BRILL *Insect Systematics & Evolution (2020) DOI 10.1163/1876312X-bja10013* brill.com/ise

Systematic revision of the caddisfly genus *Machairocentron* Schmid (Trichoptera: Psychomyioidea: Xiphocentronidae)

Albane Vilarino[a,*] and Ralph W. Holzenthal[b]

[a]Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. dos Bandeirantes, 3900, CEP14040-901, Ribeirão Preto, SP, Brazil

[b]Department of Entomology, University of Minnesota, 1980 Folwell Ave., St. Paul, Minnesota 55108, USA

*Corresponding author, e-mail: albanevilarino@gmail.com

Abstract

The genus *Machairocentron* is revised and its included species, *M. ascanius* Schmid 1982, *M. echinatum* (Flint 1981), *M. falciforme* Pes & Hamada 2013, *M. lucumon* Schmid 1982, *M. tarpeia* Schmid 1982, and *M. teucrus* Schmid 1982, are redescribed and illustrated based on type specimens. Two new species from Costa Rica, *M. chorotegae* **sp. nov.** and *M. eugeniarguedasae* **sp. nov.**, and one from Venezuela, *M. kalinae* **sp. nov.**, are described. An identification key for the *Machairocentron* genus is also provided.

Keywords

aquatic insects; biodiversity; caddisflies; Neotropical; taxonomy

ZooBank: http://zoobank.org/F98FCFDD-1EEE-4BD3-9173-D830DB90182B

Introduction

Xiphocentronidae Ross 1949 is a tube-dwelling caddisfly family comprising 183 species and seven genera. The family distribution is primarily tropical, with most of the known diversity in Southeast Asia and Mesoamerica, with some genera extending to Central Africa, the Middle East, and Japan. The New World Xiphocentronidae fauna comprises 65 species in three Neotropical taxa: *Xiphocentron* Brauer 1870, *Machairocentron* Schmid 1982, and the subgenus *Cnodocentron* (*Caenocentron*) Schmid 1982 (Holzenthal & Calor 2017).

The family was established by Ross (1949), which included Neotropical and Oriental species within *Xiphocentron*. After the description of *Xiphocentron* larvae, the family was synonymized with the Psychomyiidae by Edwards (1981) due to a strong

similarity between the larvae. Schmid (1982), in a worldwide revision, re-established the family status of Xiphocentronidae organizing it into two subfamilies: Proxiphocentroninae Schmid 1982 and Xiphocentroninae. Proxiphocentroniae includes only the genus *Proxiphocentron* Schmid 1982. Xiphocentroninae Schmid 1982, includes six genera: *Abaria* Mosely 1948, *Cnodocentron* Schmid 1982, *Drepanocentron* Schmid 1982, *Machairocentron* Schmid 1982, *Melanotrichia* Ulmer 1906, and *Xiphocentron* Brauer 1870.

Schmid (1982) separated *Machairocentron* from *Xiphocentron* by the degree of elongation of the genital appendages and by the spinous projections present on the inferior appendage of *Machairocentron*. In his revision, Schmid described five of the six currently known species in *Machairocentron*: *M. lucumon*, *M. tarpeia*, *M. teucrus*, *M. ascanius*, and *M. carmentis*, (the latter a junior synonym of *M. echinatum* (Flint 1981)). Pes et al. (2013) described *M. falciforme*, a species from the Central Amazon of Brazil, and also described the pupa and the female; the larvae were morphologically indistinguishable from those of *Xiphocentron*.

Machairocentron species (Fig. 1) occur in Mexico, Mesoamerica, northern South America, and central Amazonia. The adults of *Machairocentron* are small (3-4 mm) and the wings are narrow and apically acute, with long setal fringes along the margins; some species have one or two white spots on the forewing. The adult habits and habitats are similar to those of other genera in the family, living mainly in the headwaters of streams, constructing long silken tubes usually outside of the water on rocks and

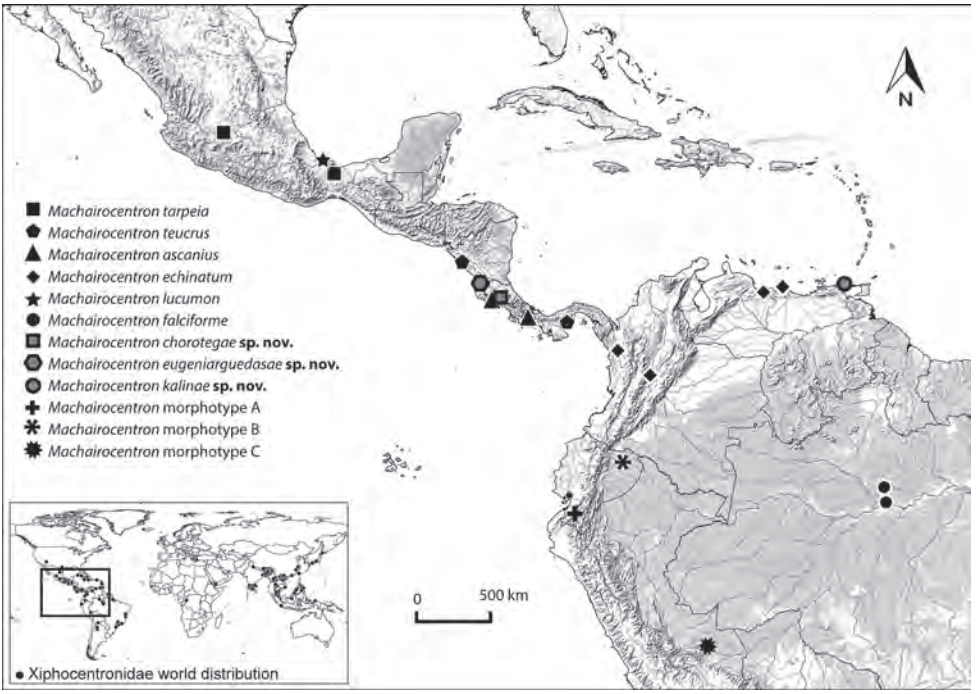

Figure 1. Distribution map: *Machairocentron* species

logs in shaded humid areas near the stream banks (Sturm 1960; Flint 1968; Pes et al. 2013). Larvae scrape the substrate to obtain their food, feeding on microalgae and debris associated with the substrate surface (Pes et al. 2013; Wiggins 1996). Adults of *Machairocentro*n, as is typical of Xiphocentronidae, are rarely collected in large numbers with light traps and often are active during daylight (Flint 1968; Schmid 1982). Flight intercept malaise traps and active collection via sweep netting are more productive methods for collecting xiphocentronids than light trapping, as Schmid (1982) collected his specimens by sweeping a net along streamside vegetation during the day, and Pes et al. (2013) collected a large type series using flight intercept traps.

In this work, we provide a revision of *Machairocentron* species, with a description of new species from Costa Rica and Venezuela. A key to males of *Machairocentron* is also provided.

Material and methods

Morphological terminology

Terminology is modified from Schmid (1982) and Nielsen (1957) for male genitalia, and Nielsen (1980) for female genitalia. Schmid's segment X is treated here as a composite structure: a membranous tergum, and a pair of sclerotized intermediate appendages (paraproctal processes *sensu* Nielsen 1957), deducing its homology with comparison to *Proxiphocentron*, Psychomyiidae, Ecnomidae, and Polycentropodidae. The terminology for head setal warts is modified from Oláh & Johanson (2007). Terminology for wing venation follows the Comstock – Needham system as interpreted for Trichoptera by Mosely & Kimmins (1953). Paired structures are referred to in the singular form. The phallus and the wing venation do not show significant differences among the species and are depicted for just a few species.

Specimens preparation and illustrations

To view wing venation, wing setae were removed using a thin artist brush and wings were mounted on slides following standard protocols outlined by Prather (2003). To observe the genitalia, the abdomens were removed and genitalia were cleared using 85% lactic acid through standard methods outlined by Blahnik et al. (2007). The prepared genitalia were transferred to microvials with 80% ethanol. Genitalia were placed in depression slides with a drop of glycerin. The bottom of the depression was covered with small glass beads to help stabilize the genitalia in the preferred position and examined using a compound microscope (Olympus BX41) at 400 X magnification. The structures were traced in pencil with the aid of a camera lucida coupled to the microscope. Final illustrations were made by scanning the pencil drawings and digitally rendering them using the software Adobe Illustrator® CS6. In the illustrations of male genitalia in lateral view, the preanal appendage and inferior appendage were rotated to allow the full visualization of the harpago structures. In the preserved specimens the inferior appendage crosses the preanal appendage at a 45° angle. Distribution map was generated using the open source software QGIS version 2.8.2.

Depositories

Types of the species described herein and other material examined are deposited, as indicated in the species descriptions, in the following institutions:

BIOUG Centre for Biodiversity Genomics, University of Guelph, Ontario, Canada.
CNC Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada.
DZRJ Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
MZSP Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.
USNM National Museum of Natural History, Washington, DC, USA.
UMSP University of Minnesota Insect Collection, Saint Paul, Minnesota, USA.

Systematics

Family Xiphocentronidae Ross 1949

Subfamily Xiphocentroninae Schmid 1982

Genus Machairocentron *Schmid 1982*

Machairocentron Schmid 1982:46 [Type species: *Machairocentron lucumon* Schmid 1982, original designation].

Generic diagnosis

Adult male *Machairocentron* can be diagnosed by the presence of sclerotized, swollen and rugose mesal and lateral projections at the base of harpago. These projections are covered with spines, and the mesal projection forms an oblong dorsal lobe and a ventral flap that surround laterally the apex of the intermediate appendage and the phallus. The coxopodite is always without spines, and well separated from the harpago. The genus is also identified by the very elongate inferior and preanal appendages, although these features are also found in *Xiphocentron torquon*, *X. polemon*, and *X. prolixum*.

The females are distinguished by having segment X darkly sclerotized (differing from the lighter sclerotized segment X in other xiphocentronids).

The pupae of *Machairocentron*, as presented in Pes et al. (2013), differ from the known pupae of *Xiphocentron*, (*X. sclerothrix*, *X. haitiense*, and *X. moncho*) and *Abaria* (*A. electa*) by the abdominal apex with longer mesal projections (4x longer than wide); middle legs not compressed and expanded; hook plates with greater number of hooks (i.e., 3rd segment: *Machairocentron* 14 hooks, *Xiphocentron* 9 hooks, *Abaria* 6–7 hooks); and the mandible apex serrated, not hooked (acutely hooked, whip-like apex in *Abaria*, *X. moncho*, and *X. haitiensis*).

The larvae are indistinguishable from *Xiphocentron* larvae (Pes et al. 2013).

Description

Adult. (Fig. 2A–F) Forewings uniformly dark brown or with one or two white spots; hindwings uniformly dark brown; wing margins covered with long, fine setae, without sexual dimorphism. Antenna scape 1/2 length of head (Fig. 2A). Maxillary palps with 5-segments in both sexes; segments in increasing order of length (I-II)-III-IV-V: segment V about 2x length of segment IV; IV longer than I+II; III about as long as I+II; I and II subequal (Fig. 2B). Labial palps with 3-segments, segments in increasing order of length I-II-III, with segment III 2x length of segment II (Fig. 2B). Head: frons with pair of large frontal setal warts (Fig. 2D); vertex, coronal and occipital sulcus well defined, coronal sulcus forking at the anterior 1/3 of head; interantennal setal wart diffuse; lateroantennal setal warts small, ocellar setal warts elongate mesally, occipital setal warts large, elongate (Fig. 2A). Tegula rounded. Prothorax: median pronotal setal warts elongate, lateral pronotal setal warts small (Fig. 2A). Mesothorax: mesoprescutum present, longer than broad, subquadrangular, divided by median sulcus; mesoscutellum anteriorly divided by median sulcus (Fig. 2A). Tibial spur formula 2-4-3 in males and 2-4-4 in females; male apical spur of hind leg without any conspicuous difference from other spurs (Fig. 2C). Body color dark brown; legs pale yellow. Venation (Fig. 2F): forewing forks II and IV present, fork II sessile, hindwing forks II and V present. Forewing discoidal cell small, thyridial cell elongate; 3 anal veins present; A2 basally merged with A3 and looped to A1. Hindwing: R1 long, reaching wing margin, without cross vein between R1 and SR. Abdominal sternum V bearing pair of anterolateral sclerotized reticulated regions around glandular opening (Fig. 2E).

Male genitalia. Tergum IX, in dorsal view triangular, tapered apically, apex cleft or not. Sternum IX elongate, in lateral view ventral margin convex, anteriorly with slender apodemes. Tergum X membranous, fused with intermediate appendage. Intermediate appendage sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, intermediate appendages separated or partially fused together mesally, with 2 pairs of setae at mid length; in ventral view, intermediate appendages fused together, apex cleft, with numerous sensillae. Preanal appendage very elongate, length 10–20 times height, covered with long, dense setae. Inferior appendage distinctly biarticulated. Coxopodite simple, with set of long setae ventrally. Harpago complex, basal region short, sclerotized; apical region elongate, narrow; basal region of harpago projected laterad and mesad, covered with small spines and tubercles; mesal projection broad, oblong dorsally, narrow ventrally; apical region of harpago elongate and narrow, length 2–5 times basal region length, mesal margin with row of setae from base to apex, apex enlarged or not, with single row of setae or multiple setae. Basal plate of inferior appendage, in lateral view broad. Phallus very long, narrow, with base reaching segment V anteriorly, slightly enlarged at base, subapical region annulate, apex slightly enlarged, similar in all species. Periphallic membrane thin, covering the phallus length in the region of the genital segments.

Female genitalia. Telescopically elongate, forming slender oviscapt. Segment VIII synscleritous, dorsally open, membranous; each anterolateral margin with thin, very

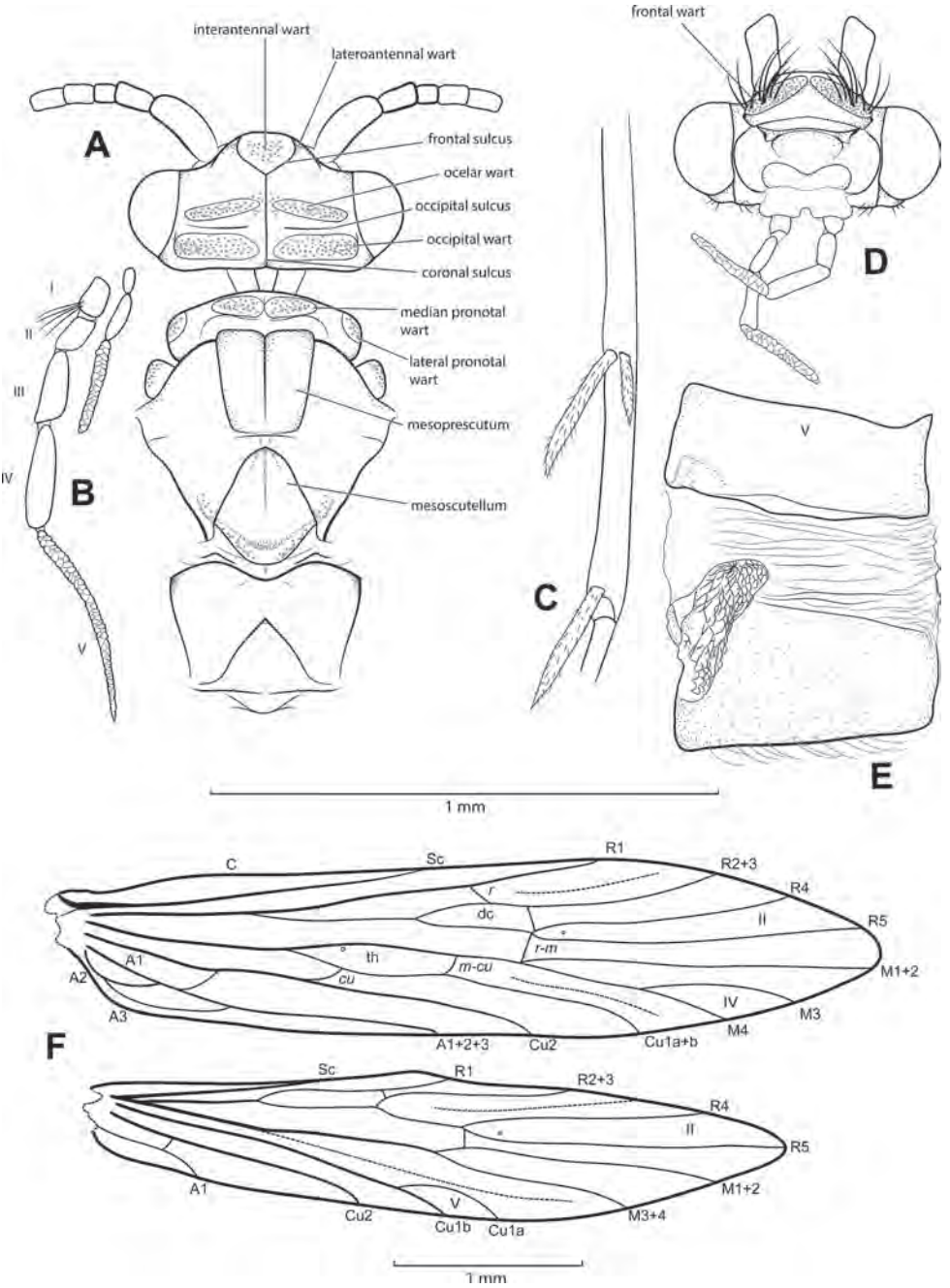

Figure 2. *Machairocentron* adult male: (A) head, pro– and mesothorax of M. falciforme, dorsal view; (B) labial and maxillary palps of *M. tarpeia*; (C) hind leg, tibial spurs of *M. tarpeia*; (D) head of *M. falciforme*, frontal view (labial palps are omitted); (E) sternum V reticulate glandular region of *M. eugeniarguedasae* **sp. nov.**, lateral view; (F) wing venation of *M. ascanius*.

elongate apodeme extending anteriorly until segment VI. Intersegmental membrane VIII–IX well developed. Segment IX tubular, slender, covered with annulated striations; longer than segment VIII, open ventrally; each anterolateral margin with thin, very elongate apodeme extending anteriorly to segment VI; strong rim present on lateral margin, extending for whole length reaching segment X. Segment X small, distinctly more sclerotized than segment IX, covered with sensillae; mesally with small rod. Cercus thin, digitiform.

Larvae. Pes et al. (2013) collected larvae *of Xiphocentron sclerothrix* and *Machairocentron falciforme* and observed no morphological differences between the larvae of the two genera. Illustration of *Machairocentron* larvae was provided by Pes et al. (2005). Descriptions of *Xiphocentron* larvae were provided by Edwards (1961), Flint (1964), Muñoz-Quesada & Holzenthal (1997) and Wiggins (1996).

Pupae [After Pes et al. (2013)]. Length 3.6–3.8 mm. Mandible triangular, apex sclerotized, elongate, tapered, inner margin serrate. Tarsi of middle leg flattened, wide. Abdomen: pair of hook plates present anteriorly on abdominal segments II–VII and posteriorly on segment V; each anterior hook plate II–V with 14–16 hooks; VI with 11 hooks; VII with 9 hooks; posterior hook plate V with 8 hooks. Anterior hook plates with hooks directed posterad, posterior hook plates with hooks directed anterad. Male abdominal apex with two pairs of projections, one short, one elongate; female abdominal apex with small projections.

Etymology. The generic etymology was not specified by Schmid (1982) in his original designation, but the name derives from the Greek: *machairi* = knife, *kéntron* = center, sharp point. Following the name pattern previously used by Brauer for the genus *Xiphocentron*, as *xiphon* means sword.

Machairocentron ascanius **Schmid 1982**

Fig. 3A–E

Machairocentron ascanius Schmid 1982:48 [Type locality: Panama, Dolega; USNM; ♂]. Aguila 1992:537 [distribution]. Armitage et al. 2015:5 [checklist]; Armitage & Cornejo 2015:193 [checklist].

Diagnosis

Machairocentron ascanius is similar to *M. teucrus*, *M. tarpeia*, *M. chorotegae* **sp. nov.** and *M. eugeniarguedasae* **sp. nov.** by the setal pad at the apex of the harpago. It can be differentiated by the apex of tergum IX divided into well separated lobes (Fig. 3B); the apex of the preanal appendage wide in lateral view (Fig. 3A); and the mesal projection of the harpago with very short spines (Fig. 3D, C).

Description

Adult. Forewing length 3.5 mm. Forewing uniformly dark brown. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

DOI 10.1163/1876312X-bja10013

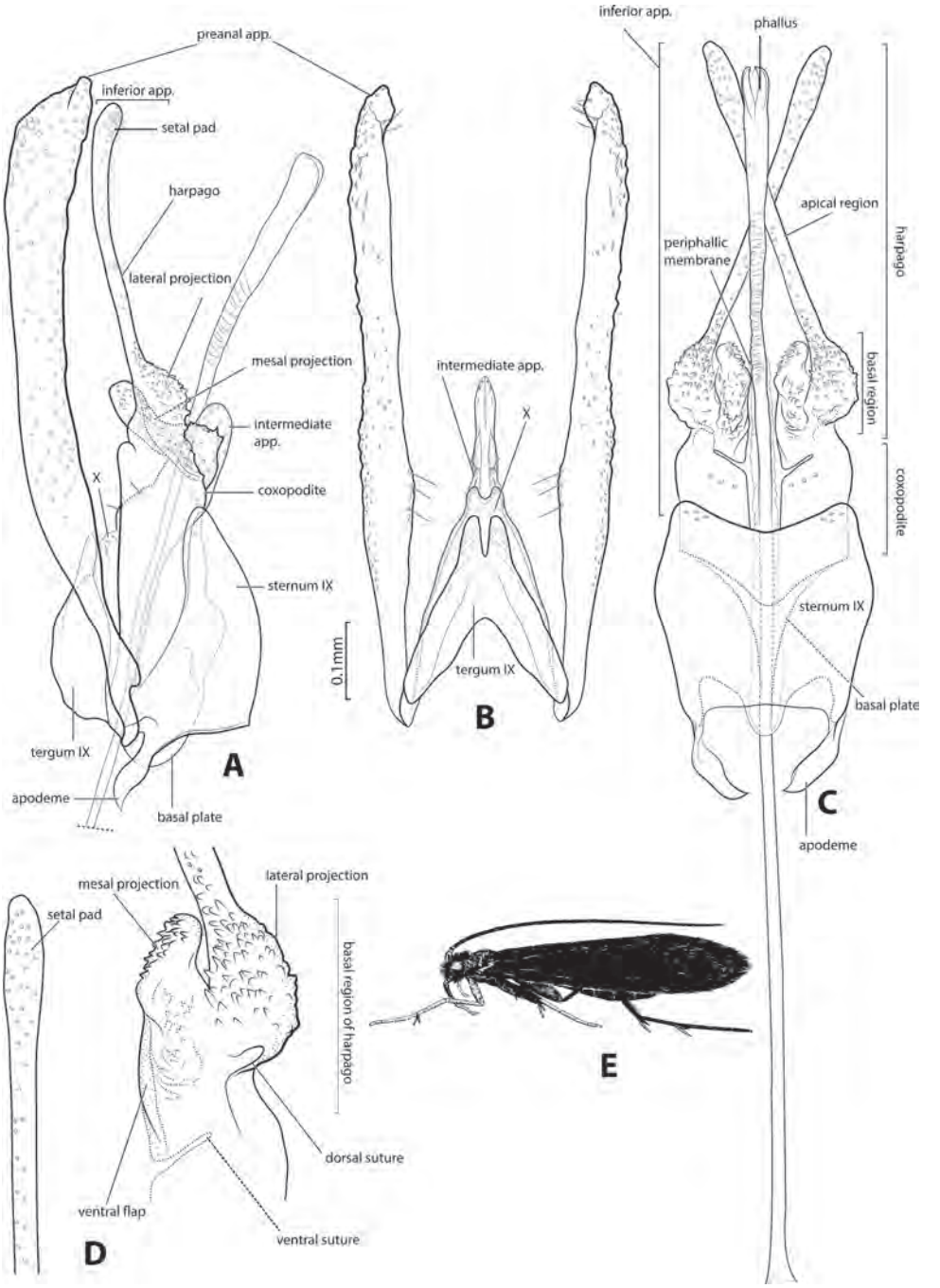

Figure 3. *Machairocentron ascanius* Schmid 1982: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult, showing wing coloration (modified from Muñoz-Quesada & Holzenthal 1997; here and throughout).

Male genitalia. Tergum IX elongate, 1.5x longer than wide; in dorsal view, anterior margin broadly concave, V-shaped, posterior margin tapered, apex divided into 2 well separated lobes (Fig. 3B). Sternum IX, in lateral view, about 2x as long as high, tapering apically; posterodorsal margin straight, ventral margin convex, anterior margin straight, with short, curved apodeme (Fig. 3A); in ventral view anterior margin nearly straight, posterior margin concave (Fig. 3C). Tergum X membranous. Intermediate appendage sclerotized; in lateral view oblong, apex rounded, with numerous sensillae (Fig. 3A); in dorsal view, tapered apically, partially fused mesally, with two pairs of setae at mid length (Fig. 3B). Preanal appendage long, 3x length of tergum IX, densely setose; in lateral view narrower at base, apically broad, apex truncate (Fig. 3A); in dorsal view straight, bent at apex. Inferior appendage longer than preanal appendage, bi-segmented. Coxopodite short, with long setae ventrally. Harpago basal region short, sclerotized; lateral projection rounded, covered with small spines; mesal projection covered with small spines, oblong and rounded dorsally; apical region of harpago, elongate, narrow, about 3x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae (Fig. 3A, 3D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged (Fig. 3C).

Material examined. **PANAMA: Dolega:** 17.vii.1967, O.S. Flint (holotype, ♂ pinned, USNMENT01028605). **COSTA RICA: Puntarenas:** Rio Cotón in las Alturas. 8.938°N 82.826°W, 18.iii.1991, el. 1360 m, R.W. Holzenthal, F. Muñoz, Y. Huisman (♂ pinned, UMSP000146117).

Distribution. Panama. Costa Rica (**new record**).

***Machairocentron echinatum* (Flint 1981)**
Figs 4A–E, 5A–D

Machairocentron echinatum (Flint 1981):17 [Type locality: Venezuela, Aragua, Maracay, Rio Limon, Estacion Piscicultura; USNM; ♂; in *Xiphocentron*]. Ríos-Touma et al., 2017:15 [checklist].
—*carmentis* Schmid 1982:48 [Type locality: Venezuela, Aragua, Ocumare; USNM]; Flint et al. 1999:81 [to synonymy].

Diagnosis

Machairocentron echinatum is similar to *M. falciforme*, and *M. lucumon* by the elongated apical region of the harpago, with the apex not enlarged and having a single row of setae (Fig. 4A, C). *M. echinatum* is diagnosed by the mesal projection of harpago dorsally with conspicuous long spines (Fig. 4D); the lateral projection of the harpago with sharp edges; the posterior margin of sternum IX undulate (Fig. 4C); and the preanal appendage with the apex slightly bent (Fig. 4A, B).

Description

Adult. Forewing length 3.5 mm. Forewing dark brown. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

DOI 10.1163/1876312X-bja10013

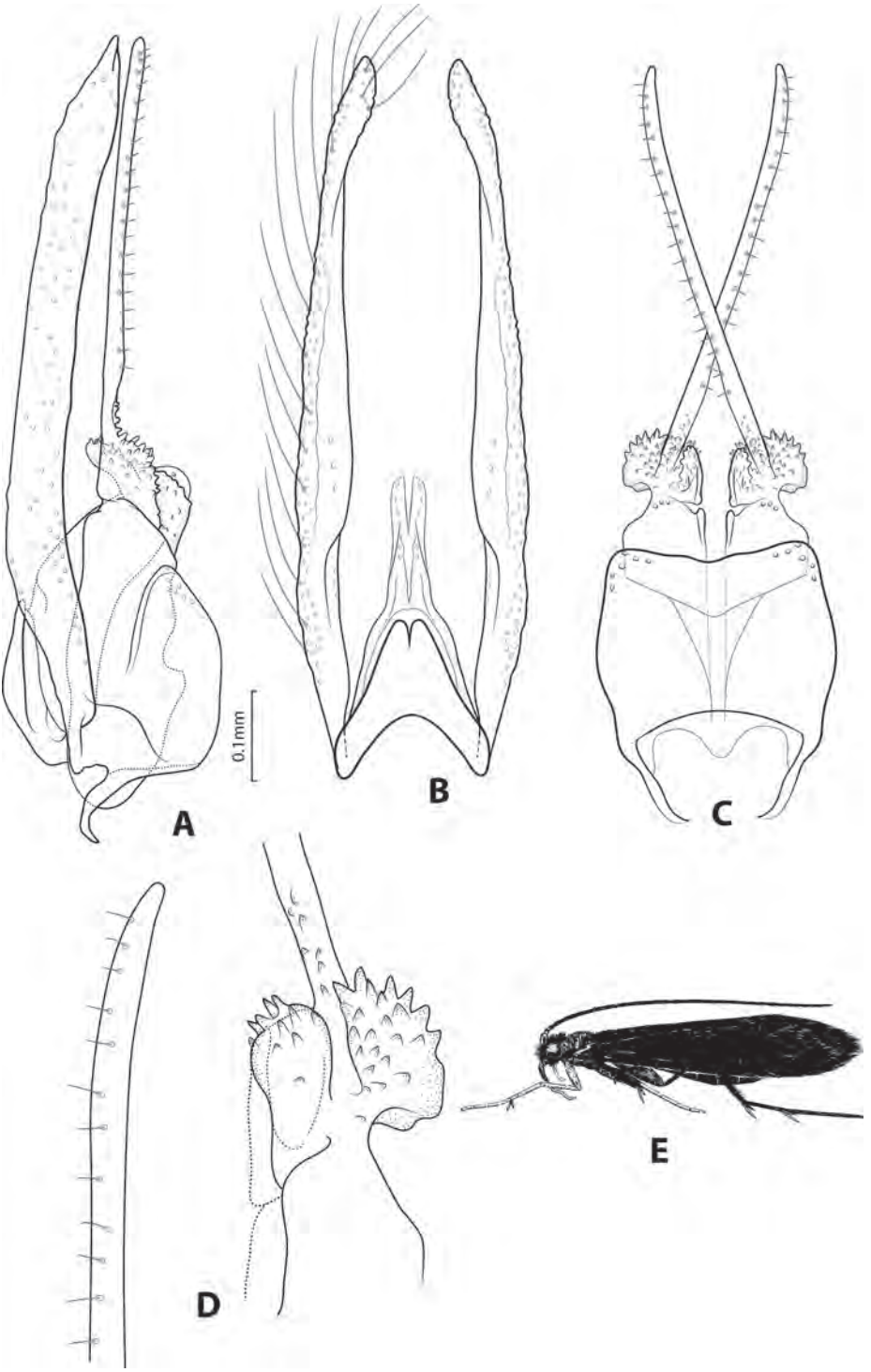

Figure 4. *Machairocentron echinatum* (Flint 1981): Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

Male genitalia. Tergum IX as long as wide; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex divided into 2 lobes (Fig. 4B). Sternum IX, in lateral view, about as long as high, tapering apically, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view (Fig. 4C), anterior margin concave, posterior margin undulated with narrow shallow mesal concavity. Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensilla; in dorsal view, tapered apically, partially fused mesally, with 2 pairs of setae mid length. Preanal appendage long, about 4x length of tergum IX, densely setose; in lateral view narrower at base, tapered apically; in dorsal view straight and apically bent (Fig. 4B). Inferior appendage longer than preanal appendage, bi-segmented. Coxopodite short with long setae ventrally. Harpago basal region short, sclerotized; lateral projection quadrate, covered with spines; mesal projection covered with conspicuously longer spines, oblong and rounded dorsally; apical region of harpago elongate, narrow, about 4x basal region length, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae (Fig. 4A, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Material examined. **VENEZUELA: Aragua:** Maracay, Rio Limon, Estacion Piscicultura, 5-6.xi.1974, F.H. Weibezahn (holotype, ♂ pinned, USNM76615); Ocumare, 19–20.ii.1969, P. & P. Spangler (2♂ alcohol, USNM); **Distrito Capital:** Río Camurí Grande, 1 km S of Camurí (Núcleo U.S.B.), 10.616°N, 66.715°W, el. 30 m, 24.i.1994, R.W. Holzenthal, C. Cressa, J. Rincón (♂ pinned, UMSP000146114). **COLOMBIA: Tolima:** Armero, near Guayabal, 2–10.ii.1977, malaise trap, E.L. Peyton (♂ pinned, USNM); **Choco:** Rio Atrato, Yuto, 18.ii.1983, O.S. Flint (2♂ pinned, USNM).

Distribution. Colombia (**new record**), Venezuela.

Remarks. While the holotype of *M. echinatum* does not have any spots on the wings, some specimens with similar genitalia (Fig. 5A–D) do possess white spots on the forewing. The presence or absence of these spots is considered here to be intraspecific variation. The genitalia of all specimens have very similar morphology with some variation, but without any conspicuous characters that would clearly indicate more than a single species (Figs 5A–D). The collection of additional material and examination of additional character data would be necessary for a more conclusive understanding of these populations. The specimen recorded as *M. echinatum* from Ecuador (Ríos-Touma et al. 2017) (accession number UMSP000098453) has much smaller spines compared to *M. echinatum*, the tergum IX is damaged, and the individual has a single white spot on the forewing. This specimen is here designated as undescribed *Machairocentron* morphotype B (Fig. 17A–D).

Machairocentron falciforme **Pes & Hamada 2013**

Figs 6A–E, 7A–D

Machairocentron falciforme Pes & Hamada in Pes et al. 2013:562 [Type locality: Brazil, Amazonas, Manaus, Reserva Ducke, Igarapé do Acará, 02°56'29.3"S, 59°56'07.4"W; INPA; ♂; ♀; pupa; biology]. Paprocki & França 2014:93 [checklist].

DOI 10.1163/1876312X-bja10013

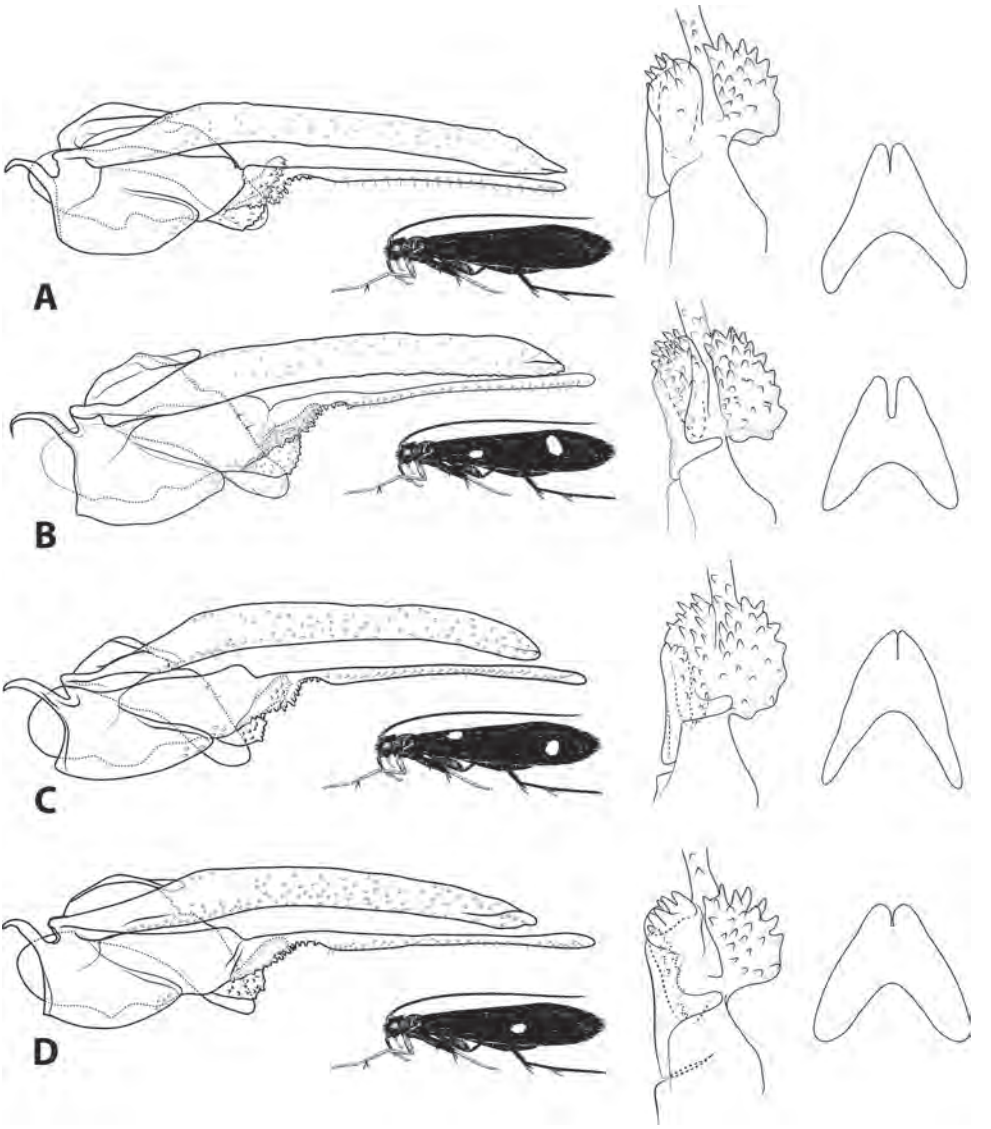

Figure 5. *Machairocentron echinatum* (Flint 1981) variations: male genitalia lateral, wing aspect, detail of basal region of harpago dorsal, tergum IX dorsal, respectively. (A) Venezuela, Aragua state (Holotype); (B) Venezuela, Distrito Capital; (C) Colombia, Choco departament; (D) Colombia, Tolima departament.

Diagnosis

Machairocentron falciforme is similar to *M. echinatum*, and *M. lucumon* by the elongated apical region of the harpago, with the apex not enlarged and having a single row of setae. *Machairocentron falciforme* can be differentiated from *M. echinatum* by the lateral projection of the harpago strongly produced anterad (Fig. 6C, D). In dorsal view, the conical preanal appendage shape, with a tapered apex (Fig. 6B), can differentiate

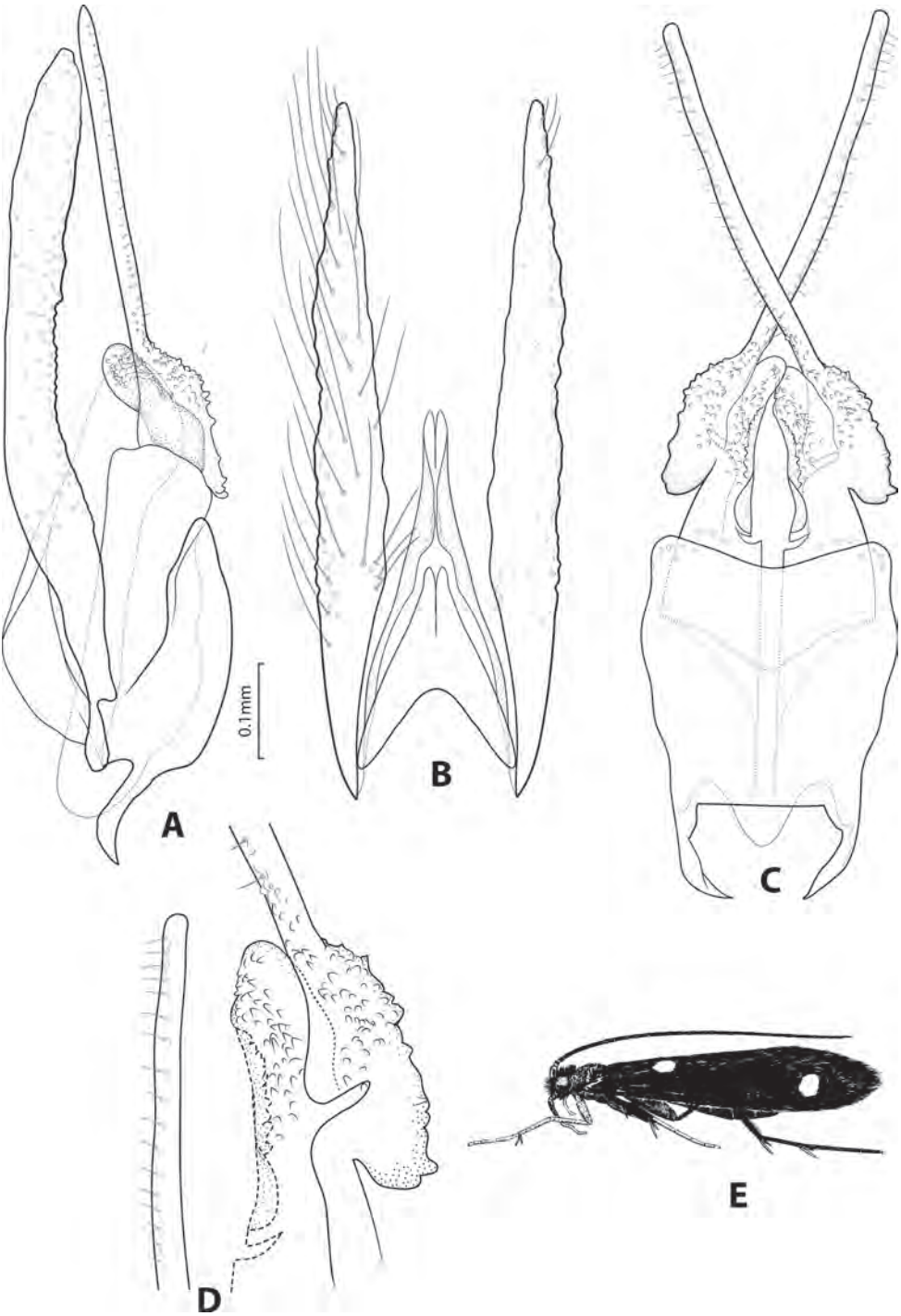

Figure 6. *Machairocentron falciforme* Pes & Hamada 2013: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

DOI 10.1163/1876312X-bja10013

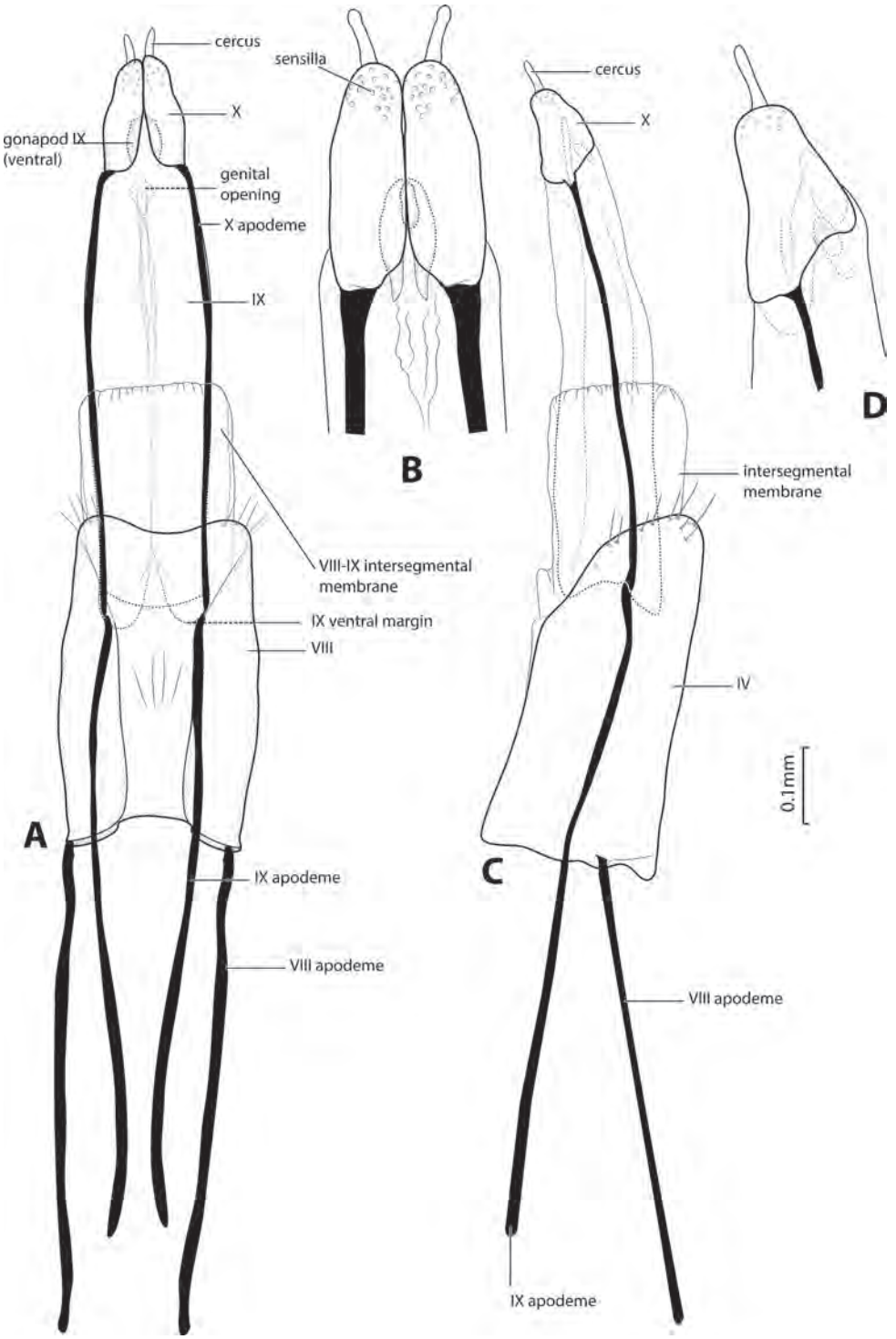

Figure 7. *Machairocentron falciforme* Pes & Hamada 2013: Female genitalia: (A) dorsal; (B) detail of X segment, dorsal; (C) lateral; (D) detail of X segment, lateral.

M. falciforme from all its congeners. The forewing with two white spots (Fig. 6E), also can separate *M. falciforme* from *M. lucumon* (which also has the harpago's lateral projection produced anterad, although, in a lesser degree).

Description

Adult. Forewing length 3 mm. Forewing dark brown with white spot near forking point of R4 and R5 and one anteriorly on costal margin. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX elongate, narrow apically; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin strongly tapered, apex cleft until about mid-length (Fig. 6B). Sternum IX, in lateral view, about 2x as long as high, tapered apically, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin straight, posterior margin concave (Fig. 6A, C). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensillae; in dorsal view, tapered apically, separated mesally throughout length, with 2 pairs of setae at mid length. Preanal appendage long, 3x length of tergum IX, densely setose; in lateral view narrower at base, slightly wider mid length, tapered apically; in dorsal view conical, strongly tapered apically. Inferior appendage longer than preanal appendage, bi-segmented. Coxopodite short, with long setae ventrally. Harpago basal region short, sclerotized; lateral projection strongly produced anterad, covered with spines; mesal projection covered with small spines, dorsally oblong, rounded dorsally; apical region of harpago elongate, narrow, about 2x length of basal region, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae (Fig. 6C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Female genitalia (Fig. 15A–D). Segment VIII synscleritous, membranous dorsally; each anterolateral margin thin, with very elongate apodeme extending anteriorly until segment VI. Intersegmental membrane VIII-IX well developed. Segment IX tubular, opened ventrally, longer than segment VIII; each anterolateral margin with thin, elongate apodeme extending anteriorly to segment VI; sclerotized rim extends along all of segment IX. Segment X small, distinctly more sclerotized, covered with sensillae; with small rod mesally. Cercus thin, digitiform.

Material examined. **BRAZIL: Amazonas:** Manaus, "Reserva Ducke; Igarapé do Acará, 02°55'51"S, 059°58'59"W, 20–30.x.2001, malaise trap, J. Vidal, (paratype, ♂ in alcohol, MZUSP000121), (♀ in alcohol, MZUSP000122).

Distribution. Brazil.

***Machairocentron lucumon* Schmid 1982**
Fig. 8A–E

Machairocentron lucumon Schmid 1982:50 [Type locality: Mexico, Ver., Rio Tacolapan, rt 180, Km 551; USNM; ♂].

DOI 10.1163/1876312X-bja10013

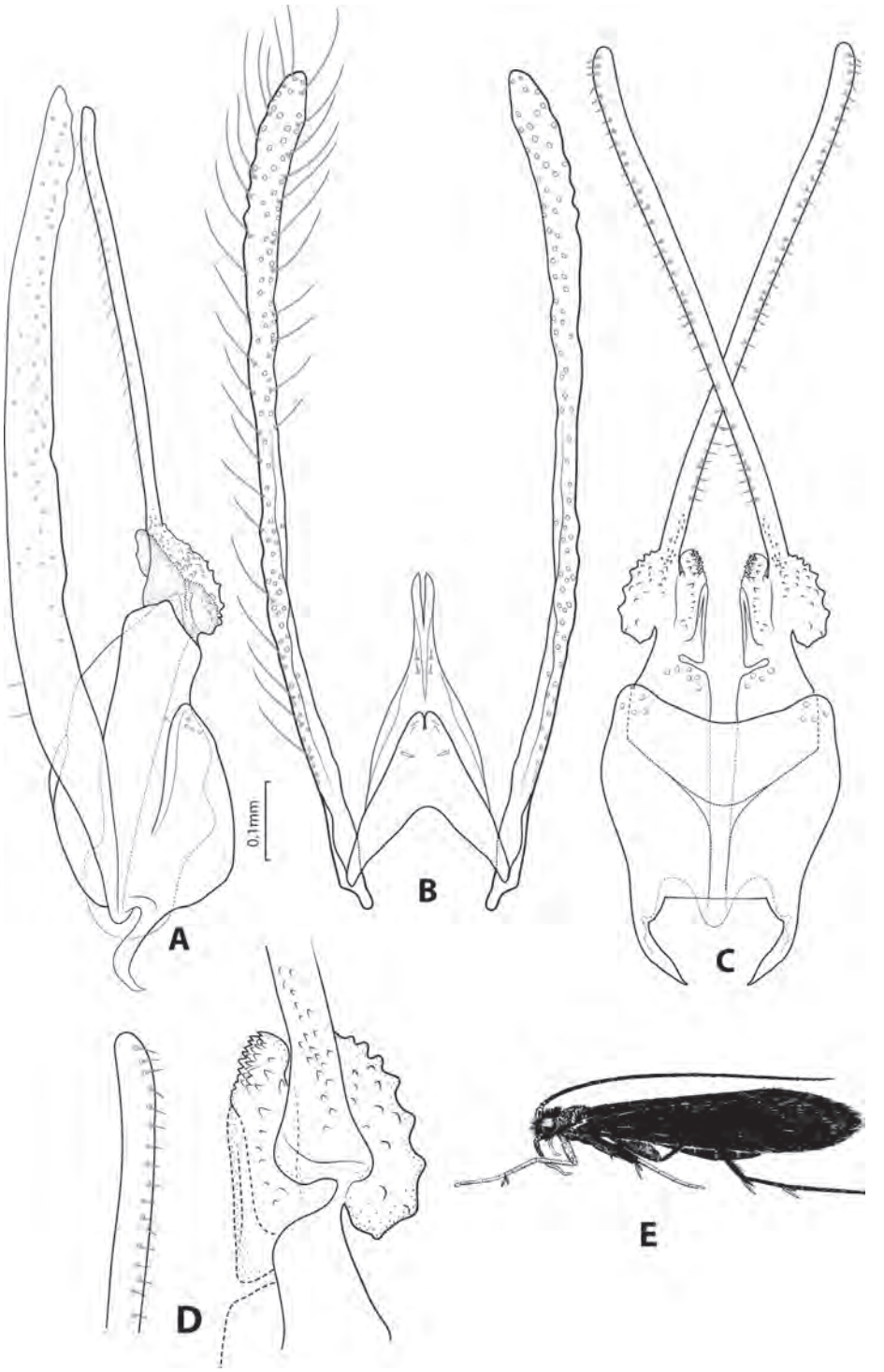

Figure 8. *Machairocentron lucumon* Schmid 1982: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

Diagnosis

Machairocentron lucumon is similar to *M. echinatum* and *M. falciforme* by the very elongate apical region of the harpago without a setal pad at the apex. *Machairocentron lucumon* has the longest apical region of the harpago among the known species, about 5x the length of the basal region and a highly sclerotized lateral projection on the basal region (Fig. 8A–C). The spines on the mesal projection of the harpago are smaller than in *M. echinatum* and the lateral projection is less produced anterad than in *M. falciforme* (Fig. 8C, D). Additionally, in dorsal view, a pair of subapical marks on the tergum IX (Fig. 8B) were seen only in *M. lucumon* specimens.

Description

Adult. Forewing length 3.5 mm. Forewing uniformly dark brown. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX elongate, narrow apically; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex with shallow cleft (Fig. 8B). Sternum IX, in lateral view about 2x as long as high, posterodorsal margin straight, ventral margin convex, anterior margin convex with short, curved apodeme; in ventral view, anterior margin straight, posterior margin concave (Fig. 8A, C). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensillae; in dorsal view, tapered apically, each intermediate appendage partially fused together mesally, with two pairs of setae at mid length. Preanal appendage long, 5x length of tergum IX, densely setose; in lateral view narrower at base, slightly wider at mid length, tapered apically; in dorsal view straight, bent apically. Inferior appendage as long as preanal appendage, bi-segmented. Coxopodite short, simple, with long setae ventrally. Harpago basal region short, sclerotized, lateral projection well developed, produced anterad, covered with spines; mesal projection covered with small spines oblong and rounded dorsally; apical region of harpago elongate, narrow, about 5x length of basal region, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae (Fig. 8A, C). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Material examined. **MEXICO: Veracruz-Llave:** Rio Tacolapan, Rt 180, Km 551, 30.VII.1966, O.S. Flint & M.A. Ortiz (holotype, ♂ pinned, USNMENT01028606); same data except, Los Tuxtlas area, Rio Maquinas, 4–14.v.1981, C.M & O.S. Flint (♂ pinned, UMNH).

Distribution. Mexico.

Machairocentron tarpeia Schmid 1982

Fig. 9A–E

Machairocentron tarpeia Schmid 1982:46 [Type locality: Mexico, Michoacán, San Lorenzo, Rt. 15, Km 206; USNM; ♂].

Diagnosis

Machairocentron tarpeia has a short apical region of the harpago as also seen in *M. teucrus*, and *M. chorotegae* **sp. nov.** (Fig. 9A, C). It differs by the rounded mesal projection of the harpago with elongate finger-like spines (Fig. 9C, D), and the wider tergum IX with a broad U-shaped concavity on the anterior margin and the well separated apical lobes (Fig. 9B).

Description

Adult. Forewing length 3.5–4.0 mm. Forewing uniformly dark brown. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX as long as wide; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex divided into well separated lobes (Fig. 9B). Sternum IX, in lateral view, about 1.5x longer than high, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin nearly straight, posterior margin concave (Fig. 9A, B). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensilla; in dorsal view, tapered apically, partially fused mesally, with 2 pairs of setae at mid length. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider mid length, tapered apically; apex rounded, in dorsal view straight enlarged. Inferior appendage as long as preanal appendage, bi-segmented. Coxopodite shortwith long setae ventrally. Harpago basal region short, sclerotized; lateral projection rounded, covered with small spines; mesal projection with finger-like spines, rounded dorsally; apical region of harpago about 2x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae (Fig. 9C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged (Fig. 9A).

Material examined. **MEXICO: Michoacán:** San Lorenzo, Rt. 15, Km 206, 14–15. vii.1966., O.S. Flint & M.A. Ortiz (holotype, ♂ pinned, USNMENT01028607), (paratype, ♂ in alcohol, CNC165710).

Distribution. Mexico.

Machairocentron teucrus Schmid 1982

Fig. 10A–E

Machairocentron teucrus Schmid 1982:48 [Type locality: Panama, Playa Santa Clara; USNM; ♂]. Aguila 1992:537 [distribution]. Armitage et al. 2015:5 [checklist]. Armitage & Cornejo 2015:193 [checklist].

Diagnosis

The short length of the apical region of the harpago (3x basal region length) of *M. teucrus* is also present in *M. tarpeia* and *M. chorotegae* sp. nov. *Machairocentron teucrus* can be differentiated by the narrow sternum IX (Fig. 10B); the rounded, smooth margin

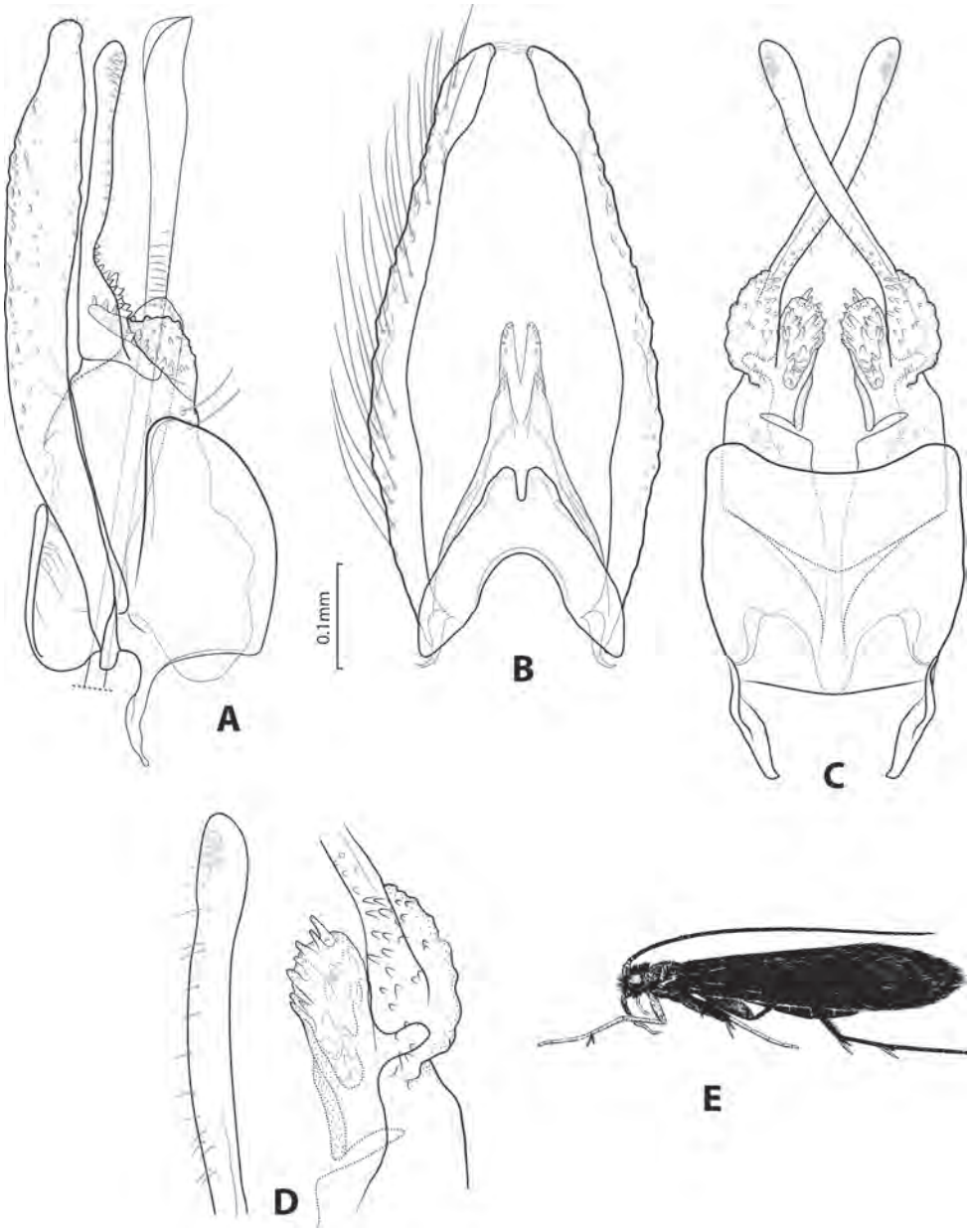

Figure 9. *Machairocentron tarpeia* Schmid 1982: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

of the lateral projection of the harpago (Fig. 10C, D), and the high density of the small spines on the ventral region of the mesal projection and the ventro-apical region of the lateral projection, which make the mesal and lateral projections appear fused (Fig. 10C, D).

DOI 10.1163/1876312X-bja10013

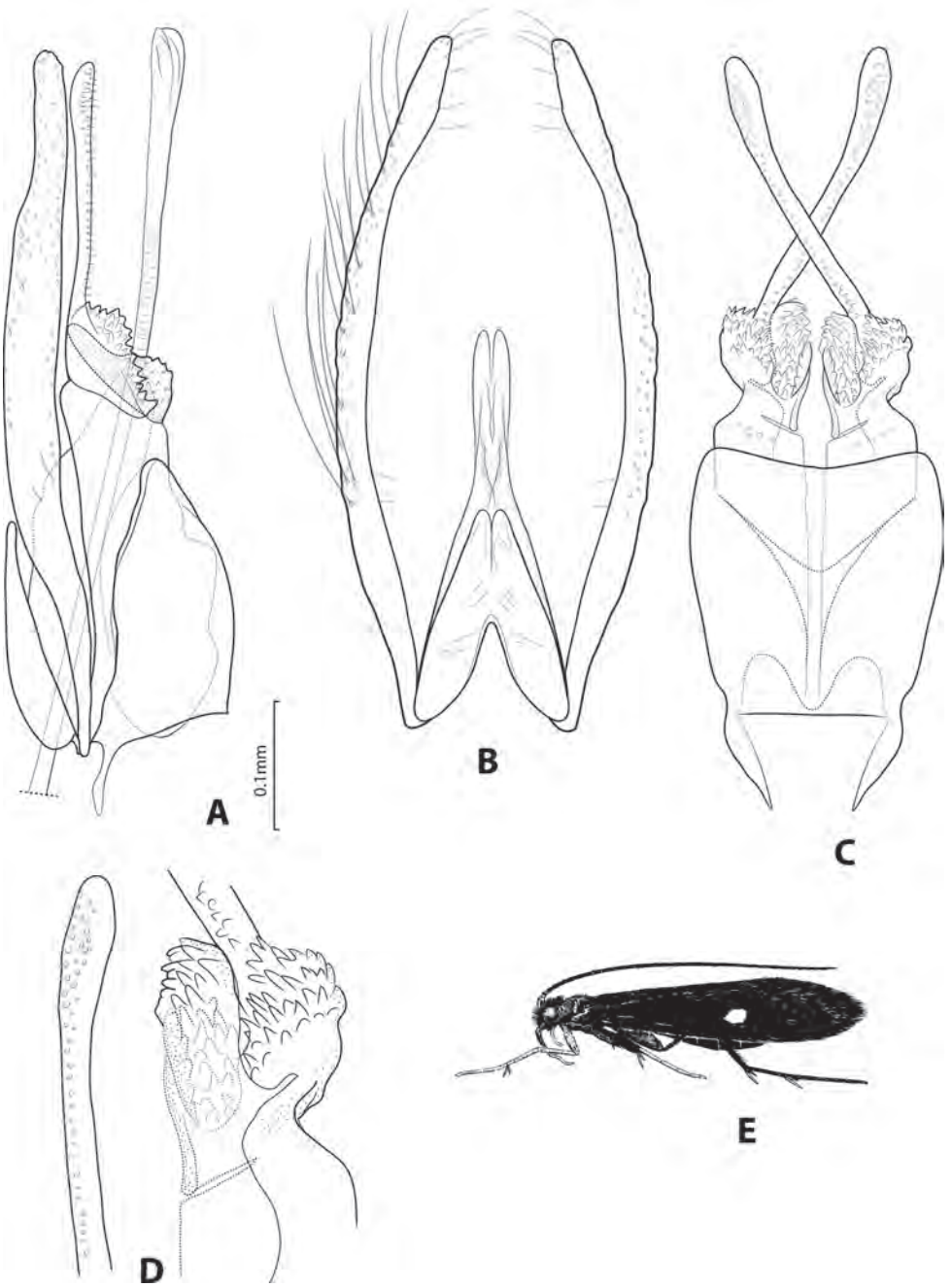

Figure 10. *Machairocentron teucrus* Schmid 1982: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

Description

Adult. Forewing length 3.5 mm. Forewing dark brown with white spot near forking point of R4 and R5. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX longer than wide; in dorsal view, anterior margin broadly concave, V-shaped, posterior margin tapered, apex incised into 2 well separated lobes (Fig. 10B). Sternum IX, in lateral view, about 1.5x longer than high, posterodorsal margin straight, ventral margin convex, anterior margin straight with short apodeme; in ventral view, anterior margin straight, posterior margin concave (Fig. 10C). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensillae; in dorsal view, tapered apically, separated mesally throughout length, with two pairs of setae at mid length. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider at mid length, tapered apically, apex rounded; in dorsal view straight, apex slightly enlarged. Inferior appendage as long as preanal appendage, bi-segmented. Coxopodite short, with long setae ventrally. Harpago, basal region short, sclerotized; lateral projection rounded, posterior margin densely covered with small spines, anterolateral margin smooth; mesal projection laterally covered with small spines, oblong, rounded dorsally; mesoventrally densely covered with small spines; apical region of harpago elongate, narrow, about 2.5x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae (Fig. 10C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged (Fig. 10A).

Material examined. **PANAMA: Cocle:** Playa Santa Clara, 2.vii.1967, malaise trap, W.W. Wirth (holotype, ♂ pinned, USNMENT01028608). **NICARAGUA: Dto. Carazo:** Quebrada on farm California, 45 km SW of Managua towards Pochomil / Montelimar, N 11°55'62.5", W 86°27'71.7", 15.viii.2000, el. 185 m, L. Chamorro & Lacayo (♂ pinned, UMSP000101033).

Distribution. Panama, Nicaragua (**new record**).

Machairocentron chorotegae **sp. nov.**

Fig. 11A–E, 12A–C
ZooBank: http://zoobank.org/CC835E2A-A0DF-4156-95AA-74DB0094FAF0

Diagnosis

The new species is similar to *Machairocentron teucrus* and *M. tarpeia* by the short length of the apical region of the harpago (3x length of basal region). It can be separated from *M. teucrus* and *M. tarpeia* by the inner margin of the basal region of the harpago bearing a radula-like dorsal projection (Fig. 11D) and tergum IX having a narrow V-shaped mesal concavity on the anterior margin (Fig. 11B).

DOI 10.1163/1876312X-bja10013

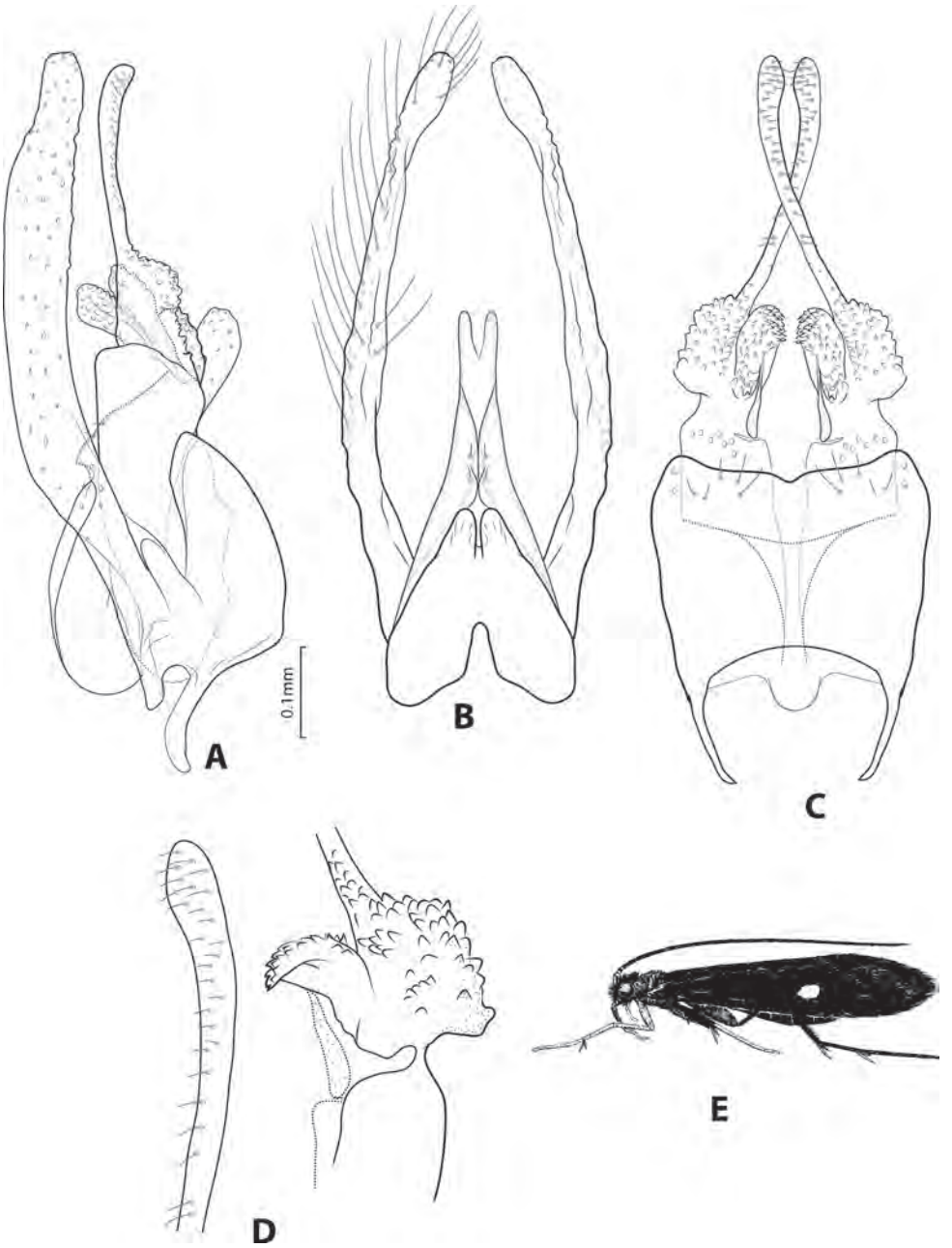

Figure 11. *Machairocentron chorotegae* **sp. nov.**: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

Description

Adult. Forewing length 3.5 mm. Forewing dark brown with white spot near forking point of R4 and R5. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX as longer as wide; in dorsal view, anterior margin with narrow V-shaped mesal concavity, posterior margin tapered, apex cleft. Sternum IX, in lateral view, more than 2x as long as high, each side with posterolateral-dorsal margin straight, ventral margin convex, with anterolateral apodeme short, curved (Fig. 11A); in ventral view, anterior margin slightly concave, posterior margin straight with very small mesal concavity, sides convex (Fig. 11C). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensillae; in dorsal view, tapered apically, separated mesally throughout its length, with 2 pairs of setae at mid length. Preanal appendage, 3x length of tergum IX, densely setose; in lateral view, narrower at base, slightly wider at mid length, tapered apically; in dorsal view, apically enlarged. Inferior appendage longer than preanal appendage, bi-segmented. Coxopodite short, simple, with long setae ventrally. Harpago basal region short, sclerotized; lateral projection angulate, square, covered with small spines; mesal projection divided in 3 lobes, dorsal lobe oblong, covered with small tubercles (Fig. 11A), in dorsal view curved mesad, covered with spines, radula-like (Fig. 11D); mesal lobe in lateral view oblong, in ventral view mesal margin rounded, apex directed posterad with small spines, mesal margin spines curved dorsad; in lateral view ventral lobe broad, with small tubercles; apical region of harpago elongate, narrow, about 3x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae (Fig. 11C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Female genitalia (Fig. 16A–C). Segment VIII synscleritous, membranous dorsally; each anterolateral margin with narrow, elongated apodeme, extending anterad until segment VI. Intersegmental membrane VIII-IX well developed. Segment IX tubular, open ventrally, longer than segment VIII, half-length included inside segment VIII; each anterolateral margin with narrow, elongate apodeme, extending anteriorly until segment VI; sclerotized rim extending along all of segment IX. Segment X short, distinctly sclerotized, covered with sensillae; with small rod mesally. Cercus thin, digitiform.

Material examined. **Holotype: COSTA RICA: Puntarenas:** Rio Bellavista, ca 1.5 km, NW Las Alturas. 8.951°N, 82.846°W, 16–17.iii.1991, el. 1400 m, R.W. Holzenthal, F. Muñoz, Y. Huisman (♂ pinned, UMSP000146097).

Paratypes: COSTA RICA: Puntarenas: same data as holotype: (6♂ pinned, UMSP000146091, 146092, 146093, 146098, 146099, 146100), (♀ pinned, UMSP000146113); **Alejuela:** Rio Toro, 3.0 km, SW Bajos del Toro, 10.204°N, 84.316°W, 3-4.ix.1990, el. 1530 m, R.W. Holzenthal, R.J. Blahnik, Y. Huisman, (7♂ pinned, UMSP000146110, 146103, 146104, 146105, 146107, 146108, 146109), (♀ UMSP000146112).

DOI 10.1163/1876312X-bja10013

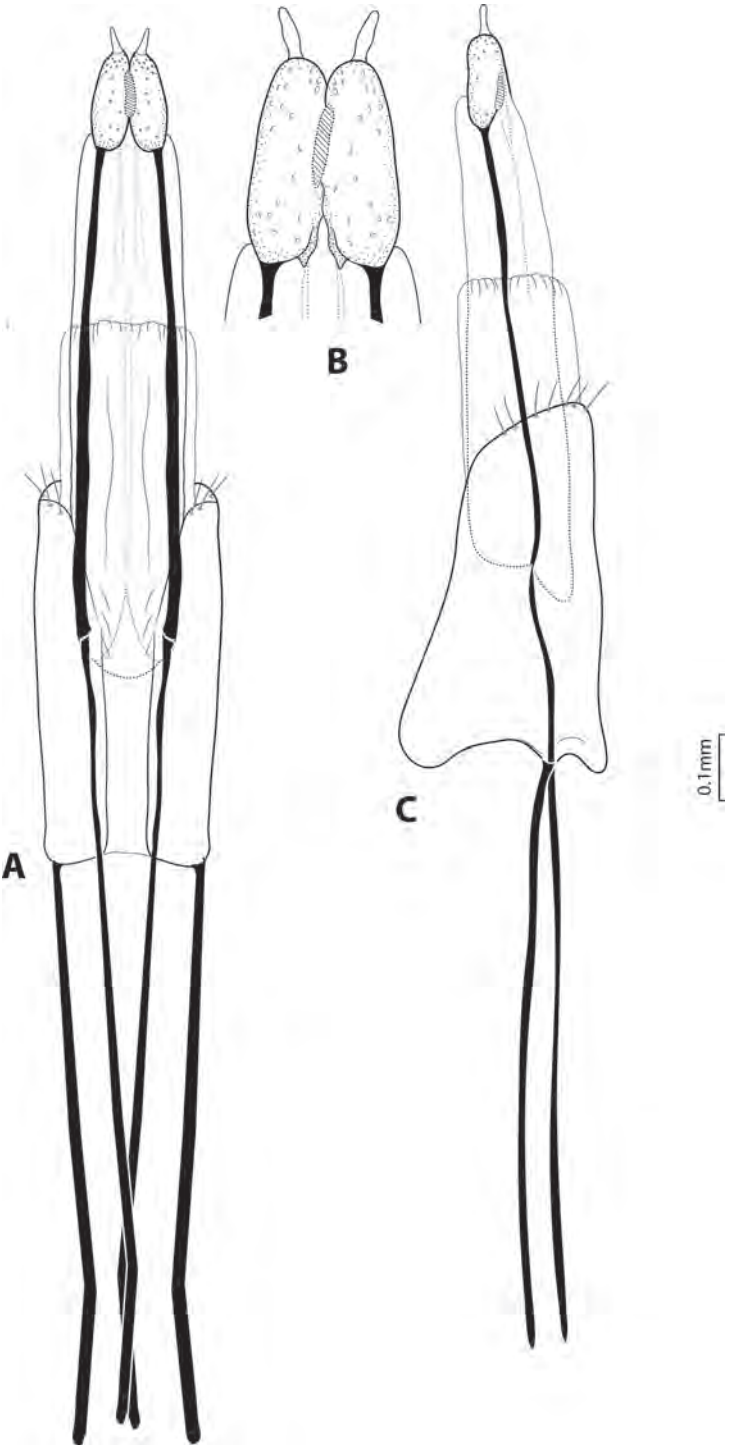

Figure 12. *Machairocentron chorotegae* **sp. nov.**: Female genitalia: (A) dorsal; (B) detail of X segment dorsal; (C) lateral.

Distribution. Costa Rica.

Etymology. The species is named after the Chorotegas, one of the eight indigenous ethnic groups that inhabited Costa Rica before Europeans arrived. The word Chorotega means "man who flees," referring to the account that the first Chorotegas escaped from war with the Huicholes, indigenous warriors of Mexico. It is said that the Chorotega emigrated between 1000 and 1100 A.D. and settled along the Pacific coast from Honduras to Panama.

***Machairocentron eugeniarguedasae* sp. nov.**

Figs 13A–D, 14A–C

ZooBank: http://zoobank.org/2B452983-FBBB-4910-9740-4AF2B19A3412

Diagnosis

Machairocentron eugeniarguedasae is similar to other species with elongate apical region of harpago (*M. echinatum*, *M. falciforme*, *M. lucumon*), particularly *M. echinatum* by the elongate spines on the mesal projection of the harpago. *M. eugeniarguedasae* can be differentiated by these spines being longer and displayed as a line of finger-like spines curving upward close to the inner margin (Fig. 13D). The spines on the lateral projection are also sparser and more pointed; and the harpago apex is enlarged and has a pad of numerous setae (Fig. 13C, D), while *M. echinatum* and other species with elongated harpago have just a simple row.

Description

Adult. Forewing length 4.0 mm. Forewing uniformly dark brown (material in alcohol, denuded, faded). Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX slightly longer than wide; in dorsal view, anterior margin with U-shaped mesal concavity, posterior margin tapered, very thin, apex cleft until near half length (Fig. 13B). Sternum IX, in lateral view, more than 2x as long as high, each side with posterolateral-dorsal margin straight, ventral margin convex, anterolateral apodeme short, curved; in ventral view, anterior margin concave, posterior margin concave, sides convex (Fig. 13A, B). Tergum X membranous. Intermediate appendage sclerotized, in lateral view oblong, apex rounded, with numerous sensilla; in dorsal view, tapered apically, separated mesally throughout its length, with 2 pairs of setae at mid length. Preanal appendage long, 5x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider at mid length, tapered apically; in dorsal view subapically angulate. Inferior appendage longer than preanal appendage, bi-segmented. Coxopodite short, with long setae ventrally. Harpago basal region short, sclerotized; lateral projection covered with elongate spines; mesal projection oblong dorsally, with finger-like spines, spines curved dorsad; apical region of harpago elongated, narrow, about 6x length of basal region, mesal margin with row of setae from base to apex, apex slightly enlarged, with pad of numerous setae (Fig. 13C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

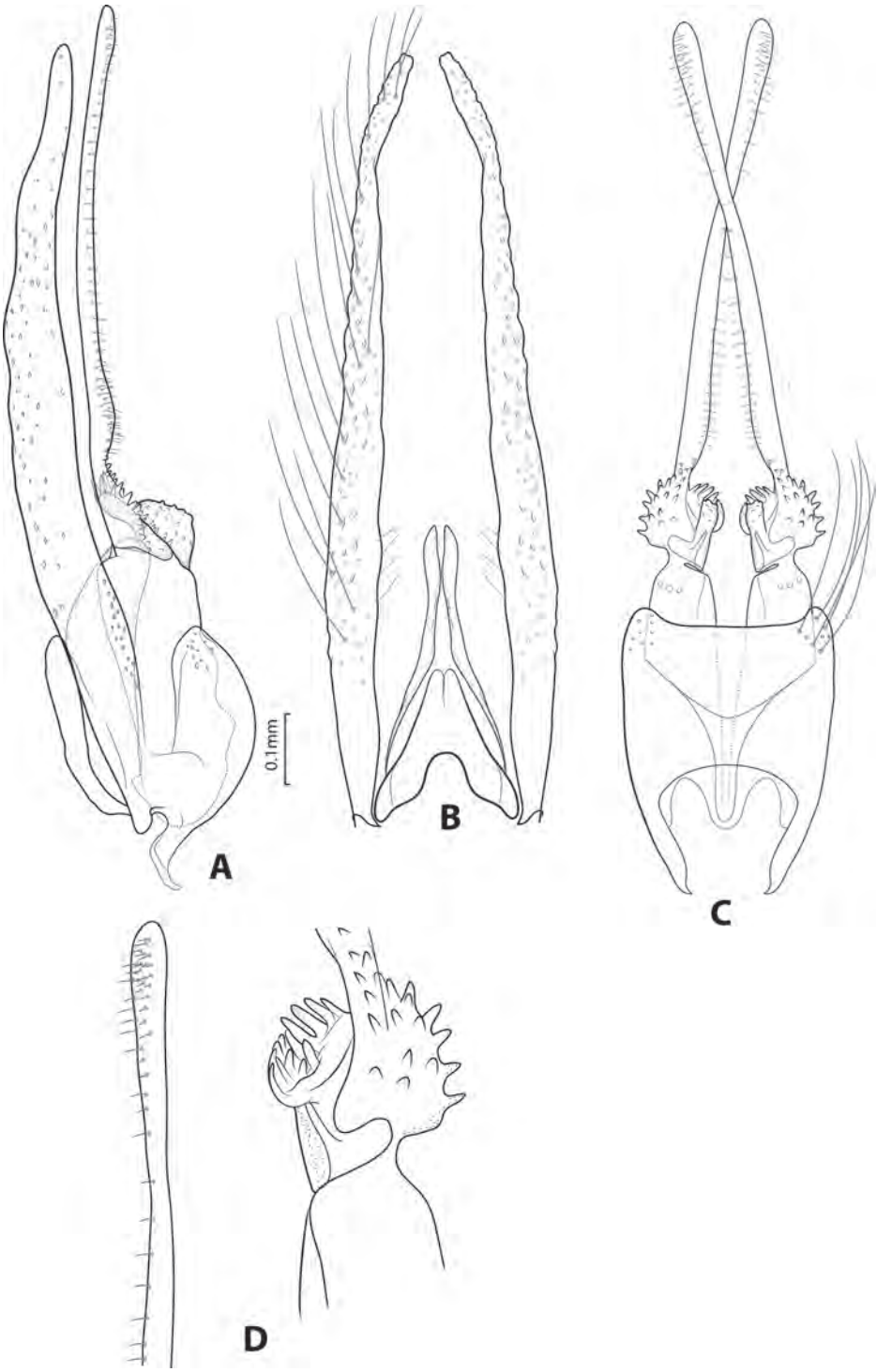

Figure 13. *Machairocentron eugeniarguedasae* **sp. nov.**: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures. Adult wing pattern is unknow.

Female genitalia (Fig. 17A–C). Segment VIII synscleritous, membranous dorsally; each anterolateral margin with thin, elongated apodeme extending anterad to segment VI. Intersegmental membrane VIII-IX well developed. Segment IX tubular, opened ventrally, longer than segment VIII, half-length included inside segment VIII; each anterolateral margin with thin, elongated apodeme extending until segment VI; apodeme of segment X fused along the sides of segment IX. Segment X short distinctly more sclerotized than the previous segment, covered with sensillae; mesally with small rod. Cerci not visible.

Material examined. **Holotype. COSTA RICA: Guanacaste**: Area de Conservacion Guanacaste; Sector San Cristobal, Estación San Geraldo, 10.8801N, -85.3889W, el. 575 m, 21.x.2013, malaise trap, D.H. Janzen & W. Hallwachs (♂ in alcohol, BIOUG20201-C08).

Paratypes. COSTA RICA: Guanacaste, same data as holotype, except, 7.x.2013 (♀ BIOUG19941-H01); 4.xi.2013 (♀ BIOUG22784-B12); 9.vii.2013 (♀ BIOUG 19725-A05).

Distribution. Costa Rica.

Etymology. Machairocentron eugeniarguedasae is named in honor of Sra. Eugenia Arguedas Montezuma in recognition of her dedication and contributions to Costa Rica's biopolitical liason between the Costa Rican Ministry of Environment and Energy, and the global Convention for Biological Diversity.

***Machairocentron kalinae* sp. nov.**

Fig. 15A–E

ZooBank: http://zoobank.org/38238D20-328F-42E5-B1E5-1115A2DBE17A

Diagnosis

Machairocentron kalinae can be distinguished from other congeners by being the only with the apex of tergum IX setose (Fig. 15B). The apical region of the harpago is short, with the apex enlarged having a line of multiple setae (Fig. 15C, D), like *M. teucrus*, *M. tarpeia* and *M. chorotegae*, but in *M. kalinae* the apex has a tapered projection (Fig. 15A).

Description

Adult. Forewing length 3.0 mm. Forewing uniformly dark brown. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX as long as wide; in dorsal view, triangular, anterior margin broadly concave, U-shaped; posterior margin tapered, apex setose, mesally cleft producing 2 well separated lobes (Fig. 15B). Sternum IX, in lateral view, narrow, about 3x longer than high, posterodorsal margin concave basally, straight apically, ventral margin convex, anterior margin with apodeme, apodeme as long as 2/3 length of sternum; in ventral view, anterior margin concave, posterior margin concave, lateral margins convex, lateral edges with long setae (Fig. 15C). Tergum X membranous. Intermediate appendage sclerotized; in lateral view, oblong, apex rounded, with numerous

DOI 10.1163/1876312X-bja10013

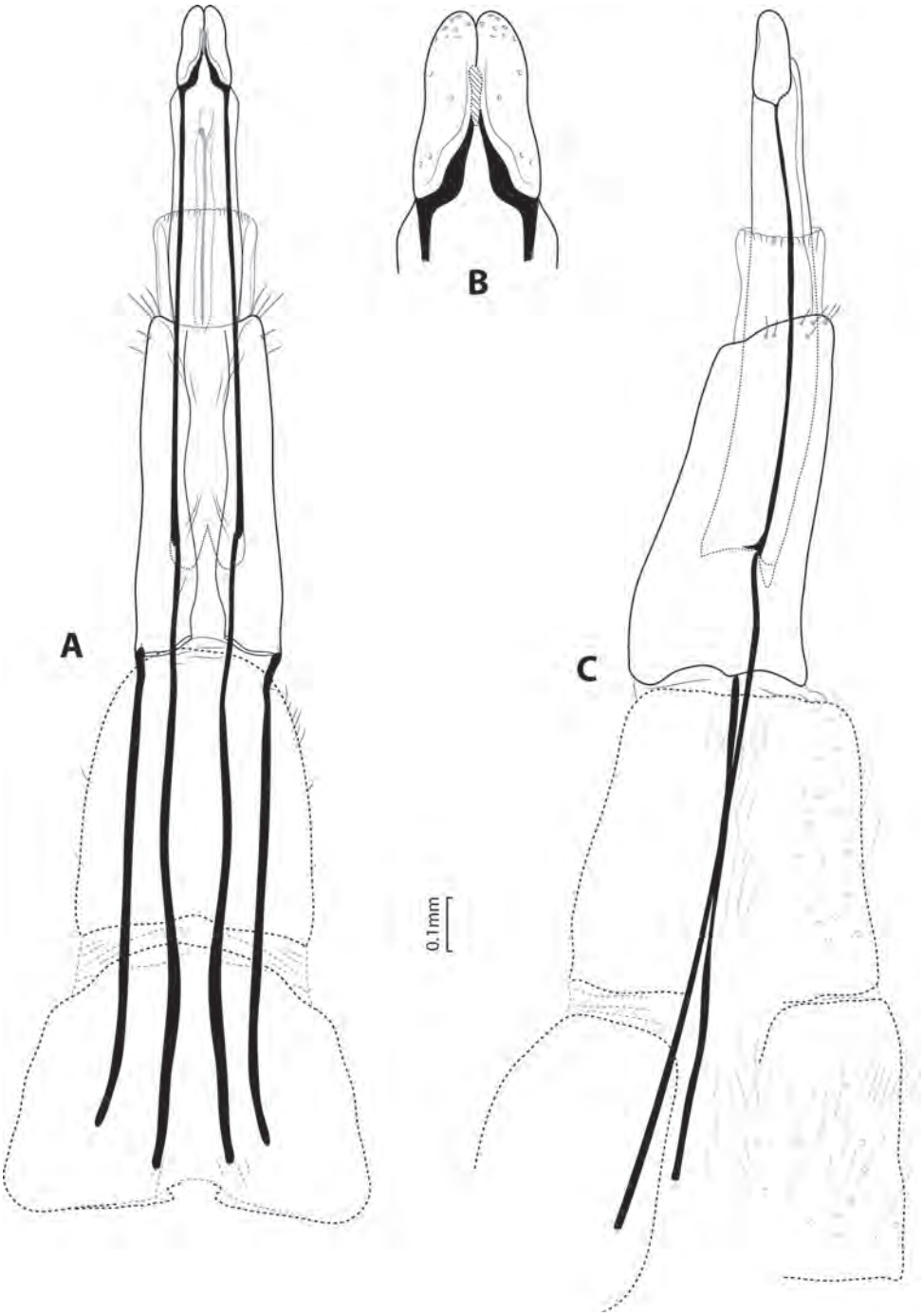

Figure 14. *Machairocentron eugeniarguedasae* **sp. nov.**: Female genitalia: (A) dorsal; (B) detail of X segment, dorsal; (C) lateral.

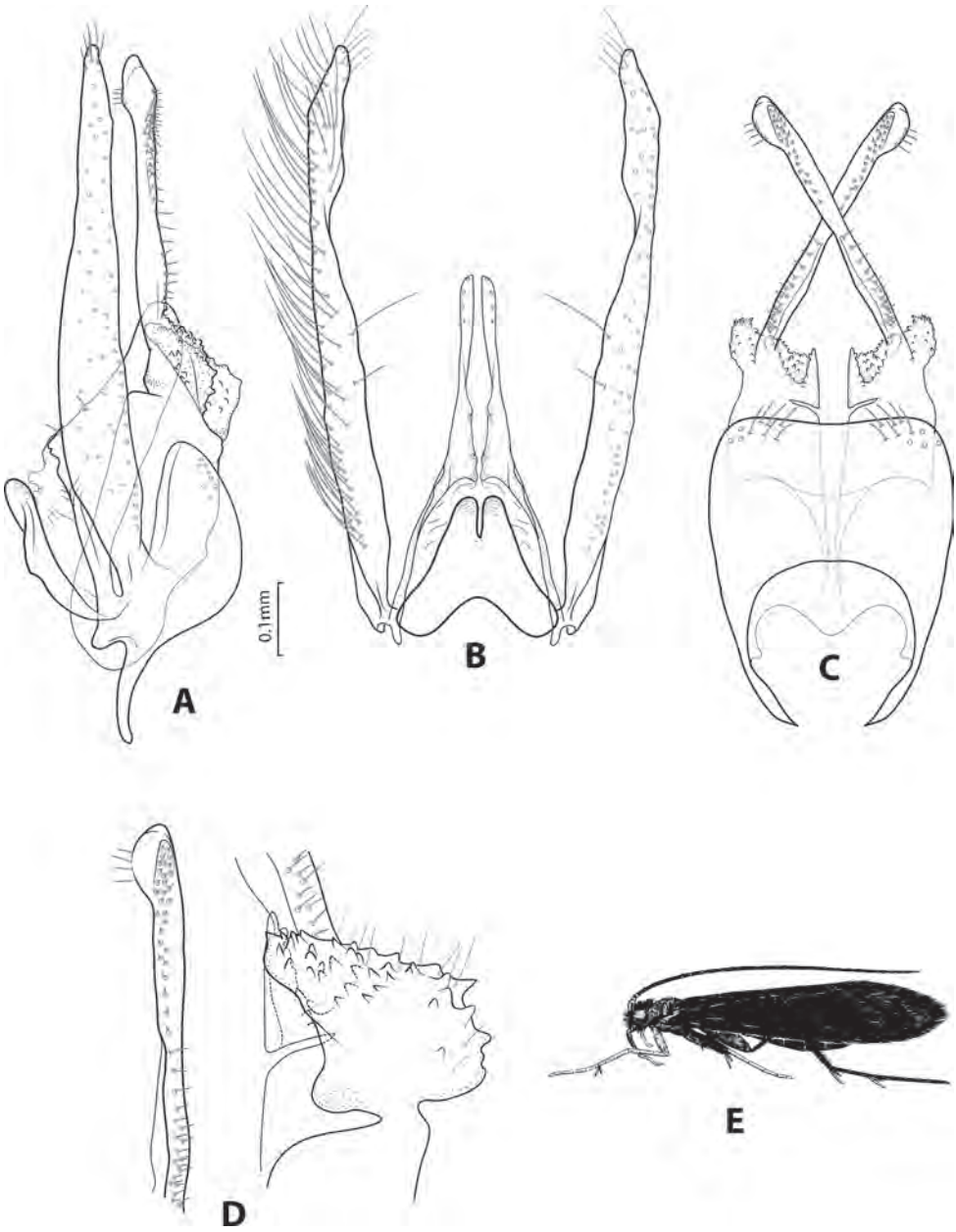

Figure 15. *Machairocentron kalinae* **sp. nov.**: Male genitalia: (A) lateral; (B) dorsal; (C) ventral; (D) detail of harpago structures, dorsal; (E) adult.

sensilla; in dorsal view, tapered apically, separated mesally throughout length, with 2 pairs of setae at mid length. Preanal appendage long, 3x length of tergum IX, densely setose; in lateral view, narrower at base, tapered apically; in dorsal view, straight, with subapical constriction, apex tapered. Inferior appendage as long as preanal appendage, bi-segmented. Coxopodite with long setae ventrally. Harpago basal region short,

DOI 10.1163/1876312X-bja10013

sclerotized; lateral projection anterior margin quadrate, covered with spines; mesal projection oblong, rounded dorsally, covered with small spines; apical region of harpago elongate, narrow, about 3x length of basal region, semimembranous basomesally, mesal margin with row of setae from base to apex, apex enlarged, with set of setae mesally and row of multiple setae ventrally (Fig. 15C, D). Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Material examined. **Holotype. VENEZUELA: Sucre:** Península de Paria, Santa Isabel, Rio Sta. Isabel, 10°44.294'N, 62°38.954'W, el. 20m, 4.iv.1995, R.W. Holzenthal, O.S. Flint, C. Cressa. (♂ pinned, USNMENT01518182 – DNA Voucher: 10OFCAD-123).

Paratypes. VENEZUELA: Puerto Viejo: "Rio el Pozo", 10°43.073'N, 62°28.569'W, 3.iv.1995 (♂ pinned, USNM), (♂ pinned, UMSP000146115 – DNA Voucher: 09MNKK0390).

Distribution. Venezuela.

Etymology. Kalina, also known as the Caribs, Caraíbas, and several other names, are an indigenous people native to the northern coastal areas of South America. The Kalina inhabited the coast from the mouth of the Amazon River to the Orinoco River, dividing their territory with the Arawak, against whom they fought during their expansion.

Additional material examined

The following specimens do not clearly fit into the species previously described. However, a single individual is available for each morphotype and some of these morphotypes have structures apparently damaged. More individuals will be needed to conclusively understand if they are different species or not.

***Machairocentron morphotype* A**
Fig. 16A–D

Material examined. **ECUADOR: El Oro:** Pinas/Zaruma, rio La Calera 19–20. viii.1977, L.E. Pena (♂ pinned, USNM).

Remarks. The specimen has the mesal lobe of the harpago similar to that of *M. chorotegae*, but the apical region of the harpago is longer and the apex not enlarged; the anterior margin of tergum IX also lacks the narrow central concavity present in *M. chorotegae*. The forewing is completely dark brown without any spots.

***Machairocentron* morphotype B**
Fig. 17A–D

Material examined. **ECUADOR: Orellana:** Reserva de Biodiversidad Tiputini, river slough, Numa Trail, 00.63954°S, 76.14836°W, el. 260m, 23.x.2011, R.W. Holzenthal & B. Rios (♂ pinned, UMSP0098453).

Remarks. Tergum IX is damaged. Spines on the harpago are very small in comparison with *M. echinatum*. The specimen has a single white spot on the forewing.

***Machairocentron morphotype* C**
Fig. 18A–D

Material examined. **PERU: Madre de Dios:** 13°251S, 70°2046W; el. 382m, 23–31. viii.2012, malaise trap, R.R. Cavichioli, J.A. Rafael, A.P.M. Santos & D.M. Takiya (♂ alcohol, DZRJ).

Remarks. Each harpago is strongly bent (apparently due to damage). The specimen is similar to *M. echinatum* although the mesal lobe of the harpago lacks the conspicuous spines, and he apex of tergum IX is elongate. The specimen is in alcohol, and the wing is devoid of hairs, hence the wing maculation is unknown.

Discussion

Machairocentron shares with *Xiphocentron* (*Xiphocentron*) *tarquon*, and *X.* (*Xiphocentron*) *polemon* the very elongate harpago, an intermediate state of fusion between the coxopodite and harpago with visible sutures, and the long setae on the lateral sides of sternum IX. The structure of the intermediate appendage of *Machairocentron* seems to be ancestral in relation to the structure in *X.* (*Xiphocentron*) *tarquon* and *X.* (*Xiphocentron*) *polemon*. The plesiomorphic condition of the intermediate appendage in Xiphocentronidae probably is similar to the one present in *Proxiphocentron* (Figs 19D, 20C) and in the Psychomyiidae: *Eoneureclipsis* (Fig. 20A) and *Tinodes* (Figs 19E, 20B), in which the two intermediate appendages are completely separated mesally. In *Proxiphocentron* each intermediate appendage has a basodorsal lobe bearing one or two stout setae (Figs 19D, 20C). In *X.* (*Xiphocentron*) *aureum*, *X.* (*Xiphocentron*) *asilas*, *X.* (*Xiphocentron*) *bilimekii*, and *Machairocentron* each intermediate appendage has a dorsal rim bearing a pair of setae (Fig 19B, C, 20D) that seems to be homologous to those basodorsal lobes of *Proxiphocentron*. *Xiphocentron tarquon*, *X. polemon*, and most Xiphocentroninae have the two intermediate appendages broadly fused together, with the vestigial basodorsal lobe appearing just as a sclerotized band (Figs 19A, 20E). The tergum IX of *Machairocentron* has the apex produced (sub-triangular) (Fig. 19B), a feature absents in *Xiphocentron* (*Xiphocentron*) subgenus (Fig. 19A, C), and common among *X.* (*Antillotrichia*), and *X.* (*Sphagocentron*) species.

Within the genus *Machairocentron*, there is a clearly defined species group comprising *Machairocentron echinatum*, *M. falciforme*, *M. lucumon*, and *M. eugeniarguedasae* characterized by the apical region of harpago very elongate (about 3x tergum IX length) and often having a single row of setae along the harpago apex. All the other species have the apical region of the harpago shorter (less than 2x tergum IX length) with the apex enlarged and bearing numerous setae (Fig. 10C–D).

Based on the distribution data (Fig. 1), *Machairocentron* is widespread in the Mesoamerica and Amazon basin, although the rarity in which the group is collected certainly biases our understanding of its actual diversity, distribution, and evolution. This revision will provide a taxonomic foundation for the placement of new species within the group.

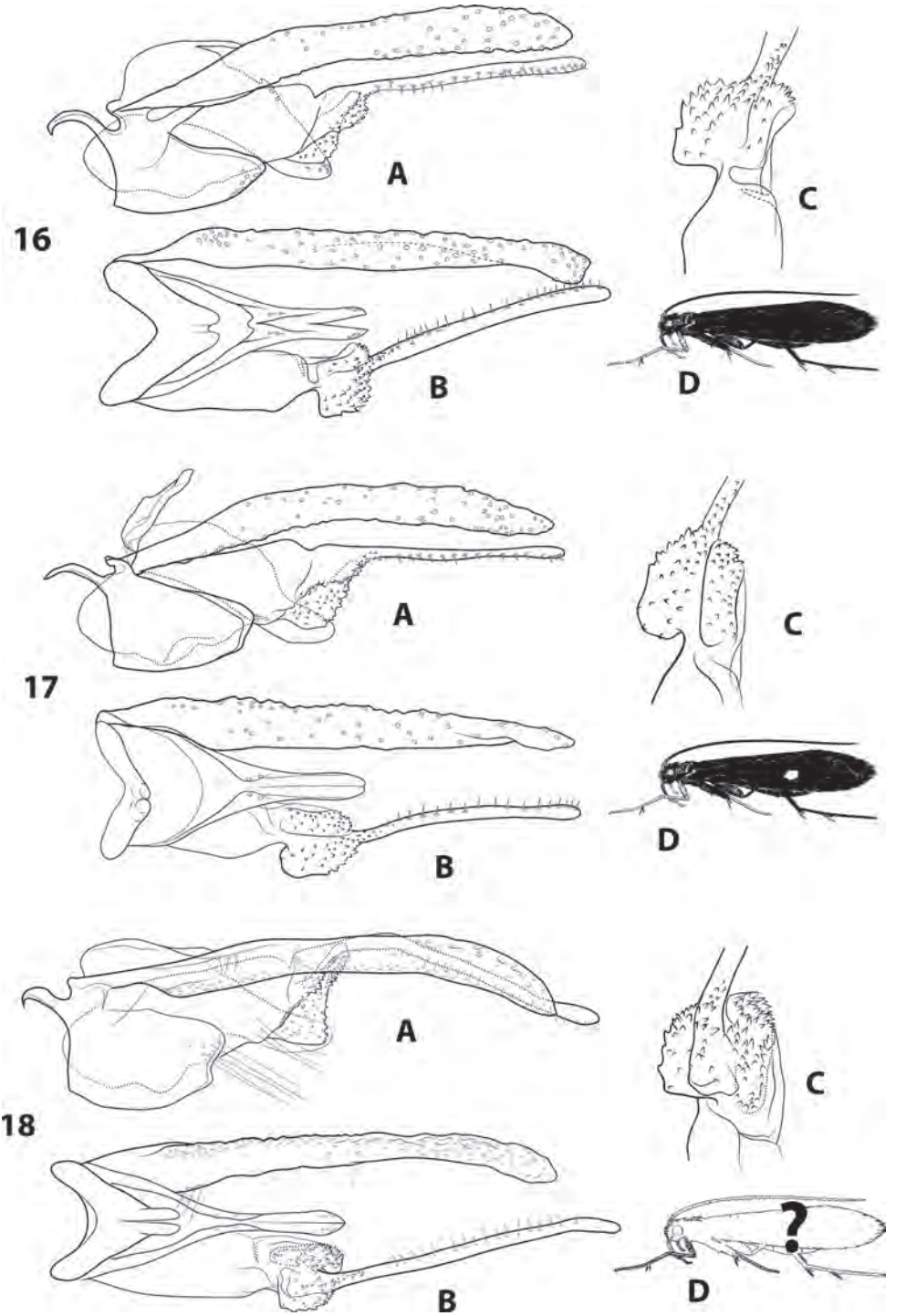

Figure 16–18. *Machairocentron* undescribed morphotypes. Male genitalia: (A) lateral; (B) dorsal; (C) detail of harpago structures, dorsal; (D) adult. (16) morphotype A, (Ecuador: El Oro); (17) morphotype B, (Ecuador: Orellana); (18) morphotype C, (Peru: Madre de Dios), adult wing pattern unknown.

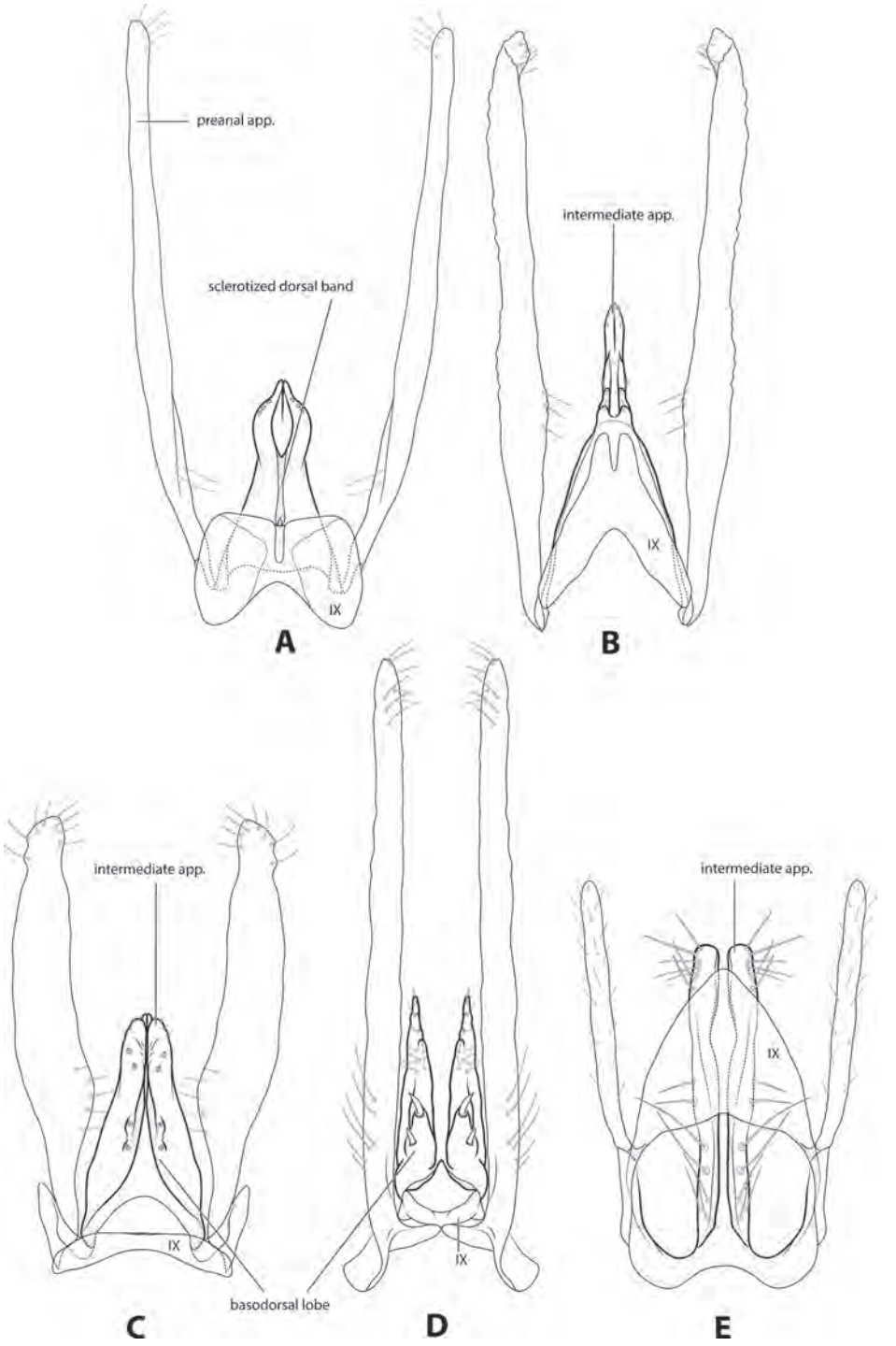

Figure 19. Psychomyioidea male genitalia, dorsal: (A) *Xiphocentron* (*Xiphocentron) tarquon*; (B) Machairocentron ascanius; (C) *Xiphocentron (Xiphocentron) aureum*; (D) *Proxiphocentron arjinae*; (E) *Tinodes consueta*.

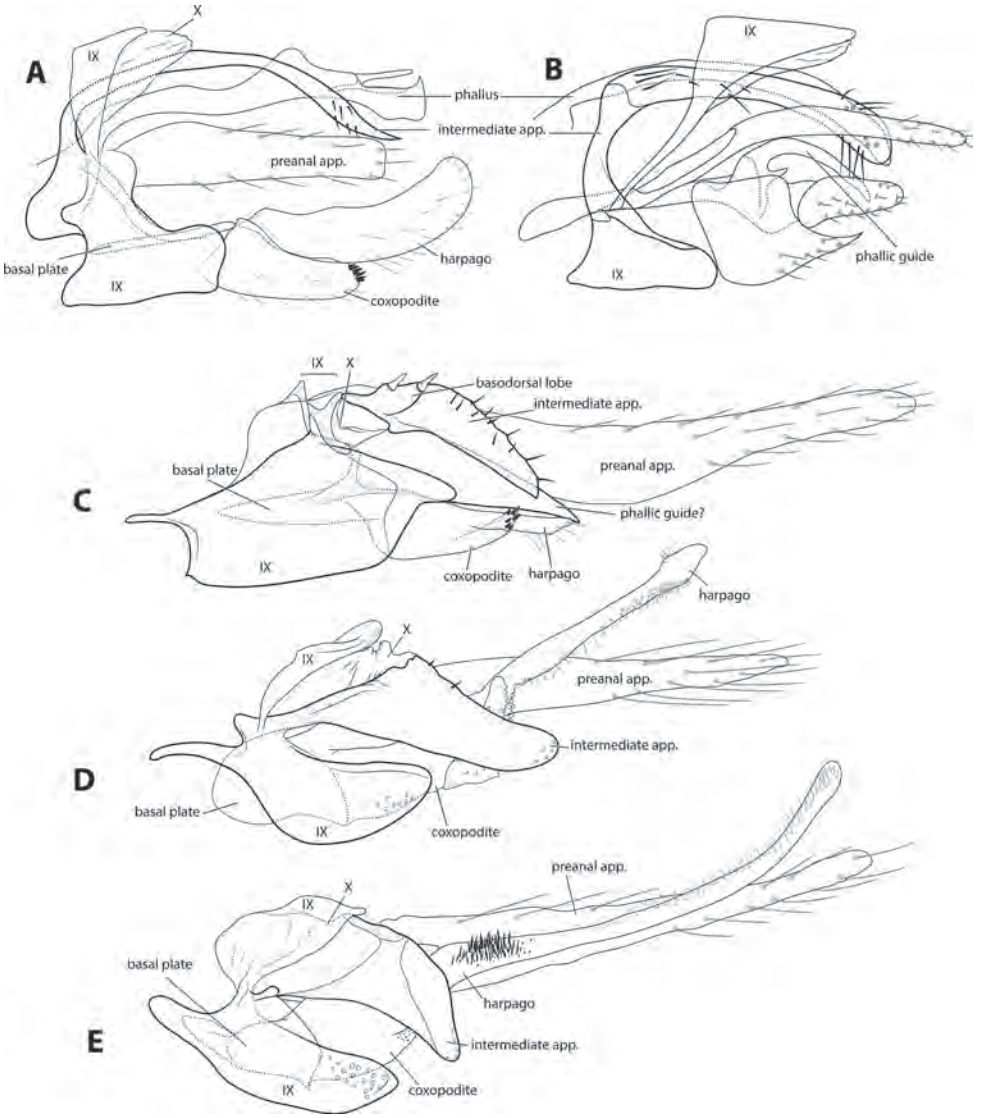

Figure 20. Psychomyidae male genitalia, lateral: (A) *Eoneureclipsis varsikiyja* (modified from Schmid 1972); (B) *Tinodes consueta.* Xiphocentronidae male genitalia, lateral: (C) *Proxiphocentron arjinae*; (D) *Machairocentron kalinae*; (E) *Xiphocentron* (*Xiphocentron*) *tarquon*.

Key to Neotropical Xiphocentronidae

1. Mesoscutal setal warts modified in a quadrate mesoprescutum. Phallus tubular, extremely elongated (reaching anterad to segment V), without phallic sclerites or spines ..... 2 (Xiphocentronidae)
   Mesoscutal setal warts absent or rounded. Phallus not so elongated, phallic sclerites and spines absent or present..... other families

2(1) Apicoventral margin of sternum IX between the inferior appendages with a patch of longate stout setae. Inferior appendage strongly bifurcated, with the gonocoxite forming a produced projection ..... ***Cnodocentron*** Schmid 1982
Apicoventral margin of sternum IX without conspicuous set of spines, or setae; gonopod linear, coxopodite not strongly produced 3

3(2) Inferior appendage with coxopodite and hapago clearly distinct, base of harpago strongly sclerotized, overall covered with tubercles and short spines, swoolen laterally and forming a broad mesal projection, harpago very elongated. (The female of *Machairocentron* can be distinguished from the other described Xiphocentronidae females by the very sclerotized segment X) .....
..... ***Machairocentron*** Schmid 1982
Inferior appendage with coxopodite and harpago fused or not, base of harpago never forming broad sclerotized projection, with rows or patches of spines, sometimes forming a distinct polyp-like mesal sclerite..... ***Xiphocentron*** Brauer 1870

Key to adult male of *Machairocentron*

1. Apical region of harpago short, less than 2x tergum IX length; apex enlarged with setae in multiple rows (Fig. 9A–C) 2
Apical region of harpago very long, about 3x tergum IX length; apex not enlarged usually with setae in a single linear row (Figs 4A–C) 6

2(1) Mesal projection of harpago with spines conspicuously elongated, finger-like (Fig. 9D) ..... ***Machairocentron tarpeia*** Schmid 1982
Mesal projection of harpago with small spines (Fig. 3D) 3

3(2) Lateral projection of harpago with margins rounded (Fig. 9D) 4
Lateral projection of harpago with margins basally angulated (Fig. 11D)..... 5

4(3) Mesal projection of harpago densely covered with spines (Fig. 10C, D); anterior margin of tergum IX in dorsal view with a narrow V-shaped concavity (Fig. 10B); preanal appendage in lateral view apically narrower than in middle-length (Fig. 10A) ..... ***Machairocentron teucrus*** Schmid 1982
Mesal projection of harpago with some sparse spines (Fig. 3C, D); anterior margin of tergum IX in dorsal view with a wide U-shaped concavity (Fig. 3B); preanal appendage in lateral view apically broader than in middle-length (Fig. 3A)
..... ***Machairocentron ascanius*** Schmid 1982

5(3) Mesal projection of harpago in dorsal view with radula-like spines (Fig. 11D); tergum X apex without setae; forewing with a white spot (Fig. 11E) .....
..... ***Machairocentron chorotegae*** **sp. nov.**
Mesal projection of harpago in dorsal view spines not radula-like (Fig. 15D); tergum IX apex setose (Fig. 15B); forewing dark brown without any white spot
..... ***Machairocentron kalinae*** **sp. nov.**

6(1) Mesal projection of harpago with elongated spines (Figs 4D, 5A–D); lateral projection in dorsal and ventral views not extending anterad (Figs 9C–D, 10C–D, 11C–D, 13C–D) 7

Mesal projection of harpago with small spines (Fig. 8D); lateral projection in dorsal and ventral views extending anterad (6C–D, 8C–D)..... 8

7(6) Mesal projection apex in dorsal view, with line of very long finger-like spines curved upward on the mesal margin, in lateral view spines as long as mesal lobe width (Fig. 13D); harpago apex enlarged, with many setae (Fig. 13C); tergum IX anterior margin with narrow U-shaped concavity (Fig. 13B) ....***Machairocentron eugeniarguedasae*** **sp. nov.**

Mesal projection apex in dorsal view, with long spines however not curved upward, in lateral view spines shorter than mesal lobe width (Fig. 4D); harpago apex not enlarged with a single row of setae; tergum IX anterior margin with broad concavity (Fig. 4B) ..... ***Machairocentron echinatum*** (Flint 1981)

8(6) Apical region of harpago more than 4x basal region length (Fig. 8C); tergum IX dorsal view with a pair of sclerotized transversal lines near the apex; preanal appendages in dorsal view enlarged at the apex; forewing wing without white spots (Fig. 8E).....***Machairocentron lucumon*** Schmid 1982

Apical region of harpago less than 3x basal region length (Fig. 6C); tergum IX dorsal view without any sclerotized transversal line near the apex; preanal appendages in dorsal view tapered at the apex; forewing wing with two white spots (Fig. 6E).....***Machairocentron falciforme*** Pes & Hamada 2013

Acknowledgements

This work was supported by the Brazilian National Council for Scientific and Technological Development (CNPq), under Grant 205447/2017-1 and 140267/2016-6. The research was also supported by University of Minnesota Agricultural Experiment Station project AES 17-094. We are grateful for the assistance of the various curators that provided access to specimens: Dr. Daniel H. Janzen (BIOUG); Dr. Owen Lonsdale (CNC); Dr. Daniela M. Takiya (DZRJ); Dr. Eliana M. Cancello (MZSP); Dr. Tobias Malm (NHRS); Dr. Torsten Dikow (USNM) and Dr. Oliver Flint (USNM), in memoriam. We also appreciate the reviewers' and the editor's valuable comments and suggestions on our manuscript.

References

Aguila, Y. (1992) Systematic catalogue of the caddisflies of Panama (Trichoptera). *In*: Quintero D, Aiello A (Eds.) Insects of Panama and Mesoamerica: Selected Studies. Oxford University Press, Oxford, 532–548.

Armitage, B.J. & Cornejo, A. (2015) Orden Trichoptera (Insecta) en Panamá: Listas de especies y su distribución por cuencas y unidades administrativas. *Puente Biológico* **7**: 175–199.

Armitage, B.J., Harris, S.C., Arefina-Armitage, T.I. & Cornejo, A. (2015) The Trichoptera of Panama. III. Updated species list for caddisflies (Insecta: Trichoptera) in the Republic of Panama. *Insecta Mundi* **0442**: 1–16.

Blahnik, R.J., Holzenthal, R.W. & Prather, A.L. (2007) The lactic acid method for clearing Trichoptera genitalia. In: Bueno-Soria, J., Barba-Álvarez, R., & Armitage, B. (Eds.), *Proceedings of the 12th International Symposium on Trichoptera*, The Caddis Press, Columbus, Ohio, pp. 9–14.

Brauer, F. (1870) Ueber *Xiphocentron*. eine neue Hydropsychidengattung. Verhandlungen der Kaiserlich-königlichen. *Zoologischen-Botanischen Gesellschaft in Wien* **20**: 66.

Edwards, S.W. (1961) The immature stages of *Xiphocentron mexico* (Trichoptera). *Texas Journal of Science* **13**: 51–56.

Flint, O.S. Jr. (1968) The Caddisflies of Jamaica. *Bulletin of the Institute of Jamaica, Science Series* **19**: 1–68.

Flint, O.S. Jr. (1981) Studies of Neotropical caddisflies, XXVIII: the Trichoptera of the Rio Limón basin, Venezuela. *Smithsonian Contributions to Zoology* **330**: 1–60. doi: 10.5479/si.00810282.330.

Flint, O.S. Jr., Holzenthal, R.W. & Harris, S.C. (1999) Nomenclatural and systematic changes in the Neotropical caddisflies. *Insecta Mundi* **13**: 73–84.

Holzenthal, R.W. & Calor, A.R. (2017) Catalog of the Neotropical Trichoptera (Caddisflies). *ZooKeys* **654**: 1–566. doi: 10.3897/zookeys.654.9516.

Mosely, M.E. (1948) Trichoptera. Expedition to South-West Arabia 1937-1938. *British Museum (Natural History)* **1**: 67–86.

Mosely, M.E. & Kimmins, D.E. (1953) The Trichoptera of Australia and New Zealand. *Trustees of the British Museum (Natural History), London*. doi:10.5962/bhl.title.118696.

Muñoz-Quesada, F. & Holzenthal, R.W. (1997) A new species of *Xiphocentron* (*Antillotrichia*) from Costa Rica with semiterrestrial immature stages (Trichoptera: Xiphocentronidae). *In*: Holzenthal, R.W., Flint, O.S. Jr. (Eds.) *Proceedings of the 8th International Symposium on Trichoptera*. Columbus, Ohio, Ohio Biological Survey. 355–363.

Nielsen, A. (1957) A comparative study of the genital segments and their appendages in male Trichoptera. *Biologiske Skrifter, Danske Videnskabernes Selskab* **8**(5): 1–159.

Nielsen, A. (1980) A comparative study of the genital segments and the genital chamber in female Trichoptera. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* **23**: 1–200.

Oláh, J. & Johanson, K.A. (2007) Trinominal terminology for cephalic setose warts in Trichoptera (Insecta). *Braueria* **34**: 43–50.

Paprocki, H. & França, D. (2014) Brazilian Trichoptera Checklist II. *Biodiversity Data Journal* 2 **e1557**: 1–109. doi: 10.3897/BDJ.2.e1557.

Pes, A.M, Hamada, N. & Nessimian, J.L. (2005) Chaves de identificação de larvas para famílias e gêneros de Trichoptera (Insecta) da Amazônia Central, Brasil. *Revista Brasileira de Entomologia* **49**(2): 181–204.

Pes, A.M., Hamada, N., Nessimian, J.L. & Soares, C.C. (2013) Two new species of Xiphocentronidae (Trichoptera) and their bionomics in Central Amazonia, Brazil. *Zootaxa* **3636**(4): 561–574.

Prather, A.L. (2003) Revision of the Neotropical caddisfly genus *Phylloicus* (Trichoptera: Calamoceratidae). *Zootaxa* **275**: 1–214.

Ríos-Touma, B., Holzenthal, R.W., Huisman, J., Thomson, R., & Rázuri-Gonzales, E. (2017) Diversity and distribution of the caddisflies (Insecta: Trichoptera) of Ecuador. *PeerJ* **5: e2851**: 1–26. doi: 10.7717/peerj.2851.

Ross, H.H. (1949) Xiphocentronidae, a new family of Trichoptera. *Entomological News* **60**: 1–7.

Schmid, F. (1982) La famille des Xiphocentronidae (Trichoptera: Annulipalpia). *Mémoires de la Société Entomologique du Canada* **121**: 1–127. doi: 10.4039/entm114121fv.

Sturm, H. (1960) Die terrestrischen Puppengehäuse von *Xiphocentron sturmi* Ross Xiphocentronidae, Trichoptera). Zoologische Jahrbücher, Abteilung für Systematic kologie und Geographie der Tiere **87**: 387–394.

Ulmer, G. (1906) Neuer beitrag zur kenntnis aussereuropäischer Trichopteren. *Notes from the Leyden Museum* **28**: 1–116.

Wiggins, G.B (1996) *Larvae of the North American caddisfly genera (Tichoptera), second edition*. University of Toronto Press, Toronto, Ontario, 457 pp.