GEOGRAPHIC DISTRIBUTION AND RECLASSIFICATION OF THE SUBFAMILY EPHEMERELLINAE (EPHEMEROPTERA: EPHEMERELLIDAE)

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ABSTRACT

The geographic distributions of the genera are included on maps and 9 latitudinal distributional zones are established, revising the system proposed by Allen and Brusca. The genera are included in 2 tribes, Ephemerellini and Hyrtanellini n. tribe, and *Acerella, Attenella, Caudatella, Cinctic ostella, Crinitella, Dannella, Drunella, Ephemerella* s.s., *Eurylophella, Hyrtanella, Serratella, Teloganopsis, Timpanoga* and *Torleya* are treated as genera. *Drunella* is composed of five subgenera: s.s., *Eatonella, Myllonella* n. subgen., *Tribrochella* n. subgen., and *Unirhachella* n. subgen.; *Cincticostella* of 3: s.s., *Rhionella* n. subgen., and *Vietnamella* NEW COMBINATION; and *Dannella* of 2: s.s. and *Dentatella* n. subgen.

GEOGRAPHIC DISTRIBUTION

Allen & Brusca (1973), in an attempt to understand the geographic distribution and distributional limits of the mayfly genera of Mexico, plotted collection records of all species on maps. It was observed that genera of both austral and boreal origins reached their most northern and southern limits in the same narrow latitudinal zones. For example, the boreal *Ephemerella* s. l. and *Centroptilum,* and the austral *Baetodes, Campsurus, Leptohyphes,* and *Thraulodes* all reach their distributional limits in North America between 30°-40° north latitude; and the boreal genera *Iron**, *Hepta-*

* The heptageniid taxa *Iron* and *Ironopsis* are herein considered to have generic rank.

genia, Isonychia, Rhithrogena and *Stenonema,* and the austral genus *Euthyplocia* all reach their distributional limits in southern Mexico and Central America between 15°-25° north latitude. Also, it was observed that five genera of austral origin, *Dactylobaetis, Lachlania, Tortopus, Traverella* and *Tricorythodes,* all reach their most northern limits in southern Canada between 45°-55° north latitude. A nomenclature was established which was based on the presumed origin of the genus and the latitudinal zone on earth where they reach their most northern or southern limits. Seven distributional zones were established to accommodate the distribution of the 21 Mexican genera.

Additional study of the geographic distribution of more than 100 genera from all parts of the world reveals that nine distributional zones must be established (Fig. 1). The proposed zones and their latitudinal limits are as follows:

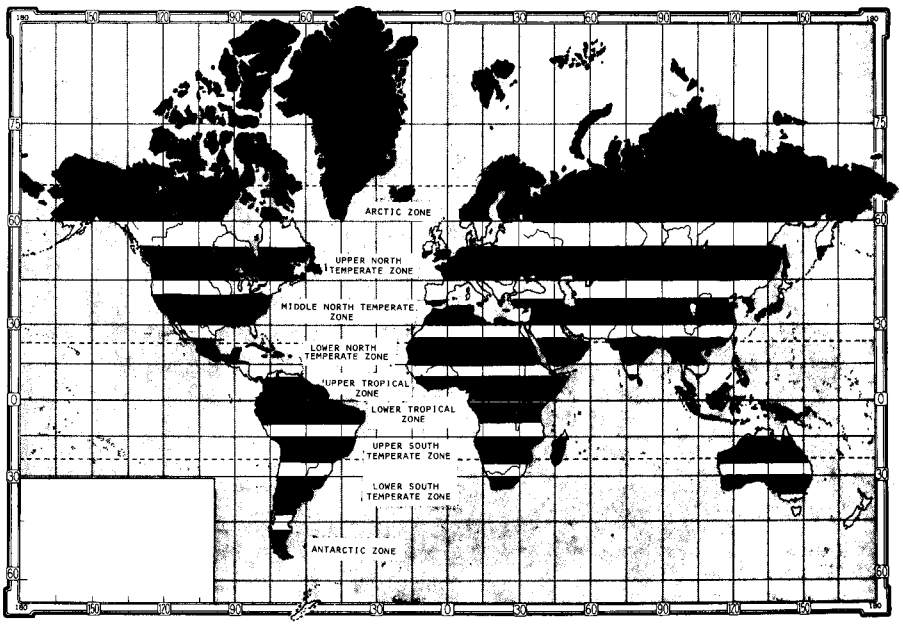

Figure 1. Mayfly distribution zones of the world.

I. ARCTIC ZONE - above 60° north latitude.
II. UPPER NORTH TEMPERATE ZONE - between 45°-55° north latitude.
III. MIDDLE NORTH TEMPERATE ZONE - between 30°-40° north latitude.
IV. LOWER NORTH TEMPERATE ZONE - between 15°-25° north latitude.
V. UPPER TROPICAL ZONE - between 0°-10° north latitude.
VI. LOWER TROPICAL ZONE - between 0°-10° south latitude.
VII. UPPER SOUTH TEMPERATE ZONE - between 15°-25° south latitude.
VIII. LOWER SOUTH TEMPERATE ZONE - between 30°-40° south latitude.
IX. ANTARCTIC ZONE - below 50° south latitude.

The paper by Allen & Brusca (1973) established the first system by which the geographic distribution and distributional limits of mayflies could be expressed in simple terms. A more exact system would designate the presumed origin, and both the northern and southern limits of the taxon. For example, the genera *Ephemerella* and *Serratella* are boreal in origin and both reach their most southern limits in the MIDDLE NORTH TEMPERATE ZONE in North America. But the northern limits of *Ephemerella* is in the UPPER NORTH TEMPERATE ZONE.

A close examination of the distributional limits of the Ephemerellinae reveals that not all species fit exactly within the designated zones dictated by the distributional limits of all the remaining species. Distributional records are good for North America, but good distributional data are lacking for most of Europe and Asia. There are 160 valid species of Ephemerellinae and only ten (*Serratella micheneri*, S. thailandensis, Torleya major*, T. nepalica, T. padunica, Drunella flavilinea*, D. gilliesi, Acerella uenoi, A. perculta,* and *Eurylophella lithuanica*) do not "fit" the proposed distributional zones. Seven species, however are known from Europe or Asia and only from the type locality. The three species with good distributional data (marked * above) do not occur more than 2-3° from the limits established by other species.

TAXONOMY

A reevaluation of nymphal and adult characters and a detailed study of geographic distribution of the Ephemerellinae by the author, and the recent publication of the descriptions of new taxa by Allen (1971, 1975, 1977), Allen & Edmunds (1976), Gose (1969), and Tshernova (1972), strongly indicate a need for reappraisal of the status of the taxa. The subfamily is divided into 2 tribes, 14 genera, and 10 subgenera.

Subfamily Ephemerellinae

The subfamily is herein divided into the tribes Ephemerellini and Hyrtanellini n. tribe.

Tribe Ephemerellini Lameere 1917

Adult Forewing with 2 intercalaries between IMP and MP_2, and between MP_2 and CuA; numerous short intercalaries along entire outer wing margin; hind wing comparatively large with abundant venation; hind wing with small, blunt, subbasal costal projection; male genital forceps with heavy, short, basal segment; long, slightly concave second segment; and long slender to heavy, short, terminal segment.

Nymph Paired dorsal abdominal gills segments 3-7 or 4-7.

Genus *Ephemerella* Walsh 1862

Type Species *excrucians* Walsh 1862

Remarks North American workers consider *Chitonophora* to be synonymous with *Ephemerella* while most Eurasians treat *E. aurivillii*, *E. krieghoffi*, and *E. mucronata* by the former generic name.

The penes of the male imago usually possess spines, but they are lacking in some species. Also, the form of the penes is variable. The lobes are rounded with a shallow notch in most, but they are elongate with a deep notch in *E. aurivillii*, *E. krieghoffi*, *E. mucronata*, *E. needhami*, and *E. septentrionalis*. The penes of *E. needhami*, *E. krieghoffi*, and *E. mucronata* are without spines, while *E. maculata* has only a shallow notch and is without spines. The nymphs of all species, except *E. septentrionalis* and *E. berneri*, possess femoral spines on the anterior surface of the fore femora, and all species have some vestige of dorsal abdominal tubercles. The nymphs of some species appear to be without tubercles, but all have at least discernible protuberances. The nymph of *E. septentrionalis* is unique in that the abdomen possesses small median tubercles.

Ikonomov (1961) described *Chitonophora* sp. *nympha unicolorata*, and in accordance with Article 5 of ICZN the name is emended to *Ephemerella unicolorata*.

Distribution *Ephemerella* is the most widely distributed genus in the subfamily as it occurs in North America, the British Isles, northern Africa, Europe, Asia and Japan (Fig. 2). In western North America, Europe, and Asia the genus has a wide latitudinal distributional range from the ARCTIC ZONE to the MIDDLE NORTH TEMPERATE ZONE. In western North America species occur from

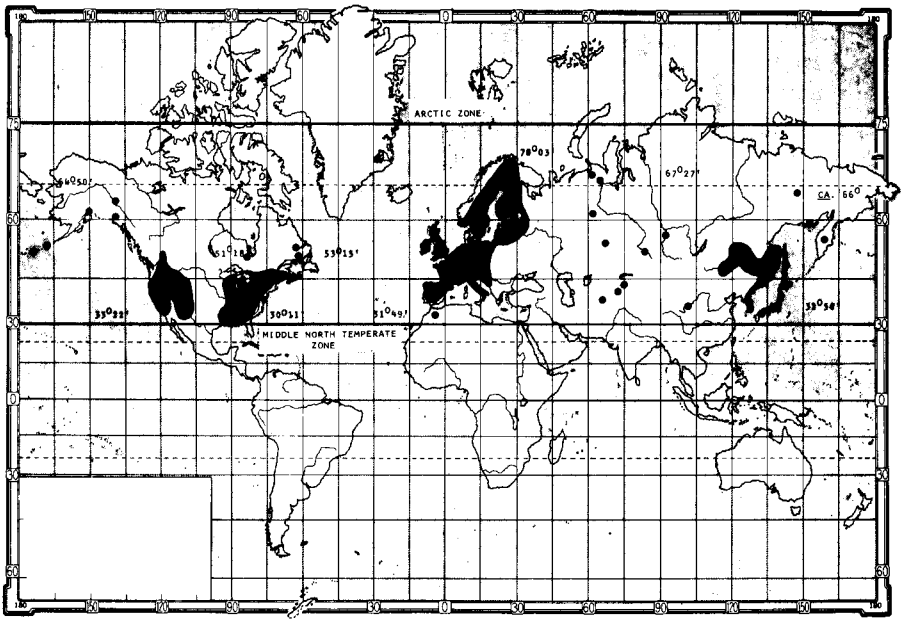

Figure 2. Distribution of the genus *Ephemerella*.

64° 50' to 33°22'; in Europe from 70° 03' to 38° 21'; and in Asia from 67° 27' to 32° 50'. In Africa the genus occurs at about 31° 50'N. latitude. The latitudinal range is narrower in eastern North America as species occur from the UPPER NORTH TEMPERATE ZONE, 53°15', to the MIDDLE NORTH TEMPERATE ZONE, 30°11', and the distribution is disjunct in North America, Europe and Asia.

Genus *Serratella* Edmunds 1959

Type Species *serrata* Morgan 1911.

Remarks The penes of the male imago resemble those of *Torleya* as they possess subapical lateral projections, except for *S. tibialis* and *S. teresa*. The nymphal head and thorax are without tubercles, except for *S. carolina*. The nymphs of *S. spiculosa* and *S. serrata* have spicules on the occiput. All nymphs, except *S. levis*, possess paired dorsal abdominal tubercles. Abdominal tubercles are barely discernible in *S. deficiens*.

Gose (1969) described and figured a nymph from Thailand which he labelled *Ephemerella* sp. TEB. This species belongs in *Serratella*

and is the second known species from Asia. It is morphologically and distributionally distinct from *S. subsolana*. I formally name it *S. thailandensis*, and designate the nymph from Chantaburi, Thailand, 20-VI-61, as the type.

Distribution *Serratella* is known only from North America and Asia (Fig. 3). The North American species are widely distributed between the UPPER NORTH TEMPERATE ZONE, 53°34', and the MIDDLE NORTH TEMPERATE ZONE, 30°26', except for one western North American species. *Serratella micheneri* nymphs have become adapted to warm water and occur in central Baja California, 27°35'N. latitude. The two Asian species are known only from their respective type localities.

Genus *Torleya* Lestage 1917

Type Species *major* Klapalek 1905

Distribution The five species of *Torleya* are known from a narrow latitudinal belt in Europe and Asia (Fig. 4). In Europe the genus occurs from the UPPER NORTH TEMPERATE ZONE, 53°03', to just

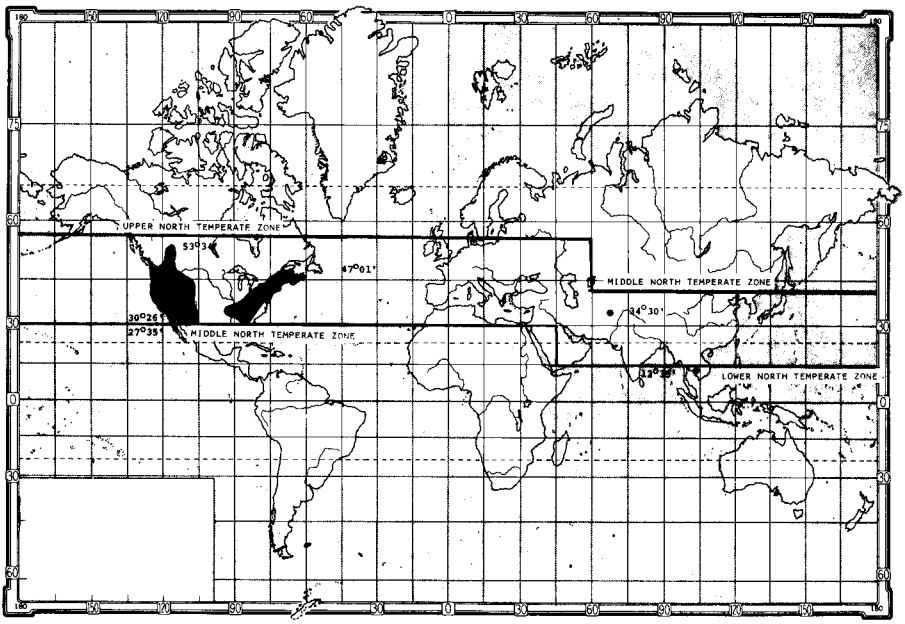

Figure 3. Distribution of the genus *Serratella*.

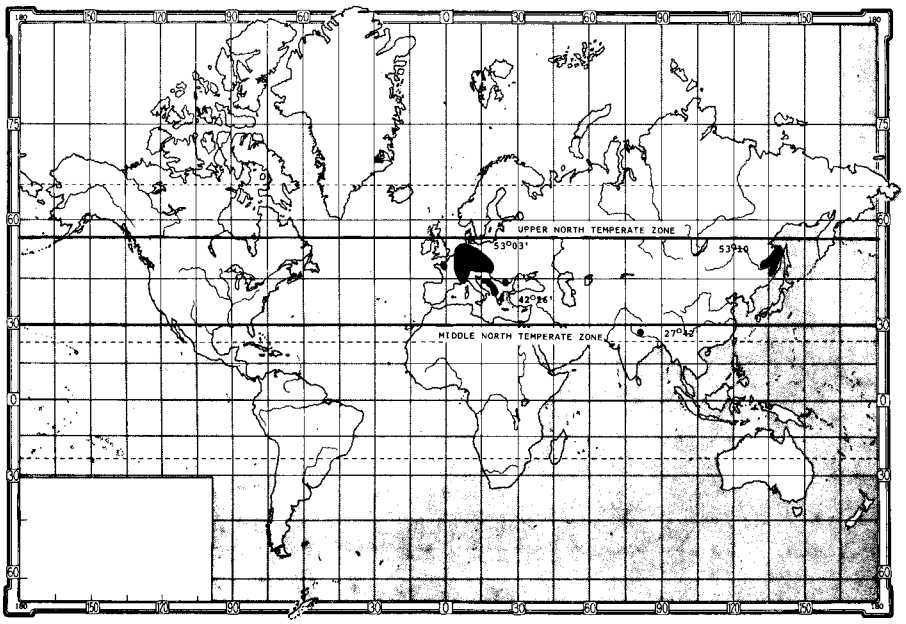

Figure 4. Distribution of the genus *Torleya*.

above the northern limits of the MIDDLE NORTH TEMPERATE ZONE, 42°26', and in Asia from the UPPER NORTH TEMPERATE ZONE, 53°10', to just below the MIDDLE NORTH TEMPERATE ZONE, 27°42' N. latitude.

Genus *Teloganopsis* Ulmer 1939

Type Species *media* Ulmer 1939

Distribution The two described species of *Teloganopsis* are allopatric (Fig. 5). The genus is restricted to eastern Asia. One species is known from the UPPER NORTH TEMPERATE ZONE, 50°12'N. latitude, and the other from the LOWER SOUTH TROPICAL ZONE, 6°57' S. latitude.

Genus *Caudatella* Edmunds 1959

Type Species *heterocaudata* McDunnough 1929

Distribution *Caudatella* is restricted to western North America, and occurs from the UPPER NORTH TEMPERATE ZONE, 50°12', to the MIDDLE NORTH TEMPERATE ZONE, 34°07' (Fig. 6).

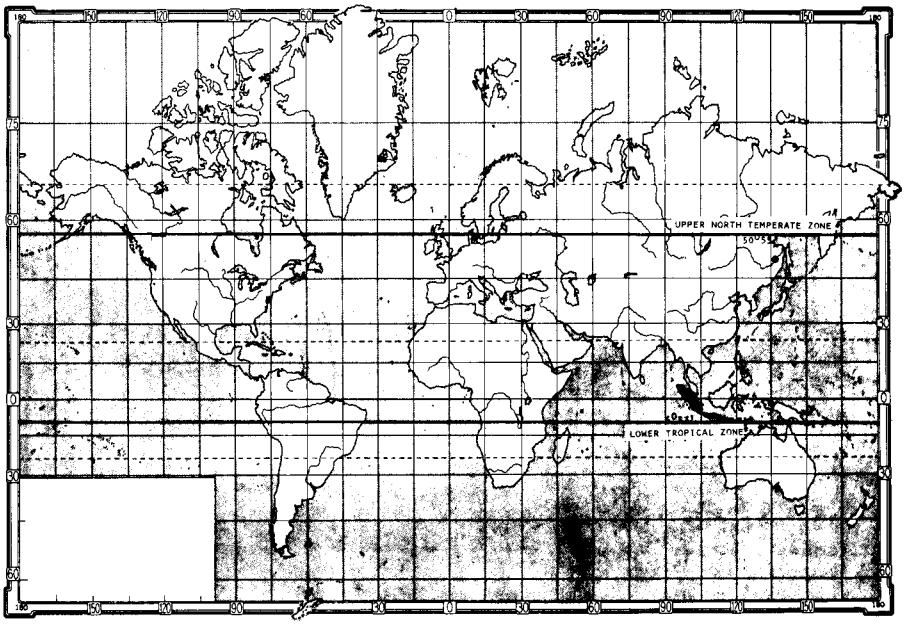

Figure 5. Distribution of the genus *Teloganopsis*.

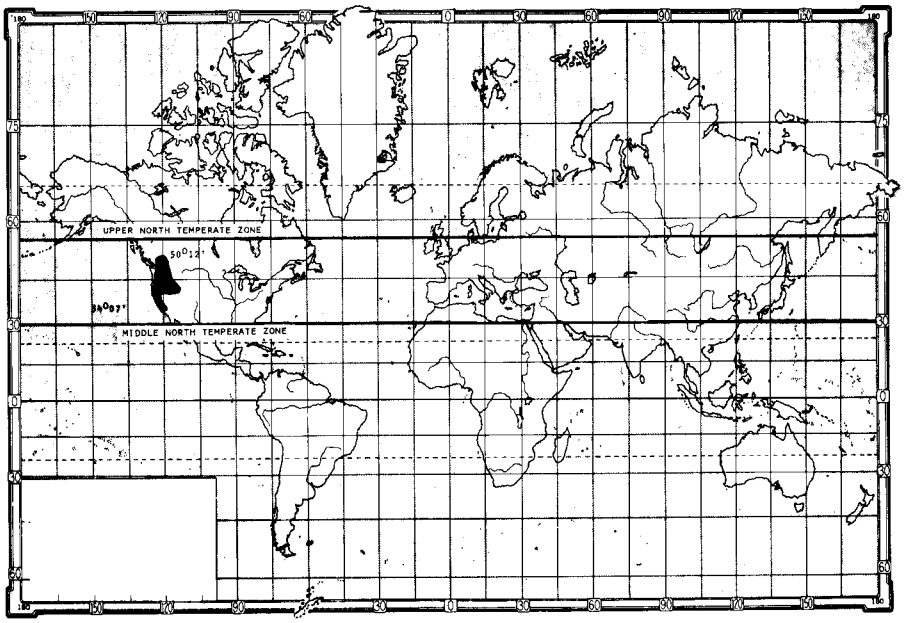

Figure 6. Distribution of genus *Caudatella*.

Genus *Drunella* Needham 1909

Type Species *grandis* Eaton 1884

Remarks The nymphs of *Drunella* are diverse in structure as species have adapted to a variety of stream habitats. Five subgenera are recognized in the genus.

Distribution The genus occurs in only North America, Asia and Japan (Fig. 7), and it has a wide latitudinal range on both continents. In North America and Asia the latitudinal range is from the ARCTIC ZONE to the MIDDLE NORTH TEMPERATE ZONE. In western North America it is known from Alaska, 61°10', to Baja California, 31°03', and northern Sonora, 30°59'. In Asia the range is from Kamchatka, 59°20', to Nepal, 27°42', and to 34°41' in Japan. The latitudinal range is narrower in eastern North America, from only the UPPER NORTH TEMPERATE ZONE, 51°18', to the MIDDLE NORTH TEMPERATE ZONE, 35°03'.

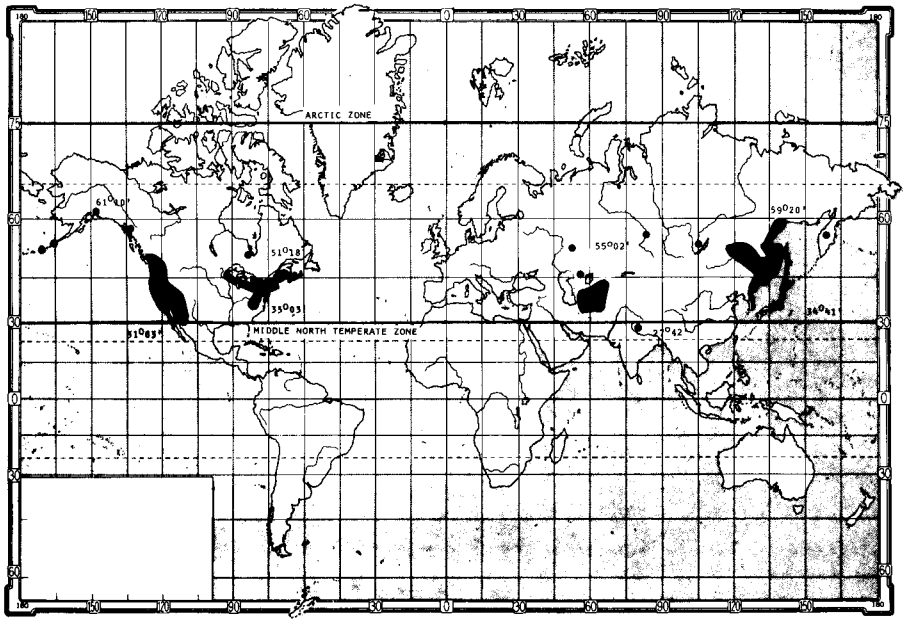

Figure 7. Distribution of the genus *Drunella*.

Subgenus *Drunella* s.s.

Remarks *Drunella pelosa* is the most aberrant species in the genus. The nymph lacks body tubercles, but possesses paired submedian tufts of setae on the occiput, thorax, and abdomen. The femora are without tubercles, but the ventral margins are lined with thick setae, and the sternum has a partial adhesive disc. The inclusion of *D. pelosa* in this subgenus is appropriate as the nymphs have features that are most similar to the other *Drunella* s.s. nymphs.

Subgenus *Tribrochella* Allen n. subgen.

trispina group Imanishi 1940: 193.

Type Species *trispina* Imanishi 1940.

Nymph Head with anteromedian and lateral frontoclypeal projections; abdominal tubercles absent, with only paired submedian ridges.

Remarks *Drunella (Tribrochella) kohnoi* is emended to *D. (T.) kohnoae* as R.W. Baumann (Brigham Young University) has informed the author that Dr. Mitsuko Kohno is female. This subgenus is the largest in the genus with 12 species, and it is the only one in which the great majority of species are in Asia.

Subgenus *Unirhachella* Allen n. subgen.

Type Species *tuberculata* Morgan 1911

Nymph Head with well developed occipital tubercles, large median metanotal tubercle, and small paired dorsal abdominal tubercles.

Subgenus *Myllonella* Allen n. subgen.

Type Species *coloradensis* Dodds, 1923

Nymph Head with small occipital tubercles, without thoracic tubercles, and with small abdominal tubercles.

Subgenus *Eatonella* Needham 1927

Type Species *doddsi* Needham 1927

Remarks McDunnough (1931) acknowledged the close relationship of *D. doddsi* and *D. walkeri* (as *fuscata*) nymphs, but he rejected *Eatonella* as a taxon. He stated that *D. walkeri* and *D. tuberculata* were closely related in the adult stage, and he was unable to understand the great diversity of characters in the nymphs

of the latter and the other two species. Of course, *D. walkeri* and *D. tuberculata* are not closely related. Allen & Edmunds (1962b) recognized the common characters of the nymphs of *D. conestee*, *D. doddsi*, *D. wayah*, and *D. walkeri* and placed them together in a species group. I herein resurrect *Eatonella* as a subgenus for *D. doddsi* and the other three species.

Genus *Crinitella* Allen & Edmunds 1963

Type Species *coheri* Allen & Edmunds 1963

Remarks It seems advisable to elevate this taxon to full generic rank along with the others that were formerly placed in *Ephemerella* s. l., but this placement is tentative until the male imago is described.

Distribution *Crinitella* is known from India, 31°34' N. latitude, in the lower limits of the MIDDLE NORTH TEMPERATE ZONE to Malaysia, 3°08' N. latitude, in the UPPER TROPICAL ZONE (Fig. 8).

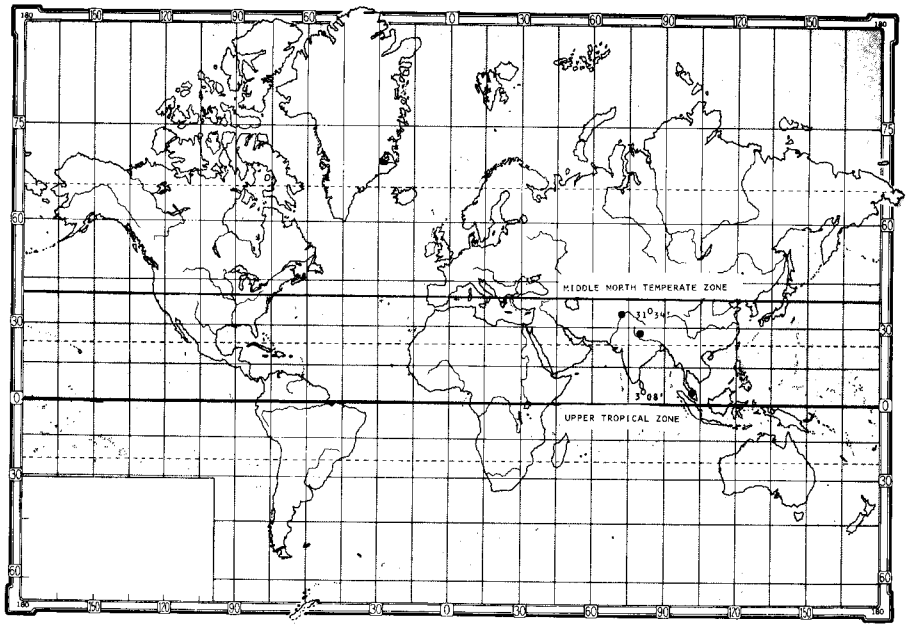

Figure 8. Distribution of the genus *Crinitella*.

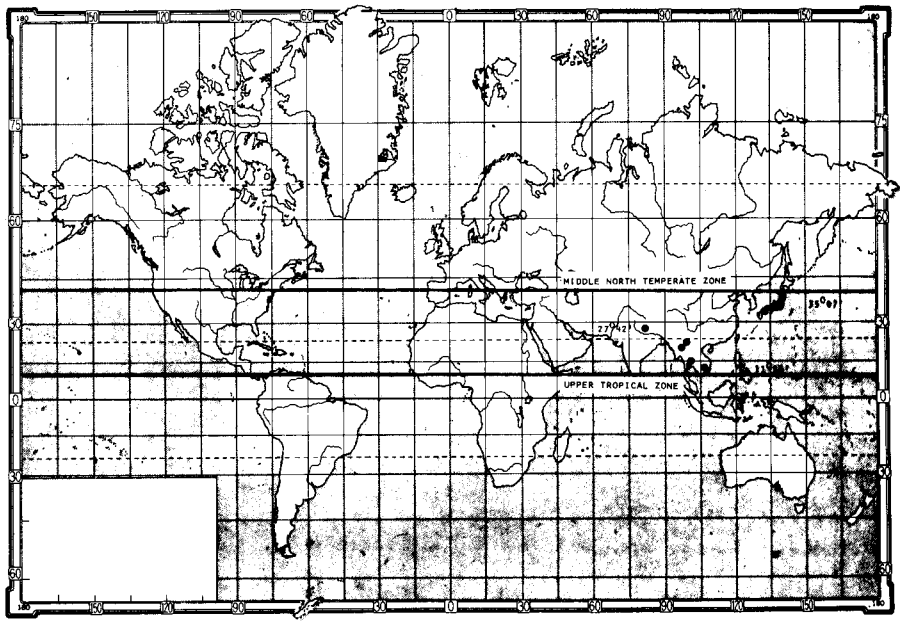

Figure 9. Distribution of the genus *Acerella*.

Genus *Acerella* Allen 1971

Type Species *longicaudata* Ueno 1928

Distribution This genus is known only from southeast Asia and Japan from the MIDDLE NORTH TEMPERATE ZONE, 35°07', to near the upper limits of the UPPER TROPICAL ZONE, 11°56' (Fig. 9).

Genus *Cincticostella* Allen 1971

Type Species *nigra* Ueno 1928

Remarks *Cincticostella* nymphs are diverse in structure and 3 subgenera are recognized, including *Vietnamella*, NEW COMBINATION.

Distribution This genus is known from western and southwestern Asia, and Japan, from the UPPER NORTH TEMPERATE ZONE, 53°44', to the LOWER NORTH TEMPERATE ZONE, 18°48' (Fig. 10).

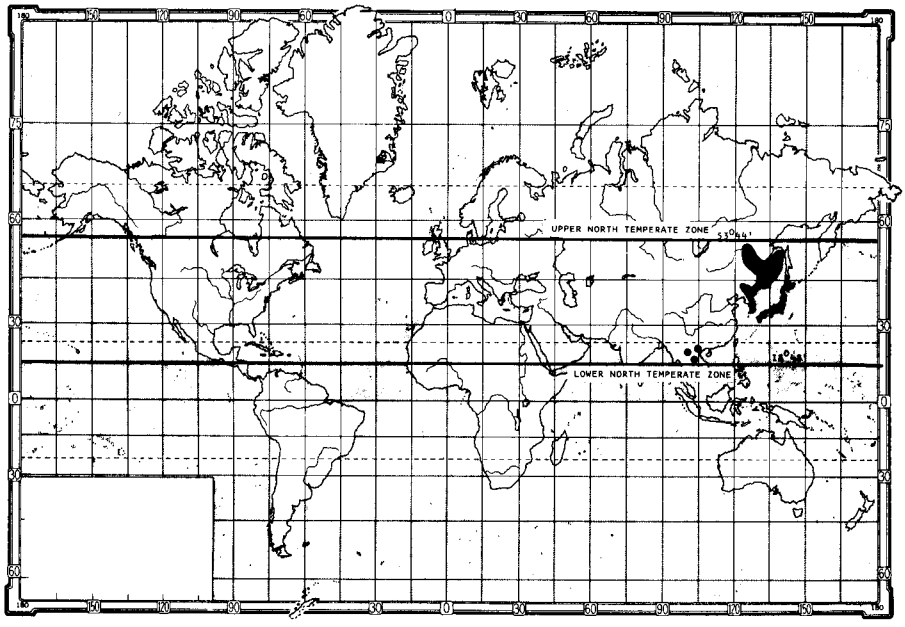

Figure 10. Distribution of the genus *Cinctícostella*.

Subgenus *Cinctícostella* s.s.

nigra group Allen 1975: 17.

Nymph Head without tubercles; femora narrow and entire.

Subgenus *Rhionella* Allen n. subgen.

insolta group Allen 1975: 17.

Type Species *insolta* Allen 1971.

Nymph Head with occipital or suboccipital tubercles; femora with serrations and protuberances; middle and hind femora expanded.

Subgenus *Vietnamella* Tshernova 1972

Vietnamella Tshernova 1972: 609. NEW COMBINATION

Type Species *thani* Tshernova 1972.

Nymph Head with long frontoclypeal projections and paired frontal tubercles; fore femora with tubercles on ventral margin and fore femora expanded; middle and hind femora without tubercles and not expanded.

Genus *Attenella* Edmunds 1971

Attenella Edmunds 1971: 152 (=*Attenuatella* Edmunds 1959: 465, *nec* Stehli 1954: 343)

Type Species *attenuata* McDunnough 1925

Distribution *Attenella* is known only from North America (Fig. 11). Species occur from the UPPER NORTH TEMPERATE ZONE to the MIDDLE NORTH TEMPERATE ZONE, between 46°11' and 30°27' N. latitude in the east and between 53°54' and 35°34' N. latitude in the west (Fig. 11).

Genus *Eurylophella* Tiensuu 1935

Type Species *karelica* Tiensuu 1935

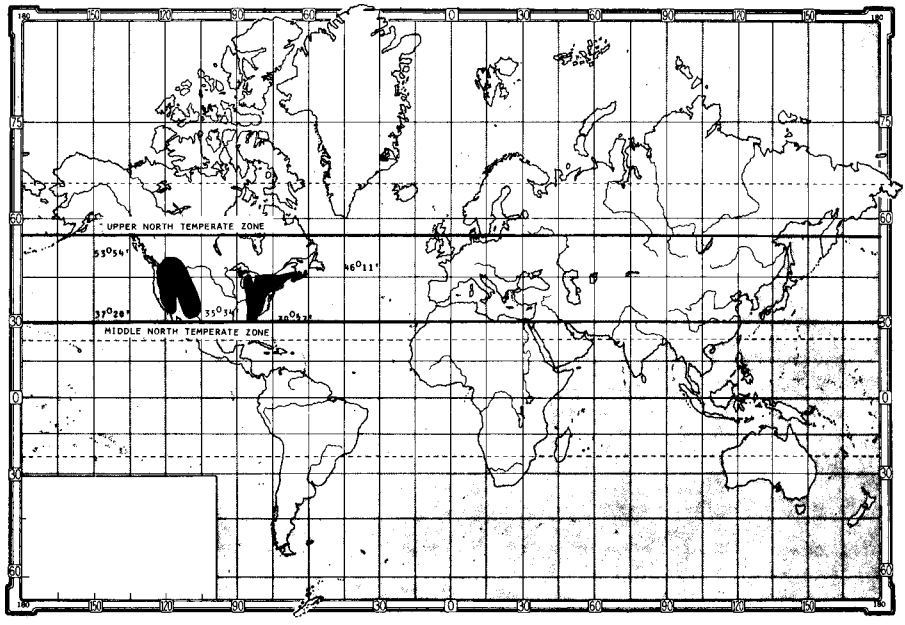

Figure 11. Distribution of the genus *Attenella*.

Remarks Edmunds, Jensen & Berner (1976) incorrectly list *E. brunnescens* Tiensuu 1935 as the type of this taxon. The type is *E. karelica* which was established by original designation.

Distribution Eleven of the 15 species of *Eurylophella* occur in eastern North America, one is known from western North America, and three from Europe. In North America the genus occurs from the ARCTIC ZONE, 59°47', to the MIDDLE NORTH TEMPERATE ZONE, 29°37'. In Europe, it is known from the ARCTIC ZONE, 64°32', to near the lower limits of the UPPER NORTH TEMPERATE ZONE, 42°31' (Fig. 12).

Genus *Dannella* Edmunds 1959

Type Species *simplex* McDunnough 1925

Remarks Allen & Edmunds (1962a) characterized the adult and nymphal stages of *Dannella* based on the characters of known species. Allen (1977) recharacterized the taxon to include *D. bartoni*, a newly described nymph, which possesses paired dorsal abdominal tubercles and dentition on the claws. McCafferty (1977) failed to include *D. bartoni* in *Dannella*, as, in his opinion, the species

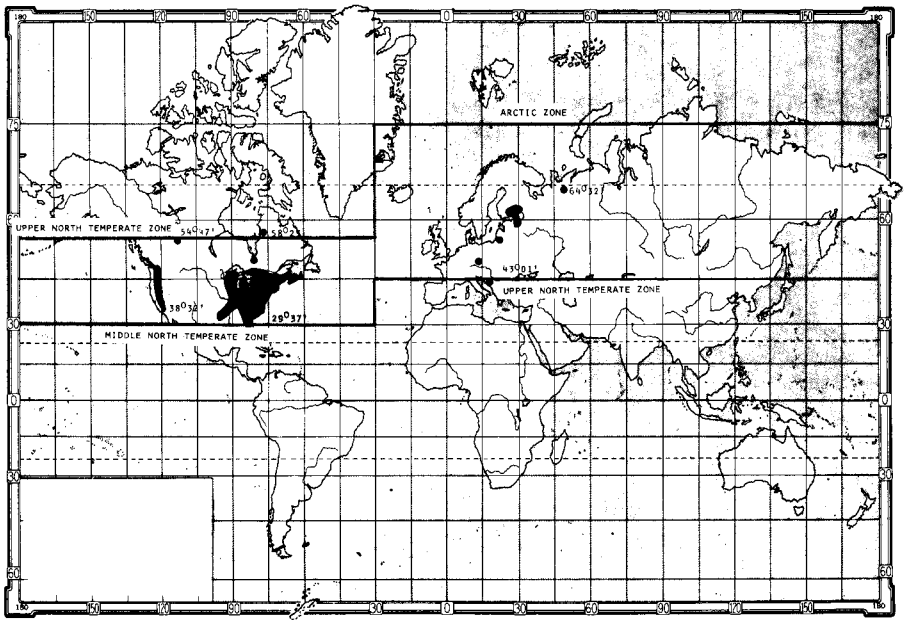

Figure 12. Distribution of the genus *Eurylophella*.

changed the concept of the taxon. Recharacterization of taxa to accommodate additional species has been done several times recently in the Ephemeroptera (see Allen & Edmunds 1962b; Allen 1967; and Allen & Brusca 1973). *Drunella* s.l. was characterized as having only head and body tubercles until *D. pelosa* was described with tufts of setae in place of tubercles. *Leptohyphes* was characterized as being without head and body tubercles, or protuberances, until *L. undulatus*, *L. dicinctus*, and *L. melanobranchus* were discovered; *Tricorythodes* was characterized as being without body tubercles until *T. bullus* and *T. cristatus* were described; and *Leptohyphes* and *Tricorythodes* were characterized as possessing only small compound eyes in both sexes until *L. mirus* and *T. dimorphus* were found.

McCafferty (MS) places *D. bartoni* in *Eurylophella* as he states, "....*E. bartoni* possesses three derived larval character states that are found in the *Eurylophella* lineage." "This evolution included the loss of maxillary palpi, the apical rounding of the gills, and the reduction of the midlength of abdominal segments 5, 6, and 7." The maxillary palpi are well developed in *D. provonshai*, reduced in *D. lita* and *D. simplex*, and absent in *D. bartoni*. Obviously there is a tendency for the reduction of this structure in *Dannella*, as is the case in the nymphs of *Acerella*, *Cinctocostella*, *Serratella*, and *Torleya*. The taxonomic significance of the rounding of the gills has not been investigated by the author. The reduction of the length of abdominal segments 5-7 does not reflect a relationship to *Eurylophella* as the nymphs of all ephemerellid genera with operculate gills possess this character, including *Hyrtanella*.

Dannella nymphs are not easily recognized since the characters which distinguish them are not as well defined as they are in *Eurylophella*. The body is extremely depressed, like *Timpanoga*, the abdomen is broad and the posterolateral projections are well developed; the body is heavily setaceous; and the abdominal segments 8-9 are subequal (Fig. 13). *Eurylophella* nymphs (Fig. 14) on the other hand, are the most easily recognized in the subfamily because of two consistent characters. First, abdominal segment 9 is considerably longer than 8, and second, the paired dorsal abdominal tubercles on segments 1-3 are blunt and those on 4-9 are sharp.

The morphological characters of the nymph of *D. bartoni* suggest that it be placed in a separate subgenus and *Dentatella* is erected to accommodate this species.

Distribution *Dannella* occurs only in North America from the ARCTIC ZONE, 58°45', to the MIDDLE NORTH TEMPERATE ZONE, 35°22'. Four species occur in eastern North America, and one undescribed species is known from Colorado (Fig. 15).

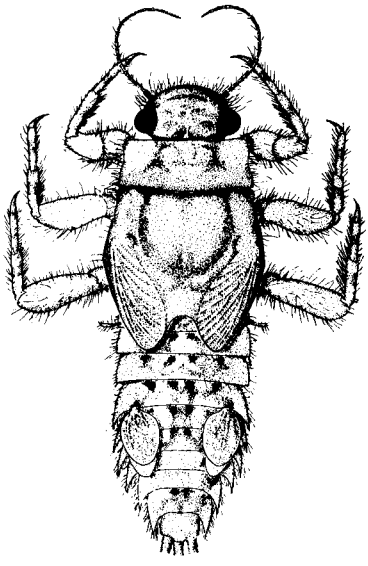

Figure 13. Nymph of *Dannella*.

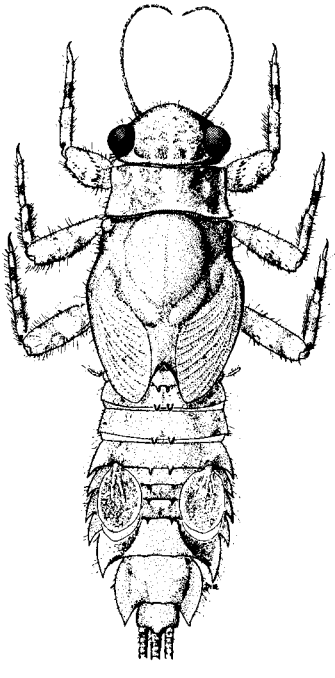

Figure 14. Nymph of *Eurylophella*.

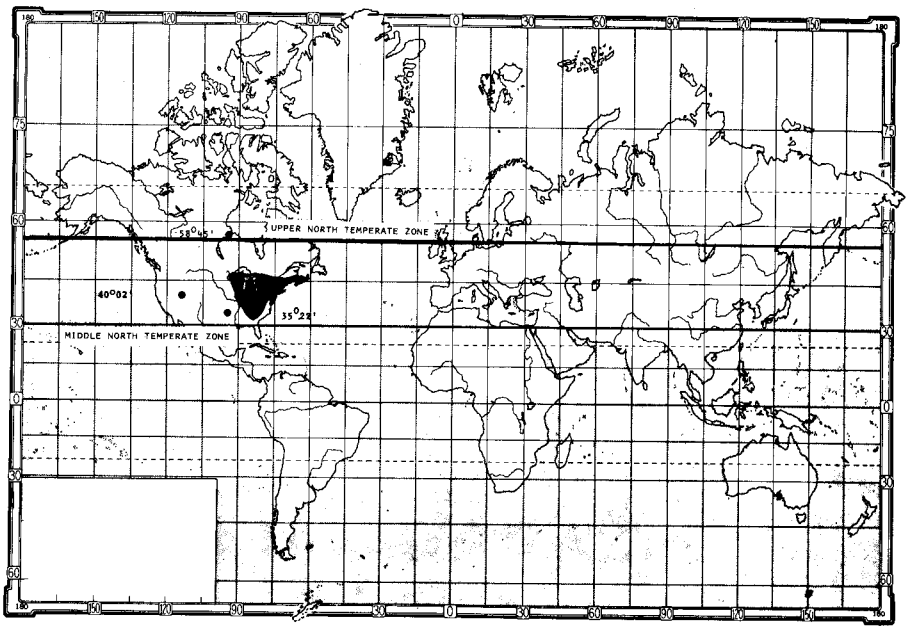

Figure 15. Distribution of the genus *Dannella*.

Subgenus *Dannella* s.s.

Nymph Abdominal terga without tubercles; claws without denticles.

Subgenus *Dentatella* Allen n. subgen

Type Species *bartoni* Allen 1977

Nymph Abdominal terga with tubercles; claws with denticles.

Genus *Timpanoga* Needham 1927

Type Species *hecuba* Eaton 1884

Distribution *Timpanoga* is known only from a single species in western North America from the UPPER NORTH TEMPERATE ZONE, 50°03', to the MIDDLE NORTH TEMPERATE ZONE, 35°34' (Fig. 16).

Tribe Hyrtanellini Allen n. tribe

Adult Forewing with 1 intercalary between IMP and MP_2, and

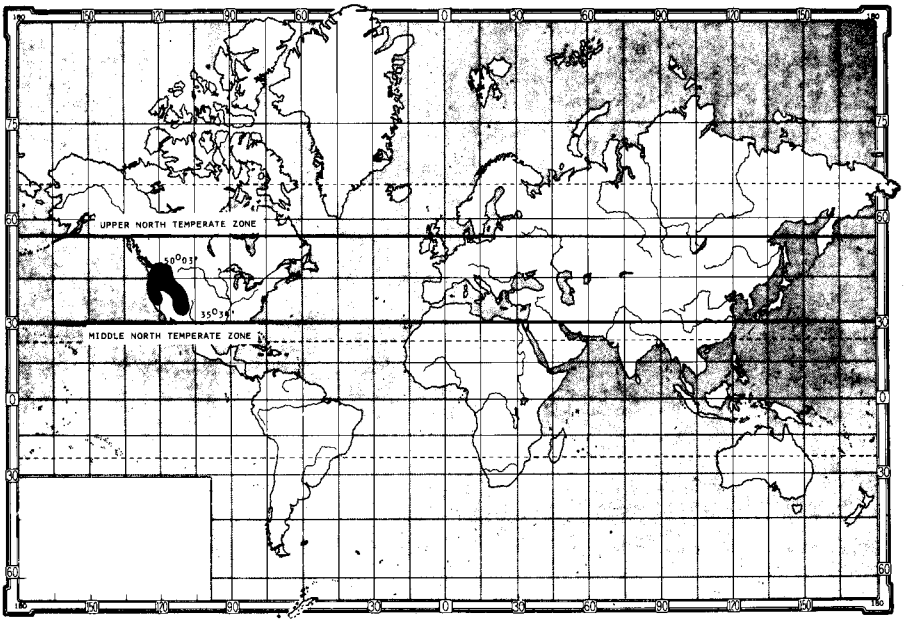

Figure 16. Distribution of the genus *Timpanoga*

without intercalaries between MP_2 and CuA; with few intercalaries along outer margin; hindwing small with sparse venation; male genitalia unknown.

Nymph Abdominal gills segments 3-6; gill operculate segment 3, imbricated 4-6; abdominal terga 4-8 depressed laterally; maxillary palpi vestigial; claws with palisade subapical denticles; caudal filaments with setae.

Genus *Hyrtanella* Allen & Edmunds 1976

Type Species *christineae* Allen & Edmunds 1976

Distribution *Hyrtanella* is known only from Malaysia, *ca.* 5° N. latitude in the UPPER TROPICAL ZONE.

RESUME

Le rapport détermine la répartition géographique des genres du sous famille des éphémérellinés ainsi que l'établissement de neuf

zones de répartition latitudinales et révise le système proposé par Allen et Brusca. Les genres font partie de deux tribus, les Ephemerellini et les Hyrtanellini, n. tribus, et *Acerella, Attenella, Caudatella, Cincticostella, Crinitella, Dannella, Drunella, Ephemerella* au sens strict, *Eurylophella, Hyrtanella, Serratella, Teloganopsis, Timpanoga* et *Torleya* sont considérés comme des genres. *Drunella* comprend cinq sous-genres: sens strict, *Eatonella, Myllonella*, n. subgen. *Tribrochella* n. subgen. et *Unirhachella* n. subgen.; *Cincticostella* comprend trois sous-genres: sens strict, *Rhionella* n. subgen., et *Vietnamella*, n. comb.; *Dannella* comprend deux sous-genres; sens strict et *Dentatella*, n. subgen.

ZUSSAMENGASSUNG

Diese Arbeit befaßt sich mit der geographischen Verteilung von Gattungen der Unterfamilie *Ephemerella* und stellt neun latitudinale Verteilungszonen auf, wobei das von Allen & Brusca vorgeschlagene System revidiert wird. Die n. Sippe, sowie *Acerella, Attenella, Caudatella, Cincticostella, Crinitella, Dannella, Drunella, Ephemerella, Eurylophella, Hyrtanella, Serratella, Teloganopsis, Timpanoga* und *Torleya* werden als Gattungen behandelt. *Drunella* besteht aus fünf subgenera: s.s., *Eatonella, Myllonella* n. subgen., *Tribrochella* n. subgen. und *Unirhachella* n. subgen., *Cincticostella* von 3: s.s., *Rhionella* n. subgen., und *Vietnamella* Neue Kombination. *Dannella* von 2: s.s. und *Dentatella* n. subgen.

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