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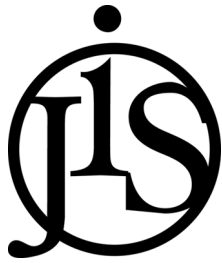
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Revision of *Heterocloeon* McDunnough (Ephemeroptera: Baetidae)

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Abstract

The North American genus *Heterocloeon* McDunnough is redefined and shown to be distinct from other two-tailed *Baetis* complex genera, including *Acentrella* Bengtsson and *Plauditus* Lugo-Ortiz and McCafferty, which are also represented in North America. *Heterocloeon* is divided into three distinct subgenera, including *Heterocloeon* s.s., *Isxaeon* McCafferty and Webb, new subgenus, and *Jubilatum* McCafferty and Jacobus, new subgenus. Cladistic analysis supports the recognition of these subgenera within a genus defined by the presence of an apomorphic secondary ridge or denticle row on the larval claw; *Heterocloeon* s.s. and *Jubilatum* being sister groups, with their stem and *Isxaeon* branching basally within the *Heterocloeon* clade. The subgenus *Heterocloeon*, which possesses larval prothoracic osmobranchiae, retains the traditional species makeup of the genus. *Isxaeon*, which possesses a basally narrowed labial palp segment 2 and tibiae, and primary claw denticles of subequal length, includes a revalidated *H. anoka* (Daggy); *H. davidi* Waltz and McCafferty, new species; and *H. rubrolaterale* (McDunnough), new combination. *Jubilatum*, which possesses an adenticulate secondary ridge on the claws and specialized tibial setation, includes *H. amplum* (Traver), new combination, and *H. grande* (Wiersema and Long), new combination. Previous confusion of *H. anoka* and *Plauditus punctiventris* (McDunnough) is also resolved, with adult color patterns in *Isxaeon* and *Plauditus* shown to be of diagnostic importance.

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Introduction

Among North American Baetidae, the genera *Acentrella* Bengtsson, *Baetis* Leach, *Barbaetis* Waltz and McCafferty, *Heterocloeon* McDunnough, *Plauditus* Lugo-Ortiz and McCafferty, and *Pseudocloeon* Klapálek are members of the *Baetis* complex grouping of genera as defined by their possession of a larval femoral villopore (Waltz and McCafferty, 1987a,b; Waltz et al., 1994; Lugo-Ortiz and McCafferty, 1998; Lugo-Ortiz et al., 1999). Some of these genera consist entirely of species with larvae that have a highly reduced median caudal filament. These are known as two-tailed baetids and include the genera *Acentrella*, *Heterocloeon*, and *Plauditus* in North America. *Plauditus* and *Heterocloeon* are strictly Nearctic, whereas *Acentrella* is also found in the Palearctic and Oriental regions (Lugo-Ortiz and McCafferty, 1999). Larvae of only two of the 22 North American species of *Baetis* have an independently evolved highly reduced median caudal filament (Moriyama and McCafferty, 1979a). Non-Nearctic two-tailed *Baetis* complex genera include the Palearctic and Oriental *Baetiella* Uéno, and the Oriental *Gratia* Thomas and *Liebebiella* Waltz and McCafferty.

Besides the reduction of the median caudal filament, larvae of North American two-tailed *Baetis* complex genera also share an absence of scales and scale bases on the abdominal terga, and the presence of smooth gill margins, and adults have a variously developed dorsally oriented anterior mesonotal process. Such characteristics, for example, distinguish these strictly two-tailed genera from *Baetis*. In addition for diagnostic purposes, two-tailed *Baetis* larvae have a developed inner thumb on labial palp segment 2, which is not developed in the strictly two-tailed *Baetis* complex genera.

Plauditus was established by Lugo-Ortiz and McCafferty (1998) to include most North American two-tailed baetids that lacked hind wings and had been traditionally but inappropriately placed in *Pseudocloeon* and then *Baetis*. Other North American species traditionally placed in *Pseudocloeon* had previously been moved to *Apobaetis* Day, *Acentrella*, and *Barbaetis* [see review of Lugo-Ortiz and McCafferty, 1998]. Wiersema (2000) moved two of the *Plauditus* species to *Acentrella* and reiterated characteristics of *Acentrella*, such as the relative development of the dorsal femoral setal row and compact nature of

the labium, that were thought to distinguish it from both *Plauditus* and *Heterocloeon*. For *Acentrella*, we take the designation of a compact labium essentially to denote a labium with short palps overlapping the paraglossae and giving a narrow, rounded appearance to the entire mouthpart [see Fig. 3 in McCafferty et al., 1994]. Differences attributed by Waltz (1994) to *Acentrella* and other North American *Baetis* complex genera with respect to the relative refinement of the anterior mesonotal process in the adults were found by Wiersema (2000) to be unstable among *Acentrella*, and we have also found the relative refinement of the apex of the process to be somewhat unstable among *Plauditus* and *Heterocloeon*, although the process is always dorsally oriented in these three genera as mentioned above.

In North America, *Plauditus* has up to this point consisted of the following species: *P. bimaculatus* (Berner), *P. cestus* (McCafferty and Provonsha), *P. cingulatus* (McDunnough), *P. dubius* (Walsh), *P. elliotti* (Daggy), *P. futilis* (McDunnough), *P. gloveri* McCafferty and Waltz, *P. grandis* Wiersema, *P. punctiventris* (McDunnough), *P. rubrolateralis* (McDunnough), *P. texanus* Wiersema, *P. veteris* (McDunnough), and *P. virilis* (McDunnough). In the same respect, *Acentrella*, which has been considered a synonym of *Baetis* at times in the past [see review of Waltz and McCafferty (1987b)], has recently consisted in North America of *A. alachua* (Berner), *A. ampla* Traver, *A. feropagus* Alba-Tercedor and McCafferty, *A. lapponica* Bengtsson, *A. parvula* (McDunnough), and *A. turbida* (McDunnough).

Heterocloeon was erected by McDunnough (1925) for baetid adults with very small hind wings, but subsequently was generally subordinated under *Baetis* or *Acentrella*. The genus was revalidated by McCafferty and Provonsha (1975) who showed that highly distinctive larvae were associated with these adults. McCafferty and Provonsha (1975) also showed *Rheobaetis* (Müller-Liebenau, 1974) to be equivalent to *Heterocloeon*. Moriyama and McCafferty (1979b) further elaborated the definition of the genus, showing it to be characterized by such features as the presence of two dissimilar rows of claw denticles and the presence of prothoracic osmobranchiae in the larvae. Moriyama and McCafferty (1979b) also hypothesized the phylogenetic relationships of its traditional species, including *H. berneri* (Müller-Liebenau), *H. curiosum* (McDunnough),

H. frivolum (McDunnough), and *H. petersi* (Müller-Liebenau). In addition to these species, *H. anoka* was recently placed in the genus via a listing of Alberta mayflies by Webb and McCafferty (2003), with explanations regarding it deferred to the present work.

The presence of two dissimilar rows of denticles on the larval claw of *H. anoka* was consistent with *Heterocloeon* characterization, but other features of *H. anoka*, such as absence of osmobranchiae and hind wings, shape of tibiae and labial palps, tail banding, and size of the claw denticles of the primary row (all of which had not been associated with a concept of *Heterocloeon*) begged an obvious question regarding the actual breadth of the genus, its relationships with other *Baetis* complex genera, character evolution, and relationships among those species with the modified claw. It also instigated a further investigation of potentially displaced species, and led to the discovery of at least one new species. Here we present the results of such research, including a more comprehensive and cladistic based concept for *Heterocloeon* with distinctive phylogenetic branches within it demarked as subgenera and the inclusion of additional species that had previously been placed in other genera or are newly described.

Taxonomy

Genus *Heterocloeon* McDunnough

Diagnosis

Larva: The head capsule is relatively narrow, as compared to the width of the labrum (similar to that typical of *Baetis* and generally narrower than the more broadened head of *Acentrella* and *Plauditus*). The clypeus and labrum are directed ventrally or angled somewhat posteriorly. The labium is somewhat variable, but never compact as is typical of *Acentrella*; and the labial palp never has an inner thumb developed as in many *Baetis*. A villopore is present at the base of the femora (as per all *Baetis* complex genera). The tibiae have short, robust setae present along the dorsal margin (Fig. 2) (not seen in *Acentrella* and variable in *Plauditus*). The claws have a primary row of denticles and additionally a secondary ridge that may be denticulate (Fig. 3) or not denticulate (high magnification is required to see this diagnostic characteristic, which differs from the single row condition seen, for example, in *Baetis*, *Plauditus* and *Acentrella*). The hind wing pad is present and

generally relatively small, or is not developed (the hind wing pad is relatively larger in *Baetis* and some *Acentrella*, and the hind wing pad is not developed in *Plauditus* and some *Acentrella*). Tergal scales and scale bases are not present on the abdomen as they are in *Baetis*. Gills are present on abdominal segments 1-7, and these gills have smooth margins (as per all two-tailed *Baetis* complex genera). The median caudal filament ranges from being minute to slightly longer than tergum 10. Adult: See subgeneric diagnoses below.

Discussion

Various aspects of the genus are taken up below under each of its three subgenera, including subgeneric taxonomy, species makeup, formal new species descriptions, and any remarks pertinent to understanding species specific issues that require resolution.

Subgenus *Iswaeon* McCafferty and Webb, new subgenus

Type species.— *Pseudocloeon anoka* Daggy.

Diagnosis

Larva: The body length ranges from about 3.0-4.0mm (differing significantly from all *Jubilatum* and only barely overlapping with the smallest size known in *Heterocloeon* s.s.). The labial palp (Fig. 1) broadens distally, with segment 2 distinctly narrowed along the inner margin toward the base, and its outer margin gently curved; segment 3 is slightly falcate (Fig. 1) (the palp is considerably different from the narrowed palp of all other *Heterocloeon*). The tibiae are distinctly narrowed at the base and increase in width to approximately midlength (Fig. 2) (generally not as such in other *Heterocloeon*, although some *H. petersi* of the subgenus *Heterocloeon* also demonstrate this characteristic but to a lesser degree), and lack specialized setae below the dorsal margin on either side (differing from *Jubilatum*). The claws (Fig. 3) have a primary row of denticles of approximately equal length, except for the smaller most basal denticles (progressively longer in all other *Heterocloeon*), and a secondary ridge with a row of fewer and less distinct denticles (secondary ridge is not denticulate in *Jubilatum*). Thoracic osmobranchiae are not present (differing from *Heterocloeon* s.s. in this regard). The hind wing pad is not developed, but some vestige may be recognizable in a slide mount under very high magnification (a small hind wing pad is evident in *Heterocloeon* s.s. and some

Jubilatum). Gills have a rounded leading edge (Fig. 4) (this characteristic is inconsistent in other subgenera, sometimes appearing with a straighter leading edge). The cercus has a darkened broad band at approximately mid length (Fig. 4), although this band and a sometimes present apical band can become faded in alcohol (not present in *Heterocloeon* s.s., variable in *Jubilatum*). The median caudal filament is made up of about six segments and is slightly longer than tergum 10 (differing from the much shorter median caudal filament associated with *Heterocloeon* s.s. and the variable but at least shorter median caudal filament of *Jubilatum*).

Male adult: Anterior mesonotal process appears subtriangular in lateral view, with a rounded dorsal apex (variable in other subgenera). The hind wing is entirely lacking (present but relatively small in *Heterocloeon* and some *Jubilatum*). Distinct, single, central spots are located on several abdominal sterna, usually sterna 2- or 3-6 or -7, but occasionally fewer (no spotting as such in all other *Heterocloeon*).

Etymology

An arbitrary combination of letters, but incorporating the name Iswa, meaning “from the river” and given as the name of a band of Native Americans that occupied part of South Carolina and that were eventually absorbed into the Catawba tribe. The name is neuter in gender.

Included species

Three species as per their treatments below.

Distribution

Nearctic, specifically eastern and western Canada (lower provinces), and northwestern, northeastern, and southeastern USA.

Material examined

See species treatments below.

Heterocloeon (Iswaeon) anoka (Daggy)

Pseudocloeon anoka Daggy, 1945

Heterocloeon anoka (Daggy): Webb and McCafferty, 2003

Discussion

Pseudocloeon anoka Daggy (1945) had been placed as a junior synonym of *Plauditus punctiventris* (McDunnough) (previously *Pseudocloeon*, then *Baetis*) by McCafferty and Waltz (1990). Our more recent studies include male adult-type material of

P. anoka and reared associated larval exuviae housed at the University of Minnesota. These indicate that, despite some color-pattern similarities with certain *Plauditus*, a distinct species that did not belong to *Plauditus* was represented. Ontario adults that we have examined from the Royal Ontario Museum (Singhampton, VII-12-1930; Erindal, VII-16-1934) and that were originally identified by Fred Ide as *P. punctiventris* were found to be referable to *H. anoka*. It is therefore highly probable that the larvae that were associated with *P. punctiventris* and originally described as such by Ide (1937) (and to a large degree considered as such by workers since that time) are also referable to *H. anoka*. Further supporting this contention are observations that the adults referred to above were taken from the same locality (different dates) as those adults that Ide (1937) associated with larvae, and that Ide (1937) described the larvae as having centrally located abdominal sternal spotting (which can sometimes be found in larvae of *H. anoka* but not *Plauditus*). Indeed, our reexamination of considerable materials previously identified as *P. punctiventris* has shown that many of these specimens from throughout much of North America are actually referable to *H. anoka*, as will be documented in various faunistic studies in process. Thus far, *H. anoka* has been found in Alberta, Iowa, Manitoba, Minnesota, North Carolina [seven larvae, Henderson Co, Mills R, 11-2001, in the Purdue Entomological Collection (PERC)], Oklahoma, Ontario, Pennsylvania, Saskatchewan, Tennessee [two larvae, Scott Co, Big South Fork NRR, Clear Fork R at Burnt Mill Bridge, VI-11-2003 (PERC)], Virginia [one larva, Carroll Co, New R, XI-26-1976 (PERC)], and Wisconsin [male adult, Pierce Co, Rush R, upstream STH 10 bridge, IX-02-2004 (PERC)]. See also materials examined by McCafferty et al. (2004).

Heterocloeon (Iswaeon) davidi Waltz and McCafferty, new species

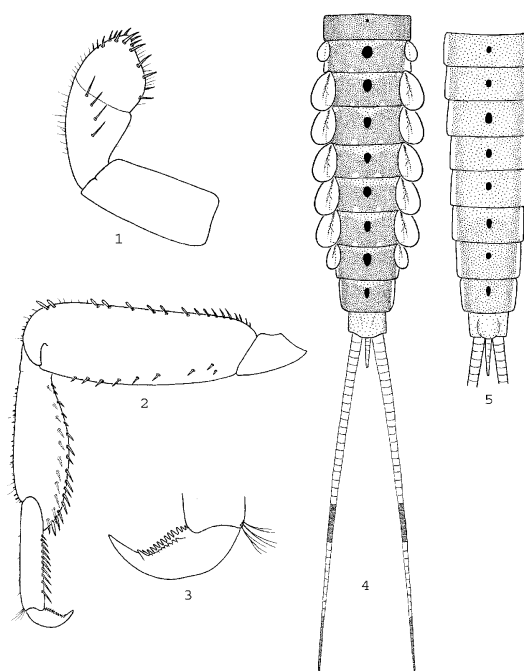
Mature larva: Body length 3.8-4.0mm. Cercus length 3.0mm. General coloration cream to light brown. Head: Antenna ca. 1.5 times length of head capsule. Labrum 1+3-5 setae. Angulate mandible 3(1)+1+3. Planate mandible 4+1+3 (innermost denticle with multiple dentition to base). Maxillary palp two segmented, extending beyond galealacinia. Labial palp (Fig. 1) segment 2 with inner margin strongly tapered toward base, not paralleling outer margin, and with four prominent

setae on dorsal surface; segment 3 length subequal to width, with apex offset dorsally, creating oblique inner margin. Thorax: Meso- and/or metanota sometimes with large central spots similar to those of most abdominal terga (see below); distinctive spots also often laterally above meso- and metacoxae. Hind wing pad not developed, or if discernible under high magnification, then pustulate vestige only. Femora (Fig. 2) with ca. 14-16 spatulate setae dorsally, and with two rows of robust setae ventrally. Tibiae (Fig. 2) wider in distal half, narrower at base, with two rows of robust setae ventrally (longer than ventral femoral setae), and with small robust setae and fine setae ventrally. Foretarsus (Fig. 2) with 8-11 robust setae ventrally (increasing in size distally); meso- and metatarsi with 12-15 robust setae ventrally (increasing in size distally). Claws (Fig. 3) with two dissimilar rows of denticles; prominent row with 11-15 distinctive denticles (all subequal except basal two or three); less prominent, somewhat shorter, ridgelike row with two to six less distinctive denticles (row and individual denticles discernible only under high magnification). Abdomen: Tergal surfaces without scales, with pores and fine setae (under very high magnification, surface cuticular surface with sparsely scattered, slightly curved, slender microtrichiae measuring ca. 15 microns, and with dense fields of narrow, attenuated, sharp microspines measuring ca. 5.0-10.0 microns); posterior marginal spines of terga blunt, broader than long on anterior terga and becoming more elongate on posterior terga; terga (Fig. 4) marked with large distinctive spots (slightly anterior of midpoint) usually on terga 2-9, with smaller spot on tergum 1. Sterna (Fig. 5) usually marked with prominent central spots on sterna 1-8 (always smaller than main dorsal spots, and sometimes slightly anterior of midpoint); ventral spotting sometimes faded or absent on sterna, more commonly absent on anterior sterna. Gills (Fig. 4) elliptical with curved leading margin, apically rounded; margins smooth with scattered, fine setae. Paraproct with 14-17 marginal spines; surface with fine setae, without robust setae, but sometimes with spines near margin. Cercus (Fig. 4) with submedial dark, broad band and with or without apical band; median caudal filament slightly longer than tergum 10.

Male adult (in alcohol): Body length 4.3mm. Cercus length unknown. Wing length 4.5mm. Head: Color medium-dark brown, except ocelli, turbinate portion of eye, and antennal flagellum light.

Thorax: Color medium-dark brown. Anterior mesonotal process directed dorsally, point somewhat rounded. Hind wing absent. Abdomen: Color mostly whitish (segments 2-6) with extensive tracheal markings evident (not drawn in Figs. 6, 7); segments 1 and 7-10 contrasting medium brown. Terga (Fig. 6) with large, distinctive, centrally located (slightly anterior of midpoint) spots on terga 2-7; terga 1 and 8 with very small, similarly located dots. Sterna (Fig. 7) with large, distinctive spots on sterna 2-8 (spots on sterna 2-6 slightly anterior of midpoint, and spots on sterna 7 and 8 posterior of midpoint). Genital forceps whitish.

Fig 1-5. *Heterocloeon (Iswaeon) davidi*, larva. 1, Labial palp (dorsal). 2, Foreleg. 3, Foreclaw. 4, Dorsal abdomen. 5, Ventral abdomen.

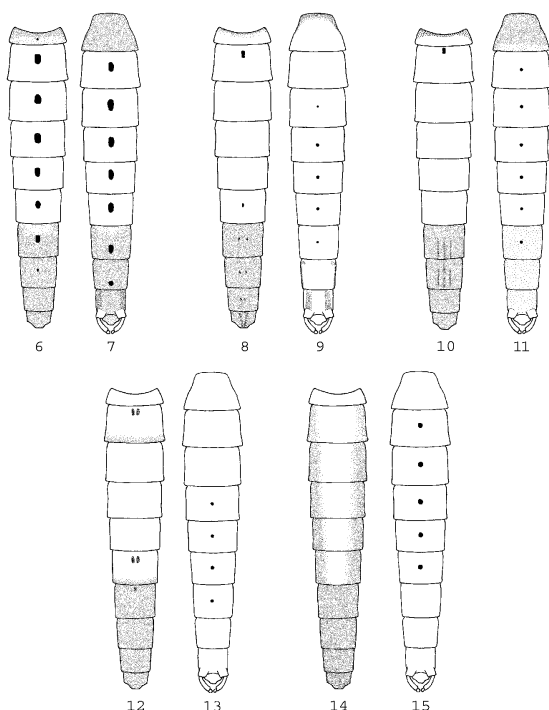


Material examined

Holotype: larva in alcohol, North Carolina, Swain Co, Oconoluftee R above Bryson Dam, IX-2001, TJ Wilda (PERC). Paratypes: one larva, North Carolina, Swain Co, Oconoluftee R below Bryson Dam, IX-2001, TJ Wilda (PERC); 1 larva (slide mounted with parts dissected), Henderson Co, Mills R, VII-1992, D Lenat (PERC). Other material: one male adult, North Carolina, Swain Co, Oconoluftee R, 50m from confluence with Raven's Fork, in light trap, VI-18-2001 (PERC) (associated by having identical color pattern to larval

holotype); three larvae, North Carolina, Cherokee Co, Hiwassee R, below Mission Dam, IX-2001 (PERC); three whole larvae and two slide mounted larvae (dissected), North Carolina, Henderson Co, Mills R, VII-2001 (PERC).

Fig. 6-15. *Heterocloeon (Iswaeon)* male adult dorsal and ventral abdomens. 6 and 7, *H. davidi*. 8 and 9, *H. anoka* (variant 1, holotype). 10 and 11, *H. anoka* (variant 2). 12 and 13, *H. anoka* (variant 3). 14 and 15, *H. rubrolaterale* (holotype).



Etymology

The species is named in honor of David R. Lenat, who originally brought the unusual species to our attention, and who has for many years contributed largely to our understanding of mayfly biodiversity in North Carolina.

Diagnosis

With respect to larvae, extensive dorsal, centrally located, large tergal spotting is typical of *H. davidi* (Fig. 4), but not *H. anoka*. Dorsal single spotting on the terga is often not evident on *H. anoka* larvae, and when it is, it is usually limited to a somewhat anterior spot on tergum 2 or one each on tergum 6 and 2 (and such spots sometimes appear more or less divided), and there may or may not be pairs of small submedial dots on intermediate terga. In

addition, the dorsal larval color pattern of *H. anoka* usually includes a median pale stripe running longitudinally on the abdomen set against a somewhat darker background. No such stripe has been seen in *H. davidi*. Dorsal abdominal spotting can also be found on some individuals of *H. curiosum*, a species that also is found within the range of *H. davidi*. The two species are easily distinguished by any of several subgeneric differences, e.g., progressive claw denticle length, hind wing pads, and osmobranchiae in *H. curiosum*. Dorsal abdominal color patterns can also be similar in *H. anoka* and some *Plauditus*. But the former can always be easily distinguished from the latter, for example, by the basally narrowed tibiae and the even rather than progressive claw denticle length.

Among male adults of *Iswaeon*, abdominal central tergal spotting is extensive in *H. davidi* (Fig. 6); whereas in *H. anoka*, such large spots are limited to tergum 2 or 2 and 6 (although small dots sometimes appear on terga 3-5 and 7), and the tergum 2 spot is clearly anterior in position (Figs. 8, 10, 12). The number of ventral abdominal sterna with spots is somewhat variable in *H. anoka* as previously discussed, and therefore could possibly be variable in other species in which we have seen relatively little material (see below).

Heterocloeon (Iswaeon) rubrolaterale (McDunnough), new combination

Pseudocloeon rubrolaterale McDunnough, 1931.

Baetis rubrolateralis (McDunnough): McCafferty and Waltz, 1990.

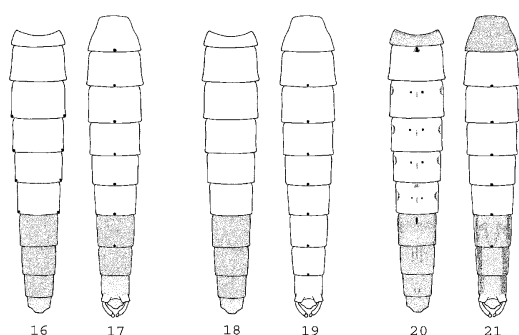
Plauditus rubrolateralis (McDunnough): Lugo-Ortiz and McCafferty, 1998.

Discussion

The male adult holotype of *Pseudocloeon rubrolaterale* McDunnough (a little known North American baetid species) that is housed in the Canadian National Collection (CNC) was recently examined by Jacobus and McCafferty (2002). The species was similar to *H. anoka* and *H. davidi* in terms of having a series of distinctive, centrally located spots (one per segment) on several abdominal sterna (Figs. 7, 9, 11, 13, 15), at least sterna 4-7 (rarely this few in some *H. anoka*), but usually on 2- or 3-7 or -8 in *H. anoka*, and usually 2-8 in *H. davidi*, and 2-6 or -7 in *H. rubrolaterale*. *Plauditus* spp. have no such spots, or if central spots are expressed on the male adult abdominal

sterna, they are located adjacent to the sternal posterior margins [in *P. punctiventris* and its many variants (Figs. 17, 19, 21) and in *P. veteris* (McDunnough)], or they are limited to sterna 5-6 [*P. virilis* (McDunnough)]. These latter three *Plauditus* species can also have double central spotting dorsally on abdominal terga 2-6 or fewer terga in this area [some *P. punctiventris* variants (Fig. 16, 18, 20)], whereas such double spotting is rare in *H. anoka*, and apparently non-existent in *H. davidi* and *H. rubrolaterale*.

Fig 16-21. Mortality of uziflies in tetracycline treated and control batches.



Although the larvae of *H. rubrolaterale* are unknown at this time, it is clear to us, based on abdominal markings discussed above, that this species is very closely related to *H. anoka* and *H. davidi*, and should be included in *Heterocloeon* (*Iswaeon*) at this time. Jacobus and McCafferty (2002) believed *H. rubrolaterale* to be known at that time from only the original material taken in Alberta (McDunnough, 1931), and thus considered it possibly extinct. They also stated that the species was distinctive by the presence of the medially located central spots on the abdominal sterna. Although we now know that characteristic is common to all known *Iswaeon* male adults, we continue to consider *H. rubrolaterale* a distinctive species within the subgenus *Iswaeon* because it lacks any dorsal single spotting on the abdominal terga (Fig. 14). The species is not extinct, as evidenced by recently sampled specimens housed in PERC as follows: one male adult, Montana, Cascade Co, Missouri R at Great Falls at lights, VII-27-2002; and one male adult, North Carolina: Swain Co, unnamed tributary of Raven's Fork, in light sample, VII-16-2001. We also have a male adult of *H. rubrolaterale* from Virginia with no

other data associated with it. In view of these new reports, especially from the Southeast, an early and often dismissed report of the species from Sevier Co, Tennessee by Berner (1977) must again be taken seriously.

Although the dried type material of *H. rubrolaterale* shows pigmented shading along the sides of the dorsal abdominal segments as in Fig. 14 that is not found in *H. davidi* or *H. anoka*, we have seen material of *H. rubrolaterale* in alcohol (e.g., our specimen from Montana cited above) with little or undetectable lateral pigmentation. When larvae of *H. rubrolaterale* become known through rearing to male adult, we expect that they will prove to be most similar to those of *H. anoka*; we do not know if individuals that may not express the adult spotting patterns will be morphologically discernible.

Subgenus *Heterocloeon sensu stricto*

Type species: *Centroptilum curiosum* McDunnough.

Diagnosis

Larva: The body length ranges from about 4.0-8.0mm (most species are distinctly larger than *Iswaeon*). Labial palp (Fig. 5, in Morihara and McCafferty, 1979b; Figs. 1D, 13D, in Müller-Liebenau, 1974) is narrowed throughout; segment 2 is parallel sided; and segment 3 is slightly to strongly pointed (the palp clearly differs from that of *Iswaeon*). The tibiae are generally parallel sided (Fig. 6, in Morihara and McCafferty, 1979b; Figs. 2A, 14A, in Müller-Liebenau, 1974) (differing from *Iswaeon*, although there may be a lesser basal narrowing in at least one species of *Heterocloeon* s.s.), and lack specialized setae below the dorsal margin on either side (as found in *Jubilatum*). The claws have a primary row of denticles that become progressively longer apically (differing from those of *Iswaeon*), and a secondary denticulate row (differing from *Jubilatum*). A papilla-like osmobranchia is found near the base of the foreleg (e.g., Fig. 13F, in Müller-Liebenau, 1974) (differing from all other *Heterocloeon* in this respect, although they can be difficult to see and may be subject to breakage). The hind wing pad is present but very small and never larger than that shown in Fig. 7 of Morihara and McCafferty (1979b) (differing from all *Iswaeon* and some *Jubilatum*). The cercus lacks banding near the midlength (differing from *Iswaeon* and some *Jubilatum*). The median caudal filament is reduced to a single

segmented vestige (distinctly differing from the less reduced median caudal filament of *Iswaeon*). Male adult: The hind wing is present but relatively small (differing from all *Iswaeon* and some *Jubilatum*). Extensive central abdominal sternal spotting is not present (differing from *Iswaeon*).

Included species

Heterocloeon (*Heterocloeon*) *berneri* (Müller-Liebenau); *H.* (*H.*) *curiosum* (McDunnough); *H.* (*H.*) *frivolum* (McDunnough); and *H.* (*H.*) *petersi* (Müller-Liebenau).

Distribution

Nearctic, specifically eastern Canada (lower provinces), and northeastern, northwestern (Colorado only), and southeastern USA.

Material examined

H. curiosum: Indiana, Harrison Co, Blue R, 1 mi E White Cloud, VIII-23-1973, PERC (larvae & reared adults); New Hampshire, Hillsboro Co, Otter Br, 0.8 mi E jct 202 & 136, nr Peterborough, VI-20-1999, PERC (larvae); Ontario, Ottawa, VIII-22-1922, CNC (male adult holotype), (larvae, IV-31-1930 & VI-12-1930). *H. frivolum*: Colorado, Jackson Co, North Platte R, 9 mi SE Waldren, VII-31-1992, PERC (male adults); Quebec, Wakefield, VI-25-1924, CNC (male adult holotype); Tennessee, Scott Co, Big South Fork NRR, Big South Fork Cumberland R at Leatherwood Ford, VI-10-2003, PERC (larva). *H. petersi*: North Carolina, Madison Co, Ivy R, IX-1993, PERC (larvae); Tennessee, Scott Co, Big South Fork NRR, Clear Fork R at Burnt Mill Bridge, VI-11-2003, PERC (larvae).

Discussion

The four species of *Heterocloeon* s.s. can be identified using Morihara and McCafferty (1979b) and Müller-Liebenau (1974).

Subgenus *Jubilatum* McCafferty and Jacobus, new subgenus

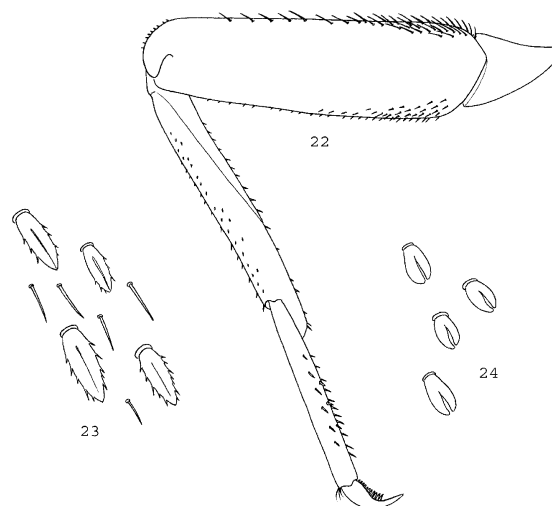
Type species: *Acentrella ampla* Traver.

Diagnosis

Larva: The body length ranges from about 7.0-9.0 mm (distinctly larger than *Iswaeon*). The labial palp (Fig. 15a, in Morihara and McCafferty, 1979b, Fig. 6, in Wiersema and Long, 2000) is narrow throughout; segment 2 is parallel sided or with the outer margin slightly convex; segment 3 is slightly pointed (clearly differing from *Iswaeon*). The tibiae (Fig. 22) are parallel sided (differing from *Iswaeon*)

and have small, deeply forked, broadly spatulate setae (Fig. 23) on the anterior face below the dorsal margin, and small, stout, fimbriate setae (Fig. 24) on the posterior face below the margin. The claws have a primary row of denticles, with denticles progressively longer distally (differing from the generally subequal denticulation of *Iswaeon*), and a secondary ridge that is devoid of denticulation (differing from the at least slightly denticulate secondary ridge of all other *Heterocloeon*). A pair of prothoracic osmobranchiae are not present (differing from *Heterocloeon* s.s.). The hind wing pad is either small or not developed. The cercus may or may not have a broad, dark middle band. The median caudal filament is either very short and limited to one segment or has three to five segments but is shorter than tergum 10. Male adult: The hind wing is either present and very small or not present. Extensive central sternal spotting is not present on the abdomen (differing from *Iswaeon*).

Fig 22-24. *Heterocloeon (Jubilatum) amplum*, larva. 22, Hindleg. 23, submarginal setae of the anterior face of tibia. 24, Submarginal setae of the posterior face of tibia.



Etymology

Latin masculine for “shout for joy.”

Included species

Heterocloeon (Jubilatum) amplum (Traver), new combination; and *H. (J.) grande* (Wiersema and Long), new combination.

Distribution

Nearctic, specifically northeastern, southeastern, and southwestern (west Texas only) USA.

Material examined

H. amplum: Indiana, Morgan Co, Bryant Cr, above state forest, IV-11-1975, PERC (male and female adults); Kentucky, Leslie Co, Cutchins Cr, 3.7 mi NNE Perry/Leslie County line on KY 699, V-10-1978 (larvae); Tennessee, Scott Co, Big South Fork NRR, Big South Fork Cumberland R at Leatherwood Ford, III-18-2003, PERC (larva). *H. grande*: Tennessee, Rutherford Co, Middle Fork Stones R at Hwy 269 & Short Creek Church, III-21-1997, PERC (male adult holotype, with larval cast skin), Rutherford Co, Dry Fork Cr at Brother d, III-21-1997, PERC (paratype larvae).

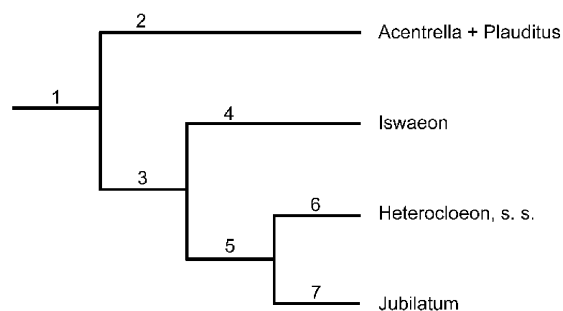
Discussion

As per all *Heterocloeon*, diagnosis of those species placed in *Jubilatum* will ideally require the use of ultramorphological characteristics, for example, to note the presence of a secondary ridge on the claw. This ridge can be especially difficult to detect. The following, however, may be of some assistance in identifying *Heterocloeon* (*Jubilatum*) larvae: These are relatively large species among two-tailed *Baetis* complex mayflies in general, and particularly with respect to the fact that they have either very small or no hind wing pads. Other larvae that are this large include three of the *Heterocloeon* s.s. species, but they will have osmobranchiae near the base of the forelegs. Any *Acentrella* that may approach this size have fundamentally different claws and labial palps, among other things. Also, below the dorsal margin of the tibiae of both *Jubilatum* species, specialized setae are evident on either face even at relatively low magnification, although the detailed structure of these setae are only evident under very high magnification. Although the head capsule of *H. grande* may appear somewhat broader than that of typical *Heterocloeon*, the combination of easy to detect characteristics, such as the large body size, the absence of hind wing pads, the absence of prothoracic osmobranchiae, the minute median terminal filament, the medially banded cerci, and the relatively narrow labial palps should make this species readily identifiable. In the same respect, *H. amplum* may be easily identified by the combination of large size, small hind wing pads, absence of prothoracic osmobranchiae, a miniature tail-like median caudal filament, non-banded cerci, and parallel sided and narrow labial palps.

Phylogeny

Our hypothesized cladogram of *Heterocloeon* is given in Fig. 25. Using *Baetis* as the outgroup, we analyzed the cladistic relationships of the North American groupings of the two-tailed *Baetis* complex mayflies, keeping in mind that *Plauditus* and *Heterocloeon* are both restricted to North America. Classical cladistic methodology (e.g., Ross, 1974) was used, and no particular ancillary programs were necessary for analysis of apomorphy distribution or resolution of parsimony due to the small number of operational taxonomic units under investigation (four) and the small number of characters used (11) (see below). The following discussion reviews all apomorphies used and their distribution, as were used in our cladistic analysis. Character state distribution, while not given separately in a matrix per se, can be derived directly from the accumulative apomorphies associated with the numbered stems and associated taxa (Fig. 25). The small size and relative simplicity of the analysis has allowed such distribution to be covered comprehensively in the narrative.

Fig 25. Hypothesized cladogram of species groups of North American two-tailed *Baetis* complex mayflies. See text for synapomorphies designated by stem numbers.



North American two-tailed *Baetis* complex baetids, the identifiable subgroup of Baetidae (Fig. 25, stem 1) to which *Heterocloeon* belongs, demonstrate the following defining synapomorphies: in the larva, reduction of the middle tail, loss of tergal scales and scale bases, smooth gill margins, and reduction of the medial thumb of labial palp segment 2; and in the adults, dorsal orientation of the anterior mesonotal process. While all such characteristics are subject to homoplasy in various clades of Baetidae, these are relatively stable apomorphies within the *Baetis* complex. The first branching

within this grouping involves the dichotomy of *Acentrella* and *Plauditus* as one of the basal clades, and *Heterocloeon* the other. *Acentrella* + *Plauditus* demonstrate the synapomorphy of the larval head broadening in relationship to the labral width (Fig. 25, stem 2). This was a characteristic first shown by Morihara and McCafferty (1979b) to separate certain other two-tailed North American baetids from *Heterocloeon*. The *Heterocloeon* clade demonstrates the synapomorphies of the presence of a secondary ridge with a row of denticles on the larval claws (Fig. 25, stem 3) (presumed by parsimony to have been modified from the initial denticulate condition in some subsequent apotypic lineages, see below). Hind wings are either reduced in size compared to that seen, for example, in *Baetis*, or are completely absent, and ancestrally within the branch are presumed to have been reduced in size.

Within the *Heterocloeon* clade, the initial basal branching resulted in the *Isxaeon* branch and the *Heterocloeon* s.s.- *Jubilatum* branch. The *Isxaeon* branch (Fig. 25, stem 4) demonstrates the synapomorphies of a strongly narrowed base of the larval tibia, and medial and distal denticles of the primary row of claw denticles being approximately of equal length. A narrowing of the base of the tibia can also be found in *H. petersi*, but is not nearly as pronounced and is taken by parsimony to be an independent event. *Isxaeon* also entirely lost the hind wings. This is reductionist evolution that has occurred numerous times independently throughout Baetidae, and even within the *Baetis* complex has apparently occurred at different times within *Acentrella* and at different times within *Heterocloeon* (see below). The extensive central sternal spotting seen in the male adults of *Isxaeon* may have developed independently as another synapomorphy for the group. Species relationships within *Isxaeon* remain unknown, because only two of the three are known in the larval stage.

The branch leading to *Heterocloeon* s.s. and *Jubilatum* (Fig. 25, stem 5) demonstrates a narrowed labial palp in the larva and a median caudal filament that is somewhat more reduced to highly reduced. Branching from the *Heterocloeon* s.s.- *Jubilatum* stem, *Heterocloeon* s.s. demonstrates the synapomorphy of having a pair of prothoracic osmobranchiae in the larvae (Fig. 25, stem 6). The species relationships within *Heterocloeon* s.s. were shown by Morihara and McCafferty (1979b) and demonstrate, among other

things, progressive hind wing reduction but not a complete loss. The *Jubilatum* branch (Fig. 25, stem 7) demonstrates the synapomorphies of the presence of submarginal rows of highly specialized setae present below the dorsal margin on both the anterior face (forked, spatulate setae) and posterior face (stout, fimbriate setae) of the larval tibiae, and the loss of denticulation on the secondary ridge of the claws. Both species of *Jubilatum* are also relatively large for two-tailed *Baetis* complex mayflies, and all but one species of *Heterocloeon* s.s. are also large, perhaps indicating that the immediate common ancestor to the *Heterocloeon* - *Jubilatum* branch was large and *H. frivolum* became secondarily reduced in size. In the same respect, the median caudal filament is reduced to one segment in all *Heterocloeon* s.s. and in one species of *Jubilatum* (*H. grande*), perhaps indicating that the immediate common ancestor to the *Heterocloeon* - *Jubilatum* branch had the severely reduced tail, which secondarily recovered some size in *H. amplum*.

The hypothesized branching sequence allows the recognition of subgeneric taxa as per the classification revised herein. Generic rank may be possible, depending on the relationships among the *Acentrella* - *Plauditus* clade, which has yet to be resolved.

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