

## The Significance of Nymphal Stages in the Study of Ephemeroptera<sup>1</sup>

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### ABSTRACT

The aquatic nymphs and aerial adults offer 2 different sets of characters for study. Knowledge of the nymphs is essential for clarifying relationships and testing the validity of species concepts. The demand for specific identifications also is greatest for the nymphs, and the long-lived nymphs are more abundant in collections than are the short-lived adults. Despite the greater need for knowledge of nymphs, the adults are much better known. Field and laboratory rearing is needed in almost all parts of the world to associate adults and nymphs and provide the

knowledge necessary for an adequate taxonomy. Association of adults and nymphs collected together in the field is useful if rigid precautions are observed. The authors suggest that the naming of species from nymphs only is useful when an appropriate effort is made to associate adults and nymphs of all species and the studies are revisional. Analysis of the cause of synonymies where some species have been described from nymphs only and some from adults only shows that very few synonymies result from such practices.

The study of Ephemeroptera (mayflies) considers 2 ecologically and morphologically distinct stages, nymphs adapted to an aquatic environment, and subimagos and imagoes adapted for aerial reproduction and egg-laying. The history of mayfly systematics is unique among insects in that evidences from the nymphal stages were considered by Eaton (1883-1888) in the first sound classification of the group and in various degrees by all subsequent students of the order.

The study of characters from both the winged and aquatic stages allows an excellent opportunity for reconstructing probable phylogenies in those mayfly groups where a reasonably high percentage of the species are known in both stages. Nymphal mayflies are generally richer in taxonomically useful characters than are the adults, although in some groups the adult stages show more useful characters. A knowl-

edge of the immature stages is essential to the entire task of reconstructing the probable phylogeny and establishing a classificatory arrangement consistent with it. In any case, in this insect order the 2 stages offer an excellent opportunity for evaluating the numerous hypotheses involved in constructing probable phylogenies. A relatively large number of genera throughout the world are known in both stages, and the characters studied are not confined to a few superficial exoskeletal features.

Numerous genera now considered as having highly uncertain relationships will undoubtedly be correctly placed only when the nymphs are known. Almost three-fourths of all described genera now are known as nymphs from 1 or more species, and the known number is increasing rapidly; however, this figure is less meaningful than it appears because the generic arrangements will undoubtedly change as more species become known in the nymphal stage.

The study of nymphs and adults is valuable also in studies within a genus. As an example, the 4 spe-

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cies of the *Ephemerella bicolor*-complex (*E. bicolor* Clemens, *E. minimella* McDunnough, *E. verisimilis* McDunnough and *E. aestiva* McDunnough) are easily distinguishable as nymphs, but the species are separable as adults only with extremely careful study, and even then there is often uncertainty about the identity of some collections. In contrast, *Ephemerella inermis* Eaton and *E. infrequens* McDunnough are readily separable by means of the male genitalia, but there is no completely satisfactory means of distinguishing the nymphs. The validity of the species concept within a genus is greatly clarified when both the nymphs and adults are known.

There is a great need for identification of the nymphs of Ephemeroptera in aquatic ecology, stream pollution biology, and fisheries studies. The length of the nymphal life varies from as little as 14 days (in *Parameletus columbiae* McDunnough) to as much as 2-3 years in some of the larger burrowing species of the superfamily Ephemeroidea. The adult life is usually only a few hours to a few days, although rarely the females of *Callibaetis* Eaton and *Cloeon* Leech live for 3-8 weeks. Despite the brevity of this stage, most of the taxonomic work has been concentrated on the adults. A brief survey of the described genera illustrates the point. Between 1758 and 1850, 9 genera were described; 8 of these were characterized by adults and only 1, *Prosopistoma* Latreille (1833), was described from the nymph (as a crustacean). Between 1850 and 1900, 43 genera were described; of these, only 6 were described from nymphs and adults and the remainder were based solely upon adults. The trend has changed very little from 1900 to the present. A total of 133 genera have been described during this period; 38 of these were based upon both adults and nymphs, 82 upon adults only, and 13 were based solely upon nymphs. Of the 186 described genera, 46 remain unknown in the immature stage, while only 4 of those described from nymphs remain unknown in the adult stage.

The current descriptions of the genera of the Ephemeroptera are usually based upon study of adults of most of the included species, but frequently generic characterizations of the nymphs are drawn from only 1 to a few of the species of the genus. To attain a correct concept of the range of the characters of each genus, all the species should be studied in both stages; however, much more rearing is necessary before this ideal can be approached.

The order Ephemeroptera is composed of approximately 2000 described species, and it is estimated that less than 20% of the species are known from the nymphal stage. The current knowledge of the North American fauna is more advanced than that of other areas of the world, except perhaps for Europe. The only comprehensive treatment of the North American Ephemeroptera (Needham et al. 1935) treated 507 species. Of these, only 218, or about 40%, were well enough known to be included in keys, and many of the nymphs that were keyed still remain undescribed. A reasonable amount of work has been done since

this time, but a vast amount of systematic study must be done to achieve a reasonably good understanding of the group in North America. The most obvious deficiency is unquestionably the poor knowledge of the immature stages.

The necessary studies of the immature stages can be done in any combination of several ways. Adults may be reared from nymphs in the field by using rearing cages placed in the natural aquatic habitat. This is an ideal method, as ecological and emergence data can be incorporated with the taxonomic findings. Although field rearing can be done in many local areas, and is a subject well-suited for undergraduate and graduate dissertations, it generally has been neglected by entomologists. Field rearing presents many problems, not the least of which is that of finding suitable rearing sites free from public interference.

The rearing of adults from nymphs in the laboratory is also feasible. It also presents many problems, and the number of species is further limited by one's ability to transport living specimens to the laboratory. Some species can be transported most easily in water, but many others survive better when in wet burlap or other coarse cloth in a saturated atmosphere, with care taken to prevent nymphs' being submerged in water. Survival is always highest if low temperatures are maintained during the transfer. Many mayflies are difficult to rear under artificial conditions, and the mortality is greatest just prior to emergence of the subimago. In our laboratories we are able to rear the nymphs in either standing or running water in closed systems with controlled temperature. Bacterial growth is a constant and serious problem, often directly killing the nymphs or interfering with the emergence of the subimagoes from the nymphal skin. In any rearing study it is essential to allow the subimago to transform to the imago stage to insure specific identification.

Many associations of nymphs and adults may be made by collecting both from the same locality, and then associating such stages through the observation of adult characters developing in the nymphs. This method is very useful but must be applied with extreme caution, as attested by numerous serious errors that have resulted from such associations. When unique color or structure can be used for the association, the method seems reasonably sound. Comparative study of details of the egg chorion of various species (see Degrange 1960) suggest that those are very useful in correlating mature associated female nymphs with adults.

There is an additional methodology that can be used to describe the diversity of Ephemeroptera so as to make the names available for other disciplines. It is an acceptable and recognized practice to name and describe species from adults only, so it should be an equally acceptable and even more valuable practice to describe the nymphal forms and name them, establishing the associations of nymphs and adults where possible, and to leave the completion of this task to subsequent works. At its worst, this would lead to an

admittedly undesirable system, with 1 set of names for nymphs and another for adults, and subsequent study would result in a series of synonymies. Usually, however, many associations will be established and the synonymy will be minimal. There is a possible personal stigma attached to the idea of creating synonymous names, but the names are useful biologically, and the task of combining all the data on the nymph and adult under a single name at a later date is slight. Certainly, the attachment of such epithets as species A, B, C, or 1, 2, 3, does not solve the problem any more satisfactorily than the use of scientific names.

A recent study of the tricorythid genus *Leptohyphes* Eaton by one of us (R. K. A.) exemplifies the problem. At present the genus is known from 14 species, all of which were described from the adults only. The nymphs of 4 species, which are unassociated with known adults, have been described; Needham and Murphy (1924) described 2 as species 1 and 2, and Traver (1944) described 2 others as species A and B. The total available nymphal collections greatly exceed the number of adults in numbers of species and individuals. Study of the nymphal material has revealed more than 30 distinct species, 3 of which have been associated with previously described adults, and 2 which have been associated with adults of new species. Most of the unassociated nymphs are from areas where it is highly unlikely that they represent the nymphs of species already described as adults.

The primary argument against giving scientific names to these nymphal stages is that synonyms will be created, because all other named species are based upon descriptions of the adults. These objections are well founded, but they must be weighed against the value of having a series of comparable descriptions and keys enabling one to appreciate the evolutionary diversity and adaptations in the genus, and to apply names to collections of nymphs being studied by other aquatic biologists.

The genus *Ephemerella* Walsh (Ephemerellidae) has had a relatively high percentage of its included species named and described from the nymphal stage only, and is a good group to examine to judge the impact of naming some species from adults and others from nymphs in a single genus. In North America the genus is represented by more than 70 species, and 27 (20 of which are still valid) of them have been described from the nymphs. There have been 29 synonymies in the genus, but an analysis of the reasons for each synonymy shows that only a single synonymy was caused by the separate naming of the adult and the nymph of a single species. Those remaining are all accountable by one or more of the classic causes of synonymy, i.e., inadequate allowance for individual variation, lack of knowledge of geographic variation, inadequate review of the named species, etc.

Except for the historical fact that the concentration of effort by taxonomists has been on the adults, the nymphs appear to be the most useful stage for study. The nymphs are more prevalent than adults in collec-

tions and long series are more often available. The duration of the nymphal stages is longer and allows collection over a much longer season, and it is usually the most interesting stage for the study of the adaptive evolution and ecology. The availability of the nymphal stages in relation to that of the adult stages is exemplified by some western North American species of *Ephemerella*. *Ephemerella coloradensis* Dodds is a common species of which we have records of nymphs from more than 200 localities, but only 17 locality records of adults. Collections of nymphal *E. doddsi* Needham are from 196 localities, but adults are available from only 12 sites. *Ephemerella grandis* Eaton was studied as nymphs from many more than 200 localities, but less than 15 adult collections were available. *Ephemerella tibialis* McDunnough is known from 159 localities as nymphs, but only 5 localities as adults. The overwhelming availability of nymphal collections is even more striking when the number of specimens per collection is considered.

The description and naming of species from the nymphs only has been used to a limited extent. Of approximately 565 valid North American species, 27 were described originally from nymphs. Except for Eaton (1883-1888) who apparently inadvertently applied a name to a nymph (*Ephemerella hecuba*), Morgan (1911) was the first worker to describe new North American species from nymphs when she named *Ephemerella lata* and *E. tuberculata*. Needham (1918) described *Brachycercus lacustris* (as *Caenis*) from nymphs, and in 1927 described 2 more species of the genus *Ephemerella* from the nymphs. Traver described *Baetisca callosa* from nymphs in 1931, and in 1934 described 4 additional species of the genus *Ephemerella*. Ide described *Baetis hudsonica* in 1937, and Spieth described *Homoeoneuria ammophila* (as *Oligoneuria*) the following year. Since 1946, 7 different authors have described 19 species of *Ephemerella*, 4 species of *Baetisca* Walsh, and a new genus and species, *Dolania americana* Edmunds and Traver, from the nymphal stage only.

Despite our viewpoint that the describing and naming of mayfly species on the basis of nymphs only is more useful than when based on adults only, we would interject some serious precautions in such procedures. In most genera the species are known principally from the adult, so when describing a new species a reasonably good judgment can be made in estimating which characters will serve most effectively for species discrimination. Unless a reasonably large number of species have the nymphal stage described, or unless a major study of all nymphal material is undertaken at the time, it seems questionable that the characters needed for discrimination of species will be included in the nymphal descriptions. In some cases, the descriptions of a genus and species based on nymphs can be justified on the basis of the extreme biological or phylogenetic significance of the form. Such interesting genera as *Behningia* Lestage, *Dolania* Edmunds and Traver, *Protobehningia* Tshernova, *Acanthametropus* Tshernova, *Murphyella* Les-

tage, and *Prospistoma* were described and named from nymphs, and 3 of them are still known only as nymphs. Most certainly, the naming of species from nymphal specimens in large genera with few species known as nymphs will create more problems than it solves unless it is done as a major revisional study. Although there are many cases where the naming of species from nymphs is clearly justified, and others where it seems undesirable, each systematist is left a large problem area where his individual judgment is his only guide as to acceptable procedure. Whenever nymphal stages are described, be it with a scientific name, an informal epithet, or without distinctive designation, there is considerable doubt as to the usefulness of descriptions without comparisons with a reasonably large number of species.

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