

Phylogenetics and the classification of the *Timpanoga* complex (Ephemeroptera:Ephemerellidae)

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Abstract. The *Timpanoga* complex is a holophyletic group of mayflies in the subfamily Ephemerellinae consisting of 21, mostly North American species, distinguished by the absence of lamellate gills on abdominal segment 3 in the larvae, and associated absence of the gill socket remnants in subimagos and adults. A phylogenetic reclassification is proposed, based on a cladistic analysis, and is an example of reclassification necessary in much of the Ephemeroptera. Of the options available for generic classification, the one proposed is both informative in terms of expressing diversity within the complex and practical in terms of allowing morphological differentiation in all life stages, including both sexes of alate stages. Three main sequential lineages are recognized as the genera *Attenella*, *Eurylophella*, and *Timpanoga* [= *Dannella* n. syn.]. The two main phylogenetic branches in *Eurylophella* are treated as subgenera *Dentatella* and *Eurylophella* s.s. The two main phylogenetic branches of *Timpanoga* are treated as subgenera *Dannella* and *Timpanoga* s.s. A key to known stages of genera and subgenera incorporates newly discovered characteristics of gill socket and postero-lateral projection remnants in adults and subimagos, and polar cap characteristics of eggs. A cladogram of the four species of *Attenella* indicates that *A. soquele* and *A. attenuata* are sister species commonly derived with a sister branch represented by *A. margarita*, and that these three species represent a sister group of *A. delantala*.

Key words: *Timpanoga* complex, Ephemerellidae, cladistics, phylogenetic reclassification, *Attenella*, *Eurylophella*, *Timpanoga*.

The mayfly group, or taxon, we refer to as the *Timpanoga* complex includes species that have been classified in the genus *Ephemerella* Walsh (subgenera *Timpanoga* Needham, *Eurylophella* Tiensuu, *Attenella* Edmunds [originally as *Attenuatella*], and *Dannella* Edmunds), or more recently in the genera *Timpanoga*, *Eurylophella*, *Attenella*, and *Dannella*. Revisions of *Timpanoga* (Allen and Edmunds 1959), *Eurylophella* (Allen and Edmunds 1963), *Attenella* (Allen and Edmunds 1961), and *Dannella* (Allen and Edmunds 1962) provided species-level interpretations that have remained remarkably stable. Currently, 21 species (19 North American, 2 European) are placed in this complex. Furthermore, only two new species belonging to this group have been described (Allen 1977, McCafferty 1977), and only two names have fallen to synonymy (Berner 1984), since the revisionary studies of Allen and Edmunds.

McCafferty (1977) showed that the *Timpanoga* complex was a monophyletic group defined by the unique synapomorphic loss of the gill pair on abdominal segment 3 (larvae having lamellate gills only on segments 4-7). Allen (1984) recognized this taxon as the subtribe Timpanogae of the tribe Ephemerellini (Ephemerellidae: Ephemerellinae). Divisions and rankings of

higher taxa within the family Ephemerellidae (see Hubbard 1990) have not been phylogenetic, but instead have had only a roughly defined, phenetic basis. For this reason recognition of the *Timpanoga* complex as a subtribe or any other hierarchical category remains tenuous until phylogenetic studies of the pannote mayflies are completed. Such phylogenetic revisions of Ephemeroptera are in keeping with the philosophy and techniques elaborated by McCafferty (1991).

Edmunds (1959) divided the genus *Ephemerella* into several subgenera, including those of the *Timpanoga* complex cited above. McCafferty (1977) showed that each of these *Timpanoga* complex subgenera was monophyletic and also deduced their phylogenetic relationships cladistically based on several larval and adult characters. Allen (1977) described a new species, *Ephemerella bartoni*, in the *Timpanoga* complex and placed it in the subgenus *Dannella*. McCafferty (1978) showed that *E. bartoni*, despite some superficial resemblance to *Dannella* based on symplesiomorphies, had none of the apomorphies found in the lineage leading to *Dannella*, but instead had apomorphies common to the opposite lineage leading to the *Eurylophella*. Allen (1980) raised the *Timpanoga* complex sub-

genera to the rank of genus, and they have generally been recognized as such since that time. Allen (1980) also redefined *Dannella* so that it would continue to include *bartoni*, and he erected the subgenus *Dentatella* for *bartoni*. Allen's revised concept of *Dannella*, however, is apparently polyphyletic as will be shown below.

Historically, generic classifications of Ephemeroptera have been proposed on the basis of little or no phylogenetic information and have often incorporated certain "gap" criteria, as proposed, for example, by Edmunds (1962). McCafferty (1991) thoroughly discussed this method and its inherent limitations in expressing phylogenetic relationships. The increase in nominal genera of already known taxa of Ephemerelellidae (Allen 1980) has been paralleled somewhat in Baetidae (e.g., Waltz and McCafferty 1987) and Heptageniidae (e.g., Flowers 1980). Other recent treatments of Baetidae (Novikova and Kluge 1987) and Heptageniidae (Kluge 1988) have resulted in extreme lumping of genera. We mention this because such disparities among classificatory interpretations are often a concern to the users of taxonomy, and thus they require prompt and practical resolution. Arguments over splitting or lumping of genera, however, are moot if phylogeny has not been detailed. In the case of Ephemerelellinae, we intend to offer at least a partial resolution of the classification issue here. In the case of Baetidae and Heptageniidae, phylogenetic data remain inconclusive; however, it appears that splitting into groups to express the monophyletic nature of those groups is provisionally preferable to lumping of such groups solely because they apparently lack character "gaps" in one of their life stages.

The relatively straightforward phylogeny of the *Timpanoga* complex provides the necessary basis, and thus an excellent opportunity, for formulating a phylogenetic generic classification. The main purpose of this study therefore, is to re-evaluate the present superspecific classification of the species of the *Timpanoga* complex in light of this phylogeny and to revise the classification as necessary. The cladogram is to a large extent deduced from characters that have been discussed previously by McCafferty (1977, 1978) but not presented in strict cladistic fashion as here. In addition, we provide a first stage-associated diagnostic key to the known

life stages of all higher taxa of the *Timpanoga* complex, incorporating some newly discovered characteristics of adults, subimagos, and eggs. We also cladistically analyze the interspecific relationships of *Attenella* for the first time.

Methods

Eighteen of the 19 nominal North American species of the *Timpanoga* complex were examined for comparative morphological characters (see details in Material examined section, below). In the few cases where known stages of species were not available to us, we relied on published descriptions. Voucher specimens are in the Purdue Entomological Research Collection, West Lafayette, Indiana.

Standard cladistic methods (including the determination of character polarity by the outgroup method, the inference of common ancestry by common possession of derived character states, and the resolution of possible conflicting data by parsimony) are essentially after Hennig (1966), Ross (1974), and Wiley (1981). Because of relatively low numbers of operational taxonomic units (OTUs) analyzed and characters used, no computer-aided analytical programs were necessary for generating branching sequences. Outgroups are explained under the phylogeny sections, below.

Material examined

The following is a short-form accounting of the species (listed alphabetically), life stages (a = adult, e = egg, l = larva), and geographic regions (abbreviated) represented by the material we were able to examine for this study. Note that generic classification of species are after the revision proposed here. More detailed information regarding this material is available from us upon request. *A. attenuata*: 1, a, e, AR, GA, MA, PA, VA; *A. delantala*: 1, CA; *A. margarita*: 1, ID; *A. soquele*: 1, CA; *Ephemerelella maculata*: a, e, CA; *Eurylophella aestiva*: 1, AR, IN; *E. bartoni*: 1, ON; *E. bicolor*: 1, a, e, GA, IN, ME, NC, ON, SC, TN; *E. coxalis*: 1, IN, NC; *E. funeralis*: 1, a, e, AR, GA, IN, MA, MD; *E. lodi*: 1, WA; *E. lutulenta*: 1, GA, ON, MI, NC, TN; *E. prudentialis*: 1, a, e, ME, MA, NC, NS, PQ, SC; *E. temporalis*: 1, a, e, GA, IN, KY, ME, NC, NH, VT; *E. verisimilis*: 1, a, e, MA, ME, NS, SC; *T. hecuba*: 1, a, AZ, BC, MT;

T. lita: 1, a, e, IN, NC, WI; *T. provonshai*: 1, AR; *T. simplex*: 1, a, e, IN, MA, MI, NB, VA, WI. Numerous outgroup genera and species representatives were also studied in general but are not elaborated here.

Diagnosis of the *Timpanoga* complex

As stated above, the taxonomic rank of the *Timpanoga* complex is dubious until its relative position among the pannote mayflies is known. Allen (1984) evidently believed that the adults of the complex could not be distinguished as a group since he placed the taxon as a subtribe, stating in that same paper that subtribes should be groups recognizable in one life stage but not the other, as per the same philosophy and reasoning he applied in naming subgenera. Such hierarchical limitations are subjective and artificial because they incorporate a gap criterion. Nevertheless, the basis for recognizing the taxon, regardless of its rank, involves an important apomorphic character state of the larval stage that defines the taxon as a natural grouping and is evident in the alate stages as well.

Larvae of the *Timpanoga* complex lack gills on abdominal segment 3 (Figs. 2–4, 15–17). We have discovered that adults and subimagos retain a clear indication of the distribution of the lamellate gills that were present on the larval abdomen. In Ephemerellinae adults and subimagos, remnants of *gill sockets* are recognizable as cuticular excavations posterolaterally on abdominal terga (Figs. 5, 7, 9) where gills occurred in the larvae. Therefore adults and subimagos of the *Timpanoga* complex can be differentiated from other Ephemerellinae by their lack of gill socket remnants on abdominal segment 3.

Edmunds (1959) and Allen and Edmunds (1959) characterized adults of the subgenus *Timpanoga* as having vestiges of larval gills on abdominal segments 4–7. We have found that these structures are actually small fingerlike remnants of the well-developed abdominal posterolateral projections of the larva (Figs. 6, 8). McCafferty (1977), in comparing the adult stage of species of the subgenus *Dannella*, found these structures in additional species and showed them to be somewhat variable in size between species. Because these structures do not originate from the gill socket remnants, it is clear they are not gill vestiges. Although these pro-

jections are distinct on adult segments 4–7 on some species (Figs. 6, 8); they are poorly developed on other species (Fig. 10), being barely discernible on segments 6 and 7.

Smith (1935) was the first to describe eggs of any species of the *Timpanoga* complex (considered species of *Ephemerella* at that time). He noted that eggs of *Attenella attenuata* possessed a single polar cap, were ovoid, and had a somewhat smooth chorion. He noted that eggs of *Eurylophella prudentalis*, *E. temporalis*, and *E. verisimilis* lacked a polar cap, were somewhat "dumbbell" shaped, and had a reticulate chorion. He noted that eggs of *Timpanoga hecuba* possessed a single polar cap, were ovoid, and had a reticulate chorion. We can corroborate the descriptions of *Eurylophella* eggs given by Smith (1935), and additionally have found this type of egg in other species of *Eurylophella*. We cannot corroborate Smith's description of *Attenella* eggs, however, because eggs we studied of *A. attenuata* lack the polar cap. We have not seen eggs of *T. hecuba*, but we have examined eggs of two species that have variously been known as the genus or subgenus *Dannella*, and these possess two polar caps (one at each end), are ovoid, and have reticulate chorions.

It is now clear that the eggs of the *Timpanoga* complex demonstrate considerable variation and that the taxon cannot be differentiated from other Ephemerellinae on the basis of a single egg characteristic. Eggs of different lineages of the complex, however, may be differentiated from other Ephemerellinae. For example, the absence of any polar cap in a number of species and the presence of two polar caps in a few others, which we are reporting for the first time here, may be unique egg characteristics among the Ephemerellinae. With respect to the absence of polar caps in Ephemerellinae, Smith (1935) noted that *Ephemerella maculata* (not a member of the *Timpanoga* complex) atypically lacked a polar cap. Our examination of eggs of this species, on the contrary, revealed a small single polar cap.

Phylogeny of species groups

Our OTUs for cladistic analysis consisted of five, at least somewhat distinctive, groupings of species, each of which have been shown to be monophyletic (see McCafferty 1977, 1978).

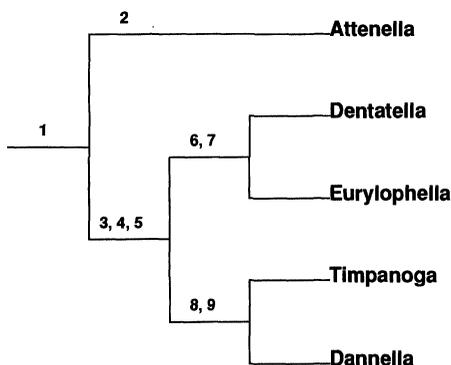


FIG. 1. Cladogram of species groups of the *Timpanoga* complex (see text for explanations of OTUs, and see Table 1 for numbered apomorphies).

These OTUs may be conveniently indicated by superspecific names with which they have been associated in the past, without assuming any particular superspecific classification or biasing classificatory revision. Thus, the OTUs are designated "Attenella" (species: *attenuata*, *delantala*, *margarita*, *soquele*); "Dannella" (species: *lita*, *provonshai*, *simplex*); "Dentatella" (species: *bartoni*); "Eurylophella" (species: *aestiva*, *bicolor*, *coxalis*, *funeralis*, *karelica*, *lithuanica*, *lodi*, *lutulenta*, *minimella*, *prudentialis*, *temporalis*, *verisimilis*); and "Timpanoga" (species: *hecuba*).

The cladogram of these OTUs is given in Figure 1, and the synapomorphies that define the common ancestry of lineages are given in Table 1. The only autapomorphy we have indicated is for the "Attenella" lineage, whose species relationships are additionally considered below. The outgroup used for establishing character state polarities included all Ephemerellinae other than the *Timpanoga* complex; the plesiomorphies deduced from the outgroup are also shown in Table 1. McCafferty (1977, 1978) gave a complete discussion of polarities of most character states used here. Adult and subimago remnant characters associated with larval characters are not counted as separate characters for cladistics; these are bracketed and listed with their associated, numbered larval character in Table 1. Character states are illustrated in Figures 2-17 and cited in Table 1.

Egg characters were not used in deducing the cladogram for three reasons. First, eggs of a number of species are not known or have not been described adequately. Second, as noted above, there are some inconsistencies with re-

spect to independent observations of egg structure, and thus further study is necessary to sort out possible intraspecific variability from erroneous observations. Third and perhaps most significant, as pointed by Bae and McCafferty (1991), egg morphology in Ephemeroptera appears to be highly subject to convergence, and thus of limited use in phylogeny reconstruction. This becomes apparent in the *Timpanoga* complex if known egg morphology is overlaid on the cladogram. Considering that the egg of the outgroup possessed one polar cap, the immediate common ancestor of the complex must have lost the polar cap (a character state found in the "Attenella" lineage and the "Eurylophella" branch of the opposite lineage). Because a two-cap and one-cap condition is found in the relatively apotypic "Dannella" and "Timpanoga" branches of the "Timpanoga-Dannella" lineage, opposite the "Eurylophella-Dentatella" lineage, one must conclude that polar caps not only reappeared but they did so as two distinct and possibly independent variations. Eggs of the "Dentatella" branch are unknown, and although the cladogram predicts that they will lack polar caps as do the eggs of the "Eurylophella" branch of the same lineage, we would not be surprised to find any of the highly mutable states of this character.

Chorionic surfaces of Ephemeroptera eggs often vary even among closely related species. For example, the symmorphous sister species of North American *Ephoron* (Polymitarciidae) are distinguished by highly dimorphic egg chorion sculpturing (Koss 1968). Ironically, in the case of the *Timpanoga* complex, based on the presence of somewhat smooth chorion in the outgroup, the entire "Dentatella-Eurylophella-Dannella-Timpanoga" clade apparently possesses a synapomorphic reticulate chorion. Otherwise, this character state shows up innumerable times as a plesiomorphy or apomorphy in the Ephemeroptera, and should not always be assumed to be reliable for formulating cladograms.

Classification of the species groups

Adherence to a strict phylogenetic classification method (e.g., see Wiley 1981), but allowing for sequencing conventions (Nelson 1972, 1973) as suggested by McCafferty (1991), generates a number of alternative arrangements

TABLE 1. Character states used to formulate the cladogram of the *Timpanoga* complex. Numbers of apomorphies appear at their occurrence on the cladogram (Fig. 1). Character states asterisked represent a multiple-state phenocline.

Apomorphy	Plesiomorphy
1 = Larval gills on third abdominal segment lost (Figs. 2-4, 15-17). [Adult and subimaginal gill socket remnants on third abdominal segment lost (Figs. 5-10).]	- Lamellate gills on abdominal segments 3-7. [Gill socket remnants present on third abdominal segment.]
2 = Male adults with third segment of genital forceps elongated (Fig. 11).	- Third segment of genital forceps short (Fig. 12).
3 = *Larval gills on abdominal segment 4 relatively enlarged (covering much of remaining gill lamellae) (Figs. 2, 3). [Adult and subimaginal gill socket remnant on abdominal segment 4 relatively large (Figs. 5, 7).]	- *Gills 4 not larger than others (Figs. 4, 15-17). [Gill socket remnants on abdominal segment 4 relatively small (Fig. 9).]
4 = Larval posterolateral projections of abdominal segments 4-9 enlarged (Figs. 2, 3). [Adult and subimaginal fingerlike posterolateral projection remnants well developed (Figs. 6, 8).]	- Posterolateral projections only moderately extended (Figs. 4, 15-17). [Fingerlike posterolateral projection remnants only poorly developed on abdomen (Fig. 10).]
5 = Larval posterolateral projections with setaceous margins (Figs. 2, 3).	- Lateral setae short and sparse (Figs. 4, 15-17).
6 = Larval maxillary palpi lost.	- Maxillary palps present.
7 = *Larval lamellate gills on abdominal segment 4 operculate (other gill lamellae usually not exposed) (Fig. 2).	- *Gills on segment 4 semi-operculate (Fig. 3).
8 = Larval medial maxillary setae sparse (5 or less).	- Maxillae generally with many setae medially.
9 = Larval claw denticles lost.	- Claw denticles present.

based on the cladogram (Fig. 1). Obviously, the entire *Timpanoga* complex could be considered a single genus. The two primary lineages (the "Attenella" lineage and the "Dentatella-Eurylophella-Timpanoga-Dannella" lineage) could each be considered a genus. By using a sequencing convention, three genera could also be designated, representing the "Attenella" lineage, the "Eurylophella-Dentatella" lineage, and the "Timpanoga-Dannella" lineage. Technically, sequencing would also allow a four-genera arrangement, representing the "Attenella" lineage along with either the "Eurylophella-Dentatella" lineage, the "Timpanoga" branch of the "Timpanoga-Dannella" lineage, and the "Dannella" branch of the "Timpanoga-Dannella" lineage, or the "Timpanoga-Dannella" lineage, the "Dentatella" branch of the "Eurylophella-Dentatella" lineage, and the "Eurylophella" branch of the "Eurylophella-Dentatella" lineage. Classification into five genera is not an allowable option unless the two basal dichotomous lineages within the complex are also de-

lineated at some supergeneric level, which is not now possible.

We do not find either of the four-genera classifications advisable at this time because there are insufficient grounds for choosing between them. One of the lineages somewhat arbitrarily would have to be considered a genus group while the branches of the opposite lineage would be considered two genera. The degree of difference between branches of either lineage does not appear sufficient to favor either one for splitting, and adults of the "Dentatella" branch remain unknown. In this case, the sequencing convention actually presents a dilemma rather than obviating a classificatory complication.

Given the three remaining alternatives, secondary criteria may be employed for choosing among them because they each satisfy all requirements for phylogenetic classification. Secondary criteria could, for example, include considerations of practicality in terms of taxon distinctiveness, or tradition in terms of select-

TABLE 2. Classification of the *Timpanoga* complex.

Genus <i>Attenella</i> Edmunds, 1959
<i>Attenella delantala</i> (Mayo), 1952
<i>Attenella attenuata</i> (McDunnough), 1925
<i>Attenella margarita</i> (Needham), 1927
<i>Attenella soquele</i> (Day), 1954
Genus <i>Timpanoga</i> Needham, 1927 [= <i>Dannella</i> Edmunds, n. syn.]
Subgenus <i>Dannella</i> Edmunds, 1959
<i>Timpanoga lita</i> (Burks), 1949 n. comb.
<i>Timpanoga provonshai</i> (McCafferty), 1977 n. comb.
<i>Timpanoga simplex</i> (McDunnough), 1925 n. comb.
Subgenus <i>Timpanoga</i> s.s.
<i>Timpanoga hecuba</i> (Eaton), 1884
Genus <i>Eurylophella</i> Tiensuu, 1935
Subgenus <i>Dentatella</i> Allen, 1980
<i>Eurylophella bartoni</i> (Allen), 1977 n. comb.
Subgenus <i>Eurylophella</i> s.s.
<i>Eurylophella aestiva</i> (McDunnough), 1931
<i>Eurylophella bicolor</i> (Clemens), 1913
<i>Eurylophella coxalis</i> (McDunnough), 1926
<i>Eurylophella funeralis</i> (McDunnough), 1925
<i>Eurylophella lodi</i> (Mayo), 1952
<i>Eurylophella karelica</i> Tiensuu, 1935
<i>Eurylophella lithuanica</i> (Kazlauskas), 1959
<i>Eurylophella lutulenta</i> (Clemens), 1913
<i>Eurylophella minimella</i> (McDunnough), 1931
<i>Eurylophella prudentalis</i> (McDunnough), 1931
<i>Eurylophella temporalis</i> (McDunnough), 1924
<i>Eurylophella verisimilis</i> (McDunnough), 1930

ing a system requiring the least necessary revision. None of the classificatory alternatives would entirely satisfy a secondary criterion of tradition because, up until about 14 years ago, North American species of the *Timpanoga* complex were known as *Ephemerella*, and thus none of the names that would apply (*Timpanoga* for one genus, *Timpanoga* and *Attenella* for two genera; or *Timpanoga*, *Attenella*, and *Eurylophella* for three genera) have much of a tradition as generic names. All appeared only as subgeneric names in the last complete compendium of North American mayfly species (Edmunds et al. 1976). Nonetheless, of the three alternatives, the three-genera system comes the closest to satisfying a tradition criterion.

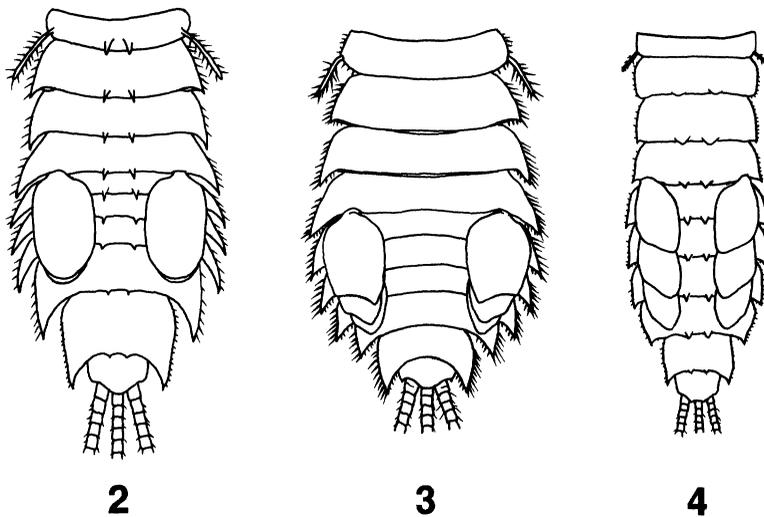
Depending on one's point of view, each of the alternatives could be deemed more practical. However, whereas a single genus, which would be equivalent to the entire *Timpanoga* complex as discussed above, would be easy to

differentiate, no additional taxonomic information about the diversity within the group would be rendered by the generic nomenclature in a one-genus system. Although it could be argued that subgeneric delineation would satisfy this lack of information content, it should be remembered that it is the generic nomen that is incorporated in the binomial species name and thus carries inherent information with it. Recognition of two genera, *Attenella* and *Timpanoga*, might result in groups easily identifiable in all life stages and sexes (adults of the "Dentatella" branch remain unknown), but again the classification would not relay information about the considerable diversity of the "Eurylophella-Dentatella-Timpanoga-Dannella" lineage. Besides this, a two-genera system would be less traditional than the three-genera system, as mentioned above.

We are thus recognizing three genera in the *Timpanoga* complex (Table 2). This classification imparts considerable diversity information via the resultant species binomials but at the same time results in generic concepts applicable to larvae, male subimagos and adults, and female subimagos and adults when eggs are available (see key, below). Most importantly, it sequentially denotes the three major clades of the *Timpanoga* complex (Fig. 1) while conserving the name *Eurylophella*, in which the majority of species reside. In doing this, we synonymize *Dannella* with the genus *Timpanoga*.

If the adults of the "Dentatella" branch of the "Eurylophella-Dentatella" lineage (Fig. 1) should prove to be highly distinctive from the "Eurylophella" branch, for example, by retaining a number of the plesiomorphic character states that have become modified in the latter branch, then a future modification of the three-genera system to a four-genera system would be within the realm of possibility while still maintaining a phylogenetic arrangement, as discussed above.

Subgenera have often been used in the classification of the Ephemerellidae; however, they have been only arbitrarily defined in the past. To show the next level of phylogenetic branching (Fig. 1), we are further subordinating the classification of the *Timpanoga* complex by recognizing the two distinctive, base phylogenetic branches both within the genus *Eurylophella* (the "Eurylophella" branch and "Dentatella" branch of the "Eurylophella-Dentatella" lineage) and



FIGS. 2-4. Larvae, dorsal abdomen. 2.—*Eurylophella* (*E.*) *funeralis*. 3.—*Timpanoga* (*Dannella*) *lita*. 4.—*Attenella margarita*.

within the genus *Timpanoga* (the "Timpanoga" branch and "Dannella" branch of the "Timpanoga-Dannella" lineage) as subgenera.

The complete new phylogenetic classification of the *Timpanoga* complex species is shown in Table 2. Status changes, new synonyms, and new combinations are also formally given in Table 2.

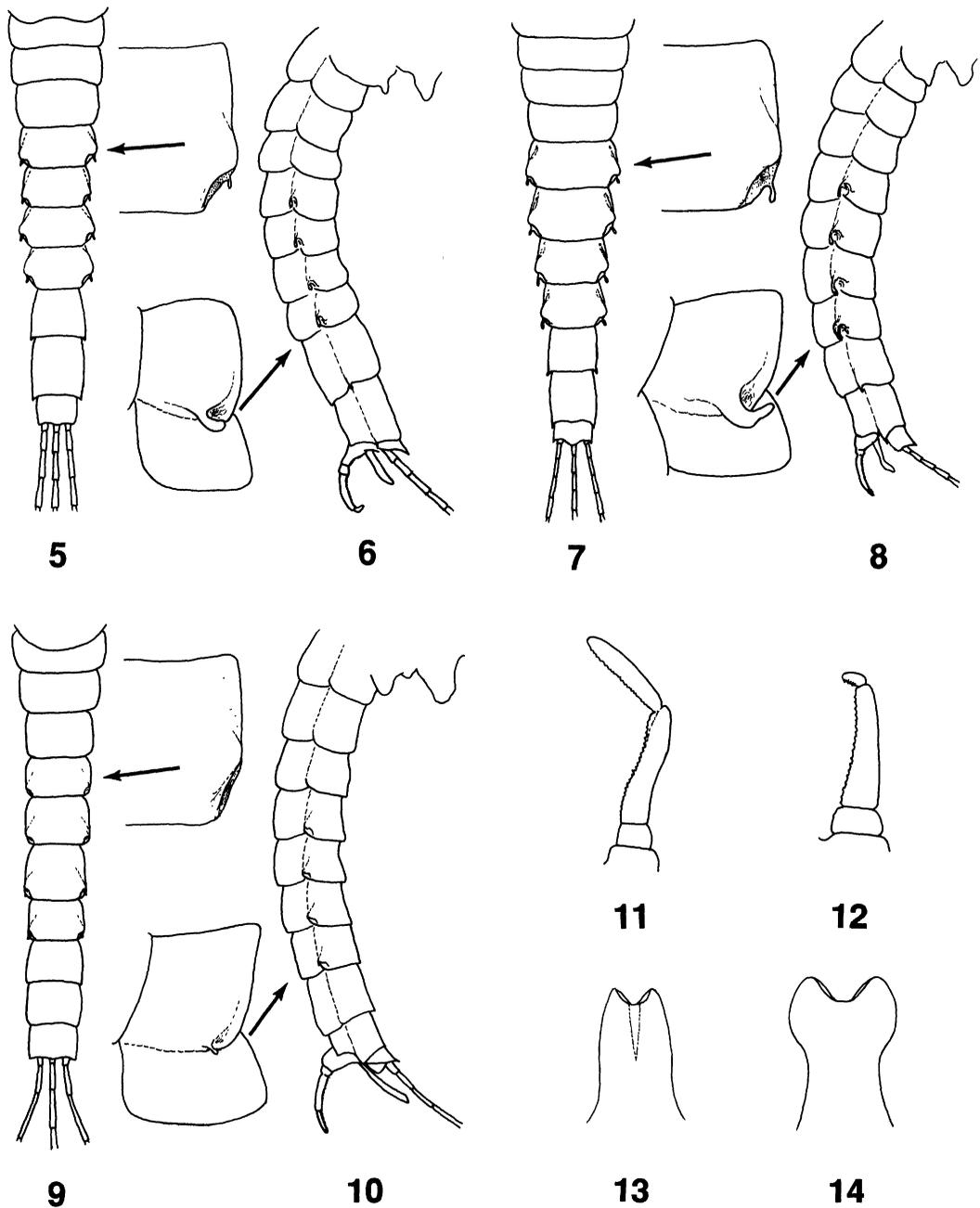
Among the Ephemerellidae of North America and Europe, the species groups of the *Timpanoga* complex may be recognized by using the following key.

**Key to the *Timpanoga* complex,
its genera, and subgenera**

- 1 Larva (Figs. 2-4) without gills on abdominal segment 3. Adult (Figs. 5, 7, 9) and subimago without gill socket remnants on abdominal segment 3. Egg without polar caps, having two polar caps; or if one polar cap present, then chorion reticulate. ***Timpanoga* complex, 2**
- 1' Larva with gills on abdominal segment 3. Adult and subimago with gill socket remnants on abdominal segment 3, although poorly developed in some. Egg with one polar cap and somewhat smooth chorion. **other Ephemerellinae**
- 2 Larva (Figs. 4, 15-17) with posterolateral projections on no more than two abdominal segments being longer than

midlengths of same segments; gill 4 not operculate (covering less than half of gill 5) and not reaching posterior margin of abdominal tergum 7. Adult and subimago with poorly developed fingerlike remnants of posterolateral projections on abdominal segments 6 and 7 (compare Fig. 10 with Figs. 6, 8); gill socket remnant on abdominal segment 4 relatively small (compare Fig. 9 with Figs. 5, 7). Male adult with terminal segment of genital forceps relatively elongate, as in Figure 11. Egg without polar caps and having somewhat smooth chorion. **genus *Attenella***

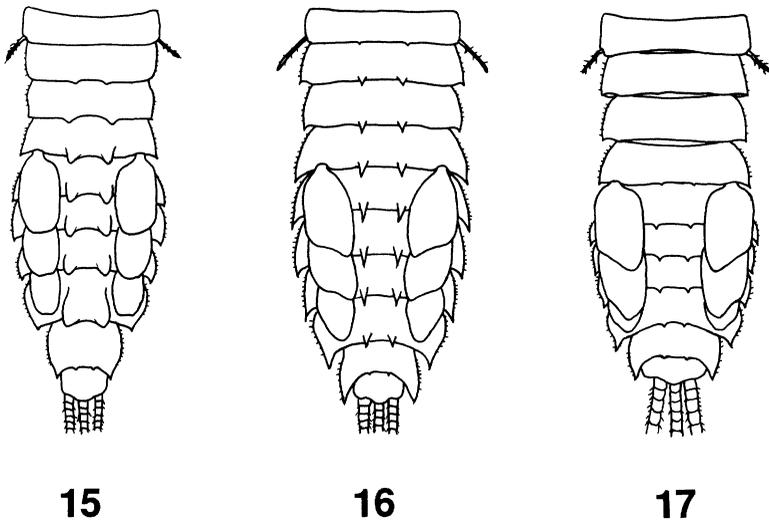
- 2' Larva (Figs. 2, 3) with three or more abdominal posterolateral projections longer than midlength of respective terga; gill 4 more-or-less operculate (covering more than half of gill 5) and reaching to about posterior margin of tergum 7 or beyond. Adult and subimago with at least abdominal segment 7, but often preceding segments also, with well-developed fingerlike remnants of posterolateral projections (Figs. 6, 8); gill socket remnant on abdominal segment 4 relatively well developed (compare Figs. 5, 7 with Fig. 9). Male adult (Fig. 12) with terminal segment of genital forceps relatively short (length always less than 3 × width). Egg with



FIGS. 5-14. Adults. 5-10: Abdomen. 5.—*Eurylophella* (*E.*) *prudentalis*, dorsal. 6.—*E. prudentalis*, lateral. 7.—*Timpanoga* (*T.*) *hecuba*, dorsal. 8.—*T. hecuba*, lateral. 9.—*Attenella attenuata*, dorsal. 10.—*A. attenuata*, lateral. 11, 12: Left ventral forceps, male. 11.—*A. attenuata*. 12.—*E. (E.) bicolor*. 13, 14: Ventral penes, male. 13.—*E. (E.) temporalis*. 14.—*T. (Dannella) simplex*.

reticulate chorion and with zero, one, or two polar caps. 3
 3 Larva with claw denticles; maxillae without palpi. Male adult of known species

with penes broadest at base, narrowing apically (Fig. 13). Female adult of known species with eggs without polar caps. **genus *Eurylophella*, 4**



FIGS. 15-17. Larvae, dorsal abdomen. 15.—*Attenella delantala*. 16.—*A. soquele*. 17.—*A. attenuata*.

- 3' Larva without claw denticles; maxillae with palpi. Male adult with penes laterally expanded apically, somewhat narrower basally (Fig. 14). Female adult with eggs having polar caps.
 **genus *Timpanoga*, 5**
- 4 Larva (Fig. 2) with abdominal tergum 9 relatively elongate (midlength ~1.4 × midlength of terga 8 or 10); operculate gills relatively narrow, ovate, and broadly rounded apically.
 **subgenus *Eurylophella* s.s.**
- 4' Larva with abdominal midlength of tergum 9 subequal to midlength of terga 8 or 10; operculate gills relatively broad (Allen 1977, fig. 3) but more narrowly rounded at apex (somewhat falcate) than shown in Allen's figure.
 **subgenus *Dentatella***
- 5 Larva (McCafferty 1977, fig. 6) with filamentous gills on abdominal segment 1 originating sublaterally on tergum; posterolateral abdominal processes extremely developed; paired dorsal abdominal tubercles present or rarely absent. **subgenus *Timpanoga* s.s.**
- 5' Larva (Fig. 3) with filamentous gills on abdominal segment 1 originating at approximately lateral margin of tergum; posterolateral abdominal processes not as extremely developed as above; paired dorsal abdominal tubercles absent.
 **subgenus *Dannella***

Species phylogeny

The phylogeny of the four species of *Timpanoga* was given by McCafferty (1977). The phylogeny of species of *Eurylophella*, the study of which is currently in progress, is not completely resolved at this time because the species taxonomy in this genus appears problematic. Funk et al. (1988) presented electrophoretic data from populations in far eastern North America suggesting that 15 rather than nine species may actually be represented there. We suggest that careful morphological comparisons are needed to corroborate the specific delimitation generated by such molecular data.

We have completed a cladistic analysis of the currently recognized species of *Attenella*. The results are given in Figure 18. Synapomorphies

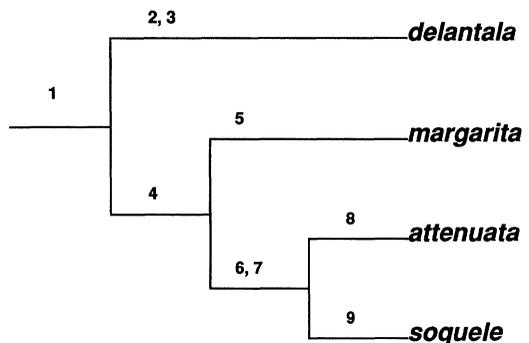


FIG. 18. Cladogram of *Attenella* species (see Table 3 for explanations of numbered apomorphies).

TABLE 3. Character states used to formulate the cladogram of *Attenella* species. Numbers of apomorphies appear at their occurrence on the cladogram (Fig. 15). Asterisked character states represent a multiple-state phenocline.

Apomorphy	Plesiomorphy
1 = Male adult with third segment of forceps elongated (Fig. 11).	– Third segment of forceps short (Fig. 12).
2 = Larva with broad, blunt dorsal abdominal tubercles (Fig. 15).	– Small dorsal abdominal tubercles (Figs. 2, 4, 15).
3 = Larva with lamellate gills somewhat truncate apically (Fig. 15).	– Gills slightly falcate to asymmetrically emarginate (Figs. 3–4, 16, 17).
4 = *Larva with small paired protuberances on pro- and mesonotum.	– *No paired protuberances on pro- and mesonotum.
5 = Larva with caudal filaments having broad, dark, medial transverse band.	– Caudal filaments variable but not medially banded.
6 = *Larva with dorsal thoracic protuberances well developed as tubercles.	– *Small paired protuberance on the pro- and mesonotum.
7 = Larva with abdominal posterolateral projections, especially of segment 8, elongated (Figs. 16, 17).	– Abdominal posterolateral projections only moderately extended (Figs. 4, 15).
8 = Female larvae with pair of dorsal tubercles on head.	– Female larva without pair of dorsal tubercles on head.
9 = Larva with dorsal abdominal tubercles sharp and elongated (Fig. 16).	– Small dorsal abdominal tubercles (Figs. 2, 4, 15).

and autapomorphies depicting ancestry of species in the cladogram are elaborated in Table 3. We have found no character state distributions among species that suggest any other arrangement at this time. Character state polarity was established using *Eurylophella* and *Timpanoga* as the major outgroup. Deduced plesiomorphies are also shown in Table 3. Phenoclines of characters with more than two progressive character states are distinguished in Table 3 with an asterisk. Most character states listed in Table 3 are illustrated in this paper.

As will undoubtedly be the case in other major lineages of Ephemereididae and perhaps other lineages of Pannota, there are some instances of homoplasy that require explanation. Characters that appear to be prone to such homoplasy include relative development of paired dorsal tubercles of the head, thorax, and abdomen. Based on the outgroup, these tubercles were not initially present on the head and thorax of this lineage, but they were developed on the abdomen similarly to those shown in Figures 4 and 17. It appears that in the lineage that includes *A. soquele*, *A. margarita*, and *A. attenuata* (Fig. 18) such tubercles became developed on the pronotum and mesonotum. In *A. attenuata* and *A. soquele*, they became much larger on the

thoracic nota, and in *A. attenuata* they additionally became developed on the dorsal head. Such tubercles are found variously in other lineages of Ephemereididae (e.g., *Drunella*). In the lineage represented by *A. delantala*, the abdominal tubercles became unusually broadened (Fig. 15), while in *A. soquele*, the abdominal tubercles became elongated (Fig. 16). In *Ephemereididae* species and other lineages of the *Timpanoga* complex (Fig. 1, Table 1), abdominal tubercles are also highly variable. For example, in some *Timpanoga* species, they are entirely lost on the abdomen (Fig. 3). Such character states may be adaptive, but we know virtually nothing regarding this possibility.

The new classification presented in Table 2 lists species of *Attenella* and *Timpanoga* according to their known phylogenetic relationships. The linear arrangement of species of *Eurylophella* s.s., however, remains alphabetical until interrelationships can be elucidated.

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