

Larva and Adult of *Teloganella* (Ephemeroptera: Pannota) and Assessment of Familial Classification

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Ann. Entomol. Soc. Am. 88(3): 324–327 (1995)

ABSTRACT The mayfly genus *Teloganella* Ulmer was originally described from a female subimago. Adults (both sexes) and larvae of *Teloganella* Ulmer collected in Malaysia form the basis of the first descriptions of the larva, adult, and egg of *T. umbrata* Ulmer and of the genus. Although *Teloganella* has historically been placed in the family Ephemerellidae and subfamily Teloganodinae, characteristics of larval forefemoral armature, male adult compound eyes, orientation of ICuA in the forewings, shape of adult tarsal segment 3, and male genitalia forceps segmentation strongly suggest placement in the family Tricorythidae, where it is classified here. Traditional ephemerellid characteristics of detached marginal venation in the forewings and the presence of dorsal abdominal tubercles in the larvae are found in *Teloganella* but are not reliable indicators of relationships. *Teloganella* is not placed in any subfamily because resolution of the exact phylogenetic relationships of subgroups in Ephemerellidae and Tricorythidae require further cladistic analysis.

KEY WORDS Ephemeroptera, *Teloganella*, classification

HIGHER CLASSIFICATION WITHIN the mayfly family Ephemerellidae has been considered by numerous Ephemeroptera workers (e.g., Lestage 1917; Tien-suu 1935; Traver 1935; Demoulin 1955; Edmunds 1959; Allen 1965, 1980, 1984; Tshernova 1972; McCafferty & Wang 1994). Nevertheless, critical problems in determining species relationships and generic limits remain unsolved because of species or supposed species groups that are unknown as either larvae or adults. The lack and misinterpretation of characters have made it difficult to corroborate certain superspecific taxa as monophyletic groupings. The genus *Teloganella* Ulmer is representative of such a problem.

Ulmer (1939) based his description of *Teloganella* on a female subimago taken from southern Sumatra. Not knowing the larval or male adult stage, Ulmer placed his genus in the family Ephemerellidae because it possessed detached marginal intercalary veins in the forewings. Unfortunately, Ulmer's description was necessarily incomplete for classificatory analysis, lacking characters of the adults (such as tarsal segment characteristics and male genitalia) and larvae (such as gill and femoral characteristics) that we now realize are crucial to resolving relationships and placement of pannote mayflies. Essentially, only the illustrated wing venation was available as a source of comparative data for *Teloganella*, although the species description of *Teloganella umbrata* Ulmer included distinctive size and color

pattern characteristics that would eventually allow association of unknown stages and sexes of the genus and species.

Allen (1965), based on the available incomplete data, further indicated a provisional placement of *Teloganella* in the subfamily Teloganodinae, family Ephemerellidae. Edmunds & Polhemus (1990) transferred *Teloganella* to the family Tricorythidae based on males and immatures seen from north Celebes, South India, Borneo, Sabah, and the Malay Peninsula. The basis for their reclassification was not given, and morphological information and detailed locality data were not provided at the time of publication. Peters & Peters (1993) stated that *Teloganella* "did not fit perfectly" into any family or subfamily and, therefore, returned the genus to Ephemerellidae (Teloganodinae). Their opinion was based on characteristics of the larvae and male adults that they interpreted as being more in agreement with those of Ephemerellidae. Again, no morphological data or other details were given.

The resolution of this issue should be based on complete comparative morphological data analyzed from a phylogenetic perspective. The ability to use the greatest number of comparative characters for deducing phylogenetic relationships ultimately depends on the association of larvae and adults. It is by such an association of stages and sexes of *Teloganella* and the resultant descriptions, detailed for the first time below, that we are able to suggest a substantiated resolution of the placement of *Teloganella* within the presently recognized familial classification of pannote mayflies.

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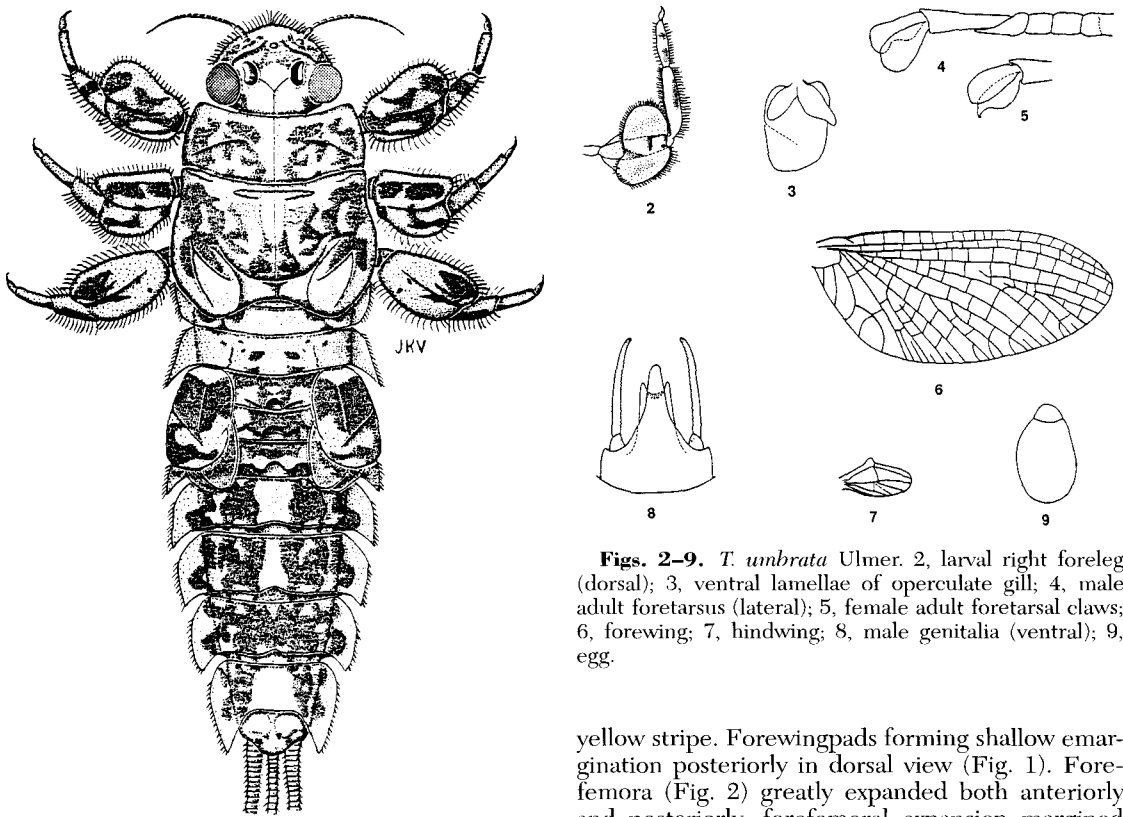
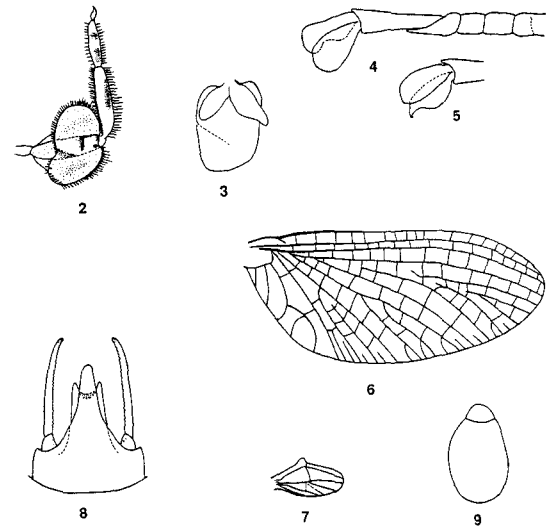


Fig. 1. *T. umbrata* Ulmer larva.

In 1978, G.F.E., along with Christine Edmunds, collected male and female adults of *T. umbrata* from Sabah, East Malaysia (both sexes match the original color pattern as well as wing venation description of Ulmer's female subimago). Among collections that G.F.E. provided to Purdue University was one larval specimen from Sabah collected in 1972 by W. M. Beck and one from West Malaysia collected by G.F.E. in 1978 that also match in color pattern. Furthermore, structures of the larval abdomen, including gills on segments 2–5 (large and operculate gill 2) match the position and size of the vestiges of these characters found in the adults. Finally, eggs taken from both the female adults and larvae are identical. Thus, it is clear to us that this material represents a correct association of stages and sexes of *Teloganella*, the descriptions of which follow.

***Teloganella umbrata* Ulmer**
(Figs. 1–9)

Larva. Body length 4.5–5.0 mm. Head without projections or tubercles; vertex with median longitudinal yellow stripe. Eyes widely separated. Maxillary palps absent. Labial palps small, with three segments; segment 3 poorly developed. Thoracic nota with continuous median longitudinal



Figs. 2–9. *T. umbrata* Ulmer. 2, larval right foreleg (dorsal); 3, ventral lamellae of operculate gill; 4, male adult foretarsus (lateral); 5, female adult foretarsal claws; 6, forewing; 7, hindwing; 8, male genitalia (ventral); 9, egg.

yellow stripe. Forewingpads forming shallow emargination posteriorly in dorsal view (Fig. 1). Forefemora (Fig. 2) greatly expanded both anteriorly and posteriorly; forefemoral expansion margined with row of well-developed spatulate and bristle-like setae as shown in Fig. 2. Mid- and hindfemora with posterior margin greatly expanded (Fig. 1). Tarsal claws without denticles. Abdomen (Fig. 1) with anterior terga with median longitudinal yellow stripe; dorsal color pattern changing in terga 6–10 as shown in Fig. 1. Terga 3–8 with paired small tubercles; terga 2–9 expanded laterally and with well-developed projections and hair-like setae. Gills present on segments 1–5; first pair of gills minute and vestigial; gills on segment 2 operculate (although tips of remaining gills exposed), more or less elongate-rectangular with truncate apices, nearly reaching tergum 6, and each with pair of elongate underlying lamellae (Fig. 3). Three caudal filaments present.

Male Adult. Body length 4.0–4.5 mm. Forewing length 4.0–4.5 mm; hindwing length 0.8–0.9 mm. Caudal filaments 9.0–10.0 mm. Eyes uniform in size, not subdivided into larger upper portion. Forefemora slightly twisted, subequal in length to foretibiae. Tarsal segments in order of decreasing length: 4-1-2-3, with venter of third foretarsal segment $2.0\text{--}3.0 \times$ length of dorsum (Fig. 4); mid- and hindtarsal segment 4 longer than total of first three segments, with venter of tarsal segment 3 more than $4.0 \times$ length of dorsum. Tarsal claws dissimilar on all legs, but appearing almost similar on forelegs (Fig. 4). Forewings (Fig. 6) with ICuA attached to CuP or detached basally, curving and terminating at approximate juncture of hind and

anal margin. CuP strongly curved and terminating at midpoint of anal margin. Marginal intercalaries arranged as in Fig. 6. Hindwings (Fig. 7) with broad costal projection medially. Abdomen with gill sockets clearly present on segments 2-5, with gill sockets 2 relatively large. Genital forceps (Fig. 8) two segmented, with basal segment very short. Penes (Fig. 8) concave apically, giving appearance of having two sharp apical projections. Three subequal caudal filaments present; each segment of caudal filaments with black bands alternately narrow and wide on segments of basal third of filaments, becoming uniform in width on segments of apical half of filaments.

Female Adult. Body length 4.5-5.0 mm. Forewing length 4.5-5.0 mm; hindwing length 0.9-1.0 mm. Caudal filaments 6.5-7.5 mm. Similar to male in wing venation, general leg segmentation traits, and color pattern described above, except abdomen slightly darker and pattern slightly less contrasting, and caudal filaments somewhat lighter. Claws distinctly dissimilar on all legs (Fig. 5). Posterolateral projections of abdominal segment 9 well developed. Subanal plate smoothly convex apically.

Egg. One polar cap present (Fig. 9).

Material Examined. Five male and three female adults, E. Malaysia, Sabah, Trib. of Moyog River, 11 mi E Panampung, Mile 17, IX-29-1978, G. F. and C. H. Edmunds. One male adult, E. Malaysia, Sabah, Moyog River, 3 mi E Panampung, IX-28-1978, G. F. and C. H. Edmunds. One larva, W. Malaysia, side pool of Selangor River, Mile 42, IX-13-1978, G. F. and C. H. Edmunds. One larva, E. Malaysia, Sabah, Moyog River, 3 mi W Panampung (NE Kota Kinabalu), ca. 300 m, VIII-18-1972, W. M. Beck. All of the above specimens are presently deposited in the Purdue Entomological Research Collection, West Lafayette, Indiana.

Discussion

Teloganella does possess certain characteristics that commonly have been associated with members of the Ephemerellidae, i. e., some detached marginal intercalaries in the forewings and the presence of dorsal abdominal tubercles or processes in the larva. However, *Teloganella* also possesses a number of characteristics that we associate with the Tricorythidae. These latter characteristics include the following: (1) larval forefemora with a row of well-developed broad, spatulate setae, (2) adult tarsi with the venter of segment 3 much longer than the dorsum, (3) compound eyes of male adult not divided into distinctive upper and lower portions, (4) cubital forewing venation in which ICuA is strongly recurved, and (5) male genitalia with an elongate terminal segment of the forceps (with no defined small third segment). We currently interpret all of the above, with the exception of the male eye character state, to represent apomorphies. Among the apomorphies, the loss of the

small terminal segment of the male forceps and the presence of spatulate setae on the larval forefemora are apparently subject to homoplasy, both in Pannota and other mayflies. Nevertheless, together the apomorphies, and in particular the adult tarsal and wing venation characters states, would appear to indicate a major (tricorythid) lineage within the Pannota, not including the Ephemerellidae.

Regarding the characteristics of *Teloganella* normally associated with Ephemerellidae, the possession of detached marginal intercalaries is repeated in numerous, sometimes unrelated lineages of Ephemeroptera, including the nonpannote mayfly taxa Baetidae and certain Ephemeroidea, and the pannotes Ephemerellidae, Baetiscidae, and *Ephemerythus* (Tricorythidae). The possession of dorsal abdominal tubercles in the larvae also is found in many lineages of Ephemeroptera, including Baetidae, Heptageniidae, Ephemerellidae, Tricorythidae, and Caenidae. These characteristics are obviously subject to homoplasy. It may be that they represent apomorphies that have arisen independently in Ephemerellidae and certain Tricorythidae, or it may be that they evolved in a common ancestor of the Ephemerellidae and Tricorythidae and subsequently have been retained in Ephemerellidae but lost in all but certain Tricorythidae and Leptohephidae. In any case, these characteristics do not outweigh the evidence given above for placing *Teloganella* in the Tricorythidae, not the Ephemerellidae or Teloganodinae.

Operculate gills are present in most Tricorythidae, but they are also present in Ephemerellidae, both on abdominal segment 2 (certain Teloganodinae) and abdominal segment 4 (certain *Timpanoga* complex). Their presence in *Teloganella*, therefore, does not give explicit evidence for placement in any family. The characteristic demonstrates a repeated trend in Pannota (see Caenidae and Neophemeridae also), but at this time we do not know the exact number of independent versus common derivations of the character state among the major lineages.

The condition of vein ICuA in the forewing of *Teloganella* varies on an individual basis between being attached basally to CuP, as we show in Fig. 6 to being detached basally, as shown by Ulmer's (1939) figure 82. We have also seen this latter variation among some of our alate specimens. This vein, however, is gradually curved in all of our specimens and not perfectly straight as shown by Ulmer. Any attempt to associate the attached or unattached variation with either Tricorythidae or Ephemerellidae would be untenable, based on the fact that it has been demonstrated to be individually variable. We do not know if the straight ICuA condition shown by Ulmer represents a variation or an incorrect drawing. We have found such slight differences between actual wing venation and Ulmer's drawings of such previously, for example, of

the single alate type specimen of *Melanemerella* described by Ulmer (1920).

The precise relationships of *Teloganella* within the tricorythid lineage is not known at this time; however, a cladistic evaluation of the phylogenetic relationships of the pannote mayflies is currently in progress. Furthermore, we cannot suggest a placement in any subfamily because we do not know if presently recognized subfamilies of Tricorythidae (see e.g., McCafferty & Edmunds 1979, Peters & Peters 1993) will continue to be recognized as such within the scheme of phylogenetic reclassification (as recommended by McCafferty [1991]), if some of them will require a change of rank, or perhaps will not warrant any supergeneric rank. Also, the phylogenetic positions and classifications of Teloganodinae and Melanemerellinae (both presently classified in Ephemerellidae) are problematic because they appear to be relatively primitive groups that possess some traditional characteristics of both Ephemerellidae and Tricorythidae. Only a clear assessment of character state polarity and homoplasy will lead to the resolution of these current problems in Pannota.

Acknowledgment

Purdue Agricultural Research Program Journal No. 14358.

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Received for publication 22 September 1994; accepted 3 January 1995.