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A revision of the Neotropical genus *Cacaohelea* Wirth & Grogan (Diptera: Ceratopogonidae)

Ревизия неотропического рода *Cacaohelea* Wirth & Grogan (Diptera: Ceratopogonidae)

Art Borkent[1] & Annia Picado[2]
Арт Боркент, Анния Пикадо

[1] Royal British Columbia Museum, American Museum of Natural History and Instituto Nacional de Biodiversidad. 691 — 8th Ave. SE, Salmon Arm, British Columbia, V1E 2C2, Canada. E-mail: aborkent@sunlite.ca

[2] Instituto Nacional de Biodiversidad, 400 Mts Oeste del Cementerio, A.P. 22-3100, Santo Domingo de Heredia, Costa Rica. E-mail: hpicado@inbio.ac.cr

KEY WORDS: *Cacaohelea*, new species, revision, male, Costa Rica, biting midges, phylogeny, cladistic analisys, aquatic.

КЛЮЧЕВЫЕ СЛОВА: *Cacaohelea*, новые виды, ревизия, самец, Коста-Рика, мокрецы, филогения, кладистический анализ, водный.

ABSTRACT. A redescription of the Costa Rican genus *Cacaohelea* Wirth & Grogan recognizes four species, three of which are new. *Cacaohelea glukhovae* **sp.n.** is described as both males and females, *C. adusta* **sp.n.** from a male, and *C. curva* **sp.n.** from a female. The female of the type species, *C. youngi* Wirth & Grogan, is redescribed. A key to the species is provided. An analysis of the phylogenetic position of the genus indicates that it is the sister group of *Parastilobezzia* Wirth & Blanton and that these two genera are the sister group of *Camptopterohelea* Wirth & Hubert plus the extinct genus *Eohelea* Petrunkevitch.

РЕЗЮМЕ. Выполнены переописание и ревизия рода *Cacaohelea* Wirth & Grogan, известного из Коста-Рики. Род включает четыре вида, три из которых описаны как новые. *Cacaohelea glukhovae* **sp.n.** описана по самцу и самке, *C. adusta* **sp.n.** — по самцу, *C. curva* **sp.n.** — по самке. Переописана самка типового вида, *C. youngi* Wirth & Grogan. Составлен ключ для определения видов. Анализ филогенетического положения рода *Cacaohelea* свидетельствует о том, что он является сестринской группой рода *Parastilobezzia* Wirth & Blanton, и что эти два рода являются сестринской группой другой ветви, состоящей из современного рода *Camptopterohelea* Wirth & Hubert и вымершего рода *Eohelea* Petrunkevitch.

RESUMEN: La redescripción del género de Costa Rica *Cacaohelea* Wirth & Grogan reconoce cuatro especies, tres de las cuales son nuevas. *Cacaohelea glukhovae* **sp.n.** se describe a partir de machos y hembras, *C. adusta* **sp.n.** a partir de un macho, y *C. curva* **sp.n.** a partir de una hembra. Se redescribe la hembra de la especie tipo, *C. youngi* Wirth & Grogan. Se provee una clave de especies. Un análisis de la posición filogenética del género indica que el mismo es el grupo hermano de *Parastilobezzia* Wirth & Blanton y que estos dos géneros son el grupo hermano de *Camptopterohelea* Wirth & Hubert sumado al género extinto *Eohelea* Petrunkevitch.

Introduction

Our exploration of the Costa Rican ceratopogonid fauna over the past 15 years has allowed us to study some rare and poorly known members of this family. The diminutive genus *Cacaohelea* Wirth & Grogan, 1988 is a case in point. This previously monotypic genus was known only from two Costa Rican females collected, as the name suggests, from flowers of cacao. In this paper we redescribe the genus and describe three new species, including the first males reported for the genus. Some character states allow for further hypotheses regarding the phylogenetic position of *Cacaohelea*.

Materials and methods

Specimens were examined, studied, measured and drawn using a Wild M3 dissecting microscope and a Zeiss Jenaval compound microscope. Photomicrographs were taken with a Nikon CoolPix 995 through a Zeiss Jenaval compound microscope.

All specimens were mounted on microscope slides using the technique described by Borkent & Spinelli [2007]. Terms for structures generally follow those in the Manual of Nearctic Diptera [McAlpine et al., 1981].

Terms for wing veins follow the same system, with modifications proposed by Szadziewski [1996] and summarized by Spinelli & Borkent [2004]. The length of female abdominal segment 8 is the distance from the base of sternite 8 to its apex (apex of one of the two lobes on either side of the oviduct opening). The width of the pale spermatheca was measured by its greatest width, perpendicular to an imaginary line extending from the duct to the apex of the spermatheca. Measurements are given as ranges generally followed by mean values.

Specimens are deposited in the following collections: CNCI — Canadian National Collection of Insects, Ottawa, Ontario, Canada; INBC — Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; USNM — U.S. Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. Material housed at INBC has labels including Lambert numbers and lot numbers (number of a given sample).

Phylogenetic methods are cladistic but follow the approach presented by Borkent [1984].

Descriptions of taxa

Genus *Cacaohelea* Wirth & Grogan

Cacaohelea Wirth & Grogan, 1988: 33.

Type species: *Cacaohelea youngi* Wirth & Grogan, 1988, by original designation.

DIAGNOSIS. Male: the only genus of Ceratopogonidae with the following combination of features: antenna female-like (Figs 2A–B), with flagellomeres 9–13 longer than flagellomeres 1–8 and without plume, wing (Fig. 1A) plain (without distinctive pigmentation), costal ratio 0.72–0.76, with two radial cells, the first radial cell small, nearly oval and the second radial cell elongate, M petiolate, forking well beyond r-m, hind first tarsomere with one row of palisade setae parallel to a second row of strong setae extending about half-length of tarsomere, and with large, well-developed cerci extending beyond apex of tergite 9 (Figs 2E–F).

Female: the only genus of Ceratopogonidae with the wing with a single darkened, nearly circular patch of elongate macrotrichia covering most of cell r_3 and situated distal to r-m and nearly abutting CuA_1 (Fig. 1B).

DESCRIPTION. **Male**. Head: Uniformly light to medium brown. Ommatidia separated dorsomedially (by distance equal to diameter of about 3 ommatidia), with interommatidial macrotrichia. With a single vertex seta. Antenna (Figs 2A–B) female-like (including scape and pedicel), without plume, with 13 separate flagellomeres; flagellomeres 1, 9–13 more elongate than flagellomeres 2–8; all flagellomeres without sensilla coeloconica. Mouthparts short. Mandible and lacinia simple. Palpus (as in Fig. 2D) with 5 segments, each short, segment 3 with about 8–10 capitate sensilla grouped in a shallow pit. Thorax: Uniformly light to medium brown. With three anterior pronotal apodemes. Scutum with elongate setae. Scutellum rounded in dorsal view. Ventral portion of anapleural cleft broad. Anapleural suture short. Wing (Fig. 1A): Uniformly infuscated, dark grey. Membrane without macrotrichia, with abundant moderately elongate microtrichia. Alula without fringe of macrotrichia. Costa extending, at most, slightly beyond apex of R_3; costal ratio 0.72–0.76. Two radial cells present. First radial cell small, nearly oval. Second radial cell broad, elongate. R_3 and r-m thick. r-m oblique to R_1. M bifurcating distal to r-m, base of M_2 poorly defined. Halter light brown. Legs: Uniformly yellowish or light brown, lacking armature. Femora and tibiae slender. Fore- and midleg trochanter with a pair of thick setae. Fore tibia with apical spur. Midleg tibia without apical spur. Apex of hind tibia with two rows of spines and a spur. First tarsomere of hind leg without basal spine, with one row of palisade setae and a parallel row of thick setae extending about half-length of tarsomere. Fourth tarsomeres slightly cordiform. Claws on fore-, mid-, and hind legs equal in size, equal on each leg, apically bifid. Empodium absent. Abdomen (Figs 1C–D) uniformly light brown or with segments 1–8 pale, the genitalia dark brown.

Genitalia (Figs 2E–F): Tergite 9 well developed, sternite 9 as a narrow transverse band, concave. Apicolateral process absent. Gonocoxite moderately elongate, dorsomedial margin with a short subbasal, medially directed apodeme. Gonostylus moderately elongate, apical spine absent. Parameres separate, each elongate, with bifid base, tapering distally to pointed apex, subapically bent ventrolaterally. Aedeagus very pale, difficult to discern, not articulated basally, without basal arms or arch, apparently attached by membrane to remainder of genitalia, apically either shallowly bifid or so poorly defined as to be uncertain. Cercus large, laterally compressed, directed posteriorly beyond margin of tergite 9.

Female as for male, except as follows. Head: Clypeus separated from margin of eye by membrane. Mandible with 7–8 large teeth. Lacinia slender, without apical teeth or spicules. Wing (Fig. 1B): infuscated but with single, darker, nearly circular patch of elongate macrotrichia covering most of r_3, situated distal to r-m, nearly abutting CuA_1; M_1 and M_2 barely discernable; costal ratio 0.71–0.75. Legs: first tarsomere of hind leg with a row of palisade setae and parallel row of thick setae. Single, short claw on each leg, equal or nearly equal in size, each claw with small subbasal tooth. Abdomen (Figs 1E–G): segments 1–7 pale (or just sternite 7 light brown), segments 8–10 medium brown; sternite 7 forming a narrow band.

Genitalia (Figs 2G–I): Tergite and sternite 8 fused, forming a single, tapering unit; tergite 8 shorter than sternite 8. Posterior margin of sternite 8 bilobed. Tergite 9 well developed. Sternite 9 with each half well-developed, thick, tapering medially, fused medially with enlarged, heavily sclerotized medial portion (possibly part of anterior margin of opening of oviduct). Segment 10 with 2–4 pairs of subbasal short setae and a subapical pair of elongate setae. Cercus moderately elongate. Two large spermathecae, both with well-developed tube-like necks; largest one spherical, dark with clear spots; smaller one nearly or entirely spherical, pale; third spermatheca very reduced, pale or lightly pigmented. Segment 8 with internal sclerotization well-developed or barely discernable.

Larva and pupa unknown.

Egg elongate, length/width = 7.3–8.6 (n = 2); no obvious sculpturing of surface (known only for *C. youngi*).

DISTRIBUTION AND BIONOMICS. The four included species are known only from the eastern lowlands of Costa Rica (Figs 3A–B). The types of *C. youngi* were collected from the flowers of cacao. All but one of the other specimens of *Cacaohelea* were collected with light traps. The single remaining specimen, of *C. adusta*, was collected with a sweep net. Adults of this genus have been collected from 50(possibly 20)–300 metre in elevation in wet lowland tropical rainforests.

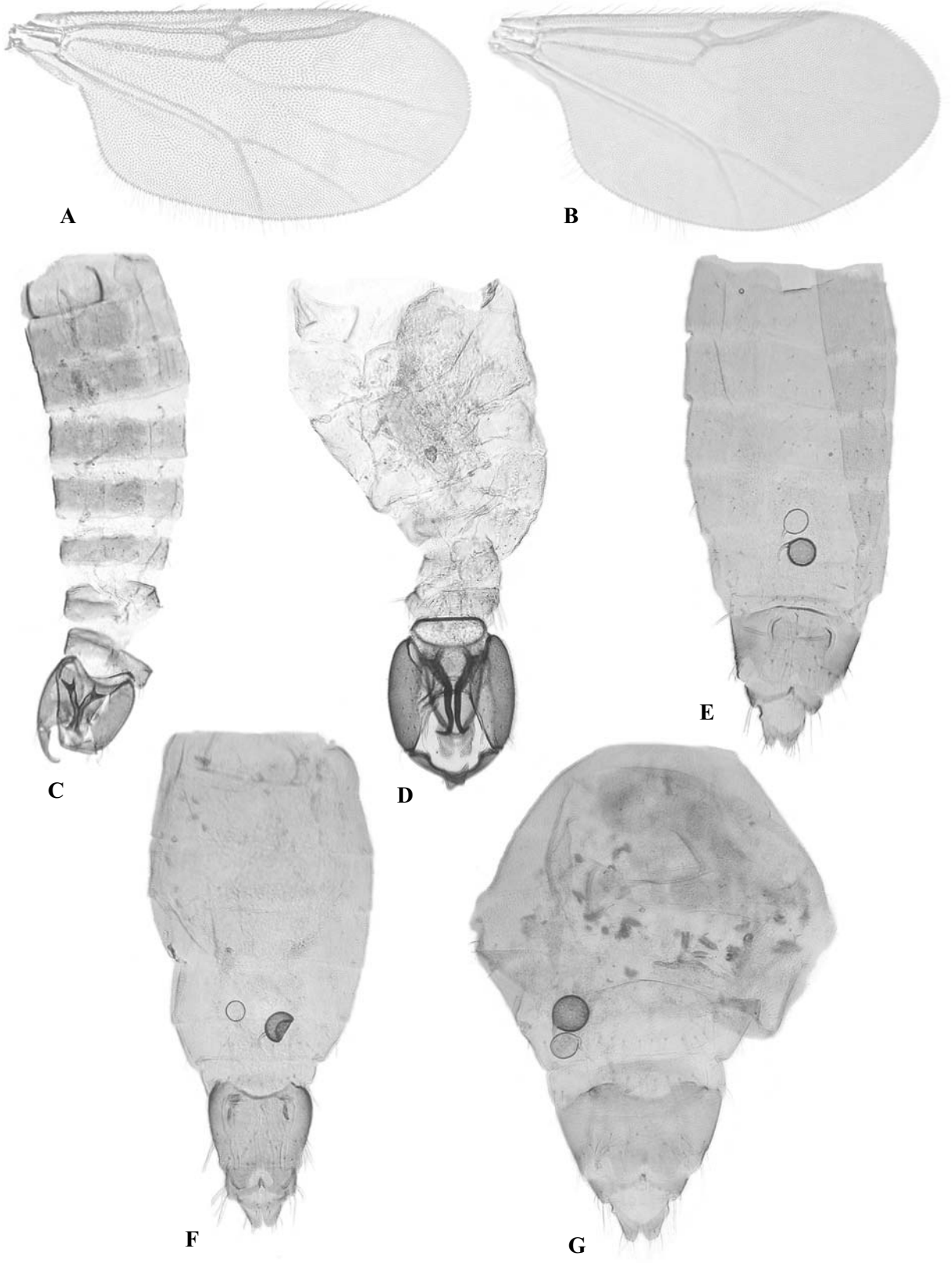

Fig. 1. Structures of adult *Cacaohelea*: A–B, D–E — *C. glukhovae*; C — *C. adusta*; F — *C. youngi*; G — *C. curva*; A–B — wing; C–G — abdomen, in ventral view; A, C–D — males; B, E–G — females.

Рис. 1. Детали строения имаго *Cacaohelea*: A–B, D–E — *C. glukhovae*; C — *C. adusta*; F — *C. youngi*; G — *C. curva*; A–B — крыло; C–G — брюшко, снизу; A, C–D — самцы; B, E–G — самки.

Although the two females composing the type series of *C. youngi* were collected from cacao flowers, all other specimens of *Cacaohelea* reported here were from habitats devoid of cacao, a plant introduced to Costa Rica. Therefore, it is likely that the adults of at least *C. youngi* also imbibe nectar from other, native plants and that their association with cacao was opportunistic.

The coarsely toothed mandibles and simple laciniae (without teeth) of all female *Cacaohelea* indicate that they likely feed on hemolymph of other invertebrates of nearly equal size [Borkent, 1995, 2000]. In addition, females have a single claw on each leg, a feature also restricted to female predaceous ceratopogonids that feed on insects of similar size.

TAXONOMIC NOTES. *Cacaohelea* was previously monotypic but now includes four species. Because all species have been collected in Costa Rica at low elevations, it seems likely that more species await discovery in at least Central and South America. The genus was keyed to the generic level in Borkent et al. [in press] for the Central American Region and in Borkent & Spinelli [2007] for the Neotropical Region. The illustration of the male genitalia in both publications was that of *C. glukhovae*.

Wirth & Grogan [1988] noted in their description of the female of this genus that abdominal sternite 9 was inconspicuous (their "genital lobes"), but in fact they are well-developed. In addition, they reported the presence of only one spermatheca because the pale second spermatheca was missed.

Cacaohelea adusta Borkent & Picado, **sp.n.**
Figs 1C, 2A, 2E, 3A

TYPE MATERIAL. Holotype: ♂ — adult on microscope slide, labelled "HOLOTYPE *Cacaohelea adusta*, Borkent and Picado", "Costa Rica, Prov. Cartago, Turrialba, P.N. Barbilla. Send. El Felino. 300 m. 17 ABR 2001, E. Rojas. Red de Golpe, LN217500 596893 #62196" (INBC).

DIAGNOSIS. Male: the only species of *Cacaohelea* with apex of gonostylus slender and tapering; also, the only species with tergites 1–9 uniformly medium brown (males of only two species known). Female unknown.

DESCRIPTION. **Male**. Head light brown. Antenna with flagellomeres as in Fig. 2A; antennal ratio 0.50 (n = 1). Thorax medium brown. Wing: length 0.58 mm (n = 1), costal ratio 0.72 (n = 1). Abdomen (Fig. 1C) with all tergites and the genitalia medium brown.

Genitalia (Fig. 2E) about as wide as preceding segments. Tergite 9 tapering distally from base to narrow, truncated apex. Gonocoxite 2.7 times as long as its greatest width, with small, slender apodeme on dorsomedial surface situated about 0.7 of total length from base of gonocoxite; gonostylus about 0.5 times as long as gonocoxite, thick basally, with apical third slender and curved. Aedeagus small, light brown, nearly evenly broad; its apex poorly defined, shape uncertain.

Female unknown.

TAXONOMIC NOTES. The male of *C. adusta* **sp.n.** differs from that of *C. glukhovae* **sp.n.** in having a uniformly darkly pigmented abdomen (among other differences). The male of *C. glukhovae* **sp.n.** and the females of the other three species of *Cacaohelea* all have pale basal abdominal segments and contrasting dark genitalia. Therefore, unless there is sexual dimorphism in *C. adusta* **sp.n.**, the presently unknown female will be distinguished from other *Cacaohelea* by a uniformly brown abdomen.

DISTRIBUTION AND BIONOMICS. *Cacaohelea adusta* **sp.n.** is known only from the type locality in eastern Costa Rica (Fig. 3A) at an elevation of 300 metres. The holotype was collected with a sweep net in an area of very wet lowland rainforest.

ETYMOLOGY. The species name *adusta* ("tanned" in Latin) refers to the distinctive uniformly medium brown abdomen of the male of this species.

Cacaohelea curva Borkent & Picado, **sp.n.**
Figs 1G, 2H, 3B

TYPE MATERIAL. Holotype: ♀ — adult on microscope slide, labelled "*Cacaohelea curva*, Borkent and Picado", "Costa Rica, Prov. Alajuela, San Carlos, Pital, Boca Tapada, Finca de Sergio Murillo, 50−100 m. 21 JUL, 2004, B. Hernández. Tp. Luz/Balde, LN293857 514072 #77932" (INBC).

DIAGNOSIS. Female: the only species of *Cacaohelea* with abdominal segment 8 length/width about 0.6 and anterior margin of abdominal sternite 8 concave. Male unknown.

DESCRIPTION. **Female**. Head light brown. Antennal ratio 0.99 (n = 1). Palpus: ratio of segments 4/5 = 0.47 (n = 1). Thorax light brown. Wing: length 0.82 mm (n = 1), costal ratio 0.75 (n = 1). Abdomen (Fig. 1G) with entire segments 1–6 and tergite 7 pale, sternite 7 light brown, segment 8 medium brown with darker lateral margins, and segments 9–10 medium brown.

Genitalia (Fig. 2H): Anterior margin of sternite 8 concave, with sublateral thicker bend. Segment 8 length/width = 0.64. Diameter of dark spermatheca / width of pale spermatheca = 1.39. Segment 8 with sclerotized internal structure barely discernable (under phase contrast, with light lateral striae).

Male unknown.

TAXONOMIC NOTES. As discussed under *C. glukhovae* **sp.n.**, it is possible that the female of *C. curva* **sp.n.** is actually conspecific with one or more male specimens described as *C. glukhovae* **sp.n.**.

DISTRIBUTION AND BIONOMICS. *Cacaohelea curva* **sp.n.** is known only from a single female from northern Costa Rica (Fig. 3B) collected at an elevation of 50–100 metres. It was collected with a mercury vapour light placed over a pan of soapy water in an area of primary and very wet lowland forest. There were no cacao in the area [B. Hernández, personal communication].

ETYMOLOGY. The name *curva* ("curved" or "bent" in Latin) refers to the distinctive concavity on the anterior margin of sternite 8 of the female of this species.

Cacaohelea glukhovae Borkent & Picado, **sp.n.**
Figs 1A–B, D–E, 2B–D, 2F, 2G, 3A

TYPE MATERIAL. Holotype: ♂ — adult on microscope slide, labelled "HOLOTYPE *Cacaohelea glukhovae*, Borkent and Picado", "Costa Rica, Prov. Alajuela, San Carlos, Pital, Boca Tapada, Finca de Sergio Murillo, 50−100 m. 21 JUL, 2004, B. Hernández. Tp. Luz/Balde, LN293857 514072 #77932" (INBC). Paratypes: 3 ♂♂, 3 ♀♀ — adults on microscope slides, with same data as holotype (2 ♂♂, 2 ♀♀, INBC [1 ♀ designated as allotype]; 1 ♂, 1 ♀, CNCI); 2 ♀♀ — adults on microscope slides, labelled "Costa Rica, Prov. Heredia, R.V.S. Corredor Fronterizo C.R.−Nicaragua, Lagunas a la par de rio San Juan, 20−50 m, 16 SET, 2004, B. Hernández, Tp. Luz. LN306850 519443 #78168" (INBC).

DIAGNOSIS. Male: the only species of *Cacaohelea* with apex of gonostylus expanded distally and sharply bent medially (males of only two species known). Female: the only species of *Cacaohelea* with anterior margin of abdominal sternite 8 straight or slightly convex anteriorly.

DESCRIPTION. **Male**. Head light brown. Antenna with flagellomeres as in Fig. 2B; antennal ratio 0.54–0.60 (n = 2). Thorax light brown. Wing (Fig. 1A): length 0.45–0.49 mm (0.47 mm, n = 4), costal ratio 0.74–0.76 (0.75, n = 4). Abdomen (Fig. 1D) with segments 1–7 pale, segment 8 light

brown, and the genitalia dark brown.

Genitalia (Fig. 2F) significantly wider than preceding segments. Tergite 9 tapering from base to narrow, truncated apex. Gonocoxite 2.5 times as long as its greatest width, with slender apodeme on dorsomedial surface situated about 0.35 of total length from base of gonocoxite; gonostylus about 0.6 times as long as gonocoxite, straight in basal three-fourths, sharply curved in apical fourth and expanded subapically, with pointed apex. Aedeagus small, pale, difficult to discern, broad at base, tapering to U-shaped, bifid apex.

Female. Antenna with flagellomeres as in Fig. 2C; antennal ratio 0.94–1.02 (0.98, n = 5). Palpus (Fig. 2D): ratio of segments 4/5 = 0.67–0.82 (0.74, n = 5). Wing (Fig. 1B): length 0.80–0.83 mm (0.81 mm, n = 5), costal ratio 0.71–0.74 (0.72,

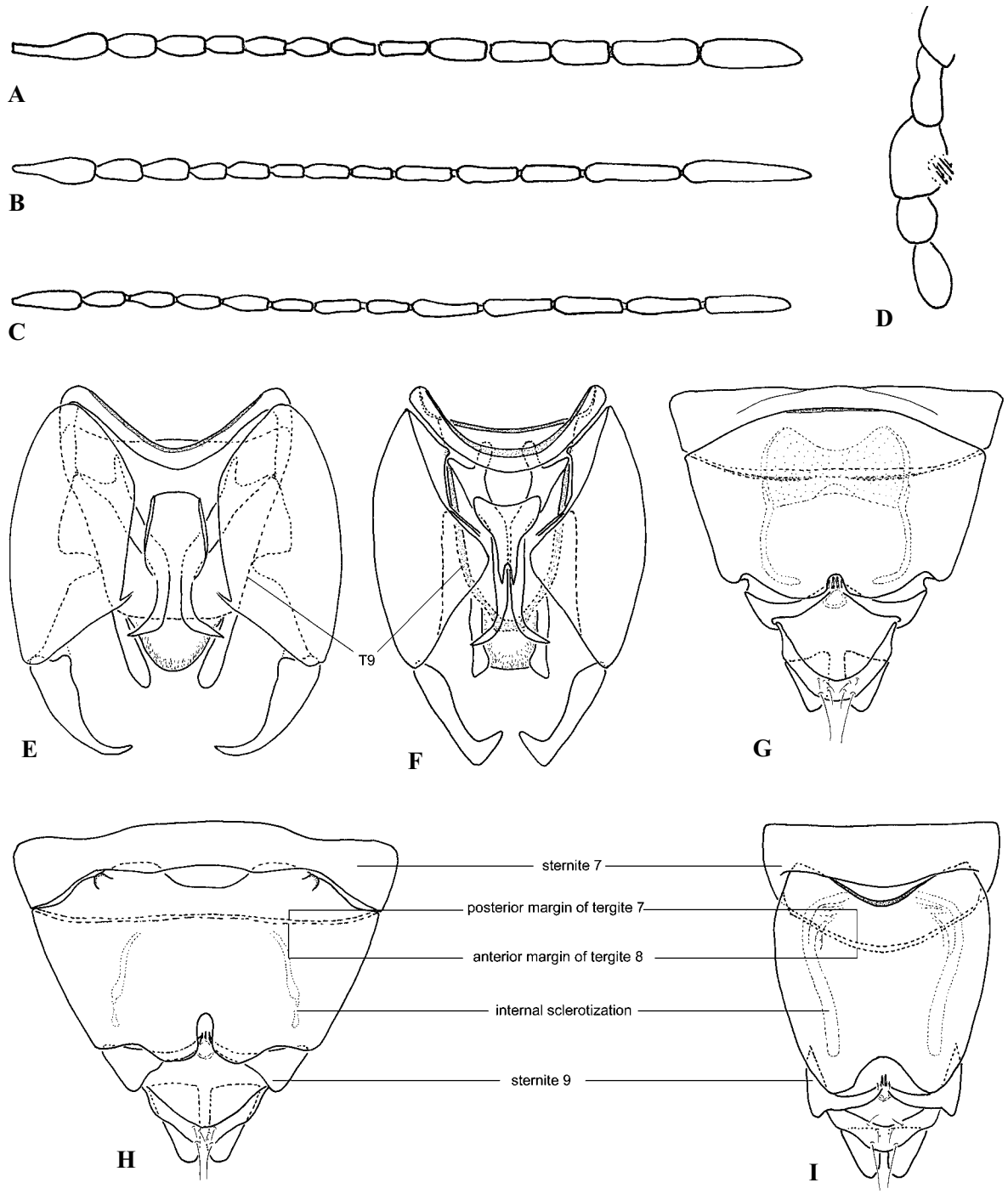

Fig. 2. Structures of adult *Cacaohelea*: A, E — *C. adusta* **sp.n.**; B–D, F–G — *C. glukhovae* **sp.n.**; H — *C. curva* **sp.n.**; I — *C. youngi*; A–C — antenna; D — right palpus; E–I — genitalia, in ventral view; A–B, E–F — males; C–D, G–I — females; T9 — tergite 9.

Рис. 2. Детали строения имаго *Cacaohelea*: A, E — *C. adusta* **sp.n.**; B–D, F–G — *C. glukhovae* **sp.n.**; H — *C. curva* **sp.n.**; I — *C. youngi*; A–C — антенна; D — правый щупик; E–I — гениталии, снизу; A–B, E–F — самцы; C–D, G–I — самки; T9 — 9-й тергит.

n = 5). Abdomen (Fig. 1E) with entire segments 1–6 and tergite 7 pale, sternite 7 light brown, segment 8 medium brown with darker lateral margins, and segments 9–10 medium brown.

Genitalia (Fig. 2G): Anterior margin of sternite 8 straight or convex. Segment 8 length/width = 0.64–0.75 (0.68, n = 5). Diameter of dark spermatheca / width of pale spermatheca = 1.14–1.24 (1.18, n = 5). Segment 8 with sclerotized internal structure nearly quadrate in general outline, somewhat bilobed anteriorly.

TAXONOMIC NOTES. All four males and three of the five females were collected at the same place and time at Pital, July 21, 2004, suggesting that they are correctly associated. The two females from the province of Heredia appeared inseparable from those of the other females. The

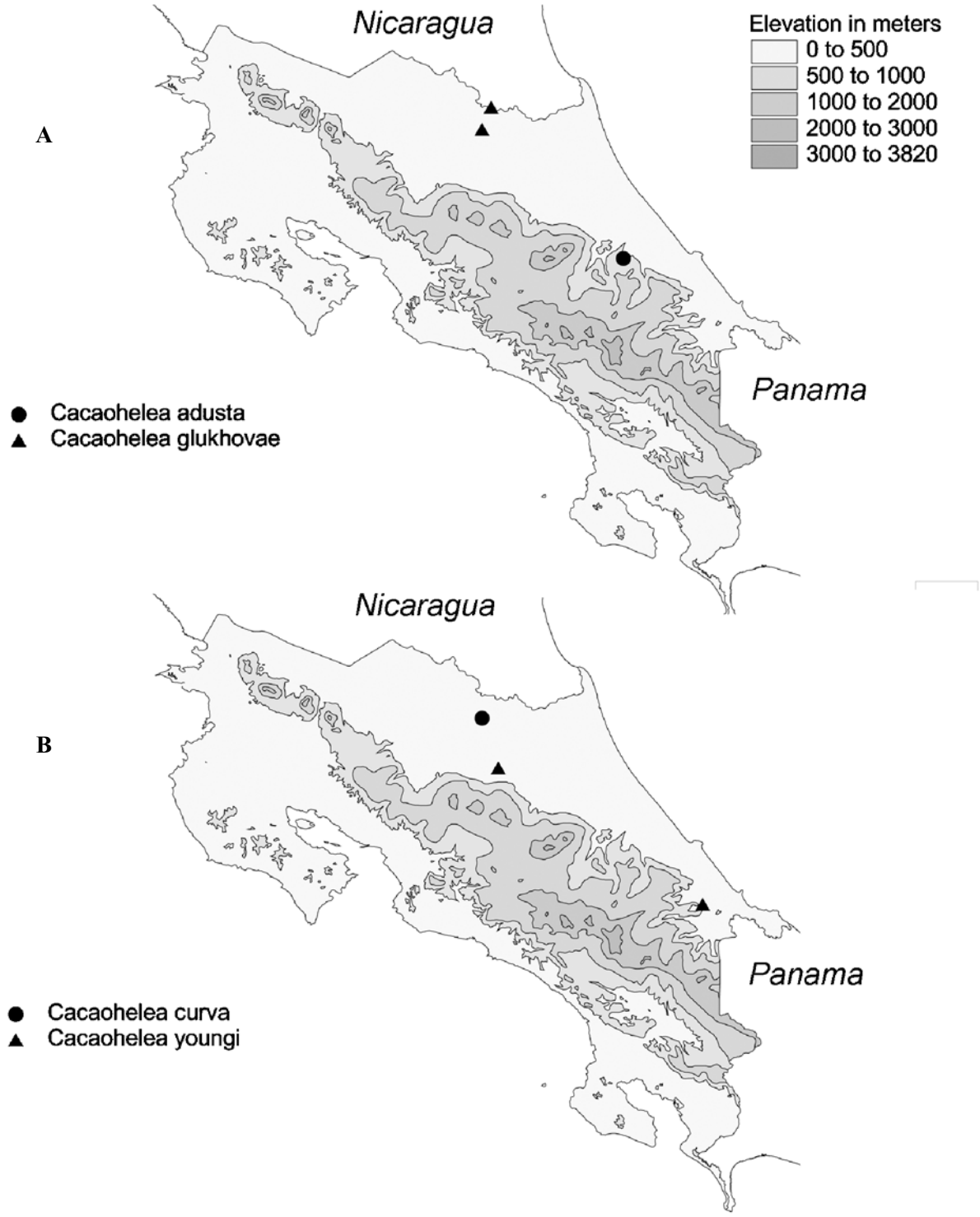

Fig. 3. Known distribution of species of *Cacaohelea*.
Рис. 3. География известных к настоящему времени находок *Cacaohelea*.

holotype female of *C. curva* **sp.n.** was also collected at Pital on July 21, 2004 with some of the types of *C. glukhovae* **sp.n.**, and it is possible that it is conspecific with one or more of the males described here as *C. glukhovae* **sp.n.**

The male genitalia of *C. glukhovae* **sp.n.** were illustrated in Borkent & Spinelli [2007] and in Borkent et al. [in press] but were redrawn here to include some more recently discovered features and to make it more comparable to that of *C. adusta* **sp.n.** The aedeagus of *C. glukhovae* **sp.n.** was very difficult to see and not identifiable in one paratype. It was in a different position in the holotype and in two paratypes, suggesting that it is loosely attached, at least after being cleared in KOH.

DISTRIBUTION AND BIONOMICS. *Cacaohelea glukhovae* **sp.n.** is known only from northern Costa Rica (Fig. 3A) at elevations of about 20–100 metres (labels gave 20–50 or 50–100 m). Specimens were collected with light traps. The specimens from Pital were sampled with a mercury vapour light placed over a pan of soapy water in an area of primary and very wet lowland forest. There were no cacao trees in either of the two areas sampled [B. Hernández & D. Solano, personal communication].

ETYMOLOGY. The species name *glukhovae* is proposed in honour of the life and work of Valentina M. Glukhova. During her lifetime she made tremendous improvements to our understanding of the systematics and bionomics of Ceratopogonidae, including the groundwork for interpreting the larvae of this diverse family.

Cacaohelea youngi Wirth & Grogan
Figs 1F, 2I, 3B

Cacaohelea youngi Wirth & Grogan, 1988: 34.

MATERIAL EXAMINED. Holotype: ♀— adult on microscope slide, labelled "HOLOTYPE, *Cacaohelea youngi* Wirth & Grogan, Costa Rica, Heredia Prov. nr. La Virgen, Finca La Tigra, 84°70'N 10°24'W, 5 MAR, 1982, 8 AM, A.M. Young, in cacao flower, 69" (USNM). 1 ♀ — adult on microscope slide, labelled "Costa Rica, Prov. Limón, R.B. Hitoy Cerere, 120 m, 20−21 OCT, 2004. B. Gamboa, D. Briceño, M. Moraga, Y. Cárdenas. Tp. Luz de Mercurio / Balda, N184120 643471 #78506" (INBC).

DIAGNOSIS. Female: the only species of *Cacaohelea* with elongate abdominal segment 8, with length/width ratio about 1.0. Male unknown.

DESCRIPTION. **Female**. Head light brown. Antennal ratio 0.98–1.06 (n = 2). Palpus: ratio of segments 4/5 = 0.73–0.80 (n = 2). Thorax light brown. Wing: length 0.80–0.91 mm (n = 2), costal ratio 0.72–0.73 (n = 2). Abdomen (Fig. 1F) with segments 1–7 pale and segments 8–10 medium brown.

Genitalia (Fig. 2I): Anterior margin of sternite 8 concave. Segment 8 length/width = 1.01–1.06 (n = 2). Diameter of dark spermatheca / width of pale spermatheca = 1.56–1.73 (n = 2). Segment 8 with elongate sclerotized internal structure paired, each half near lateral margin of segment, with anterior portion with darker pigmentation.

Male unknown.

Egg as described above for the genus.

TAXONOMIC NOTES. Wirth & Grogan [1988] have noted the type locality at Finca La Tigra, Heredia, Costa Rica to be at 10°24'N 84°70'W, but this farm is actually located at 10°24'N 84°07'W. Similarly, the label on the holotype mistakenly reads "84°70'N 10°24'W". We were unable to examine the single paratype female of *C. youngi* because it could not be located in the USNM [T. Gaffigan, personal communication].

Wirth & Grogan [1988] have noted that the female abdomen was "yellowish brown", but reexamination of the holotype indicates that segments 1–7 are pale, contrasting with the medium brown genitalia.

DISTRIBUTION AND BIONOMICS. *Cacaohelea youngi* is known only from the type series (holotype and paratype, both females) and an additional female from southeastern Costa Rica (Fig. 3B) collected at elevations of 120–185 metres. Although the two females in the type series were collected from cacao flowers, the third specimen from Hitoy Cerere was collected with a mercury vapour light placed over a pan of soapy water in an area of very wet lowland forest, with no cacao trees nearby.

ETYMOLOGY. The species name *youngi* was given in recognition of the contributions of the collector, Allen M. Young.

KEY TO ADULT *CACAOHELEA*

1 Male (those of *C. youngi* and *C. curva* **sp.n.** unknown) 2
— Female (that of *C. adusta* **sp.n.** unknown) 3
2 Abdominal tergites and the genitalia uniformly medium brown (Fig. 1C); gonostylus tapering from base to curved, pointed apex (Fig. 2E) ..... *C. adusta* **sp.n.**
— Abdominal tergites 1–7 pale, tergite 8 light brown and the genitalia dark brown (Fig. 1D); gonostylus swollen for most of length and sharply bent subapically (Fig. 2F) .. .. *C. glukhovae* **sp.n.**
3 Abdominal segment 8 elongate, its length/width ratio 1.01–1.06; internal sclerotization of segment 8 forming a pair of lateral bands, each close to its lateral margin (Fig. 2I); dark spermatheca 1.56–1.73 times as large in diameter as pale spermatheca (Fig. 1F) ..... *C. youngi*
— Abdominal segment 8 squatter, its length/width ratio 0.64–0.75; internal sclerotization of segment 8, if present, forming a central structure, anteriorly somewhat bilobed and with lateral margins more distant from lateral margins of segment (Figs 2G, 2H); dark spermatheca 1.13–1.39 times as large in diameter as width of pale spermatheca (Figs 1E, 1G) 4
4 Anterior margin of abdominal sternite 8 concave (Fig. 2H); internal sclerotized structure barely discernable; palpal segments 4/5 ratio 0.47; dark spermatheca 1.39 times as large in diameter as width of pale spermatheca (Fig. 1G) ..... *C. curva* **sp.n.**
— Anterior margin of abdominal sternite 8 straight or convex (Fig. 2G); segment 8 with internal structure; palpal segments 4/5 ratio 0.66–0.82 (Fig. 2D); dark spermatheca 1.13–1.24 times as large in diameter as width of pale spermatheca (Fig. 1E) ..... *C. glukhovae* **sp.n.**

Phylogenetic interpretation

The genus *Cacaohelea* belongs to the tribe Ceratopogonini, a group which is paraphyletic [Borkent, 1995]. The phylogenetic relationships between most of the 58 extant and 11 extinct genera in this tribe are poorly understood, and there is a great need for comparative morphological study and cladistic interpretation of this group. In this section we provide evidence of the cladistic relationships between *Cacaohelea* and other genera of Ceratopogonidae, as well as relationships between the species of *Cacaohelea*.

Borkent [1995] demonstrated that some Ceratopogonini are more closely related to the tribes Heteromyiini, Sphaeromiini, Palpomyiini and Stenoxenini than they are to other Ceratopogonini. Some Ceratopogonini have females in which the clypeus is fused to the lateral

margins of the eyes, a feature shared with the aforementioned tribes, and these were interpreted by Borkent et al. [2008]. Another, more inclusive synapomorphy described by Borkent [1995] (as his character 42) groups some further genera of Ceratopogonini, now including *Cacaohelea*, with the above-noted taxa (Fig. 4). The following provides evidence for the relationships between the taxa of Ceratopogonidae considered herein. Numbers below refer to synapomorphies depicted in Fig. 4.

1. Male adult cerci small, located ventrally on membranous patch which is itself ventral to tergite 9 (plesiomorphic); male cerci large, laterally compressed, directed posteriorly beyond margin of tergite 9 (apomorphic).

Although the derived condition is unique within the Culicomorpha, this feature is somewhat difficult to interpret because the plesiomorphic and apomorphic conditions do not appear to be entirely discrete. It may be that there are further intermediate states which need to be better defined, and some taxa examined may have secondarily reduced cerci. In addition, some taxa have very modified male genitalia and this can make them difficult to interpret. Regardless, nearly all Heteromyiini, Sphaeromiini, Palpomyiini and Stenoxenini have the derived condition; only *Dibezzia* Kieffer, 1911 and *Mackerrasomyia* Debenham, 1970, both with modified ninth tergite, have smaller, more ventral cerci, even though these are still laterally placed. The newly described males of *Cacaohelea* were discovered to have large, extended cerci, placing this genus in the group with the apomorphic state. The study of male *Allohelea* Kieffer, 1917 indicates that they also exhibit the derived condition.

Males of *Eohelea* Petrunkevitch, 1957 were not examined but Szadziewski [1988: 166] illustrated the male of *E. gedanica* Szadziewski, 1988 with well-developed projecting cerci. Only a single male of *Camptopterohelea* Wirth & Hubert, 1960 is known (*C. admirabilis* Das Gupta & Sarkar, 1982), and its genitalia are in need of further study. The male of *Metacanthohelea cogani* Wirth & Grogan, 1988 was also not examined but was hypothesized to be the sister group of *Serromyia* Meigen, 1818 by Borkent & Bissett [1990].

The type series of *Parastilobezzia leei* Wirth & Blanton, 1970 includes the only known male of this genus. Although it is said to be deposited in the USNM [Wirth & Blanton, 1970], it cannot be located there now [Tom Gaffigan, personal communication]. The drawing of the male genitalia of this species by Wirth & Grogan [1988], however, shows large, posteriorly directed cerci.

All species with the derived condition lack apicolateral processes, and this is likely related to the elongate cerci. However, the presence or absence of apicolateral processes is otherwise variable in other, more basal Ceratopogonidae.

2. Male hind leg claws equal, short (plesiomorphic); hind leg with single, elongate claw (apomorphic).

The males of all other families of nematocerous Diptera have a pair of small, equal claws on their hind legs. Within the Ceratopogonidae, the apomorphic condition is restricted to all male *Allohelea* and a pair of species of *Stilobezzia* Kieffer, 1911 (where it is clearly independently derived) [Downes, 1990]. The elongate hind claw of male *Allohelea* is identical to that of the female and this feature is clearly a result of feminization. An elongate claw is otherwise present in the females of a number of other ceratopogonid genera.

3. Adult hind leg femur more or less slender and bare of stout bristles, or femur may be stout and if bristles present, these arranged in scattered pattern or in one row (plesiomorphic); hind femur swollen, with 2–4 rows of strong bristles (apomorphic).

This character was discussed by Borkent & Bissett [1990].

4. If 2–4 rows of strong bristles present on femur of male hind leg, then these restricted to less than 0.58 of the femur length (plesiomorphic); bristles extending more than 0.58 the length of the male hind femur (apomorphic).

This character was discussed by Borkent & Bissett [1990].

5. Female without distinctive patch of microtrichia on wing (plesiomorphic); with distinctive patch of elongate microtrichia (apomorphic).

There are three genera of Ceratopogonidae with the derived condition: *Cacaohelea*, *Camptopterohelea* and some members of the extinct genus *Eohelea*. In each genus, the feature is sexually dimorphic with corresponding males having unmodified wings. In female *Cacaohelea*, the enlarged microtrichia are only moderately elongate and form a single, nearly round, uniformly dark patch on the wing. Females of *Camptopterohelea* and of some *Eohelea* have varying arrangements of elongate and/or thick microtrichia, and two of these, *Camptopterohelea hoogstraali* Wirth & Hubert, 1960 and *Eohelea sakhalinica* Szadziewski, 1990 have wing modifications approximating that found in *Cacaohelea* [Wirth & Hubert, 1960; Wirth & Wada, 1979; Das Gupta & Sarkar, 1982; Szadziewski, 1988, 1990, 1993]. Two species of *Eohelea* do not have modified wings, and others just have ridges apparently composed of thickened wing membrane. As hypothesized here, we consider the bare wings of these two species of *Eohelea* to be due to loss of the derived condition. Similarly, the ridged condition of some other species of *Eohelea* would likely be an extreme adaptation originating from modified microtrichia.

The wing of female *Parastilobezzia* Wirth & Blanton, 1970 has a small patch of somewhat thicker microtrichia at the wing apex, just posterior to the apex of the costa. We were unable to examine the male of this genus to determine if the feature is sexually dimorphic. Regardless, we consider the condition in *Parastilobezzia* to be a reduced variant of the apomorphic state.

6. Base of well-developed aedeagus articulated or abutting laterally against base of gonocoxite (plesiomorphic); aedeagus small, present only as a non-articulating sclerite (apomorphic).

The plesiomorphic condition is present in nearly all other Ceratopogonidae. Although the aedeagus is

modified in many different ways in the family, in nearly all cases it is basally articulated with the gonocoxite by heavily sclerotized basal arms and forming a well-defined ventral sclerite. In *Parastilobezzia* (not seen by authors), it is apparently well-defined although very reduced. In *Cacaohelea*, the aedeagus is weakly sclerotized, barely discernable and surrounded by thin membrane. From the few specimens available, it appears to be flexible in position (after clearing in KOH), and this may be a further derived state of this genus. Further study of *Parastilobezzia* is needed in this regard. In addition, it is important to know that only two of four species of *Cacaohelea* are known in the male stage.

7. Female abdominal sternite 7 moderately to well-developed, nearly as long as or only somewhat shorter than segment 8 (plesiomorphic); sternite 7 very short (apomorphic).

Female *Cacaohelea* are unique within Ceratopogonidae in having a very short sternite 7. Some *Stilobezzia* have a relatively short sternite 7, but not as reduced as in *Cacaohelea*. We consider the condition in these few species of *Stilobezzia* to be independently reduced. Similarly, female *Echinohelea* Macfie, 1940

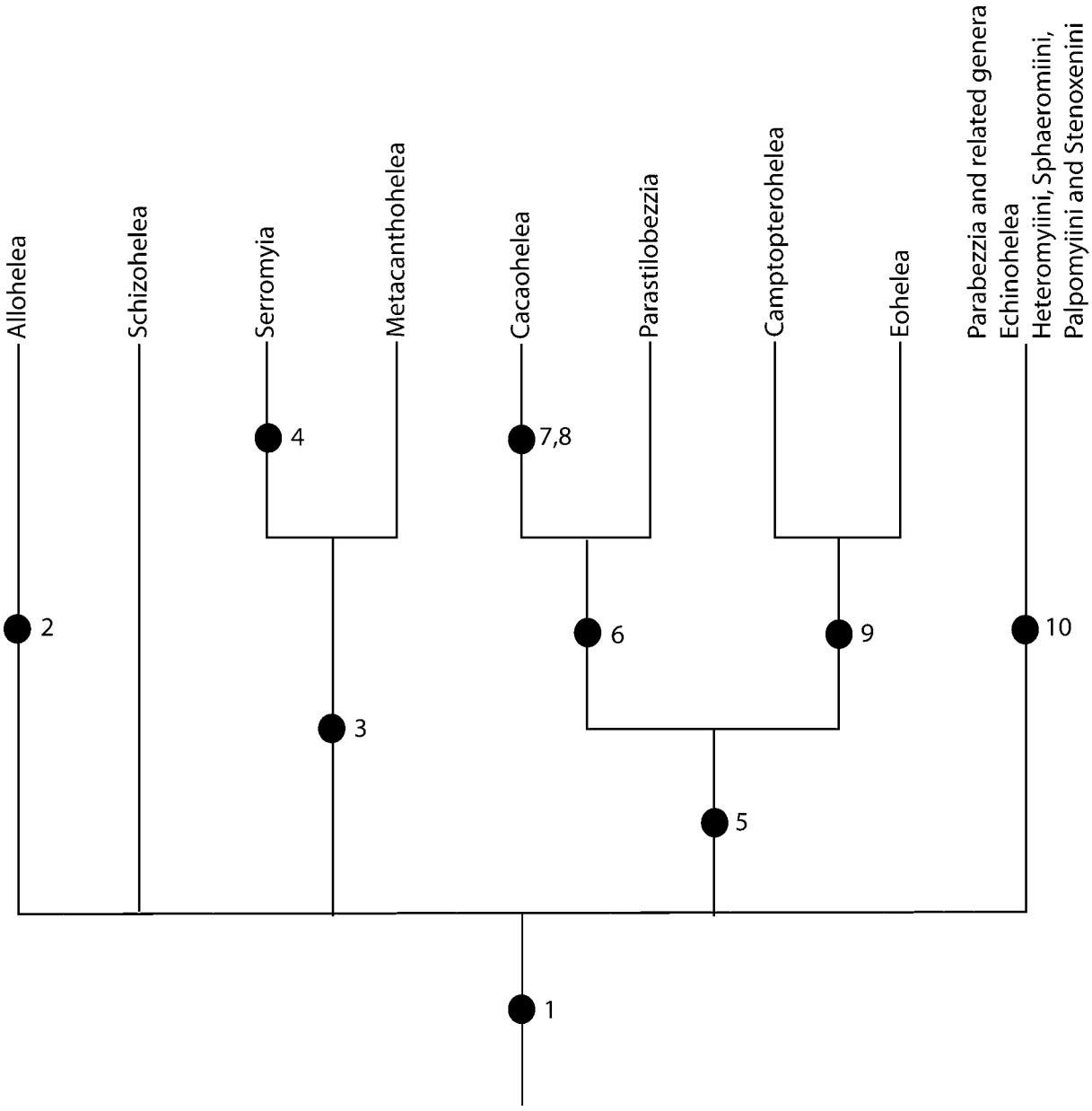

Fig. 4. Cladogram depicting proposed phylogenetic relationships between *Cacaohelea* and related genera. Numbers refer to synapomorphies discussed in the text.

Рис. 4. Кладограмма, отображающая предполагаемые филогенетические отношения между *Cacaohelea* и близкими родами. Номера соответствуют синапоморфиям, которые обсуждаются в тексте.

have a somewhat shortened sternite 7, but not to the extent as is present in *Cacaohelea*. Because the female of *C. adusta* is unknown and this species is the sister group of the remaining species of *Cacaohelea*, it is possible that this synapomorphy groups only three of the four species of *Cacaohelea*.

8. Those females with 2–3 spermathecae with all of these equally pigmented (plesiomorphic); female with one dark and one completely pale spermatheca (apomorphic).

The majority of Ceratopogonidae have two well-developed spermathecae and most often a very reduced third one. Of these, the two larger spermathecae are similarly pigmented, mostly a medium to dark brown. We found pale spermathecae only in some species of *Stilobezzia* and in these species most of, or all of the abdomen is also pale; in those instances where two spermathecae were present, both were pale. The condition in *Cacaohelea*, with one dark and one pale spermatheca, is unique within the Culicomorpha. As for character state 6, it is possible that this synapomorphy groups only three of the four species of *Cacaohelea*.

It is impossible to compare the derived state to those Ceratopogonidae with only one spermatheca, but we do not believe *Cacaohelea* is closely related to any of these.

9. Male antenna with 13 flagellomeres (plesiomorphic); male antenna with 11 or 12 flagellomeres (apomorphic).

The antennae of nearly all female Ceratopogonidae are composed of 13 separate flagellomeres (12 only in *Rhynchohelea* Wirth & Blanton, 1970 and some *Brachypogon* Kieffer, 1899), but those of the male have been reduced in several genera: some *Atrichopogon* Kieffer, 1906 [Borkent & Picado, 2004], *Baeohelea* Wirth & Blanton, 1970, *Baeodasymyia* Clastrier & Raccurt, 1979, *Nannohelea* Grogan & Wirth, 1980, *Notoceratopogon* de Meillon & Downes, 1986, and *Heterohelea* Clastrier, 1985 [Wirth & Grogan, 1988]. The antennae of these genera are composed of varying numbers of fused and/or lost flagellomeres. *Nannohelea*, as least, is most closely related to taxa in which the males have 13 flagellomeres [Borkent, 1992] and the others have short male cerci, indicating that they are not related to the taxa at hand. Males of *Camptopterohelea* and *Eohelea* have feminized antennae with 11 and 12 flagellomeres, respectively, with the four terminal flagellomeres elongate in both genera. Because female ceratopogonids generally have five elongate terminal flagellomeres, this suggests the loss of one elongate subterminal flagellomere in the male of both *Camptopterohelea* and *Eohelea* as well as an additional loss of one of the shorter, more basal flagellomeres in *Camptopterohelea*. We consider the loss to be unique within the family.

Das Gupta & Sarkar [1982] reported 11 flagellomeres in their description of the male of *Camptopterohelea distincta* Das Gupta & Sarkar, 1982 (as antenna 13-segmented, including the pedicel and scape) but illustrated 12 flagellomeres in their figure 2A. Das Gupta [personal communication] reported that their figure showed flagellomere 6 twice (the antenna was drawn in two parts).

10. Female adult with clypeus separated by membrane from margin of eye (plesiomorphic); female clypeus fused with ventromedial margin of eye (apomorphic).

This character appears to be unique within the Culicomorpha and is a complex and convincing indicator of the relationship between the genera possessing it. The relationships between *Parabezzia* Malloch, 1915 and related genera were discussed by Borkent et al. [2008].

The species of *Cacaohelea* can be partially interpreted phylogenetically. We consider *C. adusta* to be the sister group to the remaining three species on the basis of its uniformly dark abdomen. The pale basal abdominal segments contrasting with the dark genitalia (both in male and female) of *C. glukhovae*, *C. curva* and *C. youngi* is likely a synapomorphy of this group. This character state is otherwise found in only some species of *Stilobezzia*, female *Neurobezzia* Wirth & Ratanaworabhan, 1972, and a few Heteromyiini (e.g. some *Pellucidomyia* Macfie, 1939) and Sphaeromiini. The elongate, cylindrical abdominal segment 8 of female *C. youngi* is nearly unique and likely derived. Should further species of *Cacaohelea* be discovered, which seems very likely, this feature may become a synapomorphy.

The palpi of *Parastilobezzia* and *Camptopterohelea* have segments 3 and 4 nearly fused and enlarged, and this condition is unique in the family. Some other genera have one segment beyond the capitate sensilla bearing third segment, and the partially fused condition of *Parastilobezzia* and *Camptopterohelea* may be considered an intermediate state, but not in the scenario presented here. If this feature is a synapomorphy grouping these two genera, the reduced aedeagi of *Cacaohelea* and *Parastilobezzia* have evolved independently.

We cannot confidently propose a synapomorphy for *Schizohelea* Kieffer, 1917, but there is a potential feature worthy of further study. The gonocoxite of *S. leucopeza* (Meigen, 1804) and an unidentified species from Turkey both have an inner basal lobe bearing setae. This condition is unique within the Ceratopogonidae and therefore likely derived. It is also present in the drawings of *S. armata* (Remm, 1993) [Remm, 1993] and *S. pekae* (Remm, 1980) [Remm, 1980]. The feature is not shown in drawings of *S. lampropeza* (Remm, 1967) with an apparently bare lobe [Remm, 1967], and *S. spathulata* (Remm, 1993) [Remm, 1993], which appears to lack a lobe. The last remaining species of *Schizohelea*, *S. incerta* (Clastrier, 1963) is known only as female. It is possible that the apomorphic condition was not noticed in *S. lampropeza* and *S. spathulata*, and that this feature is a synapomorphy of the genus. Alternately, it may group only some species of *Schizohelea.* Further study is needed.

The males of *Cacaohelea*, *Parastilobezzia*, *Camptopterohelea*, and *Eohelea* have feminized antennae,

with the terminal five or, in the case of *Camptopterohelea* and *Eohelea*, the terminal four flagellomeres elongate and all lacking a plume. This feature occurs in a number of other genera and cannot be presently interpreted. However, in the context of the taxa depicted in Fig. 4, only males of *Leptohelea* Wirth & Blanton, 1970, a genus related to *Parabezzia*, have fully feminized antennae. Other, earlier lineages of Ceratopogonini with feminized antennae include *Fanthamia* de Meillon, 1939, *Afrohelea* Wirth, 1965, *Calcarhelea* Wirth & Grogan, 1988, *Luciamyia* de Meillon, 1937, and *Stiloculicoides* Wirth & Grogan, 1988.

Borkent [1995] discussed the character states of female abdominal sternite 9, which is divided medially in the apomorphic condition (his character 26). Although there are a few exceptions in the group defined by the synapomorphy, these are clearly reversals to the plesiomorphic condition. The apparently fused sternite 9 of *Cacaohelea* reported here is also likely a reversal. Although simply described as fused, it is possible that this sclerotization might actually be a thickening of the anterior margin of the opening of the oviduct. It would be valuable to study this feature more closely with sectioned material.

Similarly, our report of internal sclerotizations in segment 8 of the female abdomen of species of *Cacaohelea* warrants further study. Other Ceratopogonidae also have internal structures which are likely homologous to that reported here (e.g. some *Leptoconops* Skuse, 1889, *Austroconops* Wirth & Lee, 1958, some *Culicoides* Latreille, 1809, *Alluaudomyia* Kieffer, 1913, and others). Careful histological study is needed to better interpret this feature.

In addition to a complete row of palisade setae, adult *Cacaohelea* have a second row of strong setae (less well-developed in male). A survey of other Ceratopogoninae indicates that the feature is homoplastic, with some species of *Stilobezzia*, *Downeshelea* Wirth & Grogan, 1988, *Monohelea* Kieffer, 1917, *Austrohelea* Wirth & Grogan, 1988, *Leptohelea*, and numbers of genera in the tribes Heteromyiini, Sphaeromiini, and Palpomyiini with a second row of strong setae present.

Conclusions

Taxonomists with significant field experience never cease to be amazed at how apparently well sampled areas can yield previously unknown species. The combined efforts of sampling ceratopogonids in Costa Rica by the authors and staff at INBio have been based on many thousands of hours of field work and careful extraction of material during the past 15 years. In all that time, only 12 specimens of *Cacaohelea* have been discovered, one in 2001 with a sweep net, and the remainder in 2004 with light traps. This may be due in part to sampling technique. Most previous samples were based on Malaise traps, sweep nets and some above-ground light traps. Only recently have lights placed over ground-level pans of soapy water been utilized. The technique warrants greater use by collectors to see what further treasures might be discovered.

The fresh material of *Cacaohelea* reported here, well-mounted on microscope slides and including the first known males, allowed for a reexamination of character states of phylogenetic importance. There are presently 26 monotypic genera of Ceratopogonini, and most of these are based on few specimens, mounted in such a way that their thoraces are distorted. There is a great need of further specimens of these genera so that various character states may be determined and their phylogenetic relationships better understood.

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