

THE CLASSIFICATION OF EPHEMEROPTERA IN RELATION TO THE  
EVOLUTIONARY GRADE OF NYMPHAL AND ADULT STAGES

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Ephemeroptera imagos have been subject to natural selection associated primarily with reproduction. Nymphal features have evolved for life in a diversity of aquatic habitats. Most of the structures evolve semi-independently in the two stages. Inferences concerning phylogeny which are drawn from the adults thus may be tested by comparison with inferences drawn from the nymphs. Groups that are separated from their nearest relatives by extremely wide gaps in one stage may show only slight differentiation in the other stage; no rule may be formulated as to which stage evolves more rapidly.

Any classification that is based on one life history stage is at times inconvenient for considering the other stage because the size and position of the character gaps employed in hierarchic categorization are different in the adult and nymphal stages. Following are some of the outstanding examples from the Ephemeroptera.

In the Tricorythidae, such unique and specialized nymphs as *Diceromyzon* and *Machadorythus* might well be placed as the sole members of monotypic families, except that the known adult structures appear to be rather typical of the Tricorythidae. A more striking case is seen in the Neophemeridae and Caenidae. These two families are almost indistinguishable in the nymphal stage, being virtually impossible to separate except on size and the presence or absence of the developing hind wings. But the families are so completely different in the adults that as yet no characters have been found in the exoskeleton that will serve to characterize the group. Thus, although the nymphal evidence suggests that there is no justification for two families, the immense character gap between the adults of the two groups favors the separation into two families.

In the family Siphonuridae (including Isonychiidae) the nymphs have evolved more rapidly than have the adults. Such subfamilies as Ameletopsinae, Oniscigastriinae and Coloburiscinae each have many unique nymphal characters and would seemingly be more convenient to regard as distinct families, except that the adult characters appear to be few even for their segregation as subfamilies. Another type of problem arises in the Siphonuridae because it appears highly probable that the nymphal traits of most other families of Heptagenioidea can be traced into the Siphonuridae. Thus some of the nymphs now placed in the Siphonuridae would be best considered as primitive members of other families except for the fact that the adults largely retain Siphonurid characters.

The phylogenetic interrelationships of most genera of Ephemeroptera are now reaching fairly reliable levels of probability. This has been possible because of the wide range of characters studied by various investigators, the extensive geographic areas represented, and the fact that about 80% of the named genera are known in the nymphal stage by one or more described species. The probable phylogenetic sequence is best represented by means of a phylogenetic tree diagram, but the classification must consider not only phylogeny but historical stability, utility, and the conceptual value of the generalization expressed by the hierarchic arrangement as it applies to both nymphal and adult stages.

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