

Toward a Phylogenetic Classification of the Ephemeroptera (Insecta): A Commentary on Systematics

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ABSTRACT Higher classifications of Ephemeroptera formulated in light of phylogenetic hypotheses have been essentially evolutionary in that they have incorporated paraphyletic taxa. The term "paraphyletic" has had a confused history because systematists have applied it to different concepts; for Ephemeroptera, it has denoted one type of nonpolyphyletic grouping. Such paraphyletic taxa were used so that large degrees of character (presumably adaptive) differentiation could be expressed, but resulting classifications lack any means of consistently expressing such gaps, and their ability to express genealogy is compromised. Phylogenetic classifications are now strongly advocated. Not only can the increasing number of phylogenetic hypotheses based on cladistic analysis be objectively expressed, but many traditional taxa and categories can be conserved by employing sequencing conventions. The philosophy and history of competing classificatory systems are discussed. A phylogenetic methodology is employed when possible in proposed revisions of the higher taxa of Ephemeroptera. New cladistic data are presented and previous data reviewed. Major lineages formerly part of the paraphyletic family Siphonuridae are classified as families within several higher taxa to express phylogeny and at the same time maintain other traditional family units. Assignment of superfamilies within the new suborder Pisciforma (new infraorder Arenata [Acanthametropodidae, Ametropodidae, Analetrididae, Metretopodidae, Pseudironidae] and new infraorder Imprimata [Ameletidae, Ameletopsidae, Baetidae, Metamoniidae, Rallidentidae, Siphlaenigmatidae, Siphonuridae]) awaits additional cladistic analysis. Considerable evidence is available, however, for the new suborder Rectracheata (new infraorder Vetulata [Oniscigastridae, new infraorder Lanceolata [Leptophlebioidea, Behningioidea, Ephemeroidea], and infraorder Pannota, new status [Caenoidea, Neoephemeroidea, Baetiscoidea]), and new suborder Setisura (Coloburiscidae, Isonychiidae, Oligoneuriidae, Heptageniidae). A new revision of Ephemeroidea serves as a *prima facie* example of phylogenetic classification in the order. Changes in Ephemeroidea include the removal of Behningiidae, the addition of the new fossil family Australiphemeridae, incorporation of the former Euthyplociidae and the new fossil subfamily Pristiplociinae in Polymitarciidae, and the incorporation of Pentageniinae and Palingeniinae (formerly Palingeniidae) and the new subfamily Hexageniinae in Ephemeridae. Derivations are expressed mainly by sequencing of taxa recognized at the subfamily rank. Phylogenetic systematics is shown to have predictive and heuristic value for interpreting comparative biology, inferring adaptive evolution and biogeography, and also to have an important function in paleontological and ecological analyses.

KEY WORDS Insecta, Ephemeroptera, phylogenetic systematics, systematic methodology

"At any rate, in biology nothing makes sense except in the light of evolution."

(Dobzhansky 1970)

A VERBAL EXCHANGE took place at a symposium on the phylogeny and higher classification of the Ephemeroptera held at Tallahassee, Fl., in 1970. It is highly illustrative of critical concerns and perhaps misunderstood intentions regarding Ephemeroptera classifications—concerns and intentions that have continued to fester in the subsequent 20 yr.

George Edmunds had finished his keynote presentation (Edmunds 1973) and was being questioned by Lars Brundin with respect to the relationship between Edmunds' phylogenetic diagram

(Fig. 1) and his higher classification. The essence of this exchange follows:

Brundin: "What did you say about the connections between classification and a phylogenetic system—that it is impossible to combine them? I think you must be wrong there because it is quite easy to explain all known phylogenetic relationships in a group classification."

Edmunds: "You have said that you can explain relationships by a linear system, and on another page of your same book you said it can only be done by means of a phylogenetic schedule."

Brundin: "But you have four groups here and they are related to one another [Fig. 1 herein]. You can express exactly that in a linear system in a book, in print, in a classification . . . in your diagram there you showed Baetidae as a sister group for

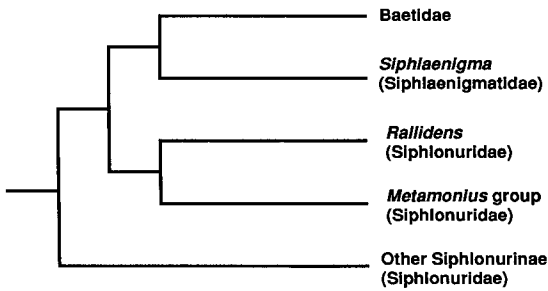


Fig. 1. Phylogram representing Edmunds' (1973) concept of the phylogeny of some Southern Hemisphere derivatives of Siphonurinae and their familial classification.

one New Zealand genus *Siphlaenigma*. . . . You can put this New Zealand genus into Baetidae and make a subfamily or you can raise this New Zealand group to a family."

Edmunds: "It is now a family. Do I then have to raise the *Metamonius* group to a family?"

Brundin: "Only such an arrangement can give a sound classification."

Edmunds: "Can I call Siphlaenigmatidae one family and *Metamonius* group one family without calling *Rallidens* one family?"

Brundin: "No, but do the other Siphonurinae, *Metamonius* group, and *Rallidens* now belong to the Siphonuridae?"

Edmunds: "Yes."

Brundin: "Then your diagram must be wrong . . . the whole thing is impossible according to your diagram."

Edmunds: "Yes, it is impossible in the Hennig-Brundin system, according to my diagram."

The primary issue underlying this exchange was whether classifications should reflect phylogenetic branching sequences or not. Edmunds' working premise was that phylogenies can stand on their own and classifications need not be restricted by them, a view philosophically broached by Mayr (1974) and explained by McCafferty & Edmunds (1976). Such an idea, however, was taken as counterproductive by Brundin, whose working premise was that classifications should reflect the best estimate of the evolutionary history of organisms (Brundin 1966) vis-à-vis phylogenetic branching sequences. This philosophy was discussed as a rebuttal to Mayr (1974) by Hennig (1975).

An important and related issue more subtly raised by the exchange was whether all taxa need to be monophyletic, or whether some taxa may be represented by some but not all of the lineages derived from a common ancestor. Advocates of either view have been prominent in the literature and elsewhere, particularly in the 1970s.

Certain tête-à-têtes I have had with other systematists, particularly specialists of some other insect groups, and correspondence with certain European ephemeropterists and journal editors have reaffirmed the dichotomies exemplified by the Ed-

munds-Brundin exchange and have also uncovered doubts as to whether or not current Ephemeroptera higher classifications were, indeed, natural. The present work is offered, first, to ameliorate the situation and suggest an uncompromised framework for Ephemeroptera classifications, and second, to begin to put such a classificatory methodology into operation and to evaluate it.

Background and Problem

Rationales were presented by Edmunds (1962) and McCafferty & Edmunds (1976, 1979) for adopting an essentially "evolutionary" taxonomy (sensu Michener 1957; Simpson 1961; Mayr 1969, 1974; Ashlock 1979) for establishing higher classifications in Ephemeroptera. The thrust of such arguments has been that, in addition to phylogenetic relationships, the expression of major character gaps, often indicative of major adaptive shifts or the lack thereof, should also be a function of the classification. Large morphological gaps in at least one life stage are common and often profound in recent Ephemeroptera (McCafferty & Edmunds 1979), perhaps due in part to the antiquity and presumed large degree of extinction, or decimation, in the order (see below). In any case, the higher classifications of Ephemeroptera that have been constructed in light of cladistic epistemology have incorporated paraphyletic taxa. This was intentional in the classification of McCafferty & Edmunds (1979), which generally has been followed in other major Ephemeroptera works since (e.g., Landa & Soldán 1985, Hubbard 1987, Berner & Pescador 1988), and has been incorporated into general entomological treatises (e.g., McCafferty 1981, Stehr 1987, Borror et al. 1989).

It is important to emphasize that the classification of McCafferty & Edmunds (1979) was not polyphyletic. Any misinterpretation as such may be related to the considerable confusion that has existed in the application of the term paraphyletic. Concepts applied to that term unfortunately differ among authors (Wiley 1981). McCafferty & Edmunds (1979) followed the concepts of Ashlock (1971, 1972), Farris (1974), and Ross (1974): a paraphyletic group is a group derived from a common ancestor but does not include all the progeny of that ancestor. As such, it is one type of natural (nonpolyphyletic) group and fits within the interpretation of Ross (1956) that all members of a nonpolyphyletic group arise from a common ancestor, but not all the lineages arising from that ancestor must necessarily be members of the designated group. Ashlock (1971) hence considered two kinds of monophyletic groups: holophyletic (containing all progeny) and paraphyletic.

The confusion arises from the fact that Hennig (1966), the major protagonist of phylogenetic systematics (e.g., see Dupuis 1984), used a more restricted definition of a monophyletic group, that is, to include the common ancestor and all descendants. Moreover, Hennig (1966, 1975) considered

both a methodological and genealogical definition for a paraphyletic group. Methodologically, it was taken to be a group based on symplesiomorphy rather than synapomorphy. Genealogical definitions of paraphyletic groups by both Hennig (1966) and Nelson (1971) equate them with unnatural polyphyletic groups. These concepts obviously are very different from those used by certain other authors in the recent past.

Most Ephemeroptera systematists currently involved in formulating higher classifications now generally appear to employ a nonphenetic theoretical framework for hypothesizing relationships. To this degree, there appears to be some general solidarity, but because analytical methodology is not necessarily stated by these workers, I can only assume that their phylogenetic data are always derived from accepted precepts of cladistic methodology (Ross 1937, 1974; Hennig 1950, 1966); i.e., monophyly, or common descent, deduced from synapomorphy. Some early phylogenetic studies of Edmunds (1972, 1973) and Landa (1973) did not always distinguish symplesiomorphy from synapomorphy and were phenetic to some degree; Riek (1973), although distinguishing the two types of character states, used either equally to deduce ancestry.

Only one ephemeropterist publishing higher classification today is clearly a "traditional" taxonomist with no particular theoretical framework (my reference is anonymous for the sake of maintaining simpatia among colleagues, and lest my intent be viewed as an aspersion). Although such workers can make, and have made, important descriptive contributions, their reliance on arbitrary characters or otherwise unstated criteria often leads to unnatural classifications. Attempts to rationalize these in the face of solid phylogenetic data, particularly by invoking past practices and other ill-defined classifications in their own repertoire, is reminiscent of how, in the history of science, traditional dogma often continues to be used for some time after contrary evidence emerges. The implication of Scilla's (1670) tongue-in-cheek title of his revolutionary treatise on the nature of fossils: "La Vana Speculazione disingannata dal Senso" (see Rudwick 1976) apparently continues to find application in some late 20th century systematics.

Given the preponderance of mayfly systematists who are purposefully influenced by phylogeny, and given the increasing availability of data resulting from cladistic analyses, a question, more important than ever regarding the future of the higher classification of Ephemeroptera, is whether to continue to devise evolutionary classifications or abnegate them and adopt strict phylogenetic (nonparaphyletic as well as nonpolyphyletic) precepts as the "principium divisionis" (Ax's [1987] term) of our classifications. Although the evolutionary and phylogenetic systems of classification actually have a tremendous amount in common (Wiley 1981), their differences have caused proponents of evolutionary

classification (e.g., Bock 1973; Ashlock 1974, 1979; Mayr 1974, 1982, 1988; Michener 1977; Brothers 1978) and of phylogenetic classification (e.g., Hennig 1966, 1975; Nelson 1972; Cracraft 1974; Mickevich 1978; Farris 1979; Wiley 1979, 1981; Ax 1987) to argue their points of view vehemently and with considerable clamor (see below).

The dilemma faced by Ephemeroptera systematists, of course, has been faced by specialists of other groups. One excellent and archetypical example of the problem is from the taxonomy of birds and reptiles. Although perhaps trite to some, this analogy from generally more familiar organisms has explanatory and heuristic value. Essentially, should birds be classified with the reptiles, particularly their sister lineage, the crocodiles, or should they be placed separately in a group equal in rank to the reptiles? (See, for example, Romer [1966] and Gorman et al. [1971], for some pertinent data.) The first choice (for example, placing Aves and Crocodylia in Archosauria separate from the other reptiles) gives a phylogenetic classification by disallowing the traditional paraphyletic class Reptilia. The second choice would give an evolutionary classification by reflecting the considerable character and adaptive gap between birds and all their phylogenetic relatives but would retain Reptilia as a paraphyletic group, and the sequence of phylogenetic branching could not be reproduced from a linear classification of the vertebrates.

Phylogenetic classifiers have argued that only their classifications are fully predictive of phylogeny. Evolutionary classifiers have argued that classifications should express more than just phylogeny and that a phylogeny and a classification can each stand alone. Phylogenetic classifiers have argued that, in attempting to express more than phylogeny, evolutionary classifications lose their ability to reflect anagenesis and at the same time associated predictive value. Evolutionary classifiers have argued that phylogenetic classifications are not practical because they result in an overbearing increase in infracategories and taxa. Phylogenetic classifiers have devised conventions that circumvent the need for such increases. Although neither camp appears to have had the last word (e.g., Bottjer 1980), I believe the denouement of this drama is at hand, as I shall attempt to exemplify in this paper.

Turning, in particular, to ephemeropterists, why have they been reluctant to adopt phylogenetic classifications?

A major reason, in my opinion, has been the existence of an overriding philosophy that supra-specific taxa should be separable from each other to some predetermined degree, depending on the taxonomic category involved. Edmunds (1962), as an example, predicated his higher classification system for Ephemeroptera to a large extent on various "distinct gaps" having to be present between taxa at similar ranks, a larger gap at the family level than at the subfamily level, etc. Such definitions generally follow the criteria set forth by Mayr et

al. (1953), who indicated that the various higher categories are separated from similar units by "decided gaps." Edmunds (1962) stated that such criteria were subjective, but that "the history of mayfly classification shows rather clearly that they are practical."

The gap concept, or criterion, in this regard is taken to be some measure of the degree of evolutionary differentiation, often reflected by obvious morphological differences. In practice, the gaps generally have been tantamount to some degree of ease in differentiating taxa. In any case, what makes a gap distinct appears to be in the eyes of the beholder; i.e., a function of the extent to which pertinent species are known and the analytical tools and experience available to the systematist. Even arbitrary definitions, were they to be quantified, would be difficult to follow objectively.

The interpretation of gaps by Ephemeroptera systematists has been exacerbated by the fact that in mayflies (but not necessarily in other groups) there are apparently many instances of different rates of evolution in the larval (aquatic) stage and the adult (terrestrial) stage. This means that there may be a phenotypic gap demonstrated by one of these stages but not necessarily the other. As a result, Edmunds (1962) stated that a mayfly genus should be separated from other genera by a distinct gap in both adult and larval characters; however, when the distinct gap is evident in only one or the other stage, he felt subgenera were more appropriate. This criterion was restated in essence and practiced in revisionary works, for example, in the Leptophlebiidae monograph by Peters & Edmunds (1970); yet for the Baetidae, it was mollified by Traver & Edmunds (1968) to attain a "natural classification arrangement." Although there have been additional recent tendencies away from such restrictions of genera for various reasons (e.g., Allen 1980; Flowers 1980; Waltz & McCafferty 1987a,b), Novikova & Kluge (1987), and Kluge (1988a) have evoked rigorous gap criteria for genera and subgenera in their respective revisionary classifications of certain Baetidae and Heptageniidae; their gaps are clearly equivalent to ease of differentiation. Essentially, if adults of a species group are difficult to key or otherwise identify, then their taxon is relegated to subgeneric status.

Whether gap criteria have an evolutionary connotation or a purely phenetic connotation, they cannot be the bases of phylogenetic classifications, which by their nature are based exclusively on historical sequences of phylogenetic branching. Thus, Wiley (1981) explicitly pointed out that because phylogenetic classifiers reject gaps, they also must reject any of the definitions of taxonomic categories based on gaps.

A belief that an inordinate number of taxa and taxonomic categories would be required for a phylogenetic classification of the Ephemeroptera undoubtedly has been another reason for the reluctance to accept phylogenetic classifications. The

sensitivity about this point was apparent in Edmunds (1962) and was elucidated by McCafferty & Edmunds (1976): "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."

This idea was actually a misconception by the authors because they assumed that every branch point in a phylogeny had to be named, such as in the completely subordinated classification of mammals given by McKenna (1975). This is not necessarily the case; the accepted use of a phyletic sequencing convention such as that of Nelson (1972, 1973) allows holophyletic groups sequentially branching along a similar, asymmetrical line of a phylogenetic tree to be placed at the same categorical rank and listed in order of their sequence of derivation. Sequencing in the classification can be substituted for rank category subordination and thus can reflect exactly the same phylogeny. Not only does the convention minimize the number of changes that have to be made in converting traditional classifications, but classifications can be relatively conservative, such as the highly sequenced classifications of vespid wasps given by Carpenter (1982, 1987).

Variable uses of the sequencing convention can also mitigate some of the controversy between evolutionary and phylogenetic classifiers about what can or should be reflected by a classification. In essence, there could be more than just the required branching information expressed in the classification once the phylogenetic criteria have been satisfied; e.g., major adaptive events and biogeographic vicariance events (Wiley 1979, Nelson & Platnick 1981). Such factors influenced my choice of available options for Ephemeroptera that I present below.

As for increasing the number of families in a revised, phylogenetic classification of Ephemeroptera, that would be strictly up to the classifier and would be based on the degree to which conventions were applied (Hennig 1975, Wiley 1981) and the degree to which conservation was practiced. For example, in attempting to maintain traditional family concepts for certain well-defined and long-held groups that happen to represent relatively distally (more recently, or apotypic) branched lineages, it would be necessary to recognize the preceding, more basally (earlier, or pleiotypic) branched lineages in that part of the phylogeny at an equivalent rank, if sequencing, or even higher rank, if subordinating. Therefore, these lineages would be recognized at least as families. Such a situation is illustrated by the phylogeny of the Heptagenioidea (Fig. 2). Because of the historical integrity and the morphologically, ecologically, and behaviorally distinctive nature of the large family Heptageniidae, I found it preferable to retain it as a family (McCafferty 1990, 1991a). This meant that

the earlier derived lineages along the line leading to Heptageniidae were also at least of family rank. Incidentally, the resultant Coloburiscidae and Isonychiidae would not have fit the family-gap criteria of Edmunds (1962).

The net gain in families in a phylogenetic classification of Ephemeroptera actually may be negligible, if that is desirable. For example, along with the mandatory revocation of traditional families that have been shown to be paraphyletic, certain graded lineages that have been recognized as families and perhaps do not reflect discrete adaptive units could be conveniently represented at subfamilial or lesser ranks with the use of a sequencing convention. This has been done to a large extent in the revision of the higher classification of the Ephemeroidea, given below.

Perspectives for Revising Ephemeroptera

As indicated above, I have recently adopted a phylogenetic classification of the superfamily Heptagenioidea (McCafferty 1991a) based on a detailed cladistic analysis of these mayflies and the resulting cladogram given in Fig. 2. A more conservative, evolutionary classification would perhaps have been to place the first, and second derived, coloburiscid and isonychiid lineages together in a single paraphyletic family, or to place them together with the third derived, oligoneuriid lineage in an even more encompassing paraphyletic family. This latter possibility was essentially the classification used by McCafferty & Edmunds (1979), although exact early branching sequences had not been hypothesized at that time.

I have become convinced that so-called practicality should not govern the formulation of higher classifications of mayflies. Accounting for morphological gaps or lack thereof, and the measurement of such gaps to decide what is distinct and what is not, are inexact exercises, as explained above. They are further compounded by gaps reflected in one metamorphic stage but not the other. Phylogenetic classifications cannot be biased by a priori judgments about the significance of such gaps for establishing taxonomic groups. In my experience, maintaining paraphyletic taxa on the basis of gap criteria or possibly for the sake of conserving older classifications has not been productive, and this practice is no longer defensible. Moreover, a consistent, definable methodology is needed, not only for the sake of stabilizing semantics among workers but for validating systematics as a reproducible science. I view my rejection of evolutionary classification and adoption of phylogenetic classification as a necessary metamorphosis and take some comfort in Gould's (1989) reminder that "obsolescence is a fate devoutly to be wished, lest science stagnate and die."

Although others have articulated cogent arguments for adopting phylogenetic classification (e.g.,

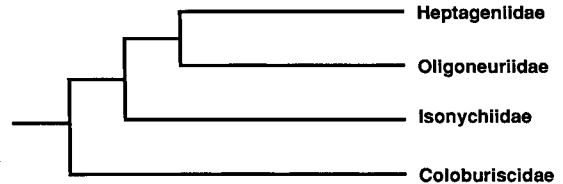


Fig. 2. Cladogram of the major lineages of Heptagenioidea (Setisura).

Cracraft 1974; Farris 1979, 1980) and have fairly weighed the pros and cons of classificatory alternatives (Holmes 1980, Wiley 1981), additional credibility for my use of phylogenetic classification is perhaps best realized when the system is viewed within a historical framework. Although recent breaks from classificatory tradition have been inflammatory (e.g., Sokal & Sneath's [1963] assessment of the use of hypothetical reasoning in hypothesizing phylogeny as "utter rubbish," Ross' [1964] reference to numerical taxonomy as "an excursion into futility," and Michener's [1977] opinion that cladistic methods "do violence to most biological attributes"), this history, nonetheless, may be viewed as a progression culminating in phylogenetic classification. As such, this progression has contributed to what Kuhn (e.g., 1962) and others have often referred to as the "revolutions" of science and cosmology.

A long-standing, intuitive, and nonhierarchical system of classification (often associated with the ancient Greek scholars) was replaced in the 18th century, when, Linnaeus (1758) introduced the now universal method of hierarchical nesting, and Adanson (1763) importantly suggested that all possible characteristics be used to ascertain groupings. Classification, however, remained, preevolutionary. Although Adanson is often identified with the modern nonevolutionary system of classification known as numerical phenetics, Adanson clearly weighted characters, whereas numerical pheneticists do not, ostensibly to obviate any subjectivity in their use of algorithms to devise taxonomic groupings.

In the late 19th century, the Darwin-Wallace principle of evolution provided a watershed for classification; many classifiers attempted to devise taxa that were natural in an evolutionary sense, and the evolutionary classification system of the 20th century eventually developed. Mayr (1988) specifically equated evolutionary classification with Darwin, but, as pointed out by Ferris & Ferris (1987), Darwin's own classificatory concepts can be linked to a number of methodologies now in use, including phenetics and cladistics. Darwin's (1859) statement that, "Our classifications will come to be, as far as they can be made, genealogies," perhaps reflects his realization of temporality more than anything else.

Until relatively recently, evolutionary classifications were often related to genealogies that had

been deduced without necessarily having distinguished between ancestral and derived characteristics. However, as the logical epistemology of rigid cladistic techniques became elaborated, those techniques were incorporated into phylogeny reconstruction, but the expression of common descent has remained compromised in evolutionary classifications by attempts to express additional data, as explained above. Finally, in the middle of this century, phylogenetic classifications began to be used for precisely expressing phylogenetic relationships.

Significant progress in classificatory methodology might continue in time only if the restrictive Linnaean system is replaced with a more sophisticated means of organization that allows additional facets of relatedness to be expressed. Such would be needed to accommodate Huxley's (1942) prediction that "new classificatory systems that are destined to arise . . . will give due weight to gradients of change, their different directions, and their variations in steepness." These facets must now be expressed by other means; for example, relative ancestor-descendant relationships can be depicted with a Wagner groundplan-divergence phylogram (see Wagner 1969).

Finally, with regard to perspectives, it is important to remember that, although evolutionary classification is arguably an outdated method, certain facets commonly associated with it must not be indiscriminately discarded. Cracraft (1974) critiqued evolutionary classifications as being little more than expressions of the intuition, experience, or art of the investigator. The real concern in this regard, however, is that, at the point of deriving a classification from a phylogeny, these expressions should not supersede ground rules that ensure the consistent translation of phylogeny from the classification. That does not preclude them from playing a role in the analytical aspects of systematics. Lewis Thomas (1990), in writing about natural science, stated, "It is in the abrupt, unaccountable aggregation of random notions, intuitions, known in science as good ideas, that the high points are made." Those humanisms singled out by Cracraft actually contribute significantly to one's ability to investigate phylogeny and no doubt have affected analyses of Ephemeroptera.

Considerations for Revising Ephemeroptera

The adoption of phylogenetic classifications that I advocate for mayflies may present some problems in morphologically differentiating certain life stages of some taxa, as suggested earlier. A case in point involves the traditional family Siphonuridae, a group that has been based on symplesiomorphic character states, particularly with regard to wing venation. McCafferty & Edmunds (1979) indicated that the ancestry of all extant mayflies could be traced to one of the many evolutionary lineages

constituting the Siphonuridae. Several families once included in the paraphyletic Siphonuridae are designated in List 1 with an asterisk. Some of this fractionation already has been suggested by others (e.g., Campbell 1988); it was actually started some time ago by Riek (1973) with regard to the more ancestral families of my Heptagenioidea. One by-product of splitting Siphonuridae is a greater degree of difficulty in differentiating the adults of the resultant new families. This problem unquestionably requires attention. But it should not pre-empt a classificatory system that aims to resolve a long-standing, critical problem in Ephemeroptera phylogeny.

Another by-product of splitting the Siphonuridae is the small size of the resultant families. Although not directly related to their anagenesis, the size of these lineages is a function of the relative history of adaptive radiations and extinctions; i.e., they are not now broadly radiated, and if they ever had been, they now are relict in nature. Paleontological data indicate that Siphonuridae, as here restricted, historically may have been more diverse and indeed more widespread in the Mesozoic (McCafferty 1990). Others of these families are not known from the Mesozoic, except possibly Ameletopsidae (Jell & Duncan 1986, McCafferty 1990) and Coloburiscidae (Sinitschenkova 1985), which are known from too limited or dubious data to draw conclusions. The now extinct siphonurid cognate Hexagenitidae apparently represents the largest and most pervasive group of mayflies on earth before the end of the Mesozoic.

These aspects of Ephemeroptera history, if I may digress somewhat, are noteworthy in supporting some important historical evolutionary theories that have recently come to the forefront. The observations that several families and subfamilies of mayflies did not survive the Mesozoic, and others have since disappeared from large land masses in the Southern Hemisphere (McCafferty 1990), generally support theories of mass extinction at the end of the Cretaceous that have been based on studies of marine animals (e.g., Raup & Sepkoski 1982) and tetrapods (reviewed by Colbert 1986), although the exact timing and degree of universality of the phenomenon are still to be resolved (Clemens 1986, Raup 1988).

In addition, this history of Ephemeroptera preliminarily appears to fit Gould's (1989) concept of decimation, albeit on a much smaller scale than his comparison of today's Animalia with the more diverse array displayed by fossils in the Cambrian Burgess Shale (see also Briggs & Fortey 1989, Morris 1989). Nevertheless, an iconography of mayfly evolution as an inverted cone of progressive diversification through time is apparently not what would be represented by a phylogenetic tree of Ephemeroptera if extinct lineages were accurately depicted as abbreviated or attenuating branches. Stanley (1979) indicated that birds and insects have had too poor a fossil record for evaluating theories

List 1. Revised higher classification of recent Ephemeroptera families; listings are phylogenetic, except families within parentheses require additional study. Asterisked families are equivalent to taxa that since 1954 have been placed by various authors in the previously paraphyletic family Siphonuridae

Order Ephemeroptera
Suborder Rectracheata
Infraorder Vetulata
*Family Oniscigastridae
Infraorder Lanceolata
Superfamily Leptophlebioidea
Family Leptophlebiidae
Superfamily Behningioidea
Family Behningiidae
Superfamily Ephemeroida
Family Polymitarciidae
Family Potamanthidae
Family Ephemeridae
Infraorder Pannota
Superfamily Caenoidea
Family Ephemerellidae
Family Tricorythidae
Family Caenidae
Family Prosopistomatidae
Superfamily Neoephemeroidea
Family Neoephemeridae
Superfamily Baetiscoidea
Family Baetiscidae
Suborder Setisura
*Family Coloburiscidae
*Family Isonychiidae
Family Oligoneuriidae
Family Heptageniidae
Suborder Pisciforma
Infraorder Arenata
(Families *Acanthametropodidae, Ametropodidae,
*Analetrididae, Metretopodidae, *Pseudironidae)
Infraorder Imprimata
(Families *Ameletidae, *Ameletopsidae, Baetidae,
*Metamoniidae, *Rallidentidae, Siphlaenigmatidae,
*Siphonuridae)

of historical instability of taxa, but recent discoveries of insects, including mayflies, from the Lower Cretaceous (see treatments in Grimaldi [1990]) would appear to begin to remedy this situation.

Before suggesting specific phylogenetic alternatives for the Ephemeroptera, it is important to understand that the stability of phylogenetic classification is directly related to the strength of the phylogenetic hypothesis on which it is based. Like all hypotheses in science, genealogical hypotheses are subject to review, corroboration, modification, and rejection. In the historical sciences, hypotheses are testable by observation and comparison rather than by experimentation (Gould 1984). How strong a hypothesis must be before formulating a phylogenetic classification is a subjective decision, and many organisms may not yet be classified phylogenetically with any confidence. I have taken the liberty of presenting an outline of higher classification, some components of which can be expressed phylogenetically but other components of which must await further cladistic analysis. In List 1, phylogenetic hypotheses are represented by the vertical sequence of names in the classification; however, when relationships among more than two

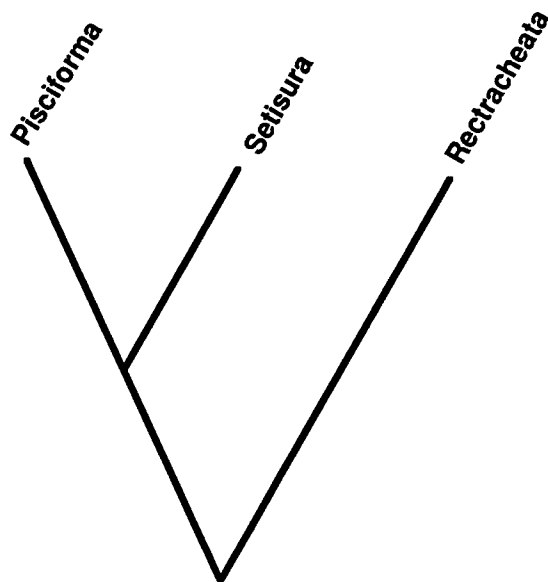


Fig. 3. Hypothesized branching sequence of the three suborders of recent Ephemeroptera.

subordinate taxa are not hypothesized, these taxa are run alphabetically. Conventions followed regarding redundancy and phyletic sequencing are those suggested by Wiley (1979).

Suborders, Infraorders, and Superfamilies of Ephemeroptera

The subordinal classification introduced by McCafferty & Edmunds (1979) requires modification to comply with a phylogenetic system. The suborder Pannota was a holophyletic grouping, but the suborder Schistonota as it was constituted is paraphyletic and must be disallowed. "Pannote" and "schistonote" remain useful descriptive terms as used, for example, by McCafferty et al. (1990), but they denote only gradations of evolution with respect to certain characteristics such as larval thoracic development, gill orientation, and certain aspects of internal anatomy (McCafferty & Edmunds 1979, Landa & Soldán 1985). Only the term pannote retains a clear genealogical connotation, whereas schistonote actually indicates the retention of certain plesiomorphic traits.

I suggest new suborders and infraorders (List 1) to express the major branches of Ephemeroptera. From Fig. 3, a sequencing convention is used to recognize three suborders rather than two. Fig. 3 basically is a consolidation of Landa's (1973) diagram. His branch representing my suborder Rectracheata was shown to be deduced on the basis of synapomorphies. However, synapomorphies previously have not been identified for his opposite branch representing my suborder Setisura plus suborder Pisciforma.

The Rectracheata (nominally, an allusion to the advanced tracheal system) is clearly defined by

synapomorphies involving internal anatomy (Landa & Soldán 1985), particularly the change from the plesiomorphic state of having ventral tracheal anastomoses present only in abdominal segments 8 or 9 or both (all nonrectracheate mayflies) to having such anastomoses present additionally in at least segments 4, 5, 6, and 7 (all rectracheate mayflies). This branch, except for Oniscigastridae, was recognized by McCafferty & Edmunds (1979); however, the common possession of dramatically increased ventral tracheal anastomoses in Oniscigastridae (Landa 1969, 1973; Landa & Soldán 1985) had been overlooked. Oniscigastridae has previously been classified in the Siphonuridae, and its new status is an example of the reclassification necessary to reflect the phylogenetic position of many components comprising the traditional Siphonuridae.

The Setisura and Pisciforma are phenetically much closer to each other than either is to Rectracheata, and together evidently have been interpreted as an opposite, monophyletic branch by default rather than by demonstrable synapomorphy. However, whereas there are numerous symplesiomorphies shared by Setisura and Pisciforma, there has also remained the probability that some of their common character states would prove to be synapomorphic.

I have found one character state that I can interpret as such an applicable synapomorphy; thus, based on their hypothesized sister relationship, it provisionally allows me to accept Setisura and Pisciforma as adelphotaxa (see Ax 1987). The character involves the relative presence of visceral tracheae in the abdomen. Landa & Soldán (1985) indicated, and I agree, that the plesiomorphic state is the presence of visceral tracheae in segments 1–8. This condition is found in its simplest form in Oniscigastridae, the most ancestral lineage of the Rectracheata. Acanthametropodidae, Ameletidae, Amelotopsidae, Coloburiscidae, Heptageniidae, Metamoniidae, Metretopodidae, Pseudironidae, Rallidentidae, and Siphonuridae, along with plesiotypic Baetidae, possess the apomorphic state of visceral tracheae in segments 2–8. This includes almost all of the nonrectracheate families (no data were available on Isonychiidae and Oligoneuridae). The major exception is the Ametropodidae. This family and apotypic genera of Baetidae have visceral tracheae in segment 1. However, observations that the ancestral *Callibaetis* lineage of Baetidae (McCafferty & Waltz, unpublished data) shows the loss in segment 1, and that Ametropodidae is clearly a member of the psammophilous branch of Pisciforma (see below), would suggest that the presence of such tracheae in segment 1 in some Pisciforma represents an anomalous reversion.

Further regarding visceral tracheae, the preponderant character states in the Rectracheata are presence in segments 3–8 and 4–8. Only in the highly apotypic genera *Eurylophella* and *Timpa-*

noga of Ephemerellidae (McCafferty 1977) is there a convergent presence in segments 2–8. Some ephemerellids have visceral tracheae in segment 1 also but have a peculiar situation where such tracheae are missing or weak in segments 3–5 (Landa & Soldán 1985).

As seen in List 1, the three major branches within the Rectracheata (Fig. 4) are sequenced as infraorders. Infraorder Vetulata (nominally, an allusion to the older [earlier derived] position of the lineage) represents the ancestral lineage, Oniscigastridae. The infraorders Lanceolata (nominally, an allusion to the lanceolate gill lamellae of the larvae of the burrowing mayflies and certain, presumably primitive, leptophlebiids) and Pannota (nominally, an allusion to the fused forewingpads of the larvae and the modified thorax of both the adults and larvae) are more derived sister branches. The phylogenetic relationship of the latter two groups was discussed in some detail by McCafferty & Edmunds (1979); the visceral tracheae condition discussed herein could be added to the synapomorphies demonstrating their relationship. The previous subordinal status of Pannota is changed and superfamilies within Lanceolata and Pannota are modified substantially to accommodate a phylogenetic classification.

Regarding the Lanceolata, McCafferty & Edmunds (1979) had indicated that Leptophlebiidae was possibly paraphyletic, in that a lineage within it may have given rise to the Ephemeroidea; however, more recent interpretations of data show Leptophlebiidae to be holophyletic. My placement of the Behningiidae in a separate superfamily for the first time is consistent with its phylogenetic position within the Lanceolata, the evidence for which was given by McCafferty (1979). This small, specialized group is very distinctive in both the adult and larval stages because of its many autapomorphies.

Regarding the Pannota, considerable cladistic analysis must still be conducted to gain more confidence in hypothesizing family-level derivations; however, preliminary data suggest the arrangement shown in Fig. 4. This differs significantly from that of McCafferty & Edmunds (1979) and in part from Landa & Soldán (1985). The highly specialized families Neoephemeridae and Baetiscidae may represent one major lineage, based on shared internal anatomical apomorphies treated by Landa (1969, 1973) and Landa & Soldán (1985), especially the ureterlike modification of the Malpighian tubules. The carapacelike development of the larval thorax in Baetiscidae and Prosopistomatidae is fundamentally different and therefore does not support a previous hypothesis that these two families are sister groups. In the same respect, the operculate gills of Neoephemeridae and Caenidae, although square-shaped, are fundamentally different and do not support a previously hypothesized sister relationship.

In the other hypothesized major lineage (Ephemerellidae, Tricorythidae, Caenidae, and

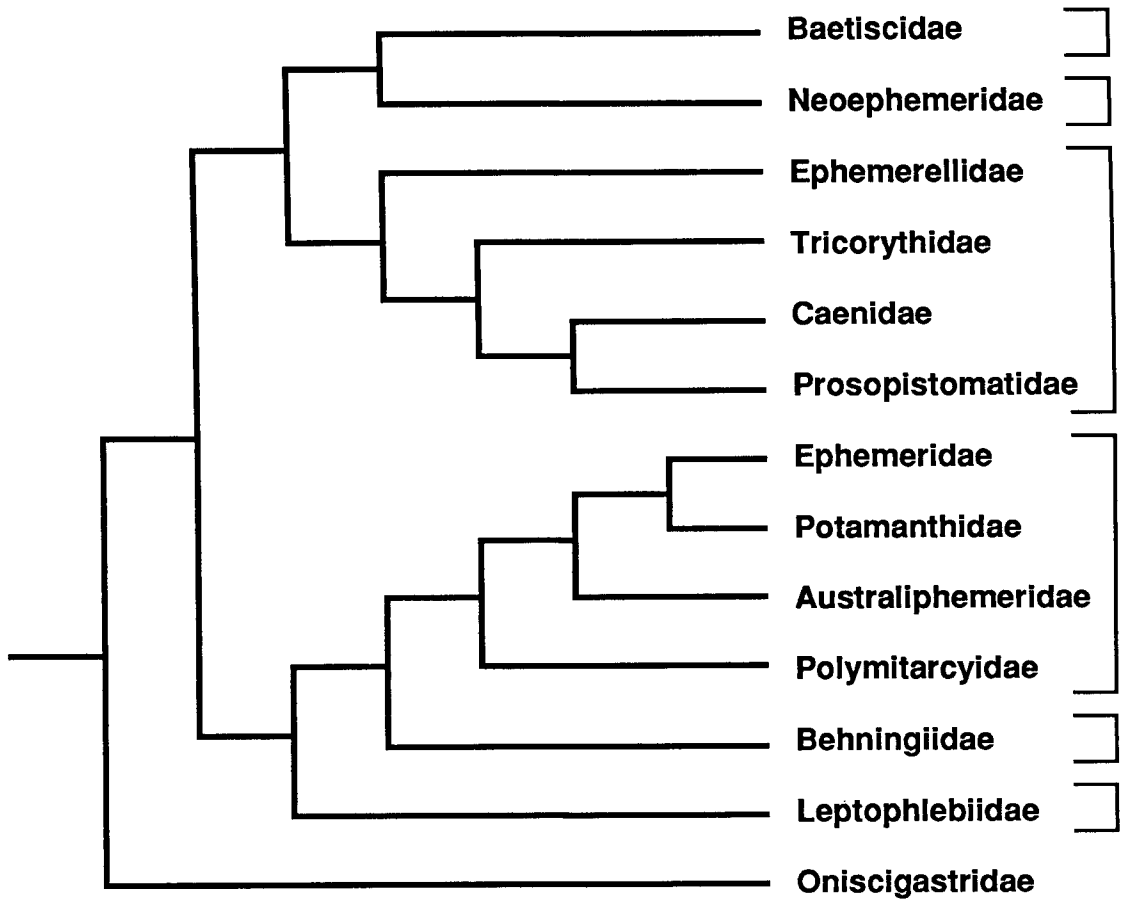


Fig. 4. Cladogram of the major lineages of Rectracheata, with proposed superfamily groups bracketed at right.

Prosopistomatidae) of Pannota, CuP in the forewing basally runs very close to, or is connected to, CuA or an intercalary thereof and distally curves strongly toward the posterior or inner margin of the wing. In the more apotypic Tricorythidae–Caenidae–Prosopistomatidae lineage, crossvenation is reduced, the recurved CuP is elongated into a more developed anal area, and the hindwings are correspondingly either lost or reduced. Furthermore, there are striking similarities in flight behavior and the resting wing position in these groups that I have observed recently in southern Africa (unpublished data). The Caenidae and Prosopistomatidae have additional reduction of crossvenation and share apomorphies involving internal anatomy (Landa & Soldán 1985). In addition, these latter families are the only pannotes that have become reproductive as female subimagos, a clear apomorphy (Edmunds & McCafferty 1988) probably present in their immediate common ancestor. The apparent inconsistency of some internal anatomical data (that suggest an alternative Neophemeridae–Baetiscidae–Caenidae–Prosopistomatidae grouping [Landa & Soldán 1985]), with the data presented here will remain problematic

until convergences that would explain the inconsistency are clearly identified.

By sequencing, I have placed the families of Pannota into three superfamilies for the present. Although the Baetiscidae and Neophemeridae could have been placed together in the same superfamily, the large degree of external morphological differences in the larvae and adults of the two groups can be additionally reflected by superfamily distinction. The inclusion of the remaining four families in Caenoidea would appear to be an appropriate alternative because of the character phenoclines clearly demonstrated in going from Ephemerellidae to Tricorythidae to Caenidae–Prosopistomatidae, and also from the fact that when all genera of Ephemerellidae, Tricorythidae, and Caenidae are considered, there is only weak family-level demarcation present within this clade.

The suborder Setisura (Fig. 3) is equivalent to the superfamily Heptagenioidea (Fig. 2), as discussed above. Numerous morphological and behavioral synapomorphies define this holophyletic group (see McCafferty 1991a). Nominally, Setisura is an allusion to the possession of filtering foreleg setae in the larvae of its ancestral lineages. Within

the higher classification proposed here, the rank category of superfamily within the suborder *Setisura* is redundant and thus does not appear in List 1.

Relationships among taxa placed in the suborder *Pisciforma* (nominally, an allusion to the minnow-like bodies and actions of the larvae) are not very clear. Edmunds (1972, 1973) and McCafferty & Edmunds (1979) have presented some hypotheses of relationships; however, there now appears to be two major groups, indicated as infraorder *Arenata* and infraorder *Imprimata* in List 1. This represents a significant departure from the most recent line of thought (e.g., McCafferty & Edmunds 1979). I recognize as synapomorphies the many characteristics of leg segment proportions, claw development, ambulatory and swimming behavior, as well as certain cubital venation common among several psammophilous mayflies that have been classified in different families. Thus, within the *Pisciforma*, I recognize these psammophilous mayflies as a separate holophyletic group, the infraorder *Arenata* (nominally, an allusion to the sand-dwelling nature and adaptations of the larvae). This basically agrees with an earlier grouping concept of Burks (1953).

All major lineages of *Arenata* have been at one time or another recognized as part of, or cognates of, the traditional family *Siphonuridae*, except that the pseudironid lineage has more often been considered in the *Heptageniidae*, beginning with Edmunds & Traver (1954). My phylogenetic data from the study of *Heptagenioidea* (McCafferty 1991a) showed that the pseudironid lineage is not related to *Heptageniidae*. Based on internal anatomy, Landa & Soldán (1985) have also removed it from the *Heptageniidae*. Although the possible synapomorphies common to all the families of *Arenata* are apparent, I am aware that some of the characteristics associated with sand dwelling are prone to convergence in distantly related mayfly lineages. I have just begun a careful cladistic study of these mayflies, but preliminarily, it appears that it may be difficult to find subsequent synapomorphies to deduce branching sequences of daughter lineages within the *Arenata*. This may very well be the consequence of a highly decimated group (sensu Gould 1989).

Although the branch referred to here as the infraorder *Imprimata* (nominally, meaning among the first, thus alluding to the retention of many primitive characteristics typifying the group) has been generally recognized in other workers' phylogenies (e.g., Edmunds 1973, Landa 1973, Riek 1973), synapomorphies that clearly define the group have yet to be proposed. Because *Imprimata* admittedly is very generalized and plesiotypic, and constitutes a "negative" grouping in the terminology of Woodley (1989), synapomorphies must be found to validate it as a holophyletic taxon. Similarly constituted groupings may be found in many insect orders for which additional cladistic information is required; for example, the systematic

position of *Imprimata* among *Ephemeroptera* is somewhat analogous to that of *Nematocera* among the *Diptera* (see Wood & Borkent 1989). Of additional note, the order *Ephemeroptera*, itself, is analogous to the *Imprimata* in that currently and almost exclusively it is defined by retained plesiomorphies, yet there would appear to be little doubt as to the order's integrity, at least with respect to post-Paleozoic forms (McCafferty 1990).

Imprimata contains most of the families that had been included in *Siphonuridae*. A reason for my recognition of several families rather than subfamilies within *Imprimata* is related to the arguments given above and exemplified by the *Heptagenioidea*. In this case, although exact phyletic sequencing cannot yet be detailed, it is apparent from available data that the baetid lineage is another example of a large, very distinctive taxon (family *Baetidae*) that has a most distal (apotypic) branched position in part of the phylogenetic tree (Edmunds 1973, McCafferty & Edmunds 1979). Therefore, to maintain it as a family, those lineages derived before it must have at least equal rank. As a possibility, see the Edmunds-Brundin exchange quoted herein and the phylogeny depicted in Fig. 1.

Because exact phylogenetic branching sequences for the families in either *Imprimata* or *Arenata* are not formally hypothesized at this time, no attempt has been made to list the families phylogenetically. Furthermore, although superfamilies have been a useful and commonly used category in *Ephemeroptera*, they cannot be formulated in these groups at this time for the same reason. Revision of the suborder *Pisciforma* will be required if it should prove to be paraphyletic. This, of course, also holds for the *Imprimata* and *Arenata*.

Kluge (1988b) has independently suggested two suborders for *Ephemeroptera*. His suborder *Furcatergalia* is equivalent to my *Rectracheata*, except it does not include *Oniscigastridae*. It therefore equals my combined infraorders *Lanceolata* and *Pannota*, or ancestor B and derivatives of McCafferty & Edmunds (1979). Kluge's suborder *Costatergalia* includes all other mayflies and is equal to my *Pisciforma* plus *Setisura* plus *Vetulata* (*Oniscigastridae*).

Kluge's suborders essentially are based on what he perceives to be fundamental differences in gills (his *tergalia*). The condition of his *Furcatergalia* (forked gill) appears to be an important additional synapomorphy substantiating a generally accepted phylogenetic hypothesis first suggested by Landa (1973) and generally accepted since. Kluge's conclusion that his *Furcatergalia* is a young group occurring only since Late Cretaceous is erroneous because at least two lineages of *Ephemeroidea* have been discovered from Lower Cretaceous deposits in Brazil, and *Leptophlebiidae* apparently is of Jurassic origin (McCafferty 1990).

I do not follow Kluge's classification because, for one, the inclusion of *Oniscigastridae* in his *Costatergalia* (bordered gills) gives it paraphyletic status.

If the phylogeny shown in Fig. 4 is followed, then to recognize Furcatergalia as a suborder requires that Vetulata (Oniscigastridae) also be recognized as a suborder. This would then require another rank category between order and suborder to distinguish the Vetulata-Furcatergalia branch from the Setisura-Pisciforma branch, and the system would be too cumbersome. Or Setisura together with Pisciforma might be considered one suborder (e.g., Costatergalia) and a sequencing convention might be used, but this, I believe, does not reflect the large adaptive units of mayflies as well as the subordinal classification that I have proposed. An alternative would be to recognize Vetulata and Furcatergalia as infraorders within Rectracheata; however, I would prefer to sequence three infraorders in Rectracheata, as discussed above, because the classification within an infraorder Furcatergalia would have to be subordinated with an additional rank category between infraorder and superfamily to distinguish the Lanceolata branch from the Pannota branch.

If it can be demonstrated that Kluge's presumed gill apomorphy applies also to Oniscigastridae (this does not appear to be the case), and Oniscigastridae should thus also be placed in his Furcatergalia, then I would gladly yield Rectracheata to his Furcatergalia, although no nomenclatural rules apply. Even with the latter modification, however, I would not adopt Kluge's Costatergalia. This is not because the gill condition defining that group is probably plesiomorphic, something I cannot unequivocally demonstrate at this time. It is instead simply because I can argue that the three suborders presented herein are in keeping with the constructs of phylogenetic classification and are more indicative of significant evolutionary events in the history of Ephemeroptera. For example, the recognition of Setisura as a distinct suborder additionally reflects a major evolutionary event, probably in the Jurassic, involving adaptation to running water and to passive filter feeding and other subsequent feeding adaptations in one of the largest groups of mayflies (McCafferty 1991a).

Even when workers agree on the details of phylogeny, they need not agree on the details of classification. As Hennig (1975) has pointed out, phylogenetic classification is a relatively straightforward process, but classifications of the same phylogeny will vary in the conventions applied and the kind of conveniences that such conventions may provide. Perhaps fittingly, it has been Hennig's fellow dipterists, in their quest to systematize the numerous diverse and intricate Zweiflüger (see reviews in McAlpine 1989), who, more than any other set of systematists, have proven him to be correct in this assessment. For example, the large disparity between Hennig's (1973) classification of Nematocera and the more recent interpretation by Wood & Borkent (1989), although due in part to differences in phylogenetic inferences, the use of additional characters, and some difference of opinion

about homology, to a large degree reflects personal choices within the purview of phylogenetic classification.

Phylogenetic Revision of Ephemeroidea

A phylogeny of major lineages of Ephemeroidea based on cladistic analysis was presented by McCafferty (1979). The classification of the Ephemeroidea, however, has retained paraphyletic families, in particular the families Ephemeridae and Euthyplociidae. Classificatory modifications are, therefore, in order and can be accomplished with some confidence because phylogenetic hypotheses are supported by considerable cladistic research.

The revised classification, presented in List 2 and based on the cladistic relationships given in Fig. 5, shows the composition of the four families now recognized in the Ephemeroidea. The new family Australiphemeridae includes only fossil genera. The concept of Potamanthidae is unmodified from previous treatments. Polymitarciidae and Ephemeridae are, however, more inclusive than in other recent classifications, and these concepts are used in the following discussion. Bases for this revision will be detailed or reviewed below. The cladistic evidence demonstrating that each of the three extant families is holophyletic is very strong and was given for the most part by McCafferty (1979) but supplemented by Gillies (1980) and Landa & Soldán (1985).

The branching sequence of these major lineages of Ephemeroidea has been difficult to ascertain because of the dearth of clear apomorphies shared by any subset of the lineages. Landa (1973) and Landa & Soldán (1985) derived the Potamanthidae with the Ephemeridae; however, I interpret all the synapomorphies inferred by those workers to constitute symplesiomorphies. McCafferty (1979) surmised a possible synapomorphy shared by Polymitarciidae and Ephemeridae that placed these lineages as sisters. Based on internal anatomical data reported by Landa (1969), it was interpreted that all members of those two lineages possessed an additional ventral tracheal anastomosis in abdominal segment 2. I no longer consider that deduction valid, because Landa & Soldán (1985) have since indicated that this additional anastomosis does not occur in *Ichthybotus* and some *Ephemer* (both relatively ancestral genera of the ephemerid lineage) or in *Asthenopus* and *Povilla* (relatively derived genera of the polymitarciid lineage).

At least two traits of forewing venation are interpreted here as synapomorphies in the Potamanthidae and Ephemeridae. Mayflies in general have longitudinal veins that run straight from their base. But in Ephemeroidea, veins MP_2 and CuA are variously arched posteriorly at their bases. In the Polymitarciidae, these veins are only gently arched, and these arches closely parallel each other. In Potamanthidae and Ephemeridae, however, MP_2

List 2. Supraspecific classification of the recent and fossil Ephemeroidea^a

Superfamily Ephemeroidea

- Family Polymitarciidae Banks
 Subfamily Pristiplociinae McCafferty [SA]
 Genus *Pristiplocia* McCafferty [Cretaceous]
 Subfamily Euthyplociinae Lestage [MA, OR, SA]
 (Genera *Campylocia* Needham & Murphy, *Euthyplocia* Eaton, *Mesoplocia* Demoulin, *Polylocia* Lestage, *Proboscidoplocia* Demoulin)
 Subfamily Exeuthyplociinae Gillies [AF]
 Genus *Afroplocia* Lestage
 Genus *Exeuthyplocia* Lestage
 Subfamily Asthenopodinae Edmunds & Traver [PA, PT]
 Genus *Asthenopodichnium* Thenius [Paleogene]
 Genus *Asthenopus* Eaton
 Genus *Povilla* Eaton
 Subfamily Campsurinae Traver [NA, SA]
 Genus *Campsurus* Eaton
 Genus *Tortopus* Needham & Murphy
 Subfamily Polymitarciinae Banks [AF, HO, OR]
 Genus *Ephoron* Williamson
 Family Australiphemeridae McCafferty [SA]
 Genus *Australiphemera* McCafferty [Cretaceous]
 Genus *Microphemera* McCafferty [Cretaceous]
 Family Potamanthidae Albará [HO, OR]
 Genus *Rhoenanthus* Eaton
 Subgenus *Rhoenanthus*
 Subgenus *Potamanthidus* Lestage
 Genus *Anthopotamus* McCafferty & Bae
 Subgenus *Potamanthus* Pictet
 Subgenus *Potamanthus*
 Subgenus *Stygifloris* Bae, McCafferty & Edmunds
 Subgenus *Potamanthodes* Ulmer
 Family Ephemeridae Latreille
 Subfamily Ichthybotinae Demoulin [NZ]
 Genus *Ichthybotus* Eaton
 Subfamily Ephemerinae Latreille [AF, HO, OR]
 Genus **Ephemer* Linnaeus [Paleogene]
 Subgenus **Ephemer*
 Subgenus *Aethephemera* McCafferty & Edmunds
 Genus *Afromera* Demoulin
 Subfamily Hexageniinae McCafferty [AF, HO, OR, SA]
 Genus *Denina* McCafferty [Paleogene]
 Genus **Hexagenia* Walsh [Paleogene]
 Subgenus **Hexagenia*
 Subgenus *Pseudeatonica* Spieth
 Genus **Litobranca* McCafferty [Paleogene]
 Genus *Eatonigenia* Ulmer
 Genus *Eatonica* Navas
 Subfamily Pentageniinae McCafferty [NA]
 Genus *Pentagenia* Walsh
 Subfamily Palingeniinae Albará [AF, MA, OR, PA]
 Genus *Palingenia* Burmeister
 (Genera *Anagenesia* Eaton, *Chankagenesia* Buldovskij, *Cheirogenesia* Demoulin, *Mortogenesia* Lestage, *Plethogenesia* Ulmer)

^a Authorships are appended. Asterisked genera contain both recent and fossil species, with fossil period indicated. Classification is phylogenetic, except relationships of genera within parentheses require analysis. World distributions are indicated in brackets: AF, Afrotropical; HO, Holarctic; M, Madagascar; NA, Nearctic; NZ, New Zealand; OR, Oriental; PA, Palearctic; PT, Palearctic; SA, Neotropical. Geological periods of fossil genera are indicated in brackets as either Cretaceous or Paleogene.

is extremely arched, more so than CuA. It is so strongly arched that the apex of its arch is juxtaposed with CuA, and in some individuals MP₂ actually becomes directly connected to CuA at this point and the base of the arch is lost or appears as a crossvein. Considering mayflies in general (all

nonephemeroids except Neophemeridae and others with highly specialized wings) for outgroup comparison, this venation has to be interpreted as apomorphic, with the gently arched condition retained in the Polymitarciidae representing a transitional state. The only exceptions to this characteristic in the Ephemeridae are found in some highly derived genera that have evolved atypically broadened forewings (i.e., *Eatonigenia* and *Palingenia*), where CuA has also become strongly directed posteriorly at the base to accommodate such broadening.

A possible additional synapomorphy involves the cubital venation of the forewing. Considering the Behningiidae and Leptophlebiidae as the nearest related taxa for use as outgroups (Fig. 4), it appears that the plesiomorphic cubital venation in Ephemeroidea included some longitudinal intercalary veins (posterior to CuA and paralleling CuA distally). This is generally also the case in Polymitarciidae, including early fossils from the Lower Cretaceous (McCafferty 1990). The lack of such intercalaries in Potamanthidae and in all the more ancestral genera of Ephemeridae would appear to represent a synapomorphy. The lack of such intercalaries in some *Euthyplocia* would represent an independent loss in that genus. I do not feel as confident about the polarity of this character as I do about the arch of MP₂, because there are several ancestral lineages of mayflies that possess cubital veinlets instead of intercalaries. Although this casts some doubt on the actual state of the cubital area in the common ancestor of Ephemeroidea, this polarity does parallel the more easily deduced polarity of the venational arches discussed above.

Overall, the cladistic evidence for hypothesizing a sister relationship of Potamanthidae and Ephemeridae is admittedly limited. Nevertheless, I can find no synapomorphies for Potamanthidae and Polymitarciidae or for Polymitarciidae and Ephemeridae that would falsify the hypothesis at this time. Soldán (1981) reported a slight difference in relative position of the gonads in Potamanthidae (lateral) and Ephemeridae and Polymitarciidae (ventrolateral). However, the positions appear essentially similar and to represent the same shift from the plesiomorphic dorsal position of gonads in mayflies. Furthermore, this slight difference within Ephemeroidea did not influence the phylogenetic reconstruction of Landa & Soldán (1985). The synapomorphy of a "forked" ligula in Ephemeridae and Polymitarciidae proposed by Tomka (1991) does not hold because labia are too variable in this respect. Preliminarily, I have found several genera of Ephemeridae from different lineages to have the unforked condition, and certain *Anthopotamus* (Potamanthidae) have a forked condition.

Landa & Soldán (1985) indicated, without details, that a departure from the basic arrangement of larval head tracheation in Ephemeroptera occurred in Ephemeridae, Palingeniidae, and Potamanthidae. Further investigation into this possibly unique anatomical evolution may uncover an im-

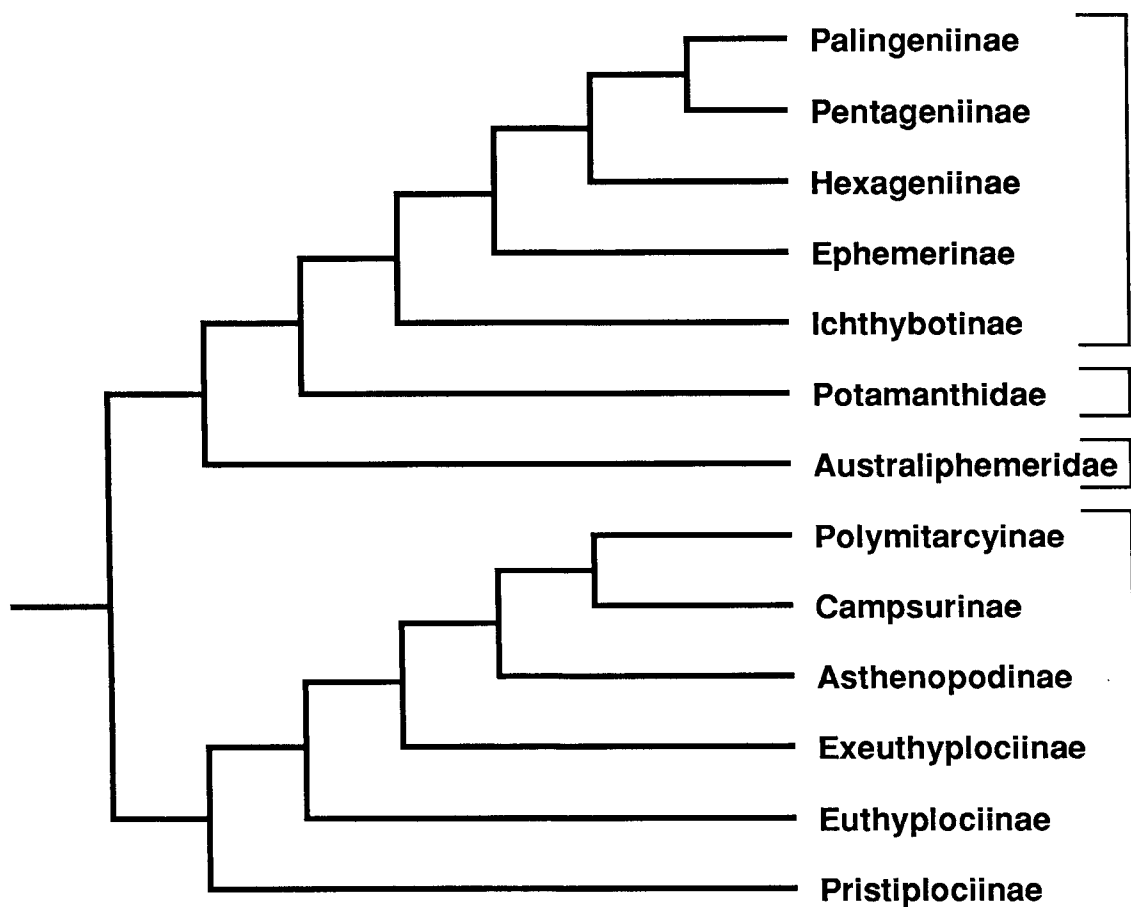


Fig. 5. Cladogram of the major lineages of Ephemeroidea, with proposed family groups bracketed at right.

portant substantiating synapomorphy for my hypothesis (Fig. 4 and 5).

The fossil genera *Australiphemera* and *Microphemera*, known from impressions taken from Lower Cretaceous deposits in Brazil, would belong to the same major branch as Potamanthidae and Ephemeridae based on forewing cubital venation, but the basal arch of MP_2 in these genera does not appear to be as extremely developed as in those others, and they lack the forked A_1 typical of Potamanthidae. Their MP_2 arch places them on the branch, but derived before the bifurcation resulting in the potamanthid and ephemerid lineages (Fig. 4 and 5). I therefore erect the new family Australiphemeridae for the lineage represented by these fossils. Also, hereafter I shall refer to the australiphemerid-potamanthid-ephemerid branch as the A-E branch.

Cladistic evidences for the branching sequences within part of the A-E branch were given by McCafferty (1972, 1979). A phylogenetic classification of families and subfamilies (List 2) is based on the resultant cladogram (Fig. 5), which also incorporates the new hypotheses regarding Australiphemeridae and Potamanthidae. Using the classification of McCafferty & Edmunds (1979) as

the baseline, the primary revision of taxa of the A-E branch involves the creation of the family Australiphemeridae and subfamily Hexageniinae and the placement of the Pentageniinae and Palingeniinae in the Ephemeridae rather than in a separate family Palingeniidae.

Ephemeridae and Palingeniidae have been regarded as distinct taxa of equal rank since Klapálek (1909). McCafferty (1972), however, showed that *Pentagenia*, which had always been considered in the Ephemeridae, was a sister lineage to the Palingeniidae (sensu lato) as demonstrated by numerous synapomorphies found in the larvae. The adults of *Pentagenia*, on the other hand, retain all of the plesiomorphic adult characteristics typical of the Ephemeridae (sensu lato), and a separate family was proposed for the genus. Later, McCafferty & Edmunds (1976) placed *Pentagenia* as a subfamily of the Palingeniidae.

Given the cladogram, viable classificatory options for the A-E branch hinge primarily on the taxonomic level which is used to express the most derived major lineage bifurcation. In other words, if a family Palingeniidae is recognized, then other major lineages in this branch must also be regarded at least as families to avoid paraphyly. Even if

Pentagenia is included in a family Palingeniidae, the only other option would be also to place the lineage represented by *Hexagenia* and its closely allied genera (Hexageniinae) in the Palingeniidae.

In being conservative and at the same time avoiding paraphyly, I have chosen to use the phyletic sequencing convention and regard the five more derived lineages of this branch as individual subfamilies within a single family Ephemeridae. If more than one family is to be recognized, divisions would have to proceed from the base. Thus, to maintain the integrity of Potamanthidae, the new family Australiphemeridae is called for. Other possibilities of family recognition in this branch (i.e., of four, five, six, or seven families), although certainly possible, would unnecessarily fractionate the family-level taxonomy. Although the lineages of Ephemeridae reflect distinct gradations, these gradations represent a fairly even phenocline along the sequence (Fig. 5), and additional families are difficult to justify.

Phylogenetic data for the polymitarcyid branch has been presented by McCafferty (1979) and Gillies (1980). The phylogeny (Fig. 5) given here, however, differs significantly from that given by McCafferty (1979). The exethyplociine lineage shown by Gillies (1980) is added, and the newly discovered pristiplociine lineage is also added, as is discussed below.

With respect to the more derived lineages (the traditional Polymitarcyidae), I no longer consider Campsurinae and Asthenopodinae to be sister lineages. At least two synapomorphies, however, indicate that Campsurinae and Polymitarcyinae actually represent the terminal sister lineages, or adelphotaxa. These include the shared additional ventral tracheal anastomoses in abdominal segment 2 (Landa & Soldán 1985) and the loss of the adult stage in females (Edmunds & McCafferty 1988). Certain characters of the internal anatomy of Polymitarcyinae remain enigmatic; i.e., I regard the loss of a Malpighian tubule trunk pair to be convergent with a similar loss in Euthyplociinae.

I use Landa & Soldán's (1985) classification as the baseline to discuss taxonomic revision in the polymitarcyid branch because it included the subfamily Exethyplociinae (in Euthyplociidae). The primary revision (List 2) involves the recognition of one family rather than two. To have maintained the status quo also would have maintained a paraphyletic family Euthyplociidae, considering the apomorphic relationship of the Exethyplociinae with traditional Polymitarcyidae, as shown by Gillies (1980). The present revision results in a more diffuse Polymitarcyidae; however, application of the same reasoning and sequencing convention used for classifying the Ephemeridae has allowed major lineages to be expressed as subfamilies.

The new subfamily Pristiplociinae has necessarily been created for the Lower Cretaceous genus *Pristiplocia* because of its hypothesized earliest derived position in the phylogeny (Fig. 5). This po-

sition is suggested by an apparent venational synapomorphy in all other polymitarcyids. *Pristiplocia* forewings possess three or four well-developed, free, marginal intercalary veins between each of the major longitudinal veins from IMA to CuA; such veins are lost or severely reduced in other polymitarcyids. The known age of this lineage and its hypothesized phylogenetic position are congruent.

Finally, a few additional comments are pertinent to augmenting the generic classification presented in List 2. Generic revisions are still required for the Polymitarcyidae and Palingeniinae. *Asthenopodichnium* was based on fossilized wood burrows only (Thenius 1979, 1988) and has a dubious placement in Asthenopodinae. I follow the recent synonymy of *Asthenopodes* Ulmer with *Asthenopus* as proposed by Hubbard & Dominguez (1988). Certain genera listed under Palingeniinae are expected to fall to synonymy. I do not now recognize *Heterogenesia* Dang described in Palingeniidae and have shown it to be a synonym of the ephemerid genus *Eatonigenia* (McCafferty 1991b).

The classification of potamanthid genera is based on a phylogenetic revision by Bae et al. (1990), McCafferty & Bae (1990), and Bae & McCafferty (in manuscript). The classification of Hexageniinae genera is based on phylogeny discussed by McCafferty (1973, 1987), McCafferty & Gillies (1979), and McCafferty & Sinitshenkova (1983).

I do not consider *Parabaetis* Haupt (Tertiary) and *Mesogenesia* Tshernova (Jurassic) as Ephemeroidea. The drawings of *Mesogenesia* by Tshernova (1977) suggest that the gills are more typical of Pisciforma gills such as those found in the fossil family Hexagenitidae, and that the forelegs may be raptorial rather than fossorial (McCafferty 1990). According to Demoulin (1957), the wing fragment on which *Parabaetis* was based is part of an ephemerid hindwing. The arrangement of what might be interpreted as the MP triad (labeled as CuA by Demoulin), although suggestive of the arrangement found in *Ephemer* and *Rhoenanthus*, is fundamentally different in that it would lack the actual MP₂.

Postscript

Concomitant with any revision of classification is a necessary adjustment in the language of biological discourse—the names used for imparting and recording comparative information associated with species and the higher taxa in which they are nested. These new nomenclatures, which some users and instigators alike might feel are necessary evils, result from the need to express improved interpretations of the relationships of organisms, usually based on additional knowledge about them. Improved interpretations, of course, can affect concepts of taxa, and in the case of phylogenetic classification, it is interpretations of evolutionary origins and their sequences (phylogeny expressed in its purest form as a cladogram) that equate relation-

ships and the taxa recognized. In addition to providing a basis for classification, however, such phylogeny can be shown to have many other important applications in biology.

In my opinion, the classification of the Ephemeroptera has been improved herein, if only by the fact that the classification now has a more definable basis. But perhaps most important, the enhanced evolutionary hypotheses, as ultimately expressed by phylogeny and phylogenetic classification, have gained considerable predictive and heuristic value. For example, in the Ephemeroidea, the evolution of burrowing and the history of microhabitat relationships and feeding relationships, along with the ponderable adaptation, preadaptation, or preadaptation of tusks, can be explained from the study of comparative behavior, ecology, and functional morphology (e.g., Keltner & McCafferty 1986) that now can be analyzed within the context of phylogeny.

Other striking examples already exist of the power and importance of mayfly phylogeny in the explanation not only of evolutionary history but also of some other realms of science. The phylogeny of certain Amphinotic mayflies worked out by Edmunds was explicable, considering the low vagility of mayflies, only by a deduced sequence of continental breakup of a formerly contiguous Transantarctica involving Chile-Patagonia, New Zealand, and Australia. This, in fact, was one of the first bits of zoological data (later elaborated by Edmunds [1973, 1975]) to give impetus to the eventual geologic confirmation of continental drift. Conclusions regarding the possible function of the subimaginal life stage in primitive insects and the preadaptation of hydrofuge wings in mayfly subimagos (Edmunds & McCafferty 1988) were possible only within the theoretical framework provided by knowledge of mayfly phylogeny. The historical invasion of flowing waters and its relationship to passive filter feeding and seston utilization and subsequent bottom feeding in streams could not have been inferred without the prerequisite basis provided by the phylogenetic systematics of the Setisura (McCafferty 1991a).

Besides these applications of phylogeny, there should be mentioned also the important interplay of paleontology and phylogeny (deduced from neontology) of mayflies (e.g., McCafferty 1990). Not only does the relationship demonstrate another interpretive role that phylogeny can play, but it may ultimately provide a quintessential example of how data derived from two investigative viewpoints may complement each other (see Cracraft & Eldredge 1979, Donoghue et al. 1989). The significance of the morphological diversity of the fauna of the Burgess Shale would hardly have been realized had it not been for the perspective provided by neontology (Morris 1989).

And finally, the phylogeny of mayflies could potentially play an important role in the conservation of their ecological diversity. Although tropical bi-

otas have been highlighted in conservation efforts because of rapid destruction of their habitats and high species diversity, Franklin (1988) has pointed out an additional dire need for protecting the diversity of temperate freshwater ecosystems (of which the mayflies are a major component). The importance of descriptive taxonomy in ecology has been appreciated for some time (Elton 1947), but more that just lists of species are needed to understand the intricacies of biodiversity (Ray 1988). For example, Funk & Pipoly (1990) suggested that it is information from phylogenetic systematics that allows ecologists to pose the most meaningful questions about the mechanics of the evolution of biota, and Ross (1974) showed that phylogeny plays a key role in understanding the evolution of ecological communities, including the coevolution of their components.

One tactic of ecologists for documenting the need for conservation has been to emphasize species interdependencies. I would suggest that, in addition to this, an accounting of the geographic, geologic, and ecologic peregrinations of species should also (and might even better) serve the cause to conserve them. This, of course, points to the essential role of phylogeny because only it will lead to the unraveling of such peregrinations. I expect the phylogenetic systematics of mayflies to play out its role proportionately in this task.

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References Cited

- Adanson, M. 1763. Les familles naturelles des plantes, vol. I. Vincent, Paris.
- Allen, R. K. 1980. Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae), pp. 71-92. In J. F. Flannagan & K. E. Marshall [eds.], *Advances in Ephemeroptera biology*. Plenum, New York.
- Ashlock, P. H. 1971. Monophyly and associated terms. *Syst. Zool.* 20: 63-69.
1972. Monophyly again. *Syst. Zool.* 21: 430-437.
1974. The uses of cladistics. *Annu. Rev. Syst. Zool. Ecol.* 5: 81-99.
1979. An evolutionary taxonomist's view of classification. *Syst. Zool.* 28: 441-450.

- Ax, P.** 1987. The phylogenetic system. Wiley-Interscience, New York.
- Bae, Y. J., W. P. McCafferty & G. F. Edmunds, Jr.** 1990. *Stygifloris*, a new genus of mayflies (Ephemeroptera: Potamanthidae) from Southeast Asia. *Ann. Entomol. Soc. Am.* 83: 887-891.
- Berner, L. & M. L. Pescador.** 1988. The mayflies of Florida, rev. ed. University Florida Press, Gainesville.
- Bock, W. J.** 1973. Philosophical foundations of classical evolutionary taxonomy. *Syst. Zool.* 22: 375-392.
- Borror, D. J., C. A. Triplehorn & N. F. Johnson.** 1989. An introduction to the study of insects, 6th ed. Saunders, Philadelphia.
- Botjter, P. D.** 1980. Farris' "information content" and phylogenetic versus evolutionary classification: the philosophical differences remain. *Syst. Zool.* 29: 382-386.
- Briggs, D.E.G. & R. A. Fortey.** 1989. The early radiation and relationships of the major arthropod groups. *Science* 246: 241-243.
- Brothers, D. J.** 1978. How pure must cladistic classification be? A response to Nelson on Michener. *Syst. Zool.* 27: 118-122.
- Brundin, L.** 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. *K. Sven. Vetenskapsakad. Handl.* 11: 1-472.
- Burks, B. D.** 1953. The mayflies, or Ephemeroptera, of Illinois. *Bulletin of the Illinois Natural History Survey* 26.
- Campbell, I. C.** 1988. Ephemeroptera, pp. 1-22. *In* W.W.K. Houston [ed.], *Zoological catalogue of Australia*, vol. 6. Bureau of Flora and Fauna, Canberra.
- Carpenter, J. M.** 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Syst. Entomol.* 7: 11-38.
1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). *Syst. Entomol.* 12: 413-431.
- Clemens, W. A.** 1986. Evolution of the terrestrial vertebrate fauna during the Cretaceous-Tertiary transition, pp. 63-85. *In* D. K. Elliott [ed.], *Dynamics of extinction*. Wiley, New York.
- Colbert, E. H.** 1986. Mesozoic tetrapod extinctions: a review, pp. 49-62. *In* D. K. Elliott [ed.], *Dynamics of extinction*. Wiley, New York.
- Cracraft, J.** 1974. Phylogenetic models and classification. *Syst. Zool.* 23: 71-90.
- Cracraft, J. & N. Eldredge.** [eds.] 1979. *Phylogenetic analysis and paleontology*. Columbia University Press, New York.
- Darwin, C.** 1859. On the origin of species by means of natural selection or the preservation of favored races in the struggle for life. Murray, London.
- Demoulin, G.** 1957. A propos de deux insectes Eocenes. *Bull. Inst. R. Sci. Nat. Belg.* 33(45): 1-4.
- Dobzhansky, T.** 1970. *Genetics of the evolutionary process*. Columbia University Press, New York.
- Donoghue, M. J., J. A. Doyle, J. Gauthier, A. G. Kluge & T. Rowe.** 1989. The importance of fossils in phylogeny reconstruction. *Annu. Rev. Ecol. Syst.* 20: 431-460.
- Dupuis, C.** 1984. Willi Hennig's impact on taxonomic thought. *Annu. Rev. Ecol. Syst.* 15: 1-24.
- Edmunds, G. F., Jr.** 1962. The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Syst. Zool.* 11: 22-31.
1972. Biogeography and evolution of Ephemeroptera. *Annu. Rev. Entomol.* 17: 21-42.
1973. Some critical problems of relationships in the Ephemeroptera, pp. 145-154. *In* W. L. Peters & J. G. Peters [eds.], *Proceedings of the first international conference on Ephemeroptera*. Brill, Leiden.
1975. Phylogenetic biogeography of mayflies. *Ann. Mo. Bot. Gard.* 62: 251-263.
- Edmunds, G. F., Jr. & J. R. Traver.** 1954. An outline of reclassification of the Ephemeroptera. *Proc. Entomol. Soc. Wash.* 56: 236-240.
- Edmunds, G. F., Jr., & W. P. McCafferty.** 1988. The mayfly subimago. *Annu. Rev. Entomol.* 33: 509-529.
- Elton, C.** 1947. *Animal ecology*. Sidgwick & Jackson, London.
- Farris, J. S.** 1974. Formal definitions of paraphyly and polyphyly. *Syst. Zool.* 23: 548-554.
1979. The information content of the phylogenetic system. *Syst. Zool.* 28: 483-519.
1980. The efficient diagnoses of the phylogenetic system. *Syst. Zool.* 29: 386-401.
- Ferris, V. R. & J. M. Ferris.** 1987. Phylogenetic concepts and methods, pp. 346-353. *In* J. A. Veech & D. W. Dickson [eds.], *Vistas on nematology*. Soc. Nematol., Hyattsville, Md.
- Flowers, W.** 1980. Two genera of Nearctic Heptageniidae (Ephemeroptera). *Fl. Entomol.* 63: 296-307.
- Franklin, J. F.** 1988. Structural and functional diversity in temperate forests, pp. 166-175. *In* E. O. Wilson [ed.], *Biodiversity*. National Academy Press, Washington, D.C.
- Funk, V. A. & J. J. Pipoly III.** 1990. Can systematics and ecology work together to broaden our collective biodiversity agenda? *Assoc. Syst. Coll. Newslet.* 18: 48-49.
- Gillies, M. T.** 1980. The African Euthyplociidae (Ephemeroptera) (Euxeuthyplociinae subfam. n.). *Aquat. Insects* 2: 217-224.
- Gorman, G. C., A. C. Wilson & M. Nakanishi.** 1971. A biochemical approach towards the study of reptilian phylogeny: evolution of serum albumin and lactic dehydrogenase. *Syst. Zool.* 20: 167-186.
- Gould, S. J.** 1984. Balzan prize to Ernst Mayr. *Science* 223: 255-257.
1989. *Wonderful life: the Burgess Shale and the nature of history*. Norton, New York.
- Grimaldi, D.** [ed.] 1990. *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. *Bull. Am. Mus. Nat. Hist.* 195.
- Hennig, W.** 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
1973. *Ordnung Diptera (Zweiflüger)*. *Handb. Zool.* 4(2): 1-337.
1975. "Cladistic analysis or cladistic classification?": a reply to Ernst Mayr. *Syst. Zool.* 24: 244-256.
- Holmes, E. B.** 1980. Reconsideration of some systematic concepts and terms. *Evol. Theory* 5: 35-87.
- Hubbard, M. D.** 1987. *Ephemeroptera. Fossilium catalogus, I: Animalia, pars 129*. Kugler, Amstelveen, The Netherlands.
- Hubbard, M. D. & E. Dominguez.** 1988. Synonymy of the Neotropical mayfly genera *Asthenopus* and *Asthenopodes* (Ephemeroptera: Polymitarciidae: Asthenopodinae). *Fl. Entomol.* 71: 207-210.
- Huxley, J.** 1942. *Evolution: the modern synthesis*. Harper, London.
- Jell, P. A. & P. M. Duncan.** 1986. Invertebrates, mainly insects from freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumburra Group), South

- Gippsland, Victoria. *Memoirs of the Association of Australasian Paleontologists* 3: 111-205.
- Keltner, J. & W. P. McCafferty.** 1986. Functional morphology of burrowing in the mayflies *Hexagenia limbata* and *Pentagenia vittigera*. *Zool. J. Linn. Soc.* 87: 139-162.
- Klapálek, F.** 1909. Ephemerida, eintagsfliegen, pp. 1-32. In A. Brauer [ed.], *Die Süßwasserfauna Deutschlands*. Fischer, Jena.
- Kluge, N.** 1988a. Revision of genera of the family Heptageniidae (Ephemeroptera). I. Diagnosis of tribes, genera and subgenera of the subfamily Heptageniinae. *Entomologicheskoye Obozreniye* 67: 291-313 (in Russian).
- 1988b. A question of the homology of the tracheal gills and paranotal processes of mayfly larvae and wings of insects with references to the taxonomy and phylogeny of the order Ephemeroptera, pp. 47-77. In *Proceedings of the 1st annual lectures in memory of N. A. Kholodkovskogo*, Leningrad Acad. Sci. 1988 (in Russian).
- Kuhn, T. S.** 1962. The structure of scientific revolutions. University of Chicago Press, Chicago.
- Landa, V.** 1969. Comparative anatomy of mayfly larvae (Ephemeroptera). *Acta Entomol. Bohemslav.* 60: 289-316.
1973. A contribution to the evolution of the order Ephemeroptera based on comparative anatomy, pp. 155-159. In W. L. Peters & J. G. Peters [eds.], *Proceedings of the first international conference on Ephemeroptera*. Brill, Leiden.
- Landa, V. & T. Soldán.** 1985. Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. Academia, Prague.
- Linnaeus, C.** 1758. *Systema naturae per regna tria naturae secundum classes, ordines, genera, species cum caracteribus, differentiis, synonymis, locis*, 10th ed. Stockholm.
- Mayr, E.** 1969. *Principles of systematic zoology*. McGraw-Hill, New York.
1974. Cladistic analysis or cladistic classification. *Z. Zool. Syst. Evolutionsforsch.* 12: 94-128.
1982. The growth of biological thought, diversity, evolution, and inheritance. Belknap, Cambridge, Mass.
1988. *Toward a new philosophy of biology*. Harvard University Press, Cambridge, Mass.
- Mayr, E., E. G. Linsley & R. L. Usinger.** 1953. *Methods and principles of systematic zoology*. McGraw-Hill, New York.
- McAlpine, J. F. [ed.]** 1989. *Manual of Nearctic Diptera*, vol. 3. Agriculture Canada Monograph 32. Hull, Quebec.
- McCafferty, W. P.** 1972. Pentageniidae: a new family of Ephemeroidea (Ephemeroptera). *J. Ga. Entomol. Soc.* 7: 51-56.
1973. Systematic and zoogeographic aspects of Asiatic Ephemeridae (Ephemeroptera). *Orient. Insects* 7: 49-67.
1977. Biosystematics of *Dannella* and related subgenera of *Ephemerella* (Ephemeroptera: Ephemerellidae). *Ann. Entomol. Soc. Am.* 70: 881-889.
1979. Evolutionary trends among the families of Ephemeroidea, pp. 45-50. In K. Pasternak & R. Sowa [eds.], *Proceedings of the second international conference on Ephemeroptera*. Panstwowe Wydawnictwo Naukowe, Warsaw.
1981. *Aquatic entomology*. Jones & Bartlett, Boston.
1987. New fossil mayfly in amber and its relationships among extant Ephemeridae (Ephemeroptera). *Ann. Entomol. Soc. Am.* 80: 472-474.
1990. Chapter 2: Ephemeroptera, pp. 20-50. In D. A. Grimaldi [ed.], *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bull. Am. Mus. Nat. Hist. 195.
- 1991a. The cladistics, classification, and evolution of the Heptagenioidea. In J. Alba-Tercedor & A. Sanchez-Ortega [eds.], *Overview and strategies of Ephemeroptera and Plecoptera*. Sandhill Crane Press, Gainesville, Fla. (in press).
- 1991b. Synopsis of the Oriental mayfly genus *Eatonigenia* (Ephemeroptera: Ephemeridae). *Oriental Insects* (in press).
- McCafferty, W. P. & Y. J. Bac.** 1990. *Anthopotamus*, a new genus for North American species previously known as *Potamanthus* (Ephemeroptera: Potamanthidae). *Entomol. News* 101: 100-102.
- McCafferty, W. P. & G. F. Edmunds, Jr.** 1976. Redefinition of the family Palingeniidae and its implications for the higher classification of Ephemeroptera. *Ann. Entomol. Soc. Am.* 69: 486-490.
1979. The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Am.* 72: 5-12.
- McCafferty, W. P. & M. T. Gillies.** 1979. The African Ephemeridae (Ephemeroptera). *Aquat. Insects* 1: 169-178.
- McCafferty, W. P. & N. D. Sinitshenkova.** 1983. *Litobranca* from the Oligocene in eastern Asia (Ephemeroptera: Ephemeridae). *Ann. Entomol. Soc. Am.* 76: 205-208.
- McCafferty, W. P., B. P. Stark & A. V. Provonsha.** 1990. Ephemeroptera, Plecoptera, and Odonata, pp. 43-58. In M. Kosztarab & C. W. Schaefer [eds.], *Systematics of the North American insects and arachnids: status and needs*. Virginia Agricultural Experiment Station, Information Series 90-1. Virginia Polytechnic Institute and State University, Blacksburg.
- McKenna, M. C.** 1975. Toward a phylogenetic classification of the Mammalia, pp. 21-46. In W. P. Luckett & F. S. Szalay [eds.], *Phylogeny of the primates*. Plenum, New York.
- Michener, C. D.** 1957. Some bases for categories in higher classification. *Syst. Zool.* 6: 160-173.
1977. Discordant evolution and the classification of allodapine bees. *Syst. Zool.* 26: 32-56.
- Mickevich, M. F.** 1978. Taxonomic congruence. *Syst. Zool.* 27: 143-158.
- Morris, S. C.** 1989. Burgess Shale faunas and the Cambrian explosion. *Science* 246: 339-346.
- Nelson, G. J.** 1971. Paraphyly and polyphyly: redefinitions. *Syst. Zool.* 20: 471-472.
1972. Phylogenetic relationships and classification. *Syst. Zool.* 21: 227-231.
1973. Classification as an expression of phylogenetic relationships. *Syst. Zool.* 22: 344-359.
- Nelson, G. & N. Platnick.** 1981. *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Novikova, E. A. & N. Kluge.** 1987. Systematics of the genus *Baetis* (Ephemeroptera: Baetidae) with description of a new species from middle Asia. *Vestn. Zool.* 1987(4): 8-19 (in Russian).
- Peters, W. L. & G. F. Edmunds, Jr.** 1970. Revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). *Pac. Insects* 12: 157-240.

- Raup, D. M. 1988.** Diversity crisis in the geological past, pp. 51–57. *In* E. O. Wilson [ed.], *Biodiversity*. National Academy Press, Washington, D.C.
- Raup, D. M. & J. J. Sepkoski, Jr. 1982.** Mass extinction in the marine fossil record. *Science* 215: 1051–1053.
- Ray, G. C. 1988.** Ecological diversity in coastal zones and oceans, pp. 36–50. *In* E. O. Wilson [ed.], *Biodiversity*. National Academy Press, Washington, D.C.
- Riek, E. F. 1973.** The classification of the Ephemeroptera, pp. 160–178. *In* W. L. Peters & J. G. Peters [eds.], *Proceedings of the first international conference on Ephemeroptera*. Brill, Leiden.
- Romer, A. S. 1966.** Vertebrate paleontology. University of Chicago Press, Chicago.
- Ross, H. H. 1937.** A generic classification of the Nearctic sawflies (Hymenoptera, Symphyta). *Ill. Biol. Monogr.* 15: 1–173.
- 1956.** Evolution and classification of the mountain caddisflies. University of Illinois Press, Urbana.
- 1964.** Review: Principles of numerical taxonomy, by Robert R. Sokal & Peter H. A. Sneath. *Syst. Zool.* 13: 106–108.
- 1974.** Biological systematics. Addison-Wesley, Reading, Mass.
- Rudwick, M. J. S. 1976.** The meaning of fossils: episodes in the history of paleontology, 2nd ed. University of Chicago Press, Chicago.
- Scilla, A. 1670.** La vana speculazione disingannata dal senso. Lettera responsiva circa i corpi marini, che petrificata si trovano in varii luoghi terrestri, Napoli.
- Simpson, G. G. 1961.** Principles of animal taxonomy. Columbia University Press, New York.
- Sinitshenkova, N. D. 1985.** Jurassic mayflies (Ephemeroptera) of southern Siberia and western Mongolia. *Transactions Paleontol. Inst. (Moscow)* 211: 11–23 (in Russian).
- Sokal, R. R. & P.H.A. Sneath. 1963.** Principles of numerical taxonomy. Freeman, San Francisco.
- Soldán, T. 1981.** Comparative anatomy of the internal reproductive organs of mayflies (Ephemeroptera). *Stud. Czech. Acad. Sci.* 6: 1–120.
- Stanley, S. M. 1979.** Macroevolution: pattern and process. Freeman, San Francisco.
- Stehr, F. W. [ed.] 1987.** Immature insects. Kendall Hunt, Dubuque, Iowa.
- Thenius, E. 1979.** Lebensspuren von Ephemeropterenlarven aus dem Jung-Tertiär des Wiener Beckens. *Ann. Natur. Mus. Wien* 82: 177–188.
- 1988.** Lebensspuren von aquatischen Insectenlarven aus dem Juntertiär Niederösterreichs. *Beitr. Paläont. Österr.* 14: 1–11.
- Thomas, L. 1990.** A long line of cells. Book-of-the-Month Club, New York.
- Tomka, I. 1991.** Problems in the phylogeny of the Ephemeroptera. *In* J. Alba-Tercedor & A. Sanchez-Ortega [eds.], *Overview and strategies of Ephemeroptera and Plecoptera*. Sandhill Crane Press, Gainesville, Fla. (in press).
- Traver, J. R. & G. F. Edmunds, Jr. 1968.** A revision of the Baetidae with spatulate-clawed nymphs (Ephemeroptera). *Pac. Insects* 10: 629–677.
- Tshernova, O. A. 1977.** Unusual new larval mayflies (Ephemeroptera: Palingeniidae, Behningiidae) from the Jura Mountain area of the Transbaykal. *Paleontol. Zh.* 1977(2): 91–96 (in Russian).
- Wagner, W. H., Jr. 1969.** The construction of a classification, pp. 67–103. *In* *Systematic biology*. National Academy of Sciences Publication 1692, Washington, D.C.
- Waltz, R. D. & W. P. McCafferty. 1987a.** New genera of Baetidae for some Nearctic species previously included in *Baetis* Leach (Ephemeroptera). *Ann. Entomol. Soc. Am.* 80: 667–670.
- 1987b.** Systematics of *Pseudocloeon*, *Acentrella*, *Baetiella*, and *Liebebiella*, new genus (Ephemeroptera: Baetidae). *J. N. Y. Entomol. Soc.* 95: 553–568.
- Wiley, E. O. 1979.** An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* 28: 308–337.
- 1981.** Phylogenetics: the theory and practice of phylogenetic systematics. Wiley, New York.
- Wood, D. M. & A. Borkent. 1989.** Phylogeny and classification of the Nematocera, pp. 1333–1370. *In* J. F. McAlpine [ed.], *Manual of Nearctic Diptera*, vol. 3. Agriculture Canada Monograph 32. Hull, Quebec.
- Woodley, N. E. 1989.** Phylogeny and classification of the "Orthorrhaphous" Brachycera, pp. 1371–1395. *In* J. F. McAlpine [ed.], *Manual of Nearctic Diptera*, vol. 3. Agriculture Canada Monograph 32. Hull, Quebec.

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