

Deutsche
Entomologische

Zeitschrift

66 (2) 2019

Deutsche Entomologische Zeitschrift

An International Journal of Systematic Entomology

Editor-in-Chief

Dominique Zimmermann

Natural History Museum Vienna
dominique.zimmermann@nhm-wien.ac.at

Managing Editor

Lyubomir Penev

Pensoft Publishers, Sofia, Bulgaria
phone: +359-2-8704281
fax: +359-2-8704282
e-mail: penev@pensoft.net

Editorial Secretary

Boryana Ovcharova

Pensoft Publishers, Sofia, Bulgaria
e-mail: journals@pensoft.net

Editorial Board

Ulrike Aspöck, Vienna, Austria

Roger L. Blackman, London, United Kingdom

Claudia Hemp, Bayreuth, Germany

Harald Letsch, Vienna, Austria

James Liebherr, Ithaca, United States of America

Wolfram Mey, Berlin, Germany

Alessandro Minelli, Padova, Italy

Michael Ohl, Berlin, Germany

Ralph Peters, Bonn, Germany

Susanne Randolph, Vienna, Austria

Dávid Rédei, Tianjin, China

Nikolaus Szucsich, Vienna, Austria

Jan van Tol, Leiden, Netherlands

Sonja Wedmann, Messel, Germany

Frank Wieland, Bad Dürkheim, Germany

Michael Wilson, Cardiff, United Kingdom

Dominique Zimmermann, Vienna, Austria

Deutsche Entomologische Zeitschrift

2019. Volume 66. Issue 2

ISSN: 1435-1951 (print), 1860-1324 (online)

Abbreviated keys title: Dtsch. Entomol. Z.

In Focus

The cover picture shows *Tropopterus peckorum* sp. nov.

See paper of **Liebherr JK** Revision of *Tropopterus* Solier: A disjunct South American component of the Australo-Pacific Moriomorhini (Coleoptera, Carabidae)

Cover design

Pensoft



Deutsche Entomologische Zeitschrift
An International Journal of Systematic Entomology

Content of volume **66 (2)** 2019

Meierotto S, Sharkey MJ, Janzen DH, Hallwachs W, Hebert PDN, Chapman EG, Smit MA A revolutionary protocol to describe understudied hyperdiverse taxa and overcome the taxonomic impediment	119
Liebherr JK Revision of <i>Tropopterus</i> Solier: A disjunct South American component of the Australo-Pacific Moriomorphini (Coleoptera, Carabidae)	147
Prathapan KD, Poorani J, Kumari SA, Anuradha C, Padmanaban B, Thanigairaj R Species composition and diagnoses of leaf- and fruit-scarring beetles (Coleoptera, Chrysomelidae) infesting bananas and plantains (Zingiberales, Musaceae) in the Indian subcontinent	179

Abstract & Indexing Information

Biological Abstracts® (Thompson ISI)
BIOSIS Previews® (Thompson ISI)
Cambridge Scientific Abstracts (CSA/CIG)
Web of Science® (Thompson ISI)
Zoological Record™ (Thompson ISI)

A revolutionary protocol to describe understudied hyperdiverse taxa and overcome the taxonomic impediment

Sarah Meierotto¹, Michael J. Sharkey¹, Daniel H. Janzen², Winnie Hallwachs², Paul D. N. Hebert³, Eric G. Chapman¹, M. Alex Smith⁴

¹ Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA

² Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

³ Centre for Biodiversity Genomics, Guelph, ON, N1G 2W1, Canada

⁴ Department of Integrative Biology, University of Guelph, Guelph, Canada

<http://zoobank.org/FDA33662-0595-4AC1-B9BA-9F2C1311D114>

Corresponding author: Sarah Meierotto (s.meierotto@uky.edu); Michael J. Sharkey (msharkey@uky.edu)

Academic editor: D. Zimmermann ♦ Received 21 March 2019 ♦ Accepted 2 July 2019 ♦ Published 25 July 2019

Abstract

Here we elucidate and justify a DNA barcode approach to insect species description that can be applied to name tens of thousands of species of Ichneumonoidea and many other species-rich taxa. Each description consists of a lateral habitus image of the specimen, a COI barcode diagnosis, and the holotype specimen information required by the International Code of Zoological Nomenclature. We believe this approach, or a slight modification of it, will be useful for many other underdescribed hyperdiverse taxa, especially in the tropics. Due to the extreme species-richness of the Ichneumonoidea, the very low percentage of described species, and the lack of detailed biological information for most described species, the standard taxonomic approach is inefficient and overwhelmingly time consuming. A DNA barcode-based approach to initial description will provide a solid foundation of species hypotheses from which more comprehensive descriptions can be developed as other data, time, and budgets permit. Here we elucidate this view and detailed methodology that can generally be applied to species-rich underdescribed taxa. A real example is given by describing species in two genera, *Hemichoma* and *Zelomorpha*, reared from the Área de Conservación Guanacaste in northwestern Costa Rica. The generic type species *Zelomorpha arizonensis* is given a DNA barcode diagnosis and the following new species are described: *Zelomorpha angelsolisi*, *Zelomorpha bobandersoni*, *Zelomorpha danjohnsoni*, *Zelomorpha donwindsori*, *Zelomorpha effugia*, *Zelomorpha johnchemsaki*, *Zelomorpha kellyanneae*, *Zelomorpha larrykirkendalli*, *Zelomorpha mariyavladmirovnae*, *Zelomorpha mikeiviei*, *Zelomorpha myricagaleae*, *Zelomorpha noahjaneae*, *Zelomorpha paulgoldsteini*, *Zelomorpha terryerwini*, *Zelomorpha willsflower-si*, *Hemichoma donwhiteheadi*, *Hemichoma frankhovorei*, and *Hemichoma johnkingsolveri*.

Key Words

Agathidinae, barcode, Braconidae, COI, *Hemichoma*, Hymenoptera, Ichneumonoidea, *Zelomorpha*

Introduction

Systematists have many powerful tools at their disposal for discovering, delimiting and describing new species, and an integrated taxonomic approach, combining morphological characters, identification keys, phylogenetic analyses with multiple molecular markers, and ecological data, is currently the gold standard for quality descrip-

tions of new species (Will et al. 2005; Burns et al. 2008; Pante et al. 2014; Janzen et al. 2017). Such detailed investigation will produce high quality species hypotheses and should be the long-term goal in the taxonomic study of most organisms. However, this approach is highly labor- and resource-intensive, a fact well understood by

those who champion it. When this reality is paired with decreasing manpower and financial support for taxonomic work (Godfray 2007), integrated taxonomic workflows cannot meet the demand for new species documentation produced by the current ecological crises nor by modern technology-assisted exploration of the incredibly species-rich tropics (e.g., Smith et al. 2006, 2008; Fernandez-Triana et al. 2014).

We propose the description of new species based primarily on the DNA barcode molecular marker as a first step in the systematic study of terminal taxa in the highly diverse superfamily Ichneumonoidea. These descriptions are meant to encourage and accelerate 1) the accumulation of additional information on the described species, 2) scientific discussion of the groups treated, 3) opportunities for the refinement of presented species hypotheses as well as those long believed to be established (e.g., Smith et al. 2006), and 4) a species-based framework on which the collateral information of literally hundreds of similar species can be organized. As an example of necessity for a dramatic change in our approach to species descriptions, we elucidate the state of affairs in the Ichneumonoidea below.

The superfamily Ichneumonoidea contains the two most species-rich families of Hymenoptera, i.e., Braconidae and Ichneumonidae. As parasitoids, ichneumonoids exert strong top-down control on their hosts, contributing to ecosystem stability and diversity (Janzen 1981; LaSalle and Gauld 1993; Condon et al. 2014). Many species have economic importance as biological control agents (Sharkey 1997) and display extreme host specificity (Fernandez-Triana et al. 2014).

The Ichneumonoidea contains over 44,000 valid species as of 2016 (Yu et al. 2016). The true number of species can only be crudely estimated, but the superfamily may include as many as 1,000,000. Estimates of total species richness for this group are variable and have increased greatly over recent decades. Dolphin and Quicke (2001) estimated there to be 30,000–50,000 braconid species, using species description rates and comparisons to mammalian diversity patterns. Based on decades of experience working on the morphologically based taxonomy of the family, van Achterberg (in Ghahari et al. 2006) estimated a minimum of 120,000 braconid species in the world, and a roughly equal number of ichneumonids. Rodriguez et al. (2013) used the ratio of described wasp species to Lepidoptera hosts from relatively well-studied sites to estimate the total number of species in the subfamily Microgastrinae, which currently has about 2,000 described species. They predicted between 17,000 and 46,000+ species of Microgastrinae, but noted this was likely an underestimate due to the many undescribed species of Microgastrinae from the well-studied sites used to make the estimations. Extrapolating from the Ichneumonoid database Taxapad (Yu et al. 2016), five of every 100 described ichneumonoid species are microgastrines. Assuming that this ratio holds true for undescribed species and that the estimates made by Rodriguez et al. (2013) are sound, there are between 300,000 and 900,000 species

of Ichneumonoidea. From 2000 to 2011, an average of 468 species of ichneumonoids were described per year (Fig. 1). Given the current rate of species description and these estimates of species diversity, all ichneumonoids, that manage to remain extant, would be described somewhere between the years 2560 and 3842.

Recent revisions of ichneumonoids in the subfamilies Agathidinae and Microgastrinae have investigated the utility of the DNA barcoding region of the gene cytochrome *c* oxidase subunit I (COI) for species delimitation, paired with morphological and ecological host-use characters (e.g., Fernandez-Triana et al. 2014). Kang et al. (2017) created initial molecular operational taxonomic units (MOTUs) for the genus *Lytopylus* using neighbor joining and maximum likelihood trees, clustering species with boundaries at a sequence divergence of 2%. The MOTUs matched the final species concepts for *Lytopylus* at 96.6%. Similarly, revisionary studies of the agathidine genera *Alabagrus* (Sharkey et al. 2018), *Aerophilus* (Sharkey and Chapman 2016), *Euagathis* (Achterberg et al. 2014), *Aphelegathis* (Sharkey et al. 2015), and *Cremnops* (Tucker et al. 2015) used COI data for formation of preliminary MOTUs for species delimitation and found high concordance between MOTUs and final species delimitations. An investigation of the Microgastrinae of Área de Conservación Guanacaste in Costa Rica (again using morphology, COI DNA barcodes, and ecological host data) found all morphological species concepts perfectly corroborated by barcodes (Smith et al. 2008). Additionally, in all of the above cases, DNA barcodes accurately distinguished morphologically cryptic but ecologically distinct species.

While there have been some calls to use molecular species descriptions (Cook et al. 2010; Jörger and Schrödl 2013), few arthropod species have been described based on molecules (Pante et al. 2014) even though DNA sequences are likely more diagnostic than any other trait. There is no stipulation in the International Code of Zoological Nomenclature that prevents or discourages DNA-based descriptions and diagnoses (ICZN 1999). Requirements for the publication of new species include that they be properly named, properly published, have a designated type deposited in an identified place, and that they be accompanied by either a description or diagnosis which can separate them from any known species with which they are likely to be confused. Obviously the diagnosis cannot distinguish them from the many hundreds of species not yet encountered, many of which are now being discovered in modern year-round tropical bioinventory by resident-based biomonitoring (e.g., Janzen and Hallwachs 2016). Barcode-based descriptions are more accurate than morphological descriptions, especially when dealing with diverse, understudied taxa. The COI barcode approach also allows species hypotheses to be posited and data accumulated by employing clear and reproducible methods. By naming these species, we give them a permanent and traceable human-readable record in the literature and electronic databases, and a basis by which they can be back-referenced to information from previous centuries

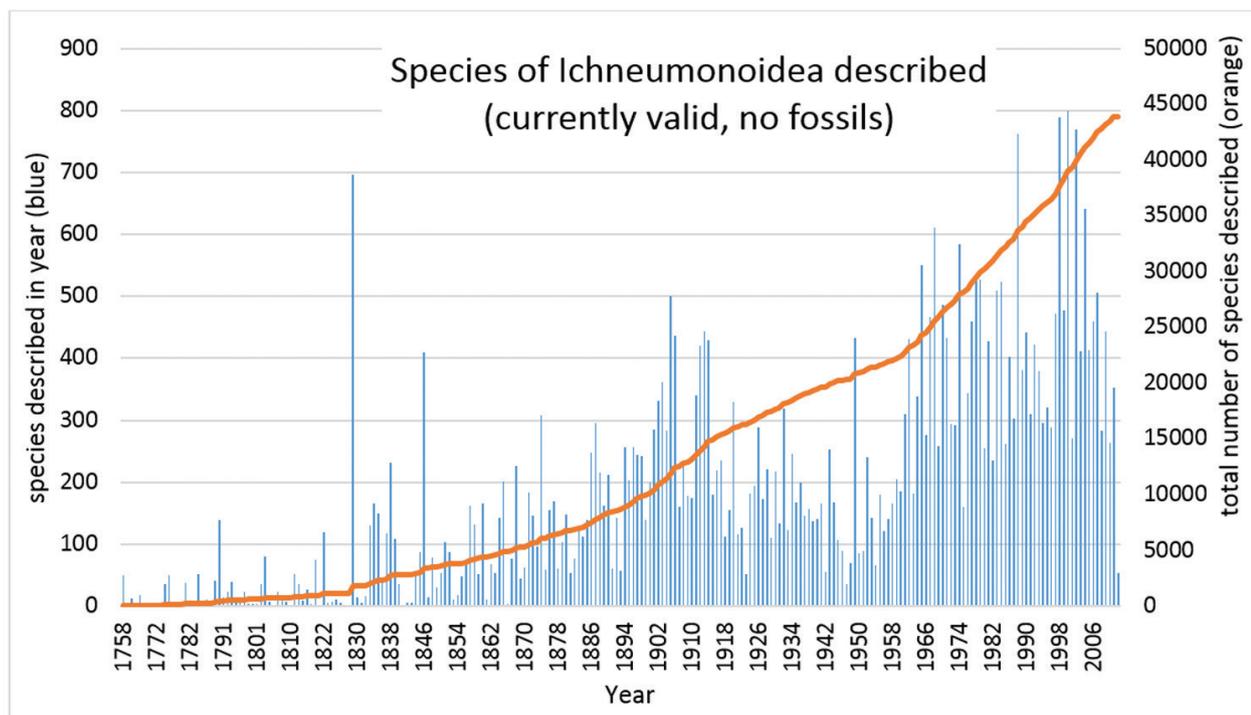


Figure 1. Description rate of Ichneumonoidea species. Data from Taxapad (Yu et al. 2016).

of taxonomic and biological study. Unlike provisional names or simple unique codes, the official names allow the species concepts to be discussed and revised by the scientific community without ambiguity. We do not discourage the standard taxonomic approach. However, we believe that the method outlined here will facilitate such treatments. Furthermore, we find that the barcode-based approach greatly streamlines the ease and accuracy of the standard approach when resources and/or urgency call for it to be applied. We further note that even before standard human-readable names are applied through our suggested barcode-approach, an enormous amount of ecological and natural history study can be conducted with the voucher-based unique codes, and their groupings into BIN codes (Ratnasingham and Hebert 2013) that link the barcode to a scientific name (Janzen and Hallwachs 2016; in prep).

Methods

Specimen collection and documentation

Most specimens were collected by rearing host caterpillars in Área de Conservación Guanacaste (ACG) in north-western Costa Rica (Janzen and Hallwachs 2016). Caterpillar hosts were collected by a team of parataxonomists (Janzen and Hallwachs 2011) as part of the ongoing project to document all ACG non-leaf-mining Lepidoptera larvae, their food plants, and their parasitoids (Janzen and Hallwachs 2016). These caterpillars were databased with collection information, food plant information, and often a photograph, and they were reared to adults. When an

adult moth, butterfly, or parasitoid emerged, the specimen was preserved oven-dried or frozen in 95% ethanol, and a leg was sent to the Centre for Biodiversity Genomics (CBG) (<http://biodiversitygenomics.net>) for DNA barcoding at a cost ranging from \$3–\$10 USD per specimen. Barcodes are deposited with their collateral specimen voucher data in the Barcode of Life Data System (www.boldsystems.org). A generic assignment was confirmed for all specimens of *Hemichoma* and *Zelomorpha* using morphological characters (and both genera form their own monophyletic group in a standard Hymenoptera NJ tree of thousands of species). Focus-stacked images of specimens were taken using a JVC digital camera mounted on a Leica microscope and compiled with the program Automontage. Image post-processing was done in Adobe Photoshop.

DNA extraction and sequencing

Molecular work was carried out at the Centre for Biodiversity Genomics (CBG) using their standard protocols. A leg of each specimen was destructively sampled for DNA extraction using a glass fiber protocol (Ivanova et al. 2006). Extracted DNA was amplified for a 658-bp region near the 5' terminus of the CO1 gene using standard insect primers LepF1 (5'-ATTCAACCAATCATAAAGATATTGG-3') and LepR1 (5'-TAAACTTCTGGATGTC-CAAAAATCA-3') (Ivanova and Grainger 2007). If initial amplification failed, additional amplifications were conducted following the established protocols using internal primer pairs, LepF1-C113R (130 bp) or LepF1-C-ANTMR1D (307 bp) and MLepF1-LepR1 (407 bp) to

generate shorter overlapping sequences. Amplified products were sequenced using Sanger technology.

Sequence analysis and species determination

Sequences (barcodes) were assigned to operational taxonomic units called barcode index numbers (BINs) that were generated in tandem with the neighbor-joining tree of the barcodes themselves (Appendix 1).

Morphology and host information were compared to BIN assignments that package the NJ tree. Specimen groupings, a BIN, suggested by all data sources were considered to be species. However, for other higher taxa there are cases where several obvious species are packaged into one BIN (e.g., Hebert et al. 2004; Janzen et al. 2017), basically because the BIN algorithm separates groups at about a 2% difference, while in the early stages of evolutionary separation, the species became distinctive before the barcodes attained 2% difference. *Zelomorpha arizonensis*, as discussed below, may be such a case in this study. Type specimens of all previously described *Zelomorpha* and *Hemichoma* species were examined by MJS and his notes were used to verify that *Z. arizonensis* is the sole previously described species in the genus.

Consensus barcodes were created for each species using BioEdit (Hall 1999) and aligned to the *Drosophila melanogaster* complete mitochondrial genome from the NCBI Reference Sequence Database, accession number NC_024511. Consensus barcodes for all species in each genus were compared to all other species in the genus. Nucleotides that were shared by all specimens of a species and by no specimens of any other species were recorded as diagnostic characters. Diagnostic characters are called by their position in the alignment with the *D. melanogaster* reference sequence.

For *Zelomorpha arizonensis*, the only previously described species that we included in the dataset, a number of specimens collected in the southwestern USA and Mexico were included in the NJ tree in addition to the sequences of specimens from ACG.

Specimen information

Holotypes are deposited in the insect collection in the Biology Department of Utah State University in Logan, Utah (EMUS), formerly the insect collection of the American Entomological Institute, Gainesville, Florida. Paratypes are divided between the EMUS and the Hymenoptera Institute Collection (HIC). Detailed specimen records are available on Janzen and Hallwach's database (<http://janzen.sas.upenn.edu/caterpillars/database.lasso>) by searching for specimen voucher codes (DHJPARxxxxxxx), and equally, for a reduced set of specimen collateral in BOLD. Additional specimen information on host caterpillars can be found by search-

ing for their yy-SRNP-xxxxx voucher codes at <http://janzen.sas.upenn.edu/caterpillars/database.lasso>; there are no data (other than name) for the caterpillar host in BOLD because the cadaver was not barcoded, but rather, identified by its morphology, food plant and other ecological collateral.

Some host species are still awaiting full identification and are given interim names, generally based on their barcodes, just as is the case with the wasps described here. For example, *Hemiceras plusiata*DHJ01 is identified to the genus *Hemiceras* by classical morphology-based criteria. However, it is one of the two reared in a species complex that used to be known as *H. plusiata*. One of the two is the actual *H. plusiata*, and the other is new, but which is which cannot be determined until the holotype is barcoded, or more closely examined morphologically. This was the case with *Udranomina kikkawai*DHJ01, *H. kikkawai*DHJ02 and *H. kikkawai*DHJ03, recently rendered into three species (Janzen et al. 2017). *Udranomina kikkawai* was described from a Venezuelan holotype in 1906. It retained the holotype name through being confirmed by its barcode. When such interim-named species are assigned an official epithet (scientific name) in the future, the barcode and BIN will remain searchable in Janzen's database as well as BOLD, GenBank, and any other public repository. Complete DNA sequence and specimen information is available at dx.doi.org/10.5883/DS-ASZELO.

Results

Species delimitation

Three hundred thirty-six specimens of *Zelomorpha* and *Hemichoma* with COI barcodes were determined to represent 20 species in two genera by their barcodes, their BINs, and by concomitant morphological inspection. BIN assignments were the same as final species hypotheses (Appendix 1), except in one case in which two species are included in one BIN, i.e., *Z. johnchemsaki* and *Z. bobandersoni*. *Zelomorpha johnchemsaki* parasitizes only *Hemiceras pallidula* (Notodontidae) feeding on *Inga*, while *Z. bobandersoni* parasitizes only on two species of *Hemiceras plusiata* feeding on *Tachigali costaricensis* (Fabaceae) in the same ecosystem. Although these two species have a low interspecific p-distance (2.29%), there is a clear gap between them due to the low variation within species: maximum intraspecific p-distances are 0.30% and 0.16% for *Z. johnchemsaki* and *Z. bobandersoni*, respectively. The separation of these two species is also supported by host plant and host caterpillar differences (Appendix 1). *Hemichoma frankhovorei* contains the greatest intraspecific p-distance and the barcodes are conspicuously variable in length, which obviously results in a high intraspecific p-distance (0.93%), but with no clear subgroupings by morphology, barcode, or ecology (and all parasitize the

same genus of caterpillars). *Zelomorpha arizonensis* is the only previously described species in this dataset. We describe all other species as new.

Systematics

Zelomorpha Ashmead, 1900

Type species. *Zelomorpha arizonensis* (by monotypy) (Ashmead 1900).

Diagnosis. *Zelomorpha* can be distinguished from all other Agathidinae genera by the following combination of morphological characters: fore tarsal claws cleft and not pectinate; foretibial spur shorter than first tarsomere; ovipositor shorter than half the length of the metasoma; frons bordered by carinae; hind trochantellus with one or two longitudinal ridges; notauli variable, usually distinct; gena not elongate.

Biology. The species of *Zelomorpha* are koinobiont solitary endoparasitoids of free-living, late instar medium-small Lepidoptera larvae (Sharkey 1997). Larvae emerge from pre-pupal caterpillars after the caterpillars have spun their cocoons. The parasitoid larvae then spin pale silk cocoons within the host cocoons, next to the host cadavers.

Distribution. *Zelomorpha* occur only in the New World, from the southern USA to Argentina and are pri-

marily Neotropical (Sharkey et al. 2006; Sharkey and Chapman 2017).

Species richness. Including the fifteen new species described here, there are 67 described species of *Zelomorpha* (Yu et al. 2016).

Zelomorpha angelsolisi Meierotto, sp. nov.

<http://zoobank.org/82FC9D54-84E0-470B-8A02-2F80FBFAC5B6>

Figure 2

Molecular diagnosis. Nucleotides 43–45 TTA, 54–57 CTTT, 75 G, 136–138 GTG, 165 T, 321 G, 417 G, 462 G, 477 C, 561 G, 684 G.

Biology. This species has characteristics associated with nocturnal habits: pale coloration, large compound eyes and ocelli. Specimens were reared from caterpillars in the family Erebidae feeding on Fabaceae: *Azeta ceramina* on *Acosmium panamense*, *Chabora repugnalis* DHJ01 on *Indigofera costaricensis*, and *Coenipeta bibitrix* on *Enterolobium cyclocarpum*. Host caterpillars were collected in April, May, and November.

Notes. Many specimens of this species were originally identified as *Zelomorpha arizonensis* by MJS based on morphology. However, p-distances between *Z. arizonensis* and *Z. angelsolisi* are greater than 8%.

Type material. Holotype ♀: DHJPAR0009310 (ASBR577-06), Costa Rica, Área de Conservación Gua-



Figure 2. Lateral image of *Zelomorpha angelsolisi* holotype female.

nacaste, Sector Mundo Nuevo, Punta Plancha, GPS: 10.7416, -85.42734, 420 m elevation, Mariano Pereira coll., reared from *Azeta ceramina* 05-SRNP-56517, host collected 30 May 2005, wasp eclosed 17 June 2005, (EMUS). Paratypes: DHJP0009321 (ASBR588-06), DHJP0009322 (ASBR589-06), DHJP0009314 (ASBR581-06), DHJP0009315 (ASBR582-06), DHJP0009316 (ASBR583-06), DHJP0009313 (ASBR580-06), DHJP0009318 (ASBR585-06), DHJP0009317 (ASBR584-06), DHJP0009311 (ASBR578-06), DHJP0009312 (ASBR579-06), DHJP0009319 (ASBR586-06), DHJP0009320 (ASBR587-06), DHJP0009323 (ASBR590-06), DHJP0021152 (ASBC964-07), DHJP0028276 (ASHYF038-09), DHJP0028275 (ASHYF037-09), DHJP0015578 (ASAG264-07), DHJP0015593 (ASAG279-07), DHJP0015584 (ASAG270-07), DHJP0015592 (ASAG278-07), DHJP0015579 (ASAG265-07), DHJP0015577 (ASAG263-07), DHJP0015556 (ASAG242-07), DHJP0029184 (ASHYE591-09), DHJP0015590 (ASAG276-07), DHJP0015588 (ASAG274-07).

Etymology. *Zelomorpha angelsolisi* is named in honor of Angel Solís of INBio and the Museo Nacional de Costa Rica, a master taxonomist of Coleoptera and curator who has massively contributed to the inventory of Costa Rican Coleoptera.

Zelomorpha arizonensis Ashmead, 1900.

Figure 3

Molecular diagnosis. Nucleotides 515 C, 648 T

Biology. Adults of this species have characteristics associated with nocturnal habits: pale coloration, large compound eyes and large ocelli. All individuals were reared from *Bulia mexicana* (Erebidae) caterpillars feeding on mature leaves of *Prosopis juliflora* (Fabaceae) at the edge of ACG mangrove swamps in the month of July.

Notes. The host of *Z. arizonensis* from the type locality in the southwestern United States is unknown. However, the range of *Prosopis juliflora* extends northwards through Mexico and into the United States, where it is fed upon by several species of *Bulia*. P-distances between specimens from Costa Rica and the US are close to 1.5% (Fig. 2), which is more than separates many morphologically and ecologically distinctive ACG species (Hebert et al. 2004; Burns et al. 2007; Janzen et al. 2017), including *Z. johnchemsaki* and *Z. bobandersoni*. We have elected to identify this ACG species as being *Z. arizonensis* because of its morphological similarity to *Z. arizonensis* and because its DNA barcode differs from that species by only 1.5% in the sample of six ACG specimens and two Arizona specimens (NJ tree in Appendix 1). However, because there are hundreds of morphologically and ecologically distinctive ACG sympatric or parapatric insect species pairs that show similar or less divergence (e.g., Hebert et

al. 2004; Burns et al. 2007; Janzen and Hallwachs 2016; Janzen et al. 2017), it is possible that two cryptic species will eventually be confirmed within this name, with the Costa Rican species being new.

Material examined. Figured specimen ♀: DHJP00052709 (ASHYM2063-13), Costa Rica, Área de Conservación Guanacaste, Sector Santa Rosa, Argelia, GPS: 10.78004, -85.66405, 5 m elevation, Guillermo Pereira coll., reared from *Bulia mexicana* 13-SRNP-17758, host collected 13 July 2013, wasp eclosed 29 July 2013, (EMUS). Other specimens: Costa Rica: DHJP00052704 (ASHYM2058-13), DHJP00052702 (ASHYM2056-13), DHJP00052703 (ASHYM2057-13), DHJP00052708 (ASHYM2062-13; EMUS), DHJP00052705 (ASHYM2059-13), DHJP00052707 (ASHYM2061-13; HIC). Arizona: HICH015113 (GBMIN73766-17; HIC), HICH015114 (GBMIN142474-18; HIC), BIOUG02486-B12 (BBHYA1354-12), BIOUG02486-C01 (BBHYA1355-12), BIOUG02486-C02 (BBHYA1356-12), BIOUG02580-A06 (BBHYA1778-12), BIOUG02580-B07 (BBHYA1791-12), BIOUG02580-C06 (BBHYA1802-12), BIOUG02580-C08 (BBHYA1804-12), BIOUG02580-C09 (BBHYA1805-12), BIOUG02587-B02 (BBHYA2356-12), BIOUG02587-B03 (BBHYA2357-12), BIOUG02644-H11 (BBHYA3007-12), BIOUG02645-A09 (BBHYA3016-12), BIOUG02645-D12 (BBHYA3055-12), BIOUG02645-E02 (BBHYA3057-12), BIOUG02645-E09 (BBHYA3064-12), BIOUG02645-E10 (BBHYA3065-12), 10BBHYM-0795 (BBHYG795-10), 09BBHYM-158, 09BBHYM-159, 09BBHYM-1106, 09BBHYM-1107, 09BBHYM-1108, 09BBHYM-1109, 09BBHYM-1110, 09BBHYM-1111 (BIOUG). New Mexico: BIOUG02644-G07 (BBHYA2991-12; BIOUG). Texas: 09BBHYM-1112 (BIOUG).

Etymology. *Zelomorpha arizonensis* was named for its holotype locality.

Zelomorpha bobandersoni Meierotto, sp. nov.

<http://zoobank.org/AB75E8BD-A06E-401E-8CAB-060558F66DF1>

Figure 4

Molecular diagnosis. Nucleotides: 72–75 GGGT, 163 G, 222–225 GGGG, 264 G

Biology. All known individuals were reared from *Hemiceras plusiata*DHJ01 or *Hemiceras plusiata*DHJ02 (Notodontidae) feeding on *Tachigali costaricensis* (Fabaceae); the caterpillars are indistinguishable without barcoding them. Host caterpillars were collected in January, February, April, and June through October.

Type material. Holotype ♀: DHJP00028037 (ASHYE274-08), Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, Estacion Quica, GPS: 10.99697, -85.39666, 470 m elevation, Mauricio Sieszar coll., reared from *Hemiceras plusiata*DHJ01 08-SRNP-71265, host collected 10 July 2008, wasp eclosed 11 August 2008, (EMUS). Paratypes: DHJP0009346 (ASBR613-06), DHJP0009345 (ASBR612-06), DHJP0036332



Figure 3. Lateral image of *Zelomorpha arizonensis* female.



Figure 4. Lateral image of *Zelomorpha bobandersoni* holotype female.

(ASHYD1523-09), DHJPARG0036330 (ASHYD1521-09), DHJPARG0036331 (ASHYD1522-09), DHJPARG0052686 (ASHYM2040-13)

Etymology. *Zelomorpha bobandersoni* is named in honor of Bob Anderson of the Canadian Museum of Nature, Ottawa, in recognition of his taxonomic and curatorial support for understanding the Curculionidae of Costa Rica.

***Zelomorpha danjohnsoni* Meierotto, sp. nov.**

<http://zoobank.org/946520CB-DEB7-437C-84F5-5E2F7C05A3CB>

Figure 5

Molecular diagnosis. Nucleotides: 98 G, 111 G, 264 C, 310 G, 375 A, 452 T, 495 A, 507 G, 513 G, 648 G

Biology. The host of the holotype and one additional specimen lacking COI data were collected in June. Both were reared from *Diastema morata* (Noctuidae) on feeding on *Lantana camara* (Verbenaceae).

Type material. Holotype ♀: DHJPARG0009409 (ASBR676-06), Costa Rica, Área de Conservación Guanacaste, Sector Cacao, Quebrada Otilio, GPS: 10.88996, -85.47966, 550m elevation, Dunia Garcia coll., reared from *Diastema morata* 05-SRNP-45510, host collected 7 June 2005, wasp eclosed 14 July 2005, (EMUS).

Etymology. *Zelomorpha danjohnsoni* is named in honor of C. Dan Johnson (RIP) of Arizona State University, in recognition of his taxonomic support for understanding the Bruchinae (Chrysomelidae) of Costa Rica.

***Zelomorpha donwindsori* Meierotto, sp. nov.**

<http://zoobank.org/77937C61-D022-4671-A5F4-3E67F5ABCCAC>

Figure 6

Molecular diagnosis. Nucleotides: 78 A, 213 C, 243 A, 390 G, 429 G, 456 G, 506–507 CT, 513 T, 585 G, 588 G, 603 C, 636 C, 660 G, 678–679 TG

Biology. The two specimens of this species were reared from caterpillars in the Euteliidae, *Paectes lunodes* feeding on very young leaves of *Ocotea veraguensis* (Lauraceae) and *Paectes fuscescens* feeding on young leaves of the introduced species *Anacardium occidentale* (Anacardiaceae). Host caterpillars were collected in November and July.

Type material. Holotype ♀: DHJPARG0048721 (ACGBA2263-12), Costa Rica, Área de Conservación Guanacaste, Sector El Hacha, Los Almendros, GPS: 11.03226, -85.52776, 290 m elevation, Elieth Cantillano coll., reared from *Paectes fuscescens* 11-SRNP-23258, host collected 15 November 2011, wasp eclosed 9 January 2012, (EMUS). Paratype: DHJPARG0052679 (ASHYM2033-13).

Etymology. *Zelomorpha donwindsori* is named in honor of Don Windsor of the Smithsonian Tropical Research Institute in Panama, a master taxonomist in Chrysomelidae who also contributed to the early development of ACG. The timbers from his original house are part of an ACG caterpillar rearing barn.

***Zelomorpha effugia* Meierotto, sp. nov.**

<http://zoobank.org/7032E109-6070-4617-ADCA-A76C6660E3A6>

Figure 7

Molecular diagnosis. Nucleotides: 46 A, 96–97 TG, 102 T, 124–127 TTAA, 130 G, 285 G, 352–353 TC

Biology. This species has been reared only from *Cosmosoma hercyna* (Erebidae) caterpillars feeding on mature leaves of *Lacistema aggregatum* (Lacistemataceae), and *Lozania pittieri* (Lacistemataceae). Hosts were collected in September, November, January, and February.

Type material. Holotype ♀: DHJPARG0015541 (ASAG227-07), Costa Rica, Área de Conservación Guanacaste, Sector Rincon Rain Forest, Vochysia, GPS: 10.86666, -85.24528, 320 m elevation, Minor Carmona coll., reared from *Cosmosoma hercyna* 05-SRNP-43568, host collected 30 November 2005, wasp eclosed 27 December 2005, (EMUS). Paratypes: DHJPARG0015535 (ASAG221-07), DHJPARG0009432 (ASBR699-06), DHJPARG0009431 (ASBR698-06), DHJPARG0015538 (ASAG224-07), DHJPARG0009381 (ASBR648-06), DHJPARG0009336 (ASBR603-06), DHJPARG0015546 (ASAG232-07), DHJPARG0015552 (ASAG238-07), DHJPARG0009328 (ASBR595-06), DHJPARG0015553 (ASAG239-07), DHJPARG0015547 (ASAG233-07), DHJPARG0009329 (ASBR596-06), DHJPARG0009330 (ASBR597-06), DHJPARG0009331 (ASBR598-06), DHJPARG0009332 (ASBR599-06), DHJPARG0015551 (ASAG237-07), DHJPARG0015550 (ASAG236-07), DHJPARG0009333 (ASBR600-06), DHJPARG0015548 (ASAG234-07), DHJPARG0009334 (ASBR601-06), DHJPARG0015544 (ASAG230-07), DHJPARG0009335 (ASBR602-06), DHJPARG0015545 (ASAG231-07), DHJPARG0015549 (ASAG235-07), DHJPARG0009337 (ASBR604-06), DHJPARG0009338 (ASBR605-06), DHJPARG0009339 (ASBR606-06), DHJPARG0009340 (ASBR607-06), DHJPARG0009341 (ASBR608-06), DHJPARG0009342 (ASBR609-06), DHJPARG0009343 (ASBR610-06), DHJPARG0009379 (ASBR646-06), DHJPARG0009380 (ASBR647-06), DHJPARG0017282 (ASBD387-07), DHJPARG0017281 (ASBD386-07), DHJPARG0017283 (ASBD388-07), DHJPARG0017275 (ASBD380-07), DHJPARG0017278 (ASBD383-07), DHJPARG0017280 (ASBD385-07), DHJPARG0017279 (ASBD384-07), DHJPARG0054489 (ASHYD3654-14), DHJPARG0054516 (ASHYD3681-14), DHJPARG0054472 (ASHYD3637-14), DHJPARG0054473 (ASHYD3638-14), DHJPARG0054481 (ASHYD3646-14), DHJPARG0054479 (ASHYD3644-14), DHJPARG0054484 (ASHYD3649-14), DHJPARG0054483 (ASHYD3648-14), DHJPARG0054477 (ASHYD3642-14), DHJPARG0054475 (ASHYD3640-14), DHJPARG0054482 (ASHYD3647-14), DHJPARG0054476 (ASHYD3641-14), DHJPARG0054478 (ASHYD3643-14), DHJPARG0054474 (ASHYD3639-14), DHJPARG0056359 (MHMYC2439-15), DHJPARG0057453 (ACGBA5363-15), DHJPARG0057454 (ACGBA5364-15), DHJPARG0057455 (ACGBA5365-15), DHJPARG0057456 (ACGBA5366-15), DHJPARG0057452 (ACGBA5362-15), DHJPARG0056979 (ACGBA4889-15).



Figure 5. Lateral image of *Zelomorpha danjohnsoni* holotype female.



Figure 6. Lateral image of *Zelomorpha downwindsori* holotype female.



Figure 7. Lateral image of *Zelomorpha effugia* holotype female.

Etymology. *Zelomorpha effugia* is named in honor of the podcast Escape Pod, whose short science fiction stories provided the first author with inspiration and motivation during the production of this manuscript.

***Zelomorpha johnchemsaki* Meierotto, sp. nov.**

<http://zoobank.org/05EA3708-DFE6-4FCD-81B4-33D4EDE323BB>

Figure 8

Molecular diagnosis. Nucleotides: 261 G, 279 C, 537–538 GC, 571 G

Biology. All 24 rearing records for this species are from *Hemiceras pallidula* (Notodontidae) feeding on mature leaves of *Inga vera* and *Inga oerstediana* (Fabaceae). Two of the hosts were collected in October and the others in July.

Notes. Members of *Z. johnchemsaki* are similar to *Z. bobandersoni* in COI sequence and morphology, but the large samples of the two species show consistent differences in color pattern and host preference, and fall in different BINs. They are an excellent example of a shallow split in an NJ tree that definitely represents two species.

Type material. Holotype ♀: DHJPAR0040547 (ASHYE2683-11), Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, Bullas, GPS: 10.9867, -85.38503, 440 m elevation, Ricardo Calero coll., reared from *Hemiceras pallidula* 09-SRNP-71580, host collected 14 July 2009, wasp eclosed 10 August 2009, (EMUS). Paratypes: DHJPAR0023296 (ASHYM048-08), DHJPAR0036326 (ASHYD1517-09), DHJPAR0040539 (ASHYE2675-11), DHJPAR0040536 (ASHYE2672-11),

DHJPAR0040540 (ASHYE2676-11), DHJPAR0040546 (ASHYE2682-11), DHJPAR0040537 (ASHYE2673-11), DHJPAR0040543 (ASHYE2679-11), DHJPAR0040541 (ASHYE2677-11), DHJPAR0036325 (ASHYD1516-09), DHJPAR0040535 (ASHYE2671-11), DHJPAR0036369 (ASHYD1560-09), DHJPAR0040538 (ASHYE2674-11), DHJPAR0040542 (ASHYE2678-11), DHJPAR0040545 (ASHYE2681-11), DHJPAR0040544 (ASHYE2680-11), DHJPAR0036327 (ASHYD1518-09), DHJPAR0036328 (ASHYD1519-09), DHJPAR0036368 (ASHYD1559-09).

Etymology. *Zelomorpha johnchemsaki* is named in honor of John Chemsak (RIP) of the University of California, Berkeley, in recognition of his taxonomic support for understanding the ACG Cerambycidae and teaching DHJ about them in the 1960's.

***Zelomorpha kellyanneae* Meierotto, sp. nov.**

<http://zoobank.org/0C60342A-4476-4526-983A-648B9B1D1C2D>

Figure 9

Molecular diagnosis. Nucleotides: 348 C, 421 A

Biology. This species has been reared only from *Nephodia* Janzen18 (Geometridae) feeding on *Heteropterys macrostachya* and *Heteropterys laurifolia* (Malpighiaceae). Host caterpillars were collected in November, February, and May.

Type material. Holotype ♀: DHJPAR0015536 (ASAG222-07), Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, Quebrada Raiz, GPS: 11.02865, -85.48669, 280 m elevation, Lucia Ríos coll., reared from *Nephodia* Janzen18, 05-SRNP-25234, host collected

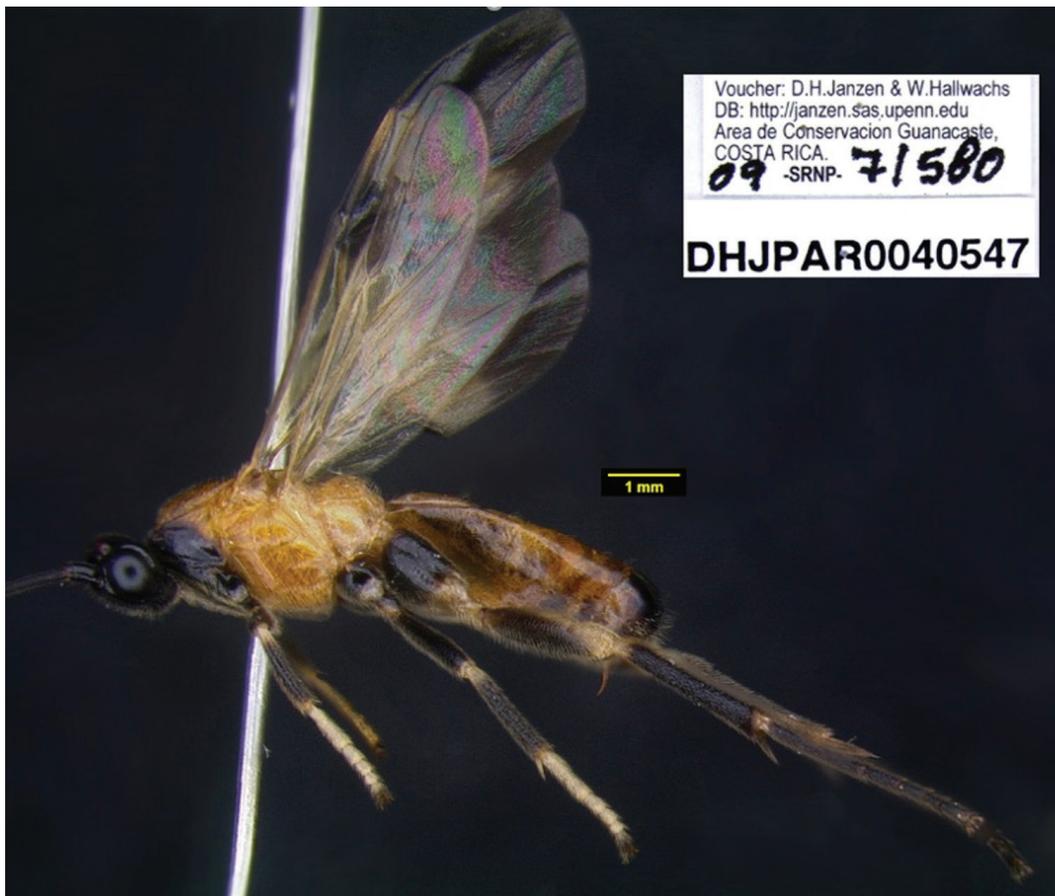


Figure 8. Lateral image of *Zelomorpha johnchemsaki* holotype female.



Figure 9. Lateral image of *Zelomorpha kellyanneae* holotype female.

21 November 2005, wasp eclosed 10 December 2005, (EMUS). Paratypes: DHJPAR0029301 (ASHYE708-09), DHJPAR0009395 (ASBR662-06), DHJPAR0009394 (ASBR661-06), DHJPAR0015543 (ASAG229-07), DHJPAR0015542 (ASAG228-07), DHJPAR0042809 (ASHYH567-11), DHJPAR0042806 (ASHYH564-11).

Etymology. *Zelomorpha kellyanneae* is named in honor of Kelly Meierotto, sister of SM and up and coming archaeologist.

***Zelomorpha larrykirkendalli* Meierotto, sp. nov.**

<http://zoobank.org/14D4279C-C434-45E0-A5C5-2D6148C30406>

Figure 10

Molecular diagnosis. Nucleotides: 81 G, 273 G, 324 T, 369 A, 432 G, 522 A, 662 G

Biology. This species has been reared from three species of *Opisthoxia* (Geometridae) feeding on very young leaves of three species of Primulaceae: *O. molpadia* on *Parathesis glabra*, *O. bella* on *Ardisia compressa*, and *O. uncinata* on *Ardisia auriculata*. Caterpillars were collected in February, March, June, July, and September.

Type material. Holotype ♀: DHJPAR0015540 (ASAG226-07), Costa Rica, Área de Conservación Guanacaste, Sector San Cristobal, Rio Blanco Abajo, GPS: 10.90037, -85.37254, 500 m elevation, Yessenia Men-

doza coll., reared from *Opisthoxia bella* 04-SRNP-4505, host collected 6 September 2004, wasp eclosed 26 September 2004, (EMUS). Paratypes: DHJPAR0055988 (ASHYH2725-14), DHJPAR0055084 (ASHYH1631-14), DHJPAR0052087 (ASHYH1199-13), DHJPAR0055981 (ASHYH2718-14).

Etymology. *Zelomorpha larrykirkendalli* is named in honor of Larry Kirkendall of the University of Bergen, Norway, in recognition of his intense taxonomic interest in Neotropical Scolytidae and Platypodidae, and now, those of ACG.

***Zelomorpha mariyavladmirovnae* Meierotto, sp. nov.**

<http://zoobank.org/029D3E7C-77FA-4F91-8491-70AC1D4E8B98>

Figure 11

Molecular diagnosis. Nucleotides: 250 A, 354 G, 462 C, 543 G

Biology. The single specimen of this species was reared from *Ormetica sicilia* (Erebidae) feeding on mature leaves of *Inga vera* (Fabaceae). Unexpectedly, it appears that this wasp eclosed from the moth pupa rather than from a wasp cocoon spun inside the moth cocoon.

Type material. Holotype ♀: DHJPAR0023528 (ASHYM280-08), Costa Rica, Área de Conservación Guanacaste, Sector Mundo Nuevo, GPS: 10.77175,



Figure 10. Lateral image of *Zelomorpha larrykirkendalli* holotype female.

-85.434, 305 m elevation, Jose Cortez coll., reared from *Ormetica sicilia* 07-SRNP-61364, host collected 28 December 2007, wasp eclosed 14 January 2008, (EMUS).

Etymology. *Zelomorpha mariyavladmirovnae* is named in honor of Mariya Frahm, for her guidance and support to SM.

***Zelomorpha mikeiviei* Meierotto, sp. nov.**

<http://zoobank.org/EC79D207-970B-49F9-AD1F-C9CC1A76B156>

Figure 12

Molecular diagnosis. Nucleotides: 111 C, 411 G, 549 G, 567 G, 661 T

Biology. This species has been reared from three unidentified, different species of host feeding on two different host plants: a species of Geometridae feeding on *Ruellia inundata* (Acanthaceae) and another on *Solanum hayesii* (Solanaceae), and a species of Erebidae feeding on *Colubrina spinosa* (Rhamnaceae). Host caterpillars were collected in January and June.

Type material. Holotype ♀: DHJPAR0029297 (ASHYE704-09), Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, Pasmompa, GPS: 11.01926, -85.40997, 440 m elevation, Calixto Moraga coll., reared from Erebidae 04-SRNP-30170, host collected 12 January 2004, wasp eclosed 6 February 2004, (EMUS). Paratype: DHJPAR0040325 (ASHYE2461-11).

Etymology. *Zelomorpha mikeiviei* is named in honor of Mike Ivie of Montana State University, a master taxonomist in Coleoptera of who has massively contributed to the knowledge base of the inventory of Caribbean Coleoptera and ACG biodiversity inventory.

***Zelomorpha myricagaleae* Meierotto, sp. nov.**

<http://zoobank.org/72D356D0-7744-4C2A-96C5-653CC49588DE>

Figure 13

Molecular diagnosis. Nucleotides: 44 C, 55 A, 64 G, 98 C, 126 C, 135 G, 163 T, 168 G, 183–186 GGTA, 246 C, 258 G, 357–358 GG, 369 G, 381 C, 400–401 AA, 505 T, 519–520 CG, 525 G, 570 A, 603 G, 606 G

Biology. The single specimen of this species was reared from *Speocropia* Poole01 Noctuidae feeding on mature leaves of *Smilax spinosa* (Smilacaceae).

Notes. Known from a single specimen. Holotype is somewhat damaged, missing antennae.

Type material. Holotype ♀: DHJPAR0028033 (ASHYE270-08), Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, Quebrada Trigoal, GPS: 11.02681, -85.49547, 290 m elevation, Lucia Ríos coll., reared from *Speocropia* Poole01 08-SRNP-21458, host collected 11 June 2008, wasp eclosed 8 July 2008, (EMUS).

Etymology. *Zelomorpha myricagaleae* is named in honor of Myrica Gale Meierotto, cousin of SM and fierce competitor.

***Zelomorpha noahjaneae* Meierotto, sp. nov.**

<http://zoobank.org/30902D70-7645-4071-A153-0D045619A81D>

Figure 14

Molecular diagnosis. Nucleotides: 108 G, 123 G, 333 G, 519 A, 693 CG

Biology. Specimens of this species were reared from three species of Euteliidae feeding on young leaves of Anacardiaceae: *Paectes fuscescens* on introduced *Anacardium occidentale*, *Eutelia chrysotermina* on *Anacardium excelsum*, and *Paectes* Poole10 on *Mosquitoxylum jamaicense*. Caterpillars were collected in July and November.

Type material. Holotype ♀: DHJPAR0048720 (ACGBA2262-12), Costa Rica, Área de Conservación Guanacaste, Sector El Hacha, Estacion los Almendros, GPS: 11.03226, -85.52776, 290 m elevation, Elieth Cantillano coll., reared from *Paectes fuscescens* 11-SRNP-23262, host collected 15 November 2011, wasp eclosed 30 December 2011, (EMUS). Paratypes: DHJPAR0048723 (ACGBA2265-12), DHJPAR0048719 (ACGBA2261-12), DHJPAR0052678 (ASHYM2032-13), DHJPAR0028023 (ASHYE260-08), DHJPAR0028024 (ASHYE261-08).

Etymology. *Zelomorpha noahjaneae* is named in honor of Noah Jane Meierotto, cousin of SM and an aspiring scientist and possible future entomologist.

***Zelomorpha paulgoldsteini* Meierotto, sp. nov.**

<http://zoobank.org/016912DC-0078-4D19-8472-4DF6F5A9C4A2>

Figure 15

Molecular diagnosis. Nucleotides: 216 G, 327 G, 345–346 AA, 352–354 ACA, 517 C

Biology. This species has been reared from a relatively wide range of hosts in the families Erebidae and Noctuidae, but all hosts feed on leaves of ferns. Caterpillars of paratype specimens were collected in every month except March and April.

Type material. Holotype ♀: DHJPAR0040222 (ASHYE2389-11), Costa Rica, Área de Conservación Guanacaste, Sector Del Oro, Quebrada Serrano, GPS: 11.00025, -85.45614, 585 m elevation, Roster Moraga coll., reared from *Callopietria mexicana* 10-SRNP-21839, host collected 5 August 2010, wasp eclosed 29 August 2010, (EMUS). Paratypes: DHJPAR0044986 (ACGAZ207-11), DHJPAR0057443 (ACGBA5353-15), DHJPAR0057447 (ACGBA5357-15), DHJPAR0057458 (ACGBA5368-15), DHJPAR0057460 (ACGBA5370-15), DHJPAR0015539 (ASAG225-07), DHJPAR0009404 (ASBR671-06), DHJPAR0057649 (ASBR966-15), DHJPAR0030382 (ASHYB1121-09), DHJPAR0054469 (ASHYD3634-14), DHJPAR0054470 (ASHYD3635-14), DHJPAR0054485 (ASHYD3650-14), DHJPAR0036684 (ASHYE1595-09), DHJPAR0028032 (ASHYE269-08), DHJPAR0041152 (ASHYF1067-11), DHJPAR0041153 (ASHYF1068-11), DHJPAR0041159 (ASHYF1074-11), DHJPAR0042357 (ASHYH121-11), DHJPAR0042808



Figure 11. Lateral image of *Zelomorpha mariyavladimirovnae* holotype female.



Figure 12. Lateral image of *Zelomorpha mikeiviei* holotype female.

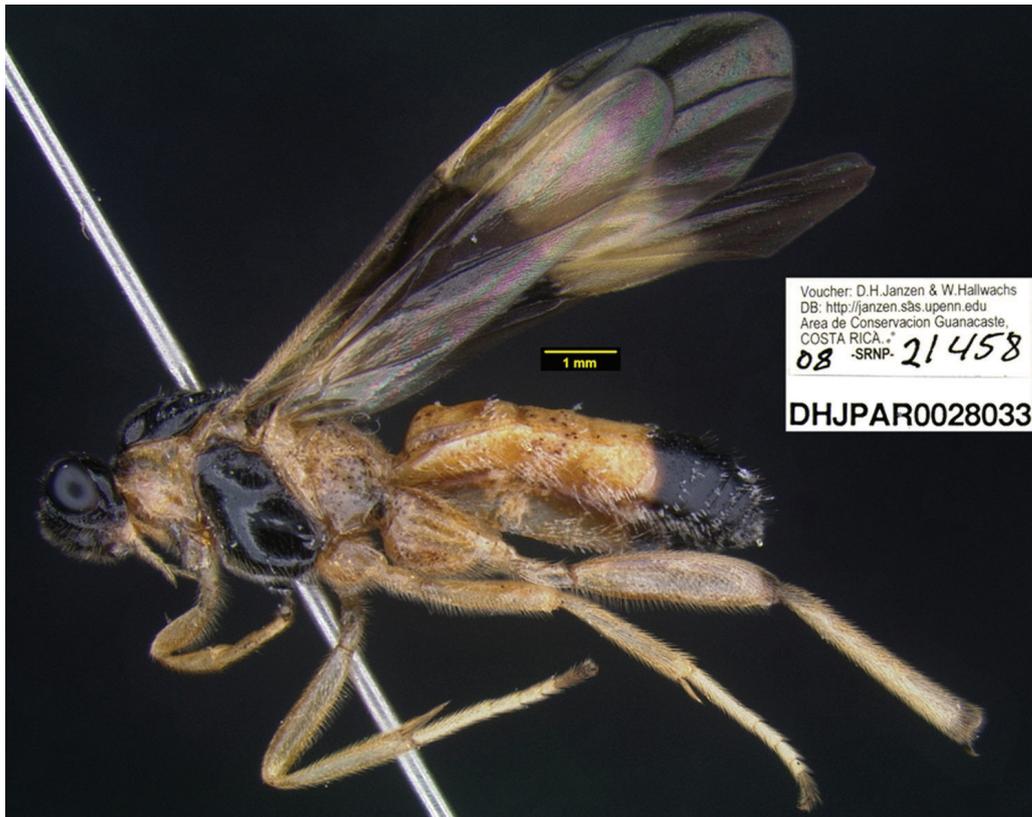


Figure 13. Lateral image of *Zelomorpha myricagaleae* holotype female.



Figure 14. Lateral image of *Zelomorpha noahjaneae* holotype female.



Figure 15. Lateral image of *Zelomorpha paulgoldsteini* holotype female.

Table 1. Host caterpillars and their food plants of *Zelomorpha paulgoldsteini*.

Host family	Host species	Food plant family	Food plant species
Erebidae	<i>Nicetas antonalis</i>	Cyatheaceae	<i>Cyathea multiflora</i>
	<i>Nicetas</i> Janzen02	Woodsiaceae	<i>Diplazium myriomerum</i>
	<i>Nicetas</i> Poole22	Dryopteridaceae	<i>Elaphoglossum doanense</i>
	<i>Rejectaria</i> Janzen02	Cyatheaceae	<i>Cyathea multiflora</i>
	<i>Rejectaria</i> Janzen02	Lomariopsidaceae	<i>Lomariopsis vestita</i>
	<i>Rejectaria</i> Janzen06	Cyatheaceae	<i>Alsophila firma</i>
	<i>Rejectaria</i> Poole11	Cyclanthaceae	<i>Cyclanthus bipartitus</i>
	<i>Rejectaria splendida</i>	Cyclanthaceae	<i>Asplundia utilis</i>
	<i>Rejectaria splendida</i>	Cyclanthaceae	<i>Carludovica costaricensis</i>
	<i>Rejectaria splendida</i>	Cyclanthaceae	<i>Asplundia utilis</i>
	<i>Nicetas</i> Poole21	Dryopteridaceae	<i>Didymochlaena truncatula</i>
Noctuidae	<i>Callopietria floridensis</i>	Blechnaceae	<i>Blechnum occidentale</i>
	<i>Callopietria floridensis</i>	Davalliaceae	<i>Nephrolepis biserrata</i>
	<i>Callopietria mexicana</i>	Dryopteridaceae	<i>Bolbitis portoricensis</i>
Erebidae	<i>Nicetas</i> Poole20	Dennstaedtiaceae	<i>Hypolepis repens</i>

(ASHYH566-11), DHJPAR0042810 (ASHYH568-11), DHJPAR0052697 (ASHYM2051-13), DHJPAR0016425 (ASTAP454-06), DHJPAR0016426 (ASTAP455-06).

Etymology. *Zelomorpha paulgoldsteini* is named in honor of Paul Goldstein of the USDA Systematic Entomology Laboratory at the Smithsonian Institution, in honor of his inordinate fondness for the fern-eating caterpillars parasitized by this wasp.

***Zelomorpha terryerwini* Meierotto, sp. nov.**

<http://zoobank.org/01931B54-7D54-4788-8BF5-A706D6104B3C>

Figure 16

Molecular diagnosis. Nucleotides: 66 G, 359 G, 492 C, 621 G

Biology. Hosts of type specimens were collected in January and May through November.

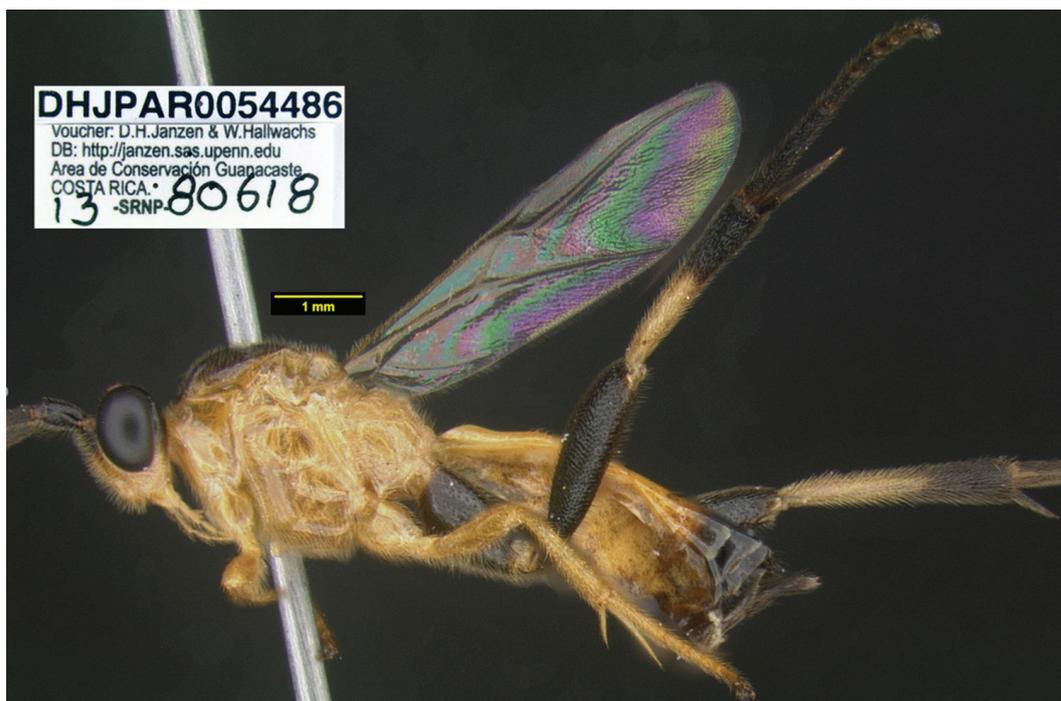


Figure 16. Lateral image of *Zelomorpha terryerwini* holotype female.

Table 2. Host caterpillars and their young leaf food plants, for *Zelomorpha terryerwini*.

Host family	Host species	Host plant family	Host plant species
Noctuidae	<i>Cropia cedica</i>	Cordiaceae	<i>Cordia alliodora</i>
	<i>Cropia cedica</i>	Cordiaceae	<i>Cordia panamensis</i>
	<i>Cropia connecta</i>	Cordiaceae	<i>Cordia alliodora</i>
	<i>Cropia europs</i>	Cordiaceae	<i>Cordia alliodora</i>
	<i>Cropia phila</i>	Cordiaceae	<i>Cordia panamensis</i>
	<i>Cropia rivulosa</i>	Cordiaceae	<i>Cordia alliodora</i>
	<i>Cropia rivulosa</i>	Cordiaceae	<i>Cordia panamensis</i>
	<i>Cropia rivulosa</i>	Cordiaceae	<i>Cordia bicolor</i>
	<i>Heterodelta nea</i>	Hypericaceae	<i>Vismia baccifera</i>
	<i>Nephelistis</i> Poole01	Asteraceae	<i>Lepidaploa tortuosa</i>
Nolidae	<i>Perigea agnonia</i>	Asteraceae	<i>Lepidaploa patens</i>
	<i>Iscadia</i> Poole02DHJ03	Hypericaceae	<i>Vismia baccifera</i>

Type material. Holotype ♀: DHJPAR0054486 (ASHYD3651-14), Costa Rica, Área de Conservación Guanacaste, Sector Rincon Rain Forest, Jacobo, GPS: 10.94076, -85.3177, 461 m elevation, Edwin Apu coll., reared from *Iscadia* Poole02DHJ03 13-SRNP-80618, host collected 13 November 2013, (EMUS). Paratypes: DHJPAR0009349 (ASBR616-06), DHJPAR0015554 (ASAG240-07), DHJPAR0022188 (ASTAT1326-07), DHJPAR0023284 (ASHYM036-08), DHJPAR0009420 (ASBR687-06), DHJPAR0009419 (ASBR686-06), DHJPAR0009422 (ASBR689-06), DHJPAR0009421 (ASBR688-06), DHJPAR0015555 (ASAG241-07), DHJPAR0021145 (ASBC957-07), DHJPAR0028156 (ASHYE393-08), DHJPAR0057947 (MHMYK10647-15), DHJPAR0009382 (ASBR649-06), DHJPAR0009383 (ASBR650-06), DHJPAR0009384 (ASBR651-06), DHJPAR0021203 (ASBC1015-07), DHJPAR0053595 (ASHYM2949-13), DHJPAR0054480 (ASHYD3645-14), DHJPAR0009423 (ASBR690-06), DHJPAR0041605

(ASHYF1511-11), DHJPAR0040343 (ASHYE2479-11), DHJPAR0041606 (ASHYF1512-11), DHJPAR0041183 (ASHYF1089-11), DHJPAR0049658 (ASHYB2452-12).

Etymology. *Zelomorpha terryerwini* is named in honor of Terry Erwin of the Smithsonian Institution, a master taxonomist of Coleoptera who has massively contributed to the inventory of Latin American Coleoptera and pesticide-fogged more trees than any other entomologist.

***Zelomorpha willsflowersi* Meierotto, sp. nov.**

<http://zoobank.org/63D1264F-E390-4174-809E-ACE25BBCADBC>

Figure 17

Molecular diagnosis. Nucleotides: 207 G, 303 G, 345 G, 360 G, 398 G, 579 G, 661–663 GTG, 678 G

Biology. This species was reared from three species of Erebidae feeding on young leaves of Fabaceae: *Coenipeta bibitrix* on *Enterolobium cyclocarpum* and *Samanea saman*,

Goniohelia Poole02 on *Senegalia tenuifolia*, and *Tyrissa acygonia* on *Senegalia tenuifolia*. Host caterpillars were collected in May, June, and July.

Type material. Holotype ♀: DHJPAR0009415 (ASBR682-06), Costa Rica, Área de Conservación Guanacaste, Sector Santa Elena, Entrada Santa Elena, GPS: 10.9257, -85.608, 270 m elevation, Elieth Cantillano coll., reared from *Coenipeta bibitrix* 05-SRNP-21918, host collected 5 June 2005, wasp eclosed 22 June 2005, (EMUS). Paratypes: DHJPAR0021205 (ASBC1017-07), DHJPAR0010194 (ASBC475-06), DHJPAR0021146 (ASBC958-07), DHJPAR0009412 (ASBR679-06), DHJPAR0009413 (ASBR680-06), DHJPAR0009414 (ASBR681-06), DHJPAR0009418 (ASBR685-06), DHJPAR0057944 (MHMYK10644-15).

Etymology. *Zelomorpha willsflowersi* is named in honor of Wills Flowers of Florida State University, a master taxonomist of Coleoptera who has massively contributed to the inventory of Costa Rican Chrysomelidae.

Hemichoma Enderlein, 1920

Type species. *Hemichoma fenestratum* Enderlein, 1920.

Diagnosis. *Hemichoma* shares diagnostic morphological characters with *Zelomorpha* except: notauli absent, mesoscutum lacking distinct lobes; gena greatly produced posteroventrally.

Biology. Members of *Hemichoma* are, like *Zelomorpha*, koinobiont endoparasitoids of late instar lepidop-

teran larvae. The solitary wasp larva emerges from the prepupal larva after it has spun its cocoon, and spins its own cocoon inside the host cocoon next to the cadaver.

Distribution. Restricted to the New World, known from Mexico to Argentina.

Species richness. Including the three species described here, there are eight described species of *Hemichoma*.

Hemichoma donwhiteheadi Meierotto, sp. nov.

<http://zoobank.org/E9A8F205-0BB9-426E-A478-74A176B59585>

Figure 18

Molecular diagnosis. Nucleotides: 72 G, 78 G, 90 G, 114 G, 162 T, 168 A, 204 C, 207 G, 216 G, 225 G, 306 G, 318 T, 322 T, 346 G, 357 T, 409–410 GC, 414 G, 492 A, 516 G, 564 A, 585 GC

Biology. All specimens of this species were reared from *Pelochyta misera* (Erebidae: Arctiinae). Food plants include *Heliocarpus appendiculatus* (Malvaceae), the introduced species *Psidium guajava* (Myrtaceae), *Inga oerstediana*, and *Erythrina costaricensis* (Fabaceae). Host caterpillars were collected in June, August, November, and October.

Notes. This species has a sexually dimorphic color pattern: females have bicolored wings and a mostly orange mesosoma, while males have infusate wings and a black mesosoma.

Type material. Holotype ♀: DHJPAR0016918 (ASBR891-07), Costa Rica, Área de Conservación Guanacaste, Sector San Cristobal, Sendero Huerta, GPS: 10.9305,

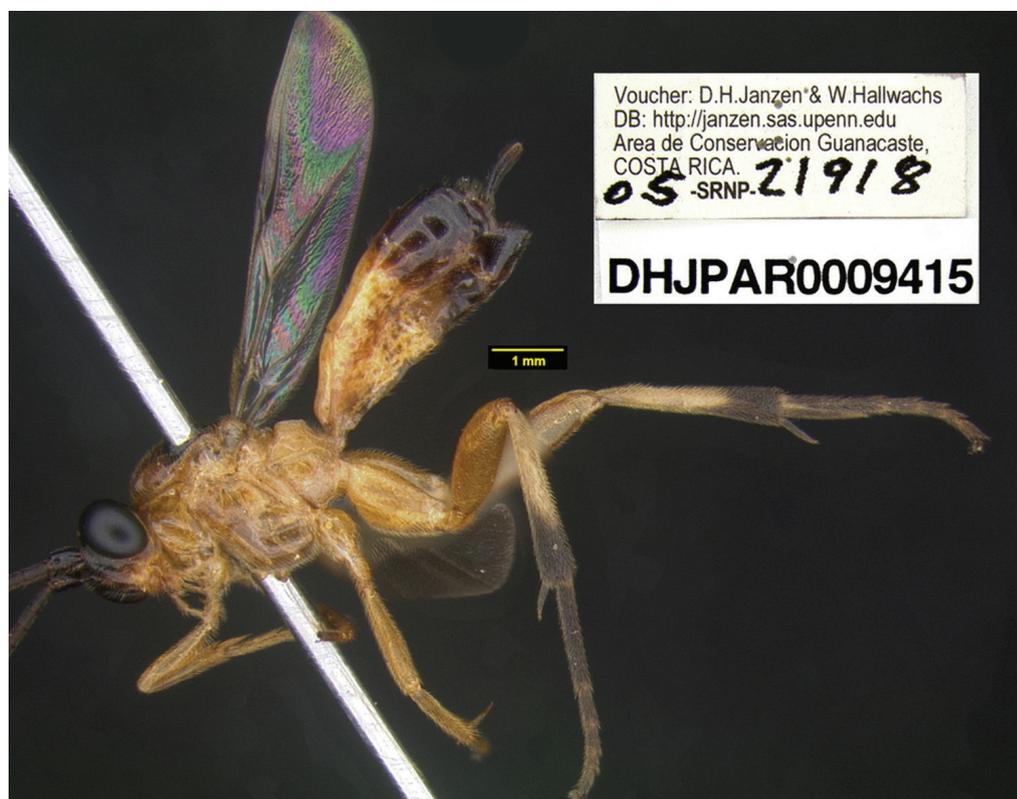


Figure 17. Lateral image of *Zelomorpha willsflowersi* holotype female.



Figure 18. Lateral image of *Hemichoma donwhiteheadi* holotype female.

-85.37223, 527 m elevation, Elda Araya coll., reared from *Pelochyta misera* 06-SRNP-9643, host collected 27 November 2006, (EMUS). Paratypes: DHJPAR0021147 (ASBC959-07), DHJPAR0016917 (ASBR890-07), DHJPAR0029296 (ASHYE703-09), DHJPAR0022191 (ASTAT1329-07).

Etymology. *Hemichoma donwhiteheadi* is named in honor of Don Whitehead (RIP) of the Smithsonian Institution, a master weevil taxonomist who helped greatly with the taxonomy of ACG Curculionidae.

***Hemichoma frankhovorei* Meierotto, sp. nov.**

<http://zoobank.org/03ECEB9C-16EC-4BBF-93F1-6BAAE30FEDC3>

Figure 19

Molecular diagnosis. Nucleotides: 117 G, 228 C, 243 A, 357 A, 414 A, 477 T, 513 T, 570 A, 615 G, 645 T, 60 A, 663 T

Biology. Multiple species of *Halysidota* (Erebidae; Arctiinae) are the hosts for this wasp: *H. orientalis*, *H. pectenella*, *H. schausi*, and *H. underwoodi* feeding on mature leaves of *Trema micrantha* (Cannabaceae), *Bernardia nicaraguensis* (Euphorbiaceae), and *Acalypha macrostachya* (Euphorbiaceae). Host caterpillars of type specimens were collected between the months of September and December.

Type material. Holotype ♀: DHJPAR0054503 (ASHYD3668-14), Costa Rica, Área de Conservación Guanacaste, Sector Pitilla, Medrano, GPS: 11.01602, -85.38053, 380 m elevation, Ricardo Calero coll., reared from *Halysidota schausi* 13-SRNP-71924, host collected 2 December 2013, wasp eclosed 12 January 2014,

(EMUS). Paratypes: DHJPAR0015563 (ASAG249-07), DHJPAR0030385 (ASHYB1124-09), DHJPAR0030386 (ASHYB1125-09), DHJPAR0037925 (ASHYC4670-10), DHJPAR0037926 (ASHYC4671-10), DHJPAR0054501 (ASHYD3666-14), DHJPAR0054502 (ASHYD3667-14), DHJPAR0036689 (ASHYE1600-09), DHJPAR0036708 (ASHYE1619-09), DHJPAR0036713 (ASHYE1624-09), DHJPAR0028242 (ASHYF004-09), DHJPAR0028243 (ASHYF005-09), DHJPAR0028244 (ASHYF006-09), DHJPAR0028247 (ASHYF009-09), DHJPAR0028248 (ASHYF010-09), DHJPAR0028249 (ASHYF011-09), DHJPAR0028252 (ASHYF014-09), DHJPAR0028254 (ASHYF016-09), DHJPAR0028258 (ASHYF020-09), DHJPAR0028260 (ASHYF022-09), DHJPAR0028263 (ASHYF025-09), DHJPAR0028264 (ASHYF026-09), DHJPAR0041156 (ASHYF1071-11), DHJPAR0041160 (ASHYF1075-11), DHJPAR0041161 (ASHYF1076-11), DHJPAR0029304 (ASHYE711-09).

Etymology. *Hemichoma frankhovorei* is named in honor of Frank Hovore (RIP) of California, a master cerambycid taxonomist who helped greatly with the taxonomic inventory of Costa Rican Cerambycidae.

***Hemichoma johnkingsolveri* Meierotto, sp. nov.**

<http://zoobank.org/9E2998AB-2431-473F-B4B7-835243A6240E>

Figure 20

Molecular diagnosis. Nucleotides: 77 C, 84 G, 108 T, 111 A, 122 C, 141 T, 297 T, 327 G, 357 G, 414 T, 465 A, 579 G, 582 G, 591 G, 648 G, 678 GC

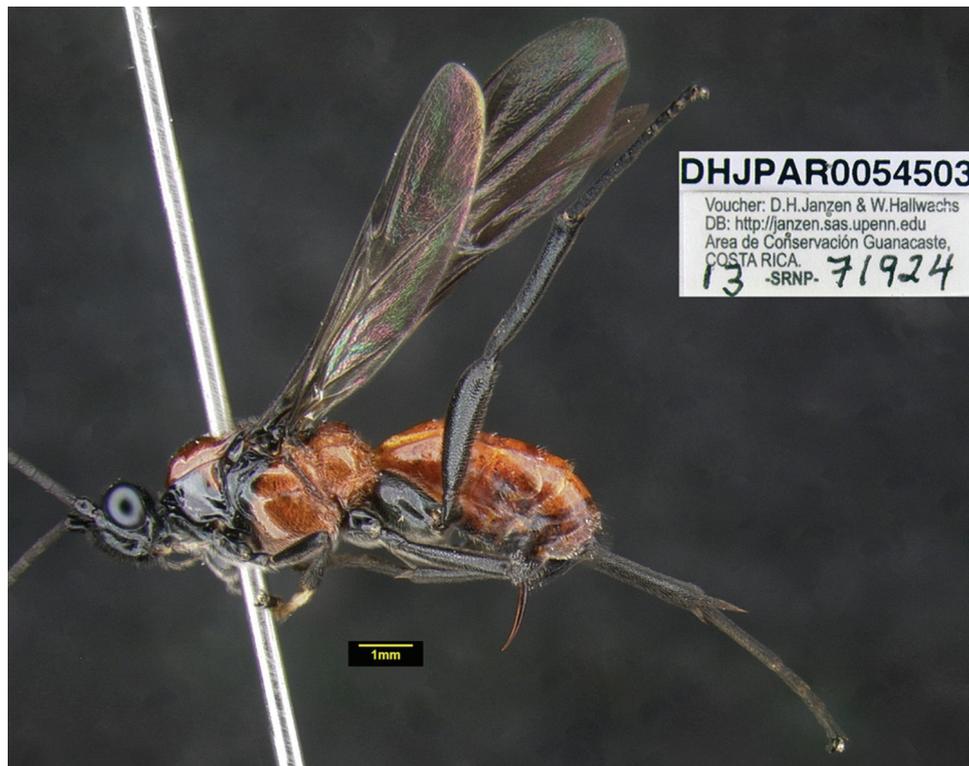


Figure 19. Lateral image of *Hemichoma frankhovorei* holotype female.

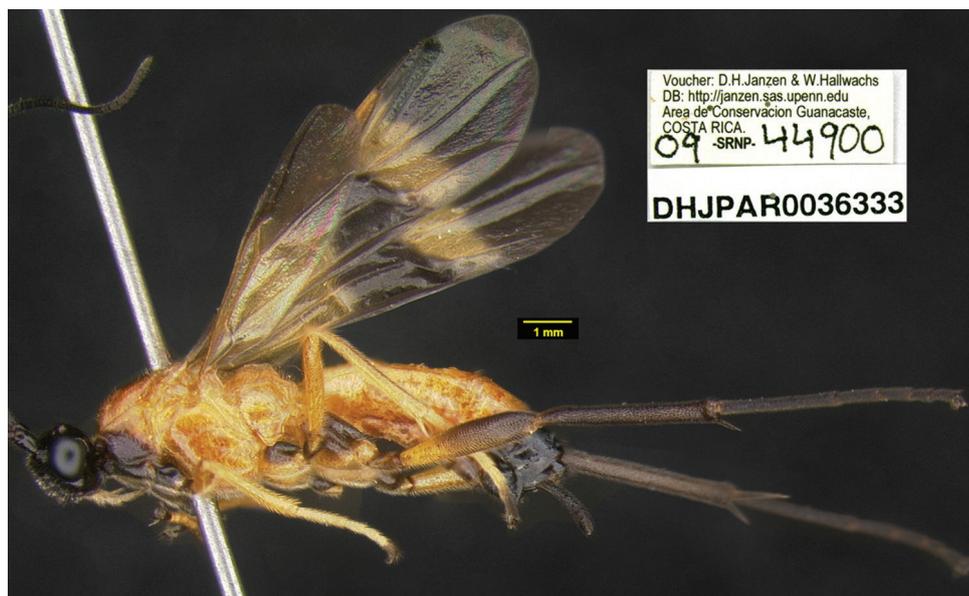


Figure 20. Lateral image of *Hemichoma johnkingsolveri* holotype female.

Biology. This species has been reared from *Carathis septentrionalis* (Erebidae) feeding on mature leaves of *Ocotea cernua* (Lauraceae) and *Pachydota saduca* (Erebidae) feeding on several species of *Ocotea* and *Nectandra* (Lauraceae). Host caterpillars of type specimens were collected throughout the year, except between March and May.

Type material. Holotype ♀: DHJPAR0036333 (ASHYD1524-09), Costa Rica, Área de Conservación

Guanacaste, Sector Rincon Rain Forest, Estacion Llanura, GPS: 10.93332, -85.25331, 135 m elevation, Keiner Aragon coll., reared from *Pachydota saduca* 09-SRNP-44900, host collected 4 July 2009, wasp eclosed 8 September 2009, (EMUS). Paratypes: DHJPAR0022195 (ASTAT1333-07), DHJPAR0057457 (ACGBA5367-15), DHJPAR0046730 (ACGBA903-12), DHJPAR0046731 (ACGBA904-12), DHJPAR0046732 (ACGBA905-12),

DHJP0015558 (ASAG244-07), DHJP0015559 (ASAG245-07), DHJP0015560 (ASAG246-07), DHJP0057646 (ASBR963-15), DHJP0038613 (ASHYD2186-10), DHJP0041168 (ASHYF1083-11), DHJP0042358 (ASHYH122-11), DHJP0042359 (ASHYH123-11), DHJP0057945 (MHMYK10645-15), DHJP0058547 (MHMYN8147-16), DHJP0058548 (MHMYN8148-16), DHJP0060427 (ACGBA6848-17), DHJP0060428 (ACGBA6849-17), DHJP0060429 (ACGBA6850-17).

Etymology. *Hemichoma johnkingsolveri* is named in honor of John Kingsolver (RIP) of the USDA Systematic Entomology Laboratory at the Smithsonian Institution, a master taxonomist of Bruchinae (Chrysomelidae) and long-time supporter of ACG biodiversity inventory.

Discussion

Ichneumonoid taxonomists have remained in a taxonomic paradigm that was created for a well-known and largely extra-tropical fauna and flora. For example, there is great utility in a morphological key to the 30 species of butterflies that occur in a suburban backyard in eastern North America; however a key to the 100+ species of 1–4 cm long amber-colored nocturnal highly host-specific species of *Enicospilus* parasitic wasps (Ichneumonidae: Ophioninae) that occur within 3 km of the Administration Area of Área de Conservación Guanacaste is much less useful because, a) they mostly look the same, b) 90% are undescribed, and c) knowing the species name would not give you much additional information, i.e., life history, geographic range, or phenology. Now there is an alternative to morphological keys and complex prose descriptions (Hebert et al. 2003; Ratnasingham and Hebert 2013). The effort and need to create traditional descriptions can be reserved for situations where there is demand for them or until a fairly complete dataset is believed to have been accumulated. However, a species still needs to have a unique identifier, be it a database code or a formal scientific name, so that it can be compared with other species and their collateral.

With online public databases such as BOLD accumulating hundreds of thousands of specimen and species based barcodes (Hebert et al. 2003; <http://ibol.org>), DNA sequences from holotype specimens can be instantly accessed and compared among themselves and with other specimens. If new specimens are delivered with their COI barcodes, taxonomists can rapidly identify new or previously described species. In combination with high quality images and other digitized specimen attributes, online molecular data can enable much revisionary work without the need for physically visiting museums or shipping loaned specimen. Physical collections remain essential as repositories for types, voucher specimens, specimens for further study, and vouchers for the barcodes themselves.

We recognize that DNA barcodes may fail to delimit all species, or all specimens of all species, just as there are

no morphological characters capable of unfailingly separating species. There are drawbacks to using a portion of the single gene COI as a barcode, including potential confusion with nuclear mitochondrial paralogs, *Wolbachia* mediated introgression, hybridization, and incomplete lineage sorting (Rubinoff et al. 2006; Trewick 2008; Calvignac et al. 2011; Klopstein et al. 2016); however, in our opinion, these are trivial problems compared to the efficacy of the approach, and they apply to any other standardized single gene. Most can be overcome by laboratory protocols for recognizing the barcodes alone. Pragmatically, as revealed by the between-species barcode differences for unarguable different species by their morphology and other easy traits, barcodes are easily as reliable for discriminating species as are other traits long used for this purpose and they are superior for discriminating members of tropical complexes of sibling species (e.g., Hebert et al. 2004; Smith et al. 2006, 2008; Burns et al. 2007, 2008, 2010; Bertrand et al. 2014; Janzen et al. 2017).

We demonstrate a novel approach to species descriptions for hyperdiverse, underdescribed taxa, such as those within Ichneumonoidea. The descriptions consist of a high-quality lateral habitus photograph, latitude and longitude coordinates, and the diagnostic characteristics of the COI barcode region, along with details of the holotype as required by the International Code of Zoological Nomenclature (ICZN 1999). The purpose of the lateral habitus images is to allow others who have identified specimens with DNA barcodes to check the plausibility of their determination while they are not meant to assure the species-level identification of specimens based on the images alone. Much more could be included in the species treatments, e.g., extensive images of all body parts, genitalic images (if informative), or SEM images of microsculpture. However, these all take time that is better spent on documenting the tens of thousands of undescribed species. Furthermore, these details will be only poorly informative with respect to the hundreds to thousands of further confamilials that are yet to be discovered in hyperdiverse tropical countries. To effectively solve the problem of the “taxonomic impediment” within Ichneumonoidea, thousands of new species will need to be described annually by many taxonomists. Even with the minimalist approach suggested here, this is a daunting challenge for the future.

Acknowledgments

We gratefully acknowledge the unflagging support of the team of ACG parataxonomists (Janzen et al. 2009; Janzen and Hallwachs 2011) who found and reared the specimens used in this study, and the team of biodiversity managers who protect and manage the ACG forests that are home to these wasps and their caterpillar hosts. The study has been supported by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from

the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, Permian Global, individual donors, and University of Pennsylvania (DHJ and WH). This study has been supported by the Government of Canada through its ongoing support to the Canadian National Collection, and by grants from Genome Canada and Ontario Genomics to PDNH in support of the Centre for Biodiversity Genomics at the University of Guelph, and to the Natural Sciences and Engineering Research Council of Canada.

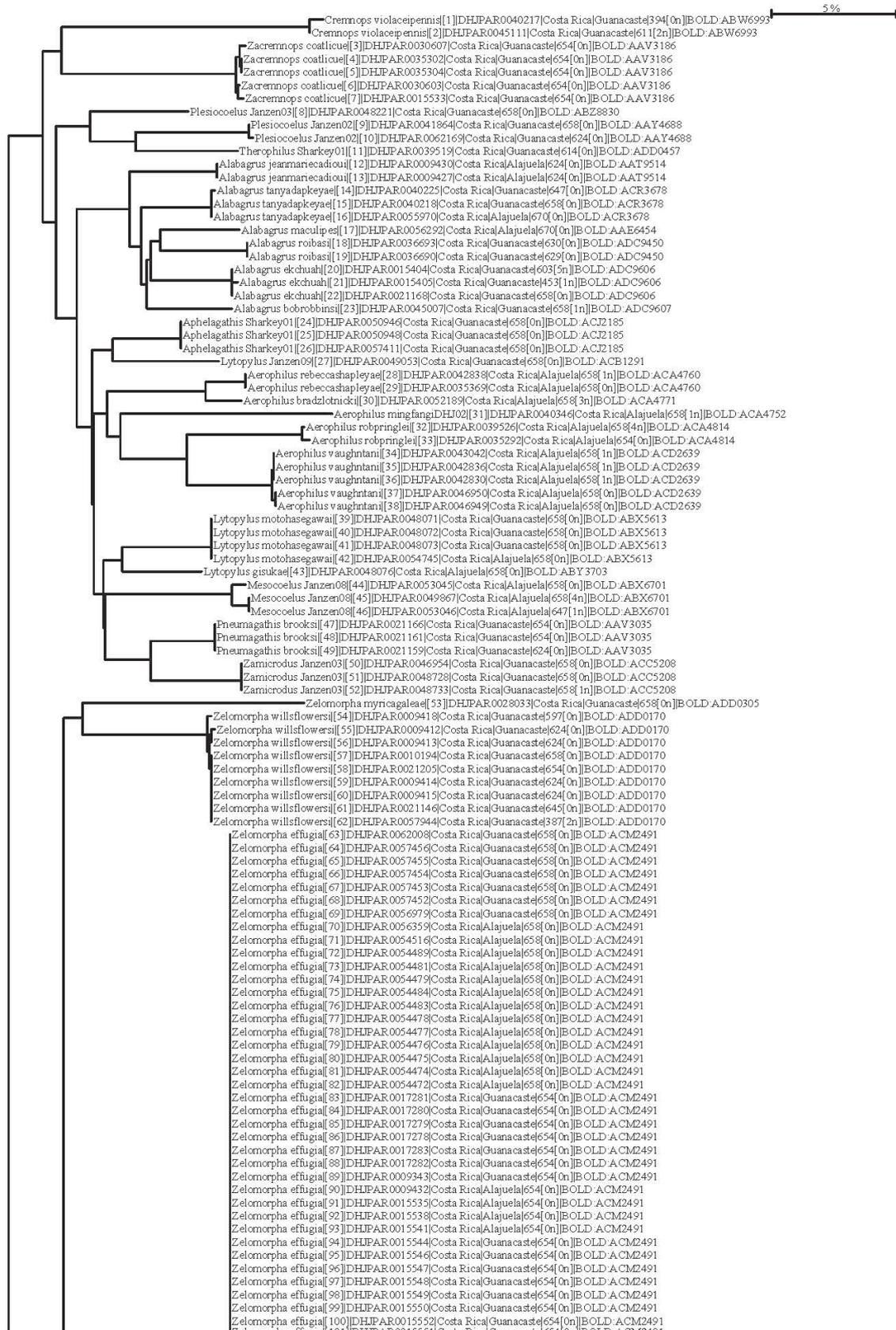
References

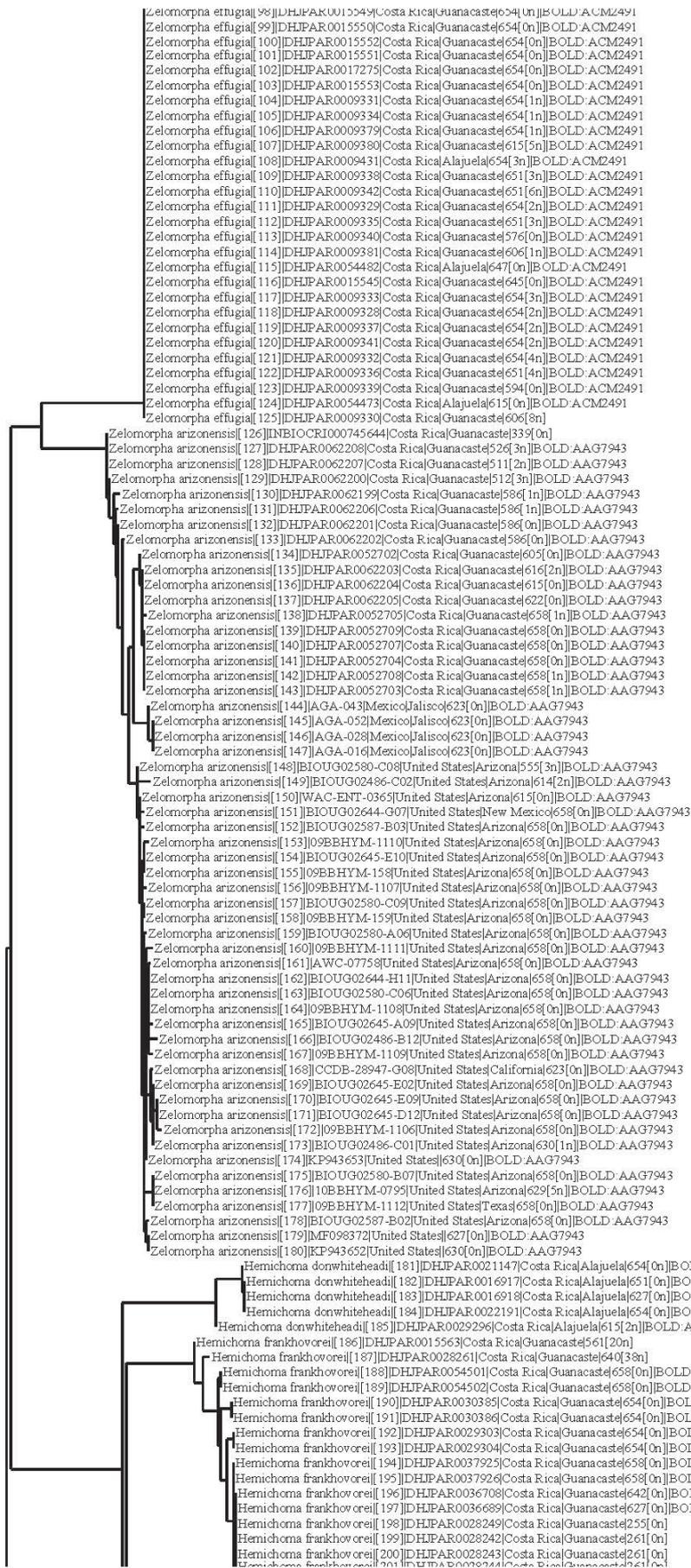
- Achterberg C van, Sharkey MJ, Chapman EG (2014) Revision of the genus *Euagathis* Szépligeti (Hymenoptera, Braconidae, Agathidinae) from Thailand, with description of three new species. *Journal of Hymenoptera Research* 36: 1–25. <https://doi.org/10.3897/jhr.36.5658>
- Ashmead WH (1900) Classification of the ichneumon flies, or the superfamily Ichneumonoidea. *Proceedings of the United States National Museum* 23: 1–220. <https://doi.org/10.5479/si.00963801.23-1206.1>
- Bertrand C, Janzen DH, Hallwachs W, Burns JM, Gibson JF, Shokrala S, Hajibabaei M (2014) Mitochondrial and nuclear phylogenetic analysis with Sanger and next-generation sequencing shows that, in Area de Conservación Guanacaste, northwestern Costa Rica, the skipper butterfly named *Urbanus belli* (family Hesperidae) comprises three morphologically cryptic species. *BMC Evolutionary Biology* 14: 153. <https://doi.org/10.1186/1471-2148-14-153>
- Burns JM, Janzen DH, Hajibabaei M, Hallwachs W, Hebert PDN (2007) DNA barcodes of closely related (but morphologically and ecologically distinct) species of skipper butterflies (Hesperidae) can differ by only one to three nucleotides. *Journal of the Lepidopterists Society* 61: 138–153.
- Burns JM, Janzen DH, Hajibabaei M, Hallwachs W, Hebert PDN (2008) DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. *Proceedings of the National Academy of Sciences* 105: 6350–6355. <https://doi.org/10.1073/pnas.0712181105>
- Calvignac S, Konecny L, Malard F, Douady CJ (2011) Preventing the pollution of mitochondrial datasets with nuclear mitochondrial paralogs (numts). *Mitochondrion* 11(2): 246–254. <https://doi.org/10.1016/j.mito.2010.10.004>
- Condon MA, Scheffer SJ, Lewis ML, Wharton R, Adams DC, Forbes AA (2014) Lethal Interactions Between Parasites and Prey Increase Niche Diversity in a Tropical Community. *Science* 343(6176): 1240–1244. <https://doi.org/10.1126/science.1245007>
- Cook LG, Edwards RD, Crisp MD, Hardy NB (2010) Need morphology always be required for new species descriptions? *Invertebrate Systematics* 24(3): 322–326. <https://doi.org/10.1071/IS10011>
- Dolphin K, Quicke DL (2001) Estimating the global species richness of an incompletely described taxon: an example using parasitoid wasps (Hymenoptera: Braconidae). *Biological Journal of the Linnean Society* 73(3): 279–286. <https://doi.org/10.1111/j.1095-8312.2001.tb01363.x>
- Fernandez-Triana JL, Whitfield JB, Rodriguez JJ, Smith MA, Janzen DH, Hallwachs W, Hajibabaei M, Burns JM, Solis MA, Brown J, Cardinal S, Goulet H, Hebert PDN (2014) Review of *Apanteles* sensu strictu (Hymenoptera, Braconidae, Microgastrinae) from Area de Conservación Guanacaste, northwestern Costa Rica, with keys to all described species from Mesoamerica. *ZooKeys* 383: 1–565. <https://doi.org/10.3897/zookeys.383.6418>
- Ghahari H, Yu D, Achterberg C van (2006) Bibliography of the family Braconidae (Hymenoptera: Ichneumonoidea) (1964–2003). *NNM Technical Bulletin* 8: 1–293.
- Godfray H CJ (2007) Linnaeus in the information age. *Nature* 446(7133): 259–260. <https://doi.org/10.1038/446259a>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hanson P, Janzen D, Knapp S, Scoble M, Wahl D, West-Eberhard MJ (2009) Obituary. Ian Gauld FLS (1947–2009). Master taxonomist and morphologist. *The Linnean, Newsletter and Proceedings of the Linnean Society of London* 25(2): 46–47.
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B, Biological Sciences* 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astrartes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America* 101(41): 14812–14817. <https://doi.org/10.1073/pnas.0406166101>
- ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, 306 pp.
- Ivanova NV, Dewaard JR, Hebert PD (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Resources* 6(4): 998–1002. <https://doi.org/10.1111/j.1471-8286.2006.01428.x>
- Ivanova NV, Grainger CM (2007) CCDB protocols, COI amplification. [Online] http://ccdb.ca/docs/CCDB_Amplification.pdf
- Ivanova NV, Grainger CM (2007a) CCDB protocols, COI amplification. http://www.dnabarcoding.ca/CCDB_DOCS/CCDB_Amplification.pdf [accessed 15 July 2010]
- Janzen DH (1981) The peak in North American ichneumonid species richness lies between 38 and 42 degrees North latitude. *Ecology* 62: 532–537. <https://doi.org/10.2307/1937717>
- Janzen DH, Burns JM, Cong Q, Hallwachs W, Dapkey T, Manjunath R, Hajibabaei M, Hebert PDN, Grishin NV (2017) Nuclear genomes distinguish cryptic species suggested by their DNA barcodes and ecology. *Proceedings of the National Academy of Sciences of the United States of America* 114(31): 8313–8318. <https://doi.org/10.1073/pnas.1621504114>
- Janzen DH, Hallwachs W, Blandin P, Burns JM, Cadiou J, Chacon IS, Dapkey T, Deans AR, Epstein ME, Espinoza B, Franclemont JG, Haber WA, Ibañaei MH, Hall JP, Hebert PDN, Gauld ID, Harvey DJ, Hausmann A, Kitching IJ, Lafontaine D, Landry J-F, Lemaire C, Miller JE, Miller JS, Miller L, Miller SE, Montero J, Munroe E, Green SR, Ratnasingham S, Rawlins JE, Robbins RK, Rodriguez JJ, Rougerie R, Sharkey MJ, Smith MA, Solis MA, Sullivan JB, Thiaucourt P, Wahl DB, Weller SJ, Whitfield JB, Willmott KR, Wood DM, Woodley NE, Wilson JJ (2009) Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Molecular Ecology Resources* 9 (Supplement 1): 1–26. <https://doi.org/10.1111/j.1755-0998.2009.02628.x>

- Janzen DH, Hallwachs W (2011) Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. *PLoS ONE* 6(8): e18123. <https://doi.org/10.1371/journal.pone.0018123>
- Janzen DH, Hallwachs W (2016) DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservación Guanacaste, northwestern Costa Rica. *Genome* 59: 641–660. <https://doi.org/10.1139/gen-2016-0005>
- Janzen DH, Burns JM, Cong Q, Hallwachs W, Dapkey T, Manjunath R, Hajibabaei M, Hebert PDN, Grishin NV (2017). Nuclear genomes distinguish cryptic species suggested by their DNA barcodes and ecology. *Proceedings of the National Academy of Sciences* 114(31): 8313–8318. <https://doi.org/10.1073/pnas.1621504114>
- Jörger KM, Schrödl M (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology* 10(1): 59. <https://doi.org/10.1186/1742-9994-10-59>
- Kang I, Chapman EG, Janzen DJ, Hallwachs W, Solis MA, Sharkey MJ (2017) Revision of the species of *Lytopylus* from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Braconidae, Agathidinae). *ZooKeys* 721: 93–158. <https://doi.org/10.3897/zookeys.721.20287>
- Klopfstein S, Kropf C, Baur H (2016) *Wolbachia* endosymbionts distort DNA barcoding in the parasitoid wasp genus *Diplazon* (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* 177: 541–557. <https://doi.org/10.1111/zoj.12380>
- LaSalle J, Gauld ID (Eds) (1993) *Hymenoptera and Biodiversity*. CAB International, Wallingford, 368 pp.
- Pante E, Schoelink C, Puillandre N (2014) From integrative taxonomy to species description: one step beyond. *Systematic Biology* 64(1): 152–160. <https://doi.org/10.1093/sysbio/syu083>
- Quicke DL (2012) We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology. *PLoS ONE* 7(2): e32101. <https://doi.org/10.1371/journal.pone.0032101>
- Ratnasingham S, Hebert PD (2013) A DNA-based registry for all animal species: The Barcode Index Number (BIN) System. *PloS ONE* 8(7): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Rodriguez JJ, Fernández-Triana JL, Smith MA, Janzen DH, Hallwachs W, Erwin TL, Whitfield JB (2013) Extrapolations from field studies and known faunas converge on dramatically increased estimates of global microgastrine parasitoid wasp species richness (Hymenoptera: Braconidae). *Insect Conservation and Diversity* 6(4): 530–536. <https://doi.org/10.1111/icad.12003>
- Rubinoff D, Cameron S, Will K (2006) A genomic perspective on the shortcomings of mitochondrial DNA for “barcoding” identification. *Journal of Heredity* 97(6): 581–594. <https://doi.org/10.1093/jhered/esl036>
- Sharkey MJ (1997) Subfamily Agathidinae. In: Wharton R, Sharkey MJ, Marsh PM (Eds) *Manual of the New World genera of the family Braconidae (Hymenoptera)*. Special publication of the International Society of Hymenopterists 1. The International Society of Hymenopterists, Washington, DC, 68–83.
- Sharkey MJ, Chapman EG (2016) Revision of *Aerophilus* Szépligeti (Hymenoptera, Braconidae, Agathidinae) from eastern North America, with a key to the Nearctic species. *Contributions in Science* 524: 51–110.
- Sharkey MJ, Chapman EG (2017) Phylogeny of the Agathidinae (Hymenoptera: Braconidae) with a revised tribal classification and the description of a new genus. *Proceedings of the Entomological Society of Washington* 119: 823–842. <https://doi.org/10.4289/0013-8797.119.SpecialIssue.823>
- Sharkey MJ, Chapman EG (2018) Revision of *Zosteragathis* Sharkey of Thailand (Hymenoptera, Braconidae, Agathidinae, Agathidini). *Deutsche Entomologische Zeitschrift* 65(2): 225–253. <https://doi.org/10.3897/dez.65.25772>
- Sharkey MJ, Chapman EG, Janzen DH, Hallwachs W, Smith MA (2015) Revision of *Aphelagathis* (Hymenoptera, Braconidae, Agathidinae, Agathidini). *Zootaxa* 4000(1): 73–89. <https://doi.org/10.11646/zootaxa.4000.1.3>
- Sharkey MJ, Laurenne NM, Sharanowski B, Quicke DLJ, Murray D (2006) Revision of the Agathidinae (Hymenoptera: Braconidae) with comparisons of static and dynamic alignments. *Cladistics* 22: 546–567. <https://doi.org/10.1111/j.1096-0031.2006.00121.x>
- Sharkey MJ, Meierotto S, Chapman EG, Janzen DJ, Hallwachs W, Dapkey T, Solis MA (2018) *Alabagrus* Enderlein (Hymenoptera, Braconidae, Agathidinae) species of Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. *Contributions in Science* 526: 31–180. <https://doi.org/10.3897/zookeys.130.1569>
- Smith MA, Woodley NE, Janzen DH, Hallwachs W, Hebert PDN. (2006) DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). *Proceedings of the National Academy of Sciences* 103: 3657–3662. <https://doi.org/10.1073/pnas.0511318103>
- Smith MA, Rodriguez JJ, Whitfield JB, Deans AR, Janzen DH, Hallwachs W, Hebert PDN (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proceedings of the National Academy of Sciences of the United States of America* 105(34): 12359–12364. <https://doi.org/10.1073/pnas.0805319105>
- Trewick SA (2008) DNA Barcoding is not enough: mismatch of taxonomy and genealogy in New Zealand grasshoppers (Orthoptera: Acrididae). *Cladistics* 24(2): 240–254. <https://doi.org/10.1111/j.1096-0031.2007.00174.x>
- Tucker EM, Chapman EG, Sharkey MJ (2015) A revision of the New World species of *Cremnops* Förster (Hymenoptera: Braconidae: Agathidinae). *Zootaxa* 3916(1): 1–83. <https://doi.org/10.11646/zootaxa.3916.1.1>
- Will KW, Mishler BD, Wheeler QD (2005) The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology* 54(5): 844–851. <https://doi.org/10.1080/10635150500354878>
- Yu DSK, van Achterberg C, Horstmann K (2016) *Taxapad*, Ichneumonoidea. Vancouver. <http://www.taxapad.com>

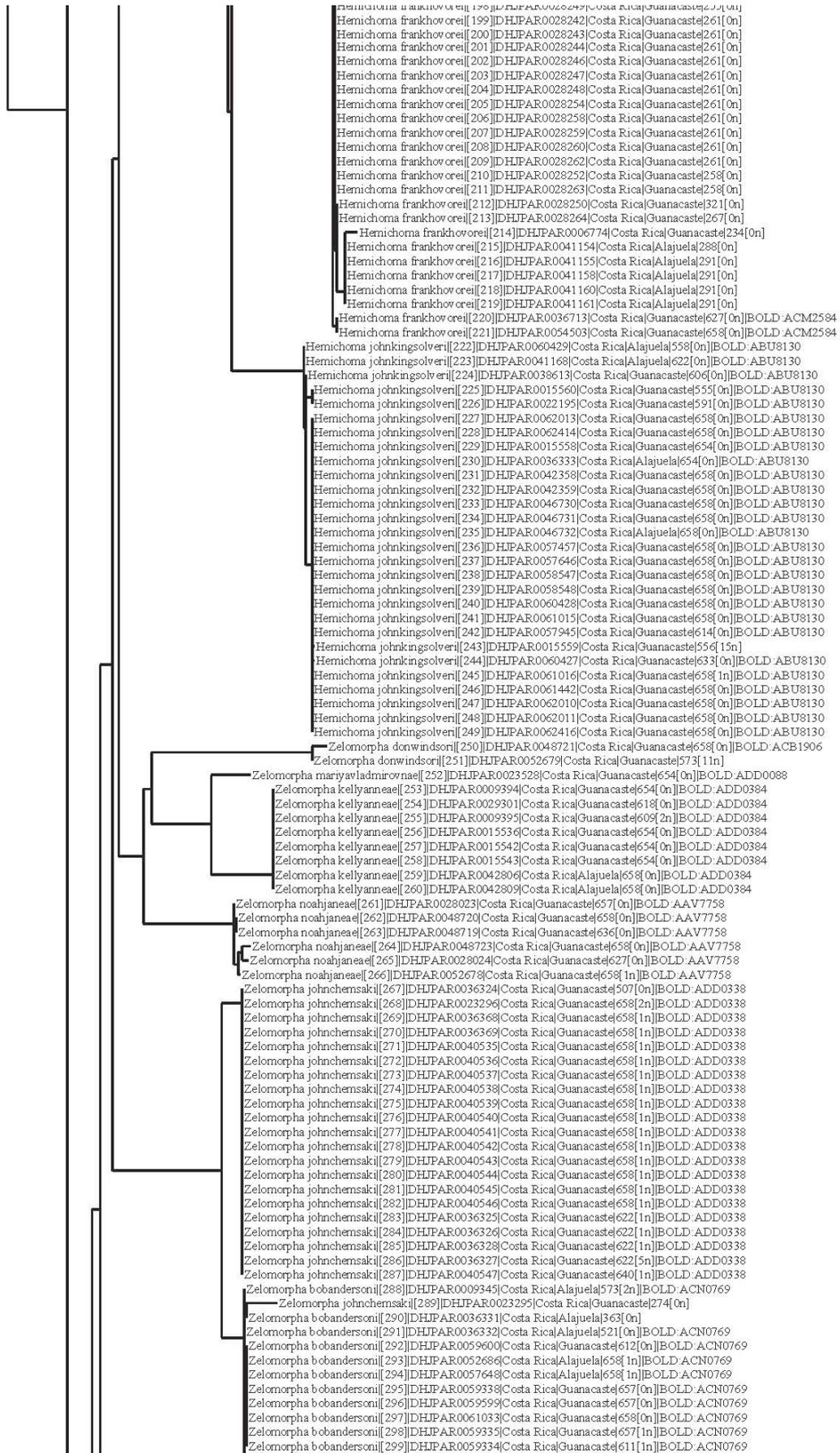
Appendix 1

Neighbor joining (NJ) tree of *Zelomorpha* and *Hemichoma*. The distance model employed was the Kimura 2 parameter.

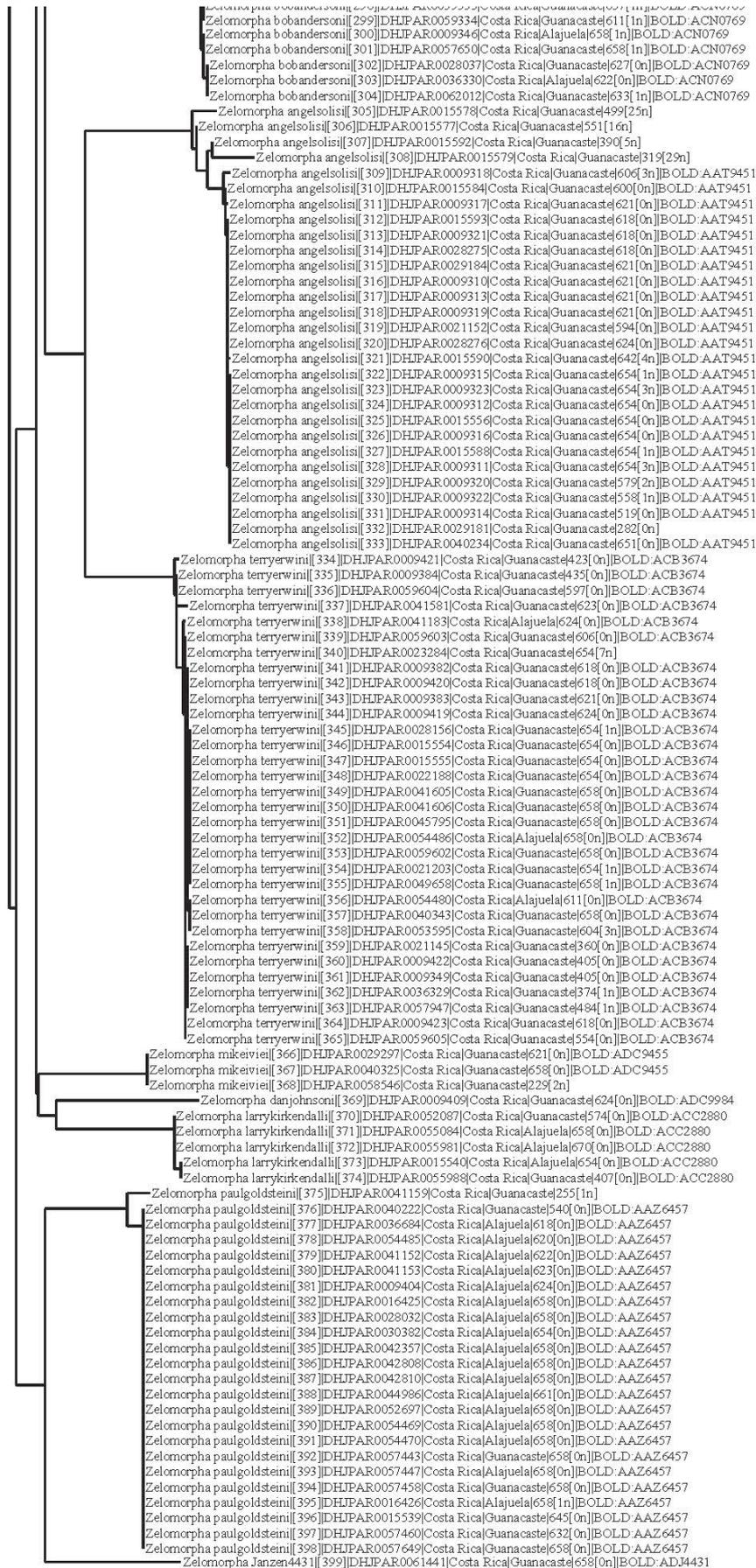




Continued.



Continued.



Continued.

Revision of *Tropopterus* Solier: A disjunct South American component of the Australo-Pacific Moriomorphini (Coleoptera, Carabidae)

James K. Liebherr¹

¹ Department of Entomology, Comstock Hall, 129 Garden Ave., Cornell University, Ithaca, NY 14853-2601, USA

<http://zoobank.org/1C96C480-B8BA-4D63-BBF4-68566D57EA73>

Corresponding author: James K. Liebherr (JKL5@cornell.edu)

Academic editor: Dominique Zimmermann ♦ Received 5 July 2019 ♦ Accepted 20 August 2019 ♦ Published 5 November 2019

Abstract

Tropopterus Solier, 1849, precinctive to southern South America, is taxonomically revised. Six new species are described: *T. peckorum* sp. nov., *T. robustus* sp. nov., *T. canaliculus* sp. nov., *T. trisinuatus* sp. nov., *T. minimicro* sp. nov., and *T. fieldianus* sp. nov. *Merizodus catapileanus* Jeannel, 1962, is synonymized with *T. montagnei* Solier, 1849. Lectotypes are designated for *T. montagnei*, *T. giraudyi* Solier, *T. duponchelii* Solier, and *T. nitidus* Solier (= *T. duponchelii*). *Tropopterus peruvianus* Straneo is noted as a *nomen dubium*, with its identity and taxonomic placement to be substantiated via neotype designation. Phylogenetic relationships among *Tropopterus* spp. are hypothesized based on 37 morphological characters, the distributions of which are analyzed under the parsimony criterion, with the cladogram root established between *Tropopterus* and its adelphotaxon from New South Wales, Australia. Speciation in the group has occurred predominantly at a limited geographical scale relative to the overall generic distribution, with three pairs of sister species sympatric. However phylogenetic divergence between taxa in the more northern, sclerophyllous forest characterized by *Nothofagus obliqua* (Brisseau de Mirbel) and those occupying the Valdivian and North Patagonian Rain Forest dominated by *N. dombeyi* (Brisseau de Mirbel) is observed in two instances of phylogenetic history. Using specific collecting locality records, it is shown that *Tropopterus* beetles have been collected syntopically and synchronically with species of *Glypholoma* Jeannel (Coleoptera, Staphylinidae), *Anaballetus* Newton, Švec & Fikáček (Coleoptera, Leiodidae), *Andotypus* Spangler (Coleoptera, Hydrophilidae), and *Novonothrus* Balogh (Acari, Oribatida). These concordant ecological occurrences document a cohesive *Nothofagus* forest leaf-litter community. These genera plus other Valdivian Rain Forest invertebrate taxa all exhibit an Austral disjunct biogeographical pattern that corroborates trans-Antarctic vicariance between the *Nothofagus* forests of southern South America and Australia. Male genitalic antisymmetry is shown to be a synapomorphy of *Tropopterus*, though the female reproductive tract retains the plesiomorphic orientation observed in all other moriomorphine taxa.

Key Words

Austral biogeography, dispersal, genitalic antisymmetry, vicariance, Western Antarctica

Introduction

The carabid beetle tribe Moriomorphini exhibits an aggregate geographical distribution that includes Australia, New Zealand, New Caledonia, the Sunda Islands, the Society and Hawaiian Islands in Polynesia, and Chile. The greatest generic diversity in the tribe is centered in Australia with representatives of 21 genera (Liebherr 2020) and New Zealand with six genera represented (Larochelle and Larivière 2013, Liebherr 2018a, 2020). Conversely,

the bulk of species-level diversity in the tribe is represented by species of the genus *Mecyclothorax* Sharp, with that genus represented by 239 species in Hawaii (Liebherr 2015) and 108 species in Tahiti and Moorea (Liebherr 2012, 2013). These two Polynesian radiations commenced on the islands of Maui and Tahiti Nui, respectively, indicating very rapid speciation in the radiations of both archipelagoes. Thus the total diversity of the tribe has been built both by relatively slower, generic-level evolution on geologically old Australia and New Zealand, but explo-

sive speciation on the younger, geologically more ephemeral islands of Polynesia. An adjunct to this disparate mix is *Tropopterus* Solier, which is geographically restricted to South America and isolated across the Pacific Ocean from the rest of the members of its tribe.

Tropopterus was described by Solier (1849), who placed it immediately after species now assigned to the genus *Incagonum* Liebherr (tribe Platynini) because he considered the two taxa to be closely related due to shared tarsal configuration (Solier 1849: 212). Reed (1874), Chaudoir (1876), and Germain (1911) followed suit with this tribal placement. Bates (1874) and Broun (1880, 1882) expanded the generic concept by describing New Zealand taxa in combination with *Tropopterus*. Sloane (1898) then proposed *Tropopterus* as a member of an Australian assemblage of genera assignable to today's Moriomorphini, while considering three Australian species to represent *Tropopterus*. This trans-Pacific interpretation of *Tropopterus* unravelled over time, with Broun proposing several precinctive New Zealand genera to hold species he previously described under *Tropopterus* (summarized in Larochelle and Larivière 2013), and Moore (1963) removing the Australian species from *Tropopterus* and placing them in the precinctive Australian genus *Theprisa* Moore. Most recently, Liebherr (2020) conducted a cladistic analysis of the tribe Moriomorphini, finding that *Tropopterus* exhibits a sister-taxon relationship with a monotypic Australian genus. This contribution revises *Tropopterus* based on substantial new material collected by field surveys conducted from the 1980s to the present. Phylogenetic relationships among *Tropopterus* species are hypothesized based on parsimony analysis of morphological characters. It is shown that the *Nothofagus*-dominant Valdivian Rain Forest supports a cohesive assemblage of leaf-litter inhabiting taxa, with *Tropopterus* beetles living alongside beetle and mite taxa also exhibiting the Austral disjunct biogeographical pattern involving Chile and Australia. Thus, we can now recognize an Austral disjunct ground litter fauna of the Valdivian Rain Forest, the members of which take part in trans-Antarctic biogeographical relationships. Finally, male genitalic antisymmetry, rarely observed among carabid beetles (Liebherr and Will 2015), is shown to be a synapomorphy for *Tropopterus*.

Nomenclatural disclaimer. *Pharetis* Liebherr and *Pharetis thayerae* Liebherr are disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3) and are unavailable until published (Liebherr 2020).

Material and methods

Taxonomic material

This revision is based on 162 specimens borrowed from the following institutions (institutional acronym and responsible curators in parentheses): California Academy of Sciences (CAS, David H. Kavanaugh); Carnegie Mu-

seum of Natural History, Pittsburgh, PA (CMNH, Robert Davidson); Essig Museum of Entomology, University of California, Berkeley, CA (EMEC, Kipling W. Will); Field Museum of Natural History, Chicago, IL (FMNH, Al Newton and Margaret Thayer); Florida State Collection of Arthropods, Gainesville, FL (FSCA, Paul Skelley); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ, Philip D. Perkins and Crystal Maier); Museum national d'Histoire naturelle, Paris (MNHN, Thierry Deuve); Department of Geosciences, North Dakota State University, Fargo, ND (NDSU, Allan C. Ashworth); and Oregon State Arthropod Collection, Oregon State University, Corvallis, OR (OSAC, David R. Maddison). Specimens stored as whole bodies in 100% ethanol for DNA sequencing are noted by "etoh" following the institutional coden. Specimens were requested from the Museo Nacional de Historia Natural, Santiago, but none were available.

Laboratory methodology

Specimens were relaxed for dissection in nearly boiling distilled water held in shell vials placed in a double boiler, the water containing a drop of Kodak Photo-Flo® detergent. For males, the aedeagal median lobe, associated parameres and 9th laterotergite and antecostal apodeme, and 8th ventral apodeme when possible, were disassociated from the abdomen using minuten pins mounted on wooden dowels. The genitalic apparatus was removed, cleared overnight in cold 10% KOH, deacidified in 10% acetic acid, and then placed in glycerin. The male internal sac, or endophallus, was everted in KOH using modified minuten nadeln. Female dissections involved removal of the entire abdomen, and clearing in cold 10% KOH overnight. After removal from the abdominal ventrites and dorsal membranous tergites, the reproductive tract assembly was deacidified briefly in dilute 10% acetic acid, cleared and stained in a mixture of Kodak Chlorazol Black stain suspended in methyl cellosolve for as long as it took for the associated fat tissue to dissipate. The cleared dissection was viewed in glycerin on a microslide. Macrophotography was accomplished using a Microoptics (now Visionary Digital) photographic apparatus employing a Nikon D1 camera, the K2 lens system, and a three-wand photographic strobe fiber-optic light source. Female dissections were photographed in ventral view, with the gonocoxites additionally presented as line drawings.

Descriptive conventions and characters

Previously described species are provided an extensive diagnosis sufficient for identification, whereas new species are also provided with a description that complements the diagnosis. Male genitalic terminology follows that of Liebherr (2018b, 2020), with abbreviations used in the figures presented in Table 1. Terminology of the female

Table 1. Key to abbreviations for morphological structures labelled in illustrations of male genitalia (Figs 3–5), female reproductive tracts (Fig. 7), and female gonocoxae (Fig. 8).

Abbreviation	Structure
acIX	antecostal apodeme of abdominal IX, male
afs	apical fringe setae, basal gonocoxite
ans	apical nematiform setae, apical gonocoxite
bc	female bursa copulatrix
co	female common oviduct
des	dorsal ensiform seta, apical gonocoxite
fl	flagellum, male aedeagal internal sac
fs	flagellar sheath, male aedeagal internal sac
gc1	basal gonocoxite, female
gc2	apical gonocoxite, female
hg	hindgut
les	lateral ensiform setae, apical gonocoxite
mu	micro on aedeagal median lobe apex
pub	pleated ostial border, male
r	ramus, basal gonocoxite
sd	spermathecal duct, female
sg	spermathecal gland, female
sp	spermatheca, female
vss	ventrobasal spiracular sclerite, male

reproductive tract characters (Table 1) follows Liebherr and Will (1998). The numbers of individuals used as the basis for describing male and female genitalia are indicated at the start of descriptive sections for those structures. Several ratios are used to describe body conformation (Table 2). To describe eye configuration three ratios are used: (1) ocular ratio (MHW/mFW), or the maximal head width across the eyes divided by the minimal frons width between the eyes; (2) ocular lobe ratio (EyL/OLL), or eye length measured in dorsal view, divided by the distance from the anterior margin of the eye to the inflection at the juncture of the ocular lobe and the gena, also measured in dorsal view; and (3) eye convexity (EyL/EyD), or the eye length measured as above, divided by the depth of the convex eye, with the eye's dorsal margin uppermost in the field of view. Eye development was also quantified by counting the number of ommatidia crossed by a diametric line passing across the maximal horizontal dimension of the eye, that number assessed in lateral view. Pronotal shape was described using two ratios: (1) maximal pronotal width divided by the basal pronotal width, measured between the hind angles (MPW/BPW); and (2) maximal pronotal width divided by pronotal median length (MPW/PL). The relative shape of the elytra was described using the ratio of maximal elytral width measured where that occurs, divided by elytral length, defined as the distance from the base of the raised scutellar surface to the elytral apex, measured along the suture (MEW/EL). The range of specimens chosen for measurement included both the largest and smallest individuals, males and females, and representatives from multiple localities where available. Standardized body length is defined as the sum of three linear measurements: (1) the distance from the anterior labral margin to the cervical ridge, a transverse carina posterad the vertex; (2) the medial length of the pronotum; and (3) elytral length as defined above.

Holotype label data are presented verbatim, including typeface. Individual labels are indicated by a double slash “//”, and lines within labels by a single slash “/”. Nomenclatural actions conform to the International Code of Zoological Nomenclature (ICZN 1999). Institutional repositories for holotypes were assigned based on the earliest collections of the newly described species, thereby recognizing those collectors who first discovered them.

Cladistic analysis. An hypothesis of phylogenetic relationships among the species was generated using parsimony analysis implemented by the Winclada data platform (Nixon 2002) running NONA (Goloboff 1999) and the parsimony ratchet (Nixon 1999). The complete data matrix, character states, and single most parsimonious tree (Fig. 10) are presented in Suppl. material 1.

Characters. The analysis was based on 37 morphological characters; 22 binary two-state characters, and 15 ordered multistate characters of 3 or 4 states.

- Character 0 Antennomere 9 length/width ratio: $1.42 < x < 1.98$, Figs 7, 8 (0; Fig. 1D); $2.0 < x < 2.8$ mm (1; Fig. 1F).
- Character 1 Number of ommatidia-horizontal diameter: 12–17 (0); 18–21 (1; Fig. 1C); 23–26 (2; Fig. 2C).
- Character 2 Paraglossae relative to ligula: adjacent (0); set off laterally from basal portion of glosal sclerite (1).
- Character 3 Mentum paramedial depression: broad, shallowly depressed (0); deep but without abrupt pit (1); deep with narrow, distinct pit at depth (2).
- Character 4 Labral apical margin: straight (0); moderately concave (1); deeply concave (2).
- Character 5 Ocular ratio: < 1.30 (0); $1.30–1.40$ (1; Fig. 1C); $1.41–1.50$ (2; Fig. 1B).
- Character 6 Ocular lobe ratio: < 0.70 (0); $0.76–0.83$ (1; Fig. 1C); $0.85–0.90$ (2; Fig. 2C); $0.91–0.94$ (3; Fig. 1F).
- Character 7 Anterior pronotal margin: smooth medially, margined laterally (0; Fig. 1F); with marginal bead medially and laterally (1; Fig. 1E).
- Character 8 Pronotal median base: coplanar with disc medially (0); depressed relative to disc medially (1).
- Character 9 Pronotal basal margin: straight (0; Fig. 2B); trisinate (1; Fig. 2A).
- Character 10 Lateral setal position: 1 setal diameter from lateral marginal depression (0); 2 setal diameters from lateral marginal depression (1).
- Character 11 Pronotal breadth ratio MPW/PL: $1.20–1.32$ (0; Fig. 1D); $1.33–1.40$ (1; Fig. 2C).
- Character 12 Prosternum and prosternal process: broadly depressed medially in basal half of prothorax (0); deeply and narrowly depressed medially in basal half (1).

- Character 13 Apex of scutellum: extended onto elytral disc between elytral bases (0); not or only slightly extended onto disc, mostly in basal groove (1).
- Character 14 Elytral shape MEW/EL: 0.66–0.68 (0; Fig. 1C); 0.69–0.74 (1; Fig. 1E); 0.75–0.81 (2; Fig. 1D).
- Character 15 Elytral humeral angle: broadly rounded (0); narrowly rounded to obtuse-angulate (1).
- Character 16 Elytral basal groove: present from scutellum to humeral angle (0; Fig. 1); absent medially, at most present just mesad humeral angle (1; Fig. 2).
- Character 17 Elytral striae on disc: 1–4 shallow, punctate, and 5–7 progressively obsolete (0; Fig. 1D); 1–2 shallow, punctate, and 3–7 progressively obsolete (1; Fig. 1F); only sutural stria 1 present, and 2–7 obsolete (2; Fig. 2); all discal striae obsolete (3; Fig. 1A, B).
- Character 18 Elytral striae on apex: 1–3 to 1–5 traceable on apex, 7 evident mesad subapical sinuation (0; Fig. 1D); only striae 1–2 and 7 visible near apex 3–6 obsolete (1; Fig. 2); only sutural stria or no striae traceable near apex (2; Fig. 1B).
- Character 19 Sutural stria at apex (when present): uniformly punctate (0); with antepical punctate section and apical canalicula (1); absent antepically, smooth apically (2).
- Character 20 Elytral stria 8: smooth throughout length, deep at midlength (0); smooth throughout, shallow at midlength (1); deep fore and aft, isolated punctures at midlength (2); present fore and aft, absent at midlength (3).
- Character 21 Mesepisternum: smooth to 3 small punctures (0); with ~4–7 punctures in 1 row (1); with 8–18 punctures in 2–3 rows (2).
- Character 22 Metepisternum width/length: < 0.75 (0); 0.78–0.83 (1); 0.85–0.88 (2); 1.0 (3).
- Character 23 Metathoracic flight wing: foreshortened, stenopterus (0); vestigial, apex not extended past metanotum (1).
- Character 24 Lateral abdominal suture between ventrites 1 and 2: straight or slightly sinuate (0); sinuate with ventrite 2 depressed within sinuosity (1).
- Character 25 Base of ventrites 4–6: smooth, small punctures may be present along basal margin (0); sulcate, the sulcus lined with distinct punctures (1).
- Character 26 Apical abdominal ventrite 6 (male): with 1 seta each side (total of 2) (0); with 2 setae each side (total of 4) (1).
- Character 27 Metatarsomere 4 apex: truncate apically (0); emarginate, outer lobe longer than inner lobe (1).
- Character 28 Male aedeagal orientation: plesiomorphic, right side ventral (0); inverted left side ventral (1) (Figs 3–6).
- Character 29 Abdominal IX antecostal apodeme: distinctly angulate distally, extension may be present (0; Figs 3B, F, H, 4B, D); rounded or obtusely rounded distally (1; Fig. 4G).
- Character 30 Aedeagal median lobe apex: smoothly rounded or acuminate (0); with small mucro on ventral margin (1; Fig. 5A, C, E); with large mucro on ventral margin (2; Figs 3A, E, 4E, F).
- Character 31 Male aedeagal median lobe ostial opening: surrounded by smooth membrane (0); surrounded by pleated membrane (1; Fig. 4A).
- Character 32 Female basal gonocoxite 1: with one apical fringe seta each side (0; Fig. 8E); with two apical fringe setae each side (one may be smaller) (1; Fig. 8A–C).
- Character 33 Microsculpture of vertex between eyes: evident isodiametric mesh (0); shallow isodiametric mesh (1); indistinct, surface glossy (2).
- Character 34 Microsculpture of pronotum: dense transverse mesh (0); transverse lines (1).
- Character 35 Microsculpture of elytra: transverse mesh, up to 3–4 × (0); elongate transverse mesh to transverse lines causing spectral iridescence (1).
- Character 36 Standardized body length: < 5.0 mm (0); 5.0–6.1 mm (1); 6.7–8.4 mm (2).

Table 2. Ratios of dimensions of the head, pronotum, and elytra for *Tropopterus* spp., along with number of ommatidia intersecting a line crossing horizontal diameter of eye. Abbreviations described in Material and Methods. Number of specimens denotes those measured to establish ranges of ratios.

Species	No. specimens	MHW/mFW	EyL/OLL	EyL/EyD	No. ommatidia	MPW/BPW	MPW/PL	MEW/EL
<i>T. montagnei</i>	4	1.32–1.36	0.83–0.90	3.0–3.3	18	1.21–1.26	1.21–1.27	0.70–0.72
<i>T. giraudyi</i>	5	1.41–1.47	0.83–0.89	2.6–3.0	23	1.25–1.31	1.21–1.25	0.69–0.74
<i>T. peckorum</i>	3	1.30–1.33	0.82–0.83	3.1–3.2	18–20	1.23–1.25	1.21–1.31	0.66–0.68
<i>T. robustus</i>	5	1.35–1.48	0.90–0.92	3.1–3.3	20	1.18–1.21	1.36–1.41	0.74–0.81
<i>T. canaliculus</i>	5	1.40–1.50	0.85–0.93	2.9–3.3	25	1.21–1.33	1.20–1.25	0.70–0.74
<i>T. duponchelii</i>	5	1.37–1.46	0.91–0.94	2.5–3.1	20–25	1.20–1.24	1.25–1.32	0.70–0.75
<i>T. trisinuatus</i>	2	1.36	0.76–0.81	2.7–2.8	25–26	1.22–1.24	1.30–1.36	0.72–0.74
<i>T. minimucro</i>	5	1.41–1.45	0.85–0.89	3.0–3.3	25	1.24–1.33	1.27–1.37	0.70–0.73
<i>T. fieldianus</i>	2	1.42–1.44	0.87–0.88	2.4	26	1.18–1.25	1.37–1.39	0.74–0.75

Results

Taxonomic treatment

Genus *Tropopterus* Solier, 1849

Tropopterus Solier 1849: 211; Reed 1874: 58; Chaudoir 1876: 124; Sloane 1898: 471; Sloane 1903: 585.

Tropidopterus Gemminger and Harold 1868: 385 (unjustified emendation).

Type species. *Tropopterus giraudyi* Solier by subsequent designation (Enderlein 1909).

Diagnosis. *Tropopterus* may be placed in the Moriormorphini based on: presence of a seta in the mandibular scrobe; frontal grooves present mesad eyes and traversing the frons anteromedially to the frontoclypeal suture; clypeus narrower than distance between antennal insertions; penultimate maxillary palpomeres glabrous, not setose over the entire surface; apical palpomeres fusiform and as long and broad as penultimate palpomere; head with two pairs of supraorbital setae; procoxal cavities closed posteriorly; mesocoxal cavities conjunct; prothoracic leg bearing an antennal cleaner with a distal zone of short, separated setae, and a basal arc of confluent setae that performs the cleaning function (Grade C of Hlavac 1971). The first eight characters will place *Tropopterus* within Psydrini in the system of Roig-Juñent and Domínguez (2001). The last antennal cleaner character differentiates the Psydrini from Moriormorphini (Baehr 1998; Liebherr 2020), as Psydrini exhibit a shorter, less well-developed antennal cleaner (Grade B of Hlavac 1971) versus that observed in Moriormorphini. The morphological results conform to phylogenetic hypotheses based on molecular sequence data (Maddison et al. 1999, 2019).

Within Moriormorphini *Tropopterus* may be diagnosed by the inversion of the male aedeagus, a character observed in several other Moriormorphini: *Mecyclothorax storeyi* Moore (1963) of Queensland; and polymorphically within Western Australian populations of *Mecyclothorax punctipennis* (MacLeay) (Liebherr and Will 2015). Nowhere else in Moriormorphini does this character define a monophyletic grouping of species. Other characters supporting monophyly of *Tropopterus* include deep, pit-like paramedial depressions of the mentum, also observed in *Meonis* spp. of Australia (Moore 1963; Liebherr 2020). The metathoracic scutellum projects little onto the disc of the elytra, whereas it is more narrowly triangular and elongate in the sister group *Pharetis* (Liebherr 2020). The elytral basal groove (when present) meets the lateral marginal depression at a distinct angle, whereas this juncture is more rounded in *Pharetis thayerae*. Both *Pharetis* and *Tropopterus* are characterized by a tooth along the dorsal margin of the humerus. Though the elytral striae vary in configuration among *Tropopterus* spp., their reduction is derived, and the presence of only the first, or sutural stria in a fully developed condition on the elytral apex is a synapomorphy. All species of *Tropopterus* are characterized by vestigial flight wings, and the metepister-

num is correspondingly foreshortened. That sclerite's dimensions range from length 1.2× breadth to length and breadth subequal; length measured along lateral margin and maximal breadth measured perpendicular to that line. Relative to *Pharetis*, the fourth metatarsomere is more emarginate, with the outer, lateral lobe longer than the inner, mesal lobe. Finally, the setal configuration across the dorsal body is diagnostic, though not synapomorphic, with: presence of both anterior and posterior supraorbital setae; presence of both lateral and basal pronotal setae; presence of the parascutellar setae; absence of any dorsal elytral setae; and presence of both subapical and apical setae near the elytral apex. Consistent with most other moriomorphines there are seven (rarely eight) anterior lateral elytral setae bordering the eighth stria, and six posterior setae: though the posterior two setae of the anterior series, or the anterior two setae of the posterior series may be isolated from their respective series' partners in *T. robustus*, sp. nov. Also, males, where known for the various species, have two setae each side of the apical abdominal ventrite, representing a potential synapomorphy for the genus relative to its Australian adelphotaxon, *Pharetis thayerae* Liebherr (2020). The male aedeagal median lobe is robust, i.e. broad dorsoventrally, with the internal sac flagellar apparatus also large (e.g. Fig. 4A). The aedeagal median lobe of males, for all species so far examined, bears dense longitudinal pleating across the sclerotized surface surrounding the ostium (Fig. 4A, C), with this pleating allowing broad extension of the aedeagal surface during eversion of the internal sac. Females also have two setae each side along the apical margin of ventrite 6 accompanied by four median setae of length subequal to the more lateral setae, these variously arranged in an apically broad trapezoid or in a straight line. The female reproductive tract is characterized by absence of a helminthoid sclerite; a sclerotized projection at the junction of the bursa copulatrix wall, common oviduct, and spermathecal duct (Liebherr and Will 1998). The derived loss of the helminthoid sclerite, observed across many other moriomorphine taxa, is shared with *Raphetis* Moore of southeastern Australia (Liebherr 2020).

Nomenclatural notes. Although *Tropopterus* Solier (1849) was used by major authorities throughout the 19th century (see synonymy above), Gemminger and Harold's (1868) unjustified emendation *Tropidopterus* was adopted by Enderlein (1909), Moore (1963), and subsequently followed by Baehr (1998). The original spelling of *Tropopterus* has also been used more recently (Straneo 1954; Roig-Juñent and Domínguez 2001; Maddison and Ober 2011; Larochelle and Larivière 2013). Though both variants have been used, the original spelling predominates and so the unjustified emendation *Tropidopterus* cannot be considered “in prevailing usage” (ICZN 1999, Article 33.2.3.1). Thus *Tropidopterus* must be rejected in favor of the original spelling.

In addition to the three *Tropopterus* spp. described by Solier (1849), Germain (1911) listed “*T. plicicollis*” ms. name, as an undescribed species held in the Museo

Nacional de Historia Natural, Santiago, Chile, assigning it his “N.^{os} del Catálogo primitivo” entry 500. This combination was never validly described (Lorenz 2005). However a specimen labelled as per Germain’s protocol (“459 / Catapilcanus / P. G. (ined.)”) was described as *Merizodus catipileanus* by Jeannel (1962). That name is synonymized below with *T. montagnei* Solier. Germain’s (1911) list also includes undescribed specimens labelled with his catalog numbers 458 and 460, bracketing the number assigned to “Catapilcanus.” Germain assigned those numbers to his manuscript names *Trechus ebeninus* and *Trechus araucanus*, with Jeannel subsequently describing those specimens as *Trechisibus araucanus* (Jeannel 1962: 562) and *Trechisibus ebeninus* (Jeannel 1962: 577). Thus, some of the undescribed Germain (1911) material was used by Jeannel as the basis for new species he described in 1962, but there is no evidence that any specimens assigned to “*T. plicicollis*”, catalog entry 500, were part of Jeannel’s working material, nor was Germain’s name validated in any subsequent publication. Thus Germain’s (1911) “*Tropopterus plicicollis* (P. G. ined.)” has no nomenclatural standing.

Straneo (1954) described *Tropopterus peruvianus* from two specimens (Sivia, Peru, 13-v-1936, 520 m. el.) collected during the Südperu-Expedition of the Naturhistorisches Museum, Hamburg. Although Straneo’s description was published in 1954, the material had been originally de-

scribed in 1942, with the specimens returned to the Hamburg museum and subsequently destroyed in the Allied firebombing of 1943. That the types of this species were lost in the destruction of the museum was documented by Weidner (1976; Dr. M. Husemann pers. comm.). Straneo (1954) recorded the female type used as the basis for the description as being of 8 mm body length. His diagnosis for *T. peruvianus*, translated from the Italian, follows:

“It differs from *T. giraud[y]i* Sol. by the basally non-sinuate pronotum; it also has distinctly obtuse pronotal basal angles; the 1st stria is strongly impressed from approximately 1/6 of the elytra length, immediately commencing as a distinct impression and not with isolated punctures; the eighth stria is about as long as the 1st; the third interstria has a small puncture present the apical half; the two basal antennal articles extend beyond the pronotal base, etc. From *T. duponcheli[i]* Sol. it differs by the first and second striae stria reaching the elytral base, and because the lateral pronotal [margin] is very gradually enlarged from the anterior setal pore towards the base.”

This diagnosis does not fit any of the species treated below. Indeed the presence of a puncture in the third interval does not fit the diagnosis of *Tropopterus*, suggesting phylogenetic placement outside the presently treated taxa. Thus *T. peruvianus* Straneo is to be treated as an available *nomen dubium* with its identity to be stabilized through new collection and designation of a neotype.

Key to the adults of *Tropopterus* Solier recorded from Chile and Argentina

- 1 Elytral microsculpture of transverse mesh or dense transverse lines, the surface iridescent, or discal surface glossy, sculpticells difficult to discern..... 2
- 1' Elytral microsculpture isodiametric, sculpticells distinct, surface granulate with silvery reflection (Fig. 1A)..... 1. *Tropopterus montagnei* Solier
- 2 At least sutural stria evident in basal half of elytral length, the sutural stria indicated by isolated punctures or distinct punctures connected by longitudinally impressed strial segments..... 3
- 2' All elytral striae reduced, elytra smooth basally; sutural stria represented at most by very small isolated punctures on basal half of length versus very distinct in apical half, with distinct isolated punctures subapically and a deep continuous impression apically (Fig. 1B)..... 2. *Tropopterus giraudyi* Solier
- 3 Body robust, broad, eyes moderately to very convex, MEW/EL = 0.70–0.81, ocular ratio = 1.35–1.50; standardized body length 5.2–8.4 mm (those beetles of *T. robustus*, sp. nov. and *T. canaliculus* sp. nov. that overlap in body length with *T. peckorum*, **sp. nov.** below, differ greatly in MEW/EL and ocular ratios)..... 4
- 3' Body narrow, eyes little convex, MEW/EL = 0.66–0.68, ocular ratio = 1.30–1.33 (Fig. 1C); standardized body length 5.5–6.0 mm..... 3. *Tropopterus peckorum* sp. nov.
- 4 Elytra with well-developed basal groove extended from laterad scutellum to angulate humerus..... 5
- 4' Elytra lacking basal groove, elytra smoothly depressed mesad humeral angles from disc to depressed anterior elytral margin..... 7
- 5 Vertex with indistinct to well-developed transverse mesh microsculpture, the surface glossy to iridescent; pronotum at most moderately transverse, MPW/PL = 1.20–1.33 (Fig. 1E, F)..... 6
- 5' Vertex covered with distinct mesh of isodiametric and transversely stretched sculpticells, the surface appearing granulate; pronotum rather transverse, MPW/PL = 1.36–1.41 (Fig. 1D)..... 4. *Tropopterus robustus* sp. nov.
- 6 Prosternum with deep, narrow, canaliculate depression medially from prosternal process anterad more than half length of prosternum; discal elytral intervals 1–3 with glossy surface, sculpticells difficult to discern except near strial punctures, surface not iridescent (Fig. 1E)..... 5. *Tropopterus canaliculus* sp. nov.
- 6' Prosternum broadly, medially flattened anterad prosternal process, a shallow longitudinal depression present over a portion of the flattened area in some individuals; discal elytral intervals 1–3 covered with dense transverse-line microsculpture, surface iridescent (Fig. 1F)..... 6. *Tropopterus duponcheli* Solier

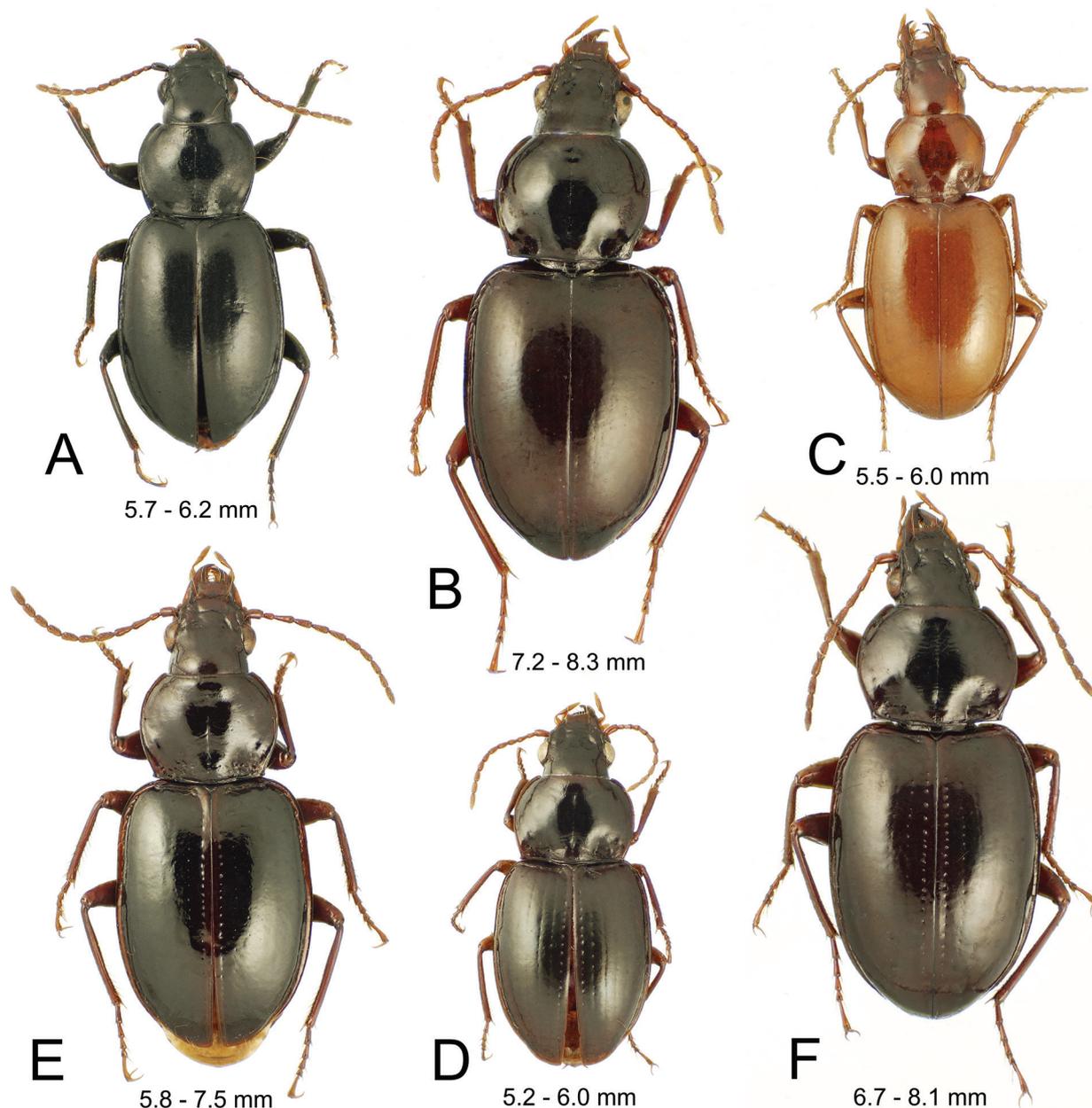


Figure 1. *Tropopterus* spp., dorsal view; range of standardized body lengths in mm. **A.** *T. montagnei* female; Petorca Prov., Q. Tigre Zapallar, Catapilco (MNHN). **B.** *T. giraudyi* female; Valdivia Prov., Chaihuin (EMEC). **C.** *T. peckorum* male; Quillota Prov., P. N. La Campana (FMNH). **D.** *T. robustus* female; Malleco Prov., M. N. Contulmo (FMNH). **E.** *T. canaliculus* female; Malleco Prov., P. N. Nahuelbuta (FMNH). **F.** *T. duponchelii* male; Arauco Prov., Caramavida (MCZ).

- 7 Pronotal basal margin straight, or anteriorly curved laterally so that hind angles lie anterad margin of median base; eyes moderately to very convex, ocular ratio = 1.41–1.45, ocular lobe ratio = 0.85–0.89, juncture of ocular lobe and gena slightly obtuse in dorsal view 8
- 7' Pronotal basal margin trisinate, inflexed anteriorly behind very deep laterobasal depressions, posteriorly expanded laterally to acute hind angles (Fig. 2A); eyes small, little convex, ocular ratio = 1.36, ocular lobe ratio = 0.76–0.81, juncture of ocular lobe and gena very obtuse in dorsal view 7. *Tropopterus trisinuatus* sp. nov.
- 8 Sutural stria deep, narrow, continuous at elytral apex, stria 2 obsolete there except for broad, very shallow depression just mesad apical seta; pronotum more quadrate, MPW/PL = 1.27–1.37 (Fig. 2B)..... 8. *Tropopterus minimicro* sp. nov.
- 8' Both sutural stria 1 and stria 2 impressed at elytral apex, both of them punctate anteapically; pronotum more transverse, MPW/PL = 1.37–1.39 (Fig. 2C)..... 9. *Tropopterus fieldianus* sp. nov.

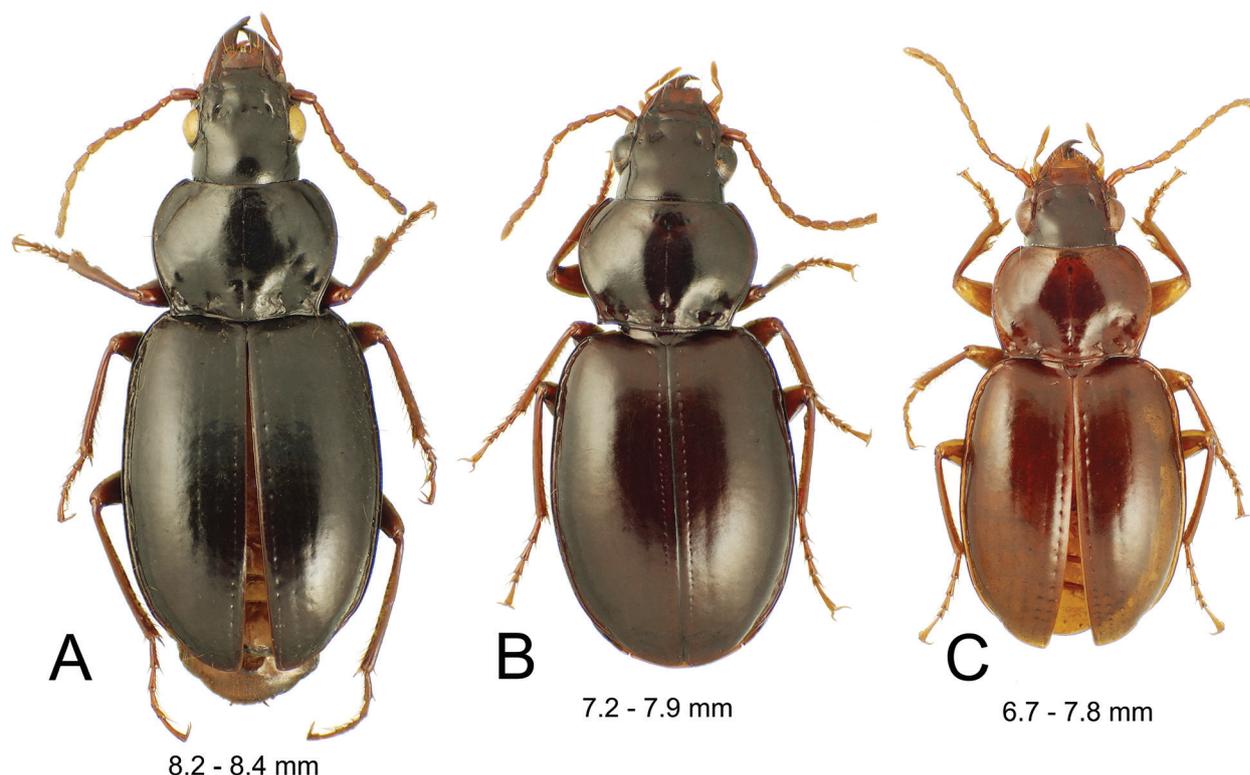


Figure 2. *Tropopterus* spp., dorsal view; range of standardized body lengths in mm. **A.** *T. trisinuatus* female; Cautín Prov., Villarrica (CAS). **B.** *T. minimicro* female; Valdivia Prov., P. N. Oncol (OSAC). **C.** *T. fieldianus* male; Osorno Prov., Maicolpue (FMNH).

1. *Tropopterus montagnei* Solier

Figures 1A, 7A, 8A, 9A, 10

Tropopterus montagnei Solier 1849: 214; Reed 1874: 58.

Tropidopterus montagnei Gemminger and Harold 1868: 385 (unjustified emendation).

Merizodus catapileanus Jeannel 1962: 606 (New synonymy).

Diagnosis ($n = 3$). These somber-colored, small-bodied beetles – standardized body length 5.7–6.2 mm – can be recognized by the isodiametric elytral microsculpture that gives the surface a granulate appearance. The legs are dark, with the femora and tibial apices as dark as the piceous head, pronotum, and elytra. The pronotum is moderately transverse (MPW/PL = 1.21–1.27) with the pronotal hind angle obtuse, the lateral margin straight anterad the hind angle. The elytral striae 1–4 are obsolete, only traceable on the disc and without punctuation. Only the first, sutural stria is \pm traceable on the elytral apex. The eyes are small (ocular ratio = 1.32–1.36) with about 18 ommatidia crossed along a horizontal diameter of the eye. The vertex is glossy, contrasted with the transverse mesh microsculpture of the pronotum, and the granulate isodiametric microsculpture of the elytra. Ventrally the prosternum is broadly flattened to moderately depressed medially from the prosternal process anterad to 2/3 of the prosternal length, and the mesepisternum is smooth, with 2–3 irregular punctures dorso-ventrally arranged on its concave surface.

Female reproductive tract ($n = 1$). Bursa copulatrix columnar, length twice breadth, compressed under microslide cover slip (Fig. 7A), bursal walls relatively thick, translucent; spermatheca globose (separated in single dissection); basal gonocoxite 1 with apical fringe of two setae (Fig. 8A); apical gonocoxite 2 broadly triangular, base extended laterally, with two moderate lateral ensiform setae and one dorsal ensiform seta; apical sensory fossa with two nematiform setae.

Type information. *T. montagnei* lectotype female (MNHN) hereby designated: S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus* / *montagnei* / Sol. Sn. Iago (handwritten white label) // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr 2019 // LECTOTYPE / *Tropopterus* / *montagnei* / Solier / des. Liebherr 2019 (black-margined red label). PARALECTOTYPE female (MNHN): MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // *Tropopterus* / Measured / Specimen #2 / det. J.K. Liebherr 2019 // PARALECTOTYPE (as above).

Merizodus catapileanus holotype female (MNHN): Catapilco // 459 // Chili / Aconcagua / Catapilco // *Catapilcanus* / P. G. (ined.) / 459 // *Merizodus* / *catapileanus* / m. (hand written cursive) // *Tropidopterus* / *catapileanus* / det. P. M. Johns // 163 // *Tropopterus* / Measured / Specimen #3 / det. J.K. Liebherr 2019 // HOLOTYPE / *Merizodus* / *catapileanus* / Jeannel 1962 (black-margined

red label) // *Tropopterus / montagnei / Solier / det. J.K. Liebherr 2019*. Because Jeannel (1962) stated this species name was based on “une femelle,” he designated a holotype by monotypy. This female was card-mounted with the abdomen missing. As Jeannel routinely mounted dissected genitalia on separate pins (see the *Tropopterus giraudyi* paralectotype) it appears this species was dissected with the abdomen plus genitalia mounted separately, the latter subsequently disassociated. The data on the specimen agree with those provided in Jeannel’s (1962: 606) description. Also, Jeannel’s textual description fits the specimen with regard to size, wing configuration, general habitus, and absence of dorsal elytral setae. However, the illustration accompanying the text deviates significantly from the specimen by showing the penultimate palpomere as setose, and the elytra with eight lateral elytral setae (arranged as 4 + 4). In fact the penultimate palpomere is glabrous, and the lateral elytral setae are arranged as 6 + 1 + 6; i.e. a single seta separated from the anterior and posterior series of six setae each. Admittedly, there was excessive mucilage filling the elytral marginal depression, and so the setae were apparently missed. The consequence of these mistakes was Jeannel’s placement of this species in a genus of the Zolini.

Date locality information for all specimens. Chile: Petorca Prov. (labelled “Aconcagua”), Catapilco, 32°34.10'S, 71°16.52'W, Germain (MNHN, 1); Q. Tigre Zapallar (= Catapilco), 13-vii-1966, Pena (MNHN, 1). Santiago Prov., Santiago (lectotype and paralectotype), 33°26.75'S, 70°40.12'W, Solier (MNHN, 2).

Distribution and habitat. No habitat data are associated with the types of either names representing this species. This species is restricted to the Santiagan entomofaunal region (Fig. 9A; O’Brien 1971).

2. *Tropopterus giraudyi* Solier

Figures 1B, 3A, B, 6A, B, 7B, 8B, 9B, 10

Tropopterus giraudyi Solier 1849: 212 (*Tropoptertus giraudyi*, printer’s error); Reed 1874: 58.

Tropidopterus giraudi Gemminger and Harold 1868: 385 (unjustified emendations).

Diagnosis ($n = 5$). This large-bodied species (standardized body length 7.2–8.3 mm) is easily diagnosed by the smooth elytra with the sutural stria completely effaced to irregularly punctate basally (Fig. 1B), the punctures, when present, broad, very shallow, and irregularly distributed. Conversely, the sutural stria is distinctly punctate behind the elytral midlength, transforming to a very narrow canaliculate depression near the elytral apex. The eyes are moderately convex (ocular ratio = 1.41–1.47) with about 23 ommatidia crossed by a horizontal diameter of the eye. The pronotal hind angles are right to obtuse, sharp, with the lateral margins subparallel anterad the angles. The pronotal apical margin is finely, continuously margined medially, and the pronotum is relatively narrow

(MPW/PL = 1.21–1.25) compared to the similar-appearing *T. duponchelii* (MPW/PL = 1.25–1.32; Fig. 1F) and *T. minimucro* (MPW/PL = 1.27–1.37; Fig. 2B). Ventrally the prosternum is deeply depressed medially, the broad depression extended from the prosternal process more than halfway toward the front margin, and the mesepisternum is broadly punctate, with 8–9 punctures in 2–3 dorsoventral rows. The glossy vertex contrasts with the pronotum that bears a dense, shallow transverse mesh, and the iridescent elytra covered with dense transverse lines.

Male genitalia ($n = 13$). Aedeagal median lobe robust, broad dorsoventrally from base to apex, the broadly rounded apex bearing a well-developed mucro on its ventrobasal aspect (Fig. 3A); internal sac lightly sclerotized (sac not everted), with a sinuous spicular sclerite that would be positioned on the sac apex when everted. Antecostal apodeme of laterotergite IX (Deuve 1993) broadly angulate distally, the apex of the apodeme not extended much beyond lateral arms of the apodeme (Fig. 3B). Right paramere of median lobe elongate, slightly broader medially, with one or two long setae apically, six to eight setae along ventral margin, and several more smaller setae apically (Figs 6A, B); left paramere broad basally, variously narrowed apically into a parallel-sided extension (Fig. 6A), or an evenly narrowed apex (Fig. 6B), the apex of the paramere bearing two or three longer setae plus several shorter subapical setae.

Female reproductive tract ($n = 2$). Bursa copulatrix columnar, length 2.5× breadth, compressed under microslide cover slip (Fig. 7B), bursal walls relatively thick, translucent; spermatheca ovoid; spermathecal gland elongate, broadest distally; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with two apical fringe setae (Fig. 8B); apical gonocoxite 2 narrowly triangular, base little extended laterally, with one or two (Fig. 8B) lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Type information. Lectotype female (MNHN) hereby designated (card mounted): S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // TYPE (red label) // *Tropopterus / Giraudyi / Sol.* Sn. Iago (handwritten white label) // 9 / 45 (pale blue circle) // LECTOTYPE // *Tropopterus / giraudyi / Solier / des. Liebherr 2019* (black-margined red label). Paralectotype male (MNHN) (card mounted, genitalia dissected and removed): MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 / 45 (pale blue circle) // *Tropidopterus / giraudi Sol.* // PARALECTOTYPE (as above). Male genitalia (card mounted): *Tropidopt. / Giraudi / Chili / '71* // PARALECTOTYPE (as above).

Date locality information for all specimens. Argentina: Neuquén Prov., Pucará to Lago Venados road, Lago Lacar, 40°10.50'S, 71°21.50'W, 24–25-i-1972, Herman (NMNH, 1). Chile: Cautín Prov., Bellavista, Lago Villarrica, 39°12.55'S, 72°08.14'W, 250 m el., 8-i-2006, Will (EMEC, 1); Villarrica, 30 km NE, 39°09.23'S, 71°51.82'W, 1–30-i-1965 (MCZ, 1). Chiloé Prov., Chepu (det. Straneo, see Straneo [1969]), 42°02.03'S,

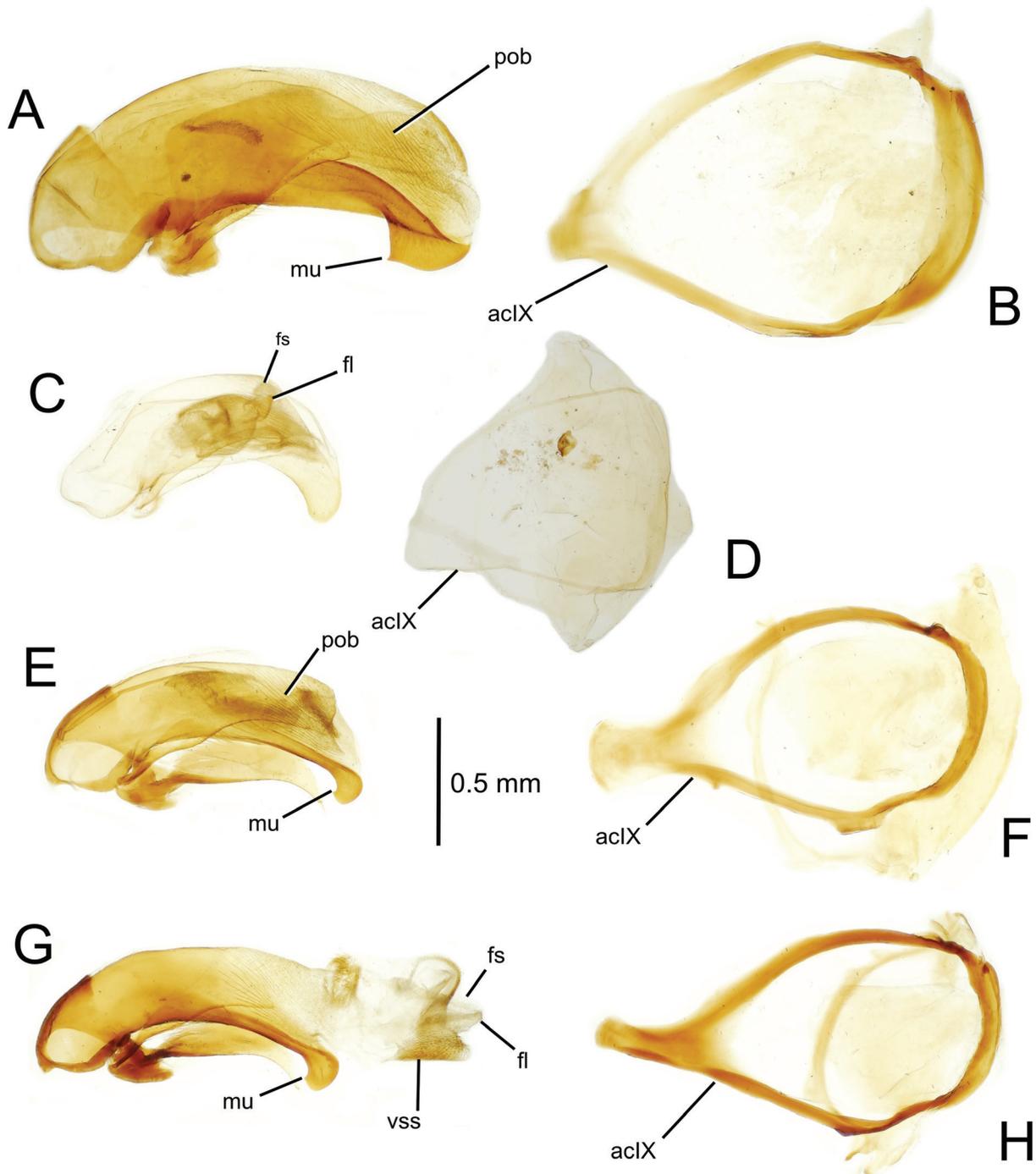


Figure 3. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. **A–B.** *T. giraudyi*; Chile, “*Tropopterus nitidus* Sol.”, Chaudoir Coll. (MNHN). **C, D.** *T. peckorum*; Quillota Prov., P. N. La Campana (FMNH) (**D** darkened to allow viewing of teneral dissection). **E–H.** *T. robustus*; Malleco Prov., M. N. Contulmo. **E–F.** (CMNH). **G, H.** (FMNH). For abbreviations used to label structures see Table 1.

73°58.31'W, 9-x-1958, Kuschel (MNHN, 1); P. N. Chiloé, under logs/rocks, 42°36.84'S, 74°06.25'W, 20-i-2002, Will & Lew (EMEC, 1), Rio Cipresal, above, lot DRM 06.085, 42°34.70'S, 74°04.98'W, 195 m el., 20–21-i-2006, Maddison & Will (OSAC etoh, 2), Quemchi, 11 km w of, 11 km E Hwy. 5, Valdivian rainforest remnant w/ thick bamboo understory, beating vegetation, 42°10.40'S, 73°35.73'W, 140 m el., 10-

xii-2002, Clarke (FMNH, 3). Llanquihue Prov., P. N. Vicente Pérez Rosales, Ensenada, 9.2 km NE, on road to Petrohué, Valdivian rainforest w/ *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 2-i-1997, Newton & Thayer (FMNH etoh, 1), 28-i-1997, Newton & Thayer (FMNH etoh, 1), 4–28-i-1997, Newton & Thayer (DRM DNA voucher DNA0532, FMNH on loan to OSAC, 1), Volcán Osor-

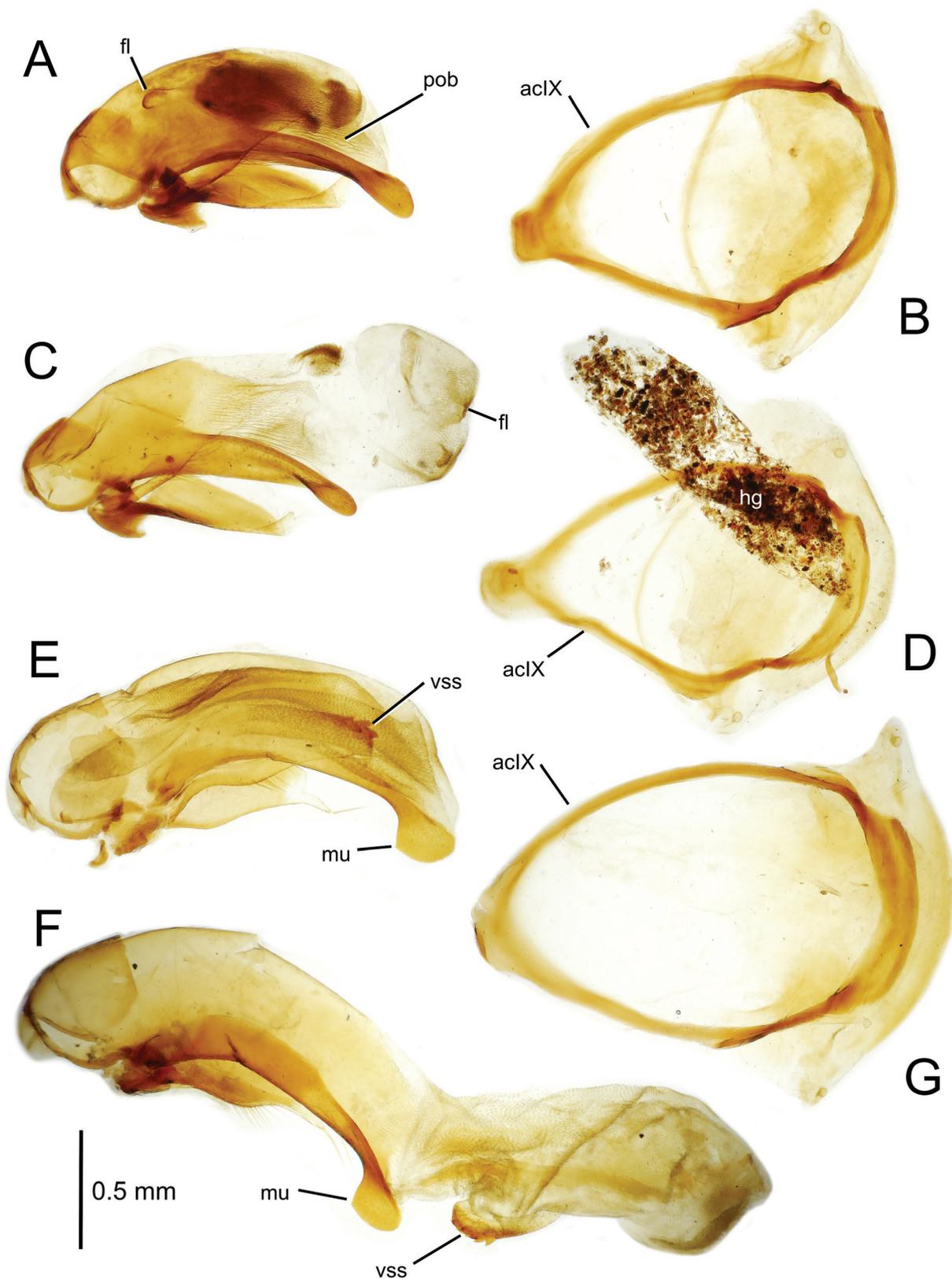


Figure 4. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. A–D. *T. canaliculus*; Malleco Prov., P. N. Nahuelbuta. A, B. (FMNH). C, D. (OSAC). E–G. *T. duponchelii*; Arauco Prov., Caramavida. E. (NMNH). F–G. (MCZ). For abbreviations used to label structures see Table 1.

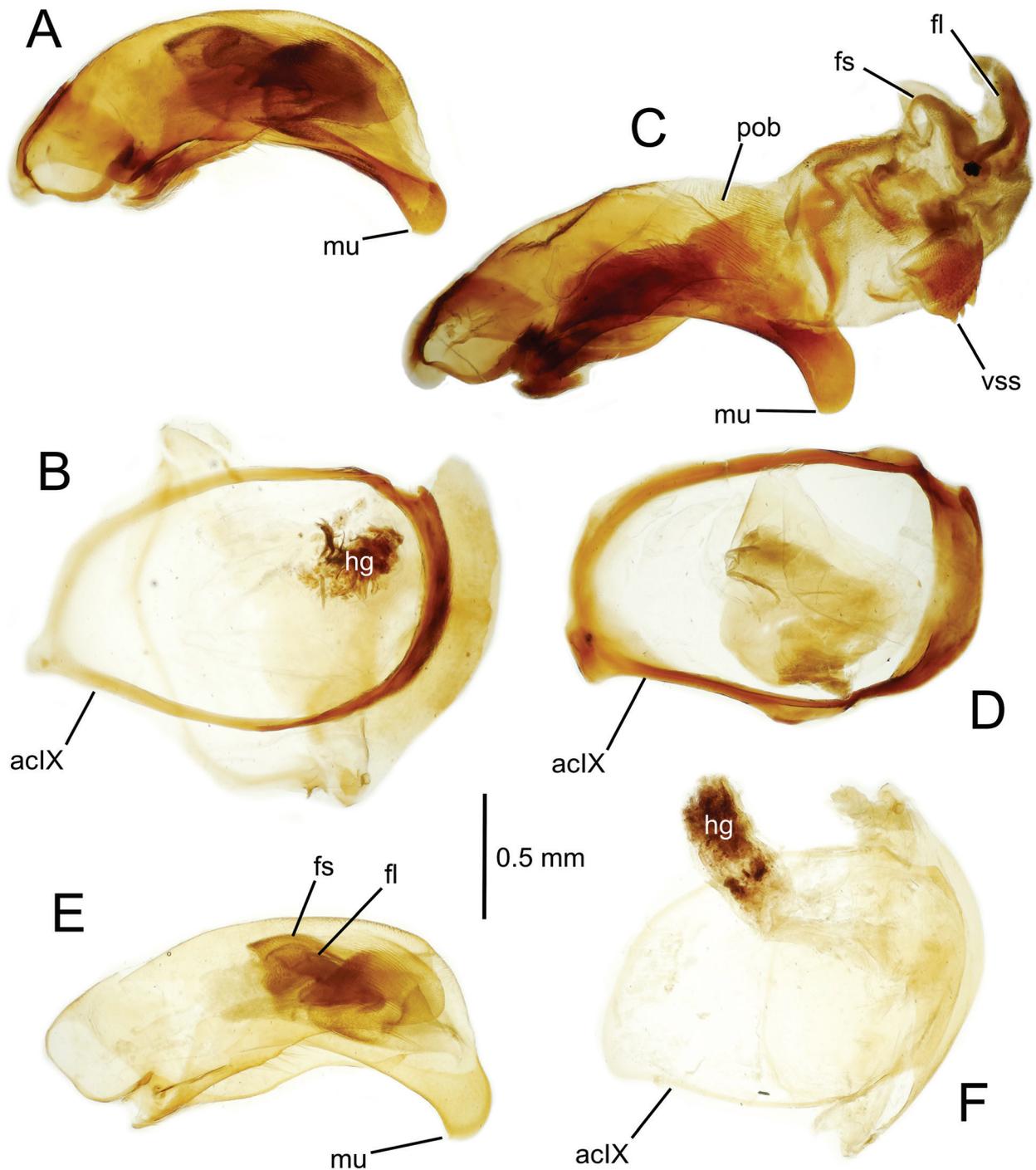


Figure 5. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. **A–D.** *T. minimucro*. **A, B.** Cautín Prov., Bellavista (EMEC). **C, D.** Llanguihue Prov., P. N. Vicente Pérez Rosales (FMNH). **E, F.** *T. fieldianus*. **E.** Osorno Prov., Maicolpue (FMNH). **F.** Valdivia Prov. La Unión (FSCA). For abbreviations used to label structures see Table 1.

no, SW slope, c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton & Thayer (FMNH, 3). Malleco Prov.: P. N. Nahuelbuta, Los Portones entrance, 2.3 km W, *Nothofagus dombeyi* + ?*antarctica*, mostly open understory, lot 1057, pyr. fogging old *Nothofagus*

logs, 37°49.41'S, 72°58.95'W, 1150 m el., 25-xii-2002, Newton, Thayer & Chani (FMNH, 1). Osorno Prov., P. N. Puyehue, Aguas Calientes, forest litter on trail, lot P#85-43, sifting 40°43.66'S, 72°18.11'W 500 m el. 20-xii-1984, S. & J. Peck (FMNH, 1), Anticura, 4 km E, 40°39.73'S, 72°08.1'W, 460 m el., 31-xii-1996, Newton & Thayer (DRM 97-021, DNA voucher DNA0459,

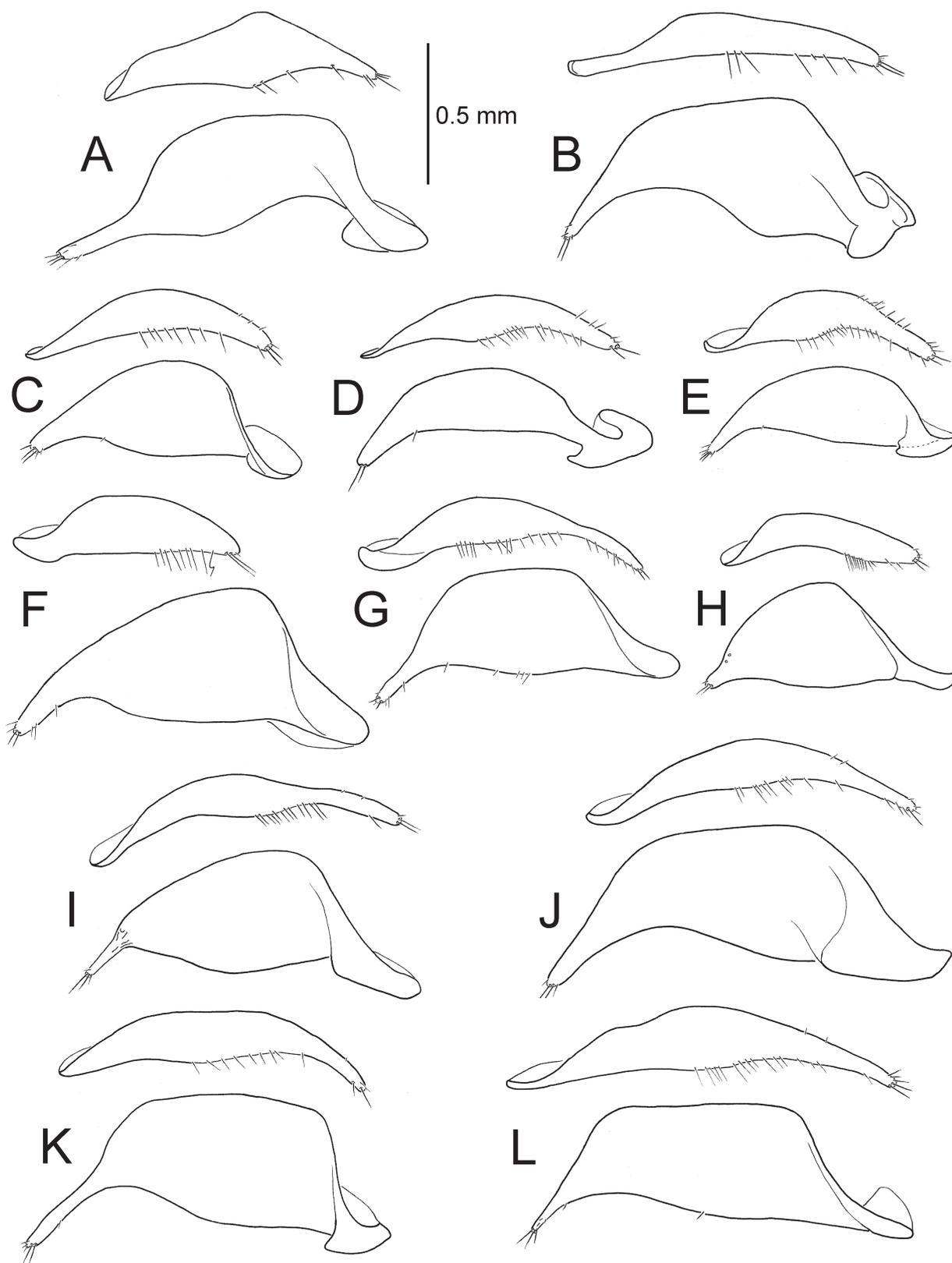


Figure 6. Paired sets of left parameres (above) and right parameres (below), ectal view, for male specimens of *Tropopterus* spp. Parameres are in anatomically correct orientation with ventral surface toward bottom of drawing. **A, B.** *T. giraudyi*. **A.** Malleco Prov., P. N. Nahuelbuta (FMNH). **B.** Chili, “*Tropopterus nitidus* Sol.” [sic], Chaudoir Coll. (MNHN). **C.** *T. peckorum*; Quillota Prov., P. N. La Campana (FMNH). **D, E.** *T. robustus*. **D.** Malleco Prov., P. N. Contulmo (CMNH). **E.** Cautín Prov., Bellavista (CAS). **F, G.** *T. canaliculus*. **F.** Malleco Prov., P. N. Nahuelbuta (FMNH). **G.** Arauco Prov., Caramavida (NMNH). **H–I.** *T. duponchelii*. **H.** Talca Prov., Altos de Vilches (MNHN). **I.** Arauco Prov., Caramavida (MCZ). **J, K.** *T. minimicro*. **J.** Cautín Prov., Bellavista (EMEC). **K.** Llanquihue Prov. P. N. Vicente Pérez Rosales (FMNH). **L.** *T. fieldianus*; Valdivia, La Union (FSCA).

FMNH on loan to OSAC, 1), rainforest w/ large *Saxegothaea*, lot 985-2, pyr.-fogging old logs, 40°39.73'S, 72°08.10'W, 460 m el., 30-i-1997, Newton & Thayer (FMNH etoh, 1), Puyehue, 10 km E, 40°37.00'S, 72°30.68'W, 24-i-1951, Ross & Michelbacher (CAS, 2), 20 km E, 40°36.66'S, 72°24.83'W, 26-i-1951, Ross & Michelbacher (CAS, 1). San Antonio Prov., Santo Domingo, 33°35.50'S, 71°36.33'W, 1-xi-1972 (MNHN, 1). Santiago Prov., Santiago (lectotype, paralectotype), 33°26.75'S, 70°40.12'W, Solier (MNHN, 2). Valdivia Prov., Chaihuin, Res. Costera Valdiviana, lot CH2006.13.H.i.2, 40°03.71'S, 73°35.32'W, 443 m el., 14-i-2006, Will (EMEC etoh, 1), lot CH2006.16.i.2, 40°01.67'S, 73°31.85'W, 511 m el., 16-i-2006, Will (EMEC etoh, 1), headlamp search, 39°58.32'S, 73°39.23'W, 77 m el., 10-xi-2008, Will (EMEC, 1), Corral, 39°53.25'S, 73°25.69'W, xii-1905, Thaxter (MCZ, 3), i-1906, Thaxter (MCZ, 1). Valdivia Prov., P. N. Oncol, Mirador Pilocura, Sendero, 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC, 2), road to P. N. Oncol, 39°41.98'S, 73°20.65'W, 513 m el., 9-xi-2008, Will (EMEC, 1), Cerro Oncol trail, 39°41.89'S, 73°18.07'W, 500 m el., 11-i-2006, Maddison & Seago (OSAC, 2), Puerto Fui, 12 km SSE, Lago Pirehueico, Site F, Coigue-Lenga Forest, *N. dombeyi*, *N. alpina*, *N. pumilio*, under *Nothofagus* bark 39°58'S, 71°50'W, 1030 m el., 10-i-1988, Ashworth, Figiseth & Maliscke (NDSU, 1), Valdivia Res., Punta Curiñanco, CH2006.13.i.2, 39°41.25'S, 73°21.50'W, 150 m el., 13-i-2006, Will (EMEC etoh, 1). No other data except “x-70” (MNHN, 1); “1611”, Chaudoir colln. (MNHN, 1); “Chili // *Tropopterus nitidus* [sic]”, Bates colln. (MNHN, 1).

Distribution and habitat. This is the most widely distributed species of *Tropopterus*. with localities ranging in latitude from 33°27'S–42°37'S (Fig. 9B). Known localities thus occur within the Santiagan, Northern Valdivian, and the northern portion of the Southern Valdivian entomofaunal provinces (O'Brien 1971). Specimens have been collected by sifting in Valdivian rainforest with *Nothofagus*, by pyrethrin fogging of old *Nothofagus* logs, under logs and rocks, and by beating vegetation. *Tropopterus giraudyi* has been contemporaneously collected in localities shared with: *Metacorneolabium exuberatum* Thayer (1985; Argentina: Neuquén Prov., Pucara, 24–25-i-1972, Herman, NMNH); *Glypholoma chepuense* Thayer (1997; Chile: Chiloé Prov., Chepu, MNHN); *Andotypus ashworthi* Spangler (Fikáček et al. 2014; Chile: Llanquihue, P. N. Vicente Pérez Rosales, 9.2 km NE Ensenada on road to Petrohué, FMNH); *Anaballatus chilensis* (Newton et al. 2017; Chile: Cautín Prov., Bellavista, N. shore Lago Villarrica, FMNH); Chile: Malleco Prov., P. N. Nahuelbuta, 2.3 km W Los Portones entrance, FMNH; and Chile: Osorno Prov., P. N. Puyehue, 4.1 km E Anticura, FMNH). The Neuquén Province, Argentina record from Lee Herman, above, represents the only Argentine record for both *Tropopterus* and *Metacorneolabium* Steel (Thayer 1985).

3. *Tropopterus peckorum* sp. nov.

<http://zoobank.org/2E5BF389-1E6B-4C7D-A3CA-5ACF5E7A536F>
 Figures 1C, 3C, D, 6C, 9C, 10

Diagnosis ($n = 3$). Beetles of this species are distinguished by their small size (standardized body length 5.5–6.0 mm) and narrow bodies. The latter is evidenced by: very flat eyes, ocular ratio = 1.30–1.33; a narrow, quadrate pronotum, MPW/PL = 1.21–1.31; and narrow, relatively flat elytra, MEW/EL = 0.66–0.68. The pronotal median base is longitudinally wrinkled near the narrow basal marginal bead, whereas the anterior margin is smooth medially, with an anterior marginal bead present only in the lateral half of each side. The sutural stria is evident as a series of minute, isolated punctures on the elytral disc, whereas it is effaced on the elytral apex. The elytral basal groove is present, continuous from laterad the parascutellar seta to the obtuse angle where it joins the lateral marginal depression. Ventrally the prosternum is broadly flattened to slightly depressed medially anterad the prosternal process, and the mesepisternum bears 7 or 8 linearly arranged punctures in the dorsoventral depression. The vertex is glossy, the pronotum glossy with indistinct transverse lines, and the elytral disc is covered with an elongate transverse mesh, the sculpticells 2–4× as broad as long.

Description. Head capsule narrow; eyes flat, ocular lobe little-protruded, compound eye covering 0.82–0.83 length of ocular lobe, 18–20 ommatidia across horizontal diameter of eye; antennomeres broadened apically, moderately elongate, antennomere 9 length 1.83× greatest diameter; mandibles elongate, distance from anterior condyle to apex of left mandible 1.91× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.86× length from lateral apex to base, paramedial pits deep; ligular apex truncate, broad, two setae separated by three setal diameters; paraglossae extended as far beyond ligular margin as distance from paraglossal base to ligular margin. Pronotum relatively narrow, lateral margins straight to slightly sinuate before right to slightly acute hind angles; anterior transverse impression broad and shallow across width; front angles only slightly protruded; lateral marginal depression narrowest at midlength, slightly broader at front angle, broadened progressively toward hind angle; lateral seta separated from lateral marginal depression by one diameter of articulatory socket; laterobasal depression quadrate, oblique with deep inner groove and upraised tubercle in middle of depression. Elytra smooth, striae 2–4 traceable on disc as longitudinal series of minute lenticular punctures, striae 5–7 obsolete; stria 8 present anteriorly near posterior portion of anterior lateral setal series, very shallow at midlength, and deep, continuous inside posterior setal series; lateral marginal depression broad, lined with transverse sculpticells; subapical sinuation broad, shallow, elytral plica evident in lateral view. Metepisternum equitrapezoidal, the maximal width and lateral length subequal; metasternal process rounded apically, apex

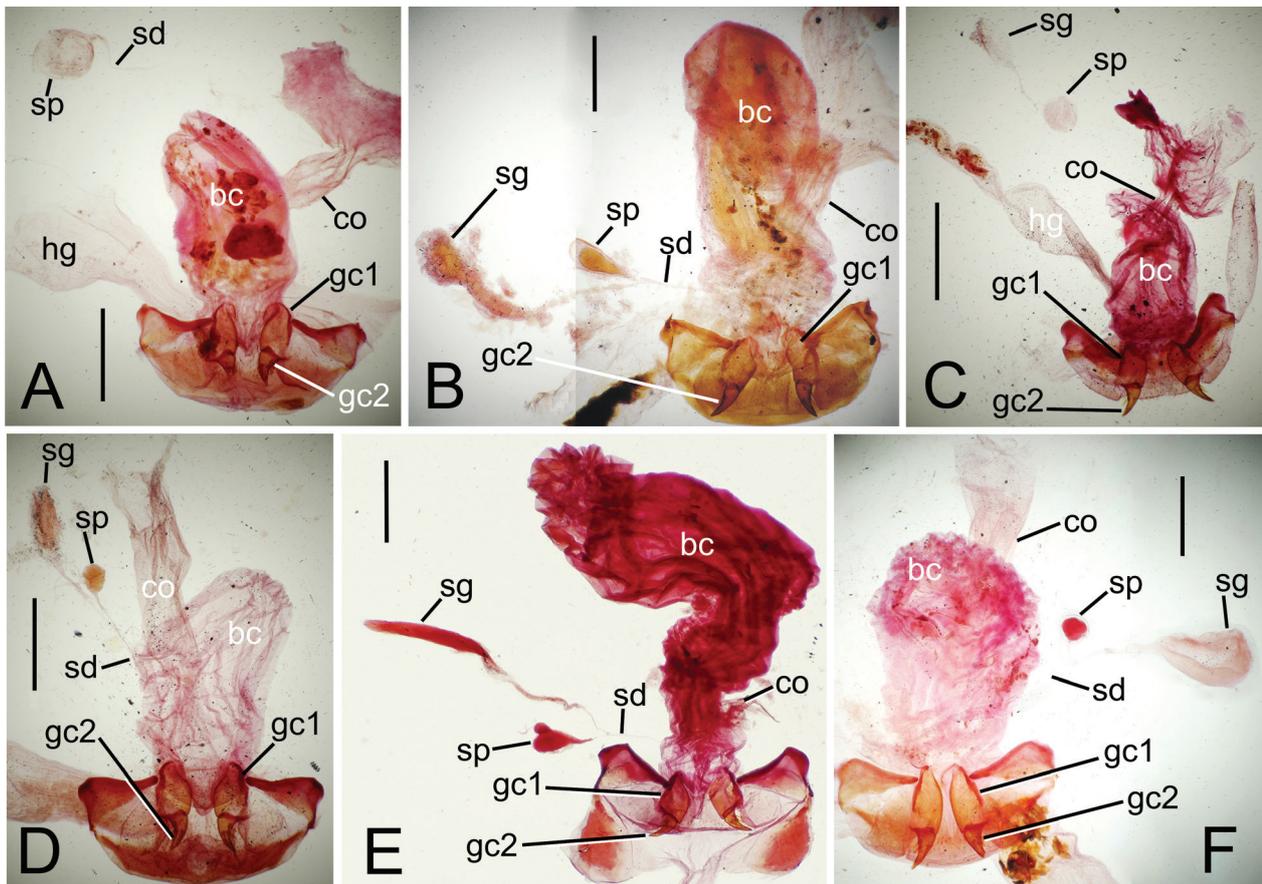


Figure 7. Female reproductive tract and gonocoxae of abdominal segment IX, ventral view. **A.** *T. montagnei*; Petorca Prov., Q. Tigre Zapallar, Catapilco (MNH). Spermatheca disassociated from bursal assemblage. **B.** *T. giraudyi*; Llanquihue Prov., P. N. Vicente Pérez Rosales (FMNH). **C.** *T. robustus*; Malleco Prov., M. N. Contulmo (FMNH). **D.** *T. canaliculus*; Malleco Prov., P. N. Nahuelbuta (FMNH). **E.** *T. duponchelii*; Arauco Prov., Caramavida (MCZ). **F.** *T. minimucro*; Valdivia Prov., P. N. Oncol (EMEC). For abbreviations used to label structures see Table 1. Vertical scale bars: 0.5 mm.

broadly and the side narrowly upraised in a lateral bead. Abdominal ventrites 3–6 broadly depressed laterally, suture between ventrites 1 and 2 nearly straight, surface of ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 depressed, intersegmental membranes punctate; female apical abdominal ventrite with two setae each side, four shorter medial setae arranged in an apically broader trapezoid. Body coloration pale (specimens appear teneral), concolorous rufobrunneous, legs not paler; ventral surface concolorous, with elytral epipleura, metepisternum, and apical half of ventrite 6 paler, rufoflavous.

Male genitalia ($n = 1$). Aedeagal median lobe broadest dorsoventrally at base, narrowed slightly to a narrowly rounded apex (Fig. 3C); internal sac with a sclerotized flagellar complex (teneral specimen), with a putative, short flagellum visible. Antecostal apodeme of abdominal IX narrowly rounded, the apex not extended beyond lateral arms (Fig. 3D, although teneral specimen may not have sclerotized fully to attain mature configuration; e.g. Song 2004). Right paramere elongate, slightly broader at midlength with broadly rounded apex, two longer apical

setae complemented by eight setae along ventral margin and several very small setae on the dorsoapical surface (Fig. 6C); left paramere broad basally, with short narrow apical extension that bears two longer apical setae plus several very small subapical setae.

Holotype male (FMNH): CHILE: Quillota Prov. / Olmue, La Campana / N.P., 2.XII.1984 // FMHD#85-889, / hygrophilous forest / leaf litter, S.&J. / Peck, P#85-4, Berlese / FIELD MUSEUM NAT. HIST. // Tropopterus / Measured / Specimen #2 / det. J.K. Liebherr 2019 // HOLOTYPE / Tropopterus / peckorum/ J.K. Liebherr 2019 (black-margined red label).

Paratypes: Chile: Quillota Prov., P. N. La Campana (Sector Granizo), Cajón La Opositora, 685 m el., 32°58.80'S, 71°06.93'W, 29.xi–29.xii.2002, sclerophyll forest, ?w/*Nothofagus obliqua*, FMHD#2002-019, flight intercept trap, Thayer, Newton, Solodovnikov, 1045, FIELD MUSEUM NAT. HIST. (FMNH, 2)

Etymology. This species is named to honor Stewart Peck and Jarmila Kukalova-Peck for their immense contributions to systematic entomology, and their numerous discoveries of Austral biodiversity.

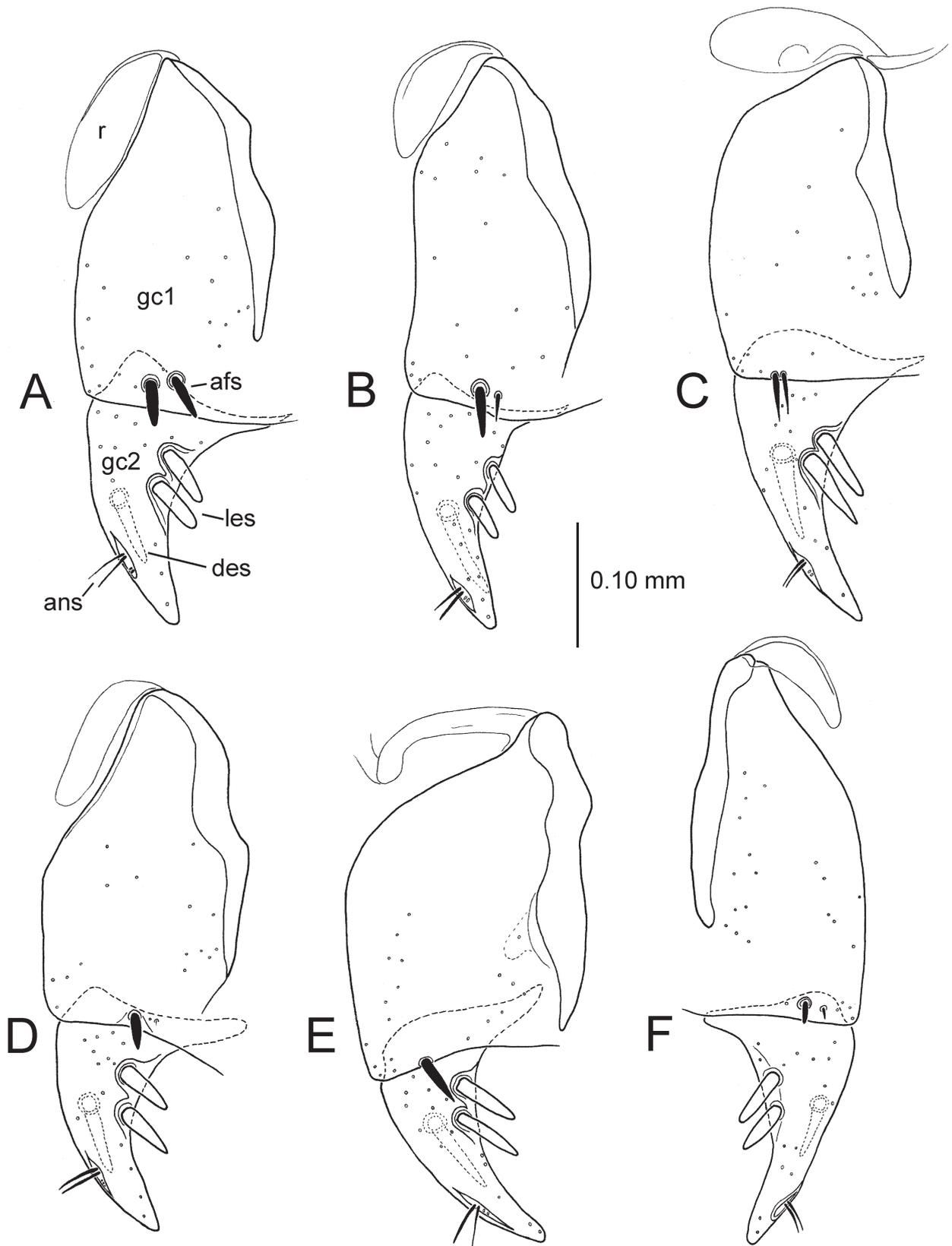


Figure 8. Left gonocoxa (except where noted), ventral view, for *Tropopterus* spp. Specimen information is parallel to that in Figure 7A–F. For abbreviations used to label structures see Table 1. **A.** *T. montagnei*. **B.** *T. giraudyi*. **C.** *T. robustus*. **D.** *T. canaliculus*. **E.** *T. duponchelii*. **F.** *T. minimucro* (right gonocoxa).

Distribution and habitat. This species is known from localities in the Santiagan entomofaunal province (O'Brien 1971) at latitudes near 33°S (Fig. 9C). Both collecting events are associated with ground-level microhabitats, either in forest litter via Berlese sifting, or in an octopus-baited carrion trap in sclerophyll forest with *Nothofagus obliqua* (Briseau de Mirbel).

4. *Tropopterus robustus* sp. nov.

<http://zoobank.org/A6E5A597-16AB-45C9-BBC8-7F6448078F50>

Figures 1D, 3E–H, 6D–E, 7C, 8C, 9D, 10

Diagnosis ($n = 5$). The combination of small, very broad body, and punctate discal elytral striae 1 and 2 (Fig. 1D) diagnoses this species: standardized body length 5.2–6.0 mm; pronotal MPW/PL = 1.36–1.41; and elytral MEW/EL = 0.74–0.81. The pronotal hind angle is right to acute, the apex of the angle denticulate, and the lateral margins convergent just before the angles. The pronotum anterior margin is beaded only along the lateral 1/3 to 1/4 each side. The parascutellar striole is absent, and instead the sutural stria continues to the well-developed basal groove laterad the scutellum. These small beetles have the most well-developed elytral striae in the genus, striae 3–7 traceable on the disc, and the sutural stria is narrowly and smoothly grooved apically. Ventrally the prosternum is deeply depressed medially from the prosternal process 2/3 of the way to the anterior prothoracic margin. The mesepisternum is mostly smooth, with only 2 or 3 punctures in a furrow at the deepest part of the sclerite's concave surface. And the metepisternum and metepimeron are fused along the lateral margins of those sclerites; a derived character otherwise only observed in *T. fieldianus*. The microsculpture is distinctive, with the vertex covered with well-developed isodiametric to slightly transverse microsculpture, the pronotum covered with a dense transverse mesh, sculpticell breadth 3–4× length, and the elytral disc covered with dense transverse lines connected into a mesh over only portions of the surface.

Description. Head capsule broad, eyes moderately convex, ocular ratio 1.35–1.48, eyes covering most of moderately protruded ocular lobe, ocular lobe ratio 0.90–0.92, horizontal diameter of eye crossing 20 ommatidia; antennae relatively stout, antennomere 9 length 1.67× maximal diameter; mandibles short, distance from anterior condyle to apex of left mandible 1.67× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.75× length from lateral apex to base, paramedial pits moderately deep; ligular apex truncate, two setae separated by four setal diameters, paraglossae elongate, extended beyond ligular apex more than distance from base to ligular margin. Pronotum broad, lateral margins convergent before minutely denticulate hind angles; basal margin lined with well-developed marginal bead, median base anterad bead longitudinally, shallowly strigose medially, minutely punctate laterally; median longitudinal impression with

elongate lenticular pit at front of median base, narrow and shallow on disc, deep near anterior transverse impression; anterior transverse impression broad and shallow across width; anterior margin beaded only in lateral 1/3 to 1/4 each side, smooth medially; front angle protruded, subangulate mesally, rounded laterally; lateral seta separated from very narrow lateral marginal depression by two diameters of setal articulatory socket; laterobasal depression broadly subquadrate, central tubercle connected anteriorly to disc, mesal surface irregular near punctate median base. Elytra broadly hemiovoid, basal groove deep, slightly irregular at bases of striae, angle with lateral marginal depression obtuse-rounded; sutural stria deeply punctate on disc, the punctures isolated, smooth and moderately deep apically, the sutural striae of the two elytra bordering an upraised sutural callus at conjoined elytral apices; stria 8 deep mesad anterior and posterior series of lateral setae, shallow at midlength, variously interrupted there; lateral elytral setal series variable, with either: anterior series of 5 setae, 2 intermediate setae, and 6 apical setae; or 6 anterior setae, 2 intermediate setae, and 6 posterior setae; or 7 anterior setae, 2 intermediate setae, and 4 posterior setae; lateral marginal depression narrow anteriorly, broadened in apical half, lined with transverse sculpticells apically; subapical sinuation distinctly concave, elytral plica visible in dorsolateral view. Metepisternum slightly elongate, maximal width 0.82× lateral length. Abdomen with visible ventrites 3–6 broadly depressed laterally; suture between ventrites 1 and 2 nearly straight, ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 slightly depressed, but no punctures visible along suture; female apical abdominal ventrite with two setae each side, four shorter medial setae arranged in an apically broader trapezoid. Coloration of dorsal surfaces rufopiceous to piceous with silvery reflection; palpomeres, antennae, legs, and pronotal and elytral margins rufobrunneous; ventral body surface rufopiceous, though proepipleuron dark rufous, elytral epipleuron dark anteriorly and rufobrunneous posteriorly, and apical half of ventrite 6 rufobrunneous.

Male genitalia ($n = 5$). Aedeagal median lobe broad dorsoventrally, apex broadly downturned apicad ostium, with a small mucro on ventrobasal face of apex (Fig. 3E); internal sac with sclerotized spicular fields (Fig. 3E), including a ventrobasal spicular sclerite (Fig. 3G); short flagellum and flagellar sheath both present. Antecostal apodeme of abdominal IX extended distally, the extension ranging from broad and expanded distally (Fig. 3D), to narrow and parallel-sided (Fig. 3H). Right paramere varying slightly in length, the ventral surface lined with many (14–18) setae, the apex bearing two longer setae, and the apicodorsal surface lined with five to eight small setae (Fig. 6D, E); left paramere broadly rounded dorsally, with length varying in concert with right paramere (Fig. 6D, E), apex of variable length and breadth, bearing two longer apical setae and also small subapical setae of variable position and number.

Female reproductive tract ($n = 1$). Bursa copulatrix broader basally, with narrow apex, length twice breadth, compressed under microslide cover slip (Fig. 7C), surface relatively thick, translucent; spermatheca globose; spermathecal gland ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with apical fringe of two slender setae (Fig. 8C); apical gonocoxite 2 triangular, base moderately extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype male, dissected (FMNH): CHILE: Malleco Prov., / Puren Nat. Mon. / Contulmo, 350 m, / 13.II.1985 // FMHD#85-1001, mixed / forest litter, S. & J. / Peck, P#85-118. / berlese / FIELD MUSEUM NAT. HIST. // dissection vial // *Tropopterus / robustus / Liebherr* ♂4 / J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus / robustus / J.K. Liebherr* 2019 (black-margined red label).

Paratype: Chile: Cautín Prov., Bellavista, Lago Villarrica, N shore, Berlese wet forest litter, 39°12.55'S, 72°08.14'W, 30-i-1986, Platnick & Schuh (CAS, 1), Villarrica, upper Flor del Lago, lot CH2002/3.41, 39°10.00'S, 71°59.07'W, 700 m el., 12-i-2003, Will (EMEC etoh, 5), Villarrica, 15 km S, *Nothofagus* woods, 39°24.62'S, 72°13.69'W, 14-ii-1993, Ward (CMNH, 2). Malleco Prov., M. N. Contulmo, Sendero Lemu Mau, *Nothofagus obliqua-Eucalyptus cordifolia* ++ w/ fern & bamboo understory, lot 1059, FMHD#2002-063, Berlese leaf and log litter, 38°00.74'S, 73°11.13'W, 410 m el., 8-xii-2002, Newton & Thayer (FMNH, 13), lot 1059, FMHD#2002-061, Flight intercept trap, 38°00.74'S, 73°11.13'W, 410 m el., 8-24-xii-2002, Thayer, Newton, Solodovnikov, Chani & Clarke (FMNH, 1), M. N. Puren, Contulmo, lot FMHD#85-1001, Berlese mixed forest litter, 38°00.90'S, 73°13.76'W, 13-ii-1985, S. & J. Peck (FMNH, 1), no other data, lot CH2002/3.124, Will (EMEC etoh, 1). Valdivia Prov., Huilohuilo, Neltume, 1 km WSW, Site B, Valdivian Rain Forest, leaf litter, sifting/photoeclector, 39°51'S, 71°57'W, 390 m el., 28-xi-1987, Ashworth, Figiseth & Maliscke (NDSU, 1), 7-i-1988, Ashworth, Figiseth & Maliscke (NDSU, 1), Pte. Blanco, Choshuenco, 8 km NW, Site A, Valdivian Rain Forest, leaf litter, sifting/photoeclector, 39°48'S, 72°05'W, 180 m el., 25-xi-1987, Ashworth, Figiseth & Maliscke (NDSU, 1).

Etymology. The adjectival species epithet *robustus* is used to denote the broad body form of beetles of this species.

Distribution and habitat. This species is distributed from latitude 38°S–39°51'S (Fig. 9D), within the Northern Valdivian entomofaunal province (O'Brien 1971). It has been recovered from Berlese samples of mixed forest litter, wet forest litter, or combined leaf and log litter. One specimen was collected in a ground-level collecting pan associated with a flight intercept trap. This species has been collected contemporaneously with the leiodid beetle *Anaballetus chilensis* (Newton et al. 2017: Chile: Cautín Prov., Bellavista, N shore Lago Villarrica, FMNH; and Chile: Malleco Prov., N. M. Contulmo, Sendero Lemu Mau, FMNH).

5. *Tropopterus canaliculus* sp. nov.

<http://zoobank.org/93355D10-1B12-42EA-9907-ED6D43477E92>

Figures 1E, 4A–D, 6F, G, 7D, 8D, 9E, 10

Diagnosis ($n = 5$). Both this species and *T. duponchelii* exhibit subparallel elytra with the sutural stria represented by a series of isolated punctures on the disc, and the second stria much reduced though still visible as a series of minute punctures (Fig. 1E, F). Individuals of *T. canaliculus* with more reduced second elytral striae could be confused with those of *T. minimucro*; however, that species is characterized by the absence of a basal elytral groove, the elytral surface smoothly convex inside the humeral tooth at the anterior end of the lateral marginal depression (compare Figs 1E, 2B). Compared to *T. duponchelii*, *T. canaliculus* can be characterized by the prosternum bearing a median, canaliculate depression that extends from the ventral face of the prosternal projection 2/3 the distance toward the anterior pronotal margin, whereas the prosternum of *T. duponchelii* is medially flattened to broadly depressed, not narrowly canaliculate. The two species can also be told by individuals of *T. canaliculus* exhibiting a narrower pronotum (MPW/PL = 1.20–1.25 versus 1.25–1.32 for *T. duponchelii*) and a glossier upper body surface. *Tropopterus canaliculus* has the vertex glossy with indistinct transverse sculpticells over portions of the surface, the pronotum also glossy, and the elytral disc glossy with indistinct transverse sculpticells visible near depressed portions of the surface such as the stria punctures, and minute micropunctures regularly distributed across the glossy surface. The dorsal microsculpture of *T. duponchelii* is much more developed, with both the pronotum and elytra bearing dense transverse lines that cause iridescence of the latter. In this species the pronotum is sparsely punctate in the laterobasal depressions and lateral portions of the median base, versus smooth in *T. duponchelii*, and the anterior pronotal margin is completely beaded, versus smooth and unmarginated across the median half in *T. duponchelii*. The standardized body length = 5.8–7.5 mm; a smaller though not diagnostic range of sizes compared to *T. duponchelii* (below).

Description. Head capsule broad basally, eyes moderately convex, ocular ratio 1.40–1.50; eyes covering much of abruptly protruded ocular lobe, ocular lobe ratio 0.85–0.90; horizontal diameter of eye crossing 25 ommatidia; antennomeres moderately elongate, length of antennomere 9 2.0× maximal diameter; mandibles moderately elongate, distance from anterior condyle to apex of left mandible 1.81× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.86× length from lateral apex to base, deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by four setal diameters; paraglossae extended as far beyond ligular margin as distance from their base to ligular margin. Pronotal lateral margins convex, hind angles distinctly denticulate; basal margin with complete marginal bead, median base sparsely punctate across breadth, the punctures continuing across lateroba-

sal depressions; median longitudinal impression with lenticular depression at front of median base, narrow and deep on disc; anterior transverse impression broad and shallow medially, traceable to front angles, anterior callosity broadly convex; anterior margin completely beaded, the bead continuous medially; front angle slightly protruded, right angled; lateral marginal depression very narrow in apical half, broadened from lateral seta to laterobasal depression; lateral seta separated from lateral marginal depression by the diameter of setal articulatory socket; laterobasal depression rugosely punctate, surface upraised in middle of depression; surface of proepisternum slightly irregular, as if beaten by a ball-peen hammer. Elytra broad, sides subparallel, humeri broad; basal groove deep, continuous from anterad parascutellar seta to tightly rounded humeral angle; parascutellar striole absent, sutural stria reaching basal margin mesad parascutellar seta; sutural stria a series of isolated punctures on disc, continuous and smooth apically, the striae of both elytra bordering upraised sutural callus associated with conjoined elytra; surface of elytra depressed mesad subapical and apical elytral setae; stria 8 continuous throughout length; lateral marginal depression broad, lined with transverse sculpticells; subapical sinuation broad, moderately excavated, elytral plica evident in dorsolateral view. Mesepisternum with broad vertical depression lined with ~8 punctures in 2 or 3 vertical rows; metasternal process narrowly rounded apically, apex broadly and sides more narrowly upraised; metepisternum somewhat elongate, maximal width 0.78× lateral length. Abdomen with ventrites 3–6 broadly depressed laterally, suture between ventrites 1 and 2 nearly straight, ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 depressed, intersegmental membranes punctate; apical female abdominal ventrite with 2 setae each side, plus a median group of two to four setae, subequal in length; if two nearly in line with lateral setae, if four aligned in an apically broader trapezoid. Coloration of dorsal body surface subtly tricolored, head and pronotum dark rufous, elytra darker, rufopiceous, elytral lateral marginal depressions translucent rufobrunneous; antennae, mouthparts, and legs rufobrunneous; ventral body surface rufopiceous, apex of elytral epipleuron slightly paler, apex of abdominal ventrite 6 narrowly paler to concolorous.

Male genitalia ($n = 8$). Aedeagal median lobe broad dorsoventrally, but with sclerotized ventral surface of shaft narrow and terminated in a narrow, smooth, spoon-like apex (Fig. 4A, C); internal sac with flagellum small, apical. Antecostal apodeme of abdominal IX broadly angulate distally, the short distal extension very broad (Fig. 4B, D). Right paramere of variable length, length not associated with length of left paramere (Fig. 6F, G), ranging from shorter and broader to more elongate with an attenuated apical extension, the ventral surface bearing from 8–20 setae, two longer setae present near or at apex; left paramere much broader basally, with apical extension ranging from an evenly narrowed projection (Fig. 6F) to a narrow, parallel digitiform extension (Fig. 6G),

two longer setae present at apex, plus a variable number of subapical and ventral setae.

Female reproductive tract ($n = 1$). Bursa copulatrix columnar, broadly rounded apically, length 1.75× breadth, compressed under microslide cover slip (Fig. 7D), bursal walls thin, nearly transparent; spermatheca globose; spermathecal gland elongate-ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with one large apical fringe seta, a second small seta also present unilaterally (Fig. 8D); apical gonocoxite 2 falciform, base extended laterally, with two lateral ensiform setae, one dorsal ensiform setae, and two apical nematiform setae.

Holotype male dissected (CAS): Crest of Sierra / Nahuelbuta / Elev. 1200 m // W. of Angol / CHILE, I-3-51 // Ross and / Michelbacher / Collectors // dissection vial // Tropopterus / canaliculus / Liebherr ♂4 // HOLOTYPE / Tropopterus / canaliculus / J.K. Liebherr 2019 (black-margined red label). The type locality is in Malleco Prov., with geographic coordinates estimated to be 37°47.76'S, 73°02.27'W.

Paratypes. Chile: Arauco Prov., San Alfonso, Carmañavida, above, 37°42.75'S, 73°09.00'W, 16–17-x-1969, Flint & Barria (NMNH, 1). Malleco Prov., P. N. Nahuelbuta, lot DRM 06.046, DRM DNA2200, 37°48.98'S, 73°05.7'W, 1312 m el., 7-i-2006, Maddison (OSAC, 1), Los Portones entrance, 4.5 km W, emergent *Nothofagus* spp., *Araucaria aurucana*, *Chusquea* understory, lot 975, pyr.-fogging old logs, 37°49.25'S, 72°59.82'W, 1300 m el., 7-ii-1997, Newton & Thayer (FMNH etoh, 1), Guarderia Pichinahuel, E of, *Araucaria-Nothofagus dombeyi* w/ *Chusquea* bamboo, lot 1054, in rotten logs, 37°48.20'S, 73°01.41'W, 1290 m el., 7-xii-2002, Clarke & Solodovnikov (FMNH, 5), lot 1054, pyr. fogging live *Araucaria*, 37°48.20'S, 73°01.41'W, 1290 m el., 24-xii-2002, Newton & Solodovnikov (FMNH, 1), lot 1054, FMHD#2002-094, Berlese debris under bark large *Araucaria* log, 37°48.20'S, 73°01.41'W, 1290 m el., 24-xii-2002, Newton & Solodovnikov (FMNH, 4), Los Portones entrance, 2.3 km W, *Nothofagus dombeyi* + ?*antarctica*, mostly open understory, lot 1057, pyr. fogging old *Nothofagus* logs, 37°49.41'S, 72°58.95'W, 1150 m el., 25-xii-2002, Newton, Thayer & Chani (FMNH, 6).

Etymology. The species epithet *canaliculus* references the narrow, deep median prosternal depression present in these beetles. The epithet is to be treated as a noun.

Distribution and habitat. This species' distribution lies near 38°S (Fig. 9E) in the Northern Valdivian entomofaunal province (O'Brien 1971). Most records are from forest-floor microhabitats, either by pyrethrin fogging of old, rotten *Nothofagus* logs, or in Berlese siftate from under bark of a large *Araucaria* log. One specimen was collected via pyrethrin spraying onto a live *Araucaria* trunk. This species was collected with *Anaballatus chilensis* at two sites (Newton et al. 2017: Chile: Malleco Prov., P. N. Nahuelbuta, 2.3 km W Los Portones entrance, FMNH, and P. N. Nahuelbuta, E of Guarderia Pichinahuel, FMNH).

6. *Tropopterus duponchelii* Solier

Figures 1F, 4E–H, 6G, I, 7E, 8E, 9F, 10

Tropopterus duponchelii Solier 1849: 213; Reed 1874: 58.

Tropidopterus duponcheli Gemminger and Harold 1868: 385 (unjustified emendations).

Tropopterus nitidus Solier 1849: 213 (synonymy Chaudoir 1876: 124).

Diagnosis ($n = 5$). To distinguish this species from *T. canaliculus* see that species' diagnosis above. From all others, this species can be recognized by the medially, broadly flattened to broadly depressed prosternum, the depression not narrow and deep. The elytra bear a well-developed, dense, transverse-line microsculpture that results in a distinctly iridescent surface, whereas the vertex is covered with a shallow isodiametric mesh transversely stretched in parts, and the pronotum is covered with shallow transverse lines that result in only subtle iridescence. The eyes are moderately convex, ocular ratio = 1.37–1.46, with 20–25 ommatidia crossed by a horizontal diameter of the eye. The pronotal hind angles are obtuse and sharp, with the lateral margins slightly sinuate before the angles, and the pronotal median base and laterobasal depressions are smooth (Fig. 1F). The elytra are broad basally, with the basal groove well developed and meeting the lateral marginal depression at a distinct, obtuse angle, with a minute tooth projected posterad from that juncture. The mesepisternum is smooth throughout the dorsoventral depression of that sclerite. Standardized body length = 6.7–8.1 mm.

Male genitalia ($n = 4$). Aedeagal median lobe broad dorsoventrally to broadly rounded apex, the apex with broad, blunt mucro on ventrobasal surface (Fig. 4E, F); aedeagal internal sac with stout, serrate ventrobasal spicular sclerite and elongate, moderately sclerotized flagellum. Antecostal apodeme of abdominal IX rounded distally, the juncture of the lateral arms only slightly broader (Fig. 4G). Right paramere of variable length, ranging from short and broadly parallel-sided, to more elongate with an apical attenuated apex (Fig. 6H, I), ventral surface with about 13 setae in apical half, apex with two longer setae, and apicodorsal surface with several very small setae of variable position; left paramere varying in length in concert with right paramere, ranging from short and stout with a very short apical extension, to longer with a narrow, digitiform extension connected to body of paramere by semiflexible membrane, two longer apical setae present plus one to several short subapical setae.

Female reproductive tract ($n = 1$). Bursa copulatrix elongate, broader distally, length nearly 4× breadth, compressed under microslide cover slip (Fig. 7E); spermatheca an ovoid heart-shape; spermathecal gland elongate, fusiform; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with single apical fringe seta (Fig. 8E); apical gonocoxite 2 falciform, base extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Type information. *Tropopterus duponchelii* lectotype female (MNHN) hereby designated: S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus / Duponchelii / Sol.* Sn. Iago (handwritten white label) // LECTOTYPE / *Tropopterus / duponchelii / Solier / des.* Liebherr 2019 (black-margined red label). *Tropopterus nitidus* lectotype female (MNHN) hereby designated (pinned specimen with mouthparts mounted beneath on point): S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus / nitidus Sol. / Sn.* Iago (handwritten white label) // LECTOTYPE / *Tropopterus / nitidus / Solier / des.* Liebherr 2019 (black-margined red label). The types would have come into the Chaudoir Collection in 1876 directly from Philibert Germain (Ball and Erwin 1982). Given Chaudoir's interest in mouthpart characters (Basilewsky 1982), and his synonymization of *T. nitidus* under *T. duponchelii* in that year, it seems likely that the mouthpart dissection of the *T. nitidus* lectotype was made by Chaudoir himself.

Date/locality information, all specimens: Chile: Arauco Prov., Caramavida, Nahuelbuta (W), 37°40.99'S, 73°21.00'W, 750 m el., 25–31-xii-1953, Peña (MCZ, 2; MNHN, 1); Curanilahue, 37°28.58'S, 73°20.58'W, 10-xii-1967, Cekalov[ic] (MNHN, 1); San Alfonso, above Caramavida, 37°42.75'S, 73°09.00'W, 16–17-x-1969, Flint & Barria (NMNH, 1). Santiago Prov., Santiago, 33°26.75'S, 70°40.12'W, Solier (lectotypes *T. duponchelii* plus *T. nitidus*), 33°26.75'S, 70°40.12'W, Solier (MNHN, 1). Talca Prov., Altos de Vilches, 35°36.25'S, 71°04.30'W, 19-ix-1968, Ramirez (MNHN, 1), 26-i-1969, Valencia (MNHN, 1), 11-x-1971, Valencia (MNHN, 1). No data except "81", Chaudoir Colln. (MNHN, 1).

Distribution and habitat. This species is distributed from 33°27'S–37°41'S (Fig. 9F), spanning the Santiagan and Northern Valdivian entomofaunal provinces (O'Brien 1971). Specimens have been found by sifting litter in Valdivian rainforest with *Nothofagus*, via pyrethrin fogging of old *Nothofagus* logs, under logs and rocks, and by beating vegetation. Thus this species is most often encountered in ground-level microhabitats; however, there is evidence that the beetles can climb onto vegetation. *Tropopterus duponchelii* and the leiodid beetle *Anaballatus chilensis* are both known from Alto de Vilches, Talca Prov., Chile (Newton et al. 2017).

7. *Tropopterus trisinuatus* sp. nov.

<http://zoobank.org/CF674F9C-289B-49FE-A307-0B0478E28DCE>

Figures 2A, 9G, 10

Diagnosis ($n = 2$). Although the pronota of all *Tropopterus* have the basal margin slightly undulated and medially convex, beetles of this species exhibit an exaggeration of this situation, with the base profoundly concave just mesad the acute hind angles in association with the deep

laterobasal depressions (Fig. 2A). This *Tropopterus* also exhibits the largest body size; standardized body length of 8.2–8.4 mm larger than all but the largest individuals of *T. giraudyi*. The eyes are large in diameter though little convex, with an ocular ratio = 1.36 and a horizontal diameter crossing the eye intersecting 25–26 ommatidia. The sutural stria is punctate, the isolated punctures joined in part by indistinctly depressed strial connections, and the parascutellar striole is absent, the sutural stria vaguely continued to the elytral base as a broad depression. The outer elytral striae are progressively reduced, with striae 2 and 3 traceable as a series of minute, isolated punctures, and a very few minute punctures visible in the position of stria 4. Stria 8 just dorsad the lateral elytral setae is continuous throughout its length. As in *T. minimucro* and *T. fieldianus*, the elytral basal groove is absent; the elytral surface evenly and smoothly convex inside the anterior termination of the lateral marginal depression at the toothed humerus. Ventrally, the prosternum is broadly and deeply depressed from the prosternal process anterad 2/3 the distance to the pronotal anterior margin, and the mesepisternum is punctate, with ~18 punctures arranged in 2 or 3 vertical rows broadly distributed across its surface. Microsculpture of the vertex is an evident isodiametric mesh with sculpticells arranged in transverse rows in part. The pronotum is covered with a dense transverse mesh with sculpticells of breadth 3–4× length, complemented by transverse lines, and the elytra are covered with dense transverse lines producing iridescence.

Description. Head capsule broad, ocular lobe little protruded; antennae moderately robust, length of antennomere 9 2.0× maximal diameter; mandibles elongate, but given large head, distance from anterior condyle to apex of left mandible only 1.80× distance from that condyle to lateroapical margin of labrum; mentum basal breadth 3.05× length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by four setal diameters; paraglossae extended beyond ligular margin slightly more than distance from their base to ligular margin. Pronotum moderately transverse, lateral margins distinctly sinuate anterad right to slightly acute hind angles; base with complete marginal bead, median base smooth medially, with approximately eight small punctures each side mesad laterobasal depression; median longitudinal impression with lenticular depression on median base, finely etched on disc; anterior transverse impression traceable medially, broad and shallow laterally; anterior margin smooth in medial 1/3, margined in lateral 1/3 each side; front angle protruded, subangulate; lateral marginal depression narrow from apex to lateral seta, widened in basal 1/3 of length; lateral seta separated from lateral marginal depression by diameter of setal articulatory socket; laterobasal depression margined medially by deep, sinuous impression, an upraised tubercle in middle of depression; proepisternum smooth dorsally, with broad irregular punctures near prosternal suture. Elytra broad basally, sides sub-

parallel; humerus angulate with short extension of basal groove mesad angle; sutural stria with closely set yet isolated punctures on disc, punctures larger toward apex, but stria deep, narrow and smooth distad subapical situation; stria 8 deep and continuous throughout length; seven or eight anterior lateral elytral setae, six posterior setae; lateral marginal depression very narrow anteriorly, broader in apical half, lined there with transverse sculpticells; subapical situation broad and shallow, elytral plica visible in lateral view. Metepisternum equitrapezoidal, maximal width subequal to lateral length; metasternal process with a rounded apical knob, the lateral margins narrowly upraised. Abdomen with ventrites 3–5 longitudinally depressed laterally; suture between ventrites 1 and 2 sinuate, ventrite 2 depressed posterad situation; ventrites 4–6 depressed basally, the intersegmental membranes minutely punctate; female apical ventrite with two setae laterally each side and an elongate quadrangle of subequally-lengthed setae medially. Coloration of body dark, head, pronotal disc and elytra piceous, the latter with iridescent surface; antennae, mouthparts and legs brunneous; ventral surface piceous, pterothoracic and abdominal ventrites, and elytral epipleura iridescent, only apical 1/6 of apical abdominal ventrite paler, rufobrunneous.

Female reproductive tract ($n = 2$; females not dissected, only accessible gonocoxal characters described). Basal gonocoxite 1 with one apical fringe seta; apical gonocoxite 2 narrowly triangular, base not extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype female (CAS): CHILE: Cautin Province, / Villarrica, 1250 m, trap / site 653, 15 – 29 Jan 1982 / *Nothofagus domb.-pumilio* / forest w/ *Chusquea* / A.F. Newton & M.K. Thayer // *Tropopterus* / *trisinuatus* / sp. nov. ♀1 photo / det. J.K. Liebherr 2019 // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr // HOLOTYPE *Tropopterus* / *trisinuatus* / J.K. Liebherr 2019 (black-margined red label). The type locality is Volcán Villarrica, 1250 m el.; geographic coordinates 39° 22.8'S, 71° 56.4'W (A.F. Newton, pers. comm.).

Paratype with identical data (CAS, 1).

Etymology. The adjectival species epithet *trisinuatus* signifies the trisinate basal pronotal margin that unique characterizes this species among those known.

Distribution and habitat. This species is known only from the type locality in the Northern Valdivian entomofaunal province (O'Brien 1971). The two specimens were collected in a mixed forest of large *Nothofagus dombeyi* (Brisseau de Mirbel), *N. pumilio* (Poepig and Endlicher), and *Chusquea* bamboo. The forest was near a recent lava flow, and the soil was thin. The specimens were collected from the ground-level microhabitat, either in a flight intercept trap catch pan, or in a leaf litter sift sample. The two types were collected at the same place and time as part of the type series of the oribatid mite *Novonothrus puyehue* Casanueva and Norton (1997).

8. *Tropopterus minimicro* sp. nov.

<http://zoobank.org/115C452A-2872-4623-A3C6-67178AB5F548>

Figures 2B, 5A–D, 6J–K, 7F, 8F, 9H, 10

Diagnosis ($n = 5$). These larger sized beetles – standardized body length = 7.2–7.9 mm – can be distinguished by the closely punctate sutural stria which becomes a fine, narrow impression on the elytral apex, and the broadly impressed and smooth stria 2 which is obsolete apically (Fig. 2B). The basal elytral groove is absent across most of the elytral base, though it extends for a short distance medially from the elevated humeral tooth at the base of the elytral lateral marginal depression. The pronotum is moderately transverse (MPW/PL = 1.27–1.37) and the pronotal base is smooth except for 5–8 shallow punctures mesad the laterobasal depression. The parascutellar striole is present as a broad smooth groove mesad the parascutellar seta, the groove not continuous with the base of the sutural stria. Ventrally the prosternum is broadly and deeply depressed medially from the prosternal process ventral face anterad 2/3 toward the prothoracic anterior margin, and the mesepisternum is irregularly punctate with 8–9 punctures in 2 or 3 vertical rows. The dorsal body surface bears well-developed microsculpture: 1, the vertex with an evident isodiametric mesh in transverse rows; 2, the pronotum with a dense transverse mesh, sculpticell breadth 2–3× length, accompanied by transverse lines over portions of the surface; and 3, the elytra with dense transverse lines resulting in iridescence.

Description. Head capsule broad with moderately convex eyes, ocular ratio = 1.41–1.45, 25 ommatidia crossed by a horizontal diameter of eye; ocular lobes slightly protruded, their posterior margin obtusely meeting gena, ocular lobe ratio 0.85–0.89; antennae elongate, antennomere 9 length 2.30× maximal diameter; mandibles moderately elongate, distance from anterior condyle to apex of left mandible 1.76× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.8× length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by 4 setal diameters; paraglossae extended beyond ligular margin slightly more than distance from their base to ligular margin. Transverse pronotum with sides sinuate before acute, projected and denticulate hind angles; median base completely margined, base smooth medially anterad marginal bead, with ~8 minute punctures each side mesad laterobasal depressions; median longitudinal impression with deep, lenticular depression on median base, finely engraved on disc; anterior transverse impression broad and shallow medially, deeper laterally toward front angles; anterior margin smooth medially, margined in outer half of breadth each side; front angles only slightly protruded, rounded; lateral marginal depression very narrow in anterior 2/3 of length, gradually widened to hind angle; lateral setae separated from lateral marginal depression by diameter of articulatory socket; laterobasal depression subquadrate, a smooth tubercle upraised in middle of depression. Elytra broader

in apical half, humeri narrowly rounded; lateral marginal depression ended blindly at humerus; parascutellar striole absent, sutural stria indicated by series of isolated punctures, those punctures more closely spaced in apical half, the stria smooth, narrow and deep on apex; subapical and apical setae together in depressed remnant of stria 7; stria 8 greatly reduced, broad and shallow among anterior lateral elytral setae, absent to shallow medially, and shallow, interrupted to deeper and continuous between setae of posterior series; lateral marginal depression moderately broad, lined with transverse sculpticells; subapical sinuation broad and shallow, elytral plica evident in lateral view. Metepisternum slightly elongate, maximal width 0.83× lateral length. Abdomen with ventrites 3–6 broadly depressed laterally; suture between ventrites 1 and 2 slightly sinuate, ventrite 2 depressed within sinuation; base of ventrites 4–6 depressed, no evidence of punctures associated with the intersegmental membranes; female apical ventrite with two long setae each side and four shorter setae in a more basally situated transverse row medially. Coloration of dorsal body dark rufous, antennae, mouthparts and legs rufobrunneous; ventral body surface also dark rufous, proepipleuron and elytral epipleuron concolorous to paler, rufobrunneous, apex of abdomen not paler.

Male genitalia ($n = 10$). Aedeagal median lobe broad dorsoventrally, the ostial opening narrowed to a rounded apex that bears a very small mucro on the ventrobasal surface (Fig. 5A, C); a large, distally serrate ventrobasal spicular sclerite present (Fig. 5C); flagellum elongate, associated with membranous flagellar sheath. Antecostal apodeme of abdominal IX broadly rounded distally, juncture of two lateral arms asymmetrically offset toward left side, the distal extension short. Right paramere elongate with narrow apical extension (Fig. 6J, K), ventral surface lined with 10–14 small setae, one or two larger setae at apex, and from one to several small setae on dorsoapical surface; left paramere broad basally, the apex ranging from a gradually narrow apex (Fig. 6J) to a very narrow, digitiform extension (Fig. 6K), two longer apical setae accompanied by several short setae.

Female reproductive tract ($n = 1$). Bursa copulatrix ovoid, expanded apically, length about 1.6× greatest breadth, compressed under microslide cover slip (Fig. 7F); spermatheca globose; spermathecal gland large, ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with apical fringe of one larger seta and one smaller seta (Fig. 8F); apical gonocoxite 2 broadly triangular, base moderately extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype male, dissected (MCZ): PucaTrihue / Orsono Prov. / III-23-62 / CHILE Pena // dissection vial // *Tropopterus* / *minimicro* / Liebherr ♂2 / det. J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus* / *minimicro* / J.K. Liebherr 2019 (black-margined red label). The geo-

graphic coordinates for the type locality are 40°32.10'S, 73°41.53'W.

Paratypes: Chile: Cautín Prov., Bellavista, Lago Villarrica, 39 12.55'S, 72 08.14'W, 250 m el., 8-i-2006, Will (EMEC, 4). Chiloé Prov., Degán, 10.3 km E, rte. W33, lot CH2006.18.1.1, 42°10.37'S, 73°36.72'W, 166 m el., 18-i-2006, Will (EMEC etoh, 1), Huillinco, 5.4 km S, Rio Terahuin, 42°43.12'S, 73°53.87'W, 36 m el., 22-i-2006, Will (EMEC, 2), P. N. Chiloé, Cucao, lot CH2002/3.53, 42°38.47'S, 74°07.00'W, 23 m el., 20-i-2003, Will (EMEC etoh, 3). Llanquihue Prov., Lago Chapo, near SE end, km 9.9 on road to Rollizo, Valdivian rainforest on steep slope, lot 989; pyr.-fogging old logs, 41°30.63'S, 72°23.98'W, 385 m el., 26-i-1997, Newton & Thayer (FMNH etoh, 1), P. N. Vicente Pérez Rosales, Volcán Osorno, SW slope ca. km 11 to La Burbuja, low *Nothofagus dombeyi* w/ mixed understory, lot 1005, FMHD #97-35, Berlese leaf and log litter, 41°07.91'S, 72°32.16'W, 1065 m el., 27-i-1997, Newton & Thayer (FMNH, 1), Ensenada, 9.2 km NE, on road to Petrohué, Valdivian rainforest with *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 28-i-1997, Newton & Thayer (FMNH etoh, 1), Volcán Osorno, SW slope c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton & Thayer (FMNH, 1). Osorno Prov., P. N. Puyehue, lot CH2002/3.192, 40°40.22'S, 72°10.07'W, 300 m el., 23-i-2003, Will (EMEC etoh, 1), lot CH2002/3.187, 40°40.22'S, 72°10.07'W, 300 m el. 23-i-2003, Will (EMEC etoh, 2), P. N. Puyehue, Anticura, Repucura Tr., lot P#85-113, FMHD #85-996, Berlese forest litter, 40°39.97'S, 72°10.47'W, 500 m el., 6-ii-1985, S. & J. Peck (FMNH, 2), Volcán Casablanca, E shore Lago Puyehue, Site 36, tundra-forest transition, 40°44'S, 72°10'W, 1270 m el., 18-xii-1977, Ashworth, Hoganson & Mooers (NDSU, 1), Osorno, 40°34.50'S, 73°07.00'W, xii-1977 (NMNH, 2). Valdivia Prov., Curiñanco, road to, 39°42.90'S, 73°23.77'W, 112 m el., 9-xi-2008, Will (EMEC, 1), La Union, 34 km WNW, lot P#85-36, FMHD #85-921, Berlese mixed forest litter, 40°15.00'S, 73°23.75'W, 700 m el., 17-xii-1984, S. & J. Peck (FMNH, 1), P. N. Oncol, Cerro Oncol trail, lot DRM 06-044, 39°41.89'S, 73°18.07'W, 525 m el., 10-i-2006, Maddison & Will (OSAC, 1; OSAC etoh, 1), lot DRM 06.045, 39°41.89'S, 73°18.07'W, 500 m, 11-i-2006, Maddison & Seago (OSAC etoh, 1), Sendero Oncol, 39°41.50'S, 73°18.25'W, 600 m el., 10-i-2006, Will (EMEC, 1), lot CH2006.10.i.2, 39°41.50'S, 73°18.25'W, 600 m el., 10-i-2006 (EMEC etoh, 2), 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC, 8), pitfall trap, 39°41.55'S, 73°18.86'W, 690 m el., 10-23-i-2006, Will et al. (EMEC, 2), 39°41.67'S, 73°18.25'W, 513 m el., 9-xi-2008, Will (EMEC, 2), 600 m el., 8-xi-2008, Will (EMEC, 1), Puerto Fui [sic Fuy], 14 km SE, Lago Pirehueico, Site G, Lenga Forest, *Nothofagus pumilio*, standard pitfall trap, 39 58'S, 71 48'W, 1230 m el., 5-xii-1987, Ashworth, Fugiseth & Maliscke (NDSU, 1), leaf litter, photoelector, 39°58'S,

71°48'W, 1230 m el., 11-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1), window/pitfall trap, 39°58'S, 71°48'W, 1230 m el., 11-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1), standard pitfall trap, 39°58'S, 71°48'W, 1230 m el., 15-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1).

Etymology. The species epithet *minimucro* describes the very small mucro on the apex of the male aedeagal median lobe, that character amply diagnosing this species. The name is to be treated as a noun.

Distribution and habitat. All records for this species are clustered from 39°13'S–42°39'S (Fig. 9H), straddling the transition between the Northern and Southern Valdivian entomofaunal provinces (O'Brien 1971). Collecting sites range from 23 m elevation on Isla Chiloé to 1270 m elevation in the forest-tundra transition zone on Volcán Casablanca (Ashworth and Hoganson 1987). Beetles have been found in Berlese siftate of mixed forest litter, leaf and log litter, and via pyrethrin fogging of old logs with or without moss. The species is broadly sympatric with the southern portion of the range of *T. giraudyi*. Moreover, both *T. minimucro* and *T. giraudyi* have been collected during the same collecting events four different times, suggesting intense sympatry at both macro- and microsympatric scales. The four identical collecting series include: Cautín Prov., Bellavista, Lago Villarrica, 39°12.55'S, 72°08.14'W, 250 m el., 8-i-2006, Will (EMEC); Valdivia Prov., P. N. Oncol, Mirador Pilocura, Sendero, 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC); Llanquihue Prov., P. N. Vicente Pérez Rosales, Volcán Osorno, SW slope c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton and Thayer (FMNH); and Llanquihue Prov., P. N. Vicente Pérez Rosales, Ensenada, 9.2 km NE on road to Petrohué, Valdivian rainforest with *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 28-i-1997, Newton and Thayer (FMNH). *Tropopterus minimucro* has been collected alongside the leiodid *Anaballetus chilensis* two times (Newton et al. 2017; Chile: Cautín Prov., Bellavista, N shore Lago Villarrica, FMNH; and Chile: Valdivia Prov., La Union, 34 km WNW, FMNH).

9. *Tropopterus fieldianus* sp. nov.

<http://zoobank.org/2358ECB7-472F-4371-9FF2-26D51633AFF4>

Figures 2C, 5E–F, 6L, 9I, 10

Diagnosis ($n = 2$). Like *T. minimucro* this species lacks the basal elytral groove and has the sutural stria punctate on the elytral disc. But unlike that species, *T. fieldianus* has both elytral stria 1 and 2 punctate subapically: stria 1 is deeply and narrowly impressed at the apex, whereas stria 2 is broadly, shallowly continuous there. The pronotum of this species is broad (MPW/PL = 1.37–1.39) and rather quadrate, broad basally with MPW/BPW = 1.18–1.25 (compared to the basally narrowed, more cordate prono-

tum of *T. minimucro*; MPW/BPW = 1.24–1.33). The eyes are very convex with 26 ommatidia intersected by a horizontal diameter, and an eye convexity ratio, $EyL/EyD = 2.4$. The pronotal median base is rugosely punctate mesad the laterobasal depressions, and the anterior pronotal margin is smooth medially and margined along the outer 1/3 of each side. Ventrally the prosternum is broadly, moderately depressed medially, the depression extended 2/3 the distance from prosternal process to anterior margin, with the depression shallow and broad between the coxae. The mesepisternum bears a single dorsoventral row of 4–6 punctures, and the metepisternum and metepimeron are fused laterally, the suture difficult to trace except mesally near the metacoxa. Dorsally the head is glossy with very shallow isodiametric sculpticells visible across the surface, and the pronotum and elytra bear dense elongate transverse sculpticells and transverse lines resulting in iridescence. Standardized body length = 6.7–7.8 mm.

Description. Head capsule broad, eyes convex, ocular ratio = 1.42–1.44; antennae moderately elongate, antennomere 9 length $1.96\times$ maximal diameter; mandibles elongate, distance from anterior condyle to apex of left mandible $1.96\times$ distance from condyle to lateroapical margin of labrum; mentum basal breadth $3.0\times$ length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by 4 setal diameters; paraglossae extended beyond ligular margin as far as distance from their base to ligular margin. Pronotum transverse, lateral margins nearly straight basally, briefly concave anterad right to slightly obtuse, denticulate hind angles; basal marginal bead complete, well developed medially; median base smooth; median longitudinal impression continued to basal marginal bead, lenticularly depressed near front of median base, finely inscribed on disc; anterior transverse impression obsolete medially, broad and shallow approaching front angle; front angles slightly protruded, obtuse-rounded; lateral marginal depression narrow in anterior half of length, evenly broadened from lateral seta to base; lateral seta separated from lateral marginal depression by diameter of setal articulatory socket. Elytra broad, lateral margins subparallel; parascutellar striole absent, sutural stria interrupted basally, terminated in broad, irregular depression surrounding parascutellar seta; stria 8 present near posterior setae of anterior lateral elytral setal series, shallow and interrupted near midlength, deep and continuous mesad posterior setal series; lateral marginal depression moderately broad from humerus to midlength, gradually narrowed to subapical situation; subapical situation broadly concave, moderately deep, plica well evident in dorsolateral view. Metepisternum slightly elongate, maximal width $0.83\times$ lateral length. Abdomen with ventrites 3–6 longitudinally depressed laterally; suture between ventrites 1 and 2 slightly sinuate laterally, ventrite 2 depressed within slight situation; abdominal ventrites 4–6 depressed basally, minutely strigose along intersegmental membranes; male apical abdominal ventrite with two setae each side, in one specimen median two setae more basally positioned, in

the other two bilateral pairs of apical setae complemented by three shorter medial setae in the position usually observed in female specimens. Coloration (based on apparently, slightly teneral individuals) paler, head capsule rufopiceous, pronotum and elytra rufobrunneous; legs paler, rufoflavous; thoracic and abdominal ventrites brunneous, proepipleuron and elytral epipleuron paler, rufoflavous.

Male genitalia ($n = 2$). Aedeagal median lobe broad dorsoventrally with broadly rounded apex, a minute mucro on the ventrobasal margin of the apex (Fig. 5E); internal sac armature including flagellum and flagellar sheath. Antecostal apodeme of abdominal IX broadly rounded distally, with juncture of two lateral arms asymmetrically offset toward left side, distal extension broadly rounded (teneral specimen). Right paramere elongate, broader near midlength, narrowed evenly to apex, ventral surface lined with 16 small setae, two larger setae at apex, three subapical setae, and two very small setae on dorsal surface; left paramere very broad for much of length, terminated apically by a evenly narrowed projection with two larger apical setae, a third smaller subapical seta, plus several very small setae on apical process or ventral margin.

Holotype male (FMNH), point mounted with left mesotarsomeres glued to point: CHILE: Osorno Prov., 3 / km S Maicolpue, Bahia / Mensa, 200 m, / 21.XII.1984 // FMHD#85-933, mixed forest litter, S. & J. / Peck, P85-48 / berlese / FIELD MUSEUM NAT. HIST. // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr 2019 // dissection vial // *Tropopterus* / fieldianus / Liebherr ♂1 / det. J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus* / fieldianus / J.K. Liebherr 2019 (black-margined red label).

Paratype: CHILE: Valdivia, 35 km WNW La Union, 7.xi.1985, 700m el., Mixed forest, S. Peck, P#85-114, FIELD MUSEUM (FSCA, 1)

Etymology. The species epithet *fieldianus* combines the noun *field* with the adjectival ending *-anus*, thereby signifying that this species belongs to the Field Museum. This “belonging” is based on the Field Museum’s institutional dedication to Coleoptera systematics signified by a long succession of beetle curators: John E. Liljeblad, Rupert L. Wenzel, Henry S. Dybas, Harry G. Nelson, Larry E. Watrous, Steve Ashe, Alfred F. Newton, and Margaret K. Thayer.

Distribution and habitat. This species is known only from two localities (Fig. 9I) distributed near latitude 40°S in the northern portion of the Southern Valdivian entomofaunal province (O’Brien 1971). It has been recovered from Berlese siftate of mixed forest litter. At the La Union site in Valdivia Prov., it was collected alongside the leiodid species *Anaballetus chilensis* (Newton et al. 2017).

Cladistic analysis

Submitting the 10 taxon by 37 ordered-character data matrix to Winclada running NONA for 200 ratchet runs results in one tree of step-length = 97; CI = 57, RI = 47 (Fig. 10). This identical tree is returned when 1000 ratch-

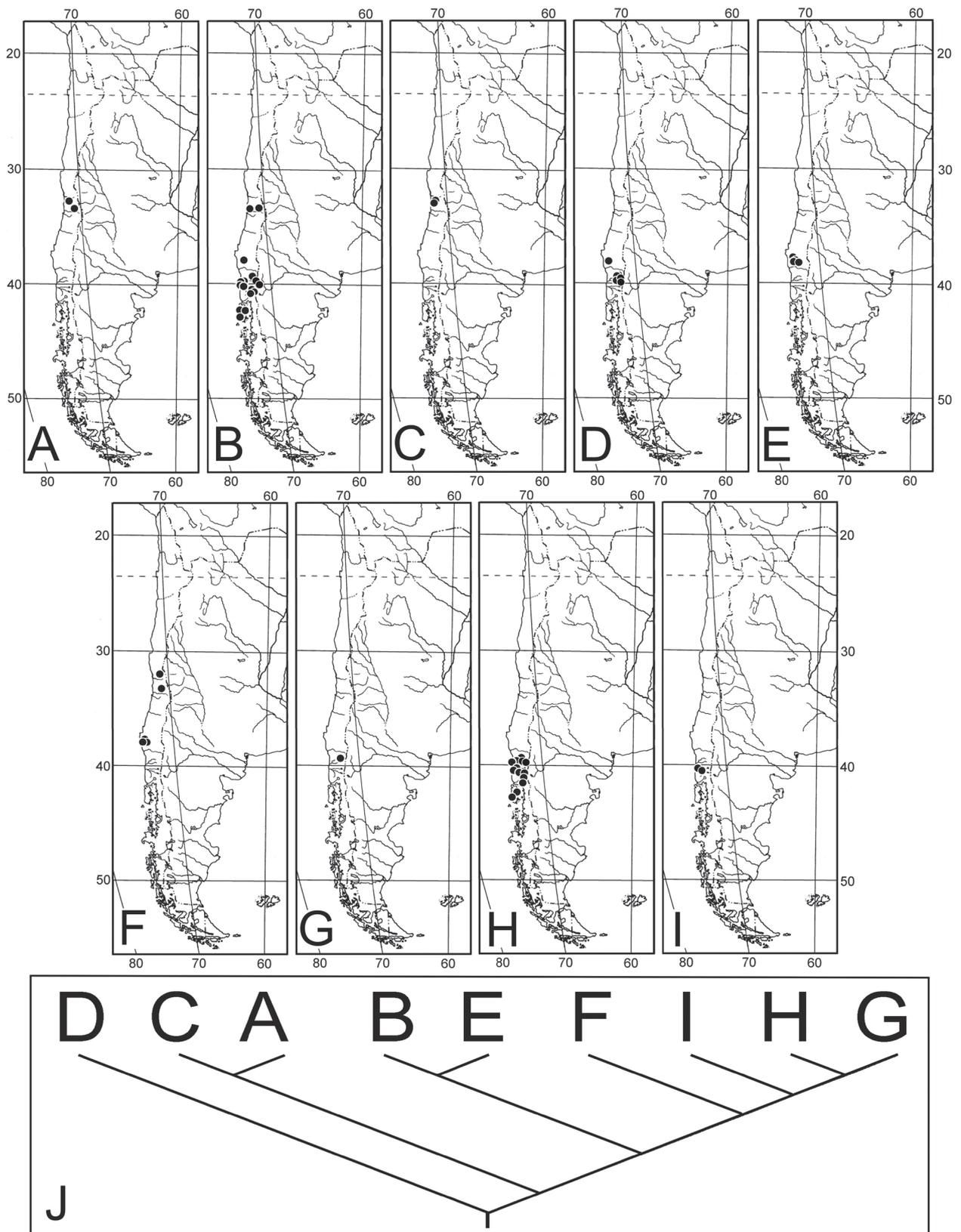


Figure 9. A–I. Geographic distributions of *Tropopterus* spp. **A.** *T. montagnei*. **B.** *T. giraudyi*. **C.** *T. peckorum*. **D.** *T. robustus*. **E.** *T. canaliculus*. **F.** *T. duponchelii*. **G.** *T. trisinuatus*. **H.** *T. minimicro*. **I.** *T. fieldianus*. **J.** Geographical distributions of *Tropopterus* spp., labeled as per figures above, hierarchically arranged by phylogenetic relationships of the taxon cladogram, Fig. 10.

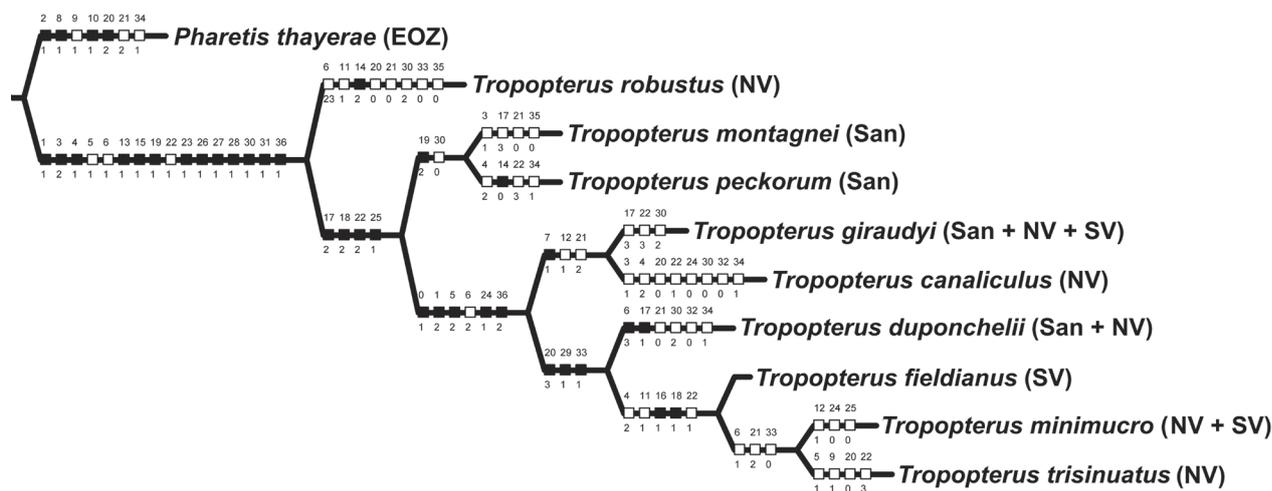


Figure 10. Cladogram returned under all cladistic protocols described in text; tree length = 97, CI = 57, RI = 47, fast character optimization shown. Outgroup choice of *Pharetis thayerae* based on results in Liebherr (2020). Geographic region abbreviations after taxon name include: eastern Australia (EOZ); Santiagan entomofaunal province (San); Northern Valdivian entomofaunal province (NV); Southern Valdivian Entomofaunal province (SV).

et replicates are run using NONA within Winclada. The outgroup *Pharetis thayerae* establishes the root of the *Tropopterus* phylogeny between *T. robustus* and the remaining eight species. Monophyly of *Tropopterus* relative to *Pharetis* is supported by 15 unambiguously optimized synapomorphies, most of which are presented in the generic diagnosis: **1**, mentum paramedial depressions deep (character 3, state 2); **2**, scutellum little projected onto elytral disc (13, 1); **3**, elytral humerus tightly rounded to angulate (15, 1); **4**, sutural stria modified apically (19, 1); **5**, metepisternum foreshortened (22, 1); **6**, male apical ventrite bisetose each side (26, 1); **7**, metatarsomere 4 emarginate apically (27, 1); **8**, male aedeagus inverted (28, 1); and **9**, male aedeagal median lobe with pleated ostial border (31, 1). Five other synapomorphies relative to the *Pharetis* outgroup include three associated with larger eyes; **1**, 18 or more ommatidia (character 1, state 1); **2**, ocular ratio > 1.30 (5, 1), and **3**, ocular lobe ratio > 0.76 (6, 1). The two additional synapomorphies include: **4**, labrum apical margin moderately concave (4, 1); and **5**, body size larger than 5.0 mm (36, 1). A final character listed on the cladogram edge leading to *Tropopterus* (aedeagal median lobe with mucro; character 30, state 1)—is reversed in *T. peckorum* and *T. canaliculus*, or not known in *T. montagnei* or *T. trisinuatus* for which we lack male specimens. In addition, all *Tropopterus* beetles are vestigially winged; a condition more derived than the stenopterous flight wing condition of *Pharetis thayerae* (character 23). However, given *P. thayerae* as the lone outgroup, that character cannot be unambiguously polarized on this cladogram except under fast optimization.

Several character transformation series support the present phylogenetic hypothesis of *Tropopterus* spp. (Fig. 10). Elytral striation is least reduced in *T. robustus* (characters 17, 18, states 0; Fig. 1D), supporting its placement

as adelphotaxon to the other seven *Tropopterus* (Figs 1A–C, E, F, 2). Eye size (character 1) increases during *Tropopterus* phylogeny, with all *Tropopterus* exhibiting larger eyes than the outgroup *Pharetis*, and species of the clade bracketed by *T. giraudyi* and *T. trisinuatus* exhibiting the largest number of ommatidia; 23–26 ommatidia (character 1, state 2). Within this crown clade of six species, the sister species status of *T. giraudyi* and *T. canaliculus* is supported by a pronotal anterior margin that is completely beaded side to side (character 7, state 1). Monophyly of their respective sister group of four species is supported by the synapomorphic, distally rounded antecostal apodeme of the male abdominal ventrite IX (character 29, state 1), though our lack of knowledge regarding males of *T. trisinuatus* must invoke the prediction that those males, when examined, will also exhibit the distally rounded antecostal apodeme. Monophyly of the three-species clade of *T. fieldianus* + (*T. minimucro* + *T. trisinuatus*) is supported by shared loss of the elytral basal groove (character 16, state 1; Fig. 2). Several other characters may represent attributes phylogenetically associated with the reduction of metathoracic flight wings. Body size (character 36, states 1, 2) increases throughout *Tropopterus* phylogeny, consistent with the evolutionary trend observed across brachypterous carabid beetle taxa (Liebherr 1988). The six-taxon *T. giraudyi*–*T. trisinuatus* clade is characterized by the largest body sizes, with the single exception being broad body size variation within *T. canaliculus*, where the smallest males of that species fall near the top of the body-size range for *T. robustus*, *T. montagnei*, and *T. peckorum*. Associated with this phyletic increase in body size is the reduction of the metepisternum (character 22, states 1, 2), though that character is highly homoplasious, changing states six times within *Tropopterus*. Also, the antennae are more elongate (char-

acter 0, state 1) within the larger-bodied *T. giraudyi*–*T. trisinuatus* clade, a finding in keeping with allometric increase in antennal length as body size increases.

Discussion

Tropopterus diversity (Fig. 9A–I) is centered in the Northern Valdivian and the northern portion of the Southern Valdivian entomofaunal regions (O’Brien 1971). The ranges of two of the geographically more widespread species, *T. giraudyi* (Fig. 9B) and *T. minimucro* (Fig. 9H), extend the furthest south, into the North Patagonian Rain Forest (Clarke 1964) and onto Isla Chiloé. Where recorded, the ecological associates of these species include *Nothofagus dombeyi*, *Chusquea* bamboo, and the podocarp *Saxegothaea conspicua* Lindley. To the north, four species have been recorded from the more mesic Santiagan entomofaunal province, though the Solier type localities “near Santiago” for *T. montagnei*, *T. giraudyi*, and *T. duponchelii* (Fig. 9A, B, F) have not been recently corroborated. Northern localities within N. P. La Campana have recently produced *T. peckorum*, with this species found in *Nothofagus obliqua* forest.

That our knowledge of the generic distributional range of *Tropopterus* is more or less accurate can be ascertained by the combination of: syntopic collections of *Tropopterus* beetles and other Coleoptera within the known *Tropopterus* range; and absence of *Tropopterus* beetles from samples outside the known range that comprise beetle species found in sympatry with *Tropopterus*. For example, *T. giraudyi* was collected at Chepu, Chiloé by W. Kuschel, 9-x-1958, and he collected *Glypholoma pustuliferum* Jeannel the day before at the same locality (Thayer 1997). *Tropopterus* is not found further south than Chiloé, though *G. pustuliferum* has been collected, using similar methodology, at numerous localities further south in Magallanes and Tierra del Fuego Provinces. Other entomological survey programs in southern Chile have also not recovered any *Tropopterus* species south of localities presented here (Fig. 9A–I) (Domínguez et al. 2006; Niemalä 1990).

Tropopterus sympatry is greatest near 40°S, with seven of the nine species distributed near this latitude (Fig. 9). Thus any attempt to hypothesize past episodes of allopatric speciation are complicated by secondary sympatry. A limited amount of information suggests that speciation has occurred across relatively limited geographic distances in this group. The three sister-species pairs (Fig. 9J), one in the northern sclerophyllous forest (Fig. 9A, C) and the two in the Valdivian forest (Fig. 9B, E, and 9G, H, respectively), all exhibit little geographic isolation between the paired species. In the two southern examples, both sister-species pairs consist of a more widespread species (Fig. 9B, H) plus a geographically restricted sister (Fig. 9E, G). In the northern sister-species pair, both species are known from a limited range, although agricultural land conversion in this region (O’Brien 1971) may have

greatly reduced primordial distributions. Sympatry is also observed within the three-species clade of *T. fieldianus* + (*T. minimucro* + *T. trisinuatus*) (Fig. 9G–I), though their sister, *T. duponchelii* (Fig. 9F), exhibits narrow allopatry based on its more northerly distribution within the Northern Valdivian and Santiagan entomofaunal regions.

Pleistocene glaciation has influenced geographical distributions of both plants and animals in the region of highest diversity near 40°S. The beetle fauna of the lowland Lake Region (latitude 40°S–42°S) consisted of cold-adapted species immediately following glacial retreat 19,500 yr B.P., with fossils from older assemblages comprising species typical of both forest and more open riparian habitats: for Carabidae this included *Bembidion* Latreille spp. (tribe Bembidiini) (Hoganson and Ashworth 1992). More recent stratigraphic layers from 13,000 yr B.P. to the present yielded forest-adapted species representing genera such as *Ceroglossus* Solier (tribe Carabini), *Cascellius* Curtis (tribe Broscini), *Parhyptes* Motschulsky & *Trirammatus* Chaudoir (tribe Pterostichini), and *Bradycellus* Erichson & *Pelmatellus* Bates (tribe Harpalini) (Ashworth and Hoganson 1987, Ashworth and Markgraf 1989, Hoganson and Ashworth 1992). The Quaternary pollen record synchronously reflects this warming, with the increase of Chenopodiaceae and Amaranthaceae pollen, indicative of warmer conditions, increasing dramatically in the Lake Region from 14,500 yr B.P. to the present (Heusser 1983). Along with the warming came dramatic increases in charcoal deposition during the past 6,000 years, indicating human modification of the landscape.

Tropopterus is the only polytypic taxon within Moriomorphini to uniformly exhibit antisymmetric male genitalia; i.e., the orientation of the male aedeagus is inverted 180° from the plesiomorphic condition in the tribe, and indeed the entire family Carabidae, wherein the anatomical right side is oriented ventrally when the genitalia are in repose within the abdomen (Jeannel 1955: 75). *Mecyclothorax punctipennis* MacLeay exhibits infraspecific variation in male genitalic orientation, with populations in Western Australia variably polymorphic for either the normal left-everting aedeagus (right side ventral), or the inverted right-everting (left side ventral) condition (Liebherr and Will 2015). Just as in *M. punctipennis*, the male genitalic inversion of *Tropopterus* is not reflected in inverted orientation of the female reproductive tract. *Tropopterus* females retain the plesiomorphic condition of the spermathecal duct entering the bursal–common oviduct juncture from the right side (Fig. 7). From a genetic viewpoint then, the orientation of the male and female genitalia are decoupled. Moreover, any functional difference in the inverted male aedeagus is not associated with change from the plesiomorphic condition in the female reproductive tract.

How inverted male genitalia originated in this geographically disjunct clade remains an open question. Liebherr and Will (2015) argued that the antisymmetric genitalic orientation of *Tropopterus* supported the

hypothesis of colonization of Chile over water, assuming a small colonizing propagule became fixed for the alternative, apomorphic left side ventral genitalic orientation during founding of the initial population. However, knowledge that the adelphotaxon *Pharetis* retains the plesiomorphic right side ventral orientation (Liebherr 2020) begs the question of how the switch in orientation might have occurred. If it happened after colonization in a polymorphic population, why was the plesiomorphic condition lost from South America? In Western Australia, maximally 58% of *Mecyclothorax punctipennis* individuals in population samples exhibit antisymmetric genitalia. What conditions would drive the plesiomorphic condition to zero in the primordial Chilean *Tropopterus* population? Moreover, the only other moriomorphine species to monomorphically exhibit antisymmetric male genitalia, *Mecyclothorax storeyi* Moore (1963), evolved the condition on Mt. Bellenden Ker in the Queensland Alps. Closely related species exhibiting the plesiomorphic genitalic orientation occupy adjacent mountains (Baehr 2003), showing that such a transition can occur over limited distances within a terrestrial situation. Given these questions and contradictions, it seems best to consider the origin of antisymmetry agnostic with regard to the history of *Tropopterus* in South America.

Conversely, knowledge of the community within which *Tropopterus* occurs may be more relevant to understanding its colonization history in South America. *Tropopterus* beetles have been collected syntopically with *Glypholoma* staphylinid beetles (Thayer 1997), *Andotypus* hydrophilid beetles (Fikáček et al. 2014), and *Anaballetus* leiodid fungus beetles (Newton et al. 2017), establishing a modern ecological association. The middle Jurassic fossil species, *Juroglypholoma antiquum* Cai et al. (2012) dates the origin of the Glypholomatinae to before 165 Myr ago, supporting placement of *Glypholoma* in Australia and southern South America prior to Gondwanan vicariance. *Andotypus* and its sister genus *Austrotypus* also exhibit an Austral disjunction (Fikáček et al. 2014) involving Australia and western South America, supporting a trans-Antarctic vicariant relationship. The leiodid genus *Anaballetus* is hypothesized to be most closely related to presently undescribed taxa from Australia and New Zealand (Newton et al. 2017). Colloff (2011) explicated a trans-Antarctic area relationship involving Chile, Tasmania, and New South Wales for the *Novonothrus puyehue* species group (Acari, Oribatida); litter-inhabiting mites resident in cool temperate *Nothofagus* Rain Forest. Type specimens of *Novonothrus puyehue* Casanueva and Norton (1997) were collected syntopically and synchronically with the two type specimens of *Tropopterus trisinuatus*. The moss-inhabiting hemipterous Peloridiidae represent another taxon of *Nothofagus* associates exhibiting Austral disjunctions consistent with Gondwanan vicariance, with specimens of several species of *Peloridora* China

(Burkhardt 2009) collected at localities represented by *Tropopterus* collections reported above. All of these taxa represent the long-recognized Austral-disjunct Western Antarctic biogeographical track that housed *Nothofagus* forest (Schlinger 1974; Humphries et al. 1986). The modern crown groups of *Nothofagus* began diversifying 55–40 Myr ago (Cook and Crisp 2005), well before the break up of Australia, Antarctica, and South America via vicariance across the Tasman Sea and Drake Passage (San Martín and Ronquist 2004; Livermore et al. 2005). This history is consistent with the broad distribution of specialist *Nothofagus* herbivorous taxa across the range of *Nothofagus* (McQuillan 1993), and the lack of any significant overlap between the herbivore faunas of the *Nothofagus* and *Eucalyptus* dominant communities in Australia. Burgeoning fossil evidence verifies the presence of an Eocene to Late Eocene flora on the Antarctic Peninsula that consisted of *Nothofagus* dominated vegetation with some podocarp conifers (Dawson et al. 2014; Warny et al. 2019). That forest was extremely similar in composition to the Valdivian and North Patagonian forest assemblages found in Chile today (Clarke 1964). The concordance between the ecological distribution of *Tropopterus* and its leaf-litter associates in South American *Nothofagus* forest, and the Austral biogeographical disjunction shown by *Tropopterus* and its New South Wales sister group, *Pharetis*, supports a legacy membership for *Tropopterus* in this vicariant, Austral *Nothofagus* forest community.

Acknowledgements

That this study could be undertaken at all is due to the concerted efforts of the dedicated individuals who collected the bulk of the specimens. These collections were commenced by Stewart Peck and Jarmila Kukalova-Peck, and Allan Ashworth, followed by Alfred Newton and Margaret Thayer, and then David Maddison and Kipling W. Will. Collecting series for *Tropopterus* are generally small, and so numerous other persons who were fortunate enough to collect even a few specimens have added to our current knowledge of this group. I gratefully recognize these people for their lifelong pursuits of biodiversity: Dave Clarke, Lee Herman, Willi Kuschel, A. E. Michelbacher, Luis Peña, Norman Platnick, Ed Ross, Randall T. Schuh, Alexey Solodovnikov, and Roland Thaxter. Peter Johns is thanked for recognizing *Merizodus catapileanus* Jeannel as a *Tropopterus*, and so labelling it. I thank Al Newton and Margaret Thayer for information regarding the collecting locality of *T. trisinuatus*. Martin Husemann educated me regarding the fate of the types of *Tropopterus peruvianus*, and others. I thank Chris Carleton, Louisiana State University, and Ashley Dowling, University of Arkansas for information regarding the S. L. Straneo Collection. This research was supported by N.S.F. Award DEB-0315504.

References

- Ashworth AC, Hoganson JW (1987) Coleoptera bioassociations along an elevational gradient in the Lake Region of southern Chile, and comments on the postglacial development of the fauna. *Annals of the Entomological Society of America* 80: 865–895. <https://doi.org/10.1093/aesa/80.6.865>
- Ashworth AC, Markgraf V (1989) Climate of the Chilean channels between 11,000 to 10,000 yr B.P. based on fossil beetle and pollen analyses. *Revista Chilena de Historia Natural* 62: 61–74.
- Baehr M (1998) A preliminary survey of the classification of Psydrinae (Coleoptera: Carabidae). In: Ball GE, Casale A, Vigna Taglianti V (Eds) *Phylogeny and classification of Caraboidea (Coleoptera: Adephega)*. Atti Museo Regionale di Scienze Naturali, Torino, 359–368.
- Baehr M (2003) Psydrine ground beetles (Coleoptera: Carabidae: Psydrinae), excluding Amblytelini, of eastern Queensland rainforests. *Memoirs of the Queensland Museum* 49: 65–109. <https://www.biodiversitylibrary.org/part/243680>
- Ball GE, Erwin TL (1982) The Baron Maximilien de Chaudoir: inheritance, associates, travels, work, and legacy. *The Coleopterists Bulletin* 36: 475–501.
- Basilewsky P (1982) Baron Maximilien de Chaudoir (1816–1881). *The Coleopterists Bulletin* 36: 462–474.
- Bates HW (1874) On the geodephagous Coleoptera of New Zealand. *Annals and Magazine of Natural History (series 4)* 13: 233–246, 270–277. <https://doi.org/10.1080/00222937408680859>
- Broun T (1880) *Manual of the New Zealand Coleoptera (Part I)*. Government Printer, Wellington, 651 pp. <https://doi.org/10.5962/bhl.title.32505>
- Broun T (1882) On the New Zealand Carabidae. *New Zealand Journal of Science (Dunedin)* 1: 215–227.
- Burkhardt D (2009) Taxonomy and phylogeny of the Gondwanan moss bugs or Peloriidiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift* 56: 173–235. <https://doi.org/10.1002/mmnd.200900019>
- Cai C, Huang D, Thayer MK, Newton AF (2012) Glypholomatine rove beetles (Coleoptera: Staphylinidae): a southern hemisphere recent group recorded from the Middle Jurassic of China. *Journal of the Kansas Entomological Society* 85: 239–244. <https://doi.org/10.2317/JKES120531.1>
- Casanueva ME, Norton RA (1997) New nothroid mites from Chile: *Novonothrus covarrubiasi* n. sp. and *Novonothrus puyehue* n. sp. (Acari: Oribatida). *Revista Chilena de Historia Natural* 70: 435–445.
- Chaudoir M de (1876) Notes et additions au mémoire de M Reed sur les Carabiques du Chile inséré dans les Proceedings of the Zoological Society of London. *Annales de la Société entomologique de Belgique* 19: 105–124.
- Clarke D (1964) The forests of southern Chile and the Argentine (2). *Quarterly Journal of Forestry* 58: 120–134.
- Colloff MJ (2011) A review of the oribatid family Nothridae in Australia, with new species of *Novonothrus* and *Trichonothrus* from rain forest and their Gondwanan biogeographical affinities (Acari: Oribatida). *Zootaxa* 3005: 1–44. <https://doi.org/10.11646/zootaxa.3005.1.1>
- Cook LG, Crisp MD (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proceedings of the Royal Society B* 272: 2535–2544. <https://doi.org/10.1098/rspb.2005.3219>
- Dawson M, Francis J, Carpenter R (2014) New views of plant fossils from Antarctica: a comparison of X-rays and neutron imaging techniques. *Journal of Paleontology* 88: 702–707. <https://doi.org/10.1666/13-124>
- Deuve T (1993) L'abdomen et les genitalia des femelles de Coléoptères Adephega. *Mémoires du Muséum national d'Histoire naturelle, Serie A, Zoologie* 155: 1–184.
- Domínguez MC, Roig-Juñent S, Tassin JJ, Ocampo FC, Flores GE (2006) Areas of endemism of the Patagonian steppe: an approach based on insect distributional patterns using endemicity analysis. *Journal of Biogeography* 33: 1527–1537. <https://doi.org/10.1111/j.1365-2699.2006.01550.x>
- Enderlein G (1909) 9. Des Insektenfauna der Insel Neu-Amsterdam. In Enderlein G (ed). *Die Insekten des Antarktischen Gebietes*, 10. Druck und Verlag von Georg Reimer, Berlin: 486–492.
- Fikáček M, Minoshima YN, Newton AF (2014) A review of *Andotyplus* and *Austrotyplus* gen. nov., rygmoline genera with an austral disjunction (Hydrophilidae: Rygmolinae). *Annales Zoologici* 64: 557–596. <https://doi.org/10.3161/000345414X685893>
- Gemminger M, Harold B de (1868) Cicindelidae–Carabidae. *Catalogus Coleopterorum* 1, 424 pp. [+ 8 pp index]
- Germain P (1911) *Catalogo Coleopteros Chilenos del Museo Nacional*. Boletín del Museo Nacional de Historia Natural, Chile 3: 47–73.
- Goloboff PA (1999) NONA (NO NAME). Tucumán, Argentina, Published by the author. <http://www.softpedia.com/get/Science-CAD/NONA.shtml> [accessed 6-ix-2016]
- Heusser CJ (1983) Quaternary pollen record from Laguna de Tagua Tagua, Chile. *Science* 219: 1429–1431. <https://doi.org/10.1126/science.219.4591.1429>
- Hlavac T F (1971) Differentiation of the carabid antennal cleaner. *Psyche* 78: 51–66. <https://doi.org/10.1155/1971/927545>
- Hoganson JW, Ashworth AC (1992) Fossil beetle evidence for climatic change 18,000–10,000 years B.P. in south-central Chile. *Quaternary Research* 37: 101–116. [https://doi.org/10.1016/0033-5894\(92\)90009-8](https://doi.org/10.1016/0033-5894(92)90009-8)
- Humphries CJ, Cox JM, Nielsen ES (1986) *Nothofagus* and its parasites: a cladistic approach to coevolution. In: Stone AR, Hawksworth DL (Eds) *Coevolution and Systematics. The Systematics Association Special Volume No. 32*. Oxford University Press, New York, NY, 55–76.
- ICZN [International Commission on Zoological Nomenclature] (1999) *International Code of Zoological Nomenclature. Fourth Edition*. The International Trust for Zoological Nomenclature, London, 306 pp. <http://iczn.org/iczn/index.jsp> [accessed 26-vi-2018]
- Jeannel R (1955) L'Édage, initiation aux recherches sur la systématique des coléoptères. *Publications du Muséum national d'Histoire naturelle no. 16*: 155 pp.
- Jeannel R (1962) Les tréchides de la Paléantarctide occidentale. In: Debutteville CD, Rapoport E (Eds) *Biologie de l'Amérique Australe I: Etudes sur la faune du sol*. Éditions du Centre national de la Recherche scientifique, Paris, 527–655.
- Larochelle A, Larivière M-C (2013) Carabidae (Insecta: Coleoptera): synopsis of species, Cicindelinae to Trechinae (in part). *Fauna of New Zealand / Ko te Aitanga Pepeke o Aotearoa* 69: 193 pp.
- Liebherr JK (1988) Brachyptery and phyletic size increase in Carabidae (Coleoptera). *Annals of the Entomological Society of America* 81: 157–163. <https://doi.org/10.1093/aesa/81.2.157>

- Liebherr JK (2012) The first precinctive Carabidae from Moorea, Society Islands: new *Mecyclothorax* spp. (Coleoptera) from the summit of Mont Tohiea. *ZooKeys* 224: 37–80. <https://doi.org/10.3897/zookeys.224.3675>
- Liebherr JK (2013) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Tahiti, Society Islands. *ZooKeys* 322: 1–170. <https://doi.org/10.3897/zookeys.322.5492>
- Liebherr JK (2015) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Haleakalā, Maui: Keystone of a hyperdiverse Hawaiian radiation. *ZooKeys* 544: 1–407. <https://doi.org/10.3897/zookeys.544.6074>
- Liebherr JK (2018a) Cladistic classification of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriormorphini) and taxonomic revision of the New Caledonian subgenus *Phacothorax* Jeannel. *Deutsche Entomologische Zeitschrift* 65: 1–63. <https://doi.org/10.3897/dez.65.21000>
- Liebherr JK (2018b) Taxonomic review of Australian *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriormorphini) with special emphasis on the *M. lophoides* (Chaudoir) species complex. *Deutsche Entomologische Zeitschrift* 65: 177–224. <https://doi.org/10.3897/dez.65.27424>
- Liebherr JK (2020) Phylogenetic placement of the Australian *Pharetis*, gen. nov. and *Spherita*, gen. nov., in a revised classification of the circum-Antarctic Moriormorphini (Coleoptera: Carabidae). *Invertebrate Systematics*. [in press]
- Liebherr JK, Will KW (1998) Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. In: Ball GE, Casale A, Vigna Taglianti V (Eds) *Phylogeny and classification of Caraboidea* (Coleoptera: Adephaga). *Atti Museo Regionale di Scienze Naturali, Museo Regionale di Scienze Naturali, Torino*, 107–170.
- Liebherr JK, Will KW (2015) Antisymmetric male genitalia in Western Australian populations of *Mecyclothorax punctipennis* (Coleoptera: Carabidae: Moriormorphini). *Insect Systematics & Evolution* 46: 393–409. <https://doi.org/10.1163/1876312X-45042124>
- Livermore R, Nankivell A, Eagles G, Morris P (2005) Paleogene opening of Drake Passage. *Earth and Planetary Sciences Letters* 236: 459–470. <https://doi.org/10.1016/j.epsl.2005.03.027>
- Lorenz W (2005) *Nomina Carabidarum*, a directory of the scientific names of ground beetles. Published by the author, Tutzing, Germany, 993 pp.
- Maddison DR, Baker MD, Ober KA (1999) Phylogeny of carabid beetles as inferred from 18S ribosomal DNA (Coleoptera: Carabidae). *Systematic Entomology* 24: 103–138. <https://doi.org/10.1046/j.1365-3113.1999.00088.x>
- Maddison DR, Kanda K, Boyd OF, Faille A, Porch N, Erwin TL, Roig-Juñent S (2019) Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): unexpected clades, isolated lineages, and morphological convergence. *Molecular Phylogenetics and Evolution* 132: 151–176. <https://doi.org/10.1016/j.ympev.2018.11.006>
- Maddison DR, Ober KA (2011) Phylogeny of minute carabid beetles and their relatives based upon DNA sequence data (Coleoptera, Carabidae, Trechitae). *ZooKeys* 47: 229–260. <https://doi.org/10.3897/zookeys.147.1871>
- McQuillan PB (1993) *Nothofagus* (Fagaceae) and its invertebrate fauna – an overview and preliminary synthesis. *Biological Journal of the Linnean Society* 49: 317–354. <https://doi.org/10.1111/j.1095-8312.1993.tb00910.x>
- Moore BP (1963) Studies on Australian Carabidae (Coleoptera) – 3. The Psydrinae. *Transactions of the Royal Entomological Society of London* 115: 277–290. <https://doi.org/10.1111/j.1365-2311.1963.tb00810.x>
- Newton AF, Švec Z, Fikáček M (2017) A new genus and two new species of Leiodinae from Chile, with keys to world genera of Sogdini and Leiodinae from Chile and Argentina (Coleoptera: Leiodidae). *Acta Entomologica Musei Nationalis Pragae* 57: 121–140. <https://doi.org/10.1515/aemnp-2017-0061>
- Niemälä J (1990) Habitat distribution of carabid beetles in Tierra del Fuego, South America. *Entomologica Fennica* 1: 3–16. <https://doi.org/10.33338/ef.83348>
- Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414. <https://doi.org/10.1111/j.1096-0031.1999.tb00277.x>
- Nixon KC (2002) *WinClada*. Ithaca, NY. Published by the author. <http://www.softpedia.com/get/Science-CAD/WinClada.shtml> [accessed 16-ix-2016]
- O'Brien CW (1971) The biogeography of Chile through entomofaunal regions. *Entomological News* 82: 197–207.
- Reed EC (1874) 7. On the Coleoptera Geodephaga of Chile. *Proceedings of the Zoological Society of London* 1874: 48–70. [+ 1 pl.] <https://doi.org/10.1111/j.1096-3642.1874.tb02451.x>
- Roig-Juñent S, Domínguez MC (2001) Diversidad de la familia Carabidae (Coleoptera) en Chile. *Revista Chilena de Historia Natural* 74: 549–571. <https://doi.org/10.4067/S0716-078X2001000300006>
- Sanmartín I, Ronquist F (2004) Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53: 216–243. <https://doi.org/10.1080/10635150490423430>
- Schlíngler EI (1974) Continental drift, *Nothofagus*, and some ecologically associated insects. *Annual Review of Entomology* 19: 323–343. <https://doi.org/10.1146/annurev.en.19.010174.001543>
- Sloane TG (1898) On Carabidae from West Australia, sent by Mr A M Lea (with descriptions of new genera and species, synoptic tables, &c.). *Proceedings of the Linnean Society of New South Wales* 23: 444–520.
- Sloane TG (1903) *Studies in Australian Entomology*. no. XII. New Carabidae (Panageini, Bembidiini, Pogonini, Platysmatini, Platynini, Lebiini, with revisional lists of genera and species, some notes on synonymy, &c.). *Proceedings of the Linnean Society of New South Wales* 28: 566–642.
- Solier AJJ (1849) Orden III. Coleopteros. In: Gay C (Ed.). *Historia Física y Política de Chile* 4: 105–508. En Casa del Autor, Paris; Museo de Historia Natural de Santiago, Chile.
- Song H (2004) Post-adult emergence development of genitalic structures in *Schistocerca* Stål and *Locusta* L. *Proceedings of the Entomological Society of Washington* 106: 181–191.
- Straneo SL (1954) Pterostichini e Tropopterini (Col. Carabidae). In: Titschack E (Ed.) *Beiträge zur Fauna-Perus*, Jena 4: 95–108. [G. Fischer, Jena]
- Straneo SL (1969) Sui Carabidi del Chile, raccolti dal Dr Holdgate della Royal Society Expedition (1958–1959) e dal Prof Kuschel. *Annales de la Société entomologique de France (NS)* 5: 951–974.

- Thayer MK (1985) Revision, phylogeny and biogeography of the austral genus *Metacorneolabium* Steel (Coleoptera: Staphylinidae: Omaliinae). In: Ball GE (Ed.) Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. Dr W Junk Publishers, Dordrecht, 113–179.
- Thayer MK (1997) *Proglypholoma aenigma* gen. et sp. nov., *Glypholoma* spp. nov. and new records, and a phylogenetic analysis of Glypholomatinae (Coleoptera: Staphylinidae). *Annales Zoologici* 47: 157–174.
- Warny S, Kymes CM, Askin R., Krajeski KP, Tatur A (2019) Terrestrial and marine floral response to latest Eocene and Oligocene events on the Antarctic Peninsula. *Palynology* 43: 4–21. <https://doi.org/10.1080/01916122.2017.1418444>
- Weidner H (1976) Die Entomologischen Sammlungen des Zoologischen Instituts und Zoologischen Museums der Universität Hamburg, IX Teil, Insecta VI. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 73: 87–264.

Supplementary material 1

Cladistic analysis of *Tropopterus* spp.

Author: James K. Liebherr

Data type: phylogenetic data

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/dez.66.38022.suppl1>

Species composition and diagnoses of leaf- and fruit-scarring beetles (Coleoptera, Chrysomelidae) infesting bananas and plantains (Zingiberales, Musaceae) in the Indian subcontinent

Kaniyarikkal D. Prathapan¹, Janakiraman Poorani², S. Amritha Kumari¹, C. Anuradha², Balakrishnan Padmanaban², Ramalingam Thanigairaj²

¹ Department of Entomology, Kerala Agricultural University, Vellayani, Trivandrum 695522, Kerala, India

² ICAR – National Research Centre for Banana, Thogamalai Road, Thayanur Post, Tiruchirappalli 620102, Tamil Nadu, India

<http://zoobank.org/85572917-1A87-4F97-8476-912B7B5CD580>

Corresponding author: J. Poorani (poorani@gmail.com)

Academic editor: D. Zimmermann ♦ Received 19 October 2019 ♦ Accepted 3 December 2019 ♦ Published 13 December 2019

Abstract

Leaf- and fruit-feeding chrysomelids (Coleoptera) on bananas and plantains (Musaceae, Zingiberales) cause major losses to banana growers in the northern and northeastern regions of India, Bangladesh, and other parts of Southeast Asia. The species composition of these beetles has not been studied so far in India and wrong names or wrong name combinations in the literature have caused confusion. Most particularly, the Central and South American species of *Colaspis hypochlora* Lefèvre (Chrysomelidae, Eumolpinae) has been erroneously reported as occurring in India and Bangladesh, and this name has been used for the Indian species. Based on extensive surveys for leaf- and fruit-feeding chrysomelids in the northern and northeastern regions of India from 2015 to 2019, three species of banana-feeding chrysomelids, namely, *Basilepta subcostata* (Jacoby) (Eumolpinae), *Bhamoina varipes* (Jacoby), and a new species, *Sphaeroderma cruenta* sp. nov. (Galerucinae, Alticini), are documented. Of these, the latter two are recorded as pests of banana in India for the first time. An illustrated diagnostic account of these three species is given to facilitate their identification by economic entomologists. COI sequences of populations of *B. subcostata* from Assam and Uttar Pradesh showed 98–100% homology, indicating that these populations are conspecific and that COI sequences can be used for rapid species determination. Brief notes on the biology and available management options for these pests are also given.

Key Words

COI sequences, leaf beetles, *Sphaeroderma cruenta* sp. nov., new records, South Asia, pest management

Introduction

India is one of the major centres of diversity for bananas and plantains (Zingiberales, Musaceae) and the largest producer of bananas in the world, with its annual production greater than what the rest of the world produces for export (Promusa 2019). The term “plantain” is often used specifically to refer to cooking bananas while “banana” is mainly used to refer to dessert bananas (Promusa 2019). Data from the Food and Agriculture Organization of the United Nations indicate the area under banana cultivation in India in 2017 was 860000 ha with a production of 30.48

million metric tonnes (FAOSTAT 2019). Rhizome weevil (*Cosmopolites sordidus* (Germar)) and pseudostem weevil (*Odoiporus longicollis* (Olivier)) (Coleoptera, Curculionidae) are considered as the most economically important insect pests of banana in this region. Besides these, leaf- and fruit-scarring beetles (Coleoptera, Chrysomelidae) are major seasonal pests of bananas and plantains in many states of northern, eastern, and north-eastern India, Bangladesh, and parts of Southeast Asia.

At present, there is no systematic study on the species composition of leaf and fruit feeding chrysomelids from the Indian subcontinent. Ostmark’s (1974) review of the

economic insect pests of banana was restricted to insect pests of mainly Central and South America and did not focus on the major South Asian pests of bananas, including the fruit-scarring beetles. The name “*Colaspis hypochlora* Lefèvre” (Coleoptera, Chrysomelidae) has been most extensively associated with bananas in the literature, but it is known to be a pest only in South and Central American countries (Ostmark 1975). Gowdey (1926) gave an overview of the biology of *C. hypochlora*. Ostmark (1975) gave an account of four species of *Colaspis* considered to be established pests of banana leaves and fruits in Central and South America. He also listed three more species of *Colaspis* collected in association with banana. He reported *C. hypochlora* as “common on plants near banana plantations” (Ostmark 1975: 2), but as only occasional or accidental feeders on banana. He recorded it as a frequent feeder on banana candelas in newly planted orchards in Panama and as an occasional pest of banana fruits. Hill (2008: 309) also referred to *C. hypochlora* as “a pest of some past importance in C. and S. American banana-growing areas”. Hill (1983: 518) listed “*Colaspis* spp.” as banana fruit scarring beetles in India, Central and South America with a note “larvae scar fruits”. *Myochrous melancholicus* Jacoby is another potentially serious banana fruit-feeding chrysomelid reported from Mexico (Cruz-Zapata et al. 2018).

In South and Southeast Asia, three of the 24 chrysomelid genera on Musaceae are known to feed on banana (Jolivet and Hawkeswood 1995): *Basilepta*, *Bhamoina*, and *Sphaeroderma*. *Basilepta subcostata* (Jacoby) (Chrysomelidae, Eumolpinae) is rated as one of the major seasonal pests of regional importance in India, particularly in the northeastern region, which is host to a wide diversity of bananas. The extent of damage to banana bunches by this pest has been estimated at 30% (Ahmad et al. 2003) and 11.47–95.68% (Choudhary et al. 2010) in Bihar, north India, and is as high as 80% in Assam, northeastern India (unpublished observations) in the rainy and post-rainy seasons.

Despite its economic importance, the nomenclature has not been clarified and incorrect names have been used for this species in literature. Indian workers have erroneously applied the name “*Colaspis hypochlora*” to the Indian scarring beetles (e.g. Verghese and Kamala Jayanthi 2001), and Sah et al. (2018) used both “*Basilepta* sp.” and “*Colaspis* sp.” to refer to the leaf- and fruit-scarring beetle of banana occurring in Bihar. The names *Nodostoma* spp., *Nodostoma (Basilepta) subcostatum*, *Nodostoma subcostatum*, and *Nodostoma viridipenne* have been used for the common fruit-scarring beetle in the northeastern region even though *Nodostoma* is a junior synonym of *Basilepta* (Weise 1922; Kimoto and Gressitt 1982). Furthermore, taxonomic treatments of *B. subcostata* are sparse; Kimoto and Gressitt (1982) provided a key to *Basilepta* spp. of Thailand, Vietnam, and Laos which included *B. subcostata*, but a recent redescription of *B. subcostata* with illustrations of the genitalia is not available. Besides

B. subcostata, the other chrysomelid species feeding on bananas were not identified.

The aim of this study is a) to determine the species composition of leaf- and fruit-scarring beetles infesting bananas and plantains in the Indian subcontinent, b) to describe or redescribe these species, and c) to provide a determination key facilitating their correct identification. In this way, we hope to provide a basis for a reliable identification of the banana-feeding chrysomelids, which is needed for species-specific, effective pest management strategies in future.

Materials and methods

Field collections

Surveys were carried out over a period of five years (2015–2019) for banana-feeding chrysomelids in seven states of India, namely, Uttar Pradesh, Bihar, Assam, Manipur, Meghalaya, West Bengal, and Odisha. Banana fruit-scarring beetles are major pests in the states surveyed (unpublished data from All India Co-ordinated Research Project on Fruits, operated by the Indian Council of Agricultural Research (ICAR), New Delhi).

Taxonomy

Morphological terminology follows Konstantinov (1998), Jolivet and Verma (2008), and Moseyko (2008). Males and females of *B. subcostata* were distinguished by the basitarsomeres having closely arranged capitate setae bordered by long, pointed setae on the ventral side in males, and only pointed setae in females. In the other two species, sexes were separated by the apical abdominal ventrites. Male and female genitalia of all species, including different colour morphs of *B. subcostata* from various Indian states, were dissected, photographed, and stored in glycerine in microvials pinned with the respective specimens.

The endophallus was everted using a KK-3 type C fine nozzle as follows. The endophallus was pushed towards the apical opening using the blunt end of a flexible fine needle through the basal opening and the tip of the fine nozzle, filled with K-Y gel, and affixed at the base of the aedeagus proper with a cyanoacrylate glue (Fevikwik). The assembly was allowed to dry for 5 min. and kept in water for 1 min. to relax the endophallic membrane. Then the aedeagus was immersed in K-Y gel on a glass slide and the endophallus was everted under controlled pressure of a syringe filled with K-Y gel.

Imaging

Photographs of whole specimens and their diagnostic characters were taken using a Leica M205A stereo microscope fitted with a Leica DMC 4500 digital camera. Im-

age stacks were processed into composite, high resolution images using CombineZP software. Types of *Basilepta* spp. at the Natural History Museum, London, were studied and photographed with a Canon EOS 1500D DSLR camera fitted with a Canon MP-E 65 mm macrolens and processed with Helicon Focus Pro.

COI sequencing and analysis

Sequencing of a 660-base pair (bp) fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) was done for samples of *B. subcostata* from Assam and Uttar Pradesh. Morphologically identified specimens were used for extraction, amplification and sequencing of 5' end of COI mtDNA. Genomic DNA was extracted using QiagenDNeasy kit, following the manufacturer's protocols using the following primers: forward primer (LCO 1490 5'-GGTCAACAAATCATAAAGATATTGG-3'), and reverse primer (HCO 2198 5'-TA- AACTTCAGGGTGACCAAAAAATCA-3'). Amplified products were sequenced using Sanger technology and the sequences were submitted to GenBank and accession numbers obtained.

Sequence identity matrix and alignment of COI sequences of *B. subcostata* from Assam and Uttar Pradesh were executed using the CLUSTAL W multiple alignment tool of BioEdit sequence alignment editor 7.0.5.3. Phylogenetic analysis was performed using the Maximum likelihood phylogenetic tree construct in MEGA X. Sequences of *Basilepta leechi* (MN343857), *B. variable* (MN344143), *Eumolpinae* sp. (KF946194), *Chrysomelidae* (MK083043), *Oryctes rhinoceros* (L.) (KP898260), and *Coccinella septempunctata* L. (MH976795) from GenBank were used for phylogenetic analysis with the last two forming outgroup taxa..

Specimen repositories

The specimens studied are deposited in the following collections:

BMNH	Natural History Museum, London, UK [formerly British Museum (Natural History)]
NPC	National Pusa Collection, Indian Agricultural Research Institute, New Delhi, India
ICAR-NBAIR	ICAR-National Bureau of Agricultural Insect Resources, Bangalore, India
KAU	Travancore Insect Collection, Kerala Agricultural University, Vellayani
UASB	University of Agricultural Sciences, Bangalore, India
USNM	National Museum of Natural History, Washington DC, USA
ICAR-NRCB	ICAR-National Research Centre for Banana, Tiruchirappalli, India

Results

About 1200 specimens of leaf and fruit feeding chrysomelids were collected on banana from seven states of India. The genera and species were identified by the keys given by Jacoby (1908), Kimoto and Gressitt (1982) (for *Eumolpinae*), Maulik (1926), and Scherer (1969) (for *Alticini*). One species, *Basilepta subcostata* (*Eumolpinae*), was collected from all seven states and was the most predominant and economically important leaf- and fruit-feeding chrysomelid in all locations. Two species, *Bhamoina varipes* (Jacoby) and a hitherto undescribed species of *Sphaeroderma* Stephens (*Galerucinae*, *Alticini*), were found to be restricted to the northeastern region. *Bhamoina varipes* was collected from the states of Assam and Meghalaya, and *Sphaeroderma* was collected only from the state of Meghalaya. These two species are recorded for the first time on banana in India.

Taxonomy

Chrysomelidae

Eumolpinae

Basilepta subcostata (Jacoby, 1889)

Figs 1–8

Nodostoma subcostatum Jacoby, 1889: Jacoby 1889: 164; Jacoby 1908: 334.

Nodostoma cyanipenne: Lefèvre 1893: 120; Kimoto and Gressitt 1982: 51 (synonymy).

Basilepta subcostatum: Kimoto 1967: 69; Medvedev 1990: 8–9; Chûjô 1964: 268–269.

Basilepta subcostata: Kimoto and Gressitt 1982: 51; Sprecher-Uebersax 1997: 144; Medvedev and Sprecher-Uebersax 1999: 288; Kimoto 2001: 27; Medvedev 2001: 608; Kimoto 2005: 31–32; Moseyko and Sprecher-Uebersax 2010: 639.

Material examined. *Type material*: syntype female, "SYNTYPE (blue bordered circular label)/ Bhamò, Birmania, Fea, VII.1886/ Jacoby Coll. 1909-28a/ *Nodostoma subcostatum* Jac./ abdomen missing, S.L. Shute 1976/NHMUK014016383" (BMNH). *Other material*: 64016/Birmah, Momeit/Doherty/Fry Coll. 1905-100, 1 ex.; Tharrawaddy, Burma/ Andrewes Bequest 1922-221/ *Nodostoma subcostatum* Jac., 1 male with genitalia glued to the same card; Assam, Sudiya/ Doherty/ Fry Coll. 1905-100, 1 male; Assam, Patkai Mts./ Doherty/ Fry Coll. 1905-100/ Jacoby det., 1 ex.; Thailand, Lot 1830, Nakhonratchasima, June 15, 1912/24/To B.M. List 153.10/ C.I.E. Coll. A1720/ Pres. By Com. Inst. Ent. B.M.1967-2, 2ex. (BMNH); S.INDIA, Mysore, Vittal 1964, Arecanut Res. Stn., on banana/ C.I.E. Coll. No.19658, 2 ex; Deccan/ 67.56, 1 ex; NEPAL: Rampur, 14.vii.1981, Ex. Banana, 6 ex; NEPAL: Dhunibesi, 22.vi.65, Banana, Dept. Agric. C.I.E. A.573, Col.161/ Pres. By Com. Inst. Ent. B.M. 1966-22, 2 females and 2 unsexed; 61647/ Doherty/ Assam, Patkai Mts/ Fry Coll. 1905-100, 4 ex; Bacan, N. India/ 67.56, 3 ex.; Calcutta

/ Atkinson Coll. 92-3, 2 ex; Doherty/ Tenasserim, Mergui/ Fry Coll. 1905-100; W. Almora Divn., Kumaon, UP, Aug. 1917, HGC/ E8/ H.G. Champion Coll. B.M. 1953-156, 4 ex; Lansdowne Division, UP, India, F.W.C./ H.G. Champion Coll. B.M. 1953-156, 1 ex.; Ind./ Baly Coll., 1 ex.; Khasis/ Coll. Kraatz/ Pres. by Imp. Inst. Ent. BM 1938-351/ *Nodostoma occipitale* Jac., Det. G.E. Bryant, 1 ex. (BMNH). India: Assam: 7 ♂ and 5 ♀ Balipara 74 m msl/26°49'56"N, 92°46'41.1"E/17.v.2019/ K D Prathapan Coll.; 3 ♂ Jorhat /19–22.xi.2007/ Prathapan K D Coll.; 4 ♂ and 10 ♀, Assam: Dergaon, 26°42'01.00"N, 093°54'01.26"E/2.x.2018, R. Thanigairaj; Assam: 2 ♂, 2 ♀ Nameri Nat. Park 85 m msl/ 26°55'27.4"N, 92°49'38.9"E/17.v.2019/ K D Prathapan Coll.; Assam: 17 ♂, 13 ♀ and 7 unsexed, Tezpur 72 m msl/ 26°37'33.4"N, 92°48'41.5"E/19.v.2019/ K D Prathapan Coll.; 25 ♂ and 14 ♀, Assam: Kaziranga, Kohora 70 m msl/ 26°35'29.6"N, 93°23'56.1"E/18.v.2019/ K D Prathapan Coll./Ex Banana; 2 ♂ same data, except Host *Canna* sp.; Meghalaya: 11 ♂, 13 ♀, Barapani/25°41'17.6"N, 91°55'5.1"E/5.vi.2013 993 m/Prathapan K D Coll./Ex. Banana; 3 ♂, 1 ♀, Meghalaya: Nongpoh 587 m msl/25°50'34.4"N, 91°52'34.4"E/22.v.2019/ K D Prathapan Coll.; 1 ♂, 6 ♀ Meghalaya: Cherrapunjee 1426 m msl/ 25°17'11.0"N, 91°43'07.8"E/21.v.2019/ K D Prathapan Coll.; 3 ♂, 3 ♀ Meghalaya: Umroi/2.xii.2007/Prathapan K D Coll.; 4 ex, Meghalaya: Jorabat, 04.x.2018, 26°04'59.52"N, 091°52'36.59"E, R.Thanigairaj; Meghalaya: 2 ex, Umi-am/19.vii.2019/D. M. Firake/Ex ginger; 3 ♂ and 10 ♀, West Bengal: Cooch Behar, x.2016, B. Padmanaban; Uttar Pradesh: 4 ♂, 9 ♀ Faizabad Dist, 27°37'06.96"N, 081°36'29.54"E, 12.xi.2018, J. Poorani; Bihar: 6 ♂ and 1 ♀ Bhagalpur, 6.iii.2016, B. Padmanaban; Bihar: Falka, 11–12.x.2017, B. Padmanaban; Odisha: 4 ex, Bhubaneswar, 29.v.2015, Sangeetha.

Generic diagnosis. Body oblong; head mildly sulcate above eyes; antennae filiform or distal antennomeres widened; pronotum wider than long, widest posteriorly, lateral margins often angulate; anterior margin of proepisternum concave; legs long, all femora dilated, minutely dentate ventrally, tibia longitudinally sulcate with a sharp ridge along dorsal side; intermediate and posterior tibiae emarginated preapically; metatibia with a pair of short apical spines; prosternum broader than long. Claws appendiculate; bursa sclerites present in female genitalia.

Related species. *Basilepta makiharai* Kimoto, described from Nepal, is stated to “resemble *B. subcostata* in having the elytron with humeral ridge but differs by its shorter body length and in having the surface of vertex finely shagreened” (Kimoto 2001: 26). It is generally pitchy black to dark reddish brown with entirely yellowish-brown antenna. *Basilepta viridipennis* (Motschulsky), another species widely distributed in Southern Asia and erroneously reported as the banana fruit-scarring beetle from India and Bangladesh, is also externally similar to *B. subcostata*, but its antenna is almost fully blackish except for the first four antennomeres and the posterolateral callosity of pronotum does not project beyond lateral margin, and hence, the posterolateral corners of pronotum

are obtuse and not angulate as in *B. subcostata*. Besides, the elytra are metallic green to violaceous and shinier and lack a distinct lateral costa.

Nodostoma obscurum Jacoby, 1908 and *Basilepta sakaii* Takizawa, 1987 were listed as synonyms of *B. subcostata* in the catalogue of Nepalese Chrysomelidae by Medvedev and Sprecher-Uebersax (1997: 288), but they did not mark it as a new synonymy. This appears to be incorrect because the type of *N. obscurum* is not even morphologically similar to *N. subcostatum*, whereas *B. sakaii* is a smaller insect according to the description (Alexey Moseyko, personal communication).

Description. Length 2.34–3.00 mm, width 1.36–1.86 mm, 1.6–1.7× longer than broad. Body (Fig. 1a–c) oblong ovate, shiny. Colour highly variable from red-brown to dark blue, black, or their mixtures without any spots, stripes or maculations; head entirely red-brown to tinted black except vertex red-brown, palpomeres light yellow to brown, some specimens with apex of last palpomere black; basal 4–6 antennomeres light brown and rest gradually turning piceous to black; colour of pronotum and elytra varies from red-brown or dark blue to shiny black, pronotum concolorous with elytra or not, general color of legs red-brown to dark brown or testaceous, tibia distally and tarsomeres darker.

Three major color morphs and their intermediates were commonly observed:

1. Head and pronotum red-brown; elytra blue, blue-black, dark green, or black; all ventrites dark (Fig. 1a). A syntype, images of which were made available by the Museum of Comparative Zoology (http://140.247.96.247/mcz/Species_record.php?id=9291), belongs to this category.
2. Entirely red-brown, except distal antennomeres, legs and palpi piceous to black (Fig. 1c);
3. Entirely dark blue, blue-black, dark green, or black (Figs 1b, 2), except head medially red-brown; metasternum and abdominal ventrites piceous to black; all entirely dark variants observed were females.

Head (Fig. 3a, b) distinctly punctured with impunctate areas on vertex and frons; punctures bold, slightly smaller than those on pronotum. Coronal suture weak but evident. Supraorbital pore adjacent to dorsal margin of eye, rounded, with a long seta. Orbital sulcus with deep, bold punctures. Frons hardly differentiated from vertex, supra frontal sulcus weak. Frons with a few bold punctures, impunctate medially. Antennal calli trapezoidal, raised; supracallinal sulcus well developed with a few bold punctures. Clypeus forms narrow transverse band with strongly concave anterior margin; frontoclypeal suture with a few small punctures. Labrum broader than long, with a pair of broadly placed setose punctures in middle and a pair of setae anterolaterally; anterior margin with thick short setae on either side of middle, apical margin emarginate medially. Antennae hardly extend up to middle of elytra; first antennomere thick, longer than second; second antennomere thinner than first, thicker than 3rd and 4th separately; 5th onwards antennomeres progressively thicker; basal four anten-

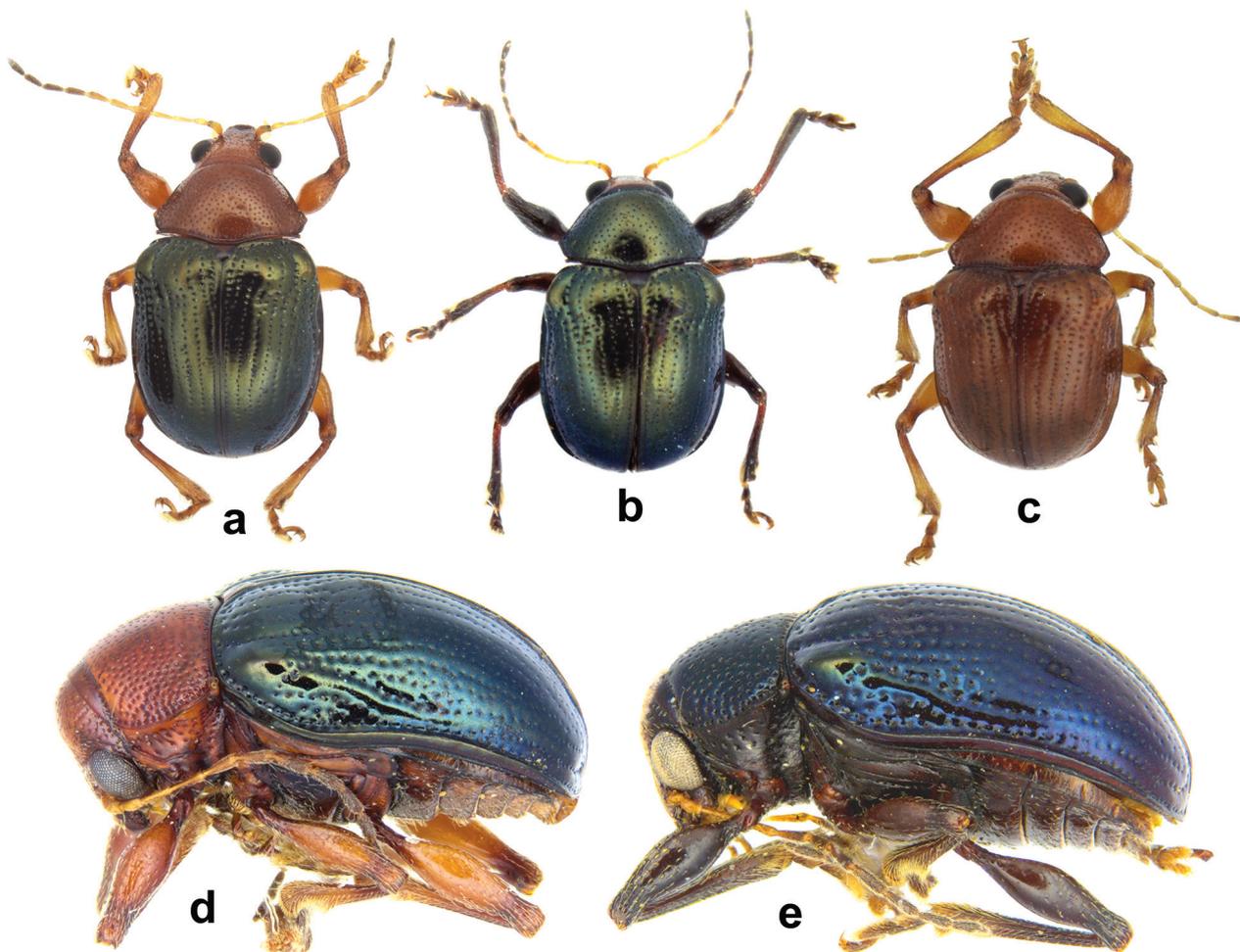


Figure 1. *Basilepta subcostata* (Jacoby). **a–c.** Habitus, dorsal: **a.** Nominate form, male; **b.** Female; **c.** Rufous form, male; **d.** Male, lateral view; **e.** Female, lateral view.



Figure 2. Syntype (female) of *Basilepta subcostata* (Jacoby) (BMNH). **a.** Dorsal view; **b.** Lateral view.

nomeres smooth, shiny, sparsely setose; distal seven thickly covered with short pointed setae, proportion of antennomeres as follows: 1 : 0.80 : 1.13 : 1.33 : 1.27 : 1.20 : 1.20 : 1.27 : 1.20 : 1.13 : 1.33.

Compound eyes with inner margin feebly emarginate, transverse diameter about 1.4–1.5× vertical. Distance between eyes 1.8× distance between antennal sockets, shortest distance between compound eye to adjacent an-

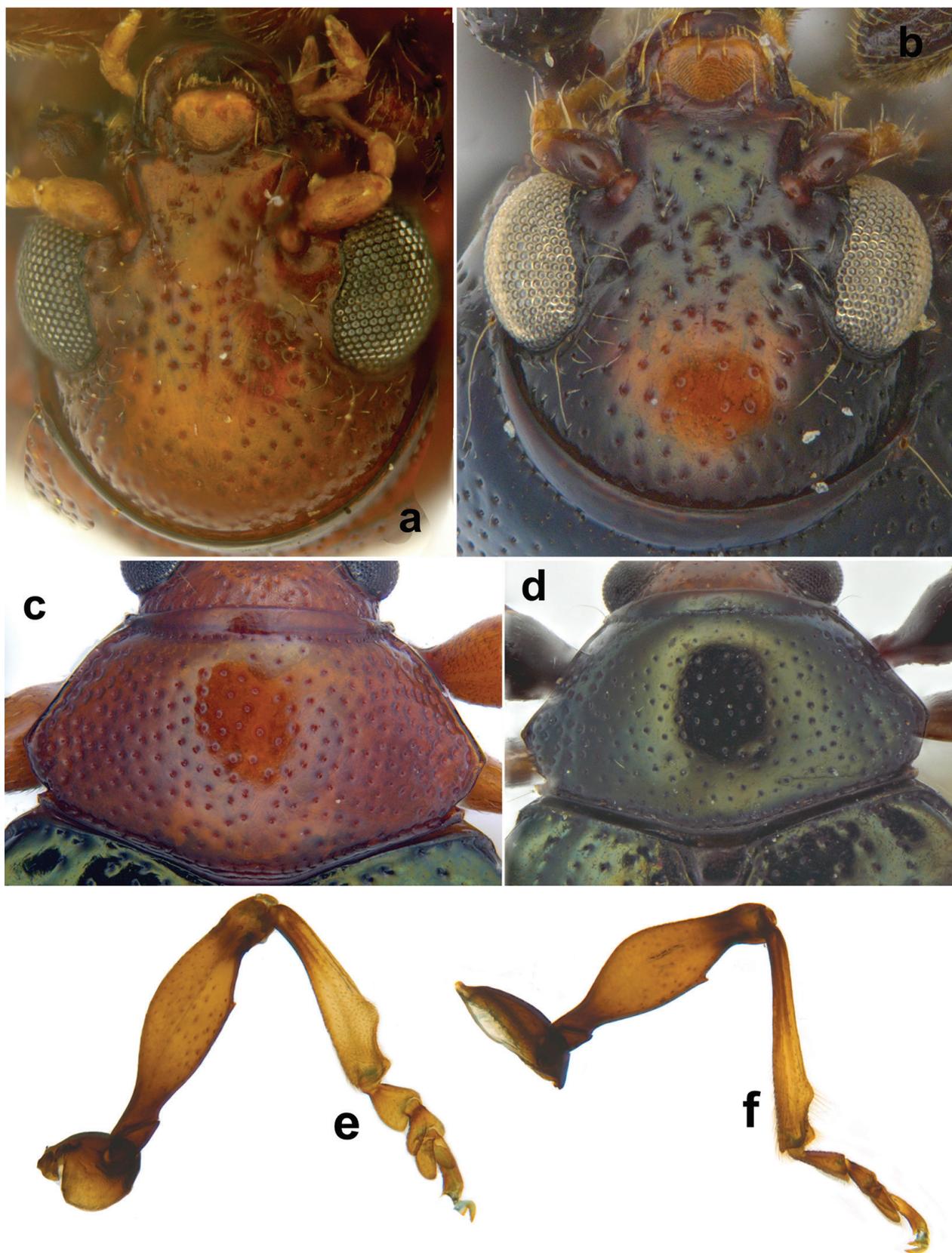


Figure 3. *Basilepta subcostata* (Jacoby). **a.** Head, dorsal view, male; **b.** Head, dorsal view, female; **c.** Pronotum, male; **d.** Pronotum, female; **e.** Middle leg; **f.** Hind leg.

tennal socket about $3.5\times$ distance between antennal sockets. Mandibles with two large denticles; maxillary palpi three-segmented excluding palpifer; last palpomere lon-

gest, penultimate palpomere less than half length of last palpomere. Labial palpi with three palpomeres, excluding palpiger, first palpomere being shortest and last longest.

Pronotum (Fig. 3c, d) about 1.6× broader than long, posteriorly 1.6–1.7× wider than anteriorly, somewhat trapeziform in outline, narrowed anteriorly, with posterolateral callosity laterally projecting beyond lateral margin, hence posterolateral corners appear sharply angulate, lateral margins angulate at posterior one-third presenting octagonal appearance, densely punctate, punctures larger than those on head and smaller than those on elytra, posterior margin gently lobed in middle, anterior sulcus and posterior sulcus distinct with a row of punctures, posterior sulcus deeper than anterior. Scutellum wider than long, broadly rounded posteriorly, sparsely and minutely punctate. Elytra 1.2× longer than wide, punctate striate, punctation weaker towards apex, punctures regular post medially with 10 striae; partially confused and semiregular in anterior half of elytra due to incomplete or broken striae; distance between punctures in a row less than distance between adjacent rows; extreme lateral row of elytral punctures regular, complete, extending up to apex; second row merged with first row from anterior one-fourth to middle of elytra; third row arising from humerus extending up to apex of elytra; interstice between 2nd and 3rd lateral rows distinctly costate, extending as far as middle of elytra or beyond, costa variable in prominence, strongly convex and sinuate in the syntype female (Fig. 2b) (BMNH, examined), but only moderately prominent in most of the Indian material examined. Humeral calli well developed, post basal depression shallow but distinct; basal calli distinct, vary in prominence. Elytral apex narrowly convex. Epipleura outwardly oblique with sparse and fine punctures, narrowing beyond proximal one-third, hardly reaching elytral apex.

Prosternum broader than long, broader posteriorly than anteriorly, with bold punctures, posterior margin straight; mesosternum nearly twice as broad as long with a few punctures smaller than those on prosternum. Proepisternum depressed; hypomeron with bold punctures. Legs long; all femora dilated, minutely dentate ventrally beyond middle (Fig. 3e, f); tibia (Fig. 3f) with eight sharp carinae, variable in prominence: three each dorsally and ventrally, one each on either side laterally. Tarsomeres ventrally fringed with diverse forms of setae, basitarsomere with closely arranged capitate setae bordered by long pointed setae in males and only pointed setae in females, second tarsomere ventrally with pointed setae, bilobed third tarsomere with triangular or inverted arrowhead-shaped setae ventrally.

Ventrites sparsely punctate, pubescent; first ventrite medially longer than following two combined, ventrites 3 and 4 subequal, shorter than 2 and 5 separately which are subequal, last ventrite hardly sexually dimorphic, last tergite without longitudinal groove medially.

Male genitalia: aedeagus in lateral view (Fig. 4a, c, e, h, k, m, n, o) sharply bent almost at right angle near base of aedeagus proper, apical portion acutely narrowed and slightly recurved dorsally; in ventral view (Fig. 4b, d, f, g, i, j, l), depressed along ventral surface, apex narrowed forming obtuse denticle; apical opening wide, partial-

ly covered by a lamina with a pair of sclerotized stripes fused basally and joining dorsal surface. Tegmen (Fig. 4q) flat, membranous, lightly sclerotized, bilobed distally, proximally with a pair of arms which turn narrowed and encircle base of aedeagus proper. Spiculum gastrale (second spiculum of Jolivet and Verma 2008) Y-shaped, sclerotized. Tergite VIII semicircular with spindle-shaped sclerotization on either side, with short setae apically. Spiculum relictum (sensu Slipinski and Escalona 2013) spoon-shaped, distally dilated (Fig. 4p).

Endophallus (Fig. 5a) long, membranous, tubular, about 3.7–3.9× longer than aedeagus proper; with three distinct regions: basal phallomere (BP), median phallomere (MP), and apical phallomere (AP); basal phallomere (Fig. 5b) very short with a lateral lobe on either side, followed by two inwardly curved central sclerites (CS) dorsally; median phallomere (Fig. 5c) longest, tubular, with setae or hair like spicules, a few circular spicules present near apical region; apical phallomere (Fig. 5d) much wider than other two regions, asymmetrical, with spicules varying in shape such as triangular, angular, oval; apical region proximally with three minute lobes facing median phallomere, apex with large lateral lobes and several smaller lobes medially.

Female genitalia (Fig. 6) with spermathecal capsule sickle-shaped (Fig. 6a, b), proximal portion very short, constricted medially, dumbbell-shaped where spermathecal duct and spermathecal gland join side by side, distal portion sickle-shaped, sharply curved, subacutely narrowed towards distal end; spermathecal gland long and tubular, length of spermathecal capsule 7.7× its maximum width. Bursa copulatrix (Fig. 6c) sac like, longer than wide, with a long bursa sclerite (BS) on either side, spermathecal duct joins bursa copulatrix between these sclerites, median oviduct attached on the other side of bursa copulatrix. Ovipositor (Fig. 6d) elongate, sclerotized distally, with almost 10–16 long setae, stylus absent; 8th sternite and 8th tergite fused laterally to form a membranous cylinder with mild sclerotizations laterally (Fig. 6f); 8th sternite with a long tignum *sensu* Konstantinov, 1998 (spiculum ventrale *sensu* Slipinski & Escalona, 2013) longer than ovipositor (Fig. 6e); collateral gland (CoG) present (Fig. 6g).

Distribution. India [Karnataka (new record); Delhi (Batra 1952); Uttarakhand; Uttar Pradesh; Bihar; Odisha; West Bengal; Sikkim; Assam; Manipur; Meghalaya]. Bangladesh. Myanmar, Thailand, Laos, Cambodia (Kimoto and Gressitt 1982; Vansilalom 2016); Nepal (Medvedev 1990; Sprecher-Uebersax 1997; Kimoto 2001). A distribution map is available at this link: https://www.google.com/maps/d/edit?hl=en&mid=1QgHVswL3eaPJ2soJ16_R5BTkIu8mRM6z&ll=23.692266951458954%2C78.67937627596257&z=6.

Host plants. *Musa* spp. (*Musa sapientum*, *M. acuminata*; Musaceae, Zingiberales) are principal hosts. Beetles were observed feeding on ginger (*Zingiber officinale* Roscoe; Zingiberaceae, Zingiberales) in Meghalaya (D.M. Firake, personal communication). In Assam, northeastern India, adult beetles were observed feeding on *Canna indica* L. (Cannaceae, Zingiberales) and tur-

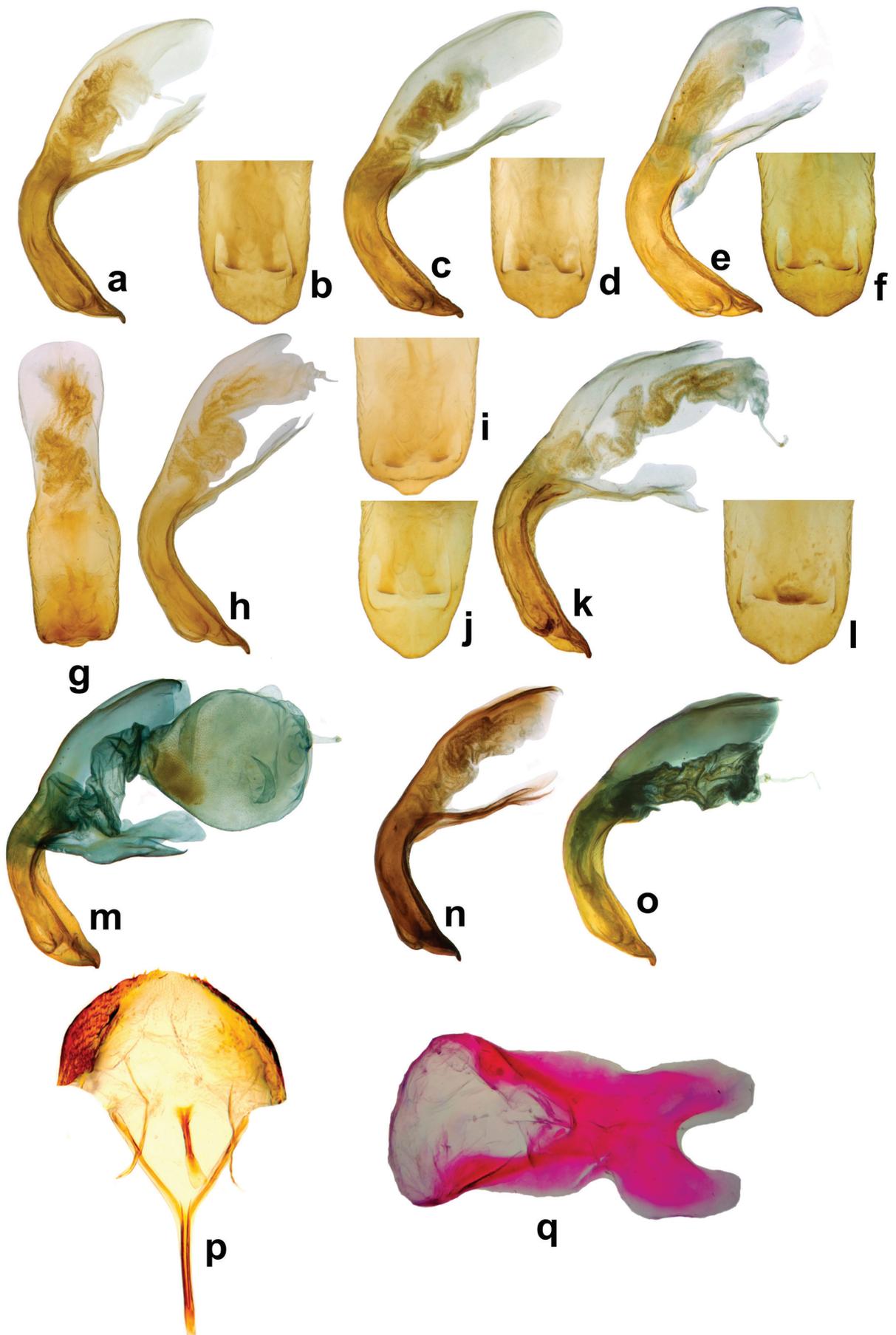


Figure 4. Male genitalia of different populations of *Basilepta subcostata* (Jacoby). **a, c, e, h, k, m–o.** Aedeagus, lateral view; **b, d, f, g, i, j, l.** Apex of aedeagus, ventral view; **p.** Male: tergite VIII, sternite VIII and IX; **q.** Male genitalia, tegmen.

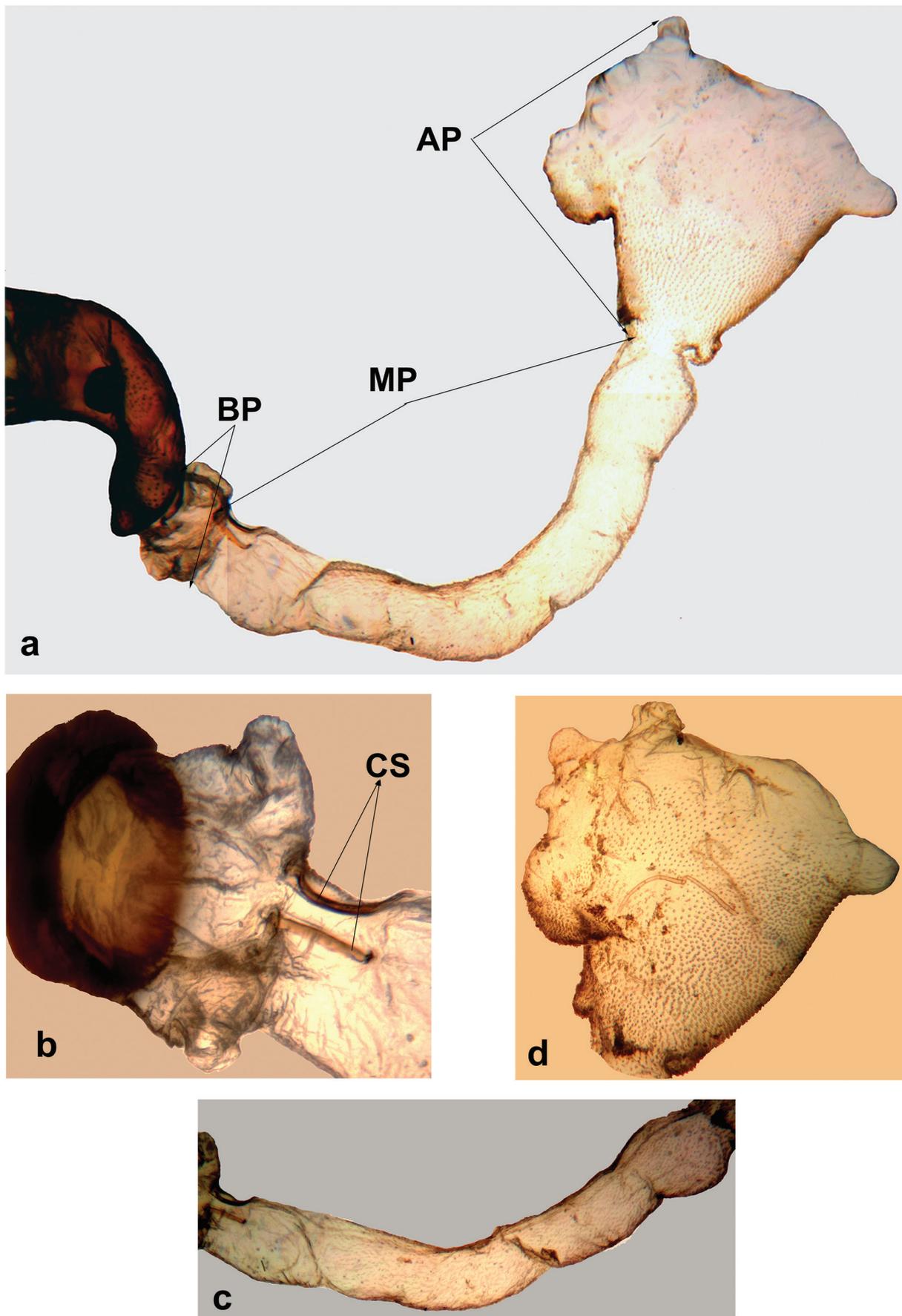


Figure 5. Endophallus of *Basilepta subcostata* (Jacoby). **a.** Endophallus completely everted, lateral view; **b.** Basal phallomere and central sclerite, dorsal view; **c.** Median phallomere, lateral view; **d.** Apical phallomere, dorsolateral view. Abbreviations: BP = Basal phallomere; MP = Median Phallomere; AP = Apical phallomere; CS = Central Sclerite.

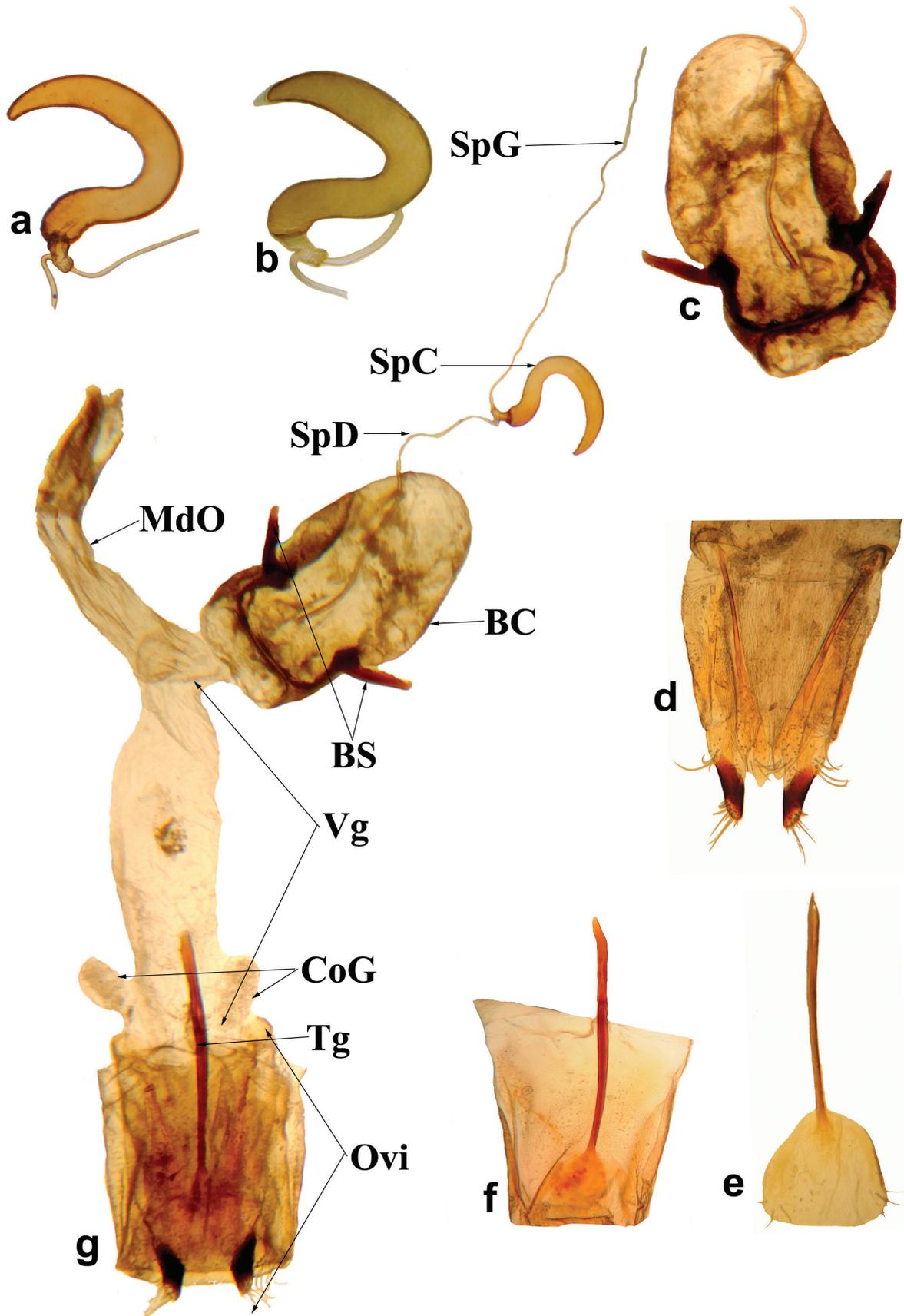


Figure 6. Female genitalia of *Basilepta subcostata* (Jacoby). **a, b.** Spermatheca; **c.** Bursa copulatrix; **d.** Ovipositor; **e.** Eighth sternite and tignum; **f.** Eighth sternite and 8th ventrite along with tignum; **g.** Female genitalia. Abbreviations: SpG = spermathecal gland; SpC = spermathecal capsule; SpD = spermathecal duct; MdO = median oviduct; BC = Bursa copulatrix; BS = bursa sclerite; Vg = vagina; CoG = collateral gland; Tg = tignum; ovi = ovipositor.

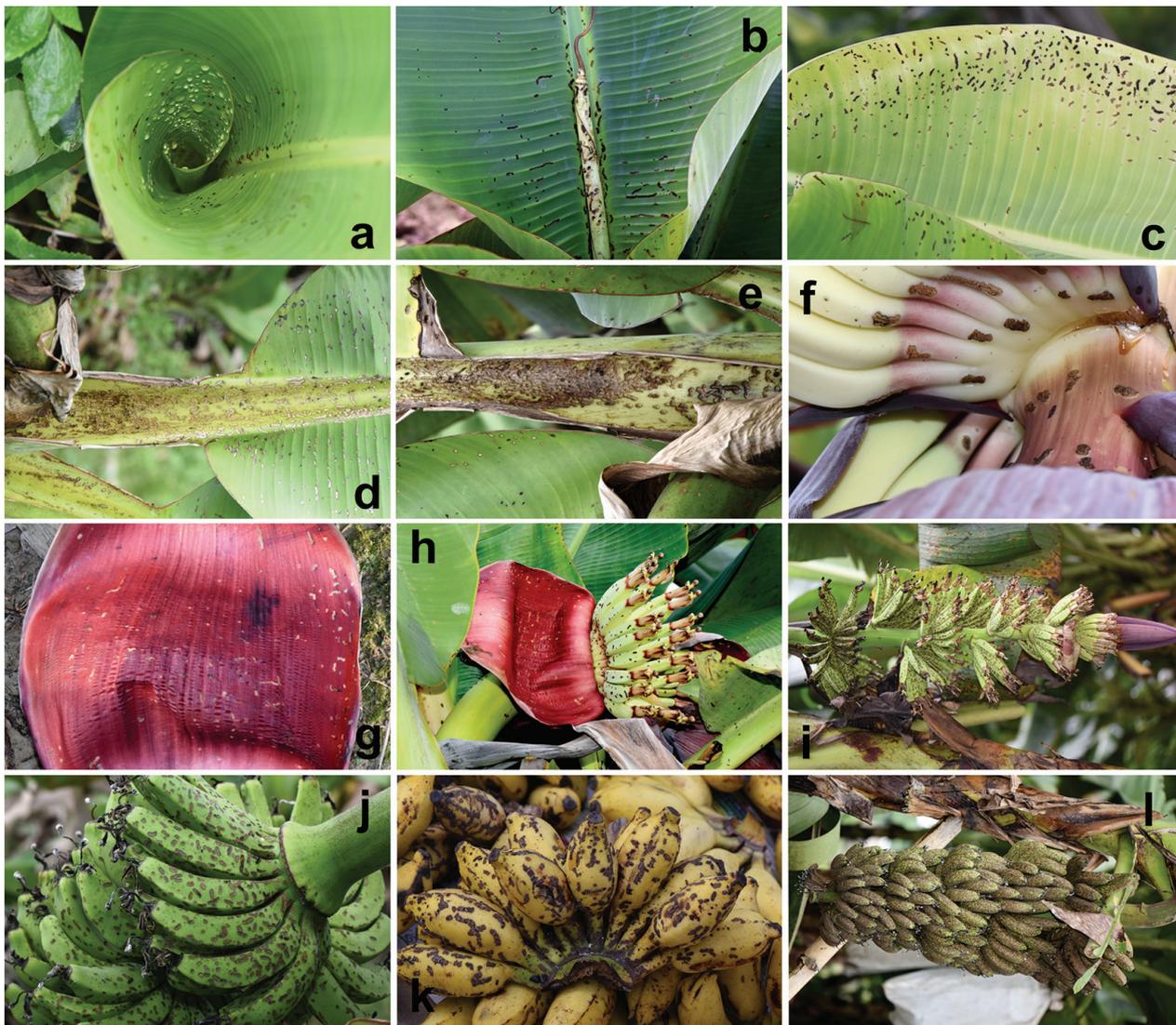


Figure 7. Damage caused by *B. subcostata* (Jacoby) on banana. **a.** Leaf whorl showing scarring damage; **b.** Scars on spindle leaf; **c.** Scars on leaf; **d., e.** Scarring on leaf petiole; **f.** Flower damage; **g.** Bract damage; **h–i.** Damage on young fruits and emerging bunch; **j–l.** Fruit damage.

meric (*Curcuma longa* L., Zingiberaceae) and characteristic feeding marks were observed on the latter. This is the first documentation of other hosts of *B. subcostata* besides banana. Adults were also found to be resting on taro (*Colocasia* sp., Araceae, Arales) (unpublished data).

Bioecology. The adult beetles are most active during the monsoon and post-monsoon seasons and summer. They are nocturnal and usually found hiding inside the leaf whorls and come out only when disturbed. They feed on the young unfurled leaves (Fig. 7a), leaf petioles (Fig. 7d, e), and stems of banana, and the emerging leaves (Fig. 7b, c) are badly scarred. Feeding damage was also observed on flowers (Fig. 7f) and bracts (Fig. 7g), as well as young, developing fruits (Fig. 7h, i). For more images of the damage symptoms on cultivated banana, see the website of ICAR-National Research Centre for Banana (2019). In severe cases, the developing bunches and fruits (Fig. 7j–l) are so badly scarred that they lose their market value.

Eggs are laid in the soil and the larvae feed on the roots of grasses and other weeds. Pupation takes place in the soil. Emerging adults feed on young leaves and fruits. Adults hibernate during winter. Seasonal incidence and population dynamics of fruit scarring beetles have been studied from some parts of India, including Assam (Mishra et al. 2015) and Bihar (Ahmad et al. 2010; Sah et al. 2018).

Pest status. Mukherjee et al. (2006) reported that meteorological factors accounted for about 85% of the beetle incidence in Bihar (India) and minimum temperature and maximum relative humidity had a positive and significant effect on scarring beetle populations. Though damage due to scarring beetles is believed to be mainly cosmetic, the fruit quality is also badly affected. Zahan et al. (2001) and Sah et al. (2018) reported that scarring beetle infestation significantly delayed fruit ripening, reduced the fruit weight, and adversely affected the skin colour and thickness of fruits and the



Figure 8. Naturally occurring epizootic of fungal pathogen, *Beauveria bassiana* on *Basilepta subcostata*.

taste and smell of the pulp. This damage considerably affects the consumption value.

Natural enemies. In Uttar Pradesh, North India, adults of the predatory beetle, *Paederus fuscipes* Curtis (Coleoptera, Staphylinidae), were found to be commonly associated with *B. subcostata*. Natural epizootics of entomofungal pathogens, such as *Beauveria bassiana*, are commonly observed on *B. subcostata* in the northeastern region of India (Fig. 8) and exert some control in the post-monsoon months.

Basilepta viridipennis (Motschulsky, 1860)

Fig. 9

Nodostoma viridipenne Motschulsky, 1860: Motschulsky 1860: 177; Jacoby 1908: 349; Kimoto 1967: 69.

Nodostoma frontale: Baly 1867: 253; Medvedev 2006: 412 (synonymy).

Nodostoma occipitale: Jacoby 1908: 335–336; Kimoto and Gressitt 1982: 36 (synonymy).

Nodostoma haroldi: Jacoby 1908: 331 (new name for *Nodostoma aeneipenne* Baly); Kimoto and Gressitt 1982: 36 (synonymy).

Nodostoma aeneipenne: Baly 1867: 235; Jacoby 1908: 331 (synonymy)

Nodostoma haroldi var. *apicipes*: Jacoby 1892: 87; Jacoby 1908: 331.

Basilepta viridipenne: Medvedev 2006: 412.

Basilepta viridipennis: Moseyko and Sprecher-Uebersax 2010: 639.

Basilepta occipitalis: Moseyko and Sprecher-Uebersax 2010: 639.

Material examined. *Type material* of *Nodostoma occipitale* Jacoby: 62590/ Type (red bordered circular label)/ Doherty/ Tenasserim, Mergui/ Fry Coll. 1905-100/ *Nodostoma occipitale* Jac., Type (blue label)" (BMNH). **Other material:** Fea/ Birmah, Carin Cheba/ Fry Coll. 1905-100/ NHMUK0114016244, 1 ex; Doherty/ Tenasserim, Javoy/ Fry Coll. 1905-100/ NHMUK014016300, 1 ex (BMNH).

Remarks. *Basilepta viridipennis* (Fig. 9) has been erroneously reported in the literature as a pest of banana in the Indian Subcontinent (India and Bangladesh), and Waterhouse (1993) also listed it as a major pest of banana in Southeast Asia. All reports of its occurrence in northeastern India (Das and Baruah 2018), Bangladesh (Ahmed 1963; Zahan et al. 2001, 2003, 2004; Rahman et al. 2004), and Thailand (Wongsiri 1991) are most likely to refer to *B. subcostata*. The type of *N. occipitale* Jacoby (Fig. 9a, b) (BMNH, examined), a synonym of *B. viridipennis*, has only a superficial resemblance to *B. subcostata* and can be easily separated from the latter by the pronotum forming an obtuse angle posterolaterally (Fig. 9b) and its lateral margins abruptly converging an-

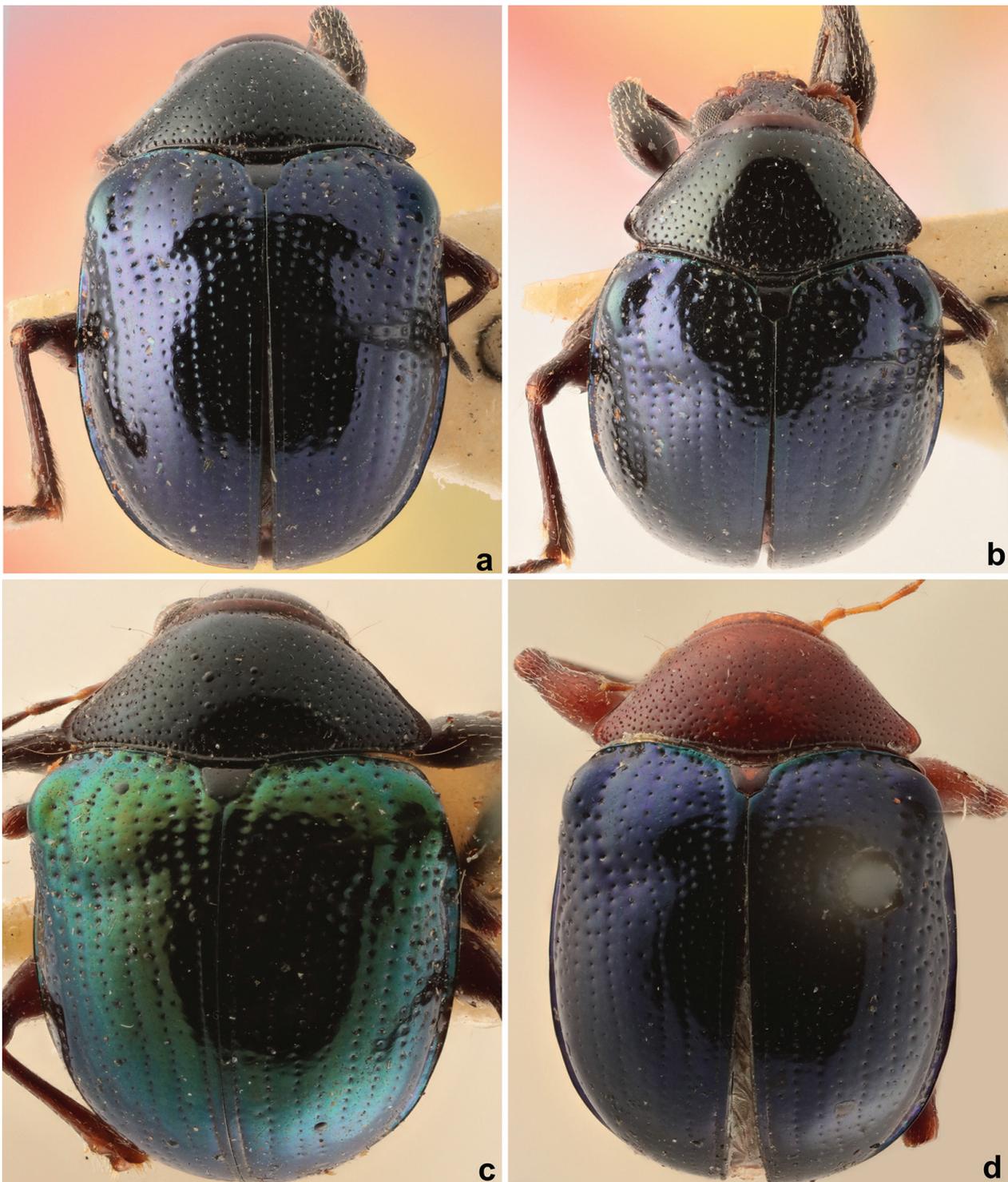


Figure 9. *Basilepta viridipennis* (Jacoby). **a, b.** Syntype of *Nodostoma occipitale* Jacoby, a synonym of *B. viridipennis* (BMNH); **c, d.** Colour forms of *B. viridipennis*.

teriorly in almost a straight line. Besides, pronotal punctures in *B. viridipennis* are smaller than average elytral punctures and finely and more closely impressed on lateral part and more sparsely and finely so on median and anterior parts. *Basilepta viridipennis* is of variable coloration and includes reddish, brownish, bluish, greenish,

violaceous, and blackish forms. Medvedev (2006) designated a lectotype for *N. viridipenne* and synonymised *Basilepta frontalis* (Baly) with it, as he found the types of both species were identical.

Distribution. India, Nepal, Myanmar (= Burma), Thailand, Laos, Vietnam, Hainan, Malaya, Sumatra.

Chrysomelidae
Galerucinae
Alticini

***Bhamoina varipes* (Jacoby, 1884)**

Figs 10–12

Eucycla varipes Jacoby, 1884: Jacoby 1884: 210 (Sumatra; Mus. Leiden); Duvivier 1885: 42 (Is. Bodjo).

Sphaeroderma varipes: Jacoby 1889: 193 (N Burma: Teinzo, Bhamo; Tenasserim: Meetan); Maulik 1926: 318, 328 (Burma: Karen Mts., Assam: Khasi Hills).

Bhamoina varipes: Bechyné 1958: 91; Scherer 1969: 202–203; Döberl 2010: 505.

Bhamonia [sic] *varipes*: Kimoto 2005: 80.

Sphaeroderma varipennis Jacoby 1892: 928 (Carin Cheba, Palon, Rangoon; Mus. Genova); Maulik 1926: 318, 325; Scherer 1969: 202 (synonymy).

Material examined. *Type material* of *Sphaeroderma varipennis* Jacoby: “Type (H.T.) (red bordered circular label) / Carin Cheba, 900–1100 m, L. Fea, v.XII.88 / Jacoby Coll. 1909-28a / Sphaerod. varipennis Jac. (blue label)” (BMNH); Others: “Sumatra / Jacoby Coll. 1909-28a / varipennis Jac. In B.M. Coll. C.M.F. Von Hayek det. 1967 / *Bhamoina varipennis* (Jacoby), G. Scherer det. 1967” (BMNH). India: Assam: 5♂, 6♀♀, Balipara 74 m msl; 26°49'56.0"N, 92°46'41.1"E; 17.V.2019; K. D. Prathapan Coll. (KAU); Meghalaya: 3♂, 8♀ Barapani 993 m msl; 25°41'17.6"N, 91°55'5.1"E; 5.vi.2013; K. D. Prathapan Coll. Ex banana (KAU); Meghalaya: 11♂, 16♀, Ri Bhoi Dst., Saiden 540 m msl; 25°52'41.0"N, 91°53'1.4"E; 4.vi.2013; K. D. Prathapan Coll. Ex banana (KAU); Meghalaya: 5♂, 2♀, Nongpoh, 587 m msl; 25°50'34.4"N, 91°52'34.4"E; 22.v.2019; K. D. Prathapan Coll. (KAU).

Remarks. The genus *Bhamoina* closely resembles *Sphaeroderma* (see below for the generic diagnosis of *Sphaeroderma*). *Bhamoina acutangula* (Jacoby), the type species of the genus, was originally described in *Sphaeroderma*. *Bhamoina* can be easily separated from *Sphaeroderma* by the anteriorly produced anterolateral corners of pronotum (in *Sphaeroderma*, the anterolateral corners of pronotum are not produced forward, or only slightly produced). *Sphaeroderma varipennis* Jacoby, treated as a synonym of *B. varipes* by Scherer (1969), is bicolored (Fig. 11a) with the elytra fully black and the head and pronotum reddish. It has a slightly more robust body form, and the anterolateral corners of pronotum (Fig. 11b, c) are less produced and somewhat obtusely rounded compared to those of *B. varipes*.

Scherer (1969) gave a key to the Oriental species of *Bhamoina*. *Sphaeroderma varipennis* has been known to be a pest of banana in Thailand, and adults defoliate banana (Hill 2008). Dean (1978) recorded “*Sphaeroderma varipennis*” on banana in Laos. Although *B. varipes* is distributed in India, there has been no previous records of its host plant association from India.

Description. Entirely red-brown (Fig. 10a, b), except eyes and distal portion of mandibles black. Elytra darker in a few examples. Proximal 5–7 antennomeres lighter than distal ones. Anterolateral corners of pronotum, palpi, fore- and midfemora, tarsomeres, and last abdominal ventrites often lighter than dorsum.

Length 2.71–3.41 mm, width 1.97–2.80 mm, 1.34× longer than broad. In lateral view vertex weakly convex, forming a concavity where it joins frons; frons strongly arched, joining clypeus at an obtuse angle. In frontal view vertex moderately flat, sparsely punctate with a mixture of small and minute punctures. Supraorbital pore circular, without shallow groove surrounding it, placed just above orbital sulcus, two or three smaller punctures anterior to supraorbital pore present. In frontal view (Fig. 10c), frontal ridge broad and raised between antennal sockets; narrowed dorsally entering between antennal calli; ventrally narrower than dorsally; frontolateral area anteriorly with a few setae; anterofrontal area flat, not forming ridge, with long and short setae. Antennal calli transverse-oblique, trapezoidal, slightly higher than vertex, narrowly separated dorsally; anteromesal ends acutely angulate, entering into interantennal space. Supracallinal sulcus deep, gently convex, oblique, narrower than orbital sulcus. Suprafrontal, supraorbital, supraantennal sulci well developed, all weaker than supracallinal sulcus. Distance between antennal sockets 1.57× diameter of a socket, antennal sockets separated from adjacent eye by a distance 0.38× transverse diameter of a socket. Labrum wider than long, dorsal surface convex anteriorly, anterior margin convex, with three pairs of labral setae arranged in a transverse row. First antennomere longer than second and third combined, second a little longer than third and fourth separately, sixth onwards antennomeres progressively thickened. Proportionate length of antennomeres I to XI: 1 : 0.48 : 0.41 : 0.52 : 0.56 : 0.44 : 0.59 : 0.52 : 0.52 : 0.52 : 0.8. Maxilla with penultimate palpomere thicker and longer than last and preceding palpomeres separately. Labium with penultimate palpomere thickened, subequal in length to thin, pointed last palpomere.

Pronotum (Fig. 10d) convex, distinctly narrowed anteriorly, 0.30× as long as wide, posteriorly 1.65–1.76× wider than anteriorly, profusely, uniformly covered with small punctures. Pronotal punctures as small as half of elytral punctures. Lateral margin weakly convex proximally, gently concave at anterolateral seta bearing pore; broader anteriorly than posteriorly. Anterior margin deeply concave, except gently convex in middle. Posterior margin bisinuate, forming a distinct lobe in middle. Anterolateral callosity (Fig. 10e) projecting forward on either side of head; seta bearing pore on dorsal posterior face of callosity. Posterolateral callosity not protruding laterally, with seta bearing pore on lateral face.

Scutellum triangular, acutely angulate posteriorly, shiny, flat on top, minutely punctate. Elytra as wide as pronotum at base, widened postbasally, lateral margin entirely visible in dorsal view. Elytral apex convex. Elytral punctures confused in mesal half, tend to form rows in

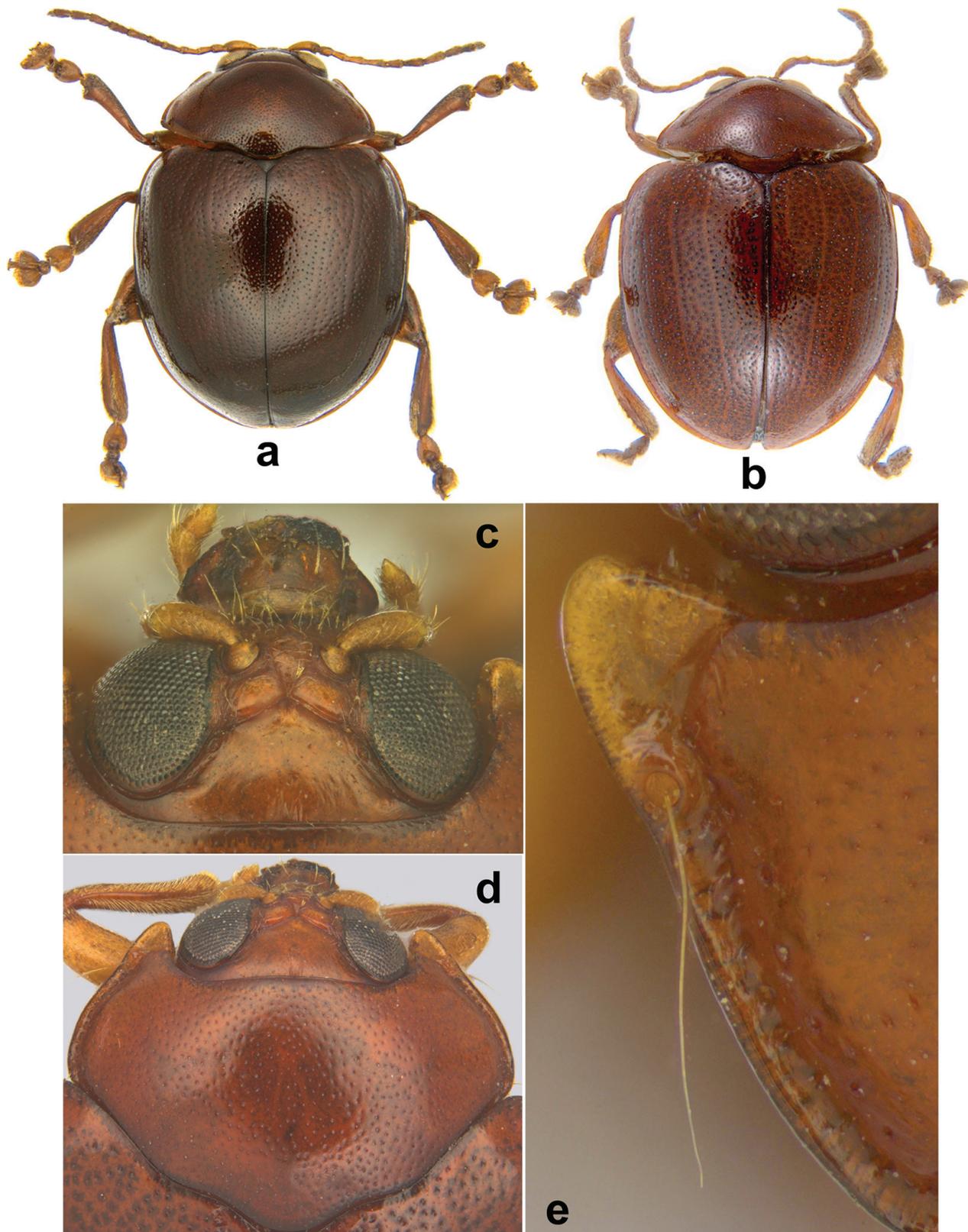


Figure 10. *Bhamoina varipes* (Jacoby). **a, b.** Dorsal view; **c.** Head, dorsal view; **d.** Pronotum, dorsal view; **e.** Lateral margin of pronotum.

lateral half, outermost punctures forming a regular row. Each elytral puncture surrounded by a dark halo, distance between adjacent punctures less than diameter of one puncture, including dark halo.

Maximum width of elytral epipleura subequal to that of midfemur. Epipleura subhorizontal, visible in lateral view, widest at proximal one-fourth, gradually narrowing till distal one-third and then abruptly narrowed, hardly

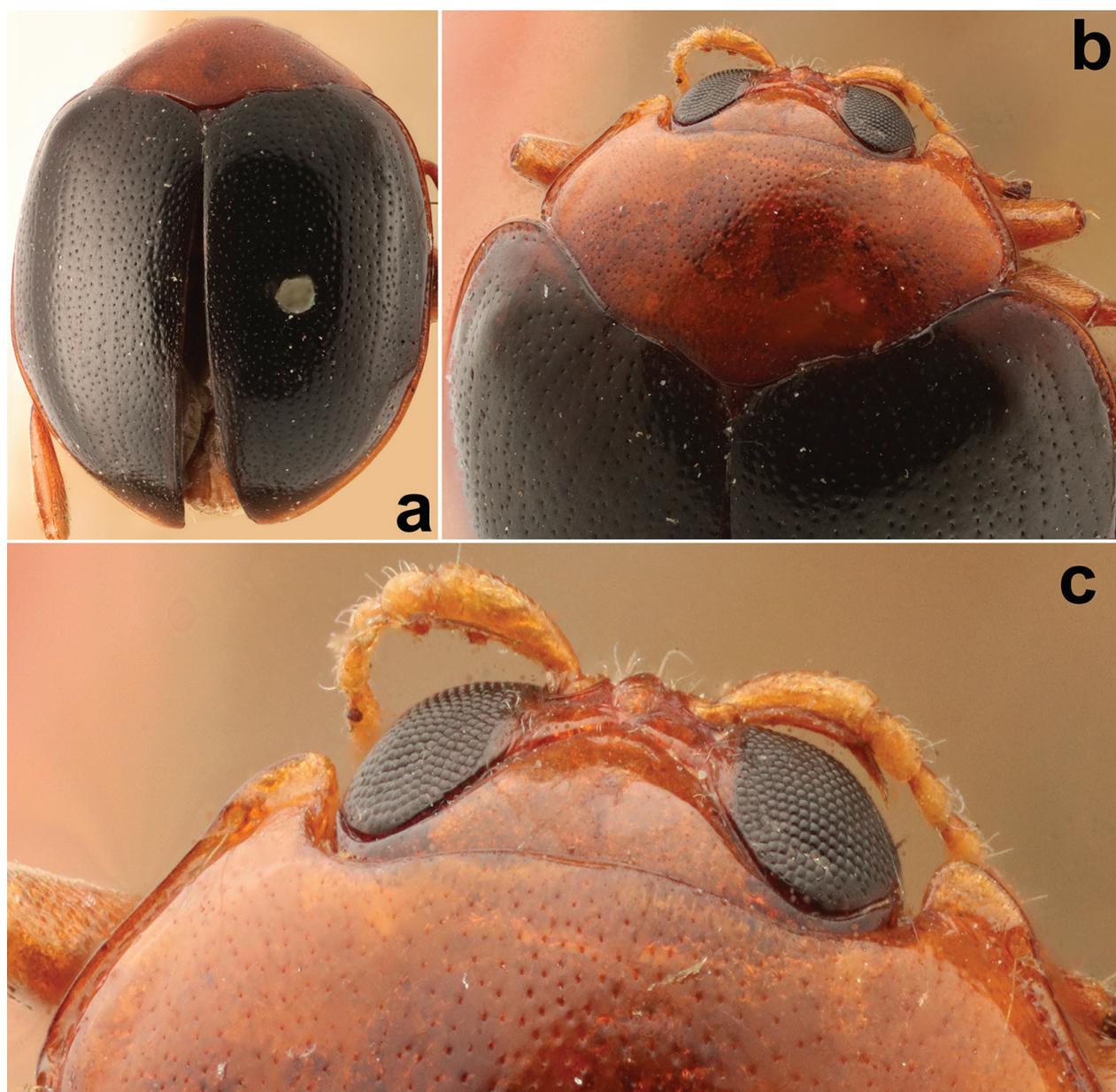


Figure 11. Type of *Sphaeroderma varipennis* Jacoby (= *B. varipes*) (female). **a.** Dorsal view; **b.** Pronotum of *S. varipennis*; **c.** Anterolateral corners of pronotum (magnified).

reaching apex. Prosternum gently depressed on top, setose, coarsely but shallowly punctate; minimum distance from anterior margin of prosternum to coxal cavity less than half of minimum width of prosternal intercoxal process; prosternal intercoxal process longer than wide, narrowed in middle, widened apically, posterior margin concave. Mesosternum transverse, nearly three times wider than long, with concave posterior margin; metasternum profusely setose medially, coarsely punctate. First abdominal ventrite profusely setose medially, coarsely punctate; in length, medially subequal to next three combined. Last ventrite a little longer than preceding two combined. Last visible tergite medially with a broad longitudinal groove not reaching apex.

Foretibia without apical spine. Mid- and hind tibiae with apical spine. First pro-, meso-, and metatarsomeres

distinctly wider in male than in female; with capitate setae ventrally in male and pointed setae in female. Posterior margin of last ventrite entire in female; forms a lobe notched on either side, in middle in male. Last ventrite internally with a longitudinal apodeme along mid-line in male (Fig. 12a), externally visible as a dark line; apodeme absent in female (Fig. 12b).

Male genitalia with aedeagus in lateral view (Fig. 12f) curved, apex acutely pointed, recurved dorsally. In ventral view (Fig. 12g), aedeagus with a longitudinal depression along middle of ventral side, depression being stronger distally; aedeagus narrowed apically forming a triangular denticle. Dorsal opening (Fig. 12h) partially covered with three laminae.

Female genitalia with spermathecal receptacle (Fig. 12e) oblong, widest in middle, narrowed to-

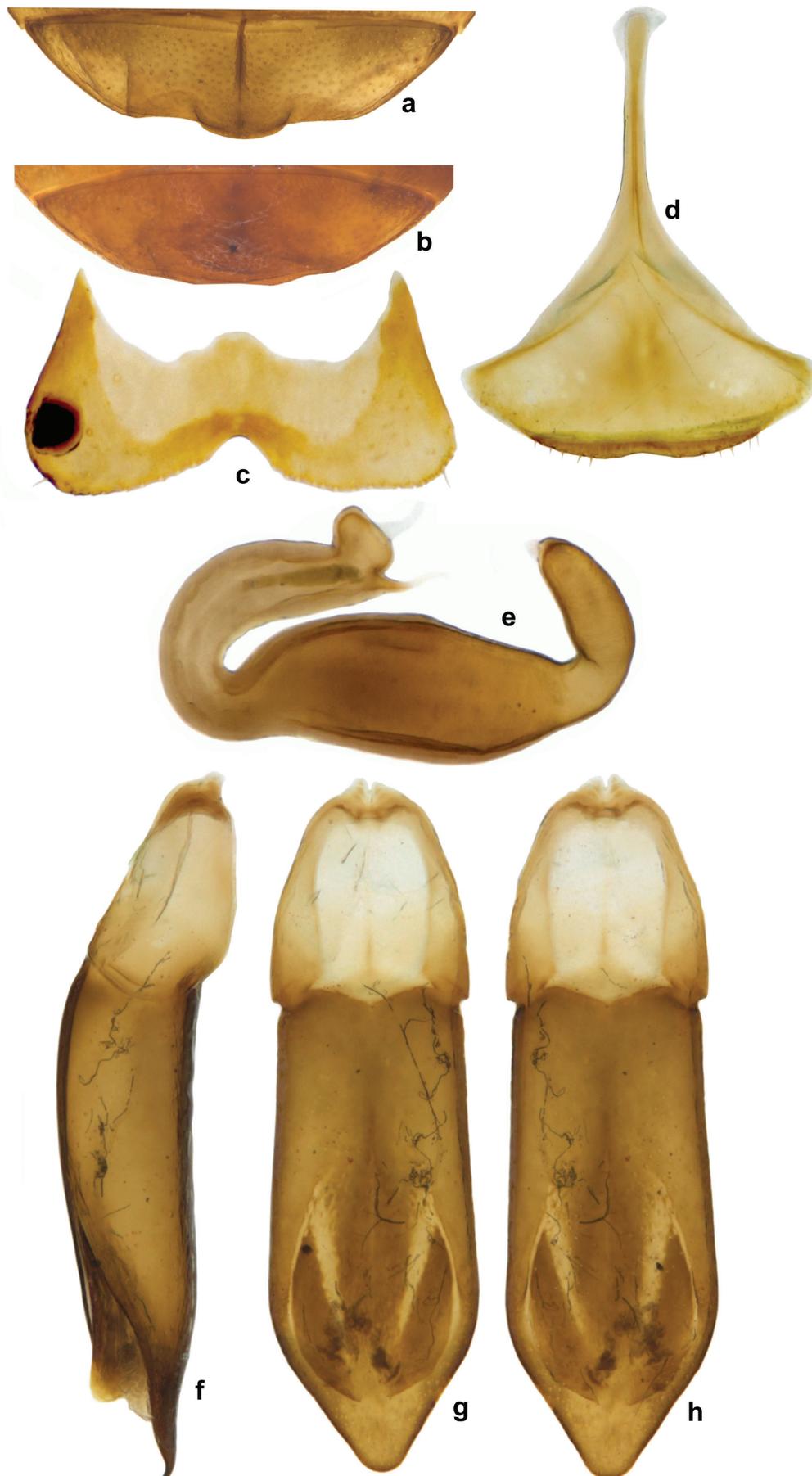


Figure 12. *Bhamoina varipes* (Jacoby). **a.** Abdominal apex, male; **b.** Abdominal apex, female; **c.** Vaginal palpi; **d.** Tignum; **e.** Spermatheca; **f–h.** Male genitalia: **f.** Aedeagus, lateral view; **g.** Aedeagus, ventral view; **h.** Aedeagus, dorsal view.

wards both ends, 2.2× longer than broad. Vaginal palpi (Fig. 12c) medially fused, both together 1.75× broader than long, posterior margin deeply emarginate with a seta on either side. Tignum (Fig. 12d) channeled along middle, posterior membranous area broadened greatly with posterior margin emarginate medially with a few short setae; tignum gently broadened anteriorly.

Nature of damage. Adults feed on the abaxial surface of the leaf lamina, making transverse, narrow linear scars. Feeding by *Basilepta subcostata* results in much shorter and broader feeding troughs, which is very different from that of *Bhamoina varipes*.

Distribution. India (Assam; Meghalaya; Uttarakhand (Dehra Dun)); Myanmar; Nepal (Medvedev 2000); Vietnam; China (Döberl 2010); Sumatra; Laos.

Sphaeroderma spp.

Notes. Unidentified species of *Sphaeroderma* Stephens have been reported from Laos as defoliators of banana (Dean 1978; Hill 2008; Vansilalom 2016). We collected a new species of *Sphaeroderma* feeding on banana from the state of Meghalaya, northeastern region of India, during our surveys, which is described and illustrated here.

Generic diagnosis. Small to medium sized flea beetles, convex and broadly oval. Red brown to black with

or without spots or stripes on elytra. Head hypognathous, frontal ridge raised, forming T-shaped ridge with apical margin of head capsule. Antennal calli well delineated by sulci, supracallinal sulcus deep. Pronotum broader than long, without impressions or furrows. Posterior margin bisinuate with a lobe in middle. Procoxal cavity open behind. Anterolateral corners of pronotum not greatly produced forward. Metatibia dorsally flat or concave, with lateral and mesal margins forming ridge. Third tarsomere broad, its anterior margin entire, not bilobed. First metatarsomere short, not longer than next two combined. Intercoxal part of first abdominal ventrite truncate. Vaginal palpi broader than long.

Sphaeroderma cruenta Prathapan & Kumari, sp. nov.

<http://zoobank.org/3EC3F062-239F-4436-9647-EB5032384C7F>

Figs 13, 14

Material examined. Holotype: ♂: India: Meghalaya: Barapani, 25°41'17.6"N, 91°55'5.1"E; 5.vi.2013, 993 m; Prathapan K D Coll., Ex Banana (BMNH). **Paratypes:** (17♂, 8♀): India: Meghalaya: Barapani, 25°41'17.6"N, 91°55'5.1"E; 5.vi.2013, 993 m; Prathapan K D Coll., Ex Banana (2 BMNH; 2 USNM; 17 ICAR-NBAIR; 2 NPC; 2 UASB).

Diagnosis. This species closely resembles *S. mandarensis* Jacoby (Jacoby 1900: 123–124), from Mandar in

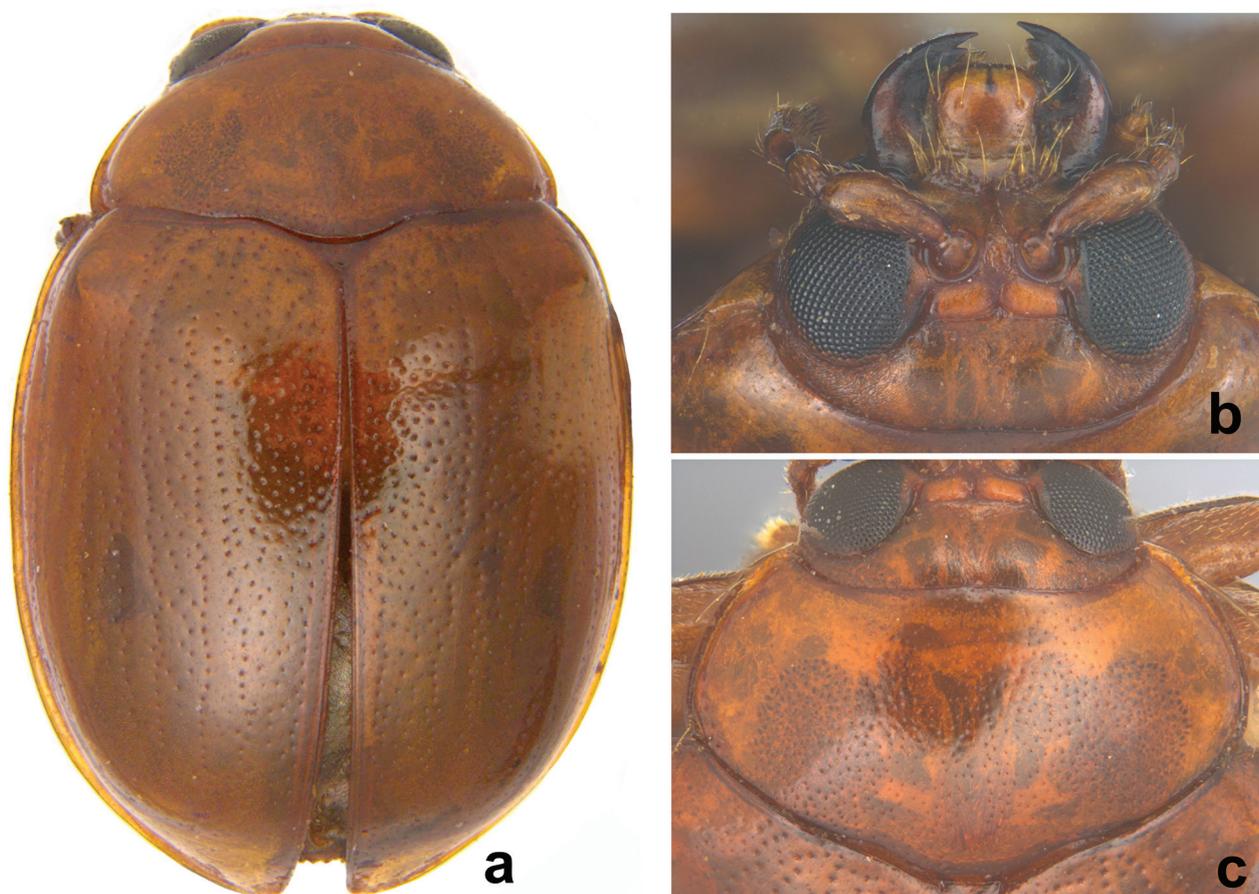


Figure 13. *Sphaeroderma cruenta* sp. nov. Paratype (female) a. Adult, dorsal view; b. Head, dorsal view; c. Pronotum, dorsal view.

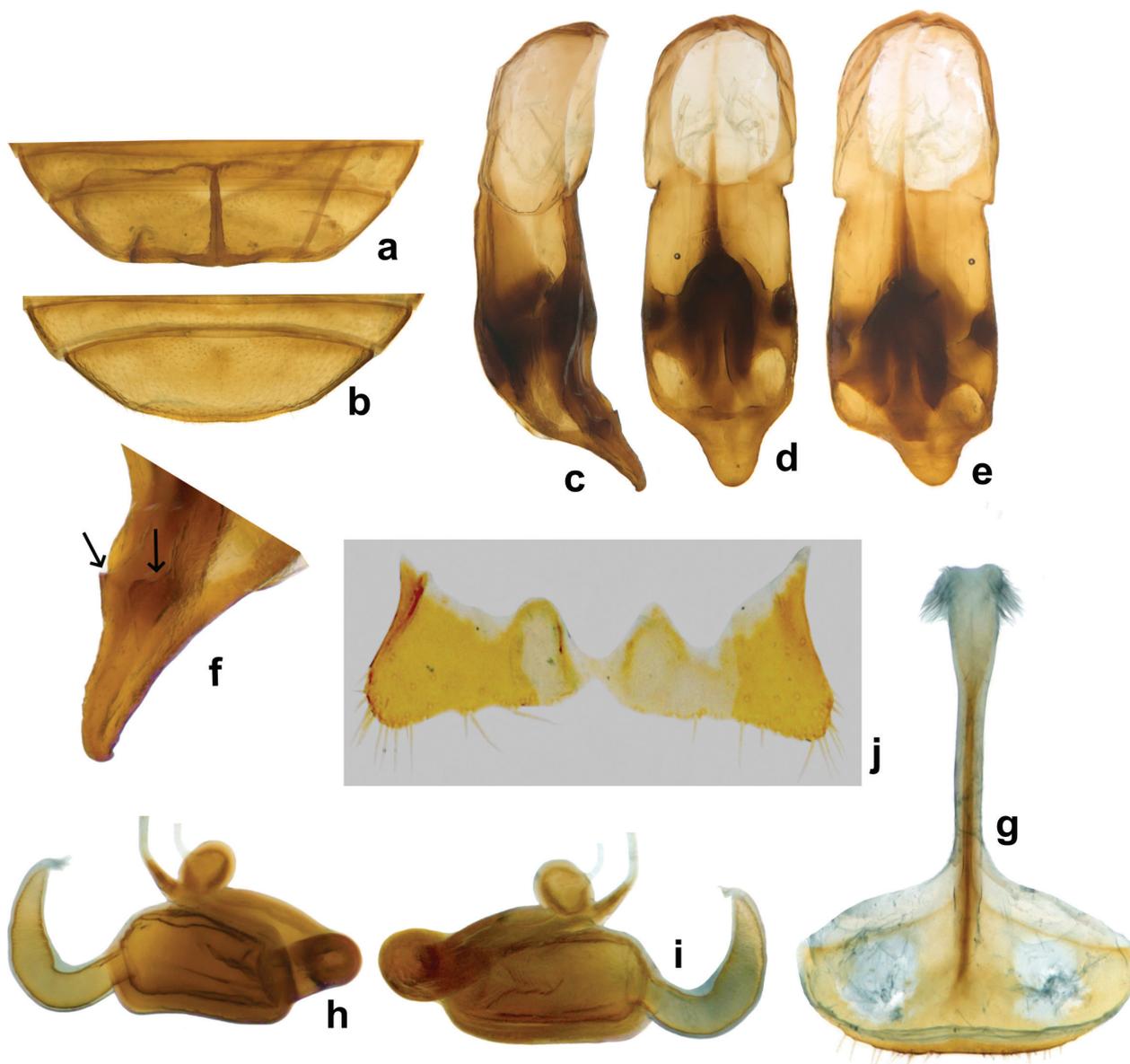


Figure 14. *Sphaeroderma cruenta* sp. nov. **a.** Abdominal apex, male; **b.** Abdominal apex, female; **c–f.** Male genitalia: **c.** Aedeagus, lateral view; **d.** Aedeagus, ventral view; **e.** Aedeagus, dorsal view; **f.** Aedeagus apex, lateral view; **g.** Tignum; **h, i.** Spermatheca; **j.** Vaginal palpi.

West Bengal, India, especially in size, coloration, structure of head and punctation. However, the pronotum is more narrowed anteriorly than in *S. mandarensis*. The male genitalia are diagnostic (Fig. 14c–f).

Description. Entirely red-brown (Fig. 13), except distal antennomeres darker. Length 2.97–3.33 mm, width 2.08–2.26 mm, ca 1.40× longer than broad. In lateral view, vertex and antennal calli form a gently curved line with an emargination at their meeting point; frontal ridge forms a strongly convex line that joins anterofrontal ridge at an obtuse angle. In frontal view (Fig. 13b), vertex gently convex on sides, flat in middle, with small punctures and indistinct rugosities. Antennal calli subhorizontal, laterally slightly narrower than medially, about twice wider than long, subquadrate. All sulci surrounding antennal calli well developed. Supracallinal sulcus gently convex.

Supraorbital pore circular, with a long seta on a convex tubercle, not surrounded by shallow groove. Frontal ridge sharply raised, narrower ventrally than dorsally. Frontoclypeal suture with closely placed, irregularly arranged long setae. Anterior margin of clypeus straight. Frontolateral area concave, without long setae or bold punctures. Anterofrontal ridge poorly developed, not convexly raised. Distance between antennal sockets 0.84× diameter of a socket, antennal sockets separated from adjacent eye by a distance 0.36× transverse diameter of a socket. Labrum distinctly wider than long, anterior margin convex, with three pairs of transversely arranged setae.

Maxillary palpi with four palpomeres, penultimate palpomere being thicker and longer than last palpomere. First palpomere smallest, second subequal to last. Labial palpi three-segmented with the second palpomere thicker

than last, subequal to last in length. Proportionate length of antennomeres I to XI: 1 : 0.61 : 0.57 : 0.61 : 0.74 : 0.70 : 0.74 : 0.70 : 0.70 : 0.70 : 1.09.

Pronotum (Fig. 13c) distinctly narrowed anteriorly, 0.38× times longer than wide, posterior margin 1.59× as wide as anterior margin, anterolateral corners only slightly produced forward, not reaching eye. Lateral margin gently and evenly curved, anteriorly as wide as posteriorly. Anterolateral callosity longer than wide, not forming denticle at pore, pore situated on posterior dorsal face of callosity. Posterolateral callosity not laterally protruding. Disc profusely covered with small punctures, much smaller than those on elytra.

Scutellum as broad as long, obtusely narrowed posteriorly, surface very minutely punctate. Elytra as broad as pronotum at basal margin, widening near humerus. Humerus convex, weakly depressed posteriorly. Elytra with a mixture of small and large punctures. Punctures confused, tend to form uncountable rows. Lateral most row regular, followed by one or two countable adjacent rows. Distance between adjacent punctures smaller than diameter of a puncture. Elytral apex convex. Maximum width of epipleura at anterior one-third; subequal to forefemur in width. Epipleura subhorizontal, narrowing posterior to anterior one-third, not reaching elytral apex.

Prosternum widened posteriorly, posterior margin concave medially, slightly depressed on top, setose with coarse shallow punctures. Mesosternum setose, transverse, with concave posterior margin. Metasternum with moderate sized, deep punctures, thickly setose on either side. First abdominal ventrite longest, 2–4 each shorter than fifth separately; fifth longer than preceding two combined, shorter than preceding three combined. Last visible tergite with a shallow groove along middle, not reaching apex. All tibiae with apical spine.

First pro-, meso-, and metatarsomeres slightly wider with capitate setae ventrally in male. In female, all first tarsomeres ventrally with pointed setae. Posterior margin of last ventrite entire in female, forms a lobe notched on either side in middle in male. Last ventrite internally with a longitudinal apodeme along mid-line in male (Fig. 14a), externally visible as a dark line; apodeme absent in female (Fig. 14b).

Male genitalia (Fig. 14c–f) with aedeagus in lateral view gently bent at middle (Fig. 14c), apex acutely narrowed, recurved (Fig. 14f). In ventral view (Fig. 14d), ventral surface depressed preapically, narrowed to apex, forming a broad denticle. Dorsal side (Fig. 14e) of aedeagus convex, dorsal opening partially covered by a lamina; a characteristic, narrowly elongate, bifid sclerotization present preapically on dorsal side, it laterally extends forming an internal ring around aedeagus.

Female genitalia with spermathecal receptacle (Fig. 14h, i) 1.5× as long as broad, outer margin concave, inner margin convex; pump with unsclerotized denticle apically, horizontal part longer than vertical. Duct twisted proximally, curved over receptacle, reaching a little beyond middle of receptacle. Vaginal palpi (Fig. 14j) narrowly connected medially, both together 2.4× as wide as long. Tignum (Fig. 14g) straight, channeled along middle, gently broadened anteriorly, posterior membranous part broadened greatly with a few short setae along posterior margin, unsclerotized on either side of middle of posterior membranous part.

Etymology. The specific epithet is a Latin adjective in nominative case in reference to the reddish colour of this species.

Distribution. India (Meghalaya).

Biology. Adults feed on the foliage of banana (*Musa* spp.).

Key to chrysomelids feeding on bananas and plantains in the Indian Subcontinent

- 1 Form oblong-oval, metallic red and blue or entirely reddish, dark green, or blue (Fig. 1a–c). Antennal calli poorly developed, not delimited by deep sulci (Fig. 3a, b). Lateral margin of pronotum sharply angulate at distal-third (Fig. 3c, d). Elytra with a sharply raised costa/ridge running parallel with lateral margin to about middle (Fig. 2b). Forecoxal cavities closed behind. Legs with all femora dilated and ventrally with a small tooth, mid- and hind tibiae preapically emarginate (Fig. 3e, f) *Basilepta subcostata* (Jacoby)
- Form elongate-oval, entirely reddish to dark reddish brown, not metallic. Antennal calli well developed, delimited by deep sulci. Lateral margins of pronotum curved, not angulate. Elytra without a lateral ridge/costa. Forecoxal cavities open behind. Hind femora greatly enlarged compared to fore- and midfemora, tibiae preapically not emarginate, without a ventral tooth 2
- 2 Form broad oval, reddish to dark reddish brown (Fig. 10a, b). Anterolateral angles of pronotum distinctly produced forward (Fig. 10d, e); lateral margin of pronotum in dorsal view convex in proximal two-thirds, gently concave behind anterolateral callosity (Fig. 10e); male genitalia with apex of aedeagus gently recurved and slightly curved dorsad in lateral view (Fig. 12f); preapical, ring-like sclerotization absent on aedeagus (Fig. 12f–h); spermathecal duct not twisted proximally (Fig. 12e) *Bhamoia varipes* (Jacoby)
- Form more elongate and less robust, entirely reddish (Fig. 13a). Anterolateral corners of pronotum rounded, not produced forward (Fig. 13c); lateral margin of pronotum in dorsal view evenly convex throughout; male genitalia with apex of aedeagus strongly bent ventrad in lateral view (Fig. 14c); a characteristic, narrowly elongate, bifid sclerotization present preapically on dorsal side of aedeagus (Fig. 14f), which laterally extends forming an internal ring around aedeagus; spermathecal duct twisted proximally (Fig. 14h, i) *Sphaeroderma cruenta* Prathapan & Kumari, sp. nov.

Molecular characterization of *B. subcostata*

In total 10 COI sequences of *B. subcostata* (six from Assam and four from Uttar Pradesh) were deposited in GenBank and accession numbers obtained (KY908365.1, MK414475.1, MK414474.1, MK414473.1, MK414472.1, K414470.1, MK414469.1, MK414468.1, MK414467.1 and MK414466.1). The pairwise nucleotide sequence identity of COI sequences of *B. subcostata* from Assam and Uttar Pradesh ranged from 98 to 100%, indicating that they were conspecific. The phylogenetic tree constructed by the maximum likelihood method based on COI gene sequence alignments revealed two clusters, with *B. subcostata* from Assam and UP forming one cluster (Group I), and the sequences from the outgroup taxa falling in another cluster (Group II) (Fig. 15).

Discussion

The chrysomelids recorded by us on banana here are also included in the host plants listed by Jolivet and Hawkeswood (1995). Of the three species of banana feeding chrysomelids studied by us, *B. subcostata* is the most predominant and widespread pest in northern and north-eastern regions of India and Bangladesh. The other two appear to be of minor importance as banana pests with a much more restricted distribution. *Bhamoina varipes* and *Sphaeroderma* are known from Thailand and Laos as defoliators of banana (Dean 1978; Hill 2008) but have not been reported from India until now. *Sphaeroderma cruenta* sp. nov. was collected from northeastern India; it still needs to be determined if the *Sphaeroderma* species reported from Laos (Dean 1978; Hill 2008; Vansilalom

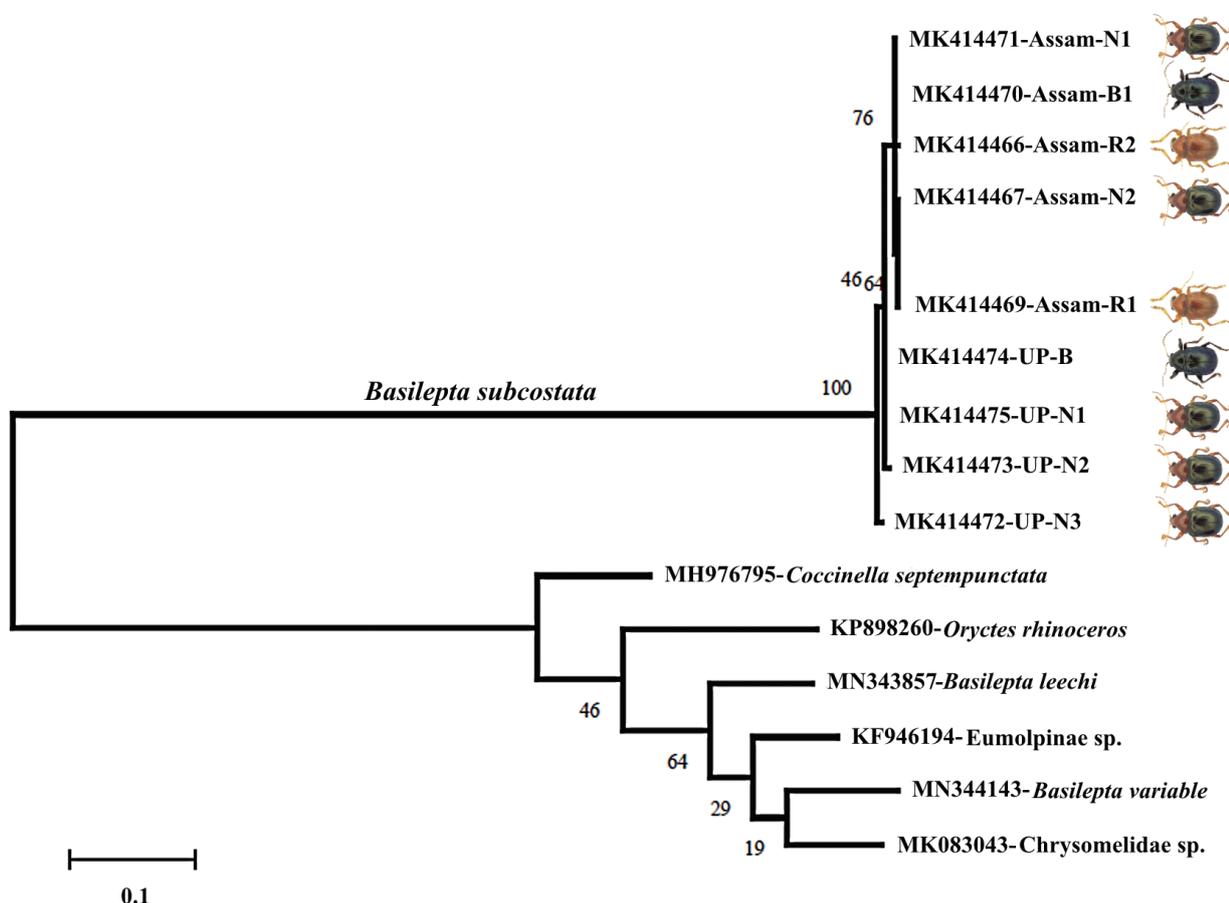


Figure 15. Maximum Likelihood phylogeny of *B. subcostata* populations from Assam and Uttar Pradesh, India. The evolutionary history was inferred by using the Maximum Likelihood method and Tamura-Nei model. The tree with the highest log likelihood (-3489.32) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 16 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. There was a total of 660 positions in the final dataset. Evolutionary analyses were conducted in MEGA X.

2016) are conspecific with this new species or belong to a different species.

It is noteworthy that three species of chrysomelids belonging to two systematically distant subfamilies (Galerucinae and Eumolpinae) are feeding on the same host plant. More studies are needed to determine the nature and extent of damage to bananas caused by *B. varipes* and *S. cruenta* sp. nov. and to clarify their distribution in India, as they are not common pests. Taro (*Colocasia esculenta* L.) has been recorded as a host plant of *B. subcostata* [as "*Nodostoma subcostatum*"] in West Bengal (Bhattacharyya and Mandai 2006) and Manipur (Prasad and Singh 1987). We observed a few adults resting on taro, which is commonly grown with banana in homesteads and as an intercrop, but did not see any feeding damage. There is some doubt regarding the reliability of records of *B. subcostata* from Nepal (Medvedev 1990), as the specimens are not conspecific with *B. subcostata* and seem to belong to the genus *Pseudostonopa* Jacoby, 1903, which is closely related to *Basilepta* and probably can be included as a subgenus (Alexey Moseyko, personal communication). However, the specimens in the holdings of BMNH studied by JP seem to be conspecific with *B. subcostata*. The elytral costa characteristic of *B. subcostata* is highly variable in different populations and is distinctly convex and strongly sinuate in the female syntype (BMNH) and other specimens from Myanmar, but the Indian specimens have only a moderately convex and less sinuate costa. COI sequences of *B. subcostata* populations from Assam and Uttar Pradesh showed 98–100% similarity indicating they are conspecific and can be used as a rapid diagnostic tool by economic entomologists and plant protection workers. Morphological studies also did not show any major variations among different populations of *B. subcostata* and the genitalia of material from all locations surveyed were identical.

Although *Basilepta subcostata* is known to be a serious pest of bananas and plantains in the northeastern, eastern, and northern regions of India, there is no published record of its occurrence in any part of peninsular India. However, two specimens collected on banana from Vittal, Karnataka (South India), and one specimen from "Deccan" were examined by JP in the collections of the Natural History Museum, London. These specimens indicate that this pest is present in peninsular India albeit in very small numbers and highlights the importance of museum collections in determining the geographic range of economically important insect pests. Its occurrence in peninsular India is a major concern for banana growers, and it is essential to conduct more systematic surveys to acquire data on the extent of its presence there. Plant protection workers and applied entomologists in peninsular India need to be alerted about the presence of *B. subcostata*, as it is virtually unknown in peninsular India, although it has a huge potential to cause devastation. Management options for *B. subcostata* mainly involve removal of grassy weeds, application of insecticides, neem-based biopesticides, entomofungal pathogens like

Beauveria bassiana, and covering fruit bunches with polythene sleeves (Das and Baruah 2018; Rituraj et al. 2018). Soil application of entomofungal pathogens and entomophilic nematodes targeting the larvae and pupae may be more effective in controlling this pest.

It is a matter of concern that systematic revisions of pests and related species important in agriculture and horticulture are lacking in biodiversity-rich countries like India, as well as the rest of Asia, and even for cash crops like banana. The International Plant Protection Convention (IPPC) stipulates that contracting parties should "conduct surveillance for pests and develop and maintain adequate information on pest status in order to support categorization of pests, and for the development of appropriate phytosanitary measures" (Cock 2011: 22) which can be done only if a country's pests, including newly introduced ones, can be identified and necessary facilities like reference collections and diagnostic capabilities are put in place (Cock 2011). The clarification of the nomenclature of leaf and fruit feeding chrysomelids of the Indian region provided in this paper is essential for future phytosanitary, quarantine and management purposes, as most of the available literature on *Basilepta* spp. as banana pests in Asia use wrong names, and we hope the illustrations provided here and the COI sequences will be useful for economic entomologists and non-taxonomists in identifying these insects. Future studies, including further field surveys and focused systematic studies, for identifying the chrysomelid species feeding on banana in other Asian countries are much needed.

Acknowledgements

We thank Dr S. Uma, Director, ICAR-National Research Centre for Banana, Trichy, for the facilities and support in carrying out this work. The second author gratefully acknowledges the Museum of Comparative Zoology, Harvard University, Massachusetts, for enabling her visit to Natural History Museum, London, funded by an Ernst Mayr travel grant and Dr Max Barclay, Dr Michael Geiser, and Dr Keita Matsumoto of the Natural History Museum, London, for facilitating the study and imaging of type material of Chrysomelidae. We thank the Museum für Naturkunde, Berlin, for waiving the fees for publishing this paper. We are grateful to Dr Elisabeth Geiser and an anonymous reviewer for their thorough and constructive reviews which greatly helped in improving the manuscript.

References

- Ahmad MA, Singh PP, Singh B (2003) Efficacy of certain synthetic insecticides and plant products used as foliar and whorl application against the scarring beetle (*Nodostoma subcostatum* Jacoby) on banana. *Journal of Entomological Research* 27: 325–328.
- Ahmad MA, Mandal SK, Mukherjee U (2010) Population dynamics of *Basilepta subcostatum* Jacoby on banana. *Annals of Plant*

- Protection Sciences 18: 349–352. <https://doi.org/10.5958/0974-8172.2015.00047.4>
- Ahmed A (1963) Notes on the Biology of Banana Leaf and Fruit Beetle, *Nodostoma viridipennis* Mots. A review of research, Division of Entomology. Published by Agricultural Information Service, Dhaka, 187–190.
- Baly JS (1867) Phytophaga Malayana; a revision of the phytophagous beetles of the Malay Archipelago, with descriptions of the new species collected by Alfred R. Wallace. Transactions of the Entomological Society of London 4(3): 1–300. <https://biodiversitylibrary.org/page/14694380>
- Batra HN (1952) Occurrence of three banana pests of Delhi. Indian Journal of Entomology 14: 1–60.
- Bechyné J (1958) Contribution à l'étude des Chrysomeloidea des lies Mascareignes. II. Alticinae. The Mauritius Institute Bulletin 5(3): 83–93.
- Bhattacharyya A, Mandai SK (2006) Pests infesting tare (*Colocasia esculenta* L.) in West Bengal. Indian Agriculturist 50: 153–156.
- Choudhary SK, Mukherjee U, Ahmed MDA (2010) Efficacy of biopesticides against banana scarring beetle, *Basilepta subcostatum* Jacoby. Pest Management in Horticultural Ecosystems 16(2): 120–123. <http://www.aapmhe.in/index.php/pmhe/article/view/106>
- Chûjô M (1964) Coleoptera from Southeast Asia. 32. Chrysomelidae. Nature & Life SE Asia 3: 252–315.
- Cock MJW (2011) Strategic entry points for funding taxonomic support to agriculture in developing countries. CABI Working Paper 3: 1–32. <https://www.cabi.org/Uploads/CABI/expertise/CABI-WP3-TaxAg.pdf>
- Cruz-Zapata G de la, Moreno-Jiménez M, Osorio-Osorio R, Hernández-Hernández LU, Márquez-Quiroz C, Cruz-Lázaro E de la, Valdez-Carrasco JM (2018) Fruit-scarring beetle *Myochrous melancholicus* Jacoby as a potential new pest of banana. Southwestern Entomologist 43(1): 57–66. <https://doi.org/10.3958/059.043.0124>
- Das D, Baruah K (2018) Management of banana leaf and fruit scarring beetle *Nodostoma viridipennis* Motsch. in Assam. Indian Journal of Entomology 80(3): 703–705. <https://doi.org/10.5958/0974-8172.2018.00226.2>
- Dean GJ (1978) Insects found on economic plants other than rice in Laos. PANS 24(2): 129–142. <https://doi.org/10.1080/09670877809411603>
- Döberl M (2010) Subfamily Alticinae Newman, 1835. In: Lobl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera (Vol. 6). Apollo Books, Stenstrup, 491–562.
- Duvivier A (1885) Catalogue des chrysomelides, halticidés et galericides décrites. Mémoires de la Société Royale des Sciences de Liège 2 11(15): 1–64. <https://biodiversitylibrary.org/page/27434462>
- FAOSTAT (2019) Food and Agriculture Data. <http://www.fao.org/faostat/en/#home> [Accessed on: 18-11-19]
- Gowdey CC (1926) The banana fruit-scarring beetle (*Colaspis hyperchlora*, Lef.). Bulletin of Entomological Research 17: 1–137. <https://doi.org/10.1017/S0007485300019167>
- Hill DS (1983) Agricultural Insect Pests of the Tropics and Their Control. Cambridge University Press, Cambridge, 758 pp.
- Hill DS (2008) Pests of Crops in Warmer Climates and Their Control. Springer, Dordrecht, 679 pp. <https://doi.org/10.1007/978-1-4020-6738-9>
- ICAR-National Research Center for Bananas (2019) Banana fruit and leaf scarring beetles, *Basilepta* spp. <http://nrcb.res.in/album/Fruit%20and%20leaf%20scarring%20beetles/index.html>
- Jacoby M (1884) Description of new genera and species of phytophagous Coleoptera collected by Dr. B. Hagen at Serdang (East Sumatra). Notes from the Leyden Museum 6: 201–230. <https://biodiversitylibrary.org/page/9635686>
- Jacoby M (1889) Viaggio di Leonardo Fea in Birmania e Regioni Vicine, 17. List of the Phytophagous Coleoptera obtained by Signor L. Fea at Burmah and Tenasserim, with descriptions of the new species. Annali del Museo Civico di Storia Naturale de Genova, ser. 2, 27: 147–237. <https://biodiversitylibrary.org/page/35995817>
- Jacoby M (1892) Description of the new genera and species of the phytophagous Coleoptera obtained by Sign. L. Fea in Burma. Annali del Museo Civico di Storia Naturale di Genova 32: 869–999. <https://biodiversitylibrary.org/page/30084319>
- Jacoby M (1900) New species of Indian Phytophaga principally from Mandar in Bengal. Mémoires de la Société Entomologique de Belgique 7: 95–140. <https://biodiversitylibrary.org/page/10981179>
- Jacoby M (1903) Descriptions of the new genera and species of phytophagous Coleoptera obtained by Mr H. L. Andrewes and Mr T. R. D. Bell at the Nilgiri Hills and Kanara. Annales de la Société Entomologique de Belgique 47: 80–128. <https://biodiversitylibrary.org/page/12371882>
- Jacoby M (1908) The Fauna of British India Including Ceylon and Burma. Coleoptera. Chrysomelidae (Vol. 1). Taylor and Francis, London, 534 pp. <https://biodiversitylibrary.org/page/50883892>
- Jolivet P, Hawkeswood TJ (1995) Host-Plants of Chrysomelidae of the World: an Essay About the Relationships Between the Leaf-Beetles and Their Food-Plants. Backhuys Publishers, Leiden, 281 pp.
- Jolivet P, Verma KK (2008) Eumolpinae – a widely distributed and much diversified subfamily of leaf beetles (Coleoptera, Chrysomelidae). Terrestrial Arthropod Reviews 1: 3–37. <https://doi.org/10.1163/187498308X345424>
- Kimoto S (1967) A list of the chrysomelid specimens from the Himalayas and Kashmir, preserved in the Zoological Museum, Berlin. Esakia 6: 65–75. https://catalog.lib.kyushu-u.ac.jp/opac_download_md/2356/65.pdf
- Kimoto S (2001) The Chrysomelidae (Insecta: Coleoptera) collected by the Kyushu University Scientific Expedition to the Nepal Himalaya in 1971 and 1972. Bulletin of Kitakyushu Museum of Natural History 20: 17–80. http://www.kmnh.jp/wp-content/themes/kmnh_jp/images/pdf/20-17-E-Kimoto.pdf
- Kimoto S (2005) Systematic Catalog of the Chrysomelidae (Coleoptera) from Nepal and Bhutan. Bulletin of the Kitakyushu Museum of Natural History and Human History, Series A 3: 13–114. http://www.kmnh.jp/wp-content/themes/kmnh_jp/images/pdf/A3-13-E-Kimoto.pdf
- Kimoto S, Gressitt L (1982) Chrysomelidae (Coleoptera) of Thailand, Cambodia, Laos and Vietnam. III. Eumolpinae. Esakia 18: 1–141. https://catalog.lib.kyushu-u.ac.jp/opac_download_md/2421/1.pdf
- Konstantinov AS (1998) Revision of the Palearctic Species of *Aphthona* Chevrolat and Cladistic Classification of the Aphthonini (Coleoptera: Chrysomelidae: Alticinae). Memoirs on Entomology International (Vol. 11). Associated Publishers, Gainesville, 429 pp.
- Kumar S, Stecher G, Li M, Knyaz C, and Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549.
- Lefèvre E (1893) Contribution à la faune indo-chinoise. 12c Mémoire (1). Clytrides & eumolpides (2^e mémoire). Annales de la Société

- Entomologique de France 62: 111–134. <https://biodiversitylibrary.org/page/8236945>
- Maulik S (1926) The Fauna of British India, Including Ceylon and Burma. Coleoptera. Chrysomelidae (Chrysomelinae and Halticinae). Taylor and Francis, London, 442 pp. <https://biodiversitylibrary.org/page/43810441>
- Medvedev LN (1990) Chrysomelidae from the Nepal Himalayas, II (Insecta: Coleoptera). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 453: 1–46. <https://biodiversitylibrary.org/page/33385513>
- Medvedev LN (2000) Chrysomelidae from the Nepal Himalayas, with revision of the genus *Haplosomoides* (Insecta: Coleoptera). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 616: 1–32. <https://www.naturkundemuseum-bw.de/sites/default/files/publikationen/serie-a/A616.pdf>
- Medvedev LN (2001) Jacoby's types of Chrysomelidae (Coleoptera) from Burma in the Museo Civico di Storia Naturale "Giacomo Doria", Genova Part 2. Annali del Museo civico di Storia naturale di Genova 93: 607–616.
- Medvedev LN (2006) To the knowledge of Chrysomelidae (Coleoptera) described by V. Motschulsky. Russian Entomological Journal 15: 409–417. http://zmmu.msu.ru/files/images/spec/Russ%20Ent%20J/REJ_15-4_409-417%20%28Medvedev%29.pdf
- Medvedev LN, Sprecher-Uebersax E (1999) Katalog der Chrysomelidae von Nepal. Entomologica Basiliensia 21: 261–354.
- Mishra H, Bora DK, Bhattacharyya B, Das D, Baruah K (2015) Population dynamics of banana leaf and fruit scarring beetle, *Nodostoma subcostatum* Jacoby in Assam. Indian Journal of Entomology 77: 226–229. <https://doi.org/10.5958/0974-8172.2015.00047.4>
- Moseyko AG (2008) The Reproductive Apparatus of Female Leaf Beetles (Coleoptera, Chrysomelidae) and its Importance for the Systematics of the Group. Unpublished PhD dissertation, Russian Academy of Sciences, Zoological Institute, St. Petersburg, 148 pp.
- Moseyko A, Sprecher-Uebersax E (2010) Subfamily Eumolpinae Hope, 1840, In: Lobl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera (Vol. 6). Apollo Books, Stenstrup, 619–643.
- Motschulsky V (1860) Dr. L. von Schrenk's Reisen und Forschungen im Amur-lande, II, 2, Coléoptères de la Sibérie Orientale et en Particulier des Rives de l'Amour. St. Petersburg, 77–258. <https://biodiversitylibrary.org/page/33519815>
- Mukherjee U, Bharati RC, Arun K, Ranjan R (2006) Influence of weather factors on the incidence of scarring beetle, *Basilepta subcostatum* Jacoby (Coleoptera: Chrysomelidae) on banana in Bihar. Pest Management in Horticultural Ecosystems 12: 98–102. <http://www.aapmhe.in/index.php/pmhe/article/view/614/569>
- Ostmark HE (1974) Economic insect pests of banana. Annual Review of Entomology 19: 161–176. <https://doi.org/10.1146/annurev.en.19.010174.001113>
- Ostmark HE (1975) Banana pests in the genus *Colaspis*, including description of a new species (Coleoptera: Chrysomelidae). Florida Entomologist 58: 1–8. <https://doi.org/10.2307/3493857>
- Prasad B, Singh OL (1987) Insect pests of banana and their incidence in Manipur. Indian Journal of Hill Farming 1: 71–73.
- Promusa (2019) Promusa. <http://www.promusa.org/Musapedia> [Accessed on: 18-11-19]
- Rahman MA, Hossain M, Islam KS (2004) Effectiveness of weeding and bunch covering in controlling banana leaf and fruit beetle, *Nodostoma viridipennis* Mots. Journal of Bangladesh Agricultural University 2(2): 237–243. <https://ageconsearch.umn.edu/record/276357/?ln=en>
- Rituraj S, Bora DK, Baruah K, Mishra H (2018) Ecofriendly management of banana leaf and fruit scarring beetle *Basilepta subcostatum* Jacoby in Assam. Indian Journal of Entomology 80(3): 794–797. <https://doi.org/10.5958/0974-8172.2018.00108.6>
- Sah SB, Prakash S, Parasnath, Kumar R (2018) Occurrence of leaf and fruit scarring Beetle, (*Basilepta* sp., *Colaspis* sp.) on banana in Koshi region of Bihar, India. International Journal of Current Microbiology and Applied Sciences, Special Issue 7: 2778–2784. <https://www.ijcmas.com/special/7/Shyam%20Babu%20Sah,%20et%20al.pdf>
- Scherer G (1969) Die Alticinae des indischen Subkontinentes. Pacific Insects Monograph 22: 1–251. <http://hbs.bishopmuseum.org/pim/pdf/pim22.pdf>
- Slipinski A, Escalona HE (2013) Australian Longhorn Beetles (Coleoptera: Cerambycidae) (Vol. 1). CSIRO Publishing, Melbourne, 504 pp. <https://doi.org/10.1071/9781486300044>
- Sprecher-Uebersax E (1997) Blattkäfer aus Nepal in den Sammlungen des Naturkunde-museum Erfurt (Insecta: Chrysomelidae). Veröffentlichungen Naturkunde-museum Erfurt 453: 138–171.
- Takizawa H (1987) Notes on chrysomelid beetles (Coleoptera: Chrysomelidae) of India and its neighboring areas. Part V. Proceedings, Japanese Society of Systematic Zoology 35: 40–58.
- Vansilalom V (2016) Bananas, Laos and economic development: farming practice and farmers' perceptions. Ph.D. Thesis, James Cook University, Townsville. <https://researchonline.jcu.edu.au/46825/>
- Verghese A, Kamala Jayanthi PD (2001) Integrated pest management (IPM) in major fruit crops. In: Reddy PP, Verghese A, Krishna Kumar NK (Eds) Integrated Pest Management in Horticultural Ecosystems. Capital Publishing Company, New Delhi, 23 pp.
- Waterhouse DF (1993) The Major Arthropod Pests and Weeds of Agriculture in Southeast Asia: Distribution, Importance and Origin. Monograph No. 21, ACIAR, Canberra, 141 pp. <https://www.aciar.gov.au/node/7856>
- Weise J (1922) Chrysomeliden der Indo-Malayischen Region. Tijdschrift voor Entomologie 65: 39–130. <https://biodiversitylibrary.org/page/10857673>
- Wongsiri N (1991) List of Insect, Mite and Other Zoological Pests of Economic Plants in Thailand. Entomology and Zoology Division, Department of Agriculture, Bangkok.
- Zahan ZMS, Ahad MA, Bari MS, Hossain MA, Islam MJ (2001) Estimation of yield and quality of banana fruit affected by banana leaf and fruit beetle, *Nodostoma viridipennis* (Coleoptera: Eumolpidae) in Bangladesh. Pakistan Journal of Biological Sciences 4: 1118–1119. <https://doi.org/10.3923/pjbs.2001.1118.1119>
- Zahan ZMS, Ahad A, Bari S, Sardar MA (2003) Estimation of leaf damage of banana affected by banana leaf and fruit beetle, *Nodostoma viridipennis* Mots. (Coleoptera: Eumolpidae) in Bangladesh. Pakistan Journal of Scientific and Industrial Research 46(4): 261–264. <http://agris.fao.org/agris-search/search.do?recordID=PK2004000101>
- Zahan ZMS, Ahad A, Bari S, Sardar MA (2004) Abundance and fruit damage estimation of banana leaf and fruit beetle, *Nodostoma viridipennis* (Coleoptera: Eumolpidae) on amrita sagar (*Musa* spp.) variety in Bangladesh. Journal of Science and Technology 2: 74–76.