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Comparative Mouthpart Morphology and Evolution of the Carnivorous Heptageniidae (Ephemeroptera)[1]

by

W. P. McCAFFERTY and A. V. PROVONSHA

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Mouthparts of the carnivorous mayfly larvae in the family Heptageniidae are detailed and compared to each other as well as to generalized, non-carnivorous heptageniid mouthparts. The three carnivorous forms are presently classified in the genera *Anepeorus, Spinadis,* and *Pseudiron,* although proper application of these names to larval stages is tentative. Autapomorphies in each of the carnivores are numerous. General loss of setae and development of impaling structures are not used as phyletic data since they are subject to convergence in carnivores in general; however, synapomorphies involving maxillary crown spinal plates, the superlinguae, and labial palpi suggest a common carnivorous ancestor for the group and strongly suggest that *Spinadis* and *Pseudiron* are sister groups. General facies support this. Behavioral studies indicate that, contrary to previous reports and drawings, the legs of live *Pseudiron* larvae orient forward and the femoral setal row is posterior, just as in other heptageniids.

W. P. McCAFFERTY and A. V. PROVONSHA, Department of Entomology, Purdue University, West Lafayette, IN 47907, U.S.A.

The family Heptageniidae is a major group of mayflies consisting of some 28 genera and 340 species distributed primarily in the Holarctic and Afrotropical regions but with some representation in the Oriental region and in Middle America. The vast majority of these mayflies belong to the well-known subfamily Heptageniinae. The larvae of Heptageniinae are typically flatheaded forms that are sprawling benthic bottom-feeders on periphyton and/or fine detritus.

Also included in the Heptageniidae, however, are three very distinctive carnivorous forms of larvae. These historically enigmatic mayflies are currently classified respectively as the genera *Pseudiron* McDunnough, *Spinadis* Edmunds and Jensen, and *Anepeorus* McDunnough (possibly with one or two species each), and these genera have been traditionally placed in three separate subfamilies (McCafferty and Edmunds, 1979). They are apparently restricted to North America, and their relationships to each other and the Heptageniinae have been poorly known (Jensen and Edmunds, 1973; McCafferty and Provonsha, 1985). The generic nomenclature applied to those larval forms currently known as *Spinadis* and *Anepeorus* remains provisional because association with nominally based adult forms is tentative (McCafferty and Provonsha, 1985).

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The larvae of the three genera as presently known have been generally described by Edmunds et al. (1976). Also included in that work were whole, dorsal larval figures of all three forms as well as a review of what little biological information was available. Mouthparts of the three forms have not been thoroughly described, and mouthpart figures of *Spinadis* surprisingly have not been published. This is unfortunate since mouthpart adaptations appear to be highly reflective of the derived habit of carnivory and may be particularly informative for deciphering relationships and functional morphology. For this reason a comparative morphology and detailed figures are provided here.

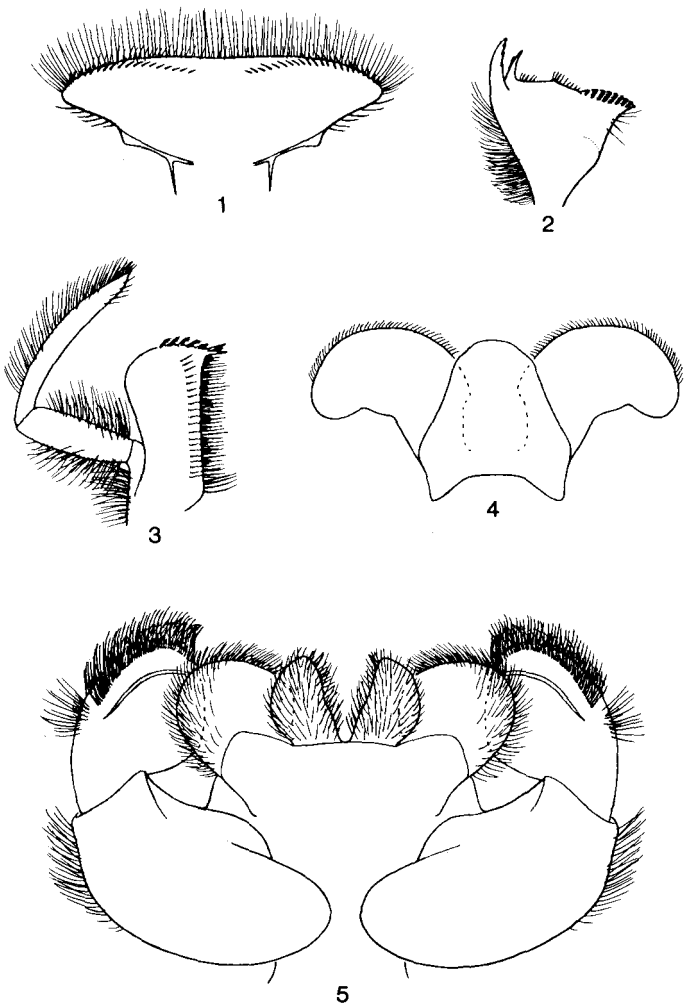
The carnivorous genera of Heptageniidae appear to have evolved from a more generalized, non-carnivorous Heptageniidae ancestor. They share with all other Heptageniidae the distinctive prognathous head with dorsally oriented eyes and antennae in the larvae, and forewings with two pairs of cubital intercalaries in the adults. This fundamental adult mayfly synapomorphy clearly places their affinity with the family Heptageniidae. They are differentiated from Heptageniinae by apomorphic mouthparts associated with carnivory and quite unlike those of other mayflies in general, unique gill structure/orientation, and various spination, setation, and leg segment proportion modifications (see Edmunds et al., 1976). As to whether these three genera are independently or commonly derived we can only speculate at this time. Some fundamental mouthpart and gill similarities among the three carnivorous forms would suggest that they form a monophyletic grouping, although the possibility of convergences between them cannot be entirely ruled out since some reductionist tendencies concomitant with a predatory habit, such as the loss of setae, can be particularly subject to convergence. In regards to the point of origin relative to Heptageniinae, we cannot determine at this time if the carnivorous lineage, or lineages, are a sister group(s) sharing a proto-Heptageniidae ancestor with a seperate Heptageniinae lineage, or if they have evolved from a particular lineage within the Heptageniinae proper. No higher classificatory changes are recommended until such phylogenetic questions are resolved; however, our data, below, suggest that an eventual revision may be necessary.

Figures of typical generalized mouthparts in Heptageniinae (Fig. 1-5) are included for comparative purposes.

The labra of carnivorous heptageniids are generally similar and relatively short and broad (Fig. 10). They are not unique, nor do they appear to offer any advantage for handling prey; however, they do differ from Heptageniinae in being considerably less setiferous than their filter-feeding counterparts (Fig. 1).

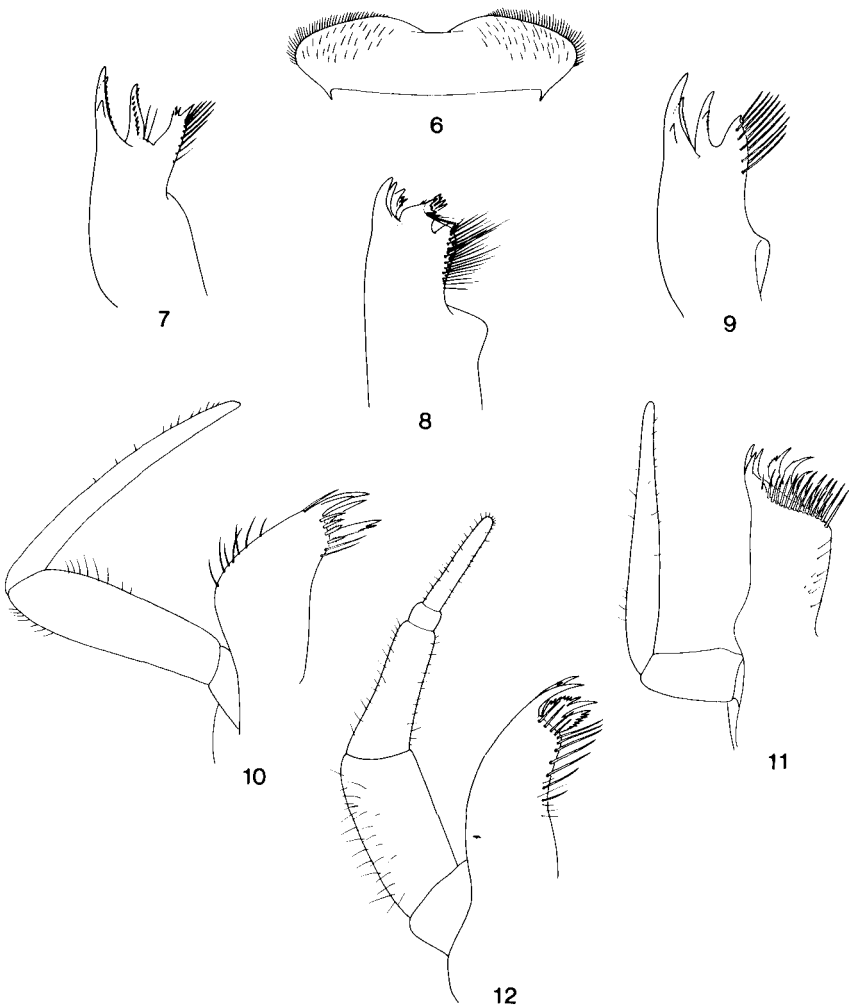
The mandibles of carnivorous heptageniids (Fig. 7-9) are highly evolved from the generalized form (Fig. 2). Essentially, a grinding or packing structure has become an impaling structure. The molar regions of all three are entirely reduced, and the medial region has been produced apically to form a process analogous with the incisors but having medial stout setae. The incisors, themselves, appear most derived in *Spinadis* (Fig. 8), whereas the medial process is most extensively developed in *Anepeorus* (Fig. 7). The seeming lack of synapomorphies when comparing the three carnivorous mandibles precludes a deduction about relationships based on this mouthpart.

The galealaciniae of the carnivores (Fig. 10-12) are all narrowed and equipped with well-developed apical spination, as opposed to the hair setae or small spine-



Figs. 1-5: *Stenonema* sp. larva: 1, labrum; 2, right mandible; 3, right maxilla; 4, hypopharynx; 5, labium.

like setae found apically in the Heptageniinae (Fig. 3). The medial row of setae that is generally highly developed in Heptageniinae (Fig. 3) is represented by scattered sparse setae in *Spinadis* (Fig. 11), a row of a few primarily stout setae in *Pseudiron* (Fig. 12), and has been essentially lost in *Anepeorus* (Fig. 10). Only *Anepeorus* possesses any lateral setae on the galealacinia. A few non-carnivorous genera have various setae laterally in this area, but there is no clue as to whether this is an ancestral or derived state in *Anepeorus*. The apex of the galealaciniae of *Anepeorus* and *Pseudiron* is more narrowed than that of *Spinadis*, and *Pseudiron* is equipped with a well-developed spinal plate. The maxillary palpi of all the carnivores have lost most of the setae common in Heptageniinae (Fig. 3) and are



Figs. 6-12: *Anepeorus* sp., *Spinadis* sp., *Pseudiron* sp. larvae: 6, labrum, *Anepeorus*; 7-9, right mandible: 7, *Anepeorus*; 8, *Spinadis*; 9, *Pseudiron*; 10-12, right maxilla: 10, *Anepeorus*; 11, *Spinadis*; 12, *Pseudiron*.

more slender. In *Spinadis* (Fig. 11), segment one is shortened, and in *Pseudiron* (Fig. 12), the palpi are uniquely four-segmented, with a very short third segment.

The loss of setae and the development of sharp spines as reflected in the maxilla are obviously closely associated with the carnivorous habit, but they do not help resolve the question of independent vs. common evolution. Details of the spination, however, may be at least somewhat revealing. Although the carnivorous maxillae generally appear to present an array of only autapomor-

phies when compared to each other, the fact that *Pseudiron* possesses a well-developed spinal plate and *Spinadis* possesses an apparently homologous rudimentary spinal plate represented by three flat and serrate spines having a common base (Fig. 11) may indeed indicate a common ancestry.

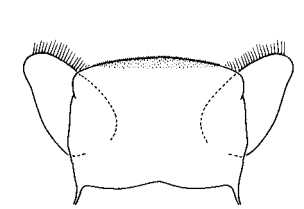
The relative development of the hypopharynx in the carnivorous forms and the Heptageniinae is perhaps the most phylogenetically informative of all the mouthpart variations. The superlinguae of the hypopharynx are reduced in *Anepeorus* (Fig. 13), even more highly reduced in *Spinadis* (Fig. 14), and completely lost in *Pseudiron* (Fig. 15), suggesting a possible evolutionary phenocline from the plesiomorphic state of Heptageniinae (Fig. 4) and mayflies in general, where superlinguae are generally well developed, often more so than the lingua. There are also strong similarities in the shapes of the lingua of *Spinadis* and *Pseudiron*.

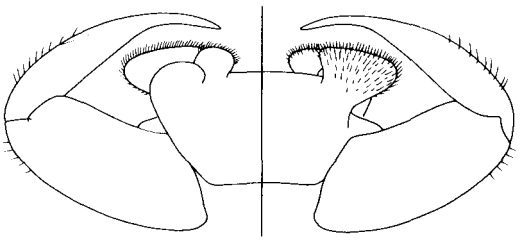
Again, in comparison with Heptageniinae (Fig. 5), the labia of carnivores show a distinct reduction in the amount and extent of setae, especially affecting compact rows or brushes of setae (Fig. 16-18). The glossae and paraglossae appear most ancestral in *Anepeorus*, but the palpi of *Anepeorus* have become uniquely derived raptorial structures (Fig. 16). In *Spinadis*, the glossae and paraglossae have elongated, and the palpi have become highly reduced (Fig. 17). Finally, in *Pseudiron*, the paraglossae are reduced, and the palpi are broadened basally but highly reduced terminally. The palpi of *Anepeorus* have apparently become adapted for impaling or manipulating prey, whereas the entire labium of *Spinadis* and *Pseudiron* has instead perhaps assumed a lower liplike function, especially evidenced by the broadened basal segment of the palpi and the narrowed terminal segment.

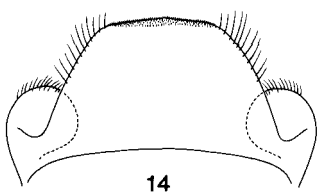
From all of the above, the cladistic evidence that can be gleaned indicates that *Spinadis* and *Pseudiron* are sister groups sharing a common carnivorous ancestor. If all three carnivorous forms are monophyletic, sharing a carnivorous ancestor, as may be indicated from the hypopharynx, then *Anepeorus* represents the earliest derived form. This genus possesses a number of relative ancestral states as well as many autapomorphies associated with mouthpart structure.

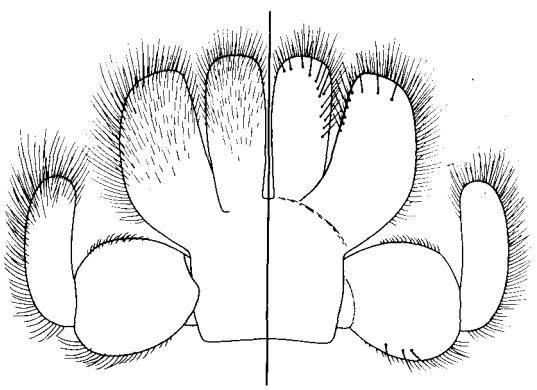
Other larval characters and the general facies of these carnivores do not falsify the phylogenetic hypothesis. The broad, flat head and body form of *Anepeorus* is typical of the Heptageniinae. The most conspicuous apparent autapomorphy is the ventral orientation of the entire series of abdominal gills in *Anepeorus*. The contention then that *Anepeorus* is the most ancestrally derived carnivore, based on mouthpart morphology, would appear to be obvious from its general facies. Given the flattened femora and their resemblance to most Heptageniinae, one may assume that *Anepeorus* is a bottom sprawler group as are most Heptageniinae.

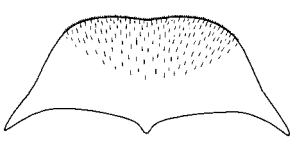
Spinadis and *Pseudiron* share a relatively narrowed head and long slender legs. Among the carnivores, *Spinadis* has uniquely lost the median terminal filament and has developed median, dorsal abdominal tubercles. These two hypothesized sister genera are not as different as one might assume based on the figures of *Pseudiron* by Edmunds et al. (1963, Fig. 67) and Edmunds et al. (1976, Fig. 406) because the legs of *Pseudiron* have been drawn in an unnatural position. Our extensive behavorial observations and stop-action photography of *Pseudiron centralis* McDunnough larvae from the Niobrara River in western

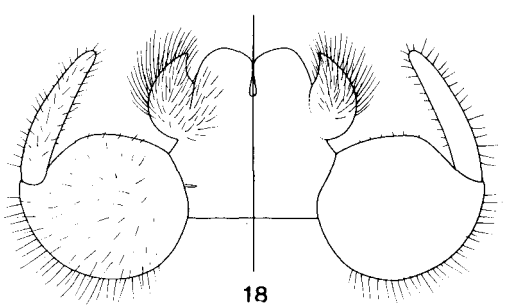












Figs. 13-18: *Anepeorus* sp., *Pseudiron* sp., *Spinadis* sp. larvae: 13-15, hypopharynx: 13, *Anepeorus*; 14, *Spinadis*; 15, *Pseudiron*; 16-18, labium: 16, *Anepeorus*; 17, *Spinadis*; 18, *Pseudiron*.

Nebraska clearly indicated that the legs of live larvae are oriented forward as are those of other heptageniids. Larvae maintain this orientation when at rest or moving crablike sideways and backwards over their sand substrate. When swimming, their legs are tightly folded against the thorax with the femora directed posteriorly and the tibiae and tarsi directed anteriorly. Only when

killed or removed from water were their legs oriented posteriorly as shown in drawings. Edmunds et al. (1976) indicated that posteriorly directed legs anchored the larvae in sand. Our observations did not confirm this. It should also be noted that this unnatural position is attained by a rotation of the legs at the coxa-trochanter joints, and therefore the supposed anterior row of setae on the femora, as it has been drawn, is actually a posterior row in nature, homologous with the posterior femoral setal rows in *Anepeorus* and *Spinadis*.

Based on our studies, it appears that the carnivorous Heptageniidae are much more closely related than has been previously thought. Additional substantiating data from other character sources would perhaps necessitate some revisionary consolidation of the present subfamilial classification. The proper application of the names, *Anepeorus* and *Spinadis* still requires resolution, which can only be attained via rearings and precise adult associations. Adult characters should then yield additional phyletic data. In any case, adult morphology should be very valuable in determining a specific phyletic point of origin. The carnivorous larvae are so modified that they provide no help in this regard. Biogeographically, a North American origin may logically be presumed. Finally, further behavioral observations could be most informative, particularly to determine the degree of sprawling and possibly swimming characteristics of *Spinadis*.

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