RELATIONSHIPS OF THE ARTHROPLEIDAE, HEPTAGENIIDAE, AND PSEUDIRONIDAE (EPHEMEROPTERA: HEPTAGENIOIDEA)[1]

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ABSTRACT: Phylogenetic relationships indicate that *Pseudiron* represents a sister lineage to all other genera that have traditionally been placed in the family Heptageniidae. Among the latter lineage, *Arthroplea* represents a sister lineage to a lineage including all other genera. Recognition of the families Pseudironidae *(Pseudiron),* Arthropleidae *(Arthroplea),* and Heptageniidae *sensu stricto* is suggested within the framework of a strictly phylogenetic classification. The deduced cladogram of the three lineages and their apomorphic characterization is presented.

The superfamily Heptagenioidea is a monophyletic grouping of Ephemeroptera that was shown by McCafferty (1990) to include, as far as is now known, the extant families Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae. This fundamental relationship has been recognized by other workers (Edmunds 1973, Landa 1973, McCafferty and Edmunds 1979, Landa and Soldán 1985) and a first cladistic hypothesis was offered by McCafferty (1991a). Although a close relationship of the fossil family Epeoromimidae and Heptageniidae had been suggested by Tshernova (1970), McCafferty (1990) excluded Epeoromimidae from the Heptagenioidea because it apparently lacked larval synapomorphies that defined the superfamily. Although the Heptagenioidea clearly appear to have arisen from a minnowlike (pisciform) ancestor, the exact point of origin remains problematic; however, if it is derived at the base of the pisciform lineage, its provisional consideration as a separate suborder Setisura (McCafferty 1991b) would be appropriate. Also, although there is little question as to the monophyletic nature of the Heptagenioidea, we are not completely sure that it is holophyletic at this time since some problematic pisciform families may eventually prove to share its common ancestry. More cladistic research is expected to resolve these latter questions.

The family Heptageniidae is by far the largest and most apotypic of the major lineages of Heptagenioidea. It constitutes a familiar group of "flatheaded" mayflies that are distributed mainly in streams throughout the "world continent" [i.e., excluding only South America and the Australian regions; see Wilson (1992)]. These mayflies may have evolved from stream-dwelling, minnowlike, passive filter feeders (see McCafferty 1991a). A relatively consistent concept of the Heptageniidae as a distinct taxon of mayflies began with Eaton's (1883) informal grouping, but it was not until the reclassification of Edmunds and Traver (1954) that the group was universally recognized at the family level.

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[1] Received April 29, 1995. Accepted May 29, 1995.

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There are two genera of highly specialized mayflies, *Arthroplea* Bengtsson and *Pseudiron* McDunnough, that have been placed either in separate subfamilies of Heptageniidae or in separate families. Recent treatments of these genera may be found in Studemann *et al.* (1987) and Pescador (1985), respectively. The Holarctic genus *Arthroplea* was considered to constitute the separate family Arthropleidae by Balthasar (1937), and this classification has sometimes been followed in Europe. In North America, for the most part, the taxon has been considered only a subfamily of Heptageniidae. The Nearctic genus *Pseudiron* was considered to constitute the subfamily Pseudironinae of Heptageniidae by Edmunds and Traver (1954). Landa and Soldán (1985) and McCafferty (1990) did not believe that *Pseudiron* was related to the Heptageniidae. Landa and Soldán (1985) considered Pseudironinae in the family Siphlonuridae *sensu lato,* but this was done on the basis of unreliable internal anatomical characters. McCafferty (1991b) gave it familial status within a particular group of pisciform families outside the Heptagenioidea, mainly because of the similarity of certain larval characteristics associated with the sand-dwelling larvae. It now appears that this grouping of psammophilous mayflies in the provisional infraorder Arenata may represent an artificial construct because defining apomorphies are highly adaptive and may not have been commonly derived (see also McCafferty 1991c, McCafferty and Wang 1994).

The main purpose of this paper is to demonstrate the phylogenetic relationships of *Arthroplea* and *Pseudiron* to Heptageniidae *sensu stricto.*

FAMILIES OF THE HEPTAGENIIDAE COMPLEX

Our detailed comparison of *Arthroplea, Pseudiron,* and the numerous genera that have unquestionably been considered in the Heptageniidae has revealed that together they form a monophyletic group within the Heptagenioidea. *Pseudiron* shares a number of apomorphies common to this entire grouping (see below). Thus the placement of *Pseudiron* in, or as a cognate of, the Heptageniidae, as initially suggested by Edmunds and Traver (1954), is validated. For purposes of discussion below, we will refer to this monophyletic grouping as the Heptageniidae complex.

Shared characteristics of the Heptageniidae complex that distinguish it from other Heptagenioidea are as follows: Larvae have bodies that are generally depressed with outspread legs, and associated with this condition is a head capsule that has lost a considerable amount of its convexity and thus become relatively flattened and flanged. The head is prognathous with dorsal eyes and antennae, but the associated prognathous mouthpart orientation along with a reduced clypeus was already apparent in the related heptagenioid family Oligoneuriidae, as was some primordial tendency towards the flanging of the head capsule. The apomorphic depression of the larvae has independently evolved from the plesiomorphic fusiform shaped body to various degrees in

some other mayfly lineages outside the Heptagenioidea, especially within certain lineages of the extremely diverse family Leptophlebiidae. Maxillary gills and filtering foreleg setae that are present in certain plesiotypic families of Heptagenioidea are absent in the Heptageniidae complex and presumably evolved in an early ancestor of the Heptagenioidea. The absence of these features in the Heptageniidae complex therefore may represent a reversion to the general outgroup condition widespread throughout the Ephemeroptera. A row of usually well-developed hairlike setae is present posteriorly along the forefemora. This characteristic, however, is highly subject to homoplasy among mayflies.

The alate stages of the Heptageniidae complex reflect the flattened condition of the larvae with a corresponding broadening of the thorax and various shortening and broadening of the adult head capsule. The broadening of the thorax in the alate stages is expressed by the relative width of the medio-elongate depression of the furcasternum of the mesothorax. In the Heptageniidae complex, this depression is variously broadened compared to a narrow-elongate depression found in the alate forms of mayflies with narrow elongate larval bodies. Alate stages of the Heptageniidae complex also have forewings in which both CuP and A_1 are more elongated than that found in other Heptagenioidea and the more primitive pisciform mayflies. This is best expressed by CuP ending variously beyond the midlength of the anal margin (with very few exceptions in certain species). Two pairs of cubital intercalaries are also present in the forewings of the Heptageniidae complex (rarely reduced to one pair, for example, in a species of *Rhithrogena* Eaton) and at least the first pair ends in the outer margin. McCafferty (1991a) hypothesized that this basic cubital venation evolved in a common ancestor of the Oligoneuriidae and Heptageniidae complex because it is present in the most plesiotypic Oligoneuriid subfamily Chromarcyinae (more apotypic lineages of Oligoneuriidae having become highly specialized for rapid flight with geminated elongate veins and loss of crossveins). The presence of two pairs of cubital intercalaries may be subject to homoplasy in mayflies. For example, two pairs of cubital intercalaries are also found in the Ametropodidae and some Metretopodidae; however, the exact relationships of these latter families must be further researched. The relative length of CuP may be variously represented outside the Heptagenioidea.

In order to resolve the higher classification within the Heptageniidae complex, we subjected the genera of the Heptageniidae complex to a cladistic analysis. It is critical that the cladistic position of *Arthroplea* and *Pseudiron* be determined if a phylogenetic classification is to be followed. For example, if either of these lineages originated from within Heptageniidae *sensu stricto*, then that particular lineage would necessarily be disqualified from consideration as a separate family because such a classification would also establish Heptageniidae as paraphyletic. The branching sequence would also obviously have an impact on the consideration of lineages as subfamilies.

Our analysis indicated that *Pseudiron, Arthroplea,* and all other genera of the Heptageniidae complex form three monophyletic lineages, respectively. The deduced branching sequence of the three lineages is shown in Figure 1. The evidentiary apomorphies are indicated by letters on Figure 1 and are detailed in Table 1. Our conclusions apparently are in some agreement with previous conclusions by Jensen and Edmunds (1973), wherein they stated that *Pseudiron* and *Arthroplea* arose independently from near the base of the "proto-Heptageniidae." Jensen and Edmunds (1973), however, gave no phylogenetic data to substantiate their conclusions, and a third conclusion that *Raptoheptagenia* Whiting and Lehmkuhl (treated as *Anepeorus* McDunnough) was also derived basally is not supportable. Our additional cladistic data (McCafferty and Wang,

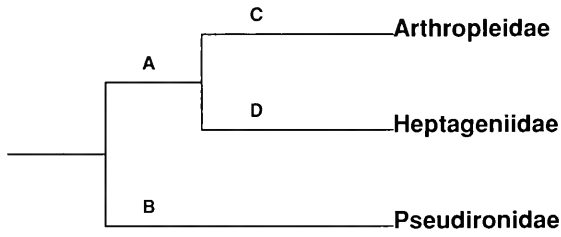

Fig. 1. Cladogram of the Heptageniidae complex (letters represent synapomorphies listed in Table 1).

Table 1. Apomorphies used in configuring the cladogram of the major lineages of the Heptageniidae complex (Fig. 1), with respective plesiomorphies indicated.

Apomorphy	Plesiomorphy
A. Adult hindtarsal segment 1 completely articulated with tibiae (clearly 5-segmented) (Fig. 235: Edmunds *et al.* 1976)	- Hindtarsus segment 1 fused or partially fused to tibiae (tarsus apparently 4-segmented) (Figs. 234, 236: Edmunds *et al.* 1976).
B. Larval tarsal claws subequal to tibiae (Fig. 406: Edmunds *et al.* 1976).	- Tarsal claws much shorter than tibiae.
Larval gills lamellae with elongate appendage (Fig. 406: Edmunds *et al.* 1976).	- Gills without elongate appendage.
C. Male genital forceps with 3 small terminal segments.	- Forceps with 2 small terminal segments.
Larval maxillary palps extremely elongated (Fig. 405: Edmunds *et al.* 1976).	- Maxillary palps not elongate.
D. Larval labial base broad and enlarged, with thickened labial palp segment 1 obliquely and subterminally fitted to base (Fig. 20: McCafferty 1991a).	- Labial base and palps not developed as such and palps articulated terminally (Figs. 12, 14, 16, 18: McCafferty 1991a).

in preparation) will show *Raptoheptagenia* to be derived from within the Heptageniinae.

By incorporating a sequencing convention (see, *e.g.,* Wiley 1981), we propose that the three distinctive lineages depicted in Figure 1 be recognized as separate families. Not only is this in compliance with the precepts of a phylogenetic classification, but the three families are easily keyed out as such in both the larval and alate stages. In recent family keys to adult mayflies of North America (*e.g.,* Edmunds *et al.* 1976, Edmunds 1984), Heptageniidae *sensu lato* had to be keyed out at two different places in those keys, *i.e.,* at one point as Heptageniidae in part (= Heptageniidae *sensu stricto*) and at another point as Heptageniidae in part (= Pseudironidae). This situation is now obviated by the revised classification.

As pointed out above, in addition to the families Heptageniidae, Arthropleidae, and Pseudironidae, the mayfly families Ametropodidae and Metretopodidae also possess adults with paired elongate cubital intercalary veins in the forewings. All of these families also have relatively elongate CuP and A 1 veins in the forewings. Presently, we are not sure of the relationships of the latter families with each other or with the former three families of the Heptagenioidea. Adults of all of these groups can be easily keyed using the taxonomic keys of Edmunds *et al.* (1976) and Edmunds (1984), for example, Ametropodidae adults possess a developed median caudal filament and those of the others do not. Adults of Chromarcyinae (Heptagenioidea, Oligoneuriidae), a group known only from southeast Asia, possess a cubital wing venation similar to the latter five families, however, they are told by the possession of more than four elongate MP1 intercalary veins and CuP and A 1 veins that do not extend quite as far along the anal margin of the forewing. Adults of some species of the large and diverse families Baetidae and Leptophlebiidae can be found to have paired elongate cubital intercalaries, but they are otherwise highly distinctive and should not be confused with the families that consistently show this cubital characterization.

ACKNOWLEDGMENT

This paper has been assigned Purdue Agriculture Research Program journal number 14644.

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