

Heptageniidae (Ephemeroptera) of the World. Part I: Phylogenetic Higher Classification

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ABSTRACT

Twenty-nine monophyletic species groups based on the study of nearly 200 species of the Ephemeroptera family Heptageniidae from North and Central America, Africa, Eurasia, and Southeast Asia were subjected to cladistic analysis in order to hypothesize their interrelationships and produce a framework for a strict phylogenetic higher classification for the family. As a result, three sequentially derived major clades are recognized as the subfamilies Ecdyonurinae, Heptageniinae, and Rhithrogeninae. The Ecdyonurinae is divided into four tribes: the Ecdyonurini, containing the genera *Nixe* Flowers and *Ecdyonurus* Eaton; the Leucrocutini, n. trib., containing the genera *Siberionurus* McCafferty and *Leucrocuta* Flowers; the Notacanthurini, n. trib., containing the genera *Notacanthurus* Tshernova and *Electrogena* Zurwerra and Tomka; and the Atopopini, n. trib., containing the genera *Afronurus* Lestage [= *Cinygmina* Kimmins, n. syn.], *Asionurus* Braasch and Soldán, *Thalerosphyrus* Eaton [= *Compsoneuriella* Ulmer, n. syn.], [= *Notonurus* Crass, n. syn.], and *Atopopus* Eaton. The Heptageniinae is divided into four tribes: the Compsoneuriini, n. trib., containing the genera *Compsoneuria* Eaton and *Trichogenia* Braasch and Soldán; the Heptageniini, containing the genera *Heptagenia* Walsh, *Dacnogenia* Kluge, n. stat., and *Raptoheptagenia* Whiting and Lehmkuhl; the Kageroniini, n. trib., containing the genera *Kageronia* Matsumura [= *Parastenacron* Kluge, n. syn.] and *Stenacron* Jensen; and the Stenonematini, n. trib., containing the genera *Macdunnovia* Lehmkuhl, *Maccaffertium* Bednarik, n. stat., and *Stenonema* Traver. The Rhithrogeninae is divided into four tribes: the Rhithrogenini, containing the genera *Paegniodes* Eaton, *Rhithrogena* Eaton [= *Rhithrogeniella* Ulmer, n. syn.], and *Cinygmula* McDunnough [- *Epeiron* Demoulin, n. syn.; = *Ororotsia* Traver, n. syn.]; the Cinygmatini, containing the genus *Cinygma* Eaton [= *Cinygmoides* Matsumura, n. syn.]; the Epeorini, n. trib., containing the genera *Bleptus* Eaton, *Ironodes* Traver, and *Epeorus* Eaton [= *Epeorella* Ulmer, n. syn.]; and the Anepeorini, containing the genera *Anepeorus* McDunnough [= *Acanthomola* Whiting and Lehmkuhl, n. syn.] and *Spinadis* Edmunds and Jensen. The nomenclatural history of the higher classification of the family, bases for the new classification and synonymies, and the biogeography and evolution of the genera are discussed.

INTRODUCTION

Heptageniidae is a family of mayflies distributed mainly in the Holarctic, Oriental, and Afrotropical regions, but also in the Central American tropics, extreme northern South America, and possibly the northern Australian tropics. There are over 500 nominal species of extant Heptageniidae recognized as valid, with another 12 species known from fossils. The flatheaded mayflies, as the Heptageniidae are sometimes known in reference to their conspicuously flattened larval head and body, are regular members of the benthic assemblages of streams and rivers (less commonly lake shores), where they may be major consumers of fine detritus and diatoms (a few are specialized predators). As a result, they are often important components of most lotic ecosystems.

The phylogenetic origin of the Heptageniidae was treated in detail by McCafferty (1991a) and Wang and McCafferty (1995a), where the family was shown by cladistic analysis to represent a most apotypic clade of a monophyletic group of families, which includes Coloburiscidae, Isonychiidae, Oligoneuriidae, Pseudironidae, and Arthropleidae. This grouping of families, known as the superfamily Heptagenioidea, is possibly related to the pisciform mayflies—either derived from within the Pisciforma, or representing a sister group of the Pisciforma. Thus, the Heptagenioidea has been recognized as the separate suborder Setisura (McCafferty 1991b), but as a suborder it remains provisional, pending additional cladistic study of the Pisciforma families. On-going molecular studies are expected to shed further light on the precise origin of the Heptagenioidea.

The relatively consistent recognition of the Heptageniidae as a distinct taxon of mayflies began with Eaton's (1883) informal groupings and continued with Needham's (1901) formal recognition of subfamilial status and formal authoring of the family-group name. Although Bengtsson (1913) was the first to use the familial rank for the taxon, it was not until the reclassification of Edmunds and Traver (1954) that the group was universally recognized at the family level.

There are two taxa of mayflies that have been considered either as subfamilies of Heptageniidae or as separate families. These are Arthropleidae and Pseudironidae. *Arthroplea* Bengtsson was considered to constitute the separate family Arthropleidae by Balthasar (1937), and generally this classification has been followed in Europe in recent years, but otherwise the taxon was considered only a subfamily of Heptageniidae until Wang and McCafferty (1995a) further established familial delineation.

Pseudiron McDunnough was considered to constitute the subfamily Pseudironinae of Heptageniidae by Edmunds and Traver (1954). McCafferty (1991b) gave it familial status and provisionally placed it within the Pisciforma. Later, Wang and McCafferty (1995a) suggested that its correct affinity was with the Heptagenioidea (Setisura), in essence following after Edmunds and Traver (1954). Wang and McCafferty (1995a) further showed that the currently more restrictive application of Heptageniidae is a valid phylogenetic concept.

Only four strictly fossil genera of Heptageniidae have been proposed: *Succinogenia* Demoulin, *Miocoenogenia* Tshernova, *Pseudokageronia* Masselot and Nel, and *Amerogenia* Sinitshenkova. Only the latter is known from the Mesozoic (upper Cretaceous), whereas the former three are known from the Tertiary, as are other species that have been placed in *Cinygma* Eaton, *Heptagenia* Walsh, *Rhithrogena* Eaton, and *Stenonema* Traver. Heptageniidae certainly can be con-

sidered a relatively recent group of mayflies, given the high diversity of the family today, its general restriction to Arctogaea, its apotypic phylogenetic position among the Setisura, and the fact that fossils are mostly present subsequent to the K-T boundary and rarely just prior to that boundary.

Well over 50 different genus-group names have been proposed for extant Heptageniidae. Whereas many of these have been considered equivalents of each other, only a relatively few synonymies have been axiomatic, and among workers, there has been significant disagreement as to how inclusive (or exclusive) generic concepts should be in the Heptageniidae. For example, Jensen (1972), in the only comprehensive (at the time), but unpublished study of the genera of the Heptageniidae, considered 22 extant genera of Heptageniidae, excluding *Arthroplea* and *Pseudiron*. An additional 13 genera have been described in Heptageniidae since 1972, resulting in 35 extant genera that could be recognized if the interpretations of Jensen were to be followed. On the other hand, Kluge (1988), in a partial revisionary study, recognized only six extant genera of Heptageniidae, excluding *Arthroplea* and *Pseudiron*, and only provisionally allowed another eight genera that he did not study.

For lack of decisive studies on the higher classification of the Heptageniidae applicable to the Western Hemisphere fauna, McCafferty et al. (1990), McCafferty and Lugo-Ortiz (1996), McCafferty (1996), McCafferty and Randolph (1998), and Randolph and McCafferty (2000), as well as all other North American workers, continued to use a *status quo* liberal generic classification with respect to documenting the Ephemeroptera fauna. Likewise, many workers in other parts of the world, for example, Studemann et al. (1992) in Switzerland, Belfiore (1994) in Italy, Kang and Yang (1994) in Taiwan, McCafferty and de Moor (1995) in South Africa, Dudgeon (1999) in tropical Asia, Bauernfeind and Humpesch (2001) in middle Europe, and Haybach and Malzacher (2002) in Germany, have not followed the highly conservative generic classification.

Both the Jensen (1972) and the Kluge (1988) studies of heptageniid genera made excellent contributions to our knowledge of variation and radiation within the family. They, as well as Tshernova et al. (1986), also recognized certain nomenclatural problems resulting from the fact that earlier workers had not taken a global perspective and therefore had sometimes used different taxonomies for the same taxa in different parts of the world. The Kluge (1988) work, in particular, introduced many new morphological characters of potential value in comparing taxa. Still, choosing between the overall interpretations of generic limits in the Jensen or Kluge revisions is tedious and laden with ambiguity not only because the interpretations are so disparate, but also because any cladistic basis of either is not apparent and strict rules of phylogenetic classification were not incorporated. Heptageniidae taxonomy can be additionally exasperating because of the recent inordinate number of generic assignments that have been applied to many species and the seeming lack of consensus among Ephemeroptera taxonomists. To give an extreme example of this situation, the Asian species originally described as *Epeorus levis* Navás has been placed in five different genera in recent years. Equivalent names have included *Cinygmula zachvatkini* Tshernova, *Cinygma zachvatkini*, *Ecdyonurus zachvatkini*, *Cinygmia zachvatkini*, and *Ecdyonurus levis* (Tshernova 1974, Tshernova et al. 1986, Braasch and Soldán 1988a, Kluge 1988).

Although Jensen and Edmunds (1973) proposed a tentative phylogeny for

certain of the genera treated in Jensen's (1972) work, it was to a large degree based on phenetics and the equal weighting of ancestral and derived characteristics. The basis of Kluge's (1988) recognition of numerous synonymies was not always clear, but he apparently followed an arbitrary gap rule that genera had to be clearly separable in both the larval and adult stage, although there were inconsistent cases where he synonymized monophyletic groups of species that were separable as such (e.g., *Stenonema* Traver). The inappropriateness of gap criteria for recognizing taxa in phylogenetic systems was addressed by Wiley (1981) in general and by McCafferty (1991b) and McCafferty et al. (2003) with particular reference to Ephemeroptera. Kluge (1988) also discounted the use of a character state for defining genera if it was not diagnostically unique, essentially disallowing the use of any apomorphy if it was apparently convergent in any other lineage. This strict and, we believe, untenable philosophy would make ascertaining the phylogeny of almost all large taxonomic groups intractable, and it evidently resulted in an unresolved phylogeny of Heptageniidae (Kluge 1993). Presumption that Kluge's (1988) higher classification of Heptageniidae was based on phylogeny is not supportable. Regarding Kluge's (1993) proposed phylogeny, it suffers because two or more possible origins of certain branches were given, apomorphies used were not always consistently present throughout his hypothesized branches, and a considerable number of species and species groupings were not considered.

Other attempts at determining relationships among Heptageniidae, such as analyses by Zurwerra et al. (1987), Whiting and Lehmkuhl (1987b), Tomka and Elpers (1991), Masselot and Nel (1999), and Chun (2000) were based on only a fraction of the taxa, were often geographically limited, and were fragmentary to various degrees. Thus, they may not be reliable in describing evolution within the Heptageniidae, and some have little application to global higher classification. Tomka and Elpers (1991) did, however, suggest some alternatives for large groupings of genera that were left unresolved.

Another factor contributing to the historical confusion regarding Heptageniidae taxonomy involves the generic assignment of several Southeast Asian species. Works such as those of Braasch and Soldán (e.g., 1986abc) and Soldán and Braasch (1986) undoubtedly contributed considerable new descriptive data regarding this particular fauna and have been invaluable in our current study. Nonetheless, our preliminary work indicated that correct generic identification was problematic in some of these papers, and such problems often could be traced to problems originating in Ulmer's (1924, 1939) studies of the Sunda Islands fauna.

Our primary objective in this study is to help rectify the tenuous state of the higher classification of the Heptageniidae by providing workers with the most informative higher classification possible, including the recognition of all monophyletic species groups defined by apomorphies and recognizable at appropriate taxonomic levels within the constraints of phylogenetic classification. To accomplish this, we corroborate or refute previous generic synonymies, and establish any new generic synonyms as necessary, thus generating a working group of operational taxonomic units for the purposes of cladistic analysis and comparison. From the most parsimonious cladogram of these units, we present a strict phylogenetic higher classification of monophyletic genera within a scheme of infracategories that facilitates use of the classification for hypothesizing and un-

derstanding the historical evolution of the family. Our results, below, show that many of the previously named genera of Heptageniidae are not only monophyletic groups, but can be considered valid genera within the framework of phylogenetic classification. The phylogeny and classification presented provide a framework for any further classification of yet to be discovered taxa, particularly in terms of species placement and resolving whether or not any possibly new genera are allowable within the construct of a strict phylogenetic classification.

Our treatment herein is limited to cladistic characters and therefore neither includes comprehensive comparative morphology of each taxon nor presumes to duplicate applicable parts of the descriptive works of Jensen (1972), Kluge (1988) and many others. We have necessarily concentrated our effort on type species (the *bona fide* representatives) of our operational taxonomic units because it would be impossible to examine material of all described species in the family. Fortunately, we have had vast materials from throughout the world to examine, some of this being borrowed genotypes from European museums, but mainly consisting of the large holdings of the Purdue Entomological Research Collection, including the collections studied and later donated to us by S. L. Jensen and George F. Edmunds. Still, because there remain numerous dubious or poorly documented species that we have been unable to study or that are based on only the larval or adult stage, it will be up to regional specialists in the future to determine the proper generic classification of many species within the framework given here. We cannot cite formal new combinations for every species possibly affected by the generic revision, although generic assignment will be implied for many nominal species, and new combinations affecting species that we have examined are given herein, under Material Examined.

This paper will be followed by two complimentary studies on the world Heptageniidae. Although diagnoses of taxa, other than via cladistic characteristics, are not covered herein and illustrations are not given at this time, the first of the following complementary studies will include illustrated diagnoses and keys to the genera, and as such will provide additional clarification of phylogenetic characterization as well as introduce many other characteristics of purely diagnostic value. The second complementary study will involve a world catalogue of Heptageniidae species, covering their entire nomenclatural history, and updating necessary specific recombinations and synonyms.

DEFINITION OF THE STUDY GROUP

The Heptagenioidea is characterized by external morphology as follows (modified from McCafferty 1991a): In the larvae, the maxillary and labial vestiture tends to be highly developed, segments 2 and 3 of both the maxillary and labial palps are fused to various degrees, the labial palps are broadened, the forewingpads are not broadly separated at the base, and at least abdominal gills 2-5 consist of a lamella, with a basal filamentous tuft. In the adults, the hindtibiae are relatively elongate, and some cubital intercalaries of the forewing run nearly parallel to CuA (not at near right angle to CuA).

Apomorphies associated with the Heptageniidae complex (Heptageniidae + Arthropleidae + Pseudironidae) include in the larvae, a dorsoventrally flattened body and a depressed and laterally expanded epicranium. These characteristics are also evident in the alate stage, particularly in terms of relative head flattening

and the relative width of the medio-elongate depression of the furcasternum of the mesothorax. Larval flattening is also independently present in some Leptophlebiidae and pannote mayflies (members of the suborder Furcatergalia) that are very distantly related to the Heptagenioidea. Also in larvae of the Heptageniidae complex, filtering foreleg setae and maxillary gills, which are generally present in more plesiotypic Heptagenioidea families, are absent. Although filtering setae (present along the front margin of the larval forelegs of plesiotypic Heptagenioidea) are absent in the Heptageniidae complex, there is a strong tendency for well-developed hairlike setae to be present along the hind margin.

In the alate stages of the Heptageniidae complex, CuP and A_1 veins of the forewing are more elongate than in other Heptagenioidea; for example, CuP can be seen as ending variously beyond the midlength of the anal margin. Two pairs of intercalary veins are also present (rarely secondarily reduced to one pair) and at least the first pair ends in the outer margin of the forewing. The relative length of CuP varies outside the Heptagenioidea, and two pairs of cubital intercalaries are found in common with ancestral lineages of the Oligoneuriidae, the nearest familial relative of the Heptageniidae complex [secondarily lost in apotypic Oligoneuriidae due to the development of vein gemination (McCafferty 1991a)]. Two pairs of cubital intercalaries are also found in the pisciform families Ametropodidae and Metretopodidae, which otherwise are generally dissimilar to the Heptageniidae complex.

The cladistic relationships within the Heptageniidae complex were shown by Wang and McCafferty (1995a). The Heptageniidae s.s. is further defined, and differentiated from the Pseudironidae, by complete articulation of the first tarsal segment of the adult hindleg with the tibia. It is further and ultimately defined, and differentiated from the Arthropleidae and Pseudironidae, by the base of the larval labium being enlarged and the broad labial palp segment 1 being obliquely and subterminally fitted to the labial base. Additional characteristics that will differentiate Heptageniidae include the relatively short larval claws in combination with genital forceps with two, rather than one, relatively short terminal segments (occasionally segment 3 elongated); gill lamellae without an elongate central appendage (present in Pseudironidae); and maxillary palps that are not extremely elongated (extremely elongated in Arthropleidae).

GENUS-GROUP SYNONYMS

Previously demonstrated and herein confirmed objective genus-group synonyms in the Heptageniidae include the following: The name *Cosmetogenia* was inadvertently used by Eaton (1883) for *Compsoeuria* Eaton (1881). Eaton (1868b) emended the name *Ecdyonurus* Eaton (1868a) to *Ecdyurus*, which was later shown by Schoenemund (1930) to be an unnecessary emendation. The type of *Sigmoneuria* Demoulin (1964), *S. amseli* Demoulin, was synonymized with *Heptagenia perflava* Brodsky by Kluge (1987), thereby creating a synonymy of *Sigmoneuria* with *Heptagenia* Walsh (1863), which was only later formally cited by Kluge (1988). Braasch and Soldán (1984a) referred the type species of *Ecdyonuroides* Dang (1967), *Ecdyonurus sumatranus* Ulmer (1939), to the genus *Thalerosphyrus* Eaton (1881). The resultant objective synonymy of the genus *Ecdyonuroides* with *Thalerosphyrus* appears substantial.

Ali (1970) proposed the name *Eatonia* as a genus of the family Heptageniidae.

However, not only was that name preoccupied as *Eatonia* Bengtsson (1904) [= *Parameteletus* Bengtsson (1904) (Siphonuridae), see Bengtsson (1930)], but the species to which Ali's genus was referable belongs to *Isonychia* Eaton (1871), in the family Isonychiidae (see Hubbard and Peters 1978).

Gillies (1963, 1984) proposed the synonymy of *Notonurus* Crass (1947) with *Compsoneriella* Ulmer (1939). As elucidated by Gillies (1984), this synonymy is based on substantial morphological evidence. We have corroborated that equivalency with our observation of the same apomorphic character states associated with both names, despite Demoulin's (1970) argument that the two are distinct. Braasch and Soldán (1986b) further synonymized *Compsoneriella* (and *Notonurus*) with *Compsoneria* Eaton (1881). That proposed revision is not supportable because the type species of *Compsoneria*, *C. spectabilis* Eaton, is phenetically and, as will be shown below, phylogenetically far removed from *Compsoneriella* and *Notonurus*. However, it should be noted that whereas the type species of *Compsoneria* is distinct, all other species that have been described or placed in *Compsoneria* are referable to other genera, possibly including, for example, *Thalerosphyrus* (see below), *Atopopus* Eaton (1881) (see Wang and McCafferty 1995b), *Asionurus* Braasch and Soldán (1986a) (see below), or even *Ecdyonurus* (see below and McCafferty 2004). For instance, the most recently described species placed in *Compsoneria*, *C. taipokauensis* Tong and Dudgeon (2003) from Hong Kong, is clearly not related to *Compsoneria* and can be placed to the *simplicioides* group of *Ecdyonurus*, as *E. taipokauensis*, n. comb., based on the species description. Some additional Asian species that must be re-examined before they are accurately placed to genus include, for example, *Afronurus javanicus* Ulmer, *A. sangangensis* You et al., and *Asionurus petersi* Braasch and Soldán.

Eaton (1881) based the genus *Thalerosphyrus* on adults of *T. determinatus* (Walker). Ulmer (1924, 1939) studied additional material from Southeast Asia, including larvae (Ulmer 1939), that he identified as this species. This material, however, is not *T. determinatus*, but instead is representative of an additional species of *Thalerosphyrus* that Ulmer (1939) identified and recombined as *T. sinuosus* (Navás) (originally *Ecdyonurus sinuosus* Navás). Ulmer (1939) also described the genus *Compsoneriella* from Southeast Asia on the basis of adults and reared larvae of its type, *C. thienemanni* Ulmer. The adult of the true *C. thienemanni*, however, is essentially similar to the adult of the true *T. determinatus*, and in fact may be the same species. A larval comparison of the two can not be made because the true larval stage of *T. determinatus* remains unknown. Nevertheless, it is obvious from comparison of other *Thalerosphyrus* larvae that *Compsoneriella* is equivalent to *Thalerosphyrus*, n. syn. Obviously then, *Notonurus* (see above) is also equivalent to *Thalerosphyrus*, n. syn. We do not recognize the synonymy of *Thalerosphyrus* with *Ecdyonurus* by Kluge (1988) because both are distinguishable by apomorphies and worthy of cladistic consideration.

For the same reason, we also do not recognize the synonymy of *Ecdyonuroides* Dang (1967) (author sometimes incorrectly cited as Thanh) with *Ecdyonurus* by Kluge (1988). We do, however, recognize the objective synonymy of *Ecdyonuoides* with *Thalerosphyrus* resulting from the recombination by Braasch and Soldán (1984a) of the type species of *Ecdyonuroides*, *Ecdyonurus sumatranus* Ulmer, in the genus *Thalerosphyrus* Eaton. Our *Thalerosphyrus* concept is therefore re-

stricted to *T. determinatus* and *T. sinuosus*, along with species originally described as *Thalerosphyrus* from Africa and Madagascar (see McCafferty 2003a), species that historically have been placed in *Compsoeuriella* and *Notonurus* [e.g., see African species recombinations (McCafferty 2003a)], and species originally placed in *Ecdyonuroides*. Certain other species that have been described or placed in *Thalerosphyrus*, i.e., *T. bishopi* Braasch and Soldán and *T. torridus* (Walker), can not be confirmed as *Thalerosphyrus* because critical data associated with them have not been available. They may possibly belong to *Asionurus* as it is discussed below.

Our conclusion that Ulmer (1939) incorrectly associated the larvae he referred to as *Thalerosphyrus sinuosus* and *T. determinatus* is based on our observation that the dorsal abdominal color patterns of the adult he referred to as *T. sinuosus* matches that of the larva he referred to as *T. determinatus*, not *T. sinuosus*. Braasch and Soldán (1986a), also recognizing that the larvae Ulmer called *T. sinuosus* were not associated correctly with the adults of that species, gave those larvae the new name *Asionurus ulmeri* Braasch and Soldán. We maintain that the adults and the larvae that Ulmer (1924, 1939) called *T. determinatus* are referable to *T. sinuosus*. The larvae of *Asionurus* appear distinct from those referable to *Thalerosphyrus*; however, the only species that are clearly referable to the strict concept of *Asionurus*, *A. primus* Braasch and Soldán (the type of the genus) and *A. ulmeri*, remain unknown in the adult stage. *Asionurus* is not equivalent to our concept of *Ecdyonurus*, although it should be noted that Kluge (1988) proposed a synonymy of *Asionurus* with his broad concept of *Ecdyonurus*.

The name *Afghanurus* was proposed by Demoulin (1964) for adults only. Kluge (1980) claimed to have discovered the larvae associated with Demoulin's concept [described as *Ecdyonurus vicinus* (Demoulin)]; however, we believe Kluge's species was different than Demoulin's, and we believe it is actually a species that would have been attributable to *Paracinygmula* Bajkova (1975). Nevertheless, McCafferty (2004) showed that indeed Demoulin's and Kluge's concepts of *Afghanurus*, Bajkova's concept of *Paracinygmula*, and the concept of *Nixe* [subgenus *Akkarion* Flowers (1980)] were all encompassed within the concept of *Ecdyonurus* as it is treated herein. Although all of the above constitute a distinctive grouping of species (the *simplicioides* species group) within *Ecdyonurus*, they could not be clearly shown to represent a monophyletic grouping separate from those specialized *Ecdyonurus* having developed thoracic flanges in the larvae and extreme sclerotization of the penes. Thus, the *simplicioides* species group can not stand alone as a separate genus or subgenus under rules of strict phylogenetic classification, and synonymies are corroborated as had been presented by Tshernova (1978), Kluge (1980), and Tshernova et al. (1986). However, we do not agree with the synonymies of *Electrogena* Zurwerra and Tomka (1985), *Leucrocota* Flowers (1980), *Nixe* s.s. Flowers (1980), and *Notacanthurus* Tshernova (1974) with *Ecdyonurus* as first proposed by Tshernova et al. (1986). All of these are monophyletic groups distinct from *Ecdyonurus* that should be cladistically analyzed.

Maccaffertium Bednarik (1979), *Macdunnoa* Lehmkuhl (1979), *Stenacron* Jensen (1974), and *Stenonema* Traver (1933) were synonymized with *Heptagenia* Walsh (1863) by Kluge (1988) and considered part of a so-called *Stenonema* subgeneric group. We are able to substantiate all of these groups, however, as distinct monophyletic entities worthy of cladistic analysis. *Kageronia* Matsamura

(1931) was placed as an objective junior synonym of *Heptagenia* by Imanishi (1935) via the synonymy of the type species of *Kageronia* (*K. suzukiella* Matsumura) with *H. kihada* Matsumura. *Kageronia* was later relegated to subgeneric status under *Heptagenia* by Tshernova et al. (1986). We have been able to demonstrate that *Kageronia* is a clearly separable monophyletic group worthy of cladistic analysis. *Parastenacron* Kluge (1983b), from an unpublished abstract, was listed by Braasch and Soldán (1988b) as a subgenus of *Heptagenia*. The name *Parastenacron*, although technically unavailable, is equivalent to *Kageronia* Matsumura (1931), n. syn.

Evans et al. (1985) described the extremely specialized species *Heptagenia culacantha* Evans, Botts and Flowers from eastern North America. Although this species might presumably be placed as a separate new genus on the basis of phenetic characteristics associated with its larval stage, our study indicates that such a move would lead to a paraphyletic *Heptagenia* lacking a separate apomorphy consistent throughout but not found in *H. culacantha*. Therefore *H. culacantha* is considered a specialized lineage within *Heptagenia*. Other such instances in Heptageniidae, involving very specialized and therefore distinctive lineages that are present within genera but whose nominal segregation would result in paraphyletic classification, are found, e.g., in *Epeorus* Eaton and *Cinygmula* McDunnough (see below). Other examples of purposely avoiding paraphyletic generic classification may be found in a number of Ephemeroptera families [see, for instance, a classic example involving the variously specialized Baetidae genus *Acanthiops* Waltz and McCafferty (Lugo-Ortiz et al. 2001)].

Burks (1953) first synonymized the names *Iron* Eaton (1883) and *Ironopsis* Traver (1935) with *Epeorus* Eaton (1881). The former two names have had a vacillating history of being and not being recognized as genera. We have not been able to associate consistent concepts of these names with synapomorphies that are not subject to clinal variation, and therefore we are recognizing these two synonymies. Burks (1953), Edmunds et al. (1976), and Kluge (1988) have relegated the names *Iron* and *Ironopsis* to subgeneric status under *Epeorus*, and if they are recognized as such, such taxa assume questionable phylogenetic status by injecting paraphyly into subgeneric concepts. Our present analysis is in agreement with Jensen's (1972) refutation of these names as either genera or subgenera, based on findings of numerous undescribed species or stages that are characteristically intermediate. In other words, any homogeneous characterization that may be suggested by localized taxonomic comparisons belies the clinal gradation that becomes evident on a global scale.

Some Asian species of *Epeorus* have been treated by Tshernova (1981) and others as an additional subgenus *Belovius* Tshernova (1981) [cited as a genus by Hubbard (1990)] under the genus *Epeorus*. However, until a clarification of species relationships is provided via a world revision of *Epeorus*, as suggested by Edmunds and Allen (1964), we are obliged to continue to treat *Epeorus* as a large genus encompassing several specialized species lineages within it, with any currently suggested nominal subgroups or derived genera either being unstable and grading to each other or resulting in paraphyletic classification.

Ironodes Traver (1935) is a genus that was placed into synonymy with *Epeorus* but retained as a subgenus of the latter by Burks (1953) and others. Jensen (1972) and others (e.g., Edmunds et al. 1976), however, have considered it a full and separate genus based on its distinctive larval characterization. We have

confirmed that it is a legitimate monophyletic group worthy of cladistic analysis. Lestage (1924) described the genus *Afronurus* Lestage from Africa. Kimmins (1937) proposed the name *Cinygmina* Kimmins for a single species from India known from adults only with somewhat different penes. The subsequent description of the larvae of *Cinygmina* by Wu et al. (1986) shows that there are no substantive larval differences between the two, and recent descriptions of numerous additional species classified as *Afronurus* or *Cinygmina* from Asia indicate, at most, species level differences with considerable character gradation, including size, shape and degree of separation of the penes. Because of this and the fact that we cannot identify a consistent apomorphy in *Afronurus* that would delineate it as a group from *Cinygmina*, we must consider *Cinygmina* synonymous with the genus *Afronurus*, n. syn. Furthermore, by recognizing *Afronurus* as a distinct monophyletic entity worthy of cladistic consideration, we do not recognize a previous synonymy of *Cinygmina* with *Ecdyonurus* by Tshernova et al. (1986) or the previous synonymy of *Afronurus* with *Ecdyonurus* by Kluge (1988).

Matsumura (1931) proposed the name *Cinygmoides* for a Japanese species based only on the adult stage. Ueno (1931) considered the name of doubtful status, and Edmunds and Traver (1954) listed the name as a junior synonym of *Ecdyonurus*, but no explanation was given, and we presume this was a new synonymy at the time. In any case, the synonymy is not supportable. Although Matsumura's description of *Cinygmoides* is very incomplete, and the specimen is not available to us for study, the whole dorsal habitus figure accompanying the description has provided us with enough information to hypothesize its affinities. Characters, including the relative length of the foreleg, foreleg segmentation, and, most importantly, the distinctive anastomose venation in the distal costal area of the forewing that gives rise to two layers of cellules, have led us to conclude that *Cinygmoides* is equivalent to *Cinygma* Eaton (1885), n. syn.

Although the larval stage is unknown, the adults of *Epeiron* Demoulin (1964) are similar in all essential respects to *Cingymula* McDunnough (1933), including details of the mesonotum, tarsal segment size in the forelegs, and male genitalia. We thus consider *Epeiron* to be equivalent to *Cinygmula*, n. syn. A synonymy of *Epeiron* with *Epeorus* given by Jensen (1972) and first published by Tshernova and Belov (1982) is not supportable. Our examination of the vestige of the median terminal filament of the paratype of the type species *Epeiron umseli* Demoulin indicated that the median terminal filament was developed in the larval stage. This is not the case in *Epeorus* larvae. A synonymy of *Epeiron* with *Rhithrogena* Eaton (1881) (as subgenus *Rhithrogena* s.s. of genus *Rhithrogena*) was first proposed by Kluge (1988) and elaborated by Sartori and Sowa (1992). The Sartori and Sowa concept of *Rhithrogena*, however, was very broad and included our current concept of the genus *Cinygmula*. Along with *Cinygmula*, Kluge (1988) also considered *Paegniodes* Eaton (1881) as a subgenus of *Rhithrogena*.

The monobasic *Ororotsia* Traver (1939) was placed into synonymy with *Cinygmula* by Jensen (1972), but retained under new status as a subgenus of the latter. Kluge (1988) also placed *Ororotsia* in synonymy with *Cinygmula*, which he considered a subgenus of *Rhithrogena*. Although larval apomorphies associated with *Ororotsia* would appear to be sufficient for its recognition as a separate superspecific taxon, there are no consistent apomorphies associated with *Cinygmula* that are not also present in *Ororotsia*, indicating that the single species previously known as *O. hutchinsoni* Traver is a specialized, large-headed

form within *Cinygmula* and that any recognition of *Ororotsia* as a separate taxon would essentially result in a restricted, paraphyletic *Cinygmula*. This is not an option under rules of strict phylogenetic classification, and complete dissolution of *Ororotsia* is warranted. Because Jensen's (1972) synonymy is technically not published, we here formalize the synonymy of *Ororotsia* under *Cinygmula*, n. syn.

The name *Epeorella* was proposed for male and female adults of a heptageniid species from Borneo by Ulmer (1939). Ulmer believed them similar to *Epeorus*, but because that genus was not known from Southeast Asia at that time, he erected a new genus for them. Several species of *Epeorus* are now known from the region, and our examination of Ulmer's type specimens of *Epeorella borneonia* Ulmer, indeed, shows them to belong to *Epeorus*. We therefore find *Epeorella* to be equivalent to *Epeorus*, n. syn. Adult characteristics of Ulmer's *E. borneonia* are in agreement with those associated with the genus *Epeorus*, including male genitalia and forelegs. Also, the vestiges associated with the adults indicate that the larvae were two-tailed, and that median tubercles were present on at least larval abdominal terga 6-8. This latter characteristic was found in *Epeorus* from Vietnam by Braasch and Soldán (1984b).

The name *Rhithrogeniella* was proposed by Ulmer (1939) for a single Southeast Asian species known only in the adult stage. The type species of *Rhithrogeniella*, *R. ornata* Ulmer, possesses the essential characteristics associated with *Rhithrogena*. We therefore recognize *Rhithrogena ornata* (Ulmer), n. comb., and thereby place *Rhithrogeniella* as a synonym of *Rhithrogena*, n. syn. *Rhithrogeniella tonkinensis* Soldán and Braasch, however, is clearly characteristic of the genus *Ecdyonurus*, as demonstrated by characteristics of the subimago, larva, and egg, which formed the basis of the original description of this species (Soldán and Braasch 1986). *Ecdyonurus tonkinensis*, n. comb., is thus established.

Our final consideration of generic synonymy results from a new species synonym. Whiting and Lehmkuhl (1987b) and McCafferty and Provonsha (1988) suggested that *Acanthomola* Whiting and Lehmkuhl (1987b), which had been known only from the larval stage of the type species *A. pubescens* Whiting and Lehmkuhl, represented the unknown larval stage of *Anepeorus rusticus* McDunnough. We concur based on compelling circumstantial evidence, and because *A. rusticus* is the type species of *Anepeorus*, the formal synonymy of the two species, *Anepeorus rusticus* [= *Acanthomola pubescens*, n. syn.], also places *Acanthomola* as a junior objective synonym of *Anepeorus*, n. syn. The combination of similar unique locales of the adults and larvae in large rivers of the western Missouri, Colorado, and Saskatchewan River Drainages, and the uniquely specialized morphologies of adults and larvae, both of which occupy the same precise cladistic position amongst Heptageniidae, have led us to this conclusion.

Anepeorus simplex (Walsh) is related to *A. rusticus* and is the only other species that has historically been placed in *Anepeorus*. Although for many years (and in all previous broad-scale studies of heptageniid genera), larvae of what are now known to be those of *Raptoheptagenia cruentata* (Walsh) (see Whiting and Lehmkuhl 1987a) were mistakenly thought to be the larvae of *A. simplex*, the actual larval stage of *A. simplex* was first described as *Spinadis wallacei* Edmunds and Jensen (1974) and designated as the type species of the monotypic *Spinadis* Edmunds and Jensen (1974). McCafferty and Provonsha (1988) showed by a reared association (McCafferty and Provonsha 1984) that the larva of *Spinadis*,

which had been undescribed in the adult stage, and the adult of *A. simplex*, which had actually been undescribed in the larval stage, were in fact stages of the same species, and thus synonymized *S. wallacei* with *A. simplex* (and thereby *Spinadis* with *Anepeorus*). We are able to recognize a reestablished monotypic *Spinadis* (represented by *S. simplex*, n. comb.) and the monotypic *Anepeorus* (represented by *A. rusticus*) as lineages distinctive in both the larval and adults stages (see McCafferty and Provonsha 1985) and worthy of further cladistic consideration.

OPERATIONAL TAXONOMIC UNITS

The 29 species group operational taxonomic units (OTUs) of Heptageniidae that we can identify as monophyletic species groups are listed in Table 1. They correspond to many genus group taxa (genera and subgenera) that have been historically proposed for the family Heptageniidae, and they are sustained by having a unique cumulative set of apomorphies associated with them. In order to clarify our OTU concepts, the relevant type, or reference species of each OTU is also listed in Table 1 along with references to the first appropriate larval or adult description or applications for these life history stages if they appeared subsequent to the original description. Synonyms, including those given above, or other name equivalencies with references and type species are also indicated as necessary for each OTU. A history of genus group synonymy, the numerous synonyms we recognize here, and those synonyms we institute at this time are detailed above. Their morphological bases are in part expressed by the character state distributions used for cladistic analysis. Morphology will be more completely elucidated in Part II of this study, which will deal with diagnoses. Although there are phenetic and apomorphic characters states that would distinguish each of these OTUs as genera, only cladistic analysis can show if they are allowable as such within a scheme of strict phylogenetic higher classification (see e.g., Wiley 1981), and this indeed has been much of the challenge of the present study.

PHYLOGENY

The deduced, most parsimonious cladogram of our operational taxonomic units of Heptageniidae is given in Figure 1. Each end point in the cladogram represents a monophyletic species group definable by a cumulative series of apomorphies associated with it and its parental branches. The numbers shown on branches of the cladogram indicate shared apomorphy sets associated with subsequent nodes or OTUs. These apomorphies along with associated plesiomorphies are detailed in Table 2. The outgroup used to deduce character state polarity included other non-specialized Heptagenioidea. Any instances of homoplasy, which are inevitable in the phylogeny of a taxon of this size, are indicated in Table 2. Although cladistic hypotheses and morphological character bases for them are self-evident by using Figure 1 and Table 2 in conjunction with each other, further elucidation of the morphology associated with the clades and lineages will be presented in Part II, which will deal primarily with higher taxa diagnoses. The *Asionurus* branch in Figure 1 is shown as a dashed line, because the absence of adult characteristics precludes cladistic confirmation of its proposed phylogenetic position, which had to be deduced from the overall similarity of its larvae with those of *Thalerosphyrus* and *Atopopus*.

CLASSIFICATION AND DISCUSSION

The phylogenetic classification derived from the cladogram is given in Table 3. Taxonomic categories are either strictly subordinated (each pair of daughter lineages considered taxa at the next lower taxonomic category) or sequenced (lineages sequentially branching along a similar asymmetrical line of the cladogram placed at the same categorical rank) [for the explanation of this phylogenetic classificatory convention, see Nelson (1972, 1973)]. In either case, the higher classification we have adopted is strictly phylogenetic because the cladogram can be exactly reproduced from the linear Linnaean hierarchical classification presented in Table 3 (when sequencing, taxa at the same rank are listed in order of their sequence of derivation, and thus any numerical coding system of taxa is unnecessary). The recognition of appropriate subfamilial and tribal infracategories has allowed each of the 29 operational taxonomic units to be recognized at the genus level of classification.

Within the Heptageniidae, three major groupings are sequenced as subfamilies of Heptageniidae. One initial basal branch of the cladogram of Heptageniidae (Fig. 1) forms a clade in which all lineages have a unique mesosternum in the adult stage and subquadrate glossae and outer incisors with a single tooth in the larval stage. This concept is recognized as the subfamily Ecdyonurinae. This earliest available family-group name for such a grouping was provided by Ulmer (1920), but technically it takes the 1905 date of Jacobson and Bianki's (1905) Ecdyurinae, which had been rooted with the unnecessary replacement genus-group name *Ecdyurus* (= *Ecdyonurus*) (see discussion of generic synonymies, above). Ecdyonurinae encompasses the following genera: *Afronurus*, *Asionurus*, *Atopopus*, *Ecdyonurus*, *Electrogena*, *Leucrocuta*, *Nixe*, *Notacanthurus*, *Siberionurus* McCafferty, and *Thalerosphyrus*. The opposite branch (Fig. 1), typified by larvae that are devoid of any scattered or non-ordered setae on the ventral face of the galealacinia is further divided into two basal daughter branches, each of which form additional large clades of genera. By use of the sequencing convention, both of these latter clades are also recognized at the subfamilial rank. The clade recognized as the subfamily Heptageniinae Needham (1901), s.s., consists of the following genera: *Compsoeuria*, *Dacnogenia* Kluge, n. stat., *Heptagenia*, *Kageronia*, *Maccaffertium*, n. stat., *Macdunnoa*, *Raptoheptagenia*, *Stenacron*, *Stenonema*, and *Trichogenia* Braasch and Soldán. The clade recognized as the subfamily Rhithrogeninae consists of the following genera: *Anepeorus*, *Bleptus* Eaton, *Cinygma*, *Cinygmula*, *Epeorus*, *Ironodes*, *Paegniodes*, *Rhithrogena*, and *Spinadis*. Rhithrogeninae Lestage (1917) is the earliest available family-group name that can be applied to this latter group of genera.

Within the Ecdyonurinae, we recognize clades resulting from the initial four sequenced branches (Fig. 1) as the tribes Ecdyonurini, s.s., Leucrocutini, n. trib., Notacanthurini, n. trib., and Atopopini, n. trib. The tribe Ecdyonurini, which represents one of the initially branched clades within Ecdyonurinae, has well-sclerotized penes and is further divided into two branches (Fig. 1) forming sister clades recognized as the Holarctic genus *Nixe* and the Holarctic-Oriental-Neotropical genus *Ecdyonurus* [see further details in McCafferty (2004)]. The tribe Leucrocutini has differently specialized genitalia and is divided into two branches (Fig. 1) recognized as the northern Asian genus *Siberionurus* and the North American genus *Leucrocuta* [see further characteristics of these genera in McCafferty

(2004)]. The tribe Notacanthurini is divided into two branches (Fig. 1), the first being a clade recognized as the Asian genus *Notacanthurus* and the second being a clade recognized as the Palearctic genus *Electrogena*. The branch opposite the Notacanthurini clade is recognized as the tribe Atopopini and is further sequentially branched (Fig. 1) into four clades, recognized respectively as the mainly Oriental-Afrotropical genus *Afronurus*, the Oriental genus *Asionurus*, and the sister clades consisting of the Oriental-Afrotropical genus *Thalerosphyrus* and the Oriental and ostensibly northern Australian genus *Atopopus* (see Wang and McCafferty 1995b).

The biogeography of the Ecdyonurinae, with consideration of the Laurasian origin of the family Heptageniidae, supports the hypothesized cladistic relationships and the resultant phylogenetic classification. For example, from the above, it can be seen that the plesiotypic tribes in the Ecdyonurinae are essentially concentrated in the Holarctic area with some minor infiltration into the Oriental region and Neotropical region. In particular, evolution of northern Asian *Siberionurus* and North American *Leucrocuta* sister genera may have been associated with Northern Hemisphere geographic vicariance. The Holarctic nature of both genera of the Ecdyonurini, including certain circumpolar species (McCafferty 2004), supports the presumed Laurasian history of the family, suggesting some relatively old Holarctic lineages and possibly some trans-Bering dispersal or colonization during the Tertiary, particularly in that *Ecdyonurus* species in the Nearctic are restricted to western North America. The two most atypically positioned tribes of the Ecdyonurinae, Notacanthurini and Atopopini, are restricted to the Old World, with the most atypical tribe Atopopini being radiated primarily in the tropics, including a possible dispersal and colonization of *Atopopus* into northern Australia. In addition, *Afronurus* has penetrated northward into parts of the Palearctic region.

Phenetic subgroups within the genus *Ecdyonurus* are easily identifiable [for example, the *simplicoides* species group (McCafferty 2004) versus the European species groups (e.g., Bauernfeind and Humpesch 2001)]. The lack of consistent synapomorphies associated with each of the groups, however, precludes their separation into cladistically supportable taxa that do not result in paraphyly.

Within the subfamily Heptageniinae, whose members share somewhat modified maxillae, one of the two basal branches (Fig. 1) forms a clade recognized as the tribe Componeurini, n. trib., and further branches into sister lineages recognized as the Oriental genera *Componeuria* and *Trichogenia*. The three sequential branches in the opposite clade (Fig. 1) form daughter clades that are recognized respectively as the tribes Heptageniini, s.s., Kageroniini, n. trib., and Stenonematini, n. trib. The tribe Heptageniini consists of three sequential branches (Fig. 1) that are recognized respectively as the clade equivalent to the mainly Holarctic genus *Heptagenia*, and a pair of sister branches equivalent to the Palearctic and Oriental clade (based on undescribed species we have examined from Thailand and Afghanistan) that forms the genus *Dacnogenia* and the Nearctic lineage that represents the genus *Raptoheptagenia*. The Kageroniini consists of sister clades (Fig. 1) recognized as the Palearctic genus *Kageronia* and the eastern and central Nearctic genus *Stenacron*. Stenonematini is an essentially eastern and central Nearctic grouping that consists of three sequential branches (Fig. 1), a basal clade recognized as the genus *Macdunnoa*, and opposite it, sister branches represented by the lineage recognized as the genus *Stenonema* and by the clade

represented by the genus *Maccaffertium*, the latter of which has one lineage that has infiltrated western North America and another that has infiltrated the Neotropics.

Within the Heptageniidae, the *Heptagenia* clade is both the most generalized and the most widespread geographically, being Holarctic but also having penetrated somewhat the Oriental region. Presumably the hypothetical common ancestor of the subfamily was very *Heptagenia*-like. The basal branched tribe Compsoeuriini is restricted to the Oriental region. Other generic and tribal groups are made up of either Eastern or Western Hemisphere lineages, but predominantly Western Hemisphere lineages. Just as in the Ecdyonurinae, there are significant Old and New World pairs of sister genera whose origins may have been facilitated by vicariance, i.e., *Dacnogenia* and *Raptoheptagenia* in the Heptageniini and *Kageronia* and *Stenacron* in the Kageroniini. The apotypic tribe Stenonematini is restricted to the Nearctic, with some slight infiltration into the Neotropics. Bednarik and McCafferty (1979) indicated a relatively recent Nearctic origin and post-glacial radiation in this group.

Of note is the progression of larval adaptations in the major branches of the tribe Heptageniini. The basal branched *Heptagenia* clade has larvae with generalized collector-gatherer mouthparts typical of the Ecdyonurinae and the vast majority of Heptageniinae. In *Dacnogenia*, which shares with *Raptoheptagenia* gill lamellae that have become considerably narrowed, the mandibles, galealacinae and linguae are intermediate between the generalized plan found in *Heptagenia* and the highly specialized predatory mouthparts found in *Raptoheptagenia*. Although the ecology of *Dacnogenia* is unknown, larvae may be presumed from morphology to be facultative carnivores. In any case, *Dacnogenia* is clearly intermediate in certain morphological respects between the relatively plesiotypic *Heptagenia* and the relatively apotypic *Raptoheptagenia*, and as such was one of the important links in discovering the cladistic origin of the highly specialized *Raptoheptagenia*.

Within the subfamily Rhithrogeninae, whose members share modified apices of the larval femora, the four major basal sequential branches (Fig. 1) form clades that are recognized respectively as the tribes Rhithrogenini, s.s., Cinygmatini [based on a family-group name first made available but incorrectly formed by Kluge (1988) as Cinygmini; emended here based on declension of its particular neuter gender genotype root], Epeorini, n. trib., and Anepeorini [based on a family-group name first made available by Edmunds (1962)]. The tribe Rhithrogenini consists of three sequential branches (Fig. 1), the most basal being a lineage recognized as the Asian genus *Paegniodes*. Branching opposite of *Paegniodes*, are two sister clades recognized as the mainly Holarctic genus *Rhithrogena* (with some minor representation in the Oriental and Neotropical regions) and the Nearctic and eastern Palearctic genus *Cinygmula*. In the remaining tribes the larval femoral apices are further modified. The tribe Cinygmatini contains only the clade recognized as the western Nearctic and eastern Palearctic genus *Cinygma*. The remaining two tribes share a severe reduction of the median caudal filament and are known as the two-tailed flatheaded mayflies. The tribe Epeorini consists of three sequential branches (Fig. 1), the most basal being a lineage recognized as the eastern Palearctic genus *Bleptus*. Branching opposite of *Bleptus*, are two sister clades recognized as the western Nearctic genus *Ironodes* and the Holarctic-Oriental-Neotropical genus *Epeorus*. The tribe Anepeorini consists of a pair of

North American sister lineages (Fig. 1) recognized as the genera *Anepeorus* and *Spinadis*.

The subfamily Rhithrogeninae is most diverse in the Holarctic, with most genera found in the Nearctic and eastern Palearctic regions. Palearctic distributions are extended in the Oriental region in the single species of the genus *Paegniodes* and to a considerable extent in the relatively widespread *Rhithrogena* and *Epeorus*. In addition, *Epeorus* is the only genus of flatheaded mayflies known to have infiltrated South America, other Neotropical-represented Heptageniidae (*Ecdyonurus*, *Maccaffertium*, *Rhithrogena*) being found no farther south than Central America. The subfamily Rhithrogeninae is also the best represented of the entire family in high gradient streams often associated with mountainous environments. This involves *Cinygma*, *Cinygmula*, *Ironodes*, *Bleptus*, and most species of *Rhithrogena* and *Epeorus*. Mountain chains have to a large extent facilitated southern penetrations of boreal originated flatheaded mayflies and others into more tropical areas (McCafferty 1998). The Holarctic distributions within *Rhithrogena*, *Cinygmula*, *Cinygma*, and *Epeorus*, suggest Laurasian origins and possibly Palearctic-Nearctic dispersal events. For example, disjunction of *Cinygmula* in western Nearctic/eastern Palearctic and southeastern Nearctic, especially considering the distribution of *C. subaequalis* (Banks) in Alaska and the southern Appalachians, along with an Alaskan/Siberian distribution of *Cinygma lyriforme* (McDunnough), may suggest dispersal events via the Arcto-Tertiary Forest (see McCafferty 1985). *Paegniodes* and *Ironodes* apparently originated in the Eastern and Western Hemispheres, respectively. Possible *Ironodes* spp. from Asia (see e.g., Dudgeon 1999) are most likely misidentifications but require further study.

Reduction of the median caudal filament in many Ephemeroptera larvae is often associated with habitation of swift currents in high gradient streams, as has been repeatedly derived in various lineages in the family Baetidae (e.g., see McCafferty and Baumgardner 2003, McCafferty 2003b), and as is apparently also the case with the Epeorini. Other adaptations related to benthic exposure to swift currents (see also periphyton feeding, below) include the gill lamellae forming a friction disc ventrally as seen in all *Rhithrogena* larvae (which on the other hand retain the plesiomorphic developed median caudal filament), and in certain lineages of *Epeorus* with a somewhat similar friction disc that has evolved independently.

Except for the strict predators within the Rhithrogeninae, larvae of this subfamily differ from other flatheaded mayflies in that they generally have mouthparts adapted for periphyton grazing and scraping rather than the collection and gathering of fine detritus, which typify the subfamilies Ecdyonurinae and Heptageniinae [see, e.g., feeding behavior and functional morphology studies of *Stenacron* and *Rhithrogena* by McShaffrey and McCafferty (1986, 1988)]. This adaptation for periphyton feeding is perhaps best exemplified by the field of scraping armature seen on the maxillary palps.

Predation is highly developed among the Heptageniidae in the Rhithrogeninae, as seen in the tribe Anepeorini, although it independently also evolved within the Heptageniini (Heptageniinae), see above. Although the microhabitat of the Anepeorini is not clear, larvae may hunt on substrate in considerable current and sometimes at considerable depths in mainly large rivers. This

may account for the fact that their larvae exhibit the two-tailed condition derived in common with the Epeorini.

As mentioned previously, the genus *Epeorus* does not appear to be divisible into additional cladistically sound species groups, each with exclusive synapomorphies. However, the group is in severe need of a global revision at the species level, which could possibly yield data revealing such additional groupings. Within the strict rules of phylogenetic classification (Wiley 1981), additional genera would only be possible if they were sequentially derived with *Epeorus*, given the present cladogram (Fig. 1) and the position within the Epeorini that *Epeorus* has been shown to occupy.

MATERIAL EXAMINED

Included below is a concise accounting of the species examined as part of this study. Additional details are available from WPM. Abbreviations used include standard two-letter codons for USA states and Canada provinces (see McCafferty and Randolph 1998), L for larva(e), M for male adult(s), and F for female adult(s).

Previously *Afghanurus*: See *Ecdyonurus*.

Afronurus: *A. assamensis* (Kimmins), n. comb. (from *Cinygmina*) [Thailand-M]; *A. philippinensis* Flowers and Pescador [Philippines-L,F]; *A. spp.* [Afghanistan-L; China-M,F; F. R. Congo-F,L; Ghana-L; Hong Kong-M,L; India-M,L; Kenya-M,F,L; Lebanon-L; Malaysia-M,F,L; Nepal-M,F; Nigeria-I; Philippines-M,F,L; South Africa-M,F,L; Taiwan-M,F; Thailand-M,F,L].

Anepeorus: *A. rusticus* McDunnough [SA-L; UT-M]. See also previous *Anepeorus* under *Spinadis*.

Asionurus: *A. sp.* [Thailand-L].

Atopopus: *A. edmundsi* Wang and McCafferty [Malaysia-M,L]; *A. tibialis* Ulmer [Philippines-M,L].

Bleptus: *B. fasciatus* Eaton [Japan-M,L; Korea-M,L].

Cinygma: *C. dimicki* McDunnough [ID-M,F]; *C. integrum* Eaton [ID-L; UT-L]; *C. lyriforme* (McDunnough) [AK-M,L; Russia-L]; *C. spp.* [China-L; India-L].

Previously *Cinygmina*: See *Afronurus*.

Cinygmula: *C. amseli* (Demoulin), n. comb. (from *Epeiron*) [Afghanistan-M]; *C. cava* (Ulmer) [Russia-M,L]; *C. gartrelli* McDunnough [BC-M,F; UT-M]; *C. grandifolia* Tshernova [Russia-I.]; *C. hirasana* (Imanishi) [Japan-M,L; Russia-L]; *C. hutchinsoni* (Traver), n. comb. (from *Ororotsia*) [India-M,F,L]; *C. kootenai* McDunnough [UT-M]; *C. kurenzovi* (Bajkova) [Russia-L]; *C. mimus* (Eaton) [ID-M,F; UT-M,F]; *C. par* (Eaton) [AB-M,F; CO-I.; ID-M; NM-M,F; UT-M,L]; *C. ramaleyi* (Dodds) [CO-L; UT-M]; *C. reticulata* McDunnough [ID-M; UT-M]; *C. subaequalis* (Banks) [AK-L; KY-L; ME-M; NC-M,F,L; NH-L; NY-M,L; PE-M,F; TN-M,L]; *C. tarda* (McDunnough) [ID-M,F; MT-M]; *C. uniformis* McDunnough [ID-M; YU-M]; *C. spp.* [India-M].

Compsoneria: *C. spectabilis* Eaton [Malaysia-M].

Previously *Compsoneriella*: See *Thalerosphyrus*.

Dacnogenia: *D. coeruleans* (Rostock), n. comb. (from *Heptagenia*) [Czech Republic-L]; *D. sp.* [Afghanistan-L; Thailand-L].

Previously *Ecdyonuroides*: See *Thalerosphyrus*.

Ecdyonurus: *E. bellus* (Allen and Cohen) [Guatemala-L; Mexico-L]; *E. criddlei* (McDunnough) [AZ-L; CO-L; ID-M,I; NM-L; SD-L]; *E. dispar* (Curtis) [Ireland-M,L]; *E. insignis* (Eaton) [Belgium-L]; *E. kibuenis* Imanishi [Korea-M]; *E. levis* (Navás) [Russia-M]; *E. simplicoides* (McDunnough) [AZ-L; CO-L; ID-M; NM-L; UT-M]; *E. torrentis* Kimmins [Belgium-L]; *E. yoshidae* Takahashi [Japan-L]; *E. spp.* [Afghanistan-L; France-L; Germany-L; Greece-L; India-F; Italy-M; Pakistan-L; Philippines-L; Taiwan-M,F; Thailand-L].

Electrogena: *E. lateralis* (Curtis) [England-M]; *E. spp.* [Germany-L, Italy-M; Lebanon-L; Nepal-L].

Previously *Epeiron*: See *Cinygmula*.

Previously *Epeorella*: See *Epeorus*.

Epeorus: *E. aesculus* (Imanishi) [Japan-M,L; Korea-M,L]; *E. albertae* (McDunnough) [ID-M,L; ON-L]; *E. assimilis* Eaton [Belgium-M,I; Czech Republic-L; Germany-L; Slovakia-L; Switzerland-M]; *E. borneonia* (Ulmer), n. comb. (from *Epeorella*) [Malaysia-M]; *E. curvatus* Matsumura [Japan-L]; *E. deceptivus* (McDunnough) [CO-L; ID-L; NM-L; OR-M,F]; *E. dispar* (Traver) [NC-L; TN-L]; *E. dulciana* (McDunnough) [CA-M]; *E. fragilis* (Morgan) [NY-L; TN-L; VT-L]; *E. frisoni* Burks [NY-M]; *E. grandis* (McDunnough) [BC-L; CA-M,F,L; CO-L; ID-L; SD-L; WA-M]; *E. ikanonsis* Takahashi [Japan-M,L]; *E. latifolium* Ueno [Japan-M,L]; *E. longimanus* (Eaton) [AZ-L; CO-L; ID-M,F; NM-L; SD-M,F; UT-L]; *E. margarita* Edmunds and Allen [AZ-L; NM-L]; *E. metlacensis* Traver [Mexico-I.]; *E. namatus* (Burks) [IN-L; KY-L; OH-L]; *E. packeri* Allen and Cohen [Honduras-L]; *E. pellucidus* (Brodsky) [Russia-M]; *E. pleuralis* (Banks) [MA-L; MD-L; NF-M,L; NY-M; PA-L; PE-M; TN-L]; *E. punctatus* (McDunnough) [AR-M,F]; *E. subpallidus* (Traver) [TN-L]; *E. suffusus* (McDunnough) [ME-L; NY-M]; *E. vitreus* (Walker) [KY-L; ME-L; NB-I; NC-M,F,L; NY-L; PA-L; TN-M,F,L; VT-M; WI-L]; *E. spp.* (Afghanistan-L; China-M,F; Hong Kong-L; India-M,F,L; Korea-L; Lebanon-F; Nepal-L; Pakistan-F; Thailand-M,F,L).

Previously *Epeorus* (*Belovius*): See *Epeorus s.s.*

Heptagenia: *H. adaequata* McDunnough [AB-M; ID-M; OR-M; SA-M,F,L]; *H. culacantha* Evans, Botts and Flowers [NY-L; PA-M,F,L]; *H. diabasia* Burks [IA-L; IN-M,L; NE-M,F,L; SD-M,F; WI-L]; *H. elegantula* (Eaton) [AZ-L; CO-L; ID-L; NE-M,F,L; NM-M; NV-L]; *H. flavescens* (Walsh) [AR-M, IA-L; NE-M; NY-L; TX-L]; *H. julia* Traver [NC-L; NY-L]; *H. marginalis* Banks [OH-L; NY-L; SC-M]; *H. nasuta* Ulmer [Malaysia-F]; *H. patoka* Burks [IL-M; IN-M]; *H. pulla* (Clemens) [IA-L; IN-L; MI-L; NB-M; NY-L; WI-L]; *H. solitaria* McDunnough [AZ-L; ID-L; NM-M; UT-L]; *H. sulphurea* (Muller) [England-M,F; Ireland-L; Russia-L]; *H. spp.* [China-F]. See also previous *Heptagenia* under *Dacnogenia* and *Kageronia*.

Ironodes: *I. nitidus* (Eaton) [CA-M,F,L; OR-M,L]; *I. flavipennis* Traver [BC-M].

Kageronia: *K. fuscogrisea* (Retzius), n. comb. (from *Heptagenia*) [Ireland-M,L]; *K. kihada* (Matsumura), n. comb. (from *Heptagenia*) [Japan-M,L]; *K. orbitocola* (Kluge), n. comb. (from *Heptagenia*) [Sweden-M,L].

Leucrocota: *L. aphrodite* (McDunnough) [AR-M,F,L; IN-L; KY-L; NY-L; OH; VA-M; VT-M]; *L. hebe* (McDunnough) [AR-M,F,L; GA-M; IA-L; IN-L; KY-L; ME-M; MI-L; NY-M,L; OH-L; OK-M,L; PA-M; SC-M; TN-M; VT-L; WI-L]; *L. juno* (McDunnough) [IA-L; IN-L; NY-L; OK-M,F; TN-M]; *L.*

maculipennis (Walsh) [AR-M,L; IA-M,L; NB-L; NE-M,L; NH-M; NY-L; OK-M; SD-M,F; TX-L]; *L. minerva* (McDunnough) [AR-M,L; KY-L; OK-L; PA-L]; *L. petersi* (Allen) [NM-F,L]; *L. umbratica* (McDunnough) [AR-M,L; NY-M,L]; *L. thetis* (Traver) [NC-L; NY-M; TN-L]; *L. walshi* (McDunnough) [OH-L].

Maccaffertium: *M. bednariki* (McCafferty), n. comb. (from *Stenonema*) [KY-L; MO-L; OK-L]; *M. carlsoni* (Lewis), n. comb. (from *Stenonema*) [GA-L; KY-L; SC-M,L]; *M. exiguum* (Traver), n. comb. (from *Stenonema*) [AL-M,F,L; AR-M,L; FL-M,F,L; GA-M,F; IA-I; IL-L; IN-M,F,L; KY-L; LA-L; MI-L; MN-M; NC-M; NE-L; NY-L; OH-L; TX-L; WI-L]; *M. ithaca* (Clemens and Leonard), n. comb. (from *Stenonema*) [KY-M,L; MA-M; NC-M,L; NJ-M; NY-M,F,L; OH-I; PQ-M,L; TN-M; VA-M,L; VT-L]; *M. lenati* (McCafferty), n. comb. (from *Stenonema*) [NC-L]; *M. luteum* (Clemens), n. comb. (from *Stenonema*) [IA-M; IL-M; IN-M,L; MI-L; NY-L; OH-L; OK-L; ON-M,F,L; PQ-M; WI-M,L]; *M. mediopunctatum* (McDunnough), n. comb. (from *Stenonema*) [AL-L; AR-M,F,L; CT-M; IA-L; IL-M,L; IN-M,L; KY-L; MA-M; MD-L; MO-L; NY-M,L; OH-M,L; OK-L; ON-M,L; PA-M; PQ-M,F,L; SD-L; TN-L; TX-L; VA-M; WI-L; WV-L]; *M. meririvulatum* (Carle and Lewis), n. comb. (from *Stenonema*) [KY-L; NY-L; PA-M,L; VA-M,F,L]; *M. mexicanum* (Ulmer), n. comb. (from *Stenonema*) [AL-M; AR-L; Costa Rica-M,L; FL-F,L; GA-M; Guatemala-L; IA-M,L; IL-M,L; IN-M,F,L; KY-L; KS-M; KY-M; LA-M; Mexico-M,L; MS-M; NC-M,F; NE-L; NY-L; OH-L; SC-M,F; TN-M,F; TX-M,F,I; WI-L; WV-M]; *M. modestum* (Banks), n. comb. (from *Stenonema*) [AL-L; AR-M,F; CT-M; DC-M; GA-M,L; IN-L; KY-L; MA-M; MD-M; ME-F,L; MI-M,L; NC-M,F,L; NY-L; OH-M,F; OK-L; ON-M,F,L; PA-M,F,L; PQ-M,F,L; SC-M; TX-L; VA-M,F,L; WI-L]; *M. pudicum* (Hagen), n. comb. (from *Stenonema*) [DC-M; KY-L; MA-M; MD-M,L; NC-M,F,L; NY-F,L; PA-M; SC-L; TN-M,L; VA-M; VT-L]; *M. pulchellum* (Walsh), n. comb. (from *Stenonema*) [AR-L; IA-L; IL-M,L; IN-M,L; KY-L; MI-L; MO-L; MN-M; NE-L; NY-M,L; OH-M,L; ON-M,F,L; PA-M; WI-L]; *M. sinclairi* (Lewis), n. comb. (from *Stenonema*) [TN-M,F,L]; *M. smithae* (Traver), n. comb. [AL-M,F,L; FL-M,F,L; GA-L]; *M. terminatum* (Walsh), n. comb. (from *Stenonema*) [AR-L; GA-M,F,L; IA-M,L; ID-L; IL-M,F; IN-M,F,L; KY-L; MA-M,F; MB-M,F; MI-M,L; MN-M,L; MO-L; MT-M; NE-M,L; NF-L; NS-M; NV-L; NC-M; NY-M,L; OH-M,F,L; OK-L; ON-M,F; OR-M; PE-L; PQ-M; SC-M, TX-L; UT-M,L; WA-M; WI-L; WY-F]; *M. vicarium* (Walker), n. comb. (from *Stenonema*) [CT-F; IA-L; IL-M,L; IN-M,F,L; KY-L; MA-L; MB-M; MD-I; ME-L; MI-M,F,L; NB-L; NC-M; NE-M; NF-M,L; NH-M,F,L; NS-M,F,L; NY-M,L; OH-M,F,L; OK-L; ON-M,F; PA-M,L; PQ-M,F,L; VA-M,L; WI-M,L; WV-M].

Macdunnoa: *M. brunnea* Flowers [AL-M; GA-M,L; NC-L; SC-M]; *M. persimplex* (McDunnough) [CO-M,L; NE-M].

Nixe: *N. flowersi* McCafferty [IN-M,F,L; KY-L; OK-L]; *N. inconspicua* (McDunnough) [AR-M,L; IA-L; IN-M,F,L; KY-L; NY-M; OH-L; OK-L; WI-L]; *N. kennedyi* (McDunnough) [CA-M]; *N. lucidipennis* (Clemens) [IN-M; WI-L]; *N. perfida* (McDunnough) [AR-L; IA-L; IN-L; NC-M; OH-L; OK-L]; *N. rusticalis* (McDunnough) [IA-M; OH-M]. *N. spp* [Taiwan].

Notacanthurus: *N. spp.* [Afghanistan-L; Nepal-L].

Paegniodes: *P. cupulatus* (Eaton) [Hong Kong-M,F].

Raptoheptagenia: *R. cruentata* (McDunnough) [IA-M,I; IN-L; KY-L; MT-L; NE-M,L; SA-L].

Rhithrogena: *R. amica* Traver [NY-M; TN-L]; *R. anomala* McDunnough

[NY-M]; *R. fasciata* Traver [NC-M,L]; *R. fuscifrons* Traver [NC-L]; *R. guspeensis* McDunnough [PQ-M]; *R. hageni* Eaton [CO-L; ID-L]; *R. hybrida* Eaton [Switzerland-M]; *R. impersonata* (McDunnough) [IN-L; ME-M,F; MI-L; OK-L; WI-L]; *R. japonica* Ueno [Japan-M,F,L]; *R. jejuna* Eaton [IA-L; NH-M; OK-L; WI-L]; *R. loyolae* Navás [Czech Republic-L]; *R. manifesta* Eaton [AR-M,F,L; IA-L; IN-L; MI-L; MO-L; WI-L]; *R. morrisoni* (Banks) [AZ-L; ID-M,L; NM-L; OR-M,F]; *R. notialis* Allen and Cohen [Guatemala-L]; *R. ornata* (Ulmer), n. comb. (from *Rhithrogeniella*) [India-M; Malaysia-F]; *R. plana* Allen [NM-L]; *R. robusta* Dodds [CO-L; WA-M; WY-L]; *R. semicolorata* (Curtis) [Belgium-M,L; England-M]; *R. trispina* Zhou and Zheng [China-M]; *R. uhari* Traver [NY-L]; *R. undulata* (Banks) [MI-L; NM-L; UT-M,F,L; WI-L]; *R. spp.* [China-M; Germany-L; India-M,F; Korea-L; Nepal-L; Thailand-F,L].

Previously *Rhithrogena* (*Ororotsia*): See *Cinygmula*.

Previously *Rhithrogeniella*: See *Rhithrogena*.

Siberionurus: *S. asperus* (Kluge) [Mongolia-L].

Spinadis: *S. simplex* (Walsh), n. comb. (from *Anepeorus*) (GA-M,L; IN-M,F,L).

Stenacron: *S. interpunctatum* (Say) [AR-M,F,L; IA-L; IL-M; IN-L; KY-L; MI-L; NE-M,L; NF-M,F,L; NY-L; OH-L; OK-L; PA-M; PE-L; TX-L; WI-L]; *S. candidum* (Traver) [IA-L; IN-L; KY-L; NY-M,F,L; PA-M,F]; *S. carolina* (Banks) [IA-L; NY-L; OH-L; PA-M,F]; *S. gildersleevei* (McDunnough) [IN-L; KY-L; NY-M]; *S. minnetonka* (Daggy) [IN-L; KY-L; PA-M]; *S. pallidum* (Traver) [KY-L; NY-L; OH-M,F].

Stenonema: *S. femoratum* (Say) [AL-M,F,L; AR-M,F; GA-M,L; IA-L; IL-L; IN-L; KY-M,L; MB-L; MI-M,L; MN-L; MO-M,L; NE-L; NF-M; NY-L; NC-M,L; NY-L; OH-M,L; OK-M,F,L; ON-M,L; PA-M; PQ-F,L; TN-M,F,L; TX-M,F,L; VA-M,L; WI-L; WV-L]. See also previous *Stenonema* under *Maccaffertium*.

Thalerosphyrus: *T. bequaerti* (Navás) [F. R. Congo-M]; *T. determinatus* (Walker) [Borneo-M]; *T. njalensis* (Kimmins) [South Africa-M,F,L]; *T. sinuosus* Navás [Malaysia-M,L; Philippines-I.]; *T. sumatranus* (Ulmer) [Malaysia-M,L; Thailand-F,L]; *T. thienemanni* (Ulmer), n. comb. [Malaysia-M]; *T. spp.* [F. R. Congo-F; India-M; Madagascar-M,F; Malaysia-F,L; South Africa-M,F,L; Sri Lanka-M,L; Thailand-L].

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Table 1. Alphabetical list of defined species group operational taxonomic units of Heptageniidae subjected to cladistic analysis.

- AFRONURUS** = *Afronurus* Lestage (1924), type—*Ecdyurus peringueyi* Esben-Petersen; larva: Barnard (1932). [= *Cinygmia* Kimmins (1937), type—*Cinygmia assamensis* Kimmins; larva: Wu et al. (1986)].
- ANEPEORUS** = *Anepeorus* McDunnough (1925), type—*Anepeorus rusticus* McDunnough; larva: Whiting and Lehmkuhl (1987b) as *Acanthomola pubescens* Whiting and Lehmkuhl; monotypic. [= *Acanthomola* Whiting and Lehmkuhl (1987b), type—*Acanthomola pubescens* Whiting and Lehmkuhl].
- ASIONURUS** = *Asionurus* Braasch and Soldán (1986a), type—*Asionurus primus* Braasch and Soldán; restricted to larvae of *Asionurus primus* and *Asionurus ulmeri* Braasch and Soldán; adult unknown.
- ATOPOPUS** = *Atopopus* Eaton (1881), type—*Atopopus tarsalis* Eaton; larva: Wang and McCafferty (1995b).
- BLEPTUS** = *Bleptus* Eaton (1885), type—*Bleptus fasciatus* Eaton; larva: Ueno (1931); monotypic.
- CINYGMA** = *Cinygma* Eaton (1885), type—*Cinygma integrum* Eaton; larva: McDunnough (1933). [= *Cinygmoides* Matsumura (1931), type—*Cinygmoides heckachii* Matsumura]
- CINYGMULA** = *Cinygmula* McDunnough (1933), type—*Ecdyurus ramaleyi* Dodds. [= *Epeiron* Demoulin (1964), type—*Epeiron amseli* Demoulin; = *Ororotsia* Traver (1939), type—*Ororotsia hutchinsoni* Traver]
- COMPSONEURIA** = *Compsoneuria* Eaton (1881), type—*Compsoneuria spectabilis* Eaton; larva: Ulmer (1939); restricted to *Compsoneuria*

spectabilis.

DACNOGENIA = *Heptagenia (Dacnogenia)* Kluge (1988), type–*Heptagenia coeruleans* Rostock; monotypic.

ECDYONURUS = *Ecdyonurus* Eaton (1868a), type–*Ephemera venosa* Fabricius; larva: Eaton (1885). [= *Afghanurus* Demoulin (1964), type–*Afghanurus vicinus* Demoulin; larva(?): Kluge (1980) as *Ecdyonurus vicinus* (Demoulin); = *Paracinygmula* Bajkova (1975), type–*Paracinygmula zhiltzovae* Bajkova; adult: Kluge (1983a) as *Ecdyonurus zhiltzovae* (Bajkova), nec Tshernova (1972) (= *Ecdyonurus bajkovae* Kluge); = *Nixe (Akkarion)* Flowers (1980), type–*Heptagenia simplicioides* McDunnough].

ELECTROGENA = *Electrogena* Zurwerra and Tomka (1985), type–*Baetis lateralis* Curtis.

EPEORUS = *Epeorus* Eaton (1881), type–*Epeorus torrentium* Eaton; larva: Eaton (1885). [= *Iron* Eaton (1883), type–*Epeorus longimanus* Eaton; = *Ironopsis* Traver (1935), type–*Iron grandis* McDunnough; = *Epeorella* Ulmer (1939), type–*Epeorella borneonia* Ulmer; = *Epeorus (Belovius)* Tshernova (1981), type–*Epeorus latifolium* Ueno].

HEPTAGENIA = *Heptagenia* Walsh (1863), type–*Palingenia flavescens* Walsh; larva: Eaton (1885). [= *Sigmoneuria* Demoulin (1964), type–*Sigmoneuria anseli* Demoulin]

IRONODES = *Ironodes* Traver (1935), type–*Iron nitidus* Eaton.

KAGERONIA = *Kageronia* Matsumura (1931), type–*Kageronia suzukiella* Matsumura (= *Heptagenia kihada* Matsumura); larva: Lestage (1917) as *Ecdyurus fuscogriseus* (Retzius). [= *Parastenacron* Kluge (1983b), unavailable].

LEUCROCUTA = *Leucrocuta* Flowers (1980), type–*Heptagenia maculipennis* McDunnough.

MACCAFFERTIUM = *Stenonema (Maccaffertium)* Bednarik (1979), type–*Heptagenia integer* McDunnough (= *Heptagenia mexicana* Ulmer).

MACDUNNOA = *Macdunnoa* Lehmkuhl (1979) type–*Macdunnoa nipawinia* Lehmkuhl.

NIXE = *Nixe (Nixe)* Flowers (1980), type–*Ecdyonurus lucidipennis* Clemens.

NOTACANTHURUS = *Notacanthurus* Tshernova (1974), type–*Ecdyonurus zhiltzovae* Tshernova.

PAEGNIODES = *Paegniodes* Eaton (1881), type–*Heptagenia cupulata* Eaton; larva: Tshernova (1976); monotypic.

RAPTOHEPTAGENIA = *Raptoheptagenia* Whiting and Lehmkuhl (1987a), type–*Heptagenia cruentata* Walsh; monotypic.

RHITHROGENA = *Rhithrogena* Eaton (1881), type–*Baetis semicoloratus* Curtis; larva: Eaton (1885). [= *Rhithrogeniella* Ulmer (1939), type–*Rhithrogeniella ornata* Ulmer; restricted to type].

SIBERIONURUS = *Siberionurus* McCafferty (2004), type–*Ecdyonurus aspersus* Kluge (1980).

SPINADIS = *Spinadis* Edmunds and Jensen (1974), type–*Spinadis wallacei* Edmunds and Jensen (= *Heptagenia simplex* Walsh); adult: Walsh (1863) as *Heptagenia simplex*; monotypic.

STENACRON = *Stenacron* Jensen (1974), type–*Baetis interpunctatus* Say.

STENONEMA = *Stenonema* Traver (1933), type–*Heptagenia tripunctata*

Banks (= *Baetis femorata* Say).

THALEROSPHYRUS = *Thalerosphyrus* Eaton (1881), type-*Baetis determinatus* Walker; larva: Ulmer (1939) as *Thalerosphyrus determinatus* (Walker). [= *Compsoeuriella* Ulmer (1939), type-*Compsoeuriella thienemanni* Ulmer; = *Notonurus* Crass (1947), type-*Notonurus cooperi* Crass; = *Ecdyonuroides* Dang (1967), type-*Ecdyonurus sumatranus* Ulmer].

TRICHOGENIA = *Trichogenia* Braasch and Soldán (1988b), type *Trichogenia maxillaris* Braasch and Soldán; adult unknown; monotypic.

Table 2. Examples of characters used to derive the cladogram of Heptageniidae operational taxonomic units. Apomorphies in numbered sets (also referred to by numbers appended to branches of the cladogram in Figure 1) are stated first and followed by bracketed precedent plesiomorphies; A = adult character; L = larval character; * = subject to convergence elsewhere in Heptageniidae.

1. Mesothoracic furcasternum medial depression parallel sided (A) [mesothoracic furcasternum medial depression narrowed anteriorly].
Glossa subquadrate (L)* [glossa subtriangulate].
Mandible outer incisor with single terminal denticle (L) [mandible outer incisor with multiple terminal denticles].
2. Galealacinia lacking scattered, non-rowed setae on ventral face (L) [galealacinia at least some non-rowed setae].
3. Penes with highly developed lateral and apical marginal sclerites (A) [penes without both lateral and apical marginal sclerites highly developed].
4. Caudal filaments with lateral setae reduced (L)* [caudal filaments with lateral setae developed for the most part].
5. Titillators relatively thick and spindle shaped (A)* [titillators not spindle shaped and generally attenuated].
Egg chorion reticulate [egg chorion not reticulate].
6. Penes dorsally with lateral marginal sclerite well developed and strongly extended medially (A)* [penes dorsally with lateral sclerite not extended].
7. Penes dorsolateral spines well developed (A) [penes dorsolateral spines not well developed].
Penes lobe strongly developed medioapically (A)* [penes lobe not strongly developed medioapically].
8. Penes lobe angulations, sclerotization and titillators tending to be reduced (A)* [penes lobe angulations or sclerotization or titillators at least moderately developed].
Whorls of spines well developed (L)* [whorls of spines moderately

developed].

9. Forceps segment 3 relatively long (A)* [forceps segment 3 not relatively long].
10. Male eye distinctly reduced in size (eyes well separated) (L&A) [male eye not reduced in size].
11. Maxillary palp segment 1 lacking setae on inner margin (L)* [maxillary palp segment 1 with setae on inner margin].
12. Foretarsal segment 1 long (usually over one-half of segment 2) (A) [foretarsal segment 1 less than one-half of segment 2].
13. Male head capsule longer than diameter of eye (A) [male head capsule shorter than diameter of eye].
Claw long with more than one basal denticle (L). [claw with only one basal denticle].
14. Penes lobe tear-drop (egg) shape or subtruncate and lacking distal sclerotization (A)* [penes lobe with some distinctive angulated or interrupted margin, with variable sclerotization].
Some gill lamellae bluntly attenuated distally (L)* [lamellae shape variable].
PMG (phosphoglucomutase) levels lowered [PMG levels normal].
15. Egg with large and small coiled threads [egg with only small coiled threads].
16. Male hindtarsus length two-thirds or more hindtibia (A) [male hindtarsus length about one-half of hindtibia].
17. Gill 7 greatly elongated (L) [gill 7 not greatly elongated].
18. Hindtarsus segment 1 greatly elongated (A) [hindtarsus segment 1 not greatly elongated].
19. Middle and hind supracoxal processes acute or subacute (L) [supracoxal processes bluntly pointed, rounded or truncate].
20. Hindwing outer margin distinctly pigmented (A) [hindwing outer margin not pigmented].
Gill I lamella reduced (L)* [gill I lamella not reduced].
21. Galealacinia ventrally with submarginal setal row reduced basally along inner setate margin, or if row longer, then sparse, especially basally (usually with less than 25 setae in row) (L)* [galealacinia ventrally with submarginal setal row dense and extensive (usually with more than 25 setae in total)].

- Maxillary palp segment 2 inner margin with inward curvature (L)*
[maxillary palp segment 2 inner margin without inward curvature].
22. Forefemur with dorsal apical process projected and narrower than ventral process (L) [forefemur with dorsal apical process not projected, and ventral process narrower than dorsal process].
 23. Mandible with two tufts of setae on outer margin (L) [mandible with one row of setae on outer margin].
 24. Labrum reduced in width (less than six times length) (L)* [labrum width seven or more times length].
 25. Lingua with deep U-shaped median notch (L) [lingua without deep U-shaped median notch].
 26. Mandible terminal denticles well separated (L) [mandible terminal denticles contiguous].
 27. Gill tufts highly developed (L) [gill tufts not highly developed].
 28. Gill 7 reduced and dissimilar to anterior gills (L)* [gill 7 smaller than, but similar to, anterior gills].
 29. Superlingua lyre shaped (L)* [superlingua not exactly lyre shaped].
 30. Gill lamellae slender (L) [gill lamellae not all slender].
Lingua shortened, with approximately straight distal margin (L) [lingua generally longer than wide and with rounded or multi-lobular distal margin].
 31. Superlingua distolateral tip not defined (rounded and not indented or recurved) (L) [superlingua distolaterally with variously defined tip].
 32. Labial palp segment 2 slender, sharp, with sparse setae (L)* [labial palp segment 2 broad, rounded, with dense setae].
Maxillary palp setae short and sparse (L) [maxillary palp setae long and dense at least in some areas].
 33. Penes laterally with subapical cluster of small to large spines (A)* [penes without subapical cluster of spines].
Gill lamellae with a narrowed, sharp point (L) [gill lamellae without narrowed, sharp point].
 34. Gill lamellae 1-6 broad apically (L)* [gill lamellae 1-6 variously bluntly narrowed apically or broadly attenuate].
 35. Forefemur hindmargin with short setae (L) [forefemur hindmargin with long setae or short and long setae].

36. Forewing with two or three crossveins immediately below bulla connected or nearly connected by pigment band (A) [forewing without banded crossveins below bulla].
37. Gill 7 vestigial or absent (L)* [gill 7 slender but well formed].
38. Penes distinctly L-shaped (A) [penes not distinctly L-shaped].
Maxillary crown with hairlike setae (L)* [maxillary crown without hairlike setae].
39. Gill lamellae 1-6 truncate (L) [gill lamellae 1-6 not truncate].
Gill 7 tracheation absent (L) [gill 7 tracheation present].
40. Penes lobe inner margin incurved (A) [penes lobe inner margin straight or outcurved].
Claw with small denticles (L)* [claw without small denticles].
41. Maxillary palp segment 2 with hooked pectinate spinules (L) [maxillary palp segment 2 without hooked pectinate spinules].
Mandibles with broadened subapical lobes (L) [mandibles without broadened subapical lobes].
42. Forefemur dorsal apical process angulate (L) [forefemur dorsal apical process rounded].
43. Hindwing smaller than cubital area of forewing (A) [hindwing larger than cubital area of forewing].
44. Maxillary palp with pigmented rib outlining armature field (L) [maxillary palp without pigmented rib outlining armature field].
Galealacinia ventral row of setae curved distally (L) [galealacinia ventral row of setae not curved distally].
45. Gill lamellae forming ventral friction disc (L)* [gill lamellae not forming ventral friction disc].
46. Head capsule anteriorly with medial notch or indentation (L) [head capsule without medial notch or indentation].
47. Labrum extremely narrowed (width less than length) (L) [labrum distinctly wider than long].
Glossa strongly divergent from base (L) [glossa not strongly divergent from base].
48. Median caudal filament reduced (two tailed) (L) [median caudal filament developed (three tailed)].
Hypopharynx narrowed, superlingua reduced distolaterally (L) [hypopharynx not narrowed, superlingua not reduced distolaterally].

49. Mesonotum without apparent transverse suture (A) [mesonotum with apparent transverse suture].
Cerci intersegmental setation on inner margin absent or sparse (L)* [cerci intersegmental setation well developed].
50. Maxillary palp segment 2 extremely slender (L) [maxillary palp segment 2 somewhat broad].
Galealacinia without crown (L)* [galealacinia with crown].
51. Glossae subrectangulate* and well separated (L) [glossac subtriangulate and usually closely oriented].
Gill lamellae margin entirely ribbed (L) [gill lamellae margin not entirely ribbed].
Head capsule thickened (L) [head capsule not thickened].
52. Head capsule anterior margin with dense setae (L) [head capsule anterior margin with no setae or only sparse setae].
53. Gill 7 small, not much longer than abdominal segment 8 (L)* [gill 7 at least as long as abdominal segments 8 and 9].
Abdominal terga 1-9 with paired submedial tubercles (L) [abdominal terga with single median tubercles or with paired tubercles on some but not each of terga 1-9].
54. Galealacinia crown weakly developed, crown setae reduced; medioapical spines strongly developed (L)* [galealacina crown well developed, with crown setae; medioapical spines not strongly developed].
55. Maxillary palp setae absent (L) [maxillary palp setae present].
Titillators apically denticulate (A) [titillators not apically denticulate].
56. Head and thorax with dorsal tubercles (L) [head and thorax without dorsal tubercles].
Head capsule lateral margin nearly straight and not produced (L) [head capsule lateral margin convex or produced laterally].

Table 3. Phylogenetic higher classification of the Heptageniidae.

- Subfamily Ecdyonurinae Ulmer
- Tribe Ecdyonurini, *s.s.*
 - Genus *Nixe* Flowers
 - Genus *Ecdyonurus* Eaton
 - Tribe Leucrocotini, n. trib.
 - Genus *Siberionurus* McCafferty
 - Genus *Leucrocota* Flowers
 - Tribe Notacanthurini, n. trib.
 - Genus *Notacanthurus* Tshernova
 - Genus *Electrogena* Zurwerra & Tomka
 - Tribe Atopopini, n. trib.
 - Genus *Afronurus* Lestage
 - Genus *Asionurus* Braasch & Soldán
 - Genus *Thalerosphyrus* Eaton
 - Genus *Atopopus* Eaton
- Subfamily Heptageniinae Needham
- Tribe Compsoneriini, n. trib.
 - Genus *Compsoneria* Eaton
 - Genus *Trichogenia* Braasch & Soldán
 - Tribe Heptageniini *s.s.*
 - Genus *Heptagenia* Walsh
 - Genus *Dacnogenia* Kluge
 - Genus *Raptoheptagenia* Whiting & Lehmkuhl
 - Tribe Kageroniini, n. trib.
 - Genus *Kageronia* Matsumura
 - Genus *Stenacron* Jensen
 - Tribe Stenonematini, n. trib.
 - Genus *Macdunmoa* Lehmkuhl
 - Genus *Maccaffertium* Bednarik
 - Genus *Stenonema* Traver
- Subfamily Rhithrogeninae Lestage
- Tribe Rhithrogenini *s.s.*
 - Genus *Paegniodes* Eaton
 - Genus *Rhithrogena* Eaton
 - Genus *Cinygmula* McDunnough
 - Tribe Cinygmatini Kluge
 - Genus *Cinygma* Eaton
 - Tribe Epeorini, n. trib.
 - Genus *Bleptus* Eaton
 - Genus *Ironodes* Traver
 - Genus *Epeorus* Eaton
 - Tribe Ancpeorini Edmunds
 - Genus *Anepeorus* McDunnough
 - Genus *Spinadis* Edmunds & Jensen

