Redefinition of the Family Palingeniidae and Its Implications for the Higher Classification of Ephemeroptera[1]

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ABSTRACT

The family Palingeniidae is reclassified to include Eastern Hemisphere Palingeniinae and Western Hemisphere Pentageniinae. The reclassification is based on both phyletic and phenetic criteria; and recommendations for the evolutionary classification of genera, which are phylogenetically intermediate between traditional family groups, are presented. The family and respective subfamilies are morphologically redefined and their diagnosis reviewed.

The Palingeniidae was first recognized as a taxon by Eaton (1883–88) as Subsection A of Section 1 of *Palingenia*. Familial status was first given to the taxon by Klapálek (1909). The family has since been reviewed by Lestage (1923) and Demoulin (1965). Workers have considered the family taxonomically sound because of the definitive characteristics common to adults. Larval information has been sketchy, and delimitation of this stage at the family level has not been well understood.

The family Pentageniidae was erected by McCafferty (1972) for the genus *Pentagenia* Walsh 1863, which possesses adult characteristics typical of the Ephemeridae (where it had traditionally been placed), but at the same time possesses larval characteristics typical of the genera of the Palingeniidae. These larval affinities were also alluded to by Edmunds (1972), but were only apparent after we had made a comprehensive study of the comparative morphology of ephemerid genera. The recent study of palingeniid larvae from Madagascar (McCafferty and Edmunds 1976) has further substantiated the observation that *Pentagenia* is essentially palingeniid-like in the larval stage.

McCafferty (1972) indicated that the palingeniid-like character states of the larval stage of *Pentagenia* were derived relative to the Ephemeridae, and that the ephemerid-like character states of the adult stage were ancestral relative to the Palingeniidae. Evidence for the evolutionary origin of the Palingeniidae from within the Ephemeridae and hence the paraphyletic nature of the latter group has been presented by McCafferty (1976). The relationships under discussion are depicted in Fig. 1.

The phylogenetic position of *Pentagenia* can be explained by apparent differential rates of morphological change at different times in the adult and larval stages of the lineages involved. The evolution of the hypothetical common ancestor of Old World palingeniids and *Pentagenia* involved a great deal of morphological adaptation in the larval stage but very little in the adult stage. Adult evolution has been extensive in the palingeniid lineage since the origin of *Pentagenia*, and hence *Pentagenia* remains as an "evolutionary intermediate." The relative position of *Pentagenia* has served as a valuable phylogenetic landmark, and has made possible an understanding of the relationship of the Ephemeridae and Palingeniidae.

DISCUSSION

Although this interesting position of *Pentagenia* is fortunate for the elucidation of relationships, it poses a most critical problem concerning higher classification. Where should *Pentagenia* be classified? The problem is even more basic, however, since within the Ephemeroptera other analogous situations are already known and as knowledge concerning generic relationships accumulates others are likely to arise. Edmunds (1962) proposed that for the Ephemeroptera "the gaps within a family are small enough that the relationships are readily evident, but the gaps between families are so large that the relationship can be discerned only by detailed study." This practical definition is not foolproof, however, since detailed study reveals intermediates between the families as defined. Although the following arguments deal with the classification of *Pentagenia* they should be of broader application in formulating philosophies of higher classification.

The classificatory alternatives under consideration are (1) to maintain *Pentagenia* in the Ephemeridae, (2) to recognize the separate family established recently for *Pentagenia*, (3) to recognize the family Ephemeridae which would include *Pentagenia* and traditional palingeniids, and possibly be divided into infra-categories, or (4) to place *Pentagenia* within the Palingeniidae.

We maintain that the higher classification should be expressive of phylogeny as far as possible without becoming biologically impractical (even though the 2 qualities may be neither mutually exclusive nor completely compatible). Such a compromise requires that the careful subjective weighting of various factors be undertaken, including phyletic and phenetic relationships [respectively the "genealogical" and "genetic" relationships of Mayr (1965)], rates of evolution, ecological roles, etc.

Since phylogeny reconstruction is in part a criterion for our higher classification, it is important to note that the methodology utilized by McCafferty (1976) is essentially after Ross' (1974) modification of Hennig (1950, 1966). We agree with Cracraft (1974) that the strictly phylogenetic (cladistic) clas-

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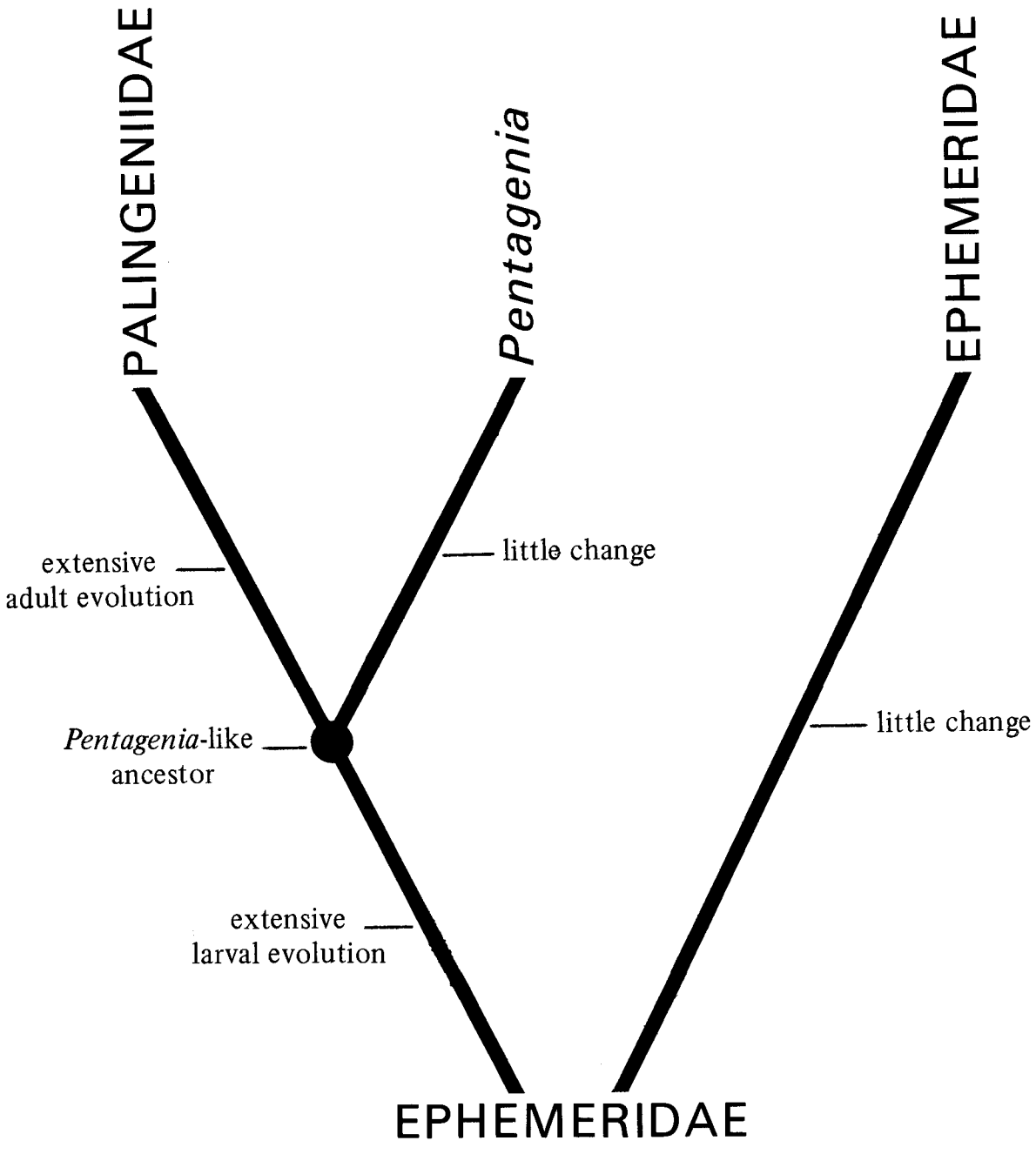

Fig. 1.—Phyletic diagram of Ephemeridae-Palingeniidae.

sifications derived from such "models" are the most useful in terms of information retrieval, since only inferences about phyletic relationship and relative points of origin can be stored in a taxonomic hierarchical classification with any precision. We believe the model itself can be axiomatic for these purposes, whereas a resulting cladistic classification at times may be of little practical use for biologically classifying taxa at the various superspecific hierarchical levels. As was first intimated by Michener (1957), ideally phenetic ("static") and phyletic information should be independently indicated for taxa. In the final analysis, however, only one classification can be conveniently used for indexing purposes.

With our objective of an evolutionary classification in mind, we reject the 1st 3 classificatory alternatives for *Pentagenia* as follows:

The retention of *Pentagenia* in the Ephemeridae would appear to be a misrepresentation of the evolutionary affinities of the group in terms of its recently

discovered, highly derived characteristics. This would be the case even if *Pentagenia* were to be placed in a separate subfamily. It may be most convenient not to tamper with familiar classifications, but higher classification must be responsive to increasing information content and therefore be flexible in nature. There are neither phyletic nor phenetic grounds for this alternative.

The placement of *Pentagenia* in a separate family equal in status to Ephemeridae would be an extreme move, although it may draw attention to the phylogeny, as had been the primary intent of McCafferty (1972). Such a classification may not be practical in the sense that it could set a precedent for the establishment of a number of new families in the Ephemeroptera. It would become increasingly difficult to accommodate hierarchical inflation within the order.

A classification which combines the Palingeniidae and Ephemeridae because an intermediate has been found would discount the large morphological gaps which exist between the groups, and obscure the evolution involved, i.e., a major adaptive shift to the Palingeniidae. The magnitude of the differences between the Ephemeridae and Palingeniidae can be seen in the fact that Tshernova (1970) and Edmunds and Traver (1954) placed the Palingeniidae next to the Polymitarcidae, and Demoulin (1958) placed the Ephemeridae and Palingeniidae in separate superfamilies.

Such a retrogressive, combining classificatory trend would, if pursued, theoretically lead to a marked decline in the usefulness of familial rank in Ephemeroptera. This alternative does not appear to meet either the criterion of practicality or predictability. We agree with Mayr (1969) that when the divergent elements are so large and the connecting element so small, that it would completely defeat the objectives of sound classification to combine the 2 families into one. Further, the communicative concepts of Palingeniidae would be lost, and we think such a taxonomic change would find little acceptance. Edmunds (1962) has previously stated that conceptual value is a major criterion in choosing the hierarchic level of family groupings.

We propose the reclassification of *Pentagenia* within the Palingeniidae. We furthermore propose that *Pentagenia* be placed in a separate subfamily within the Palingeniidae. The distinct morphological gap in the adult stage along with some character state differences between the larvae of *Pentagenia* and other Palingeniidae warrants the subfamilial classification.

The proposed classification (1) conserves the stability of the family level classification, (2) expresses phyletic relationships (Fig. 1), (3) invokes an arbitrary rule of thumb for the ranking of intermediate taxa which accounts for phenetic relationships, and (4) offers a practical, albeit subjective criterion for the subfamily category in the Ephemeroptera.

When genera are found to be intermediate between family groups because of retained ancestral characteristics in one stage and derived characteristics in the other stage (in terms of the adults and larvae), then we recommend that these genera be classified with the family which represents the most recently, commonly derived sister group. Any similarity to cladistic ranking is coincidental because, in the special case of an intermediate, the phyletic relationship weighs heavily in the classificatory decision. The phylogenetic position of a genus (or genus group) could theoretically be analogous to that of *Pentagenia,* but at the same time the group could be very closely related phenetically to the parental family in both stages (obviously on the basis of relatively ancestral character states). When no distinct gap exists in either stage, regardless of the phylogenetic position, the genus should be classified with the parental family, e.g., the *Hexagenia* group of the Ephemeridae (McCafferty 1973, 1976).

Another critical case in Ephemeroptera has come to light with the recent interpretations of the phylogenetic position of the genus *Isonychia* between the parental Siphlonuridae and the more derived Oligoneuriidae [systemic viewpoints have been given by Edmunds (1973) and Riek (1973)]. These phylogenetic findings and similar ones should lead to practical, evolutionary classifications if the above recommendations are followed, i.e., with the phenetic and adaptive position of stages also taken into account.

Once the family limits are arrived at, subfamilies may be instituted to reflect distinct gaps between genus groups. We propose that the subfamily incorporate genera as Edmunds (1962) proposed that subgenera incorporate species, i.e., the gap between groups (of genera or species) is very distinct in one stage but weak in the other. Use of these infracategories would therefore be somewhat analogous for operational taxonomic units at the 2 levels. These criteria should not be the only ones for subfamilial classification but could be employed in special cases such as that illustrated by *Pentagenia* and Palingeniidae. In other situations it may be convenient for subfamilies to be based on moderately distinct gaps between both stages of genus groups.

Within this conceptual framework for higher classification and based on known morphological limits, we redefine the Palingeniidae and its subfamilial components as follows:

Family Palingeniidae.—Adult.—Pronotum of male usually much wider than long. Legs of male developed with fore-legs reduced to ½ or less length of body. Legs of female well developed or obsolescent. Fore-wings with position of MA fork variable, A_1 not forked, if connected to anal margin then never by more than 3 veinlets. Hind wings with costal angulation obtuse or reduced, R_1 sometimes attached basally to MA. Penes well-developed and deeply separated. Both sexes with terminal filaments never as long as body.

Larva.—Frons of head produced anteriorly into distinct frontal process, slightly to strongly emarginate with anterior margin with variable number of teeth or sometimes smooth. Supra-antennal processes of head distinct with at least one angulate protuber-

ance above base of antennae. Mandibular tusks with distinct lateral carina with series of spurs and spines or modified into large undulating crenulations. Maxillae and labium robust with palpi rounded apically. Fore-legs with femora with posteroproximal angle distinctly produced from trochanters, and tibiae with anterior margin with distinct row of spurs, spurs and spines, or large developed processes, and at least one large process anterodistally.

Remarks.—This formal description encompasses those character states common to known Palingeniidae not including those shared by all Ephemeroidea. The adults of the family are largely a heterogeneous group, particularly in regards to wing venation and genital forceps. The larvae, on the other hand, are a relatively homogeneous and easily delimited group.

The reduced fore-legs of the males will serve to identify the group on a world basis. The larvae of Palingeniidae can be distinguished by any of several characters. The conditions of the lateral carina of the tusks and the condition of the fore femora [e.g., see figures in McCafferty (1972) and Landa (1969)] are easily recognizable diagnostic characteristics.

It should be noted here that the comprehensive key to the families and subfamilies of mayfly larvae by Edmunds et al. (1963) will not adequately distinguish the Palingeniidae from the Ephemeridae since both families possess tibial processes of the hind legs, and the labial palpi are more or less in the same plane as the labium in both families.

Subfamily Palingeniinae.—Adult.—Head usually retaining atrophied remnants of frontal process, supra-antennal processes, and tusks. Wings translucent, longitudinal veins usually geminating and outer margins sometimes appearing somewhat scalloped or sinuate. Fore wings with Sc usually hidden in fold of membrane ventral to R_1, being visible only at base; CuA usually diverging into CuA_1 and CuA_2. Forceps of ♂ genitalia with 3 or more segments, basal segment longest, sometimes followed by several small terminal segments. Terminal filament rudimentary in both sexes.

Larva.—Supra-antennal processes variable with median protuberances reduced or absent; additional processes dorsally on head between antennal bases and compound eyes. Tibiae of fore-legs with series of large crenulations similar to anterodistal process, or with pair of distal processes (one distinctly posterior and one anterior to tarsus) and series of spurs along anterior margin. Abdominal segments 3–7 produced into elongated lateral lobes.

Remarks.—This subfamily represents the Eastern Hemisphere component of the Family Palingeniidae. Species are known from widespread localities in the Palearctic and Oriental Regions including Asia Minor. The only Southern Hemisphere records for the family and subfamily include Madagascar and New Guinea.

Highly derived adult characteristics are seen in the group as a whole and more so in certain genera particularly regarding wing venation and ♂ genitalia. It is most distinctive as a subfamily in the adult stage, but the larval characters stated above are sufficient for its diagnosis.

The genera which are included in this subfamily are *Anagenesia* Eaton 1883, *Chankagenesia* Buldovskij 1935, *Cheirogenesia* Demoulin 1952, *Mortogenesia* Lestage 1923, *Palingenia* Burmeister 1839, and *Plethogenesia* Ulmer 1920. The larvae of *Mortogenesia* remain unknown.

Subfamily Pentageniinae.—Adult.—Head lacking larval frontal process, supra-antennal processes, or tusks. Wings hyaline, longitudinal veins not geminating, and outer margins smooth. Fore wings with Sc visible for entire length; CuA singular for entire length. Forceps of ♂ genitalia 4-segmented, 2nd segment longest. Terminal filament of both sexes shorter than cerci or body, moreso in male but never rudimentary.

Larva.—Supra-antennal processes distinctly bifurcate above antennal bases. Tibiae of fore-legs each with anterodistal process and subdistal anterior process followed proximally by series of spurs along anterior margin. Abdominal segments 3–7 only slightly produced laterally.

Remarks.—This subfamily is known only from North America and currently is monogeneric. A review of the biology of the genus has recently been presented by McCafferty (1975).

All of the characteristics stated in the above descriptions are convenient and diagnostic for separating the 2 subfamilies. Reliable keys to *Pentagenia* and hence the subfamily Pentageniinae and New World Palingeniidae will be found in McCafferty (1975) and Edmunds et al. (1976).

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