an unresolved but monophyletic bush, represented in analysis by only the mesoleuca OTU.

OTUs apopsis, braaschi, changbaishanensis, fusongensis, indica, longforceps, longipennis, nigromaculata and tianmushanensis were excluded from any analysis due to their having extremely few of no associated phylogenetic data in this study. OTU braaschi is known only as a poorly described larva; OTU indica is known only as a female adult; and the remaining seven are known only as male adults. Of these nine, it was possible for us to examine specimens of only the apopsis OTU directly. Each of these OTUs is treated in the Classification section, however, based on the few taxonomic characters that are associated with them (Kapur and Kripalani 1961, Xu et al. 1980, Braasch 1981, Su and You 1988, McCafferty 1992, Zhou et al. 1997a, Gui et al. 1999).

PAUP* (Swofford 2002) was utilized to conduct phylogenetic analyses of subsets of the data matrix, as outlined below. The entire data matrix was executed in PAUP*, and the add or delete taxa functions were used to acquire the subsets subjected to analysis. The factory default settings were employed, except that multiple states were to be interpreted as polymorphisms (Swofford 2002).

OTU attenuata was used to root all resultant trees. OTUs berneri and teresa were included as additional outgroups in the analysis of the nigra clade. OTUs berneri and teresa were chosen based on the intuitive assumption that both are closely related to, but not part of, the nigra clade. This assumption was based on the hypothetically pleisiotypic characterization of both OTUs' mouthparts relative to the nigra clade, the hypothetically pleisiomorphic nature of OTU teresa's eggs and male genitalia, and the hypothetically synapotypic characterization of the ventral lamellae of gills 6 of OTU teresa, OTU berneri and the nigra clade.

Each analysis consisted of a heuristic search for the set of best trees under the parsimony criterion and then the generation of a consensus tree from this set of most parsimonious trees. Consensus trees can provide a useful insight into underlying phyletic relationships when numerous best trees are encountered (Stevens and Wall 1996).

First, each of the clades grandis, heterocaudata and nigra was analyzed separately. The resulting consensus trees were examined, and the OTU occuring the fewest number of nodes away from the base of the tree was noted from each. These hypothetically most pleisiomorphic OTUs were used as proxies for their respective clades in subsequent analyses.

The entire fused-gill clade was analyzed following the analyses of the grandis, heterocaudata and nigra clades. In order to do this, all fused-gill OTUs not assigned to the grandis, heterocaudata or nigra clades were included; also included were the exemplar OTUs of the grandis, heterocaudata and nigra clades. The resulting consensus tree was examined, and the most basal OTU was noted for use as a proxy in the subsequent analysis.

Finally, the exemplar of the fused-gill clade, the exemplar of the mesoleuca clade and all other OTUs not part of the fused-gill clade were analyzed together. The resulting tree was used as the basis for creating a composite tree of all OTUs analyzed, in which trees replaced proxies. The composite tree was treated as a monophyletic sister group of Timpanoginae for the purposes of using sequencing conventions (Nelson 1972, 1973) to establish a classification. In one instance, a polytomy was resolved based on phenetic characters; for further explanation, see Remarks under *Quatica*, new genus, in the Taxonomy section. The sequencing conventions determined the application of established supraspecific taxonomic names, the necessity for creating any new names and the taxonomic rank of names. All such nomenclature follows the rules established by the International Commision on Zoological Nomenclature (1999).

RESULTS

Data Matix

The matrix (Figs. 87–92) is divided into six sections for the purpose of presentation. Character states are indicated by numerals, as indicated in the Characters section, above. Missing or unknown data are indicated by a question mark (?). Inapplicable character states are indicated by a dash (–); these include, for example, states that cannot be scored because the characters in question are not present. Polymorphisms are indicated by an ampersand (&).

Trees

Analysis of the heterocaudata clade produced three most parsimonious trees (MPTs), and the consensus tree is shown in Figure 93. Analysis of the nigra clade produced 431 MPTs, and the consensus tree is shown in Figure 94. Analysis of the grandis clade produced 1735 MPTs, and the consensus tree is shown in Figure 95. Analysis of the fused-gill clade produced 8338 MPTs, and its consensus tree is shown in Figure 96. Analysis of the exemplars of the fused-gill and mesoleuca clades, and all other OTUs not part of the fused-gill clade, produced 29603 MPTs; the consensus tree for this group is shown in Figures 97–99.

In Figures 93–99, consensus values are indicated below each branch. These values represent the percentage of times that the respective cluster of OTUs appears together among the group of MPTs acquired from analysis and "can be taken as a rough measure of relative support" (Stevens and Wall 1996).

Classification

In the Taxonomy section, the new and revised higher taxa of Ephemerellinae are discussed based on their branching sequence within the composite tree described in the Analysis section. McCafferty and Wang (2000) emphasized that any classification "should be viewed as a state of knowledge and hypothesis at the time the research was performed, and as for all science, is to some extent, provisional. Most importantly, the study will have been worthwhile if only it serves as a catalyst for further research on a world level and a foundation upon which further precision in systematics can be based." This statement also applies to the revised classification scheme that follows.

REVISED TAXONOMY OF EPHEMERELLINAE

Tribe **EPHEMERELLINI**, s. s.

Diagnoses.—Eggs vary greatly in form, having the chorion smooth or reticulate, but it is never dimpled. The tribe is defined by the apomorphic form of the ventral lamella of gill 6 (Fig. 57) in larvae; it has the medial cleft greatly reduced or absent. Male adults have penes that almost always lack dorsomedial projections.

Genus **DRUNELLA** Needham, 1905: 42

Type species: *Ephemerella grandis* Eaton

Eatonella Needham, 1927: 108, new synonym (type species: *Ephemerella doddsii* Needham)
Myllonella Allen, 1980: 80, new synonym (type species: *Ephemerella coloradensis* Dodds)
Tribrochella Allen, 1980: 80, new synonym (type species: *Ephemerella trispina* Imanishi)
Unirhachella Allen, 1980: 80, new synonym (type species: *Ephemerella tuberculata* Morgan)

Description.— Egg (Fig. 9): Chorion smooth, without reticulations. Larva: Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with single row of denticles, sometimes numerically reduced. Forefemur (Figs. 46, 47) usually expanded and usually with stout chalazae on leading margin. Mesothorax without prominent anterolateral projections. Abdominal terga (Figs. 51, 52) with or without paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna sometimes with prominent friction disk (Fig. 48). Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 81): Forceps segment 3 elongate. Forceps segment 2 straight or bowed, sometimes swollen. Penes lobes compact, separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Distribution.— Holarctic (excluding western Palearctic), Oriental.

Species included.—*D. aculea* (Allen, 1971) [=*Ephemerella aculea*]; *D. allegheniensis* (Traver, 1934) [=*Ephemerella allegheniensis*]; *D. basalis* (Imanishi, 1937) [=*Ephemerella basalis*]; *D. coloradensis* (Dodds, 1923) [=*Ephemerella coloradensis*; = *Ephemerella wilsoni* Mayo, 1952]; *D. cryptomeria* (Imanishi, 1937) [=*Ephemerella cryptomeria*]; *D. doddsii* (Needham, 1927) [=*Ephemerella doddsii*]; *D. flavilinea* (McDunnough, 1926) [=*Ephemerella flavilinea*; =*Ephemerella lapidula* McDunnough, 1935]; *D. grandis* (Eaton, 1884) [=*Ephemerella grandis* Eaton, 1884; =*Ephemerella flavitincta* McDunnough, 1934; =*Ephemerella ingens* McDunnough, 1934; =*Ephemerella glacialis* Traver, 1934; =*Ephemerella Proserpina* Traver, 1934; =*Ephemerella Yosemite* Traver, 1934; =*Ephemerella glacialis carsona* Day, 1952]; *D. ishiyamana* Matsumura, 1931 [=*Ephemerella latipes* Tshernova, 1952; =*Ephemerella yoshinoensis* Gose, 1963]; *D. kohnoi* (Allen, 1971) [=*Ephemerella kohnoi*]; *D. lata* (Morgan, 1911)

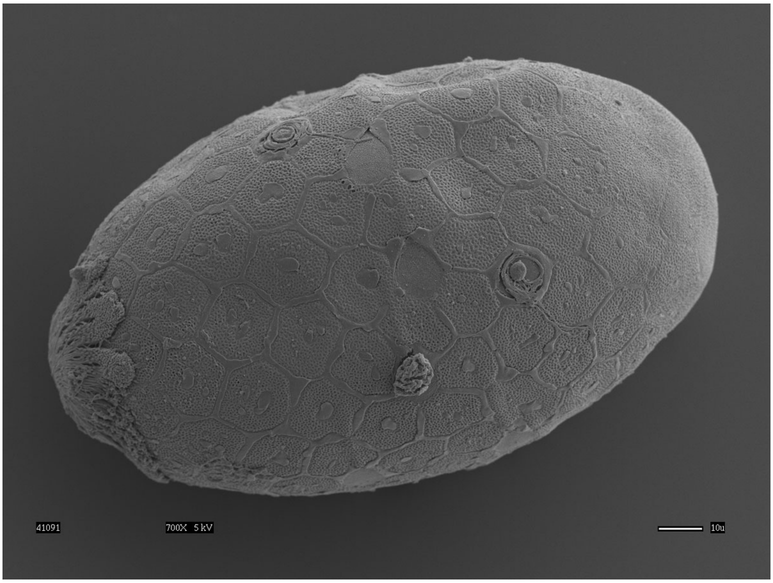


Fig. 1. Egg, *Matriella teresa*.

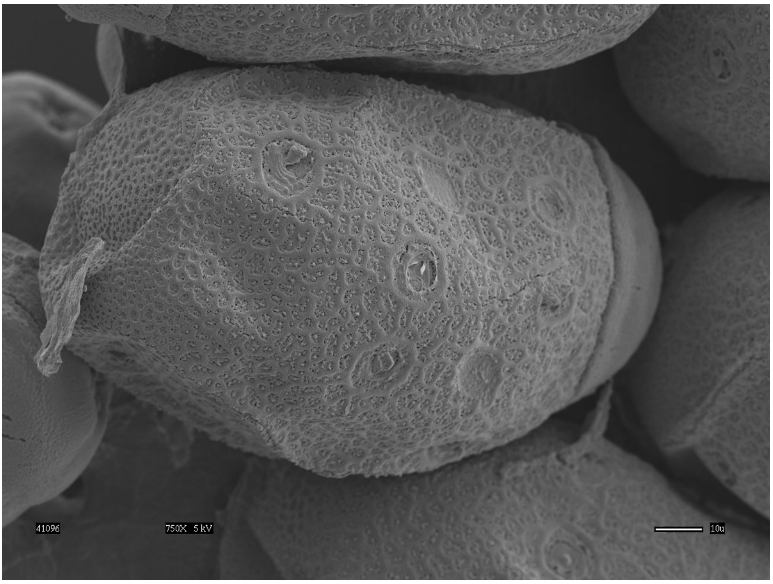


Fig. 2. Eggs, *Ephemerella* (*Hosoba*) *atagosana*.

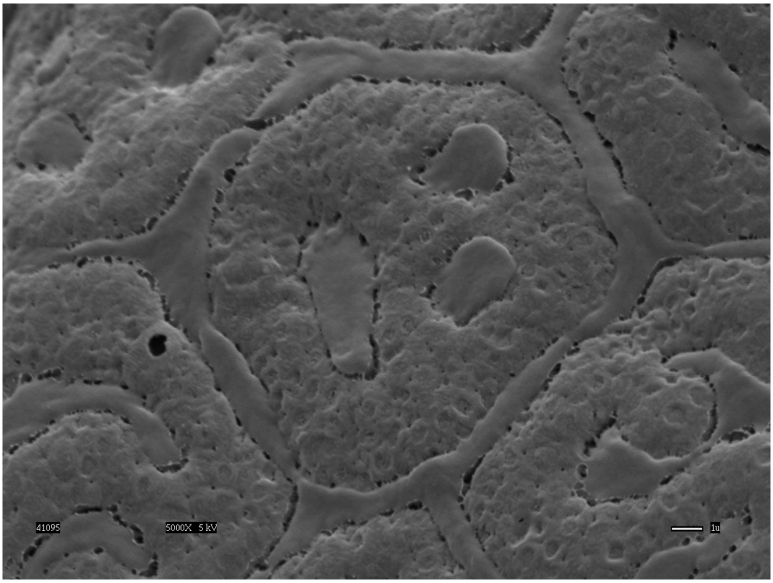


Fig. 3. Egg surface, *Cincticostella orientalis*.

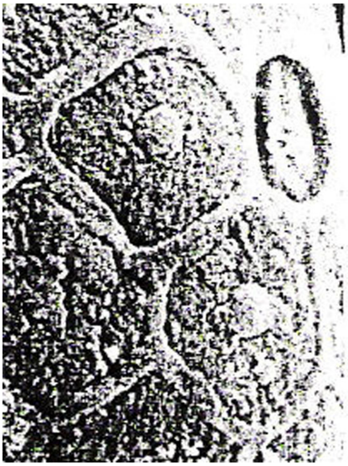


Fig. 4. Egg surface, *Cincticostella fusca* (from Kang and Yang 1995)

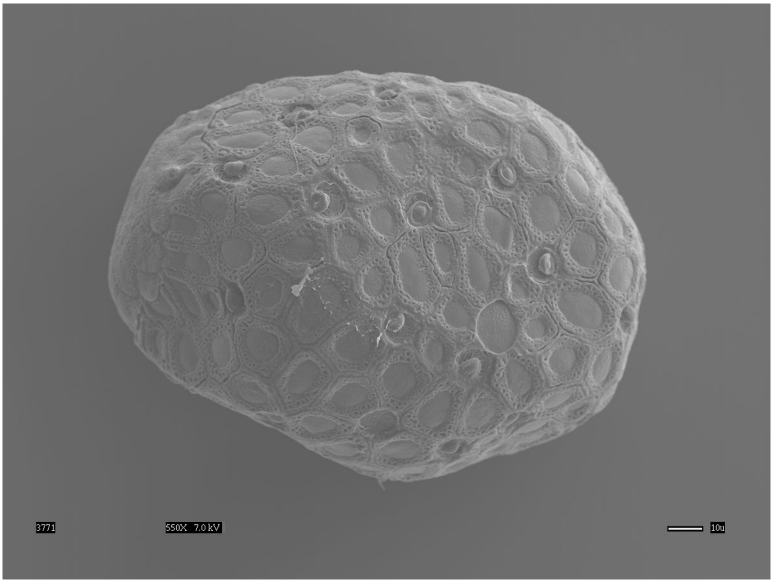


Fig. 5. Egg, *Tsalia berneri*.

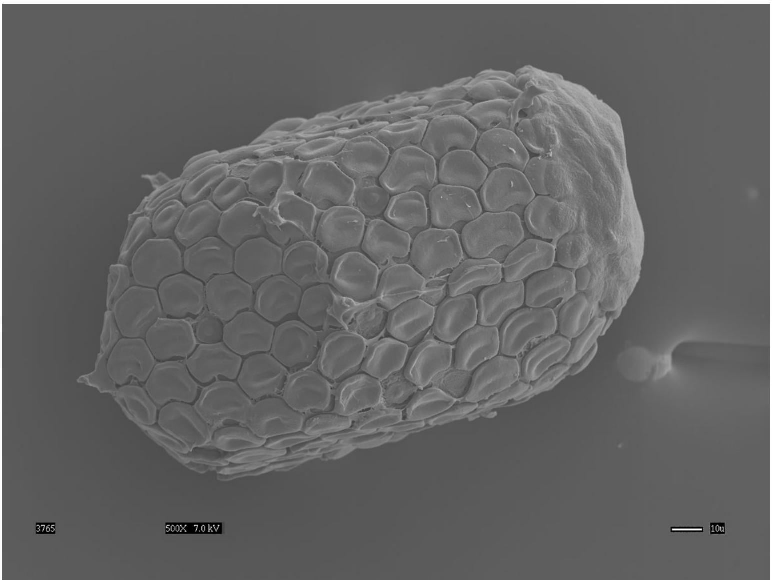


Fig. 6. Egg, *Ephemerella* (*Draeconia*) *needhami*.

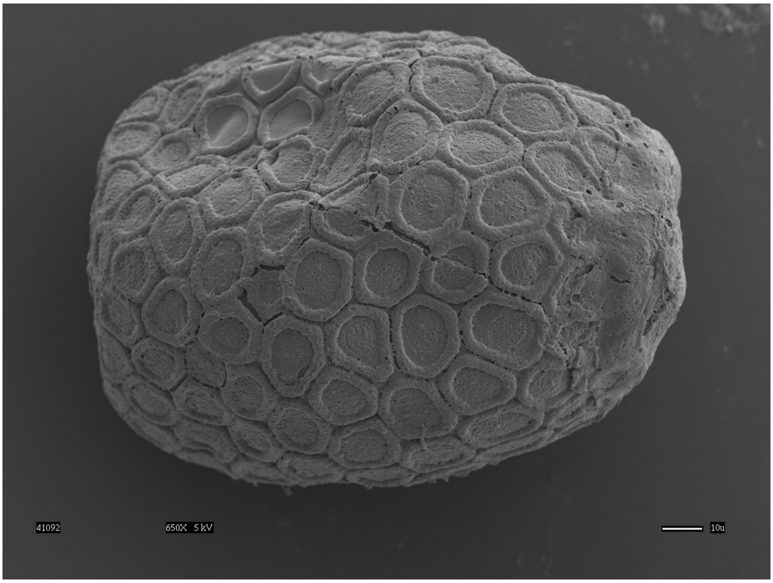


Fig. 7. Egg, *Ephemerella* (*Draeconia*) *maculata*.

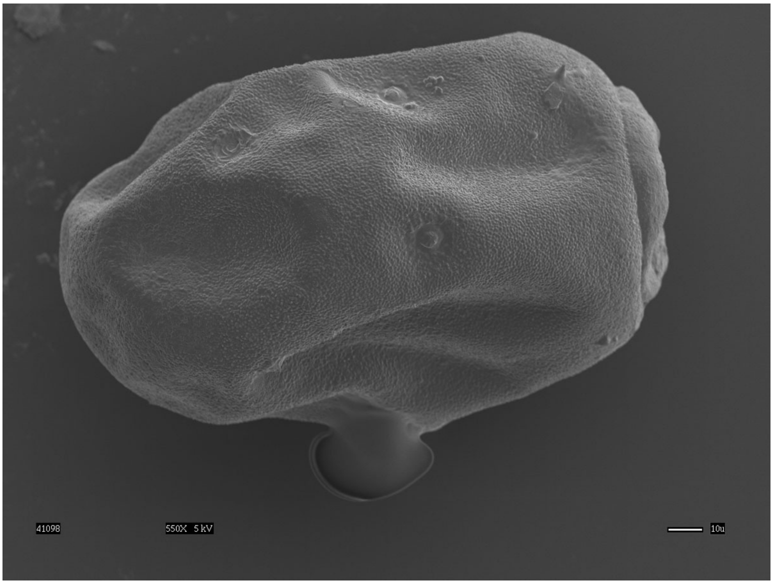


Fig. 8. Egg, *Caudatella hystrix* (*cascadia* variant).

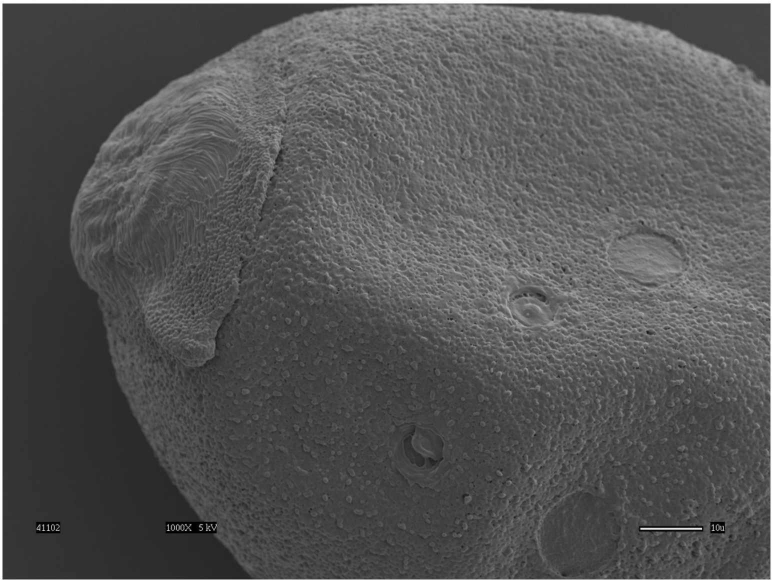


Fig. 9. Egg, *Drunella tuberculata* (*conestee* variant).

Fig. 10. Eggs, *Ephemerella* (*Scholitza*) *verruca*.

Fig. 11. Egg, *Ephemerella* (*Ephemerella*) *invaria*.

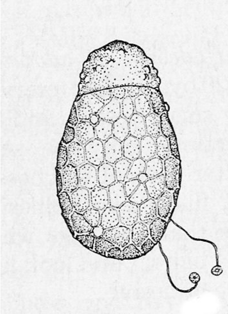


Fig. 12. Egg, *Penelomax septentrionalis* (from Smith 1935).

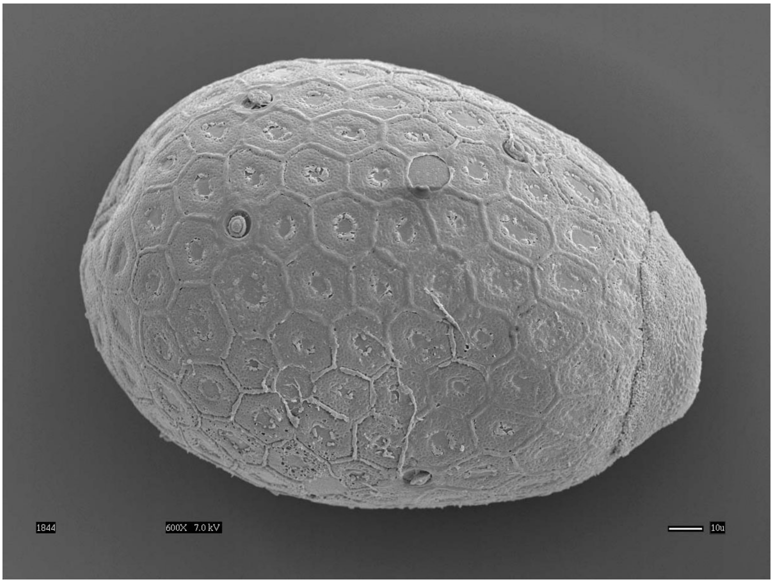


Fig. 13. Egg, *Caurinella idahoensis*.

Fig. 14. Egg, *Serratella uenoi*.

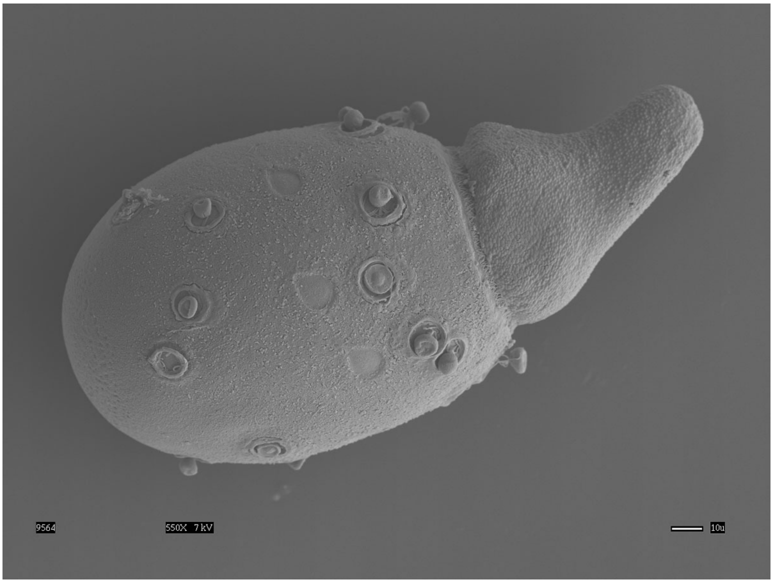


Fig. 15. Egg, *Serratella serrata*.

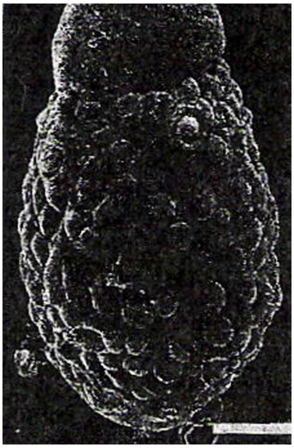
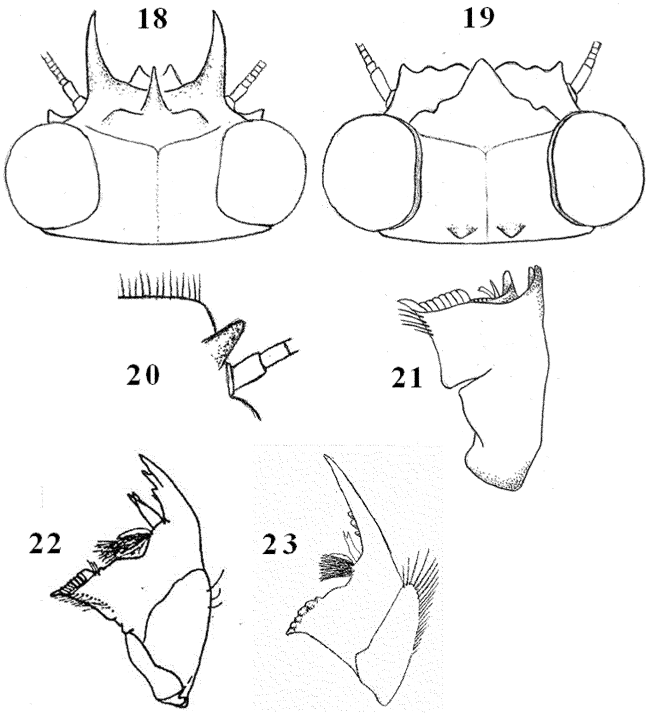


Fig. 16. Egg, *Teloganopsis hispanica* (from Studemann and Landolt 1997).

Fig. 17. Egg, *Teloganopsis* sp., nr. *media*.

[=*Ephemerella lata*; =*Ephemerella cornuta* Morgan, 1911; =*Ephemerella cornutella* McDunnough, 1931a; =*Ephemerella depressa* Ide, 1930; *Ephemerella longicornis* Traver, 1932]; *D. lepnevae* (Tshernova, 1949) [=*Ephemerella lepnevae*; =*Ephemerella longipes* Tshernova, 1952; =*Ephemerella bicornis* Gose, 1980; =***Drunella fuso***, new name (=*Ephemerella fusongensis* Su and Gui, 1995 nec *Ephemerella fusongensis* Su and You, 1988)]; *D. pelosa* (Mayo, 1952) [=*Ephemerella pelosa*]; *D. sachalinensis* (Matsumura, 1931) [=*Ephemerella sachalinensis*; =*Ephemerella bifurcata* Allen, 1971]; *D. solida* (Bajkova, 1980) [=*Ephemerela solida*]; *D. spinifera* (Needham, 1927) [=*Ephemerella spinifera*; *Ephemerella autumnalis* McDunnough, 1934; =*Ephemerella sierra* Mayo, 1952]; *D. submontana* (Brodsky, 1930) [=*Ephemerella submontana*; =*Ephemerella svenhedini* Ulmer, 1936; =*Ephemerella traverae* Allen and Edmunds, 1963; =*Ephemerella nasiri* Ali, 1971; =*Ephemerella borakensis* Allen, 1971; =*Ephemerella kabulensis* Allen, 1973]; *D. triacantha* (Tshernova, 1949) [=*Ephemerella triacantha*; =*Ephemerella tenax* Tshernova, 1952; =*Ephemerella ezoensis* Gose, 1980]; *D. trispina* (Ueno, 1928) [=*Ephemerella trispina*]; *D. tuberculata* (Morgan, 1911) [=*Ephemerella tuberculata*; =*Ephemerella conestee* Traver, 1932; =*Ephemerella cherokee* Traver, 1937]; *D. walkeri* (Eaton, 1884) [=*Baetis fuscata* Walker, 1853; =*Ephemerella walkeri*; =*Ephemerella bispina* Needham, 1905; =*Ephemerella wayah* Traver, 1932].

Remarks.— Although part of the *Drunella* tree (Fig. 95) remains unresolved based on present data, none of the polyspecific subgenera indicated by Allen (1980) were recovered as monophyletic. Therefore, they are placed into strict synonymy under *Drunella*. Some putatively polytypic *Drunella* species may be, in fact, complexes of cryptic species (e.g., Funk et al., unpublished). Further investigation is needed.

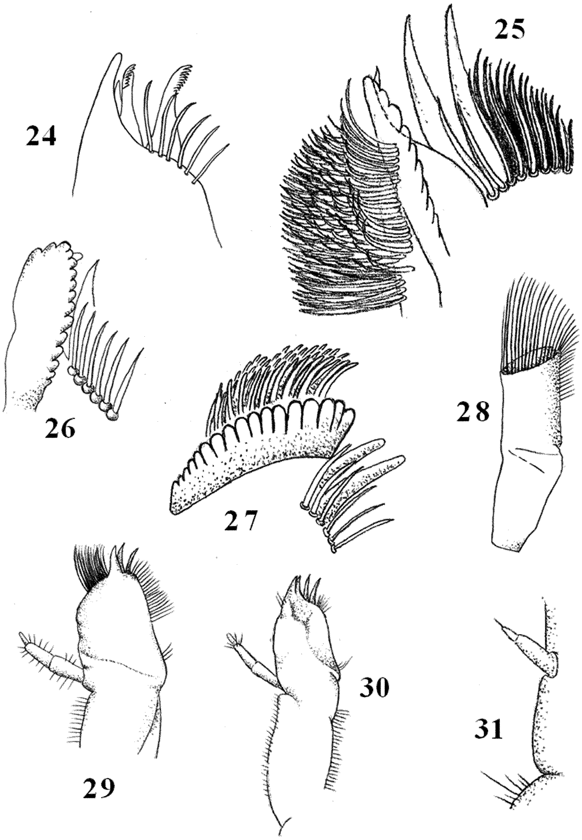


Figs. 18–20. Larval heads. 18, *Drunella aculea*. 19, *Drunella submontana*. 20, Subantennal spine, *Drunella lata*.
Figs. 21–23. Mandibles. 21, *Torleya nepalica*. 22, *Teloganopsis punctisetae*. 23, *Teloganopsis brocha*.

Genus **CAURINELLA** Allen, 1984: 245

Type species: *Caurinella idahoensis* Allen

Description.—Egg (Fig. 13): Chorion with reticulations; strands ridged; mesh with central, recessed disk margined by papillae. Larva: Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota without star-like setae. Pronotum without prominent anterolateral projections. Claw with single row of denticles. Forefemur not expanded and with very few or no stout chalazae on leading margin. Mesothorax without prominent anterolateral projections. Abdominal terga without paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 greatly elongate and upturned (Fig. 55). Cerci subequal to medial filament. Adult male genitalia (Fig. 78): Forceps segment 3 ovoid. Forceps segment 2 straight. Penes lobes compact, separated by slight cleft;



Figs. 24–27. Apices of maxillae. 24, *Teloganopsis mesoleuca*. 25, *Notacanthella* (*Notacanthella*) *quadrata*. 26, *Spinorea montana*. 27,*Cincticostella fusca*.

Figs. 28–31. Maxillae. 28, *Teloganopsis punctisetae*. 29, *Spinorea gilliesi*. 30, *Ephemerella* (*Ephemerella*) *invaria*. 31, Palp, *Matriella teresa*.

anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Distribution.— Western Nearctic.

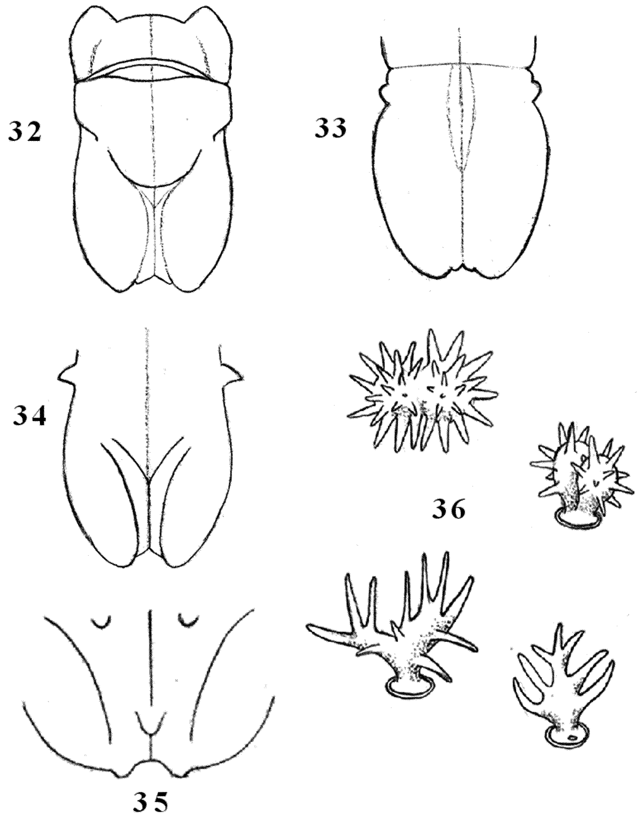
Species included.—*C. idahoensis* Allen, 1984.

Genus **EPHEMERELLA** Walsh, 1862: 377

Type species: *Ephemerella excrucians* Walsh

Chitonophora Bengtsson, 1909: 6 (type species: *Chitonophora aurivillii* Bengtsson), synonymized by Walley (1930)

Description.— Egg (Figs. 2, 6, 7, 10, 11): Chorion with or without reticulations; if present, strands furrowed and mesh smooth. Larva: Maxilla with palp;



Figs. 32–36. Larval thoracic structures. 32, Pro- and mesonota, *Cincticostella nigra*. 33, Mesonotum, *Cincticostella fusca*. 34, Mesonotum, *Ephacerella longicaudata*. 35, Mesal plate, *Spinorea montana*. 36, Starlike setae, *Quatica paradinasi*.

palp with or without medial whorl of setae (Fig. 30); crown setae not numerically increased; canines sharp, usually without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections, but sometimes slight projections present. Claw with single row of denticles. Forefemur (Fig. 45) not expanded and without stout chalazae on leading margin. Mesothorax without prominent anterolateral projections, but slight projections sometimes present. Abdominal terga with or without paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Figs. 70–75, 79): Forceps segment 3 globular or ovoid. Forceps segment 2 straight, sometimes with apical quadrate expansion (Figs. 74, 75), rarely with medial crease (Fig. 79). Penes lobes either compact and separated by shallow cleft or elongate and separated by deep cleft; anteromedial, dorsomedial and lateral stout setae (Fig. 75) present or absent; dorsolateral projection absent. Cerci subequal to medial filament.

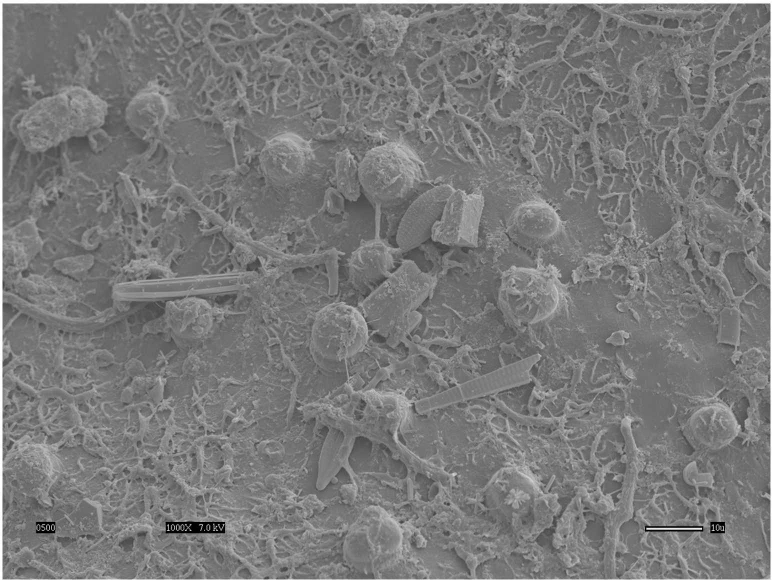


Fig. 37. Excrescences on larval mesonotum, dorsal view, *Ephemerella* (*Vittapallia*) *tibialis*.

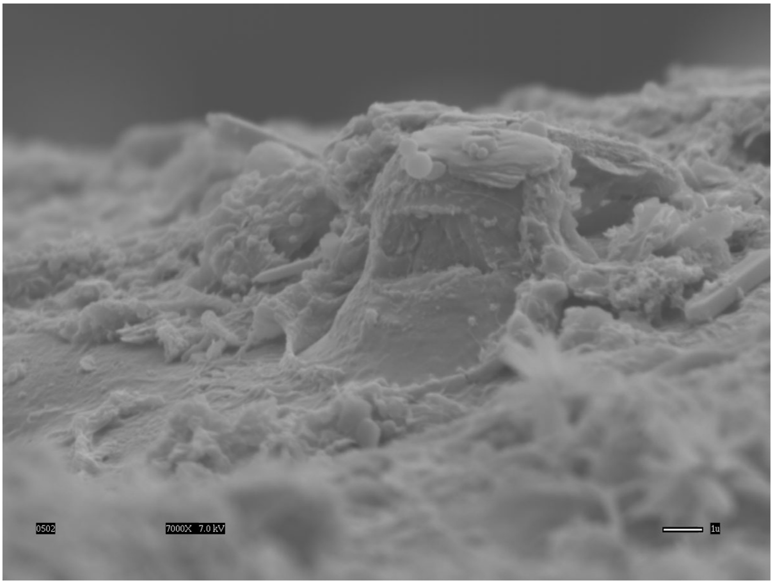
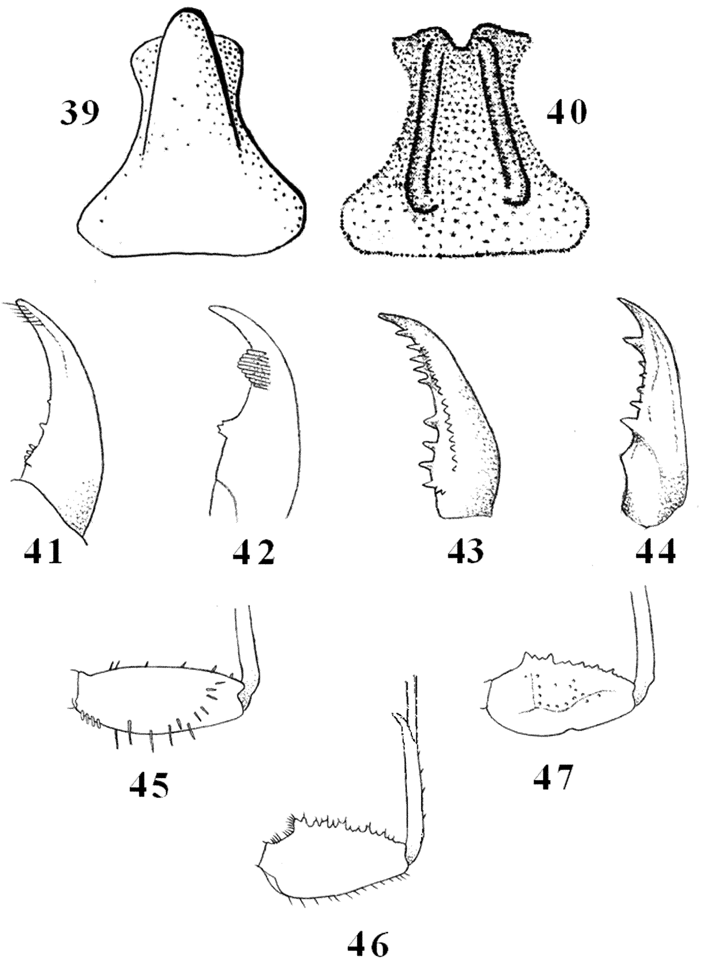


Fig. 38. Excrescences on larval mesonotum, lateral view, *Ephemerella* (*Vittapallia*) *tibialis*.



Figs. 39–40. Larval prosterna. 39, *Drunella grandis*. 40, *Notacanthella* (*Notacanthella*) *quadrata*.

Figs. 41–44. Larval claws. 41, *Torleya major*. 42, *Torleya coheri*. 43, *Caudatella edmundsi*. 44, *Teloganopsis punctisetae*.

Figs. 45–47. Larval forefemora. 45, *Ephemerella* (*Draeconia*) *needhami*. 46, *Drunella lata*. 47, *Drunella submontana*.

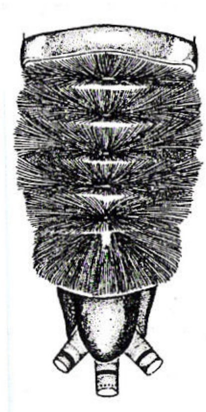
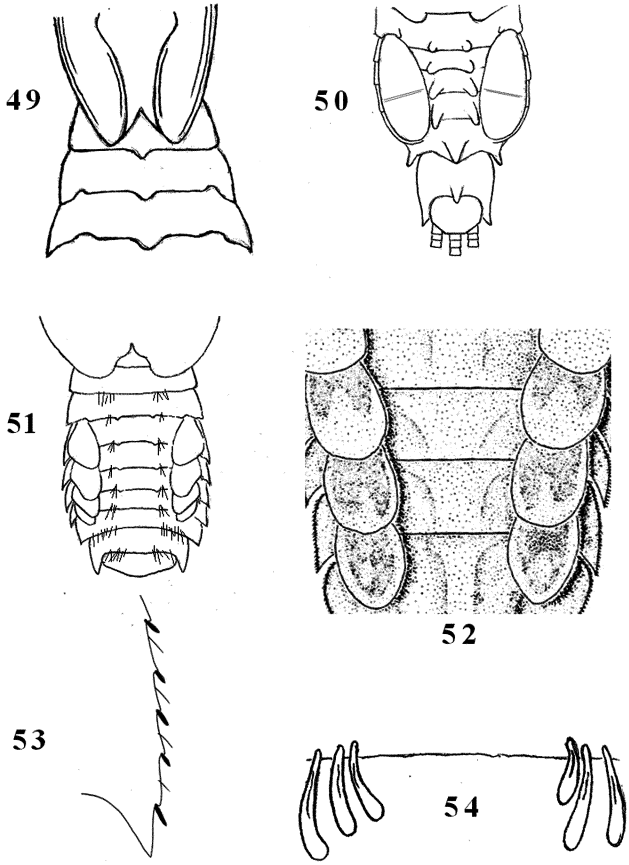


Fig. 48. Friction disc on larval abdominal sterna, *Drunella pelosa* (from Mayo 1952).

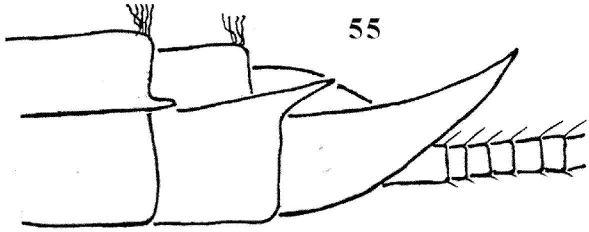
Distribution.— Holarctic.

Subgenera included.— **ZONADIA**, new subgenus (type species: *Ephemerella kozhovi* Bajkova) [*Description*.— Egg: Chorion without reticulations, surface smooth. Larva: Head without suboccipital spines. Maxillary canines without lateral serrations. Thoracic nota without excrescences. Abdominal terga with blunt paired spines not situated unusually close together; lateral margins of abdominal segments slightly upturned. Lateral lobules of gill 6 ventral lamella not enlarged. Adult male genitalia (Fig. 70): Forceps segment 2 straight and without apical expansion. Penes lobes each with short apicolateral protuberance; stout, spinelike setae absent. *Etymology*.— The subgenus name is an arbitrary combination of letters involving the Latin *zona* (belt), a reference to the abdominal coloration of the type species.]; **HOSOBA**, new subgenus (type species: *Ephemerella atagosana* Imanishi) [*Description*.— Egg (Fig. 2): Chorion without reticulations, surface rough and pitted. Larva: Head without suboccipital spines. Maxillary canines without lateral serrations. Thoracic nota without excrescences. Abdominal terga with sharp paired spines not situated unusually close together; lateral margins of abdominal segments upturned. Lateral lobules of gill 6 ventral lamella not enlarged. Adult male genitalia (Fig. 71): Forceps segment 2 straight and without apical expansion. Penes lobes slightly expanded and rounded apically; stout, spinelike setae absent. *Etymology*.— The subgenus name is the Japanese name of the type species.]; **DRAECONIA**, new subgenus, (type species: *Ephemerella needhami* McDunnough) [*Description*.— Egg (Figs. 6, 7): Chorion with strands furrowed. Larva: Head without suboccipital spines. Maxillary canines without lateral serrations. Thoracic nota without excrescences. Abdominal terga with or without paired spines; if present, spines not unusually close together; lateral margins of abdominal segments not upturned. Lateral lobules of gill 6 ventral lamella not enlarged. Adult male genitalia: Forceps segment 2 straight and rarely with apical expansion. Penes usually with deep, medial cleft and long lobes; stout, spinelike setae absent. *Etymology*.— The subgenus name is an arbitrary combination of letters referring to a dragon.]; **SCHOLITZA**, new subgenus (type spe-



Figs. 49–54. Larval abdominal structures. 49, Terga 1–3, *Teloganopsis gracilis*. 50, Dorsal view, *Hyrtanella christineae*. 51, Dorsal view, *Drunella aculea*. 52, Terga 5–8, *Drunella doddsii*. 53, Outer margin of posterolateral projection, *Ephemerella* (*Ephemerella*) *catawba*. 54, Setal tufts on tergum, *Torleya lutosa*.

cies: *Ephemerella verruca* Allen and Edmunds) [*Description.*— Egg (Fig. 10). Chorion without reticulations, surface smooth. Larva: Head with suboccipital spines. Maxillary canines without lateral serrations. Thoracic nota without excrescences. Abdominal terga with very sharp, paired spines, situated unusually close together; lateral margins of abdominal segments not upturned. Lateral lobules of gill 6 ventral lamella not enlarged. Adult male genitalia (Fig. 72): Forceps segment 2 straight and without apical expansion. Penes lobes each with slight apical protuberance; stout, spinelike setae absent. *Etymology.*— This subgenus is named to honor the mother of Chief Seattle, a Native American.]; **VITTAPALLIA**, new subgenus (type species: *Ephemerella tibialis* McDunnough) [*Description.*— Egg. Chorion without reticulations, surface smooth. Larva: Head without suboccipital spines. Maxillary canines with lateral serrations. Thoracic nota with excrescences (Figs. 37, 38). Abdominal terga with paired spines, not situated un-



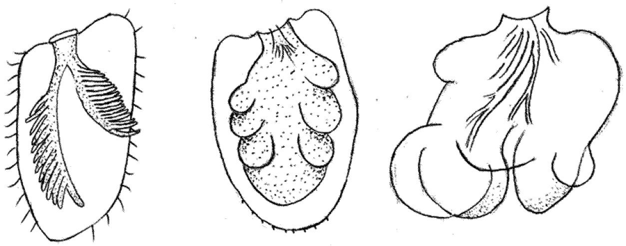


Fig. 55. Posterior abdominal segments and proximal segments of caudal filaments, lateral view, *Caurinella idahoensis* larva.

Figs. 56–58. Abdominal gills 6, ventral views. 56, *Torleya major*. 57, *Cincticostella nigra*. 58, *Ephemerella* (*Vittapallia*) *nuda*.

usually close together; lateral margins of abdominal segments not upturned. Lateral lobules of gill 6 ventral lamella enlarged (Fig. 58). Adult male genitalia (Fig. 79): Forceps segment 2 slightly swollen and with medial crease but without apical expansion. Penes lobes broad; stout, spinelike setae absent. *Etymology.—* The subgenus name is based on the Latin *vitta* and *pallia*, together meaning striped cloak.]; **EPHEMERELLA**, s.s. (=*Chitonophora*) [*Description.—* Egg: Chorion without reticulations, surface smooth (Fig. 11). Larva: Head usually without suboccipital spines. Maxillary canines without lateral serrations. Thoracic nota without excrescences. Abdominal terga usually with paired spines, paired spines rarely situated unusually close together; if abdominal spines unusually close, suboccipital spines absent from head; lateral margins of abdominal segments not upturned. Lateral lobules of gill 6 ventral lamella not enlarged. Adult male genitalia (Figs. 74, 75): Forceps segment 2 straight and usually with quadrate apical expansion. Penes lobes variable in shape and with stout, spinelike setae.].

Species included.— E. (E.) alleni Jensen and Edmunds, 1966; *E. (D.) apopsis* McCafferty, 1992; *E. (H.) atagosana* Imanishi, 1937a [=*Ephemerella dentata* Bajkova, 1967; =*Ephemerella denticula* Allen, 1971; =*Ephemerella keijoensis* Allen, 1971]; *E. (E.) aurivillii* (Bengtsson, 1909) [=*Chitonophora aurivillii*; =*Ephemerella aronii* Eaton, 1909; =*Ephemerella norda* McDunnough, 1924; =*Ephemerella concinnata* Traver, 1934; =*Ephemerella taeniata* Tshernova, 1952; =*Ephemerella maxima* Allen, 1971; =*Ephemerella ezoensis* Gose, 1980]; *E. (E.)*

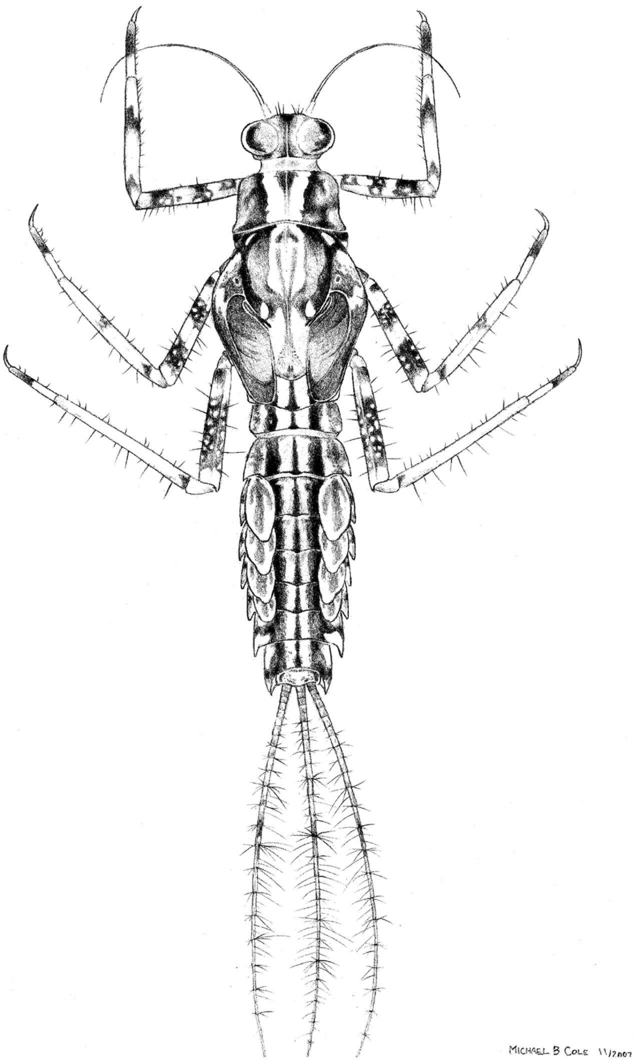
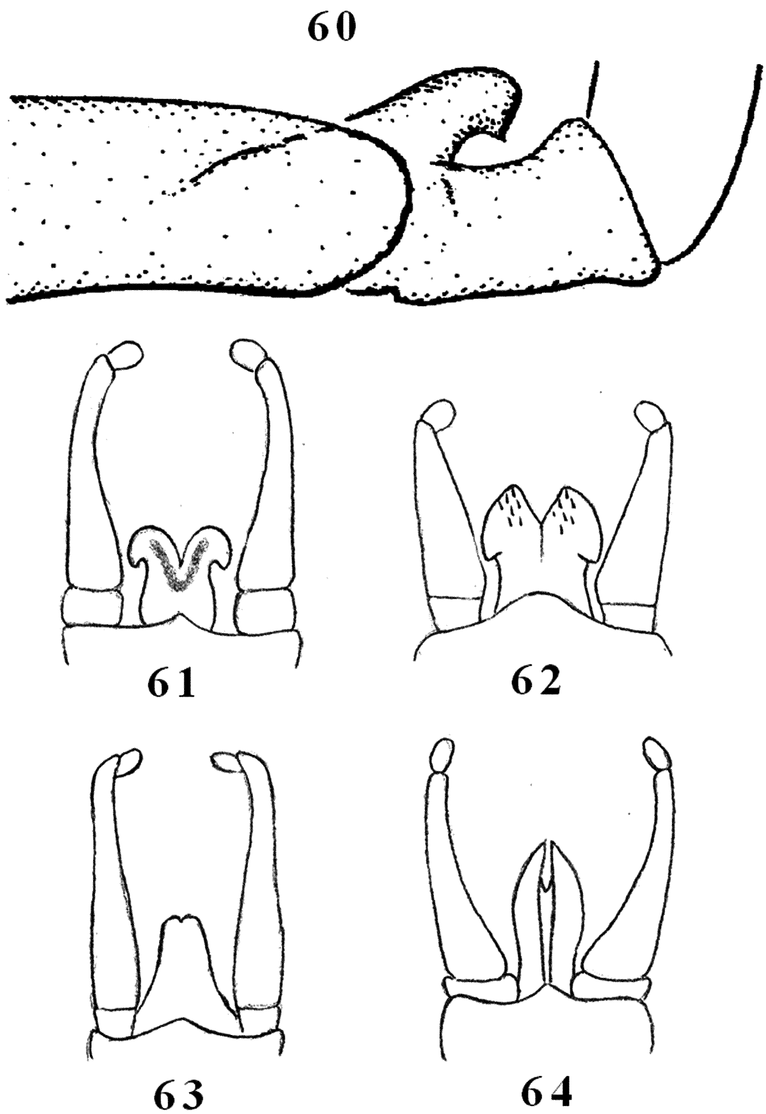


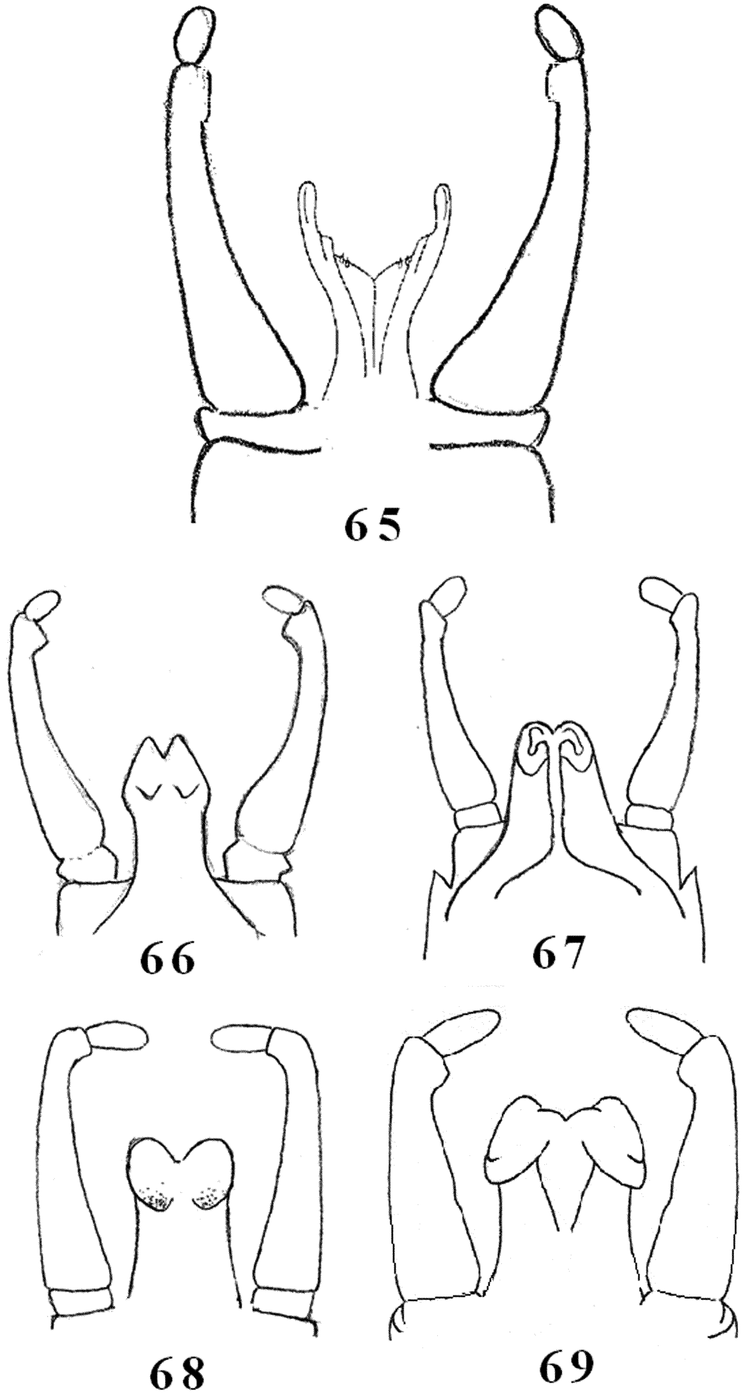
Fig. 59. Dorsal habitus,

catawba Traver, 1932; *E. (E.) dorothea* Needham, 1908 [=*Ephemerella infrequens* McDunnough, 1924; =*Ephemerella mollitia* Seeman, 1927]; *E. (E.) excrucians* Walsh, 1862 [=*Ephemerella inermis* Eaton, 1884; =*Ephemerella semiflava* McDunnough, 1926; =*Ephemerella argo* Burks, 1947; =*Ephemerella ora* Burks, 1949; =*Ephemerella crenula* Allen and Edmunds, 1965; =*Ephemerella lacustris* Allen and Edmunds, 1965; =*Ephemerella rossi* Allen and Edmunds, 1965; =*Ephemerella rama* Allen, 1968]; *E. (E.) hispida* Allen and Edmunds, 1965; *E. (E.) invaria* (Walker, 1853) [=*Baetis invaria*; =*Ephemerella rotunda* Morgan, 1911; =*Ephemerella vernalis* Banks, 1914; =*Ephemerella feminina* Needham, 1924;

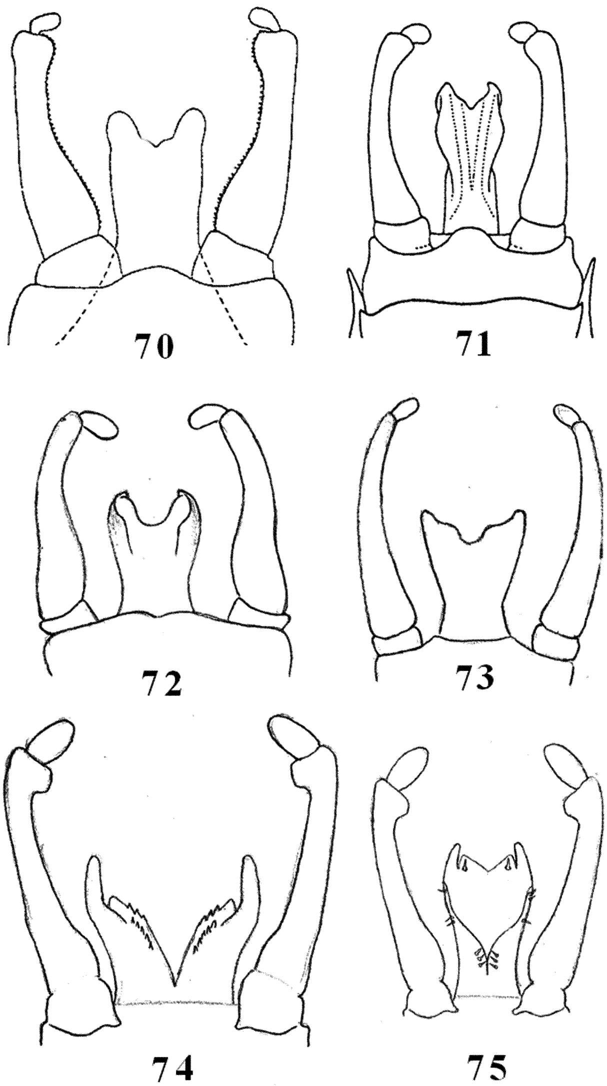


Figs. 60–64. *Teloganopsis* spp. 60, Proximal hook on adult tarsus. 61–64. Adult male genitalia. 61, *T. media*. 62, *T. changbaishanensis*. 63, *T. hispanica*. 64, *T. mesoleuca*.

=*Ephemerella fratercula* McDunnough, 1925c; =*Ephemerella inconstans* Traver, 1932; =*Ephemerella choctawhatchee* Berner, 1946; =*Ephemerella simila* Allen and Edmunds, 1965; =*Ephemerella floripara* McCafferty, 1985]; *E. (Z.) kozhovi* Bajkova, 1967 [=*Ephemerella notofascia* Yoon and Bae, 1988]; *E. (D.) maculata* Traver, 1934 [=*Ephemerella euterpe* Traver, 1934]; *E. (D.) mucronata* (Bengtsson, 1909) [=*Chitonophora mucronata*; =*Chitonophora kreighoffi* Ulmer, 1920; =*Chitonophora unicolorata* Ikonomov, 1961; =*Ephemerella moffatae* Allen,

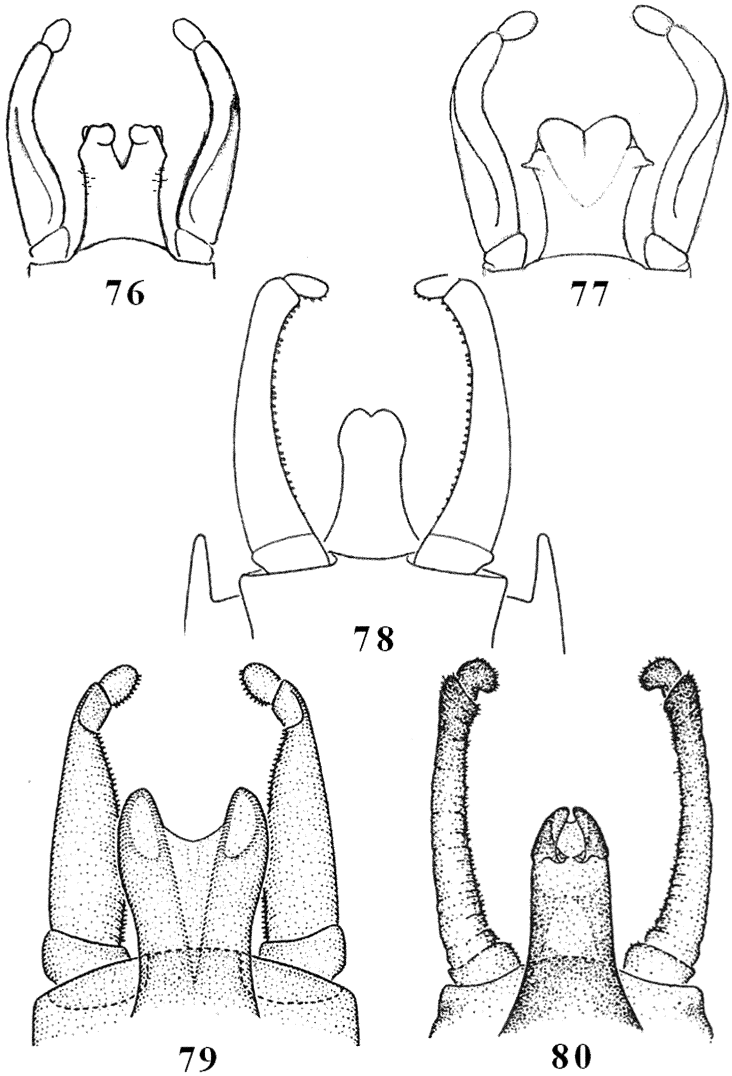


Figs. 65–69. Adult male genitalia. 65, *Penelomax septentrionalis*. 66, *Torleya nepalica*. 67, *Quatica ikonomovi*. 68,*Hyrtanella grandipennis*. 69, *Torleya major*.



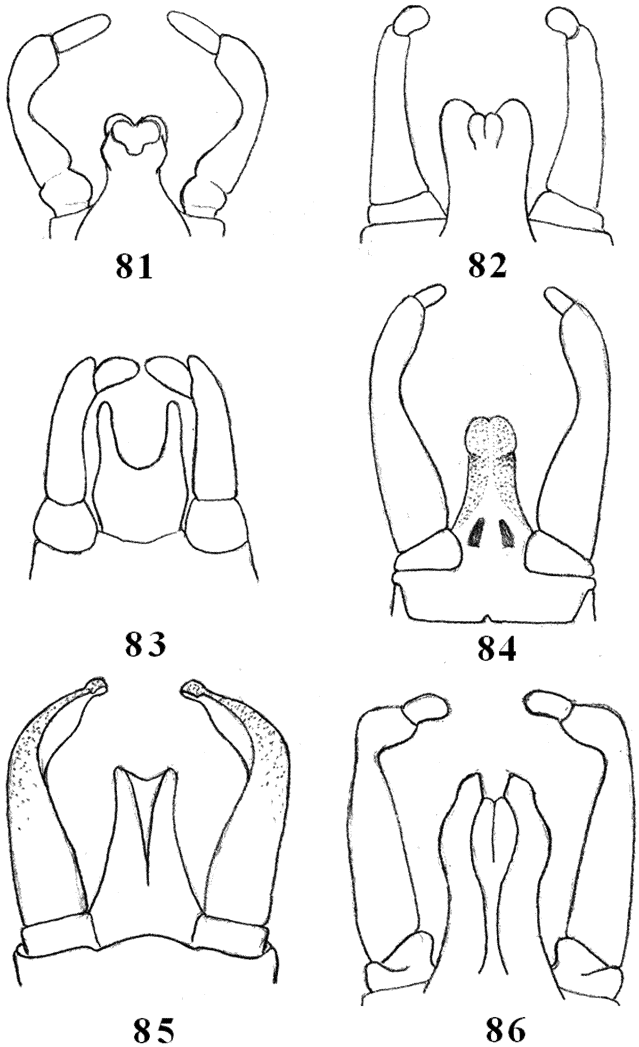
Figs. 70–75. Adult male genitalia, *Ephemerella* spp. 70, *E.* (*Zonadia*) *kozhovi* (from Bajkova 1967). 71, *E.* (*Hosoba*) *atagosana* (from Imanishi 1937b). 72, *E.* (*Scholitza*)

1977b; =*Ephemerella kreighoffi intermedia* Keffermüller, 1979]; *E. (D.) needhami* McDunnough, 1925a; *E. (D.) notata* Eaton, 1887; *E. (V.) nuda* Tshernova, 1949 [=*Ephemerella thymalli* Tshernova, 1952; =*Ephemerella verrucosa* Kluge, 1980]; *E. (E.) subvaria* McDunnough, 1931a; *E. (V.) tibialis* McDunnough, 1924, reinstated combination [=*Ephemerella angusta* Traver, 1934; =*Ephemerella sequoia* Allen and Collins, 1968]; *E. (E.) velmae* Allen and Edmunds, 1963a, reinstated combination; *E. (S.) verruca* Allen and Edmunds, 1965.



Figs. 76–80. Male genitalia. 76, *Serratella ignita*. 77, *Serratella serratoides*. 78, *Caurinella idahoensis*. 79, *Ephemerella* (*Vittapallia*) *tibialis*. 80, *Caudatella hystrix*.

Remarks.— The subgenus *Draeconia* corresponds approximately to the "needhami group" of Traver (1935) and includes *E. needhami*, *E. notata*, *E. maculata* and *E. mucronata*. These four species have eggs with furrowed strands (Figs. 6, 7). *Ephemerella apopsis* probably belongs to this subgenus, based on its similarity to *E. needhami* (McCafferty 1992). *Ephemerella maculata* apparently has the penes lobes secondarily reduced (Fig. 73) relative to other members of this clade. Beginning with Smith (1935), *E. maculata* had been assumed to have eggs with no polar cap, until McCafferty and Wang (1994) reported otherwise.



Figs. 81–86. Male genitalia. 81, *Drunella lata*. 82, *Matriella teresa*. 83, *Tsalia berneri*. 84, *Notacanthella nigromaculata*. 85, *Ephacerella longicaudata*. 86, *Cincticostella nigra*.

Our examination of *E. maculata* eggs (Fig. 7) corroborates McCafferty and Wang's (1994) observations and confirms that all known Ephemerellinae eggs have single polar caps that are easily visible in ethanol-preserved specimens. However, polar caps sometimes are difficult to discern when the eggs have been preserved in other media.

Chitonophora sometimes has been applied as a subgenus name to the needhami group. The type species of *Chitonophora*, *Chitonophora aurivillii*, shares apomorphies with species included in *Ephemerella*, s.s., and therefore, *Chitonophora* is retained in strict synonymy under *Ephemerella*. *Ephemerella*, s.s., is equivalent to McDunnough's (1925a) excrucians group, in which all species have stout, spinelike setae on the penes (Fig. 74, 75). Several putatively polytypic species included in *Ephemerella*, s.s., namely *E. aurivillii*, *E. dorothea*, *E. excrucians*, and *E. invaria*, have complex population structures and need evaluation for the presence of cryptic species within their current concepts (Alexander et al., unpublished; Xin Zhou et al., unpublished).

Ephemerella nuda and *E. tibialis* together form the subgenus *Vittapallia*, a monophyletic group that is defined by unique excrescences on the thorax of larvae (Tshernova 1952: Fig. 89; Figs. 37, 38 herein) and some synapomorphies presumably convergent with species included in the the clade containing the genus *Cincticostella* (Fig. 94), such as the denticulation of the maxillary canines and a medial crease on male genital forceps segment 2. The shape of the penes (Fig. 79), the setation of the maxillary palp and the structure of the egg chorion of *E. nuda* and *E. tibialis* (Studemann et al. 1995, Studemann and Landolt 1997) are, however, consistent with other *Ephemerella*. The structure of gills 6 (Fig. 58), as discussed in the Analysis section, is unique.

Genus **MATRIELLA**, new genus

Type species: *Ephemerella teresa* Traver

Description.— Egg (Fig. 1): Chorion with reticulations; strands ridged; mesh with multiple central tubercles. Larva: Maxilla with vestigial palp (Fig. 31); crown setae not numerically increased; canines sharp, with lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with two rows of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 82): Forceps segment 3 ovoid. Forceps segment 2 straight. Penes lobes compact with small, broad apical projections, separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Etymology.— The name means "little mother."

Distribution.— Western Nearctic.

Species included.— M. teresa (Traver, 1934), new combination [=*Ephemerella teresa*; =*Ephemerella cognata* Traver, 1934].

Genus **TSALIA**, new genus

Type species: *Ephemerella berneri* Allen and Edmunds

Description.— Egg (Fig. 5): Chorion with reticulations; strands ridged; mesh with central, recessed disc. Larva: Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, with lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 83): Forceps segment 3 ovoid. Forceps segment 2 straight with apparent apical projection on outer margin, due to point of attachment of segment 3. Penes lobes elongate, separated by deep, U-shaped cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Etymology.— This genus is named to honor Tsali, the founder of the Eastern Band of the Cherokee, a group of Native Americans from the southern Appalachian Range.

Distribution.— Eastern Nearctic, restricted to the southern part of the Appalachian Range.

Species included.— T. berneri (Allen and Edmunds, 1958), new combination [=*Ephemerella berneri*].

Genus **CAUDATELLA** Edmunds, 1959: 546

Type species: *Ephemerella heterocaudata* McDunnough

Description.— Egg (Fig. 8): Chorion smooth. Larva: Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, usually with lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one or two (Fig. 43) rows of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci reduced relative to medial filament. Adult male genitalia (Fig. 80): Forceps segment 3 globular. Forceps segment 2 straight. Penes lobes compact, separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projections sometimes present. Cerci reduced relative to medial filament.

Distribution.— Western Nearctic.

Species included.— C. edmundsi (Allen, 1959) [=*Ephemerella edmundsi*]; *C. heterocaudata* (McDunnough, 1929) [=*Ephemerella heterocaudata*; =*Ephemerella columbiella* McDunnough, 1935; =*Ephemerella heterocaudata californica* Allen and Edmunds, 1961; =*Ephemerella heterocaudata circia* Allen and Edmunds, 1961]; *C. hystrix* (Traver, 1934) [=*Ephemerella hystrix*; =*Ephemerella spinosa* Mayo, 1952; =*Ephemerella cascadia* Allen and Edmunds, 1961]; *C. jacobi* (McDunnough, 1939) [=*Ephemerella jacobi*; =*Ephemerella orestes* Allen and Edmunds, 1961].

Remarks.— The species taxonomy of this genus may change if subspecies and junior synonyms are subjected to critical evaluation.

Genus **NOTACANTHELLA**, new genus

Type species: *Ephemerella quadrata* Kluge and Zhou

Description.— Egg: Unknown. Larva: Maxilla (Fig. 25) with palp; palp covered with setae; crown setae numerically increased; canines sharp or spoonlike, with or without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum usually with prominent anterolateral projections. Claw with one row of denticles, sometimes numerically reduced. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax with medially notched anterolateral projections (as in Fig. 33). Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 84): Forceps segment 3 ovoid. Forceps segment 2 with medial crease. Penes lobes compact and scooplike, separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Distribution.— Oriental.

Subgenera included.— **NOTACANTHELLA**, s.s. [*Description.—* Larva with maxillary canines serrate laterally.]; **SAMIOCCA**, new subgenus (type species: *Ephemerella perculta* Allen) [*Description.—* Larva with maxillary canines smooth laterally.

Etymology.— The new subgenus name is an arbitrary combination of letters from the Latin words *samio* (smooth) and *occa* (harrow), a reference to the morphology of the larval maxillary canines.].

Species included.— N. commodema (Allen, 1971), new combination [=*Ephemerella commodema*]; *N. nigromaculata* (Xu, You and Su, 1980), new combination [=*Ephemerella nigromaculata*]; *N. perculta* (Allen, 1971), new combination [=*Ephemerella perculta*]; *N. quadrata* (Kluge and Zhou [in Kluge, Zhou, Jacobus and McCafferty], 2004), new combination [=*Ephemerella quadrata*]; *N. tianmushanensis* (Xu, You and Su., 1980), new combination [=*Ephemerella tianmushanensis*]; *N*. sp. A.

Remarks.— In order to maintain taxonomic stability and reduce confusion, we formally establish *Notacanthella* as a valid name here, because its original description (Kluge 2004) came before the name of the type species was available (Kluge et al. 2004) (Soldán 2007). The new subgenus *Samiocca* is established for the species *N. commodema* and *N. perculta*, whose larvae share an apomorphic loss of the lateral serrations of the maxillary canines. Male adults are assigned to this genus based on the associated metamorphic stages of a species from Thailand (Phitsanulok Prov., Phu Hin Rongkla NP, Waterwheel Falls, 1280m, 16°59’N, 101°00’E, VI-2002 [ISUI]) which is called *Notacanthella* sp. A, until stages can be associated for other species in the genus and compared to type specimens.

Genus **SPINOREA**, new genus

Type species: *Ephemerella gilliesi* Allen and Edmunds

Description.— Egg: Chorion with reticulations; strands ridged; mesh with central, recessed disc. Larva: Maxilla (Figs. 26, 29) with palp; palp covered with setae; crown setae numerically increased; canines reduced to denticulate blade, with its length subequal to its width (Fig. 26). Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles, sometimes numerically reduced. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax with medially notched anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia: Unknown.

Etymology.— The genus name is an arbitrary combination of letters derived from the Latin *spina* (spine) and *oreas* (mountain nymph).

Distribution.— Oriental.

Species included.— S. gilliesi (Allen and Edmunds, 1963c), new combination [=*Ephemerella gilliesi*]; *S. glebosa* (Kang and Yang, 1995), new combination [=*Acerella glebosa*]; *S. montana* (Kang and Yang, 1995), new combination [=*Acerella montana*].

Genus **ADORANEXA**, new genus

Type species: *Drunella soldani* Allen

Description.— Egg: Unknown. Larva: Maxilla with palp; palp covered with setae; crown setae numerically increased; canines reduced to denticulate blade, it length much less than its width. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax with medially notched anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia: Unknown.

Etymology.— The name is derived from the Latin *adoratus* and *nexus*, meaning honored tie. The name is a double entendre, referring to the resolution of the type species' hypothetical phylogenetic position and honoring friends and former colleagues of LMJ at the Nexus Corp., Ltd., Morioka, Japan.

Distribution.— Oriental.

Species included.— A. soldani (Allen, 1986), new combination [=*Drunella soldani*].

Genus **EPHACERELLA** Paclt, 1994: 283

Type species: *Ephemerella longicaudata* Ueno

Acerella Allen, 1971, nec *Acerella* Berlese, 1909 [Protura], name replaced by Paclt (1994)

Description.— Egg: Undescribed. Larva: Maxilla with palp; palp with numerous setae; crown setae numerically increased; canines reduced to denticulate blade, its length less than its width. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax with medially notched anterolateral projections; posterior portion of projection sharp and elongate (Fig. 34). Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 85): Forceps segment 3 globular. Forceps segment 2 with medial crease. Penes lobes compact, with large notch on ventral face; lobes separated by shallow apical cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Distribution.— Eastern Palearctic, Oriental (one record from Vietnam: Allen 1986).

Species included.— E. longicaudata (Ueno, 1928) [=*Ephemerella longicaudata*].

Genus **CINCTICOSTELLA** Allen, 1971: 513

Type species: *Ephemerella nigra* Imanishi

Asiatella Tshernova, 1972: 611 (type species: *Ephemerella nigra* Imanishi), synonymized by Tshernova (1972) at time of publication
Rhionella Allen, 1980: 83, new synonym (type species: *Ephemerella insolta* Allen)

Description.— Egg (Figs. 3, 4): Chorion with reticulations; strands ridged; mesh with single (Fig. 4) or multiple (Fig. 3) central tubercles. Larva: Maxilla usually with palp; palp, if present, covered with setae; crown setae numerically increased; canines reduced to denticulate blade (Fig. 27), its length much less than its width. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum with prominent anterolateral projections (Fig. 32). Claw with one row of denticles, sometimes numerically reduced. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax with with prominent, paddlelike anterolateral projections (Fig. 32); projection almost always without medial notch. Abdominal terga almost always with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 86): Forceps segment 3 globular. Forceps segment 2 with medial crease. Penes lobes compact, usually separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Distribution.— Eastern Palearctic, Oriental.

Species included.— ***C. braaschi***, new name [=*Ephemerella serrata* Braasch, 1981: 85, nec *E. serrata* Morgan, 1911: 109. Etymology: The new name is in honor of Dietrich Braasch, who originally described this species.]; *C. colossa* Kang and Yang, 1995; *C. corpulenta* (Braasch, 1981), new combination [=*Ephemerella corpulenta*]; *C. elongatula* (McLachlan, 1875) [=*Leptophlebia elongatula*; =*Ephemerella okumai* Gose, 1980]; *C. femorata* (Tshernova, 1972) [=*Asiatella femorata*; =*Ephemerella boja* Allen, 1975]; *C. fusca* Kang and Yang, 1995; *C. gosei* (Allen, 1975) [=*Ephemerella gosei*; =*Serratella thailandensis* Allen, 1980]; *C. indica* (Kapur and Kripalani, 1961), new combination [=*Ephemerella indica*]; *C. insolta* (Allen, 1971) [=*Ephemerella insolta*]; *C. levanidovae* (Tshernova, 1952) [=*Ephemerella levanidovae*; =*Ephemerella swatensis* Ali, 1971; =*Ephemerella castanea* Allen, 1971; =*Ephemerella delicata* Allen, 1971]; *C. nigra* (Ueno, 1928) [=*Ephemerella nigra*]; *C. orientalis* (Tshernova, 1952) [=*Ephemerella orientalis*; =*Ephemerella tshernovae* Bajkova, 1962; =*Ephemerella imanishii* Gose, 1980].

Remarks.— *Cincticostella indica* is included in this genus based on the coloration of the abdomen of the female adult (Kapur and Kripalani 1961), which is similar to that of several other *Cincticostella* species. *Cincticostella braaschi* is included in this genus based on its similarily to *C. femorata* and *C. insolta*, with respect to the larval femora (Braasch 1981).

These latter three species form an apparently monophyletic group, to which the name *Rhionella* would be applied; however, recognizing the nominal group would render the rest of *Cincticostella* paraphyletic (Fig. 94). Thus, *Rhionella* is placed into strict synonymy with *Cincticostella*.

Tribe **HYRTANELLINI** Allen, 1980: 88

Diagnosis.— Eggs usually have the chorion smooth or dimpled. The tribe is defined by the pleisiotypic form of the ventral lamella of gill 6 in larvae (Fig. 56), in which the medial cleft is deep and wide. Male adults usually have penes with dorsomedial projections.

Genus **PENELOMAX**, new genus

Type species: *Ephemerella septentrionalis* McDunnough

Description.— Egg (Fig. 12): Chorion with reticulations; strands ridged; mesh smooth. Larva (Fig. 59): Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles. Forefemur thin and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with medial spine on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia: Forceps segment 3 globular. Forceps segment 2 straight. Penes (Fig. 65) with long apical arms; anteromedial stout setae present; dorsomedial and lateral stout setae absent; dorsolateral projection absent. Cerci subequal to medial filament.

Etymology.— This genus is named in honor of the parents of LMJ, Max and Penelope.

Distribution.— Eastern Nearctic, restricted to the Appalachian Range and its vicinity.

Species included.— P. septentrionalis (McDunnough, 1925a), new combination [=*Ephemerella septentrionalis*].

Remark. Our attempts to examine *P. septentrionalis* eggs via SEM were not successful, and thus, we relied on Smith's (1935) observations. New SEM examination of eggs may provide additional insights into the relationships of this genus to other Ephemerellidae (Ogden et al. 2008).

Genus **TELOGANOPSIS** Ulmer, 1939: 513

Type species: *Teloganopsis media* Ulmer

Amurella Kluge, 1997: 235, new synonym (type species: *Ephemerella gracilis* Tshernova)
Uracanthella Belov, 1979: 577, new synonym (type species: *Ephemerella lenoki* Tshernova)
Kangella Sartori, 2004: 76, new synonym (=*Eburella* Kang and Yang, 1995, nec *Eburella* Monné and Martins, 1973 [Coleoptera]) (type species: *Eburella brocha* Kang and Yang)

Description.— Egg (Fig. 17): Chorion dimpled, rarely covered with globular tubercles (Fig. 16). Larva: Maxilla usually without palp (Fig. 28); if palp present, palp without medial setae; crown setae often numerically increased (Fig. 28); canines usually greatly reduced or vestigial (Fig. 28), rarely sharp; if sharp canines present, without lateral serrations along entire margin (Fig. 24). Mandibular canines sometimes enlarged (Figs. 22, 23). Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles and large, stout preapical denticle (Fig. 44). Forefemur not enlarged and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with no spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Figs. 61–64): Forceps segment 3 globular. Forceps segment 2 straight. Penes lobes sometimes elongate and separated by relatively deep cleft, but usually broad and separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection usually present. Cerci subequal to medial filament.

Distribution.— Holarctic, Oriental.

Species included.— T. albai (Gonzales del Tanago and Garcia de Jalon, 1983), new combination [=*Serratella albai*]; *T. bauernfeindi* (Thomas, Marie and Dia [in Marie, Dia and Thomas], 1999), new combination [=*Serratella bauernfeindi*]; *T. brocha* (Kang and Yang, 1995), new combination [*Eburella brocha*]; *T. changbaishanensis* (Su and You, 1988), new combination [*Ephemerella changbaishanensis*]; *T. chinoi* (Gose, 1980) [=*Ephemerella chinoi* Gose, 1980]; *T. deficiens* (Morgan, 1911), new combination [=*Ephemerella deficiens*; =*Ephemerella atrescens* McDunnough, 1925b]; *T. gracilis* (Tshernova, 1952), new combination [=*Ephemerella gracilis*]; *T. hispanica* (Eaton, 1887), new combination [=*Ephemerella hispanica*]; *T. jinghongensis* (Xu, You and Hsu, 1984), new combination [=*Ephemerella jinghongensis*; =*Serratella hainanensis* She, Gui and You, 1995; =*Serratella albostriata* Tong and Dudgeon, 2000]; *T. media* Ulmer, 1939; *T. mesoleuca* (Brauer, 1857), new combination [=*Potamanthus mesoleucus*; =*Ephemerella maculocaudata* Ikonomov, 1961]; *T. oriens* (Jacobus and McCafferty, 2006a), new combination [=*Uracanthella oriens*]; *T. punctisetae* (Matsumura, 1931), new combination [=*Drunella punctisetae*; *Ephemerella rufa* Imanishi, 1937a; =*Ephemerella lenoki* Tshernova, 1952; =*Ephemerella markevitshi* Belov, 1979; =*Ephemerella yixingensis* Wu and Gui, 1993]; *T. subsolana* (Allen, 1973), new combination [=*Ephemerella subsolana*].

Remarks.— *Teloganopsis changbaishanensis* is recombined under this genus based on the structure of the male genitalia (Fig. 62) being similar to that of *T. punctisetae*.

Genus **SERRATELLA** Edmunds, 1959: 544

Type species: *Ephemerella serrata* Morgan

Description.— Egg (Figs. 14, 15): Chorion smooth. Larva: Maxilla with palp; palp almost always without medial setae, very rarely covered with setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with one row of denticles. Forefemur not expanded and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Figs. 76, 77): Forceps segment 3 globular. Forceps segment 2 usually somewhat flattened and twisted (Figs. 76, 77). Penes lobes compact, separated by cleft of variable depth; anteromedial stout setae sometimes present; dorsomedial stout setae sometimes present; lateral stout setae usually present (Fig. 76); dorsolateral projection present (Fig. 77). Cerci subequal to medial filament.

Distribution.— Holarctic.

Species included.— *S. frisoni* (McDunnough, 1927) [=*Ephemerella frisoni*]; *S. fusongensis* (Su and You, 1988), new combination [=*Ephemerella fusongensis*]; *S. ignita* (Poda, 1761) [=*Ephemera ignita*; =*Ephemera erythrophalma* Schrank, 1798; =*Ephemera apicalis* Stephens, 1835; =*Ephemera diluta* Stephens, 1835; =*Ephemera fusca* Stephens, 1835; =*Baetis obscura* Stephens, 1835; =*Ephemera rosea* Stephens, 1835; =*Ephemera rufescens* Stephens, 1835; =*Potamanthus aeneus* Pictet, 1844; =*Potamanthus dilectus* Pictet, 1844; =*Potamanthus gibbus* Pictet, 1844; =*Ephemerella lactate* Bengtsson, 1909; =*Ephemerella torrentium* Bengtsson, 1917; =*Ephemerella sibirica* Tshernova, 1952; =*Drunella karasuensis* Kustareva, 1976; =*Ephemerella antuensis* Su and You, 1989]; *S. ishiwatai* (Gose, 1985), new combination [=*Ephemerella ishiwatai*]; *S. karia* (Kazanci, 1990), new combination [=*Drunella karia*]; *S. levis* (Day, 1954) [=*Ephemerella levis*]; *S. longipennis* Zhou, Gui and Su, 1997; *S. micheneri* (Traver, 1934) [=*Ephemerella micheneri*; =*Ephemerella altana* Allen, 1968 (adult nec larva)]; ***S. occiprens***, new name [=*Ephemerella imanishii* Gose, 1980: 367, nec *Ephemerella imanishii* Allen, 1971: 517. *Etymology.—* The specific epithet is an arbitrary combination of letters that refers to the meaning of kanji characters in the surname of Kenji Imanishi; it borrows from the Latin *presens* (now) and *occidentalis* (west).]; *S. serrata* (Morgan, 1911) [=*Ephemerella serrata*; =*Ephemerella sordida* McDunnough, 1925b; =*Ephemerella carolina* Berner and Allen, 1961; =*Ephemerella spiculosa* Berner and Allen, 1961]; *S. serratoides* (McDunnough, 1931a) [=*Ephemerella serratoides*]; *S. setigera* (Bajkova, 1967) [=*Ephemerella setigera*]; ***S. tsuno***, new name, [=*Ephemerella cornuta* Gose, 1980: 367, nec *E. cornuta* Morgan, 1911: 114. Etymology: *Tsuno*, a noun in apposition, is part of the Japanese name of this species, and it means horn or antler.]; *S. uenoi* (Allen and Edmunds, 1963c), new combination [=*Ephemerella uenoi*; =*Ephemerella undatella* Allen, 1971]; *S. zapekinae* (Bajkova, 1967) [=*Ephemerella zapekinae*].

Remarks.— Serratella longipennis and *S. fusongensis* are included here based on their penes being similar to those of *S. ishiwatai* and *S. setigera*, respectively (Su and You 1988, Zhou et al. 1997a, Ishiwata 2000). Discovery of undescribed stages (i.e., male adult, egg) of other *Serratella* species may indicate alternate generic placement for these other species.

Genus **QUATICA**, new genus

Type species: *Ephemerella ikonomovi* Puthz

Description.— Egg: Chorion smooth or dimpled. Larva: Maxilla with palp; palp without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota sometimes with starlike setae (Fig. 36). Pronotum usually with prominent anterolateral projections. Claw with one row of denticles. Forefemur not enlarged and without stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines on posterior margins. Gills 3 without medial transverse band of weakened membrane. Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 67): Forceps segment 3 globular. Forceps segment 2 relatively straight. Penes lobes compact, separated by moderate cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection sometimes present. Cerci subequal to medial filament.

Etymology.— This name is an anagram derived from the English word, aquatic.

Distribution.— Western Palearctic.

Species included.— Q. euphratica (Kazanci, 1987), new combination [=*Drunella euphratica*]; *Q. ikonomovi* (Puthz, 1971), new combination [=*Ephemerella spinosa* Ikonomov, 1961; =*Ephemerella ikonomovi*; =*Drunella andaluciana* Kazanci, 1990]; *Q. paradinasi* (Gonzales del Tanago and Garcia de Jalon, 1983), new combination [=*Drunella paradinasi*].

Remarks.— Quatica paradinasi is included here on the basis of its having male genitalia similar to those of the other two species (Studemann and Tomka 1987, Studemann et al. 1989). Its placement is tentative, and, as such, the genus may not be monophyletic.

Genus **HYRTANELLA** Allen and Edmunds, 1976: 133

Type species: *Hyrtanella christineae* Allen and Edmunds

Description.— Egg: Chorion smooth. Larva: Maxilla usually with palp; palp, if present, without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged. Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw with two rows of denticles, second row usually forms preapical palisade. Forefemur usually not greatly enlarged and with few or no stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with paired spines and often with medial spine on posterior segments (Fig. 50). Gills 3 often with medial transverse band of weakened membrane (Fig. 50). Abdominal sterna without friction disc. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Fig. 68): Forceps segment 3 elongate. Forceps segment 2 relatively straight. Penes lobes not elongate, separated by shallow cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection present. Cerci subequal to medial filament.

Distribution.— Oriental.

Species included.— *H. christineae* Allen and Edmunds, 1976; *H. grandipennis* (Zhou, Su and Gui, 2000), new combination [=*Torleya grandipennis*]; *H. pascalae* Jacobus and Sartori, 2004.

Remarks.— Ogden et al. (2008) indicated an alternate phylogenetic relationship of *Hyrtanella* relative to the nominal groups *Crinitella* and *Torleya*. Please note further discussion, below.

Genus **TORLEYA** Lestage, 1917: 366

Type species: *Torleya belgica* Lestage

Crinitella Allen and Edmunds, 1963c: 17, new synonym (type species: *Ephemerella coheri* Allen and Edmunds)

Description.— Egg: Chorion dimpled. Larva: Maxilla with or without palp; if present, palp without medial setae; crown setae not numerically increased; canines sharp, without lateral serrations. Mandibular canines not enlarged (Fig. 21). Thoracic nota without starlike setae. Pronotum without prominent anterolateral projections. Claw (Fig. 42) usually with two rows of denticles, second row forming preapical palisade; claw rarely with only one row (Fig. 41). Forefemur not enlarged and usually without any stout chalazae on leading margin. Mesothorax without anterolateral projections. Abdominal terga with or without paired spines on posterior margins. Gills 3 usually without medial transverse band of weakened membrane; faint band rarely present. Abdominal sterna without friction disc, although long setae sometimes present. Posterolateral projections 9 not greatly elongate and not upturned. Cerci subequal to medial filament. Adult male genitalia (Figs. 66, 69): Forceps segment 3 ovoid. Forceps segment 2 straight or with triangular apical expansion. Penes lobes usually compact and separated by moderate cleft; anteromedial, dorsomedial and lateral stout setae absent; dorsolateral projection usually present. Cerci subequal to medial filament.

Distribution.— Palearctic, Oriental.

Species included.— *T. coheri* (Allen and Edmunds, 1963c), new combination [=*Ephemerella coheri*; =*Crinitella permkami* Wang and Sites, 1999]; *T. japonica* (Gose, 1980) [=*Ephemerella japonica*]; *T. lacuna* (Jacobus, McCafferty and Sites, 2007), new combination [=*Crinitella lacuna*]; *T. longforceps* (Gui, Zhou and Su, 1999), new combination [=*Serratella longforceps*]; *T. lutosa* Kang and Yang, 1995; *T. major* (Klapálek, 1905) [=*Ephemerella major*; =*Torleya belgica* Lestage, 1917; =*Torleya nazarita* Alba-Tercedor and Derka, 2003]; *T. mikhaili* Tiunova, 1995; *T. naga* Jacobus and McCafferty (in Jacobus et al.), 2004; *T. nepalica* (Allen and Edmunds, 1963c) [=*Ephemerella nepalica*; =*Ephemerella wahensis* Ali, 1971; =*Torleya glareosa* Kang and Yang, 1995; =*Serratella tumiforceps* Zhou and Su, 1997; =*Torleya arenosa* Tong and Dudgeon, 2000]; *T. padunica* Kazlauskas, 1963.

Remarks.— *Torleya longforceps* is placed in this genus on the basis of its male genitalia being similar to those of *T. coheri*, *T. lacuna* and *T. mikhaili* (Tiunova 1995, Gui et al. 1999, Jacobus et al. 2007). Ogden et al. (2008) indicated alternate phylogenetic relationships of the nominal groups *Crinitella*, *Hyrtanella* and *Torleya*, based on their analysis of three OTUs representing these groups. We propose validity for *Hyrtanella* and synonymy for *Torleya* and *Crinitella* based on the analysis of twelve OTUs representing the three nominal groups and based on the strong support for the placement of the type species deep within two distinctive clusters of OTUs (Fig. 99).

IDENTIFICATION OF RECENT EPHEMERELLIDAE GENERA

Key to Eggs

(Notes: Eggs of *Notacanthella*, *Adoranexa* and *Ephacerella* are undescribed. The eggs of *Timpanoga* and *Penelomax* are included tentatively.)

1 At least one polar cap present 2
1’ Polar caps absent (Studemann and Landolt 1997: Figs. 1–8; Burian 2002: Fig. 6) .... *Dentatella, Eurylophella*

2 Two polar caps present (Studemann and Landolt 1997: Fig. 9) .... *Dannella*
2’ One polar cap present 3

3 Chorion with large, round, protruding tubercles (Fig. 16) .... *Teloganopsis hispanica*
3’ Chorion without such tubercles 4

4 Chorion with strands (Figs. 1, 3–7, 12, 13) 5
4’ Chorion without strands (Figs. 2, 8–11, 14, 15), but it may have dimples (Fig. 17) 9

5 Strands furrowed (Figs. 6, 7) .... *Ephemerella* (in part)
5’ Strands ridged (Figs. 1, 3–5, 13) 6

6 Mesh with circle of papillae (Fig. 13) .... *Caurinella*
6’ Mesh without circle of papillae 7

7 Mesh with central tubercle(s) (Figs. 1, 3–5) 8
7’ Mesh with no central tubercles (Fig. 12; Smith 1935: Fig.29) .... *Penelomax*, *Timpanoga*

8 Mesh with single, central tubercle, sometimes enlarged to form recessed disk (Figs. 4, 5; Studemann and Landolt 1997: Fig. 15) ... *Tsalia, Spinorea*, *Cincticostella* (in part), ... *Attenella* (in part)
8’ Mesh usually with more than one small tubercle (Figs. 1, 3; Studemann and Landolt 1997: Figs. 13, 14) .... *Matriella, Cincticostella* (in part), *Attenella* (in part)

9 Chorion with dimples (Fig. 16) .... *Teloganopsis* (in part), *Quatica* (in part), *Torleya*
9’ Chorion without dimples (Figs. 2, 8–11, 14, 15) ...... *Serratella, Quatica* (in part), *Hyrtanella, Drunella, Ephemerella* (in part), *Caudatella*

Key to Larvae (Late Instars)

1 Gills 1 absent and gills 3 present 2
1’ Gills 1 present and gills 3 absent (following couplets modified from Waltz and Burian 2008) 24

2 With any of the following: dense disk of setae on abdominal sterna (Fig. 48), stout chalazae on leading margin of forefemora (Figs. 46, 47), distinctive anterior projection on prosternum (Fig. 39) .... *Drunella*
2’ Abdominal sterna without such disc, although a felt of setae may be present; forefemora without stout chalazae on leading margin; *and* prosternum without distinctive anterior projection 3

3 Claw with large, very stout, preapical denticle (Fig. 44) .... *Teloganopsis*
3’ Claw otherwise 4

4 Body and legs thin and elongate (Fig. 59) [eastern Nearctic] .... *Penelomax*
4’ Body (e.g., Figs. 50–52) and legs (e.g., Figs. 45–47) relatively robust 5

5 Medial filament much stouter and longer than cerci [western Nearctic] .... *Caudatella*
5’ Medial filament and cerci nearly subequal 6

6 Mesothorax with prominent anterolateral projection(s) (Figs. 32–34) [eastern Palearctic, Oriental] 7
6’ Mesothorax without such prominent projection(s) 11

7 Maxilla with length of canines greater than their respective width; canines not reduced (Fig. 25) .... *Notacanthella*

7' Maxilla with length of canines not greater than their respective width; canines fused and reduced to denticulate blade (Figs. 26, 27) 8

8 Blade length subequal to width (Fig. 26) .... *Spinorea*

8' Blade length much less than width (Fig. 27) 9

9 Anterolateral projections of mesothorax long and sharp (Fig. 34); abdominal gills distinctly falcate .... *Ephacerella*

9' Anterolateral projections of mesothorax relatively short and blunt (Figs. 32, 33); abdominal gills not falcate or only slightly falcate 10

10 Anterolateral projections of mesothorax always notched mediolaterally (as in Fig. 33) *and* prothorax without prominent anterolateral projections (as in Fig. 35) *and* mesal plate with paired spines or ridges ....*Adoranexa*

10' Anterolateral projections of mesothorax with or without (Fig. 32) notch; if notched, then prothorax with prominent anterolateral projections (as in Fig. 32) *and* mesal plate without paired spines or ridges ....*Cincticostella*

11 Claws with distal palisade of long denticles (Fig. 42) [eastern Palearctic, Oriental] 12

11' Claws without such palisade of denticles, although two rows may be present 14

12 Abdominal terga 8 and 9 with single stout, medial spine (Fig. 50) [Borneo] ....*Hyrtanella* (in part)

12' Abdominal terga 8 and 9 with paired spines or no spines 13

13 Abdominal terga with paired spines elongate [Oriental] ....*Hyrtanella grandipennis*

13' Abdominal terga paired spines small or absent [eastern Palearctic, Oriental] .... *Torleya* (in part)

14 Abdominal tergum 9 with distinctively long, upturned posterolateral projections (Fig. 55) [western Nearctic] ....*Caurinella*

14' Abdominal tergum 9 with posterolateral projections otherwise 15

15 Distribution Nearctic 16

15' Distribution Oriental and Palearctic 20

16 Maxillary palp vestigial (Fig. 31) or absent [western Nearctic] .... *Matriella*

16' Maxillary palp present and segmented 17

17 Abdominal terga with large, arching spines and forefemora without distal band of setae [southeastern Nearctic] .... *Tsalia*

17' Abdominal terga with small, paired spines or without armature; distal band of setae on forefemur present (Fig. 45) or absent 18

18 Maxilla with canines strongly serrate laterally; thoracic nota with numerous brown excrescences (Figs. 37, 38), expecially between forewingpads [western Nearctic] .... *Ephemerella* (in part; *E. tibialis* and *E. nuda*)
18' Maxillary canines without lateral serration; thoracic nota usually with excrescences very few or absent [transcontinental] 19

19 Ventral lamella of gills 6 with medial cleft very deep (as in Fig. 56) .... *Serratella*
19' Ventral lamella of gills 6 without such deep, medial cleft (as in Fig. 57) .... *Ephemerella* (in part)

20 Abdominal terga with paired spines or ridges [Palearctic & Oriental] ... 21
20' Abdominal terga without paired spines or ridges [Palearctic] .... *Torleya major*

21 Maxilla with canines strongly serrate laterally; thoracic nota with numerous brown excrescences (as in Figs. 37, 38), expecially between forewingpads [central and eastern Palearctic] .... *Ephemerella nuda*
21' Maxillary canines without lateral serration; thoracic nota usually with excrescences very few or absent [Palearctic and Oriental] 22

22 Ventral lamella of gills 6 with deep medial cleft (as in Fig. 56) [Palearctic and Oriental] 23
22' Ventral lamella of gills 6 with medial cleft tiny or absent (as in Fig. 57) [Palearctic] .... *Ephemerella* (in part)

23 Pronotum with anterolateral projections (similar to Fig. 32) or thoracic nota with robust, starlike setae (Fig. 36) .... *Quatica*
23' Pronotum without anterolateral projections; any robust setae present on thoracic nota not distinctly starlike .... *Serratella*

24 Gills 4 covering most of subjacent gills, with no more than one-third of any of these visible 25
24' Apical half of gills 5 and 6 visible from beneath gills 4 .... *Attenella*

25 Claws without denticles; maxilla with palp 26
25' Claws with denticles; maxilla without palp 27

26 Filamentous gills 1 originate at lateral margins of tergum; posterolateral abdominal processes not extremely developed .... *Dannella*
26' Filamentous gills 1 originate sublaterally on dorsal surface of tergum; posterolateral abdominal processes extremely developed .... *Timpanoga*

27 Paired median spines present on abdominal terga 1 through 7; abdominal tergum 9 approximately 1.4 times midlength of terga 8 or 10; operculate gills relatively narrow, ovate and broadly rounded distally .... *Eurylophella*
27' Paired median spines present only on abdominal terga 5 through 7; abdominal tergum 9 subequal to midlength of terga 8 or 10; operculate gills broad, but more narrowly rounded distally .... *Dentatella*

Key to Male Adults

(Note: Male adults of *Adoranexa* and *Spinorea* are undescribed)

1 Distribution Nearctic 2
1’ Distribution Palearctic and Oriental 19

2 Abdominal segment 3 with vestiges of gill sockets laterally 3
2’ Abdominal segment 3 with no vestiges of gill sockets (following couplets modified from Waltz and Burian 2008) 15

3 Genital forceps segment 3 elongate (Fig. 81) .... *Drunella*
3’ Genital forceps segment 3 length no more than 2x width 4

4 Forceps segment 3 attached at inner margin of segment 2; penes with deep U-shaped medial cleft (Fig. 83) [southeastern] .... *Tsalia*
4’ Forceps and penes not as above 5

5 Penes with long apical arms and stout spinelike setae in medial cleft (Fig. 65) [eastern] .... *Penelomax*
5’ Penes not exactly as above 6

6 Medial filament longer and stouter than cerci [western] .... *Caudatella*
6’ Medial filament and cerci subequal 7

7 Penes with some variety of sharp projections dorsolaterally (as in Figs. 62, 77) 8
7’ Penes without dorsolateral projections 9

8 Forceps relatively straight (as in Fig. 62) [eastern] .... *Teloganopsis*
8’ Forceps curved and somewhat twisted (as in Fig. 77) [transcontinental] .... *Serratella*

9 Penes with stout, spinelike setae or forceps segment 2 with apical quadrate expansion, or both (as in Figs. 74, 75) .... *Ephemerella* (in part)
9’ Penes without stout spinelike setae and forceps segment 2 without apical quadrate expansion 10

10 Penes lobes long with deep medial cleft .... *Ephemerella* (*E. needhami* and *E. apopsis*)
10’ Penes lobes not so long and divided (Figs. 72, 73, 78, 79, 82) [western] 11

11 Forceps segment 2 slightly swollen and with crease subdisally (Fig. 79); abdominal sterna usually with ganglionic marks .... *Ephemerella* (*E. nuda* and *E. tibialis*)
11’ Not exactly as above 12

12 Penes relatively narrow, compact and apically rounded (Fig. 78) [western] .... *Caurinella*
12' Penes usually broader, with apical projections or medial cleft (as in Figs. 72, 73, 82) 13

13 Penes broad and relatively blunt (Fig. 73); abdominal sterna with extensive dark markings .... *Ephemerella maculata*
13' Penes not as broad and blunt; abdominal sterna without such markings . 14

14 Genitalia as in Figure 82 .... *Matriella*
14' Genitalia as in Figure 72 .... *Ephemerella verruca*

15 Genital forceps segment 3 elongate (length nearly six times width); abdominal segments 6 and 7 with poorly developed fingerlike remnants of posterolateral projections .... *Attenella*
15' Genital forceps segment 3 subovoid (length less than three times width); abdominal segment 7, and often preceeding segments, with with well-developed fingerlike remnants of posterolateral projections 16

16 Penes broadest at base 17
16' Penes laterally expanded apically 18

17 Caudal filaments pale, unbanded; distinctive black shading on coxae and trochanters .... *Dentatella*
17' Caudal filaments variably banded; occasionally some shading on coxae and trochanters, usually not black .... *Eurylophella*

18 Penes with long apical lobes .... *Timpanoga*
18' Penes with short and rounded apical lobes .... *Dannella*

19 Abdominal segment 3 with vestiges of gill sockets laterally 20
19' Abdominal segment 3 with no vestiges of gill sockets .... *Eurylophella*

20 Forceps segment 3 elongate (as in Figs. 68, 81) 21
20' Forceps segment 3 length less than 2x width 23

21 Penes without dorsolateral projections; forceps segment 2 sometimes greatly swollen and bowed (Fig. 81) .... *Drunella*
21' Penes with dorsolateral projections (Figs. 66, 68, 69); forceps segment 2 neither greatly swollen nor bowed 22

22 Distribution Oriental .... *Hyrtanella*
22' Distribution Palearctic .... *Torleya* (in part; *T. major* and *T. padunica*)

23 Penes with apical or lateral stout, spinelike setae (as in Figs. 65, 74–76) 24
23' Penes without such spinelike setae 25

24 Penes with dorsolateral projections (similar to Fig. 77) .... *Serratella*
24' Penes without dorsolateral projections (Fig. 74) .... *Ephemerella aurivillii*

25 Forceps segment 2 with medial (Figs. 84–86) or subdistal crease (Fig. 79) 26
25' Forceps segment 2 relatively straight, sometimes with apical expansion (as in Figs. 74, 75) 29

26 Forceps segment 2 with crease subdistally (Fig. 79) .... *Ephemerella nuda*
26' Forceps segment 2 with crease medially (Figs. 84–86) 27

27 Penes elongate and distally scooplike (Fig. 84) [Oriental] .... *Notacanthella*
27' Penes not exactly as above [eastern Palearctic, Oriental] 28

28 Penes with deep, V-shaped notch on ventral face (Fig. 85) .... *Ephacerella*
28' Penes with medial, longitudinal suture on ventral face (Fig. 86) .... *Cincticostella*

29 Forceps segment 2 with quadrate apical expansion (similar to Fig. 74) and penes without dorsolateral projections .... *Ephemerella mucronata*
29' Genitalia not exactly as above 30

30 Penes lobes somewhat elongate and without dorsolateral projection (Fig. 64) .... *Teloganopsis* (in part; *mesoleuca* group)
30' Penes not exactly as above 31

31 Distribution restricted to Europe and extreme western Asia (Turkey) 32
31' Distribution restricted to Central and East Asia 34

32 Penes with dorsolateral projections (similar to Figs. 62, 67) 33
32' Penes without dorsolateral projections (Figs. 63) ... *Teloganopsis hispanica*

33 Penes lobes distinctly divided and somewhat expanded distally (as in Fig. 62) .... *Teloganopsis albai*
33' Penes lobes fused for almost entire length and not expanded distally (Fig. 67) .... *Quatica*

34 Penes without dorsolateral projection (Figs. 70, 71) .. *Ephemerella* (in part)
34' Penes with dorsolateral projections (Figs. 61, 62, 66) 35

35 Foretarsus with proximal hook (Fig. 60); penes lobes apicolaterally expanded (Figs. 61, 62) .... *Teloganopsis* (in part)
35' Foretarsus without proximal hook; penes lobes usually without such expansion (Fig. 66) .... *Torleya*

	1									10										20										30					35
attenuata	0	0	1	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
aculea	?	?	0	1	1	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	0	0	-	0	1	1	1	0	0
albai	4	-	0	0	0	0	0	0	1	-	1	1	2	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	-	0	0	0	0
allegheniensis	?	?	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0
alleni	3	-	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
apopsis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
atagosana	3	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aurivillii	3	-	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
basalis	3	-	0	1	1	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	0	0	-	0	1	1	0	0	0
bauerfeindi	?	?	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	2	0	0	0	0	0
berneri	0	2	1	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
braaschi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?
brocha	4	-	0	0	0	0	0	2	1	-	1	2	2	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	-	0	0	0	0
catawba	?	?	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	&	0	0	0	0	1
changbaishanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
chinoi	?	?	0	0	0	0	0	2	1	-	1	2	2	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	-	0	0	0	0
christineae	?	?	1	0	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	&	0	0	0	1	-
coheri	4	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	-	1	1	0	0
coloradensis	3	-	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0
colossa	0	0	0	0	0	0	0	0	0	2	1	1	1	1	1	1	1	0	0	1	?	0	0	0	0	?	0	0	-	0	?	?	?	0	0
commodema	?	?	1	0	0	0	0	0	0	2	1	1	0	-	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-
corpulenta	?	?	0	0	0	0	0	0	0	2	1	2	1	1	-	1	1	0	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
deficiens	4	-	0	0	0	0	0	0	1	-	1	1	2	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	-	0	0	0	0
doddsii	3	-	&	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	0	0	-	2	1	0	0	0	0
dorothea	3	-	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	&	0	0	0	0	0
edmundsi	3	-	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	0	0	1
elongatula	0	2	0	0	0	0	0	0	0	2	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
euphraticus	?	?	1	0	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	?	0	0	0	0	0	?	?	0	0	?	?	?	0	0
excrucians	3	-	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	&	0	0	0	0	0
femorata	?	?	&	0	0	0	0	0	0	2	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
flavilinea	?	?	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0
frisoni	?	?	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fusca	0	0	0	0	0	0	0	0	0	2	1	1	1	1	1	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
fusongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
gilliesi	?	?	1	0	0	0	0	0	0	2	1	1	1	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
glebosa	0	2	1	0	0	0	0	0	0	2	1	1	1	0	1	1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
gosei	?	?	0	0	0	0	0	0	1	-	1	2	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
gracilis	?	?	1	0	0	0	0	0	1	-	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	-	0	0	0	0
grandipennis	?	?	1	0	0	0	0	0	&	-	0	0	0	-	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	&	&	0	0
grandis	?	?	1	0	1	0	1	0	0	0	0	0	0	-	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0
heterocaudata	?	?	&	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-
hispanica	4	-	0	0	0	0	0	0	1	-	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	-	0	0	0	0
hispida	?	?	0	0	0	0	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
hystrix	3	-	1	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-
idahoensis	0	2	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	1	1	0	0
ignita	3	-	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ikonomovi	4	-	1	0	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
indica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Fig. 87. Data matrix, Section 1/6.

ACKNOWLEDGMENTS

Mike Cole (Greenfield, Massachusetts) kindly prepared many of the line drawings and the dorsal habitus of *Penelomax septentrionalis*. Y. Jae Bae (Seoul, Korea), Ed Becker (Ottawa, Ontario), Dietrich Braasch (Potsdam, Germany), Ethan Bright (Ann Arbor, Michigan), Greg Courtney (Ames, Iowa), R. Ed DeWalt (Champaign, Illinois), the late George Edmunds (Salt Lake City, Utah), Sanaa Enhktaivan (Ulaanbaatar, Mongolia), Colin Favret (Champaign, Illinois), Toshihito Fujitani (Osaka, Japan), Jean-Luc Gattolliat (Lausanne, Switzerland), Adam Glazacow (Poznan, Poland), David Goodger (London, England), Arne Haybach (Koblenz, Germany), Stephen Hiner (Blacksburg, Virginia), Brad Hubley (Toronto, Ontario), Raymond Hutchinson (Ottawa, Ontario), Shinichi Ishiwata (Kanagawa, Japan), Nikita Kluge (St. Petersburg, Russia), Boris Kondratieff (Ft. Collins, Colorado), Reimo Lieske (Schlitz, Germany), John MacDonald (West Lafayette, Indiana),

	1 10 20 30 35
insolta	? ? 1 0 1 0 0 0 0 - 1 1 1 1 1 1 1 0 1 1 0 1 1 1 1 0 0 0 0 0 0 0 0 1 -
invaria	3 - 0 0 0 0 0 0 0 1 0 0 0 - 0 0 & 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
ishiwatai	? ? 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 ? ? ? 0 0 0 0 0 0
ishiyamana	3 - & 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 1 0 0 - 0 1 1 0 0 0
jacobi	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 -
japonica	? ? 0 0 0 0 0 0 1 - 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0
jinghongensis	? ? 0 0 0 0 0 0 1 - 1 1 2 - - 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 - 0 0 0 0
karia	? ? 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
kohnoae	3 - 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 1 0 1 1 0 0 0 0 1 1 1 0 0
kozhovi	3 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
lacuna	? ? 1 0 0 0 0 0 1 - 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0
lata	3 - 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 2 1 1 1 0 0
lepnevae	3 - 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 0 0 0 0
levanidovae	0 0 0 0 0 0 0 0 0 2 1 1 1 1 1 1 1 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
levis	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 & 0 0 0 0 0
longforceps	? ?
longicaudata	? ? 0 0 0 0 0 0 0 2 1 1 1 1 1 1 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
longipennis	? ?
lutosa	4 - 0 0 1 0 0 0 1 - 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0
maculata	1 3 0 0 0 0 0 0 0 0 0 1 0 - 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 2 - 0 0 0 0
major	4 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 1 1 0 0
media	4 - 0 0 0 0 0 0 1 - 1 1 2 - - 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 - 0 0 0 0
mesoleuca	4 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 - 0 0 0 0
micheneri	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
mikhaili	? ? 0 0 ? 0 0 0 1 - 0 0 0 - 0 0 0 ? 0 0 ? 0 0 0 0 0 ? ? ? & 0 1 0 0 0
montana	0 2 1 0 0 0 0 0 0 2 1 1 1 0 1 1 0 0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
mucronata	1 3 0 0 0 0 0 0 0 0 0 0 0 - 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
naga	4 - 0 0 1 0 0 0 1 - 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0
needhami	1 3 0 0 0 0 0 0 0 1 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
nepalica	4 - 1 0 0 0 0 0 1 - 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0
nigra	0 2 0 0 0 0 0 0 0 2 1 1 1 1 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
nigromaculata	? ?
notata	1 3 0 0 0 0 0 0 0 1 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
nuda	3 - 0 0 0 0 0 0 0 - 0 0 0 - 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
occiprens	? ? 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
oriens	? ? 0 0 0 0 0 0 1 - 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 - 0 0 0 0
orientalis	0 0 0 0 0 0 0 0 0 2 1 2 1 1 1 1 1 0 1 1 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0
padunica	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 1 0 0
paradinasi	4 - 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
pascalae	3 - 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 & 1 0 0 0 1
pelosa	? ? 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 -
perculta	? ? 1 0 0 0 0 0 0 2 1 0 0 - 0 1 0 0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 1 -
punctisetae	4 - 0 0 0 0 0 1 1 - 1 2 2 - - 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0
quadrata	? ? 1 0 0 0 0 0 0 2 1 1 0 - 1 1 1 0 1 2 0 0 0 0 0 0 0 0 - 0 0 0 0 1 -
sachalinensis	? ? 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 1 1 0 0 0
septentrionalis	0 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 & 0 0 0 0 0
serrata	3 - 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
serratoides	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Fig. 88. Data matrix, Section 2/6.

Michael Meyer (Newport News, Virginia), John Morse (Clemson, South Carolina), Robert Newell (Polson, Montana), Mark O'Brien (Ann Arbor, Michigan), Jan Peters (Tallahassee, Florida), Wojciech Pulawski (San Francisco, California), Michel Sartori (Lausanne, Switzerland), Bill Shepard (Sacramento, California), Hans Silfverberg (Helsinki, Finland), Kris Simpson (Columbia, Missouri), Robert Sites (Columbia, Missouri), Ian Smith (Ottawa, Ontario), Tomas Soldán (Czech Republic), Sven-Erik Spichiger (Harrisburg, Pennsylvania), Denise Studemann (Fribourg, Switzerland), Lu Sun (Bethesda, Maryland), John Thurman (Norris, Tennessee), J. Reese Voshell (Blacksburg, Virginia), Jeff Webb (Wondonga, Victoria, Australia), Bob Wisseman (Corvallis, Oregon), Kazunori Yoshizawa (Sapporo, Japan), and Changfa Zhou (Nanjing, China) assisted by locating, loaning or donating specimens. Ellen Alers (Washington, D.C.) provided details from C. P. Alexander's field notebooks. Jan Peters and Tianqi Wang (North Andover, Massachusetts) suggested some characters for phylogenetic analysis. Jan Peters donated the figure of the

	1 10 20 30 35
setigera	3 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
soldani	? ? 1 0 0 0 0 0 0 2 1 1 1 1 1 1 0 0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
solida	? ? 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 0 1 1 0 0 - 0 1 1 0 0 0
spinifera	? ? 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 1 0 0 0 1 0 1 0 1 0 0 0 0 1 1 1 0 0
submontana	3 - 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 1 0 0 - 0 1 0 0 0 0
subsolana	? ? 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 - 0 0 0 0
subvaria	3 - 1 0 0 0 0 0 0 1 0 0 0 - 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
teresa	0 0 0 0 0 0 0 0 0 - 0 0 0 - 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0
tianmushanensis	? ?
tibialis	3 - 0 0 0 0 0 0 0 1 0 0 0 - 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
triacantha	3 - ? 0 1 1 1 0 0 0 0 0 0 - 0 0 ? ? ? ? ? 1 1 1 1 1 ? ? ? 0 ? ? ? ? ?
trispina	3 - 1 0 1 1 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 1 0 0 - 0 1 1 1 0 0
tsuno	? ? 1 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
tuberculata	3 - 1 0 1 0 1 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 1 1 1 0 0
uenoi	3 - 1 0 0 0 0 0 0 2 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0
velmae	? ? 0 0 0 0 0 0 0 1 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
verruca	3 - 1 0 0 0 0 0 0 1 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
walkeri	3 - 1 0 1 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 1 1 0 0
zapekinae	3 - 0 0 0 0 0 0 0 0 0 0 0 - 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Fig. 89. Data matrix, Section 3/6.

adult *Teloganopsis* tarsus, and Nikita Kluge sent a photograph of the gill of *E. nuda*, from which the line drawing was made. Steve Jensen (Springfield, Missouri) granted permission to use some figures from his thesis. Heath Ogden (Pocatello, Idaho) provided valuable consultation on technical issues and facilitated the loan of some specimens. Nikita Kluge graciously discussed and debated the use and interpretation of various characters for phylogenetic inference. Greg Hass (Bad Axe, Michigan) helped build a rearing apparatus for field studies. Virginia Ferris (Lafayette, Indiana), Chris Oseto (West Lafayette, Indiana), Arwin Provonsha (West Lafayette, Indiana), Michel Sartori (Lausanne, Switzerland), Anne Spacie (West Lafayette, Indiana), Bob Waltz (Indianapolis, Indiana) and Michael Zannis (West Lafayette, Indiana) provided counsel. The encouragement and intellectual contributions of Jeff Webb, Michael Meyer (Newport News, Virginia), Jami Schrock Guenther (Michigan), Lu Sun (Bethesda, Maryland), Pat Randolph (Davis, California), Carlos Lugo-Ortiz (Puerto Rico), Jeong-mi Hwang (Seoul, Korea), Sanaa Enhktaivan, Helen Barber-James (Grahamstown, South Africa), Jean-Luc Gattolliat and Changfa Zhou also should be acknowledged. Discover Life In America, Inc. and the U. S. National Park Service provided funding and facilities for some fieldwork. This study was funded in part by USEPA fellowship 91601701-0 and CanaColl Grant 178. This material is based upon work supported under a National Science Foundation Graduate Research Fellowship.

LITERATURE CITED

Alba-Tercedor, J. 1981[1982]. RecopilaciÛn bibliográfica de citas de EfemerÛpteros en la PenÌnsula Ibérica e islas Baleares. Trabajos y MonografÌas del Departamento de ZoologÌa Universidad de Granada (New Series) 4(2): 41–81.

Alba-Tercedor, J. and T. Derka. 2003. *Torleya nazarita* sp. n., a new species from southern Spain (Ephemeroptera: Ephemerellidae). Aquatic Insects 25: 23–32.

Alba-Tercedor, J. and A. Sánchez-Ortega. 1982. Presencia del género *Torleya* Lestage, 1917 (Insecta, Ephemeroptera, Ephemerellidae) en la PenÌnsula Ibérica. Boletin de la Real Sociedad Espanola de Historia Natural Seccion Biologica 80: 81–88.

Ali, S. R. 1971. Certain mayfly nymphs (Order; Ephemeroptera) of Azad Kasmir and Swat. Pakistan Journal of Science 23: 209–214.

Allen, R. K. 1959. A new species of *Ephemerella* from Oregon (Ephemeroptera: Ephemerellidae). Journal of the Kansas Entomological Society 32: 59–60.

	36				40										50
attenuata	0	1	-	0	0	?	1	0	0	1	&	0	0	0	0
aculea	1	0	0	1	0	1	1	0	0	1	5	0	0	0	0
albai	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
allegheniensis	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
alleni	1	0	0	1	0	0	1	0	0	0	&	0	0	1	1
apopsis	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0
atagosana	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
aurivillii	1	0	0	1	0	0	2	0	0	0	4	0	0	1	1
basalis	1	0	0	1	0	1	1	0	0	1	5	0	0	0	0
bauerfeindi	1	0	0	0	?	?	?	0	?	?	?	?	?	?	?
berneri	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
braaschi	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
brocha	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?
catawba	1	0	0	1	0	0	1	0	0	0	4	0	0	0	&
changbaishanensis	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0
chinoi	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?
christineae	1	0	1	0	?	0	1	0	?	?	?	?	?	?	?
coheri	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0
coloradensis	1	0	0	1	0	1	2	0	0	1	0	0	0	0	0
colossa	1	0	0	?	?	?	1	0	?	?	?	?	?	?	?
commodema	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
corpulenta	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
deficiens	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
doddsii	1	0	0	1	0	1	1	0	0	1	5	0	0	0	0
dorothea	1	0	0	1	0	0	1	0	0	0	4	0	0	1	1
edmundsi	1	0	0	1	0	0	2	1	0	0	0	1	0	0	0
elongatula	1	0	0	1	0	0	2	0	0	0	2	0	0	0	0
euphraticus	1	0	0	?	?	?	1	0	?	0	?	1	0	0	0
excrucians	1	0	0	1	0	0	1	0	0	0	&	0	0	&	1
femorata	1	0	0	1	0	1	2	0	?	?	?	?	?	?	?
flavilinea	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
frisoni	1	0	0	0	0	0	1	0	?	0	1	1	0	0	0
fusca	1	0	0	1	0	0	1	0	?	?	?	?	?	?	?
fusongensis	?	?	?	?	?	?	?	?	0	0	1	?	1	0	0
gilliesi	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
glebosa	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
gosei	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
gracilis	1	0	0	0	0	0	1	0	?	?	?	?	?	?	?
grandipennis	1	0	0	0	0	&	1	0	0	1	0	1	0	0	0
grandis	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
heterocaudata	1	0	0	1	0	0	2	1	0	0	0	1	0	0	0
hispanica	1	0	0	0	0	0	1	0	?	0	0	0	0	0	0
hispida	1	0	0	1	0	0	2	0	0	0	4	0	0	0	1
hystrix	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0
idahoensis	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0
ignita	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0
ikonomovi	1	0	0	0	0	0	2	0	0	0	0	1	0	0	0
indica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Fig. 90. Data matrix, Section 4/6.

Allen, R. K. 1965. A review of the subfamilies of Ephemerellidae (Ephemeroptera). Journal of the Kansas Entomological Society 38: 262–266.

Allen, R. K. 1968. New species and records of *Ephemerella* (*Ephemerella*) in western North America (Ephemeroptera: Ephemerellidae). Journal of the Kansas Entomological Society 41: 557–567.

Allen, R. K. 1971. New Asian *Ephemerella* with notes (Ephemeroptera: Ephemerellidae). Canadian Entomologist 103: 512–528.

	36				40										50
insolta	1	0	0	1	0	1	2	0	?	?	?	?	?	?	?
invaria	1	0	0	1	0	0	1	0	0	0	4	0	0	&	1
ishiwatai	1	0	0	0	0	0	2	0	0	0	4	1	1	0	0
ishiyamana	1	0	0	1	0	1	2	0	0	1	5	0	0	0	0
jacobi	1	0	0	1	0	1	2	1	?	0	0	1	0	0	0
japonica	1	0	0	0	1	0	1	0	?	0	0	1	0	0	0
jinghongensis	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
karia	1	0	0	0	1	0	1	0	?	?	?	?	?	?	?
kohnoae	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
kozhovi	1	0	0	1	0	0	1	0	0	0	0	?	0	0	0
lacuna	1	0	0	0	0	0	1	0	?	0	0	1	?	?	?
lata	1	0	0	1	0	1	1	0	0	1	5	0	0	0	0
lepnevae	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
levanidovae	1	0	0	1	0	0	2	0	0	0	2	0	0	0	0
levis	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0
longforceps	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0
longicaudata	1	0	0	1	0	0	2	0	0	0	2	0	0	0	0
longipennis	?	?	?	?	?	?	?	?	?	0	?	1	?	?	?
lutosa	1	0	0	0	1	0	0	0	?	?	?	?	?	?	?
maculata	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
major	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0
media	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
mesoleuca	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0
micheneri	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0
mikhaili	1	0	0	0	?	0	0	0	?	0	0	?	0	0	0
montana	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
mucronata	1	0	0	1	0	0	1	0	0	0	4	0	0	0	0
naga	1	0	0	0	0	0	0	0	0	0	3	1	0	0	0
needhami	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
nepalica	1	0	0	0	1	0	1	0	0	0	3	1	0	0	0
nigra	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0
nigromaculata	?	?	?	?	?	?	?	?	0	0	2	0	0	0	0
notata	1	0	0	1	0	0	1	0	?	0	0	0	0	0	0
nuda	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0
occiprens	1	0	0	0	1	0	2	0	?	?	?	1	1	0	0
oriens	1	0	0	0	0	0	2	0	?	?	?	?	?	?	?
orientalis	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0
padunica	1	0	0	0	?	0	1	0	?	1	0	?	0	0	0
paradinasi	1	0	0	0	0	0	1	0	?	0	0	1	0	0	0
pascalae	1	0	1	0	1	0	1	0	?	1	?	?	?	?	?
pelosa	1	0	0	1	0	1	2	0	0	1	0	0	0	0	0
perculta	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
punctisetae	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
quadrata	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
sachalinensis	1	0	0	1	0	1	2	0	0	1	5	0	0	0	0
septentrionalis	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
serrata	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0
serratoides	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0

Fig. 91. Data matrix, Section 5/6.

Allen, R. K. 1973. New Ephemerellidae from Madagascar and Afghanistan (Ephemeroptera). Pan-Pacific Entomologist 49: 160–164.

Allen, R. K. 1974. The present status of *Ephemerella borakensis* (Ephemeroptera: Ephemerellidae). Canadian Entomologist 106: 1227.

	36				40										50
setigera	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0
soldani	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
solida	1	0	0	1	0	1	1	0	?	1	5	0	0	0	0
spinifera	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
submontana	1	0	0	1	0	1	1	0	0	1	5	0	0	0	0
subsolana	1	0	0	0	0	0	2	0	?	?	?	?	?	?	?
subvaria	1	0	0	1	0	0	1	0	0	0	4	0	0	&	1
teresa	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
tianmushanensis	?	?	?	?	?	?	?	?	0	0	2	0	0	0	0
tibialis	1	0	0	1	0	0	1	0	0	0	2	0	0	0	0
triacantha	?	?	0	1	?	?	?	0	0	1	5	0	0	0	0
trispina	1	0	0	1	0	1	2	0	?	?	?	?	?	?	?
tsuno	1	0	0	0	0	0	1	0	0	0	1	1	1	1	0
tuberculata	1	0	0	1	0	1	2	0	0	1	0	0	0	0	0
uenoi	1	0	0	0	0	0	2	0	?	?	?	?	?	?	?
velmae	1	0	0	1	0	0	2	0	?	?	?	?	?	?	?
verruca	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
walkeri	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
zapekinae	1	0	0	0	1	0	2	0	0	0	1	1	1	1	0

Fig. 92. Data matrix, Section 6/6.

Allen, R. K. 1975. *Ephemerella* (*Cincticostella*): A revision of the nymphal stages (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 51:16–22.

Allen, R. K. 1977a. A review of *Ephemerella* (*Dannella*) and the description of a new species (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 53: 215–217.

Allen, R. K. 1977b. New species of *Ephemerella (Ephemerella)* from Alberta (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 53: 286.

Allen, R. K. 1980. Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae). Pp. 71–91, in: Flannagan, J. F. and K. E. Marshall (eds). Advances in Ephemeroptera Biology. Plenum, New York.

Allen, R. K. 1984. A new classification of the subfamily Ephemerellinae and the description of a new genus. Pan-Pacific Entomologist 60: 245–247.

Allen, R. K. 1986. Mayflies of Vietnam: *Acerella* and *Drunella* (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 62: 301–302.

Allen, R. K. and D. L. Collins. 1968. A new species of *Ephemerella* (*Serratella*) from California (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 44: 122–124.

Allen, R. K. and G. F. Edmunds, Jr. 1958. A new species of *Ephemerella* from Georgia (Ephemeroptera: Ephemerellidae). Journal of the Kansas Entomological Society 31: 222–224.

Allen, R. K. and G. F. Edmunds, Jr. 1959. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). I. The subgenus *Timpanoga*. Canadian Entomologist 91: 51–58.

Allen, R. K. and G. F. Edmunds, Jr. 1961. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). II. The subgenus *Caudatella*. Annals of the Entomological Society of America 54: 603–612.

Allen, R. K. and G. F. Edmunds, Jr. 1962. A revision of the genus *Ephemerella* (Ephemeroptera, Ephemerellidae). V. The subgenus *Drunella* in North America. Miscellaneous Publications of the Entomological Society of America 3: 145–179.

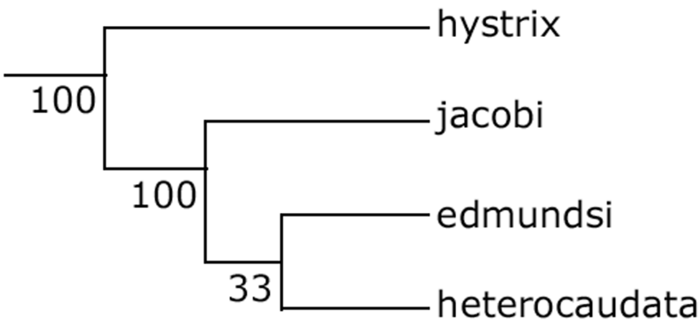


Fig. 93. Majority rule consensus of three trees, heterocaudata group (= genus *Caudatella*).

Allen, R. K. and G. F. Edmunds, Jr. 1963a. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VI. The subgenus *Serratella* in North America. Annals of the Entomological Society of America 56: 583–600.

Allen RK, Edmunds GF, Jr. 1963b. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VII. The subgenus *Eurylophella*. Canadian Entomologist 95: 597–623.

Allen, R. K. and G. F. Edmunds, Jr. 1963c. New and little known Ephemerellidae from southern Asia, Africa and Madagascar (Ephemeroptera). Pacific Insects 5: 11–22.

Allen, R. K. and G. F. Edmunds, Jr. 1965. A revision of the genus *Ephemerella* (Ephemeroptera, Ephemerellidae) VIII. The subgenus *Ephemerella* in North America. Miscelaneous Publications of the Entomological Society of America 4: 244–282.

Allen, R. K. and G. F. Edmunds, Jr. 1976. *Hyrtanella*: A new genus of Ephemerellidae from Malaysia (Ephemeroptera). Pan-Pacific Entomologist 52: 133–137.

Bae, Y. J., N. Kluge and D. J. Chun. 1998. New synonymy and new data on the distribution of the mayflies from Korea and the Russian Far East (Ephemeroptera). Zoosystematica Rossica 7: 89–94.

Bae, Y. J., J. E. Lee and I. B. Yoon. 2000. Northeast Asian Ephemeroptera in Imanishi's 1940 report. Entomological Science 3: 391–397.

Bajkova, O. 1962. New species of the genus *Ephemerella* Walsh. (Ephemeroptera, Ephemerellidae) from Gornikh Pritokov Amur Basin. Izvestiya Tikhookeanskogo Nauchno-Issledovatel'skogo Rybokhozyaistvennogo Tsentra 48: 202–205.

Bajkova, O. 1967. New species of *Ephemerella* Walsh (Ephemeroptera, Ephemerellidae) from the Far East and East Siberia. Entomologicheskoe Obozrenie 46: 327–335.

Bajkova, O. 1972. Contribution to the knowledge of mayflies (Ephemeroptera) from the Amur Basin. I. Imagines (Ephemeroptera: Ephemerellidae). Izvestiya Tikhookeanskogo Nauchno-Issledovatel'skogo Rybokhozyaistvennogo Tsentra 77: 178–206.

Bajkova, O. 1980. A new species of mayfly (Ephemeroptera, Ephemerellidae) from Primorye Region. Entomologicheskoe Obozrenie 59: 796–799.

Banks, N. 1914 [1915]. New neuropteroid insects, native and exotic. Proceedings of the Academy of Natural Sciences of Philadelphia 66: 608–632, 28 pl.

Barber-James, H. M., J.-L. Gattolliat, M. Sartori and M. D. Hubbard. 2008. Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater. Hydrobiologia 595: 339–350.

Beketov, M. A. and N. Kluge. 2003. Mayflies of Southwestern Siberia, Russia (Ephemeroptera). Opuscula Zoologica Fluminensia 211: 1–6.

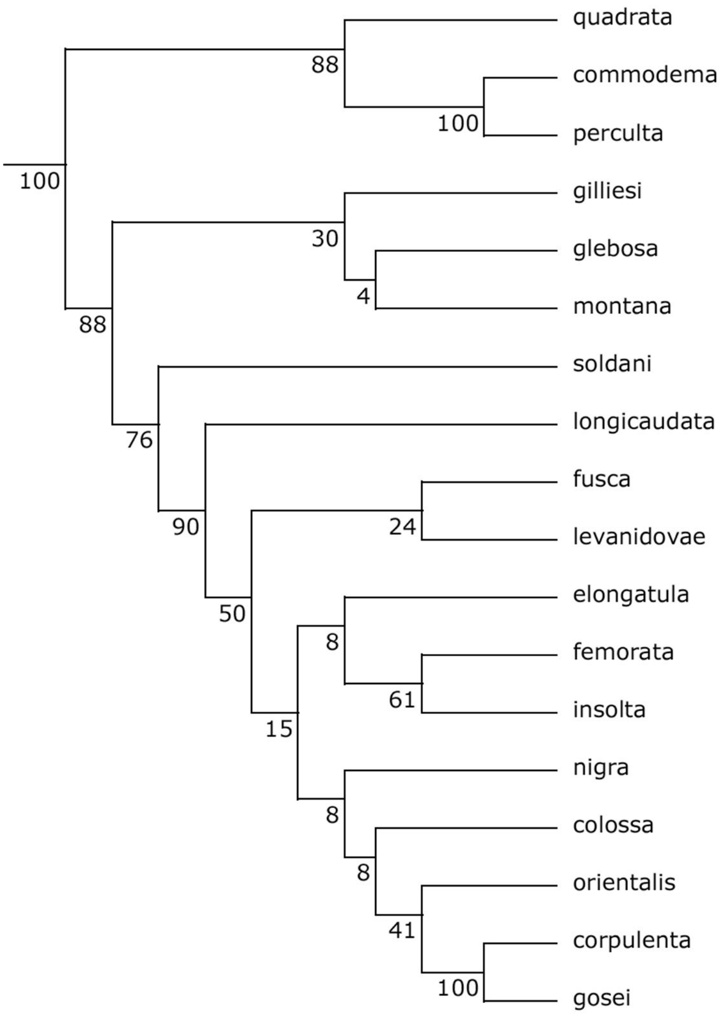


Fig. 94. Majority rule consensus of 431 trees, nigra group (= genera *Notacanthella*, *Spinorea*, *Adoranexa*, *Ephacerella* and *Cincticostella*).

Bell, J. G., C. Ghioni and J. R. Sargent. 1994. Fatty-acid compositions of 10 freshwater invertebrates which are natural food organisms of Atlantic salmon parr (*Salmo salar*): A comparion with commercial diets. Aquaculture 128: 301–313.

Belov, V. V. 1979. A new mayfly genus (Ephemeroptera, Ephemerellidae) in the USSR fauna. Dopovidi Adadmeii Nauk Ukrainskoi RSR Seriya B—Geologichni Khimichni ta Biologichni Nauki 1979(7): 575–578.

Bengtsson, S. 1909. Beitrage zur Kenntnis der Palaarktischen Ephemeriden. Lunds Universitets Arsskrift, N. F., Afd. 2, Bd. 5: 1–19.

Bengtsson, S. 1917. Weitere Beiträge zur Kenntnis der nordischen Eintagsfliegen. Entomologisk Tidskrift 38: 174–194.

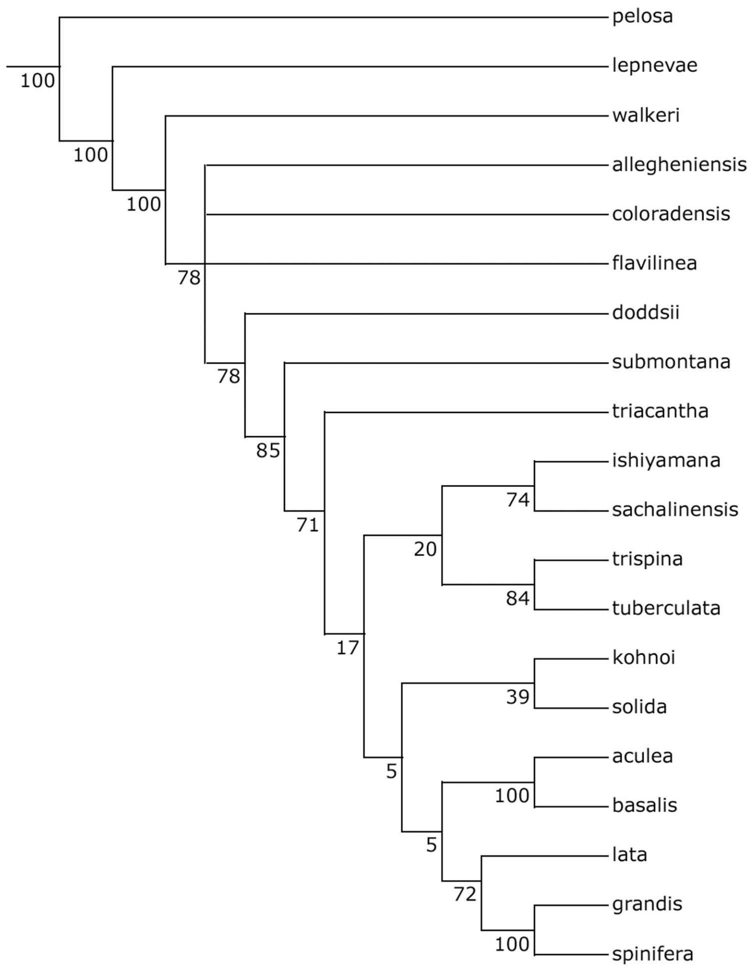


Fig. 95. Majority rule consensus of 1735 trees, grandis group (= genus *Drunella*).

Bennett, H. H., M. W. Mullen, P. M. Stewart, J. A. Sawyer and E. C. Webber. 2004. Development of an invertebrate community index for an Alabama coastal plain watershed. Journal of the American Water Resources Association 40: 43–51.

Berlese, A. 1909. Monografia dei Myrientomata. Redia 6: 1–182.

Berner L. 1946. New species of Florida mayflies (Ephemeroptera). Florida Entomologist 28: 60–82.

Berner, L. and R. K. Allen. 1961. Southeastern species of the mayfly subgenus *Serratella* (*Ephemerella*: Ephemerellidae). Florida Entomologist 44: 149-158.

Beutel, R. G. and H. Pohl. 2006. Endopterygote systematics—where do we stand and what is the goal (Hexapoda, Arthropoda)? Systematic Entomology 31: 202–219.

Braasch, D. 1981. Beitrag zur Kenntnis der Ephemerellidae des Himalaya. Reichenbachia 19: 85–88.

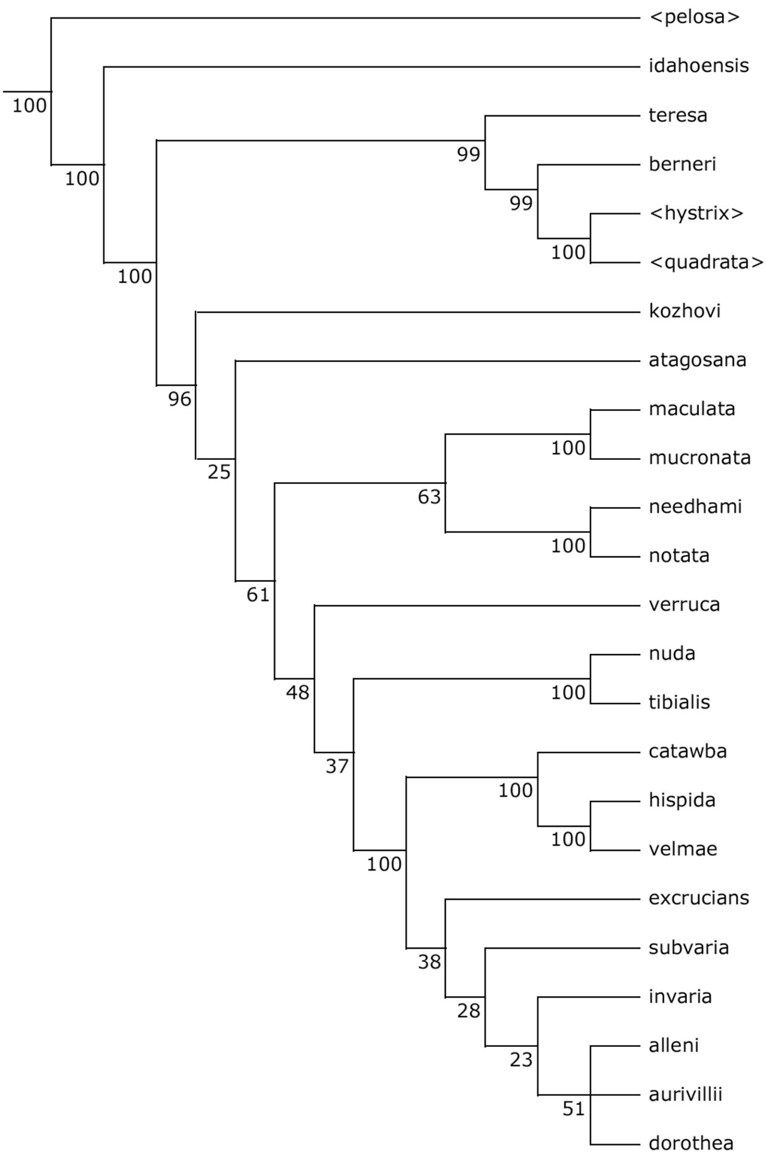


Fig. 96. Majority rule consensus of 8338 trees, fused-gill ephemerelline group (= genera *Drunella*, *Caurinella*, *Ephemerella*, *Matriella*, *Tsalia*, *Caudatella* + *Cincticostella* complex of genera); exemplar OTUs indicated by <>.

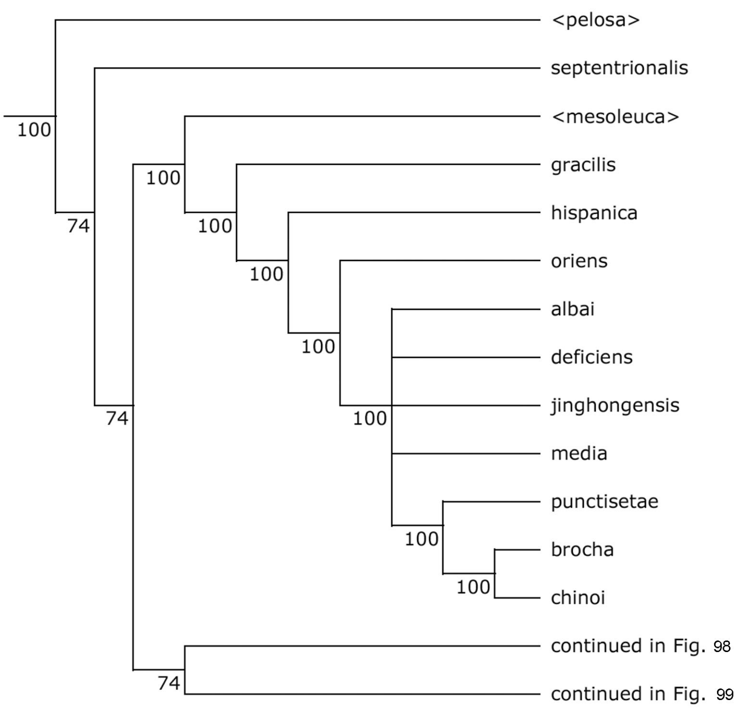


Fig. 97. Majority rule consensus of 29,603 trees, Ephemerellinae group (= tribe Ephemerellini + genera *Penelomax*, *Teloganopsis* and others in figures 98, 99); exemplar OTUs indicated by <>.

Brauer, F. 1857. Neuroptera austriaca. Carl Gerold's Sohn, Wien, 75 pp.

Brauer, F., J. Redtenbacher and L. Ganglbauer. 1889. Fossile Insekten aus der Juraformation Ost-Sibiriens. Mémoires de l'Academie Impériale des Sciences de St.-Petersbourg (7), 36(15): 1–20, 2 pl.

Brittain, J. E. and M. Sartori. 2003. Ephemeroptera (Mayflies). Pp. 373–380, in: Resh, V. H. and R. T. Cardé. (eds). Encylopedia of Insects. Academic Press, Amsterdam.

Brodsky, K. 1930. Zur Kenntnis der mittelasiatischen Ephemeropteren I. (Imagines). Zoologische Jahrbuecher. Abteilung fuer Systematic Oekologie und Geographie der Tiere 59: 681–720.

Buchwalter, D. B., D. J. Cain, W. H. Clements, and S. N. Lucima. 2007. Using biodynamic models to reconcile differences between laboratory toxicity tests and field biomonitoring with aquatic insects. Environmental Science & Technology 41: 4821–4828.

Burian, S. K. 2002. Taxonomy of *Eurylophella coxalis* (McDunnough) with notes on larval habitat and behavior (Ephemeroptera:Ephemerellidae). Journal of the North American Benthological Society 21: 602–615.

Burks, B. D. 1947 [1949]. New species of *Ephemerella* from Illinois (Ephemeroptera). Canadian Entomologist 79: 232–236.

Burks, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bulletin of the Illinois Natural History Survey 26 (Art. 1): 1–216.

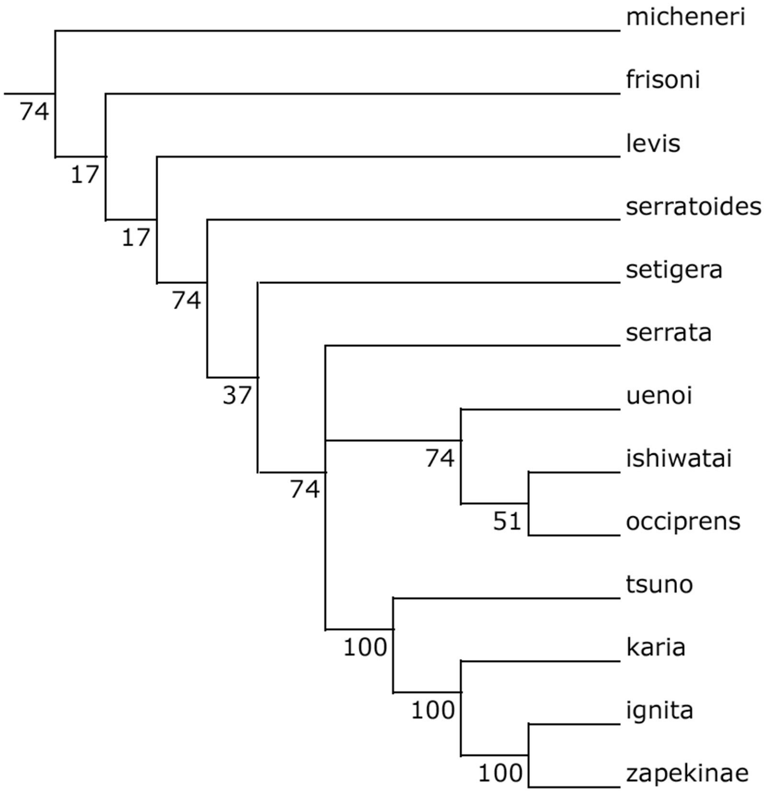


Fig. 98. Continued from figure 97. Equivalent to genus *Serratella*.

Cain, D. J., S. N. Luoma and W. G. Wallace. 2003. Linking metal bioaccumulation of aquatic insects to their distribution patterns in a mining-impacted river. Environmental Toxicology and Chemistry 23: 1463–1473.

Chandler, D. S., G. D. Whitmore, S. K. Burian and J. F. Burger. 2006. The mayflies (Ephemeroptera) of New Hampshire: Seasonality and diversity of the stream fauna. Transactions of the American Entomological Society 132: 25–73.

Clifford, H. F. 1980. Numerical abundance values of mayfly nymphs from the Holarctic region. Pp. 503–509, in: Flannagan, J. F. and K. E. Marshall (eds). Advances in Ephemeroptera Biology. Plenum, New York.

Dakki, M. and A. El Agbani. 1983. Ephéméroptères d'Afrique du Nord. 3, éléments pour la connaissance de la faune marocaine. Bulletin de l'Institut Scientifique Rabat 7: 115–126.

Day, W. C. 1952. New species and notes on California mayflies (Ephemeroptera). Pan-Pacific Entomologist 28: 17–39.

Day, W. C. 1954. New species and notes on California mayflies. II (Ephemeroptera). Pan-Pacific Entomologist 30: 15–29.

Day, W. C. 1956. Chapter 3, Ephemeroptera. Pp. 79–105, in: Usinger, R. L. (ed.). Aquatic Insects of California. Berkeley and Los Angeles: Univ. Calif. Press.

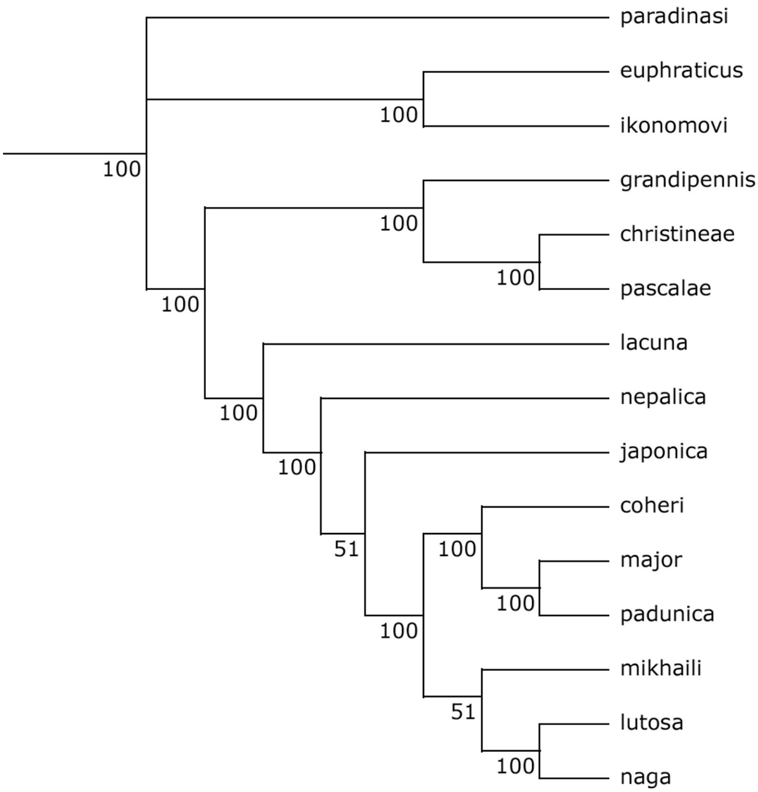


Fig. 99. Continued from figure 97. Equivalent to genera *Quatica*, *Hyrtanella* and *Torleya*.

Demoulin, G. 1954. Les Ephéméroptéres jurassiques du Sinkiang. Bulletin et Annales de la Société Entomologique de Belgique 90: 322–326.

Demoulin, G. 1968. Duexiéme contribution la connaissance des …phéméroptéres de l'ambre oligocéne de la baltique. Deutsche Entomologische Zeitschrift 15: 233–276.

Dodds, G. S. 1923. Mayflies from Colorado. Descriptions of certain species and notes on others. Transaction of the American Entomological Society 49: 93–114, pl. 8–9.

DomÌmguez, E. (ed). 2001. Trends in research in Ephemeroptera and Plecoptera. Kluwer Academic/Plenum Publishers, New York. 490 pp.

DomÌmguez, E. and M. G. Cuezzo. 2002. Ephemeroptera egg chorion characters: A test of their importance in assessing phylogenetic relationships. Journal of Morphology 253: 148–165.

Eaton, A. E. 1883–1888. A revisional monograph of recent Ephemeridae or mayflies. Transactions of the Linnean Society, London, Zoological Series 3: 1–352.

Eaton, A. E. 1908 [1909]. Description of a new species of Ephemeridae. Pp. 149-151, in: Esben-Peterson, P. (ed). Bidrag til en Fortegnelse over arktisk norges Neuropterfauna. Troms Museums Arshefter 25 (1902): 119–153.

Edmunds, G. F., Jr. 1959. Subgeneric groups within the mayfly genus *Ephemerella* (Ephemeroptera: Ephemerellidae). Annals of the Entomological Society of America 52: 543–547.

Edmunds, G. F., Jr. 1962. The principles applied in determining the hierarchical level of the higher categories of Ephemeroptera. Systematic Zoology 11: 22–31.

Edmunds, G. F., Jr. 1971. A new name for a subgeneric homonym in *Ephemerella* (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 73: 152.

Edmunds, G. F., Jr. 1973. Invitational lecuture: trends and priorities in mayfly research. Pp. 7–11. *In:* Peters, W. L. and J. G. Peters (Eds). Proceedings of the first international conference on Ephemeroptera. E. J. Brill, Leiden, Netherlands.

Edmunds, G. F. Jr. and R. K. Allen. 1957. A checklist of the Ephemeroptera of North America north of Mexico. Annals of the Entomological Society of America 50: 317–324.

Edmunds, G. F., Jr., and C. M. Murvosh. 1995. Systematic changes in certain Ephemeroptera studied by R. K. Allen. Pan-Pacific Entomologist 71: 157–160.

Edmunds, G. F., Jr., and D. A. Polhemus. 1990. Zoogeographical patterns among mayflies (Ephemeroptera) in the Malay Archipelago, with special reference to Celebes. Pp. 49–56, in: Knight, W. J. and J. D. Holloway (eds). Insects and the rain forests of South East Asia (Wallacea). Royal Entomological Society of London. 343 pp.

Edmunds, G. F., Jr., and J. R. Traver. 1954. An outline of a reclassification of the Ephemeroptera. Proceedings of the Entomological Society of Washington 56: 236–240.

Edmunds, G. F., Jr., and R. D. Waltz. 1996. Ephemeroptera. Pp. 126–163, in: Merritt, R. W. and K. W. Cummins (eds). An Introduction to the Aquatic Insects of North America, Third Edition. Kendall Hunt, Dubuque, Iowa.

Edmunds, G. F., Jr., R. K. Allen and W. L. Peters. 1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). University of Utah Biological Series 13: 1–49.

Engblom, E. 1996. Ephemeroptera, Mayflies. Pp. 13–53, in: Nilsson, A. N. (ed). Aquatic insects of North Europe—A taxonomic handbook. Part. 1. Apollo Books, Stenstrup. 274 pp.

Feck, J. and R. O. Hall. 2004. Response of American dippers (*Cinclus mexicanus*) to variation in stream water quality. Freshwater Biology 49: 1123–1137.

Fochetti, R., I. Amici and R. Argano. 2003. Seasonal changes and selectivity in the diet of brown trout in the River Nera (Central Italy). Journal of Freshwater Ecology 18: 437–444.

Funk, D. H. and B. W. Sweeney. 1994. The larvae of eastern North American *Eurylophella* Tiensuu (Ephemeroptera: Ephemerellidae). Transactions of the American Entomological Society 120: 209–286.

Funk, D. H., J. K. Jackson and B. W. Sweeney. 2008. A new parthenogenetic mayfly (Ephemeroptera:Ephemerellidae:*Eurylophella* Tiensuu) oviposits by abdominal bursting in the subimago. Journal of the North American Benthological Society 27: 269–279.

Funk, D. H., B. W. Sweeney and R. L. Vannote. 1988. Electrophoretic study of eastern North American *Eurylophella* (Ephemeroptera: Ephemerellidae) with the discovery of morphologically cryptic species. Annals of the Entomological Society of America 81: 174–186.

Gagneur, J. and A. G. B. Thomas. 1988. Contribution la connaissance des Ephéméroptéres d'Algérie. I. Répartition et écologie (1ere partie)(Insecta, Ephemeroptera). Bulletin de la Societe d'Histoire Naturelle de Toulouse 124: 213–223.

Gonzalez del Tanago, M. and D. Garcia de Jalon. 1983. New Ephemerellidae from Spain (Ephemeroptera). Aquatic Insects 3: 147–156.

Gose, K. 1963. Two new mayflies from Japan. Konty˚ 31: 142–145.

Gose, K. 1980. The mayflies of Japan. 9. Key to families, genera and species. Kaiyo to Seibutsu 2: 366–368.

Gose, K. 1985. Ephemeroptera. Pp. 7–32, in: Kawai, T. (ed). An Illustrated Book of Aquatic Insects of Japan. Univ. Tokai Press, Tokyo, Japan.

Gotelli, N. J. 2004. A taxonomic wishlist for community ecology. Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences 359: 585–597.

Gui, H., C.-F. Zhou and C.-R. Su. 1999. Ephemeroptera. Pp. 324–346, in: Huang, B.-K. (ed). Fujian Insect Fauna, Vol. 1. Fujian Science & Technology Press, Fuzhou, China.

Harper, F. and P. P. Harper. 1981. Northern Canadian mayflies (Insecta; Ephemeroptera), records and descriptions. Canadian Journal of Zoology 59: 1784–1789.

Harper, F. and C. P. Hawkins. 1984. Description of the imagines of *Ephemerella verruca* Allen and Edmunds (Ephemeroptera: Ephemerellidae). Aquatic Insects 6: 13–16.

Hilsenhoff, W. L. 1972. Aquatic insects of the Pine-Popple River, Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin 54: 1–44.

Hilsenhoff, W. L. 1982. Using a biotic index to evaluate water quality in streams. Wisconsin Department of Natural Resources Technical Bulletin 132: 1–22.

Hilsenhoff, W. L. 1988. Rapid field assessment of organic pollution with a family-level biotic index. Journal of the North American Benthological Society 7: 65–68.

Hubbard, M. D. 1990. Mayflies of the World: A Catalog of the Family and Genus Group Taxa. Flora & Fauna Handbook no. 8. Sandhill Crane Press, Gainesville, Florida. viii + 119 pp.

Hubbard, M. D. 2008. Bibliography of the Ephemeroptera: Virtual library and working bibliography of literature on the mayflies (Insecta: Ephemeroptera) of the world. Available Online: < http://www.famu.org/mayfly/mfbib.php>. [Accessed: 22 February 2008].

Ide, F. 1930. Contribution to the biology of Ontario mayflies with descriptions of new species. Canadian Entomologist 62: 204–213, 218–231.

Ikonomov, P. 1961. Eintagsfliegen (Ephemeroptera) Mazedoniens. Fam. Ephemerellidae. Acta Musei Macedonici Scientiarum Naturalium 8(3):1–22, 53–74.

Imanishi, K. 1937a. Mayflies from Japanese torrents. VII. Notes on the genus *Ephemerella*. Annotationes Zoologicae Japonenses 16: 321–329.

Imanishi, K. 1937b. Mayflies from Japanese torrents. VIII. Notes on the genera *Paraleptophlebia* and *Baetis*. Annotationes Zoologicae Japonenses 16: 330–339.

International Commission on Zoological Nomenclature. 1999. Int. Code Zool. Nomenclature, Fourth Edition. Intl. Trust Zool. Nomenclature, London.

Ishiwata, S.-I. 1987. Structure and keys of the family Ephemerellidae (1). Structure and keys to genera from the family Ephemerellidae. Aquatic Organisms of Kanagawa Prefecture 9: 27–34.

Ishiwata, S.-I. 2000. Notes on mayflies in Kanagawa Prefecture. Natural History Report of Kanagawa 21: 73–82.

Ishiwata, S.-I. 2001. A checklist of Japanese Ephemeroptera. Pp. 55–84, in: The 21st Century and Aquatic Entomology in East Asia: Proceedings of the 1st Symposium of Aquatic Entomologists in East Asia. The Korean Society of Aquatic Entomology, Korea. 146 pp.

Ishiwata, S.-I. 2003. A revision of the genus *Cincticostella* (Insecta: Ephemeroptera: Ephemerellidae) from Japan. Species Diversity 8: 311–346.

Ishiwata, S.-I., T. M. Tiunova and R. B. Kuranishi. 2000. The mayflies (Insecta: Ephemeroptera) collected from the Kamchatka Peninsula and the North Kuril Islands in 1996–1997. Natural History Research Special Issue 7: 67–75.

Jacob, U. 1993. Zur systematik und verbreitung der europäischen Ephemerellidae (Ephemeroptera). Verhandlungen Westdeutscher Entomologentag Tag 1992, S. 101–110.

Jacobus, L. M. and W. P. McCafferty. 2000. Variability in the larvae of *Serratella serrata* (Ephemeroptera: Ephemerellidae). Entomological News 111: 39–44.

Jacobus, L. M. and W. P. McCafferty. 2001. Adult description and commentary for two species of southeastern Nearctic *Ephemerella* (Ephemeroptera: Ephemerellidae). Entomological News 112: 294–298.

Jacobus, L. M. and W. P. McCafferty. 2002a. Analysis of some historically unfamiliar Canadian mayflies (Ephemeroptera). Canadian Entomologist 134: 141–155.

Jacobus, L. M. and W. P. McCafferty. 2002b. Provancher's *quebecensis* mayfly species (Ephemeroptera: Leptophlebiidae, Siphlonuridae). Entomological News 113: 315–317.

Jacobus, L. M. and W. P. McCafferty. 2003a. A new synonym of *Caudatella hystrix* (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 105: 776–777.

Jacobus, L. M. and W. P. McCafferty. 2003b. Revisionary contributions to North American *Ephemerella* and *Serratella* (Ephemeroptera: Ephemerellidae). Journal of the New York Entomological Society 111: 174–193.

Jacobus, L. M. and W. P. McCafferty. 2003c. Revisions to the genus *Crinitella* (Ephemeroptera: Ephmerellidae). Journal of the New York Entomological Society 111: 48–50.

Jacobus, L. M. and W. P. McCafferty. 2004a. Contribution to the morphology and descriptive biology of *Caurinella idahoensis* (Ephemeroptera: Ephemerellidae). Western North American Naturalist 64: 101–108.

Jacobus, L. M. and W. P. McCafferty. 2004b. Revisionary contributions to the genus *Drunella* (Ephemeroptera: Ephemerellidae). Journal of the New York Entomological Society 112: 127–147.

Jacobus, L. M. and W. P. McCafferty. 2006a. A New Oriental Species of *Uracanthella* (Ephemeroptera: Ephemerellidae) from Thailand and Vietnam. Entomological News 117: 276–280.

Jacobus, L. M. and W. P. McCafferty. 2006b. Reevaluation of the phylogeny of the Ephemeroptera Infraorder Pannota (Furcatergalia), with adjustments to higher classification. Transactions of the American Entomological Society 132: 81–90, 429–430.

Jacobus, L. M. and W. P. McCafferty. 2007. Reinstatement of *Serratella serratoides* and status of *Ephemerella molita* (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 109: 730–732.

Jacobus, L. M. and M. Sartori. 2004. Review of the genus *Hyrtanella* (Ephemeroptera: Ephemerellidae). Zootaxa 785: 1–12.

Jacobus, L. M., W. P. McCafferty and R. W. Sites. 2005a. A new synonym and new Thailand records of *Cincticostella femorata* (Tshernova) (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 107: 733–734.

Jacobus, L. M., W. P. McCafferty and R. W. Sites. 2005b. Significant range extensions for *Kangella* and *Vietnamella* (Ephemeroptera: Ephemerellidae, Vietnamellidae). Entomological News 116: 268–270.

Jacobus, L. M., W. P. McCafferty and R. W. Sites. 2007. New species and stage associations in the genus *Crinitella* (Ephemeroptera: Ephemerellidae). Zootaxa 1611: 45–53.

Jacobus, L. M., W. P. McCafferty and S. Spichiger. 2002. First adult description for *Ephemerella hispida* (Ephemeroptera: Ephemerellidae). Entomological News 113: 342–343.

Jacobus, L. M., R. W. Newell and W. P. McCafferty. 2006. First adult and egg descriptions of *Caudatella edmundsi* (Ephemeroptera: Ephemerellidae), from Montana (U.S.A.), with habitat notes. Entomological News 117: 175–180.

Jacobus, L. M., C.-F. Zhou and W. P. McCafferty. 2004. Revisionary contributions to the genus *Torleya* (Ephemeroptera: Ephemerellidae). Journal of the New York Entomological Society 112: 153–175.

Jacobus, L. M., B. C. Kondratieff, M. D. Meyer, and W. P. McCafferty. 2003. Contribution to the biology and systematics of *Ephemerella alleni* (Ephemeroptera: Ephemerellidae). Pan-Pacific Entomologist 79: 207–211.

Jenkins, R. K. B. and S. J. Omerod. 1996. The influence of a river bird, the dipper (*Cinclus cinclus*), on the behaviour and drift of its invertebrate prey. Freshwater Biology 35: 45–56.

Jensen, S. L. and G. F. Edmunds, Jr. 1966. A new species of *Ephemerella* from western North America (Ephemeroptera: Ephemerellidae). Journal of the Kansas Entomological Society 39: 576–579.

Kang, S.-C. and C.-T. Yang. 1995. Ephemerellidae of Taiwan (Insecta, Ephemeroptera). Bulletin of National Museum of Natural Science 5: 95–116.

Kapur, A. P., and M. B. Kripalani. 1961. The mayflies (Ephemeroptera) from the northwestern Himalaya. Records of the Indian Museum 59: 183–221.

Kazanci N. 1987. New *Drunella* (Ephemeroptera, Ephemerelliidae) species from Turkey. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 60: 379–382.

Kazanci N. 1990. *Drunella karia* n. sp. a second species of the genus *Drunella* (Ephemeroptera: Ephemerellidae) from Turkey. Hydrobiologia 199: 35–42.

Kazanci N. 1991. Contribution on the zoogeography of Asia Minor based on the distribution of *Drunella* (Ephemeroptera: Ephemerellidae) species. Pp. 271–276, in: Alba-Tercedor, J. and A. Sánchez-Ortega. (eds). Overview and strategies of Ephemeroptera and Plecoptera. Sandhill Crane Press, Gainesville, Florida.

Kazlauskas, R. 1963. New and little known mayfly (Ephemeroptera) species of the USSR fauna. Entomologicheskoe Obozrenie 42: 582–592.

Keffermüller, M. 1979. Ein Vergleich von zwei *Ephemerella*-arten (Ephemeroptera: Ephemerellidae). Pp. 67–71 & 2 pl., in: Pasternak, K. and R. Sowa (eds). Proceedings of the Second International Conference on Ephemeroptera. Panstwowe Wydawnictwo Naukowe, Warszawa-KrakÛw.

King, R. S. and C. J. Richardson. 2002. Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. Journal of the North American Benthological Society 21: 150–171.

Kitchin, P. L. 2005. Measuring the amount of statistical information in the EPT index. Environmetrics 16: 51–59.

Klapálek, F. 1905. Ephemeridarum species quatuor novae. Casopis Ceské Spolecnosti Entomologické 2: 1–5.

Klapálek, F. 1909. Ephemeridae, Eintagsfliegen. In: Brauer, A. (ed). Die Süsserwasserfauna Deutchlands 8: 1–32.

Kluge, N. 1980. To the knowledge of mayflies (Ephemeroptera) of Taimyr National District. Entomologichekoe Obozrenie 59: 561–579.

Kluge, N. 1995. A catalogue of the type-specimens in the collection of the Zoological Institute, Russian Academy of Sciences. Insecta, Ephemeroptera. Zoological Institute, Russian Academy of Sciences, St.Petersburg. 52 pp.

Kluge, N. 1997. New subgenera of Holarctic mayflies (Ephemeroptera: Heptageniidae, Leptophlebiidae, Ephemerellidae). Zoosystematica Rossica, 1996, 5(2): 233–235.

Kluge, N. 2004. The Phylogenetic System of Ephemeroptera. Kluwer Academic Publishers, Dordrecht. 442 pp.

Kluge, N., D. Studemann, P. Landolt and T. Gonser. 1995. A reclassification of Siphlonuroidea (Ephemeroptera). Bulletin de la Société Entomologique Suisse 68: 103–132.

Kluge, N., C.-F. Zhou, L. M. Jacobus and W. P. McCafferty. 2004. A new Southeast Asian mayfly species (Ephemeroptera: Ephemerellidae: Ephemerellinae). Journal of the New York Entomological Society 112: 148–152.

Kondratieff, B. C., J. W. S. Foster, III, and J. R. Voshell, Jr. 1981. Description of the adult of *Ephemerella berneri* Allen and Edmunds (Ephemeroptera: Ephemerellidae) with biological notes. Proceedings of the Entomolgical Society of Washington 83: 300–303.

Koss, R. K. 1968. Morphology and taxonomic use of Ephemeroptera eggs. Annals of the Entomological Society of America 61: 696–721.

Koss, R. K. and G. F. Edmunds, Jr. 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zoological Journal of the Linnean Society 55: 267–349.

Kreivi, P., T. Muotka, A. Huusko, A. Maki-Petays, A. Huhta and K. Meissner. 1999. Diel feeding periodicity, daily ration and prey selectivity in juvenile brown trout in a subarctic river. Journal of Fish Biology 55: 553–571.

Kustareva, L. A. 1976. Mayflies (Ephemeroptera, Ephemerellidae, Heptageniidae) in the rivers of Issyk-Kul Hollow. Entomologicheskoe Obozrenie 60: 58–68.

Laine, A. 2001. Effects of peatland drainage on the size and diet of yearling salmon in a humic northern river. Archiv für Hydrobiologie 151: 83–99.

Landa, V. 1969. Fauna SSR. Svazek 18. Jepice—Ephemeroptera. Academia Nakladatelstvi eskoslovenské, Akademie Vd, Prague.

Landa, V. 1973. A contribution to the evolution of the order Ephemeroptera based on comparative anatomy. Pp. 155–159, in: Peters, W. L. and J. G. Peters (Eds). Proceedings of the first international conference on Ephemeroptera. E. J. Brill, Leiden, Netherlands.

Landa, V. and T. Soldán. 1985. Distributional patterns, chorology and origin of the Czechoslovak fauna of mayflies (Ephemeroptera). Acta Entomologica Bohemoslovaca 82: 241–268.

Landa, V., T. Soldán and G. F. Edmunds. 1982. Comparative anatomy of larvae of the family Ephemerellidae (Ephemeroptera). Acta Entomologica Bohemoslovaca 79: 241–253.

Leonard, J. W. and F. A. Leonard. 1962. Mayflies of Michigan trout streams. Cranbrook Institute of Science, Bloomfield Hills, Michigan. x+137 pp.

Lestage, J. A. 1917. Contribution l'étude des larves d'Ephéméres paléarctiques. Séries 1. Annales de Biologie Lacustre 8: 213–457.

Lestage, J. A. 1925. Contribution l'étude des larves des Ephéméres, série III. le groupe Ephémérellidien. Annales de Biologie Lacustre 13: 229–319.

Licht, O., D. Jungmann, K. U. Ludwichowski and R. Nagel. 2004. Long-term effects of fenoxycarb on two mayfly species in artificial indoor streams. Ecotoxicology and Environmental Safety 58: 246–255.

Lin, Q.-B. 1986. Early Mesozoic fossil insects from South China. Palaeontologia Sinica 170 (N.S. B21): i–iii, 1–112, 20 pl.

Linnaeus, C. 1758. Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th Edition. Vol. 1. Salvii, Holmiae. 824 pp.

Maddison, D. R. and W. P. Maddison. 2005. MacClade 4: Analysis of phylogeny and character evolution. Version 4.07 for OS X. Sinauer Associates, Sunderland, Massachusetts.

Maret, T. R., D. J. Cain, D. E. MacCoy and T. M. Short. 2003. Response of benthic invertebrate assemblages to metal exposure and bioaccumulation associated with hard-rock mining in northwestern streams, USA. Journal of the North American Benthological Society 22: 598–620.

Marie, V., A. Dia and A. Thomas. 1999. Compléments et corrections la faune des Ephéméroptéres du Proche-Orient. 3. *Serratella bauernfeindi* n. sp. du Liban: Description comparativement *S. mesoleuca* (Brauer, 1857) et écologie [Ephemeroptera, Ephemerellidae]. Ephemera 1: 93–103.

Matsumura, S. 1931. [Ephemerida]. 6000 Illustrated Insects of the Japanese Empire: 1465–1480.

Mayo, V. K. 1951 [1952]. New western Ephemeroptera II. Pan-Pacific Entomologist 27: 121–125.

McCafferty W. P. 1977. Biosystematics of *Dannella* and related subgenera of *Ephemerella* (Ephemeroptera: Ephemerellidae). Annals of the Entomological Society of America 70:881–889.

McCafferty W. P. 1978. A natural subgeneric classification of *Ephemerella bartoni* and related species (Ephemeroptera: Ephemerellidae). Great Lakes Entomologist 11: 137–138.

McCafferty, W. P. 1981. Aquatic Entomology. Jones and Bartlett, Sudbury, Massachusetts.
McCafferty, W. P. 1985. New spiny crawlers from headwaters of the Savannah River (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 87: 421–425.
McCafferty, W. P. 1990. Chapter 2: Ephemeroptera. Pp. 20–50, in: Grimaldi, D. A. (ed). Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History 195.
McCafferty, W. P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. Annals of the Entomological Society of America 84: 343–360.
McCafferty, W. P. 1992. *Ephemerella apopsis*, a new species from Rocky Mountain high (Ephemeroptera: Ephemerellidae). Entomological News 103: 135–138.
McCafferty, W. P. 1997. Ephemeroptera. Pp. 89–117, in: Poole, R. W. and P. Gentili (eds). Nomina Insecta Nearctica, a checklist of the insects of North America. Volume 4: Non-holometabolous orders. Entomological Information Services, Rockville, Maryland.
McCafferty W. P. 2000. A hierarchical classification of the Timpanoginae (Ephemeroptera: Ephemerellidae) and description of a new species from Quebec. Annales de Limnologie 36: 157–161.
McCafferty, W. P. 2001. Status of some historically unfamiliar American mayflies (Ephemeroptera). Pan-Pacific Entomologist 77: 210–218.
McCafferty, W. P. 2004. Higher classification of the burrowing mayflies (Ephemeroptera: Scapphodonta). Entomological News 115: 84–92.
McCafferty, W. P. and G. F. Edmunds, Jr. 1979. The higher classification of the Ephemeroptera and its evolutionary basis. Annals of the Entomological Society of America 72: 5–12.
McCafferty, W. P. and T.-Q. Wang. 1994. Phylogenetics and the classification of the *Timpanoga* complex (Ephemeroptera: Ephemerellidae). Journal of the North American Benthological Society 13: 569–579.
McCafferty, W. P. and T.-Q. Wang. 1997. Phylogenetic systematics of the family Teloganodidae (Ephemeroptera: Pannota). Annals of the Cape Provincial Museums (Natural History) 19(9): 387–437.
McCafferty, W. P. and T.-Q. Wang. 2000. Phylogenetic systematics of the major lineages of Pannote mayflies (Ephemeroptera: Pannota). Transactions of the American Entomological Society 126: 9–101.
McCafferty, W. P., T. Hubbard and J. M. Webb. 2006. Insecta, Ephemeroptera: range extensions and new Iowa state records. Check List 2(1): 40–41.
McCafferty, W. P., L. M. Jacobus and T.-Q. Wang. 2003. Phylogenetics and the reconfirmation of
Dentatella Allen (Ephemeroptera: Ephemerellidae). Proceedings of the Entomological Society of Washington 105: 786–788.
McDunnough, J. 1924. New North American Ephemeridae. Canadian Entomologist 56: 221–226.
McDunnough, J. 1925a. New Canadian Ephemeridae with notes, III. Canadian Entomologist 57: 168–176, 185–192.
McDunnough, J. 1925b. New *Ephemerella* species (Ephemeroptera). Canadian Entomologist 57: 41–43.
McDunnough, J. 1925c. The Ephemeroptera of Covey Hill, Que. Transactions of the Royal Society of Canada 19: 207–223.
McDunnough, J. 1926. Notes on North American Ephemeroptera with descriptions of new species. Canadian Entomologist 58: 184–196.
McDunnough, J. 1927. New *Ephemerella* from Illinois (Ephemeroptera). Canadian Entomologist 59: 10.
McDunnough, J. 1929. Notes on North American Ephemeroptera with descriptions of new species. II. Canadian Entomologist 61: 169–180.

McDunnough, J. 1930. The Ephemeroptera of the north shore of the Gulf of St. Lawrence. Canadian Entomologist 62: 54–62.

McDunnough, J. 1931a. New species of North American Ephemeroptera. Canadian Entomologist 63: 82–93.

McDunnough, J. 1931b. The eastern North American species of the genus *Ephemerella* and their nymphs (Ephemeroptera). Canadian Entomologist 63: 187–197, 201–216.

McDunnough, J. 1934. New species of North American Ephemeroptera IV. Canadian Entomologist 66: 154–164, 181–188.

McDunnough, J. 1935. Notes on western species of Ephemeroptera. Canadian Entomologist 67: 95–104.

McDunnough, J. 1938. New species of North American Ephemeroptera with critical notes. Canadian Entomologist 70: 23–34.

McDunnough, J. 1939. New British Columbian Ephemeroptera. Canadian Entomologist 71: 49–54.

McLachlan R. 1875. A sketch of our present knowledge of the Neuropterous fauna of Japan (excluding Odonata and Trichoptera). Transactions of the Entomological Society 1875: 167–190.

Milne, L. and M. Milne. 1980. The Audubon Society fieldguide to North American insects and spiders. Alfred A. Knopf, New York.

Mitter, C. 1999. Sketches of U.S. systematic entomology, circa 1850–2000: Return of a Golden Age? Annals of the Entomological Society of America 92: 798–811.

Monné, M. A. and U. R. Martins. 1973. Notas e descriãoes em Eburiini (Coleoptera, Cerambycidae). Papéis Avulsos de Zoologia (Sao Paulo) 27: 145–155.

Morgan, A. H. 1911. May-flies of Fall Creek. Annals of the Entomological Society of America 4: 93–119, pl. 6–12.

Molineri, C., and E. DomÌnguez. 2003. Nymph and egg of *Melanemerella brasiliana* (Ephemeroptera: Melanemerellidae), with comments on its systematic position and the higher classification of Ephemerelloidea. Journal of the North American Benthological Society 22: 263–275.

Needham, J. G. 1905. Ephemeroptera. Pp. 17–62, in: Needham, J. G., K. J. Morton and O. A. Johannsen. Mayflies and Midges of New York. New York Museum Bulletin 86: 1–352.

Needham, J. G. 1908. New data concerning May flies and dragon flies of New York. May flies (Ephemeridae). Bulletin of the New York State Museum 1908: 188–194.

Needham, J. G. 1924. The male of the parthenogenetic may-fly, *Ameletus ludens*. Psyche 31: 308–310.

Needham, J. G. 1927. The Rocky Mountain species of the mayfly genus *Ephemerella*. Annals of the Entomological Society of America 20: 107–117.

Needham, J. G. and R. O. Christenson. 1927. Economic insects in some streams of northern Utah. Bulletin of the Utah Agricultural Experiment Station 201: 1–36.

Nelson, G. J. 1972. Phylogenetic relationships and classification. Systematic Zoology 21: 227–231.

Nelson, G. J. 1973. Classification as an expression of phylogenetic relationships. Systematic Zoology 22: 344–359.

Ogden, T. H. and M. F. Whiting. 2003. Phylogeny of Ephemeroptera: molecular evidence. Entomologische Abhandlungen 61: 126–127.

Ogden, T. H. and M. F. Whiting. 2005. Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. Molecular Phylogenetics and Evolution 37: 625–643.

Ogden, T. H., J. T. Osborne, L. M. Jacobus and M. F. Whiting. 2008. Combined molecular and morphological phylogeny of Ephemerellinae (Ephemeroptera: Ephemerellidae), with remarks about classification. Zootaxa, IN REVIEW.

Okazaki, H. 1984. Observation of the eggs of Japanese mayflies by scanning electron microscope. Biology of Inland Waters 3: 19–27.

Paclt, J. 1994. *Ephacerella*, a replacement name for *Acerella* Allen, 1971 (Ephemeroptera), nec Berlese, 1909 (Protura). Entomological News 105: 283–284.

Parker, C. R., O. S. Flint, Jr., L. M. Jacobus, B. C. Kondratieff, W. P. McCafferty, and J. C. Morse. 2007. Ephemeroptera, Plecoptera, Megaloptera, and Trichoptera of Great Smoky Mountains National Park. Southeastern Naturalist, Special Issue 1: 159–174.

Pictet, F.-J. 1843–1845. Histoire naturelle générale et particuliére des insectes néuroptères. Famille des éphémérines. Chez J. Kessmann et Ab. Cherbuliz, Geneva. 300 pp., xix + 47 pl.

Ping C. 1935. On four fossil insects from Sinkiang. Chinese Journal of Zoology 1: 107–115.

Poda, N. 1761. Insecta musei Graecensis, quae in ordines, genera et species juxta systema naturae. Caroli Linnaei digessit. Graecii. 127 pp.

Poff, N. L., P. L. Angermeier, S. D. Cooper, P. S. Lake, K. D. Fausch, K. O. Winemiller, L. A. K. Mertes, M. W. Osgood, J. Reynolds and F. J. Rahel. 2001. Fish diversity in streams and rivers. Pp. 315–349, in: Chapin, F. S., III, O. E. Sala and E. Huber-Sannwald (Eds.). Global biodiversity in a changing environment: Scenarios for the 21st Century. Ecological Studies 152. Springer, New York. xii + 376 pp.

Prusha, B. A. and W. H. Clements. 2004. Landscape attributes, dissolved organic C, and metal bioaccumulation in aquatic macroinvertebrates (Arkansas River Basin, Colorado). Journal of the North American Benthological Society 23: 327–339.

Puthz, V. 1971. Namensänderung einer Eintagsfliegenart (Ephemeroptera). Mitteilungen der Dentschen Entomologischen Gesellschaft 29: 43.

Quan, Y.-T., Y. J. Bae, J.-C. Jung and J.-W. Lee. 2002. Ephmeroptera (Insecta) fauna of Northeast China. Insecta Koreana 19: 241–269.

Randolph, R. P. and W. P. McCafferty. 2005. The mayflies (Ephemeroptera) of Alaska, including a new species of Heptageniidae. Proceedings of the Entomological Society of Washington 107: 190–199.

Revenga, C., J. Brunner, N. Henninger, R. Payne and K. Kassem. 2000. Pilot analysis of global ecosystems (PAGE): Freshwater systems. World Resources Institute, Washington, DC. 100 pp.

Sala, O. E., F. S. Chapin III and E. Huber-Sannwald. 2001. Potential biodiversity change: Global patterns and biome comparisons. Pp. 351–367, in: Chapin, F. S., III, O. E. Sala and E. Huber-Sannwald (eds). Global biodiversity in a changing environment: Scenarios for the 21st Century. Ecological Studies 152. Springer, New York. xii + 376 pp.

Sartori, M. 2004. *Kangella* nom. nov. (Ephemeroptera, Ephemerellidae), Replacement Name pro *Eburella* Kang & Yang, 1995 nec Monné & Martins, 1973 (Coleoptera, Cerambycidae). Aquatic Insects 26:75–76.

Schrank, F. von P. 1798. Fauna Boica, durchgedachte Geschichte der in Baiern einheimischen und zahmen Thiere. Erster Band. Stein: Nürnberg, Germany. 720 pp., xii + 1 pl.

Seeman, T. 1927. Ephemerida. Pp. 40–51, in: Dragonflies, mayflies and stoneflies of southern California. Journal of Entomology & Zoology, Pomona College 19–22: 1–69.

Sharkey, M. J. 2001. The All Taxa Biological Inventory of the Great Smoky Mountains National Park. Florida Entomologist 84: 556–564.

She, S., H. Gui and D. You. 1995. A research on the mayflies from Hainan Province, China (Insecta: Ephemeroptera). Journal of Nanjing Normal University (Nature Science) 18: 72–82.

Silfverberg H. 1989. Lists of the insect types in the Zoological Museum, University of Helsinki. 10. Ephemeroptera. Acta Entomologica Fennica 55:1–2.

Smith, B. D., P. S. Maitland, M. R. Young, and M. J. Carr. 1981. The littoral zoobenthos. Pp. 155–203, in: P. S. Maitland (ed). The Ecology of Scotland's Largest Lochs: Lomond, Awe, Ness, Morar and Shiel. Monographiae Biologicae 44: i–xiv + 1–297. Dr. W. Junk, The Hague.

Smith, O. R. 1935. The eggs and egg-laying habits of North American mayflies. Pp. 67–89, in: Needham, J. G., J. R. Traver and Y.-C. Hsu. The biology of mayflies. Comstock, Ithaca, New York.

Soldán, T. 2007. Book review, Kluge N.: The Phylogenetic System of Ephemeroptera. European Journal of Entomology 104: 351–352.

Spieth, H. T. 1940. The North American species of Francis Walker. Annals of the Entomological Society of America 33: 324–338

Stephens, J. F. 1835. Illustrations of British entomology. Mandibulata 6: 53–70, 29 pl.

Stevens, J. and R. Wall. 1996. Classification of the genus *Lucilia* (Diptera: Calliphoridae): a preliminary parsimony analysis. Journal of Natural History 30: 1087–1094.

Studemann, D. and P. Landolt. 1997. Eggs of Ephemerellidae (Ephemeroptera). Pp. 362–371, in: Landolt, P. and M. Sartori (eds). Ephemeroptera & Plecoptera: Biology—Ecology—Systematics. MTL, Fribourg, Switzerland.

Studemann, D. and I. Tomka. 1987. Contribution to the study of European Ephemerellidae (Ephemeroptera). I. Completion of description of three endemic Iberian species. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 60: 361–378.

Studemann, D. and I. Tomka. 1989. Contribution to the study of European Ephemerellidae (Ephemeroptera). III. Synonymy of *Ephemerella maculocaudata* Ikonomov, 1961. Syn. n. with *Ephemerella mesoleuca* (Brauer, 1857). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 62: 129–130.

Studemann, D., P. Landolt and I. Tomka. 1989. Contribution to the study of European Ephemerellidae (Ephemeroptera). II. Description of the winged stages of *Ephemerella ikonomovi* Puthz, 1971, and *Serratella albai* Gonzales del Tanago & Garcia de Jalon, 1983. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 62: 119–127.

Studemann D, Landolt P, Tomka I. 1988. Morphology and taxonomy of imagines and eggs of Central and Northern European Siphlonuridae (Ephemeroptera). Bulletin de la Société Entomologique Suisse 61:303–328.

Studemann, D., P. Landolt, and I. Tomka. 1995. Eggs of the European Ephemerellidae (Ephemeroptera). Pp. 407–422, in: Corkum, L. and J. Cibrowski (eds). Current directions in research on Ephemeroptera. Canadian Scholar's Publishing, Toronto.

Studemann, D., P. Landolt, M. Sartori, P. Hefti, and I. Tomka. 1992. Ephemeroptera. — Fauna Helvetica 9: 1–176. Societé Entomologique Suisse (ed.), Fribourg.

Su, C.-R., and H. Gui. 1995. The first record of the genus *Drunella* in China with description of a new species (Ephemeroptera: Ephemerellidae). Acta Zootaxonomica Sinica 20: 451–454.

Su, C.-R., and D.-S. You. 1988. Two new species of genus *Ephemerella* subgenus *Ephemerella*. Journal of Nanjing Normal University (Natural Science) 3: 63–67.

Su, C.-R., and D.-S. You. 1989. A new species of *Ephemerella* subgenus *Ephemerella* from Jilin Province, China (Ephemeroptera: Ephemerellidae). Acta Zootaxonomica Sinica 14: 181–185.

Swofford, D. L. 2002. PAUP* Phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Thomas, A., Masselot, G., and Brulin, M. 1999. Les Ephéméres de France: complément bibliographique l'inventaire des espéces signalées et des espéces potentielles par départements (Thomas et Masselot, 1996) (Ephemeroptera). Ephemera 1: 119–122.

Tiensuu, L. 1935. On the Ephemeroptera-fauna of Laatokan Karjala (Karelia Ladogensis). Suomen Hynteistieteellinen Aikakauskirja 1:3–23.

Tiensuu, L. 1939. A Survey of the distribution of mayflies (Ephemeroptera) in Finland. Suomen Hynteistieteellinen Aikakauskirja 5(2): 97–124.

Tiunova, T. M. 1988. On the new mayflies of the family Ephemerellidae (Ephemeroptera) of the fauna Far East. Pp. 3–6, in: Fauna, sistematika i biologija presnovodkykh bespozvonochnykh, Vladivostok.

Tiunova, T. M. 1995. A new species of *Torleya* Lestage, 1917 (Ephemeroptera: Ephemerellidae) from the Far East of Russia. Aquatic Insects 17: 51–56.

Tomka, I. and C. Elpers. 1991. Problems in the phylogeny of the Ephemeroptera. Pp. 115–119, in: Alba-Tercedor, J. and A. Sánchez-Ortega (eds). Overview and strategies of Ephemeroptera and Plecoptera. Sandhill Crane Press, Gainesville, Florida.

Tong, X. and D. Dudgeon. 2000. Ephemerellidae (Insecta: Ephemeroptera) from Hong Kong, China, with descriptions of two new species. Aquatic Insects 22: 197–207.

Traver, J. R. 1932. Mayflies of North Carolina. Journal of the Elisha Mitchell Scientific Society 47: 85–236, pl. 5–12.

Traver, J. R. 1934. New North American species of mayflies (Ephemerida). Journal of the Elisha Mitchell Scientific Society 50: 189–254.

Traver, J. R. 1935. Part II: Systematic. North American mayflies order Ephemeroptera. Pp. 237–739, in: Needham, J. G., J. R Traver and Y.-C. Hsu. The biology of mayflies. Comstock, Ithaca, New York.

Traver J. R. 1937. Notes on mayflies of the southeastern United States (Ephemeroptera). Journal of the Elisha Mitchell Scientific Society 53: 27–86, pl. 6.

Tshernova, O. A. 1949. Mayfly nymphs of waters flowing into Lake Teletskoe and of the R. BiÌa. Trudy Zoologicheskogo Instituta Akademiya Nauk SSSR 7: 139–158.

Tshernova, O. A. 1952. Mayflies (Ephemeroptera) of the Amur river basin and adjacent waters and their role in the nutrition of Amur fishes. Trudy Amurskoy Ichtiologicheskogo Ekspeditsii 3: 229–360.

Tshernova, O. A. 1962. Order Ephemeroptera. Mayflies. Pp. 55–64, in: Rohdendorf, B. B. (ed). Fundamentals of Paleontology. Arthropoda Tracheata and Chelicerata. Izdatel'stvo Akademii Nauk SSSR, Moscow, 560 pp.

Tshernova, O. A. 1969. New Early Jurassic mayflies (Ephemeroptera, Epeoromimidae and Mesonetidae). Entomologicheskoe Obozrenie 48: 153–161.

Tshernova, O. A. 1972. Some new Asiatic species of mayflies (Ephemeroptera, Heptageniidae, Ephemerellidae). Entomologicheskoe Obozrenie 51: 604–614.

Tshernova, O., N. Kluge, N. D. Sinitshenkova and V. V. Belov. 1986. Order Ephemeroptera. In: Opredelitel' nasekomyh Dal'nego Vostoka SSSR [Key to the insects of the USSR Far East], vol. 1, Leningrad, "Nauka".

Ueno, M. 1928. Some Japanese mayfly nymphs. Memoirs of the College of Science, Kyoto Imperial University, Series B, 4(1): 19–63, pl. 3–17.

Ueno, M. 1931. Contributions to the knowledge of Japanese Ephemeroptera. Annotationes Zoologicae Japonenses 13: 189–231.

Ueno, M. 1953. Fauna and flora of Nepal Himalaya. Scientific results of the Japanese expeditions to Nepal Himalaya. Fauna and Flora Reseach Society, Kyoto Univ., Kyoto, Japan 1: 301–316.

Ulmer, G. 1919 [1920]. Neue Ephemeropteren. Archiv für Naturgeschichte (A) 85(11): 1–80.

Ulmer, G. 1936. Neue chinesische Ephemeropteren, nebst ubersicht uber die bischer aus China bekannten Arten. Peking Natural History Bulletin 10: 201–215.

Ulmer, G. 1939. Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. Archiv für Hydrobiologie Supplement 16: 443–692.

Vidinova, Y. and B. Russev. 1997. Distribution and ecology of the representatives of some ephemeropteran families in Bulgaria. Pp. 139–146, in: Landolt, P. and M. Sartori (eds). Ephemeroptera & Plecoptera: Biology—Ecology—Systematics. MTL, Fribourg.

Walker, F. 1853. Ephemerinae. List of the specimens of neuropterous insects in the collection of the British Museum, Part III (Termitidae- Ephemeridae). pp. 533–585.

Walley, G. S. 1930. A review of the *Ephemerella* nymphs of Western North America (Ephemeroptera). Canadian Entomologist 62: 12–20.

Walsh, B. D. 1862. List of the Pseudoneuroptera of Illinois contained in the cabinet of the writer, with descriptions of over forty new species, and notes on their structural affinities. Proceedings of the Academy of Natural Sciences of Philadelphia 1862: 361–402.

Waltz, R. D. and S. K. Burian. 2008. Ephemeroptera. Pp. 181–236, in: Merritt, R. W., K. W. Cummins and M. B. Berg (eds). An Introduction to the Aquatic Insects of North America, Fourth Edition. Kendall Hunt, Dubuque, Iowa.

Wang, T.-Q., and R. W. Sites. 1999. Description of a new species of *Crinitella* (Ephemeroptera: Ephemerellidae) from Thailand. Journal of the New York Entomological Society 107: 73–77.

Wang, T.-Q., W. P. McCafferty and Y. J. Bae. 1997. Sister relationships of the Neoephemeridae and Caenidae (Ephemeroptera: Pannota). Entomological News 108: 52–56.

Webb, J. M., D. W. Parker, D. M. Lehmkuhl and W. P. McCafferty. 2004. Additions and emendations to the mayfly (Ephemeroptera) fauna of Saskatchewan, Canada. Entomological News 115: 213–218; 116: 92 (errata).

Wheeler, Q. D. 2004. Taxonomic triage and the poverty of phylogeny. Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences 359: 571–584.

Williams, H. C., S. J. Ormerod and M. W. Bruford. 2006. Molecular systematics and phylogeography of the cryptic species complex *Baetis rhodani* (Ephemeroptera, Baetidae). Molecular Phylogenetics and Evolution 40: 370–382.

Wu, T., and H. Gui. 1993. A new species of genus *Ephemerella* (Ephemeroptera: Ephemerellidae). Journal of Nanjing Normal University (Nature Science) 16: 72–74.

Xu, J.-Z., D.-S. You and C.-R. Su.1980. Two new species of genus *Ephemerella* (Ephemeroptera: Ephemerellidae). Journal of Nanjing Normal College (Nature Science) 2: 60–63.

Xu, J.-Z., D.-S. You and Y.-C. Hsu. 1984. A new species of *Ephemerella* (Ephemeroptera: Ephemerellidae). Acta Zootaxonomica Sinica 9: 413–415.

Yoon, I. B. and Y. J. Bae. 1988. I. Order Ephemeroptera. Pp. 95–184, in: Yoon, I. B. Illustrated encyclopedia of fauna & flora of Korea. Vol. 30. Animals (Aquatic Insects). Ministry of Education, Seoul.

Yoon, I. B. and M. L. Kim. 1981. A taxonomical study on the larvae of Ephemerellidae (Ephemeroptera) in Korea. Bulletin of Entomological Research (Korean Entomological Institute) 8: 33–59.

Yoon, I. B., Y. J. Bae and S. J. Aw. 1985. A study on the aquatic insects community structure of Paegun Mountain Torrents in Kynggi-do. Pp. 119–128, in: A Report on the Scientific Survey of Mt. Paegun and its Surrounding Regions.

You, D.-S. and H. Gui. 1995. Economic Insect Fauna of China, Fasc. 48. Ephemeroptera. Science Press, Beijing.

Zaika, V. V. 2000. An atlas guide to the aquatic invertebrates of Tuva and West Mongolia, Part 1: Mayflies—Insecta, Ectognatha, Ephemeroptera. Kyzyl. 60pp.

Zhang, J.-F. and N. Kluge. 2007. Jurassic larvae of mayflies (Ephemeroptera) from the Daohugou Formation in Inner Mongolia, China. Oriental Insects 41: 351–366.

Zhou, C.-F. and C.-R. Su. 1997. A new species of *Serratella* from China (Ephemeroptera: Ephemerellidae). Journal of Nanjing Normal University (Nature Science) 20(3): 42–44.

Zhou, C.-F., H. Gui and C.-R. Su. 1997a. Three new species of Ephemeroptera (Insecta) from Henan Province of China. Entomotaxonomia 19: 268–272.

Zhou, C.-F., L. M. Jacobus and W. P. McCafferty. 2006. New Synonyms of *Serratella jinghongensis* (Ephemeroptera: Ephemerellidae). Entomological News 117: 237–238.

Zhou, C.-F., C.-R. Su and H. Gui. 1997b. A study on the genus *Serratella* of China (Ephemeroptera: Ephemerellidae). Journal of Nanjing Normal University (Nature Science) 20(4): 124–127.

Zhou, C.-F., C.-R. Su and H. Gui. 2000. The first record of the genus *Torleya* in China with description of a new species (Ephemeroptera: Ephemerellidae). Acta Zootaxonomica Sinica 25(3): 312–314.