

The Higher Classification of the Ephemeroptera and Its Evolutionary Basis^{1,2}

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ABSTRACT

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The higher classification of the extant Ephemeroptera of the world is reviewed. The suborders Schistonota (to include the Baetoidea, Leptophlebioidea, and Ephemerioidea) and Pannota (to include the Ephemerelloidea, Caenoidea, and Prosopistomatoidea) are introduced and defined on the basis of thoracic structure and other characters. The families Ephemerellidae and Tricorythidae are removed from the Leptophlebioidea and placed as the Ephemerelloidea. The phyletic basis for this classification and the evolutionary history of the superfamilies is presented. The Siphonuridae and Leptophlebiidae are paraphyletic groups as constituted. All extant mayfly lineages take their origin within the Siphonuridae and their derivations are discussed. The Leptophlebiidae gave rise to the Ephemerioidea. Classificatory modifications in the makeup of the Siphonuridae, Siphlaenigmatidae, Baetidae, Ametropodidae, Oligoneuriidae, Ephemerellidae, and Tricorythidae are discussed. On the basis of phyletic intermediacy, the Siphlaenigmatinae is recognized as a subfamily of Baetidae, 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 indicate the existence 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 larvae 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 Tricorythidae, and Caenoidea), the legs (Tricorythidae: Diceromyzinae), 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. Pannote larvae are generally slow moving, relatively inactive crawlers or clingers. They are often secretive in habit and tend to be inconspicuous among the vegeta-

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Table 1.—Higher classification of the extant Ephemeroptera of the world, including suborders, superfamilies, families, and subfamilies. Distributional realms for each subfamily are indicated. Amphinotic distribution is southeastern Australia, Tasmania, New Zealand, and Chile and adjoining Argentina.

Suborder SCHISTONOTA	
Superfamily Baetoidea	
Family Siphonuridae	
Subfamily Oniscigastrinae (Amphinotic)	
Subfamily Ameletopsinae (Amphinotic)	
Subfamily Siphonurinae (Holarctic, Amphinotic)	
Subfamily Rallidentinae (New Zealand)	
Subfamily Acanthametropodinae (Holarctic)	
Family Ametropodidae (Holarctic)	
Family Baetidae	
Subfamily Siphlaenigmatinae (New Zealand)	
Subfamily Baetinae (Widespread, except New Zealand)	
Family Metretropodidae (Holarctic)	
Family Oligoneuriidae	
Subfamily Isonychiinae (Holarctic, Oriental)	
Subfamily Chromarcyinae (Oriental)	
Subfamily Coloburiscinae (Amphinotic)	
Subfamily Oligoneuriinae (Ethiopian, Neotropical, Holarctic)	
Family Heptageniidae	
Subfamily Arthropleinae (Holarctic)	
Subfamily Pseudironinae (Nearctic)	
Subfamily Heptageniinae (Holarctic, Oriental, Ethiopian)	
Subfamily Anepeorinae (Nearctic [Holarctic?])	
Subfamily Spinadinae (Nearctic)	
Superfamily Leptophlebioidea	
Family Leptophlebiidae (Widespread)	
Superfamily Ephemeroidea	
Family Behningiidae (Holarctic)	
Family Potamanthidae (Holarctic, Oriental)	
Family Euthyplociidae (Oriental, Ethiopian, Neotropical)	
Family Polymitarcyidae	
Subfamily Polymitarcyinae (Holarctic, Ethiopian, Oriental)	
Subfamily Campsurinae (Neotropical, Nearctic)	
Subfamily Asthenopodinae (Neotropical, Ethiopian, Oriental)	
Family Ephemeridae (Holarctic, Ethiopian, Oriental, New Zealand, Neotropical)	
Family Palingeniidae	
Subfamily Pentageniinae (Nearctic)	
Subfamily Palingeniinae (Palearctic, Oriental, Ethiopian)	
Suborder PANNOTA	
Superfamily Ephemerelloidea	
Family Ephemerellidae	
Subfamily Teloganodinae (Ethiopian, Oriental, Palearctic, Australian)	
Subfamily Ephemerellinae (Holarctic, Oriental)	
Subfamily Melanemerellinae (Neotropical)	
Family Tricorythidae	
Subfamily Leptohiphinae (Neotropical, Nearctic, Ethiopian)	
Subfamily Ephemerythinae (Ethiopian)	
Subfamily Tricorythinae (Ethiopian, Oriental)	
Subfamily Diceromyzinae (Ethiopian)	
Subfamily Machadorythinae (Ethiopian)	
Superfamily Caenoidea	
Family Neophemeridae (Holarctic, Oriental)	
Family Caenidae (Widespread, except New Zealand)	
Superfamily Prosopistomatoidea	
Family Baetiscidae (Nearctic)	
Family Prosopistomatidae (Ethiopian, Oriental, Palearctic)	

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 climbers. 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 anteroventral origin to the posterodorsal 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

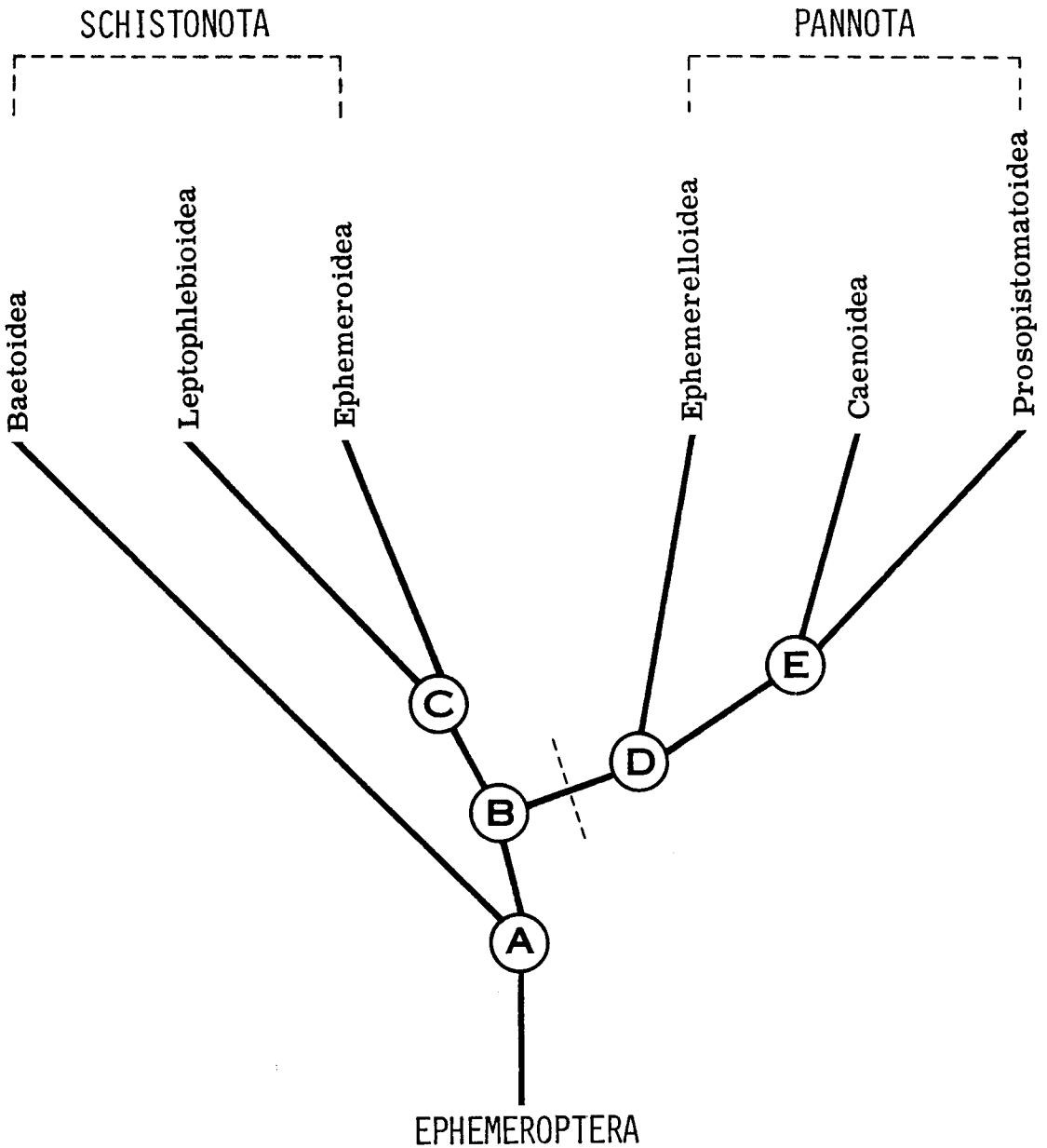


FIG. 1.—Phylogeny of the extant superfamilies and suborders of Ephemeroptera (ancestors lettered).

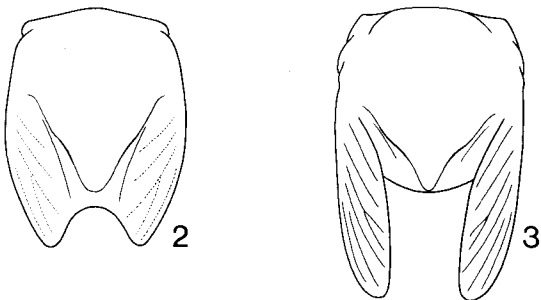


FIG. 2-3.—Larval mesonotum and wing pads of generalized mayflies. 2. Pannota. 3. Schistonota.

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 schistonote 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

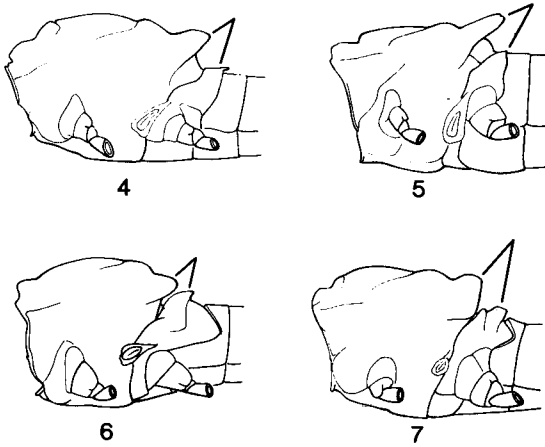


FIG. 4-7.—Lateral thorax of adult mayflies (pointers to apex of mesoscutellum and to metanotum). 4. *Ephemera* sp. (Pannota). 5. *Tricoryth* sp. (Pannota). 6. *Baetis* sp. (Schistonota). 7. *Heptagenia* sp. (Schistonota).

was no explanation of this evidence. However, if it proves to be substantive and involves commonly derived character states (as intimated by Landa), then it would reinforce our systematic conclusions considerably.

Both adult and larval convergences have been found among the Schistonota, and others will probably be discovered as various groups are surveyed further. In the Siphonuridae (Schistonota), the larvae of 2 coloburiscine genera, *Murphyella* (of Chile) and *Coloburiscoides* (of Australia) have the wing pads fused for a considerable distance along the midline. Interestingly, this is strong phyletic evidence for the sibling status of these 2 genera and is biogeographically pertinent since *Coloburiscus* (New Zealand) does not share this derived state. In *Traverella* (Schistonota: Leptophlebiidae), the adult metathorax is relatively short and the mesonotum is generally pannota-like. The relatively large sized adults of *Neophemera* (Pannota: Neophemeridae) possess a thorax more of the schistonote type. This apparent reversion of the adult is probably related to its size. The larvae of *Neophemera* are typical of Pannota. We suggest that other convergences, if they are found, will be among the Siphonuridae or Leptophlebiidae.

Most extinct Ephemeroptera will apparently fall within one of our extant suborders. However, if additional suborders are deemed necessary for fossil groups, the most anomalous larvae and hence the most obvious candidates for such recognition are those which had subequally developed fore and hind wing pads very narrowly attached to the thorax, and possessed more than 7 pairs of abdominal gills. These primitive larvae, according to reconstructions (Handlirsch 1906-8, Kukulova 1968), had little if any notal fusion of the wing pads except for the wing articulation area. The thorax is therefore an extreme schistonote (precursor) type, and along with the gill number and large hind wings, is suggestive of pre-Schistonota. Evolutionary grades, as reflected by fundamental larval thoracic morphology, can be conveniently extended to include these pre-Schistonota in basically a pre-Schistonota-Schistonota-Pannota progression.

The fossil genus, *Triplosoba*, 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-prosopistomatoid lineage and an ephemerellid-tricorythid lineage, and derived them independently (although very close in grade) from pre-leptophlebiid ancestors. As a result Edmunds et al. (1976) also recognized the Ephemerellidae and Tricorythidae together with the Leptophlebiidae in the superfamily Leptophlebioidea. Obviously such a classification is contrary to the findings presented herein. Since the ephemerellid-tricorythid lineage can now be shown to be derived from a common ancestor (Fig. 1D) with the superfamilies Caenoidea and Prosopistomatoidea, the Ephemerellidae and Tricorythidae should not be placed in the Leptophlebioidea, but either in the Caenoidea or as Ephemerelloidea. We classify them as Ephemerelloidea.

The hypothetical common ancestor D of the Pannota was most probably ephemerelloid-like, while the hypothetical common ancestor E of the caenoid and prosopistomatoid 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 Leptophlebioidea. The name Heptagenioidea (in the sense of Edmunds) is changed to Baetoidea 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 Baetoidea. Besides the Baetoidea, ancestor A gave rise to the common ancestor (B) of the remainder of the modern Ephemeroptera. Ancestor B was most likely leptophlebioid-like, and gave rise on the one hand to the Pannota and on the other hand to the common ancestor of the Leptophlebioidea and Ephemeroidea. This latter ancestor was most likely a leptophlebioid.

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 Siphonuridae is such a group and corresponds in part to Fig. 1A. The family Leptophlebiidae is also such a group and corresponds in part to Fig. 1C. It should be noted here that parphyly 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 Siphonuridae. This family is therefore of pivotal importance in understanding the evolution of the Ephemeroptera. The separate sources of non-siphonurid mayflies are depicted diagrammatically by arrows in Fig. 8.

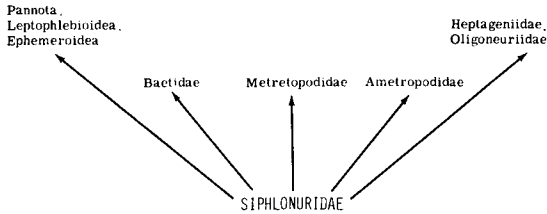


FIG. 8.—Separate origins of Ephemeroptera lineages from siphonurid ancestors.

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 Siphonuridae is represented by the present-day survivors of the earliest ephemeropteran adaptive radiation. Because of its basal phyletic 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 siphonurids 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 Siphonurinae and especially *Parameletus*. *Parameletus* larvae agree with the ancestral form in that the body is generally machiloid, the legs are relatively unmodified, and the gills are oyal 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 *Siphonurus*. The adults possessed hind wings more nearly as long as the forewings, and most likely possessed 3 caudal filaments as in *Siphuriscus*.

One paraphyletic lineage within the Siphonuridae appears to be represented by the Oniscigastrinae. This subfamily has retained many ancestral siphonurid 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 oniscigastrine Siphonuridae.

Another paraphyletic lineage from the Siphonuridae gave rise to the large and widespread Baetidae. The evidence clearly indicates a common origin of this family with the *Metamonius*-group of the Siphonurinae. 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 *Siphlaenigma* between these siphonurines and the more highly advanced Baetidae will be discussed below.

The small family Metretopodidae was also derived from within Siphonurinae. Because of behavioral and gill structure similarities, its most probable common ancestry was with the *Siphonurus-Parameletus* cluster (the Holarctic siphonurines excluding *Ameletus-Metretetus*). 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 siphonurid subfamily Acanthametropodinae than with any other group. Unfortunately, most shared character states of the Ametropodidae and Acanthametropodinae 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, adenticulate 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 Oligoneuriidae and Heptageniidae) must have originated relatively very early from a siphonurine 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 Siphonuridae (as will be discussed below). Thus, other than the hypothetical ancestor, we know of no "siphonurids" 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 Ephemeroidea (Fig. 1B) was a pre-leptophlebiid; 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 leptophlebiid.

The highly derived superfamily Ephemeroidea 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 leptophlebiids 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 Polymitarciidae, and the Ephemeridae-Palingeniidae lineages (McCafferty 1978). Tendencies 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 *Probosciodoplocia* (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 Ephemeroidea.

Families and Subfamilies

Our discussion of families and subfamilies will be limited to those groups that are affected by our classificatory modifications (Table 1), and those groups that remain highly tentative in classification because of insufficient 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 distinct 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 hierarchical 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 generalized group. Such small annectant groups have been classified either as separate families, or as part of either the generalized or derived family.

When McCafferty (1972) recognized the actual phyletic position of *Pentagenia* as derived from the *Hexagenia*-group of the Ephemeridae, and also as having acquired many larval palingeniid character states, he placed it in a new family. Subsequently, McCafferty and Edmunds (1976) placed the genus as a subfamily, Pentageniinae, of the family Palingeniidae and formulated the rule that groups known to be clearly intermediate between two other groups, should be placed with their derived relatives (possibly as a subgroup). The evolutionary basis of this classificatory philosophy (which admits paraphyletic taxa) as well as the pros and cons of alternative strategies were discussed in some detail by McCafferty and Edmunds (1976).

Since more and more instances of such phyletic intermediacy are becoming known, the rule has 2 decided advantages for higher classification. It tempers classificatory inflation and at the same time allows the evolutionary position of groups to be reflected somewhat by their classification. When this rule is applied throughout the Ephemeroptera, it leads to the taxonomic shifts presented herein. These involve placement of the subfamilies Siphlaenigmatinae, Isonychiinae, and Coloburiscinae.

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

sition is shown in Fig. 9. Although retaining several siphonurine 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 experienced workers upon seeing or collecting *Siphlaenigma* in the field for the first time could easily dismiss the larvae as being *Baetis*.

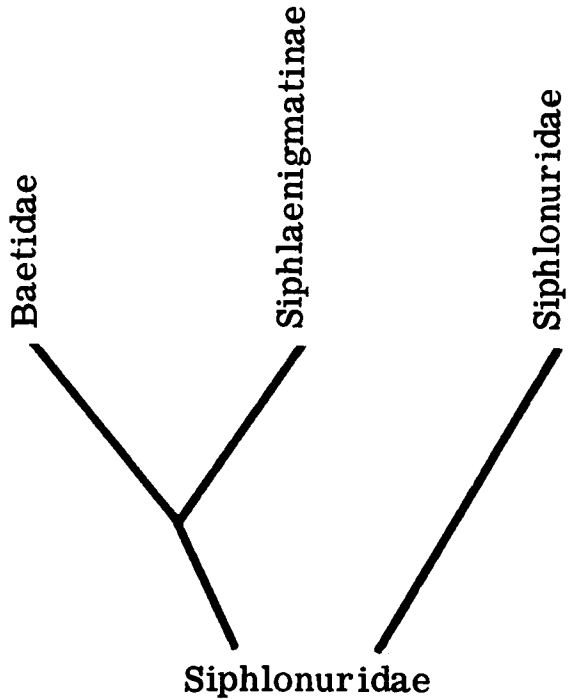


FIG. 9.—Phyletic relationships of the Siphlaenigmatinae.

Riek (1973) reduced the monogeneric family Siphlaenigmatidae 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 Siphonuridae has been generally accepted. However, these groups are clearly intermediate between the ancestral Siphonuridae and the derived Oligoneuriidae, and we now recognize the Isonychiinae (monogeneric) and Coloburiscinae (three genera) as members of the Oligoneuriidae. Riek (1973) had earlier introduced such a classification and McCafferty and Edmunds (1976) alluded to this probable classificatory change.

Early in the lineage which originated from ancestral Siphonuridae and led to the Oligoneuriidae and Heptageniidae, 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 heptageniid 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 oligoneuriid 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 oligoneuriids. These phyletic relationships are diagrammatically depicted in Fig. 10.

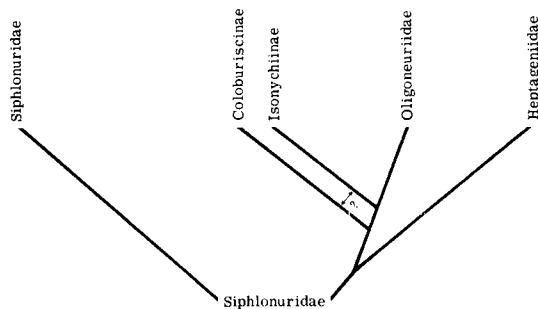


FIG. 10.—Phyletic relationships of the Isonychiinae and Coloburiscinae among the Baetoidea.

Because of their adaptations for swift flight, the Oligoneuriinae 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 Oligoneuriinae 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 *Homoeneuria* or *Oligoneurisca*. They more closely resemble the active strong swimming larvae of *Isonychia*, both in general form and behavior. W. L. Peters (pers. comm.) has noted that *Chromarcys* (Oligoneuriidae: Chromarcyinae) is also a rapid swimmer. This latter group appears to be a sister lineage of the Oligoneuriinae, but not so highly derived as the Oligoneuriinae.

The Coloburiscinae and the Chromarcyinae-Oligoneuriinae 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 re-

lationship of the subfamily Acanthametropodinae to the Ametropodidae can be confirmed, and if intermediacy between the Siphonuridae and Ametropodidae becomes evident, then the Acanthametropodinae 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 Ephemerelloidea. As presently constituted, the Teloganodinae (ephemerellids having gills on abdominal segment 2) appears to be the most ancestral group of ephemerelloids. It also appears to be paraphyletic, with both the Ephemerellinae 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 Leptohiphinae have been considered a separate family by Landa (1973) and Riek (1973).

REFERENCES CITED

- Demoulin, G. 1958. Nouveau schéma de classification des Archodonates et des Ephéméroptères. Bull. Inst. Roy. Sci. Nat. Belg. 34 (27): 1-19.
- Edmunds, G. F., Jr. 1962. The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. Syst. Zool. 11: 22-31.
1972. Biogeography and evolution of Ephemeroptera. Annu. Rev. Entomol. 17: 21-42.
1973. Some critical problems of family relationships in the Ephemeroptera. Proc. 1st. Internat. Conf. Ephem., Tallahassee, Fla. 1970: 145-54.
- Edmunds, G. F., Jr., and J. R. Traver. 1954. An outline of a reclassification of the Ephemeroptera. Proc. Entomol. Soc. Wash. 56: 236-40.
- Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The Mayflies of North and Central America. Univ. Minn. Press. Minneapolis, x + 330 pp.
- Handlirsch, A. 1906-8. Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Leipzig. 1430 pp.
- Koss, R. W., and G. F. Edmunds, Jr. 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zool. J. Linn. Soc. 55: 267-349.
- Kukalova, J. 1968. Permian mayfly nymphs. Psyche 75: 310-27.
- Landa, V. 1969. Comparative anatomy of mayfly larvae (Ephemeroptera). Acta Entomol. Bohemslav. 66: 289-316.
1973. A contribution to the order Ephemeroptera based on comparative anatomy. Proc. 1st. Internat. Conf. Ephem., Tallahassee, Fla. 1970: 155-9.
- McCafferty, W. P. 1972. Pentageniidae: a new family of Ephemeroidea (Ephemeroptera). J. Ga. Entomol. Soc. 7: 51-6.
1975. The burrowing mayflies of the United States (Ephemeroptera: Ephemeroidea). Trans. Am. Entomol. Soc. 101: 447-504.
1978. Evolutionary trends among the families of Ephemeroidea. Proc. 2nd Intern. Conf. Ephem., Kraków, 1975. (In press).
- McCafferty, W. P., and G. F. Edmunds, Jr. 1976. Redefinition of the family Palingeniidae and its implications for the higher classification of Ephemeroptera. Ann. Entomol. Soc. Am. 69: 486-90.
- Peters, W. L., and G. F. Edmunds, Jr. 1970. Revision of the generic classification of the eastern hemisphere Leptophlebiidae. Pac. Ins. 12: 157-240.

- Riek, E. F. 1973.** Classification of the Ephemeroptera. Proc. 1st, Internat. Conf. Ephem., Tallahassee, Fla. 1970: 160–78.
- Tshernova, O. A. 1970.** On the classification of the fossil and recent Ephemeroptera. (in Russian) Entomol. Obozr. 49: 124–45.
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