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MORIBAETIS: A NEW GENUS OF NEOTROPICAL BAETIDAE (EPHEMEROPTERA)[1]

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Abstract—A new genus, ***Moribaetis***, erected for four species of Neotropical Baetidae, including *M. **ellenae*** (Mayo), new combination; *M. **maculipennis*** (Flowers), new combination; *M. **salvini*** (Eaton), new combination, and *M. **macaferti*** Waltz, new species. The subgenus ***Mayobaetis*** is proposed to include *M. ellenae,* whereas the remainder of the known species are placed in the subgenus *Moribaetis* s.s. Presumed but unassociated larvae of *M. salvini* (Eaton) are described and redescriptions of the larvae of *M. ellenae* and *M. maculipennis* are given. Keys to the four species in the larval stage and three species known as adults are provided, and new distribution records are cited. Phylogenetic relationships of the cited species are proposed.

The study of Central and South American collections of mayflies for the analysis of the generic relationships within the family Baetidae has led to the discovery of several new taxa. One of these taxa is described below as a new genus. Not only is this new genus morphologically striking, primarily because of its relatively large size and unique larval claw and gill structure, but its species demonstrate a biological trait apparently unique among baetids. Larvae are splash-zone dwellers that are frequently found exposed on wet surfaces above the water line of tropical streams. Further notes on biology and species relationships follow the generic and species descriptions.

Moribaetis Waltz and McCafferty, NEW GENUS

Type species: Baetis maculipennis Flowers, 1979: 187.

Adult diagnosis.—Adults will key to couplet 36 in Edmunds et al. (1976) as *Baetis*. Species of *Moribaetis* may, however, be distinguished from other known Baetidae by the following combination of characters: 1) a body length of 10–12 mm; 2) short-stalked turbinate eyes; 3) brown infuscations in male forewing (as in Fig. 43); 4) cubitoanal cells often with three or four marginal intercalaries; 5) paired marginal intercalaries shorter than cell width (Fig. 13) to often exceeding cell width (Fig. 43) by at least one member of the pair; 6) hindwings present with two or three veins and costal process; and 7) male genitalia of modified *intercalaris*-type (sensu Needham et al., 1935).

Larval diagnosis.—Larvae of *Moribaetis* will key to couplets 41 and 42 in Edmunds et al. (1976) as *Baetis,* from which they may be distinguished by the

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following combination of characters: 1) a peculiar claw structure (Fig. 40) with one to three stout unpaired subapical setae that are distinctly different than paired subapical setae discussed by Morihara and McCafferty (1979) and Corkum and Clifford (1981); 2) a relatively large body size of 9–12 mm; 3) deflected antennae; 4) a labrum that is basally narrowed (Figs. 6, 15, 25, 34) and with long plumose marginal setae; 5) a hypopharynx with a broadened and tongue-like lingua and without a dorso-median tuft of setae; 6) the presence of a pigmented anteromedial membrane of the abdominal terga that appears as a dark posteromedial border of the preceding tergum; 7) abdominal terga with rectangulate-based, broadly pointed scales; 8) asymmetric gills with gill 1 smallest (subequal to other gills in final instar); and 9) the presence of a well-developed median terminal filament.

Etymology.—Masculine gender. *Moribaetis* is named in recognition of Dennis Morihara for his revisionary contributions to the systematics of Baetidae.

Subgenus *Mayobaetis* Waltz and McCafferty, New Subgenus

Type species: Baetis ellenae Mayo, 1973: 285.

Adult male.—Body 10–11 mm long. Forewing (Fig. 13) with paired marginal intercalaries shorter than the marginal cell width. Hindwing (Fig. 14) with 2 longitudinal veins; 2nd vein not forked; costal margin with process; intercalaries and crossveins few or absent. Forceps with terminal segment elongate and ovoid.

Adult female.—Similar to male except body sometimes more darkly pigmented and wings may not always be pigmented.

Mature larva.—Head capsule round in frontal view (Fig. 1). Antenna subequal to head in length; pedicel and scape (Fig. 11) with longitudinal row of fine setae on outer margin, strongly dorso-ventrally flattened (pedicel broadened), with dorsal side having large blunted scale-like tuberculations. Labrum (Fig. 6) without basal-medial raised area. Mandibular denticles (Fig. 8) of outermost incisor group distinct. Maxillary palp (Fig. 9) often with indication of 3rd segment. Prothorax without coxal osmobranchia. Median terminal filament less than or subequal to ½ length of cerci.

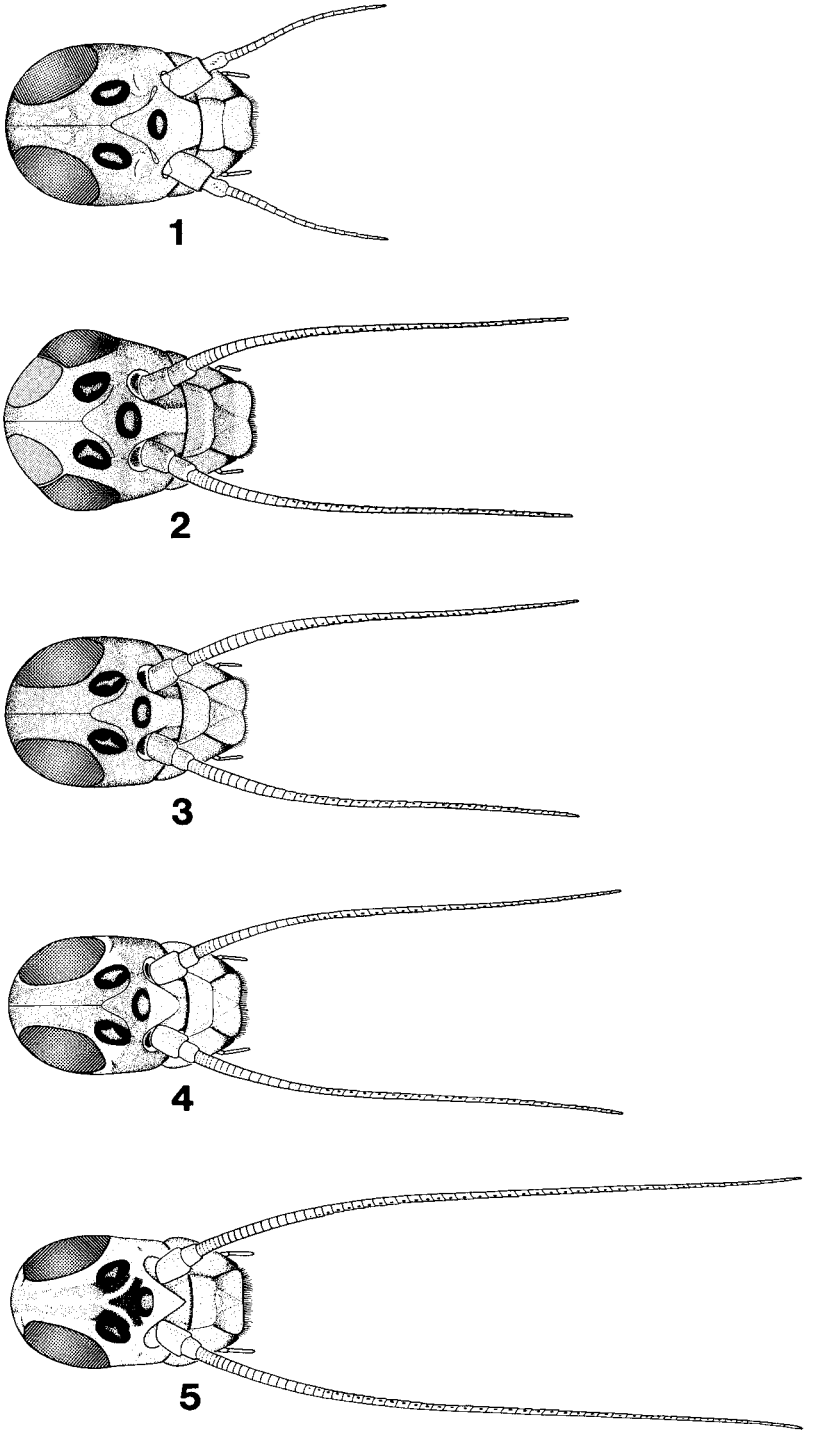
Etymology.—Masculine gender. This subgenus is named in honor of the ephemeropterist Mrs. Velma Knox Mayo.

Moribaetis (*Mayobaetis*) *ellenae* (Mayo), New Combination

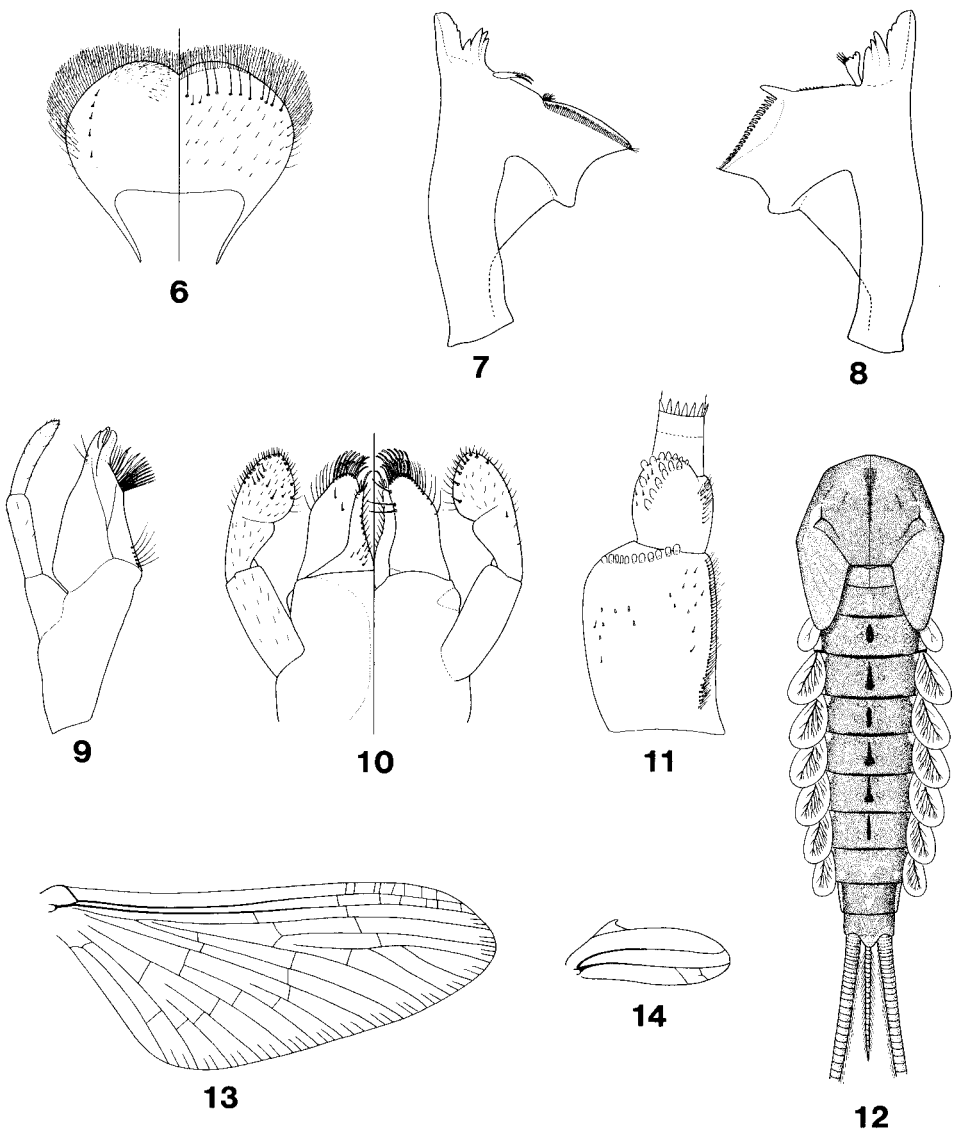
Baetis sp. 1 Roback, 1966: 137.
Baetis ellenae Mayo, 1973: 285; Berner, 1980: 190.

Adult male.—Adequately characterized by Mayo (1973).

Mature larva.—Head capsule (Fig. 1) rounded, uniformly colored. Antennae subequal to length of head capsule; pedicel ca. ½ length of scape; both scape and pedicel (Fig. 11) dorsoventrally flattened with scales, fine setae, and scale-like tuberculations and with longitudinal row of fine setae on outer margin; flagellum with subapical scales dorsally and clumped setae ventrally. Labrum (Fig. 6) with rounded anterior margins, strongly narrowed basally, without basomedian raised area, and with submarginal setae 1+9–10. Mandible (Figs. 7, 8) with divided incisors joined basally; prostheca of right mandible slender, bifurcate; thumb of left mandible elongate, narrow. Maxilla (Fig. 9) with palp exceeding galea-lacinea, and often with indication of 3rd segment. Segment 2 of labial palp (Fig. 10)



Figs. 1–5. *Moribaetis* larval head capsules (females). 1, *M. ellenae.* 2, *M. macaferti* (Guatemalan male). 3, *M. macaferti.* 4, *M. salvini.* 5, *M. maculipennis.*



Figs. 6–14. *Moribaetis ellenae*. 6, Labrum (left-ventral; right-dorsal). 7, Right mandible, ventral. 8, Left mandible, ventral. 9, Maxilla. 10, Labium (left-ventral; right-dorsal). 11, Antennal scape and pedicel (right side, dorsal view). 12, Dorsal color pattern. 13, Forewing, male imago. 14, Hindwing, male imago (not to scale).

subequal to segment 3; paraglossa with 3 apparent rows of apical setae; glossa with broadened (scraper type) setae and spine-like stout setae medially.

Diagnosis.—Larvae of *M. ellenae* may be separated from other species of this genus by the apically divided mandibular incisors (Figs. 7, 8); distinctive color pattern of the abdomen (Fig. 12); short stout antennae (Fig. 1); labial palp (Fig. 10) with segments 2 and 3 subequal; and a relatively round anterior margin of the labrum (Fig. 6). Adults of this species may be distinguished by a hindwing

venation that consists of two veins with the second undivided (Fig. 14) and by the elongate terminal segment of the male forceps.

Known distribution.—Ecuador (type), Peru, Costa Rica, from 1400 m to 2000 m.

Material examined.—♀ larva (Paratype): Ecuador, Macuchi, Catopaxi Prov., Rio Amayo, VI-30-1943, 6000 ft. elev., V. K. Mayo. One larva: Costa Rica, San Jose, 12 mi N San Isidro del Genekal (Pan Amer. Hwy.), 5200 ft. VII-20-1962. G. G. Musser.

Subgenus *Moribaetis* sensu stricto

Adult male. Body 10–11 mm long. Forewing (Fig. 43) with ano-cubital cells frequently with 3 or 4 marginal intercalaries; all intercalaries long, equal to ½ cell width or more. Hindwing (Fig. 44) with 3 longitudinal veins, 2nd vein forked in known species and with few crossveins and intercalaries. Forceps of genitalia with terminal segment small, ovoid to nearly spherical.

Adult female.—Similar to male except sometimes more darkly pigmented and wings may not always be pigmented.

Mature larva.—Head capsule round to elongate in frontal view (Figs. 2–5). Antennae (Figs. 2–5) variable in length; pedicel and scape moderately dorsoventrally flattened, without (Figs. 22, 30) scale-like tuberculations, and without longitudinal row of fine setae on outer margin. Labrum (Figs. 15, 25, 34) with basomedial raised area. Mandibular denticles (Figs. 16, 17) of outermost incisor group fused. Maxillary palp (Fig. 28) 2-segmented. Prothorax with short, stout coxal osmobranchia (Fig. 31). Median terminal filament ½ to subequal length of cerci.

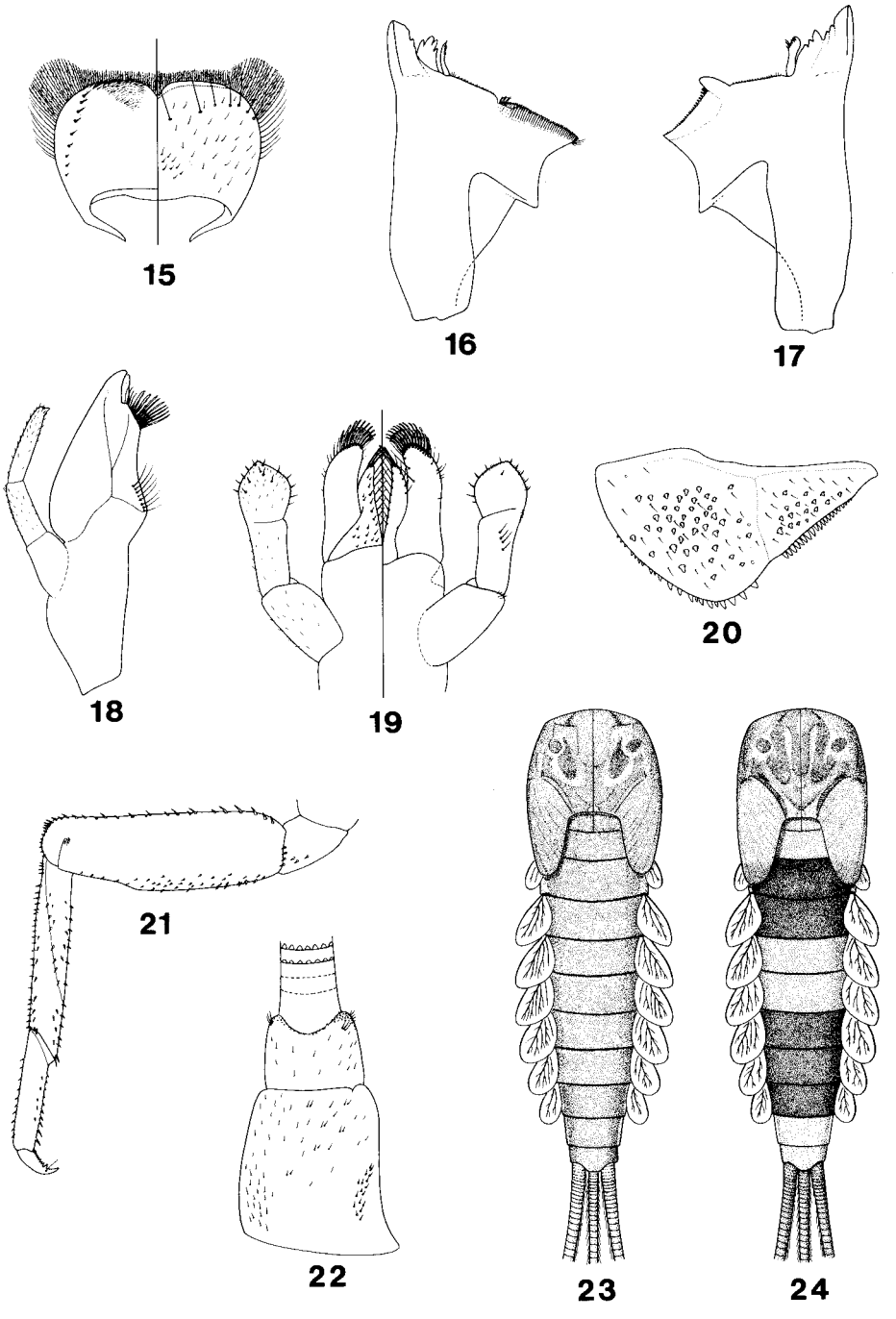
Subgeneric Diagnosis.—The two subgenera may be most easily distinguished as larvae by the following: the presence of procoxal osmobranchia (Fig. 31) [terminology after Shepard and Stewart (1983)] in *Moribaetis* versus none such in *Mayobaetis*; longer antennae relative to the head capsule (Figs. 2–5) in *Moribaetis* s.s. and a median terminal filament that is longer relative to the cerci in *Moribaetis* s.s.

The presence of three veins in the hind wing, the second of which is forked, in *Moribaetis* s.s. (Fig. 44) versus only two veins in *Mayobaetis* (Fig. 14), neither of which is forked; and a small spherical terminal genital forceps segment in *Moribaetis* s.s. versus an elongate, ovoid segment in *Mayobaetis,* will easily distinguish the known adults of the two subgenera.

Moribaetis (*Moribaetis*) *macaferti* Waltz, New Species

Adult.—Unknown.

Mature larva.—Body 8–9 mm long. Cerci 4.5–5.0 mm long. Terminal filament 3.5–4.0 mm long. Head (Fig. 2) rounded, yellow-brown to tan, without darkening between ocelli. Antennae deflected downward, paler ventrally, moderately long, reaching gill 3 to 5; scape and pedicel (Fig. 22) with random fine setae and clumped setae; pedicel with subapical scaling. Labrum (Fig. 15) with raised basal median area, and with rounded anterior margin; 1 + 5–6 stout submarginal setae; marginal setae long and plumose; sublateral row of ventral spines increasing in size from base to margin. Mandible (Figs. 16, 17) with row of fine spine-like setae between prostheca and molar area, outermost incisor denticles fused (few denticles may



Figs. 15–24. *Moribaetis macaferti.* 15, Labrum (left-ventral; right-dorsal). 16, Right mandible, ventral. 17, Left mandible, ventral. 18, Maxilla. 19, Labium (left-ventral; right-dorsal). 20, Paraproct. 21, Fore leg. 22, Antennal scape and pedicel (right side; dorsal view). 23, Dorsal color pattern. 24, Dorsal color pattern, Guatemalan male.

be discernible on margin), and innermost incisor tridentate or quadridentate, fused apically with outermost incisor on left mandible, free apically from outermost incisor on right mandible; thumb of left mandible broadly triangulate and blunt. Maxillary palp (Fig. 18) 2-segmented, subequal to galea-lacinea in length. Segment 3 of labial palp (Fig. 19) bulbous; segment 2 ca. 2–3× length of segment 3, with weak inner apical lobe and 4 dorsal setae; paraglossa with 3 apical rows of setae. Thorax tan and lacking medial stripe dorsally; procoxal osmobranchia present. Legs cream to tan, setation as in Fig. 21, tibia and tarsus uniformly colored, with spine-like setae and fine setae on dorsal and ventral margins; claws with 8 to 10 denticles and a strong subapical seta. Abdominal terga (Fig. 23) uniformly colored, without distinct patterning; posterior tergal margins with sharp spines. Gills asymmetric, with sclerotized anterior and posterior margins, and distinct tracheae; anterior margin serrate, with fine setae between serrations. Paraproct as in Fig. 20. Cerci and median terminal filament uniformly colored.

Variant.—A single larva from Guatemala possesses a unique color pattern (Figs. 2, 24) but is structurally identical with other specimens of *M. macaferti.*

Diagnosis.—*Moribaetis macaferti* may be distinguished from other species of this genus by the combination of characters as follow: shape of the mandibles (Figs. 16, 17) with distinctly denticled innermost incisors, right innermost incisor free apically from outermost incisor, left innermost incisor fused apically to outermost incisor; segment 2 of labial palp (Fig. 19) ca. 2–3× length of segment 3, and with four dorsal setae; paraglossa with three apical rows of setae (Fig. 19); submarginal row setal pattern of 1+5–6 stout setae on labrum (Fig. 15); antennae reaching gill 3 to 5 (Figs. 2, 3); and frons without medial pigment spot between ocelli. Adults are unknown.

Type material.—Holotype larva: Costa Rica, Guanacaste Pro., Rio Tenorio at Finca La Pacifica, E of Pan Amer. Hwy. II-2-1969. W. P. McCafferty, deposited in the Purdue University Entomological Research Collection. Three larval paratypes: same data and deposition as holotype, with one whole-mount slide preparation (3 slides), Hoyer's medium (water). One larval paratype: Guatemala, Escuiutla, VI-15-1962, G. G. Musser, with leg and mouthparts slide mounted in euparal (abs. alc.), deposited in the University of Utah Collections.

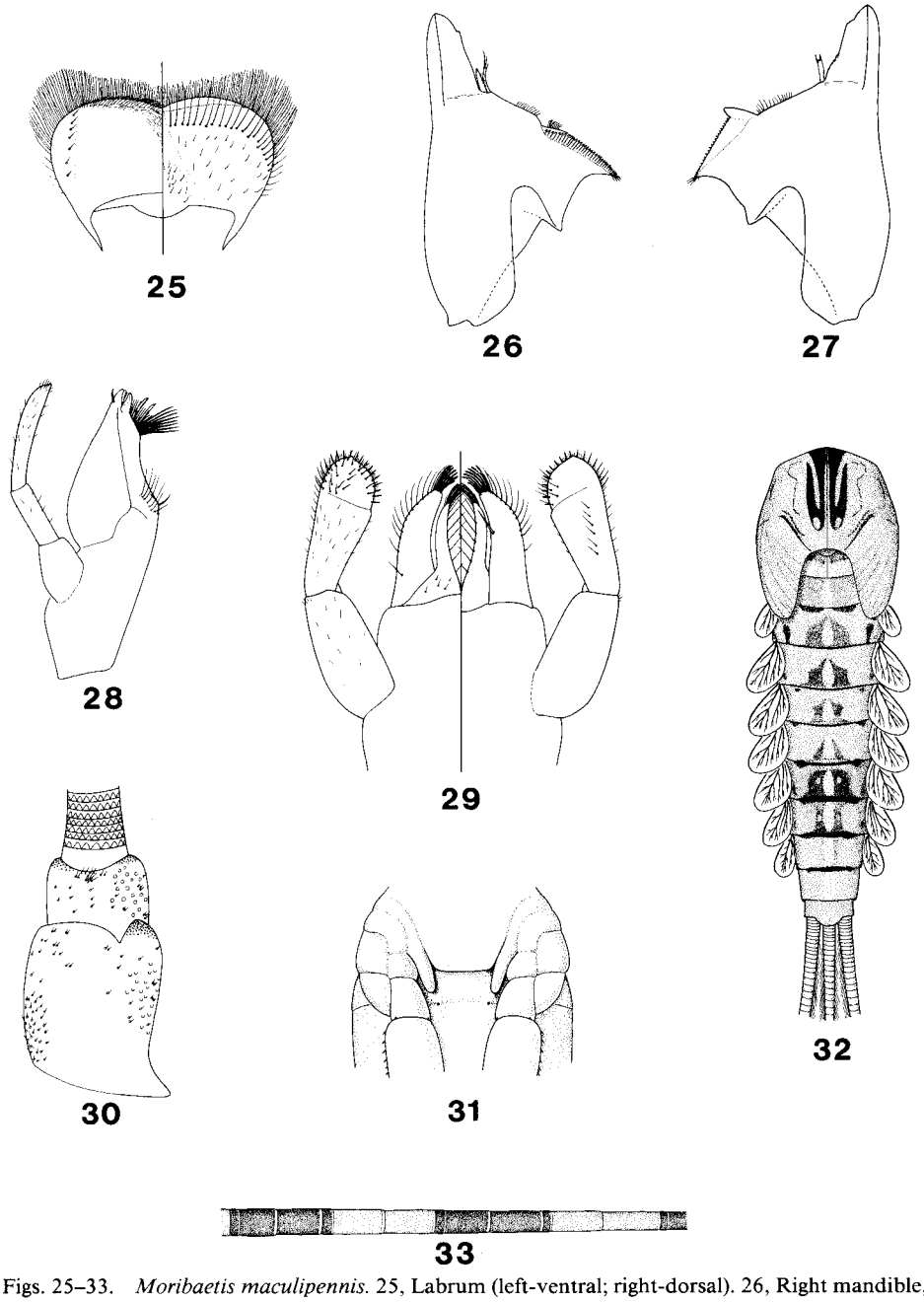
Etymology.—The specific epithet is a phonetic spelling of the collector's last name, McCafferty.

Moribaetis (*Moribaetis*) *maculipennis* (Flowers), New Combination

Baetis maculipennis Flowers, 1979: 187.

Adult male.—Adequately characterized by Flowers (1979).

Mature larva.—Antennal scape (Fig. 30) subequal to pedicel in length, with scales, clumped setae, and random fine setae; flagellum with dorsal scales and ventral clumped setae. Labrum (Fig. 25) truncate apically, narrowed basally with prominent basal median raised area, and with submarginal setae 1+12–20. Mandible (Figs. 26, 27) with fine spine-like setae between prostheca and molar area; incisors of left mandible completely fused into single blade-like structure, innermost incisor of right mandible discernible as a smaller secondary blade near prostheca; prostheca slender, ribbonlike with apical furcations. Maxillary palp (Fig. 28) subequal to galea-lacinea in length, 2-segmented; galea-lacinea relatively



Figs. 25–33. *Moribaetis maculipennis*. 25, Labrum (left-ventral; right-dorsal). 26, Right mandible, ventral. 27, Left mandible, ventral. 28, Maxilla. 29, Labium (left-ventral; right-dorsal). 30, Antennal scape and pedicel (right side; dorsal view). 31, Prothorax ventral, procoxal osmobranchia. 32, Dorsal color pattern. 33, Male imago cercus (basal).

slender. Segment 2 of labial palp (Fig. 29) 2.5–3.0× length of segment 3 and with 6 or 7 dorsal setae; paraglossa with 2 apparent rows of apical setae; glossa narrowed, with serrate setae apically and long fine setae medially. Procoxal osmobranchia present (Fig. 31).

Diagnosis.—Larvae of *M. maculipennis* may be easily separated from other species of this genus by the distinctive abdominal color pattern (Fig. 32); the highly fused mandibular incisors forming a single blade (Figs. 26, 27), the relative second segment lengths and relation of the labial palp (Fig. 29); the relatively long antennae that may reach gill 7; and the distinct medial spot located on the frons (Fig. 5). Adults of this species may be recognized by the hindwing venation that includes a forked second vein with relatively few intercalaries within the fork; the abdominal color pattern; and cerci with an alternating pattern of one white segment then three darkened segments (Fig. 33).

Known distribution.—Costa Rica, Panama (Type).

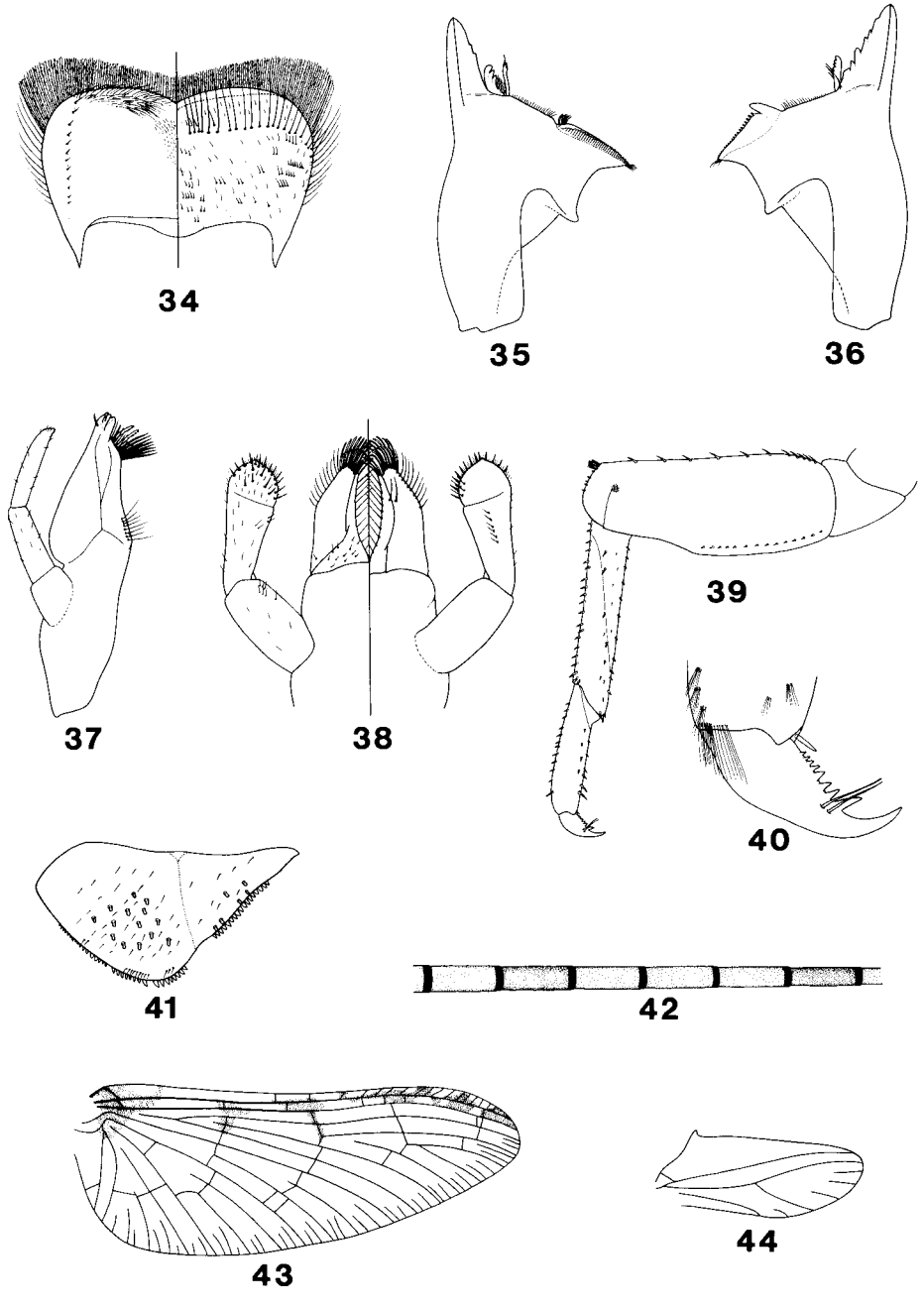
Material examined.—♂ adult paratype: Panama, Chiriqui, Fortuna, 8°44'N: 82°15'W. VI-8/14-1977 (light trap). Henk Wolda. Numerous larvae: Costa Rica, San Jose, 12 mi N San Isidro del Genekal (Pan Am. Hwy.) 5200 ft. elev. VIII-20-1962; G. G. Musser. Puntarenus Pro., 10 km N of San Vita at quarry waterfall, III-16-1969, W. P. McCafferty. Contago, Moravia, 1116 m elev. VI-24-1962, G. G. Musser.

Moribaetis (*Moribaetis*) *salvini* (Eaton), New Combination

Baetis salvini Eaton, 1885: 170; 1892: 13; Kimmins, 1934: 347; 1960: 289; Edmunds et al., 1976: 164.

Adult male.—Adequately characterized by Eaton (1885).

Mature larva.—Larvae that appear to match the adult color pattern of *M. salvini* and that fit the classification scheme concordant with the relationship of *M. salvini* to that of *M. maculipennis* are described as *M. salvini* as follows: Body 8–9.5 mm long. Head capsule (Fig. 4) elongated; yellow-brown to tan, vertex darker, without darkening between ocelli. Antenna deflexed, paler ventrally, 3× length of head capsule, reaching gill 3 to 5; scape and pedicel (as in Fig. 30) with clumped fine setae and random fine setae; pedicel with subapical scaling. Labrum (Fig. 34) with raised basal median area, with anterior margin slightly more projecting than in *M. maculipennis* and with submarginal setal pattern 1+7–9 (not including lateral field setae); marginal setae long, plumose; sublateral row of ventral spines 8–10. Mandible (Figs. 35, 36) with row of fine spine-like setae between prostheca and molar area, with outermost incisor denticles fused (few denticles may be discernible on margin), and with innermost incisor tridentate, fused apically with outermost incisor on left mandible, and free apically from outermost incisor on right mandible, thumb of left mandible elongate and blunt. Maxillary palp (Fig. 37) 2-segmented, subequal to galea-lacinea in length. Segment 3 of labial palp (Fig. 38) bulbous; segment 2 with weak inner apical lobe and 6 to 8 dorsal setae; paraglossa with 2 apical rows of closely set setae. Thorax tan, with medial stripe on pro- and mesonotum (as in Fig. 32); procoxal osmobranchia present. Legs cream colored and with setation as in Fig. 39; tibia and tarsus jointly graded from cream to tan distally, with spine-like setae dorsally and ventrally; claws (Fig. 40) with 8 or 9 denticles and 1 to 3 stout subapical seta(e) reaching apex. Abdominal tergal pattern with distinct lateral oblique bars; medial areas of terga with broken pigmented pattern similar to *M. maculipennis*; posterior margins of terga with sharp scales. Gills asymmetric, with sclerotized anterior and posterior margins, and distinct tracheae; apical margin serrate with several fine setae between teeth;



Figs. 34–44. *Moribaetis salvini*. 34, Labrum (left-ventral; right-dorsal). 35, Right mandible, ventral. 36, Left mandible, ventral. 37, Maxilla. 38, Labium (left-ventral; right-dorsal). 39, Foreleg. 40, Foreclaw. 41, Paraproct. 42, Male imago cercus (basal). 43, Forewing, male. 44, Hindwing, male (not to scale).

gill on segment one smaller than those on remaining segments. Paraproct (Fig. 41) with sharp marginal denticles, not clustered apically, and with surface having fine setae and clumped setae. Cerci and median terminal filament unicolored.

Diagnosis.—Larvae of *M. salvini* may be separated from other species of the genus by the antennal length that reaches to gill 3–5 (Fig. 4); form of the mandibles (Figs. 35, 36), with distinctly denticled innermost incisors; frons without pigment spot between ocelli (Fig. 4); paraglossae with two apical rows of setae (Fig. 38); and paraproct (Fig. 41) denticles not clustered apically. Adults of *M. salvini* may be distinguished by the forked second vein of the hindwing (Fig. 44) with several relatively prominent marginal intercalaries; color pattern of the abdomen; and cerci (Fig. 42) of adult male, that have one darkened segment alternating with three light-colored segments.

Known distribution.—Costa Rica (type), Guatemala(?).

Material examined.—Lectotype male adult: Costa Rica: Volcan de Irazu, 6000 to 7000 ft. H. Rogers. Female adult: Guatemala: Panima, Vera Paz, no date, det. A. E. Eaton [Identification of this specimen is questionable]. Larvae: Costa Rica, San Jose. 12 mi N San Isidro del Genekal, (Pan Amer. Hwy.) 5200 ft. VIII-20-1962, G. G. Musser. One male adult specimen in relatively poor condition that we have examined from Huatusco, Vera Cruz Pro., Mexico, agrees with the type in abdominal maculation pattern and hindwing venation but lacks other characters (especially of cerci and legs) that are found in other known adults of this species.

Key to Male Adults of *Moribaetis* Species

1. Hindwing with two longitudinal veins (Fig. 14); forewing with little mottling; abdominal terga patterned on posterior margin with black-brown on either side of midline and laterally near pleural fold; terminal segment of forceps elongate-ovoid ..... *M. ellenae*
– Hindwing with three longitudinal veins (Fig. 44); forewing patterned; abdominal terga with varied color patterns; terminal segment of forceps spherical, small 2
2. Hindwing with marginal intercalaries reduced, usually with one distinct intercalary and two minor intercalaries; cerci (Fig. 33) banded in alternating pattern of one white segment with three darkened segments .... *M. maculipennis*
– Hindwing with marginal intercalaries more apparent, usually with two distinct intercalaries and two or three minor intercalaries (Fig. 44); cerci (Fig. 42) banded in alternating pattern of one lightly darkened segment with three white segments ..... *M. salvini*

Key to Mature Larvae of *Moribaetis* Species

1. Antennae short, subequal to head capsule in length (Fig. 1); segment 2 of labial palp subequal in length to segment 3 (Fig. 10); procoxal osmobranchia absent; median terminal filament less than or subequal to one-half length of the cerci; abdominal color pattern as in Fig. 12 ..... *M. ellenae*
– Antennae distinctly longer than head capsule; segment 2 of labial palp longer than segment 3; procoxal osmobranchia present (Fig. 31); median terminal filament greater than or subequal to one-half length of cerci; abdominal color pattern varied 2

2. Incisors of mandible fused into one blade-like structure lacking denticles (Figs. 26, 27); antennae often reaching or surpassing gill 6 or 7; color pattern as in Fig. 32; frons with distinct medial pigmented area between ocelli (Fig. 5) ..... *M. maculipennis*
- Incisors of mandible with easily discernible denticles (Figs. 16, 17 and 35, 36); antennae reaching gill 3 to 5; frons without medial pigmented area 3
3. Paraglossa (Fig. 19) with three apical rows of setae; segment 2 of labial palp with four dorsal setae (Fig. 19); abdominal terga without distinct color patterning (Figs. 23, 24) ..... *M. macaferti*
- Paraglossa (Fig. 38) with two apical rows of setae; segment two of labial palp with six dorsal setae (Fig. 38); abdominal terga with distinctive color pattern similar to Fig. 32 ..... *M. salvini*

Species Relationships

It is difficult at this time to determine the derivation of *Moribaetis* and therefore have use of the appropriate outgroup comparison for deciphering character state polarity. Nonetheless, certain evidence appears to support convincingly the relationships described below.

The common possession of procoxal osmobranchia and a labrum with a uniquely elevated basal medial area in *M. macaferti, M. maculipennis,* and *M. salvini* strongly suggests a synapomorphy tying these species (subgenus *Moribaetis*) to a common branch separate from a *M. ellenae* lineage (subgenus *Mayobaetis*). The short antennae of *M. ellenae,* among other character states, would appear to be an autapomorphy. Within the subgenus *Moribaetis,* the extremely reduced apices of the paraglossae and two apical rows of paraglossal setae of *M. maculipennis* and *M. salvini* would indicate that these species form a sister group on a branch separate from the *M. macaferti* lineage.

The above relationship predicts the polarity of other character states within the genus and indicates a number of possible evolutionary trends. These include the fusion of the mandibular incisors and independently a fusion of the denticles of the incisors, both lengthening and shortening of the antennae, increase in the distribution and intensity of abdominal pigmentation, elongation of the clypeus, narrowing of the intraantennal frontal process, and an increase in the size of the medial basal region of the labrum (possibly in conjunction with increased musculature). Furthermore these deductions may allow the origin of the genus to be hypothesized once more information on related baetid genera is available.

Biology

On the basis of collections taken in Ecuador and reported by Mayo (1973), observations discussed by Peters (1973), and field notes by W. P. McCafferty, the species of this genus frequent the upper surfaces of rocks in fast water, the bases of waterfalls in the splash zone, or rocks along the shoreline of fast-water areas. Peters (1973) states that the Peruvian baetid (*M. ellenae*?) he observed "could be found on the top of rocks instead of in the water." Peters also reported that when disturbed, the larvae would flip into the air up to 3 feet and escape into the water. Riek [see ref. Peters (1973)] and Edmunds et al. (1976) have also noted a similar phenomenon in species of Siphlonuridae.

The species of *Moribaetis* have sympatric distributions in Central America. Three of the species (*M. maculipennis, M. salvini,* and *M. ellenae*) have been collected together. Differences in habitat partitioning that may be attributed to specific mouthpart structure differences and possible related feeding behavior are at present unknown.

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