

Phylogeny and classification of the *Baetodes* complex (Ephemeroptera:Baetidae), with description of a new genus

C. R. LUGO-ORTIZ AND W. P. McCAFFERTY

Department of Entomology, Purdue University, West Lafayette, Indiana 47907 USA

Abstract. The *Baetodes* complex is a distinct, monophyletic grouping of Neotropical and southwestern North American baetine (Ephemeroptera:Baetidae) genera having subapical setae on the lateral margin of the tarsal claws of the larvae and a distinct distomedial projection on the basal segment of the genital forceps of male adults. The complex comprises *Moribaetis* sensu stricto, *Mayobaetis* new status, *Prebaetodes* new genus, and *Baetodes*. *Moribaetis* is the most plesiotypic lineage, and its larvae have autapomorphic labral and frontal interantennal character states. *Mayobaetis* shares synapomorphies involving antennal and paraproct armature with *Prebaetodes* and *Baetodes*, and its larvae have autapomorphic antennal and cerci character states. *Prebaetodes* and *Baetodes* are sister lineages sharing numerous synapomorphies, some of which appear associated with the evolution of more specialized larval clinging behavior in torrential habitats. *Prebaetodes* is morphologically intermediate between the more plesiomorphic *Mayobaetis* and the apotypic *Baetodes*, and its larvae have autapomorphic labral and mandibular character states. Larvae of *Baetodes* have autapomorphic gill and median caudal filament character states. Within the construct of a strict phylogenetic classification, the generic concept of *Moribaetis* is restricted, and *Mayobaetis*, formerly a subgenus of *Moribaetis*, is elevated to generic rank. *Prebaetodes* and its type species, *P. sitesi* new species, are described from larvae from Colombia and Ecuador. A generic key to the larvae of the *Baetodes* complex is provided.

Key words: *Baetodes* complex, phylogenetics, *Prebaetodes sitesi*, new genus, new species, *Mayobaetis*, new status, *Moribaetis*, *Baetodes*.

Needham and Murphy (1924) erected the genus *Baetodes* (Ephemeroptera:Baetidae) for *B. serratus* Needham and Murphy, a Brazilian species described from larvae only. They considered the genus distinctive because of the presence of elongate legs, ventrally oriented gills on abdominal segments 1-5, and tergal tubercles. Subsequent work in the Neotropics and southwestern North America dealing with the 30 nominal species now recognized in *Baetodes* (Mayo 1968, 1972, 1973, Koss 1972, Cohen and Allen 1978, McCafferty and Provonsha 1993, Lugo-Ortiz and McCafferty 1995) has demonstrated that the morphology of the legs and the arrangement of the gills are consistent within the genus, but that the shape and number of the tergal tubercles are highly variable.

Although larvae of *Baetodes* are distinctive, adults of the genus are less understood. Traver (1943) described the first adults based on *B. spinifer* Traver. Her generic assignment of this species was tenuous because it was based on limited material that had not been reared from known larvae. Koss (1972) described adults from reared larvae of *B. edmundsi* Koss, and considered the expanded anal region in the forewings to be diagnostic of the genus. Based on

rearing of additional species of *Baetodes*, Flowers (1987) confirmed Traver's (1943) original assignment of adults. He indicated that a distomedial process of the basal segment of the genital forceps and an elongate foretibiae of male adults, along with a poorly developed metanotum, are generic characteristics, but that the expanded anal region of the forewings is not.

Gillies (1991) restricted the concept of the subfamily Baetinae of the family Baetidae to include only those taxa that have double marginal intercalaries in the forewings. Based on the possession of this characteristic, *Baetodes* is now considered to belong to Baetinae. Other than this characteristic, the relationships of *Baetodes* have remained an anomaly because of its unusual larvae. The only previous information having any possible phylogenetic consequence was the suggestion by McCafferty et al. (1992) that *Baetodes* was probably related to the Neotropical genus *Moribaetis* Waltz and McCafferty. McCafferty et al. (1992) also suggested that the subgenus *Mayobaetis* Waltz and McCafferty of *Moribaetis* probably deserved generic rank because it appeared to be more closely related to *Baetodes* than to *Moribaetis* sensu stricto. However, no supporting phylogenetic data were given.

While recently engaged in an intensive study of the Baetidae of South America, we discovered a new taxon from the highlands of Colombia and Ecuador whose larvae are morphologically intermediate between *Mayobaetis* and *Baetodes*, and therefore potentially the phylogenetic "missing link" that might tie *Baetodes* to other Baetinae. This discovery prompted us to undertake a formal cladistic analysis of the taxonomic species groups that were potentially related, i.e., *Baetodes*, *Moribaetis* (*Moribaetis*), *Moribaetis* (*Mayobaetis*), and the newly discovered taxon. We were able to demonstrate that the grouping is monophyletic (see below), and we refer to it as the *Baetodes* complex.

Elucidation of the phylogeny of the *Baetodes* complex is important because it provides an objective basis for any necessary revision of higher classification, which in Ephemeroptera should be based on strict phylogenetic constraints as recommended by McCafferty (1991). Only recently has there been a concerted effort to replace old classificatory schemes in Ephemeroptera based on subjective phenetic criteria with consistent phylogenetic criteria. In Baetidae, in particular, the subjective use of differential character gaps in larval and adult stages has resulted in the proposed lumping of many genera (e.g., Novikova and Kluge 1987, Kluge 1992a, 1992b) that potentially masks detailed genealogical relationships of the taxa involved and thus any other biological information that may be inherent in discrete phyletic lineages. McCafferty and Wang (1994) argued against such lumping of genera prior to phylogenetic analysis because they are often monophyletic species groups that serve as the initial taxonomic units for cladistic study (e.g., McCafferty and Waltz 1990, 1995).

Deposition of the material examined in this study is variously noted as the entomological collection of Florida A&M University (FAMU), Tallahassee; the Purdue Entomological Research Collection (PERC), West Lafayette, Indiana; the entomological collection of the University of Missouri (UM), Columbia; and the National Museum of Natural History (NMNH), Washington, D.C.

Taxonomy

Baetodes complex

This monophyletic group is distinguished by the presence of subapical setae on only one lat-

eral margin of the tarsal claws of the larvae (Figs. 9, 15, 32, 39). These setae originate above the apical denticle of the claws, and are distinctly different from the paired subapical setae discussed by Morihara and McCafferty (1979) and Corkum and Clifford (1981) that arise almost at the tip of the claws in some species of *Baetis* Leach. Larvae also lack the villopore (see Waltz and McCafferty 1987: figs. 1, 2), thus separating the group from the *Baetis* complex (see Waltz et al. 1994). Known male adults possess a distinct small distomedial projection on the basal segment of the genital forceps (Figs. 11, 17, 42).

Moribaetis Waltz and McCafferty

Moribaetis (*Moribaetis*) Waltz and McCafferty 1985: 243.

Diagnosis

Larvae: Antennae are more than 2.0× the length of the head capsule (Fig. 7; see also Waltz and McCafferty 1985: figs. 2, 3, 5), and the subcylindrical scapes and pedicels (Fig. 1) lack a dorsolateral row of setae; the lateral margins of the frons (Fig. 7) are abbreviated and do not reach the base of the clypeus; the labrum (Fig. 2) is somewhat narrow basally and distinctly raised basomedially; the paraprocts (Fig. 3) have marginal spines; and the median caudal filament (Fig. 10) is 0.5–1.0× the length of the cerci. Male adults: 3 longitudinal veins are present in the hindwings, the 2nd of which is forked (Fig. 8); and the distal segment of the genital forceps (Fig. 11) is round and short.

Distribution

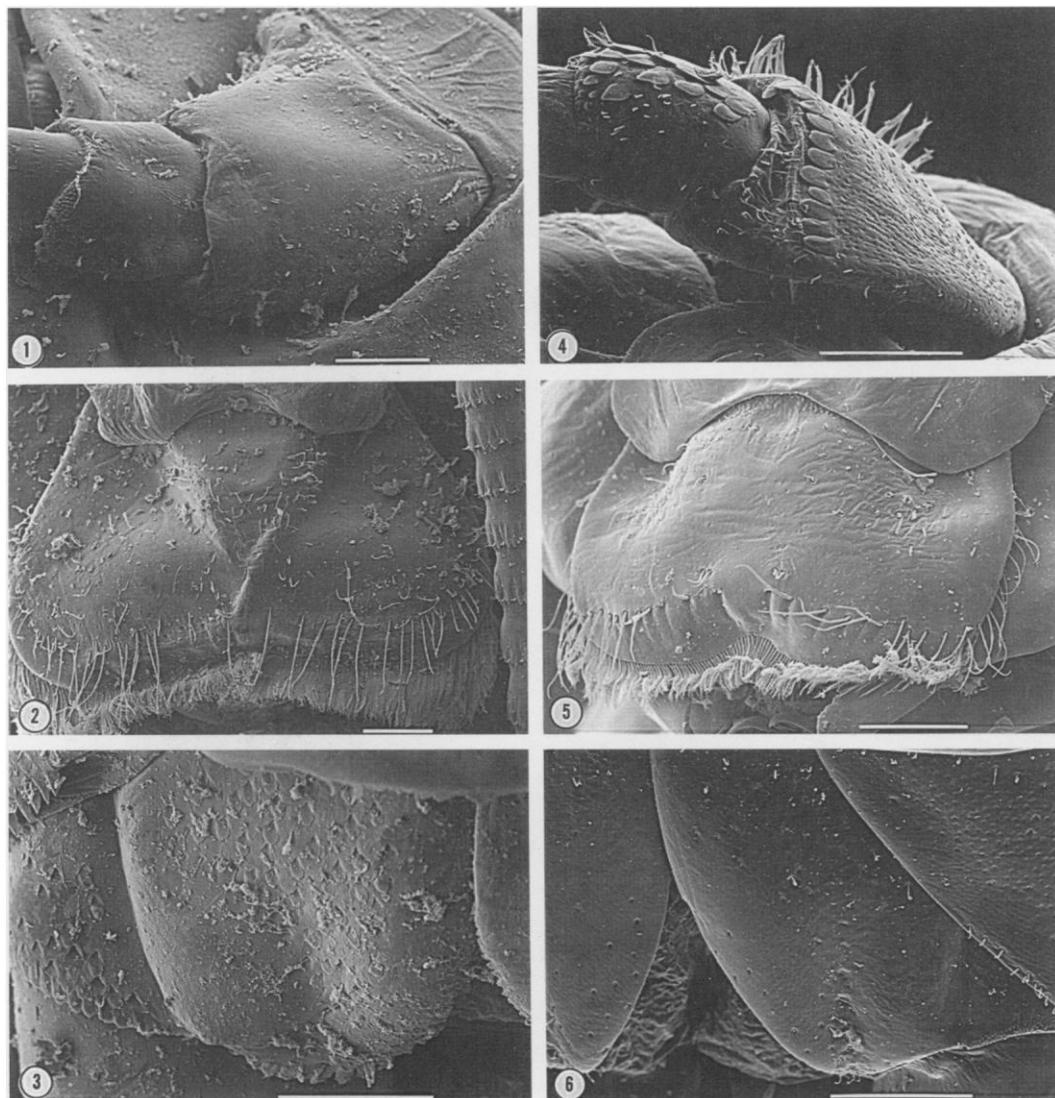
Southern Mexico, Central America, tropical South America.

Included species

Moribaetis macaferti Waltz, *M. maculipennis* (Flowers) (*type species*), *M. salvini* (Eaton).

Material examined

Moribaetis macaferti: holotype larva, Costa Rica (PERC); larvae: Guatemala (PERC); larvae: Mexico, Chiapas, Oaxaca, and Veracruz States (PERC); *M. maculipennis*: larvae and male



FIGS. 1-6. *Moribaetis macaferti* and *Mayobaetis ellenae*, larvae. 1-3.—*Moribaetis macaferti*: 1.—Antennal scape and pedicel (bar = 100 μ m). 2.—Labrum, dorsal (bar = 100 μ m). 3.—Paraproct (bar = 100 μ m). 4-6.—*Mayobaetis ellenae*: 4.—Antennal scape and pedicel (bar = 100 μ m). 5.—Labrum, dorsal (bar = 100 μ m). 6.—Paraproct (bar = 100 μ m).

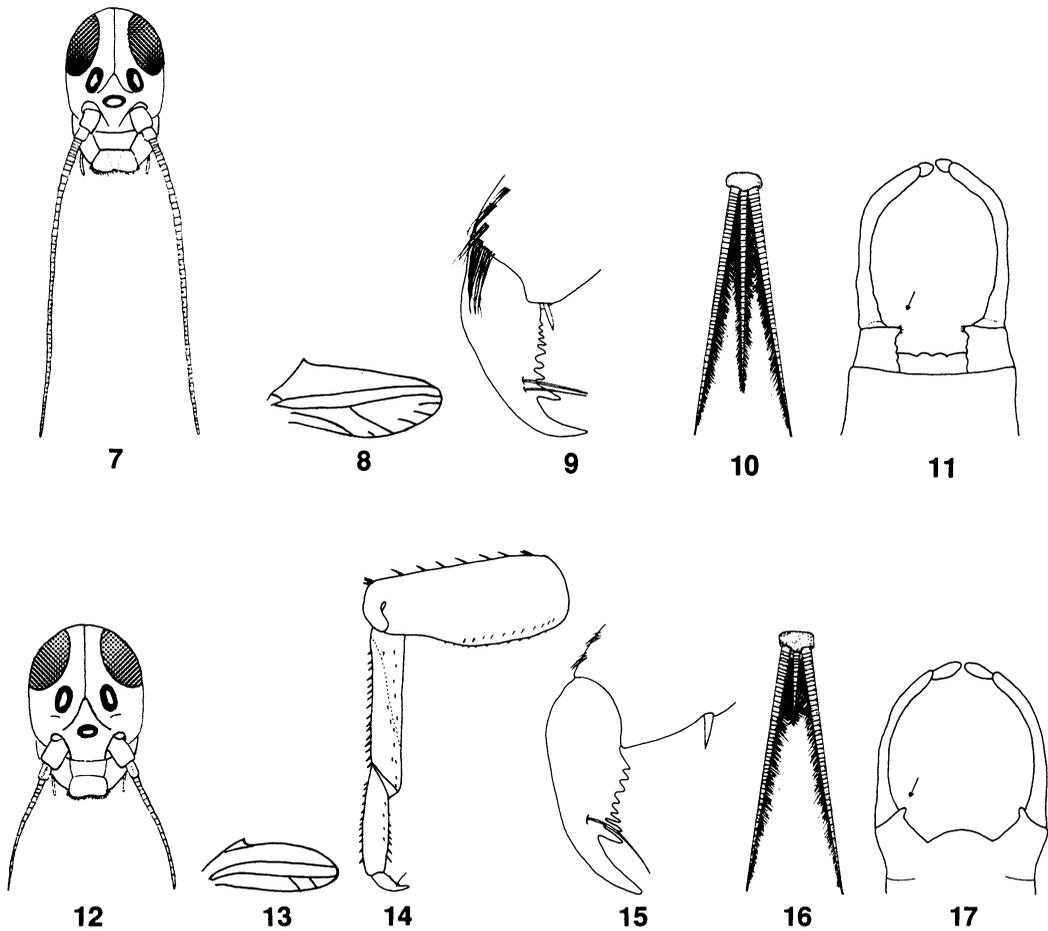
adults: Costa Rica (PERC); *M. salvini*: larvae: Costa Rica (PERC).

Mayobaetis Waltz and McCafferty, new status
Moribaetis (*Mayobaetis*) Waltz and McCafferty 1985:
 240.

Diagnosis

Larvae: Antennae are subequal to the length of the head capsule (Fig. 12); the dorsoventrally

flattened scapes and pedicels (Fig. 4) have scales, fine setae, scale-like tuberculations and a dorsolateral row of long, fine, simple setae; the lateral margins of the frons (Fig. 12) are broadly connected to the clypeus; the labrum (Fig. 5) is somewhat basally narrow and basomedially flattened; the paraprocts (Fig. 6) lack marginal spines; lateral spines are present on the cerci (Fig. 18); and the median caudal filament (Fig. 16) is $<0.5\times$ but $\geq 0.25\times$ the length of the cerci.



FIGS. 7-17. *Moribaetis* spp. and *Mayoabaetis ellena*. 7-11.—*Moribaetis* spp.: 7-9.—*M. salvini*: 7.—Head, frontal. 8.—Hindwing. 9.—Tarsal claw, larva. 10-11. *M. maculipennis*: 10.—Caudal filaments, larva. 11.—Genitalia, male adult, ventral (arrow to distomedial projection). 12-17.—*Mayoabaetis ellena*: 12.—Head, frontal. 13.—Hindwing. 14.—Right foreleg, larva. 15.—Tarsal claw, larva. 16.—Caudal filaments, larva. 17.—Genitalia, male adult, ventral (arrow to distomedial projection).

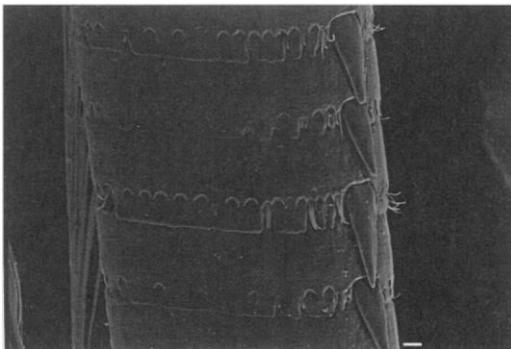


FIG. 18. *Mayoabaetis ellena*, larva: Cercus (bar = 10 μ m; lateral spines on right side).

Male adults: 2 longitudinal, unforked veins are present in the hindwings (Fig. 13); and the distal segment of the genital forceps (Fig. 17) is elongate and ovoid.

Distribution

Central America, tropical South America.

Included species

Mayoabaetis ellena (Mayo) new status (*type species*).

Material examined

Larva: Costa Rica (PERC); larvae: Ecuador (UM).

Prebaetodes Lugo-Ortiz and McCafferty, new genus

Diagnosis

Larvae: Antennal pedicels (Fig. 19) have a dorsolateral row of long, fine, simple setae; the labrum (Figs. 20, 21, 25) is narrow basally and expanded laterally; the mandibles (Figs. 27, 28) have somewhat curved lateral margins and fan-like denticles, and the right prosthema is pointed and medially-serrate; the hindwingpads are rudimentary (Fig. 33); the legs (Fig. 31) are elongate and outstretched, and the tibiae are somewhat twisted; the paraprocts (Fig. 22) lack marginal spines, but have ill-defined submarginal spines; and the median caudal filament (Fig. 37) is $<0.25\times$ but $\geq 0.20\times$ the cerci length, and has rudimentary marginal setae.

Description

Larva.—Antennal scapes and pedicels (Fig. 19) with numerous small, simple setae; dorso-lateral row of long, fine, simple setae present on scapes. Lateral margins of frons broadly connected to clypeus (Fig. 25). Labrum (Figs. 20, 21, 25) basally narrow, laterally expanded; antero-medial emargination shallow. Hypopharynx (Fig. 26) with broad, somewhat rectangular lingua with single distomedial projection; superlinguae narrow and elongate. Left mandible (Fig. 27) with incisors fused, fan-like; prosthema with distal setae, very close to incisors; lateral margin curved, with long, simple setae not extending beyond basal half. Right mandible (Fig. 28) with incisors fused, fan-like; prosthema spine-like, median margin serrate; tuft of setae at base of mola; lateral margin curved, with long, simple setae not extending beyond basal half. Maxillae (Fig. 29) broad, with median hump near midregion; palps 2-segmented, extending beyond galealacinae; galealacinae with elongate denticles; row of long, simple setae at base of denticles, ventrally oriented. Labium (Fig. 30) with 3-segmented palps; palp segment 1 as long as segments 2 and 3 combined; segment 2 short, nearly half length of segment 3, medially concave; segment 3 ellip-

soidal; glossae broadly based, nearly $0.75\times$ length of paraglossae, distally round; paraglossae almost rectangular, medially concave, with long, pectinate setae ventrodistally. Legs (Fig. 31) without villopore; femora elongate, anterior and posterior margins subparallel, distally round; tibiae, somewhat twisted, elongate and slender, as long as femora; tarsi slender, $0.33\times$ length of tibiae; tarsal claws (Fig. 32) elongate, with one row of denticles and lateral subapical seta. Hindwingpads rudimentary (Fig. 33). Abdominal terga (Fig. 34) with scale bases and triangular spination on posterior margin. Gills (Fig. 35, 36) on abdominal segments 1–7, plate-like, held dorsolaterally (Fig. 33); gill 1 highly reduced. Paraprocts (Fig. 22) lack marginal spines. Median caudal filament (Fig. 37) is $<0.25\times$ but $\geq 0.20\times$ length of cerci, with rudimentary setation; cerci with long, simple setae medially.

Adult.—Unknown.

Etymology

Masculine, an arbitrary combination of letters consisting of the Latin prefix *pre* and the generic name *Baetodes*. It is an allusion to the precursor evolutionary relationship of *Prebaetodes* with *Baetodes*.

Distribution

Tropical South America.

Included species

Prebaetodes sitesi Lugo-Ortiz and McCafferty, new species (*type species*).

Material examined

See under *P. sitesi*.

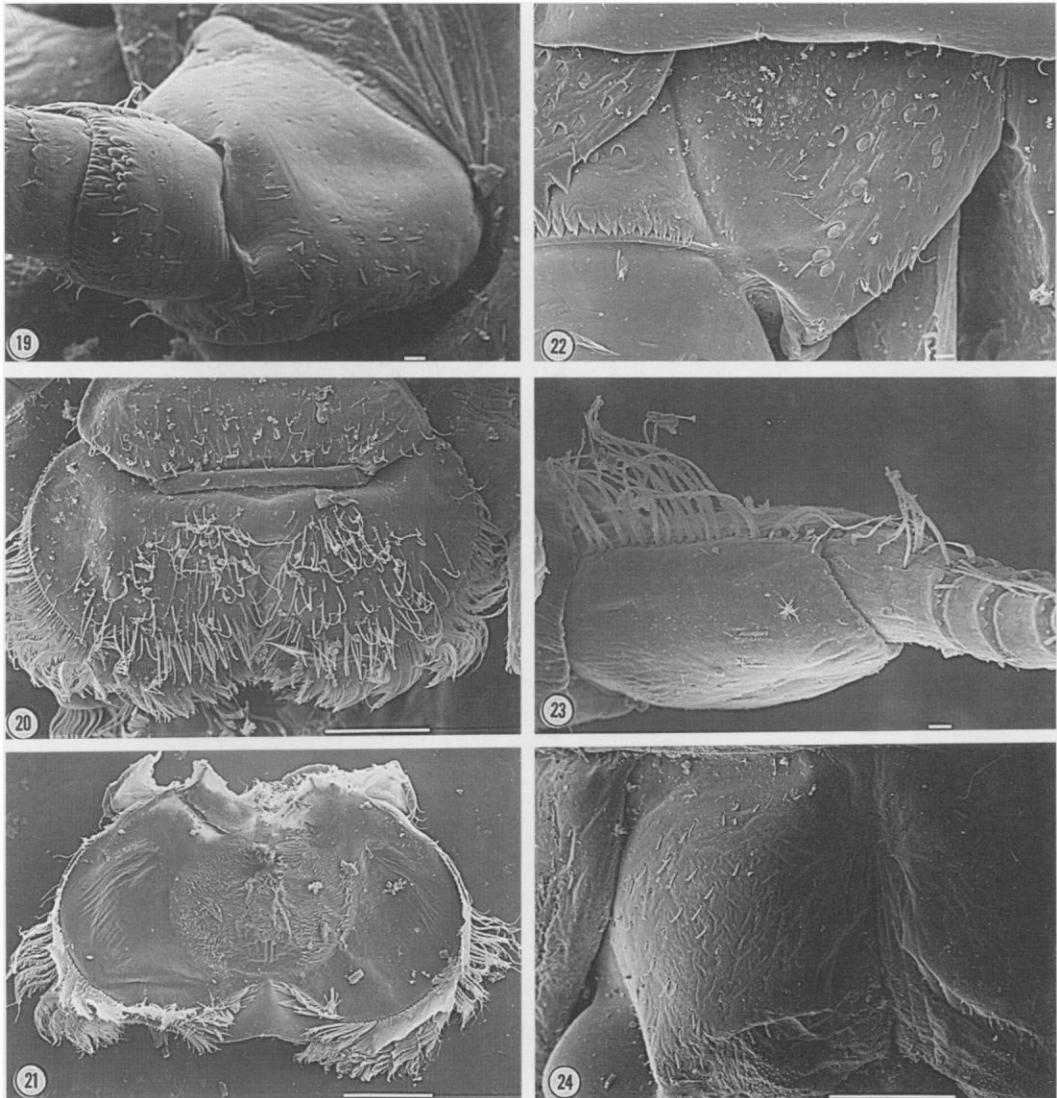
Prebaetodes sitesi Lugo-Ortiz and McCafferty, new species

Diagnosis

This is the only known species of the genus. See generic diagnosis.

Description

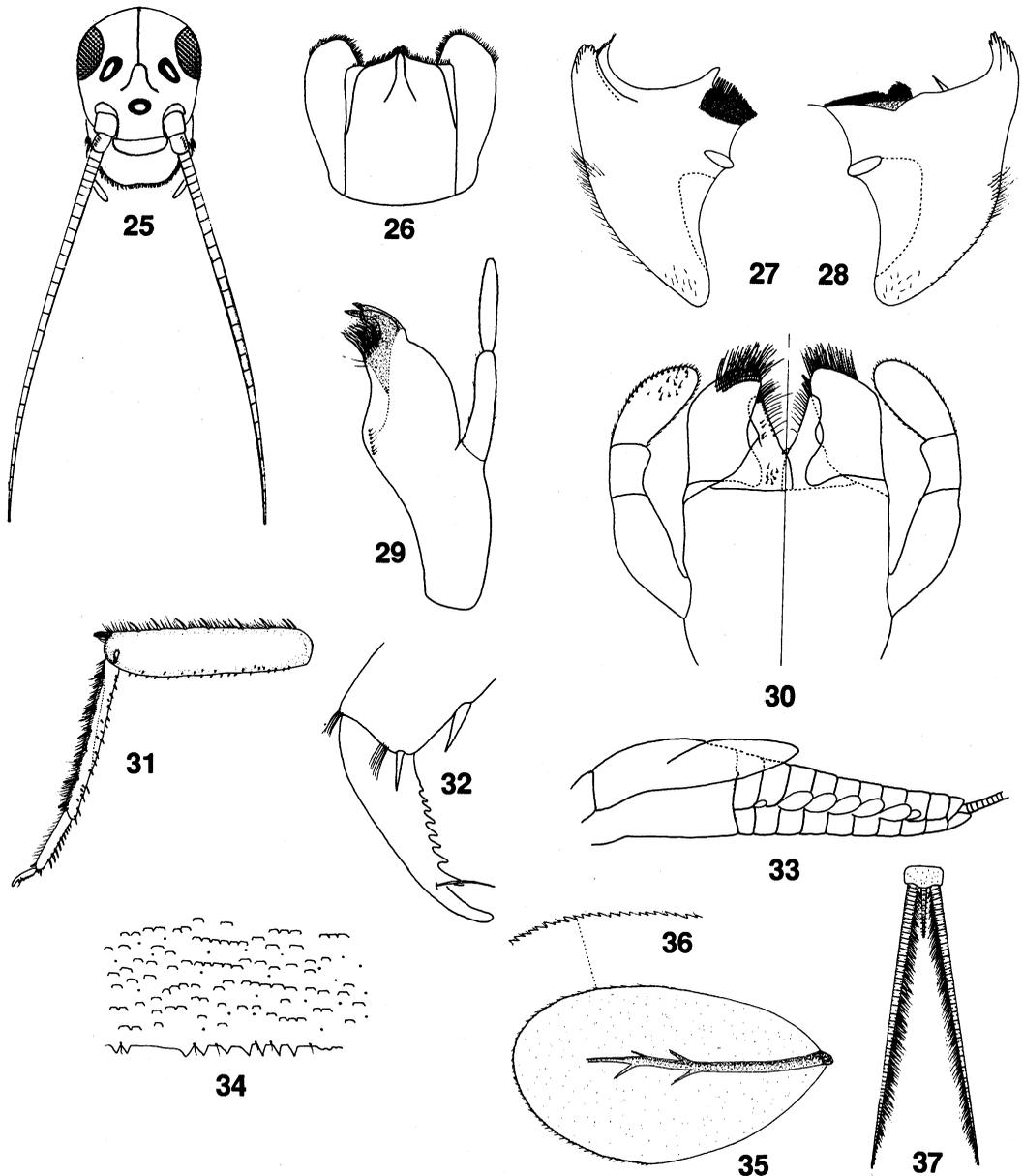
Larva.—Body length: 5.5–6.3 mm; caudal filaments: 4.2–5.0 mm. Head (Fig. 25): Coloration



FIGS. 19–24. *Prebaetodes sitesi* new species and *Baetodes* spp., larvae: 19–22. *P. sitesi*: 19.—Antennal scape and pedicel (bar = 10 μ m). 20.—Labrum, dorsal (bar = 100 μ m). 21.—Labrum, ventral (bar = 100 μ m). 22.—Paraproct (bar = 10 μ m). 23–24.—*Baetodes* spp.: 23.—*B. velmae*: Antennal scape and pedicel (bar = 10 μ m). 24.—*B. tritus*: Paraproct (bar = 100 μ m).

yellow-brown, clypeus and area around compound eyes cream. Antennae nearly $3.0\times$ length of head capsule. Labrum (Figs. 20, 21, 25) with numerous long, fine, simple setae dorsally, forming submarginal cluster anteriorly. Hypopharynx as in Fig. 26. Left mandible (Fig. 27) with 9 denticles. Right mandible (Fig. 28) with 7 denticles. Maxillae (Fig. 29) with 4 sharp denticles on galealaciniae and 5–6 long, simple setae on medial hump; palp segment 1 somewhat

longer than segment 2. Labium (Fig. 30) with glossae with scattered short, simple setae ventrally; paraglossae with 3 ventrodistal rows of long, pectinate setae. Thorax: Coloration yellow-brown, variably mottled with cream. Legs (Fig. 31) yellow-brown, with variable cream and medium brown markings; femora dorsally with 9–10 long, robust, simple setae (last 2 contiguous) and numerous long, fine, simple setae, ventrally with numerous short, stout, simple setae; tibiae



FIGS. 25-37. *Prebaetodes sitesi* new species, larva: 25.—Head, frontal. 26.—Hypopharynx. 27.—Left mandible. 28.—Right mandible. 29.—Left maxilla. 30.—Labium (left-ventral; right-dorsal). 31.—Right foreleg. 32.—Tarsal claw. 33.—Thorax and abdomen, lateral. 34.—Detail of tergum 4. 35.—Gill 4. 36.—Detail of gill margin. 37.—Caudal filaments.

dorsally with 9-10 long, robust, simple setae and numerous long, fine, simple setae, ventrally with numerous simple setae of medium length and short, stout, simple setae; tarsi dorsally with numerous long, fine, simple setae; ventrally with 9-10 simple setae of increasing length

and girth; tarsal claws (Fig. 32) with 8-9 denticles, distal denticle largest. Abdomen (Fig. 33): Coloration yellow-brown to medium brown; terga 9-10 usually paler than 1-8; terga 2-8 usually with pale anteromedial areas. Terga (Fig. 34) with abundant scale bases; posterior margin

with irregular triangular spination. Sterna yellow-brown to medium brown. Gills (Figs. 35, 36) 1–7 marginally serrate and with fine, simple setae. Paraprocts (Fig. 22) with ill-defined submarginal spines and scattered scales and scale bases. Caudal filaments (Fig. 37) yellow-brown.

Adult.—Unknown.

Material examined

Holotype.—Larva: **ECUADOR. Napo Prov:** 5.6 km E of Papallacta, 2880 m, 11°C, roadside stream, 20.vii.1993, Sites, Linit, Nichols (PERC).

Paratypes.—**ECUADOR. Carchi Prov:** 2.1 km W of Santa Bárbara, 2603 m, 17°C, fast stream passing under road, 15.vii.1993, Sites, Linit, Nichols, 2 larvae (UM); **Pichincha Prov:** 25.3 km W of Barrio de la Libertad, on old road to Quito, 2316 m, 12°C, small gravel stream, 25.vii.1993, Sites, Linit, Nichols 11 larvae (2 in UM, 3 in NMNH, 6 in PERC); 20.2 km W of Barrio de la Libertad, on old road to Quito, 2707 m, 12°C, rocky stream, 25.vi.1993, Sites, Linit, Nichols, 3 larvae (PERC); 14.2 km W of Barrio de la Libertad, on old road to Quito, 3097 m, 11°C, roadside stream with vegetation, 25.vii.1993, Sites, Linit, Nichols, 6 larvae (2 in NMNH, 4 in PERC).

Additional material.—**COLOMBIA. Cundinamarca Dept:** 23 km E of El Colegio, 9.ii.1969, P. and P. Spangler (PERC); Caño at Los Alpes Albán, on Hwy 166, 3.iv.1969, W. P. McCafferty, larva (PERC). **ECUADOR. Carchi Prov:** 2.1 km W of Santa Bárbara, 2603 m, 17°C, fast stream passing under road, 15.vii.1993, Sites, Linit, Nichols, 2 larvae (PERC); 33.7 km W of Tufiño, 3158 m, 11.5°C, silty, vegetated stream riffle, 16.vii.1993, 3 larvae (PERC); **Napo Prov:** Río Maspa, 13.5 km E of Papallacta, 2975 m, 9°C, gravel and large rocks, 20.vii.1993, Sites, Linit, Nichols, 2 larvae (PERC); **Pichincha Prov:** 20.2 km W of Barrio de la Libertad, on old road to Quito, 2707 m, 12°C, rocky stream, 25.vii.1993, Sites, Linit, Nichols, 3 larvae (PERC); 14.2 km W of Barrio de la Libertad, on old road to Quito, 3097 m, 11°C, roadside stream with vegetation, 25.vii.1993, Sites, Linit, Nichols, 5 larvae (UM).

Etymology

We name this species after R. W. Sites, who provided us Ecuadorian samples of the species.

Remarks

Prebaetodes sitesi was collected at high altitudes in Colombia and Ecuador, in riffles and, less often, in stream pools (perhaps through drift) with water temperatures ranging from 9° to 17°C. The species appears to be endemic to highlands of Colombia and Ecuador, because we have examined extensive baetid material from other South American countries and have yet to find it elsewhere.

Baetodes Needham and Murphy

Baetodes Needham and Murphy 1924: 55.

Diagnosis

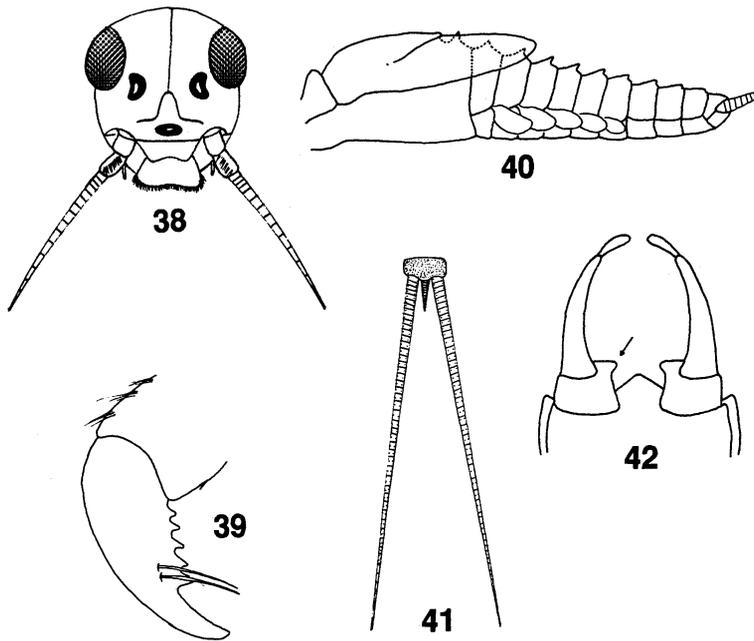
Larvae: Antennae are subequal to, or shorter than, the head capsule, and the pedicels (Fig. 23) have a dorsolateral row of long, fine, simple setae; the lateral margins of the frons are broadly connected to clypeus (Fig. 38); the legs (similar to Fig. 31) are elongate and outstretched, and the tibiae are somewhat twisted; there are 5 pairs of ventrally oriented gills (Fig. 40); the tergal tubercles range from weakly developed (see Cohen and Allen 1978: figs. 12, 24) to well developed (Fig. 40); the paraprocts lack marginal spines (Fig. 24); and the median caudal filament is <0.20× the length of the cerci (Fig. 41). Male adults: Forelegs are relatively elongate; the hindwings are rudimentary (similar to Fig. 32) or absent (Fig. 39); the metanotum is poorly developed (see Flowers 1987: figs. 4–7); and there is a distinct distomedial projection on the basal segment of the genital forceps (Fig. 42).

Distribution

Southwestern United States, Mexico, Central America, tropical South America.

Included species

Baetodes adustus Cohen and Allen; *B. andamaensis* Mayo; *B. alleni* McCafferty and Provonsha; *B. arawak* (Traver); *B. arizonensis* Koss; *B. bibranchius* McCafferty and Provonsha; *B. caritus* Cohen and Allen; *B. chilloni* (Mayo); *B. deficiens* Cohen and Allen; *B. deludens* Lugo-Ortiz and McCafferty; *B. edmundsi* Koss; *B. fortinensis* Mayo; *B. fuscipes* Cohen and Allen; *B. inermis* Cohen and Allen; *B. itatayanus* Demoulin; *B. lev-*



FIGS. 38-42.—*Baetodes* spp.: 38.—*B. levis*: Head, frontal. 39.—*B. tritus*: Tarsal claw, larva. 40.—*B. bibranchius*: Thorax and abdomen, larva, lateral. 41.—*B. velmae*: Caudal filaments, larva. 42.—*B. bibranchius*: Genitalia, male adult, ventral (arrow to distomedial projection).

is Mayo; *B. longus* Mayo; *B. noventus* Cohen and Allen; *B. obesus* Mayo; *B. pallidus* Cohen and Allen; *B. peniculus* Mayo; *B. pictus* Cohen and Allen; *B. proiectus* Mayo; *B. sancticatarinae* Mayo; *B. serratus* Needham and Murphy (*type species*); *B. solus* Mayo; *B. spinae* Mayo; *B. spinifer* Traver; *B. tritus* Cohen and Allen; *B. velmae* Cohen and Allen.

Material examined

Baetodes alleni: holotype larva: USA, Texas (PERC); larvae, USA, Arizona (PERC); *B. bibranchius*: holotype larva, USA, Texas (PERC); paratype larvae, USA, Texas (PERC); *B. deficiens*: larvae, Costa Rica (PERC); larvae, Mexico, Sonora (PERC); *B. deludens*: holotype larva, Costa Rica (PERC); *B. fuscipes*: larva, Guatemala (PERC); *B. levis*: larvae, Colombia (PERC); larvae, Ecuador (UM); *B. longus*: larvae, Mexico, Nuevo León (PERC); *B. noventus*: larva, Costa Rica (PERC); *B. pictus*: male adults, Mexico (PERC); *B. proiectus*: larvae, Ecuador (UM); *B. solus*: larvae, Colombia (PERC); *B. spinae*: larvae, Colombia (PERC); larvae, Ecuador (UM); *B. tritus*: larvae, Costa Rica

(FAMU); *B. velmae*: larvae, Costa Rica; *B. spp.*: larvae, Ecuador (UM).

Generic key to the larvae of the *Baetodes* complex

1. Tarsal claws with 1 or 2 setae on lateral margin, situated between base of distal-most denticle and convex margin (Figs. 9, 15, 32, 39); villopore absent *Baetodes* complex, 2
- 1'. Tarsal claws not as above; villopore present or absent other Baetidae (not keyed further)
2. Labrum basomedially raised (Fig. 2); lateral margins of frons abbreviated, not reaching clypeus (Fig. 7); paraprocts with marginal spines (Fig. 3); median caudal filament length $\geq 0.5 \times$ cerci length (Fig. 10); antennal pedicel without dorsal row of setae (Fig. 1); segment 2 of labial palps longer than segment 3 *Moribaetis*
- 2'. Labrum basomedially flattened (Figs. 5, 20); lateral margins of frons broadly con-

- nected to clypeus (Figs. 12, 25, 38); paraprocts without marginal spines (Figs. 6, 22, 24); median caudal filament length $<0.5\times$ cerci length (Figs. 16, 37, 41); antennal pedicels with dorsal row of setae (Figs. 4, 19, 23); segment 2 of labial palps usually subequal to, or shorter than, segment 3 3
3. Cerci with lateral spines (Fig. 18); scapes and pedicels dorsoventrally flattened, with scales and scale-like tuberculations (Fig. 4); median caudal filament length $<0.5\times$ but $\geq 0.25\times$ cerci length (Fig. 16); legs robust, with straight tibiae (Fig. 14); hindwingpads well developed *Mayobaetis*
- 3'. Cerci without lateral spines; scapes and pedicels subcylindrical and without scales or scale-like tuberculations (Figs. 19, 23); median caudal filament length $<0.25\times$ cerci length (Figs. 37, 41); legs slender and elongate, with partially twisted tibiae (Fig. 31); hindwingpads rudimentary (Fig. 33) or absent (Fig. 40) 4
4. Lateral margin of mandibles somewhat curved (Figs. 27, 28); labrum laterally expanded (Fig. 25); gills on abdominal segments 1-7, held dorsolaterally (Fig. 33); median caudal filament length $<0.25\times$ but $\geq 0.20\times$ cerci length (Fig. 37); abdominal tergal tubercles absent *Prebaetodes*
- 4'. Lateral margin of mandibles somewhat straight; labrum not laterally expanded (Fig. 38); gills on abdominal segments 1-5, held ventrally (Fig. 40); median caudal filament length $<0.20\times$ cerci length (Fig. 41); abdominal tergal tubercles usually present, variously developed (Fig. 40) *Baetodes*

Phylogeny

Methods

The operational taxonomic units, or OTUs, used for comparative cladistic analysis consisted of the traditional species groups *Baetodes*, *Moribaetis* [= *Moribaetis* (*Moribaetis*)], and *Mayobaetis* [= *Moribaetis* (*Mayobaetis*)], and the newly discovered taxon, *Prebaetodes*. Larvae of all OTUs were examined, and adults of all but *Prebaetodes*

(adults remain unknown) were examined (see Taxonomy section).

Standard cladistic methods employed are after Hennig (1966), Ross (1974), and Wiley (1981). Neither the use of computer programs to analyze the phylogeny nor the generation of a character matrix was necessary because of the small number of OTUs and available comparative characters. The outgroup used to determine character state polarities consisted of all Baetinae exclusive of the *Baetodes* complex.

Nineteen comparative characters and their plesiomorphic and apomorphic states are given in Table 1. Two character states are evident for all characters except 1, in which a distinct, 3-step, unidirectional gradation of the larval median caudal filament length was evident among the OTUs (see discussion). The phenoclinical states of this character are listed under numbers 7, 10, and 17 in Table 1.

Phylogenetic results and discussion

The deduced cladogram depicting the relationships of the OTUs is given in Fig. 43. Numbers along the branches of the cladogram (Fig. 43) show apomorphies that define the respective lineages and are described in Table 1. The cladogram is based on complete parsimony and no alternative branching sequences at any probability level were possible from our evidential data.

Apomorphies 1 and 2 in Table 1 and Fig. 43 define the *Baetodes* complex as a monophyletic group within Baetinae. With respect to apomorphy 2, which is associated with the adult stage, we infer that adults of *Prebaetodes* will demonstrate this genitalic apomorphy when adults become known. The relative apotypic position of *Prebaetodes* within the complex, as deduced from its larvae, is certainly predictive of such.

Cladistic analysis showed that the subgenera *Mayobaetis* and *Moribaetis* are phyletically distinct, with *Mayobaetis* having a more recent common ancestry with *Prebaetodes* and *Baetodes* (Table 1, Fig. 43). *Prebaetodes* and *Baetodes* share numerous synapomorphies indicating a sister relationship, but both OTUs also possess autapomorphies that clearly distinguish them from each other (Table 1 and Fig. 43). *Prebaetodes* and *Baetodes* may be interpreted as the most specialized lineages within the complex, because they reflect reductive trends in body size,

TABLE 1. Structural characters and character state polarities used to formulate the cladogram of the *Baetodes* complex in Fig. 1. Numbered characters correspond to the numbered apomorphies distributed on the cladogram. Stepwise character states, or phenoclines, are asterisked. All characters refer to the larval stage, except character 2, which refers to adults.

Character	Plesiomorphy	Apomorphy
1. Tarsal claw lateral setation	Absent	Present (Figs. 9, 15, 32, 39)
2. Male genital forceps basal segment	Without distomedial projection	With distomedial projection (Fig. 11, 17, 42)
3. Labrum shape	Basomedially flat (Figs. 5, 20)	Basomedially raised (Fig. 2)
4. Frons lateral margins	Broad, reaching clypeus (Figs. 12, 25, 38)	Abbreviated, not reaching clypeus (Fig. 7)
5. Paraproct spination	Present (Fig. 3)	Absent (Figs. 6, 22, 24)
6. Antennal pedicel setation	Absent (Fig. 1)	With dorsal row of long, fine, simple setae (Figs. 4, 19, 23)
7. Median caudal filament length	>0.5× cerci length (Fig. 10)	*<0.5× cerci length (see 10)
8. Cercus lateral spination	Absent	Present (Fig. 18)
9. Antennal scape and pedicel shape	Cylindrical to subcylindrical (Figs. 1, 19, 23)	Dorsoventrally flatten (Fig. 4)
10. Median caudal filament length	*<0.5× but $\geq 0.25 \times$ cerci length (Fig. 16)	*<0.25× cerci length (see 17)
11. Leg shape	Robust (Fig. 14)	Slender and elongate (Fig. 31)
12. Tibia rotation	Straight (Fig. 14)	Partially twisted (Fig. 31)
13. Hindwingpad	Well developed	Rudimentary (Fig. 33) or absent (Fig. 40)
14. Median caudal filament setation	Well developed (Figs. 10, 16)	Reduced (Figs. 37, 41)
15. Mandibular shape	Lateral margins somewhat straight	Lateral margins somewhat curved (Figs. 27, 28)
16. Labrum shape	Not expanded (Figs. 7, 13, 38)	Expanded (Fig. 25)
17. Median caudal filament length	*<0.25× but $\geq 0.20 \times$ cerci length (Fig. 37)	<0.20× cerci length (Fig. 41)
18. Gill number	On abdominal segments 1-7 (Fig. 33)	On abdominal segments 1-5 (Fig. 40)
19. Gill orientation	Dorsolateral (Fig. 33)	Ventral (Fig. 40)

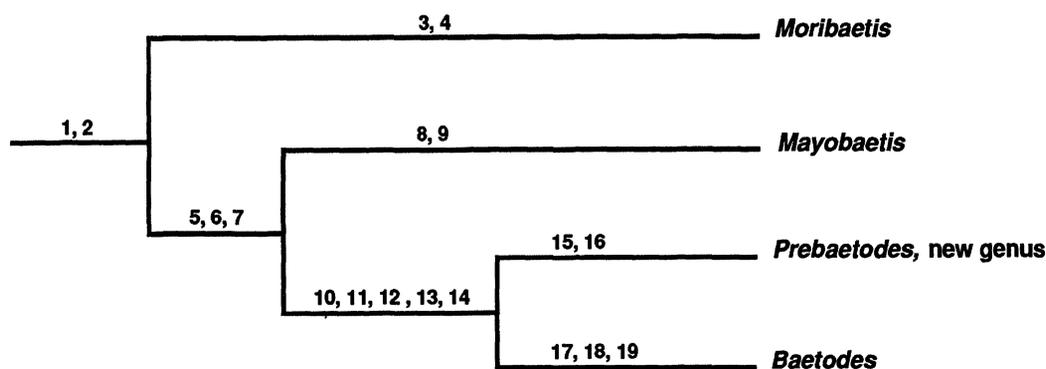


FIG. 43. Cladogram of the taxa of the *Baetodes* complex. Numbered apomorphies correspond to the numbered characters in Table 1. See text for explanation of OTUs.

number and size of gills, loss of hindwings, length of median caudal filament, and setation of caudal filaments. Additionally, *Prebaetodes* and *Baetodes* have relatively long legs as larvae.

The phenoclinical change in the morphology of the caudal filaments is important in hypothesizing behavioral and ecological evolution in the *Baetodes* complex. *Moribaetis* shows the most plesiomorphic condition, with the cerci and median caudal filament fully developed, and with abundant, interlocking setae on the median margins of the cerci and lateral margins of the median caudal filament (Fig. 10). These features are similar to the ancestral condition in Ephemeroptera (e.g., Sinitshenkova 1984 and McCafferty 1990), where such setaceous tails were associated with primordial swimming (Edmunds and McCafferty 1988). Larvae of *Mayobaetis* also have 3 caudal filaments with abundant setation, but the median caudal filament is substantially shorter than that of *Moribaetis* (Fig. 16). Larvae of both lineages are known to occur often on exposed parts of stones above the water surface of tropical streams or in the splash zone near banks and waterfalls, and they will jump into the stream and swiftly swim away when disturbed (McCafferty unpublished, Waltz and McCafferty 1985). Larvae of *Prebaetodes* (McCafferty unpublished; Sites, University of Missouri, personal communication) and *Baetodes* (Edmunds et al. 1976) predominantly occur in riffle areas of streams, where they are clingers. Larvae of *Prebaetodes* have well-developed cerci and abundant setae medially, but have a median caudal filament that is shorter than that of *Mayobaetis* and with rudimentary setation (Fig. 37). These conditions are clearly transitional be-

tween those found in *Mayobaetis* and *Baetodes*. Larvae of *Baetodes* have well-developed, bare cerci and a rudimentary median caudal filament (Fig. 41). The transition of caudal filament structure therefore appears to parallel the functional and habitat transition from clinger/swimmer in variable currents (*Moribaetis* and *Mayobaetis*) to predominantly clinging larvae in riffles (*Prebaetodes* and *Baetodes*).

Additional functional morphology supporting the hypothesized evolution from clinger/swimmers to predominantly clingers in the *Baetodes* complex involves larval legs. *Prebaetodes* and *Baetodes* have relatively long and laterally oriented legs (Fig. 31), whereas *Moribaetis* and *Mayobaetis* have relatively short and more ventrally oriented legs (Fig. 14). Long, laterally oriented legs are apparently an adaptation for clinging, as is seen in other baetid mayflies such as certain *Acentrella* (McCafferty et al. 1994). We also suspect that the ventrolateral orientation of the gills of *Baetodes* (Fig. 40) is related to behavioral clinging in riffles, such as has been observed in certain Heptageniidae mayflies where ventral gills function as friction devices for gripping substrate in torrential habitats (e.g., Hynes 1970, Ward 1992).

Another noteworthy trend is found in the reductive evolution of the hindwings of lineages in the *Baetodes* complex. In *Moribaetis*, adults possess relatively large hindwings with 3 longitudinal veins, 1 of which is forked. Hindwings of *Mayobaetis* are somewhat smaller than those of *Moribaetis*, and they have only 2 unforked longitudinal veins. Larvae of *Prebaetodes* possess only rudimentary hindwingpads (Fig. 33), and we infer that adults of *Prebaetodes* lack hind-

wings because larvae of *Baetodes* that also have rudimentary hindwingpads lack hindwings as adults. Most larvae of *Baetodes*, however, lack hindwingpads entirely (Fig. 40).

Phylogenetic classification

Based on the cladogram (Fig. 43), and allowing for sequencing conventions (Nelson 1973), 4 phylogenetic generic classifications are allowable for the OTUs in the *Baetodes* complex. The historical generic classification of the involved taxa is not one of these, and some revision is therefore necessary. An alternative would be to consider the 4 taxa in the complex as 1 genus. A 2nd alternative would be to consider *Moribaetis* as one genus and *Mayobaetis*, *Prebaetodes*, and *Baetodes* as another genus. A 3rd alternative would be to consider *Moribaetis* and *Mayobaetis* as 2 separate genera and *Prebaetodes* and *Baetodes* together as a 3rd genus. The final alternative would be to consider each taxon in the complex as a separate genus.

We maintain that the choice of a phylogenetic classificatory alternative should be based on the information content and practicality of the resulting generic classification. The first 2 alternatives are not preferable because they would not convey information on the intrinsic diversity of the complex. The 3rd alternative is more preferable in that it would convey more information regarding the diversity of the complex; however, the concept of the large and relatively well-known genus *Baetodes* would become too diffuse because it would incorporate the morphologically distinctive *Prebaetodes*. In our opinion, the 4th alternative is the most preferable because it reflects the diversity and uniqueness of each lineage within the complex. This alternative also involves the least amount of revision, with the restriction of the generic concept of *Moribaetis* and the elevation of *Mayobaetis* to generic rank as the only taxonomic changes.

Acknowledgements

We thank R. W. Sites (University of Missouri, Columbia) for the donation of part of the material used in this study. We also thank R. D. Waltz (Indiana Department of Natural Resources, Indianapolis) for discussing this paper with us. The scanning electron microscope was made available by the Electron Microscopy Cen-

ter at Purdue University with support of grant PCM-8400133 from the National Science Foundation. This paper has been assigned Purdue Agricultural Research Program Journal No. 14874.

Literature Cited

- COHEN, S. D., AND R. K. ALLEN. 1978. Generic revisions of mayfly nymphs III. *Baetodes* in North and Central America. *Journal of the Kansas Entomological Society* 51:253-269.
- CORKUM, L. D., AND H. F. CLIFFORD. 1981. Function of the caudal filaments and correlated structures in mayfly nymphs, with special reference to *Baetis* (Ephemeroptera). *Quaestiones Entomologicae* 17: 129-141.
- EDMUNDS, G. F., AND W. P. MCCAFFERTY. 1988. The mayfly subimago. *Annual Review of Entomology* 33:509-526.
- EDMUNDS, G. F., S. L. JENSEN, AND L. BERNER. 1976. *Mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- FLOWERS, R. W. 1979. A new species of *Baetis* from Panama. (Ephemeroptera:Baetidae). *The Pan-Pacific Entomologist* 55:187-191.
- FLOWERS, R. W. 1987. The adult stage of three Central American *Baetodes* (Ephemeroptera:Baetidae) with notes on the genus. *Aquatic Insects* 9:1-10.
- GILLIES, M. T. 1991. A diphyletic origin for the two-tailed baetid nymphs occurring in east African streams with a description of the new genus and species *Tanzaniella spinosa* gen. nov. sp. nov. Pages 175-187 in J. Alba-Tercedor and A. Sánchez-Ortega (editors). *Overview and strategies of Ephemeroptera and Plecoptera*. Sandhill Crane Press, Gainesville, Florida.
- HENNIG, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- HYNES, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Toronto.
- KLUGE, N. Y. 1992a. Cuban mayflies of the family Baetidae (Ephemeroptera). 2. Subgenera *Caribaetis* subgen. n. and *Americabaetis* subgen. n. of the genus *Baetis* s.l. *Zoologicheskii Zhurnal* 71:13-20 (in Russian).
- KLUGE, N. Y. 1992b. Cuban mayflies of the family Baetidae (Ephemeroptera). 3. Subgenus *Falliceon* of the genus *Baetis* s.l. *Zoologicheskii Zhurnal* 71: 38-48 (in Russian).
- KOSS, R. W. 1972. *Baetodes*: new species and new records for North America (Ephemeroptera:Baetidae). *Entomological News* 83:93-102.
- LUGO-ORTIZ, C. R., AND W. P. MCCAFFERTY. 1995. New species, stage description, and records of *Baetodes* (Ephemeroptera:Baetidae) from Mexico

- and Central America. *Entomological News* 106: 81–86.
- MAYO, V. K. 1968. Two new species of the genus *Baetodes* from Ecuador (Ephemeroptera:Baetidae). *The Pan-Pacific Entomologist* 44:251–257.
- MAYO, V. K. 1972. New species of the genus *Baetodes* (Ephemeroptera:Baetidae). *The Pan-Pacific Entomologist* 48:226–241.
- MAYO, V. K. 1973. Four new species of the genus *Baetodes* (Ephemeroptera:Baetidae). *The Pan-Pacific Entomologist* 49:308–314.
- MCCAFFERTY, W. P. 1990. Chapter 2: Ephemeroptera. Pages 20–50 in D. A. Grimaldi (editor). *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. *Bulletin of the American Museum of Natural History* 195.
- MCCAFFERTY, W. P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. *Annals of the Entomological Society of America* 84:343–360.
- MCCAFFERTY, W. P., AND A. V. PROVONSHA. 1993. New species, subspecies, and stage descriptions of Texas Baetidae (Ephemeroptera). *Proceedings of the Entomological Society of Washington* 95: 59–69.
- MCCAFFERTY, W. P., AND R. D. WALTZ. 1990. Revisionary synopsis of the Baetidae (Ephemeroptera) of North and Middle America. *Transactions of the American Entomological Society* 116:769–799.
- MCCAFFERTY, W. P., AND R. D. WALTZ. 1995. *Labio-baetis* (Ephemeroptera:Baetidae): new status, new North American species, and related new genus. *Entomological News* 106:19–28.
- MCCAFFERTY, W. P., AND T.-Q. WANG. 1994. Phylogenetics and the classification of the *Timpanoga* complex (Ephemeroptera:Ephemerellidae). *Journal of the North American Benthological Society* 13:569–579.
- MCCAFFERTY, W. P., R. W. FLOWERS, AND R. D. WALTZ. 1992. The biogeography of Mesoamerican mayflies. Pages 173–193 in S. P. Darwin and A. L. Welton (editors). *Biogeography of Mesoamerica: proceedings of a symposium*. Tulane University Studies in Zoology and Botany, Supplementary Publication 1. Tulane University, New Orleans.
- MCCAFFERTY, W. P., M. J. WIGGLE, AND R. D. WALTZ. 1994. Systematics and biology of *Acentrella turbida* (Ephemeroptera:Baetidae). *The Pan-Pacific Entomologist* 70:301–308.
- MORIHARA, D. K., AND W. P. MCCAFFERTY. 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). *Transactions of the American Entomological Society*. 105:139–221.
- NEEDHAM, J. G., AND H. E. MURPHY. 1924. Neotropical mayflies. *Bulletin of the Lloyd Library of Botany, Pharmacy and Materia Medica*, 24, *Entomological Series* 4:1–79.
- NELSON, G. J. 1973. Classification as an expression of phylogenetic relationships. *Systematic Zoology* 22:344–359.
- NOVIKOVA, E. A., AND N. Y. KLUGE. 1987. Systematics of the genus *Baetis* (Ephemeroptera:Baetidae) with descriptions of a new species from middle Asia. *Vestnik Zoologii* 1987(4):8–19 (in Russian).
- ROSS, H. H. 1974. *Biological systematics*. Addison-Wesley, Reading, Massachusetts.
- SINITSHENKOVA, N. D. 1984. The Mesozoic mayflies (Ephemeroptera) with special reference to their ecology. Pages 61–66 in V. Landa, T. Soldán, and M. Tonner (editors). *Proceedings of the Fourth International Conference on Ephemeroptera*. Institute of Entomology, Czechoslovak Academy of Sciences, Prague.
- TRAVER, J. R. 1943. New Venezuelan mayflies. *Boletín de Entomología Venezolana* 2:79–98.
- WALTZ, R. D., AND W. P. MCCAFFERTY. 1985. *Moribaetis*: a new genus of Neotropical Baetidae (Ephemeroptera). *Proceedings of the Entomological Society of Washington* 87:239–251.
- WALTZ, R. D., AND W. P. MCCAFFERTY. 1987. New genera of Baetidae for some Nearctic species previously included in *Baetis* Leach (Ephemeroptera). *Annals of the Entomological Society of America* 80:667–670.
- WALTZ, R. D., W. P. MCCAFFERTY, AND A. THOMAS. 1994. Systematics of *Alainites* n. gen., *Dipheter*, *Indobaetis*, *Nigrobaetis* n. stat., and *Takobia* n. stat. (Ephemeroptera:Baetidae). *Bulletin de la Société d'Histoire Naturelle de Toulouse* 140:33–36.
- WARD, J. V. 1992. *Aquatic insect ecology: 1. Biology and habitat*. John Wiley and Sons, New York.
- WILEY, E. O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley-Liss, New York.

Received: 1 February 1996

Accepted: 26 May 1996