

## Phylogenetic Systematics of the Major Lineages of Pannote Mayflies (Ephemeroptera: Pannota)

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### ABSTRACT

The phylogeny of 14 monophyletic groupings of known pannote mayfly genera are presented based on a cladistic analysis. From this, a strictly phylogenetic hierarchical classification of supergeneric taxa is presented, and previous paraphyletic and polyphyletic concepts in the Pannota are corrected. Revised superfamilies, families, and subfamilies are described, illustrated, and discussed in terms of makeup, distribution, and diagnosis. Superfamilies represent the two major cosmopolitan clades: Caenoidea (divided into sister clades recognized as the Caenidae and Neophemeridae) and Ephemerelloidea (further divided into a sequential series of clades recognized at the family rank and including Ephemerellidae, Austremerellidae, n. stat., Teloganodidae (restricted), Teloganellidae, n. fam., Ephemerithidae, n. stat., Machadorythidae, n. stat., Tricorythidae (restricted), and the measurably most apotypic pannote family Leptohephidae. The first major branching within the Ephemerelloidea results in a Laurasian clade (Ephemerellidae sensu stricto) and all other lineages, which constitute a Gondwanan clade. Such vicariance suggests a Pangaeian origin about 200 million years old for the Ephemerelloidea, and probably an even older origin for Pannota. A sequence of lineages in Caenidae are recognized as the Caeninae, Madecocercinae, n. subfam., and Brachycercinae (restricted); sister lineages in the Ephemerellidae are recognized as the Ephemerellinae (restricted) and Timpanoginae, n. stat.; and sister lineages in Tricorythidae are recognized as Tricorythinae and Diceromyzinae. Ranorythinae and Madecassorythinae are provisionally placed as synonyms of Tricorythinae and Diceromyzinae, respectively, because of lack of larval data associated with them. The unrelated families Prosopistomatidae and Baetiscidae must be excluded from the Pannota. Taxonomic keys are constructed to superfamilies, families, and subfamilies of Pannota for both known larvae and adults.

## INTRODUCTION

McCafferty and Edmunds (1979) divided extant Ephemeroptera into two suborders (Schistonota and Pannota). McCafferty (1991) subsequently proposed that Ephemeroptera higher classification be strictly phylogenetic. He showed that because Schistonota was a paraphyletic group it must be disallowed, and at the same time showed that Pannota was indeed a monophyletic group but placed it as an infraorder within the suborder Furcatargalia [= Rectracheata], a higher grouping which also contained the leptophlebiid and burrowing mayflies. Evidence now indicates that the Pannota shared a most recent common ancestor with the burrowing mayflies (infraorder Scaphodonta) (McCafferty 1997), with several characters shared by the two groups, including the essentially synapomorphic gill structure. Notably, what were previously considered anomalies in the two groupings are now explicable as either larval plesiomorphies common throughout pannote mayflies but also retained in the primitive burrowing group family Potamanthidae, or adult plesiomorphies common throughout burrowing mayflies but also retained in the plesiotypic pannote family Neophemeridae (see also Bae and McCafferty 1998).

The original concept of Pannota (generally referred to as the pannote mayflies) included the traditional families Baetiscidae, Caenidae, Ephemerellidae, Neophemeridae, Prosopistomatidae, Tricorythidae, and the more recently recognized families Leptohyphidae and Teloganodidae. The sister families Baetiscidae and Prosopistomatidae (Wang et al. 1997, Wang and McCafferty unpublished) were excluded from the Pannota and placed in a separate suborder, Carapacea, by McCafferty (1997) based on their wing venation, which is fundamentally more primitive than that of all other extant mayflies, and their larval morphology, which is uniquely specialized. Essentially, all extant groups other than the Carapacea share the apomorphic position of A1 vein in the forewings ending in the anal margin rather than in the more primitive position of the outer margin. On the other hand, the Carapacea demonstrate a number of synapomorphies, especially the thoracic shield structuring in the larvae. Our present study has confirmed additional differences between Carapacea and other extant suborders with respect to mouthparts and hindwing venation. Kluge et al. (1995) had, by way of a diagram but with no other explanation, also considered Prosopistomatidae and Baetiscidae in a lineage separate from other extant mayflies.

Pannota (literally fused back) includes those mayflies characterized primarily by the situation where less than half of the developing forewingpads in mature larvae freely extend beyond their fusion to each other (McCafferty and Edmunds 1979). Even though they may be highly

fused in Pannota, the wingpads remain externally recognizable as do the pro- and mesothoracic segments. This is unlike the thorax that is fused into a carapace in the Prosopistomatidae and Baetiscidae, and which was originally thought to represent an extreme pannote condition (McCafferty and Edmunds 1979). All other mayflies, with very few exceptions in some aberrant species or genera (see McCafferty and Edmunds 1979), retain the plesiomorphic condition of having the forewingpads separate from each other for over half their length in mature larvae.

The abdominal gill series in pannote larvae tend to be modified and protected in various ways. Gills are usually recumbent dorsally on the lateral shelves of abdominal terga. Respiratory surfaces are protected either by gill lamellae on the same gills, strong overlapping of lamellae, specialized operculate gills (for which there is a high propensity and homoplasy throughout numerous lineages of the major pannote clades), a gill chamber that incorporates both operculate gills and dorsally upturned abdominal flanges, or expanded hindfemora. The gill series of most other mayfly larvae tend not to be recumbent on lateral abdominal shelves, and are rarely protected as described above. Gills of the highly apotypic African genus *Dicercomyzon* Demoulin of the Tricorythidae (Dicercomyzinae) are an exception to the usual characteristic recumbent gill lamellae on lateral extensions of the abdomen. Instead, the gills of *Dicercomyzon* have an extended lateral position and the lamellae have been reduced and become fringed with fibrillae. In life, these unusual pannote gills are protected by the greatly enlarged hindfemora of the larva (McCafferty unpublished).

Pannote larvae are also somewhat distinctive behaviorally, being generally very slow crawlers and poor swimmers. They often are secretive in habit, and can be very inconspicuous among vegetation, debris, or while on, or partially buried in, sand and silt. There likely is a strong adaptive correlation between structure and function considering that the protected respiratory gill surfaces are well suited to such potentially abrasive environments. Some leptohyphids are commonly covered with fungal growth that camouflages them (McCafferty 1981), and caenids can be difficult to find (Provonsa 1990), as can be certain ephemereclids that climb about filamentous algae and aquatic mosses (e.g., McShaffrey and McCafferty 1991).

Distinct differentiating synapomorphies have not been identified for all pannote adults taken together. Some carry-over from larval thoracic morphology is evident in adults (McCafferty and Edmunds 1979), but in general adult thoracic morphology in Ephemeroptera is highly subject to convergence related to body and wing size reduction, as well as flight behavior variability. It should be remembered that with respect to body size, the smallest extant mayflies known are found among the Pannota in the family Caenidae. Nonetheless, each family of

pannote mayflies is highly distinctive in the adult stage, as will be seen below.

Although the families of pannota mayflies historically have been relatively stable [e.g., see reviews of Burks (1953), Edmunds et al. (1976), and Landa and Soldán (1985)], some genera have not been easily placed, and there has been little agreement regarding the phylogenetic relationships of higher taxa. The previous proposals of relationships were based on incomplete data and were highly speculative. Some were deduced only from restricted character sets, such as eggs (Koss 1973), internal anatomy (Landa and Soldán 1985), or gills (Kluge 1988); and some were based on symplesiomorphies (Riek 1973, Landa and Soldán 1985), thus making them essentially phenetic based and apt to include paraphyletic and polyphyletic taxa. The most recent review of the differences in these interpretations was given by McCafferty (1991), wherein an additional speculation was given, but at the same time it was emphatically pointed out that, regarding Pannota, considerable cladistic analysis must still be conducted to gain confidence in hypothesizing family-level derivations.

The familial classification of certain pannota genera has been problematic largely because symplesiomorphic characters have been used to define families, and because larval and adult stage correlations have been lacking. Examples of historical misplacement of taxa involving the Pannota (to be discussed in full in the Systematic Account) include *Melanemerella* Ulmer (see Wang and McCafferty 1996a), *Ephemerellina* Lestage and *Vietnamella* Tshernova (see Wang and McCafferty 1995), *Austremrella* Riek and *Teloganella* Ulmer (see Wang et al. 1995), *Coryphors* Peters (see Peters and Peters 1993), *Manobypbella* Allen (see below), and *Provonsbaha* McCafferty and Wang [= *Madecocercus* Malzacher] (see below).

The only comprehensive biogeographical studies of pannota mayflies were those of McCafferty and Wang (1997) for the Teloganodidae sensu lato, and of Bae and McCafferty (1998) for the Neophemeridae, although specific references to dispersal and vicariance of pannota genera in the Western Hemisphere were reviewed in detail by McCafferty (1998). McCafferty and Wang (1997) showed the major lineages then included in Teloganodidae sensu lato to be of Mesozoic Gondwanan origin prior to the initial breakup of Gondwana, based on phylogenetic generic relationships deduced therein. While those biogeographic deductions hold for each of the major lineages mentioned (Austremellinae sensu lato and Teloganodinae sensu lato), we will show below that the family in its prior sense was paraphyletic and that Teloganodinae sensu lato is derived separately with a larger grouping of Southern Hemisphere pannotes. We will present phylogenetic biogeographic evidence below for a Pangaeian origin of the Pannota and the most major clades within it.

Bae and McCafferty (1998) based their biogeographic conclusions

on their species cladogram and reduced area cladogram incorporating Holarctic-Oriental distributions within the group. They demonstrated both Asiatic and Euramerican elements of more recent Paleogene origin for the major lineages of Neophemeridae. Relationships between North and South America were due primarily to dispersal events of Pleistocene and Holocene, with Leptohyphidae having its recent center of dispersal in South America, Ephemerellidae in North America, and Caenidae (of apparently older origin) with centers in both North and South America (McCafferty 1998) as well as elsewhere in the world.

Paleontological data on the Pannota are very sparse and fragmentary. Fossils have been described for three species, currently known as *Potamantellus rubensis* Lewis (Neophemeridae) from the Oligocene Neartic (Montana), *Timpanoga viscata* (Demoulin) (Ephemerellidae, Timpanoginae) from Eocene Palearctic (Baltic amber), and *Turfanarella tingi* (Ping) (Ephemerellidae) from Jurassic Palearctic (China). The neophemerid is reliably placed (Lewis 1977) and is significant from a biogeographic standpoint because it reveals a previous Holarctic Tertiary distribution of a genus now restricted to Asia (Bae and McCafferty 1998). McCafferty (1990) indicated that placement of the Jurassic fossil in the Ephemerellidae by Demoulin (1954) was highly doubtful. The age and location of this family, however, would certainly be possible based on the phylogenetic biogeography deduced herein. The subimago of *T. viscata* (see Demoulin 1968) apparently is correctly placed to subfamily, but cannot be reliably placed to any genus.

Seldom has it been possible to bring together for comparison and analysis the bulk of genera of such a large group as the Pannota from throughout the world. Recent acquisitions to the Purdue Entomological Research Collection, mainly from the collections of G. F. Edmunds, collections made in southern Africa by the first author, and the kind loans of materials from cooperators throughout the world have made comparative analysis possible. That has allowed the hypothesis of the phylogenetic relationships of the major lineages of pannota mayflies and establishment of a phylogenetic higher classification that reflects such relationships. Herein we provide cladistic data; a systematic account of revised superfamilies, families, and subfamilies; and a key to discriminate the currently known larvae and adults at these higher taxonomic levels.

Although the historically dubious nature of the higher classification of the Pannota has been resolved to a large extent by our research, some differentiation of the adult stages of taxa may be regarded as subtle by some, particularly regarding wing venation, and additional variability may be found in the future. Also, we have no doubt that additional genera of Pannota will be discovered and described and may or may not conveniently fall to the higher taxa as described herein. The eventual discovery of larval stages of certain Afrotropical taxa currently known

only as adults, and unknown stages of Neotropical taxa known only as adults or larvae, may also be cause for some future descriptive or classificatory adjustments. Of course, as in any work of this sort, it should be viewed as a state of knowledge and hypothesis at the time the research was performed, and as for all science, is to some extent, provisional. Most importantly, the study will have been worthwhile if only it serves as a catalyst for further research on a world level and a foundation upon which further precision in systematics can be based.

#### METHODS AND MATERIALS

Operational taxonomic units (OTUs) analyzed by us consisted of 16 evidently monophyletic groupings of pannote genera. All such groupings have previously been recognized as taxa at the family, subfamily, tribe, subtribe, or complex level (see listing of OTUs below), with the exception of one (referred to herein as the *Madecocercus* group OTU). Those genera or stages of genera not represented in the Purdue Entomological Research Collection (PERC), or not elaborated completely in the literature, were borrowed from various other researchers and curators (see Acknowledgments) for comparative examination.

Of more than 100 characters initially explored as possibly comparative at our OTU group level, 49 were eventually found to be of some cladistic use or unique to lineages. The distribution of character states of these characters among the OTUs were plotted in a matrix for cladistic analysis as per Bae and McCafferty (1991) and McCafferty and Wang (1994). Polarity of character states were determined by standard outgroup analysis. Essentially all non-pannote mayflies are available as the outgroup. However, other Furcatergalia (especially Leptophlebiidae and pleistotypic Ephemeroidea such as Potamanthidae) took priority when the outgroup character state varied among non-pannote mayflies. Cladograms were generated based on common occurrences of apomorphies (synapomorphies). There were some incongruent character state distributions in the most parsimonious cladogram, explicable as homoplasy. Techniques of analysis are essentially after Hennig (1966), Ross (1937, 1974), Wiley (1981) and McCafferty (1991).

A strictly phylogenetic higher classification of pannote mayflies was derived from the cladogram according to the rules outlined by Wiley (1981), in that the cladogram can be exactly reproduced from the linear classification that we present. Phyletic sequencing conventions (Nelson 1972, 1973) were incorporated to obviate unnecessary increases in taxa and to provide some flexibility in choosing obviously more practical schemes, while adhering to the strict rules of phylogenetic classification.

Systematic accounts are presented in the resultant phylogenetic order. The treatment of each taxon includes a short synonymy indicating the first usage of the taxon at any rank (the authorship of the taxon

is noted for families and is applicable to other taxonomic level names similarly rooted), a comparative formal description of adults and mature larvae (and eggs if consistently useful), a diagnosis, a statement or list of the next lower level of taxa included (if genera, they are listed alphabetically, and type species are also indicated), general world distribution, material examined (only under the lowest level taxon treatment, i.e., either family or subfamily), and any remarks we deemed pertinent. Abbreviations for states in the USA used in the Material Examined sections are those of the U.S. Postal Service. Furthermore to conserve space herein we detail only the taxonomic name, stage and sex, and distribution of materials examined in most cases.

#### PHYLOGENETICS

##### Cladistics

The OTUs are named for the oldest, best known, or most typical named genus among them. In the following alphabetical listing of our OTUs, the most recent recognized equivalent higher taxa is given in brackets if existent, with references to the concepts. All genera in each of the OTUs are also given, although some remain provisional to various degrees either because they could not be examined, or more commonly because they remain unknown in the larval stage.

1. *Austremerella* group OTU [= *Austremerellinae* (McCafferty and Wang 1997)], including *Austremerella* Riek and *Vietnamella* Tshernova.
2. *Brachycercus* group OTU [= *Brachycercinae* in part (Malzacher 1987)], including *Brachycercus* Curtis, *Cercobrachys* Soldán, and *Insulibrachys* Soldán.
3. *Caenis* group OTU [= *Caeninae* (Needham et al. 1935), excluding *Brachycercinae*], including *Afrocaenis* Gillies, *Amercaenis* Provonsha and McCafferty, *Barnardata* McCafferty, *Brasilocaenis* Puthz, *Caenis* Stephens, *Caenoculis* Soldán, *Caenopella* Gillies, *Clypeocaenis* Soldán, *Tasmanocaenis* Lestage and *Wundacaenis* Suter.
4. *Diceromyzon* group OTU [= *Diceromyzinae* (Edmunds and Traver 1954)] including *Diceromyzon* Demoulin.
5. *Ephemerella* group OTU [= *Ephemerellidae* (McCafferty and Wang 1997), excluding *Timpanogae*], including *Caudatella* Edmunds, *Caurinella* Allen, *Cinctocostella* Allen, *Crinittella* Allen and Edmunds, *Drumella* Needham, *Eburella* Kang and Yang, *Ephacrerella* Paclt, *Ephemerella* Walsh, *Hyrtanella* Allen and Edmunds, *Serratella* Edmunds, *Teloganopsis* Ulmer, *Torleya* Lestage, and *Uracantibella* Below.
6. *Ephemerythbus* group OTU [= *Ephemerythinae* (Gillies 1960)], including *Ephemerythbus* Gillies.
7. *Leptotyphbes* group OTU [= *Leptotyphbidae* (Landa and Soldán 1985)], including *Allenhyphbes* Hofmann and Sartori, *Coryphorus* Peters, *Cotopaxi* Mayo, *Haplohyphbes* Allen, *Leptotyphbes* Eaton, *Leptotyphbodes*

- Ulmer, *Tricorythodes* Ulmer, and *Tricorythopsis* Traver.
8. *Machadorythus* group OTU [= *Machadorythinae* (Edmunds et al. 1963)], including *Machadorythus* Demoulin.
  9. *Madecassorythus* group OTU [= *Madecassorythinae* (Elouard and Oliariny 1997)], including *Madecassorythus* Elouard and Oliariny.
  10. *Madecocercus* group OTU including *Madecocercus* Malzacher, and provisionally *Afrocerus* Malzacher.
  11. *Neophemera* group OTU [= *Neophemeridae* (Burks 1953)], including *Neophemera* McDunnough, *Ochternova* Bae and McCafferty, and *Potamanthellus* Lestage.
  12. *Ranorythus* group OTU [= *Ranorythinae* (Oliariny and Elouard 1997)], including *Ranorythus* Oliariny and Elouard.
  13. *Teloganella* group OTU [= *Teloganella* complex in part (Wang et al. 1995)], including *Teloganella* Ulmer.
  14. *Teloganodes* group OTU [= *Teloganodinae* (McCafferty and Wang 1997)], including *Ephemerellina* Lestage, *Lestagella* Demoulin, *Lithogloea* Barnard, *Macafertella* Wang, *Manobypella* Allen, *Nadinella* McCafferty and Wang, and *Teloganodes* Eaton.
  15. *Timpanoga* group OTU [= *Timpanogae* (see *Timpanoga* complex, McCafferty and Wang 1994)], including *Attenella* Edmunds, *Eurylophella* Tiensuu, and *Timpanoga* Needham.
  16. *Tricorythus* group OTU [= *Tricorythinae* (Edmunds and Traver 1954)], including *Tricorythus*.

Evidentiary apomorphies used are given in Table 1. Fifty-one characters are listed, two are synapomorphic for all pannota mayflies, others are either autapomorphic for individual OTUs or constitute critical cladistic evidence for determining common origins among OTUs. Outgroup homoplasy is common among mayflies, including the Pannota; however, such characters possibly provide important cladistic information for analyzing relationships within groups. For example, the reduction of segments in forceps or palps, or reduction of the median caudal filament or loss of hindwings, terminal gills, crossvenation or major venation may be found independently in numerous infraorders, superfamilies and families of Ephemeroptera. Nonetheless, these character states and others may or may not be highly valuable and necessary in deducing phylogenetic relationships within any particular group such as the pannota mayflies. Thus, they should not be discarded indiscriminately because of outgroup homoplasy. Sometimes such characters may be the only data available for assessing relationships.

Ingroup homoplasy can also be common within a group such as the Pannota. For example, the use of a character such as presence or absence of maxillary palpi, might be questioned because the loss of such palpi - already reduced appreciably in the Pannota as a whole is extremely subject to homoplasy. Such homoplasy within a grouping, however,

cannot be demonstrated without first conducting a cladistic analysis. Indeed, there have been numerous independent losses of these palpi within the Pannota based on the results of our study (see character 20, Fig. 1). Palpi have apparently been lost independently in the *Madecocercus*, *Teloganodes*, *Teloganella*, and *Ephemerythus* group OTUs, and in some but not all of the *Ephemerella*, *Austremrella*, and *Leptobyphes* group OTUs. It is of some importance in expressing derivations between the sister *Madecocercus* and *Brachycercus* group OTUs, but otherwise simply is an ancillary character data associated with the cladogram.

Development of operculate gills, loss of gills 2 and 3, presence of the ommation, and certain venation traits, such as marginal intercalary venation and the cubital system, especially attachment, length, curvature, and orientation of ICuA1, are paramount among the pannota mayflies. Certain evolutionary gain tendencies become obvious in the Pannota (in addition to losses, such as the reduction and loss of maxillary palpi as discussed above). For example, the most anterior pair of lamellate gills often becomes operculate. This is apparently an adaptive based tendency, easily attained genetically by modification of recumbent lamellate gills, and it has been repeated independently several times. Not only has it involved gills 2 (several times), but also other anterior lamellae when gills 2 are not present.

Another tendency is for the cubital intercalary veins in the forewings to become reduced in number and in their attachments to CuA. This is seen independently in the *Caenis* + *Madecocercus* + *Brachycercus* group OTUs and in the common ancestor of the *Teloganodes* + *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptobyphes* group OTUs (see character 14). We have seen this character state also in the smaller sized representatives of the *Ephemerella* group OTU, where it appears clearly to be related to the reduction of the cubital area in the forewings.

Generally in accompaniment of this latter trend is the associated tendency for the longest cubital intercalary vein to have the same orientation as CuA. Such orientation brings the detached base of ICuA1 in proximity to the next main vein, such as ICuA2 or CuP, and leads to an eventual attachment that forms a distinct forking. Such forking is present in the cubital region of the forewings of the more apotypic lineages of the latter grouping of OTUs mentioned above. Hence, within the clade consisting of the *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptobyphes* group OTUs, forking is manifested either as a ICuA1-CuP fork, a ICuA1-ICuA2 fork, or both. Although the smaller forewings within the *Teloganodes* group OTU have a cubital venation suggestive of an eventual cubital fork, the most rudimentary forking is found in some of the *Teloganella* group OTU. In the *Teloganella* group OTU, there can be both a crude and shallow ICuA1-CuP fork and a very shallow ICuA1-ICuA2

fork. The forking is not entire or the forking is bridged by a crossvein in others of the *Teloganella* group OTU. In the very apotypic grouping consisting of *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptotyphes* group OTUs, any existent forks have become deepened and ICuA2 has become longer, so that in *Tricorythus* group and some of the *Diceromyzon* group OTUs, there is both a deep ICuA1-CuP fork and a ICuA1-ICuA2 fork. In the *Leptotyphes* group OTU, however, the ICuA1 attachment to CuP is either extremely basal or has been lost and replaced entirely by a deep ICuA1-ICuA2 fork, or occasionally both forks have been broken and secondarily no longer formed. In some specialized genera of this latter grouping, e.g., *Leptotyphes*, the cubital region has secondarily become reduced in depth, ICuA2 is thus shortened, and the cubital forking present in plesiotypic members of this OTU has been lost.

The various modifications of the cubital region as discussed above are apparently associated with the relative expansion of the cubital region of the forewings, except in the case of the few very small members of the *Ephemera* group OTU, which contrary to the others actually have a reduced cubital area. These latter species, however, do not develop any cubital forking, but are strictly subject to intercalary reduction and loss of attachments. In terms of the many groups that demonstrate the expanded cubital area, we maintain that this expansion is an evolutionary compensation for the loss or severe reduction of the hindwings, which occurs concomitantly in these particular groups.

Our hypothesized cladogram, as generated from the data set, is represented in Fig. 1. Numbers along branches indicate the respective evidentiary apomorphies noted in Table 1. Apomorphies that appear more than once independently are given in parentheses on the cladogram at that branch or branches that involve fewer resultant major lineages, or on all such branches if a similar number of lineages have resulted from each instance. For example, (5) appears at the branch in the cladogram leading to the *Neophemera* + *Caenis* + *Madecocercus* + *Brachycercus* group OTUs and represents the fact that the gills 7 have been lost independently at that point in addition to the loss at the branch leading to *Teloganodes* + *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Diceromyzon* + *Leptotyphes* group OTUs and presumably *Ranorythus* and *Madecassorythus* group OTUs (the latter two remain unknown as larvae). In the few instances when an apomorphy number is accompanied by an asterisk, it indicates that the apomorphy appears in only some but not all members of the resultant lineage. For example, (20\*) on the last branch leading to *Ephemera* group OTU and that leading to the *Leptotyphes* group OTU indicates that maxillary palpi have been lost in some but not all species in those groups, although they are entirely lost in certain other lineages.

If the apomorphy is accompanied by a double asterisk in Fig. 1, it

indicates that the condition is not maintained entirely in some distant and apotypic lineages. The instances of this include the following: The presence of 2\*\* indicates that dorsally recumbent gills are found throughout the Pannota, except that they have secondarily become modified and laterally oriented in the highly apotypic *Diceromyzon* group OTU. The presence of 28\*\* indicates that the basal forceps segment is elongated in the large grouping of *Austremarella* + *Teloganodes* + *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptotyphes* group OTUs, with exception that it is secondarily either highly reduced or otherwise modified in the *Teloganella* and the *Machadorythus* group OTUs and in some species of the *Ranorythus* and *Leptotyphes* group OTUs. The presence of 26\*\* indicates that the distal (third) segment of the forceps has been lost in the large grouping including the *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptotyphes* group OTUs, with the exception that within the *Leptotyphes* group OTU there is a redevelopment of a small third segment (articulated or not articulated), which may be plesiotypic or apotypic within the OTU itself, and rarely some supposed basal sub-segmentation or other aberrance in the forceps, which are certainly apomorphic within the lineage. Lastly, the presence of 50\*\* and 51\*\* indicates the deepening of cubital forks and lengthening of ICuA2 in the *Tricorythus* + *Ranorythus* + *Diceromyzon* + *Madecassorythus* + *Leptotyphes* group OTUs, with the exception that these traits are secondarily reduced in some highly apotypic species of the highly radiated *Leptotyphes* group OTU, especially in those where the wing is also secondarily narrowed.

Many other characters and thus parsimony bear out these five cases of so-called secondary reversion in highly apotypic lineages. With respect to the cladistic use of such characters states that subsequently revert, it is important to remember that, when cladistically analyzing lineages above the species level, it is the most plesiotypic species of each lineage that must be considered and used for any comparison between lineages. This was emphatically shown by Wiley (1981). Our methods have been consistent regarding this operational technique, which validates the use of characters 2, 26, 28, 50, and 51, as discussed in the preceding.

Branches representing the first dichotomy in the cladogram are compelling because of the number and type of synapomorphies involved that define the *Neophemera*, *Caenis*, *Madecocercus*, and *Brachycercus* group OTUs as one major clade, and all other OTUs as another major clade (Fig. 1). Within the first clade, the character data remain strong for the lineage branches as deduced. In addition, however, some remarkable homoplasy is found between some lineages of this clade and the *Machadorythus* group OTU, and within the *Leptotyphes* group OTU (see discussions below).

The second clade (Fig. 1) is also well defined and includes a large gradation of lineages from the plesiotypic extreme to the apotypic extreme, thus expressing a sequence of stepwise transitions that additionally indicates and explains the intermediacy of some of the OTUs, such as the *Teloganella* group and *Ephemerythus* group. Although these latter groups have contentiously been placed either with the ephemerellid type pannotes or the tricorythid type pannotes, depending on one's particular viewpoint, our cladistic analysis appears to have now resolved this question. Although there is some obvious degree of ingroup and outgroup homoplasy in the second major clade, all deduced lineages are substantiated by at least one synapomorphy that is not found elsewhere in the Pannota. The only exceptions are the *Ephemera* group OTU, which is otherwise clearly defined by its relative basal position and the autapomorphy defining its sister lineage (see character 30, Fig. 1), and *Teloganodes* group OTU, which is otherwise clearly defined by the synapomorphies common to its large and diverse sister branch (see characters 25, 26, and 44, Fig. 1).

Several phenoclines became evident in the phylogeny of the major lineages of the Pannota. These involve more than two transitional or connected apomorphic character states. Note in Table 1 that in such cases, the immediately previous, more plesiomorphic character state is listed as the plesiomorphic state for subsequent changes. For example, the ultimate plesiomorphic condition of gills 2 is that they are not operculate. In the Pannota certain lineages develop gills 2 into operculate gills that cover the following gills (character 35). Character 43 involves the modification of the shape of these operculate gills, and therefore the plesiomorphic state involves non quadrate operculate gills, although obviously the ultimate plesiomorphic condition involved non-operculate gills.

One phenocline was found with respect to what are referred to as character 8 and character 15 in Table 1 and Fig. 1. Marginal intercalary venation in the forewings grades from being developed and attached to other main veins, to being detached from main veins (although attached to crossveins in some) (8), to being absent (15) in the outer margin. Such ultimate reduction is often associated with size reduction in general and thus is also seen among the *Caenis* + *Madecocercus* + *Brachycercus* group OTUs in addition to the *Machadorythus* + *Tricorythus* + *Ranorythus* + *Dicercomyzon* + *Madecassorythus* group OTUs. It should be noted, however, that the reduction type venation is retained in larger *Tricorythus* adults. These two disparate groupings of pannote lineages (Fig. 1) with similar reduction tendencies also share the tendencies for the modification of the cubital system as discussed in some detail above, again evidently related to the expansion of the cubital region of forewings in compensation for the also convergent loss (character 13) or severe reduction in size of the hindwings in various lineages of the

Pannota.

Another phenocline involves the MP2 vein of the forewings. The plesiomorphic relative length of MP2 in the pannote forewing is generally much longer than the several short ICuA veins (see outgroups and plesiotypic lineages in both major clades, for example). In the *Machadorythus* + *Tricorythus* + *Ranorythus* + *Dicercomyzon* + *Madecassorythus* + *Leptobyphes* group OTUs, the MP2 vein is subequal in comparison with the remaining longest ICuA vein, which is also sometimes forked in this grouping. In the *Leptobyphes* group OTU, MP2 tends to become even further shortened in relation to the entire stalked and forked ICuA.

Some other phenoclines involve sequential gill loss. The loss of gills 2, seen in the *Ephemera* + *Timpanoga* group OTUs, is followed by the additional loss of gills 3 in the *Timpanoga* group OTU (see characters 27 and 30, Fig. 1). Another example is the loss of gills 7 in the *Teloganodes* + *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Dicercomyzon* + *Leptobyphes* group OTUs (and presumably *Ranorythus* + *Madecassorythus* group OTUs), followed by the additional loss of gills 6 in the *Teloganodes* group OTU, the *Teloganella* group OTU, and certain of the *Leptobyphes* group OTUs. Certain of the *Teloganodes* group OTU exhibit a further loss of gills 5.

One character was found to involve bipolar modification from the plesiomorphic character state. In the plesiomorphic condition, the male genital forceps have three or four fully articulated segments. This is found in the *Neopthemera* group OTU of the one major clade (although there is some reduction in some species) and in the *Ephemera*, *Timpanoga*, *Astremerella*, and *Teloganodes* group OTUs of the other major clade. In the case of the *Caenis* + *Madecocercus* + *Brachycercus* group OTUs compared to the former group OTUs, the forceps become somewhat aberrant by lacking segmentation (character 11). The plesiomorphic forceps condition is independently modified to two articulated segments in the *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Dicercomyzon* + *Madecassorythus* + *Leptobyphes* group OTUs (26\*\*), with only a reappearance of a third, poorly articulated segment within the highly apotypic *Leptobyphes* lineage (as discussed above). The aberrance seen in the forceps of the *Leptobyphes* group genus *Cotopaxi* (Mayo 1968) remains enigmatic.

Two common homoplasies that to some extent typify the tendency for homoplasy within the Pannota involve first and last gill pairs loss. As alluded to above, in the *Ephemera* group OTU, the filamentous gills on abdominal segment 1 are lost (character 29). The same loss occurs variably in some of the *Astremerella* group OTU, in some of the *Teloganodes* group OTU, and throughout the *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Dicercomyzon* + *Leptobyphes* group OTUs (and presumably the *Ranorythus* and *Madecassorythus* group OTUs, which remain unknown in the larval stage), and reportedly (but unconfirmed by us) as

occasionally within the *Timpanoga* group OTU. This trend is repeated many times independently, but still is of considerable cladistic importance for grouping the most apotypic lineages within the second major clade, i.e., those equivalent to the historical concept of the Tricorythidae sensu lato (Fig. 1). The ancestral terminal gills (gills 7) are also lost independently in the *Neophemera* + *Caenis* + *Madecocercus* + *Brachycercus* group OTUs and the *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Diercomyzon* + *Leptohyphes* group OTUs (character 5) (and presumably in the *Ranorythus* and *Madecassorythus* group OTUs), indicating two independent modifications. Such losses of already somewhat reduced first and last gill pairs, however, are a common and expected tendency also seen in such unrelated, large families as Baetidae and Heptageniidae.

Less parsimonious cladograms that could be generated would variously group the traditional family Caenidae and the traditional family Tricorythidae (or Tricorythidae sensu lato + *Teloganella* group OTU) together in an apotypic clade. This is untenable, however, in light of the majority of the data available. Also, dioptic eyes are found in several groups of mayflies, including other Furcatergalia, e.g., certain Leptophlebiidae and Ephemerioidea, indicating that this character state may be reversible to some degree and that the dioptic or holoptic condition might be considered either apomorphic or plesiomorphic, depending on the relative position in the phylogeny of mayflies. However, our present and critical interpretation based on the examination of outgroups within the Furcatergalia is that within the Pannota proper, the dioptic condition was present in the immediate common ancestor of the Pannota and that the apomorphic holoptic condition (see character 25) independently evolved in the *Caenis* + *Madecocercus* + *Brachycercus* group OTUs and the *Teloganella* + *Ephemerythus* + *Machadorythus* + *Tricorythus* + *Ranorythus* + *Diercomyzon* + *Madecassorythus* + *Leptohyphes* group OTUs. The dioptic condition was also considered plesiomorphic by Wang et al. (1995). If, however, the dioptic condition is alternatively considered apomorphic within the Pannota, it would suggest a monophyletic group consisting of the *Ephemera* + *Timpanoga* + *Anstremerella* + *Teloganodes* group OTUs, and indicate that the dioptic condition evolved independently in the *Neophemera* group OTU. This latter scenario would suggest an *Ephemera* + *Timpanoga* + *Anstremerella* + *Teloganodes* group OTU clade separate from the Tricorythidae sensu lato + *Teloganella* group OTU and also possibly require separate superfamily distinction. It would not, however, explain the obvious intermediate and transitional characterization that is found in certain groups such as the *Anstremerella* group OTU, the *Teloganodes* group OTU, the *Teloganella* group OTU, and the *Ephemerythus* group OTU. This intermediality is more logically explained as stepwise intermediate grades within the clade, which is obvious in our hypothesized cladogram (Fig. 1).

Another alternative to our hypothesized cladogram would place the *Teloganella* and *Ephemerythus* group OTUs together as sister groups rather than in sequence as shown in Fig. 1. Possible arguments for this alternative would include the fact that both groups have known male adults with subgenital plates with a narrow medial projection, and they have very short, broad labra as larvae. We believe both characters are convergent in this instance. Subgenital plate projections are also found in some of the *Tricorythus* group OTU, and the short, broad labrum shows up occasionally within several groups of Pannota. Instead, the loss of filamentous gills 1 appears compelling for grouping the *Ephemerythus* group OTU sequentially with the *Machadorythus* + *Tricorythus* + *Diercomyzon* + *Leptohyphes* group OTUs (including presumably *Ranorythus* and *Madecassorythus* group OTUs). Venational trends in the cubital region would also tend to support our hypothesis.

Additional comments on cladistic interpretations will be presented under the various taxa in the Systematic Account section, below.

#### HIGHER CLASSIFICATION

A revised, strictly phylogenetic hierarchical supergeneric classification is outlined in Table 2. Its construction complies with the strict style elaborated and endorsed by Wiley (1981) in general, and McCafferty (1991) in particular with respect to Ephemeroptera. The two traditional superfamilies Caenoidea and Ephemerelloidea are substantiated by the two major clades within our cladogram (Fig. 1). The stepwise and transitional nature of the hypothesized sequence of derivation of the major lineages within the second clade does not justify a separate superfamily Tricorythoidea, because there would be no clear demarcation point for separating another superfamily due to the transitional nature of the *Anstremerellidae*, the *Teloganodidae*, the *Teloganellidae*, and the *Ephemerythidae*. Furthermore, by rule, the only division possible would be to separate the *Ephemereillidae* sensu stricto out from the remainder of the families in this major clade.

Essential revision (described in detail in the Systematic Account, below) within the superfamily Caenoidea includes erection of the new subfamily *Madecocercinae* in the family *Caenidae*, which also involves a restriction of the subfamily *Brachycercinae*. The Afrotropical caenid genus *Afrocerus* Malzacher, which remains unknown in the larval stage, is placed only provisionally within the subfamily *Madecocercinae*, and that placement cannot be further substantiated until the larvae become known (see further discussion below). The cladogram substantiates the status quo for the family *Neophemeriidae*.

Within the superfamily *Ephemerelloidea*, new subfamily status is given to the *Timpanoginae* within the restricted family *Ephemerellidae*. *Anstremerellidae* is given full family status based on its relatively basal



and sequential position in the clade, and thereby restricts the family Teloganodidae. The genus *Manobryphella* Allen is placed within the family Teloganodidae. Teloganellidae is restricted to the Oriental genus *Teloganella* Ulmer but also includes at least one undescribed genus from Madagascar (see further discussions below). Full family status is given this lineage because of its intermediate sequential position in the cladogram. The intermediacy is manifested by apomorphic characteristics that are associated with what have traditionally been known as the Tricorythidae sensu lato, along with the retention of certain plesiomorphic states associated with the traditional Ephemerellidae sensu lato. Ephemerithidae attains full family status as does Machadorythidae because of their relatively intermediate cladistic position, although progressively more apotypic that Teloganellidae. The highly apotypic family Tricorythidae is restricted from previous concepts and includes the subfamily Tricorythinae and Diceromyzinae. These latter two subfamilies could, by rule of their phylogenetic position (Fig. 1), be given full family status; however, we are taking a conservative stance with respect to more apotypic lineages within the Ephemerelloidea. In addition, there is currently insufficient cladistic information (from lack of larval data) to maintain the former subfamilies Ranorythinae and Madecassorythinae as separate supergeneric taxa, as erected respectively by Elouard and Oliarinony (1997) and Oliarinony and Elouard (1997). Based only on the known adults, the former falls by default with Tricorythinae, and the latter to the Diceromyzinae, both in the family Tricorythidae. Only if significant cladistic evidence from the larvae is eventually found, could Ranorythinae and Madecassorythinae be possibly justified. While that is certainly possible, we feel the interim provisional classification herein is most appropriate.

The highly apotypic Western Hemisphere family Leptohiphidae is confirmed and must remain undivided into subfamilies at this time, although it is tempting to consider the extremely apotypic genus *Coryphorus* Peters as a separate group from the other genera taken together. The fact remains, however, that whereas *Coryphorus* has numerous apomorphies that could define it as a separate monophyletic subfamily, we could not identify one apomorphy that the other genera together share that would define them as a monophyletic group. Thus the origin of *Coryphorus* could be anywhere within the other Leptohiphidae, making any taxonomic grouping of them paraphyletic. *Coryphorus* remains unknown in the adult stage, and the genus *Cotopaxi* Mayo, which is highly enigmatic in the adult stage, remains unknown as larvae. Any similarities between the larvae of *Coryphorus* in South America and Machadorythidae in Africa, and for that matter, Brachycercinae (Caenidae) in the Northern Hemisphere (such as gill chambers, dorsally protruding sensory structures on the head, and crab-like legs) are clearly due to some remarkable convergent evolution (see

further discussion of this convergence in Remarks under Machadorythidae, below).

We maintain that the revised classification is not only strictly phylogenetic but is also practical in that superfamilies, families, and subfamilies are easily distinguishable in both the larval and adult stages. Only the fact that certain Afrotropical genera of Caenidae and Tricorythidae remain unknown in the larval stage and certain Neotropical genera of Leptohiphidae remain unknown in either the larval or adult stage presents a possible caveat in this respect. Nevertheless, the taxonomic keys to the higher taxa presented below are workable for all known stages of higher taxa. World distribution augments the keys as an additional aid in diagnostics.

#### SYSTEMATIC ACCOUNT

##### Superfamily Caenoidea

Figs. 2-5, 16-38

Coenidae Newman, 1853:187.

Caenoidea, Spieth, 1933:356 (in part).

Caenoidea, Edmunds and Traver, 1954:239.

*Larva*.—Maxillary palpi two or three segmented or absent (Figs. 16, 24, 32, 36). Notal margin between mature forewingpads without submedial lobes (Figs. 2-5). Filamentous abdominal gills 1 present (Figs. 2-5); gills 2 approximate, meeting, overlapping, or interlocking (Figs. 2-5), more or less quadrate and operculate (Figs. 2-5); gills 3-6 fringed with fibrillae or hairs and with (Fig. 19) or without (Fig. 26) underlying gill branches; gills 7 absent. Abdominal terga 3-6 shortened. Median caudal filament developed (Figs. 2-5).

*Adult*.—Ommation present on mesonotum (Figs. 20, 28). Forewings (Figs. 21, 29) with MP2 long, originating from wing base or curving from near base of MP1; CuP slightly curved and ending in outer margin or in or near posterior margin; marginal intercalaries present or absent in outer margin; if present, many marginal intercalaries connected to main longitudinal veins. Forceps of male genitalia segmented (Figs. 22, 23) or not segmented (Figs. 30, 31, 35, 38). Median caudal filament developed.

*Diagnosis*.—Larvae of Caenoidea can be distinguished from all other mayfly superfamilies by a combination of the presence of filamentous abdominal gills 1 and broad, quadrate operculate gills 2 that meet or nearly meet medially. The latter characteristic is particularly useful for field recognition. The families Teloganellidae and Machadorythidae, both in the superfamily Ephemerelloidea, demonstrate some remarkable convergence with certain Caenidae in the larval stage (see discussions below). Adults can be distinguished from all other mayfly super-

families by the presence of the ommation on the mesonotum and by forewing venation.

*Families included.* - Neophemeridae, Caenidae.

*Distribution.* - Cosmopolitan.

*Remarks.* - The advent of operculate gills 2, the quadrate shape of the operculate gills, and the loss of abdominal gills 7 are convergent within certain lineages of the Ephemerelloidea (Fig. 1). The loss of terminal gills on the abdomen is also subject to considerable homoplasy outside the Pannota.

Neophemerid mayflies, the large squaregills (McCafferty 1981), were considered among the burrowing mayflies in the first half of the twentieth century. For example, Traver (1935) considered them one of the subfamilies of Ephemeridae [= families of Ephemerioidea], and Ulmer (1939) considered them in the family Potamanthidae. This association was based on the common possession of basally arched MP2 and CuA veins in the forewings. Edmunds and Traver (1954) placed the neophemerids with the Caenidae, the small squaregills (McCafferty 1981), in a separate superfamily Caenoidea. This classification was based on larval morphology, in particular the similar gill structure. Since that time, all workers, with the exception of Demoulin (1958), have grouped Neophemeridae with Caenidae rather than with the Ephemerioidea. Inclusion of Neophemeridae with Caenidae is based on shared apomorphies, whereas any inclusion of Neophemeridae with burrowing mayflies would have to be based on shared plesiomorphies, although it is now obvious that the burrowing mayflies and pannote mayflies represent sister clades (see discussion, Introduction). Further discussion about the historical taxonomy related to Caenoidea can be found in Bae and McCafferty (1991, 1998) and Wang et al. (1997).

McCafferty and Edmunds (1979) recognized Neophemeridae as a sister group of Caenidae. Landa and Soldán (1985), however, placed Neophemeridae as a sister group of Baetiscidae, with the two derived with another clade consisting of Caenidae and Prosopistomatidae. McCafferty (1991) followed Landa and Soldán (1985) but derived this clade from near the base of the Pannota (see also Tshernova 1970). The Landa and Soldán scheme was based on data from internal anatomy, especially the ureter-like characteristics of Malpighian tubules in the case of Neophemeridae and Baetiscidae, and the arrangement of the alimentary canal in the case of Prosopistomatidae and Caenidae. Although these characteristics provided some valuable descriptive data for certain pannote mayflies, the interpretation of many of them as synapomorphic leads to polyphyletic classification and does not appear tenable in light of all other data. Furthermore, their consistency is suspect because of the small number of exemplars upon which descriptions were derived (Landa 1969). Although all such arguments are now essentially moot because of the recent elaboration of the suborder

Carapacea (families Baetiscidae + Prosopistomatidae) in the Ephemeroptera, any similarity in Malpighian tubules or alimentary canals in the suborders Carapacea and Furcatergalia may be regarded as either symplesiomorphic or convergent in light of the data regarding the critical basal position of Carapacea as discussed in the Introduction, above.

Wang et al. (1997) indicated that the operculate gills in Neophemeridae and Caenidae were fundamentally similar and uniquely associated medially. Although the operculate condition in itself is subject to both ingroup and outgroup homoplasy (McCafferty and Wang 1995), the superfamily Caenoidea is nonetheless well founded by larval characteristics. However, adults of the two families are so dissimilar in body size, wings, male genitalia, and compound eyes, that adult synapomorphies had never been found to support the monophyletic status of Caenoidea. Wang et al. (1997) identified one such synapomorphy: the ommation. This unique, central structure on the mesonotum of the adults has proven an excellent character for not only defining the Neophemeridae + Caenidae clade but diagnosing the superfamilial concept used by Edmunds and Traver (1954) and McCafferty and Edmunds (1979) that has now been substantiated by our comprehensive cladistic analysis herein.

The current concept of Caenoidea takes into account the recent discovery of the larvae of the Madagascar caenid *Madecocercus* Malzacher [= *Provoisshaka* McCafferty and Wang], by McCafferty and Wang (1995), which was initially misplaced in the family Tricorythidae sensu lato (see discussions below).

### Family Neophemeridae

Figs. 2, 16-23

Group II, Series III, Section 7 (type of Caenis) Eaton, 1883:137.  
Ephemeridae (Neophemeridae) Needham et al., 1935:234.  
Neophemeridae, Burks 1953:42.

*Larva.* - Compound eyes of male dioptic. Maxillary palpi three segmented (Fig. 16). Labial palpi three segmented (Fig. 17). Hindwingpads present. Abdominal gills 2 (Fig. 2) interlocked medially; lamellate gills with underlying gill branches (Figs. 18, 19).

*Adult.* - Compound eyes of male dioptic. Ommation not membranous (Fig. 20). Forewings (Fig. 21) with marginal intercalaries in outer margin, mostly attached to main veins; MA2 and MA1 with common stem; CuP slightly curving and ending in posterior margin; A1 forked; margins without cilia. Hindwings present. Male genital forceps three or four segmented (two terminal segments) (Figs. 22, 23), or reduced but segmented in some.

**Diagnosis.**—The larvae of Neophemeridae can be distinguished from Caenidae and other mayfly families by their uniquely medially interlocked, quadrate operculate gills on abdominal tergum 2. Underlying gill branches on all lamellate gills also distinguish them from Caenidae. Adults are distinguished from all other pannote mayflies by their basally curved MP2 and CuA and forked A1 in the forewings. They may be distinguished from Potamanthidae of the Ephemerioidea (with similar venation) by the slight asymmetric nature of the A1 fork, but most significantly by the presence of an ommation on the mesonotum.

**Genera included.**—*Neophemera* McDunnough (type: *N. bicolor* McDunnough) [= *Neophemeropsis* Ulmer, = *Rboenanthodes* Lestage]; *Potamanthellus* Lestage (type: *P. horai* Lestage) [= *Caenomera* Demoulin, = *Leucorboenanthus* Lestage, = *Oreianthus* Traver]; *Ochernoza* Bae and McCafferty (type: *Neophemera tshernoozae* Kazlauskas).

**Distribution.**—Holarctic; Oriental.

**Material examined.**—*Neophemera purpurea* (Traver), larvae, male and female adults, NC, SC; *N. youngi* Berner, larvae, male and female adults, AL, FL, SC; *Potamanthellus* spp., larvae, Malaysia, Thailand). Bae (pers. comm.) examined material of the Asian genus *Ochernoza* for us.

**Remarks.**—Neophemeridae currently consists of 11 extant nominal species and was recently revised by Bae and McCafferty (1998). There are evidently additional undescribed species in the Oriental region. The historical confusion of the placement of this family either with the burrowing mayflies or the caenids was taken up somewhat in the Introduction and in greater detail under the superfamily Caenoidea, above. Although Holarctic biogeographic patterns studied by Bae and McCafferty (1998) can be explained by Paleogene vicariant events in the Northern Hemisphere, we suggest that Neophemeridae or a neophemerid-like precursor must have been at least of Mesozoic Laurasian origin, and probably considerably older, given its retention of ephemeroid adult characteristics (see McCafferty 1990) and the age of Gondwanan lineages of other Pannota (McCafferty and Wang 1997), along with the probability of its sister family Caenidae being Pangaean in origin (e.g., McCafferty 1998) and the ancestral Ephemerelloidea (Fig. 1) being Pangaean in origin (see below). All other aspects of the family have been taken up recently by Bae and McCafferty (1998).

Finally, it should be noted that a common reference in the literature to fused operculate gills in this group is technically incorrect. Close examination has revealed that the operculate gills are actually held together by an interlocking system mediated by interlocking cuticular outgrowths and that they can be pried apart. In other words, there is no fusion as may be intimated by the fused descriptor of the past.

## Family Caenidae

Figs. 3-5, 20-38

Coenidae Newman, 1853:187.

Caenidae, Klápálek, 1909:14.

Ephemeridae (Caenidinae), Handlirsch, 1925:415 (in part).

Baetidae (Caeninae), Needham et al., 1935:234.

**Larva.**—Compound eyes of both sexes holoptic. Maxillary palpi two or three segmented or lacking (Figs. 24, 30, 34). Labial palpi two or three segmented (Figs. 25, 31, 35). Hindwings absent. Abdominal gills 2 not interlocked at midline of abdomen but overlapping, meeting, or approximate medially (Figs. 3-5); gills 3-6 fringed with fibrillae or hairs, without underlying gill branches (Fig. 26).

**Adult.**—Compound eyes of both sexes holoptic, usually but not always small and remote. Ommation membranous (Fig. 28). Forewings (Fig. 29) with MA fork incomplete and asymmetric (MA2 not originating with MA1); marginal intercalaries absent; CuP slightly curved and ending in posterior margin; posterior marginal cilia present. Hindwings absent. Genital forceps of male unsegmented (Figs. 30, 31, 35, 38), more or less straplike, bowed, or aberrant. All caudal filaments long in males (> 2x body length), short in females (< body length).

**Diagnosis.**—The larvae of Caenidae can be easily distinguished from those of Neophemeridae by the absence of hindwings, the overlapping or approximate but never interlocking operculate gills, and the absence of underlying gill branches. The generally small adults of the subfamily Caeninae are superficially similar to those of *Prosopistoma* Latreille (Prosopistomatidae), and the two have a similar forewing shape and are even commonly found flying at the same time of night and predawn in Africa (McCafferty unpublished). Unique wing venation together with the presence of the ommation distinguish Caenidae adults.

**Subfamilies included.**—Caeninae; Madecocercinae; Brachycercinae.

**Distribution.**—Cosmopolitan.

**Remarks.**—Our hypothesized cladogram of the pannote groups (Fig. 1) indicates that the condition of the longest ICuA vein paralleling CuA was independently acquired in the immediate common ancestor of the grouping made up of the Teloganodidae, Teloganellidae, Ephemerithidae, Machadorythidae, Tricorythidae, and Leptohyphidae (Fig. 1). The fact that it also is such in Prosopistomatidae suggests that the characteristic is probably associated with reduction in body size and the often expanded cubital areas of the forewing in association with the loss or severe reduction of the hindwing in many of these groups. Distal crossveins have also been lost independently in Caenidae and the most atypical Ephemerelloidea (Machadorythidae, Tricorythidae, and Leptohyphidae). This probably is also related to reductionism. Hindwings have been entirely lost independently in Caenidae, Machadorythidae,

and Tricorythidae, and some Leptoxyphidae, among the pannote mayflies as well as many other lineages of mayflies, especially small Baetidae.

Caenidae, also known as small squaregills generally (McCafferty 1981), or as cainflies in Africa (e.g., Agnew 1985), are well known mayflies that historically have been classified in the Baetoidea (Ulmer 1920, Needham et al. 1935), Ephemerelloidea (Demoulin 1958), Prosopistomatoida (Landa and Soldán 1985), and Caenoidea. The body size of caenids is usually relatively very small. Edmunds et al. (1976) reported the body size to be 2.0-7.0 mm, but we have seen caenids not much over one millimeter and believe they are the smallest of all extant mayflies. One problem associated with small body size in mayflies is that many taxonomic characters are associated with reductionism in the adult stage (e.g., loss of hindwings), and such reductionism involves several commonly repeated adaptations. Reduction of eyes in many male adults of Caenidae is probably associated with the fact that most are night swimmers. Thew (1960) gave suggestions for further taxonomic research in the family; Soldán (1986) presented some preliminary work on Brachycercinae; Provonsha (1990) provided a significant revision of the genus *Caenis* in North America; and Malzacher (1993) and Provonsha and McCafferty (1995) presented significant descriptive data for the rich African fauna.

Malzacher (1995) described the genus *Madecocercus* based only on adults from Madagascar. Slightly later in that same year, McCafferty and Wang (1995) described the genus *Provonshaka* from Madagascar based on larvae only. *Provonshaka* had been provisionally placed in the Tricorythidae because although the larvae agreed with the Caenidae in many respects they lacked maxillary palps and some other larval characteristics that had historically been associated with Caenidae. *Madecocercus* adults were clearly members of the Caenidae. One of us (WPM) has been informed by J.-M. Elouard (pers. comm.) that *Provonshaka* larvae have recently been reared out and that they have proven to be the larvae of *Madecocercus*, thus resolving the familial placement of the Madagascar larvae described by us.

Most genera of Caenidae can be clearly placed to either the subfamily Caeninae or Brachycercinae as per the original concept of these groups by Malzacher (1987). Certain genera, however, are problematic in this respect. The problematic genera include the Southern Hemisphere genera *Afrocerus*, *Madecocercus*, *Wundacaenis*, and *Tasmanocoenis*. The African genus *Afrocerus* is problematic because it is known only in the adult stage, and its placement to any subfamily must thus remain provisional. It is possible that its larvae will prove to be either typical of Brachycercinae (some members of this group are known from the Oriental region, which often shows a close relationship with African mayfly fauna), or typical of the genus *Madecocercus* from Madagascar (where strong biogeographic relationships also exist with Africa). Based

on male genitalia, Malzacher (1995) believed *Madecocercus* and *Afrocerus* to be closely related, and because of that assessment, we provisionally place *Afrocerus* in the same subfamily with *Madecocercus*.

*Madecocercus* shows several characteristics typical of Brachycercinae in the adult stage (Malzacher 1995) but does not share the many larval apomorphies that have traditionally been associated with Brachycercinae (see McCafferty and Wang 1995, as *Provonshaka*). Nonetheless, the larvae of *Madecocercus* are only superficially similar to Caeninae sensu stricto, in that it is the many plesiomorphies (giving the typical *Caenis* appearance) that are shared. We place *Madecocercus* as a separate, new subfamily Madecocercinae in the Caenidae, based on the fact that it cannot reside satisfactorily with either Brachycercinae or Caeninae and that it is allowable phylogenetically. It appears to share apomorphic genitalia with Brachycercinae of the type 2 as discussed by Malzacher (1997), and thus is considered herein a primitive sister group of the Brachycercinae. The strongly arched condition of the forceps, however, may well prove to be relatively plesiomorphic within Caenidae. Importantly, it does not share an adult triangular prosternum with Caeninae, nor does it share the ventral submarginal row of minute palmate outgrowths that occurs on the gills 2 of Caeninae.

Whereas *Madecocercus* and possibly *Afrocerus* appear to be primitive genera sharing a common ancestor with the Brachycercinae, *Tasmanocoenis* and evidently *Wundacaenis* may represent a basal branch within the Caeninae lineage. Although they share the apomorphic prosternum and the ventral row of minute outgrowths, mentioned above, on the gills 2 (microtrichia of Malzacher 1997) with Caeninae proper, their male genitalia appear somewhat similar to the type found in Brachycercinae and Madecocercinae according to Malzacher (1997). We maintain *Tasmanocoenis* and *Wundacaenis* in the Caeninae because of shared fundamental larval apomorphies and because SEM study of the male genitalia of *Tasmanocoenis* by A. V. Provonsha (pers. comm.) indicates that the so-called longitudinal groove of the forceps is actually the inner part of a longitudinal folding of the forceps (see also Malzacher 1991). Unlike the forceps of the *Brachycercus* type, which are folded longitudinally outwardly, those of *Tasmanocoenis* (and presumably *Wundacaenis*) are folded inwardly, indicating the independent and fundamental difference from the Brachycercinae. Another possibly important observation is that in terms of the forceps shape that are found in *Tasmanocoenis* and *Wundacaenis* of the Caeninae, the Madecocercinae, and the Brachycercinae, those of the former have a strong bow basally, those of Madecocercinae are bowed more distally, and those of the Brachycercinae have a more slightly and evenly distributed curvature. Malzacher (1997) also gave arguments for placing *Tasmanocoenis* and *Wundacaenis* in Caeninae. Madecocercinae may prove to have the outwardly directed fold similar to that of Brachycercinae if our hypothesized relationships

of the two groups (Fig. 1) are correct.

There is no doubt that an intensive genus-level cladistic analysis of the family Caenidae is called for. Apparently there is an abundance of ultrastructure armature and chaetotaxy in the larvae that may be of consequence if examined at the SEM level. Genitalia also need to be studied at the SEM level (A. V. Provonsha, pers. comm.).

Finally, two cases of rather remarkable convergence in the larval stage of mayflies involve members of the family Caenidae. *Madecocercus* of the subfamily Madecocercinae is adaptively very similar to larvae of the ephemeropteroid family Teloganellidae. Brachycercinae larvae are adaptively similar to the larvae of the subfamily Machadorythidae and a specialized Neotropical genus of the family Leptohyphidae (see thorough discussion of the convergence under Machadorythidae, below).

### Subfamily Caeninae

Figs. 3, 24-31

Coenidae Newman, 1853:187 (in part).

Baetidae (Caeninae), Needham et al., 1935:234 (in part).

Caenidae (Caeninae), Edmunds and Traver, 1954:239 (in part).

Caenidae (Caeninae), Malzacher, 1987:1.

**Larva.**- Head without ocellar tubercles (Fig. 3). Maxillary palpi two or three segmented (Fig. 24). Labial palpi three segmented (Fig. 25). Prosternum width less than half width of mesosternum. All legs similar in length (Fig. 3); claws robust, usually with denticles. Abdominal segments poorly developed laterally (Fig. 3). Gills 2 with ventral submarginal row of minute palmate outgrowths.

**Adult.**- Prosternum short, triangular (Fig. 27), less than 2.5 times as long as wide. Forceps mostly without longitudinal fold (groove) and usually not bowed (Fig. 30); when longitudinal fold present, forceps folded inwardly and bowed basally (Fig. 31); forceps highly reduced in some species.

**Eggs.**- Length less than 2.5 times width.

**Diagnosis.**- The larvae of Caeninae can be distinguished from those of Brachycercinae by their lack of ocellar tubercles and their three-segmented labial palpi. They can be separated from known Madecocercinae larvae by the presence of maxillary palps, poorly developed abdominal lateral processes and narrow prosternum, among other characteristics. Adults are distinguished by the triangular shaped prosternum. Known eggs are distinct from known eggs of Brachycercinae in their relative shortness.

**Genera included.**- *Afrocaenis* Gillies (type: *Caenopsella major* Gillies); *Amercaenis* Provonsha and McCafferty (type: *Caenis ridens* McDunnough); *Barnardara* McCafferty (type *B. demoori* McCafferty); *Brasilocaenis* Puthz

(type: *B. irmleri* Puthz); *Caenis* Stephens (type *C. macrura* Stephens) [= *Oxygypsa* Burmeister, = *Ordella* Campion, = *Caenodes* Ulmer, = *Austrocaenis* Barnard, = *Caenomedeia* Thew]; *Caenoculis* Soldán (type: *C. bisbopi* Soldán); *Caenopsella* Gillies (type *C. meridies* Gillies); *Clypeocaenis* Soldán (type: *C. bisetosa* Soldán); *Tasmanocoenis* Lestage (type: *T. tonnoiri* Lestage) [= *Pseudocaenis* Soldán]; *Wundacaenis* Suter (type: *W. dostini* Suter).

**Distribution.**- Cosmopolitan.

**Material examined.**- *Afrocaenis browni* Gillies, larvae, Kenya; *A. major* (Gillies), larvae, Kenya; *Amercaenis ridens* McDunnough, larvae, female adults, CO, KS, NE; *Barnardara demoori* McCafferty, larvae, Kenya, South Africa; *Brasilocaenis* sp., larvae, Brazil; *Caenis amica* (Hagen), larvae, male and female adults, AL, AR, AZ, CA, CN, CO, FL, GA, ID, IL, IN, IA, KY, MA, MS, NC, NJ, NY, OH, OR, WA, WV, WY, Alberta, Ontario; *C. capensis* (Barnard), larvae, South Africa; *C. latipennis* Banks, larvae, male and female adults, AL, AZ, CA, IL, IN, MD, MS, MT, WA, Alberta; *C. sp.*, male adults, Senegal; *C. sp.*, male and female adults, Ethiopia, New Guinea; *Clypeocaenis umgeni* Provonsha and McCafferty, larvae, South Africa; *Tasmanocoenis* sp., larvae, male and female adults, Australia.

**Remarks.**- Many species and two genera are unfortunately known only from either the adult or larval stage. This makes it particularly difficult to assess relationships among the genera of Caeninae. Nevertheless, we are retaining all genera listed above at this time because they all apparently have autapomorphic characteristics. One clear monophyletic lineage within Caeninae that was identified by Provonsha and McCafferty (1995) is made up of the so-called brush-legged caenids, consisting of *Amercaenis*, *Clypeocaenis*, and *Barnardara*. *Caenis* is a large and apparently very old genus found throughout the world. As pointed out by McCafferty (1998), it could well be of Pangaea origin. In southern Africa and perhaps elsewhere, the Caeninae, although often secretive as larvae, surely make up a large portion of the benthic riverine biomass and thus a good deal of the secondary productivity in these streams as evidenced by the overwhelming number of adults seen daily in light traps (McCafferty unpublished).

### Subfamily Madecocercinae, new subfamily

Figs. 4, 32-35

**Larva.**- Head without ocellar tubercles (Fig. 4). Maxillae lacking palpi (Fig. 32). Labial palpi three segmented (Fig. 33). Prosternum width more than one-half width of mesosternum. Forelegs about as long as mid- and hindlegs (Fig. 4). Claws robust and curved, without denticles (Fig. 4). Abdomen with narrow laterally produced projections on some segments, not upturned (Fig. 4). Gills 2 without ventral submarginal row of minute palmate outgrowths; gills 3-6 fringed with hairs, not fibrillae.

**Adult.**- Prosternum rectangular (Fig. 34), more than half width of mesosternum. Forceps bowed distally (Fig. 35).

**Egg.**- Unknown.

**Diagnosis.**- Based on the genus *Madecocercus* (*Afrocerus* is unknown as larvae), this subfamily in the larval stage differs from both Caeninae and Brachycercinae in the absence of maxillary palpi and the lack of fibrillae on gills 3-6. It is reminiscent of Caeninae, except that it is hairy throughout, has very broad femora, and a peculiar arrangement of abdominal lateral processes on segments 2, 6, and 7 especially. Adults have the unique combination of a rectangular shaped prosternum, along with forceps that are strongly bowed.

**Genera included.**- *Madecocercus* Malzacher (type: *M. tauroides* Malzacher) [= *Provonshaka* McCafferty and Wang]; *Afrocerus* Malzacher (type: *A. forcipatus* Malzacher) (provisional inclusion).

**Distribution.**- Madagascar; Africa(?).

**Material examined.**- *Madecocercus* sp. larvae, Madagascar.

**Remarks.**- For the history and relationships of the unusual genus *Madecocercus*, see the remarks under the family Caenidae, above. *Afrocerus* is only provisionally included in the subfamily because it remains unknown in the critical larval stage. McCafferty and Wang (1995) compared the larvae of Madecocercinae (as *Provonshaka*) in detail with a larva from Madagascar presumed to be *Manolophella* Allen, a genus placed by us herein in the family Teloganodidae of the Ephemerelloidea (see further discussion below).

#### Subfamily Brachycercinae

Figs. 5, 36-38

Brachycercidae Lestage, 1924b:62 (in part).  
Caenidae (Brachycercinae), Malzacher, 1987:1.

**Larva.**- Head with well-developed ocellar tubercles (Fig. 5). Maxillary palpi two segmented (Fig. 36). Labial palpi two segmented (Fig. 37). Prosternum rectangular, with width more than one-half width of mesosternum. Forelegs relatively short (Fig. 5); mid- and hindlegs longer than forelegs; claws long and very slender. Abdominal segments produced into laterally broad, flat, upcurved projections (Fig. 5). Gills 2 lacking ventral submarginal row of minute palmate outgrowths.

**Adult.**- Prosternum (Fig. 35) rectangular, more than half width of mesosternum (as in Fig. 34). Forceps moderately bowed and longitudinal fold (groove) outward and somewhat shortened (Fig. 38).

**Egg.**- Elongate, length more than three times width.

**Diagnosis.**- Brachycercinae larvae can be distinguished from Caeninae and Madecocercinae larvae by the presence of well-developed ocellar tubercles, two-segmented labial palpi, short forelegs, and upturned

lateral abdominal processes. Adults can be distinguished from Caeninae by their rectangular shaped prosternum. They can be distinguished from Madecocercinae by forceps that are neither stout nor strongly bowed. The eggs of Brachycercinae are distinctly more elongate than those of Caeninae.

**Genera included.**- *Brachycercus* Curtis (type: *B. harrisellus* Curtis) [= *Eurycaenis* Bengtsson]; *Cercobrachys* Soldán (type: *C. etowah* Soldán); *Insulibrachys* Soldán (type: *I. neebhami* Soldán).

**Distribution.**- Holarctic; Neotropical; Oriental.

**Material examined.**- *Brachycercus edmundsi* Soldán, larvae, WY; *B. maculatus* Berner, larvae, NC; *B. nasutus* Soldán, larvae, female adults, IN; *B. prudeus* (McDunnough), larvae, WY; *B. nitidus* (Traver), larvae, NC; *B. spp.*, larvae, male and female adults, IA, MD, MI, NE, TX, Ontario; *Cercobrachys* spp., larvae, MT, SC.

**Remarks.**- The Brachycercinae are surely one of the most apotypic groupings of Pannota and of mayflies in general, demonstrating numerous larval apomorphies (Fig. 1). The group is not known from Africa; however, the African genus *Machadorythus* Demoulin (Machadorythidae) not only is to a great extent convergent with this group, but is found in much the same habitat (larvae partially covered by silt bottoms in slight to moderate current of streams) (McCafferty unpublished), apparently filling much the same niche that typifies brachycercines in other parts of the world (see more complete discussion under Machadorythidae, below).

Barnard (1932) stated that the South African genus *Austrocaenis* Barnard was related to *Brachycercus*. We examined specimens identified by Barnard as *Austrocaenis* and they proved to be typical *Caenis* (Caeninae). McCafferty and de Moor (1995) placed *Austrocaenis capensis* Barnard, the type of the genus, in the genus *Caenis*, thereby essentially synonymizing *Austrocaenis* with *Caenis*.

#### Superfamily Ephemerelloidea

Figs. 6-15, 39-116

Ephemerellidae Klápálek, 1909:13.

Leptophlebioidea, Edmunds and Traver, 1954:238 (in part).

Ephemerelloidea, Demoulin, 1958:10 (in part).

Ephemerelloidea, McCafferty and Edmunds, 1979:6.

**Larva.**- Maxillary palpi absent, or one to three segmented (Figs. 40-44, 50, 54, 55, 58, 73, 78, 85, 92, 101-104). Notal margin between forewingpads with (Figs. 6-9) or without (Figs. 10-15) well-developed submedian lobes. Filamentous gills 1 present or absent; lamellate gills present on abdominal segments 2-5, 2-6, 2-7, 3-7, or 4-7; gill 2 if present operculate or not, variously shaped, and never interlocking and only rarely meeting along longitudinal midline of abdomen (Figs. 6-15), if

quadrate or meeting or approximate, then filamentous gills 1 absent. Median caudal filament developed or reduced.

*Adult.*— Mesonotum without ommation. MP2 of forewings (Figs. 45, 56, 57, 59, 60, 67-69, 75, 82, 88, 112, 113) not extending to base nor curving from near base of MP1; CuP strongly curved toward anal margin; marginal intercalaries in outer margin of wing single (Figs. 45, 56, 59, 60, 67-69) or double (Fig. 75) and mostly detached from main veins, or absent (Figs. 82, 88, 98, 112, 113). Male genital forceps with two or three completely articulated segments (Figs. 47-49, 62, 70, 76, 83, 89, 90, 99, 100, 114-116). Median caudal filament developed or reduced.

*Diagnosis.*— Larvae of Ephemerelloidea can generally be distinguished from those of Caenoidea by not having gills 2 operculate and quadrate and meeting or interlocking dorsally on the abdomen. The Neotropical genus *Coryphors* Peters is the only known exception to this because it has quadrate, operculate gills 2 that meet. Unlike the caenooids, however, this atypical ephemerelloid does not possess filamentous gills 1. Adults can always be distinguished from those of Caenoidea by the MP2 vein of the forewings that does not extend to the base nor curve from near the base of MP1, along with other venation traits mentioned in the descriptions of the superfamilies and the key to adults. In those ephemerelloids that lack marginal intercalaries, the crossvenation is not restricted to the basal region of the wing as it is in the Caenoidea, but extends more distally at least in the anterior area of the wing. In those ephemerelloids with marginal intercalaries in the outer margin of the forewings, most intercalaries will not be attached to main longitudinal veins, as they are in the Neoephemeridae of the Caenoidea. The intercalaries will either be mostly detached or attached to crossveins, and with relatively few, if any, attached to main veins.

*Families included.*— Ephemerellidae; Austremereillidae; Teloganodidae; Teloganellidae; Ephemerithidae; Machadorythidae; Tricorythidae; Leptohyphidae.

*Distribution.*— Cosmopolitan.

*Remarks.*— Ephemerelloidea is a very primitive group. Its most plesiotypic members have, for the most part, a preponderance of plesiotypic characteristics (see especially Austremereillidae larvae). Biogeographic and cladistic analysis of genera of Teloganodidae sensu lato by McCafferty and Wang (1997) would give the immediate common ancestor of the entire clade at least an early Mesozoic ancestry. Our present analysis is even more revealing with respect to possible historical biogeography of the group. The most ancestral major dichotomy in the clade, which gave rise to the Ephemerellidae sensu stricto on the one hand and the immediate common ancestor of the remainder on the other ephemerelloid clade on the other hand (Fig. 1), strongly suggests that this event coincided with a major world geographic vicariant event. The Ephemerellidae proper are essentially a Laurasian group, whereas the

remainder of the clade, represented by seven other families, is essentially Gondwanan in distribution, with only recent incursions into the Holarctic, i.e., Leptohyphidae into the Nearctic (see e.g., McCafferty 1998). This strongly suggests that the initial major dichotomy of the clade corresponded to the initial breakup of Pangaea into Laurasia and Gondwana, and thus a Pangaeal and probably Paleozoic origin for the Ephemerelloidea, as well as the Pannota in general.

Historically, Ephemerelloidea has included Ephemerellidae (including Teloganodidae) and Tricorythidae (sensu McCafferty and Edmunds 1979, Landa and Soldán 1985). Wang and McCafferty (1996a) recently removed the South American genus *Melanemerella* Ulmer from Ephemerellidae and Pannota because it appears more reasonably to be an aberrant member of Leptohyphidae. McCafferty and Wang (1997) erected Teloganodidae to familial status, and the analysis herein indicates that Austremereillidae and Teloganodidae must be recognized as separate families because of their relatively basal and sequential positions in the hypothesized cladogram (Fig. 1). The relative positions of Teloganodidae, Teloganellidae, and Ephemerithidae (Fig. 1) also explain some of the historical confusion in the classification or misidentification of these mayflies either as traditional Ephemerellidae sensu lato or Tricorythidae sensu lato (see further discussions under the taxa below, and under Phylogenetics, previously).

Several published descriptive mistakes were discovered during our study, including the incorrect counts of abdominal gills in several original descriptions of genera. For example, after checking topotypic specimens, the larvae of *Austremereilla* and *Hyrtanella* Allen and Edmunds were found to have abdominal gills 7, despite original descriptions that they were absent. Such data have proven pertinent to cladistic analysis.

Allen (1965, 1980, 1984) proposed higher classifications for Ephemerellidae sensu lato. Unfortunately, his higher classifications were phenetic based, biased by often arbitrary limits (gap criteria) that were assigned to higher categories, and included incorrectly assigned genera and species.

### Family Ephemerellidae

Figs. 5, 6, 39-53

Ephemerellidae Klápálek, 1909:13.

Ephemeridae (Ephemerellini), Handlirsch, 1925:415.

Baetidae (Ephemerellinae), Needham et al., 1935:234.

Ephemerellidae, Edmunds et al., 1963:16 (in part).

*Larva.*— Mature male eyes dioptic. Maxillary palpi one to three segmented or absent (Figs. 39-44, 50). Filamentous gills absent or present on abdominal segment 1 (Figs. 5, 6); lamellate gills on abdominal segments 3-7 or 4-7 (Figs. 5, 6). Median caudal filament developed.

**Adult.**— Male eyes dioptic. Forewings (Fig. 45) with MP2 generally longer than longest ICuA; usually three or more CuA intercalaries present, longest not paralleling CuA, or at least attached to CuA at angle; the first and/or second cubital intercalary usually attached to CuA, and all usually basally oriented toward CuA (cubital system sometimes highly reduced in very small individuals); marginal intercalaries single and mostly detached in outer margin, sometimes attached to crossveins, only rarely with some attached to main longitudinal veins. Abdominal segment 2 without gill socket vestiges (Figs. 46, 52). Male forceps with segment 1 relatively short, less than twice as long as wide (Figs. 47-49, 53). Median caudal filament developed.

**Diagnosis.**— Larvae of Ephemerellidae can be distinguished from all other mayfly families by the absence of gills 2. Adults differ from some other families of ephemerelloids in that they have marginal intercalary veins and well developed hindwings. They can be distinguished from ephemerelloid adults that similarly also possess marginal intercalaries (Austremerellidae, Teloganodidae, Teloganellidae, Ephemerithidae) by their lack of gill socket vestiges on abdominal segment 2, and by the shape and relative size of the male forceps basal segment. Cubital wing venation is not a definitive diagnostic character for this group because small sized genera, e.g., *Teloganopsis* Ulmer, can have a very reduced cubital region with as few as two intercalaries, similar to some Teloganodidae.

**Subfamilies included.**— Ephemerellinae; Timpanoginae.

**Distribution.**— Holarctic; Oriental.

**Remarks.**— The first concept of Ephemerellidae dates to section 6 of *Ephemerella* (Eaton 1883-88), which included the Holarctic and Oriental genus *Ephemerella* Walsh and the Oriental genus *Teloganodes* Eaton, as they were known at that time. Klapálek (1909) first used the family rank designation, but included only *Ephemerella*. Ulmer (1920) added the South American genus *Melanemerella* to the family, and Lestage (1924a) added the South African genus *Ephemerellina* Lestage. Various other genera were described in the family thereafter. Edmunds et al. (1963) regarded the Ephemerellidae as having two subfamilies and six genera. *Ephemerella*, *Ephemerellina*, *Teloganella* Ulmer, *Teloganodes*, and *Teloganopsis* were placed in the Ephemerellinae, and *Melanemerella* was placed in the Melanemerellinae. The placement of *Melanemerella* in the family Leptophlebiidae was resolved by Wang and McCafferty (1996a), the placement of *Ephemerellina* and *Teloganodes* was reviewed by McCafferty and Wang (1997), and the classification of *Teloganella* in the new family Teloganellidae is presented herein.

The unique absence of gills 2 in the larvae and absence of vestiges of such in the adults defines the family within the Ephemerelloidea in a cladistic sense. The family represents the Laurasian element among the Ephemerelloidea, and North America has been a particularly rich center

of evolution in both the subfamilies Ephemerellinae and Timpanoginae. Fossils assigned to the family Ephemerellidae include a larva from the Jurassic in China known as *Turfanerella tingi* (Ping) and a male subimago from Eocene Baltic amber that is known as *Timpanoga viscata* (Demoulin). The family classification of the former cannot be confirmed (McCafferty 1990). Based on gill vestiges apparent on the abdomen of the latter, a placement in the Timpanoginae of the Ephemerellidae appears to be correct (Demoulin 1968). There is insufficient evidence, however, to place this putative timpanogine to a particular genus with any confidence.

### Subfamily Ephemerellinae

Figs. 6, 39-49

Ephemerellidae Klapálek, 1909:13 (in part).

Baetidae (Ephemerellinae), Needham et al., 1935:234.

Ephemerellidae (Ephemerellinae), Edmunds and Traver, 1954:250 (in part).

**Larva.**— Maxillary palpi absent, or one to three segmented (Figs. 39-44). Filamentous gills 1 absent (Fig. 6); lamellate gills present on abdominal segments 3-7 (Figs. 6) (gills 7 sometimes minute and under gills 6).

**Adult.**— Abdominal segment 3 with gill socket vestiges (Fig. 46).

**Diagnosis.**— Ephemerellinae can be distinguished from Timpanoginae by the presence of gills 3 in the larval stage, and by the presence of gill socket vestiges on abdominal segment 3 in the adult stage.

**Genera included.**— *Caudatella* Edmunds (type: *Ephemerella heterocaudata* McDunnough); *Cawrinella* Allen (type: *C. idahoensis* Allen); *Cincticostella* Allen (type: *Ephemerella nigra* Uéno) [= *Asiatella* Tshernoval; *Crinittella* Allen and Edmunds (type: *Ephemerella coheri* Allen and Edmunds); *Drunella* Needham (type: *Ephemerella grandis* Eaton); *Eburrella* Kang and Yang (type: *Eburrella brocha* Kang and Yang); *Ephacrerella* Paclit (type: *Ephemerella longicaudata* Uéno) [= *Acerella* Allen, nec *Acerella* Berlese]; *Ephemerella* Walsh (type *E. excrucians* Walsh) [= *Chitonophora* Bengtsson]; *Hyrtanella* Allen and Edmunds (type: *H. christinae* Morgan); *Teloganopsis* Ulmer (*Serratella* Edmunds (type: *Ephemerella serrata* Morgan); *Teloganopsis* Ulmer (type: *T. media* Ulmer); *Tortya* Lestage (type: *T. belgica* Lestage); *Turfanerella* Demoulin (type: *Ephemeropsis tingi* Ping); *Uracanthella* Belov (type: *Ephemerella lenoki* Tshernova).

**Distribution.**— Holarctic; Oriental.

**Material examined.**— *Cincticostella nigra* Uéno, larvae, Japan; *C. sp.*, larvae, Korea; *Caudatella jacobi* (McDunnough), larvae, OR; *Cawrinella idahoensis* Allen, larvae, ID, MT; *Crinittella coheri* Allen and Edmunds, holotype and paratypes, larvae, Nepal; *C. sp.*, larvae, Malaysia; *Drunella allegheniensis* (Traver), larvae, GA, SC; *D. coloradensis* (Dodds), larvae,



CO, ID, MT, NV, OR, UT, WA, WY, Alberta; *D. cornuta* (Morgan), larvae, GA, NC, NH, VA, VT; *D. cornutella* (McDunnough), larvae, GA, NC, PA, WV; *D. doddsi* (Needham), larvae, CA, CO, ID, MT, NM, UT, WA, OR, WY; *D. flavilinea* (McDunnough), larvae, female subimagos, CA, CO, MT, OR, UT, WA, WY, Alberta; *D. gilliesi* (Allen and Edmunds), holotype and paratypes, larvae, Nepal; *D. grandis* (Eaton) larvae, male and female adults, AZ, CA, CO, ID, NM, MT, OR, UT, WA, WY, British Columbia; *D. kabulensis* Allen, paratypes, larvae, Afghanistan; *D. kohnoae* Allen, paratypes, larvae, Japan; *Ephemerella commoda* (Allen), paratypes, larvae, Thailand; *E. longicaudata* (Uéno), larva, Vietnam; *Ephemerella aliciana* Allen, larvae, AZ; *E. inconstans* Traver, larvae, GA, ME, MD, NC, SC, VA; *E. inermis* Eaton (AZ, CO, ID, MT, NM, OR, SD, UT, WA, WY; *E. infrequens* McDunnough, male and female adults, CA, CO, ID, OR, UT, WA, WY; *E. invaria* (Walker), larvae, male and female adults, GA, IN, NC, NY, SC, Ontario; *E. lacustris* Allen and Edmunds, paratypes, larvae, male adult, WY; *E. maculata* Traver, larvae, CA; *E. mollitia* Seemann, larvae, CA; *E. needhami* McDunnough, larvae, male and female adults, IN, MI, VA; *E. rossi* Allen and Edmunds, larvae, NC; *E. rotunda* Morgan, larvae, male and female adults, GA, KY, MA, MD, MI, NC, NY, PA, VT, Ontario; *E. septentrionalis* McDunnough, larvae, male and female adults, MA, NC; *E. subvaria* McDunnough, larvae, male and female adults, GA, MA, MD, IN, MI, NY, PA, SC, Ontario; *Hyrtanella christinae* Allen and Edmunds holotype and paratypes, larvae, female adults, Malaysia; *Serratella carolina* (Berner and Allen), paratypes, larvae, NC; *S. sp.*, larvae, IN; *Teloganopsis media* Ulmer, larvae, male and female adults, Malaysia; *Torteya* sp., larvae, Malaysia, Thailand; *Uracanthella* sp. larvae, Korea.

**Remarks.**—Klapálek (1909) first used the subfamily rank designation for *Ephemerella*. Since then, several genera have been added to this grouping. In addition, the status of Ephemerellinae has changed several times (see Remarks under Ephemerellidae), and some of the genera have necessarily been transferred to other groupings upon further, more detailed study (Wang and McCafferty 1995, McCafferty and Wang 1997). Ephemerellinae represents one of the most speciose groups of Pannota, and mayflies in general, in the Northern Hemisphere. Many of its members are well known for being associated with clean-water streams.

### Subfamily Timpanoginae, new status

Figs. 7, 51-53

Ephemerellidae (Timpanogae) Allen, 1984:246.  
Timpanoga complex, McCafferty and Wang, 1994:569.

**Larva.**—Maxillary palpi three segmented (Fig. 147). Filamentous gills 1 generally present (Fig. 7); lamellate gills present on abdominal segments 4-7 (Fig. 7).

**Adult.**—Abdominal segment 3 without gill socket vestiges (Fig. 51). **Diagnosis.**—Larvae of Timpanoginae can be distinguished from those of Ephemerellinae by the absence of gills 3 and, in most if not all cases, the presence of filamentous gills 1. Adults of Timpanoginae can be distinguished from those of Ephemerellinae by the absence of gill socket vestiges on abdominal segment 3.

**Genera included.**—*Attenella* Edmunds (type: *Ephemerella attenuata* McDunnough) [= *Attenuatella* Edmunds, nec *Attenuatella* Stehli]; *Eurylophella* Tiensuu (type: *E. karelica* Tiensuu) [= *Melanameteletus* Tiensuu]; *Timpanoga* Needham (type: *Ephemerella hecuba* Eaton) [= *Dannella* Edmunds].

**Distribution.**—Holarctic.

**Material examined.**—*Attenella attenuata* (McDunnough), larvae, male and female adults, AR, GA, MA, PA, VA; *A. delantala* (Mayo), larvae, CA; *A. margarita* (Needham), larvae, IN; *A. soquele* (Day), larvae, CA; *Eurylophella aestiva* (McDunnough), larvae, AR, IN; *E. bartoni* (Allen), larvae, Ontario; *E. bicolor* (Clemens), larvae, male and female adults, GA, IN, ME, NC, SC, TN, Ontario; *E. coxalis* (McDunnough), larvae, IN, NC; *E. funerals* (McDunnough), larvae, male and female adults, AR, GA, IN, MA, MD; *E. lodi* (Mayo), larvae, WA; *E. lutulenta* (Clemens), larvae, GA, MI, NC, TN, Ontario; *E. prudentialis* (McDunnough), larvae, male and female adults, MA, MN, NC, PA, SC; *E. temporalis* (McDunnough), larvae, male and female adults, GA, IN, KY, MN, NC, NH, VT; *E. verisimilis* (McDunnough), larvae, male and female adults, MA, ME, NC, SC; *Timpanoga hecuba* (Eaton), larva, male and female adults, AZ, MT, British Columbia; *T. lita* (Burks), larvae, male and female adults, IN, NC, WI; *T. provonsbai* (McCafferty), larvae, AR; *T. simplex* (McDunnough), larvae, male and female adults, IN, MA, MI, NE, VA, WI.

**Remarks.**—Divisions and ranking of higher taxa within the family Ephemerellidae historically have not been phylogenetic, nor have they claimed to be, but instead have had a roughly defined phenetic basis. The species now placed in the subfamily Timpanoginae had, for the most part, been placed in *Ephemerella* and later assigned to the subgenera *Attenella*, *Dannella*, *Eurylophella*, and *Timpanoga* within *Ephemerella* sensu lato. McCafferty (1977) showed that this was a monophyletic group defined by the loss of gills 3. McCafferty (1977) deduced phylogenetic relationships within the taxon based on several larval and adult charac-

ters. Allen (1984) recognized this taxon as the subtribe Timpanogae of the tribe Ephemerellini (Ephemerellidae: Ephemerellinae), stating that subtribes should be groups recognizable in one life stage but not in the other. Such a rule, however, is neither a precept of phylogenetic classification nor is it applicable to this grouping of species.

McCafferty and Wang (1994) discovered a universally diagnostic characteristic for distinguishing all adults of the *Timpanoga* complex [=Timpanoginae herein] from the adults of other Ephemerellidae. This characteristic of gill socket vestiges on the adult abdomen is obvious and simple to use. Although McCafferty and Wang (1994) gave a thorough review of this group, including generic level cladistics, the question of hierarchical category remained. New cladistic data herein indicate that recognition of this taxon at the subfamily level is consistent with the phylogenetic higher classification of the Pannota.

Edmunds (1959) in reference to this grouping of genera, stated that a rudimentary gill was often present on segment 1. In all the mature larvae that we have examined, we have been able to detect the presence of filamentous gills 1. There perhaps, however, are immature larvae or larvae of some species we have not seen that have independently lost the filamentous gills 1. McCafferty (1977) showed that filamentous gills 1 were displaced dorsally in *Timpanoga* hecuba, whereas they remained laterally oriented in all other Timpanoginae. Until the possibility that gills 1 are actually absent in some larvae can be confirmed, a (29\*) is left off the Timpanoginae branch in Fig. 1.

Although the Timpanoginae is a Holarctic subfamily, its greatest diversity by far is found in the Nearctic, probably at least in part due to the relative greater survival of the lineage in North America during recent circumpolar glacial events in the Northern Hemisphere. The report of the genus *Eurylophella* in Madagascar, based on a male subimago, by Allen and Edmunds (1963) is probably due to a labeling mistake, or possibly as the venation would suggest, it is actually a member of the Teloganodidae, although the subimaginal genitalia does not at this time support this latter proposition.

#### Family Austremerebellidae, new status

Figs. 7, 54-57

Teloganodidae (Austremerebellinae) McCafferty and Wang, 1997:392.

*Larva.*— Mature male eyes dioptic. Maxillary palpi absent or three segmented (Figs. 54, 55). Filamentous gills 1 present or absent; lamellate on abdominal segments 2-7 (Fig. 7), although gills 7 sometimes difficult to detect; gills 2 neither operculate nor semi-operculate. Median caudal filament developed. Inner margins of cerci with long, relatively dense, and sometimes forked, hairlike setae.

*Adult.*— Male eyes dioptic. Forewings (Figs. 56, 57) with MP2 considerably longer than longest ICuA; complex stigmatic area longitudinally subdivided by secondary vein into upper and lower rows of subequal sized cellules between C and Sc; three or more cubital intercalaries at angle with CuA, the first and/or second cubital intercalary attached to CuA, and all basally oriented toward CuA; middle marginal intercalaries single and detached or attached to crossveins. Gill socket vestiges on abdominal segment 7, although relatively obscure in some. Male forceps with segment 1 relatively long, more than twice as long as wide. Median caudal filament developed.

*Diagnosis.*— Larvae of Austremerebellidae can be distinguished from other ephemerelloids by the presence of lamellate gills 2-7 (although the small gills 7 may be difficult to detect, see discussion below). Other ephemerelloid families with gills 2 do not possess gills 7, and still others with gills 7 do not possess gills 2. The genus *Vietnamella* is very distinctive as larvae (see McCafferty and Wang 1997: Fig. 3). Adults of Austremerebellidae can be distinguished from other families with complex venation, dioptic male eyes, and middle tails, i.e., Ephemerellidae and some Teloganodidae, by the complex stigmatic area that is longitudinally subdivided by a secondary vein into upper and lower rows of several subequal sized cellules between C and Sc. Some species of Ephemerellidae and Teloganodidae may have some stigmatic reticulation or poorly formed upper, divided cells, but Ephemerellidae will not have gill socket remnants on abdominal segment 2, and Teloganodidae will not have gill socket remnants on abdominal segment 7. The generally greater number of cubital intercalaries and attachments to CuA in Austremerebellidae can also be used to distinguish adults from those of Teloganodidae.

*Genera included.*— *Austremerebella* Riek (type: *A. picta* Riek); *Vietnamella* Tshernova (type: *V. thani* Tshernova).

*Distribution.*— Australian; Oriental.

*Material examined.*— *Austremerebella picta* Riek, larvae, female adult, Australia; *Vietnamella thani* Tshernova, larvae, Vietnam.

*Remarks.*— Tshernova (1972) described the Oriental genus *Vietnamella* in the family Ephemerellidae, and although Allen (1980, 1984) placed this genus in the Ephemerellinae, Edmunds and Murvosh (1995) recognized that it was more closely related to the Teloganodinae sensu lato. Wang and McCafferty (1995) showed that all Oriental species that were previously known as adults and that were called *Ephemerellina* were in fact *Vietnamella*. The large number of autapomorphies of *Vietnamella* (McCafferty and Wang 1997) indicates that it is a relatively apotypic genus within a relatively plesiotypic family. The distinctiveness of the larvae, especially with respect to outgrowths of the head (see McCafferty and Wang 1997), could be considered aberrant, and it is not surprising that all workers previous to Edmunds and Murvosh (1995) considered

it in Ephemerellidae (Ephemerellinae). The taxonomy of the species is somewhat dubious at the present time because species have not been adequately compared with each other. For example, the known alate forms of *V. ornata* (Tshernova), a species unknown as larvae, may prove to be associated with the larvae of *V. thani*.

Gills 7 in the Austremereillidae are relatively very small and inserted sublaterally and dorsally at about mid length of segment 7, rather than at the posterior border, as are other lamellae. Such an insertion of terminal gill pairs may also be found in at least some Neoephemeridae and Ephemerellidae. This insertion position in Austremereillidae and some Ephemerellidae means that gills 7 can be essentially hidden under the small gills 6, as shown in Fig. 8. This is probably the reason that both Riek (1963), in his original description, and later Allen (1965) had previously miscounted gills in this group.

The Austremereillidae appears to be an ancient Gondwanan element represented in the southern Orient and Australia. The Australian genus *Austremereilla* is clearly the more generalized genus in the family (see also McCafferty and Wang 1997), and in many respects is perhaps the extant taxon closest to the hypothetical precursor of the entire superfamily Ephemerelloidea.

#### Family Teloganodidae

Figs. 8, 58-62

Ephemerellidae (Teloganodinae) Allen, 1965:163.  
Teloganodidae, McCafferty and Wang, 1997:390 (in part).

**Larva.** - Male eyes dioptic. Maxillary palpi absent (Figs. 58). Claws with denticles. Forefemora variously expanded or not expanded. Filamentous gills 1 absent or present; lamellate gills on abdominal segments 2-4, 2-5 (Fig. 8) or 2-6; gills 2 operculate or semi-operculate (Fig. 8). Median caudal filament developed or reduced.

**Adult.** - Male eyes dioptic. Forewings (Figs. 59, 60) with MP2 often considerably longer than longest ICuA vein; zero, one, or rarely two cubital intercalaries connected to CuA; middle marginal intercalaries single and mostly detached. Abdominal segment 2 with gill socket vestiges (Fig. 61); segment 7 without such vestiges. Male forceps with segment 1 relatively long, more than twice as long as wide (Fig. 62). Median caudal filament developed or reduced.

**Diagnosis.** - Larvae of Teloganodidae are distinguished from those of Ephemerellidae by the presence of gills 2, from those of Austremereillidae by the absence of gills 7, and from other ephemerelloids by the dioptic eyes of the males. They may be additionally distinguished in Africa from the somewhat similar larvae of Ephemerithidae by the labrum of the former, which is not nearly as short and broad, and by the presence of

submedial lobes or a margin offset from the wingpads on the notal margin between the forewingpads in mature individuals. Male and female larvae of known Teloganellidae differ from those of Teloganodidae in lacking claw denticles and submedial lobes on the posterior margin between the mature forewingpads. Adults of Teloganodidae differ from those of other ephemerelloids with marginal intercalaries in the outer margin of the forewings and dioptic eyes in the males by the combination of presence of gill socket vestiges on abdominal segment 2, their male forceps, and the reduced basal attachments of cubital intercalaries with CuA. They may be distinguished from all other ephemerelloids by the male dioptic eyes and the shape and segmentation of the forceps. Male and female adults of those ephemerelloids with holoptic male eyes and single marginal intercalaries (i.e., family Teloganellidae) should be distinguishable by a crossvein in the forewings that attaches CuA and the longest ICuA1 at about mid length of ICuA1, and often the presence of a cubital fork (see Teloganellidae, below).

**Genera included.** - *Ephemerellina* Lestage (type: *E. barnardi* Lestage); *Lestagella* Demoulin (type: *Litbogloea penicillata* Barnard); *Litbogloea* Barnard (type: *L. harrisoni* Barnard); *Macafertiella* Wang (type: *M. insignis* Wang and McCafferty); *Manohyphella* Allen (type: *M. keiseri* Allen); *Nadinella* McCafferty and Wang (type: *Ephemerellina crassi* Allen and Edmunds) [= *Nadinella* McCafferty and Wang, nec *Nadinella* Penard]; *Teloganodes* Eaton (type: *Cloc tristis* Hagen).

**Distribution.** - Afrotropical; Oriental.

**Material examined.** - *Ephemerellina barnardi* Lestage, larvae, male and female adults, South Africa; *Nadinella crassi* (Allen and Edmunds), larvae, male and female adults, South Africa; *Lestagella penicillata* (Barnard), larvae, male subimago, South Africa; *Litbogloea harrisoni* Barnard, larvae, male and female adults, South Africa; *Macafertiella insignis* Wang and McCafferty, larvae, Sri Lanka; *Teloganodes tristis* (Hagen), larvae and male subimagos, Malaysia, Sri Lanka; *Teloganodes* spp., larvae, Indonesia, Thailand; undescribed genus, female larva (possibly *Manohyphella*), Madagascar, Prov. Fianar., Tsaratango R., 9 km E Ranomafana.

**Remarks.** - Teloganodidae is a group of pannote mayflies that generally have not been well known in the past, and incomplete and sometimes erroneous information has resulted in a history of divergent interpretations. The family, however, has been recently comprehensively revised (as the subfamily Teloganodinae of the family Teloganodidae), including the incorporation of a cladistic based generic classification (McCafferty and Wang 1997). The original subfamily Teloganodinae traditionally had been included in the Ephemerellidae. Allen (1965) erected the subfamily Teloganodinae within the Ephemerellidae, and included the genera *Teloganodes* and *Ephemerellina*. He considered *Austremereilla*, from Australia, to be synonymous with

*Ephemerellina*; he did not mention *Lithogloea*. Wang and McCafferty (1995) showed, however, that those Oriental species placed in *Ephemerellina* (Tshernova 1972) were in actuality members of *Vietnamella* (Austremereidae herein). Allen (1973) described the genus *Manobryphella* Allen from Madagascar and added it to the Teloganodinae along with *Teloganella*. Although never stated by Allen, *Lestagella* was also, by default, considered in the subfamily Teloganodinae, because he did not include it in Ephemerellinae of Ephemerellidae (Allen 1980, 1984). Wang et al. (1995) removed *Teloganella* from the Ephemerellidae and Teloganodinae, and our present study places it in the new family Teloganellidae. McCafferty and Wang (1995) also removed *Manobryphella* from Ephemerellidae and Teloganodidae because it was at that time presumed to be a member of the same grouping as *Teloganella*. McCafferty and de Moor (1995) re-established the genus *Lithogloea*, thus adding it to the Teloganodinae. Finally, the Sri Lanka genus *Macaferiella* Wang was described recently in the Teloganodinae (see Wang and McCafferty 1996b).

We have recently reconsidered the genus *Manobryphella* from Madagascar from a large comparative base and are able to confirm that the forewing figure of Allen (1973), presumably of the holotype or paratype female adult, shows venation characteristics, particularly the cubital system, that would place it in Teloganodidae, not Teloganellidae. Male adults and thus genitalia, however, remain unknown for *Manobryphella*. We are in possession of the paratype that Allen (1973) designated for *Manobryphella keiseri* (type of the monospecific genus) and which was originally deposited at the University of Utah. This paratype was collected in 1971 from Madagascar, whereas the holotype had been collected in 1958 from a different locality in Madagascar. The paratype is neither the same genus nor family as the holotype, but instead represents an undescribed genus of Teloganellidae in Madagascar (see further Remarks under Teloganellidae, below). Based on just the examination of the paratype, McCafferty and Wang (1997) excluded what they assumed was *Manobryphella* from consideration in Teloganodidae at that time, because what supposedly was its wing venation (Fig. 67) was essentially similar to that of *Teloganella* (Figs. 68, 69).

A female larva from Madagascar in our possession that was presumed to be the larvae from *Manobryphella* was collected from a third locality in Madagascar by G. F. Edmunds in 1971, and was assumed by him to be the larva of *Manobryphella*. This assumption was followed by Wang et al. (1995) when they gave some details of this larvae; however, because the larva had not been associated with any adult by rearing, it cannot definitively be placed to any genus although we agree that it is probably *Manobryphella*. Because it cannot now be ascertained whether the male eyes are dioptic, as they are in Teloganodidae, or holoptic, as they are in

Teloganellidae, there might be some doubt as to which of these families it belongs. Although immature, there is a slight indication of submedial lobes between the forewingpads as found in the known mature Teloganodidae larvae, but not in the known Teloganellidae. There are claw denticles present in the undescribed Madagascar larva as in Teloganodidae but not present in known Teloganellidae. The robust medial row of dorsal abdominal tubercles is reminiscent of some of the Teloganodidae, but not the known Teloganellidae. Other mouthparts and lamellate gill distribution (2-5) are not suggestive of one or the other family; however, the forelegs and gills 1 are very reminiscent of those of the South African teloganodid *Lestagella* (McCafferty and Wang 1997: Fig. 7), and the head capsule and lamellate gills are reminiscent of the teloganodid genus *Nadinetella* (Fig. 9). These similarities and the presence of a developed median caudal filament suggests to us a close relationship with the South African members of the Teloganodidae.

There are only 13 species currently described in the family. This may, in part, be attributed to the relict nature of the group, which was thoroughly discussed by McCafferty and Wang (1997); however, we anticipate that several more species will be described from the more apotypic Oriental fauna within the family. For example, we have examined at least five new species of *Teloganodes* from the Southeast Asia.

#### Family Teloganellidae, new family

Figs. 10, 63-70

**Larva.**—Mature male eyes holoptic. Labrum short and broad (Fig. 63). Mandibles slender (Fig. 64). Maxillary palpi absent (Fig. 65). Labial palpi three segmented (Fig. 66). Claws without denticles. Forefemora greatly expanded anteriorly and margined by short, stout setae (Fig. 10). Hindwingpads present and minute. Filamentous gills 1 present; lamellate gills present on abdominal segments 2-5; gills 2 operculate (Fig. 10). Median caudal filament developed.

**Adult.**—Male eyes holoptic. Forewings (Fig. 67-69) with simple, mostly detached marginal intercalaries in mid region; MP2 considerably longer than longest ICuA; ICuA1 and CuA connected by crossvein about mid length of ICuA1; ICuA1 either attached directly to CuP (Fig. 68), or ICuA1-CuP connection bridged by crossvein (Fig. 69), or connection not quite entire (Fig. 67), either forming or suggesting cubital fork; often shallow ICuA1-ICuA2 fork also formed. Minute hindwings present. Known male genitalia (Fig. 70) with highly elongate medial subgenital process and with short basal forceps segment and elongate distal segment. Median caudal filament developed.

**Diagnosis.**—The larvae of Teloganellidae can be distinguished from those of other ephemerelloids with holoptic male eyes and that lack

submedial lobes on the posterior margin between the mature forewingpads by the presence of filamentous gills 1. Males and females of known larval of Teloganellidae can be distinguished from those of Teloganodidae, which also may have filamentous gills 1, lamellate gills on abdominal segments 2-5, and a developed median caudal filament, by the lack of claw denticles and submedial lobes on the posterior margin between the mature forewingpads. The adults of Teloganellidae can be distinguished from other ephemerelloids with holoptic male eyes by having single marginal intercalaries in the forewings. Males and females can be told from other ephemerelloids with single marginal intercalaries in the outer margin of the forewing by the presence of, or strong suggestion of, a cubital fork, albeit shallow, in the forewings in addition to the medial connection of ICuA1 and CuA by a crossvein.

*Genera included.*- *Teloganella* Ulmer (type: *T. umbrata* Ulmer); undescribed genus.

*Distribution.*- Madagascar (undescribed genus); Oriental (*Teloganella*).

*Material examined.*- *Teloganella umbrata* Ulmer, larvae, male and female adults, Malaysia; undescribed genus, adult female, Madagascar (originally incorrectly identified as *Manohybella keiseri* Allen, paratype).

*Remarks.*- Historical confusion surrounding this group has involved the occasional placement of *Teloganella* in the Teloganodinae sensu lato of the family Ephemerellidae sensu lato based on symplesiomorphies (e.g., Peters and Peters 1993), and the incorrect association of certain Madagascar larvae now known to belong to the family Caenidae (subfamily Madecocercinae) (McCafferty and Wang 1995) or the Teloganodidae (see Teloganodidae, above). The caenid, named *Provonshaka* McCafferty and Wang, has proven to be the larval stage of *Madecocercus* (J.-M. Elouard, pers. comm.), which had originally been based on adults from Madagascar described in the same year by Malzacher (1995). Obviously, Caenidae and Teloganellidae belong to entirely different major clades (superfamilies) as shown in Fig. 1 and classified herein.

In adult specimens of both *Teloganella* from the Orient and an unnamed genus from Madagascar that we have studied, the ICuA1 of the forewings is connected to CuA by a medial crossvein (see Figs. 67-69). Figure 2 of Allen (1973) of the *Manohybella* forewing (presumably the female holotype of the type species *M. keiseri* Allen), places that genus in Teloganodidae, and not as a cognate of *Teloganella*, which would have been concluded based on our examination of what proved to be the incorrectly identified paratype of *M. keiseri*. The latter actually represents an undescribed genus of Teloganellidae from Madagascar, and its forewing is illustrated herein (Fig. 67). The larva from Madagascar that McCafferty and Wang (1995) considered *Manohybella* for comparative purposes is provisionally considered a teloganodid, and possibly the true *Manohybella* (see Remarks under Teloganodidae, above).

### Family Ephemerithidae, new status Figs. 11, 71-76

Tricorythidae (Ephemerythinae) Gillies, 1960:35.

*Larva.*- Mature male eyes holoptic. Labrum short and broad (Fig. 71). Mandibles stout, with developed incisors (Fig. 72). Maxillary palpi absent (Fig. 73). Forefemora only moderately expanded, with subapical row of spatulate setae (Fig. 11). Hindwingpads present and minute. Filamentous gills 1 absent; lamellate gills present on abdominal segments 2-5; gills 2 operculate, narrow-oblong (Fig. 11). Median caudal filament developed.

*Adult.*- Male eyes holoptic. Forewings (Fig. 75) with middle marginal intercalaries short, detached, and double; ICuA1 attached to CuP, forming moderately developed cubital fork, never attached to CuA by crossvein, and not forming additional cubital fork with ICuA2. Minute hindwings present. Male genitalia (Fig. 76) with medial subgenital process moderately developed; forceps segments subequal in length; penes highly reduced. Median caudal filament developed.

*Diagnosis.*- The larvae of Ephemerithinae are easily distinguished from those of Teloganellidae, which also have operculate gills 2 and lamellate gill formula 2-5, by the lesser development and setation of the forefemora, and the absence of filamentous gills 1. The shape of the operculate gills, the absence of maxillary palpi, and the absence of gills 6 can be used to distinguish them from other ephemerelloid larvae in Africa that lack submedial lobes on the posterior margin between the mature forewingpads and that have operculate gills (i.e., Machadoriithidae). The adults of Ephemerithidae can be distinguished from all other Pannota by the presence of detached, double marginal intercalaries in the outer margin of the forewings.

*Genera included.*- *Ephemerythus* Gillies (type: *E. niger* Gillies).

*Distribution.*- Afrotropical (Africa).

*Material examined.*- *Ephemerythus kiboensis* Gillies, male adults, Tanzania; *E. spp.*, larvae, male adults, Congo, South Africa, Morocco, Nigeria, Tanzania.

*Remarks.*- This taxon initially appeared so bizarre that Kimmins (1955) did not name the species he had when describing its larvae, but believed it possibly to belong to Ephemerellidae. McCafferty and Wang (1997) indicated that many *Ephemerythus* were misidentified in collections and reported in the literature as certain teloganodid genera (Ephemerellidae sensu lato). Gillies (1960) first described the adult of *Ephemerythus*, which is quite intermediate in a number of respects between the ephemerelloids with dioptic eyes (the traditional ephemerellids) and those more apotypic ephemerelloids with holoptic

eyes (the traditional tricorythids). Kopelke (1981) further associated the larvae and adult of *Ephemerythus*, and confirmed that Kimmins' ephemerellid larvae belonged to Gillie's tricorythid adult. The taxon can now be shown to be closely related to the Teloganellidae, and essentially intermediate between the latter and the other ephemerelloids with holoptic male eyes and highly fused mature forewingpads (lacking the submedial lobes on the posterior border between forewingpads).

It may seem feasible to place the Teloganellidae and Ephemerythidae together as sister lineages (and in the same family) because of short, broad labra in the larvae, the medial projection of the subgenital plate, and some other shared characteristics as discussed above under Higher Classification. The loss of the filamentous gills 1, however, and venation trends argue for a sequential relationship as hypothesized in Fig. 1. Also, adults of Ephemerythidae lack a transverse suture on the mesonotum, whereas those of Teloganellidae have such a transverse suture. Although the family Ephemerythidae clearly shares an immediate common ancestor with more apotypic ephemerelloids, our data now show that it represents a lineage certainly more closely related to the Teloganellidae and the more pleistotypic, dioptic eyed ephemerelloids than may have been previously thought.

#### Family Machadorythidae, new status

Figs. 12, 77-83

Tricorythidae (Machadorythinae) Edmunds et al., 1963:17.

**Larva.**- Mature male eyes holoptic. Compound eyes protruding dorsally above convergently narrowed vertex (Figs. 12, 77). Galealaciniae (Fig. 78) narrow, with setae restricted to crown or margin; maxillary palpi two segmented. Labium (Fig. 79) with glossae fused with paraglossae; palpi robust, two or three segmented, segment 3 when present, very short and indistinct. Forefemora (Fig. 15) highly reduced, with poorly developed basal setae. Hindwingpads absent. Flanges of mid abdominal segments extended and strongly upturned dorsally, forming gill chamber (Figs. 12, 80). Filamentous gills 1 absent; lamellate gills on abdominal segments 2-6; gills 2 operculate, with underlying gill branches as in Fig. 81. Median caudal filament developed.

**Adult.**- Male eyes holoptic. Forewings (Fig. 82) without marginal intercalaries in outer margin; with ICuA1 subequal in length to MP2, attached to CuP at ca. mid length of CuP, forming broad, moderately deep cubital fork. Hindwings absent. Male forceps (Fig. 83) two segmented, with short, globular basal segment. Median caudal filament developed.

**Diagnosis.**- Larvae of Machadorythidae can be distinguished from those of all other mayflies by the dorsal protrusion of the closely set eyes

on a narrowed and raised vertex, the presence of the gill chamber, the fused glossae and paraglossae, and the lack of filamentous gills 1. The Holarctic/Oriental Brachycercinae (Caenidae) are superficially similar, but lack the peculiar head and narrow set eyes and have the filamentous gills 1. The Neotropical genus *Coryphorus* Peters of the Leptohephyidae is also superficially similar, but the head and eye set is fundamentally different, and there are considerable other differences (see Leptohephyidae, below, and the key to larvae). The adults of Machadorythidae can be distinguished from other ephemerelloids with holoptic male eyes, cubital forks, no outer marginal intercalaries in the forewings, and sometimes no hindwings, by the absence of a well-developed ICuA2 and ICuA1-ICuA2 fork.

**Genera included.**- *Machadorythus* Demoulin (type: *M. palanquin* Demoulin).

**Distribution.**- Afrotropical (Africa).

**Material examined.**- *Machadorythus maculatus* Kimmins, larvae, South Africa; *Machadorythus* spp. larvae, South Africa.

**Remarks.**- A monogeneric Afrotropical Machadorythinae traditionally has been included in Tricorythidae sensu lato (Edmunds and Traver 1954). At the time that Peters (1981) described the genus *Coryphorus* from South America, he placed it in Machadorythinae. Later, however, Peters and Peters (1993) transferred *Coryphorus* into Leptohephyidae sensu lato. Cladistic analysis shows that Machadorythidae, although highly specialized in the larval stage with numerous adaptive autapomorphies, is essentially intermediate between the more plesiomorphic ephemerelloids with holoptic male eyes and highly fused forewingpads (without submedial lobes) (Teloganellidae and Ephemerythidae) and the more apotypic members with such characteristics (Tricorythidae and Leptohephyidae). Machadorythidae is the most pleistotypic family of ephemerelloids without marginal intercalaries in the outer margin of the forewings.

The larvae of Machadorythidae are among the most specialized of mayflies. One of us (WPM) has collected the larvae in South Africa in the very same kind of riverine habitat where he has collected the genus *Brachycercus* (Caenidae: Brachycercinae) in North America. *Machadorythus* larvae were found near the sand-silt substrate surface in slow to moderate current while kicking for burrowing mayflies. The narrow, crablike legs may be an adaptation for moving rapidly over the substrate, as has been observed for the genus *Pseudiron* (Pseudironidae) in North America (McCafferty and Provonsha 1986). The protruding eyes may allow vision in the water as the rest of the body may become covered with silt-sand. The eyes of the Neotropical genus *Coryphorus* (Leptohephyidae) are also protuberant but are set broadly and dorsolaterally on a broad vertex. The ocelli of the Brachycercinae, which are raised on tubercles, may function somewhat similarly. The gill chamber, formed by upturned lateral extensions of the mid abdominal segments and found

exclusively in Machadorythinae, Brachycercinae, and *Coryphorus*, would appear to give added protection to the gills, possibly again because of the habit of partial submergence in the sand/silt substrate. There are striking similarities in body shape, leg size and orientation, head sensory structure orientation, and gill and abdominal structure. WPM was also struck by the similarity of the behavior of live larvae collected of Brachycercinae and Machadorythidae. Short forelegs of both appear to be used for head cleaning. This then appears to be a classical case of adaptive convergence, and parallelism demonstrated by three different lineages, in three different parts of the world, associated with similar evolutionary specialization for similar habitat.

### Family Tricorythidae

Figs. 13, 14, 84-100

Tricorythidae Lestage, 1942:15 (in part).

Tricorythidae (Tricorythinae), Edmunds and Traver, 1954:238 (in part).

Tricorythidae (Diceromyzinae) Edmunds and Traver, 1954:238 (in part).

Leptohyphidae (Diceromyzinae), Landa and Soldán, 1985:104 (in part).

**Larva.** - Male eyes holoptic. Maxillae (Figs. 85, 92) with galealaciniae robust, with well-developed subapical setae on surface; palpi two or three segmented. Labium (Figs. 87, 94) with paraglossae expansive, and entirely fused with glossae in some. Width of forefemora variable (Figs. 13, 14), and femora with or without row of spatulate setae. Hindwingpads absent. Abdominal segments 2-6 (Figs. 13, 14, 95) without well-developed lateral flanges. Filamentous gills 1 absent; lamellate gills on abdominal segment 2-6; gills 2 not operculate or semi-operculate (Figs. 13, 14). Median caudal filament reduced or developed.

**Adult.** - Male eyes holoptic. Forewings (Figs. 88, 98) with marginal intercalaries absent from outer margin; MP2 subequal in length to entire stalked ICuA; ICuA1 attached to CuP, forming cubital fork, with stalk attached to CuA by basal crossvein; ICuA2 well developed and in most forming secondary ICuA1-ICuA2 fork. Hindwings absent. Male genitalia with forceps as in Figures 89, 90, 99, 100; penes with or without auxiliary processes, variously developed when present. Median caudal filament developed or reduced.

**Diagnosis.** - Known larvae of Tricorythidae may be distinguished from those of other ephemerelloids that have holoptic male eyes and that lack submedial lobes along the notal margin between the mature forewingpads, i.e., Teloganellidae, Ephemerithidae, Machadorythidae, and Leptohyphidae, by the lack of operculate gills and by broad maxillae that have well-developed subapical setae on the surface. They may be additionally distinguished from Leptohyphidae and Machadorythidae by not having abdominal segments 2-6 expanded laterally into flanges,

and from Teloganellidae and Ephemerithidae by the presence of gills 6 and absence of hindwingpads. The adults of Tricorythidae can be easily distinguished from other ephemerelloids with male holoptic eyes and no marginal intercalaries in the outer margin of the forewings, i.e., Machadorythidae and Leptohyphidae, by the combination of having a short-stalked and broadly angled ICuA1-CuP fork and an MP2 subequal in length to the entire ICuA in the forewings. Machadorythidae have the CuP stalk of such a fork about as long as the fork, and Leptohyphidae, which also lack the hindwings in some, tend to have their entire forked ICuA distinctly longer than MP2, although it may not be surprising to find some variation in this as more genera become known. Nevertheless, Leptohyphidae is restricted to the Western Hemisphere, and Tricorythidae is restricted to the Eastern Hemisphere. The short globular basal segment of the forceps can also be used to distinguish Machadorythidae from Tricorythidae in Africa.

**Subfamilies included.** - Tricorythinae; Diceromyzinae.

**Distribution.** - Afrotropical; Oriental.

**Remarks.** - Tricorythid mayflies have been classified in Caenidae, Ephemerellidae, and as a separate family with polyphyletic components. Larvae are diverse and quite specialized within the family in its present sense. Wing venation is relatively consistent throughout the family, although the ICuA1-ICuA2 fork is not entire in all of them. Diversity in adults is seen mainly in male genitalia differences and in the variable presence or absence of the median caudal filament. Known larvae within the family are highly specialized with respect to each genus, although gills are not operculate in the group, and maxillae also are characteristic of the group in terms of the orientation of surface setae.

The phylogenetic position of the two main lineages making up the Tricorythidae (Tricorythinae and Diceromyzinae) could, by phylogenetic rule, be considered at the family level. Because of the relatively homogeneous adults in the family Tricorythidae and fundamental similarities in the known larvae, we are taking a conservative stance in this respect.

Certain genera recently discovered from Madagascar by Elouard and Oliariny (1997) and Oliariny and Elouard (1997) were described from adults only. The characteristics of these adults, described as *Ranorythus* and *Madecassorythus*, clearly place them with the Tricorythidae in the cladogram (Fig. 1). Those authors placed these Madagascar genera, and apparently at least one other undescribed Madagascar genus (referred to prematurely as *Spinirythus*), into two new subfamilies, Ranorythinae and Madecassorythinae (although only the name appeared in the article title and no formal description of Ranorythinae was given). This apparently was done mainly on the basis of some unusual modification of the male genitalia, particularly regarding the penes. Such modifications have historically been viewed mainly as species or

generic level characteristics because they are associated with sexual isolation, which is a species level phenomenon. Ranorythinae and Madecassorythinae may indeed prove to be warranted once larval characterization becomes known, and might even prove justifiable as separate phylogenetic families. For the time being, however, we are including these Madagascar genera in the family Tricorythidae sensu stricto. See further discussion under the subfamilies Tricorythinae and Dicercomyzinae, below. The only genus of Tricorythidae in Madagascar that we know for sure will key out using the larval key provided herein is *Tricorythus*. (*Neurocaenis* Navás, a generic name historically used in both Madagascar and Africa, is considered a junior synonym of *Tricorythus*.)

### Subfamily Tricorythinae

Figs. 13, 84-90

Tricorythidae Lestage, 1942:15 (in part).

Tricorythidae (Tricorythinae), Edmunds and Traver, 1954:238.

Tricorythidae (Ranorythinae) Ollariomy and Elouard, 1997:439 (n. syn.).

**Larva** (based on *Tricorythus*): Mandibles expanded and flat, with well-developed, elongate filtering setae along outer margin (Fig. 84). Hypopharynx as in Fig. 86. Labium (Fig. 88) with paraglossae and glossae fused, with setaceous palpi. Pro- and mesosternum without disc of friction hairs. Forefemora slightly expanded, with row of spatulate setae (Fig. 13).

**Adult**:—Penes (Figs. 89, 90) entire basally and variably divided distally, without auxiliary processes. Median caudal filament developed or reduced.

**Diagnosis**.—The known larvae of Tricorythinae can be distinguished from the known larvae of Dicercomyzinae by the highly specialized mandibles, whose filtering setae flare into a distinctive fan when exposed to current (McCafferty and C. Palmer unpublished), the narrower femora, and the lamellate nature of the gills. The adults of Tricorythinae can be distinguished from those of Dicercomyzinae by their lack of auxiliary processes associated with the penes.

**Genera included**.—*Ranorythus*Ollariomy and Elouard (type: *R. violletae* Ollariomy and Elouard) (provisional inclusion); *Tricorythus* Eaton (type: *Caenis variaecauda* Pictet) [= *Neurocaenis* Navás, = *Tricorythus* Lestage].

**Distribution**.—Afrotropical; Oriental.

**Material examined**.—*Tricorythus jacobsoni* Ulmer, male and female adults, Indonesia; *T. spp.*, larvae, male and female adults, Madagascar, South Africa.

**Remarks**.—The fact that the relative development of the median

caudal filament is not of importance in the classification of the Tricorythidae or for subfamilies within it is borne out by our observations of *Tricorythus* from Madagascar. Some species have a reduced medial caudal filament (two tailed) as adults and some have a well-developed median caudal filament (three tailed). The genitalia we have observed are similar and typical of the genus in adults of both tail types. We have not yet, however, seen larvae with two tails. *Ranorythus* adults reportedly have a reduced median caudal filament (Ollariomy and Elouard 1997), and although the larvae and adults are usually in agreement in this respect in other taxa of Ephemeroidea, there obviously is a distinct probability that the larvae of *Ranorythus* are three tailed. A somewhat similar diversity of median caudal filament development in the Pannota can be found within the family Teloganodidae *sensu stricto* (McCafferty and Wang 1997).

As indicated above, the placement of *Ranorythus* in Tricorythinae is provisional and determined somewhat by default because, based only on the known adults, this is where it would fall in the cladogram (Fig. 1). It should be noted that the autapomorphy defining this subfamily is a characteristic associated with the adaptive filter feeding of the larvae and thus we cannot be confident it is associated also with *Ranorythus*. An adult synapomorphy was not identified for the subfamily, although the sister lineage Dicercomyzinae indeed possesses at least one adult autapomorphy found in all known genera, which involves the development of auxiliary processes associated with the penes. The lack of that synapomorphy in *Tricorythus* and *Ranorythus* suggests by default that *Ranorythus* belongs in the Tricorythinae lineage.

### Subfamily Dicercomyzinae

Figs. 14, 91-100

Tricorythidae (Dicercomyzinae) Edmunds and Traver, 1954:238.

Leptohyphidae (Dicercomyzinae), Landa and Soldán, 1985:104.

**Larva** (based on *Dicercomyzon*): Mandibles (Fig. 91) narrow-elongate, not fitted with long filtering setae. Superlinguae of hypopharynx (Fig. 93) highly developed laterally. Labium (Fig. 94) with well-developed paraglossae and reduced palpi. Pro- and mesosternum with disc of friction hairs (Fig. 95). All femora expanded (Fig. 14) (hindfemora often covering abdominal gills). Gills 2-6 fibrillate and more or less oriented laterally (Figs. 14, 96, 97).

**Adult**.—Penes (Figs. 99, 100) slightly to deeply divided, with auxiliary processes. Median caudal filament developed or reduced.

**Diagnosis**.—Known larvae of Dicercomyzinae can be distinguished from known larvae of Tricorythinae by the highly expanded femora, dorsoventrally flattened body, and ventral friction disc. The adults of



Diceromyzinae can be distinguished from those of Tricorythinae by the presence of auxiliary processes associated with the penes.

*Genera included.*- *Diceromyzon* Demoulin (type: *D. femorale* Demoulin); *Madecassorythus* Elouard and Olliaromy (type: *M. hertwi* Elouard and Olliaromy) (provisional inclusion).

*Distribution.*- Afrotropical.

*Material examined.*- *Diceromyzon femorale* Demoulin, larvae, paratype adults, Congo; *D. spp.*, larvae, Nigeria, South Africa, Tanzania.

*Remarks.*- Larvae of *Diceromyzon* are specialized sprawler/clingers with depressed bodies that are also broadened, owing mostly to the wide femora that are held juxtaposed to the lateral line of the body. Such a depressed body type has been associated primarily with the flatheaded mayflies, family Heptageniidae. A low profile of the body in benthic insects is generally associated with sprawlers, allowing them to live in crevices, or clingers, allowing them to live within the boundary layer of the current (see McCafferty 1981). Like certain other ephemeroptera in disparate groups such as Leptohephidae and Teloganodidae, there is a fringe of setae anteriorly on the head in *Diceromyzon*.

This subfamily could be justified at full familial rank based on its phylogenetic position. However, based on the rather uniform adults, we are maintaining it with its sister lineage in the family Tricorythidae (also see the numerous larval characteristics in common, under the description of the family). The larvae of certain Madagascar genera (e.g., *Madecassorythus*) remain unknown, but, based on adult male genitalia, they would appear to be related to the Diceromyzinae. This provisional placement may require revision in the future as larvae become known in Madagascar.

### Family Leptohephidae

Figs. 15, 101-116

Tricorythidae (Leptohephinae) Edmunds and Traver, 1954:238.  
Leptohephidae, Landa and Soldán, 1985:103 (in part).

*Larva.*- Mature male eyes holoptic. Galealacinae (Figs. 101-104) narrow, with setae restricted to crown or margin; maxillary palpi absent (Fig. 104) or one to three segmented (Figs. 101-103). Labium (Figs. 105, 106-108) with glossae very small, or fused with paraglossae; palpi two or three segmented, with terminal segment (whether segment 2 or 3) relatively weak. Forefemora (Figs. 15) not expanded to moderately expanded, usually with well-developed basal, medial, or subapical row of spatulate, bifurcate, or bristlelike setae. Hindwingpads present or absent. Various developed flanges on abdominal segments 2-6, usually laterally oriented (Figs. 15, 110), or rarely dorsally upturned to form gill chamber (Fig. 109); posterolateral projections not developed or devel-

oped on segments 7-9. Filamentous gills 1 absent; lamellate gills on abdominal segments 2-6, or rarely 2-5; gills 2 operculate (Figs. 15, 109), variously shaped. Median caudal filament developed.

*Adult.*- Forewings (Figs. 112, 113) without marginal intercalaries in the outer margin; cubital fork often consisting of deep ICuA1-ICuA2 fork (Figs. 112, 113), although this fork not entire or evident in some; if ICuA1-CuP connection maintained, then usually very near base of wing and not strongly angled at base (Fig. 112); entire stalked ICuA longer than MP2, distinctly longer when only ICuA1-CuP fork present, or ICuA1, itself, distinctly longer than MP2 when no cubital forks present. Hindwings present or absent. Male forceps (Figs. 112-114) either two segmented, or with additional small, third, distal segment; basal segment elongate or somewhat shortened in some; forceps rarely aberrant (Traver 1958: Fig. 4; Mayo 1968: Fig. 5). Median caudal filament developed.

*Diagnosis.*- Larvae of Leptohephidae are the only larvae of ephemeroptera in the Western Hemisphere with operculate gills 2 together with no filamentous gills 1 (see also larval key, below). The adults of Leptohephidae are the only pannote mayfly adults in the Western Hemisphere having no marginal intercalaries in the forewings together with lacking an ommatium on the mesonotum. A combination of characters would have to be used in order to differentiate all leptohephid adults from all tricorythid adults; however, this is not a practical problem considering that their world distributions do not overlap.

*Genera included.*- *Allenhephes* Hofmann and Sartori (type: *Leptohephes flinti* Allen); *Coryphorus* Peters (type: *C. aquilus* Peters); *Cotopaxi* Mayo (type: *C. macuchae* Mayo); *Haplohephes* Allen (type: *H. huallaga* Allen); *Leptohephes* Eaton (type: *L. eximius*) [= *Bruchella* Navás]; *Leptohephodes* Ulmer (type: *Potamanthus inanis* Pictet); *Tricorythodes* Ulmer (type: *Tricorythus explicatus* Eaton) [= *Caenopsis* Needham, = *Needhamocoenis* Leatage, = *Tricorythofer* Lestage]; *Tricorythopsis* Traver 1958 (type: *T. aritigas* Traver).

*Distribution.*- Nearctic; Neotropical.

*Material examined.*- *Cotopaxi macuchae* Mayo, holotype male adult, Ecuador; *Haplohephes huallaga* Allen, larvae, holotype and paratype male adult, Peru; *H. aquilonius* Lugo-Ortiz and McCafferty, holotype and paratype larvae, Costa Rica, Colombia; *Leptohephes curvius* Lugo-Ortiz and McCafferty, larvae, Costa Rica; *L. dolani* Allen, larvae, NC; *L. liniti* Wang, Sites, and McCafferty, larvae, Ecuador; *L. nicholsae* Wang, Sites, and McCafferty, larvae, Ecuador; *L. zalope* Traver, larvae, NM; *L. spp.*, larvae, male and female adults, Argentina, Brazil, Uruguay, Venezuela; *Tricorythodes allectus* (Needham), male and female adults, IN; *T. atratus* (McDunnough), larvae, male and female adults, AR, IN; *T. conchylius* Allen, larvae, NM; *T. corpulentis* Kilgore and Allen, larvae, CO; *T.*

*dimorphus* Allen, larvae, male and female adults, AZ, NM; *T. explicatus* (Eaton), larvae, AZ, UT; *T. minutus* Traver, larvae, male and female adults, AR, AZ, CO, NM, SD, WY; *T. peridius* Burks, *T. stygiatus* McDunnough, larvae, male and female adults, IN; *T. spp.*, larvae, male and female adults, CA, CO, ID, NM, WA, WY; *Tricorythopsis arigas* (male adults), Uruguay; *T. sp.*, larvae, male and female adults, Brazil.

*Remarks.*— This group has traditionally been classified in the Tricorythidae sensu lato. Although Edmunds and Traver (1954) and McCafferty and Edmunds (1979) recognized it as a separate subfamily, and Landa and Soldán (1985) recognized it as a separate family (including with it Diceromyzinae), a single diagnostic characteristic had not been identified for the grouping (the recognition of the Leptohephidae sensu lato was based only on its New World distribution).

Peters and Peters (1993) removed the highly specialized Neotropical genus *Coryphorus* from the Machadorythinae sensu lato to the Leptohephinae sensu lato, where Peters (1981) had originally considered it. The meticulous description and figures of the larvae of the *Coryphorus* that accompanied its description have allowed our confirmation of its placement in the Leptohephidae. The adult of *Coryphorus* remains unknown, and *Cotopaxi*, a seemingly aberrant genus, remains unknown in the larval stage.

Aberrations of cubital venation and male genital forceps are present in the Leptohephidae, likely because it is both old (see below) and relatively highly radiated. Such aberrations make it difficult to find unqualified characters to diagnose this family from the closely related family Tricorythidae, and to find entirely stable character states for cladistic use. Nonetheless, the family can be consistently keyed by use of character state combinations (see key to adults), and fundamental characters that are plesiomorphic within the family, itself, are valid for cladistic analysis. As emphasized by Wiley (1981), when performing a cladistic analysis of superspecific lineages or taxa above the species level, such units must be represented by the character states found in the most plesiotypic members (species) of those units.

It would be tempting to recognize the highly specialized genus *Coryphorus* as a separate subfamily within the family Leptohephidae. However, whereas several apomorphies exist that would show such a subfamily to be a monophyletic group, we could not find any apomorphies exclusive to the remainder of the Leptohephidae. This indicates that *Coryphorus* could have originated virtually from anywhere within the other lineages, and such a subfamily classification would surely result in a paraphyletic grouping of the other genera.

There are apparently a number of undescribed genera in the Leptohephinae in both North and South America, and in fact some are in the process of being described by other workers as the current monograph is being written (N. A. Wiersema and McCafferty unpub-

lished; C. Molineri unpublished). It will be important to research generic level cladistics in this grouping in conjunction with such future descriptions. The familial characteristics, especially in terms of male genitalia, may require modification with the discovery and description of the new genera of Leptohephidae.

If one were to use a measure of the number of changes in character from the hypothetical ancestor of the Pannota as a quantitative indicator of the relative amount of evolution undergone, the Leptohephidae would surely be considered the most highly evolved, or most apotypic of all the pannote families. Based only on Fig. 1, there have been 25 character shifts from the hypothetical ancestor resulting in the Leptohephidae, while by comparison there have been only six in the case of Neophemeridae, and seven in the case of Ephemereidae. As can be seen with the Baetidae within the mayfly suborder Pisciforma, this most apotypic lineage may also prove to be one of the most speciose, if not the most speciose, group within its higher grouping.

The sister group to the Leptohephidae is the Tricorythidae. The former is found exclusively in the Western Hemisphere, with its center of evolution undoubtedly in South America (McCafferty 1998). The latter is strictly found in the Eastern Hemisphere, with its center of evolution being in Africa/Madagascar plus possibly the Indian subcontinent (given its present Afrotropical and Oriental distribution). From this it may be hypothesized that the common ancestor of these two clades was in West Gondwana after the split of Gondwana from Laurasia (when the ephemerelloids probably originated; see Remark under the superfamily Ephemerelloidea, above), and after the subsequent split of East from West Gondwana. It would follow that the origin of the two clades corresponded to the subsequent breakup of South America from the African area within West Gondwana. This vicariant event is generally thought to have been initiated approximately 135 million years ago, further allowing a reasonable hypothesis of the origin of the Leptohephidae.

#### KEY TO THE HIGHER TAXA OF PANNOTE MAYFLIES (LARVAE)

- 1 Gills 2 (Figs. 2-5) operculate, quadrate, and large, meeting, interlocking, or approximate on dorsal abdomen; filamentous gills 1 present. Segment 3 of labial palpi, when present, not greatly reduced (Figs. 17, 25, 33). [cosmopolitan].....
- 1' Gills 2 present (Figs. 8-15, 107) or absent (Figs. 6, 7), when present, operculate, semi-operculate, or not operculate, variably shaped, if quadrate and meeting, then filamentous gills 1

- absent. Segment 3 of labial palpi, when present, greatly reduced (Figs. 66, 74, 87, 94, 107, 108). [cosmopolitan].....
- ..... Superfamily Ephemerelloidea, **5**
  
- 2 Gills 2 interlocked (Fig. 2), without posterior fringe of setae or spines; gills 2-5 with underlying gill branches (Fig. 19). [Holarctic; Oriental]..... **Family Neophemeridae**
- 2' Gills 2 meeting or approximate but not interlocked (Figs 3-5), with posterior fringe of setae or spines; lamellate gills without underlying gill branches (Figs. 26). [cosmopolitan].....
- ..... Family Caenidae, **3**
  
- 3. Forelegs (Fig. 3) not highly reduced nor with greatly expanded femora. Maxillary palpi three segmented (Figs. 24). Operculate gills with submarginal ventral row of minute palmate outgrowths. [cosmopolitan]..... **Subfamily Caeninae**
- 3' Forelegs, especially femora, modified by reduction or expansion (Figs. 4, 5). Maxillary palpi two segmented or absent (Figs. 32, 36). Operculate gills without ventral row of minute palmate outgrowths. [Holarctic; Oriental; Afrotropical]..... **4**
  
- 4 Forefemora greatly expanded (Fig. 4); legs generally fringed with long setae. Head without ocellar tubercles (Fig. 4). Maxillary palpi lacking (Fig. 32). Labial palpi three segmented (Fig. 33). [Afrotropical]..... **Subfamily Madecocercinae**
- 4' Forelegs (Fig. 5) highly reduced; legs not fringed with long setae; head with ocellar tubercles (Fig. 5). Maxillary palpi two-segmented (Fig. 36). Labial palpi two segmented (Fig. 37). [Holarctic; Oriental]..... **Subfamily Brachycercinae**
  
- 5 Mature male eyes dioptic. Mature forewingpads generally with small submedial lobes or offset area on notal margin between well-defined forewingpads (Figs. 6-9); gills 2 and 7 present, or gills 2 absent and gills 7 present, or gills 2 present and gills 7 absent. [Holarctic; Oriental; Australian; Afrotropical]..... **6**
- 5' Mature male eyes holoptic. Mature forewingpads generally highly fused, without small submedian lobes or distinctive offset area on notal margin between forewingpads (Figs. 10-15, 109); gills 2 present and gills 7 absent. [Nearctic, Neotropical, Oriental, Afrotropical]..... **9**
  
- 6 Gills 2 absent (Figs 6, 7). [Holarctic; Oriental].....
- ..... Family Ephemerellidae, **7**
- 6' Gills 2 present (Figs. 8, 9). [Afrotropical; Australian; Oriental]..... **8**

- 7 Gills 3 present (Fig. 6). [Holarctic; Oriental].....
- ..... **Subfamily Ephemerellinae**
- 7' Gills 3 absent (Fig. 7). [Holarctic]..... **Subfamily Timpanoginae**
  
- 8 Gills 7 absent; gills 2 operculate or semi-operculate (Fig. 9). [Afrotropical; Oriental]..... **Family Teloganodidae**
- 8' Gills 7 present (but inserted sublaterally and dorsally at about mid length of abdominal segment 7); gills 2 not operculate or semi-operculate (Fig. 8). [Australian; Oriental].....
- ..... **Family Austremerelellidae**
  
- 9 Filamentous gills 1 present. [Oriental; Madagascar].....
- ..... **Family Teloganellidae**
- 9' Filamentous gills 1 absent. [Afrotropical; Nearctic; Neotropical; Oriental]..... **10**
  
- 10 Gills 2 operculate, narrow, elongate (Fig. 11); gills 6 absent. Maxillary palpi absent (Fig. 73). [Africa].....
- ..... **Family Ephemerithidae**
- 10' Gills 2 not operculate (Figs. 13, 14) or operculate (Figs. 12, 15), approaching narrowly rounded and elongate only in some Western Hemisphere forms; gills 6 present, or absent only in some rare Neotropical forms. Maxillary palpi present (Figs. 86, 92, 101-103, 108), or absent only in some Neotropical forms (Fig. 104). [Afrotropical; Neotropical; Nearctic; Oriental].. **11**
  
- 11 Lateral margins of head capsule strongly raised and converging dorsally (Fig. 77), with narrowly set eyes protruding above narrowed vertex (Figs. 12, 77). Labial palpi segment 2 robust, subequal to segment 1 (Fig. 79). Gills 2 operculate; gill chamber formed by upturned lateral flanges of mid abdominal segments (Figs. 12, 80). [Africa]..... **Family Machadorythidae**
- 11' Lateral margins of head capsule not strongly raised and converging dorsally, with eyes widely separated or dorsolateral on broad vertex (Figs. 13-15). Labial palpi segment 2 not robust, either very short (Fig. 94), very slender (Fig. 87), or much reduced compared to segment 1 (Figs. 105-108). Gills 2 not operculate (Figs. 13, 14) in Eastern Hemisphere forms, or operculate (Figs. 15, 109) in Western Hemisphere forms; latter either with (Fig. 109) or in most without (Fig. 15) gill chamber formed from upturned lateral flanges of mid abdominal segments. [Afrotropical; Neotropical; Nearctic; Oriental]..... **12**

- 12 Gills 2 not operculate (Figs. 13, 14). [Afrotropical; Oriental].  
.....Family Tricorythidae, **13**
- 12' Gills 2 operculate (Figs. 15, 109). [Neotropical; Nearctic].....  
.....**Family Leptohiphidae**
- 13 Mandibles flat and with long marginal setae (Fig. 84). Gills 2-6 lamellate (Fig. 13). Thorax without ventral friction disc. (Some Madagascar forms unknown as larvae.) [Afrotropical; Oriental]  
.....**Subfamily Tricorythinae**
- 13' Mandibles neither flat nor broad nor with long marginal setae (Fig. 91). Gills 2-6 fibrillate (Figs. 14, 96, 97). Thorax with ventral friction disc (Fig. 95). (Some Madagascar forms unknown as larvae.) [Afrotropical]  
.....**Subfamily Dicercomyzinae**

KEY TO THE HIGHER TAXA OF PANNOTE MAYFLIES  
(ADULTS)

- 1 Mesonotum with ommation (Figs. 20, 28). Forewings (Figs. 21, 29) with MP2 extending to base or curving from near base of MP1; CuP not strongly curved toward inner margin of wing. [cosmopolitan].....**Superfamily Caenoidea, 2**
- 1' Mesonotum without ommation. Forewings (Figs. 45, 56, 59, 60, 67, 75, 82, 88, 98, 112, 113) with MP2 not extending to base nor curving from near base of MP1; CuP strongly curved to inner margin of wing. [cosmopolitan].....**Superfamily Ephemerelloidea, 5**
- 2 Forewings (Fig. 21) with crossveins well developed; marginal intercalaries well developed; MP2 curving from near base of MP1. Hindwings present. Male forceps segmented (Figs. 22, 23). [Holarctic; Oriental].....**Family Neophemeridae**
- 2' Forewings (Figs. 29) with crossveins restricted to basal and anterior areas; marginal intercalaries lacking; MP2 originating straight from base. Hindwings absent. Male forceps not segmented (Figs. 30, 31, 35, 38). [cosmopolitan].....**Family Caenidae, 3**
- 3 Prosternum triangular (Fig. 27), with width less than one-half that of mesonotum. [cosmopolitan].....**Subfamily Caeninae**
- 3' Prosternum rectangular (Fig. 34), with width more than one-half that of mesonotum. [Holarctic; Oriental; Afrotropical].....**4**
- 4 Male forceps (Fig. 35) somewhat stout, and strongly bowed. [Afrotropical].....**Subfamily Madecocercinae**
- 4' Male forceps (Fig. 38) more straplike, only gradually bowed. [Holarctic; Oriental].....**Subfamily Brachycercinae**
- 5 Male eyes dioptic. Forewings with single marginal intercalaries in outer margin (Figs. 45, 56, 59, 60); either cubital intercalary veins at distinct angle with CuA (Figs. 45, 56, 57), or longest ICuA more or less paralleling CuA but never attached to CuA by single medial crossvein and never forming cubital forks by attaching to CuP or another ICuA vein at broad angle (Figs. 59, 60). Hindwings present and often well developed. Forceps (Figs. 47-49, 53, 62) with three well-articulated segments. [Holarctic; Oriental; Australian; Afrotropical].....**6**
- 5' Male eyes holoptic. Forewings with single (Figs. 67-69), or double (Fig. 75), or no (Figs. 82, 88, 98, 112, 113) marginal intercalaries in outer margin; longest ICuA paralleling CuA or curving toward CuP, often with ICuA1 attaching to CuP or another ICuA vein to form cubital fork(s), or if no fork formed or not entire, then ICuA1 attached to CuA by medial crossvein (Figs. 67, 69). Hindwings present and minute, or absent. Forceps (Figs. 70, 76, 83, 89, 90, 99, 100, 116) generally with two articulated segments; some with poorly defined small, apical, third forceps segment (Figs. 114, 115), or rarely entirely aberrant forceps (Mayo 1968: Fig. 5). [Nearctic, Neotropical, Oriental, Afrotropical].....**9**
- 6 Abdominal segment 2 without gill socket vestiges (Figs. 46, 51). Forceps with basal segment short, less than twice as long as wide (Figs. 47-49, 53) [Holarctic; Oriental] Family Ephemerellidae, **7**
- 6' Abdominal segment 2 with gill socket vestiges (Fig. 61). Forceps with basal segment long, more than twice as long as wide (Fig. 62). [Afrotropical; Australian; Oriental].....**8**
- 7 Abdominal segment 3 with gill socket vestiges (Fig. 46) [Holarctic; Oriental].....**Subfamily Ephemerellinae**
- 7' Abdominal segment 3 without gill socket vestiges (Fig. 51) [Holarctic].....**Subfamily Timpanoginae**
- 8 Forewings (Figs. 59, 60) with zero, one, or rarely two ICuA veins attached to CuA; stigmatic area not divided by secondary longitudinal vein into upper and lower series of many subequal cellules, some with poorly formed upper cellules or stigmatic area appearing anastomosed. Abdominal segment 7 without gill socket vestiges (Fig. 61) [Afrotropical; Oriental].....**Family Teloganodidae**
- 8' Forewings (Figs. 56, 57) with two or more, usually several,

cubital intercalaries attached to CuA; stigmatic area divided by secondary longitudinal vein into upper and lower series of many subequal sized cellules. Abdominal segment 7 with gill socket vestiges (similar to Fig. 46). [Australian; Oriental].....  
**Family Austremerelellidae**

- 9 Forewings (Fig. 67-69) with single marginal intercalaries in outer margin; ICuA1 attached to CuA by medial crossvein. [Oriental; Madagascar].....  
**Family Teloganelidae**  
 9' Forewings with zero (Figs. 82, 88, 98, 112, 113) or double (Fig. 75) marginal intercalaries in interspaces of outer margin; ICuA1 not attached to CuA by medial crossvein. [Afrotropical; Neotropical; Nearctic; Oriental]..... **10**
- 10 Forewings with double marginal intercalaries in outer margin (Fig. 75). [Africa].....  
**Family Ephemerithidae**  
 10' Forewings with no marginal intercalaries in outer margin (Figs. 82, 88, 98, 112, 113). [Afrotropical; Neotropical; Nearctic; Oriental]..... **11**
- 11 Forewings (Fig. 82) with cubital fork consisting of ICuA1-CuP fork only, with long stem about as long as fork, and no, or poorly developed, ICuA2 vein. Male forceps basal segment short, with rounded lateral margins (Fig. 82). [Africa].....  
**Family Machadorythidae**  
 11' Forewings with cubital fork consisting of ICuA1-CuP fork (Fig. 98), ICuA1-ICuA2 fork (Fig. 112, 113), or both (Fig. 88), or forks not formed but MP2 distinctly longer than ICuA1 in some Western Hemisphere forms; stem of cubital fork(s), when present, always shorter than fork. Male forceps basal segment (Figs. 89, 90, 114-116, Traver 1958: Fig. 4, Mayo 1968: Fig. 5) of various length but with more or less straight lateral margins. [Afrotropical; Neotropical; Nearctic; Oriental]..... **12**
- 12 Cubital fork of forewings consisting of ICuA1-CuP fork (Figs. 88, 98) with base of fork broadly angled; ICuA2 well developed and in many forming additional fork with ICuA1 (Fig. 88); entire stalked ICuA usually subequal to, or shorter than, MP2. Hindwings absent. Male forceps two segmented (Figs. 89, 90, 99, 100). Median caudal filament developed or not developed. [Afrotropical; Oriental].....  
**Family Tricorythidae, 13**  
 12' Cubital fork of forewings often consisting of deep ICuA1-ICuA2 fork (Figs. 112, 113), but no cubital forks present in some; if ICuA1-CuP connection present, then usually near base of wing and not strongly angled at base (Fig. 112); entire stalked

ICuA longer than MP2, distinctly longer when cubital forks not present. Hindwings present or absent. Male forceps usually two or three segmented (Figs. 114-116), rarely aberrant (Traver 1958: Fig. 4, Mayo 1968: Fig. 5). Median caudal filament developed. [Neotropical; Nearctic].....  
**Family Leptohyphidae**

- 13 Penes with auxiliary processes (Figs. 99, 100). [Afrotropical].....  
**Subfamily Diceromyzinae**  
 13' Penes without auxiliary processes (Figs. 89, 90). [Afrotropical; Oriental].....  
**Subfamily Tricorythinae**

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Table 1. Characters used to analyze cladistic relationships of the major lineages of Pannota (A = adult stage, L = larva stage). Double asterisk\*\* indicates some subsequent reversion within highly apotypic lineages, see text.

#### Apomorphy

1. Forewingpads fused basally over one-half their length. Forewingpads not fused or less fused.
2. Gill lamellae dorsally recumbent.\*\* Gills not dorsally recumbent.
3. Gills 2 meeting or nearly meeting at midline of abdomen. Gills 2 well separated.
4. Mesonotum with ommatium. Mesonotum without ommatium.
5. Gills 7 absent. Gills 7 present.
6. MP2 of forewings not extending to base or near base. MP2 of forewings extending to base.
7. CuP of forewings distinctly curved to inner margin. CuP not distinctly curved to inner margin.

8. Marginal intercalaries of forewings mostly detached from main veins. Marginal intercalaries mostly attached to main veins.
9. Gills 2 pair interlocked. Gills 2 pair not interlocked.
10. MA2 of forewings not directly attached to MA1. MA2 and MA1 with common stem.
11. Forceps unsegmented and straplike. Forceps segmented.
12. Forewing crossveins restricted to basal crossveins connecting major veins. Crossveins well developed.
13. Hindwings absent. Hindwings present.
14. Cubital intercalary veins of forewing reduced in number and attachments to CuA. Two or more cubital intercalaries derived from CuA.
15. Marginal intercalaries of forewings absent in outer margin. Marginal intercalaries present in outer margin.
16. Prosternum triangular (A); relatively narrow (L). Prosternum rectangular (A); relatively broad (L).
17. Submarginal, outer ventral row of minute palmate outgrowths on gills 2. Without such a row of palmate outgrowths.
18. Forceps bowed. Forceps not bowed.
19. Forceps with longitudinal fold. Forceps without longitudinal fold.
20. Maxillae without palpi. Maxillae with palpi.
21. Forefemora with convex hyperextension posteriorly. Forefemora not broadened as such.
22. Ocellar tubercles present (L). Ocellar tubercles not present.
23. Forelegs highly reduced (L). Forelegs not highly reduced.
24. Labial palps two segmented. Labial palps three segmented.
25. Male eyes holoptic (L & A). Male eyes dioptic.
26. Forceps reduced to two completely articulated segments.\*\* Forceps with three completely articulated segments.
27. Gills 2 absent. Gills 2 present.
28. Forceps segment 1 longer than wide.\*\* Segment 1 not longer than wide.
29. Filamentous gills 1 absent. Filamentous gills 1 present.
30. Gills 3 absent. Gills 3 present.
31. Stigmatic area of forewings divided into rows of subequal cells. Stigmatic area not modified exactly as such.
32. Head narrowly raised and Head shape not modified.



- convergent dorsally (L).  
 33. Gills 6 absent. Gills 6 present.  
 34. Segment 1 of forceps short and globular. Segment 1 of forceps not short and globular.  
 35. Gills 2 operculate. Gills 2 not operculate  
 36. Abdominal segments 2-6 expanded laterally. Abdomen not modified as such.  
 37. MP2 of forewings distinctly shorter than entire stalked ICuA if forked, or entire ICuA1 if not forked. MP2 not distinctly shorter than entire forked ICuA.  
 38. Lateral flanges of abdominal sterna 2-6 curved dorsally (L). Abdominal flanges not curved dorsally.  
 39. Forewings with double marginal intercalaries. Forewings without double marginal intercalaries.  
 40. Mandibles flattened and expanded, with long filtering hairs on outer margin. Mandibles neither expanded nor with long filtering hairs.  
 41. Thoracic sternum with friction disc (L). Sternum without friction disc.  
 42. Penes with well-developed auxiliary processes. Penes without such processes.  
 43. Operculate gills 2 quadrate. Operculate gills 2 not quadrate.  
 44. Longest ICuA of forewing basally curved toward or approaching CuP, forming or very nearly forming cubital fork. ICuA not strongly curved toward or approaching CuP to form cubital fork.  
 45. Galealaciniae broadened, with well-developed subapical setae on surface. Galealaciniae narrow, setae not developed, or restricted to crown and/or margin.  
 46. Longest ICuA and CuA of forewings attached by medial crossvein. Longest ICuA and CuA not attached as such.  
 47. Labium with palpi segment 3 narrowed and reduced. Palpi segment 3 not narrowed and reduced.  
 48. Glossae reduced. Glossae well developed.  
 49. Apical articulated segment of labial palpi broad and robust. Apical articulated segment of labial palpi not broad and robust.  
 50. Cubital fork of forewings deepened (ICuA1 attaching in basal half of attachment vein).\*\* Cubital fork shallow (ICuA1 attaching to CuP at ca. mid length of CuP.  
 51. ICuA2 of forewings well developed.\*\* ICuA2 relatively short.

**Table 2.** Phylogenetic higher classification of the Pannota.

Superfamily Caenoidea
Family Neophemeridae
Family Caenidae
Subfamily Caeninae
Subfamily Madecocercinae
Subfamily Brachycercinae
Superfamily Ephemerelloidea
Family Ephemerellidae
Subfamily Ephemerellinae
Subfamily Timpanoginae
Family Austremereleididae
Family Teloganodidae
Family Teloganellidae
Family Ephemerythidae
Family Machadorythidae
Family Tricorythidae
Subfamily Tricorythinae
Subfamily Diceromyzinae
Family Leptohyphidae

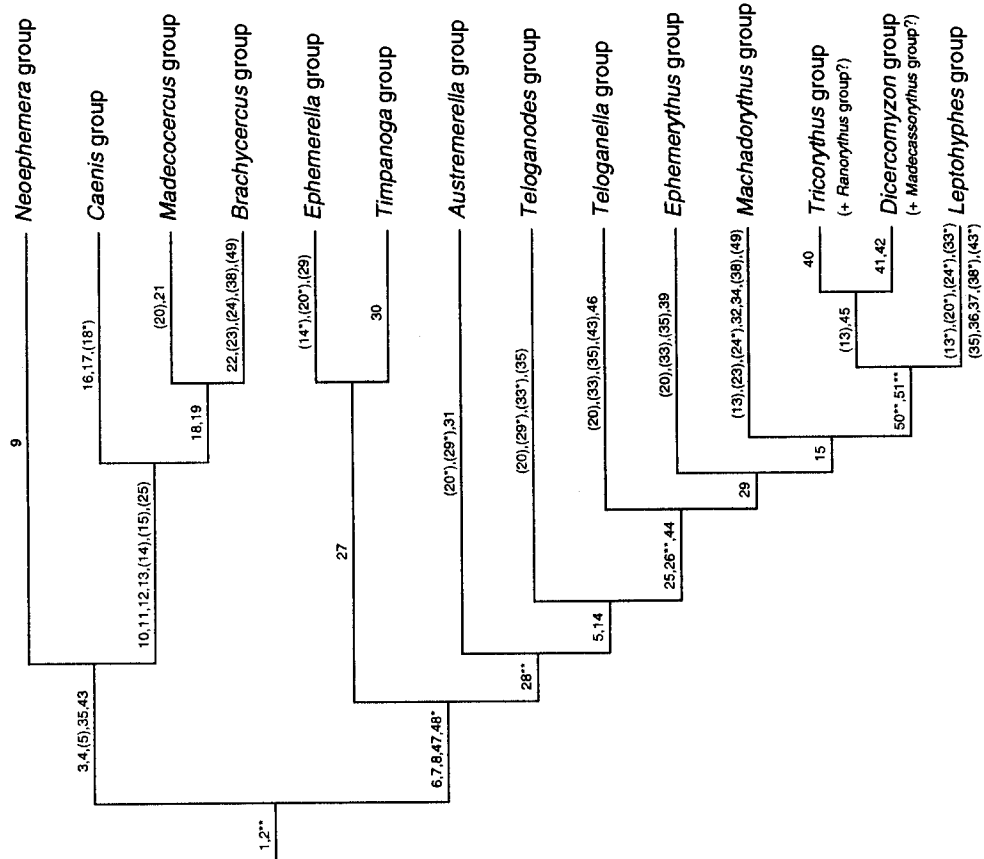


FIGURE 1. Cladogram of the major lineages of Pannota. Numbers represent apomorphies itemized in Table 1. Parenthetical numbers are repeated apomorphies. Single asterisk indicates apomorphy not present in all species. Double asterisk indicates aberrant reversion occurs within highly apotypic lineage.

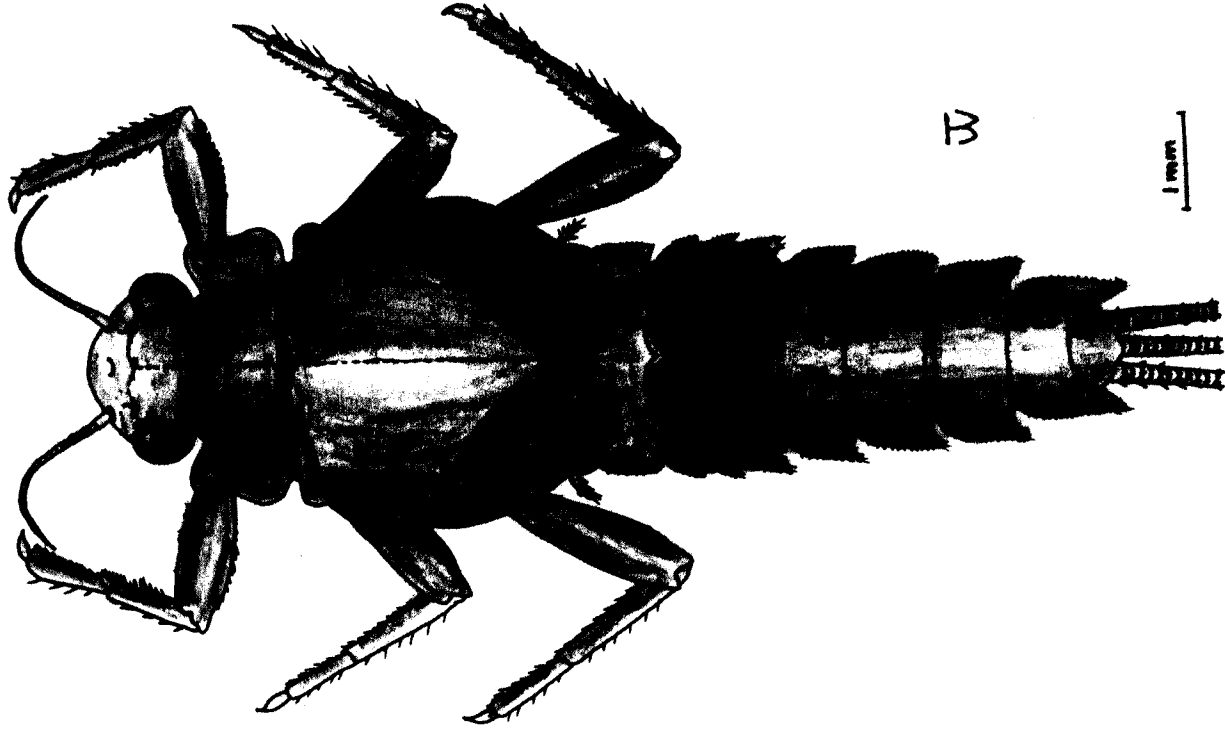


FIG. 2. *Neopphemera youngi* Berner larval habitus.

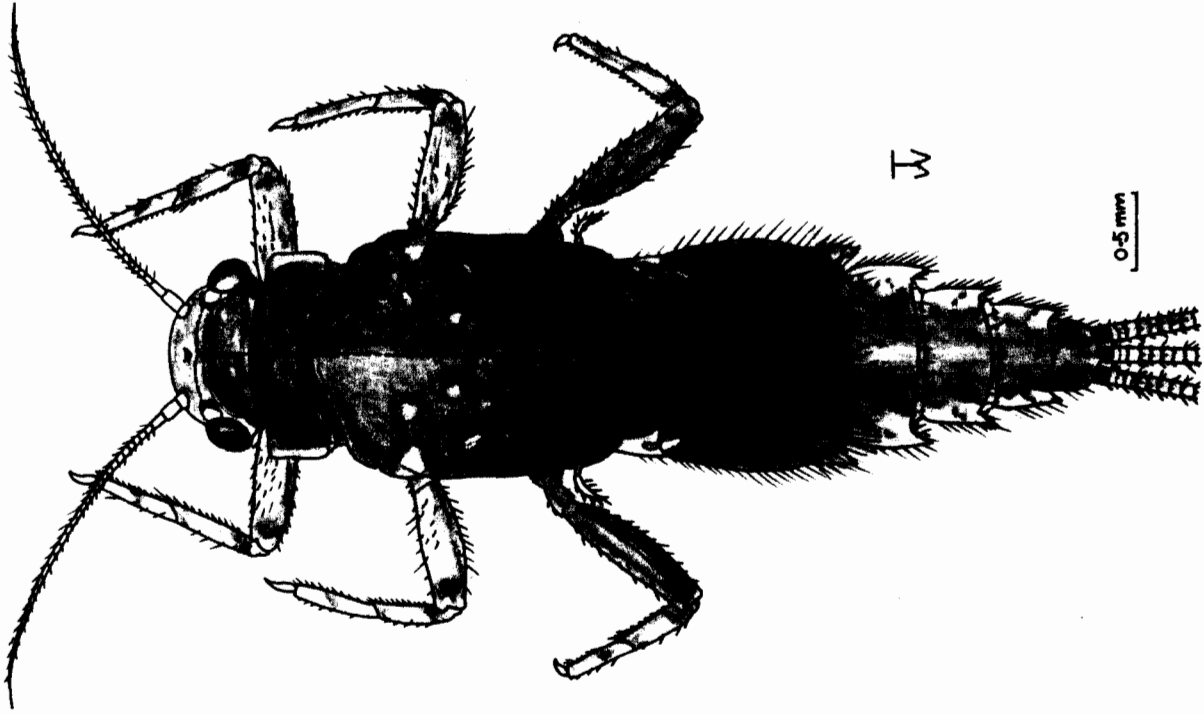


FIG. 3. *Caenis amica* Hagen larval habitus.

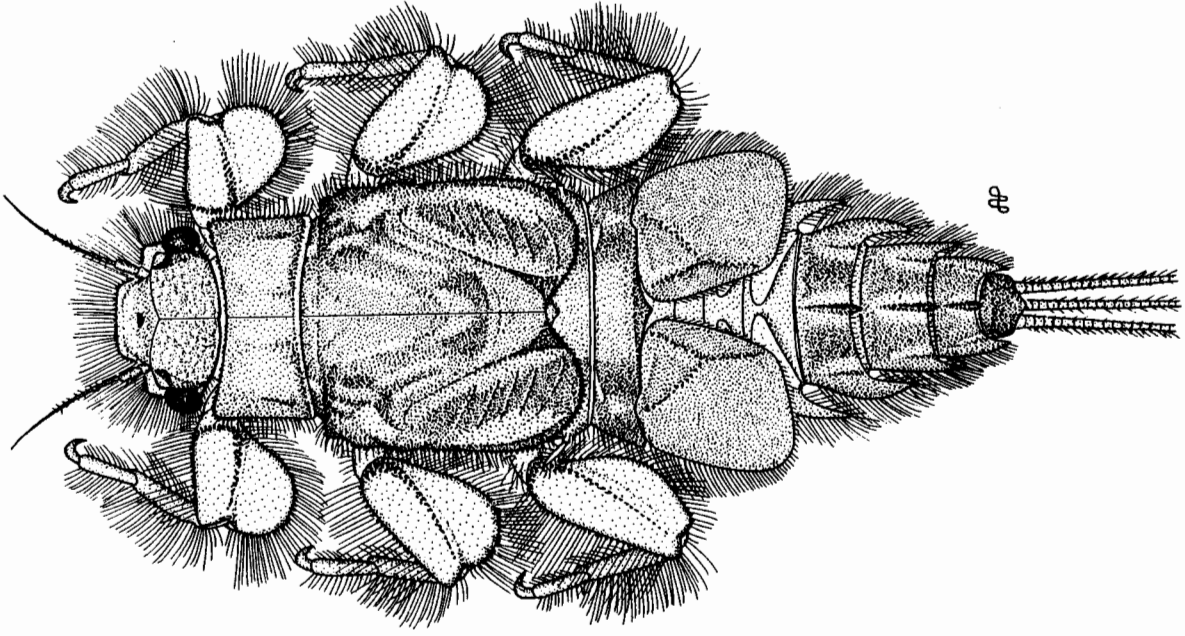


FIG. 4. *Madecocercus* sp. larval habitus.

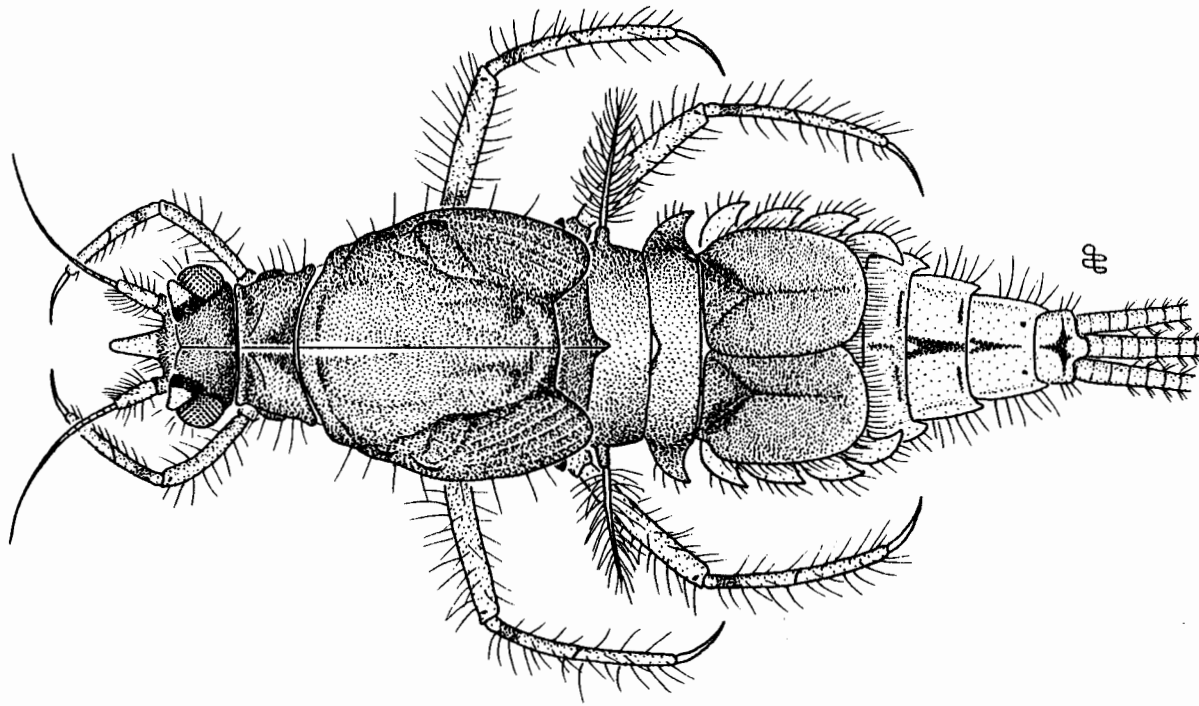


FIG. 5. *Brachyercus* sp. larval habitus.

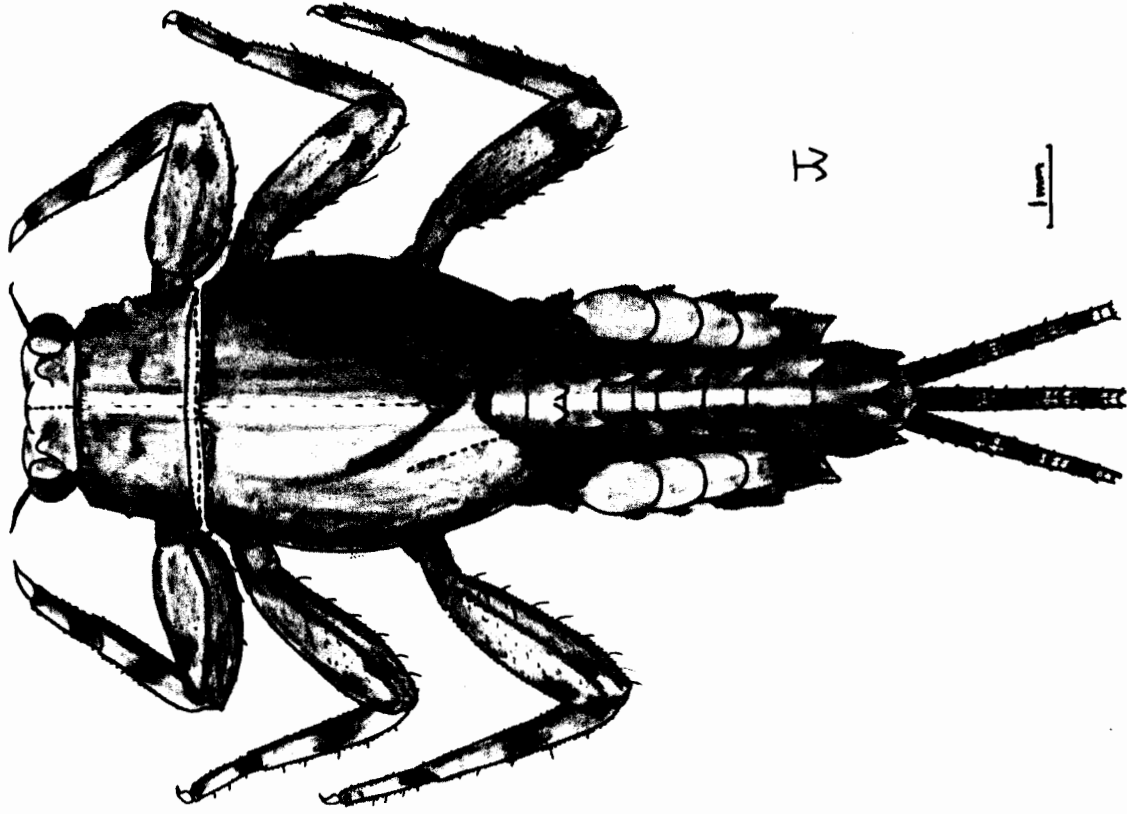


FIG. 6. *Drunella grandis* (Eaton) larval habitus.

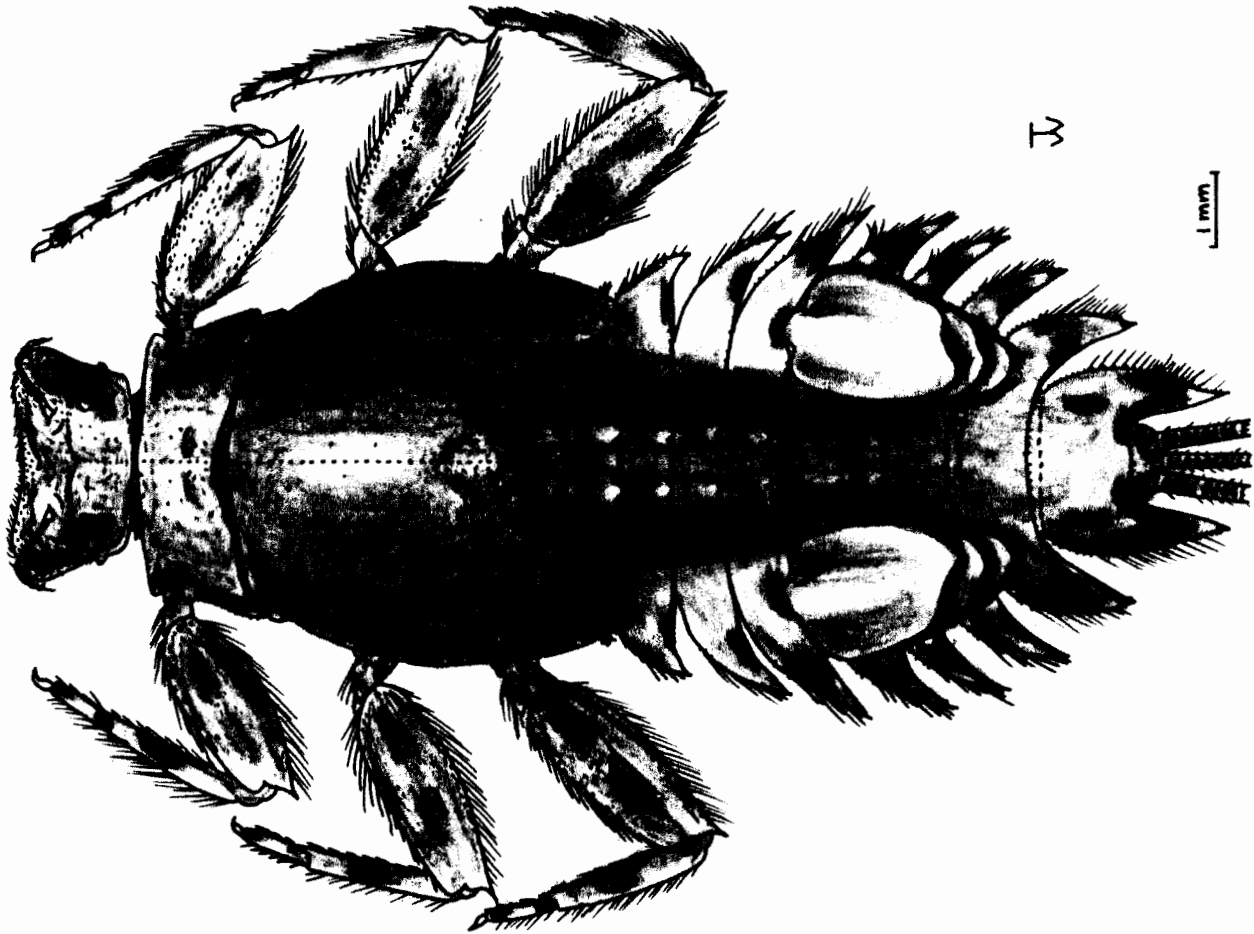


FIG. 7. *Timpanoga hecuba* (Eaton) larval habitus.

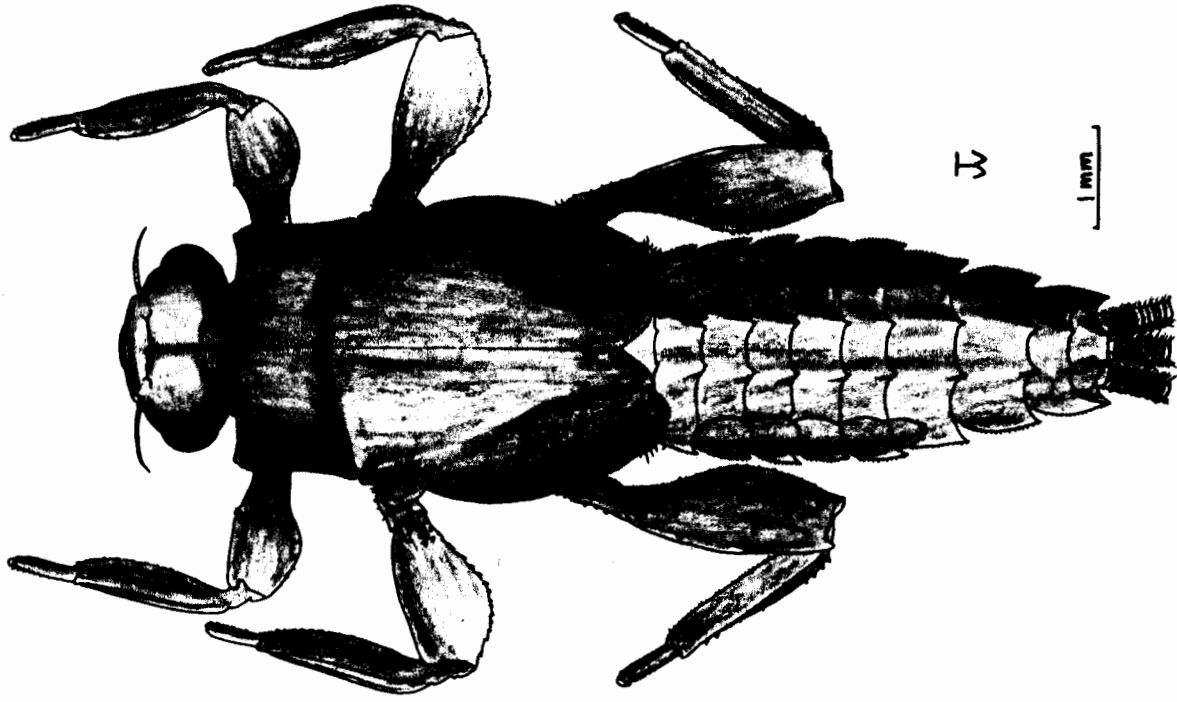


FIG. 8. *Austremarella picta* Riek larval habitus.

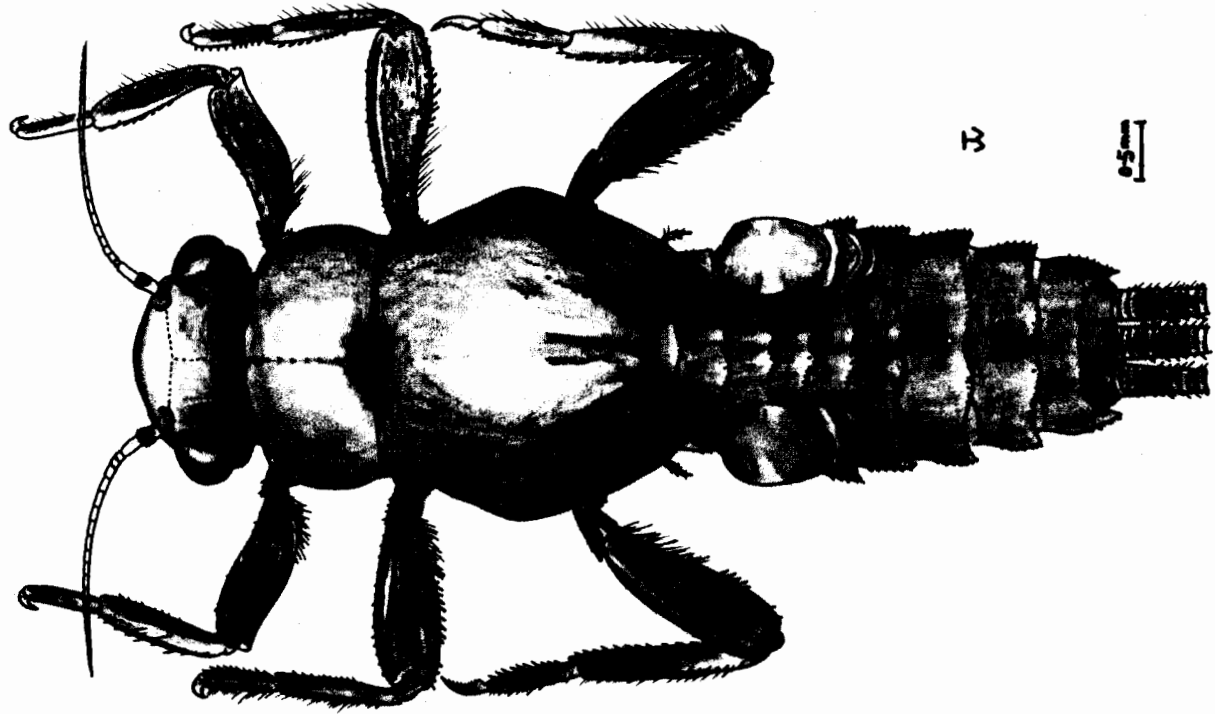


FIG. 9. *Nadinetella crassi* (Allen and Edmunds) larval habitus.

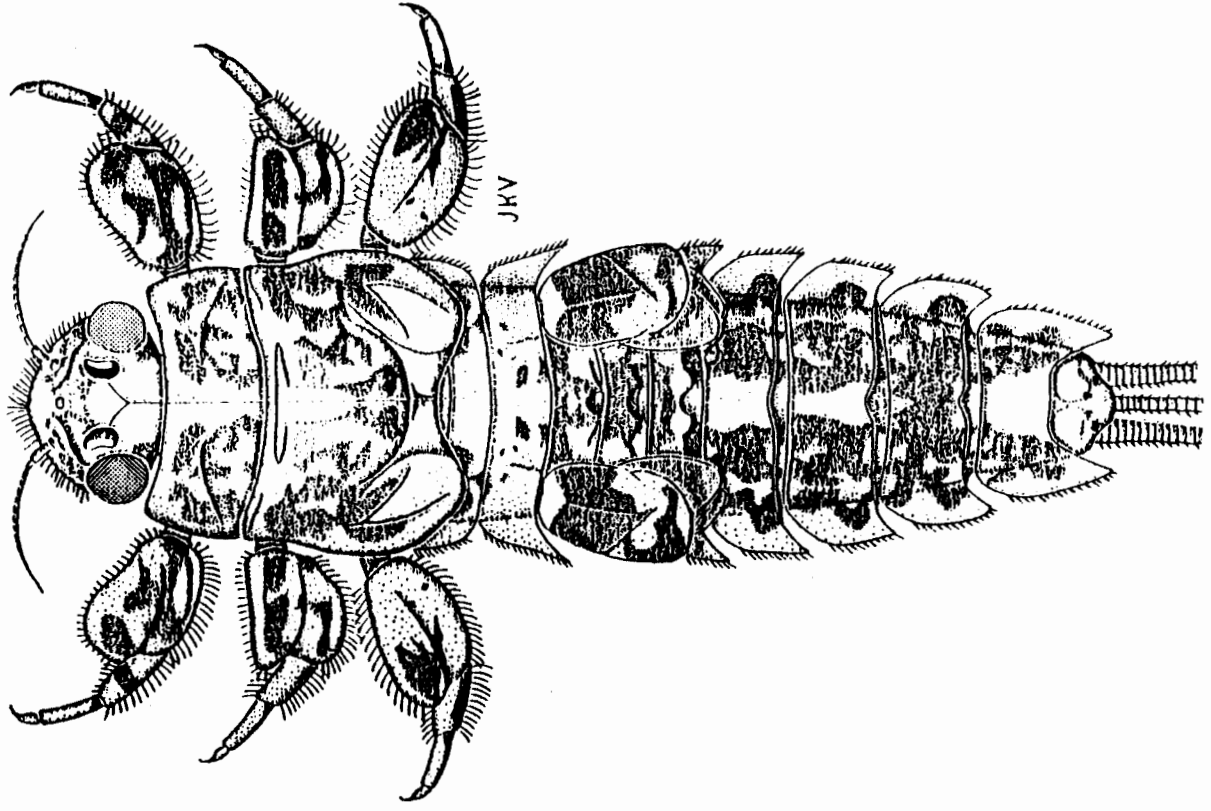


FIG. 10. *Teloganella umbrata* Ulmer larval habitus.

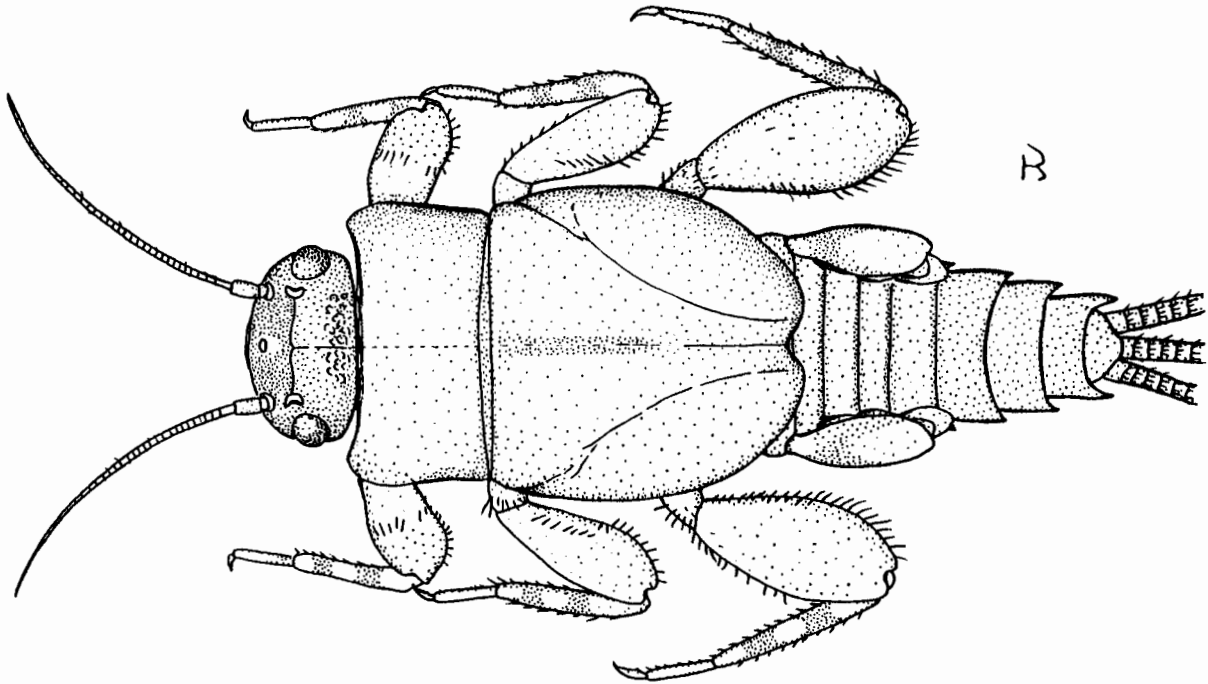


FIG. 11. *Ephemeriythys* sp. larval habitus.

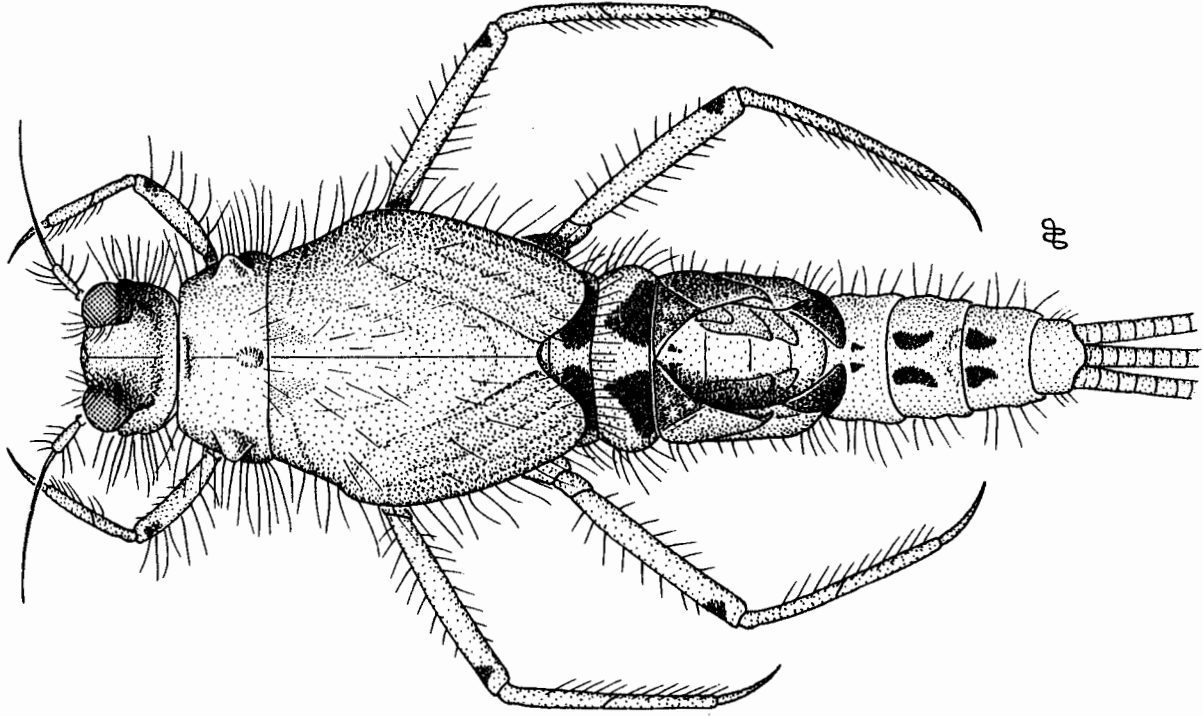


FIG. 12. *Machadorythys* sp. larval habitus.

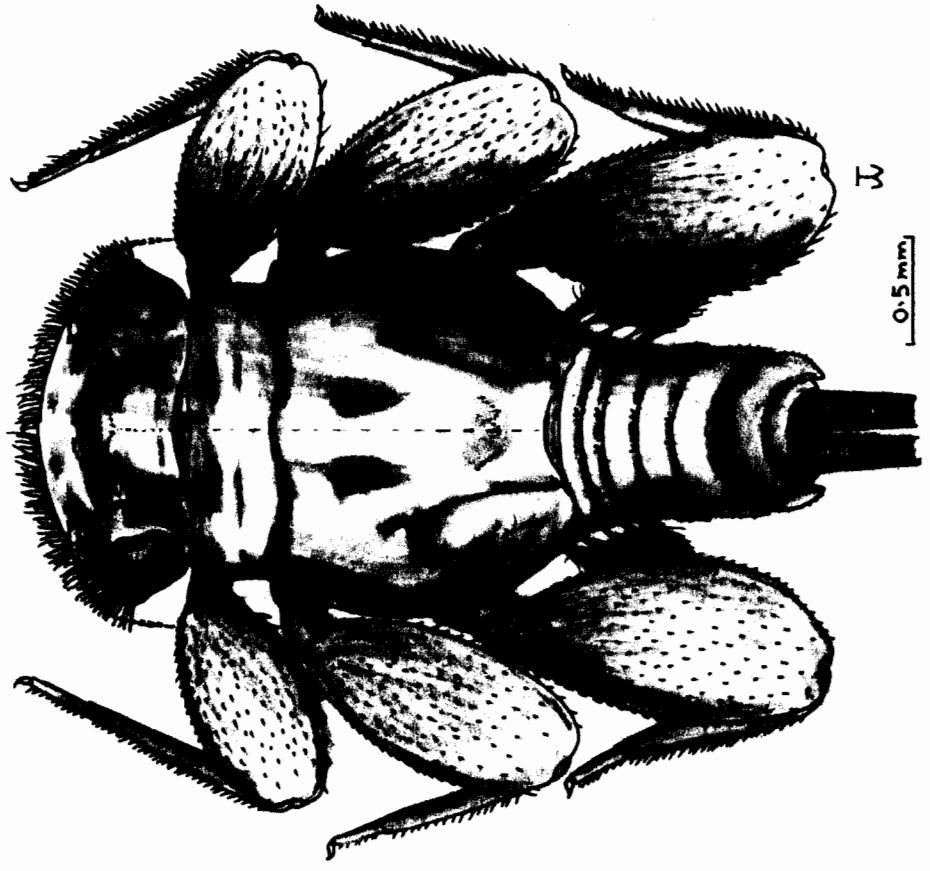


FIG. 14. *Diceromyzon* sp. larval habitus.

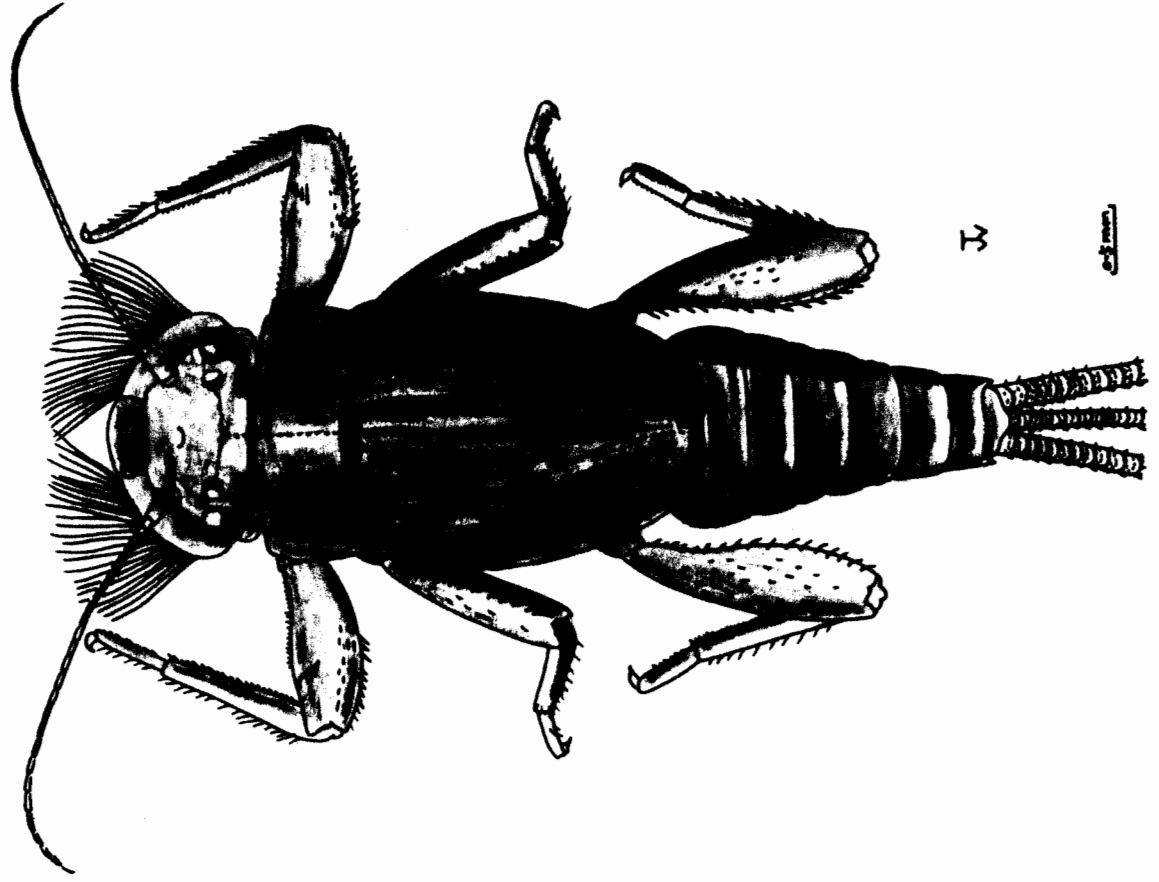


FIG. 13. *Tricorythus* sp. larval habitus.



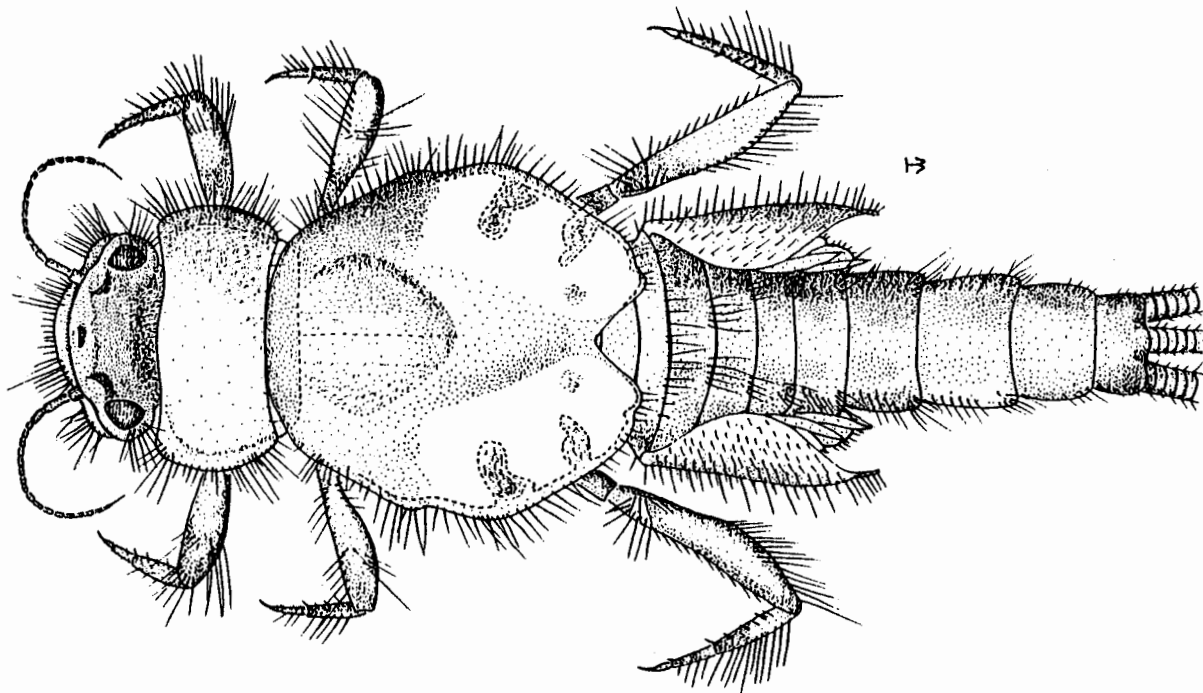
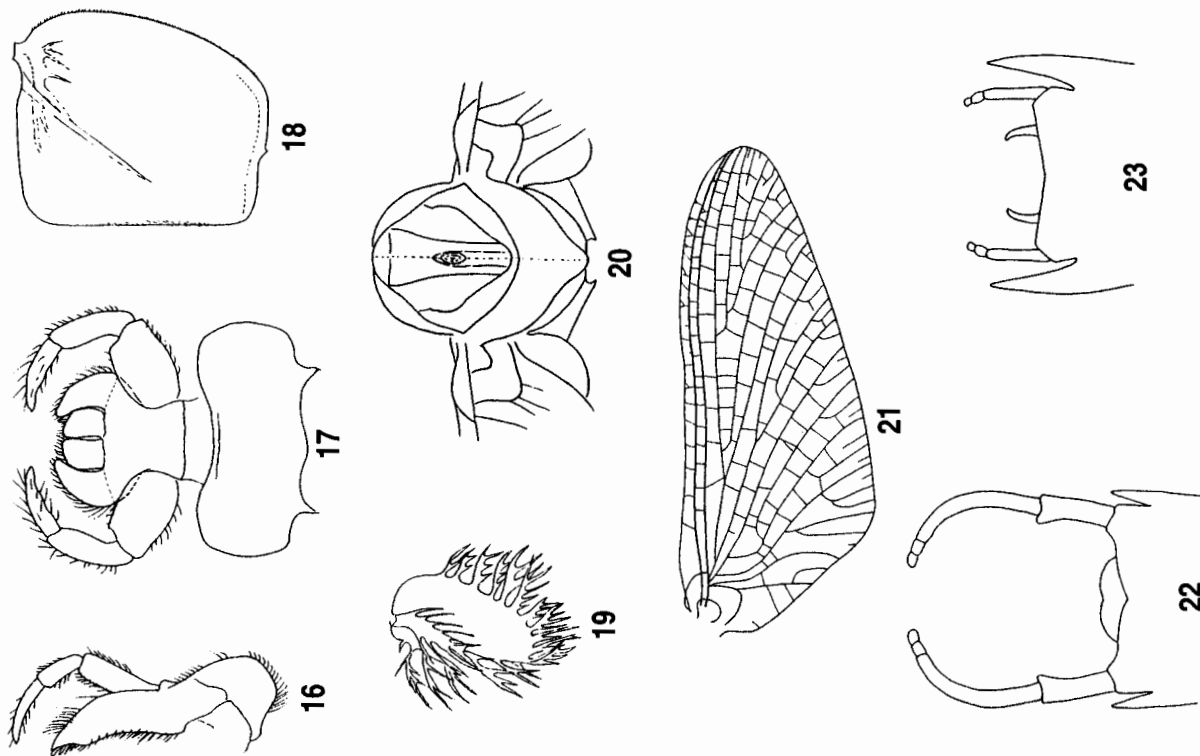
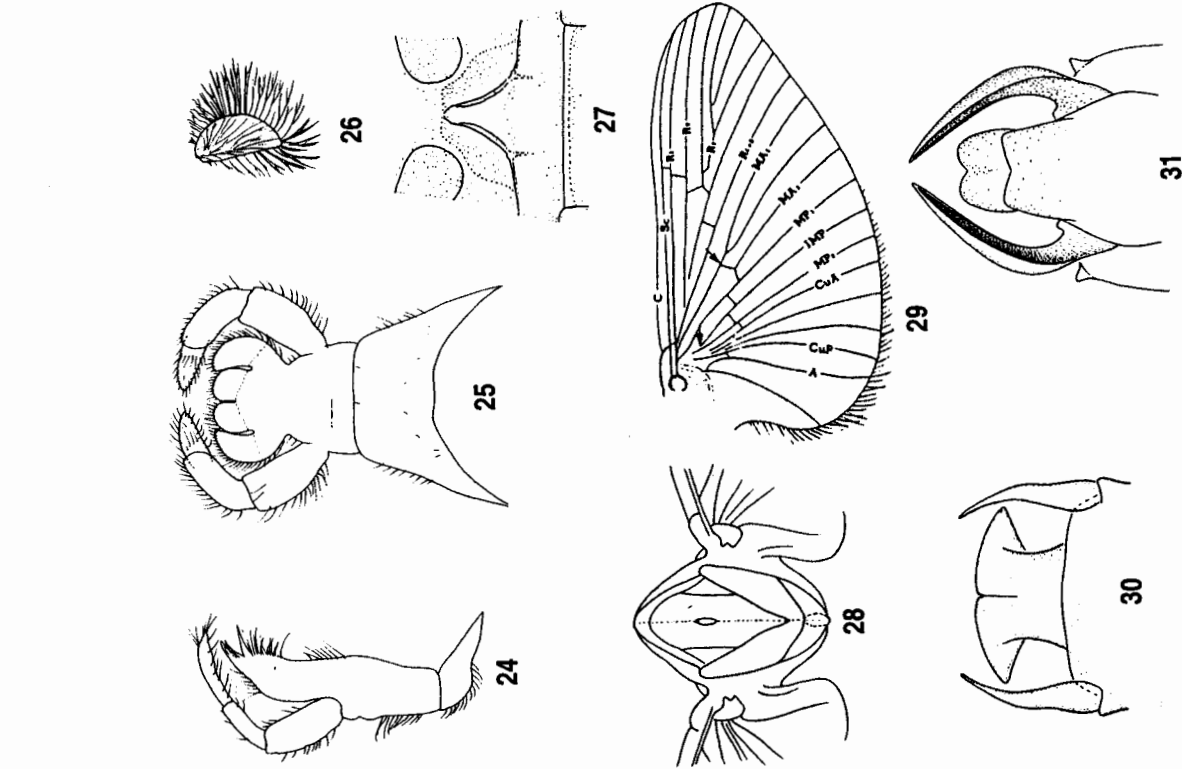


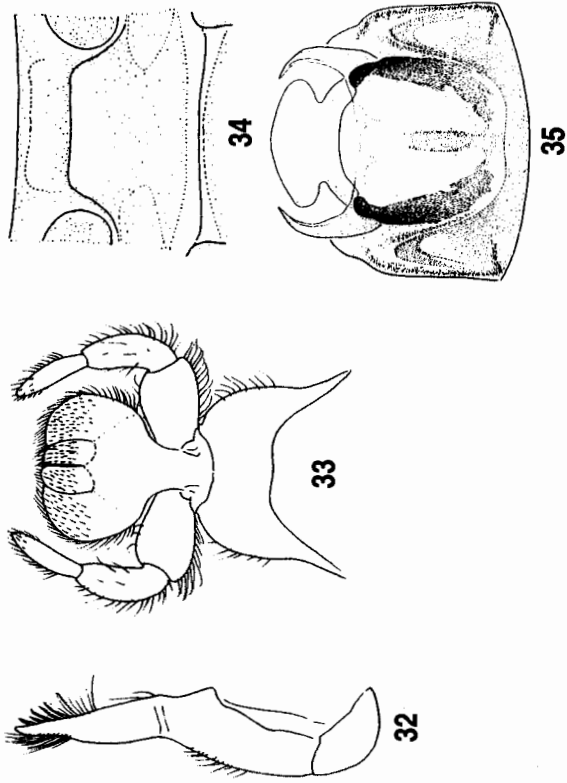
FIG. 15. *Haplohyphes* sp. larval habitus.



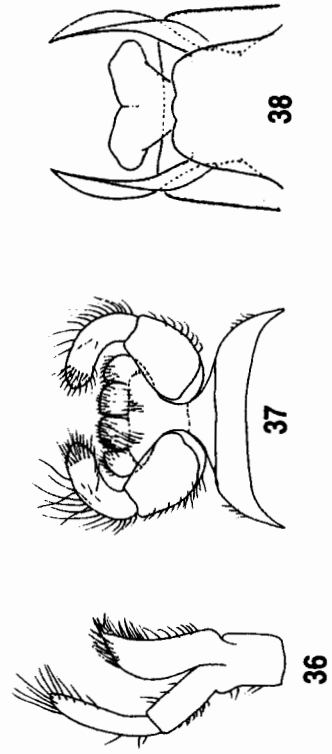
FIGS. 16-23. Neophemeridae. 16-20: *Neophemera* sp. 16, Maxilla. 17, Labium. 18, Gill 2, ventral. 19, Gill 4, ventral. 20, Adult thorax, dorsal. 21, *N. purpurea* (Traver) forewing. 22, *N. youngi* Berner male genitalia. 23, *Potamanthellus chinensis* (Hsu) male genitalia.



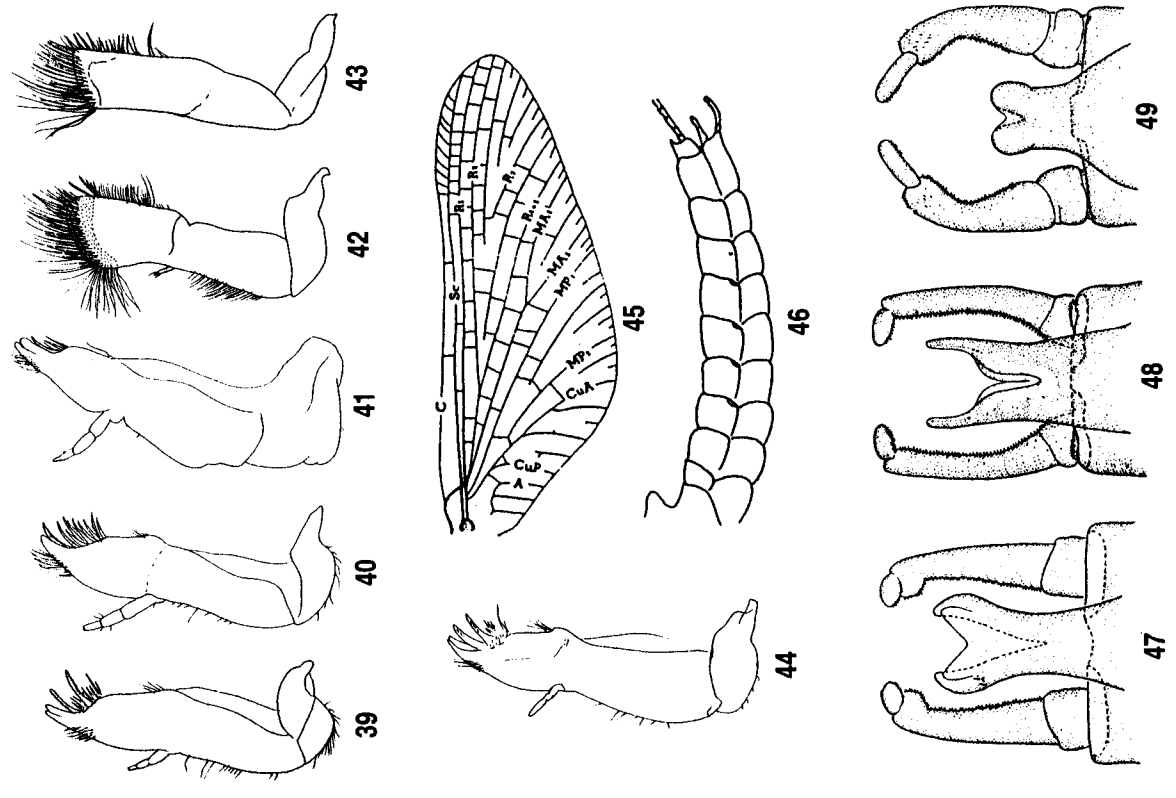
FIGS. 24-31. Caenidae (Caeninae). 24, *Caenis latipennis* Banks maxilla. 25, *C. latipennis* labium. 26, *C. latipennis* gill 4, ventral. 27, *C. capensis* (Barnard) adult prosthema. 28, *C. sp.* adult thorax, dorsal. 29, *C. amica* Hagen forewing, after Edmunds et al. (1976). 30, *C. amica* male genitalia. 31, *Tasmanocoenis* sp. male genitalia, drawn from SEM.



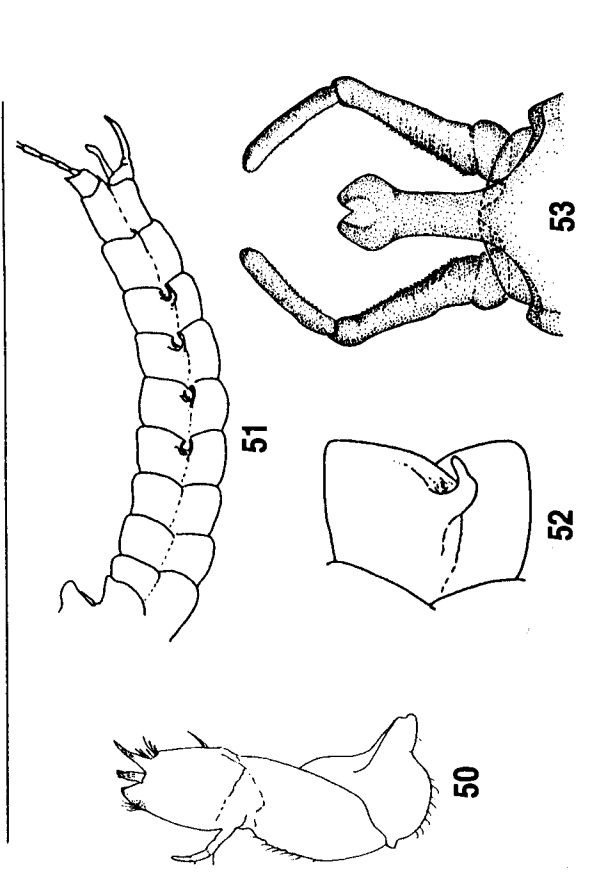
FIGS. 32-35. Caenidae (Madecocercinae). 32, *Madecocercus* sp. maxilla. 33, *M. sp.* labium. 34, *Afrocerus forcipatus* Malzacher adult prosthema. 35, *M. tauroides* Malzacher male genitalia, after Malzacher (1995).



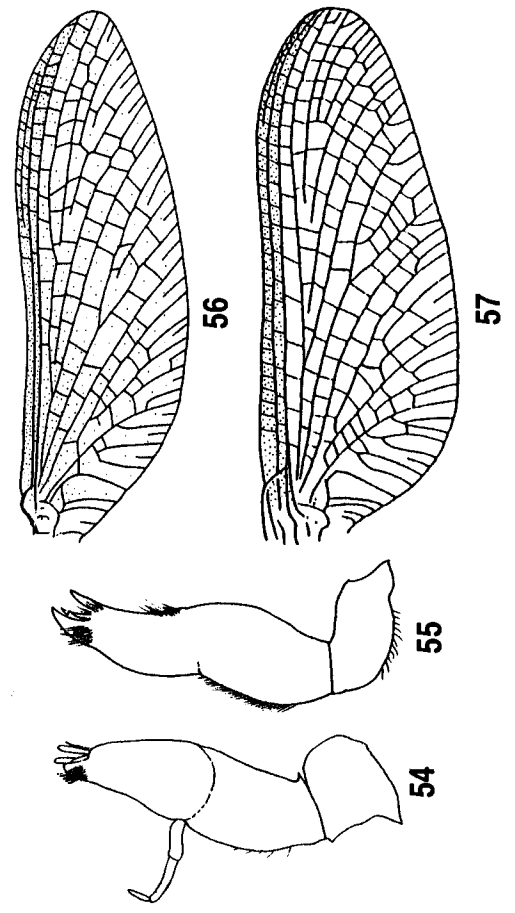
FIGS. 36-38. Caenidae (Brachycercinae). 36, *Cercobrachys* sp. maxilla. 37, *C. sp.* labium. 38, *Brachycercus* sp. male genitalia.



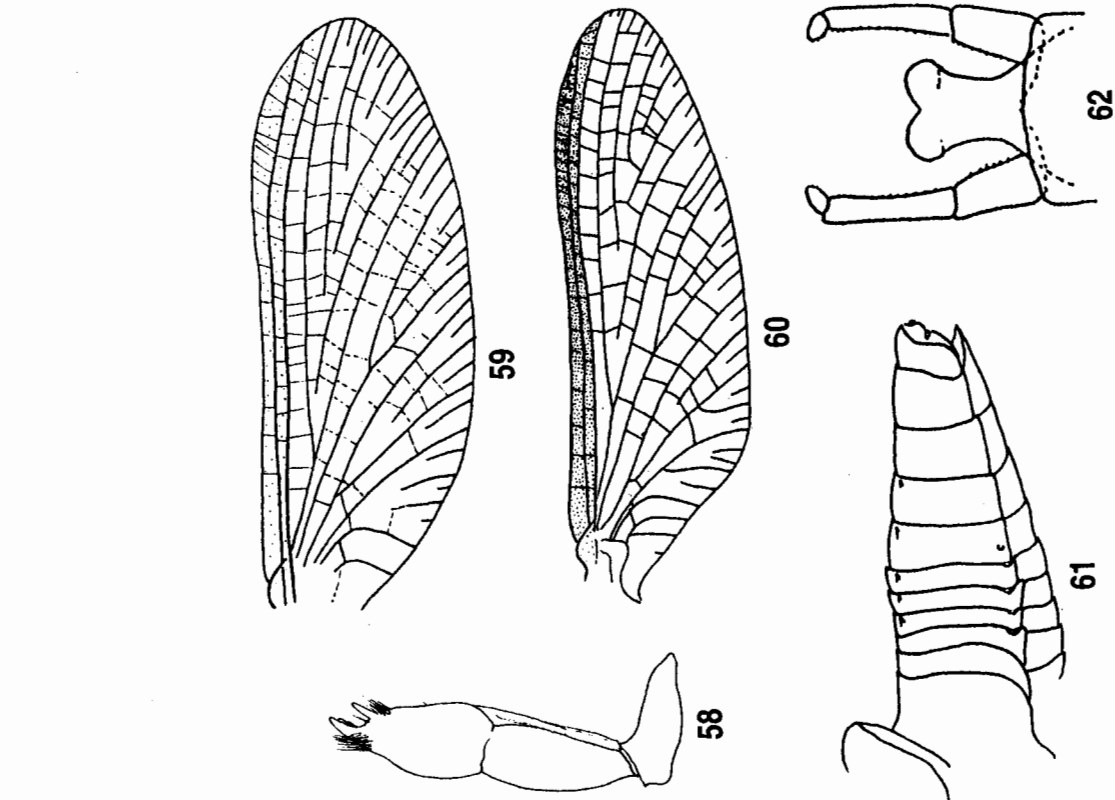
FIGS. 39-49. Ephemerellidae (Ephemerellinae). 39, *Drunella grandis* (Eaton) maxilla. 40, *Ephemerella needhami* McDunnough maxilla. 41, *Caudatella heterocaudata* (McDunnough) maxilla. 42, *Cincticostella* sp. maxilla. 43, *Uracanthella* sp. maxilla. 44, *Serratella* sp. maxilla. 45, *E. inermis* forewing, after Edmunds et al. (1976). 46, *Ephemerella* sp. adult abdomen, lateral. 47, *Ephemerella catamba* Traver male genitalia. 48, *Ephemerella needhami* male genitalia. 49, *Drunella grandis* male genitalia.



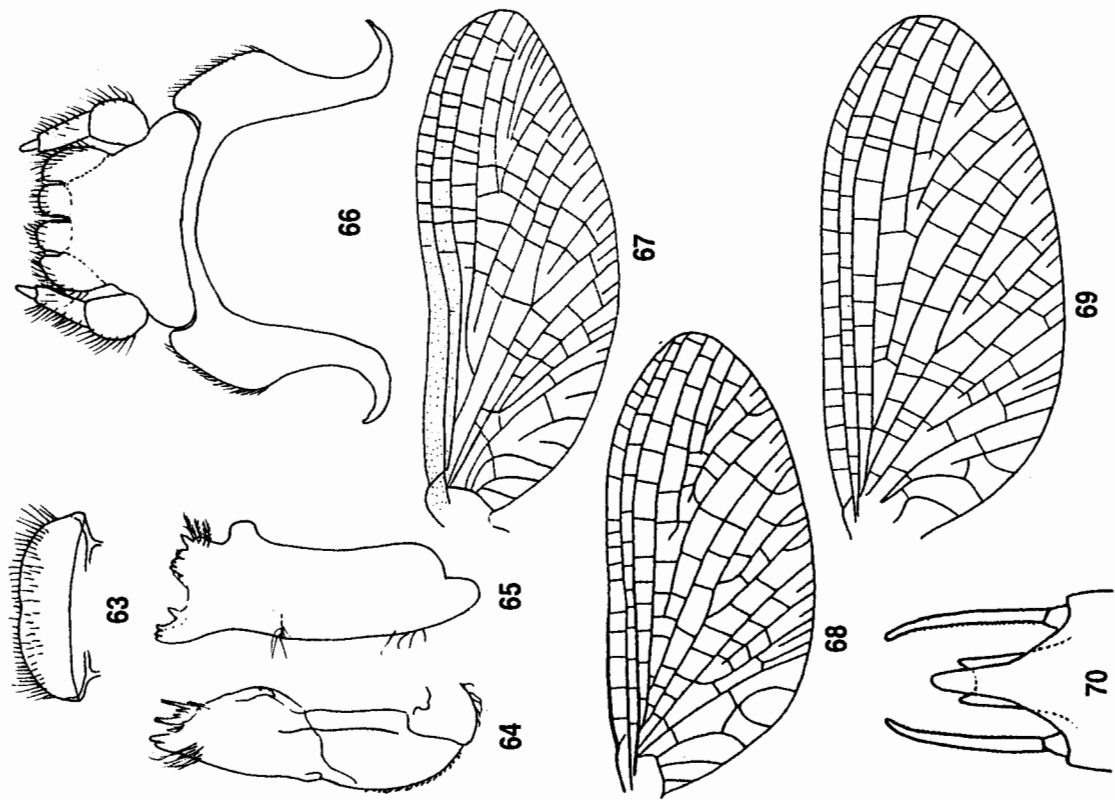
FIGS. 50-53. Ephemerellidae (Timpanoginae). 50-52: *Timpanoga bacuba* (Eaton). 50, Maxilla. 51, Adult abdomen, lateral. 52, Adult abdominal segment 7, lateral. 53, *Attenella attenuata* (McDunnough) male genitalia.



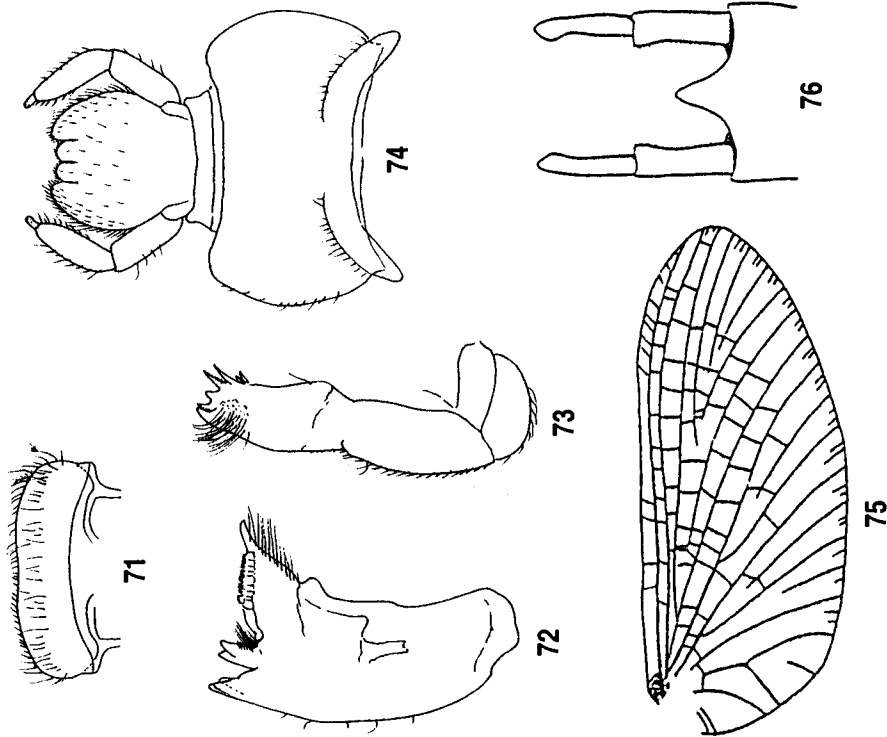
FIGS. 54-57. Austremerellidae. 54, *Vietnamella thani* Tshernova maxilla. 55, *Austremerella picta* Riek maxilla. 56, *A. picta* forewing. 57, *Vietnamella ornata* (Tshernova) forewing, after Tshernova (1972).



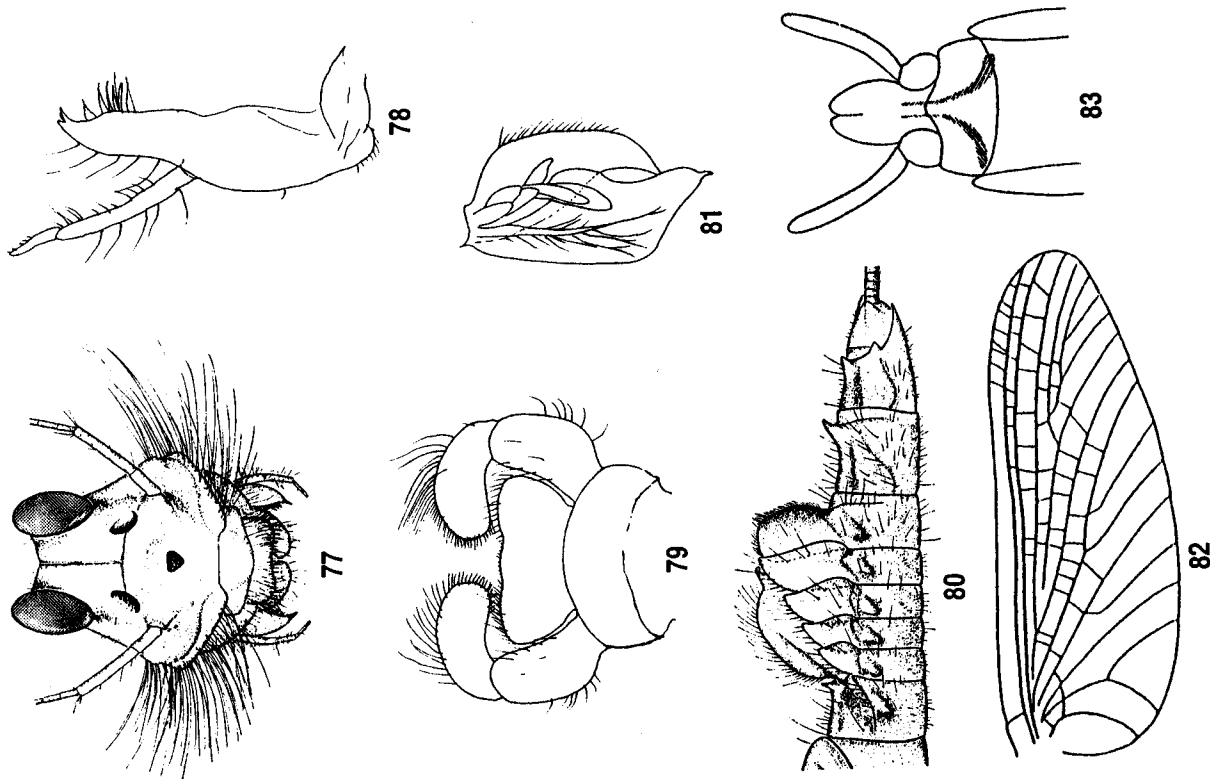
FIGS. 58-62. Teloganodidae. 58, *Ephemerebella barmardi* Lestage maxilla. 59, *Teloganodes tristis* (Hagen) forewing. 60, *Lithogloea barrisoni* Barnard forewing. 61, *E. barmardi* adult abdomen, lateral. 62, *Nadinetella crassi* (Allen and Edmunds) male genitalia.



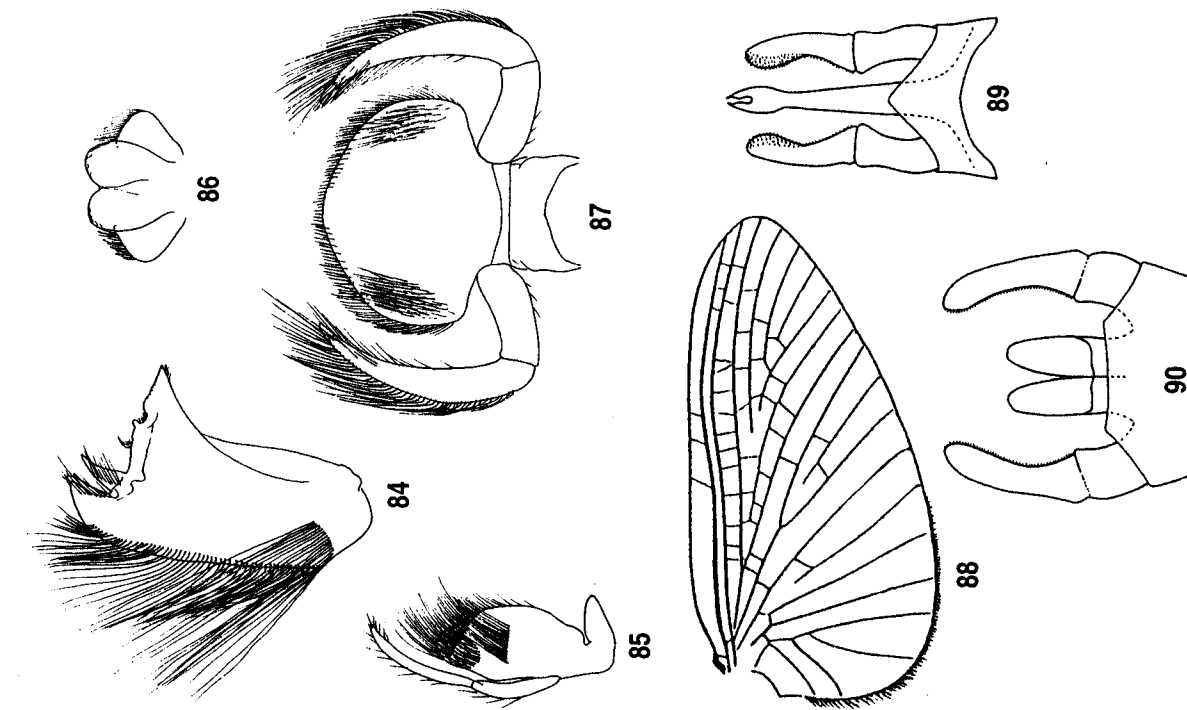
FIGS. 63-70. Teloganellidae. 63-66: *Teloganella umbrata* Ulmer. 63, Labrum. 64, Maxilla. 65, Right mandible. 66, Labium. 67-69: Forewings. 67, Teloganellidae sp. female (from Madagascar). 68, *T. umbrata* male. 69, *T. umbrata* female, after Ulmer (1939). 70, *T. umbrata* male genitalia.



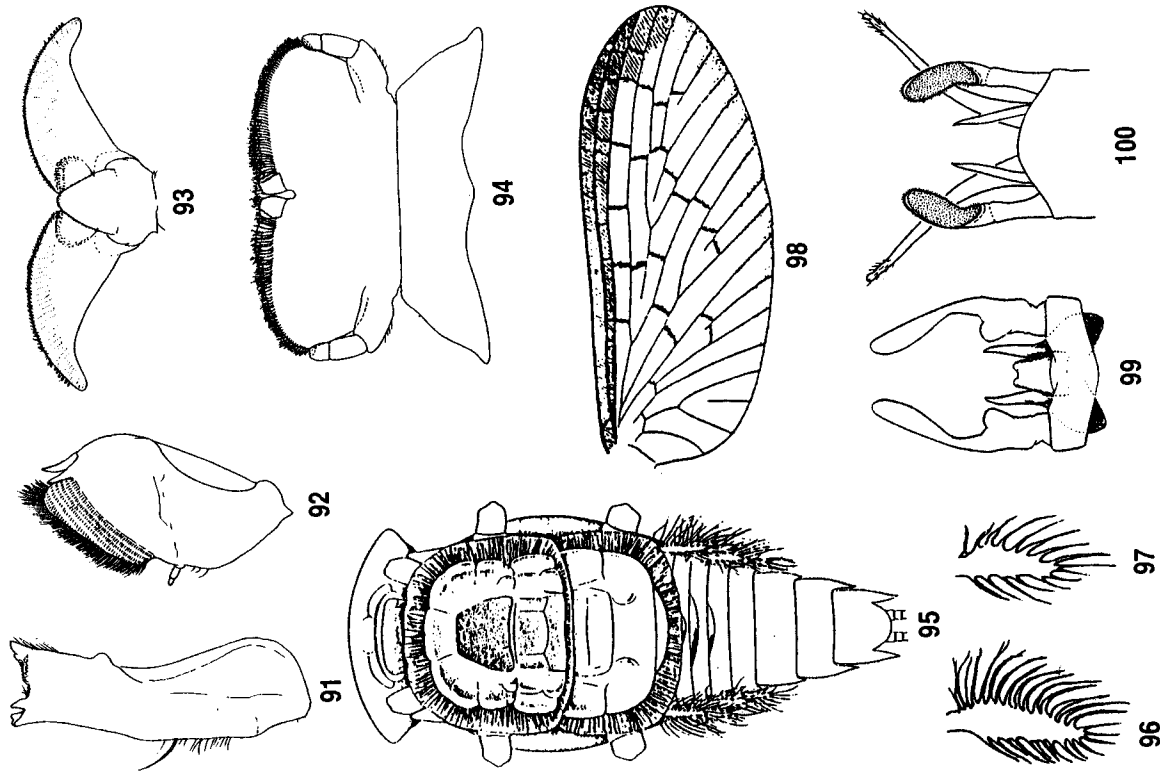
FIGS. 71-76. Ephemerythidae. 71-74: *Ephemerythus* sp. 71, Labrum. 72, Right mandible. 73, Maxilla. 74, Labium. 75, *Ephemerythus niger* Gillies forewing, after Gillies (1960). 76, *E. niger*, male genitalia, after Gillies (1960).



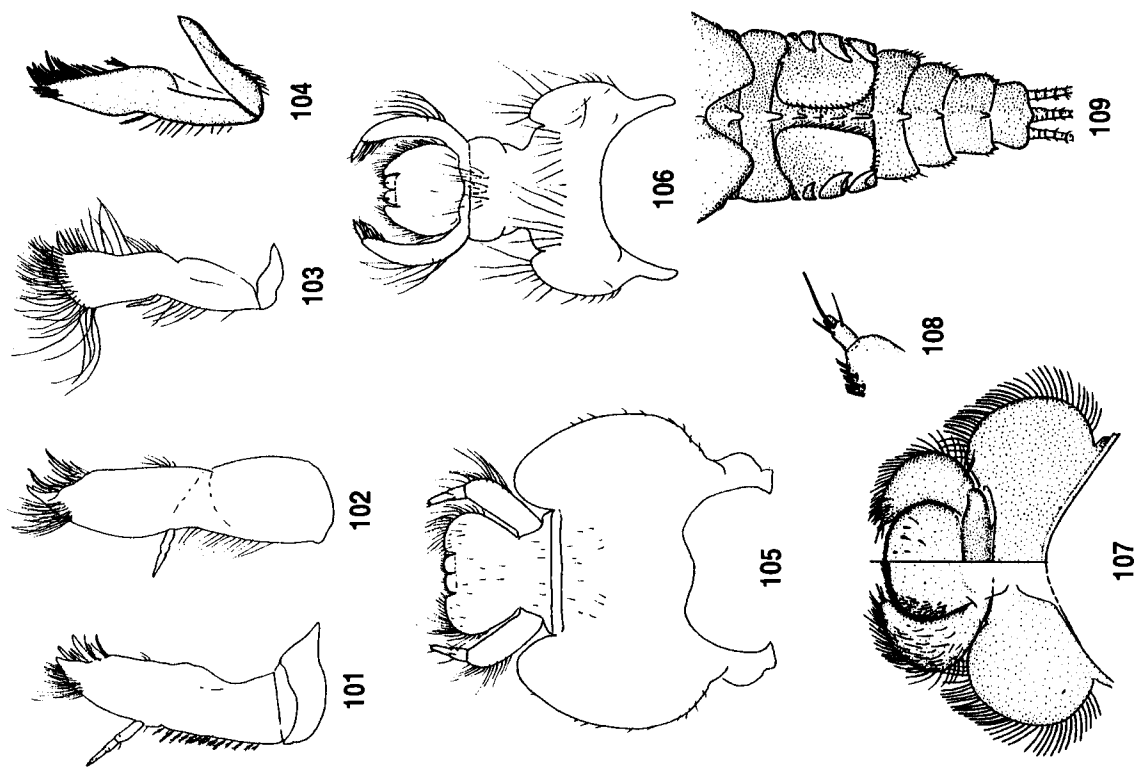
FIGS. 77-83. Machadorythidae. 77-81: *Machadorythus* sp. 77, Larval head, after Edmunds et al. (1963). 78, Labium. 79, Maxilla. 80, Larval abdomen, lateral, after Edmunds et al. (1963). 81, Gill 2, ventral. 82, *M. maculatus* (Kimmins) forewing, after Kimmins (1949). 83, *M. maculatus* male genitalia, after Kimmins (1949).



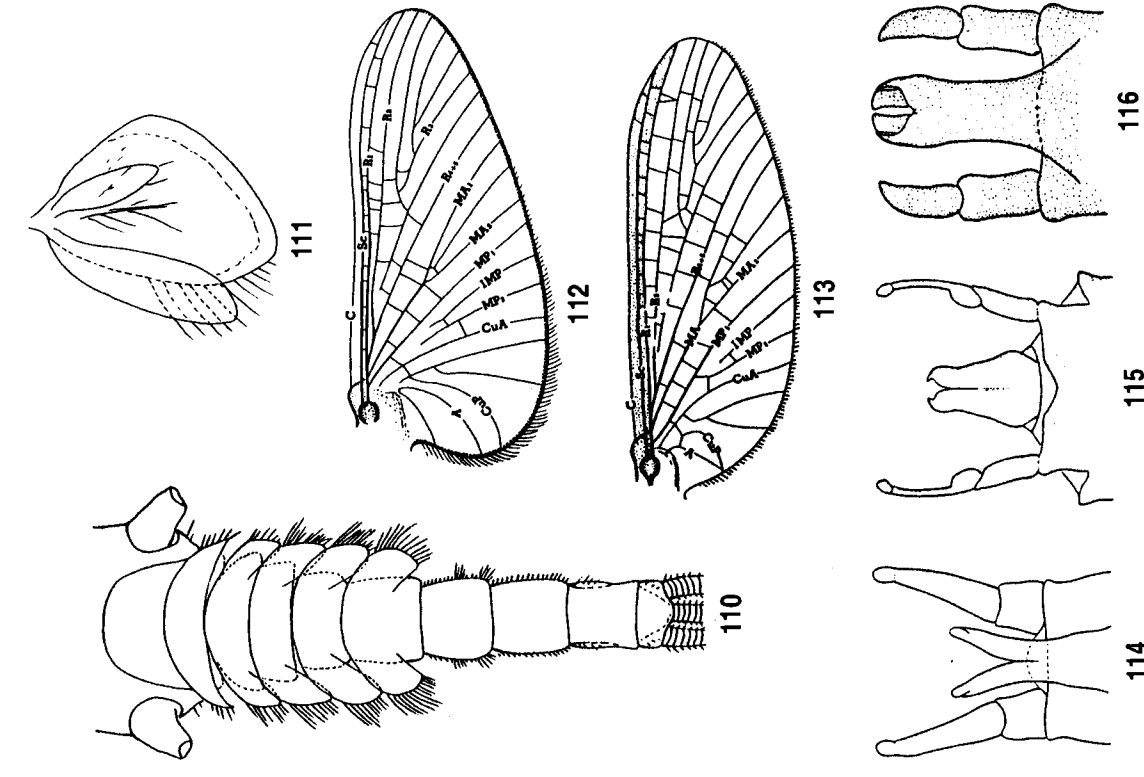
FIGS. 84-90. Tricorythidae (Tricorythinae). 84-88: *Tricorythus* sp. 84, Right mandible. 85, Maxilla. 86, Hypopharynx. 87, Labium. 88, *T. tinctus* Kimmins forewing, after Kimmins (1956). 89, *T. tinctus* male genitalia, after Kimmins (1956). 90, *Ranopythus violettai* Ollariuony and Elouard male genitalia, after Ollariuony and Elouard (1997).



FIGS. 91-100. Tricorythidae (Diceromyzontinae). 91-97: *Diceromyzon* sp. 91, Right mandible. 92, Maxilla. 93, Hypopharynx. 94, Labium. 95, Larva, ventral. 96, Gill 2, ventral. 97, Gill 4, ventral. 98, *D. costata* Kimmins forewing, after Kimmins (1957). 99, *D. costata* male genitalia, after Kimmins (1957). 100, *Madecassorythus lineae* Elouard and Ollariuony male genitalia, after Elouard and Ollariuony (1997).



FIGS. 101-116. Leptobryphinae. 101-104: Maxilla. 101, *Leptobryphes zalope* Traver. 102, *Tricorythodes dimorphus* Allen. 103, *Haplobryphes* sp. 104, *Coryphobus aquilus* Peters, after Peters (1981). 105-108: Labium. 105, *T. dimorphus*. 106, *H. sp.* 107, *C. aquilus*, after Peters (1981). 108, *C. aquilus*, detail of palp. 109, *C. aquilus* larval abdomen, dorsal, after Peters (1981).



FIGS. 110-116. 110, *H. sp.* larval abdomen, ventral. 111, *T. dimorphus* gill 2, ventral. 112, *T. explicatus* (Eaton) forewing, after Edmunds et al. (1976). 113, *H. huallaga* Allen forewing, after Edmunds et al. (1976). 114-116: Male genitalia. 114, *L. mollipes* Needham and Murphy. 115, *T. explicatus*. 116, *H. huallaga*.