The Higher Classification of the Ephemeroptera and Its Evolutionary Basis

W. P. McCafferty and George F. Edmunds, Jr.

ABSTRACT


The higher classification of the extant Ephemeroptera of the world is reviewed. The suborders Schistonota (including the Baelidae, Leptophlebioida, and Ephemeroidea) and Pannota (including the Ephemerelloida, Caenoida, and Prosopistomatoidea) are introduced and defined on the basis of thoracic structure and other characters. The families Ephemerellidae and Tricorythidae are removed from the Leptophlebioida and placed as the Ephemerelloidea. The phyletic basis for this classification and the evolutionary history of the superfamilies is presented. The Siphlonuridae and Leptophlebiidae are paraphyletic groups as constituted. All extant mayfly lineages take their origin within the Siphlonuridae and their derivations are discussed. The Leptophlebiidae gave rise to the Ephemeroidea. Classificatory modifications in the makeup of the Siphlonuridae, Siphlaenigmatidae, Baelidae, Ametopodidae, Oligoneuriidae, Ephemerellidae, and Tricorythidae are discussed. On the basis of phyletic intermediacy, the Siphlaenigmatinae is recognized as a subfamily of Baelidae, and the Isonychiinae and Coloburiscinae are recognized as subfamilies of Oligoneuriidae.

Evolutionary relationships are becoming relatively well understood among higher groups of Ephemeroptera. Thus, this group of insects is a model for studies integrating phylogeny, classification, and biogeography. Reasons for this level of understanding are many. The order's size has helped make systematic studies approachable from a world perspective. In addition, systematic conclusions are often testable with a wide range of characters from different character sources. These include exoskeletal, soft anatomy, and behavioral data from adult, larval, and egg stages. Fossil data, although extremely sparse, have also been considered.

In the past 25 yr, higher classification systems have been proposed or reviewed by Edmunds and Traver (1954), Demoulin (1958), Tshernova (1970), Edmunds (1972), Riek (1973), Landa (1973), and Edmunds et al. (1976). All these workers have had at least some interest in the phylogeny of mayflies. Precise criteria for the formulation of higher classification in Ephemeroptera have been suggested by Edmunds (1962) and McCafferty and Edmunds (1976). Phyletic relationships were an important consideration among these criteria. Furthermore, data are being generated from several on-going studies of certain families or superfamilies. Some of these data have been published (e.g., Peters and Edmunds 1970, McCafferty 1972, Edmunds 1973, McCafferty and Edmunds 1976).

Table 1 represents our higher classification of the extant Ephemeroptera of the world. This classification is modified from Edmunds et al. (1976) for 2 primary purposes. First, it more fully reflects the evolutionary relationships of the major phyletic lineages (superfamilies). Second, it accommodates evolutionarily intermediate lineages into a practical familial classification in accordance with our suggested rules (McCafferty and Edmunds 1976).

The classification introduces 2 fundamental suborders of Ephemeroptera, and recognizes the reclassification of several families and subfamilies. The interpretive bases for these modifications, along with evidences for the paraphyletic nature of major stem-groups are treated herein.

Suborders

New evidence from the thorax along with other data indicates the presence of a derived monophyletic grouping of families which represents a major and distinctive evolutionary grade within Ephemeroptera. We designate this grouping as the suborder Pannota. It is given equal hierarchical status to a grouping of all other families which we designate as the suborder Schistonota (see Table 1).

Phyletic relationships of the suborders and their superfamilies are depicted in Fig. 1. The common ancestor (D) of the Pannota had evolved radically from the ancestral structural pattern of mayflies by a fusion of the larval wing pads along the mesonotum, and a general enlargement of the mesonotum. Mature larvae of Pannota are usually easily recognized since, in most, less than half the developing forewing pad freely extends beyond its fusion to the thorax (Fig. 2). Maximum expression of the fusion is seen in the "carapace" of the Prosopistomatoidea. The Schistonota have generally retained the ancestral condition of the larval thorax, and mature Ilaecea usually have forewing pads free from notal fusion for one half or more of their length (Fig. 3).

The gill series in pannote larvae tend to be reduced and protected in various ways. Gills usually lie flattened somewhat along lateral shelves of the abdomen. Respiratory surfaces are protected either by other plates on the same gill (many Ephemerellidae), specialized operculate gills (some Ephemerellidae, most Tricitythidae, and Caenoida), the legs (Tricitythidae: Dicercomyzinae), or the fused mesothorax (Prosopistomatoidea). The gill series of Schistonota are usually well developed, highly variable, and expressive of a number of different adaptive modes and diverse lineages.

The larvae of Pannota tend to be behaviorally as well as structurally homogeneous, and there is most likely a strong adaptive correlation between the 2 character sets. Pannota larvae are generally slow moving, relatively inactive crawlers or clingers. They are often secretive in habit and tend to be inconspicuous among the vegeta-
Table 1.—Higher classification of the extant Ephemeroptera of the world, including suborders, superfamilies, families, and subfamilies. Distributional realms for each subfamily are indicated. Amphitonic distribution is southeastern Australia, Tasmania, New Zealand, and Chile and adjoining Argentina.

<table>
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<tr>
<th>Suborder SCHISTONOTA</th>
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<tr>
<td>Family Baetidae</td>
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<tr>
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<td>Subfamily Palingeniinae (Palearctic, Oriental, Ethiopian)</td>
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Suborder PANNOTA

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<td>Family Tricorythidae</td>
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<td>Family Nesoephemeridae (Holarctic, Oriental)</td>
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<td>Family Caenidae (Widespread, except New Zealand)</td>
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<td>Superfamily Prosopistomatoidae</td>
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<td>Family Baetiscidae (Nearctic)</td>
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<td>Family Prosopistomatidae (Ethiopian, Oriental, Palearctic)</td>
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... tion, debris, or other substrates with which they may occur. The swimming habit has been retained (or secondarily acquired), but is seldom used in the prosopistomatoids. Schistonote larvae are variously swimmers, sprawlers, burrowers, or occasionally crawlers or clingers. Most tend to be relatively active.

The adults of Pannota and Schistonota are not as easily distinguishable or as consistently expressive of their relative evolutionary grades as are the larvae. Although there is some obvious carry-over from larval thoracic differences, adult thoracic morphology has evidently evolved many times in relation to body and wing size modifications (primarily reduction), and flight behavior evolution. Such changes have occurred in many diverse lineages of Ephemeroptera. In the adults of Pannota, the margins of the mesoscutellum are highly tapered from their relatively anterovernal origin to the posteriorodorsal apex of the mesoscutellum. Although there are exceptions, the mesoscutellum often extends posteriorly for over half of the length of the relatively short metanotum. Fig. 4 and 5 are two examples of thoracic types that are most apt to be encountered in the Pannota. The adults of...
Schistonota tend to have a mesoscutellum which is not highly tapered; however, when it is tapered, usually more than half of the metanotum of the relatively large metathorax is exposed. Typical schistoneote thoracic types are shown in Fig. 6 and 7. These adult differences must be regarded only as general tendencies in the 2 suborders, and because of possible convergences and the complexities of thoracic morphology, we recommend that adult mayflies continue to be initially keyed by familial characters.

Using evidence from internal anatomy, Landa (1973) recognized the Ephemeroptera encompassed by our Pannota as a single phyletic branch in which "an improved tracheal system begins to appear." Unfortunately, there
The fossil genus, *Triposoba*, was placed as a separate suborder by Demoulin (1958). Because of the absence of larval morphological evidence regarding it, its equivalency within our subordinal scheme cannot be determined at this time.

**Superfamilies**

We recognize three superfamilies within the suborder Pannota (Table 1 and Fig. 1). Edmunds (1972) and Edmunds et al. (1976: Fig. 19) recognized a caenoid-prosopomatoid lineage and an ephemerrilid-tricorythid lineage, and derived them independently (although very close in grade) from pre-leptoplebiid ancestors. As a result Edmunds et al. (1976) also recognized the Ephemerellidae and Tricorythidae together with the Leptoplebiidae in the superfamily Leptoplebioidea. Obviously such a classification is contrary to the findings presented herein. Since the ephemerrilid-tricorythid lineage can now be shown to be derived from a common ancestor (Fig. 1D) with the superfamilies Caenoidae and Prosopomatoidae, the Ephemerellidae and Tricorythidae should not be placed in the Leptoplebioidea, but either in the Caenoidae or as Ephemerellioidea. We classify them as Ephemerellioidea.

The hypothetical common ancestor D of the Pannota was most probably ephemeraloid-like, while the hypothetical common ancestor E of the caenoid and prosopomatoid lineages was caenoid-like. Thus, within the Pannota there are three progressive evolutionary gradations expressed by the 3 superfamilies.

The suborder Schistonota is a much larger and more diverse group than the Pannota, containing at the same time the most primitive and some of the most highly advanced extant mayflies. As in the Pannota, we recognize 3 superfamilies in the Schistonota. The only conceptual modification of these from Edmunds et al. (1976) is the exclusion of Ephemerellidae and Tricorythidae from the Leptoplebioidea. The name Heptagenioidea (in the sense of Edmunds) is changed to Baetioidea to comply with rules governing the formation of family-group names by priority.

In general and in reference to Fig. 1, hypothetical ancestor A was the common ancestor of all modern mayflies, and was most likely an ancestral Baetioidea. Besides the Baetioidea, ancestor A gave rise to the common ancestor (B) of the remainder of the modern Ephemeroptera. Ancestor B was most likely leptoplebioid-like, and gave rise on the one hand to the Pannota and on the other hand to the common ancestor of the Leptoplebioidea and Ephemeroidae. This latter ancestor was most likely a leptoplebioid.

**Major Stem-Groups**

The phylogeny of the major groups of Ephemeroptera cannot be fully explained without a more complete examination of the major stem-groups of the Schistonota. These are groups that have given rise to lineages which became highly evolved into other recognizable groups. These stem-groups are therefore paraphyletic taxa. The family Siphlonuridae is such a group and corresponds in part to Fig. 1A. The family Leptoplebiidae is also such a group and corresponds in part to Fig. 1C. It should be noted here that paraphyly is common in our classifica-
tory scheme of the Ephemeroptera (this subject will be discussed below), and a failure to accept paraphyletic taxa would lead to extreme fragmentation of the higher classification.

All modern mayflies have an origin traceable to within the Siphlonuridae. This family is therefore of pivotal importance in understanding the evolution of the Ephemeroptera. The separate sources of non-siphlonurid mayflies are depicted diagrammatically by arrows in Fig. 8.

Four of these lineages led to other families of baetoid mayflies, while the remaining lineage led to all other superfamilies (the descendants of the leptophlebiid-like ancestor B of Fig. 1).

The Siphlonuridae is represented by the present-day survivors of the earliest ephemeropteran adaptive radiation. Because of its basal phylectic position and highly paraphyletic nature, the family is delimited primarily by ancestral characteristics. Its members have evolved relatively little in comparison to the other mayfly groups to which it gave rise. For example, each of the 5 lineages shown in Fig. 8 also contains commonly derived siphlonurids at their bases.

Although all ancestral ephemeropteran character states cannot be found in any one modern genus, the ancestor of the extant Ephemeroptera was probably most similar to the Siphlonurinae and especially Parameletus. Parameletus larvae agree with the ancestral form in that the body is generally machioid, the legs are relatively unmodified, and the gills are oval and found on abdominal segments 1 through 7. Whether the primitive gills did or did not have a fibrilliform portion is open to question. The ancestral labium was more similar to that of Siphlonurus. The adults possessed hind wings more nearly as long as the forewings, and most likely possessed 3 causal filaments as in Siphlonurus.

One paraphyletic lineage within the Siphlonuridae appears to be represented by the Oniscigasterinae. This subfamily has retained many ancestral siphlonurid features, but the increased number of ventral tracheal connectives in the abdomen (Landa 1969) suggests that it shares a common ancestry with a much more highly derived leptophlebiid-like ancestor (B). If this is true, then all non-baetoid mayflies were derived from a common lineage with the oniscigastirine Siphlonuridae.

Another paraphyletic lineage from the Siphlonuridae gave rise to the large and widespread Baetidae. The evidence clearly indicates a common origin of this family with the Metamorphus-group of the Siphlonurinae. These groups all share an unusual derived nerve cord in which the ganglion of abdominal segment 1 is fused with the metathoracic ganglion, ganglia are present in abdominal segments 2 through 8, and the entire nerve cord is fused into a single flat ribbon. The crucial intermediate position of Siphaenogiga between these siphlonurines and the more highly advanced Baetidae will be discussed below.

The small family Metrotropodidae was also derived from within Siphlonurinae. Because of behavioral and gill structure similarities, its most probable common ancestry was with the Siphlonurus-Parameletus cluster (the Holarctic siphlonurines excluding Ameletus-Metereletus). Additional study is required in order to clarify this origin more fully, however.

The origin of the Ametropodidae remains obscure. Available data are more suggestive of a common derivation with the siphlonurid subfamily Acanthometropodinae than with any other group. Unfortunately, most shared character states of the Ametropodidae and Acanthometropodinae are ancestral, and characteristics which define the Ametropodidae are largely unique. The 2 groups do share a derived type of fused male penes; and in the larvae, they share short tibiae on the legs, and elongate curved, adventiculate claws on the meso- and metathoracic legs. When these larvae swim, the legs are revolved to the side and under the body, and trail behind. We regard this evidence as weak because the fused penes is a pattern too frequently repeated in the Ephemeroptera. Also, such leg and claw modifications appear to be strongly selected in sand-dwelling larvae, and the same tendencies occur in other families.

The remaining lineage indicated in Fig. 8 (to the Oligonuridae and Heptageniidae) must have originated relatively very early from a siphlonurine ancestor. Here there occurred a broadening of the maxillae and labium and their palpi, and the 2nd and 3rd segments of the palpi became partially fused. We do not now recognize any mayflies with these derived character states as Siphlonuridae (as will be discussed below). Thus, other than the hypothetical ancestor, we know of no "siphlonurids" which are left to represent this particular paraphyletic lineage.

The extremely diverse Leptophlebiidae represents the other major stem-group within the Ephemeroptera. This family consists of relatively ancestral and highly derived components, with a number of ancestral character states being found in the genus Paraleptophlebia and its allies.

As stated earlier, we feel the most recent common ancestor of the Pannota, Leptophlebioidea, and Ephemeroidae (Fig. 1B) was a pre-leptophlebid; in other words, a form that was probably more leptophlebiid-like than anything else but had not yet acquired all of the characteristics by which we define the family. This ancestor cannot, however, be completely excluded from consideration as a leptophlebid.

The highly derived superfamily Ephemeroida has its origin within the Leptophlebiidae. The associated paraphyletic lineage of Leptophlebiidae is most probably represented by Paraleptophlebia and related genera. An early gill pattern in the leptophlebids appears to have been a simple fork. The capacity of this basic gill to be modified into an array of forms is seen among diverse members of the extant Leptophlebiidae as well as the
invariably fringed gill form of the Ephemeroidea.

Within the Ephemeroidea burrowing throughout the larval stage became fully developed independently in the Behningiidae, the Polymitarcyidae, and the Ephemeri- 
dae-Paligenidae lineages (McCafferty 1978). Tend- 
encies towards burrowing were most certainly present in the 
first ephemeroid. Among the “non-burrowing” 
families young larvae of Potamanthus (Potamanthidae) 
burrow (McCafferty 1975) and larvae of Probsociplo- 
cia (Euthyplociidae) in Madagascar seem to burrow and 
may remain within gravel substrates to maturity. Similar 
tendencies are present in some little known leptophlebiids (W. L. Peters, pers. comm.), and further studies of the habits of Paraleptophlebia and its relatives may 
add support to our suggested origin of the Ephemero- 
idea.

Families and Subfamilies

Our discussion of families and subfamilies will be 
limited to those groups that are affected by our classifi- 
catory modifications (Table 1), and those groups that 
remain highly tentative in classification because of in- 
sufficient phyletic data at the present.

When a family is a relatively derived group and has 
not given rise to other groups, its classification as a dis- 
tinct taxon presents no problem, no matter what the 
philosophy of the classifier. When a relatively derived family 
is linked to a more generalized family by a small, 
remote, or poorly known intermediate group, the hier- 
archial placement of the groups presents a taxonomic 
problem, particularly if the small group tends to obscure 
the definition of either the derived group or the general- 
ed group. Such small annexant groups have been 
classified either as separate families, or as part of either 
the generalized or derived family.

When McCafferty (1972) recognized the actual phy- 
etic position of Pentagenia as derived from the Hexa- 
genitidae-group of the Ephemeroidea, and also as having ac- 
quired many larval paligeniid character states, he placed 
it in a new family. Subsequently, McCafferty and Ed- 
munds (1976) placed the genus as a subfamily, Pentageni- 
idae, of the family Paligeniidae and formulated the 
rule that groups known to be clearly intermediate be- 
tween two other groups, should be placed with their de- 
ferred relatives (possibly as a subgroup). The evolution- 
ary basis of this classificatory philosophy (which admits paraphyletic taxa) as well as the pros and cons of alter- 
native strategies were discussed in some detail by 
McCafferty and Edmunds (1976).

Since more and more instances of such phyletic inter- 
mediacy are becoming known, the rule has 2 decided 
advantages for higher classification. It tempers classifi- 
catory inflation and at the same time allows the evolu- 
tionary position of groups to be reflected somewhat by 
their classification. When this rule is applied throughout 
the Ephemeroptera, it leads to the taxonomic shifts pre- 
sented herein. These involve placement of the subfami- 
lies Siphlaenigmatae, Isonychiinae, and Coloburis- 
cinae.

As discussed previously, the Baetidae are derived 
from within the Siphlonurinae. The genus Siphlaenigma 
is clearly intermediate between the ancestral Siphlonu- 
rinae and the derived Baetidae. Its relative phyletic po-

sition is shown in Fig. 9. Although retaining several 
siphlonurine character states, it possesses labia which 
have narrow glossae and paraglossae (but less so than 
Baetinae), detached veins IMA and MA2 in the adult 
wing venation, and reduced penes in the male. Further 
evidence of its intermediate position is its Baetis-like 
larval behavior. Siphlaenigma larvae are found in streams 
where they usually cling to vegetation, and like Baetis, 
they slowly swing the abdomen from side to side. Most 
expected workers upon seeing or collecting Siphlae- 
nigma in the field for the first time could easily dismiss 
the larvae as being Baetis.

Riek (1973) reduced the monogenic family Siphlae- 
nigmatae to a subfamily of the Baetidae. This change 
fits our criteria for the inclusion of intermediates with 
their derived sister groups, and we have incorporated 
this into our classification.

The placement of the subfamilies Isonychiinae and 
Coloburiscinae in the family Siphlonuridae has been 
generally accepted. However, these groups are clearly 
intermediate between the ancestral Siphlonuridae and 
the derived Oligoneuridae, and we now recognize the 
Isonychiinae (monogenic) and Coloburiscinae (three 
genera) as members of the Oligoneuridae. Riek (1973) 
had earlier introduced such a classification and Mc- 
caffert y and Edmunds (1976) alluded to this probable 
classificatory change.

Early in the lineage which originated from ancestral 
Siphlonuridae and led to the Oligoneuridae and Hepta- 
genidae, a split occurred which can be documented by 
a large number of uniquely derived character states in 
each of the resultant daughter lineages. In the heptagen- 
iiid lineage the larval body became characteristically
strongly depressed, and the femora became more or less flattened and appressed to the surface. In the adult wings, the cubital veins became distinctive. Certain features of internal anatomy (Landa 1973) and eggs (Koss and Edmunds 1974) are also unique to this lineage.

In the oligoneurid lineage a double row of long setae evolved on the larval prothoracic femora and tibiae (an apparent adaptation for filter feeding). Also in this lineage, gills occur on the maxillae, the tracheal system lacks the ventral cephalic branch, and the maxillae and labium are highly setaceous. Since all these characteristics are common to Isonychiinae and Coloburiscinae, the derived affinities of these subfamilies are obvious. However, the intermediate phyletic position of these subfamilies is evident because they retain many siphonurid adult characteristics and do not share additional derived character states found in other oligoneurids. These phyletic relationships are diagrammatically depicted in Fig. 10.

![Phyletic relationships of the Isonychiinae and Coloburiscinae among the Baetoidea.](image)

Because of their adaptations for swift flight, the Oligoneurinae are perhaps the most highly evolved adult mayflies. Students of Ephemeroptera in Europe or North America are likely also to regard the larvae as strongly differentiated. However, the most ancestral larvae of the Oligoneurinae are those of the genus *Elassoneuria* which occurs in Africa and Madagascar. These larvae are unlike either the slow crawlers of *Lachlania* or *Oligoneuriella*, or the soft bodied sand-dwellers of *Homoneuria* or *Oligoneurisca*. They more closely resemble the active strong swimming larvae of *Isonychia*, both in both in general form and behavior. W. L. Peters (pers. comm.) has noted that *Chromarcy* (Oligoneuridae: Chromarcyinae) is also a rapid swimmer. This latter group appears to be a sister lineage of the Oligoneurinae, but not so highly derived as the Oligoneurinae.

The Coloburiscinae and the Chromarcyinae-Oligoneurinae apparently are derived independently from *Isonychia*-like ancestors. Both lineages show several derived advances over *Isonychia* but none of the derived character states of either lineage is shared by the other. Thus, the precise points of phyletic origin of the Isonychiinae and Coloburiscinae, relative to each other, are unclear. Riek (1973) and Landa (1973) showed the Coloburiscinae diverging earliest among related groups.

Other possible classificatory modifications that involve evolutionarily intermediate groups may become necessary as we learn more. For example, if a close relationship of the subfamily Acanthometropodinae to the Ametropodidae can be confirmed, and if intermediacy between the Siphlonuridae and Ametropodidae becomes evident, then the Acanthometropodinae could be placed as the primitive subfamily of the Ametropodidae.

Among the Pannota, basic questions regarding phyletic relationships and classification at the family and subfamily levels remain to be resolved in the Ephemeroidea. As presently constituted, the Teloganodinae (epimeletrids having gills on abdominal segment 2) appears to be the most ancestral group of epimeletrids. It also appears to be paraphyletic, with both the Ephemereidae and Tricorythidae being derived from within it. Since these relationships and those within the very diverse Tricorythidae are unclear, the familial position of Teloganodinae or segments of it may eventually require modification. The Leptohyphinae have been considered a separate family by Landa (1973) and Riek (1973).

REFERENCES CITED


