

SUBGENERIC GROUPS WITHIN THE MAYFLY GENUS EPHEMERELLA (EPHEMEROPTERA: EPHEMERELLIDAE)

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ABSTRACT

The currently recognized *Ephemerella* species are assigned, as far as possible, to nine subgenera based on nymphal and imaginal characters. New subgenera are **SERRATELLA** (type *serrata* Morgan), **CAUDATELLA** (type *heterocaudata* McDunnough), **ATTENUATELLA** (type *attenuata* McD.), and **DANNELLA** (type *simplex*

McD.); those previously named are *Ephemerella* Walsh, s.s., *Torleya* Lestage, *Drunella* Needham, *Eurylophella* Tiensuu, and *Timpanoga* Needham. Thirteen of the species can not be assigned subgenerically without further study.

There is considerable difference of opinion among Ephemeropterists concerning the number of generic or subgeneric categories to be recognized within the Holarctic Ephemerellidae. Generally the specialists in Western Europe have placed a small number of species in three or four genera, while workers in North America and Asia have generally included a much larger number of species within the single genus *Ephemerella*. The nymphs of the complex show great diversity and the adults a moderate diversity of characters, so it is not difficult to find large morphological gaps between a small number of species within any geographic area. It is only when the world fauna is examined that there is great difficulty in recognizing gaps between groups of species.

Eaton (1883-1888) included all the Holarctic Ephemerellidae in the genus *Ephemerella* or as allies of *Ephemerella*. Needham (1905) split off

one group as the genus *Drunella*, but later (1927) gave it only subgeneric rank. Bengtsson (1909) erected the genus *Chitonophora*. Lestage (1917) named the genus *Torleya* from Europe, and Needham (1927) named two subgenera of *Ephemerella*, *Drunella* and *Eatonella*, from western North America. Tiensuu (1935) erected the genera *Eurylophella* and *Melanameletus*. Traver (1935) placed all the North American species in the genus *Ephemerella* but recognized a number of groups and noted (op. cit.: 565) that proper application of the above mentioned names "awaits a better definition of the groups of species, based on a more complete knowledge of them in all stages, and especially of the type species of *Ephemerella*, *E. excrucians*." Edmunds and Traver (1954: 238) listed the Holarctic Ephemerellidae as being one genus with six subgenera. Demoulin (1958: 10) followed this arrangement.

American workers generally have recognized a single genus *Ephemerella* with a variable number of species-groups, but they have not applied subgeneric names to such groups.

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In my opinion there are moderately well definable natural groups within the genus that should be designated as subgenera, leaving the term species-group to apply to the smaller clusters of related species within each subgenus.

To be functional and phylogenetically significant, subgenera should be definable in both nymphal and male imago stages. Knowledge of the characters of the nymphal stage are then useful in predicting what an unknown male imago stage would be like, or vice versa. If this predictability breaks down in a classification, there is a strong probability that the separation of the groups has been done on superficial characters.

Difficulty in the classification of the genus *Ephemerella* stems in part from the fact that the rate of evolution in nymphal forms is in most cases rapid, while the adults remain essentially conservative. Within the subgenus *Drunella* there are striking morphological differences between various groups of species, but the adults are remarkably monotonous, with little structural differentiation between species or groups of species.

The subgeneric groupings proposed in this paper are based largely on a study of the North American species, but the Eurasian species have been considered.

This study of subgeneric groupings is still in progress by the writer and Mr. R. K. Allen, but it is hoped that this paper will serve as a stimulus to others to publish their own findings on this subject. Certainly, there is a great need for additional knowledge of the systematic position of many of the species considered in this paper.

The distinguishing characters of the subgenera can be ascertained from the keys following the discussions of the groups. Under each subgenus I have listed all the nominal species, but have placed those previously considered invalid in italics following the valid name to which the synonym is referred. Some additional species either are known to be invalid or are questionably valid, but these problems will be treated elsewhere.

Subgenus **Ephemerella** Walsh, s.s.

1862 Walsh, Proc. Acad. Nat. Sci. Philadelphia 13-14: 377; type species: *excrucians* Walsh.

There has been considerable doubt for some time whether *Ephemerella* s.s. and *Chitinophora* can be maintained even as subgenera. There seems little doubt that this separation should not be maintained on the characters first suggested by Bengtsson (1908), but it might be desirable on the basis of characters suggested by Traver (1935) (using the terms "invaria group" for *Ephemerella* and "needhami group" for *Chitinophora*). It appears to me that while such a division may still have merit for the North American fauna, the division may break down completely in the Eurasian forms. For this reason I am not at

present inclined to recognize *Chitinophora* as distinct from *Ephemerella*, although I leave the final decision open. The best basis of separation in the adult males appears to be the form of the penes, which in *Ephemerella* s.s. have the lateral penes rounded with only a shallow notch between them, while in *Chitinophora* the penes are longer and more slender with a deep apical notch between them.

According to Traver (op. cit.: 566) the nymphs of *Ephemerella* s.s. have "rather long spines along the posterior margins of the femora, and on the upper surface of the fore femur, where they are arranged in an irregular transverse band near the apical end; tails never with a whorl of spines at the base." *Chitinophora* has "only short and inconspicuous spines along the margins of the femora; usually no spines on the upper surface of the fore femur, but if present, generally distributed and not in an apical band; tails may have whorls of spines in the basal half."

If a separation of the group into two subgenera is attempted, the following North American species appear to belong to the subgenus *Ephemerella* s.s.: *argo* Burks, *dorothea* Needham, *excrucians* Walsh (= *semiflava* McDunnough), *fratercula* McDunnough, *inconstans* Traver,² *inermis* Eaton, *infrequens* McDunnough, *invaria* Walker, *mollitia* Seeman, *ora* Burks, *rotunda* Morgan (= *feminina* Needham, *vernalis* Banks²), and *subvaria* McDunnough. The Eurasian species tentatively assigned here would be *lactata* Bengtsson and *torrentium* Bengtsson.

The North American species which might be separable as *Chitinophora* (type species: the Holarctic *aurivillii* Bengtsson) are *aurivillii* Bengtsson (= *aaroni* Eaton, *concinatta* Traver, *norda* McDunnough), *berneri* Allen and Edmunds, *catawba* Traver, *choctawhatchee* Berner, *euterpe* Traver, *maculata* Traver, *needhami* McDunnough and *septentrionalis* McDunnough. Eurasian species which I tentatively associate with this group are *ignita* Poda (= *aenea* Pictet, *erythrophthalma* Schrank, *gibba* Pictet), *krieghoffi* Ulmer, *mesoleuca* Brauer, *notata* Eaton, *sibirica* Tshernova, and *sven-hedini* Ulmer.

Subgenus **Serratella**, new subgenus

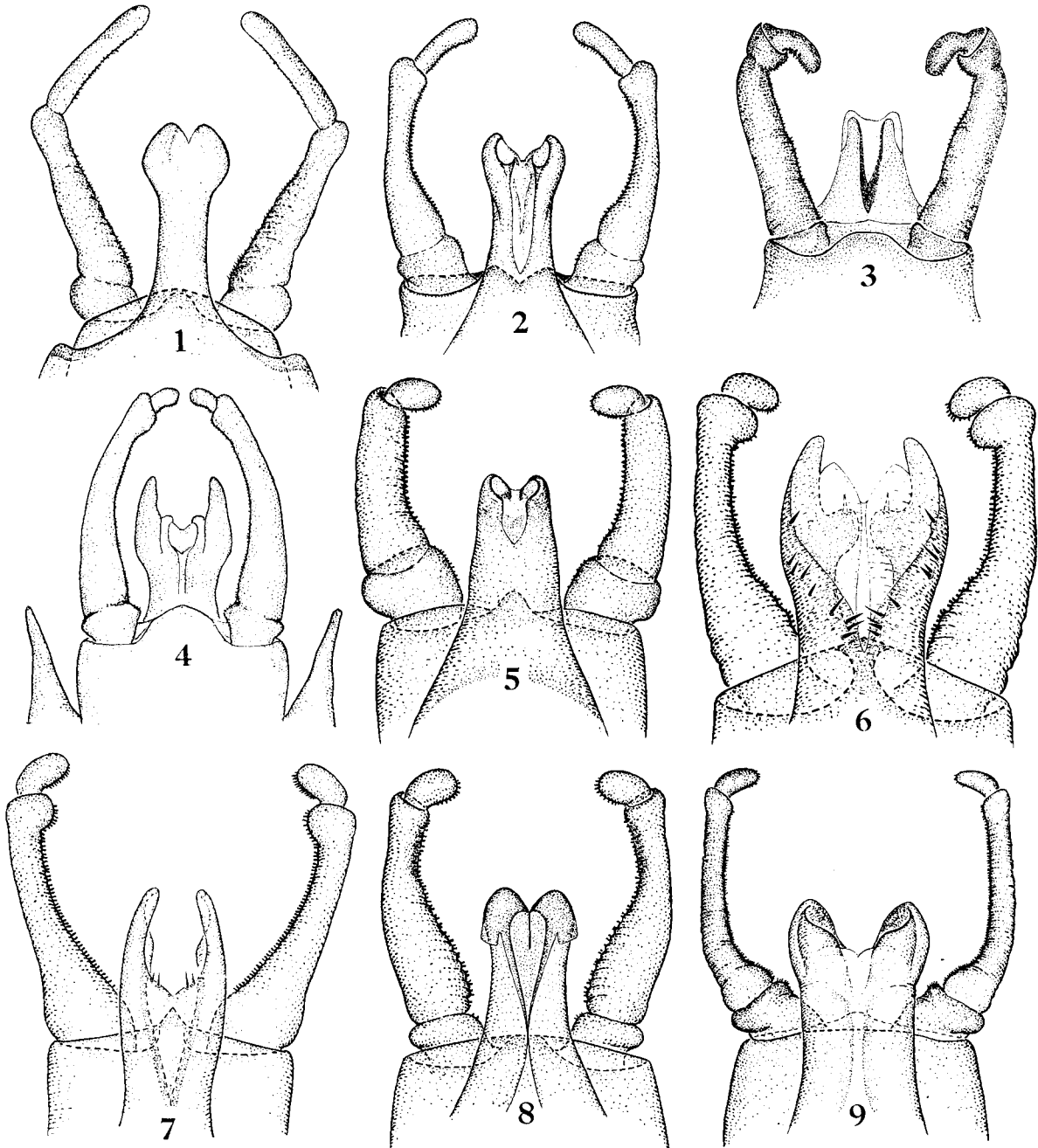
Type species: *serrata* Morgan.

Although this group may eventually prove to be inseparable from the European *Torleya*, it presently appears to be quite distinct. Additional studies of the species in Eastern Asia will probably clarify this point.

²With the generous aid of Dr. W. L. Brown, I was able to examine the type of *Ephemerella vernalis* Banks at the Museum of Comparative Zoology in May 1958, and to determine that it is a junior synonym of *E. rotunda* rather than a senior synonym of *E. inconstans*. The figure which I give as the male genitalia of *E. rotunda* Morgan was drawn from the holotype of *E. vernalis* Banks.

The North American species assigned to the subgenus are *cognata* Traver, *deficiens* Morgan (= *atrescens* McDunnough), *frisoni* McDunnough, *levis* Day, *micheneri* Traver, *molita* McDunnough, *serrata* Morgan, *serratoides* McDunnough, *sordida*

McDunnough, *teresa* Traver, and *tibialis* McDunnough (= *angusta* Traver). Eurasian species which I tentatively place in the subgenus are *levanidovae* Tshernova, *longicaudata* Ueno, and *orientalis* Tshernova.



EXPLANATION OF FIGURES

Male genitalia of representatives of several subgenera of *Ephemerella*; figure 3 in ventral view, all others in dorsal view.

FIG. 1.—*E. (Attenuatella) attenuata*. FIG. 2.—*E. (Drunella) coloradensis*. FIG. 3.—*E. (Torleya) belgica*. FIG. 4.—*E. (Timpanoga) hecuba*. FIG. 5.—*E. (Eurylophella) bicolor*. FIG. 6.—*E. (Ephemerella) rotunda*, drawn from the holotype of the synonymous *E. (E.) vernalis* Banks. FIG. 7.—*E. (Ephemerella) septentrionalis*. FIG. 8.—*E. (Serratella) deficiens*. FIG. 9.—*E. (Dannella) simplex*, from specimen not treated with KOH.

The subgeneric name *Serratella* is formed by adding the diminutive suffix *ella* to the name of the type species.

Subgenus **Torleya** Lestage

1917 Lestage, Ann. Biol. Lacustre 8: 366; type species: *belgica* Lestage.

This subgenus is known only from Europe where it is represented by two species, *belgica* Lestage and *major* Klapalek.

Subgenus **Caudatella**, new subgenus

Type species: *heterocaudata* McDunnough.

This subgenus is at present known only from western North America where it is represented by *columbiella* McDunnough, *edmundsi* Allen, *heterocaudata* McDunnough, *hystrix* Traver (= *spinosa* Mayo), and *jacobi* McDunnough.

The subgeneric name is formed by the diminutive of the latter part of the Greek-Latin hybrid name of the type species.

Subgenus **Drunella** Needham

1905 Needham, New York State Mus. Bull. 86: 42; type species: *grandis* Eaton. (= *Eatonella* Needham 1927, Ann. Ent. Soc. America 20: 108; type species *doddsi* Needham.)

The North American species assigned to this subgenus are *allegheensis* Traver, *autumnalis* McDunnough, *cherokee* Traver, *coloradensis* Dodds, *conestee* Traver, *cornuta* Morgan, *cornutella* McDunnough, *depressa* Ide, *doddsi* Needham, *flavilinea* McDunnough, *flavincta* McDunnough, *glacialis* Traver, *glacialis carsona* Day, *grandis* Eaton, *ingens* McDunnough, *lapidula* McDunnough, *lata* Morgan (= *inflata* McDunnough), *longicornis* Traver, *pelosa* Mayo, *proserpina* Traver (= *yosemite* Traver), *sierra* Mayo, *spinifera* Needham, *tuberculata* Morgan, *walkeri* Eaton (= *bispina* Needham, *fusca* Walker), *wayah* Traver, and *wilsoni* Mayo.

The species from Eastern Asia which appear to fall in this subgenus are *basalis* Imanishi, *cryptomeria* Imanishi, *ishiyama* Matsumura, *latipes* Tshernova, *punctisetae* Matsumura, *tenax* Tshernova, *tricantha* Tshernova, and *trispina* Ueno.

Subgenus **Attenuatella**, new subgenus

Type species: *attenuata* McDunnough.

This is a small subgenus of which the named species are all North American. Dr. Herman T. Spieth has shown me a male of an undescribed species of this subgenus from China.

The species of this subgenus are *attenuata* McDunnough, *delantala* Mayo, *margarita* Needham, *hirsuta* Berner, and *soquele* Day.

The subgeneric name is formed from the diminutive of the type species.

Subgenus **Dannella**, new subgenus

Type species: *simplex* McDunnough.

Only two North American species are placed

in this subgenus at the present time, *simplex* McDunnough and *lita* Burks.

Because the diminutive of the name of the type species of this group is preoccupied, I have made the name from the diminutive of the middle name of Benjamin Dann Walsh, author of the genus *Ephemerella*. In this I am following the practice used by J. G. Needham in naming *Drunella* for Theodore Dru Allison Cockerell.

Subgenus **Eurylophella** Tiensuu

1935 Tiensuu, Ann. Ent. Fennici 1: 20; type species: *karelica* Tiensuu. (? = *Melanameletus* Tiensuu 1935, op. cit. 15; type species: *brunnescens* Tiensuu.)

The type species of this subgenus, *karelica* Tiensuu, appears to be a typical member of the same complex as the North American *bicolor*-group except for a single feature of the nymph. The North American species have no maxillary palpi, but these structures are present in *E. karelica*.

When the adult is known, the relationship of *E. karelica* to the other species might be clarified. The presence or absence of maxillary palpi does not in and of itself seem to provide adequate reason for recognizing two subgenera.

Besides the Finnish species *karelica* Tiensuu (? = *brunnescens* Tiensuu), the North American species of the subgenus are *aestiva* McDunnough, *bicolor* Clemens, *bicoloroides* McDunnough, *coxalis* McDunnough, *doris* Traver, *funeralis* McDunnough, *lodi* Mayo, *lutulenta* Clemens (= *lineata* Clemens), *minimella* McDunnough, *prudentialis* McDunnough, *temporalis* McDunnough, *trilineata* Berner and *verisimilis* McDunnough.

Subgenus **Timpanoga** Needham

1927 Needham, Ann. Ent. Soc. America 20: 108; type species: *hecuba* Eaton.

Only the single species *E. hecuba* with two subspecies, *E. h. hecuba* and *E. h. pacifica* Allen and Edmunds, is assigned to this subgenus.

UNASSIGNED SPECIES

Although all the North American species have been assigned to subgenus except for three *nomina dubia* (*consimilis* Walsh, *quebecensis* Provancher, and *unicornis* Needham), I feel that specimens of many Eurasian species must be examined before they can be placed. This is true even of some species which have been placed provisionally in subgenera.

The species which I leave unassigned are *atagosana* Imanishi, *elongatula* McLachlan, *gracilis* Tshernova, *hispanica* Eaton, *lenoki* Tshernova, *longipes* Tshernova, *nigra* Ueno, *rufa* Imanishi, *sachalinensis* Matsumura, *sinensis* Hsu, *submontanus* Brodsky, *taeniata* Tshernova, and *thymalli* Tshernova.

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KEYS TO THE SUBGENERA

Male Imagoes

1. Lateral cerci one-fourth to three-fourths as long as the median terminal filament. **Caudatella**
2. Cerci subequal in length to the terminal filament. **Attenuatella**
3. Terminal segment of genital forceps six times as long as broad; penes slender (fig. 1) **Attenuatella**
4. Terminal segment of genital forceps less than four times as long as broad, penes variable (figs. 2-9) **Attenuatella**
5. Terminal segment of genital forceps more than twice as long as broad (figs. 2-3) **Attenuatella**
6. Terminal segment of genital forceps less than twice as long as broad (figs. 4-9) **Attenuatella**
7. Inner margin of long segment of genital forceps distinctly incurved or strongly bowed (fig. 2) **Drunella**
8. Inner margin of long segment of genital forceps nearly straight or gently incurved, sharply incurved at apex (fig. 3) **Torleya**
9. Vestigial nymphal gills retained on abdominal segments 4-7; well developed posterolateral projections on segments 8-9, genitalia as in fig. 4 **Timpanoga**
10. Vestiges of nymphal gills wanting; posterolateral projections poorly developed or wanting, genitalia variable **Timpanoga**
11. Penes without dorsal or ventral spines, apical notch shallow; penes distinctly narrower at apex than at base (fig. 5) **Eurylophella**
12. Penes not as above, either with dorsal or ventral spines or subapical tubercles, apical notch deep or penes as wide or wider at apex than at base **Eurylophella**
13. Lateral apical margins of penes project apically as distinct processes or lobes; dorsal or ventral spines may be present (figs. 6-7) **Ephemerella**
14. Penes without such projecting lobes apically; without such spines except that a subapical, lateral tubercle may be present on each lobe (figs. 8-9) **Ephemerella**
15. Penis lobes usually bearing a subapical, lateral tubercle on lobe; if tubercles lacking, no tubercle present between forceps bases (fig. 8) **Serratella**
16. Penis lobes without such tubercles on lobe; a tubercle present between forceps bases (fig. 9) **Dannella**

Nymphs

1. Gills present on abdominal segments 3-7 **2**
2. Gills wanting on segment three, present on 4-7 only, a rudimentary gill often present on segment 1 **6**
3. The lateral cerci one-fourth to three-fourths as long as the median terminal filament. **Caudatella**
4. The cerci subequal in length to the terminal filament **3**
5. Distinct tubercles and/or spines usually present on anterior margin of the fore femur, if absent the abdomen with an adhesive disc of hairs ventrally, or head, thorax and abdomen with distinct paired dorsal spines **Drunella**
6. Distinct tubercles or spines absent on anterior margin of the fore femur, abdomen without a ventral adhesive disc, paired dorsal spines lacking on either head, thorax, or abdomen **4**

7. A whorl of spines or hair-like spines at the joinings of the segments of caudal filaments; no fringe of hairs along the lateral edges of caudal filaments. **5**
8. Whorls of spines or hair-like spines absent, present only at base, or if extending to the apex of the caudal filaments a fringe of hairs present along the lateral edges, at least in the apical third **Ephemerella** s.s.
9. Gills on tergite 3 semioperculate; only the first three pairs of gills visible; without paired dorsal abdominal spines **Torleya**
10. Gills on tergite 3 not as above, the gills imbricate; four or five pairs of gills visible; paired dorsal abdominal spines present in most species. **Serratella**
11. The apex of each femur terminating in a sharp spine; nymph very broad and flat, abdominal segment 5 at least two-thirds as broad as abdomen is long **Timpanoga**
12. Apex of each femur without such a spine; nymph variable in form, but fifth segment less than half as broad as abdomen is long **7**
13. Abdominal segment 9 distinctly longer than 8; maxillary palpi wanting (except in *E. karelica* of Finland) **Eurylophella**
14. Abdominal segment 9 not longer than 8, maxillary palpi present **8**
15. Abdominal tergites 1 or 2 to 9 with paired dorsal spines or tubercles; tarsal claws with denticles **Attenuatella**
16. Abdominal tergites without paired dorsal spines or tubercles; tarsal claws without denticles **Dannella**

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