UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA

Phylogeny of Xiphocentronidae Ross, 1949 and taxonomy of Neotropical Xiphocentroninae (Trichoptera: Annulipalpia : Psychomyioidea)

Filogenia de Xiphocentronidae Ross, 1949 e taxonomia de Xiphocentroninae neotropicais (Trichoptera : Annulipalpia : Psychomyioidea)

Albane Vilarino Santos da Silva

Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor em Ciências, obtido no Programa de Pós-Graduação em Entomologia

Ribeirão Preto - SP

2020

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Orientador: Dr. Pitágoras C. Bispo

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NOTA

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In accordance with the criteria of the International Code of Zoological Nomenclature (ICZN - Chapter 3, articles 8 and 9), this thesis does not characterize publication and therefore any new names proposed here or acts that affect the nomenclature are not valid

DEDICATION

This dissertation is dedicated to the memory of my godfather João Bosco de Barros, and the trichopterologist Oliver S. Flint Jr., whom passed away while I was finishing this study

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ABSTRACT

The Psychomyioidea are the most diverse annulipalpian clade comprising 7 families and about 2.200 species. The larvae construct short silken retreats or long galleries covered with sand and detritus. The net-tube caddisfly families Xiphocentronidae Ross, 1949 (185 species and 7 genera) and Psychomyidae Walker, 1852 (8 genera, 608 spp.) have their phylogenetic proximity undisputed, sharing many adult and larval characters and being most of times placed as sister-taxa. The monophyly of Xiphocentronidae including the genus Proxiphocentron (Proxiphocentroninae) is based on genitalia characters, since Proxiphocentron lack much of the autoapomorphies of the other Xiphocentronidae, having a plesiomorphic wing venation and body characters like in Psychomyiidae. The placement of Xiphocentronidae as a distinct evolutionary lineage from Psychomyidae has been subject to debate, and the synonymization with Psychomyidae was already proposed in the past. The family status of Xiphocentronidae was restated by Schmid in 1982 that established the present taxonomic organization of the family. The description of the larvae of the psychomyid *Eoneureclipsis* that present foreleg tibia and tarsus fused as in Xiphocentronidae larvae, brought additional doubt about the evolutionary relationship between Xiphocentronidae and Psychomyiidae. In this study we investigated the relationship of Xiphocentronidae and Psychomyiidae through a parsimony morphological phylogeny (106 species, 168 characters). Has the aim of proposing a first phylogeny for Xiphocentronidae; testing the hypotheses of monophyly of the families; and infering the evolutionary relations of the established groups. The monophyly of Psychomyiidae, as currently defined, was rejected without including Xiphocentronidae. Being Xiphocentronidae lowered to subfamily level. Among the subfamilies previously established for Psychomyiidae, Eoneureclipsinae (*Eoneureclipsis*) was recovered as the first cladogenesis of family. The monophyly of Psychomyiinae (*Metalype*, *Paduniella* and *Psychomyiia*) was also recovered under implied weighting but not Tinodinae (*Tinodes, Lype*), with *Lype* placed as a clade right after *Eoneureclipsis,* and *Tinodes* as sister group of the xiphocentronids. The fossil genus *Palerasnitsynus* from early Cretaceous was placed at within the Xiphocentroninae, and the Australian genus *Zelandoptila* was placed as an Ecnomidae as shown in previous molecular phylogenies. The monophyly of *Xiphocentron* and *Cnodocentron* was not recovered. In addition to the phylogeny, species-level revisions for *Machairocentron* and *Xiphocentron* species from Brazil were also presented; including morphological data on species polymorphism, comparative illustrations, new species, new distribution records, and species keys. In the revision of *Xiphocentron* from Brazil *X. steffeni* (Marlier, 1964) and X. *ilionea* Schmid are redescribed. Additional 5 new species are described: *X.* **sp.n.** 1 (Paraná, Rio de Janeiro, São Paulo). *X.* **sp.n.** 2 (Goiás, Mato Grosso), *X.* **sp.n.** 3 (Paraná), *X.* **sp.n.** 4 (Santa Catarina), *X.* **sp.n.** 5 (Santa Catarina). New state records of *X. acqualume*, *X. jaguare*, *X. kamakan*, *X. maracanan*, and *X. steffeni* are presented. In the revision of the genus *Machairocentron*, *M. ascanius* Schmid, *M. echinatum* (Flint), *M. falciforme* Pes & Hamada, *M. lucumon* Schmid, *M. tarpeia* Schmid, and *M. teucrus* Schmid are redescribed and illustrated based on type specimens. Two new species from Costa Rica, *M. chorotegae* **sp.n.** and *M. eugeniarguedasae* **sp.n.**, and one from Venezuela, *M. kalinae* **sp.n.**, are described. This study is the first attempt to provide a hypothesis of the xiphocentronids relationship, bringing new insights about the Psychomyiidae evolution, as well as new questions about their evolutionary history.

Keywords: Comparative morphology; phylogenetic inference; weighted parsimony; aquatic insects; caddisflies; *Xiphocentron*; *Machairocentron*; tube-dweller larvae.

RESUMO

A superfamília Psychomyioidea é a mais diversa da subordem Annulipalpia possuindo 7 famílias e cerca de 2.200 espécies. As larvas constroem abrigos de seda curtos ou longas galerias tubulares cobertas por areia e detritos. As famílias construtoras de galerias Xiphocentronidae Ross, 1949 (7 gêneros, 185 espécies viventes) e Psychomyidae Walker, 1852 (9 gêneros, 608 spp. viventes) tem proximidade filogenética inquestionável, partilhando vários caracteres morfológicos e sendo tradicionalmente posicionados como grupos irmãos. A monofilia de Xiphocentronidae incluindo *Proxiphocentron* (Proxiphocentroninae) é apenas baseada em caracteres de genitália, já que *Proxiphocentron* carece de várias autapomorfias do restante da família possuindo venação alar plesiomórfica e caracteres de corpo como de Psychomyiidae. O posicionamento de Xiphocentronidae como um ramo evolutivo distinto de Psychomyioidea já foi alvo de questionamento, com a sinonimização das famílias tendo sido proposta quando a larva de *Xiphocentron* foi descrita. O status de Xiphocentronidae como família foi reestabelecido por Schmid, que em 1982 realizou a revisão do grupo, estabelecendo a atual organização taxonômica. A descrição da larva do Psycomyiidae *Eoneureclipsis* que apresenta a perna anterior com tíbia e tarso fundidos como em Xiphocentronidae, adicionam ainda mais dúvidas sobre o posicionamento de Xiphocentronidae. O presente estudo realizou uma análise filogenética do relacionamento de Xiphocentronidae e Psychomyiidae baseada em caracteres morfológicos (106 espécies, 168 caracteres). Este estudo tem como objetivos a proposição da primeira filogenia para Xiphocentronidae; testar as hipóteses de monofilia das famílias; e inferir os relacionamentos evolutivos dos grupos previamente estabelecidos. A monofilia de Psychomyiidae foi rejeitada sem a inclusão de Xiphocentronidae. Sendo então, a família Xiphocentronidae passa ao nível de subfamília dentro de Psychomyiidae. Entre as subfamílias previamente estabelecidas para Psychomyiidae, Eoneureclipsinae (*Eoneureclipsis*) foi recuperada como primeira cladogênese da família. A monofilia de Psychomyiinae (*Metalype*, *Paduniella* e *Psychomyiia*) também foi recuperada nas análises com pesagem implícita, no entanto, o clado Tinodinae (*Tinodes*, *Lype*) não foi recuperado, com *Lype* sendo posicionado como uma cladogênese logo depois de *Eoneureclipsis*, e *Tinodes* como grupo irmão dos xiphocentronideos. O gênero fóssil *Palerasnitsynus* do início do Cretáceo, foi posicionado junto aos Xiphocentroninae; e o gênero Australiano *Zelandoptila* foi posicionado fora de Psychomyiidae e dentro de Ecnomidae como previamente indicado em análises moleculares. A monofilia dos gêneros de Xiphocentroninae: *Xiphocentron* e *Cnodocentron* não foi recuperada. Adicionalmente à filogenia, os gêneros neotropicais *Machairocentron* e as espécies de *Xiphocentron* do Brasil foram revisados, incluindo dados de polimorfismo, ilustrações comparativas, novas espécies, novos registros e chaves de identificação. Na revisão das espécies de *Xiphocentron* do Brasil, *X. steffeni* (Marlier) e *X. ilionea* Schmid são redescritas e 5 novas espécies são descritas: *X.* **sp.n.** 1 (Paraná, Rio de Janeiro, São Paulo). *X.* **sp.n.** 2 (Goiás, Mato Grosso), *X.* **sp.n.** 3 (Paraná), *X.* **sp.n.** 4 (Santa Catarina), *X.* **sp.n.** 5 (Santa Catarina). Além disso são apresentados novos registros de distribuição de *X. acqualume*, *X. jaguare*, *X. kamakan*, *X. maracanan*, e *X. steffeni*. Na revisão do gênero *Machairocentron*, as espécies: *M. ascanius* Schmid, *M. echinatum* (Flint), *M. falciforme* Pes & Hamada, *M. lucumon* Schmid, *M. tarpeia* Schmid, e *M. teucrus* Schmid, são redescritas e ilustradas com base em espécimes tipos. Também são descritas duas novas espécies da Costa Rica, *M. chorotegae* **sp.n.** e *M. eugeniarguedasae* **sp.n.**, e uma espécies da Venezuela, *M. kalinae* **sp.n.**. O presente estudo é um primeiro esforço para o entendimento da evolução do grupo, apresentando uma primeira hipótese filogenética sobre relacionamento dos xiphocentronideos e trazendo novos perguntas sobre a história evolutiva dos tricópteros psychomyioides.

Palavras-chave: Morfologia comparada; inferência filogenética; parcimônia com pesagem; insetos aquáticos; tricópteros; *Xiphocentron*; *Machairocentron*; larvas tubícolas.

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General Introduction

Trichoptera is a cosmopolitan aquatic insects order with more than 14,500 species (Morse 2019) being one of the most species-rich insect groups with primarily aquatic larvae (Malm et al. 2013). The insects of this order have complete metamorphosis, with well distinct larva, pupa and adult stages (Holometabola). Together with the Mecoptera (scorpionflies), Siphonaptera (fleas), Diptera (true flies) and Lepidoptera (moths and butterflies) they form the clade Panorpida and share a last common ancestor from the Carboniferous (Misof et al. 2014). From the panorpid ancestor a same branch gave rise to the aquatic Trichoptera and the primarily terrestrial Lepidoptera (superorder Amphiesmenoptera) (Beutel et al. 2011). The divergence between both orders occurred in the Triassic (Malm et al. 2013), with the formation and radiation of Trichoptera being associated to the specializations of the larvae for a fully aquatic living in freshwater and the diversification in the use of the silk that is produced from their labial glands (Holzenthal et al. 2007a; Malm et al. 2013).

The caddisflies are divided in two extant monophyletic suborders, the portable case builders Integripalpia Martynov, 1924 and the net-spinning caddisflies Annulipalpia Martynov, 1924 (Kjer et al. 2016). Although, the relationship of the four families that previously were grouped in the paraphyletic “Spicipalpia” Weaver, 1984 has been strongly debated and still under dispute (Kjer et al., 2001, 2002, 2016; Holzenthal et al., 2007a, 2007b; Malm et al., 2013) being placed sometimes within Integripalpia (Kjer et al., 2016) and sometimes at the base of Trichoptera phylogeny (Malm et al., 2013).

Annulipalpians larvae usually lives in running waters where they spin fixed silken retreats and filtering nets used to catch debris or small animals carried by the stream flow, being predators and/or detritivorous filter-feeders (Holzenthal et al. 2007a). Adult annulipalpians are easily diagnosed due to the frequently elongated and striated apical segment of maxillary palps (Ross 1967). The suborder Annulipalpia has 10 extant families that are divided into three evolutionary branches: the superfamilies Hydropsychoidea Curtis, 1835, Philopotamoidea Stephens, 1829 and Psychomyioidea Walker, 1852 (Malm et al. 2013, Kjer et al. 2016).

The Psychomyioidea are the most diverse annulipalpian clade comprising seven living families and about 2.200 species, while Hydropsychoidea (1808 spp.) has only the family Hydropsychidae, and Philopotamoidea (1262 spp.) has two families: Philopotamidae and Stenopsychidae (Morse 2019, Holzenthla et al. 2011). The monophyly of Psychomyioidea has been well supported in most morphological (Frania

& Wiggins 1997, Ivanov 2002) and molecular phylogenies of Trichoptera (Kjer et al. 2016, Malm et al., 2013, Holzenthal et al. 2007b, Kjer et al. 2002). Synapomorphic characters of Psychomyioidea as discussed in Frania & Wiggins (1997) and Ivanov (2002) are: 1) larvae pronotum with hind angles that joint sternite behind coxa; 2) the usually long spinneret (labium); and 3) the larval antenna with only one basiconic sensilla. The larvae construct short silken retreats or long galleries covered with sand and detritus and are predacious or detritivorous (Holzenthal et al. 2007a). The adults can be diagnosed by their mesoscutal rounded setal warts (with exception of some Xiphocentronidae and Dipseudopsidae). The most recent molecular phylogenies support Hydropsychoidea as the sister group of all other Annulipalpia, and Psychomyioidea as sister group of Philopotamoidea (Malm et al. 2013, Johanson et al. 2012, Kjer et al. 2016).

Long-tube-dweller caddisflies

Among the Psychomyioidea the families Pseudoneureclipsidae, Dipseudopsidae, Psychomyiidae and Xiphocentronidae share the larvae behavior of constructing long galleries covered with detritus, while other families with known larvae (Polycentropodidae, and Ecnomidae) construct short tube nets or funnel-shaped nets (Merrit et al. 2008). Considering the phylogenetic proximity to xiphocentronids and psychomyids (Johanson et al. 2012, Malm et al. 2013), another family that possibly has a long-tube dweller larva is Kambaitipsychidae. This family is represented only by the genus *Kambaitipsyche,* which has oriental distribution and 2 species described (the larvae is unknown) (Morse 2019). All these gallery builders' families present larvae with elongated labium and without labial palpi (Frania & Wiggins 1997, Li & Morse 1997, Weaver & Malicky 1994, Chamorro & Holzenthal 2011) and all except Pseudoneureclipsidae have shorter and ticker legs with a foreleg tarsal brush (Tachet et al. 2001).

Pseudoneureclipsidae

Pseudoneureclipsidae include the Old-World genus *Pseudoneureclipsis* (123 spp.) and *Antillopsyche* (8spp. (4† Miocene)) from Greater Antilles and Meso-America (Holzenthal et al. 2007a, Morse 2019). Their larvae present a combination of characters that induce an ambiguous placement (Tachet et al. 2001): the meso and metanota sclerotization and the narrow and elongate thoracic legs place them close to Ecnomidae; the tube construction and the very elongate labium without palpi, approximate them to

Dipseudopsidae; the presence of fore trochantin separated from episternum by a suture is common to Psychomyiidae and Xiphocentronidae (Chamorro & Holzenthal 2011). Some phylogenies place them close to Dipseudopsydae (Li et al. 2001, Malm et al. 2013) while other place them close to Ecnomidae (Johanson & Espeland 2010, Johanson et al. 2012, Kjer et al. 2016). The fossils specimens of the family were found in Miocene Mexican amber (Morse 2019).

Dipseudopsidae

Dipseudopsidae present 5 genera: *Protodipseudopsis* (5 spp. Afrotropical) *Dipseudopsis* (82 spp. Afrotropical and Oriental), *Hyalopsyche* (13 spp. Afrotropical, Oriental and Australasian), *Phylocentropus* (20spp.,8† Oligocene and late Cretaceous, from Nearctic, Oriental, and Palearctic), and *Limnoecetis* (1 spp. Afrotropical) (Morse 2019). Their larvae construct siphon-like elongate silken tubes, which are buried in the sediment with the tube openings above the substrate working like a filter device with the larva occupying a lateral branch (Gibbs 1968, Wallace et al. 1976). The dipseudopsids larvae have the tibia and tarsus of all the legs very enlarged and with ventral brush of setae, the tibia and tarsus are almost fused but there is a clear suture (Gibbs 1968, Sturkie & Morse 1998, Wells & Cartwright 1993). Higher-level phylogenies (Johanson et al. 2012, Kjer et al. 2016) suggest that the genus *Phylocentropus* is one of the first Dipseudopsidae cladogenesis. The oldest Dipseudopsidae fossil is from *Phylocentropus* found on the Nearctic region in New Jersey Cretaceous amber (Morse 2019).

Psychomyiidae

Psychomyiidae Walker 1852 occurs in all biogeographical regions except the Neotropics, it has fewer Australasian species and is highly diverse on the Oriental region where all the 8 genera occur: *Eoneureclipsis* (17 spp. Oriental), *Tinodes* (305 spp. occurring in all regions except Neotropical), *Padangpsyche* (1 sp. Oriental), *Trawaspsyche* (1 sp. Oriental), *Paduniela* (81 spp. occurring in all regions except Neotropical and Australasian), *Psychomyia* (168 spp. mainly Oriental, but with Nearctic and Palearctic species), *Metalype* (11 spp. Oriental and Palearctic), *Lype* (22 spp., 6† from Eocene) from all regions except Neotropical and Australasian), and *Zelandoptila* (2 spp. Australasian) (Morse 2019). The Psychomyiidae as Pseudoneureclipsidae and Dipseudopsidae have larvae with elongated labium, and the larvae construct silken galleries covered with sand and detritus (Merrit et al. 2008). These galleries are placed on the surface of the substrate, as rocks and logs, similar to Pseudoneureclispsidae and differing from Dipseudopsidae. The trochantin is separated from the episternum by a suture, and the fore-trochantin has distinct hatchet-shape in most of the species (but acute in some larvae of *Eoneureclipsis* (Thamsenanupap et al. 2005)). The submentum is separated in 2 sclerites (Tachet et al. 2018). The legs are not as thickened as in dipseudopsids and not as thin and elongate as pseudoneureclipsids, ecnomids and polycentropodids, and also present a ventral brush on the fore-tarsus as in dipseudopsids (Merrit et al. 2008). The pupae mandible has the apex elongated whip-like, also present in Xiphocentronidae, and the segment II, pre-segmental hook-plates are present only in Psychomyiidae and Xiphocentronidae (Merrit et al. 2008). Another similarity with the Xiphocentronids is the fused tibia-tarsus of *Eoneureclipsis* larvae forelegs (Thamsenanupap et al. 2005, Torii & Nakamura 2016). Many fossils of *Lype* were found in Eocene Baltic amber (Wichard et al. 2009), and the oldest psychomyid fossil is †*Palerasnitsynus* Wichard et al. 2011 (10 spp.) from Oriental mid-Cretaceous Burmese amber, this species has wing vein reduction similar to some xiphocentronids, the genitalia is somewhat similar to *Eoneureclipsis*, by the free and narrow paraproctal processes, and narrow preanal appendages.

Xiphocentronidae

Xiphocentronidae Ross 1949, differing to Psychomyiidae are mostly restrict to warm streams of tropical areas of the world being most diverse in the Neotropical and Oriental regions, with the Oriental genera *Proxiphocentron* Schmid (5 spp.), *Drepanocentron* (41 spp.), *Melanotrichia* (30 spp.); *Abaria* (39 spp. also with Afrotropical species), *Cnodocentron* (13 spp. with Neotropical and Oriental subgenera) and the exclusively Neotropical genera *Xiphocentron* (51 spp.) and *Machairocentron* (6 spp.) (Morse 2019). The only described Xiphocentronidae fossil, belongs to *Xiphocentron* (*Xiphocentron*) subgenera and was found in the Miocene Mexican amber (Wichard et al. 2006). Xiphocentronids despite building galleries like those of Pseudoneureclispsidae and Psychomyiidae, commonly place their construction in humid areas outside the water on the splash zone (Sturn 1960, Pes et al. 2013), this semiaquatic habitat with larvae living in humid substrate possibly was the habit of the Trichoptera and Lepidoptera ancestor (Kristensen 1997). The larvae submental sclerites are completely absent in xiphocentronids, and the fore-trochantin is short and acute like in pseudoneureclipsids; the mesopleuron has a flat process unique to Xiphocentronidae, and the tibia and tarsus are fused in all the legs (Sturn 1960, Flint 1964, Barnard & Dudgeon 1984, Pes et al. 2013). The pupae lack pre-segmental hook-plates on the segment VIII, which are present in all other Psychomyioidea (Flint 1964, Munoz-Quesada & Holzenthal 1997, Pes et al. 2013). The female genitalia is elongated, with very elongated apodemes on segments VIII, IX and X, and the lateral papillae are absent like in Psychomyiidae (Schmid 1982). The adult male genitalia has patches of spines on the inner margin of the inferior appendages, which also occur in some Psychomyiidae (†*Palerasnitsynus,* and *Eoneureclipsis*) and Dipseudopsidae (*Phylocentropus*). The phallus is narrow and extremely elongated reaching the segment V of the abdomen, and unlike most caddisflies it has no articulations with any structure of the genitalia. The phallus is enclosed by the paraproctal processes forming a tubular structure around the phallus. The typical rounded mesoscutal warts of the adult Psychomyioidea is only present in the genus *Proxiphocentron,* being absent in the genus *Abaria.* In all other xiphocentronid genera the mesoscutal warts are modified, the mesoscutum parapsidal lines are well developed, and the warts were apparently stretched out. Another curious feature of xiphocentronids is a pair of cuticular plates on the sternum V, these plates are associated with glandular openings, and are present in most Neotropical xiphocentronid species. In oriental species these plates are mostly absent with exception of *Melanotrichia forficula* and *M. darcha*, although in *M. darcha* the plates have a totally different aspect. The genus fossil †*Archaeotinodes* Ulmer (20 spp.) (Ecnomidae) from Eocene Baltic amber as described for †*Archaeotinodes reveraverus* Melnitsky & Ivanov 2010 has strong parapsidal lines surrounding the mesoscutal warts, and a cuticular plate on abdominal sternum V, what could be intermediate states of the xiphocentronid structures. †*A. augusta*, †*A. tenuis* and †*A. securifera* (Ulmer 1912) have similar male genitalia to *Lype* and †*Palerasnitsynus*, and the female of †*A. grossa* do not present lateral papillae on segment X like xiphocentronids and psychomyiids (Ulmer 1912). The genus †*Archaeotinodes* was placed in Ecnomidae based on the plesiomorphic spurs formula and wing venation (Ulmer 1912), which are not conclusive to place them in this family, therefore, they might be Psychomyiidae instead. As stated by Melnitsky (2009) a revision of the genus with the reexamination of Ulmer’s types would be important to clarify this and other questions.

JUSTIFICATION AND OBJECTIVES

The family Xiphocentronidae was erected by Ross (1949) to place three species from Central America and China that by the set of characters was speculated to have an affinity with Rhyacophilidae, Philopotamidae and Psychomyiidae but belonging to a distinct group. When Edwards (1961) described the first larvae of *Xiphocentron* was clear the closer affinity with Psychomyiidae. Because of the strong similarity of the larvae of both families Edwards proposed the synonymization of Xiphocentronidae. The family status of Xiphocentronidae was reestablished after the revision of Schmid (1982). In his revision were included 93 species, 4 new genera were established and the family was organized in two subfamilies Proxiphocentroninae including only *Proxiphocentron* and all other 6 genera were placed in Xiphocentroninae. A morphological phylogeny for Psychomyiidae is provided by Li & Morse (1997), including Xiphocentronidae as outgroup. Despite appearing in higher-level phylogenies, the relation of Psychomyidae and Xiphocentonidae was never investigated including a broader species sample, and including *Eoneureclipsis*, *Proxiphocentron* and other rare psychomyiid and xiphocentronid. In addition, phylogenetic hypothesis for Xiphocentronidae was never been proposed. Given the above, this study has the following objectives:

1) To investigate the phylogenetic relationship and monophyly of Xiphocentronidae and Psychomyiidae through morphological characters; and to test the monophyly of the genera of Xiphocentronidae.

2) To review species of *Xiphocentron* from Brazil and describe new species.

3) To review and describe new species of the genus *Machairocentron*.

In order to achieve these objectives, this PhD thesis was structure in three chapters:

Chapter I. Morphological phylogeny of the net-tube caddisflies reveals xiphocentronids within Psychomyiidae (Trichoptera: Psychomyioidea)

Chapter II. Taxonomy of *Xiphocentron* Brauer from Brazil, with new species and records (Trichoptera: Psychomyiidae)

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

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Chapter I. Morphological phylogeny of the net-tube caddisflies reveals xiphocentronids within Psychomyiidae (Trichoptera: Psychomyioidea)

INTRODUCTION

The Xiphocentronidae and Psychomyiidae are among the seven living families that comprise the superfamily Psychomyioidea, which is the most diverse annulipalpian clade with about 2.200 species (Morse 2019). Psychomyioid larvae construct short silken retreats or long galleries covered with sand and detritus. The adults can be diagnosed (with exception of Xiphocentronidae) by their rounded mesoscutal setal warts.

The family Xiphocentronidae was established by Ross, 1949, including Neotropical and Oriental species within a single genus, *Xiphocentron* Brauer, 1870. After the description of *Xiphocentron* larvae, the family was synonymized by Edwards (1961) with the Psychomyiidae due to the strong similarity between the larvae. Schmid (1982), in a worldwide revision, re-established the family status of Xiphocentronidae and organized the family into two subfamilies: 1) Proxiphocentroninae Schmid, 1982, including only the genus *Proxiphocentron* Schmid, 1982, and; 2) Xiphocentroninae Schmid, 1982, including 6 genera, *Abaria* Mosely, 1948, *Cnodocentron* Schmid, 1982, *Drepanocentron* Schmid, 1982, *Machairocentron* Schmid, 1982, *Melanotrichia* Ulmer, 1906, and *Xiphocentron* Brauer, 1870. Currently, the family comprises 185 species and seven genera widespread in the tropical regions of the world: being two genera exclusively Neotropical (*Machairocentron*, *Xiphocentron*), and five genera occur in the Oriental Region (*Abaria*, *Cnodocentron*, *Drepanocentron*, *Melanotrichia*, *Proxiphocentron*), with *Cnodocentron* occurring in both Oriental and Neotropical regions (Morse 2019).

Xiphocentronids and psychomyiids larvae share many morphological characters and have the same feeding habits and retreat construction style (Flint 1964; Bernard & Dudgeon 1984). Xiphocentronidae larvae usually build long tubular galleries made of silk and sediments, which are placed on humid rocks or other wet surfaces outside the water, being found mainly in hygropetric environments (Sturm 1960, Flint et al. 1991). Their larvae have short legs and thickened tibia and tarsus, but in Xiphocentronidae tibia and tarsus of all legs are fused as a single article. In both families, in the prothoracic legs, the tarsus has a ventral brush of setae that possibly is used in their foraging, scraping on detritus and grazing algae that grow within or in the surroundings of their retreats (Ings et al. 2010, Bernard & Dudgeon 1984, Pes et al. 2013).

The family Xiphocentronidae is indisputably closely related to Psychomyidae Walker, 1852 (8 genera, 469 spp.) being recovered as sister taxa in most of the phylogenies (Kjer et al. 2016, Malm et al. 2013). The family status of Xiphocentronidae was restated by Schmid in 1982 based on genitalia characters, and the present taxonomic organization of the family was established without the use of formal phylogenetics methods. Some findings have raised doubts about the evolutionary relationship of Xiphocentronidae and Psychomyiidae, including: 1) the genus *Proxiphocentron* that has the male genitalia with a xiphocentronid pattern but body characters similar to psychomyiids (Schmid 1982); and 2) the description of the larvae of the psychomyid *Eoneureclipsis* that present the tibia and tarsus of the foreleg fused as in Xiphocentronidae (Thamsenanupap et al. 2005, Torii & Karamura 2016). Therefore, a phylogenetic analysis is necessary to clarify the relationships between the two families.

Relationship and classification of Xiphocentronidae

When the family Xiphocentronidae was established by Ross (1949), the combination of traits as the mesopraescutum, the female ovipositor, and head sutures, motivated comparisons with Rhyachophilidae and Philopotamidae. On the other hand, the lack of ocelli, and details of the genitalia (as the reduced tergum IX and preanal appendages elongated) showed an affinity with Psychomyiidae. When the first larvae of *Xiphocentron* was described, the closer relationship with Psychomyiidae became clear (Edwards 1961). Thus, the family Xiphocentronidae was synonymized with Psychomyiidae (Edwards 1961). The family status of Xiphocentronidae was reestablished after the revision of Schmid (1982). Both, Ross (1949) and Schmid (1982) understood that the characters presented by xiphocentronids would indicate that Xiphocentronidae originated next to the stem group of Psychomyiidae but as a distinct clade. In general, comprehensive phylogeny of Trichoptera includes only few taxa from Xiphocentronidae and Psychomyiidae, being that most of the morphological and molecular evidences placed both families as sister groups (Figure 1A-F) (Frania & Wiggins 1997; Holzenthal et al. 2007b; Malm et al. 2013; Kjer et al. 2016; Zhou et al. 2016). In some analyses although, Xiphocentronidae was recovered within Psychomyiidae, as in Kjer et al. (2002) using combined data (morphological and molecular); and in Johanson et al. (2012) based on protein-encoding genes (Figure1D). Frandsen et al. (2016) in a likelihood analysis using only COI data found Xiphocentronidae closer to the Psychomyiidae subfamily Tinodinae. Molecular dating studies indicate that the family divergence from the Psychomyiidae occurred during the early Cretaceous (Figure 1E) (Malm et al. 2013). As the sister group (Psychomyiidae) presents Holarctic and Oriental distribution, and Xiphocentronidae has a greater diversity in the Oriental region (where occurs five of the seven genera), Schmid (1982) proposed a probable Oriental origin of the group with later dispersion to the Neotropical region.

Relationship and classification of Psychomyiidae

The family Psychomyiidae was established by Walker (1852) and in initially the family included most of the taxa of Annulipalpia other than Philopotamidae and Hydropsychidae, later, as other families in Annulipalpia were recognized, the name encompassed a smaller number of taxa. (Holzenthal et al. 2007a). Currently, it comprises 9 living genera and about 600 species occurring in all regions, except the neotropics, and being more diverse in the regions Palearctic and Oriental (Morse 2019). The family is organized in the subfamilies Eoneureclipsinae Mey 2013, Tinodinae Li & Morse 1997 and Psychomyiinae Walker 1852. The subfamily Eoneureclipsinae includes the genus *Eoneureclipsis* Kimmins 1955 (17 spp.), whose adults lack much of the characters of the rest of the family. The larvae of *Eoneureclipsis* was described by Thamsenanupap et al. (2005) and Torii & Karamura (2016) and share Psychomyiidae and Xiphocentronidae traces, having the foreleg tibia and tarsus fused like in Xiphocentronidae. Tinodinae comprises *Tinodes* Curtis 1834 (305 spp.), *Lype* McLachlan 1878 (22 spp. (6†)), *Padangpsyche* Malicky, 1993 (1 sp. Indonesia) and *Trawaspsyche* Malicky 2004 (1 sp. Indonesia). Psychomyiinae includes *Metalype* Klapálek 1898 (11spp.), *Psychomyia* Latreille 1829 (168 spp.) and *Paduniella* Ulmer 1913 (81 spp.). *Zelandoptila* Tillyard 1924 (2 spp.) from Australia and New Zealand was not formally removed from Psychomyiidae, although, there are evidences that the genus is positioned within the family Ecnomidae (Johanson & Espeland, 2010; Frandsen et al. 2016). Additionally, Psychomyiidae has three fossil genera: 1) two based on larvae (†*Cretolype* Ivanov 2006) and retreat (†*Trichopterodomus* Erickson 1983); and 2) one fossil genus with male and female (†*Palerasnitsynus* Wichard et al. 2011 (10 spp.)) described from Burmese amber (from lower and middle Cretaceous). In †*Palerasnitsynus*, the forewing forks I and III are absent as occur in most xiphocentronids (Wichard et al. 2018).

A phylogenetic study of Psychomyiidae based on the adults and the immature stages using generalized groundplan taxa was published by Li & Morse (1997a) (Figure1C). In this study, 6 out of the 9 current Psychomyidae living genera were included; *Eoneureclipsis*, *Trawaspsyche*, and *Zelandoptila* were not included in the analysis. The analysis of Li & Morse (1997a) recognized as synapomorphic characters of the family the lack of fork I in both wings, larvae protrochantin broad at apex, and larvae with submental sclerite split messaly. Also, the family was divided in two subfamilies: 1) Psychomyiinae including *Psychomyia*, *Metalype*, and *Paduniella* (characters: larvae anal claw with a comb of spines, hindwing costal margin with a prominent point, ovipositor short, presence of female apodeme and phallus j-shaped apically); and 2) Tinodinae including *Tinodes*, *Lype*, and *Padangpsyche* (character: male genitalia with phallic sclerite).

The current classification of Psychomyiidae and Xiphocentronidae is presented at table 1, showing living and fossil species and their respective species number and geographic distribution.

In this study, we mapped and coded immature and adult morphological characters of Xiphocentronidae and Psychomyiidae in order: 1) to propose a phylogeny; 2) to test the hypotheses of monophyly of the families; 3) to infer the evolutionary relations of the established groups.

Table 1. Classification of Psychomyiidae and Xiphocentronidae according with Li & Morse (1997) and Schmid (1982), respectively. With the number of species in each genus currently recognized, and their geographical distribution. AT= Afrotropical, AU=Austral, NT=Neotropical, NA=Nearctic, EP=East Palearctic, WP=West Palearctic, OR=Oriental. Species number according to Morse (2019).

Families	Subfamilies	Genera	spp.	Distribution
Psychomyiidae	Eoneureclipsinae	*Eoneureclipsis* Kimmins, 1955	17	OR
	Tinodinae	*Tinodes* Curtis, 1834	305(1†)	AT(31), OR(141), EP(11), WP(101), AU(10), NA(14).
		Lype Mclachlan, 1878	22(6†)	AT(2), OR(5), EP(5), WP(4+6†), NA(1).
		Trawaspsyche Malicky, 2004	1	OR
		Padangpsyche Malicky, 1993	1	OR
	Psychomyiinae	*Psychomyia* Latreille, 1829	168	OR(143), EP(21), WP(5), NA(3)
		Metalype Klapálek, 1898	11	OR(8), EP(1), WP(2)
		Paduniella Ulmer, 1913	81	AT(10), OR(62), EP(7), WP(3), NA(1)
	unplaced	*Zelandoptila* Tillyard, 1924	2	AU
	-	†*Palerasnitsynus* Wichard, Ross & Ross, 2011	10†	OR
	-	†*Arkharia* Sukatsheva, 1982	1†	EP
	-	†Trichopterodomus Erickson, 1983	1†	NA

Table 1. Continued.

Families	Subfamilies	Genera	spp.	Distribution
Xiphocentronidae	Proxiphocentroninae	*Proxiphocentron* Schmid, 1982	5	OR
	Xiphocentroninae	*Abaria* Mosely, 1948	39	AT(2), OR(37)
		Cnodocentron Schmid, 1982	13	OR(6), NT(6), NA(1)
		Drepanocentron Schmid, 1982	41	OR
		Machairocentron Schmid, 1982	6	NT
		Melanotrichia Ulmer, 1906	30	OR(27), EP(3)
		Xiphocentron Brauer, 1870	51(1†)	NT, NA(7)

MATERIAL AND METHODS

Specimens preparation

Analyzed specimens were conserved in 80% ethanol. Wing venation, and body characters were studied in stereomicroscopy. Photographs were taken using a camera coupled to the stereomicroscope or traced in pencil using a camera lucida and then digitalized with Adobe Illustrator® CS6. To study the genitalia, the entire abdomens were removed and genitalia were cleared using 85% lactic acid through standard methods outlined by Blahnik *et al.* (2007). The prepared genitalia were transferred to microvials with 80% ethanol. Genitalia were placed in excavated slides with a drop of glycerin, covered with coverslips and examined using optical microscopy at 400 X magnification, and then illustrations were traced in pencil using a camera lucida coupled to the microscope, and posteriorly digitalized with Adobe Illustrator® CS6.

Morphological terminology

Terminology for head and thoracic setal warts is modified from Oláh & Johanson (2007). Terminology for male genitalia is modified from Schmid (1982) and Nielsen (1957), and for female genitalia from Nielsen (1980). Terminology for wing venation follows the Comstock – Needham system as interpreted for Trichoptera by Mosely & Kimmins (1953). Paired structures are referred to in singular form.

Taxon selection

Taxa included in the phylogeny are presented in Table 2. The ingroup included 90 species in 17 genera from Xiphocentronidae (7/7 genera, 66/185 spp. sampled) and Psychomyiidae (10/12 genera, 24/620 spp. sampled). The outgroups included 16 species: 13 species representatives of all the five families within the superfamily Psychomyioidea; one species of Stenopsychidae from Philopotamoidea; and two species of Hydropsychidae from Hydropsychoidea. Representatives of fossil species from Xiphocentronidae and Psychomyiidae were also included.

Table 2. Species of Xiphocentronidae, Psychomyiidae and outgroup taxa analyzed, with respective indication of locality, depository collection (or literature source) and sex of the individuals.

Genera	**Species**	**Locality**	**Collection or literature source**	**Sex**
PSYCHOMYIIDAE				
Psychomyia	*arthit*	Thailand, Surat Thani	NMNH	♂
	chompu	Thailand, Chiang Mai Doi Tnthanon N.P.	UMSP000094808	♂, ♀
	cruciata	Russia, Far East, Primorye Territory	UMSP000208625	♂
	flavida	USA, Minnesota	UMSP000025024	♂, ♀
	nomada	USA, VAVirginia, Prince Willian Co.	UMSP000113776	♂, ♀
	schefterae	Bhutan, Thimpu Dreychhu	UMSP000174635	♂
Metalype	*holzenthali*	India, Assan, Borghat	Schmid 1997	♂
	ucatissima	Russia, Primorsky Krai Narva River	UMSP000138195	♂
Lype	†*essentia*	Ukraine, Rovno amber; Late Eocene	Melnitsky & Ivanov 2013	♂, ♀
	†*prolongata*	Baltic amber, Eocene	after Ulmer 1912	♂, ♀
	auripilis	Portugal, Serra Do Caramulo	UMSP173422	♂
	diversa	USA, VirginiaA, Prince Willian Co.	UMSP113770	♂, ♀
Tinodes	*consueta*	USAsa, California, Morgan Hill	UMSP102966	♂
	ragu	Thailand, Surat Thani	NMNH	♂
	unicolor	Greece, Euboa Dirfis	UMSP173984	♂
	waeneri	Norway, Hordaland	UMSP21783	♂, ♀
Paduniella	*kalamos*	Indonesia, Bali, Munduk	UMSP000172879	♂
	sampati	Thailand, Ubon Ratchathani Pha Taem	UMSP000093295	♂, ♀
Zelandoptila	*yuccabina*	New Zealand, North Island	UMSP000102987	♂,larvae
Eoneureclipsis	*akrichalakchmi*	India, Assan	Schmid 1972	♂
	montanamontanus	Shizuoka, Japan, Shizuoka	CBM-ZI-138373	♂, ♀
	okinawaensis	Okinawa, Japan, Okinawa	CBM-ZI-138382	larvae
†*Palerasnitsynus*	*ohlhoffi*	Myanmar, Cretaceous Burmese amber	Wichard et al. 2011, 2018	♂, ♀
	spinosus	Myanmar. Cretaceous Burmese amber	Wichard et al. 2018	♂
XIPHOCENTROIDAE				
Drepanocentron	*birghu*	India, Assam, Bhairabkunda	CNC165714	♂
	curmisagius	Thailand	OMNZ	♂
	jiska	Vietnam	HNHM	♂
	vang	Vietnam	HNHM	♂, ♀
Proxiphocentron	*arjinae*	Thailand, Taleban N.P.p OMNZ	OMNZ	♂
	prathamajam	India, Sikkim	CNC165712	♂
Melanotrichia	*attia*	Thailand	OMNZ	♂, ♀
	chichupala	India, Kandalur	CNC165702	♂
	darcha	India, Sabah, Sungai Bilanut	OMNZ	♂
	drupada	India	CNC165704	♂
	kachika	India, Huiahu	CNC165705	♂
	kibuneana	Japan	NMNH	♂
	pachupati	India	CNC165706	♂
	prajapati	India, Assam, Bhairabkunda	CNC165707	♂
	samaconius	Indonesia, Jawa	OMNZ	♂
	samaconius	Vietnam	HNHM	♂

Table 2. Continued.

Genera	**Species**	**Locality**	**Collection or literature source**	**Sex**
	taiwanensis	Taiwan	OMNZ	♂
Machairocentron	*ascanius*	Panama, Dolega	NMNH	♂
	echinatum	Venezuela, Sucre	UMSP103781	♂
	falciforme	Brazil, Amazonas	MZSP	♂, ♀
	tarpeia	Mexico, Mich, San Lorenzo	CNC165710	♂
Abaria	*cuna*	Vietnam	HNHM	♂
	electa	Congo	Marlier 1960	♂, ♀
	hemdan	Thailand	NMNH	♂, ♀
Xiph. (Xiphocentron)	†*chiapasi*	Mexican amber, Miocene	Wichard et al. 2006	♂
	asilas	Mexico, Tiera Blanca	CNC165713	♂
	aureum	Panama	UMSP171589	♂, ♀
	polemon	Mexico, Pedregal	NMNH	♂
	tarquon	Mexico, Ixtacomitan	NMNH1028630	♂, ♀
Xiph. (Sphagocentron)	*evandrus*	Costa Rica, Juan Vinas	NMNH1028615	♂
Xiph. (Glyphocentron)	*euryale*	Costa Rica	NMNH1028621	♂
	alcmeon	Guatemala	Schmid 1982	♂
Xiph. (Rhamphocentron)	*lavinia*	Guatemala, Dept. Izabal	NMNH1028618	♂
	messapus	United States, Texas	NMNH	♂
Xiph. (Antillotrichia)	*acqualume*	Brazil, Goias	MZSP	♂
	albolineatum	Dominica, Pont Casse	NMNH1028609	♂
	borinquensis	Puerto Rico, El Yunque	NMNH	♂
	cubanum	Cuba, Province Pinar del Rio	NMNH	♂
	cuyensis	Holotype, Argentina, Prov. Tucuman	NMNH1028613	♂
	fuscum	Dominica, Brantridge	NMNH1028616	♂
	haitiense	Haiti, Camp Perin, Haiti	NMNH	♂
	insulare	Trinidad and Tobago, Simla, Arima valley	NMNH	♂
	jaguare	Brazil, Goias	MZSP	♂♀
	kamakan	Brazil, Bahia, Varzedo	UFBA	♂
	maeteae	Brazil, Bahia, Varzedo	UFBA	♂,
	maracanan	Brazil, Espirito Santo	MZSP	♂
	mnesteus	Venezuela, Barinitas	NMNH1028619	♂
	nesidion	Jamaica, Trelawny	NMNH1028622	♂
	parentum	Martinique, Ravine l'Abbé	NMNH	♂
	pintada	Argentina, Prov. Tucuman	NMNH1028624	
	prolixum	Holotype, Trinidad and Tobago, Trinidad	NMNH1028626	♂
	regulare	Holotype, Colombia, Antioquia	NMNH1028627	♂
	sclerothrix	Brazil, Amazonas	MZSP	♂
	steffeni	Brazil, São Paulo State, Boracéia	NMNH	♂, ♀
	sturn	Ecuador, Napo	NMNH	♂
	surinamense	Suriname, Brokopando District	NMNH101148	♂
Cnodo. (Cnodocentron)	*bhuja*	India, Sikkim, Tikjak	CNC165709	♀
	brogimarus	Thailand, Tung Yaw	OMNZ	♂
	girika	India, Assam	Schmid 1982	♂
	tchaturbhuja	India, Sikkim	Schmid 1982	♂

Table 2. Continued.

Genera	**Species**	**Locality**	**Collection or literature source**	**Sex**
Cnodo. (Cnodocentron)	*vrisaparvan*	Assam, Rupa	CNC165711	♀
Cnodo. (Caenocentron)	*immaculatum*	Colombia, Dpto. Antioquia	NMNH	♂
	lausus	Nicaragua, Villa Somoza	NMNH	♂
	pallas	Panama, Canal Zone, Gamboa	NMNH	♂, ♀
	trilineatum	Mexico, Teapa	NMNH	♂
	yavapai	Arizona, Yavapai Co., Bubbling Springs	UMSP000021747	♂, ♀
OUTGROUPS				
Nyctiophylax	*affinis*	USA, Minnesota	UMSP000145728	♂, ♀
Neureclipsis	*bimaculata*	USA, Minnesota	UMSP000051352	♂
Pseudoneureclipsis	*arkananos*	Thailand, Ubon Ratchathani Pha Taem N.P.	UMSP000094849	♂, ♀
	hai	Thailand, Ubon Ratchathani Pha Taem N.P.	UMSP000094853	♂
Phylocentropus	*placidus*	USA, Minnesota	UMSP000051494	♂, ♀
	harrisi	USA, Alabama	UMSP000113745	♂
	ngoclinh	Vietnan, Quang Nam	Arefina & Armitage 2011	♂
Dipseudopsis	*robustior*	Thailand, Chaiyaphum, Tat Tone N.P.	UMSP000093272	♂
Kambaitipsyche	*hykrion*	Thailand	Malicky & Chantaramongkol 1991	♂
	schmidi	Myanmar (Burma)	Malicky 1992, Chamorro & Holzenthal 2011	♂, ♀
Stenopsyche	*marmorata*	Russia, Perevoznaya	UMSP000138178	♂
Arctopsyche	*grandis*	USA, Utah	UMSP000158943	♂, ♀
Hydropsyche	*betteni*	USA, Minnesota	UMSP000051511	♂
Austrotinodes	*picada*	Chile, Viii Region Del Bio-Bioestero Pichinahuel	UMSP000208523	♂
Ecnomus	*tenellus*	Russia, Primorsky Krai Utinoye Lake	UMSP000138143	♂

Depositories

Material examined is deposited at the following institutions:

CBM	Natural History Museum and Institute, Chiba, Japan.
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada.
HNHM	Hungarian Natural History Museum, Dr. Oláh Private Collection, Budapest, Hungria.
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
NMNH	Smithsonian Institution National Museum of Natural History, Washington, DC, USA.
OMNZ	Oberösterreichisches Landesmuseum, Dr. Hans Malicky Private Collection, Lunz am See, Austria.
UFBA	Museu de Zoologia, Universidade Federal da Bahia, Salvador, Brazil
UMSP	University of Minnesota Insect Collection, Saint Paul, USA.

Morphological characters

The phylogenetic dataset comprises 106 taxa (90 ingroup taxa, 16 outgroup) and 168 characters (Table 4). Were utilized characters of the adult male genitalia (74 characters), wing (23), adult body (head, thorax, legs and abdomen) (30), female genitalia (7), pupae (5), and larvae (29). Characters of larvae, and female are mostly conserved within the genera level, therefore were generalized for all species of the same genus, information source for larvae, pupae and female is listed on table 3. In addition to the characters newly established, the following earlier works were consulted as character source: Trichoptera higher-level phylogeny (Frania & Wiggins 1997); Polycentropodidae phylogeny (Chamorro & Holzenthal 2011); Psychomyiidae phylogeny (Li & Morse 1997a); placement of Pseudoneureclipsinae (Li et al. 2001); and *Dipseudopsis* phylogeny (Weaver & Malicky 1994). Characters were modified and coded to address the objectives of this study. The character states construction were based on Sereno (2007). A reference to the publication where the character first appeared and the character number as it appeared in the original text is indicated where applicable in the following form: e.g. Frania & Wiggins 1997, #11; Weaver & Malicky 1994, #5. Characters were coded from literature rather than direct observation for (16 taxa): *Abaria electa*, *Cnodocentron* (*Cnodocentron*) *girika*, *Cnodocentron* (*Cnodocentron*) *tchaturbhuja*, *Eoneureclipsis akrichalakchmi*, *Kambaitipsyche*, *Metalype holzenthali*, *Pandangpsyche*, *Phylocentropus ngonlinh*, *Trawaspsyche*, *X.* (*Glyphocentron*) *alcmeon*, and also, for the fossil taxa included for the genera: †*Palerasnitsynus*, †*Lype* and †*Xiphocentron chiapasi*.

Table 3. Sources of larvae and pupae data of included genera.
For taxa marked with * immature also were directedly analyzed.

Taxa	Source of larvae data	Source of pupae data
*Eoneureclipsis**	Torii & Nakamura 2016, Thamsenanupap, et al. 2005	Unknown
Lype	Vieira-Lanero 1998	Unknown
Tinodes	Edington & Alderson 1973, Wells 1995	Wells 1995
Psychomyia	Tachet et al. 2018	Merrit et al. 1996
Metalype	Tachet et al. 2018	Torii 2011
Paduniella	Mathis & Bowles 1994; Tachet et al. 2018	Mathis & Bowles 1994
Xiphocentron haitiensis	Flint 1964	Flint 1964
Xiphocentron mexico	Edwards 1961	Edwards 1961
*Xiphocentron moncho**	Muños & Holzenthal 1997	Muños & Holzenthal 1997
Machairocentron falciforme	Pes et al. 2005	Pes et al. 2013
Drepanocentron sp.	Genco et al. 2018	unknown
Abaria electa	Marlier 1960	Marlier 1960
Melanotrichia serica	Barnad & Dudgeon 1984	unknown
Cnodocentron yavapai	Moulton & Stewart 1997	unknown
Phylocentropus	Sturkie & Morse 1998	Merrit et al. 1996

Table 3. Continued.

Taxa	Source of larvae data	Source of pupae data
Dipseudopsis	Akagi, 1953	unknown
Stenopsyche	Ismail et al. 1996, Frania & Wiggins 1997	Ismail et al. 1996
Ecnomus	Lepneva 1970, Frania & Wiggins 1997	Lepneva 1970, Frania & Wiggins 1997
Austrotinodes	Flint 1973	Flint 1973
*Zelandoptila**	Analized	unknown
Pseudoneureclipsis	Vieira-Lanero 2000, Tachet et al. 2001	Tachet et al. 2001
Neureclipsis	Lepneva 1970	Lepneva 1970
Nyctiophylax	Wiggins 1996	Wiggins 1996
Holocentropus	Lepneva 1970, Vieira-Lanero 2000	Lepneva 1970, Vieira-Lanero 2000
Arctopsyche	Frania & Wiggins 1997, Zhou 2009	Frania & Wiggins 1997
Hydropsyche	Frania & Wiggins 1997	Frania & Wiggins 1997

Phylogenetic analysis

The phylogenetic inference was based on morphological data, using the principle of parsimony for the resolution of characters distribution conflicts. This option aims to find the topology with the fewest number of *ad hoc* hypotheses (topology with fewer steps) (Farris 1983). Two datasets were analyzed, one including all taxa (TOTAL dataset, 106 spp.), and to evaluate the bias of missing data, a dataset excluding the taxa which the immature stages is unknown, therefore using a matrix with more complete information, although with less information (REDUCED dataset, 95 spp.) (all fossils and the genera *Proxiphocentron*, *Trawaspsyche*, *Pandangpsyche* and *Kambaitipsyche* were excluded, totalizing 11 species)). The cladistic analyzes were performed through the “Tree analysis using New Technology” software (TNT) version 1.1 (Goloboff et al. 2008). Heuristics searches were performed using sectorial search (Goloboff 1999) in default mode, 200 iterations of ratchet (Nixon 1999), 20 cycles of drift (Goloboff 1999) and ten rounds of tree fusing (Goloboff 1999). This procedure was repeated until hit the minimum length 100 times. Characters were analyzed under equal weighting and implied weighting. In the implied weighting approach allows to weight characters against homoplasy, in a way that characters are weighted during tree searches and the resultant most parsimonious trees are compared to determine the maximum total character fit (Goloboff 1993). Character fit can be adjusted using a concavity constant (K), where K determines how much a character is downweighted based on its number of homoplastic steps. Therefore, low values of K strongly downweight homoplasy, whereas larger values allow for some signal to come from homoplasy. Goloboff at al. (2008) showed that downweighting characters according to their homoplasy improves phylogenetic results when properly rescaled to the utilized matrix. As the maximum number of extra steps can vary depending on the matrix dataset, a mild K in a given matrix can actually have a strong weighting in another matrix, completely eliminating many characters. Therefore, the value of K was calculated as a function of the ratio of the cost of an extra step for the less homoplastic and for the most homoplastic character. We used the TNT script *setk.run*, written by Salvador Arias, to calculate the value of K through the formula proposed by Goloboff et al. (2008). A value of 14.785 was returned for the TOTAL dataset, and 13.828 for the REDUCED dataset and subsequently used in the implied weighting scheme. The resulting trees were rooted with the Hydropsychidae taxa, following the placement of this family among the first Annulipalpia cladogenesis according to recent phylogenies (Malm et al. 2013; Kjer et al. 2016). The characters' dataset matrix was built and the cladograms were viewed and edited using Winclada/Asado 1.1 software (Nixon 2002). Most of the characters were binary and all multistate characters were treated as unordered. Branch support was measured using symmetric resampling (Goloboff et al. 2003) expressed as the difference in the CG (contradicted/present groups) frequency (1000 replications) and relative bremer support (Goloboff & Farris 2001), with branch-swapping of suboptimal trees up to 10 steps longer and relative fit of 0.9%.

RESULTS

Characters and states used in the phylogenetic inference:

Larval characters

1. *Larvae construction, length*: (0) short retreats; (1) elongate tubular galleries. Dipseudopsids, pseudoneureclipsids, psychomyiids and xiphocentronids build elongate galleries.
2. *Prelabio-hypopharyngeal lobe, sclerotization* (Figure 2A)*:* (0) membranous; (1) sclerotized. Synapomorphy of Psychomyioidea (Frania & Wiggins 1997, # 7; Chamorro & Holzenthal 2011, #2).
3. *Foreleg tarsus, ventral margin:* (0) without setal brush; (1) with a dense brush of setae (Figures 2G, H) (State 1 present in dipseudopsids, psychomyiids and xiphocentronids).
4. *Labium (spinneret), length:* (0) short; (1) longer than other mouthparts (Figure 2A). An elongate labium is observed in psychomyiids, xiphocentronids, pseudoneureclipsines and dipseudopsids. All these taxa construct dwelling tubes with associated matter, such as large sand grains (Weaver & Malicky 1994, #5; Chamorro & Holzenthal 2011, #3).

5. *Labial palpi:* (0) present; (1) absent. State 1 is characteristic of taxa having an elongate labium (Frania & Wiggins 1997, #8; Chamorro & Holzenthal 2011, #4).
6. *Labial palpi, aspect:* (0) prominent; (1) appressed to sides of prelabio-hypopharyngeal lobe. State 1 is characteristic of polycentropodines. (Frania & Wiggins 1997, #8; Chamorro & Holzenthal 2011, #5).
7. *Right mandible, brush of setae:* (0) right mandible never with a brush of setae; (1) both mandibles with a brush of setae. State 1 is synapomorphy of Dipseudopsidae (Chamorro & Holzenthal 2011, #6).
8. *Anterior tentorial pits:* (0) in contact with anterior arms of dorsal ecdysial line; (1) arising on dorsal (frontoclypeal) apodeme distant from mesad line. All Psychomyioidea present state 0 (Frania & Wiggins 1997, #11; Chamorro & Holzenthal 2011, #7).
9. *Head ventral apodemes, posterior apodeme:* (0) absent; (1) presente. Posterior apodemes present in Hydropsychidae (Frania & Wiggins 1997, #12; Chamorro & Holzenthal 2011, #9).
10. *Shape of anterior apodeme*: (0) elongated laterally; (1) small, not elongating laterally (Figure 2E). State 1 is a *Psychomyia* synapomorphy (after Tachet et al. 2018)
11. *Submental sclerites* (Chamorro & Holzenthal 2011, #10): (0) absent (Figure 2A); (1) present (Figure 2B-F). Xiphocentronids lack submental sclerites.
12. *Submental sclerites, state of fusion*: (0) fused; (1) separate (Figures 2B-F). Psychomyiids have separated submental sclerites (Chamorro & Holzenthal 2011, #11).
13. *Pronotum, tergal ridge*: (0) absent; (1) present, entire. Pronotal tergal ridge entire only in Hydropsychidae. (Frania & Wiggins 1997, #16; Chamorro & Holzenthal 2011, #12).
14. *Pronotum, hind angles.* (0) not prominent separated by entire width of sternum; (1) extending ventrally and coming into contact on sternum. (Frania & Wiggins 1997, #18; Chamorro & Holzenthal 2011, #13).
15. *Larval fore-trochantin*: (0) free from episternum; (1) fused with episternum, with or without suture (Figures 2J-P). (Li et al. 2001, #13).
16. *Suture of larval fore-trochantin*: (0) absent; (1) with suture distinguishing trochantin from episternum (Figures 2J-P) (Li et al. 2001, #13; Chamorro & Holzenthal, #15).
17. *Fore-trochantin, two very small lobes:* (0) absent; (1) present (Figures 2K-L).

18. *Trochantin, suture betwen propleuron and trochantin.* (0) only one vertical suture visible (Figure 2M); (1) forked with two vertical sutures visible (Figure 2O).
19. *Shape of trochantin apex*: (0) acute; (1) broad (Figures 2N, O, P). An acute and elongate trochantin is present in ecnomids, dipseudopsids and polycentropodines. Psychomyiids have a truncate and broad trochantin (Li et al. 2001, #14; Weaver & Malicky 1994, #1).
20. *Mesonotum, sclerotization*: (0) membranous (Figure 2I); (1) sclerotized, dorsal ecdysial line present or absent. A membranous mesonotum is characteristic of psychomyiids, xiphocentronids, dipseudopsids and polycentropodines (Frania & Wiggins 1997).
21. *Metanotum, sclerotization*: (0) membranous (Figure 2I); (1) sclerotized, dorsal ecdysial line present or absent (a membranous mesonotum is characteristic of psychomyiids, xiphocentronids, dipseudopsids and polycentropodines) (Frania & Wiggins 1997, #23).
22. *Larval mesopleuron, flat process extending anteriorly*: (0) absent; (1) present (this is a synapomorphy of xiphocentronids, absent in psychomyiids) (Chamorro & Holzenthal 2011, #18).
23. *Foreleg, tibia and tarsus*: (0) not fused (Figures 2G); (1) fused (Figure 2H). Foreleg fused tibia and tarsus is present in *Eoneureclipsis* and xiphocentronins, and absent in other psychomyiids.
24. *Midleg, tibia and tarsus*: (0) not fused; (1) fused. Fused tibia and tarsus of meso and hindlegs is a synapomorphy of xiphocentronids.
25. *Larvae foreleg*: (0) not thickened; (1) thickened (Figures 2G, H). Dipseudopsids, psychomyiids and xiphocentronids present state 1.
26. *Larval abdominal gills*: (0) absent; (1) present (present only in hydropsichids). (Wiggins 1996, Chamorro & Holzenthal 2011, #26).
27. *Pleural region of abdominal segments II-VIII, fringe of secondary setae*: (0) absent; (1) present. (Frania & Wiggins 1997, #36).
28. *Anal claw, spines on ventral margin*: (0) absent; (1) present (Figure 2Q). (Tachet et al. 2018).
29. *Anal claw, dorsal accessory spine*: (0) absent; (1) present. (Wiggins 1996, Chamorro & Holzenthal 2011, #29).

Pupal characters

30. *Apex of pupal mandible, whip-like process*: (0) absent (Figure 2V); (1) present (Figures 2S, T, U). State 1 is exclusive of psychomyiids and xiphocentronids. Mandibles are used to clean pupal cases and for emergence during eclosion. (Chamorro & Holzenthal 2011, #33).
31. *Pupal mandible, inner tooth:* (0) absent; (1) present. State 1 is synapomorphy of Pseudoneureclipsidae. (Chamorro & Holzenthal 2011, #34).
32. *Abdominal segment VIII, pre-segmental hook-plates:* (0) absent; (1) present.
33. *Abdominal segment II, pre-segmental hook-plates:* (0) absent; (1) present. Present in Psychomyiidae and Xiphocentronidae.
34. *Abdominal segment V, post-segmental hook-plates:* (0) absent; (1) present. Only absent in *Hydropsyche*.

Female genitalia characters

35. *Segment VIII, tergum- sternum:* (0) divided in tergum and sternum; (1) synscleritous (without pleural suture between tergum and sternum). *Lype*, *Paduniella* and most xiphocentronids (except *Abaria* and *Proxiphocentron*) have synscleritous segment VIII. (Li et al. 2001, #2; Chamorro & Holzenthal, #120).
36. *Segment VIII, dorsum:* (0) dorsally closed and sclerotized; (1) dorsally opened or membranous. Character (1) is present only in xiphocentronines except *Abaria*. Schmid (1982) hypothesized that the tergum VIII was lost and that the sternum VIII covered the whole segment, explaining the dorsal opening. Although, *C.* (*Cnodocentron*) *bhuja* and *C.* (*C.*) *vrisaparran* have small pleural incisions that seems to indicate that tergum and sternum VIII were actually fused, and that the tergum VIII got secondarily membranous to opened.
37. *Ovipositor, length:* (0) short (Figure 3C); (1) elongate (Figure 3A).
38. *Sternum VIII:* (0) entire; (1) separated into a pair of lobes. An undivided or incised female sternum VIII is present in dipseudopsids, xiphocentronids, psychomyiids and pseudoneureclipsids. (Li et al. 2001, #3; Chamorro & Holzenthal 2011, #119).
39. *Segment IX, apodemes:* (0) absent (Figure 3C); (1) present (Figure 3A). (Xiphocentronidae, Psychomyiinae and Philopotamoidea have ovipositor apodemes).

40. *Segment VIII, apodemes:* (0) absent (Figure 3C); (1) present (Figure 3A). (Xiphocentronidae, Psychomyiinae and Philopotamoidea have ovipositor apodemes).
41. *Segment X, lateral papillae:* (0) absent (Figure 3A); (1) present (Figures 3B, C). State 0 is a synapomorphy for the clade Xiphocentronidae + Psychomyiidae (Frania & Wiggins 1997, #68; Weaver & Malicky 1994, #3; Chamorro & Holzenthal 2011, #122).

Adult characters

42. *Setae between ommatidia*: (0) absent; (1) present (Figure 4G). Small setae are present between the facets of the compound eye in *Kisaura*, *Kambaitipsyche*, *Psychomyia*, *Metalype,* and *Paduniella*. (Chamorro & Holzenthal 2011, #37).
43. *Oceli:* (0) absent; (1) present.
44. *Preocellar setal wart*: (0) absent or very difuse; (1) present, well distinct (Chamorro & Holzenthal 2011, #40).
45. *Preocellar setal wart and ocellar wart, state of fusion*: (0) preocellar and ocellar warts separated; (1) preocellar and ocellar warts fused (Figure 4K). In *Pseudoneureclipsis,* the preocellar setal wart is fused to the ocellar wart. (Li et al. 2001, #5).
46. *Preocellar wart, size*: (0) prominent (Figures 4K, L); (1) small (Figures 4K, L) (Chamorro & Holzenthal 2011, #41).
47. *Ocellar and occipital warts, angle*: (0) angulated to the coronal line; (1) mostly parallel to each other and perpendicular to the coronal line (Figure 4H).
48. *Ocellar wart, shape*: (0) oblong (Figures 4N-O); (1) deltoid (Figures 4G, I, P) (Chamorro & Holzenthal 2011, #42).
49. *Occiptal wart, length in relation to eye midline*: (0) not extending beyond eye midline; (1) long, at or extending beyond eye midline (Figure 4J) (Chamorro & Holzenthal 2011, #45).
50. *Postoccipital wart:* (0) absent; (1) present (Chamorro & Holzenthal 2011, #44).
51. *Occipital line*: (0) not evident (Figures 4M, N); (1) well distinct (Figures 4A,F,G,H).
52. *Postoccipital line*: (0) meeting with occipital line, near occipital warts (1) meeting with occipital line high on the head, near ocellar warts.
53. *Mesoscutal wart*: (0) absent; (1) present (Figure 4N).
54. *Mesoproscutum, parapsidal lines:* (0) absent; (1) present.

55. *Mesoscutal wart, edges:* (0) sharp, rectangular; (1) smooth, rounded.
56. *Mesoscutal wart, shape:* (0) rounded; (1) elliptical; (2) elongated until mesoscutelum.
57. *Mesoscutal warts, state of reduction:* (0) regular (Figures 4I, J, L); (1) very reduced (Figures 4K, P).
58. *Mesoscutellum anterior margin, shape:* (0) acute (Figures 4G-K).; (1) rounded (Figures 5O, P), (2) truncate (Figure 4A). Most species have the anterior margin acute; it is more rounded in *Proxiphocentron* and *Abaria*; and some *Melanotrichia* have a truncate, quadrate mesoscutellum.
59. *Median pronotal wart, shape:* (0) oblong; (1) ovoid; (2) quadrate to broadly rectangular. *Kambaitipsyche*, *Austrotinodes*, Psychomyiidae and *Proxiphocentron* have ovoid pronotal warts. Polycentropodid, dipseudopsids have more quadrate pronotal warts. *Pseudoneureclipsis*, Ecnomidae, and xiphocentronids other than *Proxiphocentron* have oblong warts (Modified from Chamorro & Holzenthal 2011, #50).
60. *Maxillary palp segments, number:* (0) 5; (1) 6. *Paduniella* has an additional palpomere.
61. *Maxillary palpomere 2, shape*. (0) cylindrical, length greater than twice the diameter (Figures 4C, D, F); (1) ovoid, length approximately equal the diameter (Figure 4E) (Frania & Wiggins 1997, #45; Chamorro & Holzenthal 2011, #52).
62. *Apex of maxillary palpomere 2, setose cushion*: (0) absent; (1) present. (Chamorro & Holzenthal 2011, #53).
63. *Maxillary palpomere 3, stout setae*: (0) absent; (1) present. †*Palerasnitsynus* synapomorphy (Wichard et al. 2018).
64. *Maxillary palpomere 3, length*: (0) palpomere 3 shorter than twice palpomere 2; (1) palpomere 3 length more than twice palpomere 2. Polycentropodids have state 1 (Chamorro & Holzenthal 2011, #56).
65. *Maxilary palpomere 4, length:* (0) palpomere 4 shorter than palpomere 3; (1) palpomere 4 longer than palpomere 3.
66. *Adult fore tibia, preapical spurs*: (0) absent; (1) present (modified from Li et al. 2001, #7; Chamorro & Holzenthal 2011, #60).
67. *Adult fore tibia, number of apical spurs*: (0) 2 spurs; (1) reduced to 1 or 0 spur (modified from Li et al. 2001, #7; Chamorro & Holzenthal 2011, #60).
68. *Male hind tibia, spurs number*: (0) 4 spurs; (1) 3 spurs.

69. *Hind leg apical spur, aspect:* (0) similar to other spurs (Figure 3F); (1) modified spurs, distinct from spurs of other legs (distinctly enlarged and\or twisted) (Figures 3E, G). Modified spurs are present in *Dipseudopsis*, *Metalype*, *Drepanocentron*, *X.* (*Ramphocentron*), *Xiphocenton* (*Xiphocentron*), (except *X.* (*X.*) *tarquon* and *X.* (*X.*) *polemon*).
70. *Abdominal vesicle, 2 pairs of vesicles opening on tergum III and IV:* (0) absent; (1) present. This is a synapomorphy of *X.* (*Ramphocentron*) *mexico* group as presented by Schmid (1982). These vesicles are absent in *X.* (*R.*) *lavinia* group and all other xiphocentronids. These vesicles are not homologous with the ones present in some hydropsychids, as their opening are near the base of abdomen and dorsally in *Xiphocenton* (segments III and IV) and posterior and more ventrally on hydropsychids (segments VII and VI).
71. *Sternum V, pair of reticulated sclerotized cuticular plates:* (0) absent; (1) present (Figure 3D). This structure is present most Neotropical Xiphocentroninae except *X.* (*Ramphocentron*), *X.* (*Xiphocentron*), (although present on *X.* (*X.*) *tarquon,* and *X.* (*X.*) *polemon*). These plates can be produced laterally forming elongate processes as in *X. piscicaldum*. The species *Melanotrichia forficula* (Kobayashi, 1964) from Japan also has these cuticular plate laterally on sternum V. *Melanotrichia dakcha* Schmid, 1982 has a pale rounded area, but as it is not sclerotized and reticulate, the character was coded as absent for this species. The fossil genus *Archaeotinodes* Ulmer, 1912 (Ecnomidae) also show a reticulated sclerotized cuticular area on sternum V (Melnitsky 2013).

Wing characters

72. *Forewing Sc looped in R_1:* (0) absent; (1) present (Figure 5G). (State 1 present in *X.* (*Rhamphocentron*), *X.* (*Xiphocentron*), *X.* (*Sphagocentron*), *Abaria* in part, *Drepanocentron* in part, and *Melanotrichia* in part).
73. *Forewing, R_1 forked:* (0) absent; (1) present (Figure 5E).
74. *Forewing, fork I (R_2 and R_3):* (0) absent; (1) present (Figures 5A,E,F,G).
75. *Forewing, fork I in relation to discoidal cell:* (0) sessile; (1) petiolate.
76. *Forewing, Discoidal cell size (ratio of discoidal cell to Rs-radial sector):* (0) discoidal cell about 2 times smaller than the cell between R1 and Rs (Figures 5F-H); (1) discoidal cell more than 3 times smaller than the cell between R1 and Rs (Figures 5A, B, C, E).

77. *Forewing, median cell:* (0) open (Figure 5C); (1) closed (Figure 4B).
78. *Forewing, fork II forewing:* (0) sessile; (1) petiolate or with nygma isolated.
79. *Forewing with nygma surrounded by a cell*: (0) absent; (1) present.
80. *Forewing, fork III:* (*M_1 and M_2*) (0) present; (1) absent.
81. *Forewing, fork IV:* (0) present; (1), absent. *Abaria* and *Drepanocentron* do not have the fork IV.
82. *Forewing, fork IV (M_3 and M_4) in relation to m crossvein:* (0) petiolate; (1) sessile (Figures 4A,E).
83. *Forewing, fork V (Cu_{1a} and Cu_{1b})*: (0) present; (1) absent (Figures 5G,H). (Li et al. 2001, #6)
84. *Forewing, thyridial cell and medial fork, distance*: (0) thyridial cell not very separated from medial fork (Figures 5A, D, E); (1) medial fork separated by at least one-quarter length of thyridial cell (Figures 5B, C, F, G, H). (Frania & Wiggins 1997, #58).
85. *Forewing, anal vein 2A:* (0) present; (1) absent (Figures 5H). State 1 present in *Abaria*, *X. (Rhampocentro*n), and *Drepanocentron druhyu* group.
86. *Forewing, anal veins 2A position:* (0) meeting 1A (Figures 5C, G); (1) meeting 3A.
87. *Hindwing, costa, pointed curvature:* (0) absent; (1) present (Figures 5C, D).
88. *Hindwing, fork II in relation to crossvein r-m:* (0) sessile or short petiolate; (1) long petiolate.
89. *Hindwing, crossvein r_1-rs/R_{2+3}:* (0) absent; (1) present. The hindwing *r_1-rs* in xiphocentronids and psychomyiids can be fused to R_1 therefore the *r_1-rs* is being considered homologous to R_{2+3} in these taxa.
90. *Hindwing, discoidal cell:* (0) absent; (1) present (Figures 5A, F).
91. *Hindwing, Fork I:* (0) absent; (1) present.
92. *Hindwing, Fork III (M_1 and M_2):* (0) present; (1) absent (Figure 5F).
93. *Hindwing M bifurcation in relation to crossvein r-m:* (0) sessile; (1) petiolate (Figure 5H).
94. *Forewing, apex shape:* (0) rounded; (1) acute (Figures 5D, H). Some xiphocentronids, *Psychomyia* and *Paduniella* have acute wing apex.
95. *Forewing, color pattern:* (0) forewing with 1 or none white spot; (1) forewing numerous spots (2 to 4 white spots). (All *Cnodocentron* (*Caenocentron*) have 3 spots, *Abaria* species have forewings with 2 to 4 spots; some South American *Machairocentron* have 2, *Melanotrichia* and *Xiphocentron* can have one or none,

sometimes with sex variation in *Melanotrichia* with the female having the spot and the male not).

Male genitalia characters

96. *Tergum VIII, posterior margin:* (0) not produced; (1) produced. State 1 present in *X. tarquon,* and *Abaria.*
97. *Tergum IX, state of fusion with sternum VIII*: (0) well separated from tergum VIII; (1) fused or intimately associated to tergum VIII anterior margin. State 1 present in *Abaria,* and *Drepanocentron*.
98. *Tergum IX, dorsal crest:* (0) absent; (1) present State 1 present in *Lype*, *Kambaitipsyche*, and *Dipseudopsis*.
99. *Tergum IX, state of reduction:* (0) well developed; (1) extremely reduced, or absent (Figure 6A). State 1 present in Polycentropodids, *Zelandoptila*, *Austrotinodes*, *Kisaura*, Pseudoneureclipsids, *Proxiphocentron*, and *Abaria*.
100. *Tergum and sternum IX, separation:* (0) well separated; (1) broadly fused.
101. *Tergum IX, posterior margin:* (0) not produced, tergum short (Figure 6G); (1) produced, tergum elongate (Figures 6D, H).
102. *Tergum IX, posterior margin lobes, length:* (0) 1short; (1) very elongate.
103. *Tergum IX, posterior margin incision width:* (0) narrow to moderately wide; (1) very wide (apical lobes very far from each other).
104. *Tergum IX, posterior margin incision:* (0) shallow or absent; (1) deep.
105. *Tergum IX, anterior margin incision:* (0) shallow or absent; (1) deep.
106. *Tergum and sternum IX articulation aspect (lateral view):* (0) tergum IX hinged over the sternum (leaving some free anterior margin of the sternum) (Figure 6C, F); (1) tergum IX very reduced and contiguously articulated with the foremost edge of sternum (Figure 6E).
107. *Tergum IX and tergum X, state of fusion:* (0) tergum IX well distinct; (1) tergum IX broadly fused to tergum X. State 1 present in Hydropsychidae, Dipseudopsidae, Kambaitipsychidae, *Neureclipsis,* and *Pseudostenopsyche.*
108. *Sternum IX, apodeme:* (0) present (Figures 6K-P); (1) absent. Apodeme present and well developed in Xiphocentronidae.
109. *Sternum IX, apodeme shape:* (0) narrow; (1) broad and contiguous with sternum IX margins. Narrow in *Abaria, Machairocentron,* some *Cnodocentron* (*Caenocentron*) and many *Xiphocentron.*

110. *Sternum IX, medial suture:* (0) absent; (1) present. Present in *Kisaura*, Ecnomidae, Pseudocenureclipsidae, and *Nyctiophylax*.
111. *Sternum IX, ventro-apical margin:* (0) without a small medial point; (1) with a small medial point. Small point present in some *Melanotrichia*.
112. *Sternum IX, ventro-apical projection, length:* (0) short (Figure 6B); (1) elongate, about half inferior appendage length (Figures 6A, N). Elongate in *Drepanocentron* and some *Cnodocentron*.
113. *Sternum IX, ventro-apical margin:* (0) with smooth concavity to linear; (1) with indentations or elongate projections (Figures 6A, B).
114. *Sternum IX, ventro-apical margin projection, position:* (0) lateral (Figure 7B); (1) mesal (Figure 7A).
115. *Sternum IX, lateral margin:* (0) not produced; (1) produced posterad (Figure 6A). Produced in *Stenopsyche*, *Neureclipsis* and *Proxiphocentron*.
116. *Sternum IX, upper margin, shape (in lateral view):* (0) linear; (1) produced dorsad (Figures 7M). State 1 present in most *C. (Caenocentron)* subgenus.
117. *Sternum IX, upper margin, incision:* (0) absent; (1) present (Figures 7O, P). Incision near preanal appendage present in most *Melanotrichia* and partially in *X. cubanum* (Figure 7P).
118. *Preanal appendage shape (dorsal view):* (0) subapically without any distinct mesal rouded expansion; (1) subapically with mesal rouded expansion. State 1 present in X. steffeni, X. pintada.
119. *Preanal appendage, length (in lateral view):* (0) not elongate; (1) elongate (length more than 4x base width).
120. *Preanal appendage, width (in lateral view):* (0) slender; (1) broad (1/3 of the segment).
121. *Preanal appendage and tergum IX, separation:* (0) well separated; (1) broadly fused. State 1 is a Psychomyia synapomorphy.
122. *Preanal appendage, apical sclerotized point:* (0) absent; (1) present. State 1 is a *Metalype* synapomorphy.
123. *Preanal appendage, shape (lateral view):* (0) clavate, apex rounded or truncate; (1) subapically enlarged, and acute at apex. *X.* (*Sphagocentron*) subgenus and some *Xiphocentron* (*Antillotrichia*) species from Antilles have state 1.

124. *Preanal appendage, longitudinal keel:* (0) absent; (1) present. *Melanotrichia* presents a longitudinal keel on the preanal appendage on the region where the fan-shaped mesal sclerite touch the preanal appendage.
125. *Inferior appendage, harpago and coxopodite state of fusion:* (0) broadly fused, with or without partial remnant suture; (1) harpago and coxopodite well separated.
126. *Inferior appendage, length:* (0) short; (1) elongate.
127. *Each coxopodite:* (0) well separated; (1) mostly fused (fused in *Eoneureclipsis, Pandangpsyche, Trawaspsyche,* and *Proxiphocentron*).
128. *Coxopodite, length:* (0) very reduced (less than 1\3 gonocoxite lenght); (1) elongate. *Metalype* and *Psychomyiia* as well some †Palerasnitsynus have very short coxopodite (state 0), by the remnant suture on *Drepanocentron*'s inferior appendage, they also present short coxopodite.
129. *Harpago, length:* (0) short (less than half coxopodite length); (1) elongate.
130. *Harpago, overall shape:* (0) flat and not cylindrical, (1) oblong, cylindrical.
131. *Harpago, apex, width:* (0) about as wide as the base (Figures 6A, C, E, F); (1) apex narrowly elongate, finger-like (Figures 7C-I).
132. *Harpago, position*: (0) apical to the coxopodite; (1) displaced from the apex of coxopodite (latero-basal). State 1 present in Pseudoneureclipsidae.
133. *Basal plate of inferior appendage,dorsal process (phallic guide):* (0) absent (Figure 6F); (1) present (Figures 6A, C). Present in *Tinodes*, and in some Ecnomidae.
134. *Basal plate of inferior appendage, apodeme length:* (0) short; (1) elongate (Figures 6A, C, F). *Tinodes*, *Padangpsyche*, *Trawaspsyche*, *Eoneureclipsis,* and Xiphocentonids (except *Abaria*) have very elongate basal plate.
135. *Coxopodite, basomesal margin:* (0) not projected; (1) projected mesad (Figure 7I).
136. *Coxopodite, each basomesal projection, state of fusion:* (0) separated (Figure 7A); (1) fused (Figure 7I).
137. *Coxopodite, shape:* (0) not produced; (1) produced posterad. *Cnodocenton*, and *Kambaitopsyche* have coxopodite produced posterad, sometimes giving a biforked aspect to the inferior appendage. State 1 is a *Cnodocentron* synapomorphy (Schmid 1982).
138. *Coxopodite, projection shape:* (0) acute (present in *C.* (*Cnodocentron*) subgenus); (1) smooth, rounded (present in most *C.* (*Caenocentron*) subgenus, except *C. yavapai*, *C. trilineatum*).

139. *Coxopodite, basomesal face:* (0) smooth, without any noticeable roughness; (1) setose\granulose (Figures 7E, I).

140. *Coxopodite, setae length:* (0) short to very short setae (granulose area) (Figure 7E); (1) elongate, bristle like setae present (Figure 7I).

141. *Harpago, spine-like setae:* (0) absent; (1) present.

142. *Inferior appendage, spines length:* (0) short, or tubercle like (Figures7E-G); (1) elongate or bristle like (Figures 7C, D).

143. *Inferior appendage spines density:* (0) fewer sparse spines; (1) many dense spines.

144. *Harpago, basal region, aspect:* (0) harpago base contiguous with inferior appendage length and/or without any distinct spine concentration; (1) harpago base broad rounded and sclerotized/ setose area (Figures 7C, G, H). *Melanotrichia chichulapa* group, *Machairocentron* and *X.* (*Xiphocentron*) *aureum, X. asilas,* and †*X. chiapasi* have the basal area broad and mostly covered with spines.

145. *Harpago, basal region:* (0) without any sclerotized lateral lobe; (1) with a sclerotized lateral lobe (Figure 7H). State 1 is synapomorphy of *Machairocentron*.

146. *Harpago, mesal sclerite or projection:* (0) absent; (1) present.

147. *Harpago, group of elongate setae on the same position of the mesal sclerite (when mesal sclerite absent):* (0) absent; (1) present (Figure 7D).

148. *Harpago, mesal projection:* (0) narrow sclerite-like (Figures 7E-G); (1) broad lobe-like (Figure 7H). State 1 is synapomorphy of *Machairocentron*.

149. *Harpago, mesal sclerite:* (0) acute process, without spines (Figure 7B); (1) covered with spines (Figures 7E-G). *Melanotrichia kibuneana*, *M. tawanensis*, and *C. girika* have an acute sclerite without spines (Figure 7B).

150. *Mesal sclerite, spines length*: (0) short; (1) elongate.

151. *Inferior appendage, harpago, mesal sclerite stalk:* (0) narrow, oblong; (1) rounded (Figure7E). Rounded in in *X.* (*Rhamphocentron*) subgenus.

152. *Harpago, mesal sclerite spines shape:* (0) acute, spine-like; (1) broad, process fan-shaped. Mesal sclerite is fan-shaped shaped in most *Melanotrichia*.

153. *Harpago, ventro-mesal sclerite:* (0) absent; (1) present. Some *Melanotrichia* have 2 or more additional mesal sclerites.

154. *Harpago, subbasal region aspect*: (0) linearly contiguous with base and apex; (1) bent in an elbow-like shape, usually with a group of spines on the region.

155. *Harpago, apical region:* (0) without spine-like setae; (1) with spine-like setae (Figure 7J).

156. *Paraproctal process, dorsal setae/ spines:* (0) absent; (1) present (Figures 6B, G, H).

157. *Paraproctal process and tergum X, state of fusion:* (0) paraproct as a free lateral structure usually with a semi-membranous tergum X at middle; (1) paraproct fused with the tergum X, or absent. In some taxa the paraproctal process is not present as a free structure but is fused with other structures, being noticed as a sclerotized rim or spinous outgrowths on the structure. In Dipseudopsidae, *Kambaitipsyche*, and *Hydropsyche* the paraproct might be fused to the tergum X, as it is membranous in all analyzed species and only is sclerotized when any free paraproctal structure is not visible. In *Psychomyia* and *Metalype* the paraproctal process is possibly fused on the tergum X that is also fused to the preanal appendage and appear as a sclerotized mesal process in *Psychomyia*.

158. *Paraproctal process, position in relation to the phallus:* (0) paraproctal process distant to the phallus, with or without punctual articulation with the phallus; (1) closely associate, paraproctal process closely appressed to along phallus (Figures 8A, C). Xiphocentronidae and *Tinodes* have the paraproctal processes appressed around the phallus. *Tinodes* lack any phallic musculatures (Nielsen 1957), and the paraprocts and the dorsal process of basal plate (phallic guide) likely help with the placement and orientation of the phallus. The same may occur in the xiphocentronids.

159. *Paraproctal process, shape:* (0) broad; (1) acute, hornlike (Figure 6F). Many species possess an acute and elongate paraproctal process, Chamorro & Holzenthal (2011), named the various latero-dorsal and latero-mesal outgrowths of polycentropodids as ‘processes of preanal appendage’ considering as intermediate appendage only the mesal most process, herein all these outgrowths are collectively referred as paraproctal processes as in Nelsen (1957). These structures are very labile in Trichoptera showing great variation and possibly evolved different times. Following the appendicular theory of the formation of the genital structures (Snodgrass, 1957), by their appearance and strong modification, these structures may be endites/exites of the ancestral appendages fused along the remaining genital segments.

160. *Paraproctal process, lateral spines/setae:* (0) absent; (1) present (Figures 6B, D, G, H). In *Tinodes* and *Drepanocentron*, *X*. (*Glyphocentron*), and some *C.* (*Caenocentron*) the paraproctal process bears many spines or spine-like setae.

161. *Phallus, width (lateral view):* (0) broad (Figures 8L, J), (1) very slender (Figures 8A-I). Most of the psychomyiids and all xiphocentronids have very slender phallus.

162. *Phallus, length:* (0) elongate (length proportional to the genital segments) (Figures 8A, B, H, I, J, L); (1) very elongate (length extending for many abdominal segments) (Figures 8D, K). Xiphocentronids have extremely elongate phallus.

163. *Phallus, articulation with elements of paraproctal process:* (0) absent; (1) present (Figure 8L). Polycentropodidae, Pseudoneureclipsidae, and some Ecnomidae have phallus articulated with the paraprocts that usually form ear-like lobes mesally to the preanal appendages.

164. *Phallus, posterior region, shape*: (0) straight or not strongly bent; (1) strongly bent, S-shaped (Figure 8H). *Psychomyia* and *Metalype* have strongly curved phallus. (Li & Morse 1997a, #16).

165. *Phallus, sclerotized strip articulating to IX segment:* (0) absent; (1) present (Figure 6F). *Eoneureclipsis* and *Paduniella* have a sclerotized strip connecting the phallus to the sternum IX, in *Psychomyia* and *Metalype* the dorso-lateral margin of sternum IX is curved and articulated to the phallus basally, in *Lype auriplis* a sclerotized strip leave the subapical portion of phallus articulate with the sclerotized rim of tergum X (probably of paraproctal origin) that articulates with the dorso-lateral margin of sternum IX. *Tinodes* and xiphocentronids do not have any articulation with the phallus and other genital structures. Nelsen (1957) analyzing the phallus musculature noted the absence of any anterior or posterior musculature on the phallus of *Tinodes*, while *Psychomyia* and *Lype* present anterior muscles but not posterior ones. Polycentropodidae (i.e. *Holocentropus*, *Polycentropus*), and Ecnomidae (i.e. *Ecnomus*) presented both anterior and posterior phallus musculature.

166. *Phallus, apex shape:* (0) apex rounded (Figure 8C); (1) apex pointed and totally curved upward (Figures 8C, D, F). *Melanotrichia* that present pointed phallus (state 1) while most of xiphocentronids have a rounded one.

167. *Phallic parameres:* (0) absent or very short; (1) elongate (Figures 8I, 8K) *Proxiphocentron* has clear parameres, *Paduniella* has a single structure that may be the fused paired parameres (Li & Morse 1997b). In other xiphocentronids the elongated parameres of *Proxiphocentron* seem to be completely fused along the phalloteca, the structure that Schmid (1982) refers as intermediate appendage (paraproctal process) in *Drepanocentron* is likely part of the phallotheca, and may be homologous to the paramere in *Proxiphocentron* rather than to the paraproctal process, as the structure does not have any articulation to the segment IX.

168. *Endothecal spines\sclerites:* (0) absent; (1) present (Figures 8F, K). In many psychomyids and xiphocentronids the endotheca is obliterated and any sclerite of spine is present. *Lype*, *Eoneureclipsis*, *Proxiphocentron*, *Drepanocentron*, and some *Tinodes* present some endothecal sclerites.

Phylogenetic results

Consensus trees summarizing results for each dataset are shown in the figures 9-10. Phylogenetic analysis of the complete dataset (106 taxa, 168 characters) under equal weighting yielded 969 trees, length 468, consistence index (CI): 0.36, retention index (RI): 0.87 (Figure 9A). The same dataset under implied weighting resulted in 9 trees, length 468, CI: 0.36, RI: 0.87 (Figure 9B). The reduced dataset (95 taxa, 168 characters) under equal weightings resulted in 820 equally parsimonious trees, length 420, CI: 0.41, RI: 0.89 (Figure 10A). Under implied weighting 90 trees were obtained, length 421, CI: 0.41, RI: 0.89 (Figure 10B). Support values (Relative Bremer and Symmetric Resampling) for a given clade are displayed along the internodes (Figures 9-10).

The TOTAL dataset (Figure 9) presented a topology better resolved than the REDUCED dataset (Figure 10), but the exclusion of the terminals with many missing data (REDUCED dataset) despite being less resolved, resulted in clades in general with stronger support, being a more conservative result. Results from analyses of both the reduced and total datasets showed Psychomyiidae paraphyletic without including the taxa from Xiphocentronidae (Figures 9-10). Also, *Zelandoptila* was placed within the outgroup taxa among the Ecnomidae. The subfamily Eoneureclypsinae Mey (2013) was supported as a clade at the base of the family. Psychomyiinae *sensu* Li & Morse (1997) was recovered but not Tinodinae Li & Morse (1997), with *Lype* being placed in a polytomy (in the reduced dataset), or as an isolate clade after *Eoneureclipsis* (in the TOTAL dataset). Analyses of the TOTAL dataset under implied weighting showed *Tinodes* + *Trawaspesyche* + *Padangpsyche* grouped in a clade with the xiphocentronids, this group would place xiphocentronids within Tinodinae, although the clades had very low support values and were not recovered in the REDUCED dataset, or the equal weighting analyses of both datasets. Xiphocentronidae including *Proxiphocentron* is only recovered in the TOTAL dataset under implied weighting in which *Proxiphocentron* is placed at the base of the xiphocentronid clade followed by the Cretaceous genera †*Palerasnitsynus* that present the same reduction in forewing venation as most xiphocentronids, with fork III absent. Therefore, Xiphocentronidae *sensu* Schmid (1982) is only monophyletic when including †*Palerasnitsynus.*

The Xiphocentroninae *sensu* Schmid (1982) were recovered in all analyses as a monophyletic group with high support values (57/96, 72/100; relative bremer/symmetric resampling in TOTAL and REDUCED dataset respectively) (Figures 9B, 10B). The genera *Abaria*, *Drepanocentron*, *Machairocentron*, and *Melanotrichia* were always recovered as monophyletic. *Cnodocentron* as a whole was not recoverd as monophyletic, however each subgenus, *Cnodocentron* (*Caenocentron*) and *Cnodocentron* (*Cnodocentron*), was individually monophyletic. *Xiphocentron* appears or in an unsolved polytomy (equal weighting analyses) or as a paraphyletic group. *Cnodocentron* (*Cnodocentron*), *X*. (*Xiphocentron*) (in part) and *X*. (*Rhamphocentron*) were placed associated with *Melanotrichia* and *Drepanocentron*; while *Cnodocentron* (*Caenocentron*) and *Machairocentron* appeared grouped with all other *Xiphocentron* subgenera (Figures 9, 10, 11, 13). However, most of the clades showing relationship between xiphocentronid groups showed very low support values (Figures 9B, 10B), being supported under implied weighting with few characters (1–2), and under equal weighting the genera relationship appeared totally unsolved (Figures 9A, 10A).

TAXONOMIC CONCLUSIONS

Genus ***Zelandoptila*** Tillyard, **stat. nov.**

Zelandoptila Tillyard, 1924 [Type species: Zelandoptila moselyi Tillyard, 1924]

The resulting topologies corroborate the placement of *Zelandoptila* (2 species, 1 sampled) in the family Ecnomidae, as shown in previous molecular phylogenies (Johanson & Espeland 2010, Frandsen et al. 2016).

The genus was placed within ecnomids and pseudoneureclisids by (Figure 11): larvae with meso and metanotum sclerotized (#20, 21); and the adult median pronotal wart oblong (#59). Nine characters (#50, 61, 62, 64, 76, 88, 119, 133, 168) supported the placement of *Zelandoptila* among the ecnomids, being the character #88, hindwing R_4 and R_5 (fork II) bifurcating very far from the crossvein *r-m* a unique character state change for the clade.

Family **PSYCHOMYIIDAE** Walker

Psychomyiidae Walker, 1852. [Type genus: *Psychomyia* Latreille]

Our phylogenetic results indicate that Psycomyiidae includes Xiphocentronidae. Given this, the new definition of Psycomyiidae can be diagnosed by considering the following synapomorphies (based on the phylogeny with REDUCED dataset and implied weighting, Figure 11):

Larvae: submental sclerites separated (#12), larvae with suture separating fore-trochantin from episternum (#16), shape of trochantin broad (#19) (occurs reversal in xiphocentronids), elongate oviscapte (#37) (occurs reversal in Psychomyiinae). Female: segment X lateral papilla absent (#41). Adult: postoccipital setal wart vestigial or absent (#50), occipital line well distinct (#51). Pronotal setal wart ovoid (#59) (state modified in xiphocentronids), maxillary palpomere II elongate, twice as long as wide (#61), tergum IX well distinct from X (#107) (reversed in *Lype*), inferior appendage 2-segmented (#125) (secondarily fused in many different species)

The characters that traditionally have been used to define the Psychomyiidae hold only the other taxa not including *Eoneureclipsis*, but they are useful, in combination, to identify the family: foretibia apical spur absent (#66), forewing fork I absent (#74), forewing fork IV petiolate (#82), thyridial cell well separated from Ms bifurcation (#84), hindwing discoidal cell absent (#90), hindwing fork I absent (#91), and phallus very slender (#161).

Xiphocentronids within Psychomyiidae

All the results place Xiphocentronidae within Psychomyiidae, with suggestion of relationship of xiphocentronids and *Tinodes* in the TOTAL dataset under implied weighting. To keeps with the Xiphocentronidae at the family level, according to this result at least 3 genera and a subfamily (*Eoneureclipsis*, *Lype*, Psychomyiinae and *Tinodes*) would be elevated to family level, alternatively, a more parsimonious taxonomic change would be lower Xiphocentronidae rank. The not inclusion of taxa like *Eoneureclipsis* and *Proxiphocentron* in previous molecular phylogenies (e.g., Kjer at al. 2016, Malm et al. 2013) might be the reason of the placement of Xiphocentronids as a different family instead as a same group, both taxa show larval and adult intermediate characters between the two families.

The clade *Pandangpsyche, Trawaspsyche, Tinodes,* Xiphocentronids + †*Palerasnitsynus* (Figure 12) is supported by the characters: 1) harpago shorter than coxopodite (#129); 2) inferior appendage basal plate elongate (#134); and 3) the absence of the articulation between the phallus and the sternum IX (#165). The genus *Tinodes* is grouped with the xiphocentronids based on the character: paraproctal process position, closely associate with the phallus (#158), and a broader paraproctal process (#159). Being xiphocentronids and *Tinodes* closely related, possibly the dorsal process of the inferior appendage basal plate of *Tinodes* (phallic guide) is homologous to the ventral part of paraproctal process in *Proxiphocentron.* The molecular phylogeny of Malm et al. (2013) and Frandsen et al. (2016) COI phylogeny also placed xiphocentronids as closer to *Tinodes* (Figure 1E). Although in our results this placement only appeared in the TOTAL dataset analyses and with very low support values. The lack of information about the genera *Pandangpsyche* and *Trawaspsyche* and immatures of *Proxiphocentron* contribute to the uncertainty about this hypothesis of relationship. Nevertheless, all results indicate that xiphocentronids are within Psychomyiidae, therefore the family Xiphocentronidae should be lowered to subfamily level and the previously established subfamilies Xiphocentroninae and Proxiphocentroinae to tribe.

Subfamily **XIPHOCENTRONINAE** Ross **stat. nov.**

Xiphocentronidae Ross 1949 [Type genus: *Xiphocentron* Brauer 1870]

The monophyly of the subfamily including *Proxiphocentron* and †*Palerasnitsynus,* which many characters are unknown, is supported only by the male characters (TOTAL dataset): elongate apodemes on the sternum IX (#108), and by the very elongated phallus (#162). Although, synapomorphic characters of immatures and female are shown in the REDUCED dataset, including 23 characters (Figure 11), those of immature and females are: larvae: submental sclerites absent (#11), trochantin acute (#19), mesopleuron presenting an elongate process (#22), fore leg tibia and tarsus fused (#23), meso and hind legs with tibia and tarsus fused (#24). Pupae: abdominal segment 8 without pre-segmental hook plates (#32). Female: with elongate apodemes on segment IX (#39), and on segment VIII (#40).

†*Palerasnitsynus,* as *Proxiphocentron,* has the rounded mesoscutal setal warts, and the spur formula 2-4-4, but lacks the forewing fork III (#80), a synapomorphy of xiphocentronids other than *Proxihocentro*n. †*Palerasnitsynus* was collected from Lower

Cretaceous (Albian) Burmese amber (Wichard et al. 2011), agreeing with the molecular dating of Malm et al. (2013) that indicated the split of Xiphocentroninae and the other psychomyiids to occur during the early Cretaceous. According to the same molecular dating the radiation, and the emergence of all families of the superfamily Psychomyioidea occurred during the early Cretaceous.

Tribe **PROXIPHOCENTRONINI** Schmid **stat. nov.**

Proxiphocentroninae Schmid 1982 [Type genus: *Proxiphocentron* Schmid 1982]

With only one genus *Proxiphocentron* Schmid, 1982 (5 species, 2 sampled), presenting 5 species from Malaysia, Borneo, Thailand and Northeast India, the subtribe was placed as the first xiphocentronid cladogenesis in all analyses (Figures 9, 11).

The synapomorphies for the tribe Proxiphocentronini are (Figure 12): ocellar wart deltoid (and divided in two) (#48); forewing fork I present (#74); sternum IX with latero-apical margin produced (#115); paraproctal process, dorsal setae/spines present (#156); and phallic parameres present (#167); endothecal spines present (#168).

Proxiphocentron present broad process articulated with the basal plate of inferior appendage, by the phylogenetic placement of the Xiphocentroninae closer to *Tinodes* (Figure 12), this structure may be homologous to the dorsal process of basal plate of *Tinodes*. In some species the dorsal process of basal plate is hook-like but in other (*T. unicolor*, *T. antonioi*, *T. valvatus*, *T. polifurculatus*, e.g.) this process is broad like in *Proxiphocentron*. The immature of *Proxiphocentron* are not known, their description could help to clear the relation between the xiphocentroids and the other Psychomyidae.

Tribe **XIPHOCENTRONINI** Schmid **stat. nov.**

Xiphocentroninae Schmid 1982 [Type genus: *Xiphocentron* Brauer 1870]

The monophyly of Xiphocentronini following the phylogeny of TOTAL dataset under implied weighting (figure 12) is supported by the characters: median pronotal setal wart oblong (#59); maxillary palpomere IV longer than palpomere III (#65); foretibia apical spurs with single spur (#67) (reduced to zero spurs in some *Abaria*); forewing fork V absent (#83); forewing A2 absent (#85) (absent only on *Drepanocentron*, *Abaria*, and *X*. (*Rhamphocentron*)); forewing A2 looped in A1 (#86); wing apex acute (#94).

Tribe †**PALERASNITSYNINI** Wichard, Ross & Ross **stat. nov.**

[Type genus: †*Palerasnitsynus* Wichard, Ross & Ross, 2011]

The genus †*Palerasnitsynus* was placed as sister group of the living Xiphocentronini by 5 characters (#77, 80, 126, 129, 141), being the absence of forewing fork III (#80), a unique character state change.

†*Palerasnitsynus* genitalia has significative differences from the living species, and many typical characters of Xiphocentronini are not accessible in the fossils, the genus is here placed in a different tribe. Synapomorphic characters of the tribe were: maxillary palpomere 3 with stout setae (#63); discoidal cell more than 3 times smaller than the cell between R1 and Rs (#76); forewing thyridial cell not very separated from medial fork (#84); harpago and coxopodite well separated (#125); inferior appendage with sparse spines (#143).

Genus ***Abaria*** Mosely

Abaria Mosely 1948 [Type species: *Abaria tripunctata* Mosely 1948]

The genus *Abaria* (39 species, 3 sampled) is recovered as monophyletic. The monophyly is supported by following synapomorphies on the TOTAL dataset topology (Figure 13): mesoscutal setal wart absent (#53); forewing fork II petiolate (#78); basal plate of inferior appendage, apodeme short (#134).

Abaria has strong wing venation reduction, and fusions and reductions in male genitalia structures, therefore, Schmid (1982) was very uncertain about the relation of *Abaria* and other xiphocentronids. According with our results *Abaria* is placed near the base of the subfamily after *Proxiphocentron* and †*Palerasnitsynus*, lacking much of the synapomorphies of other xiphocentronids (Figure 13) as the membranous dorsum of female segment VIII (#36), the mesopraescutum well delimited (#54), and the elongate finger-like harpago of male genitalia (#131) (Figures 7C-I). *Abaria* has similarities with *Drepanocentron* as the female segment VIII with division between tergum and sternum (#35) that supported the placement of *Drepanocentron* as the first cladogenesis after *Abaria* in the TOTAL datased under implied weigting (Figure 13). Also, the larval trochantin of *Abaria* has an irregular shape with two apical lobes (Fig. 2L) that seems to be present in *Drepanocentron* (Fig. 2K), and the head of both genera does not have strong occipital lines, differing of the strong lines of *Xiphocentron* and *Melanotrichia*.

Genus ***Melanotrichia*** Ulmer

Melanotrichia Ulmer 1906 [Type species: *Melanotrichia singularis* Ulmer 1906]

The genus *Melanotrichia* (30 species, 10 sampled) is recovered as monophyletic. The monophyly based on the phylogeny with TOTAL dataset under implied weighting is supported by following synapomorphies (Figure 13): broad sternum IX apodeme (#109); and the longitudinal keel on preanal appendage (#124).

The fan-shaped mesal sclerite (#152) (Figure 7G) that is characteristic of *Melanotrichia* is not present in all species, being absent in species of the *Melanotrichia singularis* group (Schmid 1982) as well as in some isolated species from Japan and Taiwan (*M. kibuneana*, *M. tanzawaensis*, *M. taiwanensis*) (Figure 7B), these species also present hind leg with 4 spurs in both males and females (#64) a plesiomorphic condition only presented by the Afrotropical *Abaria electa*, and are placed at the base of *Melanotrichia*. *Xiphocentron* species of the Great Antilles (*X. haitiensis* and *X. cubanum*) also present a broad sternum IX apodeme (#109) (Figures 7P, O), and *X. cubanum* shows a vestigial incision on the latero-dorsal margin of the sternum IX (#117) (Figure 7P), although not as deep as occurs in *Melanotrichia* (Figure 7O).

Melanotrichia is placed as the sister group of *C.* (*Cnodocentron*) (Figure 11) in all implied weighting analyses based on: 1) the lateral position of the projections on the apical margin of sternum IX (#114); 2) the incision on the latero-dorsal margin of the sternum IX (#117); and 3) by presenting a mesal process (#146). The mesal process is secondarily lost in *C. brongimarus*, and *M. samaconius*.

Genus ***Drepanocentron*** Schmid

Drepanocentron Schmid 1982 [Type species: *Drepanocentron druhyu* Schmid 1982]

The genus *Drepanocentron* (41 species, 4 sampled) is recovered as monophyletic. The monophyly based on the phylogeny with TOTAL dataset under implied weighting is supported by following synapomorphies (Figure 13): modified spurs (#69); hindwing M bifurcation petiolate in relation to crossvein r-m (#93); sternum IX apodeme broad (#109); base of coxopodite with mesal projection (#135); paraproctal process with lateral spines (#160); phallus with spines (#168).

One of the most distinctive diagnostic characters of *Drepanocentron*, the apical margin of the sternum IX produced in an elongate medial process (Figures 7A, N) (#112) is also present in some *Cnodocentron* and *X*. (*Xiphocentron*) *aureum*, *X*. *asilas* and †*X*. *chiapasi*. Although in these other groups this process is bifid while it is mostly entire in *Drepanocentron*. The phallus has an abundant membranous endotheca with spines (#168), absent in all Xiphocentroninae except *Proxiphocentron* (Figure 8K).

Two different hypotheses of placement of *Drepanocentron* are presented: 1) placed within a clade with *Xiphocentron* (*Xiphocentron*) and *X*. (*Rhamphocentron*) (Figure 11) or 2) in a cladogenesis right after *Abaria* (Figure 13). *Drepanocentron* do not present syncleritous female segment VIII as *Abaria*, supporting the cladogenesis right after *Abaria*. Alternatively, *Drepanocentron* shares modified spurs (#69) with *Xiphocentron* (*Xiphocentron*) and *X*. (*Rhamphocentron*) and forewing veination reduction with *X*. (*Rhamphocentron*) (#85).

Genus ***Machairocentron*** Schmid

Machairocentron Schmid 1982 [Type species: *Machairocentron lucumon* Schmid 1982]

The genus *Machairocentron* (6 species, 4 sampled) is recovered as monophyletic. The monophyly based on the phylogeny with TOTAL dataset under implied weighting is supported by following synapomorphies (Figure 13): sternum ix apical margin smooth without incisions (#113); inferior appendage 2-segmented (#125); harpago base with broad mesal sclerotized\spinous region (#144); harpago with lateral sclerotized region (#145); harpago mesal projection lobular (#148); paraproctal process with vestigial dorsal process with setae (#156).

Under implied weighting *Machairocentron* was placed among the Neotropical *Xiphocentron* that also have sclerotized plate on sternum V. In the reduced dataset *Machairocentron* was placed with *Xiphocentron* species with lower density of spines on inferior appendage (#143) and with mesal sclerite having shorter spines (#150). In the total dataset some of the species in this group (*X. maite* and *X. mnesteus*) moved to other clades and the synapomorphy holding the species was the coxopodite without setae or setae vestiges (#139).

Genus ***Cnodocentron*** Schmid

Cnodocentron Schmid 1982 [Type species: *Cnodocentron girika* Schmid 1982]

The genus *Cnodocentron* (13 species, 9 sampled) was not recovered as monophyletic in any analyses. But each subgenera *C.* (*Cnodocentron*) and *C.* (*Caenocentron*) were individually monophyletic. As the clades where each subgenus was placed had very low to no support, further evidences would be necessary for conclusive changes on the group taxonomy, and so, the definition of Schmid (1982) is maintained.

C. (*Cnodocentron*) subgenus is recovered as monophyletic based on the characters (TOTAL dataset, implied weighting) (Figure 13): preanal appendage slender (#120); harpago and coxopodite separated (#125); coxopodite produced posterad (#137).

C. (*Caenocentron*) subgenus is recovered as monophyletic based on the characters (Figure 13): preanal appendage slender (#120); coxopodite with basomesal projection (#135); paraproctal process bearing lateral spines (#160).

The *C.* (*Cnodocentron*) subgenus was placed as sister group of *Melanotrichia* in all implied weighting analyses. As *Melanotrichia* they do not have the reticulate plates of sternum V, that are present in all Neotropical *C.* (*Caenocentron*) subgenus. Some *C.* (*Cnodocentron*) (*C. vrisaparvan*, and *C. girika*) present the incision near the preanal appendage (#117) that is common to *Melanotrichia,* but they do not have the preanal appendage keel. Oriental and Neotropical *Cnodocentron* are traditionally recognized as a group by the coxopodite produced posterad (#137) (Figure 7I), and the spines and projections on the apical margin of sternum IX, although these structures seem to be not homologous in the two subgenera. In the Neotropical *C.* (*Caenocentron*) subgenus instead of the sternum IX projections, brushes of long setae arise actually from a basal lobe of coxopodite (Figure 7I). In the Oriental *C.* (*Cnodocentron*) subgenus large spines are present and fused to the sternum margin, the connection with the coxopodite is not clear as in *C.* (*Caenocentron*), and so, according with our result these structures are not homologous.

Genus ***Xiphocentron*** Brauer

Xiphocentron Brauer 1870 [Type species: *Xiphocentron bilimeki* 1870]

Xiphocentron (51 species, 33 sampled) monophyly was not recovered in any analyses. The results under equal weights recovered the genus in an unsolved polytomy.

The results under implied weighting add some resolution placing the genus as paraphyletic, although, all the clades had very low to none support. Therefore, more evidences including broader sampling and additional characters would be necessary for conclusive decisions and no taxonomic changes are proposed, maintaining previous Schmid (1982) taxonomic definition.

Nevertheless, the phylogeny gave some suggestions about the subgenera relationships: The *X.* (*Ramphocentron*) subgenus and *X.* (*Xiphocentron*) *aureum*, *X.* (*Xiphocentron*) *asilas* do not have the reticulate plate on sternum V (#71) and were not grouped with the other Neotropical species (Figure 13). The species *X.* (*Xiphocentron*) *tarquon* and *X.* (*X.*) *polemon* have the sternum V plates and possibly do not belong to this subgenus and were grouped with *X.* (*Glyphocenron*) *euryale,* both having coxopodite setose region (#139), sternum apex straight without any projection (#113), and elongate spines on harpago (#142). About the *X.* (*Antillotrichia*) from Meso-America, most of them as the *X.* (*Sphagocentron*) subgenus have elongate spine-like setae on the harpago, and do not present the polyp-like mesal sclerite, but just spine-like setae (#147). Also, *X. boriquensis*, *X.* (*S.*) *evandrus* and *X. fuscum* have all the same preanal appendage shape (#123). Therefore, these species within the clade weld by the character #147 are suggested to be *X.* (*Sphagocentron*) instead. According to the implied weighting results these Meso-American and Antillean *X.* (*Antillotrichia*) species with long spine-like setae and without a mesal sclerite are related.

BIOGEOGRAPHIC IMPLICATIONS

The Psychomyiidae are very abundant in the Oriental region where all the genera occur, *Lype*, the Psychomyiinae and *Tinodes* reach a wide distribution in all Old-World regions, with some few species also occurring on the Nearctic region (Table 1), and *Tinodes* even presenting Australasian species. However, all these groups are completely absent in the Neotropics.

The Xiphocentroninae on the other hand are the only Psychomyiidae with Neotropical representatives, occurring throughout the tropical regions of the world. But, contrary to the other Psychomyiidae, the subfamily is absent in the West Palearctic and other temperate regions (Figure 14). According to the antiquity of †*Palerasnitsynus* and the molecular dating of Malm et al. 2013; the group was present at least since the early Cretaceous. The phylogenetic hypothesis presented in the REDUCED dataset (Figure 11), shows a cladogenesis event of *Abaria* followed by the radiation of all other

Xiphocentronini, which are placed in two clades: 1) one including most Neotropical species of *Xiphocentron*, as well as *Cnodocentron* (*Caenocentron*) and *Machaircentron* and; 2) a clade including Oriental genera and subgenera and the Nearctic and Neotropical subgenera *X.* (*Xiphocentron*) and *X.* (*Ramphocentron*) subgenera. This topology suggests a vicariant origin of the Neotropical species from a widespread pantropical ancestor. The non-monophyly of *Xiphocentron* therefore would indicate that other genera differentiated from a *Xiphocentron*-like ancestor that posteriorly differentiate into the present genera.

Alternatively, according with phylogenetic hypothesis of the TOTAL dataset (Figure 13), the Oriental *Drepanocentron* is placed right after *Abaria*, as sister group of the Nearctic distributed *Xiphocentron* (*Rhamphocentron)* followed by the radiation of a Neotropical species clades and an Oriental and Nearctic species clade. The *Xiphocentron* subgenera with Nearctic species (*X.* (*Rhamphocentron*), *X.* (*Xiphocentron*)) were always grouped with Oriental *Melanotrichia* and *Cnodocentron*, differing from the clade with other New World species by the absence of sternum V reticulate plate (#71). The only *Xiphocentron* fossil, *Xiphocentron* (*Xiphocentron*) *chiapasi*, from middle Miocene Mexican amber (Wichard et al. 2006) also belongs to these Oriental related *Xiphocentron* subgenera. By the *Drepanocentron* current distribution restrict to the Oriental region the topology of the TOTAL dataset (Figure 13) supports a cladogenesis event between Oriental and Nearctic species, with the new world species entering the New World through the Nearctic (Figure 11).

The caddisfly fauna from Nearctic and East Palearctic has one of the highest similarities (in terms of shared genera and subgenera), only surpassed by the similarities between Oriental and East Palearctic, and West and East Palearctic caddisfly faunas (de Moor & Ivanov 2008). This support that caddisflies were able to disperse between Asia and North America. A dispersion through the Beringia land bridge was the hypothesis proposed for Schmid (1982) for the xiphocentronids based on the diversity of Oriental genera and the many plesiomorphic features of the Oriental genus *Proxiphocentron*. During the early Palaeogene a warm climate occurred on high-latitudes (Paleocene–Eocene Thermal Maximum) and the presence of land bridges connecting Eurasia and North America turn possible the dispersion of thermophilic species as the Xiphocentroninae across the Holarctic (Brikiatis 2014; Brunk et al. 2017).

Curiously, the genera *Proxiphocentron*, *Drepanocentron* and *Abaria* are present in islands of Indonesia, Borneo and Philippines with *Abaria* even occurring in New Guinea, however, the genus *Melanotrichia* that is very diverse on the continental Asia is absent on these islands (Figure 14). This suggest that *Proxiphocentron*, *Drepanocentron* and *Abaria* were present on the Southeast Asia before than *Melanotrichia* and so, they could disperse between these islands during the Pleistocene glacial periods, when the sea level were low and there were connectivity among Borneo, Java, and Sumatra to the Malay Peninsula and mainland Asia (Hanebuth et al. 2000). This support our results with *Melanotrichia* and *C.* (*Caenocentron*) clades originating from a New World ancestor (Figure 13), with a subsequent dispersal and radiation in the Oriental region.

CONCLUSIONS

The present morphology-based study is the first to hypothesize phylogenetic relationships among xiphocentronid caddisflies. As a result of this study, the hypothesis brought by Edwards (1961) about xiphocentroid taxa being a Psychomyiidae was corroborated under the current available evidences. Therefore, Xiphocentonidae was lowered to subfamily level, with †*Palerasnitsynus* also included in this subfamily. Additionally, the genus *Zelandoptila* is transferred to Ecnomidae. This study also improves the previous Psychomyiidae morphological phylogeny of Li & Morse (1997) increasing the number of characters and analyzed species, and provide the first evolutionary hypothesis for the Xiphocentroninae genera and subgenera. The understanding of phylogenetic relationships within Psychomyiidae, although, still with important gaps as the morphology of immature stages for important taxa remain unknown (i.e., *Kambaitipsyche, Proxiphocentron, Trawaspsyche*, *Padangsyche*). About the Xiphocentroninae, the monophyly of *Machairocentron, Drepanocentron, Abaria*, *Melanotrichia* and the subgenera *C.* (*Cnodocentron*) and *C.* (*Caenocentron*) were supported. *Xiphocentron* and *Cnodocentron* were suggested to be paraphyletic groups, the low support of their topology indicate that further evidences are necessary for a conclusive understanding of the relationship of the species within these genera. Future studies aimed at obtaining this knowledge will only improve our phylogenetic estimates. Nevertheless, this study is a positive contribution towards the evolutionary relationships of psychomyiids caddisflies and their relatives rooted in cladistic principles.

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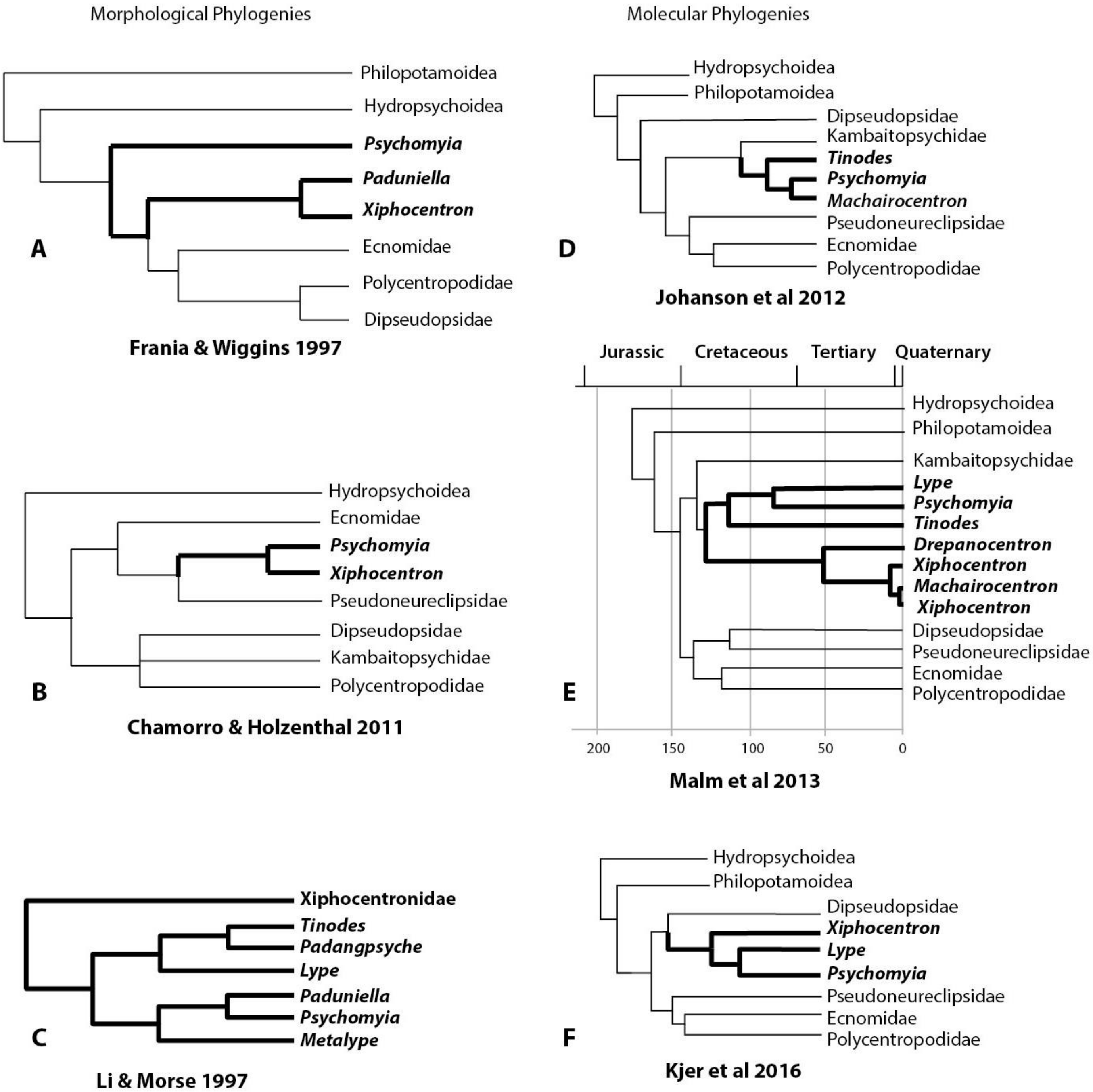

Figure 1. High-level phylogenetic relationships proposed for the Psychomyiioidea, showing the placement of Xiphocentronidae and Psychomyiidae taxa.

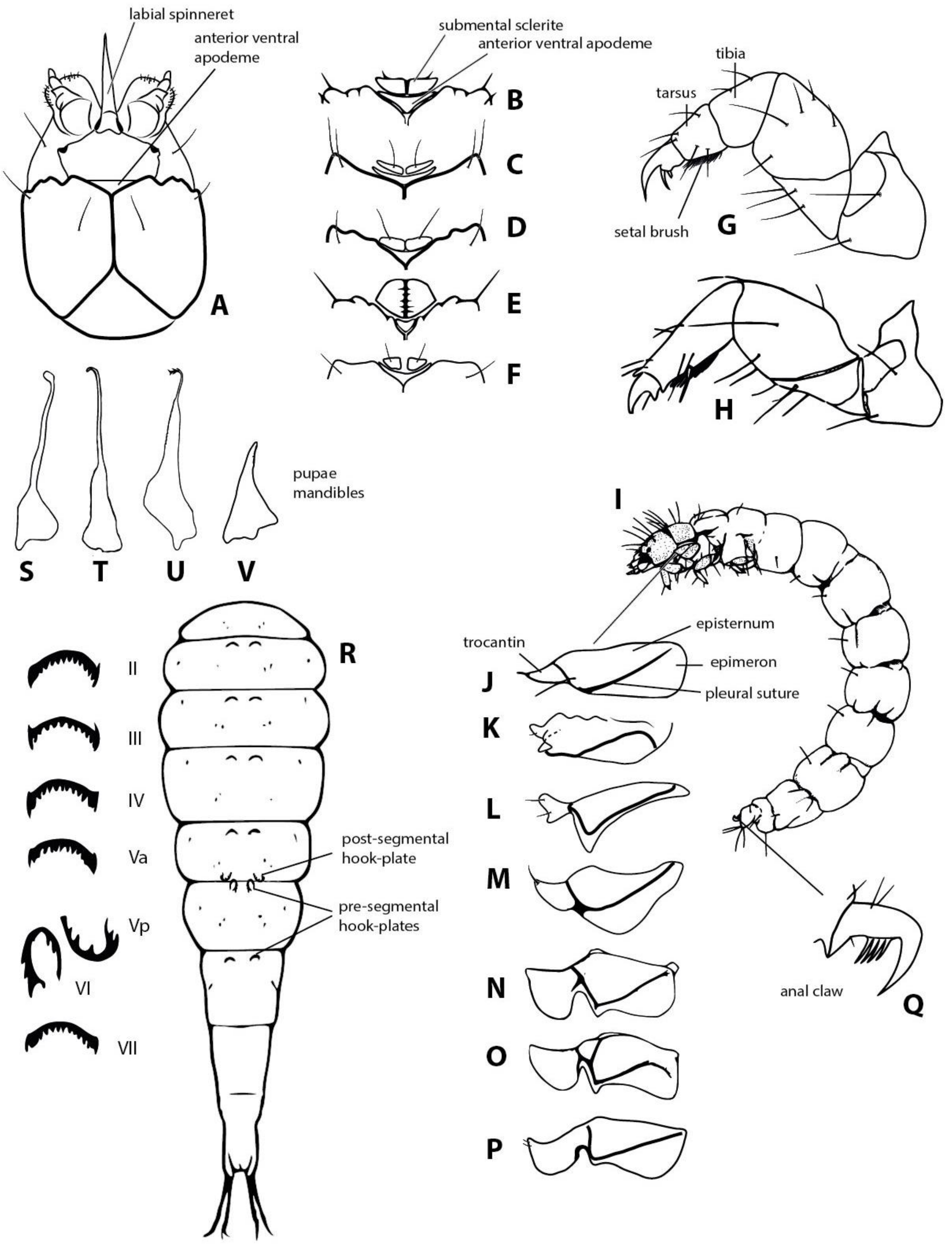

Figure 2. Immatures of Psychomyiidae and Xiphocentronidae. A-Q larvae structures: A. *Drepanocentron* sp. head, ventral (after Genco et al. 2018); B-F submental sclerites: B. *Tinodes* sp. (after Merrit et al. 2008), C. *Eoneureclipsis* sp. (after Torii & Nakamura 2016), D. *Metalype* sp. (after Tachet et al. 2018), E. *Psychomyia* sp. (after Merrit et al. 2008), F. *Paduniella neartica* (after Mathis & Bowles 1994); G. foreleg of *Metalype uncatissima* (after Tachet et al. 2018); H. foreleg of *Xiphocentron haitiensis* (after Flint 1964); I. larvae of *Machairocentron* (after Pes et al. 2005); J. trochantin of *Xiphocentron haitiensis* (after Flint 1964), K. trochantin of *Drepanocentron* sp. (after Genco et al. 2018), L. trochantin of *Abaria electa* (after Marlier. 1960), M. trochantin of *Menalotrichia serica* (after Barnard & Dudgeon 1984), N. trochantin of *Lype* sp., O. trochantin of *Tinodes* sp. P. trochantin of *Eoneureclipsis montanus* (after Torii & Nakamura 2016); Q. anal claw of *Psychomyia* sp. with comb of inner spines (after Merrit et al. 2008); R-V pupae structures: R. dorsal view of abdomen of *Xiphoceniron* sp. pupae with details of hook plates (after Merrit et al. 2008); S-V pupal mandible: S. *Abaria electa* (after Marlier. 1960), T. *Tinodes*, U. *Paduniela neartica* (after Mathis & Bowles 1994), V. *Machairocentron falciforme* (after Pes et al. 2013).

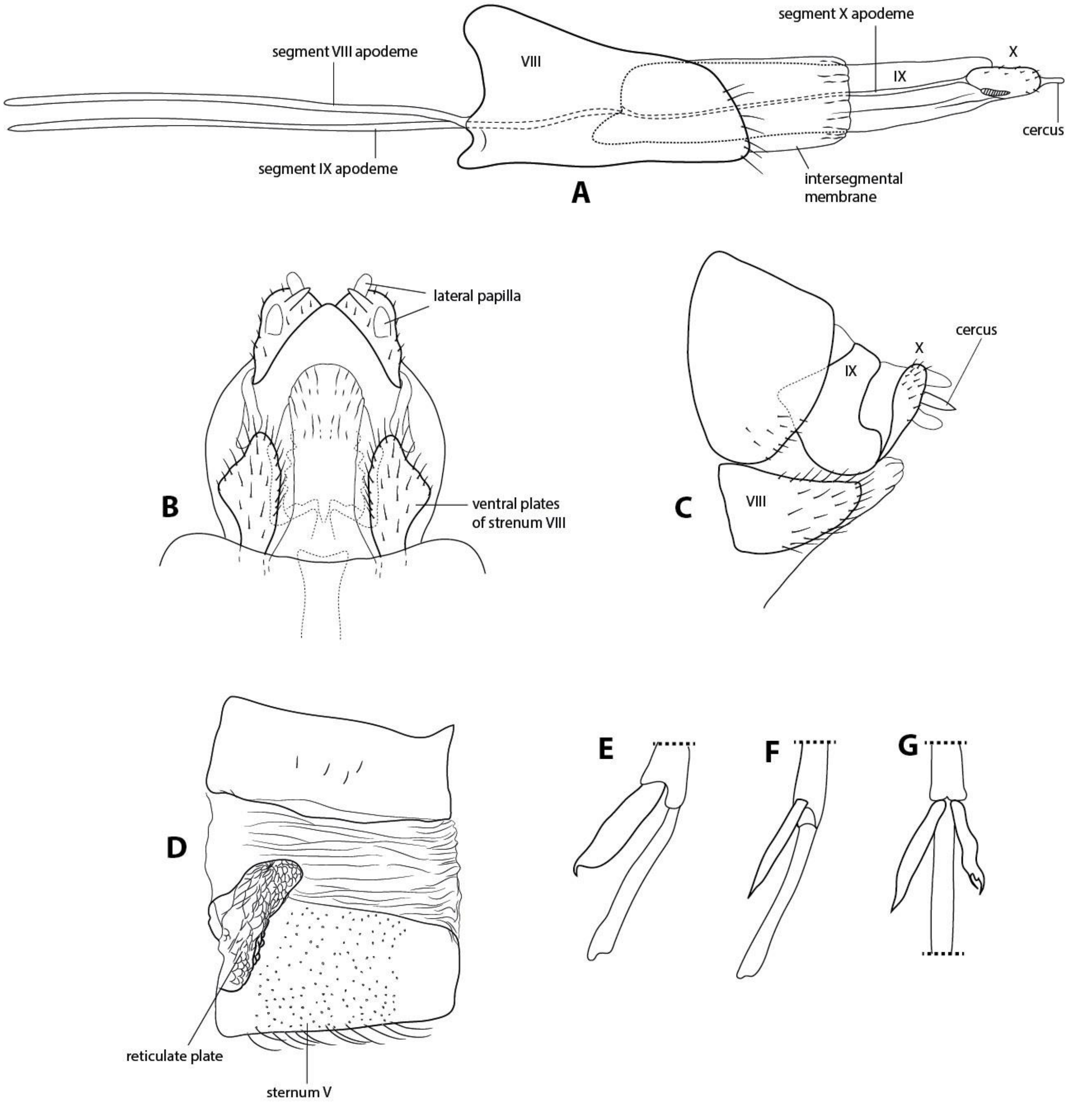

Figure 3. Female genitalia, abdomen and tibial spurs. A-C. female genitalia: A. *Machairocentron* sp., lateral; B. *Pseudoneureclipsis* sp., ventral, C. *Pseudoneureclipsis* sp., lateral (after Schmid 1980); D. reticulate plate at sternum V of *Machairocentron* sp.; E-G. hind leg apical spurs: E. modified spur of *Drepanocentron vang*, F. spur of *Machairocentron* sp., G. spurs of *Metalype uncatissima* (after Qiu et al. 2017).

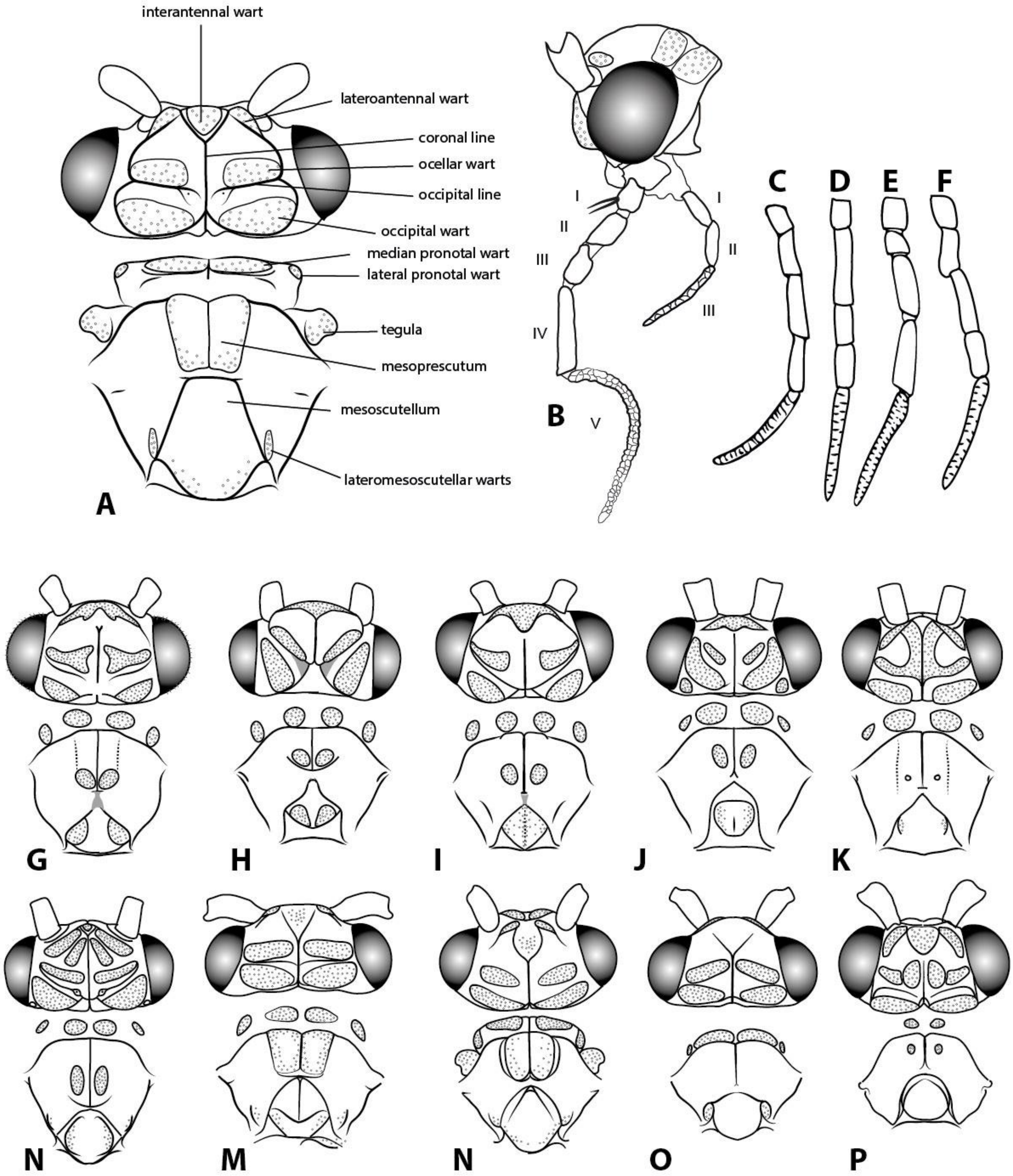

Figure 4. Head, palp and thorax of psychomyioidea species. A. head, proscutum, and mesoscutum of *Melanotrichia attia*, dorsal; B. same lateral, showing labial and maxylary palps; C-F maxilary palps: C. *Eoneureclipsis montanus*; D. *Lype diversa*; E. *Proxiphocentron prathamajam*; F. *Tinodes ragu*; G-P setal warts: G. *Psychomyia chompu*; H. *Tinodes waeneri*; I. *Lype diversa*; J. *Phylocentropus harrisi*; K. *Pseudoneureclipsis hai*; L. *Ecnomus tenellus*; M. *Xiphocentron* sp.; N. *Drepanocentron tamdaona*; O. *Abaria damgiaca*; P. *Proxiphocentron prathamajam.*

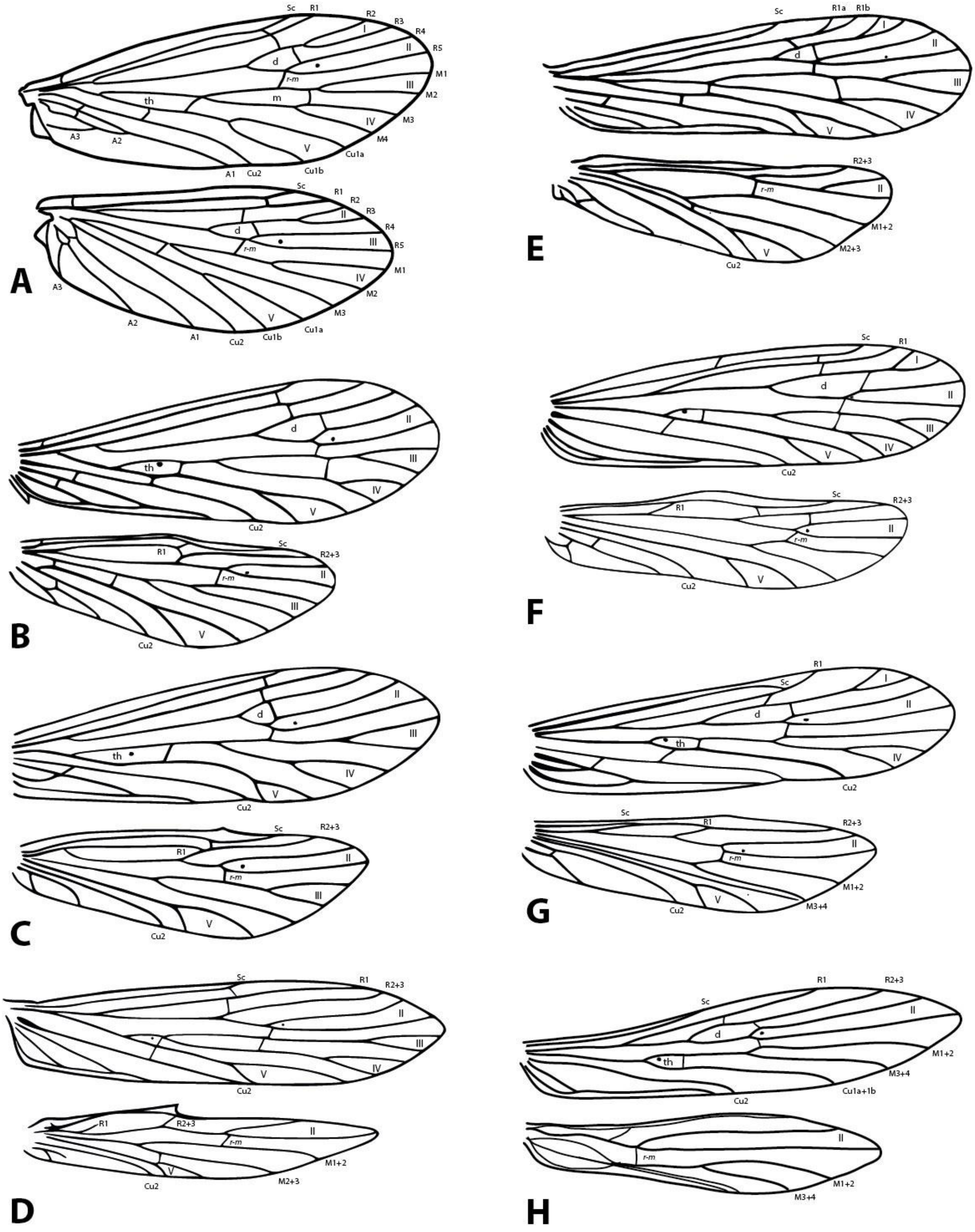

Figure 5. Wing venation of Psychomyioidea species. A. *Eoneureclipsis montanus*; B. *Tinodes provo* (after Schmid 1980); C. *Psychomyia schefterae*; D. *Paduniella communis*; E. *Ecnomus tenellus*; F. *Proxiphocentron prathamajam*; G. *Xiphocentron* (*Xiphocentron*) *aureum*; H. *Drepanocentron birghu*.

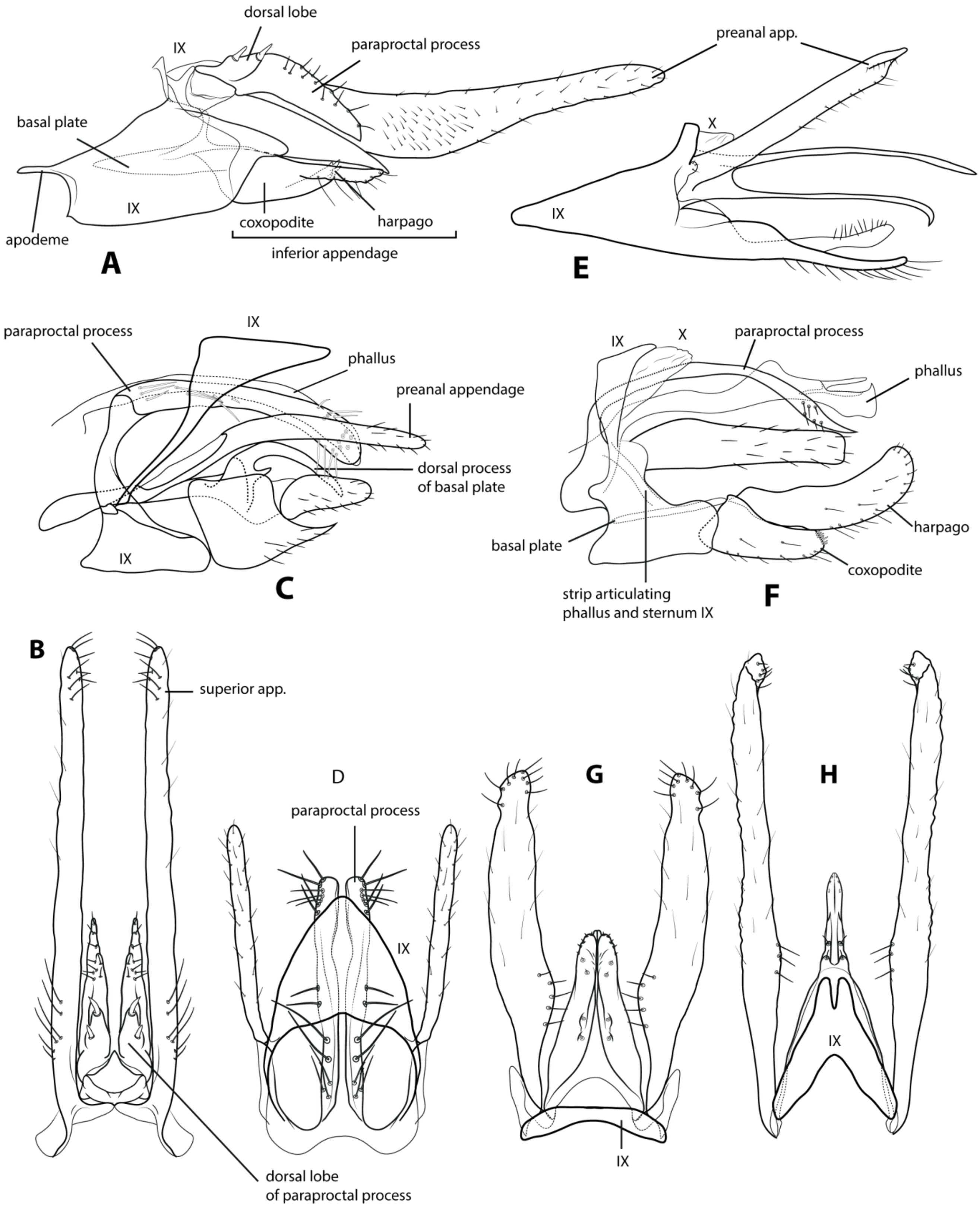

Figure 6. Male genitalia of Psychomyioidea taxa. A-B *Proxiphocentron arjinae:* A. lateral, B. dorsal. C-D *Tinodes consueta:* C. lateral, D. dorsal. E. *Zelandoptila yuccabina*, lateral. F. *Eoneureclipsis acrichalakchmi*, lateral (after Schmid 1972). G. *Xiphocentron* (*Xiphocentron*) *aureum*, dorsal. H. *Machairocentron ascanius*, dorsal.

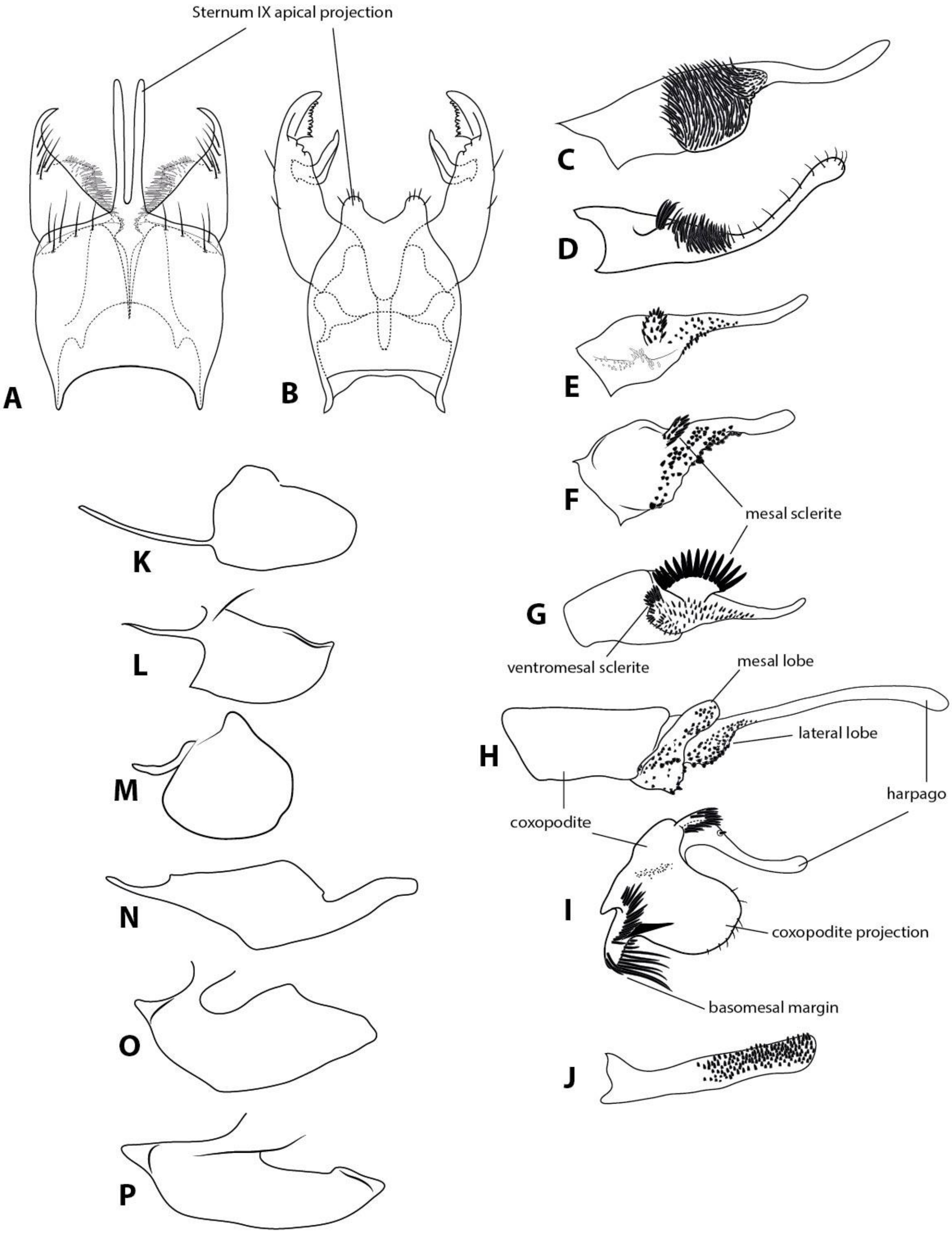

Figure 7. Xiphocentronidae male genitalia. Ventral view A. *Cnodocentron* (*Caenocentron*) n.sp. aff *yavapai* B. *Melanotruchia forficula*. C-J inferior appendage lateral: C. *Xiphocentron* (*Xiphocentron*) *aureum*, D. *X*. (*Sphagocentron*) evandrus, E. *X*. (*Rhamphocentron*) *numanus*, F. *X*. (*Antillotrichia*) *steffeni*, G. *Melanotrichia pachupati*, H. *Machairocentron ascanius*, I. *Cnodocentron* (*Caenocentron*) *pallas*, J. *Abaria achwatirtha*. K-P sternum IX, lateral: K. *Abaria achwatirtha*, L. *X*. (*Rhamphocentron*) *numanus*, M. *Cnodocentron* (*Caenocentron*) *pallas*, N. *Drepanocentron vang*, O. *Melanotrichia forficula*, P. *X*. (*Antillotrichia*) *cubanum*.

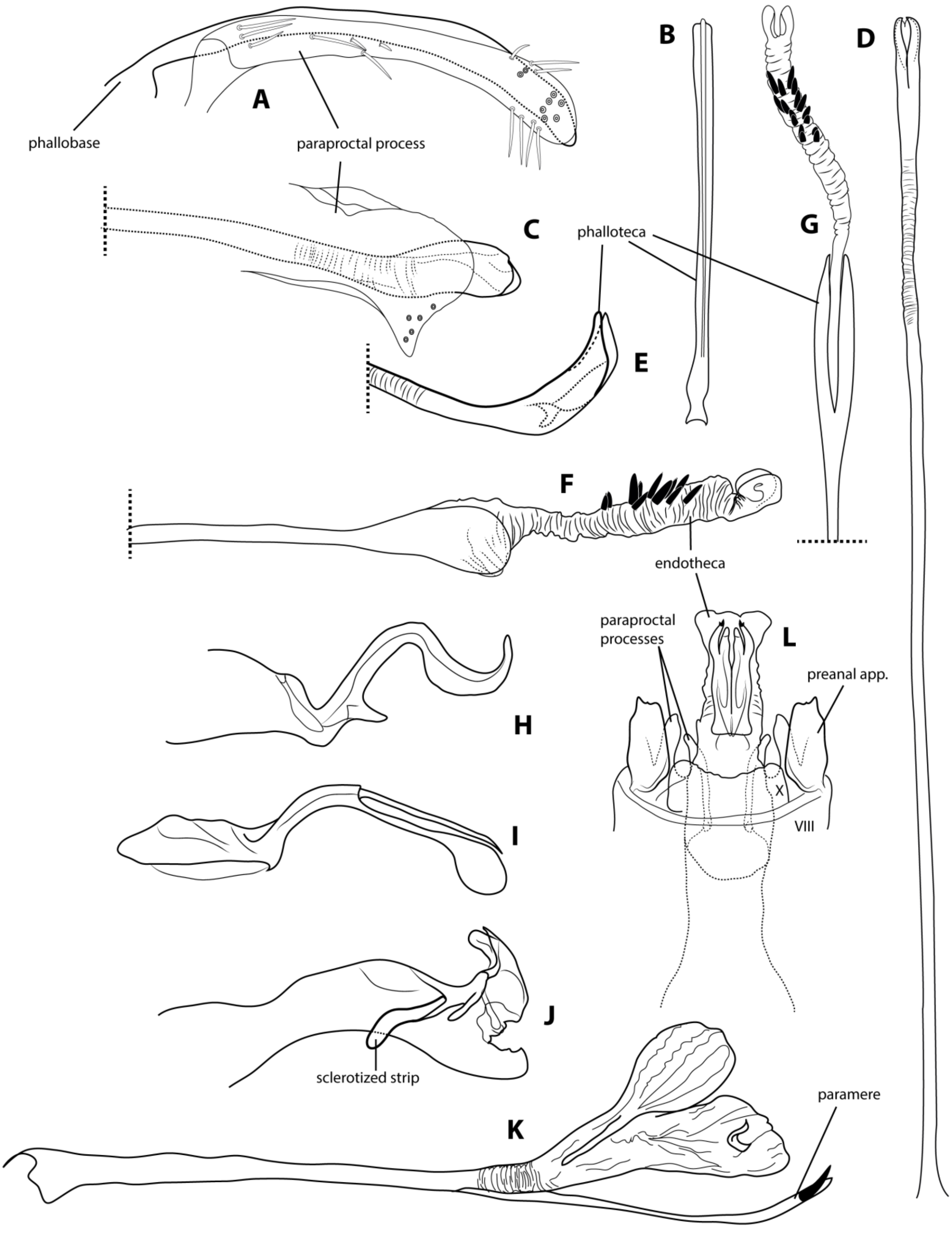

Figure 8. Phallus of Psychomyioidea taxa. *Tinodes consueta*: A. lateral, showing placement between each paraproctal process; B. dorsal. *X*. (*Antillotrichia*) *steffeni*: C. lateral, showing paraproctal process; D. dorsal in full length. E. *Melanotrichia forficula*, lateral. *Drepanocentro vang*: F. lateral, G. dorsal. H. *Psychomyia amphiaraos*, lateral. I. *Paduniella koehleri*, lateral. J. *Lype auripis*, lateral. K. *Proxiphocentron arjinae*, lateral. L. Male genitalia of *Pseudoneureclipsis hai*, dorsal.

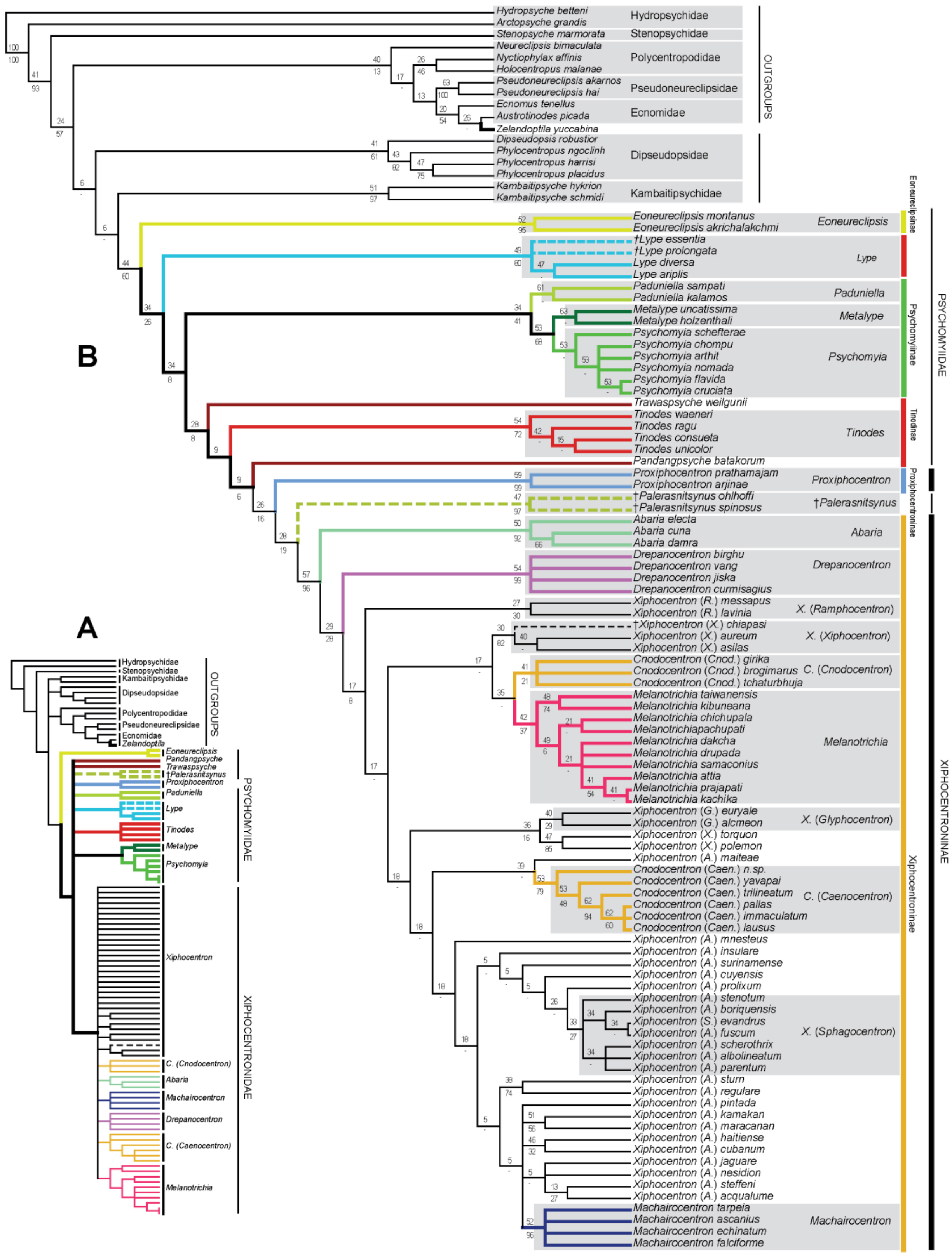

Figure 9. Phylogeny of Psychomyiidae, Xiphocentronidae and related taxa obtained from the TOTAL dataset (106 species, 168 characters). A. strict consensus of 269 most parsimonious topologies under equal weighting analyses. B. strict consensus of the 9 most parsimonious topologies under implied weighting analyses (adjusted K=14,785). Genera and subgenera clades are highlighted. Values displayed above branches correspond to Relative Bremer support and below branches to Symmetric Resampling support.

Figure 10. Phylogeny of Psychomyiidae, Xiphocentronidae and related taxa obtained from the REDUCED dataset (95 species, 168 characters). A. strict consensus of 820 most parsimonious topologies under equal weighting analyses. B. strict consensus of the 90 most parsimonious topologies under implied weighting analyses (adjusted K=13,828). Genera and subgenera clades are highlighted. Values displayed above branches correspond to Relative Bremer support and below branches to Symmetric Resampling support.

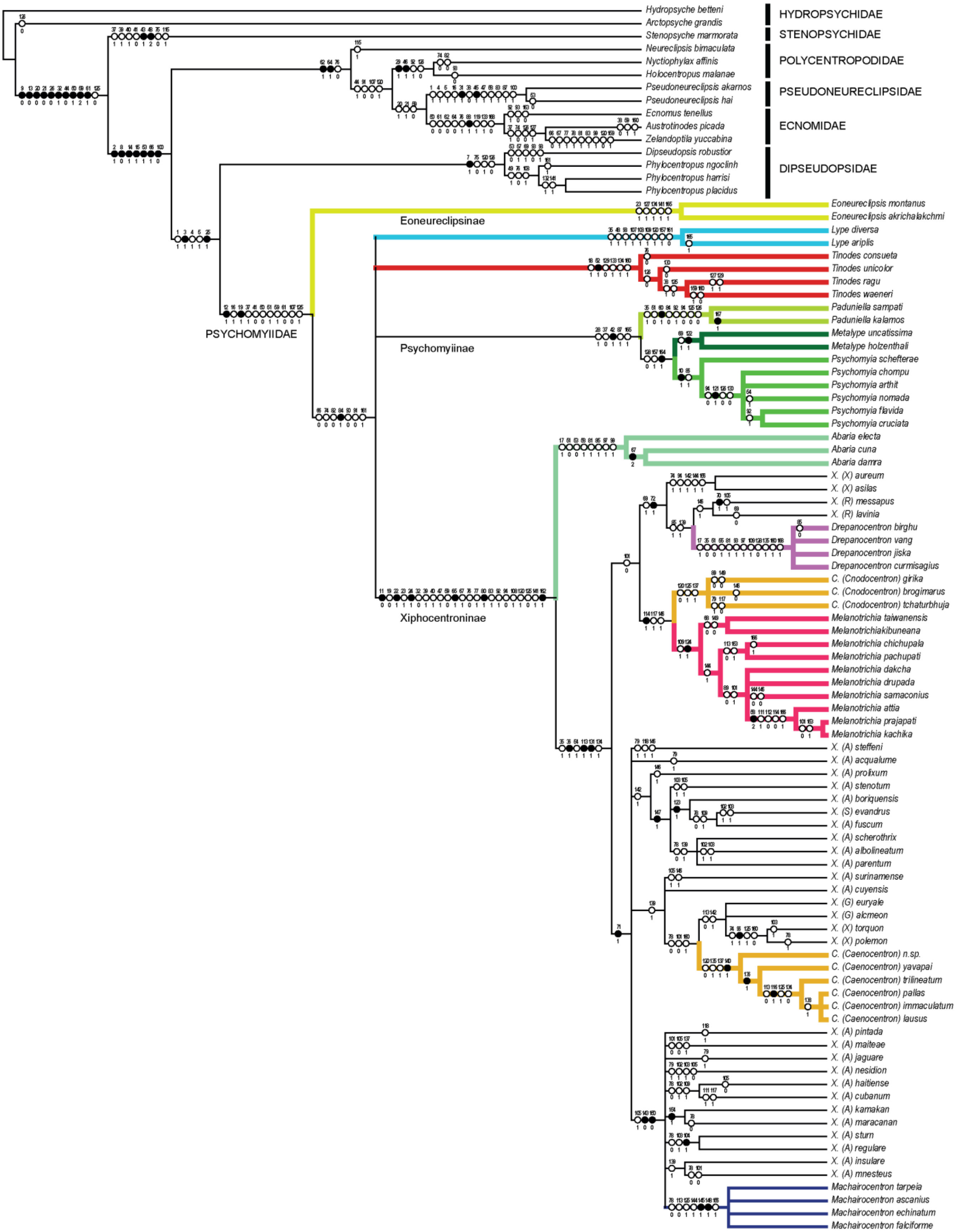

Figure 11. Phylogenetic relationships of Psychomyiidae and related taxa, implied weighting, REDUCED dataset (adjust K=13.828). Strict consensus of 90 trees, character state transformations are presented along each branch.

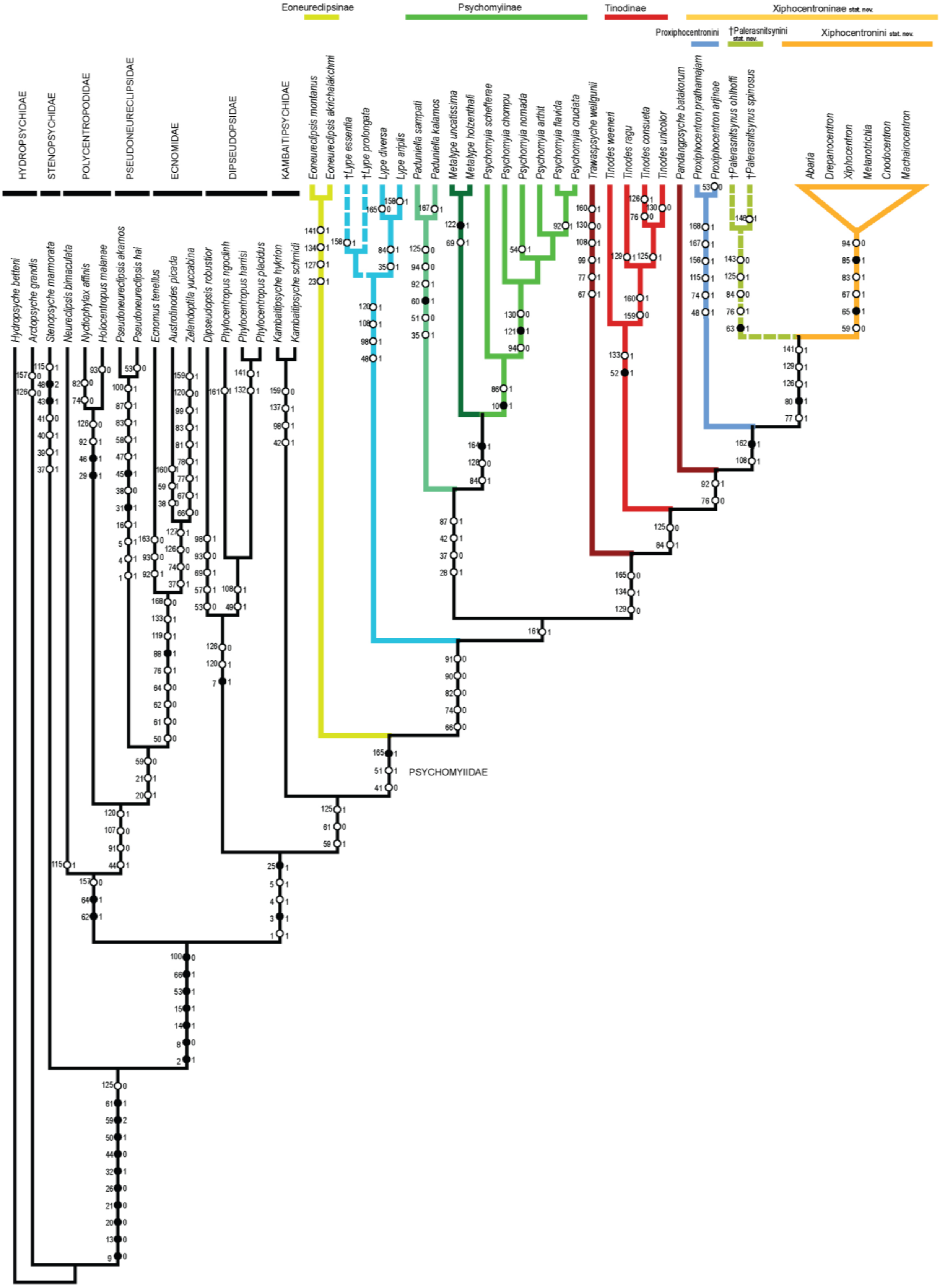

Figure 12. Phylogenetic relationships of Psychomyiidae, implied weighting, TOTAL dataset (adjust K=14.785). Strict consensus of 9 trees, character state transformations are presented along each branch.

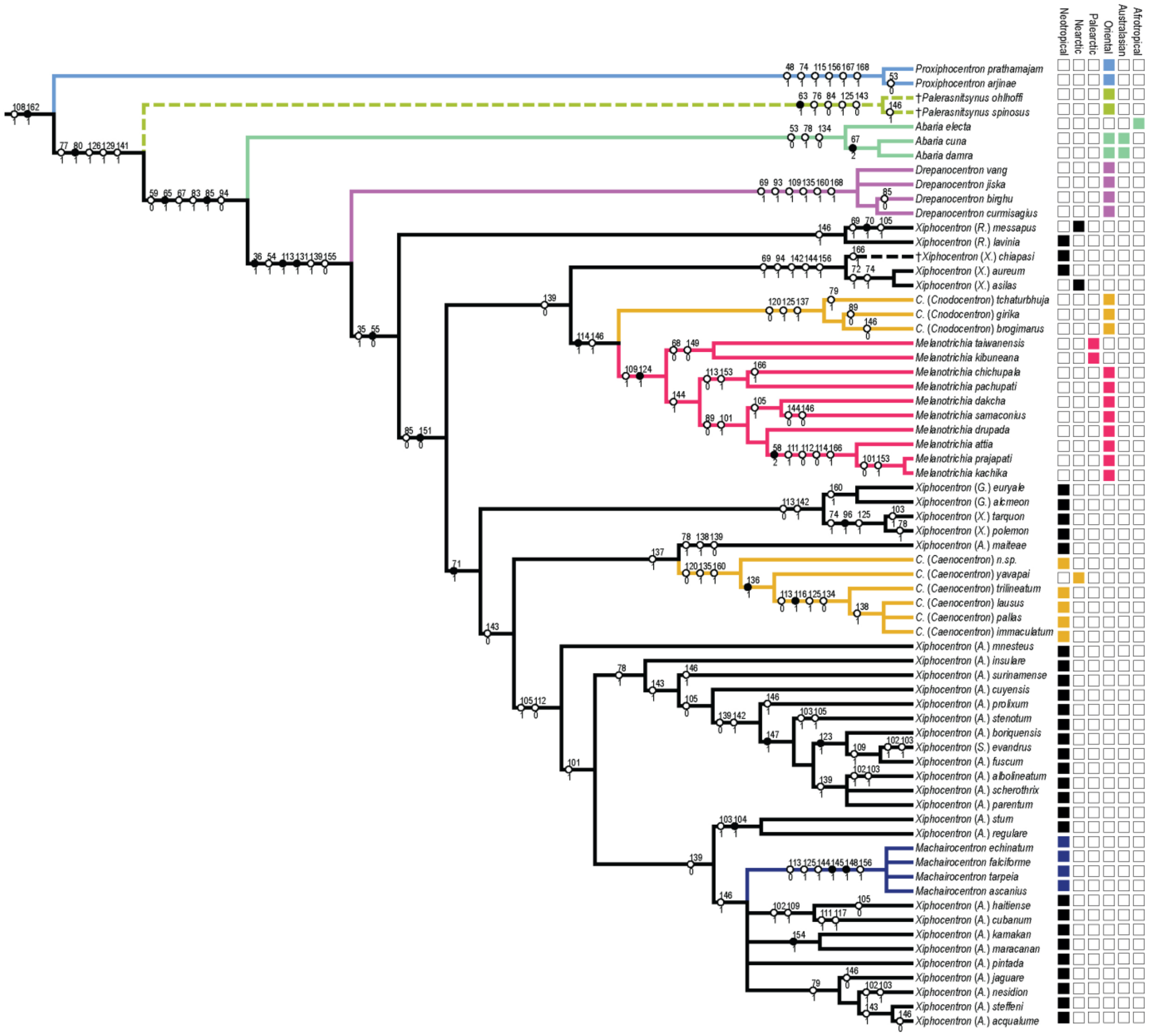

Figure 13. Phylogenetic relationships of Xiphocentroninae, implied weighting, TOTAL dataset (adjusted K=14,785). Consensus strict of 9 trees, character state transformations are presented along each branch. Species biogeographic distribution is presented in front of each species. Biogeographical regions according to Morse (2019).

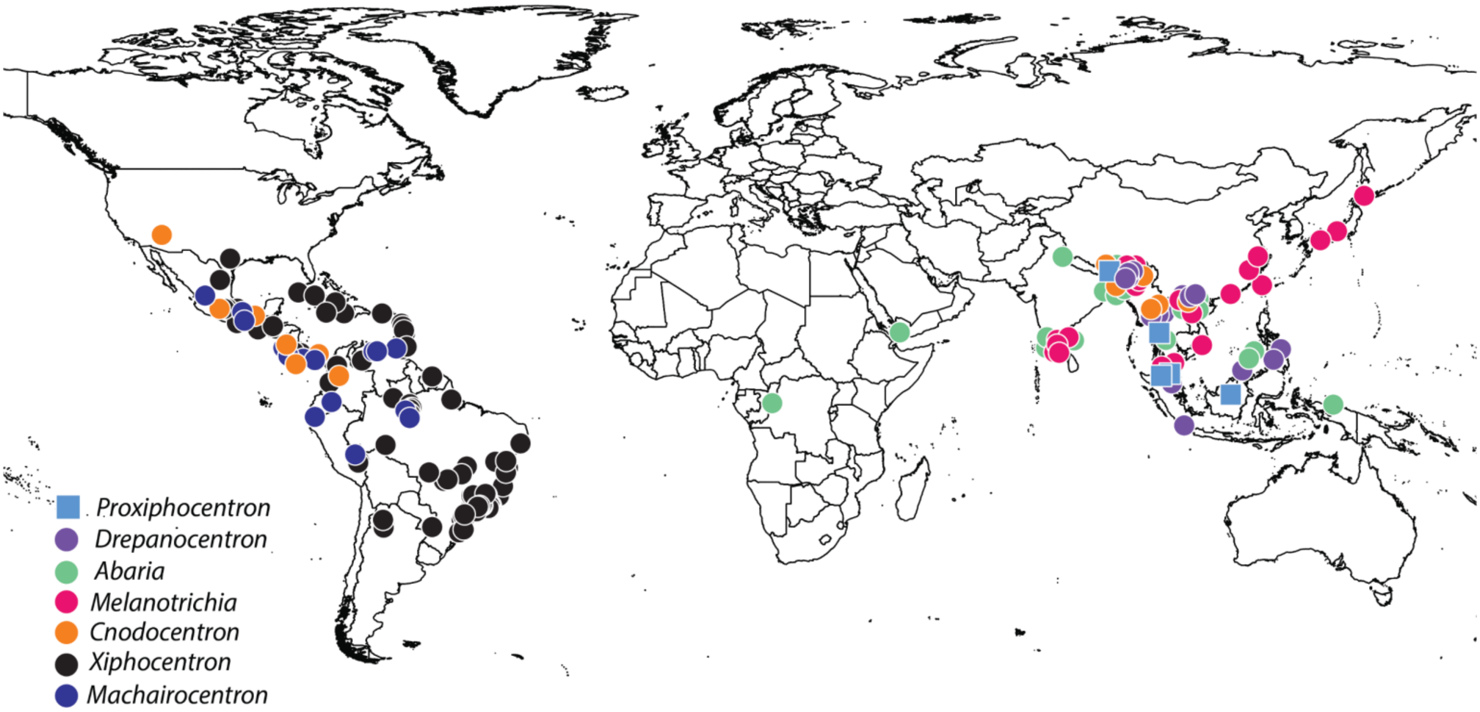

Figure 14. World distribution of Xiphocentroninae genera. Including data from new species presented in this dissertation.

Table 4. Data matrix utilized in the phylogenetics analyses.

Species \ Characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**
Hydropsyche betteni	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	-	0	-	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Arctopsyche grandis	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	-	0	-	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Stenopsyche marmorata	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0
Neureclipsis bimaculata	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Nyctiophylax affinis	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0
Holocentropus malanae	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0
Ecnomus tenellus	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	-	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0
Austrotinodes picada	?	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	-	0	1	1	0	0	0	0	0	1	1	0	?	?	?	?	?	0	0	1	0	1	1	1	0
Zelandoptila yuccabina	?	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	-	0	1	1	0	0	0	0	0	1	1	0	?	?	?	?	?	?	?	1	1	-	-	1	0
Pseudoneureclipsis akarnos	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0
Pseudoneureclipsis hai	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0
Phylocentropus harrisi	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Phylocentropus placidus	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Phylocentropus ngoclinh	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Dipseudopsis robustior	1	1	1	1	1	0	1	0	0	0	1	-	0	1	1	0	0	-	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Kambaitipsyche hykrion	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0	-	1	0	0	1	1
Kambaitipsyche schmidi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0	-	1	0	0	1	1
Psychomyia flavida	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Psychomyia cruciata	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Psychomyia chompu	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Psychomyia arthit	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Psychomyia nomada	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Psychomyia schefterae	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Metalype uncatissima	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Metalype holzenthali	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1
Paduniella sampati	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1
Paduniella kalamos	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1
Euneureclipsis montanus	?	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	?	?	?	?	?	0	0	1	0	0	0	0	0
Euneureclipsis akrichalakchmi	?	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	?	?	?	?	?	0	0	1	0	0	0	0	0
Pandangpsyche batakorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trawaspsyche weilgunii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lype diversa	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	1	0	1	0	0	0	0	0
Lype ariplis	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	1	0	1	0	0	0	0	0
†Lype essentia	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	0	0	1	0	0	0	0	0
†Lype prolongata	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	-	0	1	0	0	0	0	0
Tinodes consueta	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0
Tinodes unicolor	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0
Tinodes ragu	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0
Tinodes waeneri	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0
Prox. prathamajam	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	0
Prox. arjinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	0

Table 4. Continued

Species \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Abaria cuna	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0
Abaria damra	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0
Abaria electa	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0
Drepanocentron birghu	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	?	?	?	?	1	0	1	1	0	1	1	0	0
Drepanocentron vang	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	?	?	?	?	1	0	1	1	0	1	1	0	0
Drepanocentron jiska	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	?	?	?	?	1	0	1	1	0	1	1	0	0
Drepanocentron curmisagius	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	?	?	?	?	1	0	1	1	0	1	1	0	0
Machairocentron tarpeia	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Machairocentron ascanius	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Machairocentron echinatum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Machairocentron falciforme	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Cnod.) girika	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Cnod.) brogimarus	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Cnod.) tchaturbhuja	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) yavapai	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) n. sp.	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) pallas	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) immaculatum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) lausus	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Cnod. (Caen.) trilineatum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia chichupala	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia dakcha	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia drupada	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia prajapati	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia kachika	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia samaconius	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia taiwanensis	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia kibuneana	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia pachupati	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
Melanotrichia attia	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Rhamphocentron) messapus	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Rhamphocentron) lavinia	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Xiphocentron) aureum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Xiphocentron) asilas	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
†X. (Xiphocentron) chiapasi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0
X. (Xiphocentron) torquon	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Xiphocentron) polemon	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Glyphocentron) euryale	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Glyphocentron) alcmeon	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) steffeni	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) pintada	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0

Table 4. Continued

Species \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
X. (Antillotrichia) maiteae	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) kamakan	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) maracanan	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) acqualume	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) jaguare	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) surinamense	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) insulare	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) sturn	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) prolixum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) regulare	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) cuyensis	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) scherothrix	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Sphagocentron) evandrus	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) albolineatum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) parentum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) fuscum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) stenotum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) boriquensis	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) haitiense	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) cubanum	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) nesidion	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
X. (Antillotrichia) mnesteus	1	1	1	1	1	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0
†Palerasnitsynus ohlhoffi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	0	0
†Palerasnitsynus spinosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	0	0

Table 4. Continued

Species \ Characters	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Hydropsyche betteni	0	1	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Arctopsyche grandis	0	1	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Stenopsyche marmorata	1	0	-	-	0	2	0	1	0	0	0	0	-	-	-	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Neureclipsis bimaculata	0	0	-	-	0	0	1	1	0	0	1	0	1	0	0	0	2	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Nyctiophylax affinis	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	2	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Holocentropus malanae	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	0	2	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Ecnomus tenellus	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
Austrotinodes picada	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	-	1	0	0	0	0	0
Zelandoptila yuccabina	0	-	-	-	-	-	0	-	0	0	1	0	1	1	0	0	0	0	-	-	0	-	0	0	1	0	0	-	-	0	0	0	-	1	1	1	0	0	1
Pseudoneureclipsis akarnos	0	1	1	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Pseudoneureclipsis hai	0	1	1	0	1	0	0	1	0	0	0	0	1	-	-	1	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Phylocentropus harrisi	0	0	-	-	0	0	1	1	0	0	1	0	1	1	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Phylocentropus placidus	0	0	-	-	0	0	1	1	0	0	1	0	1	1	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Phylocentropus ngoclinh	0	0	-	-	0	0	1	1	0	0	1	0	1	1	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dipseudopsis robustior	0	0	-	-	0	0	0	1	0	0	0	0	-	-	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Kambaitipsyche hykrion	0	0	-	-	0	0	0	?	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Kambaitipsyche schmidi	0	0	-	-	0	0	0	?	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Psychomyia flavida	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Psychomyia cruciata	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Psychomyia chompu	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Psychomyia arthit	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Psychomyia nomada	0	0	-	-	0	1	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Psychomyia schefterae	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Metalype uncatissima	0	-	-	-	-	-	-	0	-	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-	1	0	0	0	0	0
Metalype holzenthali	0	-	-	-	-	-	-	0	-	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-	1	0	0	0	0	0
Paduniella sampati	0	0	-	-	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0
Paduniella kalamos	0	0	-	-	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0
Euneureclipsis montanus	0	0	-	-	0	0	0	0	1	0	1	0	1	0	0	-	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Euneureclipsis akrichalakchmi	0	0	-	-	0	0	0	0	1	0	1	0	1	0	0	-	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Pandangpsyche batakorum	?	?	?	?	?	?	?	?	?	0	1	0	1	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Trawaspsyche weilgunii	?	?	?	?	?	?	?	?	?	0	1	0	1	0	0	-	-	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	1	1	0	0	0	0
Lype diversa	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Lype ariplis	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
†Lype essentia	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
†Lype prolongata	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Tinodes consueta	0	0	-	-	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
Tinodes unicolor	0	0	-	-	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Tinodes ragu	0	0	-	-	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Tinodes waeneri	0	0	-	-	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0
Prox. prathamajam	0	0	-	-	1	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Prox. arjinae	0	0	-	-	1	1	0	0	1	0	0	0	1	-	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0

Table 4. Continued

Species \ Characters	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
Abaria cuna	0	0	-	-	1	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	-	0	1	1	0	1	1
Abaria damra	0	0	-	-	1	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	-	0	1	1	0	1	1
Abaria electa	0	0	-	-	1	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	-	0	1	1	0	1	1
Drepanocentron birghu	0	0	-	-	1	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	-	0	1	0	0	1	1
Drepanocentron vang	0	0	-	-	1	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	-	0	1	0	0	1	1
Drepanocentron jiska	0	0	-	-	1	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	-	0	1	0	0	1	1
Drepanocentron curmisagius	0	0	-	-	1	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	-	0	1	0	0	1	1
Machairocentron tarpeia	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Machairocentron ascanius	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Machairocentron echinatum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Machairocentron falciforme	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Cnod.) girika	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Cnod. (Cnod.) brogimarus	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Cnod. (Cnod.) tchaturbhuja	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	1	1	0
Cnod. (Caen.) yavapai	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Caen.) n. sp.	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Caen.) pallas	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Caen.) immaculatum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Caen.) lausus	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Cnod. (Caen.) trilineatum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
Melanotrichia chichupala	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia dakcha	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia drupada	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia prajapati	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia kachika	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia samaconius	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia taiwanensis	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia kibuneana	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia pachupati	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
Melanotrichia attia	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	0	1	0	0	1	0
X. (Rhamphocentron) messapus	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	-	0	1	0	0	1	0
X. (Rhamphocentron) lavinia	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	-	0	1	0	0	1	0
X. (Xiphocentron) aureum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0
X. (Xiphocentron) asilas	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0
†X. (Xiphocentron) chiapasi	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	-	0	1	0	0	1	0
X. (Xiphocentron) torquon	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	-	0	1	0	0	1	0
X. (Xiphocentron) polemon	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	-	0	1	1	0	1	0
X. (Glyphocentron) euryale	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Glyphocentron) alcmeon	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) steffeni	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	1	1	0
X. (Antillotrichia) pintada	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0

Table 4. Continued

Species \ Characters	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
X. (Antillotrichia) maiteae	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) kamakan	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) maracanan	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) acqualume	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	1	1	0
X. (Antillotrichia) jaguare	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	1	1	0
X. (Antillotrichia) surinamense	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) insulare	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) sturn	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) prolixum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) regulare	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) cuyensis	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) scherothrix	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Sphagocentron) evandrus	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) albolineatum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) parentum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) fuscum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) stenotum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) boriquensis	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	0	1	0
X. (Antillotrichia) haitiense	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) cubanum	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
X. (Antillotrichia) nesidion	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	1	1	1	0
X. (Antillotrichia) mnesteus	0	0	-	-	1	0	0	0	1	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	-	0	1	0	0	1	0
†Palerasnitsynus ohlhoffi	0	?	?	?	?	?	?	?	?	0	1	?	1	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	1	0
†Palerasnitsynus spinosus	0	?	?	?	?	?	?	?	?	0	1	?	1	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	1	0

Table 4. Continued

Species \ Characters	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
Hydropsyche betteni	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	-	-	-	-	-	-	1	0	-	0	0	-	0	-	0
Arctopsyche grandis	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	-	-	-	-	-	-	1	0	-	0	0	-	0	-	0
Stenopsyche marmorata	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	-	-	-	-	-	-	1	0	-	0	0	-	0	-	1
Neureclipsis bimaculata	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	-	1	0	-	-	-	-	-	-	1	0	-	0	0	-	0	-	1
Nyctiophylax affinis	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	-	1	0	-	-	-	-	-	-	0	0	-	1	0	-	0	-	0
Holocentropus malanae	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	-	1	0	-	-	-	-	-	-	0	0	-	0	0	-	0	-	0
Ecnomus tenellus	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	-	-	-	-	1	0	0	-	1	0	-	0	-	0
Austrotinodes picada	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	-	-	-	-	1	0	0	-	1	0	-	0	-	0
Zelandoptila yuccabina	-	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	-	1	0	-	-	-	-	-	1	-	0	-	-	0	-	0	-	0
Pseudoneureclipsis akarnos	1	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	-	-	-	-	-	-	0	0	-	1	0	-	0	-	0
Pseudoneureclipsis hai	1	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	-	-	-	-	-	-	0	0	-	1	0	-	0	-	0
Phylocentropus harrisi	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	-	0	-	0
Phylocentropus placidus	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	-	0	-	0
Phylocentropus ngoclinh	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	1	1	0	0	0	-	0	-	0
Dipseudopsis robustior	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	1	-	-	-	-	0	1	0	-	0	0	-	0	-	0
Kambaitipsyche hykrion	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	0	-	0	0	-	0	-	0
Kambaitipsyche schmidi	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	0	-	0	0	-	0	-	0
Psychomyia flavida	0	0	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Psychomyia cruciata	0	0	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Psychomyia chompu	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Psychomyia arthit	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Psychomyia nomada	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Psychomyia schefterae	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Metalype uncatissima	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Metalype holzenthali	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Paduniella sampati	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Paduniella kalamos	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Euneureclipsis montanus	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Euneureclipsis akrichalakchmi	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Pandangpsyche batakorum	0	0	1	0	1	0	0	1	0	0	1	0	1	-	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Trawaspsyche weilgunii	-	0	0	0	0	0	0	1	0	0	0	0	1	-	0	0	-	1	0	-	-	-	-	-	0	0	1	1	0	0	-	0	-	0
Lype diversa	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	1	1	0	0	-	0	-	0
Lype ariplis	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	1	1	0	0	-	0	-	0
†Lype essentia	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	1	1	0	0	-	0	-	0
†Lype prolongata	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	-	-	-	-	0	1	1	1	0	0	-	0	-	0
Tinodes consueta	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Tinodes unicolor	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Tinodes ragu	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Tinodes waeneri	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	0	0	0	-	0	0	-	0	-	0
Prox. prathamajam	0	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	-	1	0	-	-	-	-	-	0	0	1	0	0	0	-	0	-	1
Prox. arjinae	0	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	-	1	0	-	-	-	-	-	0	0	1	0	0	0	-	0	-	1

Table 4. Continued

Species \ Characters	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
Abaria cuna	-	1	1	1	-	0	0	1	0	0	1	0	0	-	0	1	-	1	0	-	-	-	-	-	0	0	1	0	0	0	-	0	-	0
Abaria damra	-	1	1	1	-	0	0	1	0	0	1	0	0	-	0	1	-	1	0	-	-	-	-	-	0	0	1	0	0	0	-	0	-	0
Abaria electa	-	1	1	1	-	0	0	1	0	0	1	0	0	1	0	1	-	1	0	-	-	-	-	-	0	0	1	0	0	0	-	0	-	0
Drepanocentron birghu	-	1	1	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	-	0	0	0	0	0	1	1	0	0	1	1	0	0
Drepanocentron vang	-	1	1	1	1	0	0	1	0	0	1	1	0	-	0	1	0	0	0	0	-	0	0	0	0	0	1	1	0	0	1	1	0	0
Drepanocentron jiska	-	1	1	1	1	0	0	1	0	0	1	1	0	-	0	1	0	0	0	0	-	0	0	0	0	0	1	1	0	0	1	1	0	0
Drepanocentron curmisagius	-	1	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	-	0	0	0	0	0	1	1	0	0	1	1	0	0
Machairocentron tarpeia	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	0	-	0
Machairocentron ascanius	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	0	-	0
Machairocentron echinatum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	0	-	0
Machairocentron falciforme	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	0	-	0
Cnod. (Cnod.) girika	-	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	-	0
Cnod. (Cnod.) brogimarus	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	1	0
Cnod. (Cnod.) tchaturbhuja	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	1	0
Cnod. (Caen.) yavapai	-	1	1	0	1	0	0	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	-	0
Cnod. (Caen.) n. sp.	-	1	1	0	1	0	0	1	0	0	1	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	-	0
Cnod. (Caen.) pallas	-	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
Cnod. (Caen.) immaculatum	-	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
Cnod. (Caen.) lausus	-	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
Cnod. (Caen.) trilineatum	-	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
Melanotrichia chichupala	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1	0	0	-	0	-	0
Melanotrichia dakcha	-	1	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	1	0
Melanotrichia drupada	-	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	1	0	0	1	1	1	0
Melanotrichia prajapati	-	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1	0	1	0	1	0	0
Melanotrichia kachika	-	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1	0	1	0	1	0	0
Melanotrichia samaconius	-	1	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	1	0
Melanotrichia taiwanensis	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1	0	0	1	1	1	0
Melanotrichia kibuneana	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	-	0	0	1	1	0	0	1	1	1	0
Melanotrichia pachupati	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1	0	0	-	0	-	0
Melanotrichia attia	-	1	1	0	1	0	0	-	-	0	1	0	0	-	0	0	0	0	0	1	0	0	0	-	0	0	1	1	0	1	0	1	0	0
X. (Rhamphocentron) messapus	-	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	1	0	0	0	-	-	-	0
X. (Rhamphocentron) lavinia	-	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	-	-	0
X. (Xiphocentron) aureum	-	1	1	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	-	0	0	0	0	0	1	-	0	0	1	1	0	0
X. (Xiphocentron) asilas	-	1	1	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	-	0	0	0	0	0	1	-	0	0	1	1	0	0
†X. (Xiphocentron) chiapasi	-	1	1	0	1	0	0	-	0	0	1	0	1	-	0	0	0	0	0	0	-	-	0	-	-	0	1	-	0	0	1	1	0	0
X. (Xiphocentron) torquon	-	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	-	1	0	0	0	0	1	0	0	0	-	0	-	0
X. (Xiphocentron) polemon	-	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
X. (Glyphocentron) euryale	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
X. (Glyphocentron) alcmeon	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	0	-	0	-	0
X. (Antillotrichia) steffeni	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) pintada	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	-	1	0	0

Table 4. Continued

Species \ Characters	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**
X. (Antillotrichia) maiteae	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) kamakan	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) maracanan	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) acqualume	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) jaguare	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) surinamense	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) insulare	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) sturn	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) prolixum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) regulare	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) cuyensis	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) scherothrix	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	-	0	-	0	0	1	0	0	0	-	1	0	0
X. (Sphagocentron) evandrus	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0
X. (Antillotrichia) albolineatum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) parentum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	0	1	0	0	0	-	1	0	0
X. (Antillotrichia) fuscum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0
X. (Antillotrichia) stenotum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0
X. (Antillotrichia) boriquensis	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0
X. (Antillotrichia) haitiense	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0
X. (Antillotrichia) cubanum	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	1	0	0
X. (Antillotrichia) nesidion	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0
X. (Antillotrichia) mnesteus	-	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	1	0	0	0	0	1	0	0
†Palerasnitsynus ohlhoffi	-	0	0	0	1	0	0	1	1	0	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	0	-	-
†Palerasnitsynus spinosus	-	0	0	0	1	0	0	1	1	0	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	-	0	-	-

Table 4. Continued

Species \ Characters	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145
Hydropsyche betteni	0	0	0	0	-	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Arctopsyche grandis	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Stenopsyche marmorata	0	0	0	1	0	0	0	0	0	0	1	0	-	-	-	0	-	0	0	0	-	0	-	0	-	0	-	-	-	0
Neureclipsis bimaculata	0	0	0	0	0	0	0	0	0	0	1	0	-	-	-	0	-	0	0	0	-	0	-	0	-	0	-	-	-	0
Nyctiophylax affinis	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	1	0	0	0	-	0	-	0	-	0	-	-	-	0
Holocentropus malanae	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	1	0	0	0	-	0	-	0	-	0	-	-	-	0
Ecnomus tenellus	0	0	0	1	1	0	0	0	0	0	1	0	-	-	-	0	1	1	0	0	-	0	-	0	-	0	-	-	-	0
Austrotinodes picada	0	0	0	1	1	0	0	0	0	0	0	1	-	-	-	0	0	1	0	0	-	0	-	0	-	0	-	-	-	0
Zelandoptila yuccabina	0	0	0	1	0	0	0	0	0	-	0	1	-	-	-	0	-	1	0	0	-	0	-	0	-	0	-	-	-	0
Pseudoneureclipsis akarnos	0	0	0	0	1	0	0	0	0	0	1	0	-	-	-	0	1	0	0	0	-	0	-	0	-	0	-	-	-	0
Pseudoneureclipsis hai	0	0	0	0	1	0	0	0	0	0	1	0	-	-	-	0	1	0	0	0	-	0	-	0	-	0	-	-	-	0
Phylocentropus harrisi	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	1	0	0	0	-	0	-	0	-	1	1	1	0	0
Phylocentropus placidus	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	1	0	0	0	-	0	-	0	-	1	1	1	0	0
Phylocentropus ngoclinh	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Dipseudopsis robustior	0	0	0	0	1	0	0	0	0	0	0	0	-	-	-	0	-	0	0	0	-	0	-	0	-	0	-	-	-	0
Kambaitipsyche hykrion	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	1	-	0	-	0	-	-	-	0
Kambaitipsyche schmidi	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	1	-	0	-	0	-	-	-	0
Psychomyia flavida	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Psychomyia cruciata	0	0	0	1	0	1	0	0	0	1	0	0	0	1	-	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Psychomyia chompu	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Psychomyia arthit	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Psychomyia nomada	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Psychomyia schefterae	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Metalype uncatissima	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Metalype holzenthali	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Paduniella sampati	0	0	0	1	0	0	0	0	0	0	0	0	1	-	-	0	-	0	0	0	-	0	-	0	-	0	-	-	-	0
Paduniella kalamos	0	0	0	1	0	0	0	0	0	0	0	0	1	-	-	0	-	0	0	0	-	0	-	0	-	0	-	-	-	0
Euneureclipsis montanus	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	-	0	-	0	-	1	1	1	0	0
Euneureclipsis akrichalakchmi	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	-	0	-	0	-	1	1	1	0	0
Pandangpsyche batakorum	0	0	0	1	0	0	0	0	0	0	0	1	-	-	-	0	0	0	1	0	-	0	-	0	-	0	-	-	-	0
Trawaspsyche weilgunii	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	-	0	-	0	-	0	-	-	-	0
Lype diversa	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Lype ariplis	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
†Lype essentia	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
†Lype prolongata	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	-	0	-	0	-	0	-	-	-	0
Tinodes consueta	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	-	0	-	0	-	0	-	-	-	0
Tinodes unicolor	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	-	0	-	0	-	0	-	-	-	0
Tinodes ragu	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	-	0	-	0	-	0	-	-	-	0
Tinodes waeneri	0	0	0	1	0	0	0	0	0	0	0	0	-	0	-	0	0	1	1	0	-	0	-	0	-	0	-	-	-	0
Prox. prathamajam	0	0	0	1	1	0	0	0	0	0	0	1	-	0	-	0	0	0	1	0	-	0	-	0	-	0	-	-	-	0
Prox. arjinae	0	0	0	1	1	0	0	0	0	0	0	1	-	0	-	0	0	0	1	0	-	0	-	0	-	0	-	-	-	0

Table 4. Continued

Species \ Characters	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145
Abaria cuna	0	0	0	1	1	0	0	0	0	0	1	0	-	-	-	0	0	0	0	0	-	0	-	0	-	1	0	-	0	0
Abaria damra	0	0	0	1	1	0	0	0	0	0	1	0	-	-	-	0	0	0	0	0	-	0	-	0	-	1	0	-	0	0
Abaria electa	0	0	0	1	1	0	0	0	0	0	1	0	-	-	-	0	0	0	0	0	-	0	-	0	-	1	0	-	0	0
Drepanocentron birghu	0	0	0	1	1	0	0	0	0	0	1	0	0	-	1	1	0	0	1	1	0	0	-	1	0	1	0	-	0	0
Drepanocentron vang	0	0	0	1	1	0	0	0	0	0	1	0	0	-	1	1	0	0	1	1	0	0	-	1	0	1	0	-	0	0
Drepanocentron jiska	0	0	0	1	1	0	0	0	0	0	1	0	0	-	1	1	0	0	1	1	0	0	-	1	0	1	0	-	0	0
Drepanocentron curmisagius	0	0	0	1	1	0	0	0	0	0	1	0	0	-	1	1	0	0	1	1	0	0	-	1	0	1	0	-	0	0
Machairocentron tarpeia	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	1
Machairocentron ascanius	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	1
Machairocentron echinatum	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	1
Machairocentron falciforme	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	1
Cnod. (Cnod.) girika	0	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	1	0	0	-	1	0	-	0	0
Cnod. (Cnod.) brogimarus	0	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	1	0	0	-	1	0	-	0	0
Cnod. (Cnod.) tchaturbhuja	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	1	0	0	-	1	0	-	0	0
Cnod. (Caen.) yavapai	0	0	0	1	0	0	0	0	0	0	1	0	-	1	-	1	0	0	1	1	1	1	0	1	1	1	0	-	0	0
Cnod. (Caen.) n. sp.	0	0	0	1	0	0	0	0	0	0	1	0	-	1	-	1	0	0	1	1	0	1	0	1	1	1	0	-	0	0
Cnod. (Caen.) pallas	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	-	0	0
Cnod. (Caen.) immaculatum	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	-	0	0
Cnod. (Caen.) lausus	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	-	0	0
Cnod. (Caen.) trilineatum	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	0	1	1	1	0	-	0	0
Melanotrichia chichupala	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia dakcha	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia drupada	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia prajapati	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia kachika	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia samaconius	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	0	0
Melanotrichia taiwanensis	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	0	0
Melanotrichia kibuneana	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	0	0
Melanotrichia pachupati	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
Melanotrichia attia	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	-	1	0
X. (Rhamphocentron) messapus	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	-	0	0
X. (Rhamphocentron) lavinia	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	-	0	0
X. (Xiphocentron) aureum	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	1	0
X. (Xiphocentron) asilas	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	1	0
†X. (Xiphocentron) chiapasi	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	-	1	1	1	0
X. (Xiphocentron) torquon	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Xiphocentron) polemon	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Glyphocentron) euryale	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Glyphocentron) alcmeon	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Antillotrichia) steffeni	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	1	0	0
X. (Antillotrichia) pintada	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0

Table 4. Continued

Species \ Characters	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145
X. (Antillotrichia) maiteae	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	1	1	0	-	1	0	0	0	0
X. (Antillotrichia) kamakan	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) maracanan	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) acqualume	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	1	0	0
X. (Antillotrichia) jaguare	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) surinamense	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	1	0	0
X. (Antillotrichia) insulare	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	0	0	0
X. (Antillotrichia) sturn	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) prolixum	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	0	0
X. (Antillotrichia) regulare	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) cuyensis	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	1	0	0
X. (Antillotrichia) scherothrix	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Sphagocentron) evandrus	0	0	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	0	0
X. (Antillotrichia) albolineatum	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Antillotrichia) parentum	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	1	1	0	0
X. (Antillotrichia) fuscum	0	0	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	0	0
X. (Antillotrichia) stenotum	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	0	0
X. (Antillotrichia) boriquensis	0	0	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	1	1	0	0
X. (Antillotrichia) haitiense	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) cubanum	0	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) nesidion	0	0	-	1	1	0	0	-	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	0	-	1	0	0	0	0
X. (Antillotrichia) mnesteus	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	-	0	-	1	0	1	0	0	0	0
†Palerasnitsynus ohlhoffi	-	-	0	1	0	0	0	0	0	1	1	0	0	1	1	-	0	0	-	0	-	0	-	-	-	1	-	0	0	0
†Palerasnitsynus spinosus	-	-	0	1	0	0	0	0	0	1	1	0	0	1	1	-	0	0	-	0	-	0	-	-	-	1	-	0	0	0

Table 4. Continued

Species \ Characters	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
Hydropsyche betteni	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	0	0	0	0
Arctopsyche grandis	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	0	0	0	0	0	0	0	1
Stenopsyche marmorata	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	0	0	0	-
Neureclipsis bimaculata	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	0	0	-	0	0	0	0	1
Nyctiophylax affinis	0	-	-	-	-	-	-	0	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1
Holocentropus malanae	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	0	0	1	0	0	0	0	1
Ecnomus tenellus	0	-	-	-	-	-	-	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Austrotinodes picada	0	-	-	-	-	-	-	0	0	-	0	0	0	0	1	0	0	1	0	0	0	0	0
Zelandoptila yuccabina	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	0	0	-	0	0	0	0	0
Pseudoneureclipsis akarnos	0	-	-	-	-	-	-	0	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1
Pseudoneureclipsis hai	0	-	-	-	-	-	-	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
Phylocentropus harrisi	0	-	-	-	-	-	-	0	0	1	0	1	0	-	0	0	0	0	0	0	0	0	0
Phylocentropus placidus	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	0	0	0	0
Phylocentropus ngoclinh	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	0	0	0	0	0
Dipseudopsis robustior	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	0	0	0	0
Kambaitipsyche hykrion	0	-	-	-	-	-	-	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	1
Kambaitipsyche schmidi	0	-	-	-	-	-	-	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	1
Psychomyia flavida	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Psychomyia cruciata	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Psychomyia chompu	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Psychomyia arthit	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Psychomyia nomada	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Psychomyia schefterae	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Metalype uncatissima	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Metalype holzenthali	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	1	0	0	1	1	0	0	0
Paduniella sampati	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	1	0	0	0	1	0	0	0
Paduniella kalamos	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	1	0	0	0	1	0	1	0
Euneureclipsis montanus	0	-	-	-	-	-	-	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Euneureclipsis akrichalakchmi	0	-	-	-	-	-	-	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Pandangpsyche batakorum	0	-	-	-	-	-	-	0	0	-	0	0	0	1	0	1	0	0	0	0	0	0	0
Trawaspsyche weilgunii	0	-	-	-	-	-	-	0	0	-	0	0	0	1	1	1	0	0	0	0	0	0	0
Lype diversa	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	0	0	0	0
Lype ariplis	0	-	-	-	-	-	-	0	0	-	0	1	1	-	0	0	0	0	0	1	0	0	0
†Lype essentia	0	-	-	-	-	-	-	0	0	-	0	1	1	-	0	0	0	0	0	1	0	0	0
†Lype prolongata	0	-	-	-	-	-	-	0	0	-	0	1	0	-	0	0	0	0	0	1	0	0	0
Tinodes consueta	0	-	-	-	-	-	-	0	0	-	0	0	1	0	1	1	0	0	0	0	0	0	0
Tinodes unicolor	0	-	-	-	-	-	-	0	0	-	0	0	1	0	1	1	0	0	0	0	0	0	0
Tinodes ragu	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Tinodes waeneri	0	-	-	-	-	-	-	0	0	-	0	0	1	1	0	1	0	0	0	0	0	0	0
Prox. prathamajam	0	-	-	-	-	-	-	0	0	-	1	0	1	0	0	1	1	0	0	0	0	1	1
Prox. arjinae	0	-	-	-	-	-	-	0	0	-	1	0	1	0	0	1	1	0	0	0	0	1	1

Table 4. Continued

Species \ Characters	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
Abaria cuna	0	-	-	-	-	-	-	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0
Abaria damra	0	-	-	-	-	-	-	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0
Abaria electa	0	-	-	-	-	-	-	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0
Drepanocentron birghu	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1
Drepanocentron vang	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1
Drepanocentron jiska	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1
Drepanocentron curmisagius	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1
Machairocentron tarpeia	1	0	1	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Machairocentron ascanius	1	0	1	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Machairocentron echinatum	1	0	1	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Machairocentron falciforme	1	0	1	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
Cnod. (Cnod.) girika	1	0	0	0	-	0	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Cnod. (Cnod.) brogimarus	0	-	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Cnod. (Cnod.) tchaturbhuja	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Cnod. (Caen.) yavapai	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Cnod. (Caen.) n. sp.	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Cnod. (Caen.) pallas	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Cnod. (Caen.) immaculatum	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Cnod. (Caen.) lausus	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Cnod. (Caen.) trilineatum	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
Melanotrichia chichupala	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
Melanotrichia dakcha	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia drupada	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia prajapati	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
Melanotrichia kachika	1	0	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
Melanotrichia samaconius	0	-	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia taiwanensis	1	0	0	0	-	0	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia kibuneana	1	0	0	0	-	0	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia pachupati	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
Melanotrichia attia	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
X. (Rhamphocentron) messapus	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Rhamphocentron) lavinia	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Xiphocentron) aureum	0	-	-	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
X. (Xiphocentron) asilas	0	-	-	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0
†X. (Xiphocentron) chiapasi	0	-	-	-	-	-	-	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0
X. (Xiphocentron) torquon	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Xiphocentron) polemon	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Glyphocentron) euryale	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
X. (Glyphocentron) alcmeon	0	-	-	-	-	-	-	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
X. (Antillotrichia) steffeni	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) pintada	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0

Table 4. Continued

Species \ Characters	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
X. (Antillotrichia) maiteae	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) kamakan	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) maracanan	1	0	0	-	-	-	-	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) acqualume	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) jaguare	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) surinamense	1	0	0	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) insulare	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) sturn	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) prolixum	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) regulare	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) cuyensis	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) scherothrix	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Sphagocentron) evandrus	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) albolineatum	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) parentum	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) fuscum	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) stenotum	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) boriquensis	0	1	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) haitiense	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) cubanum	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) nesidion	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
X. (Antillotrichia) mnesteus	0	-	-	-	-	-	-	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0
†Palerasnitsynus ohlhoffi	0	-	-	-	-	-	-	0	0	1	-	0	-	1	0	1	-	-	0	-	0	-	0
†Palerasnitsynus spinosus	1	0	0	1	1	1	0	0	0	1	-	0	-	1	0	1	-	-	0	-	0	-	0

Chapter II – Taxonomy of *Xiphocentron* Brauer from Brazil, with new species and records (Psychomyiidae: Xiphocentroninae)

INTRODUCTION

Following the phylogenetic results of the preceding chapter the family Xiphocentronidae Ross, 1949 was synonymized with Psychomyiidae Walker, 1852 and the member of the family were included in the subfamily Xiphocentroninae. Xiphocentroninae Ross, 1949 with 178 know species in 7 genera. This subfamily occurs in small streams along the tropics having most of its diversity in the Oriental region, where occurs 5 of the 7 genera. Three genera occur in the Neotropical region: *Cnodocentron* (*Caenocentron*), *Machairocentron* and *Xiphocentron*. The Neotropical fauna comprises 64 species, most of them represented by the genus *Xiphocentron* Brauer, 1870, which is the most species-rich of the family, with 51 species. The *Xiphocentron* species distribution including data analyzed in the present study is shown in the figure 1.

The phylogeny of Xiphocentroninae (chapter 1) reveals that *Xiphocentron* is not monophyletic and that species of this genus are spread among different clades, which are associated with other genera. As many of these clades have little support and as there is a need to redefine other genera, in the present study, the understanding of *Xiphocentron* as defined by Schmid (1982) is maintained. Thus, broader phylogeny including broader sampling and new morphological (e.g. ultrastructural data) and molecular data are needed before the genus *Xiphocentron* is resolved. Schmid (1982), without using phylogenetic approaches, organized the genus *Xiphocentron* into 5 subgenera, *Glyphocentron*, *Rhamphocentron*, *Sphagocentron*, *Xiphocentron*, and *Antillotrichia*. Considering the chapter 1, the subgenera *Xiphocentron*, and *Antillotrichia* were not recovered as monophyletic. The *X*. (*Antillotrichia*) species included in the phylogeny (chapter 1) formed two main groups: 1) A group of species bearing dense patch of spines on the inferior appendage from Amazon and Mesoamerica, that included the subgenus *Sphagocenton*. 2) and a group with *Antillotrichia* species with mesal process on the inferior appendage of Great Antilles and South America, which also included the species of the genus *Machairocentron*. All species in Brazil and South America have been placed in *Antillotrichia* subgenus, and only *X. sclerothrix* Pes & Hamada, 2013 belongs to the the group of Amazon and Mesoamerica species.

Adults of *Xiphocentron*, with exception to *X. aureum* Flint, 1967 that can reach 8.5 mm, are mostly small-sized (2.8–5.5 mm). They have wings with pointed apex, generally black to dark brown in color, with pubescent surface and forewings covered by fine long dark setae generally with a circular patch of white setae near the nygma. They usually are active during the day, and are not commonly attracted to light, being very scarce in collections (Flint 1968, Schmid 1982). Day light capture methods as active swiping and flight interception traps are more appropriate ways to collect larger number of specimens (Pes et al. 2013, Vilarino et al. 2018).

In Brazil, there are 12 described species: *X. ilionea* Schmid, 1982, *X. steffeni* (Marlier, 1964), *X. sclerothrix* Pes & Hamada, 2013, *X. kamakan* Vilarino & Calor, 2015, *X. maiteae* Vilarino & Calor, 2015, *X. acqualume* Rocha, et al., 2017 and *X. jaguare* Rocha, et al., 2017. *X. copacabana* Vilarino et al., 2018, *X. maracanan* Vilarino et al., 2018, *X. redentor* Vilarino et al., 2018, *X. tijuca* Vilarino et al., 2018 and *X. saltuum* (Müller, 1921), a *nomem dubium* (Flint *et al*. 1999) which the description was based only on the pupae mandible.

Herein we present a taxonomic revision of the *Xiphocentron* species occurring in Brazil, with the description of five new species and the redescription of *X. ilionea,* and *X. steffeni*. The new species are one from central Brazil in Cerrado (Brazilian savanna), three from southeastern and one from southern Brazil in Atlantic forest.

MATERIAL AND METHODS

Species delimitation.

In this study, species were delimitated based primarily on characters of the male genitalia and wing venation. Species were recognized based on the presence of a combination of constant morphological character states since intra and interpopulation variation seems to be common in *Xiphocentron*. For example, *X. cubanum* has different morphotypes, which were described to different regions of Cuba as subspecies (*X. cubanum caimitense*, *X. cubanum cubanum* and *X. cubanum orientale*). On the other hand, it is important to note that the morphological differences observed for these subspecies (e.g. in spines, and in tergum and sternum shapes) can also be good indicators of different species. Thus, phylogeny and molecular studies would be necessary to understand how significant these morphological variations are in terms of phylogeneticlineages and genetic distances between populations. Additionally, specimens usually have soft and light sclerotized structures (parts of tergum IX and paraproctal process), which are subject to some deformations; and long movable structures (e.g. preanal and inferior appendages), which are prone to rotations. Faced with these questions, delimiting species of the genus *Xiphocentron* is a difficult task. Therefore, in this study, we tend to be conservative avoiding taxonomic inflation. Thus, we grouped as the same species the individuals that share a main pattern of genitalia. However, all variations in wing and genitalia were described and illustrated as part of the species plasticity. The phallus in *Xiphocentron* show very few variations among the species, most concerning the degree of enlargement at the apex. So, the phallus is not depicted in most of the descriptions. Here we present in full length only the phallus of *X.* (*Antillotrichia*) sp. n. 3 as an example, for other species it is basically the same. The cuticular reticulated region on the abdominal sternum V also do not show variation among the species herein described.

Aiming to make easier the species comparison they are here presented organized according to the overall similarity of male genitalia rather than in alphabetical order: Species that present inferior appendage with polyp-like mesal sclerite (with many spines) and harpago not very elongate (*X. steffeni*, *X. ilionea*, *X.* sp. n. 1, *X.* sp. n. 2); species with very elongate harpago (*X.* sp. n. 3, *X. kamakan*, *X. acqualume*); species with inferior appendage with the coxopodite projected posterad (*X. copacabana*, *X. maiteae*, *X.* sp. n. 4); species with small spine-like mesal sclerite (*X. jaguar*, *X. tijuca*, *X. redentor*, *X. maracanan*, *X.* sp. n. 5); and species with dense and long setae on the inferior appendage (*X. sclerothrix*).

Morphological terminology.

Terminology for head and thoracic setal warts followed Oláh (2007). Terminology for male genitalia was based on Nielsen (1957) and Schmid (1982). Terminology for wing venation followed the Comstock – Needham system as interpreted for Trichoptera by Mosely & Kimmins (1953). Paired structures are referred to in the singular form.

Specimens preparation and illustrations.

All the specimens were conserved in 80% ethanol. To analyze the wing venation, right wings were removed and studied in stereomicroscopy. Photographs of wings were taken using a Leica Camera (DFC450) coupled to a Leica stereomicroscope (M205A) and then digitalized with Adobe Illustrator® CS6. To study the genitalia, the entire abdomens were removed and genitalia were cleared using 85% lactic acid through standard methods outlined by Blahnik *et al.* (2007). The prepared genitalia were transferred to microvials with 80% ethanol. Genitalia were placed in excavated slides with a drop of glycerin, covered with coverslips and examined using optical microscopy (Leica DM2500) at 400 X magnification. The structures were traced in pencil with the aid of a camera lucida (drawing tube) coupled to the microscope. Final illustrations were made scanning the pencil drawings and digitalizing with the software Adobe Illustrator® CS6. Distribution maps were generated using the open source software QGIS version 2.8.2.

Depositories

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

DZRJ	Coleção Entomológica Professor José Alfredo Pinheiro Dutra, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.
UFBA	Museu de Zoologia da Universidade Federal da Bahia, Salvador, Brazil.
UFMG	Coleção de Insetos do Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.
NMNH	Smithsonian National Museum of Natural History, Washington, D.C., USA.

RESULTS

Systematics

Family **PSYCHOMYIIDAE** Walker, 1852

Genus ***Xiphocentron*** Brauer, 1870

Xiphocentron steffeni (Marlier, 1964)

Figures 2A–F, 3A–C, 4A–F, 5A–D, 12A–F

Melanotrichia steffeni Marlier, 1964: 6

Xiphocentron steffeni Schmid, 1982:114 —Paprocki et al., 2004:16 [checklist]. —Dumas et al., 2009:361 [distribution]. —Dumas et al., 2010:9 [distribution]. —Calor, 2011:323 [checklist]. —Dumas & Nessimian, 2012:24 [checklist]. —Paprocki & França, 2014:93 [checklist]. —Vilarino & Calor, 2015:52 [♂; key].

Neotype designation

We contact the Institut royal des Sciences Naturelles de Belgique, Bruxelles, where Marlier deposited the types of *X. steffeni* although we were informed that the material is lost. We analyzed material from the exactly same locality that Marlier described *X. steffeni*, the specimens agree with the description and drawings with the same shape of preanal appendage, length of spines of inferior appendage and wing pattern. In this case, it is herein designated a neotype to *Xiphocentron steffeni* following the provisions of ICZN (1999; Article 75.3).

Material examined

Neotype male. **BRAZIL: São Paulo:** ♂ (MZSP001261) Salesopolis: Estação Biológica de Boracéia, Casa Grande, Ribeirão Coruja, 08.x.1977 (CG Froehlich).

Paraneotypes. **BRAZIL: São Paulo:** ♂ (MZSP001259) Same data as neotype. 3♂ (MZSP001260), (MZSP001254), (MZSP001257) Campos do Jordão: Parque Estadual, rio Galharada, 2.x.1986. (CG Froehlich & LGO). **Rio de Janeiro:** 14♂ (DZRJ) Parque Nacional Itatiaia: rio Maromba, Véu da Noiva, 22º25′38,60″S, 44º37′09,70″W, 1140m, 08.xii.2015–06.i.2016, malaise trap (DM Takiya, APM Santos, LS Barbosa). **Santa Catarina:** 3♂ (MZSP) Grão Pará: *Parque* Nacional Serra Furada, rio Capea, 28º11′26″S, 49º23′30″W, 15.x–16.xi.2012, malaise trap (LC Pinho, LS Gomes, AL Schlindwein). 1♂ (UFBA) Urubici: Morro da Igreja, 17.viii–06.i.2006, malaise trap (LC Pinho & L Bizzo). 2♂ (MZSP) Grão Pará: same data except: 16.ii–6.iv.2013 (morphotype I).

Diagnosis

X. steffeni can be distinguished from its congeners mainly by the elongated and dense spines on the inner face of inferior appendage, and on the mesal sclerite. Additional characters that can help to differentiate *X. steffeni* are the apical margin of tergum IX with shallow incision and smooth lobes; and the preanal appendage clavate, enlarged subapically.

Redescription

Adult male. Forewing length 4.4-4.7 mm; brown to dark brown in alcohol. Legs pale yellow, tibia of hind legs darker. Spur formula 2,4,3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; fork II petiolate, with closed cell around the nygma; thyridial as long as discoidal cell; three anal veins present. Hindwing fork II and fork V present. Sternum V with pair of anteroventral cuticular reticulated areas.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a broad v-shaped incision; posterior margin roof-like, with pair of smooth lobes divided by a shallow incision. Sternum IX, in lateral view, about 2x longer than tall, apex deltoid, anterior apodeme filiform, straight, tapering to slender flange; in ventral view, almost rounded, posterior margin with concave incision and mesal deeper incision. Paraproctal process in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, tapering apically, apex membranous, with sensilla, medially cleft until sclerotized band. Preanal appendage more than 2x longer than tergum IX, setose; in lateral view, strongly bent about mid-length; in dorsal view, clavate, enlarged subapically. Inferior appendage less than 2x tergum IX length, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region about as long as basal region; in dorsal view, inner face with set of stout long spines; mesal sclerite large, broadly covered with elongate spines; in lateral view polyp-like. Phallus tubular, long and slender, in lateral view phallobase wide; apex straight enlarged apically, weakly sclerotized.

Distribution. Brazil (Rio de Janeiro, Santa Catarina, São Paulo).

Remarks. All the characters from the specimens from Salesópolis fits with the original description of Marlier (1964). Specimens from other locality also have the same aspect of spines on the inferior appendage. Some specimens from southern Brazil have these spines in a larger density (Figure 12F). The forewing fork II oscillate in different populations, varying from sessile to petiolate (Figures 2D-E, 3A-C). The specimens from Rio de Janeiro, Itatiaia from a same locality show darker and lighter colors (Figure 5D).

Xiphocentron ilionea **Schmid, 1982**

Figures 6A-E, 11A-E

Xiphocentron ilionea (Antillotrichia) Schmid, 1982:70 [Type locality: Brazil, [São Paulo], Estacion Biol. Boraceia, Pedreira; NMNH; ♂; in Xirocentron]. —Paprocki et al., 2004:16 [checklist]. —Dumas et al., 2009:361 [distribution]. —Calor, 2011:323 [checklist]. —Paprocki & França, 2014:93 [checklist]. —Vilarino & Calor, 2015:52 [♂; key].

Material examined.

Holotype. **BRAZIL: São Paulo:** ♂ (NMNH1028617) Salesópolis: Estação Biológica Boraceia, Pedreira, 3.iv.1977, 850m (C.M. & OS.Flint, Jr.)

Paratype. 2♂ (NMNH) same data as holotype.

Diagnosis

X. ilionea is very similar to *X. steffeni*, it can be differentiated from *X. steffeni* and other species with polyp-like mesal sclerite by the tergum IX apical lobes acute and with deeper mesal incision; the inferior appendage with short and sparse spines; the preanal appendage straight in dorsal view and the apical margin of sternum IX without incision.

Redescription

Adult male. Forewing length 3-4.3 mm; brown in alcohol. Legs pale yellow, tibia of hind legs darker. Spur formula 2,4,3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; fork II petiolate, with closed cell around the nygma; thyridial as long as discoidal cell; three anal veins present. Hindwing fork II and fork V present. Sternum V with pair of anteroventral cuticular reticulated areas.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a v-shaped incision; posterior margin produced as a pair of acute lobes. Sternum IX, in lateral view, about 2x longer than tall, apex deltoid, anterior apodeme filiform, straight, tapering to a slender flange; in ventral view, almost rounded, posterior margin with concave incision. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, tapering apically, apex membranous, with sensilla, medially cleft until sclerotized band. Preanal appendage more than 2x longer than tergum IX, setose; in lateral view, narrower at mid-length; in dorsal view, narrow basally. Inferior appendage less than 2x tergum IX length, setose; coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region about 1,5x longer than basal region; in dorsal view, inner face with a set of stout spines; mesal sclerite with crown of spines; in lateral view polyp-like. Phallus tubular, long and slender, in lateral view, phallobase wide; apex straight enlarged apically, weakly sclerotized.

Remarks. The types of *X. ilionea* were collected at the same locality as *X. steffeni* and could perhaps be considered within the specter of variation of *X. steffeni*, although *X. ilionea* has diagnosable features that allows to differentiate each other. So, both specimens should be kept valid until more information about morphological and molecular variability are available.

Xiphocentron **sp. n. 1**

Figures 7A–D, 8A–J, 9A–B, 13A–E

Type material

Holotype. **BRAZIL: Rio de Janeiro**: ♂ (DZRJ) Itatiaia: Penedo, rio Palmital, 22º25′34.00″S, 44º32′52.00″W, 637m, 07.iii.2008 (LL Dumas, MR de Souza, RB Braga, JL Nessimian).

Paratypes. **BRAZIL: Rio de Janeiro**: 4♂ (DZRJ) Itatiaia: same as holotype. **São Paulo**: 3♂ (DZRJ) Ubatuba: P.E. Serra do Mar, Núcleo Picinguaba, casa de farinha, rio da fazenda, 23º20′46.01″S, 44º50′59.61″W, 52m, 31.v.2014 (LL Dumas, JL Nessimian). **Paraná**: 1♂ (DZRJ) Morretes: Porto de cima, tributário do rio Nhundiaquara, 25º25′04.00″S, 48º54′05.20″W, 91m, 23.i.2011 (JL Nessimian, LL Dumas).

Diagnosis

This species is very similar to *X. ilionea*, the preanal appendage has a similar shape and the spines on the inferior appendage have the same density and length. The new species can be distinguished by *X. ilionea* and other congeners by the tergum IX in dorsal view having rounded apical lobes with a blunt mesal notch; the apical margin of sternum IX has an undulate incision (smooth concave incision in *X. ilionea* and *X.* sp n. 2); and the preanal appendage in dorsal view is mostly straight and subbasally bears a distinct mesal projection.

Description

Adult male. Forewing length 3.5-3.6 mm; yellowish brown in alcohol. Legs pale yellow, tibia of hind legs distinctly darker, except at the proximal end. Maxillary palp in increasing order of length (I-II-III)-IV-V, segment IV shorter than sum of segments I-II-III. Spur formula 2, 4, 3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; Sc reaching C subapically, apically bent and meeting R1; fork II short, petiolate in relation to discoidal cell; thyridial cell as long as discoidal cell; three anal veins present. Opaque pterostigma present. Hindwing fork II and fork V present; R1 absent. Sternum V bearing pair of anteroventral reticulated regions.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a shallow concave incision; posterior margin produced as a pair of rounded lobes, divided medially, lobes lateral edges soften, inner edges abrupt, forming a quadrate incision. Sternum IX, in lateral view, about 2x longer than tall, apex deltoid, anterior apodeme filiform, straight, tapering to a slender flange; in ventral view, almost rounded, posterior margin with median shallow flange and submedially concave. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, each side fused, with sclerotized band on fusion region, wide basally, narrowing until midlength, straight toward apex, apex divided mesally until the sclerotized band, that also is divided medially. Preanal appendage about 3x longer than tergum IX, setose; in lateral view, sigmoid, narrower at mid-length, enlarged at apex; in dorsal view, basally produced mediad, narrow submedially. Inferior appendage about 2x longer than tergum IX, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region about as long as basal region, with a set of spines forming a distinct rosette-like agglomeration ventrally below mesal sclerite; in dorsal view, inner face with numerous spines; mesal sclerite polyp-like with a grown of spines; in lateral view, finger-like with lateral and apical spines. Phallus tubular, long and slender, in lateral view phallobase wide; apex straight, slightly enlarged subapically, weakly sclerotized.

Distribution

Brazil (Paraná, Rio de Janeiro, São Paulo).

Remarks

The species from São Paulo State (Ubatuba) and Paraná State (Morretes) have shorter lobes on the posterior margin of tergum IX, in dorsal view, and the tergum is more hoof-like. Although this and other structures are very membranous as the specimens from São

Paulo and Paraná are weakly sclerotized than the specimens from Rio de Janeiro State (Itatiaia), so the sclerotized band on paraproctal process also is not visible. The wing venation and the pattern of spines and mesal sclerite on the inferior appendage are quite the same in all morphotypes.

Xiphocentron **sp. n. 2**

Figures 9C, 10A–H, 14A–E

Type material

Holotype male. **BRAZIL: Goiás**: ♂ (DZRJ) Pirenópolis: RPPN Vargem Grande, Ribeirão dos Infernos, prox. Sede, 15º48′43,90″S, 48º55′09,50″W, 934m, 4.ii.2015, pensilvania trap, (DM Takiya, APM Santos).

Paratypes. **BRAZIL: Goiás** 3♂ (DZRJ) Pirenópolis: same data as holotype. 9♂ (DZRJ) Mineiros: 17º16′ 46.00″S, 52º44′47.50″W, 532m, 19.ii.2019, penselvania trap, (LFS, APM Santos, ER). 1♂, Caiapônia: 16º51′53.00″S, 51º39′31.70″W, 639m, 29.ii.2012 (LFS, APM Santos, ER). 2♂ (DZRJ), same data except, 16º51′47.80″S, 52º01′45.90″W, 594m, 28.ii.2012. 1♂ (DZRJ), same data except, 17º10′15,50″S, 51º51′13,10″W, 793m, 14.ii.2012. 1♂(DZRJ) Portelândia: 17º10′15.16″S 52º38′56.98″W, 544m, 21.ii.2012 (LFS, APM Santos, ER). **Mato Grosso**: 3♂ (DZRJ) Cuiabá: PN Chapada dos Guimarães, Córrego Coxipozinho, abaixo da cachoeira Véu de Noiva, 15º24′27.20″S, 55º50′04.40″, 532m, 21.vii.2013 (ALH Oliveira, BHL Sampaio, B Clarkson, N Ferreira-JR). 1♂(DZRJ), same data except, córrego Independencia, Degraus/ prainha, 15º24′58.70″S, 55º50′23.40″W, 601m, 19.vii.2013.

Diagnosis

The species differs from others species with a polyp-like mesal sclerite as *X. steffeni* by having the inferior appendage with a longer apex, the spines of shorter, grain-like, and the mesal process about 2x longer. At the tergum IX the apical lobes also are more produced than in *X. steffeni*. On the forewing the cell enclosing the nygma is generally absent.

Description

Adult male. Forewing length 3.3-3.7 mm; pale brown in alcohol. Legs pale yellow, tibia of hind legs distinctly darker, except at the proximal end. Maxillary palp in increasing order of length (I-II-III)-IV-V, segment IV shorter than sum of segments I-II-III. Spur formula 2, 4, 3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; Sc reaching C subapicaly, apically bent and meeting R1; fork II petiolate at discoidal cell; thyridial cell slightly shorter than discoidal cell; three anal veins present. Opaque pterostigma present. Hindwing fork II and fork V present; R1 absent. Sternum V bearing pair of anteroventral reticulated regions.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a broad concave incision; posterior margin produced as a pair of lobes with undulate to rounded margins, lobes divided by an incision that reaches the transversal line of tergum IX. Sternum IX, in lateral view, about 2x longer than tall, apex deltoid, anterior apodeme filiform, straight, tapering to a slender flange; in ventral view, almost rounded, posterior margin with a shallow concave incision. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, tapering apically, apex membranous, with sensilla, medially cleft until sclerotized band. Preanal appendage more than 2x longer than tergum IX, setose; in lateral view, sigmoid, slightly enlarged apically; in dorsal view, subbasally enlarged. Inferior appendage more than 2x tergum IX length, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region 2x longer than basal region; in dorsal view, inner face with a set of stout spines, spines enlarged near the region of the mesal sclerite; mesal sclerite simple with about two apical points; in lateral view, as a conspicuous spine. Phallus tubular, long and slender, in lateral view phallobase wide; apex straight enlarged apically, weakly sclerotized.

Distribution

Brazil (Goiás, Mato Grosso).

Xiphocentron **sp. n. 3**

Figures 15A–F, 17A–D, 19A

Type material

Holotype. **BRAZIL: Paraná**: ♂ (DZRJ) Guaraqueçaba: Ribeirão do Engenho, 25º10′31.00″S, W48º22′16.20″W, 25m, 25.i.2011 (JL Nessimian, LL Dumas).

Diagnosis

The diagnostic characters are the very elongated inferior appendage (about three times longer than tergum IX), inner face of inferior appendage without pointed spines, just with a crenulated area with a rounded mesal sclerite without any spine. Also, the posterior margin of sternum IX has a short and deeper apical incision. The fork II is sessile on fore and hindwings.

Description

Adult male. Forewing length 4.6 mm; yellowish brown in alcohol. Legs pale yellow, tibia of hind legs distinctly darker, except at the proximal end. Maxillary palp in increasing order of length (I-II-III)-IV-V, segment IV shorter than sum of segments I-II-III. Spur formula 2, 4, 3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; Sc reaching C subapically, apically bent, meeting R1; fork II sessile at discoidal cell, with a crossvein between R4 and R5; thyridial cell shorter than discoidal cell; three anal veins present. Opaque pterostigma present. Hindwing fork II and fork V present; R1 absent. Sternum V bearing pair of anteroventral reticulated glandular regions.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a shallow concave incision; posterior margin produced as a pair of rounded lobes divided by a concave incision. Sternum IX, in lateral view, about as long as tall, truncated at apex with a small projection, anterior apodeme filiform, straight, tapering to a slender flange; in ventral view, almost rounded, posterior margin hoof-like with a small concave incision. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, wide basally, tapering apically, apex membranous, with sensilla, medially cleft. Preanal appendage about 3x longer than tergum IX, setose; in lateral view, sigmoid, width most sub equal throughout the length, slighly tapering at apex, apex truncate; in dorsal view, sub-basally slightly produced mediad, narrow at mid-length, slightly tapering apically. Inferior appendage about 3x longer than tergum IX, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate, apex slightly enlarged; in lateral view, apical region about 2x longer than basal region; in dorsal view, inner face crenulated, without conspicuous spines; mesal sclerite small, rounded; in lateral view tooth–like, without spines. Phallus tubular, long and slender, in lateral view, phallobase wide; apex straight enlarged apically, weakly sclerotized.

Distribution

Brazil (Paraná).

Xiphocentron kamakan **Vilarino & Calor, 2015**

Figures 16A–D, 19B

Xiphocentron kamakan (Antillotrichia) Vilarino & Calor, 2015:47 [Type locality: Brazil, Bahia, Camacan, RPPN Serra Bonita, Córrego 3, Chuchuzeiro, 15°23′03″S, 039°34′00″W; MZUSP; ♂].

Material examined. **BRAZIL: Alagoas**: 1♂, 1♀ (DZRJ) Quebrangulo: REBIO de Pedra Talhada, Rio Caranguejo, acima do alojamento, 09º15′26,00″S; 36º25′07,90″W, 574m, 19.vi.2014, pensilvânia trap (APM Santos, DM Takiya, WRMS, ACD). **Minas Gerais**, 2♂ (UFMG) Nova Lima: 19°58′7.4″, S 43°51′22.7″W, malaise trap, 12–26.iv.2015 (AR Lima). 1♂ (UFMG) Itabirito: Vale dos Tropeiros, cachoeira dos cascalhos, 20º12′26,30″S, 43º38′34,10″W, 996m, 10.x.2010, (N Ferreira Jr.). **Bahia**: 1♂ (UFBA) Camacan: RPPN Serra Bonita, malaise trap I, iv.2011. Same data except: 1♂ (UFBA) viii.2011; 1♂ (UFBA) x.2011; 1♂ (UFBA) xii.2011; 1♂ (UFBA) iv.2012. 1♂ (UFBA) Varzedo: Fazenda Baixa da Areia (Sr. Getúlio). Ponto 4, 12º52′12.7″S, 39º28′32.4″W 510 m, 09.iv.2015. Malaise (ES Dias & R Campos).

Description. See Vilarino & Calor 2015

Distribution. Brazil (Alagoas [new record], Bahia, Minas Gerais [new record]).

Remarks. This is the only species in Brazil with very elongate inferior appendage that present a polyp-like mesal process. It is similar to the Caribbean species *X. prolixum* Flint, 1996 from Trinidad and Tobago, although *X. kamakan* has shorter inferior appendage, smaller spines and have an elbow shape curve before the narrow apical region. The species occurs along the São Francisco river Basin from northeastern Brazil until Minas Gerais state.

Xiphocentron acqualume **Rocha, Dumas & Nessimian, 2017**

Figures 18A–D, 19C

Xiphocentron acqualume (*Antillotrichia*) Rocha, Dumas & Nessimian, 2017:2 [Type locality: Brazil, Minas Gerais, Delfinópolis, surrounding area of Parque Nacional da Serra da Canastra, Ribeirão Dona Candinha (Pousada Acqualume), 20°19′56.5″S, 46°49′07.9″W; MZUSP; ♂].

Material examined. **BRAZIL: Goiás:** (DZRJ) 2♂ Alto Paraiso: PARNA Chapada dos Veadeiros, Córrego Rodoviarinha, 14º09′35,40″S; 47º49′33,40″W, 901m, 25–28.iii.2013, malaise trap, (APM Santos, DM Takiya).

Description. See Rocha et al. 2017

Distribution. Brazil (Minas Gerais, Goiás [new record]).

Remarks. X. acqualume has inferior appendage length and the inferior appendage spines like the Caribbean *X. prolixum*, however, *X. acqualume* has no mesal sclerite, differing from *X. prolixum* and *X. kamakan.* Also, the forewing has a cell enclosing the nygma. The species occurs on the Paraná and Tocantins Basins, with records from southern Minas Gerais and northern Goiás.

Xiphocentron copacabana **Vilarino & Cavalcante, 2018**

Figures 20A–B

Xiphocentron copacabana (*Antillotrichia*) Vilarino et al, 2018:4 [Type locality: Brazil, Rio de Janeiro State, Rio de Janeiro, Parque Nacional da Tijuca, Rio Archer, Cascata Gabriela, 22º57′16.0″S, 43°17′20.2″W; DZRJ; ♂].

Material examined. **BRAZIL: Rio de Janeiro:** 1 ♂ (MZSP 5411) Rio de Janeiro: Parque Nacional da Tijuca, 22º56′96.7″ S, 43°17′67.9″W, 786 m, x.2016 (L Silveira, S Vaz, B Clarkson).

Description. See Vilarino et al. 2018

Distribution. Brazil (Rio de Janeiro).

Remarks. This species is very similar to *X. maitea,* however, it has the forewing fork II sessile, a conspicuous mesal spine, and a narrower projection than *X. maitea*. *Xiphocentron maiteae* together with *X. copacabana*, and *X. saltuum* present the ventral margin of coxopodite produced posterad, a character typical of the *Cnodocentron* (*Caenocentron*), although the spines on the ventral margin of coxopodite that also are typical from *Cnodocentron* (*Caenocentron*) are not present in these species.

Xiphocentron maiteae **Vilarino & Calor, 2015**

Figures 21A–C

Xiphocentron maiteae (*Antillotrichia*) Vilarino & Calor, 2015:50 [Type locality: Brazil, Bahia, Camacan, RPPN Serra Bonita, Córrego 3, Chuchuzeiro, 15°23′03″S, 039°34′00″W; MZUSP; ♂].

Material examined. **BRAZIL: Bahia:** 1♂ (UFBA) Camacan: Serra Bonita, Malaise I, xii.2011. Same data except: 6♂(UFBA) Malaise III, ii.2009; 3♂(UFBA) Malaise I, x.2011; 3♂, 1♀(UFBA) Malaise I, ix.2012; 2♂(UFBA) Malaise I, x.2012. 1♂ (UFBA) Uruçuca: Serra Grande, Parque Estadual Serra do Conduru, Cachoeira da Trilha Principal, 14º29′48.5″S, 39º07′53.1″W, 227m. 18.i.2014. light pan trap (ES Dias & T Pereira).

Description. See Vilarino & Calor 2015

Distribution. Brazil (Bahia)

Remarks. X. maitea differs from other species with ventral projection of inferior appendage by the forewing fork II petiolate, by the shape of the coxopodite projection wider than *X. copacabana*, and by the absence of any conspicuous mesal sclerite.

***Xiphocentron* sp. n. 4**

Figures 22A–C, 23A, 24A–F

Type material

Holotype. **BRAZIL: Santa Catarina**: ♂ (UFBA) Florianópolis: Córrego Pantanal, 13.vii.2012, sweeping net (LC Pinho).

Paratypes. **BRAZIL: Santa Catarina**: 1♂ (UFBA), same data as holotype. 4♂, 1♀ (MZSP) Grão Pará: Parque Nacional Serra Furada, 30.ix.2016 (T Duarte, V Gomes, CB Floriano). **São Paulo**: 1♂ (MZSP) Iporanga: P.E. Intervales, i.2015, light trap, (PC Bispo et al).

Diagnosis

The new species can be differentiated from its congeners by the inferior appendage with the basoventral margin squarely projected with stout spines on the inner face, the mesal sclerite is seem as a more conspicuous spine with about three apical points.

Description

Adult male. Forewing length 3.5-3.6 mm; pale brown in alcohol. Legs pale yellow, tibia of hind legs darker. Maxillary palp in increasing order of length (I-II-III)-IV-V, I-II-III subequal, segment IV as long as II+III. Spur formula 2, 4, 3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; fork II sessile at discoidal cell; thyridial cell as long as discoidal cell; three anal veins present. Hindwing fork II and fork V present. Sternum V with pair of anteroventral cuticular reticulated regions.

Male genitalia. Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with a broad v-shaped incision; posterior margin produced as a pair of small rounded lobes divided by a concave incision that reaches near the transversal line of tergum IX. Sternum IX, in lateral view, about 2x longer than tall, truncated at apex, anterior apodeme filiform, straight, tapering to a slender flange; in ventral view, almost rounded, posterior margin with a shallow concave incision. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, wide basally, tapering apically, apex membranous, with sensilla, medially cleft. Preanal appendage about 2x longer than tergum IX, setose; in lateral view, slightly sigmoid, width most sub equal throughout the length, apex crenulated; in dorsal view, clavate, basally slightly produced mediad, narrow basally, enlarged at mid-length and apex. Inferior appendage less than 2x longer than tergum IX, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region about as long as basal region, ventral margin of basal region produced in a quadrate shape; in dorsal view, inner face with numerous spines; mesal sclerite as a longer spine with about 3 points; in lateral view, as a conspicuous spine. Phallus tubular, long and slender, in lateral view, phallobase wide; apex straight enlarged apically, weakly sclerotized.

Distribution

Brazil (Santa Catarina, São Paulo).

Xiphocentron jaguare **Rocha, Dumas & Nessimian, 2017**

Figures 25, 26A–E, 31A

Xiphocentron jaguare (*Antillotrichia*) Rocha, Dumas & Nessimian, 2017:5 [Type locality: Brazil, Minas Gerais, São João Batista do Glória, surrounding area of Parque Nacional da Serra da Canastra, Córrego da Taquara (Cachoeira do Oratório), 20°32′03.7″S, 46°22′50.5″W; DZRJ; ♂].

Material examined. **BRAZIL: Goiás**: (DZRJ) 148♂♀ Alto Paraiso: PARNA Chapada dos Veadeiros, córrego Rodoviarinha, 14º09′35,40″S; 47º49′33,40″W, 901m, 25–28.iii.2013, malaise trap, (APM Santos, DM Takiya).

Description. See Rocha et al. 2017

Distribution. Brazil (Minas Gerais, Goiás [new record]).

Remarks. The species bear a very distinctive diagnostic character on the maxillary palps in which the segment V is very reduced, being smaller than all other preceding segments (Figure 25). The eyes also are larger than in other species. Intrapopulation variations were observed on the forewing nygma that can be total, partially or not enclosed in a cell.

Xiphocentron redentor **Vilarino et al, 2018**

Figures 28A–E, 31C

Xiphocentron redentor (*Antillotrichia*) Vilarino et al, 2018:9 [Type locality: Brazil, Rio de Janeiro State, Rio de Janeiro, Parque Nacional da Tijuca, Gruta Paulo e Virgínia, Rio Archer, 22°57′15.3″S, 43°17′29.9″W; DZRJ; ♂].

Material examined. **BRAZIL: Rio de Janeiro:** 1♂ (DZRJ) Rio de Janeiro: Jardim Botânico, acima da represa, 12.iv.2000, (AA Huamantinco).

Description. See Vilarino et al. 2018

Distribution. Brazil (Rio de Janeiro)

Remarks. This specimen shows the dorsal sclerotized band on paraproctal process more clearly visible, and slightly variations on the apodemes of sternum IX and inferior appendages.

Xiphocentron tijuca **Vilarino et al, 2018**

Figure 24A–E

Xiphocentron tijuca (*Antillotrichia*) Vilarino et al, 2018:12 [Type locality: Brazil, Rio de Janeiro State, Rio de Janeiro, Parque Nacional da Tijuca, Gruta Paulo e Virgínia, Rio Archer, 22°57′15.3″S, 43°17′29.9″W; DZRJ; ♂].

Material examined. Paratype. **BRAZIL: Rio de Janeiro**: 1♂(DZRJ 7339), Rio de Janeiro, Parque Nacional da Tijuca, Cachoeira das Almas, Rio das Almas, 22°56′55.8″S, 43°17′09.6″W, 583 m, 11.x.2014, (BM Silva, LL Dumas, JL Nessimian, KA Estevão, F Quintarelli).

Additional material: **BRAZIL: Rio de Janeiro**: 9♂(DZRJ), Teresópolis. PN Serra dos Orgãos, Trecho de 2a ordem do Rio Paquequer, Trilha para Pedra do Sino, 22º27′26″S, 43º01′24″W, 2017m, 9.i–13.ii.2016 (DM Takiya, L Silveira). 3♂(DZRJ) same data except: 13.ii-05.iii.2016 (APM Santos, L Silveira).

Description. See Vilarino et al. 2018

Distribution. Brazil (Rio de Janeiro)

Remarks. The specimens from Teresópolis (Rio de Janeiro State), has the subbasal region mesally produced but not as abrupt as on the holotype, and the apex of inferior appendage also is not strongly bent. The species could be recognized by the sclerotized lateral regions on tergum IX (that forms the V-line at the middle of the tergum), the small and sparse spines on inferior appendage, and by the petiolate forewing fork II.

Xiphocentron maracanan **Vilarino et al, 2018**

Figures 26A–E, 28A–F, 29A–K

Xiphocentron maracanan (*Antillotrichia*) Vilarino et al, 2018:7 [Type locality: Brazil, Rio de Janeiro State, Rio de Janeiro, Parque Nacional da Tijuca, Rio Taquaruçú, 22°57′36.2″S, 43°17′36.2″W; DZRJ; ♂].

Analized material: **BRAZIL: Bahia**: 1♂ (UFBA) Varzedo: Faz. Baixa da Areia, malaise trap, 9.iv.2015 (ES Dias & R Campos). 10♂ (UFBA) Camacan: Serra Bonita, Malaise I, iv.2011. **Espírito Santo**: 1♂, 1♀(DZRJ) Pinheiros: Reserva Biológica Córrego dos Veados, Riacho Água Limpa, 10.ii.2009 (APM Santos). 1♂ (DZRJ) Domingos Martins: Pedra Azul, Rota do lagarto, 20º23′36.00″S, 41º01′01.20″W, 1170m, 31.iii.2011 (LL Dumas, CA Jardim). **Minas Gerais**: 6♂, 13♀ (UFMG) Nova Lima: Mata, 19°58′7.4″S, 43°51′22.7″W, 29.xi–13.xii.2015, malaise trap (AR Lima). **Rio de Janeiro**: 1♂ (DZRJ) Itatiaia: Penedo, afluente do rio das pedras, 22º25′02,00″S,44º32′50,00″W, 689m, 06.iii.2008 (LL Dumas, MR de Souza, RB Braga, JL Nessimian). 1♂ (DZRJ) Rio de Janeiro: Parque Nacional da Tijuca, 22°56′48.9″S, 43°17′32.3″W, 11.x.2014 (BM Silva, LL Dumas, JL Nessimian, KA Estevão & F Quintarelli).

(Morfotype II) - **Santa Catarina**: 2♂ (MZSP) Grão Pará: Parque Nacional Serra Furada. Rio Capea 28º11′26″S, 49º23′30″W, 15.x–16.xi.2012, malaise (LC Pinho, LS Gomes, AL Schlindwein). **São Paulo**: 1♂ (MZSP) Iporanga: P.E.T.A.R., Nucleo Ouro Grosso, Trilha Figureueiras, light pan-trap,13.ii.2017, LH Almeida. 1♂ (DZRJ) Iporanga: Estrada Apiaí-Iporanga, tributario 1ª ordem do rio Betani, 24º31′S, 48º41′W, 10.x.2011. LL Dumas, JL Nessimian.

Description. See Vilarino et al. 2018

Remarks.

The *Xiphocentron maracanan* can be differentiated from its congeners by the posterior margin of tergum IX, which has acute lobes with a deep v-shaped incision and the inferior appendage with a sclerotized elbow-shaped region at half-length, with small spines on the inner face and a small mesal sclerite with tinny spines apically.

The morphotypes from Bahia State (forewing length 3.7-3.6 mm) have slightly broader preanal appendage than the morphotypes collected in other states (Figure 33C), also the fork II of forewing was not distinctly narrower near the nygma (Figure 32A); in Minas Gerais State (forewing length 3.4-3.5 mm) in the same location, specimens with and without the narrowing region in the fork II were found, showing that there is a variation on this character. Additionally, the morphotype from Espírito Santo (forewing length 3.7mm), have inferior appendages slightly shorter (Figure 33F). Specimens from São Paulo State (Iporanga) (forewing length 4.1-4.3mm), and Santa Catarina State (Grão Pará) (forewing length 4.7mm) have a dorsal hump on the paraproct (Figure 33I), and the apical lobes of tergum IX are narrow, finger-like (Figure 33J). These lobes of tergum IX are long on a yellowish-brown species from São Paulo State (Iporanga) and short on the dark-brown species also from Iporanga, and from Santa Catarina State. The species show a broad distribution along the Atlantic coast from northeastern Brazil to southern Brazil.

Distribution

Brazil (Bahia [new record], Espírito Santo [new record], Minas Gerais [new record], Rio de Janeiro, Santa Catarina [new record], São Paulo [new record]).

***Xiphocentron* sp. n. 5**

Figures 30A–E, 31D, 35A–G

Type material

Holotype. **BRAZIL: Santa Catarina:** ♂ (UFBA) Urubici: Morro da Igreja, 17.viii-06.i.2006, malaise trap, (LC Pinho & L Bizzo).

Paratypes. 8♂, 5♀ (UFBA), same data as holotype.

Diagnosis

This species can be recognized by the stout spines mainly near the mesal sclerite, the mesal sclerite simple, the apical lobes of tergum IX undulated, with the medial incision reaching the transversal line of tergum IX, and the fore and hindwing fork II sessile.

Description

Adult male. Forewing length 4.3-4.4 mm; translucid in alcohol. Legs pale yellow, tibia of hind legs distinctly darker, except at the proximal end. Maxillary palp in increasing order of length (I-II-III)-IV-V, segment IV shorter than sum of segments I-II-III. Spur formula 2, 4, 3; hind legs with unmodified apical spur. Forewing fork II and fork IV present; Sc reaching C subapicaly, apically bent and meeting R1; fork II sessile at discoidal cell; thyridial cell slightly shorter than discoidal cell; three anal veins present. Wing with an opaque region on the anterior margin between Sc and R1 veins. Hindwing fork II and fork V present; R1 absent. Sternum V bearing pair of anteroventral reticulated regions.

Male genitalia.

Tergum IX, in lateral view, wider basally, narrower apically; in dorsal view, anterior margin with broad concave incision; posterior margin produced with pair of lobes with undulate to rounded margins, lobes divided by incision that reaches the transversal line of tergum IX. Sternum IX, in lateral view, about 2x longer than tall, apex deltoid, anterior apodeme filiform, straight, tapering to slender flange; in ventral view, almost rounded, posterior margin with shallow concave incision. Paraproctal process, in lateral view, oblong, apically produced in narrow ventral lobe; in dorsal view, each side fused, with sclerotized band on fusion region; wide basally, tapering apically, apex membranous, with sensilla, medially cleft until sclerotized band. Preanal appendage more than 2x longer than tergum IX, setose; in lateral view, sigmoid, slightly enlarged apically; in dorsal view, subbasally enlarged. Inferior appendage less than 2x tergum IX length, setose, coxopodite and harpago completely fused; broad basally, apical region slender, digitate; in lateral view, apical region slightly shorter than basal region; in dorsal view, inner face with set of stout spines, spines enlarged near the region of the mesal sclerite; mesal sclerite simple with about two apical points; in lateral view as conspicuous spine.

Phallus tubular, long and slender, in lateral view phallobase wide; apex straight slightly enlarged apically, weakly sclerotized.

Distribution

Brazil (Santa Catarina).

Xiphocentron sclerothrix Pes et al. 2013

Figure 36A–E, 37A–C

Xiphocentron sclerothrix (*Antillotrichia*) Pes & Hamada in Pes, et al., 2013:568 [Type locality: Brazil, Amazonas, Presidente Figureueiredo, igarapé da Caverna do Maroagoa, km 6 AM 240, 01°04′20.33″S, 59°58′54.24″W; INPA; ♂; ♀; pupa; biology]. —Paprocki & França, 2014:93 [checklist]. —Vilarino & Calor, 2015a:52 [♂; key].

Material examined.

Paratype. **BRAZIL: Amazonas**: 1♂, 1♀ (MZSP) Presidente Figueiredo: ″ramal do Castanhal, igarapé Canoas″; 11º49′51″S, 601º04′15″W, 04–18.viii.2008 (A.M.O. Pes; J.O. da Silva, A.P. dos Santos).

Description. See Pes et al. 2013

Distribution. Brazil (Amazonas, Amapá).

Remarks. This species has the inferior appendage spines elongate, dense and arranged in line along the harpago, a stalked mesal sclerite is not formed, but instead a group of conspicuously elongate spines occur in the same position. This kind of arrangement of spines is the same that occurs in *Sphagocentron* and in most species from the Antilles.

CONCLUSIONS

For a long time only two possibilities were available when someone tried to determine a *Xiphocentron* collected in Brazil, they were fitted into *X. steffeni* or *X. ilionea*. The rarity in which *Xiphocentron* species are collected in regular light traps (rendering few individuals for comparative analysis), in addition to the subtle although diverse differences present on the genitalia shape and inferior appendage spines makes very challenging a taxonomic work in this group. Only recently taxonomic studies on *Xiphocentron* has been performed on the Brazilian fauna with the works of Pes et al. (2013) on Amazon species; Vilarino & Calor (2015) on northeastern Brazil species; Rocha et al. (2017) on southern Minas Gerais species; and Vilarino et al. (2018) on southeastern Brazil Atlantic coast species. In this current study, we provide a comprehensive documentation of the regional morphological diversity of this genus in Brazil (which now has 17 species recorded). Species polymorphism was characterized, from color, to venation and genitalia, giving a foundation for future comparative studies aiming to clarify the dynamics of these variations and their significance or not as a marker for species genetic flow. Therefore, the species here presented might be split apart or lumped as more morphological information (e.g. ultrastructure) and new molecular data are available, and all this variation become better understood. We hope this study spurs new researches on this poorly known insect group and further improves our knowledge and understanding of their diversity, morphology, and ecology.

Key to Neotropical genera of Xiphocentronini

1. Mesoescutal setal warts modified in a quadrate mesoprescutum. Phallus tubular extremely elongated (reaching the segment V), without internal sclerites… (Xiphocentronini)..2

\- Mesoescutal setal warts absent or rounded. Phallus not so elongated, sclerite and spines absent or present... **other groups**

2(1) Apicoventral margin of sternum IX, between the inferior appendages, with a patch of points, lobes, or stout setae. Inferior appendage strongly bifurcated, with the basal article (gonocoxite) forming a long lobe ....***Cnodocentron***

\- Apicoventral margin of sternum IX without conspicuous set of spines, or setae; inferior appendage linear, basal article broad not strongly produced, apically elongated and digitate 3

3(2) Inferior appendage with coxopodite and hapago clearly distinct, base of harpago strongly sclerotized, overall covered with tubercles and short spines and forming a mesoventral flap, apical portion extremely elongated ....***Machairocentron***

\- Inferior appendage with coxopodite and harpago fused or not, base of harpago (apical article) never forming a mesoveltral flap, with lines or patches of spines, sometimes forming a distinct mesal sclerite ....***Xiphocentron***

Key to *Xiphocentron* species from Brazil.

1 Inferior appendage ventral margin produced posterad (Figures 20–22A).............. 2

\- Inferior appendage ventral margin linear to wavy, not conspicuously produced 4

2(1) Inferior appendage ventral projection quadrate ....***X.* sp. n. 4**

\- Inferior appendage ventral projection rounded..3

3(2) Forewing fork II petiolate, inferior appendage spines broad, dentate, placed at the margins of the ventral projection ....***X. maiteae***

\- Forewing fork II sessile, inferior appendage spines sort, tubercle-like, placed at the margins of the ventral projection, at the base of the finger-like dorsal projection, and some spines spread on the mesal area ....***X. copacabana***

4(1) Inferior appendage with a polyp-like mesal sclerite, with apex covered of spines..5

\- Inferior appendage with more or less conspicuous mesal spines.............................9

5(4) Inferior appendage very elongate (more than 2x tergum IX length), with a sclerotized elbow-like spinous region near the base of finger-like projection...***X. kamakan***

\- Inferior appendage not so elongated (2x or less tergum IX length), spines spread along mesal margin, without a sclerotized elbow-like spinous region 6

6(5) Inferior appendage spines elongate and occurring in high density; preanal appendage subapically enlarged; sternum IX posterior margin with an acute incision ....***X. steffeni***

\- Inferior appendage spines shorter and sparser; preanal appendage subapically linear or enlarged; sternum IX posterior margin concave to undulate.....................7

7(6) Tergum IX apical margin with a concave mesal incision; sternum IX posterior margin concave; preanal appendage subbasally without conspicuous mesal projection...8

\- Tergum IX apical margin with a squared mesal notch, sternum IX posterior margin undulate; preanal appendage subbasally with conspicuous mesal projection..***X.* sp. 1**

8(7) Tergum IX apical margin with acute lobes, and closer to each other, preanal appendage not enlarged subapically, inferior appendage spines acute ......***X. ilionea***

- Tergum IX apical margin with rounded lobes, and spaced from each other; preanal appendage enlarged subapically, inferior appendage spines mostly rounded, tubercle like..***X*. n. sp. 2**

9(4) tergum IX apical margin with acute lobes; inferior appendage with a sclerotized elbow-like spinous region near the base of finger-like projection; sternum IX posterior margin with a deep concave incision..................................***X. maracanan***

- tergum IX apical margin with smooth rounded lobes; inferior appendage without a sclerotized elbow-like spinous region near the base of finger-like projection; sternum IX posterior margin straight, wavy, or smoothly concave 10

10(9) Inferior appendage very elongate, apical region length about 2x or more than basal region length...11

- Inferior appendage not so elongated, apical region length about as long as basal region length...12

11(10) Inferior appendage without spines, with simple mesal sclerite without apical spines. Apical region of inferior appendage not more than 2x basal region..***X*. sp n. 3**

- Inferior appendage mesal margin with spines, without any mesal sclerite. Apical region of inferior appendage more than 2x basal region.....................***X. acqualume***

12(10) Inferior appendage with dense elongate setae mesaly, region of mesal sclerite with a patch of elongate setae (Figure 36D) ....***X. sclerothrix***

- Inferior appendage with sparse, long or short spines, region of mesal sclerite with a single more conspicuous spine or without any spine 13

13(12) Inferior appendage spines elongated; tergum IX apical lobes very short and smooth; maxillary palp apical segment very short..................................***X. jaguare***

- Inferior appendage spines short to very short; tergum IX apex with produced rounded lobes; maxillary palp apical segment elongated 14

14(13) Inferior appendage ventral margin wavy to slightly produced.............***X. redentor***

- Inferior appendage ventral margin linear 15

15(14) Tergum IX with lateral sclerotized regions forming a V-shaped line at the middle of the tergum, apical lobes rounded; sternum IX posterior margin straight; inferior appendage spines in dorsal, ventral view, broad and numerous ....***X. tijuca***

\- Tergum IX without lateral sclerotized regions, apical lobes wavy; sternum IX posterior margin concave; inferior appendage spines, in dorsal and ventral views, sparse...***X.* sp. n. 5**

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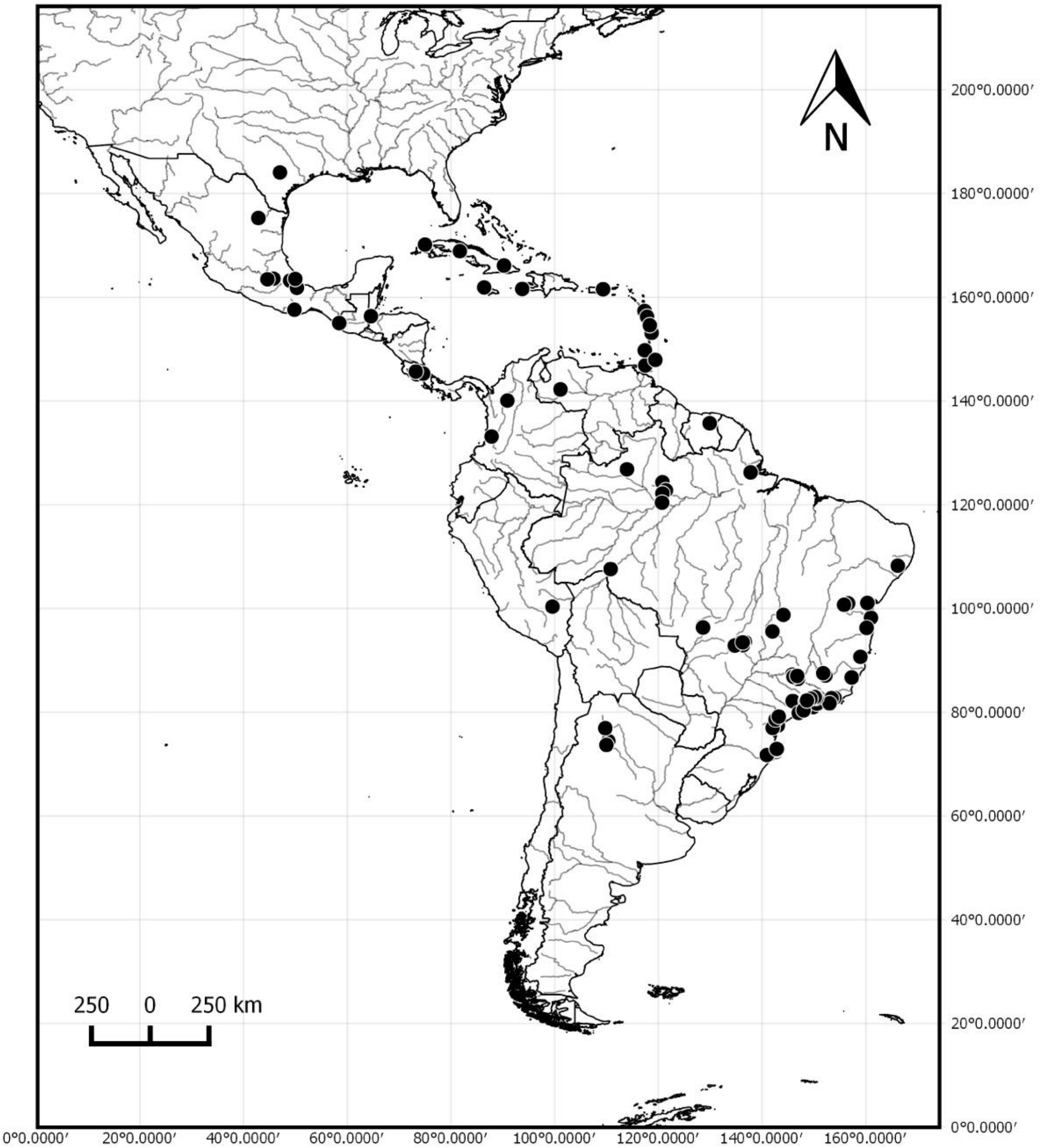


Figure 1. Distribution map of *Xiphocentron* species, including species analyzed on the present study.

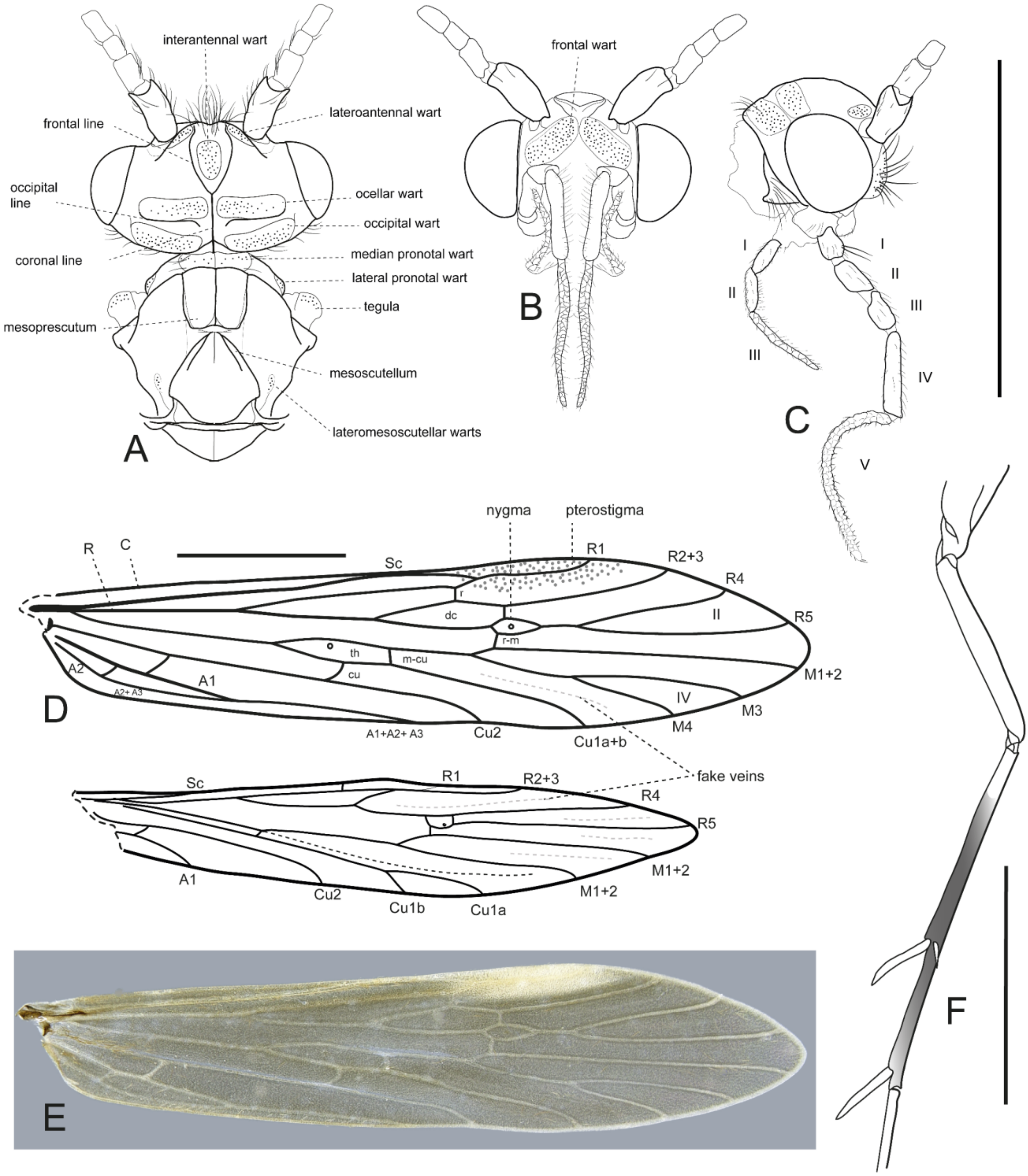


Figure 2. Adult of *Xiphocentron steffeni*: A. head, pro– and mesothorax, dorsal view; B. head, frontal view; C. head, right maxillary palp, lateral view; D. right forewing venation; E. right forewing aspect; F. hind leg, tibial spurs. Scale bar = 1 mm.

Figure 3. *Xiphocentron steffeni*: Forewing fork II variation: A. Santa Catarina (Grão Pará). B. Rio de Janeiro (Itatiaia). C. São Paulo (Campos do Jordão).

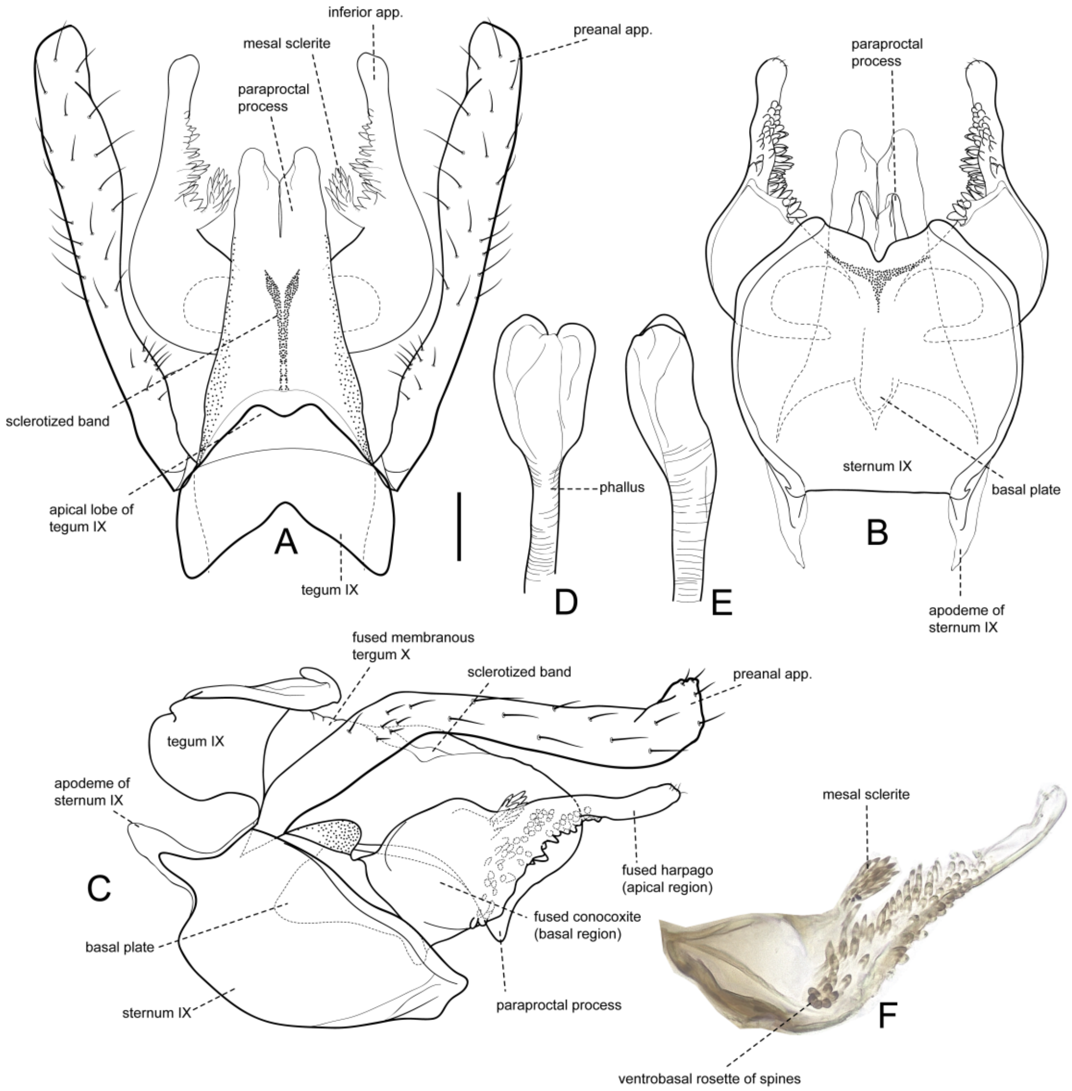


Figure 4. *Xiphocentron steffeni* from type locality. Male genitalia: A. dorsal; B. ventral; C. lateral; D. phallus, dorsal; E. phallus, lateral; F. photo showing detail of inferior appendage, latero-ventral. App. = appendage Genitalia scale bar = 0.1 mm.

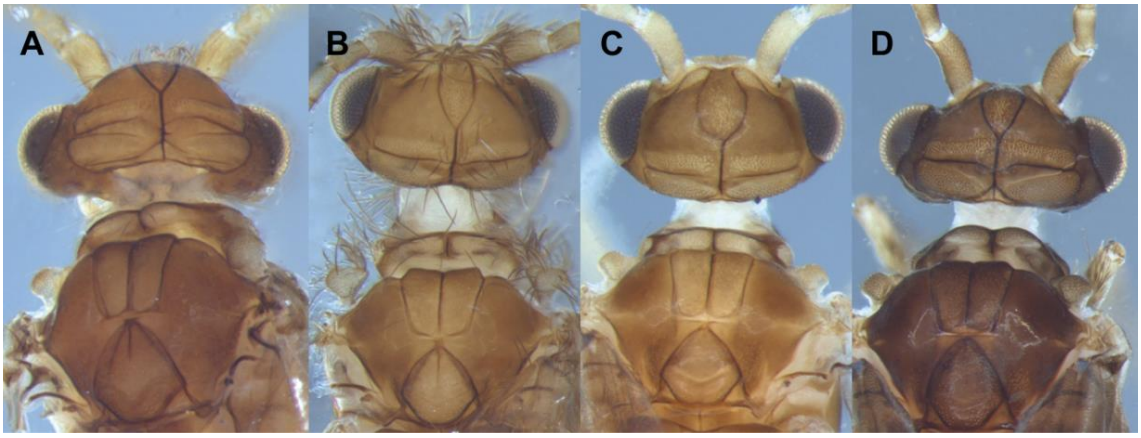


Figure 5. *Xiphocentron steffeni* aspect head and thorax, dorsal, morphotypes: A. São Paulo (Salesópolis); B. Santa Catarina (Grão-Pará); C-D. Rio de Janeiro (Itatiaia).

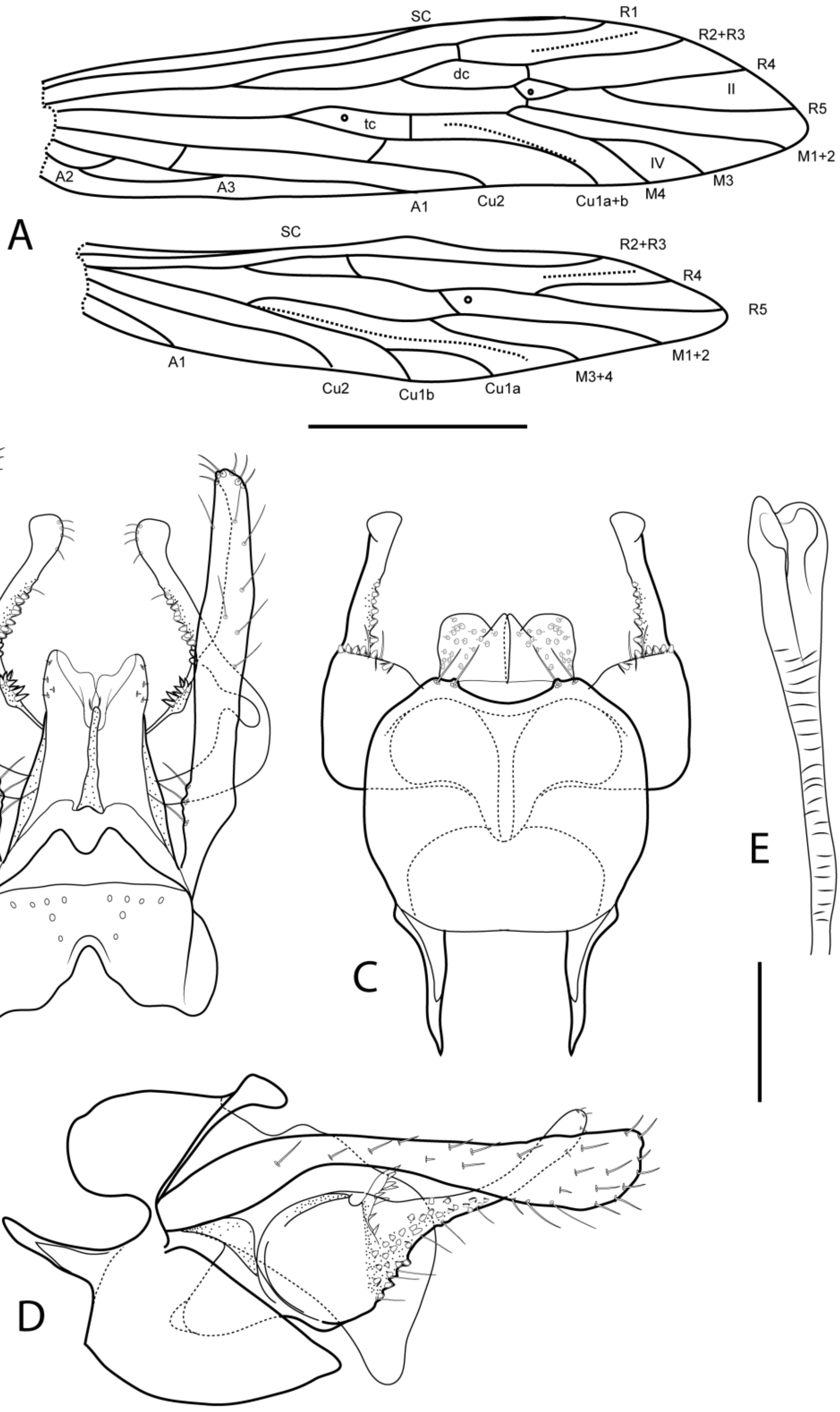


Figure 6. *Xiphocentron ilionea* Schmid, 1982, holotype male: A. forewing venation. Genitalia: B. dorsal; C. ventral; D. left lateral; E. phallus lateral. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm.

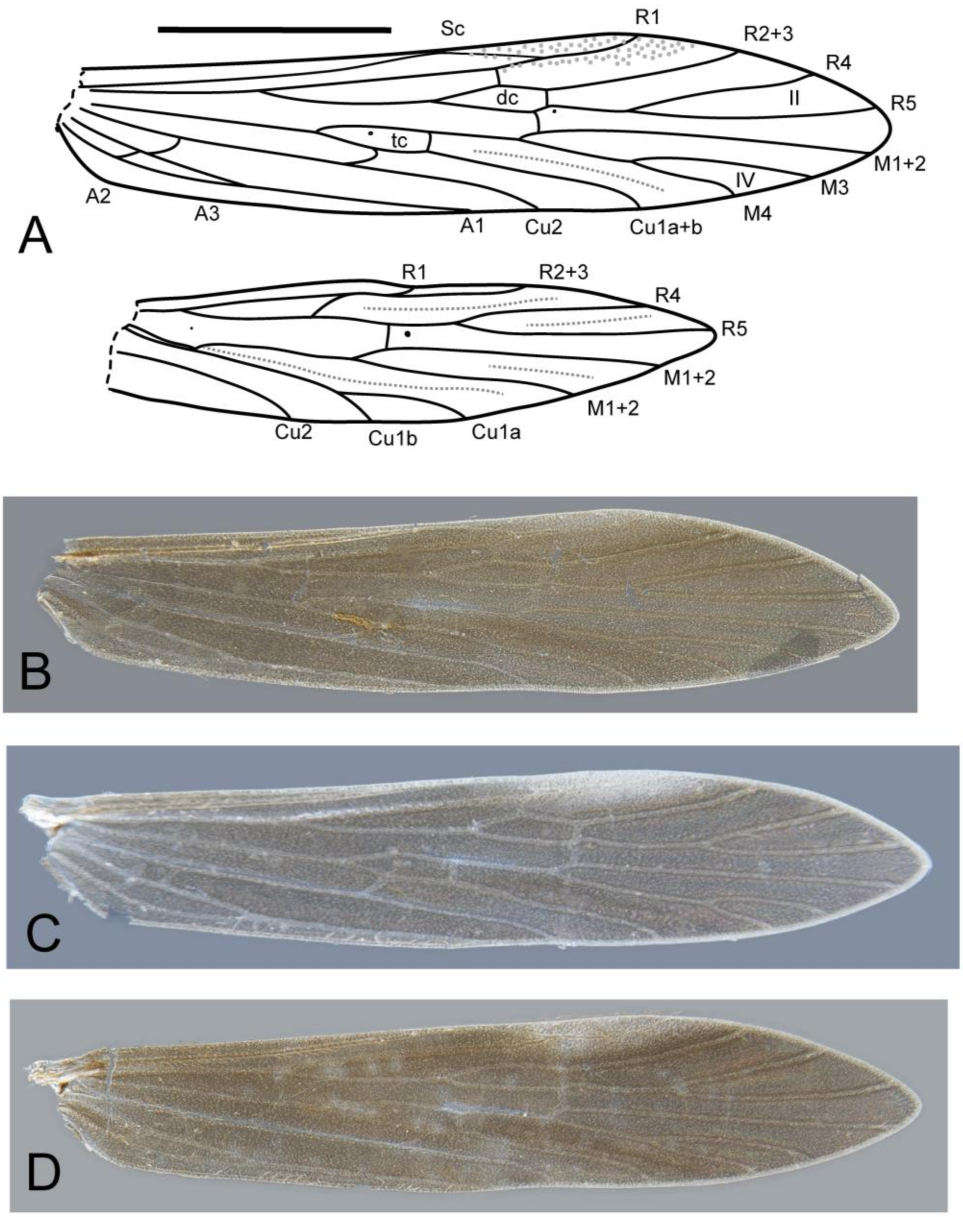


Figure 7. *Xiphocentron* sp. n. 1, Forewing: A. holotype male venation; B. aspect. C. aspect morphotype from Paraná (Morretes); D. aspect morphotype from São Paulo (Ubatuba). Wing scale bar = 1 mm.

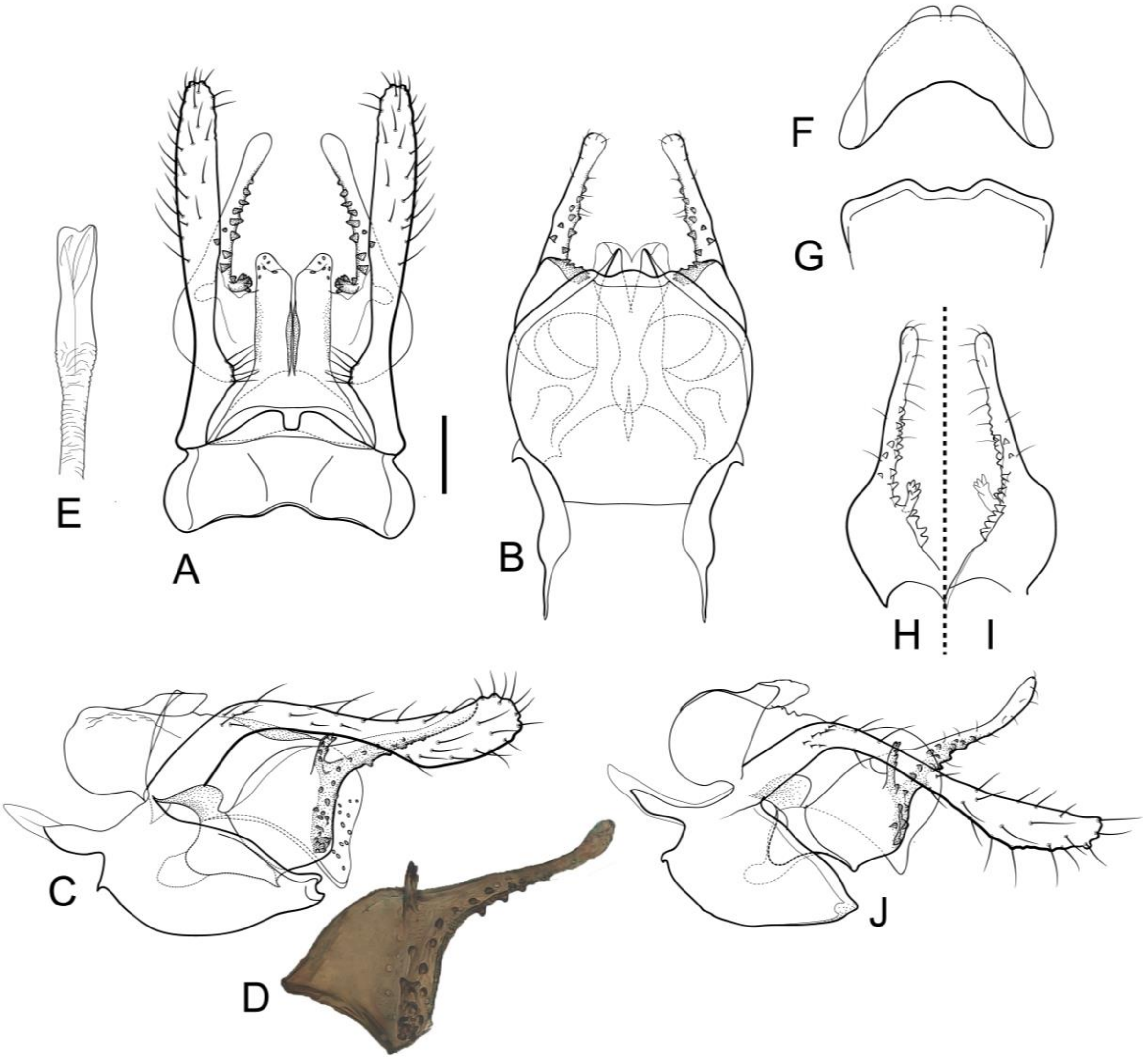


Figure 8. *Xiphocentron* sp. n. 1, Genitalia holotype male: A. dorsal; B. ventral; C. left lateral. D. photo of inferior appendage, lateral; E. phallus dorsal. F–J. Variations of morphotype from Paraná: F. tergum IX; G. sternum IX posterior margin; Inferior appendages: H. dorsal; I. ventral, J. genitalia left lateral. Genitalia scale bar = 0.1 mm.

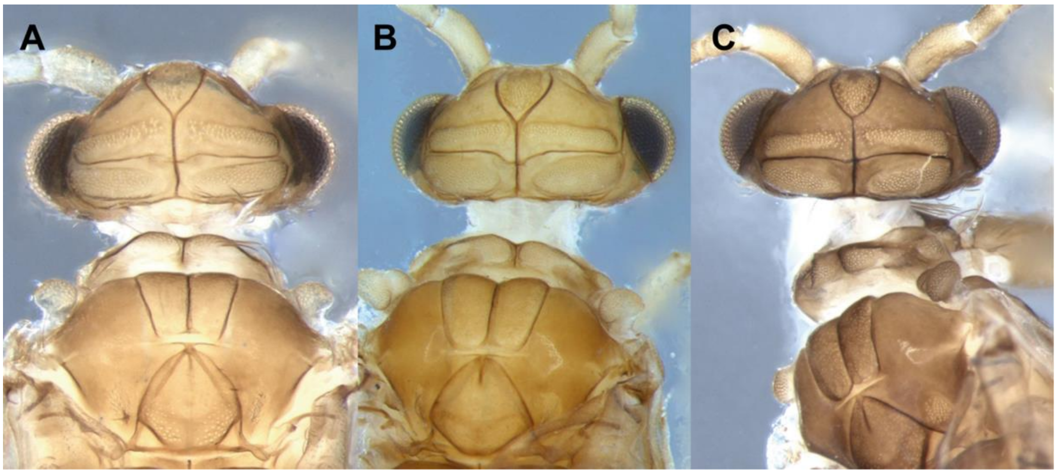


Figure 9. *Xiphocentron* n. sp. head and thorax, dorsal: A-B. *Xiphocentron* new species 1: A. specimen from Rio de Janeiro (Penedo); B. specimen from Paraná (Morretes). C. *Xiphocentron* new species 3, from Goiás, (Pirenópolis).

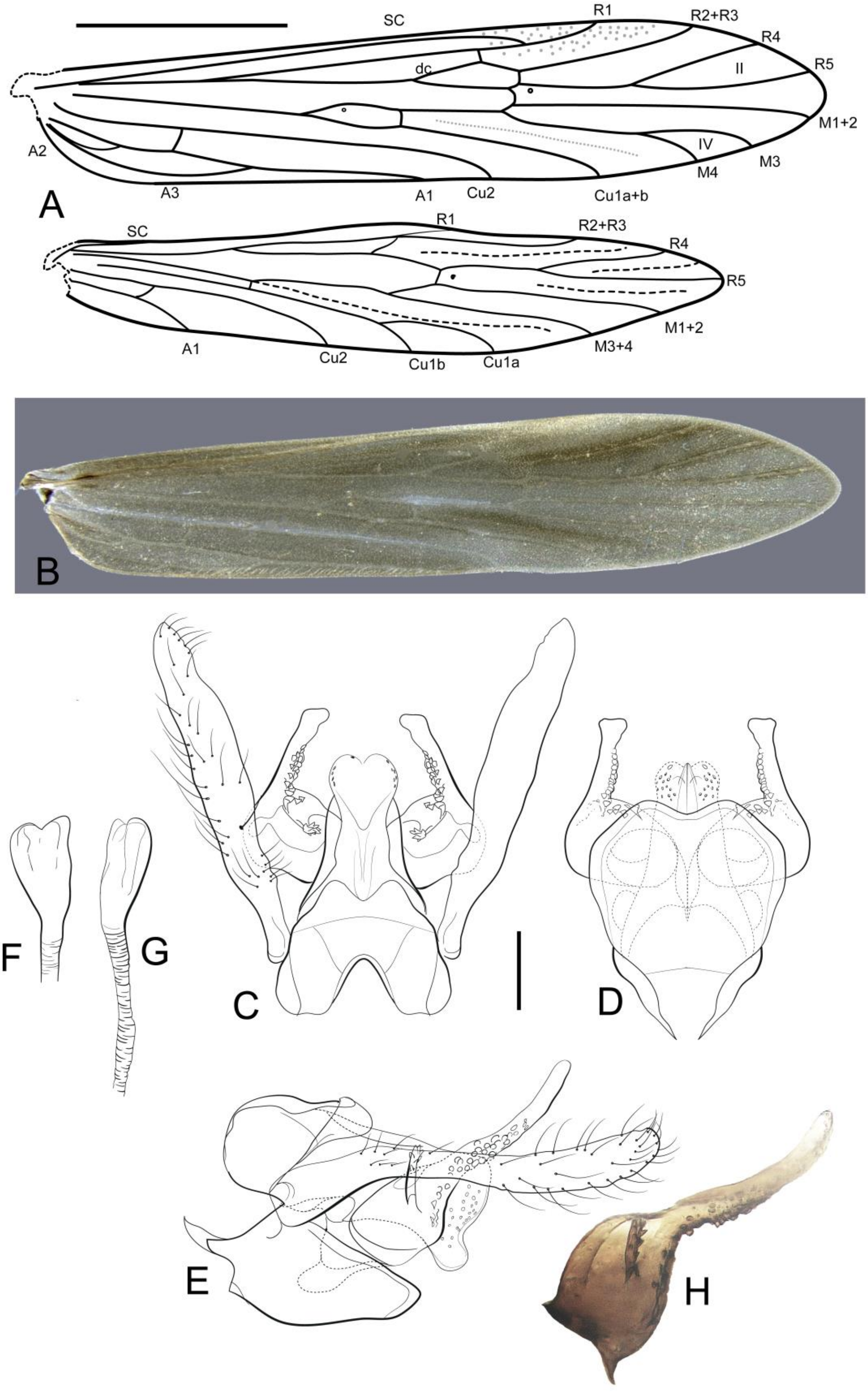
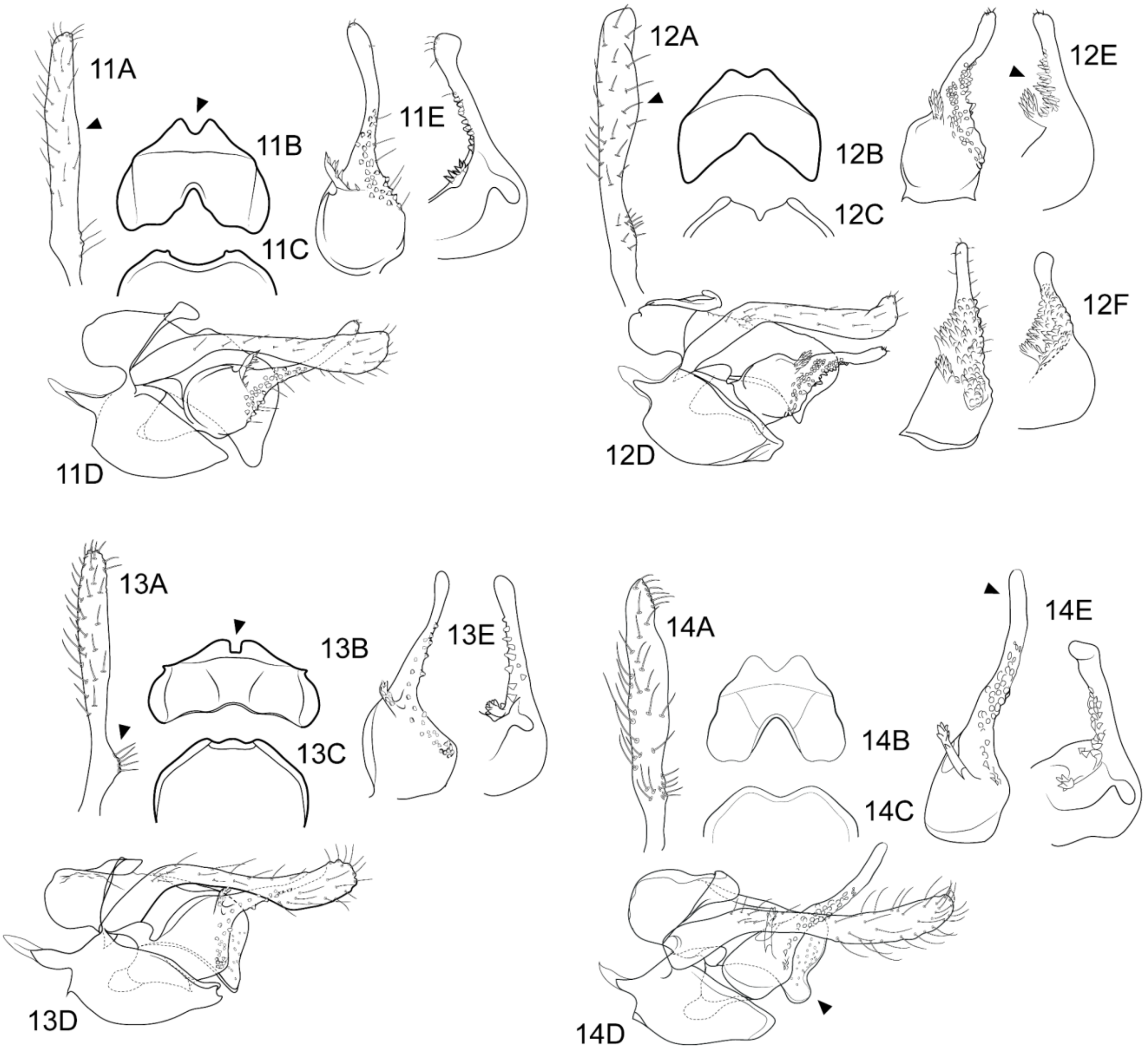


Figure 10. *Xiphocentron* sp. n. 2, holotype male: A. forewing venation; B forewing aspect. Genitalia: C. dorsal; D. ventral; E. left lateral; F. phallus dorsal; G. phallus lateral left. H. photo showing detail of inferior appendage, latero-ventral. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm



Figures 11-14. Species comparison, male genitalia. Arrows highlight diagnosable attributes. (11) *X. ilionea*; (12). *X. steffeni*; (13) *X.* sp. n. 1; (14) *X.* sp. n. 2. A. preanal appendage, dorsal; B. tergum IX, dorsal C. sternum IX posterior margin, ventral; D. genitália, lateral; E. inferior appendage lateral and dorsal respectively. F. *X. steffeni* inferior appendage variation from Santa Catarina (Grão Pará).

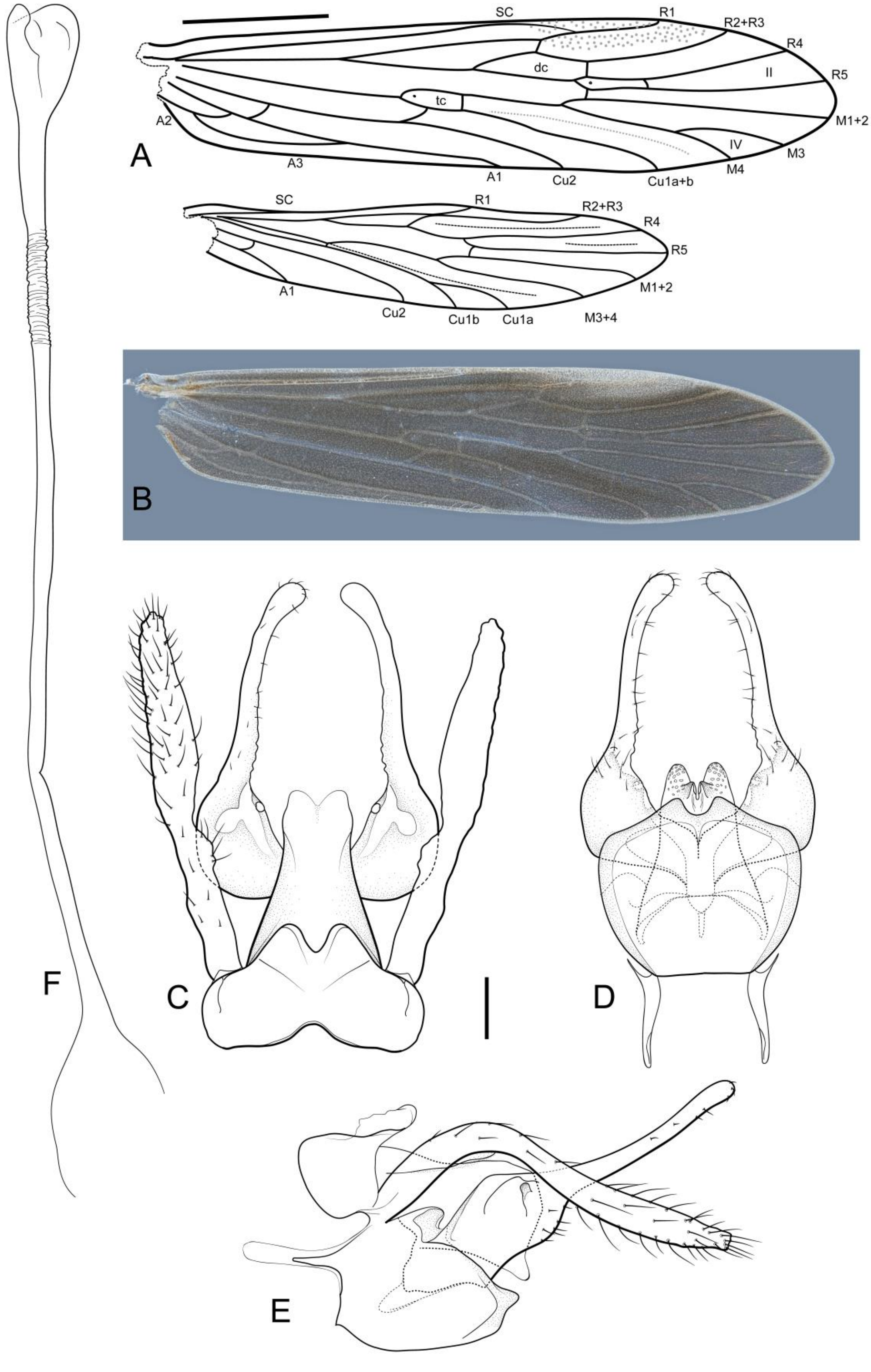
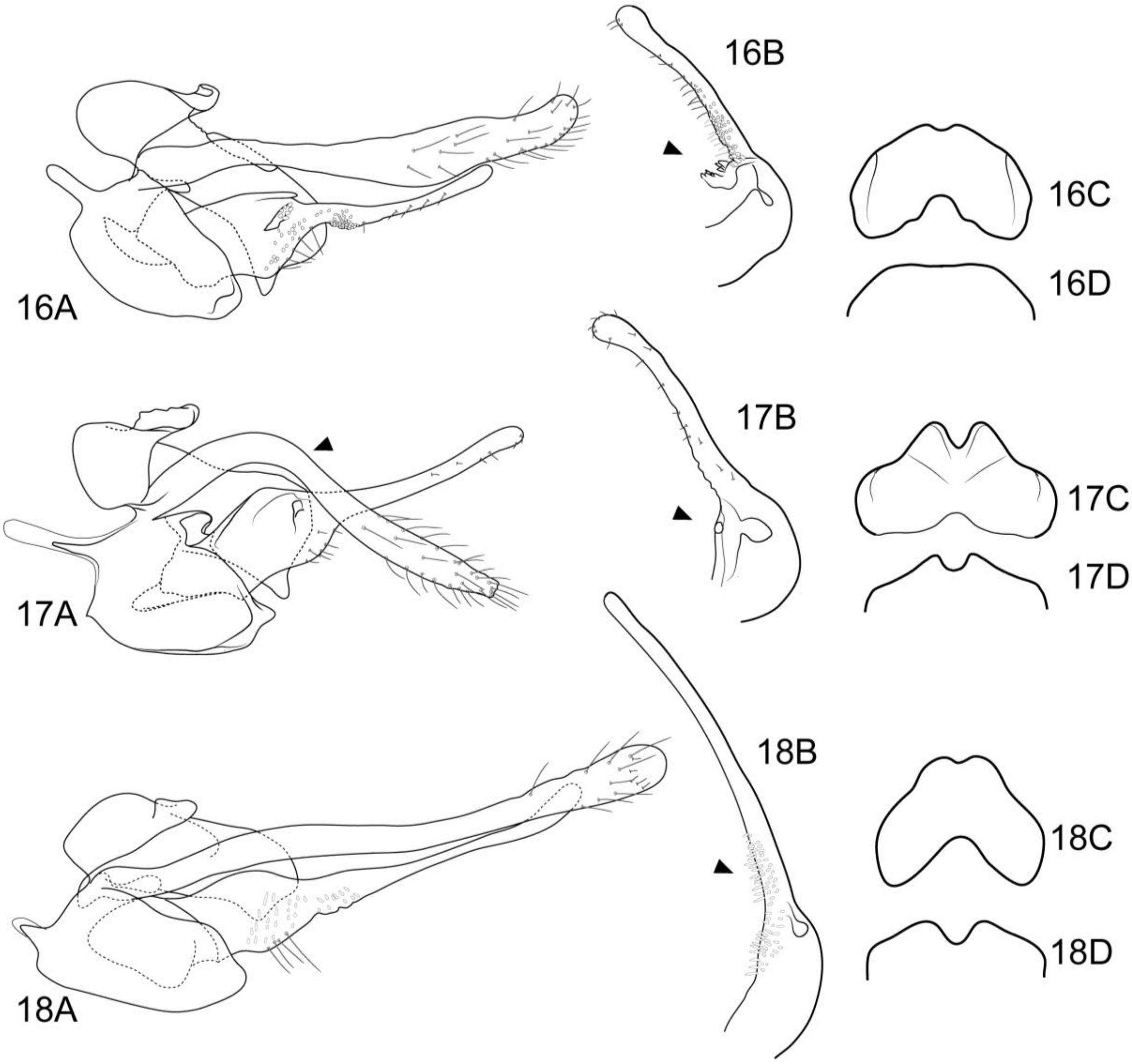


Figure 15. *Xiphocentron* sp. n. 3, holotype male: A. forewing venation; B forewing aspect. Genitalia: C. dorsal; D. ventral; E. left lateral; F. phallus in full length, dorsal. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm.



Figures 16-18. Species comparison, male genitalia. Arrows highlight diagnosable attributes. (16) *X. kamakan*; (17). *X.* sp. n.3; (18) *X. acqualume* (modified from Rocha et al. 2013): A. genitália, lateral; B. inferior appendage dorsal; C. tergum IX, dorsal D. sternum IX posterior margin, ventral.

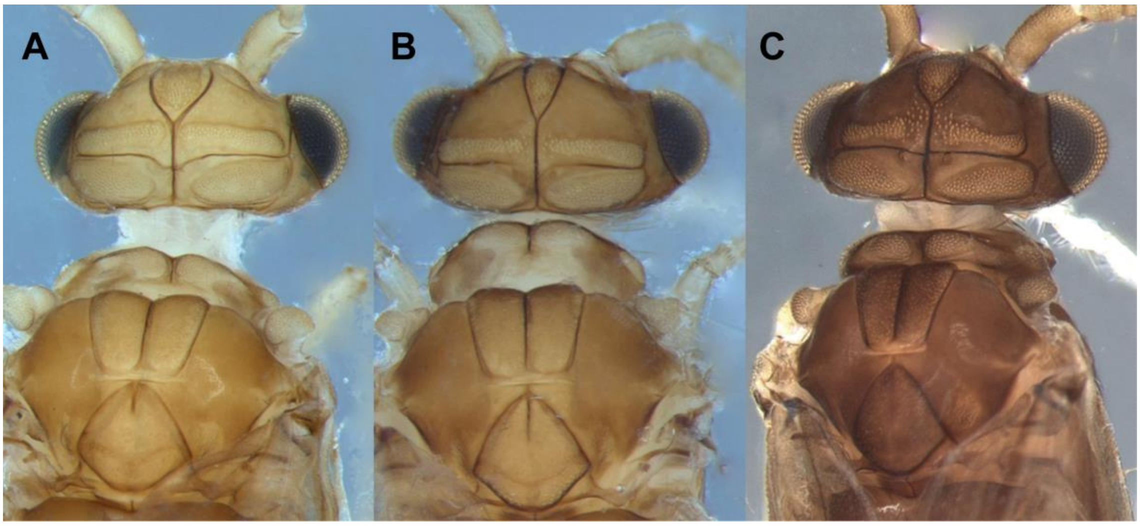
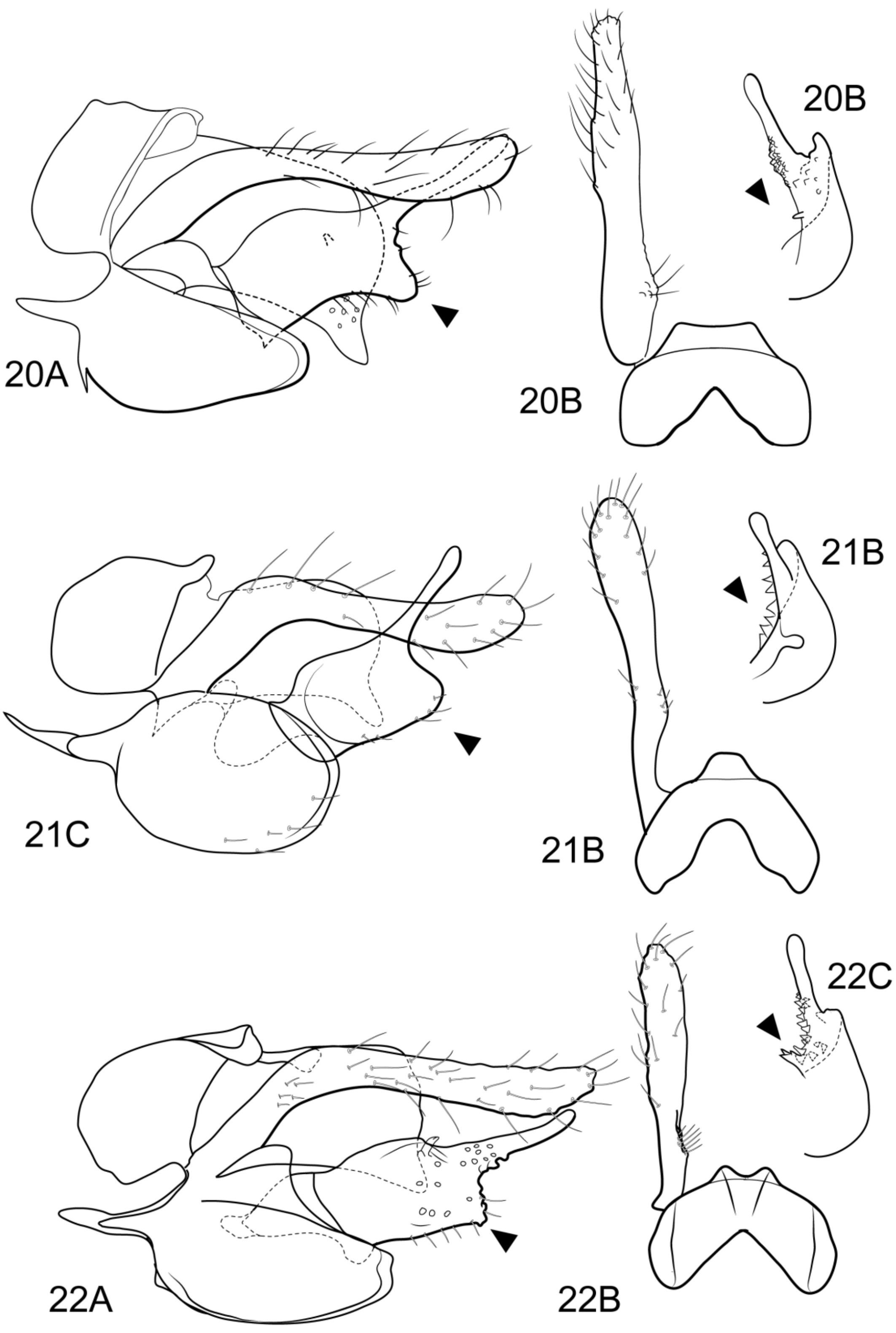


Figure 19. Adult *Xiphocentron* aspect head and thorax, dorsal, comparison: A. X. sp. n. 3; B. *X. kamakan*; C. *X. acqualume.*



Figures 20-22. Species comparison, male genitalia. Arrows highlight diagnosable attributes. (20). *X. copacabana* (modified from Vilarino et al. 2018); (21) *X. maeteae* (22) *X.* sp. n. 4: A. genitalia, lateral; B. preanal appendage and tergum IX, dorsal; C. inferior appendage, dorsal.

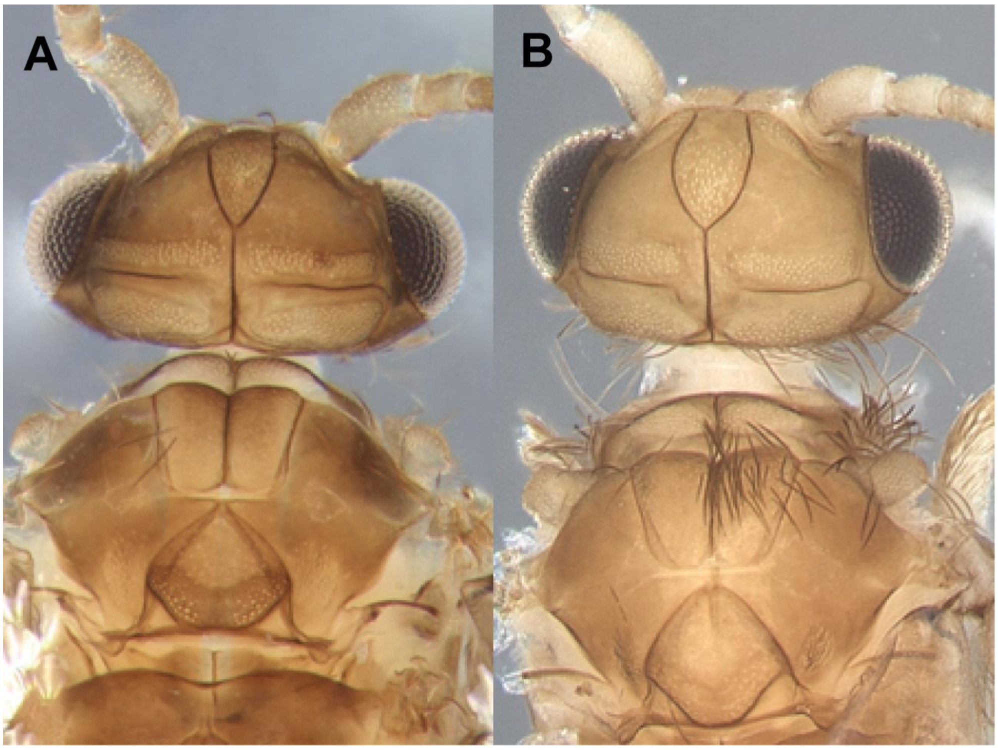


Figure 23. *Xiphocentron* head and thorax, dorsal: A. *X.* sp.n.4; B. *X. maiteae.*

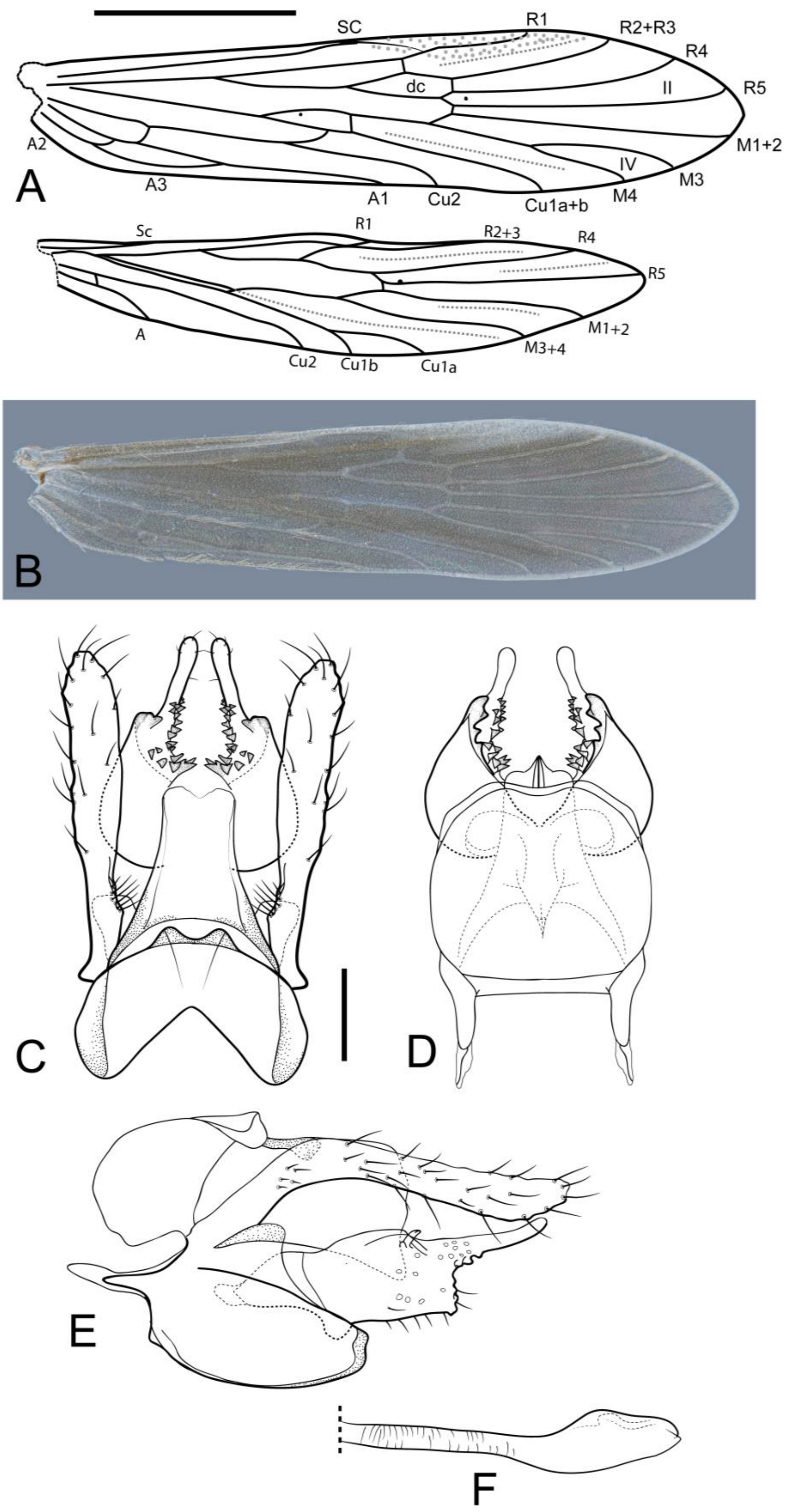
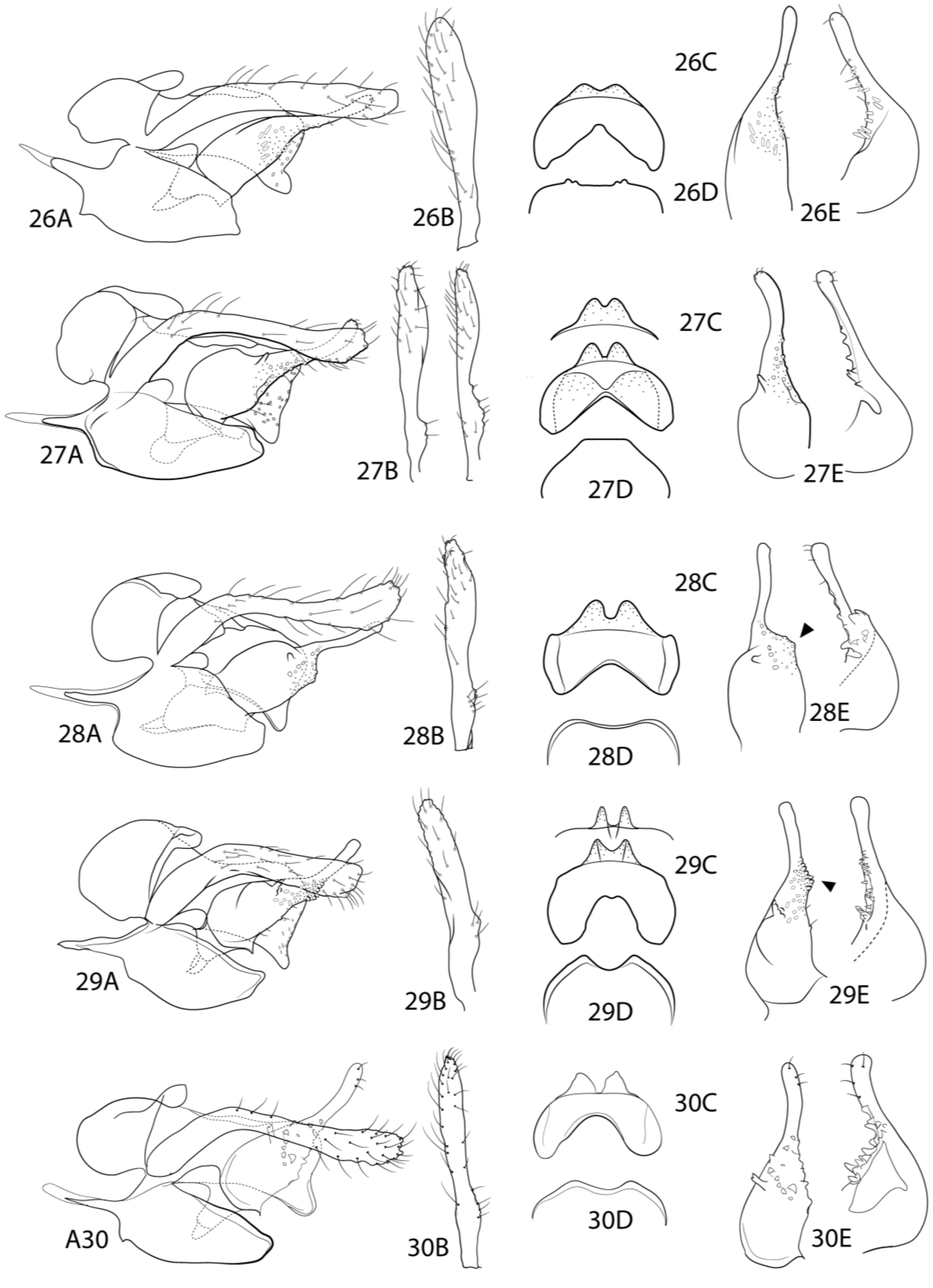


Figure 24. *Xiphocentron* sp. n. 4 holotype male: A. forewing venation; B forewing aspect. Genitalia: C. dorsal; D. ventral; E. left lateral; F. phallus lateral. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm.

Figure 25. *Xiphocentron jaguare* Rocha, Dumas & Nessimian, 2017. Head frontal and lateral respectively, showing the reduced length of 5th segment of maxillary palp.



Figures 26-30. Species comparison, male genitalia. Arrows highlight diagnosable attributes. A. genitalia, lateral; B. preanal appendage; C. tergum IX, dorsal; D. sternum IX, ventral. E. inferior appendage, lateral and dorsal, respectively. (26). *X. jaguare* from Goiás; (27) *X. tijuca* from Rio de Janeiro (Teresópolis), showing variation of B. preanal appendage and C. tergum IX from paratype; (28) *X. redentor*; (29) *X. maracanan* showing in C. variation of tergum IX, (30) X. sp. n. 5.

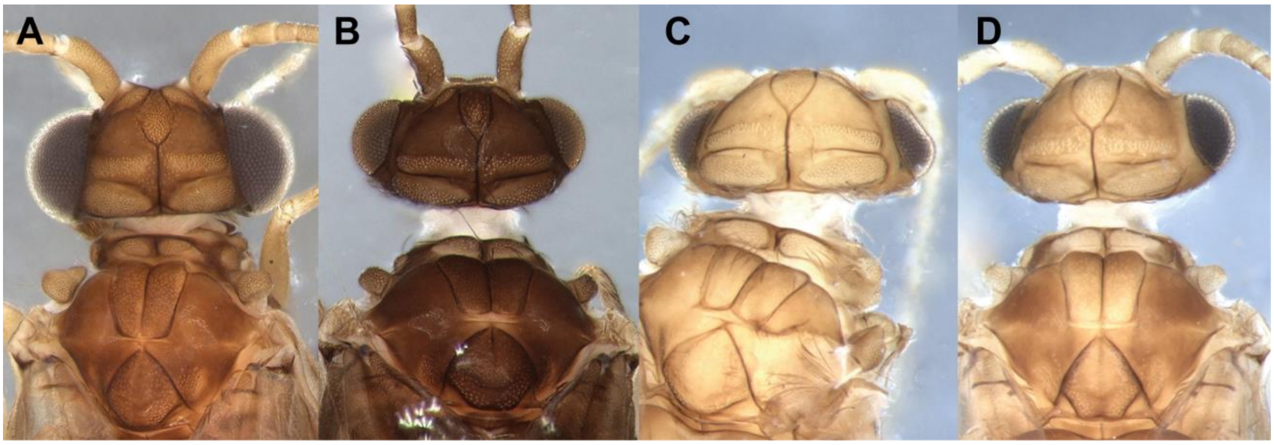


Figure 31. *Xiphocentron* head and thorax, dorsal, comparison: A. *X. jaguare*; B. *X. tijuca;* C. *X. redentor;* D. *X.* sp n. 4.

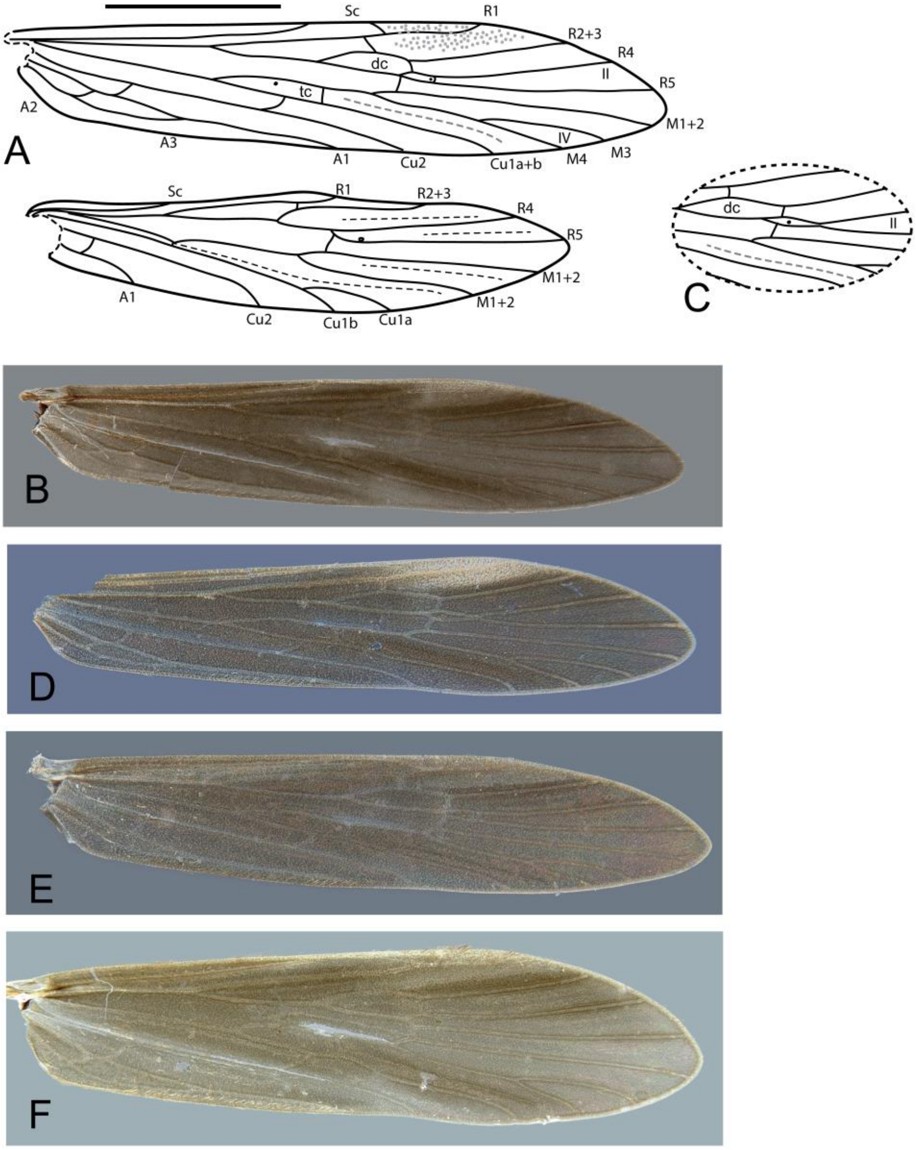


Figure 32. *Xiphocentron maracanan*, wings: A-B. specimen from Bahia: A. wing venation; B. forewing aspect. C-D. specimen from Espírito Santo: C. detail of variation; D. forewing aspect. E. specimen from Minas Gerais, forewing aspect. F. morphotype from São Paulo, forewing aspect. Wing scale bar = 1 mm.

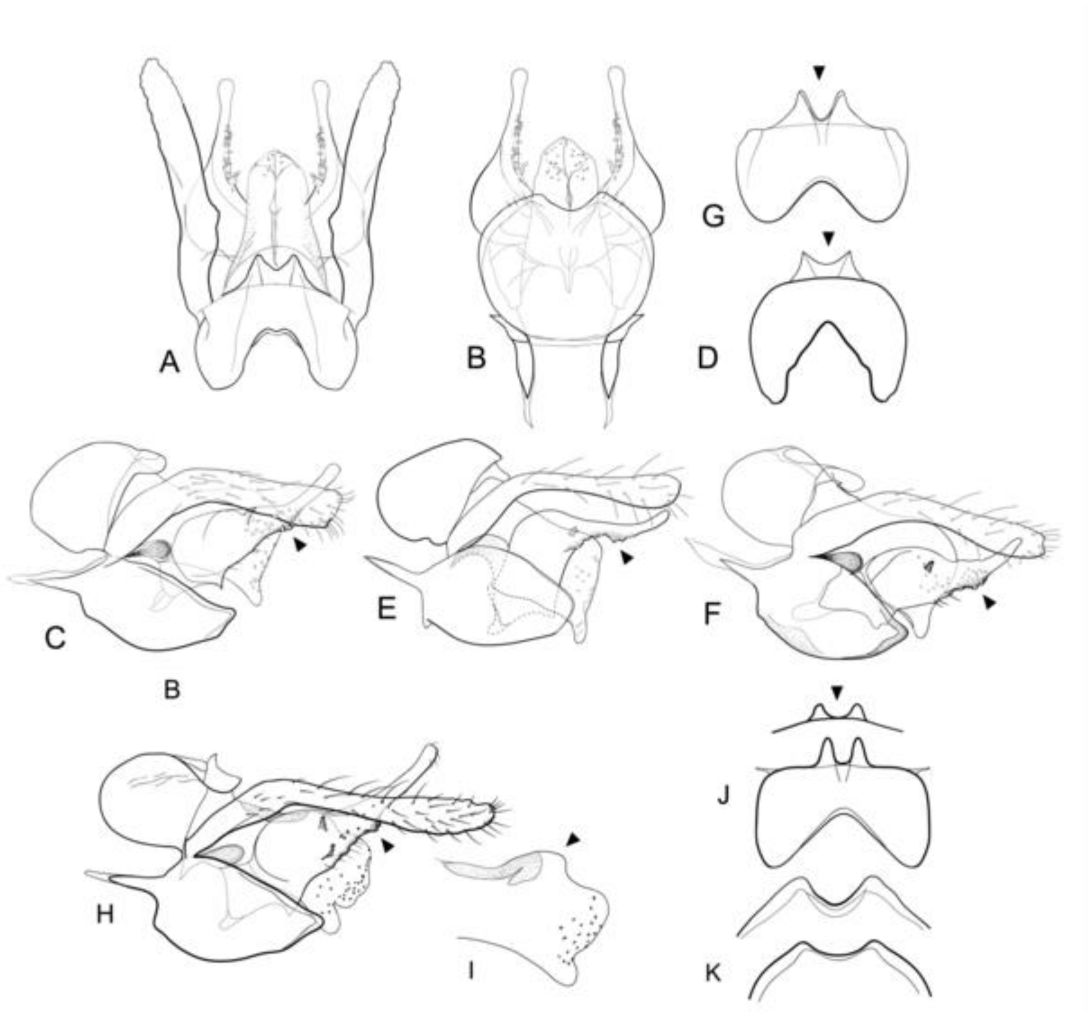


Figure 33. *Xiphocentron maracanan* male, genitalia variations: A-C. specimen from Bahia: A. Dorsal, B. ventral, C. lateral. D-E. specimen from Rio de Janeiro (holotype, after Vilarino et al. 2018) D. dorsal E. lateral. F-G. specimen from Espirito Santo: F. dorsal, G. lateral. H-K. morphotype from São Paulo and Santa Catarina. H. lateral, I. detail of paraproctal process, J. tergum IX, dorsal showing variation, K. sternum IX, ventral showing variation.

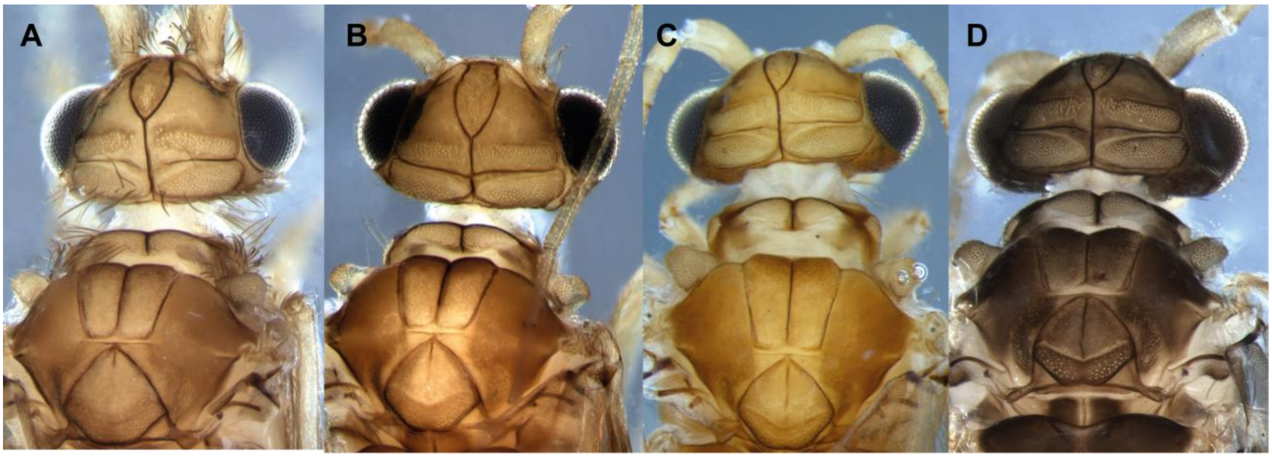


Figure 34. *Xiphocentron maracanan* head and thorax: Morphotypes from A. Bahia (Mucuge); B. Espirito Santo (Domingues Martins); C. São Paulo (Iporanga); D. Santa Catarina (Grão-Pará).

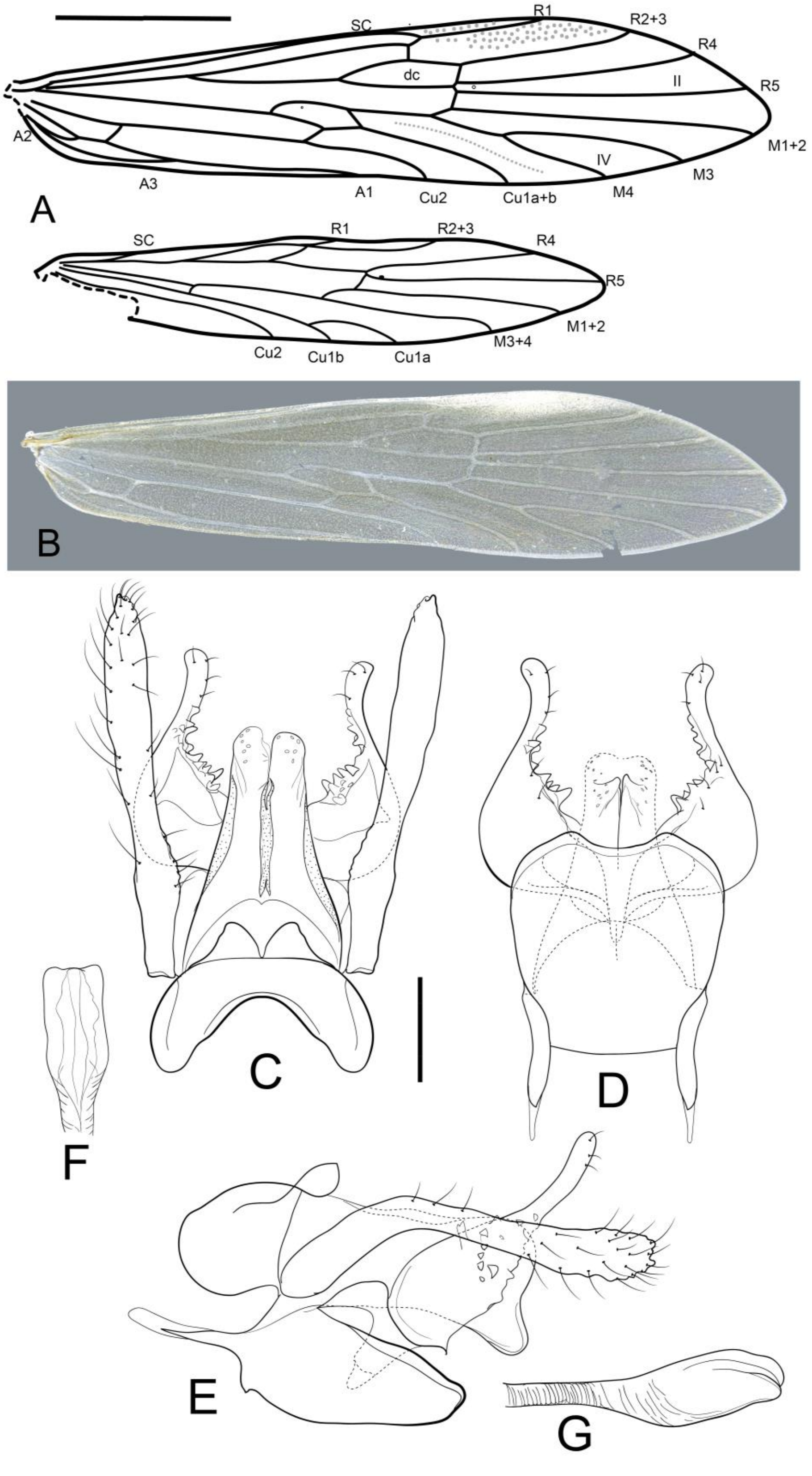


Figure 35. *Xiphocentron* sp. n. 5, holotype male: A. forewing venation; B forewing aspect. Genitalia: C. dorsal; D. ventral; E. left lateral; F. phallus dorsal; G. phallus lateral. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm.

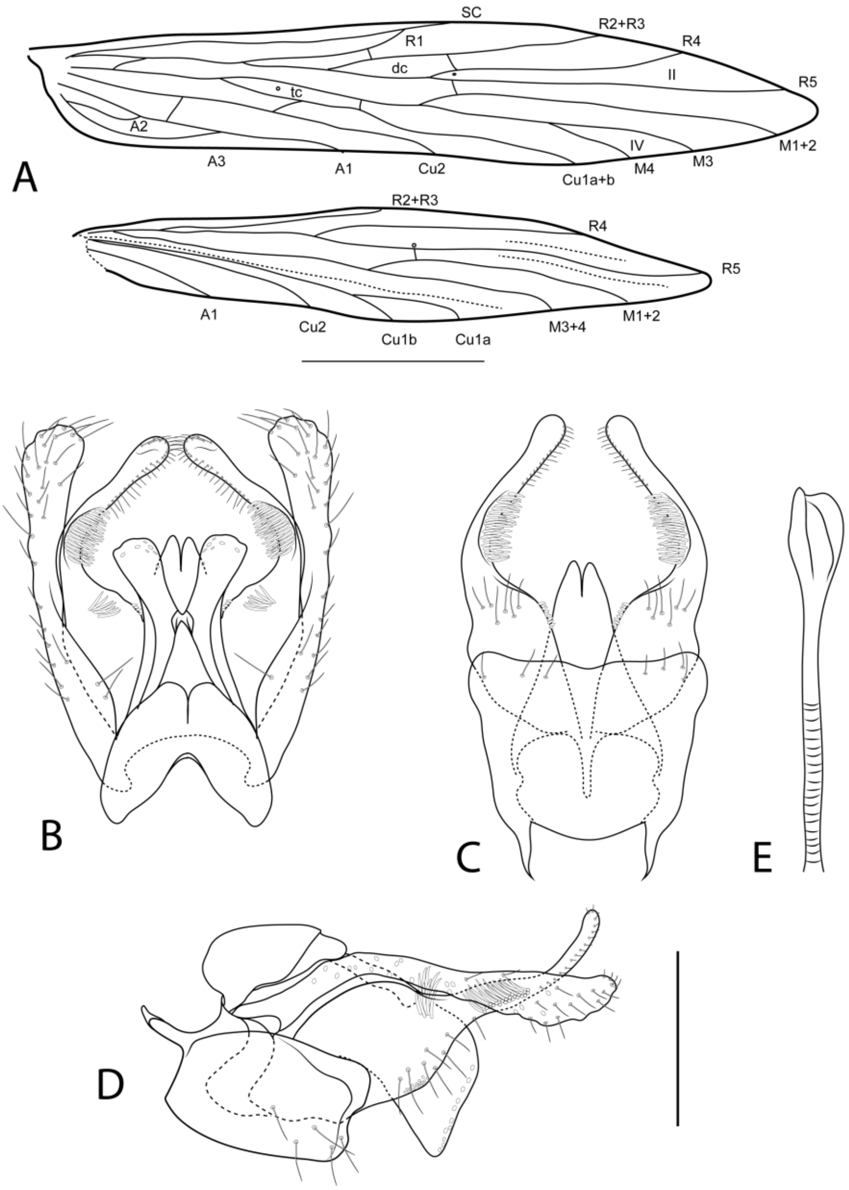


Figure 36. *Xiphocentron sclerothrix* Pes et al. 2013, paratype male: A. forewing venation. Genitalia: B. dorsal; C. ventral; D. left lateral; E. phallus dorsal. Wing scale bar = 1 mm. Genitalia scale bar = 0.1 mm.

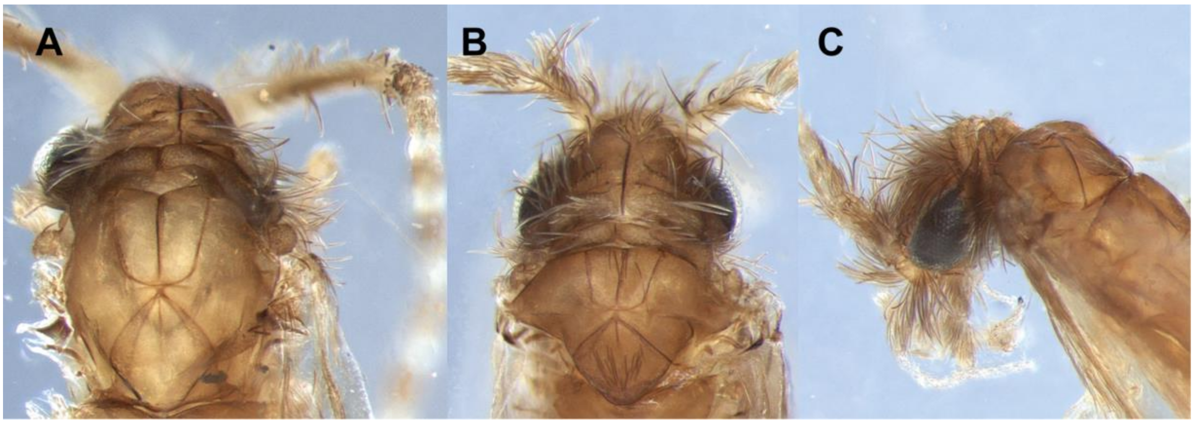


Figure 37. *Xiphocentron sclerothrix* Pes et al. 2013 paratype, head and thorax: A male dorsal; B. female dorsal; C. female lateral.

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

--Manuscript Draft—

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

INTRODUCTION

Xiphocentronidae Ross, 1949 is a tube-dwelling caddisfly family comprising 183 species and seven genera. The family distribution is primarily tropical, with most of the known diversity in Southeast Asia and Mesoamerica, with some genera extending to Central Africa, the Middle East, and Japan. The Neotropical Xiphocentronidae fauna comprises 63 species in three exclusively Neotropical taxa: *Xiphocentron* Brauer, 1870, *Machairocentron* Schmid, 1982, and the subgenus *Cnodocentron* (*Caenocentron*) Schmid, 1982 (Holzenthal & Calor, 2017).

The family was established by Ross, 1949, including Neotropical and Oriental species within a single genus, *Xiphocentron*. After the description of *Xiphocentron* larvae, the family was synonymized by Edwards (1961) with the Psychomyiidae due to the strong similarity between the larvae. Schmid (1982), in a worldwide revision, re-established the family status of Xiphocentronidae organizing it into two subfamilies: Proxiphocentroninae Schmid, 1982, including only the genus *Proxiphocentron* Schmid, 1982, and Xiphocentroninae Schmid, 1982, including 6 genera, 3 newly established by Schimd, *Abaria* Mosely, 1948, *Cnodocentron* Schmid, 1982, *Drepanocentron* Schmid, 1982, *Machairocentron* Schmid, 1982, *Melanotrichia* Ulmer, 1906, and *Xiphocentron* Brauer, 1870.

Schmid (1982) separated *Machairocentron* from *Xiphocentron* by the degree of elongation of the genital appendages and by the spinous projections present on the inferior appendage of *Machairocentron*. In his revision, Schmid described 5 of the 6 currently known species in *Machairocentron*: *M. lucumon*, *M. tarpeia, M. teucrus, M. ascanius*, and *M. carmentis*, (the latter a junior synonym of *M. echinatum* (Flint, 1981)). Additionally, Pes et al. (2013) described a species from the Central Amazon of Brazil, *M. falciforme*, describing also the pupa and the female; the larvae were morphologically indistinguishable from those of *Xiphocentron*.

Machairocentron species (Figure 1) occur in Mexico, Mesoamerica, northern South America, and central Amazonia. The adults of *Machairocentron* are small (3-4 mm) and the wings are narrow and apically acute, with long setal fringes along the margins; some species have one or two white spots on the forewing. The adult habits and habitats are similar to those of other genera in the family, living mainly in the headwaters of streams, constructing long silken tubes usually outside of the water on rocks and logs in shaded humid areas near the stream banks (Sturm 1960; Flint 1964; Pes et al. 2013). Larvae scrape the substrate to obtain their food, feeding on microalgae and debris associated with the substrate surface (Pes et al. 2013; Wiggins 1996). Adults of *Machairocentron,* as is typical of Xiphocentronidae, are collected rarely in large numbers with light traps and often are active during daylight (Flint 1968; Schmid 1982). Flight intercept malaise traps and active collection via sweep netting are more productive methods for collecting xiphocentronids than light trapping, as Schmid (1982) collected his specimens by sweeping a net along streamside vegetation during the day, and Pes et al. (2013) collected a large type series using flight intercept traps.

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

MATERIAL AND METHODS

Morphological terminology

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

Specimens preparation and illustrations

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

Depositories

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

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

RESULTS

Systematics

Family XIPHOCENTRONIDAE Ross, 1949

Subfamily Xiphocentroninae Schmid, 1982

Genus *Machairocentron* Schmid, 1982

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

Generic diagnosis

The unequivocal synapomorphy of *Machairocentron* are the swollen and rugose basal projections of the harpago. The mesal surface is covered with spines and forms an oblong dorsal projection and a ventral flap that surround laterally the apex of the paraproctal process. The coxopodite does not bear any spines. The genus is also identified by the very elongate inferior and preanal appendages and the very distinct suture line between the coxopodite and harpago, although these features are also found in *Xiphocentron torquon*, *X. polemon*, and *X. prolixum*. The females have segment X sclerotized (differing from the lighter sclerotized segment X in other Xiphocentronidae genera).

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

Description

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

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

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

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

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

Etymology. The generic etymology was not stated by Schmid (1982) in his original designation, but the name probably derives from the Greek: *machairi* = knife, *kéntro* = centre, perhaps referring to the elongate phallus or other appendages of the male genitalia.

***Machairocentron* ascanius Schmid, 1982**

Figure 3A–E

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

Material examined

Holotype: (♂ pinned, NMNH 01028605) PANAMA: Dolega 17.vii.1967, O.S. Flint.
Additional material: COSTA RICA: Puntarenas: Rio Cotón in las Alturas. 8.938ºN 82.826ºW, 18.iii.1991, el. 1360 m, Holzenthal, Muñoz, Huisman (♂ pinned, UMSP000146117).

Diagnosis. *Machairocentron ascanius* is similar to *M. teucrus*, *M. tarpeia*, *M. chorotegae* **sp.n.** and *M. eugeniarguedasae* **sp.n.** by the setal pad at the apex of the harpago. It differs from these species by the apex of tergum IX divided into well separated projections, the apex of the preanal appendage wide in lateral view, and the mesal projection of the harpago with very short spines.

Description

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

Male genitalia. Tergum IX, elongate, 1.5x longer than wide; in dorsal view, anterior margin broadly concave, V-shaped, posterior margin tapered, apex divided into well separated projections. Sternum IX, in lateral view, about 2x as long as high, tapering apically; posterodorsal margin straight, ventral margin convex, anterior margin straight, with short, curved apodeme; in ventral view, anterior margin nearly straight, posterior margin concave.

Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized; in lateral view oblong, apex rounded; in dorsal view, tapered apically, each paraproctal process partially fused mesally, with two pairs of setae at mid length; in ventral view each preanal appendage fused, apex cleft with numerous sensilla. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, apically broad, apex truncate; in dorsal view straight, bent at apex. Inferior appendage longer than preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongate, narrow; basal region lateral projection rounded, covered with small spines; mesal projection dorsally oblong and rounded, mesally covered with small spines, ventrally narrow, flap-like, covered with small spines; apical region of harpago about 3x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

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

Machairocentron echinatum **(Flint, 1981)**

Figure 4A–E, 5A–D

Machairocentron echinatum (Flint), 1981:17 [Type locality: Venezuela, Aragua, Maracay, Rio Limon, Estacion Piscicultura; NMNH; ♂; in *Xiphocentron*]. — Ríos-Touma et al., 2017:15 [checklist].

> —*carmentis* Schmid, 1982:48 [Type locality: Venezuela, Aragua, Ocumare; NMNH; ♂]. —Flint et al. 1999:81 [to synonymy].

Material examined.

Holotype: (♂ pinned, NMNH76615) VENEZUELA: Aragua, Maracay, Rio Limon, Estacion Piscicultura, 5-6.xi.1974, F.H. Weibezahn.

Additional material: VENEZUELA: Distrito Capital: Río Camurí Grande, 1 km S of Camurí (Núcleo U.S.B.), 10.616ºN, 66.715ºW, el. 30 m, 24.i.1994, Holzenthal, Cressa, Rincón col. (♂ pinned, UMSP000146114); Venezuela, Aragua, Ocumare 19-20.ii.1969, P. & P. Spangler, (2♂ alcohol, NMNH). COLOMBIA: Tolima, Armero, nr. Guayabal, 2-10.ii.1977, Malaise trap, E.L. Peyton, (♂ pinned, NMNH); Choco, Rio Atrato, Yuto, 18.ii.1983, O.S. Flint, (2♂ pinned, NMNH).

Diagnosis.

Machairocentron echinatum is similar to *M. falciforme*, and *M. lucumon* by the very elongated apical region of the harpago, with the apex not enlarged and having a single row of setae. *Machairocentron echinatum* differs by the mesal projection of harpago dorsally with conspicuous long spines, the lateral projection of the harpago with sharp edges, and the undulate posterior margin of sternum IX.

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

Male genitalia. Tergum IX as long as wide; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex divided into well separated projections. Sternum IX, in lateral view, about as long as high, tapering apically, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin concave, posterior margin undulate with narrow and shallow mesal concavity. Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, each paraproctal process partially fused mesally, with two pairs of setae at mid length; in ventral view each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, about 4x length of tergum IX, densely setose; in lateral view narrower at base, tapered apically; in dorsal view straight and apically bent. Inferior appendage longer than preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongate, narrow; basal region lateral projection quadrate, covered with spines; mesal projection dorsally oblong and rounded, dorsally covered with conspicuously longer spines, ventrallynarrow, , laterally covered with small spines; apical region of harpago about 4x basal region length, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

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

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

***Machairocentron falciforme* Pes & Hamada, 2013**

Figures 6A–E, 7A–D

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

Material examined.

Paratype: BRAZIL. Amazonas, Manaus, “Reserva Ducke; Igarapé do Acará, 02º55’51”S, 059º58’59”W, 20–30.x.2001, Malaise trap, J. Vidal, (♂ in alcohol, MZUSP000121), (♀ in alcohol, MZUSP000122).

Diagnosis. Machairocentron falciforme is similar to *M. echinatum*, and *M. lucumon* by the very elongated apical region of the harpago, with the apex not enlarged and having a single row of setae. *Machairocentron falciforme* can be differentiated from these species mainly by the lateral projection of the harpago strongly produced anterad. Additionally, the preanal appendage in dorsal view is conical with a tapered apex and the forewing has a white spot at the center of the wing and other anteriorly on the costal margin.

Adult. Forewing length 3 mm. Forewing dark brown with white spot near the nygma. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX elongate, narrow apically; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin strongly tapered, apex cleft until about mid-length. Sternum IX, in lateral view, about 2x as long as high, tapered apically, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin straight, posterior margin concave. Tergum X membranous, fused with paraproctal process; paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, separated mesally throughout length, with two pairs of setae at mid length; in ventral view, each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider at mid length, tapered apically; in dorsal view conical, strongly tapered apically. Inferior appendage longer than preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongated, narrow; basal region lateral projection strongly produced anterad, covered with spines; mesal projection dorsally oblong, rounded, mesally covered with small spines, ventrally flap-like, laterally covered with small spines; apical region of harpago about 2x length of basal region, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

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

Distribution. Brazil.

Machairocentron lucumon **Schmid, 1982**

Figure 8A–E

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

Material examined.

Holotype: (♂ pinned, NMNH1028606) MEXICO, Veracruz-Llave, Rio Tacolapan, Rt 180, Km 551, 30.VII.1966, O.S. Flint Jr. and Ortiz B., M. A.

Additional material: MEXICO: same data except, Los Tuxtlas area, Rio Maquinas, 4-14.v.1981, C.M & O.S. Flint Jr., (♂ pinned, UMNH).

Diagnosis. Machairocentron lucumon is similar to *M. echinatum* and *M. falciforme* by the very elongate apical region of the harpago without a setal pad at the apex. *Machairocentron lucumon* has the most elongated apical region of the harpago among the known species, about 5x the length of the basal region and a highly sclerotized lateral projection on the basal region. The spines on the mesal projection of the harpago are smaller than in *M. echinatum* and the lateral projection is less projected anterad than in *M. falciforme*.

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

Male genitalia. Tergum IX elongate, narrow apically; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex with swallow cleft. Sternum IX, in lateral view, about 2x as long as high, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin straight, posterior margin concave. Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, each paraproctal process partially fused mesally, with two pairs of setae at mid length; in ventral view each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, 5x length of tergum IX, densely setose; in lateral view narrower at base, slightly wider at mid length, tapered apically; in dorsal view straight, apically bent. Inferior appendage as long as preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongate, narrow; basal region lateral projection well developed, rounded, covered with spines; mesal projection dorsally oblong and rounded, mesally covered with small spines, ventrally flap-like, laterally covered with small spines; apical region of harpago about 4x length of basal region, mesal margin with row of setae from base to apex, apex not enlarged, with single row of setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Distribution. Mexico.

Machairocentron tarpeia **Schmid, 1982**

Figure 9A–E

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

Material examined.

Holotype: (♂ pinned, NMNH1028607) MEXICO: Michoacán, San Lorenzo, Rt. 15, Km 206, 14-15.vii.1966., O.S. Flint Jr. & B. Ortiz, M. A.

Paratype: MEXICO: same data as holotype, (♂ in alcohol, CNC165710).

Diagnosis. Machairocentron tarpeia has a short apical region of the harpago as also seen in *M. teucrus*, and *M. chorotegae* **sp.n.** It differs mainly by the elongate finger-like spines apically on the mesal projection of the harpago, and also the wider tergum IX with a broad concavity on the anterior margin and the well separated projections at the apex.

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

Male genitalia. Tergum IX as long as wide; in dorsal view, anterior margin broadly concave, U-shaped, posterior margin tapered, apex divided into well separated projections. Sternum IX, in lateral view, about 1.5x longer than high, posterodorsal margin straight, ventral margin convex, anterior margin straight with short, curved apodeme; in ventral view, anterior margin nearly straight, posterior margin concave.

Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, each paraproctal process partially fused mesally, with 2 pairs of setae at mid length; in ventral view each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider at mid length, tapered apically, apex rounded; in dorsal view straight, apex enlarged. Inferior appendage as long as preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongated, narrow; basal region lateral projection rounded, covered with small spines; mesal projection dorsally oblong, rounded, dorsally with finger-like spines, ventrally narrow, flap-like, laterally covered with small spines; apical region of harpago about 2x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Distribution. Mexico.

Machairocentron teucrus **Schmid, 1982**

Figure 10A–E

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

Material examined.

Holotype (♂ pinned, NMNH1028608): PANAMA, Cocle, Playa Santa Clara 2.vii.1967, malaise trap, Wirth, W.W.

Additional material: NICARAGUA: Dto. Carazo, Quebrada on farm California, 45 km SW of Managua towards Pochomil /Montelimar, N 11º55’62.5’’, W 86º27’71.7”, 15.viii.2000, el. 185 m, Chamorro & Lacayo, (♂ pinned, UMSP000101033).

Diagnosis. The short length of the apical region of the harpago (3x basal region length) of *M. teucrus* is also present in *M. tarpeia* and *M. chorotegae* ***sp.n.*** *Machairocentron teucrus* can be differentiated from these species by the narrow sternum IX, the rounded margin of the lateral projection of the harpago, and the high density of the small spines on the ventral region of the mesal projection and the ventro-apical region of the lateral projection, which make the mesal and lateral projections appear fused.

Adult. Forewing length 3.5 mm. Forewing dark brown with white spot near the nygma. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX longer than wide; in dorsal view, anterior margin broadly concave, V-shaped, posterior margin tapered, apex divided into well separated projections. Sternum IX, in lateral view, about 1.5x longer than high, posterodorsal margin straight, ventral margin convex, anterior margin straight with short apodeme; in ventral view, anterior margin straight, posterior margin concave. Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, separated mesally throughout length, with two pairs of setae at mid length; in ventral view, each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, 3x length of tergum IX, densely setose, in lateral view narrower at base, slightly wider at mid length, tapered apically, apex rounded; in dorsal view straight, apex slightly enlarged. Inferior appendage as long as preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongated, narrow; basal region lateral projection rounded, posterior margin densely covered with small spines; mesal projection, dorsally oblong, rounded; mesoventrally densely covered with small spines; ventrally narrow, flap-like; laterally covered with small spines; apical region of harpago about 2.5x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

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

***Machairocentron chorotegae* sp.n.**

Figure 11A–E, 12A–C

Material examined.

Holotype (♂ pinned, UMSP000146097): COSTA RICA: Puntarenas, Rio Bellavista, ca 1.5 km, NW Las Alturas. 8.951ºN, 82.846ºW, 16-17.iii.1991, el. 1400 m Holzenthal, Muñoz, Huisman.

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

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

Diagnosis. The new species is similar to *Machairocentron teucrus* and *M. tarpeia* by the short length of the apical region of the harpago (3x length of basal region). It can be diagnosed by the inner margin of the basal region of the harpago bearing a radula-like dorsal projection. Also, tergum IX has a very narrow central concavity on the anterior margin and a tiny apical cleft.

Description.

Adult. Forewing length 3.5 mm. Forewing dark brown with white spot near the nygma. Tibial spurs not modified. Sclerotized reticulated region on sternum V present.

Male genitalia. Tergum IX as longer as wide; in dorsal view, anterior margin with narrow central concavity, posterior margin tapered, apex cleft. Sternum IX, in lateral view, more than 2x as long as high, each side with posterolateral-dorsal margin straight, ventral margin convex, with anterolateral apodeme short, curved; in ventral view, anterior margin slightly concave, posterior margin straight with very small central concavity, sides convex. Tergum X membranous, fused with paraproctal process. Paraproctal process sclerotized, in lateral view oblong, apex rounded; in dorsal view, tapered apically, separated mesally throughout its length, with 2 pairs of setae at mid length; in ventral view, each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage, 3x length of tergum IX, densely setose; in lateral view, narrower at base, slightly wider at mid length, tapered apically; in dorsal view, apically enlarged. Inferior appendage longer than preanal appendage, bi-segmented, coxopodite short, simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongated, narrow; basal region lateral projection angulate, square, covered with small spines; mesal projection divided in 3 projections, dorsal projection in ventral view oblong, covered with small tubercles, in dorsal view curved mesad, covered with spines, radula-like; mesal projection in lateral view oblong, in ventral view mesal margin rounded and apex directed posterad with small spines, mesal margin spines curved dorsad; ventral projection in lateral view broad, with small tubercles, in ventral view narrow, flap-like; apical region of harpago about 3x length of basal region, mesal margin with row of setae from base to apex, apex enlarged, with pad of numerous setae. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

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

Distribution. Costa Rica.

Machairocentron eugeniarguedasae **sp.n.**

Figures 13A–D, 14A–C

Material examined.

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

Paratypes. COSTA RICA: Same data as holotype, except, (♀ BIOUG19941-H01) Guanacaste, 7.x.2013; (♀ BIOUG22784-B12) Guanacaste, 4.xi.2013; (♀ BIOUG19725-A05) Guanacaste, 9.vii.2013.

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

Diagnosis. The new species is similar to *M. echinatum* by the elongate spines on the mesal projection of the harpago. The new species can be differentiated by these spines being longer and displayed as a line of finger-like spines curving upward close to the inner margin. Also, the spines on the lateral projection are sparser and more pointed, and the harpago apex has a pad of numerous setae, while *M. echinatum* has just a simple row.

Description.

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

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

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

Distribution. Costa Rica.

Machairocentron kalinae **sp.n.**
Figure 15A–E

Material examined.
Holotype (♂ pinned, NMNH01518182): VENEZUELA: Sucre, Península de Paria, Santa Isabel, Rio Sta. Isabel, 10º44.294’N, 62º38.954’W, el. 20m, 4.iv.1995, Holzenthal, Flint, Cressa. (DNA Voucher: 10OFCAD-123).
Paratypes: VENEZUELA: same data as holotype except: Puerto Viejo, “Rio el Pozo”, 10º43.073’N, 62º28.569’W, 3.iv.1995 (♂ pinned, NMNH); same data: (♂ pinned, UMSP000146115), (DNA Voucher: 09MNKK0390).

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

Diagnosis. The new species is similar to *M. echinatum* and differs by the setose apex of tergum IX; the shorter apical region of the harpago, with the apex enlarged with a line of multiple setae; and the mesal projection of the harpago without the conspicuous mesal spines present in *M. echinatum*.

Description.

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

Male genitalia. Tergum IX as long as wide; in dorsal view, triangular, anterior margin broadly concave, U-shaped, posterior margin tapered, apex cleft into well separated projections, apex setose. Sternum IX, in lateral view, narrow, about 3x longer than high, posterodorsal margin concave basally, straight apically, ventral margin convex, anterior margin with apodeme, apodeme as long as 2/3 length of sternum; in ventral view, anterior margin concave, posterior margin concave, lateral edges with long setae. Tergum X membranous, partially fused with paraproctal process. Paraproctal process sclerotized; in lateral view, oblong, apex rounded; in dorsal view, tapered apically, separated mesally throughout length, with 2 pairs of setae at mid length; in ventral view, each preanal appendage fused, apex cleft, with numerous sensilla. Preanal appendage long, 3x length of tergum IX, densely setose; in lateral view, narrower at base, tapered apically; in dorsal view, straight, with subapical constriction, apex tapered. Inferior appendage as long as preanal appendage, bi-segmented; coxopodite simple, with long setae ventrally; harpago complex, basal region short, sclerotized; apical region elongate, narrow; basal region lateral projection anterior margin quadrate, covered with spines; mesal projection dorsally oblong, rounded, dorsally with spines; ventrally narrow, laterally covered with small spines; apical region of harpago about 3x length of basal region, semimembranous basomessaly, mesal margin with row of setae from base to apex, apex enlarged, with set of setae mesally and row of multiple setae ventrally. Phallus very long, slender, conical at base, subapically annulate, apex slightly enlarged.

Distribution. Venezuela.

Additional material examined

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

Machairocentron morphotype A

Figure 16A–D

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

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

Machairocentron morphotype B

Figure 17A–D

Material examined. (♂ pinned, UMSP0098453) ECUADOR: Orellana. Reserva de Biodiversidad Tiputini, river slough, Numa Trail, 00.63954ºS, 76.14836ºW, el. 260m, 23.x.2011, Holzenthal & Rios.

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

Machairocentron morphotype C

Figure 18A–D

Material examined. (♂ alcohol, DZRJ) PERU: Madre de Dios, 13º251S, 70º2046W; el. 382m, 23-31.viii.2012, malaise trap, RRC, JAR, APMS, DMT.

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

DISCUSSION

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

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

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

Key to Neotropical Xiphocentronidae

1. Mesoscutal setal warts modified in a quadrate mesoprescutum. Phallus tubular, extremely elongated (reaching anterad to segment V), without phallic sclerites or spines.. 2 (Xiphocentronidae)

\- Mesoscutal setal warts absent or rounded. Phallus not so elongated, phallic sclerites and spines absent or present...other families

2(1). Apicoventral margin of sternum IX between the inferior appendages with a patch of elongate stout setae. Inferior appendage strongly bifurcated, with the gonocoxite forming a produced projection.................................... *Cnodocentron* Schmid, 1982

- Apicoventral margin of sternum IX without conspicuous set of spines, or setae; gonopod linear, coxopodite not strongly produced...3

3(2) Inferior appendage with coxopodite and hapago clearly distinct, base of harpago strongly sclerotized, overall covered with tubercles and short spines and forming a broad mesal projection, harpago very elongated. (The female of *Machairocentron* can be distinguished from the other described Xiphocentronidae females by the very sclerotized segment X).. *Machairocentron* Schmid, 1982

- Inferior appendage with coxopodite and harpago fused or not, base of harpago never forming broad sclerotized projection, with rows or patches of spines, sometimes forming a distinct polyp-like mesal sclerite..................***Xiphocentron*** Brauer, 1870

Key to adult male of *Machairocentron*

The species can be recognized mainly by the spines and projections of the inferior appendage

1 Apical region of harpago short, less than 2x tergum IX length; apex enlarged with setae in multiple rows (Figures 9A–C) 2

- Apical region of harpago very long, about 3x tergum IX length; apex not enlarged usually with setae in a single linear row (Figures 4A–C).......................................6

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

- Mesal projection of harpago with small spines (Figure 3D)...................................3

3(2) Lateral projection of harpago with margins rounded (Figure 9D)...........................4

- Lateral projection of harpago with margins basally angulated (Figure 11D)..........5

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

- Mesal projection of harpago ventrally with some sparse spines (Figure 3C, D); tergum IX in dorsal view, anterior margin with a wide concavity (Figure 13B);

preanal appendage in lateral view apically broader than in middle-length (Figure 3A) .... *Machairocentron ascanius* Schmid, 1982

5(3) Mesal projection of harpago in dorsal view radula-like spines (Figure 11D); tergum IX apex without setae; forewing with a white spot (Figure 11E) ....*Machairocentron chorotegae* **sp.n.**

\- Mesal projection of harpago in dorsal view not radula-like; tergum IX apex setose (Figure 15B); forewing dark brown without any white spot..................................... ....*Machairocentron kalinae* **sp.n.**

6 (1) Mesal projection of harpago with conspicuously elongated spines (Figures 4D, 5) 7

\- Mesal projection of harpago with small spines (Figure 8D)....................................8

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

\- Mesal projection apex in dorsal view, with some conspicuously long spines not distinctly curved, in lateral view spines shorter than mesal lobe width (Figure 14D); harpago apex not enlarged with a single row of setae; tergum IX anterior margin with broad concavity (Figure 14B) ....*Machairocentron echinatum* (Flint)

8(6) Apical region of harpago more than 4x basal region length (Figure 8C); lateral projection of harpago not markedly produced anterad ....*Machairocentron lucumon* Schmid, 1982

\- Apical region of harpago less than 3x basal region length; lateral projection of harpago very produced anterad (Figure 6D) ....*Machairocentron falciforme* Pes & Hamada, 2013

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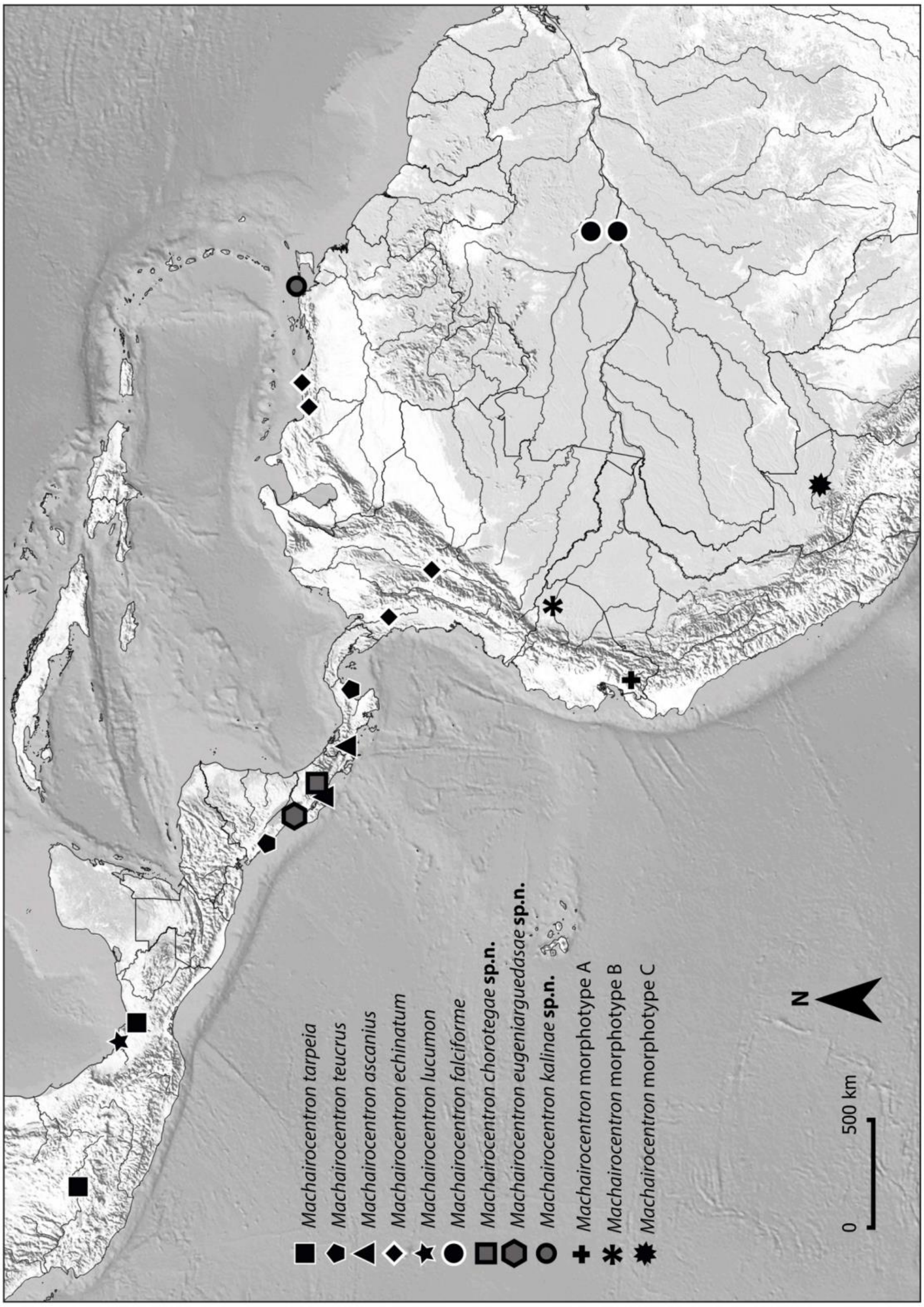

Figure 1. Distribution map: *Machairocentron* species

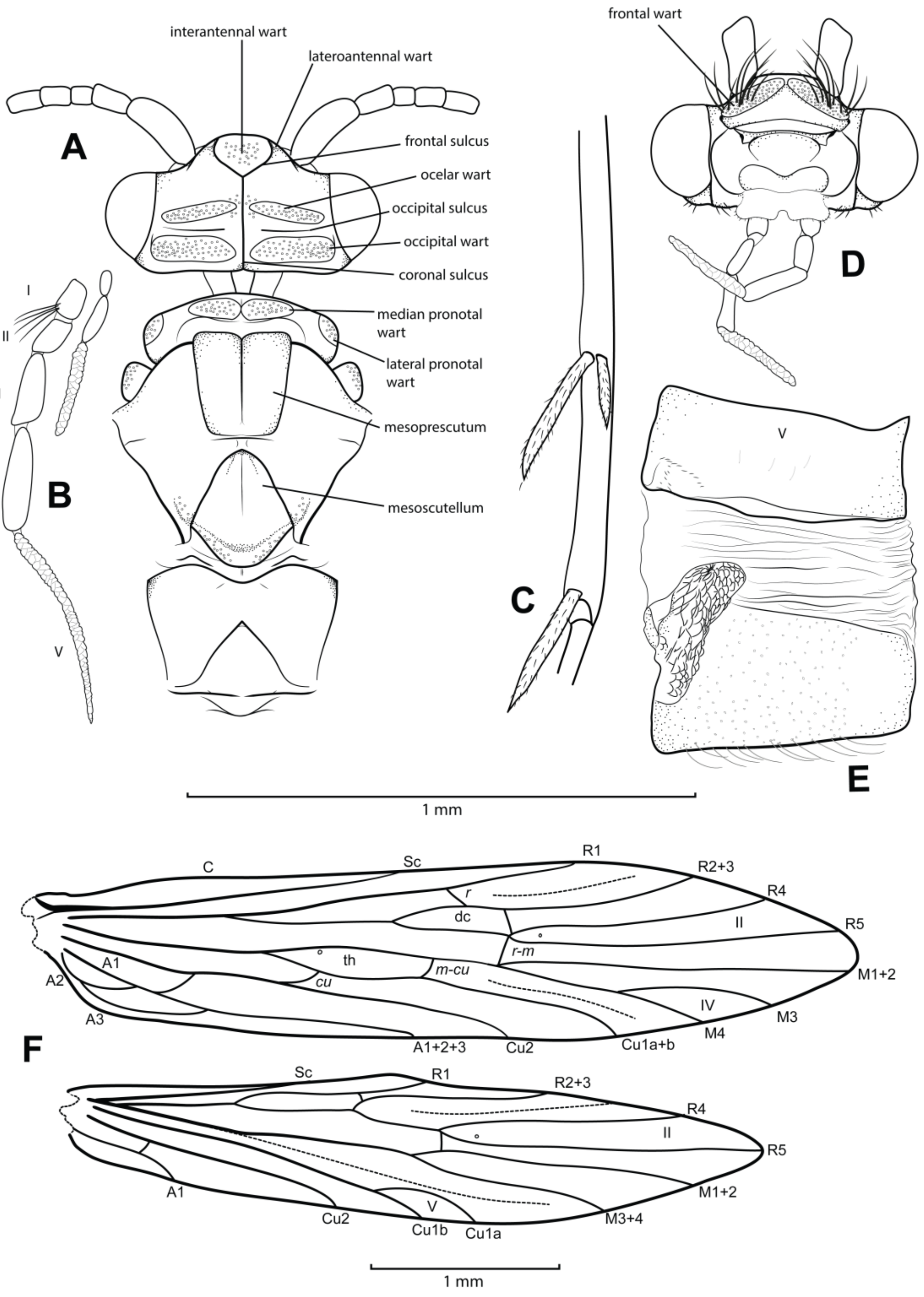

Figure 2. *Machairocentron* adult male: A. head, pro– and mesothorax of *M. falciforme*, dorsal view; B. labial and maxillary palps of *M. tarpeia*; C. hind leg, tibial spurs of *M. tarpeia*; D. head of *M. falciforme*, frontal view (labial palps are omitted); E. sternum V reticulate glandular region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

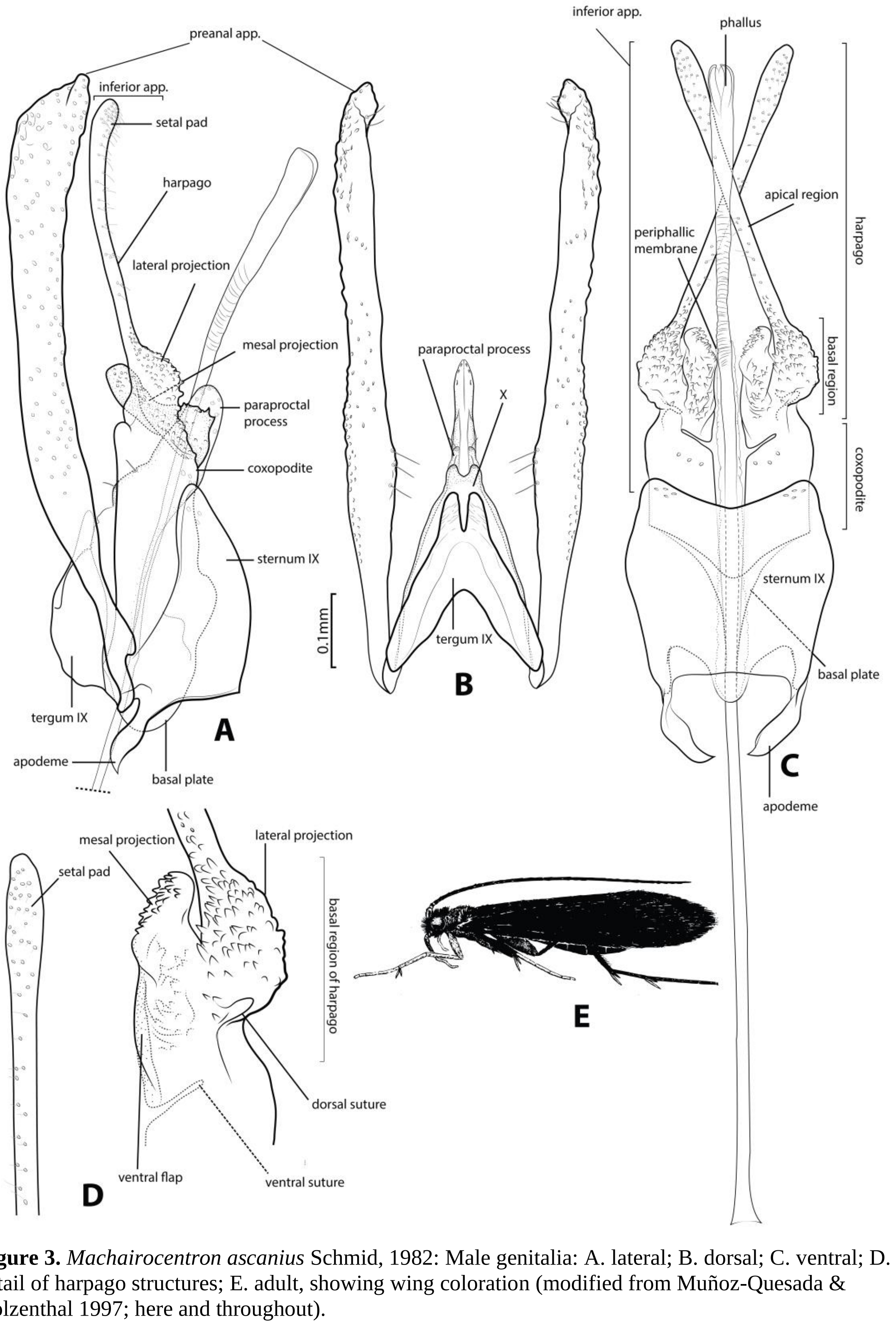

Figure 3. *Machairocentron ascanius* Schmid, 1982: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult, showing wing coloration (modified from Muñoz-Quesada & Holzenthal 1997; here and throughout).

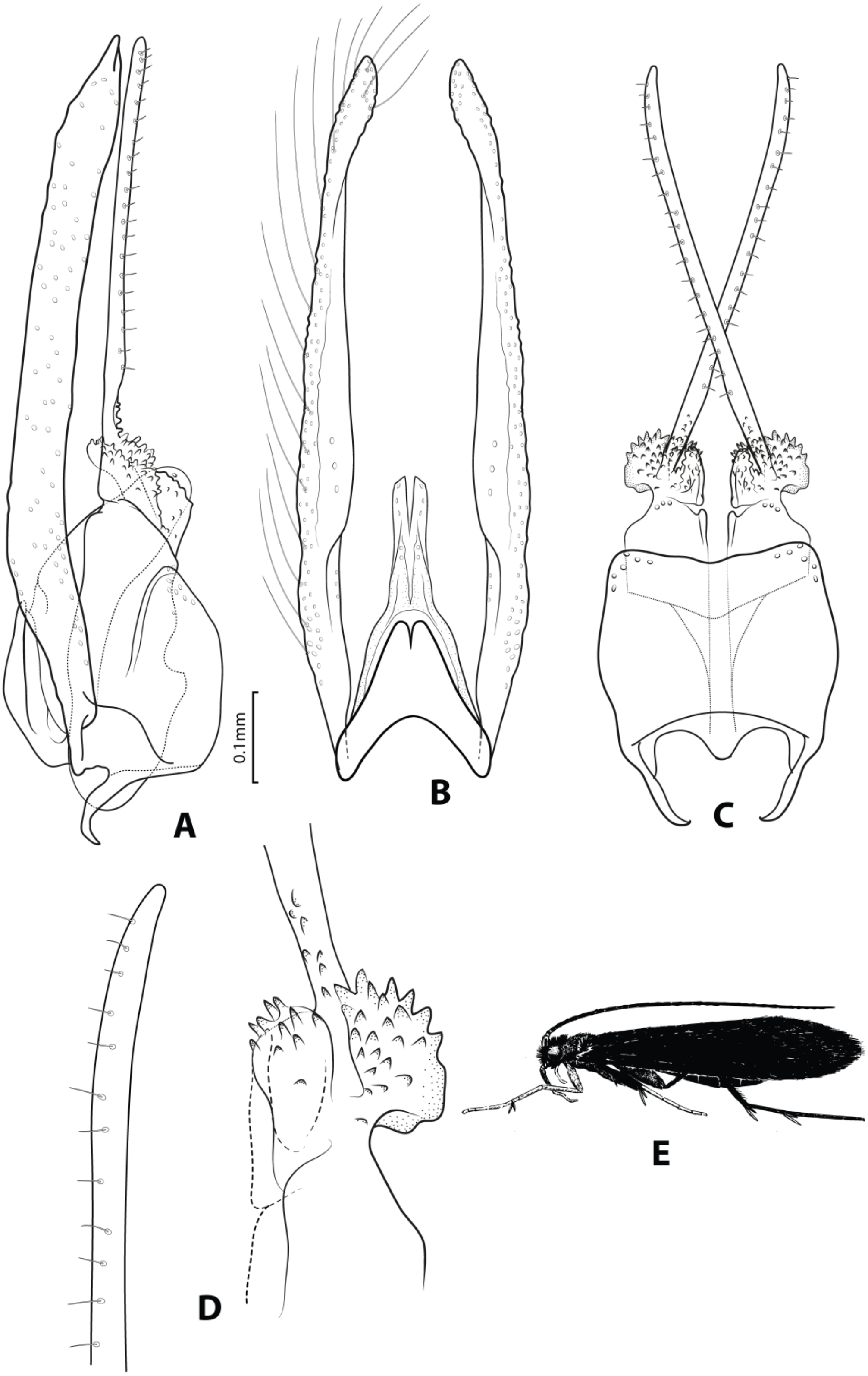

Figure 4. *Machairocentron echinatum* (Flint, 1981): Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

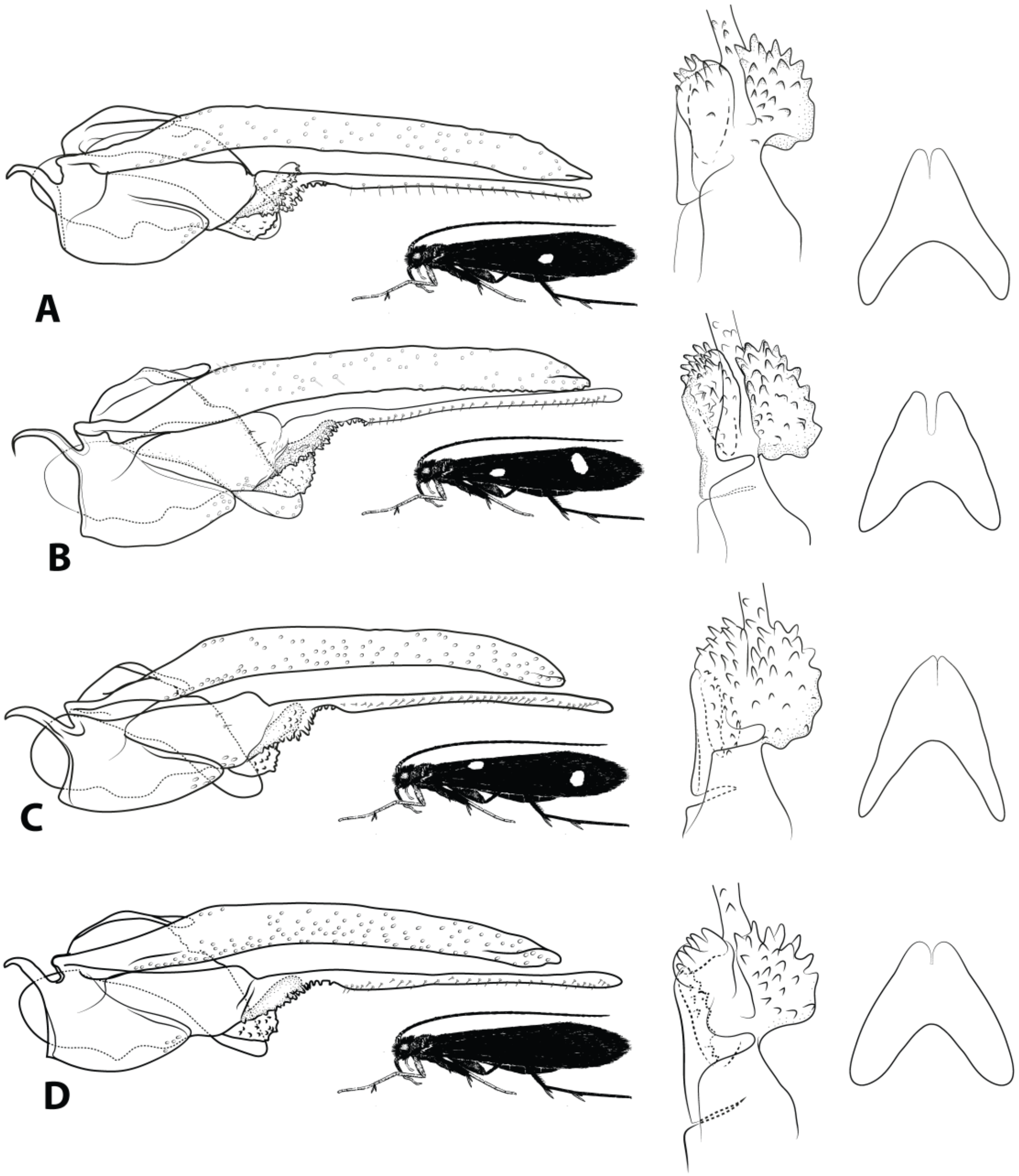

Figure 5. *Machairocentron echinatum* (Flint, 1981) variations: male genitalia lateral, wing aspect, detail of basal region of harpago dorsal, tergum IX dorsal, respectively. A. Venezuela, Aragua state (Holotype); B. Venezuela, Distrito Capital; C. Colombia, Choco departament; D. Colombia, Tolima departament.

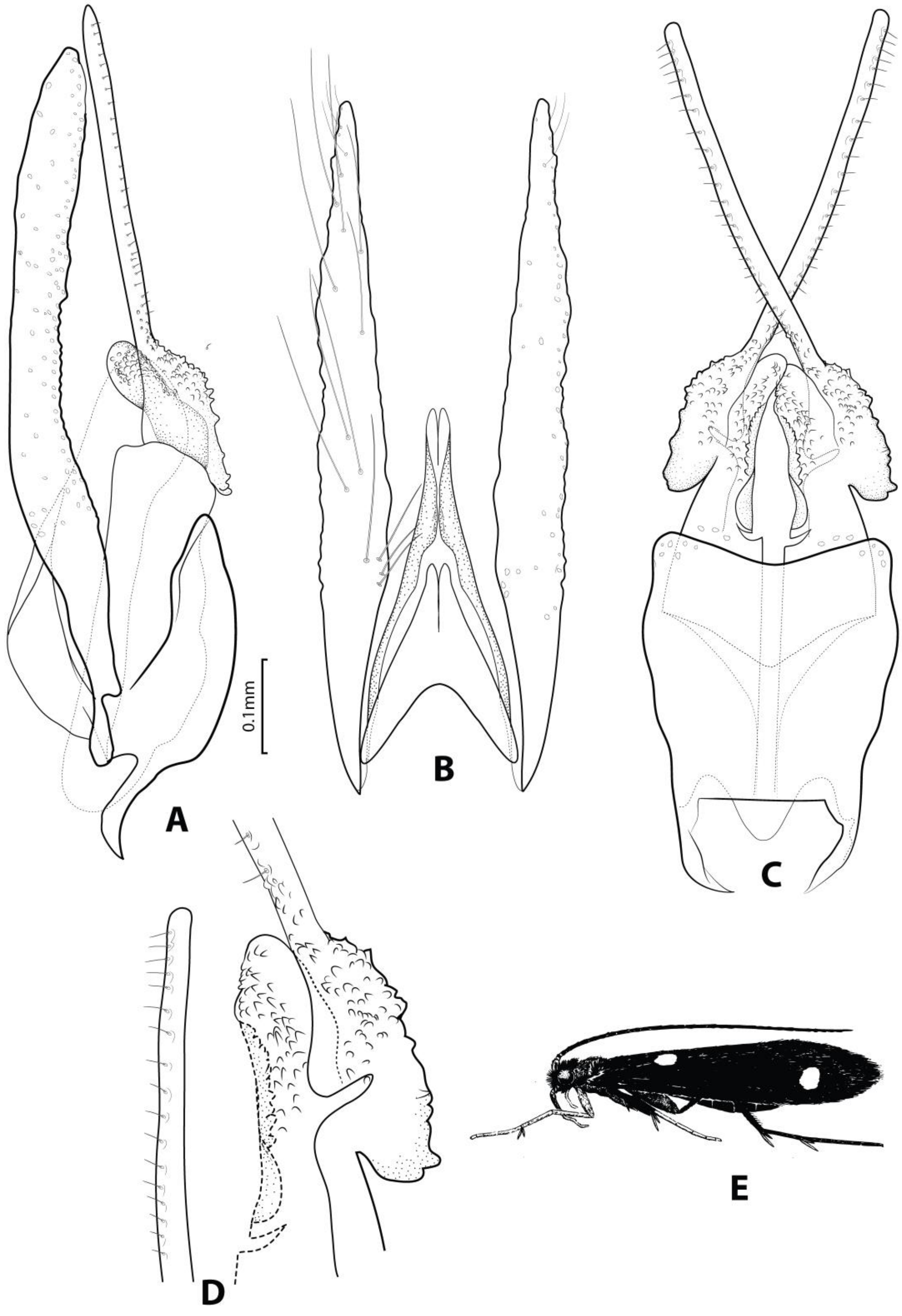

Figure 6. *Machairocentron falciforme* Pes & Hamada, 2013: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

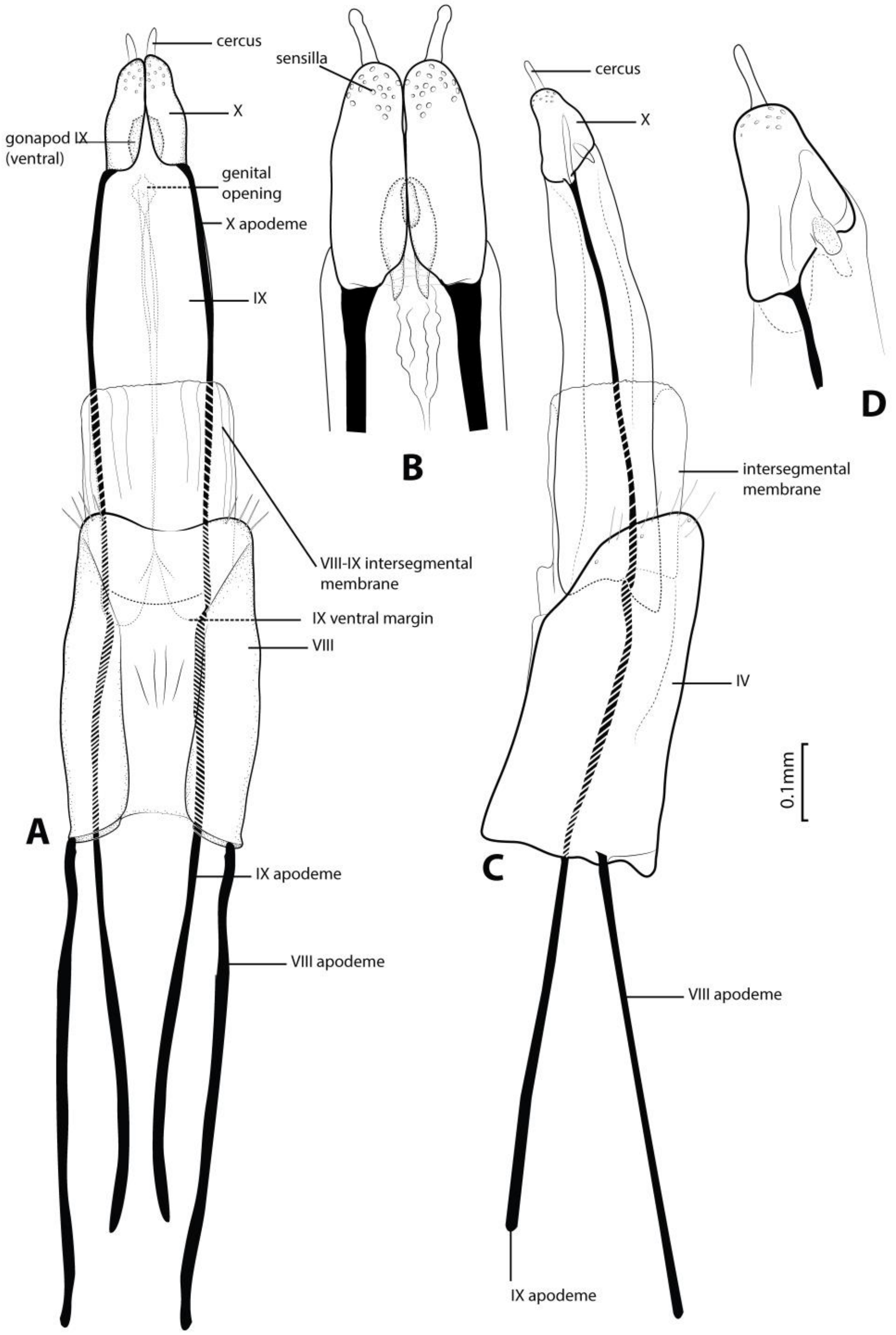

Figure 7. *Machairocentron falciforme* Pes & Hamada, 2013: Female genitalia: A. dorsal; B. lateral; C. detail of X segment, dorsal; D. same, lateral.

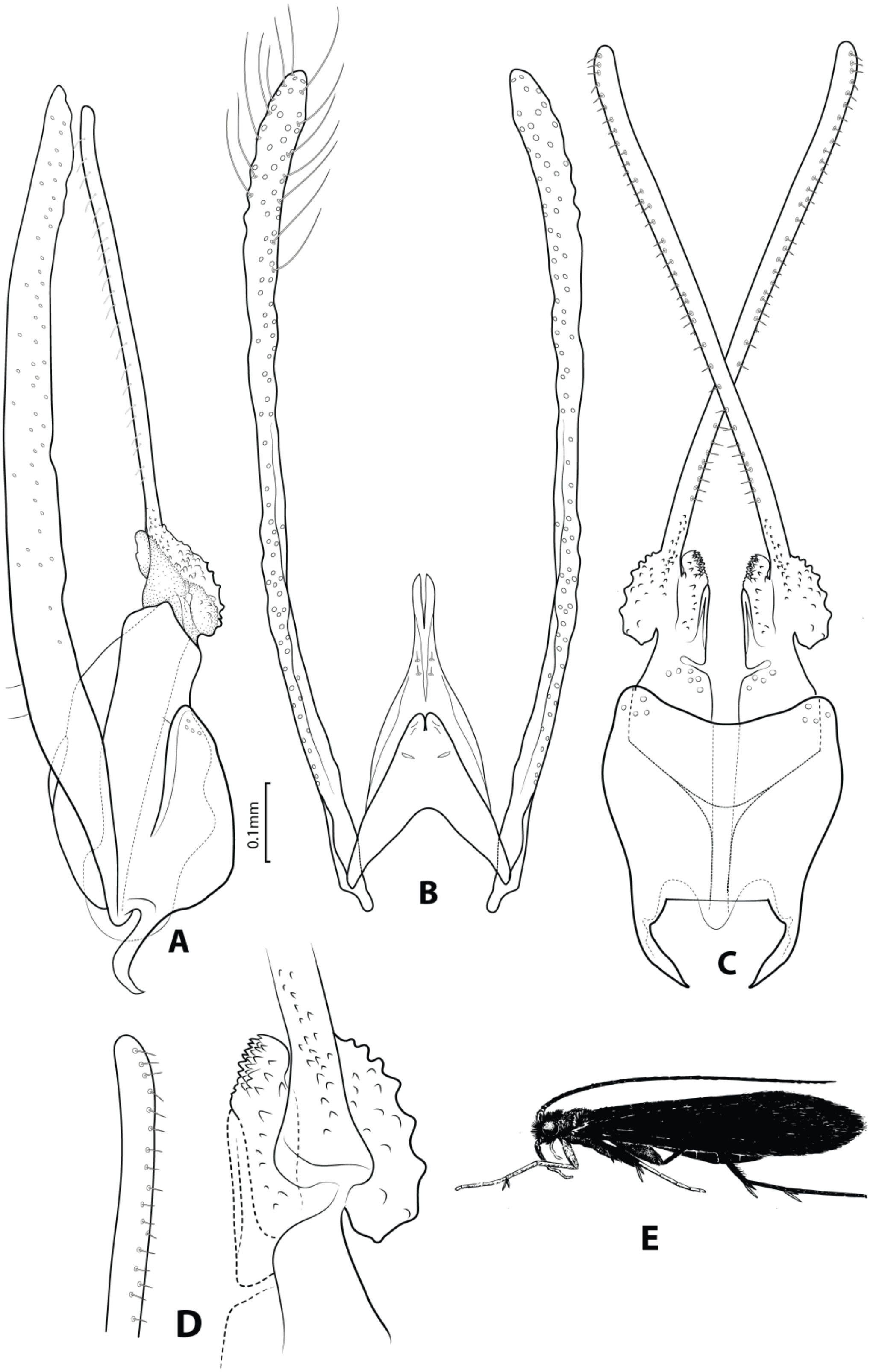

Figure 8. *Machairocentron lucumon* Schmid, 1982: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

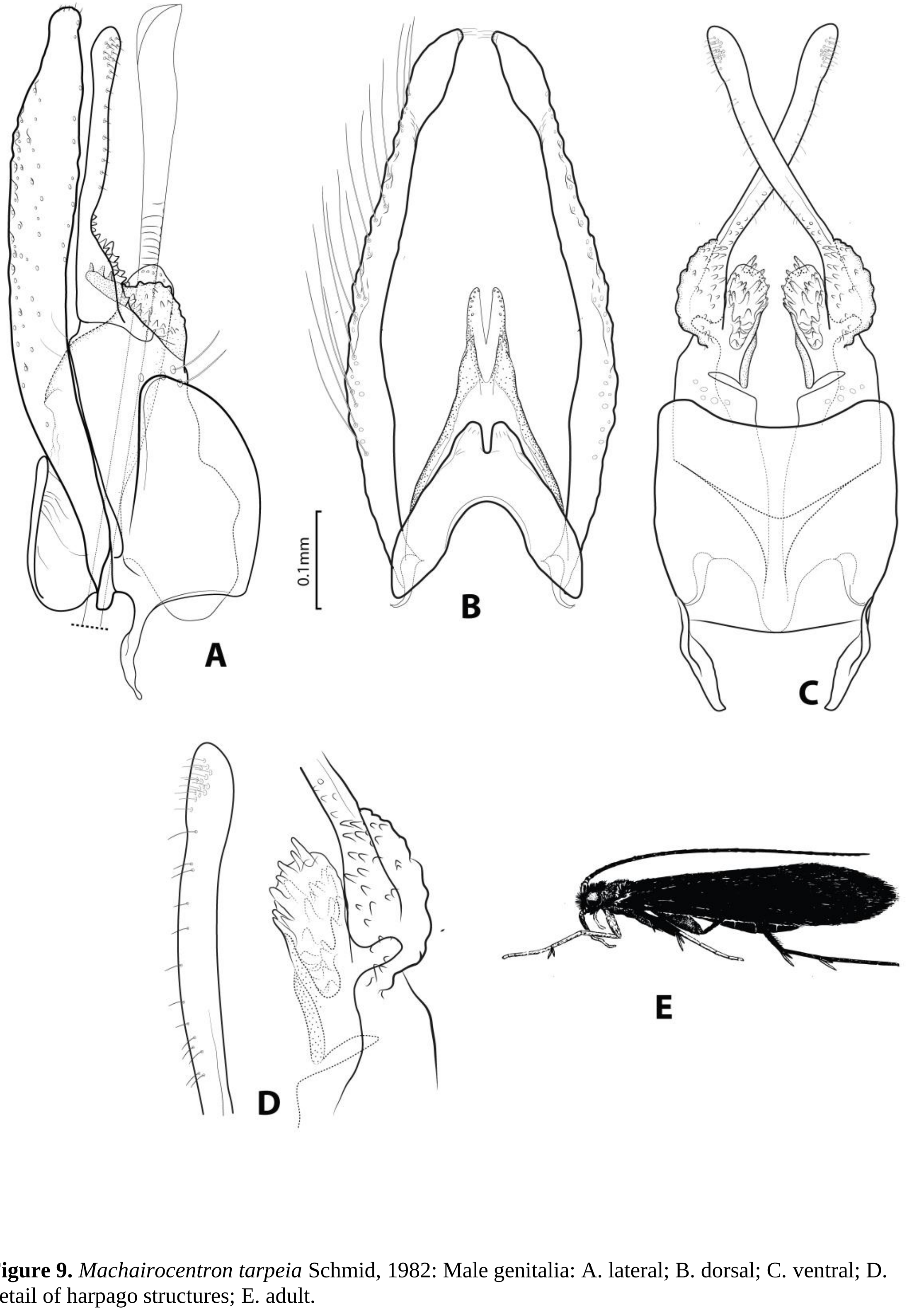

Figure 9. *Machairocentron tarpeia* Schmid, 1982: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

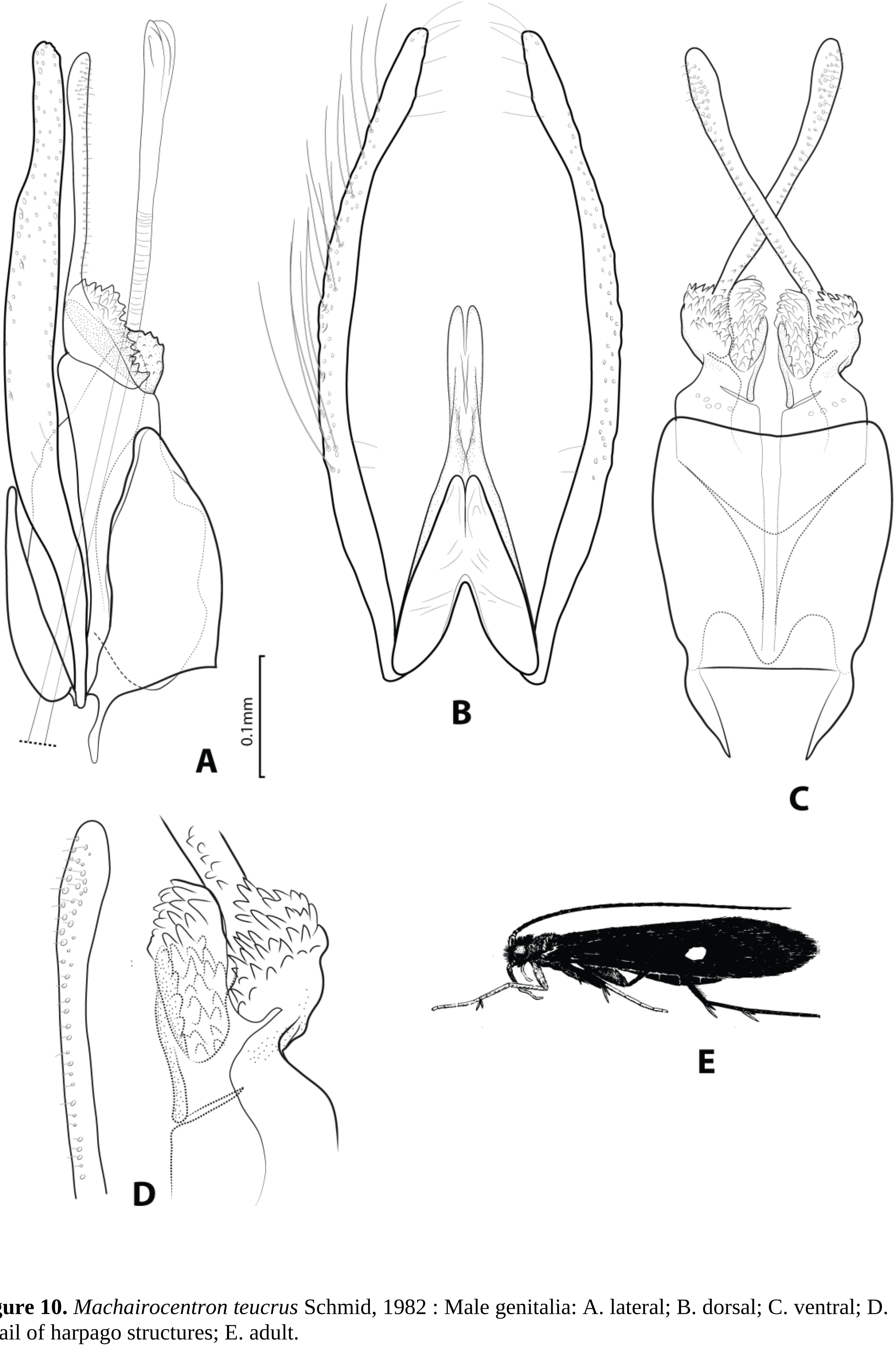

Figure 10. *Machairocentron teucrus* Schmid, 1982 : Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

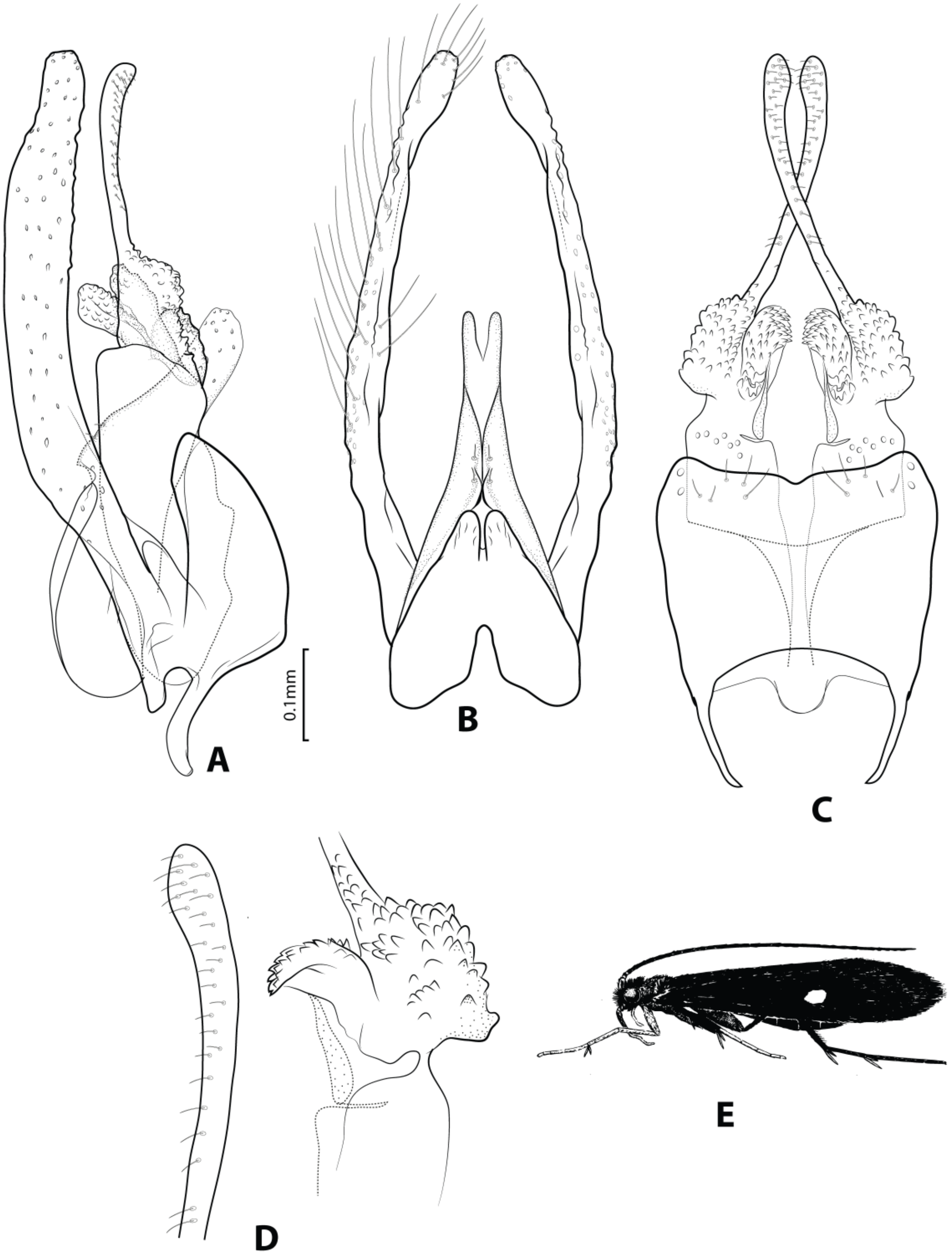

Figure 11. *Machairocentron chorotegae* **sp.n.**: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

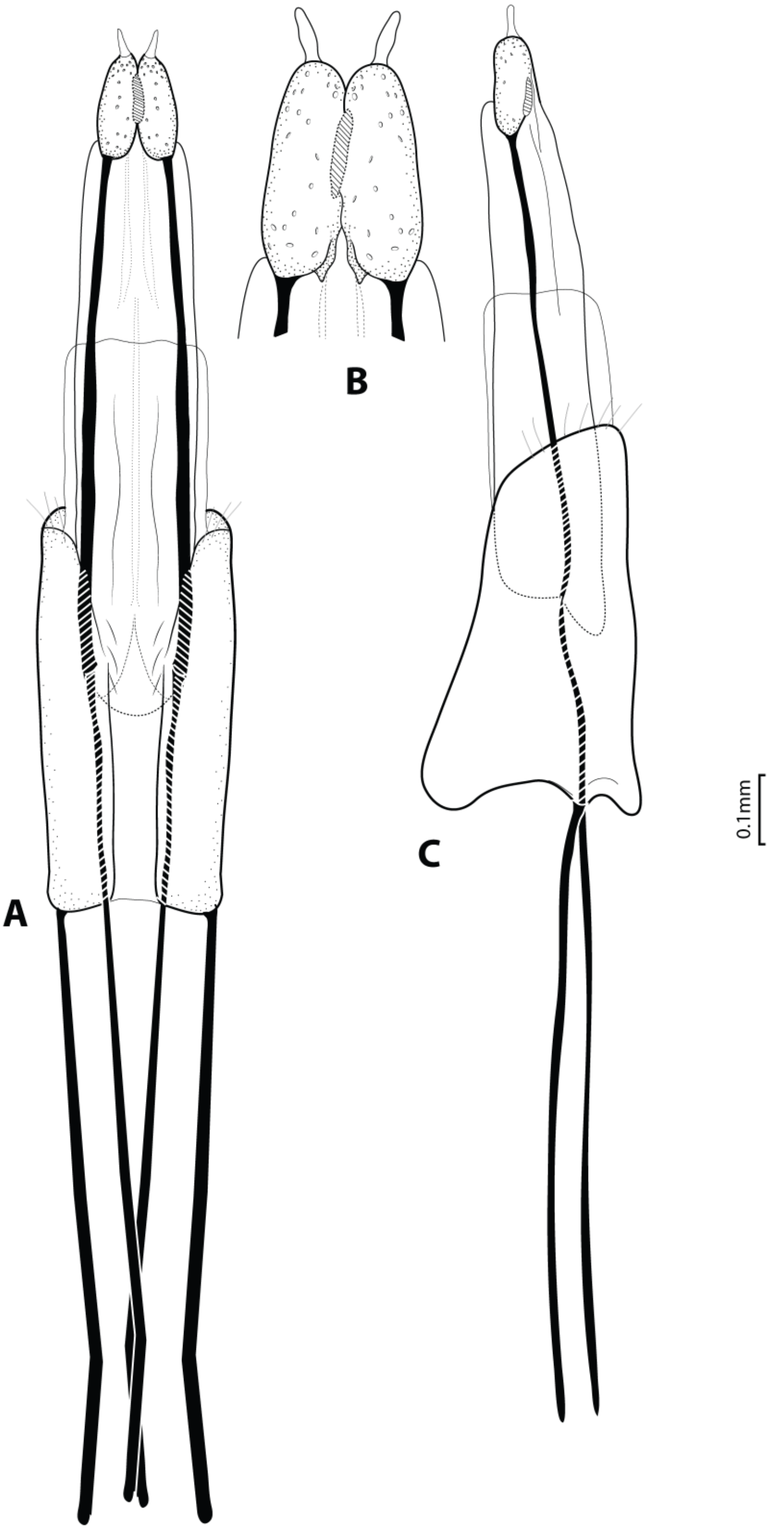

Figure 12. *Machairocentron chorotegae* **sp.n.**: Female genitalia: A. dorsal; B. lateral; C. detail of X segment dorsal.

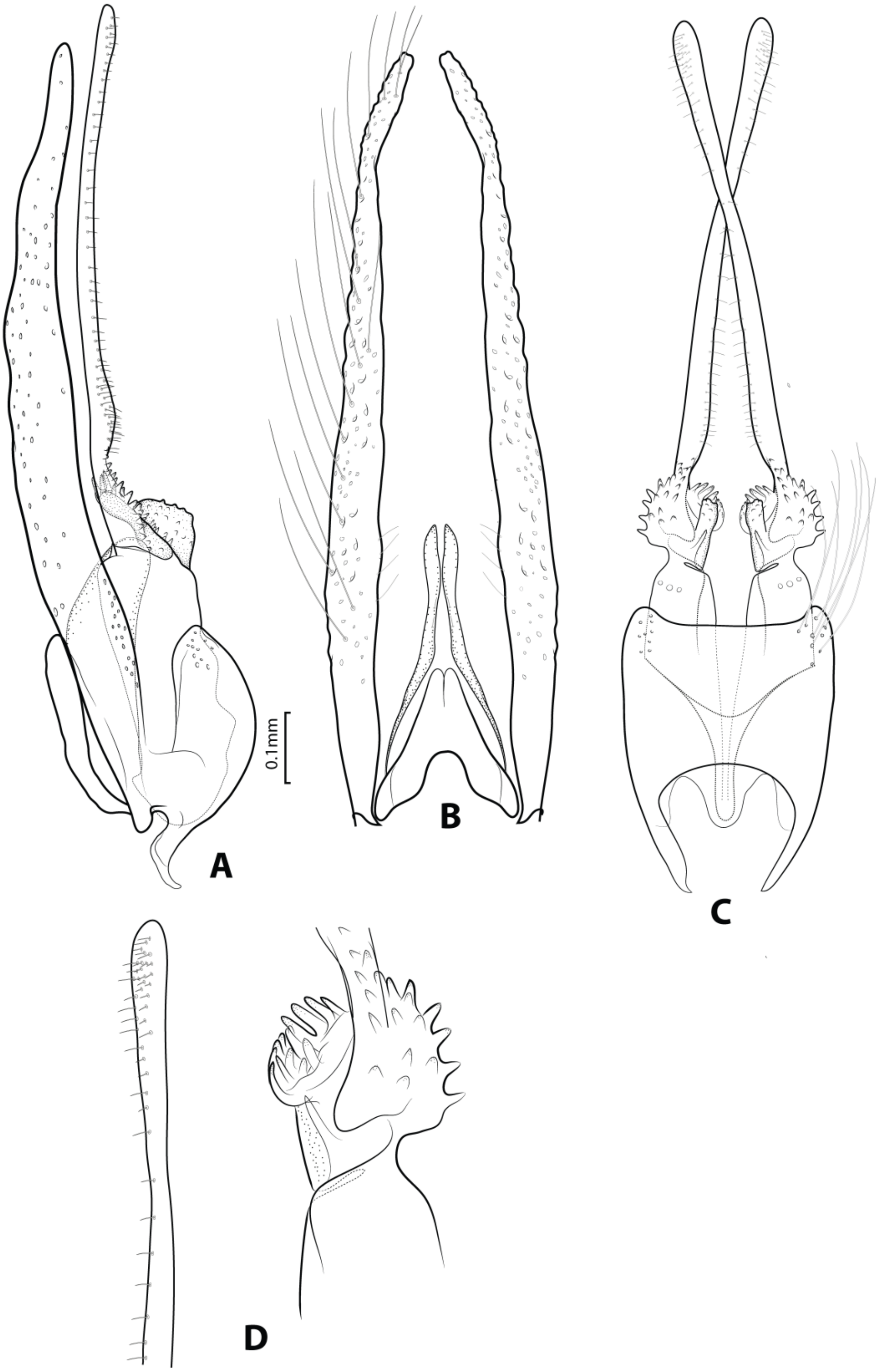

Figure 13. *Machairocentron eugeniarguedasae* **sp.n.**: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures. Adult wing pattern is unknow.

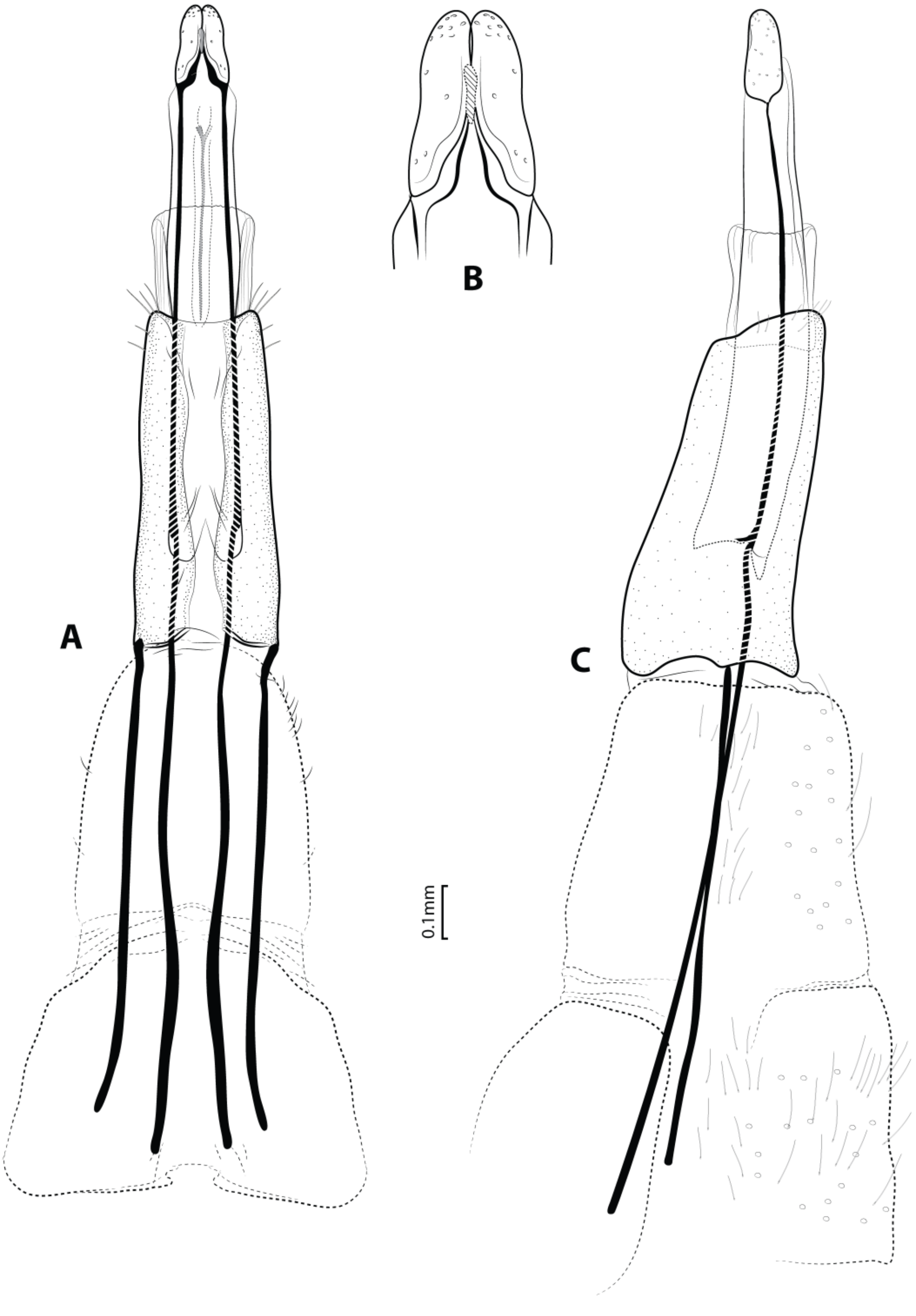

Figure 14. *Machairocentron eugeniarguedasae* **sp.n.**: Female genitalia: A. dorsal; B. lateral; C. detail of X segment, dorsal.

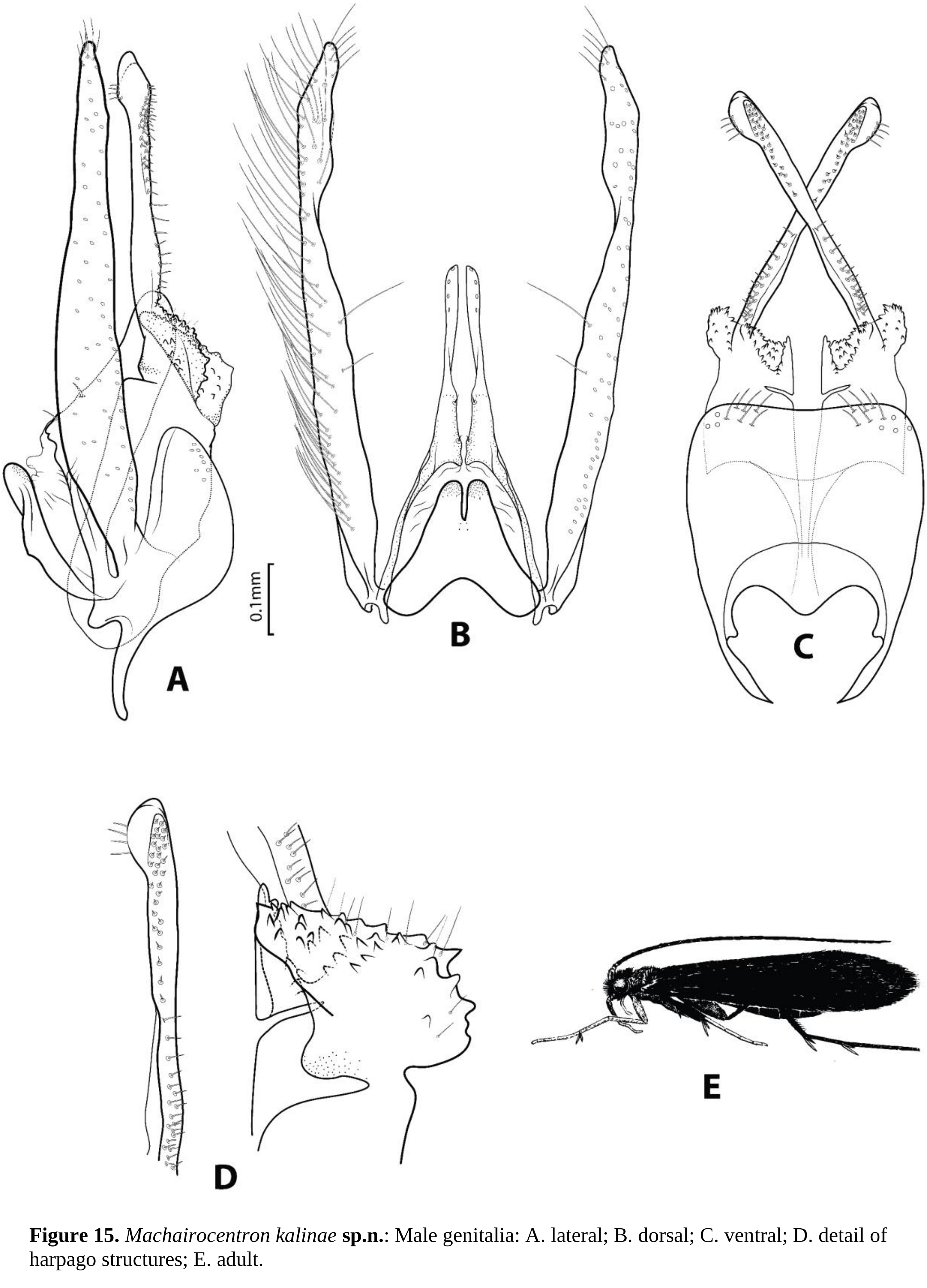

Figure 15. *Machairocentron kalinae* **sp.n.**: Male genitalia: A. lateral; B. dorsal; C. ventral; D. detail of harpago structures; E. adult.

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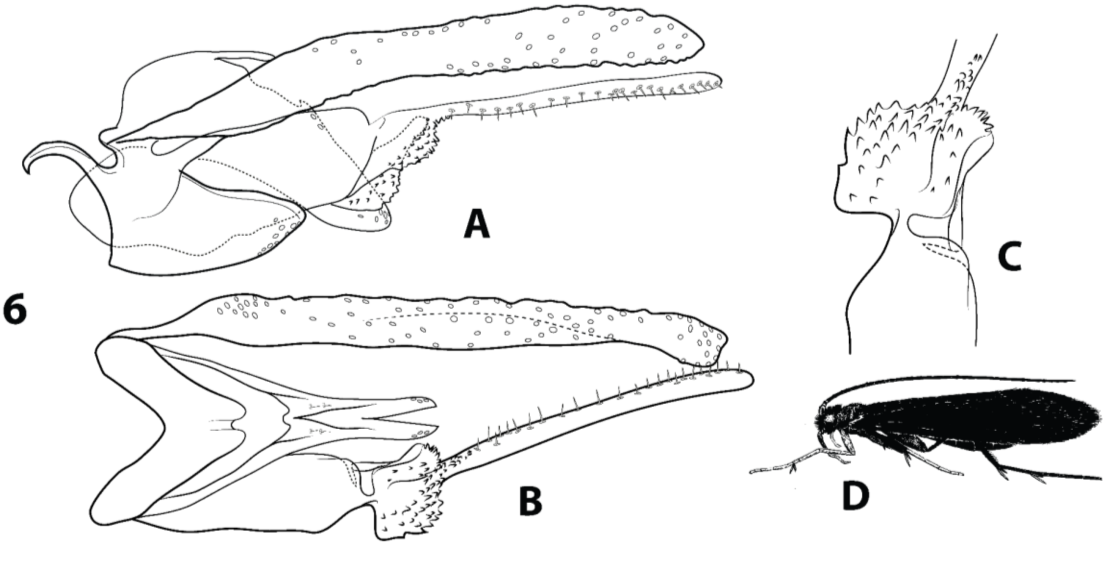

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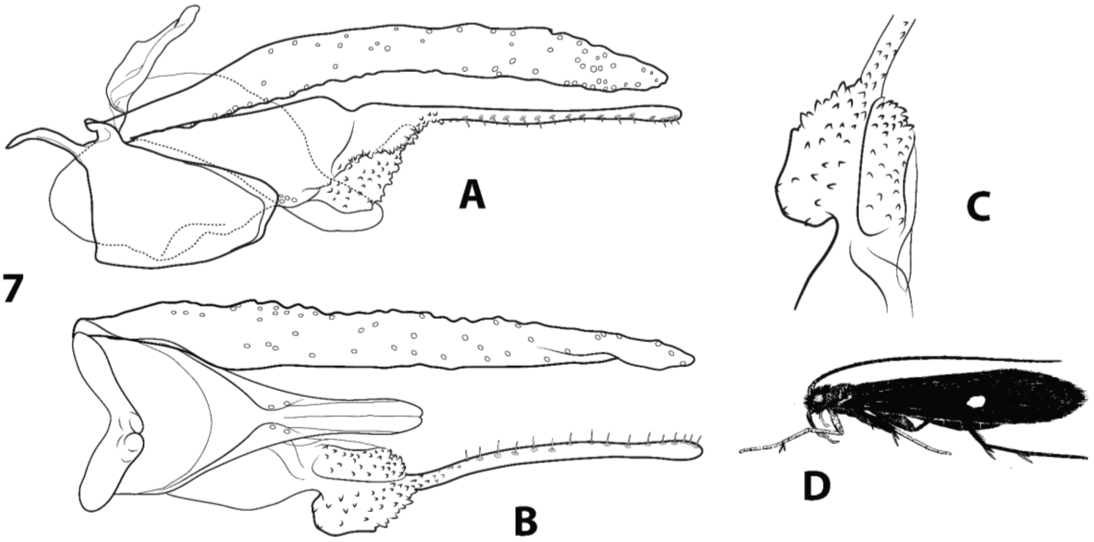

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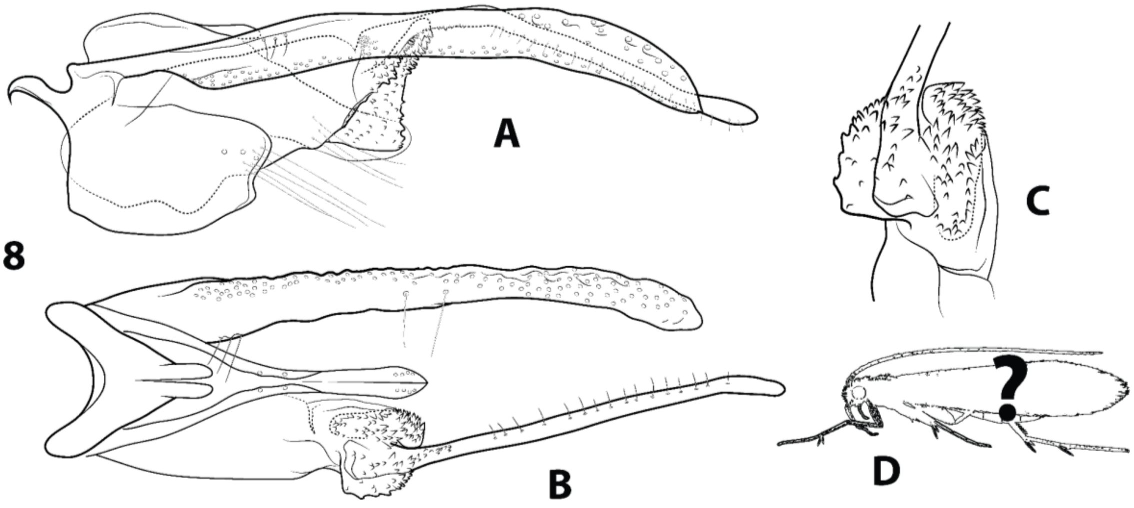

Figures 16–18. *Machairocentron* undescribed morphotypes. Male genitalia: A. lateral; B. dorsal; C. detail of harpago structures; D. adult, respectively. (16) morphotype A, (Ecuador: El Oro); (17) morphotype B, (Ecuador: Orellana); (18) morphotype C, (Peru: Madre de Dios), adult wing pattern unknown.

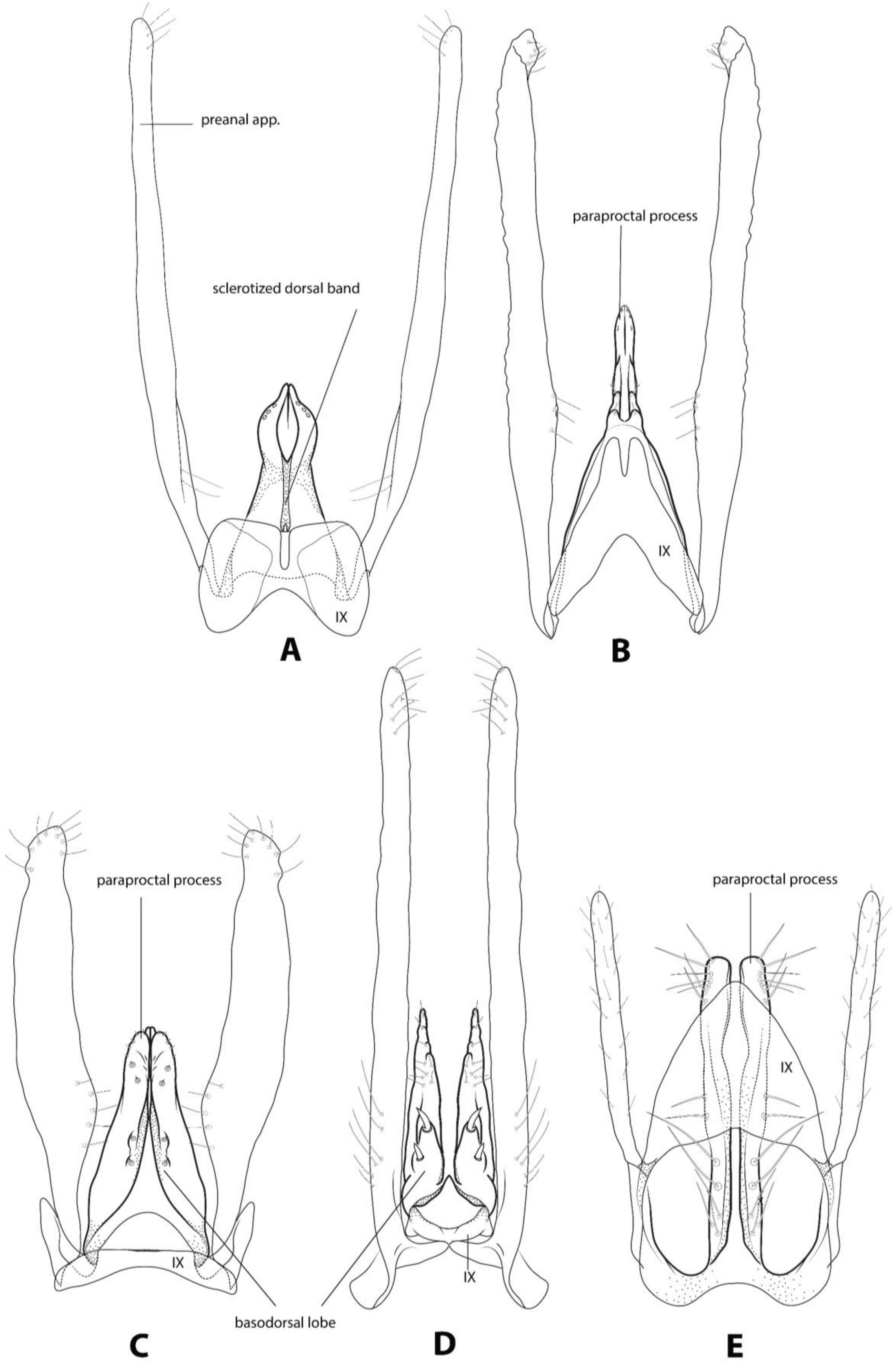

Figure 19. Psychomyioidea male genitalia, dorsal: A. *Xiphocentron* (*Xiphocentron*) *tarquon*; B. *Machairocentron ascanius*; C. *Xiphocentron* (*Xiphocentron*) *aureum*; D. *Proxiphocentron arjinae*; E. *Tinodes consueta.*

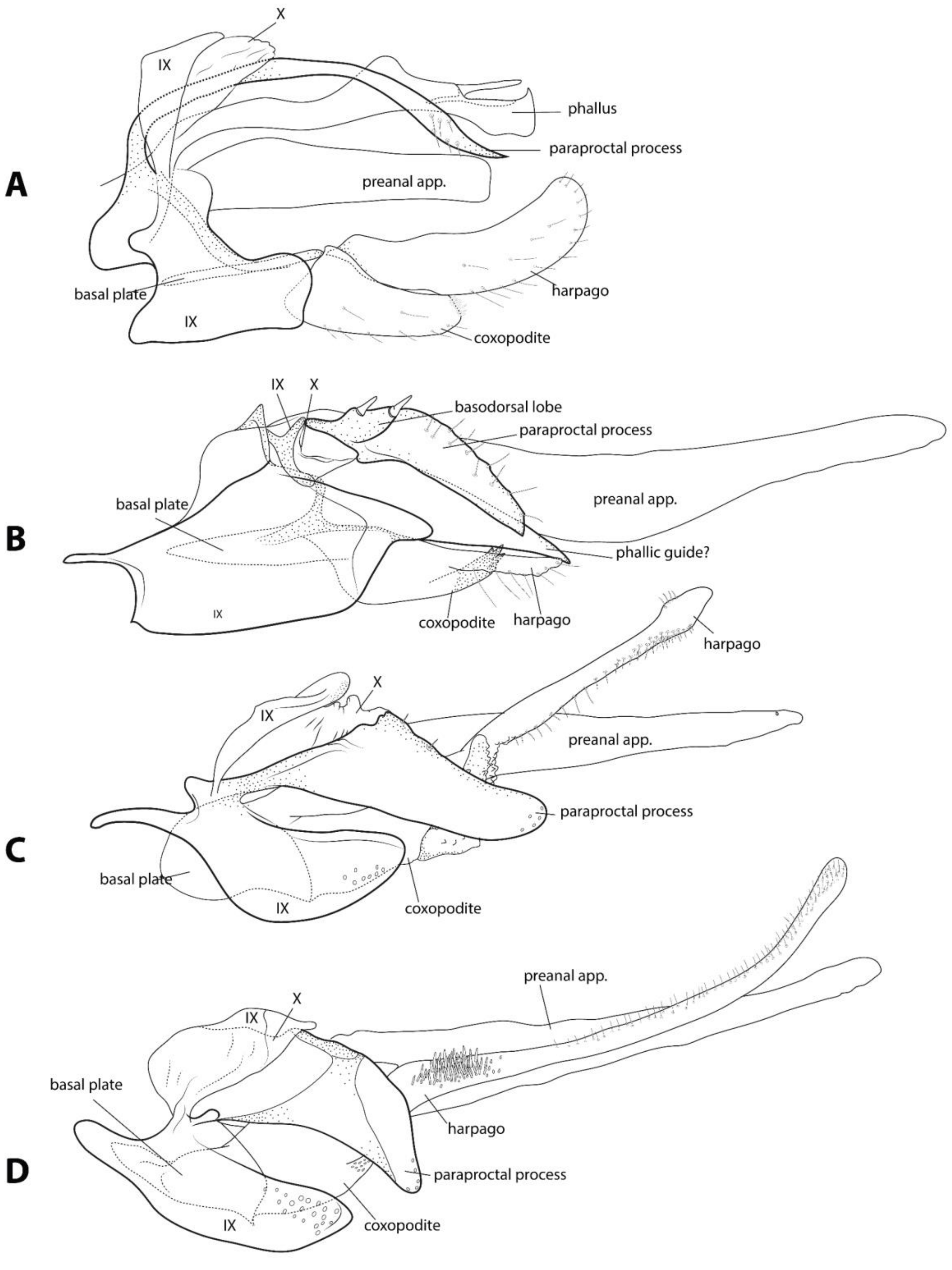

Figure 20. Psychomyioidea male genitalia, lateral: A. *Eoneureclipsis varsikiyja* (modified after Schmid 1972); B. *Proxiphocentron arjinae*; C. *Machairocentron piaroa*; D. *Xiphocentron* (*Xiphocentron*) *tarquon*.

Conclusive Remarks and Perspectives

This study aimed to improve our understanding of the xiphocentroid clade evolution and their relationship with related taxa. Our research provided a first comprehensive phylogenetic proposition for Psychomyiidae and the Xiphocentronidae, revealing the placement of Xiphocentronidae within the Psychomyiidae, confirming Edwards (1961) hypothesis, being the family lowered to subfamily level. Also following the phylogenetic results, the genus *Zelandoptila* previously included in Psychomyiidae now was transferred to Ecnomidae. Additionally, this study proposes the first hypothesis of the evolutive relationship of the xiphocentroid taxa. Despite the low support results of some xiphocentroid clades do not conclusively resolve the relationship of all the xiphocentroid genera and subgenera, the results confirm the placement of *Proxiphocentron* among the first cladogenesis of the group as proposed by Schmid (1982), and suggest the paraphyly of the genera *Xiphocentron* and *Cnodocentron*, as well as the placement of the fossil genera *Palerasnitsynus* as a xiphocentroid.

Additionally, the taxonomy of the group since Schmid (1982) revision did not have many extensive works on the Neotropical fauna, with isolated descriptions of few species (Flint 1991, Flint 1996; Pes et al. 2013; Mey et al. 2018; Muñoz & Holzenthal 1997; Rocha et al. 2017; Vilarino & Calor 2015). The present study provided descriptive taxonomic revisions for *Machairocentron* and Brazilian *Xiphocentron* species adding 8 new species, helping to standardize descriptions and illustration, and stating questions concerning species polymorphism and blurry species limits, that besides mentioned in the case of the subspecies of *Xiphocentren cubanum* (Banks), 1941 (Kumanski 1987; Botosaneanu 1993), were not properly discussed in previous works and seems to be common among *Xiphocentron* and *Machairocentron* species.

The results of this research highlight the importance of the Xiphocentroninae for achieving a big picture of the tube-dweller caddisflies evolutionary history and for understand the early evolution of the superfamily Psychomyioidea. This research also provides a foundation for further studies on Psychomyiidae evolution and Xiphocentroninae taxonomy.

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