# The Principles Applied in Determining the Hierarchic Level of the Higher Categories of Ephemeroptera

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THE ORDER Ephemeroptera (mayflies) is small enough (about 2,000 extant species and 170 genera described) to be readily comprehensible to a single worker. Since 1950, I have been engaged with several colleagues in a revision of the higher classification of the order. Some of the results of this study have been published (Edmunds and Traver, 1954a, 1954b, 1959; Edmunds, 1957, 1959). Since outlining my views on higher classification of the Ephemeroptera (Edmunds and Traver, 1954b), new findings have caused me to slightly modify the earlier classification. At the present time I view the mayflies as comprised of five superfamilies and 19 families. Figure 1 illustrates in a necessarily diagrammatic and incomplete way my concept of the relationships among the families. This diagram attempts to present two pieces of information. The lines indicate the most probable origins and communities of origin of the families and the depths of the forks give an indication of the degree of divergence in so far as this is compatible with the first purpose. The depths of the forks also are somewhat related to the time that the groups diverged since there is a general correlation, albeit not absolute, between the amount of morphological divergence and the time of the origin of a group. Such diagrams commonly have been called phylogenetic trees, but some authors prefer to limit this term either to diagrams based in part on knowledge of fossil forms which give direct evidence of ancestral connections of the various branches or to those based on fossils which allow the times at which the groups arose to be precisely determined. Either of these restrictions would effectively preclude any phylogenetic tree of the Ephemeroptera; the fossils are largely wing prints only, and the study of wings alone yields only a distorted view of mayfly relationships. I view these as excessive restrictions of the use of the term phylogeny. Although fossil mayflies have aided in determining homologies of wing veins and in ascertaining which characters are primitive, they have been of little value in determining relationships of extant forms. Except for those assignable to extant families, evidence is inadequate to place the fossils in the present classification and probable phylogenetic tree.

After establishing and diagramming the probable relationships as in Figure 1, the problem remains of applying the taxonomic hierarchies to the various levels of differentiation and constructing a useful classification consistent with this interpretation of phylogeny.

The extant mayflies form a distinctive and isolated order of insects, so that the taxonomic hierarchy to be applied falls clearly below the ordinal level. In these circumstances, I have felt that if the levels of the highly utilitarian hierarchies of genus and family are established by practical and definable criteria, other tax-

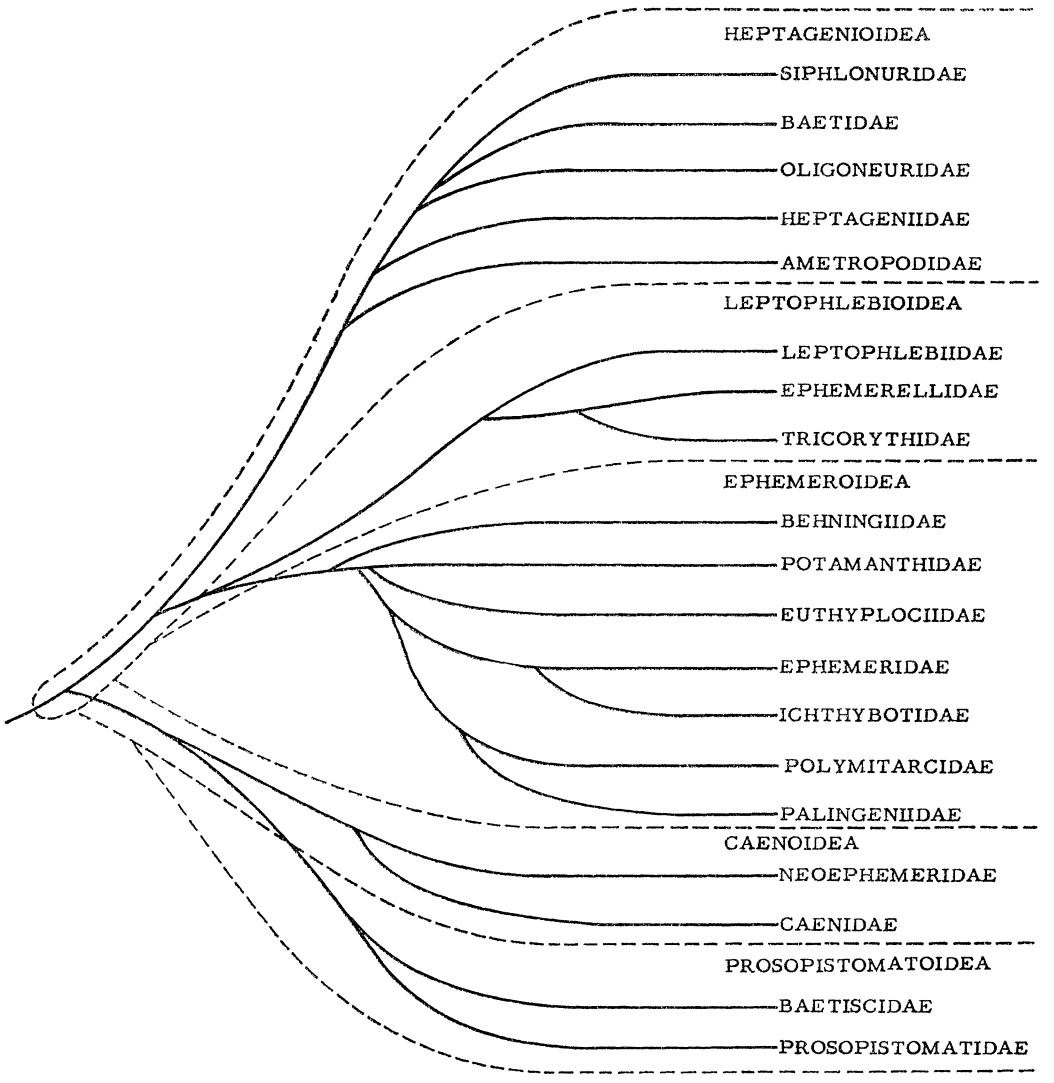


FIG. 1. A diagram of the probable phylogeny of the families of Ephemeroptera. The superfamilies are enclosed by dash-lines. Groups retaining the most primitive characters are indicated by continuing lines; diverging lines indicate specialization. Extinct families are not included in the diagram or discussion.

onomic levels are readily intercalated into this system.

In the mayflies I contend that the genus should be separated from other genera by a *distinct gap* evident in *both* adult and nymphal characters. When groups are separated by a distinct gap in nymphal structure, but this gap is very weakly indicated or absent in the adults, I prefer to call the groups subgenera. The same applies equally when the gap appears only in the adult stage. Subgenera may also be designated for groups weakly differentiated in both adults and nymphs. This results in my being more conservative than most of my colleagues in applying generic names to the groups I have studied. Many groups are either inade-

quately studied, not known in all stages, or only a small percentage of extant species is described. When the data are so obviously incomplete it becomes necessary to recognize many genera on the inference that they will meet the stated criteria. Such an inference is, of course, inherent in varying degrees in the recognition of any taxonomic category.

For application of the family level of the hierarchy, I have chosen a level in which the gaps *within* the family are small enough so that the relationships are readily evident, but the gaps *between* families are so large that the relationships can be discerned only by detailed study. These are subjective criteria, but a review of the history of mayfly classification shows rather clearly that they are practical. The taxa defined at the family level of differentiation as I conceive it by these standards are rather uniformly recognized by specialists but the level of differentiation which I call the superfamily is characterized by extreme instability of content and recognition.

In reviewing the degree of stability, I am covering a historical period in which the hierarchic classificatory position of the mayflies has changed from a family of the Neuroptera to an order with several to many families. The sections of Eaton's (1883–1888) classification generally approximate the present families. So do the tribes of Lameere's (1917) and Banks' (1900) classifications, although some of Banks' tribes are much more inclusive. The three subfamilies of Needham's (1901) classification accord rather well with the families of his 1935 work, but bear little relation to the present familial classification. The subfamilies of Jacobsen and Bianchi (1905) and of Lestage (1917) also approximate the present families. In the classifications by Klapálek (1909), Ulmer (1914, 1920), Burks (1953), and Demoulin (1958) the family level is in general accord with my views. Burks' classification is more conservative than the others, recognizing a minority of the groups only as subfamilies.

Some entomologists familiar only with the three-family classification that has prevailed in American literature on mayflies mistakenly have attributed to the paper by Edmunds and Traver (1954b) a sudden inflation of subfamilies to families. The present family concept in Ephemeroptera dates back to Klapálek (1909) and has been widely accepted everywhere but in North America since publication of Ulmer's 1920 paper. The Edmunds and Traver (1954b) paper elevated two subfamilies to family rank, but Edmunds (1957) returned one to subfamily rank. What the 1954 paper *did* do was to present a radically new superfamilial grouping.

### *Stability of the Families*

In the following discussion, I am attempting to review the degree of stability of recognition and the uniformity of the limits of the zoological groups that I and others place as the family in the taxonomic hierarchy. If in these discussions, I also attempt to deal with the problem of the hierarchic level assigned in the history of the classification, then the discussion becomes unnecessarily involved. The same problem arises in the subsequent discussion of the zoological groups that I consider to be superfamilies. To simplify the discussion and avoid the continued use of involved phrases I have taken the liberty of using the word "family" (in quotes) and "superfamily" (in quotes) to designate the zoological groups which I, in my classification, call families and superfamilies respectively, but which in the classifications which I am reviewing have been designated at a different hierarchic level.

*Siphlonuridae.* This "family" was recognized first by Eaton (1883–1888) as Section 10 of *Siphlurus,* and Banks (1900) established authorship of the family name (as Siphlurini). Klapálak (1909) recognized the group as a family, Siphluridae, although Jacobsen and Bianchi (1905) previously had used the name for a more

inclusive group. The name Siphluridae is based on Eaton's unnecessary emendation of *Siphlonurus* to *Siphlurus;* with restoration of the original spelling, the name is Siphlonuridae. Since 1909 the group has been recognized almost universally but the hierarchic position has varied from tribe to family. Lameere (1917) placed *Oniscigaster* in a tribe separate from the other members of the "family" and placed *Isonychia* with the oligoneuriids. Burks recognized the siphlonurids as a subfamily of Baetidae and placed *Isonychia* in a separate subfamily. Edmunds and Traver (1954b) expanded the latter subfamily by adding several genera of paleantarctic dispersal and recognized a separate family Isonychiidae, but Edmunds (1957) reduced the group to a subfamily in the Siphlonuridae. Demoulin (1958) and Kimmins (1960) continue to recognize the isonychiine mayflies as a family and Demoulin has placed them in a different superfamily than the other Siphlonuridae.

*Baetidae.* This "family" was recognized by Eaton (1883–1888) as Section 9 of *Baetis* but the authorship dates to Leach (1815) who used it (as Baetida) for a very extensive grouping. The hierarchic level has varied from tribe to family but the limits of the family have been practically universal since the time of Eaton's revisional monograph.

*Oligoneuriidae.* Eaton placed this "family" as Subsection B of Section 1 of *Palingenia.* Ulmer (1914) named it as a family. Since then it has been recognized at hierarchic levels varying from subtribe to family. The genus *Chromarcys* Navas (=*Pseudoligoneuria* Ulmer, 1939) has been a subject of dispute. Ulmer placed *"Pseudoligoneuria"* in a monotypic subfamily of Siphlonuridae, but Spieth (1943) transferred the subfamily to the Oligoneuriidae, noting that the nymphs are "oligoneurid in all structural details and to a total extent that cannot be explained by parallelism but represents close generic relationship." I have recently studied a female imago of *"Pseudoligoneuria" feuerborni* Ulmer and confirmed the suspected synonymy of *Pseudoligoneuria* and *Chromarcys.* The imago has several peculiarities, but its venation is essentially of a modified siphlonurid type with abundant venation rather than a reduced venation as in the other Oligoneuriidae. Although Edmunds and Traver (1954b) regard *Chromarcys* as a member of the Oligoneuriidae, Demoulin (1958) places it with several fossil genera in the Paedephemeridae. I am of the opinion that the evidence for this latter grouping is rather fragmentary and unconvincing.

The genus *Behningia* (see Behningiidae) was included in the family for a short time, but it bears only superficial resemblance to the Oligoneuriidae.

*Heptageniidae.* Eaton (1883) first recognized this "family" as Section 14 of *Ecdyurus.* Needham (1901) established authorship of the family name by proposing the subfamily Heptageniinae. The "family" has been almost universally recognized although its hierarchic level has varied, and the name Ecdyuridae or Ecdyonuridae has been used in place of Heptageniidae. The correct name is Heptageniidae, not Ecdyonuridae (or the variant Ecdyuridae based upon Eaton's unnecessary emendation of the spelling of *Ecdyonurus*). The fact that Kimmins (1960), a leading British worker, has now used the name Heptageniidae will help in establishing usage of the proper name for this family. Balthasar (1937) proposed removing *Arthroplea* to a separate family but this has not been followed except by Demoulin (1956) who placed *Arthroplea,* I believe correctly, in a separate subfamily of the Heptageniidae. The genus *Pseudiron* has been classified in the Ametropodidae by most workers, but Edmunds and Traver (1954b) have placed it in a monotypic subfamily of the Heptageniidae.

*Ametropodidae.* This family was recognized and named by Bengtsson (1913)

and has been recognized nearly universally since. Needham et al. (1935) separated off a separate subfamily Metretopinae; Lestage (1938) divided the family into three, Ametropodidae, Metretopodidae, and Siphloplectonidae. This latter arrangement is clearly unnatural, as it places the very closely related genera *Metretopus* and *Siphloplecton* in different families. There is little agreement on the composition of Ametropodidae, with various authors at times including the genera *Pseudiron* (e.g., Needham et al., 1935; Lestage, 1938), *Metreletus,* which is doubtfully distinct from the siphlonurid genus *Ameletus* (e.g., Demoulin, 1951 but not 1958), and *Acanthametropus* (=*Metreturus*) (e.g., Tshernova, 1948, Burks, 1953, and Demoulin, 1955b, 1958).

Thus, the family Ametropodidae has been nearly universally recognized but the limits have varied. Actually the genus *Ametropus* has no known close relatives and every genus, except for the type genus *Ametropus,* has been removed by one or more workers.

*Leptophlebiidae.* This family was recognized first by Eaton (1883–1888) as Section 5 of *Leptophlebia.* The authorship of the family name was established by Banks (1900) (as Leptophlebiini). The hierarchic level has varied since from subfamily to family, but the family limits have almost universal stability.

*Ephemerellidae.* The family was recognized first by Eaton (1883–1888) as Section 6 of *Ephemerella* and authorship was established by Klapálek (1909). The limits have been nearly universally recognized. The genus *Melanemerella* has been transferred by Demoulin (1955a) to the Tricorythidae where it was placed in a monotypic subfamily, an action that can be evaluated more safely when the nymphal stage of *Melanemerella* becomes known. Also, an unnamed African nymph placed in the Ephemerellidae by Kimmins, has recently been named as *Ephemerythus* and placed in a monotypic subfamily in the Tricorythidae. The uncertainty of the familial assignment of *Melanemerella* and the mistaken assignment of the tricorythid genus *Ephemerythus* to the Ephemerellidae has resulted from the close relationship of the two families. They may prove inseparable as our knowledge of the two groups increases. (See the Tricorythidae for further remarks.)

*Tricorythidae.* This family was erected by Lestage (1942) for a group of genera that had been placed with the Caenidae. Ulmer (1920) was first to recognize that the Caenidae was composed of two groups, one of which (*Tricorythus* and its allies) was closely related to the Ephemerellidae, and Spieth (1933) transferred *Tricorythodes* from the Caenidae to the Ephemerellidae. The family has been enlarged and diversified by the description of new genera and the transfer to it of *Melanemerella.* Although its recognition has been obscured by the superficial resemblance of some of its members to the Caenidae, it is rapidly being recognized as a family closely allied to the Ephemerellidae.

*Behningiidae.* This family was proposed by Motas and Băcesco (1938) for the genus *Behningia.* Lestage (1938) synonymized it by placing *Behningia* in the Oligoneuriidae, but Motas and Băcesco (1940) placed it in a separate monotypic subfamily of the Oligoneuriidae. Demoulin (1952) restored the group to family status; Edmunds and Traver (1954b, 1959) also recognized it as a family. It now contains three genera. The placement of this group as a family is hardly open to question, but its position in relation to the other families is difficult to establish.

*Potamanthidae.* This group was recognized first by Eaton (1883) as Section 4 of *Potamanthus.* The authorship of the name was established by Jacobsen and Bianchi (1905) as Potamanthinae, but Klapálek (1909) first regarded it as a family. The group has been recognized almost universally as a family or sub-

family with quite stable limits. Ulmer (1939) included the neoephemerids as a subfamily of the Potamanthidae.

*Euthyplociidae.* The genera of this family have been placed traditionally in the Polymitarcidae, but Lestage (1921) recognized them as a separate subfamily. The group remained in the Polymitarcidae until Edmunds and Traver (1954b) placed them in a separate family. Demoulin (1958) also has recognized this group as a family.

*Ephemeridae.* The family name was proposed by Leach (1815) for a much broader group, but the "family" was delineated in its present sense by Eaton (1883) as Section 3 of *Ephemera.* The group has been recognized at levels from tribe to family with quite stable limits since Eaton defined it.

*Ichthybotidae.* This monotypic family was proposed by Demoulin (1957) for the unique New Zealand genus *Ichthybotus,* which was formerly included in the Ephemeridae. It seems closely related to the Ephemeridae and the necessity for separating it as a separate family needs critical evaluation. Kimmins (1960) has not recognized this family.

*Polymitarcidae.* This "family" was recognized first by Eaton as Section 2 of *Polymitarcys.* Banks (1900) established authorship of the family by erecting the tribe Polymitarcini, and the family level was first used for this group by Klapálek (1909). Needham et al. (1935) and Burks (1953) separated the Campsurinae from the "family," but Edmunds and Traver (1954b) and Demoulin (1958), have retained them. Edmunds and Traver (1954b) also removed *Euthyplocia* and its allies and placed them in a separate family. The "family" has been designated also as Ephoronidae or Ephoridae by authors who regard *Polymitarcys* as a junior synonym of *Ephoron.*

*Palingeniidae.* This "family" was characterized first by Eaton (1883–1888) as Subsection A of Section 1 of Palingenia. Jacobsen and Bianchi (1905) established authorship by erecting the subfamily Palingeniinae and the group was elevated to family status by Klapálek (1909). The family has been recognized at the levels of subfamily or family and its limits have been universally agreed upon.

*Neoephemeridae.* Members of this family were made known when Joly (1870) described the nymph of *Neoephemera maxima* (Joly) as a *Caenis* from France. Eaton (1883–1888) provisionally referred it to *Tricorythus.* McDunnough (1925) first described the adult and Traver (1931) made known the association of the nymphs and adult. The nymphal stage closely resembles *Caenis* in all details of structure to a degree that precludes the similarity being a result of convergent evolution, but the wing venation of the adult is very similar to that of the Potamanthidae.

Needham et al. (1935) erected a subfamily for the group, and it has been since recognized as a family or subfamily. Ulmer (1939) placed it as a subfamily of the Potamanthidae.

*Caenidae.* This group was recognized first by Eaton as Section 7 of *Caenis.* The authorship of the family was established by Newman (1853). The family was restricted by the removal of the Tricorythidae, but otherwise has been universally recognized at hierarchic levels of tribe to family with its limits stable.

*Baetiscidae.* This monotypic "family" was recognized by Eaton as Section 11 of *Baetisca* and the authorship of the name established by Lameere (1917) as tribe Baetiscini. The "family" has been universally recognized since at hierarchic levels of subfamily to superfamily.

*Prosopistomatidae.* This monotypic "family" was recognized by Eaton as Section 8 of *Prosopistoma* and authorship of the name was established by Lameere (1917) as tribe Prosopistomini. Lestage (1917) first recognized it at the family level. The family has been universally recognized since, at the level of subfamily or family.

*Summary*

It is evident that the groupings to which I believe family names should apply in the Ephemeroptera have more stability of recognition and limits than have groups above or below this level of differentiation. The level in the hierarchy recognized for the groups has differed in various classification systems but the degree of differentiation from other such units and obvious relationships within each group have led most investigators to use this level as the fundamental working unit or organizational category.

Eleven of the mayfly families have practically universal recognition and limits, three of these being monobasic. Four others have universal recognition, but the inclusion or exclusion of one or more aberrant or little known genera places the limits in dispute. The Caenidae have been universally recognized but dispute over whether or not to include the tricorythid genera has caused instability of the limits. The inclusion or exclusion of two of the subfamilies has caused some instability in the limits of the Polymitarcidae, and the isonychiine genera have been variously excluded from or included in the Siphlonuridae. The most disputed family is the Ametropodidae; although it has been universally recognized since being proposed, no two classifiers agree on its limits.

There can be little doubt but what the fragmentation of recognized insect families makes it difficult for the non-specialist and it is best if specialists can use a family concept that is most useful to the non-specialist. In the classification of the mayflies by Needham et al. (1935) only three families were recognized and this arrangement has appeared in several text books. Why should we not continue to use this for the convenience of the non-specialist? My answer is simply that it does not group related forms together and as one becomes familiar with the mayflies, he finds that the subfamilies are the usable units in this classification. In Needham's arrangement the Heptageniidae are a natural unit, the Ephemeridae are in my opinion diphyletic (the Neoephemerinae have affinities with the Caeninae and the nymphs will not key to the family Ephemeridae) and the Baetidae are a collection of diverse types classified and identified in the keys by default, namely, failure to be either Heptageniidae or Ephemeridae.

If we consider the classifications of mayflies from the standpoint of the superfamilies, the various schemes have so little agreement that comparison serves to illustrate only systematic chaos.

Eaton grouped his fourteen sections into nine groups and three series. Lameere arranged nine tribes into five subfamilies and two families. Jacobsen and Bianchi (1905) classified their subfamilies into three families; the subfamilies of Lestage (1917) were grouped into five families and two groups, and Needham et al. (1935) arranged the subfamilies into three families. Ulmer (1920) placed the families in three superfamilies, Edmunds and Traver (1954b) put them in five, and Demoulin (1958) in six superfamilies. The only "superfamily" that might be agreed upon by several investigators is the Ephemeroidea. But the placement of three of the "families" in this group is in dispute. The Neoephemeridae have been included here by most, but removed to the Caenoidea by Edmunds and Traver (1954b). The Behningiidae are a clearly aberrant family but appear to me to be most closely allied to the families that constitute the Ephemeroidea. The discovery of the more primitive *Protobehningia* by Tshernova and Baikova (1960) has in my opinion only strengthened the views expressed by Edmunds and Traver (1959). Demoulin (1958) has removed the Behningiidae and the Palingeniidae from the Ephemeroidea and placed them with several fossil genera in a separate superfamily.

Let me illustrate the taxonomic chaos at the "superfamily" level used in vari-

ous classifications by Eaton (1883-1888), Ulmer (1920), Needham et al. (1935), Burks (1953), Edmunds and Traver (1954b), and Demoulin (1958). Only five of the nineteen "families" have received unanimous superfamilial placement in all six classifications; four of these are Ephemeroidea as cited above, and the other one, Heptageniidae, manages unanimous placement only by the nomenclatural accident of being the type "family" of the "superfamily." Two "families" have been placed in only two different "superfamilies"; five have been in three, six of them have been in four different "superfamilies" and one has been placed in five. The Behningiidae have been considered in only three of the classifications and have been in three different "superfamilies." *Of the six superfamilies delineated by Demoulin* (1958) *not one corresponds to the content of any of the five superfamilies proposed by Edmunds and Traver* (1954b). By contrast, even though these two superfamilial arrangements bear little resemblance to one another, the content of the families in the two classifications is very nearly identical except for the placement of occasional poorly known or aberrant genera.

It would appear then that any "conservative" classification of the mayflies into a smaller number of families by reducing the groups currently called superfamilies to family level can result only in having the limits of the families highly fluid and controversial. In contrast, about 20 families can be recognized with a high degree of stability in placement of well-known genera, although some poorly known genera will undoubtedly be transferred from one family to another. The advantages of stability at the family level clearly outweigh the considerations of the number of families recognized.

The families of Ephemeroptera are apparently equivalent to long-recognized families in other insect orders. To anyone familiar with the mayflies the families are easily recognized by their general facies without detailed examination of key characters, and in general the family name conveys an image of the structure, habitus, and behavior of the named group. The families owe their naturalness and their clear separation from other such groups to the apparent fact that each represents a major adaptive trend in the nymphal stage, adult stage, or both.

Evidence from geographic distribution indicates that the family unit is not overly-restricted. The Ephemeroptera, being short lived and easily subject to desiccation, are apparently not easily dispersed by air as they are virtually absent from Micronesia and Polynesia and are poorly represented on such island groups as the West Indies and Seychelles. Despite their poor dispersal, three of the families are found in all six of the major zoogeographic realms (Nearctic, Palearctic, Ethiopian, Oriental, Australasian, and Neotropical), six of the families are in all but one region, two are dispersed over four regions, and four are found in only three of the zoogeographic realms. Two small families are Holarctic (Nearctic plus Palearctic) and two monotypic families are restricted to a single realm, the Baetiscidae to the Nearctic region and the Ichthybotidae to New Zealand (Australasian).

Although the concept of *family* is difficult to define, it has acquired a major function in permitting man to comprehend related groups of animals. Historically, the hierarchic levels of superfamily and subfamily have not gained this level of importance in man's conceptual view of animal groups. It therefore is important that a level of differentiation be selected for family status that conveys a concept of a group of animals that is most meaningful to the persons acquainted with the animals. To recognize a larger number of families that are more or less readily associated with zoological concepts is certainly preferable to the formation of a smaller number of families whose names are more readily memorized but have little conceptual value. In the clas-

sification of the Ephemeroptera the present concept of the family seems generally most useful to those that classification should be serving, namely, the specialists or non-specialists that study these insects.

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