PHYLOGENY OF THE LEPTOPHLEBIIDAE (EPHEMEROPTERA): AN INTRODUCTION

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ABSTRACT

Work has been done to revise the genera of the Leptophlebiidae and to determine the higher classification and phylogeny of monophyletic groups within the family. Detailed criteria must be imposed if such studies are to be consistent. Our phylogenies are based on the possession of several, presumed derived, character states for each monophyletic daughter line. The most primitive furcation in the evolution of the extant Leptophlebiidae is discussed. Based on this phylogeny, the need for and usefulness of subfamilies and tribes within the family are also discussed. A new subfamily: the Atalophlebiinae is proposed.

INTRODUCTION AND METHODS

In 1960, while a graduate student at the University of Utah, I began to revise the generic classification of the Leptophlebiidae on a worldwide basis. I also hoped to study the phylogeny and zoogeography of the family.

At that time only 44 genera and 13 subgenera were established in the literature. Except for 6 Holarctic genera, all were known from tropical Asia and the Southern Hemisphere. Of these 38 latter genera, exactly one-half were established on adults alone and 17 were monotypic. Further, none of the generic descriptions were consistent and any two descriptions had little comparative value.

While I had at my disposal unstudied collections of Leptophlebiidae from tropical Asia, South America, Australia and a

few other areas, most material was not reared and contained only nymphs or adults. Since 1960, I and others have reared Leptophlebiidae all over the world. Based on these collections and others either loaned or given to me, I estimate there may be some 300 genera and 4,000 species of Leptophlebiidae. Except for possibly the Baetidae, the Leptophlebiidae are the most diversified family, occurring in all areas of the world except for a few distant oceanic islands.

An example of this diversity occurs in the Leptophlebiidae of New Caledonia. This Pacific island some 400 km long x 40 km wide contains a mayfly fauna consisting entirely of Leptophlebiidae (except for some introduced Baetidae) representing about 20 new genera and over 65 species. The nymphs of these mayflies have adapted to many river and stream habitats and some superficially resemble nymphs of other mayfly families, such as Heptageniidae, Baetidae, Ephemerellidae and Ephemeridae. These Leptophlebiidae are being described in a series of papers (Peters *et al.* 1978, Peters and Peters, in press).

Many of the earlier publications concerned the leptophlebiid genera of the Eastern Hemisphere excluding Australia (Peters *et al.* 1964, Peters and Edmunds 1964, 1970). In these papers and others, consistency is stressed so that all generic descriptions are consistent and comparable; however, for certain phyletic lineages additional characters have been added when needed. Illustrations are also consistent and comparable. When interpretation of morphological characters has been better understood with further study, additional detail figures have been added. For example, many small structures of nymphal mouthparts are now used in our phylogenetic analyses.

The first phylogenetic analysis of any group of Leptophlebiidae was published in Peters and Edmunds (1970). Our phylogenetic diagram represented the probable phylogeny of the Eastern Hemisphere genera, excluding Australia. While this phylogeny was developed by evaluating weighted phenetic similarities, it is surprising how close this diagram is to those that have recently been developed in our studies using presumed shared, derived character states.

Although the phylogeny of any group is incomplete until all Recent species are described and studied, this task is often larger than the time one can apply to it. Sometimes in a large monophyletic group such as Leptophlebiidae with a high diversity of genera and species, time is not available in any one person's lifetime to describe and study all species. However, based on the studies of some species and the delineation of genera and subgenera, the phylogeny of the inter-group ancestors of the Leptophlebiidae can be determined. For example, Peters and Edmunds (1972) studied the generic limits of certain cool-adapted Leptophlebiidae in southern South

America based on a review of the literature and available species, and later Pescador (1976) completely revised the species of these genera and others. The delineation of genera and the phylogenetic conclusions on the inter-group ancestors are similar in both studies.

Since a number of persons are studying various groups of Leptophlebiidae, or Leptophlebiidae of specific geographical areas, detailed criteria must be imposed if phylogenetic and classificatory studies are to be consistent. Such criteria have been developed and examples of our criteria and methods will be presented at this conference and discussed in a series of papers in press or in preparation.

The three basic systems of phylogenetic reconstruction are: (1) methods of phenetics, (2) methods of cladistics, and (3) evolutionary methods. The basic system of phenetics was developed by Sokal and Sneath (1963) and is not used in our work. The cladistic approach was best developed by Hennig (1966), while the evolutionary or morphological system was outlined in detail by Mayr (1969). Recently Ross (1974) developed a system of phylogenetic reconstruction which incorporated much of the thinking of both the cladistic and evolutionary systems. While other series of methods have been proposed, most are combinations of the three basic systems.

Hennig (1966), Mayr (1969), and Ross (1974) all claimed to develop phylogenies based on shared, derived characters. While Hennig (1966) developed the rule of shared, derived characters, Ross (1937) used the same rule and similar methods some 29 years earlier. Hennig (1966) developed a set of rigid principles and methods for phylogenetic reconstruction and classification; however, many of these methods remain in a theoretical stage of development. Mayr (1969) contended that precise and rigid methods for phylogenetic reconstruction were nearly impossible to write and would not allow taxonomists to express clearly their ideas concerning evolution of groups. Therefore, much of Mayr's system involves evaluating weighted phenetic similarities.

The methods of Ross (1974) gave a precise but flexible system for phylogenetic reconstruction and classification. Basically, these methods, with some modifications, are used for our phylogenetic studies of the Leptophlebiidae.

It is Ross's tenet that only characters with known ancestral and derived states should be used in phylogenetic analysis. In all cases, derived character states arise from ancestral ones, not vice versa. Taxa that share particular derived states are grouped together on the assumption that they arose from a common ancestor possessing that state. As groups are joined together by this method, there should result a gradual progression of groups having more and more derived states arising from the group ancestor in which all

states are ancestral (Fig. 1). Hennig (1966) restricts this method of shared, derived character states so that each daughter line of any furcation, even at the level of the recent taxa, possesses at least one derived state (Fig. 2).

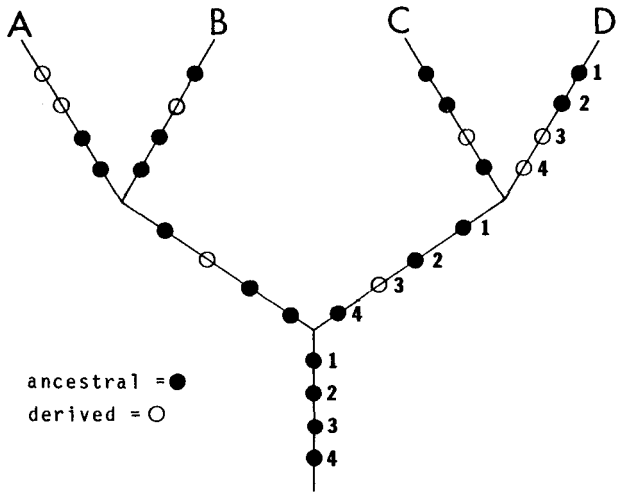

Figure 1. Phylogenetic analysis as developed by Ross (1974).

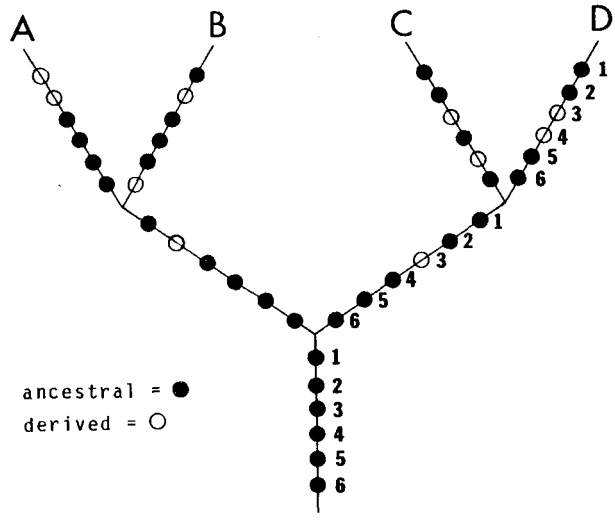

Figure 2. Phylogenetic analysis as developed by Hennig (1966).

In our phylogenetic studies of the Leptophlebiidae, we analyze 300 to 500 morphological characters from both the nymphs and adults for any assumed furcation. Based on such a large number of characters, our phylogenetic diagrams approach more the rigid Hennig diagrams than those of Ross. Sometimes for a given furcation, a derived character state is not known for one daughter line. The lack of a particular derived character state should not delay publication of a phylogenetic analysis, but the search for the derived character state should continue. Further, in some more primitive and basal furcations, not all taxa of a large monophyletic group might possess a given derived character state which we use, although other derived character states can demonstrate the monophyletic relationship. Often a character state which is not possessed by all members of a group needs only redefinition to be useful in phylogenetic analysis (or the exceptions clearly noted).

Once a formal phylogenetic analysis has been developed by using shared, derived character states, then the evolution of character complexes within the groupings should be discussed in detail. If the rate of evolution is hypothesized based on these data and shown in the phyletic diagram, then such data should be discussed for each furcation. In actuality, the phenetic similarities and differences among taxa can be given in a matrix, table, or diagram. In both the formal phylogenetic analysis and the statement of phenetic similarities and differences, it is important that all data be given in the publication.

To date, the higher classificatory limits within the Leptophlebiidae have been confined to genera and subgenera. A higher classification should be expressed as simply as possible and correspond to the phylogenetic analysis in order to express various sets of phylogenetic and evolutionary data.

Generic and subgeneric limits for the Leptophlebiidae are defined by criteria given in Peters and Edmunds (1970). These criteria use the degree of morphological difference in both nymphs and adults to differentiate genera and subgenera.

ANCESTRAL EVOLUTION

McCafferty and Edmunds (1979) recently published a phylogeny of the extant superfamilies and suborders of Ephemeroptera and the resulting higher classification. They stated that the most recent common ancestor of the Pannota, Leptophlebioidea, and Ephemeroidea was a pre-leptophlebiid; however, this ancestor could be a leptophlebiid. Further they stated that the highly derived superfamily Ephemeroidea had its origin within the Leptophlebiidae, thus making the Leptophlebiidae paraphyletic. While I agree that the most recent common ancestor of Leptophlebioidea and Ephemeroidea was at least

leptophlebiid-like, the paraphyletic nature of the Leptophlebiidae remains problematical and will be considered in detail, in a future paper. Herein, I will concern myself only with the most primitive leptophlebiid ancestors within the Leptophlebiidae.

Peters and Edmunds (1970) discussed the uniqueness of the *Paraleptophlebia*-type genera with respect to all other genera of the Eastern Hemisphere Leptophlebiidae based on morphology of both the nymphs and adults. Based on my additional studies, the *Paraleptophlebia*-type genera represent the basal most primitive furcation within the Leptophlebiidae. Zoogeographical studies indicate this furcation occurred before the breakup of Laurasia and Gondwanaland during the middle Cretaceous. The group presently occurs only in the Northern Hemisphere and includes *Paraleptophlebia*, *Leptophlebia*, *Habroleptoides*, *Habrophlebia*, *Calliarcys*, *Habrophlebiodes*, *Dipterophlebiodes*, and *Gilliesia*.

Herein I designate the above eight genera to represent the subfamily Leptophlebiinae Banks. The remaining known extant genera of Leptophlebiidae are herein placed in a NEW SUBFAMILY Atalophlebiinae Peters (Fig. 3). Table 1 presents character states delineating each daughter line leading to these subfamilies.

Table 1. Character states of Figure 1.

Character	Character state in "A"	Character state in "B"
Styliger plate of ♂	● deeply cleft or deeply cleft ventrally.	O fused.
Composition of brush on anterior margin of maxillae.	● hairs or spines scattered or unevenly arranged.	O hairs or spines evenly arranged in rows.
Lingua of hypopharynx:		
lateral margins	● without lateral projections.	O with lateral projections (except *Castanophlebia*, *Terpides*, *Fittkaulus*).
venter	O with submedian, subapical patches of hair (except *Paraleptophlebia*).	● with to without scattered hairs. (Hair patterns, if present, occur on apical margin or dorsum.)
Anteromedian emargination of labrum:		
anterolateral margins	O with heavy, thickened, pointed to blade-like setae or spines.	● without modification of marginal setae.
shape of emargination	● smooth, without denticles; shallowly to moderately curved.	O with denticles or with acute median cleft; straight to acutely cleft.*

* Character is best seen in freshly molted nymphs other than those in last instar. Denticles are frequently worn (*Thraulus*, *Choroterpes*) and secondarily lost in some genera with straight labral margins (*Choroterpides*, *Kirrara*).

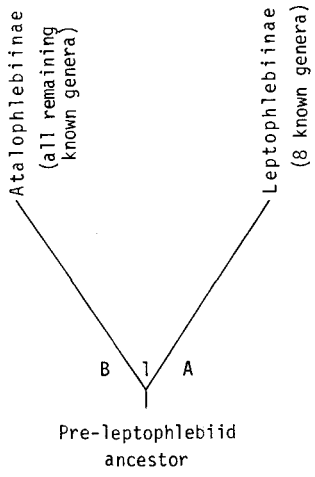

Figure 3. Phylogenetic diagram of most basal primitive furcation within the recent Leptophlebiidae (see Table 1 for character states).

The Atalophlebiinae are composed of a good number of primitive to highly specialized phyletic lineages. All of these lineages represent distinct assemblages of genera and each lineage occurs over more than one continent. While a higher classification should express various phylogenetic entities, recognition of each of these lineages as subfamilies would lead to extreme fragmentation at the subfamilial level. Therefore I propose that since each of these lineages are distinctly delineated in the literature, they be called tribes. While tribes are not now commonly used in the classification of the Ephemeroptera, I feel the tribal level will become more important as we better understand the evolution of various groups of Ephemeroptera.

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RESUME

Les chercheurs qui révisent les genres des leptophlébiidés et cherchent à déterminer une classification et une phylogénie mieux articulées des groupes monophylétiques au sein de cette famille,

doivent pouvoir se baser sur des critères détaillés pour que les résultats de leurs études s'accordent avec les faits. Nos théories actuelles sur la phylogénèse reposent sur un certain nombre de caractéristiques découlant d'observations portant sur chacune des lignées monophylétiques. Il est question de la plus ancienne ramification dans l'évolution des leptophlébiidés qui existent encore. En se basant sur cette phylogénèse, l'auteur traite de la nécessité et de l'utilité de sousordres et de tribus rattachés aux ordres.

ZUSSAMENFASSUNG

Um die Leptophlebiidengattungen revidieren und die höhere Klassifizierung und Phylogenie monophyletischer Gruppen innerhalb der Familie bestimmen zu können, werden detaillierte Kriterien benötigt, damit solche Studien Konsistenz erlangen. Unsere Phylogenien basieren auf dem Besitz einiger, vermutlich abgeleiteter Merkmale für jede monophyletische Tochterlinie. Die aller primitivste Gabelung bei der Evolution der noch vorhandenen Leptophlebiident wird in der vorliegenden Studie abgehandelt. Gegründet auf diese Phylogenie, wird ebenfalls der Bedarf an und die Nützlichkeit von Unterfamilien und Klassen innerhalb der Familie erörtert.

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