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New Genera of Baetidae for Some Nearctic Species Previously Included in *Baetis* Leach (Ephemeroptera)

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ABSTRACT Certain Nearctic species originally described in the genus *Baetis* Leach lack the apomorphy possessed by other species described in *Baetis* and several related genera. This apomorphy is a patch of setae ventral on the femora of larvae. As a result, *Baetis* is here restricted to a more monophyletic concept, to include species with a patch of setae ventrally on the femora; and the nonconforming species that lack this character are placed in three new genera as follows: *Fallceon*, n. gen., type species *Baetis quilleri* Dodds as *Fallceon quilleri* (Dodds), n. comb., also includes *Fallceon buenoi* (Allen), n. comb., *Fallceon byblis* (Allen & Murvosh), n. comb., and *Fallceon eatoni* (Kimmins), n. comb.; *Acerpenna*, n. gen., type species *Baetis macdunnoughi* (Ide), n. comb., also includes *Acerpenna macdunnoughi* (Ide), n. comb., also includes *Saltes nageni* Eaton as *Diphetor hageni* (Eaton), n. comb., also includes *Diphetor devinctus* (Traver), n. comb.

KEY WORDS Baetis, Fallceon, Acerpenna, Diphetor, Ephemeroptera, Baetidae, taxonomy

THE EXTENT to which the mayfly genus Baetis Leach may or may not be a natural (monophyletic) entity has never been cladistically demonstrated, although some obvious problems in the group have been recognized or suggested by several workers. The genus name has been widely applied to baetid species throughout the world, primarily because adults possess two character states: paired marginal intercalaries in the forewings, and a well-developed hindwing, which also generally bears a costal process. We and others have found characters involving presence or absence of paired marginal intercalaries and presence or absence of hindwings to be of little use for natural generic classifications because of repeated convergences (e.g., Müller-Liebenau 1981, Waltz & McCafferty 1987a,b). Different adult characters are required for use in cladistic analyses.

As larvae, species of *Baetis* have been reviewed in both the Palearctic (Müller-Liebenau 1970) and the Nearctic (Morihara & McCafferty 1979). Among the Nearctic species, Morihara & McCafferty (1979) introduced six species groups, which were similar to Palearctic species groups recognized by Müller-Liebenau (1970); but 10 species were not clearly assignable to any species group.

We have reviewed larval exemplars of all described genera of the family Baetidae for which larvae are known. We have also studied the larvae and adults of *Baetis fuscatus* L., the type species of *Baetis*. Our studies indicate at least one distinctive larval synapomorphy useful in grouping *Baetis* and related genera. This synapomorphy, however, has also required the exclusion of certain species previously described in *Baetis*. This study treats the Nearctic species only; *Baetis* from other parts of the world, although studied, will be dealt with subsequently.

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Taxonomic Treatment

Larvae of many species heretofore placed in the genus *Baetis*, as well as all known larvae of the genera *Acentrella* Bengtsson, *Barbaetis* Waltz & McCafferty, *Baetiella* Ueno, *Heterocloeon* Mc-Dunnough, and *Platybaetis* Müller-Liebenau, possess a patch of setae at the ventral base of each femur (Fig. 1 and 2). This patch is absent in all other described Baetidae and in the family Siphlonuridae including the *Metamonius* genus group, which is generally regarded as the ancestral outgroup of the Baetidae (Edmunds 1972, 1973, Edmunds et al. 1976, McCafferty & Edmunds 1979). Thus, the presence of a ventral femoral patch of setae is interpreted as apomorphic and its absence is interpreted as plesiomorphic.

Some of the Nearctic species of *Baetis* found by Morihara & McCafferty (1979) not to fit into any species group lack the ventral femoral patch of setae and, therefore, do not share an immediate common ancestor with *Baetis* or with the other genera possessing the patch. Because these species are neither congeneric with *Baetis* nor any other described baetid genus, we place them in new genera.

Most species treated have been previously described and illustrated by Morihara & McCafferty

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Fig. 1. Foreleg of *Heterocloeon curiosum* (Mc-Dunnough) indicating location of ventral femoral patch of setae (sp).

(1979). Because the intent of this paper is to provide a more natural generic classification of Nearctic species and not to redescribe particular species, we have made reference freely in our text to the recently reviewed and illustrated species descriptions of Morihara & McCafferty (1979) as "MM 1979."

Fallceon, n. gen.

Type Species. Baetis quilleri Dodds, 1923: 112. Diagnosis. Larvae of Fallceon are distinguished by the combined characteristics of no ventral femoral patch of setae, the shape of the labial palps (MM 1979: fig. 37b), and presence of a tuft of setae between the prostheca and molar region on at least the right mandible. In the adults this genus is distinguished by the combined presence of paired marginal intercalaries in the forewing and a hindwing with a hooked costal process (Day 1954: fig. 1; Edmunds et al. 1976: fig. 252). Adults of Fallceon may be confused with Neotropical species of Cloeodes Traver, specifically Paraguayan and Uraguayan species; however, adult males may easily be separated by the form of the genitalia (e.g., Day 1954: fig. 2; for *Cloeodes* see Waltz & McCafferty 1987a,b). Larvae of the two genera are distinct.

Description. *Larva.* Antennal scape (MM 1979: fig. 37a) with robust setae. Segment 2 of labial palps



Fig. 2. Scanning electron micrograph of ventral femoral patch (*Baetiella japonica* (Imanishi)) $550 \times$ viewing magnification (scale bar = 10 μ m).

(MM 1979: fig. 37b) poorly developed. Mandibles with incisors fused, denticles distinct; with patch of feathered setae between prostheca and molar region, at least on right mandible. Maxillary palp 2-segmented, subequal to or extending beyond apex of galealacinea. Margins of femora subparallel, not broadened medially, without ventral femoral patch. Seven gill pairs rounded apically, with serrate margins. Median terminal filament present, variable in length.

Adult. Forewings with paired marginal intercalaries. Hindwings reduced, with 2–3 longitudinal veins, and with distinctly hooked costal process (Edmunds et al. 1976: fig. 252). Male forceps (e.g., Day 1954: fig. 2) with elongate distal segment ca. 4-fold longer than wide and subequal to 0.5-fold length of segment 3; basal segment of forceps weakly tapered distally; interbasal area of forceps with distinctive, bilobed median projection.

Included Species. Fallceon quilleri (Dodds, 1923: 112), n. comb.; Fallceon eatoni (Kimmins, 1934: 349), n. comb.; Fallceon buenoi (Allen, 1985: 332), n. comb.; and Fallceon byblis (Allen & Murvosh, 1983: 427) n. comb.

Etymology. Masculine, an arbitrary combination of letters based in part on the Latin *fallax*, meaning false or deceptive.

Remarks. As has been described for species of at least two other genera lacking a ventral femoral patch (e.g., *Callibaetis* Eaton [Check 1982] and *Cloeodes* Traver [Waltz & McCafferty 1987a,b]), the larvae of *Fallceon* (and the other newly described genera herein) show very few distinctive



Fig. 2. Scanning electron micrograph of ventral femoral patch (*Baetiella japonica* (Imanishi)) $550 \times$ viewing magnification (scale bar = 10 μ m).

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and intrageneric character shifts in mouthpart morphology. Characters for species-level recognition of larvae must include a reevaluation of tergal and leg armature and, to a lesser extent, distinctions in color patterns. It is possible that a reevaluation of reared larvae from the western Nearctic may result in the recognition of distinct species now regarded as synonyms of *F. quilleri* (see Morihara & McCafferty 1979). The Mexican species *F. eatoni* and *F. buenoi* are not known as larvae, but the adults are similar both generically and specifically to *F. quilleri*. We suspect that *Baetis poyei* (Eaton) from Cuba and *Baetis garcianus* Traver from Puerto Rico will prove to belong to *Fallceon* upon further study.

Diphetor, n. gen.

Type Species. Baetis hageni Eaton, 1883–88: 169; Edmunds 1962: 4.

Diagnosis. Larvae of *Diphetor* are distinguished by the absence of gills on abdominal segment 1 in combination with the reduced prostheca of the right mandible (MM 1979: fig. 34b) and the absence of the ventral femoral patch of setae. As adults, the character of a forked second vein in the hindwing (Day 1956: fig. 3.26j; Edmunds et al. 1976: fig. 251) in combination with the form of the male genitalia (Day 1956: fig. 3.26g) will distinguish *Diphetor*.

Description. Larva. Antennal scape without robust setae. Segment 2 of labial palps (MM 1979: fig. 34d) poorly developed. Mandibles (MM 1979: fig. 34b) with incisors fused, denticles distinct; without patch of feathered setae between prostheca and molar region. Prostheca of right mandible (MM 1979: fig. 34b) deeply furcate. Maxilla (MM 1979: fig. 34c) with palp 2-segmented and extending beyond galealacinea. Margins of femora subparallel, not broadened medially, without ventral femoral patch. Gills absent on abdominal segment 1. Median terminal filament (MM 1979: fig. 35 a and b) present, slightly shorter than cerci.

Adult. Forewings with paired marginal intercalaries. Hindwings (Day 1956: fig. 3.26j; Edmunds et al. 1976: fig. 251) relatively broad (compared with the majority of *Baetis* species) with pointed costal process and forked vein 2. Male forceps (Day 1956: fig. 3.26g) with elongate distal segment subequal to 0.5-fold length of segment 3; basal segment with tubercle on inner margin or without tubercle.

Included Species. Diphetor hageni (Eaton, 1883– 88: 169), n. comb.; and Diphetor divinctus (Traver, 1935: 684), n. comb.

Etymology. Masculine, from the Greek *diphetor*, meaning searcher.

Remarks. The loss of the first pair of gills in *Diphetor* is not unique in the Baetidae. The first pair of gills has been lost independently even within certain genera (e.g., *Baetis* (Müller-Liebenau 1984) and *Baetiella* [unpublished data]). Therefore, we do not deem the presence or absence of abdominal gill 1 as a generic character, although in the case of *Diphetor* it is useful diagnostically at least with respect to the presently included species.

The condition of the forked vein 2 of the hindwing is not unique to the genus *Diphetor*, for it occurs in various Neotropical, Palearctic, and Oriental baetid species. However, in the Nearctic, adults of only *Baetis diablis* Day may be confused with adults of *Diphetor* because of this character (Day 1954: fig. 4); male genitalia of *B. diablis* (Day 1954: fig. 3) are clearly distinct. We regard the relatively broad hindwing with a forked vein 2 as a plesiomorphy among baetids compared with the more apomorphic, reductionistic condition of reduced hindwing size and venation that arises in other widely disparate baetid lineages. Nevertheless, the hindwing may be useful in identifying field collections of this genus in North America.

The new combination of *D. devinctus* is based on our study of the reared but undescribed larval stage of this species.

Acerpenna, n. gen.

Type Species. *Baetis macdunnoughi* Ide, 1937: 230; McCafferty & Morihara 1979: 27.

Diagnosis. Larvae of Acerpenna are distinguished by the apically pointed seventh pair of abdominal gills (MM 1979: fig. 31f and 32g), thumblike process of the second labial palp segment (MM 1979: fig. 31a and 32c), and absence of the ventral femoral patch of setae. In field samples, larvae may appear to have darkened ring segments of the cerci similar to those described for larvae of Centroptilum Eaton. Adult males may be separated from most other Baetidae with paired marginal intercalaries by the combined characteristics of an elongate apical segment of the forceps (ca. 4-fold longer than wide), conical base of the forceps, and hindwing with a costal process and an undulate anterior margin beyond the costal process (McCafferty & Morihara 1979: fig. 1 and 2).

Description. Larva. Antennal scape rarely with robust setae. Segment 2 of labial palps (MM 1979: fig. 31a and 32c) with anteromedial thumblike process. Mandibles (as in MM 1979: fig. 32b) with incisors fused, denticles distinct; with patch of feathered setae between prostheca and molar region. Maxillary palp 2-segmented, subequal in length to galealacinea. Margins of femora subparallel, not broadened medially, without ventral femoral patch of setae. Seven gill pairs, gills 1–6 rounded apically, gills 7 pointed apically (MM 1979: fig. 31f and 32g). Median terminal filament (MM 1979: fig. 32g) present, subequal to cerci.

Adult. Forewings with paired marginal intercalaries. Hindwings (McCafferty & Morihara 1979: fig. 1) with pointed costal process and undulate anterior margin beyond costal process. Male forceps (McCafferty & Morihara 1979: fig. 2) with elongate distal segment ca. 4-fold longer than wide; basal segment of forceps conical, narrowed distally.

Included Species. Acerpenna macdunnoughi (Ide, 1937: 230), n. comb. and Acerpenna pygmaea (Hagen, 1861: 54), n. comb.

Etymology. Feminine, from the Latin acer, meaning sharp, and *penna*, meaning plate, an almeaning sharp, and *penna*, meaning plate, an al-lusion to the pointed seventh pair of abdominal sharper of the seventh pair of the

Remarks. The condition of the seventh pair of gills in larvae of the two species of Acerpenna is strikingly similar to that of the Palearctic species pair Baetis digitatus and Baetis niger (see Müller-Liebenau 1970). The shape of the labial palps clearly separates the two species pairs.

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