Systematics, Morphology, and Evolution of the New World Conoderinae Schoenherr, 1833

(Coleoptera: Curculionidae)

by

Salvatore Anzaldo

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Graduate Supervisory Committee:

Nico Franz, Chair
Emilia Martins
Kathleen Pigg
Christian Rabeling

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ABSTRACT

Weevils are one of the most diverse groups of animals with thousands of species suspected to remain undiscovered. The Conoderinae Schoenherr, 1833 are no exception, being especially diverse and unknown in the Neotropics where they are recognizable for their unique behaviors and color patterns among weevils. Despite these peculiarities, the group has received little attention from researchers in the past century, with almost nothing known about their evolution. This dissertation presents a series of three studies that begin to elucidate the evolutionary history of these bizarre and fascinating weevils, commencing with an overview of their biology and classificatory history (Chapter 1).

Chapter 2 presents the first formal cladistic analysis on the group to redefine the New World tribes Lechriopini Lacordaire, 1865 and Zygopini, Lacordaire, 1865. An analysis of 75 taxa (65 ingroup) with 75 morphological characters yielded six equally parsimonious trees and synapomorphies that are used to reconstitute the tribes, resulting in the transfer of sixteen genera from the Zygopini to the Lechriopini and four generic transfers out of the Lechriopini to elsewhere in the Conoderinae.

Chapter 3 constitutes a taxonomic revision of the genus *Trichodocerus* Chevrolat, 1879, the sole genus in the tribe Trichodocerini Champion, 1906, which has had an uncertain phylogenetic placement in the Curculionidae but has most recently been treated in the Conoderinae. In addition to redescriptions of the three previously described species placed in the genus, twenty-four species are newly described and an identification key is provided for all recognized species groups and species.

Chapter 4 quantitatively tests the similarity in color pattern among species hypothesized to belong to several different mimicry complexes. The patterns of 160 species of conoderine weevils were evaluated for 15 categorical and continuous characters. Non-

metric multidimensional scaling (NMDS) is used to visualize similarity by the proximity of individual species and clusters of species assigned to a mimicry complex in ordination space with clusters being statistically tested using permutational multivariate analysis of variance (PERMANOVA).

ACKNOWLEDGMENTS

There are many people who supported and assisted me over the past six years that I would like to thank, for I could not have completed this dissertation without them.

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Without the labors of previous weevil workers to uncover the mysteries of these fascinating insects there would have been no foundation to develop the projects of this dissertation on. Special thanks go to the Arizona State University library staff for their timely fulfillment of the hundreds of interlibrary loan requests I have made in the past six years, thus making this prior research available to me.

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CHAPTER 1

INTRODUCTION TO THE CONODERINAE SCHOENHERR, 1833[1]

The Conoderinae Schoenherr, 1833 (*sensu stricto*; Conoderitae *sensu* Prena *et al.* 2014) are one of the most diverse and conspicuous groups of weevils in the New World tropics. Despite this fact they have remained relatively unstudied. Research on the group is hindered by an unnatural classification, with poorly defined tribes and genera and numerous undescribed species that don't fit into existing genera as they are currently circumscribed. The individual projects of this dissertation take a first step toward achieving a phylogenetic classification of the Conoderinae and understanding the evolutionary history of the group. A cladistic analysis of the Lechriopini Lacordaire, 1865 and the Zygopini Lacordaire, 1865 (Chapter 2) aims to redefine the tribes based on phylogenetically tested morphological characters. A taxonomic revision and overview of the morphology of the only genus placed in the enigmatic conoderine tribe Trichodocerini Champion, 1906 (Chapter 3) describes new species and evaluates the placement of the genus in the Conoderinae. Finally, convergent color patterns thought to represent different mimicry complexes are quantitatively analyzed (Chapter 4). This chapter presents an overview of the New World Conoderinae and provides the foundation of classificatory and biological knowledge that the subsequent chapters build off of.

[1] The section "Review of classificatory history" was previously published in: **Anzaldo SS. 2017**. Review of the genera of Conoderinae (Coleoptera, Curculionidae) from North America, Central America, and the Caribbean, *Zookeys* 683: 51-138. doi: 10.3897/zookeys.683.12080. The text in this section is reproduced with minor emendations (e.g. removing references to tables occurring in that document, adding authorities for the first appearance of taxa in this document).

Review of classificatory history

The first treatment of genera now included in Conoderinae was by Schoenherr (1825, 1826) who included *Cratosomus* Schoenherr, 1825, *Zygops* Schoenherr, 1825 (including the subgenera *Copturus* Schoenherr, 1825, *Piazurus* Schoenherr, 1825, and *Coryssopus* Schoenherr, 1826), *Mecopus* Schoenherr, 1825, *Lechriops* Schoenherr, 1825, and *Pinarus* Schoenherr, 1826 under "Divisio 3. Cryptorhynchides" for having a curved rostrum and a more-or-less distinctly deep rostral channel. This classification was refined by Schoenherr (1837, 1838), where the Cryptorhynchides were split into two "*Cohortes*", I (1837: 1; including *Cratosomus* and *Lechriops*) which has the prosternum distinctly canaliculate, continuous on the mesoventrite and distinctly terminated, and II (1837: 360, which included *Zygops*, *Copturus*, *Piazurus*, *Timorus* Schoenherr, 1838, *Pinarus*, and *Mecopus* in 1838) containing those with a less distinctly canaliculate prosternum that is usually not continuous on the mesoventrite and never distinctly terminated. This classification was largely unchanged in the subsequent influential work by Schoenherr (1845), which saw the addition of numerous species, several of which became type species of subsequently described genera but only two more New World conoderine genera (*Lobops* Schoenherr, 1845 and *Peltophorus* Schoenherr, 1845).

Lacordaire's (1865) classification represents the first grouping of genera into the three largest New World tribes recognized today mainly based on sternal modification to receive the rostrum in repose. He divided the New World representatives of "Tribu *Zygopides*" – those having both a broad metanepisternum that extends between the metacoxae and the elytra, large eyes, a canaliculate prosternum, and an antennal funicle of seven articles (as summarized by Pascoe 1871: 199) – into three groups: the "*Piazurides*", the "*Lechriopides*" and the "*Zygopides vrais*". Pascoe (1871: 198) noted the inadequacy of this system but provided no alternative classification.

Lacordaire's classification was amended only slightly by K.M. Heller (1894) to accommodate the thirty-three mainly Old World genera described by Pascoe since Lacordaire's work as well as the two genera and many species newly described by Heller therein. In Heller's key (1984: 3) the New World Conoderinae are characterized by an antennal funicle composed of seven articles and the presence of a rostral channel at least on the prosternum, but are not further separated morphologically from several Old World genera that share those characters. Heller (1895) further amended this to accommodate seventeen new New World genera, and provided an identification key based largely on eye shape, the modification to the mesoventrite and the relative lengths of the antennal funicular articles.

Champion's (1906b) "Zygopina" section of the *Biologia Centrali-Americana* represents the most recent major taxonomic treatment of Central American Conoderinae, in which he authored 14 genera and 194 species (also in 1909, 1910) pertaining to the Conoderinae as currently recognized. Champion noted that his arrangement of the genera would have been presented in the order given by Heller (1895) "...were it not more convenient, to avoid delay in publication, to deal with the genera seriatim, irrespective of their relationships..." (Champion 1906b: 1). Despite this, the order the genera are presented by Champion do seem to have been done so with consideration of potential relationships, and the next catalog of Conoderinae, Hustache's pars 134 of the Coleopterorum Catalogus (1934), presented a classification in nearly the exact order arranged by Champion, with genera treated on Champion's pages 2–21 representing the Piazurini Lacordaire, 1865, 21–87 representing the Zygopini Lacordaire, 1865, and 87–130 the Lechriopini Lacordaire, 1865, with the single exception of *Euzurus* Champion, 1906 on page 45 placed in the Lechriopini.

Many of those genera were grouped in Lacordaire's tribes without bearing the characters originally indicated, and no updated tribal diagnoses were presented to redefine them.

This classification scheme remained almost completely unchanged, despite a foreshadowing of its probable inadequacy in reflecting the evolutionary history of numerous lineages of Conoderinae by Böving (1926) and Hustache (1938), until several genera of Zygopini were transferred to the Lechriopini by Lyal *et al.* (2006). Böving's (1926) comparative study of larvae and pupae (representing the only comparative study of conoderine immatures) of the genera *Peltophorus*, *Cylindrocopturus* Heller, 1895, and *Eulechriops* Faust, 1896, all of which at the time were included in the Zygopini, revealed *Cylindrocopturus* and *Eulechriops* to share multiple larval and pupal characters, suggesting a closer relationship to each other than either is to *Peltophorus*. Böving later (1927) created the tribe Cylindrocopturini to include both *Cylindrocopturus* and *Eulechriops*. The current classification includes *Eulechriops* in the Lechriopini and *Cylindrocopturus* and *Peltophorus* in the Zygopini due to the presence of modification to the mesoventrite in *Eulechriops* in the form of a carinate channel and an unmodified or only slightly modified mesoventrite (not a carinate channel) in *Cylindrocopturus* and *Peltophorus*. *Cylindrocopturus* was included in the Lechriopini by Kissinger (1964) and Hatch (1971) but in the Zygopini in all subsequent works – the genus was not among the lechriopines moved by Lyal *et al.* (2006) due to both an unmodified mesoventrite and lack of sclerolepidia (modified scales along the metanepisternal suture), while other genera that are possibly related to *Cylindrocopturus* that have sclerolepidia (e.g. *Macrocopturus* Heller, 1895) were moved.

Further examination of external and internal morphological character systems have revealed characters that seem to conflict with the original classification scheme, and until now had not been tested phylogenetically to reveal the classificatory hypothesis best

supported by synapomorphies. Many of the genera traditionally in the Zygopini are shown to be more closely related to lechriopines than to *Zygops*, *Peltophorus*, and a few additional South American genera (e.g. *Parazygops* Desbrochers, 1890, *Colpothorax* Desbrochers, 1890) that make up the "true zygopines", as Böving's work implied. Hustache (1938: 58) noted the interesting distribution of "granules" on the metathoracic episterna (i.e. sclerolepidia) and suggested that a further study of these structures may provide an updated classification from that of Lacordaire; Lyal *et al.* 2006 based several generic transfers from the Zygopini to the Lechriopini based on these structures and/or the presence of modification to the mesoventrite. The classification used as the framework for this dissertation follows that provided by Anzaldo (2017), accommodating a recent addition by Kuschel (2017).

Natural history, behavior, and mimicry

The Conoderinae have long been recognized as having interesting behaviors among the weevils (e.g. Quoy and Gaimard 1824, Champion 1906b), especially for being active and alert to potential threats (e.g. Lyal 1986). Very little is known about the natural history of most species, likely in part a result of the most effective methods of their collection being passive trapping (e.g. Malaise traps) and by hand as they perch on tree trunks (Hespenheide 1995) that are not thought to be the host plant. Many species are thought to be wood boring as larvae (Prena *et al.* 2014), though species are known to be associated with seeds and fruits (Sanz-Veiga *et al.* 2017, Hespenheide 2018b, Anzaldo & O'Brien 2019 *in press*), and galls (Hanson *et al.* 2014, Hespenheide 2018c) and utilize a variety of plant families (Anderson 1993, Anzaldo 2017 and references therein).

Similar color patterns were frequently commented upon in the original descriptions of species (e.g. Champion 1906b: 87) but weren't hypothesized to have adaptive significance

until Hespenheide (1973, 1980, 1984, 1986, 1995, 1996a, 2005, 2017, 2018c) identified several such patterns as belonging to different mimicry complexes. These putative mimicry complexes have never been experimentally tested or quantified though they have the potential for fascinating and controversial evolutionary explanations (e.g. Ruxton *et al.* 2004).

Certainly, much remains unknown about the biology and classification of the New World Conoderinae. It is hoped that the projects contained within this dissertation can generate interest in this group of incredible weevils and provide a starting point to base future analyses on these topics.

CHAPTER 2

SYSTEMATICS OF THE LECHRIOPINI LACORDAIRE, 1865 (COLEOPTERA: CURCULIONIDAE: CONODERINAE)

ABSTRACT

The two largest New World tribes of the Conoderinae Schoenherr, 1833, the Lechriopini Lacordaire, 1865 and the Zygopini Lacordaire, 1865, are poorly defined and contain many genera that appear out of place. The Lechriopini are here redefined following a morphological cladistic analysis of 75 taxa (65 ingroup) and 75 morphological characters. The analysis yielded six equally parsimonious trees (L = 95, CI = 82, RI = 96). Synapomorphies revealed by the analysis are used to reconstitute the tribes Lechriopini and Zygopini. The following transfers from the Zygopini to the Lechriopini are made: *Acopturus* Heller, 1895, *Arachnomorpha* Champion, 1906, *Archocopturus* Heller, 1895, *Copturosomus* Heller, 1895, *Chileops* Kuschel, 2017, *Cylindrocopturus* Heller, 1895, *Helleriella* Champion, 1906, *Hemicolpus* Heller, 1895, *Hypoplagius* Desbrochers, 1891, *Larides* Champion, 1906, *Lissoderes* Champion, 1906, *Macrotimorus* Heller, 1895, *Phileas* Champion, 1906, *Philenis* Champion, 1906, *Timorus* Schoenherr, 1838, and *Zygopsella* Champion, 1906, all **new placements**. The genera *Mnemyne* Pascoe, 1880, *Paramnemyne* Heller, 1895, *Paramnemynellus* Hustache, 1932, and *Psomus* Casey, 1892 are transferred from the Lechriopini to the Conoderinae *incertae sedis*, **new placements**.

Introduction

The Conoderinae Schoenherr, 1833 (*sensu* Alonso-Zarazaga and Lyal 1999; Conoderitae *sensu* Prena *et al.* 2014) are among the most diverse of the subfamilies of Curculionidae Latreille, 1802, containing over 2,000 species arranged into 210 genera (Anzaldo 2017; with addition of Kuschel 2017) and 14 tribes. This diversity is especially prevalent in the New World tropics where there are hundreds of undescribed species and many genera in their current concept are insufficiently delimited to accommodate these new species (Hespenheide 2007, Anzaldo 2017). Despite conoderine weevils being one of the most recognizable subfamilies of Curculionidae due to their characteristic large eyes and frequently long legs, the classification below the level of subfamily is inadequate and remains relatively unchanged from what was originally proposed by Lacordaire (1865).

Within the Conoderinae are understudied behaviors (Lyal 1986) and mimicry systems (Hespenheide 1973, 1995; Anzaldo, in preparation), the study of which is hindered by the lack of a phylogenetic classification. Conoderines as a whole have received little attention from taxonomists in the past century and have been poorly represented in molecular phylogenies aimed at resolving higher-level relationships within the Curculionoidea Latreille, 1802 (e.g. Gunter *et al.* 2016, two conoderines; Shin *et al.* 2017, no conoderines). Within the subfamily a phylogenetic hypothesis has never been proposed for any of the 14 tribes. In the New World, conoderine diversity is dominated by two tribes, the Lechriopini Lacordaire, 1865 and the Zygopini Lacordaire, 1865, which together contain 46 extant genera and 678 described species (Table 1). The generic composition of these tribes has been suspect for decades (e.g. Böving 1926) but the tribes have never been revised. This study presents the first formal cladistic analysis focusing on the Conoderinae and redefines the Lechriopini and

the Zygopini resulting in twenty generic transfers and progress towards a phylogenetic classification.

Taxonomic history of the New World Conoderinae

The taxonomic history of the New World tribes of Conoderinae was outlined in detail by Anzaldo (2017). Lacordaire's (1865) original concepts for the three largest New World tribes was based in part on the type of ventral modification to receive the rostrum in repose, being a posteriorly closed channel in the Lechriopini Lacordaire, 1865 (Fig. 2.1A), a posteriorly open channel in the Piazurini Lacordaire, 1865 (Fig. 2.1B), and without any ventral modification to the meso- or metaventrite in the Zygopini Lacordaire, 1865 (Fig. 2.1C). Soon after this classification was established, 31 of the New World genera were described by Heller (1895) and Champion (1906) and placed into Lacordaire's tribes without reference to the characters that originally defined them. The next significant change to the generic composition of the Lechriopini and the Zygopini came from Lyal *et al.* (2006), who transferred 12 genera from the Zygopini to the Lechriopini based in part on the presence of a rostral channel and thus reapplying Lacordaire's tribal characters. Anzaldo (2017) transferred four other genera out of the Lechriopini and discussed conflict between characters found among the genera in the Zygopini that likely underlie their improper placement.

Materials and Methods

General morphological terminology largely follows Oberprieler *et al.* (2014) in part supplemented with specific terminology for the prosternum (Chamorro-Lacayo and Konstantinov 2004, Davis 2011), mouthparts (Ting 1936), abdominal ventrites (Thompson

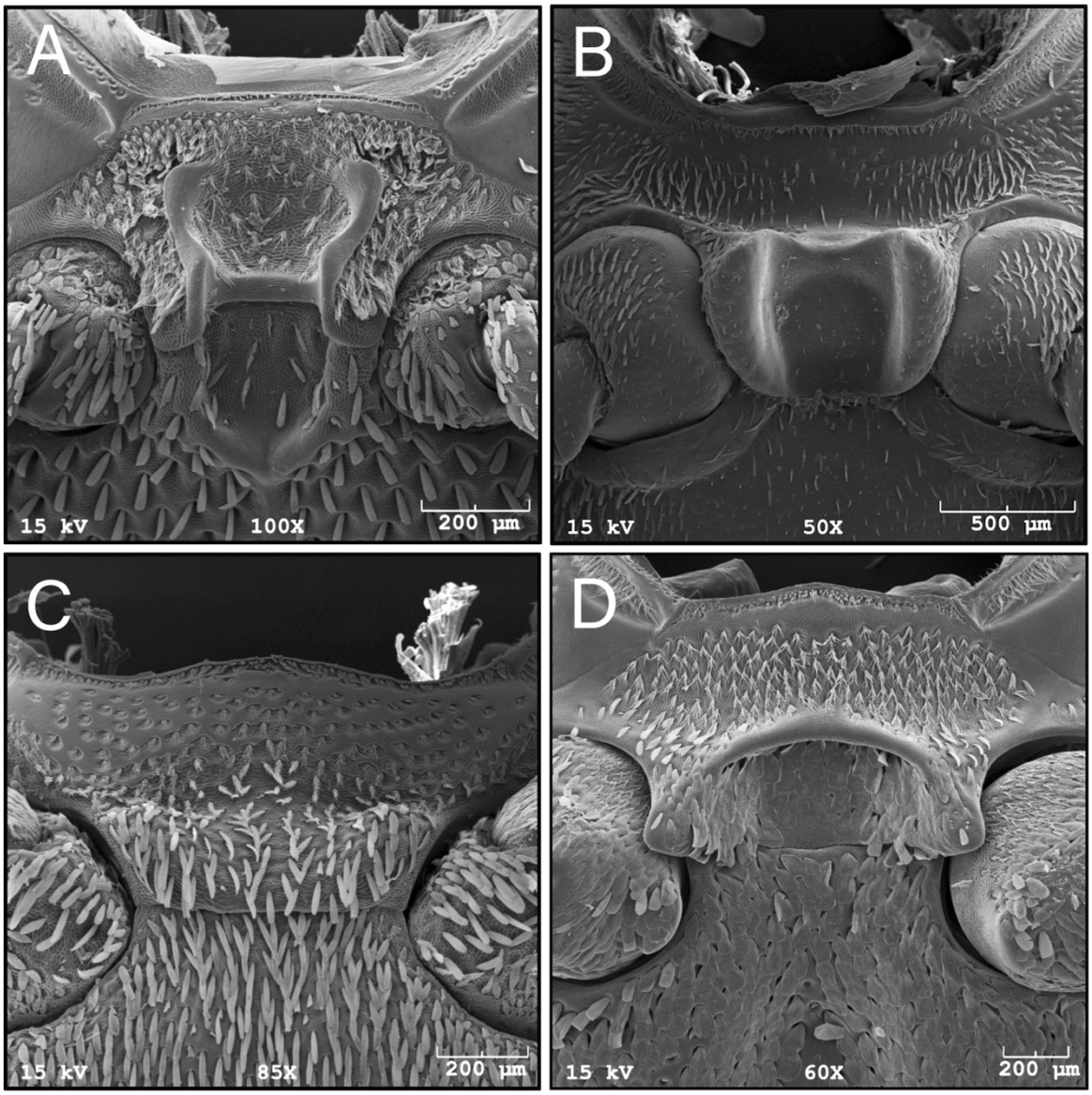

Figure 2.1. Modification to the mesoventrite in the New World Conoderinae. A) *Lechriops vestitus*; B) *Piazurus maculipes*; C) *Zygops tridentatus*; D) *Hoplocopturus javeti*.

1992), female terminalia (Howden 1995, Aslam 1961), male terminalia (Wanat 2007), and the hind wing (Zherikhin and Gratshev 1995).

Mouthpart images (Figs 2.2-2.3) were taken with Confocal Laser Scanning Microscopy (CLSM) at the Arizona State University College of Liberal Arts and Sciences Keck Bioimaging Facility with a Leica TCS SP5 AOBS Spectral Confocal System. Samples were prepared on a glass slide in glycerin jelly and excited with a 488 nm argon laser. Autofluorescence was collected at 500–580 nm and 580–700 nm and pseudocolored green and red, respectively. Channels were merged in FIJI (Fiji Is Just ImageJ; Schindelin *et al.* 2012) with a maximum intensity Z-projection. Scanning Electron Microscopy was done with a JEOL JSM 6300 Scanning Electron Microscope at the Arizona State University Eyring Materials Center.

Specimens used in the cladistic analysis or observed from limited material were obtained from the following collections:

ASUHIC Arizona State University Hasbrouck Insect Collection, Tempe, AZ, USA

ASUCOB Arizona State University Charles W. O'Brien Collection, Tempe, AZ, USA

CMNC Canadian Museum of Nature Collection, Ottawa, Canada

MIUP Museo de Invertebrados G.B. Fairchild, Universidad de Panamá, Panamá

MTD Museum für Tierkunde, Dresden, Germany

NHM Natural History Museum, London, UK

NMNH National Museum of Natural History, Washington DC, USA

PCMENT Programa Centroamericano de Maestria en Entomología, Universidad de Panamá

SSAC Salvatore S. Anzaldo Collection, Tempe, AZ, USA

Taxon sampling. Despite efforts to include as many of the genera of New World Conoderinae as possible in the analysis, only 26 of the 46 extant New World genera currently placed in the Lechriopini and Zygopini (Anzaldo 2017 with the addition of Kuschel 2017; Table 1; Appendix A) were included. As a result, this sampling is not deemed complete enough to propose a subtribal classification, even though these genera represent a small fraction of the described species-level diversity. Of the genera not included, only *Timorus* Schoenherr, 1838, *Hemicolpus* Heller, 1895 (Hespenheide 2018b) and *Philenis* Champion, 1906 (Hespenheide 2018c) contain more than three species (Table 1). Sampling did however target the three most diverse genera, *Eulechriops* Faust, 1896 (with 9 species included), *Lechriops* Schoenherr, 1825 (7 species included), and *Macrocopturus* Heller, 1895 (7 species included), each of which was suspected to not be a monophyletic grouping of species and greatly confound the classification of the lechriopines (Anzaldo 2017).

Outgroups were selected from other tribes of Conoderinae (Appendix A) and the tree was rooted on the species *Conotrachelus suturalis* Champion, 1904 (Molytinae Schoenherr, 1823). Since the relationships of the tribes of Conoderinae have no proposed phylogenetic hypothesis, and the relationship of the Conoderinae to other frequently proposed subfamilies such as the Baridinae Schoenherr, 1836 have little phylogenetic corroboration, characters used in the analysis were surveyed for broadly in the Curculionidae. As such, many more taxa than could feasibly be included in the analysis were observed and analyzed for certain characters to reduce the possibility that the Lechriopini as redefined here was artificially recovered as monophyletic due to limited outgroup comparisons. A complete set of voucher specimens is deposited in the ASUHIC (Tempe, AZ).

Cladistic analysis. A character matrix for 75 taxa was scored for 75 characters (Appendix A) in ASADO (Nixon 2008). An unconstrained heuristic search was run in NONA (Goloboff 1999) using the commands hold 100000, mult*1000, hold/100, mult*max. Bootstrap support was calculated in NONA with 1000 replications and the commands hold 1000, mult*10, hold/100 and "don't do max*".

Previous cladistic analyses on weevils (especially Franz 2006, 2012, Davis 2011, 2014) were useful for identifying character systems potentially having phylogenetically informative signal. Only 10 of the 75 characters included are external characters not requiring dissection or special preparation to view. Throughout the process of assembling the matrix characters were rescoped to reflect more precise statements of homology in light of emerging phylogenetic signal (Franz 2014).

Results

The analysis yielded six equally parsimonious trees of length 95 (CI = 82; RI = 96). A strict consensus resulted in 4 collapsed nodes and 3 extra steps (L = 98). Bootstrap support was generally low (Fig. 2.7) except for major clades identifying the Piazurini, Zygopini, Zygopini+Piazurini, Lechriopini, *Copturus* Schoenherr, 1825, and a less inclusive lechriopine clade excluding *Copturus*.

Morphological characters. Character state optimizations are based on the preferred most parsimonious tree (Fig. 2.7; 73 unambiguous, 2 fast). Clades are named by the sequence of taxa presented on this tree. The sequence of characters is modeled after Franz (2006).

Scales

1. *Shape of scales, lateral and ventral surfaces*: (0) scales absent, piliform to broad and flattened, with margins entire; (1) scales round, flattened, with minute projections giving a frayed appearance. Synapomorphy for the *Mecopus helleri* – *Acoptus suturalis* LeConte, 1876 clade. Unambiguous optimization (CI = 100; RI = 100).

Mandible

2. *Shape of mandible*: (0) relatively flat, with one cutting surface; (1) scoop-shaped, with the anterior and posterior faces in contact when closed. Synapomorphy for the Piazurini and Zygopini. Unambiguous optimization (CI = 100; RI = 100).

3. *Shape of mandible*: (0) variously toothed and in contact along mesal surface; (1) somewhat falcate, when closed only in contact at apex. Synapomorphy for the *Mecopus helleri* Marshall, 1930 – *Acoptus suturalis* clade. Unambiguous optimization (CI = 100; RI = 100).

4. *First incisor, dorsally*: (0) dorsal margin straight to evenly curved; (1) dorsal margin with a small to large dentate process. Coded as inapplicable for taxa with scoop-shaped mandibles (character 2). Synapomorphy for *Pseudolechriops* Champion, 1906. Unambiguous optimization (CI = 100; RI = 100).

Maxilla

5. *Cardo, shape*: (0) short, not considerably longer than wide; (1) elongate, much longer than wide. Synapomorphy for the Piazurini and Zygopini. Unambiguous optimization (CI = 100; RI = 100).

6. *Cardo, setation*: (0) without any setae or with a single, elongate, straight seta; (1) with a longitudinal row of 2-6 curved setae originating in an indentation (Fig. 2.2B); (2) with a single curved setae originating in an indentation. Coded as additive, implying a transformation series from a relatively simple state with a single or no seta to a series of curved setae in a longitudinal row, then a reduction to a single seta of similar form. State 1 is an apomorphy for the Piazurini and Zygopini with the derived state 2 is present in the *Zygops maculipes* Desbrochers, 1891 – *Z. tridentatus* Gyllenhal, 1838 clade. Unambiguous optimization (CI = 100; RI = 100).

7. *Proximal lacinial tooth, ventral view*: (0) variably thin, elongate, straight or falcate; (1) broad at the base, triangular (Fig. 2.2B). Synapomorphy for the *Parazygops luctuosus* (Desbrochers, 1890) – *Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

8. *Mala, proximal setal tuft, dorsal*: (0) arising in plane with lacinial tooth, continuous with malar cutting surface; (1) offset from lacinial plane, obliquely directed towards base of stipes (Fig. 2.2B). Synapomorphy for the *Peltophorus polymitus seminiveus* LeConte, 1884 – *Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

9. *Palpiger, central region, setation, dorsal view*: (0) without setae or multiple adjacent setae; (1) with a single isolated seta (Fig. 2.3E). Synapomorphy for a clade of four *Eulechriops* species and *Arachnomorpha circumlineata* Champion, 1906. Unambiguous optimization (CI = 100; RI = 100).

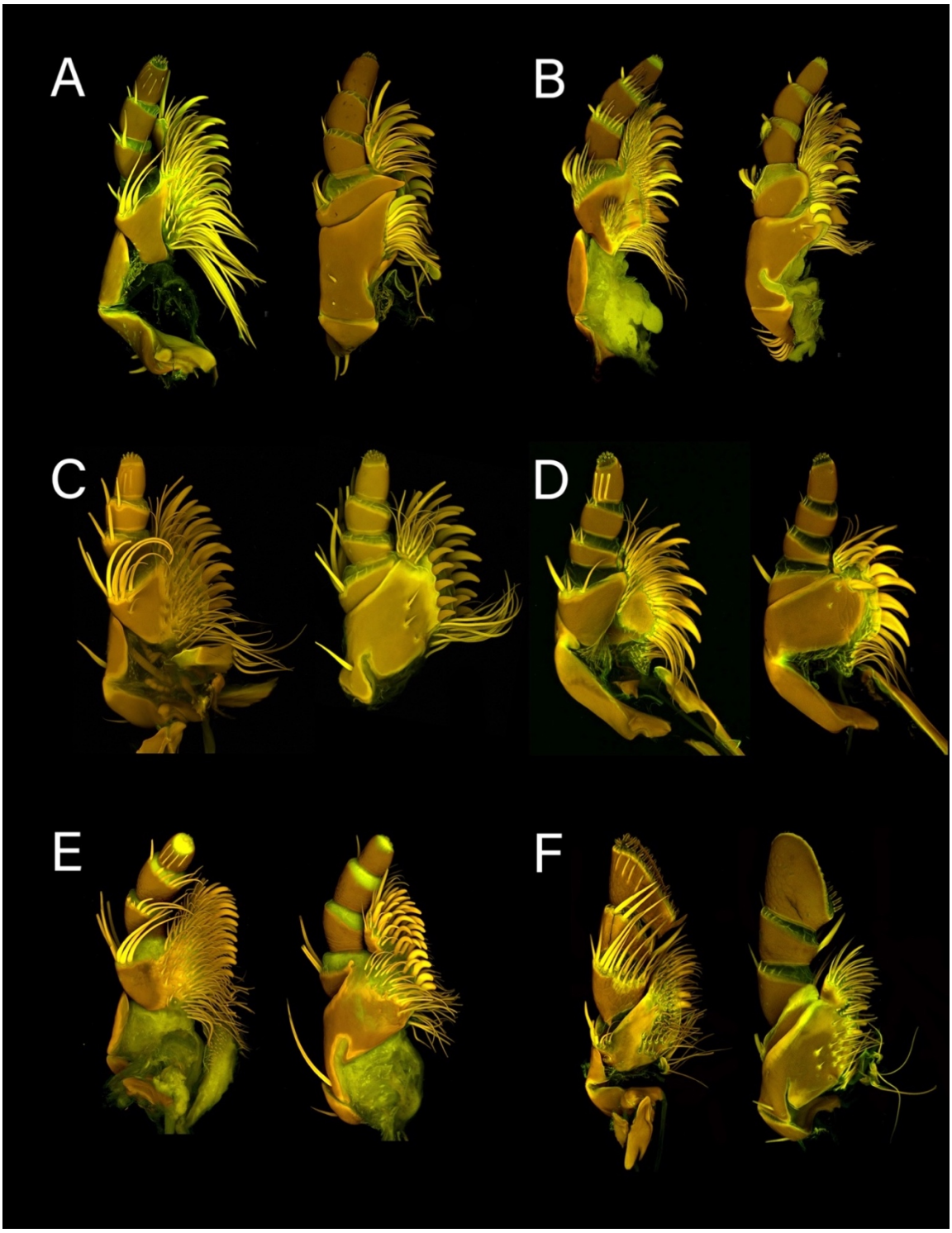

Figure 2.2. Maxillae of the Conoderinae, Part I. Left image is dorsal, right is ventral. A) *Piazurus alternans*; B) *Zygops mexicanus*; C) *Acoptus suturalis*; D) *Trichodocerus "leptodontus"*; E) *Copturus aurivillianus*; F) *Microzygops nigrofasciatus*.

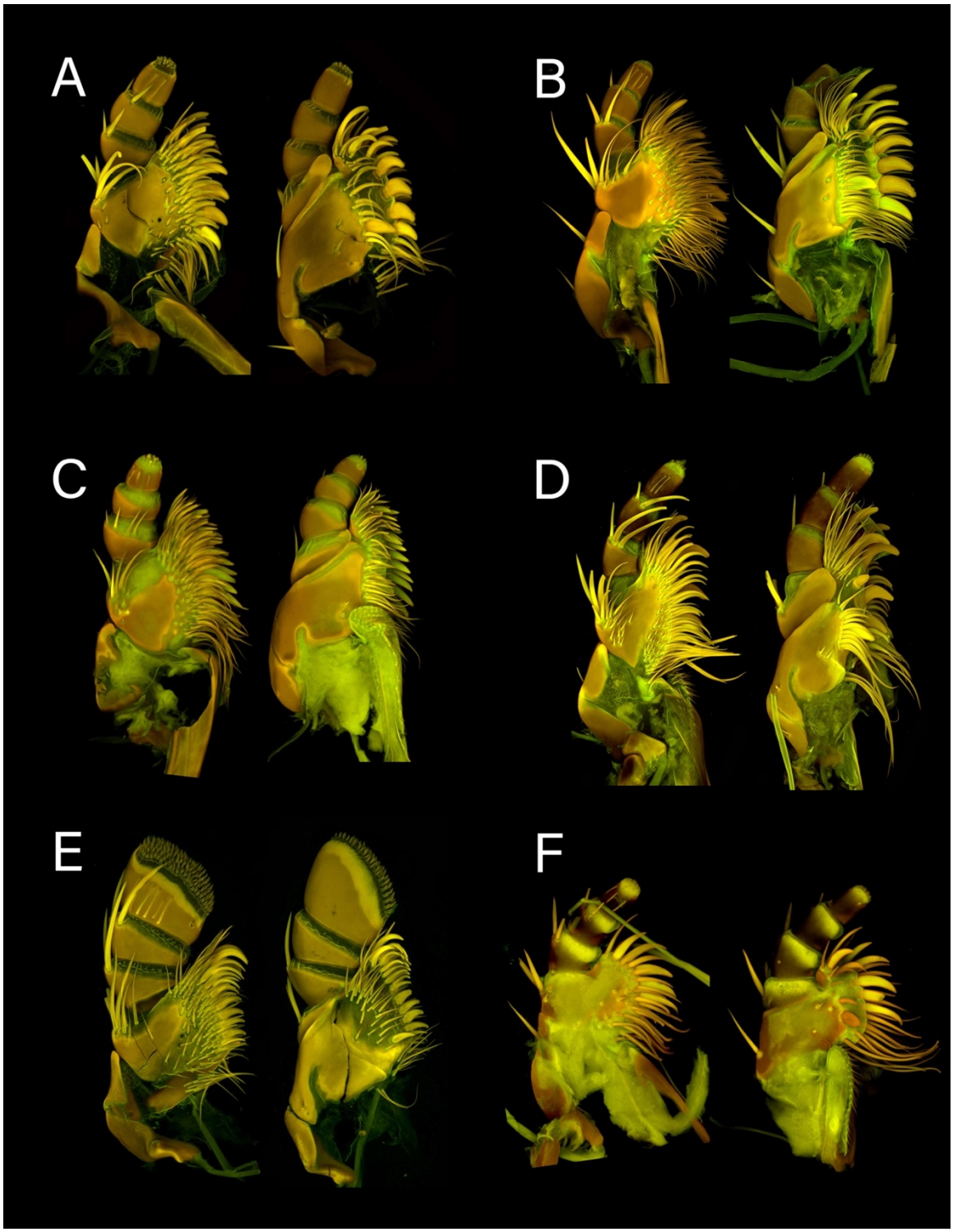

Figure 2.3. Maxillae of the Lechriopini, Part II. Left image is dorsal, right is ventral. A) *Lechriops vestitus*; B) *Macrocopturus floridanus*; C) *Hoplocopturus armatus*; D) *Archocopturus regalis*; E) *Arachnomorpha circumlineata*; F) *Helleriella longicollis*.

10. *Palpiger, shape entally, ventral view*: (0) not projecting towards palpomeres; (1) slightly to broadly projecting (e.g. Fig. 2.3C-D). Convergently present in *Mecopus helleri* and in the *Archocopturus regalis* (Boheman, 1845) – *Lechriops excavatus* Champion, 1906 clade with a single reversal in *Helleriella longicollis* Champion, 1906. Unambiguous optimization (CI = 33; RI = 94).

11. *Mala, ental surface, ventral view*: (0) continuous; (1) interrupted by projecting palpiger (Fig. 2.1A). Synapomorphy for the *Pseudopiazurus centraliamericanus* (Heller, 1906) – *Piazolechriops bicristatus* Heller, 1906 clade. Unambiguous optimization (CI = 100; RI = 100).

12. *Palpomere I, setation*: (0) setae lateral, paired or multiple in transverse row; (1) setae paired, more central, inner setae longer, thicker, displaced proximally. Synapomorphy for the *Crassocopturus* Rheinheimer, 2011 sp. – *Poecilogaster brevis* (Waterhouse, 1879) clade. Unambiguous optimization (CI = 100; RI = 100).

13. *Shape of palpomere III*: (0) narrow, cylindrical, not apically widened; (1) expanded, apical sensory region large, with dense small pappilate sensillae (Fig. 2.3E). Synapomorphy for the *Arachnomorpha circumlineata* – *Eulechriops* sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

Labium

14. *Number of labial palpomeres*: (0) 3 (e.g. Fig. 2.4K); (1) 2 (Fig. 2.4L). Convergently present in *Microzurus* nr. *rhombus* Heller, 1895 and the *Helleriella longicollis* – *Cylindrocopturus quercus* (Say, 1831) clade. Unambiguous optimization (CI = 50; RI = 66).

15. *Shape of prementum*: (0) roughly transversely rectangular to longitudinally rectangular with setae interrupting the outline of the lateral margins; (1) longitudinally rectangular, setal attachments not interrupting outline of lateral margins (Fig. 2.4J). Synapomorphy for the *Archocopturus regalis* – *Microzurus* sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

16. *Palpomere I, setation of posterolateral region, ventral view*: (0) setae absent or single, stout; (1) with one elongate curved seta. Synapomorphy for *Pseudolechriops*. Unambiguous optimization (CI = 100; RI = 100).

17. *Postmentum, shape medially*: (0) relatively parallel to slightly constricted at middle; (1) very strongly constricted, postmentum a thin line at middle. Synapomorphy for the *Cylindrocopturus biradiatus* Champion, 1906 – *Cylindrocopturus quercus* clade. Unambiguous optimization (CI = 100; RI = 100).

Prothorax

18. *Subapical constriction*: (0) absent to slightly impressed; (1) sulcate. Synapomorphy for the *Peltophorus polymitus seminiveus* – *Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

19. *Proendosternite, shape (posterior view)*: (0) terminating in a straight to rounded lobe; (1) posterior face projecting posteriorly and curving medially. Synapomorphy for the

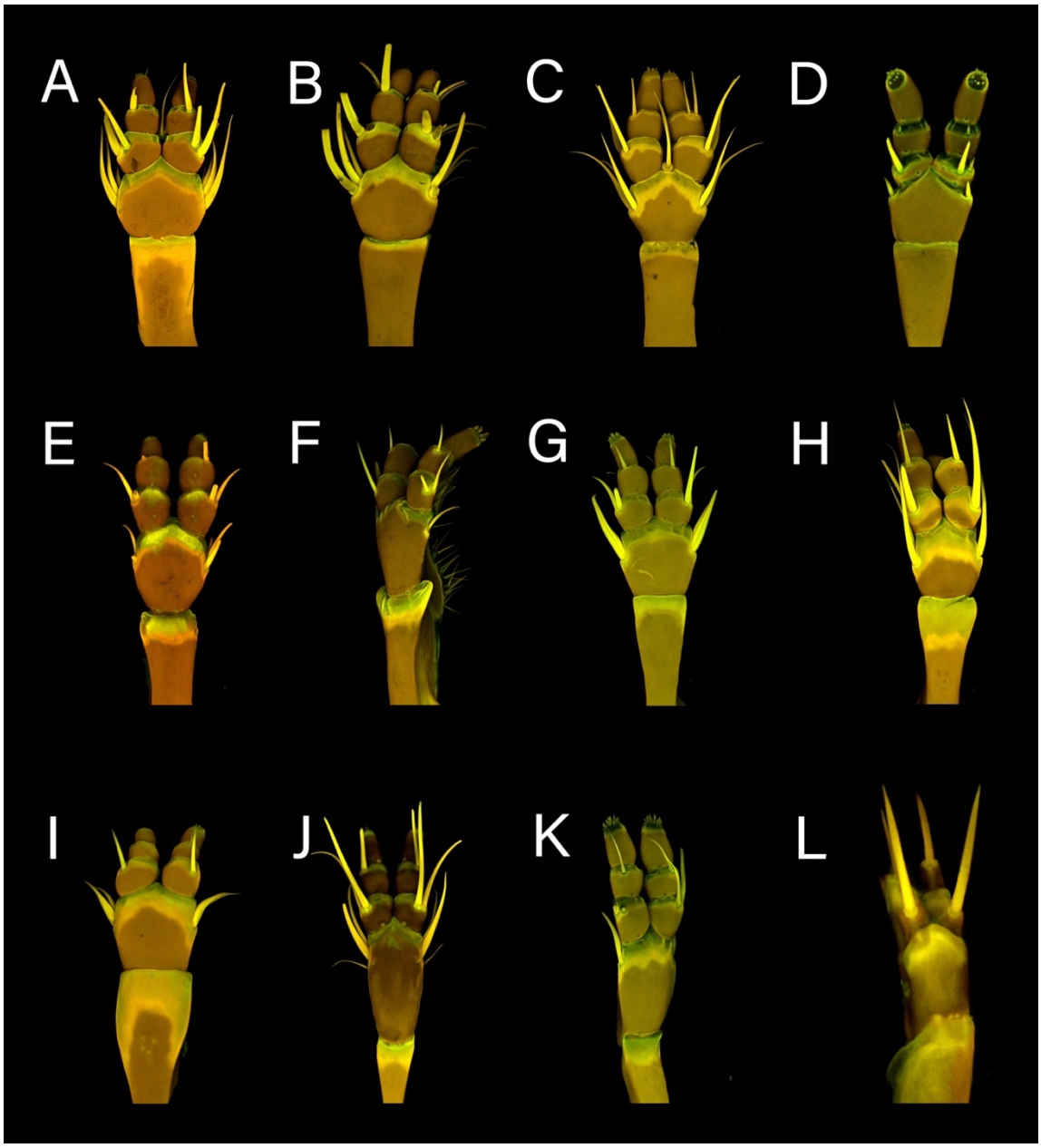

Figure 2.4. Variation in the labium of Conoderinae. A) *Piazurus alternans*; B) *Zygops mexicanus*; C) *Acoptus suturalis*; D) *Trichodocerus "leptodontus"*; E) *Copturus aurivillianus*; F) *Microzygops nigrofasciatus*; G) *Lechriops vestitus*; H) *Macrocopturus floridanus*; I) *Hoplocopturus armatus*; J) *Archocopturus regalis*; K) *Arachnomorpha circumlineata*; L) *Helleriella longicollis*.

Cratosomus multipunctatus Gyllenhal, 1837 – *Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

20. *Prosternum, sternellum, anterior margin*: (0) not or partially (only medially) subducting the posterior margin of the basisternum; (1) entirely subducting the posterior margin of the basisternum (Fig 2.5D). Synapomorphy for the *Lissoderes subnudus* Champion, 1906 – *Eulechriops* sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

21. *Prosternum, sternellum, anterior margin*: (0) transverse, flush with the posterior margin of the basisternum or slightly thickened; (1) strongly deflected posteriorly (Fig. 2.5I-J). Coded as inapplicable for taxa with the anterior margin subducting the basisternum (character 19). Synapomorphy for the *Lechriops* sp. – *L. excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

22. *Prosternum, posterior margin*: (0) relatively straight to slightly concave at middle; (1) strongly concave at middle (Fig. 2.5I). Synapomorphy for the *Pseudolechriops klopferi* Hespenheide & LaPierre, 2006– *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

23. *Prosternum, anterior margin of hypomeral arms*: (0) straight, flush with posterior margin of sternellum; (1) extending slightly anteriorly, overlapping posterior margin of sternellum. Synapomorphy for the *Macrocopturus cognatus* Heller, 1895 – *M. sannio* (Gyllenhal, 1838) clade. Unambiguous optimization (CI = 100; RI = 100).

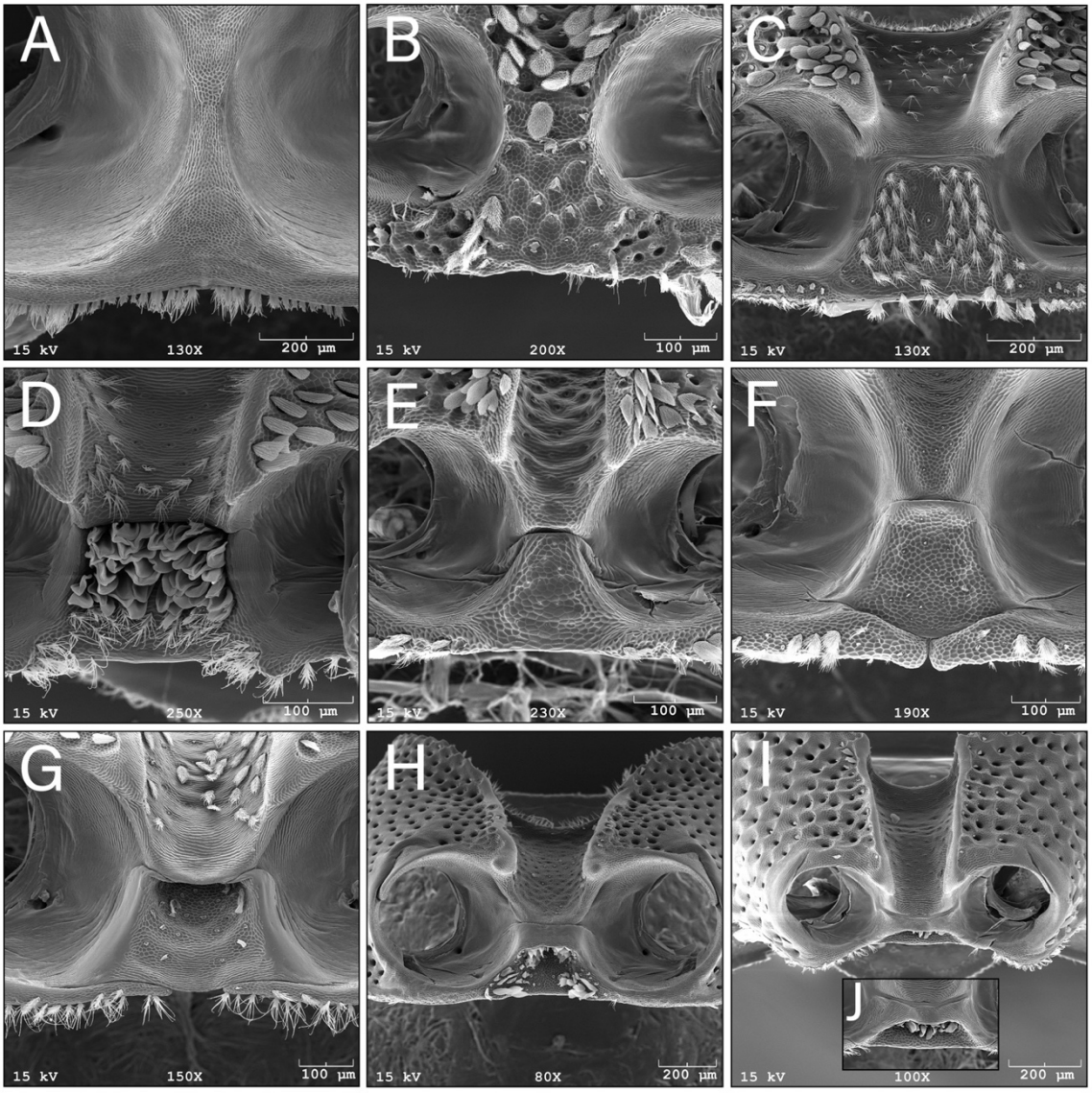

Fig. 2.5. A) *Zygops mexicanus*; B) *Acoptus suturalis*; C) *Copturus aurivillianus*; D) *Macrolechriops "moreyi"*; E) *Cylindrocopturus quercus*; F) *Copturomimus cinereus*; G) *Macrocopturus floridanus*; H) *Hoplocopturus armatus*; I) *Lechriops vestitus*; J) *L. vestitus*, close-up of sternellum.

24. *Apex of cryptopleuron*: (0) anterior and posterior extensions absent or present and extending from the same height; (1) dorsal margin strongly sinuous, anterior and posterior extensions not at same level. Convergently present in *Paramnemyne decemcostata* Champion, 1906 and the *Peltophorus polymitus seminiveus – Zygops maculipes* clade. Unambiguous optimization (CI = 50; RI = 83).

Mesothorax

25. *Mesendosternite, shape at middle*: (0) with a broad anteriorly or mesally produced lobe (Fig. 2.6A); (1) with an anteriorly produced arm (Fig. 2.6B). Putative synapomorphy for the Lechriopini, unreversed in the *Copturus–Lechriops* clade. Unambiguous optimization (CI = 100; RI = 100).

26. *Mesonotum, posterolateral margin of mesoscutellum (concealed part)*: (0) pleural hook broadly fused with posterolateral margin of mesoscutellum (Fig. 2.6C); (1) pleural hook slender, fused only at base with posterolateral margin of mesoscutellum (Fig. 2.6D). Synapomorphy for the *Lissoderes subnudus – Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

27. *Mesonotum, posterolateral margin of mesoscutellum (concealed part), setation*: (0) margin bare or with simple or multifurcate setae; (1) margin with a single scale. Coded as inapplicable for taxa with a pleural hook broadly fused with the posterolateral margin of the mesoscutellum (character 26:0). Synapomorphy for the *Cylindrocopturus nanulus* (LeConte, 1876) – *C. quercus* clade. Unambiguous optimization (CI = 100; RI = 100).

28. *Mesonotum, mesoscutellum, median longitudinal carina*: (0) absent; (1) present (Fig. 2.6E). Synapomorphy for the *Copturus aurivillianus* – *C. sanguinicollis* (Champion, 1906) clade. Unambiguous optimization (CI = 100; RI = 100).

29. *Mesonotum, punctures at mesoscutum-mesoscutellum border*: (0) absent or variously arranged, not in isolated, clearly defined oblique row; (1) in isolated, clearly defined oblique row. Synapomorphy for the *Lechriops* nr. *lebasii* (Boheman, 1838) – *L. excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

30. *Mesonotum, shape of mesoscutellum*: (0) variously dorsally produced, apically rounded; (1) short, relatively flat, transversely rectangular (Fig. 2.6F). Synapomorphy for the *Eulechriops manihoti* Monte, 1938 – *Microzurus* sp. 1 clade. The scutellum is slightly more dorsally produced and exposed in *E. manihoti* and flatter and concealed in *Microzurus* Heller, 1895, though hypothesized to be homologous due to similarity in shape. *Peltophorus* Schoenherr, 1845 and some included species of *Zygops* Schoenherr, 1825 have a much larger transversely rectangular scutellum that is deemed non-homologous. Unambiguous optimization (CI = 100; RI = 100).

31. *Left elytron, production of the mesal flange*: (0) Not produced (Fig. 2.6G) to variously produced only in apical half; (1) abruptly produced at base, strongly produced to apex (Fig. 2.6H). Synapomorphy for the *Copturus aurivillianus* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

32. *Left elytron, mesal flange, shape at middle*: (0) indented; (1) straight (Fig. 2.6H). Coded as inapplicable for taxa without a strongly, basally abruptly produced mesal flange. Synapomorphy for the *Lissoderes subnudus* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

33. *Mesoventrite, modification in form of carinae*: (0) absent or with longitudinal, parallel carinae; (1) with a complete, arcuate carina originating in posterolateral margins (Fig. 2.1D). Synapomorphy for the *Hoplocopturus varipes* Champion, 1906 – *Mnemynurus poeciloderes* Champion, 1906 clade. Unambiguous optimization (CI = 100; RI = 100).

34. *Mesoventrite, shape of arcuate carina*: (0) carina uniformly flat throughout; (1) carina strongly produced posteriorly, posterior part of mesoventrite invaginated (Fig. 2.1D). Coded as inapplicable for taxa without an arcuate carina (character 32). Synapomorphy for the *Mnemynurus longispinis* Champion, 1906 – *M. poeciloderes* clade. Unambiguous optimization (CI = 100; RI = 100).

35. *Mesoventrite, modification in form of carinae*: (0) absent or variously complete to anterior margin; (1) paired longitudinal carinae at posterior margin, incomplete to anterior margin, anteriorly slightly curving mesally (Fig. 2.1A). Coded as inapplicable for taxa with an arcuate carina (character 32). Synapomorphy for the *Pseudolechriops klopferi* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

36. *Mesoventrite, modification in form of carinae*: (0) absent or variously present and not extending to anterior margin; (1) paired longitudinal carinae at anterior margin extending variously

posteriorly. Synapomorphy for the *Copturomorpha* sp. 1 – *Eulechriops* sp. 1 clade with a reversal in *Arachnomorpha circumlineata*. Unambiguous optimization (CI = 50; RI = 92).

37. *Mesoventrite, carinae at anterior margin, shape*: (0) carinae joining thickened anterior margin of mesoventrite; (1) carinae uniform in width to anterior margin. Inapplicable in taxa without carinae complete to the anterior margin of the mesoventrite. Apomorphy for the *Cylindrocopturinus vanessae* Anderson, 1994 – *Eulechriops* sp. 4 clade. Unambiguous optimization (CI = 100; RI = 100).

38. *Mesoventrite, carinae at anterior margin, integument lateral to carinae*: (0) carinae laterally excavated along entire length; (1) carinae not excavated or only slightly excavated anteriorly. Coded as inapplicable for taxa without carinae complete to the anterior margin of the mesoventrite. Convergently present in the *Crassocopturus* sp. – *Eulechriops* sp. 4 clade and in *E.* sp. 1. Fast optimization preferred, which hypothesizes that the carinae became unexcavated in the common ancestor of the *Arachnomorpha circumlineatus* – *Eulechriops* sp. 4 clade, and then the carinae were altogether lost in *Arachnomorpha*, instead of independently lost and unexcavated (CI = 50; RI = 80).

Metathorax

39. *Excavation anterior to metacoxa, vestiture*: (0) bare or with sparse scales or setae; (1) with a dense cluster of yellow to yellowish white scales. Apomorphy for the *Archocopturus regalis* – *Cylindrocopturus elongatus* Champion, 1906 clade with a reversal in *Helleriella longicollis*. Unambiguous optimization (CI = 50; RI = 80).

40. *Metendosternite, shape of basal stalk*: (0) lateral margins variously parallel, slightly (Fig. 2.6I) to strongly converging; (1) lateral margins converging, roughly equilateral triangle shaped (Fig. 2.6J). Synapomorphy for the *Cratosomus multipunctatus – Piazolechriops bicristatus* clade. Unambiguous optimization (CI = 100; RI = 100).

41. *Metathoracic wing, shape of second radial sclerite*: (0) variously shaped, not triangular or small and rectangular; (1) triangular, with three distinct points and the sides of the triangle variously inflexed; (2) small, roughly rectangular. Coded as non-additive, as the states don't appear related in a transformation series. State 1 is an apomorphy for the *Cratosomus multipunctatus – Piazolechriops bicristatus* clade and state 2 is an apomorphy for the *Copturus aurivillianus – Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

42. *Metathoracic wing, length of radiomedial sclerotization*: (0) short, not extending halfway or more to the base of the radial cell; (1) long, extending halfway or more to the base of the radial cell. Convergently present in *Mecopus helleri* and the *Lissoderes subnudus – Lechriops excavatus* clade. Unambiguous optimization (CI = 50; RI = 93).

Male terminalia

43. *Post-tegminal membrane, large lateral lobes*: (0) absent; (1) present. Synapomorphy for the *Peltophorus polymitus seminiveus – Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

44. *Aedeagus, shape at apex*: (0) lateral margins converging to point or rounded apex; (1) with a broad, flattened plate. Synapomorphy for the *Piazurus maculipes* – *Piazolechriops bicristatus* clade. Unambiguous optimization (CI = 100; RI = 100).

45. *Endophallus, endophallic sclerites, anterior region*: (0) unsclerotized or with various small to medium-sized teeth or plates; (1) with multiple large, curved, dentate plates. Synapomorphy for the *Pseudopinarus condyliatus* (Boheman, 1838) – *Piazolechriops bicristatus* clade. Unambiguous optimization (CI = 100; RI = 100).

46. *Endophallus, sclerotization, posterior region*: (0) unsclerotized or with various small to medium-sized teeth or plates; (1) with paired regions of dense rugulose sculpturing to microdenticles. Apomorphy for the *Macrocopturus floridanus* – *Lechriops excavatus* clade with reversals in the *Pseudolechriops klopferi* – *P. megacephala* Champion, 1906 and *L. rugicollis* Champion, 1906 – *L excavatus* clades. Unambiguous optimization (L = 3; CI = 33; RI = 60).

47. *Endophallus, sclerotization*: (0) unsclerotized or variously unevenly sclerotized; (1) fairly uniformly, very densely microdenticulate. Synapomorphy for the *Crassocopturus* sp. – *Poecilogaster brevis* clade. Unambiguous optimization (CI = 100; RI = 100).

48. *Aedeagus, shape ventrally*: (0) flat or evenly rounded to lateral surface; (1) concave medially at least in basal one-third. Synapomorphy for the *Lechriops californicus* (LeConte, 1876) – *L. excavatus* clade with a reversal in *Lechriops excavatus*. Unambiguous optimization (CI= 50; RI = 75).

49. *Aedeagus, shape (dorsal view)*: (0) of relatively even width throughout or angularly constricted; (1) constricted near middle, rounded. Synapomorphy for the *Hoplocopturus javeti* Champion, 1906 – *Mnemynurus poeciloderes* clade with a reversal in *M. championi* Heller, 1933. Unambiguous optimization (CI = 50; RI = 50).

50. *Aedeagus, shape laterally*: (0) lateral margins mostly unsclerotized to continuously rounded from ventral surface; (1) lateral margin concave. Synapomorphy for the *Macrocopturus* sp. 18 – *M. sannio* clade. Unambiguous optimization (CI = 100; RI = 100).

51. *Aedeagus, shape subapicoventrally*: (0) flat, continuous to apex, without process; (1) with ventrally projecting process. Synapomorphy for the *Macrocopturus* sp. 18 – *M. sannio* clade. Unambiguous optimization (CI = 100; RI = 100).

52. *Aedeagus, lateral margin at base*: (0) continuous with temones or evenly expanded; (1) abruptly expanded. Synapomorphy for the *Eulechriops* nr. *elongatus* – *E.* sp. 4 clade. Unambiguous optimization (CI = 100; RI = 100).

53. *Aedeagus, apicodorsal region*: (0) without setae; (1) with cluster of erect setae. Synapomorphy for *Acoptus suturalis* – Othippiini gen. 2 sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

54. *Sternite IX, base of spiculum gastrale*: (0) variously bifurcate, or transversely to quadrately expanded; (1) very slightly expanded, basal plate mostly membranous. Synapomorphy for

the *Copturosomus affaber* (Boheman 1838) – *C. rorulentus* (Boheman, 1838) clade. Unambiguous optimization (CI = 100; RI = 100).

55. *Tergite VIII, sclerotization of posteromedial region*: (0): relatively evenly sclerotized with the lateral and apical regions; (1) unsclerotized. Synapomorphy for *Lissoderes subnudus* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

56. *Tergite VIII, shape*: (0) roughly "D"-shaped, short (Fig. 2.6K); (1) somewhat longitudinally elongate, slightly constricted medially (Fig. 2.6L) to "U"-shaped. Inapplicable in taxa with a posteromedially sclerotized tergite VIII (character 54). Synapomorphy for the *Archocopturus regalis* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

57. *Tergite VIII, shape*: (0) semicircular to broadly rounded; (1) circular, lateral margins strongly arcuate. Inapplicable in taxa with a longitudinally elongate, slightly constricted medially to "U"-shaped tergite VIII (character 55). Synapomorphy for the *Macrolechriops "moreyi"* – *Eulechriops* nr. *tenuirostris* Champion, 1906 clade. Unambiguous optimization (CI = 100; RI = 100).

58. *Sternite VIII, shape*: (0) variously shaped, separate sclerites (hemisternites); (1) single, fused transverse sclerite. Synapomorphy for the *Acoptus suturalis* – Othippiini gen. 2 sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

59. *Tergite VIII*: (0) concealed to narrowly exposed; (1) broadly exposed. Synapomorphy for the *Cratosomus multipunctatus* – *Zygops maculipes* clade. Unambiguous optimization (CI = 100; RI = 100).

60. *Tergite VII, setation posteriorly*: (0) setae at posterior region similar to setae elsewhere; (1) setae at posterior region larger, fusiform. Inapplicable in taxa with a broadly exposed tergite VII (character 59). Synapomorphy for the *Lechriops vestitus* (Boheman, 1838) – *L. excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

Female terminalia

61. *Bursa copulatrix, sclerotization*: (0) entirely membranous to variously sclerotized, not with small flat tooth-like sclerites; (1) with small, ovoid, flat, apically tooth-like sclerites. Apomorphy for the *Lechriops* sp. 1 – *L. excavatus* clade with a reversal in the *Pseudolechriops klopferi* – *P. megacephala* clade. Fast optimization preferred, which treats the derived state as present in the *Lechriops* sp. 1 – *L. excavatus* clade with a secondary reversal in *Pseudolechriops* (CI = 50; RI = 83).

62. *Gonocoxite, sclerotization*: (0) variously broad to somewhat constricted subapically; (1) abruptly constricted subapically, very thin and elongate. Synapomorphy for the *Mnemynurus championi* – *M. poeciloderes* clade. Unambiguous optimization (CI = 100; RI = 100).

63. *Gonostylus, shape*: (0) short, nearly as long as wide to elongate and cylindrical; (1) elongate, narrowing apically. Convergently present in the *Eulechriops* nr. *elongatus* – *E.* sp. 4 clade and in *Copturomorpha* sp. 1. Unambiguous optimization (CI = 50; RI = 50).

64. *Spermatheca, apex of cornu*: (0) rounded to pointed; (1) with thin rounded process. Synapomorphy for the *Microzurus* nr. *rhombus* – *M.* sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

65. *Spermatheca, shape of ramus*: (0) not produced to variously produced, tube-like or tumescent with duct insertion ventral; (1) strongly tumescent, duct insertion apical. Synapomorphy for the *Copturus aurivillianus* – *C. sanguinicollis* clade. Unambiguous optimization (CI = 100; RI = 100).

66. *Spiculum ventrale, shape apically*: (0) variously straight to apically expanded and rounded; (1) triangularly expanded. Synapomorphy for the *Eulechriops* sp. 2 – *E.* sp. 3 clade. Unambiguous optimization (CI = 100; RI = 100).

67. *Spiculum ventrale, shape posteriorly*: (0) variously bifurcate; (1) bifurcate, with lamina lateral to arms of spiculum ventrale broadly sclerotized. Synapomorphy for the *Pseudolechriops klopferi* – *P. megacephala* clade. Unambiguous optimization (CI = 100; RI = 100).

68. *Spiculum ventrale, shape posteriorly*: (0) variously broadly bifurcate, flattened, explanate, or parallel-sided; (1) narrowly bifurcate, lightly sclerotized on lamina lateral to arms of apodeme. Inapplicable in taxa with a broadly sclerotized lamina (character 67).

Synapomorphy for the *Hoplocopturus costatipennis* Champion, 1906 – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

69. *Spiculum ventrale, shape posteriorly*: (0) explanate at apodeme-lamina junction, subparallel to posterior margin; (1) bifurcate, broadly rounded. Inapplicable in taxa with the spiculum ventrale narrowly bifurcate, lightly sclerotized (character 68) and broadly sclerotized (character 67). Synapomorphy for the *Eulechriops nitidus* – *Eulechriops* sp. 1 clade. Unambiguous optimization (CI = 100; RI = 100).

70. *Tergite VIII, posterior margin*: (0) variously rounded to truncate or slightly emarginate; (1) medially emarginate, posterolateral margins acuminate. Synapomorphy for the *Pseudolechriops klopferi* – *P. megacephala* clade. Unambiguous optimization (CI = 100; RI = 100).

71. *Tergite VIII, posterior margin*: (0) rounded or continuously sclerotized, with setae or small cuticular projections; (1) with stout socketed teeth; (2) with socketed, flattened, apically rounded teeth. Coded as non-additive. State 1 is an apomorphy for the *Piazurus maculipes* Gyllenhal, 1838 – *Piazolechriops bicristatus* clade and state 2 is an apomorphy for the *Copturus aurivillianus* – *C. sanguinicollis* clade. Unambiguous optimization (CI = 100; RI = 100).

72. *Tergite VIII, shape*: (0) broadly rounded; (1) elongate. Convergently present in *Eulechriops* nr. *tenuirostris*, the *Cylindrocopturus filicornis* (Fall, 1906) – *C. elongatus* clade, and the

Copturomimus cinereus (Heller, 1895) – *Lechriops excavatus* clade. Unambiguous optimization (L = 3; CI = 33; RI = 93).

73. *Tergite VIII, subapical setae*: (0) setae absent or scattered; (1) setae in transverse, medially incomplete and anteriorly curving row. Inapplicable in taxa with a broadly rounded (character 72) or an apically modified (character 70) tergite VIII. Synapomorphy for the *Hoplocopturus costatipennis* – *Lechriops excavatus* clade. Unambiguous optimization (CI = 100; RI = 100).

74. *Sternite VIII, spiculum ventrale – lamina junction*: (0) variously slightly flattened to explanate; (1) strongly flattened, arms connate halfway to posterior margin of sternite VIII. Apomorphy for the *Hoplocopturus nigripes* Champion, 1906– *Mnemynurus poeciloderes* clade with a reversal in the *Balaninurus longipes* Heller, 1895 – *M. poeciloderes* clade. Unambiguous optimization (CI = 100; RI = 100).

Abdominal sternites

75. *Sternite VII, carinae*: (0) without carinae or with arcuate, sharp, somewhat posteriorly produced carina; (1) with an arcuate, smooth, not posteriorly produced carina. Synapomorphy for the *Cylindrocopturus biradiatus* – *C. quercus* clade. Unambiguous optimization (CI = 100; RI = 100).

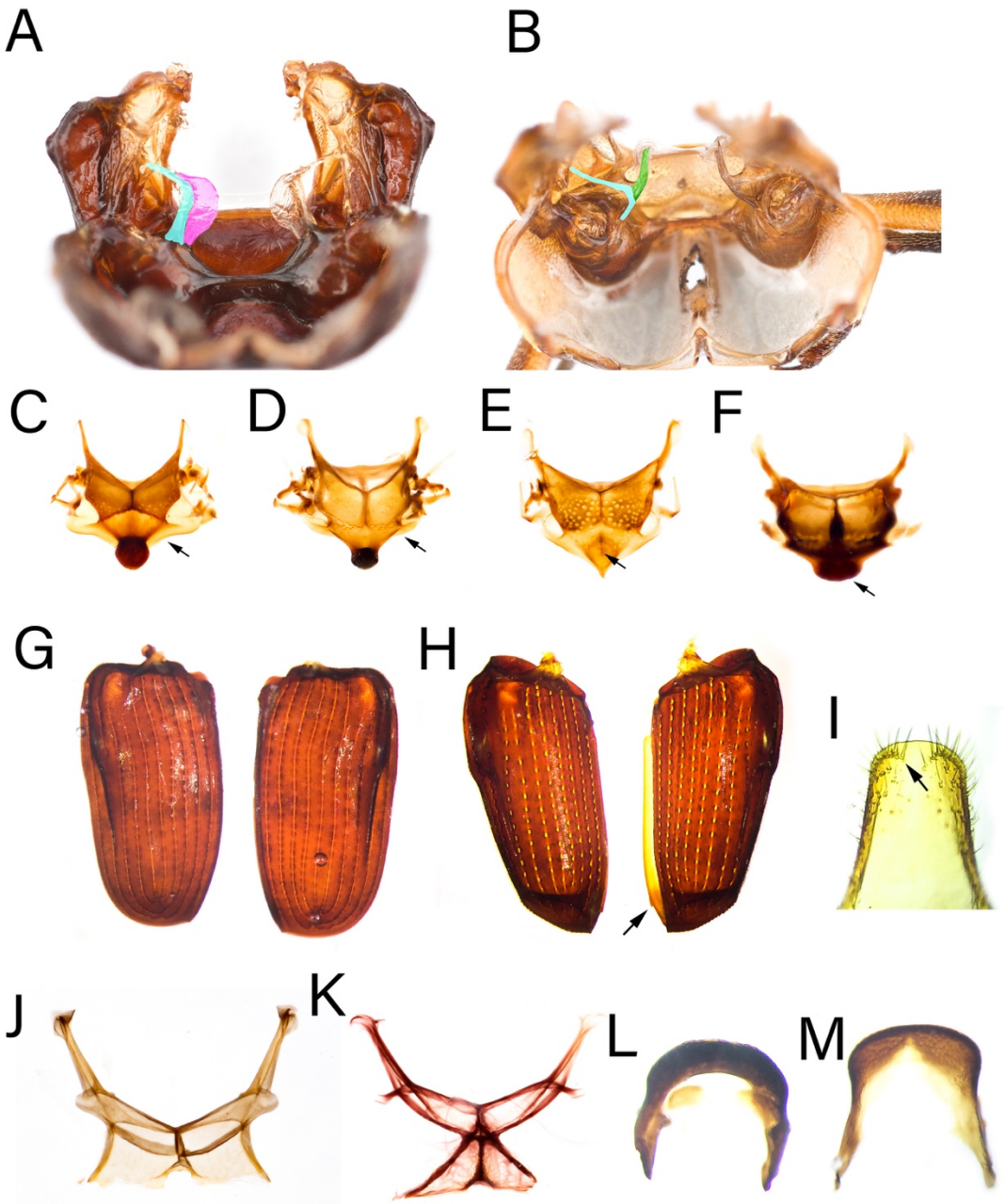

Figure 2.6. Various morphological structures in the New World Conoderinae. A-B: mesendosternite, left side with overlay. A) *Piazurus maculipes*, showing a broad lobe (pink overlay); B) *Mnemynurus championi*, showing an anterior arm (green overlay). B-F: mesonota. C) *Pseudopinarus condyliatus*; D) *Hoplocopturus costatipennis*; E) *Copturus aurivillianus*; F) *Eulechriops manihoti*. G-H: elytra, ventral view. G) *Zygops tridentatus*; H) *Hoplocopturus javeti*. I) *Macrocopturus cincticollis*, posterior margin of female tergite VIII; J-K: metendosternite. J: *Hoplocopturus armatus*; K: *Piazurus maculipes*. L-M: male tergite VII. L) *Eulechriops* nr. *elongatus*; M) *Macrocopturus sannio*.

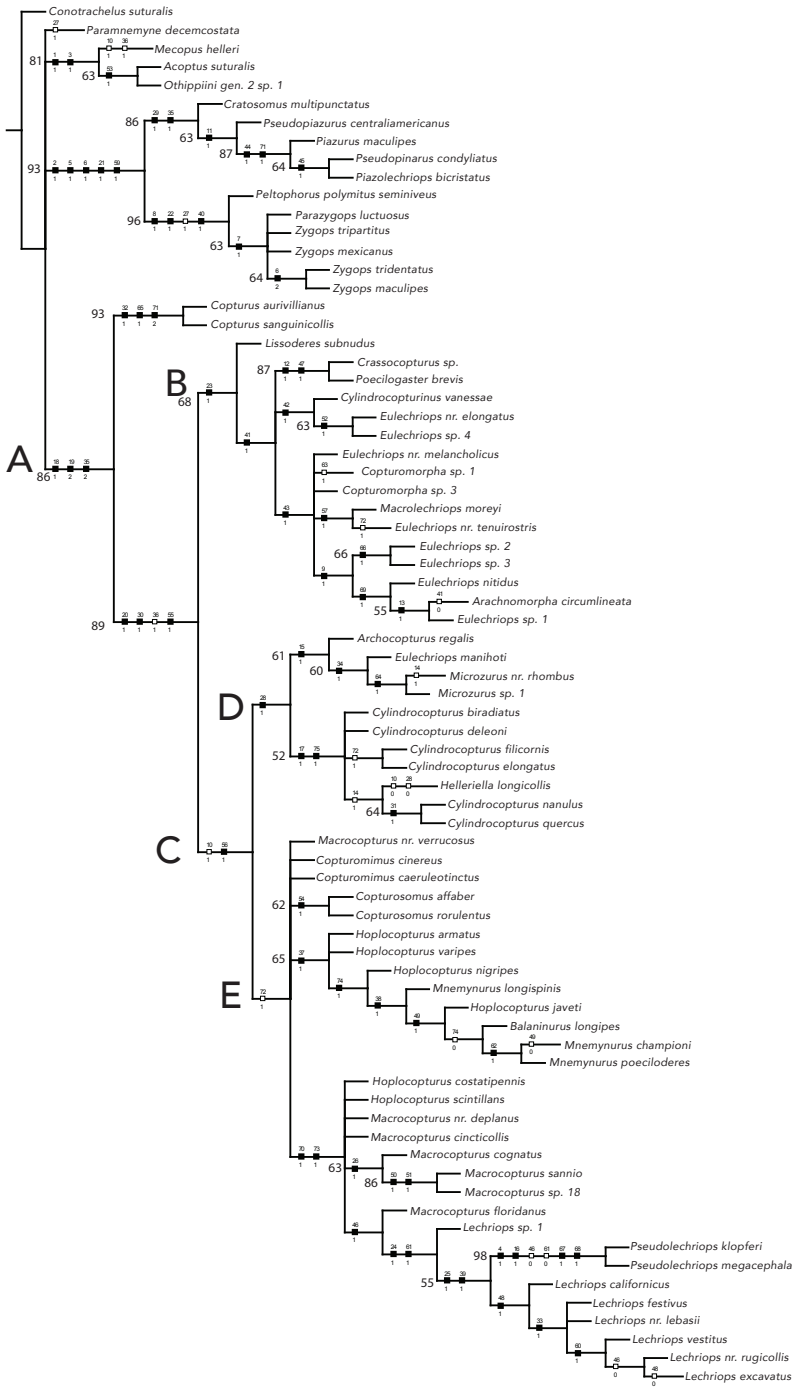

Figure 2.7. Preferred tree out of six equally parsimonious trees (L = 95; CI = 82; RI = 96). All unsupported nodes are shown as collapsed. Bootstrap support over 50% is shown to the left of a branch.

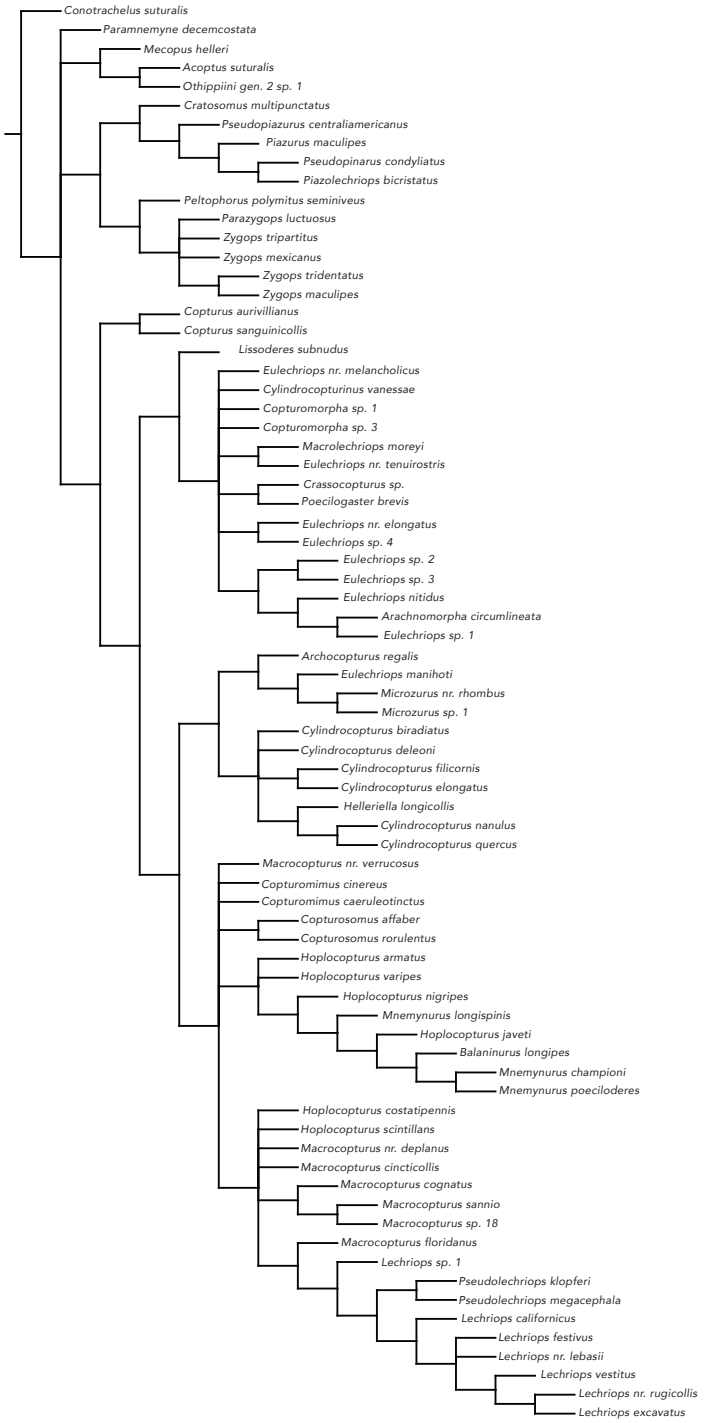

Fig. 2.8. Strict consensus of six equally parsimonious trees. All unsupported nodes are shown as collapsed.

Discussion

This study represents the first cladistic analysis focusing on the Conoderinae and the first major reorganization of currently recognized genera based on phylogenetically tested morphological characters, representing a major step towards understanding the evolutionary history of the Lechriopini and acquiring a phylogenetic classification. A large clade was recovered in the analysis supported by three unreversed synapomorphies that contains most genera included from the Lechriopini and several genera from the Zygopini and forms the basis of the new classification presented herein.

Updated classification of the Lechriopini and Zygopini.

Lechriopini Lacordaire, 1865

The lechriopines are redefined here as a much larger group than previously treated (Alonso-Zarazaga and Lyal 1999, Lyal *et al.* 2006, Anzaldo 2017), now containing 39 genera, 16 of which are newly transferred from the Zygopini. The tribe is supported in the preferred cladogram (Fig. 2.7, Clade A) by the following unreversed synapomorphies: elytral sutural flange abruptly prominent at base and greatly expanded to the apex (character 31:1; Fig 2.6H), the mesendosternite with a distinct anteriorly projecting arm instead of a rounded lobe (character 25:1; Fig 2.6B), and a rectangular second radial sclerite (character 41:1). Externally, the lechriopines can be differentiated from zygopines and piazurines by the concealed pygidium and the strongly ascending abdominal ventrites. Zygopines have a broadly exposed pygidium that is more dorsally oriented and visible in dorsal view, while piazurines have a slightly to broadly exposed pygidium that is visible in lateral or ventral view only.

Copturus was recovered as the earliest divergent lechriopine genus, with the following unreversed synapomorphies identifying a less inclusive monophyletic clade containing the remainder of the Lechriopini: male tergite VIII posteromedially unsclerotized (character 55:1; Fig. 2.6L-M), the elytral sutural flange is straight and not medially indented (character 32:1), and the base of mesonotal pleural hook is offset from the posterolateral margin of mesoscutellum (character 26:1; Fig. 2.6E). Interestingly, the genus *Microzurus*, which also has a concealed scutellum, was recovered in a different clade and otherwise has a very different mesonotal structure (similar to Fig. 2.6F). An additional homoplasious character that identifies this group is the radiomedial sclerotization on the metathoracic wing (character 42:1) which is elongate, extending halfway or more to the base of the radial cell.

The remainder of the lechriopines are organized into two main clades, here termed the "*Eulechriops* group" (Clade B) and the "*Cylindrocopturus* + *Macrocopturus* group" (Clade C). The *Eulechriops* group contains the large and evidently polyphyletic genus *Eulechriops* as well as the smaller genera *Arachnomorpha* Champion, 1906, *Lissoderes* Champion, 1906, *Copturomorpha* Champion, 1906, *Macrolechriops* Champion, 1906, *Crassocopturus*, *Cylindrocopturinus* Sleeper, 1963, and *Poecilogaster* and likely also the unincluded genera *Chileops* Kuschel, 2017, and *Hemicolpus*. The structure of the prosternum is shared in this group, having a posterior margin of the basisternum overhanging the anterior margin of the sternellum (character 20:1; Fig. 2.5D). The shape of the eighth tergite is short and roughly "D"-shaped and not elongate (character 56:0). The placement of the genera *Larides* Champion, 1906 and *Phileas* Champion, 1906 is currently uncertain, though it seems likely they are related to this group as the observed *Larides cavifrons* Champion, 1906 has the same short tergite VIII, though a differently structured prosternum.

Table 2.1. Summary classification of the herein redefined Lechriopini and Zygopini. An asterisk (*) indicates an Old World taxon not observed in this study, and a dagger (†) indicates an extinct taxon. Number of described species are taken from Anzaldo (2017) and from Wibmer and O'Brien 1986 for taxa only recorded from South America. Species counts were amended with the following recent references: *Chileops* (Kuschel 2017), *Hemicolpus* (Hespenheide 2018b), *Microzygops* (Hespenheide 2018a), *Philenis* (Hespenheide 2018c), *Timorus* (Vanin and Guerra 2012).

Lechriopini Lacordaire, 1865	Described species
Acopturus Heller, 1895, **new placement**, from Zygopini	1
Arachnomorpha Champion, 1906, **new placement**, from Zygopini	1
Archocopturus Heller, 1895, **new placement**, from Zygopini	5
Balaninurus Heller, 1895	5
Chileops Kuschel, 2017, **new placement**, from Zygopini	1
Copturomimus Heller, 1895	17
Copturomorpha Champion, 1906	24
Copturosomus Heller, 1895, **new placement**, from Zygopini	9
Copturus Schoenherr, 1825	33
Coturpus Anderson, 1994	1
Crassocopturus Rheinheimer, 2011	1
Cylindrocopturinus Sleeper, 1963	4
Cylindrocopturus Heller, 1895, **new placement**, from Zygopini	43
Damurus Heller, 1895	1
Eulechriops Faust, 1896	88
Euzurus Champion, 1906	1
Helleriella Champion, 1906, **new placement**, from Zygopini	5
Hemicolpus Heller, 1895, **new placement**, from Zygopini	5
Hoplocopturus Heller, 1895	30
Hypoplagius Desbrochers, 1891, **new placement**, from Zygopini	1
Larides Champion, 1906, **new placement**, from Zygopini	1
Lechriops Schoenherr, 1825	91
Lissoderes Champion, 1906, **new placement**, from Zygopini	7
Machaerocnemis Heller, 1895	1
Macrocopturus Heller, 1895	157
Macrolechriops Champion, 1906	6
Macrotimorus Heller, 1895, **new placement**, from Zygopini	1
Microzurus Heller, 1895	7
Microzygops Champion, 1906	2
Mnemynurus Heller, 1895	11
Phileas Champion, 1906, **new placement**, from Zygopini	1
Philenis Champion, 1906, **new placement**, from Zygopini	13
Poecilogaster Heller, 1895	2
Pseudolechriops Champion, 1906	10
Rhinolechriops Hustache, 1939	1
Tachylechriops Heller, 1895	3
Timorus Schoenherr, 1838, **new placement**, from Zygopini	7
Turcopus Anderson, 1994	1
Zygopsella Champion, 1906, **new placement**, from Zygopini	2

Zygopini Lacordaire, 1865	
Colpothorax Desbrochers, 1890	1
†*Geratozygops* Davis and Engel, 2006	4
**Isocopturus* Hustache, 1931	1
Parazygops Desbrochers, 1890	3
Peltophorus Schoenherr, 1845	3
**Xeniella* Hustache, 1931	1
Zygops Schoenherr, 1825	52

Conoderinae *incertae sedis*	
Mnemyne Pascoe, 1880, **new placement**, from Lechriopini	2
Paramnemyne Heller, 1895, **new placement**, from Lechriopini	5
Paramnemynellus Hustache, 1932, **new placement**, from Lechriopini	1
Philides Champion, 1906	3
Philinna Champion, 1906	2
Psomus Casey, 1892, **new placement**, from Lechriopini	4

Clade D is the "*Cylindrocopturus* group", containing the genera *Cylindrocopturus* Heller, 1895, *Helleriella* Champion, 1906, *Microzurus*, *Archocopturus* Heller, 1895, and the species *Eulechriops manihoti*, which all share a patch of dense yellow to yellowish white scales in the excavation on the metaventrite anterior to the metacoxa (character 39:1). The genus *Zygopsella* also shares this feature and is likely closely related. *Cylindrocopturus* has been suspected to be a polyphyletic assemblage of species adapted to arid environments (Hespenheide 1980) and contains species with very different host plants and larval development strategies. Included in this analysis are six species with diverse hosts (including Pinaceae, Cactaceae, and Asteraceae), selected to minimize the chances that the genus would be artificially recovered as monophyletic. Along with *Helleriella longicollis*, this group can be identified by the strongly constricted postmentum of the labium (character 17:1).

Clade E is a large and poorly resolved clade with the relationships between species included in the genera *Copturomimus* Heller, 1895, *Copturosomus* Heller, 1895 and *Macrocopturus* uncertain. The genera *Hoplocopturus* Heller, 1895 (including the type species *Hoplocopturus armatus* (Gyllenhal, 1838)), *Balaninurus* Heller, 1895, and *Mnemynurus* Heller, 1895 were recovered as a group within this clade, supported by the arcuate carina on the mesoventrite (character 33:1; Fig. 2.1D), and an apical clade consisting of most included species of *Lechriops* and *Pseudolechriops* was supported based on the shape of the posterior margin of the prosternum (character 22: 1; Fig. 2.5I) and the shape of the parallel carinae of the mesoventrite anteriorly (character 35:1; Fig. 2.1A).

Of the genera newly transferred to the Lechriopini, the positions of *Timorus*, *Macrotimorus* Heller, 1895, *Philenis*, *Hypoplagius* Desbrochers, 1891 and *Acopturus* Heller, 1895 within the tribe is currently uncertain. *Macrotimorus* was the only genus not observed, however based on the original description (Heller 1895: 59, Fig. 21) the correct placement is

in the lechriopines due to the structure of the abdominal ventrites. Of the genera already in the Lechriopini, only the monotypic *Rhinolechriops* Hustache, 1939 was not observed and thus cannot be commented on further.

Note on taxa no longer included in the Lechriopini

The genus *Acoptus* was transferred from the Lechripini to the Othippiini Morimoto, 1962 (Anzaldo 2017) based on similarities with the othippiine genus *Rimboda* Heller, 1925. The taxon included in the analysis as "Othippiini gen. 2 sp. 1" is more similar to *Rimboda* than to *Othippia* Pascoe, 1874. Confounding the issue of the placement of these genera are the genera *Emexaure* Pascoe, 1871 (Conoderinae: Mecopini) and *Elassophilus* Faust, 1899 (Conoderinae: Sphadasmini), which are all very similar and likely closely related. It is currently uncertain whether they all require a new tribe or if these four genera are better placed in one of the tribes that currently accommodates them.

Paramnemyne is herein transferred out of the Lechriopini as it lacks all of the characters newly defining the lechriopine tribe. Its placement within the Conoderinae is uncertain, as some features are similar to the Zygopini while others resemble Piazurini such as *Pseudopinarus*. It cannot be transferred to either tribe as currently recognized, and the very similar South American genera *Mnemyne* Pascoe, 1880 and *Paramnemynellus* Hustache, 1932, though not included in the analysis, must be moved with it.

Zygopini Lacordaire, 1865

In this new, restricted circumscription, the Zygopini is composed of *Zygops*, *Parazygops* Desbrochers, 1890, *Peltophorus*, *Colpothorax* Desbrochers, 1890, and the extinct *Geratozygops* Davis and Engel, 2006. Two monotypic African genera, *Isocopturus* Hustache,

1931 and *Xeniella* Hustache, 1931, have not been examined and are thus retained in the tribe for now though they are likely to belong elsewhere. Species in this tribe were found to have the pygidium broadly exposed (shared with the Piazurini; character 59:1), a sulcate subapical constriction of the prothorax (character 18:1), a large, elongate lobe arising from the post-tegminal membrane on either side of the aedeagus (character 43:1), and the proximal malar setal tuft of the maxilla obliquely offset from the cutting face of the galeo-lacinial complex (character 8:1). All observed taxa except for *Peltophorus polymitus seminiveus* share the broad, triangular shape of the proximal lacinial tooth (character 7:1; Fig. 2.2B), potentially signifying the basal position of the genus *Peltophorus* within this tribe. The Zygopini were shown in the analysis to be much more closely related to the Piazurini than to the Lechriopini *sensu novo*, a relationship supported by characters of the mouthparts (characters 2:1, 5:1, 6:1) and the proendosternite (character 19:1).

While a sister taxon for the Lechriopini *sensu novo* was not identified in this analysis, the characters supporting the monophyly of the group were broadly surveyed for among Old World tribes of Conoderinae and in the weevil subfamilies Baridinae and Ceutorhynchinae Gistel, 1856, which have been proposed to form a higher-level entity (e.g. Zherikhin and Gratshev 1995, Prena *et al.* 2014). The character states were not found in any other taxon but those in the Lechriopini, further supporting the results of this study. Within the Lechriopini, the modification to the meso- and metaventrite was found to be a character that, while incongruent with the newly proposed classification in the broad presence/absence delimitation used by Lacordaire, has multiple distinct states that were informative for different groups of Lechriopini (characters 33-38). With the limited sampling of this study it was not possible to properly assess evolutionary transformations of different forms of

modification and they were mostly treated as independent characters. For example, it is possible that the arcuate carina found in species of *Hoplocopturus*, *Mnemynurus*, and *Balaninurus* (character 33:1) is related to the posteriorly parallel, slightly anteromesally curving carinae found in *Lechriops* and *Pseudolechriops* (character 35:1), but the polarity of these states is not apparent with the current phylogenetic hypothesis.

The analysis further revealed species out of place in their current generic placement (e.g. *Eulechriops manihoti*). In the absence of well-defined, monophyletic genera to transfer them to, any lower-level transfers will await a more focused treatment of the clades they were recovered in. The genera *Macrocopturus* and *Eulechriops* will need to be split into multiple smaller genera as other genera currently recognized (e.g. the monotypic *Arachnomorpha*) were recovered as derived within those larger, poorly resolved clades. A taxon as diverse as the Lechriopini will require many targeted analyses to resolve certain regions of the phylogeny, in concert with taxonomic revisions to better understand the relationships between species. Many genera of lechriopines remain largely unknown morphologically - upon their inclusion into a cladistic analysis they will potentially add new major clades (e.g. subtribes) to the tree or necessitate the modification of character state circumscriptions defining the clades presented here.

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CHAPTER 3

REVISION OF THE WEEVIL GENUS *TRICHODOCERUS* CHEVROLAT, 1879 (CURCULIONIDAE: CONODERINAE: TRICHODOCERINI)

ABSTRACT

The enigmatic genus *Trichodocerus* Chevrolat, 1879 is revised. The type species *T. spinolae* Chevrolat, 1879, as well as *T. brevilineatus* Champion, 1906 and *T. antiquus* (Bondar, 1946), are redescribed and the following 24 species are described as new: *T. atheatomerus* **sp. nov.**, *T. browni* **sp. nov.**, *T. chrysochaetus* **sp. nov.**, *T. condylothecus* **sp. nov.**, *T. corystochion* **sp. nov.**, *T. fazerangrus* **sp. nov.**, *T. gorgonarium* **sp. nov.**, *T. hespenheidei* **sp. nov.**, *T. hybophrictus* **sp. nov.**, *T. lathrios* **sp. nov.**, *T. leptodontus* **sp. nov.**, *T. mariae* **sp. nov.**, *T. mecistotarbus* **sp. nov.**, *T. musathrus* **sp. nov.**, *T. obrieni* **sp. nov.**, *T. ochromae* **sp. nov.**, *T. plataleaculus* **sp. nov.**, *T. prionasceles* **sp. nov.**, *T. selenion* **sp. nov.**, *T. sobetes* **sp. nov.**, *T. stockwelli* **sp. nov.**, *T. torquatus* **sp. nov.**, *T. woldai* **sp. nov.**, and *T. yavinivensis* **sp. nov.** All 27 species are arranged into six species groups: the *spinolae* group, the *brevilineatus* group, the *ochromae* group, the *antiquus* group, the *mecistotarbus* group, and the *obrieni* group. The lectotype of *T. brevilineatus* is herein designated. Distribution maps are provided for each species and an identification key is provided to all recognized species groups and species.

Introduction

The genus *Trichodocerus* Chevrolat, 1879 has had an uncertain phylogenetic position in the Curculionidae Latreille, 1802, since its original description. First proposed by Chevrolat (1879) to be related to the genus *Conotrachelus* Dejean, 1835 (most recently placed in the Cleogonini Gistel, 1856, of the Molytinae Schoenherr, 1823; see Lyal 2014), the genus has since been treated in several different subfamilies of weevils (*sensu* Alonso-Zarazaga and Lyal 1999). *Trichodocerus* was created to accommodate two species from French Guiana, *T. spinolae* Chevrolat, 1879, and *T. lateralis* Chevrolat, 1879. In the next treatment of the genus, G.C. Champion (1906a) considered *T. lateralis* to be a junior synonym of *T. spinolae* and described one other species, *T. brevilineatus* Champion, 1906. Here *Trichodocerus* was included at the end of his volume treating the Cryptorhynchinae Schoenherr, 1825 (*sensu* Alonso-Zarazaga and Lyal 1999; most recently placed in the Molytinae, Lyal 2014), as the sole genus of Section "Trichodocerides". The third species to be included in the genus, *Trichodocerus antiquus* (Bondar, 1946), was originally described in the Baridinae Schoenherr, 1846, and subsequently transferred to *Trichodocerus* (Bondar 1947). Since, *Trichodocerus* has been treated variously in the Cryptorhynchinae (e.g. Thompson 1992: 875, Zherikhin and Gratshev 1995) and the Conoderinae Schoenherr, 1833 (e.g. Prena *et al.* 2014).

Perhaps the greatest contribution to the knowledge of the diversity and biology of *Trichodocerus* was through an intensive UV-light trapping study carried out at six localities in Panama from 1976-1978 (Wolda *et al.* 1998). Light traps were running in some localities every night during those three years, yielding 488 specimens of *Trichodocerus* in six morphospecies (Wolda *et al.* 1998). This material, as well as material collected at light traps in other years and localities by the authors of that study, represented a significant fraction of the 818 total specimens observed during this project.

A revision of the genus has been undertaken as part of a larger project on the systematics of the New World Conoderinae, wherein the nominal tribe Trichodocerini has been treated most recently (Prena *et al.* 2014, as Conoderitae), and also most frequently since it was first transferred (Wibmer and O'Brien 1989). This contribution describes new species of *Trichodocerus* and provides an identification key to all included species and species groups.

Materials and Methods

General morphological terminology follows Oberprieler *et al.* (2014); in part supplemented for specific terminology of the abdominal ventrites (Thompson 1992), tibial apex (Thompson 1992, Anzaldo 2017), sclerolepidia (Lyal *et al.* 2006), male terminalia (Wanat 2007), female terminalia (Howden 1995) and spermatheca (Aslam 1961). Species were delimited according to the phylogenetic species concept (Wheeler and Platnick 2000).

Habitus images were taken using a Visionary Digital Passport II imaging system with a Canon EOS 5D Mark II camera and aligned and stacked with Zerene Stacker. SEM micrographs were taken with a JEOL JSM 6300 Scanning Electron Microscope at the Arizona State University CLAS Bioimaging Facility. Genitalia were dissected by removing the abdomen with a #0 insect pin after relaxing the specimens in warm water and clearing soft tissues in warm KOH. Genitalia were prepared on a slide in glycerin jelly and imaged with a Leica DFC450 camera attached to a Leica M205C stereomicroscope and stacked with LAS core software. Body length (the distance from the anterior margin of the head to the posterior margin of the elytra) and width (distance across elytral humeri) measurements were also taken with LAS core software.

All referenced botanical names are the accepted name from The Plant List (2013; theplantlist.org) at the time of access. Distribution maps were created using SimpleMappr

(Shorthouse 2010). Coordinates for localities given by Champion (1906) are taken from Selander and Vaurie (1962).

Type Material. Labels for new type specimens include the genus and specific epithet, author, and the sex of the specimen. Type labels are red for the holotype and yellow for paratypes. A backslash with a space on either side " / " separates individual labels on specimens. Specimens were examined from the following collections:

ASUCOB Arizona State University Charles W. O'Brien Collection, Tempe, AZ

ASUHIC Arizona State University Hasbrouck Insect Collection, Tempe, AZ

CHAH Henry A. Hespenheide Collection, Los Angeles, CA

CMNC Canadian Museum of Nature Collection, Ottawa, Canada

CUAC Clemson University Arthropod Collection, Clemson, SC

FMNH Field Museum of Natural History, Chicago, IL

MNCR Museo Nacional de Costa Rica, San Jose, Costa Rica

NHM Natural History Museum, London, UK

NMNH Smithsonian National Museum of Natural History, Washington D.C.

PCMENT Programa Centroamericano de Maestria en Entomología, Universidad de Panamá

SSAC Salvatore S. Anzaldo Collection, Tempe, AZ

Phenotypic uniqueness of *Trichodocerus*

The reason for the uncertainty in phylogenetic placement lies in the many "structural peculiarities" (Champion 1906a: 713) that are either not found elsewhere in the

Curculionidae or appear similar to different groups of weevils. The most conspicuous external features are discussed below.

Antenna. The most salient and bizarre of these features is the antenna, which in *Trichodocerus* is elongate and delicate, terminating in a loose club (Figs. 3.1-3.2), and bearing long setae in the apical half. Synapomorphies for adult Curculionidae (*sensu* Oberprieler 2014) include a geniculate antenna and a compact antennal club (Oberprieler 2014: 423), both of which have been subject to contradictory interpretations in *Trichodocerus*. The antenna of *Trichodocerus* was originally described by Chevrolat as linear ("*Antennes lineares*..."; Chevrolat 1879: XCII) and by Bondar as filiform ("...*antenas longas, filiformes*..."; Bondar 1946: 86), both of which imply a non-geniculate state, and by Marvaldi and Lanteri as "almost straight due to shortened scape" (2005: 81). The distinction between geniculate and non-geniculate antennae lies in the point of insertion of the first funicular article on the scape, being apical in orthocerous weevils and shifted ventrally in those with geniculate antennae (Davis 2014, Clarke *et al.* 2018). In *Trichodocerus* the insertion point is indeed in this ventrally shifted position (Fig. 3A, the apex of the scape is visible and rounded, with the insertion of the first funicular article hidden underneath), allowing the antenna to be classed as geniculate.

The antennal club in weevils typically consists of 3-4 visible, expanded articles that in the "higher" Curculionoidea (Curculionidae *sensu lato*, Oberprieler 2014) form a compact club. The club of *Trichodocerus* was discussed by Champion in his redescription of the genus (1906a: 713) where he states that it is "...composed of four smooth, slender, elongate joints, the tip of each of which is more or less swollen"; it was also interpreted by Thompson (1992: 875) as "...consisting of 3 (apparently 4) very slender pilose segments" and Prena *et al.* (2014: 295) considered the club to be loose and bearing "conspicuous secondary

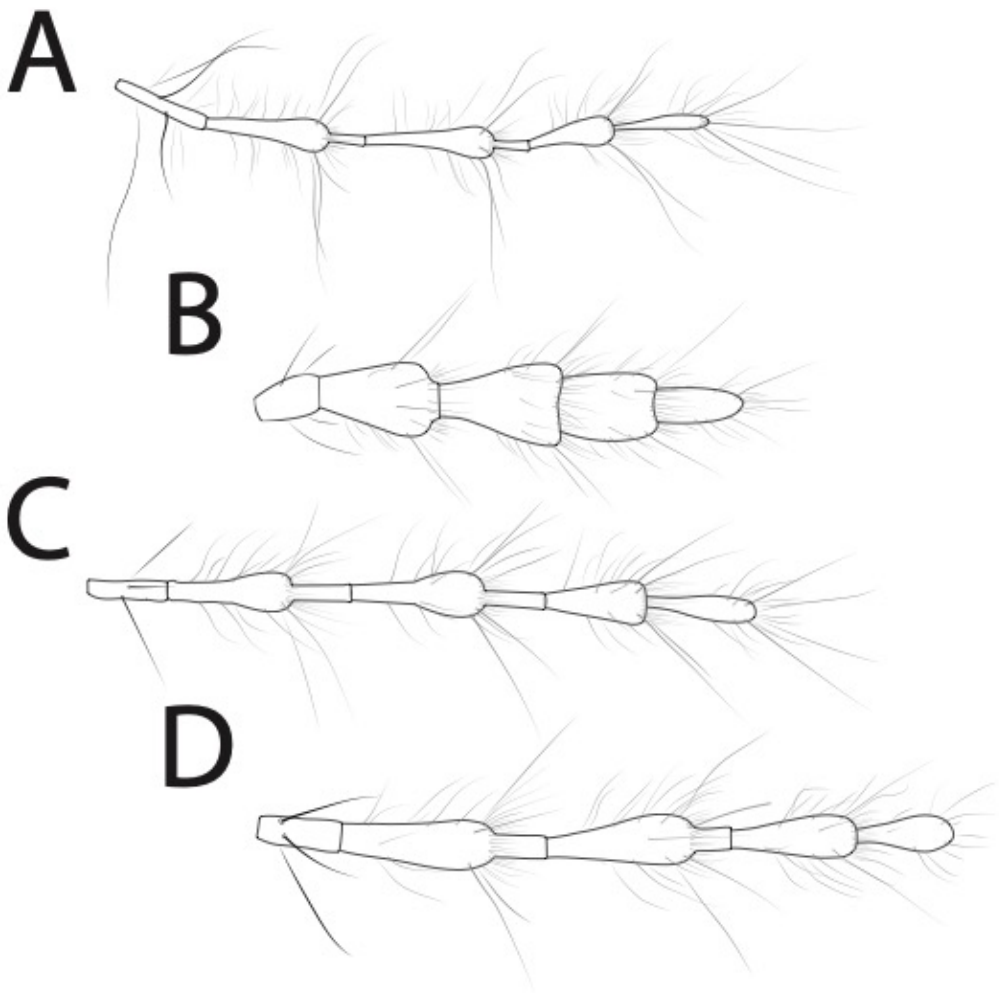

Figure 3.1. Line illustrations of the antennal club and funicular article 7, part I. A) *T. spinolae*; B) *T. lathrios*; C) *T. brevilineatus*; D) *T. ochromae*.

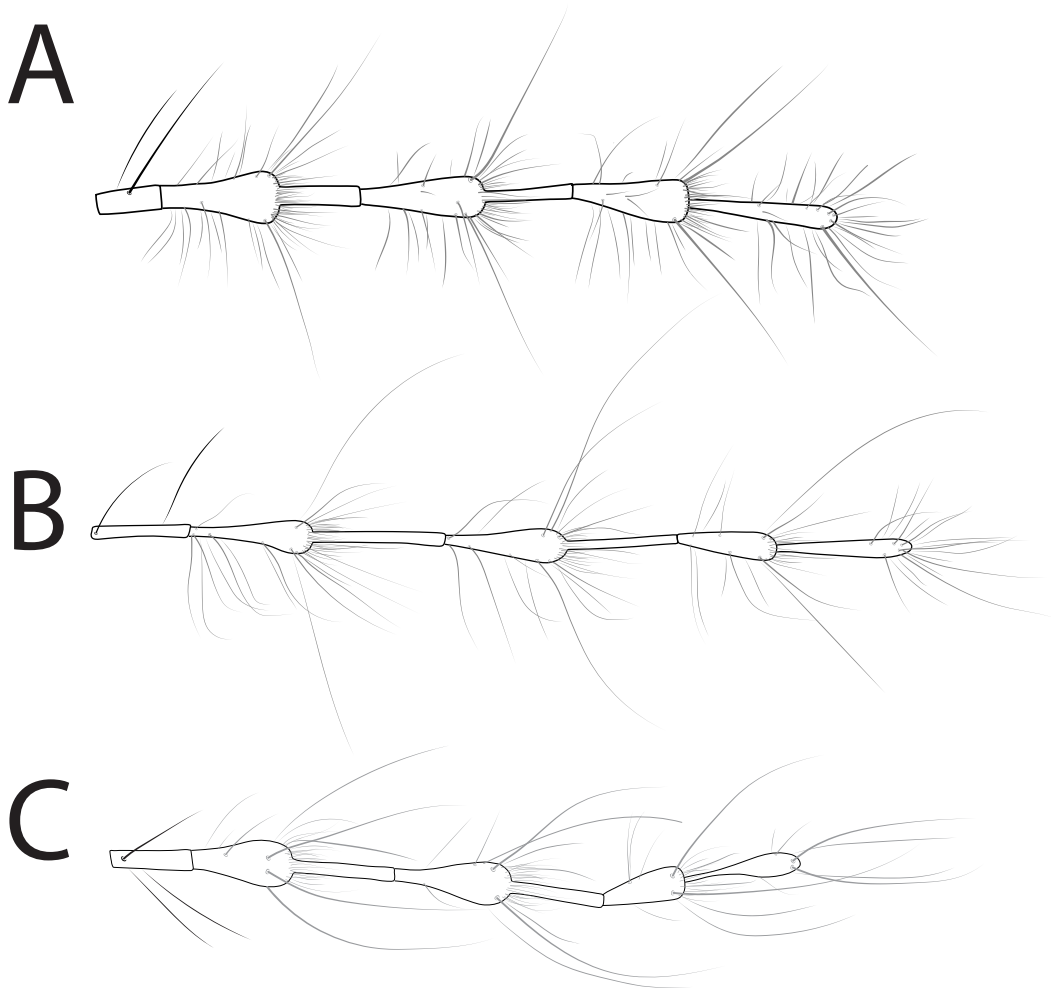

Figure 3.2. Line illustrations of the antennal club and funicular article 7, part II. A) *T. antiquus*; B) *T. chrysochaetus*; C) *T. obrieni*.

annulation". The club of *Trichodocerus* is not compact as is typical in Curculionidae, and in all species has four distinct articles (Figs. 3.1-3.2); in most species each one is articulating. At least the basal article – usually the basal two – is ventricose-rostrate in shape with a narrow basal stalk becoming swollen at the middle and then narrowed again in an apical "rostrum". The base of the second article is of a similar width to the apex of the first, and the base of the rostrate portion is obscured by a ring of short, dense setae, making it easy to assume Champion's (1906a) interpretation where the swollen part is the apex of the article, not the middle, and each article has an even longer basal stalk. The third article is shaped basally as the ventricose-rostrate ones but lacks the rostrate portion, and the fourth article is generally more linear. As the fourth club article in weevils is often thought to represent a secondary annulation of the third article (Davis 2009), in *Trichodocerus* this can be seen as a third article being ventricose-rostrate as the first two of most species and the fourth article representing the rostrate portion that has become articulating on the basal part.

Prosternum. Many groups of weevils have ventral modification in the form of a channel of varying degrees of development that can receive the rostrum in repose, allowing the weevil to become more compact for defensive purposes and protect its antenna. In *Trichodocerus* there is a channel present on the anterior region of the prosternum only, modified into a "rostral sheath" (Prena *et al.* 2014). The channel is widest anteriorly (Figs. 3.3G-D), being able to receive the rostrum and the short scape. Beyond this wider anterior part of the sheath appears to function more to hold the elongate antenna (and is usually narrower than the rostrum) and is variously constricted and converging to the a pointed and often impressed apex. The apex is usually situated below the contiguous procoxae, subapically fused with the

anterior coxal rim. The form of the prosternum is very similar to that of *Rhyssomatus* Schoenherr, 1837 (Molytinae: Cleogonini *sensu* Lyal 2014).

Mesoventrite (Figs. 3.3B, E, H, I). Species of *Trichodocerus* have a transverse ventral process on the mesoventrite anterior to the mesocoxae that is variously shaped but never apparently with the function of having the rostrum rest on it. A similar mesoventrite has been observed in species of *Conotrachelus* and other Molytinae. Posterior to the ventral process, in the narrow intercoxal region and in adjacent mesal faces of the mesocoxae are dense, small, circular yellow scales (Fig. 3.3E). In *Trichodocerus* these scales are always present in this region and variously on the pro- and metacoxae.

Taxonomic treatment

Trichodocerini Champion, 1906

Trichodocerus Chevrolat, 1879

Type species: *Trichodocerus spinolae* Chevrolat, 1879 [by subsequent designation: Champion 1906a: 713].

= *Mallerus* Bondar, 1946 [Syn.: Bondar 1947: 294]. Type species: *Mallerus antiquus* Bondar, 1946 [by original designation: Bondar 1946].

Diagnosis. *Trichodocerus* can be separated from all other curculionids by the loose antennal club with at least the first article ventricose-rostrate (Figs. 3.1-3.2). Additional characteristics are the triangular prosternal rostral sheath, the presence of yellow scales posterior to the mesosternal process and mesal faces of the mesocoxae, and deep punctures with a crustose

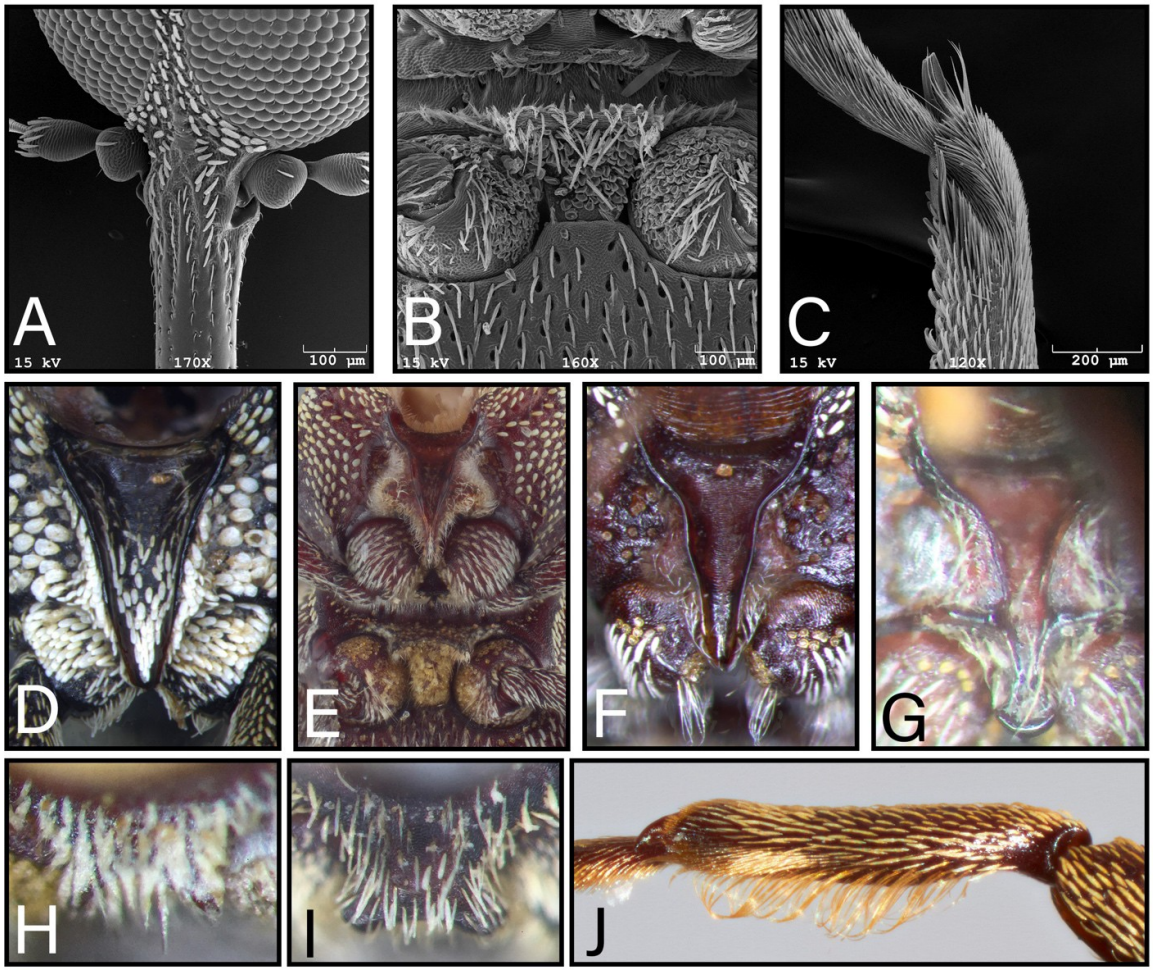

Figure 3.3. Miscellaneous morphological features of *Trichodocerus*. A) *T. woldai* head, rostral base, antennal scape and funicular article 1; B) *T. woldai* mesoventrite, ventral view; C) *T. leptodontus* protibial setal brush; D) *T. spinolae* prosternal sheath; E) *T. brevilineatus* prosternum and mesoventrite; F) *T. hybophrictus* prosternal sheath; G) *T. condylothecus* prosternal sheath; H) *T. selenion* ventral process of mesoventrite, anterior view; I) *T. leptodontus* ventral process of mesoventrite, anterior view; J) *T. chrysochaetus*, male protibia.

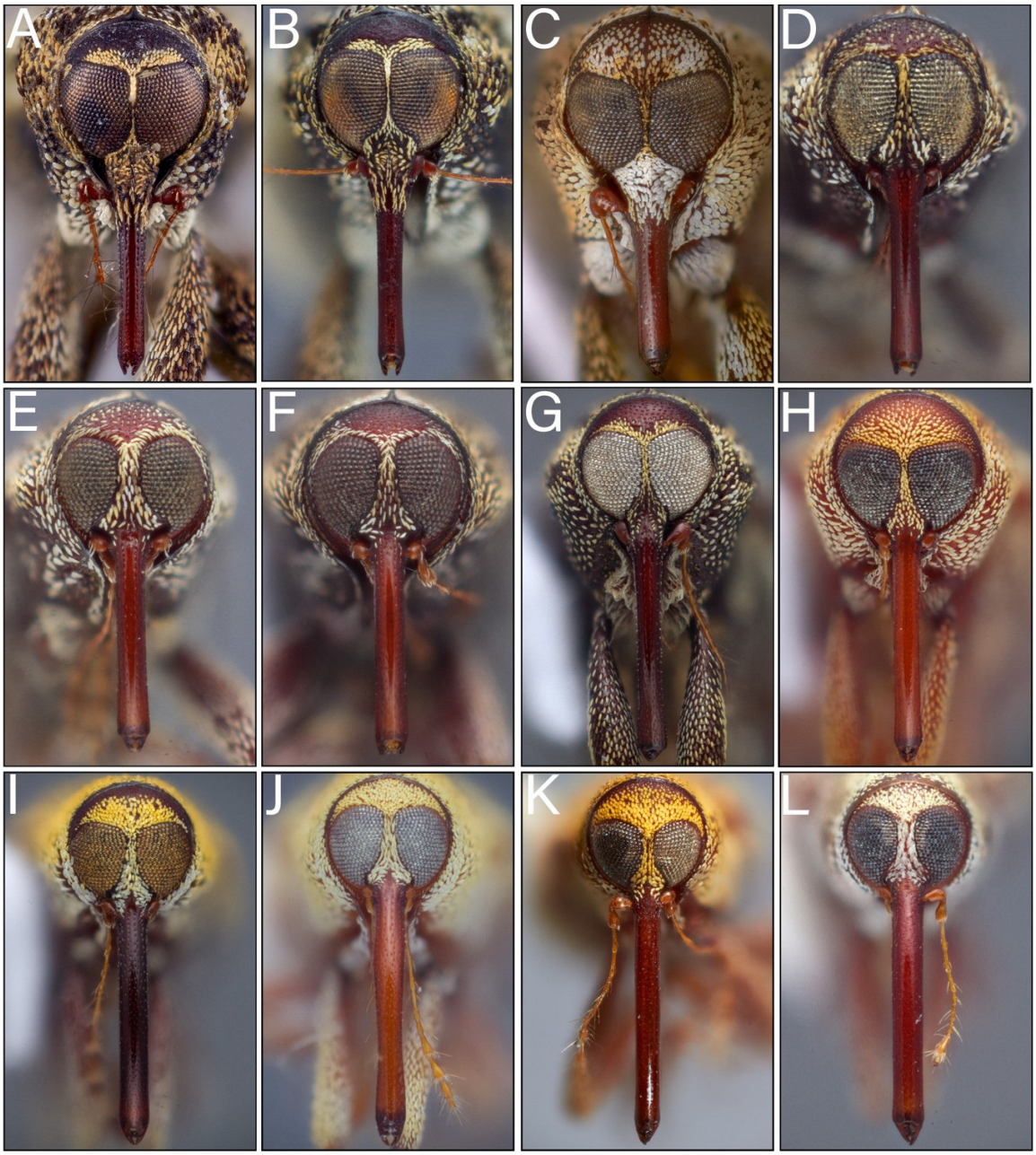

Figure 3.4. Head and rostrum, frontal view. A) *T. spinolae*; B) *T. leptodontus* male, paratype; C) *T. choristochion* male, holotype; D) *T. yavinivensis* female, paratype; E) *T. browni* female, paratype; F) *T. lathrios* female, holotype; G) *T. brevilineatus*; H) *T. hespenheidei*, paratype; I) *T. ochromae* female, holotype; J) *T. atheatomerus* female, paratype; K) *T. musathrus* female, holotype; L) *T. prionasceles* female, paratype.

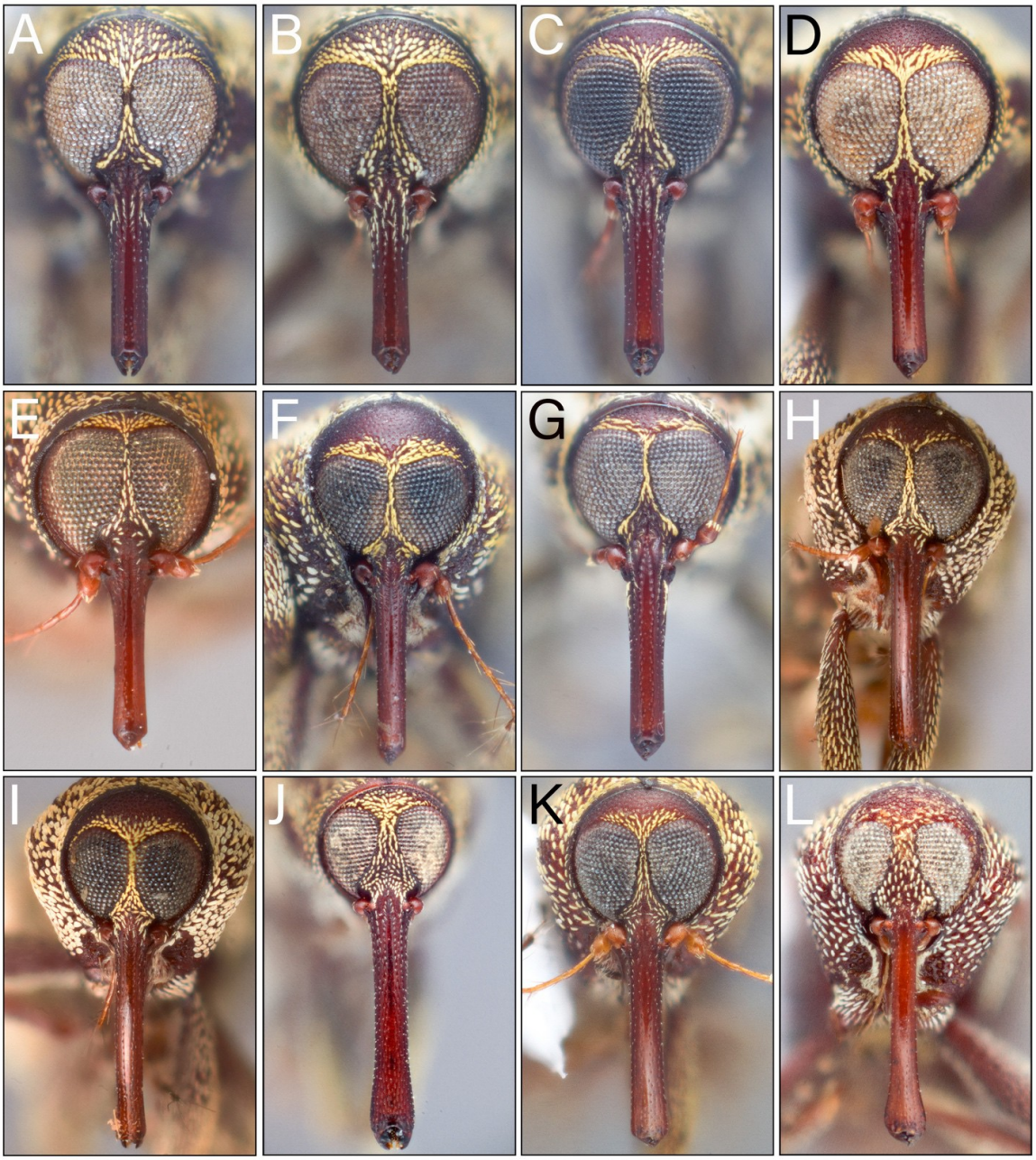

Figure 3.5. Head and rostrum, frontal view. A) *T. antiquus*; B) *T. woldai* female, holotype; C) *T. sobetes* female, holotype; D) *T. mecistotarbus* female, paratype; E) *T. hybophrictus* male, holotype; F) *T. stockwelli* female, paratype; G) *T. chrysochaetus* male, paratype; H) *T. obrieni* female, holotype; I) *T. selenion* female, holotype; J) *T. mariae* female, holotype; K) *T. condylothecus* male, paratype; L) *T. plataleaculus* female, holotype.

exudate on the lateral portion of the rostral sheath anteriorly, posteriorly on the lateral face of the prothorax, and variously on the meso- and metathoracic pleura, metaventrite, and abdominal ventrites. *Trichodocerus* is most likely to be confused for slender, flighted Cryptorhynchinae (e.g. *Mantias* Champion, 1906), which tend to also have large, coarsely faceted eyes and dark, cryptic coloration but can be easily separated by the form of the antennal club and the mesoventrite, which is typically modified in cryptorhynchines into an apically closed receptical for receiving the rostrum (Riedel *et al.* 2016). Affinity has also been noted between *Trichodocerus* and *Hedycera* Pascoe, 1870 (Champion 1906: 713), which both have slender antennal funicles with elongate setae, though the latter genus shares much more in common with the piazurine genera *Piazolechriops* Heller, 1906 and *Pseudopinarus* Heller, 1906 (Conoderinae: Piazurini; Anzaldo 2017). Another interesting feature of *Trichodocerus* is the elytro-tergal stridulatory apparatus (Type I; Lyal & King 1996), with stridulatory plectra present in parallel rows down the middle of the seventh tergite of the male only (visible in Figs. 3.19E, F). This type of stridulation is common throughout Curculionidae though stridulation is otherwise unknown in the Conoderinae (Lyal and King 1996). Elytro-tergal stridulation is widespread in the Molytinae (*sensu* Lyal 2014, including Cryptorhynchini) though in the cryptorhynchines it is not known to be present only in males (Lyal and King 1996).

Redescription – female. Length 2.26-6.02 mm, width 0.80-2.29 mm, length/width ratio 2.35-3.33. Integument light reddish brown to black, variably lighter on tarsi, rostrum, antennal scape, funicle, and sometimes club. Dorsal vestiture composed of flattened to longitudinally slightly curled, adpressed, apically truncate, rounded or emarginate scales and suberect to erect linear scales that are short and inconspicuous to conspicuous and arising

from shallow, crater-like punctures; scales sparse to dense and imbricate; scales various shades of yellow to white, tan, beige to dark coppery brown and black. Vestiture of lateral and ventral surfaces mostly linear, white, posteriorly directed scales and ventral suberect to erect setae. **Head.** Spherical to slightly impressed anteriorly at rostral insertion. Eyes large, coarsely faceted, somewhat reniform to pyriform, much narrower in lower half than upper half, distinctly constricted mesally around rostral base into a ventral lobe or gradually tapering into a rounded point, briefly contiguous at top to separated by the width of the rostrum at mid-length. Scales limited to border with eye or extending on vertex above eyes in dorsally rounded patch. Vertex above scales densely punctate. *Rostrum*: short to elongate (0.69-1.78x pronotal length), straight to evenly arcuate, ventrally flattened only basally before antennal insertion or throughout length, of even width from antennal insertion to apex or apex slightly dilated to spatulate, with or without integument flared in triangular to subquadrate process ventral to antennal insertion. Dorsally at base integument smooth to rugose, slightly to strongly impressed on either side to broadly transversely impressed; without carinae, with short basal median carina or with short basal median carina splitting to two with a third in between arising from proximal end of median dorsal smooth area. Apically integument smooth with longitudinal rows of punctures or irregularly arranged punctures, punctures with or without small curved setae. *Antenna*: inserted on rostrum in basal fourth to subbasally. Scape short and clavate to very short and globular, glabrous or with 2-3 small linear white scales. Funicular article 1 short, widest near middle and shorter than article 2 to longer, widest subapically and longer than article 2, apically ringed with small linear white scales; articles 2-7 slender and cylindrical, setae becoming longer distally. Club with 4 distinct articles; article 1 ventricose-rostrate, 2 ventricose-rostrate to ventricose, 3 ventricose, 4 elongate and linear to apically ovoid; articles 1 and 2 basally glabrous to setae

erect and dense, ventricose portion subapically ringed with elongate setae projecting at ~45 degree angle, rostrate portions glabrous; articles 1-3 with apex of ventricose portion ringed with dense setae; article 4 with setae densest apically. **Prothorax**. Ocular lobes very slightly developed. *Pronotum*: constricted subapically, evenly rounded to converging to base, disk evenly convex to irregular and with oblique impressions, median longitudinal carina absent to prominent and dorsally flattened. Lateral surfaces with crustose punctures along posterior margin to posterior half, squamose anteriorly. *Prosternum*: rostral sheath roughly triangular, widest and deepest at base, barely (Fig. 3.3D) to distinctly (Fig. 3.3F) constricted one-third from base, evenly converging to apex or slightly dilated at junction with coxal rim (Fig 3.3E), apically pointed to knobbed (Fig. 3.3G), terminating below or anterior to procoxae. Lateral margins and interior with sparse to dense multifurcate setae or white scales. **Mesothorax**. Scutellum exposed, circular to subtriangular, mostly glabrous to completely covered with small multifurcate setae. *Elytra*. Elongate, lateral margins parallel in basal two-thirds to four-fifths, rounded to apex, evenly convex on disk to transversely longitudinally impressed subbasally. Striae deep to shallow, with punctures deep and circular to ovoid or indistinct, punctures with seta or linear white scale. Interval 9 flat and evenly squamose to subcostate posteriorly and laterally glabrous and interval 10 below reduced. *Mesoventrite*: with short to prominent process anterior to mesocoxae (Figs. 3.3B, H-I), ventrally concave to conxex, ventrolateral corners rounded to produced and pointed. Intercoxal region with dense small, round yellow scales. *Mesanepisternum*: scales or crustose punctures densest bordering mesepimeron, impressed along border to coarsely sculptured, distinct from mesepimeron to apparently fused. *Mesepimeron*: scales sparse to dense, linear to flat and broad, integument flat to having deep, coarse punctures. **Metathorax**. *Metaventrite*: ventrally flat to convex, rounded to lateral region, glabrous ventrally to sparse scales, scales becoming denser at rounded side

or lateral portion, without crustose punctures laterally or with punctures scattered or along borders of sclerite. *Metanepisternum*: scales generally smaller anteriorly, becoming larger and denser posteriorly but may be uniform throughout. Sclerolepidia Type I or Type II. **Legs**. Elongate and cylindrical to short and stout, metafemur extending to sternite VI or VII. Scales unicolorous or with dark maculae at middle. Procoxa with or without mesal setal tuft. Femora ventrally unarmed or with small to large tooth on all femora or just the meso- and metafemora. Tibial apex with uncus arising from posterior margin to middle of apex, inner flange variously developed into small tooth to large triangular process, anterior margin with or without small tooth. Protibia with dense apicoventral setal brush covering distal one-fourth to one-half of ventral surface. Tarsomere 1 elongate, 3-4x longer than the 2, 1 and 2 with linear white scales dorsally only at apex or with linear white scales largest at apex. Tarsal claws angularly dilated at base or with broad triangular basal tooth. **Abdomen**. Pygidium concealed. Abdominal sternites III-VII visible, length of sternite III at sides longer than or equal to IV, IV shorter than V and VI combined, V and VI subequal in length. Sternites III-IV flat to slightly convex. Vestiture composed of setae to sparse white scales. Crustose punctures present only in single row along lateral portions of sternites or in multiple rows along entire posterior margin.

Female terminalia: spiculum ventrale elongate, longer than lamina, uniform in width or expanded at base or apex; apodeme narrowly to widely bifurcate at base of lamina, unsclerotized in between at base or somewhat laminate. Lamina of sternite 8 sclerotized only at lateral arms, setose apically. Gonostylus of even width throughout to widest apically. Bursa copulatrix entirely membranous or with large plate-like sclerite. Spermatheca falcate, subfalcate, J-shaped, or U-shaped; collum not to strongly produced, straight to curved;

ramus not to slightly produced; cornu hooked, of even width to apex, tapering to narrow rounded point or ventrally constricted subapically.

Male. Length 2.45-5.62 mm, width 0.80-2.89 mm, length/width ratio 2.40-3.15. As female except: rostrum generally shorter (0.69-1.33x pronotal length) but can be equal or longer than female, of similar shape or more straight, basal scales sometimes extending more distally; ventrally without setae to dense erect setae; metasternite ventrally slightly convex to concave, rounded at lateral margins to angulate; pro- and mesocoxa, pro- and mesotrochanter, and base of pro- and mesofemur with or without ventral setae, pro- and metafemur rarely with elongate ventral setae along entire length, tibial apex with uncus arising from posterior apical margin to inner apical margin; posteromedial margin of tergite VII emarginate, with at least one pair of stridulatory plectra; pygidium concealed or narrowly exposed; sternites III, IV and VI with or without median impression. *Male terminalia*: aedeagus strongly to slightly arcuate in lateral profile, shorter than temones, apex pointed, rounded, or truncate. Endophallus with large to small spines or small plate-like scales in patches, or complex series of variously shaped sclerites, with or without transfer apparatus. Tegmen forming complete, sclerotized ring around aedeagus or not, with lateral region of ring continuous with parameroid lobe; parameroid lobes narrow and sclerotized, approximate or widely separated; manubrium straight, thin apodeme or greatly reduced, with the posteroventral region of the tegmen broad and flattened. Base of spiculum gastrale slightly to strongly asymmetrically bifurcate, apodeme elongate, thin to broad, arcuate, expanded apically.

Natural history. The vast majority of specimens were obtained from UV light trapping. Only one species, *T. hespenheidei*, has rearing records from balsa logs (*Ochroma pyramidale* (Cav. ex Lam.) Urb.) (Malvaceae: Bombacoidea). Other species have been collected from leaves and branches of balsa (*T. brevilineatus*, *T. ochromae*) or on the trunk of a *Ceiba glaziovii* (Kuntze) K.Schum (Malvaceae: Bombacoidea) (*T. antiquus*). The only record not associated with a bombacoid is one specimen of *T. woldai* collected by canopy fogging a *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae).

Distribution. Widely distributed in the neotropics, from southern Mexico to southern Brazil, Paraguay, and northern Argentina.

Comments. Champion's redescription of the genus (1906a: 713) is inaccurate for the species described at the time in one particular: "…[femora] unarmed, the anterior pair sometimes with an indistinct tooth". *Trichodocerus spinolae* has a small tooth on the ventral surface of each femur, although it is often obscured by scales; *T. brevilineatus* has a minute tooth on the fore femora only. Most of the new species have unarmed femora.

Etymology. The name *Trichodocerus* is composed of the Greek *trichos* meaning hair and the *keros* meaning horn, referring to the elongate setae of the antennal funicular and club articles (Brown 1956).

I. The *Trichodocerus spinolae* group. This species group includes the type species of the genus, *T. spinolae*, and five newly described species: *T. leptodontus, T. corystochion, T. yavinivensis*, *T. browni*, and *T. lathrios*. All species have distinct Type I (squamose) sclerolepidia, a

prominent, crest-like, dorsally flattened pronotal carina, a ventrodistal region of the scrobe without a flared cuticular process, a prosternal rostral sheath lined laterally with regular scales and not multifurcate setae (also in the *antiquus* group and in *T. chrysochaetus* of the *mecistotarbus* group), the prosternal region lateral to sheath is not deeply impressed, the scutellum is not densely covered with multifurcate setae but has integument exposed around sparse multifurcate setae, the pygidium is exposed in the male (not observed in *T. yavinivensis* and *T. browni* but likely to occur due to their close relationship with *T. lathrios*), the rostrate portion of club articles I and II are short (especially so in *T. yavinivensis*, *T. browni*, *T. lathrios*) and elytral strial punctures bear a scale instead of a seta (also found in the *antiquus* group, in part). *Trichodocerus yavinivensis*, *T. browni*, and *T. lathrios* are likely closely related and could be treated as a separate species group, though *T. choristochion* has several intermediate features between these species and *T. spinolae*.

Trichodocerus spinolae Chevrolat, 1879

= *Trichodocerus lateralis* Chevrolat, 1879 [Syn.: Champion 1906a: 714]

Figs. 3.1A, 3.3D, 3.4A, 3.6A–B, 3.8A, 3.8C, 3.9B-C, 3.25A.

Diagnosis. *Trichodocerus spinolae* as treated here is restricted to South America, with all Central American records pertaining to the next species, *T. leptodontus*. Externally it is very difficult to distinguish from *T. leptodontus* – both species can be easily recognized by the grey chevron-shaped fascia at the middle of the elytra. *Trichodocerus spinolae* differs from *T. leptodontus* externally mainly in elytral scale pattern, with *T. spinolae* having less black scales in the anterior half, with a roughly "X" shaped patch over the first three elytral intervals at the base and the posterior margin of the "X" not extending in a more-or-less oblique fascia to

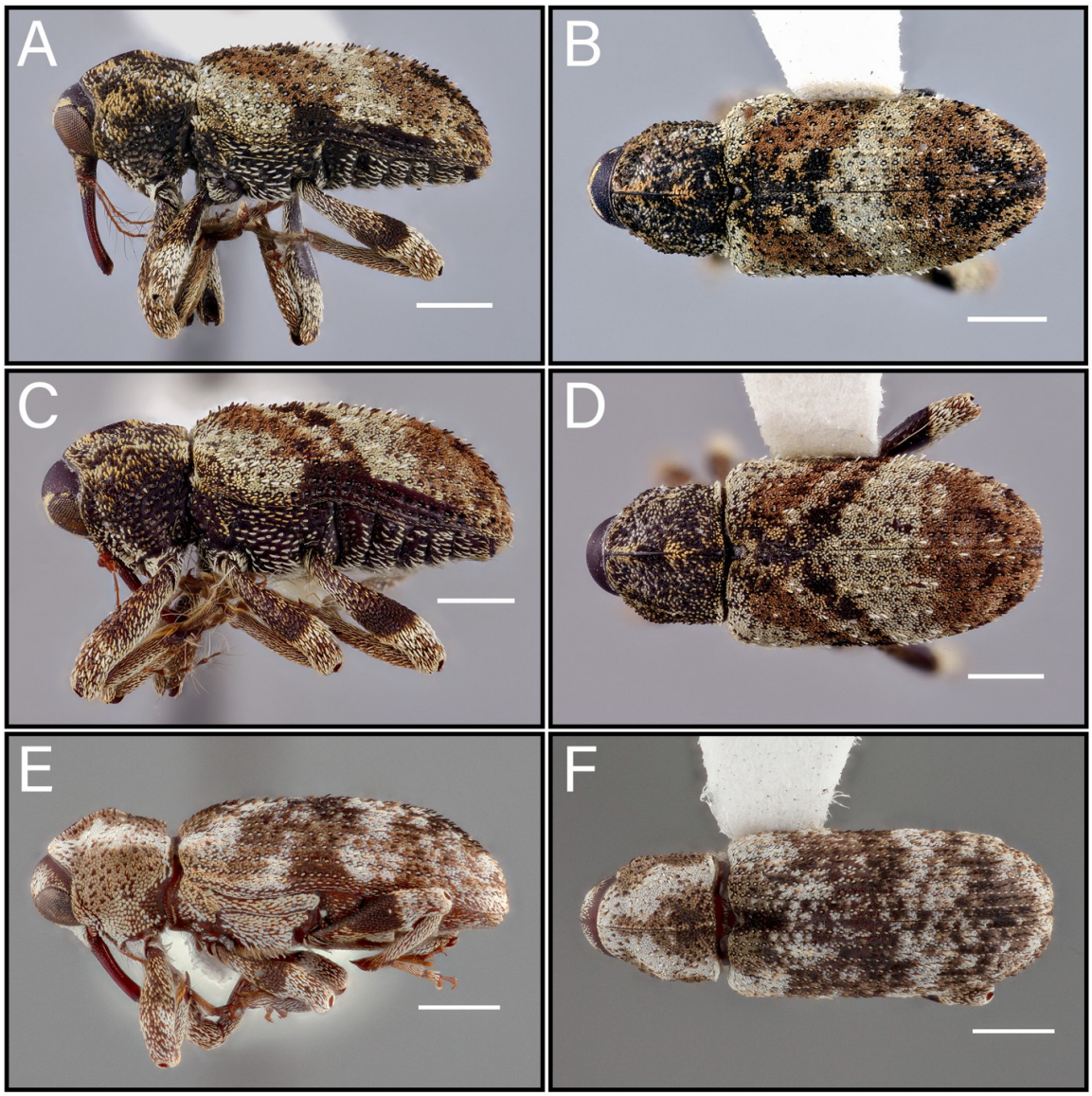

Figure 3.6. Dorsal and lateral habitus of species in the *spinolae* group. Scale bars = 1 mm. A-B) *T. spinolae* male; C-D) *T. leptodontus* holotype male; E-F) *T. choristochion* holotype male.

the black scales on interval 9 along the anterior border of the grey chevron-shaped patch (but may have small, isolated maculae on intervals 4-8). *Trichodocerus leptodontus* has the posterior margin of the "X" extending into more of an oblique fascia towards the posterior end of the dark stripe on interval 9, and though never in a completely black band, black scales are usually present on intervals 4, 5, and 7. The male genitalia is the most reliable way to distinguish the species, with *T. spinolae* having a dense patch of endophallic spines (absent in *T. leptodontus*), a flat transfer apparatus (two thin, parallel, arcuate sclerites in *T. leptodontus*), and an arcuate dorsal margin of the aedeagus in lateral profile (angulate in *T. leptodontus*).

Redescription – male. Length 4.89-5.62mm, width 1.86-2.89mm, length/width ratio 2.52-2.69. Integument dark brown to black, lighter on the tarsi, rostrum, and antenna. Dorsal scales greyish tan to grey with an opalescent tint, light brown and dark brown to velvety black. Laterally and ventrally scales white and tan. **Head**. Eyes separated by ~2 very small, narrow scales at closest point, ventral lobe extending below ventral margin of rostral insertion. Scales above eyes limited to border with eyes, with a small, unconnected patch of scales bordering eyes dorsolaterally. *Rostrum*: 0.92-0.95x pronotal length, evenly arcuate distal to antennal insertion, flattened ventrally at base and cylindrical to apex. Widest, rugose, and dorsally transversely impressed at base, impression strongest between short arcuate lateral carina and short median carina. Tan scales extending past antennal insertion in basal one-third. Integument smooth in distal two-thirds. *Antenna*: scape short, clavate. Funicle with article 1 clavate, apically narrower than scape, shorter than article 2. Article 2-4 subequal, 5-7 shorter and subequal. Club with four distinct articles, 1 and 2 ventricose-rostrate, rostrate portions very short and basal stalk of 2 very long, article 3 ventricose, 4 shorter than 3, flat, lateral margins straight on one side and arcuate on the other, apically rounded. **Prothorax**.

Pronotum: apically constricted, widest and rounded posterior to constriction, slightly constricted at middle, rounded to base. Median longitudinal carina an elevated, dorsally flattened crest in anterior two-thirds, reduced to base. Disk irregularly sculptured, with small round impressions on either side of carina at middle and subapically, and obliquely impressed anterolaterally. Scale pattern with oblique band of light scales, scales larger and whitish posterolaterally, becoming more diffuse, smaller, and somewhat transparent anteriorly; scales bordering median carina yellowish in anterior third and again at apex of carina; surrounding pattern mottled tan to yellowish to coppery brown, extending along lateral face anteriorly, becoming white adjacent to prosternal sheath. *Prosternum*: rostral sheath widest anteriorly, slightly constricted at middle, convergent to apex. Sheath lateral margins and ventral surface covered with linear white scales. **Mesothorax**. Scutellum with sparse setae. *Elytra*: slightly wider than widest part of pronotum, parallel-sided in anterior two-thirds. Pattern with vaguely "X"-shaped basal patch of dark brown scales from suture to interval 3, short dark brown stripe on interval 9 slightly posterior to "X", scales between short dark stripe and "X" in oblique light coppery brown band, with or without dark brown scales along posterior margin of brown band in small maculae on intervals 4, 5, or 7. Scales tan at humeri anterior to and at middle of elytra in chevron-shaped fascia posterior to coppery oblique band; posterior to chevron-shaped fascia scales coppery brown with a diffuse dark brown patch at declivity; scales surrounding scutellum small, yellow. Interval 9 prominent, subcostate in posterior half. Striae with deep punctures, each with a broad flat white to tan scale. *Mesoventrite*: ventral process slightly concave along ventral margin, posterolateral corners blunt, projecting laterally. Anterior and ventral face with elongate, linear white scales. *Mesanepisternum*: coarsely sculptured, appearing fused with mesepisternum, scales sparse. *Mesepimeron*: scales white to tan, densest bordering metanepisternum and elytra.

Metathorax. *Metaventrite*: ventrally concave in posterior half, rounded to sides. Ventrally scales linear, white, becoming broader at sides. Laterally with scattered crustose punctures. *Metanepisternum*: scales anteriorly small, somewhat metallic yellow, becoming larger and yellowish white anteriorly. Metanepisternal suture with Type I sclerolepidia. **Legs**. Hind femora extending to sternite VII. Procoxae with mesal tuft of linear white scales. All femora with small tooth ventrally. Scales yellowish white basally, with a dark coppery brown macula at middle laterally and dorsally, distinct on metafemora, diffuse on pro- and mesofemora, apically tan and brown with suberect white scales. Protibial setal brush covering one-third apicoventral surface. Metatibial apex with uncus arising from anterior margin. Tarsi slender, metatarsal article 1 slightly longer than twice length of article 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal in length at sides, V and VI subequal, combined longer than IV. Pygidium narrowly exposed. Sternite III strongly and IV slightly anteriorly impressed, VII with a circular median impression. Crustose punctures present laterally on each sternite, densest along posterior margin. Scales linear, white to tan.

Male terminalia. Aedeagus in lateral view strongly arched, dorsal margin arcuate; truncate apically, constricted subapically and slightly at middle, fringed with setae apicolaterally. Endophallus with dense patch of spines apically, scattered smaller teeth, a dense basal patch of small teeth; transfer apparatus elongate, flat, laterally sclerotized. Tegmen forming continuously sclerotized, circular ring, parameroid lobes long, sclerotized, widely separated, manubrium elongate. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Female. Length 4.31–6.02 mm, width 1.58–2.29 mm, length/width ratio 2.47-2.66. Similar to male except for the following: rostrum longer (1.08-1.24x pronotal length), abdominal sternites III, IV, and VII not impressed down middle, pygidium concealed, metatibial apex with uncus arising from posterior margin. *Female terminalia* (Fig. 3.9B-C): spiculum ventrale elongate, straight, apically slightly widened, longer than lamina. Lamina sclerotized at base, sclerotization limited to lateral arms posteriorly, arms narrow, slightly sinuous, slightly expanded and rounded at apex, with cluster of setae ventrally at apex. Tergite 8 lightly sclerotized, sclerotization mainly along lateral and posterior margin. Gonostylus of even width throughout. Spermatheca falcate, collum produced and curved, ramus not produced, cornu hooked and tapering to a narrow rounded point.

Distribution. Ecuador, Guyana, French Guiana, Brazil, Peru, Bolivia. Recorded from Paraguay by Wibmer & O'Brien (1986); no Paraguayan specimens were observed during this study.

Natural History. Host unknown. The majority of examined specimens examined were obtained from UV light traps.

Material examined. Seventeen specimens. Holotype (only images seen – the specimen is located in the Naturhistoriska Riksmuseet, Stockholm, Sweden, NHRS). Additional specimens: "Guyane" (1♂, NMNH); "BRIT. GUIANA. Berbice. Blairmont H.E. Box." (1♂, NHM); "ECUADOR:Pastaza;Ashuara Rio Macuma, 10km. from Rio Morona, 300m. VII 7-16:1971, leg.B.Malkin / forest night sweep" (1♂, FMNH); "BRAZIL:Rondonia,62 km.SW.Ariquemes,nr.Fzda.RanchoGrande, 30-III-10-IV-1992 / Coll. J.E.Eger" (5♂ 4♀,

ASUCOB); "BRAZIL:Rondonia,62km.SWArique- mes,Fzda.Rancho Grande,UV trap / X-5-17-1993 J.E.Eger" (1♀, ASUCOB); BRAZIL:Rond.UVtrap,62km.SW.Ariquemes, Fzda.RanchoGrande, xi-10-1994,C.O'Brien" (1♀, ASUCOB), "BOLIVIA:Santa Cruz, 3.7kmSSEBuenaVista Hotel Flora & Fauna 430m. 15-22-XI-2001 / B.K. Dozier, coll. Tropical transition forest blacklight trap" (1♂, ASUCOB).

***Trichodocerus leptodontus* Anzaldo, sp. nov.**

Figs. 3.3C, 3.3I, 3.4B, 3.6C–D, 3.8B, 3.8D, 3.9A, 3.9D-E, 3.25A.

Diagnosis. Very similar externally to *T. spinolae*. In this species there is usually more dark scales bordering the median grey chevron-shaped elytral fascia than in *T. spinolae*. The aedeagus in lateral profile is angulate (Fig. 3.8D; compare with *T. spinolae*, Fig. 3.8C), the endophallus is without a posterior patch of spines (Fig. 3.8B; compare with Fig. 3.8A) and with a transfer apparatus that is two parallel, arcuate sclerites (visible in Fig. 3.8B; compare with single, more flattened plate in Fig. 3.8A).

Description – holotype male. Length 5.52 mm, width 2.18 mm, length/width ratio 2.53. Integument dark brown to black, lighter on the tarsi, rostrum, and antenna. Dorsal scales greyish tan to grey with an opalescent tint, light brown and dark brown to velvety black. Laterally and ventrally scales white and tan. **Head**. Eyes separated by ~2 very small, narrow scales at closest point, ventral lobe extending below ventral margin of rostral insertion. Scales above eyes limited to border with eyes, with a small, unconnected patch of scales bordering eyes dorsolaterally. *Rostrum*: 1.01x pronotal length, evenly arcuate distal to antennal insertion, flattened ventrally at base and cylindrical to apex. Widest, rugose, and dorsally

transversely impressed at base, impression strongest between short arcuate lateral carina and short median carina. Tan scales extending past antennal insertion in basal one-third. Integument smooth in distal two-thirds. *Antenna*: scape short, clavate. Funicle with article 1 clavate, apically narrower than scape, shorter than article 2. Article 2-4 subequal, 5-7 shorter and subequal,4-7 with erect setae mostly along ventral surface. Club with four distinct articles, 1 and 2 ventricose-rostrate, rostrate portions very short and basal stalk of 2 very long, article 3 ventricose, 4 shorter than 3, flat, lateral margins straight on one side and arcuate on the other, apically rounded. **Prothorax**. *Pronotum*: apically constricted, widest and rounded posterior to constriction, slightly constricted at middle, rounded to base. Median longitudinal carina an elevated, dorsally flattened crest in anterior two-thirds, reduced to base. Disk irregularly sculptured, with small round impressions on either side of carina at middle and subapically, and obliquely impressed anterolaterally. Scale pattern with diffuse oblique band of light scales, scales larger and whitish posterolaterally, becoming smaller and somewhat transparent anteriorly; scales bordering median carina yellowish in anterior third and again at apex of carina; surrounding pattern mottled tan to yellowish to coppery brown, extending along lateral face anteriorly, becoming white adjacent to prosternal sheath. *Prosternum*: rostral sheath widest anteriorly, slightly constricted at middle, convergent to apex. Sheath lateral margins and ventral surface covered with linear white scales. **Mesothorax**. Scutellum with sparse setae. *Elytra*: slightly wider than widest part of pronotum, parallel-sided in anterior two-thirds. Pattern with vaguely "X"-shaped basal patch of dark brown scales from suture to interval 3, short dark brown stripe on interval 9 slightly posterior to "X", scales between short dark stripe and "X" in oblique light coppery brown band, with dark scales along posterior margin of brown band in partially connected maculae on intervals 4, 5, or 7. Scales tan at humeri anterior to and at middle of elytra in chevron-shaped fascia

posterior to coppery oblique band; posterior to chevron-shaped fascia scales coppery brown with a diffuse dark brown patch at declivity; scales surrounding scutellum small, yellow. Interval 9 prominent, subcostate in posterior half. Striae with deep punctures, each with a broad flat white to tan scale. *Mesoventrite*: ventral process slightly concave along ventral margin, posterolateral corners blunt, projecting laterally. Anterior and ventral face with elongate, linear white scales. *Mesanepisternum*: coarsely sculptured, appearing fused with mesepisternum, scales sparse. *Mesepimeron*: scales white to tan, densest bordering metanepisternum and elytra. **Metathorax**. *Metaventrite*: ventrally concave in posterior half, rounded to sides. Ventrally scales linear, white, becoming broader at sides. Laterally with scattered crustose punctures. *Metanepisternum*: scales anteriorly small, somewhat metallic yellow, becoming larger and yellowish white anteriorly. Metanepisternal suture with Type I sclerolepidia. **Legs**. Hind femora extending to sternite VII. Procoxae with mesal tuft of linear white scales. All femora with small tooth ventrally. Scales yellowish white basally, with a dark coppery brown macula at middle laterally and dorsally, distinct on metafemora, diffuse on pro- and mesofemora, apically tan and brown with suberect white scales. Protibial setal brush covering one-third apicoventral surface. Metatibial apex with uncus arising from anterior margin. Tarsi slender, metatarsal article 1 slightly longer than twice length of article 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal in length at sides, V and VI subequal, combined longer than IV. Pygidium narrowly exposed. Sternite III strongly and IV slightly anteriorly impressed, VII with a circular median impression. Crustose punctures present laterally on each sternite, densest along posterior margin. Scales linear, white to tan.

Male terminalia. Dorsal margin of aedeagus angulate in lateral view. Aedeagus rounded apically, slightly constricted subapically and one-third from apex, fringed with setae apicolaterally. Endophallus with dense microsclerites anteriorly, becoming slightly larger and toothlike posteriorly, and a region of small, circular, plate-like sclerites; transfer apparatus two thin, arcuate, parallel sclerites. Tegmen forming continuously sclerotized, circular ring, parameroid lobes long, sclerotized, widely separated, manubrium elongate. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Variation. Males length 4.18-5.46 mm, width 1.60-2.19 mm, length/width ratio 2.46-2.61, rostrum 0.92-1.03x longer than pronotum. Female length 4.34-5.98 mm, width 1.68-2.34 mm, length/width ratio 2.50-2.62, rostrum 1.02-1.10x pronotal length. Females male except abdominal sternites not impressed, pygidium concealed, metatibial uncus arising from posterior margin. *Female terminalia* (Fig. 3.9D-E): spiculum ventrale elongate, straight, apically slightly widened, longer than lamina. Lamina sclerotized at base, sclerotization limited to lateral arms posteriorly, arms narrow, slightly sinuous, slightly expanded and rounded at apex, with cluster of setae ventrally at apex. Tergite 8 lightly sclerotized, sclerotization mainly along lateral and posterior margin. Gonostylus of even width throughout. Spermatheca falcate, collum produced and curved, ramus not produced, cornu hooked and tapering to a narrow rounded point.

Distribution. Costa Rica, Panama.

Material examined. One hundred and sixty-one specimens. Holotype male: "CANAL ZONE,Barro Colorado Is.,UV trap 3(26m.high) 1May1978H.Wolda" (ASUCOB). Paratypes

(152): same as holotype except “24May1976” (2♂ 2♀, ASUCOB), “trap 1 (3m.high) 1 June1976” (1♀, ASUCOB), “3June1976” (1♂, ASUCOB), “13June1976” (1♂, ASUCOB), “1Oct1976” (1♀, ASUCOB), “trap 3 (26m.high) 13 May 1977” (1♂, ASUCOB), “23May1977” (5♂ 3♀, ASUCOB), “24 May1977” (6♂ 9♀, ASUCOB), “trap 1 (3m.high)” (5♂ 7♀, ASUCOB; 2♀, CMNC), “25 May1977” (4♂ 2♀, ASUCOB), “trap 3 (26m.high)” (1♂, ASUCOB), “28 May1977” (1♂, ASUCOB), “29 May1977” (2♂, ASUCOB), “trap 1 (3m.high)” (5♂ 1♀, ASUCOB), “30May1977” (1♀, ASUCOB), “2June1977” (1♂ 2♀, ASUCOB), “trap 3 (26m.high)” (1♂ 2♀, ASUCOB), “trap 1 (3m.high) 3June1977” (1♂, ASUCOB), “4June1977” (1♀, ASUCOB), “5June1977” (2♂ 1♀, ASUCOB), “6June1977” (1♂, ASUCOB), “trap 3 (26m.high)” (1♀, ASUCOB), “trap 1 (3m.high) 9June1977” (1♀, ASUCOB), “10June1977” (1♂, ASUCOB), “11June1977” (1♀, ASUCOB), “16June1977” (1♂ 1♀, ASUCOB), “trap 3 (26m.high)” (1♂ 1♀, ASUCOB), “trap 1 (3m.high) 18June1977” (1♂, ASUCOB), “3 July1977” (1♀, ASUCOB), “trap 3 (26m.high) 4 July1977” (1♀, ASUCOB), “25Aug.1977” (1♂, ASUCOB), “trap 1 (3m.high)” (1♀, ASUCOB), “16 Oct.1977” (1♀, ASUCOB), “20Nov.1977” (1♀, ASUCOB), “18Apr.1978” (1♂ 2♀, ASUCOB), “trap 3 (26m.high)” (1♂ 2♀, ASUCOB), “20Apr.1978” (1♀, ASUCOB), “trap 1 (3m.high)” (1♂ 1♀, ASUCOB), “trap 3 (26m.high) 21Apr.1978” (1♀, ASUCOB), “trap 1 (3m.high) 10May1978” (1♀, ASUCOB), “trap 3 (26m.high) 19May1978” (1♀, ASUCOB), “20May1978” (8♂ 10♀, ASUCOB), “30-IV-1981” (1♀, ASUCOB), “V-20-1981” (1♀, ASUCOB), “V-1-1982” (1♀, ASUCOB); “Panamá, Isla Barro Colorado Light trap Week, 18 M. III N 29 IV-5 V 1987” (1♀, PCMENT); as previous but “Week 20 N. III N 11-17 V 1988” (1♂ 1♀, PCMENT), “Week 21 N III N 18-24 V 1988” (1♂ 1♀, PCMENT), “Week 22 N. III N 25-31 V 1988” (2♂ 2♀, PCMENT); “Panamá: Canal Zone, Barro Colorado Is. 9°10’N, 79°50’W / 29.V.1977 H.A. Hespenheide (1♀, CHAH); same data as previous but

dates “15.VI.1977” (1♂, CHAH), “17.VI.1977” (1♀, CHAH); “PANAMA,Pan., Isla Maje,Lake Bayano 14.v.1976 H. Wolda” (1♀, ASUCOB); same as previous but date “28.v.1976” (1♂ 2♀, ASUCOB); “CANAL ZONE,Fort Gulick,Qts.40, Feb.1979 at light H.J.Harlan” (1♂, ASUCOB); same as previous but date “March 1979” (1♂ 1♀, ASUCOB); “CANAL ZONE,Fort Gulick, at light IX-1979” (1♂, ASUCOB); “PANAMA: CANAL ZONE Ft. Gulick, Qtrs. 40A 12-15.V.1981,H.J. Harland black lt. tp. FMHD #81-738” (1♂, CMNC); as previous but date “16-20.V.1981” (1♂, CMNC); “PAN.Panama LasCumbres UVtrap April28 1976 H.Wolda” (1♀, ASUCOB); same as previous but dates “May 8” (1♂, ASUCOB), “May 31” (1♂, ASUCOB); “PANAMA,Pan., Las Cumbres,at wall lights J. Wolda April 25, 1979” (1♂, ASUCOB); “PANAMA, dist. Chepo Altos de Maje 17 May 75 at lights Stockwell-Engleman” (1♂ 1♀, CHAH; 1♂ 1♀, NMNH; 2♀, CMNC). Additional specimens: “CANAL ZONE,Barro Colorado Is.,UV trap 1(3m.high) 1 June1976H.Wolda” (1♂, ASUCOB); same as previous but “23May1977” (1♀, ASUCOB), “trap 3 (26m.high) 24 May1977” (1♂ 2♀, ASUCOB), “25 May1977” (1♀, ASUCOB), “trap 1 (3m.high) 22May1978” (1♂, ASUCOB); “Panamá, Isla Barro Colorado Light trap Week 22 N. III N 25-31 V 1988” (1♀, PCMENT);

Comments. A single specimen from Antioquía, Colombia agrees with the elytral pattern consistent with this species, however it is a female so it cannot be confidently assigned to either *T. leptodontus* or *T. spinolae* based on aedeagal characters.

Etymology. From the Greek *leptos* meaning “small, subtle” and *dontos* meaning “tooth”, the name refers to the reduced sclerotization on the endophallus compared to *T. spinolae* (Brown 1956).

***Trichodocerus corystochion* Anzaldo, sp. nov.**

Figs. 3.4C, 3.6E–F, 3.25A.

Diagnosis. *Trichodocerus corystochion* is the most distinct species of the *spinolae* group with dense white scales on the rostral base and in sinuous, anteriorly converging vittae on the pronotum that extend to the elytral base, the tibial uncus with a small ventral tooth (possibly only in the male), and the strongly concave metaventrite (likely only in the male).

Description – holotype male. Length 5.15 mm, width 1.72 mm, length/width ratio 3.00. Integument brown to light reddish brown, lighter on tarsi, rostrum, antennal scape and funicle. Dorsal scales flat, apically rounded, imbricate white, beige, dark brown and black. Vestiture of legs, lateral and ventral surfaces white, beige and dark brown scales. **Head**. Eyes subcontiguous, separated by ~4 very narrow linear scales at closest point, ventral lobe extending below ventral margin of rostral insertion. Scales above eyes in dense, dorsally rounded patch of scales, becoming smaller and sparser farther from eyes; scales beige and dark brown laterally and above interocular space, white to vertex; between eyes scales small and narrow beige and dark brown and larger and white above rostral insertion. *Rostrum*: short (0.73 x length of pronotum), very slightly arcuate, flattened ventrally at base and cylindrical to apex. Dorsally transversely impressed at base, with dense white scales becoming narrower and light beige at antennal insertion. Smooth, with minute punctures in longitudinal rows mostly laterally, punctures each with one minute curved seta. *Antenna*: scape clavate, with three linear white scales. Funicle with article 1 clavate, narrower than scape, shorter than article 2. Articles 2-7 cylindrical; 2 longer than 3, 3 slightly longer than 4, 6 longer than 5 and 7. Articles 4-7 with erect perpendicular setae. Club with four distinct articles, 1 and 2

ventricose-rostrate, rostrate portions very short, article 3 ventricose, article 4 shorter than 3, sides rounded and widest in apical half. **Prothorax**. *Pronotum*: lateral margins roughly parallel, slightly rounded and widest in basal half, slightly constricted medially and one-fourth from anterior margin, constricted at apex. Median longitudinal carina an elevated, narrow, prominent crest, dorsally flattened in anterior two-thirds, absent posteriorly. Scale pattern a distinct, sinuous anteriorly converging white vitta, between vitta scales beige with a round dark brown macula at base and two small white maculae on either side of posterior margin of median carina, scales bordering carina white; suberect scales white or tan in white vittae, dark brown elsewhere; beige scales extending down most of lateral surface becoming white adjacent to rostral sheath. *Prosternum*: rostral sheath widest anteriorly, sides slightly constricted one-third from anterior margin and slightly dilated at junction with rim of coxal cavity, convergent to apex. Sheath lateral margins and interior densely covered with white scales. **Mesothorax**. Exposed portion of scutellum anteriorly declivous, posteriorly rounded, with sparse, small linear scales at posterior margin. *Elytra*: slightly wider than widest part of pronotum, parallel-sided from humeri to one-fifth from apex, rounded to apex. Integument slightly, transversely impressed on interval 2 one-fifth from base. Scale pattern with white humeral patch continuous with pronotal vittae, extending in diffuse arc to suture, a broad diffuse white fascia posterior to middle composed of small white maculae interspersed with tan and dark brown scales, and another diffuse, predominantly white area at apex; dark scales in short longitudinal stripes mainly bordering white areas and a short longitudinal vitta posterior to scutellum; scales at base between humeral white patch and dark scutellar stripe beige. Interval 9 tumescent in posterior half, evenly squamose, interval 10 below narrow. Striae with small, deep circular punctures, each bearing a single tan to white scale. *Mesoventrite*: ventral process short, ventrally concave, ventrolateral corners slightly laterally

produced. Anterior face and ventral margin with ventrally produced setae, posterior face with ventrally produced linear white scales. *Mesanepisternum*: with broad, flat, beige and white scales, densest bordering mesepimeron. *Mesepimeron*: with broad, flat, beige white and brown scales. **Metathorax**. *Metaventrite*: strongly concave ventrally, rounded to sides. Vestiture ventrally sparse suberect and erect setae, becoming densest at rounded lateral margins, laterally with linear and round, flattened white scales above setae becoming smaller, mottled with tan below metanepisternal suture. *Metanepisternum*: anteriorly with dense, small, linear scales, becoming larger, flat, and round, densest posteriorly, scales tan and white. **Legs**. Hind femora extending to sternite VII. Pro- and mesocoxae with mesal tuft of elongate setae, pro- and mesotrochanters ventrally with elongate setae. Femora ventrally with a tooth, largest on hind femur. Meso- and metafemoral scale pattern ventrally and laterally at the base with mottled white and tan scales, a large dark brown macula laterally and dorsally at middle and dorsally at base, apex mottled tan and white; profemur with dorsal diffuse dark brown and tan macula, mottled tan and white elsewhere. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering about one-half of apicoventral surface. Metatibial apex with uncus arising at anterior margin, uncus angularly dilated along posterior face. Metatibial apical setal comb elongate, arcuate, extending from anterior apical margin to subapical posterior margin, scales becoming darker proximally. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white and tan scales dorsally, largest at apex. Claws angularly dilated at base. **Abdomen**. Sternite III at the sides longer than IV, V and VI subequal, combined longer than IV. Integument medially concave on sternite III and slightly impressed on sternite VII. Crustose punctures present laterally and along posterior margin except medially. Vestiture composed of linear, white and tan scales, smaller in impression on sternite VII, suberect setae in concavity on sternite III. Pygidium narrowly exposed.

Female. Unknown.

Natural history. The only known specimen was collected at a mercury vapor and ultraviolet light.

Material examined. One specimen. Holotype male: "PARAGUAY: Dept. Canindeyu, Reserva Natural del Bosque Mbaracayú 2-5-XII 2017, J.E. Eger / S24°08'03" W55°31'43", 598 ft. MV & UV Light".

Etymology. This name is derived from the Greek *korystos* meaning "crested" and *chion* meaning "snow", referring to the prominently crested and distinctively snow-white pronotum (Brown 1956). The epithet is treated as a noun in apposition.

***Trichodocerus yavinivensis* Anzaldo, sp. nov.**

Figs. 3.4D, 3.7A–B, 3.25B.

Diagnosis. This species is most similar to *T. browni* and *T. lathrios* with the antennal scrobe extending to the head, the elongate, narrow body form, funicular article 1 longer than the scape and ventrally sulcate femora. *Trichodocerus yavinivensis* can be differentiated from *T. browni* and *T. lathrios* by the short median carina extending from the rostral base to between the eyes, and the distinct elytral vestiture, notably having only a small lateral triangular dark area on each elytron.

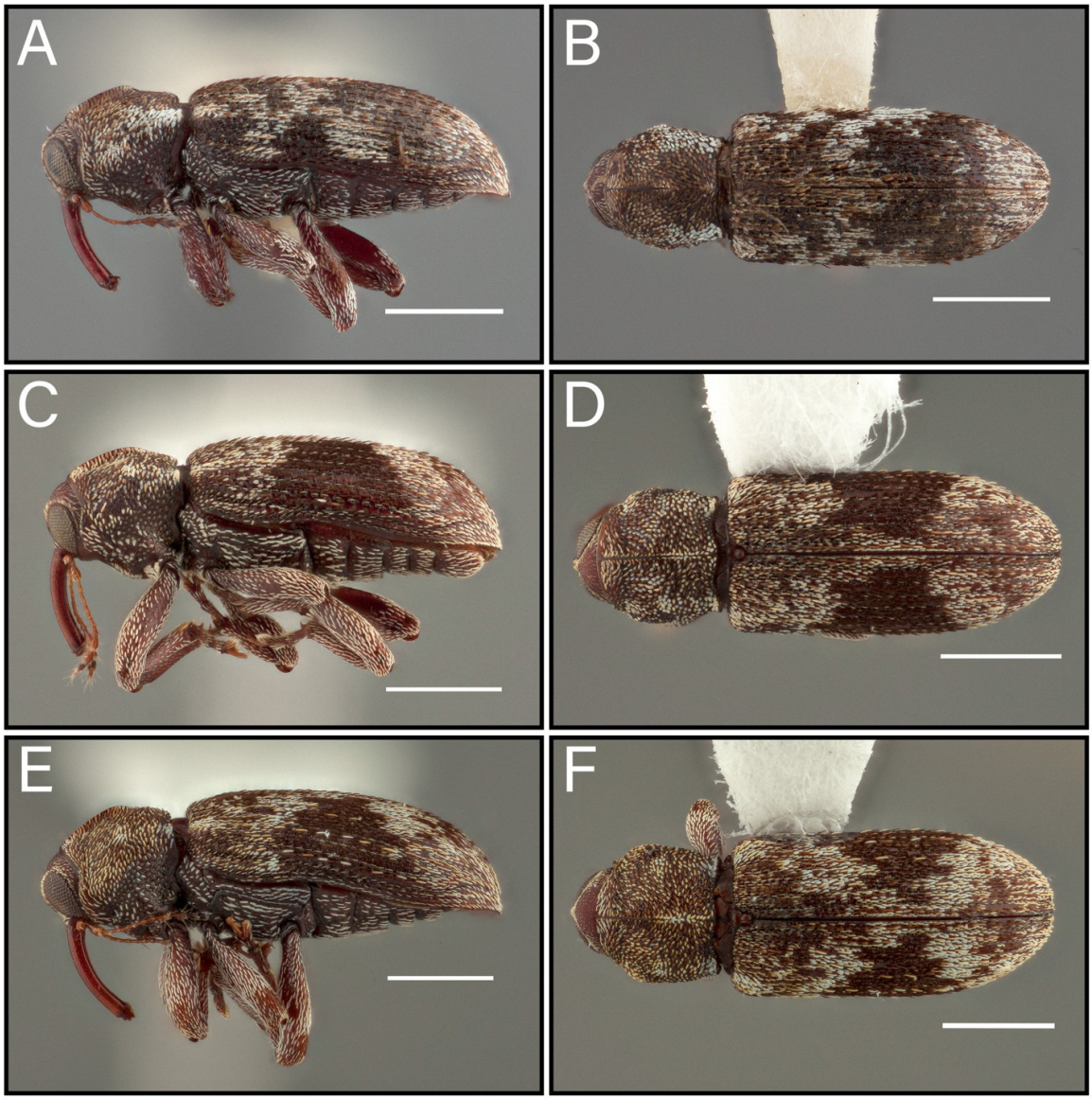

Figure 3.7. Dorsal and lateral habitus of species in the *spinolae* group. Scale bars = 1 mm. A-B) *T. yavinivensis* holotype female; C-D) *T. browni* holotype female; E-F) *T. lathrios* holotype female.

Description – holotype female. Length 3.64 mm, width 1.13 mm, length/width ratio 3.22. Integument dark brown, becoming lighter on the rostrum and antenna. Dorsal scales elongate, flat, mainly white and various shades of brown from tan to dark coppery brown. Lateral and ventral scales linear to broad, white. **Head**. Eyes subcontiguous, separated by ~4 narrow, linear scales at closest point, ventral lobe small, ending above ventral margin of rostral insertion. Antennal scrobe extending to head capsule, with round impression adjacent to ventral lobe of eye. Vestiture above eyes tan, densest bordering eyes and sparse above eyes, becoming mottled with brown between eyes and white above rostral insertion. *Rostrum*: short (0.83x pronotal length), slightly curved, somewhat flattened ventrally at base and cylindrical to apex. Dorsally at base with faint median carina extending to head between eyes, slightly impressed on either side of carina. Integument smooth, with somewhat straight longitudinal rows of punctures to apex. Antenna inserted subbasally. *Antenna*: scape short, clavate, with one long white linear scale. Funicle with article 1 clavate, longer than article 2, with linear tan scales becoming white at apex. Articles 2-7 slender, cylindrical; articles 2 and 3 subequal, slightly longer than 4, 4 slightly longer than 5, 6 slightly longer than 5 and 7. Club broad, flat, with four distinct articles; 1 ventricose-rostrate with rostrate portion very short, 2-3 ventricose, 4 narrower and shorter than 3, apically rounded. **Prothorax**. *Pronotum*: apically constricted, widest and rounded posterior to constriction, evenly converging to base. Median longitudinal carina an elevated, dorsally flattened crest in anterior two-thirds, reduced posteriorly. Scale pattern with lateral white vitta in basal half, vitta curving to lateral face; surrounding scales on disk various shades of tan to dark brown; suberect scales inconspicuous, same color as surrounding scales. *Prosternum*: rostral sheath widest anteriorly, sides converging in anterior third, parallel to junction with coxal rim, converging and flattened to apex. Sheath lateral margins and ventral surface covered with linear white scales.

Mesothorax. Scutellum with sparse setae. *Elytra*: slightly wider than widest part of pronotum, parallel-sided from humerus to apical third, rounded to apex. Pattern with a large dark transverse fascia composed of dark coppery brown scales one-third from apex, extending anteriorly on intervals 3 and 5 to middle of elytra; small, roughly triangular macula of dark coppery brown scales at middle extending from lateral margin of elytra and narrowing to interval 7; white and tan scales surrounding dark regions, humerus white, basal region between humeri tan to brown. Interval 9 slightly tumescent in posterior half. Striae indistinct, with mostly tan to brown linear scales in punctures. *Mesoventrite*: ventral process short, posterolateral corners deflected posteriorly, with a small tumescent process on ventral margin at middle. Anterior and ventral face and intercoxal region with elongate white linear scales. *Mesanepisternum*: with sparse white scales. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides, with linear white scales ventrally becoming broader laterally, laterally with scattered crustose punctures. *Metanepisternum*: white scales becoming denser posteriorly. **Legs**. Hind femora extending to sternite VI. Procoxae without mesal setal tuft. All femora ventrally unarmed, sulcate in distal half, with large lateral and dorsal macula of linear coppery brown scales at middle and a smaller one dorsally at apex, surrounding scales white. Protibial setal brush covering one-third apicoventral surface. Metatibia slightly dilated apically, with a small, curved uncus at posterior margin, inner flange rounded, anterior margin with small tooth. Tarsi stout, article 1 less than twice length of article 2, with linear white scales dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal in length at the sides, V and VI subequal, combined longer than IV, VII flat. Crustose punctures scattered throughout each sternite, densest along posterior margin except at middle of sternites III and IV. Scales linear, white.

Variation. Female length 3.64-4.30 mm, width 1.13-1.39 mm, length/width ratio 3.10-3.22, rostrum 0.83-0.89x pronotal length. Dorsal scales of female paratype with coppery brown scales having a more metallic pinkish hue. Male unknown.

Distribution. Mexico (Veracruz), Guatemala (Petén).

Natural History. Host unknown. The paratype was collected "at light".

Material Examined. Two specimens. Female holotype: "GUATEMALA: Petén: Ruinas Tikal 245m 7/10July77 E.M. & J.L. Fisher". Paratype (1): "MEXICO,Ver.,250' LosTuxtlas,Biol.Sta. UNAM,17May1983C& L.O'Brien&GMarshall / at light" (1♀, ASUCOB).

Etymology. The name is in reference to the type locality, the Tikal Ruins of northern Guatemala, which served as the filming location for the moon Yavin IV in *Star Wars: Episode IV – A New Hope*. The epithet is constructed from *yavin+iv* and is given the suffix *–ensis*, signifying place of origin.

***Trichodocerus browni* Anzaldo, sp. nov.**

Figs. 3.4E, 3.7C–D, 3.25B.

Diagnosis. This species is most similar in scale pattern to *T. lathrios* but has more widely separated eyes (Fig. 3.4E), a less irregularly outlined dark triangular elytral patch (Fig. 3.7D), the linear scales of the strial punctures light colored and conspicuous in the dark patch

(suberect interval scales light colored in *T. lathrios*), and the smaller apicoventral protibial setal brush.

Description – holotype female. Length 3.62 mm, width 1.16 mm, length/width ratio 3.12. Integument reddish brown, lighter on tibiae, tarsi, rostrum, and antenna. Dorsal scales white, tan, and dark coppery brown; lateral and ventral scales white. **Head**. Eyes separated by nearly three-quarters rostral width at middle, ventral lobe small, ending above ventral margin of rostral insertion. Antennal scrobe extending to head capsule, with round impression adjacent to ventral lobe of eye. Scales above eyes narrow, white, densest bordering eyes, broader and sparser on vertex, mottled with few tan and brown scales between eyes, white above rostral insertion. *Rostrum*: short (0.88x pronotal length), evenly arcuate, somewhat flattened ventrally at base, cylindrical to apex. Dorsally at base transversely impressed, smooth distal to antennal insertion with somewhat straight longitudinal rows of punctures to apex. Antenna inserted subbasally. *Antenna*: scape short, clavate, with three linear white scales. Funicle with article 1 clavate, longer than article 2, with sparse linear white scales. Articles 2-7 slender, cylindrical; articles 2-4 subequal, 5-7 subequal, short. Club broad, flat, with four distinct articles; 1 ventricose-rostrate with rostrate portion very short, 2-3 ventricose, 4 narrower and shorter than 3, apically rounded. **Prothorax**. *Pronotum*: apically constricted, widest and rounded posterior to constriction, evenly converging to base. Median longitudinal carina an elevated, dorsally flattened crest in anterior two-thirds, reduced posteriorly. Scale pattern with white scales in diffuse arcuate lateral band, longitudinal from posterolateral margin to middle, curving towards middle of apex, a small white macula anterolaterally before apical constriction, and a thin vitta from posterior margin at middle to apex of carinal crest; surrounding scale pattern mottled with white, tan and brown, extending

on lateral face in anterior half, becoming white adjacent to prosternal sheath. Suberect scales tan to brown, in shallow round punctures. *Prosternum*: rostral sheath widest anteriorly, sides converging in anterior third, parallel to junction with coxal rim, converging and flattened to apex. Sheath lateral margins and ventral surface covered with linear white scales.

Mesothorax. Scutellum with sparse setae. *Elytra*: slightly wider than widest part of pronotum, parallel-sided from humerus to apical third, rounded to apex. Pattern with large, roughly triangular fascia of dark coppery brown scales at middle extending from lateral margin of elytra and narrowing to interval 2; scales at base between humeri and in a diffuse thin fascia at declivity dark coppery brown; scales in surrounding areas white. Suberect scales mostly tan, dark brown in darker areas. Interval 9 tumescent in posterior half. Stria with small, shallow punctures, each with a linear scale, scales tan, conspicuously contrasting in dark triangular region. *Mesoventrite*: ventral process short, posterolateral corners deflected posteriorly ventral margin at middle slightly tumescent. Anterior and ventral face and intercoxal region with elongate white linear scales. *Mesanepisternum*: with white scales densest in impression bordering mesepimeron, elsewhere scales and crustose punctures sparse.

Metathorax. *Metaventrite*: ventrally flat, rounded to sides, scales linear and white, becoming broader on lateral face, laterally with scattered crustose punctures. *Metanepisternum*: white scales becoming denser posteriorly, metanepisternal suture with Type I sclerolepidia. **Legs**. Hind femora extending to sternite VII. Procoxae with mesal tuft of sparse linear white scales. All femora ventrally unarmed, sulcate in distal half. Scales linear, white, dorsally tan on profemora, with small tan to brown macula apically on meso- and metafemora. Protibia dilated apically, setal brush covering one-fourth apicoventral surface. Metatibial apex with short curved uncus at posterior margin, inner flange slightly produced, rounded, adjacent to small tooth at anterior margin; apical setal comb short, oblique. Tarsi stout, article 1 less than

twice length of article 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal at sides, V and VI subequal, combined longer than IV, VII tumescent. Crustose punctures scattered throughout each sternite, densest along posterior margin except at middle of sternites III and IV. Scales linear, white.

Variation. Female length 3.62-3.89 mm, width 1.16-1.13 mm, length/width ratio 3.12-3.16, rostrum 0.88-0.98x pronotal length.

Male. Unknown.

Distribution. Mexico (Veracruz).

Material Examined. Two specimens. Holotype female: "El.Palmar,16km.W. Tetzonapa, Ver. MEX. VI-9/15-1948 Werner-Nutting". Paratype: same data as holotype (1♀, ASUCOB).

Etymology. This species is named in honor of John W. Brown, former research entomologist and tortricid moth taxonomist of the United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Lab, whose mentorship inspired my career as an insect systematist.

Figure 3.8. Male terminalia of the *spinolae* group. A) *T. spinolae* aedeagus, dorsal view; B) *T. leptodontus* aedeagus, dorsal view; C) *T. spinolae* aedeagus, lateral view; D) *T. leptodontus* aedeagus, lateral view; E) *T. lathrios* aedeagus, dorsal view.

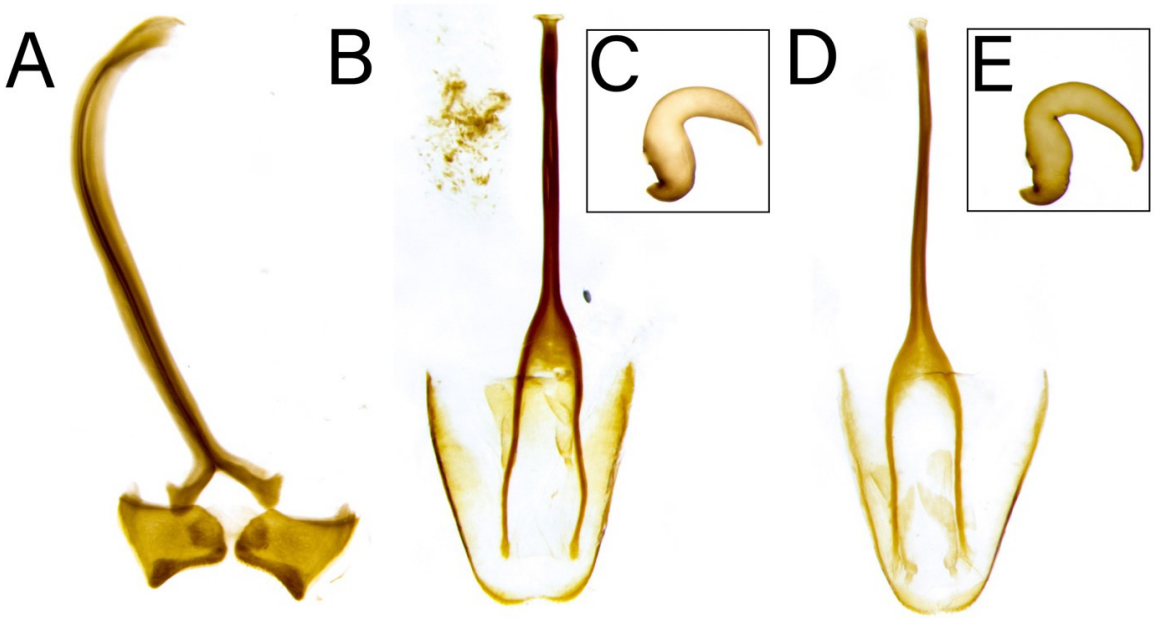

Figure 3.9. Male and female terminalia of the *spinolae* group. A) *T. leptodontus* sternite 8 and spiculum gastrale; B-C) *T. spinolae* female terminalia (B) and spermatheca (C); D-E) *T. leptodontus* terminalia (D) and spermatheca (E).

***Trichodocerus lathrios* Anzaldo, sp. nov.**

Figs. 3.1B, 3.4F, 3.7E–F, 3.8E, 3.25B.

Diagnosis. Most similar to *T. browni*, but with more approximate eyes (Fig. 3.4F) a more irregularly outlined dark triangular elytral patch (Fig. 3.7F), the contrasting light colored scales in the dark elytral patch are the suberect scales on intervals 5, 7 and 9 (not the linear scales of the strial punctures), and the larger apicoventral protibial setal brush.

Description – holotype female. Length 4.02 mm, width 1.28 mm, length/width ratio 3.14. Integument reddish brown, becoming lighter on the legs, rostrum, and antenna. Dorsal scales white, tan, and dark coppery brown; lateral and ventral surfaces with white scales and setae. **Head**. Eyes separated by about half rostral width, ventral lobe small, ending above ventral margin of rostral insertion. Antennal scrobe extending to head capsule, with round impression adjacent to ventral lobe of eye. Scales above eyes narrow, white, densest bordering eyes, with circular bare patch on vertex surrounded by sparse scales; between eyes scales tan, brown, and white, becoming white above rostral insertion. *Rostrum*: short (0.90x pronotal length), evenly arcuate, somewhat flattened ventrally at base, cylindrical to apex. Dorsally at base transversely impressed, smooth distal to antennal insertion with somewhat straight longitudinal rows of punctures to apex. Antenna inserted subbasally. *Antenna*: scape short, clavate, with two linear white scales. Funicle with article 1 clavate, longer than article 2, with sparse linear white scales. Articles 2-7 slender, cylindrical; article 2 longer than 3, 3 and 4 subequal and longer than 5, 5-7 subequal. Club broad, flat, with four distinct articles; 1 ventricose-rostrate with very short rostrate portion, 2-3 ventricose, 4 narrower and shorter than 3, apically rounded. **Prothorax**. *Pronotum*: apically constricted, widest and rounded

posterior to constriction, evenly converging to base. Median longitudinal carina an elevated, dorsally flattened crest in anterior two-thirds, absent posteriorly. Scale pattern consisting of thin, longitudinal stripe of white scales at middle of base extending to apex of median carina and three small lateral white macula in a longitudinal row, at the posterolateral corner, middle, and apex before constriction; surrounding scales on disk tan to coppery brown, on lateral prothoracic face becoming white adjacent to prosternal sheath. Scales adpressed, narrow, white scales broadest, without suberect scales. *Prosternum*: rostral sheath widest anteriorly, sides converging in anterior third, parallel to junction with coxal rim, converging and flattened to apex. Sheath lateral margins and ventral surface covered with linear white scales. **Mesothorax**. Scutellum with sparse setae. *Elytra*: slightly wider than widest part of pronotum, parallel-sided from humerus to apical third, rounded to apex. Pattern with large, roughly triangular fascia of dark coppery brown scales at middle extending from lateral margin of elytra and narrowing to interval 2; scales at base between humeri and in diffuse macuale at declivity darker; scales surrounding darker areas mostly white, roughly in an "X" shape at middle. Suberect scales white to tan in lighter areas, coppery brown in darker areas except scales on intervals 5, 7 and 9 white to tan in dark triangular region. Interval 9 tumescent in posterior half. Stria with small, shallow punctures, each with a linear scale. *Mesoventrite*: ventral process short, posterolateral corners deflected posteriorly, with a small tumescent process on ventral margin at middle. Anterior and ventral face and intercoxal region with elongate white linear scales. *Mesanepisternum*: with white scales in impression mostly bordering mesepimeron and sparse crustose punctures. *Mesepimeron*: white scales in impressions. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides. Vestiture composed of elongate white scales and setae ventrally, becoming broader white scales laterally, laterally with scattered crustose punctures. *Metanepisternum*: white scales becoming denser posteriorly,

metanepisternal suture with Type I sclerolepidia. **Legs**. Hind femora extending to sternite VII. Procoxae with mesal tuft of sparse linear white scales. All femora ventrally unarmed, sulcate in distal third to half, profemur thickened in basal half. Scales linear, white, with tan and brown macula dorsally at apex. Tibiae with white scales dorsally and setae ventrally, protibia becoming gradually wider towards apex, with setal brush covering about one-third apicoventral surface. Metatibial apex with a short, curved uncus at posterior margin, inner flange produced in a small triangular tooth, anterior margin with smaller tooth. Tarsi stout, article 1 less than twice length of article 2, with linear white scales dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternite III and IV subequal in length at sides, V and VI subequal, combined longer than IV, VII slightly tumescent. Crustose punctures scattered throughout each sternite, densest along posterior margin except at middle of sternites III and IV. Scales linear, white.

Female terminalia. Spiculum ventrale elongate, much longer than lamina, expanded at apex. Lamina of sternite 8 sclerotized only at lateral arms, arms bifurcate at base of spiculum ventrale, abruptly converging halfway to posterior margin. Tergite 8 narrow, very weakly sclerotized. Gonostylus of even width throughout.

Male. Length 3.33 mm, width 1.11 mm, length/width ratio 2.99, rostrum 0.70x pronotal length. Similar to female except rostrum shorter, scales on rostrum extending slightly distal to antennal insertion, metaventrite ventrally with denser setae, metatibial apex with uncus at anterior margin, abdominal ventrite III impressed at middle, pygidium narrowly exposed. *Male terminalia*: lateral margins of aedeagus rounded, widest one-third from base. Apex flat, truncate, slightly laterally expanded. Endophallus with posterior patch of small teeth,

anteriorly with elongate patch of small, ovoid, scale-like plates, no transfer apparatus. Tegmen not forming continuously sclerotized ring, sclerotization of ring continuous with elongate parameroid lobes. Spiculum gastrale thick, arcuate, apically expanded, basally slightly asymmetrically bifurcate.

Distribution. The only three known specimens are from Barro Colorado Island, Panama.

Natural History. Host unknown. All observed specimens were collected at light traps.

Material Examined. Three specimens. Holotype female: "Panamá, Isla Barro Colorado Light trap Week 21 M. III N 20-26 V 1987" (PCMENT). Paratype (1): "Panamá, Isla Barro Colorado Light trap Week 14 O. III N 4-10 IV 1990" (1♂, PCMENT). Other specimens: "Panamá, Isla Barro Colorado Light trap Week, 16 M. III N 15-21 IV 1987" (1♀, PCMENT).

Etymology. From the Greek *lathrios* ("stealthy"; Brown 1956) referring to the fact that this is the only species of *Trichodocerus* known from Barro Colorado Island that was not collected during the intensive light-trapping study by Wolda *et al.* (1998), despite the few known specimens having been collected at light traps. The name is treated as a noun in apposition.

II. The *Trichodocerus brevilineatus* group. The two species presently placed in this group are similar in appearance, with short dark elytral stripes at the middle of intervals 3 and 5 and short white stripes anteriorly and posteriorly. *Trichodocerus hespenheidei* in some respects is more similar to species of the *ochromae* group, for example the broader female

eighth tergite (Fig. 3.14F) and scales above the eyes that extend dorsally on the vertex (also in other species groups). Both species are widespread in Central and South America (Figs. 3.26 A, B).

***Trichodocerus brevilineatus* Champion, 1906**

Figs. 3.1C, 3.3E, 3.4G, 3.10A–B, 3.13A, 3.14A, 3.14D-E, 3.26A.

Diagnosis. *Trichodocerus brevilineatus* is most similar in dorsal pattern to *T. hespenheidei* and *T. hybophrictus* with short longitudinal stripes on the elytral intervals but can be easily separated from both by the longer, apically flattened rostrum, more approximate eyes, the more prominent pronotal carina, and the profemur ventrally with a small tooth (unarmed in *T. hespenheidei*). Other differences with *T. hespenheidei* include dark stripe on the third interval is situated more anteriorly, the denser ventral setae in particular on the rostral sheath (without anterior white scales); the elongate, tube-like, anteriorly arcuate endophallic sclerites; the transfer apparatus is without two small anteriorly-directed spines; the third pair of stridulatory plectra on the male seventh tergite is larger than the others (all other observed species have equally sized plectra); the much narrower female eighth tergite (Fig. 3.14D); the produced, curved spermathecal collum (Fig. 3.14E); and the cylindrical gonostylus (narrowed basally in *T. hespenheidei*).

Redescription – female. Length 2.31-4.59 mm, width 0.80-1.68 mm, length/width ratio 2.73-2.99. Integument dark brown, reddish brown on tarsi, rostrum and antennal scape and funicle. Dorsal scales small, apically truncate, emarginate or rounded, white, yellowish white and dark coppery brown, scales larger on the pronotum. Vestiture of lateral and ventral

surfaces mostly white scales and setae. **Head** (Fig. 3.4G). Eyes subcontiguous, separated by ~2 short, linear scales at closest point, with ventral lobe extending to sides of rostrum. Scales above eyes densest along border with eye, limited to small triangular patch of yellowish scales, densest along border with eye, extending dorsally in small triangular patches of sparse scales above each eye. Vertex above scales bare, shining. *Rostrum*: elongate (1.00-1.33x pronotal length), evenly arcuate, ventrally flat, ovoid in cross section in apical half. Dorsally slightly impressed on either side at base and with yellowish scales in impression up to antennal insertion. Smooth, with punctures in longitudinal rows in basal two-thirds, denser and irregular at apex. *Antenna*: Scape clavate. Funicle with article 1 clavate, narrower than scape, shorter than article 2. Articles 2-7 cylindrical; article 2 slightly curved and shorter than 3, article 3 longer than 4, 4 longer than 5, 6 longer than 5 and 7. Club with four distinct articles, 1 and 2 ventricose-rostrate, rostrate portion of 1 elongate, longer than one-third entire article length, rostrate portion of article 2 elongate, about one-third entire article length, article 3 gradually widening, article 4 elongate, fusiform. **Prothorax.** *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina present in anterior half, flattened dorsally. Integument evenly convex on disk around carina. Vestiture consisting of two lateral, complete vittae of white and tan scales, centrally on disk scales brown and interrupted by two lighter complete vittae on either side of the median carina, broadest anteriorly, made up of tan to white scales; posterior margin with thin border of tan scales, thin vitta of tan scales from apex of median carina to posterior margin of pronotum. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging. Coxal rim distinctly raised at junction with sheath, creating lateral triangular processes. Sheath interior and lateral margins covered with dense multifurcate

setae. **Mesothorax**. *Elytra*: Slightly wider than widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Scales small, surrounding integument mostly exposed; pattern mostly mottled white to tan to brown scales with short stripes of dark brown scales at interval 1 posterior to scutellum, 3, 5 and 7 near middle and of varying sizes and sometimes joined by smaller stripes on intervals 2 and 4, intervals 3 and 5 one-third from apex, 9 lateral to humerus, and 9 and 10 about one-third from base. Interval 9 subcostate one-third from apex, interval 10 below narrow, with reduced scales. Striae with deep, round punctures bearing a single seta. *Mesoventrite*: ventral process short, ventrally slightly concave, ventrolateral corners produced somewhat laterally. Anterior face with sparse multifurcate setae, ventral surface and intercoxal region with elongate, fine ventrally produced setae. *Mesanepisternum*: white scales along border with mesepisternum, somewhat receded and separated from rest of sclerite. *Mesepimeron*: scales flat, adpressed, white to yellowish white. **Metathorax**. *Metaventrite*: ventrally slightly convex, rounded to sides. Vestiture sparse, linear, curved white scales at middle, becoming densest at rounded lateral margin with elongate fine setae, smaller and linear laterally below metepisternal suture. *Metanepisternum*: anteriorly with dense, small, linear white scales, larger and sparser at middle, broader, and denser at posterior margin. **Legs**. Hind femora extending to anterior margin of sternite VII. Procoxae with mesal tuft of fine setae. All femora ventrally with a small tooth, with sparse, white adpressed scales becoming larger subapically, then smaller and more linear apically. Hind femur with a lateral or dorsal dark patch one-third from apex. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering one-third of apicoventral surface. Metatibial apex with large uncus arising from posterior apical margin, inner flange produced into small, basally broad tooth closer to anterior margin, anterior margin with adjacent tooth of similar height. Tarsi slender, article 1 three times as long as 2,

articles 1 and 2 with linear white scales dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV equal in length at the sides, V and VI equal in length and combined longer than IV. Pygidium concealed. Crustose punctures present in single row along posterior margin of each sternite except absent medially on sternites III and IV and in multiple rows on sternites V-VII. Vestiture sparse, linear white scales.

Female terminalia (Figs. 3.14D-E). Spiculum ventrale elongate, much longer than lamina, straight, slightly expanded at apex, becoming broader and flatter towards lamina, narrowly bifurcate. Lamina of sternite 8 sclerotized only at lateral arms, gradually diverging posteriorly, with small cluster of setae at apex. Tergite 8 narrow, lightly sclerotized, sclerotization mainly along lateral and posterior margin, posterior margin at middle with small, round emargination. Gonostylus of even width throughout. Spermatheca subfalcate, collum produced and slightly curved, ramus not produced, cornu hooked, becoming slightly narrower towards apex, apex rounded.

Male. Length 3.48 – 4.55 mm width 1.24 – 1.62 mm, length/width ratio 2.80-2.97. Similar to female except rostrum 1.27-1.39x pronotal length, ventrally the elongate, fine setae are denser on the procoxae, meso- and metaventrite, the metaventrite and middle of abdominal sternites III-IV are concave with erect multifurcate setae, the metatibial apex has the uncus more produced anteriorly, anterior margin below middle of apex, with an inner flange produced into a small, apically rounded tooth that is more separate from the small tooth at the anterior margin than in female. *Male terminalia* (Fig. 3.13A): lateral margins of aedeagus of relatively even width throughout, apically converging to rounded point. Endophallus with complex sclerites: posterior sclerite paired, tube-like, anteriorly narrowed and arcuate; paired

curved plates with a ventral anteriorly curved spine; anterior, V-shaped sclerite; transfer apparatus slightly arcuate, bifurcate, diverging anteriorly, with each arm widest anteriorly. Tegmen forming complete, ovoid ring, greatly expanded dorsally, parameroid lobes approximate, inserted on dorsal expansion, manubrium short, broad, apically rounded. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate. Eighth sternite strongly sclerotized posteriorly with fringe of setae.

Distribution. Guatemala, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia. Recorded by Rheinheimer (2011) from French Guiana though the specimen imaged is not *T. brevilineatus*.

Natural history. Host unknown. Most specimens from UV light traps, one with label "on dead branch / 'balsa'".

Material examined. Fifty-seven specimens. Lectotype designation: "Sp. figured. / Bugaba, Panama. Champion. / ♂ / B.C.A. Col. IV. 4. Trichodocerus brevilineatus Champ." Two male specimens are mounted on the same card – the lectotype hereby designated is the specimen on the left, with clear view of the dorsum. Additional specimens: "26.4 Cacao Trece Aguas / Alta V. Paz Guatemala / Schwarz & Barber Coll" (1♂, NMNH); "COSTA RICA: Alajuela San Antonio de los Chiles Hacienda R.y R. B.L.T. 16-I-1995 R. Remmer" (1♀, ASUCOB); "COSTA RICA, Punt,R. F.GolfoDulce,10m,3k.S.Rincon,vi-1991,ma- laise trap,P.Hanson" (1♀, ASUCOB); "COSTA RICA,Her,3k. S.Pto.Viejo,100m.OTS- La Selva,X-1992,P. Hanson,malaise trap" (1♀, ASUCOB); "COSTA RICA: Heredia Pr: La Selva Biol.Sta. 3 km S Pto. Viejo 10°26'N 84°01'W / 14.VI.1991 G. Gentry TREE

TRUNK" (1♀, CHAH); "COSTA RICA: Heredia Pr: La Selva Biol.Sta. 3 km S Pto. Viejo 10°26'N 84°01'W / 18.vii.1982 H.A. Hespenheide ZYGOPINE TREE" (1♀, CHAH); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m, 10°26'N, 84°01'W Jul 1998, INBio-OET / 07 julio 1998 Bosque secundario L/17/414" (1♂ 2♀, MNCR); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m, 10°26'N, 84°01'W Sep 1998, INBio-OET / 03 Setiembre 1998 Bosque secundario L/17/462" (1♀, MNCR); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m, 10°26'N, 84°01'W Oct 1998, INBio-OET / 07 Octubre 1998 L/13/482 Bosque primario" (1♂, MNCR); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m, 10°26'N, 84°01'W Nov 1998, INBio-OET / 03 Nov 1998 L/08/501 Bosque primario" (1♂, MNCR); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m, 10°26'N, 84°01'W Mar 1999, INBio-OET / 30 Mayo 1999 L/13/482 Bosque secundario" (1♂, MNCR); same data as lectotype (4♂ 1♀ 17 unsexed, NHM; 2♂, NMNH); "Panama / Cotype / [folded label] B.C.A. Col. IV. 4. Trichodocerus brevilineatus Champ." (1♀, NMNH); "PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola 9°17'30"N 82°32'41"W H.Wolda Apr.9,1980" (1♀, ASUCOB); same data but dates "Apr.9,1980" (1♀, ASUCOB), "Apr.30/May 5,1980" (1♀, ASUCOB); "Panama: Canal Zone Albrook Forest Site Fort Clayton / Lot No. 178 March 7/8, 1968 R. Hutton Black light trap" (1♀, ASUCOB); "PANAMA, Bocas del Toro, Miramar,sea level, 82°15'W,9°N 24Mar.1979H.Wolda" (1♀, ASUCOB); "CANAL ZONE,Barro Colorado Is. UV trap 1 (3m.high) 1June1978H.Wolda" (1♂, ASUCOB); same data but dates "24 Apr.1978" (1♂, ASUCOB), "14July1978" (1♂, ASUCOB), "20Aug.1976" (1♀, ASUCOB), "10 Sept.1976" (1♂, ASUCOB), "5 Oct1976" (1♀, ASUCOB), "24-X-1977" (1♂, ASUCOB), "26 Oct1978" (1♀, ASUCOB), "29 Oct.1978" (1♀, ASUCOB), "10Nov.1977" (1♂, ASUCOB), "XI-24&25,1977" (1♂, ASUCOB); "CANAL ZONE, Barro Colorado Is.,UV trap 3(26m.high)

14July1978"; same data but dates "26 Oct1978" (1♀, ASUCOB), "10Nov.1978H.Wolda" (1♀, ASUCOB); "Panamá: Canal Zone Barro Colorado Is. 9°10'N 79°50'W / 13.VIII.1978 H.A. Hespenheide" (1♀, CHAH); "COLOMBIA 1300m Tablones Valle FincaLaFlorida / 7 i 1959 JFG Clarke" (1♂, NMNH); "1200' ,Anchicaya Dam, 70km E. Buenaventura, Valle, Colombia, II.17.1970.H.Howden" (1♀, CMNC); "1200' ,Anchicaya Dam, 70km E. Buenaventura, Valle, Colombia, VII.27.1970. H. & A. Howden" (1♀, CMNC); "Ecuador, 700' RioPalenque 47km S St. Domingo Feb.27.1976 H. & A. Howden" (1♀, CMNC); same data as previous but date "Feb 22-27 1976" (1♂, CMNC); "Ecuador Pichincha Puerto Quito 23-IV-83 Eleana Fegan" (1♀, ASUCOB); "ECUADOR,Pich.Santo Domingo (47kmS) Malaise 22-28July 1976 Jeffrey Cohen" (1♀, NMNH); "Ecu.: Pich: Prov. 47km S. Sto.Domingo Rio Palenque Sta. 2-14.VII.1975 A. Forsyth" (1♀, CMNC); "ECUADOR: Orellana Yasuni Biol. Res. Sta. ca. 0°40'S/76°24'W XI-1 to XI-7-2002 coll: E. Fisher, malaise" (2♂, ASUCOB); "ECUADOR,Napo.P., Est.Cient.Yasuni,00° 40'28"S, 76°38'50"W, IX-5-10-1999,215m. / E.G.Riley" (1♀, ASUCOB); "ECU: Pich. 500m Tinalandia, 16km SE.Sto. Domingo 4-14.vi.1976 S.& J.Peck" (1♂, ASUCOB); "PERU: Junín Pampa Hermosa Lodge 1-6-IV-2011 J.B. Heppner, C.Carrera" (1♂, ASUCOB); "PERU Madre de Dios nr. PuertoMaldonado Explorer's Inn 22 Aug.1985 J.F.Cornell UV&HID-Merc.light" (1♂, ASUCOB); "BOLIVIA,Cbb.,6mi. N. Villa Tunari April 1,1978 C.W.&L.B.O'Brien (5♂, ASUCOB).

Etymology. The specific epithet "brevilineatus" is likely derived from the Latin words *brevis*, meaning "short", and *lineatus*, meaning "of a line", and is likely in reference to the short, unconnected longitudinal stripes of dark scales on the elytra (Brown 1956).

***Trichodocerus hespenheidei* Anzaldo, sp. nov.**

Figs. 3.4H, 3.10C–D, 3.13B, 3.14B, 3.14F-G, 3.26B.

Diagnosis. This species is very similar in general appearance to *T. brevilineatus* but can be separated by several characters, the most obvious being the lighter integument, more widely separated eyes, the scales above the eyes extending farther on the vertex, the reduced pronotal carina, the vestiture on the head above the eyes not being limited to the border with the eyes, the prosternal rostral channel anteriorly with white scales, the absence of a miniscule tooth on the ventral surface of the profemora, the dark lines on elytral intervals 3 and 5 being relatively even, the longer second funicular article, and the shorter rostrate portions of the first two antennal club articles. Other differences include the endophallic transfer apparatus bearing two anteriorly directed spines, a broader female eighth tergite (Fig. 3.14F), a basally narrow gonostylus, and an unproduced spermathecal collum (Fig. 3.14G).

Description – holotype female. Length 4.70 mm, width 1.68 mm, length/width ratio 2.8. Integument light reddish brown. Dorsal scales small, apically truncate, emarginate, or rounded white, tan and dark brown, scales larger on the pronotum. **Head**. Eyes separated by ~3 narrow scales at closest point, with ventral lobe broad, extending below ventral margin of rostral insertion. Vestiture above eyes in sparse, dorsally rounded patch of small yellow scales, densest along border with eye, becoming smaller at closest distance between eyes, and then larger and yellowish white to rostral base. *Rostrum*: about as long as pronotum (1.03x pronotal length), evenly arcuate, widest at base, somewhat flattened ventrally, roughly cylindrical to apex. Dorsally slightly impressed on either side at base and with yellowish white scales in impression slightly proximal to antennal insertion. Smooth, with minute

punctures in fairly regular longitudinal rows. *Antenna*: scape clavate. Funicle with article 1 clavate, narrower than scale, shorter than article 2. Articles 2-7 cylindrical; article 2 slightly curved and longer than 3, 3 longer than 4, 4 longer than 5, 5 and 5 subequal and longer than 7. Club with four distinct articles, 1 and 2 ventricose-rostrate, rostrate portions short, about one-fourth total article length, article 3 gradually widening at base and rounded apically, article 4 elongate, narrow, fusiform. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina faint, present in anterior half. Integument evenly convex on disk around carina. Vestiture cosisting of two lateral, complete vittae of white and tan scales, centrally on the disk scales mostly narrow and tan with two complete white and tan vittae on either side of the carina, scales of vittae broader than surrounding scales. White and tan scales extending down lateral face of prothorax mostly in anterior half, with a small brown macula just before apical constriction. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging. Sheath interior and lateral margins with erect, curved setae. **Mesothorax**. *Elytra*: slightly wider than widest part of pronotum, parallel-sided from humeri to one-third from apex, rounded to apex. Integument slightly impressed at interval 2 one-third from base. Scales small, surrounding integument mostly exposed; pattern consisting of alternating longitudinal stripes of white and brown scales. Short brown stripes occur basally on interval, faintly on intervals 3 and 5 subbasally, at intervals 3, 5 and 7 near middle, and about one-fourth from elytral apex at interval 3, 5, 7, and 9. Areas between brown stripes white or tan. A small brown spot present on interval 2 adjacent to the posterior margin of the stripe at interval 3. Interval 6 white, scales imbricate basally at humerus. Interval 9 subcostate one-third from apex, interval 10 below narrow, with reduced scales. Striae with deep, large ovoid punctures bearing a single

seta. *Mesoventrite*: ventral process short, ventrally concave. Anterior face with dense, fine setae, ventral surface and intercoxal region with dense, elongate, erect setae. *Mesanepisternum*: border with mesepisternum, somewhat receded and separated from rest of sclerite. *Mesepimeron*: scales flat, adpressed, white. **Metathorax**. *Metaventrite*: flattened ventrally, rounded to sides. Vestiture ventrally consisting of linear white scales, denser and broader laterally. *Metanepisternum*: anteriorly with dense, small, linear white scales, becoming larger and sparse in front of anterior margin, then broader denser towards posterior margin. **Legs**. Hind femora extending to anterior margin of sternite VII. Procoxal mesal tuft consisting of white scales and elongate setae. Femora ventrally with minute tooth, with sparse, white to yellowish white adpressed scales becoming larger subapically, then smaller and more linear apically. Tibia dorsally with dense yellowish white scales, ventrally with setae. Metatibial apex with large uncus arising from posterior margin, the inner flange produced in a broad triangular tooth, and a smaller tooth at the anterior margin. Protibial setal brush covering one-fourth apicoventral surface of protibial. Metatibial apex with a large curved uncus arising from outer apical angle, and two smaller teeth arising at apex between uncus and inner apical angle, the one closest to uncus larger; middle tooth larger on pro- and mesotibial apices. Apical tibial setal comb short, oblique. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally, densest at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV equal in length at the sides, V and VI equal in length and combined longer than IV. Crustose punctures present along posterior margin of each sternite except absent medially on sternites III and IV, present in multiple rows on sternites V-VII and laterally at the sides on III and IV. Scales linear, white.

Female terminalia (Fig. 3.14F-G). Spiculum ventrale elongate, much longer than lamina, straight, rounded at apex, becoming broader and flatter towards lamina, narrowly bifurcate. Lamina of sternite 8 sclerotized only at lateral arms, subparallel, apex rounded, with cluster of setae ventrally at apex. Tergite 8 broad, lightly sclerotized, sclerotization mainly along lateral and posterior margin, posterior margin entire. Gonostylus narrowest at base. Spermatheca J-shaped, collum and ramus not produced, cornu hooked, becoming slightly narrower towards apex, apex rounded.

Variation. Female length 3.80-4.70 mm, width 1.34-1.68 mm, length/width ratio 2.80-2.83. Male length 3.58 mm, width 4.30 mm, length/width ratio 2.68-2.8, rostrum 0.96-1.07x length of pronotum. Male as female but the yellowish white scales at the base of the rostrum extending slightly more distally to the antennal insertion, the metatibial uncus is more directed over anterior margin of the tibial apex, and abdominal ventrites III-IV are medially impressed. *Male terminalia* (Fig. 3.12B): lateral margins of aedeagus gradually diverging from base, widest subapically, narrowed to rounded apex. Endophallus with three paired, mesally denticulate plate-like sclerites becoming smaller anteriorly; transfer sclerite arcuate, ventrally acuminate, dorsally expanded, truncate, with two small spines projecting anteriorly. Tegmen forming complete, ovoid ring, dorsally expanded, parameroid lobes separate, inserted at dorsal expansion, manubrium broad, short and flat. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Distribution. Costa Rica, Panama, Colombia, Ecuador, and Peru.

Natural History. Specimens have been reared from logs of balsa, *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Malvaceae: Bombacoidea), in Costa Rica.

Material examined. 46 specimens. Holotype female: "COSTA RICA: Heredia Pr: La Selva Biol. Sta. 3 km S Pto. Viejo 10°26'N 84°01'W / 13.v.1990 H.A. Hespenheide BALSA" (NHM). Paratypes: same as holotype (1♂ 1♀, CHAH); same data as holotype but dates "18.v.1990" (1♀, CHAH), "19.v.1980" (1♀, CHAH), "20.v.1990" (1♂, CHAH), "11.iv.1983" (1♀, CHAH); same data as holotype but second label "18.VII.1994 H.A. Hespenheide OCHROMA LEAF UNDERSIDES" (1♂ 1♀, CHAH); same data as holotype but second label "10-X-2005 H.A. Hespenheide" (1♀, CHAH); first label same as holotype, plus " / 23.VII/1994 H.A. Hespenheide / BALSA LEAF" (2♀, CHAH); "COSTA RICA: Heredia: Est. Biol. La Selva, 50-150m. 10°26'N 84°01'W / 7-IX-2006 H.A. Hespenheide" (1♂, CHAH); "COSTA RICA: Heredia 10k.S.E.La Virgen, 450-550m, 10°20'N 84°05'W 17-21.III.2003, R. Anderson INBio-OET-ALAS transect beating along trails" (1♀, CMNC); "COSTA RICA: Heredia, Est. Biol. La Selva, 50-150m. 10°26'N 84°01'W Nov. 1997 Coll. L. M. LaPierre" (1♂, CHAH); "COSTA RICA, Heredia Est. Biol. La Selva 50-150m, 10°26'N 84°01'W, INBio, OET / 1.viii.95-17.i.1996 Thunes/Vargas / Primary forest GIS 1000.950 Host: *Ochroma pyram.* Log 8" (1♂ 1♀ on same pin, CHAH); "COSTA RICA, Heredia Est. Biol. La Selva 50-150m, 10°26'N 84°01'W, INBio, OET / 1.viii.95-17.i.1996 Thunes/Vargas / Primary forest GIS 1000.950, log 2 *Ochroma pyrmidale* / Primary forest GIS 1000.950 Host: *Ochroma pyram.* Log 2" (2♂ on same pin, CHAH); "COSTA RICA, Heredia Est. Biol. La Selva 50-150m, 10°26'N 84°01'W / 1.viii.95-17.i.1996 Thunes/Vargas / Primary forest GIS 1000.950, log 8 *Ochroma pyrmidale*" (2♂ 1♀ on same pin, 1♂ 1♀ on same pin, CHAH); same data as previous but third label reads "log 2" (2♂ on same pin, CHAH); same data as

previous but third label "Primary forest GIS 1000.950 Host:*Ochroma pyram.* Log: 1" (1♂ 1♀ on same pin, CHAH); "COSTA RICA, Heredia: Est.Biol.La Selva. 50-150m.10°26'N 84°01'W Mar 1998, INBio-OET / 17 Mar 1998 L/08/334 Bosque primario" (1♂, MNCR); "COSTA RICA, Heredia: Est.Biol.La Selva. 50-150m.10°26'N 84°01'W Aug 1998, INBio-OET / 06 Agosto 1998 Bosque secondario L/18/439" (1♀, MNCR); "COSTA RICA, Heredia: Est.Biol.La Selva. 50-150m.10°26'N 84°01'W May 1999, INBio-OET / 4 Mayo 1999 Bosque secondario L/18/631" (1♀, MNCR); "PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola / 9°17'30"N, 82°32'41"W H. Wolda Mar.27,1980" (1♀, ASUCOB); same data as previous but dates "Jan.20,1980" (1♂, ASUCOB), "Mar.1,1980" (1♂, ASUCOB), "Mar.25,1980" (1♀, ASUCOB); "PANAMA, Bocas del Toro, Miramar, sea level, 82°15'W,9°N 18Nov.1978H.Wolda" (1♀, ASUCOB); same data as previous but dates "11Apr.1979" (1♂, ASUCOB), "16 Jan.1979" (1♂, ASUCOB), "31.X. 1979" (1♂, ASUCOB); "Panamá, Isla Barro Colorado Ligth trap Week, 27 N. I N 5-11 VII 1989" (1♀, PCMENT); "CANAL ZONE,Barro Colorado Is.,UV trap 3(26m.high) 18Apr.1978H.Wolda" (1♀, ASUCOB); "Bugaba, 800-1500 ft. Champion. / B.C.A. Col. IV.4. Trichodocerus brevilineatus. Champ." (1♀, NHM); "1200' ,Anchicaya Dam, 70km E. Buenaventura, Valle, Colombia, VII.26.1970. H. & A. Howden" (1♀, CMNC); "Ecu.: Pich. Prov. 47km S. Sto. Domingo Rio Palenque Sta. 18-30.V.1975 S. & J. Peck" (1♀, CMNC); "PERU Madre de Dios nr. PuertoMoldonado Explorer's Inn 22 Aug.1985 J.F. Cornell UV&HID-Merc.light" (1♀, ASUCOB).

Etymology. This species is named in honor of weevil taxonomist Henry Hespenheide, who collected the holotype of this species and provided the rearing records.

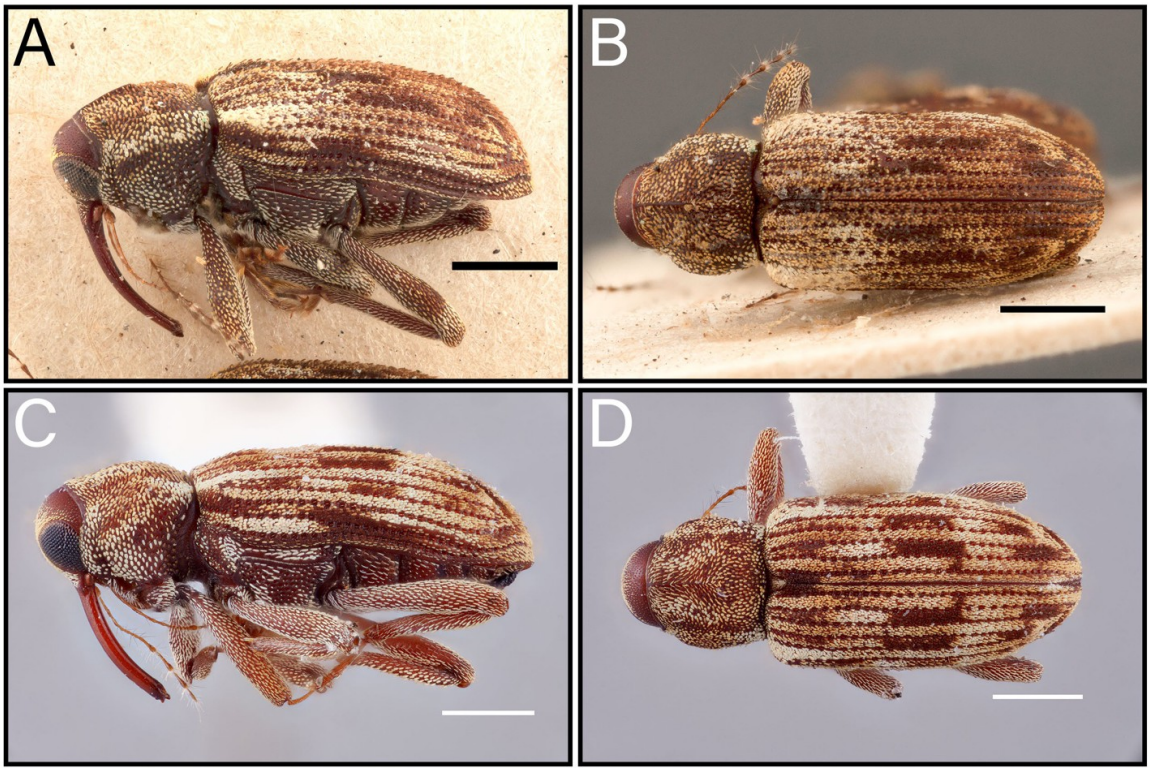

Figure 3.10. Dorsal and lateral habitus of species in the *brevilineatus* group. A-B) *T. brevilineatus* lectotype male, image shows right side of specimen, digitally flipped for ease of comparison; C-D) *T. hespenheidei* holotype female.

III. The *Trichodocerus ochromae* group. This group is composed of five new species and can be readily distinguished by the dense yellow to yellowish white dorsal vestiture. Within the group, the three South American species (*T. gorgonarium*, *T. musathrus* and *T. prionasceles*) can be easily separated from the Central American species by having basally toothed tarsal claws, a short ventral process of the metaventrite, and a large triangular tooth in the anterior half of the tibial apex in females while the Central American species (*T. ochromae* and *T. atheatomerus*) have basally angularly dilated tarsal claws (as in other *Trichodocerus* species), a prominent process of the metaventrite, and the inner flange of the tibial apex produced in an uncus-like hooked tooth.

***Trichodocerus ochromae* Anzaldo, sp. nov.**

Figs. 3.1D, 3.4I, 3.11A–B, 3.13C, 3.14C, 3.14H-I, 3.27A.

Diagnosis. This species is most similar to *T. atheatomerus*, sharing the simple tarsal claws and the protuberant ventral process of the mesoventrite. It can be separated by the distinctly separated fourth article of the antennal club, the vertical (not anteriorly directed) ventral process of the mesoventrite, and the subapically constricted spermathecal cornu (Fig. 3.14I).

Description – holotype female. Length 3.35 mm, width 1.26 mm, length/width ratio 2.65. Integument reddish brown, becoming lighter on tarsi and rostral apex and lightest on antennae. Dorsal scales flat, apically rounded, and linear, suberect mostly yellow scales with small brown elytral maculae. **Head**. Eyes subcontiguous, separated by 5 narrow scales at closest point, ventral lobe slight, extending to ventral margin of rostrum. Scales above eyes in dense, dorsally rounded patch of imbricate yellow scales, scales becoming smaller and

sparser farther from eyes. Scales whitish yellow between eyes and above rostral insertion. *Rostrum*: moderately elongate (1.57x pronotal length), evenly arcuate, widest at base, somewhat flattened ventrally, roughly cylindrical to apex. Dorsally slightly impressed on either side at base. Smooth, densely punctate from antennal insertion to apex, briefly organized into straight rows, irregularly punctate to apex. Scales whitish yellow, present basal to rostral insertion. *Antenna*: scape short, clavate. Funicle with article 1 clavate, narrower and shorter than scape. Articles 2-7 cylindrical; article 2 longer than 3, 3 longer than 4, 4 longer than 5, 6 slightly longer than 5 and 7. Club with four distinct articles, 1 and 2 ventricose-rostrate with apical portion very short, about one-quarter length of whole article, 3 with very short basal stalk, evenly rounded at sides to apex, 4 with short basal stalk, ovoid, apically rounded. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina very faint near middle. Integument mostly evenly convex on disk, slightly impressed anterolaterally. Vestiture consisting of dense, flattened, adpressed yellow scales and suberect, cylindrical yellow scales arising from shallow, round punctures. Anterior to elytral interval 4 in a short oblique patch scales smaller and surrounding integument exposed. Posterolateral corners and at posteromedial margin anterior to scutellum with a few white scales, those at posterolateral corners extending in a somewhat oblique band laterally on prothorax, extending to anterior margin and ventrally above procoxae. *Prosternum*: rostral sheath widest anteriorly, slightly constricted one-third from anterior margin, convergent to apex except for slight dilation at junction with coxal rim. Sheath interior and lateral margin with linear white scales. **Mesothorax**. *Elytra*: wider than prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument very slightly, transversely impressed one-fourth from base from suture to interval 4. Vestiture mostly dense, yellow,

imbricate scales with three brown maculae. Maculae composed of small, coppery brown adpressed scales with surrounding integument exposed, at intervals 3-4 at middle, interval 5 one-third from apex and interval 6-7 one-fourth from base. Suberect, cylindrical, yellow scales in single row along each interval, not present in brown maculae or on intervals 10 and 11 until just before apex. Interval 9 expanded, tumescent and subcostate starting at middle of elytra, scales present along inner margin of interval, outer margin glabrous; interval 10 below narrow, with reduced scales. Striae with small round punctures bearing a single seta. *Mesoventrite*: ventral process vertical, narrow, ventrally emarginate at middle, ventrolateral corners rounded. Anterior face with sparse, adpressed, white multifurcate setae, posterior face ventrally with posteriorly directed multifurcate setae. Intercoxal region flat. *Mesanepisternum*: sclerite divided by oblique, arcuate ridge, anteriorly and ventrally glabrous, with white scales bordering mesepimeron. *Mesepimeron*: scales flat, adpressed, white. **Metathorax**. Scales sparse, posteriorly directed, white. *Metaventrite*: ventrally slightly convex, rounded to sides. Scales linear and sparse ventrally at middle, wider and flattened to sides. *Metanepisternum*: anteriorly with dense, small, linear white scales becoming a single row of scales until middle, posterior half with broader, flat white scales. **Legs**. Slender, elongate, hind femora extending to anterior margin of sternite VII. Procoxae without mesal setal tufts. Femora ventrally unarmed, with sparse, white adpressed scales becoming smaller and linear at apex. Tibia dorsally with dense white scales, ventrally with sparse setae. Metatibial apex with narrow, hooked uncus at posterior margin with apex projecting over middle of tibial apex, inner flange produced into a flattened, elongate tooth, the base broader than base of uncus, and anterior margin with small tooth. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternite III at sides slightly longer than IV, V and VI equal in length and

combined longer than IV. Crustose punctures present along posterior margin of each sternite, not present medially on sternites III and IV, sternites V and VI with multiple rows. Vestiture sparse, mostly flat white scales with few linear white scales intermixed.

Female terminalia (Fig. 3.14H-I). Spiculum ventrale elongate, much longer than lamina, gradually widening towards apex. Lamina of sternite 8 sclerotized only at lateral arms, arcuate, somewhat laminate at base and again at middle, apex rounded, with cluster of setae ventrally at apex. Tergite 8 broad at base, narrowing towards apex. Gonostylus of even width throughout. Spermatheca J-shaped, collum and ramus not produced, cornu hooked, thickest at bend, abruptly constricted along ventral margin subapially, apex rounded.

Variation. Female length 2.51-3.7 mm, width 1.02-1.39 mm, length/width ratio 2.46-2.68, rostrum 1.51-1.65x pronotal length. The median longitudinal carina on the pronotum very faint in middle or absent. The size of the three basal pronotal white patches varies from just a few scales and barely discernable as in the holotype to extending about one-fourth to anterior margin. Brown elytral macula also of varying sizes: macula at middle of intervals 2 and 3 sometimes extending slightly on interval 2 at posterior margin of macula; macula at interval 5 sometimes extending from 4-6; macula at interval 7 sometimes extending to interval 8. Some specimens with a short brown streak posterior to scutellum on interval 1. *Male*: length 2.69-3.35 mm, width 1.02-1.26 mm, length/width ratio 2.63-2.66. As female except rostrum shorter (1.28-1.33x pronotal length).

Distribution. This species has been collected in low elevation forests in Panama (Bocas del Toro, Colón, Darién, Panamá).

Material Examined. Twenty specimens. Female holotype: "PANAMÁ: Las Cumbres 9°06'N, 79°32'W 23 Jan. '76 H. Wolda -at light-" (NMNH). Paratypes (17): same data as holotype but date "5 Dec '74" (1♂, NMNH); "PAN:Panama LasCumbres UVtrap June 25 1976 H. Wolda" (1♂, ASUCOB); same data as previous but date "July 25 1976" (1♂, ASUCOB); "MojingaSwamp FtShermanCZ I-3-1952 / F.S. Blanton Collector" (1♀, NMNH); "5 mi NW Gamboa Panamá, C.Z. 27 Jun. '70 H.P. Stockwell / on underside of Balsa leaf" (1♂, ASUCOB); "PANAMA,ColonP. Sabanita VII-1-1974C.W.&L. O'Brien &Marshall" (1♂, ASUCOB); "Panama: Canal Zone Albrook Forest Site Fort Clayton / May 25/26, 1967 Hutton & Llaurado Blacklight Trap" (1♀, ASUCOB); "Panamá, Isla Barro Colorado Light trap Week, 34 M. II N 19-25 VIII 1987" (1♀, PCMENT); "Panamá, Isla Barro Colorado Light trap Week 46 Q. I N 11-17 XI 1992" (1♀, PCMENT); "CANAL ZONE,Barro Colorado Is.,UV trap 1(3m.high) 4 Dec1976H.Wolda" (1♀, ASUCOB); same data as previous but dates "18May1977" (1♀, ASUCOB), "16June1977" (1♀, ASUCOB); "CANAL ZONE,Barro Colorado Is.,UV trap 3(26m.high) 18Jan.1978H.Wolda" (1♀, ASUCOB); same data as previous but date "9-10-V 1985" (1♂, ASUCOB); "PANAMA, Bocas del Toro, Miramar, sea level, 82°15'W,9°N 19Apr.1979H.Wolda" (1♂, ASUCOB), "PANAMÁ: Darién Pr. Path off Interamerican Hwy nr. Canglón apiario; on underside of *Ochroma pyramidale* leaf; 8.31135, -77.806 28.vi.2015. leg. S.S. Anzaldo" (1♂ 1♀, SSAC).c Additional specimens: "PAN:Panama LasCumbres UVtrap June 15 1976 H. Wolda" (1♀, ASUCOB); "PANAMA,Pan., Las Cumbres H.Wolda,UV trap 24-30-XII-1982" (1, ASUCOB);

Natural History. This species has been collected on the underside of foliage of *Ochroma pyramidale*. Other examined specimens collected at UV lights.

Etymology. The specific epithet *ochromae* has a twofold meaning referring to both the likely host plant *Ochroma pyramidale* and also its yellow vestiture, with *Ochroma* being derived from the Greek *okros* ("yellow") (Brown 1956). The the yellow dorsal scales are unique for the *ochromae* species group.

***Trichodocerus atheatomerus* Anzaldo, sp. nov.**

Figs. 3.4J, 3.11C–D, 3.13D, 3.14J-K, 3.27A.

Diagnosis. This species can be separated from all other species of *Trichodocerus* in having the fourth article of the club incompletely separated from the third. In addition, from *T. ochromae* it can be separated by the larger size, slightly anteriorly-directed process of the mesoventrite, and the spermathecal cornu that is of relatively even width throughout.

Description – holotype female. Length 3.71 mm, width 1.37 mm, length/width ratio 2.71. Integument reddish brown, lighter on tarsi and antennae. Dorsal scales mostly flat, apically rounded to truncate, and linear, suberect mostly yellow setae with brown elytral maculae. **Head**. Eyes subcontiguous, separated by one-third width of rostrum at antennal insertion, ventral lobe slight, extending to ventral margin of rostrum. Vestiture above eyes in dense, dorsally rounded patch of imbricate yellow scales, scales becoming smaller and sparser farther from eyes. Scales between eyes narrow, linear, whitish yellow, becoming wider above rostral insertion. *Rostrum*: moderately elongate (1.54x pronotal length), evenly arcuate, widest at base, cylindrical to apex. Dorsally slightly impressed on either side at base. Smooth, faintly, densely, irregularly punctate from antennal insertion to apex. Scales whitish yellow, present basally before rostral insertion. *Antenna*: scape short, clavate. Funicle with article 1 clavate,

narrower and shorter than scape. Articles 2-7 cylindrical; articles 2 and 3 subequal and longer than 4, 4 longer than 5, 5-7 subequal. Club with 3 apparent articles, 1 and 2 ventricose-rostrate with apical portion very short, 3 and 4 together evenly rounded at sides, fusiform. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina absent. Integument evenly convex on disk. Vestiture consisting of dense, flattened, adpressed yellow scales, becoming sparser and with more integument exposed around centrally and towards anterior margin at middle where scales are short and linear, and suberect cylindrical scales arising from shallow, round punctures. Posterolateral corners with a few white scales along basal margin, extending laterally on prothorax above procoxae, becoming yellow until anterior margin. *Prosternum*: rostral sheath widest at base, roughly triangular, only very slightly constricted one-third from anterior margin and very slightly dilated at junction with coxal rim. Sheath interior and lateral margin with linear white scales. **Mesothorax**. *Elytra*: wider than prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument very slightly impressed on interval 2 one-third from base. Vestiture mostly dense, yellow, imbricate scales with a macula on interval 3 composed of smaller, yellow-brown scales with integument surrounding scales exposed. Suberect, cylindrical, yellow scales in single row along each interval, not present on intervals 10 and 11 until just before apex. Interval 9 expanded, subcostate starting at middle and extending until one-third from apex, scales present along inner margin of interval, outer margin mostly glabrous; interval 10 below narrow, with reduced scales. Striae with small round punctures bearing a single seta. Interval 3 at base narrower than 2 and 4, becoming wider than both one-third from base. *Mesoventrite*: Ventral process narrow, prominent, apically curving anteriorly, truncate along ventral margin, posterolateral corners rounded. Anterior face with

sparse, linear white scales, posterior face with thicker, posteriorly directed white scales. Intercoxal region tumescent. *Mesanepisternum*: sclerite divided by oblique, arcuate ridge, anteriorly and ventrally glabrous, with white scales bordering mesepimeron. *Mesepimeron*: scales flat, adpressed, whitish yellow. **Metathorax**. Scales posteriorly directed, white. *Metaventrite*: ventrally flattened, rounded to sides. Ventrally scales absent except linear white scales along anterior and posterior margin, centrally with sparse setae, laterally scales broad, flat and white, becoming denser and narrower between meso- and metacoxae. *Metanepisternum*: anteriorly with dense, small, linear white scales becoming a single row of scales until middle, posterior half with broader, flat white scales. **Legs**. Slender, elongate, hind femora extending to sternite VI. Procoxae with mesal setal tuft. Femora ventrally unarmed, with sparse, white adpressed scales becoming smaller and more linear at apex. Tibia dorsally with dense whitish yellow scales, ventrally with sparse setae. Pro- and mesotibia ventrally slightly expanded at middle, protibial setal brush small, covering one-fourth tibial length. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternite III at sides slightly longer than IV, V and VI equal in length and combined longer than IV. Crustose punctures present in single row along posterior margin of each sternite. Vestiture sparse, mostly flat white scales with few linear white scales intermixed.

Female terminalia (Figs. 3.14J-K). Spiculum ventrale elongate, much longer than lamina, gradually widening towards apex. Lamina of sternite 8 sclerotized only at lateral arms, arms somewhat laminate at base, sinuate, narrowing posteriorly, with cluster of setae ventrally at apex. Tergite 8 broad at base, narrowing towards truncate apex. Gonostylus of even width throughout. Spermatheca (Fig. 3.14K) J-shaped, collum and ramus not produced and widely

separated, cornu hooked, of relatively even width, rounded at apex.

Variation. Female body length 3.71-4.02 mm, width 1.36-1.43 mm, length/width ratio 2.67-2.82, rostral length/pronotal length ratio 1.53-1.56. A slight pronotal carina is evident in the anterior half in all paratypes. The prothorax laterally has more white scales in some specimens. The specimen from Rancho Quemada, Osa Peninsula has a more distinct elytral pattern, with the macula extending from interval 2-4, and additional maculae on interval 5 about one-third from base, interval 4 posterior to the previous macula, and on interval 6 about one-third from base; other paratypes have an elytral pattern more similar to the holotype. The specimen from Rancho Quemada, Osa Peninsula also has denser scales on the metanepisternum, not being confined to a single row anteriorly. Male unknown.

Distribution. Costa Rica (Guanacaste, Puntarenas).

Natural history. One specimen is labeled as being reared from a *Cecropia peltata* L. petiole though this is most likely mislabeled (B. Jordal, personal communication).

Material Examined. Four specimens. Holotype female: "3km NO de Nacaome, 100m, P. N. Barra Honda, Prov. Guan., COSTA RICA. 3 a 30 may 1993. M. Reyes L-N-239000, 386000" (MNCR). Paratypes: same data as holotype (1♀, MNCR); "Rancho Quemado, 200m, Península de Osa, Prov. Punt. COSTA RICA. 9 a 28 feb 1993. A. Gutiérrez. L-S 292500, 511000" (1♀, MNCR); "COSTA RICA; Puntarenas Manuel Antonio N.P. 30 m 11 Sept. 1994 Leg: B. Jordal Ex: *Cecropia peltata* petiole" (1♀, ASUCOB).

Etymology. The specific epithet is derived from the Greek *atheatos*, meaning "secret" and *meros* meaning "part" (Brown 1956), referring to the fourth article of the club which is fused with the third article in this species, giving the club the appearance of having only three articles.

***Trichodocerus musathrus* Anzaldo, sp. nov.**

Figs. 3.4K, 3.12E–F, 3.13E, 3.27A.

Diagnosis. This species is most similar in appearance to *T. gorgonarium* and *T. prionasceles* in the less vibrantly yellow dorsum, the toothed tarsal claws and large triangular tooth at the anterior margin of the tibial apices. *Trichodocerus musathrus* is particularly similar to *T. gorgonarium*, indistinguishable based on the male genitalia and similar in the patterns of the prothorax and elytra but can be separated by the antennal funicle having the second and third articles subequal in length, the temones fused with the aedeagus, and an endophallic transfer sclerite that is a ring with an acuminate process.

Description – holotype female. Length 3.20 mm, width 1.10 mm, length/width ratio 2.91. Integument reddish brown, becoming lighter on distal half of tibiae, tarsi, and antennae. Dorsal scales mostly yellow to yellowish white. **Head**. Eyes subcontiguous, separated by ~5 narrow scales at closest point, ventral lobe slightly produced, broad, extending to ventral margin of rostrum. Vestiture above eyes in dense, dorsally rounded patch of imbricate yellow scales, becoming smaller and sparser farther from eyes. Scales narrow between eyes, becoming yellowish white above rostral insertion. *Rostrum*: moderately elongate (1.73x pronotal length), evenly arcuate, widest at base, flattened ventrally. Dorsally slightly

impressed on either side at base and with yellowish white scales in impression up to antennal insertion. Smooth, with minute irregular punctures to apex. *Antenna*: Scape short, clavate. Funicle with article 1 clavate, narrower than scape, shorter than article 2. Articles 2-7 cylindrical; articles 2 and 3 subequal in length, longer than 4, 4 longer than 5, 5 and 6 subequal, longer than 7. Club with four distinct articles, 1 and 2 ventricose-rostrate, apical rostrate portion of article 1 short, about one-quarter total article length, apical rostrate portion of article 2 short, less than one-quarter total article length, article 3 evenly rounded at sides, article 4 basally stalked, ovate. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina faint, present subapically only in anterior half. Integument mostly evenly convex on disk, slightly impressed anterolaterally. Scales on disk yellow, densest at the posterior margin in thin longitudinal stripe above the scutellum and elytral interval 1, subapically in a circular patch on either side of median carina, and in complete vitta above elytral interval 5; adjacent regions with scales sparser and surrounding integument exposed. Scales becoming broader and yellowish white at sides, encircling small central area of crustose punctures. *Prosternum*: rostral sheath widest anteriorly, slightly constricted one-third from anterior margin, convergent to apex except for slight dilation at junction with coxal rim, apically flattened. Sheath interior with sparse linear white scales and laterally with dense, broader white scales. **Mesothorax**. *Elytra*: wider than prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument slightly impressed on interval 2 one-fourth from base. Vestiture mostly composed of sparse, flattened scales with indistinct pattern consisting of small patches of denser, imbricate scales or darker patches composed of sparser, slightly darker scales with more integument exposed. Lighter patch of denser scales present on humeri, apex of intervals 4-6, and surrounding

darker oblique patch on intervals 2-5. Suberect, cylindrical, yellowish white scales in single row along each interval, not present on intervals 10 and 11 until just before apex. Interval 9 tumescent, subcostate in middle third, scales present along inner margin of interval, outer margin shining, with single row of small scales; interval 10 below narrow, with reduced scales. Striae with deep ovoid punctures each bearing a single seta. *Mesoventrite*: ventral process short, not produced below intercoxal region, ventrally truncate with ventrolateral corners pointed. Anterior face with dense, small multifurcate setae, ventrally with elongate, erect linear white scales. Intercoxal region flat. *Mesanepisternum*: sclerite divided by oblique, arcuate ridge, anteriorly and ventrally glabrous, with broad yellowish white scales bordering mesepimeron. *Mesepimeron*: scales flat, adpressed, yellowish white. **Metathorax**. Scales sparse, posteriorly directed, white. *Metaventrite*: ventrally flat, rounded to sides. Vestiture absent ventrally at middle, surrounded by linear white scales, wider and flattened at rounded lateral margin, smaller and sparser below metanepisternal suture. *Metanepisternum*: anteriorly with dense, small, linear white scales becoming a single row of scales until middle, posterior half with broader, flat white scales. **Legs**. Slender, elongate, hind femora extending to anterior margin of sternite VII. Procoxae with small mesal setal tuft. Femora ventrally unarmed, with sparse, yellowish white adpressed scales becoming larger subapically, then smaller and more linear apically. Tibia dorsally with dense yellowish white scales, ventrally with sparse setae. Protibial setal brush small, covering one-third ventral surface. Metatibial apex with large hooked uncus at posterior margin and anteriorly until anterior margin produced into broad flatted triangular tooth. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally at apex. Claws with a broad, flat, triangular basal tooth. **Abdomen**. Sternite III at sides same length as IV, V and VI equal in length and combined longer than IV. Crustose punctures present along posterior margin of each sternite, in single

row on sternites III and VII and a double row on sternites IV-VI. Vestiture sparse, mostly linear white scales with a few broader scales intermixed.

Male. Length 3.0 mm, width 1.0 mm, length/width ratio 3.0; rostrum shorter (1.33x pronotal length), slightly, evenly arcuate, small linear white scales extending laterally to middle, integument more densely punctured. *Male terminalia* (Fig. 3.13E): aedeagus parallel sided for most of length, slightly convergent anteriorly, constricted subapically, apex broadly truncate, posteriorly fused with temones. Endophallus with paired tube-like sclerites posteriorly, paired curved plates, and anteriorly paired comma-shaped sclerites; transfer apparatus a ring with an acuminate, curved, trough-like extension. Tegmen forming complete ovoid ring, parameroid lobes sclerotized and separate, ventral region of tegmen flat, broad, manubrium reduced.

Distribution. Ecuador (Pichincha, Santo Domingo de los Tsáchilas).

Material examined. Two specimens. Holotype female: "ECUADOR, 1km. SE. Sto.Domingo de los Colorados, V-2-1978 O'Briens&Marshall" (ASUCOB). Paratype: "ECU.: Pich. Pr. 250m 47km S Sto. Domingo RioPalenqueStation 17-25.II.1979 S.A. Marshall" (1♂, CMNC).

Etymology. The name is a portmanteau of the banana genus *Musa* L., 1753 and the Greek *sathros*, meaning "rotten" (Brown 1956), referring to the yellow and brown coloration of this species which resembles an old banana.

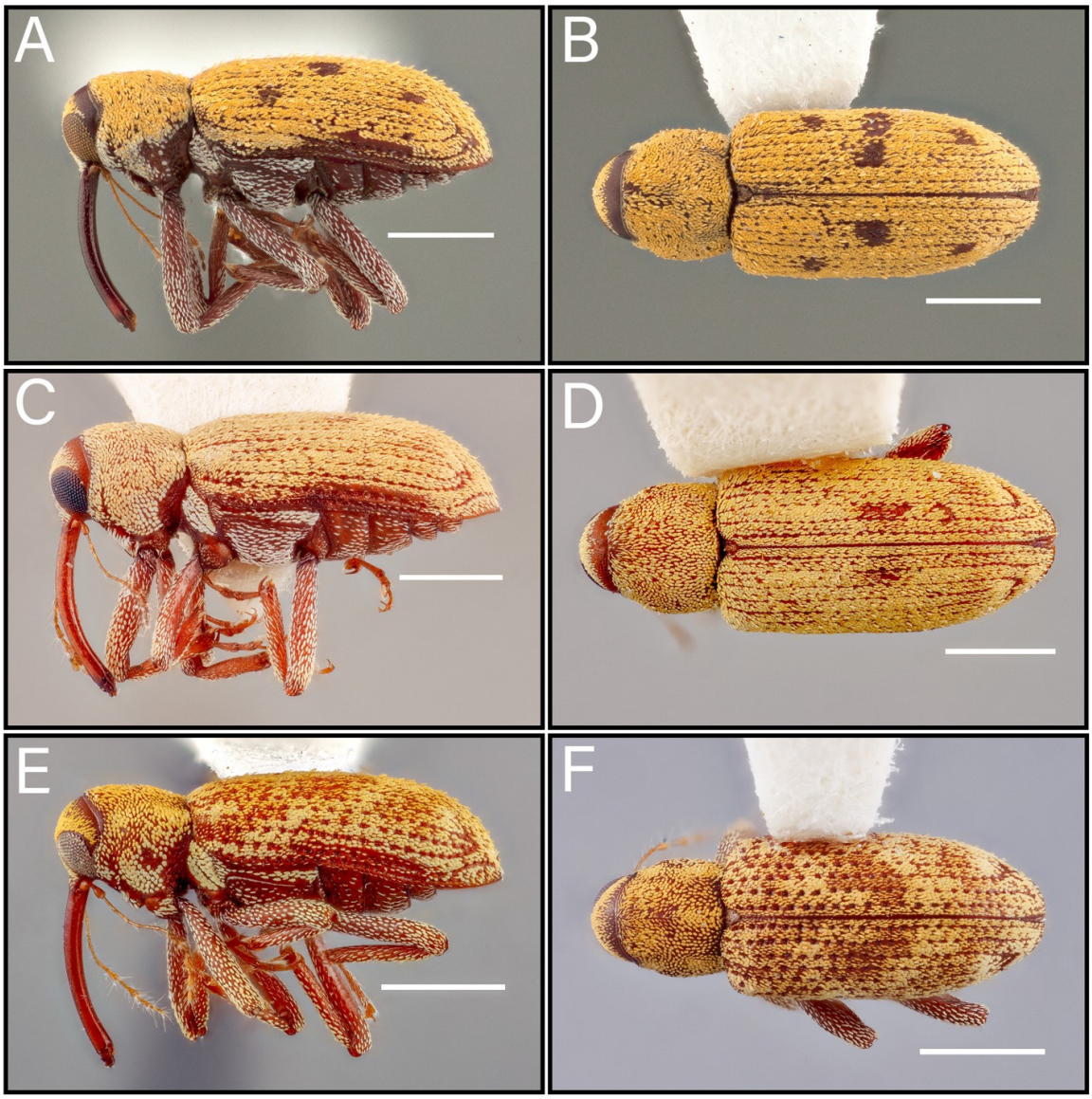

Figure 3.11. Dorsal and lateral habitus of species in the *ochromae* group. A-B) *T. ochromae* holotype female; C-D) *T. atheatomerus* holotype female; E-F) *T. musathrus* holotype female.

***Trichodocerus gorgonarium* Anzaldo, sp. nov.**

Figs. 3.12A-B, 3.13D, 3.27A.

Diagnosis. Very similar to *T. musathrus* but differs in the more whitish dorsal vestiture and the longer second funicular article.

Description – holotype female. Length 3.65 mm, width 1.29 mm, length/width ratio 2.83. Integument reddish brown, becoming darker at the femoral base and apex. Dorsal scales mostly flat, apically rounded, and linear, suberect mostly yellowish white. **Head**. Eyes subcontiguous, separated by ~5 narrow scales at closest point, ventral lobe slightly produced, broad, extending to ventral margin of rostrum. Vestiture above eyes in dense, dorsally rounded patch of imbricate yellowish white scales, scales becoming smaller and sparser farther from eyes. Scales narrow and yellowish white between eyes and white above rostral insertion. *Rostrum*: moderately elongate (1.51x pronotal length), arcuate at middle, widest and somewhat flattened ventrally at base, cylindrical to apex. Dorsally slightly impressed on either side at base and with white scales in impression up to antennal insertion. Smooth, with minute irregular punctures to apex. *Antenna*: Scape short, clavate. Funicle with article 1 clavate, narrower than scape, shorter than article 2. Articles 2-7 cylindrical; article 2 slightly longer than 3, 3 slightly longer than 4, 4 longer than 5, 6 longer than 5 and 7. Club with four distinct articles, 1 and 2 ventricose-rostrate, apical rostrate portion of article 1 short, slightly longer than one-third total article length, apical rostrate portion of article 2 short, slightly shorter than one-third total article length; article 3 evenly rounded at sides, article 4 slender, fusiform. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically

constricted. Median longitudinal carina faint, present subapically only in anterior half. Integument evenly convex on disk. Vestiture consisting of dense, flattened yellow scales with sparse, inconspicuous suberect cylindrical scales, scales sparser in patches above elytral intervals 2-4 in basal half, denser in between in narrow stripe extending to apex of median carina. Scales becoming yellowish white at sides, where suberect scales are more prominent and inserted in shallow round punctures, and extending nearly to posterior margin of lateral surface, with dense, crustose punctures at base and in small lateral patch near middle. *Prosternum*: rostral sheath widest anteriorly, slightly constricted one-third from anterior margin, convergent to apex except for slight dilation at junction with coxal rim, apically flattened. Sheath interior with sparse linear white scales and laterally with dense, broader white scales. **Mesothorax**. *Elytra*: wider than prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument slightly impressed on interval 2 one-fourth from base. Vestiture mostly dense, yellowish white except for oblique maculae of smaller, yellow scales with surrounding integument exposed on intervals 2-4. Suberect, cylindrical, yellowish white scales in single row along each interval, not present on intervals 10 and 11 until just before apex. Interval 9 tumescent in middle third, scales present along inner margin of interval, outer margin shining, with single row of small scale; interval 10 below narrow, with reduced scales. Striae with deep ovoid punctures each bearing a single seta. *Mesoventrite*: ventral process short, ventrally slightly concave. Anterior face with sparse multifurcate setae, posterior face ventrally with elongate, linear, posteriorly directed white scales. Intercoxal region flat. *Mesanepisternum*: sclerite divided by oblique, arcuate ridge, anteriorly and ventrally glabrous, with broad white scales bordering mesepimeron. *Mesepimeron*: scales flat, adpressed, white to yellowish white. **Metathorax**. Scales sparse, posteriorly directed, white. *Metaventrite*: ventrally slightly convex, rounded to sides. Scales linear and sparse ventrally at middle, wider

and flattened to at rounded lateral margin, smaller and linear laterally below metanepisternal suture. *Metanepisternum*: anteriorly with dense, small, linear white scales becoming a single row of scales until middle, posterior half with broader, flat white scales. **Legs**. Slender, elongate, hind femora extending to sternite VI. Procoxae without mesal setal tuft. Femora ventrally unarmed, with sparse, white adpressed scales becoming larger subapically, then smaller and more linear apically. Tibia dorsally with dense white scales, ventrally with sparse setae. Protibial setal brush small, covering one-third ventral surface. Metatibial apex with large hooked uncus at posterior margin and anteriorly until anterior margin produced into broad flatted triangular tooth. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally at apex. Claws with a broad, flat, triangular basal tooth. **Abdomen**. Sternite III at sides slightly longer than IV, V and VI equal in length and combined longer than IV. Crustose punctures present in single row along posterior margin of each sternite. Vestiture sparse, mostly linear white scales with a few broader, flat scales intermixed.

Male. Length 3.58 mm, width 1.25 mm, length/width ratio 2.86; rostrum shorter (1.25x pronotal length), slightly, evenly arcuate, with sparse linear white scales extending about halfway to apex. *Male terminalia*: aedeagus parallel sided for most of length, slightly convergent anteriorly, constricted subapically, apex narrowly truncate, junction with temones unsclerotized. Endophallus with paired tube-like sclerites posteriorly, paired curved plates, and anteriorly paired comma-shaped sclerites. Tegmen forming complete ovoid ring, parameroid lobes sclerotized and approximate, ventral region of tegmen flat, broad, manubrium reduced.

Distribution. Known only from Gorgona Island, Colombia.

Comments. It is currently unknown if the species is endemic to Gorgona Island or is also present on the South American mainland.

Material examined. Two specimens. Holotype female: "Gorgona Island, Colombia. Swept from herbage. Sea level. 15-x-1924. St. George Expedn. C.L. Collenette." (NHM). Paratype (1): same as holotype except date formatted as "15.10.24" (1♂, NHM).

Etymology. The name gorgonarium is in reference to the type locality of Gorgona Island, Colombia.

***Trichodocerus prionasceles* Anzaldo, sp. nov.**

Figs. 3.4L, 3.12C–D, 3.14L-M, 3.27A.

Diagnosis. *Trichodocerus prionasceles* shares with *T. gorgonarium* and *T. musathrus* the basally toothed tarsal claws, the large triangular tooth occupying the anterior part of the tibial apex, and the less densely yellow dorsal vestiture, but can be differentiated by the more widely separated eyes (Fig. 3.4L), the dense white scales on the lateral portion of the metaventrite and metanepisternum (Fig. 3.12C), the dentate ventral margin of the hind tibia, and the pronotal scales condensed into arcuate vittae (Fig. 3.12D). The spermatheca (Fig. 3.14M) is distinct from *T. ochromae* and *T. atheatomerus* in having a strongly produced collum but females of *T. musathrus* and *T. gorgonarium* were not dissected.

Description – holotype female. Length 3.44 mm, width 1.27 mm, length/width ratio 2.71. Integument reddish brown, becoming lighter on the tarsi, antennae and rostrum. Dorsal scales mostly flat, yellowish. **Head**. Eyes separated by about half subbasal rostral width, ventral lobe distinct, short, extending nearly to ventral margin of rostrum. Vestiture above eyes in dense, dorsally rounded patch of imbricate yellow scales, becoming smaller and sparser farther from eyes. Scales becoming white and narrow at closest point between eyes to rostral insertion. *Rostrum*: elongate (1.69x pronotal length), evenly arcuate, widest at base, somewhat flattened ventrally. Dorsally slightly impressed on either side at base and with yellowish white scales in impression proximal to antennal insertion. Smooth, with small irregular punctures to apex. *Antenna*: Scape short, clavate. Funicle with article 1 clavate, narrower than scape, shorter than article 2. Articles 2-7 cylindrical; articles 2 and 3 subequal in length, longer than 4, 4 longer than 5, 5 longer than 6, 6 and 7 subequal. Club with 4 distinct articles, 1 and 2 ventricose-rostrate with basal portion elongate, longer in 2, and rostrate portion very short, 3 subequal in length to 1, 4 fusiform. **Prothorax**. *Pronotum*: lateral margins in basal half slightly rounded and diverging, more strongly rounded at middle and widest just anterior to middle, apically constricted. Median longitudinal carina faint, present subapically only in anterior half. Integument evenly convex on disk, slightly impressed anterolaterally. Scales on disk yellowish white, with two arcuate vittae of dense, imbricate scales on either side of median carina, median area and area lateral to vittae sparser, with integument surrounding scales exposed. Scales at posterolateral corners white, extending to lateral face subbasally and ventrally. *Prosternum*: rostral sheath widest anteriorly, slightly constricted one-third from anterior margin, convergent to apex except for slight dilation at junction with coxal rim, apically flattened. Sheath interior and lateral margins with dense white scales. **Mesothorax**. *Elytra*: wider than prothorax, parallel-sided from humeri to one-

third from apex, rounded to apex. Integument slightly impressed on interval 2 one-fourth from base, interval 4 subbasally tumescent. Vestiture mostly composed of dense yellowish white scales with an oblique, sparse region on intervals 2-5 at middle, a stripe in front of the humeri on interval 7 and at the apex of interval 5. Suberect, cylindrical, yellowish white scales in single row along each interval except in sparser regions, not present on intervals 10 and 11 until just before apex. Interval 9 tumescent, subcostate near middle third, scales present along inner margin of interval, outer margin shining, with single row of small scales; interval 10 below narrow, receded, with reduced scales. Striae with deep ovoid punctures each bearing a single seta. *Mesoventrite*: ventral process short, ventrolateral corners slightly produced. Anterior face with dense multifurcate setae, ventral margin and intercoxal region with elongate, erect linear white setae. Intercoxal region flat. *Mesanepisternum*: sclerite divided by oblique, arcuate ridge, anteriorly and ventrally mostly glabrous, with broad yellowish white scales bordering mesepimeron. *Mesepimeron*: scales flat, adpressed, yellowish white. **Metathorax**. Ventrally concave, impressed posteriorly, rounded to sides. Setae present ventrally, lateral face with dense, broad white scales. *Metanepisternum*: anteriorly with dense, narrow white scales, scales in two rows at middle and broadening towards posterior margin. **Legs**. Slender, elongate, extending to anterior margin of sternite VII. Procoxae with mesal setal tuft. Femora ventrally unarmed, with sparse, white adpressed scales becoming larger subapically, then smaller and more linear apically. Tibia dorsally with dense yellowish white scales, ventrally with sparse setae. Protibial setal brush small, covering one-third of apicoventral surface. Metatibial apex with large hooked uncus at posterior margin and anteriorly until anterior margin produced into broad flatted triangular tooth.
Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales dorsally at apex. Claws with a broad, flat, triangular basal tooth. **Abdomen**. Sternite III at

sides same length as IV, V and VI equal in length and combined longer than IV. Crustose punctures present along posterior margin of each sternite, not present medially on sternites III and IV, sternites V and VI with multiple rows. Vestiture sparse, mostly linear white scales with a few broader scales intermixed.

Female terminalia (Figs. 3.14L-M). Spiculum ventrale elongate, much longer than lamina, slightly widened at apex, relatively even width throughout. Lamina of sternite 8 sclerotized only at lateral arms, arcuate, becoming wider apically, with cluster of setae ventrally at apex. Tergite 8 broad at base, narrowing towards truncate apex. Gonostylus of even width throughout. Spermatheca J-shaped, collum very long, slightly curved apically, ramus slightly produced, cornu hooked, rounded apically.

Variation. Female length 3.12-3.89 mm, width 1.06-1.28 mm, length/width ratio 2.71-3.03, rostral length/pronotal length ratio 1.66-1.78. Rostral sheath with sparse, linear white scales in the two paratypes. Male unknown.

Material examined. Four specimens. Holotype female: "BOLIVIA: Santa Cruz, Potrerillos del Guendá 40km NW Santa Cruz 17°40.3'S 063°27.4'W coll. B.K. Dozier" (ASUCOB) Paratypes: "Bolivia: Villa Tunari: 15-I-1981 R.C.Wilkerson malaise trap" (1♀, ASUCOB) "Peru,Madre deDios nr.PuertoMoldonado, PosadaAmazonas lodge@RTambopata / C.R.Bartlett, 609',7- 10-X-2004,S12 48. 115.W69 18.019" (1♀, ASUCOB); "ARGENTINA:La Rioja Dept.Rosaro, Penaloza Sierra de Argana El. Rocillo, 20.X.1997 Irwin & Parker, LT" (1♀, CMNC).

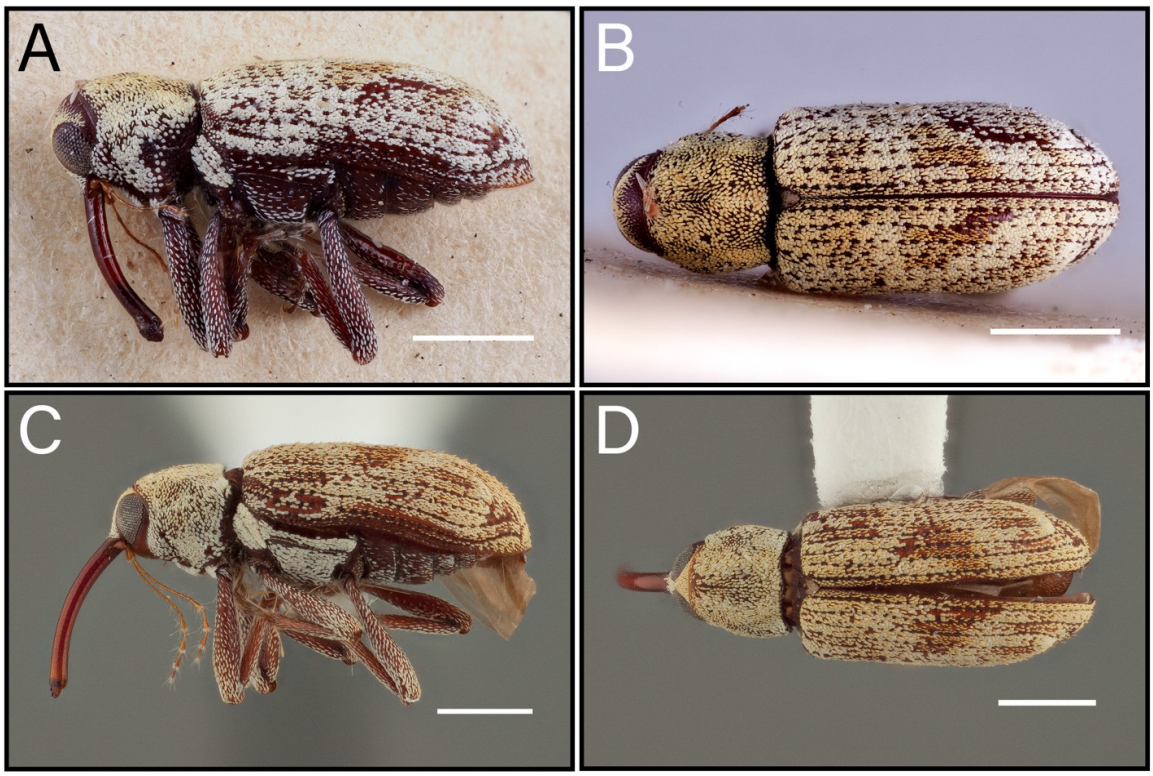

Figure 3.12. Dorsal and lateral habitus of species in the *ochromae* group. A-B) *T. gorgonarium* holotype female; C-D) *T. prionasceles* holotype female.

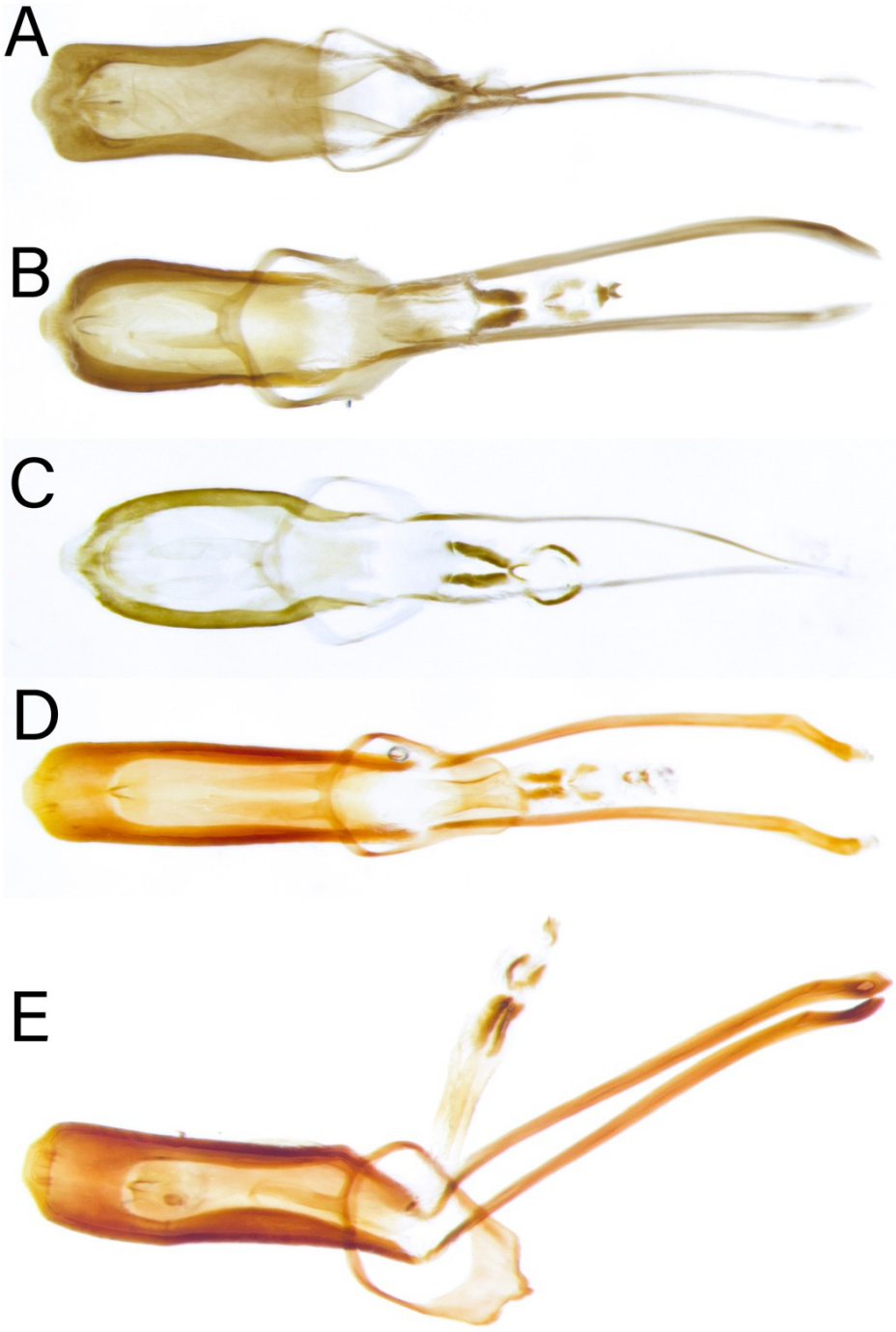

Figure 3.13. Male terminalia of the *brevilineatus* and *ochromae* group. A) *T. brevilineatus*; B) *T. hespenheidei*; C) *T. ochromae*; D) *T. gorgonarium*; E) *T. musathrus*.

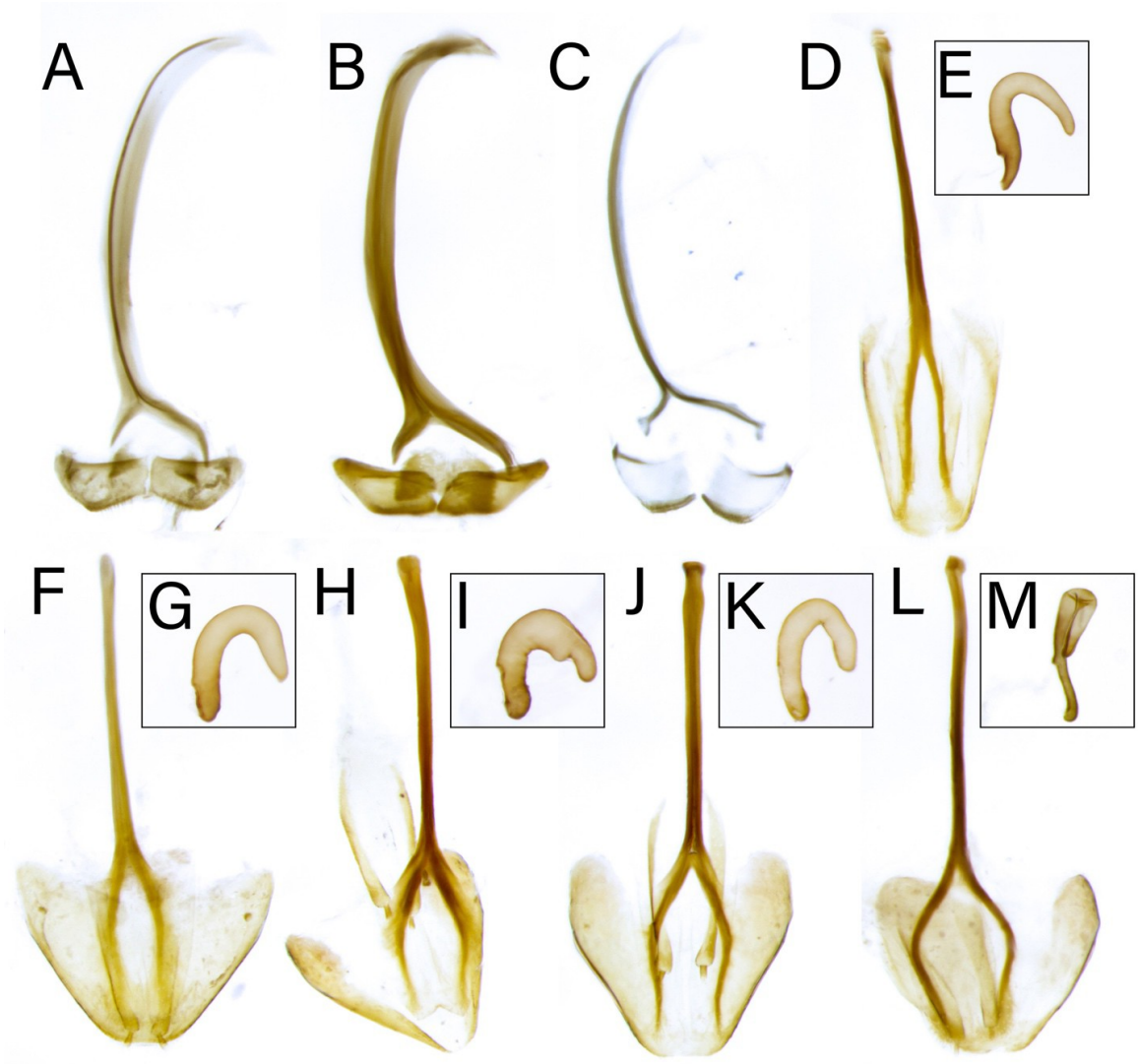

Figure 3.14. Male and female terminalia of the *brevilineatus* and *ochromae* groups. A) Sternite 8 and spiculum gastrale of *T. brevilineatus*; B) Sternite 8 and spiculum gastrale of *T. hespenheidei*; C) Sternite 8 and spiculum gastrale of *T. ochromae*; D-E) Female terminalia (D) and spermatheca (E) of *T. brevilineatus*; F-G) Female terminalia (F) and spermatheca (G) of *T, hespenheidei*; H-I) Female terminalia (H) and spermatheca (I) of *T. ochromae*; J-K) Female terminalia (J) and spermatheca (K) of *T. atheatomerus*; L-M) Female terminalia (L) and spermatheca (M; cornu collapsed) of *T. prionasceles*.

Etymology. This epithet is derived from the Greek *prion* ("saw"), referring to the denticulate ventral margin of the hind tibia and *askeles* ("dried up, withered"), referring to the coloration of the species which appears at first to represent a discolored specimen of species in the *ochromae* group with vibrant yellow scales (Brown 1956). The name is treated as a noun in apposition.

IV. The *Trichodocerus antiquus* group. The *antiquus* group contains three species, *T. antiquus*, *T. woldai*, and *T. sobetes*, and can be identified by the short, relatively straight and cylindrical rostrum, the large metafemoral tooth, the subspherical head impressed at the rostral insertion, and the rostral sheath lined with white scales (also shared by the *spinolae* group and *T. chrysochaetus*) and not multifurcate setae, and the posterior margin of the female eighth tergite is serrate (Figs. 3.16E-G; eighth tergite of female *T. sobetes* unknown). This species group is hypothesized to be related to the *mecistotarbus* and *obrieni* groups based on the presence of a triangular or subquadrate process on the rostrum below the antennal insertion and the generally shorter, more globular antennal scape.

Trichodocerus antiquus (Bondar, 1946)

= *Mallerus antiquus* Bondar, 1946 [Syn.: Bondar 1947: 294]

Figs. 3.2A, 3.5A, 3.15A–B, 3.16A, 3.16C, 3.16E-F, 3.27B.

Diagnosis. *Trichodocerus antiquus* can be easily separated from *T. woldai* by the larger size, the mottled, less distinct elytral pattern, the more sinuous inner margin of eyes around rostral insertion (Fig. 3.5A), the more numerous suberect linear scales on elytra (Fig. 3.15A), and the uneven integument of the pronotal disk with short oblique impressions on either side of the

median longitudinal carina, the lateral margins of the aedeagus are not produced to the dorsal surface (Fig. 3.16A), the broader and flatter spiculum ventrale (Fig. 3.16E) and the more robust, falcate spermatheca (Fig. 3.16F). From *T. sobetes* this species can also be separated by the less distinct elytral pattern, as well as the scales above the eyes extending dorsally on the vertex.

Redescription – male. Length 3.38-4.60 mm, width 1.31-1.91 mm, length/width ratio 2.40-2.55. Integument dark reddish brown, becoming lighter on tarsi, antennae, and rostrum. Dorsal scales short, flattened, apically truncate to rounded, white to silvery, yellowish to green, and brown, and suberect, linear, tan and brown. **Head**. Eyes subcontiguous, separated by 2-3 short linear scales at closest point, with prominent ventral lobe extending below ventral margin of rostral insertion. Vestiture above eyes in sparse, dorsally rounded patch of scales, densest bordering eyes, scales becoming smaller and more separated dorsally. Scales yellowish to whitish, brown between eyes at narrowest point. *Rostrum*: short (0.76-0.79x pronotal length), very slightly curved at middle, widest at base and flared distal to antennal insertion, cylindrical to apex. Dorsally rugose and slightly impressed laterally at base, with short basal median longitudinal carina splitting to three carinae proximal to antennal insertion and ending slightly distal to antennal insertion, smooth with relatively straight longitudinal rows of small punctures to tip. Vestiture small, flattened brown scales at base, short longitudinal rows of small, curved whitish scales between carina and extending one-third from base, glabrous to apex except for a minute, curved seta in each puncture. *Antenna*: scape short, bulbous, widest after short basal stalk. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 slender, cylindrical; article 2 longer than 3, 3 longer than 4, 4 longer than 5, 5 and 7 equal in length and shorter than 6.

Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion nearly as long as basal portion, 3 ventricose, 4 elongate, longer than 3, fusiform, widest in apical half, apically rounded. **Prothorax**. *Pronotum*: lateral margins rounded in posterior two-thirds, widest near middle, apically constricted. Median longitudinal carina most prominent in anterior half, reduced or absent in posterior half. Integument shallowly, obliquely impressed on either side of median carina in anterior half. Vestiture pattern consisting of small ovoid or apically truncate adpressed white to silvery scales in oblique vittae extending from anterior margin of pronotum on either side of carina and ending at posterolateral margin, scales larger posteriorly. Vittae near middle extending towards center. Scales between and lateral to vittae narrower, mottled dark brown to yellowish green, becoming darker laterally. Suberect linear scales on disk arising from shallow, crater-like punctures. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, converging evenly to meeting below procoxae except slight widening at junction with rim of coxal cavity. Sheath with adpressed multifurcate setae, lateral margins lined with linear white scales. **Mesothorax**. *Elytra*: scale pattern mostly indistinct, mottled with small silvery to white, greenish to yellow, and black to coppery-brown adpressed scales. Intervals with a single row of elongate, suberect linear scales. Humeri with dense white to silvery adpressed scales connected with oblique vitta of pronotum. Intervals 3-6 at middle with short longitudinal stripes of black to coppery-brown small flattened and elongate linear scales, appearing variously connected in one broad transverse fascia, dark region vaguely encircled by whitish to silvery scales. Scales generally darker on elytral declivity. Interval 9 tumescent one-third from base, interval 10 below narrow, with smaller, sparser scales. Striae with deep ovoid punctures bearing a single linear white to yellow scale, region surrounding punctures squamose and continuous with intervals. *Mesoventrite*: ventral process vertical,

ventrolateral corners slightly produced posteriorly, ventral margin strongly convex. Anterior face of ventral process with multifurcate setae, posterior face and intercoxal portion of metaventrite with elongate, linear white scales directed posteriorly. Intercoxal region flat. *Mesanepisternum*: divided in half by oblique ridge, posterior half bordering mesepimeron with variously white to brown scales, anterior half mostly smooth. *Mesepimeron*: scales variously white to brown. **Metathorax**. Scales mainly white. Metanepisternal suture with Type II sclerolepidia. *Metaventrite*: concave, separated from lateral portion by ridge between meso- and metacoxa. **Legs**. Hind femora extending just beyond anterior margin of sternite V. All femora ventrally with broad triangular tooth, largest on metafemora. Vestiture of femora with medial round patch of coppery-brown scales on lateral and dorsal face, at base, apex, and ventrally scales mostly white, broader at apex. Protibial antennal brush covering about half of ventral surface. Metatibial apex with large uncus at posterior margin, inner flange and anterior margin produced into a small tooth. Tarsal claws angularly dilated at the base. **Abdomen**. Sternite III medially impressed, III and IV at the sides subequal in length, V and VI subequal in length and combined longer than IV. Sternites III and IV with white scales and crustose punctures along posterior margin at the sides, sternites V-VII with mottled white and brown scales.

Male terminalia (Fig. 3.14A). Lateral margins of aedeagus of relatively even width throughout length, constricted subapically, apex rounded. Endophallus with large triangular sclerite surrounded by regions of dense, small teeth; transfer sclerite complex, composed of two pieces, one thin hoop-like sclerite with posterior ends acuminate, contiguous and broad, thick, flat sclerite adjacent to base of hoop. Spiculum gastrale thick, arcuate, apically

expanded, basally asymmetrically bifurcate. Tegmen forming complete, ovoid ring, parameroid lobes separate, manubrium reduced, tegmen ventrally very broad, flat.

Female. Length 3.93-5.09 mm, width 1.47-2.07. Metaventrite slightly convex, ridge separating ventral and lateral regions not prominent. *Female terminalia* (Figs. 3.16E-F). Spiculum ventrale thick, flattened, slightly widened at apex, longer than lamina of sternite 8. Lamina of sternite 8 sclerotized only at broad lateral arms, arms slightly arcuate, slightly expanded posteriorly, with cluster of setae ventrally at apex. Tergite 8 V-shaped, posterior margin rounded, serrate. Gonostylus of even width throughout. Spermatheca falcate, collum slightly produced, ramus not produced, cornu hooked, tapering to narrow rounded apex.

Variation. Mostly limited to the color of scales on the pronotum, elytra and meso- and metathoracic pleura.

Distribution. This species is known from Brazil (Rondônia, Santa Catarina, São Paulo), Bolivia (Santa Cruz), Paraguay (Boquerón, Cordillera), Argentina (Jujuy, Salta, Misiónes).

Natural History. One pair of specimens collected by botanist Karl Fiebrig in San Bernardino, Paraguay has a handwritten label that reads: "23 Nov. Ceiba glaziovii Stammerinde einer auf der andere (copula)", which suggests the double mounted specimens were collected in copula on the bark of a *Ceiba glaziovii* (Kuntze) K.Schum. (Malvaceae: Bombacoideae) tree.

Comments. Bondar described this species from a cotype series of eight specimens, two from Misiones, Argentina and six from Santa Caterina, Brazil. Four of those specimens have known whereabouts at the American Museum of Natural History (AMNH), one of which has since been designated as a lectotype (Vaurie 1953).

Material examined. 85 specimens. Lectotype male (only images seen – AMNH) from Santa Catarina, Brazil (Vaurie 1953). Other specimens:

"BRAZIL:Rondonia,62km.SW.Ariquemes,nr. Fzda.RanchoGrande 23-VIII-1992,UV trap / Coll. U.Schmitz" (1♂, ASUCOB); same data as previous but date "18-IX-1992" (1♂ 1♀, ASUCOB); "BRAZIL:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, 5-17-X-1993,JE.Eger" (2♂ 3♀, ASUCOB); same data as previous but date "8-20.xi.1994" (1♀, ASUCOB); "BRAZIL:Rondonia, 62km.SW.Arique- mes,Fzda.Rancho Grande.X-15-1993 / CW.&LB.O'Brien,at merc.vap.&UVlight" (1♂ 1♀, ASUCOB); "BRAZIL:Rondonia, 62km.SW.Arique- mes,Fzda.Rancho Grande,XI-8-1994 / UV&merc.vap.light C.W.&L.B.O'Brien" (1♂ 1♀, ASUCOB); "BRAZIL:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, xi-14-1994,C.O'Brien" (2♂ 1♀, ASUCOB); "BRAZIL:Rondonia. 62 km SW Ariquemes. Nr. Fzda.Rancho Grande 6-15-XII-1990. DA Rider & JE Eger / collected at light" (1♀, ASUCOB); BRASIL,SãoPaulo Barueri XI-1957 K.Lenko" (1♂, ASUCOB); "Ilha da Vitória, Est.S.Paulo 29.III.-6.IV.1965 Exp. Depto. Zool." (1♂ 5♀, ASUCOB); same data as previous but dates "24.III-6.IV.1965" (1♀, ASUCOB); "Ilha dos Buzios S. Paulo – Brazil 16.X-4.XI.963" (1♂, ASUCOB); "BOLIVIA: Saavedra, Dept. Santa Cruz Agr. Exp. Sta. / R. B. Cumming 27-XII-59 Blacklight Trap" (1♂ 1♀, ASUCOB); "BOLIVIA,S.C., SaavedraRes.Sta. March 23,1978 at light C.W.O'Brien" (1♀, ASUCOB); "BOLIVIA:Santa Cruz,3.7km SSEBuena Vista, Hotel Flora & Fauna,430m.,23-26-X-

2000,coll.M.C.Thomas tropical transition forest" (1♂, ASUCOB); "BOLIVIA:Santa Cruz El Refugio Los Volcanes Elev. 3363',X/1-10/08 Morris & Wappes" (1♀, CMNC); "PARAGUAY,D.Boq. LomaPlata,27-8-1986 bollweevil trapI-19-8 Whitcomb&Marengo" (1♀, ASUCOB); SBernardino Paraguay / KFiebrig Collector / [handwritten] 23 Nov. Ceiba glaziovii Stammerinde einer auf der andere (copula)" (♂ 1♀ on same pin, NMNH); SBernardino Paraguay / KFiebrig Collector / [handwritten note, illegible]" (♂ 1♀ on same pin, NMNH); "ARGENTINA: Jujuy 23.7625°S64.8510°W P.N. Calilegua, Guaraní Tr. 12.iii.2011, AKT1135 misc. hand collecting M.Caterino&A.Tishechkin (2♀, CUAC); "El Quemado Jujuy III-V,'26 / Argentina coll. G.L. Harrington" (9♂ 4♀, NMNH); same data as previous but dates "IV '26" (5♂ 1♀, NMNH), "Apr. '26" (1♂ 1♀, NMNH) "May '26(?)" (1♂ 5♀, NMNH); "Gen Ball- ivian Prov of Salta 1927-8 / Argentina coll. G.L. Harrington" (4♂ 8♀, NMNH); same data as previous but date "V-'27?" (3♂ 1♀, NMNH); "GenBALLIVIAN SaltaArgentina January 1927 GLHarrington" (1♂, NMNH); "QuemadoJujuy Arg. IV 1926 GLHarrington" (1♂ 1♀ on same pin, NMNH).

Etymology. The specific epithet *antiquus* is likely derived from the Latin noun meaning "old" (Brown 1956), although explanation of the name was not given by Bondar (1946).

***Trichodocerus woldai* Anzaldo, sp. nov.**

Figs. 3.3A–B, 3.5B, 3.15C–D, 3.16B, 3.16D, 3.16G-H, 3.28A.

Diagnosis: This species can be distinguished from *T. antiquus* and *T. sobetes* by the generally smaller size. From *T. sobetes* it can be differentiated by the scales above the eyes extending dorsally on the vertex and a smaller dark macula at the middle of the elytra. From *T. antiquus*

it can be separated by the more distinct elytra pattern, the less sinuous inner margin of the eyes around the rostral insertion (Fig. 3.5B), the less conspicuous suberect scales of the elytra, the more evenly convex pronotum, the lateral margins of the aedeagus being produced to the dorsal surface (Fig. 3.16A), the less broad spiculum gastrale (Fig. 3.16G), and the narrower, more apically pointed spermatheca (Fig. 3.16H).

Description – holotype female. Length 3.22 mm, width 1.16 mm, length/width ratio 2.77. Integument dark reddish brown, becoming lighter on tarsi, antennal scape and funicle, and rostrum. Dorsal scales short, flattened, apically truncate to rounded white, tan to golden, or coppery brown, and suberect, linear, tan and brown. **Head**. Eyes, subcontiguous, separated by 5-6 hair-like scales at closest point, with prominent ventral lobe of eye extending below ventral margin of rostral insertion. Vestiture above eyes in sparse, dorsally rounded patch of scales, densest bordering eyes, scales becoming smaller and more separated dorsally. *Rostrum*: short (0.70x pronotal length), straight, widest at base and flared distal to antennal insertion, cylindrical to apex. Dorsally rugose and slightly impressed laterally at base, with short basal median longitudinal carina splitting to three carinae proximal to antennal insertion and ending slightly distal to antennal insertion, smooth with relatively straight longitudinal rows of small punctures to tip. Vestiture small, flattened tan to yellow scales at base, becoming whiter and more linear and extending nearly halfway to apex, apical half glabrous except for a minute, curved seta in each puncture. *Antenna*: scape short, bulbous, widest after short basal stalk. Funicle with article 1 clavate, narrower apically than scape, about as long as scape. Articles 2-7 slender, cylindrical; article 2 longer than 3, 3 longer than 4, 4 longer than 5, 5-7 subequal in length. Club integument darker than funicle, with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion shorter than basal portion, 3

ventricose, 4 about as long as 3, somewhat flattened, widest in apical half, apically rounded. **Prothorax**. *Pronotum*: lateral margins rounded in posterior two-thirds, widest near middle, apically constricted. Median longitudinal carina absent. Integument evenly convex on disk. Vestiture pattern consisting of broad, flat, apically truncate to rounded adpressed white scales in sinuous oblique vittae extending from anterior margin of pronotum on either side of carina and ending at posterolateral margin, scales densest posteriorly. Scales between vittae narrower, mottled golden tan to coppery brown, scales latteral to vittae mottled golden tan to coppery brown with broad white scales, tan and brown scales extending laterally in anterior half of prothorax, becoming broad and white at anteroventral margin. Suberect scales arising from shallow, crater-like punctures. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, converging evenly to meeting below procoxae except very slight widening at junction with rim of coxal cavity. Sheath with adpressed multifurcate setae, lateral margins lined with linear white scales. **Mesothorax**. *Elytra*: general scale pattern with separate, short dark vittae near middle on interval 2, connected, offset vittae on 3-5 forming an oblique patch, and broad band of white scales connected with pronotal vittae extending from humeri and surrounding oblique patch on intervals 3-5. Basal region of intervals 1-5 between humeri appearing longitudinally striped, with single row of coppery brown suberect linear scales medially on intervals and surrounded on either side by small golden-tan scales. Intervals 5 and 6 with small round patch of coppery brown scales, followed posteriorly by a small patch of white scales at the confluence of intervals 4-6. Interval 9 tumescent one-third from base, interval 10 below narrow, with smaller, sparser scales. Striae with deep round punctures bearing a single curved seta, region surrounding punctures squamose and continuous with intervals. *Mesoventrite*: Ventral process vertical, ventrolateral corners slightly produced posteriorly, ventral margin slightly concave. Anterior

face of ventral process with multifurcate setae, posterior face and intercoxal region of mesoventrite with elongate, linear white scales directed posteriorly. Intercoxal region flat. *Mesanepisternum*: scales white to tan, broader and flat at border with mesepimeron, sparser and narrower anteriorly, with integument becoming more rugose. *Mesepimeron*: scales flat, white to tan. **Metathorax**. Scales mainly white, linear, directed posteriorly. *Metaventrite*: slightly concave, separated from lateral portion by ridge between meso- and metacoxa. Scales on lateral portion broader. *Metanepisternum*: scales broader in posterior half. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending just beyond anterior margin of sternite V. Pro- and mesofemora with small ventral tooth. Vestiture of femora and tibia white, medially thinner on femora exposing brown integument, apically on femora and on tibia scales broader. Protibial antennal brush covering about one third of ventral surface. Metatibial apex with large uncus at posterior margin, inner flange at middle of apex and anterior margin produced into a small tooth, tooth of inner flange smaller and narrower. Apical tibial setal comb oblique, setae increasing in length proximally. Tarsal article 1 three times longer than 2, articles 1 and 2 with linear white scales dorsally, larger at apex. Claws angularly dilated at base. **Abdomen**. Sternite III medially impressed, III and IV at the sides subequal in length, V and VI subequal in length and combined longer than IV. Sternites III and IV with crustose punctures along posterior margin at the sides, sternites V-VII with crustose punctures along posterior margin medially.

Female terminalia (Figs. 16G-H). Spiculum ventrale thick, flattened, longer than lamina of sternite 8. Lamina of sternite 8 sclerotized only at broad lateral arms, arms slightly arcuate, slightly expanded posteriorly, with cluster of setae ventrally at apex. Tergite 8 V-shaped, posterior margin rounded, serrate. Gonostylus of even width throughout. Spermatheca

subfalcate, collum produced and slightly curved, ramus slightly produced, cornu hooked, tapering to narrow rounded apex.

Variation. Female length 2.64-3.49 mm, width 0.90-1.26 mm, length/width ratio 2.71-2.94, rostrum 0.70-0.88x pronotal length. Male length 2.95-3.23 mm, width 1.03-1.13 mm, length/width ratio 2.80-2.90. As female except ventrite III impressed at middle, rostrum 0.65-0.71x pronotal length, tibial apex with uncus more directed towards the anterior margin, inner flange not flat, with tooth inserted higher than tooth at anterior margin. *Male terminalia* (Fig. 16B): lateral margins slightly constricted at middle, apically converging to rounded point. Endophallus with paired, triangular, convex plate-like sclerites posteriorly and anteriorly with a region of paired lightly sclerotized reticulately sculptured plates; transfer apparatus two connate sclerites forming an anterior hoop and a posterior curved acuminate process. Spiculum gastrale thick, arcuate, apically transversely expanded, basally asymmetrically bifurcate. Tegmen forming complete, ovoid ring, parameroid lobes separate, manubrium reduced, tegmen ventrally very broad, flat.

Distribution. Costa Rica, Panama.

Natural history. The single specimen from Costa Rica was collected by canopy fogging *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae) (Hespenheide, personal communication). Most of the other observed specimens were collected at UV light.

Material examined. 275 specimens. Holotype female: PANAMÁ: Las Cumbres 9°06'N, 79°32'W 27 May '74 H. Wolda -at light-" (NMNH). Paratypes: "COSTA RICA, Heredia: Est. Biol. La Selva, 50-150m, 10°26'N 84°01'W Jul 1993 INBio-OET / 4 Julio 1993 FPM/08/11 Pentaclethra macroloba" (1♀, MNCR); "CANAL ZONE,Barro Colorado Is.,UV trap 1(3m.high) 29Apr.1976H.Wolda" (1♂ 2♀, ASUCOB); same as previous but "trap 3(26m.high)" (2♀, ASUCOB), "trap 1 (3m.high) 30Apr.1976" (3♀, ASUCOB), "trap 3(26m.high)" (1♀, ASUCOB), "trap 1 (3m.high) 2May1976" (1♀, ASUCOB), "5 May 1976" (2♀, ASUCOB), "7May1976" (1♀, ASUCOB), "13May1976" (1♀, ASUCOB), "21May1976" (1♀, ASUCOB), "trap 3 (26m.high) 24May1976" (6♂ 5♀, ASUCOB), "trap 1 (3m.high) 29May1976" (1♂, ASUCOB), "30May1976" (1♂ 1♀, ASUCOB), "1 June1976" (2♂ 7♀, ASUCOB), "24June1976" (1♂ 1♀, ASUCOB), "trap 3 (26m.high) 7 July1976" (1♀, ASUCOB), "24July1976" (1♂ 1♀, ASUCOB), "trap 1 (3m.high) 25July1976" (1♂ 1♀, ASUCOB), "31July1976" (1♂, ASUCOB), "4Aug. 1976" (1♂, ASUCOB), "23Aug.1976" (1♀, ASUCOB), "6Sept.1976" (1♀, ASUCOB), "11Sept1976" (1♂, ASUCOB), "17Oct1976" (1♂, ASUCOB), "22 Oct1976" (1♂, ASUCOB), "31-X-1976" (1♂, ASUCOB), "5 Mar1977" (1♀, ASUCOB), "7 Mar1977" (1♂, ASUCOB), "20Mar1977" (1♂, ASUCOB), "27Apr1977" (1♂, ASUCOB), "trap 3 (26m.high) 28Apr.1977" (1♂, ASUCOB), "7May1977" (1♂ 2♀, ASUCOB), "8 May1977" (1♂ 1♀, ASUCOB), "trap 3 (26m.high) 22May1977" (1♀, ASUCOB), "trap 1 (3m.high) 19May1977" (4♂ 1♀, ASUCOB), "20 May1977" (1♀, ASUCOB), "23May1977" (2♂ 3♀, ASUCOB), "trap 3 (26m.high)" (17♂ 5♀, ASUCOB), "24May1977" (1♂ 2♀, ASUCOB), "trap 1 (3m.high)" (7♂ 5♀, ASUCOB), "25May1977" (1♂, ASUCOB), "trap 3 (26m.high)" (2♂, ASUCOB)", "trap 1 (3m.high) 26May1977" (1♂, ASUCOB), "29May1977" (9♂ 16♀, ASUCOB), "trap 3 (26m.high)" (3♂

1♀, ASUCOB; 1♀, CMNC), “trap 1 (3m.high) 30May1977” (1♂, ASUCOB), “2June1977” (1♂, ASUCOB), “3June1977” (1♂, ASUCOB), “5June1977” (2♀, ASUCOB), “7June1977” (1♂ 1♀, ASUCOB), “10June1977” (1♂, ASUCOB), “22June1977” (1♂, ASUCOB), “2 July1977” (1♂, ASUCOB), “10July1977” (1♀, ASUCOB), “28July1977” (1♂, ASUCOB), “Aug.41977” (1♂, ASUCOB), “2Sept.1977” (1♀, ASUCOB), “9Sept.1977” (1♀, ASUCOB), “16 Oct. 1977” (1♀, ASUCOB), “7 Dec.1977” (1♀, ASUCOB), “9 Mar.1978” (1♂, ASUCOB), “15Apr.1978” (2♂ 1♀, ASUCOB), “trap 3 (26m.high) 17Apr.1978” (2♂, ASUCOB), “18Apr.1978” (2♂, ASUCOB), “trap 1 (3m.high)” (4♂ 11♀, ASUCOB), “trap 3 (26m.high) 20Apr.1978” (1♀, ASUCOB), “trap 1 (3m.high) 21Apr.1978” (1♀, ASUCOB), “trap 3 (26m.high) 26Apr.1978” (1♂, ASUCOB),), “trap 1 (3m.high) 1May1978” (2♂ 1♀, ASUCOB), “3May1978” (2♂, ASUCOB), “trap 3 (26m.high) 9May1978” (1♂, ASUCOB), “21May1978” (1♂, ASUCOB), “trap 1 (3m.high) 22May1978” (1♂, ASUCOB), “trap 3 (26m.high) 3June1978” (1♀, ASUCOB), “trap 1 (3m.high) 25June1978” ” (1♀, ASUCOB), “trap 3 (26m.high) 8Nov.1978” (1♀, ASUCOB), “8-V-1980” (1♀, ASUCOB), “trap 1 (3m.high) 3-IX-1980” (1♀, ASUCOB), “trap 3 (26m.high) 21-IV-1981” (1♂ 1♀, ASUCOB), “22-IV-1981” (1♂, ASUCOB), “30-4-1981” (1♂, ASUCOB); “Panamá: Canal Zone Barro Colorado Is. 9°10’N 79°50’W / 29.v.1977 H.A. Hespenheide” (1♀, ASUCOB); same data as previous but dates “29.vi.1977” (1♀, ASUCOB), “3.vi.1977” (1♂, ASUCOB), “4.vi.1977” (1♀, ASUCOB), “5.vi.1977” (1♂ 2♀, ASUCOB), “9.vi.1977” (1♂, ASUCOB), “13.vi.1977” (1♀, ASUCOB), “15.vi.1977” (2♀, ASUCOB), “vi.16.1977” (1♂, ASUCOB); “Panamá, Isla Barro Colorado Light trap Week, 21 M. I N 20-26 V 1987” (1♂ 2♀, PCMENT); same data as previous but “Week, 9M. III N 25 II-3 III 1987” (1♂, PCMENT), “Week, 18 M. III N 29 IV-5 V 1987” (3♂ 3♀, PCMENT), “Week, 20 M. III N 13-19 V 1987” (1♂, PCMENT), “Week, 17 M. III N 22-28 IV 1987” (1♂, PCMENT), “Week 20M I N 11-17 V 1988” (1♂,

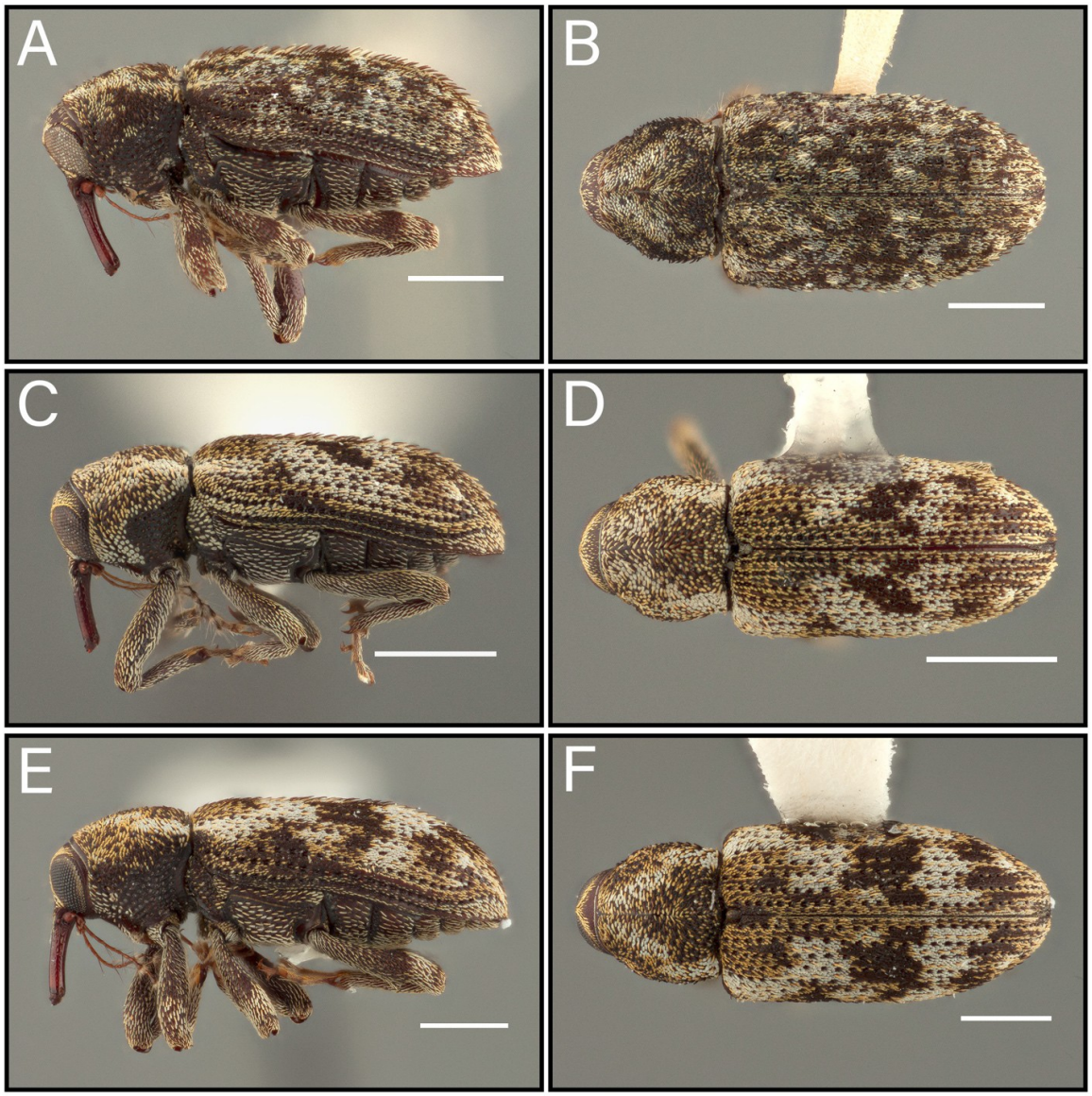

Figure 3.15. Dorsal and lateral habitus of species in the *antiquus* group. A-B) *T. antiquus*; C-D) *T. woldai* holotype female; E-F) *T. sobetes* holotype female.

PCMENT), “Week 21 N III N 18-24 V 1988” (1♀, PCMENT), “Week 22 N. III N 25-31 V 1988” (1♂ 1♀, PCMENT), “Week 39 N. III N 21-27 IX 1988” (1♂, PCMENT), “Week, 23 N. II N 8-14 VI 1988” (2♀, PCMENT), “Week 19 Q. I N 6-12 V 1992” (2♂ 1♀, PCMENT), “Week 21 Q. I N 20-26 V 1992” (1♂ 1♀, PCMENT); “PANAMA,D.Chepo, Altos de Maje,May 17,1975 Stockwell &Engleman at light” (1♀, ASUCOB); same as holotype but dates “15 Jun. ‘74” (1♀, NMNH), “25 June ‘74” (1♂, NMNH); “PAN.Panama LasCumbres UVtrapMay 2 1976 H. Wolda” (1♀, ASUCOB); same as previous but dates “May17 1976” (1♀, ASUCOB), “May22 1976” (1♂ 2♀, ASUCOB), “May23 1976” (2♂ 1♀, ASUCOB), “May24 1976” (2♂, ASUCOB), “May30 1976” (2♂, ASUCOB), “May31 1976” (1♂ 3♀, ASUCOB), “June8 1976” (1♂ 1♀, ASUCOB), “June9 1976” (1♂ 4♀, ASUCOB), “June24 1976” (1♀, ASUCOB); “PANAMA,Panama LasCumbres UVtrap 21Nov.1976H.Wolda” (1♀, ASUCOB); “BRAZIL:Rondonia, 62km.SWArique-mes,Fzda.Rancho Grande,X-13-1993” (1♂, ASUCOB).

Etymology. This species is named in honor of Henk Wolda, STRI ecologist whose UV trapping study across Panama (Wolda *et al.* 1998) yielded hundreds of specimens of *Trichodocerus* which were essential to carrying out this study. *T. woldai* was the most abundant species of *Trichodocerus* collected from that study.

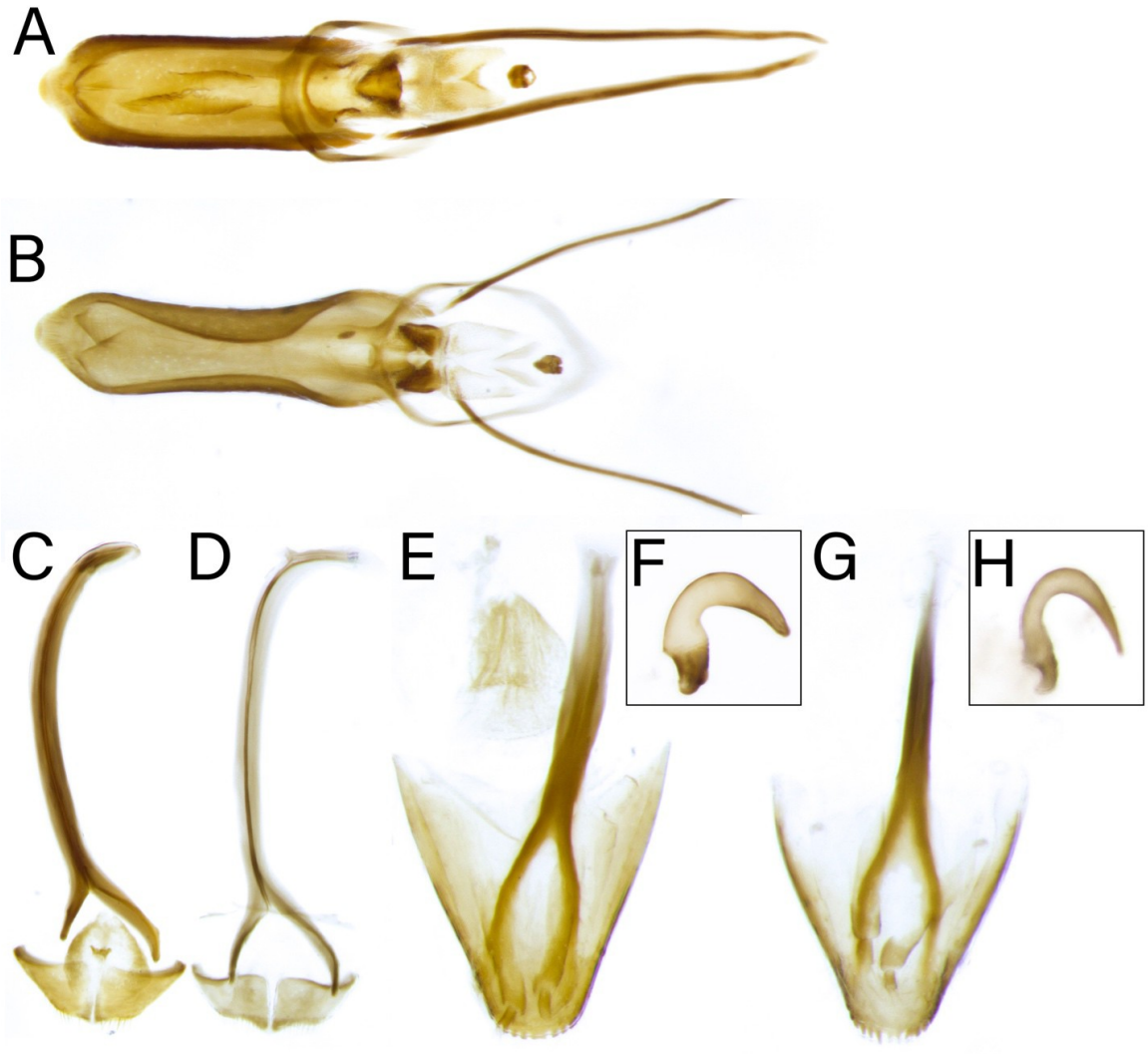

Figure 3.16. Male and female terminalia of the *antiquus* group. A) Aedeagus of *T. antiquus*; B) Aedeagus of *T. woldai*; C) Sternite 8 and spiculum gastrale of *T. antiquus*; D) Sternite 8 and spiculum gastrale of *T. woldai*; E-F) Female terminalia (E) and spermatheca (F) of *T. antiquus*; G-H) Female terminala (G) and spermatheca (H) of *T. woldai*.

***Trichodocerus sobetes* Anzaldo, sp. nov.**

Figs. 3.5C, 3.15E–F, 3.28A.

Diagnosis. This species can be separated from *T. antiquus* and *T. woldai* by the bare vertex of the head (Fig. 3.5C), the much denser vestiture especially on the elytra, the stouter funicular articles, and the distinctive elytral scale pattern (Fig. 3.13F)

Description – holotype female. Length 4.71 mm, width 1.71, length/width ratio 2.75. Integument dark reddish brown, becoming light reddish brown on the tarsi, antenna, and rostrum. Dorsal scales broad, flat, apically truncate to rounded white, tan to golden and brown and suberect, linear tan and brown. **Head.** Eyes subcontiguous, separated by 4-5 hair-like scales at closest point, with prominent ventral lobe extending below ventral margin of rostral insertion. Scales above eyes mostly limited to border of eye, with a few smaller, sparser scales extending to the vertex. Scales yellowish, becoming narrower and darker between eyes and centrally above rostral attachment, broader and white on either side above rostral attachment. *Rostrum*: short (0.71x pronotal length), straight, widest at base and flared distal to antennal insertion, cylindrical to apex. Dorsally rugose and slightly impressed laterally at base, with short basal median longitudinal carina splitting to three carinae proximal to antennal insertion and ending slightly distal to antennal insertion, smooth with relatively straight longitudinal rows of small punctures to tip. Vestiture small, flattened tan to yellow scales at base, becoming whiter and more linear and extending slightly distal to antennal insertion, apical half glabrous except for a minute, curved seta in each puncture. *Antenna*: scape short, bulbous, widest after short basal stalk. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 cylindrical; article 2 longer

than 3, 3 shorter than 4, 4 longer than 5, 5 and 7 equal in length and shorter than 6. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion short, less than half length of whole article, 3 ventricose, 4 elongate, subequal to 3, fusiform, widest near middle, apically rounded. **Prothorax**. *Pronotum*: lateral margins rounded in posterior two-thirds, widest near middle, apically constricted. Median longitudinal carina faint in anterior half, reduced in posterior half. Integument evenly convex on disk. Vestiture pattern consisting of broad, flat, apically truncate to rounded adpressed white scales in sinuous oblique vittae extending from anterior margin of pronotum on either side of carina and ending at posterolateral margin, scales densest posteriorly. Scales between and lateral to vittae narrower, mottled coppery-brown and golden-tan, with golden-tan scales densest bordering vittae and at lateral margins of pronotum. Suberect, evenly spaced, linear coppery-brown and golden-tan scales arising from shallow, crater-like punctures. *Prosternum*: rostral sheath widest anteriorly, sides sinuous, slightly constricted one-third from anterior margin, slightly dilated at junction with rim of coxal cavity, convergent to apex below procoxae. Sheath with multifurcate setae, lateral margins lined with adpressed silvery scales, densest and multifurcate at meeting with rim of coxal cavity. **Mesothorax**. *Elytra*: base color composed of golden tan and coppery brown scales with contrasting light and dark patches. Light patches composed of broad, flattened white scales, with a broad, arcuate patch extending from humeri to interval 3 about a third from base and a large transverse fascia from intervals 2-8 one third from apex. Smaller patches of white scales occur on interval 2 at middle, and intervals 6-7 at middle. Dark patches composed of short longitudinal stripes of coppery brown scales at base of interval 1 posterior to scutellum, interval 3 subbasally, interval 2 bordering arcuate white band, a large undulating fascia composed of short dark stripes on intervals 2-8 of varying lengths, 2 and 6-8 the shortest and beginning most

posteriorly. Mostly unconnected fascia of short longitudinal stripes occurring at intervals 1-7 posterior to transverse white fascia. Interval 9 tumescent one-third from base, interval 10 below narrow, with smaller, sparser scales. Striae with deep round punctures bearing a single curved seta, region surrounding punctures squamose and continuous with intervals. *Mesoventrite*: ventral process vertical, ventrolateral corners slightly produced posteriorly, ventral margin slightly concave. Anterior and ventral face of ventral process densely covered in multifurcate setae, posterior face and intercoxal region of mesoventrite with elongate, linear white scales directed posteriorly. *Mesanepisternum*: Divided in half by oblique ridge, posterior half bordering mesepimeron with tan to brown scales, anterior half smooth, mostly bare except single row of scales along anterior margin. *Mesepimeron*: scales tan along border with mesanepisternum, mostly brown dorsally. **Metathorax**. Scales mainly white, linear, directed posteriorly. *Metaventrite*: slightly concave, separated from lateral portion by ridge between meso- and metacoxa. Scales on lateral portion mottled white and tan. *Metanepisternum*: Scales at anterior margin and posterior margin white, larger posteriorly, tan in between. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending just beyond anterior margin of sternite V. All femora ventrally with broad triangular tooth. Vestiture of femora with medial round patch of coppery-brown scales on lateral and dorsal face, at base, apex, and ventrally scales mostly white, broader at apex. Protibial antennal brush covering about half of ventral surface. Metatibial apex with large uncus at posterior margin, inner flange and anterior margin produced into a small tooth. Apical tibial setal comb slightly curved distally towards middle of apical margin, longitudinal for most of length, with setae increasing in length proximally. Tarsi slender, article 1 more than twice as long as 2, articles 1 and 2 with linear white scales dorsally, larger at apex. Claws angularly dilated at base.

Abdomen. Sternite III medially impressed, III and IV at the sides subequal in length, V and VI subequal in length and combined longer than IV. Sternites III and IV with crustose punctures along posterior margin at the sides, sternites V-VII with crustose punctures along posterior margin medially.

Male. Unknown.

Distribution. Currently known only from the type locality in Jalisco, Mexico.

Comments. Female not dissected.

Material Examined. One specimen. Holotype female: "MEXICO,Jal.,UV, MismaloyaCanyon 7-25-1993,tropical decid.,C.L.Bellamy" (ASUCOB).

Etymology. This species is named for the vestiture pattern of dark scales in the posterior half of the elytra, which vaguely resembles a frightening, toothed grin. The Greek word *sobetes* means "frightener, one who scares away" (Brown 1956).

V. The *Trichodocerus mecistotarbus* group. This species group can be identified by the very elongate rostrate portions of antennal club articles 1 and 2 (e.g. Fig. 3.2B) that are longer than the basal portion and the abdominal sternites not bearing dense crustose punctures in multiple rows along the posterior margin (as in the *obrieni* group). Within the group, *T. mecistotarbus*, *T. fazerangrus*, and *T. hybophrictus* are hypothesized to be to form a monophyletic group due to the presence of apicodorsal spicules on the aedeagus and a

similarly shaped posterior endophallic sclerite. *T. chrysochaetus* and *T. stockwelli* both lack a distinct transfer apparatus of the endophallus and have similarly complex endophallic sclerites, with the anterior sclerites being paired, curved, spinose plates. This species group is hypothesized to be related to the *antiquus* and *obrieni* groups based on the presence of a triangular or subquadrate process on the rostrum below the antennal insertion and the generally shorter, more globular antennal scape.

***Trichodocerus mecistotarbus* Anzaldo, sp. nov.**

Figs. 3.5A, 3.17A–B, 3.19A, 3.19C, 3.19E, 3.20A-B, 3.28B.

Diagnosis. Most similar to *T. fazerangrus*, externally distinguishable by the lateral white vitta and the dorsally flattened pronotal carina. In the male, the posterior elongate endophallic sclerites are broadly fused anteriorly (Fig. 3.19A, C), and the seventh tergite has a less sinuate posterior margin (Fig. 3.19E).

Description – holotype male. Length 3.66 mm, width 1.18 mm, length/width ratio 3.12. Integument dark brown, lighter on tarsi, rostrum, and antennal scape and funicle. Dorsal scales small, apically truncate to rounded, greyish white, tan, and dark brown, scales larger on the pronotum. **Head**. Eyes subcontiguous, separated by ~2 very narrow linear scales at closest point, ventral lobe rounded, extending below ventral margin of rostral insertion. Vestiture above eyes bordering eyes, vertex bare. *Rostrum*: short (0.73 x pronotal length), slightly, evenly arcuate, flattened ventrally in basal half, cylindrical to apex. Integument dorsally at base roughly sculptured and impressed on either side, with a short faint median basal carina splitting subbasally into two, with a third, median carina beginning distal to split,

carinae ending about at antennal insertion; smooth distal to antennal insertion, with dense, fine punctures in longitudinal rows. Vestiture consisting of small linear yellow scales at base until rostral insertion, fine setae mostly laterally extending to mid-length. *Antenna*: scape short, bulbous. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 slender, cylindrical; article 2 longer than 3, 4 longer than 3 and 5, 6 longer than 5 and 7. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion longer than basal portion, 3 ventricose, 4 slender, longer than 3, widest in apical half, apically rounded. **Prothorax**. *Pronotum*: lateral margins in basal half gradually widening, rounded in anterior half except anterior constriction, widest just before constriction. Median longitudinal carina prominent and dorsally flattened in anterior three-fourths, faint to pronotal base. Integument evenly convex on disk around carina. Vestiture mostly consisting of greyish white scales laterally and anteriorly, with smaller, mixed greyish white and brown scales in basal half. Small greyish white scales continuing laterally in anterior half except for brown macula at greatest width. Suberect scales arising from shallow, crater-like punctures, anteriorly and laterally on disk white and basally brown. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging to apex. Sheath lateral margins with dense, erect multifurcate setae, interior vestiture sparse, present apically. **Mesothorax**. Scutellum densely covered with multifurcate scales, exposed portion ovoid and somewhat projecting dorsally. *Elytra*: nearly as wide as widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Pattern with lateral longitudinal vittae of white to greyish white scales, from humerus to apex, scales densest and vitta narrowest at humerus, widest and more diffuse apically; intervals 1-5 with median longitudinal brown stripe consisting of suberect and smaller, flattened brown scales, flattened brown scales densest and forming unconnected somewhat

arcuate dark fascia of longitudinal stripes of differing lengths at middle on intervals 1-6, and one-third from apex at intervals 2-5. Apical umbone with small white macula. Interval 9 about one-third from apex briefly subcostate, interval 10 below with reduced scales, narrower anteriorly. Striae with deep, ovoid punctures bearing a single seat. *Mesoventrite*: ventral process short, slightly concave ventrally. Anterior and ventral face and intercoxal region with dense, elongate, ventrally produced multifurcate setae. *Mesanepisternum*: region bordering mesepimeron impressed, with crustose punctures. *Mesepimeron*: scales linear to short and flat, white. **Metathorax**. *Metaventrite*: ventrally concave, rounded to sides. Vestiture composed of elongate setae, sparse ventrally and densest at rounded lateral margin, white scales laterally densest and elongate-fusiform at rounded lateral margin, smaller and linear below metanepisternum. Anterior margin of lateral region with crustose punctures. *Metanepisternum*: anteriorly with dense, small, linear white scales, becoming a single row of linear white scales at middle, and larger, broader, and denser posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending to anterior margin of sternite VII. Procoxae with mesal tuft of fine, elongate setae; elongate setae also present ventrally on the protrochanter, profemoral base, and mesotrochanter. All femora ventrally unarmed, with sparse whitish adpressed scales densest ventrally and apicodorsally, dorsally at middle with a variable patch of brown scales, scales smaller and linear at extreme apex. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering about half apicoventral surface. Metatibial apex with large curved uncus with apex projecting over anterior half of apex, a smaller tooth at the base of the anterior margin of the uncus, anterior margin of the tibial apex pointed. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales largest dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV sub equal in length at the sides, V and VI subequal in length

and combined longer than IV. Median ovoid impression present on sternite III and anteriorly on sternite IV. Crustose punctures present in single row along posterior margin of each sternite except absent medially on sternites III and IV and in multiple rows on sternites V-VII. Vestiture erect setae in impression on sternites III and IV, linear white scales elsewhere.

Male terminalia (Figs. 3.19A, C). lateral margins of aedeagus relatively even in width throughout, apex rounded and dorsally bearing spicules. Endophallus with complex sclerites: posterior sclerite broadly fused anteriorly (Fig. 3.19C); more anteriorly with two paired, curved plates; anterior with patch of small dense teeth; transfer apparatus paired elongate, anteriorly converging sclerites. Tegmen forming complete, ovoid ring around aedeagus, parameroid lobes approximate at base, manubrium short, broad, flat at base and apically rounded.

Female terminalia (Figs. 3.20A, C). Spiculum ventrale elongate, longer than lamina, slightly expanded at apex. Lamina of sternite 8 sclerotized at base between lateral arms, posteriorly limited to lateral arms, arms narrow, slighty arcuate. Tergite 8 broad, posterior margin unsclerotized at middle. Gonostylus of even width throughout. Spermatheca subfalcate, collum not produced, ramus slightly tumescent, cornu hooked, slightly narrowing towards rounded apex, annulate in apical half.

Female. As male except rostrum more evenly arcuate (0.76-0.86x pronotal length), metaventrite only slightly concave, abdominal ventrites III and IV convex and without erect

setae. Metatibial apex oblique, with a large uncus at posterior margin, a large tooth medially, and a smaller tooth at the anterior margin.

Variation. Male length 3.23-3.66 mm, width 1.03-1.18 mm, length/width ratio 3.05-3.14, rostrum 0.73-0.78x pronotal length. Female length 3.44-3.86 mm, width 1.05-1.28 mm, length/width ratio 2.95-3.29.

Distribution. Costa Rica, Panama, Colombia, Ecuador, Brazil, French Guiana.

Material examined. Twelve specimens. Holotype male: "Brazil:Rondonia, 62km.SW.Arique- mes,Fzda.Rancho Grande, XI-11-1994 / UV&merc.vap.light C.W.&L.B.O'Brien" (ASUCOB). Paratypes: same data as holotype but date "XI-13-1994" (1♀, ASUCOB); "Brazil:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, xi-10-1994,C.O'Brien" (1♀, ASUCOB); same data as previous but date "xi-16-1994" (1♂, ASUCOB); "Brazil:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, 3-15-XII-1996JE.Eger" (1♀, ASUCOB); same data as previous but date "XII.3-15.1996," (1♂, ASUCOB); "Ecuador: Napo Pr., 28 km NE Campo Cocha / 15-30.III.2001, F.T. Hovore Malaise trap, recently cut primary forest" (1♂, CHAH); "[handwritten, pink oval label] Cayenne / [upside down] Pascoe Coll. 93-60." (1♂, NHM). Other examined specimens: "COLOMBIA:Dept. of Antioquia, above Rio Anori, 15-IX-70 D.G. Young blacklight trap" (1♂ 1♀, ASUCOB). Additional specimens: "PANAMA, Bocas del Toro, CorrienteGrande RioChanguinola / 9°17'30"N 82°32'41"W H.Wolda Jan. 19, 1980" (1♀, ASUCOB), "Rancho Quemado, 200m Peninsula de Osa,Prov. Puntarenas. Costa Rica F. Quesada y G. Varela May 1992 L-S 292500,511000" (1♀, MNCR).

Etymology. The name is derived from the Greek *mekistos* meaning "longest" and *tarbos* meaning "terror" (Brown 1956), the name is in reference to the rostrate portion of antennal club articles 1 and 2, which are among the longest of all *Trichodocerus* and is diagnostic for the *mecistotarbus* species group, and the fearsome appearance of *Trichodocerus* species.

***Trichodocerus fazerangrus* Anzaldo, sp. nov.**

Figs. 3.17C–D, 3.19B, 3.19D, 3.19F, 3.20C-D, 3.29B.

Diagnosis. Very similar in appearance to *T. mecistotarbus* but without the lateral white vitta, the pronotal carina is not dorsally flattened, the posterior endophallic sclerite is only narrowly fused anteriorly (Fig. 3.19D), and the transfer apparatus is a ring formed from two nearly fused sinuous sclerites (visible in Fig. 3.19B).

Description – holotype male. Length 3.59 mm, width 1.17 mm, length/width ratio 3.07. Integument dark brown, lighter on tarsi, rostrum, and antennal scape and funicle. Dorsal scales small mostly apically truncate, tan to dark brown, scales larger on the pronotum. Vestiture of lateral and ventral surfaces and legs greyish- to yellowish white with setae.
Head. Eyes subcontiguous, separated by ~2 very narrow linear scales at closest point, ventral lobe rounded, extending below ventral margin of rostral insertion. Vestiture above eyes bordering eyes, vertex bare. *Rostrum*: short (0.90x pronotal length), slightly arcuate in apical third, flattened ventrally in basal half, cylindrical to apex. Integument dorsally at base roughly sculptured and impressed on either side, with a short faint median basal carina splitting subbasally into three and ending about at antennal insertion; smooth distal to

antennal insertion, with dense longitudinal rows of punctures. Vestiture consisting of small linear yellow scales at base until rostral insertion, and fine, curved setae in punctures becoming gradually smaller towards apex. *Antenna*: scape short, bulbous. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 slender, cylindrical; article 2 longer than 3, 4 longer than 3 and 5, 6 longer than 5 and 7. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion longer than basal portion, 3 ventricose, 4 slender, fusiform, longer than 3, widest near middle. **Prothorax**. *Pronotum*: lateral margins in basal half gradually widening, rounded in anterior half except anterior constriction, widest just before constriction. Median longitudinal carina present in anterior two-thirds, dorsally sharp. Integument broadly impressed anteriorly. Vestiture mostly mottled tan and dark brown, with tan scales densest anteriorly and laterally, tan scales laterally extending in anterior half on side of prothorax with a diffuse dark brown macula at greatest width; suberect scales arising from shallow, round punctures, mainly dark brown centrally and tan laterally. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging to apex. Sheath lateral margins with dense, erect multifurcate setae, interior vestiture sparse, present apically. **Mesothorax**. Scutellum densely covered with multifurcate setae, exposed portion ovoid and projecting dorsally. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Pattern mainly small tan scales with darker longitudinal stripes of dark brown scales at interval 1 posterior to scutellum, interval 5 one-fourth from base, 9 anterior to middle, 2-5 at middle, 2 and 4 one-fourth from apex. Interval 9 evenly squamose throughout, 10 narrow, with reduced scales. Striae with deep ovoid punctures bearing a single seta. *Mesoventrite*: ventral process short, slightly concave ventrally, with ventrolateral corners pointed, somewhat produced posterolaterally. Anterior and ventral face and

intercoxal region with dense, elongate, ventrally produced setae and short adpressed multifurcate setae. *Mesanepisternum*: region bordering mesepimeron impressed, with crustose punctures and a few whitish scales. *Mesepimeron*: with linear whitish scales. **Metathorax**. *Metaventrite*: ventrally concave, rounded to sides. Vestiture composed of elongate erect to suberect setae, setae densest at rounded lateral margin, laterally scales white, smaller and sparser bordering metanepisternum. *Metanepisternum*: anteriorly with dense, small, linear scales, becoming a single row of linear scales at middle, and larger, broader, and denser posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending to anterior margin of sternite VII. Procoxae with mesal tuft of fine, elongate setae; elongate setae also present ventrally on the protrochanter, profemoral base, and mesotrochanter. All femora ventrally unarmed, with sparse whitish adpressed scales and a variable patch of brown scales dorsally at apex, scales smaller and linear at extreme apex. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering one-third of apicoventral surface. Metatibial apex with large curved uncus with apex projecting over anterior half of tibial apex, a small tooth at the base of the uncus and at the anterior margin of tibial apex. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales largest dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV equal in length at sides, V and VI equal in length and combined longer than IV. Median ovoid impression present on sternite III and anteriorly on sternite IV. Crustose punctures present in at posterior margin and extending posteriorly at sides on articles III and IV, not conspicuous on articles V-VII. Vestiture erect setae in impression on sternites III and IV, linear white scales elsewhere.

Male terminalia (Fig. 3.17B, D). Lateral margins of aedeagus of relatively even width, convergent at apex, apex dorsally with spicules. Endophallus with complex sclerites: posteriorly with two parallel, tube-like sclerites narrowly anteriorly fused; paired, curved plates; anterior sclerites paired, spinose curved plates; transfer apparatus two sinuate sclerites, contiguous at either end, appearing as anterior ring with parallel posterior projections, and with small separate transverse sclerite ventrally. Tegmen forming complete ovoid ring, parameroid lobes approximate, manubrium broad, short, flat, apically rounded. Spiculum gastrale thick, arcuate, apically expanded into, basally asymmetrically bifurcate. Eighth sternite strongly sclerotized posteriorly with fringe of setae.

Female terminalia (Figs. 3.20C, D). Spiculum ventrale elongate, longer than lamina, slightly expanded at apex. Lamina of sternite 8 sclerotized at base between lateral arms, posteriorly limited to lateral arms, arms narrow, slightly arcuate. Tergite 8 broad, posterior margin unsclerotized at middle. Gonostylus of even width throughout. Spermatheca J-shaped, collum and ramus slightly produced, cornu hooked, slightly narrowing towards rounded apex.

Variation. Male length 3.29-3.59 mm, width 1.08-1.17 mm, length/width ratio 3.04-3.07, rostrum 0.90-0.91x pronotal length. Female length 3.53mm, width 1.18 mm, length/width ratio 2.98, rostrum 0.90x pronotal length. The dark brown scales on the elytra one-fourth from apex are sometimes denser, occurring on intervals 1-6.

Distribution. Currently known only from the type locality in Rondônia, Brazil (Fig. 3.29B).

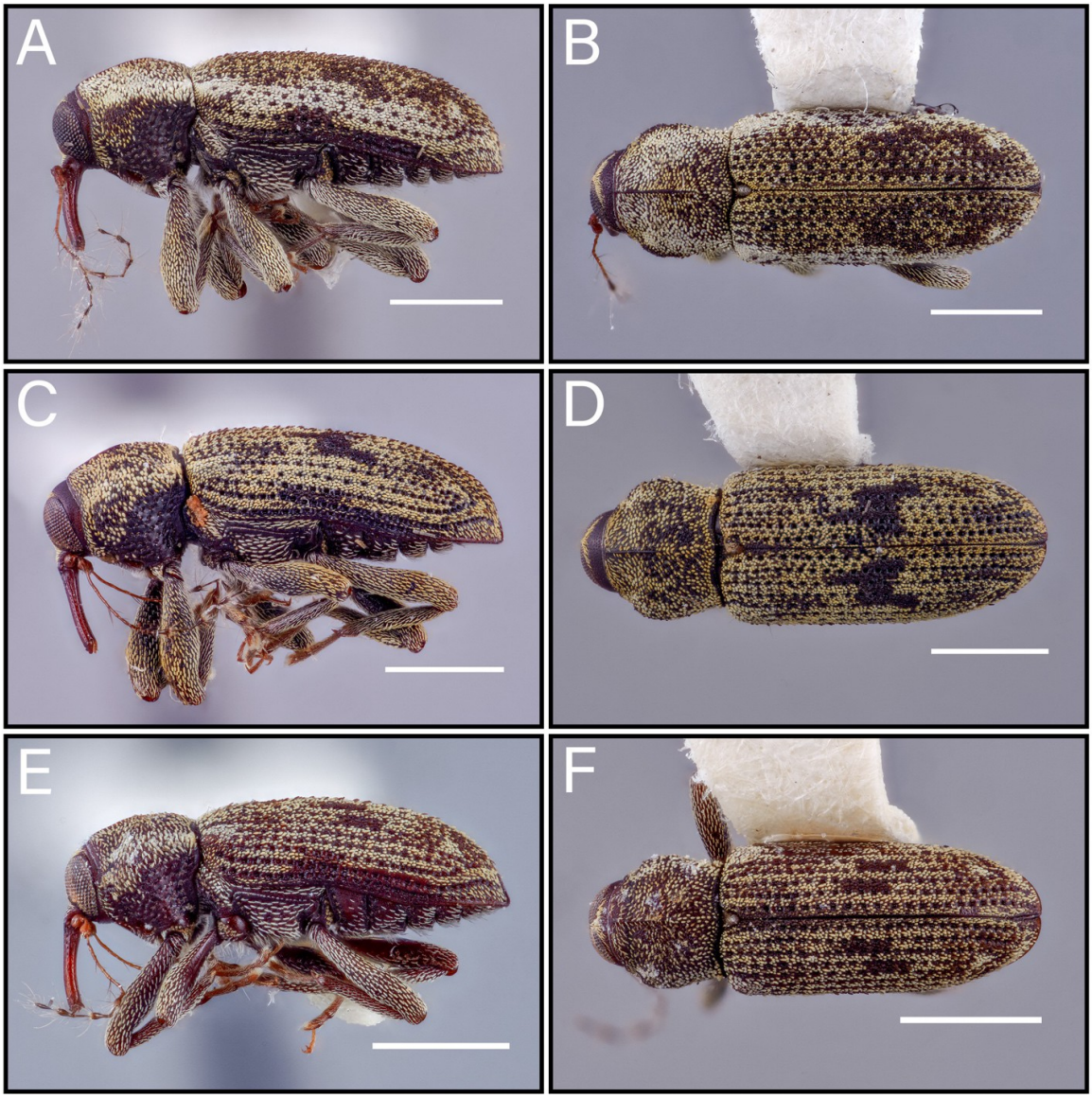

Figure 3.17. Dorsal and lateral habitus of species in the *mecistotarbus* group. A-B) *T. mecistotarbus* holotype male; C-D) *T. fazerangrus* holotype male; E-F) *T. hybophrictus* holotype male.

Material examined. Six specimens. Holotype male: "BRAZIL: Rondonia, 62km.SW.Arique-mes,Fzda.Rancho Grande,X-9-1993 / Collectors: C.W.&L.B. O'Brien" (ASUCOB). Paratypes (5): same data as holotype but with date "X-10-1993" (1♂, ASUCOB); "BRAZIL Rondonia 62kmSE Ariquemes 13-25 Apr 1992 W.J. Hanson" (1♂ 1♀, ASUCOB). Other examined specimens: Paratypes: same data as holotype but with date "X-10-1993" (1♂, ASUCOB); "BRAZIL Rondonia 62kmSE Ariquemes 13-25 Apr 1992 W.J. Hanson" (1♀, ASUCOB).

Etymology. The epithet is derived from the name of the type locality for this species, Fazenda Rancho Grande (*faze* + *ran* + *gr* + masculine ending *us*) in Rondônia, Brazil, which was an extremely productive locality for *Trichodocerus* collecting in terms of abundance and species diversity. Most of the specimens obtained from this locality were from the collecting efforts of Charles and Lois O'Brien and Joe Eger in the 1990s.

***Trichodocerus hybophrictus* Anzaldo, sp. nov.**

Figs. 3.3F, 3.5E, 3.17E, 3.19G, 3.29A.

Diagnosis. The elytral scale pattern *T. hybophrictus* is similar to *T. brevilineatus*, but the shorter rostrum and more elongate club, and lateral rostral process places the species in the *mecistotarbus* group. Hypothesized to be most closely related to *T. mecistotarbus* and *T. fazerangrus* based on the presence of apicodorsal spicules on the aedeagus. The anterior endophallic sclerite is most similar to that of *T. fazerangrus* but not fused. Can be further distinguished from other species in the *mecistotarbus* group by the prominently humped scutellum which is visible in lateral view.

Description – holotype male. Length 2.91 mm, width 0.95 mm, length/width ratio 3.06. Integument dark brown, lighter on tarsi, rostrum, and antennal scape and funicle. Dorsal scales small mostly apically truncate white, tan, and dark brown, scales larger on the pronotum. Vestiture of legs, lateral and ventral surfaces white scales and setae. **Head**. Eyes subcontiguous, separated by ~1 very narrow linear scale at closest point, ventral lobe rounded, extending below ventral margin of rostral insertion. Vestiture above eyes bordering eyes, vertex bare. *Rostrum*: short (0.83x pronotal length), slightly arcuate in apical third, flattened ventrally in basal half, cylindrical to apex. Integument dorsally rugose and impressed on either side at base, tumescent between antennal insertions; smooth distal to antennal insertion with fine punctures in longitudinal rows. Scales small, linear, yellowish white at base to antennal insertions and small curved setae arising from punctures mostly laterally extending to mid-length. *Antenna*: scape short, bulbous. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 slender, cylindrical; article 2 longer than 3, 4 longer than 3 and 5, 6 longer than 5 and 7. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion longer than basal portion, article 3 ventricose, 4 longer than 3, distinctly stalked, widest in apical half. **Prothorax**. *Pronotum*: lateral margins in basal half gradually widening, rounded in anterior half except anterior constriction, widest just before constriction. Median longitudinal carina present in anterior half, sharp. Integument slightly impressed anterolaterally. Scale pattern a lateral white vittae densest basally and diffuse anteriorly, disk between white vittae mostly mottled tan and brown with tan scales somewhat condensed into a broad vitta halfway between median carina and lateral white vitta and a narrow tan stripe connecting posterior margin of median carina with pronotal base; laterally tan scales extending ventrally in

anterior half with brown macula at greatest width. Suberect scales short, inconspicuous. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging to apex. Sheath lateral margins with dense, erect multifurcate setae, interior vestiture sparse, present apically. **Mesothorax**. Scutellum covered in dense multifurcate setae, prominently humped, apex visible in lateral view. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument slightly impressed at intervals 2-3 one-fourth from base. Pattern consisting of small tan scales contrasting with dark brown longitudinal stripes on interval 1 at base, intervals 3, 5 and 9 near middle, and surrounding white macula at apical umbone; humerus white; suberect setae mostly tan, brown in darker regions. Interval 9 tumescent posteriorly. Striae with deep, ovoid punctures bearing a single seta, punctures largest on interval 5. *Mesoventrite*: ventral process short, ventral margin slightly concave. Anterior and ventral face and intercoxal region with dense, elongate, ventrally produced setae. *Mesanepisternum*: region bordering mesepimeron impressed, with crustose punctures and a few white scales. **Metathorax**. *Metaventrite*: ventrally slightly concave, rounded to sides. Vestiture composed of erect multifurcate setae ventrally, densest at rounded lateral margin, linear white scales laterally. Anterior margin of lateral region with crustose punctures. *Metanepisternum*: anteriorly with dense, small, linear white scales, becoming a single row of linear white scales at middle, and larger, broader, and denser posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending to anterior margin of Sternite VII. Pro and meso-coxae with mesal setal tuft, pro- and mesotrochanters with ventral setae. Femora unarmed, with sparse white linear scales. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering about half apicoventral surface. Metatibial apex with large curved uncus with apex projecting over anterior half of apex, a

smaller tooth at the base of the anterior margin of the uncus, anterior margin of the tibial apex pointed. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales largest dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III and IV equal in length at the sides, V and VI equal in length and combined longer than IV. Median ovoid impression present on sternite III and anteriorly on sternite IV. Crustose punctures present laterally and in single row along posterior margin of each sternite except absent medially on sternites III and IV. Vestiture sparse suberect multifurcate setae in impression on sternites III and IV, linear white scales elsewhere.

Male terminalia (Fig. 3.19G): lateral margins of aedeagus of relatively even width throughout length, sclerotized lateral margins extending to dorsal surface, converging to rounded point apically, apically with dorsal spicules. Endophallus with complex sclerites: posterior sclerite paired, parallel, linear; paired, curved plate; anteriorly with small dense teeth; transfer apparatus arcuate, bifurcate anteriorly. Tegmen forming complete, ovoid ring, parameroid lobes separate, manubrium broad at base, tapering to apex. Spiculum gastrale thick, arcuate, apically expanded into, basally asymmetrically bifurcate. Eighth sternite strongly sclerotized posteriorly with fringe of setae.

Variation. Male length 2.76-2.97 mm, width 0.87-0.96 mm, length/width ratio 3.06-3.16, rostrum 0.83-0.87x pronotal length. Elytra darker scales in one paratype, with an additional short dark stripe on interval 5 one-fourth from base, and shorter stripes on interval 2 and 4 connecting longer stripes on intervals 3 and 5; the holotype and other paratype have brown suberect scales in these regions but adpressed scales tan. Female unknown.

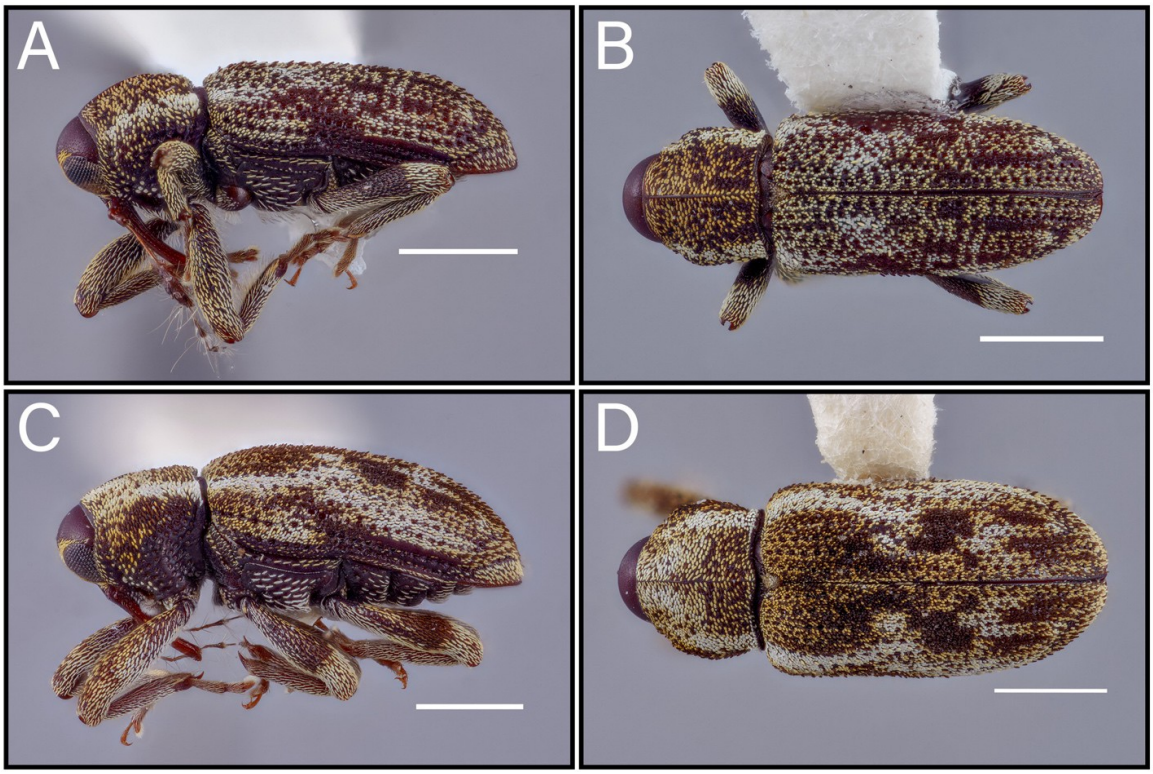

Figure 3.18. Dorsal and lateral habitus of species in the *mecistotarbus* group. A-B) *T. chrysochaetus* holotype male; C-D) *T. stockwelli* holotype male.

Distribution. Ecuador (Napo).

Material examined. Three specimens. Holotype male: "ECUADOR, 18km. S.Tena, April 28, 1978 CW&LB O'Brien&Marshall" (ASUCOB). Paratypes: same data as holotype (2♂, ASUCOB).

Etymology. This name is derived from the Greek *hybos* meaning a "hump" and *phriktos* meaning "horrible, terrible" (Brown 1956), referring to the prominently humped scutellum and the fearsome appearance of *Trichodocerus* species.

***Trichodocerus chrysochaetus* Anzaldo, sp. nov.**

Figs. 3.2B, 3.3J, 3.5G, 3.18A–B, 3.19H, 3.20E-F, 3.29A.

Diagnosis. This is the only species of *Trichodocerus* with the presence of long golden hairs on the underside of the protibiae in the males (Fig. 3.3J); *T. condylothecus* of the *obrieni* group has sparse elongate ventral setae on the profemora and tibia that are not golden, and an as yet undescribed species in the *obrieni* group has the same condition as *T. condylothecus* but on the hind leg. The rostrum being distinctly flattened laterally in the basal half bearing small yellow scales distal to antennal insertion is also distinct for this species. A prosternal rostral sheath being lined with linear white scales and not erect multifurcate setae separates it from other species in the *mecistotarbus* species group.

Description - holotype male. Length 3.47 mm, width 1.16 mm, length/width ratio 2.99. Integument dark brown, lighter on tarsi, rostrum, antennal scape and funicle. Dorsal scales

small, apically truncate to rounded, white, tan, to dark brown and black. Vestiture of legs, lateral and ventral surfaces mainly yellowish white to black scales. **Head**. Eyes subcontiguous, separated by ~2 very narrow linear scales at closest point, ventral lobe rounded, extending below ventral margin of rostral insertion. Vestiture above eyes bordering eyes, vertex bare. *Rostrum*: short (0.87x pronotal length), slightly arcuate in apical half, flattened ventrally and in the basal half flattened laterally with lateral and ventral surfaces delimited by a carina. Integument dorsally impressed on either side at base, with a short, faint, smooth median basal carina splitting into two and ending distal to antennal insertion, and a short oblique carina extending from basal impression and ending proximal to antennal insertion; smooth distal to antennal insertion, with dense, fine punctures in longitudinal rows, becoming smaller towards apex. Vestiture consisting of small linear yellow scales at base proximal to antennal insertion and a short longitudinal row of linear yellow scales distal to antennal insertion. *Antenna*: scape short, bulbous. Funicle with article 1 clavate, narrower apically than scape, shorter than article 2. Articles 2-7 slender; article 2 slightly longer than 3, 4 slightly longer than 3 and longer than 5, 6 longer than 5 and 7. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion longer than basal portion, 3 ventricose, 4 longer than 3, distinctly stalked, widest in apical half. **Prothorax**. *Pronotum*: lateral margins in basal half gradually widening, rounded in anterior half except anterior constriction, widest just before constriction. Median longitudinal carina prominent and dorsally flattened in anterior two-thirds, reduced to posterior margin. Vestiture consisting of anteriorly narrowing lateral white vittae, with the disk mainly mottled tan and dark brown, tan scales forming a diffuse vitta halfway between median carina and lateral white vitta, and a median narrow tan vitta bordering carina; mottled tan and brown scales extending on lateral prothoracic face becoming white ventrally. Suberect setae short,

indistinct. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging to apex. Sheath interior and lateral margins with dense, linear white scales. **Mesothorax**. Scutellum flat. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Integument slightly impressed on interval 2 one-fourth from base. Pattern composed of small tan scales contrasting with longitudinal stripes of dark coppery brown scales and less defined regions of white scales; white scales in a broad band on humerus continuous with lateral pronotal vitta and extending to interval three about one-third from base, and more diffuse laterally around dark areas; short longitudinal stripes of dark scales present on intervals 2, 3, 5 and 7 at about middle, a longer stripe on interval 3 about one-third from apex, and an oblique band spanning intervals 8 and 9 near middle. Interval 9 about one-third from apex briefly subcostate, interval 10 below with reduced scales, narrower anteriorly. Striae with deep circular punctures bearing a single seta. *Mesoventrite*: ventral process short, slightly concave ventrally. Anterior and ventral face and intercoxal region with elongate ventrally and posteriorly produced setae. *Mesanepisternum*: region bordering mesepimeron impressed, with crustose punctures and a few whitish scales. *Mesepimeron*: with linear whitish scales. **Metathorax**. *Metaventrite*: ventrally concave, rounded to sides. Vestiture ventrally suberect multifurcate setae encircling central glabrous area, densest at rounded lateral margin, becoming linear white scales laterally. *Metanepisternum*: anteriorly with small linear yellowish white scales, becoming a single row of linear scales at middle, and denser and smaller scales posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending to sternite VI. Pro- and mesocoxae with mesal tuft of multifurcate setae, also present on pro- and mesotrochanters, pro- and mesofemora, and metacoxa, ventrally. All femora ventrally unarmed, meso- and metafemora with scales ventrally and apically white, a large

coppery brown macula laterally and dorsally; profemoral scales yellowish white dorsally, white ventrally. Tibia dorsally with white scales, ventally with setae; profemora ventrally with elongate golden setae. Protibial setal brush covering about one-fourth apicoventral surface. Metatibial apex with apex of uncus projecting over middle of apex, a small tooth at the middle of the apex, and a smaller tooth at the anterior margin. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales largest dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternite III slightly longer than IV at the sides, V and VI equal in length and combined longer than IV. Sternite III and anteriorly on sternite IV with deep ovoid impression. Crustose punctures present laterally and in single row along posterior margin of each sternite except absent medially on sternites III and IV. Vestiture sparse setae in impression on sternites III and IV, linear white scales elsewhere.

Male terminalia (Fig. 3.19H). Aedeagus constricted at middle and at base, apex tapering to a rounded point. Endophallus with complex posterior sclerites, anterior sclerites paired, curved, bicolored spinose plates, no distinct transfer apparatus. Tegmen forming complete, ovoid ring, parameroid lobes approximate, manubrium short, broad, flat, apically rounded. Spiculum gastrale thick, arcuate, apically expanded into a flattened plate, basally asymmetrically bifurcate. Eighth sternite strongly sclerotized posteriorly with fringe of setae.

Female terminalia (Figs. 3.20E, F). Spiculum ventrale elongate, much longer than lamina, slightly expanded at apex, narrowly bifurcate at base of lamina. Lamina of sternite 8 sclerotized only at lateral arms, arms subparallel, with ventral setae along posterior margin. Bursa copulatrix with lightly sclerotized plate basally. Tergite 8 narrow, truncate apically, posterior margin lightly sclerotized at middle. Gonostylus of even width throughout.

Spermatheca subfalcate, collum produced and curved, ramus not produced, cornu hooked, slightly narrowing to rounded apex.

Variation. Male length 3.47-3.76 mm, width 1.16-1.30 mm, length/width ratio 2.90-3.06, rostrum 0.86-0.89x pronotal length. Female length 3.04-3.82 mm, width 1.00-1.34 mm, length/width ratio 2.84-3.05, rostrum 0.97-1.33x pronotal length. Paratypes with tan scales on pronotal disk darker, more golden brown and with base of elytra with longitudinal stripes of black scales in the middle of intervals between the humeri. The metatibial apex with the apex of the uncus projecting more longitudinally, with the apex over posterior half of tibial apex, a small tooth at inner flange adjacent to a similar sized tooth at anterior margin.

Distribution. Brazil (Rondônia, Mato Grosso, Amazonas). The specimen imaged and incorrectly identified as *T. brevilineatus* from French Guiana (Rheinheimer 2011: 82, Fig. 11) appears to be this species.

Material examined. Six specimens. Holotype male: "BRAZIL:Rondonia, 62km.SW.Ariquemes,Fzda.Rancho Grande,X-9-1993 / Collectors: C.W.&L.B.O'Brien" (ASUCOB). Paratypes (3): "BRAZIL: RONDONIA Fazenda Rancho Grande 62 km. S. Ariquemes 165 m. S10,32 W62,48 12-22 November 1991 E. M. Fisher collector" (1♂, ASUCOB); "Brazil:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, 5-17-X-1993,JE.Eger" (1♂, ASUCOB); "Brazil:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, xi-15-'94, CW.O'Brien" (1♀, ASUCOB). Additional material: "BRAZIL: Am. Reserva Ducke 26km NE Manaus Barbosa, M.G.V. / Plot C Malaise 2 March 1995" (1♀, NHM); "Gallery forest / BRAZIL: Mato Grosso, 12°50'S., 51°47'W. 10.x 1968 O.W. Richards" (1♀, NHM).

Etymology. The epithet is derived from the Greek *chrysochaites*, meaning "golden-haired" (Brown 1956), referring to the elongate golden hairs on the ventral surface of the protibia in the male (Fig. 3.3J).

***Trichodocerus stockwelli* Anzaldo, sp. nov.**

Fig. 3.5F, 3.18C–D, 3.19I, 3.29A.

Diagnosis. *Trichodocerus stockwelli* can be separated from other species in the *mecistotarbus* group by the wider body, denser dorsal vestiture, more strongly impressed rostral base giving the region between antennal insertions an inflated appearance, and distinct elytral scale pattern.

Description – holotype male. Length 3.98 mm, width 1.56 mm, length/width ratio 2.55. Integument dark brown, lighter on tarsi, rostrum, and antennal scape and funicle. Dorsal scales dense, small, apically truncate to rounded, white, tan, and coppery brown to black Vestiture of legs, lateral and dorsal surfaces white, tan, and coppery brown scales and setae. **Head**. Eyes subcontiguous, separated by ~2 very narrow linear scales at closest point, ventral lobe rounded, extending below ventral margin of rostral insertion. Vestiture above eyes bordering eyes, vertex bare. *Rostrum*: short (0.97x pronotal length), slightly arcuate in apical half, flattened ventrally. Integument dorsally at base rugose, very strongly impressed on either side, with a short median carina splitting into three faint carinae ending slightly distal to antennal insertion; smooth distal to antennal insertion, with dense, fine punctures in

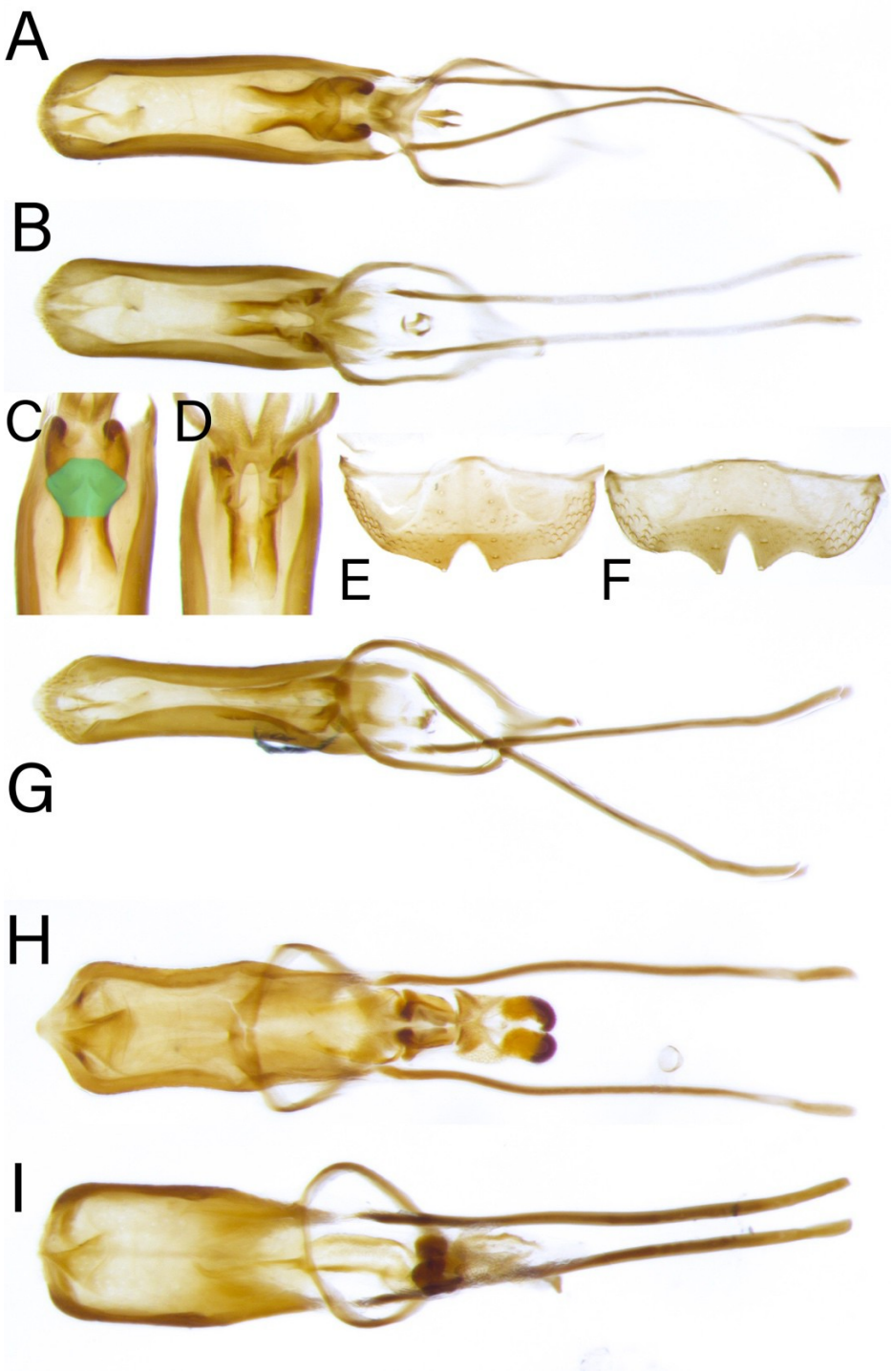

Figure 3.19. Male terminalia of the *mecistotarbus* group. A) *T. mecistotarbus* aedeagus, dorsal view; B) *T. fazerangrus* aedeagus, dorsal view; C) *T. mecistotarbus* posterior endophallic sclerite with fused portion highlighted; D) *T. fazerangrus* endophallic sclerite; E) *T. mecistotarbus* tergite 7; F) *T. fazerangrus* tergite 7; G) *T. hybophrictus* aedeagus, dorsal view; H) *T. chrysochaetus* aedeagus, dorsal view; I) *T. stockwelli* aedeagus, dorsal view.

longitudinal rows. Vestiture consisting of small linear yellow scales at base until rostral insertion, fine setae mostly laterally extending to mid-length. *Antenna*: scape short, bulbous. Funicle with article 1 clavate, narrower apically than scape, slightly shorter than article 2. Articles 2-7 slender, cylindrical; 3 longer than 2, 4 longer than 3 and 5, 6 longer than 5 and 7. Club with four distinct articles, articles 1 and 2 ventricose-rostrate with apical rostrate portion longer than basal portion, 3 ventricose, 4 slender, longer than 3, fusiform. **Prothorax**. *Pronotum*: constricted at base and apex, rounded laterally, widest at middle. Median longitudinal carina sharp in anterior half, reduced in posterior half. Integument impressed anterolaterally on disk. Vestiture consisting of a lateral white vitta, densest basally, and a diffuse oblique white stripe from the anterior margin on either side of median carina extending halfway to base and laterally somewhat merging with longitudinal vitta; scales surrounding white scales on disk mottled tan and brown, suberect scales arising from shallow, crater-like punctures ,mostly brown in posterior half, tan bordering white scales; tan scales extending laterally on prothorax in anterior half, becoming white ventrally and brown at greatest width. *Prosternum*: rostral sheath widest anteriorly, constricted one-third from anterior margin, evenly converging. Coxal rim distinctly raised at junction with sheath, creating lateral triangular processes. Sheath lateral margins covered with dense multifurcate setae, sparse in sheath interior. **Mesothorax**. Scutellum rounded, slightly dorsally prominent, covered with multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humeri to one-third from apex, rounded to apex. Pattern with white scales at humerus continuous with lateral pronotal vittae, slightly arcuate and extending to interval 5 near middle; small macula anterior to middle on interval 3; broad vitta laterally beginning on interval 7 one-third from base, spanning intervals 7-9 at middle, and ending at apex of interval 8; short offset stripes on intervals 2-4. Dark coppery brown scales occur in short

offset stripes of equal length on intervals 3-5 at middle, an adjacent small black macula on interval 2, short stripes at interval 2, 3 and 5 one-third from apex. Basal third between white humeral vittae anteriorly tan, gradually becoming dark brown at middle. Interval 9 subcostate for one-third length near middle, interval 10 below narrowed and with reduced scales. Striae with deep, round punctures each with a seta. *Mesoventrite*: ventral process short, slightly concave ventrally, ventrolateral corners slightly produced laterally. Anterior face with small adpressed multifurcate setae, ventral face and intercoxal region with dense, elongate, ventrally and posteriorly produced erect setae. *Mesanepisternum*: region bordering mesepimeron impressed, with crustose punctures and a few whitish scales. *Mesepimeron*: with yellowish hair-like scales. **Metathorax**. *Metaventrite*: ventrally slightly concave, rounded to sides. Ventral vestiture composed of sparse suberect multifurcate setae, laterally becoming linear white scales. *Metanepisternum*: anteriorly with small linear yellowish white scales, becoming a single row of linear scales at middle, and denser and smaller scales posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femora extending to anterior margin of sternite VII. Pro- and mesocoxae with mesal tuft of setae, also present on pro- and mesotrochanters ventrally. All femora ventrally unarmed, with scales ventrally and apically white, a large coppery brown macula laterally and dorsally surrounded by tan scales, brown macula diffuse and dorsal on profemora. Tibia dorsally with white scales, ventrally with setae. Protibial setal brush covering about half apicoventral surface. Tarsi slender, article 1 three times as long as 2, articles 1 and 2 with linear white scales largest dorsally at apex. Claws angularly dilated at base. **Abdomen**. Sternites III slightly longer than IV, V and VI equal in length. and combined longer than IV. Median ovoid impression present on sternite III and anteriorly on sternite IV. Crustose punctures densest laterally and along posterior

margin in outer third of each segment. Vestiture in impression on sternites III and IV short, suberect multifurcate setae, elsewhere linear white to yellowish white scales.

Male terminalia (Fig. 3.19I). Lateral margins of aedeagus parallel in apical half, apex depressed, pointed, without dorsal spicules. Endophallus with several complex, paired sclerites: posteriorly an elongate, ovoid sclerite, with border sclerotized median area containing a patch of small teeth; a strongly sclerotized plate with two flattened, dorsally projecting lobes; anterior sclerites paired, lightly sclerotized, curved spinose plates; no distinct transfer apparatus. Tegmen forming complete, circular ring, parameroid lobes sclerotized, separate, manubrium thin, elongate. Spiculum gastrale thick, arcuate, apically expanded into a flattened plate, basally asymmetrically bifurcate. Eighth sternite strongly sclerotized posteriorly with fringe of setae, unsclerotized laterally at middle.

Female terminalia. Spiculum ventrale elongate, longer than lamina, slightly expanded at apex, narrowly bifurcate and somewhat laminate at base of lamina. Lamina of sternite 8 sclerotized only at lateral arms, arms subparallel posteriorly, with cluster of setae ventrally at apex. Tergite 8 narrow, posterior margin rounded, unsclerotized along most of posterior margin. Gonostylus of even width throughout. Spermatheca J-shaped, collum slightly produced, ramus not produced, cornu hooked, of relatively even width to rounded apex.

Variation. Male length 3.98-4.26 mm, width 1.56-1.62mm, length/width ratio 2.55-2.63, rostrum 0.97-0.98x pronotal length. Female length 3.04-3.99mm, width 1.23-1.55, length/width ratio 2.47-2.57, rostrum 0.97x pronotal length.

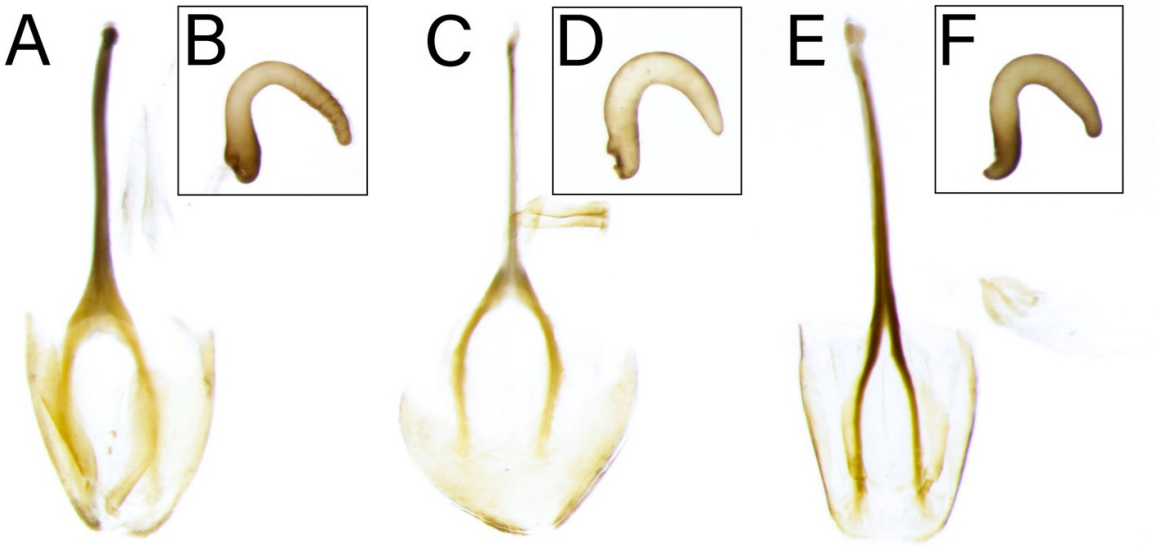

Figure 3.20. Female terminalia of the *mecistotarbus* group. A-B) Female terminalia (A) and spermatheca (B) of *T. mecistotarbus*; C-D) Female terminalia (C) and spermatheca (D) of *T. fazerangrus*; E-F) Female terminalia (E) and spermatheca (F) of *T. chrysochaetus*.

Material examined. Four specimens. Holotype male: "Panamá: Canal Zone Barro Colorado Is. 9°10'N 79°50'W / 5.viii.1974 H.A. Hespenheide" (ASUCOB). Paratypes: same data as holotype but date "9.ix.1974" (1♂ 1♀, ASUCOB); "CANAL ZONE,Barro Colorado Is., UV trap 1 (3m.high) 1 June1976H.Wolda" (1♂, ASUCOB).

Etymology. This species is named after Henry P. Stockwell, one of the authors of the Wolda *et al.* (1998) study that yielded many specimens of *Trichodocerus*.

VI. The *Trichodocerus obrieni* group. This species group is the most complicated set of species to differentiate due to their small size, very similar scale patterns, and in some cases broad and overlapping distributions. The longest setae of the antennal club are generally distinctly curved distally (Fig. 3.2C), the abdominal sternites have dense crustose punctures in multiple rows along the posterior margin, elytral interval 9 is evenly squamose and slightly tumescent posteriorly, not subcostate (except *T. selenion*), the ventral process of the mesoventrite has a small process at the middle of the ventral margin (except *T. selenion*, where it is strongly concave). The first two species are very widely distributed and likely represent complexes of sibling species. This species group is hypothesized to be related to the *antiquus* and *mecistotarbus* groups based on the presence of a triangular or subquadrate process on the rostrum below the antennal insertion and the generally shorter, more globular antennal scape.

***Trichodocerus obrieni* Anzaldo, sp. nov.**

Figs. 3.2C, 3.5H, 3.21A-B, 3.23A, 3.24D-E, 3.30A.

Diagnosis. In general appearance *T. obrieni* is most similar to *T. selenion*, from which it can be differentiated by the less dense greyish white scales, the broader, more heavily punctate rostrum, and the process of the mesoventrite that is slightly tumescent medially (not strongly concave as in Fig. 3.3H), significant differences in the largest endophallic sclerites and the shape of the transfer apparatus, and the female bursa copulatrix is without plate-like sclerotization (Fig. 3.24D). Based on the shape of the posterior rectangular plate-like sclerite of the endophallus, *T. obrieni* is likely more closely related to *T. condylothecus*, which is easily distinguishable by the apically knobbed rostral sheath.

Description - holotype female. Length 2.95 mm, width 1.02 mm, length/width ratio 2.90. Integument reddish brown, lighter on the tarsi, rostrum, and antennal funicle. **Head**. Eyes separated by ~2 linear scales at closest point (Fig. 3.5H), ventral lobe broad, extending to ventral margin of rostral insertion. Scales above eyes yellowish white, limited to dorsal border of eyes. *Rostrum*: moderately elongate (1.20x pronotal length), arcuate, slightly widened at apex. Ventrally flattened, ovoid in cross section at apex. Transversely impressed dorsally at base, between antennal insertions with median smooth, impunctate area extending to apex and laterally borded by faint carina confluent proximal to antennal insertion. Integument smooth distal to antennal insertion, with fine punctures in longitudinal rows to apex, denser at apex. *Antenna*: scape short, globular. Funicle with article 1 clavate, shorter than article 2, 3 shorter than 2 and 4, 6 longer than 5 and 7. Club with four distinct articles (Fig. 3.2C), 1 and 2 ventricose-rostrate with basal portions pyriform with apical

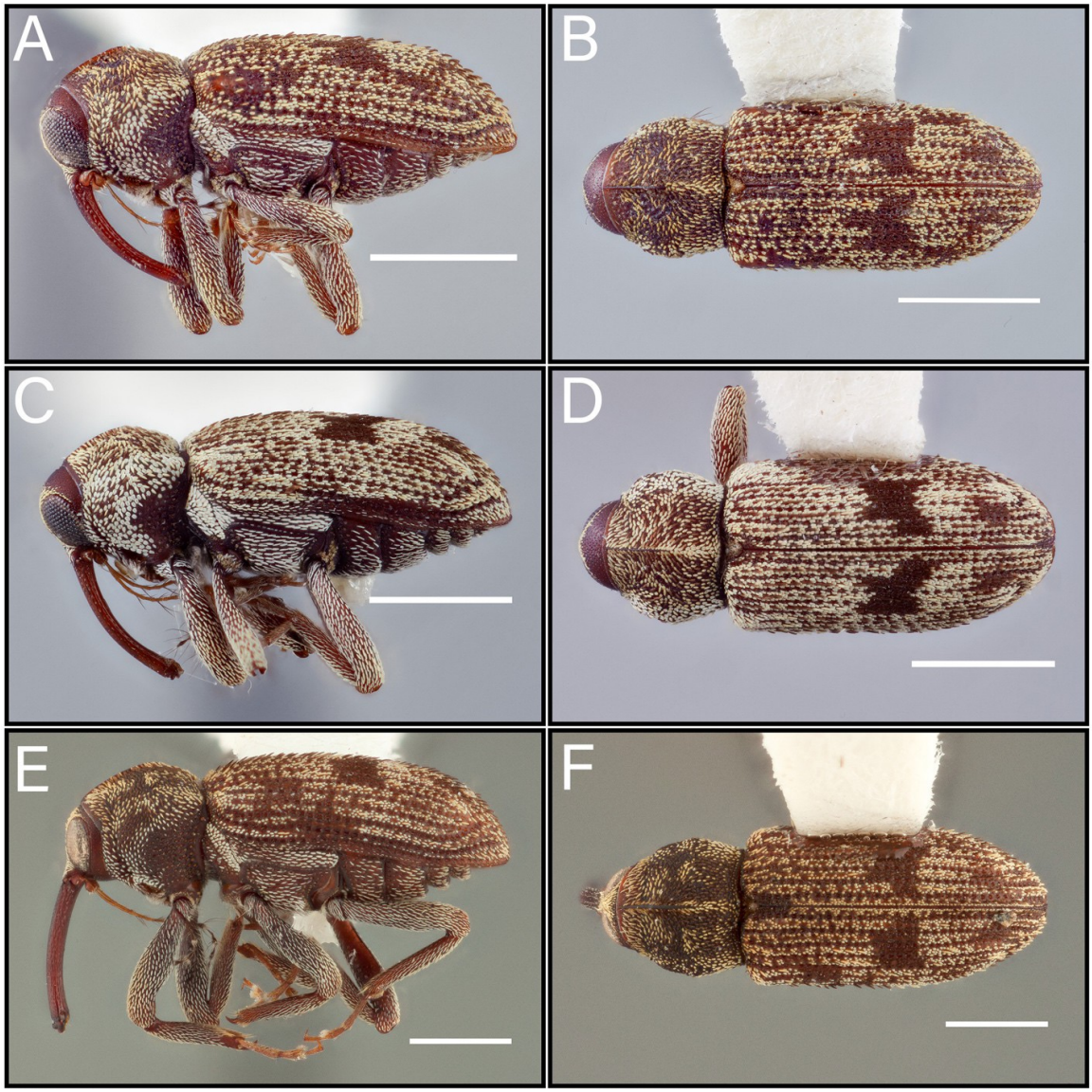

Figure 3.21. Dorsal and lateral habitus of species in the *obrieni* group. A-B) *T. obrieni* holotype female; C-D) *T. selenion* holotype female; E-F) *T. mariae* holotype.

rostrate portions shorter than basal portion, 3 pyriform, 4 stalked, apically ovoid, slightly longer than 3. **Prothorax**. *Pronotum*: apically constricted, lateral margins evenly rounded, widest at middle. Median longitudinal carina present in anterior half, elevated, dorsally flattened. Scale pattern mostly dark brown with contrasting white to tan scales present along anterior margin, lateral vitta, short posterior vitta from posterior margin at middle to apex of median carina, and diffuse, arcuate vitta spanning anterior margin on either side of carina and joining short vitta at base; laterally white scales extending in anterior half. *Prosternum*: rostral sheath constricted one-third from anterior margin, convergent to apex. Sheath lateral margins and interior with dense multifurcate setae. **Mesothorax**. Scutellum rounded, with dense multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical third. Scales small, with surrounding integument exposed; mostly tan to white with contrasting dark brown maculae at middle on interval 2-5, posterior to humerus on intervals 6-7, short basal stripe posterior to the scutellum, short stripe on the declivity on interval 3, and on interval 6 posterior to median macula. Interval 9 flat. Striae with large, deep, circular punctures each bearing a single seta. *Mesoventrite*: ventral process slightly concave with small prominence at middle, ventrolateral corners somewhat laterally produced. Anterior face with dense small multifurcate setae, ventrally and intercoxal region with longer setae. *Mesanepisternum*: border with mesepimeron impressed, with dense crustose punctures and sparse white scales. *Mesepimeron*: white scales dense. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides. Vestiture linear white scales, becoming larger and denser at rounded sides and sparse again below metanepisternum. Crustose punctures present along anterior and posterior margin of lateral surface. *Metanepisternum*: anteriorly scales small, linear, becoming larger and sparse one-fourth from anterior margin and denser at posterior margin. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femur extending to sternite

VI. Procoxae with mesal tuft of sparse elongate setae. All femora ventrally unarmed, with linear white scales. Protibial setal brush covering apicoventral half. Tarsi very slender, article 1 three times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV at the sides subequal in length, V and VI subequal, combined longer than IV. Crustose punctures dense along anterior margin of each sternite, vestiture linear white scales.

Female terminalia (Figs. 3.24D, E). Spiculum ventrale elongate, longer than lamina, slightly expanded and rounded at apex, bifurcate at base of lamina, arms at 45 degree angle. Lamina of sternite 8 sclerotized only at lateral arms, arms slightly arcuate posteriorly. Tergite 8 narrow, posterior margin rounded, with elongate setae. Gonostylus of even width throughout. Spermatheca J-shaped, collum and ramus not produced, cornu hooked, becoming slightly narrower towards apex, apex rounded.

Variation. Female length 2.51-3.39 mm, width 0.86-1.31 mm, length/width ratio 2.59-2.92, rostrum 1.10-1.23x pronotal length. Male length 2.45-2.70 mm, width 0.84-0.97 mm, length/width ratio 2.78-2.93, rostrum 0.88-0.90x pronotal length. Brown elytral markings reduced or expanded to neighboring intervals.

Male. As female, except sternite III impressed at middle, metatibial uncus more angled towards anterior margin of metatibial apex. *Male terminalia* (Fig. 3.23A): lateral margins of aedeagus parallel at middle, evenly converging to narrow truncate apex. Endophallus with large rectangular plate, slightly constricted at middle and curved ventrally at posterior margin. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Distribution. Guatemala, Costa Rica, Panama.

Comments. *Trichodocerus obrieni* is considered to be the species referred to by Champion (1906) as "brevilineatus var.?". The four specimens from Volcan de Chiriquí, Panama and Vera Paz, Guatemala are larger than any other *T. obrieni* specimens observed. Since they are all female, comparisons of the aedeagus was not possible they are not included in the type series as they may represent an additional species.

Material examined. Forty specimens. Holotype female: "CANAL ZONE,Barro Colorado Is., UV trap 3 (26m.high) 18Oct.1976H.Wolda" (ASUCOB). Paratypes (33): same as holotype but "trap 1 (3m.high) 19May1976" (1♀, ASUCOB), "trap 3 (26m.high) 24May1976" (1♀, ASUCOB), "trap 1 (3m.high) 29May1976" (1♀, ASUCOB), "4June1976" (1♀, ASUCOB), "17May1977" (1♀, ASUCOB), "trap 3 (26m.high) 19May1977" (1♀, ASUCOB), "trap 1 (3m.high) 26May1977" (1♀, ASUCOB), "trap 3 (26m.high) 29 May1977" (2♀, ASUCOB), "trap 1 (3m.high) 30May1977" (1♀, ASUCOB), "26Sept1977" (1♀, ASUCOB), "trap 3 (26m.high) 18-x-1977" (1♂, ASUCOB), "trap 1 (3m.high) 17Apr.1978" (1♀, ASUCOB), "18Apr.1978" (1♂, ASUCOB), "1May1978" (1♂, ASUCOB), "2May1978" (1♀, ASUCOB), "3May1978" (1♂, ASUCOB), "16May1978" (1♂, ASUCOB), "17May1978" (1♀, ASUCOB), "trap 3(26m.high)" (1♀, ASUCOB), "trap 1 (3m.high) 20May1978" (1♂ 1♀, ASUCOB), "21May1978" (1♂, ASUCOB), "22May1978" (1♂, ASUCOB), "27June1978" (1♂, ASUCOB), "trap 3 (26m.high) 15July1978" (1♀, ASUCOB), "trap 1 (3m.high)H. Wolda 30-IV-1981" (1♂, ASUCOB), "trap 3 (26m.high) 21-IV-1981H.Wolda" (1♀, ASUCOB), "10May1983" (1♂, ASUCOB); "Panamá, Isla Barro Colorado Light trap week 22 N. III N 25-31 V 1988" (1♂, PCMENT); as previous but

"Week 36 N. I N 6-12 IX 1989" (1♂, PCMENT), "Week 17 O. III N 25 IV-1 V 1990" (1♀, PCMENT), "Week 19Q. I N 6-12 V 1992" (1♀, PCMENT). Additional specimens: "PANAMA, Bocas del Toro, Corriente Grande, Rio Changuinola / 9°17'30"N 82°32'41"W H.Wolda Feb.17,1980" (1♀, ASUCOB); "PANAMA,Pan.,Isla Maje,Lake Bayano 4-VI-1976 in camp, H. Wolda" (1♀, ASUCOB); "V. de Chiriqui, 25-4000 ft. Champion. / B.C.A. Col. IV.4. Trichodocerus brevilineatus var. Champ." (3♀, NHM); "San Juan Vera Paz. Champion / B.C.A. Col. IV.4. Trichodocerus brevilineatus var. Champ." (1♀, NHM).

Etymology. This species is named in honor of Charles W. O'Brien, who has been exceedingly generous with loaning specimens and spreading his knowledge of and passion for weevils.

***Trichodocerus selenion* Anzaldo, sp. nov.**

Figs. 3.3H, 3.5I, 3.21C–D, 3.23B, 3.24A, 3.24F-G, 3.30B.

Diagnosis. *Trichodocerus selenion* is most similar in body shape and size to *T. obrieni*, and can be differentiated by the more slender rostrum, denser whitish grey vestiture, concave ventral process of the mesoventrite (Fig. 3.3H), the wider prosternal rostral sheath, and the subcostate ninth elytral interval in the posterior third, differently shaped endophallic sclerites and transfer apparatus, and the female bursa copulatrix with a subquadrate plate-like sclerite (Fig. 3.24F).

Description – holotype female. Length 3.01 mm, width 1.04 mm, length/width ratio 2.89. Integument dark reddish brown, lighter on the tarsi, rostrum, antennal scape and funicle.

Head. Eyes subcontiguous, separated by ~3 linear yellowish white scales at closest point (Fig. 3.5I), ventral lobe broad, extending to ventral margin of rostral insertion. Scales above eyes in 2-3 rows of linear scales, becoming narrower between eyes and white above rostral insertion. *Rostrum*: elongate (1.39x pronotal length), arcuate. Ventrally flattened, subcylindrical in cross section at apex. Transversely impressed dorsally at base, between antennal insertions with median smooth, impunctate area extending to apex and laterally borded by faint carina confluent proximal to antennal insertion. Integument smooth distal to antennal insertion, with fine punctures in longitudinal rows to apex. *Antenna*: scape short, globular. Funicle with article 1 clavate, shorter than article 2, 2 longer than 3, 3 and 4 subequal, 4 longer than 5, 6 longer than 5 and 7. Club with four distinct articles, 1 and 2 ventricose-rostrate with basal portions pyriform with apical rostrate portions shorter than basal portion, 3 pyriform, 4 fusiform. **Prothorax**. *Pronotum*: apically constricted, lateral margins evenly rounded, widest at middle. Median longitudinal carina present in anterior half. Integument convex on disk. Scales mostly tan and brown with contrasting white scales along basal margin, in lateral vitta and in short basal vitta from posterior margin to apex of carina; white scales extending ventrally in anterior half of lateral prothoracic face. Suberect scales distinct, arising from shallow, crater-like punctures. *Prosternum*: rostral sheath constricted one-third from anterior margin, convergent to apex. Sheath lateral margins and interior with dense multifurcate setae. **Mesothorax**. Scutellum rounded, with dense multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical fourth. Scales small, dense, with little surrounding integument exposed; mostly whitish grey with contrasting dark coppery brown in a somewhat oblique fascia at middle on intervals 2-5 and in a short stripe at declivity on interval 3. Suberect scales dense, in single median row; tan to dark brown, when dark brown giving interval a striped

appearance. Interval 9 subcostate in posterior third. Striae with deep, round punctures. *Mesoventrite*: ventral process short, concave ventrally (Fig. 3.3H). Anterior and ventral face with multifurcate setae. *Mesanepisternum*: border with mesepimeron impressed, with dense white scales. Mesepimeron: white scales dense. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides. Ventral vestiture sparse setae, becoming linear white scales laterally. Crustose punctures present along anterior and posterior margin laterally. *Metanepisternum*: anteriorly scales small, linear, becoming larger and sparse one-fourth from anterior margin and denser at posterior margin. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femur extending to sternite VI. Procoxae with mesal tuft of sparse elongate setae. All femora ventrally unarmed, with linear white scales. Protibial setal brush covering apicoventral half. Metatibial apex with short uncus at posterior margin, inner flange produced into a small tooth adjacent to small tooth at anterior margin. Tarsi slender, article 1 three times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV at the sides subequal in length, V and VI subequal, combined longer than IV. Crustose punctures dense along anterior margin of each sternite, vestiture linear white scales.

Female terminalia (Figs. 3.24F, G). Spiculum ventrale elongate, longer than lamina. Lamina of sternite 8 sclerotized only at lateral arms, arms at base somewhat laminate, slightly arcuate posteriorly. Tergite 8 narrow, posterior margin subtruncate, with elongate setae. Bursa copulatrix basally with large subquadrate sclerite with median striations. Gonostylus of even width throughout. Spermatheca J-shaped, collum and ramus not produced, cornu hooked, becoming slightly narrower towards apex, apex rounded.

Variation. Some specimens with additional short dark brown stripes on intervals 4-6, forming oblique fascia with short stripe on interval 2 at the declivity.

Male. *Male terminalia* (Fig. 3.23B, 3.24A): lateral margins parallel at middle in dorsal view, converging to base and to narrow, truncate apex. Endophallus with large ventrally flat sclerite with two arms curving dorsally and posteriorly, posteriorly with patches of microdenticulations, transfer apparatus bifurcate, flat. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Distribution. Currently known from Panama and Brazil (Santa Catarina, Espirito Santo, Rondônia).

Material examined. Fifty-five specimens. Holotype female: "BRASIL,Esp.Santo Linhares IX-1972 M.Alvarenga&Roppa". Paratypes (39): same data as holotype (5♂ 9♀, ASUCOB); same data as holotype, but collector "M.Alvarenga" (1♂ 3♀, ASUCOB); "BRASIL:S.Catarina Nova Teutonia 300-500 m 27°11'S 52°23'W / –.xii.1973 F. Plaumann" (3♀ 2♂, ASUCOB); same data as previous but date "–.xi.1976" (4♂, ASUCOB); "Brasilien Nova Teutonia 27°11'B 52°23'L Fritz Plaumann 300-500 m xii 1959" (2♂ 4♀, ASUCOB); same data as previous but date ".ii.1939" (1♂ 1♀, NHM); "Nova Teutonia 27°11'S, 52°23'W Brazil, 300-500m IV 1960 1973 F. Plaumann" (2♂, CMNC); same as previous but date "Jan 1973" (1♂, CMNC). Additional material: "BRASIL:S.Catarina Nova Teutonia 300-500 m 27°11'S 52°23'W / –.xii.1973 F. Plaumann" (1♂, ASUCOB); "Brasil: Nova Teutonia, Santa Catarina XII-1973 F. Plaumann" (1♂, CMNC); "BRAZIL:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.RanchoGrande, xi-10-1994,C.O'Brien" (1♀, ASUCOB); same as

previous but date "xi-17-1994" (1♂, ASUCOB); "Panamá, Isla Barro Colorado Light trap Week 19N. I N 4-10 V 1988" (1♂, PCMENT); same as previous but "Ligth trap Week, 27N. II N 28 VI-5 VII 1988" (1♀, PCMENT); same as previous but "22 N. II N 31 V-6 VI 1989" (1♂, PCMENT), "23 N. I N 7-13 VI 1989" (1♀, PCMENT); same as previous but "Light trap Week 18 O. III N 2-8 V 1990" (1♀, PCMENT), "Light trap Week 19Q. I N 6-12 V 1992" (1♂, PCMENT) ; "CANAL ZONE,Barro Colorado Is., UV trap 1 (3m. high) 17May1977H.Wolda (1♀, ASUCOB); same as previous but "29May1977" (1♂, ASUCOB), "trap 3(26m.high) 26Apr.1978H.Wolda" (1♂, ASUCOB), "1May1978" (1♀, ASUCOB), "trap 1 (3m.high) 7May1978" (1♀, ASUCOB), "trap 3(26m.high) 27June1978" (1♀,ASUCOB).

Etymology. From the Greek *selenion* meaning "moonlight" (Brown 1956), referring to the dense light-colored whitish grey scales of this species, the nocturnal habit of *Trichodocerus*, and the crescent moon-shaped (concave) ventral margin of the mesoventral process (Fig. 3.3H).

***Trichodocerus mariae* Anzaldo, sp. nov.**

Figs. 3.5J, 3.21E–F, 3.29B.

Diagnosis. Similar to *T. plataleaculus* with widely separated eyes, the scales above the eyes not limited to the border with the eyes, and the distinctly dilated rostral apex (though not spatulate as in *T. plataleaculus*), but is otherwise easily distinguished from that species by the larger size, more heavily punctate rostrum, bicolored dorsum, non-prominent scutellum, and slightly different scale pattern.

Description – holotype female. Length 3.84 mm, width 1.34 mm, length/width ratio 2.87. Integument dark brown on the pronotum and base of femora, reddish brown elsewhere. **Head**. Eyes separated by half rostral width at middle (Fig. 3.5J), ventral lobe small, not extending to ventral margin of rostral insertion. Scales above eyes small, linear, yellow, extending dorsally in small dorsally rounded patch, becoming smaller and lighter towards rostral base. *Rostrum*: elongate (1.35x pronotal length), slightly, evenly arcuate. Ventrally flattened, ovoid in cross section in distal half, apically dilate. Transversely impressed dorsally at base, between antennal insertions with median smooth, impunctate area extending one-third from apex and laterally bordered by faint carinae that join proximally to antennal insertion. Integument rugose, densely punctured, punctures confluent laterally and becoming denser and smaller apically. *Antenna*: scape short, globular. Funicle with article 1 clavate, shorter than article 2, articles 2 and 3 subequal and longer than 4, 4 slightly longer than 5, 5 and 6 subequal, longer than 7. Club with four distinct articles, 1 and 2 ventricose-rostrate with apical rostrate portions shorter than basal tumescent portion, 3 ventricose, 4 longer than 3, distinctly stalked, widest at middle, apically rounded. **Prothorax**. *Pronotum*: apically constricted, lateral margins evenly rounded, widest at middle. Median longitudinal carina prominent and dorsally flattened in anterior three-fourths, reduced to apex. Integument more strongly convex in posterior half. Scale pattern mostly dark brown with a light lateral arcuate vitta composed of white and golden tan scales, a more medial arcuate vitta of tan scales interrupted at middle, and a narrow tan basal vitta extending from posterior margin to tallest point of median carina; white scales extending in anterior half of lateral surface to rostral sheath except a dark macula anterior to middle. Suberect scales tan and dark brown, indistinct. *Prosternum*: rostral sheath slightly constricted one-third from anterior margin, convergent to apex. Sheath lateral margins and interior with dense multifurcate setae.

Mesothorax. Scutellum rounded, with dense multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical third. Scales small, with surrounding integument exposed; mostly tan to white with contrasting dark coppery brown maculae at middle on intervals 2-5, posterior to humerus on intervals 6-7, a short basal stripe posterior to the scutellum, and a short stripe on the declivity on interval 3. Interval 9 slightly tumescent at apex. Striae with large, deep, approximate circular punctures each bearing a single seta. *Mesoventrite*: ventral process short, slightly concave ventrally, with a small tumescent process ventrally on the anterior face. Anterior and ventral face and intercoxal region with dense multifurcate setae. *Mesanepisternum*: sparse white scales and crustose punctures, punctures densest bordering mesepimeron. *Mesepimeron*: white scales dense. **Metathorax**. *Metaventrite*: ventrally flat, vestiture composed of setae ventrally at middle and anterior margin and linear white scales along posterior margin, laterally with white scales becoming shorter towards metanepisternum and crustose punctures along anterior and posterior border. *Metanepisternum*: white scales in posterior half larger and denser. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femur extending to sternite VI. Procoxae with mesal tuft of sparse elongate setae. All femora ventrally unarmed, with linear white scales. Protibial setal brush covering one half apicoventral surface. Metatibial apex with apex of uncus projecting over posterior half of tibial apex, inner flange with a small tooth, anterior margin with a similarly sized tooth. Tarsi slender, article 1 three times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV at the sides subequal in length, V and VI subequal, combined longer than IV. Crustose punctures dense along anterior margin of each sternite. Scales sparse, linear, white.

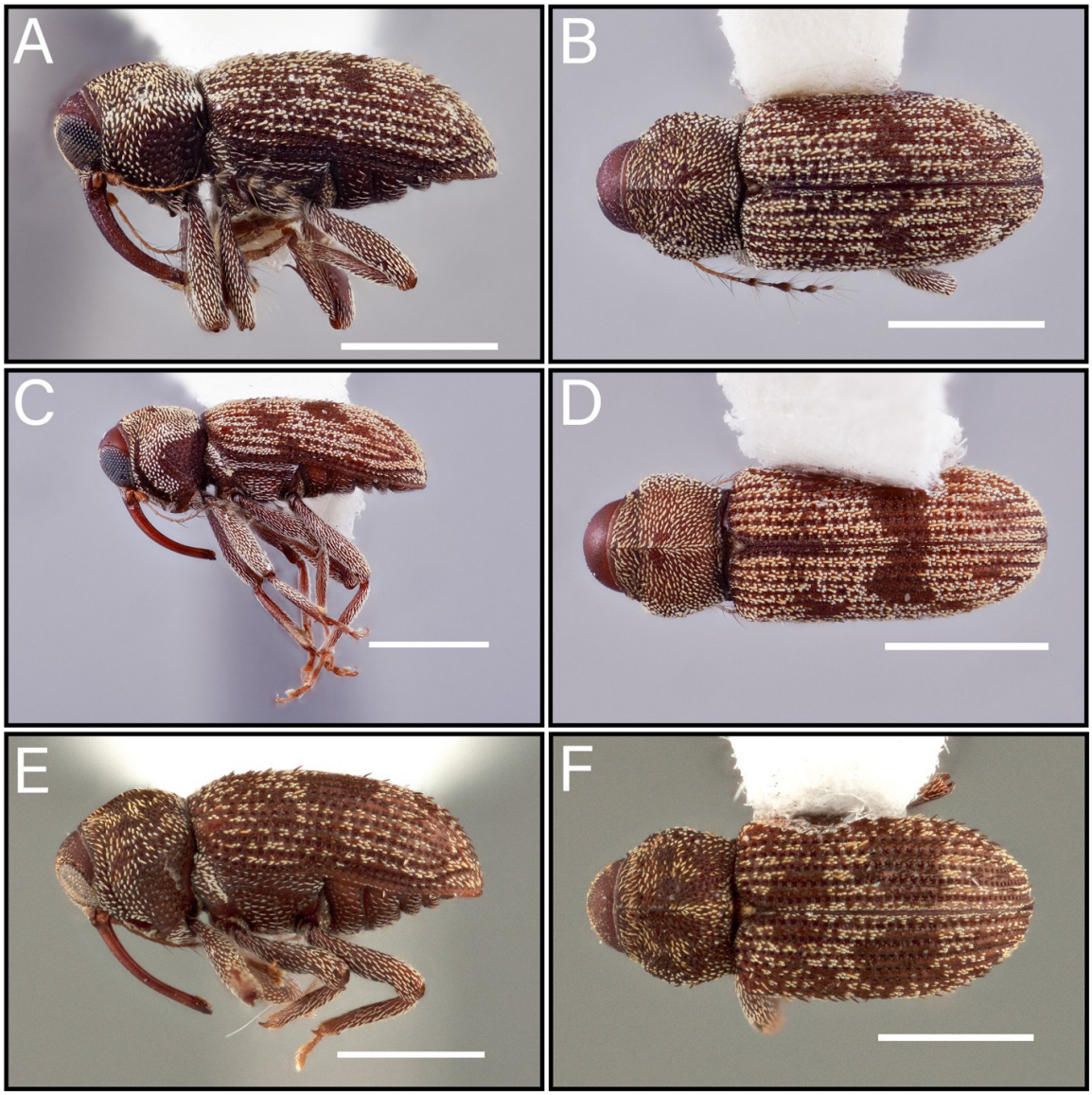

Figure 3.22. Dorsal and lateral habitus of species in the *obrieni* group. A-B) *T. condylothecus* holotype; C-D); *T. torquatus* holotype; E-F) *T. plataleaculus* holotype.

Material examined. One specimen. Holotype female: "BRAZIL: Rondonia, 62km.SW.Arique-mes,Fzda.Rancho Grande,XI-13-1994 / lot 18 C.W.&L.B.O'Brien " (ASUCOB).

Etymology. This species is named after my mother, Maria, who supported and encouraged my interest in the natural world as a child.

***Trichodocerus condylothecus* Anzaldo, sp. nov.**

Figs. 3.3G, 3.4K, 3.22A–B, 3.23C, 3.24B, 3.30A.

Diagnosis. Though similar in appearance to several species in the *obrieni* group, especially to *T. obrieni* and *T. torquatus*, *T. condylothecus* can be easily distinguished by the apically knobbed prosternal rostral sheath (Fig. 3.3G), the dentate lateral margin of the pronotum (visible in Fig. 3.19B), and the elongate setae ventrally on the profemora and protibia (probably only in the male). The aedeagus is similar to *T. obrieni*, but with a rectangular plate-like endophallic sclerite that is not constricted medially.

Description – holotype male. Length 2.60 mm, width 0.97 mm, length/width ratio 2.69. Integument dark reddish brown, becoming lighter on the tarsi, antennal scape and funiculus. Dorsal scales small, white to tan and dark brown. **Head**. Eyes subcontiguous, separated by ~3 narrow, linear scales at closest point (Fig. 3.5K), ventral lobe broad, extending to ventral margin of rostral insertion. Scales above eyes yellow, limited to border of eye, not extending laterally along border over midpoint of eye, becoming yellowish white above rostral insertion. *Rostrum*: moderately elongate (1.21x pronotal length), evenly arcuate, flattened

ventrally, ovoid in cross section in distal half, slightly dilated at apex. Dorsally at base with faint, short median carina, slightly impressed on either side of carina. Integument roughly sculptured dorsally from base to slightly beyond antennal insertion, smooth to apex, with irregular rows of punctures, punctures becoming larger towards apex. *Antenna*: scape short, clavate. Funicle with article 1 clavate, shorter than article 2. Articles 2-7 slender, cylindrical; articles 2 and 3 subequal in length and longer than 4, 4 and 5 subequal, 6 longer than 5 and 7. Club with four distinct articles; articles 1 and 2 ventricose-rostrate, apical rostrate portion of 1 about as long as basal ventricose portion, rostrate portion of 2 shorter than basal ventricose portion, 3 ventricose, 4 with distinct stalk, fusiform apically. **Prothorax**. *Pronotum*: apically constricted, rounded to base, widest at middle. Median longitudinal carina present in anterior two-thirds, reduced posteriorly. Integument evenly convex on disk, laterally denticulate. Scales white laterally in diffuse vitta, centrally with small paired comma-shaped brown maculae on either side of apex of median carina, surrounding scales tan, becoming whitish along posterior margin. *Prosternum*: rostral sheath strongly constricted one-third from anterior margin, evenly converging to procoxae, abruptly expanded at apex, apically rounded (Fig. 3.3G). Sheath lateral margins and ventral surface lined with multifurcate setae. **Mesothorax**. Scutellum with dense multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical third, rounded to apex. Scales small, with surrounding integument exposed; mostly tan except for undulating fascia on intervals 2-5 at middle and a white macula at confluence of intervals 4-6; suberect scales tan to brown. Interval 9 slightly tumescent in posterior half. Striae with deep, circular punctures each bearing a single seta. *Mesoventrite*: ventral process short, slightly convex at middle, ventrolateral corners rounded, slightly projecting laterally. Anterior and ventral face and intercoxal region with elongate multifurcate setae. *Mesanepisternum*: linear white scales and

crustose punctures bordering mesepimeron. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides. Vestiture composed of ventral setae and lateral white scales, crustose punctures present laterally along anterior and posterior margin. *Metanepisternum*: white, linear scales becoming denser posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Procoxae with mesal tuft of elongate multifurcate setae. All femora ventrally unarmed, scales white laterally and ventrally, tan dorsally. Profemora and protibia ventrally with elongate setae, protibial setal brush covering about one-third apicoventral surface. Metatibial apex with large uncus at posterior margin, inner flange produced into small tooth at middle of apex, and smaller tooth at anterior margin. Tarsi slender, article 1 three times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal at sides, V and VI subequal, combined longer than IV. Sternite III slightly impressed anteriorly. Crustose punctures present on each sternite, densest laterally and along anterior margin, absent from anterior margin at middle of sternites III and IV. Vestiture composed of linear white scales and setae.

Variation. Male length 2.60-3.03 mm, width 0.97-1.15 mm, length/width ratio 0.97-1.15, rostrum 1.14-1.26x pronotal length. Paratypes with more distinct, larger central brown pronotal markings. Specimen from Amazonas, Brazil with dark brown macula dorsally distal to middle of femora. Female unknown. *Male terminalia* (Fig. 3.23C): aedeagus in lateral view arched, dorsal margin arcuate; apically narrowed to a rounded point, gradually widening from base to widest point subapically, fringed with setae apicolaterally. Endophallus with rectangular plate-like sclerite, anteriorly with dense microdenticles. Tegmen forming continuously sclerotized ovoid ring, widened dorsally at middle, parameroid lobes

approximate, attached at widened region, manubrium absent. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Distribution. Brazil (Amazonas, Rondônia), French Guiana.

Material examined. Four specimens. Holotype male: "BRAZIL:Rondonia, 62km.SW.Arique-mes,Fzda.Rancho Grande,X-16-1993 / CW.&LB.O'Brien,at merc.vap.&UVlight" (ASUCOB). Paratypes (3): "BRAZIL:RONDONIA Fazenda Rancho Grande 62 km. S. Ariquemes 165 m. S10,32 W62,48 12-22 November 1991 E. M. Fisher collector" (1♂, ASUCOB); "BRASIL,Amazonas, Estirao do Equador, Rio Javari, X-1979 / 4°33'S,71°38'W M. Alvarenga" (1♂, ASUCOB); "FRENCH GUIANA, falls near Camp Patawa, Kaw Mountain, 4.54465°N, 52.15258°W, elev. 177m, 16-V-2006, C.R. Nelson" (1♂, ASUCOB).

Etymology. The name is derived from the Greek *kondylos* ("knob") and *theke* ("sheath") (Brown 1956), in reference to the apically knobbed prosternal rostral sheath (Fig. 3.3G).

***Trichodocerus torquatus* Anzaldo, sp. nov.**

Figs. 3.22C-D, 3.29B.

Diagnosis. One of the smallest *Trichodocerus* species, distinct in the *obrieni* group for having the apical prothoracic constriction sulcate laterally and with crustose punctures and the procoxae covered in dense elongate setae. Shares with *T. plataleaculus* (and the otherwise dissimilar *T. hybophrictus*) the prominently humped scutellum.

Description – holotype male. Length 2.55 mm, width 0.83 mm, length/width ratio 3.05. Integument reddish brown, becoming lighter on tibiae, tarsi, rostrum, and antennal scape and funicle. **Head**. Eyes subcontiguous, separated by ~3 small linear scales at closest point, ventral lobe extending below ventral margin of rostral insertion. Scales above eyes limited to border with eyes, not extending laterally along border over center of eye, yellowish, becoming smaller and narrower between eyes, larger again to rostral base. *Rostrum*: moderately elongate (1.31 x pronotal length), evenly arcuate, flattened ventrally, ovoid in cross section, slightly dilated at apex. Dorsally at base slightly impressed on either side, smooth from antennal insertions to apex, with longitudinal rows of fine punctures. *Antenna*: scape short, globular. Funicle with article 1 clavate, shorter than article 2. Articles 2-7 slender, cylindrical; articles 2 and 3 subequal in length and longer than 4, 4 longer than 5, 5-7 subequal. Club with four distinct articles; articles 1 and 2 ventricose-rostrate, apical rostrate portion of article 1 as long basal ventricose portion, apical rostrate portion of article 2 shorter than basal ventricose portion of article 2, 3 ventricose, 4 with distinct stalk, apically ovoid. **Prothorax**. *Pronotum*: apically constricted, laterally rounded and widest posterior to constriction, converging to base. Median longitudinal carina present in anterior half, narrow, raised, absent in posterior half. Scales on disk mostly linear and tan with small transverse brown macula across median carina at middle of pronotum; laterally scales lager. Apical constriction laterally sulcate, with single row of deep crustose punctures becoming multiple rows adjacent to rostral sheath. Laterally white scales extending adjacent to prosternal sheath in arcuate, "C"-shaped patch. *Prosternum*: rostral sheath strongly constricted one-third from anterior margin, evenly converging to apex. Sheath lateral margins and ventral surface lined with multifurcate setae. **Mesothorax**. Scutellum prominently humped, apex visible in lateral

view, covered with multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical third. Scales small, with surrounding integument exposed; scales mostly tan to white with brown scales in a undulating fascia between interval 6 at middle, a longitudinal stripe on interval 1 posterior to scutellum, a small macula at intervals 5-7 posterior to humerus, a small macula at intervals 2-3 one-third from apex, and a small brown stripe on interval 6 one-third from apex; suberect scales mostly tan, brown in darker regions. Interval 9 tumescent in posterior half. Striae with deep round punctures each bearing a single seta. *Mesoventrite*: ventral process short, ventrally concave with small process at middle, ventrolateral corners narrow, produced lateroventrally. Anterior face and ventral margin with short multifurcate setae, intercoxal region with elongate setae. *Mesanepisternum*: dense crustose punctures and sparse white scales bordering mesepimeron. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides, vestiture ventrally sparse setae, laterally linear white scales, scales longest at rounded sides; crustose punctures dense at anterior and posterior borders. *Metanepisternum*: scales narrow, white, evenly dense along most of length, widest at anterior margin. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femur extending to sternite VII. Pro- and mesocoxae, -trochanter, and -femoral bases ventrally with dense, elongate setae. All femora ventrally unarmed, with linear white scales. Protibial setal brush covering one half apicoventral surface. Metatibial apex with uncus projecting over anterior apical margin. Tarsi slender, article 1 three times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternites III and IV subequal at sides, V and VI subequal, combined longer than IV. Crustose punctures dense along anterior margin of each sternite. Vestiture composed of setae and sparse linear white scales on sternites III and IV, linear white scales posterior to punctures on V-VII.

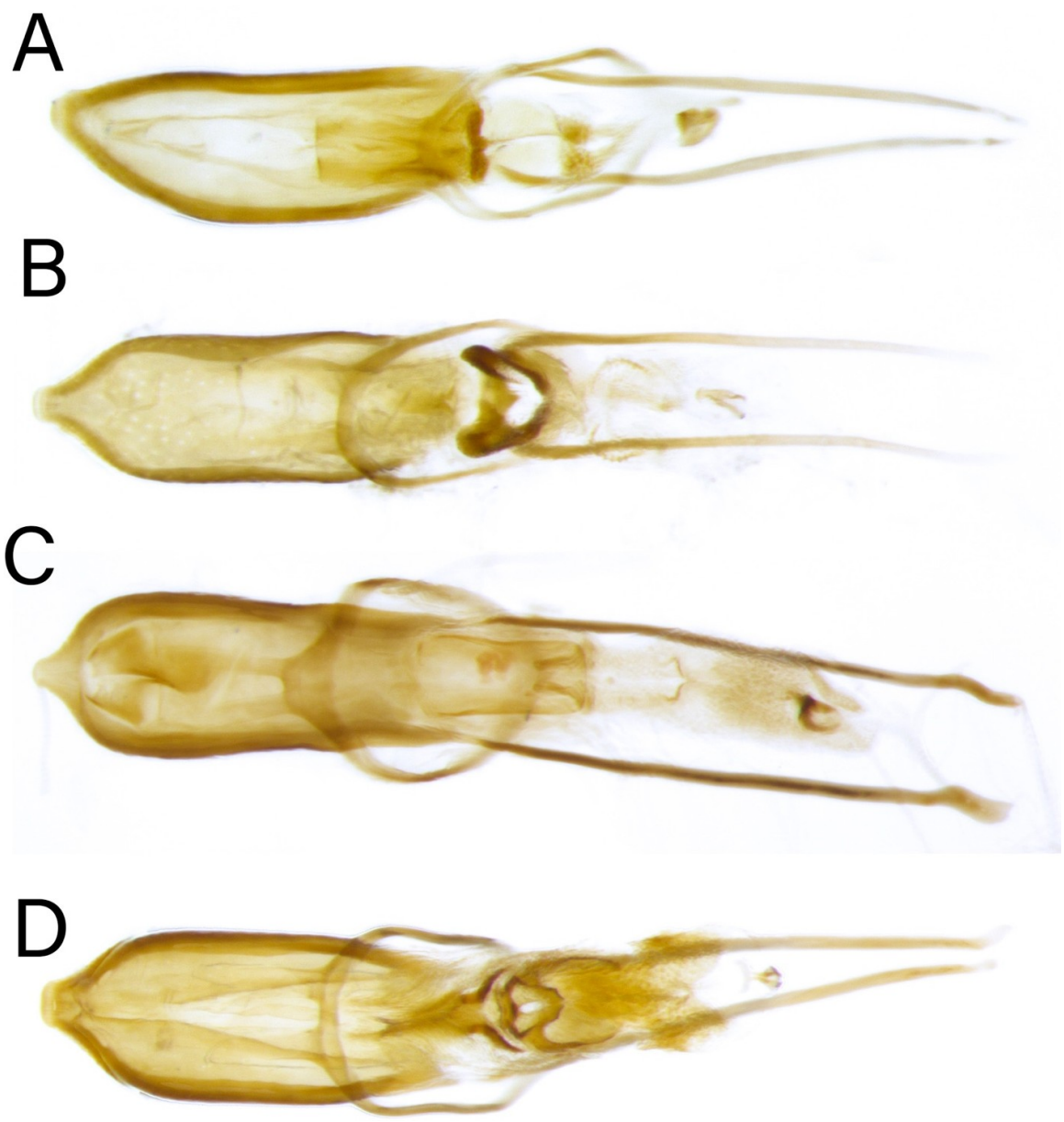

Figure 3.23. Male terminalia of the *obrieni* group. A) *T. obrieni*; B) *T. selenion*; C) *T. condylothecus*; D) *T. plataleaculus*.

Female. Length 2.40 mm, width 0.80 mm, length/width ratio 3.00. As male except rostrum longer (1.49x pronotal length), without elongate setae ventrally on leg segments except for procoxae.

Distribution. Currently known only from Brazil (Rondônia).

Material examined. Two specimens. Holotype male: "BRAZIL:Rond.UVtrap, 62km.SW.Ariquemes, Fzda.Rancho Grande, xi-10-1994" (ASUCOB). Paratype: "BRAZIL:RONDONIA Fazenda Rancho Grande 62 km. S. Ariquemes 165 m. S10,32 W62,48 12-22 November 1991 E. M. Fisher collector" (1♀, ASUCOB).

Etymology. From the Latin *torquatus*, meaning "adorned with a necklace or collar" (Brown 1956), the name refers to the laterally sulcate prothoracic apical constriction which contains a single row of crustose punctures, thus appearing as a beaded necklace.

***Trichodocerus plataleaculus* Anzaldo, sp. nov.**

Figs. 3.5L, 3.22E–F, 3.23D, 3.24C, 3.24H-I, 3.29B.

Diagnosis. The relatively small eyes separated by slightly less than the width of the rostrum at the base, the spatulate rostral apex easily separates this species from others in the *obrieni* group except *T. mariae*, which can be differentiated by the less dilated rostral apex and the larger eyes. The large subquadrate plate in the female bursa copulatrix has been observed only in *T. selenion*, but in that species it bears median striations and in *T. plataleaculus* does not (Fig. 3.24H).

Description – holotype female. Length 2.66 mm, width 1.01 mm, length/width ratio 2.66. Integument reddish brown, becoming lighter on the tibiae, tarsi, rostrum, antennal scape and funicle. Scales small, white and various shades of tan to dark coppery brown. **Head**. Eyes widely separated by width of rostrum at middle (Fig. 3.5L), ventral lobe small, extending to ventral margin of rostral insertion. Scales above eyes sparse, linear, white, extending dorsally in small, dorsally rounded patch, between eyes and above rostral insertion scales becoming slightly larger. *Rostrum*: elongate (1.36x pronotal length), slightly, evenly arcuate, flattened ventrally, ovoid in cross section in distal half, spatulate at apex. Transversely impressed dorsally at base, flattened between antennal insertions, smooth distal to antennal insertion with longitudinal rows of punctures becoming irregular at apex. *Antenna*: scape short, globular. Funicle with article 1 clavate, shorter than article 2. Articles 2 and 3 subequal in length and longer than 4, 4 longer than 5, 5-7 subequal. Club with four distinct articles; articles 1 and 2 ventricose-rostrate, basal portions pyriform with apical rostrate portions shorter than basal portion, 3 pyriform, 4 basally stalked, apically ovoid, about as long as 3. **Prothorax**. *Pronotum*: apically constricted, laterally rounded, widest at middle. Median longitudinal carina present in anterior half. Integument convex on disk, anteriorly declivous. Scales mostly brown linear scales with contrasting white to tan along anterior margin, in diffuse lateral vitta, in posterior median vitta from posterior margin to apex of median carina, and diffuse vitta from anterior margin to middle on either side of carina; white scales extend on lateral face in anterior half. *Prosternum*: rostral sheath strongly constricted one-fourth from base, gradually converging to apex. Sheath lateral margins and ventral surface lined with multifurcate setae. **Mesothorax**. Scutellum prominently humped, apex visible in lateral view, covered with multifurcate setae. *Elytra*: slightly wider than widest part of prothorax, parallel-sided from humerus to apical third. Scales small, with surrounding

integument exposed; mostly tan to white with contrasting brown maculae at middle from 2-5, smaller less well-defined macula from intervals 2-5 subbasally, and diffuse macula on elytral declivity. Interval 9 tumescent in posterior half. Striae with large, deep, approximate circular punctures each bearing a single seta. *Mesoventrite*: ventral process short, ventrally flat, with small median prominence, posterolateral corners narrow, produced ventrally. Anterior and ventral face and intercoxal region with elongate multifurcate setae. *Mesanepisternum*: dense crustose punctures and sparse white scales mostly bordering mesepimeron. **Metathorax**. *Metaventrite*: ventrally flat, rounded to sides, vestiture ventrally sparse setae, laterally linear white scales, scales longest at rounded sides; crustose punctures along anterior, dorsal, and posterior border of lateral portion. *Metanepisternum*: white scales small, linear, becoming larger and denser posteriorly. Metanepisternal suture with Type II sclerolepidia. **Legs**. Hind femur extending to sternite VI. Procoxae with mesal tuft of sparse elongate setae. All femora ventrally unarmed, with linear white scales. Protibial setal brush covering one half apicoventral surface. Metatibial apex with curved uncus at posterior margin projecting over anterior apical margin. Tarsi slender, article 1 two times longer than 2. Claws angularly dilated at base. **Abdomen**. Sternite III at sides shorter in length than IV, V and VI subequal, combined longer than IV. Crustose punctures dense along anterior margin of each sternite. Scales sparse, linear, white.

Female terminalia (Figs. 3.24H, I). Spiculum ventrale elongate, longer than lamina, dilated apically, bifurcate at base of lamina, arms at 45 degree angle. Lamina of sternite 8 sclerotized only at lateral arms, arms slightly arcuate posteriorly. Tergite 8 narrow, posterior margin rounded, lightly sclerotized, without elongate setae. Bursa copulatrix basally with large

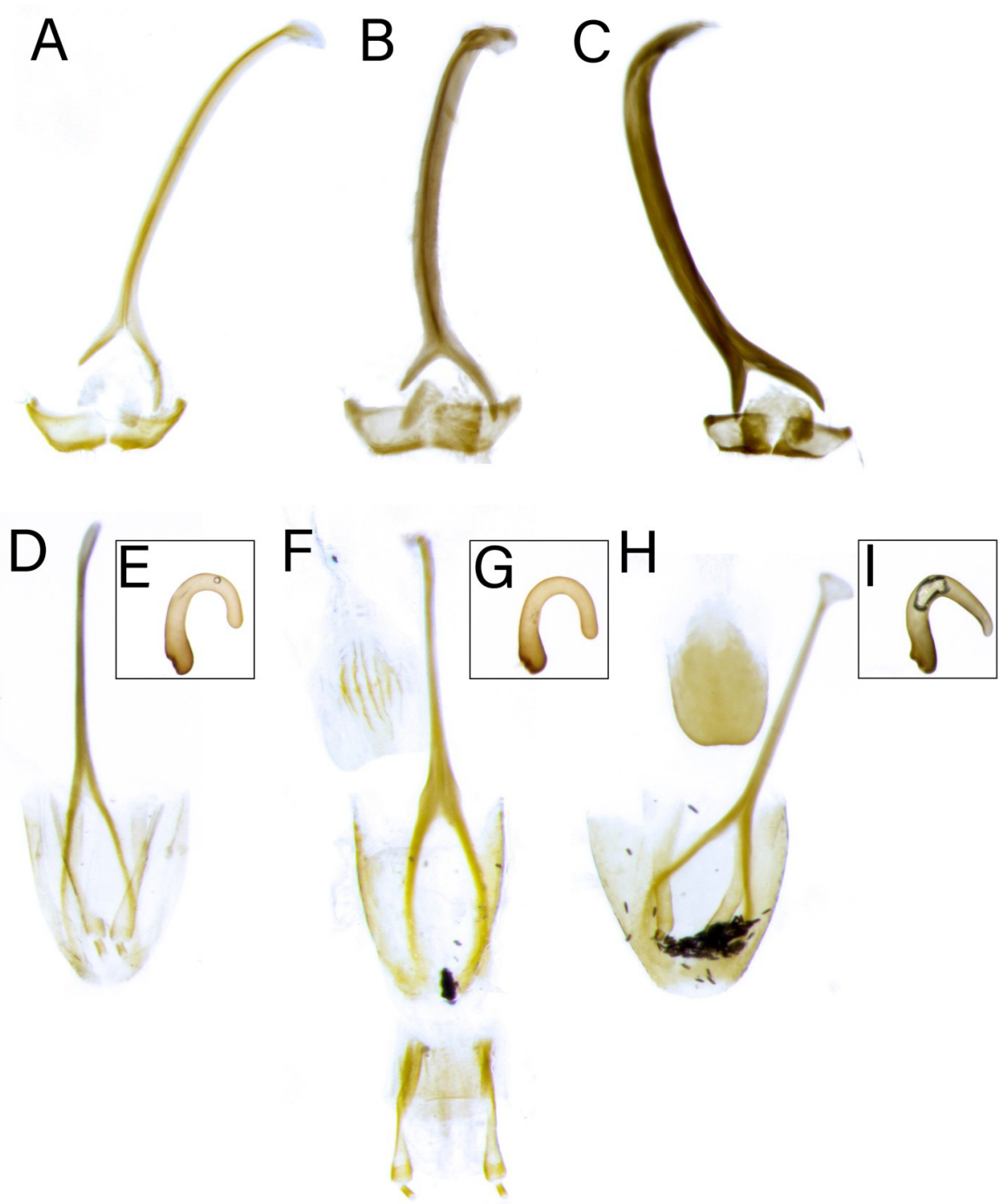

Figure 3.24. Male and female terminalia of the *obrieni* group. A) Male sternite 8 and spiculum gastrale of *T. selenion*; B) Male sternite 8 and spiculum gastrale of *T. condylothecus*; C) Male sternite 8 and spiculum gastrale of *T. plataleaculus*; D-E) Female terminalia (D) and spermatheca (E) of *T. obrieni*; F-G) Female terminalia (F) and spermatheca (G) of *T. selenion*; H-I) Female terminalia (H) and spermatheca (J) of *T. plataleaculus*.

subquadrate, flat sclerite. Gonostylus of even width throughout. Spermatheca subfalcate, collum not produced, ramus slightly produced, cornu hooked, gradually narrowing to rounded apex.

Variation. Female length 2.45-2.66 mm, width 0.923-1.01 mm, length/width ratio 2.62-2.66, rostrum 1.21-1.36x pronotal length. Variation is mainly in the extent of the brown elytral maculae, though two of the paratypes are fairly teneral.

Male. length 2.49 mm, width 1.03 mm, length/width ratio 2.41. Same as female except integument black, rostrum shorter (1.00x pronotal length), a slightly depressed ventral abdominal segment III, and smaller size. In the one male known, the cuticle is black except for the tibial apex, tarsi, and rostrum, which is reddish-brown. *Male terminalia* (Fig. 3.23D, 3.24C): arched in lateral view. In dorsal view lateral margins parallel at middle, converging to base and rounded to narrow, truncate apex, apicolaterally with fringe of setae. Endophallus with multiple large, complex sclerites and microdenticulate patch anteriorly. Tegmen forming complete, ovoid ring, manubrium broad, triangular. Spiculum gastrale thick, arcuate, apically expanded, basally asymmetrically bifurcate.

Material examined. Four specimens. Female holotype: "BRAZIL: Rondonia, 62 km.SW.Arique- mes,Fzda.Rancho Grande,X-12-1993 / Collectors: C.W.&L.B.O'Brien" (ASUCOB). Paratypes: same data as holotypes but dates "X-13-1993" (1♂, ASUCOB), "X-11-1993" (1♀, ASUCOB), "X-16-1993" (1♀, ASUCOB).

Etymology. The specific epithet "plataleaculus" is derived from *Platalea* L., the genus of threskiornithid birds commonly referred to as "spoonbills", and the diminutive suffix "-culus", forming "little spoonbill", in reference to this small species' apically spatulate rostrum.

Key to *Trichodocerus* species groups and species

1. Scrobe ventral or distal to antennal insertion not produced or at most produced in a small rounded process, antennal scape more elongate and clavate (Fig. 3.4) .....**2**, ***spinolae*, *brevilineatus*, and *ochromae* groups**

1'. Scrobe ventral to antennal insertion with prominent triangular to subquadrate process directed towards antennal insertion or flared laterally (Fig. 3.5), antennal scape shorter and more globular (Fig. 3.3A) .....**14**, ***antiquus*, *mecistotarbus*, and *obrieni* groups**

2. Dorsal vestiture mostly dense yellow to yellowish white scales.....**3**, ***ochromae* group**

2'. Dorsal vestiture various, predominantly scales in shades of brown, grey, or white.....**7**

3. Tarsal claws angularly dilated at base, mesoventral process prominent.....**4**

3'. Tarsal claws with broad basal tooth, mesoventral process short.....**5**

4. Article 4 of antennal club distinctly separated from article 3, basally stalked (Fig. 3.1D); mesoventral process vertical..... *T. ochromae* **sp. nov.**

4'. Article 4 of antennal club not distinct from article 3, basally broad; mesoventral process angled slightly anteriorly.....*T. atheatomerus* **sp. nov.**

5. Eyes separated by about half rostral width at middle (Fig. 3.4L), metatibia ventrally dentate, pronotal scales condensed in two arcuate vittae.....*T. prionasceles* **sp. nov.**

5'. Eyes more approximate, separated by less than half rostral width at middle; metatibia ventrally smooth; pronotal scales condensed in short basal median vitta.....**6**

6. Funicular article 2 subequal in length to 3.....*T. musathrus* **sp. nov.**

6'. Funicular article 2 longer than 3.....*T. gorgonarium* **sp. nov.**

7. Metanepisternal suture with distinct Type I (squamose) sclerolepidia, pygidium narrowly exposed in male.....**8**, ***spinolae* group**

7'. Metanepisternal suture without regular scales along metanepisternal suture (sclerolepidia Type II), pygidium not exposed in male.....**13**, ***brevilineatus* group**

8. Antennal club more compact, with rostrate portion of article 1 very short and apparently absent from article 2 (Fig. 3.1B) **9**

8'. Antennal club elongate, rostrate portions of articles 1 and 2 distinct (Fig. 3.1A) **11**

9. Dark triangular lateral fascia on elytra small, extending to interval 7...*T. yavinivensis* **sp. nov.**

9'. Fascia large, extending to interval 3.....**10**

10. Apicoventral protibial brush covering one-third ventral surface, elytral intervals 5, 7 and 9 without conspicuous light colored suberect scales, Mexico.....*T. browni* **sp. nov.**

10'. Apicoventral protibial brush covering one-fourth ventral surface, elytral intervals 5, 7 and 9 with conspicuous light colored scales, Panama.....*T. lathrios* **sp. nov.**

11. Elytra with grey chevron-shaped fascia at middle of elytra, pronotum without dense white scales, scales above eyes only bordering eye, metatibial apex without angular dilation along posterior face, rostrum about as long as (male) to longer than (female) pronotum.....**12**

11'. Elytra with diffuse white fascia near middle, pronotum with dense white oblique vittae, scales above eyes extending dorsally on vertex metatibial apex at least in male angularly dilated along posterior face, rostrum much shorter than pronotum (at least in male) .....*T. choristochion* **sp. nov.**

12. Elytra with black scales prominent along anterior border with grey chevron-shaped fascia particularly on intervals 4, 5, and 7 (Fig. 3.6D); endophallus of male without dense patch of spines (Fig. 3.8B), dorsal margin of aedeagus in lateral view angulate (Fig. 3.8D) .....*T. leptodontus* **sp. nov.**

12'. Elytra with anterior border of grey chevron-shaped fascia lighter in color, rarely black scales in intervals 4, 5, and 7 (Fig. 3.6B); endophallus of male with dense patch of spines (Fig. 3.8A), dorsal margin of aedeagus in lateral view rounded (Fig. 3.8C) .....*T. spinolae* Chevrolat

13. Median pronotal carina prominent, dorsally flattened; dark stripe at middle of elytral interval 5 more posterior than dark stripe on interval 3.....*T. brevilineatus* Champion

13'. Median pronotal carina faint; dark stripes at middle of elytral intervals 3 and 5 relatively even.....*T. hespenheidei* **sp. nov.**

14. Hind femur with a broad triangular ventral tooth.....**15**, ***antiquus* group**

14'. Hind femur unarmed ventrally.....**17**

15. Profemur unarmed ventrally.....*T. woldai* **sp. nov.**

15'. Profemur with a ventral tooth.....**16**

16. Elytral scale pattern mostly mottled, without large dark markings (Fig. 3.13B); scales above eyes extending dorsally on vertex (Fig. 3.5A).....*T. antiquus* Bondar

16'. Elytral scale pattern with a large dark macula at middle on intervals 2-6, bordered anteriorly and posteriorly by similar sized white maculae; scales above eyes mostly limited to border of eye (Fig. 3.5C).....*T. sobetes* **sp. nov.**

17. Abdominal sternites with crustose punctures along posterior margin mostly limited to a single row, multiple rows only at sides.....**18**, ***mecistotarbus* group**

17'. Abdominal sternites with multiple rows of dense crustose punctures along posterior margin .....**22**, ***obrieni* group**

18. Rostral sheath lined with linear white scales, rostrum laterally with short longitudinal row of yellow scales distal to antennal insertion, male with elongate, golden setae on ventral surface of protibia (Fig. 3.3J).....*T. chrysochaetus* **sp. nov.**

18'. Rostral sheath lined with multifurcate setae, rostrum laterally without longitudinal row of yellow scales, males without elongate, golden setae on ventral surface of protibia.....**19**

19. Rostrum strongly impressed on either side of base, body wide (length/width ratio ~2.5); aedeagus dorsally at apex without spicules.....*T. stockwelli* **sp. nov.**

19'. Rostrum only slightly impressed on either side at base, body narrow (length/width ratio >2.9); aedeagus dorsally at apex with spicules.....**20**

20. Scutellum prominently humped, visible in lateral view; elytral scale pattern with short, separate longitudinal stripes of dark scales on intervals 3 and 5 (Fig. 3.15F) .....*T. hybophrictus* **sp. nov.**

20'. Scutellum not visible in lateral view, elytral scale pattern with macula at middle composed of fused short longitudinal dark stripes of scales on intervals 2-5 (Figs. 3.15B, D) **21**

21. Body with a white lateral vitta, pronotal carina flat dorsally, endophallus with posterior sclerite broadly fused anteriorly (Fig. 17C), male tergite 7 posteriorly not strongly sinuate (Fig. 3.17E) .....*T. mecistotarbus* **sp. nov.**

21'. Body without a white lateral vitta, pronotal carina rounded dorsally, endophallus with posterior sclerite separate anteriorly (Fig. 3.17D), male tergite 7 posteriorly strongly sinuate (Fig. 3.17F) .....*T. fazerangrus* **sp. nov.**

22. Eyes separated by at least half rostral width at middle (Fig. 3.5J, L), rostral apex strongly dilated.....**23**

22'. Eyes subcontiguous (e.g. Fig. 3.5H), rostral apex similar in width to middle of rostrum or slightly dilated.....**24**

23. Rostrum apically spatulate, mostly smooth with small punctures, eyes widely separated by width of rostrum at middle (Fig. 3.5L).....*T. plataleaculus* **sp. nov.**

23'. Rostrum dilated apically, rugulosely punctate (Fig. 3.5J), eyes separated by about rostral width at middle.....*T. mariae* **sp. nov.**

24. Rostral sheath apically knobbed (Fig. 3.3G), protibia with a small ventral tooth .....*T. condylothecus* **sp. nov.**

24'. Rostral sheath converging to a point, protibia ventrally unarmed.....**25**

25. Subapical prothoracic constriction laterally sulcate, with row of crustose punctures .....*T. torquatus* **sp. nov.**

25'. Subapical prothoracic constriction not laterally sulcate, without crustose punctures **26**

26. Elytral scales dense, greyish white; ventral process of mesoventrite strongly concave along ventral margin (Fig. 3.3H); elytral interval 9 subcostate near middle third, without scales lateral to subcosta.....*T. selenion* **sp. nov.**

26'. Elytral scales tan, less dense; ventral process of mesoventrite flat ventrally, with small median tumescent process at middle; elytral interval 9 evenly squamose, not subcostate .....*T. obrieni* **sp. nov.**

Table 3.1. Checklist of *Trichodocerus* species and documented distributions.

T. antiquus Bondar, 1946.....Brazil, Bolivia, Argentina, Paraguay
T. atheatomerus **sp. nov.**.....Costa Rica
T. brevilineatus Champion, 1906.....Guatemala, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia
T. browni **sp. nov.**.....Mexico
T. choristochion **sp. nov.**.....Paraguay
T. chrysochaetus **sp. nov.**.....Brazil, French Guiana
T. condylothecus **sp. nov.**.....Brazil, French Guiana
T. fazerangrus **sp. nov.**.....Brazil
T. gorgonarium **sp. nov.**.....Colombia
T. hespenheidei **sp. nov.**.....Costa Rica, Panama, Colombia, Peru
T. hybophrictus **sp. nov.**.....Ecuador
T. lathrios **sp. nov.**.....Panama
T. leptodontus **sp. nov.**.....Costa Rica, Panama
T. mariae **sp. nov.**.....Brazil
T. mecistotarbus **sp. nov.**.....Costa Rica, Panama, Colombia, Ecuador, French Guiana, Brazil
T. musathrus **sp. nov.**.....Ecuador
T. obrieni **sp. nov.**.....Guatemala, Costa Rica, Panama, Brazil
T. ochromae **sp. nov.**.....Panama
T. plataleaculus **sp. nov.**.....Brazil
T. prionasceles **sp. nov.**.....Peru, Bolivia, Argentina
T. selenion **sp. nov.**.....Panama, Brazil
T. sobetes **sp. nov.**.....Mexico
T. spinolae Chevrolat, 1879.....Ecuador, Guyana, French Guiana, Brazil, Peru, Bolivia
T. stockwelli **sp. nov.**.....Panama
T. torquatus **sp. nov.**.....Brazil
T. woldai **sp. nov.**.....Costa Rica, Panama
T. yavinivensis **sp. nov.**.....Mexico, Guatemala

Discussion

Revisions of weevil genera frequently result in a significant increase in the number of included species (Oberprieler *et al.* 2007). *Trichodocerus* is no exception, having increased nine-fold in the number of described species with this treatment. Despite this increase in the knowledge on the genus there still remain many aspects of trichodocerine morphology, phylogeny, distribution, and behavior that are unknown and are a limiting factor in discovering more about these mysterious weevils. Some species are apparently quite abundant and have been collected with UV light traps in numbers (e.g. *T. woldai*; Wolda *et. al.* 1998) but little else is known about their biology; many other species, however, are known from very few specimens and host information will likely result in more specimens being collected.

It is unlikely that the correct phylogenetic placement of *Trichodocerus* is in the Conoderinae - the only similarity shared with many conoderines is the large eyes and tibial uncus, though the former is unlike any other New World conoderine in shape and in the coarse faceting, and the latter varies substantially inter- and intraspecifically in *Trichodocerus* and is common in wood-boring or arboreal weevils. Other features, such as sexually dimorphic elytro-tergal stridulation, are otherwise unknown in the Conoderinae (Lyal and King 1996). The greatest resemblance of trichodocerine character systems appears closest to various taxa of Molytinae (*sensu* Lyal 2014), though without any sister taxon currently identified, a transfer of the tribe to a different subfamily would be premature and will likely require phylogenetic analysis broadly sampling the subfamilies of Curculionidae to finally resolve.

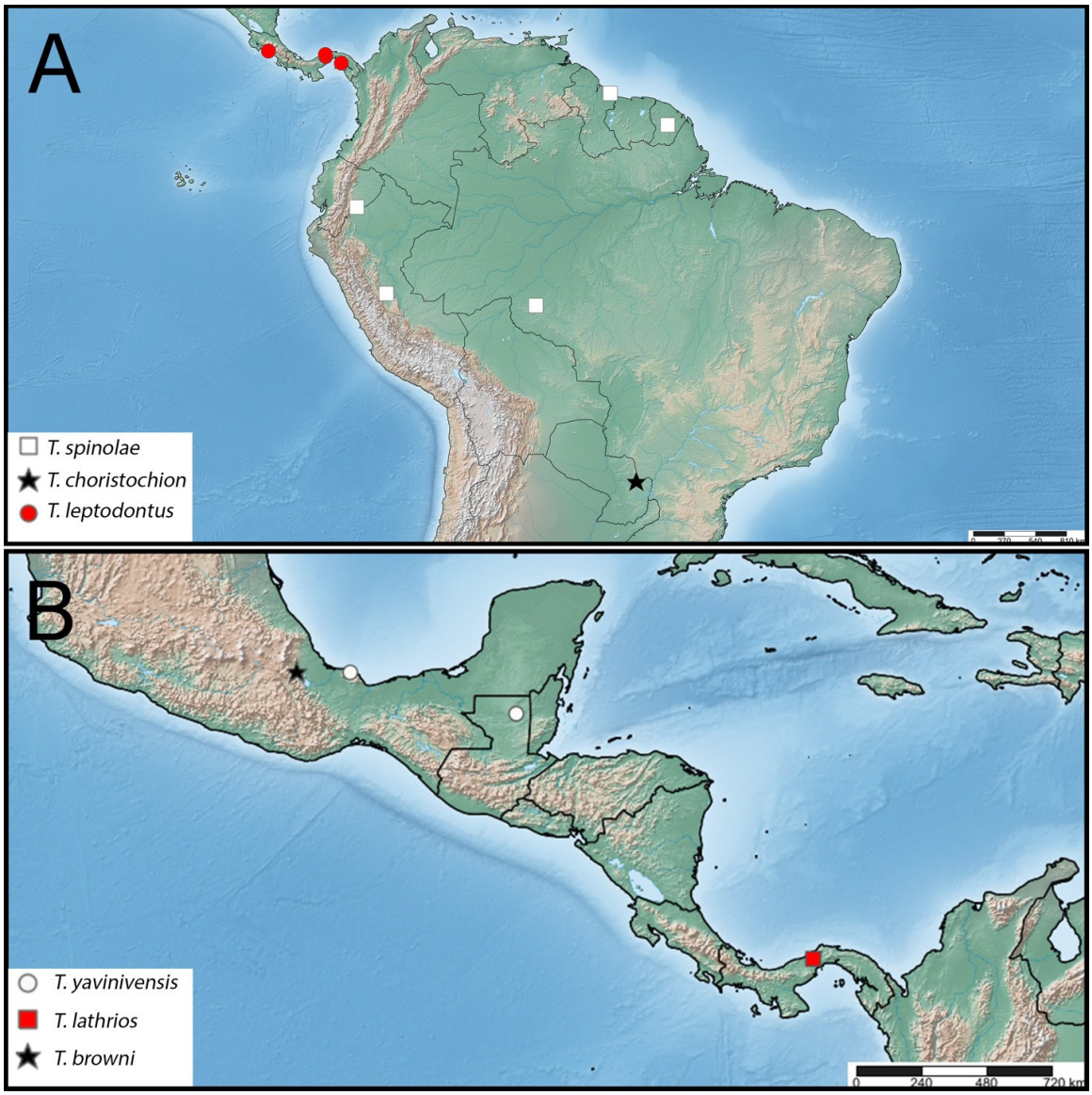

Figure 3.25. Distribution maps for the *spinolae* group. A) *T. spinolae*, *T. leptodontus*, and *T. choristochion*; B) *T. yavinivensis*, *T. browni*, and *T. lathrios*.

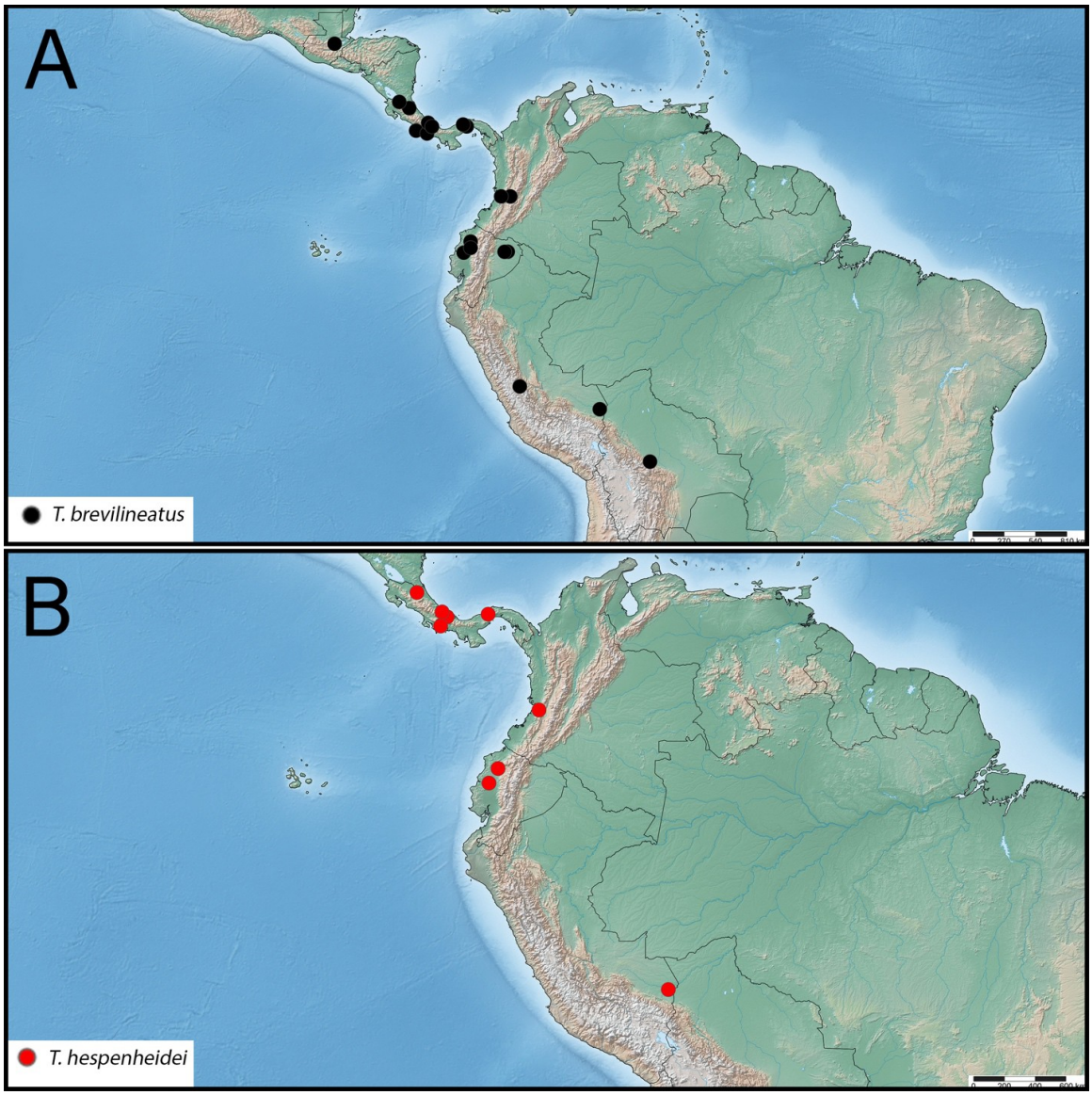

Figure 3.26. Distribution maps for the *brevilineatus* group. A) *T. brevilineatus*; B) *T. hespenheidei.*

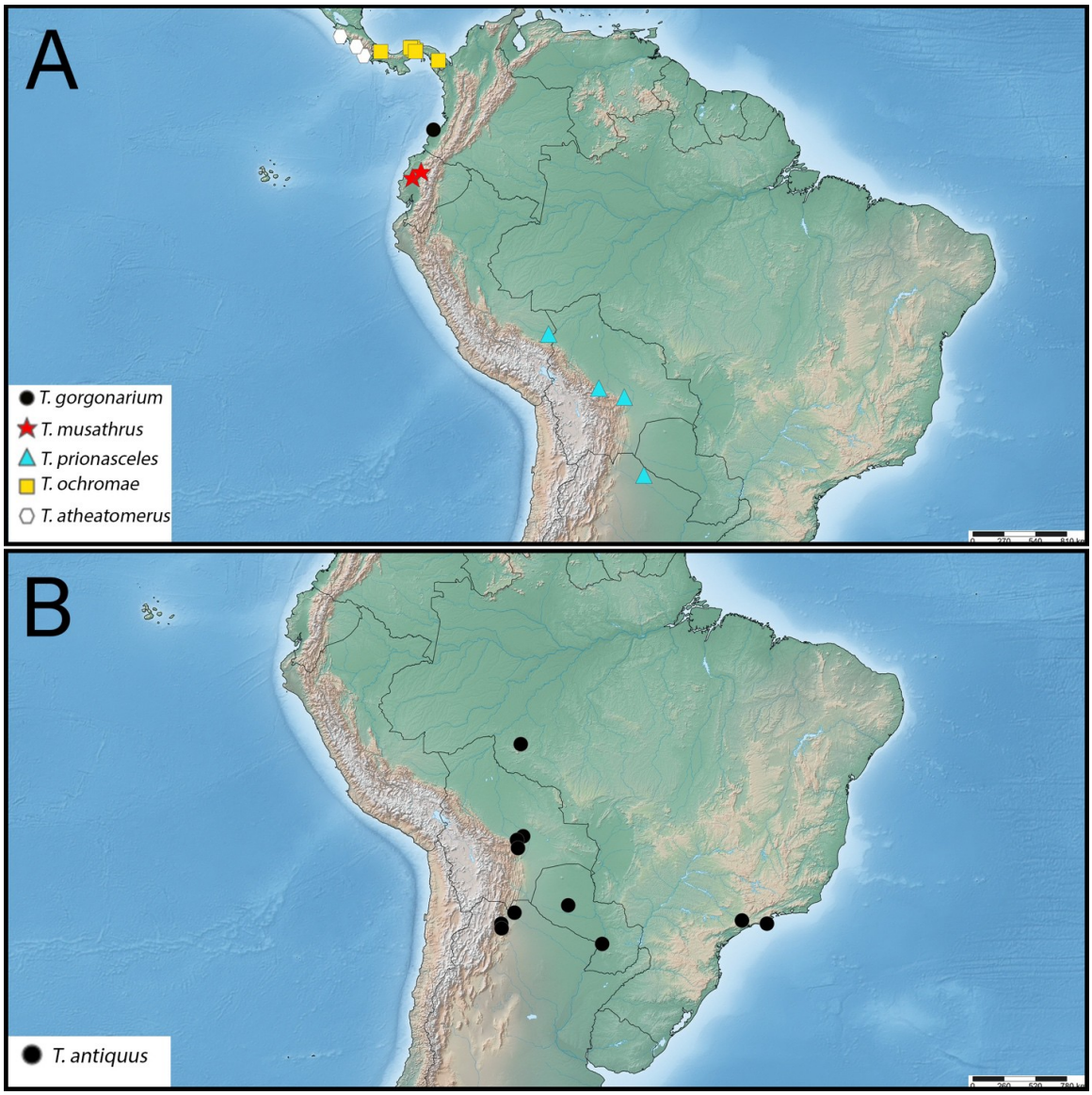

Figure 3.27. Distribution maps for the *ochromae* and *antiquus* groups. A) *T. ochromae*, *T. atheatomerus*, *T. gorgonarium*, *T. musathrus*, *T. prionasceles*; B) *T. antiquus*.

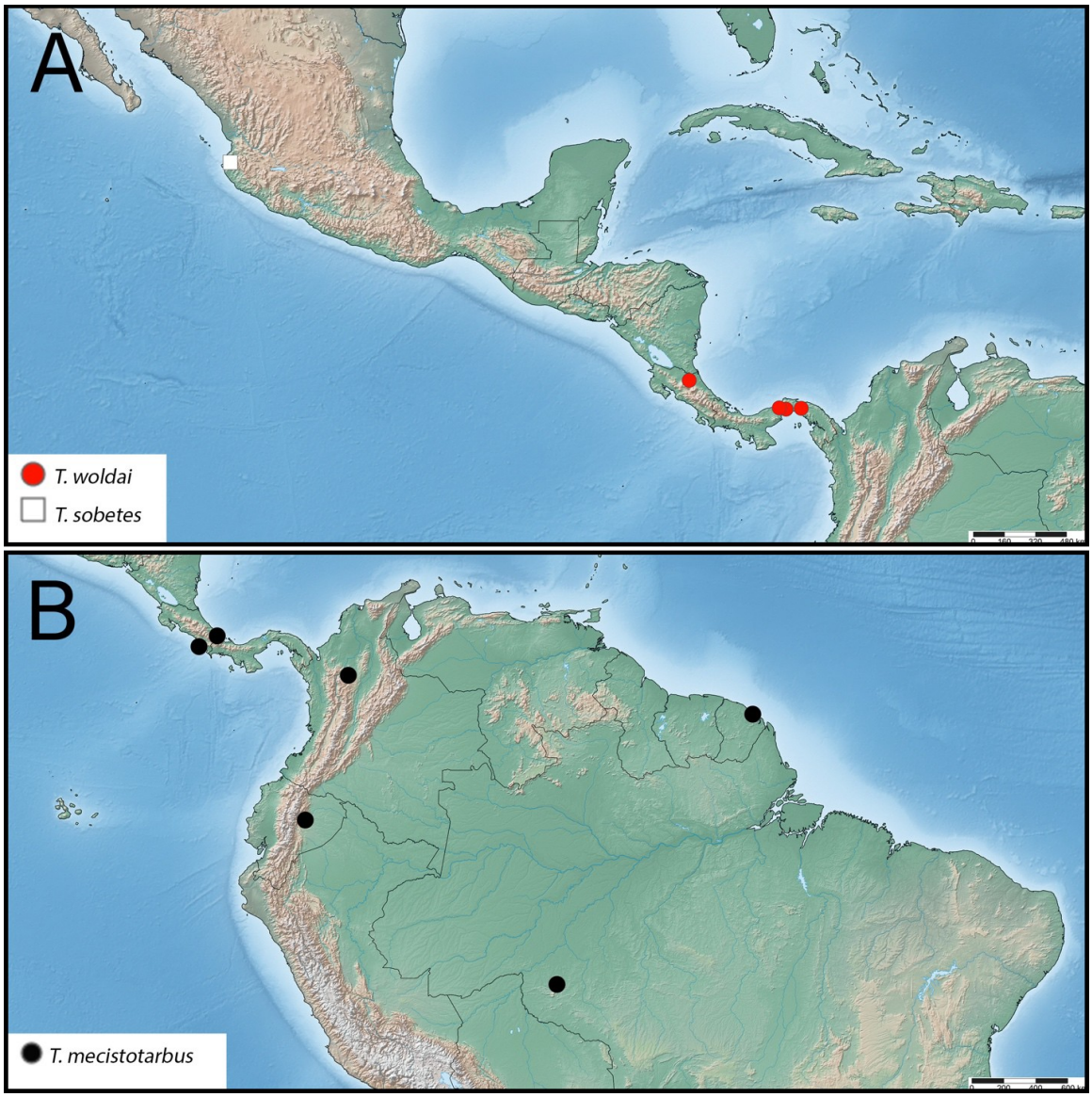

Figure 3.28. Distribution maps for the *antiquus* and *mecistotarbus* groups. A) *T. woldai* and *T. sobetes*; B) *T. mecistotarbus*.

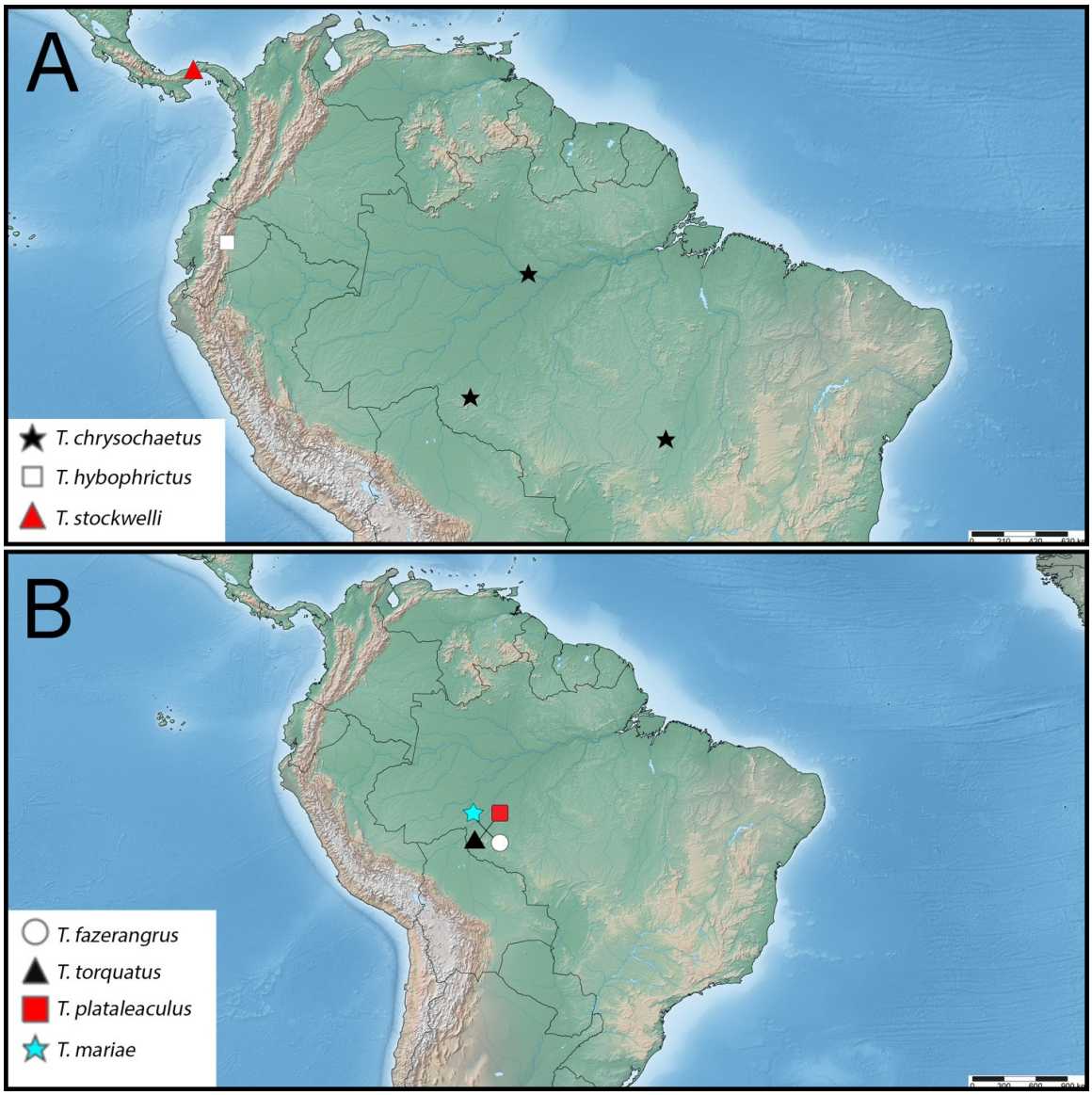

Figure 3.29. Distribution maps for the *mecistotarbus* and *obrieni* groups. A) *T. chrysochaetus*, *T. hybophrictus*, *T. stockwelli*; B) *T. fazerangrus*, *T. mariae*, *T. plataleaculus*, *T. torquatus*.

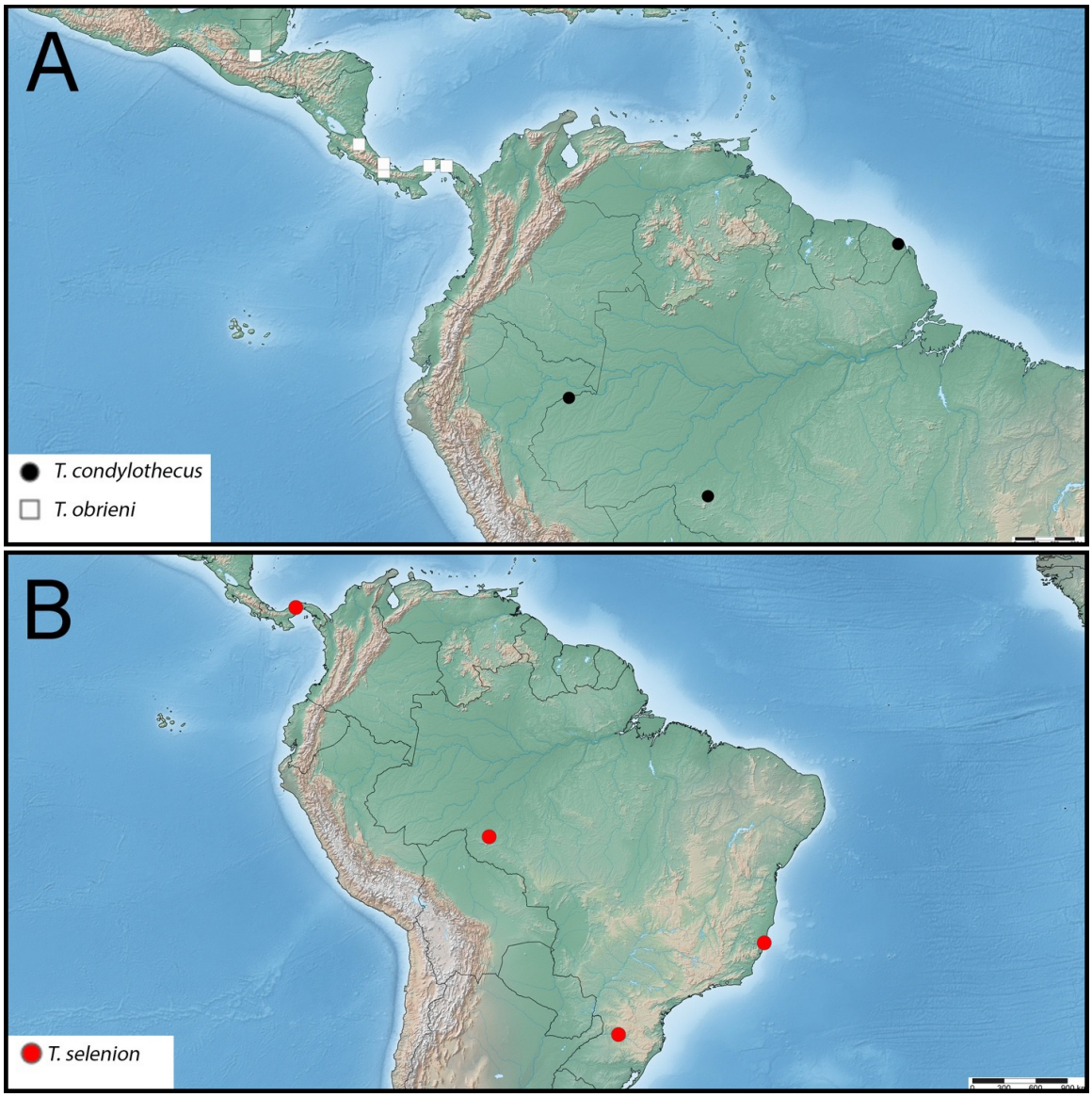

Figure 3.30. Distribution maps for the *obrieni* group. A) *T. obrieni* and *T. condylothecus*; B) *T. selenion*.

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CHAPTER 4

A QUANTITATIVE CHARACTERIZATION OF CONODERINE MIMICRY COMPLEXES (COLEOPTERA: CURCULIONIDAE)

ABSTRACT

The Conoderinae are one of the most distinctive Neotropical weevil groups in behavior and appearance, attracting numerous hypotheses regarding the evolution and function of widespread apparent mimetic convergence. One hundred and sixty species of conoderine weevils previously or herein hypothesized to belong to thirteen different groups are analyzed in the first quantitative test of conoderine mimetic complexes. Color pattern similarity is assessed using non-metric multidimensional scaling ordination plots and statistically testing the resulting clusters in ordination space. Four similar putatively mimetic complexes are emphasized in the analysis: (1) weevils that mimic red-eyed flies, (2) weevils with red or white elytral stripes or spots, (3) weevils with a metallic blue to blue-green pronotum, and (4) weevils with a red and metallic blue pronotum. The most densely sampled of these complexes were found to be significant groupings, suggesting that further sampling is needed to effectively characterize the remaining groups. Multiple avenues for future research on conoderine mimicry are discussed.

Introduction

Weevils are one of the largest groups of animals on the planet, with an estimated 220,000 species in existence (Oberprieler *et al.* 2007). Unsurprisingly, this extreme species-level diversity is also reflected in diverse evolved strategies to minimize predation. The Conoderinae Schoenherr, 1833 are among the largest subfamilies of weevils and are especially numerous in the New World tropics where they have long been recognized for their distinctive behaviors and convergently similar color patterns. The apparent convergent color patterns in the group have prompted hypotheses on their adaptive significance, yet, despite the charismatic and often vibrantly colored species of these weevils, no experimental or quantitative analyses of conoderine mimicry have been undertaken.

This study provides the first quantitative analysis of conoderine mimicry by assessing the phenotypic similarity of species hypothesized to belong to the same mimicry complex and their distinctiveness from other complexes. The herein utilized approach follows several recent studies testing mimetic convergence and mimetic fidelity to a model species (e.g. Wilson *et al.* 2012, Rodriguez *et al.* 2014, Smith *et al.* 2015).

Mimicry complexes in the New World Conoderinae

Hespenheide (1995) provided the first overview of mimicry in this group of weevils and hypothesized several complexes based on shared color patterns between unrelated species. Four hypotheses of mimetic similarity are emphasized and tested in this analysis: the "red-eyed fly" complex, the "striped/spotted" complex, the "*Medetera*" complex, and the "blue/red" complex.

Red-eyed fly complex (e.g. Figs 4.1, species 1-9). First proposed by Hespenheide (1973), this mimicry complex is also found in several other families of beetles, including other groups of weevils (e.g. Anthribidae Billberg, 1820; Hespenheide 1973, Perger and Guerra 2016) and even jumping spiders (Perger and Rubio 2018). The greatest number of species as well as the greatest number of hypothesized independent origins of red-eyed fly mimicry occurs in the New World Conoderinae, where it occurs in 14 genera distributed in the tribes Lechriopini Lacordaire, 1865 and Zygopini Lacordaire, 1865, though much phylogenetic and taxonomic progress is needed before it can be assessed in a phylogenetic framework. Since neither the flies nor the beetles are thought to be distasteful, it has been hypothesized that this apparent mimetic convergence is based not on unpalatability as in classical Batesian or Müllerian mimicry but on evasiveness: the distinctive pattern is associated with unprofitability by predators that unsuccessfully pursue the fast-flying flies and the fast-flying weevils as prey (Hespenheide 1973, 1995, Gibson 1974, Ruxton *et al.* 2004). The existence and prevalence of evasive mimicry has been a contentious issue in the literature from the past few decades (Srygley 1994, Brower 1995, Ruxton *et al.* 2004, Pinheiro and Freitas 2014, Pinheiro *et al.* 2016) but has been considered most likely to occur when predator learning is aided with aposematic coloration (Ruxton *et al.* 2004) or behavioral mimicry, such as locomotor mimicry (Srygley 1999), both of which are suspected to occur in this system (e.g. red coloration, walking style, threat response; Hespenheide 1973). Red-eyed fly mimicking weevils generally have a three-part pattern of an anterior red patch which resembles the eyes of the flies, a variably contrasting middle section resembling the often longitudinally-striped thorax of red-eyed flies, and a mottled or iridescent posterior area resembling the wings of flies.

Striped/spotted complex (e.g. Figs. 4.2, species 81-102). In the present, broad circumscription, this group (including the "red-spotted" group of Hespenheide 1995) is more of a grouping of convenience and likely contains multiple unrelated mimicry rings that share very similar components of the mimetic facies, making a distinction into multiple groups based on shared putative adaptive significance difficult. The identification of potential models for these species has likewise been difficult (Hespenheide 1995, 2017) though some species bear a resemblance to many chemically-defended Chrysomelidae Latreille, 1802 (e.g. *Omophoita* Chevrolat, 1836; A. Deczynski, pers. comm.) and others to several widespread mutillid mimicry rings (e.g. the "red-headed *Timulla*" and "black-headed *Timulla*" mimicry rings, Wilson *et al.* 2015, Fig. 1; J. Wilson, pers. comm.). Mimicry of both of these potential models is widespread in insect Batesian mimicry systems, with mimicry of mutillids also having been hypothesized to occur in other weevil groups (Lanteri and del Río 2005, del Río and Lanteri 2012). Most examined species considered to belong to this complex have a red/orange/pink patch on the prothorax and an elytral pattern consisting of contrasting stripes or white, orange, red, or pink spots.

Medetera complex (Fig. 4.2, species 121-125). Referred to as the "blue-thorax" group by Hespenheide (1995), this complex is characterized by opalescent blue to blue-green scales on the thorax and has been proposed to have dolichopodid flies of the widespread genus *Medetera* Fischer von Waldheim, 1819 as the model. For the current analysis, and since the proposed model species do not have red eyes, species with both blue and red anterior scales are treated as a separate complex (following Hespenheide 2005), also supported by the occurrence of these species in a different microhabitat from blue/red species (Hespenheide 1996b, 2005). Three species pertaining to this complex (in three genera) were observed to

have a serrate posterior margin of the female eighth sternite, a feature potentially associated with oviposition in wood (Howden 1995). This modification is not unique in the Conoderinae to *Medetera* mimics but was not found in species pertaining to the blue/red complex, further supporting a distinction between complexes based on natural history.

Blue/red complex (e.g. Fig. 4.1, species 10, 23). Species pertaining to this complex were initially treated as variation in the *Medetera* complex (Hespenheide 1995), with both being relatively small species bearing blue scales on the pronotum. The presence of red scales anteriorly on the prothorax and head renders species intermediate in appearance between the *Medetera* and red-eyed fly complexes.

Species of Conoderinae pertaining to other putative mimicry complexes as well as non-mimetic or cryptic species are included to test the distinctiveness of these four groupings not only from each other, but from the rest of the Conoderinae.

Materials and Methods

Species selection and morphological analysis. Dorsal and lateral habitus images of 160 species of conoderine weevils (Fig. 4.1-4.2) were taken using a Visionary Digital Passport II imaging system with a Canon EOS 5D Mark II camera and aligned and stacked with Zerene Stacker version 1.04. All measurements were taken in Adobe Photoshop CS6 version 13.0.

Species were identified *a priori* into thirteen mimicry complexes or unique pattern types based on perceived visual similarity or dissimilarity to species previously designated to a mimicry complex. The majority of the species pertained to the four focal complexes: the red-eyed fly complex (71 species), the spotted/striped complex (35 species), the *Medetera*

complex (5 species), and the blue/red complex (3 species). Forty-four of the remaining 46 species were divided between the following complexes: "Ant 1" (shiny black ant mimicry, five species; Hespenheide 1987, 1995), "Ant 2" (possible mimic of *Cephalotes* Latreille, 1802, 1 species; Hespenheide 1986), "Ant 3" (1 species; Hespenheide 1995), bee mimicry (1 species; Hespenheide 1995, 2018c), clytrine chrysomelid beetle mimicry (species; Hespenheide 1980, 1995, 1996a), species suspected to be non-mimetic or cryptic (33 species), and the "yellow-spotted" complex (3 species; Hespenheide 2017). Two included species with apparent aposematic coloration did not fit into any mimetic hypothesis as currently circumscribed (Fig. 4.2, species 105 and 107) and were each treated as an independent grouping, "Unknown1" (species 105) and "Unknown2" (species 106).

Each species was scored for three continuous and twelve discrete (binary or multistate) phenotypic characters. The preferred method of coding characters that applied only to a subset of taxa (e.g. character 4) was to treat them as inapplicable for the taxa without the character (Strong and Lipscomb 1999). Alternative coding methods, such as composite coding, which would have resulted in increased similarity among taxa that lack these features (e.g. for taxa that were scored as not having red/orange/pink on the pronotum/head (character 3), they were not scored as "absent" for character 4 or "0%" red/orange/pink for character 5).

Non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA). The character matrix was transformed into a distance matrix using Gower distances with the isoMDS function of the MASS package (Venables *et al.* 2002) in R and visualized in three-dimensional graphical space with NMDS, a robust ordination method that allows for the incorporation of categorical and continuous data. Similarity between

Figure 4.1A. Lateral habitus of species 1-80. See Appendix B for a list of species.

Figure 4.1B. Dorsal habitus of species 1-80. See Appendix B for a list of species.

Figure 4.2A. Lateral habitus of species 81-160. See Appendix B for a list of species.

Figure 4.2B. Dorsal habitus of species 81-160. See Appendix B for a list of species.

groups or individuals is represented by their proximity in graphical space. The grouping of species to their *a priori* assignments was tested using PERMANOVA (Anderson 2001), a non-parametric statistical method used to test the null hypothesis that the groupings are not different, implemented with the adonis function of the vegan package (Oksanen *et al.* 2018) in R. The overall effect of the groupings as well as between each pair of complexes is tested with this method. If the groupings are shown to be significant as a categorical variable, a distinct clustering of the points pertaining to each complex is expected.

The analysis was performed on the complete dataset (160 species, 13 groupings) and a separate analysis was run on a reduced dataset of the 114 species that pertain only to the red-eyed fly, striped/spotted, *Medetera*, and blue/red complexes with character 15 removed as it was uninformative for this group of species.

Phenotypic characters.

1. *Body length.* Coded as a continuous character and measured as the dorsal length from the anterior margin of the head (excluding the rostrum) and the posterior margin of the elytra or pygidium.
2. *Body length/width ratio.* Coded as a continuous character. Body length measured as in character 1, width measured as distance across elytral humeri.
3. *Red/orange/pink color on pronotum/head*: (0) absent; (1) present.
4. *Shape of red/orange/pink patch on pronotum, dorsal view*: (0) a single transverse patch mostly in the anterior two-thirds of the pronotum; (1) a single patch covering nearly all of the pronotum; (2) two separated patches; (3) more than 2 separate patches; (4) red patch encircling a transversely ovoid median black area; (5) a single patch extending completely or nearly completely to the posterior margin at the

posterolateral corners, enclosing a semicircular black space along the posterior margin at the middle. Scored as inapplicable (NA) for taxa without red (character 3, state 0).

5. *Percentage of red/orange/pink on dorsal surface*. Coded as a continuous character. Scored as inapplicable (NA) for taxa without red (character 3, state 0) except for species 107 and 158 where the coloration is present only on the elytra.
6. *Abdominal red/orange/pink*: (0) absent; (1) present, in 1 or more spots; (2) present, dominant color on abdominal sternites.
7. *Metallic blue to blue-green scales on pronotum/head*: (0) absent; (1) present.
8. *Lateral contrasting yellowish-white to yellow macula, lateral view*: (0) absent; (1) present.
9. *Dominant elytral color (by rough percentage), dorsal view*: (0) black; (1) white/grey; (2) brown/tan; (3) red/orange/pink; (4) yellow.
10. *Secondary elytral color (by rough percentage, dorsal view)*: (0) black; (1) white/grey; (2) brown/tan; (3) red/orange/pink; (4) yellow. Scored as inapplicable (NA) in taxa with unicolorous elytra.
11. *Elytral sutural stripe*: (0) absent; (1) present, incomplete; (2) present, complete.
12. *Transverse bar across elytral suture at middle to one-third from apex*: (0) absent; (1) present.
13. *Lateral/ventral pattern*: (0): mottled/indistinctly contrasting; (1) strongly contrasting, mostly white and black.
14. *Prothoracic area bordering red patch* (lateral view): (0) completely or mostly white; (1) white only anteriorly.
15. *Elytra, integument mostly bare, shining*: (0) absent; (1) present.

Results

The NMDS analyses (Figs. 4.3-4) show the clustering of species by their assignment in a mimicry complex in three-dimensional space. The plots for the reduced-complex analysis (Fig. 4.4) show a clear separation of the means for each group as well as of the clusters pertaining to each focal complex. The overall effect of these species groupings as a categorical variable was found to be significant in the full analysis ($F = 13.08$; $R^2 = 0.516$; $P < 0.001$; Fig. 4.3) and in the reduced analysis ($F = 24.398$; $R^2 = 0.400$; $P < 0.001$; Fig. 4.4). Pairwise PERMANOVAs were significant between focal complexes except between blue/red and *Medetera* groups (Table 1, Appendix C), indicating that the red-eyed fly and the striped/spotted complexes are distinct from each other and from the *Medetera* and blue/red complexes, while the smaller *Medetera* and blue/red complexes are not significantly distinct.

Table 4.1. Pairwise PERMANOVA results for the reduced analysis.

Complex 1	Complex 2	R2	F	Residual df	p
Blue/Red	Medetera	0.192	1.4	6	0.27
Blue/Red	Red-eyed Fly	0.056	4.3	72	0.01
Blue/Red	Striped/Spotted	0.204	9.2	36	0.001
Medetera	Red-eyed Fly	0.246	24.2	74	0.001
Medetera	Striped/Spotted	0.356	21	38	0.001
Red-eyed Fly	Striped/Spotted	0.437	80.8	104	0.001

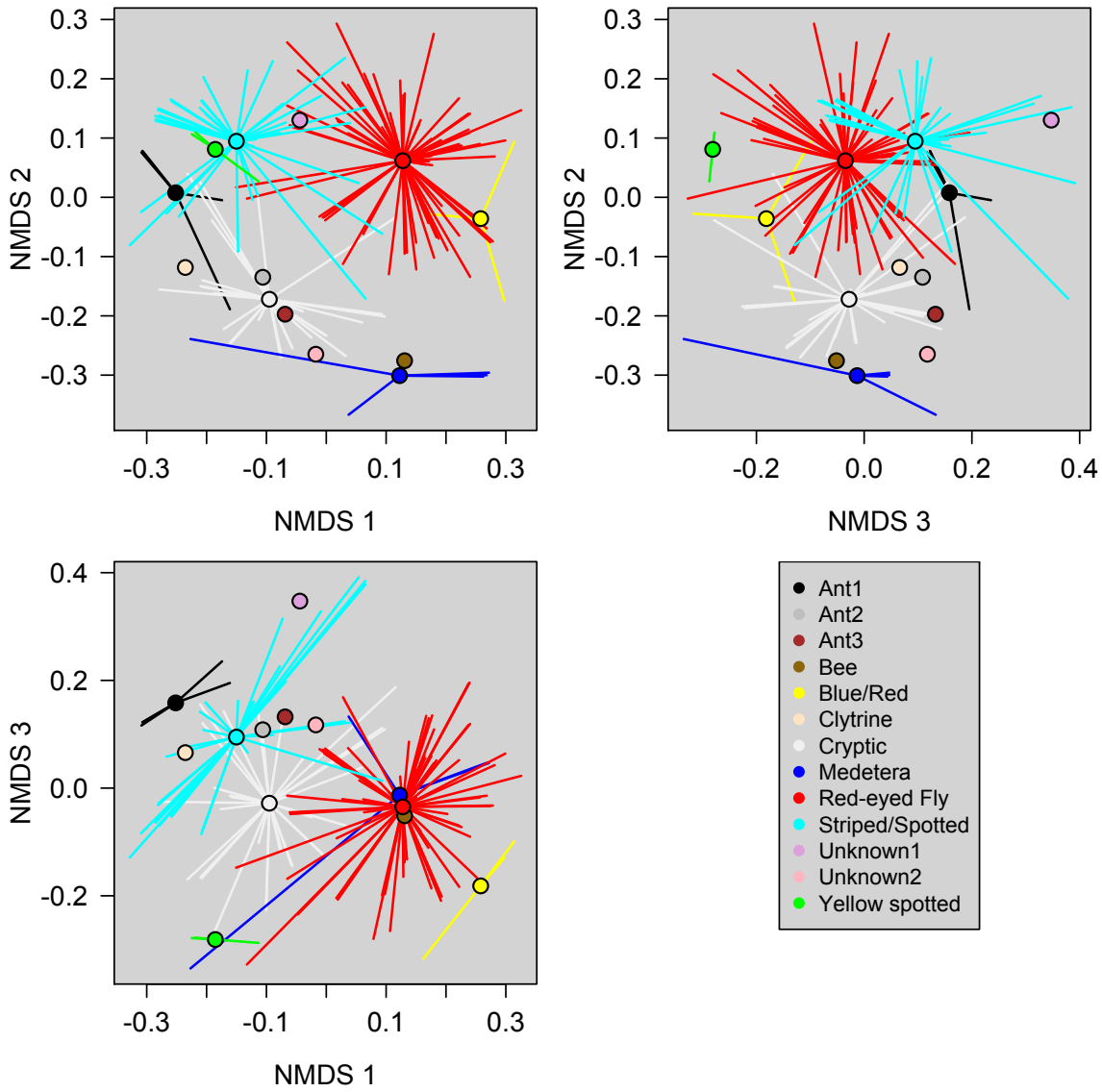

Figure 4.3. Fireworks plots based on NMDS analysis for all 13 groupings. Filled circles represent the mean value for each ring with lines from the mean to individual species values.

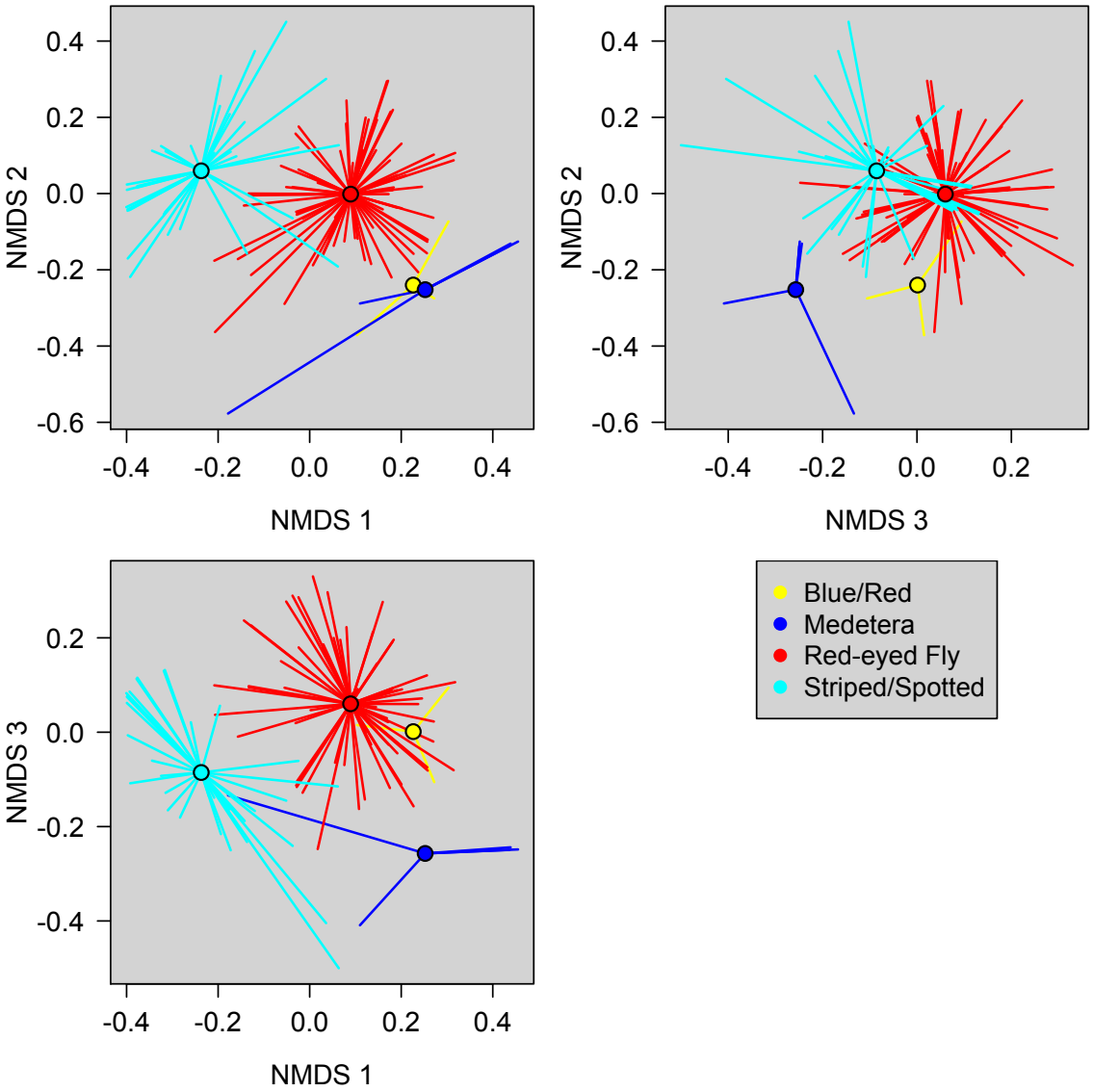

Figure 4.4. Fireworks plots based on NMDS analysis of the reduced-ring dataset. Filled circles represent the mean value for each ring with lines from the mean to individual species values.

Discussion

This study shows for the first time that species in certain mimicry complexes that could previously only be speculated to be in the complex based on perceived similarity are in fact quantitatively more similar to each other. In other words, weevils pertaining to the red-eyed fly and striped/spotted complexes are phenotypically more similar to the other species in their complex than to species in a different complex. This finding lends support to the as yet untested hypothesis that the species assigned to the red-eyed fly complex and the striped/spotted complex have convergently similar patterns due to shared selection pressures that could have arisen from similarities in behavior, the microhabitat the species spend time in (Hespenheide 1996b) thus exposing them to different potential model fly species, different types of predators to apply the selective pressure, and different types and numbers of alternative prey for those predators to pursue instead. While the inferences that can be drawn from this study about the purpose and the evolution of mimetic patterns are limited, this analysis can be used as a starting point to make further discoveries about conoderine mimicry.

Some of the characters used in the analysis were quite variable within these complexes (e.g. character 8 for the red-eyed fly complex, character 4 for the striped/spotted complex), indicating that both complexes as currently treated potentially represent several similar mimicry rings that can be delimited by an analysis looking at the species with a much finer resolution (e.g. grouping species based on size classes to test a hypothesis that patterns are more similar among similar-sized weevils).

Another layer to the variation seen in this group can potentially be explained by imperfect mimicry - it is currently unknown if species in this complex are high-fidelity mimics of a specific fly model or share general characteristics that are similar enough to the

diversity of model flies present in a given locality that they gain a selective advantage from it. A few species in this complex (e.g. Fig. 4.1A, species 4) have a red patch on their abdominal ventrites which appears to resemble the red abdominal apex of many red-eyed flies, suggesting that there are at least some species that have specific model fly species. The degree to which certain components of the patterns are constrained by phylogeny is also unknown, and will not only require phylogenetic analysis but significant revisionary taxonomic work to describe the multitude of undescribed mimetic conoderine species and arrange them in a natural classification.

The insignificant results for the *Medetera* and blue/red groups could indicate that the species assigned to these groups are not as similar as general appearance has suggested, although they are comparatively under-sampled. Additional sampling in these groups is needed to confirm whether the groupings are truly artificial or if the taxa included in the present analysis represent phenotypic extremes of otherwise similar species.

Biogeographic distribution of conoderine mimicry. The focal mimicry complexes for this study are widely distributed in the New World tropics. Though apparently much less common, species that seem to pertain to the red-eyed fly and the striped/spotted complexes have been observed among specimens from the Old World tropics (Fig. 4.1, species 29 and 61). Flies with red eyes are found in many dipteran groups worldwide, and considering how readily mimicry of them has evolved in different New World taxa it is not surprising that the Old World conoderine tribe Mecopini Lacordaire, 1865, a group with similar behaviors (Lyal 1986) to their New World relatives in the Lechriopini and Zygopini, has also evolved a similar convergent appearance. Mutillids also are a plausible group to serve as models for

Old World conoderines, with very similar Old World mimicry rings to those found in the Neotropics (Wilson *et al.* 2018).

Future directions and conclusion. The Conoderinae present an underexplored and promising system to study the evolution of different types mimicry, including evasive mimicry. There are many analyses that can provide finer resolution for the delimitation of the mimicry complexes presented here into smaller, more precisely defined groups that reflect their convergence as a product of shared selection pressures. For example, it is unknown how much imperfect mimicry (Sherratt 2002, Wilson *et al.* 2013) might be present in conoderine mimicry systems. A similar analysis can be performed with weevil species that pertain to one mimicry complex such as the red-eyed fly complex from a single locality as well as all potential model species (i.e. any red-eyed flies) from that locality in a test of mimetic fidelity (e.g. Smith *et al.* 2015). If imperfect mimicry is suspected to play a large role in this system it may be hypothesized that there will be no significant clustering in the ordination plots based on any *a priori* grouping since the weevil patterns could represent an "averaging" of the characteristics present in the flies and not resemble one specific model species (Hespenheide 1973).

Shared behaviors, microhabitats, predation pressure, and common ancestry – information that is currently unavailable for the vast majority of species – all likely play a role in shaping the evolution of convergent color patterns in the Conoderinae. Experimental field studies will undoubtedly be instrumental in uncovering critical information about mimetic species that will allow for new hypotheses to be formulated and tested, and it is hoped that future analyses can build off of this study as more knowledge is accumulated on these fascinating weevils.

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APPENDIX A

CHARACTER MATRIX USED IN CLADISTIC ANALYSIS

	1	5	10	15	20	25	30	35	40	45	50	55	60	65	70
Conotrachelus suturalis	00000	00000	00000	–000–	00000	00000	–0000	00–00	0—00	00000	000–0	——00	00000	00000	00–00
Mecopus helleri	10100	00001	00000	0000–	00000	00000	–0000	10–00	0—00	00000	000–0	——00	00000	00000	00–00
Acoptus suturalis	10100	00000	00000	0000–	00000	00000	–0000	00–00	0—00	00000	00100	—100	00000	00000	00–00
Othippiini gen. 2 sp. 1	10100	00000	00000	0000–	00000	00000	–0000	00–00	0—00	00000	00100	—100	00000	00000	00–00
Piazurus maculipes	010–1	10000	10000	0000–	10000	00010	–0001	00–00	0—10	00000	000–0	——1–	00000	00000	10–00
Pseudopiazurus centraliamericanus	010–1	10000	10000	–000–	10000	00010	–0001	00–00	0—00	00000	000–0	——1–	00000	00000	00–00
Cratosomus multipunctatus	010–1	10000	00000	0000–	10000	00010	–0001	00–00	0—00	00000	000–0	——1–	00000	00000	00–00
Pseudopinarus condyliatus	010–1	10000	10000	–000–	10000	00010	–0001	00–00	0—11	00000	000–0	——1–	00000	00000	10–00
Piazolechriops bicristatus	010–1	10000	10000	–000–	10000	00010	–0001	00–00	0—11	00000	000–0	——1–	00000	00000	10–00
Peltophorus polymitus seminiveus	010–1	10100	00000	0000–	11000	01000	–00–0	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Parazygops luctuosus	010–1	11100	00000	0000–	11000	01000	–0000	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Zygops tridentatus	010–1	21100	00000	0000–	11000	01000	–00–0	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Zygops tripartitus	010–1	11100	00000	0000–	11000	01000	–0000	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Zygops maculipes	010–1	21100	00000	0000–	11000	01000	–00–0	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Zygops mexicanus	010–1	11100	00000	0000–	11000	01000	–00–0	00–01	0—00	00000	000–0	——1–	00000	00000	00–00
Arachnomorpha circumlineata	00000	00010	00100	00121	00100	00001	00002	10–00	0—00	00000	00001	00000	00000	00010	00–00
Archocopturus regalis	00000	00001	00001	00121	00000	00101	00002	10–00	0—00	00000	00001	1–000	000??	00000	00–00
Cylindrocopturus biradiatus	00000	00001	00000	01121	00000	00101	00002	10–00	0—00	00000	00001	1–000	00000	00000	00–01
Cylindrocopturus filicornis	00000	00001	00000	01121	00000	00101	00002	10–00	0—00	00000	00001	1–000	00000	00000	01001
Cylindrocopturus nanulus	00000	00001	00010	01121	00000	00101	10002	10–00	0—00	00000	00001	1–000	00000	00000	00–01
Cylindrocopturus quercus	00000	00001	00010	01121	00000	00101	10002	10–00	0—00	00000	00001	1–000	00000	00000	00–01
Cylindrocopturus elongatus	00000	00001	00000	01121	00000	00101	00002	10–00	0—00	00000	00001	1–000	00000	00000	01001
Cylindrocopturus deleoni	00000	00001	00000	01121	00000	00101	00002	10–00	0—00	00000	00001	1–000	00000	00000	00–01
Helleriella longicollis	00000	00000	00010	01121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	00000	00–01
Hoplocopturus armatus	00000	00001	00000	00121	00000	00001	00002	11000	0—00	00000	00001	1–000	00000	00000	01000
Hoplocopturus costatipennis	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	000–1	01100
Hoplocopturus scintillans	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	000–1	01100
Hoplocopturus javeti	00000	00001	00000	00121	00000	00001	00002	11100	0—00	00010	00001	1–000	00000	00000	01010
Hoplocopturus nigripes	00000	00001	00000	00121	00000	00001	00002	11000	0—00	00000	00001	1–000	00000	00000	01010
Hoplocopturus varipes	00000	00001	00000	00121	00000	00001	00002	11000	0—00	00000	00001	1–000	00000	00000	01000
Mnemynurus championi	00000	00001	00000	00121	00000	00001	00002	11100	0—00	00000	00001	1–000	01000	00000	01000
Mnemynurus poecilocleres	00000	00001	00000	00121	00000	00001	00002	11100	0—00	00010	00001	1–000	01000	00000	01000
Mnemynurus longispinis	00000	00001	00000	00121	00000	00001	00002	11100	0—00	00000	00001	1–000	00000	00000	01010
Balaninurus longipes	00000	00001	00000	00121	00000	00001	00002	11100	0—00	00010	00001	1–000	00000	00000	01000
Macrocopturus nr. *deplanus*	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	000–1	01100
Macrocopturus nr. *verrucosus*	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	00000	01000
Macrocopturus cincticollis	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	000–1	01100
Macrocopturus floridanus	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	10000	00001	1–000	00000	000–1	01100
Macrocopturus sannio	00000	00001	00000	00121	00000	10001	00002	10–00	0—00	00001	10001	1–000	00000	000–1	01100
Macrocopturus cognatus	00000	00001	00000	00121	00000	10001	00002	10–00	0—00	00000	00001	1–000	0000?	000–1	01100
Macrocopturus sp. 18	00000	00001	00000	00121	00000	10001	00002	10–00	0—00	00001	10001	1–000	00000	000–1	01100
Copturosomus affaber	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00011	1–000	00000	00000	01000
Copturosomus rorulentus	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00011	1–000	00000	00000	01000
Copturomimus cinereus	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	00000	01–00
Copturomimus caeruleotinctus	00000	00001	00000	00121	00000	00001	00002	10–00	0—00	00000	00001	1–000	00000	00000	01–00
Crassocopturus sp.	00000	00000	01000	00121	001–0	00001	00002	10–00	10000	01000	00001	00000	00000	00000	00–00
Poecilogaster brevis	00000	00000	010??	??121	001–0	00001	00002	10–00	10000	01000	00001	00000	? ??? ?	00???	????0
Lissoderes subnudus	00000	00000	00000	00121	001–0	00001	00002	10–00	0—00	00000	00001	00000	00000	00000	00–00
Lechriops californicus	00000	00001	00000	00121	00011	00001	00002	10–10	0—00	10100	00001	1–000	10000	000–1	01100
Lechriops vestitus	00000	00001	00000	00121	00011	00001	00102	10–10	0—00	10100	00001	1–001	10000	000–1	01100
Lechriops festivus	00000	00001	00000	00121	00011	00001	00102	10–10	0—00	10100	00001	1–000	10000	000–1	01100
Lechriops nr. *lebasii*	00000	00001	00000	00121	00011	00001	00102	10–10	0—00	10100	00001	1–000	10000	000–1	01100
Lechriops sp. 1(bursera)	00000	00001	00000	00121	00010	00001	00002	10–00	0—00	10000	00001	1–000	10000	000–1	01100
Lechriops nr. *rugicollis*	00000	00001	00000	00121	00011	00001	00102	10–10	0—00	00100	00001	1–001	10000	000–1	01100
Lechriops excavatus	00000	00001	00000	00121	00011	00001	00102	10–10	0—00	00000	00001	1–001	10000	000–1	01100
Pseudolechriops klopferi	00010	00001	00000	10121	00011	00001	00002	10–10	0—00	00000	00001	1–000	00000	011—	01–00
Pseudolechriops megacephala	00010	00001	00000	10121	00011	00001	00002	10–10	0—00	00000	00001	1–000	00000	011—	01–00
Macrolechriops moreyi	00000	00000	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	01000	00000	00000	00–00
Eulechriops nitidus	00000	00010	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	00000	00010	00–00
Eulechriops manihoti	00000	00001	00001	00121	00000	00101	00012	10–00	0—00	00000	00001	1–000	00000	00000	00–00
Eulechriops nr. *elongatus*	00000	00000	00000	00121	001–0	00001	00002	10–00	11000	00000	01001	00000	00100	00000	00–00
Eulechriops nr. *melancholicus*	00000	00000	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	00000	00000	00–00
Eulechriops nr. *tenuirostris*	00000	00000	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	01000	00000	00000	01000
Eulechriops sp. 1	00000	00010	00100	00121	001–0	00001	00002	10–00	10000	00000	00001	00000	00000	00010	00–00
Eulechriops sp. 2	00000	00010	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	00000	10000	00–00
Eulechriops sp. 3	00000	00010	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	00000	10000	00–00
Eulechriops sp. 4	00000	00000	00000	00121	001–0	00001	00002	10–00	11000	00000	01001	00000	00100	00000	00–00
Cylindrocopturinus vanessae	00000	00000	00000	00121	001–0	00001	00002	10–00	11000	00000	00001	00000	? ?? ??	00???	? ??? 0
Copturomorpha sp. 1	00000	00000	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	00100	00000	00–00
Copturomorpha sp. 3	00000	00000	00000	00121	001–0	00001	00002	10–00	10100	00000	00001	00000	000??	00000	00–00
Copturus aurivillianus	00000	00000	00000	00120	00000	00000	–1002	00–00	0—00	00000	00000	—000	00001	00000	20–00
Copturus sanguinicollis	00000	00000	00000	00120	00000	00000	–1002	00–00	0—00	00000	00000	—000	00001	00000	20–00
Microzurus rhombus	00000	00001	00011	00121	00000	00101	00012	10–00	0—00	00000	00001	1–000	00010	00000	00–00

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                                1    5    10   15   20   25   30   35   40   45   50   55   60   65   70
                                |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
Microzurus sp. 1                00000 00001 00001 00121 00000 00101 00012 10–00 0—00 00000 00001 1–000 00010 00000 00–00
Paramnemyne decemcostata        00000 00000 00000 0000– 00000 01000 –0000 00–00 0—00 00000 00000 —000 00000 00000 00–00
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APPENDIX B

CHARACTER MATRIX USED FOR MIMETIC ANALYSIS

Character matrix used in the full analysis with taxon numbers matching the number of the species used in Figures 2.1-2.2. Mimicry complex codes: A1 = Ant 1, A2 = Ant 2, A3 = Ant 3, B = Bee, BR = Blue/red, Cly = Clytrine chrysomelid, C/NM = Cryptic/non-mimetic, M = Medetera, REF = Red-eyed fly, SS = Striped/spotted, U1 = Unknown 1, U2 = Unknown 2, Y = Yellow spotted.

Number	Species	Complex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Copturomimus sp. 1	REF	4.11	1.96	1	0	10.03	1	0	0	1	0	0	0	1	0	0
2	Copturomimus sp. 2	REF	3.39	1.88	1	0	12.96	0	0	0	1	0	0	0	1	0	0
3	Copturus sanguinicollis	REF	5.47	1.8	1	0	9.27	0	0	0	1	0	0	0	1	0	0
4	Euzurus ornativentris	REF	7.57	1.74	1	2	5.70	1	0	0	1	0	0	0	1	0	0
5	Hoplocopturus sp. 10	REF	4.34	1.57	1	0	13.12	0	0	0	1	0	0	0	0	0	0
6	Hoplocopturus sp. 11	REF	3.57	1.89	1	0	15.57	0	0	0	2	0	0	0	1	0	0
7	Hoplocopturus sp. 12	REF	4.67	1.81	1	0	16.04	0	0	0	2	1	1	1	1	0	0
8	Hoplocopturus sp. 13	REF	4.52	1.88	1	0	12.37	0	0	1	2	0	2	0	0	0	0
9	Hoplocopturus sp. 14	REF	4.86	1.72	1	0	15.16	0	0	0	2	0	1	1	1	0	0
10	Hoplocopturus sp. 15	BR	2.73	1.99	1	1	26.05	0	0	0	0	1	2	0	0	0	0
11	Hoplocopturus sp. 16	REF	4.98	1.71	1	0	12.78	0	0	1	1	0	0	0	0	0	0
12	Hoplocopturus sp. SSAC1	SS	2.73	1.99	1	1	26.05	0	0	0	0	1	2	0	0	0	0
13	Hoplocopturus sp. SSAC2	REF	3.76	2.01	1	0	13.20	0	0	0	0	1	1	1	0	0	0
14	Macrocopturus abnormis	REF	12.45	2.51	1	0	7.52	0	0	0	0	1	0	0	0	0	0
15	Macrocopturus cognatus	REF	4.99	2.31	1	0	7.08	0	0	1	1	4	0	0	0	0	0
16	Macrocopturus sp. 10	REF	4.98	2.19	1	2	14.38	1	0	0	1	0	0	0	1	0	0
17	Macrocopturus sp. 11	REF	6.24	1.93	1	0	6.53	0	0	1	2	1	0	0	0	0	0
18	Macrocopturus sp. 12	REF	5.13	1.94	1	0	6.88	0	0	0	2	0	0	0	0	1	0
19	Macrocopturus sp. 14	REF	2.45	1.93	1	2	12.72	0	0	0	2	0	0	0	0	0	0
20	Macrocopturus sp. 16	REF	4.32	2.11	1	0	8.67	0	0	1	2	0	1	0	0	0	0
21	Macrocopturus sp. 17	REF	5.37	1.96	1	0	8.87	0	0	1	0	2	1	1	0	1	0
22	Macrocopturus sp. 18	REF	4.77	1.99	1	2	10.51	0	0	0	2	0	1	0	1	0	0
23	Macrocopturus sp. 19	BR	2.73	1.95	1	0	12.67	0	1	1	2	1	1	0	0	0	0
24	Lechriopini genus 1 sp. 1	SS	2.73	1.95	1	0	12.67	0	1	1	2	1	1	0	0	0	0
25	Macrocopturus sp. 21	REF	4.28	2.25	1	2	6.70	0	0	0	0	2	0	0	0	0	0
26	Macrocopturus sp. 22	REF	3.32	1.9	1	0	16.31	0	0	1	0	4	0	0	0	0	0
27	Macrocopturus sp. 23	REF	5.85	2.11	1	2	8.79	0	0	1	2	0	0	1	1	0	0
28	Macrocopturus sp. SSAC1	REF	4.81	2.15	1	2	8.56	0	0	0	1	0	0	0	0	0	0
29	Mecopus sp.	REF	8.23	2.44	1	0	11.68	1	0	0	2	0	0	0	1	0	0
30	Mnemynurus sp. 10	REF	7.07	1.99	1	0	13.91	0	0	1	2	1	0	1	1	0	0
31	Mnemynurus sp. 11	REF	7.29	1.89	1	0	11.64	0	0	1	2	1	0	1	1	0	0
32	Mnemynurus sp. 12	REF	6.16	1.95	1	0	9.84	0	0	1	1	1	0	1	1	0	0
33	Mnemynurus sp. 13	REF	5.77	1.99	1	2	9.79	0	0	1	2	4	0	0	0	0	0
34	Mnemynurus sp. 14	REF	6.83	1.86	1	2	3.46	0	0	0	2	1	0	0	1	0	0
35	Mnemynurus sp. 15	REF	9.28	1.96	1	0	11.13	0	0	0	0	1	0	1	1	0	0

Number	Species	Complex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
36	Mnemynurus sp. 16	REF	9.84	1.93	1	0	13.73	0	0	0	0	1	0	0	0	0	0
37	Mnemynurus gilvipes	REF	6.85	1.7	1	0	10.79	0	0	1	1	4	0	0	0	0	0
38	Timorus sp.	REF	5.09	2.08	1	0	9.88	1	0	0	1	0	0	0	1	0	0
39	Lechriopini genus 1 sp. 2	SS	5.1	1.87	1	5	12.31	0	0	0	0	1	1	1	0	1	0
40	Lechriopini genus 2	SS	2.75	1.72	1	1	26.61	0	0	0	0	1	2	0	1	1	0
41	Lechriopini genus 3	SS	4.42	1.98	1	4	9.89	0	0	0	0	1	1	1	1	1	0
42	Hoplocopturus cavernosus	REF	7.34	1.93	1	0	7.13	0	0	1	2	0	1	1	1	0	0
43	Hoplocopturus sp. 9	REF	5.04	1.97	1	0	12.24	0	0	1	1	0	0	1	0	0	0
44	Lechriops sp. 1	REF	3.39	1.9	1	0	16.83	0	0	0	1	0	0	1	0	0	0
45	Mnemynurus sp. 9	REF	10.37	1.7	1	0	8.00	0	0	1	0	2	1	1	1	0	0
46	Parazygops luctuosus	REF	8.84	2.6	1	2	6.07	0	0	1	0	1	1	0	1	0	0
47	Philenis muscamimetica	REF	7.36	1.95	1	0	14.21	0	0	0	2	1	2	0	1	0	0
48	Balaninurus sp. 1	REF	5.71	1.75	1	0	14.04	0	0	0	2	1	0	0	0	0	0
49	Balaninurus arachnodes	REF	8.23	1.99	1	0	14.98	0	0	1	2	0	0	1	1	0	0
50	Balaninurus longipes	REF	6.29	1.94	1	0	9.38	0	0	0	0	1	0	1	1	0	0
51	Balaninurus pulex	REF	2.51	1.73	1	0	15.08	0	0	0	1	0	0	1	0	0	0
52	Hoplocopturus armatus	REF	7.26	1.69	1	2	11.28	0	0	0	2	0	0	0	1	0	0
53	Macrocopturus albotorquatus	REF	5.11	2.17	1	0	8.02	0	0	1	2	0	0	0	1	0	0
54	Macrocopturus neohispanicus	REF	5.05	2.05	1	0	9.96	0	0	0	2	0	0	0	1	0	0
55	Macrocopturus torquatus	BR	5.25	1.92	1	0	7.55	0	1	1	2	0	0	0	1	0	0
56	Macrocopturus zygopiscus	REF	7.07	2.09	1	2	5.09	0	0	0	1	0	0	0	1	0	0
57	Mnemynurus caloderes	REF	7.88	1.68	1	0	10.44	0	0	0	1	0	1	1	1	0	0
58	Mnemynurus maior	REF	10.15	1.8	1	0	5.20	0	0	0	2	1	0	0	1	0	0
59	Zygops scenicus	REF	7.49	3	1	0	13.45	0	0	1	0	4	0	0	1	0	0
60	Copturomimus rufocinctus	REF	7.84	1.98	1	2	8.27	0	0	0	1	0	0	0	1	0	0
61	Calophylaitis principalis	SS	4.46	2.23	1	0	27.24	0	0	1	0	1	0	0	0	0	0
62	Hoplocopturus densus	REF	3.2	1.84	1	0	10.51	0	0	0	2	0	0	0	0	0	0
63	Hoplocopturus nigripes	REF	3.37	1.76	1	0	16.68	0	0	0	0	1	0	0	0	0	0
64	Macrocopturus cincticollis	REF	3.59	2.02	1	0	12.12	0	0	0	2	0	1	1	1	0	0
65	Macrocopturus dufaui	REF	3.64	1.81	1	0	11.99	1	0	0	1	0	1	0	1	0	0
66	Macrocopturus ignicollis	REF	3.29	2.07	1	0	10.80	0	0	1	2	1	2	0	1	1	0
67	Macrocopturus montezuma	REF	7.14	1.87	1	0	8.40	0	0	0	2	0	2	0	1	0	0
68	Macrocopturus quadricolor	REF	4.5	2.09	1	2	9.07	0	0	1	1	0	0	0	1	0	0
69	Macrocopturus ruficollis	REF	3.43	2.03	1	0	11.85	0	0	1	2	0	0	0	1	0	0
70	Macrocopturus tricolor	REF	6.75	1.92	1	0	8.27	0	0	0	1	0	0	0	1	0	0
71	Mnemynurus erythroderes	REF	6.31	1.95	1	0	13.75	0	0	0	2	0	0	0	1	0	0
72	Mnemynurus ignifer	REF	8.72	1.85	1	0	11.15	0	0	1	2	1	0	0	1	0	0
73	Mnemynurus longispinis	REF	3.93	1.85	1	0	14.46	0	0	0	1	0	0	0	0	0	0
74	Mnemynurus phoenicoderes	REF	5.95	1.93	1	0	12.03	0	0	1	2	1	0	0	1	0	0
75	Mnemynurus poeciloderes	REF	4.15	1.97	1	0	13.14	0	0	0	0	1	0	0	0	0	0
76	Zygops albiventris	REF	8.31	2.35	1	3	8.56	0	0	1	1	4	0	0	1	0	0
77	Zygops rufitorquis	REF	8.01	3.93	1	0	10.67	1	0	1	1	0	0	0	1	0	0

Number	Species	Complex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
78	Zygops rufomaculatus	REF	13	2.36	1	2	8.25	0	0	0	1	0	0	0	1	0	0
79	Mnemynurus championi	REF	8.4	1.74	1	0	8.77	0	0	1	1	2	1	1	1	0	0
80	Macrocopturus sp 32	REF	5.14	2.06	1	0	7.48	0	0	1	1	0	0	0	1	0	0
81	Macrocopturus sp. 24	SS	8.4	1.76	1	0	9.96	0	0	0	0	1	1	1	1	1	0
82	Copturus sp. 1	SS	7.03	1.77	1	2	8.09	0	0	0	0	1	1	1	1	1	0
83	Tachylechriops sp. 1	SS	5.83	1.88	1	4	13.09	0	0	0	0	1	1	1	1	1	0
84	Lechriopini gen. 1 sp. 3	SS	5.1	1.87	1	5	16.24	0	0	0	0	1	1	1	1	1	0
85	Macrocopturus sp. 28	SS	5.76	2.04	1	5	11.78	0	0	0	0	1	1	1	1	1	0
86	Macrocopturus sp. 29	SS	4.45	1.99	1	5	13.78	0	0	0	0	1	1	1	1	1	0
87	Macrocopturus sp. 30	SS	3.75	2.01	1	0	10.05	0	0	0	0	1	1	1	1	1	0
88	Macrocopturus sp. 31	SS	4.62	1.89	1	2	8.54	0	0	0	0	1	1	0	0	1	0
89	Macrocopturus sp. 27	SS	6.5	2.05	1	2	6.86	0	0	0	0	1	1	1	1	1	0
90	Macrocopturus sp. 26	SS	5.51	1.97	1	0	23.15	0	0	1	0	3	0	0	1	1	0
91	Macrocopturus richardpackeri	SS	7.6	1.89	1	5	18.94	0	0	0	0	3	1	0	1	1	0
92	Macrocopturus sp. 25	SS	6.69	1.87	1	5	13.68	0	0	0	0	1	1	1	1	1	0
93	Copturus sp. 4	SS	4.6	1.66	1	5	13.68	0	0	0	0	1	0	0	1	1	0
94	Copturus sp. 3	SS	4.35	1.76	1	4	18.43	0	0	0	0	1	0	0	1	1	0
95	Copturus aurivillianus	SS	4.27	1.81	1	4	11.93	0	0	0	0	1	0	0	1	1	0
96	Copturus sp. 5	SS	3.87	1.82	1	4	27.52	0	0	0	0	3	0	0	1	1	0
97	Copturus sp. 2	SS	4.13	1.8	1	4	45.20	2	0	0	0	3	0	0	1	1	0
98	Macrocopturus papei	SS	6.35	1.91	1	4	13.97	0	0	0	0	1	2	0	1	1	0
99	Macrocopturus lepidus	SS	6.74	1.95	1	3	2.87	0	0	0	0	4	0	0	1	1	0
100	Paramnemyne pulchella	SS	6.09	1.81	1	3	29.59	0	0	0	0	3	1	0	1	0	0
101	Zygops amoenula	SS	7.64	2.72	1	0	23.07	0	0	0	0	3	0	0	1	0	0
102	Macrocopturus cinnabarinus	SS	6.09	1.93	1	0	29.92	0	0	0	0	3	1	0	1	1	0
103	Poecilogaster brevis	SS	7.94	1.65	1	4	61.11	2	0	0	3	3	0	0	0	NA	0
104	Poecilogaster sp. 1	SS	5.95	1.58	1	4	47.72	2	0	0	3	3	0	0	1	NA	0
105	Poecilogaster sp. 2	U1	7.96	1.67	1	4	25.96	2	0	0	0	3	0	0	1	NA	0
106	Hoplocopturus sp. 17	SS	5.72	1.88	1	3	14.85	0	0	0	0	3	1	1	0	NA	0
107	Eulechriops sp. 1	U2	4.03	1.96	0	NA	75.10	0	0	0	3	NA	0	0	0	NA	0
108	Hoplocopturus sp. 18	Y	5.16	1.82	0	NA	NA	0	0	1	0	4	1	1	1	NA	0
109	Macrocopturus corumbaensis	Y	5.36	1.99	0	NA	NA	0	0	1	0	4	1	1	1	NA	0
110	Copturus cf. aurolegulus	Y	3	1.45	0	NA	NA	0	0	1	0	4	0	1	1	NA	0
111	Copturus sp. 6	SS	3.87	1.8	0	NA	6.47	0	0	0	0	1	0	0	1	NA	0
112	Copturus sp. 7	SS	3.04	1.48	0	NA	NA	0	0	0	0	1	0	0	1	NA	0
113	Copturus sp. 8	SS	2.91	1.56	0	NA	1.21	1	0	1	0	3	0	0	1	NA	0
114	Microzurus sp. 2	A1	3.23	1.7	0	NA	NA	0	0	0	0	1	1	0	1	NA	1
115	Microzurus sp. 1	A1	2.9	1.76	0	NA	NA	0	0	0	0	1	1	0	1	NA	1
116	Arachnomorpha circumlineata	A1	3.63	1.76	0	NA	NA	0	0	0	0	1	1	0	1	NA	1
117	Lissoderes subnudus	A1	4.43	2.18	0	NA	NA	0	0	0	0	1	0	0	1	NA	1
118	Eulechriops coruscus	A1	3.34	1.67	0	NA	NA	0	0	0	0	1	0	0	0	NA	1
119	Philenis anzaldoi	B	6.52	1.93	0	NA	NA	0	0	1	2	4	0	0	0	NA	0
120	Macrocopturus lynceus	C/NM	7.68	2.13	0	NA	NA	0	0	0	2	4	2	1	1	NA	0
121	Copturomimus caeruleotinctus	M	3.77	1.89	0	NA	NA	0	1	1	0	2	0	0	0	NA	0

Number	Species	Complex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
122	Archocopturus laselvaensis	M	4.09	2.2	0	NA	NA	0	1	1	0	2	1	1	0	NA	0
123	Zygopsella ruficauda	M	3.19	1.84	0	NA	NA	0	1	1	1	0	0	0	0	NA	0
124	Archocopturus miutus	M	2.71	1.92	0	NA	NA	0	1	1	1	0	0	0	0	NA	0
125	Macrocopturus sp. 34	M	2.83	1.87	0	NA	NA	0	1	1	1	0	0	0	0	NA	0
126	Hoplocopturus basalis	C/NM	3.99	1.87	0	NA	NA	0	0	0	2	0	1	0	0	NA	0
127	Hoplocopturus nubilis	C/NM	7.25	2.03	0	NA	NA	0	0	0	2	4	0	1	0	NA	0
128	Hoplocopturus sulphureus	C/NM	5.95	2.07	0	NA	NA	0	0	0	2	4	0	1	0	NA	0
129	Larides cavifrons	C/NM	3.8	1.98	0	NA	NA	0	0	0	2	1	0	0	0	NA	0
130	Lechriops albisquamis	C/NM	4	1.76	0	NA	NA	0	0	0	1	0	0	0	0	NA	0
131	Copturomimus interrupta	C/NM	5.4	1.86	0	NA	NA	0	0	0	2	1	1	1	1	NA	0
132	Eulechriops septemnotatus	C/NM	3.33	1.94	0	NA	NA	0	0	0	2	1	1	0	0	NA	0
133	Eulechriops lugubris	C/NM	3.98	1.7	0	NA	NA	0	0	0	0	1	0	0	0	NA	0
134	Macrocopturus crassus	C/NM	3.92	1.79	0	NA	NA	0	0	0	2	1	0	1	0	NA	0
135	Macrocopturus semirufus	C/NM	4.48	2.17	0	NA	NA	0	0	0	2	1	1	1	0	NA	0
136	Macrocopturus verrucosus	C/NM	4.71	1.83	0	NA	NA	0	0	0	0	2	0	1	0	NA	0
137	Phileas granulatus	C/NM	7.74	1.8	0	NA	NA	0	0	0	2	0	0	0	0	NA	0
138	Eulechriops ductilis	C/NM	2.72	1.89	0	NA	NA	0	0	0	0	1	2	0	0	NA	0
139	Copturosomus gibbus	C/NM	6.87	1.91	0	NA	NA	0	0	0	2	1	1	1	0	NA	0
140	Timorus suturalis	C/NM	7.73	1.96	0	NA	NA	0	0	0	2	0	1	1	0	NA	0
141	Macrocopturus albidus	C/NM	5.23	1.98	0	NA	NA	0	0	0	1	0	0	0	0	NA	0
142	Macrocopturus centralis	C/NM	5.97	1.75	0	NA	NA	0	0	0	2	2	0	1	0	NA	0
143	Macrocopturus constrictus	C/NM	5.76	1.91	0	NA	NA	0	0	0	1	0	0	0	1	NA	0
144	Hoplocopturus quinquevittatus	C/NM	7.39	2.11	0	NA	NA	0	0	0	0	1	2	0	1	NA	0
145	Lechriops vestitus	C/NM	3.41	1.73	0	NA	NA	0	0	0	0	2	0	1	0	NA	0
146	Paramnemyne decemcostata	C/NM	4.43	1.68	0	NA	NA	0	0	0	0	2	0	0	0	NA	0
147	Cylindrocopturus imbricatus	C/NM	3.99	2.05	0	NA	NA	0	0	0	2	0	0	1	0	NA	0
148	Cylindrocopturus armatus	C/NM	3.96	2.08	0	NA	NA	0	0	0	2	0	0	1	0	NA	0
149	Hoplocopturus varipes	C/NM	4.58	1.7	0	NA	NA	0	0	0	0	1	0	1	0	NA	0
150	Cylindrocopturinus pictus	C/NM	4.67	1.9	0	NA	NA	0	0	0	0	1	0	0	0	NA	0
151	Coturpus arcuatus	C/NM	3.79	2.02	0	NA	NA	0	0	0	1	0	0	1	0	NA	0
152	Lechriops porcatus	C/NM	2.89	1.89	0	NA	NA	0	0	0	0	1	2	1	0	NA	0
153	Macrocopturus linter	C/NM	8.08	2.59	0	NA	NA	0	0	0	0	1	0	0	1	NA	0
154	Macrocopturus fulvomaculatus	SS	6.57	2.02	1	3	23.84	1	0	0	0	3	0	0	1	NA	0
155	Macrocopturus mexicanus	C/NM	11.68	2.35	0	NA	NA	0	0	0	0	4	2	0	0	NA	0
156	Macrocopturus sp. 33	A2	6.11	2.17	0	NA	NA	0	0	0	0	1	0	0	0	NA	0
157	Copturomimus asperatus	C/NM	4.29	1.8	0	NA	NA	0	0	0	2	0	1	1	0	NA	0
158	Helleriella longicollis	Cly	6.12	2.53	0	NA	9.40	0	0	0	0	1	1	0	0	NA	0
159	Cylindrocopturus bifasciatus	C/NM	4.8	2.38	0	NA	NA	0	0	0	2	2	0	1	0	NA	0
160	Microzygops nigrofasciatus	A3	2.94	2.23	0	NA	NA	0	0	0	0	2	0	0	0	NA	0

APPENDIX C

PAIRWISE PERMANOVA RESULTS FOR THE FULL DATASET

Complex 1	Complex 2	R2	F	Residual df	p
Ant	Ant2	0.312	1.8	4	0.333
Ant	Ant3	0.498	4	4	0.167
Ant	Bee	0.789	15	4	0.167
Ant	Blue/red fly	0.694	13.6	6	0.024
Ant	Clytrine	0.322	1.9	4	0.333
Ant	Cryptic	0.16	6.7	35	0.001
Ant	Medetera	0.512	8.4	8	0.017
Ant	Red-eyed Fly	0.198	18.3	74	0.001
Ant	Striped/Spotted	0.017	0.6	38	0.553
Ant	Unknown1	0.65	7.4	4	0.167
Ant	Unknown2	0.663	7.9	4	0.167
Ant	Yellow spotted	0.824	28.1	6	0.023
Ant2	Ant3	1	NaN	0	NA
Ant2	Bee	1	NaN	0	NA
Ant2	Blue/red fly	0.494	2	2	0.25
Ant2	Clytrine	1	NaN	0	NA
Ant2	Cryptic	0.018	0.6	31	0.728
Ant2	Medetera	0.155	0.7	4	0.333
Ant2	Red-eyed Fly	0.053	3.9	70	0.042
Ant2	Striped/Spotted	0.029	1	34	0.317
Ant2	Unknown1	1	NaN	0	NA
Ant2	Unknown2	1	NaN	0	NA
Ant2	Yellow spotted	0.939	30.5	2	0.25
Ant3	Bee	1	NaN	0	NA
Ant3	Blue/red fly	0.501	2	2	0.25
Ant3	Clytrine	1	NaN	0	NA
Ant3	Cryptic	0.024	0.8	31	0.544
Ant3	Medetera	0.116	0.5	4	0.333
Ant3	Red-eyed Fly	0.061	4.6	70	0.041
Ant3	Striped/Spotted	0.047	1.7	34	0.168
Ant3	Unknown1	1	NaN	0	NA
Ant3	Unknown2	1	NaN	0	NA
Ant3	Yellow spotted	0.953	40.2	2	0.25
Bee	Blue/red fly	0.267	0.7	2	1
Bee	Clytrine	1	NaN	0	NA
Bee	Cryptic	0.044	1.4	31	0.222
Bee	Medetera	0.014	0.1	4	1
Bee	Red-eyed Fly	0.055	4	70	0.038
Bee	Striped/Spotted	0.129	5	34	0.027
Bee	Unknown1	1	NaN	0	NA
Bee	Unknown2	1	NaN	0	NA

Complex 1	Complex 2	R2	F	Residual df	p
Bee	Yellow spotted	0.957	45	2	0.25
Blue/red fly	Clytrine	0.589	2.9	2	0.25
Blue/red fly	Cryptic	0.207	8.6	33	0.001
Blue/red fly	Medetera	0.255	2.1	6	0.122
Blue/red fly	Red-eyed Fly	0.044	3.3	72	0.027
Blue/red fly	Striped/Spotted	0.283	14.2	36	0.001
Blue/red fly	Unknown1	0.66	3.9	2	0.25
Blue/red fly	Unknown2	0.491	1.9	2	0.25
Blue/red fly	Yellow spotted	0.692	9	4	0.1
Clytrine	Cryptic	0.026	0.8	31	0.496
Clytrine	Medetera	0.247	1.3	4	0.333
Clytrine	Red-eyed Fly	0.081	6.2	70	0.027
Clytrine	Striped/Spotted	0.027	1	34	0.314
Clytrine	Unknown1	1	NaN	0	NA
Clytrine	Unknown2	1	NaN	0	NA
Clytrine	Yellow spotted	0.928	25.6	2	0.25
Cryptic	Medetera	0.135	5.5	35	0.007
Cryptic	Red-eyed Fly	0.439	79.2	101	0.001
Cryptic	Striped/Spotted	0.362	36.9	65	0.001
Cryptic	Unknown1	0.163	6	31	0.034
Cryptic	Unknown2	0.029	0.9	31	0.455
Cryptic	Yellow spotted	0.246	10.8	33	0.001
Medetera	Red-eyed Fly	0.204	18.9	74	0.001
Medetera	Striped/Spotted	0.337	19.3	38	0.001
Medetera	Unknown1	0.417	2.9	4	0.333
Medetera	Unknown2	0.062	0.3	4	1
Medetera	Yellow spotted	0.619	9.8	6	0.028
Red-eyed Fly	Striped/Spotted	0.453	86.2	104	0.001
Red-eyed Fly	Unknown1	0.075	5.7	70	0.027
Red-eyed Fly	Unknown2	0.072	5.4	70	0.031
Red-eyed Fly	Yellow spotted	0.173	15	72	0.001
Striped/Spotted	Unknown1	0.04	1.4	34	0.224
Striped/Spotted	Unknown2	0.079	2.9	34	0.044
Striped/Spotted	Yellow spotted	0.181	7.9	36	0.001
Unknown1	Unknown2	1	NaN	0	NA
Unknown1	Yellow spotted	0.967	57.8	2	0.25
Unknown2	Yellow spotted	0.961	48.9	2	0.25