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Comparative geometric morphometrics of male genitalia in *Xiphocentron* subgenera (Trichoptera: Xiphocentronidae): new species, revision and phylogenetic systematics of the subgenus *Sphagocentron*

Albane Vilarino[1], Adolfo R. Calor[1]

1 *Universidade Federal da Bahia, Instituto de Biologia, Laboratório de Entomologia Aquática, Salvador, Bahia, Brazil*

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Corresponding author: Albane Vilarino (albanevilarino@alumni.usp.br)

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Abstract

Geometric morphometric statistics have been employed to reduce the subjectivity of visual evaluations in taxonomy. Taxonomy in most insect groups relies strongly on male genitalia morphology which is often the structure with most data available, which is also true to caddisfly taxonomy. Here we revise the caddisfly subgenus *Xiphocentron* (*Sphagocentron*) adding five new species after 40 years: *X. dactylum* **sp. nov.**, *X. eurybrachium* **sp. nov.**, *X. tapanti* **sp. nov.**, and *X. tuxtla* **sp. nov.** Additionally, we describe a new *X.* (*Antillotrichia*): *X. drepanum* **sp. nov.** from French Guiana and provide new species records of Xiphocentronidae from Bolivia, Costa Rica and Ecuador. We performed exploratory geometric morphometric analysis on the male genitalia's preanal appendage to characterize the shape differences among the species, and to investigate its utility to classify species to subgenera. In order to infer species relationship and assess if shape congruences are due to phylogenetic signal or convergence data from 100 landmarks and semilandmarks, and 30 discrete characters were used to generate a phylogenetic hypothesis. The morphometry partially supports the subgenera delimitations, but the *Antillotrichia* subgenus greatly overlapped with other subgenera. The discriminant analysis overall classification correctness was 64%. Some suggested phenotypic groups were due to convergence. According to the preanal appendage morphometry, *X.* (*Antillotrichia*) *fuscum* is a *Sphagocentron* species. The phylogenetic analysis recovered *Sphagocentron* as monophyletic, but not *Antillotrichia*. *Sphagocentron* subgenus was placed within a clade of several *Antillotrichia* species, with *X.* (*A.*) *fuscum* as the sister of the other *Sphagocentron* species, although support values were low.

Keywords

Aquatic insects, Landmark, Morphology, Morphometry, Net-tube caddisfly, Taxonomy

1. Introduction

Male genitalia features play an important role in insect taxonomy as they contain the principal traits used to delineate genera and delimit species in many insect groups, and often the male genitalia is the structure with most data available (Shapiro and Porter 1989; Hosken and Stockley 2004). Moreover, the genital morphology has the potential to directly contribute to the reproductive isolation and speciation process through divergent sexual selection and mechanical or sensory incompatibility (Eberhard 1992; Arnqvist 1998). Morphometric statistics have been advocated as a tool to reduce the subjectivity of visual evaluations in taxonomy (Mutanen and Pretorius 2007). Geometric morphometrics, for instance, allows detailed analysis and visualization of shape changes in complex structures, removing size variation from the data through superimposition, while capturing all aspects of shape variation (Bookstein 1997; Rohlf and Marcus 1993). This constitutes a sophisticated method for collecting and analyzing data to address questions in anatomy and evolutionary biology (e.g., Klingenberg 2016). Genital morphology is the second most studied insect body part in morphometrics (after wings), with male genitalia accounting for most studies (Tatsuta et al. 2018; Mutanen and Pretorius 2007; Jauset et al. 2017; García-Román et al. 2019). Studies using traditional morphometry on adult caddisflies (Trichoptera) are uncommon, with notable exceptions of Goretti et al. (2005), Svensson (1975), and Bálint et al. (2008) who focused on male genitalia structures. Despite the relevance of genitalia characters in species delimitation, geometric morphometry was so far applied only to caddisfly wings by Sganga et al. (2022).

Since Nielsen (1957), several studies have discussed the morphology of Trichoptera male genitalia (e.g., Holzenthal et al. 2007; Ivanov 2005; Morse 1975; Ross and Unzicker 1977; Schmid 1970, 1979, 1989; Oláh and Johanson 2008). The genitalia is associated with abdominal segments IX, X and XI, and bears several paired appendages: the ventral inferior appendages (gonopods), often bi-articulated, are thought to have a clasping function during copulation; the mesal intermediate appendages (paraprocts) usually perform accessory copulatory and stimulatory functions, and are often fused to other structures (Oláh and Johanson 2008; Nielsen 1957); and the dorsal superior appendages (preanal appendages) are setose and thought to have a sensory function. Some authors infer that these superior appendages are homologous to the cerci (Ross 1938; Ivanov 2005; Oláh and Johanson 2008) while others have stated that Trichoptera do not possess cerci (Holzenthal et al. 2007; Nielsen 1957; Schmid 1998). The preanal appendage is often elongate, and digitate, but can be reduced to a knob-like structure or even be absent or fused to the paraprocts and tergum X (Nielsen 1957; Oláh and Johanson 2008).

Xiphocentronidae Ross, 1949 is a pantropical net-tube caddisfly family comprising 205 species, classified in eight genera: *Abaria* Mosely, 1948 with 40 species (Oriental and Afrotropical regions); *Caenocentron* Schmid, 1982 with nine species (southwestern USA to northern South America); *Cnodocentron* Schmid, 1982 with six species (India and Southeast Asia); *Drepanocentron* Schmid, 1982 with 43 species (Oriental region); *Machairocentron* Schmid, Schmid, 1982 with 10 species (Central America and northern South America), *Melanotrichia* Ulmer, 1906 with 30 species (eastern Palearctic and Oriental regions); *Proxiphocentron* Schmid, 1982 with five species (India and Southeast Asia), and *Xiphocentron* Brauer, 1870 with 62 species (Neotropical region, extending into Mexico, the southwestern USA, and the Greater Antilles) (Peng et al. 2022; Vilarino and Bispo 2020; Vilarino et al. 2023).

The majority of xiphocentronid species are found in small streams in the tropical zone, primarily in the Oriental region (with five genera) and the Neotropical region (with three genera), few species are also distributed in the Afrotropical, East Palearctic and Nearctic regions (Vilarino and Bispo 2020; Vilarino et al. 2021). The adults are small with forewings ranging from 2.5 to 8.5 mm uniformly brown or with one to three white patches on the forewing, and are often active during the day (Flint 1968; Schmid 1982). The family is inferred to have diverged from the sister group, Psychomyiidae, in the early Cretaceous (Thomas et al. 2022; Malm et al. 2013) although the only xiphocentronid fossil known is from Miocene Mexican-amber, *Xiphocentron chiapasi* Wichard et al. 2006. The male genitalia of the Xiphocentronidae is characterized by: (1) the great horizontal stretching of the genitalia; (2) the reduced tergum IX; (3) the preanal appendages very long and robust; (4) the fused segment X and paraprocts closed ventrally forming a support under the phallus; (5) the phallus reduced to a very short phallotheca and an extremely long and slender cylindrical aedeagus, while the endotheca is completely obliterated (Schmid 1982). The 2nd and 3rd characters are not exclusive to the xiphocentronids, but represent a development taken to the extreme of tendencies already present in certain Psychomyiidae (Schmid 1982).

Currently, the New World fauna comprises 81 species, most of them belonging to the genus *Xiphocentron*, making it the most species-rich genus within the family with 62 species (Vilarino et al. 2023; Bueno-Soria et al. 2022). *Xiphocentron* circumscription is based mostly on the absence of characteristics seen in other genera, although the established subgenera in general have defining traits. The genus was classified by Schmid (1982) into five subgenera: *Glyphocentron* Schmid, 1982 (3 spp.); *Rhamphocentron* Schmid, 1982 (6 spp.); *Sphagocentron* Schmid, 1982; *Xiphocentron* Brauer, 1870 (6 spp., including 1 fossil sp.); and *Antillotrichia* Banks, 1941 (47 spp.) (senior synonym of *Xirocentron* Schmid, 1982 (Botosaneanu 1988)). The last subgenus *Antillotrichia* was designated to accommodate species that could not be placed in other subgenera (Schmid 1982), so it might not be monophyletic. The *Antillotrichia* subgenus is the most heterogeneous among the subgenera established, so Schmid (1982) suggested that it would be subdivided as more species are included. Some characters of each subgenus based on Schmid (1982) descriptions are shown in Table 1.

All the five subgenera occur in Mesoamerica and Central America, while only species placed within *Antillotrichia* occur in the Caribbean islands and South America (Holzenthal and Calor 2017; Vilarino and Bispo 2020). So far, only two species were placed within the *Sphagocentron* subgenus: *Xiphocentron evandrus* Schmid, 1982 from Costa Rica and Panama, and *X. julus* Schmid, 1982 from Mexico and Panama. *Sphagocentron* is characterized mainly by the angularly curved inferior appendages, the inner face of the harpago with a large area of fine setae and the simple segment X (including the paraprocts) (Schmid 1982).

In this study we revise the subgenus *X.* (*Sphagocentron*), providing identification key, the synopses of the two

Table 1. Characters described to each *Xiphocentron* subgenus according to Schmid (1982). Abbreviations: FW, forewing; app., appendage.

	Subgenera				
Characters	***Antillotrichia* Banks, 1941**	***Glyphocentron* Schmid, 1982**	***Rhamphocentron* Schmid, 1982**	***Sphagocentron* Schmid, 1982**	***Xiphocentron* Brauer, 1870**
Male hind tibia, modified spur	absent	absent	present	absent	present
FW fork I	absent	absent	absent	rudimentarily present (some species)	present
FW thyridial cell	short	short	medium-sized	long	short
FW anal veins	3	3	2	3	3
Sternum IX posterior margin	indented	straight	with two small lobes	projecting and with two small lobes	with one or two prominent lobes (some species)
Paraproct lateral points	absent	present	absent	absent	absent
Preanal app.	moderately narrow	strong	robust and wavy	strong, pointed at apex	strong, wide and straight
Inferior app. articles	fused, vestigial suture may be visible	segments well distinct	fused, vestigial suture may be visible	fused, no suture visible	segments well distinct
Inferior app. coxopodite, zone of points	absent	present	absent	absent	absent
Inferior app. harpago, ornaments	spiny structures weakly developed, mesal sclerite present in some species	long, narrow, with subbasal zone of strong spines	long zone of tubercles, mesal sclerite present	markedly contorted with well-defined area of strong setae	wide basal zone of dense and long setae
Segments II and IV, abdominal vesicles	absent	absent	present in *X. mexico* group; absent in *X. lavinia* group	absent	absent

previously described, *X. jullus* and *X. evandrus*, and the description of five new species, *X.* (*Sphagocentron*) *dactylum* **sp. nov.** and *X.* (*S.*) *eurybrachium* **sp. nov.** from Venezuela, *X.* (*S.*) *tapanti* **sp. nov.** from Costa Rica, and *X.* (*S.*) *tuxtla* **sp. nov.** from Mexico. In addition, we describe one species, *X.* (*Antillotrichia*) *drepanum* **sp. nov.**, from French Guiana and include new distributional records of Xiphocentronidae from Bolivia, Ecuador, and Costa Rica.

We performed exploratory geometric morphometric analysis on the male genitalia's preanal appendage characterizing the shape differences among the species described, as well as among the five subgenera, in order to investigate the utility of morphometrics to classify species to subgenera. Additionally, we performed a phylogenetic analysis of *X.* (*Sphagocentron*) species combining morphometric and discrete characters, to test *Sphagocentron* subgenus monophyly, new species placement, and to verify if the preanal appendage shape congruences are due to phylogenetic signal or convergence.

2. Material and methods

2.1. Male genitalia morphology analyses

New species propositions are testable hypotheses of the distinction of separately evolving metapopulation lineages (Pante et al. 2015). Here, the new species hypotheses were based on distinct male genitalia characters which were used as an indirect indicator of reproductive isolation and evolutionary divergence. In order to visualize internal structures of the adult male genitalia, the entire abdomen of the specimen was removed and diaphonized using 85% lactic acid (Blahnik et al. 2007). The abdomens were then placed in excavated glass slides with a drop of glycerin and examined with a compound microscope at 200–400× magnification. The abdomens of the specimens were stored in microvials with 80% ethanol and kept with the specimen to which they belonged. All species were conserved in 80% ethanol. The species drawings were made by tracing the observed structures in pencil using a camera lucida attached to a compound microscope or taking multiple photographs with a digital camera attached to a microscope. Then the drawings or the photographs were used as a template and digitally traced using Adobe Illustrator CS6 software. The distribution maps were created with the software QGIS v2.8.2.

The morphological terminology for male genitalia followed Vilarino and Bispo (2020). The terminology for wing venation followed the Comstock – Needham system as interpreted for Trichoptera by Mosely and Kimmins (1953). In the descriptions, paired structures are referred to in the singular form.

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, Ontar-

Table 2. *Xiphocentron* specimens used the morphometric analysis, country, location and depository.

Species	**Country**	**Location**	**Depository/ Source**
X. cubanum	Cuba	Pinar del Rio Soroa, 22°47.7′N 83°00.1′W	USNM
X. borinquensis	Puerto Rico	El Yunque	USNM
X. dactylum **sp. nov.**	Venezuela	Falcón, Quebrada del Toro 10°49.581′N, 69°07.990′W	UMSP
X. drepanum **sp. nov.**	French Guiana	Approuague-kaw: Kaw Mtn., 104 mao, 4°33.035′N, 52°11.661′W	NHRS
X. euryale	Costa Rica	San Jose, Res. Bio. Carara, Rio del Sur, 9°46′08.4″N, 84°31′51.6″W	UMSP
X. eurybrachium **sp. nov.**	Venezuela	Falcón, Mitare river, near San Luis, 11°07.930′N, 69°39.184′W	UMSP
X. evandrus	Costa Rica	Juan Vinas, Chiz river	USNM
X. fuscum	Dominica	Brantridge	USNM
X. guanacaste **sp. nov.**	Costa Rica	Guanacaste; Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo	BIOUG
X. haitiense	Dominican Rep.	Mulito river, 21 km N Perdernales, 18°09.5′N, 71°45.4′W	USNM
X. ilionea	Brazil	São Paulo, Estação Boracéia, Pedreira	USNM
X. julus	Mexico	Veracruz, Puente Nacional	USNM
X. lavinia	Guatemala	Dept. Izabal, Matias de Galvez	USNM
X. messapus	USA	Texas, Haysco, Fern Bank Spring, near Wimberley	USNM
X. mnesteus	Venezuela	Lara, P.N. Dinira, Quebrada el Vino, 9°46.711′N, 70°02.045′W	UMSP
X. moncho	Costa Rica	Alajuela, Reserva Florestal San Ramón, San Lorencito river, 10.216°N, 84.606°W	UMSP
X. nesidion	Jamaica	St. Elizabeth Y.S. Falls, 18°09.3′N, 77°31.9′W	USNM
X. numanus	Mexico	Oaxaca, Tamazulapan	USNM
X. parentum	Martinique	Riviere Coco (Le Morn-Vert)	USNM
X. piscicaldum	Venezuela	Sucre, P.N. Peninsula de Paria, 10°42.830′N, 61°57.661′W	USNM
X. polemon	Mexico	Oaxaca, 8km S Valle Nacional	USNM
X. regulare	Colombia	Dpto. Antioquia, 12 km N Fredonia	USNM
X. sclerothix	Brazil	Amazonas, Presidente Figueiredo, 1°49′51″S, 60°04′15″W	MZUSP
X. sturmi	Ecuador	Napo, Sebundoy	USNM
X. surinamense	Suriname	Crokopondo District, Brownsberg Natuurpark, Mazaroni Plateau	USNM
X. tapanti **sp. nov.**	Costa Rica	Cartago; Tapanti Reserve, quebrada palmitos and falls, 9.72°N, 83.78°W	UMSP
X. tarquon	Costa Rica	Guanacaste; Area de Conservacion Guanacaste	BIOUG
X. tuxtla **sp. nov.**	Mexico	Veracruz; Los Tuxtlas area: Maquinas river	USNM

io, Canada; **MZUSP** – Museu de Zoloogia da Universidade de São Paulo, São Paulo, Brazil; **NHRS** – Naturhistoriska Riksmuseet Stockholm, Stockholm, Sweden; **UMSP** – the University of Minnesota Insect Collection, Saint Paul, Minnesota, USA; **USNM** – National Museum of Natural History, Washington, DC, USA. Barcode sequence identification numbers are presented whenever they are available for the analyzed specimens.

2.2. Geometric morphometric analyses

Geometric morphometry allows quantitatively evaluating the shape variation of morphological structures across a sample using standardized images and 'landmarks' (Bookstein 1991; Rohlf and Marcus 1993). For the analysis the datasets included the male genitalia of the species in Table 2 and the genitalia depicted in the original descriptions of *X. julus* and *X. evandrus*. Tps files were created from the specimens illustrations using the software TpsUtil v.1.81 (Rohlf 2021). The landmarks were digitized using TpsDig2 v.2.31 (Rohlf 2017). Curves were traced along the preanal appendage in lateral view. We utilized 97 curve points (semi-landmarks) and three landmarks aiming to get most of the shape information (Fig. 1). Curves were appended to landmarks and semi-landmark sliders files were generated with TpsUtil (File S1). All samples were aligned using Generalized Least Squares (GLS) Procrustes superimposition (Bookstein 1991) after importing the data and sliders file into TpsRelw v.1.75 (Rohlf 2021). This removed any variations in the scale, position, and orientation of the landmark coordinates. The aligned procrustes were imported into PAST 4.09 software (Hammer et al. 2001), which was used to generate shape thin-plate splines, and perform statistical analyses. To verify the congruence of the preanal appendage shape within genera, possibly misplaced species and suggested phenotypic groups we used three exploratory analyses: The Principal Component Analysis (PCA), was used to characterize the ordination of the specimens irrespective of predetermined grouping, so, it is more conservative about the assumption of shape congruence and distinction between subgenera, it also was used to visualize main contributors of shape change. We also used Discriminant Analysis (DA) in which data is addressed to a priori groups, this analysis maximizes the between-group variance and minimizes the within-group variance, therefore highlighting group differences and being more conservative about the assumption of mis-

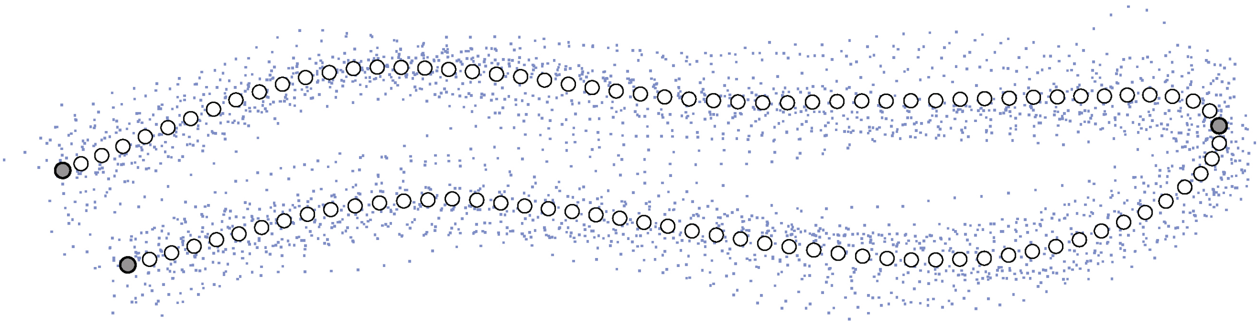

Figure 1. Location of the landmarks on the preanal appendages. Variations among samples at distinct landmarks are displayed as small dots, dark circles are landmarks and white circles are semi-landmarks.

placed species. Discriminant Analysis is affected by the sample size about the number of variables, so the analysis was made using only the ten first Principal Components (PCs). Jackknifed group assignment was verified to see the correctness of subgenera classification based on the preanal appendage shape. No formal statistical test was performed since the sample for some subgenera is rather small. The shape congruence and distinction among subgenera was observed through the degree of morphospace superimposition in the convex hulls. The overall similarities between the specimen's shape were summarized through a neighbor-joining cluster analysis based on all the PCs, which was utilized to visualize suggested phenotypic groups.

2.3. Phylogenetic analysis

The phylogenetic analysis used the same 29 taxa as the morphometric analyses (Table 2), using 30 discrete morphological characters (five non-informative) and the geometrical morphometric characters from the preanal appendage landmark configurations (Table 3). From the discrete characters, 15 were adapted from Vilarino et al. (2022). Morphological characters and character state constructions were based on Sereno (2007). When a given structure was not present in the analyzed specimens, it was coded as '–'; when the character state was not clear or could not be assessed, it was coded as '?'. All characters were binary. The morphological dataset matrix was built using Winclada 1.89 (Nixon 2002) (File S2). The TPS file with the aligned procrustes was imported into TNT 1.6 (Goloboff and Morales 2023) and combined with the matrix of discrete characters as detailed in Catalano and Goloboff (2018) (File S3). The analyses were made treating each landmark configuration as a different character (TNT default), landmark optimization, and landmark branch swapping settings also were used in default. The taxon *Xiphocentron aureum* was set as an outgroup for three rooting. The phylogenetic analysis was performed using implied weighting with the rescaled k, so that the minimum/maximum homoplasy weight ratio is 1 to 10 as implemented in TNT 1.6., with a resulting k = 5.54. Heuristic searches were performed through 'Traditional Search', with 500 replications, five trees saved per replication. The branch support was measured using symmetric resampling (Goloboff et al. 2003) expressed as the difference in the CG (contradicted/present groups) frequency (100 replications). Clades with support above 60 were considered well supported. The trees were visualized using Winclada 1.89 (Nixon, 2002) and edited in Adobe Illustrator CS6.

3. Results

3.1. Preanal appendage morphometrics

The exploratory PCA resulted in 28 PCs. The distribution of the species in the morphospace was presented over the four first PC axes (90.59% of the total variance). The PC1 (49.74%) and PC2 (17.07%) could partially separate among *Sphagocentron*, *Rhamphocentron* and *Xiphocentron* subgenera, but *Antillotrichia* morphospace overlapped most of the species. Some *Sphagocentron* were highly separated from all other subgenera by the PC2, with a wide preanal appendage bearing an acute apex. The PC3 (13.51%) and PC4 (10.27%) strongly separate *Xiphocentron* subgenus from all other subgenera, with the species having preanal appendage mostly straight with wide base tapered to a narrow apex. The PC4 also separates *Sphagocentron* from *Rhamphocentron*, but with *Antillotrichia* overlapping with both subgenera. Showing that the preanal appendage morphology allows the sub-generic distinction between *Sphagocentron*, *Rhamphocentron* and *Xiphocentron* species, but not between *Antillotrichia* and most other subgenera, except *Xiphocentron* subgenus. The main contributors to the shape changes in each PC are presented in the thin-plate splines at Figure 2.

The shape similarities were summarized in the cluster analysis dendrogram from the 28PCs distances (Fig. 3). The cluster analysis recovered most of the *Sphagocentron* subgenera except by *X.* (*S.*) *julus*, and also included *X.* (*A.*) *fuscum* and *X.* (*A.*) *borinquensis* and more distantly *X.* (*Glyphocentron*) *euryale*. In the *Xiphocentron* subgenus despite being well separate by the PC4 only *X.* (*X.*) *aureum* and *X.* (*X.*) *polemon* were clustered and in the *Rhamphocentron* only *X.* (*R.*) *lavinia* and *X.* (*R.*)

Table 3. List of morphological characters used in the cladistic analysis. Phylogenies that previously used the character and values of Consistency index (CI) of each character are shown.

1	Hind tibia apical spur: (0) simple; (1) modified (conspicuously enlarged or shape distinct from the preapical spurs). [Character 3 from Vilarino et al. (2022)] — CI = 84,7.
2	Sternum V anterior margin, reticulate cuticular region: (0) absent; (1) present. [Character 4 from Vilarino et al. (2022)] — CI = 84,7.
3	Sternum V reticulate region, elongate process: (0) absent; (1) present. — CI = 64,8.
4	Forewing fork I (R_2 and R_3): (0) absent; (1) present. — CI = 84,7.
5	Forewing fork II (R_4 and R_5): (0) rooted or sessile; (1) petiolate or with nygma isolated by cell. [Character 7 from Vilarino et al. (2022)] — CI = 58,0.
6	Forewing with nygma surrounded by a cell: (0) absent; (1) present. [Character 6 from Vilarino et al. (2022)] — CI = 73,4.
7	Forewing anal vein 2A: (0) absent; (1) present.— CI = 100.
8	Discoidal cell relative length to thyridial cell: (0) longer than thyridial cell; (1) subequal shorter than thyridial cell.— CI = 100.
9	Tergum VIII produced posterad over tergum IX: (0) absent; (1) present.— CI = 100.
10	Tergum IX, shape, in dorsal view: (0) very narrow, subrectangular (1) elongated, with apical lobes, roof shaped. [Character 18 from Vilarino et al. (2022)] — CI = 100.
11	Tergum IX, posterior margin incision: (0) shallow or absent; (1) deep.— CI = 84,7.
12	Tergum IX, anterior margin incision: (0) shallow or absent; (1) deep.— CI = 40,9.
13	Sternum IX, apodeme shape: (0) narrow, forming ~90° angle with anterior margin; (1) broad and contiguous with sternum IX. [Character 11 from Vilarino et al. (2022)] — CI = 84,7.
14	Sternum IX, relative length, in lateral view: (0) short, slightly longer than high or shorter; (1) long, 2× as long as high or longer. — CI = 100.
15	Sternum IX posterior margin projecting mesally: (0) absent; (1) present. [Character 12 (Vilarino et al. 2022)] — CI = 58,0.
16	Sternum IX posterior margin projection, incision: (0) shallow incision or not divided; (1) divided by deep mesal incision. — CI = 84,7.
17	Sternum IX apical projection length: (0) short; (1) very elongate (about half inferior appendage length). — non-informative.
18	Sternum IX, in lateral view, dorsal margin incision near preanal appendage: (0) absent; (1) present. [Character 17 (Vilarino et al. 2022)] — CI = 100.
19	Inferior appendage, articles (coxopodite and harpago), fusion: (2) articles broadly fused, indistinct; (1) articles well evident by suture line. [Character 25 from Vilarino et al. (2022)] — CI = 100.
20	Coxopodite basal region, inner face setose or granulose: (0) absent; (1) present. [Character 33 from Vilarino et al. (2022)] — CI = 64,8.
21	Harpago spine-like setae, length: (0) short or absent; (1) very long. [Character 45 from Vilarino et al. (2022)] — CI = 84,7.
22	Harpago spine-like setae, density: (0) few, sparse spines; (1) many dense spines. [Character 46 modified from Vilarino et al. (2022)] — CI = 73,4.
23	Harpago base, inner face setose area, shape: (0) narrow; (1) broad. [Character 46 modified from Vilarino et al. (2022)] — non-informative.
24	Harpago, stalked, polype-like mesal sclerite: (0) absent; (1) present. [Character 39 from Vilarino et al. (2022)] — CI = 84,7.
25	Harpago, group of conspicuously elongate setae in the same position of the mesal sclerite: (0) absent; (1) present. — CI = 100.
26	Mesal sclerite, spine-like setae, length: (0) short; (1) elongate. — CI = 100.
27	Mesal sclerite, stalk shape: (0) narrow, oblong; (1) wide, round. — CI = 100.
28	Harpago, subbasal region shape: (0) linearly contiguous with base and apex; (1) bent in an elbow-like shape (usually with a group of spines). — non-informative.
29	Paraproct dorsal band, spine-like setae: (0) absent; (1) present. — non-informative.
30	Paraproct, lateral points or spine-like setae: (0) absent; (1) present. [Character 20 from Vilarino et al. (2022)] — non-informative.
31	Geometric morphometric characters, shape of preanal appendage, in lateral view: 100 landmark configurations. — CI = 97,2.

messapus but also including other subgenera species. The results show three main clusters: (1) a cluster including species with wide preannal appendage, which are most of *Sphagocentron* species; (2) a cluster including many species with mostly straight appendage, including two *X.* (*Xiphocentron*) species, *X.* (*S.*) *julus*, *X.* (*R.*) *numanus* and a couple of *X.* (*Antillotrichia*) species from the greater and lesser Antilles; and (3) a cluster with many *X.* (*Antillotrichia*) species from South America having highly wavy appendage narrow at midlenght and wide and round at apex, but also including a cluster of species from Mexico and Central America having appendage with wider base and digitate apex with two *X.* (*Rhamphocentron*), *X.* (*X.*) *polemon* and *X.* (*A.*) *moncho*. The average overall phenotype distance was 0.137 (maximum = 0.349; minimum = 0.049). For the *Sphagocentron* subgenus (n = 7) was 0.129 (max = 0.240; min = 0.049); for *Xiphocentron* subgenus (n = 3) was 0,142 (max = 0.269; min = 0.074); for *Rhamphocentron* subgenus (n = 3) was 0.139 (max = 0.275; min = 0.067); for *Antillotrichia* subgenus (n = 15) was 0.093 (max = 0.349; min = 0.049).

The divergence of the preanal appendage shape among subgenera with groups defined a priori was visualized through the discriminant analysis over the 10 first PCs (Fig. 4). After the discriminant analysis adjusted the data to maximize between-group differences the subgenera were in general well separated except by the overlapping of *X.* (*S.*) *julus* within *Antillotrichia* and *X.* (*A.*) *fuscum* within the *Sphagocentron* subgenus morphospace. The jackknife cross-validation test had an overall correctness 64.29%, and was able to correctly classify 71% (5/7) of the *Sphagocentron*, 73% (11/15) of the *Antillotrichia*, 33% (1/3) of the *Rhamphocentron*, and 33% (1/3) of the *Xiphocentron* subgenus.

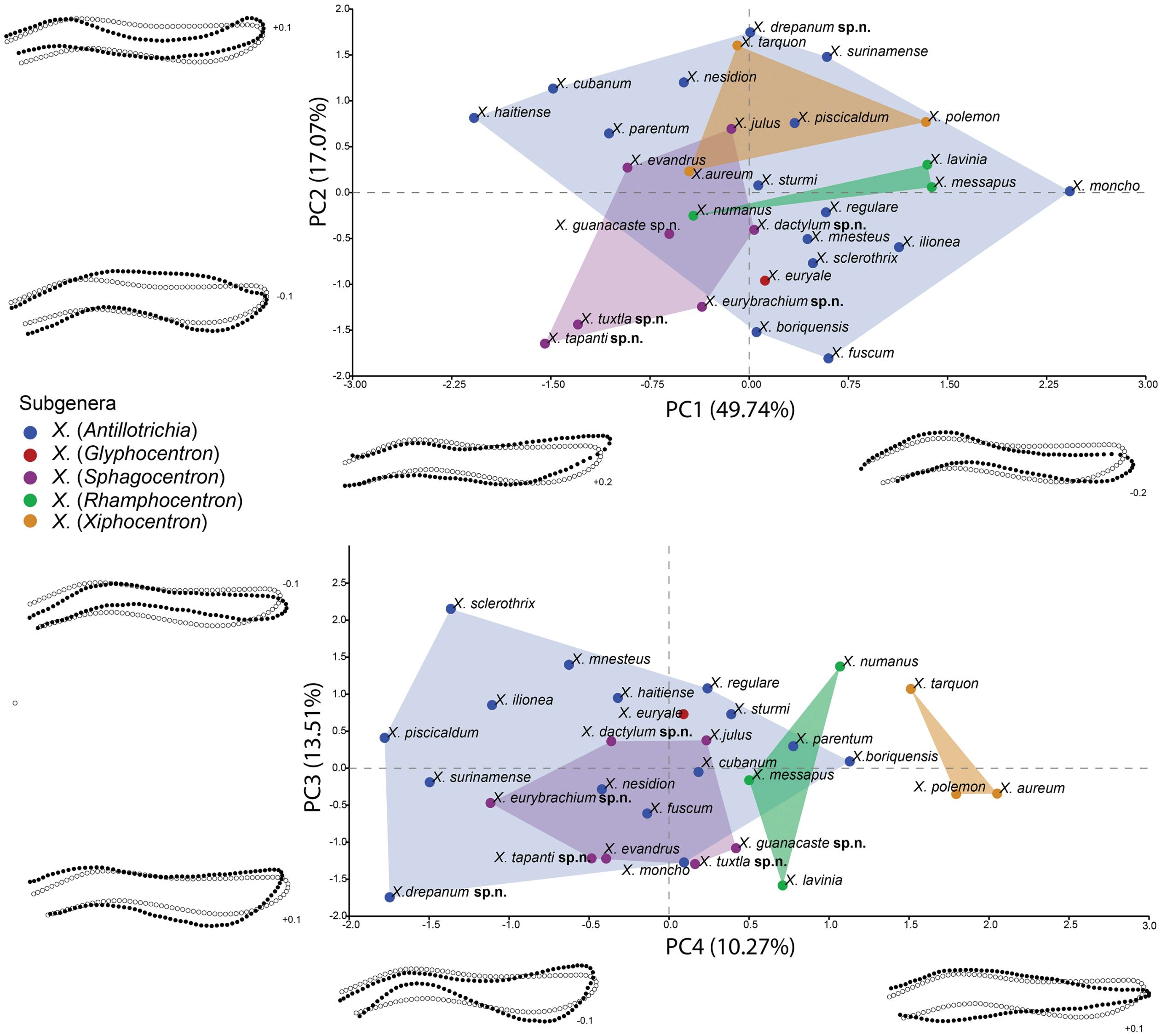

Figure 2. Principal Component Analysis (PCA) of preanal appendage shape, male genitalia. Showing the four major principal components (PCs) (90.59% of the total variance). The percentage of shape variance represented by each PC is presented along the axes. Thin-plate splines show the degree of shape deformation from the mean overall shape.

3.2. Phylogeny

The analysis ran for around four hours and examined 8,641,321 rearrangements, with one most parsimonious topology retained with a score of 3.91330. The tree topology and the distribution of the analyzed species are displayed at Figure 5. Most clades had very low or no statistical support, except *X.* (*Xiphocentron*) *tarquon* and *X.* (*Xiphocentron*) *polemon* (95%), the clade with *X.* (*Rhamphocentron*) species (68%), the clade *X.* (*Antillotrichia*) *regulate* and *X.* (*Antillotrichia*) *sturmi* (87%) and the clade with *X.* (*Antillotrichia*) species from Great Antilles (*X. haitiense* (*X. cubanum*, *X. nesidion*)). *Xiphocentron* (*Sphagocentron*) subgenus was placed in a clade including many *X.* (*Antillotrichia*) species that do not present a mesal sclerite but instead longer spine-like setae at the same position (character 25(1)). *Xiphocentron* (*A.*) *fuscum* appears as the sister clade of *X.* (*Sphagocentron*) species (support of 44%), based on the sternum IX apodeme wide and contiguous with sternum margin (character 13(1)), absence of spines at the coxopodite basal region (character 20(0)), and contributions of the preanal appendage morphometry (not shown on the cladogram). The monophyly of *X.* (*Sphagocentron*) subgenus (support of 37%) is recovered based on the character 14(1) (sternum IX, in lateral view 2× as long as high or longer) and the contributions of the preanal appendage morphometry. The new species *X. dactylum* and *X. eurybrachium* are shown as first cladogenesis of the subgenus. Clades within *X.* (*Sphagocentron*) presented very low support (<30%) (Fig. 5A). *Xiphocentron* (*Antillotrichia*) subgenus is not recovered as a monophyletic group, with the species included in the analysis being split into three different clades.

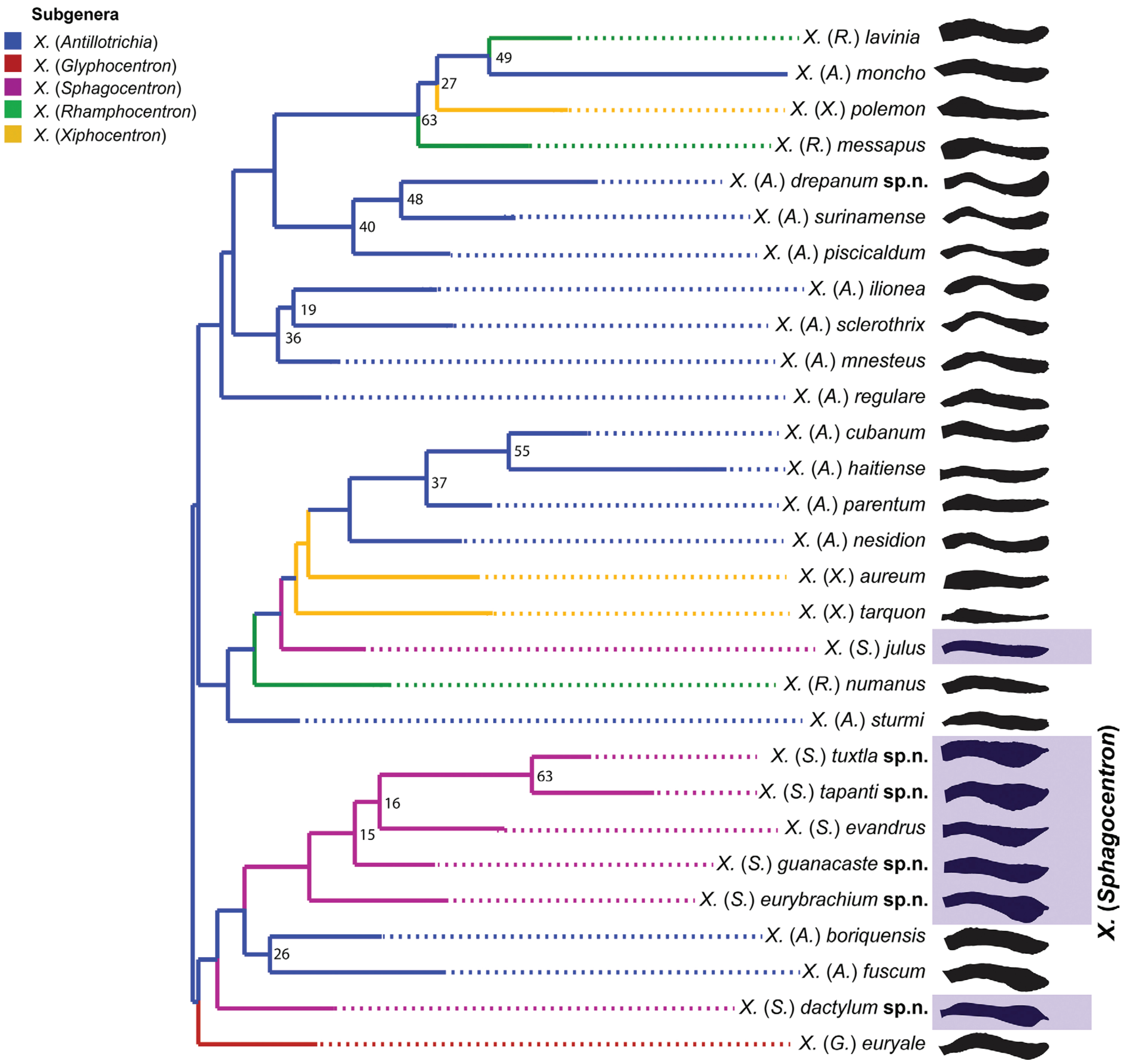

Figure 3. Neighbor-joining cluster analysis based on distance coordinates of the principal components (PCs). Representation of the preanal appendage of each species is also depicted. Bootstrap values greater than ten are shown at the nodes.

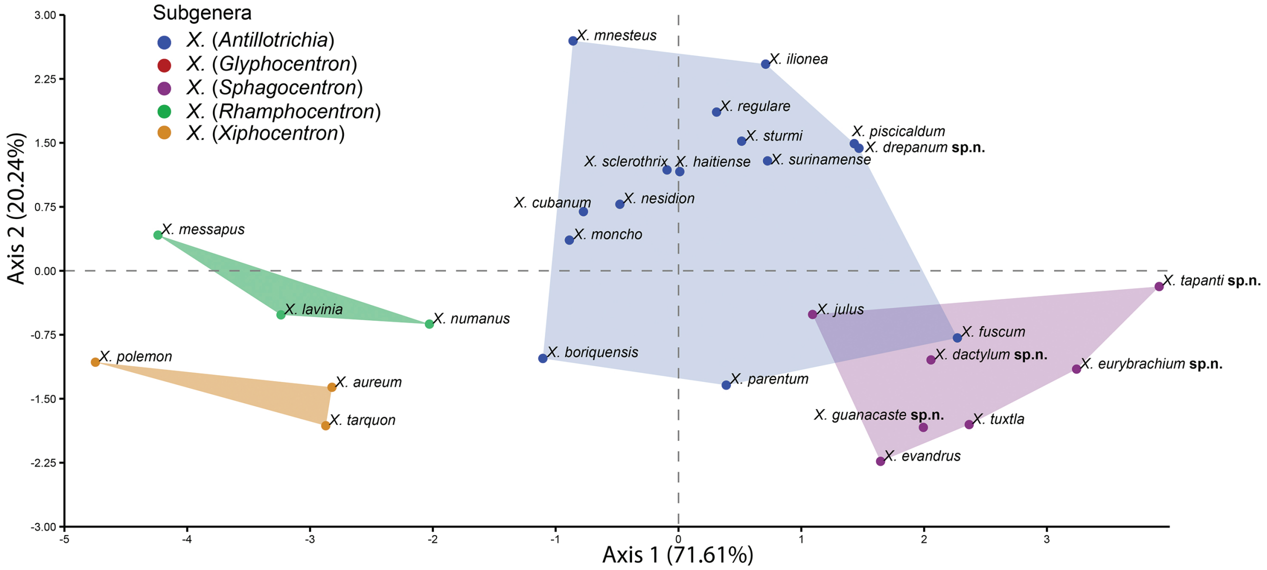

Figure 4. Discriminant analysis of preanal appendage shape over the ten first Principal Components (PCs). The percentage of shape variance is presented along the axes.

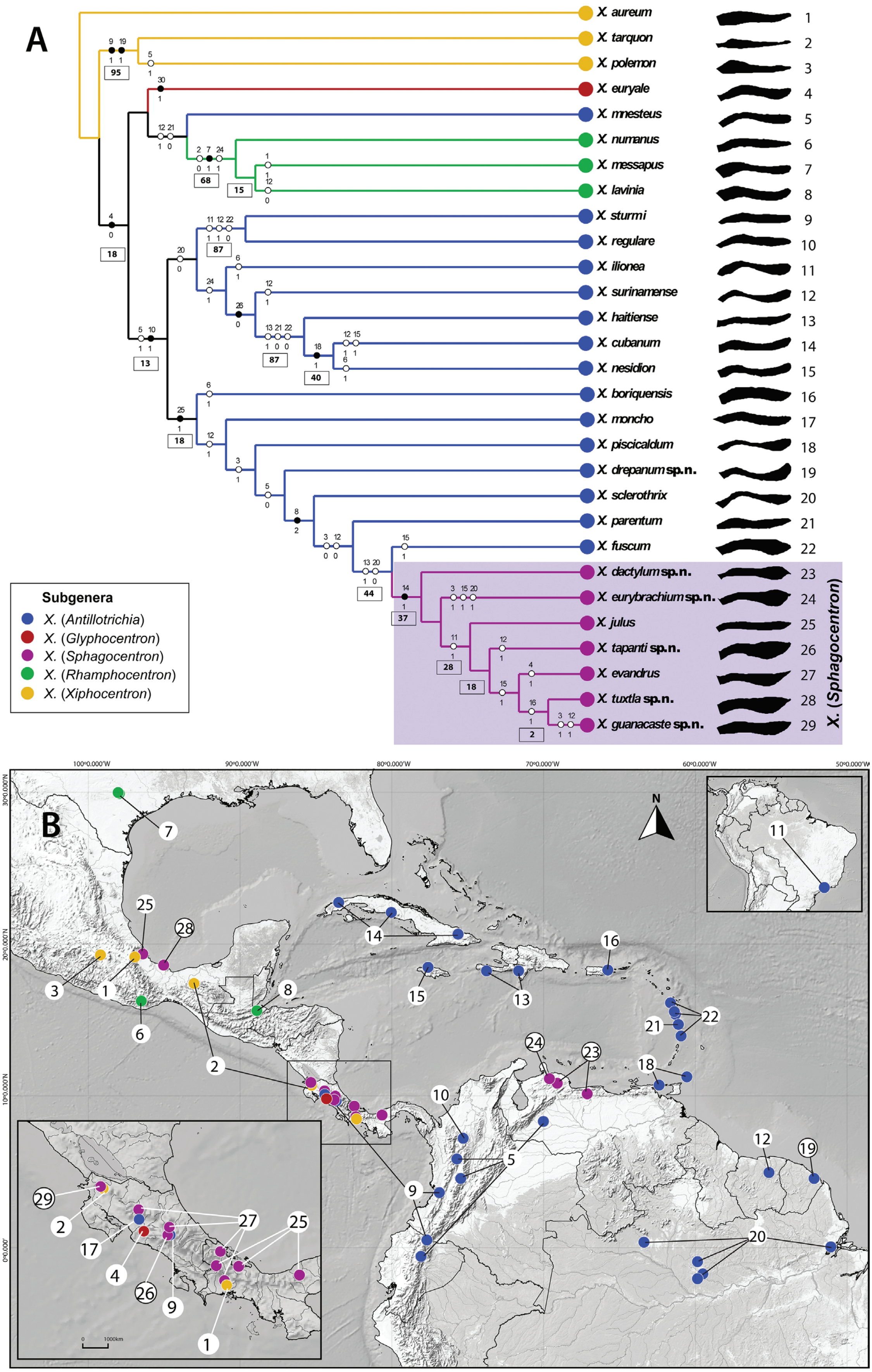

Figure 5. Phylogeny of *Xiphocentron* (*Sphagocentron*) species and other subgenera, and distribution map. **A** Implied weighting parsimony of geometrical morphometric data and 30 discrete characters, unambiguous discrete characters states are shown at the branches. Representation of the preanal appendage is depicted to each species. Symmetric resampling support values are shown at the node boxes. **B** Corresponding distributions of the analyzed species are indicated in the map with the respective number as in the phylogeny.

3.3. Taxonomy

Genus *Xiphocentron* Brauer, 1870

Subgenus *Xiphocentron* (*Sphagocentron*) Schmid, 1982

Type species. *Xiphocentron* (*Sphagocentron*) *evandrus* Schmid, 1982, by original designation.

Xiphocentron (*Sphagocentron*) *dactylum* sp. nov.

https://zoobank.org/DCC6A79D-29BB-4A0D-8850-8FF-26C2DD67F

Figures 6A–E

Type material. Holotype: VENEZUELA • ♂; Falcón, P. N. Cueva de la Quebrada del Toro, Quebrada del Toro, 10°49.581′N, 69°07.990′W, el. 530 m, 11.vi.2001, Holzenthal, Blahnik, Paprocki, Cressa leg., UMSP000075081. — **Paratypes:** VENEZUELA • 1♀; same data as holotype, UMSP000075082. • 1♂; Aragua, Tiara, 30.i.1983, Flint leg., USNMENT01518180.

Diagnosis. *Xiphocentron dactylum* **sp. nov.** is particularly similar to *Xiphocentron* (*S.*) *eurybrachium* **sp. nov.** mainly by the shape of the preanal appendage (in lateral view, straight throughout length, apically wide). However, *X. dactylum* **sp. nov.** can be differentiated from its congener by the (1) shape of sternum IX in ventral view, elongate and about as wide basally as apically, subrectangular (trapezoid, conspicuously wider apically in *X. eurybrachium* **sp. nov.**), by (2) the posterior margin of sternum IX with wide shallow V-shaped incision (absent in *X. eurybrachium* **sp. nov.**) in ventral view.

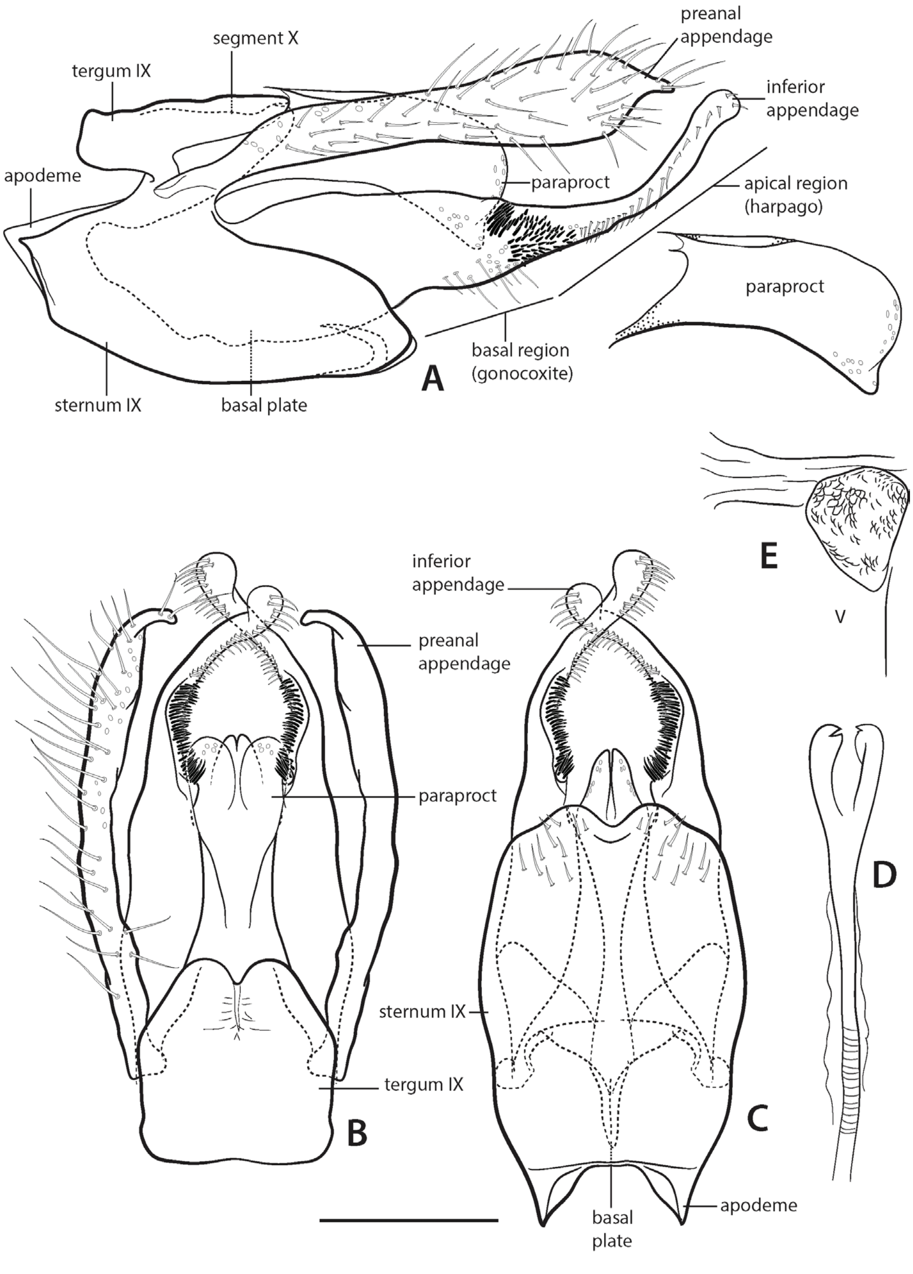

Figure 6. *Xiphocentron* (*Sphagocentron*) *dactylum* **sp. nov.**, holotype, male (UMSP). Genitalia: **A** left lateral, **B** dorsal, **C** ventral, **D** phallus dorsal, **E** sternum V left ventral reticulate region. Scale bar: 0.1 mm.

Description. ***Male***: Forewing length 3.0 mm (n = 2). Color overall dark brown, forewing uniformly dark brown. Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell half as long as thyridial cell. Hind wing forks II and V present. Sternum V with anterolateral reticulated round region (Fig. 6E).

Genitalia (Fig. 6A–D). Tergum IX, in lateral view, narrow basally, acuminate apically (Fig. 6A); in dorsal view, anterior margin straight; posterior margin with round lobes and mesal V-shaped incision, and narrow suture line (Fig. 6B). Sternum IX, in lateral view, length more than 2× as long as wide, apex subdeltoid; anterior apodeme short, wide (Fig. 6A); in ventral view, about 2× as long as wide, posterior margin with V-shaped mesal incision (Fig. 6C). Tergum X membranous fused basodorsally to each paraproct. Paraproct, in lateral view, oblong, width subequal throughout length, apex round, with narrow, short ventral lobe (Fig. 6A); in dorsal view, wide basally, narrowed mesally and wide apically, divided apicomesally, each side partially fused at base, without clear sclerotized mesal band, apex with several sensillae (Fig. 6B). Preanal appendage, in lateral view, setose, length more than 2× as long as tergum IX, wide, straight throughout length, apically wide, 1.5 as wide as base, with narrow digitate projection (Fig. 6A); in dorsal view, narrow throughout length, wide at apex with digitate projection curved mesad (Fig. 6B). Inferior appendage, in lateral view, about 2× as long as tergum IX, curved mesally in dorsal view (Fig. 6B); coxopodite and harpago completely fused to each article, inner face with longitudinal area of numerous, slightly sparse, spine-like setae, mesal sclerite region with dense, long spine-like setae, with line of regular setae from midlenght to apex (Fig. 6A); basal region (coxopodite) wide, without clear basomesal spine-like setae; apical region (harpago) narrow, digitate, about as long as basal region, apex slightly globose and curved distad (Fig. 6A); basal plate in lateral view wide (Fig. 6A). Phallus tubular, very long and narrow, reaching segment V, basally conical, subapically annulate, weakly sclerotized, apex enlarged (Fig. 6D).

Etymology. From the Greek dáktulos, ‘finger’, in reference to the conspicuous digitate projection of preanal appendage curved mesad.

Distribution. Venezuela.

Xiphocentron (*Sphagocentron*) *eurybrachium* sp. nov.

https://zoobank.org/0A3F7516-F77F-4AD0-A1DB-BECD-81B8855A

Figures 7A–F

Type material. Holotype: VENEZUELA • ♂; Falcón, Mitare river, near San Luis, 11°07.930′N, 69°39.184′W, el. 589 m, 07.vi.2001, Holzenthal, Blahnik, Paprocki, Cressa leg., UMSP000074031. — **Paratypes:** VENEZUELA • 6♂; same data as holotype, UMSP000074032, 000074033, 000074034, 000074035, 000074036, 000074037.

Diagnosis. *Xiphocentron eurybrachium* **sp. nov.** is mostly similar to *Xiphocentron* (*S.*) *dactylum* **sp. nov.**. However, *X. eurybrachium* **sp. nov.** can be differentiated mainly by the presence of the following characters: (1) the preanal appendage in lateral view conspicuously wide subapically (2× wider than basal section), without narrow digitate projection; (2) inferior appendage basal region (coxopodite) with small spine-like setae in ventral view, apex curved dorsolaterally in dorsal view; (3) paraproct ventroapical lobe wide (as wide as preanal appendage basal section) (narrow or indistinct in the other species); (4) sternum IX trapezoid, posterior margin without incision; (5) sternum V with a digitate lateral projection.

Description. ***Male***: Forewing length 3.5–3.8 mm (n = 7). Wing without spots. Color overall brown, forewing uniformly dark brown. Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell 3/4 as long as thyridial cell, very conspicuous nygmata. Hind wing forks II and V present (Fig. 7A). Sternum V with elongate, digitate, lateral glandular process (Fig. 7F).

Genitalia (Figs 7B–E). Tergum IX, in lateral view, wide basally, narrower apically (Fig. 7B); in dorsal view, anterior margin substraight; posterior margin with very narrow incision (Fig. 7C). Sternum IX, in lateral view, length more than 2× as long as high, apex subtruncate, posterior margin concave, with a posterobasal short projection, anterior apodeme short, wide (Fig. 7B); in ventral view, about as long as wide, posterior margin slightly produced posterad, mesally convex, with a posteromesal, short projection (Fig. 7D). Tergum X membranous fused dorsally to each paraproct (Figs 7B,7C). Paraproct, in lateral view, oblong, narrow basaly, wider apically, apex subtruncate, with wide round ventroapical lobe (Fig. 7B); in dorsal view, wide basally, narrowed mesally and wide apically, divided apicomesally, each side fused at midlenght, with narrow sclerotized mesal band, apex with line of sparse sensillae (Fig. 7C). Preanal appendage, in lateral view, setose, about 2.5× as long as tergum IX, wide, substraight throughout length, apically wide, 2× as wide as base, with short, narrow projection (Fig. 7B); in dorsal view, narrow and curved mesally throughout length, tapered apically (Fig. 7C). Inferior appendage, in lateral view, about 2.5× as long as tergum IX, coxopodite and harpago completely fused to each article, inner face with longitudinal area of dense, long spine-like setae, spine-like setae shorter towards base, with multiple lines of regular setae from midlenght to apex (Fig. 7B), (Fig. 7D); basal region (coxopodite) wide, with several basomesal short spine-like setae, mesal sclerite region indistinct (Fig. 7B); apical region (harpago) narrow, digitate, 2× as long as basal region, apex slightly globose and curved dorsally; (Fig. 7B); basal plate in lateral view, wide, anteriorly with long, narrow flange (Fig. 7B). Phal-

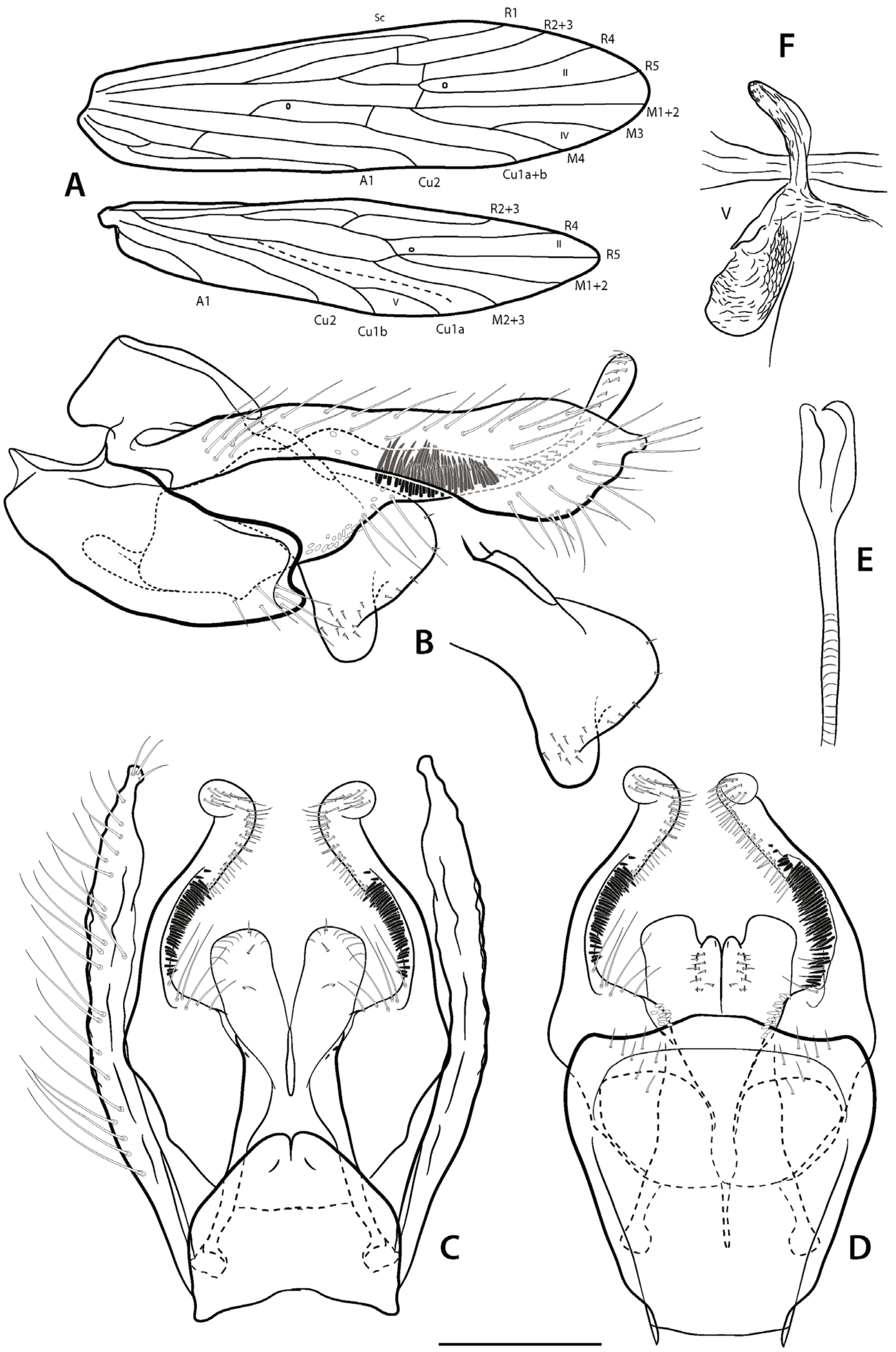

Figure 7. *Xiphocentron* (*Sphagocentron*) *eurybrachium* **sp. nov.**, holotype, male (UMSP). **A** wing venation left. Genitalia: **B** left lateral, **C** dorsal, **D** ventral, **E** phallus dorsal, **F** sternum V left ventral reticulate region. Scale bar: 0.1 mm.

lus tubular, very long and narrow, reaching segment V, basally conical, subapically annulate, weakly sclerotized, apex enlarged (Fig. 7E).

Etymology. From the Greek eurus, 'wide', and brakhíōn, 'arm' in reference to the preanal appendage shape in lateral view.

Distribution. Venezuela.

Xiphocentron (*Sphagocentron*) *evandrus* Schmid, 1982

Figures 8A–D

Schmid 1982:56 [Type locality: Costa Rica, Juan Vinas, Chiz river; USNM; ♂]. — Holzenthal 1988c:58 [distribution]. — Armitage et al. 2015a:3 [distribution]. — Armitage et al. 2015b:5 [checklist]. — Armitage and Cornejo 2015:193 [checklist]. — Harris and Armitage 2019:7 [distribution]

Material examined. COSTA RICA • ♂; Juan Vinas, Chiz river, 21.vi.1967, Flint and Ortiz leg., USNM. • ♂; Alajuela, Río La Vieja, nr. Lagarto, 2-3.vii.1967, Flint and Ortiz leg., USNM.

Diagnosis. *Xiphocentron evandrus* can be differentiated by the combination of preanal appendage subapically wide, sternum IX posterior margin produced, overall deltoid, with shallow apical incision forming very small

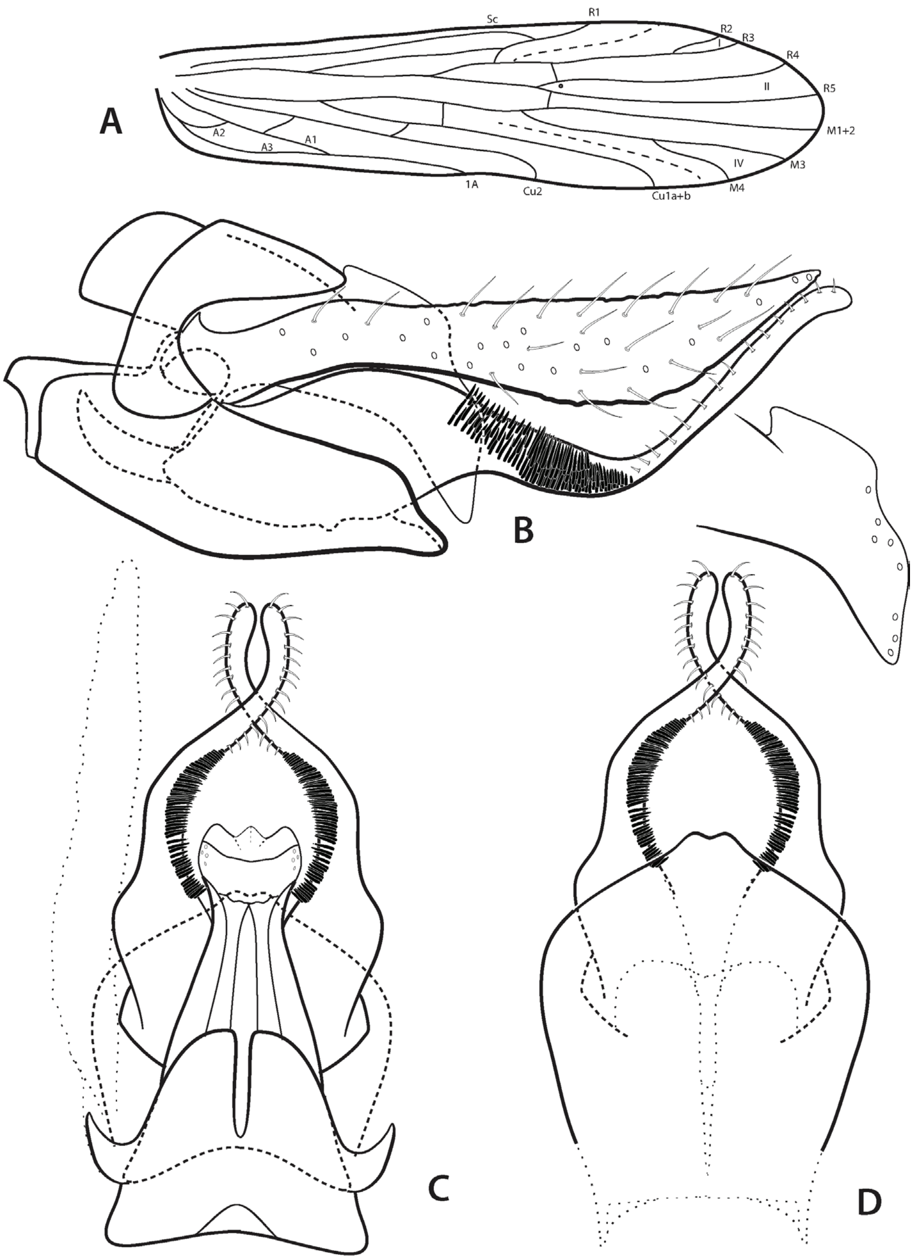

Figure 8. *Xiphocentron* (*Sphagocentron*) *evandrus* Schmid, 1982, holotype, male (USNM). **A** forewing venation. Genitalia: **B** left lateral, **C** dorsal, **D** ventral. Modified from Schmid (1982). Small dots are inferred based on other species.

lobes; tergum IX with very deep, narrow, parallel sided mesal incision.

Synopsis. Adult male. Forewing length 4-4.25 mm (n = 2). Color overall brown, forewing uniformly dark brown. Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks I, II and IV present; fork I petiolated, fork II sessile at discoidal cell; discoidal cell half as long as thyridial cell (Fig. 8A). Hind wing forks II and V present. Sternum V with anterolateral reticulated region.

Genitalia (Fig. 8B–D). Tergum IX, in lateral view, wide basally, narrower apically (Fig. 8B); in dorsal view posterior margin forming two dorsal lobes in quarter circle shaped and large lateral flanges (Fig. 8C). Sternum IX, in lateral view, about 3× as long as high, apex narrow, anterior apodeme short, truncate (Fig. 8B); in ventral view, greatly enlarged at middle length, then greatly narrowed towards posterior margin, posterior margin with two very small lobes (Fig. 8D). Paraproct, in lateral view, with apex oblique (Fig. 8B); in dorsal view, apex round, ending in three equal lobes (Fig. 8C). Preanal appendage, in lateral view, wide, strongly thickened subapically then tapering into long triangular pointed apex (Fig. 8B). Inferior appendage, in lateral view, about 2× as long as tergum IX, coxopodite and harpago completely fused to each article, inner face with longitudinal area of dense, long spine-like setae, and row of regular setae from midlenght to apex (Fig. 8B); basal region (coxopodite) wide, mesal sclerite region indistinct (Fig. 8B); apical region (harpago) narrow, digitate, 3× as long as basal region, strongly curved (Fig. 8B); in dorsal view, strongly sinuous (Fig. 8C). Phallus tubular, very long and narrow, reaching segment V, basally conical, subapically annulate, weakly sclerotized, apex enlarged.

Distribution. Costa Rica, Panama.

Remarks. Type was fixed in a permanent slide and displayed in a dorso-lateral view.

Xiphocentron (*Sphagocentron*) *guanacaste* sp. nov.

https://zoobank.org/229026A6-84A4-4D23-BDA9-52074A7DF801

Figures 9A–D

Type material. Holotype: COSTA RICA • ♂; Guanacaste, Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo, 10°52′48.00”N, 85°23′20.40”W, el. 575 m, 26.viii. 2013, Malaise Trap, D.H. Janzen, W. Hallwachs leg., [BOLD: GMAAG1127-16] BIOUG28044-C01. — **Paratypes:** Same data as holotype, except 09.ix.2013. • 2♂; 09.ix.2013, [BOLD: GMACB1559-15] BIOUG19725-A07, [BOLD: GMACB1565-15] BIOUG19725-B01. • ♂; same data, except 26.viii.2013, [BOLD: GMAAG1127-16] BIOUG28044-C01. • ♂; same data, except 31.iii.2014,

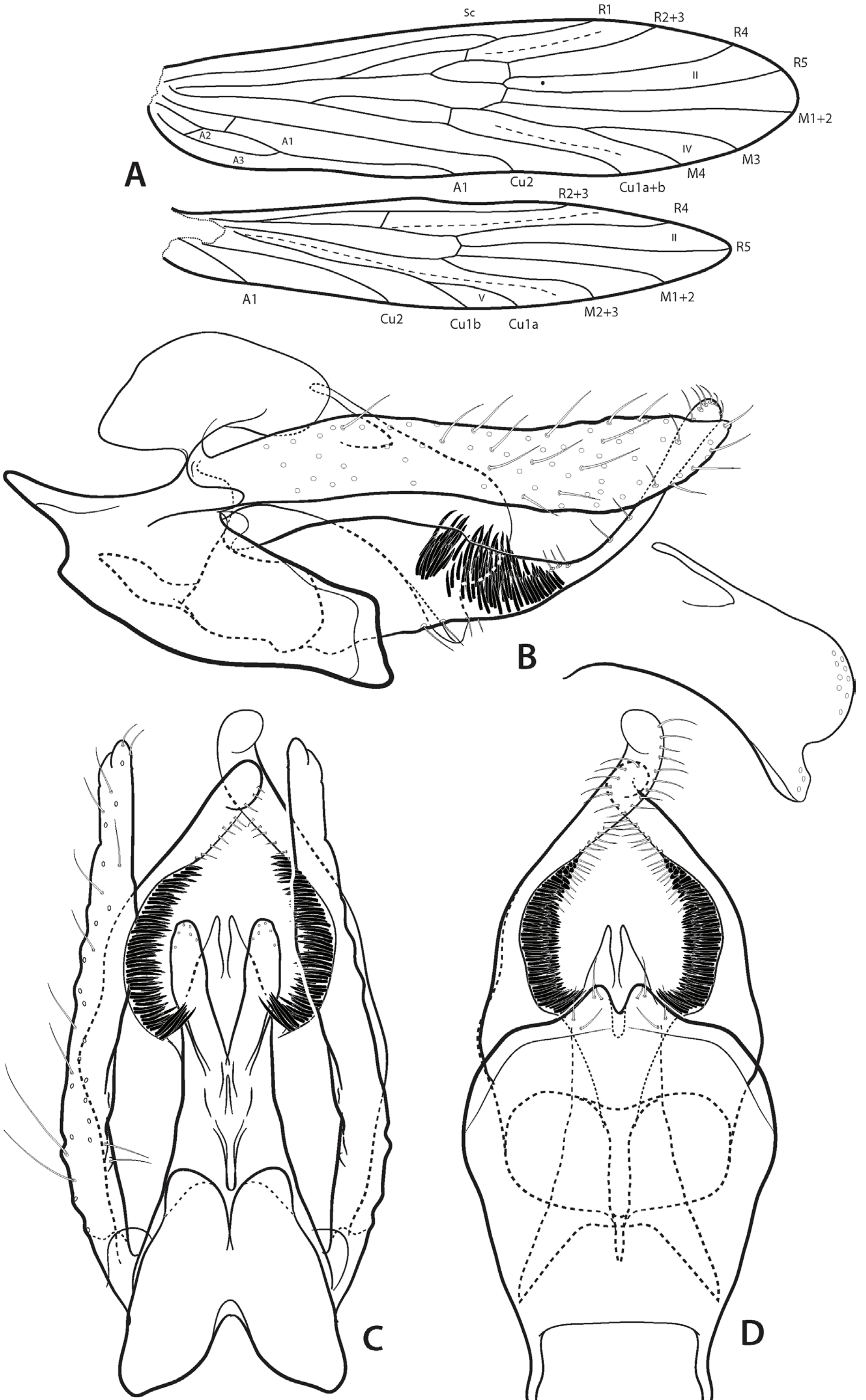

Figure 9. *Xiphocentron* (*Sphagocentron*) *guanacaste* **sp. nov.**, holotype, male (BIOUG). **A** wing venation left. Genitalia: **B** left lateral, **C** dorsal, **D** ventral. Scale bar 0.1 mm.

[BOLD: GMAAQ746-16] BIOUG28344-B02. • ♂; same data, except 11.ix.2013, [BOLD: GMACA1002-15] MZUSP.

Diagnosis. The new species is most similar to *X. tuxtla* **sp. nov.** by sharing the prominent acute lobes at the posterior margin of sternum IX and the slightly divergent lobes of tergum IX posterior margin. The new species can be diagnosed in lateral view by (1) the preanal appendage with about the same width throughout length; (2) the spine-like setae of inferior appendage numerous and very dense (sparser basely in *X. tuxtla* **sp. nov.**); and (3) the shape of paraproct apicodorsaly round (truncate in *X. tuxtla* **sp. nov.**). In dorsal view (4) the tergum IX is longer than wide (about as long as wide in *X. tuxtla* **sp. nov.**).

Description. ***Male*:** Forewing length 4–4.2 mm (n = 3). Color overall pale brown, forewing uniformly dark brown. Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present; fork II sessile at discoidal cell; discoidal cell half as long as thyridial cell. Hind wing forks II and V present (Fig. 9A). Sternum V with anterolateral reticulated region and wide sclerotized lateral projection.

Genitalia (Fig. 9B–D). Tergum IX, in lateral view, wider basally, narrower apically (Fig. 9B); in dorsal view, anterior margin with deep wide concave incision; posterior margin with round lobes and deep v-shape mesal incision (Fig. 9C). Sternum IX, in lateral view, about 3× as long as high, apex subtruncate, with narrow, straight anterior apodeme, tapering to narrow flange (Fig. 9B); in ventral view, longer than wide, posterior margin produced mesally, forming prominent acute lobes divided by v-shaped mesal incision (Fig. 9D). Tergum X membranous fused basodorsally to each paraproct. Paraproct, in lateral view, oblong, width subequal throughout length, dorsoapically round, with narrow, short ventral lobe (Fig. 9B); in dorsal view, wide basally, divided apicomesally, each side partially fused at midlenght, without clear mesal band, apex with several sensillae (Fig. 9C). Preanal appendage setose, in lateral view more than 2× as long as tergum IX, mostly straight to slightly wavy, with same width throughout length, apex tapered, acute (Fig. 9B); in dorsal view, about same width throughout length (Fig. 9C). Inferior appendage in lateral view about 3× as long as tergum IX; coxopodite and harpago completly fused, without suture line between each article, inner face with area of dense, long spine-like setae, and row of regular setae from midlenght to apex (Fig. 9B); basal region (coxopodite) wide, without basomesal spine-like setae, mesal sclerite region with dense, long spine-like setae, longer than other spinelike-setae; apical region (harpago) narrow, digitate, 1.5× as long as basal region, apex slightly enlarged (Fig. 9B); basal plate in lateral view wide, anteriorly with long, narrow flange (Fig. 9B). Phallus tubular, very long and narrow, reaching segment V, basally conical, subapically annulate, weakly sclerotized, apex slightly enlarged.

Etymology. Name in apposition; from the indigenous Nahuatl language: guaitil, 'tree', and nacaztli, 'ear'. It is the popular name of the tree *Entelorobium cyclocarpum* and also the name of the conservation area where the species was collected.

Distribution. Costa Rica.

Xiphocentron (*Sphagocentron*) *julus* Schmid, 1982

Figures 10A–C

Schmid 1982: 56 [Type locality: Holotype MEXICO • ♂; Veracruz, Puente Nacional, USNM]. — Armitage et al. 2018:3 [distribution]. — Harris and Armitage 2019: 7 [distribution]. — Armitage et al. 2021: 8 [distribution]. — Bueno-Soria et al. 2022:201 [checklist].

Material examined. MEXICO • ♂; Veracruz, Puente Nacional, 15.vi.1964, F.S. Blanton leg., USNM.

Diagnosis. *Xiphocentron julus* is particularly similar to *X. tampati* **sp. nov.** by the posterior margin of sternum IX mostly straight with very small mesal lobes; and can be differentiated from this and other species mainly by the uniform width of the preanal appendage, the posterior margin of sternum IX mostly straight with very small mesal lobes, and the paraproct apex oblique.

Synopsis. Male. Forewing length 4.0 mm. Color overall brown, forewing uniformly dark brown. Genitalia (Fig. 10A–C). Tergum IX in lateral view, wide basally, narrower apically (Fig. 10A); in dorsal view, posterior margin with two ogival shaped lobes and small lateral flanges (Fig. 10B). Sternum IX, in ventral view, posterior margin abruptly truncated, straight at its ventro-apical margin, forming two low lobes, barely produced (Fig. 10C). Paraproct, in lateral view, slender tapering to a pointed apex (Fig. 10A); in dorsal view, apex round and forming two apical lobes (Fig. 10B). Preanal appendage in lateral view, regularly narrow and pointed at apex (Fig. 10A). Inferior appendage, in lateral view, about 2.5× as long as tergum IX, coxopodite and harpago completely fused to each article, inner face with longitudinal area of dense, long spine-like setae, and row of regular setae from midlenght to apex (Fig. 10A); basal region (coxopodite) wide, mesal sclerite region indistinct; apical region (harpago) narrow, digitate 2× as long as basal region, curved dorsad (Fig. 10A); in dorsal view, strongly curved mesad, apex twisted posterad (Fig. 10B). Phallus tubular, very long and narrow, reaching segment V, basally conical, subapically annulate, weakly sclerotized, apex enlarged.

Distribution. Mexico, Panama.

Remarks. Type was fixed in a permanent slide and displayed in lateral view.

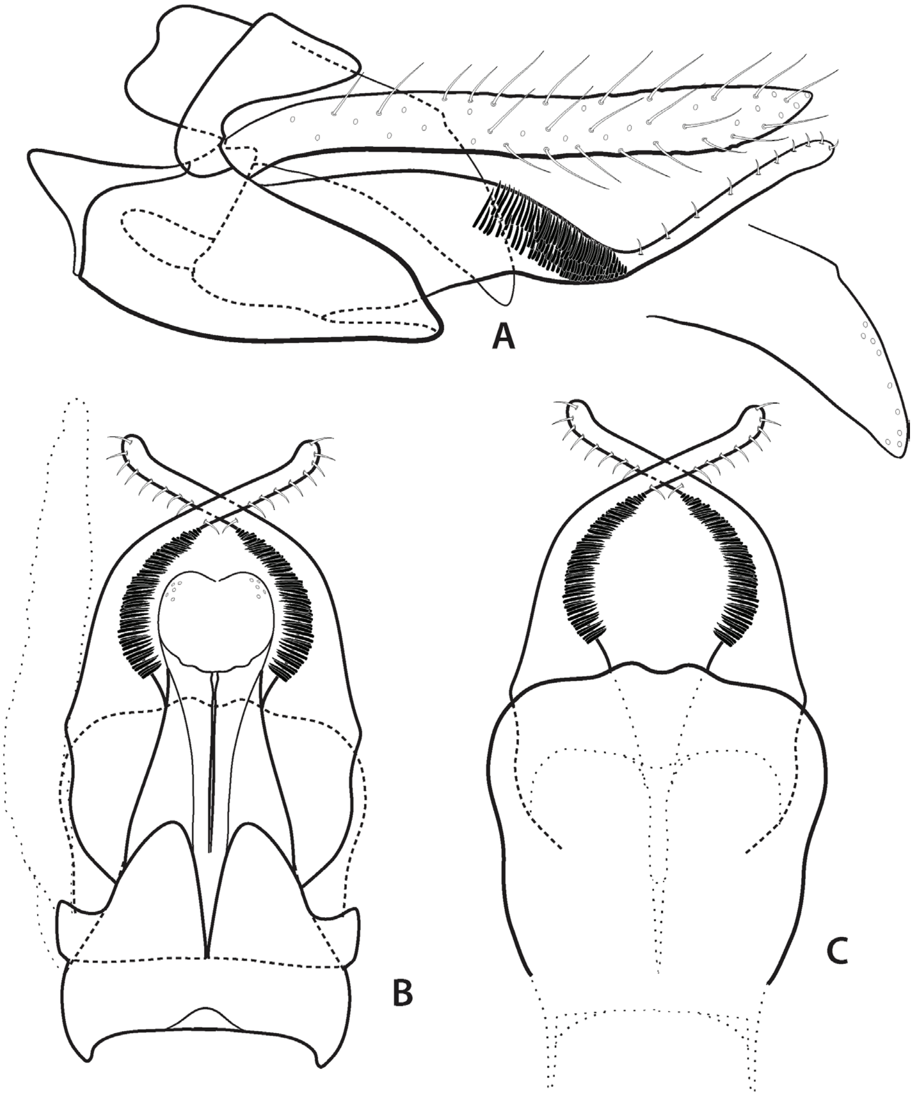

Figure 10. *Xiphocentron* (*Sphagocentron*) *julus* Schmid, 1982, holotype, male (USNM). Genitalia: **A** left lateral, **B** dorsal, **C** ventral. Modified from Schmid (1982). Small dots are inferred based on other species.

Xiphocentron (*Sphagocentron*) *tapanti* sp. nov.

https://zoobank.org/3139BEBC-6281-4133-9FD7-C410236EFBE8

Figures 11A–D

Type material. Holotype COSTA RICA • ♂; Cartago; Tapanti Reserve, quebrada palmitos and falls, 9.72°N, 83.78°W, 24–25.iii.1991, el. 1400 m, Holzenthal, Muñoz, Huisman leg., UMSP000143451. — **Paratypes** COSTA RICA • 2♂; same data as holotype, UMSP000143450, 000143452. • 9♂; same data, except 23.viii.1990, Holzenthal and Huisman leg., UMSP000143453, 000143454, 000143455, 000143456, 000143457, 000143458, 000143462, 000143463, 000143464.

Diagnosis. The new species is similar to *Xiphocentron julus* by the posterior margin of sternum IX with weakly produced mesal lobes. It can be differentiated from these and other species by the combination of the following characters: (1) the preanal appendage very wide subapically (narrow throughout length in *X. julus*); (2) shape of paraproct in lateral view, with apicodorsal margin truncate with conspicuously narrow ventral lobe (apicodorsal margin oblique, contiguous with the ventral lobe in *X. julus*); (3) tergun IX in dorsal view, posterior and anterior margins with wide deep mesal incisions.

Description. ***Male***: Forewing length 3.6–4.4 mm (n = 12). Color overall brown, forewing uniformly dark brown. Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present; fork II sessile at discoidal cell; discoidal 3/4 as long as thyridial cell. Hind wing forks II and V present (Fig. 11A). Sternum V with short, flattened projection, somewhat angular apically.

Genitalia (Fig. 11B–E). Tergum IX, in lateral view, wide basally, narrower apically (Fig. 11B); in dorsal view, anterior margin with deep concave mesal incision; posterior margin with round lobes and deep mesal incision (Fig. 11C). Sternum IX, in lateral view, about 3× as long as high, apex subround; anterior apodeme wide, straight, slightly tapering (Fig. 11B); in ventral view, slightly longer than wide, posterior margin substraight, with shallow, narrow mesal incision forming weakly produced mesal lobes (Fig. 11D). Tergum X membranous fused basodor-

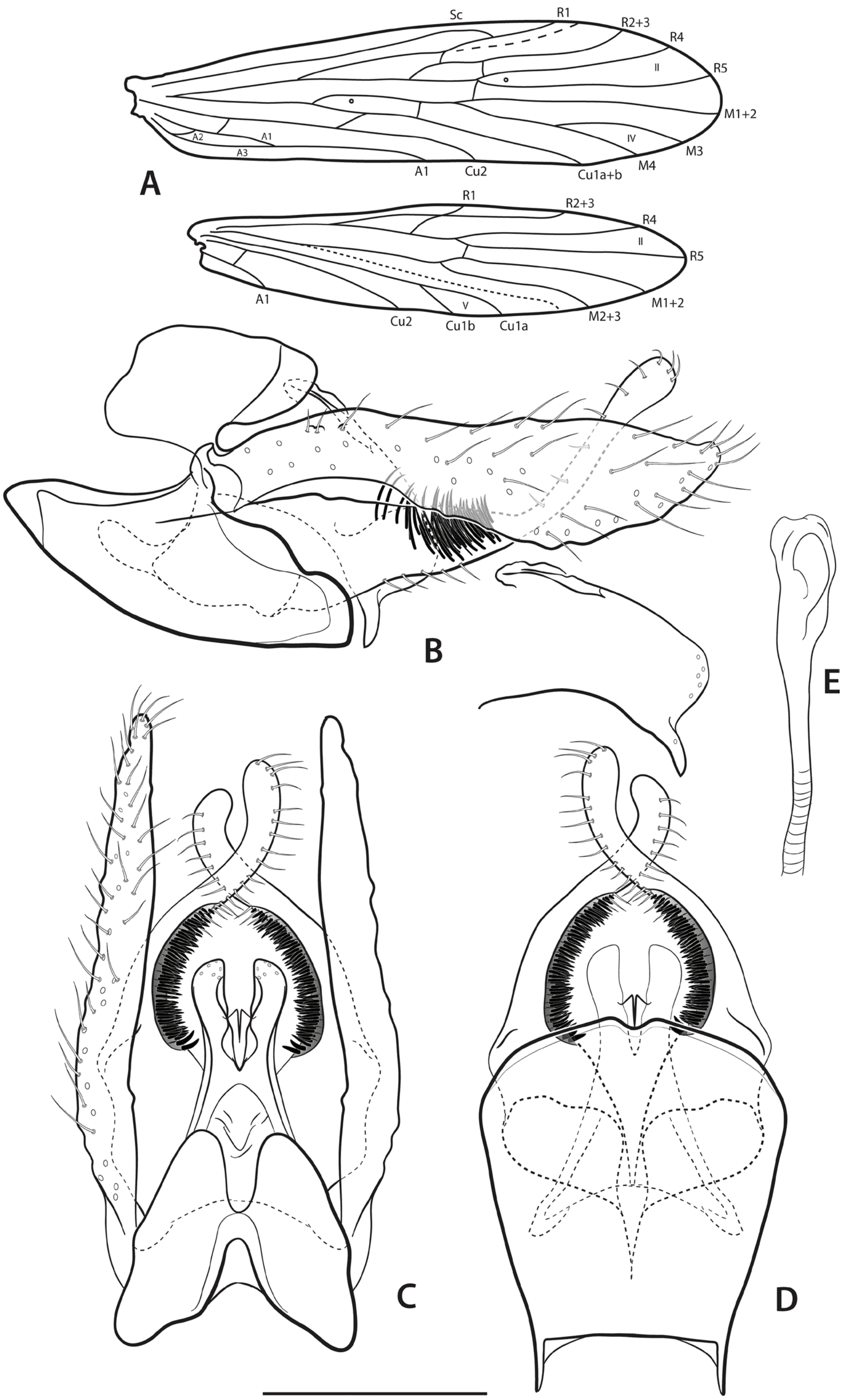

Figure 11. *Xiphocentron* (*Sphagocentron*) *tapanti* **sp. nov.** Holotype (UMSP), male. **A** wing venation. Genitalia: **B** left lateral, **C** dorsal, **D** ventral, **E** phallus lateral. Scale bar 0.1 mm.

sally to each paraproct. Paraproct, in lateral view, oblong, wide at base, narrowing apically, with narrow, ventral lobe (Fig. 11B); in dorsal view, wide basally, divided apicomesally, each side fused at midlenght, without sclerotized mesal band, apex with several sensillae (Fig. 11C). Preanal appendage setose, in lateral view about 2.5× as long as tergum IX, sigmoid, narrow at base, wide subapically, about 2× as wide as base, tapering at apex (Fig. 11B); in dorsal view, substraight, tapering apically (Fig. 11C). Inferior appendage, in lateral view, about 2.5× as long as tergum IX; coxopodite and harpago fused, with suture line between each article, inner face basally with long, dense spine-like setae, and row of regular setae from midlenght to apex (Fig. 11B); basal region (coxopodite) wide, without basomesal spine-like setae, mesal sclerite region with few difuse long spine-like setae; apical region (harpago) narrow, digitate, about as long as basal region, apex slightly enlarged, round (Fig. 11B); basal plate in lateral view wide, anteriorly with, narrow flange (Fig. 11B). Phallus tubular, very long and narrow, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged (Fig. 11E).

Etymology. Name in apposition; in reference to the Tapantí National Park where the species was collected.

Distribution. Costa Rica.

Xiphocentron (*Sphagocentron*) *tuxtla* sp. nov.

https://zoobank.org/DA100D11-3CF9-4230-A260-F8473F14A762

Figures 12A–D

Type material. Holotype MEXICO • ♂; Veracruz; Los Tuxtlas area, Maquinas river 4–14.v.1981, C.M. and O.S. Flint Jr leg., USNMENT01518157.

Diagnosis. The new species is most similar to *Xiphocentron guanacaste* **sp. nov.** by having the sternum IX posterior margin with a deep mesal incision forming two prominent lobes and is similar to *X. julus* and *X. evandrus* by the paraproct shape without the round apicodorsal margin. The species can be diagnosed from this and other congeners mainly by: (1) the shape of tergum IX with the posterior margin with wide subtruncate lobes slightly divergent, (2) the inferior appendage with sparser spine-like setae at the proximal region, and the combination of (3) the sternum IX posterior margin forming prominent mesal projections divided by a narrow incision, (4) the paraproct in lateral view truncate without round apicodorsal lobe and (5) the preanal appendage subapically wide.

Description. ***Male***: Forewing length 4.0 mm (n = 1). Color overall pale brown, forewing overall dark brown (in alcohol). Maxillary palp segment length formula (I = II = III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present, fork II sessile at discoidal cell; discoidal half as long as thyridial cell. Hind wing forks II and V present. Sternum V with anterolateral reticulated region.

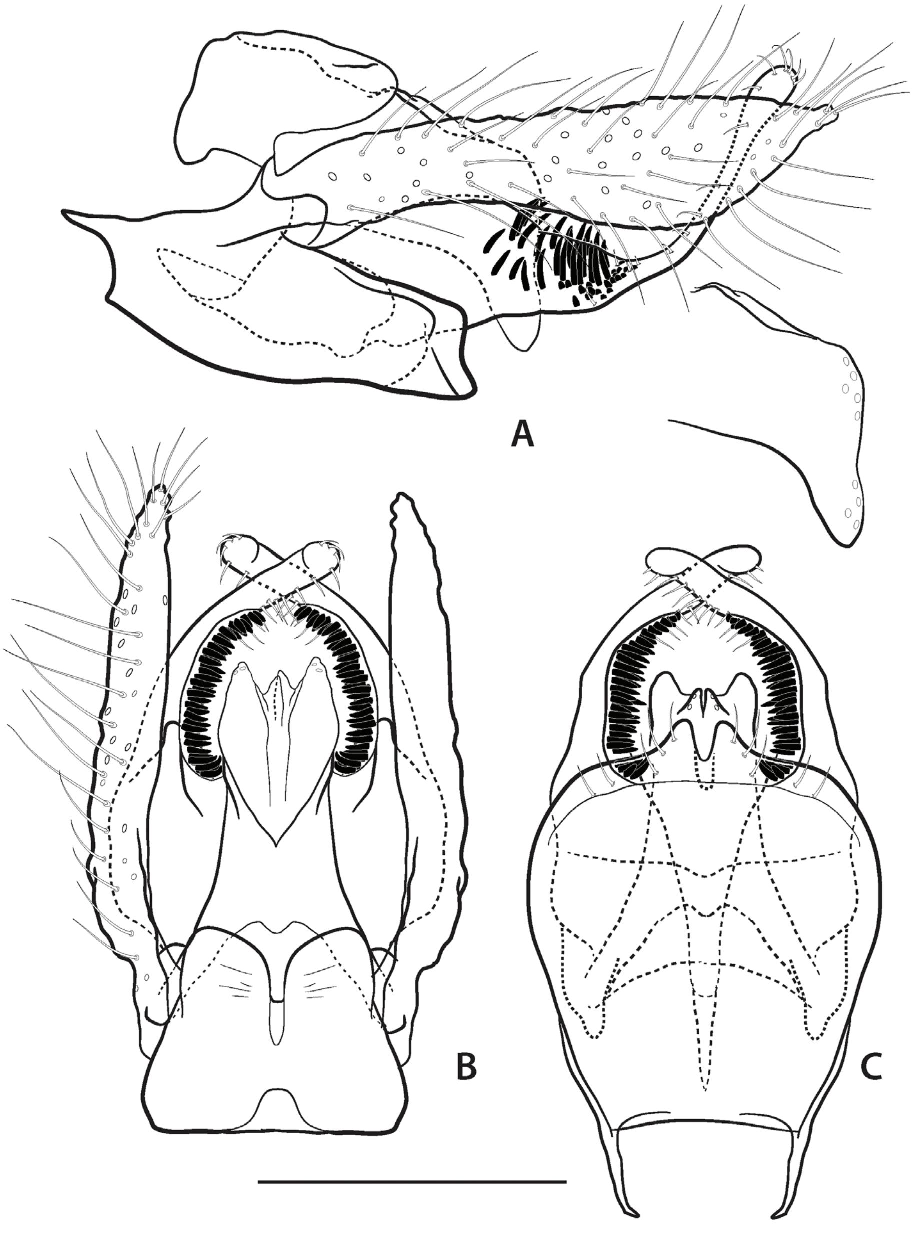

Figure 12. *Xiphocentron* (*Sphagocentron*) *tuxtla* **sp. nov.** Holotype (USNM), male. Genitalia: **A** left lateral, **B** dorsal, **C** ventral. Scale bar 0.1 mm.

Genitalia (Fig. 12A–D). Tergum IX, in lateral view, wide basally, narrowing apically (Fig. 12A); in dorsal view, anterior margin straight with mesal concave line; posterior margin with wide subtruncate lobes and narrow deep mesal incision (Fig. 12B). Sternum IX, in lateral view, about 3× as long as high, apex truncate; anterior apodeme narrow, straight, tapering to narrow flange (Fig. 12A); in ventral view, about 1.5× as long as wide, posterior margin with prominent, acute, mesal lobes devided by narrow incision (Fig. 12C). Tergum X membranous fused basodorsally to each paraproct. Paraproct, in lateral view, oblong, dorsoapically truncate, without round lobe, with narrow, ventral lobe (Fig. 12A); in dorsal view, wide basally, divided apicomesally, each side partially fused at midlenght, without clear sclerotized mesal band, apex with several sensillae (Fig. 12B). Preanal appendage setose, in lateral view about 2× as long as tergum IX, straight to slightly sigmoid, distal half wide, tapering to acute apex (Fig. 12A); in dorsal view, substraight, tapering apically (Fig. 12B). Inferior appendage, in lateral view, about 2.5× as long as tergum IX; coxopodite and harpago fused, with dorsal suture line between each article, inner face with longitudinal line of setae, area of dense, long spine-like setae, and row of regular setae from midlenght to apex (Fig. 12A); basal region (coxopodite) wide, without basomesal spine-like setae, mesal sclerite region with dense, longer spine-like setae (Fig. 12A); apical region (harpago) in lateral view narrow, digitate, 1.5× as long as basal region, inner face with longitudinal line of setae (Fig. 12A); basal plate in lateral view wide, anteriorly with narrow flange (Fig. 12A). Phallus tubular, very long and narrow, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged (Fig. 12D).

Etymology. Name in apposition; named after the type locality, tuxtla comes from the nahuatl language: 'tochtlán', meaning place of rabbits.

Distribution. Mexico.

Key to males of *Xiphocentron* (*Sphagocentron*) subgenus

1 Preanal appendage width in lateral view, subequal throughout length (Figs 9B, 10A) **2**

1' Preanal appendage width in lateral view, conspicuously enlarged subapically (Figs 7B, 8B)............................ **3**

2 **(1)** Preanal appendage width in lateral view, narrow, less than half sternum IX width; sternum IX posterior margin in ventral view, with small, inconspicuous mesal lobes; paraproct apex in lateral view oblique (Fig. 10) ....***X.* (*S.*) *julus***

2' Preanal appendage width in lateral view more than half sternum IX width; sternum IX posterior margin in ventral view, with a pair of prominent acute mesal lobes; paraproct apex in lateral view rounded apically with narrow ventral lobe (Fig. 9)..***X.* (*S.*) *guanacaste* sp. nov.**

3 **(1)** Tergum IX posterior margin with deep mesal incision (about as deep as half tergum length) (Figs 11C, 12B)... **4**

3' Tergum IX posterior margin with shallow mesal incision (as deep as less than 1/4 tergum length) (Figs 6B, 7C) **5**

4 **(3)** Sternum IX posterior margin substraight with inconspicuous mesal lobes (Fig 11D); tergum IX anterior margin with mesal incision and suture almost reaching the posterior margin incision (Fig 11C); paraproct in lateral view with narrow long ventral lobe (Fig 11B)..***X.* (*S.*) *tapanti* sp. nov.**

4' Sternum IX posterior margin acute mesaly or straight with prominent acute mesal lobes (Figs 8D, 12C); tergum IX anterior margin straight without incision and mesal suture not reaching tergum mid-lenght (Figs 8C, 12B); paraproct in lateral view oblique without conspicuous ventral lobe (Figs 8B, 12A) **6**

5 **(3)** Abdominal sternum V with membranous, digitate lateral process (Fig 7F); preanal appendage apex very wide (as wide as 2× basal region) (Fig 7B); inferior appendage basal region with small spine-like setae (Figs 7B, 7D); sternum IX posterior margin without mesal incision (Fig. 7D) ....***X.* (*S.*) *erybrachium* sp. nov.**

5' Abdominal sternum V without lateral process (Fig 6E); preanal appendage apex slightly wider than basal region (Fig 6A); inferior appendage basal region without spines (Fig 6A); sternum IX posterior margin with V-shape incision (Fig 6C)...***X.* (*S.*) *dactylum* sp. nov.**

6 **(4)** Forewing fork I (R2 and R3) present (Fig. 8A); tergum IX posterior margin lobes round, ogival-shaped (Fig. 8C); sternum IX posterior margin acute with very shallow mesal incision (Fig. 8D) ....***X.* (*S.*) *evandrus***

6' Forewing fork I (R2 and R3) absent; tergum IX posterior margin lobes, oblique, truncate (Fig. 8B); sternum IX posterior margin straight with a pair of prominent acute mesal lobes (Fig. 8C).................***X.* (*S.*) *tuxtla* sp. nov.**

Subgenus *Xiphocentron* (*Antillotrichia*) Banks, 1941: 401

Type species. *Antillotrichia cubana* Banks, 1941, original designation. — Flint 1964:25 [to synonymy]. — Botosaneanu 1988:221 [resurrected as a valid subgenus].

Xiphocentron (*Antillotrichia*) *drepanum* sp. nov.

https://zoobank.org/2C63CA4A-BDE7-46F5-882E-2CCA8F1EFCA6

Figures 13A–D

Type material. Holotype FRENCH GUIANA • ♂; Approuague-kaw, Kaw Mtn., 104 mao, 4°33.035′N, 52°11.661′W, Malaise trap, 23.i–7.ii.2007, FRG MF3, N. Jönsson leg., [BOLD: GBMIN18612-13; GenBank: JQ239839] NHRS TOBI000003833.

Diagnosis. The new species can be diagnosed mainly by the sickle-shape of preanal appendage in dorsal view, in which the mesal margin has a strong concavity and the apex is wide with a mesal pointed projection. This character is unique to this species.

Description. ***Male***: Body. Forewing length 3.5 mm (n = 1). Color overall brown, forewing pattern uniformly brown. Maxillary palp segment length formula (I = II =

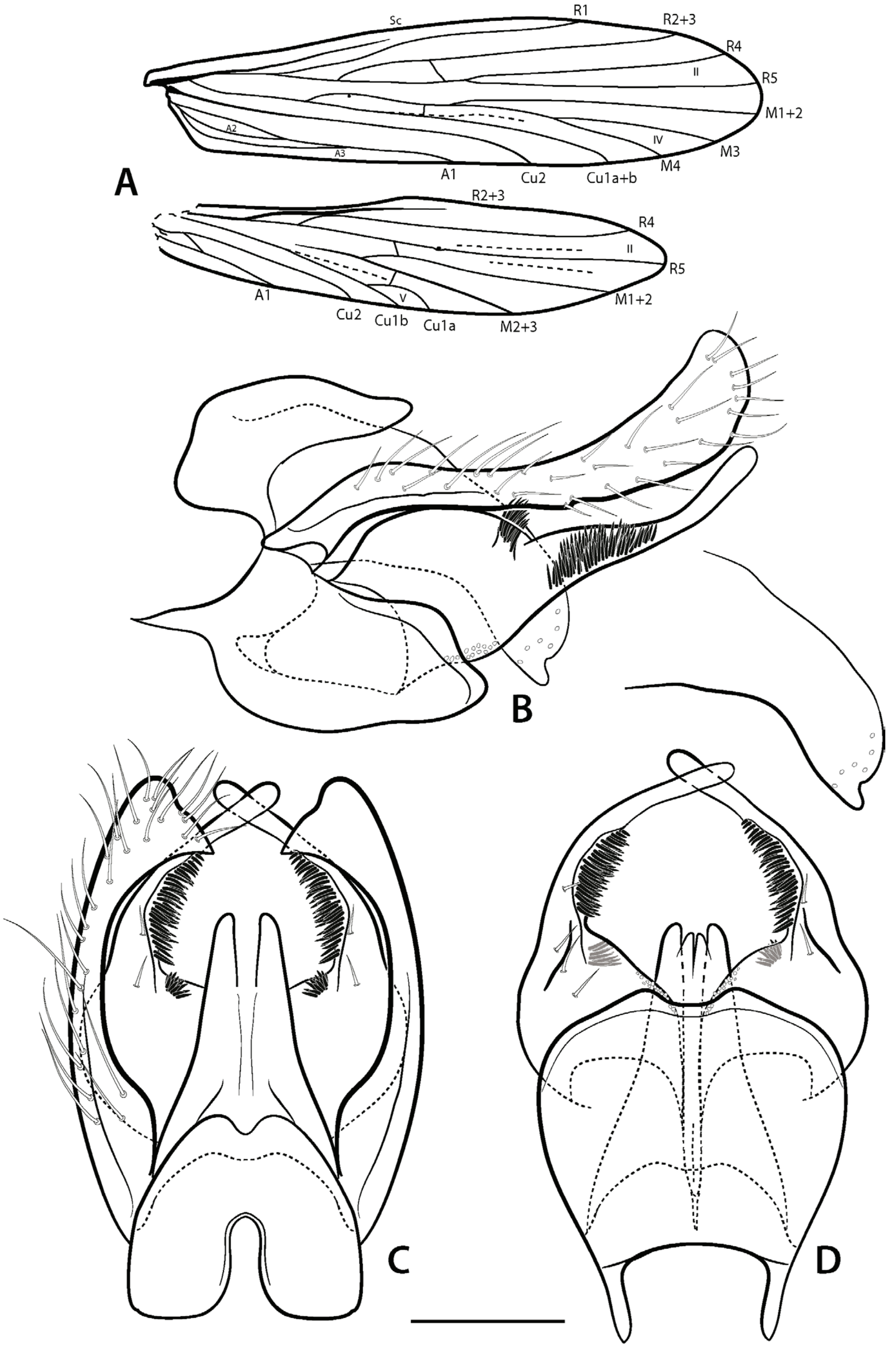

Figure 13. *Xiphocentron* (*Antillotrichia*) *drepanum* **sp. nov.** Holotype (NHRS), male. **A** wing venation. Genitalia: **B** left lateral, **C** dorsal, **D** ventral. Genitalia scale bar 0.1 mm.

III) < IV < V. Tibial spur formula 2:4:3; spurs unmodified. Forewing forks II and IV present; fork II sessile at discoidal cell; discoidal slightly shorter than thyridial cell. Hind wing forks II and V present (Fig. 13A). Sternum V with short, sclerotized anterolateral projection.

Genitalia (Figs 13B–D). Tergum IX, in lateral view, wider basally, narrower apically (Fig. 13A); in dorsal view, anterior margin with deep narrow concave incision; posterior margin with round lobes and shallow mesal incision (Fig. 13C). Sternum IX, in lateral view, about 2× as long as high, apex deltoid; anterior apodeme narrow, straight, tapering to narrow flange (Fig. 13B); in ventral view, about as long as wide, posterior margin with shallow mesal incision (Fig. 13D). Tergum X membranous fused basodorsally to each paraproct (Figs 13B, 13C). Paraproct, in lateral view, oblong, wide at base, tapering apically with submesal angle, apex round, with narrow, short ventral lobe (Fig. 13B); in dorsal view, wide basally, divided apicomesally, each side partially fused at base, without clear sclerotized mesal band, apex with several sensillae (Fig. 13C). Preanal appendage setose, in lateral view, about 2× as long as tergum IX, narrow, bent posterad at basal 1/3, apically wider and curved upward, apex round (Fig. 13B); in dorsal view, sickle-shaped, enlarged at base, narrow at midlength with concave mesal margin, wide at apex with mesal wide pointed projection (Fig. 13C). Inferior appendage, in lateral view, about 2× as long as tergum IX; coxopodite and harpago partialy fused, with shape discontinuity between each article, inner face with longitudinal area of dense, long spine-like setae (Fig. 13B); basal region (coxopodite) wide, with small basomesal spine-like setae, mesal sclerite region with dense, long spine-like setae; apical region (harpago) narrow, digitate, 1.5× as long as basal region (Fig. 13A); basal plate in lateral view wide, anteriorly with short, narrow flange (Fig. 13B). Phallus tubular, very long and narrow, reaching segment V; basally conical, subapically annulate, weakly sclerotized; apex slightly enlarged.

Etymology. From the Greek drepánē, ‘sickle’, in reference to the preanal appendage shape.

Distribution. French Guiana

3.4. New records

Xiphocentron caenina Schmid, 1982

Material examined. BOLIVIA • 3♂, 11♀; Santa Cruz Dept., PN and ANMI Amboró, Guarda Parque Mataracú, Q. Verde Uno, 17°33.136′S, 63°52.092′W, el. 374 m, 21–27.xi.2004, Malaise, Robertson, Garcia and Vidaurre leg., UMSP.

Distribution. Argentina, Bolivia (new record).

Xiphocentron mnesteus Schmid, 1982

Material examined. ECUADOR • 8♂; Pichincha 7km E Pito, el. 2950 m, 26–28.ix.1990, Flint leg., USNM. • 7♂; Azuay, Llaviuco river, el. 3010 m, 16 km W Cuenca, 18.ix.1990, Flint leg., USNM. • 4♂; Napo, 5km S Baeza, el. 1900 m, 10.ix.1990, Flint leg., USNM. • 3♂; Cañar, Chauchas river, 3 km N Zhud, el. 2910 m, 17.ix.1990, Flint leg., USNM.

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

Xiphocentron sturmi Sturm, 1960

Material examined. COSTA RICA. • ♂ Cartago, Reserva Tampati, Quebrada Palmitos and falls 9.72°N, 83.78°W, 2–3.vi.1990, el. 1400 m, Holzenthal, Blahnik, Muñoz leg. UMSP000143465. • ♂ Same data, except 1-2.viii.1990, UMSP000143460. ECUADOR: • 2♂ Napo, Sebundoy, el. 2600 m, 11–15.ix.1977, L.E. Pena G. leg., USNM; 7♂ Napo, Reventador, el. 1750 m 3–6.x.1977, L.E. Pena G. leg., USNM.

Distribution. Colombia, Costa Rica (new record), Ecuador (new record).

Xiphocentron tarquon Schmid, 1982

Material examined. COSTA RICA • 1♂; Guanacaste, Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo, 10°52′48.0”N, 85°23′20.4”W, el. 575 m, 14.iv.2014, Malaise Trap, D.H. Janzen, W. Hallwachs leg., [BOLD: GMACC652-15] MZUSP. • 1♂; same data, [BOLD: GMAAR086-16] BIOUG28246-H01.

Distribution. Costa Rica (new record), Mexico.

Xiphocentron yine Vilarino et al., 2023

Material examined. BOLIVIA • 2♂ Dept. La Paz, ANMI Madidi, Chalalan Ecolodge, Tuichi river at entrance to lodge and trib., 14°25.017′S, 67°54.378′W, el. 300 m, 29.vii.2003, Robertson and Blahnik leg., UMSP. • 3♂, 1♀; San Buenoventura–Ixiamas rd., km 23, Hacienda Chiquitos, Arroyo Chiquitos, 14°20.082′S, 67°42.204′W, el. 283 m, 13–14.vii.2003, Robertson and Blahnik leg., UMSP.

Distribution. Bolivia (new record), Peru.

Genus *Machairocentron* Schmid, 1982

Machairocentron amahuaca Vilarino et al., 2023

Material examined. BOLIVIA • 9♂. 119♀; Santa Cruz Dept.: PN and ANMI Amboró, Guarda, Parque Mataracú, Q. Verde Uno, 17°33.136′S, 63°52.092′W, el. 374 m, 21–27.ix.2004, Malaise, Robertson, Garcia and Viduarre leg., UMSP.

Distribution. Bolivia (new record), Peru.

4. Discussion

In this study new species of *Xiphocentron* (*Sphagocentron*) are described after more than 40 years. Now, the subgenus includes seven species from Central and South America. However, the preanal appendage morphometric analysis and the phylogenetic analysis suggest the inclusion of some Antillean species currently in *Antillotrichia* subgenus. Additionally, a species of *X.* (*Antillotrichia*) was also described sharing similarities with other species from northern South America. The new records expand the distribution of the genus with the first records of the family in Bolivia, which have a similar fauna to that of northern Argentina and the Peruvian Amazon. Also, the first species of *Xiphocentron* are identified in Ecuador showing a wider distribution range of *X. mnesteus* and *X. sturmi* along the northern Andean foothills, and with *X. sturmi* species occurring even in Central America.

The phenotypic groups defined by the cluster analysis (Fig. 3) only partially recovered the phylogenetic groups (Fig. 5A). The principal components of preanal appendage shape (Fig. 2) could mostly differentiate between the subgenera *Xiphocentron*, *Sphagocentron* and *Rhamphocentron* but not the *Antillotrichia* subgenus which overlapped with most of other subgenera. In the discriminant analysis (Fig. 4) the *Antillotrichia* subgenus only partially overlapped with *Sphagocentron* subgenus. The jackknife cross-validation test was around 70% to *Sphagocentron* and *Antillotrichia*, and 33% to genera with a very small sample (n = 3). Therefore, despite the overlapping, the preanal appendage shape shows a good accuracy to classify species to subgenera when an adequate sample size is used. The shape overlapping is in accordance with the initial expectations that *X.* (*Antillotrichia*) is possibly paraphyletic (or polyphyletic), which is also corroborated by the phylogenetic analysis (Fig. 5A). Only a single *Glyphocentron* was introduced in the analyses and its shape does not show any conspicuous feature, being placed closer to the *X.* (*Sphagocentron*) cluster (Fig. 3), although it was placed near *X.* (*Rhamphocentron*) species in the phylogenetic results (Fig. 5A).

The generalized shape patterns that could be recognized in the majority of the analyzed species within each subgenus are as follows: In the *Xiphocentron* subgenus species exhibit a straight preanal appendage that is wide at the base and progressively tapers to a narrow apex (indicated by the positive values of PC4). In the *Rhamphocentron* subgenus, most species have the preanal appendage conspicuously wide at the basal third, and becomes slightly wavy and equally subnarrow at the apical 2/3 with a round apex (indicated by the positive values of PC1). In the *Sphagocentron* subgenus, most species share an overall wide preanal appendage, which becomes enlarged subapically and narrows towards apex (indicated by the negative values of PC2) (Fig. 2).

The *Antillotrichia* subgenus exhibited great morphological variation, with the cluster analysis (Fig. 3) revealing three main species groups: A group of several South American species that share preanal appendage strongly curved, narrow mesally with an enlarged, round apex (seen in the negative values of the PC4). The second group includes Antillean species, that present appendage slightly wavy and subequal narrow width throughout their length (seen in the positive values of the PC2). The third are species from Lesser Antilles with overall wide preanal appendage similar to *Sphagocentron*. However, the *Antilliotrichia* subgenus groups inferred from the preanal appendage phenotype differed from the phylogenetic results (Fig. 5A). The species with wavy appendages narrow at midlenght and wide, round apex were placed at distinct clades defined more by characters of the inferior appendage setose ornaments rather than preanal appendage shape, suggesting convergent evolution of the preanal appendage.

Some species with less modified preanal appendage, such as *X.* (*S.*) *julus* and *X.* (*R.*) *numanus* were not grouped with other congeners in the morphometric analysis (Fig. 3), however, they have other characters that support their recovering within their subgenera in the phylogenetic analysis (Fig. 5A). The placement of *X.* (*A.*) *fuscum* as shown in the cluster, phylogenetic and discriminant analyses, suggests that this species belongs to *X.* (*Sphagocentron*). However, the phylogeny indicated that other species also could be included in a broader sense of the *Sphagocentron* subgenus (Fig. 5A). Nevertheless, the support for this clade was very low (18%), and many included groups had no support at all. Additionally, this clade was based only on a single discrete character and the contributions of landmarks. Therefore, we consider the evidence too weak to make conclusive taxonomic changes.

The morphofunctional aspects of the xiphocentronid genitalia are mostly unknown. Questions underlying the preanal appendage function during the copula and the selective forces related to its shape evolution have never been investigated. The copula was described to the sister group Psychomyiidae, in *Tinodes* the slender preanal appendages are loosely placed across segment IX of the female while the grasping is primarily provided by a spiny harpago of the male inferior appendages, holding onto membranous pits of the female segment VIII, and additional grasping is provided by the spiny paraprocts that are inserted with the phallus (Fisher 1977). In *Xiphocentron* the only spiny structure is often the mesal region of male inferior appendages. The long and robust preanal appendage frequently crosses the inferior appendage harpago, which should help to lock the inferior appendages in position around the female segment IX, preventing lateral movements. The paraprocts seem to have no grasping role.

Therefore, we hypothesize that the long preanal appendage in Xiphocentronidae and its different shapes should be associated with evolutionary strategies to help with additional grasping and shoring of the inferior appendage around the female, while groups in which a strong grasping is provided by structures in the phallus, paraproct or inferior appendage may have slender or reduced preanal appendages. Further research is needed to clarify the morphofunctional aspects of the preanal appendage, and test this hypothesis.

5. Conclusion

After more than 40 years since the establishment of the subgenus *Sphagocentron* new species are described, and the monophyly and relationships within the subgenus were accessed through geometric morphometry and a morphological phylogeny. This study reported the following findings:

(1) The geometric morphometric analyses of the preanal appendage were consistent with the phylogenetic results regarding the non-monophyly of the *Antillotrichia* subgenus and the proximity of certain *X.* (*Antillotrichia*) species to the subgenus *Sphagocentron*.

(2) The monophyly of *X.* (*Sphagocentron*) was recovered, although with little support. *X.* (*Antillotrichia*) species having a narrow zone of dense spine-like setae on the inferior appendages and no mesal sclerite but longer setae may represent a monophyletic group together with *X.* (*Sphagocentron*) species.

(3) Phenotypic clusters fail to fully recover the phylogenetic groups, with preanal appendage shapes evolving independently in some species.

(4) The geometric morphometry was able to highlight preanal appendage subgeneric diagnostic traits, and partially distinguishing between each subgenus, but with a greater overlapping of *X.* (*Antillotrichia*) subgenus. Despite the shape overlapping, cross-validation test was able to correctly classify around 70% of the species to subgenera in better sampled groups. Therefore, the preanal appendage shape has a good informativeness for subgeneric classification.

(5) The preanal appendage shape in xiphocentronids is hypothesized to be associated to an auxiliary grasping function.

6. Data sharing and data accessibility

The data underlying this article, including: the discrete characters matrix (.ss), the combined discrete and morphometric characters matrix (.tnt) and the morphometric procrustes (.dat) are available at the Open Science Framework (OSF) repository and can be accessed at https://osf.io/trsy3/?view_only = ff4e70d072d4462895f5c641c510958f

7. Acknowledgments

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Supplementary Material 1

File S1

Authors: Vilarino A, Calor AR (2024)
Data type: .dat
Explanation notes: Preanal appendage aligned procrustes, PAST file (morphometric).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/asp.82.e112587.suppl1

Supplementary Material 2

File S2

Authors: Vilarino A, Calor AR (2024)
Data type: .ss
Explanation notes: Morphological data matrix, discrete characters only (phylogenetic matrix).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/asp.82.e112587.suppl2

Supplementary Material 3

File S3

Authors: Vilarino A, Calor AR (2024)
Data type: .tnt
Explanation notes: Combined morphometric and discrete characters, TNT file (phylogenetic matrix).
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/asp.82.e112587.suppl3

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