

EVOLUTIONARY TRENDS AMONG THE FAMILIES OF *EPHEMEROIDEA**

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Six families are recognized as belonging to the superfamily *Ephemeroidea*. These include the *Behningiidae*, *Potamanthidae*, *Ephemeridae*, *Palingeniidae*, *Euthyplociidae*, and *Polymitarciidae*. Furthermore, the superfamily appears to be a distinct monophyletic grouping within the *Ephemeroptera*. Although this paper is concerned primarily with evolution rather than higher classification per se, it should be noted that this familial classification is compatible with the phylogeny presented herein. If anything, based on increased evolutionary data, there perhaps would be a tendency to further subdivide or split the families (McCAFFERTY, 1972). The practicality of such taxonomic maneuvers will not be debated at this time.

Recent phyletic interpretations of mayfly families including the *Ephemeroidea* have been presented by LANDA (1973) and EDMUNDS (1972 and 1973). EDMUNDS' recent views have been modified considerably from his earlier interpretations (EDMUNDS, 1962). McCAFFERTY (1972) called attention to the evolutionary position of *Pentagenia*, and views on the familial affinities of *Ichthybotus* have been discussed by DEMOULIN (1957) and EDMUNDS, *et al.* (1963).

Extensive study of the external morphology of both larvae and adults of most ephemeroid genera has provided character data upon which deductions herein are based. Published internal anatomical data (LANDA, 1969) have substantiated these findings and helped resolve certain problems. Hypothesized ancestry is based on the study of *commonly derived* (synapomorphic) character states among groups, and the analytical procedures used for deducing such are essentially after ROSS (1974).

The style of phylogenetic presentation herein and the philosophy underlying such should be pointed out: Obviously, almost all taxa possess both ancestral and derived traits. Therefore, when discussing the evolutionary relationships of extant groups of organisms, individual character states more logically than taxa are discussed in terms of being relatively ancestral or derived. Taxa are more efficiently presented in terms of their relative point of origin, relative degree of change since their origin, and their sister relationships traceable through common origin. For example, a group may have originated very early in a phylogeny but have undergone a great deal of unique evolution since that origin. On the other hand, a relatively recently derived group, in total evolution leading to it, may have experienced relatively little change through its accumulative history. Attempts have been made to approximate these relative qualities of phylogeny in the phyletic diagram (Fig. 1) by the lengths of branches which are meant to depict the relative number of character state changes observable in the morphology of the groups. Actual or relative time cannot, therefore, be indicated if one assumes that rates of organic

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evolution are subject to variability. Degree of relationship must be traced by common points of ancestry and is not affected by endpoint proximity or angles of dichotomy within the diagram.

Figure 1 represents the inferred phylogeny of the *Ephemeroidea*. The primary purpose here is to identify the hypothetical ancestors (lettered in the diagram) and to elucidate the evolutionary steps leading to each of the groups. Because of limited time, only the more important or illustrative character state changes will be discussed at this time. Although the following conclusions are stated demonstratively, it should be kept in mind that they are inferentially based.

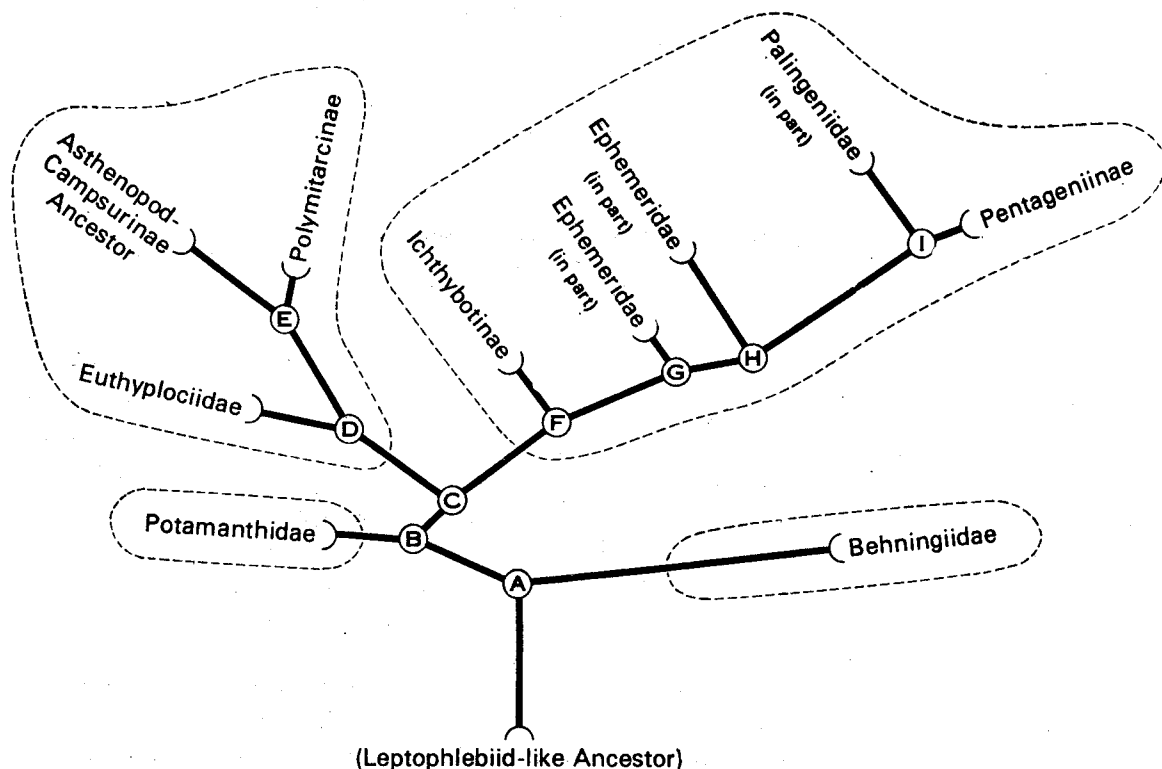


Fig. 1. Phyletic diagram of the *Ephemeroidea*

Ephemeroidea stock most likely arose from a leptophlebiid-like ancestor with double lanceolate gills on abdominal segments 2-7, oriented laterally to the abdomen. Ventral connectives of the tracheal trunks were present in abdominal segments 4-9, while imaginal thoracic spiracles were present in the metanotum. The ampullae to which malpighian tubules are attached were most likely eight in number. These conditions can all be found in certain extant leptophlebiid genera.

The *Ephemeroidea* (ancestor A, Fig. 1) had evolved at that time when the lineage had attained the unique fimbriate margined gills common to all present-day *Ephemeroidea*. This early ephemeroidean also had attained an additional ventral connective of the tracheal trunks in abdominal segment 3. Veins MP_2 and CuA of the fore wings no longer extended straight to the base as in all non-ephemeroidean mayflies (except *Neophemeridae*), but originated basally from the posteriorly oriented CuP . It is possible that ancestor A, although not adapted for burrowing, may have shown early tendencies toward subsurface substrate habit as in the very early instars of *Potamanthidae*.

Ancestor A gave rise to two lines of evolution within the *Ephemeroidea*; one line led to the *Behningiidae*, and the other, which can be considered the "main line" of evolution, led to the remainder of the *Ephemeroidea*. The *Behningiidae* have retained the ancestral character states of the internal anatomy and the basal orientation of MP_2 and CuA in the fore wings that were present in ancestor A. A relatively large number of independent evolutionary changes have occurred in this lineage since its early origin. This is exemplified by the highly modified form of the larvae: ventral oriented gills,

specialized legs and mouthparts, heavy crowns of setae, etc. This line of evolution became completely fossorial in habit.

In the "main line" of evolution from ancestor A, several character changes occurred which typify the ephemeroids in general. In the larvae, protruding mandibular tusks were developed. These were convergent anteriorly (as in the *Potamanthidae*). In the adults, CuA of the fore wings became attached to a posteriorly oriented basal crossvein so that this vein appears to extend from the base in a strongly posteriorly arched fashion. These character states must have been present in ancestor B (Fig. 1). Also in ancestor B the number of ampullae to which the malpighian tubules attach was reduced to six.

Ancestor B was probably somewhat similar to the *Potamanthidae* and gave rise to this group on the one hand. On the other hand, a commonly derived character state found in the *Ephemeridae*, *Palingeniidae*, *Euthyplociidae*, and *Polymitarciidae* clearly indicates that these families shared a more recent common ancestor (C) which evolved along another line from ancestor B. The number of ventral connectives of the abdominal tracheae was again increased so that in ancestor C and its daughter lineages an additional connective occurred in segment 2. This phyletic arrangement was not recognized by LANDA (1973) who placed the *Potamanthidae* as a sister group of the *Ephemeridae*, or EDMUNDS (1972 and 1973) who showed the *Potamanthidae* as being derived with the *Ephemeridae* and *Palingeniidae*.

Two major lineages were derived from ancestor C, one eventually leading to the *Euthyplociidae* and *Polymitarciidae* and the other to the *Ephemeridae* and *Palingeniidae*. Certain character state changes occurred in the line from ancestor C to the immediate common ancestor of the *Euthyplociidae* and *Polymitarciidae* (D), and are shared by these families. In the adults the legs of the females and all but the fore legs of the males became severely reduced, and the wings became translucent. In addition, the thoracic visceral tracheae originated in the mesonotum (a shift from the metanotum).

The *Euthyplociidae* are little changed from ancestor D. The tusks, however, are very slender and long and the maxillary palpi are more elongate. The euthyplociids remain quite "similar" to potamanthids due to the retention of many of the same ancestral character states, especially those correlated with the sprawling larval habit.

In the *Polymitarciidae* lineage leading from ancestor D many character state changes occurred. Among these were many morphological adaptations associated with attaining the complete burrowing habit. The *Polymitarciidae* also possess a very peculiar and longitudinally oriented labium unlike that of other ephemeroids. The polymitarcid ancestor (E) then gave rise to two lineages. The first led to the *Polymitarcinae* which developed dorsal unsocketed armature of the tusks but changed little from the ancestor otherwise. The second lineage was that leading eventually to the *Campsurinae* and *Asthenopodinae*. In the immediate common ancestor of these latter groups the head capsule of the larvae had become more enlarged and heavily sclerotized. The tusks in these groups are also more robust to varying degrees.

It may be noted at this time that the number of ampullae to which the malpighian tubules are attached is four in the *Euthyplociidae*, *Campsurinae*, and *Asthenopodinae* (LANDA, 1969). This is obviously a derived character state which within the *Ephemeroidea* can be traced from the eight then six ampullae states. The four ampullae state apparently evolved independently within the *Polymitarciidae* and in the euthyplociid lineage since the subfamily *Polymitarcinae* has retained the six ampullae condition. Evidence for this conclusion is the fact that all three subfamilies of the *Polymitarciidae* possess similar elaborately modified labia, among other derived morphological characteristics unique to them which indicates the family to be monophyletic. The alternative theory of the four ampullae condition evolving only once would require an explanation of an immense amount of parallel evolution and therefore seems untenable.

As stated previously, the *Euthyplociidae*-*Polymitarciidae* lineage was derived from an immediate common ancestor shared by the *Ephemeridae*-*Palingeniidae* lineage. In this latter lineage the complete fossorial habit was acquired relatively very early (ancestor F. *Ephemeridae*). Correlated with this behavior were such characteristics as the fossorial legs, frontal process, and dorsally oriented gills. In one line resulting in the *Ichthybotinae* the ancestral character state of convergent tusks was retained.

In the main line of evolution within the *Ephemeridae*, however, the tusks became divergent and upturned apically. This and other derived states were present in ancestor G.

Ancestor G gave rise to certain *Ephemeridae* (*Ephemera*) which probably changed very little from ancestor G. It also gave rise to a lineage, however, that led to the common ancestor (H) of *Hexagenia* and related ephemerid genera on the one hand and to the *Palingeniidae* on the other. The labial palpi of ancestor H had become 2-segmented, and the labium had begun to become considerably modified in shape with was subsequently further realized in the palingeniid lineage.

In the lineage leading to *Hexagenia*, uniquely derived character states regarding internal structure came about, e. g. the visceral tracheae of abdominal segment 7 disappeared; and an additional ventral connective in the abdomen developed in segment 1 (thus completing this evolutionary trend).

In the lineage leading from the ephemerid ancestor H to the *Palingeniidae* a relatively large amount of change occurred in the larval stage (McCAFFERTY, 1972). This is exemplified by the modification of mouthparts, head capsule, and legs primarily. An offshoot from this lineage is represented by the genus *Pentagenia* where ephemerid-like adult characteristics were for the most part retained. In the main line of palingeniid evolution, however, considerable adult evolution took place.

From the phyletic diagram and the discussion above it can be seen that the *Ephemeridae* could be considered a paraphyletic family in that not all of the phyletic lines resulting from ancestors within it are included in the family. The understanding of the origin of *Palingeniidae* was made possible via recognition of its derived relationships with *Pentagenia*, as shown in larval adaptations (McCAFFERTY, 1972), LANDA (1969) believed the palingeniids and ephemerids to be closely related, but this happened to be on the basis of coincidentally retained ancestral traits of the internal anatomy which could not have, in principle, indicated recent common ancestry.

Very early instars of *Potamanthidae* have recently been taken in substrate core samples at an 11 centimeter depth, indicating some limited capacity for burrowing in this early derived and relatively ancestral group. The complete fossorial habit (i. e., throughout the aquatic life) was evidently acquired at three different times in the course of ephemeroid evolution: in the *Behningiidae*, the *Polymitarciidae* (ancestor E), and the *Ephemeridae-Palingeniidae* (ancestor F) lineages. The independent evolution of this habit in each of these lineages is evidenced by the phyletic analysis as has been discussed herein. Moreover, preliminary personal study of the behavior involved and the functional morphology associated in each of these groups dismisses and obviates any theory of the common single derivation of "complete" burrowing.

In the *Behningiidae* (as observed in *Dolania*), burrowing takes place in relatively silt free, coarse sand substrate and burrows are not maintained. Burrowing proceeds in more of a vertical fashion; the gills fibrillate ventrally; there are no tusks; and the form of the body is very specialized. Thus, the behningiids are much different than any other of the burrowing groups.

Some convergent larval adaptations have occurred in the *Polymitarciidae* and the *Ephemeridae-Palingeniidae* lineages. These include the dorsally oriented gills in both groups, a distinct frontal process in most genera of both groups, fossorial adapted fore legs, and the behavior, in most genera of both groups, of digging and maintaining open ended burrows in silt to clay-like substrates.

A closer examination of attributes indicates that these lineages have acquired a similar habit in only a superficially similar manner: for the most part, the tusks in the two groups are essentially oriented differently, being convergent in the *Polymitarciidae* and divergent in the *Ephemeridae* (except in the early branching *Ichthybotus*). The tibiae of the fore legs, although expanded in both groups, is much more flangelike in the *Ephemeridae-Palingeniidae*. The tibiae of the hind legs possess a well-developed distal process in this *Ephemeridae-Palingeniidae* lineage, while such a process is completely lacking in the *Polymitarciidae*. Observations of burrowing behavior, limited to certain North American genera, have preliminarily indicated that there are subtle functional differences between these groups corresponding to the structural differences discussed above. A more detailed examination of burrowing behavior, however, is required before drawing general conclusions about the families involved.

In both the *Polymitarciidae* and *Palingeniidae*, the labial palpi are not oriented laterally as they are in all other mayflies. This has been used in the past to show the relationship of these two groups (EDMUNDS, *et. al.*, 1963). However, when both groups are studied comparatively, it is seen that although

the labial palpi have rotated ventrally in the more advanced palingeniids, the origins of the palpi have not been displaced ventrally, as is the case in the highly modified labia of the *Polymitarcidae*. These character states involve two independent adaptations which have resulted in a superficially similar structure.

Finally, the comparison of adults of these two major burrowing groups gives no evidence of a sister relationship between them, but indicates rather divergent recent paths of evolution.

SUMMARY

Evolutionary trends among the families of Ephemeroidea

Study of commonly derived morphological character states among groups of *Ephemeroidea* has provided the theoretical basis of phyletic analysis. Inferences have been further substantiated by internal anatomical data available in the literature.

Four major evolutionary lineages are recognized within the *Ephemeroidea*. The highly evolved *Behningiidae* has resulted from one of these and, although very specialized, possesses few derived character states in common with other *Ephemeroidea*. Another lineage branched early from the main line and led to the *Potamanthidae* which has retained many ancestral characteristics. The other two major lineages were derived from a common ancestor somewhat similar to the *Potamanthidae*. One lineage led to the closely related *Euthyplociidae* and *Polymitarcidae*; the other to the closely related *Ephemeridae* and *Palingeniidae*. Distinctive evolutionary grades as seen in groups of genera are discernible in the *Ephemeridae*, *Palingeniidae*, and *Polymitarcidae*; and the *Ephemeridae* represent a paraphyletic grouping.

Complete fossorial habit appears to have independently evolved three times in the history of the superfamily. Differences in structure and behaviour provide ample evidence for this conclusion.

DISCUSSION

H. J. SCHOONBEE: Is *Ephoron* a burrowing organism? I have found them (*E. savigni*) in clusters under stones in gravelly areas in Natal rivers.

W. P. McCAFFERTY: In laboratory studies we find *Ephoron* will select fine silt for burrowing over other substrates. In rivers it is often found in pockets of silt mixed with coarser gravel and rubble substrate and may indeed spend some time on the surface of the substrate.

M. D. HUBBARD: Do you then consider the *Ephemeridae* to be polyphyletic or paraphyletic?

W. P. McCAFFERTY: The *Ephemeridae* is a paraphyletic group since it is derived from a common ancestor but from within it gives rise to another group (the *Palingeniidae*). This relationship was discovered by Dr. EDMUNDS and myself by the study of *Pentagenia* and its morphological relationships.

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