SOME PHYLOGENETIC RELATIONSHIPS WITHIN THE FAMILY HEPTAGENIIDAE

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This paper is a preliminary report on a study in progress on the extant world fauna of twenty-eight genera assigned to four subfamilies of Heptageniidae. Three of these subfamilies, Anepeorinae, Pseudironiae and Arthropleinae, are highly-apomorphic derived forms and will be discussed in greater detail later in this paper. The fourth subfamily, Heptageniinae, contains twenty-five genera, and is the group studied most to date.

The subfamily Heptageniinae has evolved, for the most part, as a rather homogeneous group with relatively little morphological differentiation between the genera. Further, the most primitive genus of the subfamily is separated by a considerable gap from its hypothesized pre-Isonychiinae ancestors, thus leaving a decided gap in its evolutionary history in which no intermediate living or fossil forms are known. Ideally, the reconstruction of probable phylogenetic relationships becomes more realiable if an accurate fossil record exists; however, the available fossil evidence does not clarify the phylogeny significantly and we have relied principally upon evidence from extant forms. In the subfamily Heptageniinae the phylogeny is a perplexing problem as the degree of differentiation between the genera has been relatively slight and many of the Oriental and Asiatic genera are poorly known.

In attempting to reconstruct a meaningful phylogeny of the family, we have utilized the morphological similarities and differences of both the adults and nymphs of the extant genera with supplementary zoogeographical and ecological data. While both life stages have been utilized, the most significant evidence has been derived from the nymphal stage where evolution seems to have been faster. Even with this stage, however, it has been necessary to examine numerous morphological characteristics in minute detail before a meaningful analysis can be made. In general, the most useful characters have come from the nymphal mouthparts where patterns and types of armature have been found to be quite significant. The wings give very little information as they are all relatively alike.

LANDA (1969) reports the subfamily Heptageniiae to be composed of two basic groups with regards to internal anatomy of the nymphs. We are in agreement with his analysis as our data indicates three major phyletic lines, subdividing his plesiomorphic group into two lineages. We are presenting a tentative phylogenetic diagram of the genera that we have studied in detail (Fig. 1). As more specimens and data are available, this diagram will be altered to include all genera of the family.

Phyletic line IA represents the most plesiomorphic genera of the subfamily. The genus *Cinygmula* is the most primitive genus of this subfamily, and perhaps of the family. However, the mouthparts, gills, and internal anatomy show that it has evolved considerably from the ancestral type. It is interesting to note that the genus is far more widespread than is indicated in the literature. With the exception of three species described by Dr. TSHERNOVA from the U.S.S.R., all the reported known species are from North America. The genus actually is widespread in the Asiatic Palearctic, and further, most, if not all Palearctic species, described in the genus *Cinygma*, are probably *Cinygmula*.

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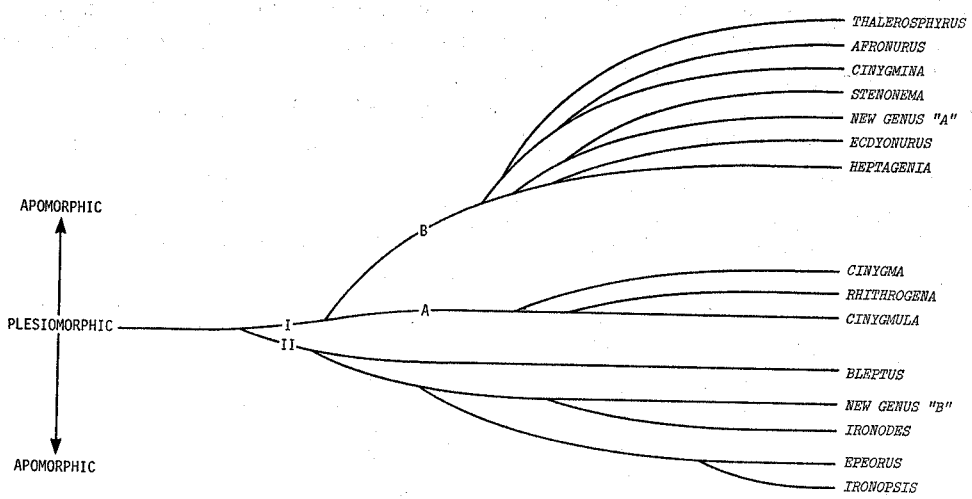

FIGURE 1. Tentative phylogenetic diagram of selected genera of the subfamily Heptageniinae.

There is little doubt that *Rhithrogena* evolved from *Cinygmula* through increased flattening of the nymph and development of its characteristic gill type which makes the genus better adapted to swifter water than is *Cinygmula*. This adaptation of the gills, extending beneath the abdominal venter to form an adhesive disc, has evolved at least two separate times in the Heptageniidae and also in the family Leptophlebiidae. In nymphs of one species of *Cinygmula* from western North America the gills partially extend beneath the abdomen. The genus *Rhithrogena* is widespread in the Holarctic and Oriental regions with species extending into the Neotropics.

The genus *Cinygma*, while the most apomorphic genus of lineage IA, still retains the mouth part characteristics common to *Cinygmula* and *Rhithrogena*, especially with regards to the hypopharynx. More data are needed on many Palearctic species to know which, if any, actually belong to this genus.

Phyletic line IB contains the derived genera of the subfamily, and represents two closely-related generic complexes. The genus *Heptagenia* represents the most plesiomorphic genus of the lineage and proto-*Heptagenia* probably gave rise to the rest of the complex. The genus is widespread in the Holarctic and Oriental regions and extends into the Neotropics.

The genus *Ecdyonurus* is very closely related to *Heptagenia*, and was undoubtedly derived from a proto-*Heptagenia* ancestor. There are a number of species assigned to *Ecdyonurus* in the Palearctic and Oriental regions that certainly are not members of that genus. We presently include only those species whose nymphs have the postero-lateral margins of the prothorax produced posteriorly, and whose adults have the typical basally-expanded penes characteristic of this genus. This genus is absent from the Neartic and Neotropical regions.

The genus *Stenonema* is closely related to *Heptagenia* and *Ecdyonurus*, and is largely restricted to the Nearctic, but extends into the Neotropics. The furcation sequence leading to this genus is quite well understood with a genus, represented as new genus "A" on the pylogenetic diagram, being intermediate in many repects between *Stenonema* and *Heptagenia*. The mouthparts of genus "A" are more similar to *Heptagenia*, especially with regards to the armature of the galealacinia of the maxillae. The gills, however, are typical of *Stenonema* with gill 7 reduced to a

slender filament. In other characteristids, it is distinct. There is little doubt that genus "A" evolved from a proto-*Heptagenia* ancestor and subsequently gave rise to the genus *Stenonema*. Genus "A" is restricted to eastern North America.

A second generic complex evolved from proto-*Heptagenia* and shows strong affinities to the slightly more plesiomorphic lineage from which it arose. The genera of this complex are closely related and have a similar zoogeographic range. The relatively poorly understood genus *Cinygmina* is known only from India and Thailand. We have studied nymphs and reared specimens of a new species. The previously unknown nymph shows that the genus is more primitive than, but closely allied to, the genus *Afronurus*.

Both *Afronurus* and *Thalerosphyrus* have common geographic ranges being known from the Sunda Islands of the Oriental region and China, and Turkey in the Palearctic. *Afronurus* is also found in East Africa and South Africa. The true relationships of these three genera are still somewhat obscure at the present time; however, both internal anatomy and mouthparts clearly demonstrate that this is a closely-related cluster.

Phyletic line II represents a plesiomorphic cluster of genera whose nymphs have two caudal filaments. The genus *Bleptus*, known only from the eastern Palearctic, is believed to most closely resemble the ancestor of the complex. While the mouthparts, gill structure, and reduced terminal filament show that the complex is more advanced than lineage IA; the genus is plesiomorphic when compared to other members of the complex. For example, the apex of the galea-lacinia of the maxillae has only a slight development of the triad of stout spines typical of the entire complex.

The relationships between *Bleptus*, new genus "B", and *Ironodes* are interesting. The genus *Ironodes* has a strong relationship to *Bleptus* as indicated by the structure of the nymphal mouthparts, gills and male genitalia. The nymphs of *Bleptus* have a single row of dorsal median abdominal spines while *Ironodes* has a double row. We have examined undescribed nymphs from Afghanistan with a single row of abdominal spines typical of *Bleptus*, but whose mouthparts are clearly more similar to those of *Ironodes*, and with gills typical of some species of the genus *Epeorus*. Further, we have studied nymphs from Pakistan which are very similar to the Afghanistan nymphs except that the abdominal spines begin as a double row on the anterior terga and gradually fuse on each succeeding tergum to form a single spine on tergum nine. Genus "B" is closely related to *Ironodes* as indicated by structure of the nymphal mouthparts and male genitalia, but is more plesiomorphic than *Ironodes* as indicated by the internal anatomy. However, the gills are more similar to those of some North American *Epeorus*. Genus "B" is apparently restricted to the Oriental region.

The Nearctic genus *Ironodes* is more apomorphic than either *Bleptus* or genus "B" on the basis of nymphal mouthparts and internal anatomy. Although BURKS (1953) reduced this genus to a subgenus of *Epeorus*, we are retaining it was a full genus on the basis of these data.

The phyletic line leading to *Epeorus* is probably relatively ancient and the genus shows a number of apomorphic advances over the ancestral type. The nymphs have the triad of stout spines on the apex of the galea-lacinia well developed and the penes of the male have well-developed median titillators, which are absent or poorly defined in *Bleptus*, genus "B" and *Ironodes*. The genus is Holarctic in distribution with one or more species extending into the Neotropical region.

The subgenus *Ironopsis* is clearly derived from *Epeorus* and its placement as a subgenus by BURKS (1953) is probably correct. The nymphx of *Ironopsis* are very similar to those of *Epeorus* in the structure of the mouthparts but the internal anatomy, as reported by LANDA (1969),

indicates that it is more apomorphic and is intermediate between what Landa refers to as the plesiomorphic and the apomorphic groups of the subfamily. The penes of the male of *Ironopsis* have retained the more primitive form of tubular penes typical of the genus *Ironodes*, with very small median titillators.

The genera of the subfamily, not included in the phylogenetic diagram, are too poorly studied to establish their affinities at this time. These include : *Afghanurus*, *Atapopus*, *Epeiron*, *Epeorella*, *Ororotsia*, *Paegniodes*, *Rhithrogeniella*, and *Sigmoneuria*, all of whose nymphs are unknown, and *Compsoneuria* and *Compsoneuriella*, of which we have inadequate material.

The three other subfamilies of Heptageniidae (Anepeorinae, Pseudironinae and Arthropleinae), represent lineages with some highly-apomorphic characters. Each is represented by a single genus and the nymphs are adapted to specialized habitats and are narrowly restricted ecologically. We are of the opinion that the three subfamilies each arose independantly from near the base of the proto-Heptageniidae. The sequence of branching from the pre-Heptageniinae is believed to be *Pseudiron*, *Anepeorus*, and then *Arthroplea*.

Anepeorus (Anepeorinae) has been extremely rare, but Dr. Dennis LEHMKUHL, University of Saskatchewan, has collected a series of nymphs from several localities in the North and South Saskatchewan Rivers. According to Dr. LEHMKUHL, the nymphs were usually collected in two or three feet of water, in moderate to swift current from firmly-compacted, rubble-laden substrate or loose gravel. In the laboratory the nymphs showed preference to rocks rather than sand substrate and were active predators. Although one species has been described from China by ULMER (1936) on the basis of a female imago, we consider the record as doubtful, and believe the genus to be restricted to North America.

The North American genus *Pseudiron* (Pseudironinae) is a highly-specialized, sand-dwelling form in which the structural modifications of the nymph, to this environment, have resulted in the placement of this genus in various families or as a separate family in itself. While the affinities of this genus are not fully understood at this time, we are presently maintaining it as a member of the family. *Pseudiron* has two non-Heptageniidae characteristics in that the hind tarsi of the adult has only four clearly-differentiated segments, and that the maxillary palpi of the nymph is three-segmented. Additional study may show that the genus is not of the same phyletic lineage of the Heptageniidae.

The Holarctic genus *Arthroplea* (Arthropleinae) too is a highly-modified form whose nymphs are restricted to standing or slow-moving waters of North America and Europe. While highly apomorphic, evidence from nymphal mouthparts and male genitalia indicates that this genus evolved later than either *Anepeorus* or *Pseudiron*.

RÉSUMÉ

Quelques relations phylogénétiques entre les Heptageniidae

La famille des Heptageniidae est constituée par quatre subfamilles et par vingt-huit genres actuels. Les subfamilles Anepeorinae, Pseudironinae et Arthropleinae représentent des lignées anciennes avec certains caractères hautement apomorphiques. Une meilleure compréhension de leurs relations avec la subfamille des Heptageniinae est nécessaire avant de proposer une interprétation de leur phylogénie. La subfamille des Heptageniinae a évolué en un groupe relativement homogène, ce qui en fait un groupe relativement avancé par rapport à leurs ancêtres hypothétiques : les pré-Isonychiinae. Trois lignées phylogénétiques peuvent être distinguées :

la lignée IA représentant les genres les plus plésiomorphiques de la subfamille, la lignée IB représentant les genres apomorphiques, et la lignée II représentant les genres plésiomorphiques dont les larves possèdent deux cerques.

Zusammenfassung

Einige phylogenetische Verwandtschaften innerhalb der Familie Heptageniidae

Die Familie Heptageniidae ist aus vier Subfamilien und achtundzwanzig wirklichen Gattungen zusammengesetzt. Die Subfamilien Anepeorinae, Pseudironinae und Arthropleinae verkörpern alte Abstammungslinien mit einigen hoch apomorphischen Charakteren. Ein besseres Verständnis von deren Verwandtschaft zu der Subfamilie Heptageniinae ist notwendig bevor eine bedeutungsvolle Analyse von deren Phylogenie vorgeschlagen werden kann.

Die Subfamilie Heptageniinae ist als eine verhaltnismässig homogene Gruppe evolviert, und ist ziemlich von den hypothetischen Pre-Isonychiinae Ahnen vorgeschritten. Drei Hauptphyletische Linien können erkannt werden : Linie IA, welche die meisten plesiomorphischen Gattungen der Subfamilie vertritt; Linie IB, welche die apomorphischen Gattungen repräsentiert; und Linie II, die die plesiomorphische Gattung, deren Nymphen zwei caudale Fäden haben, vertritt.

Discussion

R. Allen : The distribution of *Ironopsis* is different from that of *Epeorus*, *Iron*, and *Ironodes*. *Ironopsis* represents a very interesting distributional pattern in that the two North American species occur only in the upper northwestern part of North America — Oregon, British Columbia and that area. I have recently collected an *Ironopsis* is Central America and in southern Mexico. So there are two species in Oregon, British Columbia and Washington and one species in southern Mexico and Central America.

S. Jensen : I might add also that the genus has been reported in the literature in the Himalaya Mountains.

J. Jones : I notice that your phylogenetic diagram is tentative. I would like to know to what degree ?

S. Jensen : This represents about three years of concentrated effort on this family, and some of the pieces are now falling into place. This is tentative to the extent that I don't fully understand all of the relationships at this time, and there are a number of genera that I haven't included here that I hope to be able to understand. I have some very definite problems in getting material from the Oriental Region, especially China, and there is a large complex of species there that I don't really understand at this time. So when you ask how tentative the diagram is, it is subject to extensive revision.

R. Koss : What happened to *Iron* on your diagram ?

S. Jensen : It is represented by *Epeorus*. I consider *Epeorus* and *Iron* to be synonymous even so far as calling them subgenera at the present time. The true European *Epeorus* is quite a distinctive form, but when you get into North America and consider the *albertae*-type and the *longimanus*-type, there are some problems. The problem is complicated further by serveral unique forms in Europe that have been described in the wrong genus. We are currently trying to work them out.

E. RIEK : There is another very unheptageniid-like character in *Pseudiron*. That is in the caudal filaments. These are the siphlonurid-type with the hair fringes lateral; whereas, all the other Heptageniidae in your classification have hairs in whorls around the caudal filament segments.

S. JENSEN : I am aware of this. *Pseudiron* presents a perplexing problem and I hope to learn much more. I am going to work on the internal anatomy of the nymph later and try to better understand it. So far, as I mentioned in my paper, I have concentrated by efforts on the subfamily Heptageniinae. It is very possible that *Pseudiron* is not on the same lineage that gave rise to the Heptageniinae.

E. RIEK : In my classification *Pseudiron* is a Siphlonuridae or more in a siphlonurid complex. I wouldn't put it in Siphlonuridae at the moment.

L. BRUNDIN : Is group A in the diagram dependent on progressing apomorphic characters ?

S. JENSEN : Yes, it is.

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