When Ground Beetles Fly: A Taxonomic Review of the Arboreal, Myrmecophilous Neotropical Genus, Homopterus (Coleoptera: Carabidae: Paussinae) with a new Species Description, Species Diagnoses, and Insights into Species Distributions

WHEN GROUND BEETLES FLY: A TAXONOMIC REVIEW OF THE ARBOREAL, MYRMECOPHILOUS NEOTROPICAL GENUS, *HOMOPTERUS* (COLEOPTERA: CARABIDAE: PAUSSINAE) WITH A NEW SPECIES DESCRIPTION, SPECIES DIAGNOSES, AND INSIGHTS INTO SPECIES DISTRIBUTIONS

by

Angela Marie Hoover

A Thesis Submitted to the Faculty of the

GRADUATE INTERDISCIPLINARY PROGRAM IN ENTOMOLOGY AND INSECT SCIENCE

In Partial Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

2016

STATEMENT BY AUTHOR

The thesis titled *When Ground Beetles Fly: A taxonomic review of the arboreal, myrmecophilous Neotropical genus Homopterus (Coleoptera: Carabidae: Paussinae) with a new species description, species diagnoses, and insights into species distributions* prepared by Angela M. Hoover has been submitted in partial fulfillment of requirements for a master's degree at the University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that an accurate acknowledgement of the source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his or her judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Angela Marie Hoover

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

Dr. Wendy Moore
Thesis Director Name
Professor of Entomology

Defense date: *December 6, 2016*

ACKNOWLEDGEMENTS

The authors would like to acknowledge Andrea Di Giulio of the University Tre Roma for his assistance in photographing type specimens of *Homopterus steinbachi* and *Homopterus bolivianus* while visiting the Berlin Museum. A very special thanks to Charles Langford for his assistance in translating portions of journal articles pertaining to *Homopterus* written originally in Spanish. Thanks to Reilly McManus, Alan Yanahan, Garrett Hughes, Genevieve Comeau, Kirsten Verster, and Tanya Renner for their indispensable friendship and emotional support. Thanks to James Robertson for his assistance and training in Adobe Photoshop and Illustrator. Special thanks to Chip Hedgcock for his assistance in photography and imaging. Special thanks to Gene Hall for his taxonomic advice, support, and gentle goading during the writing process. A grateful thank you to Fred Skillman for his lending of recently collected *Homopterus* specimens that were used in DNA testing. Finally, thank you to Dr. Wendy Moore, Dr. Betsy Arnold, and Dr. Molly Hunter for serving as committee members during the Master's process that produced this research. This research was funded in part by the University of Arizona's Graduate Interdisciplinary Program in Entomology and Insect Science and in part by the National Science Foundation (grants DBI-1206382 to Wendy Moore and DEB-1256976 to Wendy Moore and James Robertson).

DEDICATION

This paper is dedicated to everyone who has had a hand in shaping my journey through the sciences and my development as a person. To my teachers: Mr. Ray Bivaletz for taking the time to read an entire paper written in basic Egyptian hieroglyphs. To Mr. Barry Caffery for teaching me that "the meaning of life is to give life meaning," and for the goldfish (one of them is still alive and well over a decade old at the submission of this manuscript). To Mr. Scott Smith for believing in me and not minding when I read ahead in our bio textbook during class. To Dr. Tim Holovacs for introducing me to the wonderful world of dissections and giving me an appreciation for how organisms are put together. To Dr. Carol Fishbone and Dr. Carolle Im for helping shape my writing and teaching me that history unheeded is bound to repeat itself. I could go on about each of you and some of your colleagues, but I can't for lack of space and time. Please know your guidance has been pivotal in my life and I remember your lessons even now.

To my friends. To Amelia for always reaching out to me when I am the hardest to reach--I may not respond but it means more to me that you care than you know. To Erin (Er-Bear), for her thoughtful cards and support across the miles that always seem to pile up between us. To Liz for being my long-distance sister--it's wonderful to have you in my life and I will never forget New Zealand. To John for joining in mutual shenanigans, late night snack runs, and picking me up when I was really sad. To Meltem and Rositsa for their telling me like it is and helping me pack up my nightmare of a room. To Alicia for teaching me to defend myself, see my small size as an asset, and gossiping with me late into the night after practice. To Kirsten and Genevieve for being my fierce femme fatale friends and the best gym buddies/sparring partners/boba-tea-runners a lady could ask for. And thank you to my friend Charly, as I lie on your couch with a fever and aches, for caring for me and being my partner in adventuring. There are so many stories I could share about all of you but I'm not sure there is enough space here to do so.

And lastly, to my family. To mum, dad, Tommy, Joey, Grammy and Papa, Grandma and Grandpa, Auntie Laura and Uncle Brad and Zoey, my Aunt Sharon, my Great Aunt Joyce and Great Aunt Linda. Thank you for being there for me even though I'm very far away in Arizona and for thinking of me. I miss you all and love visiting with you when I can. Thank you for being my long-distance support group!

TABLE OF CONTENTS

List of Figures

ABSTRACT

A review of the species groups of the Neotropical myrmecophilous genus *Homopterus* Westwood is presented based on the first molecular phylogenetic analysis of the genus and morphological study of 260 specimens. Two new species groups, the *H. subcordatus* group and the *H. filiko* group are erected based on the results of the molecular phylogenetic analysis and morphological analysis. The genus consists of one species known only from Dominican amber, *H. hispanolienses* Nagel, and thirteen extant species, one of which is described as new: *Homopterus filiko* n.sp. from Peru. An illustrated dichotomous identification key to species, diagnoses of the species groups and updated distribution maps are provided. The potential of several of the species groups to harbor additional cryptic diversity is discussed.

KEYWORDS

Coleoptera, *Homopterus*, taxonomic review, molecular phylogeny, myrmecophiles, new species, Neotropics

INTRODUCTION

Homopterus Westwood 1841 is one of two genera of the carabid beetle tribe Paussini known from the Western Hemisphere. It is easily distinguished from the other New World genus, *Eohomopterus* Wasmann, 1920, all of whose species have freely exposed tarsomeres and a rounded penultimate maxillary palpomere. In contrast, all species of *Homopterus* have expanded tibia covering the tarsi of all legs and a distinctly triangular penultimate maxillary palpomere (Fig 8). Adults also have distinctly flattened perfoliate antennae, and robust tank-like bodies (Fig. 2, 3, Fig 11A).

Endemic to the New World topics, species within *Homopterus* are distributed from central Mexico to San Ignacio, Argentina with a center of diversity in Panama. As with most myrmecophiles, *Homopterus* beetles are elusive and therefore we know very little about their natural history. Their larvae have not been described. As is thought to be the case for all members of the Paussini, they presumably live with ants during at least part of their life cycle. However to date there has only been one published host ant record for a *Homopterus* species. Darlington (1950) reported that a "female *Homopterus steinbachi* was collected at Muzo, Dept. Boyacá, Colombia by Dr. J. Bequaert, with *Dolichoderus (Monacis) bispinosus* Ol. (det. W.M. Wheeler)." These ants nest within myrmecophytic plants such as *Cordia* and *Tillandsia*, as well as in cavities within trees, hollow logs, and occasionally in arboreal carton termite nests (Swain 1977). Further research and collecting efforts are needed to determine if *Homopterus* is regularly associated with this ant species.

Adults are mainly collected after being attracted to ultraviolet or mercury vapour lights. However, there is some evidence that *Homopterus* species are largely arboreal. During 1977 and 1978 Henk Wolda collected weekly samples of insects with three vertically arrayed light traps in the forests of Barro Colorado Island, Panama. One trap was set at ground level, a second was suspended in the canopy 26-28 meters above the forest floor, and the third was set at an intermediate level (Wolda 1978). Wolda's collections are particularly valuable since they provide consistent quantitative weekly samples for multiple years. This study resulted in the collection of 51 *Homopterus* specimens (26 *H. subcordatus,* 17 *H. kriegi*, and 8 *H. steinbachi*) all of which were collected only by the highest traps, suggesting that these species may be arboreal.

In addition to isolated species descriptions, two previous authors have treated this genus in greater detail. Reichensperger (1938) described 4 new *Homopterus* species. Luna de Carvalho (1963) classified the extant members of the genus into three species groups, based largely on the shape of the flagellomeres.

H. steinbachi group
- *H. steinbachi* Kolbe, 1920
- *H. arrowi* Reichensperger, 1938,

H. cunctans Reichensperger, 1938
H. amplificatus Reichensperger, 1938

H. brasiliensis group
H. brasiliensis Westwood, 1938
H. subcordatus Darlington, 1950
H. bolivianus Kolbe, 1920
H. kriegi Reichensperger, 1938
H. honduriensis Darlington, 1937
H. martinezi Luna de Carvalho, 1963
H. lunacarvalhoi Martinez & Jimenez-Asua, 1965

H. proemonens group
H. proemonens Kolbe, 1920

The genus also contains a species only known from Dominican amber, *Homopterus hispanolienses* Nagel, 1987. While undoubtedly a member of the genus due to its possession of the expanded triangular subterminal maxillary segment, the placement of extinct *H. hispanolienses* among living members of the genus is enigmatic.

In this study we use molecular sequence data and comparative morphology to test Luna de Carvalho's species groups. Our taxonomic treatment includes a new subgeneric classification for the genus based on the phylogeny, new diagnoses for each species group and species, and the description of a remarkable new species. We also provide an updated distribution map to the genus, species groups and species based on the largest assembled collection of *Homopterus* studied to date.

MATERIAL AND METHODS

Specimens examined

All known specimens of *Homopterus* were examined as part of this study, including 1 fossil and 260 recent specimens. Types of all species, with the exception of of *Homopterus martinezi* Luna De Carvalho, 1963, and *Homopterus lunacarvalhoi* Martinez & Jimenez-Asua, 1965, were either examined in person or from high resolution images acquired from Dr. Wendy Moore or Dr. Andrea DiGiulio as part of this study. Specimens either came from or have been deposited in the collections listed below. Each collection's listing begins with the following codens used in the text.

USNM	National Museum of Natural History, Smithsonian Institution, Washington
MCZH	Museum of Comparative Morphology, Cambridge, Massachusetts
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
CAS	California Academy of Sciences, San Francisco, California
UCDC	Robert M. Bohart Entomology Museum, University of California Davis, Davis, California
EMEC	Essig Museum of Entomology, Berkeley, California

INBIO Instituto Nacional de Biodiversidad, Heredia Province, Santo Domingo, Costa Rica
UASM E. H. Strickland Entomological Museum, University of Alberta, Edmonton, Canada
AM Personal collection of Alan Mudge
PS Personal collection of Pat Sullivan
FS Personal collection of Fred Skillman
CWO Personal collection of Charles O'Brien
WM Personal collection of Wendy Moore

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from one mid-leg following the ATL protocol in the Qiagen DNeasy kit (Valenica, CA). Gene fragments from cytochrome c oxidase subunit I (COI), 28S ribosomal DNA (28S or 28S rDNA) were amplified using the Polymerase Chain Reaction (PCR) on an Eppendorf Mastercycler Thermal Cycler with Invitrogen Platinum Taq DNA Polymegfyurase (Carlsbad, CA). We amplified COI using primers LCO1490 and HCO2198 and 28S using primers LS30F, LS58F, LS1066R, LS1126R. We followed published protocols for PCR amplification (Moore 2008, Gilbert et al., 2007). The amplified products were cleaned, quantified, normalized and sequenced at the University of Arizona's Genomic and Technology Core Facility using an Applied Biosystems 3730 DNA Analyzer or a 3730 XL Applied Biosystems automatic sequencer. Simultaneous contig assembly and initial base calls were performed using the Phred (Green and Ewing, 2002) and Phrap (Green, 1999) programs as implemented in Mesquite 3.1 (Maddison and Maddison, 2016) in combination with the Chromaseq package vers 1.2 (Maddison and Maddison, 2016). Final base calls were made after manual inspection of individual sequences in Chromaseq; universal ambiguity (IUPAC) codes were used when multiple peaks were present at individual sites. All sequences will be deposited in DDBJ/EMBL/GenBank and accession numbers will be published in a derivative publication.

Multiple sequence alignment

Fragments of COI were not length variable and were manually aligned in Mesquite (Maddison and Maddison, 2016), and the resulting matrices were 559 bp. 28S rDNA sequences were aligned using an online version of MAFFT 7 (http://maftft.cbrc.jp/ alignment/server; Katoh and Standley, 2013) employing a Q-INS-I search strategy that accounts for RNA secondary structure (Katoh and Toh, 2008). The alignment was then inspected in Mesquite and obviously misaligned blocks were corrected manually.

Phylogenetic reconstruction

Phylogenetic trees were inferred using a model-based method on the concatenated matrix of both gene fragments. Optimal models and partitioning schemes were selected using PartitionFinder (Lanfear et al., 2012) and the Akaike Information Criterion. PartitionFinder selected the GTR+I+G model for each partition. Maximum likelihood (ML) heuristic searches were conducted using RAxML 8.0.9 (Stamatakis, 2014) on CIPRES (Miller et al., 2010). Searches based on the concatenated matrix included 1000 alternative runs repeated twice from different

starting seeds, keeping the highest likelihood tree of the three sets of runs. Non-parametric bootstrap analyses were performed separately from the ML tree searches. Bootstrap values (bs) were inferred from 1000 bootstrap replicates.

Comparative morphology

Adult beetles were examined using a Leica ES2 model microscope. Photographs were taken with a Visionary Digital BK system. Photographs were taken at different focal planes using Visionary Digital's Camlift software; these photographs were then merged using the PMax algorithm in Zerene Systems's Zerene Stacker.

Georeferencing

Geographic distributions presented for each species are based on all known specimens available at the time this study was undertaken. For specimens lacking GPS coordinates, georeferences were determined using locality information written on specimen labels. Latitude and longitude are reported as denoted on individual labels, but were converted to decimal degrees for placement on a map.

RESULTS and DISCUSSION

Phylogenetic reconstruction

The highest likelihood tree based on the concatenated matrix partitioned by gene under GTR+I+G is shown in Fig. 1. Bootstrap support values are also reported on this tree.

The genus *Homopterus* is supported as monophyletic with 100% bootstrap support. All *Homopterus* species groups that were included in our taxon sampling were recovered in the tree, with the exception of the *H. brasiliensis* group, which falls out as two separate clades.

Prior to this work, the *H. brasiliensis* group contained species that were loosely held together on the basis of flagellomere morphology and tibiae shape. With the acquisition of more specimens since the publication of the latest review, the original traits that held together the broad group are not as definitive. With the additional data from the morphological matrix, and strong morphological characters, another broad species group was established. The *Homopterus brasiliensis* group now contains *H. brasiliensis, H. honduriensis,* and *H. kriegi.* These species are united by their white elytral setation (Fig 10D), and the roughly trapezoidal shape of their first flagellomere (Fig 3). The newly established *H. subcordatus* group contains *H. bolivianus, H. subcordatus, H. lunacarvalhoi,* and *H. martinezi.* They are held together by their temple morphology, and morphology of the first flagellomere (Fig 3). The molecular matrix supports the placement of *H. bolivianus* and *H. subcordatus* into a clade together. Because exemplars of *H. lunacarvalhoi* and *H. martinezi* could not be obtained for this study, their placement in the H. subcordatus group is based upon their illustrated morphology as set forth in their original species descriptions.

Taxonomic treatment

Genus *Homopterus*, Westwood, 1841

Diagnosis.
Adult color ranges from deep rosy brown to a yellow amber. Head with slight depression between prominent round eyes. Subocular margin extends over the anterior ⅕ aspect of the eye. Scape bulbous, pedicle recessed deeply into scape. Antennae perfoliate; flagellomeres appear to wrap around a central "stem"; antennomeres transversely flattened. Subterminal mandibular maxillary segment triangular in shape, terminal mandibular maxillary segment expanded and paddle-shaped. Pronotum with faint seam down midline, and explante around lateral margins. Elytron with small, circular punctations and occasional setae. Leg segments expanded and flared along the outer apical margin; hind tibiae triangular in shape. Two small spines protrude from base of each tibiae beneath tarsal attachment. All tarsi capable of retracting into a cavity produced by the distal expansion of the hind tibiae.

Type Species: *Cerapterus brasiliensis* Westwood 1838

Remarks: Unlike many members of the Paussini, and Carabidae more generally, *Homopterus* species do not have sexually dimorphic foretarsomeres, making it challenging to determine the sex of the specimen unless the tips of the genitalia are exposed and protrude from the body. However, female *Homopterus* can be identified without the need for dissection by the presence of a row of setae in the terminal sternite just anterior to the genitalic opening.

Identification key to species

1	Antennal club with distinct gaps between each flagellomere (Fig 2A-C); Subocular margin continuously smooth from dorsal to distal margin, rounded (Fig 7A); Apical margin of the tibiae double the length of basal margin; Temples with no projection, flush with margin of eye (Fig 6A); Outer lateral margin of terminal max. palp segment rounded acutely toward midline (Fig 8B)	2 (*H. steinbachi* group, *H. filiko*)
-	Antennal club compact with flagellomeres overlapping, or touching (Fig 2D, E, Fig 3 A, C-E); Subocular margin forming an angle at dorsodistal junction, pointed (Fig 7B); Apical margin of the tibiae the same length as basal margin; Temple protruding from eye margin (Fig 6B, C)	6 (*H. subcordatus* group, *H. brasiliensis* group, *H. proemonens*)
2	Distal margin of flagellomere 9 interrupted by a triangular projection along the inner edge; Singular spikes located on the inner and outer margins of the profemur and	*H. filiko*, n.sp.

	mesofemur, metafemurs with only an outer margin spike; hook present on the outer apical margin; curved toward the posterior apical margin (11C); Clypeus with a medial length .3 of proximal margin length (Fig 11B), Mandibles outer margins straight (FIg 11B)	
-	Terminal flagellomere rounded with no protrusions, Outer margins of mandibles curved (Fig 9A); Clypeus with cluster of setae in center of distal margin (Fig 9A)	3
3	Dorsal surface of pronotum with setae barely extending past the surface of the cuticle, lateral margins of pronotum with curled golden setae (Fig 4B); Ventral surfaces and legs with conspicuous golden setae; Lateral surfaces of elytra with golden setation; Most punctations spaced apart the width of three punctations or greater, and very faint (Fig 2B, Fig 10C)	*H. amplificatus*
-	Pronotum with obvious circular punctations spaced one to two punctations' width apart (Fig 2A, C, D)	4
4	Elytra with faint punctations spaced one to one and a half punctations' widths apart; Pronotum with faint punctations spaced one punctation's width apart (Fig 4D)	*H. arrowi*
-	Elytra and pronotum with distinct punctations	5
5	Elytra with most punctations spaced the width of one punctation apart (10A)	*H. steinbachi*
-	Elytra with most punctations spaced the width of one and a half to two punctations apart (10B)	*H. cunctans*
6	Inner proximal lateral margin of flagellomeres 2-8 symmetrical to outer proximal lateral margin (Fig 2D, E); Outer lateral margin of terminal maxillary palp segment pointed acutely away from midline (Fig 8E)	*H. proemonens*
-	Inner proximal margin of flagellomere 2-8 widely rounded, each flagellomere with equal length lateral margins (Fig 3A, C-E); Lateral margins of the pronotum explanate (Fig 5A-E)	7
7	First flagellomere outer lateral margin asymmetrical to inner lateral margin, outer distal half forming an acute angle less than 45 degrees (Fig 3D, E); Flagellomere setation barely projecting above cuticle giving dorsal	8, (*H. subcordatus* group)

	surface a stippled appearance (Fig 2D, E, Fig 3D, E); Lateral margins of flagellomeres 2-9 beaded (Fig 3D)	
-	First flagellomere lateral margins roughly symmetrical; flagellomere 1 approximately trapezoidal in shape (Fig 3A, B, C); Outer distal half of segment forming a 45 degree angle (Fig 3A, B, C)	9, (*H. brasiliensis* group)
8	Temple protruding over half its width from eye margin when viewed dorsally (Fig 6C); Elytra with a microsetae arising from each punctation; Outer lateral margin of terminal max. palp segment pointed acutely away from midline (Fig 8D);	*H. subcordatus*
-	Temples raised but only projecting slightly if at all from the margin of the eye when viewed dorsally (Fig 6B); Elytra without setation on the dorsal surface	*H. bolivianus*
9	Elytra without setation; Inner proximal lateral margin flagellomeres 2-8 margin thinly rounded; inner proximal corners completely rounded (Fig 2A-C, Fig 3B)	*H. brasiliensis*
-	Elytra with setation of uniform length and even distribution (10D); Inner proximal lateral margin flagellomeres 2-8 widely rounded, each flagellomere with equal length lateral margins (Fig 3A, C-E)	10
10	Proximal and distal margins of flagellomeres 2-8 with slight apical curve, slight space between each flagellomere (Fig 3A)	*H. honduriensis*
-	Proximal and distal margins of flagellomeres 2-8 straight, antennal club compact (Fig 3C)	*H. kriegi*

***Homopterus filiko* group**

Homopterus filiko n. sp.

Type Material. Holotype (♀) labelled: “Loreto, Cocha, Shinguito, Peru, 20 May 90, Erwin et al colls, 74 45'W 05 08'S, -13.583416, -72.850772 (WM.1190, DNA 3415)”. The holotype is deposited in the National Museum of Natural History in Washington D.C.

Etymology. From the Esperanto word for “fern,” in regards to the fern-shaped antennae the species possesses.

Diagnosis. The smallest member of the *Homopterus* genus. Body is rounded unlike the elongated bodies of the currently described species in the genus. Colouration light brown. Pronotum beaded along the lateral margins, with evenly distributed golden setation, and less developed anterolateral margins than members of the *H. steinbachi* group (Fig 4E). Elytra with setation of unequal lengths, some well developed (10E). Tibiae of each leg with a long rounded hook on the outer apical margin (11C). Femur of both forelegs with blunt triangular spikes distally. Femur of mid and hind legs with a singular blunt triangular spike on the outer distal surface. Flagellomeres 2-3 with slighter bifurcation along the posterior margin than the species in the *H. steinbachi* group, similar to species in the *H. subcordatus* Group. Flagellomere 9 with margin interrupted by a projection present on the inner distal corner (Fig 2B). Mandibles possess straight outer margins, unlike those of the Steinbachi Group and more closely resembling that of the *H. brasiliensis*, *H. subcordatus*, and *H. proemonens* Groups. *H. filiko l*acks clypeal setation. Subterminal maxillary palp more compact, as seen in members of the *H. brasiliensis*, *H. subcordatus*, and *H. proemonens* Groups.

Species Description

Colouration. Head orange-brown. Flagellomeres orange-brown, spike on terminal antennomere reddish-brown. Legs orange-brown, hooks on tibiae and spikes on femurs fading to reddish-brown. Elytra orange brown at shoulders and scutellum, fading to a golden brown posteriorly.

Microsculpture. Head and pronotum with numerous punctations spaced more closely together than the width of a single puncture. Elytra with punctations set wider apart than the width of one puncture.

Setation. Setation golden in colour. Scape, head, and pronotum with short and evenly spaced setae. Setation around margins of the eyes long and curled over the eyes. Dorsal and ventral edge of flagellomeres with a thicker fringe of setae. Femur with short and evenly spaced setae. Tibiae with sparse short setae on posterior edge, longer less numerous setae on anterior edge. Tarsi with thick pads of setae. Elytra with long setae arising from each punctation. Pygidium covered in medium length setae with a denser patch of setae along the center of the basal margin.

Head. As wide as the pronotum laterally. Eyes prominent and dramatically rounded. Frons with a horizontal, large oval-shaped depression. Mandibles small and hooked slightly toward the midline. Mandibles joined to the head at a 45 degree angle to the midline. Clypeus shallow and without setae. Antennae fern-shaped and curled. Scape bulbous and prominent, pedicle concealed deeply within the scape. Flagellomere 1 lobed and tapered on the ventral side and tapered to a fine point on the dorsal side. Flagellomere 2-8 lobed and tapered on the ventral side, quadrate on the dorsal side. The dorsodistal, dorsoproximal, and ventrodistal margins of flagellomere 2-8 concave. The ventroproximal margin of flagellomere 2-8 convex. Terminal

flagellomere convex and rounded along the ventroproximal margin. Terminal flagellomere concave along the ventrodistal margin and forming a strong angle with the dorsal margin. A triangular spike is located on the ventrodistal corner of the terminal flagellomere. The spike is equipped with a small trichome at its apex.

Pronotum. Prominent medial suture on disc. Small circular depression located at the anterior end of the suture, a wider semicircular depression at the posterior end of the suture. Rounded at lateral margins. Basal margin convex and slightly flared above the prominent scutellum.

Elytra. Elytra with prominent rounded shoulders. Scutellum bluntly triangular.

Legs. All legs bearing blunt hooks above distal margins of each tibiae. The femurs of the forelegs have paired blunt triangular spikes on the distal margin, flanking each side of the femerotibial joint. The mid and hind legs have only a singular blunt triangular spike on the outside of the femerotibial joint. Each leg with a concave depression along the outer margin below each femerotibial joint.

Abdomen. Bluntly cylindrical and compact. Pygidial surface interrupted horizontally with a broad ridge placed along the middle third of the segment. Pygidium trapezoidally shaped in the bottom third of the segment.

Genitalia. Two palmate projections each equipped with a cluster of setae at the apex. A fringe of long setae marks the genitalic opening.

Remarks. We classify this new species in a species group of its own. It possesses a mixture of characteristics of both the *H. steinbachi* group and the *H. brasiliensis* group as well as a host of highly modified unique characteristics in the genus.

Two specimens were collected originally by Dr. Terry L. Erwin in 1990. However, after their collection, army ants came in through the window during the course of the evening and took one specimen from the point it was mounted upon, leaving behind just a fragment of cuticle (TLE, personal communication). While only represented by a single specimen, the fact that it is so starkly different from the rest of the species within this genus makes the authors confident in its status as a new species.

***Homopterus steinbachi* group**

Diagnosis. Robust body, largest members of this genus. Colouration deep red brown. Pronotum with rounded lateral margins, sloping anterolateral margins, and circular punctations (Fig 4). Elytra disc with circular punctations. Proximal margin of tibiae less than double the length of the apical margin. Setation on the lateral margins of flagellomeres long and visibly projecting past the margins (Fig 2A-C). Flagellomeres 2-8 unbeaded and with more numerous setae on the dorsolateral surface than across the median. Flagellomeres 2-3 with distinctive bifurcation along the posterior margin, Inner proximal lateral margins of flagellomeres 2-8 thinly rounded, inner proximal corners completely rounded (Fig 2A-C). Observable space between flagellomeres

2-8. Outer lateral margin of flagellomere 1 asymmetrical to inner lateral margin; Outer distal half forming an acute angle less than 45 degrees (Fig 2A-C). Subocular margin continuously smooth from dorsal to distal margin; Rounded (Fig 7A). Temples flush with the eye margin with no projections. Outer margins of the mandibles curved. Clypeus with a small cluster of straight golden setae in center of distal margin (Fig 9A). Subterminal maxillary palp segment thin and trapezoidal in shape. Lateral apical margin of the terminal maxillary palp forming an acute angle. Lateral margin of the terminal maxillary palp rounded toward the midline of the body. Maxillary palp with distinct golden setation. Outer angle of the penultimate maxillary palp segment extends past the lateral margin of the terminal segment (Fig 8B).

List of species:

Homopterus steinbachi Kolbe, 1920
Homopterus arrowi Reichensperger, 1938
Homopterus cunctans Reichensperger, 1938
Homopterus amplificatus Reichensperger, 1938

Remarks.

All members of the *H. steinbachi* group are very similar to one another, with *H. amplificatus* being the largest and most unique. The morphology of specimens of *H. steinbachi, H. cunctans,* and *H. arrowi* are very similar to one another. Characteristics commonly cited as useful for distinguishing among these species include the degree of elytral setation and punctation and subtle differences in hind tibiae shape. Yet in studying many specimens in this species group we find that these few characteristics do not have distinct boundaries, such that these characters alone are not sufficient for teasing apart the actual species diversity present in this group. For the purposes of this paper we did our best to assign the specimens available to us to a species. However our current understanding leaves us with the assumption that there may be multiple cryptic species represented within this group. Future work including analyses of molecular sequence data and careful comparison of the genitalia may help reveal the species boundaries.

***Homopterus amplificatus* Reichensperger, 1938**
Location of Type: British Museum
Type Locality: Paramba, Ecuador
Type Material Examined: Photos of the holotype taken from the Bonn Museum

Material Examined: COLOMBIA: Anchicaya Dam, 1200', 70 Km E. Buenaventura Valle, Feb 18, 1970, H. Howden, at light, 3.5333, -76.8675 (WM.1180, male)

Diagnosis
This species possesses all the traits of the *H. steinbachi* group, with some exceptions. Individuals of this species are larger than *H. steinbachi* and *H. arrowi*. Elytral disc with setae barely extending past surface of elytra (Fig 10C). Pronotal disc bare with very faint circular punctations, lateral dorsal surfaces of pronotum with setae of unequal length; lateral margins

of pronotum with curled golden setae (Fig 4B). Lateral margins of pronotum both beaded and explanate (Fig 4B). Ventral surfaces and legs with conspicuous golden setae. Lateral surfaces of elytra with golden setation. Most punctations spaced apart the width of three punctations or greater, and very faint (Fig 2B, Fig 10C).

***Homopterus cunctans* Reichensperger, 1938**
Location of Type: Berlin Museum
Type Locality: St. Laurent du Maroni, French Guiana
Type Material Examined: Photos of paratype from The Alexander Koenig Research Museum. Bonn, Germany

Material Examined. BELIZE: Toledo Dist., Blue Creek Village, 24 July, 1981, W. E. Steiner, 16.197001, -89.04148 (WM.1168, male), Toledo Dist., Blue Creek Village, 1 July, 1981, W. E. Steiner, 16.197001, -89.04148 (WM.1167) BRAZIL: Rondonia, 62 km S. Ariquemas, Faz. Rancho Grande, XI-11-1991, B.C. Ratcliffe, 10 32'S 62 48'W, -10.53333, 62.8 (WM.1182, male), Rondonia, 62 km, SW Ariquemas, nr. Fzda. Rancho Grande, X-16-1993, CW & LB O'Brien, at merc. vap. & UV light, -10.287383, -63.527344 (WM.1137, DNA 3417, female), Rondonia, 62 km, SW Ariquemas, nr. Fzda. Rancho Grande, 6-15-XII-1990, DA Rider & JE Eger, -10.287383, -63.527344 (ADP 112039, male) COSTA RICA: Est. Esquinas 0m, Peninsula de Osa, Prov. Punt., 8 a 27 nov 1992, A. Gutierrez, L-Sl301400, 542200, 8.680646, -83.312079 (INBIOCRI000993249, male) ECUADOR: Napo Pr., 25km E Atahualpa, 10-15 Sept 1998, F.T. Hovore coll., -0.322311, -78.108258 (WM.1188, DNA 3409, female) FRENCH GUIANA: D-5 4k SE Tngmd Jct, 24-27-VIII-1995, JE Wappes, 4.767644, -53.513081 (WM.1250, male), Montagne de Kaw, km 38, 21 SEP 1992, Carlson, Hovore, Sullivan, 4.538679, -52.136873 (WM.1249, male) PERU: Loreto, Cocha Shinguito, 140m, 26 Aug 1991, 05 08'S 74 45'W, at white light at lab tent in forest 50 m from river on Tr. Principal Lot 51, TL Erwin, 5.1333, -74.75 (ADP 71341, DNA 3418, male) VENEZUELA: San Juan, July 1900, W. Robinson bequest 1929, 8.498094, -71.35618 (WM.1178, male)

Diagnosis
This species is larger than *H. steinbachi* and *H. arrowi*. Pronotal disc bare and with distinct punctations (Fig 4B), lateral margins of pronotum with short straight golden setae (Fig 4A). Pronotum not beaded or explanate (Fig 4A). Elytra with most punctations spaced the width of one and a half to two punctations apart (Fig 10B).

Remarks
Found in Belize, Brazil, Costa Rica, Ecuador, French Guiana, and Venezuela. Specimens collected from May to December. While most specimens of this species are large, one specimen (WM.1178) collected from Venezuela has the traits of *H. cunctans*, while being the size of smaller *H. steinbachi*.

***Homopterus steinbachi* Kolbe, 1920**
Location of Type: Berlin Museum

Type Locality: Sara Province, Bolivia
Type Material Examined: Homotype, ADP 47302; Photos of the holotype taken from the Berlin Museum

Material Examined. BELIZE: Cayo Dist., Augustine, 8-VIII-1993, at black lights, William D. Shapard, 16.96716, -88.983333 (WM.1169, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1166, female), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1165, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1164, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1163, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1162, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1161, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1160, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (WM.1159, male), Toldeo District, Columbia For. St., UV-light, July 1968, W.L. Hasse coll., 16.266667, -88.95 (WM.1158, HOMOTYPE, male), Camp Sibun, 200m, Cayo District, Brit. Honduras, July 23, 1960, 17.081517, -88.650147 (WM.1157, male), Cayo District, nr. Teakettle Bank, Pook's Hill Lodge, 5-VII-2003, C.R. Bartlett, Hg Vapor/Blacklight, N17 09.26'W88 51.09', 17.154292, -88.852188 (TM 2045317, male), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (ADP 65362, female), Toledo Dist., Blue Creek Village, 6 June 1981, W.E. Steiner, 16.197001, -89.04148 (ADP 65361, female), Toldeo District, Columbia For. St., UV-light, 28 July 1968, W.L. Hasse coll., 16.280509, -89.033771 (ADP 47297, male), Orange Walk dist., Chan Chich Lodge blt. 2-VII-2004, C. Sanabria, 18.066667, -88.55 (ADP 112041, male), W. Dist,. Rio Bravo Cons. Area, UVTrap, Hdqtrs., VII-9-1996, L.B. O'Brien, 17.699945, -88.806242 (ADP 112043, male), BOLIVIA: S. Cruz, SaavedraRes. Sta., 22 Mar, 1978, UV Trap, CR Ward & CW O'Brien, -17.229445, -63.217599 (ADP 112107, male) BRAZIL: Rondonia, 62 km, SW Ariquemas, nr. Fzda. Rancho Grande, 6-15-XII-1990, DA Rider & JE Eger, -10.287383, -63.527344 (ADP 111986, female), Rondonia, 62 km, SW Ariquemas, nr. Fzda. Rancho Grande, 6-15-XII-1990, DA Rider & JE Eger, -10.287383, -63.527344 (WM.1184, male) COLOMBIA: 1936, Muzo, VII-11-36, Dept. Boyaca, alt. 900m, 5.532462, -74.100624 (WM.1179, female) COSTA RICA: Vuelta Campana, Rio Terraba, Rey Curre, Prov. Puntarenas, 300-300m, 8 Jun 1993, S. Rojas, L S 325750_544450, #2190, 8.966667, -83.25 (INBIOCRI001954063, male), Finca Jenny, 30 km N. de Liberia, Prov. Guana, 240m, 15 JUN-2 JUL 1995, E. Araya de Luz, L N 317150 363700 #5348, 10.906092, -85.43772 (INBIOCRI002236715, male) FRENCH GUIANA: PK 32, Rte. a Kaw, Aug 23-25, 1995, E. Giesbert, J. Wappes, 4.553727, -52.154285 (ADP 112047, male), kilometer point 27 on "Piste de Kaw" near Kaw Mountain, Feb. 2006, collector Francois Bondil at light trap, 4.5N 52W, 4.538679, -52.136873 (WM.1185, DNA 3408, male), Kaw Mountain Res. Amazone Lodge 4 32’ 57.8’N 52 12’49.7”W 8-18 February 2005 KB Miller, collector, 4.54939, -52.2138 (WM.0147, DNA 2020, DNA 3405, DNA 3406, DNA 3407, male), GUATEMALA: D. Izabal, Firmeza, 30 km, SE Morales, 15.416819, -88.642946 (WM.1183, male), Peten Dept., Parque Nacional El Rosario, E of Sayaxche, 30 June 2014, BL/MV lights, R.S. Zack coll., 16.52414, -90.16009 (WM.1252, male), Peten Dept., Parque Arqueologico El Ceibal, E of Sayaxche, 29-30 June 2014, 233 m, BL/MV lights, R.S. Zack coll., 16.51297, -90.06256 (WM.1253, male), Izabal Dept., ca. 20 km SSE of Morales, 7 May 2008, BL/MV light traps, R. S. Zack coll., 15.381583, -88.717383 (WM.1254, male), Peten Dept., Biotopo Cerro Cahui E of El Remate, 191m, 28 Jun 2014, BL/MV light traps,

R.S. Zack coll., 16.99765, -89.70386 (WM.1255, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1156, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1155, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1154, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1153, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1152, male), Peten: Ruinas Tikal, 245m, 7/10-July-77, E.M. & J.L. Fisher, 17.216667, -89.633333 (WM.1151, male), Tikal (Parque National), 23-VI-1974, R.W. Lundgren, 17.216667, -89.633333 (ADP 05546, male), Peden, vic. Tikal N.P., June 8-9, 1991, E. Giesbert, coll., 17.216667, -89.633333 (ADP 111966, male), Izabal, 22km SE Morales, 2400', May 21-24, 1996, E. Giesbert, J. Monzon, 15.342785, -88.670875 (ADP 111970, male), Izabal, 23km SE Morales, 800m, May 23-27, 1995, Giesbert, Monzon, 15.336394, -88.664248 (ADP 111972, male), Izabal, 25km SE Morales, 900m, May 31-June 2, 1997, E. Giesbert, J. Monzon, 15.323612, -88.650995 (ADP 111984, male) MEXICO: Chiapas, El Aguacero, 16 km W Ocozocoautla, 10-VI-2009 Skillman and Hildebrant at lights, 16.7829, -93.1362 (WM.0851, DNA 3400, male), Quintana Roo, MX307, 12km N. of Felipe Carillo Puerto, 17-VI-2009, Skillman & Hildebrant, MV & UV light, 19.717177, -88.083742 (WM.1246, male), Ver.: Estacion de Biologia los Tuxtlas, 9-13 May 1991, J.D. McCarty, P.H. Sullivan, 18.563412, -95.08864 (WM.1141, male), Chiapas, 2 kmS. Chicoasen, VI-1-1991, B. Ratcliffe, J. Ashe, M. Jameson colls., 16.934025, -93.111232 (WM.1150, male), Quintana Roo, 3.5 km W Puerto Morelas 20-21.VI.2009 Skillman & Hildebrant, at lights, near Atta nest., 20.86, -86.976 (WM.0853, male), Quintana Roo, 3.5 km W Puerto Morelas 20-21.VI.2009 Skillman & Hildebrant, at lights, near Atta nest., 20.86, -86.976 (WM.0852, DNA 3401, male), Quintana Roo, 3.5 km W Puerto Morelas 20-21.VI.2009 Skillman & Hildebrant, at lights, near Atta nest., 20.86, -86.976 (WM.0849, DNA 2144, male), Chiapas, Palenque, VI-23-1985, D.B. Thomas, 17.509036, -91.983337 (ADP 111974, male), Chiapas, 12 km S. Palenque, July 3, 1986, E. Giesbert coll., 17.400676, -91.983337 (ADP 112006, male), Tabasco 59.4 miles SE Villahermosa, VI.6-7.1966 black light, 18, -92.666667 (WM.1256, male), Tabasco 59.4 miles SE Villahermosa, VI.6-7.1966 black light, 18, -92.666667 (WM.1257, male) PANAMA: Canal Zone, BCI-STRI; beating plants; at night, Hg/UV lights; 195ft, VI-02-2013; leg. N. Franz, S. Flynn, S. Lee, 9.16371, -79.83791 (WM.1139, male), Canal Zone, Ft. Gulick, Qtrs., 40A, 6-11-V-1981, black light trap, H.J. Harlan, 9.321944, -79.869722 (WM.1186, male), Ft. Gulick Qtrs, 40-A, May-July 1981, H.J. Harlan colr., at lights, 9.321944, -79.869722 (WM.1181, male), Panama Altos (Isla) de Maje, V-28-30-1982, B.C. Ratcliffe & C. & K. Messenger, 9 08'N 78 49'W, 9.166667, -78.816667 (WM.1173, male), Colon Prov., Ft. Sherman Pavon Hill, VI-3-1995, at light, B. Ratcliffe & M. Jameson, 9.35, -79.95 (WM.1172, male), Cerro Azul, "Pinos Altos", Panama Prov., 3 JUNE 1986, F.T. Hovore coll., 9.230083, -79.403172 (WM.1174, male), Canal Zone, Barro Colorado Isl., 6 JULY 1978, Silberlied/Aiello, at light, 9.163611, -79.837778 (WM.1171, male), Panama Prov., Parq. Nac. Soberania Pipeline Rd., km 2.4, V-25-1995, B. Ratcliffe & M. Jameson, 9.128255, -79.715253 (WM.1170, male), C.Z. Coco Solo Hosp., 25 May '72, Stockwell, 9 21'N 79 51'W, 9.37, -79.881667 (ADP 47468, male), Panama pr. 7-10km N. El Llano, May 14-22, 1993, E. Giesbert coll., 9.212222, -78.964167 (ADP 111982, male), C.Z. Madden Dam, 10-13 July 1967, O.S. Flint, Jr., 9.216667, -79.616667 (ADP 01488, male), Panama pr. 6km E Puente Bayano, May 21, 1987, E. Giesbert coll., 9.182424, -78.742695 (ADP 111968, male), Canal Zone, Barro Colorado Is., 19 July 1977, 9.163611, -79.837778 (ADP 75739, male), Canal Zone, Barro Colorado Is. 27 June 1978, 9.163611, -79.837778 (ADP 75846, male), Canal Zone, Barro

Colorado Is., 27 June 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 78369, male), Canal Zone, Barro Colorado Is., 29 July 1978, 9.163611, -79.837778 (ADP 79729, male), Canal Zone, Barro Colorado Is. 27 May 1978, 9.163611, -79.837778 (ADP 83404, male), Canal Zone, Barro Colorado Is. 1 June 1978, 9.163611, -79.837778 (ADP 84349, male), Canal Zone, Barro Colorado Is. 1 June 1978, 9.163611, -79.837778 (ADP 84392, male), Canal Zone, Barro Colorado Is. 15 May 1978, 9.163611, -79.837778 (ADP 62451, male), Barro Colorado Island, 25.vi.1999. DRM 99.007. A.E. Arnold, 9.154722, -79.848056 (WM.0032, DNA 1024, DNA 1613, DNA 3403, DNA 3404, male) PERU: Loreto, Ucayali, R., Yarina Cocha, XII-4-1953, leg. Peter Hocking, -8.346418, -74.575845 (WM.1187, male) VENEZUELA: T.F. Amazonas, San Carlos de Rio Negro, 125m, 19-31-VIII-1976, J. Salcedo, Ag. Fernandez. B., 1.916667, -67.066667 (WM.1177, female), T.F. Amazonas, 27-VI-1984, Mamusavidi, Rio Pasimonia, L.J. Joly, T.J. Demarmels, 1.931667, -66.609167 (WM.1175, male), T.F. Amazonas, Sta. Lucia, 15-21-XI-1982, A. Chacon, G. Yepoz Gil coll., (WM.1176, male)

Diagnosis
Setal fringe on the lateral margins of the pronotum less pronounced than seen in *H. cunctans, H. arrowi*, and *H. amplificatus*. Lateral pronotal margins both beaded and explanate (Fig 4C). Elytra with most punctations spaced the width of one punctation apart (Fig 10A).

***Homopterus arrowi* Reichensperger, 1938**
Location of Type: Berlin Museum
Type Locality: Honduras Britanique: Colombie
Type Material Examined: Photos of paratype specimen taken from the Berlin Museum

Diagnosis. Elytra with faint punctations spaced one to one and a half punctations' widths apart. Pronotum with faint punctations spaced one punctation's width apart (Fig 4D). Pronotum both beaded and explanate.

Remarks
Very similar to *H. steinbachi*, punctations less impressed than seen in other species of the *H. steinbachi* group. Dorsal and ventral surfaces of the flagellomeres appear matte and not as shiny as other members of the *H. steinbachi* Group.

***Homopterus subcordatus* group**

Diagnosis: Colouration moderately rosy-brown. Clypeus glabrous. Temples triangular and protruding from eye margin when viewed dorsally (Fig 6C). Pronotum widely explanate and lacking distinct fringe of setae on lateral margins (Fig 5B, C). Flagellomere setation barely projecting above cuticle, giving dorsal surface a stippled appearance (Fig 3D, E). Outer lateral margin of flagellomere 1 asymmetrical to inner lateral margin; outer distal half forming an acute angle less than 45 degrees (Fig 3D, E).

List of species:

Homopterus subcordatus Darlington, 1950
Homopterus bolivianus H. Kolbe, 1920

Homopterus martinezi Luna de Carvalho, 1963
Homopterus lunacarvalhoi Martinez & Jimenez-Asua, 1965

Remarks. Because the types of *H. lunacarvalhoi* and *H. martinezi* could not be obtained for this study, their placement in the *H. subcordatus* group is based solely upon their illustrated morphology as set forth in their original species descriptions.

***Homopterus subcordatus* Darlington, 1950**
Location of Type: Museum of Comparative Zoology, Cambridge MA
Type Locality: Panama, Barro Colorado Island
Type Material Examined: Holotype, MCZ 28396; Paratype, USNM 59425

Material Examined. FRENCH GUIANA: Regina, St. Georges DZ 3, 11 Janvier 1991, piegeage lumineux, Marc Thouvenot leg., 4.057808, -52.012483 (WM.1201, DNA 3410, male) PANAMA: Canal Zone, Barro Colorado Is., 5 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 62240, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01477, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01478, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01479, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01480, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01482, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01483, male), Barro Colorado Is., 1-9.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01484, male), C.Z. Barro Colo. Isl., 6-VI-1972, at white lights, field station, 9 10'N 79 50'W, 9.163611, -79.837778 (ADP 01485, male), Barro Colorado Is., 10-17.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01486, male), Canal Zone, Barro Colorado Island, May 17, 1972, R.T. Allen, at light, 9.163611, -79.837778 (ADP 10952, male), Canal Zone, Barro Colorado Island, May 18, 1972, R.T. Allen, at lights, 9.163611, -79.837778 (ADP 10973, male), Barro Colorado Isl., Canal Zone, R.P. IV.23.1962, H. Ruckes, Collected on NSF Grant 9830, 9.163611, -79.837778 (ADP 44132, male), Canal Zone, Barro Colorado Is., VIII-6-1977, RB & LS Kimsey, 9.163611, -79.837778 (ADP 56667, female), Canal Zone, Barro Colorado Is., V-27-1981, RB & LS Kimsey, 9.163611, -79.837778 (ADP 58914, male), Canal Zone, Barro Colorado Is., 19 May, 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 62580, male), Canal Zone, Barro Colorado Is., 13 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 65726, male), Canal Zone, Barro Colorado Is., 7 Nov 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 66030, male), Canal Zone, Barro Colorado Is., 20 Nov 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 66162, male), Canal Zone, Barro Colorado Is., 13 Oct 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 76435, male), Canal Zone, Barro Colorado Is., 13 August 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 76945, male), Canal Zone, Barro Colorado Is., 12 Sept 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 77063, male), Canal Zone, Barro Colorado Is., 16 Sept 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 77145, male), Canal Zone, Barro Colorado Is., 11 June 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 77698, male), Canal Zone, Barro Colorado Is., 11 June 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 78284, male), Canal Zone, Barro

Colorado Is., 10 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 78927, male), Canal Zone, Barro Colorado Is., 11 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 78940, male), Canal Zone, Barro Colorado Is., 26 July 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 79818, male), Canal Zone, Barro Colorado Is., 29 Nov 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 82021, male), Canal Zone, Barro Colorado Is., 27 May 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 83602, male), Canal Zone, Barro Colorado Is., 7 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 ADP 83882, Canal Zone, Barro Colorado Is., 8 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 84001, male), Canal Zone, Barro Colorado Is., 23-24 August 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 90069, male), Canal Zone, Barro Colorado Is., 13 August 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 91804, male), Barro Colo. Is., C.Z., 5-4-37, S.W. Frost, 9.163611, -79.837778 (M.C.Z. 28396, male), Barro Colorado Island, 30 June 1999, collected by A.E. Arnold, light trap., 9.154722, -79.848056 (WM.0048, DNA 722, DNA 1227, DNA 2082), Barro Colorado Island, 30 June 1999, collected by A.E. Arnold, light trap., 9.154722, -79.848056 (WM.0049, male), Barro Colorado Island, 30 June 1999, collected by A.E. Arnold, light trap., 9.154722, -79.848056 (WM.0050, male), Barro Colorado Island, 30 June 1999, collected by A.E. Arnold, light trap., 9.154722, -79.848056 (WM.0051, male), Madden Forest, PANAMA Prov., 15 May 1985, at lights, F. Horvore coll., 9.094237, -79.617354 (WM.1136, male), Barro Coloarado Is., CZ, June 1940?, J. Zetek, Z-4669, 9.163611, -79.837778 (WM.1192, PARATYPE, male), Canal Zone, Barro Colorado Isl., 9 June 1978, at light, N. Woodley, 9.163611, -79.837778 (WM.1193, male), Canal Zone, Barro Colorado Is., 1 May 1978, 9.163611, -79.837778 (WM.1194, male), Canal Zone, Barro Colorado Is., 1 May 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (WM.1195, male), Zona del Canal, Barro Colorado Island, 26 Apr 1980, R. Silberglied/Aiello, at light, 9.163611, -79.837778 (WM.1198, male), Barro Colorado Is., 8 July 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 61765, male), Canal Zone, Barro Colorado Is., 26 May, 1978, H. Wolda Project, light traps, Nivel., 9.163611, -79.837778 (ADP 66233, male), Canal Zone, Barro Colorado Is., 9 Nov 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 81981, male), Canal Zone, Barro Colorado Isl., 30 June 1978, Silberglied/Aiello, at light, 9.163611, -79.837778 (WM.1196, female), Barro Colorado Island, 15-22 Nov, 1980, coll. Hank Wolda, canopy blacklight, 9.163611, -79.837778 (WM.1197, male).

Diagnosis

Elytra, pronotum, and head with micro-setae arising from each punctation. Inner proximal lateral margin of flagellomere 2 widely rounded, each flagellomere with equal length lateral margins (Fig 3E). Temples protruding over half its width from eye margin when viewed dorsally (Fig 6C). Extension of the outer angle of the penultimate maxillary palp segment extends to the lateral margin of the terminal maxillary palp segment (Fig 8D). Lateral margin of the terminal maxillary palp pointed acutely away from the midline. Outer lateral margin of terminal maxillary palp segment pointed acutely away from midline (Fig 8D) Pygidium with a distinct ridge along the basal half of the segment. Pygidial ridge with a medial depression.

Remarks

Of all the species in the genus, many exemplars exist for *H. subcordatus*.

***Homopterus bolivianus* H. Kolbe, 1920**
Location of Type: Berlin Museum
Type Locality: Sara Province, Bolivia
Type Material Examined: Photos of the holotype taken from the Berlin Museum

Material Examined. BOLIVIA: Santa Cruz, 4-6k SSE Buena Vista, F&F Hotel, 23-26 Oct. 2000, Wappes & Morris, -17.590496, -63.626724 (WM.1148, male)m Santa Cruz, Reserva Nat. Porterillo de Guenda, 6-9 Oct 2006, Wappes, Nearns & Eya,, Snake Farm, 17 40'.26S, 63 27.43'W, Elevtaion 400 meters, -17.672078, -63.466523 (WM.1147, male), Santa Cruz, Reserva Nat. Porterillo de Guenda, 16-22 Oct 2006, Wappes, Nearns & Eya, Snake Farm, 17 40'.26S, 63 27.43'W, Elevtaion 400 meters, -17.672078, -63.466523 (WM.1146, male), Santa Cruz, 4-6k SSE Buena Vista, F&F Hotel, 14-16 Oct. 2000, Wappes & Morris, -17.590496, -63.626724 (WM.1145, male), Santa Cruz Potrerillo del Guenda, 20/23-X-2011, Wappes & Skillman, Snake Farm, 17 40'S, 63 27'W, 370-400m, -17.672078, -63.466523 (WM.1144, male), Santa Cruz Potrerillo del Guenda, 14-16 October 2011, Wappes & Skillman, Snake Farm, 17 40'S, 63 27'W, 370-400m, -17.672078, -63.466523 (WM.1143, male), Santa Cruz District, Poterillos del Guenda, Preserva Natural 17 40S 63 27 W 370M 12-13 Oct 2007 A.R. Cline and J.E. Wappes collectors blacklight/mercury vapor, -17.6666667, -63.45 (WM.0848, DNA 2216, DNA 4150, male), Dept. Santa Cruz, Prov. Andres Ibanez: Potrerillos del Guenda, 370m, 23-27 October 2007, S.W. Lingafelter, day coll., 17 40'S 63 27'W, -21.983333, -64.516667 (WM.1203, male), Sta. Cruz, Ichilo, Buena Vista, 2 Oct 1994, 400m, R. Ward, m.v. light, -17.459541, -63.659683 (WM.1205, male), Santa Cruz, Ichilo Province, Buena Vista, 400 m, 3 Oct 1994, R. Ward, mercury vapor light, -17.459541, -63.659683 (WM.1206, male), Santa Cruz, Potrerillo del Guenda, 24-X-2011, Skillman & Wappes, Snake Farm, 17 40'S, 63 27'W, 370-400 meters, -17.672078, -63.466523 (WM.1247, DNA 3411, male), Santa Cruz, Potrerillo del Guenda, 24-X-2011, Skillman & Wappes, Snake Farm, 17 40'S, 63 27'W, 370-400 meters, -17.672078, -63.466523 (W.1248, male), Santa Cruz Dpt. Huaico, nr Potrerillo, October 27-29 2013, Wappes & Kuckartz, Elev 30 m, MV?UV lights, 63 26'W 17 40'S, -17.666667, -63.433333 (WM.0861, DNA 3420), Sta. Cruz, 20 km S Buena Vista, Oct. 18-25, 1992, E. Giesbert coll. (ADP 112024, male), Sta. Cruz, Buena Vista, Oct. 18-25, 1992, E. Giesbert coll., -17.459541, -63.659683 (ADP 112140, male), Santa Cruz Prov., 4-6 km SSE Buena Vista, Hotel Fauna y Flora, 400-500m, 1-10 Nov 2002, UV/MV Light, Steven W. Lingenfelter, 17 37'S 63 37'W, (WM.1207, male), Sta. Cruz, 20 km S Buena Vista, Oct. 18-25, 1992, E. Giesbert coll., -17.459541, -63.659683 (ADP 112114, male) BRAZIL: Est. Rio de Janeiro, Araruama XI, 1981, Coll. M. Alvarenga, -22.865977, -42.336229 (WM.1214, male), Rondonia, 62 km S. Ariquemas, Faz. Rancho Grande, XI-5-15-1993, C. & K. Messenger, 10 32'S 62 48'W, -10.287383, -63.527344 (WM.1210, male), Museum Paris, Bahia, P. Sierre 1913, Decembre, Janvier, (WM.1230, male) ECUADOR: Napo, 20 km E of Puerto Napo, Alinahui, 450m, Nov-Dec 1995, E.S. Ross coll., C.A.S., 1 0'S 77 25'W, -1.027719, -77.567535 (WM.1209, male) FRENCH GUIANA: 13k W D-5, Risq. Rd., 14-VIII-1995, JE Wappes, 4.916667, -52.516667 (WM.1149, male), Coralie, 2 km west, 27-29 SEp 1992, Carlson, Hovore, Sullivan, 4.508809, -52.377559 (WM.1140, male), Route de Regina, N2. PK 79km S. Cayenne, , 25-I-90, Coll. J.D. McCarty,

4.057808, -52.012483 (WM.1132, male), Risquetout Rd., pk. 4, 27 Jan 1995, F.T. Hovore coll., 4.916667, -52.516667 (WM.1199,male), R'te de Kaw, pk 37-48, 6-12 Nov 1993, F.T. Hovore coll., 4.553727, -52.154285 (WM.1200, male), R'te de Kaw, pk 37-48, 6-12 Nov 1993, F.T. Hovore coll., 4.553727, -52.154285 (WM.1202, male), 8 km W of Risquetout, 10-11-VI-2005, J.E. Eger coll., 45m, MV Light, N04 55.097' W052 33.121', 4.916667, -52.516667 (ADP 112045, male), 33 km SE Roura on Kaw Rd., 1-2-VI-2005, J. E. Eger & M. T. Messenger, coll., 227m, MV Light, N04 34.135'W052 11.150', 4.515374, -52.115811 (ADP 112049, male), 1 km S Amazon Nature Lodge, 30 km SE Roura de Kaw Rd., 3-4-VI-2005, J.E. Eger & M.T. Messenger, coll., N04 32.961' W052 12.830', 4.553727, -52.154285 (ADP 112051, male), 14 km E of N2 on rd to Degrad Correze, 6-XII-2002, J.E. Eger, 108m, MV Light, N04 29.964' W052 20.260', 4.518415, -52.32461 (ADP 112053, male) PERU: S.A. Dec 11-30, 1937, F. Woytkowski, No. 3811, Department Huanuco ,Vic. Leonpampa Jungle, 800m, -15.1747, -71.7161 (WM.1208, male) VENEZUELA: KRAN LF ? bei Groupia g. 422, 29/06/1998, leg. S. Kirmse, coll. Nagel (WM.1215, female), T.F. Amaz. Cerro de la Neblina Basecamp, 140m, 24 February 1985, at black light in rainforest clearing near Rio Baria, P.J. & P.M. Spangler, R. Faitoute, W. Steiner, 0 50'N66 10'W, 0.89044, -65.988071 (WM.1218, male), T.F. Amazonas Dept., Rio Mawarlnuma, 140m, 25-III, 15-IV-84, C. Pedilla, 0 55'N 66 10'W, V (WM.1217, male), T.F. Amazonas Dept., Rio Negro, 21-23-XI-64, S. Carlos de Rio Negro, 65m, E. Osuna, A. Chacon, 1 55'N67 1'W, 1.916667, -67.066667 (WM.1216, male)

Diagnosis
Temples raised but projecting only slightly, if at all, from the margin of the eye when viewed dorsally (Fig 5B); not as pronounced as seen in *H. subcordatus*. Elytra without setation on the dorsal surface. Lateral margin of the terminal maxillary palp parallel with the sagittal plane.

Remarks: Most specimens collected in October and November; most collected at 300-400m.

***Homopterus brasiliensis* group**

Diagnosis. Moderately sized members of *Homopterus*. Colouration ranging from deep red brown to a lighter amber brown. Pronotum dorsally flattened with lateral margins moderately explanate with setae projecting from lateral margins (Fig 5A, D, E). Most group members with circular punctations on pronota and elytra. Elytra with white setation, length varying depending on species (Fig 10D). Apical margin of tibiae the same length as basal margin. Subocular margin forming an angle at dorsodistal junction, pointed (Fig 7B). Outer margins of mandible straight (Fig 9B-C). Inner proximal margin of flagellomeres 2-8 widely rounded, each flagellomere with equal length lateral margins (Fig 3A, C-E). Lateral margins of flagellomere 1 roughly symmetrical; approximately trapezoidal in shape, Outer distal half of segment forming a 45 degree angle (Fig 3A, B, C). Margin of Flagellomere 9 continuous. Subterminal maxillary palp segment height a third of the length of the segment's distal margin (Fig 8E). Terminal maxillary palp lacking distinct setation.

List of species:

H. brasiliensis Westwood, 1938

H. kriegi Reichensperger, 1938
H. honduriensis Darlington, 1937

***Homopterus kriegi* Reichensperger, 1938**
Location of Type: Munich Museum
Type Locality: Maracay, Venezuela
Type Material Examined: Photos from Reichensperger 1938

Material Examined. BRAZIL: State of Rio, Barreira, nr. Teresopolis, 26-I-1979, R. Woodruff, swimming pool, -22.465245, -43.00495 (ADP 111976, male) COSTA RICA: Santa Rosa National Park, Guanacaste Prov., April 1983, 300m, DH Juazena & W. Hallwachs, 10.868867, -85.724596 (INBIOCRI0003017230, female), P.N. Mauel Antonio, 80 m, Quepos Prov., Puntarenas, Nov 1992, G. Varela, L-S-370900, 448800, 9.392509, -84.137223 (INBIOCRI000823165, male), P.N. Mauel Antonio, 80 m, Quepos Prov., Punt., Jun 1991, R. Zuniga, L-S-370900, 448800, 9.392509, -84.137223 (INBIOCRI001334698, male), Sector Las Pailas, Prov. Guana, 800m, 12 ABR-5 May, 1995, K. Taylor, L_N_306300_388600 #4809, 10.756366, -85.286281 (INBIOCRI002424467, male) MEXICO: Chiapas, El Aguacero, 16 km W Ocozocoautla, 10-VI-2009 Skillman and Hildebrant at lights, 16.7829, -93.1362 (WM.0854, DNA 3402, male) PANAMA: Pnma Prv, K 8-13 Lllano-Carti Rd, 21-24 May 1996, Wappes, Huether & Morris, 9.216607, -78.977772 (WM.1251, DNA 3413, male), Pearl Is., Morrison JPE, June 21 1944, collected at light, 8.357946, -78.912214 (ADP 01474, male), Barro Colo. I., CZ, Apr. 41, Collected at light, Jas Zetek, No 4781, 9.163611, -79.837778 (ADP 01475, male), Barro Colorado Isl., 10-17.V.64, WD & SS Duckworth, 9.163611, -79.837778 (ADP 01476, male), Canal Zone, Albrook Forest Site, Fort Clayton, Lot No. 105, June 8/9, 1967, Hutton & Llaurado, Black light trap, 9.004422, -79.575272 (ADP 47055, male), Canal Zone, Barro Colorado Is., 5 June 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 62239, male), Canal Zone, Barro Colorado Is., 21 July 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 75540, male), Canal Zone, Barro Colorado Is., 20 July 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 75959, male), Canal Zone, Barro Colorado Is., 21 June 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 77506, male), Canal Zone, Barro Colorado Is., 16 June 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 78562, male), Canal Zone, Barro Colorado Is., 4 July 1978, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 79212, male), Canal Zone, Barro Colorado Is., 4-5-6-May 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 83809, male), Canal Zone, Barro Colorado Is., 23 April 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 89634, male), Canal Zone, Barro Colorado Zone, 22 March 1977, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (ADP 91997, male), Canal Zone, Barro Colorado Is., 20 April 1978, H. Wolda Project, light traps, Nivel, 9.163611, -79.837778 (WM.1219, male), Barro Colo. Is., C.Z., 3-14-37, S.W. Frost, Fig: mentum, Darlington 1949, 9.163611, -79.837778 (WM.1220, male), Barro Colorado I., CZ, VI.11.1980, Hank Wolda, 9.163611, -79.837778 (WM.1221, male), Canal Zone, Barro Colorado Is., UV Trap 3, (26m high), 25 May 1977, H. Wolda, 9.163611, -79.837778 (ADP 112111, male), Canal Zone, Barro Colorado Is., 30 June 1978, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 76067, male), Canal Zone, Barro Colorado Is., 29 May 1977, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 76778, male), Canal Zone, Barro Colorado Is., 3 Sept 1978, H. Wolda Project

Light Traps, Nivel, 9.163611, -79.837778 (ADP 79488, male), Canal Zone, Barro Colorado Is., 12 July 1978, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 79671, male), Canal Zone, Barro Colorado Is., 24 July 1978, H. Wolda Project Light Traps, Nivel, 9.163611, -79.837778 (ADP 89934, male)

Diagnosis.

Flagellomeres 2-9 setation more numerous on dorsolateral surface than across the median (Fig 3C). Proximal and distal margins of flagellomeres 2-8 straight, antennal club compact (Fig 3C). Pronotum beaded (Fig 5D). Elytral setation of uniform length and evenly distributed (10D), similar to H. honduriensis. Clypeal fringe short and present along distal margin of clypeus (9B). Lateral margin of terminal maxillary palp segment parallel with the sagittal plane. Extension of the outer angle of the penultimate maxillary palp segment does not meet or extend past the lateral margin of the terminal maxillary palp segment (Fig 8C).

Remarks: Species in this group are generally more setaceous than members of the closely related *H. bolivianus* Group.

***Homopterus brasiliensis* (Westwood, 1838)**

Location of Type: Personal Collection of D. Miers
Type Locality: Mont Corcovado
Type Material Examined: Photos from Westwood 1938

Material Examined. BRAZIL: Foz. do Iguazu, 1 I 1973, L. Lautenschlager, -25.520968, -54.584521 (WM.1135, female), Rio de Jan., Acc. No. 2966, Nagel vidit 1992, -22.900115, -43.328357 (WM.1211, male), Rio de Jan., Acc. No. 2966, Nagel vidit 1992, -22.900115, -43.328357 (WM.1212, female), Rio de Jan., Acc. No. 2966, Nagel vidit 1992, -22.900115, (WM.1213, female), Foz. do Iguazu, 1 I 1973, L. Lautenschlager, -25.520968, -54.584521 (WM.1244, male) PERU: Madre de Dios, Rio Manu, BIOLAT Biol. Sta., Pakitza, 356m, 1-6 Oct 1991, M.G. Pogue Lab lights Lot 178, 11 56'47" S071 17'00"W, -12.716667, -71.283333 (BIOLAT/COLE 000013041, DNA 3412, female)

Diagnosis.

Colouration a light amber brown. Pronotum not explanate, but beaded along the lateral margins with sloping anterolateral margins (Fig 5E). Punctations on elytra and pronotum faint, white setation sparser than seen in *H. kriegi* and *H. honduriensis*. Antennal setation density sparse along dorsal surface (Fig 3B). Inner margins of flagellomeres 1-8 tapered on the ventral side, similar to members of the Steinbachi Group; inner proximal corners completely rounded (Fig 3B). Subocular margin continuously smooth from dorsal to distal margin; rounded (Fig 7A), Clypeus lacking setation. Extension of the outer angle of the penultimate maxillary palp segment extends to the lateral margin of the terminal maxillary palp segment (Fig 8A). Pygidium without distinct ridges or depressions.

Remarks:
Found in Brazil. Specimens collected in January and October.

***Homopterus honduriensis* Darlington, 1937**
Location of Type: Museum of Comparative Zoology, Cambridge MA
Type Locality: Lancetilla, Honduras
Type Material Examined: Holotype, MCZ 22502

Material Examined. BELIZE: Punta Gorda, III-1934, B. W. I., Columbia R. dist., J.J. White collector, 16.09934, -88.815106 (ADP 44153, male), Rio Grande, 16.345066, -88.969117 (WM.1226, male) GUATEMALA: Huehue Finca, Zapote, Rio Largartero, 5-VI-1991, Edmund F. Giesbert, 15.716074, -91.936567 (WM.1227, male), Huehue Finca, Zapote, Rio Largartero, 5-VI-1991, Edmund F. Giesbert, 15.716074, -91.936567 (WM.1228, male), Huehue Finca, Zapote, Rio Largartero, 5-VI-1991, Edmund F. Giesbert, 15.716074, -91.936567 (WM.1229, male) HONDURAS: Lancetilla, M. Bates Collector, 15.717963, -87.459765 (M.C.Z. 22509, HOLOTYPE) MEXICO: Teapa, Tabaco, VI-23-63, J. Doyen Collector, 17.548153, -92.952276 (WM.1134, male), Teapa, Tabaco, VI-23-63, J. Doyen Collector, 17.548153, -92.952276 (WM.1222, male), El Zapotal, 2mi. S. Tux. Gutierrez, Chias, VII-1-57, At light, J.A. Chemsak, B.J. Rannells collectors, from Powell Oct. 63, 16.728387, -93.116912 (WM.1223, male), Escarcega, Campeche, F. Islas S., trap light, 25-IV-1962, 18.607483, -90.745447 (WM.1224, male), Santo Domingo, 15 mi. S.E. Simojovel, Chiapas, VII-8-15-58, J.A. Chemsak Collector, 16.357599, -92.238459 (WM.1225, male) Quintana Roo, 3.5 km W Puerto Morelas 20-21.VI.2009 Skillman & Hildebrant, at lights, near Atta nest, 20.86, -86.976 (WM.0850, DNA 2145, male), S.L.P. Tamazunchale, June 24-27, 1965, O.S. Flint, 21.251514, -98.782467 (WM.1258, female), Palitla, S.L.P., July 21, 1970, Taken at light, Schaffner, Murray, Phelps, Hart, 21.38681, -98.990088 (WM.1259, male), Palitla, S.L.P., July 21, 1970, Taken at light, Schaffner, Murray, Phelps, Hart, 21.38681, -98.990088 (WM.1260, male), V.C. Puente National, VII-23-24-1965, Flint & Ortiz, 19.328819, -96.48231 (ADP 05545, male)

Diagnosis.
Colouration deep rosy brown. Proximal margins of each flagellomere slightly convex. Proximal and distal margins of flagellomeres 2-8 with slight apical curve, distinct space seen between each flagellomere (Fig 3A). Setation on flagellomeres similar to that of H. kriegi, more numerous on dorsolateral surface than across the median (Fig 3A). Clypeus with setae dispersed along distal margin (Fig 9B). Pronotum explanate and beaded along the lateral margins (Fig 5A). Lateral margin of the terminal maxillary palp parallel with the sagittal plane. Elytral disc setation of uniform length and evenly distributed, similar to *H. kriegi* (10D).

***Homopterus proemonens* group**

Diagnosis.
Smallest members of *Homopterus.* Colouration ranging from deep brown to light amber. Pronotum roughly square in shape with beaded lateral margins and slight setal fringe. Elytral punctations faint and small in size. Elytra disc glabrous. Tibiae with apical margin the same length as basal margin. Inner proximal lateral margin of flagellomeres 2-8 symmetrical to outer proximal lateral margin (Fig 2D, E). Flagellomere setation barely projecting above cuticle giving dorsal surface a stippled appearance (Fig 2D, E). Subocular margin forming an angle at dorsodistal junction, pointed (Fig 6B) First Flagellomere outer lateral margin asymmetrical to

inner lateral margin; outer distal half forming an acute angle less than 45 degrees (Fig 2D, E). Mandibles outer margins straight. Clypeus without setation. Outer lateral margin of terminal maxillary palp segment pointed acutely away from midline (Fig 8E).

***Homopterus proemonens* H. Kolbe, 1920**
Location of Type: Berlin Museum
Type Locality: Sara Province, Bolivia
Type Material Examined: Type not located

Material Examined. TYPE not studied. BOLIVIA: Dept. Santa Cruz, Prov. Florida, Refugio los Volcanes, 1045m, 9-13 Dec. 2008, UV/MV lights, S. Lingafelter, T. Henry, D. Windsor, 18 06'S 63 36'W, -17.673505, -63.234983 (WM.1243, DNA 3419, male), Dept. Santa Cruz, Prov. Florida, Refugio los Volcanes, 4 km N. Bermejo, 1045-1200m, 28 October-5 November 2007, S.W. Lingafelter, mv/uv lights, 18 06'S 63 36'W, -17.673505, -63.234983 (WM.1242, DNA 3416, female) COSTA RICA: La Maritza, Hda. Orosi, Gste., 500m, 2-5 June 1986, W. Hallwachs, D.H. Janzen, 10.977081, -85.464972 (INBIOCRI002611024, male), Estac. Maritza, 600m, W side Volcan Orosi Guanac., Jul 1989, GNP Biodiv. Survey, 326900, 373000, 10.977081, -85.464972 (INBIOCRI000023765, female), Est. Maritza, 600m, Lado oeste del Volcan Orosi, Prov. Guan., I curso Microlepidop. Jul 1990, L-N-326900, 37300, 10.977081, -85.464972 (INBIO/CRI000180909, female) FRENCH GUIANA: 27 km SE Roura on Kaw Rd., 14-IV-2007, D. G. Hall & J.E. Eger, coll. MV Light, 4.553727, -52.154285 (ADP 112055, male) GUATEMALA: Izabal Finca Firmesa, 30 km. SE of Morales, 22-VII-2008, Skillman + C & L O'Brien, MH & blacklight, 15.381583, -88.717383 (WM.1138, male), D. Izabal, Firmeza, 30 km, SE Morales, 23-VII-2008, at UV and metal halide light, C.W. & L.B. O'Brien & Fred Skillman, 15.416819, -88.642946 (WM.1236, male), D. Suchitepequez, Loas Tarrales Private Nature Res., Palulul, 27-VII-208, C.W. & L.B. O'Brien & Fred Skillman, N14 31'W91 08', 14.515208, -91.185955 (WM.1235, male), Huehuetenango, N. N. E. de Nenton, +/- 560m, Finca el Zapote, Rio Largarteros, 1 Junio 1997, Colec. J. Monzon y E. Giesbert, 15.716074, -91.936567 (WM.1234, female), Huehue Finca, Zapote, Rio Largartero, 5-VI-1991, Edmund F. Giesbert, 15.716074, -91.936567 (WM.1232, aDNA 0020, female), Huehue Finca, Zapote, Rio Largartero, 5-VI-1991, Edmund F. Giesbert, 15.716074, -91.936567 (WM.1231, male), Zacapa, San Enrique (Guatan), May 12, 1991, E. Giesbert coll., 14.972222, -89.530556 (ADP 111980, male), Zacapa: Sierra de las Minas, 20.3 km W of Teculutan, 13.8 km N dry oak-pine forest, 920m, at light 91-33, June 7, 1991, GE and KE Ball, D. Shepley, 14.983254, -89.906473 (WM.0859, male), Suchitepequez, nr. Patulu, Los Tarrales Preserve, 27-VII-2008, Skillman, C&L O'Brien, at light, DNA 2123, 14.515208, -91.185955 (WM.1233, DNA 2123, male), Izabal, 23km SE Morales, 800m, May 23-27, 1995, Giesbert, Monzon, 15.336394, -88.664248 (ADP 111978, male) MEXICO: Chiapas: Cinco Cerros (Hotel Paty), (860m); 13 MAY 1991, J.D. McCarty, P.H. Sullivan, 19.312049, -99.228297 (WM.1142, male), 22 mi SE Jalapa, Vera Cruz, VI-29-53, 1100ft, Univ. Kans. Mex. Expedition, 19.316392, -96.770511 (WM.1241, male), 2 miles NE of San Miguel, Cozumel, Sta. 7, 3 iv 1960, JFG Clarke, 20.446365, -86.894146 (WM.1240, male), 2 miles NE of San Miguel, Cozumel, Sta. 7, 3 iv 1960, JFG Clarke, 20.446365, -86.894146 (WM.1239, male), El Zapotal, 2mi. S. Tux. Gutierrez, Chias, VII-1-57, At light, J.A. Chemsak, B.J. Rannells collectors, from Powell Oct. 63, 16.728387, -93.116912 (WM.1238, female), Ver., Estac., Biol. Los Tuxtlas, VII-1/9-1988, JA Chemsak, at lites, 18.563412, -95.08864 (WM.1237, male), Veracruz, Puente National, 6 mi SE

Rinconada, IX-29-75 at light, J Powell & JA Chemsak collectors, 19.328819, -96.48231 (WM.1133, male), Ver., 250', Los Tuxtlas, Biol. Sta., UNAM, 21 May 1983, C&L O'Brien & G Marshall, at light, 18.563412, -95.08864 (ADP 112109, male), 7 miles W Tuxtle, Gutierrez, Chis., VI-16-68, at black light, C.D. Johnson coll., 16.782606, -93.312668 (WM.0860, female) SAN SALVADOR: VI-28-25, E.S.C.A., K.A. Salman collector, "0" (ADP 01473, HOMOTYPE, male)

Remarks: Type material was not located for this species; however, photos were analyzed of a specimen of this species identified originally by Reichensperger. There are some striking differences in antennae length and body size among specimens collected in Mexico, San Salvador, Costa Rica, and Guatemala. Based on external morphological differences, there could possibly be at least three different species represented in this species complex. To support the designation of new species, genitalic work should be undertaken. It would also be worthwhile to conduct molecular DNA studies with more recently collected specimens.

Distribution maps.

Distribution maps for the genus, species groups and species will be available as kml files distributed along with a derivative paper.

REFERENCES

Darlington PJ (1937) A new paussid beetle from Central America. Psyche 44: 56-57

Darlington PJ (1950) Paussid beetles. Transactions of The American Entomological Society 76: 47-142

Darlington PJ (1950) Two new paussid beetles from the Panama canal zone and the Philippines. Psyche 57: 68-71

De Carvalho L (1963) Paussídeos Americanos (Col. Carab. Pauss.). Memórias e Estudos do Museu Zoológico da Universidade de Coimbra 283:1-22

Eisner T, Jones TH, Aneshansley DJ, Tschinkel WR, Silberglied RE, Meinwald J (1977, May 25) Chemistry of defensive secretions of bombardier beetles (Brachinini, Metriini, Ozaenini, Paussini). Journal of Insect Physiology 23: 1383-1386. doi: 10.1016/0022-1910(77)90162-7

Gilbert MPT, Moore W, Melchior L, Worobey M (2007) DNA extraction from dry museum beetles without conferring external morphological damage. PLoS One 2, e272. DOI: http://dx.doi.org/10.1371/journal.pone.0000272.

Geiselhardt SF, Peschke K, Nagel P (2007) A review of myrmecophily in ant nest beetles (Coleoptera: Carabidae: Paussinae): Linking early observations with recent findings. Naturwissenschaften, 94: 871-894.

Green P (1999) Phrap. Version 0.990329 http://phrap.org

Green P, Ewing B (2002) Phred. Version 0.020425c http://phrap.org

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 40: 772–780

Katoh K, Toh H (2008) Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. BMC Bioinform. 9: 212

Kolbe H (1920) Die Paussiden Sudamerikas (Col.). Entomolog. Mitteilungen IX 7/9:131-156

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29: 1695–1701

Maddison DR, Maddison WP (2016) Chromaseq: A Mesquite Module for Analyzing Sequence Chromatograms. Version 1.2 http://mesquiteproject.org/packages/chromaseq

Maddison WP, Maddison DR (2016) Mesquite: A Modular System for Evolutionary Analysis. Version 3.10 http://mesquiteproject.org

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE). New Orleans, Louisiana, pp. 1-8.

Moore W (2008) Phylogeny of the Western Hemisphere Ozaenini (Coleoptera: Carabidae: Paussinae) based in DNA sequence data. Annals of the Carnegie Museum 77(1): 79-92

Nagel P (1987) Fossil ant nest beetles. Entomologische Arbeiten aus dem Museum G. Frey Tutzing bei München 35/36: 137-170

Reichensperger A (1938) Sudamerikanische Paussiden (Col.) und einige Vorbemerkungen. Rev. de Entomologia 8: 68-79

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and postanalysis of large phylogenies. Bioinformatics 30: 1312–1313

Swain RB (1977) The natural history of *Monacis*, a genus of Neotropical ants (Hymenoptera:

Formicidae). PhD thesis, Cambridge, United States of America: Harvard University

Westwood JO (1841) Synopsis of the coleopterous genus *Cerapterus*. 60: 581-585

Westwood JO (1845) Monograph of the coleopterous family Paussidae. Arcana Entomologica 13: 1-9

Wolda H (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. Journal of Animal Ecology 47: 369–381

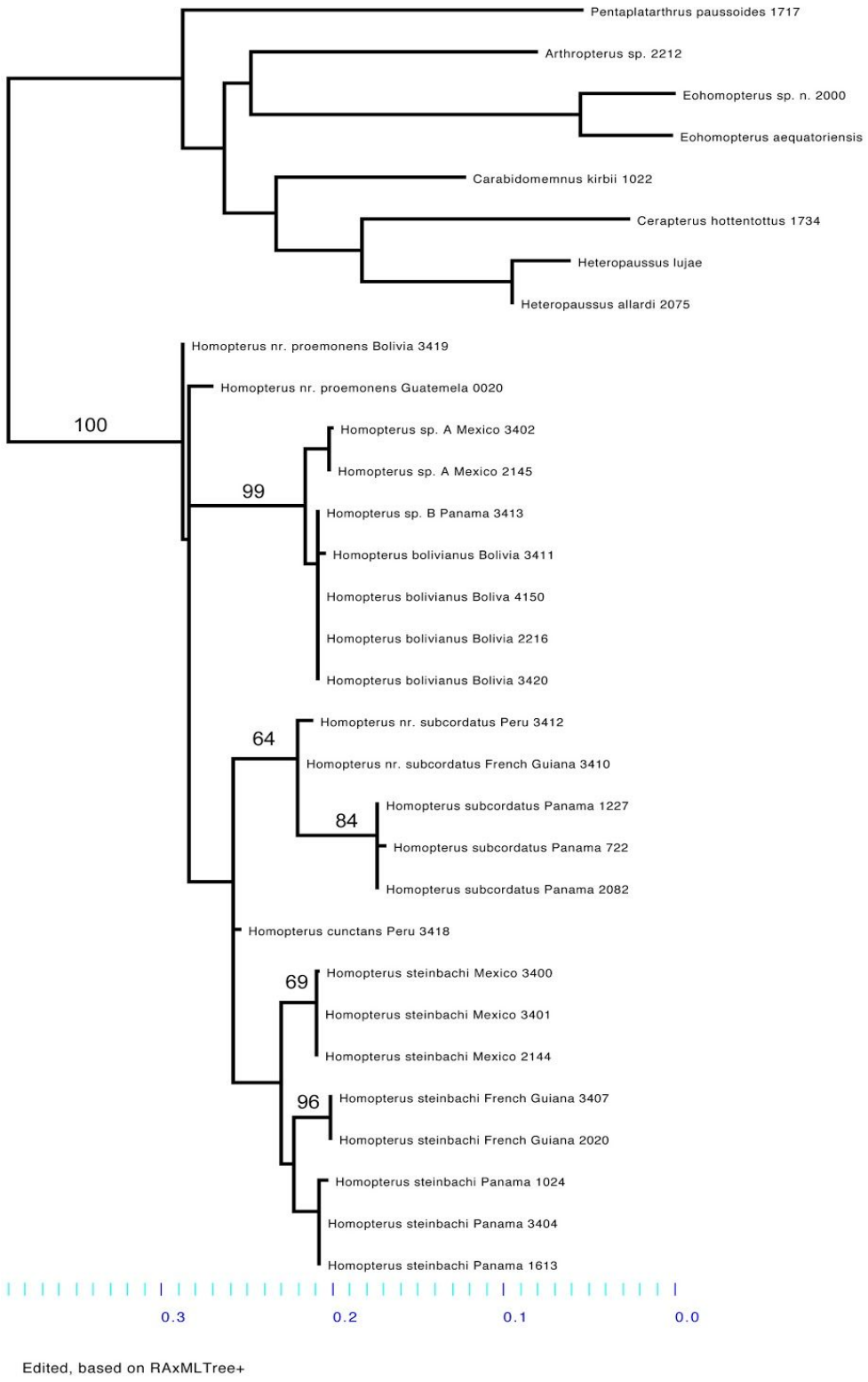

Figure 1. *Homopterus* species group phylogeny. Tree of highest likelihood as inferred by RAxML. Numbers over branches indicate bootstrap values for select clades.

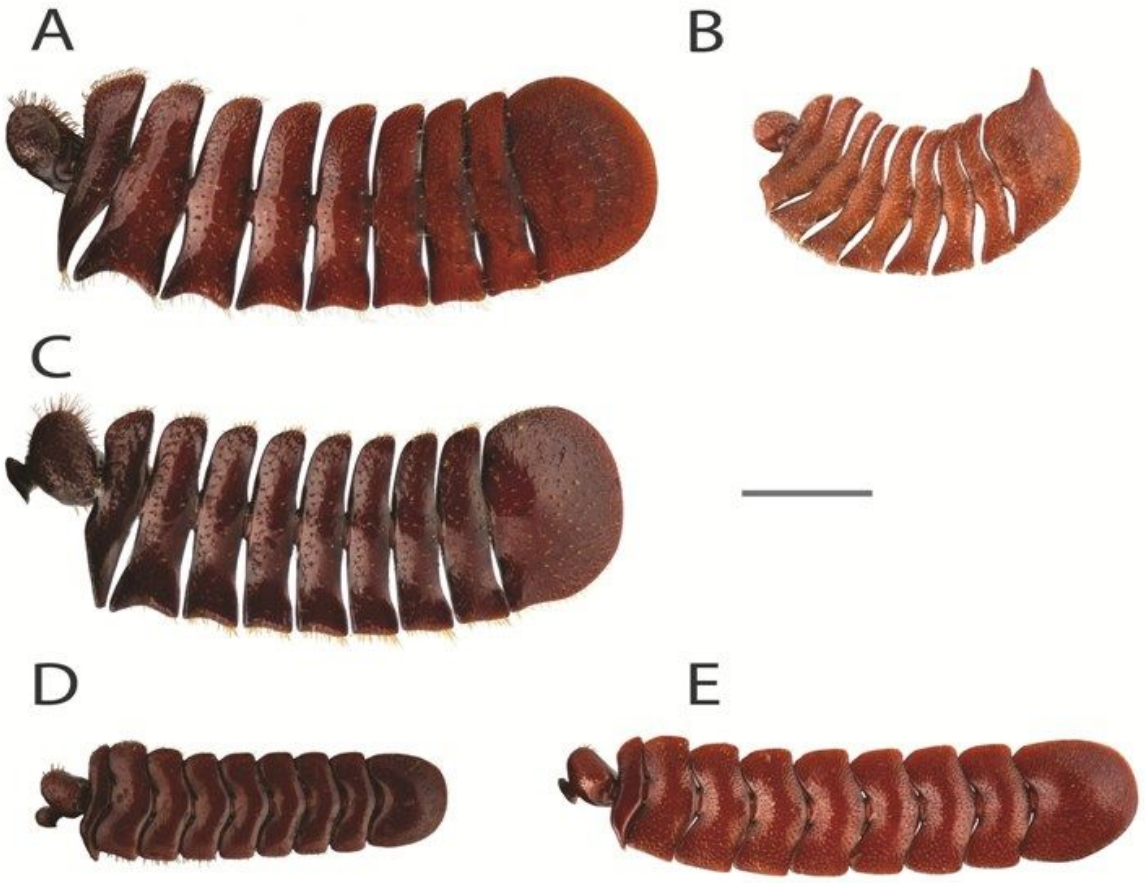

Figure 2. Antennae of the *H. steinbachi, H. fiiko,* and *H. proemonens* groups: A, *Homopterus amplificatus*; B, *Homopterus filiko,* n. sp.; C, *Homopterus cunctans*; D-E, *Homopterus proemonens.* Scale bar = 1 mm.

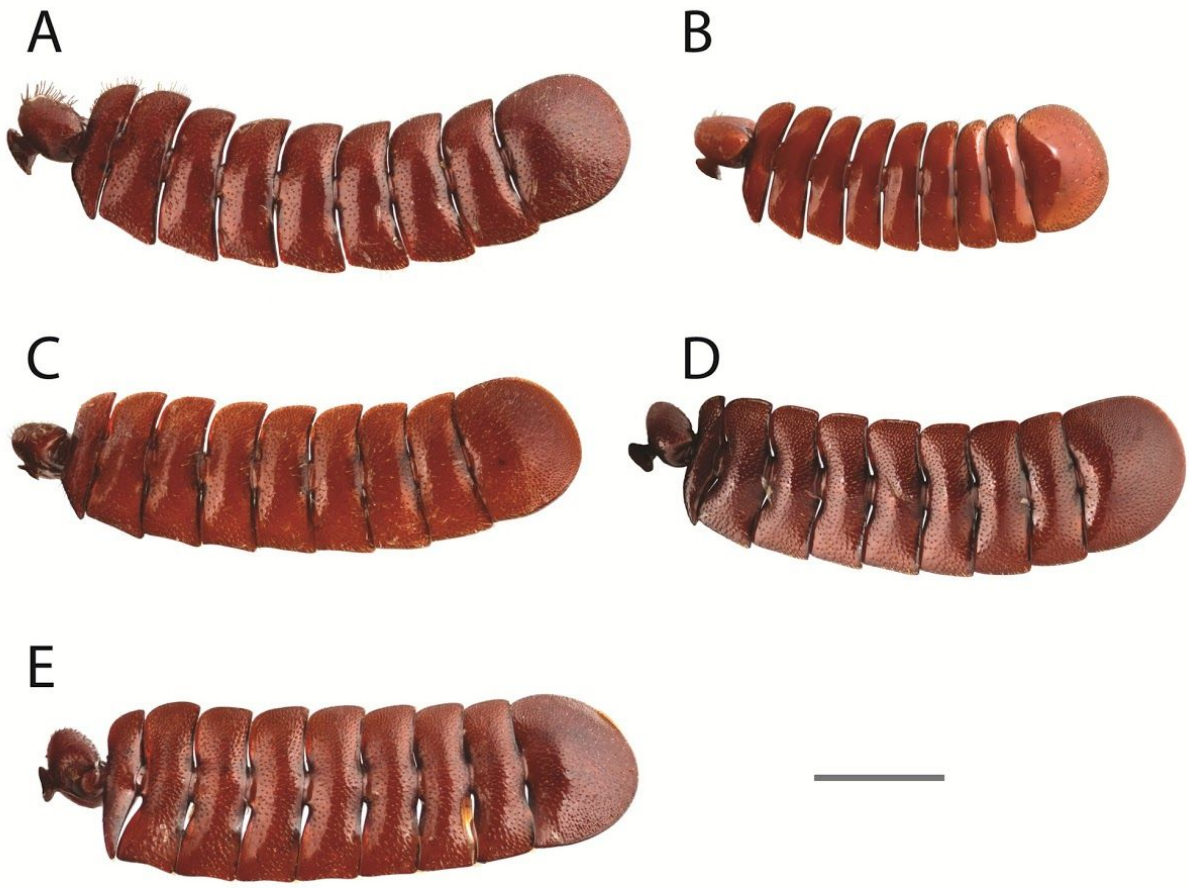

Figure 3. Antennae of the *H. brasiliensis* group and *H. subcordatus* group: A, *Homopterus honduriensis*; B, *Homopterus brasiliensis*; C, *Homopterus kriegi*; D, *Homopterus bolivianus*; E, *Homopterus subcordatus.* Scale bar = 1 mm.

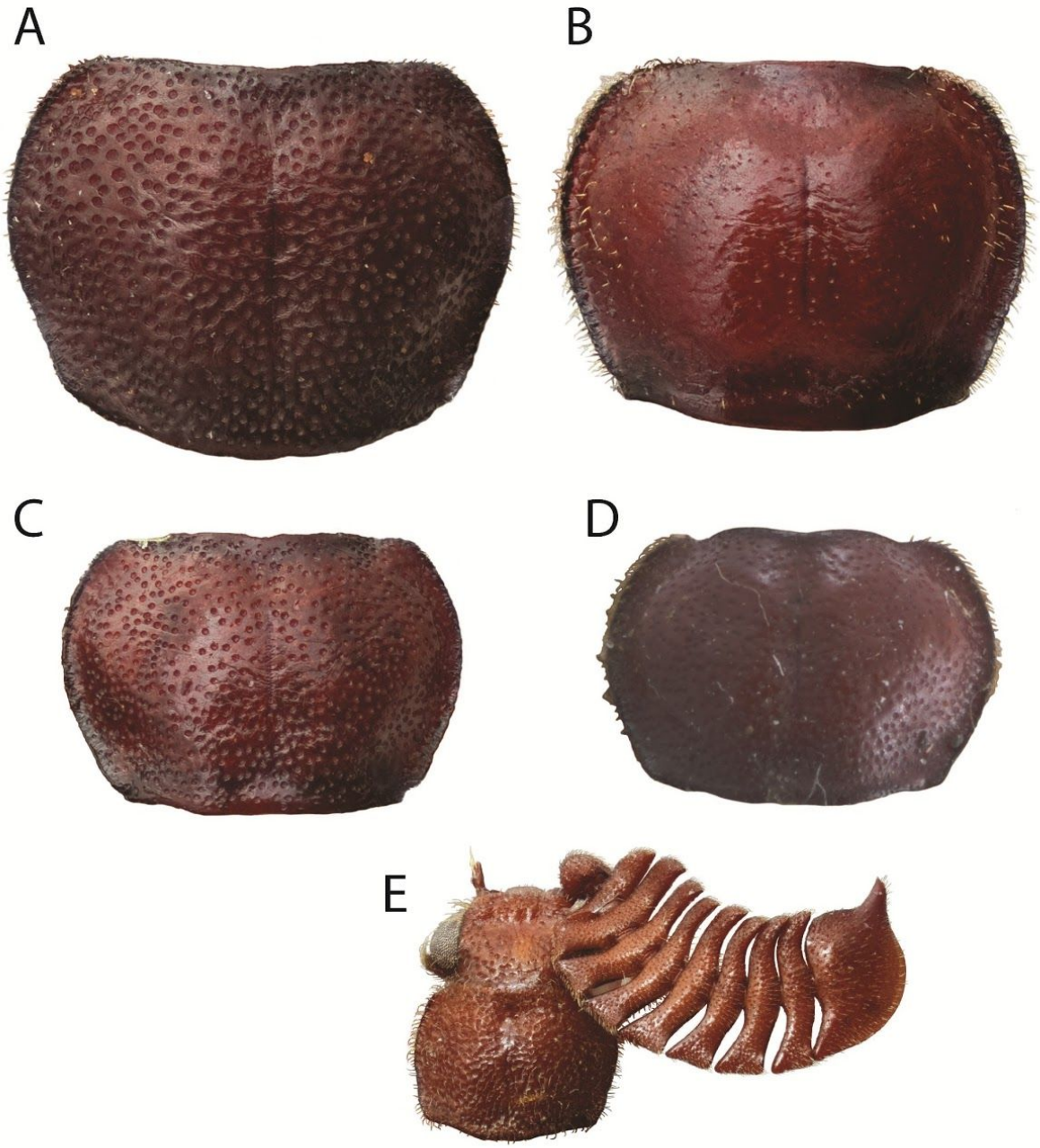

Figure 4. Pronota of the *H. steinbachi* group and *H. filiko* group: A, *Homopterus cunctans*; B, *Homopterus amplificatus*; C, *Homopterus steinbachi*; D, *Homopterus arrowi*; E, *Homopterus filiko*, n. sp.

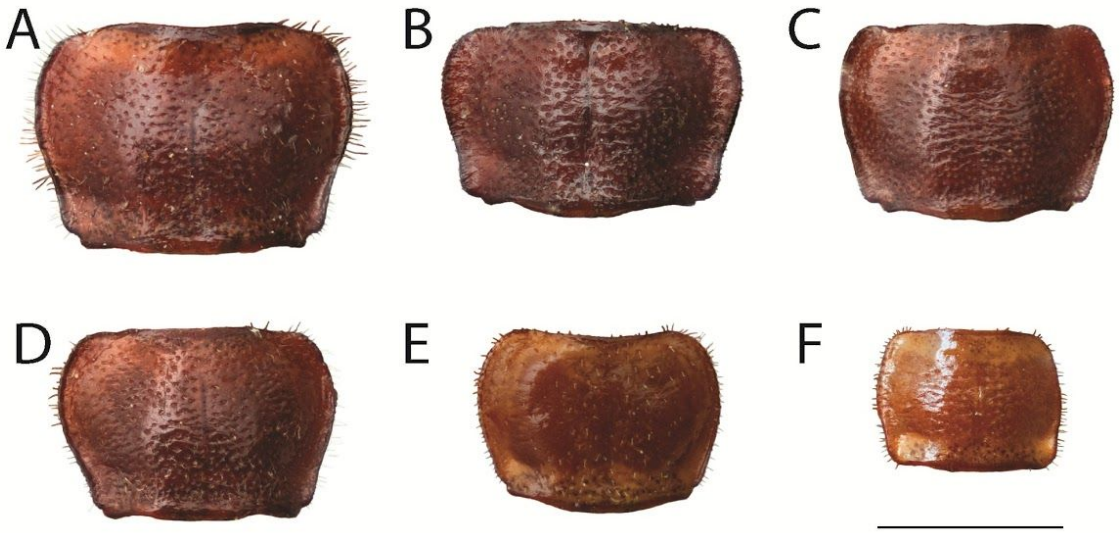

Figure 5. Pronota of the *H. brasiliensis, H. subcordatus,* and *H. proemonens* groups: A, *Homopterus honduriensis*; B, *Homopterus subcordatus*; C, *Homopterus bolivianus*; D, *Homopterus kriegi*; E, *Homopterus brasiliensis*; F, *Homopterus proemonens.* Scale bar = 1 mm.

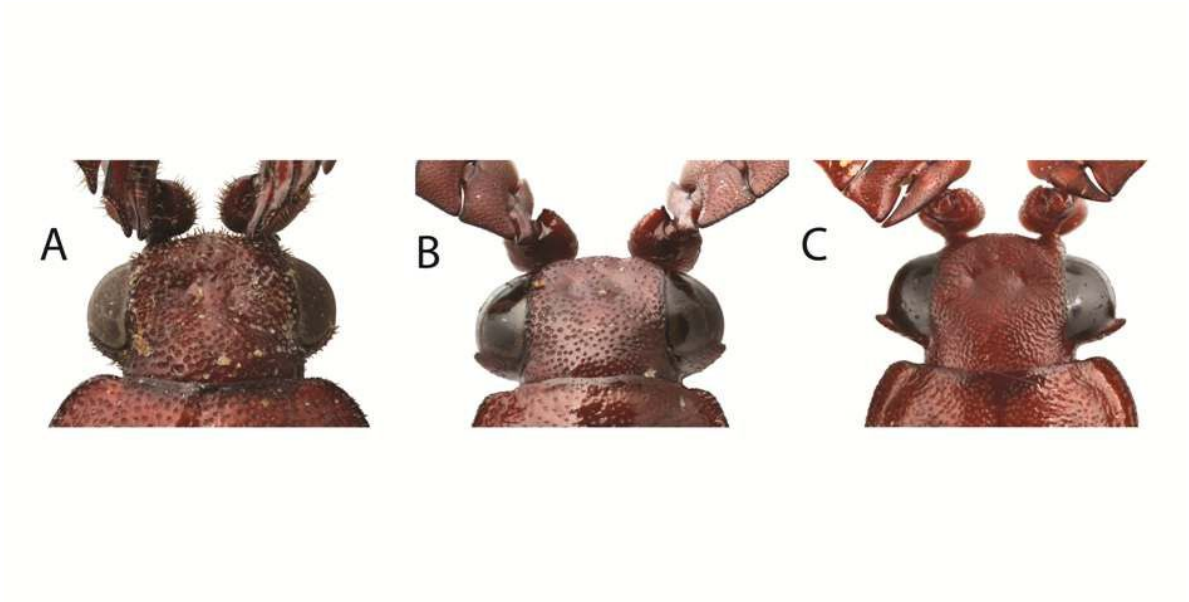

Figure 6. Temples: A, *Homopterus steinbachi;* B, *Homopterus bolivianus;* C, *Homopterus subcordatus*

Figure 7. Sub-occular margin: A, *Homopterus brasiliensis*; B, *Homopterus subcordatus*

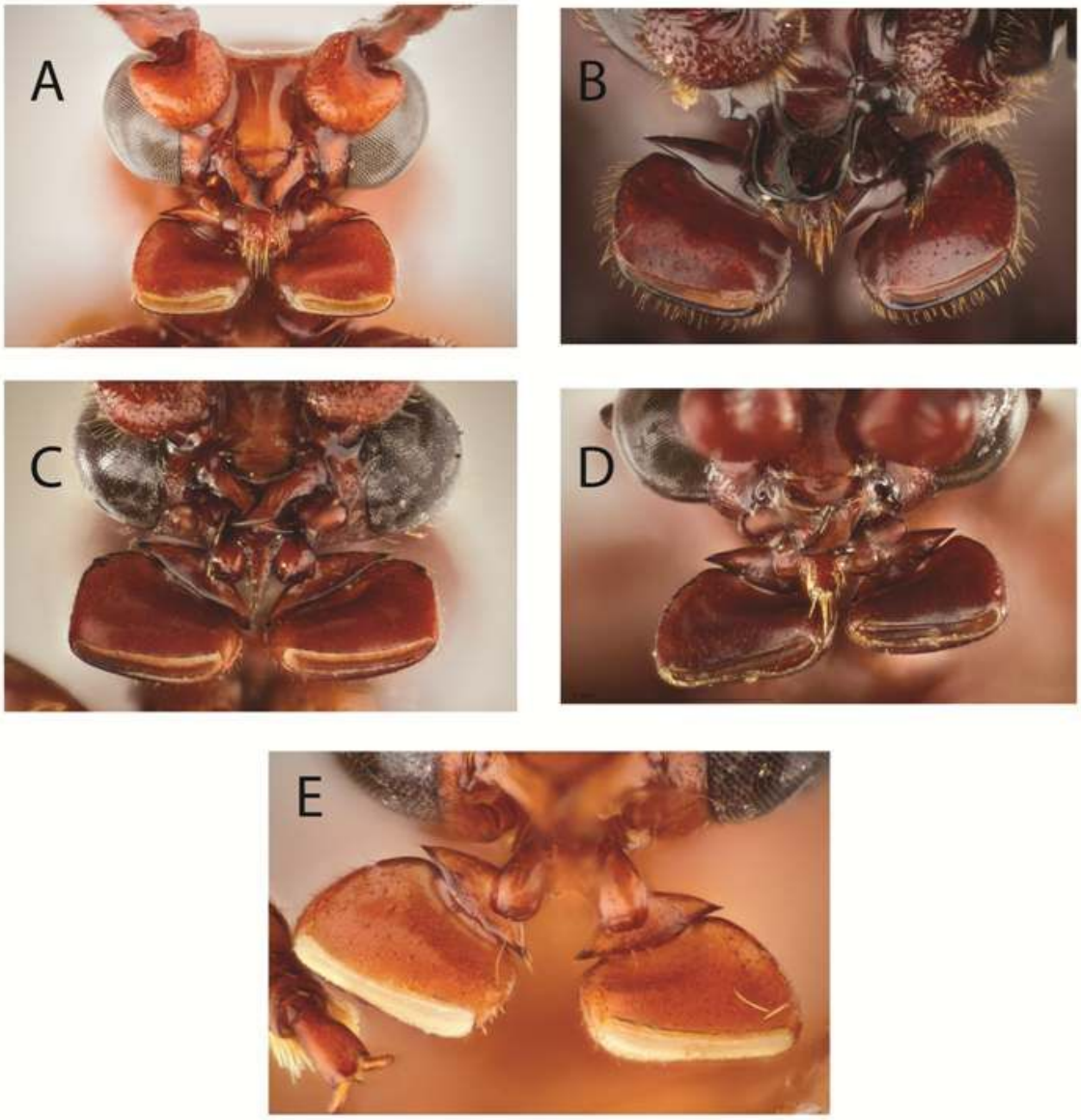

Figure 8. Maxillary palp shape: A, *H. brasiliensis*; B, *H. cunctans*; C, *H. kriegi*; D, *H. subcordatus*; E, *H. proemonens*

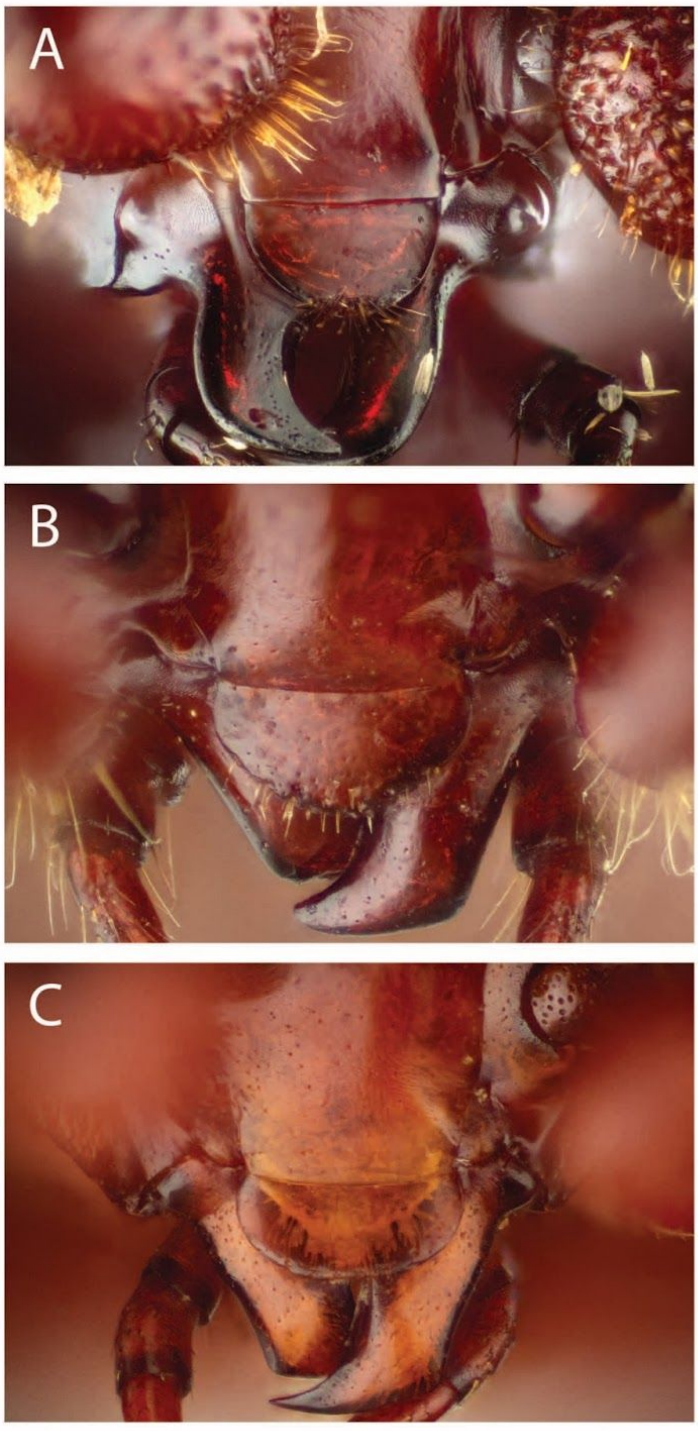

Figure 9. Clypeus states and mandibular shapes: A, *Homopterus cunctans;* B, *Homopterus honduriensis*; C, *Homopterus subcordatus*

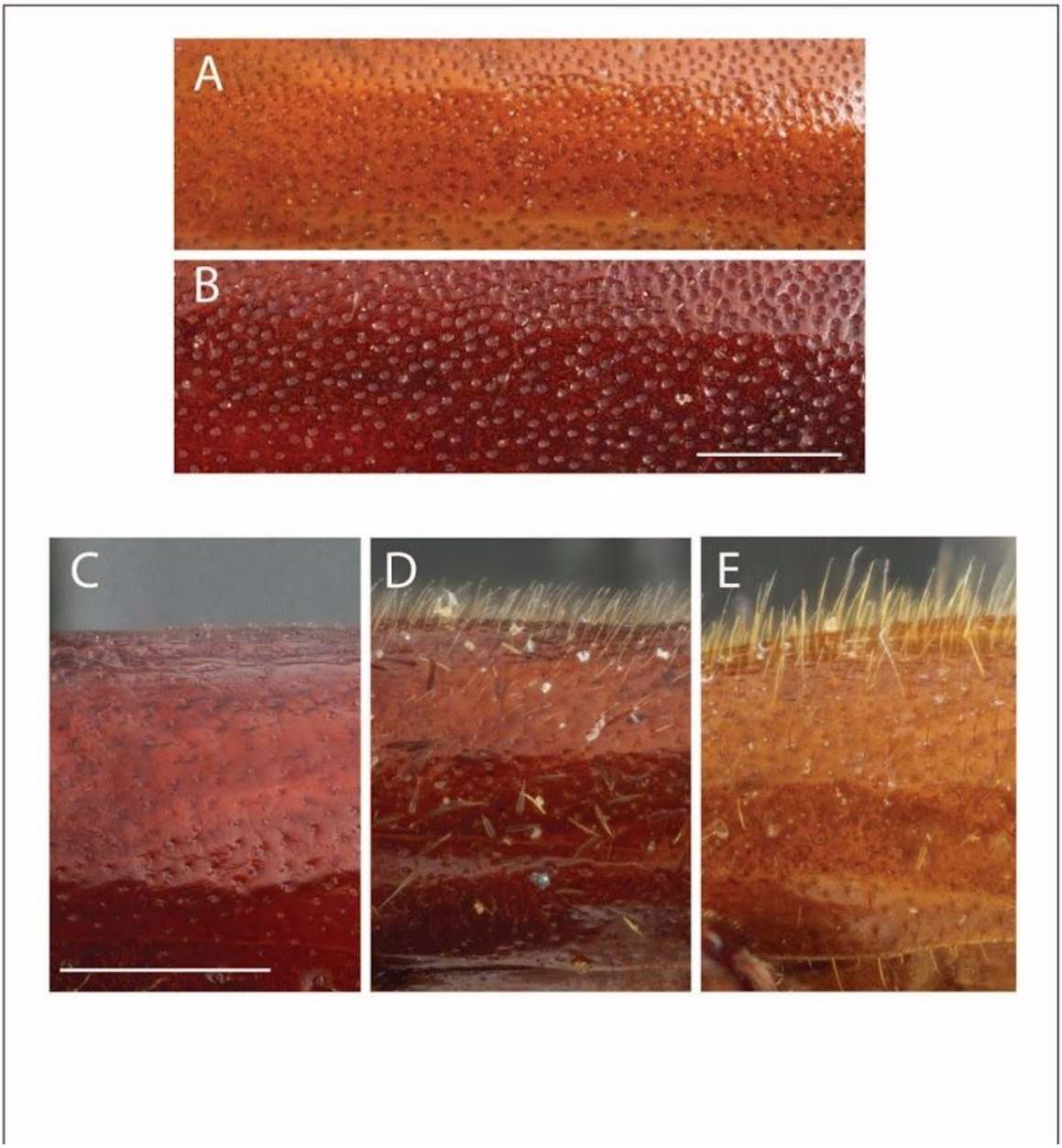

Figure 10. Elytral disc punctation and setation: A, punctation of *Homopterus steinbachi;* B, punctation of *Homopterus cunctans;* C, elytra of *Homopterus amplificatus;* D, elytra of *Homopterus honduriensis;* E, elytra of *Homopterus filiko* n. sp. Scale bar = 1 mm.

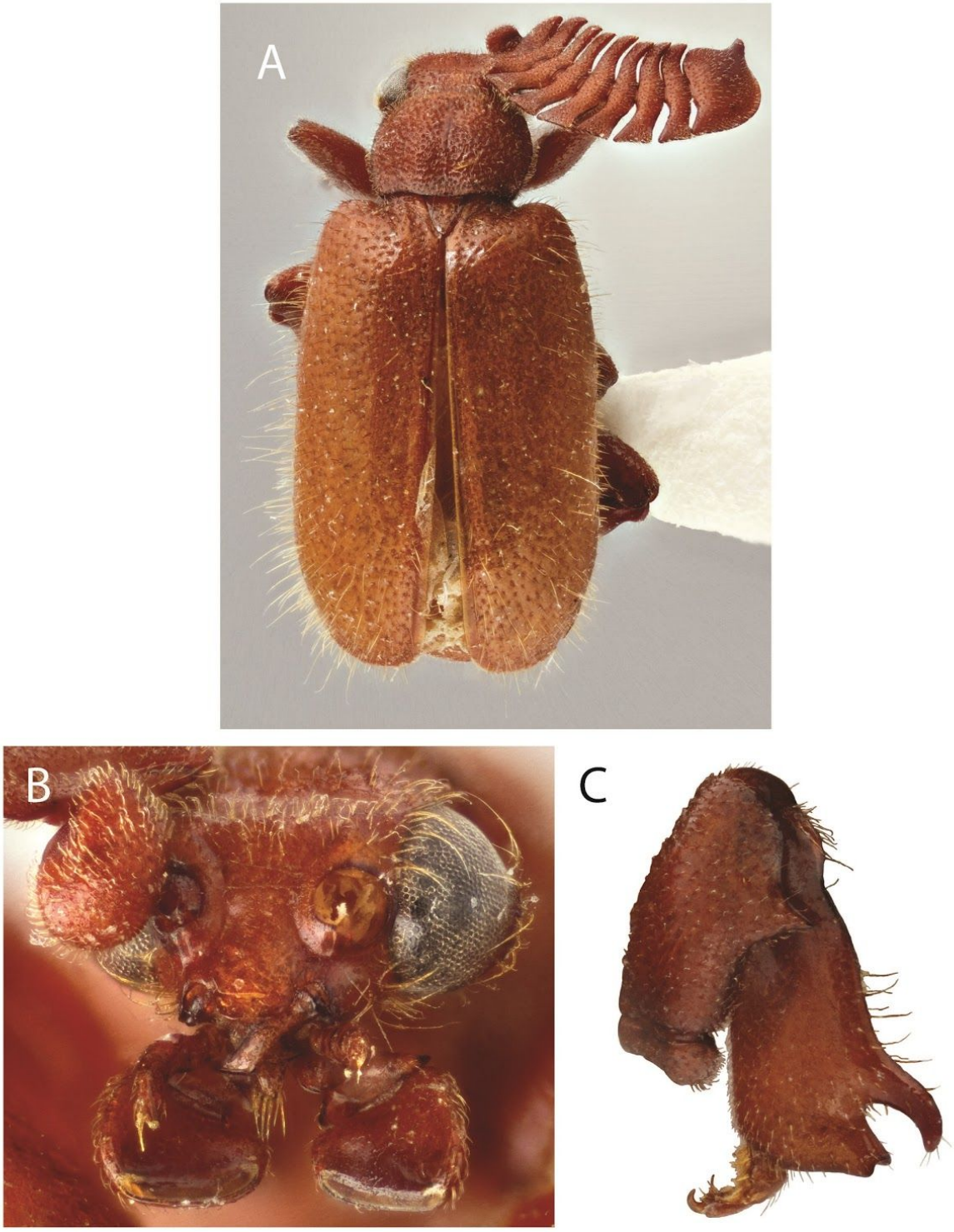

Figure 11. Characters of *Homopterus filiko,* n. sp.: A, habitus; B, frontal view of head; C, spine and hook projections on femur and tibiae