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A Revision of the Neotropical Genus *Baeodasymyia* Clastrier and Raccurt (Diptera: Ceratopogonidae) with a Discussion of Phylogenetic Relationships

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ABSTRACT

The genus *Baeodasymyia* Clastrier and Raccurt, previously known only as adults from one extant and one fossil species, now includes four more extant species. The new species are described and named *B. michaeli* Borkent, n. sp., *B. christopheri* Borkent, n. sp., *B. lydiae* Borkent, n. sp., and *B. gustavoi* Borkent, n. sp. The larvae and pupae of *B. michaeli* and *B. christopheri* are also described and bionomic information provided for these and other species. Costa Rican species (n = 3) are all restricted to springs. Males and females of *Baeodasymyia christopheri* are strikingly sexually dimorphic in their thoracic pigmentation.

A partially resolved cladogram suggests that the Dominican amber fossil species *B. dominicana* Szadziewski and Grogan is the sister group to all extant species, and that *B. lydiae* is the sister group to all remaining extant species (which are not further resolved). The presence of simple head capsule setae in larvae of *Baeodasymyia* indicates that this genus and its sister group *Baeohelea* Wirth and Blanton may be an early lineage within the Ceratopogonini. The Cretaceous genus *Brachycretacea* Szadziewski may be the sister group of *Baeohelea* + *Baeodasymyia*.

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RESUMEN

El género *Baeodasymyia* Clastrier and Raccurt, conocido previamente sólo a partir de adultos de una especie viviente y de otra fósil, incluye actualemente cuatro especies vivientes mas. Las especies nuevas son descriptas y nominadas *B. micheli* Borkent, n. sp., *B. christopheri* Borkent, n. sp., *B. lydiae* Borkent, n. sp. and *B. gustavoi* Borkent, n. sp. Se describen, asimismo, las larvas y pupas de *B. micheli* y de *B. christopheri*, y se provee de informacion acerca de la bionomía de éstas y de las restantes dos especies. Las especies presentes en Costa Rica (n = 3) se hallan restringidas a manantiales. Los machos y hembras de *Baeodasymyia christopheri* son sexualmente dimórficos en su pigmentación torácica. El cladograma resuelto parcialmente sugiere que la especie fósil del ámbar dominicano, *B. dominicana* Szadziewski and Grogan, es el grupo hermano de todas las especies vivientes, y que *B. lydiae* es el grupo hermano del grupo que incluye a las restantes especies vivientes (el cual no está completamente resuelto). La presencia de setas simples en la cápsula cefálica de las larvas de *Baeodasymyia* indica que este género y su grupo hermano, *Baeohelea* Wirth and Blanton, probablemente representan un linaje temprano dentro de los Ceratopogonini. El genero *Brachycretacea* Szadziewski, del Cretácico, puede ser el grupo hermano de *Baeohelea* + *Baeodasymyia*.

INTRODUCTION

During an eight-month scientific expedition to Costa Rica in 1993–94, the senior author had the opportunity to collect Ceratopogonidae from a wide array of habitats. Among the many delightful discoveries were three new species of the very tiny biting midges belonging to the genus *Baeodasymyia* Clastrier and Raccurt. The genus was previously known from a small series of specimens of a single species and the immatures were entirely unknown. A second species, known from two fossils, was recently described from Miocene amber in the Dominican Republic (Szadziewski and Grogan, 1994). The discovery that extant species of *Baeodasymyia* in Costa Rica appear to be restricted to springs and first order streams permitted us to find the larvae of two species and to rear these to adulthood.

We describe these species and discuss phylogenetic relationships both within the genus and to other ceratopogonids.

ACKNOWLEDGMENTS

The three children of the senior author, Chris, Mike, and Lydia Borkent, shared in a nine month collecting expedition to Costa Rica and happily spent hours extracting larvae from mud samples (they were apparently raised with the thrill of discovery!). Without their help, the senior author wouldn't have been able to rear as many ceratopogonids. The senior author's wife Annette financed part of this trip, shared a bedroom with stacks of petri dishes and a microscope (as well as the senior author), and cheerfully supported this effort to better understand the fauna of Costa Rica. The senior author expresses his heartfelt thanks to all of his family members! His brother and sister-in-law, Herman and Pieta Borkent also helped in financing a portion of the trip and we appreciate their faith in this work.

El Servicio de Parques Nacionales kindly provided permission to collect in the numerous National Parks and Reserves in Costa Rica. The senior author expresses his appreciation to Alvaro Castro, who helped organize our lives in Costa Rica and pointed out some exceptional habitats. Finally, Alvaro Vargas permitted collecting on his farm, just west of Reserva Carara, which included an exceptional virgin rainforest and some beautiful springs.

We appreciate the support of the Norwegian Agency for Development Cooperation (NORAD) through the project "Contribution to the Knowledge and Sustainable Use of Biodiversity in Costa Rica" developed by INBio and the National System of Conservation Areas (SINAC), Ministry of the Enviornment and Energy (MINAE).

We received material on loan from several museums and thank the following for their assistance with this study: Jeffery M. Cumming (CNCI), David Grimaldi (AMNH), William (Bill) L. Grogan (Salisbury State University, Maryland), Lois Matile (MNHN), Gary F. Hevel, Al L. Norrbom and Holly B. Williams (USNM), and Gustavo R. Spinelli (MLPA).

We express our thanks to Gustavo Spinelli and William (Bill) L. Grogan for critical reviews of this paper; Gustavo Spinelli also provided a Spanish translation of the abstract. Jim Troubridge produced the labels for yet another study and we express our thanks to him for his generous help.

MATERIALS AND METHODS

All specimens were examined, measured, and drawn using either a Wild M3 dissecting scope or a Carl Zeiss Jenaval compound scope. Representative specimens were examined in glycerine (especially to closely compare structures of the different species), some (including all holotypes and allotypes) mounted on microscope slides using the technique described by Borkent and Bissett (1990), and the remainder were critical point dried and mounted on pins.

Terms for structures follow the Manual of Nearctic Diptera (McAlpine, 1981). More specific larval and pupal terms follow Lawson (1951). Aedeagus length was measured as the distance from the basal lateral margin of the aedeagus to its apex (not including the small apical projection); width was the distance between the basal lateral margins.

Live larvae and pupae were extracted from mud or mud/wet leaf samples, taken with a hand trowel, by flooding the substrate with water in a shallow tray and capturing swimming larvae or floating pupae with an eyedropper. Immatures were reared in petri dishes (5 cm in diameter) with a small amount of substrate (mud and detritus) from the original habitat; in some instances nematodes (*Panagrellus redivivus*) were periodically added as potential food but some larvae were successfully reared without nematodes. The dishes were kept at ambient temperature (about 25°C) and checked every day. When needed, a small amount of water was added to the petri dish to keep the sample from drying. Upon pupation, the larval exuviae were preserved in 70% ethanol and placed in small genitalia vials. After adults emerged the pupal exuviae and adults were either preserved immediately (when the adult was dead or dying) or the adult was left for a day to allow full sclerotization.

Adults were also captured in the field by sweeping vegetation with an aerial net.

Specimens are deposited in the following collections:

AMNH	Department of Entomology, American Museum of Natural History
CNCI	Canadian National Collection of Insects, Ottawa, Ontario, Canada
MLPA	Museo de la Plata, Universidad de La Palata, Argentina
INBC	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
MNHN	Museum National d'Histoire Naturelle, Paris, France
WLGC	William L. Grogan, Salisbury State University, Salisbury, Maryland
USNM	United States National Entomological Collection, U.S. National Museum of Natural History, Washington, DC

TAXONOMY

GENUS *BAEODASYMYIA*
CLASTRIER AND RACCURT

Baeodasymyia Clastrier and Raccurt, 1979: 100. Type species: *Baeodasymyia modesta* Clastrier and Raccurt, by monotypy.

DIAGNOSIS (based on extant and extinct taxa): Adults: only Ceratopogonidae with a two segmented palpus (fig. 7A) and macrotrichiae scattered over entire wing membrane. Pupae: only Ceratopogonidae with operculum having a well-developed medial projection situated near the dorsal margin (fig. 3E) and the respiratory organ with a separate, short, expanded apical portion bearing spiracles in a single plane (fig. 3F, G). Fourth instar larvae: only Ceratopogonidae with a prognathous, fully pigmented head capsule bearing only simple setae (fig. 6A–D, 8A, B), with the two setae p very unequal in size (anterior longer than posterior one), with the two setae o very unequal in size (the anterior longer than the posterior one), and a head capsule length < 130 μm.

DESCRIPTION (based on extant and extinct taxa): *Adults*: Extremely small (wing length of males 0.41–0.58 mm, of females 0.41–0.57 mm). General body coloration pale to dark brown, some with different portions of head, thorax pigmented. Eyes pubescent, om-

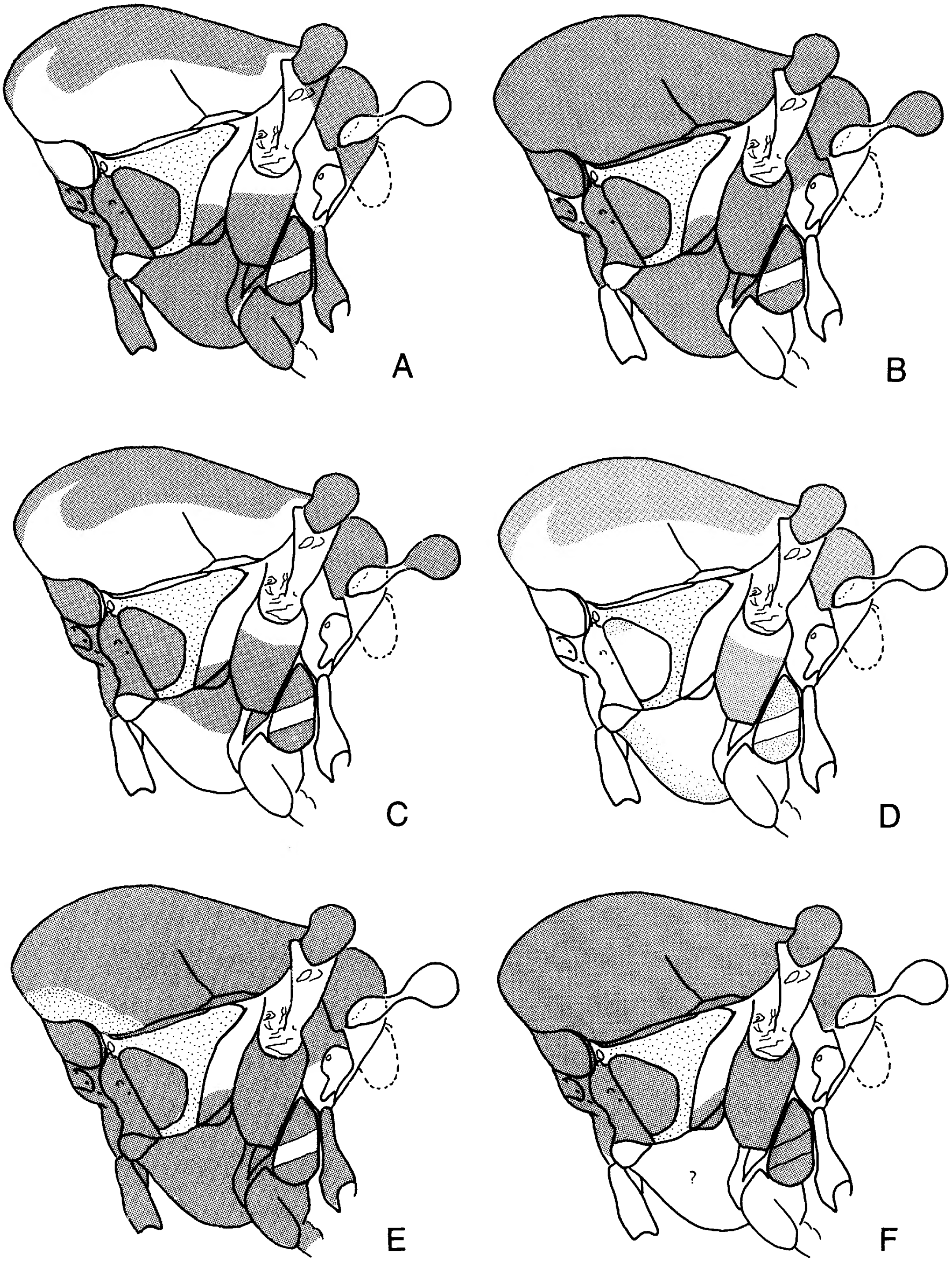

Fig. 1. Thoraces of adult *Baeodasymyia*, lateral view. **A.** *B. michaeli.* **B.** Male *B. christopheri.* **C.** Female *B. christopheri.* **D.** *B. lydiae.* **E.** *B. gustavoi.* **F.** *B. dominicana.*

matidia well separated medially, with single dorsomedial seta present. Male with moderately developed plume, 12 flagellomeres with 2–7, 8–9 fused, 10–11 fused or at least somewhat indistinct; female antenna with 13 flagellomeres, 9 slightly longer than 8, 10–13 gradually increasing in size; five sensilla coeloconica present on flagellomere 1 of both sexes. Clypeus separated laterally from head capsule by membrane. Two palpal segments (fig. 7A); basal segment with well defined pit with seven (in females) capitate sensilla (fig. 7B); apical segment small, nearly spherical to somewhat elongate. Female mouthparts reduced; mandible, laciniae not present. Thorax shiny. Scutum with elongate setae, without anteromedial tubercle; anteroventral margin of scutum with 3 elongate apodemes; humeral pit small. Anepisternum and katepisternum without setae. Scutellum with 4–6 setae. Femora, tibiae without strong bristles. Fore, midleg trochanter each with pair of setae, these thick on midleg. Female claws equal, short, without inner teeth (fig. 7D). Empodium present but small (fig. 7D). Male claws equal, short, without inner teeth, tips bifid. Foreleg tibial spur absent. Hindleg with tibial spur small or absent; first tarsomere of hindleg straight, with palisade setae on nearly full length of tarsomere (fig. 7C). Fourth tarsomeres cylindrical. Wing with abundant elongate macrotrichia on wing veins and membrane. CR 0.27–0.45 for males, 0.28–0.36 for females. Radial cells absent; medial and cubital veins poorly developed (best seen with phase contrast); stem of media not visible. Abdominal tergite 2 without anteromedial triangular apodeme. Male genitalia (fig. 2A, B) partially rotated (to about 90° or somewhat more) in some individuals of all species; apicolateral process on tergite 9 very short, bearing single seta; with well-developed, articulating gonocoxite, gonostylus; parameres absent; aedeagus more or less U-shaped, articulated laterally with base of gonocoxite, with only margin or margin and apical portion pigmented, with short, apically expanded projection situated apicodorsally; male cercus well-developed, situated on a patch of membrane, on apical margin of segment 10. Female genitalia (fig. 2C, D, 3A–C) with posterior margin of sternite 8 bilobed; sternite 9 united or divided medially; segment 10 bearing two apical or subapical bristles, two shorter setae anteriorly; cercus well-developed; one well-developed, spherical spermatheca, elongate neck bent at 90° angle to axis of spermatheca.

Pupa. Length 0.94–1.26 mm. General coloration uniformly light to medium brown. Body surface generally smooth with only a few tubercles and spicules associated with setae, a few restricted to the medioanterodorsal and medioanteroventral areas of abdominal segments 6–8 (sometimes not visible on segment 6) and anal segment. Operculum (fig. 3E) with well-developed anteromarginal seta located on tubercle, with pore at tubercle base; well-developed medial projection situated near dorsal margin. One long, one shorter anterodorsal setae on short, rounded tubercle (fig. 4B, F). One long, slender and one shorter, thick dorsolateral setae (fig. 4C, G). One short, thick dorsomedial seta (fig. 4C, H). Five dorsal sensilla, i, ii, iv elongate, slender setae, iii, v pores; i, ii on single, rounded, short tubercle, iii, iv closely approximated, v situated more posteriorly (fig. 4D, I). Ventromedian setae not visible (perhaps too minute). Two ventrolateral setae elongate, bases close (fig. 4A, E). Respiratory organ (fig. 3F, G) with three distinct sections; cylindrical basal portion light to medium brown (same as thoracic cuticle), smooth; cylindrical middle portion pale, with annulations for most of distal length; compressed apical portion pale or light brown, rounded or concave apically; one spiracle situated near base of middle portion, remaining situated apically on apical portion, opening at surface; tracheal tube of more or less equal diameter for length, dividing near base of middle portion and distal portion. Metathorax nearly completely divided medially, with medial protuberance from scutum protruding well beyond posterior margin of metathorax (fig. 3D). Abdomen with setae separate from one another (none on common tubercle), each bordered by comb-like or single elongate spicules. Segment 4 setal pattern (fig. 4J, K) with 2 d.a.s.m., 4 d.p.m., l.a.s.m. absent, 3 l.p.m., 3 v.p.m.; setae d.p.m. i–iii not clearly visible, possibly represented only by comblike spicules; setae d.p.m. iv, l.p.m. i, ii, all short, stout. Anal segment with row or patch of stout, sharp spicules (fig. 5A, B);

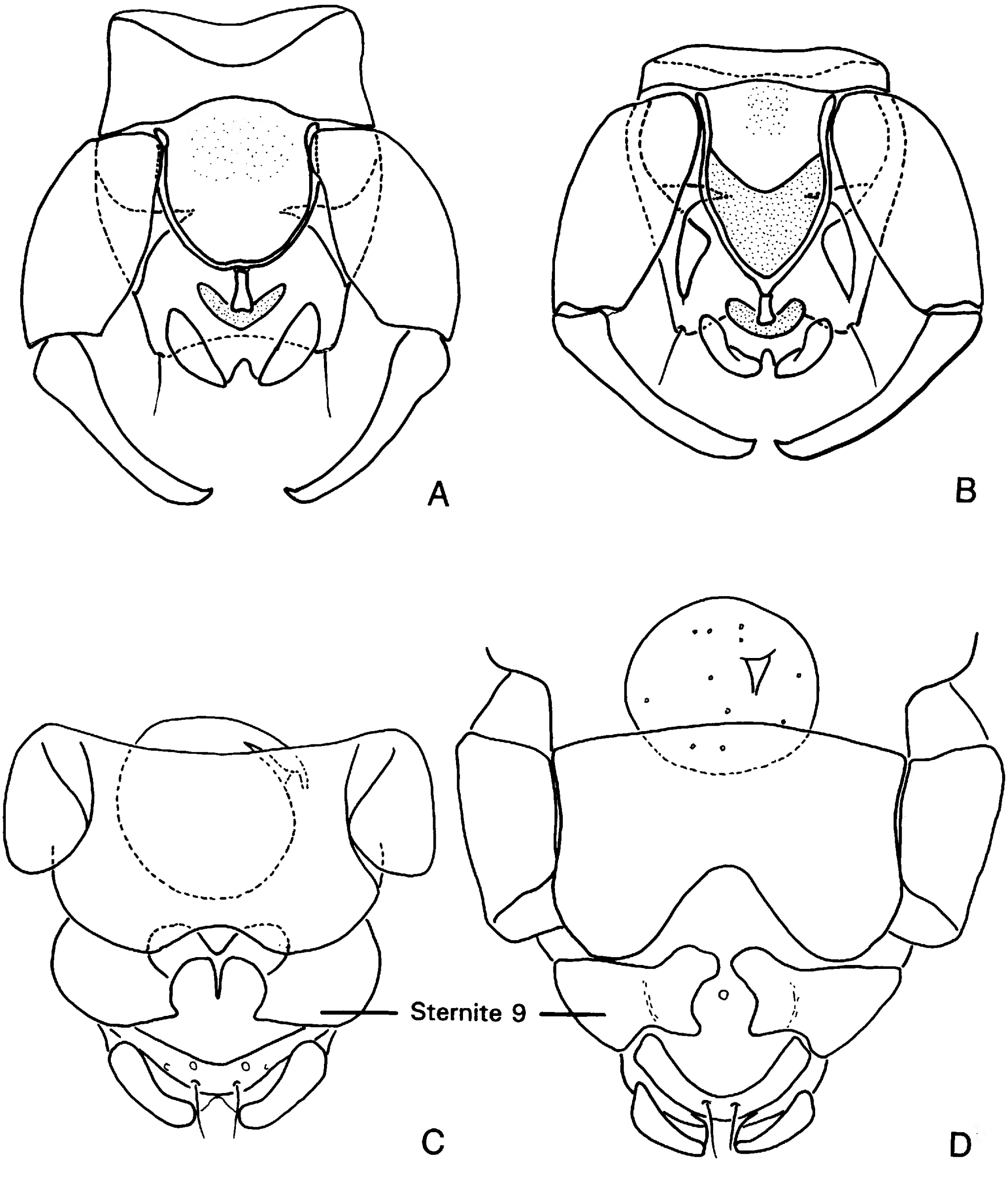

Fig. 2. Genitalia, ventral view. **A.** Male *B. michaeli.* **B.** Male *B. lydiae.* **C.** Female *B. michaeli.* **D.** Female *B. christopheri.*

caudal spine in shape of elongate triangle, sharply narrow apically, directed posterolaterally.

Fourth instar larva. Body length 1.6–2.3 mm. Head capsule (fig. 6A–D, 8A, B) relatively short (115–127 μm), blunt (head L/W 1.52–1.81), uniformly medium brown. Collar slightly darker than rest of head capsule, well-developed ventrally with expanded anterior apodeme, separated medially, dorsolateral portion thick, dorsomedial portion thin. Frontal suture extending to near anterior margin of labrum. Ventral suture barely or not visible; if present, as a short, pale slit. Setae all simple, arrangement as in fig. 6A–D, 8A, B; following sensilla more elongate, with large bases (as seen with light microscope): one of p, q, t, y, v, one of o; sensilla j represented by one very short seta (not visible in slide-mounted material); sensilla z not

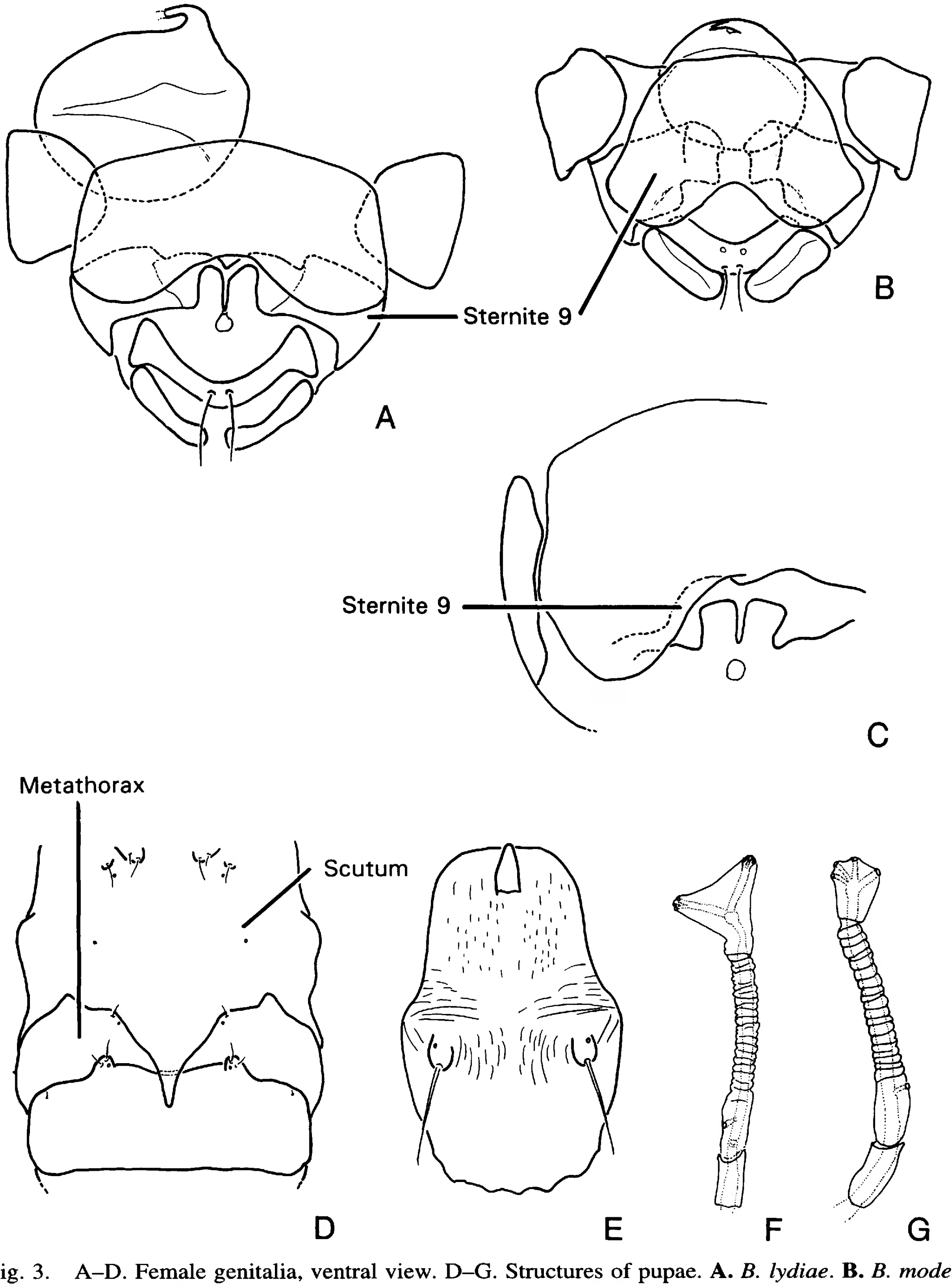

Fig. 3. A–D. Female genitalia, ventral view. D–G. Structures of pupae. **A.** *B. lydiae*. **B.** *B. modesta*. **C.** *B. gustavoi*. **D.** Posterior portion of scutum, metathorax, and first abdominal tergite of *B. michaeli*, dorsal view. **E.** Operculum of *B. michaeli*. **F.** Respiratory organ of *B. michaeli*. **G.** Respiratory organ of *B. christopheri*.

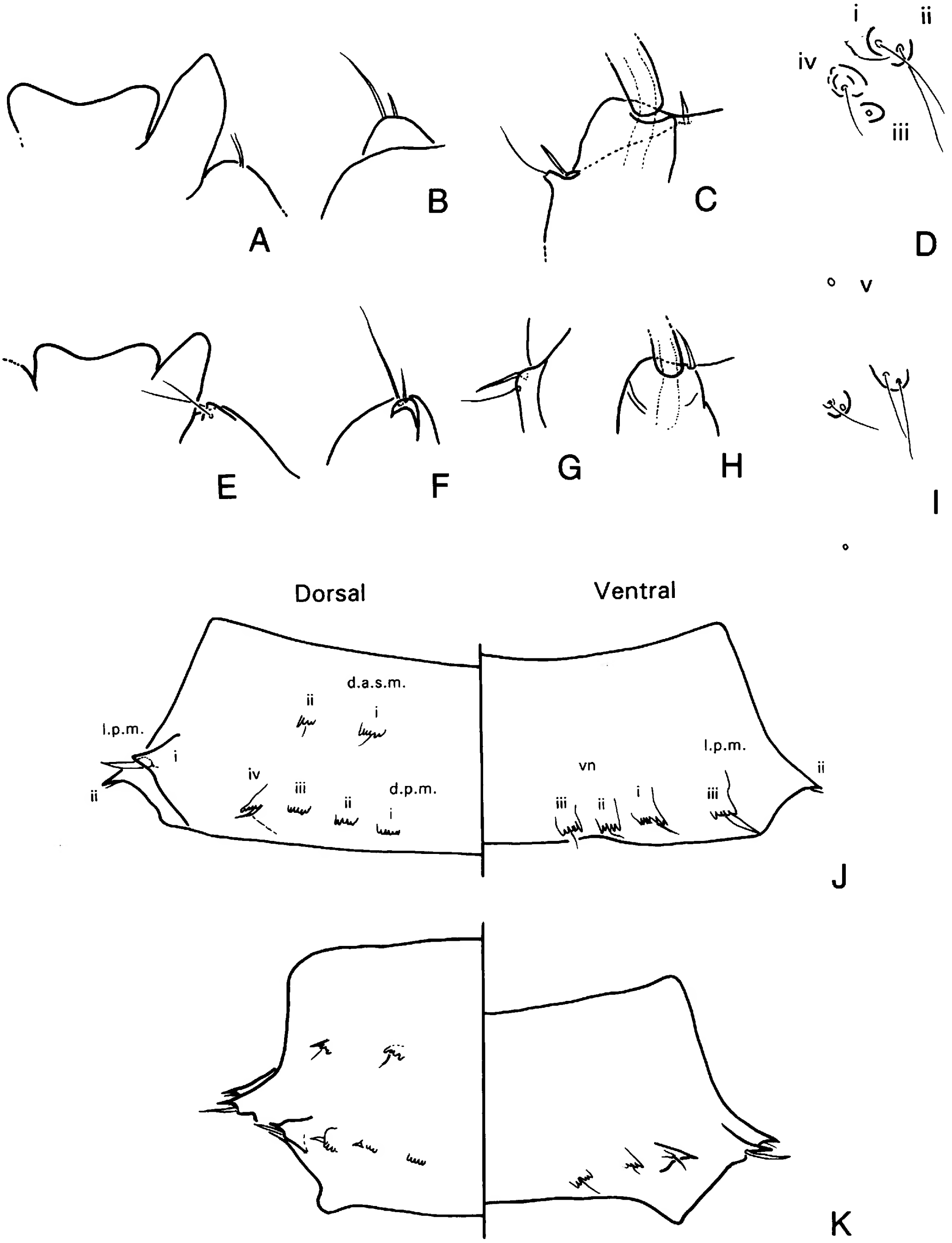

Fig. 4. A–I. Head and thoracic setae of pupae. J–K. Fourth abdominal segment of pupae. **A.** Ventrolateral setae of *B. michaeli*. **B.** Anterodorsal setae of *B. michaeli*. **C.** Dorsolateral and dorsomedial setae of *B. michaeli*. **D.** Left dorsal setae of *B. michaeli*. **E.** Ventrolateral setae of *B. christopheri*. **F.** Anterodorsal setae of *B. christopheri*. **G.** Dorsolateral setae of *B. christopheri*. **H.** Dorsomedial seta of *B. christopheri*. **I.** Left dorsal setae of *B. christopheri*. **J.** *B. michaeli*. **K.** *B. christopheri*.

present; posterior seta of p extremely thin, barely discernible. Antenna (fig. 8A, 9B) short, with eight sensilla, anterior one flattened, bearing numerous pores. Eye of moderate size, circular to kidney shaped (figure 6A). Labrum (fig. 9A) short, wide, tapering to narrow apex, with two well-developed sensilla styloconica and one associated small seta, six subapical sensilla, further details not discernible. Mandible elongate, curved with short medial lobe at midlength, apical portion slender, possibly with groove along length, with subbasal elongate seta. Maxilla (fig. 9A, C) with at least 8 sensilla, palpus short. Hypostoma (fig. 6B, D, 9A) a broadly rounded projection. Epipharynx with 1 set of serrate plates, apparently undivided medially (fig. 6B, D). Thorax, abdomen unpigmented, fat body white, without pigmentation. Caudal segment apically rounded, with short, well-separated setae (fig. 9D). Four well-developed, bifurcate anal papillae (fig. 5C).

Third instar larva. Body length 1.2–1.6 mm. Head capsule (fig. 10A, B) relatively short (88–93 µm), blunt (head L/W 1.70–1.83), uniformly medium brown. Collar slightly darker than rest of head capsule, well-developed ventrally with expanded anterior apodeme, separated medially, dorsolateral portion thick, dorsomedial portion thin. Frontal suture extending to near anterior margin of labrum. Ventral suture barely or not visible; if present, as a short, pale slit. Setae all simple, arrangement as in figure 6A–D; following sensilla more elongate, with large bases (as seen with light microscope): one of p, q, t, one of x, y, v, one of o; sensilla j represented by one very short seta (not visible in slide-mounted material); sensilla z not present; posterior seta of p extremely thin, barely discernible. Antenna (fig. 10B) short, with eight sensilla, anterior one flattened, bearing numerous pores. Eye small or of moderate size, circular to kidney shaped. Labrum (fig. 10B) short, wide, tapering to narrow apex, with two well-developed sensilla styloconica and one associated small seta, six subapical sensilla, further details not discernible. Mandible elongate, curved with short medial lobe at midlength, apical portion slender, possibly with groove along length, with subbasal elongate seta. Maxilla with at least eight sensilla, palpus short. Hypostoma broadly rounded projection. Epipharynx with one set of serrate plates, apparently undivided medially. Thorax, abdomen unpigmented. Caudal segment apically rounded, with short, well-separated setae. Anal papillae not visible.

Second instar larva. Body length 1.6–2.3 mm. Head capsule (fig. 11A, B) relatively short (115–127 µm), blunt (head L/W 1.52–1.81),uniformly medium brown. Collar slightly darker than rest of head capsule, well-developed ventrally with expanded anterior apodeme, separated medially, dorsolateral portion thick, dorsomedial portion thin. Frontal suture not clearly visible. Ventral suture not visible. Setae all simple, arrangement as in fig. 6A–D; following sensilla more elongate, with large bases (as seen with light microscope): one of p, q, t, y, v, one of o; sensilla j represented by one very short seta (not visible in slide-mounted material); sensilla z not present; posterior seta of p extremely thin, barely discernible. Antenna short, with eight sensilla, anterior one flattened, bearing numerous pores. Eye small, oval. Labrum (fig. 11B) short, wide, tapering to narrow apex, with 2 well-developed sensilla styloconica and 1 associated small seta, with four or possibly six subapical sensilla, further details not discernible. Mandible elongate, curved with short medial lobe at midlength, apical portion slender, possibly with groove along length, with subbasal elongate seta. Maxillary palpus short. Details of hypostoma, epipharynx not clearly visible. Thorax, abdomen unpigmented. Caudal segment apically rounded, with short, well-separated setae. Anal papillae not visible.

Egg. Elongate, rounded anteriorly, somewhat tapered posteriorly (based on ova within female abdomens).

DISTRIBUTION AND BIONOMICS: The genus *Baeodasymyia* is restricted to the Neotropical region and species are known from Haiti (Clastrier and Raccurt, 1979), Costa Rica, and Panama (this study), Colombia (Wirth and Grogan, 1988), Paraguay, and Argentina (Spinelli, 1997) (fig. 12A,B, 13A).

All adult *Baeodasymyia* captured by the senior author were collected near the sources of several small to medium-sized springs. Larvae and pupae of *B. michaeli* and *B. christopheri* were sampled from mud right at

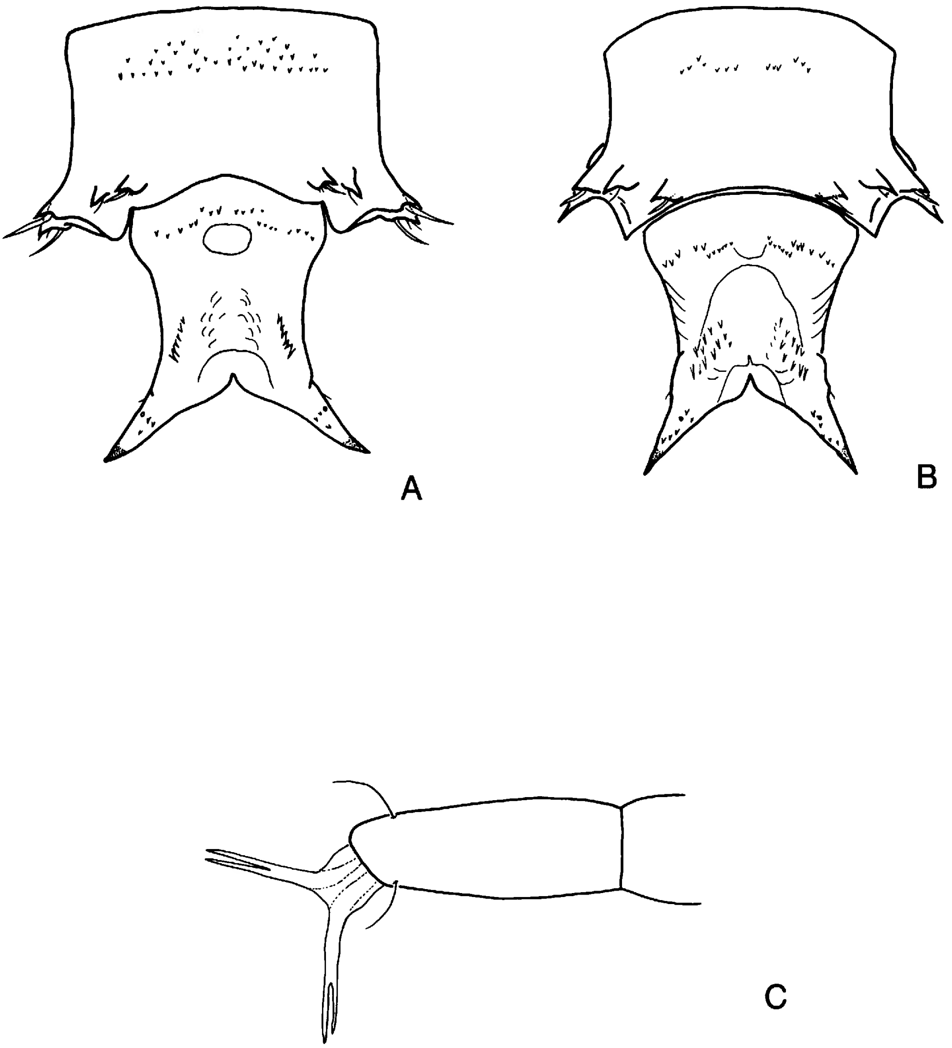

Fig. 5. Structures of immature *Baeodasymyia*. A–B. **A.** Terminal abdominal segments of female pupa of *B. michaeli*, dorsal view. **B.** Terminal abdominal segments of male pupa of *B. christopheri*, dorsal view. **C.** Terminal abdominal segments of fourth instar larva of *B. michaeli*, lateral view.

the source of a small spring in Atenas, Costa Rica and a larva of *B. christopheri* was extracted from mud on the margin of a spring-fed stream about 80 m from the mouth of the spring. Clastrier and Raccurt (1979) reported that *B. modesta* adults were reared from mud collected from a shady marsh and a shady river margin.

The behavior of immatures is further described under *B. michaeli* below. Members of *B. christopheri* were too rare to make many observations. Further information, including life cycles for some species, is given under each species.

Adult *Baeodasymyia* walk with a peculiar rapid stuttering motion. Because individuals are so small, this can be barely observed with the naked eye when specimens are in an insect net but is readily apparent when these are in a vial or under a binocular microscope.

When collected with an aerial net, adult *Baeodasymyia* remain in the bottom of the net for some time (longer than most other Ceratopogonidae) and then slowly walk upward.

All female adult *Baeodasymyia* lack functional mouthparts and therefore are not capable of blood-feeding.

TAXONOMIC DISCUSSION: There is little structural diversity among adults of different species of *Baeodasymyia* but all species may be recognized according to pigmentation patterns on the thorax. One species, *B. christopheri* is sexually dimorphic in pigmentation pattern and the sexes were only associated after considerable sampling had been completed.

Borkent and Wirth (1997) mistakenly reported the type species of the genus *B. modesta* as originally designated. Clastrier and Raccurt (1979) described the species and genus as "n. g., n. sp." indicating that the designation was actually based on monotypy.

Wirth and Grogan (1988) indicated that adult *Baeodasymyia* lack palisade setae and that the male genitalia lacked apicolateral processes. In fact, palisade setae are clearly present (fig. 7C) and the apicolateral processes are present as small knobs, bearing an apical setae (fig. 2A, B) (as reported by Clastrier and Raccurt, 1979). Szadziewski and Grogan (1994) have already pointed out that the male antenna as illustrated by Clastrier and Raccurt (1979), and reproduced by Wirth and Grogan (1988), was incorrectly drawn.

KEYS

Adult members of *Baeodasymyia* may be identified to genus using the key by Wirth and Grogan (1988), with the following modification of their couplet 8. The male antennae of the taxa were drawn by Szadziewski and Grogan (1994: fig. 13–15).

8. Foretibia with apical spur; macrotrichiae confined to margin and apex of wing (in some, also a few on apex of M veins); costal ratio > 0.40; male antenna with 6 separate flagellomeres *Baeohelea* Wirth and Blanton

– Foretibia without apical spur; macrotrichiae long and abundant over entire wing; costal ratio < 0.36; male antenna with 12 flagellomeres with 2-7, 8-9, and 10-11 fused in all extant species but 10-11 at least somewhat distinct in fossil *B. dominicana* . . . . *Baeodasymyia* Clastrier and Raccurt

The distance between the ommatidia has been used as a key character to distinguish *Baeohelea* and *Baeodasymyia* (Wirth and Grogan, 1988) but it does not differ much between females of the two genera.

There are no generic keys to larvae and pupae of Ceratopogonidae which might easily incorporate these stages of *Baeodasymyia*. The diagnoses given above must suffice until such keys are available (Borkent, in prep.). The larvae of the two known *Baeodasymyia* species could not be confidently distinguished.

KEY TO EXTANT SPECIES OF ADULT *BAEODASYMYIA*

The pigmentation patterns described below are more clearly evident in uncleared specimens in alcohol than in those cleared and mounted on microscope slides, although the key works for both.

1. Scutum dark brown, unicolorous but in some specimens slightly lighter on very anterior and lateral margins, without discrete vittae (fig. 1B, E, F) 2

– Scutum with vittae, lateral margins pale (fig. 1A, C, D) 4

2. Halter with knob dark brown (fig. 1B) . . . . male *christopheri* n. sp.

– Halter knob pale (fig. 1E) 3

3. Sclerite 9 of female divided medially (fig. 3B) . . . . *modesta* Clastrier and Raccurt

– Sclerite 9 of female connected medially (fig. 3C) (male unknown) . . . . . *gustavoi* n. sp.

4. Lateral pleural sclerites of thorax markedly pale with only anepimeron clearly more darkly pigmented (a few very light patches of pigmentation may be present on other sclerites) (fig. 1D); aedeagus pointed posteriorly, with apical portion pigmented (fig. 2B); spermatheca with neck not expanded and basal portion separate from rest of spermatheca (fig. 3A) . . . . *lydiae* n. sp.

– Lateral pleural sclerites more extensively pigmented (fig. 1A, C); aedeagus a single U-shaped band (fig. 2A); spermatheca with neck expanded and basal portion appressed to spermatheca (fig. 2C, D) 5

5. Katepisternum uniformly darkly pigmented (fig. 1A); sternite 9 fused medially (fig. 2C) . . . . *michaeli* n. sp.

– Katepisternum pale ventrally (fig. 1C); sternite 9 divided medially (fig. 2D) . . . . female *christopheri* n. sp.

KEY TO SPECIES OF PUPAE OF *BAEODASYMYIA*

Of the five extant species, pupae are known only for *B. michaeli* and *B. christopheri*. The proportional differences in width

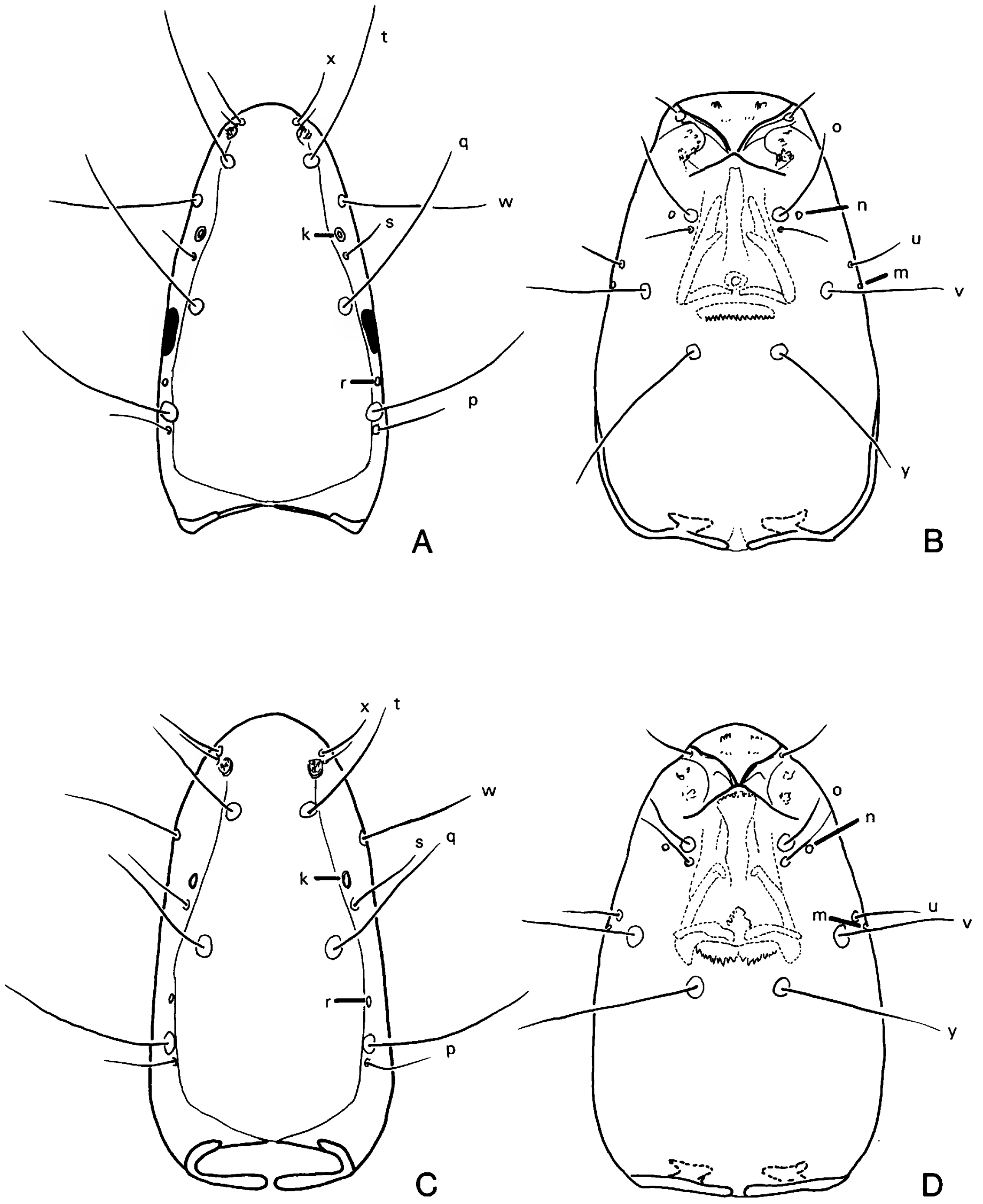

Fig. 6. Head capsules of fourth instar larvae. **A.** *B. michaeli*, dorsal view. **B.** *B. michaeli*, ventral view. **C.** *B. christopheri*, dorsal view. **D.** *B. christopheri*, ventral view.

shown in figure 4J, K are due to differences in compression of the abdominal segments by coverslips.

1. Respiratory organ apically bifid or triangular (fig. 3F); dorsolateral setae with slender, elongate seta on an elongate tubercle (fig. 4C) .... *michaeli* n. sp.
– Respiratory organ more or less rounded apically (fig. 3G); both dorsolateral setae on a low, rounded tubercle (fig. 4G) .... *christopheri* n. sp.

DESCRIPTION OF SPECIES OF *BAEODASYMYIA*

Baeodasymyia michaeli Borkent, new species

Figures 1A, 2A, C, 3D–F, 4A–D, J, 5A, C, 6A, B, 7A–D, 8A, B, 9A–D, 10A, B, 11A, B

DIAGNOSIS: *Adults*: only known *Baeodasymyia* with scutum having vittae, entire katepisternum with pigmentation and halter knob pale (fig. 1A). *Pupa*: only known *Baeodasymyia* with apex of respiratory organ triangular or somewhat bifid (fig. 3F) (only two species known). *Fourth instar larva*: not identifiable beyond generic level.

DESCRIPTION: *Male adult*. **Head**: Medium brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pale. **Thorax** (fig. 1A): Generally pale, with darker pigmentation present on the following: scutum with lateral vittae, anterior medial vittae, posterior medial vittae variably distinct or merged; scutellum but with medial portion somewhat paler than lateral portions; postnotum; most of ventral portion of lateral sclerites. Halter pale. **Wing**: Length 0.51–0.59 mm (0.55, n = 15), costal ratio 0.32–0.35 (0.33, n = 15). **Legs**: All femora, tibiae light brown with poorly defined subbasal ring and apical portion of tibiae, all tarsomeres pale. **Genitalia** (fig. 2A): Aedeagus a U-shaped band, lacking medial pigmentation, with apical club-shaped prong; L/W 0.94–1.31 (1.15, n = 13).

Female adult. Pigmentation as in male but in some, scutellum entirely pale. **Wing**: Length 0.48–0.57 mm (0.53, n = 13), wing length/width 2.22–2.47 (2.30, n = 13); costal ratio 0.32–0.36 (0.34, n = 13).**Genitalia** (fig. 2C): Sternite 9 M-shaped, connected medially. Spermatheca neck expanded, appressed against spermatheca.

Pupa. Exuviae medium brown. Total length 1.14–1.26 mm (1.21, n = 9). Respiratory organ (fig. 3F): Length 161–174 μm (169, n = 7); apex flat, expanded, triangular to somewhat bifid; apical spiracles arranged in two groups at apices of bifurcation. Dorsolateral setae with slender, elongate seta on elongate tubercle (fig. 4C).

Fourth instar larva. Not distinguishable from those of the only other known species, *B. christopheri*; thus described generically above.

Second and third instar larva. Only species for which these stages are known and therefore described generically above.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia michaeli* is known from Costa Rica and northern Panama (localities 1–6; fig. 12A) and adults have been collected from Aug. 26 until Jan. 29. Adults were collected only in association with springs and were most abundant at a small spring in Atenas, Costa Rica.

Larvae of *B. michaeli* were retrieved from mud sampled at the very head of a small spring in Atenas, Costa Rica (approximately 200 m NW of Don Yayo, a local grocery store) on Oct. 5 and 16 and Nov. 3, 1993. The wet mud surface was partially covered with wet leaves and was partially shaded by trees. Second to fourth instar larvae, disturbed during extraction from the mud samples, swam with a very rapid serpentine motion typical of so many Ceratopogoninae. When settled in substrate mud and detritus, individuals moved slowly and probed for food. The guts of whole third and fourth instar larvae contained fine particulate matter, suggesting that they feed on at least microorganisms.

Pupae immersed themselves in the mud-detritus substrate with just the anterior portion of the pupa protruding and the apices or most of the length of their respiratory organs in contact with the water surface. Pupae disturbed from their resting position would rapidly back into the detritus with circular motions of their abdomens, breaking contact with the water surface. The pupal period lasted 3–5 days (n = 6).

Repeated collections of adults at the spring at Atenas showed the presence of adults from

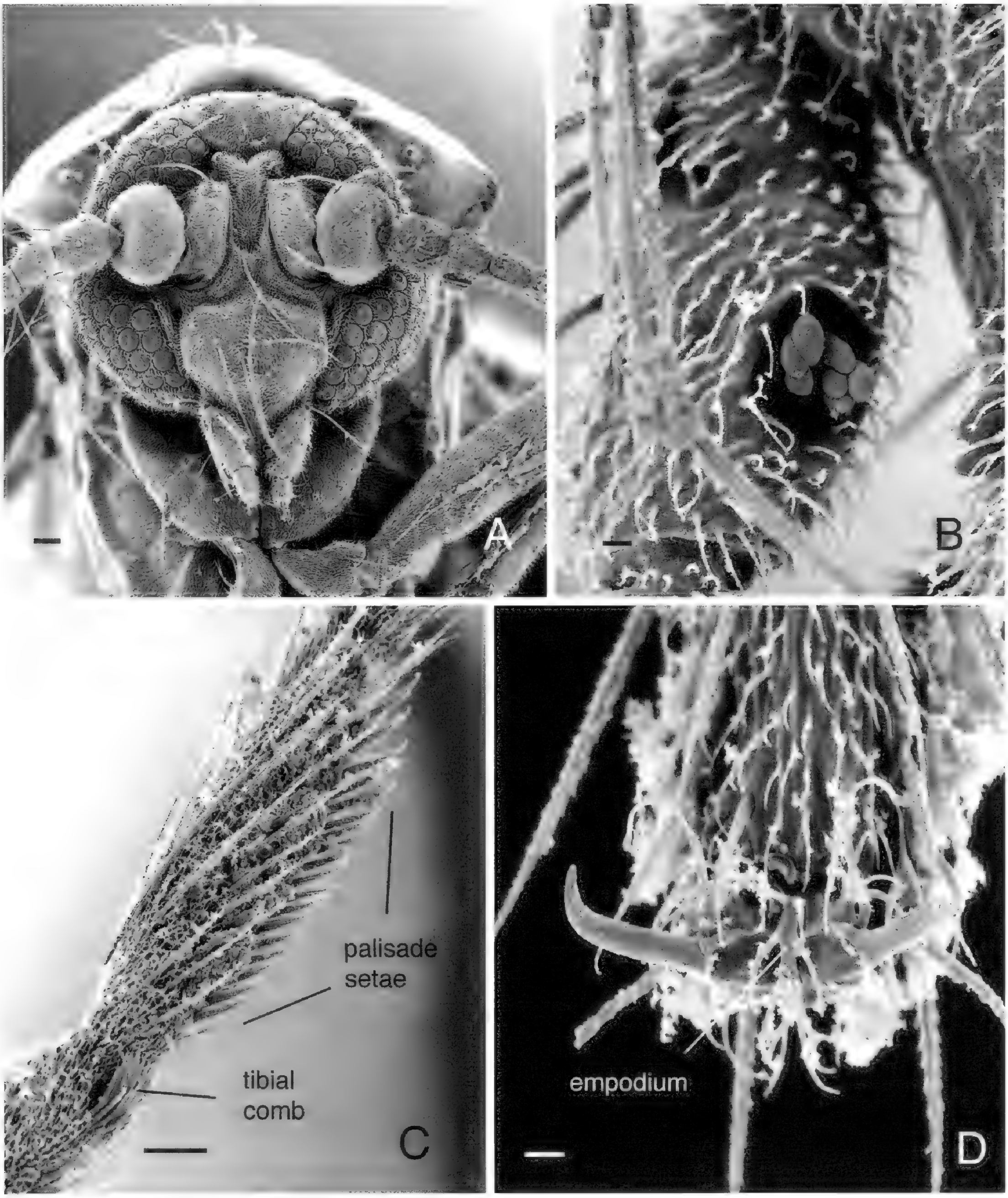

Fig. 7. Structures of female adult *B. michaeli*. **A.** Anterior view of head. **B.** Capitate sensilla in pit on right basal maxillary palpal segment. **C.** Hind first tarsomere. **D.** Ventral view of hind tarsal claws. Scales of A, C, = 10 μm, B, D = 1 μm.

Oct. 1, 1993, until Jan. 29, 1994. Throughout that period, samples (n = 6) of 15 or more adults indicated males comprised 35–53% of the samples, possibly indicating a multivoltine life cycle. A sample taken on March 27, 1999 (during the dry season) did not include any *Baeodasymyia* adults.

Taxonomic Discussion: Males and females were associated by their similar patterns of pigmentation, collection of imma-

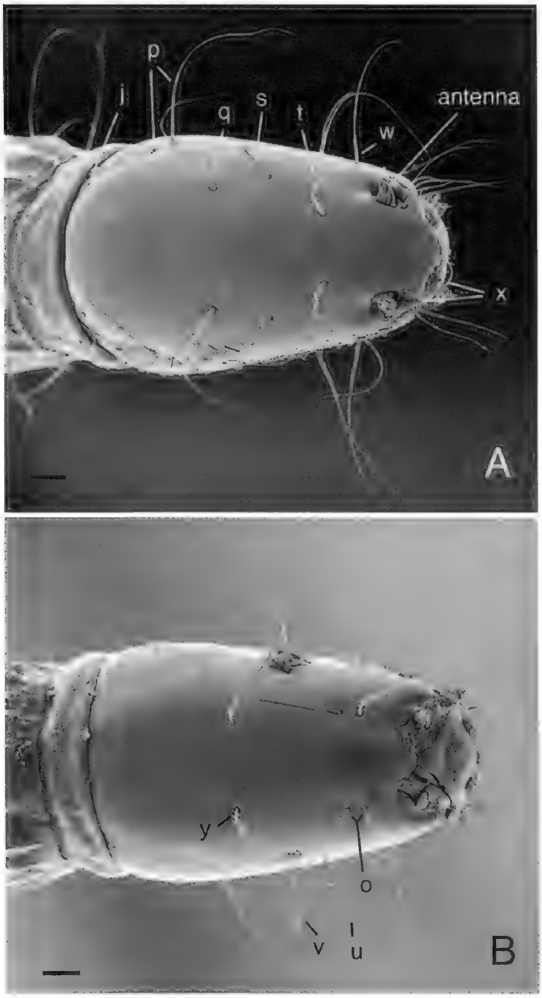

Fig. 8. Head capsule of fourth instar larva of *B. michaeli*. **A.** Dorsal view. **B.** Ventral view. Scales = 10 μm.

tures and adults from the same habitat, and rearings from pupae of similar form.

Some of the whole larvae included in the type series may include members of *B. christopheri* and *B. lydiae*, species which were also present in the same habitat. Larvae of *B. christopheri* could not be distinguished from those of *B. michaeli* and the larvae of *B. lydiae* are unknown. We have considered them all as *B. michaeli* because this was the most common species at this spring in Atenas, Costa Rica.

The three female adults of *B. michaeli* used for our SEM study (from Atenas, Costa Rica, 5-X-1993) could not be preserved in a conventional manner and are not considered to be part of the type series. The second, third and fourth larvae (one each from Atenas, Costa Rica, 16-X-1993) were removed from the stubs and placed on pins, for future SEM study; they are part of the paratype series.

TYPES: Holotype, male adult on microscope slide, labeled "HOLOTYPE Baeodasymyia michaeli Borkent, Atenas, C.R., 25-X-1993, A. Borkent CD1630" (CNCI); allotype, female adult with associated larval and pupal exuviae on microscope slide, labeled as for holotype but collected 16-X-1993 (CNCI); 126♂ 137♀, 9 pupal exuviae, 3 pupae, 12 larval exuviae, 2 second instar, 8 third instar, 10 fourth instar larvae as paratypes: 116♂ (3 with associated larval and pupal exuviae), 133♀ (5 with associated larval and pupal exuviae, 1 with pupal exuviae), 4 larval and pupal exuviae, 2 second instar, 8 third instar, 10 fourth instar larvae from type locality, adults collected 1-IX-1993, 8-IX-1993, 9-IX-1993, 4-X-1993, 5-X-1993, 7-X-1993, 16-X-1993, 20-X-1993, 25-X-1993, 2-XI-1993, 29-XI-1993, 2-XII-1993, 3-XII-1993, 7-XII-1993, 13-XII-1993, 30-XII-1993, 29-I-1994, larvae collected 5-X-1993, 16-X-1993, 3-XI-1993; 3♂ 1♀, 2 km NE Tarcoles, Costa Rica, 11-XI-1993, 14-XII-1993, 17-XII-1993; 2♂ 2♀, 10 km NW Jaco, Costa Rica, 18-X-1993; 1♂, Manuel Antonio National Park, Costa Rica, 26-VIII-1986; 3♂ 1♀, 1 km W Puerto Viejo, Limon, Costa Rica, 30-X-1993, 29-XII-1993; 1♂, 3 km SE Caldera, Panama, 22-IX-1993 (AMNH, CNCI, INBC).

DERIVATION OF SPECIFIC EPITHET: The name *michaeli* is proposed in appreciation of the senior author's younger son Michael, who spent hours peering into trays of mud and water and even found the teeny second instar larvae reported on above.

Baeodasymyia christopheri Borkent, new species

Figures 1B,C, 2D, 3G, 4E–I, K, 5B, 6C, D

DIAGNOSIS: *Male*: only known *Baeodasymyia* with halter knob and scutum dark brown (no discrete vittae) (fig. 1B). *Female*: only known *Baeodasymyia* with ventral portion of katepisternum pale and halter knob brown

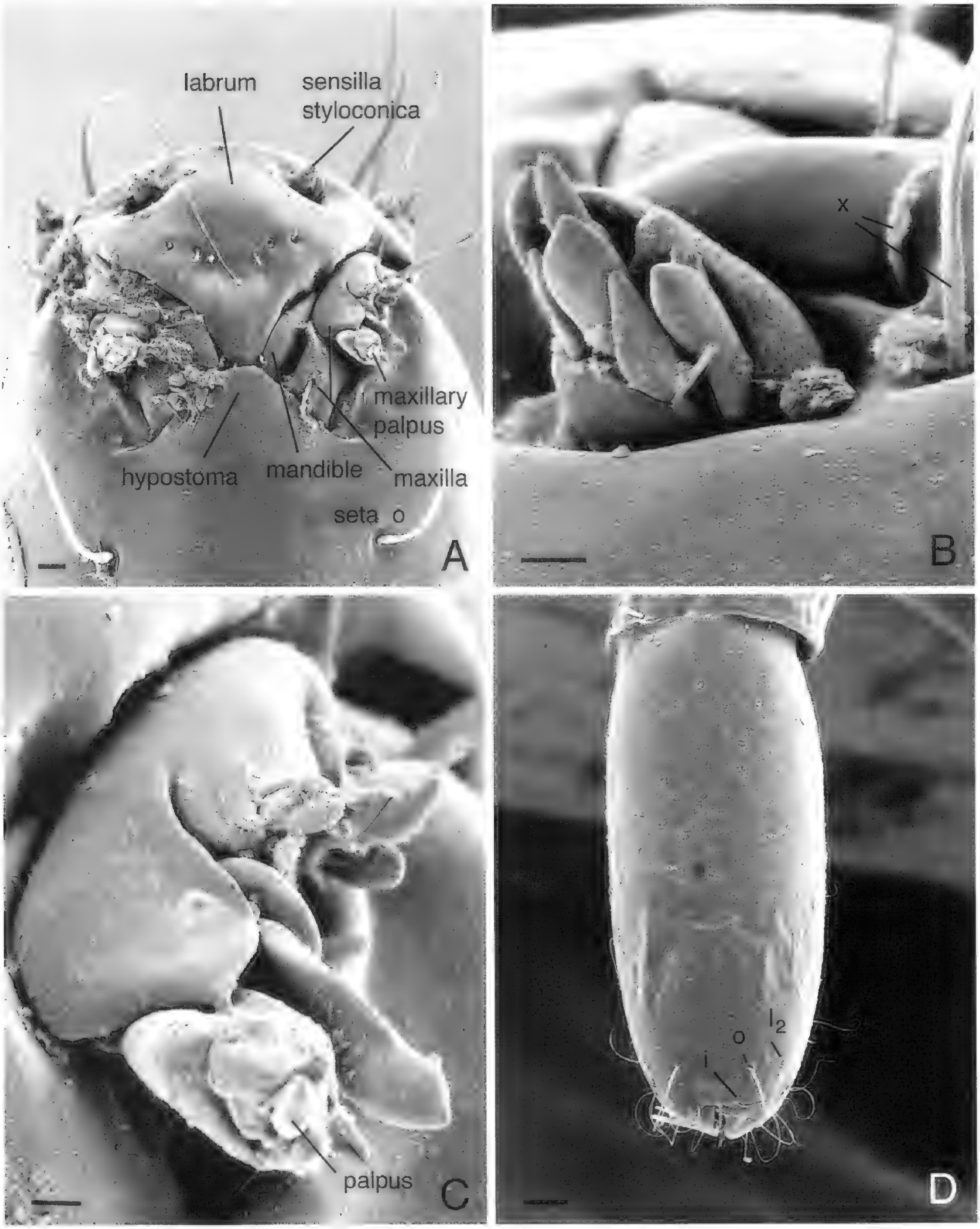

Fig. 9. Structures of fourth instar larva of *B. michaeli*. **A.** Ventral view of anterior portion of head capsule. **B.** Posteromedial view of left antenna. **C.** Ventral view of left maxilla. **D.** Ventral view of proximal abdominal segment. Scale of A = 2 μm, B, C = 1 μm, D = 10 μm.

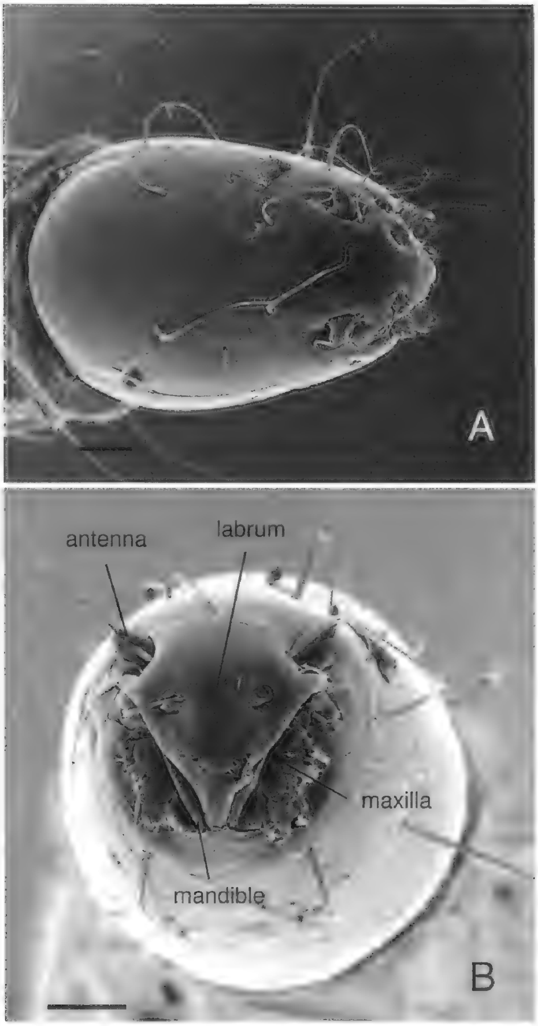

Fig. 10. Structures of third instar larva of *B. michaeli*. **A.** Anterodorsal view of head capsule. **B.** Anterior view of head capsule. Scales = 10 μm.

(fig. 1C). *Pupa*: only known *Baeodasymyia* with the apex of the respiratory organ more or less rounded (fig. 3G) (only two species known). *Fourth instar larva*: not identifiable beyond generic level.

DESCRIPTION: *Male adult.* **Head**: Dark brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pale. **Thorax** (fig. 1B): Entirely dark brown. Halter with stem pale, knob dark brown. **Wing**: Length 0.44–0.53 mm (0.49, n = 10), costal ratio 0.31–0.34 (0.32, n = 10). **Legs**: Generally pale, with slight infuscation present on apical portion of femora, all of tibiae; hindleg entirely pale in some. **Genitalia** (as in fig. 2A): Aedeagus a U-shaped band, lacking medial pigmentation, with apical club-shaped prong; L/W 0.93–1.13 (1.01, n = 11).

Female adult. **Head**: Medium brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pale. **Thorax** (fig. 1C): Generally pale, with darker pigmentation present on the following: scutum with lateral vittae, anterior medial vittae, posterior medial vittae variably distinct or merged; scutellum; postnotum; most of ventral portion of lateral sclerites but with ventral portion of katepisternum, coxae pale. Halter with stem pale, knob dark brown. **Wing**: Length 0.42–0.52 mm (0.47, n = 10), wing length/width 2.00–2.34 (2.11, n = 10); costal ratio 0.30–0.34 (0.32, n = 10). **Legs**: As in male but with pigmentation somewhat darker (remainder very pale brown). **Genitalia** (fig. 2D): Sternite 9 separated medially, with each half truncated to somewhat pointed. Spermatheca neck expanded, appressed against spermatheca.

Pupa. Exuviae pale brown. Total length 0.94–1.08 mm (n = 2). Respiratory organ (fig. 3G): Length 149–165 μm (n = 2); apex flat, expanded, somewhat roughed apically; apical spiracles arranged along width of apex. Both dorsolateral setae on low, rounded tubercle (fig. 4G).

Fourth instar larva. Not distinguishable from those of the only other known species, *B. michaeli*; thus described generically above.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia christopheri* is known from western Costa Rica (localities 1–3, fig. 12A) and adults have been collected from Sept. 8 until Dec. 17. Both adults and larvae were collected at the springs at Atenas (described more fully under *B. michaeli* above) and 2 km NE Tarcoles, Costa Rica. This latter spring was on the property of Alvaro Vargas just west of Reserva Carara and had a substantial flow. A single larva was extracted from mud on the edge of the flowing stream about 80 m below the head of the spring.

The larvae and pupae of *B. christopheri* behaved like those of *B. michaeli* reported on above. One individual had a pupal period of 4 days. Considering that adults were collected at the spring at Atenas from Sept. 8 until

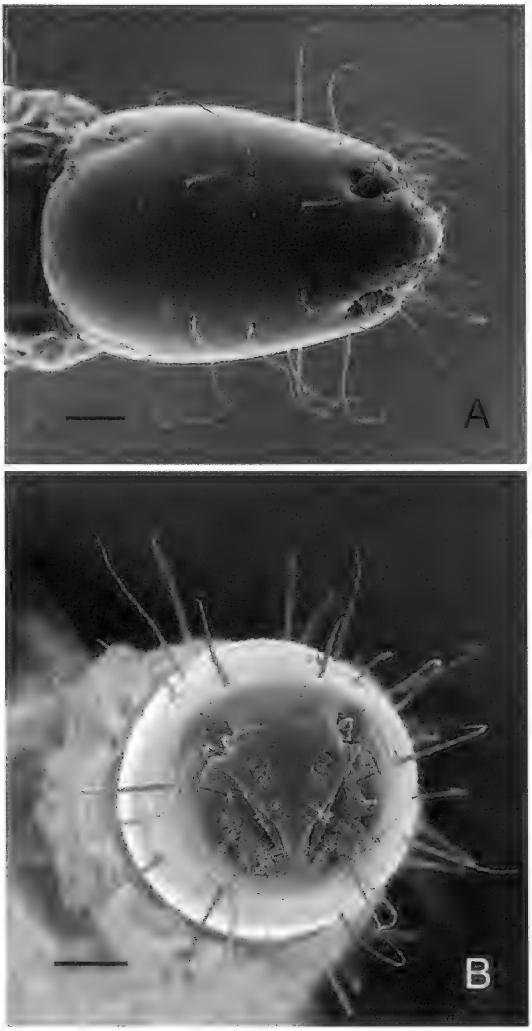

Fig. 11. Structures of second instar larva of *B. michaeli*. **A.** Anterodorsal view of head capsule. **B.** Anterior view of head capsule. Scales = 10 μm.

Dec. 7, 1993, it seems likely that the species is multivoltine at that location.

TAXONOMIC DISCUSSION: Males and females of *B. christopheri* are sexually dimorphic in their pattern of thoracic pigmentation and were associated on the basis of relative abundance at two locations. Three species of *Baeodasymyia* were present at the spring in Atenas, Costa Rica (described more fully under *B. michaeli* above). Males and females of both *B. michaeli*, the most abundant species, and *B. lydiae*, the least common species, shared similar pigmentation patterns within each species. *Baeodasymyia christopheri* was the second most common species for both sexes. Two species of *Baeodasymyia* were present at the spring 2 km NE Tarcoles, Costa Rica (on Alvaro Vargas's farm just west of Reserva Carara); *B. christopheri* was the most common species (13♂ 8♀) and *B. michaeli* the least common (3♂ 1♀). This distribution of "forms" suggests that the male and female of *B. christopheri* are correctly associated. Finally, although thoracic pigmentation was sexually dimorphic (males entirely dark, females with distinct pattern), both sexes were unique within the genus in having a brown halter knob.

The single pupal exuviae and one larval exuviae with an associated pupa were identified as *B. christopheri* on the basis of the following information. The pupae were collected at two locations where adults of *B. michaeli*, *B. christopheri*, and *B. lydiae* were present but these pupae were distinct from those of *B. michaeli* (see key above). The single pupa contained a pharate male adult and the male genitalia were typical of *B. michaeli* and *B. christopheri* (distinct from those of *B. lydiae*). We have therefore deduced that the larval exuviae and pupa and the pupal exuviae are likely those of *B. christopheri*.

Unfortunately, the associated larval exuviae and the live adult of the single pupal exuviae from Atenas, Costa Rica were lost and escaped, respectively.

The sexual dimorphic pigmentation pattern of adult *B. christopheri* is unusual and we know of no other instance of such dimorphism in the Ceratopogonini. Many members of the Sphaeromiini, Heteromyiini, and Palpomyiini are also sexually dimorphic with males often considerably darker than females.

TYPES: Holotype, male adult on microscope slide, labeled "HOLOTYPE Baeodasymyia christopheri Borkent, Atenas, C.R., 4-X-1993, A. Borkent CD1600" (CNCI); allotype, female adult on microscope slide, labeled as for holotype but collected 8-IX-1993 (CNCI); 21♂ 22♀, 1 pupal exuviae, 1 pupa and larval exuviae as paratypes: 8♂ 13♀, 1 pupal exuviae from type locality, collected 8-IX-1993, 5-X-1993, 7-X-1993, 25-X- 1993, 2-XI-1993, 2-XII-1993, 7-XII-1993; 13♂ 8♀, 1 pupa and larval exuviae, 2

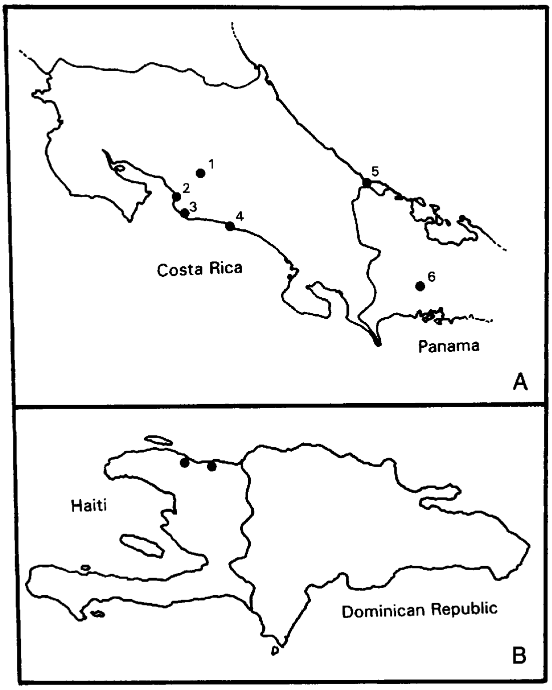

Fig. 12. Distributions of species of *Baeodasymyia*. **A.** Localities in Costa Rica and northern Panama; **1.** Atenas, **2.** 2 km NE Tarcoles, **3.** 10 km NW Jaco, **4.** Manuel Antonio, **5.** 1 km W Puerto Viejo, **6.** 3 km SE Caldera. **B.** *B. modesta.*

km NE Tarcoles, Costa Rica, 14-XII-1993, 17-XII-1993; 1♀, 10 km NW Jaco, Costa Rica, 28-IX- 1993 (AMNH, CNCI, INBC).

DERIVATION OF SPECIFIC EPITHET: The name *christopheri* is proposed to thank the senior author's oldest son, Christopher, who cheerfully helped collect ceratopogonids, including some of the larvae reared for this study, during the expedition to Costa Rica in 1993–94.

Baeodasymyia lydiae Borkent, new species

Figures 1D, 2B, 3A

DIAGNOSIS: *Adults*: only known *Baeodasymyia* with most lateral sclerites of the thorax pale (fig. 1D). *Immatures*: unknown.

DESCRIPTION: *Male adult.* **Head**: Medium brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pale. **Thorax** (fig. 1D): Generally pale, with light brown pigmentation present on the following: scutum with lateral vittae, anterior medial vittae, posterior medial vittae variably distinct or merged; scutellum; postnotum; ventral portion of anepimeron; in some, the following also very slightly pigmented: dorsal portion anepisternum, katepimeron, meron, ventral portion of katepisternum. Halter pale. **Wing**: Length 0.48–0.50 mm (0.49, n = 4), costal ratio 0.27–0.29 (0.28, n = 4). **Legs**: Pale or very slightly infuscated. **Genitalia** (fig. 2B): Aedeagus narrowly U-shaped band, with approximately apical half pigmented, with apical club-shaped prong; L/W 1.31–1.36 (1.34, n = 4).

Female adult. Pigmentation as in male. **Wing**: Length 0.45–0.48 mm (0.47, n = 3), wing length/width 2.08–2.27 (2.19, n = 3); costal ratio 0.29 (n = 3). **Genitalia** (fig. 3A): Sternite 9 M-shaped, connected medially. Spermatheca neck not expanded, not appressed against spermatheca.

Immatures. Unknown.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia lydiae* is known from western Costa Rica (localities 1, 2, 4, fig. 12A) and adults have been collected from Oct. 5 until Dec. 7. Adults were all collected with an aerial net in the vicinity of the very source or near the source of three springs at each of the collecting localities.

TAXONOMIC DISCUSSION: Males and females were associated by their shared presence of weak pigmentation of the thorax and collections from the same habitat (shared with *B. michaeli* and *B. christopheri*) at the spring in Atenas, Costa Rica (described more fully under *B. michaeli*).

TYPES: Holotype, male adult on microscope slide, labeled "HOLOTYPE Baeodasymyia lydiae Borkent, Atenas, C.R., 7-XII-1993, A. Borkent CD1697" (CNCI); allotype, female adult on microscope slide, labeled as for holotype but collected 5-X-1993 (CNCI); 3♂ 3♀ paratypes: 3♂ 1♀ from type locality, collected 7-X-1993, 2-XI-1993, 2-XII-1993; 1♀, 2 km NE Tarcoles, Costa Rica, 21-X-1993; 1♀, Manuel Antonio National Park, Costa Rica, 18-XI-1993 (CNCI, INBC).

DERIVATION OF SPECIFIC EPITHET: The name *lydiae* is proposed in appreciation of the senior author's daughter, Lydia, who as a 10 year old, spent hours looking for swimming *Baeodasymyia* larvae and would periodically shout out "Got another one!"

Baeodasymyia modesta
Clastrier and Raccurt
Figure 3B

Baeodasymyia modesta Clastrier and Raccurt, 1979: 100. Bois d'Eau, Haiti (MNHN, WLGC).

DIAGNOSIS: *Male adult*: only known *Baeodasymyia* with a more or less uniformly brown scutum (no discrete vittae) and a pale halter knob (as in fig. 1B but with halter pale). *Female adult*: only known *Baeodasymyia* with a more or less uniformly brown scutum (no discrete vittae), a pale halter knob (as in fig. 1B but with halter pale) and sclerite 9 divided medially. *Immatures*: unknown.

DESCRIPTION: *Male and female adults*. Adequately described by Clastrier and Raccurt (1979), with following additions:

Male adult. **Wing**: Length 0.42–0.45 mm (0.44, n = 5), costal ratio 0.29–0.30 (0.29, n = 5). **Genitalia** (as in fig. 2A): Aedeagus L/W 1.00–1.15 (1.07, n = 4).

Female adult. **Wing**: Length 0.41–0.46 mm (0.44, n = 8), wing length/width 1.97–2.16 (2.08, n = 8); costal ratio 0.28–0.30 (0.29, n = 8). **Genitalia** (fig. 3B): Sternite 9 separated medially, with each half truncated to slightly pointed. Spermatheca neck expanded, appressed against spermatheca.

Immatures. Unknown.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia modesta* is known from two adjacent localities in northern Haiti (fig. 12B). Wirth and Grogan (1988) reported *B. modesta* from Colombia but we were unable to locate this specimen. In the light of the further species described here, the identification of the Colombian specimen (if found) needs to be confirmed.

Clastrier and Raccurt (1979) noted that *Baeodasymyia modesta* adults were reared from mud taken from shady areas at the edge of a marsh and from a river margin. Adults reared from the mud collected from Bois d'Eau emerged the same day as the sample was taken, on Feb. 8, 1975, indicating that pupae must have been present in the original sample. The single male from Quartier Morin emerged on March 5, 1975 (Clastrier and Raccurt, 1979) from the mud sample taken on Feb. 9 (date on slide label).

TAXONOMIC DISCUSSION: Males and females were associated by their shared presence of the pigmentation patterns (as in fig. 1B but with halter pale) and having been reared from the same habitat.

Clastrier and Raccurt (1979; fig. 1E) showed female sternite 9 as medially fused but there is actually a small medial gap. These authors also mistakenly reported and illustrated the gonocoxite with a short, pointed basal apodeme; in fact these apodemes are medioventral extensions of tergite 9. Szadziewski and Grogan (1994) have already pointed out that the figure of the male antenna by Clastrier and Raccurt (1979) was inaccurate and reillustrated it.

MATERIAL EXAMINED: All type specimens were studied (MNHN, WLGC: 1♂ 1♀).

DERIVATION OF SPECIFIC EPITHET: The name *modesta* apparently refers to the small size of this species.

Baeodasymyia gustavoi Borkent,
new species
Figures 1E, 3C

DIAGNOSIS: *Male adult*: unknown. *Female adult*: only known *Baeodasymyia* with lateral sclerites of the thorax darkly pigmented, halter knob pale (fig. 1E) and sclerite 9 fused medially. *Immatures*: unknown.

DESCRIPTION: *Male adult*. Unknown.

Female adult. **Head**: Medium brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pale. **Thorax** (fig. 1E): Nearly entirely dark brown, with very anterior, anterolateral margin of scutum, medial portion of scutellum light brown or pale. Halter knob pale. **Wing**: Length 0.54–0.57 (0.56, n = 3), wing length/width 2.27–2.54 (2.38, n = 3), costal ratio 0.31–0.35 (0.33, n = 3). **Legs**: Femora, tibiae light or medium brown with apical 0.4 of tibiae pale, very slightly infuscated or as dark as rest of tibiae. **Genitalia** (fig. 3C): Sternite 9 M-shaped, connected medially. Spermatheca neck expanded, appressed against spermatheca.

Immatures. Unknown.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia gustavoi* is known from two closely approximated sites in Paraguay and Argentina (fig. 13A). The specimens were collected with a CDC light trap from both sides of the artificial lake produced by the Yacyreta dam

(Spinelli, personal commun.). Adults have been collected from Jan. 1 until March 14.

TAXONOMIC DISCUSSION: The female genitalia of *B. gustavoi* were partially crushed under coverslips and therefore could not be drawn in more detail.

TYPES: Holotype, female adult on microscope slide, labeled "HOLOTYPE Baeodasymyia gustavoi Borkent, PARAGUAY, Dept. Itapua, Aguapey, 17-I-1994, G. Spinelli" (MLPA); paratypes: 3♂ 2♀ labeled as for holotype (MLPA; CNCI); 1 from Misiones, Posadas, Argentina, 14-III-1994 (MLPA).

DERIVATION OF SPECIFIC EPITHET: The name *gustavoi* is proposed in recognition of the outstanding advances in the New World systematics of Ceratopogonidae made by our valued colleague Gustavo R. Spinelli.

Baeodasymyia dominicana
Szadziewski and Grogan
Figure 1F

Baeodasymyia dominicana Szadziewski and Grogan, 1994: 220. Dominican Republic. Miocene.

DIAGNOSIS: *Male*: only known *Baeodasymyia* with flagellomeres 10 and 11 apparently distinct (fused in other *Baeodasymyia*). *Female*: not distinguishable from other known *Baeodasymyia*. *Immatures*: unknown.

DESCRIPTION: *Male and female adults*. Adequately described by Szadziewski and Grogan (1994), with the following additions:

Male adult. **Head**: Medium brown, with very narrow pale band posterior to margin of ommatidia. Mouthparts pigmentation not visible. **Thorax** (fig. 1F): Entirely dark brown (pigmentation of katepisternum uncertain). Halter pigmentation not visible. **Legs**: Pigmentation not visible. **Genitalia**: Aedeagus present but details not clearly visible; apicolateral processes present but very short, apical seta not visible.

Immatures. Unknown.

DISTRIBUTION AND BIONOMICS: *Baeodasymyia dominicana* is known from a complete male and a few bits of a female in two separate pieces of Dominican amber. Although variably reported as Miocene, Oligocene and Eocene in age, Iturralde-Vincent and MacPhee (1996) provide reasonable evidence that this amber is 15–20 million years old (i.e. Miocene).

TAXONOMIC DISCUSSION: Males and females were associated because they are the only specimens of *Baeodasymyia* in Dominican amber. The female is represented only by an antenna and parts of a wing and hindleg. Considering the diversity in the extant fauna described here, it is conceivable that the male and female belong to different species.

Szadziewski and Grogan (1994) reported that the male had 11 flagellomeres while the key to genera and diagnosis above refer to 12. Their study counted the fused basal flagellomeres separately but did not do so for the more terminal flagellomeres. We consider the presence of a single whorl of elongate setae on flagellomeres beyond the first flagellomere as evidence of the presence of a flagellomere, regardless of whether it is fused or not and count them as such (and then report fusion).

The amber with the holotype male was ground down further to increase visibility. Unfortunately, much of the body contained gas, making viewing of pigmentation difficult. Szadziewski and Grogan (1994) noted that pigmentation of ceratopogonids in Dominican amber is well preserved, indicating that the uniform pigmentation reported here for *B. dominicana* likely reflects its original state.

MATERIAL EXAMINED: Holotype male mounted on microscope slide in Canada Balsam (AMNH) and paratype female in a loose piece of amber (USNM).

DERIVATION OF SPECIFIC EPITHET: The name *dominicana* refers the country of origin of these fossils.

DISCUSSION

When Clastrier and Raccurt (1979) first described *Baeodasymyia*, they indicated that the genus might be related to *Paradasyhelea* Macfie and *Baeohelea* on the basis of some shared features. Szadziewski and Grogan (1994), in the first cladistic analysis of *Baeodasymyia* provided good evidence that *Baeodasymyia* and *Baeohelea* were each monophyletic and sister taxa. Borkent (1995) supported these conclusions and further suggested that together, *Baeodasymyia* and *Baeohelea* represented an incompletely resolved but more basal lineage within the paraphyletic Ceratopogonini. Borkent (1995) also suggested that *Paradasyhelea* was close to *Culicoides* Latreille (details unresolved) as an earlier lineage, unrelated to *Baeodasymyia* + *Baeohelea*. The characters suggested by Clastrier and Raccurt (1979) indicating relationship with *Paradasyhelea* are either likely plesiomorphic (presence of sensilla coeloconica, small claws) or independently derived features related to their shared small size (reduced number of palpal segments, small mouthparts, loss of radial cells, short costa).

The following provides further phylogenetic analysis of the relationship between *Baeodasymyia* and *Baeohelea* and between the species within *Baeodasymyia*. The numbered character states are summarized in figure 13B.

1. Adult palpus with five segments (plesiomorphic); palpus with two segments (apomorphic).

This character state was adequately discussed by Szadziewski and Grogan (1994) and Borkent (1995: 97).

2. Male genitalia with parameres (plesiomorphic); genitalia lacking parameres (apomorphic).

This character state was adequately discussed by Szadziewski and Grogan (1994) and Borkent (1995: 97).

3. Foretibial spur present (plesiomorphic); spur absent (apomorphic).

Szadziewski and Grogan (1994) suggested that this feature was unique within the Ceratopogonidae and therefore apomorphic. Outgroup comparisons show that the feature is homoplastic within the Culicomorpha but a foretibial spur is present in most Chironomidae. Although the loss was considered unique within the Ceratopogonidae, members of *Dasyhelea* Kieffer also lack the spur, but this is almost certainly independently derived.

4. Spermatheca with neck arising in a more or less straight line with axis of spermatheca (plesiomorphic); spermatheca with neck at 90° angle to axis of spermatheca (apomorphic).

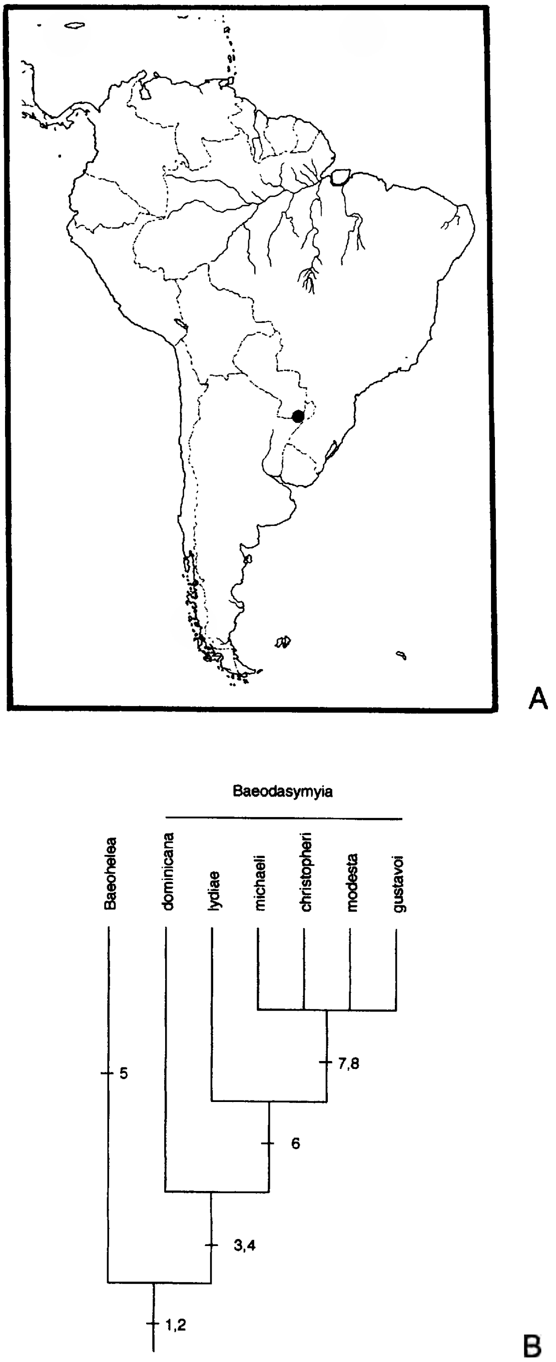

Fig. 13. **A.** Distribution of *Baeodasymyia gustavoi*. **B.** Phylogeny of *Baeohelea* and species of *Baeodasymyia*.

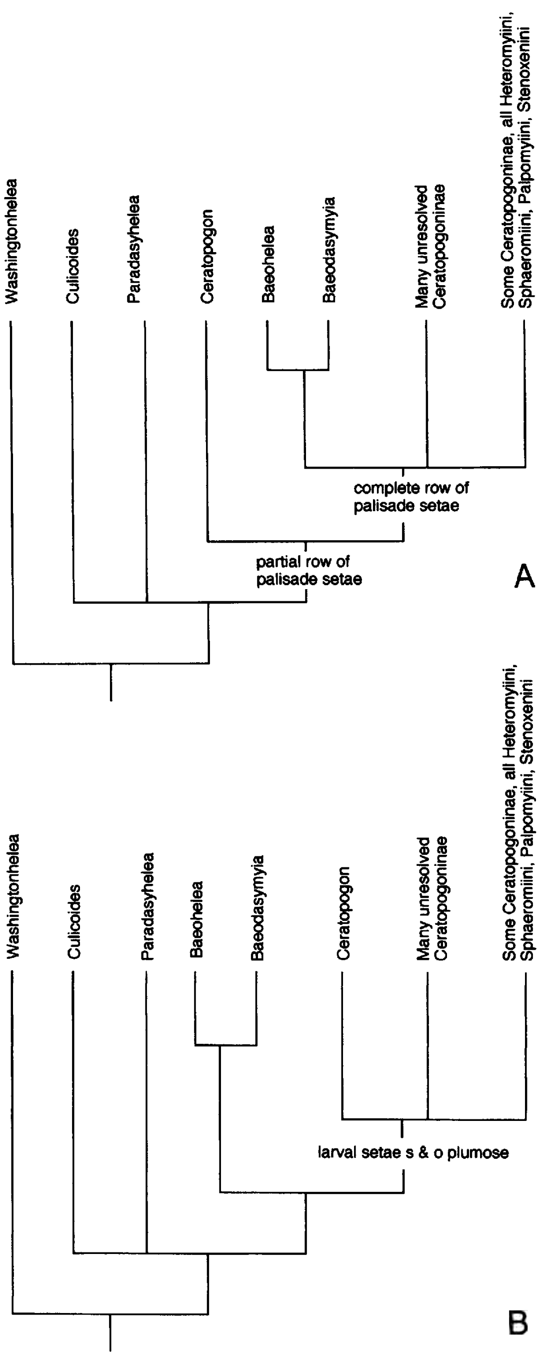

Fig. 14. **A.** Simplified phylogeny of the genera of Ceratopogoninae based on Borkent (1995). **B.** Simplified phylogeny of the genera of Ceratopogoninae showing implications of the simple larval head capsule setae character state.

This feature appears to be nearly unique within the Ceratopogonidae and at least the Culicomorpha. A few Ceratopogonidae have the neck somewhat angled from the axis of the spermatheca and a very few have the neck bent at 90° (e.g., *Washingtonhelea frommeri* Wirth and Grogan), which are almost certainly due to homoplasy.

5. Male antenna with more than six flagellomeres (plesiomorphic); antenna with six separate flagellomeres (apomorphic).

This character state was adequately discussed by Szadziewski and Grogan (1994).

6. Flagellomeres 11 and 12 separate or perhaps partially fused (plesiomorphic); flagellomeres 11 and 12 fused (apomorphic).

Nearly all male Ceratopogonidae have separate flagellomeres 11 and 12. Males of all extant *Baeodasymyia* have flagellomeres 11 and 12 fused as indicated by the presence of two whorls of elongate setae on the penultimate segment (these are referred to as flagellomeres 10 and 11 in descriptions because male *Baeodasymyia* have only 12 flagellomeres). The Miocene fossil *B. dominicana* has two separate or perhaps only partially fused flagellomeres and this suggests that *B. dominicana* may be the sister group of all extant *Baeodasymyia* (males of *B. gustavoi* are unknown). However, there is a possibility that the constriction at the midlength of the penultimate flagellomere in *B. dominicana* is an artifact of preservation and future fossil material should be studied in this regard. If further material of *B. dominicana* indicates that it too has flagellomere 11 and 12 fused, the partial fusion of flagellomeres might become a synapomorphy of *Baeohelea* + *Baeodasymyia* (with further fusion in *Baeohelea*; see character 5 above).

The Cretaceous species *Brachycretacea taimyrica* (Remm) is known from a single male in Siberian amber (Szadziewski, 1996). Flagellomeres 11 and 12 are fused in this species; however, because the antenna has only 9 flagellomeres, it cannot be certain that these flagellomeres are correctly identified. Nevertheless, the penultimate flagellomeres in males of both *Brachycretacea* Szadziewski and *Baeodasymyia* are elongate and with two whorls of elongate setae, indicating that these are composed of two fused flagellomeres. Remm (1976) originally placed *Brachycretacea taimyrica* in *Baeohelea* and the fused flagellomeres may therefore be a synapomorphy shared with *Baeohelea* + *Baeodasymyia*, a feature unique within the Ceratopogonidae. If so, the proportionally longer costa, and the presence of a radial cell would indicate that *Brachycretacea* is the sister group of *Baeohelea* + *Baeodasymyia* (with further reductions of the antenna in *Baeohelea*). Further study of *Brachycretacea taimyrica* is necessary to confirm these observations.

One difficulty with the above hypothesis is that the character state in *Baeohelea* is uncertain. The antenna has only six separate flagellomeres (the third with two whorls, indicating that this represents at least two flagellomeres) and the penultimate flagellomere has only a single whorl (suggesting either no fusion or fusion with a subsequent loss of one set of whorls).

7. Aedeagus with medial pigmentation (plesiomorphic); aedeagus with a narrow band of pigmentation (apomorphic).

The narrow band of pigmentation is found in a few other Ceratopogonidae (e.g., some *Stilobezzia* Kieffer) but is generally rare within the family. *Baeohelea nana* Wirth and Blanton males have the apical half of their aedeagus pigmented, similar to that of *B. lydiae*. Because males of *B. gustavoi* are unknown, the inclusion of this species in this clade is based on the following female feature.

8. Spermatheca neck slender (plesiomorphic); spermatheca neck enlarged (apomorphic).

The apomorphic condition is also present in a very few other Ceratopogonidae, in which the details of the enlargement appear different (e.g., *Washingtonhelea frommeri*).

Table 1

Presence (+) or Absence (−) of Plumose Setae (on head capsule of fourth instar larvae of Ceratopogonidae)

Genus	s	u	o
Leptoconops	−	−	−
Forcipomyia	+,−	−	−
Atrichopogon	−	−	−
Dasyhelea	−	−	−
Culicoides	−	−	−
Paradasyhelea	−	−	−
Ceratopogon	+	+	+
Baeodasymyia	−	−	−
Alluaudomyia	+	+	+
Brachypogon	+	+,?	+
Allohelea	+	?	+
Monohelea	+	?	+
Schizonyxhelea	+	+	?
Stilobezzia	+	+,?	+
Serromyia	−	−	−
Clinohelea	+	?	+
Pellucidomyia	+	?	+
Jenkinshelea	?	−	?
Mallochohelea	+,−	?	+
Nilobezzia	+	?	+
Probezzia	+,−	+,?	+
Sphaeromias	+	?	+
Macropeza	?	?	?
Lanatomyia	+	?	+
Bezzia	+	?	+
Palpomyia	+,−	−	+,−
Phaenobezzia	+	?	+

One feature conflicts with the relationships proposed above. Borkent (1995: 93) suggested that a medially divided sternite 9 in female Ceratopogonidae was a derived feature grouping the Ceratopogoninae (without *Washingtonhelea* Wirth and Grogan) but that reversals to the plesiomorphic condition were evident in some *Culicoides* and *Alluaudomyia* Kieffer. The discovery that some *Baeodasymyia* also have an undivided sternite 9 suggests a further instance of homoplasy. The reversal of this feature groups *B. michaeli*, *B. lydiae* and *B. gustavoi*, which conflicts with the evidence of the character states analyzed above (fig. 13B).

Two features present in pupae of the two known species of *Baeodasymyia* are probably derived. Because pupae of other species of *Baeodasymyia* and *Baeohelea* are unknown, it is not possible to determine which taxa these character states group. In addition, it is important to know that pupae are known for only 42 of a total of 102 extant genera of Ceratopogonidae (including undescribed pupa of *Schizonyxhelea* Clastrier in my collection), making conclusions regarding character state distribution somewhat uncertain. The two features are described as follows:

- Respiratory organ a single, undivided structure (plesiomorphic); respiratory organ with a distinct apical sclerite (fig. 3F, G) (apomorphic).

The respiratory organ of *B. michaeli* and *B. christopheri* appears to be unique within the Ceratopogonidae.

- Operculum without medial projection situated near dorsal margin (plesiomorphic); operculum with a well-developed medial projection situated near dorsal margin (fig. 3E) (apomorphic).

The pupae of nearly all genera of Ceratopogonidae lack a medial projection near the dorsal margin of the operculum. However, a very few species in both *Dasyhelea* and *Culicoides* appear to have a similar condition, indicating that the feature is susceptible to homoplasy (Jones, 1961; Waugh and Wirth, 1976).

There is further evidence concerning the phylogenetic position of *Baeohelea* + *Baeodasymyia* within the Ceratopogoninae. Borkent (1995) placed these sister groups, within the Ceratopogoninae as relatively unresolved lineages (fig. 14A). *Ceratopogon* Meigen was considered the sister group of most other Ceratopogoninae because many members of this genus have only a partially developed row of palisade setae (the row is secondarily lost in some species) while members of the sister group, including *Baeohelea* and *Baeodasymyia*, have a completely developed row. However, a newly discovered feature conflicts with the above conclusion. Borkent (in press) pointed out that early lineages of Ceratopogonidae, with the exception of a few *Forcipomyia* Meigen, have only simple setae on the larval head capsule and that the presence of plumose setae is therefore likely derived. Although generally stated as head capsule with or without plumose setae, only setae s, u and the most posterior of the o setae are plumose in some taxa. *Palpomyia basalis* (Walker) also has seta t plumose but it is mislabeled as seta z by Grogan and Wirth (1979). Specific details of the character state distribution are given in table 1. Seta s is plumose in most derived taxa but is simple in *Serromyia* Meigen (Borkent and Bissett, 1990), some *Mallochohelea* Wirth (Glukhova, 1979), some *Probezzia* Kieffer (Glukhova, 1979) and some *Palpomyia* Meigen (Grogan and Wirth, 1979); seta u is difficult to interpret because it is often not described in more derived lineages; and seta o is plumose in all derived lineages except for *Serromyia* and a few *Palpomyia.* This suggests that the plumose condition of seta s is derived with secondary reversals to the simple state in *Serromyia* and some *Mallochohelea*, *Probezzia* and *Palpomyia*; the condition in *Jenkinshelea* Macfie described as a single pore by Wirth nd Grogan (1979) may be a broken seta (otherwise it is unique). The plumose condition of seta u is derived but there is uncertainty about the state in many derived lineages (i.e. not reported). The plumose condition of the posteriormost seta o is also likely derived with only a few reversals in *Serromyia* and some *Palpomyia*; as is true for seta s, the condition in *Jenkinshelea* as a single pore reported by Wirth and Grogan (1979) is probably a broken seta. The larvae of *Baeodasymyia* have only simple setae and this suggests that *Baeodasymyia* + *Baeohelea* may be the sister group of all remaining Ceratopogoninae, excluding *Washingtonhelea*, *Culicoides* and *Paradasyhelea* (fig. 14B). In such a scenario, the palisade setae evolved once as a complete row, with reduction of the row in some *Ceratopogon* and *Macrurohelea* Ingram and Macfie. Further character states are required to resolve this conflict. Furthermore it should be kept in mind that the larvae of only 28 of 102 genera of Ceratopogonidae are known (including the undescribed larva of *Schizonyxhelea* in my collection).

The presence of three new species of *Baeodasymyia* in one spring in Costa Rica reflects our poor understanding of the fauna of these habitats in the tropics and elsewhere. As waters are diverted to serve human needs, such springs are disappearing or are badly polluted at an alarming rate, undoubtedly eliminating an interesting and endemic biota in many parts of the world.

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