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Research article

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Xiphocentronidae (Trichoptera: Psychomyioidea) from the Andean foothills: first species of *Machairocentron* and *Xiphocentron* described in the Peruvian Amazon

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Abstract. Neotropical Xiphocentronidae may have arrived in South America from Central America in the late Miocene or via the Greater Antilles land bridge during the Oligocene. This would give from 10 to 30 Mya of diversification of the family in South America. However, only 11 species were previously known from the Andean foothills. In this study, five new species are described from Peru, four of *Xiphocentron* (*X. ashaninka* sp. nov., *X. harakbut* sp. nov., *X. matsigenka* sp. nov., *X. yine* sp. nov.) and one of *Machairocentron* (*M. amahuaca* sp. nov.). The new species are most similar to species described from the Yungas of Argentina, and the Pacific dominion of Colombia and Venezuela. The association with species from the Pacific may suggest a species divergences prior to the major Andean uplift and the Amazon basin formation. The spine-like setae on the basal region of the inferior appendage of *Xiphocentron* were recognized as topologically homologous to the setal brushes on the ventral projection of *Caenocentron*. Furthermore, based on the morphology of male and female genitalia of *Machairocentron*, a mating position different from that described for Psychomyiidae is inferred.

Keywords. Aquatic insects, Annulipalpia, caddisflies, Neotropical, taxonomy.

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Introduction

Xiphocentronidae Ross, 1949 (Trichoptera Kirby, 1813: Psychomyioidea Ivanov, 2002) is a small net-tube caddisfly family that diverged from the Psychomyiidae lineage in the early Cretaceous (120 Mya)

(Malm *et al.* 2013; Thomas *et al.* 2020) and are now found in small streams and waterfalls throughout the tropical zone, with a high diversity in Mesoamerica and Southeast Asia (Vilarino & Bispo 2020). Unlike most Trichoptera, adults of Xiphocentronidae are active during the day (Flint 1968; Schmid 1982) and their larvae have semi-terrestrial habits, living in serpentine silken galleries often built outside the water over moist rocks and logs, feeding on microalgae and surface debris (Sturm 1960; Muñoz-Quesada & Holzenthal 1997; Pes *et al.* 2013). The family currently includes 200 species worldwide, organized in eight genera and two subfamilies. The fauna of the New World ranges from the southern United States to northern Argentina and consists of 76 species organized into three genera: *Caenocentron* Schmid, 1982 (9 spp.), *Machairocentron* Schmid, 1982 (9 spp.), and *Xiphocentron* Brauer, 1870 (58 spp.) (Holzenthal & Calor 2017; Vilarino & Bispo 2020; Vilarino & Holzenthal 2020; Vilarino *et al.* 2022; Bueno-Soria *et al.* 2022).

The classification of Xiphocentronidae was defined by Schmid (1982) through a world fauna revision, establishing new genera based on their degree of differentiation from the previous genus *Xiphocentron*. However, the new circumscription of *Xiphocentron* was poorly defined and was mainly based on the absence of characters present in the other genera. *Xiphocentron* is traditionally classified into five loosely defined subgenera: *Glyphocentron* Schmid, 1982; *Rhamphocentron* Schmid, 1982; *Sphagocentron* Schmid, 1982; *Xiphocentron* Brauer, 1870; and *Antillotrichia* Banks, 1941; with the latter serving as a receptacle for unclassified species according to Schmid (1982). Therefore, it is clear that the genus *Xiphocentron* is in need of revision. Furthermore, a phylogenetic analysis did not support the monophyly of the genus *Xiphocentron*, with clades of *Caenocentron* and *Machairocentron* diverging from a *Xiphocentron* stock (Vilarino *et al.* 2022). The genus *Machairocentron* was recently revised, and adult males are identified by sclerotized, swollen, and rugose mesal and lateral projections at the base of the harpago (Vilarino & Holzenthal 2020). *Cnodocentron* Schmid, 1982 was also recently revised, and a phylogenetic analysis revealed that *Cnodocentron* sensu Schmid was polyphyletic, resulting in the elevation of its included subgenera *Cnodocentron* (South-East Asia) and *Caenocentron* (New World) to generic status. *Caenocentron* is diagnosed mainly by the apical and ventral projections of the coxopodite, with the ventral projection bearing elongate setae (Vilarino *et al.* 2022).

In South America there are 27 known species of Xiphocentronidae, including one *Caenocentron* species from Colombia, three *Machairocentron* species from Colombia, Ecuador, Venezuela, and Brazilian Amazon, and 23 *Xiphocentron* species from Argentina, Brazil, Colombia, Venezuela, and Suriname (Holzenthal & Calor 2017; Ríos-Touma *et al.* 2017; Vilarino & Bispo 2020; Vilarino & Holzenthal 2020; Vilarino *et al.* 2022). All of the *Xiphocentron* in South America have been placed in the subgenus *Antillotrichia* (Holzenthal & Calor 2017; Vilarino & Bispo 2020). Eleven species of the three Xiphocentronidae genera are recognized in western South America, along the Northern and Central Andes foothills (Fig. 1), including an unidentified *Xiphocentron* (a female) and species of *Machairocentron* previously reported from Ecuador and Peru (Ríos-Touma *et al.* 2017; Vilarino & Holzenthal 2020).

Herein, we present the first xiphocentronids from Peru, describing five new species, being four of *Xiphocentron* (*Antillotrichia*) and one of *Machairocentron*.

Material and methods

The new species hypotheses were based on distinct male genital characters which were used as an indirect indicator of reproductive isolation and divergence of independent evolutionary units. To visualize internal structures, the entire abdomen of each specimen was removed and diaphanized using 85% lactic acid (Blahnik *et al.* 2007). The abdomen was then placed in excavated glass slides with a drop of glycerin and examined with a compound microscope at a magnification of 200–400×; it was then stored in a microvial with 80% ethanol and kept with the remainder of the respective specimen. All

species were conserved in 80% ethanol. Illustrations of the genitalia were traced in pencil using a camera lucida attached to a microscope, then scanned and digitally traced using Adobe Illustrator CS6 software. For convenience and clarity of the structures, the setae were often omitted in the illustrations, which may show only the insertion sockets. The paired appendages may also have one of their sides omitted in the illustrations. The phallus is depicted in full length only for *Xiphocentron matsigenka* sp. nov., being the same in other species. Photographs of specimen parts were taken with a digital camera attached to a compound microscope and stacked using the software CombineZP. The distribution map (Fig. 1) was created with the QGIS ver. 2.8.2 software, using the shapefiles of Morrone *et al.* (2022). The utilized biogeographic regionalization is from Morrone (2014).

The morphological terminology for male genitalia is modified from Nielsen (1957) and Schmid (1982). The segment X *sensu* Schmid (1982) is a composite structure (Nielsen 1957; Oláh & Johanson 2008) and most of it is considered homologous to the paraproctal process of Psychomyiidae, as discussed in Vilarino & Holzenthal (2020). The terminology for wing venation followed the Comstock-Needham system as interpreted for Trichoptera by Mosely & Kimmins (1953). In species descriptions, paired structures are referred to in the singular form.

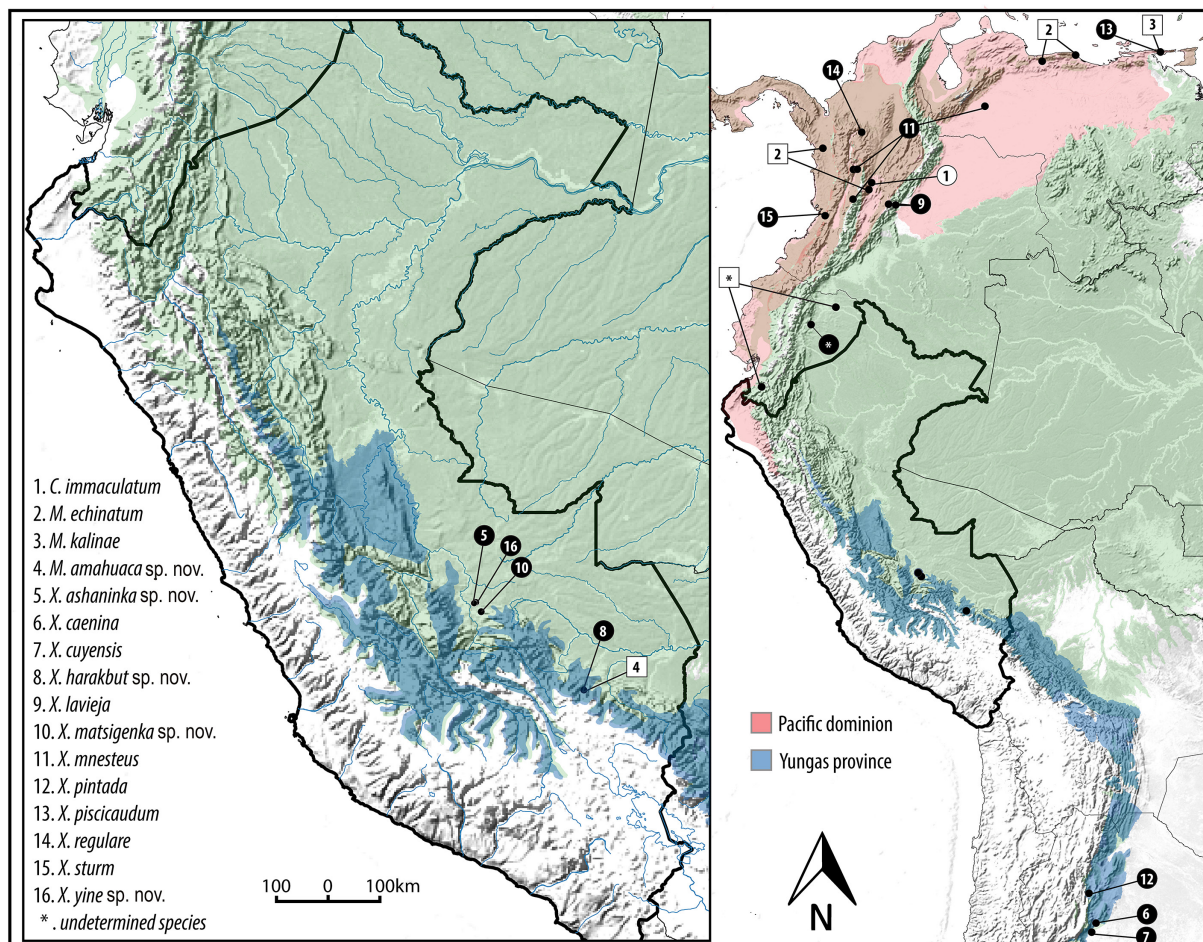


Fig. 1. Distribution of species of Xiphocentronidae Ross, 1949 in Western South America. Species of *Machairocentron* Schmid, 1982 are indicated in white boxes, those of *Xiphocentron* Brauer, 1870 in black circles and those of *Caenocentron* Schmid, 1982 in white circles. Tropical rainforests are shown in green.

The specimens examined are deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru and the Coleção Entomológica Professor José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro (DZRJ), Rio de Janeiro, Brazil. The new species were named after Peruvian indigenous peoples.

Results

Class Insecta Linnaeus, 1758
Order Trichoptera Kirby, 1813
Suborder Annulipalpia Martynov, 1924
Superfamily Psychomyioidea Ivanov, 2002
Family Xiphocentronidae Ross, 1949
Genus *Machairocentron* Schmid, 1982

Machairocentron amahuaca sp. nov.

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Figs 1, 2A, 3A, 4

Machairocentron morphotype C Vilarino & Holzenthal, 2020: 31, fig. 18.

Diagnosis

Machairocentron amahuaca sp. nov. is similar to *Machairocentron echinatum* (Flint, 1981) by the inferior appendage having a very elongated apical region, not enlarged apically, and having a single row of setae. It can be distinguished by: a) the mesal projection of the inferior appendage has shorter spines (Fig. 4B) and b) the ventral margin of the mesal projection forms a sharp right angle in lateral view (Fig. 4A), whereas it is rounded in other species.

Etymology

Named after the Amahuaca, an indigenous people whose language belongs to the Pano linguistic family. The name of the Amahuaca or “*amin waka*” has been translated as “children of the capybara”, an animal that is said to be able to “sing” in the native language of this people.

Material examined

Holotype

PERU • ♂; 19 rd km W of Cusco, Quincemil, Rio Araza tributary; 13°20'10.0" S, 70°50'57.00" W; elev. 874 m; 23–31 Aug. 2012; R.R. Cavichioli, J.A. Rafael, A.P.M. Santos and D.M. Takiya leg.; Malaise trap; MUSM-ENT-0320559.

Paratypes

PERU • 2 ♂♂; same collection data as for holotype; MUSM-ENT-0320560–0320561 • 2 ♂♂; same collection data as for holotype; DZRJ 8650–8651.

Description of male

BODY (Figs 2A, 3A). Forewing length 3.8–2.9 mm (n=5). Color overall dark brown with pale legs (in alcohol) (Fig. 2A). Maxillary palp segment length formula (I=II=III)<IV<V. Tibial spur formula 2:4:3; spurs unmodified. Venation: forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell about as long as thyridial cell. Hindwing forks II and V present. Sternum V with mammiliform reticulated projection (Fig. 3A).

GENITALIA (Fig. 4). Tergum IX, in lateral view, narrow (Fig. 4A); in dorsal view, anterior margin with deep, wide concave incision, U-shaped; posterior margin tapered, divided apicomesally by narrow incision about $\frac{1}{4}$ its length; apex of tergite rounded lobe (Fig. 4B). Sternum IX, in lateral view, about $1.5\times$ as long as high; anterior apodeme short, narrow, curved ventrad; apex deltoid (Fig. 4A); in ventral view, anterior margin strongly concave; posterior margin widely concave with very small mesal lobe (Fig. 4C). Paraproct, in lateral view, oblong, apex rounded (Fig. 4A); in dorsal view, each side unfused, with two pairs of setae at mid length (Fig. 4B); wide basally, tapering apically; divided apicomesally, with numerous sensillae on apex (Fig. 4B). Preanal appendage about $3.5\times$ as long as tergum IX, densely setose; in lateral view, wide, straight on basal $\frac{1}{3}$, slightly curved ventrad on apical $\frac{1}{3}$, tapering apically; in dorsal view, about same width throughout length, apex curved mesad (Fig. 4B). Inferior appendage longer than preanal appendage; bi-segmented, with dorsal and ventral incision between them (Fig. 4A–B). Coxopodite shorter than harpago, with long setae ventrally (Fig. 4A). Harpago basal region short, sclerotized; in lateral view, narrow and oblong dorsally, wide ventrally, posteroventral margin forming sharp right angle; apical region slender, digitate, more than $4\times$ length of basal region, bearing row of setae on mesal margin from base to apex (Fig. 4A); in ventral view, with lateral and mesal projections; lateral projection rounded, covered with small spines, with anterior margin straight and lateral margin crenulate; mesal projection oblong, mesal margin forming narrow flap, which circumscribes spiny concavity, apex rounded, densely covered with small spines (Fig. 4C). Phallus tubular, very long and slender, reaching segment V; basally conical, weakly sclerotized; in dorsal view, apex slightly enlarged, with mesal incision (Fig. 4D).

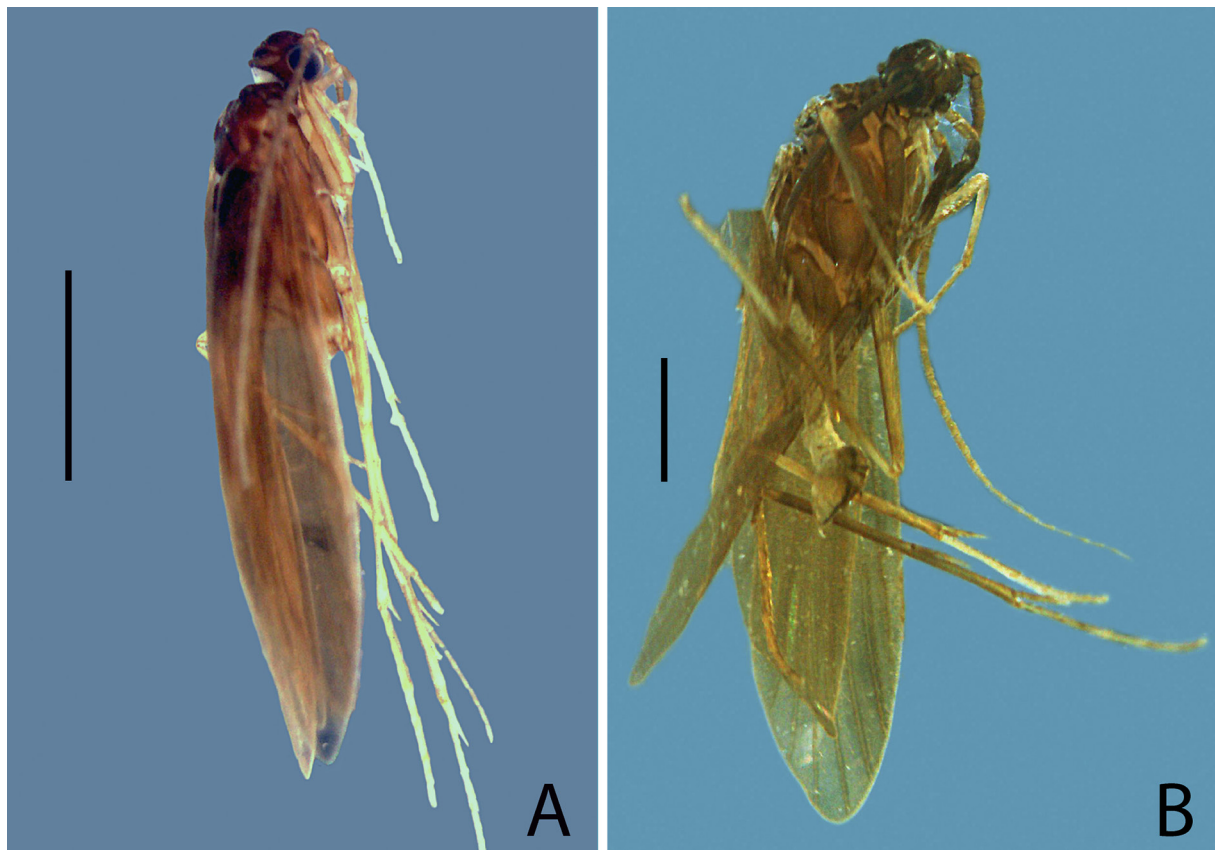


Fig. 2. Xiphocentronidae spp., adult ♂♂, habitus. **A.** *Machairocentron amahuaca* sp. nov., paratype (MUSM). **B.** *Xiphocentron harakbut* sp. nov., holotype (MUSM-ENT-03205564). Scale bars: 1 mm.

Remarks

The new species is described from the South Brazilian dominion, Yungas Province, and is most similar to *M. echinatum*, known from the Pacific dominion. This group of species is particularly recognizable by the deep concavities on the anterior and posterior margins of tergum IX. *Machairocentron amahuaca* sp. nov. corresponds to the “morphotype C” of Vilarino & Holzenthal (2020), defined on one damage specimen. Thus, more specimens were analyzed, confirming the consistency of the characters and the distinctiveness of the species.

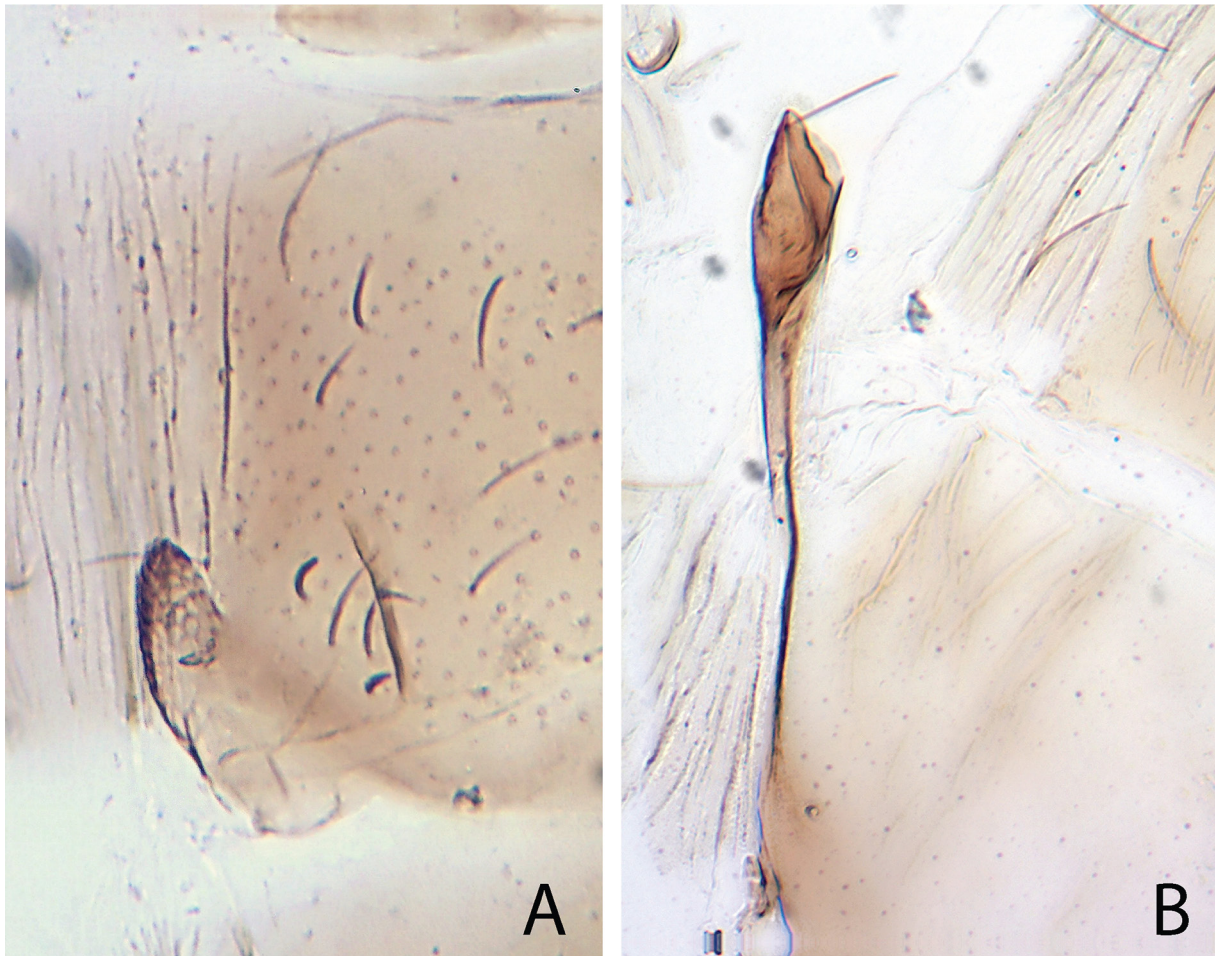


Fig. 3. Abdominal sternum V, ventral, 100× magnification. **A.** *Machairocentron amahuaca* sp. nov. (MUSM). **B.** *Xiphocentron harakbut* sp. nov. (MUSM).

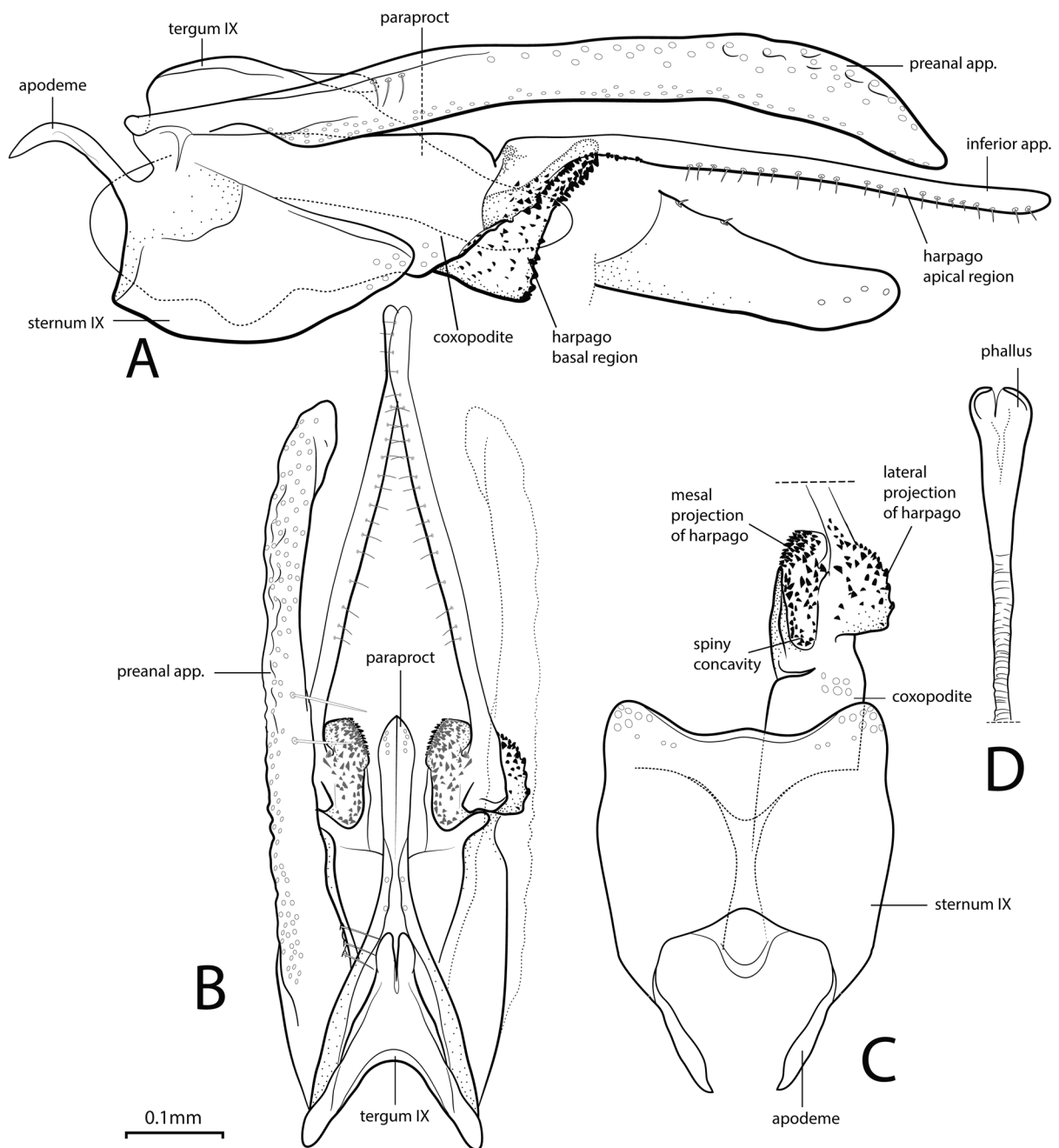


Fig. 4. *Machairocentron amahuaca* sp. nov., holotype, male genitalia (MUSM-ENT-0320559). **A.** Lateral view, with detail of paraproct. **B.** Dorsal view. **C.** Ventral view. **D.** Phallus, dorsal view.

Genus *Xiphocentron* Brauer, 1870

Xiphocentron (Antillotrichia) ashaninka sp. nov.

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Figs 1, 5

Diagnosis

Xiphocentron ashaninka sp. nov. is most similar to *X. sturmi* Sturm, 1960 and *X. regulare* Flint, 1991, based on the shape of tergum IX and the sclerotized lateral margin of the paraproct as seen in dorsal view. It can be distinguished by: a) the narrower incision at the posterior margin of tergum IX, in dorsal view (Fig. 5B) (incision wider in the other species); b) the shorter spines of the inferior appendage (Fig. 5A–C) (the other species have long spines at the mesal sclerite region); c) the narrower and longer preanal and inferior appendages, in lateral view (Fig. 5A); and d) the enlarged preanal appendage, in dorsal view (Fig. 5B).

Etymology

Named after the Ashaninka, a people from the Arawak linguistic family. The Ashaninka are the most populous native Amazonian group in Peru, with over 55 000 people in the country identifying as Ashaninka.

Material examined

Holotype

PERU • ♂; Cusco, La Convención Echarate, Pagoreni-8, Shell prospecting and development project; 11.70326° S, 72.90134° W; elev. 486 m; 27 May 1997; Córdova leg.; MUSM-ENT-0320562.

Additional material

PERU • 2 ♀♀; same collection data as for holotype; MUSM-ENT-0320563.

Description of male

BODY. Forewing length 5.2 mm (n=1). Color overall pale brown (in alcohol). Maxillary palp segment length formula (I=II=III)<IV<V. Tibial spur formula 2:4:3; spurs unmodified. Venation: forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell about half of thyridial cell length. Hindwing forks II and V present. Sternum V with flat anterolateral reticulated region.

GENITALIA (Fig. 5). Tergum IX, in lateral view, wider basally, narrower apically, about 1.5 × as long as high (Fig. 5A); in dorsal view, anterior margin with deep, wide concave incision; posterior margin with deep U-shaped mesal incision, anterior and posterior incisions almost touching each other (Fig. 5B). Sternum IX, in lateral view, about 2 × as long as high, apex deltoid; anterior apodeme narrow, straight, tapering to slender flange (Fig. 5A); in ventral view, posterior margin with shallow V-shaped mesal incision (Fig. 5C). Paraproct, in lateral view, oblong, apically rounded, with small ventral lobe (Fig. 5A); in dorsal view, each side fused, with sclerotized band on fusion region and sclerotized strips coming from lateral sides (Fig. 5B); wide basally, tapering apically; divided apicomeres until sclerotized band, with numerous sensillae on semi-membranous apex (Fig. 5B). Preanal appendage about 4 × as long as tergum IX, setose; in lateral view, narrow, bent at basal 1/3, wavy curved, slightly enlarging apically (Fig. 5A); in dorsal view, enlarged at midlength, narrow at apex (Fig. 5B). Inferior appendage about 3 × as long as tergum IX, setose; coxopodite and harpago partially fused, with dorsal incision between them; basal region wide, without spines; apical region slender, digitate (Fig. 5A–C); in lateral view, about 2 × length of basal region; inner face with various short, tubercle-like spines, more concentrated at midlength; mesal sclerite absent (Fig. 5A). Phallus tubular, very long and slender, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged (Fig. 5D).

Remarks

The new species is described from the South Brazilian dominion, Rondônia Province, and has a strong similarity with *X. regulare* and *X. sturmi*, known from the Pacific dominion, Cauca Province. This group of species is particularly recognizable by the deep concavities on the anterior and posterior margins of tergum IX.

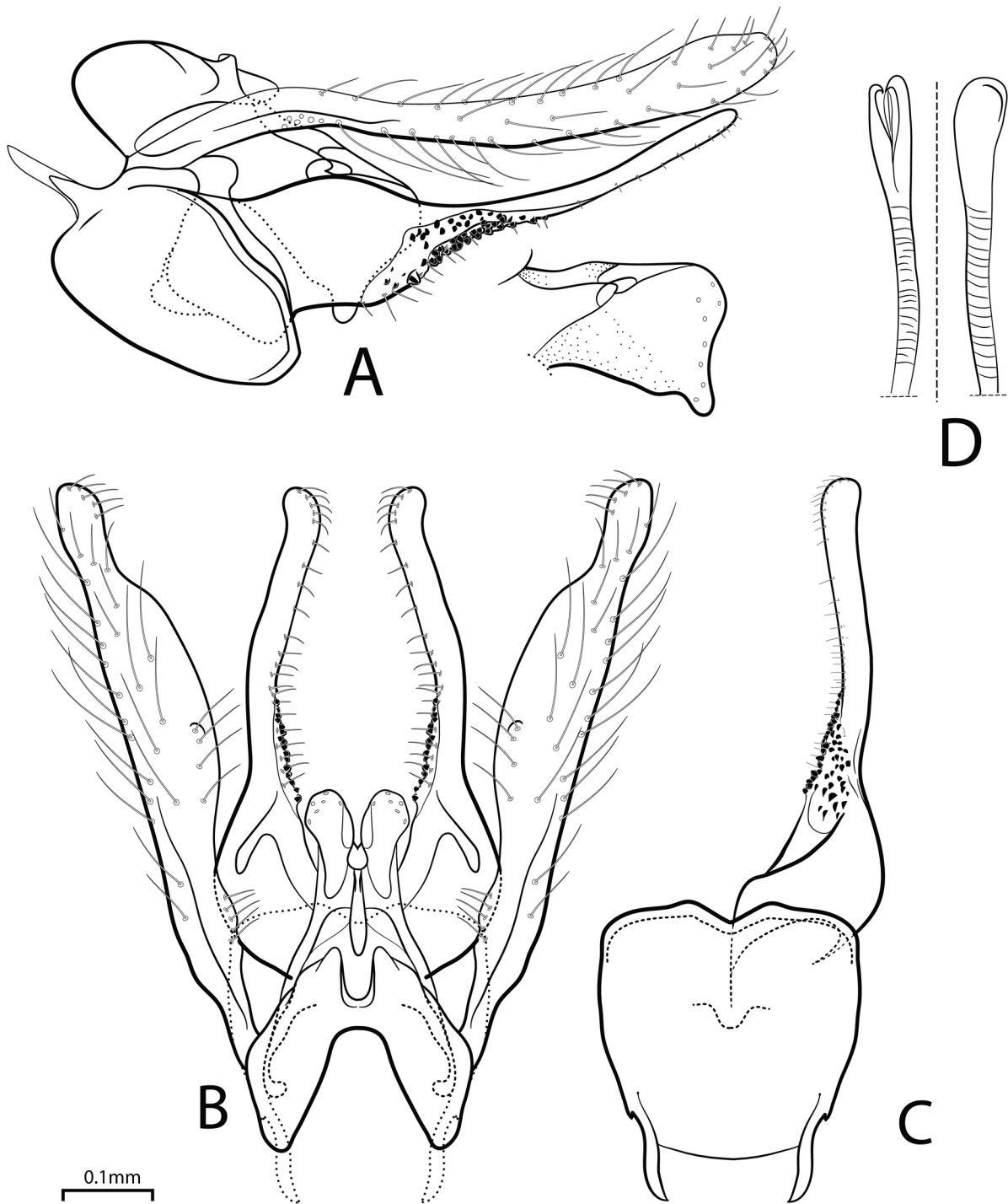


Fig. 5. *Xiphocentron ashaninka* sp. nov., holotype, male genitalia (MUSM-ENT-0320562). **A.** Lateral view, with detail of paraproct. **B.** Dorsal view. **C.** Ventral view. **D.** Phallus, dorsal and lateral views, respectively.

Xiphocentron (Antillotrichia) harakbut sp. nov.

[urn:lsid:zoobank.org:act:C5E984AA-0589-4DFA-A8D2-81A962318F8B](https://doi.org/10.21203/rs.3.rs-2811888/v1)

Figs 1, 2B, 3B, 6

Diagnosis

Xiphocentron harakbut sp. nov. is similar to *X. piscicaudum* Flint, 1996 and *X. sclerothrix* Pes *et al.*, 2013 by the inferior appendage ornamentation and the presence of a process on the abdominal sternum V. The new species can be differentiated by: a) the shape of tergum IX, which has a very shallow mesal incision on the posterior margin, and a pair of mesolateral distinctly sclerotized lobular areas, as seen in dorsal view (Fig. 6B); b) the sternum IX posterior margin, which has a V-shaped shallow mesal incision (Fig. 6C), but rectangular in *X. piscicaudum* and absent in *X. sclerothrix*; c) the process of sternum V is narrow and elongate, with a simple and rounded apex (Fig. 3B), whereas in *X. piscicaudum*, the apex is broadly forked and in *X. sclerothrix* the process is wide and short.

Etymology

Named after the Harakbut people, who live mainly in the departments of Cusco and Madre de Dios, between the Madre de Dios and Inambari rivers. Harakbut is the only member of the language family of the same name, so it is considered an isolated language.

Material examined

Holotype

PERU • ♂; 19 rd km W of Cusco, Quincemil, Rio Araza tributary; 13°20'0.00" S, 70°50'57.00" W; elev. 874 m; 23–31 Aug. 2012; R.R. Cavichioli, J.A. Rafael, A.P.M. Santos and D.M. Takiya leg.; Malaise trap; MUSM-ENT-0320564.

Paratypes

PERU • 1 ♂; same collection data as for holotype; MUSM-ENT-0320565 • 1 ♂; same collection data as for holotype; DZRJ 8652.

Description of male

BODY (Figs 2B, 3B). Forewing length 4.6–4.0 mm (n=3). Color overall brown with light brown legs, middle and foreleg with proximal ¼ of tibia pale (in alcohol) (Fig. 2B). Maxillary palp segment length formula (I=II=III)<IV<V. Tibial spur formula 2:4:3; spurs unmodified. Venation: forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell about half of thyridial cell length. Hindwing forks II and V present. Sternum V anterolateral margin bearing elongate sclerotized process, narrow basally, enlarged at apex (Fig. 3B).

GENITALIA (Fig. 6A–E). Tergum IX, in lateral view, wider basally, narrower apically, about 2 × as long as high (Fig. 6A); in dorsal view, with meso-lateral lobular area distinctly sclerotized, anterior margin with deep, wide, concave incision; posterior margin rounded with shallow mesal incision (Fig. 6B). Sternum IX, in lateral view, about 1.5 × as long as high, apex truncate; anterior apodeme narrow, straight, tapering to slender flange (Fig. 6A); in ventral view, posterior margin with shallow V-shaped mesal incision (Fig. 6C). Paraproct, in lateral view, oblong, apically truncate (Fig. 6A); in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, tapering apically; divided apicomeres until sclerotized band, with numerous sensillae on semi-membranous apex (Fig. 6B). Preanal appendage about 2.5 × as long as tergum IX, setose; in lateral view, narrow, bent at basal ⅓, slightly enlarging apically (Fig. 6A); in dorsal view, about same width throughout length (Fig. 6B). Inferior appendage about 2 × as long as tergum IX; coxopodite and harpago completely fused; basal region wide, with several short, weakly sclerotized tubercle-like spines; apical region slender, digitate; in lateral view, about 1.5 × length

of basal region, inner face with mesal sclerite and numerous long spines, more concentrated at midlength (Fig. 6A, E); mesal sclerite polyp-like, densely topped with long spines; in lateral view, about 4 × as long as high, spines concentrated at posterior face and directed posterad (Fig. 6A, E). Phallus tubular, very long and slender, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex enlarged (Fig. 6D).

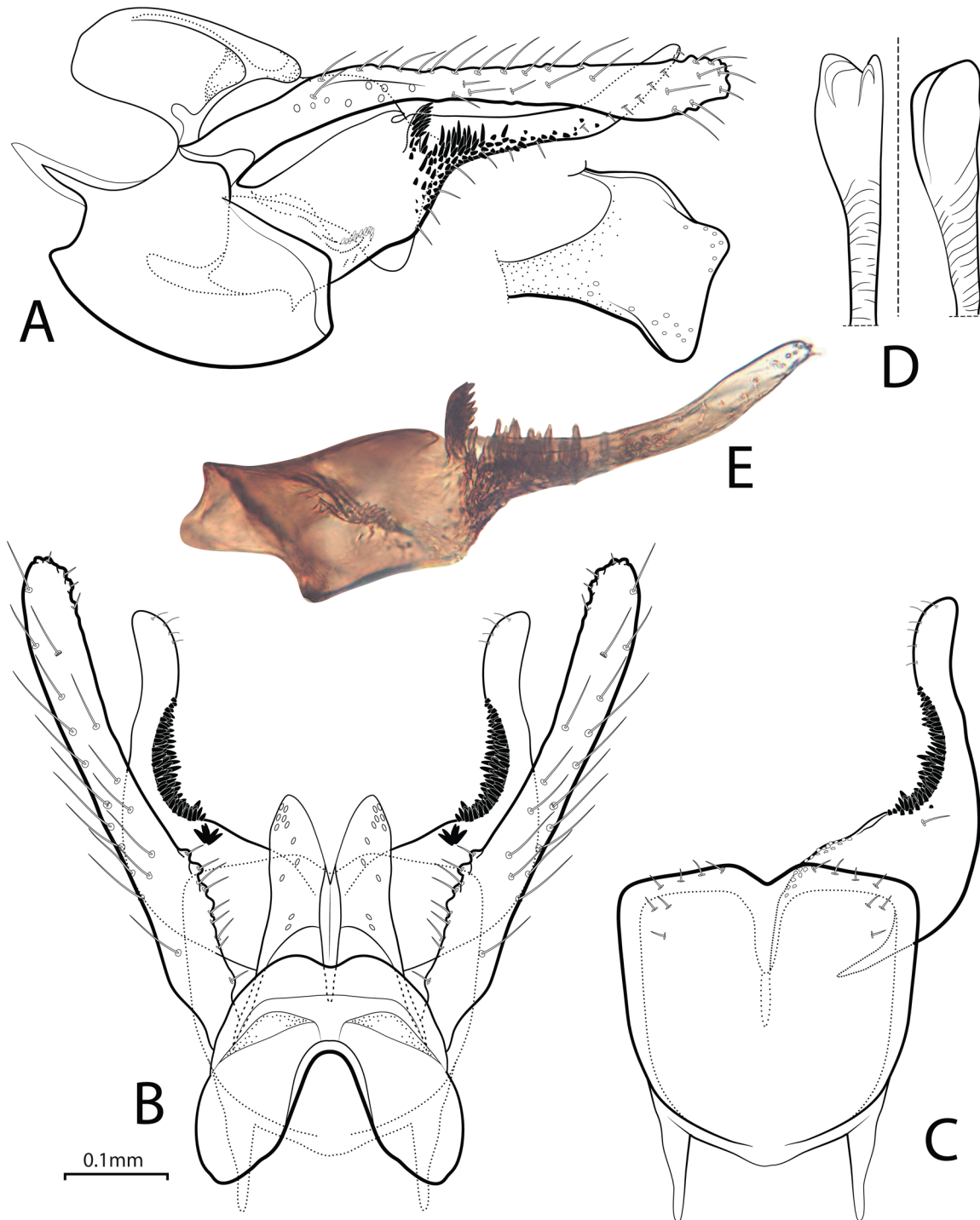


Fig. 6. *Xiphocentron harakbut* sp. nov., holotype, male genitalia (MUSM-ENT-0320564). **A.** Lateral view, with detail of paraproct. **B.** Dorsal view. **C.** Ventral view. **D.** Phallus, dorsal and lateral views, respectively. **E.** Left inferior appendage, photograph, lateroventral view.

Remarks

The new species is described from the South Brazilian dominion, Yungas Province, and is most similar to *X. piscicaudum*, known from the Pacific dominion, Venezuelan province and *X. sclerothrix* known from the Boreal Brazilian dominion, Guianan and Roraima provinces. In addition to the process on sternum V, these species have inferior appendage with long and dense brushlike spines, similar to some species from the Lesser Antilles (e.g., *X. albolineatum* Flint, 1968, *X. borinquensis* Flint, 1964 and *X. fuscum* Flint, 1968), and also very similar to the subgenus *Sphagocentron* from Mesoamerica.

Xiphocentron (Antillotrichia) matsigenka sp. nov.

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Figs 1, 7

Diagnosis

Xiphocentron matsigenka sp. nov. is similar to *X. cuyensis* Flint, 1983 and *X. caenina* Schmid, 1982 by the inner face ornamentation of the inferior appendage. The new species can be distinguished by: a) the preanal appendage wider and straight (narrow and bent in *X. cuyensis* and *X. caenina*), in lateral view (Fig. 7A); b) the paraproct shape apicodorsally, rounded with narrow ventral lobe (truncate in *X. cuyensis* and *X. caenina*), in lateral view (Fig. 7A); and c) the posterior margin of tergum IX with longer lobes and deeper mesal incision in dorsal view (lobes shorter with shallower incision in *X. cuyensis* and *X. caenina*) (Fig. 7B).

Etymology

Named after the Matsigenka, an indigenous people belonging to the Arawak linguistic family, who lives in the Amazon Basin jungle regions of southeastern Peru, east of Machu Picchu.

Material examined**Holotype**

PERU • ♂; Cusco: La Convención Echarate, Cashiriari-2, Shell prospecting and development project; 11.86425° S, 72.77933° W; elev. 579 m; 6 Apr. 1997; Córdova leg.; MUSM-ENT-0320566.

Description of male

BODY. Forewing length 3.6 mm (n=1). Color overall pale brown (in alcohol). Maxillary palp segment length formula (I=II=III)<IV<V. Tibial spur formula 2:4:3; spurs unmodified. Venation: forewing forks II and IV present; fork II petiolate at discoidal cell; discoidal cell twice as long as thyridial cell. Hindwing forks II and V present. Sternum V with flat anterolateral region reticulated.

GENITALIA (Fig. 7). Tergum IX, in lateral view, wider basally, narrower apically, about as long as high (Fig. 7A); in dorsal view, anterior margin concave, with U-shaped mesal incision; posterior margin with subdeltoid lobe, with rounded apex and deep narrow mesal incision (Fig. 7B). Sternum IX, in lateral view, about 2× as long as high, apex subangular; anterior apodeme narrow, straight, with slender flange along anterior margin (Fig. 7A); in ventral view, posterior margin with shallow rectangular mesal incision (Fig. 7C). Paraproct, in lateral view, oblong, apically rounded, with narrow ventral lobe (Fig. 7A); in dorsal view, each side fused, with sclerotized band on fusion region (Fig. 7B); wide basally, divided apicomesally until sclerotized band, with numerous sensillae on semi-membranous apex (Fig. 7B). Preanal appendage about 3× as long as tergum IX, setose; in lateral view, wide, straight and enlarged at basal 1/3 (Fig. 7A); in dorsal view, about same width throughout length (Fig. 7B). Inferior appendage about 2× as long as tergum IX, setose; coxopodite and harpago completely fused; basal region wide, with short, weakly sclerotized tubercle-like spines; apical region slender, digitate (Fig. 7A–C); in lateral view, slightly longer than basal region, inner face with stout spines, sparsely distributed at midlength, anterodorsal spines

distinctly longer; mesal sclerite absent (Fig. 7A). Phallus tubular, very long and slender, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged (Fig. 7D).

Remarks

Xiphocentron matsigenka sp. nov. is described from the South Brazilian dominion, Rondônia Province, and is most similar to *X. cuyensis* and *X. caenina*, known from the same dominion, Yungas Province. All these species have a slender flange along anterior margin of sternum IX, inferior appendage with short to medium-length stout spines, basal region spines present, and mesal sclerite absent.

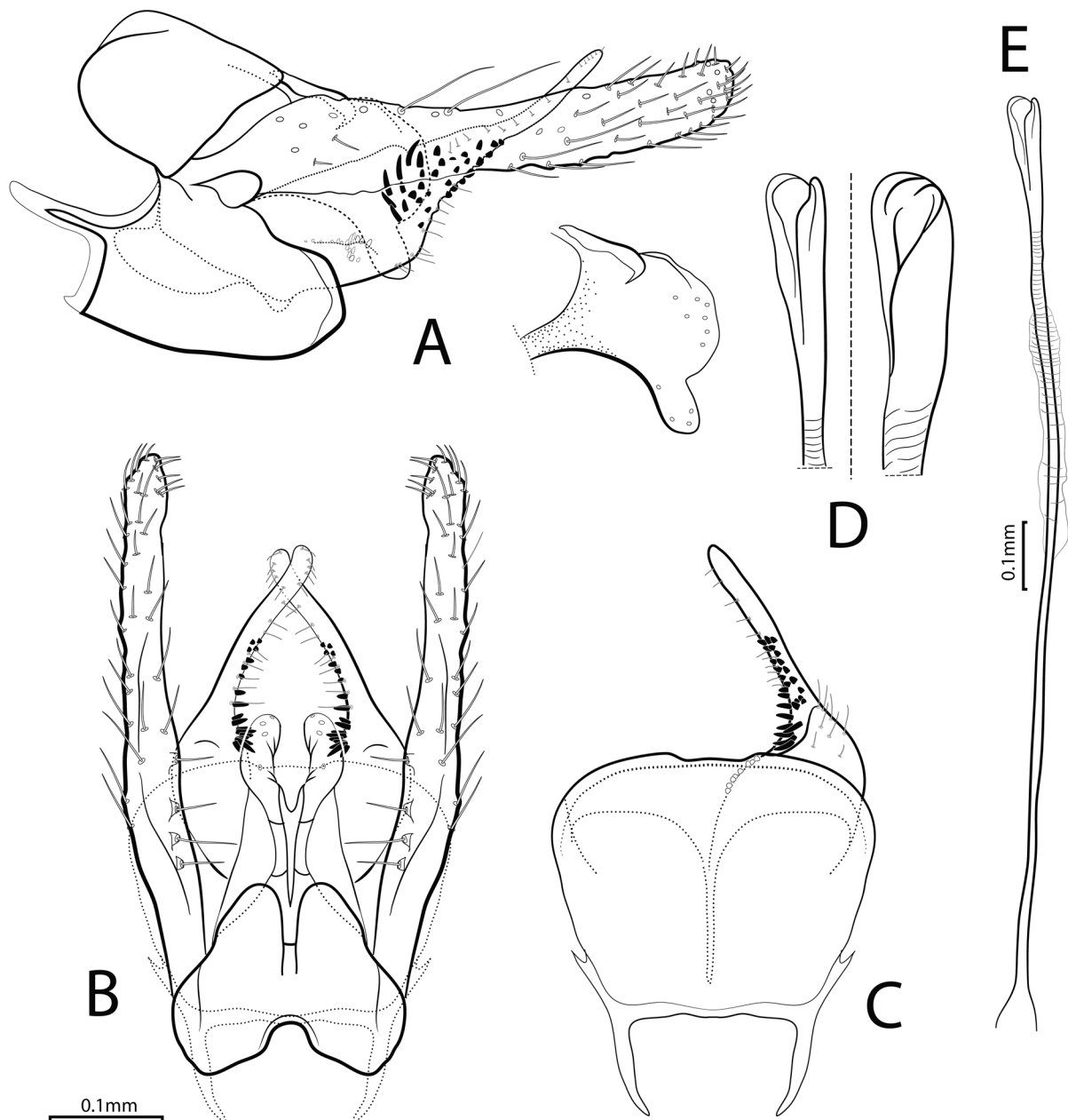


Fig. 7. *Xiphocentron matsigenka* sp. nov., holotype, male genitalia (MUSM-ENT-0320566). **A.** Lateral view, with detail of paraproct. **B.** Dorsal view. **C.** Ventral view. **D.** Phallus, dorsal and lateral views, respectively. **E.** Phallus in full length, dorsal view.

Xiphocentron (Antillotrichia) yine sp. nov.

[urn:lsid:zoobank.org:act:B1D9C9E6-CD96-4B50-ADB8-64EE87DBB98C](https://zoobank.org/act:B1D9C9E6-CD96-4B50-ADB8-64EE87DBB98C)

Figs 1, 8

Diagnosis

Xiphocentron yine sp. nov. is most similar to *Xiphocentron pintada* Flint, 1983 and *X. steffeni* (Marlier, 1964) based on the shape of preanal appendage and the ornamentation of the inferior appendage. However, the new species can be differentiated by: a) the preanal and inferior appendages about $\frac{1}{3}$ longer than in *X. pintada*, as seen in lateral view (Fig. 8A); and b) the inferior appendage with several long spines in the basal region (Fig. 8A, C), which are absent in *X. pintada* and *X. steffeni*.

Etymology

Named after the Yine people (also known as Piro), an indigenous ethnic group of Peru who have occupied the upper Ucayali River basin and the lower Urubamba River since pre-Hispanic times. The Yine are also known as the “Amazonian Phoenicians” due to their skill as navigators, traveling long distances to trade with various populations.

Material examined**Holotype**

PERU • ♂; Cusco, La Convención Echarate, Pagoreni-10, Shell prospecting and development project; 11.70462° S, 72.91256° W; elev. 460 m; 29 Sept. 1997; Córdova leg.; MUSM-ENT-0320567.

Description of male

BODY. Forewing length 4.2 mm (n=1). Color overall pale brown (in alcohol). Maxillary palp segment length formula (I=II=III)<IV<V. Tibial spur formula 2:4:3; spurs unmodified. Venation: forewing forks II and IV present; fork II petiolate at discoidal cell; discoidal cell twice as long as thyridial cell. Hindwing forks II and V present. Sternum V with flat anterolateral reticulated region.

GENITALIA (Figs 8). Tergum IX, in lateral view, wider basally, narrower apically (Fig. 8A); in dorsal view, anterior margin with deep narrow concave incision; posterior margin with pair of rounded lobes and V-shaped mesal incision (Fig. 8B). Sternum IX, in lateral view, about 1.5 × as long as high, apex deltoid; anterior apodeme narrow, straight, tapering to slender flange (Fig. 8A); in ventral view, posterior margin with concave incision (Fig. 8C). Paraproct, in lateral view, oblong, apically rounded, with narrow ventral lobe (Fig. 8A); in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, divided apicomesally until sclerotized band, with numerous sensillae on semi-membranous apex (Fig. 8B). Preanal appendage about 3 × as long as tergum IX, setose; in lateral view, narrow, bent at basal $\frac{1}{3}$, with about same width throughout length (Fig. 8A); in dorsal view, enlarged at midlength, tapering apically (Fig. 8B). Inferior appendage more than 2 × length of tergum IX, setose; coxopodite and harpago completely fused (Fig. 8A); basal region wide, with long, weakly sclerotized spine-like setae; apical region slender, digitate (Fig. 8A–C); in lateral view, 2 × length of basal region, inner face with mesal sclerite and various short, tubercle-like spines, sparsely distributed (Fig. 8A); mesal sclerite polyp-like, topped with short spines; in lateral view, about 3 × as long as high (Fig. 8A). Phallus tubular, very long and slender, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged (Fig. 8D).

Remarks

Xiphocentron yine sp. nov. is described from the South Brazilian dominion, Rondônia Province, and is most similar to *X. pintada*, known from the same dominion, Yungas Province, and *X. steffeni*, known from the Parana dominion. These species have a clavate preanal appendage and a polyp-like mesal sclerite.

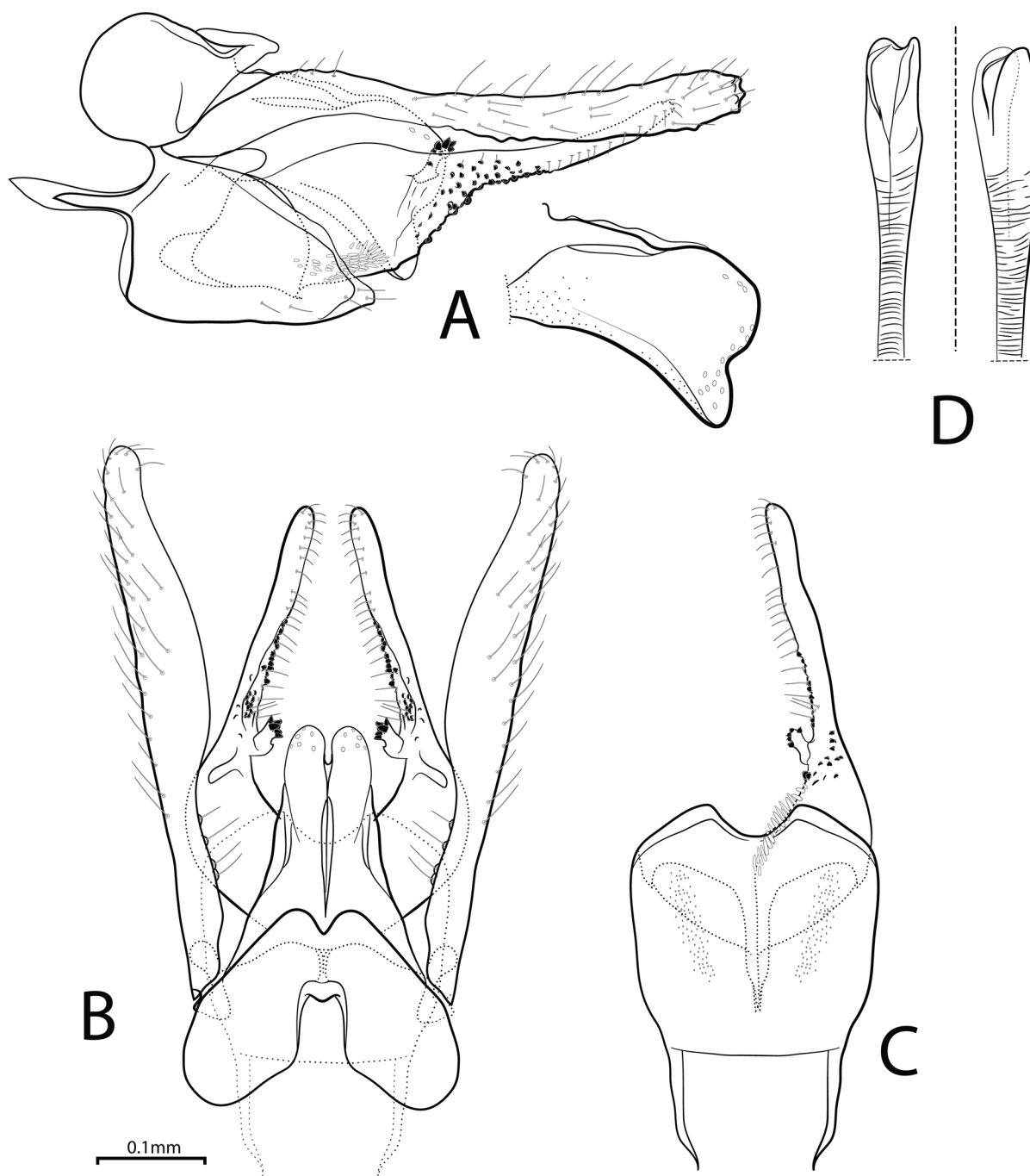


Fig. 8. *Xiphocentron yine* sp. nov., holotype, male genitalia (MUSM-ENT-0320567). **A.** Lateral view, with detail of paraproct. **B.** Dorsal view. **C.** Ventral view. **D.** Phallus, dorsal and lateral views, respectively.

Discussion

The Xiphocentronidae reached South America from Mesoamerica, with *Caenocentron* crossing the Central American seaway during the late Miocene around 10 Mya (Vilarino *et al.* 2022). The same is likely to have happened to *Xiphocentron* and *Machairocentron*, although an early colonization of South America via the Greater Antilles land bridge during the Oligocene around 30 Mya (Iturralde-Vinent & MacPhee 1999) is also a plausible scenario, since species of *X. (Antillotrichia)* are widely distributed in the Antilles and South America. Whatever the scenario, South America would have 10 to 30 million years of evolutionary history and diversification of the Xiphocentronidae. The gradual and continuous uplift of the Northern and Central Andes since the late Oligocene caused major changes on the drainage, which from a Sub-Andean river system flowing northward into the Caribbean Sea (~33–23 Mya), changed to a large wetland system in the western Amazonia (Pebas system) (~23–10 Mya), and to the present Amazon basin configuration discharging into the Atlantic (~10–7 Mya) (Hoorn *et al.* 2010; Méndez-Camacho *et al.* 2021).

The new species were described from the Peruvian Yungas (montane rain forest ecoregion) (i.e., *M. amahuaca* sp. nov. and *X. harakbut* sp. nov.) or nearby in the western Amazon Basin (i.e., *X. ashaninka* sp. nov., *X. matsigenka* sp. nov. and *X. yine* sp. nov.). *Xiphocentron matsigenka* and *X. yine* are most similar to species found in the Southern Andean Yungas, Northwest Argentina; *X. ashaninka* and *M. amahuaca* are most similar to species from the Pacific dominion in Colombia and Venezuela; while *X. harakbut* have similarities with *X. sclerothix* from the Amazon, although, even greater similarities are shared with *X. piscicaudum* from Venezuela. This demonstrates a continuum of the diversification of Xiphocentronidae along the Sub-Andean foreland basins, and could imply that these species diverged prior to the major Andean uplift and the late Miocene (~10–7 Mya) drainage shift to the current Atlantic discharge (Hoorn *et al.* 2010). Suggesting, therefore, a colonization of South America earlier than the 10 Mya of *Caenocentron* (Vilarino *et al.* 2022). However, more distributional data and phylogenetic studies would be necessary for a conclusive statement.

The species described here also contribute to the understanding of the evolution of genital characters in the Xiphocentronidae lineages. With the exception of *X. ashaninka*, all of the species of *Xiphocentron* described here have spines on the basal region of the inferior appendage. These spines are particularly intriguing. Based on their position, they must be homologous to the elongate setae on the ventral projection of the coxopodite in *Caenocentron* (see Vilarino *et al.* 2022: figs 13d, 14a, c). This character appears as shorter spines in each coxopodite in the early radiation of *Caenocentron*, as in *C. rafamoralesi* Vilarino *et al.*, 2022 and became a single large ventral projection with very long setae in the other *Caenocentron* lineages (Vilarino *et al.* 2022).

The shape of the ventral spiny concavity in the male genitalia of *Machairocentron* (Fig. 4C) suggests that it is where the female segment X (see Vilarino & Holzenthal 2020: fig. 7) is accommodated during mating, which is consistent with the female of this genus having the segment X more strongly sclerotized than other Xiphocentronidae (Vilarino & Holzenthal 2020). If this is correct, the phallus of *Machairocentron* would be inserted apically, as opposed to the mating position of *Tinodes* (Psychomyiidae), in which the female segments IX and X are raised vertically, and the phallus is inserted near the basal third of segment IX (Fisher 1977). This mating position, from the apex of the abdomen, may be related to the phallus extremely elongate of Xiphocentronidae.

Nielsen (1957, 1980) conducted the most comprehensive studies of the comparative anatomy of male and female genitalia in Trichoptera. Despite the studies of Nielsen and the fact that genital structures are the primary source of characters for the taxonomy of Trichoptera, morpho-functional studies of the genitalia are uncommon and would be necessary to make sense of the genital structures, as well to understand sexual selection forces driving the male-female genitalic evolution.

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