

**The Evolution of *Heterocloeon*,
with the First Larval Description of *Heterocloeon frivulus*
comb. n. (Ephemeroptera: Baetidae)**

by

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ABSTRACT

The larva of *Heterocloeon frivulus* (McDunnough) comb. n. is described for the first time. Larval morphology indicates that the species be removed from *Baetis* and placed in the monophyletic genus *Heterocloeon*, and indicates a relatively ancestral position of the species among congeners of *Heterocloeon*. On the basis of considerable new data, a previous phylogeny is falsified in part and a new phylogeny of *Heterocloeon* is hypothesized. *Heterocloeon petersi* and *berneri* are considered to be advanced sibling species. It is also deduced that *Heterocloeon* shared a recent common ancestor with *Pseudocloeon* and certain derived *Baetis*.

The North American genus *Heterocloeon* McDunnough (1925) was originally established for adults with reduced hind wings, and differentiated from *Pseudocloeon* Klapalek (hind wings absent) and *Baetis* Leach (hind wings relatively developed). Reduction of the hind wing has since been questioned as a valid generic criterion (Traver and Edmunds, 1968; Müller-Liebenau, 1973, and Edmunds et al., 1976). However, McCafferty and Provonsha (1975) in a review and biosystematic analysis of the genus indicated that *Heterocloeon* was a distinct and monophyletic group based on several larval characters. Müller-Liebenau (1974) had described these unique larvae as a new genus, but had not realized their adult association.

Baetis frivulus McDunnough (1925) was described from adults taken at Wakefield, Quebec. The hind wings of this species were smaller than most *Baetis* but not as minute as in *Heterocloeon*. A series of larvae also taken from Wakefield and identified as *B. frivulus* by McDunnough has recently been made available to us. These larvae possess thoracic gills and a double row of claw denticles which are taxonomically indicative of *Heterocloeon*, but their hind wing pads are not as minute as those of previously described *Heterocloeon* species.

While the larvae of *frivulus* clearly fall with *Heterocloeon*, they are also closely related to *Baetis amplus* (Traver) as evidenced by other larval characters (Mori-hara and McCafferty, 1979), and adults of the two species are symmorphic.

We transfer *frivulus* to *Heterocloeon* on the basis of synapomorphic larval characters which clearly show the species' membership with this highly derived genus. The species links *Heterocloeon* to *Baetis* and generally supports the previous hypothesis of the origin of *Heterocloeon* (McCafferty and Provonsha, 1975). Adding to this previous hypothesis and based on evidence presented below, we propose that the ancestor of *Heterocloeon* was also a recent predecessor of the genus *Pseudocloeon*. A new phylogeny of species based on the incorporation of *frivulus* and reinterpretation of character evolution is necessary.

The following larval description follows the style of Morihara and McCafferty (1979).

***Heterocloeon frivulus* (McDunnough) comb. n.**
(Figs. 1-8)

Baetis frivulus McDunnough, 1925: 174.

Body Length — 4-5 mm.

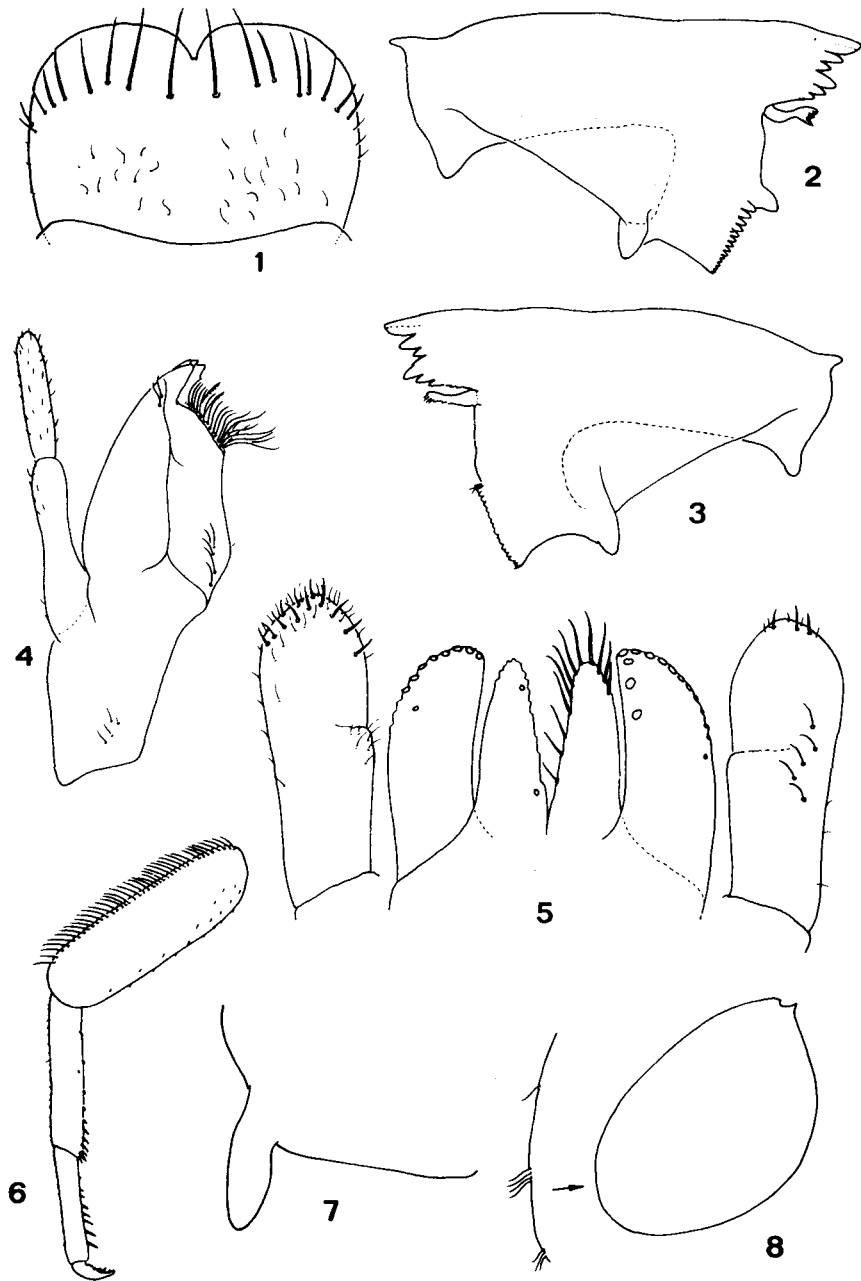
Head — Antennae: scape and pedicel with fine setae often in groups of 5 or less. Labrum (Fig. 1): 1 + 5-8 setae. Mandibles (Figs. 2 and 3): 3+3 with spines on basal denticle, distal denticle widest. Maxillae (Fig. 4): palpus usually much shorter than galea-lacinia (but sometimes extending as far), with small cone-shaped projection near apex. Labium (Fig. 5): median lobe of palpus weakly developed, segment 2 with 4-6 dorsal setae; paraglossa with 5-8 setae in innermost row and 2-3 more robust setae along apical margin.

Thorax — Pronotal Surface: with fine setae. Legs (Fig. 6): with single threadlike gill at base of procoxa; ventral setae thicker than dorsal setae on tibia and tarsus; dorsum of femur with single dense row of long, thin setae; claw with 2 dissimilar rows of denticles and 1 pair of subapical setae. Hind wing pads (Fig. 7): moderately developed.

Abdomen — Tergal Surfaces: with fine and robust setae, robust setae more numerous on anterior terga; posterior margins with blunt spines (absent on first tergum). Gills (Fig. 8): on segments 1-7; rounded posteriorly with weak, smooth margins; fine marginal setae in clumps. Paraprocts: posteromedial margin with stout, sharp spines of uniform size; surface with approximately 5 submarginal robust setae subequal in size to marginal spines, and with scattered fine setae and numerous chloride cells. Caudal Filaments: unbanded; median terminal filament reduced to 1 segment.

Figs. 1-8. Larva of *H. frivulus*:

1. labrum (dorsal surface);
2. left mandible;
3. right mandible;
4. maxilla;
5. labium (left-ventral, right-dorsal) setae on paraglossae and left glossa omitted;
6. leg;
7. left posterolateral portion of metatergum with hind wing pad;
8. 4th gill and enlargement of a section of outer margin.



Diagnosis — The moderately developed hind wing pads (Fig. 7) are much larger than those of other *Heterocloeon* species, and the tarsal claws possess two dissimilar rows of ventral denticles rather than a single row as in *Baetis*. Also, the dorsal setae on the legs (Fig. 6) of *H. frivulus* are more numerous and longer than in other *Heterocloeon* species. Caution must be employed in distinguishing this species from *B. amplus* because the thoracic gills at the base of the procoxa are very difficult to see owing to their small size and lack of pigmentation, and the smaller row of claw denticles requires slide preparation to be discernible and may sometimes not be visible because they can be obstructed by the larger row of denticles. The smaller row of denticles in *H. frivulus* is less developed than those of other *Heterocloeon* species.

Material Examined — Slide Mounts: *H. frivulus* — Lapeche River, Wakefield, Que. IV-31-1930, Walley, 3 larvae; and VI-12-1930, J. McDunnough, 1 larva, Canadian National Collection (CNC). *B. amplus* — larvae and adults, Purdue University. *Heterocloeon* spp.-collection of Dr. I. Müller-Liebenau. Specimens in alcohol: *H. frivulus*, several specimens with the same collection data as above in the CNC.

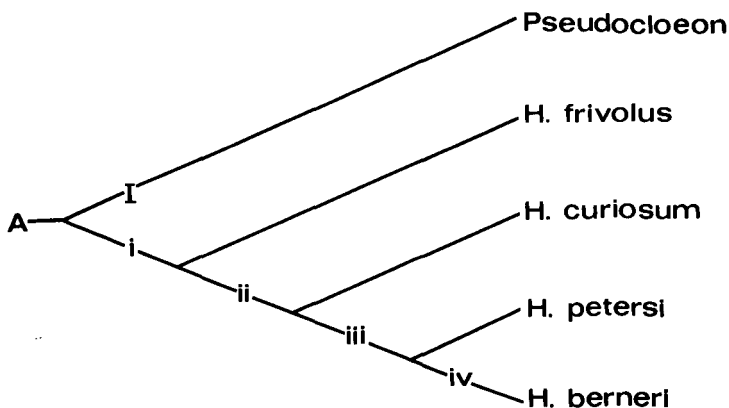


Fig. 9. Phylogeny of *Heterocloeon* species and its relationship to *Pseudocloeon*.

PHYLOGENY OF *HETEROCLOEON*

Our hypothesized phylogeny (Fig. 9) is based primarily on larval characters. Adults are poorly known or not especially diverse, and most taxonomically useful characters which are known (i.e., hind wings and genitalia) must be carefully used in phyletic analyses because they are evidently highly subject to convergences. Adult leg segment ratios may prove worthwhile in the future but have been used so irregularly in the past that inferences, or even identifications, cannot be based on this character alone. Our phylogeny is discussed below in terms of character evolution (synapomorphies I and i-iv of Fig. 9) inferred from extant species. Most morphological variation under discussion has been figured by Müller-Liebenau (1974).

CHARACTER EVOLUTION

Fig. 9, I: The head capsule became broader in proportion to the labrum and the mouthparts became directed posteriorly (see Fig. 111 in Edmunds et al., 1976). Also, the hind wing became completely lost; this loss is recognized as having occurred independently in other baetid lineages.

Fig. 9, i: Ventral thoracic gills were formed. Among other Baetidae, thoracic gills are known only from one species of *Baetodes* and some *Dactylobaetis* species, where they must have evolved independently. A slight reduction of hind wing size also occurred at i.

Fig. 9, ii: Hind wings became threadlike and lost their longitudinal veins. Also, the number and length of dorsal femoral setae became reduced. Outgroup comparisons indicate both these characters are subject to convergence with other baetid species. They, nevertheless, are useful for the ingroup analysis of *Heterocloeon*.

Fig. 9, iii: Dorsal femoral setae again became fewer and shorter. Also, the mandibular canines became increasingly fused. Distinct phenoclines are evident for both of these characters.

Fig. 9, iv: First, ventral thoracic protuberances originated. Second, large, knife-like, ventral tarsal setae were derived from the more common, smaller and symmetrically formed setae. Third, large robust setae arose on the medial area of the labrum. These ventral protuberances and tarsal setae are exclusive character states among Baetidae. The derived setal arrangement on the labrum is vaguely similar to that of *Baetis longipalpus* Morihara and McCafferty and to a few other baetids and non-baetids, but the majority of closely related species (ingroups) and more ancestral genera (i.e., *Siphlaenigma* and *Callibaetis*) indicate that any similarity is a result of convergence. *Siphlaenigma* was recently shown to belong to the more ancestral subfamily of Baetidae by McCafferty and Edmunds (1979).

HYPOTHETICAL ANCESTOR

A hypothetical ancestor (A in Fig. 9) is inferred on the basis of a number of advanced character states shared by the apotypic genera *Pseudocloeon* and *Heterocloeon*. These larval states include the loss of scales; the appearance of highly developed dorsal setae on the legs; the development of robust tarsal claws; the loss of serration along the abdominal gill margins; and the reduction of the median caudal filament.

DISCUSSION

A phylogeny of *H. curiosum*, *petersi* and *berneri* was proposed by McCafferty and Provonsha (1975). This previous phylogeny can now be clarified in regards to the specific origin of *Heterocloeon*, and falsified in regards to certain interspecific phyletic relationships which had been deduced from misinterpreted character evolution.

Baetis (sensu Müller-Liebenau, 1970 and Morihara and McCafferty, 1979)

represents an extremely diverse assemblage of species which we believe is highly paraphyletic. We now prefer to define the ancestral *Heterocloeon* stock in a narrower sense as Ancestor A with a more exclusive set of characters. Certain species such as *B. amplus* and the *alpinus*, *lutheri*, and *lapponicus* groups appear, primarily on the basis of scalelessness and the dorsal setae of the legs, to also be derived from a pre-*Pseudocloeon* -*Heterocloeon* ancestor (but not necessarily the one most recently shared by *Pseudocloeon* and *Heterocloeon*). Thus, theories of origin expressed in the former and present work (i.e., from a two-tailed *Baetis*-like ancestor vs. from an Ancestor A respectively) are essentially only semantic in difference.

McCafferty and Provonsha (1975) hypothesized the derived states of several larval characters of *Heterocloeon* species and used this as a basis of their cladistic analysis. Data from the newly discovered larvae of *H. frivulus* and the recent extensive study of *Baetis* (Moriyama and McCafferty, 1979) and outgroup diversity allow the new phyletic hypothesis (Fig. 9) which is based in part on the following reinterpretations of character evolution.

1. "Two rows of claw denticles" now appears to be an ancestral character state based on our recent outgroup examinations. *Pseudocloeon* is known to possess only a single row of denticles, and a more ancestral relative (with larger hind wings and a longer median caudal filament) possesses a double row as do all ancestral genera.

2. "A labrum with bristle-like setae scattered randomly over most of the surface" was used to characterize in part the previous hypothetical *Heterocloeon* ancestor. However, nearly all *Baetis* and *Pseudocloeon* are armed with a distinct submarginal row of labral setae. Our present phylogeny recognizes the latter condition as an ancestral state and only a single subsequent change (Fig. 9, iv).

3. "Mandibles with a series of canines produced more or less evenly throughout" was interpreted as ancestral by McCafferty and Provonsha. We now believe that the most ancestral state is a bifurcate mandibular canine because the canines of *Siphlaenigma* and *Callibaetis* are extremely bifurcate, *Baetis* and *Pseudocloeon* canines are bifurcate, and those of *H. frivulus* and *curiosum* are similar to the latter two genera.

4. Finally, we now regard the use of labial palpi segmentation and expansion, as well as tracheation patterns and median pigmentation of gills, as questionable because of observed intraspecific variability in other groups (Müller-Liebenau, 1970 and Morihiro and McCafferty, 1979).

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