

THE CLADISTICS, CLASSIFICATION, AND EVOLUTION OF THE HEPTAGENIOIDEA (EPHEMEROPTERA)

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ABSTRACT

Cladistic analysis based on 36 characters whose polarities were determinable with reference to the outgroup Siphonurinae indicated that Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae constitute a monophyletic group. The resultant highly parsimonious cladogram shows that Coloburiscidae branched earliest, and of remaining lineages, Isonychiidae branched next, with Oligoneuriidae and Heptageniidae representing sister lineages. Family status for each lineage and their classification in a separate superfamily Heptagenioidea is indicated. Consideration of behavioral and ecological data with respect to phyletics allows theorizing of evolutionary history of the superfamily, which commenced with the invasion of fast flowing habitats and development of passive suspension feeding.

INTRODUCTION

The Isonychiinae and Coloburiscinae were considered as subfamilies of Siphonuridae by Edmunds et al. (1963). Riek (1973) instead placed them in the Oligoneuriidae, first recognizing their affinities with that family. Landa (1973) considered them as families derived with the Oligoneuriidae and Heptageniidae as evidenced by internal anatomy. McCafferty & Edmunds (1979) agreed with Riek (1973) regarding family placement, but also provided additional evidence that the Heptageniidae were closely related to the Oligoneuriidae. Landa & Soldán (1985) agreed with McCafferty & Edmunds (1979). McCafferty (1990) has recognized, and herein gives evidences for, family status for Isonychiidae and Coloburiscidae.

Edmunds & Traver (1954) included a number of mainly primitive families of Ephemeroptera in the superfamily Heptagenioidea. Demoulin's (1958) concept of the superfamily was more restricted but included phyletically unrelated families. Tshernova (1970) restricted the concept of the superfamily Heptagenioidea to include only the Heptageniidae and the fossil family Epeoromimidae. McCafferty & Edmunds (1979) changed the name of Heptagenioidea (sensu Edmunds & Traver 1954) to Baetoidea. They also showed that the taxon was awkward because it contained lineages that gave rise to virtually all modern mayfly families and thus was extremely paraphyletic.

Landa & Soldán (1985) restricted the Heptagenioidea to include only Heptageniidae, Oligoneuriidae, and Epeoromimidae. McCafferty (1990) considered the Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae to constitute the Heptagenioidea, and gave reasons for excluding Epeoromimidae. Evidence for the distinctive, monophyletic nature of this grouping of families is elaborated herein.

Although workers are generally in agreement that these groups are inter-related, phylogeny reconstruction has been problematic, with branching sequences either suggested on the basis of phenetic similarities, or unresolvable. Edmunds (1973) showed Isonychiidae and Coloburiscidae as sister lineages derived in common with Oligoneuriidae. Although Riek (1973) showed Coloburiscinae branching earliest among his Oligoneuriidae, he found no apomorphy in common between the other lineages, and his conclusion was thus based only on symplesiomorphic gills. Landa (1973) drew a similar branching sequence and also included Heptageniidae as branching even earlier than Coloburiscidae. McCafferty & Edmunds (1979) suggested a similar earliest branching of Heptageniidae. They also stated that precise points of phyletic origin of Isonychiinae and Coloburiscinae, relative to each other, were unclear because synapomorphies could not be found. Landa & Soldán (1985) concurred.

A primary objective of this study was to resolve the phylogeny of the four major lineages of Heptagenioidea by employing a rigorous cladistic analysis.

METHODS

The cladistic study was based on 36 empirical characters (Table 1). All characters were structural characters having homologous states distributed among the outgroup and the study lineages. They included only characters whose polarities (Table 1) were determinable by reference to the outgroup Siphonurinae. Plesiomorphies of characters 9, 10, 17, 35, and 36 (Table 1) are actually transitional apomorphies found in some of the lineages and first expressed in characters 2, 3, 4, 8, and 13, respectively. They are all clearly intermediate between the outgroup plesiomorphy and their eventual most derived state expressed in some other lineages. Ross (1974) referred to such series as phenoclines.

Certain larval exoskeletal morphology, adult wing venation, and internal anatomy qualified as empirical characters. Data on the distribution of larval morphology were based on examination of all Isonychiidae and extant Coloburiscidae genera and most genera of Oligoneuriidae and Heptageniidae. The only critical genus unavailable to me as larvae was *Chromarcys*, for which I relied on published reports, esp. Ulmer (1939). Internal anatomy data were based on Landa & Soldán (1985). Data on wing venation were based on the examination of adults of *Isonychia* (Isonychiidae), *Coloburiscus* (Coloburiscidae), *Chromarcys* (Oligoneuriidae), most genera of Heptageniidae, and published reports on all others.

When cladistically analyzing superspecific lineages, or taxa above the

species level, they must be represented by characteristics of their most ancestral members (Wiley 1981) because of the possibility of subsequent evolution within the lineages being compared. Thus, in those few instances herein where a particular character state varies within a lineage, the state found in the ancestral genera of that lineage is used. For example, with reference to character 1 (Table 1), maxillary and labial setation is highly developed in nearly all genera of Heptageniidae, including all but the most apomorphic genera (Jensen & Edmunds 1973, McCafferty & Provonsha 1986) that have become specialized predators. Therefore in analyzing the groups under investigation, setaceous maxillae and labia characterize the heptageniid lineage.

Relative relationships within lineages are not a consideration in Iso-nychiidae because the family is monogeneric. *Coloburiscus* could qualify as ancestral in the Coloburiscidae, given the sister relationship of *Murphyella* and *Coloburiscoides* (Edmunds 1975, McCafferty & Edmunds 1979). It follows that, although abdominal gills are lost in the genus *Murphyella*, the coloburiscid lineage can still be compared with others in terms of abdominal gill characteristics (characters 5 & 25). *Chromarcys* (subfamily Chromarcyinae) qualifies as an ancestral genus in the Oligoneuriidae (Edmunds 1975, McCafferty 1990), as does *Elassoneuria* (subfamily Oligoneurinae). In fact, in terms of wing venation used herein, *Chromarcys* is the only oligoneuriid that may be used to characterize the lineage because it is the only oligoneuriid that retains basic ephemeropteran venation. Wings of other extant oligoneuriids are highly specialized by gemination of veins and reduction of venation for a rapid, sculling type of flight that is atypical of Ephemeroptera.

The principle of parsimony was used to determine cladogram feasibility. Monophyly was the primary criterion for family level recognition. From the sequence of phyletic branching indicated by the cladogram, deductions about the evolution of nonempirical characters, i.e. characters not having homologues in the outgroup, were possible. When functional, behavioral, and ecological characteristics of lineages were superimposed on the cladogram, evolutionary history could be theorized.

CLADISTICS

The results of this study are essentially given by the cladogram and distributions of apomorphies (Fig. 1). Apomorphies 1-18 are evidential synapomorphies, 19-20 are specious apomorphies whose incongruity will be explained below, and 21-36 are autapomorphies. The branching sequence is supported by 10 character distributions (apomorphies 9-18). Figure 1 is by far the most parsimonious cladogram that could be generated from the character distributions, with only two possible incongruities expressed by the distribution of characters 19 and 20. The only alternative branching sequence would show Heptageniidae branching earliest on the basis of these two apparent synapomorphies shared by the three other lineages. However, to accept such a branching sequence, one also must accept six instances of

convergent evolution occurring independently in Heptageniidae and Oligoneuriidae, and an additional four convergences between Heptageniidae and an Oligoneuriidae-Isonychiidae clade. The occurrence of such a large number and variety of convergences involving different life stages appears untenable.

The incongruent characters 19 and 20 pertain to the filtering setae on the forelegs (Fig. 8), and the gill tufts at the base of the maxillae. There are two possible explanations for their distribution. The characteristics may have evolved independently in each lineage, however, this appears to be a highly remote possibility. Rather, these characteristics had probably already evolved ancestrally in the Heptagenioidea along with apomorphies 1-8 (Fig. 1); they would have been subsequently lost (technically a reversal) in Heptageniidae. Since they are both "presence or absence" characters, the probable loss of foreleg setae and maxillary gills mimics the plesiomorphic absence of these attributes in the outgroup Siphonurinae. The latter explanation is consistent with data from ecology and behavior, discussed below.

Some evidential characters are particularly noteworthy. The advanced Malpighian tubule connections (character 12) found in all but the coloburiscid and outgroup lineages appear to be a major evolutionary advance. An exemplary phenocline is seen in characters 2 and 9 (Figs. 11, 13, 15), where there is a transition from a clearly 3-segmented maxillary palp in the outgroup, to a loss of the articulation between the second and third segments but presence of a vestigial suture in the coloburiscids, to finally the loss of any indication of the former two segments in others. The same segmentation phenocline can also be found in the labial palps (characters 3 & 10, Figs. 12, 14, 16a).

Some other important synapomorphies are those that show the sister relationship between the Heptageniidae and Oligoneuriidae. These include major modifications of the larval head (characters 13-15, Figs. 6, 7, 9, 10) from that found in Isonychiidae, Coloburiscidae, Siphonurinae, and minnowlike mayflies in general. Also, wing venation characters 16-18 (Figs. 27, 28) proved to be particularly instructive. The forewings of Heptageniidae and Oligoneuriidae (as expressed by the ancestral genus *Chromarcys*) are essentially similar.

CLASSIFICATION

With reference to the cladogram (Fig. 1) and adherence to monophyletic criteria, there are four options for a cladistic family classification. All lineages could be included in one family. I do not accept this as a viable option because of the divergence of these lineages and historical integrity of at least Heptageniidae and Oligoneuriidae, *sensu stricto*, (Table 2). In recognizing more than one family, family status for Coloburiscidae is mandated by its phyletic position. The second and third options include one or two other families besides Coloburiscidae. I reject these options for the same reasons for rejecting the first option, since in either case, Heptageniidae and Oligoneuriidae would have to be combined into one family. The fourth option,

and most acceptable cladistic classification, recognizes each lineage as a distinct family. These four families are distinguishable not only phyletically but also by a number of diagnostic autapomorphies in each lineage (characters 21-36).

The only other classification that is not artificial is also not strictly cladistic. It would recognize the isonychiid and oligoneuriid lineages together in the Oligoneuriidae. Even though this classification would technically qualify as an "evolutionary" classification, it would give such a family paraphyletic status. While it can be argued that paraphyletic classifications are sometimes more useful in showing evolutionary grades, no informative or practical purpose is served by such a paraphyletic classification in this particular instance.

The recognition of superfamily status for this grouping of families is clearly defensible. It is a monophyletic group definable by apomorphies 1-8 (Fig. 1, Table 1) shared by all its daughter lineages.

EVOLUTION

The Heptagenioidea probably originated in the Jurassic and at least the oligoneuriid grade of evolution had been reached by the Lower Cretaceous. Sinitshenkova (1985) has dated coloburiscids to the Jurassic and McCafferty (1990) has found oligoneuriids from the Lower Cretaceous. All four families are known from the Tertiary. A brief theoretical outline of the evolutionary history of the superfamily with respect to ecology and behavior is now possible given the sequence of lineage and character evolution indicated by the cladogram.

The invasion of flowing-water habitats and accompanying evolution of passive filter feeding marked the origin of the Heptagenioidea. The ancestral heptagenioids were derived from a generalist siphonurine-like ancestor that had lived in still or only gently flowing waters (Sinitshenkova 1984, Edmunds & McCafferty 1988). This "new" environment and "new" abundant source of stream food must have provided much of the impetus for further radiation of the Heptagenioidea. Passive filtering of seston was accomplished by well-developed setae on the forelegs and mouthparts. Maxillary gills were also exposed to flowing water.

This grade of evolution is represented by the Coloburiscidae and Isonychiidae, which retain minnowlike bodies, a distinct clypeus, hypognathous mouthparts, an unmodified head capsule, and relatively ancestral wing venation. Behaviorally, the coloburiscids and isonychiids can leave the water to emerge, or emerge at the water surface (Edmunds & McCafferty 1988). Such facultative behavior appears to be intermediate to the still-water siphonurine habit of leaving the water to emerge and the habit of surface emergence found in the oligoneuriids and heptageniids. Edmunds & McCafferty (1988) showed that the behavioral shift to surface emergence in most Ephemeroptera was probably related to the invasion of strong-flowing waters where larvae would have more difficulty crawling out of the water.

Although the Coloburiscidae branched earliest, the Isonychiidae have changed least. This is reflected by the number of autapomorphies found in each lineage. Moreover, although isonychiids remain fixed, facing the current, when filtering, they are also strong swimmers, as are primitive minnow-like mayflies (McCafferty 1990). Coloburiscids, on the other hand, have become less prone to swim (Edmunds pers. comm.).

The oligoneuriid-heptageniid ancestor was still minnowlike; however, along with several other apomorphies (Fig. 1), the head capsule came to form an inverted epicranial cup or hood (Fig. 6) whose peripheral ledge covered bases of the mouthparts, which significantly had also become prognathous. This grade is represented by the Oligoneuriidae. More ancestral oligoneuriids remain quite minnowlike, and Edmunds (1975) noted that the minnow-like *Elassoneuria* is similar to *Isonychia* in behavior. This is also true for *Chromarcys* (McCafferty & Edmunds 1979). One of the considerable autapomorphies in the Oligoneuriidae involved the extraordinary enlargement and fusion of the glossae to form a unique ventral plate under the head (Fig. 18).

Feeding behavior of oligoneuriids has not been studied in detail as it has for *Isonychia* (Wallace & O'Hop 1979, McShaffrey unpublished) and certain heptageniids (McShaffrey & McCafferty 1986, 1988). However, from these studies and morphological comparisons, it appears that oligoneuriid mouthparts lost much of the capacity for passive filtering. Also, reduced mandibles suggest that oligoneuriids also lost the capacity for carnivory that was maintained in earlier lineages of heptagenioids. Considering the row of gill tufts developed along the base of the labium in oligoneuriids, the thoracic area would have to remain lifted above the substrate. This would agree with the forelegs being positioned to passively filter, thus lifting the body. The epicranial cup, especially if bent down, would divert flow around the head. Such orientation along with the ventral enclosure by the labial plate suggest that many of the mouthparts would be protected from the current while processing food. Fields of setae would be maintained for such processing or removing particles from the legs.

Water diverted by the modified oligoneuriid head would create turbulence. Forelegs may not form actual catchbaskets as found in isonychiids, but being more outspread would take advantage of diverted flow and any scouring effect of turbulence. The orientation of the body to the substrate is probably directly related to body form in oligoneuriids. Highly derived, more dorsoventrally flattened forms would be expected to demonstrate a closer orientation to the substrate.

All oligoneuriids, other than *Chromarcys*, have highly specialized wings. Nevertheless, heptageniid venation (Fig. 28) shows a definite common derivation with the ancestral oligoneuriid type seen in *Chromarcys* (Fig. 27). It should also be noted that two derived genera of oligoneuriids are highly specialized sand dwellers that do not, in all respects, typify the oligoneuriid grade of evolution. In the same sense, highly derived heptageniid genera, e.g. predators, do not necessarily reflect the following discussion of the

heptageniid grade of evolution.

With respect to the advanced heptageniid lineage, larvae remained stream inhabitants, but became adapted for bottom feeding rather than passive suspension feeding. Some tendency toward this evolution was already seen in certain head and mouthpart modifications and orientation in the oligoneuriids and thus would have been present in the common ancestor to both families. Along with bottom feeding, came the possibility of a number of "new" food materials and "new" stream niches as well as flexibility in resource utilization. The realization of such ecological potentialities may have been primary factors leading to the relatively extensive adaptive radiation in the Heptageniidae.

In the Heptageniidae the epicranial cup became more flattened and expanded (Figs. 9, 10). Maxillary gills were lost, probably due to the fact that mouthparts were no longer directly exposed to the current. The body was also flattened and appressed to the substrate, and filtering setae of the forelegs were lost. The flat head and prognathous mouthparts provide a feeding system well suited to gathering food associated with the substrate. Fields of differently adapted setae on the mouthparts are used variously to brush, scrape, and collect food. McShaffrey & McCafferty (1986, 1988) found that certain fields of setae are used to process materials through the mouth. Finally, the flattened body affords access to microhabitats that were unavailable to minnowlike mayflies.

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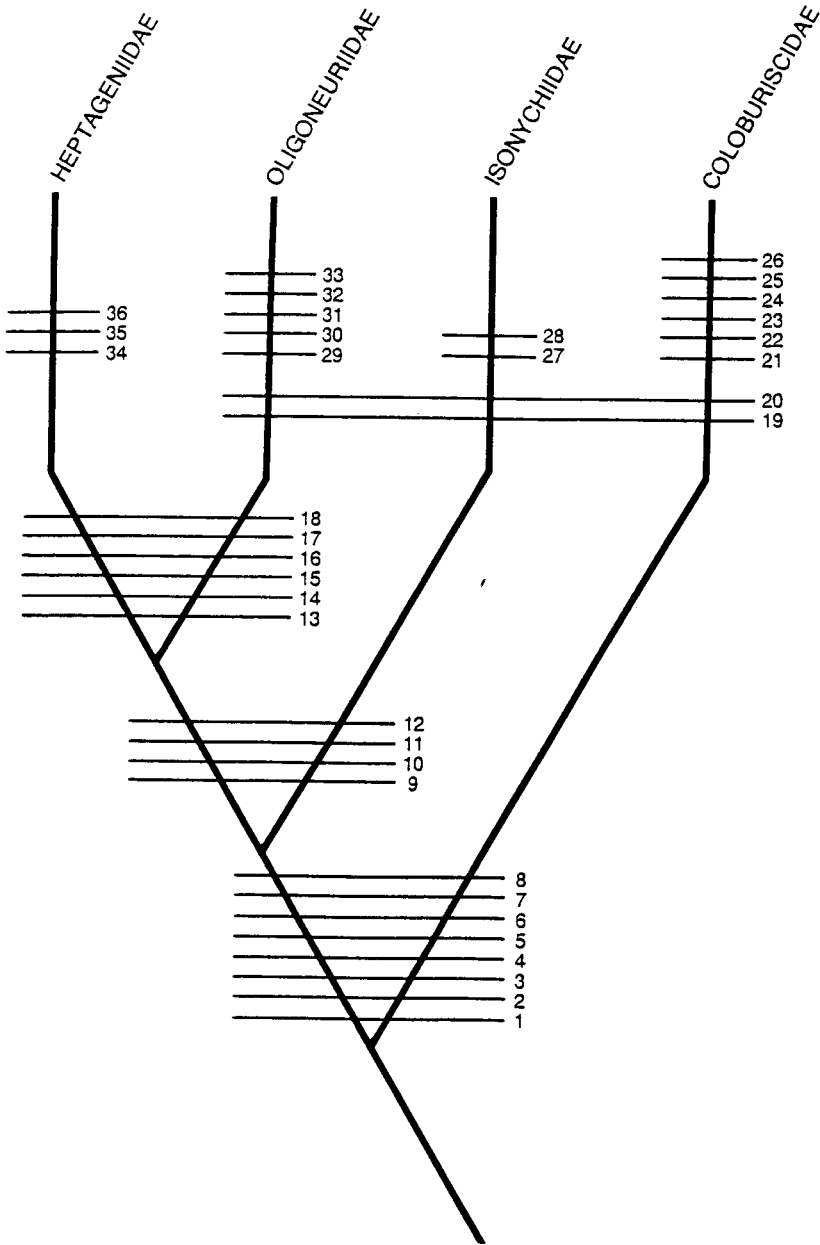
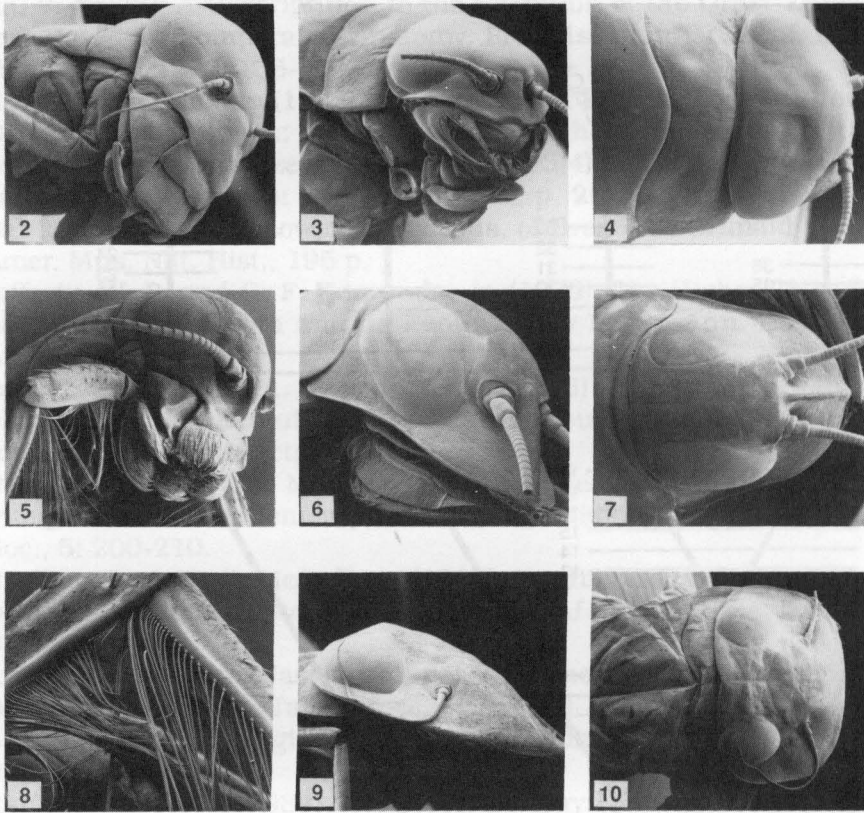
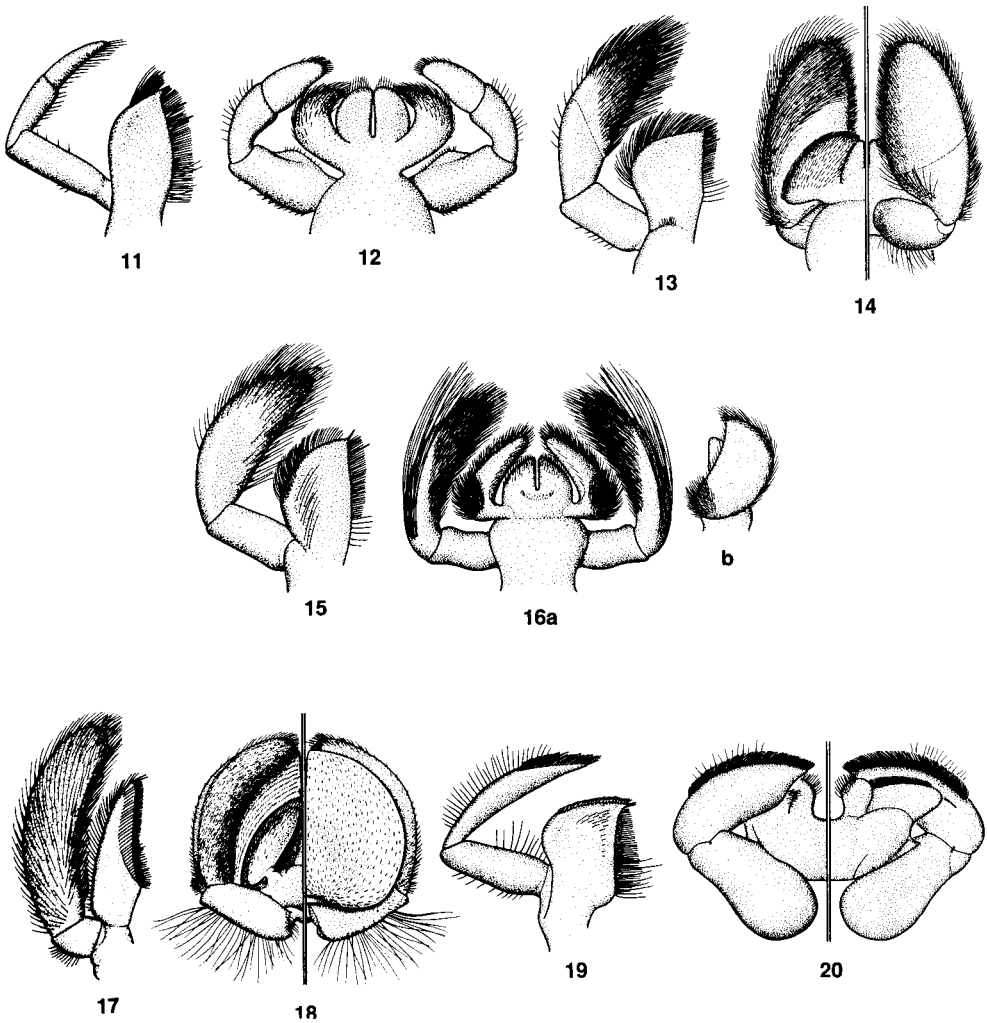


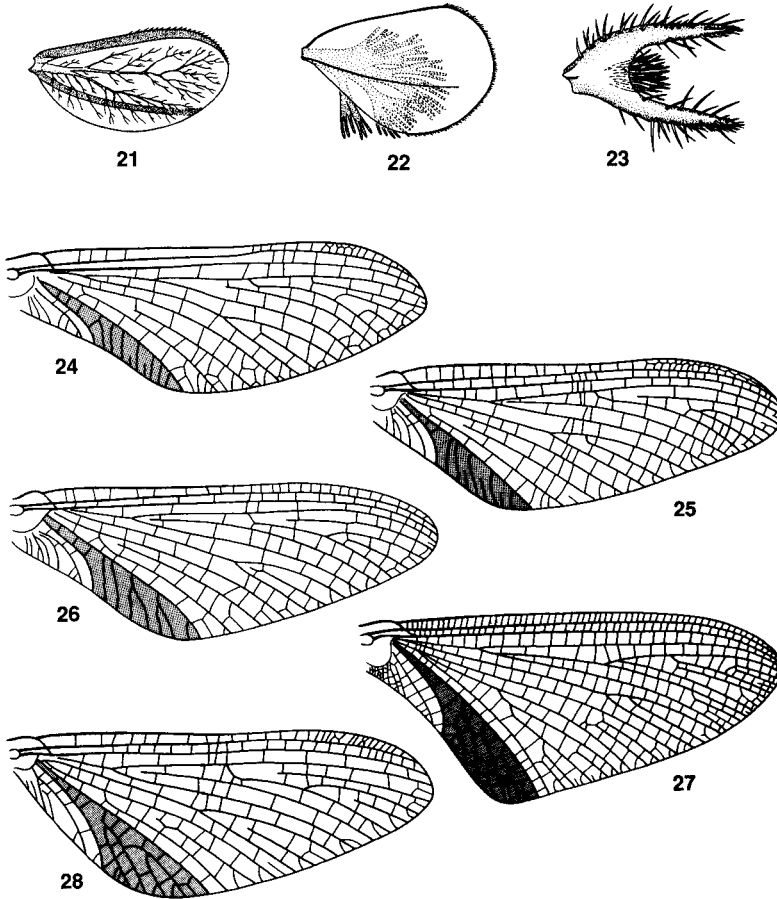
Fig. 1. Cladogram of the Heptagenioidea. Horizontal lines represent distributions of apomorphies. Numbers correspond to numbered characters in Table 1. Apomorphies 1-18 = evidential synapomorphies, 19-20 = species apomorphies (see text for explanation of incongruity), 21-36 = autapomorphies.



Figs. 2-10. Scanning electron micrographs. 2. *Siphonurus*, anterolateral head. 3-4. *Coloburiscus*: 3, anterolateral head, 4, dorsal head. 5. *Isonychia*, anterolateral head. 6-7. *Elassoneuria*: 6, anterolateral head, 7, dorsal head. 8. *Isonychia* foreleg, filtering setae. 9-10. *Stenonema*: 9, anterolateral head, 10, dorsal head.



Figs. 11-20. Maxillae & labia. 11-12. *Siphonurus*: 11, maxilla, 12, labium, dorsal. 13-14. *Coloburiscus*: 13, maxilla, 14, labium, dorsal/ventral. 15-16. *Isonychia*: 15, maxilla, 16a, dorsal labium, 16b, lateral paraglossa. 17-18. *Elassoneuria*: 17, maxilla, 18, labium, dorsal/ventral. 19-20. *Afronurus*: 19, maxilla, 20, labium, dorsal/ventral.



Figs. 21-23. Gill 4. 21. *Ameletus*. 22. *Isonychia*. 23. *Coloburiscoides*. 24-28. Forewings (cubital area shaded). 24. *Siphonurus*. 25. *Coloburiscus*. 26. *Isonychia*. 27. *Chromarcys*. 28. *Rhithrogena*.

Table 1. Structural characters and character state polarities used as empirical data for deriving cladistic relationships. Numbered characters correspond to the numbered apomorphies distributed on the cladogram, Figure 1. All characters except adult wing venational characters are referable to larvae. Character states with asterisks may be viewed as transitional states for characters with more than two character states.

Character	Plesiomorphy	Apomorphy
1. Maxillary & labial vestiture	Poorly developed (Figs. 11,12)	Highly developed (Figs. 13-20)
2. Maxillary palp segmentation	3-segmented (Fig. 11)	*2nd & 3rd segments fused (Figs. 13,15, 17,19) [see 9]
3. Labial palp segmentation	3-segmented (Fig. 12)	*2nd & 3rd segments fused (Figs. 14, 16a,18,20) [see 10]
4. Labial palp width	Narrow (Fig. 12)	*At least somewhat broadened (Figs. 14, 16a,18,20) [see 36]
5. Abdominal gills	Lamella only (Fig. 21)	Lamella & basal filamentous tufts (Figs. 22,23)
6. Main anterior branch of tracheal trunk	Leads to maxillae	Leads to labium
7. Gonads position	Dorsal to alimentary canal	Dorsolateral or lateral
8. Forewing cubital intercalaries angle	Near right angle with CuA (Fig. 24)	*Some distal veins subparallel CuA (Figs. 25-28) [see 17]
9. Maxillary palp segmentation	*2nd & 3rd segment vestiges evident (Fig. 13) [see 2]	2-segmented, fusion lines absent (Figs. 15,17,19)
10. Labial palp segmentation	*2nd & 3rd segment vestiges evident (Fig. 14) [see 3]	2-segmented, fusion lines absent (Figs. 16a,18,20)
11. Paraglossae size	Small (Figs. 12,14)	Somewhat enlarged (Figs. 16b,18,20)

Table 1, Cont.

Character	Plesiomorphy	Apomorphy
12. Malpighian tubules connections	Tubules enter narrow band around colon	Tubules enter 4 pairs of trunks
13. Epicranium	Not expanded peripherally (Figs. 2-5)	*Cuplike, expanded over mouthpart bases (Figs. 6,7,9,10) [see 35]
14. Mouthpart orientation	Hypognathous (Figs. 2,3,5)	Prognathous (Figs. 6,9)
15. Clypeus	Well developed (Figs. 2,3,5)	Reduced, indistinguishable
16. Forewing cubital crossveins	Absent (Figs. 24-26)	Present (Figs. 27,28)
17. Forewing cubital intercalaries	*Distal veins subparallel CuA (Figs. 25,26) [see 8]	All intercalaries subparallel CuA (Figs. 27,28)
18. Forewing cubital composition	Several veinlets (Figs. 24-26)	2 pairs of major intercalaries (Figs. 27,28)
19. Maxillary gill tufts	Absent	Present
20. Foreleg filtering setae	Absent	Present (Fig. 8)
21. General spination & sclerotization	Little or moderate development	Well developed
22. Mandibular vestiture	No setal patch on face	Well-developed setal patch
23. Labial palp orientation	Lateral to labium (Figs. 12,16a,18,20)	Ventral to labium (Fig. 14)
24. Filtering setae on middle legs	Absent	Present
25. Abdominal gill lamella	Somewhat oval (Figs. 21,22)	Fork shaped or absent (Fig. 23)
26. Extent of testes	In abdominal segments 1-6	In abdominal segments 3-6

Table 1, cont.

Character	Plesiomorphy	Apomorphy
27. Forecoxal filamentous gills	Absent	Present
28. Fork of MP in hindwing	Near middle or not forked	Near outer margin
29. Galealacinia	Broad apically (Figs. 11,13,15,19)	Narrow apically (Fig. 17)
30. Maxillary palps	Segments subequal (Figs. 11,13,15,19)	2nd segment much longer (Fig. 17)
31. Glossae	Small, generalized (Figs. 12,14,16,20)	Fused into large labial plate (Fig. 18)
32. Labial palps	Basally outspread (Figs. 12,14,16,20)	Juxtaposed laterally with glossae (Fig. 18)
33. Labial gill tufts	Not developed along ventral base	Developed along ventral base
34. Body	Near cylindrical	Dorsoventrally flattened
35. Epicranium	*Epicranial cup developed (Figs. 6,7) [see 13]	Cup flattened & laterally expanded (Figs. 9,10)
36. Labial palp width	*Somewhat broadened (Figs. 14,16a,18) [see 4]	Very broadened basally (Fig. 20)

Table 2. Synoptic history of the classification of the families of Heptagenioidea. Citations include the initial concept as a supergeneric group, authorship of the supergeneric named taxon if different, and the first subsequent instances of different names, ranks, or interpretations.

Family	Equivalent
Coloburiscidae	Coloburiscinae Edmunds, 1963 [in Siphonuridae] Coloburiscinae [in Oligoneuriidae] (Riek 1973) Coloburiscidae (Landa 1973)
Isonychiidae	Isonychiinae Burks, 1953 [in Baetidae] Isonychiidae (Edmunds & Traver 1954) Isonychiinae [in Siphonuridae] (Edmunds <i>et al.</i> 1963) Isonychiinae [in Oligoneuriidae] (Riek 1973)
Oligoneuriidae	Group I, Series I, Section 1, Subsection B [in Ephemeridae] (Eaton 1883) Oligoneuriidae Ulmer, 1914 Oligoneuriinae [in Ephemeridae] (Handlirsch 1925) Oligoneuriinae [in Baetidae] (Needham <i>et al.</i> 1935) Oligoneuriidae + Chromarcyidae Demoulin, 1953 (Tshernova 1970)
Heptageniidae	Group III, Series III [in Ephemeridae] (Eaton 1883) Heptageniinae Needham, 1901 [in Ephemeridae] Ecdyonuridae Klapalek, 1909 Heptageniidae (Bengtsson 1917) Ecdyurini Handlirsch, 1925 [in Siphurinae] Arthropleidae Balthasar, 1939 Heptageniidae [partim] (Edmunds & Traver 1954)